THE STRUCTURE AND DEVELOPMENT OF CRYPTOMITRIUM TENERUM.

LE ROY ABRAMS.

(WITH SIX FIGURES)

THE genus Cryptomitrium, represented by the single species *C. tenerum* (Hook.) Austin, has not yet been thoroughly studied, and as the plant has been collected in several localities near Stanford University, at the suggestion of Dr. Campbell a study of its structure and development was undertaken, in order, if possible, to determine its relationship to the other Marchantiaceæ.

The first collections were made late in the spring of 1898, at which time the plants were mature, and the spores almost ripe. Some of these plants were placed in alcohol, while others were allowed to become dry, and the earth upon which they were growing was kept until the following September, when the work upon the plant was taken up. A considerable number of the mature sporogonial receptacles were also put up dry, in order to study the germination of the spores.

Some of the pieces of earth with the dried specimens upon them were thoroughly soaked, and then kept well moistened. Within a day or two the tips of the apparently dried-up plants became green and fresh, and in about two weeks the antheridia began to form. All of the material for study was obtained in this way, until after the rains came. Then considerable material was collected from out of doors, where it developed much faster and was healthier than that grown in the laboratory.

THE THALLUS.

Cryptomitrium, like most other Marchantiaceæ, has a flat, dichotomously branched thallus, which in this species is very thin and delicate. The smooth glossy appearance, by which one can easily distinguish the sterile plants from *Fimbriaria*

Californica Hampe, a species almost always associated with it, is due for the most part to the minute stomata.

These stomata are surrounded by eight, occasionally seven, very symmetrically arranged guard cells (*a*, *fig. 1*), and not by five or six, as stated by Stephani.[1] Each opens into a well-developed air chamber (*b*, *fig. 1*), the boundaries or walls of which can be seen easily with a hand lens, forming a fine network under the epidermis.

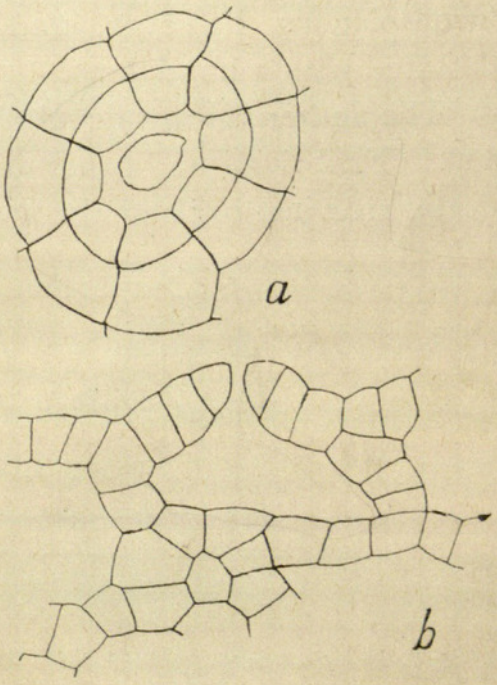

FIG. 1.—Stomata of the thallus. *a*, as seen from the surface. ×600. *b*, transverse section. × 600.

These air chambers are much the same as in *Fimbriaria Californica*. They are distributed irregularly throughout the green tissue. Only a single layer of cells separates them, and often one cavity is connected with another. Their development begins a little further back from the apical cell than in the above mentioned species as described by Campbell.[2]

The general appearance and external characters of the ventral scales have been quite thoroughly and accurately described by Stephani (*loc. cit.*), and as their development does not differ from that of other allied genera it need not be repeated here.

As might be expected, both kinds of root hairs, those with smooth thin walls and those with tuberculate walls, which are characteristic of the Marchantiaceæ, are present.

The peculiar oil bodies found in so many of the Hepaticæ were found scattered throughout the thallus, ventral scales, and sporogonial receptacle. The development and composition of these oil bodies found in the Hepaticæ have been thoroughly studied by Pfeffer.[3]

[1] BOT. GAZ. 17: 58–60. 1892.

[2] CAMPBELL, D. H.: Mosses and Ferns, p. 48. 1895.

[3] PFEFFER, W.: Die Oelkörper der Lebermoose. Flora 32: ——. 1874.

THE SEXUAL ORGANS.

Cryptomitrium tenerum is monœcious. The antheridia form a single row just back of the sporogonial receptacle. They are sunk deep in the thallus, and each one is marked on the surface by a small conical ostiolum. These ostiola are very inconspicuous, however, and their presence can scarcely be detected with a hand lens.

The antheridia are developed before the female receptacle, and in Fimbriaria and other allied genera, they are formed on the dorsal side just back of the apical cell (*a*, *fig. 2*). The primary

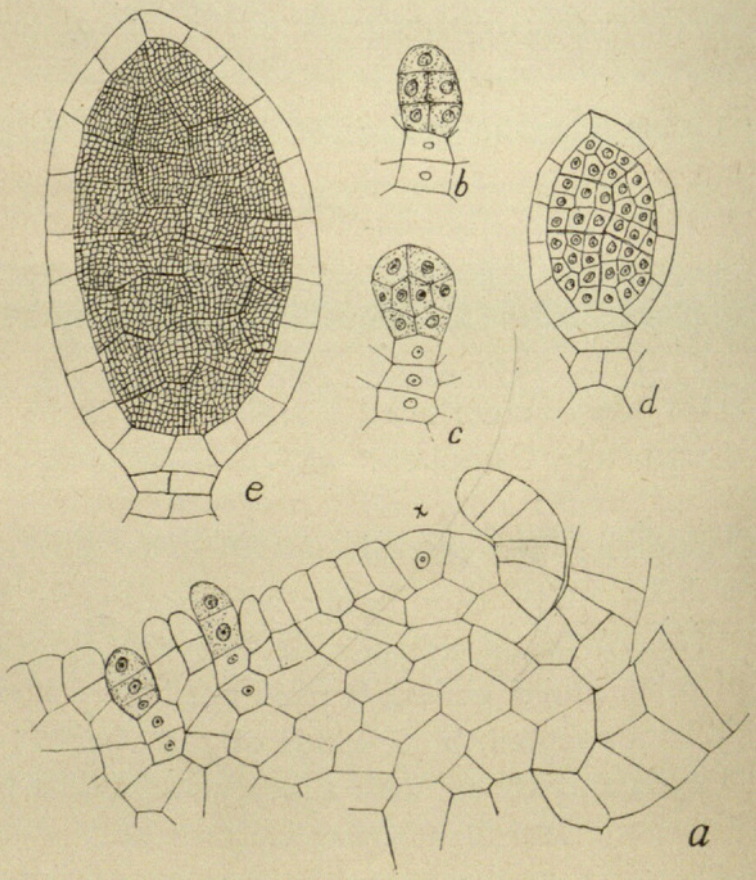

FIG. 2.— Antheridia. *a*, longitudinal section of apex of thallus with two young antheridia; *x*, apical cell. × 600. *b*, *c*, *d*, successive stages of young antheridia. × 600. *e*, full-grown antheridium. × 480.

antheridial cell, when it can first be distinguished from the initial cells around it, is a little larger and stains more deeply than these cells. The first division (*a*, *fig. 2*) is transverse and

divides the primary cell into the stalk or pedicel cell and the antheridial cell proper. The antheridial cell thus formed is then divided into three cells (*a*, *fig. 2*) by two transverse divisions. The next two divisions are longitudinal medial and are at right angles to each other, so that each of the three original cells is divided into four. In many cases, however, only the two lower cells are divided in this way (*b*, *fig. 2*), the top cell remaining undivided for a longer time. The four cells formed from the central cell by these longitudinal divisions are each again divided longitudinally, thus separating the sperm cells from those that go to make up a portion of the antheridial wall (*c*, *fig. 2*). The upper and lower cells take no part in forming the sperm cells, but form, respectively, the upper and lower portions of the antheridial wall. The remainder of the development does not differ materially from that of *Fimbriaria Californica* as described by Campbell.[4] The top of the antheridial wall is not prolonged, however, as in that species, but is only a single row of cells, as in Marchantia. In fact, the full-grown antheridium (*e*, *fig. 2*) resembles very closely that of Marchantia.

The sporogonial receptacle, or carpocephalum, is of Leitgeb's "Compositæ" type.[5] The apical cell of the thallus forms the growing point of the receptacle, but instead of remaining a single cell it divides into two cells. Each of these again divides in like manner. Finally one of the four cells thus formed divides into two, so that there are five growing points. In some cases this last division does not take place, so that there are only four growing points. Five is the usual number, however, for I found only two specimens out of the great number which I examined that had only four growing points. This branch system is somewhat emphasized in the half-grown receptacles, for, at this time, the lobes between the growing points are more developed than the rest, so that the underside of the receptacle has five quite prominent projections or folds. As the receptacle develops, however, these disappear.

[4] CAMPBELL, D. H.: Mosses and Ferns 50, 51. 1895.

[5] LEITGEB: Untersuchungen über die Lebermoose 6: 32.

The dorsal growth of the receptacle is excessive, while the ventral growth is limited to a few layers of cells. Consequently the apical cells (*a*, *fig. 3*) lie very close to the stalk. The lacunæ or airchambers are for the most part confined to a single layer. They are extremely large, however, and are separated

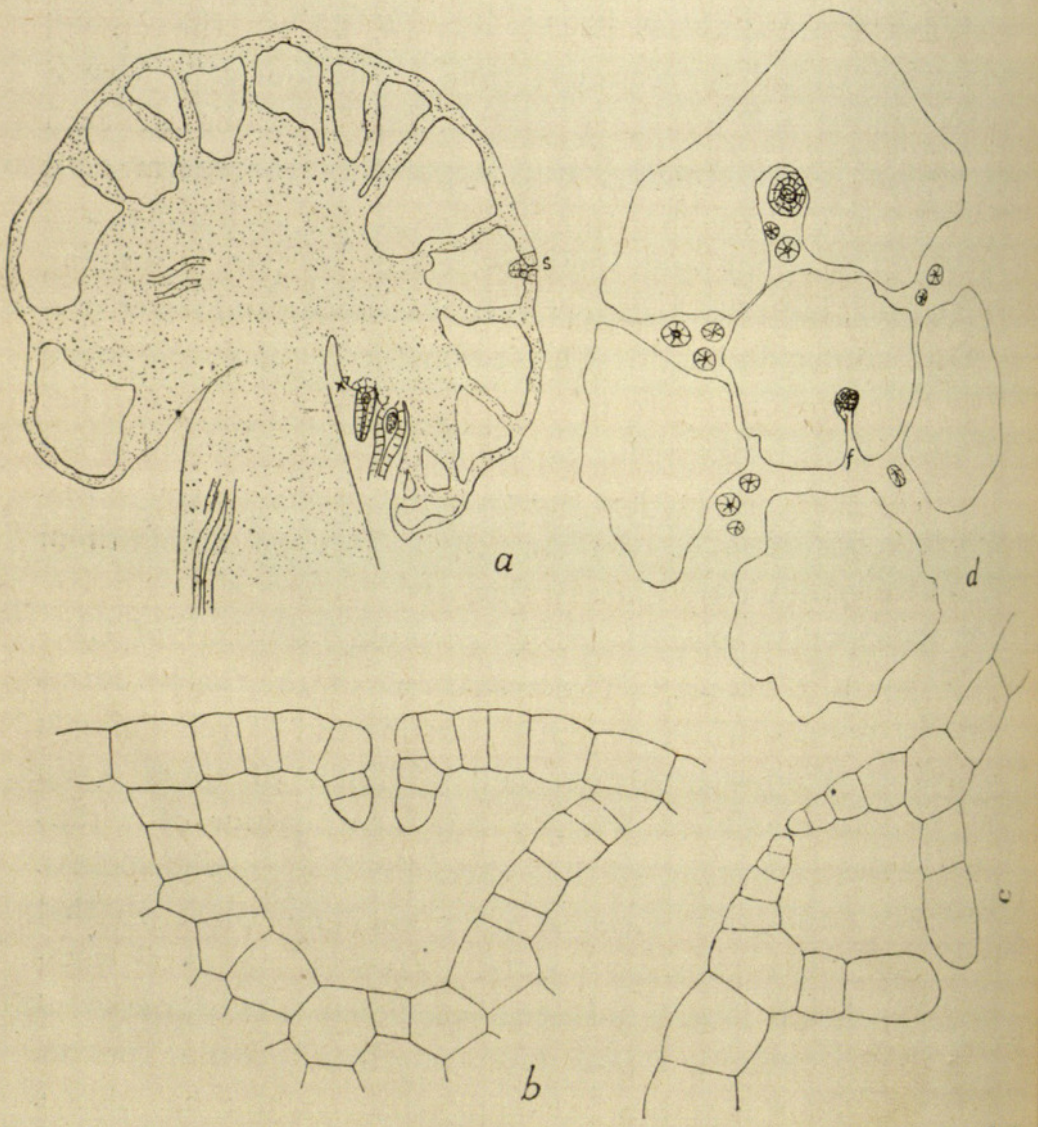

FIG. 3.—*a*, longitudinal section of sporogonial receptacle; *x*, apical cell; *s*, stoma. × 80. *b*, *c*, longitudinal section of stoma. × 600. *d*, transverse section of receptacle; *f*, furrow of peduncle. × 80.

from one another by a single row of cells. Each air-chamber is connected with the exterior by means of well-developed stomata. These peculiar breathing pores are present in several

of the Marchantiaceæ. They are almost cylindrical, and are composed of several rows of cells, which are formed from the original guard cells. These, instead of remaining single, divide by means of inclined walls into several cells. Generally four cells are cut off on the upper side (*b*, *c*, *fig. 3*), and two on the lower side of each original guard cell.

Stephani, *loc. cit.*, reports that there are two furrows on the ventral side of the stalk or peduncle of the receptacle, but I was unable to find such to be the case. In all the specimens examined there was only one. Mr. Howe,[6] also, reports only one furrow in the specimens examined by him. Seen in cross-section (*d*, *fig. 3*) it resembles very closely that of Fimbriaria and Duvalia as figured by Leitgeb.[7] The root hairs, all of which are tuberculate, are found in this furrow. At the base of the receptacle these branch, one branch going to each lobe between the growing points.

The archegonia, although they are on the underside of the receptacle, are in reality on the dorsal side, for they are formed acropetally just back of each apical cell. Hence there are five rows or groups of archegonia (*d*, *fig. 3*). In each of these rows there are usually three or four archegonia.

The development of the archegonium corresponds very closely with that of other Marchantiaceæ. The primary cell becomes much larger than the neighboring cells, and the cell contents becomes much denser, so that it stains very deeply. The first division is transverse. The outer cell forms the archegonium and the inner the stalk. Strasburger[8] states that in Marchantia this outer cell is again divided by a wall parallel to the first, and that the lower cell of the two thus formed forms the foot of the archegonium. Janczewski[9] describes the same thing in *Preissia commutata*. This second division does not take place in Crypto-

[6] Howe, M. A.: Erythea 5: 87, 88. 1897.

[7] Leitgeb: Untersuchungen über die Lebermoose 6: *pl. 4, figs. 9, 20.*

[8] Strasburger: Jahrb. f. wiss. Bot. 7: 416.

[9] Janczewski: Bot. Zeit.— : 418. 1872.

mitrium (*a*, *fig. 4*). Campbell[10] also states that it does not occur in Targionia nor in *Fimbriaria Californica*. The remainder of the development does not differ materially from that of a typical archegonium of any of the Marchantiaceæ, and it need not be repeated here.

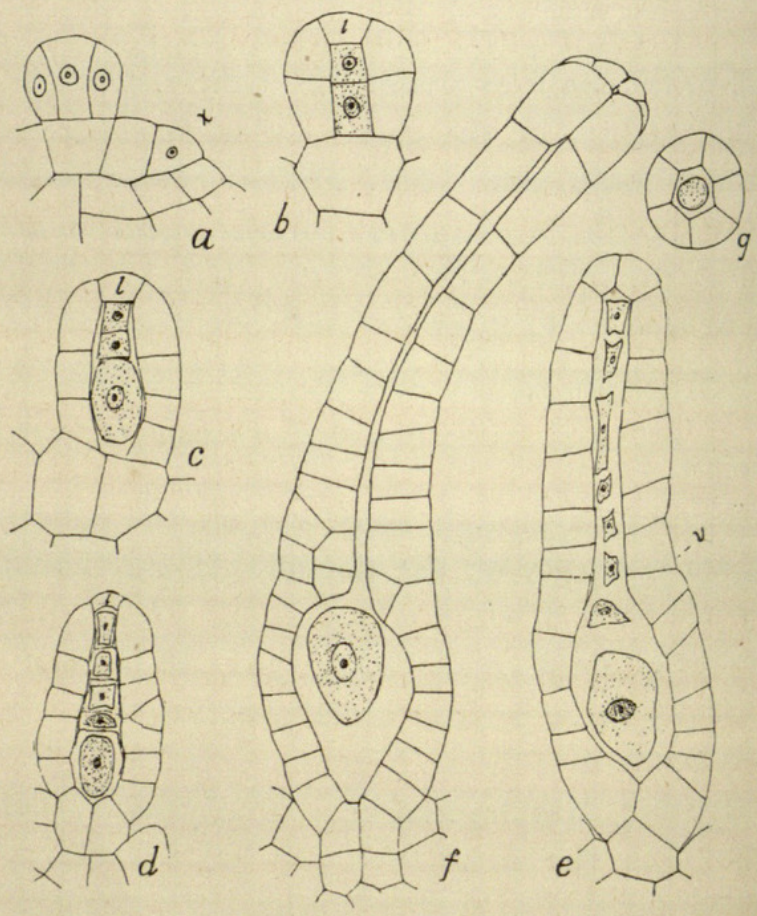

FIG. 4.—Archegonia. *a*, *b*, *c*, *d*, *e*, *f*, longitudinal sections of successive stages; *x*, apical cell; *l*, *l*, *l*, cover cell; *v*, ventral canal cell; *g*, transverse section of neck of an archegonium about the age of *e*. *a*, *b*, *c*, × 600; *d*, *e*, × 480; *f*, *g*, × 300.

The cover cell, which in other forms studied[11] divides into four cells immediately after the neck has been separated from the venter, remains undivided for a considerably longer time in this species (*b*, *c*, *d*, *l*, *fig. 4*). Unfortunately I was unable to determine just when this division took place. Several archegonia were obtained at the age of the one represented in *d*, *fig. 4*, and

[10] CAMPBELL: *op. cit.* 52. 1895.

[11] CAMPBELL: *op. cit.* 30. 1895.

in every case the cover cell still remained undivided. The stages in which the division had taken place (*e*, *fig. 4*) were too old to determine with any degree of accuracy when this division occurred, and it is to be regretted that no intermediate stages were obtained.

Gayet,[12] in a recent article, which has been reviewed by Campbell,[13] states that the archegonia of the Hepaticæ have a distinct apical growth, the same as in the Musci. His conclusions, which are contrary to those of Janczewski,[14] Campbell, and others, are not confirmed by my own observations. While I did not make a very careful study of this point, I could find nothing that indicated an apical cell. The cover cell, which Gayet claims to be the apical cell, does not have the appearance of one. It is much smaller than the upper cells of the neck, and in no way do these cells look as though they had been cut off from it. The fact that the cover cell remains undivided for a considerable time in this species might favor the idea of apical growth, were it not for the fact that the cover cell in this species is even smaller than in other species that have been studied (*d*, *fig. 4*). It looks as if it were lying dormant and not as if it were an active apical cell.

The usual number of neck canal cells is eight, as in the other Marchantiaceæ. In some cases, however (*f*, *fig. 4*), only seven are present.

THE SPOROPHYTE.

Owing to the fact that the embryo in nearly every case lies almost parallel with the stalk, its development has been comparatively easy to make out. One is at once struck with the marked similarity it shows to the embryo of Targionia.[15]

Soon after fertilization the egg cell enlarges to nearly twice its original size. The first division is transverse and divides the enlarged cell into two almost equal cells (*a*, *fig. 5*). The next

[12] GAYET: Ann. des. Sci. Nat. Bot. VIII. —: ——. 1897.

[13] CAMPBELL: BOT. GAZ. 26: 428–431. 1897.

[14] JANCZEWSKI: *loc. cit.*

[15] CAMPBELL: *op. cit.* 60, 61. 1895.

division is longitudinal (*b*, *fig. 5*). This is followed by another longitudinal division which is at right angles to it. Each of the eight cells thus formed is then divided into two slightly unequal cells by a longitudinal division (*e*, *fig. 5*). The first longitudinal wall is often inclined so that the top cell (*c*, *fig. 5*) resembles very much a two-sided apical cell. The remaining divisions are

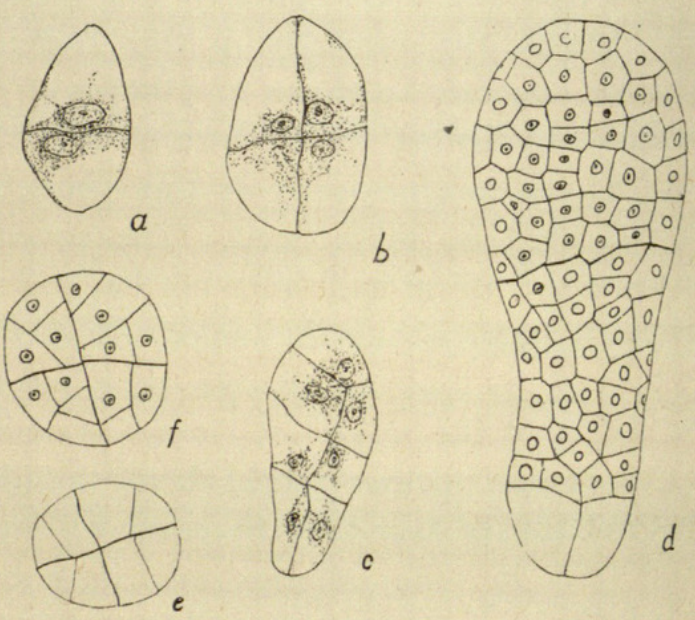

FIG. 5.—Embryo. *a*, *b*, very young stages in longitudinal section. × 600. *c* somewhat older. × 480. *d*, longitudinal section of still older stage. × 300. *e*, *f*, transverse sections. × 480.

very irregular and are difficult to follow. The young embryo takes on a more and more elongated form. Finally, the central portion almost ceases to grow, so that the embryo becomes dumb-bell-shaped (*a*, *fig. 6*). The upper portion is to form the archesporium, and at about this time, or even earlier (*d*, *fig. 5*), a definite row of cells, which becomes the capsule wall, is formed around the outside. Usually, the first transverse division marks the separation of the capsule and the foot, but in a few cases (*d*, *fig. 5*) this cell remained undivided after the first two longitudinal divisions, so that at the base of the embryo were four large cells.

Soon after the capsule wall is formed the archesporial cells can easily be distinguished, for their protoplasm becomes denser,

and both it and the cell walls, which become very gelatinous, stain deeply (*a*, *b*, *fig. 6*). These gelatinous walls soon dissolve, so that the archesporial cells are set free. Two sorts of cells can easily be made out at this time. The one, the spore

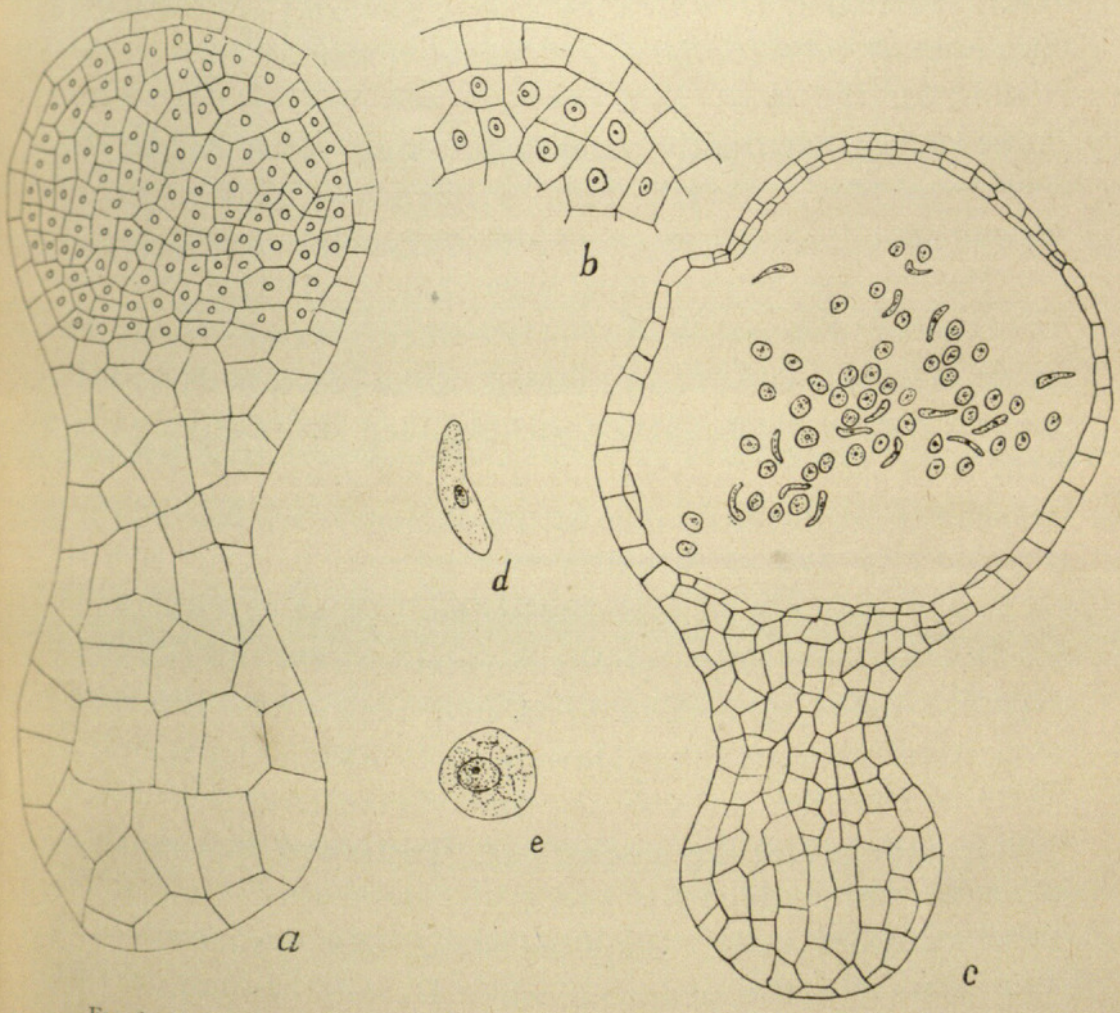

FIG. 6.—Embryo. *a*, longitudinal section of half-grown embryo. × 300. *b*, portion of transverse section showing capsule wall and archesporial cells. × 480. *c*, longitudinal section of a nearly mature sporogonium, showing spore-mother-cells and young elaters; *o*, operculum. × 150. *d*, young elater. × 600. *e*, spore-mother-cells. × 600.

mother cells, are almost spherical. Their nuclei are large and distinct (*e*, *fig. 6*), and are surrounded by closely reticulated protoplasm. The other, the young elater cells (*d*, *fig. 6*), are elongated. Their nuclei, though quite distinct, are much smaller than those of the spore-mother-cells.

The foot of the sporogonium (*c*, *fig. 6*) is not so well developed as in Targionia, being not more than one third as large as the capsule, which is large and globular. At maturity the capsule is regularly dehiscent at its apex by an operculum. This operculum, as stated by Howe (*loc. cit.*), is composed of two rows of cells (*o*, *fig. 6*), while the remainder of the capsule wall is, for the most part, only one cell thick. Near its base, however, an apparently continuous ring, composed of only two rows of very small cells occurred in all the specimens examined.

The ripe spores germinate very slowly. During the months of October, November, and December, several cultures were made of spores which had ripened in the previous April, and in no case did they germinate until eighteen or twenty days after they were sown. Their germination and manner of growth correspond very closely to that of Targionia.

SUMMARY.

In comparing *Cryptomitrium tenerum* with the other Marchantiaceæ, I found, as Stephani claimed, that it was undoubtedly very closely related to Duvalia. I had no specimens of Duvalia, however, and was dependent upon Leitgeb's[16] description. Both genera are monœcious. Both have the same minute stomata surrounded by seven or eight very symmetrically arranged guard cells. Stephani states that Cryptomitrium has two furrows in the peduncle, while Duvalia has only one; but only one furrow was present in the specimens I examined, so that neither this difference between the genera, nor the difference in number of guard cells that Stephani described, exists.

The receptacle of Duvalia is nearly spherical, while that of Cryptomitrium is disk shape. In other respects the receptacles resemble each other very much externally; but in the development of the receptacles there is a great difference. Duvalia, according to Leitgeb's account, belongs to the type of the Marchantiaceæ, which has the growing point of the receptacle at its

[16] LEITGEB: *op. cit.* 87–90.

forward margin. In Cryptomitrium the receptacle is a branch system, such as Leitgeb attributes to Marchantia and one or two other genera. This fact alone would be enough to outweigh all the minor external characters referred to, were it not for the fact that, although Leitgeb puts Fimbriaria in the same type as Duvalia, Campbell (*op. cit.*) found that the receptacle of *Fimbriaria Californica* belongs to the "Compositæ," or branching type.

While one hesitates to criticise the classical work of Leitgeb, the quality and accuracy of which is for the most part remarkable, it does not seem reasonable that plants resembling each other as closely as Cryptomitrium and Duvalia should differ so much in respect to the growth of their receptacles, to say nothing of the fact that species of the same genus, Fimbriaria, should also have this difference. It would seem more probable that Leitgeb was mistaken. Probably if one should carefully examine Duvalia and also the species of Fimbriaria which were studied by Leitgeb, it would be found that these too have as many growing points as there are groups of archegonia. Should this not be the case the apparent close relation between Duvalia and Cryptomitrium would be only apparent, and the latter would then, perhaps, have to be considered more nearly related to Marchantia, and *Fimbriaria Californica* could then no longer be considered as a Fimbriaria, for the difference in the two kinds of receptacles is too great to occur within the same genus.

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