A STUDY OF TARGIONIA HYPOPHYLLA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 156

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(WITH THIRTEEN FIGURES)

Considerable work has already been done on the morphology of *Targionia hypophylla*, LEITGEB (1) and CAMPBELL (2) being foremost among the investigators. Recently CAVERS (3) also published a paper on the same species; but with all this there still remains some little ground which has not been covered at all, as well as some which has been covered but superficially. These points it is the aim of this paper to try to clear up.

The material for this study was collected in 1908 by Drs. BARNES and LAND along the steep slopes of the canyon of the Rio Santiago in western Mexico, and also on the eastern slope of Mt. Orizaba. In both regions it was found only at an altitude of 1500 meters.

Gametophyte body

The thallus in this group is about as complex as in any of the Marchantiales. This statement is not based on any one of the several characters that usually distinguish a thallus as simple or complex, but on an average of the total amount of differentiation and complexity present.

In the first place, the thallus is formed by the segmentation of a single, cuneate apical cell (figs. 1 and 2), cutting off segments on four faces. CAVERS (3) reports a row of initials at the apex. In none of the preparations studied in this particular instance, however, could this report be verified. On the contrary, they seemed to show very distinctly a single apical cell, distinguished from its surrounding segments both as to its size, and also as to the size, plane, and position of its nucleus. Relative to the apical cells found in the other genera of the Marchantiales, the apical cell of *Targionia* is rather small.

The development of the air chamber is one feature which, as yet, has not been described. This proceeds along the lines reported by

BARNES and LAND (4) as typical for the Marchantiales. The air chambers arise by the splitting apart of the superficial cells just

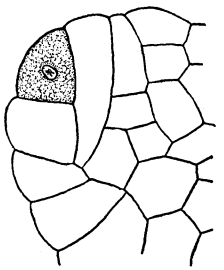

FIG. 1

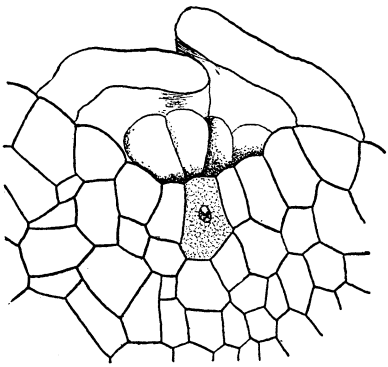

FIG. 2

FIGS. 1, 2.—Fig. 1, median longitudinal section through the apical cell; fig. 2, section in horizontal plane of thallus through the apical cell.

back of the growing point (fig. 3). However, in the other Marchantiales described, this splitting originates in an angle between the epidermal and hypodermal layers of cells, and proceeds outward toward the surface; in *Targionia* the process is reversed, the cracking apart starting at the surface between two epidermal cells and proceeding inward. Subsequent divisions enlarge the space thus formed, as well as the breadth of the roof.

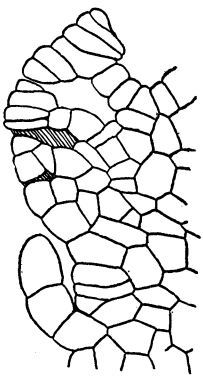

FIG. 3.—Nearly median section through growing point, showing origin of air chambers.

Early in its development the pore is closed by rapid divisions in the roof cells, and it remains closed until the chamber has almost reached maturity. The chlorophyllose filaments develop comparatively early in the history of the chamber (figs. 4–6); as soon as the chamber is 3–5 cells broad, the cells of the floor begin to project as papillae. These papillae are divided by transverse walls into filaments, which at maturity are 2–6 cells in length. They branch profusely, and in the mature chamber very

often are so long that they grow snugly up against the roof, thus giving the impression, in section, as though there were filaments depending from the roof of the chamber, as well as standing up from the floor. Directly beneath the pore the filaments are slightly modified, the distal cell being hyaline and containing no chloroplasts except one or two lying along the bottom wall. There is no modification in the form of

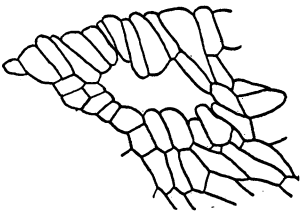

FIG. 4

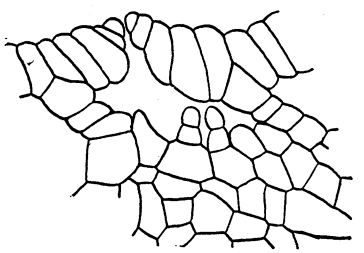

FIG. 5

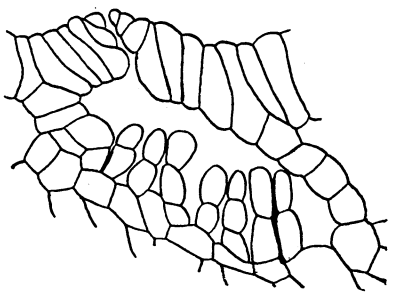

FIG. 6

FIGS. 4–6.—Fig. 4, young air chamber before appearance of the chlorophyllose filaments; fig. 5, air chamber with two chlorophyllose filaments and primordium of a third; fig. 6, later stage of air chamber, showing distortion due to unequal elongation of cells of the thallus.

these hyaline cells, as there is in *Conocephalus;* they retain the same ovoid shape found in the other cells of the filament (figs. 7 and 8).

The cells surrounding the air pore are arranged in a series of concentric rings, raised crater-like a little above the dorsal surface of the thallus. The innermost ring is composed of dead cells, collapsed and highly cutinized; and is not, as stated by CAVERS, a hardened membranous ring which has been put forth by the innermost layer of cells surrounding the pore (fig. 9).

The ventral scales are placed in two rows on either side of the midrib and are of an intense dark purple or red-brown color. They are inserted on the posterior margin, and arranged on the ventral surface in a wonderfully exact and regular fashion. On the anterior margin of the scale is borne a curious little appendage (fig. 10)

which in the younger scales overlaps the growing point of the thallus, and may serve as a protective covering. The two rows of

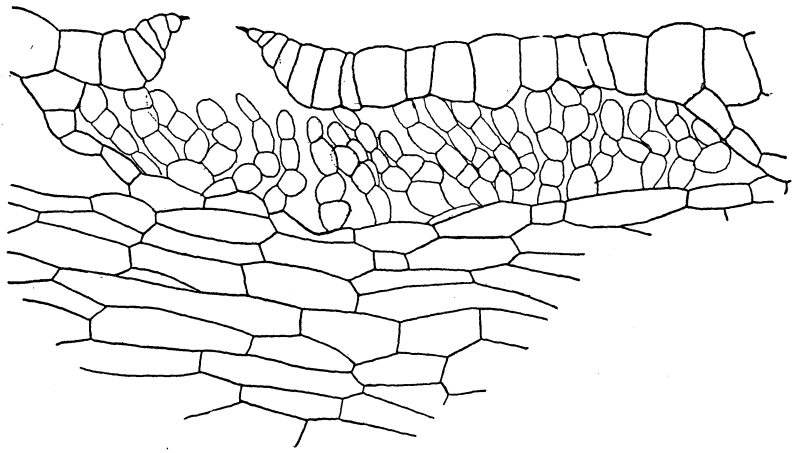

FIG. 7.—Mature air chamber in median longitudinal section

scales are separate from the first, arising from young segments close to the apical cell (CAMPBELL 2).

Both the pegged and the smooth rhizoids are present. They are extremely long, and most curiously swollen and distorted at the distal end. According to CAVERS (3) the smooth rhizoids are borne on the midrib and pass directly into the ground. The pegged rhizoids arise in great profusion in the axils of the scales and pass backward along either side of the midrib.

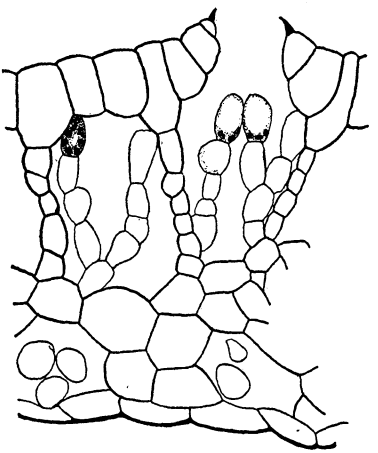

FIG. 8.—Transverse section through two air chambers, showing their extreme narrowness.

The solid, colorless tissue of the thallus is composed of elongated and, for the most part, highly vacuolate cells. These begin their elongation directly behind the growing point, and this process goes on so rapidly

that it pulls both the filaments and the vertical walls of the air chambers diagonally backward, giving the chamber a more or less distorted appearance (figs. 4–7).

A really surprising amount of differentiation is seen in the cells of the solid portion of the thallus. The commonest and most usual is a strand of stumpy cells, filled with oil globules and food granules, which passes longitudinally through the center of the thallus, and ends around the foot of the sporophyte. Besides this, there is frequently a strand composed of the ordinary elongated cells, with their walls thickened by an irregularly wound tangle of fibers, also running the entire length of the thallus.

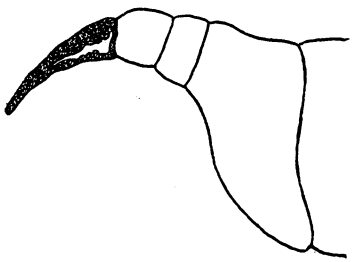

FIG. 9.—One member of the ring of collapsed cells which surround the air pore.

Vegetative reproduction.—The dichotomous branching, which is so common in the other members of the Marchantiales, is here almost entirely replaced by the occurrence of branches arising from the ventral surface. These branches have, for the most part, at maturity a stalk-like base, through the dying away of which the branches are set free as independent plants, and will then themselves multiply in the same fashion.

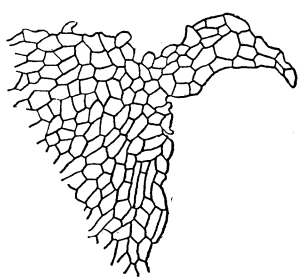

FIG. 10.—Appendage to ventral scale, which overlaps the growing point.

In their origin, these adventitious branches have absolutely nothing to do with the apical cell. This was clearly seen in several of the preparations studied, where, on a plant bearing two young branches, the older one was placed between the apical cell and the younger.

Archegonia.—The archegonia are borne terminal on the thallus. They follow so closely the general line of individual development for the Marchantiales, that it is not necessary to repeat it here. They arise in two rows in acropetal succession. The surface, or pad, on

which they are borne slopes forward and downward at the time the archegonia are mature. The development of this "fruiting surface" runs as follows. The archegonia, arising as they do in acropetal succession, check to a great extent the vegetative growth behind the growing point. The apical cell, however, is not immediately concerned, and continues its segmentation with practically no interruption. The natural result of this is that the apical cell is carried forward and out. Thus the archegonial surface is finally brought to lie in a sort of pit or depression in the anterior end of the thallus. On the lower and outer margin of this pit is the apical cell, which, when this stage is reached, ceases to function.

The involucre.—The development of the involucre is so closely allied to that of the archegonial surface, that it is extremely difficult to say just where the one leaves off and the other begins. It is simply the continued forward growth of the tissues immediately surrounding the shallow pit at the anterior end of the thallus, with the natural result that the opening to this pit is narrowed, and begins to close up. It is never completely closed, however, although in the earlier stages the edges of the wings are brought very close together. As the involucre matures, the outer surface, as well as the inner margin of the wings, becomes highly cutinized.

That the involucre is not, as reported by CAVERS (3), a result of the stimulus given by the act of fertilization is shown in one of the preparations, where it was complete and well developed, while the eggs of the archegonia it surrounded were still unfertilized.

Calyptra.—The calyptra is a simple and very delicate structure, soon ruptured by the growth of the sporophyte. At maturity it is 2–4 layers thick at the base.

Sporophyte body

Capsule.—The capsule is a comparatively simple affair. The wall consists of a single layer of cells, uniformly thickened with spiral and annular bands. There is no special mechanism for dehiscence. In his recent report on *Targionia*, CAVERS (3) figures and describes a rudimentary elaterophore, represented by a few spirally thickened cells depending from the distal portion of the capsule. This statement could not be verified in any of the sections

studied here, nor do either CAMPBELL (2) or LEITGEB (1) report such a condition.

True elaters are present, long, slender, fusiform, and thickened by usually two spiral bands.

The spores themselves have fairly thick walls, highly sculptured, and are produced in great numbers (fig. 11). CAVERS (3) has described the spore mother cells as lobing deeply before division, as happens in many of the Jungermanniales. All of the preparations studied here, however, show the ordinary tetrad formed from a spherical spore mother cell.

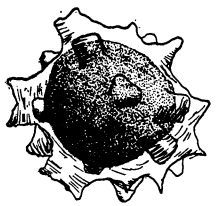

FIG. 11.—Tuberculate spore.

Seta and foot.—Both seta and foot are rather well developed. While small as compared with the size of the capsule, they are nevertheless rather massive, and well differentiated from each other. The foot is club-shaped, and bluntly pointed at the lower end (fig. 12). The surface cells project as short papillae, and are haustorial in function. These cells, as well as those of the calyptra surrounding them, show in section a very much darker stain than do the cells of the surrounding tissues. Between the calyptra and foot is interposed a fairly thick layer of mucilaginous material.

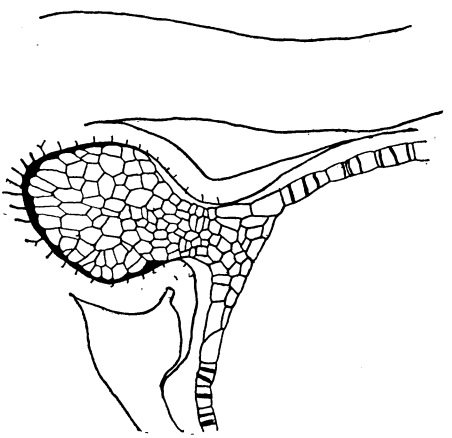

FIG. 12.—Foot and seta

Although 6–10 archegonia are produced, only one egg is fertilized. The remaining archegonia, however, persist, and are still visible after the sporophyte has matured; soon after the sporophyte has begun its development, however, their contents break down into a darkly staining mucilaginous mass.

Classification

The Marchantiaceae are at present classified according to three schemes. LEITGEB (1) gives the following:

Marchantiaceae
- *a*) Astroporae (Clevea, etc.)
- *b*) Operculatae (Plagiochasma, Fimbriaria, etc.)
- *c*) Targioniae (Targionia, Cyathodium)
- *d*) Compositae (Marchantia, Lunularia, etc.)

CAMPBELL (**2**, p. 67) gives the following:

Marchantieae
- *a*) Corsinieae
- *b*) Targionieae
- *c*) Marchantieae

GOEBEL has proposed still another classification. In this he transposes the Riellaceae to the *Marchantia* group, as follows:

- *a*) Corsiniaceae
- *b*) Targioniaceae
- *c*) Riellaceae
- *d*) Marchantiaceae

Without concerning ourselves with the relative merits of these schemes, it might be well to take up the one family, the Targionieae. This family at present contains but two genera, *Targionia* and *Cyathodium*, and it is with regard to the merits of placing these two genera within the same family that a question may be raised. In order the more clearly to present this question, the accompanying diagrams (fig. 13) have been prepared. In the key to these diagrams it will be seen that each generation (sporophyte and gametophyte) has been divided into four features, selected because of their bearing on a natural scheme of classification. Each of these divisions has been subdivided into five stages of as nearly equal importance as it was possible to find.

From the diagram it will be seen that the two lines coincide in but two points. The one of these is D4 and the other E4, which represent respectively the apical position of the archegonia accompanied by a checking of the growth of the thallus at this point, and the common involucre.

As for the former (D4), the character is not peculiar to this

group. In several other genera the archegonia are borne in a terminal cluster, notably *Grimaldia*, *Reboulia*, and *Clevea*. This narrows the situation down to a *single* character common to these two genera (*Targionia* and *Cyathodium*) and not found in others. This is the common involucre inclosing the terminal group of archegonia.

One glance at the diagrams will show how widely the two genera differ in all other respects save this. *Targionia* has perhaps as complex a thallus as is found in the entire group of Marchantiales;

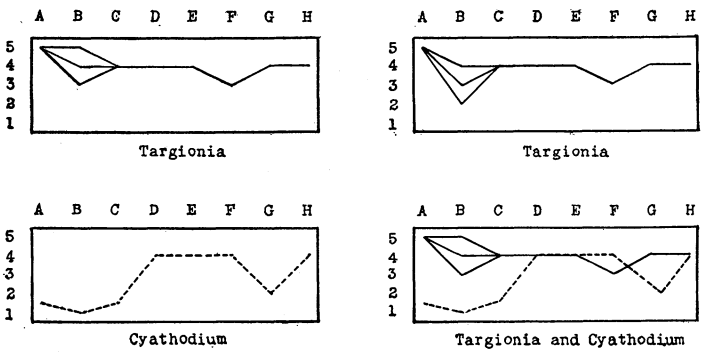

FIG. 13.—Diagrams comparing *Targionia* and *Cyathodium*

Cyathodium has perhaps the simplest, both as regards structure and the amount and character of differentiation. The thallus of *Cyathodium* consists of a simple ribbon, two layers of cells thick, the two layers slightly separated to form an air space, the air pores being simple openings in the upper layer of cells.

In *Targionia* the antheridia are borne on a special portion of a special branch; in *Cyathodium* they are scattered in clusters along the edge of the thallus. In *Targionia* the foot and seta of the sporophyte are massive and well differentiated; in *Cyathodium* both foot and seta are represented by a single filament, four cells in length.

In *Targionia* the elaters are true elaters, long pointed, and spirally banded; in *Cyathodium* the elaters, while spirally banded, are little more than dead nurse cells, short and stumpy.

In but one character is *Targionia* less advanced than *Cyathodium*, and that is in the differentiation of the capsule wall

KEY TO DIAGRAM FIG. 13

	Gametophyte body				Sporophyte body			
	Air chamber	Solid nutritive region	Antheridia	Archegonia	Protection	Capsule	Foot and seta	Sporogenous tissue
	A	B*	C	D	E	F	G	H
1....	Clefts	undiff. solid tissue	scattered	on pad	thallus over-growth	single layered	none	all forms spores
2....	Riccia type	differen. central strand of soft tissue	intermittent formation (groups)	stalked pad	antheridial pad	irregularly thickened	filament	some of the cells die and lose contents
3....	Plagiochasma type	same with central cells thickened and dead	pad or cushion	arch. at apex without interfering with growth	thallusfold	uniformly spirally thickened	quadrant-octant	these cells thickened
4....	Marchantia type	both above combined	terminal pad	apical growth checked	common involucre	thickened along lines of dehiscence	massive and comparatively small	elaters present
5....	Conocephalus type	radio-dorsi-ventral	compound receptacle	compound receptacle	separate involucre	multi-layered at top or bottom	massive and large	elaterophore present

* In case we do not accept GOEBEL's inclusion of the Riellaceae, the fifth character here given is omitted, the other four each moved up one step; while, as the lowest character, we split off from the second one here those thalli having only two layers, which are separated slightly, the space between forming an air chamber, so that the solid nutritive portion of the thallus consists of but a single layer of cells.

in the mature sporophyte. In *Cyathodium*, only the cells of the upper part of the capsule are spirally thickened, so that dehiscence occurs through the formation of 6–8 fairly regular teeth.

Of course there are several difficulties in the way of such a determining scheme as this. In the first place, it is next to impossible to select characters that will be absolutely determining. In the second place, it is impossible to select groups of characters whose determining value will be equal. Again, there is the difficulty of deciding as to which of two characters is the more advanced. And finally, there is the conflict as to the relative value of sporophytic and gametophytic characters. Is a complex gametophyte with a simple sporophyte more advanced than a simple gametophyte bearing a complex sporophyte, or vice versa; to say nothing of the different gradations in combining the two.

Leaving aside, for the present, the difficulties which a practical application of this scheme presents in general, it does seem to apply in the specific case under discussion; no matter which of the two is the higher, it seems to be fairly certain that they are widely different. According to the diagrams the two genera have but the one salient feature which is common to them and to them only, a single involucre inclosing a group of terminally borne archegonia. Now it certainly does not seem as though such a character as this should be sufficient to bind two genera differing so widely in all other respects into one family.

As to where *Cyathodium* belongs, if not with the Targionieae, the Corsinieae suggest themselves readily. But such a matter as this cannot be settled definitely without a much more extended study of *Cyathodium*, as well as the family Corsinieae, with its two genera (*Corsinia* and *Funicularia*), than has been given them.

Thanks are due Professor JOHN M. COULTER and Dr. W. J. G. LAND for assistance rendered during the progress of the work.

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