On the Morphology of *Cyathodium*¹.

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With Plates **XXI** and **XXII**.

OUR knowledge of the structure and development of *Cyathodium* is perhaps more obviously deficient than that regarding any other genus of the Marchantiaceae. Apart from systematic descriptions², which deal with the structural features of mature plants as displayed in herbarium material, the only considerable detailed description of its morphology is that given by Leitgeb³, and his observations appear to have been done upon imperfect and probably dry material. Subsequent observers⁴ have supplemented this by references to its vegetative structure, based on better preserved material, but there is a complete lack of information as to the development of the sexual organs and of the sporogonium. It has even remained uncertain whether Leitgeb's suggestion, that the antheridium differs from that of all other Archegoniatae in being a stalked unicellular structure, is correct or not.

The interest attaching to the study of this small genus of Liverworts is dependent not merely upon obtaining additional data for phylogenetic comparison, but upon the biological peculiarities of the plants composing it. The structure of the thallus in the majority of the Marchantiaceae may be regarded as adapted to life in exposed situations. The intake of water is limited to special regions of the thallus, and the system of air-chambers, communicating by definite air-pores with the external atmosphere, is such

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² Cf. Stephani, *Species Hepaticarum*, vol. i, p. 62, for a full diagnosis of the genus and species and for references to the original descriptions.

³ *Untersuchungen über die Lebermoose*, Heft 6, p. 136, Taf. XI.

⁴ Ruge, *Beitr. z. Kenntniss d. Vegetationsorgane d. Lebermoose*, *Flora*, 1893, p. 279; Stahl, *Ueber bunte Laubblätter*, *Ann. Jard. Buit.*, 1896, p. 137, note on p. 201; Kamerling, *Zür Biol. und Phys. der Marchantiaceen*, Jena, 1897; Andreas, *Ueber d. Bau d. Wand u. d. Oeffnungsweise d. Lebermoosporogons*, *Flora*, 1899.

as to limit and control the loss of water vapour. This general view of the significance of the structural peculiarities of the Marchantiaceae is confirmed by the situations in which they are found most abundantly. My own experience, when collecting Hepaticae in Ceylon and the Malay Peninsula, was that the Marchantiaceae were most abundant in open exposed situations, and almost confined to such places; that some forms also occurred by path-sides in the forest, but that they were almost absent from the depths of the forest itself, where thalloid Jungermanniaceae were abundant.

Among the Marchantiaceae there are, however, one or two genera which not only occur in relatively damp and shaded situations, but exhibit corresponding modifications in the structure of the thallus. In *Dumortiera* (and perhaps in the light of recent investigations *Monoclea* may be added) the air-chambers are rudimentary or absent, and transpiration and assimilation are carried on by the unprotected superficial cells of the thallus, which is thus physiologically comparable to that of *Aneura* or *Pellia*. In *Cyathodium* modifications of a different nature to those in *Dumortiera* appear to stand in relation to a damp and shady habitat. The few species occur in the deep shade of tropical forests, in dark caves, and sometimes in the crevices of walls or on paths in rather more exposed positions. In this genus the layer of air-chambers opening by definite pores is retained, but the basal portion of the thallus is for the most part only a single layer of cells thick. Filaments of assimilating cells are absent from the air-chambers, the epidermis of which has taken over the function of assimilation.

In the present state of our knowledge of the genus it seemed worth while to give the results of my investigation of two forms of *Cyathodium*, which bore sexual organs and sporogonia of various ages, in some detail, although this involves some repetition of known facts. The two forms investigated were collected in the Malay Peninsula and the material was preserved in alcohol. The larger form was found growing on rocks in the deep shade of the forest on Maxwell's Hill in Perak. It grew especially on the vertical faces of damp rocks, and had a distinctly phosphorescent appearance. Comparison with original specimens of *C. foetidissimum*, Schiffn., showed that while differing in some small details, it was referable to this species.

The other form was found growing in extensive patches on the walls and floor of a dimly lit limestone cave near Kuala Lumpur. The small thalli closely overlapped one another, and they also had the same phosphorescent appearance. In a preliminary statement¹ I referred this to *C. aureo-nitens*, (Griff.) Schiffn. Since then, examination of Griffith's original specimens at Kew has shown me that it cannot be referred to that species, but is practically identical with specimens of *C. cavernarum*, Kunze, from Cuba. I do not propose to enter here into the question of the

¹ British Association Report. Cambridge, 1904, p. 782.

systematic arrangement of the forms of *Cyathodium*. A number of them differ from both *C. cavernarum* and from *C. aureo-nitens* as defined by Griffith's original diagnosis and specimens. My specimens from the caves at Kuala Lumpur agree, however, so closely with examples of *C. cavernarum* from Cuba that, with this explanation as to the locality in which they were collected, I shall refer to them below under this name.

It is perhaps of greater morphological interest to make it clear at the outset that while *C. foetidissimum* is the largest and least reduced form in the genus, my specimens of *C. cavernarum* appear to be, if anything, even more reduced than those from Cuba. Thus a comparison can be made between one of the least reduced and the most reduced form in the genus.

EXTERNAL FORM AND VEGETATIVE STRUCTURE.

The thallus of *C. foetidissimum* (Fig. 1) resembles in size and general appearance that of many Marchantiaceae, though its texture is more delicate. My specimens measured about 15 mm. in length by 4 mm. across. As a rule the plants had branched dichotomously, the two branches diverging distinctly from one another. Seen from above, the surface is marked out into well-defined air-chambers. Those over the midrib are of regular outline and have the air-pore in a central position. On passing from the middle line the chambers become more irregular in shape, and the lateral ones are greatly extended over the marginal expansion of the thallus. In these lateral chambers the pore is near to the inner limit of the chamber, which is frequently divided by an imperfect septum running in from the edge of the thallus. Seen from below a narrow distinct midrib is visible, from which numerous rhizoids spring. The cells which are prolonged into rhizoids are conspicuous by reason of their dark brown colour. There are two rows of small ventral scales (cf. Fig. 9). The apical region lies in a depression owing to the greater development of the lateral portions of the thallus. The tips of the ventral scales bend up over the apex, but afford only an imperfect protection to it.

In *C. cavernarum* (Fig. 25) the whole plant is much smaller; my specimens were about 4 mm. in length. The thallus branches dichotomously, and the resulting branches may either be distinctly separated from one another, or repeated dichotomy with little separation of the branches may give a fan-shaped outline to the plant. The air-chambers are more irregular than in *C. foetidissimum*. There is no distinct midrib, its position being only indistinctly indicated by the attachment of the rhizoids and the inconspicuous ventral scales.

Adventitious branches occur in both species (Figs. 2, 3). They originate from the under surface just within the margin of the thallus. Their base is cylindrical and some six cells in thickness, but they soon acquire the ordinary dorsiventral structure.

The rhizoids in *C. foetidissimum* are of two kinds—wider thin-walled ones and others which are narrower and have well-developed peg-thickenings. In *C. cavernarum* none of the rhizoids are thickened, but some are narrower than others and probably correspond to the peg-rhizoids of the larger species.

The ventral scales in *C. foetidissimum* (Fig. 4) are small lanceolate structures, slightly concave towards the thallus and devoid of any trace of purple coloration. There is no distinction of an appendage from a basal portion. The tip is occupied by a small glandular cell, and similar cells occur at intervals round the margin. More rudimentary forms, even to single cells bearing a glandular cell at the tip (Fig. 4, a), were found on the bases of adventitious branches, and would doubtless occur on young plants. In *C. cavernarum* the ventral scales were always filamentous structures (Figs. 26, 37). They may simply terminate in a glandular cell, but in the larger ones borne on the involucre similar glandular cells occur at the junctions of the cells of the filament (Fig. 26). A comparison of these with the flat scales of *C. foetidissimum* showed that the latter could be regarded as derived from the filamentous form by a process of branching, the marginal glandular cells indicating the tips of the united branches (cf. Figs. 4 and 26).

The thallus in both species consists for the greater part of its extent of a single basal layer of cells upon which the air-chambers are borne. In *C. foetidissimum*, however, the basal tissue in the region of the midrib is several cells thick (Fig. 5). In the older portions of the thallus these cells were usually inhabited by Fungal hyphae. In *C. cavernarum* there is no indication of a midrib in the vegetative region, but when archegonia are being formed the basal tissue becomes two or three cells thick. The stomata are simple, the large pore being surrounded by five series of narrow cells. In the cells of the basal layer there are only a few small plastids; those in the cells of the septa between the air-chambers are larger, but full-sized ones are only found in the cells of the epidermis roofing over the chambers. This is the true assimilating tissue of the thallus, and, as Stahl¹ first pointed out, its cells are similarly constructed to those of the protonema of *Schistostega*, although the outer wall is not convex. The chloroplasts were sometimes distributed through the protoplasm, but at other times they were grouped around the small nucleus in the convexity of the cell which projects into the air-chamber (Figs. 6, 7). In *C. foetidissimum* there are usually only four or five large chloroplasts in each cell; they are smaller and more numerous in *C. cavernarum*. Between the assimilating cells, and sometimes in the basal layer also, smaller cells, each containing a single oil-body, were present in *C. foetidissimum* (Fig. 7). The oil-body had a protoplasmic limiting membrane, and fine strands passed across the cavity bounded by

¹ Stahl, loc. cit., p. 201.

this. Oil-bodies were absent from *C. cavernarum*. Their abundance in *C. foetidissimum* may perhaps be placed in relation to the aromatic scent of the plant when fresh.

In median longitudinal sections of the vegetative apex in both species there appeared to be a single initial cell cutting off segments parallel to its base (Fig. 8). The details of segmentation as seen in surface view were followed in *C. cavernarum* (Fig. 27). There is a single rectangular initial cell present which cuts off segments parallel to its two sides and to its base. The shape of the initial and its segmentation differs when an apex is forming archegonia, and the basal tissue immediately behind it is more than one cell thick (cf. Figs. 10 and 34).

SEXUAL ORGANS AND INVOLUCRE.

Both species were monoecious, the archegonia being formed in acropetal succession in relation to the apex of a branch of the thallus, while the antheridia are borne on small disk-shaped antheridiophores, developed from the lower surface of the thallus. In *C. foetidissimum* (Figs. 1, 9, 10) the antheridiophore springs from the midrib, and is situated a short distance behind the archegonial group or groups developed from the apex of the branch. In *C. cavernarum* (Figs. 25, *b*, 28) the antheridiophores are borne close to the margin of the thallus. The groups of archegonia are developed at the apices of branches of the thallus, and the antheridiophores very commonly alternate with them (Fig. 28). In other cases an antheridiophore may stand beside an archegonial group in the same apical depression, or it may be developed from the margin in no definite relation to the apex. In one case a young antheridiophore was seen arising from the margin of an older one.

The antheridiophore of *C. foetidissimum* is attached by a short stalk to the midrib (Figs. 9, 10). It is transversely elongated, and the upper surface of the disciform summit is crowded with the projecting openings of the chambers in which the antheridia stand. In a longitudinal section passing through the stalk the latter is seen to expand slightly into the basal region, upon which a number of narrow chambers, each containing a single antheridium, are borne. The outside is formed by a single layer of cells continuous with the basal tissue; this, unlike the septa between the antheridia, persists at maturity. The marginal cells of this peripheral layer project as a ridge circumscribing the upper face of the antheridiophore. The development of the antheridiophore in this species could not be followed in detail. A single specimen showed that it arose as a disk-shaped outgrowth from the lower surface, just behind the anterior margin, and was protected when young by large ventral scales. The two specimens that contained unopened antheridia showed that the youngest were situated at either end of the transversely extended disk. That a succession of

antheridia forms behind these ends, which for a time behave as growing points, is supported by the much greater elongation of these ends in Schiffner's specimens from Java.

The mature antheridium (Fig. 11) is essentially similar to that of other Marchantiaceae. It consists of a short stalk composed of two cells, the wall composed of a single layer of large clear cells, and the mass of spermatocytes. The antheridia throughout their development closely fill the cavities in which they stand, and at maturity have almost obliterated the septa between the chambers. Each of the latter opens by a pore raised above the general surface (Fig. 12).

The antheridiophore in *C. cavernarum* is smaller, and is situated immediately below the margin of the thallus (Figs. 28, 29). Except that no distinct stalk is present, it is similarly constructed to that of *C. foetidissimum*. The projecting rim of cells around the summit of the disk is clearly comparable, in the smaller species, to the clear rim of cells at the margin of the thallus. In the specimen figured in section in Fig. 29 the openings of the chambers in which the antheridia stand can be seen, but the septa between the chambers are obliterated; in younger stages (Fig. 30) the septa are distinct.

The antheridia are similar to those of *C. foetidissimum*. In both species the stalk-cell immediately below the base of the antheridial wall differs in the characters of its cell-wall from the others. The development of the antheridium presents no special peculiarities. The young antheridium is first divided by a number of transverse walls into a row of about six cells. The three lowest form the stalk and the base of the wall; the terminal cell forms the summit of the wall; and the two or three middle cells give rise to the spermatocytes and the other cells of the wall. It is clear from the study of the antheridia in these two species that Leitgeb's surmise that the antheridial wall was not formed of a layer of cells may be definitely put on one side. Even in material preserved in alcohol it is often difficult, in those which have opened, to detect the nature of the antheridial wall.

Comparison with *Targionia* renders it almost certain that the structures, which have been termed antheridiophores above, correspond to the specialized antheridial branches, which in that genus spring from the under side of the midrib. The comparison is closest as regards position in the case of *C. foetidissimum*. The view that the antheridiophores of *Cyathodium* are highly modified adventitious branches is further strengthened by comparison with the sub-marginal vegetative branches of both species. It is, however, difficult to carry the comparison into the details of development, and especially to place the succession of the antheridia in relation to the apical growth of a branch.

The difficulties chiefly appear in the case of the more reduced antheridiophores of *C. cavernarum*, and it is only in this form that I have

been able to study the development to some extent. The young antheridiophore is first recognizable as a projecting disk of tissue just below the margin of the thallus in the apical depression (Figs. 31, 32). Possibly it may in some cases originate from the apical cell itself, but the arrangement of its cells as seen in surface view, taken together with the positions in which the mature antheridiophores were found, makes it clear that this is not always or usually the case. It appears rather to originate from one, two, or several cells of the anterior margin close to the actual apex. In the specimen drawn in Fig. 31 two such cells seem to have been involved, and in that in Fig. 32 three segments can be traced. At this stage the antheridia have not yet appeared, but the septa between the chambers have commenced to grow up (Fig. 33). When the antheridia have developed (Figs. 29, 30) they are found to stand in a regular series, the youngest being next to the margin of the thallus and the oldest being those that stood closest to the posterior border of the young antheridiophore. These facts taken together dispose me to regard the antheridiophore as the equivalent of a much reduced ventral branch, while placing the succession of the antheridia in relation not to the apical growth of the branch, but to the marginal extension of the group of cells forming the rudiment of the antheridiophore. I have, unfortunately, not been able to study the development of the male branch in *Targionia* and *C. foetidissimum*, comparison of which may be expected to throw further light on the question.

In both species of *Cyathodium* the archegonia stand on the morphologically upper surface of the thallus, any branch of which may give rise to a group of archegonia. The actual position in which the archegonia come to stand and the mode of development of the involucre around the group differ to such an extent in the two forms that their separate description is necessary.

In *C. foetidissimum* the state of things is closely comparable to what is found in *Targionia*. By displacement of the apical region the archegonia come to stand on what is apparently the under surface of the branch, though morphologically it is a part of the upper surface. Sometimes there is only one group of archegonia in front of the antheridiophore, the position of which has been described above. Usually, however, the apex of the thallus, after the male branch has been laid down, branches dichotomously, though this dichotomy does not affect the general outline, and is evident simply by the formation of two groups of archegonia instead of a single one. Archegonia may also occur on a branch which does not bear an antheridiophore. The archegonial groups are at first protected by large ventral scales. At this stage (Fig. 9) the displaced region of the upper surface has a V-shaped outline, the initial cell being at the point of the V, while the arms of the latter correspond to the margin of the thallus, i. e. to the line of junction of dorsal and ventral surfaces (Fig. 13). The archegonia

appear in acropetal succession until the full number, about five, has been formed, so that the youngest archegonium is situated furthest from the anterior margin of the branch. This will be clear from Fig. 10, which represents a longitudinal section through the specimen in Fig. 9. The apical cell is visible some distance from the margin, and the youngest archegonium is close to it, while further forward is an older archegonium. It is also evident from this section that the basal tissue underlying the archegonia is of greater thickness than is usual even in the midrib of this species. After the full number of archegonia have been laid down the involucre commences to form around the group. The sides of the **V** (Fig. 13) first grow up as plates of cells a single layer thick. Later the growth involves the apex itself (Fig. 14), and this leads to the involucre being composed of two lobes united at the hinder end. The development of the involucre is independent of fertilization. It is throughout one layer of cells thick, and bears neither rhizoids nor ventral scales on its outer surface. Fig. 16 represents two fully developed involucre, the one on the left surrounding a group of unfertilized archegonia, while that on the right encloses two sporogonia. The involucre is roofed in above by a prolongation of the margin of the thallus bearing air-chambers (Figs. 14, 48).

In *C. cavernarum*, on the other hand, the apex does not become displaced, so that the archegonia stand on what is actually as well as morphologically the upper surface of the thallus (Figs. 34–36). The archegonia are in this case roofed in by a single layer of cells, which may be regarded as morphologically equivalent to the epidermal layer of the last formed and incomplete air-chamber (cf. Fig. 34). The basal tissue bearing the archegonia is two layers of cells thick; the further growth of the apical region produces only one layer of cells. Thus the involucre in this species is equivalent to the basal tissue of the thallus itself, and is several layers thick behind, but further forward is a single layer. The lower surface of the involucre bears ventral scales and sometimes rhizoids (Fig. 37).

The structure and development of the archegonium in the two species is like that in other Marchantiaceae. A series of developmental stages of the archegonium of *C. foetidissimum* is shown in Fig. 15, *a-d*, and a young archegonium of *C. cavernarum* in Fig. 34. One point of difference between the two species is of interest as occurring within a genus. In *C. foetidissimum* there is no stalk-cell, while in *C. cavernarum* there is a stalk-cell which from the first projects above the surface. The mature archegonium is borne on a short stalk, the wall of the venter is a single layer of cells thick, and there are six rows of neck-cells. The central series consists of ovum, ventral canal-cell, and eight or nine neck canal-cells which may not all be separated by cell-walls.

DEVELOPMENT AND STRUCTURE OF THE SPOROAGONIUM.

The structure of the mature sporogonium has been described in *C. cavernarum* by Leitgeb¹, and later by Andreas², but from the nature of the material used its development was not described. The development of the sporogonium was therefore followed in detail in *C. cavernarum*, and enough of it was seen in *C. foetidissimum* to make comparison possible.

C. foetidissimum. The first division in the fertilized ovum is transverse, and this is followed, as in the other Marchantiaceae, by longitudinal divisions in both upper and lower halves (Fig. 17). Only a few examples of stages intermediate between this and the almost mature sporogonium were seen, but these (Figs. 18, 19) resembled other Marchantiaceae, and made it almost certain that the sporogenous tissue and the greater part of the wall of the capsule were derived from the upper cell of the embryo, while the foot and the base of the capsule-wall were developed from the lower segment. By the stage represented in Fig. 19 the sporogenous tissue was clearly defined from the wall, and was conspicuous by reason of the dense and deeply-staining contents of its cells. With the first divisions of the embryo the venter of the archegonium becomes two-layered, and by this stage it is three or four cells thick. While closely investing the basal region of the sporogonium the young calyptra is separated from the upper portion of the capsule by a space which persists until the spores have been formed (Fig. 20). In the stage represented in this figure the spore-mother-cells had become rounded off and distinct from the young elaters. They are spherical and contain abundant protoplasm and a single nucleus: the elaters were somewhat elongated, but had no thickenings on their walls. The wall of the capsule is composed of a single layer of cells, except at the apex, where a disk of cells similar to that described by Leitgeb for *C. cavernarum* is present. The foot consists, as seen in longitudinal section, of two rows of vacuolated cells. At its base are larger cells densely filled with protoplasm. The calyptra is four to five cells deep around the foot, but thins off above to two layers.

The spore-mother-cells increase in size and the tetrad division takes place without the cell becoming lobed. This stage was indifferently preserved, so that no observations were made on the division. About the same time, however, a remarkable change occurs in the four cells at the base of the foot. These grow out into a number of relatively long tubular processes, each of which may branch once or oftener; these greatly increase the absorbent surface of the foot. Their general appearance will be evident from Figs. 21 and 23, which represent longitudinal and transverse sections of the foot of a sporogonium of this age. A transverse section of the stalk-like portion of the foot is seen in Fig. 22, which shows that this also consists of four rows of cells.

¹ Loc. cit.² Loc. cit.

A mature sporogonium is represented in almost median section in Fig. 24. Unfortunately the section just missed the apical disk (cf. Fig. 20). The spores are thick-walled, the exospore bearing rounded tubercles, and between them are the free elaters. The cells of the lower two-thirds of the wall of the capsule have their internal walls slightly thickened and of a brown colour, but have no thickenings on the vertical walls. Those of the upper third bear complete rings, usually thicker to the outside. The apical disk is apparently thrown off entire at dehiscence, for the open sporogonia had eight blunt teeth formed by the splitting of the upper third of the capsule wall. The sporogonium is protected until maturity by the calyptra, which keeps pace with its increase in size and is not ruptured until the time of dehiscence. More than one sporogonium may be developed from the group of archegonia, and thus be enclosed within the common involucre.

C. cavernarum. The material showing younger stages of the sporogonium of this species was more abundant, and enabled the development to be followed nearly continuously. On account of the extremely small size of the sporogonium this could be done with a precision almost impossible in the case of more bulky sporogonia, and the definite delimitation of the several regions may perhaps prove of use for comparison with the latter.

In the mature sporogonium (Fig. 44) we can distinguish a cylindrical foot, consisting of a row of cells and terminating below in a pair of larger cells, which grow out into absorbent processes (Fig. 46). The wall of the capsule, which contains relatively few large spores and some elaters, is composed of a single layer of cells. The cells of the upper third of the wall have ring-shaped thickenings, while those forming the lower two-thirds are thin-walled and of peculiar appearance. They are densely packed with starch grains and the nucleus in each is prominent and had often undergone fragmentation (Fig. 47). The appearance of these cells at once suggests a comparison with tapetal cells, and they have probably a nutritive function. At the summit of the capsule is the apical disk, the position of which is seen in Fig. 44, while its structure in median section is better shown in the adjoining section (Fig. 45). It consists of two series of four cells each, the cells being superposed, and of an inner layer of eight cells. The disk projects into the cavity of the capsule. The mode of opening of the sporogonium is similar to that of *C. foetidissimum*, and has been described and figured by Leitgeb. The spores have a dark brown exosporium, closely covered with spiny projections.

The first division in the embryo is transverse, and, unlike what usually happens in the Marchantiaceae, this is followed by transverse walls in both upper and lower segments (Figs. 38, 39). From the lowest cell of this row of four is derived the basal group of cells (usually two in number) which bear the processes. The upper cell of the lower half of the embryo gives

rise to the row of cells forming the rest of the foot and to the base of the wall of the capsule. The lower of the two cells of the upper half produces the greater part of the capsule and all the sporogenous tissue. After the quadrant divisions in this segment periclinal walls cut off the cells of the capsule wall. The central cells divide further and ultimately separate as the spore-mother-cells. From the uppermost segment of the embryo the upper two tiers of cells in the apical disk are derived. The lowest tier can, however, be traced back to the upper portion of the sporogenous tissue. A single layer of the latter at the upper limit of the group does not separate into spore-mother-cells, but remains as a continuous layer in contact with the uppermost sterile segment (Fig. 43), and forms part of the apical disk. A comparison of Figs. 40 and 41, in which the limits between the original segments are clearly recognizable, with Fig. 39 will enable the course of the segmentation to be followed; Fig. 42 shows the quadrant and periclinal divisions in the sporogenous segment.

The actual size of the sporogonia and of the spores contained in them presents some features of interest. Figs. 48 and 49 are outlines, drawn to the same scale, of longitudinal sections through the sporogonia of the two forms investigated. They are of practically the same age. In both cases the cells of the upper part of the wall had well-developed brown rings, and the walls of the spores and elaters were also thickened. The calyptra, however, was not ruptured and (as shown by measurements of opened sporogonia) the full size had not been attained. This does not, however, obscure the somewhat surprising fact that, while the sporogonium of *C. cavernarum* is much smaller than that of *C. foetidissimum*, the spores of the former are considerably larger. The sporogonium of *C. foetidissimum* figured (Fig. 48) was 625μ in length, the capsule being 525μ ; the length of mature capsules was estimated as 800μ . The sporogonium of *C. cavernarum* figured was 325μ in length, the capsule being 250μ ; the mature capsule was about 400μ long. Mature spores of *C. foetidissimum* were about 40μ in diameter, or, including the projecting thickenings of the wall, nearly 50μ . Those of *C. cavernarum* were 60μ in diameter, or, including the thickenings, 63μ . This association of proportionally large spores with a very small capsule, which has probably resulted from a process of reduction, is of interest for comparison with *Archidium*. In this genus of Mosses, as is well known, very large spores are found in a small and possibly reduced sporogonium.

CONCLUSION.

If we compare *Cyathodium* with the other Marchantiaceae in the light of the additional facts as to its vegetative structure, the structure of the antheridium, and the development of the sporogonium detailed above, the only possible conclusion seems to be that they confirm the close relationship

with *Targionia* expressed by the association of the two genera in the Targionioideae. *C. foetidissimum* stands as an intermediate link between *Targionia* and the smaller species of *Cyathodium*, being less reduced than the latter in its vegetative structure, while the position of both the male branches and of the groups of archegonia is essentially the same as in *Targionia*. The position of the archegonia on the actual upper surface in *C. cavernarum* suggests a comparison with the Corsinioideae, though the facts do not point to this being an indication of direct relationship¹.

It seems clear that *Targionia*, *C. foetidissimum*, and *C. cavernarum* form a series from a thallus of the xerophytic Marchantiaceous type bearing a large sporogonium with a well-developed bulbous foot, to a type with a small and simple thallus bearing a very small sporogonium attached by a very rudimentary foot. There is nothing to suggest that this should be regarded as an ascending series, indicating a progression from forms like *C. cavernarum* to the type of *Targionia*. The facts, on the contrary, appear to point to the series being one of reduction standing in relation to the shady and damp situations in which the species of *Cyathodium* are found, while *Targionia* occurs in open and even exceptionally exposed situations. In specimens of *T. dioica*, Schiffn., that had grown mixed with a form of *Cyathodium* on a bank in a jungle in Ceylon, the thallus was slightly thinner and the purple colour was absent, except from the extreme margin of the thallus and the tips of the ventral scales. I have observed much more extreme modifications in plants of *Fegatella conica* growing in extreme shade. The plants were reduced in size, there was great reduction of the basal tissue, the assimilating filaments were shorter, and the cells of the epidermis (which as in many Marchantiaceae contain chlorophyll) were thin-walled and bulged into the air-chamber much as in *Cyathodium*. The much more profound structural peculiarities exhibited by *Cyathodium* must of course be regarded as the result of adaptation to the changed conditions, and not as directly induced by them.

In reviewing the features presented by *Cyathodium* the persistence of the system of low flat air-chambers may be first noted and contrasted with their loss in such a hygrophytic form as *Dumortiera*. The reduction in thickness of the thallus is at the expense of the basal tissue, which (except at the midrib in *C. foetidissimum*) is only a single layer. Assimilating filaments are completely absent from the chambers. The persistence of the air-chambers and the specialization of the cells of their epidermis for assimilation suggest that *Cyathodium* is to be regarded as primarily a form adapted to shade conditions rather than as a hygrophyte. Were the function of assimilation once transferred to the most superficial layer, as so frequently happens in shade-loving plants, the preservation of the system

¹ The resemblance is increased in those exceptional cases in which the growth continues as a vegetative thallus bearing a sporogonium on its upper surface. Stephani, loc. cit., p. 63.

of air-chambers, although their original protective function had been lost, is readily comprehensible.

C. foetidissimum has been shown to resemble *Targionia* in the position of the archegonia and the development of the involucre. The fact that the archegonia in *C. cavernarum* occur on what is the actual upper face of the thallus can be placed in relation to the greater reduction of the basal tissue, which would make the displacement, as in *Targionia* and *C. foetidissimum*, difficult. The antheridiophores, which appear to correspond to what in *Targionia* are clearly modified branches, are in both species of *Cyathodium* further reduced and specialized. The sexual organs themselves do not appear to be modified.

When the reduction exhibited by the spore-producing generation in *Cyathodium* is considered it is questionable whether any adaptive explanation can be given. It is not obvious that the change of habitat would render the reduction in size of the capsule or foot advantageous, or, to put it in another form, that under the new conditions the larger sporogonium with its greater spore output would have ceased to be of value. A clearer understanding of the facts appears to be reached, if we regard the changes in the sporogonium as imposed upon it by the modifications of the thallus, upon which it is produced and by which it is nourished. The reduction in thickness of the basal tissue renders any considerable accumulation of reserve material, at the expense of which the growth of a large sporogonium could take place, impossible, and the conditions of assimilation of an extreme shade form make it unlikely that the place of such reserves could be taken by the continuous production of the necessary amount of constructive substance. Under these conditions the reduction in size of the sporogonium can be readily understood, and its degree corresponds to that of the vegetative organs. The reduction is evident not only in the capsule, but in the sterile tissue of the foot. A large bulbous foot, such as that found in *Targionia* and all the other Marchantiaceae, would indeed be impossible in connexion with the small mass of underlying tissue in *Cyathodium*. The fact that the terminal cells of the cylindrical foot have their surface greatly increased by the formation of processes after the stimulus of fertilization and of the growth of the embryo have led to the increase in thickness of the base of the calyptra indicates the need for more rapid absorption than at first was possible.

On the grounds of the facts of structure, unfortunately without the assistance of experimental data, I am therefore inclined to regard *Cyathodium* as a truly reduced form, derived from a form not unlike *Targionia* by adaptation of the gametophyte to life in shady and damp situations and by changes in the sporogonium induced by the alterations in the gametophyte upon which it is borne.

Apart from questions of genetic relationship, one point of interest may

be referred to in conclusion. When we look for sporogonia resembling that of *Cyathodium* probably the closest comparison as regards the relation between capsule and foot is presented by *Sphaerocarpus* and *Riella*. The mode of segmentation of the embryo in these genera has much in common with the Marchantiaceae, the comparison between *Sphaerocarpus* and *C. cavernarum* being particularly close. In both *Riella* and *Sphaerocarpus* the mature sporogonium consists of a small capsule connected by a narrow stalk with a small bulbous foot. In some species of *Riella* the stalk consists of a single row of cells, as in *C. cavernarum*, and the bulbous foot, which in *Riella* is composed of more numerous cells, shows a tendency to form absorbent processes. In all the Marchantiaceae and the Jungermanniaceae, with these exceptions, the foot and seta of the mature capsule appear to be relatively bulky. On the other hand, in the Ricciaceae the sporogonium shows no trace of a foot.

As has been shown above, there are reasons for regarding the sporogonium of *Cyathodium* as a reduced structure, and the same may perhaps be assumed for *Riella*. But in the absence of any other forms with a very small sterile portion of the sporogonium these genera are not without interest as indicating the sort of structure which may have characterized the stage intermediate between the Ricciaceous type and sporogonia with a well-developed foot. It is at least possible that the reduction in *Cyathodium* has taken place along the lines of differentiation, and that it may in this respect represent to some extent an intermediate stage between the Ricciaceae and Marchantiaceae.

Such reduced forms must, however, be used with caution in speculations as to the methods of descent, and further information as to the range of variation in the sporogonium under altered conditions must be accumulated before any but tentative conclusions can be drawn from their study. Without attempting further to follow out this line of comparison, the present paper may be left as a description of the main facts regarding the structure of *Cyathodium*, the full explanation of which must depend on further observations and experiments.

EXPLANATION OF FIGURES IN PLATES XXI AND XXII.

Illustrating Dr. Lang's paper on the Morphology of *Cyathodium*.

PLATE XXI.

Cyathodium foetidissimum.

Fig. 1. A plant of *Cyathodium foetidissimum* viewed from below: the thallus has branched dichotomously; an antheridiophore is seen some distance from the anterior margin of each branch, and between it and the margin there are in each case a pair of involucre enclosing sporogonia. $\times 4\frac{1}{2}$.

Fig. 2. Portion of the thallus bearing two adventitious branches.

Fig. 3. One of the adventitious branches seen from above, showing its relation to the margin of the thallus. $\times 44$.

Fig. 4. Ventral scales. *a*, *b*, reduced forms from the base of an adventitious branch; *c*, the normal form from the well-developed thallus. $\times 200$.

Fig. 5. Transverse section of the thallus in the region of the midrib; the shaded cells were occupied by Fungal hyphae. $\times 200$.

Fig. 6. Two cells of the 'epidermis' in vertical section, showing the position of the chloroplasts in the convexity of the cell. $\times 353$.

Fig. 7. Cells of the 'epidermis' in surface view; the small cell in the centre contains an oil body, the others are assimilating cells. $\times 353$.

Fig. 8. Medium longitudinal section of the apex of a vegetative branch. $\times 250$.

Fig. 9. Fertile branch seen from below, showing a mature antheridiophore and in front of it large ventral scales covering over the groups of archegonia. $\times 46$.

Fig. 10. Longitudinal section of a specimen of the same age as that in Fig. 9, passing through the shortly stalked antheridiophore, and showing the apical cell displaced towards the lower surface and in front of it two young archegonia. $\times 200$.

Fig. 11. Longitudinal section of a mature antheridium. $\times 530$.

Fig. 12. Longitudinal section through the upper part of an antheridium and the opening of the chamber of the antheridiophore that contained it. $\times 353$.

Fig. 13. Sketch showing the position of the developing archegonia and of the V-shaped ridge marking the junction of dorsal and ventral surfaces in the region of the displaced apex.

Fig. 14. Longitudinal section through an apex bearing a fully formed group of archegonia; the apex has commenced to form the hinder portion of the involucre. $\times 80$.

Fig. 15. Series of developmental stages of the archegonium in longitudinal section. $\times 640$.

Fig. 16. View of fertile branch from below, showing the spent antheridiophore and in front of it two fully developed involucre; that on the right is occupied by two sporogonia, while the one on the left contains unfertilized archegonia. $\times 23$.

Figs. 17-19. Three stages in the development of the sporogonium. $\times 375$.

Fig. 20. Median section of a sporogonium with isolated spore-mother-cells; the calyptra enclosing it is shaded. $\times 130$.

Fig. 21. Longitudinal section of the base of the calyptra, showing the absorbent processes developed from the basal cells of the foot of a sporogonium which contained tetrads. $\times 250$.

Fig. 22. Cross section of stalk-like portion of foot. $\times 375$.

Fig. 23. Cross section of basal portion of foot, showing the absorbent processes. $\times 250$.

Fig. 24. Nearly median section of a mature sporogonium; the apical cap of cells is not seen. $\times 136$.

PLATE XXII.

Cyathodium cavernarum.

Fig. 25. Plants of *C. cavernarum*. *a*, sterile plant; *b*, plant bearing three archegonial groups and two antheridiophores. $\times 7$.

Fig. 26. Two of the larger ventral scales. $\times 200$.

Fig. 27. Vegetative apex seen from below, showing the shape and mode of segmentation of the apical cell. $\times 670$.

Fig. 28. Anterior margin of a branch of the thallus seen from below, showing an antheridiophore and two involucre. The involucre to the left encloses a mature sporogonium, while that to the right bears only unfertilized archegonia. $\times 25$.

Fig. 29. Antheridiophore in vertical section; the lower antheridia are mature. $\times 375$.

Fig. 30. Younger antheridiophore, showing the septa between the antheridia. $\times 375$.

Fig. 31. Young antheridiophore in surface view. $\times 670$.

Fig. 32. Young antheridiophore, which can clearly be traced back to three marginal cells, in surface view. $\times 670$.

Fig. 33. Vertical section of a young antheridiophore similar to that in Fig. 32. $\times 670$.

Fig. 34. Median section through an apex which has produced the first archegonium. $\times 375$.

Fig. 35. Median longitudinal section through an older apex, which has formed a group of archegonia, showing the construction of the involucre in this species. This figure is based on two adjoining sections and is slightly diagrammatic. $\times 200$.

Fig. 36. Transverse section across an involucre of the same age as that in Fig. 35. $\times 200$.

Fig. 37. Involucre bearing an advanced sporogonium seen from below to show the presence of rhizoids and ventral scales upon it. $\times 64$.

Fig. 38. Embryo consisting of three cells enclosed in the archegonium. $\times 375$.

Fig. 39. Older embryo, showing the four segments; vertical walls have been formed in the upper two. The venter of the archegonium has become several cells thick. $\times 375$.

Figs. 40, 41. Young sporogonia in which the regions derived from the four first segments of the embryo can be recognized. $\times 375$.

Fig. 42. Transverse section through the lower tier of the upper half of a sporogonium about the age of those in the preceding figure. $\times 375$.

Fig. 43. Longitudinal section through the upper part of the capsule of a somewhat older sporogonium, showing the origin of the lower layer of cells of the apical disk. $\times 375$.

Fig. 44. Longitudinal section of an almost mature sporogonium. $\times 200$.

Fig. 45. The apical disk of the same sporogonium in median section. $\times 200$.

Fig. 46. Foot of a similar sporogonium, showing the processes produced from the large basal cells. $\times 200$.

Fig. 47. Cells of the lower part of the wall of the capsule in surface view. $\times 530$.

Figs. 48, 49. Longitudinal sections through sporogonia of *C. foetidissimum* (Fig. 48) and *C. cavernarium* (Fig. 49) to show their position on the thallus and their relative size. In both cases the sporogonia contained spores and elaters with their walls thickened, but had not quite attained the full size. $\times 74$.

W. H. L., del.

LANG — CYATHODIUM FOETIDISSIMUM.

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