The Development of *Fossombronia longiseta*, Aust.

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With Plates V and VI, and eight Figures in the Text.

*F*OSSOMBRONIA *longiseta* occurs in great abundance in the immediate neighbourhood of Stanford University, as well as in other parts of the state. All material used in the preparation of this paper was collected by the writer within or near the university campus. The work was taken up at the suggestion of Dr. D. H. Campbell, whose valuable advice and guidance is much appreciated. I am also indebted to Dr. Geo. J. Peirce for a number of helpful suggestions pertaining to certain physiological problems in their bearing upon Liverworts, and to Dr. A. A. Lawson for instruction and advice relative to methods, microtechnique and points of cytological interest.

With the exception of the classical work of Leitgeb¹ no comprehensive study of any member of the genus *Fossombronia* has yet appeared. Occupying as it does a position between the purely thallose Jungermanniaceae such as *Ancura* and *Metzgeria* and the higher foliose types, it was thought that a careful study of the species *F. longiseta* might disclose some interesting morphological relationships.

HABITAT AND EXTERNAL CHARACTERS.

Our species of *Fossombronia* appears to be a very adaptive one as to habitat, for while the most thrifty and largest plants are found along moist and well-shaded north-east banks or hill-sides, it is not infrequently found associated with *Sphaerocarpus cristatus* and *Anthoceros Pearsoni*, growing on soil exposed to the sun to a greater or less degree during the day. It occurs in great abundance under the somewhat open growth of the university arboretum, and this habitat seems greatly to enhance the development of antheridia and archegonia at the expense of the vegetative growth. Howe² reports it as producing stems 6 to 15 mm. long, and sometimes once dichotomous, but we have occasionally found it under

¹ Leitgeb, vol. iii, pp. 105-20.

² Howe ('99), p. 81.

especially favourable conditions attaining a length of 30 mm., and as many as three times dichotomous within one growing season. Fig. 1, Plate V, represents such a plant. A similar extra growth of the thallus has been reported by Campbell¹ for *Sphaerocarpus* under like conditions of light and moisture. *Fossombronia longiseta* is a monoecious species, though it is described by Howe² as sometimes developing antheridia to the exclusion

FIG. 1. A. Young plant bearing leaves (l) and leaf-like lobes (ll).
B. A younger plant beginning to produce leaves.

of archegonia and vice versa. Further on in his description, however, he states that it is quite probable that, in cases where the plants are perennial, archegonia occur each alternate year. The writer's observations extend over two consecutive years, and verify Howe's statement, though even here there is considerable variation. Plants growing under most favourable conditions of light and moisture quite regularly bear archegonia and antheridia on the same plant in one season, while those growing in the arboretum or in soil exposed to sunlight almost invariably produce the sex-organs separately in alternate seasons.

Among the Anacrogynae *Fossombronia*

is peculiar in that it represents something of a departure from such thallose forms as *Aneura* or *Metzgeria*, owing to the development of genuine leaves. These are disposed laterally, usually in two rows along the stem, appearing at first as mere outgrowths not greatly differing in appearance from the general structure of the young stem. But as they develop, the leaf-like character is unmistakable. In Text-Fig. 1, A and B represent different

¹ Campbell ('96), Fig. 9.

² loc. cit., p. 81.

stages of leaf-growth in very young plants. Normally the leaves range from 1 to $3\frac{1}{2}$ or 4 mm. in length, though it is not unusual to find strong, vigorous plants bearing leaves 5 or more mm. in length.

The leaves are always more or less imbricate and irregularly lobed, the apex of each lobe terminating in a relatively small, somewhat elongated mucilage-cell. These cells are further characterized by the total absence of chlorophyll, and by the presence of a few oil-bodies. Hanstein's Aniline mixture was used as a mucilage test, in each case giving the characteristic mucilage reaction—a marked scarlet red. Iodine was also employed, producing a bright yellow in the older cells, and a deeper brownish colour in the young cells. These mucilage-cells are of the same physiological

FIG. 2. A. Portion of leaf-margin showing two mucilage-cells (*m*) containing scattering oil-bodies (*ob.*). $\times 560$. B. A similar cell attached to an elevated leaf-cell. $\times 560$. C. A glandula hair. $\times 560$.

significance as the mucilage-hairs that develop upon the surface of the stem, and along with these are of undoubted value to the plant in aiding it to resist the effect of prolonged drought. Early in the autumn of 1903, before the advent of the rainy season, a quantity of the material in a thoroughly dry condition was brought into the laboratory, and a portion of it was moistened. In the course of twenty-four hours the apical ends of the more vigorous plants had revived, and were green to a length of a millimetre or more. Such a sudden revival of so much of each plant suggested the idea that one might possibly find antheridia and archegonia already fairly well developed at the inception of the dry season. Considerable material was examined shortly after being revived, and in many cases nearly mature organs were found that could only have developed before the plants were dried.

In preparing plants for the fixing solution it was noticed that in some cases the stem was more or less thickened, taking on something in the nature of a tuberos growth as shown in Text-Fig. 3. A more detailed examination of the contents of this stem-enlargement revealed the presence

FIG. 3. An example of tubercular thickening of stem. $\times 112$.

of fungal hyphae, and in every case these were always present. In fact, on close scrutiny, it is found that few plants escape infection. Just what is the true relation between the host and the fungus cannot be said, but in a later paper an attempt will be made to throw some light on the problem.

It is barely possible that the tuberos thickening of *F. longiseta*, at least as it occurs here is a pathological structure, functioning physiologically, however, as a storage organ.

No amount of desiccation seems in any way materially to affect the ability of *Fossombronia* to revive, or to influence its rate of growth. Material brought into the laboratory during the dry season was subjected for several days to the action of a powerful drying reagent, in this case glacial phosphoric acid. The material was collected in the latter part of September, from an exposed and thoroughly dry roadside embankment. In the air-dry condition the plants weighed $\cdot 107$ gr.; after treatment with glacial phosphoric acid till no further loss of weight was perceptible, they were observed to weigh $\cdot 102$ gr., or $\cdot 005$ gr. had been given up by the material, or 4.6 per cent. of its air-dry weight represents the actual water-content of the plants before subjection to the drying reagent. Upon removal from the bottle containing the glacial phosphoric acid, they were at once placed in a Petri dish upon damp earth and covered. After twenty-four to forty hours the plants were as green, and as far advanced as those not artificially dried, and within twelve days many spores had germinated that had clung to the material during the experiment. This test has not been applied to the other Archegoniates common to this region of long dry summers, but as stated by Campbell¹ they no doubt possess a degree of adaptation quite as pronounced as that seen in *Fossombronia*.

Experiments by Peirce² upon the behaviour of Lichens in this region go to show that the influence of our summer morning fogs is considerable, and it is not improbable that the Hepaticae are more or less affected, to such an extent, in fact, as to cause a slight growth.

The development of tubers or tuber-like thickening of the stem among Liverworts is not uncommon. Goebel³ has described and figured a species

¹ Campbell ('04), p. 86.

² Peirce ('99).

³ Goebel ('98), Teil ii, Heft 1.

of *Fossombronia* (*F. tuberosa*), in which well-defined tubers commonly occur. This character is also shared by *Geothallus tuberosus*, Campb., *Anthoceros dichotomus*, Raddi, *Riccia cancellata*, Taylor fide Stephani, *Riccia perennis*, Stephani, *Riccia bulbifera*, Stephani, *Anthoceros tuberosus*, Taylor, *Anthoceros phymatodes*, M. A. Howe, *Petalophyllum Preissii*, Gottsche, *Petalophyllum lamellatum*, Hooker. Howe¹ was the first to call attention to the occurrence of this fact in regard to *Fossombronia longiseta*, stating it to be especially true in specimens from Southern California. Whether the stem-thickening of plants grown in the extreme southern portion of the state is of the same character as that of plants farther north has not yet been determined, and whether the thickening is due to the disturbances set up by the fungus can be definitely ascertained only by cultures on sterilized soil. The fungus seems to be confined almost wholly to the stem and rhizoids, the latter sometimes undergoing modifications in the form of lateral swellings, some of which are strongly suggestive of short branches. In no instance have the sex-organs or sporogonium shown any evidence of infection such as is reported by Leitgeb² as occurring in the young sporogonium of *Ptilidium ciliare*; by Garber³ in *Ricciocarpus natans*; and by Cavers⁴ in *Lophocolea bidentata*, *Cephalozia bicuspidata*, *Plagiochila asplenioides* and *Radula complanata*, and in the capsules of *Pallavicinia Lyellii* and *Pallavicinia hibernica*.

Golenkin⁵ ('02), described endotrophic mycorrhiza existing in *Marchantia palmata*, *M. paleacea*, *Preissia commutata*, *Targionia hypophylla*, *Plagiochasma elongatum* and *Fegatella conica*. According to this writer the fungal hyphae are confined entirely to the compact ventral tissue, and the infected cells never show the presence of starch or chlorophyll, though they still retain their nuclei and protoplasm. In *Fossombronia longiseta* infected cells may contain chlorophyll, and in some cells starch occurs, but in those cells that have reached an advanced stage of infection, neither starch nor chlorophyll could be made out.

The occurrence of fungal hyphae in the rhizoids has been described by Janse⁶ for *Zoöpsis* and by Nemeč⁷ for *Lophozia bicrenata*, *Lepidozia reptans* and *Kantia trichomanis*. To these species Cavers⁸ has added *Cephalozia bicuspidata*, *Scapania nemorosa*, *Diplophyllum albicans*, *Plagiochila asplenioides*, *Bazzania trilobata* and *Porella platyphylla*.

METHODS.

All material was fixed either in the field, where it was at once placed in the fixing fluid, or brought into the laboratory in large sods where it was placed under a bell-jar until time of fixation. Flemming's weak solution

¹ Howe ('99), p. 80. ² Leitgeb, Heft 2, Taf. iii, Fig. 26.

⁴ Cavers ('03), p. 30. ⁵ Golenkin ('02), Bd. xc, p. 209.

⁷ Nemeč ('99), Bd. vii, p. 311.

³ Garber ('04), Pl. X, Fig. 40.

⁶ Janse ('97), vol. xiv.

⁸ loc. cit. ('03), p. 35.

gave most satisfactory results, though chrom-acetic and 1 per cent. chromic gave results quite as satisfactory in certain cases. Owing to the delicacy of the plants, thorough penetration of the fixing solution was obtained with no difficulty except in the case of the developing spores. Ordinarily, the material was left in the fixing fluid from six to twenty hours, whereupon it was washed in running water from four to seven hours, and then slowly dehydrated through a series of graded alcohols. Schleicher and Schull's diffusion shells were tried, but allowed of too rapid dehydration and a consequent shrinkage. It was found necessary to change the absolute alcohol at least twice. From the absolute alcohol the material was placed in a solution consisting of equal parts of absolute alcohol and bergamot oil. Turpentine was also tried, but seemed to render the material too brittle to section well, and was consequently dropped in favour of bergamot oil. It was found best by experiment to add bergamot oil to the alcohol gradually, and to transfer to pure bergamot after the lapse of about two hours. Material left in pure bergamot longer than two or three hours was in many cases too brittle. The receptacle containing the pure bergamot oil and the material was then placed in the paraffin bath and heated to about 45° C. To this small bits of paraffin were gradually added until a mixture of about equal parts resulted. The material was next transferred to pure paraffin at a temperature of about 55° C., after having been in the paraffin-bergamot solution from six to eighteen hours, depending upon the nature of the material. It was usually allowed to remain in the pure paraffin about twenty-four hours, and then blocked in small paper boxes and cooled in 95 per cent. alcohol which improves the grain of the paraffin for the knife. Albumen was employed throughout as a fixative. In most cases the sections were treated with the triple stain—anilin-safranin, gentian, and orange G., which gave good results throughout. In certain cases, however, as in spermatogenesis and sporogenesis material, iron haematoxylin and erythrosin or safranin as contrast stains were used with very satisfactory results. Free spermatozooids were fixed upon the slide with osmic vapour and stained with gentian violet. They were afterwards mounted in Canada balsam. The markings on the mature spores were most clearly brought into relief by placing the spores in a solution of 10 per cent. glycerine for a few days, which seemed to clear the exospore, rendering it a light brown.

GERMINATION OF SPORES.

In September, 1903, a number of capsules, already ruptured, were brought into the laboratory, and from spores clinging to these a number of cultures in different media were started. On September 14, spores were sown in distilled water and in a normal culture solution. On September 26, twelve days later, a few spores were germinating in the distilled water,

and in the course of five days the more advanced ones had reached a stage as seen in Fig. 4, B. Others of the same culture had undergone a nearly vertical division of the young germ-tube. The spores sown in the normal culture solution did not germinate, owing to the action of Bacteria.

On October 12 another set of cultures was prepared in which the above experiments were repeated, and in addition spores were sown in ordinary boiled tap-water and on sterilized soil. This time several spores, after a lapse of twelve days, had germinated in the normal culture-solution while

FIG. 4. A. A young plant grown on a soil-culture. $\times 300$. B, C, and D. Young plants grown in water-cultures. $\times 300$. D. Young plant containing within its cells numerous oil-bodies (*ob*) and chlorophyll grains (*c*). $\times 300$. E. Young plant grown on a soil-culture. Twelve days old. $\times 300$. F and G. Young plants in which the 'two-sided' apical cell (*x*) has appeared. Young rhizoid seen in the latter. $\times 112$. H. Cross-section of apical point of an old plant. $\times 560$.

none germinated in the tap-water till the nineteenth day. In a later tap-water-culture spores germinated in about half that time. After eleven days the young plants had reached a stage represented in Fig. 4, C and D. It was thought probable that spores germinating in the various water-cultures might show a tendency towards the development of a longer germ-tube than occurs in plants grown on soil, but in no water-culture did a germ-tube become longer than the one represented in Text-Fig. 4, B. Spores sown on sterilized soil germinated much more readily. In one culture

the first appearance of a germ-tube was recorded six days after sowing, but this was in a culture started in November. In May, 1904, a quantity of mature capsules were collected, and cultures of spores were started early in June on sterilized earth. These were kept in light of as near the normal intensity as possible, covered with a bell-jar which served to sustain an even condition of moisture. Spores in this culture did not germinate until late in August, and in no great numbers until the middle of October. This would seem to support the theory that, in all these forms, the spores necessarily have to pass through a certain resting period before germination. In a later study the writer intends investigating this point with reference to a number of Archegoniates, as it seems to be a somewhat mooted question as to whether the resting period is a constant character.

Text-Fig. 4, A represents a young plant grown on a soil-culture. Here an unusually long, unsegmented germ-tube has been developed, while

FIG. 5. Horizontal section through growing point of stem. Apical cell *x*, leaves 1, 1. $\times 560$.

Fig. 4, E and F represent young plants of the same culture twelve days old. In Fig. 4, D segmentation occurred at an early stage followed by a second division-wall, thus cutting off a short cell from which developed a germ-tube of considerable length. It would seem that this early segmentation is hardly to be considered as normal, since in nearly every case a germ-tube of some considerable length develops prior to any division into cells. Furthermore, in the water-

cultures in which the sporelings were subject more or less to the injurious influence of the Bacteria unavoidably present, early division occurred in the majority of cases. On the first appearance of the germ-tube it is seen to contain a very few chlorophyll-bodies, but is rich in oil-globules. As the plant advances these diminish in number, though to no great extent. Thus far the early development of *Fossombronia* agrees essentially with that of *Riccia hirta*, of *Fimbriaria californica*, and of *Sphaerocarpus terrestris*, var. *californicus*, as reported by Campbell¹. As in *Riccia*, the axis of growth is continuous with that of the germ-tube, and at an early stage (Fig. 4, F and G) the regular two-sided apical cell appears, from which a rapid growth ensues. This apical cell occurred repeatedly in young plants of about the age of those represented in the above figures. As in *Geothallus*², leaf-like lobes are seen to appear in some cases on either side of the apical cell. The leaves

¹ Campbell ('95), *Mosses and Ferns*, p. 38.

² Campbell ('96), vol. x, p. 506.

develop from lateral segments as described by Leitgeb¹ for *F. pusilla*. The apical growth of the species was carefully worked out by him, and it agrees in all essential particulars with that of *F. longiseta*.

Along the ventral surface, just behind the growing point, certain cells resulting from the divisions of the primary or inner segment of the apical cell, elongate to form glandular hairs. As a rule these are void of chlorophyll, but contain numerous oil-bodies. However, a very few have been noticed in which a few chlorophyll-bodies were present, though in a state of disintegration.

The first rhizoid, as a rule, appears rather late in the development of the young plant, though in Fig. 1, B and Fig. 4, G it is seen arising from the third cell. In a single instance it was seen to develop from the first or basal cell. It appears as a delicate, thin-walled, almost colourless structure, usually containing one or more granules and oil-globules. In one instance a number of chlorophyll-bodies were present. Young plants grown in water-cultures produced rhizoids quite as freely as those growing on soil, which fact suggests that after all the rhizoid may be other than an organ of mere attachment. To be sure it may be said that in the appearance of rhizoids on plants grown in water-cultures we have nothing more than the manifestation of the *hereditary tendency* of the plants to develop rhizoids. We are not certain that such a *tendency* is an actual fact, and until further and more conclusive light has been thrown upon this subject it will be unsafe to say positively what is the function of a rhizoid. Of the fact that it serves as a hold-fast we are certain, and the writer has found that stimulation due to continued contact has led to a more or less extensive branching of rhizoids in *Aneura* and *Cephalozia*.

The growing rhizoid of *Fossombronina*, not unlike the root-hairs of higher plants, contains protoplasm in contact with the inner surface of the rhizoid wall, and it would appear from this that there must be osmotic interchange between rhizoid and the outside medium. Peirce² considers the rhizoid as the physiological equivalent of the root-hair, hence an absorbing organ. Whether or not it is such can be demonstrated only after further experimentation and study.

It is an interesting fact that, so far as the writer's observations go, the earlier rhizoids are quite colourless, the characteristic vinous-purple rhizoids appearing after one or more pairs of leaves have developed. In a few instances young rhizoids, 50 to 70 μ in length, have been observed, containing along with oil-globules some chlorophyll, which later breaks down and disappears. These could not possibly have been glandular hairs, as the vinous-purple colour was already present. Very likely the chlorophyll had migrated into the rhizoid from the basal cell previous to the formation of the separating wall.

¹ loc. cit.

² Peirce ('03), p. 115.

THE ANTHERIDIUM.

The antheridia occur singly or in groups of two to four along the dorsal surface of the stem or near the bases of the leaves. They are spherical or somewhat oblong in outline, and are attached by means of stalks of variable length, though normally equal to the diameter of the antheridium-body. The stalk is composed of four rows of cells, and is slightly inclined to the plane of the stem surface of the thallus. Mature antheridia first appear as pale yellow or as orange-coloured organs, this change of colour being due to the breaking down of the chlorophyll in the wall-cells, and, to a certain extent, to the large mass of mature spermatozooids within. The antheridia are devoid of any envelope, thus differing from *Geothallus* or *Sphaerocarpus*, plants which in many respects resemble *F. longiseta*. In *Fossombronina* the antheridia mature in some instances within three weeks after growth of the thallus is resumed, and they appear in increasing numbers until about January 1, after which time their normal development ceases. Under certain unusual climatic conditions, such as have prevailed in California during the past winter and spring, antheridia have gone on developing and maturing in considerable numbers throughout the entire season. This, however, is to be considered as quite abnormal, and may be accounted for by the excessive late rains, and warm winter and early spring temperature.

The antheridia arise from single dorsal cells of the younger dorsal segments. In this respect their origin agrees with that of the antheridia as described by Campbell¹ for *Sphaerocarpus* and *Riccia*, and by Leitgeb² for *F. pusilla*.

Developing as they always do at the base of a leaf which in its early growth extends over the antheridium, there is thus afforded a protective covering to the young organs beneath. By the time the antheridium is nearly mature the leaf has unfurled, leaving the antheridium exposed to a normal amount of light and moisture. The initial cell of the antheridium is somewhat larger than the neighbouring vegetative cells, and is readily distinguished from them by its deeper staining qualities, no doubt accounted for by the somewhat larger nucleus and denser protoplasm. Just previous to the first division the initial cell becomes considerably elongated, extending a third or more of its total length above the surrounding cells. The first division results from the formation of a horizontal wall which cuts off the stalk from the antheridium itself. Unlike what occurs in the majority of the Jungermanniaceae, the next division, instead of being vertical, is horizontal, thus dividing the antheridium mother-cell into two superimposed cells, whereas in *Sphaerocarpus*³ and *Geothallus*⁴ another horizontal wall is formed, thus producing another cell, the two uppermost

¹ Campbell ('95), Mosses and Ferns, p. 79.

² loc. cit., Heft 3, p. 110.

³ Campbell ('96), vol. x, p. 497.

⁴ id.

dividing vertically to form the antheridium, while the basal cell, by a series of transverse walls, forms the foot.

In *Fossombronia* the development thus far agrees exactly with that in *Sphaerocarpus* and *Geothallus*, except that in *Fossombronia* only one horizontal division occurs in the antheridium-mother-cell, the stalk arising from the basal cell formed by the first horizontal division. This basal cell later divides horizontally, the uppermost segment becoming active in the formation of the stalk, while the lower ordinarily does not divide again. Following the horizontal division of the antheridium-mother-cell are two vertical

FIG. 6. A. Longitudinal section of a young antheridium. $\times 560$. B. Cross-section of one about the same age. $\times 560$. C. Cross-section of a nearly mature antheridium, primary divisions still evident. $\times 560$.

divisions forming planes at right angles to each other and dividing the antheridium into octants (Figs. 5 and 6, Pl. V). The next division results in periclinal walls for each of these octants, and there thus arise eight central cells and eight periclinal ones. The resulting divisions of the octant cells occur with considerable regularity, developing sperm-cells which are nearly perfect cubes. The primary divisions remain visible up to the early stages of spermatogenesis. Judging from the development of the antheridium, *Fossombronia* is more closely related to *Sphaerocarpus* and *Geothallus* than to the higher forms of the Jungermanniaceae. Leitgeb¹, in his

¹ loc. cit., Heft 3, p. 112.

description of *F. pusilla*, states that in this species the development of the antheridium does not in any way differ from that of the normal type for the Jungermanniaceae. Thus it seems that *Fossombronia longiseta* forms a connecting link between such forms as *Sphaerocarpus* and *Aneura*. The discharge of spermatozoids was observed under the microscope, and was found to resemble closely that occurring in *Porella*¹. The cells composing the antheridium-wall are quite hygroscopic, and within a few seconds following the addition of water, those at the top of the antheridium, which appear to be somewhat larger than the others, separate and roll outward, followed in rather rapid succession by the cells below (Fig. 13 a, Pl. V). Many of the cells are several times longer than broad, and when distended become markedly U-shaped. The form assumed by the cells on absorbing water seems to aid materially in pulling them apart, just as in *Porella*, though in a less marked degree. As the antheridium opens, the mature spermatozoids stream out, and within twenty to thirty seconds the antheridium is empty. The ripe spermatozoids soon become free and swim about actively.

SPERMATOGENESIS.

Up to the present time a number of investigators have studied the development of spermatozoids in the Hepaticae and have given more or less complete accounts². Among the most comprehensive are the studies of Schottländer³, Guignard⁴, Strasburger⁵, and the recent and exhaustive work of Ikeno⁶ on the spermatogenesis of *Marchantia polymorpha*. The development of spermatozoids in *Fossombronia*, while in many respects agreeing with Ikeno's account⁷, presents, on the other hand, some interesting differences. Mitosis in the spermatogenous tissue of half- or two-thirds-grown antheridia was studied in a number of stages and does not differ in any way from the mitosis of the spermatid mother-cell. The nucleus, at first relatively small and almost hyaline, enlarges rapidly as it approaches the spirem stage and a considerable amount of chromatin appears. At the same time the nuclear membrane becomes apparently much thicker, but this seems due to the presence of chromatic material and to the cytoplasm, which at this stage is quite granular. The nucleolus is large and conspicuous, but as the prophase advances this structure appears to become more or less vacuolate, as described by Farmer⁸ for *F. Dumortieri* in the mitosis of the sporogenous cells. The most careful study of the

¹ Campbell ('95), p. 101.

² Campbell ('87), Bd. v, p. 120.

³ Buchtien ('87), Heft 8.

⁴ Le Clerc du Sablon ('88), p. 876.

⁵ Schottländer ('92).

⁶ Guignard ('89), p. 1.

⁷ Strasburger ('92), Heft 4.

⁸ Ikeno ('03), Bd. xv, pp. 65-68.

⁹ id. ('03), Bd. xv, Pl. III, Figs. 1, 9, 10.

¹⁰ Farmer ('95), vol. ix, Pl. XVI, Fig. 4.

nucleus at this stage failed to reveal anything that might be interpreted as a centrosphere or a centrosome. In this respect *Fossombronina* certainly appears to differ from *Marchantia polymorpha*, for which Ikeno has figured a well-defined centrosome appearing first among the linin threads, afterwards moving to the surface of the nucleus from which it is discharged. It was thought most likely to appear, if present at all, at the time of elongation of the nucleus just prior to the development of the spindle, but here again the protoplasm surrounding the nucleus disclosed the presence of nothing that could be considered a centrosome. The protoplasm about the nucleus presents a rather homogeneous granular appearance, and it is barely possible that this may account for the failure to observe centrosomes were they present.

The various stages of mitosis are passed through quite rapidly, and intermediate stages between the spirem and mature spindle were not observed, consequently it is not known what structures, if any, are instrumental in bringing about the polarity of the spindle. In *Marchantia polymorpha* Ikeno figures the centrosome as active in spindle-formation, the two exerting an opposed pull upon the cytoplasm after the nuclear membrane has extended in the direction of the centrosomes and has made contact with them.

However, since no centrosome or homologous structure was seen in either of the above-named or antecedent stages, it is probable that the spindle develops in much the same way as in *Anthoceros*, where centrosomes are not known to exist.

Successive divisions of the spermatogenous tissue occur, in which the cells seem, so far as observed, to divide simultaneously, though in one antheridium all the cells in one-half of the section were in early prophase, while those in the remaining half were in metaphase. Up to the division resulting in the formation of the spermatid cells the divisions take place so as to form nearly cubical cells which are normally quite regular, following, as can be seen in many cases almost to the last division, the original lines of the primary and early divisions. Fig. 14, Plate V represents mature cells of an antheridium about two-thirds of the way along in its development. Fig. 16, Plate V represents similar cells of an antheridium just preceding the first of the last two-divisions, at which time the antheridium has attained nearly its mature size. Here we notice a considerable decrease in size as the cells divide, and it would seem that the growth of the antheridium does not parallel the increase in the number of cells¹.

After a number of successive and regular divisions in the spermatogenous tissue, the antheridium is divided into a greatly increased number of cells which undergo a final division to form the spermatid cells.

¹ Peirce ('03), pp. 165-6.

According to Ikeno¹ the spermatid mother-cells divide diagonally, thus forming spermatids of triangular outline without the formation of a wall between them. This is true of *F. longiseta* and *Aneura* as well as other Liverworts thus far observed. Each one of the spermatids thus formed develop later into spermatozoids. Up to the division of the spermatid mother-cell, all divisions are at right angles or nearly so, with the spindle lying in the long axis of the cell. In the spindles of a number of these cells the number of chromosomes could be estimated, and so far as could be ascertained they are eight.

In the case of the diagonal division (division of spermatid mother-cell) the axis of the spindle is invariably diagonal, thus dividing the cell into two daughter-cells, whose greater faces are parallel as in Fig. 23, Pl. V. As mentioned above, no division-wall is formed between these two daughter-cells, which appear to be nothing more than regular masses of protoplasm supplied with nuclei and surrounded at first by a delicate membrane, which later becomes a more evident structure. Thus inside of the spermatid mother-cell, which Ikeno also refers to as a 'tesserale Zelle,' are developed these two nucleated bodies or spermatids.

The method of division in the spermatid mother-cell is the same as that described above for other cells of the antheridium. In one or two cases bodies were seen at or near the poles of a spindle, that, so far as location goes, might have been interpreted as centrosomes, but were in all probability protoplasmic granules; for here again none of the nuclei in the spirem or prophase conditions exhibited structures such as occur at corresponding stages in *Marchantia*. The diaster phase of division was not observed in the mitosis of the spermatid mother-cell, but appeared a number of times in the younger spermatogenous cells. After the completion of mitosis in the spermatid mother-cell, the two daughter-cells (spermatids) contract, drawing away from the wall of the mother-cell though still preserving their original form for some length of time.

In *Marchantia polymorpha* Ikeno² reports the disappearance of the centrosome at the completion of mitosis in the cells of the younger spermatogenous tissue, reappearing in the early spirem stage of the next division. While in the division of the spermatid mother-cell he figures a centrosome just outside of each daughter-nucleus, instead of within as in preceding divisions. This centrosome³, he states, remains unchanged up to the time it assumes the function of a blepharoplast.

In *Fossombronia* no evidence of such a structure can be seen in the daughter-cells: in fact, not for some time after the contraction of the cell-contents of the newly formed spermatids do the blepharoplasts appear. These bodies may be made out with considerable ease, as they take up the

¹ loc. cit. ('03), p. 73, Fig. 17 of plate.

² loc. cit., p. 71, Fig. 166 of plate.

³ loc. cit., p. 86.

stain with marked avidity. In all cases examined the blepharoplast first appears in the cytoplasm, but no light can be thrown upon its origin. Much time was devoted to the study of this particular question, but without result. Shortly after the appearance of this structure it is seen to migrate towards the more acute angle of the spermatid, which in some cases faces the similar angle of the sister cell, though usually they are seen to lie as represented in Fig. 24, Pl. V. At the completion of migration the blepharoplast is seen to occupy the angle above mentioned, and appears closely applied to the cell membrane. Previous to this, however, there also appears in the cytoplasm another and considerably larger, dark-staining body, reported for the first time in the Hepaticae by Ikeno in his studies on the spermatogenesis in *Marchantia polymorpha*. It seems that Strasburger and Guignard have not reported such a structure in the plants studied by them. To this body Ikeno gives the name 'Nebenkörper.' Its behaviour in the spermatid of *Fossombronina* is somewhat different from that in *Marchantia*. It appears in the cytoplasm, Fig. 26, Pl. V, without reference to any definite position, though usually it is found occupying a position not far from the nucleus and between the nucleus and the blepharoplast, which, by the time of the appearance of the 'Nebenkörper,' has nearly completed its migration to the pole. Invariably this accessory body seems to seek a position just beneath the blepharoplast, where it is seen to elongate. Ikeno¹ states that shortly after the cilia have started to grow the 'Nebenkörper' in *Marchantia* vanish. Thus, according to his description, this structure plays no part in the formation of the spermatozoid, though his figures seem to show an elongation of the 'Nebenkörper,' and the ultimate passage of the same into the structure of the spermatozoid, apparently forming the middle piece. Further on, however, he states (p. 79) 'der cytoplasmatische Forsatz beginnt sich auszubilden und wächst nach der Richtung des vorderen Endes des jetzt sich bildenden Spermatozoids hin, um schliesslich das Zentrosom zu erreichen, so dass dieser Forsatz den letzteren mit dem Zellkern verbindet.' In *Fossombronina* several preparations were obtained, showing the attenuation of the 'Nebenkörper' as represented in Fig. 29. At this stage, Fig. 30, Pl. V, or a little before, the cytoplasm is seen to elongate in the direction of the 'Nebenkörper' and blepharoplast, apparently connecting with the former, which in its elongated form has come to lie close to the plasma-membrane of the young spermatozoid. Later the connexion seems to become complete as in Fig. 31, Pl. V, and then the developing spermatozoid elongates rapidly. Previous to the appearance of cilia the blepharoplast elongates somewhat (though a number of instances were observed in which this was not perceptible), apparently following the inner contour of the cell-membrane instead of forming a 'Cytoplasmahöcker' as described by

¹ loc. cit., p. 71.

Strasburger¹ for *Pellia calycina*. However, owing to the extreme minuteness of the organ in question, it is not impossible that the blepharoplast of *Fossombronia* grows out into a hook-like process as in *Pellia*. The cilia, in nearly all cases where they could be seen, were closely applied to the cell-membrane, and this position they retain throughout development.

As the body of the spermatozoid elongates, the chromatin of the nucleus appears to condense, and ultimately conceals the nucleolus (Fig. 31, Pl. V), which up to this time has been more or less apparent. This condensation is followed by an elongation of the nuclear chromatin, which seems to connect with the chromatic substance of the elongated 'Nebenkörper.' The spermatozoid when mature shows about one and a half complete turns of a spiral. The two cilia are relatively about as long as those in other Jungermanniaceae, and in the coiled mass of the spermatozoid are closely applied to the body.

In *Marchantia polymorpha* Ikeno describes an abnormal division of the spermatid into two rounded cells, each of which later becomes a spermatozoid. The division is amitotic, resulting in two 'Nebenkörper'; and a little later the 'Zentrosom' divides, followed by division of the nucleus. Nothing of this nature was observed to occur in *Fossombronia*. Ikeno², along with Hirase³, Belajeff⁴, and a few other investigators, holds the view that a genetic relation exists between the centrosome and blepharoplast, as opposed to the view of Webber⁵, Strasburger⁶, Mottier⁷, Shaw⁸, and others, who see no good reason why one should be considered homologous with the other. Mottier is of the opinion that the radiations of the blepharoplast primordium, described by some authors, is the only evidence they can produce in support of such an homology. According to Ikeno, the 'Zentrosom' appears constantly throughout the mitosis of the spermatogenous tissue of *Marchantia*, while Shaw and Belajeff describe the blepharoplast as first appearing in the 'grandmother' cells. In *Fossombronia* these, if they previously exist, are not evident until after the completion of division of the spermatid mother-cell, at which time they are easily made out lying in the cytoplasm not far from the nucleus. Bearing this in mind it is difficult to understand why, when employing exactly the same methods, these blepharoplasts, if present, did not appear during the divisions prior to the formation of the spermatid cells. Mottier, judging from evidence at hand, holds the opinion that the blepharoplast arises in the cytoplasm *de novo*, and the writer's studies regarding *Fossombronia* seem to support this view.

In so far as the preparations show, the 'Nebenkörper' in *Fossombronia*

¹ loc. cit., pp. 128-9.

⁴ Belajeff ('99), Bd. xvii.

⁶ loc. cit.

⁸ Shaw ('98).

² loc. cit., p. 77.

³ Hirase ('98), vol. xii, pt. 2.

⁵ Webber ('01), p. 77.

⁷ Mottier ('04), p. 47; loc. cit., p. 49.

arise *de novo*, and as above stated do not disappear as described for *Marchantia*. Shaw¹, in his studies on *Marsilia*, represents in Fig. 5 a body lying about midway between the spindle and cell-membrane, which he names a blepharoplastoid. This, as it appears in his Fig. 2, Ikeno² considers as recalling that stage of the 'Nebenkörper' in *Marchantia*, as he has represented it in his Fig. 35. Whether the two are in any way homologous, only continued study can reveal. In fact, this whole question as to the origin of the 'Nebenkörper' and its morphological and physiological significance is one upon which only the study of many Archegoniates can throw any helpful light.

The writer's work on *Fossombronia*, while agreeing in many essential respects with what occurs in *Marchantia* and *Pellia* and certain Ferns that have been investigated, still presents some important differences which bespeak the great need of continued work along the same line with a large number of forms.

THE ARCHEGONIUM.

The development of the archegonium shows a few peculiarities, but in its more essential features it agrees with the other Hepaticae. It arises in a manner not unlike that of the antheridium, and in its initial stage, Fig. 37, Pl. VI, is sometimes difficult to distinguish from the first stage of the antheridium. Usually, however, it does not extend so far above surrounding cells. The first division, being horizontal, divides the initial cell into the archegonium-cell proper and the stalk. The upper cell is usually considerably larger than the lower, differing in this respect from *Sphaerocarpus*³. The next division in all cases examined did not take place in the stalk-cell, as in *Sphaerocarpus* and *Geothallus*⁴, but in the upper cell, where a nearly vertical wall is formed (Fig. 30, Pl. VI) very much as in other Liverworts. This is followed by two similar divisions in the remaining larger cell, thus separating the archegonium-cell into four. Following this, the stalk-cell divides by a horizontal wall, and later on a vertical division occurs.

A horizontal division near the top of the axial cell cuts off (Fig. 41, Pl. VI) a central cell, that later divides horizontally forming a canal-cell and an egg-cell. Thus the axial row comes to consist of three cells, the upper of which constitutes the cover-cell. About this time two of the three peripheral cells divide vertically, thus forming five neck-cells, Fig. 46, Pl. VI, the typical number for the Jungermanniaceae. In a few instances, however, cross-sections revealed six neck-cells as in *Geothallus*⁵, Fig. 47, Pl. VI, and in the Marchantiaceae.

¹ loc. cit. ('98).

² loc. cit.

³ Campbell ('95), p. 76.

⁴ Campbell ('96), pp. 500-1

⁵ loc. cit.

The number of neck-canal-cells is, so far as observed, invariably six (Fig. 45, Pl. VI). The mature archegonium is considerably more enlarged through the venter than in *Porella*, and the egg-cell is noticeably larger than the central canal-cell in comparison with *Porella*, corresponding more nearly with these cells in *Sphaerocarpus*. The cells constituting the wall of the venter consist usually of one layer, though Text-Fig. 7, A, represents a case where two layers occur. Here again *F. longiseta* differs from *F. pusilla* as described by Leitgeb¹, where, according to him, the ventral wall

FIG. 7. A. Cross-section through venter of mature archegonium. $\times 560$. B. A similar section showing presence of spermatozoid in the egg. $\times 1200$. C. Cross-section of young embryo. $\times 560$.

is commonly two layers of cells in thickness. The development of the perianth, as described by him, agrees exactly with that of *F. longiseta*, in that it develops only after fertilization, the unfertilized archegonium bearing at its base only a chain or two of cells resembling somewhat glandular hairs. The perianth is always open anteriorly and grows much more rapidly than the young sporogonium, completely hiding it until nearly ripe.

The unfertilized egg has a well-defined receptive spot. The relatively large egg-nucleus, as well as the nuclei in other parts of the plant, as a rule possess but one nucleolus and a small amount of chromatin. Text-Fig. 7, B, represents a fertilization stage in which the spermatozoid has entered the egg-cell. Later stages were not obtained.

The neck of the mature archegonium, owing to retarded growth on one side, is always more or less curved and inclined, as are the antheridia, to the plane of the thallus. Usually a number of archegonia develop, but only in rare cases are more than one of these fertilized. Fig. 1, Pl. V, represents a plant on which two sporogonia have developed, and that, too, from parts of the thallus where one would least expect them. Usually the development of the sporogonium marks the end of the season's growth for the plant. It is usually situated just behind the growing point instead of far back on the thallus as in Fig. 2, Pl. V.

¹ loc. cit., p. 113.

THE EMBRYO.

The first division in the embryo is transverse, dividing the considerably enlarged egg-cell into two nearly equal ones, Text-Fig. 8, A, the epibasal cell later giving rise to the capsule and seta as in the typical Jungermanniaceae, and the hypobasal portion giving rise to the rather conspicuous foot. Following the primary division there next occurs a transverse wall in the epibasal cell, dividing it into two, the uppermost evidently giving rise to the archesporium, and lower one the seta.

There next occurs a third transverse division, this time dividing the epibasal cell into two, the lower one commonly dividing no further until

FIG. 8. A-D. Successive stages in development of the embryo. $\times 560$. E. Differentiation of archesporium and formation of first periclinal wall. $\times 560$. F. A later stage in development of archesporium. $\times 560$. G. An abnormal embryo. $\times 560$.

the embryo has reached an advanced stage, Text-Fig. 8, C. The embryo now consists of a tier of four superimposed cells, and the next division, Fig. 8, D, is a vertical one, followed by another at right angles to the first, thus dividing each cell into four parts. In the upper or archesporial cells are now formed periclinal walls, thus separating four archesporial cells from four wall-cells, Fig. 8, E, the initial layer of the capsule-wall. By this time a number of rather irregular divisions have occurred in the lower half of the embryo, along with an increase in size in the archesporial region, and, owing to the slow development of the stalk, the characteristic dumb-bell shape is already evident.

Further transverse divisions, followed by vertical ones, occur in the archesporium with considerable regularity, as seen in Text-Figs. 8, F, and 7, C. In *Fossombronia pusilla*, according to Leitgeb¹, the somewhat elongated egg divides by transverse walls into three cells, and then occur vertical divisions in both the end-cells, resulting in the rather rapid development of the capsular and foot regions. Further than this the two species agree in the development of the embryo. The archesporial cells rapidly increase in number, completely filling the space of the capsule. Several slides were obtained showing the early stages in the development of the elaters and spore-mother-cell. Fig. 50, Pl. VI, shows a group of archesporial cells where cells of different sizes are shown. In Fig. 53, Pl. VI, a later stage is shown, where the difference between the spore-mother-cells and the elater-initials has become very pronounced. In the latter the cell-contents seem to have contracted and elongated, while the spore-mother-cells are more regular in outline and the greater mass of cell-contents has drawn away from the cell-wall into a more spherical body, which ultimately forms the spore-tetrad. The original cell-walls persist for some time, being still faintly perceptible at the time of tetrad-formation, but finally breaking down.

The mitosis of the sporogenous cell was carefully studied and found to agree with Farmer's² account of the same in *F. Dumortieri*, with the exception of a failure to find centrospheres at any stage. Structures in a few cases were present that resembled vague radiations, but these also bore a resemblance to an irregular streaming disposition of the cytoplasm at either pole of the nucleus, as in Fig. 50, Pl. VI. Very prominent asters have been figured by Garber³ for *Ricciocarpus natans*, and it is possible that by using his methods they will be found to occur in *F. longiseta*. Anything like a complete series of satisfactory stages in the formation of spores has not yet been obtained for this species. As stated by Farmer, the sporogonia at the time of mitosis in the spore-mother-cell are fixed with great difficulty. The utmost care was employed throughout the whole process of fixation, dehydration, and embedding, but the exceedingly interesting and important matter of the mitoses that occurs in the spore-mother-cell remains a subject for subsequent study.

Stages just preceding the appearance of the spindle in the first mitosis were obtained, which are of interest here. Previous to any change in the nucleus, which usually occupies an approximately central position in the mother-cell, instead of lying in one lobe of the cell as described by Davis⁴ for *Pellia*, the wall of the spore-mother-cell constricts at four opposite points as figured by Farmer⁵ for *F. Dumortieri*, Davis for *Pellia*

¹ loc. cit., vol. iii, p. 117.

³ Garber, vol. xxxvii, Fig. 35.

⁵ loc. cit.

² Farmer, Ann. Bot. ('95), vol. ix, pp. 470-1.

⁴ Davis, vol. v, xv.

and *Pallavicinia*, and Moore¹ for *Pallavicinia*. Following this the nucleus, in which the nucleolus is relatively very large, shows a delicate, reticular structure and assumes an equi-four-angled form (Fig. 55, Pl. VI). Here again no radiations were perceptible, although different stains were employed. In one case the anilin-safranin—gentian-violet—orange G combination was employed, but more satisfactory results were obtained with the iron haematoxylin, using erythrosin as a contrast stain. A little later the nuclear protuberances are considerably elongated, extending well into each lobe of the cell. At this stage there seems to appear an accumulation of cytoplasm at the four poles, but nothing like definite radiations could be made out. At this time in all cases examined the nucleolus had begun to undergo change, in some instances appearing vacuolated, while two of the nuclear arms were somewhat longer than the others, which corresponds with Farmer's account of the spore-mother-cell nucleus in *F. Dumortieri* just preceding the appearance of the bipolar spindle. Satisfactory stages of the further behaviour of the nucleus were not obtained, so we pass to the events following mitosis. The ultimate outcome of the division in the spore-mother-cell is the tetrad, each cell of which has its own nucleus, equaling in size that of the archesporial cell, though the nucleus is relatively smaller than is true of the spore-mother-cell. Protoplasmic granules in the cytoplasm lie disposed irregularly, giving the protoplasm a somewhat vacuolated appearance. Each spore now becomes surrounded by its own proper wall, and a little later a distinct endospore becomes differentiated. Judging from its staining qualities the old spore-mother-cell wall becomes mucilaginous, and by breaking down the spores become liberated within the capsule, in which respect it agrees with the other Jungermanniaceae, with the exception of *Sphaerocarpus*. The spores have already been described by Howe² as showing considerable variation in external appearance, which leads him to think that this is significant of a possibility that we may be including under the head of *F. longiseta* more than one species. The writer's investigation can throw no light upon this point. He has found the echinate and cristate types of spores produced on plants that in no other respects appeared to differ. In the majority of cases the inner faces of the spore are nearly smooth in comparison with the outer face; the cristate ridges of the latter, at times, apparently being continuous near the limits of the inner faces, as seen in Fig. 59, Pl. VI.

Normally the spores are somewhat compressed and round-tetrahedral in outline, measuring from 38 to 50 μ in greatest diameter. The ripe sporogonium by the rapid, and relatively very great, elongation of the seta reaches a total length of 10 to 16 mm. For some time previous

¹ Moore, vol. xxxvi, Fig. 1 of plate.

² loc. cit., p. 82.

to the growth of the sporogonium above the involucre the capsule is already very dark-brown or black, and to all appearances the spores are ripe.

The capsule bursts in a manner characteristic among the Jungermanniaceae, splitting irregularly into four valves which turn back, exposing the mass of spores and elaters. The development of the elaters parallels in rate that of the spores, the spiral thickening appearing at about the time of the differentiation of the spore-crests. In a few cases much deformed nuclei were observed in elaters, in which the double spiral band was very prominent, but in the fully mature elater all trace of such a structure seems obliterated. Judging from its appearance at different stages in the development of the elater it undergoes structural changes that render it incapable of differentiation by use of stains, and, though it may still be present in the mature elater, it is not recognizable from other bodies sometimes present upon the inner surface of the wall. The mature elater attains a length varying from 150μ to nearly twice that length.

The capsule-wall is normally bistratose, the cells of both layers commonly bearing incomplete annular-like thickenings, though, in the original description of the genus, these thickenings are described as occurring only in the cells of the inner layer. In the material used in the preparation of this paper the wall in many cases appeared as in Fig. 64, Pl. VI, in which it is readily seen that the development of these bands is by no means as constant a character in the outer cells as in those of the inner layer, and might quite easily be overlooked.

Viewed *en face*, these annular bands appear as in Fig. 63, Pl. VI, and are by no means as regular as those described by Cavers¹ for *Preissia commutata*, *Targionia hypophylla*, and *Monoclea Forsteri*. The calyptra, previous to the ultimate elevation of the capsule, is very closely applied to it, in fact so closely does it fit over the capsule as to make it sometimes difficult to distinguish its individuality from the capsule-wall-cells themselves. As soon as the seta begins to lengthen the calyptra ruptures, thus exposing the nearly ripe capsule.

The foot, somewhat globular in form, attains a relatively greater size than the corresponding structure in *Sphaerocarpus*. Its basal outline is irregular, owing to the development of cells that project (Fig. 62, Pl. VI) half or more of their diameter beyond the average limits of the foot. The cells of the foot, especially those in the basal portion, are very rich in granular protoplasm, each possessing a conspicuous nucleus as in *Geothallus*². In all cases examined the foot gives evidence of a considerable growth and consequent compression of the proximate cells of the gametophyte.

¹ Cavers ('04), pp. 9, 33, 44.

² Campbell ('96), p. 504.

SUMMARY.

1. The apex of each leaf-lobe terminates in a single, smaller cell, void of chlorophyll, though always containing a few oil-globules and considerable mucilaginous fluid. These cells bear a strong resemblance to the mucilaginous hairs, and are, doubtless, of the same physiological significance to the plant.

2. The plants are susceptible to great desiccation without material injury. On being moistened they revive in a few hours. Plants that have passed through a dry season are often found bearing sex-organs in an advanced stage of development.

3. The germinating spore produces normally a germ-tube of considerable length, containing little chlorophyll, but rich in oil-globules, which diminish in number as the growth of the young plant advances. The segmentation of the germ-tube shows variation, sometimes taking place very early, as in Text-Fig. 4, D. The first rhizoids commonly appear at a later stage; these are colourless, while those of older plants are vinous purple.

4. The antheridium mother-cell divides once horizontally; this is followed by a horizontal division in the basal cell, the uppermost segment of which becomes active in forming the stalk. Following horizontal division of the mother-cell are two vertical divisions, giving rise to octants. Further divisions in the spermatogenous tissue occur with marked regularity.

5. The development of the antheridium in *Fossombronina longiseta* shows it to have a certain morphological relationship with such forms as *Geothallus* and *Sphaerocarpus*.

6. No centrosome was observed at any stage of nuclear division in spermatogenesis. The spermatid mother-cell divides to form two spermatids, between which no wall is formed.

7. Blepharoplasts appear apparently *de novo* in the cytoplasm of the spermatid. These migrate to one of the spermatid poles and later develop cilia.

8. A 'Nebenkörper' appears in the cytoplasm of the spermatid, and migrates towards the pole occupied by the blepharoplast. Here it elongates and appears to connect up with the cytoplasm and blepharoplast, thus forming the middle piece of the spermatozoid.

9. The mature sperm forms a spiral of about one and one-half turns.

10. The first division in the archegonium-mother-cell is horizontal, followed by three nearly vertical divisions in the upper cell. This is followed by horizontal and vertical divisions in the stalk-cell. Later divisions result in the formation of cap and axial-cells. The latter divide to form six canal-cells, a ventral canal-cell, and relatively large egg, bearing a well-defined receptive spot.

11. The number of neck-cells is normally five, though occasionally six.

12. The first division in the embryo results in two nearly equal cells. From the epibasal portion arise capsule and seta, the hypobasal cell giving rise to the foot.

This division is followed by another horizontal one in the epibasal cell, separating capsule and seta initials.

Another horizontal division in the hypobasal cell leaves the embryo consisting of four superimposed cells.

13. Vertical divisions now occur, giving rise to four cells from each initial, with the exception of the foot-cell, which does not divide till much later.

14. Periclinal walls now appear, one for each archesporial quadrant. This is followed by further divisions, occurring most frequently in the foot and archesporium.

15. The seta is commonly about seven cells in diameter, and elongates but little till maturity of spores.

16. The archesporial cells divide rapidly, forming, ultimately, elater-initials and spore-mother-cells. The spores develop in tetrads, separating before rupture of capsule-wall.

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EXPLANATION OF FIGURES IN PLATES V AND VI.

Illustrating Mr. Humphrey's paper on *Fossombronia longiseta*.

PLATE V.

Except when otherwise indicated, all drawings were made from microtome sections, and were drawn with the aid of an Abbé camera lucida. All sections were stained with Flemming's triple stain, except when otherwise stated.

- Fig. 1. A thrice dichotomous plant bearing three sporangia, natural size.
- Fig. 2. A plant bearing antheridia and archegonia. $\times 10$.
- Fig. 3. A mature plant bearing a single sporogonium. $\times 10$.
- Fig. 4. Initial cell of antheridium in which the first division has occurred. $\times 560$.
- Fig. 5. A later stage in the development of the antheridium in which a second horizontal division has occurred and the first vertical wall is in process of formation. $\times 560$.
- Fig. 6. Octant stage. Two vertical walls have formed at right angles to each other as indicated in Fig. 9, cross-section of an antheridium of same stage. $\times 560$.
- Fig. 7. Stage in which periclinal walls have formed. $\times 560$.
- Fig. 8. Cross-section of stage represented in Fig. 5. $\times 560$.
- Fig. 9. Cross-section of stage represented in Fig. 6. $\times 560$.
- Fig. 10. Cross-section of stage represented in Fig. 7. $\times 560$.
- Figs. 11 and 12. Cross-sections of later stages. $\times 560$.
- Fig. 13. A mature antheridium drawn shortly before discharge of spermatozooids. Crown cells much swollen. $\times$ about 300. Ad. nat.
- Fig. 13 a. An antheridium that has discharged its spermatozooids. $\times 150$.
- Fig. 14. Spirem stage of nucleus in cells of spermatogenous tissue of very young antheridium. $\times 2400$.
- Fig. 15. Diaster stage of mitosis in cells of a somewhat older antheridium. $\times 1750$.

Fig. 16. Spirem stage of nucleus in cells from which the spermatid mother-cells arise. Stained with iron haematoxylin and safranin. $\times 2400$.

Fig. 17. Metaphase in division of cells of the age of those represented in Fig. 16. Stained with Flemming's triple stain, also with iron haematoxylin. $\times 2400$.

Fig. 18. A spindle viewed *en face* showing chromosomes. $\times 2400$.

Fig. 19. A group of spermatid mother-cells; nuclei in resting-stage, though the chromatin is appearing and the nuclei are about to pass into the spirem condition. No blepharoplast apparent. Stained with iron haematoxylin and safranin. $\times 2400$.

Fig. 20. Spirem stage of spermatid mother-cell. Stained with Flemming's triple stain. $\times 1750$.

Fig. 21. Metaphase of mitosis in spermatid mother-cell. $\times 1750$. Stained with iron haematoxylin and safranin.

Fig. 22. Formation of spermatids within spermatid mother-cell; line of separation indicated between them. $\times 2400$.

Fig. 23. Separation of spermatids, and appearance of a blepharoplast in cytoplasm of each cell. $\times 2400$.

Fig. 24. Migration of blepharoplasts to opposite poles. $\times 2400$.

Fig. 25. Migration of blepharoplasts to like poles. $\times 2400$.

Fig. 26. First appearance of 'Nebenkörper' in cytoplasm. $\times 2400$.

Figs. 27 and 28. Migration of 'Nebenkörper' towards blepharoplast. $\times 2400$.

Fig. 29. Elongation of 'Nebenkörper' near blepharoplast from which cilia have developed. $\times 2400$.

Fig. 30. Elongation of cytoplasm in direction of the 'Nebenkörper.' $\times 1750$.

Fig. 31. Further elongated cytoplasm which has apparently connected up with the 'Nebenkörper' which is thus forming the middle piece of the spermatozoid. $\times 1750$.

Fig. 32. Condensation of the nucleus and elongation of spermatozoid. $\times 2400$.

Fig. 33. A later stage in the growth of the spermatozoid. $\times 2400$.

Fig. 34. Mature spermatozoid still within matrix. Stained with gentian violet. $\times$ about 1800.

Figs. 35 and 36. Free spermatozooids. $\times$ about 1800.

PLATE VI.

Figs. 37-44. Successive stages in development of archegonium. $\times 560$.

Fig. 45. Mature archegonium in which a well-marked receptive spot is seen in the egg. $\times 560$.

Figs. 46 and 47. Cross-section showing number of neck-cells. $\times 560$.

Fig. 48. Spirem stage of nucleus in archesporial cell. Nucleolus still present. $\times 1750$.

Fig. 49. Spirem stage of nucleus of similar cell in which nucleolus has disappeared. $\times 1750$.

Fig. 50. A group of archesporial cells in one of which a mature spindle is figured. $\times 1200$.

Fig. 51. Anaphase, in archesporial mitosis.

Fig. 52. Formation of daughter-cells. $\times 1750$.

Fig. 53. A group of sporogenous cells among which have appeared elater initials. The larger cells are spore-mother-cells. $\times 650$.

Fig. 54. Initial stage in the formation of a spore-tetrad. $\times 560$.

Fig. 55. A later stage in which the nucleus is elongating into each lobe.

Figs. 56, 57 and 57a. Spore-tetrads and elater of same age. $\times 560$.

Fig. 58. Section through spores of a tetrad about to separate. Mucilaginous wall between and around them. $\times 560$.

Fig. 59. A ripe spore. $\times 560$.

Fig. 60. A mature elater and median section through a ripe spore. $\times 560$.

Fig. 61. Diagram of a longitudinal section of sporogonium just previous to elongation of the seta. $\times 80$.

Fig. 62. Median longitudinal section through the foot. $\times 335$.

Fig. 63. View of a portion of inner surface of capsule wall showing annular thickenings. $\times 560$.

Fig. 64. View of capsule wall seen in longitudinal section of capsule. Showing annular bands in cells of both layers. $\times 560$.

Fig. 65. Spindle in cell of gametophyte. $\times 1200$.

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