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The Morphology of the Thallus and Cupules of Blasia pusilla

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THE MORPHOLOGY OF THE THALLUS AND CUPULES OF BLASIA PUSILLA.

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HISTORICAL.

First mention of the genus Blasia was made by Micheli Nov. Pl. Gen. 1729. Linnæus recognized the genus and added the specific name pusilla in his Species Plantarum 1753 p. 1138. In 1759 Schmidel wrote his "Dissertatio de Blasia." Hooker 1816 called the plant *Jungermannia blasia* but as this classification is much too broad it is not used today. Gottsche[8] 1828 published an account of the germination of the spores of *Blasia pusilla.* Later Grönland published his investigations of spore germination in the leafy Jungermanniæ, including Blasia in his discussion. In 1833, Nees von Esenbeck[12] made some investigations on vegetative propagation and erroneously stated that the bud-receptacles (cupules) of Blasia are closed when young and open at the top at a later period. An incorrect figure of Hedwig's had probably given rise to this error. Hofmeister[9] included in his work on The Higher Crytogamia, a short sketch of vegetative reproduction in Blasia, but some of his views are probably as faulty as those of Nees von Esenbeck.[12]

The most comprehensive study of *Blasia pusilla* was the classical work of Leitgeb[10] 1874. His work was mainly on the general characters of the thallus, and on gemma formation. The development of the gemmæ was treated in detail, following closely the work previously done by Hofmeister. He also figured a few antheridia, several archegonia, and stages in the development of the sporophyte. Further work on the species was not reported until 1913 when W. E. Woodburn published his paper on the spermatogenesis of *Blasia pusilla.*

THE THALLUS.

Blasia pusilla is a temperate zone liverwort of wide distribution. The species belongs to the Jungermanniales, which includes about 135 genera and over 3,500 species. This order of Hepatics is divided into the two sections Jungermanniaceæ Acrogynæ and Jungermanniaceæ Anacrogynæ. In the first group the apical cell is given over to the formation of archegonia, which are terminal, while in the second group, to which Blasia belongs, the archegonia are formed on the dorsal side of the thallus from segments cut off from the apical cell, so that apical growth is not hindered. The subfamily Codonioideæ includes eight genera, of widely divergent variations, namely Pellia, Calycularia, Treubia, Fossombronia, Noteroclada, Petalphyllum, Siniodon, and Blasia. The genus Blasia, according to Schiffner[5] includes but one species *B. pusilla*.

It is distinctly transitional between thallose and foliose forms of Hepatics, having a flattened, elongate thallus, which lies prostrate and firmly anchored to the substratum by rhizoids for about three-fourths of its length. The apical regions are free and grow somewhat inclined although the plants almost always point down the slope. The thallus is characterized by dichotomous branching and has a broad midrib extending throughout its entire length on the underside. Along the midrib the thallus lobes are inserted horizontally and laterally. They resemble leaves but are termed thallus lobes, not being separated from the midrib and from each other.

This dorsi-ventral thallus is relatively simple, the tissue being for the most part composed of uniform cells with thin walls. Chloroplasts are numerous in all the cells with possibly a few more in the top layer than in the lower ones. No air-chambers or pores were found. In cross section the thallus shows winglike extensions projecting out from the midrib, which is found on the underside. This midrib, slightly depressed on the dorsal surface, and bowed out on the ventral side, is eight to twelve cells in thickness and from the midrib to the point of lobe insertion, the thallus narrows gradually to the margin of the wings, which are one cell in thickness (1, figure 84).

The only differentiation in the structure of the thallus tissue was first noticed in cross section, where groups of cells varying from nine to thirty-six in number stained more deeply than the surrounding tissue. This differentiation suggested a strand of cells set apart for some special purpose, probably to function in conduction. Conducting tissue has been reported in three of the Anacrogynous Jungermanniales and nowhere else in the Liverworts. Sir William Hooker 1816 discovered the strands in Jungermannia now Pallavicinia Lyellii. Gottsche in 1864 describes a similar strand in *Symphyogyna sinnuata* and Leitgeb describes the cells of this strand in Symphyogyna and states that Blyttia (Pallavicinia) and Umbraculum (Hymenophyton) have similar strands.

In fresh young plants of Blasia the strands can barely be distinguished but in the old dead thalli they stand out on the surface as white threads. This would indicate that the cell walls

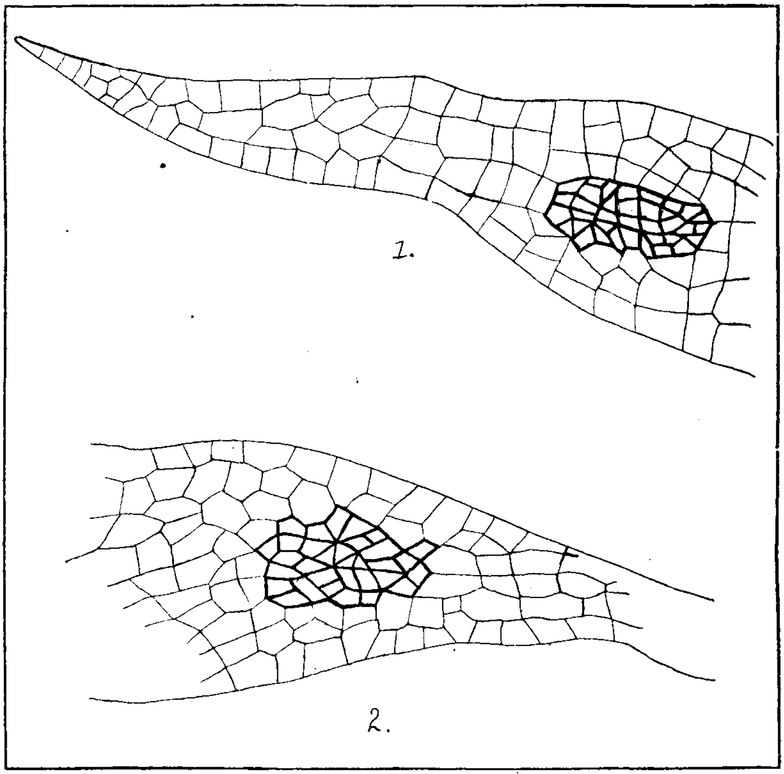

Fig. 84.—1, Cross section of thallus. 2, Cross section through conducting strand.

are more resistant in the strand than in the surrounding tissue and the few experiments tried only serve to emphasize this fact. Upon the decay of the spongy thallus tissue these strands still hold their shape and can easily be picked from the soil surface. Drying has the same effect, entirely destroying the soft portion but leaving the threads unaffected.

A weak eosin solution was used to test the conducting power of these cells, but the experiments were not wholly satisfactory as the whole thallus took the stain. There was a marked difference in the degree to which the strand stained, as they became much darker than the surrounding cells. But even this would seem to indicate that more of the fluid was retained in the strands than in the remainder of the thallus.

Generally, only two strands were found in a single thallus but the number varies from two to five, depending on the amount of branching. They are found laterally in the thickened midrib of Blasia about equidistant between the dorsal and ventral surfaces. Where the thallus branched the strand divided giving off branches to each newly formed division. The angles of the cell walls were quite sharp in the transverse section but other markings were not found here (2, figure 84).

In the longitudinal section (3, figure 85) a greater difference was noticeable. The conducting cells, averaging the same in width as those of the thallus, had a length three to five times greater and tapered to a point at each end. Cross walls in some specimens run obliquely through these long tubes. The most striking characteristic was the peculiar markings of the cell walls. The pits or depressions arranged irregularly along the walls are thin at the center and bordered by heavy darkly staining thickenings, giving the external appearance shown in 4, figure 85. These thickenings show at fairly regular intervals along the wall in the prepared sections. Where the strands join the spongy tissue on either side, only the inside walls bear the markings. The strands undoubtedly serve in a mechanical capacity, being provided with such strong walls, but it is doubtful if this is their most important function. It does not seem consistent, that a thalloid liverwort, attached by rhizoids for three-fourths its length, would need such strengthening as the strands might give. However, it is possible in the case of *Blasia pusilla*, that the resistant cells aid in giving body to the thallus upon which are found the gemmæ receptacles and large sporophytes. Gottsche found that in Symphyogyna they had no connection with the "receptacles" on which the sexual organs were seated.

These strand cells do not show nuclei, but simply a disintegrated substance, probably protoplasm, as it took the stain as readily and to about the same degree as the protoplasm in the surrounding cells.

In testing the plants in concentrated sulphuric acid, the thallus was found to melt away quite readily in from one to three hours, leaving the strands seemingly unaffected by the acid. At

II.

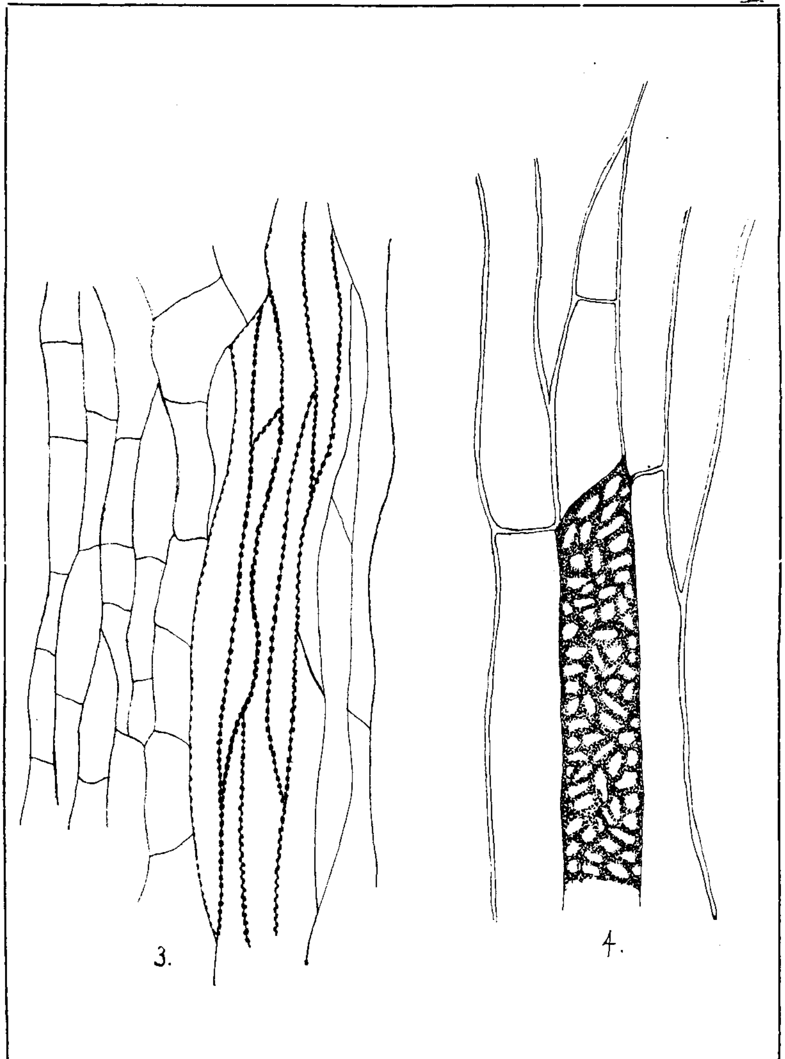

Fig. 85.—3, Longitudinal section through conducting strand. 4, Enlarged strand showing external markings.

first the tissues of the thallus swelled considerably but soon broke down and the residue assumed the consistency of jelly.

The strands, freed from the acid, were stained and mounted in balsam. They did not break down during the process but remained rigid and resistant. The mounts showed the identical markings seen in the prepared longitudinal sections.

As most liverworts thrive only in moist habitats, the whole surface, if close enough to the sub-stratum, might absorb all the water needed or the thallus might be provided with rhizoids which perform the same function. With an increase in specialization in these forms, as erect branches or parts raised above the thallus surface, it would seem almost necessary to have some sort of conducting system, more or less complex.

Chick and Tansley[14] say the following in regard to the three liverworts having conducting tissue: "The three genera Pallavicinia, Steph., Symphogyna, Nees et Mont., and Hymenophyton, Steph., differ in well-marked characters connected with the position and investment of the sporogonium, and it is perhaps most probable that the striking character they have in common—the possession of an axial strand—has developed independently in each genus. The strand cells are formed, as might be expected, by longitudinal division of the inner cells cut off from the segment of the apical cell and are differentiated very close to the apex."

The Growth of the Thallus.—The growth of the thallus proceeds by means of a wedgeshaped apical cell. This type seems characteristic of the dichotomously branching forms, for the cell can be divided into two segments alike in size and shape and like the original apical cell. As each segment cuts off segments from its inner face the two apical cells are pushed farther apart, and the dichotomous branching results. Leitgeb[10] says, "The growth of the shoot results through the division of the 'vertex cell,' which forms a four sided segment, cutting off to right and left and dorsal and ventral sides. We find the same method of growth in the segments of Aneura and Pellia and the leaf-building segments of Fossombronia and Frullania. The segments cut off from the right and left sides of the apical cell develop the side leaves, while those cut from the dorsal and ventral sides take part in developing the branches. Those on the ventral side form hair papillae and scales." Some from the dorsal side form the sex organs.

Ventral Differentiations.—The two-celled mucilage hairs, found on both sides of the thallus, originate from a superficial cell which pushes out from the surface. This cell divides once and the basal cell retains its nucleus and chloroplasts while the outer one breaks down into a mucilaginous substance which stains very deeply. These hairs usually turn inward toward the apical cell, and form a protection for the growing point and for the younger sex organs which are found near the apex. The mucilage hairs do not seem to be deciduous, for old ones are found far back on the thallus after the growing shoot has elongated and formed new hairs at its tip.

The ventral side of the thallus develops smooth, unicellular, colorless rhizoids. These hairlike structures are merely outpushings of the epidermal cells along the midrib, which function both as anchorage organs and water absorbers. They are often so numerous that they form thick mats along the midrib, and the plants can be lifted from the soil only with difficulty.

The under leaves are scalelike appendages called amphigastria. They are usually several cells in thickness at the center and one cell thick at the margin. These scales have denticulate margins in contrast to the entire margin of the thallus. They are easily detached and may give rise to new plants. No doubt the amphigastria are rudiments of the ventral row of leaves commonly found in the leafy liverworts, and may assist in holding water.

We have a final ventral differentiation in the leaf auricles. These appendages begin as plates of cells pushed out from the lower epidermis of the thallus. Their marked incurving produces a hollow, globular structure which becomes filled with Nostoc. As the cells are pushed out a mucilage papilla is formed at the outer margin which gradually curves inward. Another mucilage papilla pushes out from an epidermal cell into the hollow already formed. After the formation of the leaf auricle, it is infected with Nostoc which finds entrance at the point where the mucilage hair touches the thallus. In the young stages we find an aperture here but later the auricle is completely closed. Seen from the top of the thallus the Nostoc colonies appear as tiny black spots imbedded in the tissue.

At the time Schmidel[13] studied Blasia there was some uncertainty as to what the Nostoc might be. Schmidel in his "Dissertatio de Blasia" considered the auricles as antheridia and the individual cells as sperms.

Bischoff (1835) called the Nostoc colonies antheridia but a few years later Nees von Esenbeck found the real antheridia and called the Nostoc "Keimkörnerknötchen." Hofmeister[9] held that the organs were reproductive buds, basing his idea on their analogy with what he called "the undoubted buds of Anthoceros" developing in the same manner. He says, "It is well known that numerous reproductive buds are formed on the under side of the stem of Blasia. The contents of one of the inner cells of the tissue of the stem (which cells are only separated from the under side by a single cellular layer) become transformed into a cell occupying the whole cavity of the mother-cell. This daughter cell changes into a roundish body, composed of small cubical cells which contain numerous very small chlorophyll bodies of a dark bluish-green color. The cellular layer of the under surface of the stem which covers the reproductive buds becomes swollen to a hemispherical shape by the increase in size of the latter. I have not seen these reproductive buds develop into young plants."

Corda[4] figures the germination of the Nostoc cells and calls them new plants of Blasia. These erroneous ideas were not corrected until Leitgeb's work was published 1874. He gave a good description of the structure and origin of the peculiar chambers, but failed to show the fully developed auricle. Coker[3] says, "By pressing out the Nostoc he (Leitgeb) found that the colony was penetrated by clear cells, which he correctly deduces to be branches of the Blasia thallus that have arisen from the slime-secreting hair that was present in the young stages. There grows up from the floor of the chamber a treelike structure with a single trunk, and from the repeated ramifications of this tree the whole colony becomes interwoven with cells which doubtless serve to abstract nourishment from the algæ. This whole ramifying structure has in all probability come, as Leitgeb thought, from the subsequent growth of the slime-secreting cell. In other cases of such symbiotic relationships, as Anthoceros, there are, likewise, cells growing in from the host plant; but in all such cases, so far as I know, these outgrowths originate, not from a common base, but separately and at many points. The striking arrangement of Blasia seems to be confined to it alone."

The host plant cells no doubt take nourishment from the colonies of algæ and they may also serve as water reservoirs as do the mucilage hairs. That Nostoc is absolutely necessary to the growth of Blasia has not been ascertained, but it is true that small colonies are found in the young thalli very soon after the germination of the gemmæ.

The dorsal differentiations include the sex organs, the calyptra, and the cupules, in which the asexual reproductive bodies are produced.

CUPULES. VEGETATIVE PROPAGATION.

Asexual or vegetative reproduction in *Blasia pusilla* is accomplished in two different ways. The amphigastria or underleaves may become detached from the lower surface of the thallus and give rise to new plants. These scales are loosely attached, easily removed and well prepared to launch new thalli. The second method is by means of asexual bodies called gemmæ, which grow in special receptacles on the thallus and upon being expelled give rise to new plants.

The development of the cupule in which these gemmæ are formed is extremely interesting. The initial of the cupule is a dorsal segment of the apical cell and the mature cupule is located rather near the apex of the plant. By repeated divisions vertical to the plane of the thallus, the dorsal segment gives rise to a compact cluster of cells just back of the growing point (5, figure 86). Activity appears then to be retarded in this region and increased in the surrounding cells for they soon bulge up around the compact region, forming a rim (6, figure 86). Cell division is more rapid in the posterior part of the depression.

The development of the cupule of Blasia follows closely the first few stages in the development of the Marchantia cupule as given by Barnes and Land.[1] Here is the same compact tissue whose cells fail to divide and thus allow the surrounding cells to outgrow them. According to Barnes and Land,[1] "In Marchantia the upgrowth of cells at the rim of the depression begins on the posterior margin but later extends completely around the depression, so that at maturity the cup is circular and of almost equal height on all sides. The origin of the cupule of Lunularia has been shown to be the same as that of Marchantia, except that the development of the rim takes place only on the posterior side of the gemmiparous region, which is also more extensive. In some cases late in the development, a slight anterior elevation continues the line of the posterior rim and so suggests the circular cup of Marchantia. The superficial origin of the gemmæ is thus perfectly clear."

At the point where the posterior part of the Blasia cupule begins to increase all resemblance to Marchantia ceases (7, 8, 9, figure 86). The tissue resulting from the accelerated growth in Blasia covers the depression completely leaving only a small opening at the anterior end (10 and 11, figure 86). Because of this method of growth the resulting cavity is elongate and flask-shaped. Papillate cells are now found pushing out from all sides of the cavity and are soon cut off by transverse walls. These are differentiated either into mucilage hairs, similar to those on the thallus, or into the initials of the gemmæ (12, figure 87). Further division of the gemma initials is carried on first by transverse walls and later by vertical walls, so that the mature gemma is composed of a mass of from four to twelve cells, resembling the antheridium in its younger stages.

When the first gemmæ are mature, accelerated growth in the margin cells of the walls about the opening, forces the edges upward forming a chimney-like tube at the anterior end of the cavity (13, figure 87). This tube attains a length of 1 to 2 mm. and varies from two to four cells in thickness. At the apex the edges flare outward slightly, giving the tube a bell-shaped opening.

Most of the cupules were found on antheridial plants, although in several instances they were found on archegonial plants, where the archegonia had not been fertilized. The cupules appear later in the life cycle than do the sex organs. Leitgeb[10] held that they were antheridial pockets, for in one instance he found a half grown antheridium at the posterior end of the cupule. He tried to find other stages but was not successful. Cavers[2] thought the gemma receptacles were modified archegonial receptacles since archegonia were sometimes found in them.

The writer is inclined to think that the cupules are especially formed for gemma production and are not modified sex organ receptacles. It is true that the development of thallus tissue is parallel to the development of the sex-organ covering, but if these cupules were degenerate antheridial receptacles it seems that the tissue development would cease when it had enclosed the depression, instead of elongating to form the long necklike extension.

Leitgeb[10] says, "Gemmæ grow into male plants and those bearing flasks." The writer is not prepared to dispute this idea,

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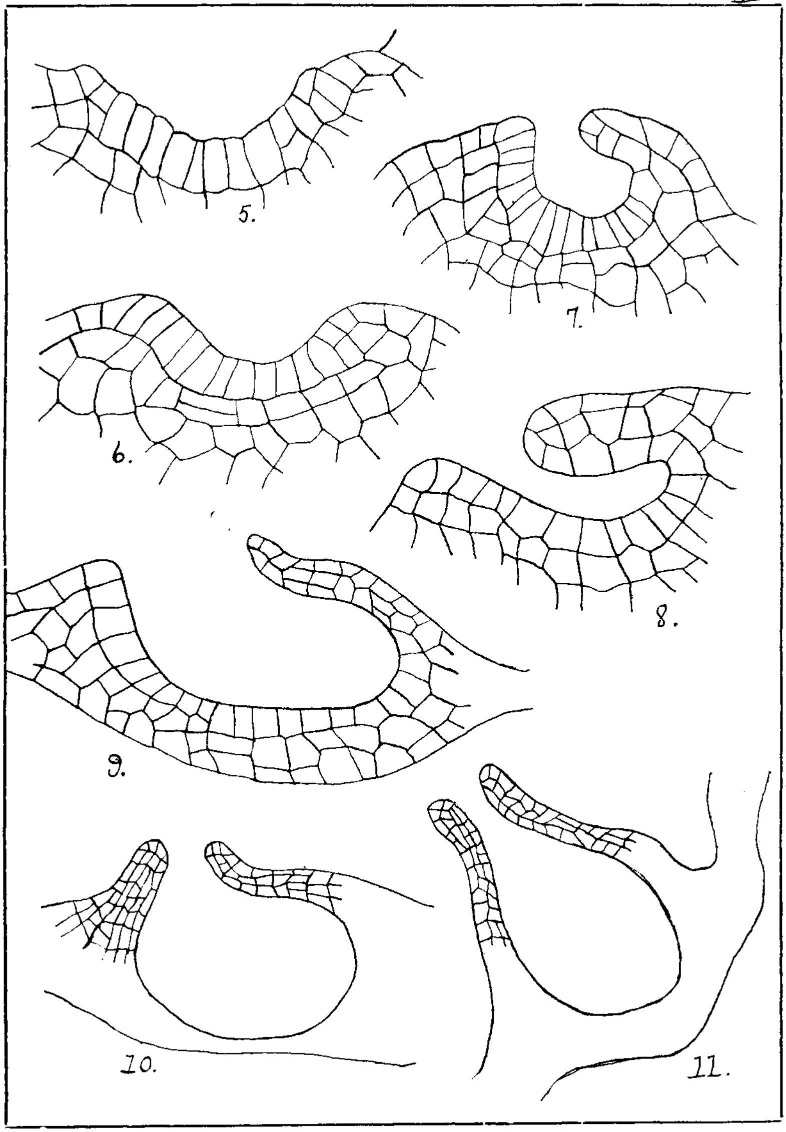

Fig. 86.—5, Compact cluster of cells beginning cupule formation. 6, Up-pushing of margin cells. 7-8-9, Stages in overgrowth of posterior portion of cupules. 10-11, Early stages in formation of cupule neck.

until further investigation has been made, but is doubtful if such is the case. The occurrence of flasks on the archegonial plants would probably be the best argument against his theory. In cultures which he made, gemmæ developed no further than a vegetative body about six cells long and two to four cells wide, in which instance it would be impossible to tell whether the plants were male or female.

The Gemmae.—The multicellular gemmæ are ovoid in form, about .14 mm. at the greatest diameter. They are held in the receptacle upon hyaline stalks, one cell in thickness, and in some cases twice the length of the gemma.

Throughout the period of gemma development the mucilage papillæ have been secreting a slimy substance which is poured out into the flask cavity. The mature gemmæ, breaking from their stalks, become imbedded in this viscid substance and are ready for expulsion from the flask. Just how this is accomplished has not been fully proven. Hofmeister[9] says, "The escape of the buds is doubtless caused by the pressure which the numerous rapidly growing young buds necessarily exert upon the mucilaginous contents of their receptacle, which contents are thereby in constant motion toward the opening in the neck." Beside the pressure of the growing gemmæ it is possible that the entrance of water into the flask causes the swelling of the mucilage forcing it from the flask neck. This conclusion is supported by the observation of drops of the exuded mucilage standing at the tops of the necks, especially when the atmosphere was moist, or when the dew was still upon the plants. After the expulsion of the mucilage drop with its load of gemmæ, they can easily be scattered.

It is probable that insects or snails might be responsible for distribution of some of the gemmæ through contact with these slime globules filled with mature brood bodies. But doubtless water splashing on the plant is the more efficient agency for gemma dispersal, as the slime dissolves quickly in water.

These little asexual bodies grow very rapidly and produce juvenile plants one to two mm. long in a few days. Their growth is extremely interesting and takes place while they are still sticking to the dorsal side of the old thallus. Leitgeb[10] was probably referring to these new plants, which are sometimes star-shaped in their earlier stages, when he described the "sternschuppen" of Blasia. Goebel[7] says the following in regard to the asexual reproduction of Blasia: "Blasia has two kinds of gemmæ: the one is a nearly spherical cell-mass produced in a flasklike receptacle with a long neck; the other is a gemma-

IV.

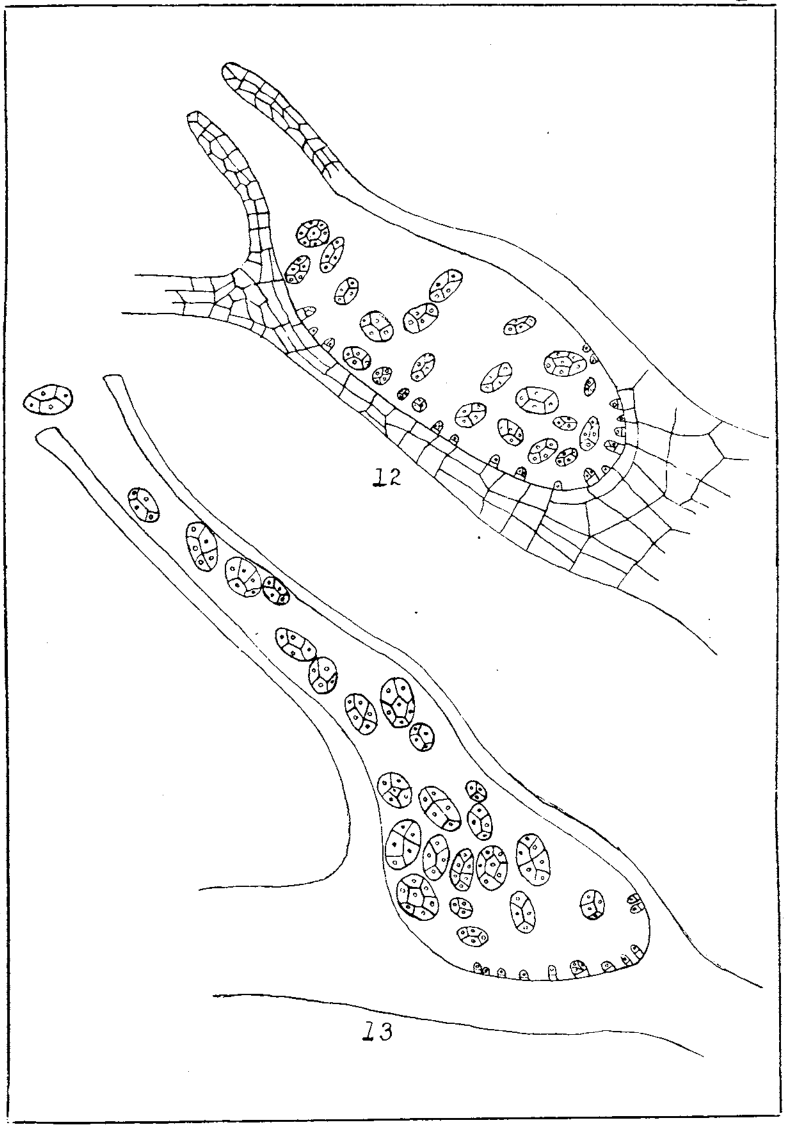

Fig. 87.—12, Cupule showing development of gemmæ. Greater development of neck. 13, Mature cupule containing mature gemmæ ready for expulsion.

scale at the base of which there is to be seen at a very early period of development the cell from which the new thallus proceeds,—this gemma-scale arises upon the upper side of the thallus, especially upon shoots which bear neither sexual organs nor receptacles for gemmæ. These gemma-scales require investigation especially in their biological relationships." No trace of these scalelike appendages showed on the dorsal surface of the specimens studied. In only one case were the gemmæ found germinating in the flask, and in this instance only a single protuberance was pushed out at the side. This flask was an old thallus and the gemmæ probably had been developed the fall before. This is an exception to the usual procedure, however, for the gemmæ are expelled at maturity, while young buds are forming at the base of the flask. Conditions for germination are not likely to be favorable when the brood-buds are tightly crowded together in the flask and surrounded by the viscid gelatinous substance produced by the mucilage papillæ.

When gemmæ are placed in a favorable situation, growth proceeds by means of the end cell which develops into the regular wedge-shaped apical cell already described for this plant. In the earlier stages of the thallus, the apical cell builds up a broad flat stem and the leaf-like lobes appear on opposite sides of this expanded portion. In very early stages the plant looks like a leafy liverwort having distinctly separated lobes set on the stemlike midrib apparently like leaves. The lobes must increase in bulk laterally for in the mature thallus they are closely set together forming a more nearly thalloid plant. At the apex of the young plant, the lobes form a rosette around the growing point. This arrangement is advantageous, as it affords protection for the bud.

Nostoc appears in the plant very soon after the gemmæ germinate. Often two or three distinct colonies may be formed on plants .25 mm. in length. It is possible that the Nostoc finds entrance into the flask and adheres to the gemmæ before they are shed. Rhizoids develop early on these little plants and soon become long and much entangled.

It would seem that the young plants could not long thrive perched on the dorsal surface of the thallus but they do grow for a time, probably upon nourishment stored in the gemma which persists at the base of each new plant. As the old thalli die these new shoots are allowed to rest on the soil where they mature into vigorous well-developed plants. Further study will probably throw light on the question as to whether these plants are fertile or sterile. Material kept in the laboratory did not prove very satisfactory for this study as conditions were not favorable for plant growth. The branches of the thallus had a tendency to grow erect and spindling, with much smaller and widely separated lobes.

Advantages of Asexual Reproduction. Cavers[2] says, "It seems probable that in both Blasia and Cavicularia we have an example of the replacement of spore production by asexual reproduction. Blasia is found more often with gemma flasks than with fruits." In the recent observations of Blasia, fruits were found quite as abundant as flasks. This problem will make an interesting study in connection with seasonal changes and the variations in environmental factors operating during these seasons. Evans[6] has found in species of Metzgeria that gemmæ are not likely to appear when the plant is growing luxuriantly.

However, it is the writer's theory that vegetative reproduction is a safeguard in tiding the plant over unfavorable periods. In times of stress for the plant sexual reproduction would be a much longer and more uncertain mode of propagation, than that of asexual gemmæ. Sex organs are formed in the summer but spores are not shed until the following spring, while gemmæ may be fully developed and shed during most months of one growing season.

In the second place it seems likely that gemmæ are better prepared to produce a plant body quickly, than are the spores, being so much larger and so abundantly supplied with food. Macvicar[11] says, "When a plant cannot obtain its normal amount of nourishment and especially moisture, it will be smaller and weaker than the type, the stems being shorter and the leaves frequently deformed. Fruit is not uncommon in this form. The other deviation is when the plant has a deficiency of light. Under this condition it is generally green or pale green, the stems are elongate and thin, the leaves distant and smaller, and if it be a thallose species the branches have a tendency to grow erect. In such plants fruit rarely occurs but gemmæ are often abundant." In this case also it would seem that gemma production is more abundant under unfavorable conditions.

SUMMARY.

1. *Blasia pusilla* is a relatively simple liverwort having a dorsi-ventral thallus with laterally inserted leaf-like lobes.

2. The growth of the thallus proceeds by means of the wedge-shaped apical cell, characteristic of the dichotomously branched forms.

3. The thallus shows distinct strands of thick-walled cells functioning as mechanical and conducting tissue.

4. The conducting strand is composed of elongate cells, tapering to a point at each end, and having pits scattered irregularly in the thick walls.

5. Mucilage hairs are found on both sides of the thallus massed at the apex for the protection of the growing region.

6. Rhizoids and scalelike amphigastria are found on the ventral surface of the thalli.

7. The leaf auricles also found on the ventral surface are filled with Nostoc colonies.

8. Blasia is dioecious, the antheridial plants being more slender and more deeply lobed than the archegonial plants.

9. Antheridia are found in two rows, one on either side of the midrib.

10. Ten or twelve archegonia are formed near the apex of the plant, the group surrounded by the upstanding side leaves.

11. Both archegonia and antheridia arise from dorsal segments of the apical cell, and the initials are similar.

12. Vegetative reproductive bodies or gemmæ are developed in cupules on the dorsal surface of the thallus.

13. These cupules have long tubelike necks from which the gemmæ are forced by the swelling of mucilage in the base of the flask.

14. The gemmæ of Blasia are multicellular, each cell containing a large nucleus and many oil globules.

15. The gametophyte of *Blasia pusilla* occupies an intermediate position between the thallose and foliose forms of liverworts.

16. This study shows that the cupules of Blasia, which are the most complex of the liverworts, are comparable to the simpler ones of Marchantia and Lunularia.

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LITERATURE CITED.

1. *Barnes, C. R.*, and *Land, W. J. G.*, Origin of Cupules in Marchantia: Bot. Gaz., 46, 401, 1908.

2. *Cavers, F.*, On Saprophytism and Mycorhiza in Hepaticae: New Phytol., 2, 30, 1903.

3. *Coker, W. C.*, Abnormalities in Liverworts: Bryologist, 12, 104, 1907.

4. *Corda*, Deutschlands Jungermannieen in Sturm's Flora, H. 26, 27, S. 137.

5. *Engler and Prantl.* (*Schiffner*), Die Natürlichen Pflanzenfamilien, I. Teil III, Abteilung I, Halfte 1895.

6. *Evans, A. W.*, Vegetative Reproduction in Metzgeria: Ann. Bot., 24, 271, 1910.

7. *Goebel, K.*, Asexual Propagation of Hepaticae, Organography of Plants, 1905.

8. *Gottsche.*, Uëbersicht der Leistungen in der Hepaticologie: Beilage zur botan., Zeit., 1828.

9. *Hofmeister, W.*, Germination, Development and Fructification of the Higher Cryptogamia, 1851.

10. *Leitgeb, H.*, Untersuchungen über die Lebermoose, Jena, 1874-1882. Dis frondosen Jungermannien, Vol. III.

11. *Macvicar, S. M.*, The Students' Handbook of British Hepatics, 1912.

12. *Nees von Esenbeck*, Naturgesch. d' Europ. Lebermoose, 1833.

13. *Schmidel.*, Dissertatio de Blasia, 1759.

14. *Tansley, A. G.*, and *Chick, Miss E.*, Notes on the Conducting Tissue System in Bryophyta: Ann. Bot., 15, 1901.