

BOTANICAL GAZETTE

MARCH, 1904

THE LIFE HISTORY OF RICCIOCARPUS NATANS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
LIV.

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(WITH FOUR FIGURES AND PLATES IX AND X)

THE beginning of the exact knowledge of the morphology of the Hepaticae dates from Hofmeister (1), who in 1850-62 published important investigations upon this group. Having discovered the egg cell in the archegonium, he traced the sperm to the surface of the egg and thus showed that the egg is fertilized by the sperm. He had previously announced his conclusion that the ordinary vegetative plants of mosses are the morphological equivalents of the prothallia of ferns, and that in mosses as well as in ferns there is a true alternation of generations.

Kny (2) gives a résumé of the literature on the morphology of Hepaticae up to 1867. He detected the apical cells and their method of segmentation in building up the thallus. He also described some stages in the development of the sex organs, and discovered the origin and manner of growth of the ventral scales. The thallus to him represented a fusion of stem and leaf.

Strasburger (3) mentions and figures the canal cells, but saw no walls separating them. He does not mention the ventral canal cell as different from the others, though one of his figures clearly shows it.

Leitgeb (6) in 1874-82 published comparative studies of the entire group of Hepaticae. In the Ricciaceae and Marchantiaceae he described the structure of the thallus and its method of

growth, the formation of air chambers and pores, and showed that the ventral scales are homologous with the walls separating the air chambers. Corda had previously suggested the separation of *Ricciocarpus natans* from *Riccia* as an independent genus. Leitgeb, after examining *Ricciocarpus*, gives the following as distinguishing characters: (1) the constant presence of definitely formed air pores similar to those of *Corsinia* and *Boschia*; (2) numerous ventral scales which are formed independently and have long-continued basal growth; (3) a rudimentary integument (Hülle) around the sporogonium; (4) antheridia collected into groups similar to those of *Marchantiaceae*. Leitgeb lays stress on the grouping of sex organs, and suggests a progressive series in which the lowest member has the sex organs scattered indiscriminately over the upper surface and the highest has the definite group of sex organs terminating a branch.

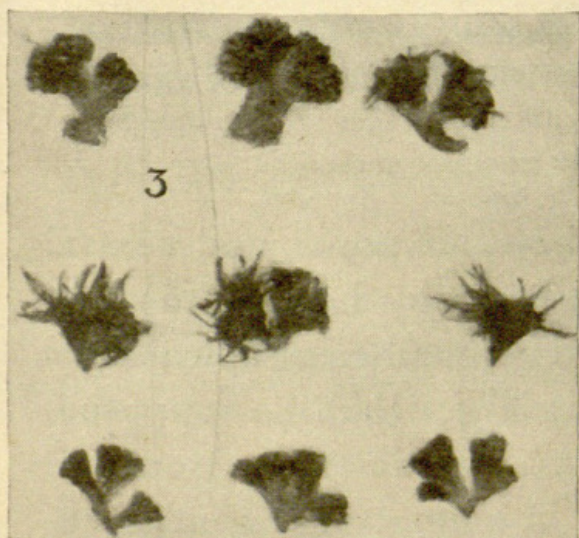
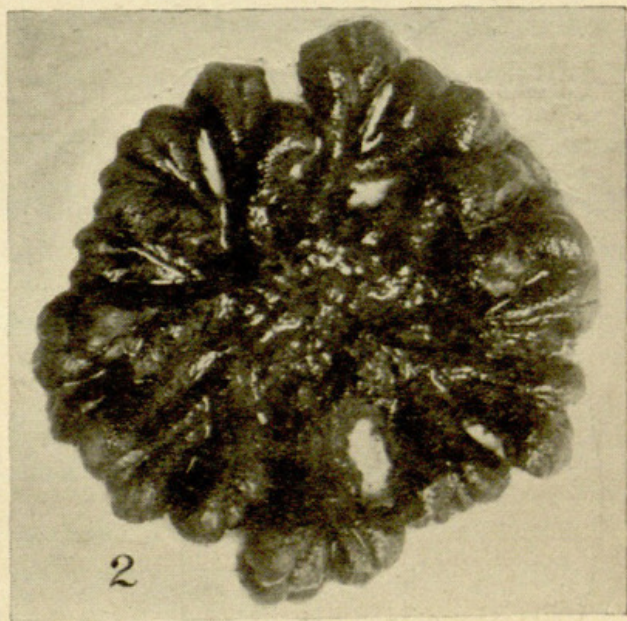
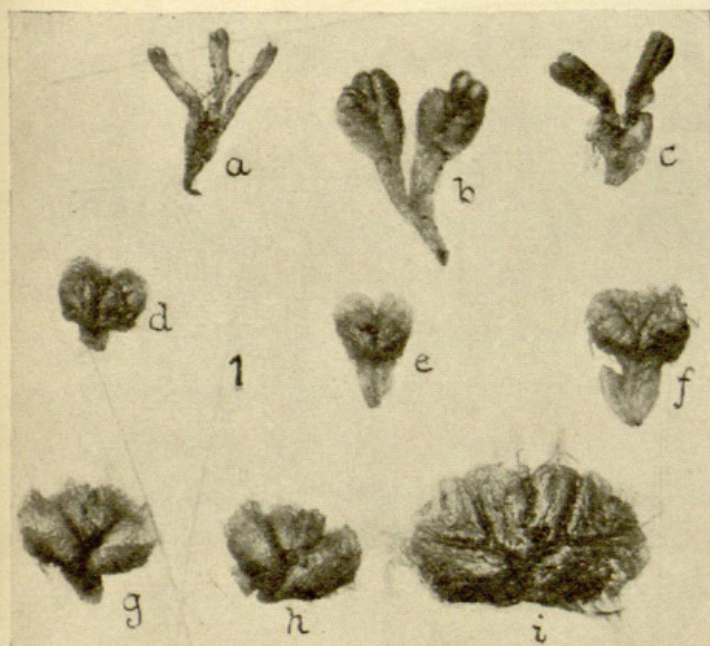
Fellner (14) studied the germination of the spore and the development of the thallus in *Riccia glauca*.

MATERIAL AND METHODS.

The material for the present study was collected during the spring and summer of 1902, and was fixed in a chrom-acetic acid mixture (1 per cent. of each) for twelve to twenty-four hours. After washing thoroughly in running water for a few hours, the plants were brought gradually into 70 per cent. alcohol. Pieces including an apex of a branch and a dorsal furrow were cut from these preserved plants. Since the loose, delicate tissues are very likely to collapse, the material should be hardened and dehydrated gradually, and the absolute alcohol should be renewed once or twice to insure perfect dehydration before any xylol is added. It is well to have xylol grades of 25, 50, and 75 per cent. in absolute alcohol, through which the material is passed with intervals of an hour between successive grades. After a short time in pure xylol, paraffin is added as fast as it is dissolved by the xylol. The paraffin should be changed three or four times during the three hours in the bath, after which the material may be imbedded. Sections perpendicular to the flat surface of the thallus and also to the median furrow are best for

all purposes except to show a series of stages in a single section, in which case the sections should be parallel to the furrow.

Delafield's haematoxylin or Heidenhain's iron-alum haematoxylin proved excellent for young stages of the sex organs, and the latter stain was especially good for older stages of the sporophyte. Flemming's safranin gentian violet combination was most satisfactory for nearly mature archegonia and the process of fertilization.



Ricciocarpus natans.

FIG. 1.—*a* and *c*, plants injured by insects, the apical cells growing independent branches; *b*, single branch of soil plant like *fig. 2*; *d-i*, successive stages in the growth of fruiting plants.

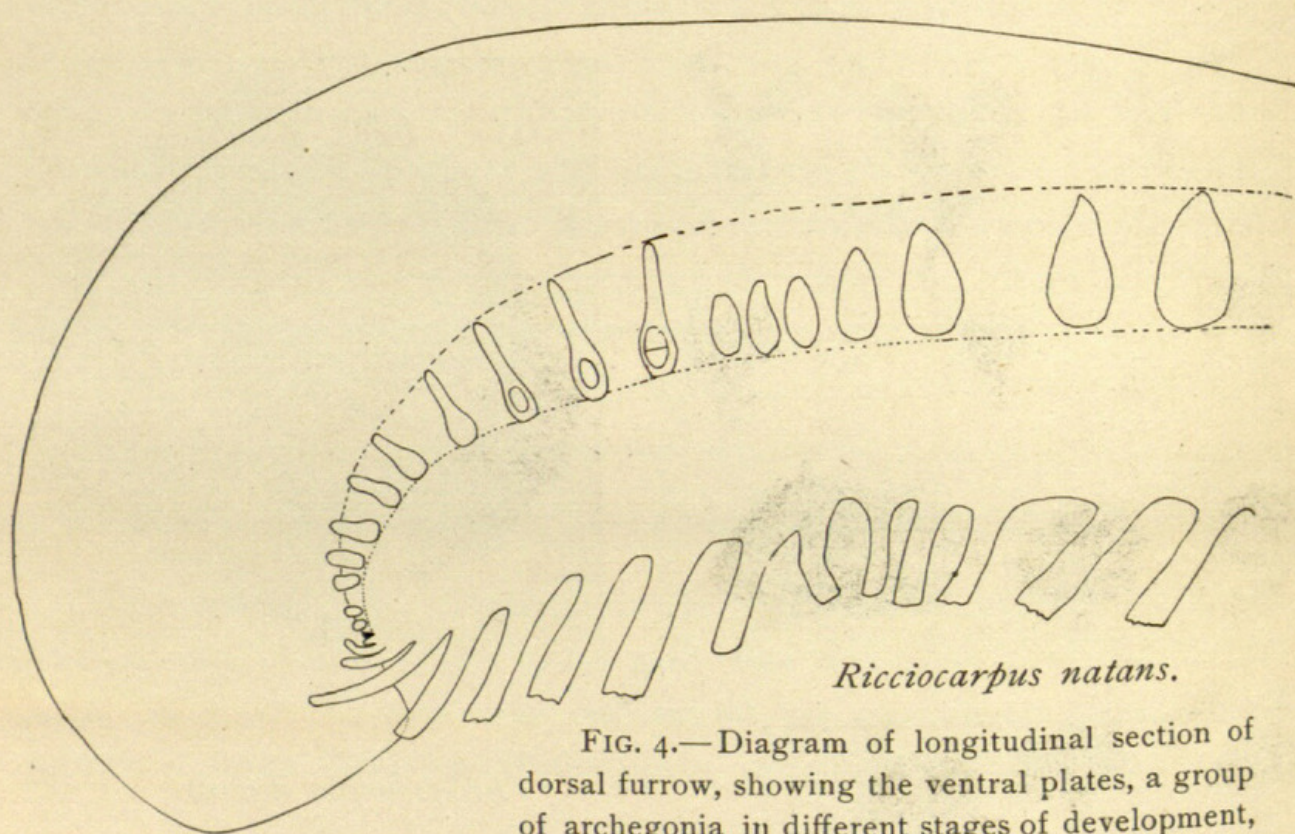
FIG. 2.—A rosette growing on the soil.

FIG. 3.—Vegetative water plants in autumn.

THE THALLUS.

The common floating form of *Ricciocarpus* is so familiar, and has been so well described by Bischoff (13) and others, that no further description of external appearance seems necessary. A series of stages in the development of the floating form is shown in *fig. 1* (*d-i*).

The upper surface of the plant is divided into small areas as in *Marchantia*, and in the center of each of these areas Leitgeb discovered a simple air pore surrounded by about six guard cells (*figs. 10, 11*). Two or three tiers of air chambers compose the green tissue, the walls and roofs of the chamber being composed of chlorophyllose cells. The storage tissue, composed of about ten layers of colorless, starch-filled cells, forms a strip beneath each dorsal furrow. The method of growth of the



Ricciocarpus natans.

FIG. 4.—Diagram of longitudinal section of dorsal furrow, showing the ventral plates, a group of archegonia in different stages of development, and further back a group of antheridia.

thallus and the formation of air chambers, air pores, and ventral scales has been so thoroughly worked out by Leitgeb (6) that there is little to add to his account. The number of apical cells at the anterior end of each furrow is larger than he supposed, averaging about five in our plants, as may be seen from the number of rudiments of ventral scales in a nearly horizontal section taken just below the apex (*fig. 9*). The position of the apical cells and their relation to the ventral scales is made clear by the sections represented in *figs. 4, 7, 8, 9*.

The dorsal furrow in cross section has somewhat the form of an inverted Y, with a more or less prominent median longitudinal ridge between the arms. Early observers supposed this ridge to

be produced by the enlarging of the sporophyte, but it occurs independently of this and is not present in purely vegetative plants. As growth proceeds, the plants become broader and thicker, and at the same time the older posterior parts decay (*fig. 1*). The decay sets free the ripened spores and provides for vegetative multiplication by separating the branches. No vegetative multiplication occurs during the spore-producing season.

THE SEX ORGANS.

It is a common statement that *Ricciocarpus* fruits only when in contact with the soil. In this vicinity no stranded fruiting plants have ever been collected except such as showed clearly that the fruiting process was already far advanced before the plant came to rest. A careful examination of abundant material in numerous localities shows that the fruiting plants normally float free on the surface of the water from germination of the spores until the spores of the next generation are ripened and discharged. The untimely withdrawal of the water often leaves mature plants stranded, and although they develop rhizoids very quickly, no change of form occurs until the spores have been discharged.

Ricciocarpus is described by Schiffner, Leitgeb, and Campbell as being strictly dioecious. Our investigations prove conclusively that it is strictly monoecious. The error of previous observers doubtless arose from the exclusive examination of mature plants, which normally bear only sporophytes because the antheridia have been lost by the decay of the older portions of the thallus. A very few plants usually produce antheridia only, and retain these until the plants are full grown, while still other plants may be quite sterile. Young plants and those formed from broken-off floating tips of soil plants very soon begin to produce antheridia in from three to five rows. The antheridia are at first superficial on the floor of the dorsal furrow just behind the apical cells. They gradually become sunken in cavities by the upgrowth of the vegetative tissue surrounding them (*figs. 4, 5*). The series may be interrupted at intervals so that the antheridia may occur in more or less definite groups,

and late in the season on plants that fail to produce sporophytes these groups may be inclosed in definite common integuments terminating above in a sort of beak. It was this kind of group on which Leitgeb (6) based his classification. The plants marked *d* and *e* in *fig. 1* have completed the series of antheridia and, if growth should continue, at once there would begin a series of from three to five rows of archegonia in position and arrangement a continuation of the antheridial rows (*figs. 4, 6*). The archegonial series is complete in a plant like *h* (*fig. 1*), from which the diagram (*fig. 4*) was made.

The cavities inclosing the sex organs are morphologically air chambers. The organ is graduated in length to the depth of the cavity, so that its apex is always approximately on a level with the floor of the dorsal furrow (*figs. 5, 6*). It may be noted that most of the antheridia are found in the narrower and less fleshy portions of the plants, while the archegonia are located in the more vigorous portions. The antheridial portions of the plant are produced early in the season, when conditions for growth are comparatively unfavorable. In this it reminds one of the prothallium of a polypod fern, which while young and delicate or in unfavorable conditions produces only antheridia, but if circumstances become more favorable, the enlarging, more vigorous plant begins the production of archegonia. Antheridia are produced during April, and by May 1 the youngest ones are half developed, the oldest having already discharged their sperms. The mature organ is a short-stalked, oval body, conical at the apex, with a wall consisting of a single layer of cells. Though antheridia are produced earlier in point of time than archegonia, their development is so much slower that both are mature at the same time. The sperms are of the usual biciliate type and have two complete coils.

A complete series of stages in the development of the archegonium was found on plants collected May 1. The course of development is the same as that outlined by Janczewski (11) for the typical liverwort archegonium. In the outer cell of the archegonium rudiment three successive vertical walls inclose a triangular cell which shortly divides by a transverse wall (*fig. 15*)

into an upper cover cell, and a central cell which is to give rise to the axial row. This latter division is quickly followed by divisions in the outer wall cells, when the archegonium is composed of two tiers of four cells each. Successive divisions in the outer cells lengthen the neck and enlarge the venter.

The upper of the first two cells of the central row by two successive divisions produces regularly four neck canal cells, the same number as that reported for the species of *Riccia* which have been studied. The lower of the first two cells enlarges very rapidly and shortly before fertilization divides, giving rise to a small ventral canal cell and the egg cell (*figs. 20-22*). The egg fills the entire venter of the archegonium, except the small portion occupied by the ventral canal cell. Its protoplasm is at first somewhat vacuolate, but it rapidly becomes denser by the increase of food materials. Starch grains inclosed in plastids are so numerous at the time of fertilization as to be conspicuous even with moderate magnification. The surface of the egg next to the ventral canal cell is concave, and this condition disappears only with the resorption of the ventral canal cell, when the egg assumes a nearly spherical or a somewhat oval shape. The breaking down and resorption of the ventral canal cell seem to be dependent upon the entrance of the sperm, for the degenerate ventral canal cell is still to be recognized in archegonia that have failed to be fertilized, and in which the egg is rapidly shrinking and approaching complete disorganization, as in *fig. 26*.

The basal cell is larger than the outer one which forms the archegonium proper (*figs. 12, 13*). Two vertical walls very early divide it into four cells (*figs. 14-16*). Later divisions in various directions form a prominent mass of cells imbedded, with the exception of the short stalk, in the storage tissue beneath (*fig. 39*). This mass of cells appears to digest the abundant starch of the storage cells, so that it may be readily transferred to the growing sporophyte. The appearance and position of this tissue in relation to the storage mass indicates that it is the physiological equivalent of the foot of the sporophyte in higher forms.

Campbell (7) states for *Riccia* in general that the basal cell

divides but a few times, forming the short stalk. For *Riccia hirta* in particular he says that "the basal cell finally divides into a single lower cell which remains undivided, completely sunk in the thallus, and an upper cell which divides into a single layer of cells forming part of the venter." For *Targionia* the same author says that "the basal cell undergoes irregular divisions and its limits are soon lost." Strasburger figures and describes the basal cell in *Marchantia polymorpha* as almost or quite superficial, forming only the stalk.

The arched ring of cells surrounding the opening through which the archegonium neck protrudes at the bottom of the dorsal furrow, regarded by Leitgeb as a rudimentary integument, appears to be merely the guard cells of the air pore belonging to the cavity in which the archegonium grows.

FERTILIZATION.

Soon after the ventral canal cell is cut off, the neck canal cells break down and the resulting mass extrudes from the tip of the neck between the separated cover cells at the bottom of the furrow. The pressure being removed from above, the cytoplasm of the egg may withdraw slightly from the venter walls and round off somewhat, the upper surface always remaining concave. The egg fills about three-fourths of the venter cavity. The shrinkage is not nearly so much in the healthy egg of *Ricciocarpus* as is figured in texts for *Riccia*, only degenerate archegonia having eggs so much shrunken (*fig. 26*). Sperms swim to the archegonium through the small quantity of water held in the furrow, which acts as a capillary tube whose ends dip to the water level. Numerous sperms were observed entangled in the mass extruded from the neck of the archegonium. The male and female nuclei were seen in various stages of fusion near the center of the egg (*figs. 23-25*). The diameter of the male nucleus is about one-half that of the female nucleus, and at the time of fusion stains darker because the chromatin elements are crowded more closely together. The male nucleus presses in the side of the membrane of the female nucleus until almost completely imbedded.

So far as I know, the observation of the phenomena of fertilization in a liverwort has been recorded only for *Riella*, studied by Kruch (9). He was, however, unable to get stages of actual fusion of the nuclei. With the entrance of the sperm, marked changes begin both in the egg and in the surrounding tissues. The oospore develops a cellulose membrane and quickly enlarges so as to fill completely the cavity of the venter. The cells of the venter begin dividing by walls parallel to the surface and make a complete double layer before the first division of the fertilized egg. A two-layered calyptra seems to be the rule among Ricciaceae, but as many as four layers occur among the Marchantiaceae.

THE SPOROPHYTE.

The first division in the sporophyte is usually transverse (*fig. 27*), but it may be oblique (*fig. 28*). The next wall may appear first in either the epibasal or hypobasal cell, and may be perpendicular to the first wall, thus forming a quadrant, or may be parallel to it, producing a row of four cells (*fig. 30*). Divisions then occur in all directions, producing a mass of thirty or forty cells, after which the amphithecium becomes distinguishable as a regular layer enclosing the spore-producing cells. Further divisions, not simultaneous (*fig. 32*), produce approximately four hundred spore mother-cells.

Up to this point the sporophyte has been a solid mass. Now the calyptra and amphithecium expand, leaving the spore mother-cells free, rounded, and separated from one another. At the same time there is excreted from the surrounding tissues a large quantity of nutritive material which fills the spaces around the mother-cells, giving them the most favorable conditions for rapid growth. Most of this nutritive material is absorbed by the spore mother-cells as they rapidly enlarge to fill again the amphithecium, and the remainder is pressed into thin plates adhering to the surface of the tetrads of spores (*fig. 38*).

The inner layer of the calyptra collapses shortly after the formation of the tetrads. The outer layer persists, while the amphithecium is distinguishable until the spores are almost ripe. All of the spore mother-cells produce spores, with no

indication of elaters or sporophyte foot of any kind. Thus, as in *Riccia*, *Ricciocarpus* presents the simplest of hepatic sporophytes, which fact, I think, should be associated with a strictly aquatic habitat. To my knowledge, all floating liverworts have this simple form of sporophyte, while nearly all of those normally living and fruiting on the soil (including the submerged *Riella*) have to some degree developed sterile structures in addition to the simple capsule wall. The soil contact rationally appears to be a necessary stimulus to any extensive sterilization of sporogenous tissue in the progressive manner contemplated by Bower (15), because only on the soil does it seem possible so to establish an independent sporophyte.

A summary of the fruiting period about Chicago in 1902 is approximately as follows:

April 10-20. Formation and development of antheridia.

April 20—May 5. Formation and development of archegonia.

April 25—May 5. Fertilization.

April 25—June 20. Growth of sporophyte, production and shedding of spores.

Any given sporophyte matures in about three weeks from the time of fertilization, and when mature exceeds the volume of the egg from which it is derived about five hundred times. In the structure of its thallus *Ricciocarpus* is much more complicated than any *Riccia*. But the most important points in classification are connected with the arrangement of the sex organs on the thallus and the structure of the sporophyte. In the lowest species of *Riccia* the sex organs are scattered indiscriminately over the surface, while in *Riccia fluitans* there is said to be a regular alternation of single antheridia and archegonia. Leitgeb based his classification of the plant on old, isolated, exceptional groups of antheridia. The antheridia should be considered as being produced in a definite region of the plant in one large group, which is followed by the production of a similar group of archegonia. These groups may be compared to the arrangement found in *Asterella*, *Sauteria*, etc., and mark the farthest advance made by *Ricciocarpus*. On the basis of its complicated thallus and definitely limited regions of sex organs, I should place *Ric-*

ciocarpus, as did Leitgeb, intermediate between Riccia and Marchantia, but with a distinct difference in conception of the arrangement of sex organs. He supposed the antheridia to be in several small groups and the archegonia to be scattered along the furrow with no attempt at grouping. All of his small groups of antheridia really belong together in one large group. The archegonia are also produced in a single region and should be regarded as a definite group.

A series of increasing concentration of sex organs into groups in specialized regions of the plant may be traced up to Marchantiaceae. Beginning with the lowest species of Riccia, sex organs are indiscriminately scattered. In *Riccia fluitans* there occurs a regular alternation of single sex organs. Ricciocarpus produces first all antheridia in a group and then all archegonia in a similar group, but with less apparent specialization of the areas bearing them than occurs in Targionia, which has the groups in special pits, and Corsinia which bears them on elevations.

On the other hand, the simple sporophyte, together with the feeding tissue derived from the basal cell of the archegonium, indicates primitive conditions not far removed from the simple sporophyte of Coleochaete.

Counts of chromosomes gave four for the gametophyte and eight for the sporophyte (figs. 21, 35). Kruch (9) gives eight and sixteen for Riella, and the same numbers are given by Farmer (5) and others for Pellia. The sporophyte spindle has very prominent and beautiful asters, but no centrosomes could be distinguished. The asters are identical with those of Pellia as described by Farmer (5), Davis (8), and Chamberlain (16), but no attempt was made to study their development.

BIOLOGY.

For biological data recourse was had to three sources, namely (1) the records of past collections, (2) the careful observation of various patches during one full season, and (3) experimentation in the laboratory.

The records of collections furnish facts as to dates and localities of fruiting in former years. With these data and by personal observation it was learned that in certain localities Ricciocarpus

reproduces sexually every year at approximately the same season, while in other localities it is to be found continually, but never reproducing sexually. The chief factor which brings about this difference seems to be the relative permanency of the water, spores being produced on temporary ponds and no spores on permanent ones.

The heavy-walled resting spore is suited to endure unfavorable conditions. When the water withdraws, the spores are left on the mud or even on dry soil, a condition which may be a necessary preparation for germination. The spores germinate early in the spring of the year following their maturity, that is, nearly a year after they have been shed. The water may remain long enough after the fruiting season for a period of vegetative multiplication to intervene, and thus many plants may be left to grow on the mud. If the mud remains very wet, there are produced beautiful rosettes like *fig. 2*, formed of numerous slender branches that remain connected at the center of the rosette.

As a rule, there seems to be little chance of survival for the stranded plants. From the under surface there is put forth a dense mass of rhizoids which anchors the plant firmly to the soil. Soil contact causes the older ventral plates to wither, but new ones continue to be produced at the apex in the usual way, though they cannot become prominent because the rhizoids pull the plant down close to the soil. If the water should return, these plants would be submerged, and, unable to float to the surface, would very likely perish, as most of the plants growing on the soil probably do. In special cases, however, the land plants have been able to endure the submergence, until by decay of the older portions the young tips of the branches are set free, when they rise to the surface and develop into the floating form again. By taking large healthy branches from the soil and placing them in water, it was found that only the extreme tip remains slightly above the water surface. The remainder extends vertically into the water and soon decays, while the young tip develops the usual floating form of the plant.

If the body of water is permanent, the surface may be covered with small plants that multiply vegetatively throughout the season,

so that countless numbers may extend over acres of water surface when the pond freezes. Large numbers of these plants probably die, but many of them, as the light and heat diminish, gradually become accustomed to submergence. The cold weather finally causes the plants to become black and apparently dead, in which condition they may float, become partially submerged, or even sink to the bottom. In this hibernating condition the plants have been taken from beneath the ice in early spring. When brought to the laboratory, the extreme apical region of each dorsal furrow grew out into a new plant. These new plants soon assume the vegetative water form and separate themselves from the old plant. Bischoff (13) mentions that *R. natans* lives over winter in a similar manner in Europe.

Rhizoids should be regarded as structures called forth by soil life, but in no sense as taking the place of ventral plates, which are always present.

The older parts of the plant possess no plasticity, but the meristematic region about the apical cell has a plasticity practically unlimited. If the plants are very much crowded, so that some are forced below the surface of the water, very commonly one or more of the apical cells will produce slender branches, which grow immediately to the surface. This is evidently an adaptation to get the plant into a favorable position again with the least possible expenditure of energy and tissue. A similar result occurred with some plants that were being kept in the laboratory. An insect ate out most of the vegetative tissues about the apex, and the restraining pressure being removed from them the apical cells grew out into independent branches (*fig. 1, a, c*). The great plasticity of the apical region in *Ricciocarpus* gives it the possibilities that one would expect to find in a transition form from aquatic to terrestrial liverworts. The gametophyte on the soil has the essential characteristics of terrestrial forms like *Marchantia*, except that it has not yet acquired the power to produce sexually there. If *Ricciocarpus* should acquire the power to produce sexually while on the land, it would become independent of the water.

A fungus belonging to the Ustilagineae frequently attacks the

young sporophytes, completely destroying them and filling the venter of the archegonium with a dense mass of the smut spores. These spores are so much smaller and so much more numerous than the *Ricciocarpus* spores that the infected sporophytes are recognized at a glance. Although the fungus enters the archegonium soon after fertilization, the young sporophyte continues to grow, apparently following the normal course of development up to the spore mother-cell stage, and even to the formation of spores. By this time, however, the mycelium and numerous spores of the fungus are tightly packed about the *Ricciocarpus* spores, which soon break down and are destroyed by the encroaching fungus (*fig. 40.*)

The life history of the fungi inhabiting various liverworts was carefully followed by Cavers (10). He states that the fungal hyphae usually grow down the neck of the fertilized archegonium, but they may pierce the venter and thus enter the sporogonium directly. In all cases where the sporogonium is invaded the relation of host plant and fungus is regarded as pure parasitism. Where the fungus penetrates only gametophyte tissue it may form a mycorrhiza, the host plant living as a saprophyte, the relation of fungus and host being apparently that of symbiosis.

I am under obligations to Professor J. M. Coulter and Dr. C. J. Chamberlain for suggestions and advice during this study.

SUMMARY.

1. When fruiting, *Ricciocarpus* is essentially a free floating plant.
2. The genus is strictly monoecious, though a small number of plants fail to produce archegonia.
3. Sex organs are produced in single definite groups as in *Asterella*, etc. Antheridia are produced on very young plants, which later produce archegonia and sporophytes.
4. The basal cell of the archegonium develops a structure which is partially imbedded in the storage tissue and acts as the physiological equivalent of the sporophyte foot in higher forms.
5. There is no rudimentary integument of the archegonium.
6. The diameter of the male nucleus is about one-half that of the female nucleus.

7. The first division of the sporophyte is transverse or oblique. The early subsequent divisions are irregular.

8. A large quantity of nutritive material is excreted into the capsule among the mother-cells.

9. There is no indication of elaters or sporophyte foot of any kind, which fact is associated with the aquatic habitat.

10. The fruiting period occurs in spring and occupies about ten weeks.

11. The gametophyte number of chromosomes is four, the sporophyte number eight.

12. Permanency of the water appears to be unfavorable to sexual reproduction.

13. Plants once established on the soil are usually unable to resume the floating condition, but under exceptional circumstances they may do so.

14. Vegetative plants hibernate at the bottom of the pond, producing new plants the following spring.

15. Rhizoids do not replace ventral plates, but are an addition to adapt the plant to a life on the soil.

16. The apical region is exceedingly plastic.

17. The sporophytes are frequently invaded and destroyed by a fungus belonging to the Ustilagineae.

LITERATURE CITED.

1. HOFMEISTER, WILHELM, On the higher Cryptogamia. Ray Society. 1862.
2. KNY, L., Ueber Bau und Entwicklung der Riccien. Jahrb. Wiss. Bot. 5: 364-386. pls. 44-46. 1867.
3. STRASBURGER, E., Die Geschlechtsorgane und die Befruchtung bei *Marchantia polymorpha*. Jahrb. Wiss. Bot. 7: 409-422. pls. 27-28. 1869.
4. FARMER, J. B., Studies in Hepaticae. Annals of Botany 8: 35-52. pls. 6-7. 1894.
5. FARMER, J. B., and REEVES, JESSE, On the occurrence of centrospheres in *Pellia epiphylla* Nees. Annals of Botany 8: 219-224. pl. 14. 1894.
6. LEITGEB, H., Untersuchungen über die Lebermoose 4: 1879.
7. CAMPBELL, D. H., Mosses and Ferns. 1895.
8. DAVIS, B. M., Nuclear studies in *Pellia*. Annals of Botany 15: 147-180. pls. 10-11. 1901.
9. KRUCH, O., Appunti sullo sviluppo degli organi sessuali e sulla fecondazione della *Riella Clausonis* Let. Malpighia 4: 403-423. pls. 17, 18. 1890.

10. CAVERS, F., On saprophytism and mycorrhiza in Hepaticae. *New Phytologist* 2: 30-35. 1903.
11. JANCZEWSKI, EDUARD V., Vergleichende Untersuchungen über die Entwicklungsgeschichte des Archegoniums. *Bot. Zeit.* 30: 377-393, 401-417, 440-443. 1872.
12. SCHIFFNER, V., Hepaticae. *Die natürlichen Pflanzenfamilien.* 1893.
13. BISCHOFF, Lehrbuch der Botanik. 1855.
14. FELLNER, FERD., Über die Keimung der Sporen von *Riccia glauca*. *Jahresb. Akad. naturwiss. Vereins in Graz.* 1875.
15. BOWER, F. O., A theory of the strobilus in archegoniate plants. *Annals of Botany* 7: 343-365. 1894.
16. CHAMBERLAIN, C. J., Mitosis in Pellia. *BOT. GAZ.* 35: 28-51. *pls. 12-14.* 1903.

EXPLANATION OF PLATES IX AND X.

The magnifications are as follows: *figs. 10 and 11*, $\times 600$; *fig. 20*, $\times 1600$; *figs. 21 and 35*, $\times ca. 2500$; *fig. 36*, $\times 850$; all others, $\times 1000$. In reproduction the drawings are reduced one-half.

FIG. 5. Diagram of cross section of dorsal furrow passing through a group of nearly mature antheridia.

FIG. 6. Diagram of cross section through group of archegonia; dotted lines indicate the limits of the starch-bearing tissue.

FIG. 7. Longitudinal section through the apex of a plant.

FIG. 8. Cross section through apical cell region.

FIG. 9. Horizontal section just below the apical cells with five rudiments of ventral scales.

FIGS. 10-11. Stages in the development of the archegonium before ventral canal cell is cut off; showing also development of tissue from basal cell.

FIGS. 20-21. Cutting off ventral canal cell.

FIG. 22. Archegonium nearly ready for fertilization.

FIG. 23. Fertilization; nuclei in contact, the male nearer to the eye in the section; egg with concave apex.

FIG. 24. Fertilization; starch grains in the plastids large and prominent.

FIG. 25. Fertilization further advanced; the male nucleus almost completely imbedded in the female nucleus, and the egg swollen out to fill compactly the venter.

FIG. 26. An unfertilized archegonium with egg and ventral canal cell degenerating.

FIG. 27. First division of the sporophyte by a transverse wall.

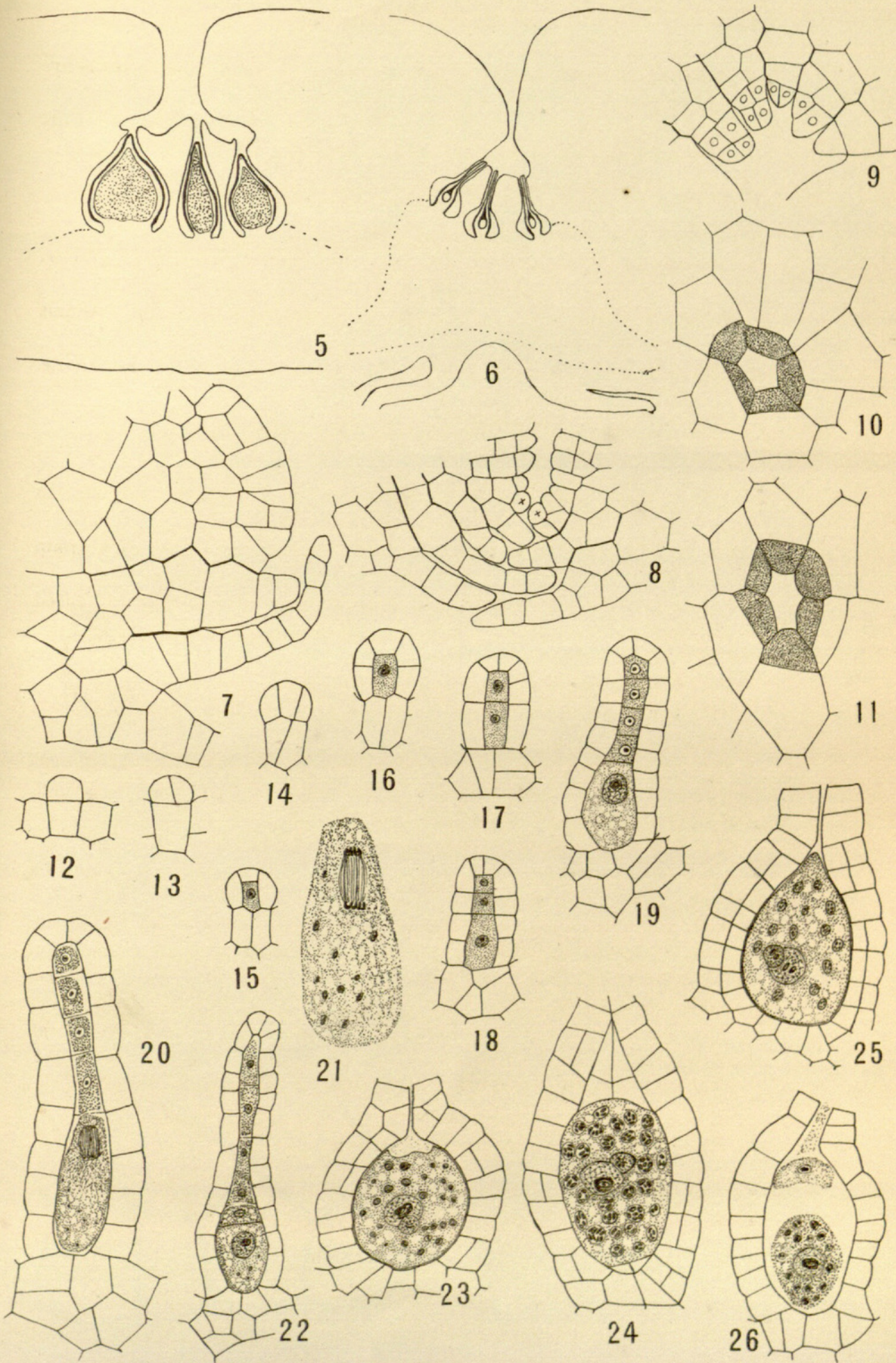
FIG. 28. First division of the sporophyte by an oblique wall.

FIG. 29. Four-celled embryo in form of quadrant.

FIG. 30. Four cells of embryo in a row.

FIG. 31. Older embryo in which quadrant can still be distinguished.

FIG. 32. Embryo beginning to form amphithecium.





Garber, John F. 1904. "The Life History of Ricciocarpus Natans." *Botanical gazette* 37(3), 161–177. <https://doi.org/10.1086/328464>.

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