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ERRATA

Page 12, 19th line from top, for mother cell of the embryo sac, read embryo sac cell.

Page 61, 9th line from top, for *megaspore*, read *megaspore mother cell*.

Page 77, 2d line from bottom, for **10** : *252*, read **30** : *221*.

Page 102, 6th line from bottom, for *and*, read *in*.

MEMOIRS
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THE
COMPARATIVE EMBRYOLOGY
OF THE
RUBIACEAE

BY

FRANCIS ERNEST LLOYD

ISSUED AUGUST 26, 1899

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I. INTRODUCTION

The following study was begun during the summer of 1898 in the laboratory of the Botanical Institute in München upon the suggestion and under the direction of Professor K. Goebel. Only a small beginning was made in München on account of a very brief visit—a few weeks only—to that city. Since then the work has been carried on in New York City.

In undertaking a comparative study of the embryology of the Rubiaceae it is expected to gain a knowledge of the life histories of a number of types sufficient to lead to a clearer understanding of the relationships between the genera of a very highly specialized and polymorphous family. It is intended at the same time to extend the studies into the supposedly allied families, and thus to contribute, if possible, to the solution of the more general problems of relationship among the higher dicotyledons.

In addition to the problems of phylogeny there are those which arise out of the physiological relations existing between the sporophyte and the gametophyte. Modern morphology has acquainted us with the main facts in regard to the process of antithetic alternation of generation in the higher plants, and the general physiological relations which are the outgrowth of interdependence of sporophyte and gametophyte. Out of this interdependence, however, a large number of phenomena of both a structural and physiological character have arisen, offering a field of investigation hitherto neglected, to a great extent, but which latterly has been attracting not a little attention. The phenomena of adaptation in this connection are not a whit less interesting if more difficult to observe. In the present study these adaptive phenomena, so far as the writer has succeeded in observing them, will be set forth. It may, however, very properly be borne in mind that these phenomena are chiefly those of nutrition, and the small

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size of the materials makes any other than morphological evidence difficult to obtain. For example, it is argued from appearances that enzymes or at least zymogens are present in the young endosperm, though that such is actually the case is not proven. Since, however, such substances have been shown to be present and have been extracted from, *e. g.*, the young date seedling * and since the action of the sucking organ of that plant on the hard endosperm is due to the ability to secrete the zymogens of a cellulose-dissolving ferment, we have a working basis for such interpretation.

The position here assumed that morphology must be regarded from a physiological point of view is the one emphasized in 1879, by M. Treub in the introductory part of his "Notes sur l'embryogenie de quelques Orchidées,"† where he expressed the hope that the readers of his paper would agree "que la manière dont les embryons absorbent les substances plastiques mérite certainement d'attirer l' attention, et sourtout d'être élucidées lors de recherches embryogéniques." That this point of view was not new with him, Treub took pains, in a detailed historical treatment, to indicate, though it remained for him to adduce the mass of evidence, embodied in the rich work above referred to, which completely substantiates the value of his position. To this historical review the reader is referred for an account of the growth of our knowledge of the suspensor. The succeeding part of the "Notes" deals with the origin, structure and function of the suspensor in eleven genera, including nineteen species of the *Orchidaceae*, in which forms the suspensor is shown to build up for the most part elaborate structures of a haustorial character which serve to absorb nutritive substances to be used by the embryo proper in its development. These structures, which attain the highest degree of specialization in *Herminium monorchis*, *Phalaenopsis grandiflora* and *Stanhopea oculata*, here take the form of tubes ("boyaux") which penetrate into the surrounding tissues of the ovule.

Two years later L. Guignard‡ ('81) published an account of his quite thorough studies on the embryology of the Leguminosae, in

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* F. C. Newcombe. Cellulose Enzymes, Ann. Bot. 13 : 49. 1899.

† Nat. Verh. d. K. Akad. van Wet. 19 1879.

‡ Recherches d'embryologie végétale comparée : Embryologie des legumineuses. Ann. sc. nat. Bot. VI. 12 : 5–166. 1881.

many species of which the suspensor attains a morphological character quite as striking as that in the *Orchidaceae*. In the *Viciae* especially the suspensor produces a great number of nuclei sometimes not separated by membranes (*Orobus*). Here, however, the endosperm is scanty and the complex suspensor appears to take its place. Guignard suggests that the principal function of the suspensor may be to contribute to the nutrition of the embryo, but admits at the same time that in certain cases the character of that organ indicates that it serves only as a means of attachment for the embryo.

It is of interest in passing to note that Schleiden and Vogel* ('38) saw the complex suspensor in *Lupinus rivularis*, but interpreted it as a development of the pollen tube in accordance with their then maintained view of the origin of the embryo.

The next work with a distinct physiological bearing dealing especially with the function of the suspensor was by S. H. Koorders† who, in 1892, investigated the embryology of the teak with especial reference to the behavior of the embryo in the matter of nutrition. In this plant a most remarkable condition occurs, which, while entirely analogous to that already found by Treub in certain orchids, was shown by Koorders to be morphologically different. The latter investigator found that the suspensor in its proximal, multicellular part is provided at the close of the "Kogelstadium" with "zuigblasen" or haustoria, which, however, are here special endosperm cells which attach themselves to the suspensor and elongate into tubular structures. Basing his inferences on the distribution of food materials in the ovule and embryo, which he found to be cuticularized till the cotyledonary phase was reached, Koorders concluded, also, that the embryo received nourishment through the agency of the suspensor until the appearance of the cotyledons, after which these organs, especially, are concerned in the absorption of foods through their peripheral membranes.

Touching more especially the rôle of the suspensor there appears to be no further work. The adoption of a similar point of

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* Beiträge zur Entwickelungsgeschichte der Blutentheile bei Leguminosen. Verhandl. der K. L.-C. D. Akad. d. Nat. **19** : 60. 1839.

† De Kiemotwickkeling van *Tectona grandis* (Djati). Natuurk. Tijdschr. voor Ned. Ind. III. **12** : 139. *pl. 1–8.* 1892.

view by workers on related matters has been productive of some important publications which we may now with profit glance at briefly.

The first paper, important in this connection, was published by M. Westermaier in 1892, entitled "Zur Embryologie der Phanerogamen insbesondere über die sogenannten Antipoden."* He embraced in his observations something like thirty four species of dicotyledons and monocotyledons, and found in the position and character of the antipodal cells and in the distribution of foodstuffs in the ovule, evidence that the view advocated by Vesque† that the antipodal cells are to be regarded as rudimentary, useless, and of only morphological worth is entirely insufficient to explain the facts, and that, on the contrary, we have here to do with a structure which, while in many cases small and apparently insignificant, are really of very considerable importance in the ultimate nutrition of the embryo. Latterly A. Osterwalder‡ ('98) by the study of *Aconitum Napellus* has established and extended Westermaier's view which he himself in a short note§ again expressed as the result of observations on *Alstroemeria* and other plants.

Mottier's ('93) observations on *Senecio aureus* || and Chamberlain's ('95) on *Aster Novae-Angliae* ¶ extended our knowledge of the antipodals by showing that in these two plants as in some other *Compositae* previously studied by others, a greater number of these cells occur than is usual. This multiplication of antipodal cells is of physiological significance, a view which is strengthened by the observations of D. H. Campbell ** ('99) on *Sparganium* and *Lysichiton*, in which these cells are numerous, reaching in the former the number of 150 at least. The author himself suggests that this great development probably indicates an important physiological rôle.

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* Verhandl. der K. L.-C. D. Akad. d. Nat. **56** : 1–39. 1892. (The literature previously published regarding the antipodals is found in this paper.)

† "Nouvelles recherches sur le développement du sac embryonnaire des phanérogames angiospermes." Ann. sc. nat. Bot. VI. **8**: 294. 1879.

‡ Beiträge zur Embryologie von *Aconitum Napellus* L. Flora **85**: 254. 1898.

§ Westermaier, Max. "Historische Bemerkungen zur Lehre von der Bedeutung der Antipoden-Zellen." Ber. d. D. B. G. **16**: 214–216. N. 1898.

|| Bot. Gaz. **18** : 245. Jl. 1893.

¶ Bot. Gaz. **20** : 205. My. 1895.

** Bot. Gaz. **27** : 153. Mr. 1899.

The work of perhaps the most interest which has recently appeared is that of Dr. Gabrielle Balicka-Iwanowska † ('99) who has studied the behavior of the embryo-sac in the Scrophulariaceae, Gesneraceae, Pedalinaceae, Plantaginaceae, Campanulaceae, and Dipsaceae. All these forms possess a more or less thickened single integument. Micropylar and chalazal haustoria, which are here for the first time shown to be of endospermic origin, penetrate more or less deeply into the integument which, under such conditions, is said to be devoid of any vascular tissue. Those plants which possess the thickest integument have the most highly developed haustoria, and these in turn have nuclei whose size and appearance show them to be active in nutrition. Their limiting membranes, moreover, are quickly "gelatinized" or become "mucilaginous." The haustoria, in some cases, reach the funicle (*Torenia*) and even the placenta (*Scoparia*). In many species a special nutritive tissue is found in the chalazal region of the ovule and the haustorium is for the most part in direct relation with such tissue. The author does not regard the "tapetes" as merely protective to the embryo-sac, as Hegelmaier held, but holds that they probably secrete a ferment and exercise a digestive function. The antipodal cells, when present, are regarded as having only a less important mission, and are at best evanescent.

While Dr. Balicka-Iwanowska's paper was in preparation at München, Mlle. M. Goldflus* ('99), was engaged in the laboratory of the University of Geneva, in a similar investigation with especial reference to the *Compositae*. Her conclusion as to the physiological value of the "epithelium," the "tapetes" of Balicka-Iwanowska, agrees with that of the latter, an opinion favored, though not fully subscribed to, by Schwere. She furthermore attributes to the antipodal cells considerable importance as agents in nutrition. These cells attain in some of the species studied a considerable size (*Leucanthemum lacustre*, *Chrysanthemum Leucanthemum*, *Helianthus Maximiliani*) and are interpreted as a haustorium (suçoir) inasmuch as they penetrate the axial part of the ovule, and stand in relation with a mass of conductive tissue which

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† Contribution à l'étude du sac embryonnaire chez certain Gamopetales. Flora, **86**: 47. 1899.

* Sur la structure et les fonctions de l'assise épithéliale et des antipodes chez les Composées. Jour. de Bot. **12**: 374. 1898; **13**: 9, 47, 87. 1899.

in turn is in a similar relation with the vascular bundle. Mlle. Goldflus bases her opinion not alone on the position of the antipodals, for she finds in the cyanophily of these cells evidence that they represent "l'intermediaire entre le sac embryonnaire et les substances digestibles élaborées par l'ovule."

The *Rubiaceae* in particular have received very little attention. Schleiden * appears to have been the earliest observer whose observations may be regarded as pertinent to the present work. He described the ovule in the *Rubiaceae* as anatropous (gemmula anatropa) and as consisting of a naked nucellus (nucleus nudus), *i. e.*, without any integument (p. 304, *l. c.*). As Warming † points out, it is easily understood how the single thick integument with the very delicate micropylar canal would have misled the earlier observers. These results seem to have remained without modification till the appearance of his "Grundriss," ‡ in which, however, it is further stated (p. 163) that in many *Rubiaceae* the integument remains at least as a thin skin which clings to the endosperm, from which it easily falls off in tatters, as in *Coffea.*

The work of Hofmeister, § as is well known, covered a very large field, and of necessity the treatment of any given group was relatively brief. The results of his work on the *Rubiaceae* are quite brief and faulty. It would, however, be very unfair to criticise him, on account of the difficulties presented by the materials, especially in view of the methods then used, methods which, by the way, in the hands of a master like Hofmeister gave surprising results. According to this pioneer in embryology the antipodals are absent from *Galium*, *Asperula* and *Crucianella*, in which the embryo-sac is attenuated and swollen at the micropyle end. The embryo-sac is quickly filled with endosperm after fertilization has taken place. Within the endosperm, the proembryo develops by forming transverse walls. The cells of a filamentous structure thus formed produce numerous branches made up of short series of cells of which the outer-

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* Einige Blicke auf die Entwickelungsgeschichte des vegetabilischen Organismus bei den Phanerogamen. Wiegmann's Archiv. 3 : 289, 414. 1837.

† De l'ovule. Ann. sc. nat. Bot. VI. 5 : 177. 1878.

‡ Grundriss der Botanik. Leipzig. W. Engelmann, 1850.

§ Neure Beobachtungen über Embryobildung der Phanerogamen. Pringsh. Jahrb. 1 : 82. 1858.

most is rounded and swollen. The cells from the middle of these branches send out secondary branches here and there, so that the proembryo as a result of this richness of branching simulates a bunch of grapes. Out of the lower end of this mass projects the primary cell row of the proembryo whose terminal cell develops into the embryo proper. Thus Hofmeister's description of the suspensor in the genera above named, one in the main correct, but requiring modification, as will hereafter be seen. He passes over without criticism and accepts as final the opinion which he attributes to Schleiden that the endosperm breaks through the integument.

In *Houstonia* and *Spermacoce* the embryo-sac is of less slender form and somewhat cylindrical, and here, on the other hand, the antipodal cells are present. The embryo-sac is here also soon filled with endosperm, although the proembryo remains a very simple thread of cells from the last of which the embryo proper arises.

It is unfortunate that no figures of these forms are given so that it is difficult to estimate exactly the value of the author's descriptions.

The only other plant of the *Rubiaceae* which has received any attention is the coffee (*Coffea arabica*), but such work as has been done does not touch upon the ground of the present paper except in a remote way. An account of the literature of this subject may be found in the footnotes of an article by T. F. Hanausek.*

I desire at this point to express my appreciation of the kindness of Professor Ignatius Urban in putting the collection of growing *Rubiaceae* in the Botanical Garden at Berlin at my disposal, and my gratitude to Professor K. Goebel for his generosity in extending to me the courtesy of the laboratory and gardens of the Botanical Institute in München during six weeks of the summer of 1898, and in expending much of his own time in discussion and suggestion when he could ill afford, on account of pressing duties, to do so.

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* Ueber symmetrische und polyembryonische Samen von Coffea arabica L. Ber. D. B. G. **13**: 73. 1895.

II. DESCRIPTIVE

Vaillantia hispida

Vaillantia is a small genus of the *Galieae* containing only two annual species, indigenous to the Mediterranean region. The plants are monoecious; the flowers are borne in threes supported by a single broadened spiny stalk. Of the three the middle is pistillate, the two lateral staminate. The three-flowered peduncles are in four vertical rows alternate with the four rows of leaves. The regularity and perfect radial symmetry of the species studied render it easy to section a growing tip so as to cut all the ovules of two opposite rows longitudinally.

The material was obtained at the Botanical Garden at Berlin.

THE ORIGIN AND DEVELOPMENT OF THE NUCELLUS

At the period of the development of the pistillate flower when the four corolla lobes have met above the hollowed out receptacles and overarch the stamens, which are as yet merely rounded knobs at the angles of the sinuses of the corolla, four elevations lying in the same vertical plane make their appearance near the base of the ovary. The outer two of these are ridge like, and by their mode of growth meet later in the transverse plane, fuse, extend upwards to form the two styles, and downward to form a partition which divides the originally unilocular ovary into two chambers. The two others are papilliform and lie on either side of the center of the floor of the ovary. These are the nucelli. As they develop, the partition above referred to passes down between them and separates them. The lower edge of the partition finally fuses with the tissues between the funicles of the two ovules, making the ovary bilocular.

We may now turn our attention to the nucellus. For a short time its growth is directly upwards. (Pl. 1. Fig. 1.) There is a well marked epidermis, and the cells are quite filled with dense cytoplasm and large nuclei. More rapid cell division upon the inner side, however, soon causes the apex of the nucellus to be directed toward the floor of the ovary. When the bending of the ovule is complete, and its definitive condition reached, the micropylar end of the ovule lies in a lower horizontal plane than does the base of the funicle. The micropyle and embryo-sac lie in a curved line, and the funicle remains short. The ovule is therefore not of the strictly anatropous type, but is campylotropous, approaching the anatropous condition. (Pl. 3. Fig. 1.) During the process of inversion the longitudinal axis comes, of course, to lie in the horizontal plane, and about this time a number of the hypodermal cells under the apex of the nucellus elongate in a direction parallel with the longitudinal axis of the nucellus. (Pl. 1. Fig. 2.) These cells, about 12 in number, constitute the archesporial tissue, and are recognizable at first only by their size. Their subsequent changes will be described below. The large number of sporogenous cells here found to constitute the archesporium recalls the condition in *Rubus caesius*, *Geum strictum* and *Sanguisorba officinalis*, in which, according to A. Fischer* ('80) numerous sporogenous cells arise. A similarly large number of these cells has also been found in *Casuarina*,† in *Loranthus*‡ and in *Ranunculus*.§ This character, which appears in several widely separated families is probably therefore not to be regarded as a persistent primitive character in the Rubiaceae at any rate, but one having a physiological meaning, as will be shown later. The sporogenous cells now elongate, and their elongation is accompanied by periclinal division in the epidermis and subadjacent cells of the tissue about the apical part of the nucellus. (Pl. 1. Fig. 3.) Only in the columnar epidermal cells immediately beneath which lie the sporogenous cells there occurs no division, periclinal or otherwise. These, therefore, remain as a cap of cells, about which arises the integument at first as a low ridge, but gradually growing over the nucellar cap and forward so as to form a canal which I shall call the micropylar canal, the outer end of which forms, in the definitive ovule, the micropyle.

The manner in which the integument has its origin recalls vividly the figures by Warming || ('78) of the nucellus of *Thesium*, one of the *Santalaceae*. In the body of the paper the author asks the question "Are these ovules in which the nucellus is not cov-

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* Jenaisch. Zeit. f. Nat. **14** : 122. 1880.

† Treub, M., Ann. de Buit. **10** : 145. 1891.

‡ Treub, M., Ann. sci. nat. Bot. VI. **13** : 274. 1882.

§ Coulter, Bot. Gaz. **25** : 73. 1898.

|| De l'ovule. Ann. sc. Nat. Bot. VI. **5**: 177. 1878.

ered by an integument," and recounts the forms in which, according to earlier students, the nucellus is naked. Some reference to this point has already been made in the introduction. In endeavoring to contribute to the answer of the question, Warming studied the development of the nucellus in the type above mentioned, and found that the epidermal cells at the apex of the nucellus, and therefore, those which cap the elongated cells which lie in the axis of the structure, have contents more granular than the remaining epidermal cells, and also that the epidermal cells surrounding these capping cells divide tangentially and "il se développe ainsi une assez forte couche de cellules de provenance épidermique qu'on doit considérer comme un tégument." His description with the exception of the reference to the more granular contents of the middle epidermal cells is exact enough to apply to the *Galieae*, and one cannot resist the conclusion that his interpretation of this collar of tissue as a rudimentary integument is correct. Guignard,[*] seven years later, published a fuller account of the behavior of the nucellus and embryo-sac of *Thesium* in which, however, he entirely overlooked Warming's work and suggestion. Guignard here makes no reference to the tangential divisions seen by Warming, nor does he show any such in his figures. Indeed he takes the position (p. 189, l. c.) that there is no integument at all in *Thesium*, though it must be said that in making the statement he is referring to the seed, rather than to the young ovule.

The bottom of the micropylar canal is formed of the few epidermal cells capping the archesporium (Pl. 1, Figs. 5, 6, 8). The walls also are formed by an epidermis continuous with and having its origin in the outer epidermis of the ovule. The endodermis[†]

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[*] Observations sur les Santalacées. Ann. sc. nat. Bot. VII. **10**: 181. 1885.

[†] This layer has its homologue in the Compositae in the inner cell-layer of the integument which, according to Hegelmaier (Ueber die Keimsack einiger Compositen und dessen Umhüllung. Bot. Zeit. **47**: 805, 821. 1889), comes to surround immediately the embryo-sac after its absorption of the nucellus is complete. For this layer Hegelmaier proposed the term *endodermis*, the types under observation and figured being *Helianthus annuus*, *Bidens leucantha* and *Zinnia tenuiflora*. Schwere (Zur Entwickelungsgeschichte der Frucht von *Taraxacum officinalis* Web. Ein Beitrag zur Embryologie der Compositen. Flora **82**: 32. 1896), however, working on *Taraxacum officinalis*, regards the layer surrounding the embryo-sac as having its origin in the outer cell-layer of the nucellus, "bei *Taraxacum* gehört diese Schicht thatsächlich zum Nucellus," a conclusion which is out of harmony with the prevailing view. For this

thus formed does not, however, have the specialized character which has been found to be so common in the *Gamopetalae*. It is not cutinized, and, as will be seen, breaks down very readily under the action of the developing embryo-sac.

Meanwhile the archesporial cells are undergoing considerable changes which will now be described.

At the time of rapid elongation of the nucellus, the archesporial cells, too, increase in length. This is accompanied by a good deal of change in the appearance of their cytoplasm and nuclei. The cytoplasm which at first and for some time is granular, becomes more and more fibrous in appearance. The fibers run approximately lengthwise. The granular character is still visible, but the stringiness becomes more marked as the cells themselves elongate (Pl. 1, Figs. 3–8). When they reach their maximum length they are spindle-shaped and appear to run under and above each other in a most perplexing fashion. Their separating membranes become less and less distinct, until they cannot be made out, and I believe them to be almost, if not entirely, absorbed. The nuclei, too, rapidly increase in size, while the chromatin, granular at first, runs through various changes, unnecessary to describe here, which are preparatory to mitosis.

It should be pointed out here that the nucellar tissue next to the archesporial tissue on its inner side is made up of cells which lengthen much more than those of the rest of the nucellus (Pl. 1, Fig. 5). The innermost of these are, indeed, as a usual thing, as long as the archesporial cells and appear to partake to a great degree of their characters. That the nucellar cells next to the archesporial cells may approach the latter in character has been noted by Coulter (l.c.) in *Ranunculus*. They may without doubt be regarded as underdeveloped sporogenous cells, which in this case disintegrate, while their substance probably contributes to the growth of the archesporium.

When the archesporial cells as above mentioned have reached

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layer he proposed the term *endothelium*, a term which is evidently inappropriate. Schwere's figures as to this detail are very unsatisfactory and unconvincing, while it is quite evident from Hegelmaier's drawings that the layer to which he gave the name *endodermis* is in reality what he thought it to be. This layer is, moreover, an *inner* layer, so that *epithelium*, the term adopted by Mlle. Goldflus, seems to me a less appropriate term, because more general.

their greatest elongation, mitosis takes place. I shall take the opportunity of describing the cytological details in a separate paper. For the present purpose it is enough to say that so far as my own observation goes four megaspores result from the division of each primitive cell. The appearance of the mass of cells which results from the division of the archesporial cells is very similar to that presented by similar cells arising in the same manner in *Helianthemum Rhodax* as described and figured by A. Fischer* according to whom two or three "mother cells" are in this form cut off, which divide each into four or sometimes six daughter cells (megaspores) one only of all these resultant cells becoming the mother cell of the embryo-sac, the rest suffering disorganization.

Several or all of the archesporial cells may divide; thus may many megaspores arise, among which there is a considerable discrepency in size (Pl. 1, Fig. 9). Of one quartette arising from one mother cell, the lowest cell may be the largest; in another, one of the middle ones; then again the uppermost may be the largest. I have not been able to determine whether there is any constancy in the selection of a megaspore to be the mother cell of the embryo-sac. The appearance of such material as I have examined seems to favor the opinion that any one of them, but more especially one of the end cells of the quartette, may be chosen.

As a rule only *one* of all the megaspores actually germinates. Exceptionally in other genera to be hereafter described, I have found two embryo-sacs completely formed and lying parallel; one of these usually lies farther forward than the other, and this one is functional.

THE DEVELOPMENT OF THE EMBRYO-SAC

At the completion of megaspore formation, the chosen megaspore commences a migration along the micropylar canal formed as above described by the forward growth of the integument. This migratory movement of the functional megaspore appears to be unique, for I have not been able thus far to find any reference in the literature which shows that such migration has hitherto been observed. The cap of epidermal cells which overlies the archesporium

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* Zur Kenntniss der Embryosackentwickelung einiger Angiospermen. Jenaische Zeitschr. **14**: 90. 1880.

seems to be a barrier to any such migration, for the migrating megaspore, so far as I have been able to determine, pushes its way to one side, as shown in Pl. 2, Fig. 1. It is reasonable to conclude that these capping cells are in a short time destroyed, for in later stages they are not usually seen. I have seen these cells once in one species of *Galium*, when the embryo-sac was mature.

The nucleus of the migrating megaspore, after passing this barrier, comes to lie in the micropylar canal about midway its length, while the accompanying cytoplasm lies in a thin layer on the walls of the canal, and so forms a large vacuole at each end of the nucleus. The whole megaspore is, roughly speaking, hour-glass-shaped (Pl. 2, Fig. 1), and its nucleus lies at the constriction. The enlarging megaspore encroaches laterally on the integument, which now for the first time is broken down. The endodermis gives way first, and is recognized a little later only by collapsed walls and the nuclei, which are the last elements of the cells to disintegrate. The persistence of nuclear substance under the action of digestive ferments suggests that the tissue which behaves thus is undergoing digestion. This is the view taken by Mlle. Goldflus (*l. c.*) in describing the behavior of the integumental tissue about the base of the embryo-sac in the *Compositae* the internal part of which is dissolved by "ferments secrétés probablement par les cellules epithéliales."

At the constriction in the hour-glass-shaped megaspore the first division of the megaspore nucleus takes place, after which one of the daughter nuclei passes forward to the micropylar end of the cavity. When it reaches this point the second division takes place in both nuclei (Pl. 2, Fig. 2). There are now four. The egg apparatus arises in the usual fashion at the micropylar end (Pl. 2, Fig. 3, 4). In the antipodal region a more unusual state of affairs occurs.

THE ANTIPODAL APPARATUS

The division of the antipodal nuclei, now two in number, results in four, one of which is, in the usual manner, concerned in the formation of the endosperm nucleus. This passes forward to coalesce with the corresponding nucleus from the egg region. Of the three which remain, one enlarges considerably and migrates backwards towards the chalazal region. Its proper cytoplasm becomes cut off by a transverse wall from the upper part of the embryo-sac (Pl. 2, Fig. 4). The other two antipodal cells surround themselves by walls, and take ultimately a lateral position. They are small and unequal in size and are usually more or less collapsed and apparently of little or no further value ; and they overstain in the manner of disintegrating cells. Not so, however, with the odd, basal antipodal, for in these forms (*i. e.*, *Vaillantia*, *Galium*, etc.), it appears to have a distinct and important physiological rôle.

It has been supposed, since the publication of Hofmeister's classical researches on the embryology of the Phanerogams (*l. c.*), that antipodals were absent in those forms of the *Rubiaceae* studied by him, excepting *Houstonia* and *Spermacoce*. I have confirmed Hofmeister's view as to *Houstonia*, but in addition I am prepared to show that antipodal cells are present in all *Rubiaceae* up to this time studied by me. The smallness of the structures in these plants, and especially the attenuated character of the basal antipodal, together with the similarity of the other two to the adjoining disintegrating integumental cells will readily account for the oversight.

The basal antipodal cell is composed at first of cytoplasm which is tenuous, scanty and difficult to see. The nucleus comes to rest on one side of the cavity some distance removed from the transverse wall.

Gradually the cytoplasm becomes more pronounced, stains more deeply and fills the elongating chalazal end. The apex becomes somewhat expanded into a knob which, as the cell lengthens, is plunged into the mass of megaspores. These are still evident, but are now on the way to disintegration as is attested by the fact that they lose all structure and become black and opaque with haematoxylin, often making it very difficult to recognize the apical, knobbed part of the long antipodal. At the time when the basal antipodal is first cut off, there is a large mass of proteinaceous food in the place of the once archesporium, which as just stated, stains very deeply. As the embryo-sac as a whole reaches maturity, before the flower opens, the cytoplasm about the endosperm nucleus becomes abundant and dense, and the archesporial food-mass is coördinately reduced, while the basal antipodal shows its maximum development during this period. The probe-like end, which, I believe, serves as a haustorium, at this time and somewhat later is filled with cytoplasm which appears finely reticulate, while the broad end which is adjacent to the upper part of the embryo-sac is occupied by a large vacuole. This large antipodal must, therefore, stand in an important relation between the food supply derived from the archesporium and the endosperm cell, and is probably active in the transportation of the food from the former to the latter. The megaspore mass thus forms a sort of nutritive tissue, partly analogous to that described by Dr. Balicka-Iwanowska (*l. c.*) as occurring in the region of the integument near the lower ends of the embryo-sac in the forms studied by her.

The archesporial tissue is now seen to bear a nutritive relation to the embryo-sac, which by this time has reached maturity.

THE DEFINITIVE EMBRYO-SAC

We may now pause to sum up the characters of the mature embryo-sac.

In shape it is fusiform and much attenuated at the lower end. The upper part, comprising one third or more of the entire length, contains the egg apparatus and the endosperm nucleus, and constitutes the expanded part of the embryo-sac. The fusion of the polar nuclei takes place at about the middle of this part of the embryo-sac, but at the time of fertilization the resultant nucleus comes to lie immediately against and partly surrounding the egg nucleus. The migration of the endosperm nucleus has been noticed by Mme. Balicka-Iwanowska (l. c.) in *Digitalis* and other related forms in which the embryo-sac is more or less attenuate. At the time it reaches the egg, the nucleolus has nearly three times its original diameter. Its size relative to that of the egg nucleus is shown in Pl. 2, Fig. 8a. The nucleus itself is larger than the egg nucleus, but the discrepancy in size is more striking between the nucleoli. This movement and growth of the endosperm nucleus must be interpreted physiologically; it is in all probability in some way connected with the nutrition of the egg.

The antipodals are three in number; two of these are small and relatively inconspicuous; the third and basal, is very long, being on the average about two thirds the length of the whole embryo-sac, though it may, in exceptional cases which I have noted, attain a considerably greater length. At its expanded upper end it is separated from the upper region of the embryo-sac by a very thin transverse wall. Its lower end is somewhat knobbed, and is embedded in a mass of degenerating megaspores. The position of the nucleus of this antipodal is always lateral and about one fourth to one half the cell's length from the upper end (Pl. 2, Figs. 7–11). It is large and prominent, and evidently active. Its function has already been discussed. The fate of the antipodals will be discussed somewhat later.

DEVELOPMENT OF THE EMBRYO

After the egg is fertilized, its vacuole enlarges considerably, pushing the cytoplasmic end rather more deeply into the endosperm stuff. Immediately the endosperm nucleus commences to divide so that before the first division of the fertilized egg takes place 20 to 30 endosperm nuclei are present (Pl. 2, Fig. 10). The proembryo now grows rapidly by the successive occurrence of approximately transverse divisions. When about five cells have been formed, the proembryo becomes bent to one side and the other. This is due to the lateral enlargement of certain of the suspensor cells, as a result of which they bulge out into the endosperm which is now of some bulk. In these enlarging suspensor cells, the cytoplasm becomes vacuolated to a considerable degree. These facts and later developments indicate that these cells are concerned in the absorption of foods in solution from the endosperm, which, however, is not broken down by the enlarging suspensor cells. The cells of the end of the embryo away from the micropyle are always smaller during the earlier development of the proembryo, while they get successively larger toward the micropylar end where the basal cell tapers off acutely, giving the young proembryo something of a spindle shape (Pl. 4, Figs. 1, 2).

When the proembryo attains the number of about six cells, longitudinal divisions occur in some of the suspensor cells. The divisions sometimes occur in two planes, and the resulting elements continue to grow and bulge out further into the endosperm and form haustorial appendages. In some cases when two longitudinal divisions have taken place in a single suspensor cell, a pair of the resulting quadrants grow out together, forming double haustoria (Pl. 4, Fig. 5). Again the haustorial cells may divide transversely ; this occurs only in the region near the embryo proper.

These haustoria, for such I regard them, are at first pronouncedly vacuolated, but as the embryo ages the vacuolation disappears, and they become densely filled with cytoplasm. After the embryo proper begins its development, the basal suspensor cell elongates considerably, increasing its length by a half and becomes less vacuolated. Its micropylar end becomes crushed by the growing endosperm, which now begins to grow into the micropylar part of the thickening integument, leaving the embryo in a more central position (Pl. 4, Figs. 9, 10). Later, the basal cell and even one or two of its neighboring suspensor cells become disorganized, but the time at which this occurs is not constant, for while I was not able to find these cells in the preparations from which Figs. 5 and 6, Pl. 4, were drawn, I did find them in another specimen of such an age as the one shown in Pl. 4, Fig. 7.

After the embryo proper has differentiated itself from the suspensor, the latter may be seen to be divided clearly into two regions which differ very markedly in structure. These two regions may be termed the micropylar and embryonal. The latter is made up of half a dozen disc-shaped cells which are very much flattened longitudinally, and show no outgrowths and are not vacuolated, and they remain so during the entire embryonic history. The cells of the micropylar region, on the other hand, become larger and thus increase their absorbing surface. When they reach their maximum development the suspensor when dissected out resembles a "bunch of grapes." These outgrowths, to which we have ascribed a haustorial function, are not unlike the suspensorial haustoria (Keimträgerblasen, boyaux) described by Treub in the *Orchidaceae* and by Hofmeister* ('49) and Guignard (*l. c.*) in *Sutherlandia*, and are analogous to the "zuigblasen" occurring in the teak (*Tectona grandis*) described by Koorders ('92). The upper part of the micropylar region, as shown above, becomes less important and is finally lost by absorption, so that the embryo

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* Die Entstehung des Embryo der Phanerogamen. Leipzig, 1849.

with its suspensorial haustoria, to which it is attached by the short row of disc-shaped cells, comes to lie entirely within the now large mass of endosperm (Pl. 4, Figs. 9, 10). The structures above described are probably to be regarded as an adaptation for the ready absorption of food for the rapid growth of the embryo. The shortness of the cells of the embryonal region of the suspensor favors the passage of food to the embryo. Whether or not the embryo is capable of absorbing food through its own surface is a question which I am unable to answer at this time. Koorders ('92), working on *Tectona*, found that the embryo till the completion of the "Kogelstadium" possessed cuticularized walls, thus preventing the absorption of food. If this be true of *Vaillantia* and its close relatives, we have a complete explanation of the significance of the haustoria. But even if the embryo is not cuticularized, it is not improbable that the amount of absorbing surface on the embryo proper alone is insufficient for its rapid development, and it may be that in this lies the explanation of many features in other forms not yet cleared up. For example, I have found that the basal cell in *Capsella*, figured years ago by Hanstein, and copied in almost every text-book, actually pushes its way into the adjacent tissue of the inner integument in the same manner that the embryo-sac itself, by its growth, in many cases encroaches upon the surrounding tissue. This fact indicates that the suspensor, in forms in which it reaches so pronounced a development, as in the *Cruciferae*, *Tropaeolum* and others, is of importance in absorbing nourishment, an opinion which we must credit to Meyen ('39).* I believe this action of the suspensor in the surrounding tissue to be correlated with the rapid growth of the embryo in *Capsella*. Before drawing any conclusions of this kind, however, it will be necessary to obtain many more data.

There can be little doubt that the rapid development of seeds is an important adaptive feature, and the study of structures which are correlated with this ability will be a fertile field for further study. Such haustorial structures as those found in the *Orchidaceae* may be correlated with the meagre integument which means a meagre store of food immediately at hand.

The further development of the embryo, which brings the

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* Neues system der Pflanzen-Physiologie 3: 331. 1839.

cotyledons into view, is accompanied by the dissolution of a zone of endosperm surrounding the embryo. The cells become mucilaginous, and the embryo is bathed in nutrient substance. The relative increase of absorbing surface by the development of the cotyledons is accompanied by the gradual loss of the haustoria of the suspensor, of which there may be found, at the time of the ripening of the fruit, only a few of the disc-shaped cells. The last of these plays a small part in the formation of the radicle

THE INTEGUMENT

The earlier development of the integument has already been described. Some time before complete maturity of the embryo-sac is reached the cells which form a zone (*d*, Fig. 1, Pl. 3) about the attachment of the funicle to the ovule become large and rounded (Pl. 3, Fig. 1, *d*) and their contents become strongly vacuolated. These cells contain a good deal of starch at quite an early condition of the ovule, and when the accumulation of starch in the integument commences, the process has its beginning here. At the end of the vascular bundle when it reaches this zone of enlarged cells, is found a mass of cells which gives the bundle a club-shaped appearance in longitudinal section. These cells, like those of the leptome of the bundle, are rich in contents, and form a center for the distribution of food, which is received by the large-celled zone above referred to, the function of which appears to be the preparation of food and the regulation and distribution of the supply to the meristematic zone. The latter is made up of smaller cells (Figs. 1*b*, 1*c*, Pl. 3), in which, after fertilization multiplication begins. Their dividing walls are periclinal, and there results a rapid thickening of the integument, with a corresponding increase of the ovary wall, accompanied by secondary changes leading to the formation of a schizocarp. Within the meristematic zone the integumental tissue shows signs of disintegration, and this process appears to be as rapid and complete in the tissue surrounding the basal antipodal as in that about the endosperm region. We may notice in this connection that the mass of disintegrated megaspores has after fertilization and before the first division of the proembryo almost disappeared (Pl. 2, Fig. 9; Pl. 3, Fig. 3) and the antipodal cells are difficult to see. In some genera they persist for some time, and vestiges may be seen after a large mass of endosperm has been formed. After the megaspore mass is absorbed, the basal antipodal appears to have no further function.

When the embryo starts to develop a small amount of starch is found in the integument, principally in those cells above referred to which form a zone between the funicle and the meristem of the integument. A very few granules are also to be found in the cells immediately about the embryo-sac. As the seed approaches maturity the starch accumulates first in the peripheral cells until all those cells of the integument which remain are replete.

THE GROWTH OF THE ENDOSPERM

During the first division of the endosperm nucleus the endosperm enlarges, becoming rounded, and encroaches upon the adjacent tissue of the integument, the cells of which become flattened and give way. At first, separating walls between the cells are not formed. The nuclei are not parietal, nor do they ever become so. The endosperm mass is always solid. A little later the parietal cells become much more densely filled with cytoplasm and stain more deeply (Pl. 3, Figs. *2b*, *2c*). This is especially true of those cells on the side of the endosperm mass facing the longitudinal axis of the ovary, which are the earliest to become dense. It is on this side that the thickness of the integument is the greatest and where the food is most abundant. After the endosperm approaches its limit of growth, these are the last of the peripheral cells to lose their dense character. The inner cells of the endosperm are strongly vacuolated, the vacuolation becoming more pronounced towards the center, where the cells ultimately break down and leave a cavity within which lies the now rapidly maturing embryo. The peripheral cells are digestive, I believe, and absorptive, for the integuments break down in advance of the growth of the end osperm, and the cell walls of the disorganized cells become thickened. These thickened walls stain readily and deeply with safranin, while the walls of the normal cells show much less affinity for that stain.

As the endosperm ages it becomes concave on its inner face, and dipping into the concavity is a mass of integument which remains undigested at the maturing of the fruit. (In Pl. 3, Fig. 2.) This mass is continuous with a thin layer of integument two cells in thickness, which surrounds the endosperm. The latter does not, contrary to the opinion of Hofmeister, break through the integument, so that the envelopes of the mature fruit consist of the wall of the ovary lined by an integument (Pl. 3, Figs. *2*, *2a*) two cells thick and loaded with starch. The endosperm cells up to a time when the embryo is large and approaching maturity, have thin walls. Starch accumulates more and more till the cells are gorged. Just before the complete maturity, however, the walls thicken so that in the mature seeds the principal foods stored in the endosperm are reserve cellulose* and starch.

The central part of the endosperm is, up to the completion of the sphere stage of the embryo, continuous, so that the embryo lies in direct contact with the endosperm cells. When, however, the cotyledons begin to appear, the endosperm immediately surrounding the embryo breaks down, so that the embryo comes to lie freely in a cavity which is filled with fluid materials. The behavior of the endosperm in this regard, as also the integument during the advance of the endosperm upon it, indicates the presence of digestive agent secreted by the embryo on one hand and by the endosperm on the other.

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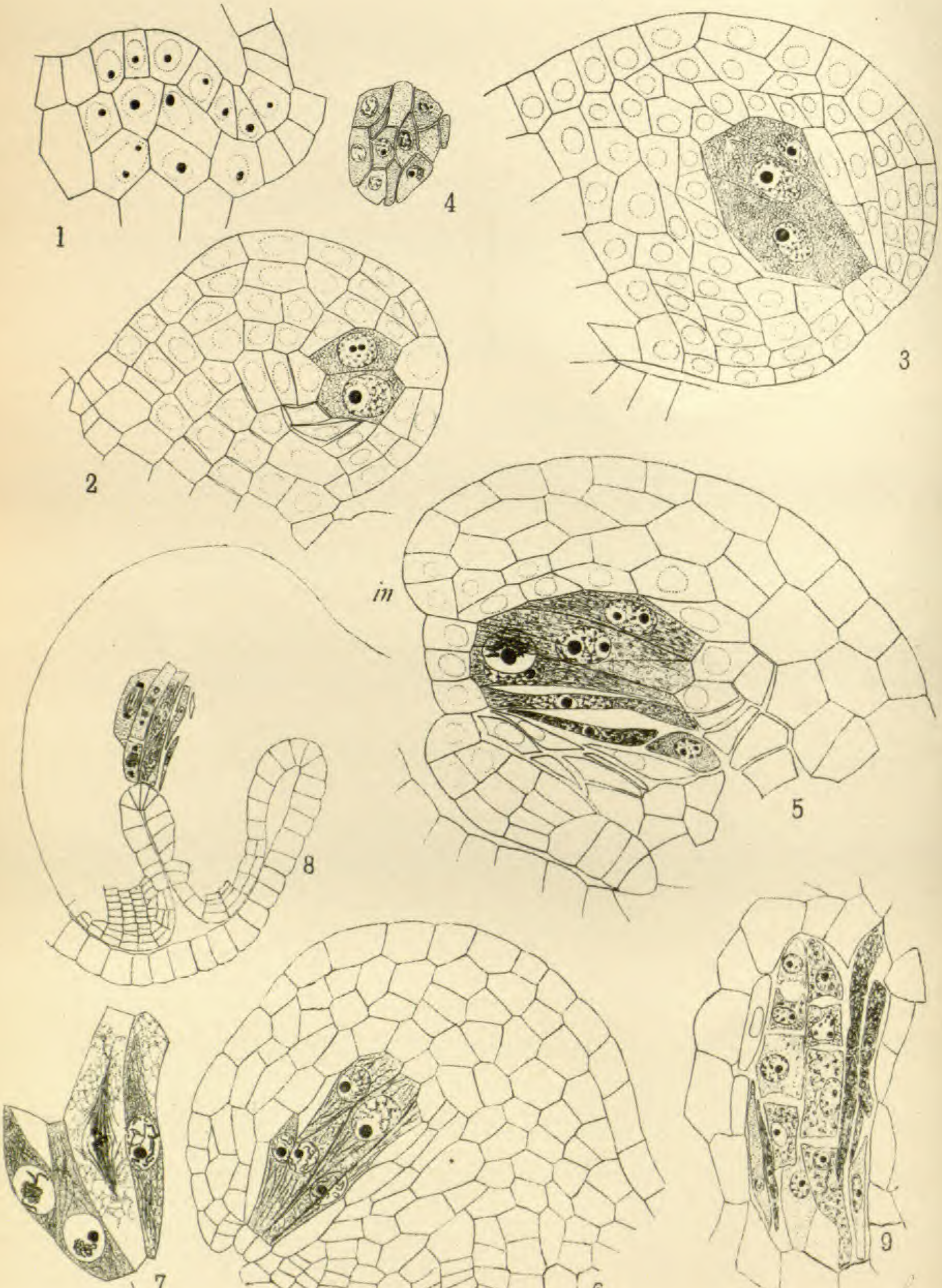
*The term 'reserve cellulose' is used here provisionally. The exact nature of the substance in the *Galieae* is, I believe, not yet determined.



VAILLANTIA HISPIDA

THE HELIOTYPE PRINTING CO., BOSTON.

Explanation of Plate I

Fig. 1. The fundament of the nucellus, × 670.

Fig. 2. The archesporial cells, of which only two are seen in the section, have begun to be differentiated. They apparently underlie only one epidermal capping cell.

Fig. 3. The archesporium more strongly developed. The periclinal divisions about the capping epidermal cells mark the beginning of the growth of the integument.

Fig. 4. Transverse section through archesporium; it is composed in this instance of twelve cells, × 670.

Fig. 5. Integument is well marked; maximal elongation of archesporial cells; disintegration of some of the inner cells has begun, × 670.

Fig. 6. Somewhat older condition of the ovule in which the archesporial cells are preparing for division; micropylar canal is begun, × 472.

Fig. 7. First division of the archesporial cells. The arrow is directed toward the position of the micropyle, × 670.

Fig. 8. A still more advanced condition of the ovule in which the micropylar canal is deep. The second division is taking place in some of the archesporial cells, × 315.

Fig. 9. Definitive megaspore. On the right one sees imperfectly formed and degenerating megaspores, × 670.

Explanation of Plate 2

Fig. 1. The embryo-sac mother cell has migrated down the micropylar canal, having passed to one side of the nucellar cells which cap the archesporium. The remaining megaspores are beginning to disintegrate, × 670.

Fig. 2. Embryo-sac with four nuclei, × 670.

Fig. 3. Embryo-sac with eight nuclei. One of the antipodals is cut off from the remaining seven nuclei by a transverse wall, × 670.

Fig. 4. Egg apparatus and antipodals definite. Approach of polar nuclei, × 472.

Fig. 5. Fusion of polar nuclei completed. The position of endosperm nucleus is near the middle of the sac, × 472.

Figs. 6 and 7. Approach of endosperm nucleus toward the egg, and their concomitant increase in size, × 472.

Fig. 8. Mature embryo-sac. The endosperm nucleus is now applied to the egg, × 670.

Fig. 8a. Egg and endosperm nuclei of the same, × 1350.

Fig. 9. After fertilization; embryo is still one-celled; several endosperm nuclei are now present; the disintegrated megaspores are now nearly absorbed; the endosperm begins to encroach on the integument, × 315.

Fig. 10. Embryo two-celled. The endosperm, in which walls begin to appear, encroaches further upon the integument, × 315.

Fig. 11. Three antipodal cells, × 670.

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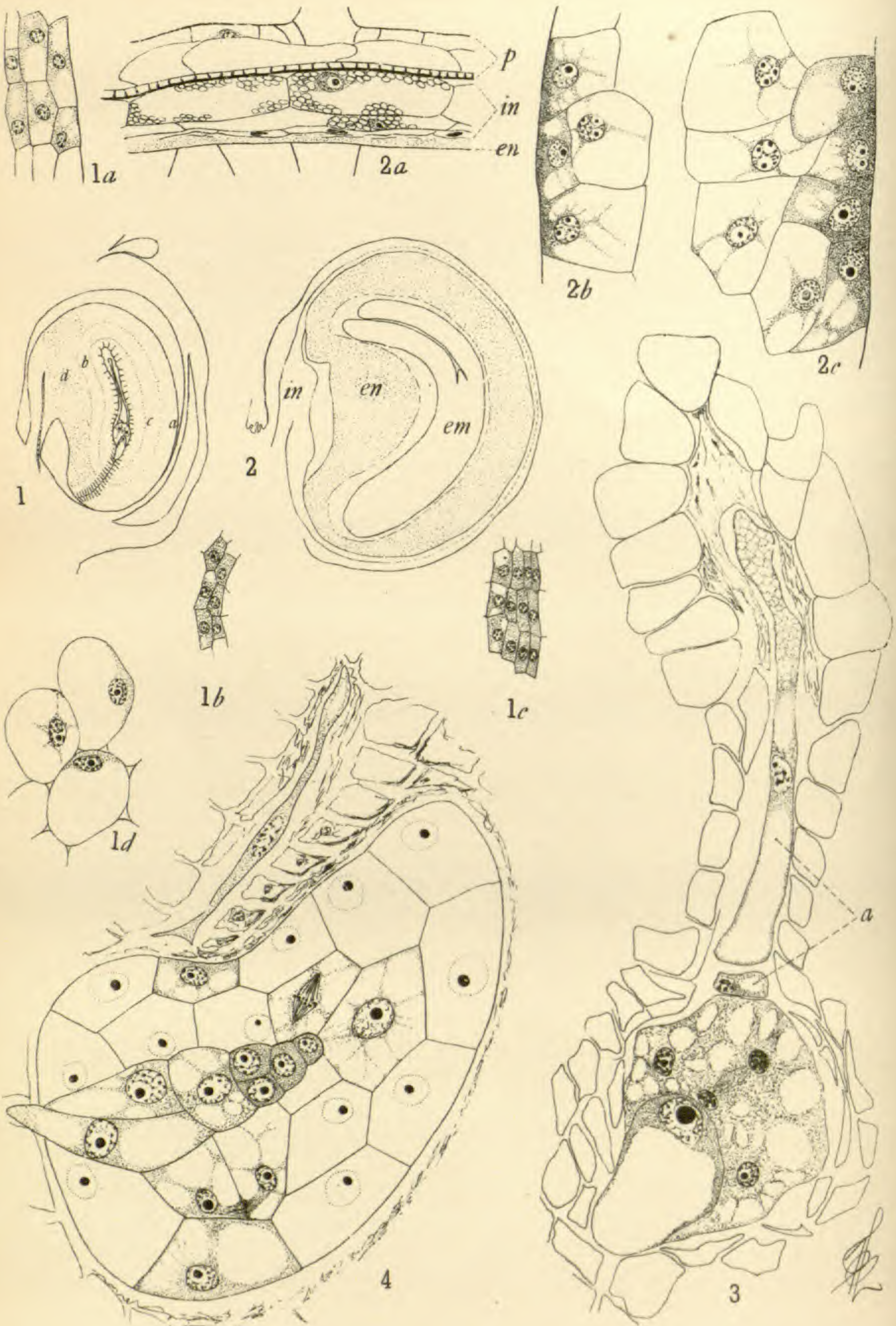

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Explanation of Plate 3

Fig. 1. Ovule just after fertilization showing areas made up of cells of different character. (*a*) Zone of cells dividing mostly by periclinal walls (see Fig. 1*a*). (*b*, *c*) Zone of rapidly multiplying cells (see Fig. 1*b*, 1*c*) forming a meristem completely surrounding the internal mass including the embryo-sac. (*d*) Mass of cells lying between the funicle and the meristem, made up of large cells (see Fig. 1*d*) containing vacuolated cytoplasm and starch grains, × 75.

Figs. 1*a*, *b*, *c* and *d*, × 670.

Fig. 2. Longitudinal section through mature fruit, in. integument, en. endosperm, em. embryo. The pericarp is seen as a thin layer without the integument.

Fig. 2*a*. Envelopes of mature fruit in detail. *p*. pericarp, *in*. integument, *en*. endosperm. The cells of the integument are still supplied with much starch, × 220.

Fig. 2*b*. Cells from periphery of endosperm on convex or dorsal aspect, × 472.

Fig. 2*c*. Cells from periphery of endosperm on concave or ventral aspect, × 472.

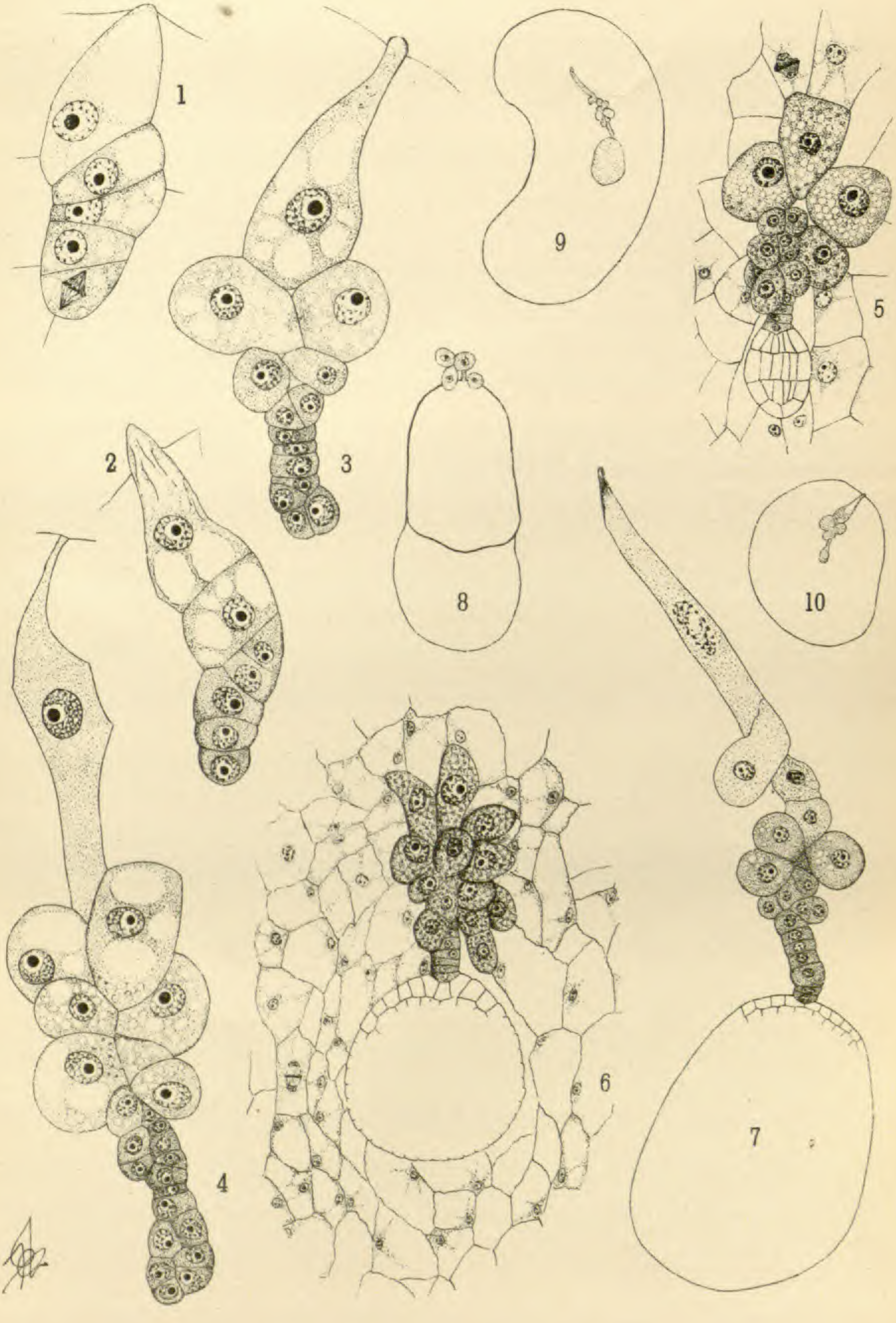
Fig. 3. After fertilization. The basal antipodal has its haustorial end embedded in a mass of refractive substance which results from the disintegrated megaspores. Embryo still one-celled, × 670.

Fig. 4. Young embryo lying in the endosperm. The latter by its growth pushes past the long antipodal into the integumental tissue as toward *c*, Fig. 1, × 472.

Explanation of Plate 4

Fig. 1. Proembryo of 5 cells, × 670.
Fig. 2.
3. × 472
4.
5.
6. × 315 Successively older stages of the embryo.
7.
8. × 75
9. × 50 Embryo, drawn on larger scale in Fig. 7, lying in the endosperm.
10. × 75 " " " " " " " 3, " " " "

A comparison of these last two figures shows the position taken by the proembryo as a result of the growth of the endosperm at the micropylar region.



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VOL. VIII NO. 1, PART 2

THE

COMPARATIVE EMBRYOLOGY

OF THE

RUBIACEAE

BY

FRANCIS ERNEST LLOYD

ISSUED FEBRUARY 15, 1902

FURTHER DESCRIPTION OF GENERA

Callipeltis cucullaria

The genus *Callipeltis* embraces three species indigenous to the Mediterranean region. In general habit they resemble closely the plants of the genus *Galium*, from which, however, they differ in their smaller size. *Callipeltis cucullaria*, the species studied, was collected in growing condition in the Botanical Garden at Berlin.

THE NUCELLI

The nucelli, two in number, arise as in *Vaillantia*, on either side the center of the floor of the ovary. Nor is their course of development different from that already described for that genus, excepting in matters of only minor moment, and these are to be found in the total number of cells in the nucellus, the greater relative amount of archesporial tissue, and in the shape of the definitive ovule.

The archesporium, the cells of which are more numerous than in *Vaillantia*, is evident when the nucellus is quite small (*pl. 5, fig. 1*). The epidermal capping cells remain without any further growth, while immediately around the area occupied by them, the integument grows out, as is made evident by the numerous periclinal divisions to be seen at this stage (*pl. 5, figs. 2 and 3*). By subsequent growth, the integument is developed so as to shut in a long micropylar canal (*pl. 5, fig. 4*). As the ovule attains its definitive form, the absence of the large special cells seen in the ovule of *Vaillantia* is noticed, and the sporogenous cells of the archesporium divide. The division into four megaspores is by no means complete for each cell. Some of them, the more centrally placed, divide more rapidly and completely, while the more peripheral lag behind and sometimes fail of division, or perhaps divide but once, and so a heterogeneous mass results, out of which the megaspore which develops into the embryo-sac makes its way into the micropylar canal. In such

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[No. 1, Part 2 (pp. 27–112), issued 15 February, 1902.]

a mixture of cells it is not easy to distinguish this cell, especially as it often happens that several pass through the initial stages of migration, and the result is very confusing. I have, however, with reasonable certainty, been able to pick out the most active cell, as in *figs. 4 and 5*. The embryo-sac cell, so far as determined, may arise out of any of the megaspores, so that we may regard these for the greater part as physiologically equivalent. The appearances presented by the archesporium at this time match closely those seen in *Alchemilla* as described by Murbeck.* Tapetal cells are not formed.

No starch is seen in the integument until the migration of the megaspore, when a slight accumulation occurs, evenly distributed throughout the whole. During the maturing of the embryo-sac, the amount of starch increases in a zone surrounding it. As the endosperm starts to grow, zonal accumulation disappears and a general distribution is again seen which becomes gradually more pronounced in the peripheral parts.

THE DEVELOPMENT OF THE EMBRYO-SAC

One of the megaspores which have developed as described above commences to enlarge and to migrate along the micropylar canal. This takes place when the ovule is well developed and has taken on its mature form. *Pl. 5, fig. 4,* shows these conditions just previous to the migration of the megaspores. It not infrequently happens in this species that two or even three megaspores commence to migrate at the same time and take paths which are nearly parallel. In such cases a good deal of confusion arises, which makes it difficult to interpret properly the preparations showing this condition. The remaining megaspores retain their character for some time, some degenerating more rapidly than others, and the resulting mass adds not a little to the difficulty of making out clearly what one sees. Occasionally two of the migrating megaspores germinate, although in no cases which I have observed has development passed beyond the four-celled stage (*pl. 5, fig. 8*) in any but the more advanced and normal one, which is set apart as the fundament of the functional embryo-sac.

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* Murbeck, Sv. Parthenogenetische Embryobildung in der Gattung *Alchemilla.* Acta Reg. Soc. Physiogr. Lund, 11 : 1–47. 1901.

More than one embryo-sac may sometimes reach perfect development, thus supplying the conditions for false polyembryony. This, however, has not been observed.

The movement of the megaspore down the micropylar canal is accompanied by histolysis of the endodermis, the cells of which degenerate and collapse. The contents of the cells are disorganized and become deeply staining. It is to be noted that the nucleus is preceded in its course by a part of the cytoplasm, while the nucleus itself travels unusually near, or along the side of the cavity formed and some little distance back from its apex (*pl. 5, fig. 6*). The amount of cytoplasm is now not great, nor does it increase markedly in amount until the complement of embryo-sac nuclei is reached. The cells of the egg apparatus, as soon as they are cut off, become rapidly different in character from the rest in attaining greater density. Their final character is reached at about the time of fusion of the polar nuclei or somewhat later. The synergids then are vacuolated at their free ends, while the egg-cell has a vacuole at its narrow basal end. The fusion of the polar nuclei occurs near the middle of the endosperm cavity (*pl. 5, fig. 8*) and is followed by a movement of the resultant nucleus toward the egg-cell with which it lies in contact till its first division. Meanwhile the cytoplasm loses its vacuolated character and becomes more dense and gorged with food material, consisting, in large part, of starch. The whole endosperm-cell becomes more rounded also.

THE ANTIPODAL CELLS

When the fusion of the polar nuclei is taking place the antipodal nuclei have arranged themselves in their definitive positions, two of them close together, each with its proper mass of cytoplasm which is thin and vacuolated, and the third some distance away in the narrowing end of the somewhat irregular cavity formed by the megaspore in its migration (*pl. 5, fig. 9*). The cytoplasm of this latter antipodal cell is at first extremely scanty, so much so that it cannot be detected with a high power except near the nucleus. The two small antipodals secrete cell walls and remain in a normal condition for some time during the development of the embryo. Their cytoplasm becomes more dense from the time they are first cut off, and numerous starch grains may then be seen. The long antipodal which occupies about three-fourths of the length of the entire embryo-sac takes on a definite club shape at its free extremity which reaches quite to the end of the megaspore cavity, and is finely granular, though not so densely filled with protoplasm as are the others. A large vacuole appears constantly at the thick end which abuts against the small antipodals. The vacuole extends as far as the nucleus. The interior of the narrow upper part is also occupied by a vacuole, though this is less evident in sections on account of the slender character of this region of the cell. A normal appearance is presented by this cell as by the other two until the proembryo has reached an eight- or ten-celled stage or even older (*pl. 6*, *fig. 5*), and an application of the iodine test demonstrates that at such a time the small antipodals are gorged with starch while the other shows a similar starch content at its thick end. The haustorial end stains deep yellow and is free from starch. No trace of the deeply staining products of disintegrated megaspores may be seen after the second or third division of the endosperm nuclei, though this is, of course, a somewhat variable matter. Disintegration of the antipodals sets in with the rapid extension of the endosperm, and they are finally lost to view.

ENDOSPERM AND INTEGUMENT

Soon after fertilization the endosperm nucleus divides. This division is followed by several others, probably five or six, before any walls are laid down. Its starch content is drawn upon during these divisions, so that at the time the cell walls are laid down, only a very little may be found or none at all. The proembryo remains unicellular till about the third or fourth division of the endosperm nuclei occurs. The growth of the endosperm is accompanied by destruction of the integument. The peripheral endosperm cells become less vacuolated, the greatest density of contents being found in those cells of the endosperm which lie towards the raphe, *i. e.*, the peripheral cells are most active where the largest amount of food is available. The accumulation of starch is gradual at first and is localized in the chalazal end of the endosperm. Later all the cells become gorged with starch, so that at the time the cotyledons appear, all the cells are well supplied with the exception of those which occupy the middle portion of the endosperm and the layer of absorbing cells next the raphe. The endosperm continues however to grow, and ceases only when there is left of the integument only a single layer of cells separating the endosperm from the pericarp. The limit of growth in extent being reached, the cells commence to secrete reserve cellulose. Their lumina, by reason of the accumulating cellulose, become more contracted and rounded in form. The increase of cellulose is accompanied by an evident reduction of the starch content, though a plentiful supply is present at the maturity of the seed.

The immediate supply of food necessary for the endosperm is to be found in the integument, of which the starch content is gradually increased as it reaches its maximum size. When the seed is ripe, a single layer of integumental cells only is left, excepting an island of tissue underlying the termination of the vascular tissue of the funicle. The endosperm is thus a concavo-convex mass, surrounded by an integumental membrane, this, in turn, being closely invested by the pericarp four cells in thickness (*pl. 6, fig. 12*). A considerable amount of starch is found in all the cells of the integument, particularly in the chalazal island.

DEVELOPMENT OF THE EMBRYO

As already pointed out, the embryo remains unicellular till the endosperm nuclei have reached the number of eight to sixteen, when it begins to develop rapidly, one transverse division following another until the embryo is composed of a cell row of ten or a dozen cells (*pl. 6, fig. 6*). The largest of these are in the suspensor. The terminal cell, the fundament of the embryo proper, is the smallest. The suspensor cells bulge out more or less. A portion of the suspensor may be composed of two rows of cells (*pl. 6, fig. 9*), though, whether this is due to transverse division or to displacement by longitudinal pressure, I cannot say. Probably, however, the latter. The arrangement and number of cells in the suspensor is by no means constant, so that it is a matter of physiological significance alone. By further growth, the bulging suspensor cells extend themselves, so as to lie between the endosperm cells, but do not cause any destruction. They are filled with cytoplasm, and have large active nuclei. The development of haustorial cells by the embryo in *Callipeltis* is not so great as in *Vaillantia*, either in point of number or size. With the development of the embryo proper and of the endosperm, the basal cell elongates, allowing the embryo to take a more central position in the endosperm. The haustorial portion is then near to the embryo. The basal cell is finally crushed between the cells of the endosperm, the haustorial portion becomes absorbed, so that only a single cell is left as a portion of the root cap of the embryo.

The development of the embryo is briefly as follows: After transverse division has ceased, the terminal-cell divides longitudinally once, then a second time. The second cell from the end follows suit, then the third and finally the fourth. Meanwhile the first three tiers of cells are giving rise to dermatogen, then to plerome in the fashion described by many authors for numerous dicotyledons. The fourth tier of cells which apparently never exceed four in number, remain so and may be recognized in the definitive embryo as a small protuberance at the top of the root cap.

A great deal of variation takes place, but the plan just set forth is followed in general and the ultimate product is the same.

Sherardia arvensis

This plant, the only species of the genus, is a small upright annual having the whorled foliage of the Galieae with small heads of several flowers with rose colored tubular corollas. It is distributed in Western Asia, Europe and North Africa. The material for study was obtained in cultivation in Germany and in New York.

The history and character of the nucelli, integument and megaspore mother-cells call for no special treatment. No evidence has been obtained pointing to differences in the division of the megaspore mother-cells, or in the selection of a given megaspore to become the embryo-sac. It thus appears that the megaspores are of potentially equivalent value. During migration down the micropylar canal the three serial divisions of the embryo-sac nuclei take place and finally a definitive embryo-sac is formed which differs somewhat from those hitherto described in form and proportion (*pl. 6, fig. 15*). The two small antipodals are concavo-convex, and are set upon the endosperm cell as a cap. They are densely filled with food materials. The third antipodal is longer relatively than in either *Vaillantia* or *Callipeltis*, and is scantily supplied with cytoplasm. The distal end is formed into a club-shaped swelling, and is buried in the mass of disintegrated megaspores. The swollen end is filled with a tenuous and finally granular cytoplasm.

The endosperm nucleus lies in the definitive embryo-sac against the egg, into which position it has moved from a distant position where fusion of the polar nuclei takes place (*pl. 6, figs. 15, 16, 17*).

The development of the embryo proceeds by the formation of transverse walls, until about a dozen cells in linear arrangement have been laid down. All but the terminal cell form then the suspensor in which two distinct regions are to be recognized. The micropylar region is composed of larger vacuolated cells, which grow out laterally into the endosperm forcing their way between the cells. The nucleus lies in the concavity of the outgrowing haustoria just as is known to occur in young root hairs (*pl. 6, fig. 19*). The proximal portion of the suspensor is composed of very short disc-shaped cells, which, while the embryo is young, retain that form. As the embryo becomes older, the more distal of these elongate, and some grow out into haustoria. When the endosperm has reached its maximum size the laying down of reserve cellulose begins in the peripheral cells first, and these cells become unfavorable for the absorption of food by the suspensorial haustoria. That portion of the suspensor, therefore, which comes to lie in the region of cellulose formation degenerates *pari passu* with the thickening of the cellulose layer. The function of absorption thus given up by the more distal part of the suspensor is then taken up by the more newly formed haustoria. The suspensor becomes loaded with food which is gradually passed on to the embryo (*pl. 6, fig. 21*).

In the development of the embryo proper there is correspondence with the process as described for *Callipeltis*. One feature appears somewhat different, namely, that the longitudinal division of the terminal cell is followed by transverse division of its quadrants, so that it appears as if the terminal five cells had gone to form the embryo proper instead of four.

The mature ovule consists of a mass of endosperm with cellulose as the chief reserve food, and one layer of integumental cells still intact. The whole is closely invested by the pericarp.

The endosperm absorbs the integument till but one or two cell layers are left, these forming a membranous lining of the pericarp.

Galium

(PLATE 7)

The species of *Galium* which have been studied are the following: *G. Aparine, recurvum, pilosum, Mollugo, verum, triflorum, tinctorum*, and *Parisiense*. As the species of this genus are very similar with regard to the characters which we are considering, it is not deemed necessary to treat them separately.

The origin of the nucelli is in all respects as in the forms already described, and the same may be said of the number of cells in the archesporium (*figs. 1, 2 and 3*), their division into megaspores by two successive divisions (*fig. 4*), and the subsequent enlargement of one of these to act as the embryo-sac cell. In occasional instances two such cells derived from different megaspores may enlarge and when germination takes place, two more or less completely formed embryo-sacs result (*fig. 11*). In one case three such were found, although here the third embryo-sac was very abnormal in appearance. The nucellar epidermal capping cells remain intact until the megaspores are fully formed, but suffer histolysis at about the time the migration of the embryo-sac mother-cell commences (*fig. 4*). The histolysis of the endodermis then follows, as the enlarged megaspore moves forward along the micropylar canal.

The condition of the definitive embryo-sac is reached in the usual manner. A two-celled condition is shown in *fig. 6*. The chief interest in this connection attaches to the form the embryo-sac takes in the various species of the genus under consideration. The various degrees of curvature seen in different species is, no doubt, due to the form of the ovule. The more strictly anatropous the ovule, the straighter the embryo-sac. In *Galium tinctorum* in which the ovule approaches the campylotrous condition, the embryo-sac is bent into an arc of ninety degrees (*fig. 10*). In other respects save in three particulars the characters of the embryo-sac are uniform namely, in the form of the endosperm cell, the shape and disposition of the antipodals and the amount of the food content. In certain species, *e. g.*, *G. Mollugo*, and *G. Parisiense*, the endosperm cell is almost spherical while in others it is oval. In *G. tinctorum* this cell is markedly constricted about midway its length and this appears to be the normal condition (*fig. 10*). In this plant also, the food content of the endosperm cell is evidently greater, and is composed for the most part of starch. The starch grains are indeed so crowded that the nucleus is very much distorted by compression (*fig. 10*). Finally the antipodal cells may take two different arrangements. They may be placed tandem ſashion as in *G. triflorum* (*fig. 7*) and *G. Mollugo* (*fig. 11*), or the two small antipodals may lie in the same transverse plane as occurs in *G. Aparine* (*fig. 8*) and *G. Parisiense* (*fig. 12*), and some others. A modification of this latter mode of arrangement is to be found in *G. tinctorum* (*fig. 10*), in which plant these cells become rounded and are placed obliquely with reference to the longitudinal axis of the embryo-sac. These cells are at the same time densely filled with starch, a good deal of which material is also to be found in the long antipodal cell.

The haustorial antipodal cell reaches, in this genus, its greatest relative length, as is illustrated by our *fig. 9* (*G. triflorum*), which shows an ovule in longitudinal section, with an embryo-sac just before fertilization.

The development of the embryo and endosperm in their earlier stages presents no differences of special note. Considerable variation is shown in the development of the suspensor in the different species. In *G. Parisiense*, for example, there is but a small haustorial apparatus formed, while the suspensor of this plant is remarkable for the unusual elongation of the basal cell (*fig. 13*). Of the species studied, the greatest development of the suspensor is reached in *G. Mollugo* (*fig. 15*).

The endosperm arises by division of the endosperm nucleus in all directions, at first without the formation of cell walls. Soon, however, these commence to form before, indeed, the suspensor produces haustoria. The histolytic changes in the integument, which take place relatively slowly at first, proceed a little later very rapidly, and, as indicated in *fig. 14*, the histolysis is not confined to the immediate vicinity of the endosperm. In the same figure we may note the antipodal cells to be still present, but they are in a dead condition, and it would not appear that they are in any way active agents in the action described, but rather that the enzyme which we may believe is secreted by the endosperm more readily passes along the course of the antipodal apparatus and is thus distributed to a distance from the endosperm.

That the behavior of the integument as the endosperm grows is indeed the result of the action of an enzyme, we have evidence in the case shown in *fig. 15*, where the cell-walls of the cells lining the micropyle remain unaffected, although the surrounding tissue has been totally destroyed.

It is to be noted also that the endosperm nucleus takes its position against the egg cell, although this does not appear to be the case in *G. tinctorum*. This may be due to the interference of the large and numerous starch grains which crowd the cell and would very naturally interfere with the movements of the endosperm nucleus (*fig. 10*).

The food mass derived from the disintegrating megaspores becomes exhausted at the maturity of the embryo-sac or soon after and no trace of this may be seen soon after fertilization. At this time, too, the fertilized egg loses its vacuole by the increase of the cytoplasm, and the synergids at the same time disintegrate.

The course of development of the embryo is, in the early stages, like that in the others previously described.

Asperula

(PLATES 8 AND 9)

Of this genus the following five species have been studied: *A. azurea*, *galioides*, *montana*, *setosa*, and *tinctoria*.

The development of the ovule and the appearances presented by the archesporium in the genus *Asperula* do not differ in general from the other *Galieae*. They present, nevertheless, some striking points of contrast, especially when compared with *Crucianella*.

The early stages of development of the ovule may be passed over without further remark. When the definitive condition of the archesporium has been attained, the further development of the ovule, especially of the integument, is such that the upper part of the sporogenous tissue becomes compressed so that the individual cells become displaced and distorted to such a degree that the whole appears almost abnormal. This appearance is accentuated during and after the division of the mother-cells, which, it would seem, is by no means as regular as in *Crucianella*. This irregularity is most striking in *Asperula montana*, in the ovule of which plant the compression appears to be greatest on the micropylar part of the archesporium. This condition is obviously the cause also of certain curious abnormalities in the behavior of the embryo-sac to be described shortly. The irregularities in the behavior of the archesporial tissue consist in the differences in rapidity with which tetrad formation takes place, in the partial or total suppression of tetrad formation in a greater proportion of the megaspores, in the early destruction, by pressure, of some of the cells, and finally are such that the accurate observation of the behavior of individual cells is rendered almost impossible.

That tetrad formation takes place normally, however, is quite sure, from the fact that, in spite of the confusion, rows of four cells each are repeatedly found. The megaspores, sister to the functional embryo-sac cell, persist in apparently normal condition for a period at least equal to that occupied by the development of the embryo-sac, and occupy, forasmuch as they do not secrete cell walls, the same cavity as the embryo-sac. It sometimes happens, too, that they have quite the appearance of the antipodal cells, so that it becomes difficult to distinguish between them.

After the functional embryo-sac cell has started to migrate (*pl. 8, fig. 2*), some of the other megaspores persist, while others degenerate. Some, further, secrete cell walls, and undergo changes which indicate that they are passing through early stages of embryo-sac development. One such cell is shown in the upper right-hand part of the figure.

It seems equally certain that the tendency is for the upper of the tetrads to become the embryo-sac. The pressure already referred to, however, modifies the ordinary mode of procedure, so that not only may some other of the megaspores rather than the upper become the embryo-sac, but it may also be forced to develop in quite the wrong direction. This is the case in *Asperula mon-*

tana, in which a completely developed embryo-sac is frequently to be found in the chalazal part of the ovule, or even in the funicle. *Text figs. 1 and 2* illustrate two such instances. In *fig. 1* two embryo-sacs are seen; one in the normal position, *i. e.*, in the micropylar canal, and one lying parallel to it, but in the funicle. Both are completely developed. In *text fig. 2* three embryo-sacs may be seen; the one normal in position, and the two others lying against each other, in the funicle, and considerably distorted. The egg poles of these two embryo-sacs are placed against the pericarp; that is to say, the embryo-sacs have grown to the surface of the ovule. In *text fig. 3* the egg apparatus and polar nuclei of one of these abnormally placed embryo-sacs may be seen to be quite normal except for a small amount of distortion. Whether the egg of such abnormally placed embryo-sacs is ever fertilized is doubtful, and no case has been observed. This plant has flowers which show a peculiar form of dimorphism caused by the abortion of the ovules in a large percentage of cases.

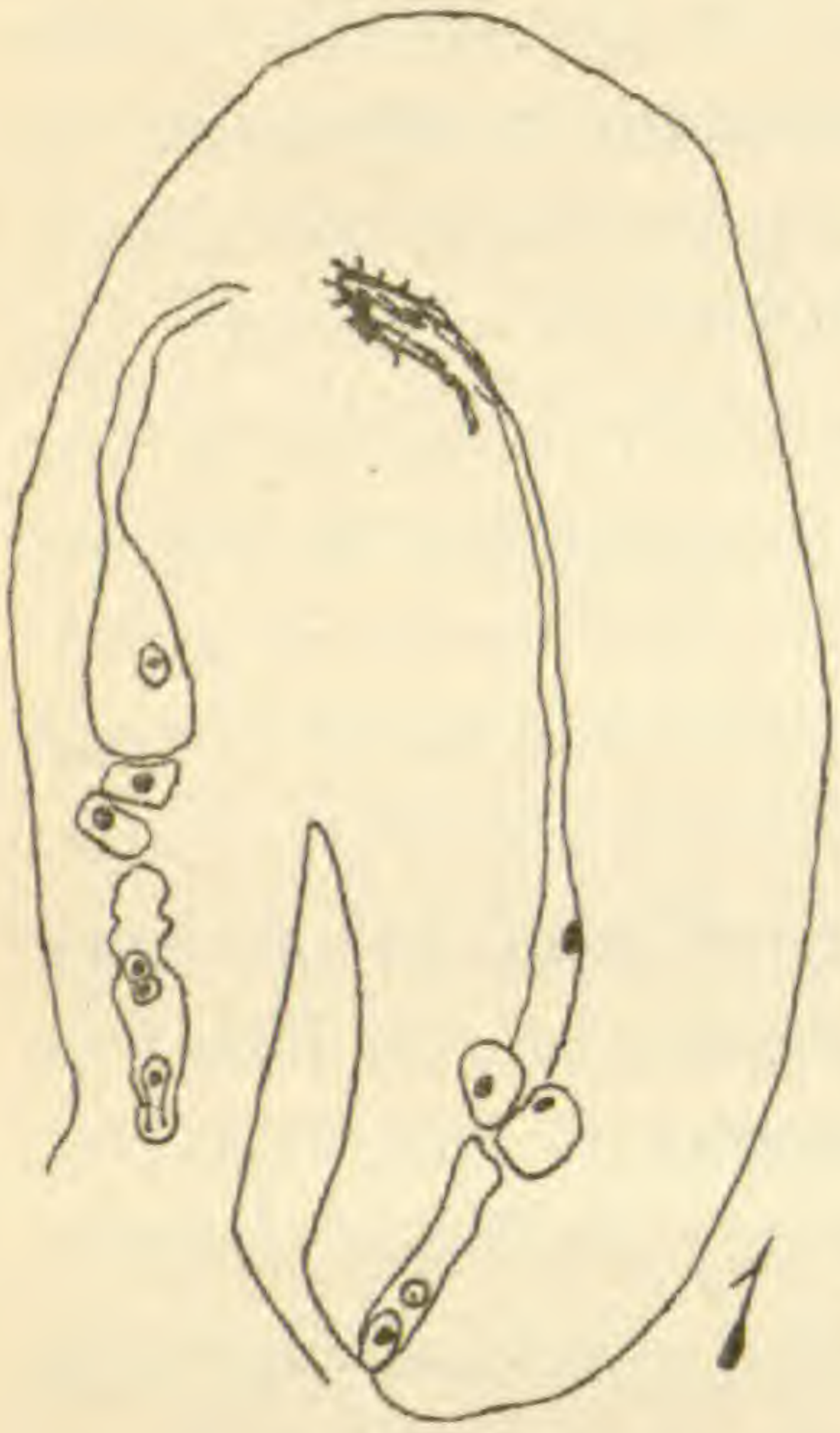


FIG. 1. Ovule with a second embryo-sac lying in the funicle.

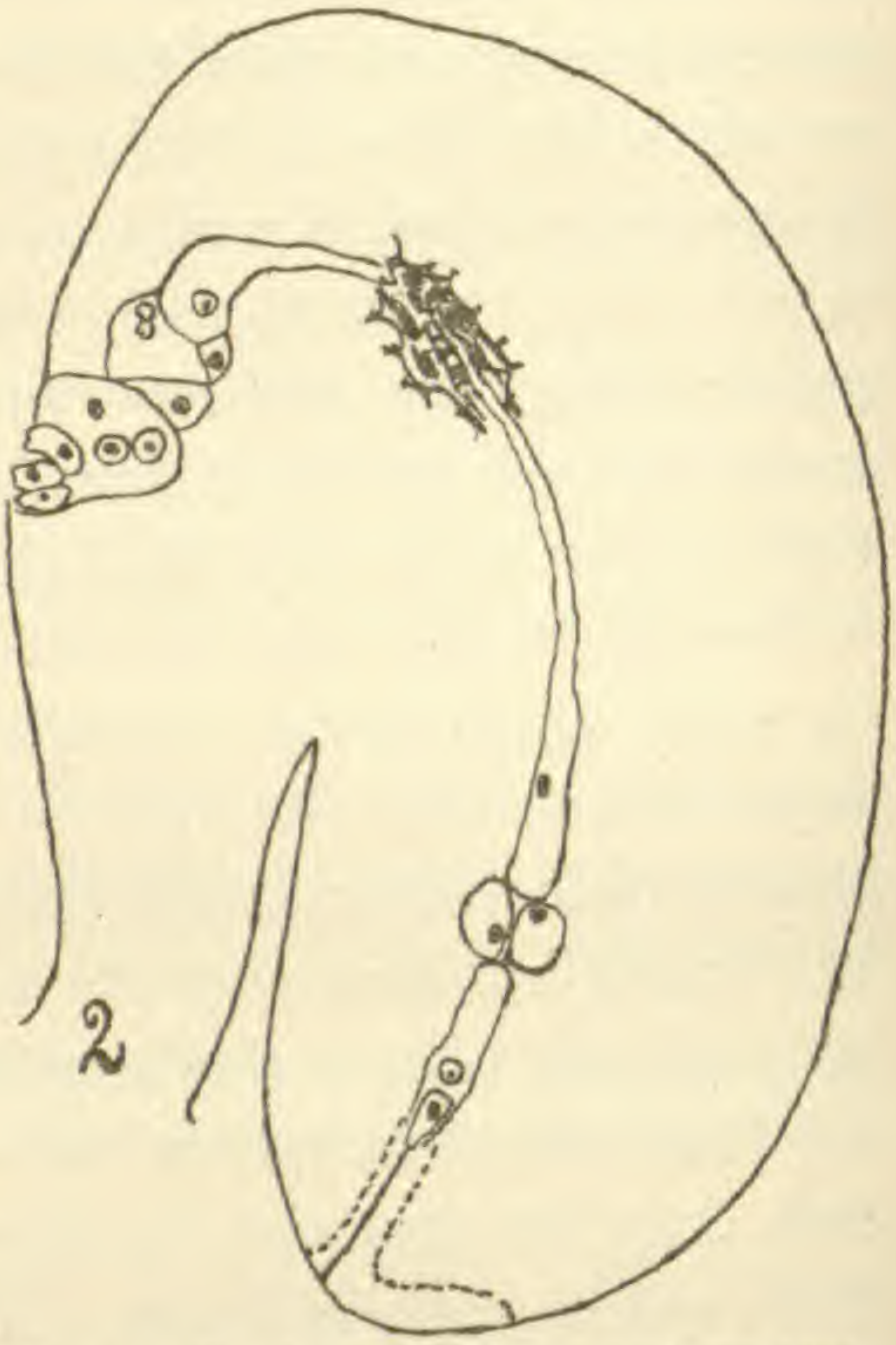


FIG. 2. Ovule with three embryo-sacs, two in the funicle and one in the usual position. The dotted line indicates the frequent protruding position of the embryo-sac.

Only relatively very few ovaries with normal ovules therefore are to be found, and from these only few seeds were produced under the cultural conditions at Bonn, where the material was collected. In view of these facts, therefore, the failure to observe fertilization in the abnormally placed embryo-sacs is not surprising. On the other hand, there are grounds for expectation that the behavior of the pollen tubes is such as to favor such an occurrence.

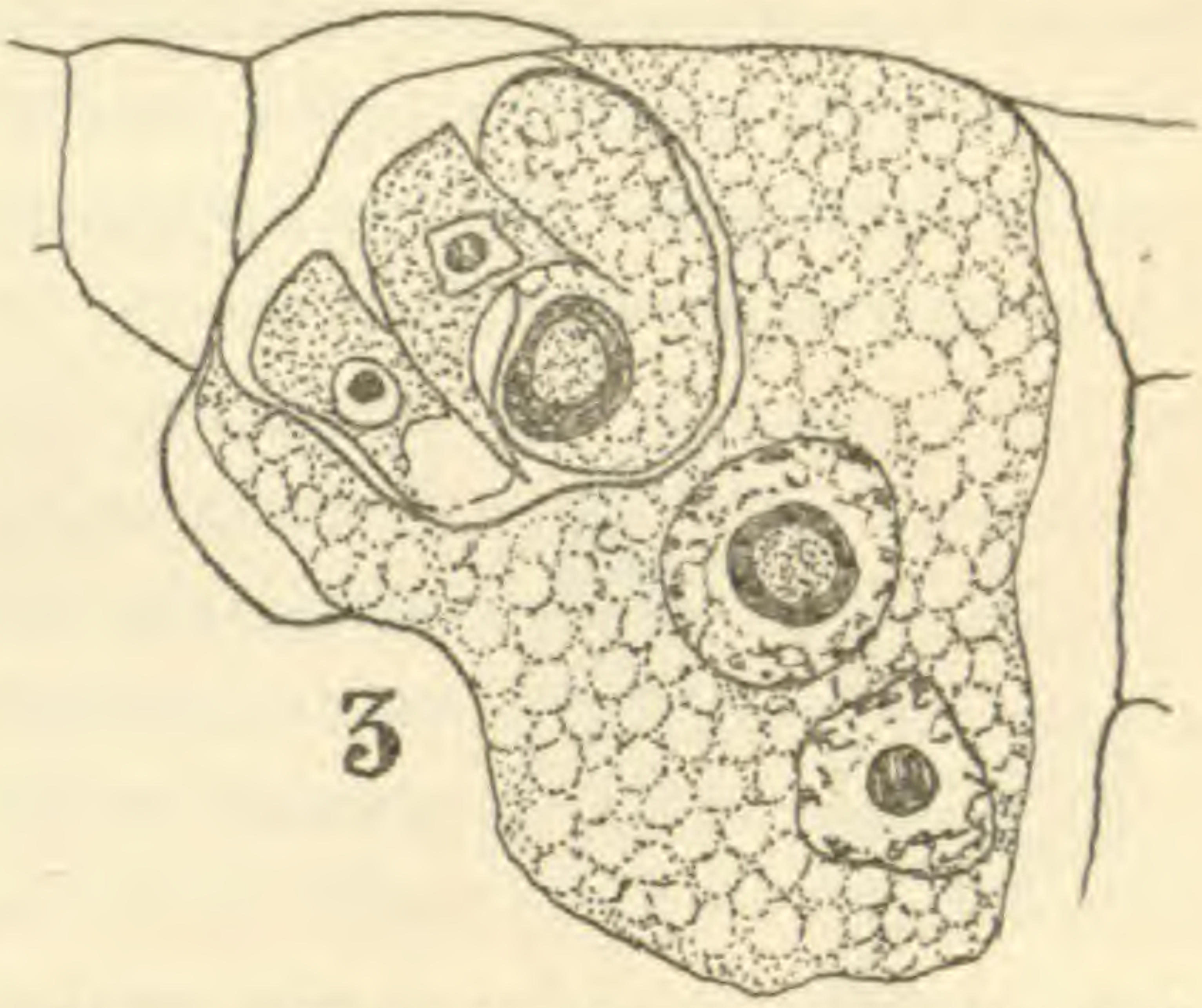
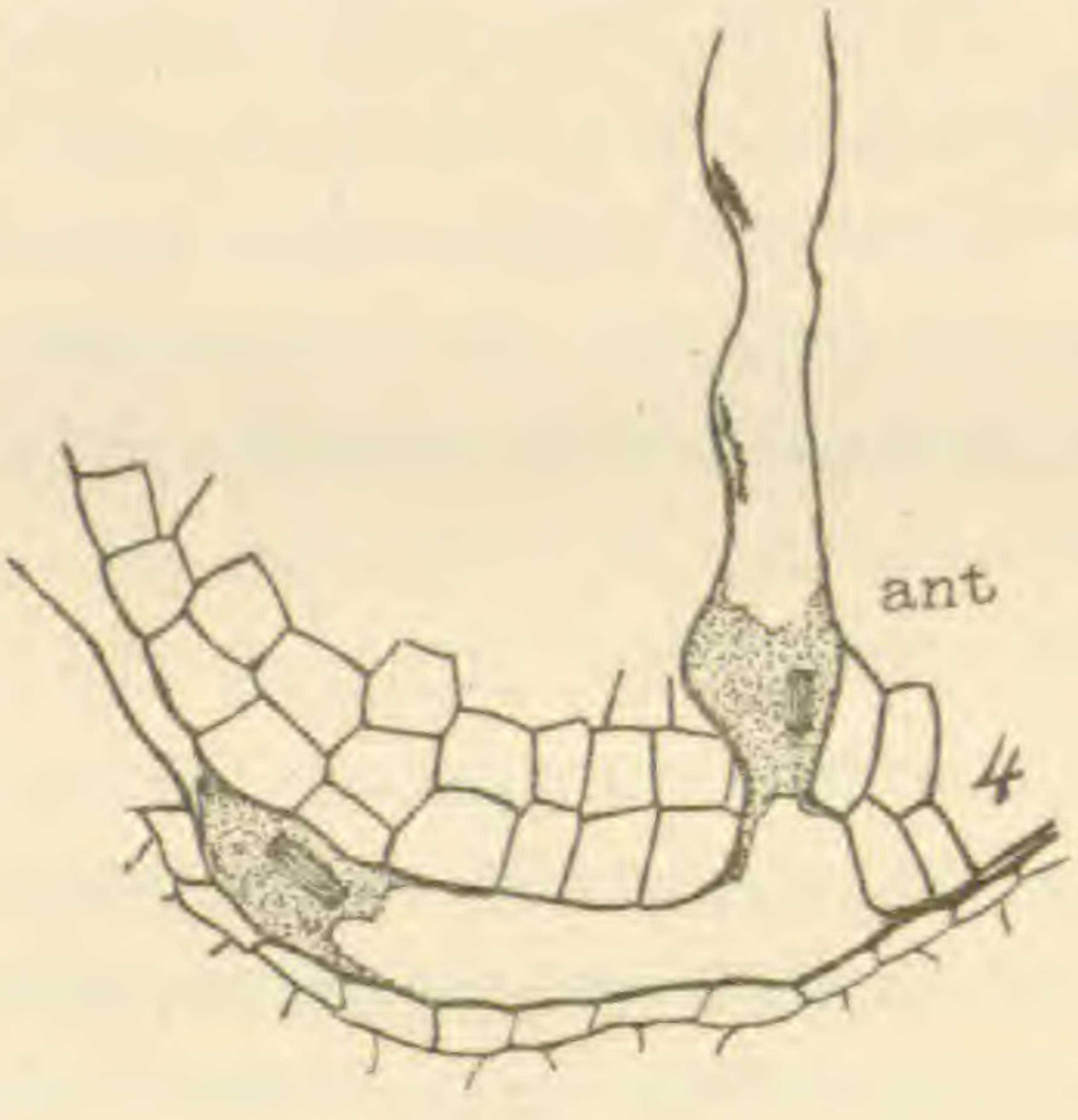


FIG. 3. Part of embryo-sac occurring in the funicle showing egg apparatus.

Further peculiarities occur in the behavior of the normally placed embryo-sac in *Asperula montana*, in that its growth continues often until the egg end projects beyond the mouth of the



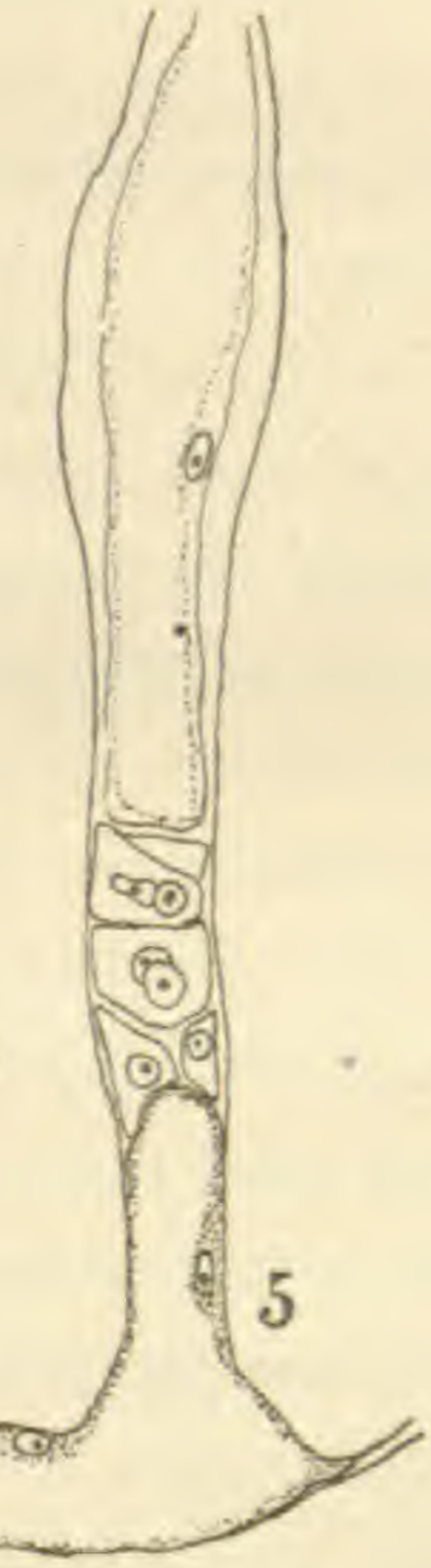


FIG. 4. Protruding embryo-sac with two nuclei in mitosis. *Ant.*, Antipodal nucleus.

FIG. 5. Protruding embryo-sac with at least seven antipodal nuclei. Polar nuclei not yet fused.

micropyle and comes to lie between the integument and the pericarp. In *text fig. 2* the dotted line indicates in a schematic way the position taken by the embryo-sac under these circumstances, and *text figs. 4 and 5* show two such embryo-sacs in detail. It is to be noted that the egg apparatus under these circumstances is always directed away from the funicle. In cases in which fertilization takes place, the egg elongates before division, and the embryo thus comes to lie within the ovule (*text fig. 6*). *Fig. 7* serves as an example, although here the egg apparatus is not as far away from the micropyle as in many other cases. The habit of the embryo of producing a long slender stalk before division is constant, and may be seen even where the embryo-sac does not protrude from the micropyle, where, namely, the embryo-sac takes the same position as in the other *Galieae* (*text fig. 7*). What the behavior of the pollen tube in this plant may be cannot be said, as no favorable material has so far been found. A study of this point cannot fail to be of interest.

FIG. 6. One-celled embryo formed in a protruding embryo-sac.

FIG. 7. One-celled embryo in embryo-sac occurring in the more usual position.

The migration of supernumerary embryo-sacs into the funicle as above described is of special interest as it bears on the question of the guidance of the embryo-sac in its movements.

Under ordinary circumstances the embryo-sac cell migrates down the micropylar canal, breaking through the thin cap of nucellar tissue. Where, however, the pressure of the integument is great enough the normal movements of the embryo-sac nucleus are prohibited, and the embryo-sac makes an irregular growth in any direction, and reaches no definite point. We may, therefore, conclude that the guidance of the embryo-sac into the micropylar canal is mechanical.

The other species of *Asperula* studied show in general the same disturbances in the archesporium due to pressure as in *Asperula montana*, though not to the same degree. This is indicated by the fact that no exception to the normal position of the embryo-sac has been seen, although similar appearances in the archesporial tissue are there.

The only other point in connection with the embryo-sac calling for special mention is the behavior of the antipodal cells. These are by no means constant in number, and may vary even in the same species, as far as observed, from three to seven. The most typical condition is shown in *pl. 8, fig. 3*, for *Asperula azurea*, and in *pl. 9, figs. 1 and 2*, for *Asperula montana*. The long antipodal has the usual appearance corresponding as it does to the homologous cell in the other *Galicae*. The other two, however, are here very much enlarged and each consists of dense cytoplasm with a large active nucleus, and a very large central vacuole. In the growth of these cells the adjacent tissues present histolytic appearances similar to those seen in the same tissue when the endosperm enlarges. There is, therefore, so much evidence that the antipodal cells are able to secrete substance which acts in the way indicated upon the living cells.

When more than three antipodal cells occur they are arranged in pairs forming an irregular double row, recalling the condition in *Aster* (Chamberlain) and in *Diodia* (*pl. 9, fig. 5*). In some species the behavior of these cells is very irregular; one frequently finds several nuclei in the same cell, and the cells are sometimes much more slender in proportion than as represented in the figure (*pl. 9, fig. 5*). In all cases, however, the same observations already made with reference to the persistance of the antipodals and their nutritive relations holds good in *Asperula*.

THE EMBRYO

Of all the *Galicae* studied, the genus *Asperula* is most remarkable for the extreme development of the suspensor. In *A. setosa* (*pl. 8, fig. 4*) the haustorial cells attain a large size, and extend to a considerable distance from the suspensor into the endosperm. The amount of cytoplasm is not great, and is collected mainly at the distal ends of the haustoria, where the nucleus is to be found. At this point the growth of the organ takes place, so that we have here a very close analogy with the root hair in which, as Haberlandt * has shown, the nucleus and cytoplasm behave similarly.

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* Ueber die Beziehung zwischen Function und Lage des Zellkernes bei den Pflanzen, Jena, 1887.

In this form, on account of the large size attained by the haustoria it is quite easy to see that, as they penetrate the endosperm, the process is accompanied by mechanical readjustment of the cells of the latter, without any destruction. *Pl. 8, fig. 5*, shows a later stage in the same or a closely related species, from which it will be seen that as the embryo grows older the haustoria becomes filled with cytoplasm. Meanwhile their proximal extremities become compressed and drawn out as a result of the pressure exerted on them by the growing endosperm. The suspensor, exclusive of the haustoria, then presents a fibrous appearance, with little cytoplasm, and is little more than an irregular tube joining the bases of the haustoria and the embryo. The haustoria in some instances are very narrow, and extend to a considerable distance, passing beyond the embryo proper. Such narrow ones remind one of fungal hyphae, which pursue an intercellular growth, or of the pollen tube with its analogous behavior.

In the other species, for example *A. azurea* and *A. galioides*, the suspensor develops haustoria which, instead of penetrating to a distance into the endosperm, confine themselves to rather narrow limits, while the immediately surrounding endosperm suffers histolysis. All the preparations of plants in which this behavior takes place show a perfectly normal structure in the haustoria, in which the cytoplasm is very dense and finely granular as in *A. galioides*, while in the material in which they are embedded no trace of structure is visible, nothing, in short, but the mucilaginous irregularly staining products of histolysis.

As the embryo becomes older the haustoria become separated from each other but still keep a normal appearance. The study of a complete series, of which *pl. 8, fig. 6*, represents a component of three sections, shows no union between several of the haustoria, although this fact cannot well be shown in a drawing.

The behavior of the suspensor in the various species of *Asperula* is therefore so different, as well as the relation between it and the endosperm, that we are prevented from interpreting the facts in the same way. In some cases, as described, the relation involves histolysis of the endosperm, which indicates that, in such cases, the suspensor secretes an enzyme.

The earlier cell divisions of the embryo proper are as described in *Callipeltis.* It is to be observed, however, that the longitudinal divisions which are generally confined to the last four cells of the young embryo here take place also in a half dozen or more of the cells of the suspensor nearest the embryo (*pl. 8, figs. 4 and 5*).

Rubia tinctoria

(PLATE 9, FIGURES 1-6)

The nucelli of *Rubia* are recognizable by their form which in the young condition, before the integument has commenced to grow, is characterized by a sharp bend on the inner side of the funicle. The megaspore mother-cells are fewer in number and are of different proportions, being shorter and thicker than the same structures in the rest of the *Galieae* studied. Their nuclei are relatively larger (*fig. 1*). The tapetal cells fail here as elsewhere, and the division of the spore mother-cells is regular (*fig. 2*) giving rise to four equivalent spores. It is a common occurrence for several of the megaspores to divide with the result that a confusion is caused. The migration of the proper embryo-sac cell along the micropylar canal is accompanied by the usual divisions and the ultimate formation of an embryo-sac (*fig. 5*). The haustorial antipodal cell is broader and shorter than those of the foregoing forms. The other antipodal cells may be very small, and placed laterally or in some cases are quite large. In the former case they are filled with cytoplasm, in the latter case they have a cytoplasmic lining and the interior is filled by a large vacuole.

It is interesting to note that the embryo-sac nuclei do not cause the disintegration of the endodermis so rapidly as in other *Galieae*, and appear to force their way along the micropylar canal, without the immediate collapse of the impinging cells (*fig. 3*).

In many respects the features of the archesporium and of the embryo-sac present the same peculiarities as have already been described in *Asperula.* There is the same tendency towards the formation of supernumerary embryo-sacs, and the same characters are shown by the persisting megaspores (*fig. 4*), the nuclei of which are supplied with a scanty amount of cytoplasm, and are found lying freely in the irregular cavities left by the megaspore mother-cells.

After fertilization the endosperm grows very rapidly, and gets a large bulk. Although the growth of the embryo is immediate, and as rapid at least as in the other plants so far described, it is proportionately slower, so that in a fruit so large that one would naturally expect to find a large embryo, one finds, on the contrary, a young embryo without cotyledons. The endosperm has large cells and contains a very small proportion of plasma. For this reason the endosperm plasmolyzes very easily.

The suspensor of this form is very fully developed (*fig. 6*). The cell divisions are, at first, solely transverse. Soon, however, they become irregular and often strictly longitudinal, while all of the suspensor cells excepting a few disc-shaped cells near the embryo proper, and still fewer at the micropylar end of the suspensor develop into haustoria. The relatively greatest development is reached by the suspensor when the embryo proper has about eight to sixteen cells. The pressure exerted by the endosperm upon the suspensor, together with the direction of growth of the same causes the suspensor to be drawn out, so that the embryo proper appears to be anchored to the endosperm, which in this way is enabled to exert a tension upon the suspensor.

Crucianella

(PLATE 10, FIGURES 7–22)

Of the genus *Crucianella*, three species, namely, *C. gilanica*, *C. macrostachya*, and *C. herbacea* have been studied. These present certain anomalies which are of not a little interest in view of the close relationship between *Crucianella* and the rest of the *Galieae*.

The archesporium consists of 12 to 15 very large embryo-sac-mother-cells, which, however, vary between themselves in size. The largest occupy the more central position, and these are also distinguished by the completeness of their nuclear divisions; the other cells divide less regularly or not at all, and the more quickly show signs of degeneration. The cell walls between the mother-cells are very delicate, but are present and easily distinguishable.

The division of the megaspore mother-cells each into four grand-daughter cells is remarkably regular, and results in the formation of four megaspores which are alike in size, but not separated by cell walls. This feature, to which only very occasional exceptions may be found, may be regarded from the phylogenetic point of view as a step further removed from the condition in Angiosperms in general in which the tendency to form cell walls may be regarded as an inheritance from forms in which the megaspores are in maturity free bodies.

Similar failure on the part of the megaspores to form cell walls has been reported to occur in *Eichhornia* * and in *Avena* † and is probably of much wider occurrence than at present supposed.

Certain authors—Juel, Murbeck and Koernicke especially—have recently concentrated attention anew to the constancy and significance of these divisions—the tetrad division. In addition to the evidence adduced from the character of the nuclear mitoses, to which reference is made in another part of this paper, the facts which speak for the morphological equivalency of the cells which justifies the use of the term megaspores as applied to them have been set forth at length by Koernicke.‡

Remarkable as is the regularity with which the megaspore mother-cell divisions take place, still more so is the further division, in very many instances, of *all the megaspores simultaneously*. If we regard these as the first embryo-sac divisions, which we are justified in doing from a comparative standpoint, we are forced to regard the eight resultant nuclei derived from a single megaspore mother-cell as representing four embryo-sacs lying tandem. It has been determined by actual count that some ovules may thus be supplied with a dozen young embryo-sacs. Of these two or three of those derived from the megaspores lying adjacent to the micropylar canal may commence to develop into functional embryo-sacs. Only one, however, normally attains full development. The very evident physiological as well as morphological equivalency of the megaspores in this plant irresistibly compels the comparison with the conditions seen in certain heterosporous vascular cryptogams, especially with *Selaginella*, in which the majority of the megaspores serve as nutriment for the functional ones.

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* Smith, W. R. A Contribution to the Life History of the Pontederiaceae. Bot. Gaz. 15 : 1898.

† Cannon, W. A. A Morphological Study of the Flower and Embryo of the Wild Oat, *Avena fatua* L. Proc. Cal. Acad. Botany, III. 1 : 329. 1900.

‡ Studien an Embryosack-Mutterzellen. Sitzungsber. Gesellsch. Natur. und Heilk. Bonn, 1901.

The occurrence of such conditions in widely separated families is, however, a fact derived from comparative study, which warns us from inferring phylogenetic continuity. We are dealing here with *recurrent morphological structures*, called out in response to physiological necessities.

Of the four megaspores formed, although as just pointed out their activity is indicated by their tendency to further division, only the upper one, namely, the one furthest removed from the chalaza, develops into a functional embryo-sac. No exception to this rule has been observed. Instead, also, of enlarging directly at the expense of the other three by destroying and absorbing them, it moves into the micropylar canal, meanwhile growing at the expense of the adjacent tissue of the ovule (*figs. 18*, *19*, *21*, *22*). In so doing the nucellar capping cells are destroyed. The fate of the remaining megaspores of the tetrad is indicated in *fig. 19*, in which they may be seen to have undergone partial disintegration, and to have been drawn forward toward the embryo-sac as if by suction. This appearance is quite constant, and is difficult to interpret in any other way. That the materials derived from them by their gradual disintegration and that of the other megaspores are used by the embryo-sac is shown by their gradual disappearance inversely to the growth of the embryo-sac.

For some time during the development of the embryo-sac, however, the tetrad masses maintain their normal appearance, and indeed elongate considerably, but generally show signs of degeneration before it is completely developed.

At the time the embryo-sac cell commences its migration down the micropylar canal certain changes take place in inner layers of the adjacent integument These consist in the rapid growth of the cells to many times their original volume, and the pronounced enlargement of the nuclei (*fig. 13*). These cells appear to be very active, and in some cases they fail to secrete cell walls, so that we find occasional cells provided with several nuclei. This behavior of cells, namely, their failure to form cell walls immediately, appears to be connected with a highly nutritive function, and recalls the conditions in young endosperm, in the suspensor of some *Leguminosae* (Guignard, *l. c.*), and in the megaspore masses described above. Examination shows that this cell mass is a specialized portion of the ovule which is especially concerned in secreting starch, of which a very large amount is present, while it is at the same time absent from the rest of the ovule.

At the base of the archesporium the cells of the chalazal tissue appear, in a very early stage, just as the remainder of the cells of the ovule. As the integument develops, however, and therefore, as the archesporial cells increase in size, these chalazal cells take on a different character (*c.c.*, *figs. 7, 9 and 13*). From being small cells with a rather scant supply of cytoplasm, and relatively small nuclei, they become larger, their nuclei grow, and they become densely filled with cytoplasm. This appearance they maintain during the periods of growth of the archesporial cells, of their division into megaspores, and of the subsequent elongation of the tetrad masses. At the close of the activity of the latter the chalazal cells lose their supply of cytoplasm and return to the condition of the rest of the cells of the ovule.

We may therefore interpret them as physiologically active in the nutrition of the archesporium. Similar specialized chalazal cells have been described in many forms, more recently, however, in *Polypompholyx* * and in *Stylidium.*†

The embryo-sac cell moves rapidly along the micropylar canal, and as it moves forward the integumental tissue closes behind it. The course taken may readily be traced by the more deeply staining cell walls of those cells lying next to the canal. The division of the embryo-sac cell follows the usual order, as heretofore described.

In this genus, however, the development of the embryo-sac is marked by the very sudden disappearance of the antipodal cells. Of all the preparations made, in not one have all three of the antipodals been seen, although they are developed, as indicated in *fig. 21*, *ant.* The polar nuclei have been seen, and several cases have been found where one antipodal nucleus appeared normal. All the evidence indicates, therefore, that the sudden death of these nuclei is a character of the genus. It must however be noted that the antipodal end of the embryo-sac extends some

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* Lang, F. K. Untersuchungen über Morphologie, Anatomie, und Samenentwickelung von *Polypompholyx* und *Biblis gigantea*. Flora, 88 : 149–206. 1901.

† Burns, G. P. Beiträge zur Kenntniss der Stilidiaceen., Flora, 87 : 313–354. 1900.

distance backwards toward the archesporial tissue, and is in connection with the same by means of the micropylar canal.

The embryo and endosperm present no points of striking difference from the same structures already described in other *Galieae.*

Diodia Virginiana

(PLATE 12, FIGURES 1–12)

I am indebted to Professor Frank S. Earle for collecting and preserving material of this and the following species described.

NUCELLUS. STROPHIOLE AND INTEGUMENT

From the account already given of the origin in the *Galieae* of the nuclei and basal partition, we have seen that the former rise independently from the floor of the ovary, and that the latter even at maturity of the ovules reaches over to one-fourth the distance from the floor to the roof of the ovarial chamber.

In the forms now to be considered, however, a somewhat different condition is to be found. Here the basal partition originates at the same time with the nucelli, so that in an appropriate longitudinal section one sees a plate of tissue rising from the floor of the ovary, from the sides of which the nucelli, seen as hemispherical masses, take their origin (*fig. 1*). With the further development of the ovary, the basal partition and that formed by the upper parts of the carpels, grow with equal rapidity, so that at the time the embryo-sac is mature the floor and roof moities of the ovarial partition fuse at a point half way from the floor to the roof of the ovary. At this point, therefore, are inserted the funicles of the ovules, whose growth is such as to give rise to the amphitropous form (*figs. 2, 8, and 9*).

Early in the development of the ovule at the time when, in assuming the amphitropous position, its axis is passing through a transverse plane, a growth which superficially suggests an integument makes its appearance first on the morphologically lower sides of the funicle. Coincident with the origin of this organ which for our present purposes we call a strophiole, the single integument commences to develop as a ring-shaped fundament about the epidermal capping cells of the archesporium. The growth of the integument is such as to form a long micropylar canal, the mouth of which is ultimately covered by the strophiole. Certain features of special interest attach to this organ which will now be described.

In the first place, the supply of vascular tissue to the ovule is confined to the strophiole. A single strand of the same passes through the funicle and upon reaching the strophiole divides, sending one branch, the chief one, to the chalazal region of the strophiole, the other toward the micropylar region (*a* and *a'*, *figs. 2, 8, 9*). The chalazal branch (*a*) presents at its extremity a sharp turn towards the spot at which lies the archesporium.

Secondly the limit of the strophiolar tissue is sharply defined by the presence of a plate of brown-walled cells (*sp.* in the figures), having the same cytological characters as the epidermal cells of the integuments, which also become brown. In the young ovule the strophiolar plate is not to be seen, and has its origin at about the time the embryo-sac reaches its definitive condition, in scattered cells which marked the position of the plate, and which increase in number until the sheet of tissue is complete. When this takes place there are no fenestrations in the plate excepting a sometimes smaller one at the extremity of the chalazal branch of the vascular supply. It ultimately becomes continuous with the epidermis (*epi, fig. 9*) and thus the ovule exclusive of the strophiole comes to be completely surrounded by a sheath of cells with scanty plasmatic content, and deep brown walls.

In the third place the strophiole is characterized by the occurrence of a large number of excretory cells which become filled with raphides. When the seed is mature the strophiole carries a heavy load of calcium oxalate. As many as two hundred of the raphide cells have been counted. The remainder of the tissue is composed of cells which do not differ materially from the parenchyma of the integument. From the foregoing facts, it must be evident that the strophiole is the seat of special metabolic activity, during the growth of the embryo and endosperm, and that the strophiolar plate is of no special hindrance to the passage of proper food materials used by the embryo and endosperm.

Archesporium and Embryo-Sac

The archesporium is laid down in certain hypodermal cells of the nucellus of any early age. No tapetal cells are cut off, nor is there any further growth of nucellar tissue above the archesporium. The conditions then, are precisely as in the *Galieae* in which the archesporium is surmounted only by a group of epidermal capping cells. In the form, here being described, the archesporium, however, contains only one functional megaspore mother-cell (*fig. 3*) surrounded by a number—about a half dozen—of cells of similar character, but reduced in size, and as their later history shows, possessing usually no ability to divide or to act as embryo-sac fundaments. No instance has been found in which two embryo-sacs have been present in a single ovule, a witness to the reduced ability of these cells as compared with their homologues in the *Galieae*.

The functional megaspore, however, grows apace and is easily to be recognized by its size and appearance. Its cytoplasm, especially at its outer end, is of a loose reticular structure which, in this form in particular, is very marked. Whether by division this cell divides to form megaspores or not, I can not at present say. In the figure shown (*fig. 3*) the synapsis stage there represented indicates that such divisions do occur since the first division of the embryo-sac nucleus takes place, in a closely related plant, at a later stage. To say that a direct development of the megaspore mother-cell into the embryo-sac takes place would, however, in the absence of positive evidence, be gratuitous. We therefore assume that such is not the case until a more favorable opportunity is presented for more careful investigation of the point.

The embryo-sac cell, when the integument is well grown, is ready to commence its development. It is to be noticed that in the case before us the subsidiary archesporial cells do not suffer disintegration during the enlargement of the functional embryo-sac cell. The latter when fully developed pushes forward, causing disintegration of the epidermal capping cells and enters the micropylar canal. Down this it moves, dividing meanwhile so as to give rise to the usual complement of embryo-sac cells. The remaining undivided megaspore mother-cells follow the moving embryo-sac cell, and arrange themselves lengthwise in the archesporial cavity and the adjacent portion of the micropylar canal in such a manner as to form a continuous strand of elongated cells connecting the embryo-sac with the archesporial cavity (*figs. 4, 5, 12*). Near this point, as above pointed out, ends the chalazal branch of the vascular tissue of the strophiole. It must be further pointed out that the chalazal tissue cells are elongated between the archesporium and the vascular tissue, completing the path along which we may believe passes a supply of food materials from the parent plant to the developing embryo-sac. The persistence of the subsidiary archesporial cells with normal appearance until the endosperm is well developed sustains this view.

The embryo-sac in form is cylindric and presents, so far as the egg apparatus and endosperm nucleus are concerned, no point of special note. The fusion of the polar nuclei takes place quite near to the egg. The synergidae have well developed beaks which have been described for many forms and which I have referred to in another part of this paper.

THE ANTIPODAL CELLS

The feature of particular note is, however, to be found in the antipodal cells, which possess the power to divide, and form a tissue of considerable extent. The number of cells has been counted in several instances, and varies from four to ten. Frequently the several component cells are not separated by a cell wall, in which cases two or more nuclei may be found in a common mass of cytoplasm. The last antipodal is tapering in form, and overlaps the adjacent subsidary archesporial cells (*figs. 6, 12*), so that there lies, between the endosperm and the chalazal end of the vascular tissue, a continuous strand of transporting cells. There can be no doubt of the activity of the antipodal cells in this regard because of the following facts: The antipodal cells exhibit a degree of active growth, they are at all times richly supplied with starch, a substance which is abundant in the embryo-sac during its whole time of development, and they do not disintegrate, but, on the contrary, maintain their form and normal appearance for a long time after fertilization, while the endosperm is in its earlier most rapid growth. In appearance they are apparently similiar to the antipodal tissue described by Chamberlain (*l. c.*) in *Aster*. The coincident persistence of the archesporial cells is also noteworthy in this connection.

THE ENDOSPERM AND EMBRYO

The endosperm is at first parietal, and arises by free cell formation. At a somewhat early stage the central cavity becomes obliterated by the growth of the endosperm cells toward the center. Walls are then secreted and the tissue then presents in the main the same appearance as the endosperm in the *Galieae*. The peripheral cells, which are more densely filled with cytoplasm than the rest, appear to play the rôles of digestive and absorptive cells before which the integument breaks down as the endosperm grows. The integument breaks down with the usual appearances accompanying histolysis, although the cells of the micropyle resist the digestive action rather more than the rest of the tissue. The cells of the middle part of the endosperm, as the latter reaches a considerable size, present, on the other hand, a quite different character. They are larger and have contents which stain in such a way as to suggest that they also are suffering histolysis. A column of such cells extends from the embryo two-thirds of the longitudinal distance through the endosperm. As the embryo grows in length it comes to occupy this space, displacing the cells.

The embryo is of remarkably slow growth in the earlier stages of its development. The early growth takes place in the usual way, forming a suspensor of a few cells which are totally devoid of such outgrowths as have been described for the *Galieae*. The spherical form of the embryo proper is reached only slowly, and meanwhile the endosperm grows so as to reach nearly its final size. The later development of the embryo during which the cotyledons are formed is more rapid.

Diodia teres

(PLATE 12, FIGURES 13–17; PLATE 13, FIGURES 1–10)

THE NUCELLUS AND STROPHIOLE

With a trifling difference in the configuration of the nucelli, due apparently to the somewhat different mechanical relations in the ovary of this species, their behavior and that of the basal partition is the same as that in *Diodia Virginiana* (*pl. 12, fig. 13*). The insertion of the funicle, however, is not so far removed from the base of the ovary on account of the somewhat less rapid development of the basal partition. Quite soon the strophiole appears on the concave side of the funicle (*pl. 12, fig. 14*), and the ridge gradually extends to the opposite side. With further development the micropyle becomes entirely closed by the strophiole, which agrees with its homologue in *Diodia Virginiana* in being possessed of special excretory cells containing raphides in large numbers, and in being the organ in which the vascular tissue of the ovule is distributed. The cells adjacent to the vascular tissue are small and are more densely filled with plasma, and increase in size in approaching the integument. The latter is not delimited from the strophiole by means of the brown cells which have been seen in *D. Virginiana*, and which are absent from the ovule entirely. The epidermal covering of the funicle and part of the strophiole is strikingly developed, and has been described more fully in another part of this paper. It is sufficient at present to point out the fact that they are deep columnar cells with thickened walls, and form a collar of tissue about the funicle, but having no relation to the nutrition of the ovule (*pl. 13, figs. 1, 7, 8*).

THE ARCHESPORIUM AND EMBRYO-SAC

The archesporium is in all respects similar to that of *Diodia Virginiana* (*pl. 12, fig. 15*). Only one functional megaspore mother-cell is present which divides to form four megaspores (*pl. 12, figs. 16, 17*). One of these, probably the basal, judging from appearances, such as are seen, for example, in *pl. 13, fig. 2*, is the embryo-sac cell. This grows rapidly, becomes loaded with starch, and commences its migration along the micropylar canal. As the nucleus passes forward, a vacuole is formed behind it. This vacuole is also present in *Diodia Virginiana* (*pl. 12, figs. 2, 4, and 5*).

The embryo-sac when mature is comparatively short, and only three antipodals are present, and we notice that, although one of these is much larger than the others, it is nevertheless much reduced in length as compared with that cell in the forms previously described. The persistence of these cells for a considerable period, together with their heavy starch contents indicate that they have a considerable amount of activity. The functional activity of the antipodal cells even in this form where, to all appearances, they are of less importance than in the other plants studied, is indicated by the distribution of starch. In the unopened flower the embryo-sac is crowded with this food material, which is, however, absent from the rest of the ovule. As the flower opens, and at the time of fertilization, the starch disappears from the embryo-sac, first from the egg pole, so that in an old flower starch is entirely absent from the embryo-sac, but has commenced to accumulate at the chalazal end of the ovule. After fertilization, starch reappears in the antipodal cells, and then in the growing endosperm, so that when the latter has considerably increased (*pl. 13, fig. 6*), the former are very rich in starch content. In this connection it is to be noticed, also, that the subsidiary archesporial cells soon disappear, and take no further part in the development of the ovule. They are, in fact, quite lost to view when the embryo-sac contains but two cells. The endosperm nucleus lies appressed against the egg cell for some time before division. The endosperm is of the parietal type (*pl. 13, fig. 6*), and its behavior is similar to that of the same structure in *Diodia Virginiana*, as is also true of the integument.

The shape of the ovary is such that the chalazal end of the integument becomes folded over the strophiole, the whole producing the curious effect shown in *pl. 13, fig. 8.*

The embryo is slow in developing, and no haustorial outgrowths occur. The cells of the suspensor are at first short, and disc-shaped and later lengthen, bringing the embryo deeper in the endosperm (*pl. 13, fig. 9*). That the suspensor is not an organ of only mechanical significance may be inferred from the occurrence in it of a great deal of starch up to the time, at least, when the cotyledons are well started.

Richardsonia pilosa

(PLATE 13, FIGURES 11–18)

Material in cultivation at the New York Botanical Garden.

In the main, this plant agrees with the two species of *Diodia* as to the development of the ovule and archesporium, and of the embryo. The following important points of difference are to be noted.

The functional megaspore enlarges and develops into the embryo-sac *in situ*. In lengthening, however, it grows forward, and destroys the nucellar cap, so that these cannot be seen after the embryo-sac nucleus divides. No migration, strictly speaking, takes place, so that the antipodal cells appear in the position previously occupied by the archesporium. The few reduced subsidiary megaspore mother-cells are soon absorbed and are lost to view.

By the usual number of divisions the eight embryo-sac nuclei are formed, and the egg apparatus, polar nuclei and antipodal cells arrange themselves in an oval cavity. The antipodals are constantly three in number, and are in this plant all nearly of a size (*figs. 14, 15*). For some time they possess a large, deeply staining nucleus, finely granular dense cytoplasm, and a vacuole at their free ends, and present the appearance of certain glandular cells, especially the stigmatic cells in some plants, and of synergidae. This fact is important, as it indicates a considerable degree of physiological activity on the part of the cells.

After fertilization the embryo develops slowly, forming first by transverse cell divisions a row of disc-formed cells. The suspensor remains always a short organ, with no special adaptations. The endosperm is at first parietal, but early fills the cavity by equal centripetal growth on all sides. At such time as this occurs, there appear at the apex of the embryo certain very much enlarged cells of endospermic origin, with nuclei considerably greater than those of the rest of the endosperm cells (*fig. 18*). Beyond their size, as just indicated, these cells do not present any peculiarities, and it is therefore difficult to any whether they possess any special physiological peculiarities, although this seems probable. They correspond in general to similarly placed cells in other types described, as having a centripetally developing endosperm, differing from them chiefly in size.

As the ovule enlarges after fertilization the limiting cells of the strophiole take on the brown coloration already noted in *Diodia Virginiana*. This change spreads to the cells surrounding the end of the vascular bundle. The peculiar function of these cells, if such they possess, remains problematical. It is certain, however, that they exert no unfavorable influence on the passage of food solutions, whether they have any positive value or not.

Houstonia

(PLATE 14)

The two species of the genus *Houstonia* which have been studied are *Houstonia coerulea* and *H. longifolia*, both of which have been found to be in essential agreement.

The style, which in *Houstonia* is single, is provided with two stigmas, and arises by the concrescence of two ridge-like fundaments which develop, as in the *Galieae*, laterally and opposite to each other, in the inside of the hollow torus (*s*, *figs. 1, 2 and 3*). During concrescence a transverse ridge (*figs. 1, 2 and 3*) is formed on the inside of the ovary roof, which, by downward growth, ultimately divides the originally single ovarial chamber into two locules. This ridge, which may be described as hanging from the roof of the ovary, unites along its free lower border with a parallel, low broader ridge developed in the floor of the ovary. This floor ridge (*b*, *figs. 2 and 3*), which must be regarded as representing two fused carpellary margins, is not evident until the two rounded fundaments of the placentae (*p*, *fig. 1*) have reached considerable size. These two structures have the same position and appearance as the fundaments of the ovules in the *Galieae*. In the latter forms, however, the two carpellary margins produce each a single ovule; in *Houstonia* a knob-shaped placenta is formed in each locule occupying the same topographic relations as the ovules in the *Galieae*.

Each placenta soon begins to show a number of protuberant growths, which may early be recognized as the primordia of ovules. The development of these is of peculiar interest.

Up till the time when the archesporium is to be distinguished the course of development of the ovule is like that in the *Galieae*. A single row of epidermal cells cap the archesporium, but these cells, which in the *Galieae* remain without further division, in *Houstonia* suffer periclinal divisions (*fig. 4*), as do also the adjacent epidermal cells. This process is continued until the archesporium comes to lie in the middle of the nucellar mass. *No integument at all is developed;* indeed, the regular periclinal cell divisions which characterize the early stage in the development of the integument in the *Galieae* are absent. The suppression of the integument accounts for the absence of the micropyle.

By growth in all directions the mass of the ovule is increased, and finally a bowl-shaped form is attained, with the concave surface turned toward the placenta. This change in form is accompanied by lengthening of the funicle, which has histologically the appearance of being a part of the placenta, but which in reality is derived by the regular division of the cells (*figs. 8 and 10, ff*), which constitute a very short stalk in the younger condition.

It is interesting to note in passing that the "*nucellus nudus*" of Schleiden, which that botanist incorrectly thought to be found in certain Rubiaceae, is realized in *Houstonia*.

It must be evident that generalizations made heretofore with reference to the occurrence of ovules without integument in degenerate plants must fall to the ground.

THE ARCHESPORIUM

The archesporium consists of a single large embryo-sac-mother-cell, surrounded by a single layer of usually about six small slender suppressed ones which show no tendency to divide. They, however, do not all degenerate, but some at least take on special cytological characters and take up their position in the cavity vacated by the functional embryo-sac-mother-cell in its development (*fig. 9*). In this figure one may see two such mother-cells which have the appearance of glandular cells, resembling in this regard the antipodal cells. From the same figure it is also evident that some of the mother-cells persist in this character for a considerable period, until, at least, the completion of the embryo-sac.

When the growth of the nucellar cap has proceeded until the archesporium comes to lie in the middle of the naked nucellus, the division of the megaspore mother-cell takes place. Four megaspores arise by two divisions, of which, contrary to the general rule among the Rubiaceae studied, the basal megaspore becomes the embryo-sac cell. In *fig. 6*, in which the arrow indicates the egg pole, are shown the four cells, of which the basal is the largest. Its sister cell is small, while the remaining pair of cells are evidently destined also to be of small dimensions.

The embryo-sac cell develops into the embryo-sac *in situ*. *fig. 7* shows the two-celled, and *fig. 8* the four-celled, condition. The definitive condition is shown in *fig. 9*. In its growth, the embryo-sac destroys the surrounding nucellar tissue (*fig. 8*), but more rapidly in the direction of the egg pole, and leaving the tissue about the archesporium intact. The suppressed megaspores, which are represented on either side the functional one in *fig. 5*, meanwhile enlarge somewhat, and a vacuole appears in the cytoplasm. In this condition they may be seen, when the embryo-sac is mature, occupying the space previously mapped out as the archesporium, behind the antipodal cells, to which they are very similar in cytological characters, differing only in size. The antipodals are all of a size, densely filled with finely granular cytoplasm, and having a large vacuole in the end adjacent to the endosperm cells. Soon after fertilization both the megaspores, which persist up till this time, and the antipodal cells degenerate, and are seen as irregular, deeply staining masses.

Before the endosperm nucleus commences to divide it is seen lying against the young embryo. The growth of the endosperm is at first parietal, remaining so until two or three irregular layers of cells have been formed. As the result of the rapid increase in amount of vacuolation, however, the endosperm cells increase in size so as to obliterate the enclosed cavity, thus passing from the parietal condition to that found in the *Galieae*, but by a different mode of development (*figs. 10, 11, and 12*).

The development of the embryo is exceedingly slow. From the condition, in which it has a rather characteristic cylindrical form, it becomes multicellular by transverse divisions which occur slowly. No haustoria are produced, nor is there any point of particular interest in the later development.

When mature the seed consists of a seed coat of a few layers of very much compressed cells derived from the outer zone of the integument, enveloping the endosperm, which, in turn, surrounds the embryo.

The cells of the endosperm are rich in proteids with a few scattered starch grains. The cell walls are moderately thick, while those of the outer layer of cells are considerably thickened.

The separation of the seed from the placenta takes place at the plane of the insertion of the funicle in the seed, along the plane, therefore, in which the growth of the funicular cells by division takes place (*ff, fig. 10*).

SUMMARY AND CONCLUSIONS

The results presented in the foregoing pages have been derived from a study of 23 species representing 9 genera of the Rubiaceae.

In view of the great size and complexity of the family as at present understood, any conclusions based upon so small a proportion of the whole segregate may be applied with probable truth only to the genera represented by the species studied.

Of the lot, the *Galieae* have been the most thoroughly studied, and this group has been found to present a high degree of homogeneity, and the characters ascertained, with one exception to be noted below under *5* may be received as applying with only slight differences to all the plants of *Galieae*.

1. In all the plants considered, excepting in those of the genus *Houstonia*, two ovules are present. Their primordia arise in the floor of the ovary on either side the floral axis, and develop in such a manner as to produce approximately anatropous ovules provided with a single integument and with a greatly reduced nucellus which is not to be distinguished except at an early age, when it takes the form of a cap consisting of a single layer of cells crowning the archesporium. In the Compositae this layer forms a complete investment of an unicellular archesporium. It would appear, then, that the nucellus in these Rubiaceae is suppressed, a view however which is hardly in accord with the facts ; for the apparent lack of a nucellus such as we find in the Compositae, may be regarded as a result of the thickening of the tissue of the primordium about the sides of the archesporium and the origin of the much thickened integument nearer the morphological apex of the primordium. According to this interpretation the nucellus is marked by the more abundant growth of its sides and its intimate relation to the integument.

This circumstance, if, as I hold, a fact, leads to a difficulty n delimiting the nucellus as ordinarily defined, a difficulty however no greater than that encountered in defining any organ when viewed in the light of modern morphological conceptions.

2. In the *Spermacoceae* there is, in addition to the integument, a second outgrowth, derived from the funiculus and here called a strophiole. This structure contains the vascular supply of the

ovules and possesses also in large numbers special excretory cells which become loaded with raphides.

Similar cells are found in some *Galieae* in the immediate vicinity of the embryo-sac for some time before and after fertilization, and the rôle which the contents play in the physiological economy of the ovule is by no means clear.

It may turn out that in both instances the calcium oxalate is of some positive value, and the term "excretory" as used above must be regarded as provisional.

3. In *Houstonia* each locule of the ovary is provided with a club-shaped placenta bearing each a number of ovules. The topographic relations of a placenta in *Houstonia* and an ovule in the *Galieae* are the same, and no differences have been observed in their origin.

The ovules in *Houstonia* are relatively very small and of a very simple type in that an *integument is wholly absent.* There is accordingly no micropyle and the archesporium becomes deeply buried in the nucellar tissue by the growth of the capping cells and of the tissue at the sides of the archesporium toward the apex of primordium. The archesporium further consists of but one functional embryo-sac-mother-cell.

Two questions arise concerning the above comparison ; first, whether we may regard the ovule of the *Galieae* and the placenta with its ovules in *Houstonia* as morphological equivalents, and secondly, whether we have here a case of correlation.

To the first we can give no positive answer at present since a more careful study of the origin of the primordia is needed. If such should prove to be the case we should have a sort of branching or compound sporangium, a most interesting condition if true.

To the second question a more decided answer in the affirmative may be given in view of the fact that *where the placenta is formed the ovules are arrested* both as regards the integument and archesporium and in total relative size. That the archesporium is really suppressed appears from the fact that commonly about seven embryo-sac-mother-cells are laid down, all but one of which fail to reach the normal size.

It must be added that the belief that a simple naked ovule, that is, one without any integument, is correlated with the parasitic habit of growth, must now be thrown aside. This conclusion was suggested inferentially by Goebel* in connection with his observation on the ovules of *Crinum Asiaticum* of which he remarked: "Sie zeichnen sich durch eine, sonst nur bei Schmarotzerpflanzen bekannte Eigenthümlichkeit aus, sie sind nackt, es fehlen die sonst in Ein- oder Zweizahl vorhandenen Integumente."

4. The archesporium throughout contains a number (7–15) of megaspore mother-cells, the largest number occurring in the species of the *Galieae*. Each megaspore—barring the arrested ones at the side of the archesporium—divides twice to form four megaspores, which, except very infrequently, are not separated by walls. This condition is comparable to that described as occurring with some frequency in *Eichhornia* † and *Avena*.‡ All the megaspores are both morphologically and physiologically equivalent. It is, in consequence, impossible to pick out with the eye the functional megaspore, which appears usually to be the outer. As Koernicke § has recently emphasized, the embryo-sac cell in the great majority of Phanerogams is derived from the last megaspore, *i. e.*, the one at the chalazal pole, because usually the divisions which give rise to the megaspores are such as to give the largest proportion of plasma to that cell, a phenomenon which he holds to be connected with its more favorable position with reference to the source of nutriment. This view finds support in the facts here summarized in so far that the larger number of megaspores and undivided megaspore mother-cells form a nutritive tissue surrounding more or less completely the embryo-sac cell which arises near the longitudinal axis of the mass. That the functional megaspore, *i. e.*, the embryo-sac cell is found near the middle, and not in the sides of the archesporium is due, I hold, to the mechanical relation between the cells brought about by the growth of the ovule which is such as to produce no unequal pressure on the archesporium.

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* Biologische Schilderungen, 1: p. 129.

† Smith, W. R. A Contribution to the Life History of the Pontederiaceae. Bot. Gaz. 15: 324. 1898.

‡ Cannon, W. A. A morphological Study of the Flower and Embryo of the Wild Oat, *Avena fatua* L. Proc. Cal. Acad. Botany, III. 1: 329. 1900.

§ Studien an Embryosack-Mutterzellen. Sitzungsber. der Niederrhein. Gesellsch. Natur- und Heilkunde zu Bonn. 1901.

That, in forms in which a pluricellular megasporangium is present, any or all of the megaspores have the ability to develop into embryo-sacs proves in a most convincing manner the morphological equality of the megaspores, and the regular division of each of the megaspore mother-cells into four megaspores must be regarded as a true tetrad division.

At this point it is of interest to compare this result with those reached by Murbeck * who has studied *Alchemilla*, a representative of the Rosaceae. The presence of a multicellular archesporium in this family was first made known by Strasburger. † According to Murbeck twelve to sixteen mother cells are present, of which the peripheral and usually one of the centrally placed, fail to divide, and moreover *never give rise to embryo-sacs.* The remainder, six to nine in number, divide at least once and of the daughter-cells some divide a second time, and the granddaughter-cells thus formed are regarded, properly, as megaspores. It may be noted in passing that here there is no reduced number of chromosomes, reproduction being parthenogenetic. Of the megaspores thus produced, two or more may develop into young embryo-sacs, and what is of immediate and special interest in this connection, *in the same sporogenous cell-row, two or more may commence their development into embryo-sacs.* It thus appears that *Alchemilla* and *Crucianella* are precisely comparable in this regard; while the evidence derived from the latter is still more final because of the actual division of all the megaspores derived from a simple mother-cell. Further cytological evidence that these are to be regarded as true tetrad divisions is presented on another page.

It is scarcely necessary to add that these facts accord an extraordinary strength to the view that the ovule is a sporangium.

In the *Spermacoceae* and *Oldenlandeae* the archesporium contains only one megaspore mother-cell of special size, from which the embryo-sac cell is derived. Several suppressed megaspores are present, surrounding the large megaspore mother-cell, which divides to form four megaspores, the basal of which forms the embryo-sac cell.

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* Parthenogenetische Embryobildung in der Gattung *Alchemilla*. Acta. Reg. Soc. Physiogr. Lund, 11 : No. 7. 1901. For a more extended examination of the relevant literature see this valuable paper.

† Die Angiospermen und Gymnospermen.

The appearance of a pluricellular archesporium may by no means be considered as primitive. It has been shown by several workers to occur in widely separated families,* and with certainty may be said to have no phylogenetic significance. On the contrary, the meaning is purely physiological, and such conditions have arisen in various forms in response to similar conditions. When present they offer favorable nutritive conditions for the chosen embryo-sac. This view comports at least with the case of *Alchemilla* as interpreted by Murbeck (*l. c.*). The archesporial tissue not directly concerned in the formation of the embryo-sac takes activity or passively a nutritive rôle. If their rôle is passive they gradually disintegrate, and are absorbed. This appears to be the case in the *Galieae*, *Diodia teres* and *Richardsonia*. In the *Diodia Virginica* they grow chiefly in length and arrange themselves as a transporting tissue. As such they connect the embryo-sac with the vascular supply of the ovule, and persist for a considerable period after fertilization. In *Houstonia* the subsidiary megaspore mother-cells appear to persist till about the time the embryo commences to develop, and undergo regular and constant changes in size and form. These changes indicate their physiological importance.

5. The embryo-sac cell behaves in two ways. In *Houstonia* and *Richardsonia* it develops *in situ*. In the *Galieae* and in *Diodia* it moves forward out of its original position, breaking through the nucellar capping cells, and passing along the micropylar canal. Its passage is intercellular, and its action is so far analogous to the movement of the pollen tube, as described by Murbeck and myself. As it moves it derives nutriment from the disintegrating cells adjacent to it. The disintegration is such as to suggest very strongly the secretion of an enzyme by the embyro-sac.

The embryo-sac presents some remarkable features as regards the antipodal cells. These, in the *Galieae*, with the possible exception of one species of *Asperula*, are three in number, one of which is very much elongated. The free end of this cell is plunged into the mass of disintegrating megaspores and absorbs the same. The physiological importance of all the antipodals is indicated by

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* For full citation of the literature see the papers of Murbeck and Koernicke (*l. c.*).

their structure, persistence, food content, and the behavior of the surrounding tissues.

The genus *Crucianella* offers an exception to the general condition in the *Galieae*. Although antipodals are developed no evidence has been obtained that they take on any special cytological characters. Indeed their tenure of life is so short that the three antipodal cells have not been seen at the same time. Their function is probably, therefore, at best but passive, and is carried out by the mere giving up of their substance in death to the embryo-sac.

In *Diodia teres*, also, the number of antipodal cells is three, but present a difference in that the long one is relatively much shorter, a feature which is undoubtedly correlated with the smaller amount of archesporial tissue. They may, however, not be considered as physiologically inactive since they secrete a large amount of starch, and persist for a long time.

In *Diodia Virginiana* the number of antipodals is greater, the number varying, so far as observed, between four and ten. These are arranged in a long series, physiologically equivalent to the single long antipodal in the *Galieae*. The subsidiary megaspore mother-cells, as above pointed out, persist and form a continuation of the series. The antipodal cells retain their normal character for a considerable period covering the earlier period of endosperm development.

In *Richardsonia* and *Houstonia* the antipodal cells are equal in all regards, and appear to have less permanent value. They acquire the cytological characters of glandular cells such as are found in certain nectarial tissues and stigmas, and are probably active in some kind of secretion. Their relative small importance as judged by their size is connected with the behavior of the embryo-sac cell and the much suppressed archesporium.

That, in the words of Westermaier (*l. c.*, Part 1), we have to do, in the antipodals, with "an anatomical-physiological apparatus, and not with a useless rudimentary structure which may be understood only from the viewpoint of comparative morphology," * is evident from the facts as here summarized :

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* It is of great interest in this connection to recall the remark of Hofmeister made over fifty years ago : "Die am Chalaza-Ende entstandenen, durch ihre beträchtliche Grösse oft sehr ausgezeichneten Zellen scheinen keine andere Bestimmung zu haben, als die der Verarbeitung des Nahrungsstoffes für den werdenden Embryo." Die Entstehung des Embryo der Phanerogamen, p. 59. 1849.

(*a*) The form and cytological structure of these cells, and the changes of their food content.

(*b*) Their tendency in some plants to multiply and form a special tissue, of the nature of conductive or nutritive tissue.

(*c*) The behavior of the surrounding tissues notably the archesporial cells, which are absorbed.

We may not overlook the case of *Crucianella*, for which evidence is lacking that the antipodals play any but a very brief, passive rôle.

7. The embryo in the *Galieae* develops rapidly, especially in its early stage, and possesses a remarkable feature in the presence of a highly developed embryonic organ, the suspensor, the cells of which elongate laterally, and penetrate the surrounding endosperm in an intercellular manner without causing any disintegration of the endosperm. These outgrowths are termed haustoria. Analogous organs are known in a number of forms, and probably occur in many more in one form or another. The function of the suspensor in these forms is therefore not alone to bring the embryo into favorable position with relation to the food supply in a mechanical sense, but to act as a temporary embryonic root. This function is secondary, the former being regarded as primary, as for example in the case of *Selaginella* * in which it appears to have no further significance.

A strikingly analogous condition appears in certain species of *Tropaeolum*, according to Dickson,† in which the embryo produces " branches from the base of the suspensor " which " serve as organs of nutrition for the developing embryo—*foetal roots*, in fact." These organs penetrate into the pericarp.

Similar organs have been described by Treub ‡ in the Orchidaceae and by Hofmeister,§ followed by Guignard ‖ in the Leguminosae.

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* Pfeffer, W. Die Entwickelung des Keimes der Gattung *Selaginella*. Hansteins bot. Abhandl. 1 : No. 4.

† On the embryogeny of *Tropaeolum peregrinum* (L.) and *T. speciosum* (Endl. and Paepp.). Trans. Roy. Soc. 17 : Part 2.

‡ Notes sur l'embryogenie de quelques Orchidees. Naturk. Verh. K. Akad. 19 : 1879.

§ Die Entstehung des Embryo der Phanerogamen, 1849.

‖ Ann. sci. nat. VI. 12: 5. 1881.

It is, further, not improbable that the peculiar features of the suspensor in some Cruciferae, *Alisma* and many other plants are connected with similar physiological conditions.

The embryo in the *Spermacoceae* and in *Houstonia* develops very slowly, especially in its early stages. We have to note here the complete absence of the adaptive characters in the suspensor seen in the *Galieae;* the suspensor is of a very simple structure, and upon anatomical evidence alone we might attribute to it only the mechanical functions above indicated. In view of the distribution of food stuffs as already described, however, we must recognize the suspensor in these forms as a less special haustorial organ than in the *Galieae*, but still an organ of that nature.

It may further be noticed that the production of haustoria from the suspensor of the embryo, and, so far as known, from no other part, is probably an expression of polarity in the embryo.

8. The endosperm is of two kinds, according to its method of development, corresponding to two of Hegelmaier's * types.

In the *Galieae*, the endosperm during its whole course of development fills completely the endosperm cavity (Hegelmaier's first type). The peripheral cells on the basis of their cytological character and the behavior of the adjacent tissues may be regarded as concerned in the secretion of an enzyme, and in the absorption of the food derived by digestion of the reserve food substances in the integument.

In the *Spermacoceae* and *Houstonia* the endosperm is at first parietal, later coming to fill completely the enclosed cavity (Hegelmaier's second type). In addition to the peripheral cells, which appear much as in the *Galieae*, the centrally placed cells in *Diodia* and *Richardsonia* take on a more special character with a problematical significance.

THE TETRAD AND EMBRYO-SAC MITOSES

(PLATES 9 AND 11)

The following account of the mitoses of the archesporium and of the embryo-sac is based upon a study of *Asperula montana*, *Crucianella macrostachya* and *C. gilanica.* Of the two genera,

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* Untersuchungen über die Morphologie des Dicotyledonen—Endosperms. Nova Acta Akad. Naturforscher., 49 : No. 1. 1885.

Crucianella offered by far the more favorable material both on account of the size of the cells and of the absence of unequal pressure due to peculiarities in the development such as occur in *Asperula*. The former has therefore received more exhaustive study, although in regard to certain points *Asperula* has given important results.

When the ovule is young the embryo-sac-mother-cells are to be distinguished only by their greater size. During the early development of the integument, however, or even earlier, their cytoplasm becomes denser. At about the same time a large number of fibers appear in the cytoplasm traversing the cells longitudinally but in somewhat irregular fashion. The fibers are more or less curved and taper off at their ends.

Inasmuch as the embryo-sac-mother-cells attain a strikingly great length before the first division takes place (*pl. 10, fig. 16*) and have their cytoplasm crowded with these fibers, they present a very unique appearance. In some cases the fibers traverse the cells from end to end, bending aside to avoid the nucleus. The condition here described apparently corresponds to that found by Mottier * and Dixon † in *Lilium*, and by Duggar ‡ in *Symplocarpus*, during the earlier development of the embryo-sac mother-cell, excepting in certain matters of detail and interpretation.

From the figures of Mottier and Duggar one would judge that the fibrillar structures result from a rearrangement of the cytoplasmic reticulum. That the large thick fibers found by me in the developing embryo-sac-mother-cell are formed in the same way seems to me not to be the case, for, in addition to their great thickness, I have not been able to see a pulling out or distortion of the adjacent cytoplasm. Reference will be made to a possible interpretation of these structures beyond.

Again, according to Mottier, the orientation of the fibers in *Lilium* is not constant in different cells of the same stage of growth. They may run in various directions or they may sometimes form a dense felt-like zone about the nucleus. Further, this cytoplasmic differentiation disappears before the commencement of mitosis, and

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* Ueber das Verhalten der Kerne bei der Entwickelung des Embryosackes und die Vorgänge bie der Befruchtung. Jahrb. wiss. Bot. 31 : 138. 1897.

† On the chromosomes of *Lilium longiflorum*. Proc. Irish Acad. III. 10 : 716.

‡ Studies in the development of the pollen grain in *Symplocarpus foetidus*, and *Peltandra undulata*. Bot. Gaz. 29 : 81. 1900.

by inference, has nothing to do with the formation of the mitotic figure. At the beginning of mitosis the cytoplasm shows again a uniform reticular structure, and the spindle of the first division takes its origin in radial or more or less irregularly placed fibers which penetrate the nuclear cavity, and form a multipolar spindle primordium.

With regard to the disappearance of the earlier formed thick fibers I am not able to establish a parallel in the Rubiaceae, for, in the embryo-sac-mother-cell in the plants studied they persist until the earlier stages of mitosis, at least through diakinesis. That they are in some way connected with the kinoplasmic figure during mitosis would appear from the circumstance that their ends on reaching the nucleus bend and run as figured in Mottier's *pl. 2, fig. 17*, of the paper referred to. This condition, as seen in *Crucianella macrostachya* is shown in *pl. 11, fig. 37*. From this and the adjoining figures it will be seen that the origin of the spindle is multipolar, and, with the possible exception of the peculiar behavior above described, corresponds to the descriptions of Osterhout * and others. The definitive spindle of the first division is strictly bipolar, and differs in the three plants in one or two details of form only.

In *Crucianella gilanica* the spindle is of very regular, broad, oval form, with sharply-pointed ends; in *C. macrostachya* it has a looser, more slender form, with attenuated ends, while in *Asperula* this character is still more accentuated. Such differences may in the main be regarded as inconstant and of no general importance, and may in many cases also be appearances referable to the plane in which the material happens to be cut. Insufficient observation of this point may very easily lead to false impressions, as Strasburger † has hinted, especially with reference to the character of the spindle poles.

Generally the ends of the spindle poles lie freely in the cytoplasm, inasmuch as the spindle axis usually lies parallel to the longitudinal axis of the cell, which, as already shown, is very long.

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* Ueber Entstehung der karyokinetischen Spindel bei *Equisetum*. Jahrb. wiss. Bot. 30: 5. 1897.

† Ueber Reductionstheilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich. Jena, 1900.

Occasionally, however, the spindle is found to lie obliquely, and one or both ends may become connected with the ectoplasm.[*]

In no case is a centrosome or centrosphere to be found. I have been able to follow finely-pointed spindles to their extreme end without finding any trace of the body which can without doubt be regarded as such. In a recent paper by Meves and von Korff on the Myriopoda,[†] the "centralkörper" are described as lying very near to the periphery of the cell, and are apparently not directly in connection with the spindle. The latter, however, is not pointed, while its fibers nevertheless are directed toward the kinetic centers.

Thus is formed a condition in which the centrosomes are considerably removed but still in control of the spindle ends.

In spite of the obvious difference in the character of the spindle itself, I was led to examine carefully every part of the cytoplasm lying in or near the spindle axis, but with a negative result.

The multipolar origin of the spindle in certain plant cells has been for some time regarded by the majority of botanists as speaking against the existence of the centrosome in plants in which the spindle has such an origin. Although a contrary view has been held by Guignard[‡] it would still appear that the former position is more consonant with the facts as they are at present understood.

For we would expect in such cases either as many centrosomes as spindle ends, or two whose influence would be exerted over the whole kinoplasmic figure (archoplasm). The former is shown to be the case in the development of the curious worm-shaped spermatozoon in *Paludina*, an account of which has lately appeared.[§] According to Meves the centrosphere of the primary spermatocyte contains a number of central granules which act as a unit. In the second mitosis the granules (Centralkörperkörner) separate and take a position in the periphery of the cell, and from these as centers are formed a number of half or partial spindles. The result is a picture which resembles in its later development to some

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[*] Ectoplasm is here used to signify the "Hautschicht" of the Germans.

[†] Meves, Fr, and von Korff, K. "Zur Kenntniss der Zelltheilung bei Myriopoda. Archiv mik. Anat. und Entwickelungsgeschichte, 57: 481–486. *pl. 21.* 1901.

[‡] Centrosomes in Plants. Bot. Gaz. 15: 158. 1898.

[§] Meves, Fr. Ueber die sog. wurmförmigen Samenfäden von *Paludina* und über ihre Entwickelung. Mitth. Verein Schles.-Holst. Aerzte. 10: No. 1. 1901.

degree the multipolar spindle primordium in plants, to which the author unhesitatingly compares it, with the inference that the plant cytologists have still overlooked the structures in question. But the comparison is without warrant, for an examination of the facts shows that we are dealing with two different modes of action.

The origin of the spindle is in the two cases quite different. In *Paludina* it is in the periphery of the cell, while in the higher plants it is at the nucleus. The development of the spindle is in the former therefore centripetal; in the latter centrifugal. We fail therefore to see any warrant for the conclusion that there is any parallel between the phenomena described by Meves, and those seen in the formation of the plant spindle of multipolar origin.

The parallel fails also in the following regard. In *Paludina* the spindle fibers develop from the centers. In plants, even admitting the existence of centers, the fibers are developed to a very considerable degree before the centrosomes, or centrosome-like bodies, when such are recognized, appear.

For the present, therefore, we must adhere to the view that the centrosome is absent from the higher plants.

We do not attempt to meet in detail the statements in certain recent papers to the contrary. * It is quite impossible to do this except by working with the same materials and methods, and this has not been done by me.

Nor, as Strasburger (*l. c.*) has shown, is positive evidence against the occurrence of the centrosome in higher plants wanting. Repeated studies on pollen development have been carried out, showing that the ends of the spindle find an insertion in the ectoplasm and the results of my own observations tend strongly to confirm the view that the ectoplasm serves in many instances as a place of connection in those cells in which the spindle is long enough to bridge the distance from side to side. One instance (*Asperula*) was seen in which a pluripolar diarch spindle had its four apices (appearing in a single section) were all inserted in the ectoplasm (*pl. 9, fig. 16*).

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* Bernard, Ch. Recherches sur les sphere attractions chez *Lilium candidum*, *Helosis guyanensis*, etc. Jour. de Bot. 14: 118, 177, 206. 1900.

Yamanuochi, S. Einige Beobachtungen uber die Centrosomen in den Pollenmutterzellen von *Lilium longiflorum*. Bot. Centralbl. Beihefte, 10: 301. 1901.

Schaffner, J. H. A Contribution to the Life History and cytology of *Erythronium*. Bot. Gaz. 31: 369. June, 1901.

When, however, the true apex of the spindle does not insert itself immediately in the ectoplasm, one may usually discover a fine strand of kinoplasm extending from the apex of the spindle to the ectoplasm (*pl. 9, fig. 10*).

In further support of the view that the spindle often stands in some intimate relation with the ectoplasm I may cite the instance from which fig. 4 of Pl. 9 was taken. The axis is here oblique to the optical plane, and one pole is seen to end distinctly at a point from which extend fibers in a somewhat radial fashion. Careful examination revealed the fact that the radially placed fibers lay in the peripheral layer of the cytoplasm, that is in the ectoplasm, and the latter therefore appears to bear a distinct mechanical relation to the spindle.

In many cases in which the dimensions of the cell are much greater relatively to the size of the spindle such attachments have not been found. This lack is especially obvious in the large embryo-sac-mother-cell of *Crucianella*, in which, however, as in the pollen spindles, extra-nuclear "supporting fibers" may be observed to run out from the spindle apices to the ectoplasm in the direction of the equator (*pl. 11, figs. 16, 17*). Similar conditions prevail in the pollen mother-cell in *Crucianella macrostachya* (*pl. 11, fig. 35*), where but a single row of sporogenous cells occurs in each locule of the anther. The cells are relatively large and the mitotic figure in both the first and second divisions lies freely in the cytoplasm. In this instance neither the insertion of the spindle poles, nor of the extra-nuclear supporting fibers in the ectoplasm could be seen with certainty. Indeed the orientation of the spindle fibers during the second division is often such as to preclude the possibility of the insertion of one of the poles at least, as will be seen in *pl. 11, fig. 35*, which shows that the axes of the two spindles lay in the same plane at right angles to each other; unless, indeed, we may expect to find the pole of one spindle passing through the body of the other.

In the developing pollen in many plants a distinct zone of very granular cytoplasm has been described by Juel,* Lawson, †

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* Die Kerntheilungen in den Pollenmutterzellen von *Hemerocallis fulva* und die bei denselben auftretenden Unregemässigkeiten. Jahrb. wiss. Bot. 30 : 204. 1897.

† Some observations on the Development of the Karyokinetic Spindle in the Pollen mother-cells of *Cobaea scandens*. Proc. Cal. Acad. Botany, III. 1 : 169. 1899.

Byxbee, * Williams, † and others, and it has been suggested by Strasburger that, in those spindles of which the ends do not reach the ectoplasm, or in the absence of other mechanical support, the pericaryoplasm (of Lawson) may serve that purpose.

I have observed this zone in the plants under consideration, but in instances the poles of the mitotic figure reach the ectoplasm (*pl. 11, fig. 2*). In this event the zone thins out as it approaches the spindle pole. In the pollen mother-cell of *Crucianella macrostachya* this zone has not been observed and the spindle appears to lie quite freely and without any special mechanical relations.

The amount of variation in the observations of the topographic relations of the spindle ends leads to the suspicion that we are yet unable to form a satisfactory explanation of them. The most far reaching interpretation among the botanists is that of the Strasburger school, and is based upon the mechanical conception that the spindle is made up of contractile fibers (Zug-fasern) which, in order to pull apart the chromosomes, must have a more or less rigid mechanical support. This has been found in the ectoplasm, in the pericaryoplasm, in the vacuoles,‡ or the spindle ends may be buttressed by extra-nuclear supporting fibers.

That such mechanical relations as described by Strasburger and others really exist we may not doubt. All the appearances lead irresistibly to that conclusion. But I am by no means convinced that we may infer from these appearances anything as to the intimate workings of the mechanism, and the contractile fiber explanation may have to undergo perhaps a considerable degree of modification before it may be accepted as satisfactory.

Reference has already been made in another part of this paper to the absence of cell walls between the megaspores. It will be seen from *pl. 11*, *fig. 20*, and *pl. 9*, *fig. 23*, that the connecting fibers are formed, and the thickenings indicative of the cell plate are present. In *Crucianella* the presence of these fibers determines the appearance of the cytoplasm for some time (*pl. 10*, *fig. 9*). At the end of the third division in the same plant the nuclei are

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* The Development of the karyokinetic Spindle in the Pollen Mother-cells of *Lavatera*. Proc. Cal. Acad. Botany, III. 2 : 63. 1900.

† The Origin of the karyokinetic Spindle in *Passiflora coerulea* Linn. Proc. Cal. Acad. Botany, III. 1 : 189. 1899.

‡ Strasburger, l. c.

arranged sometimes in two rows, and the connecting fibers run from one nucleus to the other in such a manner as to recall Mottier's* figure of the four nuclei in the upper end of the embryo-sac in *Helleborus foetidus*, and the appearances which one usually meets with during the formation of cell walls in endosperms (*pl. 10, fig. 18*).

The prophase of the first division in both pollen and embryo-sac-mother-cells is characterized by the stage known as diakinesis (of Häcker), in which the chromosome pairs become condensed into short, thick rods which lie parallel or become partially twisted about or crossed upon each other. The members of each pair may fuse at one or both ends, and as the result of more or less separation in the middle, may take also the form of rings either completely closed, or open at one point. Between these more definite forms the chromosome pairs may assume all sorts of intermediate conditions (*pl. 11, figs. 1, 14, 32, 37, 38*).

In some instances the members of the chromosome pairs may be separated from each other for a considerable distance, and the linin strands which unite their ends, may under such conditions be seen with the greatest clearness (*pl. 9, fig. 21, a*). In *Galtonia candicans*, according to Schniewind-Thies † the same behavior has been noted.

The formation of the rings takes place much more completely and earlier in *Asperula* in which genus also the condensation of the large loose rings into small thick ones may be followed with ease (*pl. 9, figs. 1 and 2*). The appearances so presented recall the figures of vom Rath ‡ of the chromosome rings in *Gryllotalpa* excepting, however, that no phenomena of tetrad formation (in the sense of the zoologists) may be observed.

During the prophase of this division the number of chromosomes may in these forms quite easily be determined and with a high degree of certainty has been found to be *one-half the usual number in the sporophyte.* The reduced number, which has been determined by counts, not only in the prophases, but in the ana-

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* Ueber das Verhalten der Kerne, etc. Jahrb. wiss. Bot. 1897.

† Die Reduction, der Chromosome Zahl und die ihr folgenden Kerntheilungen in den Embryosacmutterzellen der Angiospermen. Jena, 1901.

‡ Zur Kenntniss der Spermatogenese von *Gryllotalpa vulgaris.* Arch. Mic. Anat. 1892.

phase of the first and second pollen division and in the first, second, third and fourth embryo-sac divisions, is in *Crucianella* the hitherto unobserved and surprising number ten, in *Asperula*, twelve.

These numbers, however, are believed, on the basis of a large number of counts at different times, to be inconstant. In *Crucianella* eight to eleven have been counted, and in *Asperula* a similar amount of variation has been observed. Allowing for error in counting, which, in these plants is not great, both on account of the smallness of the cells (with the consequent frequency with which the whole nucleus appears in a single thick section) and of the number of chromosomes, I believe it must be maintained that *variation in this regard occurs*, and that this is a fact which has heretofore received insufficient recognition.

The condensation of the chromosome pairs proceeds all through the prophase until the equatorial plate has been completed, when they take the form of a double Vs, one of which lies above and one below the equatorial plane, with their angles directed toward the axis of the spindle. This arrangement is difficult to recognize in metaphase on account of the extreme condensation of the chromosome, but in very early anaphase may be seen with sufficient distinctness.

My observations and conclusions appear to coincide with those of Duggar * for *Peltandra*. That author's interpretation of his figures of the corresponding division in *Symplocarpus* as indicating a qualitative division, however, would in my judgment seem not to be justified. For the chromosomes are here, as represented in *pl. 1, figs. 7 and 7a* of Duggar's paper, of double V-form with the angle directed toward the center of the spindle. These separate first at the angle, and the degree of similarity in the two plants is so great as to render them susceptible of but a single interpretation, which is opposed to the view that there is a qualitative division, unless it can clearly be shown that the separation of the limbs of the V is a separation, not at their ends, but across the middle of the chromosomes.

Attention should further be directed to the above mentioned observation, namely, that in diakinesis and the later prophase the

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* Studies in the development of the pollen grain in *Symplocarpus foetidus* and *Peltandra undulata*. Bot. Gaz. 19: 81. 1900.

ends of the chromosome pairs do not invariably fuse even when they take the form of rings. With the approach of metaphase the two members if separated become laid together. The fixation of the fibers then takes place somewhere between and not at the ends of the chromosomes, so that the possibility of the occurrence of a transverse splitting of the chromosomes at this time, as suggested most recently by Schaffner * for *Erythronium*, seems to me to be excluded.

If the ends of the chromosome pairs always fused completely it would probably be impossible to tell whether the breaks during anaphase occurred at the points of fusion or somewhere between these. When, however, such a fusion does not take place the simpler and more obvious interpretation does not involve the idea of a reducing division.

The separation of the daughter chromosomes takes place with extreme regularity but curiously enough with quite constant differences in the two genera. In *Asperula* the ends of the daughter Vs separate simultaneously and the chromosomes take with little variation the form of a conventional heart. This is to be explained by the shortness of those bodies and the point at which the fibers are inserted (*pl. 9, figs. 3, 22*).

In *Crucianella*, on the contrary, the ends of the V-formed segments scarcely ever separate at the same time. The ones which remain united the longer are attached to each other with so great a degree of firmness that it is only after the greater mass of each daughter chromosome reaches about half the distance to the spindle poles that they finally separate (*pl. 11, figs. 2, 3, 16, 17, 18, 39*). The forms taken by the separating chromosomes under these conditions have received special study, and all of them suggest very definitely the behavior of plastic masses under tension. Examination of the detailed representations on *pl. 11* (*fig. 3, a–f; fig. 18, a–g*) will reveal this point quite clearly. Especially instructive are such forms as shown in *fig. 18, a*, as they bear on the question of transverse division. Were the chromosome here breaking transversely and not undergoing separation at united ends, it is difficult to see why such a bulge at the point of separa-

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* A Contribution to the Life History and Cytology of *Erythronium*. Bot. Gaz. 31: 369–387. 1901.

tion should occur. On the other hand, it is quite easy to understand such an appearance on the supposition that a plane of adhesion exists at that point.

Whether the unequal separation of the daughter chromosomes is due to the failure of the mantle fibers to exert an equally distributed pull upon them, or to the fact that the fusion of the chromosome ends is not equal cannot be determined. It is a further point worthy of note that the two free ends of an incompletely separated chromosome pair are always directed away from the spindle axis, as if the mantle fibers were stretched along a resistant surface. After the separation of the daughter chromosomes is complete, a readjustment of tensions takes place so that the heart-shaped form spoken of in connection with *Asperula* is approached (*pl. 11, figs. 4, 16, 17, 18, g*).

During late anaphase a second longitudinal splitting of the chromosomes is seen with a fair degree of clearness (*pl. 9, figs. 6–9*). On account of the shortness of the resulting chromosomes, however, it is not easy to determine the forms which they take. For the most part they appear as pairs of straight rods, although some evidence that they are slightly bent into a V is seen. It is not at all improbable that a considerable amount of readjustment in the relations of mantle fibers and chromosomes takes place and this would explain the change in the shape of the chromosomes.

The appearances here described have been constantly seen in a large number of cells and there is very little doubt that the first division in *Asperula* is heterotypic in the sense adopted by Strasburger (*l. c.*, 99).

The corresponding longitudinal splitting of the chromosomes in *Crucianella* does not take place so early as in *Asperula*, and may be seen with clearness only in the telophase. *Pl. 11, fig. 5*, represents such a stage. It appears not possible to resolve the chromosome pairs thus formed during the whole of the period extending from this time till the metaphase of the second division; for as shown in *pl. 11, Fig. 6*, the pairing is indistinguishable, although a completely resting condition, as described for *Larix* by Juel,* in

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* Juel, H. O. Beiträge zur Kenntniss der Tetradtheilung. Jahrb. wiss. Bot. 35: 626. 1900.

Pellia, by Davis,[*] in *Asclepias*,[†] by Strasburger, and in certain Liliaceae by Schniewind-Thies [‡] has not been observed to occur.

From the facts above presented it will be seen that in *Crucianella*, as in *Asperula*, the first splitting of the chromosomes is longitudinal. In early anaphase the daughter rods which open out from a double V-form into rings, separate finally at the ends of the limbs of the V, the angles being directed toward the pole. Later a second longitudinal splitting appears, the formation of grand-daughter rods being completed before the close of the first mitosis. This division is, therefore, heterotypic and corresponds in essential details to the heterotypical mitosis in the spermatocytes of the salamander as described by Flemming.

The final evidence for this conclusion in regard to the embryo-sac-mother-cell has not been obtained without any doubt, but I believe that we may conclude from the otherwise complete correspondence in the two cases that the first embryo-sac-mother-cell division is also heterotypic.

The resting stage occurring between the first and second divisions is characterized by its short duration, and by the varying degree of diffusion of the chromatin. This variation is considerable not only among related species, but is evident in comparing the pollen and embryo-sac tetrad divisions in the same plant, as Strasburger § has observed to be the case in *Lilium*. It is notable that in the Rubiaceae also the daughter nuclei of the pollen mother-cell enter the resting stage less completely than in the corresponding nuclei in the ovule. If this prove to be generally true we may attribute the behavior to the closer analogy between the tetrad divisions in pollen and those of cryptogams, and the greater irregularity in the tetrad divisions in the ovule to the changed conditions which have been brought about in that organ.

Although the variation in the character of the resting stage is

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[*] Davis, B. M. Nuclear Studies in *Pellia*. Ann. Bot. 15 : 147. 1901.

[†] Einige Bemerkungen zu der Pollenbildung bei *Asclepias*. Ber. deutsch. bot. Gesellsch. 19 : 450. 1901.

[‡] Schniewind-Thies, T. Die Reduction der Chromosomezahl und die ihr folgenden Kerntheilungen in den Embryosacmutterzellen der Angiospermen. Jena, 1901.

[§] Ueber Cytoplasmastructuren, Kern und Zelltheilung. Jahrb. wiss. Bot. 10 : 252. 1897.

real and considerable, all the cases studied are alike in the absence of a nucleolus, in the indistinctness of the nuclear membrane, which appears as if surrounded by an ill-defined zone of fine kinoplasmic fibers running in various directions, and in the loss, at least so far as direct observation can take us, of the individuality of the granddaughter chromosomes, even when, as in *Crucianella*, the second splitting takes place in early telophase.

The occurrence of a more or less complete resting stage at the end of the first division is a phenomenon of wide occurrence among the phanerogams. Authors are not agreed, however, as to the degree into which the daughter nuclei enter at this stage. More recently Schniewind-Thies has found a considerable amount of variations in a number of forms studied comparatively by her. It appears, therefore, that we may explain this disagreement on the ground of the occurrence of a considerable degree of variation in this regard.

It does not appear to be necessary to be concerned about the loss of individuality by the chromosomes under the circumstances at least so far as the question of reduction is involved. A second longitudinal splitting being demonstrated to occur before this takes place, we are compelled to believe in the absence of positive evidence to the contrary that the rehabilitation of the chromosomes is complete. The Weissmannian interpretation once shut out, it remains for us to explain the variable degree into which the granddaughter nuclei enter the resting condition apart from it. I cannot agree with Davis, nor do I find for him any justification in the literature of the subject, either on the zoölogical or botanical side of the question, when he remarks "This conception * is intimately concerned with, and necessarily a part of, the recent studies of Guignard and Strasburger on the double longitudinal splitting of the chromosomes." (*l. c.*, p. 159.)

Indeed Strasburger himself has recently shown that in *Asclepias* (*l. c.*) a complete resting stage, with a nucleolus, is formed between the first and second pollen divisions, without making any remark further than to call attention to the fact.

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* That the chromosomes maintain their individuality in the daughter nuclei after the first mitosis of the pollen mother-cell.

THE SECOND DIVISION

During the prophase of the second division in the embryo-sac-mother-cell delicate radiating fibers in great numbers are found surrounding the nucleus and extending from the same in all directions (*pl. 11, fig. 42*). In certain cells where the walls come into contact with the nucleus these fibers then appear in sections as if there were two distinct systems arising from the opposite sides of the nucleus. They thus simulate asters. In point of fact, however, they form a zone about the nucleus lying parallel to the compressing cell walls (*pl. 11, fig. 15*).

Such radiations have been figured and described by many authors, but accounts are, in spite of a multitude of detail, still in such a condition as not to warrant us in believing that we as yet understand fully the relation between the nucleus and these radiations.

Their resemblance, however to certain appearances is parthenogenetically developing eggs of *Toxopneustes* after treatment with magnesium chloride has led Wilson * to make the following suggestion which I give in his own words.

"The formation of a perinuclear zone in the magnesium eggs strongly suggests the accumulation of 'kinoplasm' about the nucleus in the early prophase of cell division in the higher plants, as described by Osterhout and Mottier, and a number of later observers, though the later phenomena are in many respects very different."

According to Wilson's direct observations on the living Mg-eggs, a primary radiation appears surrounding the nucleus and extending far out to the periphery of the cell. This radiation is interpreted as a flow of hyaloplasm which, in part at least, gives rise to the appearances making up the "aster." The gradual disappearance of these radiations is accompanied by the formation of a clear perinuclear zone, followed by "enlargement of the nucleus and the disappearance of the nuclear membrane accompanied by a reduction of the rays almost to the vanishing point." (*l. c.*)

The comparison is strengthened by the facts described earlier

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* Experimental Studies in Cytology, I. A cytological Study of artificial Parthenogenesis in Sea-Urchin Eggs. Archiv Entwickelungsmechanik der Organismen. **12**: 529. 1901.

in this paper in connection with the development of the embryo-sac-mother-cell. The numbers of fibers then seen and their apparent behavior with respect to the nucleus, as already indicated, in many ways harmonize with Wilson's suggestion. If further study should show this harmony to be complete, we would then have strong grounds, in the absence of direct observation of the living material, for the belief that these fibers are currents of viscid material (kinoplasm, hyaloplasm) the view first taken by Auerbach, and later adopted by Fol, Strasburger † and others in modified form.

It would appear that a further and more particular study of the behavior of the kinoplasm during the prophase in plants from the suggestive point of view just indicated would have a distinct bearing upon the vexing problem of the nature of the fibers.

In the prophase of the second division the granddaughter chromosomes reappear in *Crucianella* as pairs of rods lying parallel to or partly twisted about each other and lying on the nuclear walls (*pl. 11, fig. 21*). In *Asperula* the chromosomes are so short that they appear as pairs of spheres (*pl. 9, fig. 16*), though in metaphase they frequently appear as pairs of short rods, one lying above and one below the equatorial plate. The mantle fibers are usually attached to the chromosomes at their ends, one chromosome lying above and one below the equatorial plane (*pl. 11, figs. 8, 22 and 35*). Occasionally, however, they may be attached at some point along their length. During anaphase, therefore, the chromosomes have the form of short rods with their longitudinal axes directed toward the spindle poles (*pl. 11, fig. 24*), or less frequently of bent rods with the loop similarly directed (*pl. 11, fig. 25*). There are some minor differences between the form of the chromosomes in the second pollen- and embryo-sac-mother-cell divisions. In the latter the rods are longer and more slender (*pl. 11, fig. 24*); in the former shorter and thicker (*pl. 11, fig. 9*). On account of this fact and the further one that in *Crucianella gilanica* the spindles are very small in the pollen cells, the character of the structures is rather difficult to determine. In *Crucianella macrostachya*, in the anther locules of which but one row of pollen mother-cells is present, the opportunities

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† Zellbildung und Zelltheilung. 3 Aufl., 367.

for observations are better, and here the chromosomes are seen distinctly as paired rods, with the fibers for the most part attached to their end (*pl. 11*, *figs. 35 and 36*).

The contrast offered between the appearances seen during the first and second divisions are well seen in *pl. 11*, *figs. 16 or 17*, *and 24*, all of which have been taken from the same ovule. The spindles shown in *figs. 16 and 24*, *pl. 11*, may indeed be seen in the same field in adjacent megaspore mother-cells.

According to the interpretation here given of the behavior of the chromosomes the application of the facts to the Weissmannian view of reduction is made impossible.

That, however, a real reduction in the quantity of chromatin occurs as well as a reduction in the number of chromosomes has been held by Guignard, according to whom the second division which follows on the first without pause reduces the nuclein which the grand-daughter nuclei receive by a half, compared with the amount which the ordinary nuclei of the sporophyte have. Such reduction, however, results in equivalent cells as regards their hereditary qualities.

A reduction in this sense certainly occurs in the plants under consideration, if we may argue from the relative sizes of the nuclei. The figures which present the facts, namely, *pl. 11*, *figs. 6 and 13*, are drawn to the same scale and show that the nuclei at the end of the second division are much smaller than those at the end of the first. True, the cells themselves are also smaller and this indicates that the cause of such quantitative reduction is to be found in the rapidity with which the divisions follow each other, thus preventing an intervening period of growth.

THE THIRD DIVISION

The resting stage at the close of the second division is complete, a nucleolus is formed, and a considerable pause intervenes before the third division takes place.

It has been already pointed out on another page that in the genus *Crucianella* the megaspores are unique in that they are all functional in so far that they frequently undergo the first embryo-sac division. All the divisions which take place in this way are alike in character, that is they are typical mitoses. The further divisions of the supernumerary megaspores have not been observed in any other genus, and in all probability do not take place. It would appear from comparative study that the large size of the megaspores and the absence of compression by the surrounding tissues offer favorable conditions for the access of food materials and the equally rapid development of all the daughter and granddaughter cells, thus giving them an equal start as embryo-sac cells. The embryo-sac cell which finds itself in the most favorable position as regards the micropylar canal then commences a more rapid development, which takes place at the expense of the remaining megaspores. In the prophases of the third and succeeding divisions the chromosomes are about twice as long as those in the second division, the fibers are usually attached at about their middle point, where they are bent at a slight angle; the angle is directed toward the center of the spindle (*pl. 11, figs. 27, 30*). This division conforms, therefore, to the ordinary vegetative or typical division, differing only in the possession of the reduced number of chromosomes, which have been determined to be in *Crucianella* ten. It is not necessary for our present purpose to describe the remaining divisions in detail, more than to say that they fully correspond in character to the third.

The embryo-sac divisions in *Asperula* were not studied.

SUMMARY AND CONCLUSIONS

1. During the growth of the embryo-sac-mother-cell before the first division a large number of coarse fibers are present in the cytoplasm which persist through diakinesis of the first division. These are, in part at least, continuous with the circumnuclear complex of fibers preceding the formation of the spindle, and do not result from a rearrangement of the cytoplasmic reticulum. Further it is suggested that they be interpreted as currents of kinoplasm (hyaloplasm) corresponding to the radiations described by Wilson as occurring in the sea-urchin egg.

2. The spindle in both pollen- and embryo-sac-mother-cell is of multipolar origin. The nucleus is at first surrounded by a feltwork of curved tangentially placed fibers which gradually segregate into conical groups. By fusion of these groups a bipolar spindle is formed.

3. Centrosomes or centrosome-like bodies are not present. The poles of the spindle are finely tapering points with various topographic relations described in the body of the text. The suggestion made by Meves, prompted by his observations on *Paludina*, is not pertinent.

Under certain conditions, as for example in the pollen-mother-cell, where the proportions of the cell are not too great relatively to the size of the nucleus, the spindle ends find an insertion in the ectoplasm. At the point of insertion a small thickening may frequently be seen, and from this point run out radially placed, branching fibers in the ectoplasm. It is suggested that these are currents in the ectoplasm and may represent kinoplasm passing from the spindle into the ectoplasm during anaphase.

4. At the end of the first and second embryo-sac-mother-cell divisions, and at the end of the third division also when such occurs, as is generally the case in *Crucianella*, a system of connecting fibers arises without, however, the formation of cell walls. The megaspores and their derivatives in *Crucianella* remain in a syncytial condition.

5. A reduced number of chromosomes appears in the prophase of the first division of the pollen- and embryo-sac-mother-cells; in *Crucianella* this number is ten; in *Asperula* twelve. These numbers are maintained throughout the subsequent divisions.

The prophase of this division is characterized by the stage known as diakinesis. The metaphase offers on the whole the same characters as have been described by a number of authors for various plants and differs from them only in points of detail referable to the proportions of the chromosomes. The frequently difficult observation of the so-called ring form of the chromosome pairs in metaphase is a case in point. When the chromosomes are relatively more slender, as in the Liliaceae, the appearances are relatively more distinct. In many other plants they are less so on account of the extreme shortness and thickness of the chromosomes.

The second splitting of the chromosomes is longitudinal, and takes place in *Asperula* during the late anaphase of the first division. In *Crucianella* a similar splitting of the chromosomes takes place in the telophase of the first division and is here also longitudinal.

The first division in these plants is therefore heterotypic, in the sense of Flemming and Strasburger, and the second is homotypic, and results merely in the separation of the granddaughter rods already formed. The individuality of these bodies is, however, lost, so far as can be seen, in the resting nucleus preparatory to the second mitosis by fusion of the rods and by more or less complete diffusion of the chromatin.

It is concluded from this evidence that the divisions described are true tetrad divisions, and the four resultant cells as spores. It has on several occasions been urged that the position of these cells in the nucellus of angiosperms speaks against this interpretation, but it is not surprising that such an arrangement should occur in the ovule when we remember that the position of the spindle and through the spindle often of the cell wall is determined by growth, and that the growth of the sporogenous tissues is conditioned by a very different sort of environment from that found in the sporangium of the pteridophyta.

But the evidence is fast accumulating to show that it really frequently happens that the divisions are not such as to produce a single row of cells. This evidence has recently been collated by Max Koernicke [*] to which may be added the cases recorded by G. M. Holferty [†] as occurring in *Potamogeton.*

Adding to the above the facts derived from a cytological study of the divisions themselves, I fail to see the cogency of the statement made by Atkinson [‡] that the embryo-sac of the angiosperms "arises directly from the nucellar (sporangial) tissues or from the archesporium, without the intervention of spores." That the spores in many forms are losing or have already lost their physiological identity as spores is indeed true, but it is certainly a most remarkable fact that cannot be brushed aside that in the most extreme cases *Lilium* for example, the process of giving rise to these, cells is identical in all essential respects, to the process in all other plants, both pteridophyta and spermatophyta, in which this point has received careful study.

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[*] Studien an Embryo sac Mutterzellen. (*l. c.*)

[†] Ovule and Embryo of *Potamogeton natans.* Bot. Gaz. 13 : 339. 1901.

[‡] On the Homologies and probable Origin of the Embryo-sac. Science, II. 13 : 530. 1901.

On similar grounds the failure of the megaspores to form cell walls might be urged against the interpretation of these cells as such, but here again this character has dropped out without, it seems to me, invalidating the view that the cells in question are spores which are thereby removed one step further from their more primitive condition in which a cell wall was eminently necessary.

To be sure we are not rid of the conclusion that, in those plants in which the embryo-sac arises directly from the mother-cell the embryo-sac is constructed, so to speak, of four spores ; or that, when the mother-cell suffers one division giving rise to two daughter-cells of which one only is functional, the embryo-sac is constructed of two spores. But after all, spores, in the sense here meant, are equivalent vegetative cells of a somewhat special sort, but with no necessarily separate existence, teleologically speaking, except in those plants in which the spores are the functional equivalent of the seeds in the higher plants.

The conclusion is therefore drawn that the cells under discussion are distinguishable by their origin, that they are not cut out of the cycle of development and that their morphological persistence is connected with the function of the mitoses ; while on the other hand, the spore "*as such* * * * is wanting" * because the particular features of specialization which characterize spores have been lost in connection with the loss of the more primitive spore function.

The following question is very naturally raised at this point, namely, at what point in the life cycle does the gametophyte commence its existence.† There can of course be no categorical, or at least no final answer given under our present understanding. But we may state as fairly in accord with the facts, that the morphological identity of the gametophyte has been reduced along with the change in the function of the spores, and the two periods of development have been merged into each other, to different degrees in different plants. In the most extreme cases, as *Lilium*, the gametophyte appears to commence histologically with the embryo-

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* Atkinson, *l. c.* The italics are his.

† Coulter and Chamberlain in their recently published volume "Morphology of the Spermatophytes" (New York, 1901), take a tentative position. In their accounts they "close the history of the sporophyte with the appearance of the spore mother-cell," since it seemed to them "to be the best defined line of demarkation" (page iv).

sac-mother-cell. Against the adoption of such an interpretation it may be urged that, where each of four spores form the primordium potentially or actually of an embryo-sac, the gametophyte becomes spilt up into four individuals. To be sure there are analogies to come to our aid, such as the constant development of four embryos from a single proembryo or the much more widely distributed phenomena of vegetative reproduction.

But in spite of these analogies, it would seem more natural to regard the gametophyte as *an individual by coalescence*, having its origin in four like vegetative cells whose primitive function has been lost. These four cells become grafted on each other, so to speak. The chief difficulty seems to be due to our formal conceptional idea of an individual, which in nature, outside of our consciousness, does not exist.

In comparison with the cases at present before us we may recall the very important results obtained by Juel * and by Murbeck.†

Juel found that in *Antennaria dioica* a tetrad division takes place, and his account of the process differs in no essential detail from mine. In *Antennaria alpina*, however, in which parthenogenesis is now known to obtain, the tetrad division does not occur, and the embryo-sac-mother-cell develops directly into the embryo-sac without any reduction in the number of the chromosomes or the usual chromosome-ring formation. Nor is this process to be compared with that in some plants in which megaspores are not delimited in the usual manner, but in which parthenogenesis does not occur (*Lilium*). In such plants the first two divisions are the same in character as the two divisions occurring when four megaspores are formed.

In *Alchemilla*, as shown by Murbeck, parthenogenesis also occurs, and in such event the megaspore mother-cell divides somewhat irregularly, forming at most three cells, because of the failure of one of the daughter-cells to divide. These divisions are not different in character from ordinary divisions; or, in other words, the heterotypic and homotypic divisions fail, and the chromosome number remains constant.

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* Vergleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei der Gattung *Antennaria*. K. Sv. Vet. Akad. Handl. 33: No. 5. 1900.

† Parthenogenetische Embryobildung in der Gattung *Alchemilla*. Acta Reg. Soc. Physiogr. Lund. 11: No. 7. 1901.

In the light of the discovery of the fact that true tetrad mitoses do not occur in parthenogenetically reproduced plants * we are more than ever forced to insist upon the conclusions stated previously, that, in such plants as certain Liliaceae, the condition must not be interpreted as a suspension of spore formation, but as a reduction in the ontogeny of the gametophyte correlated with a loss of the spore function, without a loss of the morphological character of the spores so far as their development, as indicated by their mitoses, is concerned. The failure of true tetrad divisions in *Alchemilla* and *Antennaria* is a notable exception which proves the rule.

The peculiarities characteristic of the tetrad divisions are now known to occur in so many plants that we may well pause to estimate their morphological significance, apart from the relation they hold to the maintenance of a constant number of chromosomes.

In general acceptation the term archesporium has signified a cell or cell aggregate from which the spore mother-cells are developed, as first defined by Goebel.†

These cells cannot, however, be distinguished from vegetative cells except by the fact that they are richer in food and plasmic content—they have the character of embryonic cells. According to their period of growth and the number of divisions they undergo their derivatives, the spore mother-cells (taken collectively the sporogenous tissue), are few or many. Now the cells of the sporogenous tissue are different from all other cells in the life cycle in that they always suffer tetrad division, and thereby exhibit very constant morphological characters which raise them to special morphological rank. This cell, or tissue, as the case may be, by virtue of the special character attaching to it, demands special recognition in terminology, and it would seem both natural and justifiable to regard it as constituting the archesporium. The use of the term in this way seems to me simple and unmistakable.

6. The third and following divisions are typical, and the reduced number of chromosomes is preserved.

In *Crucianella* all of the four megaspores in a given series may

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* Juel (*l. c.*) interprets the phenomenon in *Antennaria alpina* as a special case of apogamy.

† Bot. Zeit. 38 : 545, 561. 1880; 39 : 681, 697, 713. 1881.

and often do develop further, and undergo a simultaneous division (the first embryo-sac division), from which the actual physiological and morphological equivalence is inferred.

THE BEHAVIOR OF THE POLLEN TUBE IN DIODIA AND RICHARDSONIA

(PLATE 15)

While engaged in the foregoing study of the embryology of certain Rubiaceae, namely, *Diodia teres*, *Diodia Virginiana* and *Richardsonia pilosa*, some conditions of rather more than usual interest attaching to the behavior of the pollen tube in these forms were met with. In view of the attention which the subject has of late received in some quarters—attention which has not by any means been barren of important results—it seems well at this time to present the outcome of a closer study of the phenomena in the above-mentioned plants, although the general subject in the Rubiaceae promises as a reward of future investigation further results of interest.

The flower in both genera presents the same chief features in common. The differences are chargeable to the different numerical relations in them, *Diodia* having a bicarpellary and *Richardsonia* a tricarpellary ovary. This fact having been mentioned, we shall from this time on ignore it, since it has no bearing in particular upon the following description and for the sake of simplicity we shall take *Diodia* as the type.

MORPHOLOGICAL RELATIONS OF THE STYLE

The locules of the inferior ovary are separated by a partition of two portions, distinct in origin and in anatomical structure. The lower portion, or basal element, arises as a ridge from the floor of the ovary, and inserted on its margin are the ovules, one in each locule. This basal element reaches to somewhat less than one-half the depth of the ovary. The remaining distance is occupied by a partition—the roof element—derived from the styles which growing out laterally from the upper part of the hollowed-out receptacles join at the middle point and grow upwards and downwards to form the style. This consists therefore of two (*Diodia*) or three (*Richardsonia*) concrescent elements. The roof and floor elements of the ovarial partition fuse at their point of meeting and so complete the separation of the originally single ovarial chamber into locules.

HISTOLOGY

When the parts above described are young, the cells are, of course, uniformly isodiametric. After all the primordia are laid down, and the period of rapid growth prior to the assumption of the definitive form sets in, the relative rapidity of growth of the several organs is accompanied by changes in the proportions of the component cells. At about the time of fertilization the histological features are as follows.

The basal element of the ovarial partition consist of thin-walled parenchyma whose elements are slightly elongated in the direction of the flower axis and contain the vascular tissue which supplies the ovules. Where the stylar portion of the partition abuts against the basal elements, the cells of the latter are flattened out transversely, this being due partly to the pressure and partly to the mode of growth. The epidermis of the basal element of the partition has, at this point, very much thickened walls. The thickening commences in the outer walls (*fig. 1*) and extends at the period of fertilization to the lateral, but not to the basal walls (*fig. 5*). At the same time the regularity of the layer of cells is lost in the process of fusion which takes place between the basal and the stylar elements of the partition.

The stylar portion of the partition is composed at the time of fertilization of three distinct tissues. The innermost of these, or that lying in the axis of the compound style, and that with which we are here concerned constitutes a conductive tissue and is composed of elongated narrow cells with transverse or slightly oblique end walls and no intercellular spaces. These cells may be further distinguished from the surrounding tissues by their denser cytoplasmic content, and thicker, more deeply staining walls. Capus (**2**) has noted that the cells of the conductive tissue in the plants studied by him have thickened walls (collenchyma), but in *Alchemilla arvensis* according to Murbeck (**10**) no such thickening is present in any part of the course of the conducting tissue, a condition which is found in the free portion of the style of the plants under consideration. Here the cells are longer than in the stylar partition, have thin walls with somewhat thinner cytoplasm, but no intercellular spaces. The conductive tissue is readily recognized in the style proper by the smaller transverse diameters of its cells. The change from this thin-walled tissue to the thick-walled is quite abrupt and takes place at the level of the roof of the ovary.

At the lower extremity of the style, at the point namely where it fuses with the basal partition, the conductive tissue suddenly expands from being long and narrow, to short, irregular and isodiametric. There is also an evident increase in the thickness of the cell-walls. The line of fusion which may be recognized easily in the young condition as represented in *fig. 1* is now so irregular as to be of itself unobservable. This irregularity and confusion of cells appears to be due to the thickening and partial gelatinization of the cell-walls or more especially of the middle lamella, for one may notice in sections that irregular lines of separation occur between the cells, thus indicating their loose relations. Such changes have been noted, also, by Capus (2) although according to him such changes are much more pronounced in the style and stigma So far as the writer's observation goes such pronounced changes do not occur in the upper portion of the style, although here the walls are a little thickened, and that they are on the more and more pronounced the deeper one penetrates the whole style.

At this point of fusion, as described in the previous paragraph, the ovules, two in *Diodia*, three in *Richardsonia*, are inserted upon the edge of the basal partition. The epidermis above described as undergoing a thickening of its walls is continuous with the epidermis of the ovules, a description of which is necessary at this point.

The ovule is, broadly speaking, anatropous, and possesses, in addition to the single integument characteristic of the gamopetalae, a second outgrowth, the origin of which has been elsewhere described (p. 53) as a secondary enlargement of the funicle, a sort of strophiole. A profile view of this organ, as seen in *Diodia teres*, is shown in text *fig. 1*, and as seen in *Richardsonia* in *fig. 9*. A striking feature of this organ with which we are at present concerned is the profound modification of the epidermis to form a special conductive tissue for the pollen tubes. When young the cells of this tissue are of an approximately cubical or columnar form (*fig. 1*) with thin walls. As the ovule develops they change into deep columnar cells with thick walls excepting at their inner ends (*fig. 5*), where the basal and lateral walls for a little distance are thin. The contents of these cells are more dense than those of the deeper lying cells and the cytoplasm is very finely granular. Their nuclei are large with very finely divided chromatin. These cells appear to correspond in general with the cells described by Capus (2) as occurring at the base of the funicle in *Dracaena elegans* and by Dalmer (3) in the placenta of *Mahonia aquifolium.* From those in *Dracaena*, however, the cells in *Diodia teres* and *Richardsonia* differ in having thick walls, and from those in *Mahonia* in the fact that they do not secrete the mucilage which, according to Dalmer, serves as food for the pollen tube. They are not glandular cells, but, strictly speaking, cells of a conductive tissue as is shown by the behavior of the pollen tube towards it. With reference to the strophiole it may be remarked that this organ is present in other members of the same family, but that, so far as known, in no other is such a special tissue present, excepting as we shall see beyond in *Diodia Virginiana*. On the upper side of the funicle these cells have somewhat different dimensions from, but otherwise are exactly like those of the lower side where they have the longest longitudinal diameter (*text figs. 8 and 9*). Here the strophiole lies against the ovules so as completely to close the micropyle. It will be seen that there is thus formed a collar of columnar epidermis which is continuous around both sides of the funicle and, as will be shown, completes the path of the conductive tissue from the style to the micropyle.

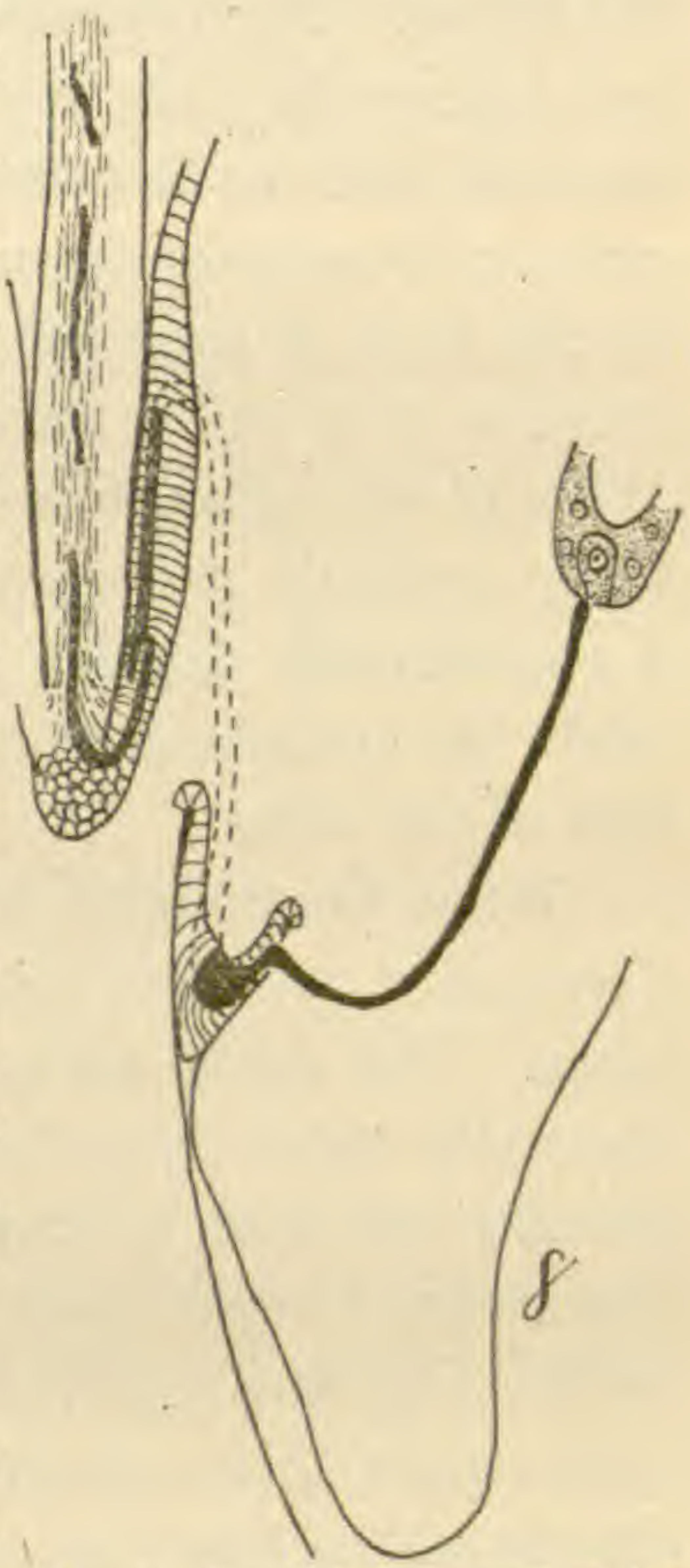

FIG. 8. Part of ovule and stylar tissue of *Diodia teres*, showing the path of the pollen tube.

THE COURSE OF THE POLLEN TUBE

In the free upper portion of the style the cells of the conductive tissue are, as above pointed out, long and very narrow. Through this tissue the pollen tube takes a somewhat devious, though on the whole direct course (*fig. 2*), and as the tube has a transverse diameter much greater than that of the neighboring conductive tissue cells, one would expect that the mechanical pressure alone would cause not a little disturbance in the conductive tissue. Such, however is not the case. The pollen tube does not destroy the cells among which it passes either by chemical influences, such as digestion, or mechanically. It is true that the cells are frequently disturbed in position, as is plentifully evidenced by the form of the nuclei when the pollen tube happens to exert pressure on a cell in such a way as to affect its nucleus (*fig. 3*). Without exception, however, the nuclei and cytoplasm stain perfectly normally and evenly. The walls of the pollen tubes are to a considerable degrees thicker than those of conducting cells, while the cytoplasm of the former is more coarsely granular than that of the latter.

When the pollen tube reaches the stylar partition it meets with conductive cells with thicker walls and of larger transverse dimensions. The nuclei are here long-oval in form. Here the path has about the same character as in the free part of the style. Occasionally one finds a sharp turn such as is shown in *fig. 3*, which represents a small part of the conductive tissue in longitudinal section showing a pollen tube cut transversely. A study of this preparation shows clearly that the effect of the pollen tube upon the tissue in this part of its course through which it passes is mechanical. Instances are frequently found in which the pollen tube passes athwart the conductive tissue, either directly or more or less obliquely. At first glance it is somewhat difficult to attribute such behavior on the part of the pollen tube to mechanical influences. When, however, we reflect upon the extreme sensitiveness of the protoplasm of the pollen tube to stimuli, it becomes less difficult. The impingement of the end of the pollen tube upon the end wall of a cell is, we believe, enough to turn it out of its direct path. Upon approaching the point of fusion of the basal and roof elements of the ovary septum the pollen tube meets with cells of similar histological characters as those of the cells through which it has immediately passed, save in dimensions and in the mucilaginous condition of the inner lamella. Here they are irregular and isodiametric as above stated, and are derived in part from each element of the septum. Through this mass of tissue the pollen tube takes a more irregular course, showing some tendency to branch, and passes from the stylar tissue into the upper part of the basal septum, into, therefore, the epidermis above described as continuous with the columnar epidermis of the strophiole. Upon meeting with the ordinary thin-walled parenchyma of this, the tube abruptly turns at right angles to its former course (*text fig. 9*). In no case does the tube penetrate beyond the thick-walled fusion cells further than to basal septum. The contents of the pollen tube may be seen well in the lower region of the style. In properly stained preparations the generative nuclei have been repeatedly found. The vegetative nucleus, however, has not been seen in this region. The cytoplasm is densely and finely granular, entirely filling the tube, while in the older parts of the same only a thin granular layer may be discerned on the wall, or none at all.

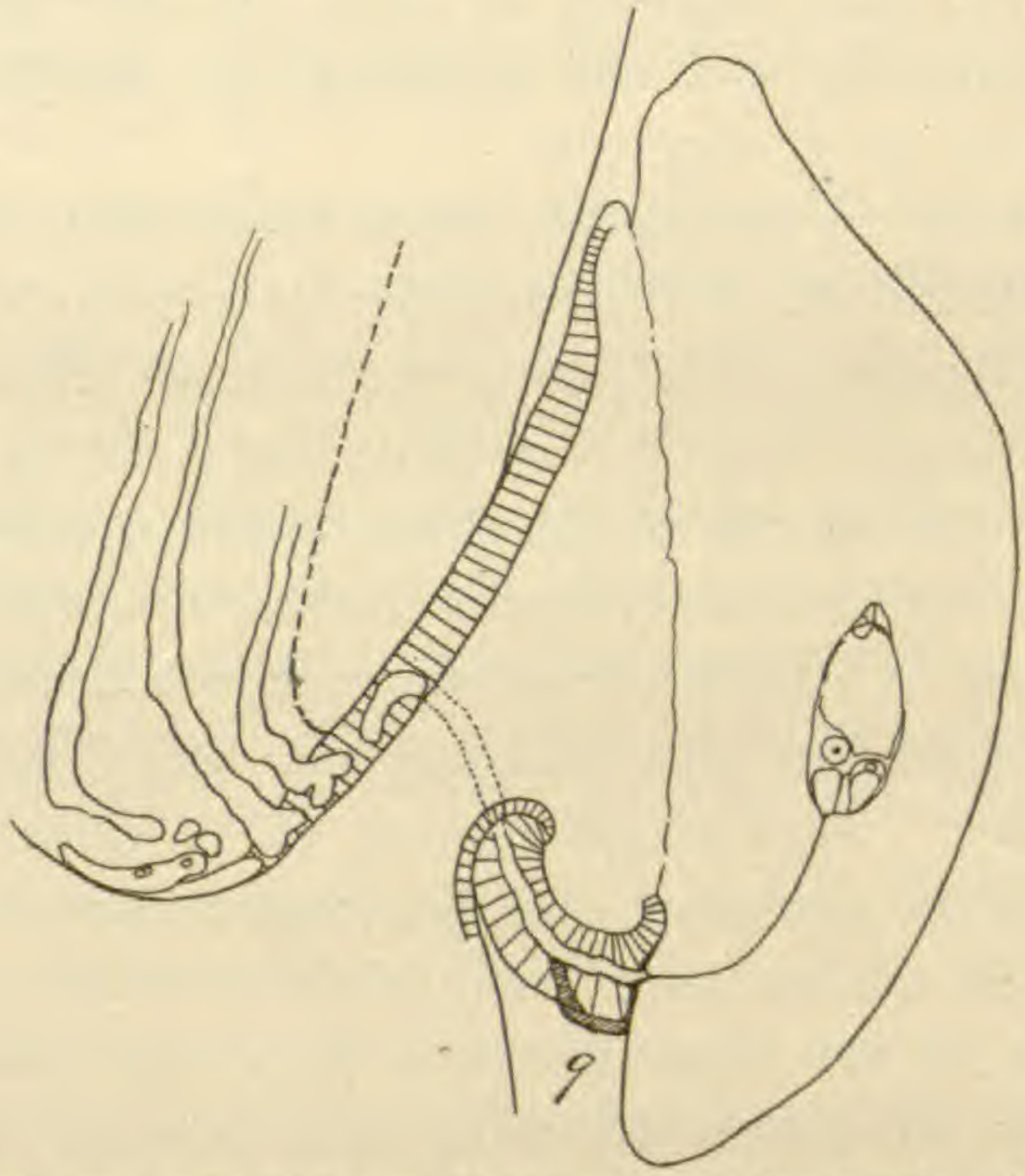

FIG. 9. Ovule and part of the stylar tissue of *Richardsonia pilosa*, showing path of the pollen tubes.

In this part of its course the pollen tubes which are usually to be found in numbers produce a destructive effect upon the cells, upon which they impinge. The effect has the appearance of being due to mechanical pressure owing in part to the number of tubes present, and in part to their larger diameter. The contents of the conductive cells thus affected appear homogeneous and deeply staining and the nuclei lose their normal appearance, while the cells are crushed out of shape (*fig. 4*). The effect of the tube is unequal, destroying cells, now here, now there, without any dissolution of the walls, showing at once the difference between a mechanical operation, and one involving the histolysis of the circumjacent tissue as by digestion.

The behavior of the pollen tubes when they reach the subepidermal parenchyma of the basal partition is quite uniform, and is strongly suggestive of a purely mechanical influence. In the case of *Richardsonia* there is formed at that point by virtue of the confluence of the funicles of the three ovules, a basin so to speak, filled with the isodiametric irregular conductive cells. Should we plant a seedling in a basin of soil the roots would penetrate till the walls of the basin had been reached, and they would then glide along the walls. Such a case appears to be quite analogous to the one before us, excepting that geotropism plays no part in the behavior of the pollen tube. In *Diodia teres* the penetration of the epidermis of the basal partition does not take place as in *Richardsonia*; but rather the tubes bend upward in the irregular cells of the stylar conductive tissue, passing at first between the walls of the style and strophiole, but soon penetrating the columnar epidermis of the latter (*text fig. 8*).

Having now reached the thick-walled epidermis, the pollen tube travels along till it enters the regular thick-walled columnar cells which constitute the collar of connective tissue about the funicle and the strophiole. It then passes out of the fusion tissue and travels in a fairly direct path upwards, that is toward the chalazal region of the ovule (*text figs. 8 and 9*). It gradually turns, however, so as to pass around one side or the other of the funicle, and then finds itself in the epidermis of the lower side of that organ. At this time the course is more or less irregular, and the pollen tube sometimes branches (*fig. 7*). Occasionally in the region of the micropyle it passes beyond the surface of the epithelium (*fig. 6*). It then glides along the surface a short distance and then passes between the conductive epidermis and the integument (*text fig. 1*). Ultimately it finds the micropyle and travels along it to the embryo-sac.

Two points of importance are to be noted at this point, the entirely or almost entirely intercellular path of the pollen tube, and the direction of its path which is not in the direction of least resistance, but at right angles to the longtudinal axis of the cells of the conducting tissue.

During this part of its course, that is, as it is passing through the fusion tissue and the strophiolar conductive tissue, the pollen tube as above pointed out not infrequently branches (*fig. 7*). Nawaschin has noted a similar tendency on the part of pollen tubes in the Birch (**11**, p. 22), to branch "wo das betreffende gewebe keine deutliche Anordnung seiner Zellen in longitudinalen Reihen aufweist." When in the strophiolar conductive tissue, the pollen tube shows more or less inability to pursue a path which is constantly at right angles to the component cells. It may then slip out to the surface. This happens most frequently in *Richardsonia* in the neighborhood of the micropyle where there is little or no pressure exerted upon the strophiole by the adjacent structures. In *Diodia teres* where the strophiole in the micropylar region is tightly wedged between the ovule and the wall of the ovary, the pollen tubes take constantly a deeper course (*text fig. 8*). These phenomena lead to the suggestion that the cause which has brought about the habit of intercellular growth in the pollen tube is a mechanical one, and this factor may probably be called upon to account for the behavior of the pollen tube in many forms. We have in mind such cases as occur, for example, in the Cannabinaceae of which Zinger (**23**) has given an account. According to this author, the intercellular node of growth is of phylogenetic significance, and, by means of such interpretation, brings his view into line with that of Nawaschin, who has vigorously supported the contention that the behavior of the pollen tube in the Amentiferae is inherited from their ancestral forms, and has endeavored, on this theory, to connect the lower Angiosperms with the Gymnosperms A discussion of this question is not pertinent here, but it may be said in passing that recently Murbeck (10) has, we believe, successfully, contested the view of Nawaschin. I believe that a study of the facts in a larger number of plants will lead to a more general recognition of the principle laid down by Murbeck (10) in the words, "Der intercellulare Wachstumsmodus des Pollenschlauches ist als eine physiologische Eigenthümlichkeit zu bezeichnen, * * *" and of the *mechanical conditions* as constituting not the least important factors in leading to such behavior. As a further illustration of peculiar mechanical conditions I would cite the instance of *Cynomorium* in which, as shown by Pirotta and Longo (18), the micropyle is completely closed and there appears in its place a cone of conductive tissue through which the pollen tube must penetrate. Zinger (21) has shown somewhat similar relations in *Cannabis*.

When, as shown above, the pollen tube passes to the surface, it travels a short distance along the conductive tissue, soon finding its way between the strophiole and the integument. Under such circumstances the wall of the pollen tube may well be seen (*fig. 6*).

The effect of the pollen tubes upon the cells of the collar of conductive tissue appears to be purely mechanical, as in the case of that in the style. Forcing its way between the cells, the pollen tube causes in them but little or no distortion and, so far as I have observed, no destruction (*figs. 5, 6*). It would appear that, although the cells of the conductive tissue form a true tissue, and are not crowded papillae, their thickened walls are nevertheless not bound together firmly but rather are loosely related by a soft, mucilaginous middle lamella.

Having reached the micropyle, the pollen tube now passes into the micropylar canal. The cells lining the latter are characterized by somewhat thicker, more deeply staining walls than those of the other integumental cells. The pollen tube eventually reaches the synergids. In the plants under discussion these cells have the "hyaline, striated tips," as described by Strasburger (21), extremely well developed. The generally accepted view that the synergids serve as a conductive apparatus is strengthened by the analogy which I venture to believe exists between their curious cellulose tips and the thickened and partially gelatinized cell walls of the conductive tissue.

Diodia Virginiana

In this species the conductive tissue is of a somewhat different character from that in the two plants already discussed. In the style both above and below the roof of the ovary the cells are cylindrical, their transverse walls being transverse, though occasionally oblique in varying degrees. The nuclei are not so much elongated, and correspondingly the length of the cells is not so great. The cell walls are thin throughout the whole range of stylar conductive tissue, excepting near the region of fusion of the basal and stylar parts of the partition where a slight thickening of the walls occurs. The conformation of the stylar conductive tissues is the same as in the other species.

In the character of the conductive tissue of the ovule, however, lies the greatest difference, a difference which, as we shall see, is connected with the behavior of the pollen tube. The tissue is disposed on the strophiole in a band around the insertion of the funicle, and extending downwards towards the micropylar region. The accompanying text figure 10 shows in a schematic way the arrangement. The component epithelial cells are approximately cubical in form (*fig. 8*), are fairly richly supplied with cytoplasm, and have a large nucleus. The outer walls are thickened, and exactly correspond in all respects to the homologous tissue in the other species studied in the young condition, before any further changes take place, *i. e.*, before the cell elongates into columnar form. At the time of pollination, a mucilaginous secretion appears so that at this time there lies on the surface of the conductive tissue a layer of mucilage of a thickness of nearly half the depth of the cells. The mucilage may be traced between the cells to some depth.

This conductive tissue corresponds in general to that which has been described by Dalmer (3) as occurring on the placenta in certain Liliaceae both in form and in the occurrence of the mucilaginous secretion through which that author has shown that the pollen tubes grow, and from which they derive nutrition which enables them to grow onward toward the micropyle. Apparently similar cells have been described by Lang (5) in *Byblis* and *Polypompholyx*.

The course of the pollen tube through the style needs no remark since what has been said above applies throughout. One point, however, needs mention, namely, that here the cellulose plugs described by Treub (22) as occurring in the pollen tubes in *Casuarina*, by Nawaschin (12, 16) in the Amentiferae and by Murbeck (10) in *Alchemilla* are here very easily and clearly seen. Two of these plugs are shown in *figs. 10 and 11*. It will be seen from the outline of the plug and the form of the somewhat shrunken pollen tube contents that these fit each other. One finds sometimes that the tube on one side of the plug is empty (*fig. 10*). In other cases cytoplasm occurs in both sides (*fig. 11*). Similar plugs occur lower down in the fusion tissue, but they have not been observed elsewhere.

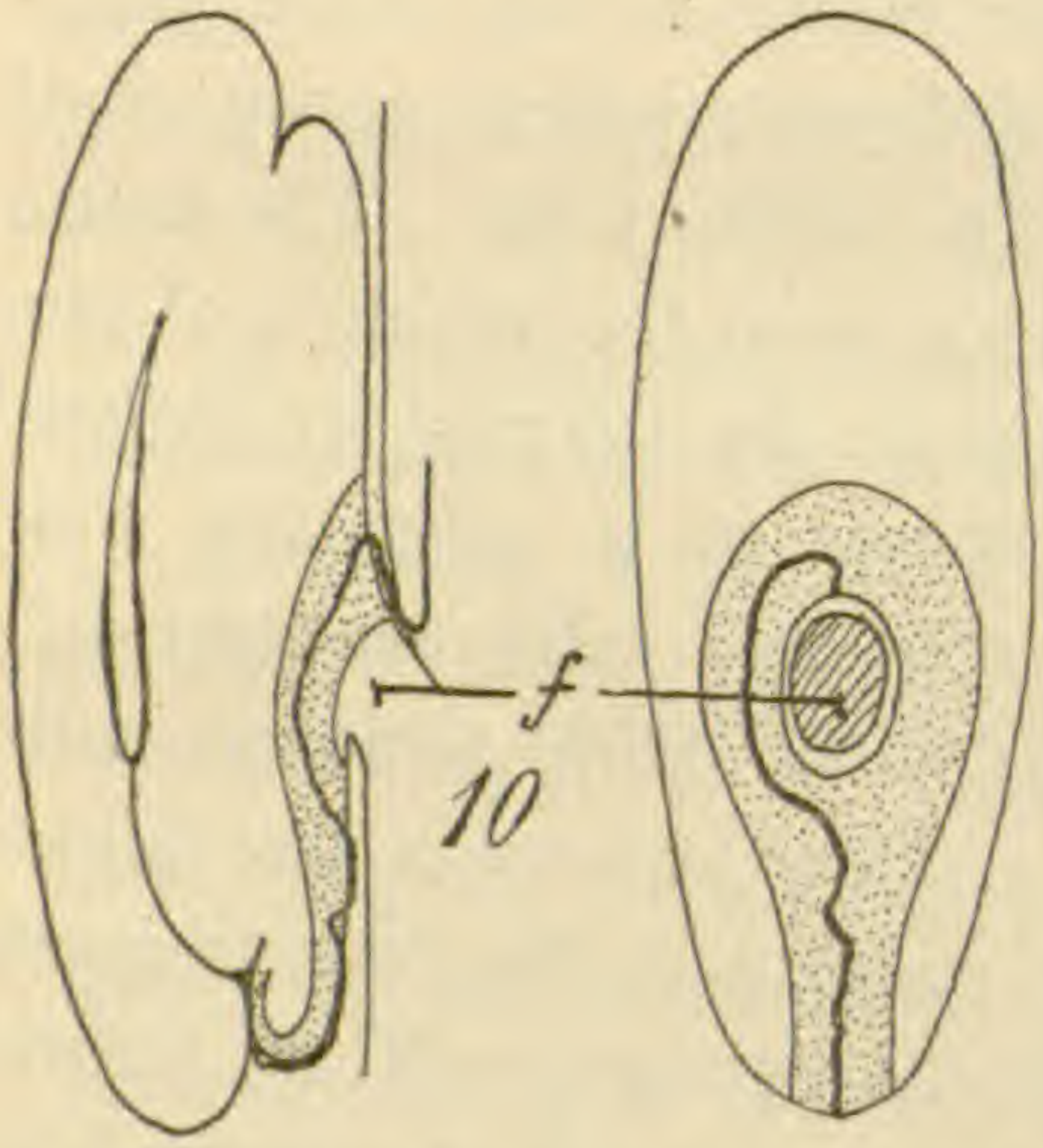

FIG. 10. Two views of the ovule of *Diodia Virginiana*, showing the conductive epidermis (dotted) and the path of the pollen tube; *f*, funicle. (*Schematic.*)

When the pollen tube reaches the epidermis of the basal partition (*text fig. 10*), it stops at that point, and does not enter between the cells as occurs in *Richardsonia*. They then bend upward and travel between the two tissue masses until they come to the collar of conductive epidermis of the strophiole, in the mucilaginous outer wall of which they pursue their way. After moving upward, *i. e.*, toward the chalaza, a little distance, they turn, following the band of secreting epidermis as shown in *text fig. 10*, and being completely buried in the mucilage, as occurs in plants studied by Dalmer (3). The behavior of the pollen tube toward the walls of the secreting cells needs particular mention in view of the fact that the wall of the former coalesces with the outer walls of the latter in such a way as to be completely indistinguishable. In one preparation the pollen tube was cut transversely at one point of its course and showed this relation especially well. In *fig. 9* this is well shown, from which it will be seen that the outer part of the tube wall is thin, thickening markedly on the sides nearer the epidermis, and, as above said, coalescing with its outer wall. It is not clear, however, whether the pollen tube wall as represented, and as it appears to the eye in the preparation belongs, properly speaking, entirely to the pollen tube. At any rate the soft character of the walls and their coalescence makes the determination of this point difficult.

When the pollen tube reaches the lower end of the strophiole, it travels, as before, superficially around and into the rift between this and the integument. This rift is filled with the slimy secretion derived entirely from the epidermis of the strophiole, inasmuch as the epidermis of the integument is not secretory. In this way the micropyle is at last reached and entered.

If now we compare the three types described as regards the development of the strophiolar conductive tissue, and the behavior of the pollen tube, we may accordingly arrange them into a series in the following order and with the characters indicated.

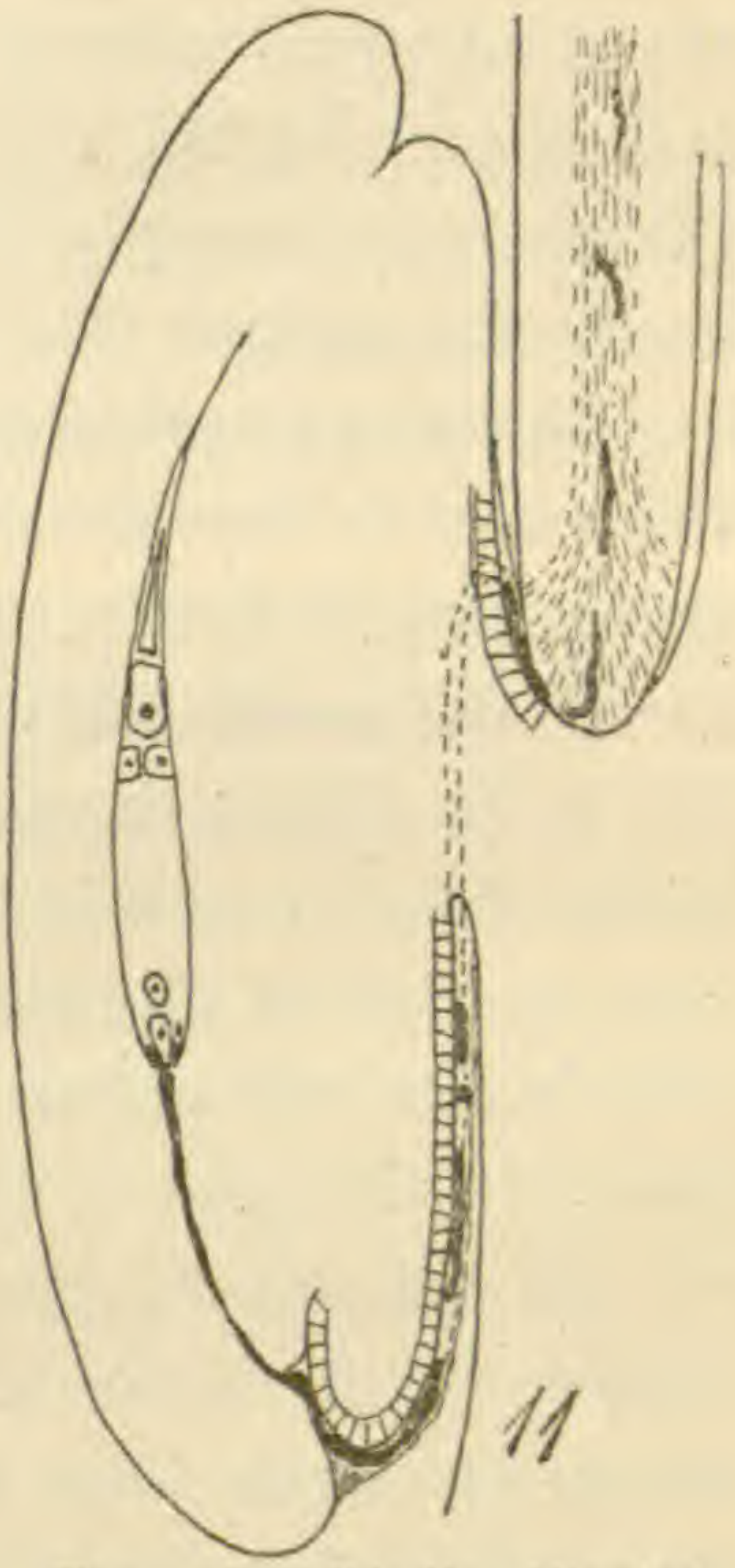

FIG. 11. *Diodia Virginiana.* Ovule and portion of the style, showing the path of the pollen tube.

1. *Diodia Virginiana.*—The conductive tissue consists of epidermal cubical cells with thickened outer walls covered with a mucilage secreted by them. The mechanical relations of the ovary are such that the pollen tubes may easily lie between the strophiole and the ovary wall. The pollen tube travels *superficially* along the funiculus and strophiolar conductive tissue, but imbedded in the mucilaginous secretion.

2. *Diodia teres.*—The conductive tissues consists of columnar epithelial cells with thickened outer and lateral walls. The middle lamella is mucilaginous. There is no secretion on the outer surface. The mechanical relations are such that the strophiolar conductive tissue is compressed between the ovule and ovary wall. The pollen tube enters the said conductive tissue immediately on commencing its upward movement along the funicle and remains within till it reaches the micropyle.

3. *Richardsonia pilosa.*—The conductive tissue as in *Diodia teres*, but somewhat different histological relations exist in the fusion tissue of the ovary septum. The mechanical relations are such that the strophiolar conductive tissue above the funicle is compressed between the ovary wall and the ovule. Below, *i. e.*, toward the micropyle, the pressure is reduced. The pollen tube enters the conductive tissue at the base of the stylar portion of the partition, travels by the intercellular method in the same till it reaches the micropylar region where it often though not always bends towards the surface.

The above-named facts speak for the mechanical conditions in the ovary as important factors in determining the course of the pollen tube, whether intercellular or not.

In review the following results and conclusions are presented:

1. In *Richardsonia pilosa* and *Diodia teres* the course of the pollen-tube is chiefly intercellular, a phenomenon clearly secondary in view of the fact that in a closely related species, *Diodia Virginiana*, the pollen tube pursues its path freely in the ovary cavity in that part of its course.

An important factor in determining such behavior of the pollen tube is found in the mechanical relations (pressure) existing between the ovule and the ovary wall. This is added as evidence supporting the contention of Murbeck to the effect that the intercellular mode of growth of the pollen tube is a matter of physiological meaning.

Inasmuch as such a difference in the behavior of the pollen-tube as has been pointed out may occur between two closely related species of the same genus, I infer, contrary to the view of Nawaschin, that the behavior of the pollen tube is of very limited significance—indeed of no practical significance—from a phylogenetic viewpoint. The condition is analogous to that of the archesporium in the angiosperms, which occurs, so far as at present known, in eight genera of the Rosaceae and in a dozen others widely scattered through the whole range of forms from the Rubiaceae (5, 6) to *Casuarina*.*

This statement does not preclude the possibility that Nawas-

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* A summary of the facts and literature pertaining thereto will be found in papers by Murbeck and Koernicke already quoted.

chin's contention, that the primitive behavior of the pollen-tube was entirely intercellular, is true.

2. The conductive tissue of the style consists of: (1) very thin-walled cylindrical cells in the upper part and (2) thicker walled cells in the lower part. The latter pass from a cylindrical to an irregular isodiametric form in the fusion tissue, in which the middle lamella is evidently soft and yielding.

3. A conductive tissue is here described which is morphologically a part of the ovule, or, more exactly, a part of a peculiar secondary outgrowth which I have designated the strophiole. It takes two histological forms: (1) In *Diodia Virginiana* it is composed of cubical, mucilage secreting cells, with thickened outer walls, corresponding to analogous cells found in many plants on the placenta. (2) In *Diodia teres* and *Richardsonia pilosa* the homologous tissue is composed of columnar, thick-walled cells (the thickening being absent from their bases only) with a soft middle lamella. No outer mucilage layer is here found.

In these plants we find a conductive tissue composed of elongate, regular cells, in which their longitudinal axes are placed at right angles to the intercellular path of the pollen tube for the direct passage of which this condition is mechanically less favorable than in the kind of conductive tissue in which the longitudinal axes of the component cells are parallel to the path of the pollen tube.

4. The pollen tube does not in general act unfavorably upon the cells with which it comes into contact. When however it does it may be referred to mechanical causes. This conclusion appears to accord with the observations of others.

5. The pollen tube shows a tendency to branch where the cells are irregular and isodiametric, or where the long axis of the conductive tissue cells are placed at right angles to the course of the pollen tube. This behavior speaks against the view of Miyoshi: "Im Griffel werden die Pollenschläuche wesentlich mechanisch zum Fruchtknoten gelenkt" (8).

6. There remains an undetermined factor in the guidance of the pollen tube. We cannot tell how the same is able to find its way to the egg in the definite way in which it does. The pollen tube is negatively aërotropic, and is chemotropic, as shown by

Molisch (9). These facts explain its behavior toward the stigma, but the later behavior in the conductive tissue remains unexplained. According to Molisch again, chemotropism "muss bei der Wanderung des pollenschlauches zur Eizelle, resp. bei der Auffindung derselben in vielen Fällen eine wichtige Rolle zufallen." But it is difficult to see how chemotropism can be an efficient factor unless there be a differential distribution of the stimulant. Miyoshi on the other hand, has maintained, in the words above quoted, that the operation is a purely mechanical one. Nawaschin (16), to whom we are indebted for a critical exposition of these two views, has pointed out that both presuppose that "der Pollenschlauch Reizbewegungen ungehindert ausführen könne," a condition which is found only where the pollen tubes have free space in which to move. If we assume that such are the conditions in *Diodia Virginiana*, in which the pollen tube moves freely in the ovarial cavity, what may we say of *Diodia teres* and *Richardsonia pilosa*, in which the pollen tube is not free to move in the ovarial cavity, but pursues an intercellular path, parallel to that which we may believe, from the case of *Diodia Virginiana*, it would take were the mechanical conditions favorable, and this in spite of the character of the conductive tissue which is mechanically unfavorable.

I believe that we may be justified in maintaining:

1. With Nawaschin, that the occurrence of a secreting conductive tissue speaks as much for the nutrition of the pollen tube as for the necessity of mechanical guidance; that, moreover, the ability of the pollen tube to secrete a cellulose-dissolving enzyme indicates the former, as in point of fact the pollen tube does not penetrate the cells of the conductive tissue; and that the assumption that in order to respond to a stimulus, the pollen tube must have unoccupied space in which to move is unnecessary and probably untrue.

2. With Molisch, that chemotropism is the important factor, and the guidance of the pollen tube; but that *the distribution of the stimulant in the conductive tissue is a differential one;* and, as Nawaschin (16) suggests, "die Verbreitung der Reizstoffe Kann zwischen den Papillen des Leitgewebes in Folge der capillarkräfte leicht zu Stande kommen," extending his statement, however, to cells as well as papillae.

The experiments of Miyoshi (8) by which he showed that pollen tubes will penetrate the cut end of a style and travel toward the stigma, and that when a lateral cut is made into the conductive tissue the pollen tubes will grow out in various directions, we maintain not only do not support his view that the pollen tubes are guided in a purely mechanical way, but also that they do not contradict the suggestion of such a differential distribution of an appropriate stimulant, inasmuch as a cut in the conductive tissue would in all probability set up disturbances by which the ordinary distribution of the stimulant might be reversed.

It may, of course, be that Miyoshi's contention is true for the style, although I believe that the case is not proven ; but that the pollen tube is guided in one way in one region of the conductive tissue, and in another way in another, seems quite improbable.

3. The suggestion is submitted that the synergidae are the source of the stimulant, and constitute the center of distribution of the stimulant. To this idea I am led by the cytological character of those cells, and by their position as the only effective center, exclusive of the egg itself. We do not forget the experiment of Strasburger (**21**) on *Torenia*, the results of which were, however, negative. Searching experimentation is still needed to throw light on the perplexing problem which we have attempted somewhat further to elucidate.

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Explanation of Plates

The letters in the following plates signify as follows:

ant., antipodal cell (or nucleus).
ar., archesporium.
c. epi., conductive epidermis.
e. s., embryo-sac.
n. c., nutritive cells of the chalaza.
p. t., pollen-tube.
s. p., strophiolar plate of brown cells.
s. t., strophiole.

PLATE 5. *Callipeltis cucullaria*

FIG. 1. An early stage in the growth of the nucellus. The archesporium is delimited and the periclinal divisions giving rise to the integument are to be seen.

FIG. 2. Older conditions of the nucellus in which the archesporial cells are approaching maturity.

FIG. 3. A nucellus cut tangentially showing a larger number of archespores than may be seen in a radial section.

FIG. 4. A radial longitudinal section through a mericarp. The formation of megaspores has been consummated and one especially large one may be seen before it has started to migrate. The micropylar canal is, therefore, intact.

FIG. 5. A group of megaspores in which one, the lowest one in the figure, has enlarged and is preparing for migration.

FIG. 6. The migrating megaspore may be seen lying in the micropylar canal, the endodermis of which has been destroyed by the activity of the moving cell.

FIG. 7. The final division of the embryo-sac cells to form the eight cells of the nearly mature condition of that organ.

FIG. 8. An instance in which two megaspores have migrated and have given rise to two imperfectly formed embryo-sacs.

FIG. 9. An embryo-sac after fertilization has taken place. The embryo is in the unicellular state and the endosperm nucleus is in its first division. The material derived from the disintegrating megaspore has completely disappeared.

PLATE 6.

FIGS. 1–12. *Callipeltis cucullaria*.

FIG. 1. Ovule in longitudinal section at the time of the migration of the embryo-sac-mother-cell, and before its division. The remains of the megaspore mass may still be seen.

FIG. 2. An example in which several megaspores have began migration. In this figure and in Fig. 1 may be seen the compressed endodermis

FIG. 3. Embryo-sac during fusion of the polar nuclei. The different cells have now taken on their definite form.

FIG. 4. Embryo-sac with one-celled embryo. One synergid remains intact.

FIG. 5. A still later condition with 11-celled embryo. Antipodals still intact.

FIGS. 6–9. Various embryos in various stages of development.

FIG. 10. Suspensor, showing perhaps its most extreme development in this species.

FIG. 11. Ovule with endosperm and embryo approaching maturity (seed condition). The endosperm cells which are still actively absorptive are drawn on the left side.

FIG. 12. Section through the pericarp (four cell layers), integument (one cell layer) and the outer cell layer of the endosperm.

FIGS. 13–23. *Sherardia arvensis.*

FIG. 13. Mass of megaspore mother-cells.

FIG. 14. Embryo-sac with the migrating embryo-sac-mother-cell.

FIG. 15. Definitive embryo-sac just previous to fertilization.

FIGS. 16, 17. Egg apparatus and fusing polar nuclei.

FIG. 18. Two-celled embryo with endosperm.

FIG. 19. Older embryo in which two regions in the suspensor are evident. The basal region produces haustoria.

FIG. 20. Shows a somewhat more developed condition of the embryo proper than that seen in *fig. 19.*

FIG. 21. Suspensor of nearly mature embryo. The basal part of the haustorium which lies embedded in the intact endosperm has degenerated. The haustoria of the part of the suspensor which lies in the digested endosperm are active.

FIG. 22. Ovule from which Fig. 21 is taken.

FIG. 23. Peripheral portion of endosperm showing outer absorbing cells.

PLATE 7. *Galium*

FIGS. 1, 2. *Galium Mollugo.* Two successive stages in the development of the nucellus.

FIG. 3. *Galium recurvum.* In this figure the archesporium has reached maturity and the integument has started its growth.

FIG. 4. *Galium recurvum.* A megaspore-mass just before the migration of the embryo-sac-mother-cell. The capping cells are not yet destroyed.

FIG. 5. The megaspore mother-cell in migration.

FIG. 6. *Galium Parisiense.* The two-celled stage of the embryo-sac.

FIG. 7. *Galium triflorum.* The embryo-sac. The same embryo-sac is shown in Fig. 9 in order to show the length of the long antipodal.

FIG. 8. *Galium Aparine.* An embryo-sac in which the endosperm has begun to form and in which the embryo is composed of six cells.

FIG. 9. *Galium triflorum.* Ovule in longitudinal section showing the proportions of the embryo-sac and the relative position of the end of the food-conducting tissue of the raphe.

FIG. 10. *Galium tinctorium.* The embryo-sac. The constriction of the endosperm cell and the irregular nucleus are to be seen.

FIG. 11. *Galium Mollugo.* Two embryo-sacs produced in the same ovule.

FIG. 14. *Galium Aparine.* Ovule with endosperm and young embryo. The remnants of the antipodals are still to be seen.

FIG. 13. *Galium Parisiense.* An embryo.

FIG. 12. *Galium Parisiense.* An embryo-sac. The embryo has begun its growth.

FIG. 15. The lower half of a mericarp of *Galium Mollugo.* The undigested walls of the cells lining the micropyle are to be seen at the end of the suspensor. *emb*, embryo ; *end*, endosperm ; *f*, funicle ; *i*, integument ; *p*, pericarp ; *s. c*, stylar column.

PLATE 8. *Asperula*

FIG. 1. *Asperula azurea.* A nucellus in an incipient stage of development.

FIG. 2. *Asperula setosa.* The migrating megaspore.

FIG. 3. *Asperula azurea.* An embryo-sac. Here two antipodals attain a spherical form.

FIG. 4. A young embryo. In this form the suspensorial haustoria reach a high degree of development.

FIG. 5. *Asperula* sp. An embryo showing the extreme development reached by the suspensor in this form. The surrounding outline represents the limit of the endosperm.

FIG. 6. *A. azurea.* This figure illustrates the persistence of the suspensor till a late stage of embryonic growth.

FIG. 7. *A. galioides*—embryo-sac.

FIG. 8. *A. galioides.* A rather early stage in the development of the embryo. The haustoria are commencing to grow out into the endosperm.

FIG. 9. *A. galioides.* The suspensor of an embryo which has reached a still greater degree of maturity than that depicted in *fig. 6.*

PLATE 9. *Asperula montana*

FIG. 1. Pollen mother-cell nucleus in the stage of diakinesis.

FIG. 2, *a*, *b*, *c*, *d*, *e*. Chromosome pairs and rings from prophases of the nucleus of the pollen mother-cell.

FIG. 3. Pollen mother-cell, early anaphase of the first division.

FIG. 4. One pole of the spindle, the end of which is seen attached to the ectoplasm ; from point of attachment are irregular radiating fibers to be seen.

FIG. 5, *a*, *b*, *c*. Chromosomes, early anaphase, first division (*p. m. c.*).

FIG. 6. Late anaphase ; chromosome pairs shown on a larger scale in the following three figures :

FIGS. 7–9. Chromosome pairs from anaphase, first division (*p. m. c.*).

FIG. 10. End of spindle (anaphase, first division) attached by means of kinoplasm strand to the ectoplasm.

FIG. 11. Telophase, first division (*p. m. c.*).

FIGS. 12, 13. End of the first division—resting stage (*p. m. c.*).

FIG. 14, *a*, *b*. Chromosome pairs, telophase, first division.

FIG. 15, *a*, *b*, *c*, *d*. Chromosome pairs during metaphase of the second division.

FIG. 16. Pluripolar diarch spindle (second division, *p. m. c.*).

FIG. 17. Polar view of chromosomes (12) metaphase, second division.

FIG. 18. Anaphase, second division.

FIG. 19. Polar view anaphase, second division.

FIG. 20. Resting stage, end of second division.

FIG. 21, *a*, *b*. Chromosome pairs, prophase, first embryo-sac-mother-cell division.

FIG. 22. Early anaphase, first embryo-sac-mother-cell division.

FIG. 23. Telophase, first division, embryo-sac-mother-cell.

PLATE 10

FIGS. 1–6. *Rubia tinctoria*

FIG. 1. Young ovule before the integument has started to grow. Two archesporial cells are shown.

FIG. 2. Daughter-cells of megaspore mother-cell in division.

FIG. 3. Embryo-sac with four cells.

FIG. 4. Embryo-sac with two cells. At *e s* a second embryo-sac is seen containing but one nucleus. Above, in the archesporial cavity are several megaspore nuclei.

FIG. 5. Embryo-sac, definitive.

FIG. 6. Embryo. The embryo proper is very young, consisting of 13 cells. The suspensor is exceedingly well developed as a haustorial organ.

FIGS. 7–22. *Crucianella*

FIG. 7. *C. gilanica.* Young ovule, showing archesporium of very large cells, and the nutritive cells at the chalazal end.

FIG. 8. Daughter-cells, at close of first division.

FIG. 9. Megaspores formed by two divisions of the archesporial cells. The end cell has become the embryo-sac cell and has begun to develop as such.

FIG. 10. *C. herbacea.* Ovule, in outline, showing its typography. Chalazal nutritive tissue and megaspore masses above and an embryo-sac below, both partially surrounded by the specialized nutritive tissue derived from the integument.

FIG. 11. Megaspore masses (seen in *fig. 10*), enlarged.

FIG. 12. Embryo-sac (seen in *fig. 10*), enlarged. One antipodal nucleus only. Polar nuclei not yet fused.

FIG. 13. Nutritive integumental tissue from another ovule; archesporium and chalazal nutritive cells above; embryo-sac below.

FIG. 14. A trinucleate cell from integumental nutritive tissue.

FIG. 15. Embryo showing, in particular, the suspensor.

FIGS. 16–22. *Crucianella macrostachya*

FIG. 16. Two embryo-sac-mother-cells. The one on the right with a spindle of the first division; on the left two spindles of the second division.

FIG. 17. Anaphase and telophase of the second division.

FIG. 18. Anaphase and telophase of a third division.

FIG. 19. Quadrinucleate embryo-sac, and three disintegrating megaspores.

FIG. 20. Eight nuclei derived from four megaspores.

FIG. 21. Nuclei (four) of an embryo-sac in mitosis. The uppermost spindle in the figure is a megaspore in mitosis.

FIG. 22. An embryo-sac (with two nuclei) and four sets of megaspores. Those of one set are in mitosis.

PLATE II

FIGS. 1–31. *Crucianella gilanica*

FIG. 1–13. Pollen tetrad divisions.

FIG. 1. Chromosome pairs seen during prophase of the first division.

FIG. 2. Anaphase of the first division; the chromosomes are in various stages of separation.

FIG. 3. The forms assumed by separating daughter chromosomes.

FIG. 4. Daughter chromosomes in later anaphase.

FIG. 5. Chromosome pairs in telophase of the first division.

FIG. 6. End of first division.

FIG. 7. Chromosome pairs as seen in metaphase of the second division.

FIG. 8. Metaphase, second division.

FIG. 9. Late anaphase, second division.

FIG. 10. Anaphase, second division, spindle showing its connection with the ectoplasm.

FIG. 11. Equatorial plate, polar view; ten chromosomes.

FIG. 12. Equatorial plate, polar view; eleven chromosomes.

FIG. 13. End of second division. Drawn to the same scale as *fig. 6*, for comparison of the size of nuclei.

FIGS. 14–25. Embryo-sac tetrad divisions.

FIG. 14. Diakinesis.

FIG. 15. Condensation of rings, the aster-like radiations correspond to those seen in Fig. 42.

FIGS. 16, 17. Anaphases, first division.

FIG. 18, a–g. Forms assumed by the chromosomes during anaphase of the first division.

FIG. 19. Telophase, first division.

FIG. 20. Telophase, first division.

FIG. 21. Prophase, second division

FIG. 22. Metaphase, second division.

FIG. 23. Chromosome pairs, metaphase, second division.

FIG. 24. Anaphase, second division.

FIG. 25. Chromosomes, anaphase, second division.

FIG. 26. Chromosomes, anaphase, first division.

FIGS. 27–30 Embryo-sac divisions.

FIG. 27. First embryo-sac division, in metaphase.

FIG. 28. Second embryo-sac division, polar view.

FIG. 29. Chromosome pairs, second embryo-sac division.

FIG. 30. Fourth (antipodal) divison.

FIG. 31. Mitotic figure from the nucellus.

FIGS. 32–44. *Crucianella macrostachya.*

FIGS. 32–36. Pollen tetrad divisions.

FIG. 32. Prophase, first division.

FIG. 33. Metaphase, first division; ten chromosomes.

FIG. 34. Very early anaphase, first division.

FIG. 35. Metaphase, second division; one spindle in lateral and one in polar view; ten chromosomes.

FIG. 36. Chromosome pair, metaphase, second division.

FIGS. 37–42. Embryo-sac tetrad division.

FIGS. 37, 38. Prophase, first division.

FIGS. 39, 40. Early anaphase, first division.

FIG. 41. Separating chromosomes, anaphase, first division.

FIG. 42. Prophase, second division. Perinuclear radiations.

FIG. 43. First embryo-sac division.

FIG. 44. Separating chromosomes of the first embryo-sac division.

PLATE 12

FIGS. 1–12. *Diodia Virginiana*

FIG. 1. Basal partition with nucelli.

FIG. 2. Ovule with one-celled embryo-sac. *a*, *a′*, branches of vascular bundle.

FIG. 3. Part of young ovule, the integument commencing, showing archesporium.

FIG. 4. One-celled embryo-sac in migration. The remaining megaspores seen above following the embryo-sac.

FIG. 5. A similar condition in another ovule.

FIG. 6. Embryo-sac with nine antipodals.

FIG. 7. The four antipodal cells of an embryo-sac.

FIG. 8. Ovule with definitive embryo-sac, showing the relation of parts. *a*, *a′*, branches of vascular tissue. The isolated cells have appeared which later form a continuous plate as seen in *fig. 9*, *sp*.

FIG. 9. Older ovule.

FIGS. 10, 11, 12. The antipodal end of three embryo-sacs showing the number and arrangement of antipodal cells in each.

FIGS. 13–17. *Diodia teres*

FIG. 13. Basal partition and young nucelli.

FIG. 14. Somewhat older condition showing the strophiole (*st*) beginning to develop.

FIG. 15. Archesporium. One large functional megaspore mother-cell flanked by a smaller one.

FIG. 16. Young ovule with archesporial cell in its second division; strophiole well marked.

FIG. 17. Second division of the megaspore mother-cell.

PLATE 13

FIGS. 1–10. *Diodia teres*

FIG. 1. Young ovule, with one-celled embryo-sac. The strophiole is seen to close the micropyle.

FIG. 2. Archesporium showing the large, functional megaspore, and the three sister cells commencing to separate. The arrow indicates position of micropyle.

FIG. 3. Embryo-sac cell elongating; at the base are seen two nutritive cells.

FIG. 4. Two-celled embryo-sac.

FIG. 5. Embryo-sac.

FIG. 6. Embryo-sac after fertilization containing a one-celled embryo. The antipodals are still normal.

FIG. 7. The ovule in longitudinal section containing the embryo-sac shown in detail in Fig. 6.

FIG. 8. Still older condition with more advanced endosperm and embryo.

FIG. 9. Embryo of *fig. 8* shown in detail.

FIG. 10. More advanced embryo, showing the suspensor after stretching.

FIGS. 11–18. *Richardsonia pilosa*

FIG. 11. Nucellus.

FIG. 12. Ovule with embryo-sac cell. The strophiole is seen.

FIG. 13. Embryo-sac cell.

FIG. 14. Embryo-sac showing small antipodals.

FIG. 15. An antipodal cell as it appears before the cell wall is secreted.

FIG. 16. Ovule with endosperm and embryo.

FIG. 17. Embryo of Fig. 16 in detail.

FIG. 18. Older embryo and the special cells of the endosperm.

PLATE 14. *Houstonia*

Lettering: *s*, stylar primordia; *p*, placental primordia; *r*, roof element of ovarial partition; *b*, basal element of ovarial partition; *ff*, plane of cell division adding to the funicle; *a*, antipodal cells.

FIG. 1. *H. coerulea.* Longitudinal section through a young flower.

FIG. 2. *H. longifolia.* Longitudinal section through an older flower.

FIG. 3. *H. longifolia.* A similar section after the fusion of the basal and roof partitions.

FIG. 4. A nucellus with a single functional megaspore mother-cell.

FIG. 5. Archesporium, showing two smaller megaspore mother-cells which do not divide. The arrow indicates the direction of the egg pole.

FIG. 6. Two megaspores formed, and the second daughter-cell in division.

FIG. 7. Embryo-sac with two cells.

FIG. 8. Ovule in which the embryo-sac contains four nuclei in telophase

FIG. 9. *H. coerulea.* Definitive embryo-sac. At the antipodal pole there are two megaspore mother-cells still persistent.

FIG. 10. *H. coerulea.* Ovule with three-celled embryo, and endosperm.

FIG. 11. One-celled embryo.

FIG. 12. Five-celled embryo.

PLATE 15

FIG. 1. Conductive epidermis (*Diodia Virginiana*) in young condition in the region of fusion between the roof and basal elements of the ovarial partition.

FIG. 2. A portion of the stylar conductive tissue penetrated by pollen tubes. Portions of three such tubes are shown.

FIG. 3. A portion of the stylar tissue showing a pollen tube taking a brief course making a large angle with the longitudinal axes of the cell (*Richardsonia pilosa*).

FIG. 4. Pollen tubes as seen in the base of the stylar tissue, turning to pass into the ovular conductive tissue (*R. pilosa*).

FIG. 5. Mouth of micropyle and adjacent conductive tissue, with a pollen tube (*R. pilosa*).

FIGS. 6, 7. Ovular conductive tissue of the kind seen in *fig. 5*, cut transversely to the longitudinal axes of the cells. Parts of pollen tubes are seen passing between the cells (*R. pilosa*).

FIG. 8. Conducting epidermis of *Diodia Virginiana*.

FIG. 9. A small portion of the surface of the conductive epidermis of *Diodia Virginiana* showing the pollen tube on the surface.

FIGS. 10, 11. Parts of pollen tube showing cellulose plugs (*Diodia Virginiana*).

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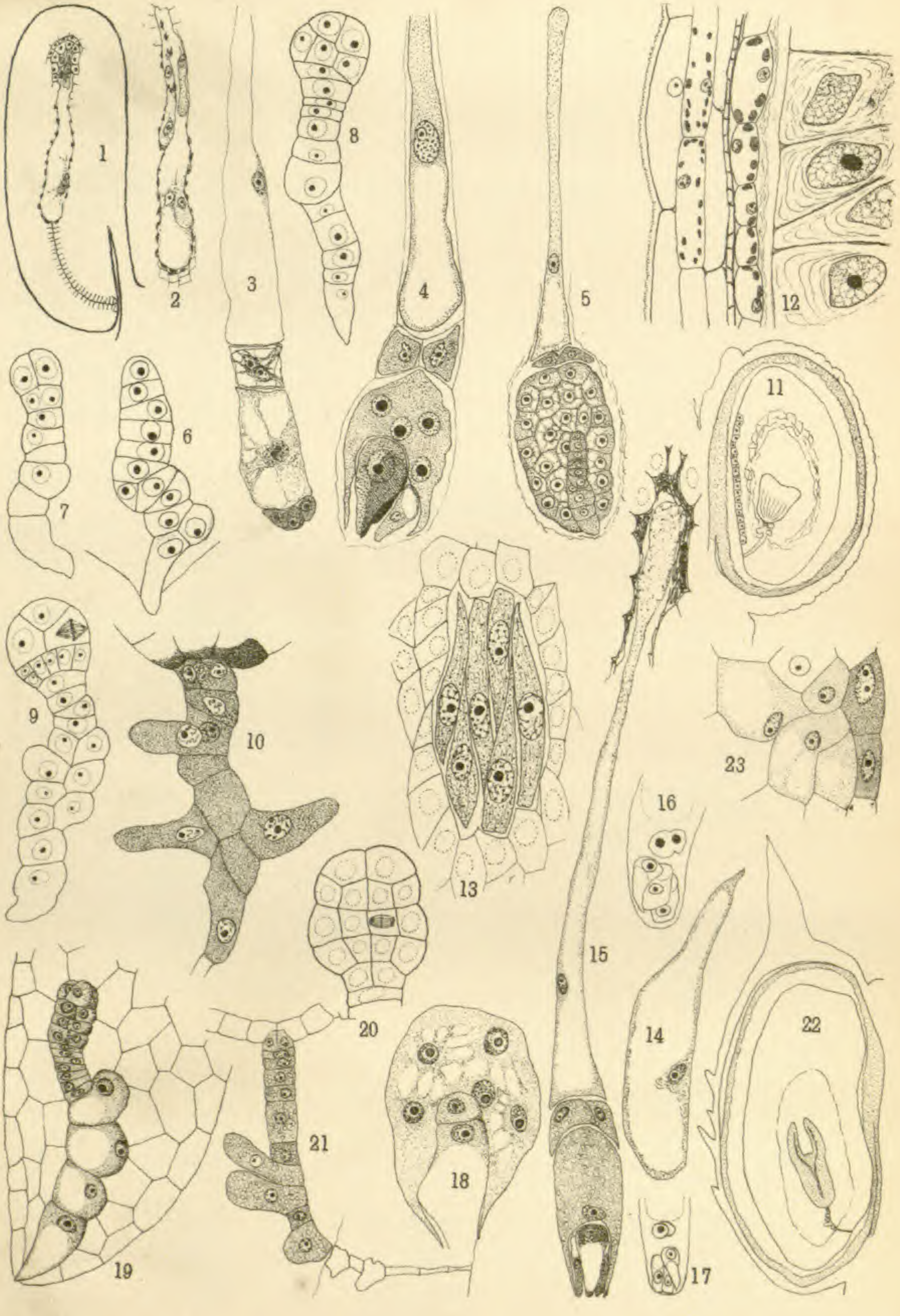

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13- 23. SHERARDIA ARVENSIS.

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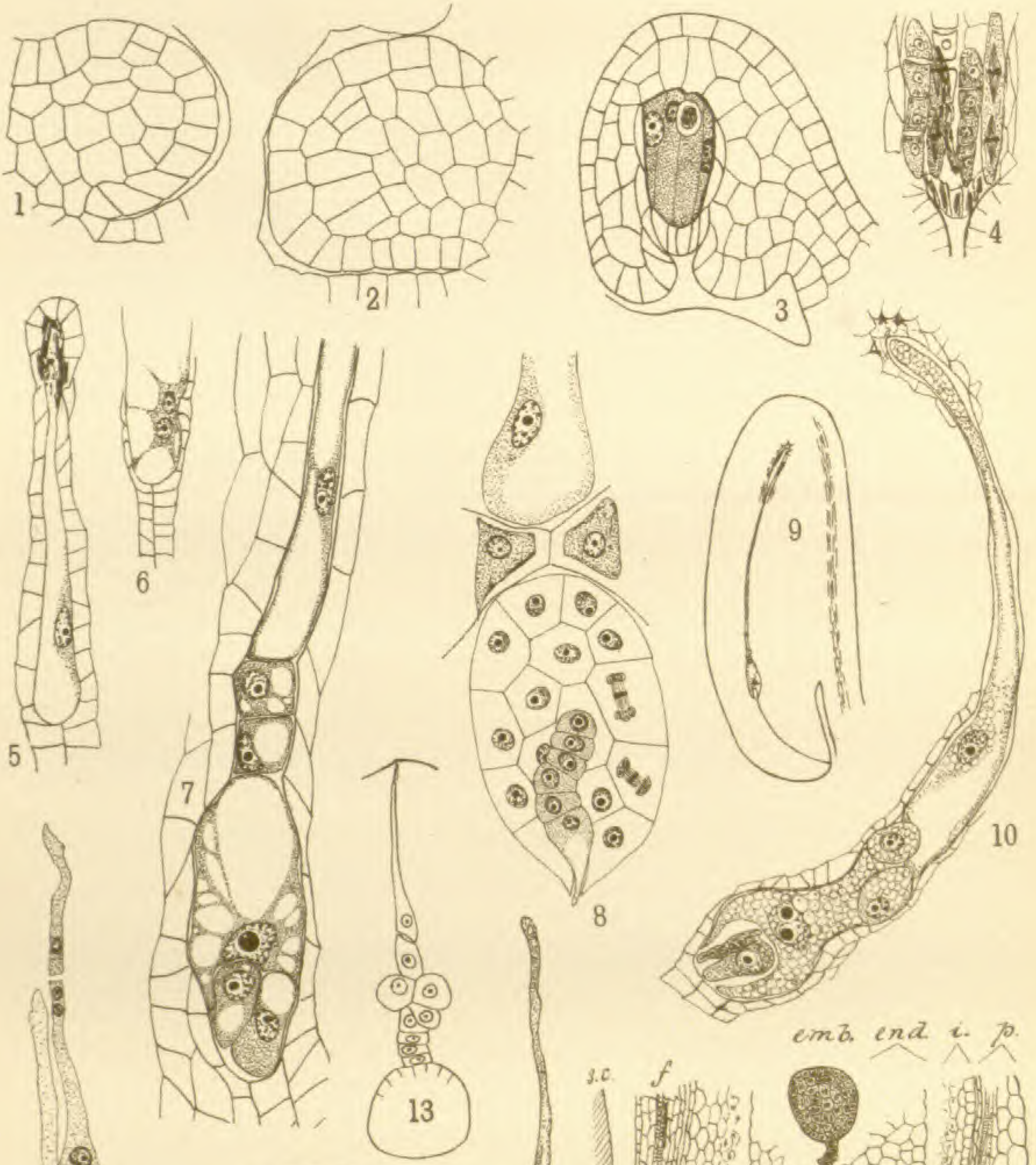

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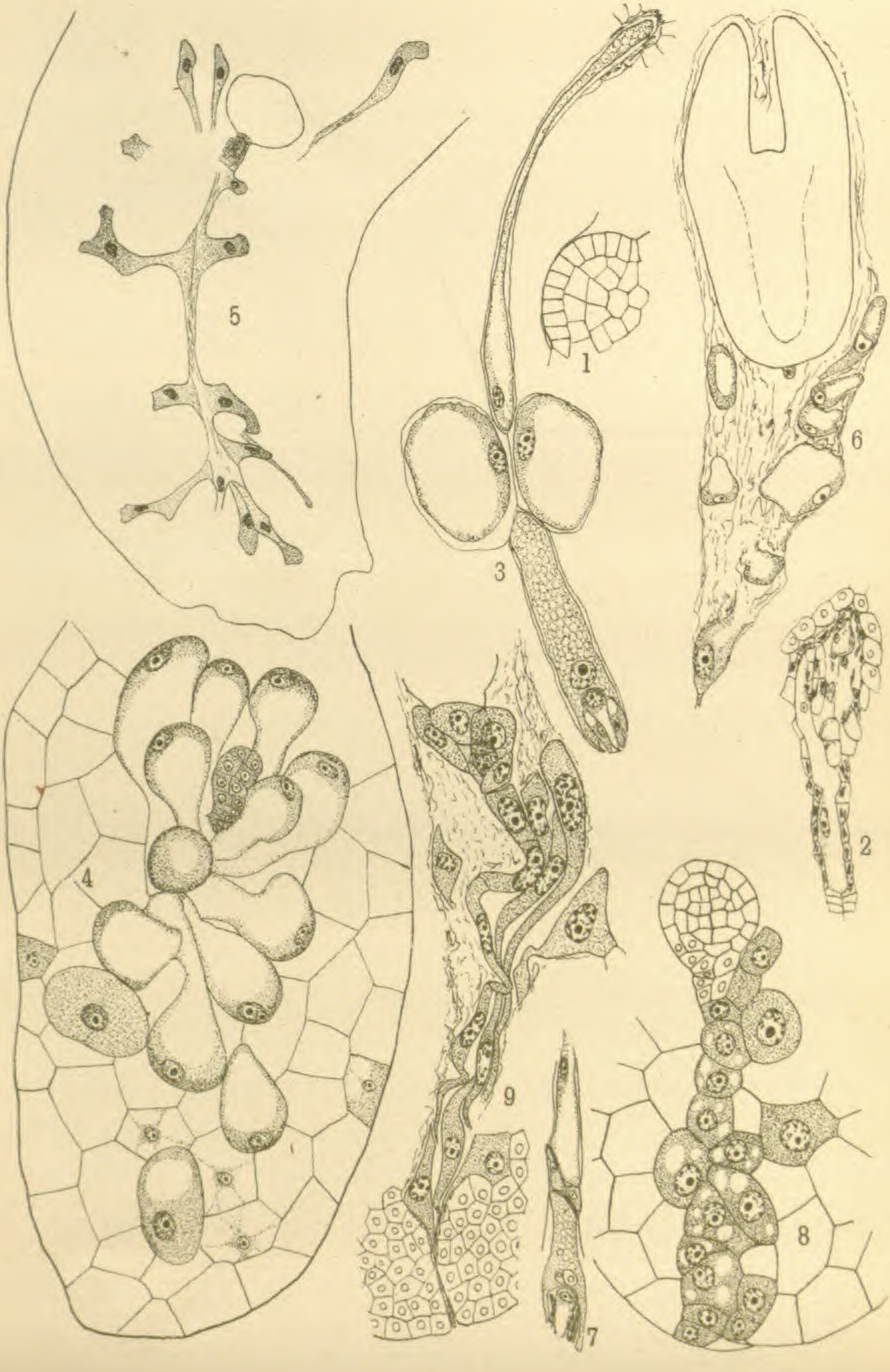
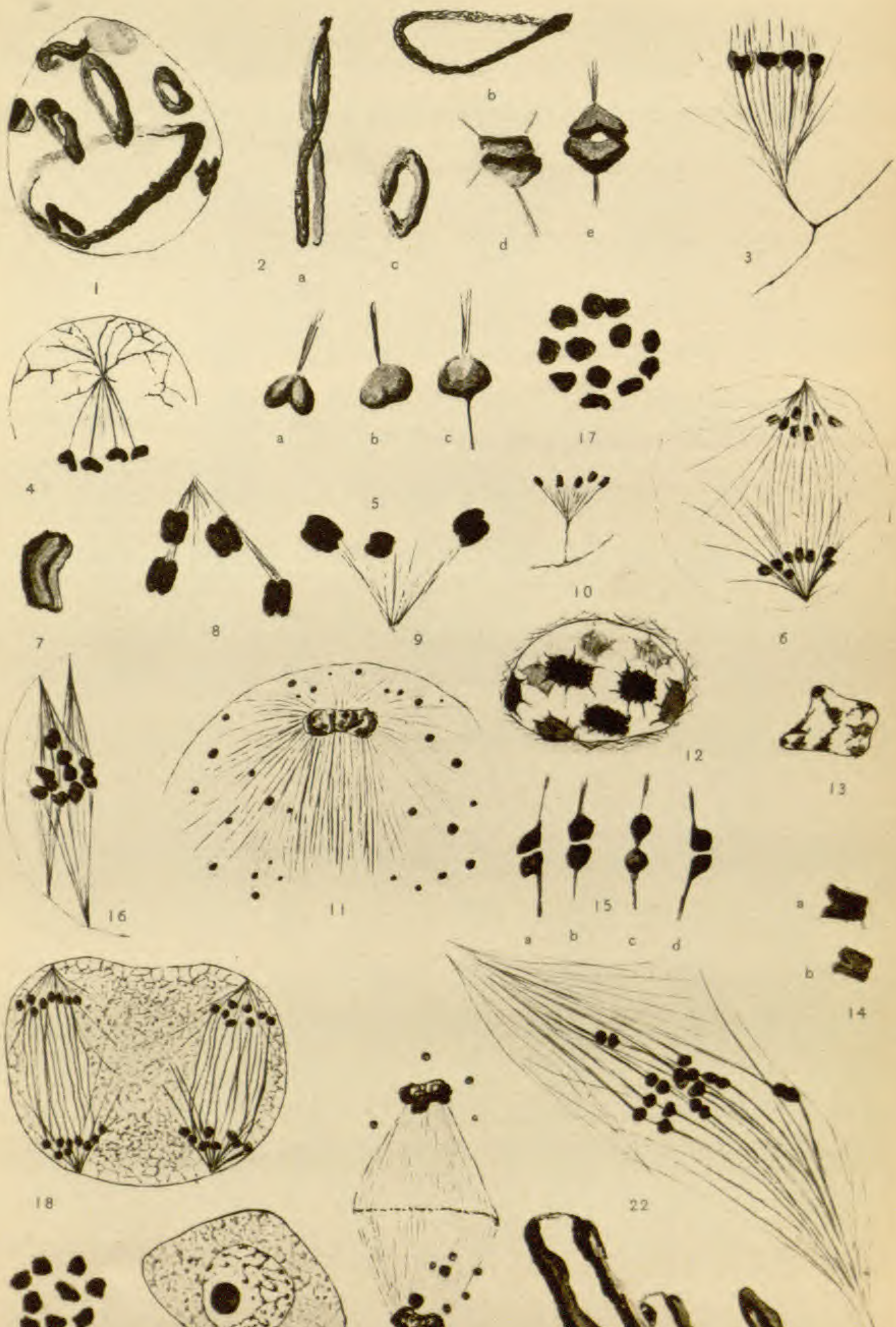


ASPERULA



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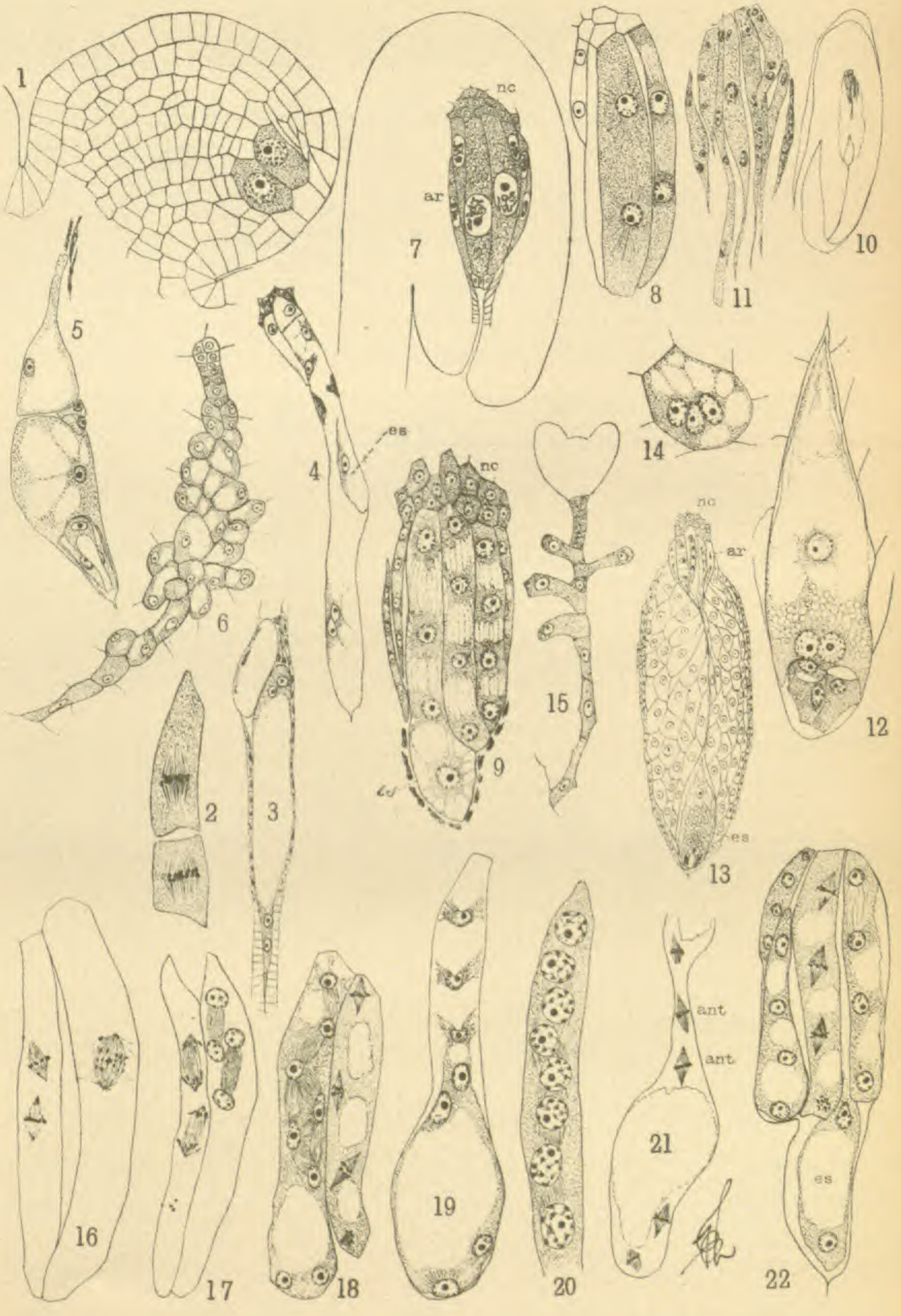
ASPERULA MONTANA



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7-22-CRUCIANELLA

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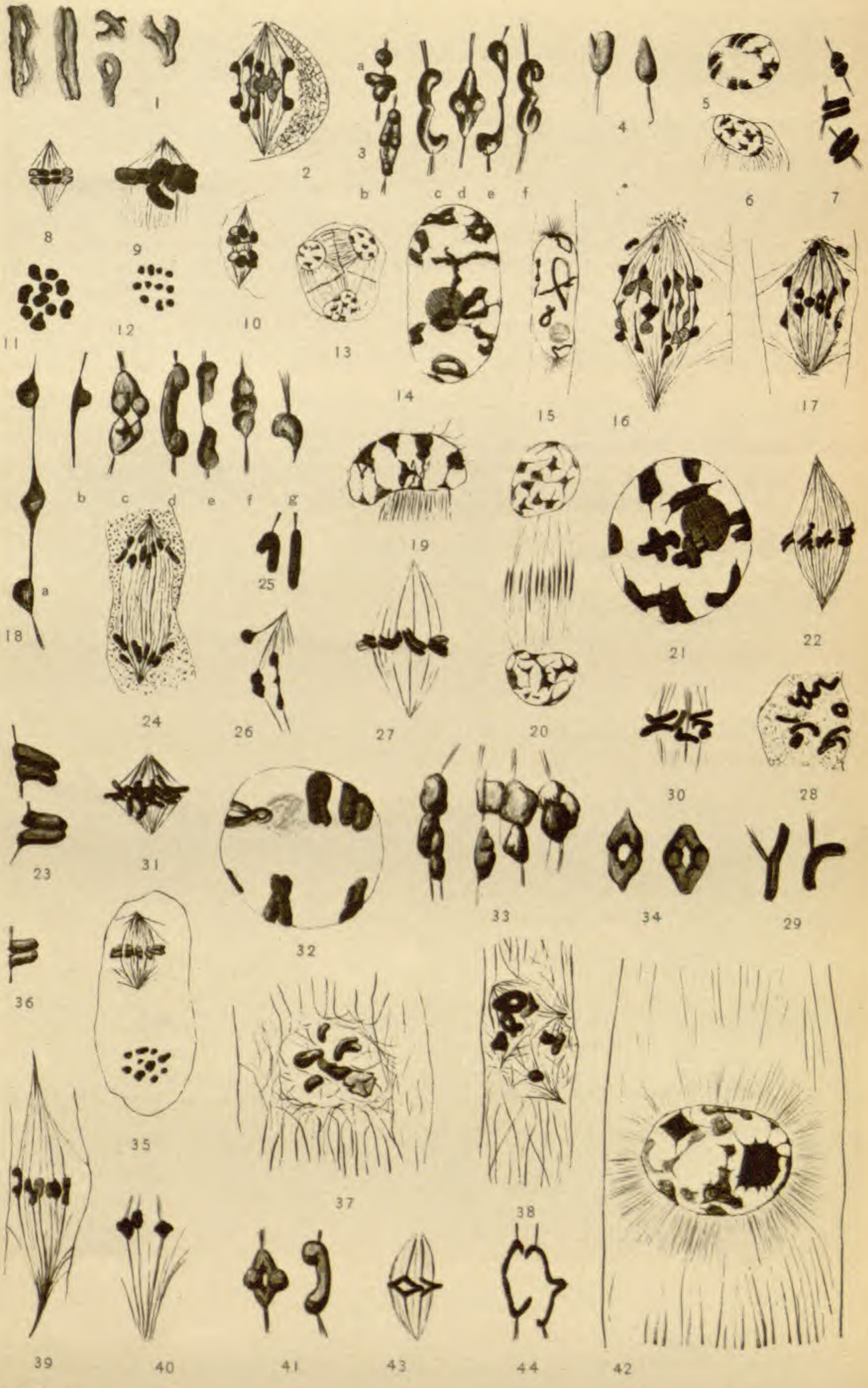

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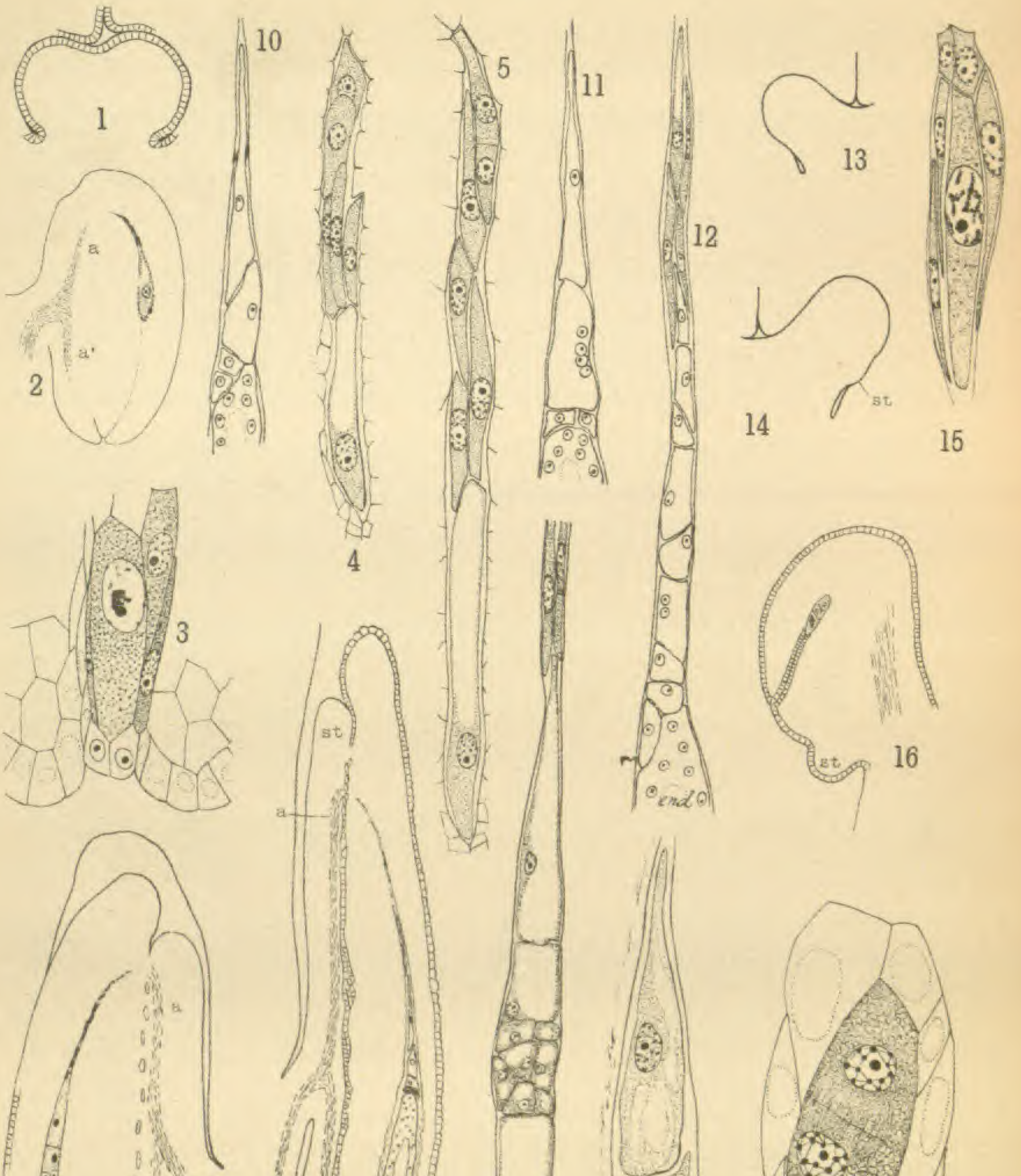
32-44-CRUCIANELLA MACROSTACHYA



1-12-DIODIA VIRGINIANA

13-17-DIODIA TERES

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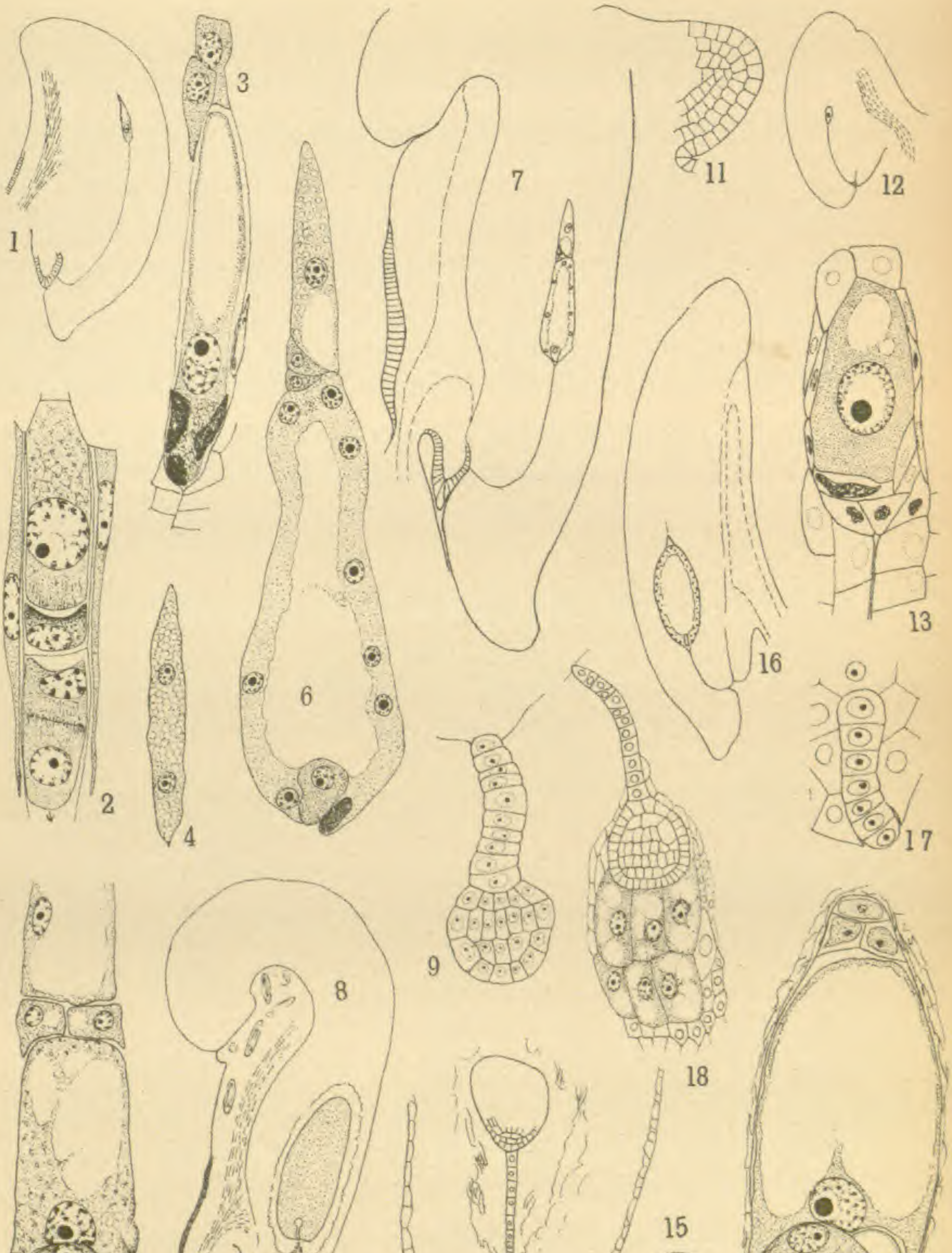

1-10-DIODIA TERES

11-18-RICHARDSONIA PILOSA

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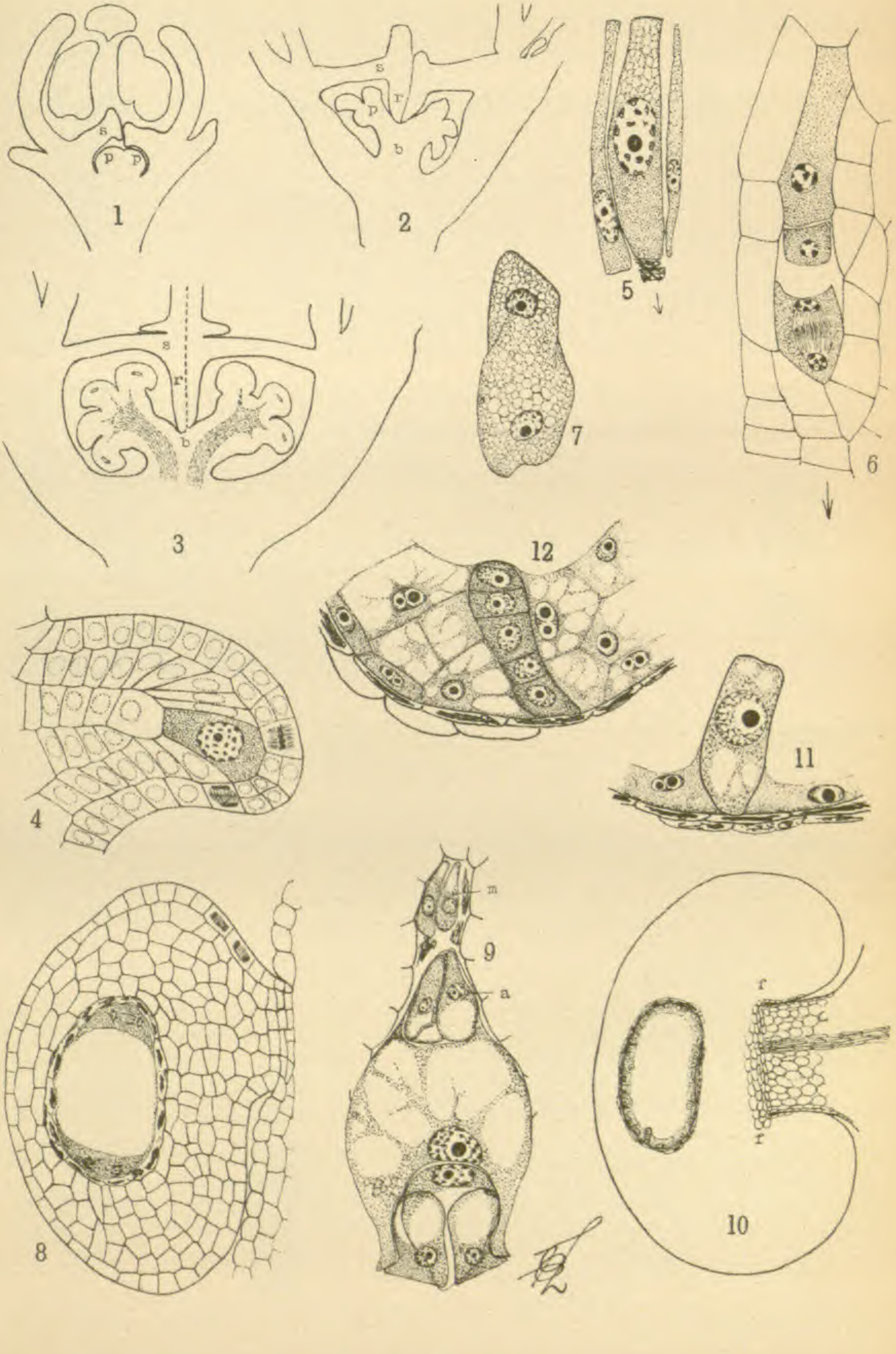

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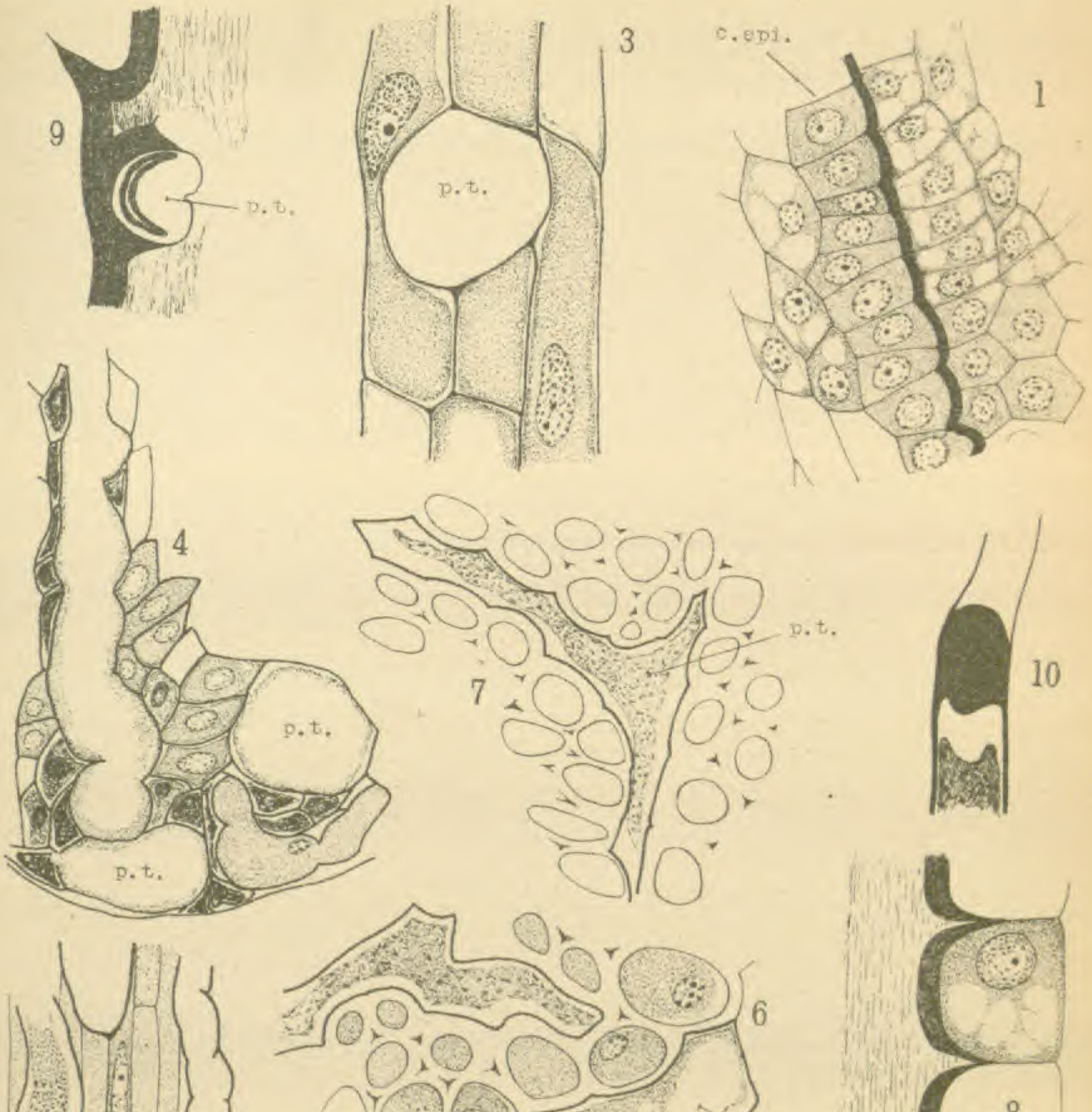

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THE LEJEUNEAE

OF THE

UNITED STATES AND CANADA

BY

ALEXANDER W. EVANS.

PRICE, $1.00

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The Lejeuneae of the United States and Canada

BY ALEXANDER W. EVANS

(PLATES 16–22)

The subtribe Lejeuneae, as defined by Schiffner, is made up of the large and comprehensive genus *Lejeunea* as understood by Spruce. The latter author divided this genus into thirty-seven natural divisions, which he looked upon as subgenera, while Schiffner raised nearly all of these subgenera to generic rank. Each of these authors has his own adherents. Writers on the hepaticae of Europe, where the Lejeuneae are poorly represented, tend to follow Spruce, recognizing but a single genus, while writers on the hepaticae of tropical regions, where the Lejeuneae attain a most luxuriant and varied development, tend to follow Schiffner. It is probable that an intermediate course would be more nearly correct, that some of Schiffner's genera are worthy of generic rank, but that others ought to be united. Until, however, the many species are more clearly defined and more accurately understood than they are at present, it seems most practicable, and perhaps wisest, to recognize Schiffner's genera as such, at least in a tentative way—a course which is adopted in the present paper.

For descriptions of the various genera, the reader is referred to the writings of Spruce[*] and of Schiffner.[†] Reference may also be made to a recent paper by the writer,[‡] where the division of the group into genera is more fully discussed.

HISTORICAL

The earliest work devoted to North American hepaticae is that of Schweinitz, published in 1821. In this paper the genus *Jungermannia* is still used in its old sense and includes the Junger-

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[*] Hep. Amaz. et And. 63–308. 1884.

[†] Engler & Prantl, Nat. Pflanzenfam. 1^3: 117–131. 1893.

[‡] The Hawaiian Hepaticae of the Tribe Jubuloideae. Trans. Conn. Acad. 10: 387–462. 1900.

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manniaceae and the Metzgeriaceae of recent American authors. Among the species referred to this genus are three which would now be included in the Lejeuneae. These are *J. serpyllifolia*, *J. transversalis* and *J. clypeata*. The first of these is a species which we share with Europe. It is the type-species of the genus *Lejeunea*, as originally described, and is now known as *Lejeunea serpyllifolia* Lib. or preferably as *L. cavifolia* (Ehrh.) Lindb. Apparently Schweinitz did not really know this species from America, the specimens so named in his herbarium being partly *Radula tenax* Lindb. and partly *Frullania Virginica* Gottsche. The second species is not the true West Indian *J. transversalis* Swartz, as Schweinitz supposed, but is the same as his *J. clypeata*, which he correctly distinguished as new. This third species is now referred to the genus *Archilejeunea*. Apparently in ignorance of Schweinitz's paper, Lehmann, in 1838, described the same species as new under the name *Lejeunea Dorotheae*.

In 1841 and in 1845 two important exsiccatae of North American bryophytes appeared in which several Lejeuneae were included. In the first of these, Drummond's Mosses of the Southern States, the specimens were determined by Wilson and Hooker and, in the case of new species, were accompanied by printed descriptions. The Lejeuneae of this collection are labeled *Jungermannia serpyllifolia*, *J. auriculata* and *J. parvula*, the last two being described as new. The first of these is not correctly determined and is in fact a mixture of two distinct species, *Euosmolejeunea duriuscula* (Nees) and *Lejeunea Americana* (Lindb.), proposed as a species in the present paper. *J. auriculata* is the type of *Mastigolejeunea auriculata* Schiffn., a species now known to have a wide distribution in tropical America. *J. parvula*, however, is apparently the same as the European *Cololejeunea minutissima* (Sm.) Schiffn., which has subsequently been collected many times in our Southern States. In the second exsiccata, Sullivant's Musci Alleghanienses, we find six Lejeuneae—*Phragmicoma clypeata*, *Lejeunea serpyllifolia*, *L. serpyllifolia* var., *L. cucullata*, *L. calcarea* and *L. minutissima*. The first and last of these are correctly determined. Of the remainder, *L. serpyllifolia* is really *L. Americana*; *L. serpyllifolia* var. is *Euosmolejeunea duriuscula*; *L. cucullata*, although compared by Sullivant with a specimen communicated by Montagne, is not the same as what we now call *Microlejeunea cucullata* (R. Bl. & N.) Jack & Steph., of Java, but is apparently to be referred to *Microlejeunea lucens* (Tayl.), a species at that time undescribed; while *L. calcarea* is not precisely the same as the European *Cololejeunea calcarea* (Lib.) Schiffn. but agrees better with the North American representative of this species, *C. Biddlecomiae* (Aust.), which was not published until 1890.

The next notes we find on our Lejeuneae are by European writers. From 1844 to 1847 Gottsche, Lindenberg and Nees von Esenbeck issued their classical Synopsis Hepaticarum in five parts. The Lejeuneae are treated in the second and third parts, which appeared in 1845, and in the fifth or supplementary part, which was published two years later. In the second and third parts the following five Lejeuneae are recorded from North America: *Phragmicoma versicolor, Lejeunea transversalis, L. catenulata, L. Dorotheae* and *L. serpyllifolia*. The first of these species is a composite; so far as American material is concerned, it is the same as *Jungermannia auriculata* Wils. & Hook., which is unjustly reduced to it as a synonym. *Lejeunea transversalis* is admitted solely on the authority of Schweinitz. *L. catenulata*, under which *Jungermannia transversalis* Schwein. strangely appears as a synonym, is *Neurolejeunea catenulata* (Nees) Schiffn. It is a species of tropical America, but there is no adequate evidence that it occurs within the United States. The last two species require no comment. In 1846 Taylor described a large number of new hepaticae from various parts of the world and among them six Lejeuneae, presumably from North America. Many years later it was proved that four of these species, viz.: *Phragmicoma testudinea, P. cyclostipa, Lejeunea polyphylla* and *L. longiflora*,* did not come from Ohio at all, as Taylor supposed, but were really collected near Pará in Brazil. A fifth species, *L. calyculata*, is a synonym of *Archilejeunea clypeata*. It is probable that the sixth species, *L. lucens*, was also originally collected at Pará. This plant, however, has a wide

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* All four of these species are reduced to synonymy by Stephani (Hedwigia, 29: 1890). *Phragmicoma testudinea* is *Pycnolejeunea macroloba* (Mont.) Schiffn., *Phragmicoma cyclostipa* is a mixture of *Archilejeunea Auberiana* (Mont.) Steph., and *Lopholejeunea Sagraeana* (Mont.) Schiffn.; *Lejeunea polyphylla* is *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn.; while *L. longiflora* is a form of the widely distributed *Euosmolejeunea trifaria* (Ness) Schiffn., of tropical regions.

range, extending into the United States and is apparently the same as Sullivant's *L. cucullata.* In the supplementary part of the Synopsis Hepaticarum these six species of Taylor are quoted with little comment, and *L. minutissima, L. calcarea* and *L. cucullata* are recorded from North America on the authority of Sullivant.

The first and second editions of Gray's Manual contain descriptions of the hepaticae by Sullivant. In the first edition, published in 1848, only four Lejeuneae are included. These are *L. serpyllifolia, L. clypeata, L. calcarea* and *L. cucullata.* In the second edition, published in 1856, species from the Southern States are added, and we find eleven Lejeuneae. The list includes the four species quoted above, Taylor's six new species, as well as *L. minutissima* and *L. auriculata. L. lucens* Tayl., however, is quoted merely as a synonym of *L. cucullata.*

In Austin's papers on hepaticae, published from 1869 to 1879, we find seven species of Lejeuneae described as new and three species recorded for the first time from the United States. Two of the new species, *L. Sullivantiae* ('72) and *L. Mohrii* ('75) are now reduced to synonymy ; the first being referable to *Euosmolejeunea duriuscula* and the second to *E. opaca* (Gottsche) Steph. A third species, *L. biseriata* ('69) proved to be a moss, as Austin himself afterwards decided. Three other species, *L. Ravenelii, L. Caroliniana* and *L. laete-fusca,* all published in 1876, are so incompletely described that we know little about them. Even the type specimens, where accessible, do not aid us ; they are very fragmentary and are either sterile or in poor condition. Under the circumstances it seems advisable to allow these three names to disappear from our literature. Austin's seventh species, the only one here retained, is *L. Jooriana* ('75), which belongs to the genus *Cololejeunea.* Of the three species which Austin first accredited to the United States, *Phragmicoma xanthocarpa* does not agree with authentic specimens of this widely distributed tropical species but should be referred to *Archilejeunea Sellowiana* Steph.; the specimens referred to the European *Lejeunea ovata,* now *Harpalejeunea ovata* (Hook.) Schiffn., are probably correctly named ; while those referred to *L. laete-virens* Mont., a West Indian species, are in too poor a condition to be definitely determined.

In 1875 the Finnish botanist, Lindberg, in a lengthy paper on

Irish hepaticae, includes interesting notes on some of the Lejeuneae in American exsiccatae. The most important of these are the following: *Lejeunea ulicina*, of Europe, is accredited to North America; *L. parvula* (the *Jungermannia parvula* of Drummond's collection) is recognized as a species, and Sullivant's *L. minutissima* is reduced to it as a synonym; the American specimens of *L. serpyllifolia* are all referred to the new var. *Americana* Lindb.; *L. Sullivantiae* Aust. is given the new name *L. Austini* Lindb., on account of the previously described *L. Sullivantii* Gottsche. The evidence that *Microlejeunea ulicina* (Tayl.) occurs in North America does not seem to be conclusive. *Lejeunea parvula* and *L. Sullivantiae* have already been commented upon. Lindberg's var. *Americana* is a composite, and, while it includes the *L. Americana* of the present paper, it includes also typical *L. cavifolia.*

In 1884 Spruce, in his important work on South American hepaticae, accredits the rare European *L. diversiloba* Spruce to North America. He apparently refers to this species the specimens which Sullivant called *L. cucullata*, although this is not definitely stated. Three years afterwards Spruce referred Sullivant's specimens somewhat doubtfully to *L. lucens* Tayl.

The numerous papers on hepaticae by Underwood contain frequent references to the Lejeuneae. In his preliminary list of North American species, published in 1882, fourteen species of Lejeuneae are noted. In his Descriptive Catalogue of 1884, descriptions are given of these fourteen species and of four others omitted from the earlier list. All of these species had been previously recorded. In the sixth edition of Gray's Manual, published in 1890, Underwood described the hepaticae, and it is interesting to note that the four Lejeuneae which he there recognizes are the same ones which Sullivant described in the first edition of the Manual, forty-two years before. In the same year Underwood published a description of *Lejeunea Macounii* Spruce, and Pearson, a plate of *L. Biddlecomiae* Aust., accompanied by descriptive notes. Both of these species belong to the genus *Cololejeunea.* Two years later Underwood recorded another *Cololejeunea*, the European *L. Rossettiana* Massal., but there seems to be no very adequate evidence that this species has been collected in America.

The last published list of North American Lejeuneae is that of

Stephani, which appeared in 1892. Twenty species are recognized; of these, *Lejeunea* (*Eu-Lejeunea*) *Underwoodii* and *L.* (*Micro-Lejeunea*) *Cardoti* are described as new, while *L.* (*Euosmo-Lejeunea*) *trifaria* Nees and *L.* (*Colo-Lejeunea*) *Wrightii* Gottsche are recorded for the first time from the United States. The first of the new species, judging from authentic specimens, is identical with *Lejeunea Sullivantiae* Aust. and is therefore a form of *Euosmolejeunea duriuscula;* the second, however, seems to be distinct. The specimens referred to *Euosmolejeunea trifaria* are dioicous and agree with *E. opaca*, while those referred to the undescribed *Lejeunea Wrightii*, from Cuba, are apparently an abnormally developed form of *Cololejeunea minutissima.* In 1895 Stephani accredited *Lejeunea flava* Swartz to Florida. The occurrence of this widely distributed species is certainly to be expected within our limits, but a specimen from Florida collected by Rau and determined as *L. flava* by Stephani himself seems to be referable to Spruce's var. *albida* of this species, a plant which the writer is unable to distinguish from *L. Americana.*

In the Hepaticae Americanae of Underwood and Cook, the first decade of which appeared in 1887, and which is still unfinished, a number of Lejeuneae have been distributed. Those from the United States or Canada will be noted in connection with the description of species.

It will be seen from the preceding account that the opinions of writers with regard to several of our species have been both varied and uncertain. This fact becomes even more evident when we consult the Lejeuneae in herbaria or in published exsiccatae. We are almost certain to find many false determinations among them. In some cases a single species will appear under several different names; in other cases several distinct species will appear under the same name. This confusion is partly because the Lejeuneae often grow mixed together, partly because certain of the species are extremely variable, and partly because the published descriptions, especially those of the older writers, are often so general and so incomplete as to be quite valueless. It becomes often necessary therefore to examine type-specimens, in order to learn upon what particular form a given species was originally founded. It becomes equally necessary, in the case of a variable species of wide range, to examine a large series of specimens from as many different localities as possible. It is only by this latter method that one can acquire a sufficient knowledge to distinguish between specific characters and those peculiarities which are simply due to variability. It should also be remembered in this connection that plants which grow under abnormal conditions tend to develop abnormally or imperfectly, and this is most strikingly true of the Lejeuneae. It may even happen that a specimen bearing perianths and capsules may utterly fail to show the foliar characters of the species, on account of the crowding together of the fruiting branches. Such abnormal specimens, although interesting from a morphological point of view, cannot always be determined with certainty, and yet it is unfortunately true that many species of Lejeuneae have been founded on just such forms. It is sometimes a question as to what should be done with species whose type-specimens are of this character, but probably in doubtful cases the best course is to discard them altogether.

DISTRIBUTION OF SPECIES

As a result of his own studies the writer is able to distinguish twenty-three species for the United States and Canada. Three of these are proposed as new, one is raised from varietal rank and six are recorded for the first time. The remaining species have all been previously noted. Four of our species occur in Europe, thirteen are more or less widely distributed in tropical America and six appear to be endemic. It should be noted, however, that two of these six species have near relatives in Europe and that the remaining four are closely allied to species of tropical America. It is very probable also that the ranges of several of these apparently endemic species will be extended into tropical regions by future explorations. Three of our species, *Lejeunea cavifolia*, *L. patens* and *Cololejeunea Macounii* are distinctly northern in their distribution. *Archilejeunea clypeata*, *A. Sellowiana* and *Cololejeunea Biddlecomiae* all have wide ranges extending from eastern Canada or New England to or beyond the Gulf States. *Harpalejeunea ovata* has been found from Virginia to northern Georgia, while *Microlejeunea Ruthii* has been collected only in Tennessee. Our other species are characteristically southern, although *Lejeunea*

Americana and *Cololejeunea Jooriana* have been found as far north as North Carolina, and *Microlejeunea lucens* apparently occurs in Virginia. Six of these southern species have not been collected outside of Florida. With the exception of *Cololejeunea Macounii*, of British Columbia, no species are known from the Pacific Coast region ; no species moreover have been reported from the Rocky Mountains nor from the Great Plains east of the Rocky Mountains, their absence or scarcity apparently being due to the dry atmospheric conditions. With regard to the number of species in individual States, Florida leads with fifteen, Louisiana ranks second with nine and Alabama third with eight. Few of the remaining States have more than three species apiece, and even east of the Mississippi River there are several States which have had no Lejeuneae whatever reported from them.

The brief notes which have just been given are mainly of temporary value. The Lejeuneae have been so largely neglected by collectors that our knowledge of their geographical distribution is at best very incomplete. The rich harvest of species which Underwood gathered in Florida shows how little we had previously known about the Lejeuneae of that state and indicates that much is still to be learned. The collections of Langlois in Louisiana and of Mohr in Alabama point to similar conclusions. Even in the north, the recent discovery of *Lejeunea patens* in Newfoundland and in Cape Breton shows how fragmentary our knowledge really is. It should be noted also that specimens exist in herbaria, too incomplete for identification and yet undoubtedly distinct from any recorded species. Some of these are probably identical with described species from tropical America, others are probably undescribed ; but for the present they must be left in doubt. It is clear, therefore, that much remains to be done to complete our knowledge of the Lejeuneae, and it is to be hoped that the present paper may incite collectors to pay more attention to these inconspicuous but beautiful plants.

The revision which follows is based largely on the collections of Lejeuneae in the Underwood herbarium, in the United States National Herbarium and in the herbaria at Yale University. The curators of other herbaria have also been most generous in allowing the writer to examine type specimens in their charge, and other correspondents have kindly furnished material for study.

Analytical Key to the Species

1\. Underleaves present, undivided. 2.
Underleaves present, bifid. 6.
Underleaves absent. 19.

2\. Plants pale, perianth five-keeled. 3.
Plants more or less tinged with brown or purple. 5.

3\. Lobule bluntly pointed at the apex or apiculate. 1. *Archilejeunea clypeata.*
Lobule with a long and slender apical tooth. 4.

4\. Lobe widely spreading, slightly convex or plane, averaging 1.2 × 0.95 mm., postical margin usually forming a distinct angle with keel. 2. *Archilejeunea Sellowiana.*
Lobe obliquely spreading, strongly convex, averaging 0.7 × 0.45 mm., postical margin usually forming a continuous line with keel. 3. *Archilejeunea conchifolia.*

5\. Lobule entire on margin or with a single apical tooth, median leaf-cells averaging 21 × 12 μ, ♀ inflorescence usually innovating or only one side, perianth trigonous throughout. 4. *Mastigolejeunea auriculata.*
Lobule crenulate on margin with about four teeth, median leaf-cells averaging 23 × 16 μ, ♀ inflorescence usually innovating on both sides, perianth six- to eight-plicate in upper part. 5. *Brachiolejeunea corticalis.*

6\. Lobe acute, at least on well developed leaves, underleaves with rounded division, and broad, shallow sinus. 6. *Harpalejeunea ovata.*
Lobe rounded or rarely obtuse, underleaves with obtuse to acute divisions and narrow sinus. 7.

7\. Plants firm in texture, yellowish- or brownish-green, inflorescence dioicous. 8.
Plants delicate in texture, whitish or pale green, varying to dark green. 10.

8\. Underleaves small, distant, narrowed toward base. 7. *Euosmolejeunea duriuscula.*
Underleaves large, contiguous to imbricated, rounded or cordate at base. 9

9\. Leaves loosely imbricated, the lobe broadly ovate, obliquely spreading. 8. *Euosmolejeunea opaca.*
Leaves densely imbricated, the lobe orbicular, widely spreading. 9. *Cheilolejeunea polyantha.*

10\. Branches sometimes flagelliform and leafless but with persistent underleaves, lobule inflated, perianth (so far as known) with a plane antical face. 11.
Branches never flagelliform. 12.

11\. Lobes without basal ocelli, median leaf-cells averaging 21 μ in diameter, inflorescence autoicous. 10. *Cheilolejeunea phyllobola.*
Lobes with basal ocelli, median leaf-cells averaging 10 μ in diameter, inflorescence dioicous. 11. *Cheilolejeunea versifolia.*

12\. Lobule filiform, not inflated, inflorescence autoicous, perianth plane or nearly so on antical face. 12. *Cheilolejeunea pililoba.*
Lobule inflated, perianth with a distinct antical keel. 13.

13\. Lobe widely spreading, inflorescence autoicous. 14.
Lobe obliquely spreading to suberect, inflorescence dioicous. 16.

14\. Lobes and underleaves distinctly crenulate on the margins, underleaves smaller than lobules. 13. *Lejeunea patens.*

Lobes and underleaves entire or nearly so. 15.

15\. Plants pale to dark green, underleaves as large as lobules or larger, not rounded at base, perianth abruptly narrowed at base. 14. *Lejeunea cavifolia.*

Plants pale, underleaves larger than lobules, rounded at base, perianth gradually narrowed toward base. 15. *Lejeunea Americana.*

16\. Median leaf-cells 18–20 μ in diameter. 17.

Median leaf-cells 12–13 *u* in diameter. 18.

17\. Underleaves longer than broad, deeply bifid, often unidentate on sides. 16. *Microlejeunea lucens.*

Underleaves as broad as long, bifid to middle, never unidentate on sides. 17. *Microlejeunea Ruthii.*

18\. Lobule much smaller than lobe, often obsolete, lobe indistinctly ocellate at base, averaging 0.25 mm. in length. 18. *Microlejeunea Cardoti.*

Lobule nearly as large as lobe, lobe not ocellate at base, averaging 0.17 mm. in length. 19. *Microlejeunea bullata.*

19\. Lobule three fourths the length of lobe or longer, lobe rounded at the apex and without hyaline cells, crenulate on the margin, stylus reduced to a single papilla, inflorescence autoicous. 20. *Cololejeunea minutissima.*

Lobule about half as long as lobe. 20.

20\. Outer surface of lobe rough from projecting cells or wart-like thickenings or both, hyaline cells absent, inflorescence dioicous or autoicous. 21.

Outer surface of lobe almost smooth, the cells scarcely if at all convex, hyaline cells often present at the apex and along antical margin, stylus usually two cells long, inflorescence synoicous or paroicous. 23. *Cololejeunea Jooriana.*

21\. Lobe narrowed toward the apex, with strongly convex or conical cells, the projecting wall sometimes thickened, stylus usually two to ten cells long. 21. *Cololejeunea Biddlecomiae.*

Lobe broad at the apex, with slightly convex cells, each bearing in the middle a large globoid thickening, stylus usually two cells long. 22. *Cololejeunea Macounii.*

DESCRIPTION OF SPECIES

1. ARCHILEJEUNEA CLYPEATA (Schwein.) Schiffn.

PLATE 16, FIGS. 1–11

Jungermannia clypeata Schwein. Spec. Fl. Amer. Sept. Crypt. Hep. 12. 1821.

Jungermannia transversalis Schwein. *l. c.* (not Swartz).

Phragmicoma clypeata Nees, Naturgesch. Eur. Leberm. 3: 248. 1838.

Lejeunea Dorotheae Lehm. Pugillus, 7: 17. 1838. G. L. & N. Syn. Hep. 332. 1845.

Lejeunea Carolinensis Mont.; G. L. & N. *l. c.* (as synonym).

Lejeunea calyculata Tayl. Lond. Jour. Bot. **5**: 388. 1846. G. L. & N. Syn. Hep. 752. 1847.

Lejeunea clypeata Sull.; Gray, Manual, Ed. I., 685. 1848.

Symbiezidium calyculatum Trevis. Mem. r. ist. Lomb. III. **4**: 403. 1877.

Lejeunea (*Archi-Lejeunea*) *clypeata* Spruce, Hep. Amaz. et And. 90. 1884.

Archilejeunea clypeata Schiffn.; Engler & Prantl, Nat. Pflanzenfam. $\mathbf{1}^3$: 130. 1893.

Pale glaucous-green or whitish, growing in broad depressed mats: stems prostrate, 0.085 mm. in diameter, closely appressed to matrix, irregularly branched: rhizoids scanty, simple or branched: leaves imbricated, the lobe obliquely spreading, slightly falcate, broadly oblong to suborbicular, convex, averaging 0.6 mm. long and 0.45 mm. wide, slightly revolute at the rounded apex, margin crenulate from projecting cells, antical margin rounded at base and arching across or just beyond axis; lobule inflated, ovate-triangular, 0.2 mm. long, 0.12 mm. wide, keel straight or slightly curved, forming a very obtuse angle with postical margin of lobe and sometimes almost continuous with it, free margin slightly curved, involute to beyond apex, then obliquely truncate to end of keel, apex blunt or subacute, consisting of a single projecting cell or rarely of two cells; cells of lobe convex with rather thick projecting walls and thin vertical walls, trigones distinct though sometimes small, acuminate, indeterminate thickenings absent except sometimes near base of lobe, cells at edge of lobe 15 μ in diameter, in the middle and at the base 19 μ: underleaves distant, orbicular, 0.2 mm. long, rounded at the apex, abruptly narrowed and neither rounded nor cordate at base, very short decurrent and attached by a slightly curved line of insertion: inflorescence autoicous or dioicous: ♀ inflorescence usually borne on a leading branch, rarely on a short branch, innovating on one or rarely on both sides, the innovations usually simple and sterile; bracts complicate, unequally bifid, scarcely or not at all winged on keel, the lobe obovate, slightly falcate, rounded at the apex, 0.75 mm. long, 0.45 mm. wide, crenulate on the margins, lobule oblong, rounded at the apex, 0.4 mm. long, 0.12 mm. wide; bracteole ovate-oblong, 0.6 mm. long, 0.4 mm. wide, slightly narrowed toward base, truncate or rarely retuse at the broad apex; perianth obovoid, 0.85 mm. long, 0.6 mm. wide, cuneate toward base, truncate above and with a short broad beak, lateral keels sharp, antical keel short and low, postical keel long, broad and sharply two-angled when young, the keels roughened from projecting cells or sometimes with narrow rudimentary wings: ♂ spikes occupying short branches, oblong; bracts closely imbricated in two to four pairs, strongly inflated, slightly and subequally bifid with rounded lobes and strongly arched keel; bracteoles similar to the underleaves but smaller, limited to base of spike: antheridia in pairs.

Type-locality, Salem, North Carolina (Schweinitz).

On rocks and trees. Connecticut (Hall, Evans); New York (Peck); Pennsylvania (James, Lea); Delaware (James, Commons); District of Columbia (Coville, Holzinger); Virginia (Mrs. Britton and Miss Vail); West Virginia (Millspaugh); North Carolina (Schweinitz); South Carolina (Green); Tennessee (Underwood); Georgia (Underwood, Small); Alabama (Mohr); Mississippi (Lloyd and Tracy); Missouri (Russell); Arkansas (Coville); Louisiana (Langlois).

EXSIC.: Musc. Alleg. 262 (as *Phragmicoma clypeata*). Hep. Bor.-Amer. 95 (as *Phragmicoma clypeata*). Hep. Amer. 50 *p.p.* (as *Lejeunea* (*Archi-Lej.*) *clypeata*).

Archilejeunea clypeata and the two following species are very closely related. They differ from typical members of the genus in their pale color, less robust habit and short antheridial spikes. In these peculiarities they show an approach to the genus *Cheilolejeunea*, from which their undivided underleaves should probably exclude them. Recent writers on the hepaticae, however, tend to ascribe less value to this character than was originally done by Spruce, and species with undivided underleaves have been described in the genera *Euosmolejeunea*, *Cheilolejeunea* and *Pycnolejeunea*. Under these circumstances the generic position of *A. clypeata* and its immediate allies cannot be regarded as thoroughly established.

In studying *A. clypeata*, the writer has been able to examine the type of *Jungermannia clypeata* from the Schweinitz herbarium, the type of *Lejeunea Dorotheae* from the Lindenberg herbarium and a portion of the type of *L. calyculata* from the Taylor herbarium. The specimens in the Schweinitz herbarium labeled *Jungermannia transversalis* have also been examined, as well as the plants which Schweinitz sent to Torrey under this name. All of these various specimens evidently belong to the same species. In *L. Dorotheae* and in the plants labeled *J. transversalis*, the apex of the lobule is sometimes composed of two superposed cells, instead of a single cell as is usual in the species. They show, however, even on robust stems, no other approach to either of the following species.

2. ARCHILEJEUNEA SELLOWIANA Steph.

PLATE 16, FIGS. 12-20

Phragmicoma xanthocarpa Aust. Hep. Bor.-Amer. 95 b. 1873. Not *Jungermannia xanthocarpa* Lehm. & Lindenb.; Lehmann, Pugillus, **5**: 8. 1832 (*Lejunea xanthocarpa* Lehm. & Lindenb.; G. L. & N. Syn. Hep. 330. 1845).

Archilejeunea Sellowiana Steph. Hedwigia, **34**: 62. 1895.

Lejeunea velata Gottsche; Stephani, *l. c.* (as synonym).

Pale glaucous-green or whitish, growing in broad depressed mats: stems prostrate, often radiating from a center, 0.17 mm. in diameter, closely appressed to matrix, irregularly branched: rhizoids abundant: leaves closely imbricated, the lobe widely spreading almost at right angles with axis, ovate-oblong, sometimes slightly falcate, plane or slightly convex, 1.2 mm. long and 0.95 mm. wide on robust individuals, slightly revolute at the rounded apex, margin entire or subcrenulate from projecting cells, antical margin rounded at base and arching across or just beyond axis; lobule somewhat inflated toward base, oblong, 0.6 mm. long, 0.25 mm. wide, keel slightly arched, forming a distinct but very obtuse angle with postical margin, free margin curved, slightly inflexed near base, otherwise plane, apex acuminate, sometimes hamately curved, the apical tooth mostly three to eight cells long and two to four cells wide at base, ending in a single row of two or three cells, sinus beyond apex deep and rounded then passing very obliquely into postical margin, free margin of lobule, except for apical tooth usually entire but, in rare cases, bearing one or two supplementary teeth between base and apex or between apex and end of keel, lobules on small branches often poorly developed; cells of lobe convex with rather thick projecting walls and thin vertical walls, trigones large, acuminate to obtuse, intermediate thickenings not infrequent in middle of lobe and abundant toward base, mostly circular in outline, cells at edge of lobe 12 μ in diameter, in the middle and at the base 18 μ: underleaves contiguous to imbricated, broadly orbicular to reniform, 0.6 mm. long, 0.7 mm. wide, rounded, truncate or retuse at the apex, rounded or subcordate at base, attached by a slightly curved line of insertion: inflorescence autoicous: ♀ inflorescence usually borne on a short branch, more rarely on a leading branch, innovating one side, the innovation simple and sterile; bracts complicate, unequally bifid, sometimes with a narrow and rudimentary wing along keel, the lobe oblong-ovate to obovate, suberect to widely spreading, rounded at the apex, 0.9 mm. long, 0.6 mm. wide, lobule oblong, rounded to subacute, 0.5 mm. long, 0.2 mm. wide; bracteole oblong to obovate, 0.5 mm. long, 0.45 mm. wide, narrowed toward base, truncate at the apex; perianth obovoid, about half exserted, 0.9 mm. long, 0.7 mm. wide, cuneate toward base, broad and truncate above and with a short, narrow beak, lateral keels sharp, antical keel short and low, postical keel long, broad and prominent, sharply two-angled when young and sometimes showing a short supplementary fold between the angles near apex, keels slightly roughened from projecting cells: ♂ spikes occupying short branches, similar to those of *A. clypeata*: spores brownish-green, angular, variable in length, with thickened walls marked by minute verruculae and small orbicular patches of low, radiating ridges, averaging 23 μ in short diameter.

Type-locality, Brazil (Sellow).

On trees and rocks: Rhode Island (Bennett); Delaware Commons); Virginia (Seymour, Mears); North Carolina (Johnson); South Carolina (Miss DuBois); Tennessee (Ruth, Scoville); Georgia (Underwood); Florida (Austin, Farlow, Lighthipe, Underwood, Straub, Nash); Alabama (Mohr, Earle and Baker, Maxon and Pollard); Mississippi (Hall, Lloyd and Tracy); Louisiana (Langlois); Texas (Mohr).

EXSIC.: Hep. Bor.-Amer. 95 b (as *Phragmicoma xanthocarpa*).

A. Sellowiana was first distinguished from *A. clypeata* by Austin, who considered it identical with *Lejeunea xanthocarpa* Lehm. & Lindenb., a widely distributed tropical and subtropical species occurring in both America and Africa. Austin distributed the plant as *Phragmicoma xanthocarpa* and it has since been known in America under this name. Through the kindness of Stephani, the writer has been enabled to study a specimen of *A. Sellowiana* collected at Petropolis, Brazil, by Rudolph. This specimen, which is quoted immediately after the type in the original description, agrees very closely with the specimens from the United States. It is probable, therefore, that the range of the species extends through Mexico and Central America into Brazil. It is worthy of note that the sterile type-specimens, collected by Sellow, were first referred doubtfully by Stephani to *A. clypeata*.*

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* Hedwigia, **29**: 20. 1890.

Austin incorrectly referred to his "*Phragmicoma xanthocarpa*," as synonyms, *Jungermannia transversalis* Schweinitz and *Lejeunea catenulata* Nees.* The first of these has already been commented upon. The second is a distinct species of the genus *Neurolejeunea*,† and its presence in the United States has not been definitely established. According to the synopsis it was found in "*Hymenophyllo ciliato* et *Neckera abietina* Hook. Americae septentrionalis." Unfortunately the genus *Hymenophyllum* is not known from the United States, *H. ciliatum* itself being found in tropical America. *Neckera abietina* (*Alsia abietina* Sull.), on the other hand, is found in California and northward along the Pacific coast, a region from which no Lejeuneae have been recorded except the recently described *Cololejeunea Macounii* of British Columbia. Under the circumstances we must exclude *Neurolejeunea catenulata* from our list.

The most important differences between *A. Sellowiana* and *A. clypeata* are drawn from their vegetative organs. *A. Sellowiana* is the more robust of the two species; the lobes of its leaves spread more widely and are at the same time more falcate; the lobule is oblong instead of ovate-triangular in outline, and its apex is acuminate instead of apiculate; the cells of the lobe have more conspicuous trigones and more numerous intermediate thickenings, the latter being practically absent in *A. clypeata;* its much broader underleaves finally are more crowded together and are usually subcordate at the base. The perichaetial bracts and perianths are so variable in both species that the slight differences between them are of little diagnostic value. In *A. Sellowiana*, however, the female flower is usually borne on a short branch, while in *A. clypeata* it is usually borne on a leading branch. Unfortunately even this difference is inconstant. The perigonial spikes are essentially the same in both species.

In the true *A. xanthocarpa* (Lehm. & Lindenb.) Steph., the lobe is much more strongly convex than in *A. Sellowiana*, and the margin is revolute both at the apex and along the entire postical side. In the lobule also the free margin is strongly involute for the greater part of its length. The leaf-cells are similar in the two

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* Syn. Hep. 323. 1845.

† Spruce, Hep. Amaz. et And. 84. 1884; Schiffner; Engler & Prantl, Nat. Pflanzenfam. 1^3: 131. 1893.

species, but intermediate thickenings in *A. xanthocarpa* are very infrequent.

3. **Archilejeunea conchifolia** sp. nov.

PLATE 17, FIGS. 1–9

Pale yellowish-green or whitish, growing in depressed mats: stems prostrate, 0.1 mm. in diameter, closely appressed to matrix, irregularly branched: rhizoids abundant: leaves densely imbricated, the lobe obliquely spreading, not falcate, ovate, very convex, 0.7 mm. long, 0.45 mm. wide, strongly revolute at the rounded apex and along the postical margin, antical margin slightly rounded at base, arching across or just beyond axis, margin entire or very vaguely and sparingly crenulate; lobule inflated, oblong, 0.45 mm. long, 0.17 mm. wide, keel more or less arched, usually forming a continuous line with the revolute postical margin but sometimes slightly indented at junction with postical margin, free margin curved, involute to or beyond apex, sinus beyond apex deep and rounded then passing very obliquely into the revolute postical margin, apex acuminate, the apical tooth mostly three to six cells long and three or four cells wide at base, ending in a single row of two or three cells; cells of lobe slightly papillose, with thickened free walls and thin vertical walls, trigones small, intermediate thickenings very scanty near base of lobe, otherwise wanting, cells at edge of lobe 14 μ in diameter, in the middle and at the base 20 μ: underleaves contiguous or imbricated, broadly orbicular, 0.25 mm. long, 0.35 mm. wide, broadly truncate at the apex, abruptly narrowed and neither rounded or truncate at base, very shortly decurrent and attached by a slightly curved line of insertion: inflorescence autoicous: ♀ inflorescence usually borne on a leading branch, rarely on a short branch, innovating on one side, the innovation usually short, simple and sterile; bracts complicate, shortly and unequally bifid, not winged on keel, the lobe ovate, obliquely or widely spreading, rounded at the apex, entire, 0.7 mm. long, 0.45 mm. wide, lobule narrowly ovate to lingulate, obtuse to acute at the apex, 0.45 mm. long, 0.17 mm. wide; bracteole obovate, 0.5 mm. long, 0.35 mm. wide, narrowed toward base, truncate or slightly retuse at the broad apex; perianth obovoid, about half exserted, 0.85 mm. long, 0.5 mm. wide, cuneate toward base, rounded or truncate above and with a short beak, lateral keels sharp, antical keel distinct, about half as long as perianth, postical keel long, broad and sharply two-angled when young, keels smooth or nearly so: ♂ spikes occupying short branches, similar to those of *A. clypeata*.

Type-locality, Orange Bend, Florida (Underwood, 60).

On trees. South Carolina (Ravenel, Miss Du Bois); Alabama (Baker); Florida (Underwood).

EXSIC.: Hep. Amer. 50 *p. p.* (as *Lejeunea* (*Archi-Lej.*) *clypeata*).

A. conchifolia is of about the same size as *A. clypeata*, and agrees with it in the position of its female flowers. It differs in its obliquely spreading, convex lobes with revolute apex and margin, in its oblong lobule with acuminate apex and in its imbricated underleaves, usually broader than long. From *A. Sellowiana* it differs mainly in its smaller size and in the characters of its convex leaf-lobes, which are not at all falcate.

A. conchifolia is perhaps closer to *A. xanthocarpa* than is the preceding species, agreeing with it in its convex leaf-lobes with revolute postical margins. It is, however, much less robust, its lobes spread more obliquely, its lobules are relatively larger and their apices can usually be made out without dissection.

4. MASTIGOLEJEUNEA AURICULATA (Wils. & Hook.) Schiffn.

PLATE 17, FIGS 10-19

Jungermannia auriculata Wils. & Hook.; Drummond, Musc. Amer. St. Merid. 170. 1841.

Phragmicoma versicolor Lehm. & Lindenb. *p. p.*; G. L. & N. Syn. Hep. 297. 1845.*

Phragmicoma teretiuscula Lindenb. & Gottsche, *p. p.*, *l. c.* 745. 1847.

Lejeunea auriculata Sull.; Gray, Manual, Ed. II., 699. 1856.

Ptycocoleus auriculatus Trevis. Mem. r. Ist. Lomb. III. **4**: 405. 1877.

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* *Phragmicoma versicolor* of the Synopsis Hepaticarum is based on specimens collected at Madras by Wight and on Drummond's Louisiana specimens, the type of *Jungermannia auriculata* Wils. & Hook. In the supplement to this work, the authors refer some of Wight's specimens to *P. repleta* Tayl. (Lond. Jour. Bot. **5**: 392. 1846) and the remainder to the newly described *P. teretiuscula* Lindenb. & Gottsche (p. 745), in which certain Mexican specimens collected by Liebman are also included. This last species, according to Stephani (Hedwigia, **29**: 8. 1890), is also a composite, the Indian specimens being referable to *P. ligulata* Lehm. & Lindenb. (Syn. Hep. 301) and the Mexican specimens to *P. versicolor*. It is evident from the above notes that the name "versicolor," although finally restricted by the authors of the Synopsis to Drummond's specimens, cannot justly supersede the older name "auriculata." According to the strict rules of priority, however, it might still be made to replace the name "repleta" of Taylor, but apparently there is enough reason for giving it up altogether. Of course the name "teretiuscula" has no claims whatever.

Lejeunea (*Mastigo-Lejeunea*) *auriculata* Spruce, Hep. Amaz. et And. 102. 1884.

Mastigolejeunea auriculata Schiffn.; Engler & Prantl, Nat. Pflanzenfam. I^3: 129. 1893.

Glaucous green, varying to brownish or purplish in older parts, growing in depressed tufts : stems prostrate or pendent, 0.15 mm. in diameter, arising from a creeping caudex, irregularly pinnate or on ♀ plants rarely dichotomous, branches widely spreading, sometimes small-leaved and flagelliform : rhizoids scanty : leaves densely imbricated, closely appressed when dry, widely spreading and subsquarrose when moist, the lobe ovate-oblong, more or less falcate, 1 mm. long, 0.5 mm. wide, apex usually obtuse, sometimes rounded or subacute, margin entire or subrepand, antical margin rounded to auriculate at base, postical margin more or less revolute, especially on robust axes ; lobule more or less inflated, very variable, averaging 0.35 mm. long and 0.2 mm. wide, on small branches ovate, the free margin more or less rounded, somewhat involute, apex apiculate, acute or obtuse, sinus beyond apex broad and shallow, passing very obliquely into postical margin of lobe, lobule on robust stems and branches often appearing simply as a broadening out of the postical margin of lobe, without showing a distinct apex, these two extreme types of lobule being connected by intermediate conditions, hexagonal or subrhomboid in outline ; cells of lobe plane, thick-walled and with distinct trigones, intermediate thickenings occasionally present toward base of lobe, cells at edge of lobe 8 μ in diameter, in the middle 21 × 12 μ, at the base 23 × 14 μ : underleaves imbricated, broadly orbicular, 0.5 mm. long, 0.55 mm. wide, with a broad, median ridge, truncate or slightly retuse at apex, cuneate toward base, indistinctly decurrent or minutely auriculate at base and attached by a slightly curved line of insertion, margin irregularly sinuate, more or less revolute at apex and near base : inflorescence autoicous or dioicous : ♀ inflorescence borne on a leading branch, innovating on one or rarely on both sides, the innovations once or repeatedly floriferous ; bracts complicate, unequally bifid, the lobe ovate, suberect to widely spreading, 1.2 mm. long, 0.6 mm. wide, the apex usually subacute, but varying from rounded to acuminate, margin irregularly sinuous, lobule oblong to obovate, bluntly pointed, truncate or retuse at apex, 0.7 mm. long, 0.35 mm. wide ; bracteole 0.8 mm. long, 0.7 mm. wide, obovate from a slightly narrowed base, at the apex rounded, truncate, retuse or emarginate with a lunulate sinus, margin sinuous, more or less revolute toward base ; perianth oval in outline, about one third exserted, 1.5 mm. long, 0.6 mm. wide, rounded at base and at apex, beak short and broad, strongly compressed and with a high, narrow, postical keel, antical surface plane or nearly so, keels not winged : ♂ inflorescence borne on ♀ plants, occupying ordinary branches or innovations, usually proliferating and sometimes repeatedly floriferous ; bracts in six to twelve pairs, similar to the leaves, but with smaller, less widely spreading lobes, more strongly arched keels and larger, more inflated lobules, truncate to retuse at apex ; bracteoles similar to underleaves, found throughout spike ; antheridia borne singly : spores greenish, thick-walled, minutely verruculose, averaging 34 μ in short diameter.

Type-locality, New Orleans and Louisiana (Drummond).

On trees. Florida (J. D. Smith, Underwood, Straub) ; Alabama (Mohr) ; Louisiana (Drummond, Langlois). The species is widely distributed in tropical America.

EXSIC.: Musc. Amer. St. Merid. 170 (as *Jungermannia auriculata*). Hep. Amer. 133 (as *Lejeunea* (*Mastigo-Lej.*) *auriculata*).

Mastigolejeunea auriculata belongs to a tropical and subtropical genus which has no other known representatives in the United States. The species bears, however, a certain superficial resemblance to *Brachiolejeunea corticalis*, with which it has been confused. The latter species is readily distinguished by its crenulate lobules, larger leaf-cells, usually double innovation and pluriplicate perianth.

According to Spruce,* *M. auriculata* can scarcely be distinguished from the Javan *M. humilis* (Gottsche) Schiffn., to which he would also reduce M. *repleta* (Tayl.). Stephani † states that all three species are amply distinct. The writer has examined a specimen of *M. humilis* and finds that this species, although very close to *M. auriculata*, differs in its smaller size, in its much less variable lobule, which ends in a long outwardly curved tooth consisting of three or eight cells in a single row, in its more emarginate underleaves and in the broader lobes and lobules of its perichaetial bracts. According to Stephani *M. repleta* is distinguished by its apiculate leaves.

5. BRACHIOLEJEUNEA CORTICALIS (Lehm. & Lindenb.) Schiffn.

PLATE 18, FIGS. 1–11

Jungermannia corticalis Lehm. & Lindenb. ; Lehmann, Pugillus, **4**: 50. 1832.

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* Hep. Amaz. et And. 103. 1884.

† Hedwigia, **29**: 9. 1890.

Frullania Leprieurii Nees & Mont.; Mont. Ann. des Sc. Nat. II. **14**: 333. *pl. 20. f. 1.* 1840.

Phragmicoma corticalis Lehm. & Lindenb.; G. L. & N. Syn. Hep. 297. 1845.

Phragmicoma melanophloea Mont. & Nees, *l. c.* 297 (as synonym).

Lejeunea linguaefolia Tayl. Lond. Jour. Bot. **5**: 390. 1846. G. L. & N. Syn. Hep. 754. 1847 (*fide* Stephani).

Phragmicoma Leprieurii Mont. Sylloge, 86. 1856.

Ptychocoleus corticalis Trevis. Mem. r. Ist. Lomb. III. **4**: 405. 1877.

Lejeunea (*Brachio-Lejeunea*) *corticalis* Steph. Hedwigia, **29**: 8. 1890.

Brachiolejeunea corticalis Schiffn. Hedwigia, **33**: 180. 1894 (in obs.).

Brownish-green, growing in depressed tufts, ♂ and ♀ plants mixed together: stems prostrate, appressed to substratum, 0.2 mm. in diameter, irregularly pinnate or on ♀ plants more or less dichotomous, branches never flagelliform, widely spreading but at less than a right angle: rhizoids often abundant: leaves imbricated, more or less appressed when dry, widely spreading when moist, the lobe ovate, falcate, 0.85 mm. long, 0.5 mm. wide, apex broad, rounded or very obtuse, margin entire, antical margin curved, arching across axis and rounded or subcordate at base, postical margin distinctly indented beyond end of keel; lobule strongly inflated about half its width, broadly ovate, measuring, when inflated, 0.45 mm. long and 0.25 mm. wide, keel straight or slightly arched, subcrenulate from projecting cells, free margin plane and appressed to lobe, rounded at inner edge, then straight or slightly curved and passing obliquely into postical margin of lobe, usually bearing four scattered papilla-like teeth, each consisting of a single blunt cell or rarely of two cells, and, near outer end, a fifth angular tooth, the last sometimes obsolete; cells of lobe plane or somewhat papillose, thin-walled, trigones distinct, usually with two convex sides and one concave side, intermediate thickenings very infrequent, cells at edge of lobe 13 μ in diameter, in the middle 23 × 16 μ, at the base 28 × 23 μ: underleaves slightly imbricated, orbicular-quadrate to reniform, 0.45 mm. long, 0.45 mm. wide, truncate or retuse at the broad apex, sides parallel or converging toward base: inflorescence dioicous: ♀ inflorescence borne on a leading branch, usually innovating on both sides, more rarely on one side, the innovations usually once or twice floriferous; bracts complicate, unequally bifid, keel broadly winged in lower half, the wing entire, semicircular to semiovate in outline, lobe ovate, obliquely spreading, rounded at apex, subcordate at base, irregularly sinuous on margin, 0.95 mm. long, 0.5 mm. wide, lobule lanceolate-ligulate, rounded at apex, sinuous on margin, 0.85 mm. long, 0.2 mm. wide; bracteole free, oblong, 0.85 mm. long, 0.4 mm. wide, truncate to retuse at apex, broadening out slightly toward base, irregularly sinuous on margin ; perianth oblong-obovoid, about one third exserted, 1.1 mm. long, 0.6 mm. wide, rounded at apex and with a short, broad beak, somewhat compressed in upper half with sharp lateral keels, postical keel broad, sharply two-angled and with a short, supplementary fold near apex, antical keels one to three, low and short: ♂ spikes spikes borne on leading branches, usually proliferating and repeatedly floriferous, bracts in about six pairs, less spreading than the leaves, the lobe not falcate, lobule nearly as long as lobe but narrower, inflated, apex blunt to subacute, margin entire ; bracteoles similar to underleaves, found throughout spike.

Type-locality, Jamaica (Herb. Lehm. & Lindenb.).

On trees. Lake Worth, Florida (Underwood). The species has a rather wide distribution in tropical America.

Brachiolejeunea corticalis has not before been recorded from the United States. The Florida specimens, however, agree closely with the type and also with the specimens from Cuba, distributed in Hep. Amer. 144. There is no danger of confusing the species with any of our other Lejeuneae except possibly *Mastigolejeunea auriculata*, under which the most important differences have already been enumerated.

The genus *Brachiolejeunea* has several representatives in tropical America, and among them *B. bicolor* (Nees) Schiffn. is perhaps most closely related to *B. corticalis*. *B. bicolor* is a more robust plant, the lobes of its leaves tend to be more sharply pointed, its underleaves are more or less auriculate at base and its perianth is regularly pluriplicate, usually with ten distinct folds in the upper part.

6. HARPALEJEUNEA OVATA (Hook.) Schiffn.

Jungermannia serpyllifolia β ovata Hook. Brit. Jung. 1816 (not figured).

Lejeunea ovata Tayl.; G. L. & N. Syn. Hep. 376. 1845.

Lejeunea (*Harpa-Lejeunea*) *ovata* Spruce, Hep. Amaz. et And. 165. 1884.

Lejeunea Molleri Steph. Hedwigia, **26**: 3. *pl. 1. f. 2.* 1887.

Harpalejeunea ovata Schiffn.; Engler & Prantl, Nat. Pflanzenfam. **1**^{3}: 127. 1893.

Pale to dark green, loosely depressed-caespitose or scattered among other hepatics: stems prostrate, 0.05 mm. in diameter, closely appressed to substratum, irregularly branched: rhizoids few: leaves contiguous or somewhat imbricated, the lobe convex, obliquely to widely spreading, falcate-ovate, 0.3 mm. long, 0.15 mm. wide, gradually narrowed beyond middle, apex often reflexed, mostly acute or short-acuminate, rarely obtuse, margin subentire or irregularly sinuate, antical margin curved, arching part way across axis and almost straight at base, postical margin slightly rounded near keel and forming with it a distinct angle varying from obtuse to acute; lobule strongly inflated, ovoid, 0.15 mm. long, 0.08 mm. wide, keel strongly arched, crenulate from convex cells, free margin slightly curved, involute to beyond apex, then obliquely truncate or lunulate to end of keel, apex tipped with a single, projecting cell, curving slightly outwards or nearly straight; cells of lobe convex, thin-walled, trigones distinct though sometimes minute, intermediate thickenings scattered, usually distinct, basal ocelli formed of two to five enlarged, thin-walled cells, cells at edge of lobe averaging 14 μ in diameter and in the middle 18 μ, cells of ocelli 30 × 24 μ: underleaves distant, broadly cuneiform, 0.08 mm. long, 0.1 mm. wide, lateral margins straight or nearly so near base, apex broad, truncate or usually emarginate-obcordate with a shallow sinus and broad, rounded or very obtuse segments, usually three to five cells long and four or five cells broad at base, margin entire: inflorescence dioicous: ♀ inflorescence on a leading branch, innovating on one or rarely on both sides, the innovations usually simple andsterile; bracts complicate, unequally bifid, sometimes narrowly winged along keel, the wing often interrupted, one or two cells wide, lobe suberect, oblong to obovate, 0.5 mm. long, 0.25 mm. wide, gradually narrowed toward the obtuse or rounded apex, often bearing scattered ocelli, lobule narrowly oblong-ovate, rounded or truncate at apex, 0.4 mm. long, 0.15 mm. wide, margins of bracts entire, bracteole slightly connate on both sides, oblong-ovate to broadly obovate, 0.3 mm. long, 0.2 mm. wide, rounded to emarginate-bifid at apex with rounded segments, sometimes sparingly ocellate, margin entire; perianth obovate-clavate, acutely five-keeled in upper part: ♂ spike occupying a short branch; bracts in one or two pairs, closely imbricated, erect, unequally bilobed, antical lobe oval, obtuse, postical lobe similar but smaller.

Type-locality, Ireland (Taylor).

On trees and fallen logs. Southern States (Sullivant, fide Austin); Virginia (Mrs. Britton and Miss Vail); Tennessee (Ruth); Georgia (Underwood). The species also occurs in western Europe but is rare. Pearson * states that it grows on shaded rocks but according to Camus † it is also found on bark.

Harpalejeunea ovata has been illustrated three times within recent years. Stephani's figure, already noted in the synonymy, was drawn from specimens collected in Portugal. The writer has illustrated the specimens from Virginia,‡ while Pearson has published figures drawn from British material.§ The perianth, known only from the brief description in the Synopsis Hepaticarum, does not appear in any of these illustrations.

The American specimens agree closely with the type-material in the Taylor herbarium but show a greater variability in the shape of the bracteole than European writers describe. There are no male specimens among them, and the description given above of the perigonial spike is taken wholly from Pearson.

There is no other species from the United States with which *H. ovata* ought to be confused. The acute lobes of its leaves and its emarginate-bifid underleaves with rounded divisions are unique among our Lejeuneae. The species, however, finds several close allies in tropical regions, where the genus *Harpalejeunea* is largely represented.

7. **Euosmolejeunea duriuscula** (Nees)

PLATE 18, FIGS. 12–13

Jungermannia serpyllifolia Wils. & Hook. *p. p.* Drummond, Musc. Amer. St. Merid. 171. 1841.

Lejeunea duriuscula Nees; G. L. & N. Syn. Hep. 364. 1845.

Lejeunea flexuosa Lindenb. *l. c.* 385. 1845 (*fide* Stephani).

Lejeunea serpyllifolia var. Sull. Musc. Alleg. 273. 1845.

Lejeunea Sullivantiae Aust. Bull. Torrey Club, **3**: 15. 1872.

Lejunea Austini Lindb. Acta Soc. Sci. Fenn. **10**: 489. 1875.

Lejeunea (*Cheilo-Lejeunea*) *duriuscula* Spruce, Hep. Amaz. et And. 259. 1884.

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* Hep. Brit. Isles, 43. 1899.

† Bull. Soc. Bot. de France, **47**: 201. 1900.

‡ Small & Vail, Mem. Torrey Club, **4**: *pl. 81.* 1894.

§ *L. c. pl. 8.*

Lejeunea (*Euosmo-Lejeunea*) *duriuscula* Steph. Hedwigia, **29**: 80. 1890.

Lejeunea (*Eu-Lejeunea*) *Underwoodii* Steph. Bot. Gazette, **17**: 171. 1892.

Cheilolejeunea duriuscula Schiffn.; Engler's Bot. Jahrb. **23**: 592. 1897 (in obs.).

Yellowish-green, sometimes tinged with brownish, depressed-caespitose: stems prostrate, loosely appressed to substratum, 0.08 mm. in diameter, sparingly and irregularly branched: rhizoids scanty: leaves slightly imbricated, the lobe convex, obliquely to widely spreading, falcate-ovate, 0.4 mm. long, 0.35 mm. wide, rounded or very obtuse at the apex, margin slightly and irregularly angular-sinuate, antical margin arching across or just beyond axis, rounded at base, postical margin forming an obtuse angle with keel; lobule strongly inflated, triangular-ovate, measuring when inflated 0.1 mm. long, 0.08 mm. wide, keel slightly arched or almost straight, somewhat decurrent, free margin strongly involute to beyond the obtusely pointed or apiculate apex, then obliquely truncate to end of keel; cells of lobe plane or slightly convex, with somewhat thickened walls and large, triangular trigones, averaging 13 μ in diameter at edge of lobe, 16 μ in the middle and 21 μ at base: underleaves distant, ovate to orbicular, 0.17 mm. long, 0.15 mm. wide, bifid about one half with acute, slightly spreading lobes and narrow usually acute sinus, cuneate and slightly decurrent at base, sometimes very minutely auriculate: inflorescence dioicous: ♀ inflorescence borne on a leading branch, innovating on one or sometimes on both sides, the innovations long, often floriferous; bracts complicate, unequally bifid, the lobe suberect to widely spreading, ovate to falcate-ovate, rounded to obtuse at the apex, margin as in leaves, 0.5 mm. long, 0.3 mm. wide, lobule ovate to lanceolate, rounded to acuminate at the apex, 0.17 mm. long, 0.08 mm. wide; bracteole free, broadly ovate to obovate, 0.45 mm. long, 0.35 mm. wide, bifid about one third with erect, acute lobes and narrow, mostly acute sinus; perianth brownish, somewhat exserted, obovoid, 0.8 mm. long, 0.5 mm. wide, rounded, truncate or slightly retuse at apex and with a short beak, somewhat compressed with sharp lateral keels and a broad, sharply two-angled postical keel, antical keel lower, surface smooth: ♂ spike borne on a leading branch or rarely on a short branch, usually proliferating at the apex; bracts in two to four pairs, very concave and strongly inflated, shortly and subequally bifid with a strongly arched keel and rounded or obtuse lobes, slightly crenulate at apex; bracteoles similar to underleaves but smaller, present only in lower part of spike.

Type-locality, Surinam (Curie).

On trees or rotten logs, often growing with mosses or other hepatics. Florida (J. D. Smith, Farlow, Underwood); Alabama (Sullivant, Mohr); Mississippi (Langlois, Lloyd and Tracy); Louisiana (Drummond, Featherman, Langlois, Faxon). The species has a wide distribution in tropical America.

EXSIC.: Musc. Amer. St. Merid. 171 *p. p.* (as *Jungermannia serpyllifolia*). Musc. Alleg. 273 (as *Lejeunea serpyllifolia* var.). Hep. Bor.-Amer. 96 (as *Lejeunea Sullivantiae*). Hep. Amer. 135 (as *Lejeunea* (*Eu-Lej.*) *Underwoodii*).

Lejeunea Sullivantiae Aust. has been more or less of a puzzle to hepaticologists, and yet the original description, although brief, is not misleading. The specimens distributed by Austin and by Sullivant, moreover, are both abundant and characteristic. Unfortunately Austin makes no note in his description of the female flowers, although they are fairly abundant in the material which he studied. The probability is that he overlooked them because they had developed no perianths.

A few years after *L. Sullivantiae* was published, Lindberg studied the specimens in Musc. Alleg. 273 and Hep. Bor.-Amer. 96 and proved that they were identical with the dark tufts in No. 171 of Drummond's exsiccata. He also stated that they could not be distinguished from *L. thymifolia* Nees, ? γ of the Synopsis Hepaticarum,[*] a plant which he knew from male specimens collected in French Guiana by Leprieur. *L. thymifolia* has since been reduced to *L. flava* Swartz,[†] and the questionable variety γ is referred by Stephani [‡] to *L. duriuscula*, a species with which Lindberg was apparently unfamiliar Objecting to the name "*L. Sullivantiae*" on account of the older *L. Sullivantii* Gottsche,[§] Lindberg gave to Austin's species the name *L. Austini*, and presumably referred to it the var. γ, to which allusion has just been made.

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[*] 373.

[†] Spruce, Hep. Amaz. et. And. 271; Schiffner, Conspect. Hep. Arch. Ind. 249. 1898.

[‡] Hedwigia, 29: 83. 1890. It should perhaps be noted that Stephani's specimens of var. γ were collected by Beyrich in Brazil and are the plants mentioned in the Synopsis. Gottsche (Mex. Leverm. 218. 1863) refers these same specimens to *L. pulvinata* Lehm. & Lindenb. (Syn. Hep. 382).

[§] Mex. Leverm. 196. 1863.

The validity of *L. Austini*, so far as the specimens from the United States are concerned, is recognized both by Underwood and by Stephani. The latter author first referred it to the subgenus *Eu-Lejeunea*, but at present considers it a *Cheilolejeunea*. With it he compares his *Eu-Lejeunea Underwoodii*, from Florida, a plant which he is now also inclined to place in *Cheilolejeunea*. It is evident from the above statements that *L. duriuscula*, *L. Austini* and *L. Underwoodii* are all considered distinct species by Stephani.

The writer has examined all the specimens which Lindberg referred to *L. Austini* with the exception of those from Guiana. He has also examined the specimens of *L. Underwoodii* distributed by Underwood and Cook and those of *Euosmolejeunea duriuscula* in Hepaticae Spruceanae, collected near Pará, in Brazil. All of these plants show female flowers without perianths, and there are no male plants among them. As a result of this study it would appear that all of these specimens are referable to the same species, for which the oldest available specific name, "duriuscula," should be retained. The differences stated by Stephani in his published papers and in his manuscript notes are not always apparent and seem hardly sufficient to separate the species. He states, for example, that *L. Austini* has much smaller leaf-cells than *L. Underwoodii*, and that the lobule of the latter species is inflated and has an arched keel, whereas in *L. Austini* the lobule is not inflated and the keel is approximately straight or concavely arched. He states also that the bracteole is free in *L. Underwoodii* and slightly connate on one side in *L. Austini*. The first of these differences does not hold, since the cells of *L. Austini* average fully as large as those of *L. Underwoodii*. The second difference is unreliable, because convexly arched, straight, and concavely arched keels may often be found on a single stem, and the degree of inflation depends largely upon the degree of development. The third difference is at best inconstant as the bracteole is uniformly free in the specimens of *L. Austini* examined by the writer. Stephani has published no descriptive notes on *Euosmolejeunea duriuscula* but has kindly furnished a drawing of this species made from the type-material. This agrees essentially with the specimens distributed by Spruce. In reducing *L. Austini* and *L. Underwoodii* to synonymy the writer regrets differing from so eminent an authority as

Stephani but feels compelled to follow the evidence drawn from the specimens themselves.

Opinions have varied with regard to the systematic position of *E. duriuscula*. By Spruce it was first placed in *Cheilo-Lejeunea*, a disposition now accepted by Stephani and by Schiffner. Spruce afterwards transferred it to *Euosmolejeunea*, thereby agreeing with an earlier view of Stephani. The plant agrees with *Euosmolejeunea* in its color and general habit, in its leaves and cell-structure and in its perianth. Its underleaves, however, are smaller than is usual in the genus and lack the basal cordations which normally occur. Since several species of *Euosmolejeunea* with equally small underleaves have been described, this difference by itself should hardly suffice to exclude *E. duriuscula*. The species certainly has less in common with either *Cheilolejeunea* or *Lejeunea* proper than it has with *Euosmolejeunea*.

E. duriuscula seems to be limited with us to the States bordering the Gulf of Mexico. The specimens from Kirkville, New York, quoted by Underwood as *L. Austini* * are referable to *Lejeunea cavifolia*. These specimens were determined by Spruce, who had apparently been misled by plants incorrectly referred to *L. Austini*. In addition to *L. cavifolia*, no fewer than four of our other Lejeuneae have been found in herbaria incorrectly determined as *L. Austini*. Our only species, however, which it at all closely resembles is *Euosmolejeunea opaca*, under which the differential characters will be noted.

8. EUOSMOLEJEUNEA OPACA (Gottsche) Steph.

PLATE 19, FIGS. 1–11

Lejeunea opaca Gottsche; G. L. & N. Syn. Hep. 362. 1845.

Lejeunea (*Omphalanthus?*) *Mohrii* Aust. Bull. Torrey Club, **6**: 20. 1875.

Lejeunea (*Euosmo-Lejeunea*) *laxiuscula* Spruce, Hep. Amaz. et And. 244. 1884.

Lejeunea (*Euosmo-Lejeunea*) *opaca* Steph. Hedwigia, **29**: 79. 1890.

Euosmolejeunea opaca Steph. Bihang Svenska. Vet.-Akad. Handl. **23**^{2}: 23. 1897.

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* Bull. Torrey Club, **19**: 299. 1892.

Yellowish-green, growing in depressed tufts: stems prostrate, loosely appressed to substratum, 0.1 mm. in diameter, sparingly and irregularly branched: rhizoids scanty: leaves loosely imbricated, the lobe convex, obliquely spreading, broadly ovate, 0.5 mm. long, 0.4 mm. wide, rounded at the apex, margin entire or sparingly crenulate from projecting cells, antical margin arching across or just beyond axis, rounded at the base, postical margin forming an angle a little greater than a right angle with keel; lobule strongly inflated, triangular-ovate, 0.15 mm. long, 0.1 mm. wide, keel slightly arched, free margin strongly involute to beyond the subacute apex, then obliquely truncate or lunulate to end of keel; cells of lobe plane or convex, with somewhat thickened walls and large, triangular trigones, averaging 13 μ in diameter at edge of lobe, 18 μ in the middle and 25 × 18 μ at the base: underleaves contiguous or imbricated, orbicular, 0.35 mm. long, bifid about one third with obtuse or acute, erect or subcontiguous lobes separated by an obtuse or acute sinus, rounded or cordate at base and attached by a long, curved line of insertion, margins entire: inflorescence dioicous: ♀ inflorescence borne on a short branch, innovating on one side with a short, simple innovation, very rarely without innovation; bracts complicate, unequally bifid, the lobe erect-spreading, unsymmetrically ovate, usually rounded at the apex, but varying to apiculate or acute, 0.6 mm. long, 0.35 mm. wide, lobule variable, mostly oblong and rounded at the apex, 0.17 mm. long, 0.07 mm. wide; bracteole free, orbicular to oblong, 0.45 mm. long, 0.4 mm. wide, bifid about one third with acute or subacute, erect lobes and narrow sinus; perianth about half exserted, oblong-obovoid, 0.9 mm. long, 0.45 mm. wide, gradually narrowed toward base, rounded at the apex and with a short beak, lateral keels sharp, postical keel about as long as perianth, broad and sharply two-angled, antical keel short, in upper part of perianth: ♂ spike borne on a short branch, sometimes proliferating; bracts and bracteoles similar to those of *E. duriuscula*, but the lobes of the bracts not crenulate at apex.

Type-locality, Surinam (Splitgerber).

On rotten logs. Florida (J. D. Smith, Lighthipe, Underwood, Faxon); Alabama (Mohr). Widely distributed in tropical America.

EXSIC.: Hep. Amer. 134 (as *Lejeunea* (*Euosmo-Lej.*) *trifaria*).

The abundant specimens of *E. opaca*, collected by Underwood in Florida, were at first confused with *E. trifaria* (Nees) Schiffn. This species is even more widely distributed, being found in the tropics of both hemispheres, and is certainly to be expected in the southern parts of Florida. It is a more robust plant than *E. opaca*, and differs from it in its autoicous inflorescence and in its leaf-cells, which are more convex on the free surface of the lobe and show much more conspicuous trigones.

The type-specimens of *Lejeunea Mohrii* in the Austin herbarium are apparently referable to *E. opaca*, although sterile and in rather poor condition. They do not agree fully with Austin's description because they show bifid underleaves, but this is a character which might have been overlooked.

E. opaca differs from *E. duriuscula* in its much larger underleaves, distinctly rounded or cordate at the base, and in the position of its sexual organs, which are borne on short branches rather than on leading branches. Occasionally one meets with specimens of *E. opaca* in which the underleaves are smaller than is normal, but in such cases a careful search will commonly show underleaves of the usual size on some of the axes.

At one time Spruce * threw doubt on the validity of *E. opaca*, suspecting that it was synonymous with *Lejeunea clausa* Mont. Later he apparently changed his mind, for he distributed specimens under both of these names in his Hepaticae Spruceanae.

9. **Cheilolejeunea polyantha** sp. nov.

PLATE 19 FIGS. 12–21

Dull green or brownish, growing in depressed tufts: stems prostrate, loosely appressed to substratum, 0.1 mm. in diameter, copiously and irregularly pinnately branched, sometimes dichotomous: rhizoids scanty: leaves densely imbricated, the lobe convex, obliquely spreading, orbicular, 0.4 mm. long, rounded at the apex, margin entire or slightly and irregularly angular-sinuate, antical margin arching across axis and rounded at base, postical margin usually rounded, forming an acute or right angle with keel; lobule strongly inflated, ovoid-cylindrical, 0.12 mm. long, 0.08 mm. wide, keel slightly arched, free margin strongly involute as far as the bluntly pointed apex, then abruptly or obliquely truncate to end of keel; cells of lobe slightly convex, with somewhat thickened walls and distinct, triangular trigones, averaging 12 μ in diameter at edge of lobe, 21 μ in the middle and 23 μ at the base: underleaves imbricated, sometimes densely so, rapidly increasing in size toward a ♀ inflorescence, plane, broadly orbicular to reniform, 0.25 mm. long, 0.35 wide, bifid about one

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* Hep. Amaz. et And. 245. 1884.

half the distance from apex to the strongly curved line of insertion, with broad, erect, triangular, obtuse to acute or apiculate lobes and obtuse to acute sinus, rounded to cordate at base, margin entire : inflorescence dioicous : ♀ inflorescence sometimes on a leading branch, sometimes on a short branch, innovating on one or occasionally on both sides, the innovations usually floriferous and sometimes repeatedly so, occasionally sterile ; bracts complicate, deeply and unequally bifid, the lobe obliquely spreading, ovate, rounded or sometimes apiculate at apex, margins as in leaves, 0.7 mm. long, 0.4 mm. wide, lobule ovate to lanceolate, rounded to acuminate at the apex, 0.25 mm. long, 0.15 mm. wide : bracteole free, oblong-elliptical to oval, convex (postically), 0.7 mm. long, 0.5 mm. wide, bifid one fourth to one third with triangular, acute or apiculate lobes and broad obtuse to acute sinus : perianth about half exserted, obovoid, 0.85 mm. long, 0.55 mm. wide, cuneate toward base, gradually narrowed toward the rounded apex and with a short beak, antical surface plane or with a low and indistinct keel near apex, postical keel long, broad and bluntly two-angled, lateral keels slightly compressed : ♂ inflorescence not seen : spores measuring 16 μ in short diameter, elongated, irregularly angular, thick-walled, with small ridge-like thickenings, arranged radiately in circles.

On bark. Eustis, Florida (Underwood, 1380 *p.p.*), the type-locality.

Cheilolejeunea polyantha resembles to a considerable extent the South American *Pycnolejeunea papulosa* Steph.,* a species described by Spruce under the name *Lejeunea* (*Pycno-Lejeunea*) *contigua*, var. *latifolia*.† The new species, however, is much less robust than *P. papulosa*, its leaves are less convex and its leaf-cells have thinner walls and less conspicuous trigones ; its underleaves are relatively longer, and its perianth has an obsolete antical keel and a longer beak.

The closely imbricated leaves and underleaves of *C. polyantha* will at once distinguish it from any of our other Lejeuneae Schizostipae, although in texture and color it somewhat resembles *Euosmolejeunea opaca* and *E. duriuscula*. From the first of these, it differs also in its more widely spreading and narrower lobules, in its broader underleaves, and in its broader perianth and perichaetial

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* Hedwigia, 35 : 126. 1896.

† Hep. Amaz. et And. 248. 1884. Afterwards distributed in Hep. Spruceanae as a distinct species under a manuscript name.

bracts. From the second it differs more particularly in its larger size and in its much larger underleaves, which are rounded or subcordate at the base.

10. CHEILOLEJEUNEA PHYLLOBOLA (Nees & Mont.) Schiffn.

PLATE 20, FIGS. 1–13

Lejeunea phyllobola Nees & Mont.; Ramon de la Sagra, Hist. fis. pol. y natur. Cuba, **9**: 281. 1845. G. L. & N. Syn. Hep. 369. 1845.

Lejeunea (*Hygro-Lejeunea*) *phyllobola* Steph. Hedwigia, **29**: 81. 1890.

Cheilolejeunea phyllobola Schiffn. Engler's Bot. Jahrb. **23**: 591. 1897.

Hygrolejeunea phyllobola Massal. Mem. dell' Accad. di Verona, **73**:—(33). *pl. 9. f. 12.* 1897.

Pale green, growing in depressed mats: stems prostrate, closely appressed to substratum, 0.07 mm. in diameter, irregularly and rather densely pinnate, the branches sometimes upright and flagelliform, leafless except at apex, but with well-developed underleaves: rhizoids somewhat abundant: leaves loosely imbricated, the lobe obliquely to widely spreading, orbicular-ovate, 0.5 mm. long, 0.45 mm. wide, rounded at the apex, margin entire or very slightly and irregularly sinuate from projecting cells, antical margin arching across axis, but almost straight near base, postical margin straight or slightly curved, forming a very obtuse angle with keel; lobule inflated, ovate, 0.1 mm. long, 0.07 mm. wide, keel almost straight, free margin involute to or just beyond apex, then obliquely truncate to end of keel, apex usually tipped with a single rounded cell, sometimes acute or even ending in a row of two or three cells, lobule often rudimentary and explanate; cells of lobe slightly convex, thin-walled, but with distinct trigones and occasional intermediate thickenings, the latter sometimes very scanty, measuring 10 μ in diameter at edge of lobe, 21 μ in the middle and 25 μ at base; ocelli wanting: underleaves distant, broadly ovate to orbicular, 0.17 mm. long, bifid to or beyond the middle, with narrow more or less spreading divisions and acute to lunulate sinus, the divisions rarely blunt, usually varying from rounded and apiculate to acute or acuminate, tipped with one or two cells, cuneate or slightly rounded toward base, margin subcrenulate, rarely with an angular tooth near the middle of one or both sides: inflorescence autoicous: ♀ inflorescence usually borne on a short branch, rarely on a leading branch, innovating on one side, the short innovation sometimes sterile, sometimes bearing another ♀ or a ♂ inflorescence, rarely absent; bracts unequally bifid, complicate, the lobe widely spreading, 0.45 mm. long, 0.35 mm. wide, ovate to orbicular, more or less falcate, rounded at apex, margin as in leaves, postical margin strongly curved, lobule ovate to lanceolate, rounded to acuminate at the apex, 0.3 mm. long, 0.1 mm. wide; bracteole free, ovate, 0.35 mm. long, 0.25 mm. wide, bifid about one third with erect, acute divisions and acute sinus, margins indistinctly angular-crenulate; perianth about half exserted, obovoid but distinctly cuneate toward base with almost straight sides, 0.6 mm. long, 0.4 mm. wide, truncate or slightly retuse at the broad apex and with a short beak, antical surface plane or nearly so, lateral keels sharp, postical keel broad and bluntly two-angled: ♂ spike variable in position, sometimes intercalary or terminal on a leading branch, sometimes occupying a short branch, sometimes on an innovation; bracts in one to five pairs, strongly concave and inflated, subequally bifid with rounded lobes and a strongly arched keel: bracteoles similar to the underleaves but a little smaller, present only in lower part of spike.

Type-locality, Cuba (Herb. Montagne).

On trees. Florida (Underwood). The species is now known from several of the West Indian Islands, from Mexico and from Costa Rica. It has also lately been reported from China.

The determination of the present species is based on the specimens in Wright's Hepaticae Cubenses. These were named by Gottsche, and the determination was afterwards confirmed by Schiffner. The type specimens have not been consulted by the writer.

C. phyllobola is remarkable for the insecure way in which its side-leaves are attached to their axes, the slightest force being sometimes sufficient to break them away. As a result leafless branches are frequent, although these are much less characteristic than in *C. versifolia*. In its leaf-cells the species exhibits considerable variation, the trigones being sometimes conspicuous and sometimes difficult to demonstrate, while the intermediate thickenings are sometimes large and abundant, sometimes smaller and more scattered and sometimes wholly absent. In all the various forms the cell-measurements remain fairly constant.

C. phyllobola has been confused with *Lejeunea cavifolia*, with *Microlejeunea lucens* and even with *Euosmolejeunea duriuscula*.

From the first of these species it differs in the shape of its leaf-lobe, in its smaller lobule, in its smaller and more deeply cleft underleaves and in its more flattened perianth, the antical face being plane or nearly so. It is a much larger plant than *Microlejeunea lucens*, and differs also in its autoicous inflorescence, in the shape of its leaves, underleaves and perichaetial bracts and in its slightly larger leaf-cells, usually with more conspicuous thickenings. From *Euosmolejeunea duriuscula*, it differs in its paler color and more delicate texture, in its autoicous inflorescence, in its slightly larger leaf-cells and in the shape of its leaves and underleaves.

The species is one of those interesting links between genera which are so frequent in the Lejeuneae. Some of the reasons for placing it in *Cheilolejeunea* rather than in *Hygrolejeunea* are stated by Schiffner,* who maintains that, although the leaves and the leaf-cells show an affinity with *Hygrolejeunea*, the underleaves and perianths are more like those of *Cheilolejeunea*. Apparently Spruce was also a supporter of this view, for he described a South American hepatic under the name *L.* (*Cheilo-Lejeunea*) *phyllobola*.† Unfortunately the plant which he studied was not *Lejeunea phyllobola* Nees & Mont. but an undescribed species, afterwards distributed under a manuscript name in Hepaticae Spruceanae. There seems to be in fact no authentic record of *C. phyllobola* from South America. Specimens from Brazil are quoted in the Synopsis, but these, according to Stephani,‡ are referable to *L. oxyloba* Lindenb. & Gottsche.

11. CHEILOLEJEUNEA VERSIFOLIA (Gottsche) Schiffn.

Lejeunea versifolia Gottsche; Wright, Hep. Cubenses (without description); Schiffner, Engler's Bot. Jahrb. **23**: 597. 1897 (as synonym).

Cheilolejeunea versifolia Schiffn. *l. c. pl. 5. f. 1–7.*

Pale olive-green, growing in depressed tufts, often in company with *C. phyllobola*: stems prostrate, 0.04 mm. in diameter, intricately mixed together, copiously bipinnately branched, some of the branches spreading from substratum, flagelliform, leafless except for two or three rudimentary leaves near apex, but with densely

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* Engler's Bot. Jahrb. **23**: 591. 1897.

† Hep. Amaz. et And. 259. 1884.

‡ Hedwigia, **29**: 81. 1890.

imbricated underleaves: rhizoids rather abundant: leaves imbricated, very fragile, distinctly smaller toward the base of the branches, the lobe subplane, widely spreading, obliquely ovate, 0.45 mm. long, 0.3 mm. wide, rounded at the apex, margin entire or subrepand, antical margin arching across but scarcely beyond axis, rounded at base, postical margin straight or nearly so, forming an obtuse angle with keel; lobule inflated, ovoid-cylindrical, 0.11 mm. long, 0.04 mm. wide, slightly constricted near apex, keel slightly arched, free margin involute to or beyond apex then truncate to end of keel, apex tipped with a long, unicellular outwardly curved tooth; cells of lobe with uniformly thickened walls, averaging 10 μ in diameter, basal ocelli 40 × 20 μ, consisting of two to six empty inflated cells: underleaves on ordinary axes contiguous or subremote, on flagelliform branches densely imbricated, plane, rotund-suboblate, often subangulate, 0.16 mm. long, 0.19 mm. wide, scarcely decurrent at the base, bifid almost to the middle with acute sinus and acute subconnivent lobes: inflorescence dioicous: ♀ inflorescence sometimes with a simple innovation; bracts unequally bifid, the lobe obliquely ovate, rounded at apex, entire, 0.47 mm. long, 0.42 mm. wide, lobule rhomboid-lingulate, apex obtuse or more rarely apiculate, 0.3 mm. long, 0.15 mm. wide; bracteole plane, broadly ovate, 0.42 mm. long, 0.35 mm. wide, slightly connate on one side with bract, shortly emarginate, bifid at the apex with rounded divisions and acute sinus, sometimes simply emarginate: perianth unknown: ♂ spikes occupying short branches or intercalary on leading branches, bracts in few pairs, large, subglobose, equally lobed, surface slightly roughened from projecting cells.

Type-locality, Cuba (Wright).

On trees. Lake Worth, Florida (Underwood).

Schiffner has described and figured this peculiar little species so fully and so accurately that the description given above is mostly compiled from his. The specimens from Florida agree closely with those distributed in Hepaticae Cubenses.

The leafless flagelliform branches with closely imbricated underleaves are not invariably found in *C. versifolia* and yet they form its most striking peculiarity. They resemble in a marked degree the flagelliform branches of *Frullania Bolanderi*,* a Pacific Coast species found in California and northward. They are much more highly specialized than the leafless branches of the related *C. phyllobola*, where the underleaves are no closer than on ordinary

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* Evans, Trans. Conn. Acad. 10: *pl. 2. f. 4.* 1897.

branches. *C. versifolia* also differs from *C. phyllobola* in its smaller size, in its much smaller leaf-cells which scarcely vary in size throughout the lobe, in its basal ocelli, in its more sharply pointed lobules and in its relatively larger underleaves.

Another West Indian species closely related to *C. versifolia* is *C. emarginuliflora* Schiffn.,* a Cuban plant likewise collected and distributed by Wright. According to its author this species has a more graceful habit than *C. versifolia*, its branches are less numerous and are never flagelliform, its leaves are more distant and their lobules are less conspicuously toothed at the apex, its basal ocelli are either wanting or very inconspicuous, its underleaves are smaller, more distant and with a broader sinus, and its female plants are repeatedly floriferous. The fragmentary material distributed in Hepaticae Cubenses shows that these slight differences certainly exist, but it would require the examination of many more specimens before it could be decided whether they were constant enough to be considered specific. In fact Schiffner himself throws doubt on the validity of the species.

12. **Cheilolejeunea pililoba** (Spruce)

Lejeunea (*Eulejeunea*) *pililoba* Spruce, Jour. Linn. Soc. Bot. **30**: 346. *pl. 23. f. 6–8.* 1894.

Pale to dark green, caespitose: stems prostrate, 0.07 mm. in diameter, irregularly branched: rhizoids few: leaves contiguous to imbricated, the lobe obliquely spreading, plane, broadly ovate to orbicular, 0.4 mm. long, 0.35 mm. wide, rounded to very obtuse at apex, margin crenulate from projecting cells or subentire, antical margin arching across or just beyond axis, rounded or sometimes abruptly contracted at base; lobule filiform from a minute, triangular base, 0.17 mm. long, 0.01 mm. wide, consisting of two to twelve cells in a single row, rarely two or three cells wide at or near base; cells of lobe slightly convex, thin-walled, trigones minute, often scarcely evident, intermediate thickenings wanting, cells averaging 14 μ at edge of lobe, 21 μ in the middle and at base: underleaves distant or contiguous, ovate or narrowly ovate, 0.25 mm. long, 0.13 mm. wide, narrowed toward base, bifid to or beyond the middle with erect, lanceolate, acuminate lobes and obtuse to lunulate sinus, margin as in leaves: inflorescence autoicous: ♀ inflorescence borne on a short branch or on a leading branch,

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* Engler's Bot. Jahrb. **23**: 585. 1897.

innovating on one side, the innovation simple and sterile; bracts complicate, unequally bifid, the lobe widely spreading, ovate to obovate, rounded at apex, 0.55 mm. long, 0.3 mm. wide, lobule with a narrowly rhomboidal base connate with lobe, running out into a subulate, acuminate point ending in a row of three or more cells, 0.25 mm. long, base 0.05 mm. wide; bracteole oblong to obovate from a narrow base, 0.35 mm. long, 0.17 mm. wide, bifid one third or less with triangular, acute, contiguous lobes and narrow sinus, perianth about half exserted, obovoid, somewhat compressed, 0.5 mm. long, 0.35 mm. wide, narrowed toward base, broad and truncate above and with a very short, broad beak, antical face plane or with a very indistinct, low keel near apex, postical keel about half as long as perianth, broad, obtusely two-angled, lateral keels blunt, keels more or less roughened from projecting cells: ♂ spike occupying a short branch, globose, bracts in about two pairs, inflated, keel strongly arched, shortly and subequally bifid with rounded divisions; bracteole at base of spike small, shortly bifid with acute divisions and narrow sinus.

Type-locality, Dominica (Elliott).

On bark or on the ground. Indian River and Cedar Keys, Florida (Herb. Austin). Also known from Cuba (Underwood).

C. pililoba presents so remarkable a character in its filiform lobule that there is little danger of confusing it with any of our other Lejeuneae. Among tropical species *Lejeunea* (*Eu-Lejeunea*) *setiloba* Spruce * is said to have a similar but shorter lobule. Through the kindness of M. B. Slater, the writer has had the privilege of examining the type-material of this species from the Spruce herbarium. These specimens show that the filiform condition of the lobule is by no means a constant feature. On some of the stems one occasionally finds a small, broadly ovate, inflated lobule of the ordinary type with the apex consisting of one or two projecting cells, and there are all gradations between such a lobule and the form described by Spruce. These specimens in fact give one the impression that the filiform lobule of *L. setiloba* is really an abnormal character. Aside from these differences in the lobule, the underleaves of *L. setiloba* are broader and usually less deeply cleft than in *C. pililoba* and are occasionally angular-unidentate on the sides. The perianth also is obovoid and scarcely compressed, and its sharp antical keel indicates that the species is a true *Lejeunea*.

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* Hep. Amaz. et And. 281. 1884.

According to Spruce *C. pililoba* should also be placed in his subgenus *Eulejeunea*, but it seems best to transfer it to *Cheilolejeunea* on account of its compressed perianth with obsolete antical keel.

According to the original description, the type-specimens of *C. pililoba* were entirely sterile, and yet on this negative evidence the species was said to be dioicous. The specimens in the British Museum, from which the published figures were drawn, show, however, flowers of both sexes on the same stem. None of the archegonia are fertilized, and the plants look as if they had grown in an unfavorable locality, where they were unable to develop normally. The specimens are not quite so large as those described by Spruce, and the filiform lobule is usually less than twelve cells long, although this length is given as one of the specific characters. The specimens from Florida and also those from Cuba (Matanzas, mixed with Hep. Amer. 145) agree closely with the British Museum specimens. Both are distinctly autoicous and the Cuban plants show well-developed perianths.

13. LEJEUNEA PATENS Lindb.

Jungermannia serpyllifolia Dicks. Fasc. Pl. Crypt. Brit. **4**: 19. 1801.

Pandulphinius serpyllifolius S. F. Gray, Nat. Arr. Brit. Plants, **1**: 689. 1821.

Lejeunea patens Lindb. Acta Soc. Sci. Fenn. **10**: 482. 1875.

Pale or sometimes darker green, slightly glossy when dry, caespitose: stems prostrate or slightly ascending, 0.08 mm. in diameter, copiously and irregularly branched: rhizoids few: leaves imbricated, the lobe ovate, widely spreading, falcate, strongly convex, 0.5 mm. long, 0.35 mm. wide, rounded and decurved at apex, margin distinctly crenulate from projecting cells, antical margin rounded or sometimes contracted at base, arching across or a little beyond axis, postical margin forming an angle of 90° or less with keel, angle in poorly developed leaves often obtuse; lobule strongly inflated, ovate, 0.17 mm. long, 0.1 mm. wide, keel arched, mostly crenulate, free margin curved and involute to beyond apex, then lunately truncate to end of keel, apex tipped with a single blunt, projecting cell; cells of lobe convex, thin-walled, but usually with conspicuous trigones and intermediate thickenings, walls sometimes thin throughout, cells averaging at edge of lobe 14 μ in diameter, in the middle 19 μ, at the base

28 × 23 μ: underleaves distant, about the size of the lobules or a little smaller, orbicular, 0.15 mm. long, strongly convex postically, gradually narrowed toward base, bifid about one half with obtuse to acute lobes separated by a sinus varying from narrow and acute to broader and obtuse, margin crenulate from projecting cells: inflorescence autoicous: ♀ inflorescence sometimes on a leading branch, sometimes on a short branch, innovating on one side, the innovation often but not always floriferous and branched; bracts complicate, unequally bifid, the lobe somewhat spreading, oblong, rounded at the apex, 0.5 mm. long, 0.3 mm. wide, margin crenulate, lobule narrowly oblong, rounded to obtuse at apex, 0.25 mm. long, 0.12 mm. wide; bracteole free or nearly so, ovate-oblong, 0.4 mm. long, 0.25 mm. wide, bifid about one fourth with acute lobes and sinus, margin crenulate; perianth about half exserted, oblong-obovoid, 0.9 mm. long, 0.5 mm. wide, gradually narrowed toward base, rounded above and with a short beak, terete below, sharply five-keeled in upper half or third, the keels crenulate from projecting cells, becoming blunter with age: ♂ spike occupying a short branch, bracts in two to four pairs, strongly inflated and with strongly arched keel, subequally bifid about one fifth with rounded lobes, cells plane; bracteoles limited to base of spike, similar to the underleaves, but smaller: antheridia in pairs.

Type-locality, Ireland (Lindberg).

On rocks. Newfoundland (Waghorne); Nova Scotia (Macoun). The species is also known from Great Britain and from Norway.

Lejeunea patens and the two species which follow are so nearly allied to one another that they have given rise to much confusion. The elucidation of their synonymy is due largely to Lindberg, who was the first to distinguish clearly between *L. serpyllifolia* Lib. and *L. patens.* Although he described the latter as a distinct species, he threw doubts on its validity, recognizing the close relationship which exists between the two species. At the time *L. patens* was published, it was taken for granted that *L. serpyllifolia* Lib. was the same as *Jungermannia serpyllifolia* Dicks.; but in 1879 Lindberg[*] discovered that the type-specimen of Dickson's species was identical with his *Lejeunea patens.* The name "*Lejeunea serpyllifolia,*" however, cannot now be taken up for *L. patens,* on account of the older *L. serpyllifolia* of Libert. At the same time

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[*] Musc. Scand. 2, footnote. 1879.

we can avoid any confusion which might arise from the use of Libert's name by restoring to Libert's species the still older name "*cavifolia*," of Ehrhart, a course which Lindberg and others have already adopted.

L. patens has not before been recorded for America. Its discovery in Newfoundland and in the neighboring island of Cape Breton shows quite conclusively that its range is northern, and that it does not belong to that group of subtropical hepaticae which are characteristic of the southwestern corner of Ireland.

The species has been illustrated by Moore * and also by Pearson.† Moore's figures bring out clearly the crenulations on the leaves and underleaves, an important character which Pearson's figures do not show.

14. LEJEUNEA CAVIFOLIA (Ehrh.) Lindb.

Jungermannia cavifolia Ehrh. Beitr. **4**: 45. 1789.

Jungermannia clavaeflora Nees; Martius, Fl. Crypt. Erl. 137. *pl. 3. f. 10.* 1817.

Lejeunea serpyllifolia Lib. Ann. Gén. Sc. Phys. **6**: 374. *pl. 97. f. 2.* 1820. G. L. & N. Syn. Hep. 374. 1845.

Lejeunea cavifolia Lindb. Acta Soc. Sci. Fenn. **10**: 43. 1871. Not Stephani.‡

Lejeunea serpyllifolia, var. *β cavifolia* Lindb. *l. c.* **10**: 485. 1875.

Lejeunea serpyllifolia, var. *γ Americana* Lindb. *p. p., l. c.* **10**: 486. 1875.

Lejeunea (*Eu-Lejeunea*) *serpyllifolia* Spruce, Hep. Amaz. et And. 262. 1884.

Eulejeunea serpyllifolia Schiffn.; Engler & Prantl, Nat. Pflanzenfam. **1**^{3}: 122. 1893.

Pale to dark green, dull or glossy when dry, growing in depressed tufts or creeping over other bryophytes: stems prostrate, 0.07 mm. in diameter, irregularly branched, the branches widely spreading, sometimes few but usually abundant: rhizoids scanty: leaves imbricated, the lobes ovate, obliquely preading, plane to convex, 0.6 mm. long, 0.35 mm. wide, rounded to very obtuse at the apex, margin en-

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* Proc. Roy. Irish Acad. II. **2**: *pl. 43.* 1877.

† Hep. Brit. Isles, *pl. 11.* 1890.

‡ Bol. da Soc. Brot. **4**: 171. *pl. 1. f. 5–7.* 1886.

tire or nearly so, antical margin arching across or just beyond axis, slightly rounded at base, postical margin usually forming an angle of 120° or more with keel, angle rarely as small as 90°; lobule strongly inflated, ovate, 0.2 mm. long, 0.14 mm. wide, keel strongly arched, scarcely or not at all crenulate, free margin more or less curved and involute as far as apex, then passing by a shallow lunulate sinus to end of keel, apex tipped with a single, blunt, projecting cell; cells of lobe almost plane, thin-walled, trigones and scattered intermediate thickenings sometimes distinct, sometimes scarcely evident, cells at edge of leaf averaging $17\ \mu$ in diameter, in the middle $24\ \mu$, at the base $30 \times 21\ \mu$: underleaves distant, as large as or a little larger than lobule, ovate-orbicular, 0.2 mm. long, 0.18 mm. wide, plane or slightly convex postically, gradually narrowed toward base and neither decurrent nor rounded, bifid about one half with rounded to acute lobes and obtuse to acute sinus, margin entire or nearly so: inflorescence autoicous: ♀ inflorescence sometimes on a leading branch, sometimes on a short branch, innovating usually on only one side, the innovation sometimes simple and sterile, sometimes floriferous; bracts complicate, unequally bifid, the lobe somewhat spreading, narrowly to broadly ovate, rounded to obtuse at the apex, entire, 0.5 mm. long, 0.3 mm wide, lobule oblong to lanceolate, rounded to acuminate at the apex, entire, 0.3 mm. long, 0.1 mm wide; bracteole free, oval-obovate, 0.4 mm. long, 0.2 mm. wide, bifid one fourth to one third with acute to obtuse lobes and sinus, margin entire; perianth about half exserted, oblong to oval-oblong from a narrowed base, 0.85 mm. long, 0.4 mm. wide, rounded or truncate at the apex with a short, slender beak, terete below, sharply five-keeled in upper part, the keels smooth, becoming blunter with age: ♂ spike as in *L. patens.*

Type-locality, near Upsala, Sweden (Ehrhart).

On rocks and trees. Ontario (Macoun); New Hampshire (Faxon, Evans); Massachusetts (Stone); Connecticut (Eaton, Hall, Evans); New York (Underwood, Cook, Mrs. Britton); Pennsylvania (Barbour); Wisconsin (Cheney); Minnesota (Holzinger). Widely distributed in Europe and recently reported from Japan.

EXSIC.: Hep. Bor.-Amer. 97 *p. p.* Hep. Amer. 8 (as *Lejeunea serpyllifolia*).

Lejeunea cavifolia is the commonest representative of the Lejeuneae in the northern United States. When well developed, it can readily be distinguished from *L. patens* and from *L. Americana.* Poorly or abnormally developed specimens, however, of these closely allied species do not always show their specific characters and cannot always be determined.

Lejeunea patens is a paler plant than *L. cavifolia;* the lobes of its leaves spread more abruptly from the lobules and are more convex, especially when dry; the underleaves are more nearly orbicular and are smaller than the lobules, while the margins of both leaves and underleaves are distinctly crenulate from projecting cells. The leaf-cells also, as a rule, are more strongly convex and show more conspicuous trigones and intermediate thickenings. Unfortunately the abrupt spreading of the lobe from the lobule is not always evident in *L. patens*, especially on the leaves of the smaller branches. Neither is this character by itself to be wholly relied upon in separating the species, for in *L. cavifolia* the lobe sometimes spreads widely also. The figures recently published by Pearson [*] show how variable both species are in this respect. It is only when the spreading lobe is found in connection with the other peculiarities of *L. patens* that it becomes of value as a differential character.

Lindberg's variety *planiuscula* of *L. cavifolia*, first distinguished simply as a form, hardly seems worthy of varietal rank.[†] According to the description, the plants of this variety are more elongated, less branched and broader than in the type, the leaves are less imbricated and less decurved, the lobules are relatively smaller and the cells have thinner walls and scarcely evident trigones. Faxon's specimens from Crawford Notch, New Hempshire, and Underwood's from Manlius, New York, agree with this description and also with the specimens which Lindberg quotes, but they are connected with typical *L. cavifolia* by intermediate conditions. Apparently their peculiarities are due to a moister habitat, which would naturally produce a laxer growth and lead to a diminution in the development of the lobules and of the cell-walls.

Two specimens of *Lejeunea* distributed in Hepaticae Americanae should perhaps be noted here. One of them is the curious submerged "*Kantia aquatica*" Underw., distributed as no. 107. As Underwood [‡] himself has shown, this plant is a true *Lejeunea*, apparently related to *L. cavifolia*. As a result of its submerged

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[*] Hep. Brit. Isles, *pl. 10, 11.* 1899.

[†] *Lejeunea serpyllifolia*, forma *α planiuscula* Lindb. Acta Soc. Sci. Fenn. **10**: 484. 1875. *Lejeunea cavifolia*, var. *β planiuscula* Lindb. Musc. Scand. 2. 1879.

[‡] Bull. Torrey Club, **23**: 383. 1896 (footnote).

habit it has lost its lobules, and, as the specimens have failed to develop perianths, it is impossible to refer them definitely. The other specimen was distributed under no. 178, as *Lejeunea* (*Eu-Lej.*) *serpyllifolia.* The plants seem to be perfectly sterile, the lobes are crenulate on the margins and both lobules and underleaves are very small, the latter being bifid beyond the middle with broad, obtuse lobes and sinus. Evidently the plant is not *L. cavifolia*, but it is in too poor a condition to be determined. Both of these specimens were collected in Florida.

15. **Lejeunea Americana** (Lindb.)

PLATE 20, FIGS. 14–26

Jungermannia serpyllifolia Wils. & Hook. *p. p.*; Drummond, Musc. Amer. St. Merid. 172. 1841. Not Dickson.

Lejeunea serpyllifolia Sull. Musc. Alleg. 272. 1845. Not Libert.

Lejeunea cavifolia Aust. *p. p.* Hep. Bor.-Amer. 97. 1873. Not Lindb.

Lejeunea serpyllifolia, var. γ *Americana* Lindb. *p. p.* Acta. Soc. Sci. Fenn. **10**: 486. 1875.

Lejeunea (*Eu-Lejeunea*) *flava*, subsp. *albida* Spruce, Hep. Amaz. et And. 269. 1884.

Pale, whitish-green or yellowish, closely appressed to substratum or growing in wide, depressed mats: stems prostrate, 0.08 mm. in diameter, irregularly pinnately branched: rhizoids often abundant: leaves imbricated, the lobe ovate, widely spreading, plane or slightly convex, 0.5 mm. long, 0.35 mm. wide, rounded to obtuse at apex, margin entire or subcrenulate from projecting cells, antical margin arching across or just beyond axis, slightly rounded at base, postical margin forming an obtuse angle with keel; lobule inflated, ovate, 0.2 mm. long, 0.15 mm. wide, keel strongly arched, scarcely or not at all crenulate, free margin slightly curved, more or less involute, apex tipped with a single projecting cell, sinus between apex and end of keel shallow and oblique; cells of lobe plane or nearly so, thin-walled, but usually with distinct trigones and occasional intermediate thickenings, averaging 15 μ in diameter at edge of leaf, 23 μ in the middle and 29 × 23 μ at the base: underleaves contiguous or subimbricated, a little larger than lobule, orbicular, 0.2 mm. long, plane or nearly so, rounded or subcordate at base, bifid about one half, segments usually acute or apiculate, occasionally obtuse, rarely rounded, sinus acute to obtuse, margin entire or irregularly sinuate, rarely with an indistinct, blunt tooth at about the middle of one or both sides: inflorescence autoicous: ♀ inflorescence sometimes on a leading branch, sometimes on a short branch, innovating on one or rarely on both sides, the innovations often floriferous, bracts complicate, unequally bifid, the lobe obliquely spreading, varying from oblong to obovate, rounded to subacute at the apex, 0.6 mm. long, 0.3 mm. wide, lobule mostly oblong and rounded or truncate at the apex, rarely indistinctly toothed or lobed with rounded divisions, 0.35 mm. long, 0.18 mm. wide; bracteole free, ovate, 0.55 mm. long, 0.35 mm. wide, somewhat narrowed at base, bifid about one half with erect, obtuse to acute divisions and narrow sinus; perianth obovoid, often distinctly dilated above middle, 0.7 mm. long, 0.35 mm. wide, gradually narrowed toward base, broad and truncate above, and with a short beak, terete below, sharply five-keeled in upper part, the keels smooth sometimes showing vague traces of wings: ♂ inflorescence usually occupying a short branch, rarely borne on a longer branch, bracts in two to eight pairs, similar to those of *L. patens*: spores greenish, angular, thick-walled, minutely verruculose, averaging 14 μ in short diameter.

Type-locality, Southern States (Austin)?

On trees. North Carolina (Johnson); South Carolina (Sullivant, Miss DuBois); Georgia (Small); Florida (Farlow, J. D. Smith, Underwood, Straub); Alabama (Underwood); Mississippi (Langlois, Lloyd and Tracy); Louisiana (Drummond, Langlois); Texas (Hall). Also known from various parts of tropical America.

EXSIC.: Musc. Amer. St. Merid. 171 *p. p.* (as *Jungermannia serpyllifolia*). Musc. Alleg. 272 (as *Lejeunea serpyllifolia*). Hep. Bor.-Amer. 97 *p. p.* (as *Lejeunea cavifolia*). Hep. Amer. 98 (as *Lejeunea* (*Micro-Lej.*) *Austini*). Hep. Amer. 137 (as *Lejeunea* (*Micro-Lej.*) *lucens*).

In proposing the present species as a variety of *Lejeunea serpyllifolia* Lib., Lindberg referred to it all the American specimens in his herbarium which presumably belonged to that species. His dictum has been followed, almost without exception, by subsequent writers on American hepaticae, who have apparently taken it for granted that typical *L. serpyllifolia* Lib. did not occur in America. Judging, however, from the specimens which Lindberg quotes, his variety was an aggregate, made up of *L. Americana*, as described above, and *L. cavifolia.* He quotes three exsiccatae, Hep. Bor.-Amer. 97, Musc. Amer. St. Merid. 171 *p. p.* (caespites pallidi) and Musc. Alleg. 272; he also quotes two plants not distributed in exsiccatae, Cleve's specimens from Catskill, New York, and Macoun's from Belleville, Canada. Of the first-mentioned specimen, Austin gives as a habitat, "on rocks and roots of trees; chiefly on mountains." He does not tell, therefore, in what part of the country they were collected. The writer has examined this number in two sets of Hep. Bor.-Amer., and finds in both cases pale tufts, which are clearly *L. Americana*, and darker tufts, which agree perfectly with the European specimens of *L. cavifolia* quoted by Lindberg, as, for example, Hep. Eur. 435. Sullivant's specimens from Charleston, South Carolina, are a poorly developed form of *L. Americana.* They show characteristic perianths, but their leaves and underleaves indicate that they grew in a moist locality, and their thin-walled leaf-cells, with small and often scarcely evident trigones, point to the same conclusion. Drummond's Louisiana specimens are also a poorly developed *L. Americana.* Cleve's specimens have not been examined by the writer, but specimens in the Underwood herbarium from Belleville, collected by Macoun, are typical *L. cavifolia.* It is a little difficult to say what should be considered the type of Lindberg's variety, and consequently of the present species. The writer would suggest, however, that the pale tufts in Hep. Bor.-Amer. 72 be so regarded. Austin's plants are the first ones quoted by Lindberg, and these pale specimens, except for certain characters drawn from the leaf-cells, agree closely with the original description.

Few of our species have been the cause of quite so much confusion as *L. Americana.* It has been referred to *L. cavifolia*, to *Euosmolejeunea duriuscula* and also to *Microlejeunea lucens* and is to be found under one or more of these various names (or their equivalents) in most of our large herbaria.

The characters which separate it from *L. cavifolia*, although slight, are sufficiently distinct when well developed specimens are examined. *L. Americana* is a paler plant than the northern species, the lobes of its leaves spread more widely from the axis, the lobules are relatively smaller, and the underleaves are broader, more or less sinuous on their margin and tending to be rounded or subcordate at the base. The perianth, however, offers the best points of difference; in the new species this is much broader in the upper part than at the base and frequently flares out abruptly above the middle, its keels also are sharper than in *L. cavifolia* and sometimes shows rudimentary wings. In the United States *L. Americana* seems to be confined to the bark of trees, while *L. cavifolia* is more at home on rocks, at the roots of trees, and creeping over other hepatics.

L. Americana is a much paler and more delicate plant than *Euosmolejeunea duriuscula*. Its leaves spread more widely from the axis, and its lobules are relatively larger with their free margins more involute, so that the apical teeth cannot usually be seen without dissection; its underleaves also are larger and not cuneate at the base. In *L. Americana*, moreover, on account of its autoicous inflorescence, perianths are frequently developed, whereas in the other species they are extremely rare.

L. Americana should hardly be confused with *Microlejeunea lucens*. It is in the first place a much larger plant and has an autoicous inflorescence. It differs markedly also in the more conspicuous thickenings of its cell-walls and in its larger and broader underleaves, which are never sharply unidentate on their lateral margins.

Spruce's *L. flava*, subsp. *albida* should apparently be referred to the present species, although his specimens are a little larger and were found on living leaves instead of on bark. Spruce afterwards recognized that the plant was specifically distinct from *L. flava* and distributed it in Hep. Spruceanae as a manuscript species. The writer has carefully compared these specimens with typical plants of *L. Americana* and finds no essential differences between them.

16. **Microlejeunea lucens** (Tayl.)

PLATE 21, FIGS. 1–10

Lejeunea cucullata Sull. Musc. Alleg. No. 274. 1845. Not Nees.

Lejeunea lucens Tayl. Lond. Jour. Bot. 5: 399. 1846. G. L. & N. Syn. Hep. 764. 1847.

Lejeunea (*Micro-Lejeunea*) *lucens* Spruce, Hep. Amaz. et And. 288. 1884.

Lejeunea (*Eu-Lejeunea*) *lucens* Steph. Hedwigia, **29** : 84. 1890.

Pale green, scattered or growing in depressed tufts : stems prostrate, 0.05 mm. in diameter, sparingly and irregularly branched, the branches sometimes microphyllous : rhizoids scanty : leaves distant to imbricated, the lobe obliquely spreading, ovate, on well-developed axes 0.25 mm. long, 0.17 mm. wide, plane, rounded at the apex or sometimes varying to obtuse, margin entire or subcrenulate from projecting cells, antical margin arching partially across axis, slightly rounded or almost straight at base, postical margin forming a continuous line or a very obtuse angle with keel; lobule on well-developed axes about half as long as lobe, on microphyllous branches sometimes as long as lobe, strongly inflated, ovoid, 0.01 mm. long, 0.09 mm. wide, keel strongly arched, free margin involute to apex, then passing by an obliquely truncate or lunulate sinus to end of keel, apex tipped with a single slightly projecting, almost straight cell ; lobule often poorly developed ; cells of lobe thin-walled throughout or sometimes with minute trigones and scattered intermediate thickenings, averaging 14 μ in diameter at edge of lobe, 20 μ in the middle and at the base : underleaves distant, ovate, 0.14 mm. long, 0.1 mm. wide, plane, narrowed toward base and not decurrent, bifid to about the middle, with subulate, acute or acuminate divisions ending in a single cell or in a row of two cells and separated by a narrow, obtuse sinus, lateral margins variable, sometimes rounded, sometimes angular, sometimes unidentate, especially on slender branches, the tooth consisting of a single projecting, rounded to acute cell, margin otherwise entire or nearly so : inflorescence dioicous : ♀ inflorescence on a short branch, innovating on one or on both sides, the innovations short and simple, inflorescence very rarely without innovation ; bracts complicate, subequally or somewhat unequally bifid, the lobe suberect, oblong-obovate, rounded or very obtuse at the apex, margin entire or subcrenulate, 0.4 mm. long, 0.2 mm. wide, lobule rounded to acuminate at the apex, 0.4 mm. long, 0.2 mm. wide, sometimes narrower ; bracteole free or nearly so, ovate, 0.45 mm. long, 0.25 mm. wide, bifid about one third with acute lobes and obtuse sinus, margin subentire, sometimes bearing a blunt lobe-like tooth on one side near the base ; perianth scarcely exserted, broadly pyriform, 0.5 mm. long, 0.3 mm. wide, slightly compressed, five-keeled, the keels smooth, beak short : ♂ spike julaceous, occupying the base of an elongated branch ; bracts in five or six pairs, as large as the leaves, turgid, the lobule half as large as lobe.

Type-locality uncertain.

On trees or moist rocks : Virginia (Sullivant); Florida (Miss Biddlecome, J. D. Smith, Underwood); Mississippi (Lloyd and

Tracy), Louisiana (Langlois). Widely distributed in tropical America.*

EXSIC.: Musc. Alleg. 274 (as *Lejeunea cucullata*). Hep. Bor.-Amer. 98 (as *Lejeunea cucullata*).

There has been a great deal of confusion about this little species and many specimens have been referred to it which really belong elsewhere. The writer ventures, therefore, to relate its history in some detail.

The specimens in the Taylor herbarium, which are presumably the type, consist of a few fragmentary stems. In the small envelope which contains them there is written in Wilson's handwriting: "*Jung. cucullata* Nees? Ohio, Sullivant, 147. I have very little of it and all barren. W." On the sheet upon which this envelope is pasted Taylor has written: "*Jungermannia lucens* Tayl. Mss. No. 147. Sullivant, Ohio. *Jung. cucullata* Nees? No. 25 Jan.? 1846. W. Wilson." The specimens are not only fragmentary and sterile but on most of the leaves show poorly developed lobules, indicating that they grew in an unfavorable locality. From the notes it would appear that these specimens were collected somewhere in Ohio, and Taylor, in his original description of *Lejeunea lucens*, states that the species came from the vicinity of Cincinnati. The evidence, however, is against this view, as the following facts will show. The more abundant specimens distributed by Sullivant in Musc. Alleg. agree perfectly with those in the Taylor herbarium, and the same may be said of Austin's specimens in Hep. Bor.-Amer. Sullivant's specimens came from Cheat Mountain, Virginia, and Austin's are labeled, "On moist rocks in the Alleghany Mountains, Sullivant." In the second edition of Gray's Manual, Sullivant limits the range of his "*L. cucullata*" to the Alleghany Mountains and quotes Taylor's *L. lucens* as a synonym. Apparently then no one has collected the species in the northern United States with the exception of Sullivant, and, as all of his specimens came from the Alleghany

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* *Lejeunea cucullata* is listed as a Massachusetts plant by Tuckerman and Frost in their "Catalogue of Plants growing without cultivation within thirty miles of Amherst College" (1875, p. 53). Unfortunately the specimens are now inaccessible, so that it is impossible to say whether they represented *Microlejeunea lucens* or merely a small form of *Lejeunea cavifolia*, the latter of course being much more probable.

Mountains, those in the Taylor herbarium could not have come from Ohio.

All of these specimens from the Alleghany Mountains are perfectly sterile and many different conclusions have been drawn from them. As we have already seen they were referred by Sullivant to *L. cucullata* Nees and by Taylor to his *L. lucens.* Spruce thought at first that they were the same as the Mexican *L. diversifolia* Gottsche [*] and afterwards transferred them to his *L. diversiloba.*[†] Still later he referred them with some hesitation to *L. lucens.*[‡] Carrington suggested that they were probably the same as *L. crenulifolia* Gottsche Ms. from the island of Trinidad.[§]

If these specimens, which are so doubtful, are to be regarded as the type-specimens, the species is certainly unfortunate. Spruce, however, considered that the type of *Lejeunea lucens* was a specimen which Taylor had deposited in the Kew herbarium.[||] This specimen came from Brazil and was labeled: "Pará, in cortice (T. L. R.) in Herb. Hook." In his original description Taylor states that his specimens came from the Hooker herbarium, and this fact would of course support Spruce's view. Spruce was able to identify with this Kew specimen a fertile plant which he himself had collected near Pará and in this way gave the species a firm footing. The specimens from Florida and Louisiana agreeing closely with this South American plant, perhaps it would be wisest to follow Spruce and consider the Pará plant at Kew as the type of *Microlejeunea lucens.* We can then refer tentatively to this species the doubtful Alleghany Mountain specimens, until something more definite is learned about them.

The generic position of the present species is not altogether definite. By Spruce it was first placed in the subgenus *Micro-*

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[*] Mex. Leverm. 227. 1863. Not *L. diversifolia* Mitt. Spruce (Jour. Bot. 5: 198, footnote. 1876) at first referred to this Mexican species not only Sullivant's Alleghany Mountain specimens but also the minute plant from Ireland which later became the type of his *L. diversiloba.* He decided afterwards that all three were distinct and that the Mexican plant was really the same as his *L. erectifolia* from South America.

[†] Jour. Bot. 5: 235. 1876.

[‡] *L. c.* 25: 37, 39. 1887.

[§] Trans. Bot. Soc. Edin. 13: 469. 1879. *Microlejeunea crenulifolia* Steph. Hedwigia, 35: 114. 1896.

[||] Hep. Amaz. et And. 288. 1884. Jour. Bot. 25: 37. 1887.

Lejeunea, while Stephani * considered it a *Eu-Lejeunea.* Both of these opinions were afterwards reversed, Spruce † placing it in *Eu-Lejeunea* and Stephani ‡ in *Micro-Lejeunea.* As a matter of fact it is intermediate between the two genera, and it is here placed in *Microlejeunea* because it seems to have more in common with our other species of this genus that it does with our species oı *Lejeunea* proper. Its differential characters will be discussed in connection with the remaining species of *Microlejeunea.*

17. **Microlejeunea Ruthii** sp. nov.

PLATE 21, FIGS. 11–19

Pale or dull green, scattered among other hepatics or loosely depressed-caespitose : stems prostrate, 0.04 mm. in diameter, sparingly and irregularly branched, the branches widely spreading : rhizoids scanty : leaves distant to loosely imbricated, the lobe obliquely spreading to suberect, ovate or broadly ovate, 0.35 mm. long, 0.25 mm. wide, rounded at the apex, margin subentire or slightly angular-sinuate, antical margin extending partially across axis, almost straight or slightly rounded at base, often a little contracted just above insertion, postical margin almost straight, forming a continuous line or sometimes on robust axes a very obtuse angle with keel ; lobule about half as long as lobe, strongly inflated, ovoid, 0.17 mm. long, 0.13 mm. wide, keel more or less arched, free margin curved, strongly involute to apex, then passing by an oblique and lunulate sinus to end of keel, apex tipped with a single projecting, sometimes outwardly curved cell ; cells of lobe plane or slightly convex, walls somewhat thickened with indistinct trigones and occasional intermediate thickenings, averaging 12 μ in diameter at the edge of lobe, 18 μ in the middle and at the base : underleaves distant, orbicular, 0.14 mm. long, narrowed toward base and neither rounded nor decurrent, bifid to about the middle with broad, suberect, triangular lobes and obtuse sinus, lobes subacute or acute, ending in a single cell or in a row of two cells, or robust stems usually four cells long and four cells wide at base, margin entire or subcrenulate from projecting cells, lateral margins rounded, never toothed : inflorescence dioicous : ♀ inflorescence borne on a leading branch, innovating on one side, the innovation usually long and sterile ; bracts complicate, deeply and unequally bifid, the lobe obliquely spreading, ovate to oblong, 0.5 mm. long,

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* Hedwigia, 29 : 84. 1890.

† Jour. Linn. Soc. Bot. 30 : 348. 1894.

‡ Bot. Gazette, 17 : 171. 1892.

0.25 mm. wide, rounded or very obtuse at the apex, margin as in leaves but usually more sinuate, lobule mostly ligulate, rounded at the apex, varying to subacute, 0.3 mm. long, 0.1 mm. wide, keel wingless or nearly so; bracteole free, ovate from an abruptly contracted base, 0.5 mm. long, 0.35 mm. wide, bifid about one third with sharp, more or less contorted segments and narrow sinus, margin as in bracts: perianth and ♂ inflorescence unknown.

On bark. Big Frog Mountain, Tennessee (A. Ruth), the type-locality.

Microlejeunea Ruthii is closely related to the European *M. ulicina* (Tayl.), agreeing with it in its general habit and dioicous inflorescence. In *M. ulicina*, however, the lobes of the leaves are more convex and tend to be more or less pointed, the leaf-cells have thinner walls, and the underleaves are more deeply divided, the narrower divisions being as a rule only two cells wide at the base. The bracts also are more distinctly winged at the keel, their lobes are more pointed and are often denticulate on the margin, while the bracteole is narrower.

Although firmer in texture than *M. lucens* and darker in color, *M. Ruthii* resembles this species in several respects. It may be distinguished by the less widely spreading lobes of its leaves, by its slightly smaller cells with thicker walls, and by its broader underleaves, which have broader segments and are never unidentate on the sides. The ♀ inflorescence also is borne on a leading branch instead of on a short branch as is usual in *M. lucens*.

18. **Microlejeunea Cardoti** (Steph.)

Lejeunea (*Micro-Lejeunea*) *Cardoti* Steph. Bot. Gazette, **17**: 172. 1892.

Dark green, loosely depressed-caespitose: stems prostrate, 0.03 mm. in diameter, copiously and irregularly branched, the branches widely spreading: rhizoids scanty: leaves distant to loosely imbricated, the lobe obliquely spreading, ovate, 0.25 mm. long, 0.17 mm. wide, plane, apex broad and rounded, margin entire or subcrenulate from projecting cells, antical margin arching across axis and rounded at base, postical margin usually forming a continuous line with keel; lobule inflated, ovoid, 0.14 mm. long, 0.08 mm. wide, keel strongly arched, more or less involute to apex, then passing by a lunulate sinus to end of keel, apex tipped with a single projecting, straight or outwardly curved cell; lobule often poorly developed; cells of lobe plane or nearly so, thin-walled throughout or with very indistinct trigones, averaging 13 μ in diameter, ocelli at base of lobe usually present in robust leaves, consisting of one to three enlarged cells, 25 μ in diameter: underleaves distant, ovate, 0.07 mm. long, 0.05 mm. wide, narrowed toward base and neither rounded nor decurrent, bifid beyond middle with narrow, lanceolate divisions and acute sinus, the divisions about two cells broad at base and ending in a row of two to four cells: inflorescence dioicous: ♀ inflorescence borne on a leading branch, innovating on one side, the innovation mostly simple and sterile; bracts complicate, somewhat unequally bifid, the lobe obliquely spreading, oblong to obovate, 0.35 mm. long, 0.15 mm. wide, rounded to very obtuse at apex, margin entire, lobule ovate, obtuse to subacute, 0.3 mm. long, 0.1 mm. wide, keel wingless or with a very narrow and indistinct interrupted wing; bracteole free, ovate, 0.25 mm. long, 0.12 mm. wide, bifid about one third with subacute lobes and sinus; perianth somewhat exserted, pyriform from a narrowed base, inflated, 0.5 mm. long, 0.35 mm. wide, rounded at apex and with a short beak, obtusely five-keeled: ♂ spike occupying a short branch, sometimes proliferating and giving off short branches beyond inflorescence; bracts in about two pairs, inflated, subequally bilobed with obtuse divisions: bracteole at base of spike similar to underleaves: spores greenish, with a thickened minutely verruculose wall, averaging 23 μ in short diameter, varying in length.

On bark of willow. Pointe a la Hache, Louisiana (Langlois), the type-locality; also reported from Mexico.

The specimens of *M. Cardoti* at the writer's disposal are so poorly developed that it is impossible to gain from them a clear idea of the species. On this account, no figures are given. The plants from Louisiana, collected by Langlois, are presumably the type specimens, as they are the ones first quoted by Stephani. They are perfectly sterile and all their lobules are apparently rudimentary. They seem to lack also the basal ocelli which are ascribed to the species. In the plants from Mexico (Hep. Amer. 136), a few of the stems bear perianths and some of the lobes show ocelli, but even here a well developed lobule is rare. The original description was probably drawn from the Mexican specimens.

Stephani compares *M. Cardoti* with *M. ulicina*, *M. bullata* and *M. lucens*; it is also related to *M. Ruthii*. It can be distinguished from *M. ulicina* by its relatively smaller lobule, by its slightly smaller leaf-cells, and by the rounded lobes and entire margins of its perichaetial bracts. The same peculiarities of the bracts will also serve to separate it from *M. bullata*, which is a much smaller plant with more erect lobes and relatively larger lobules. It differs from *M. lucens* in its darker color, in its smaller leaf-cells, and in its smaller and differently shaped underleaves. Its underleaves will also distinguish it from *M. Ruthii*, a larger plant, the leaf-cells of which are also larger and have slightly thickened walls.

19. **Microlejeunea bullata** (Tayl.)

PLATE 21, FIGS. 20–29

Lejeunea bullata Tayl. Lond. Jour. Bot. **5**: 398. 1846.

Lejeunea (*Micro-Lejeunea*) *bullata* Spruce, Hep. Amaz. et And. 289. 1846.

Pale or bright green, scattered or loosely depressed-caespitose: stems prostrate, closely appressed to substratum, 0.03 mm. in diameter, sparingly and irregularly branched, the branches widely spreading: rhizoids scanty: leaves distant, the lobe erect or slightly spreading, ovate, 0.17 mm. long, 0.1 mm. wide, rounded to obtuse at the apex, margin entire or subcrenulate from projecting cells, antical margin variable, sometimes arching across axis and rounded at base, sometimes almost straight and reaching just beyond edge, postical margin forming a continuous line with keel; lobule strongly inflated, ovoid, 0.14 mm. long, 0.08 mm. wide, keel strongly arched, free margin entire, plane or usually involute to apex, then obliquely lunulate to end of keel, apex tipped with a single, straight or outwardly curved projecting cell; cells of lobe more or less convex, thin-walled throughout or sometimes with very minute trigones, averaging 12 μ in diameter: underleaves distant, ovate to orbicular, 0.06 mm. long, 0.05 mm. wide, narrowed toward base and not decurrent, bifid to beyond the middle with obtuse to lunulate sinus and subulate, erect or connivent lobes, three to five cells long, two cells wide at base and ending in a row of two cells, margin entire: inflorescence dioicous: ♀ inflorescence on a leading branch with a single, sterile and simple innovation; bracts complicate, subequally bifid, the keel wingless or with a narrow, crenulate wing, lobe obliquely spreading, oblong, 0.36 mm. long, 0.12 mm. wide, rounded to acute at the apex, crenulate on margins, lobule narrower, 0.33 mm. long, 0.08 mm. wide, usually acute, crenulate on margin or sometimes with a blunt tooth near apex; bracteole slightly connate on both sides, oblong, 0.3 mm. long, 0.15 mm. wide, bifid about two fifths, sinus variable, divisions acute to acuminate, margins crenulate, sometimes denticulate in upper part; perianth pyriform, 0.4 mm. long, 0.2 mm. wide, rostellate, sharply five-keeled, smooth: ♂ inflorescence occupying a short branch, often proliferating at the end; bracts in two to four pairs, larger than the leaves, imbricated, strongly inflated, subequally bifid with a very shallow sinus, the lobes rounded at the apex and entire; bracteoles similar to underleaves, present only at base of spike.

Type-locality, St. Vincent (Guilding).

On bark: South Carolina (Sullivant); Florida (J. D. Smith, Mrs. Russell, Underwood, Straub). Found also at various places in tropical America.

EXSIC.: Hep. Amer. 132 *p. p.* (as *Lejeunea* (*Colo-Lej.*) *minutissima*).

Microlejeunea bullata is our smallest representative of the Lejeuneae. It has not before been recorded for the United States, but seems to be common in Florida. When growing by itself its minute size makes it almost invisible, but as it often grows in company with other species it has been collected several times. The type-specimens agree closely with those from Florida.

According to Lindberg, *M. ulicina* occurs in Sullivant's Musc. Alleg. 272, mixed with *Lejeunea Americana*. In one example of this exsiccata examined by the writer, there seems to be no admixture whatever; in another example there is a single sterile stem of *M. bullata*, and it is probable that Lindberg confused this species with *M. ulicina*. At all events it seems advisable to omit the latter species from our lists until its presence is more definitely established.

M. ulicina is about twice as large as *M. bullata*, its leaves spread a little more from the axis and tend to be more pointed, the cells of the lobe are considerably larger, averaging 18 μ in diameter, the cell-walls are thicker and usually show minute trigones, while the lobules are relatively smaller. The perichaetial bracts of the two species, except for the difference in size, resemble each other very closely, but the bracteole of *M. ulicina* is entire or nearly so, while that of *M. bullata* is crenulate or denticulate.

M. bullata has also been confused with *Cololejeunea minutissima*, with which it often grows. The presence of underleaves will at once distinguish it from this species, and there is little danger of confusing it with any of our other Lejeuneae.

20. COLOLEJEUNEA MINUTISSIMA (Smith) Schiffn.

Jungermannia minutissima Smith, Eng. Bot. *pl. 1633.* 1806.

Jungermannia inconspicua Raddi, Mem. Mat. e Fis. Soc. Ital. Sci. Mod. **18**: 34. *pl. 5. f. 2.* 1820.

Lejeunea minutissima Dumort, Comm. Bot. 111. 1822. G. L. & N. Syn. Hep. 387. 1845.

Lejeunea minutissima β inconspicua Nees, Naturgesch. Eur. Leberm. **3**: 279. 1838.

Jungermannia parvula Wils. & Hook.; Drummond, Musc. Amer. St. Merid. 172. 1841.

Lejeunea Taylori Spruce, Ann. Nat. Hist. II. **4**: 116 (footnote). 1849.

Lejeunea inconspicua De Not. Mem. Acc. Tor. II. **22**: 386. *pl. 5. f. 27.* 1865.

Lejeunea parvula Aust.; Lindb. Acta Soc. Sci. Fenn. **10**: 481. 1875.

Lejeunea (*Colo-Lejeunea*) *minutissima* Spruce, Hep. Amaz. et And. 293. 1884.

Lejeunea (*Colo-Lejeunea*) *parvula* Steph. Bot. Gazette, **17**: 171. 1892.

Cololejeunea minutissima Schiffn.; Engler & Prantl, Nat. Pflanzenfam. **1**^{3}: 122. 1893.

Dark green, varying to yellowish, scattered or loosely depressed-caespitose: stems prostrate, geniculate at nodes, 0.05 mm. in diameter, irregularly branched: rhizoids somewhat abundant: leaves distant to subimbricated, the lobe obliquely to widely spreading, convex, ovate to subrotund, 0.22 mm. long, 0.19 mm. wide, rounded or very obtuse at the apex, margin crenulate from projecting cells, antical margin arching wholly or partially across axis and slightly rounded at the very short base, postical margin forming a continuous line with keel; lobule strongly inflated, ovoid, 0.19 mm. long, 0.12 mm. wide, keel strongly arched, free margin curved, involute about half its length, bearing an obtuse or rounded tooth just beyond middle, then obliquely truncate or lunulate with a tooth composed of two rounded cells midway between the obtuse tooth and end of keel; lobule often imperfectly developed, in such cases sometimes plane or nearly so, with an almost straight keel and one or both of the marginal teeth obsolete; stylus reduced to a single papilla, sometimes borne on the basal marginal cell of the lobule, early obsolete; cells of lobe convex on both surfaces, thin-walled and without trigones, averaging 18 μ in diameter: inflorescence autoicous: ♀ inflorescence on a leading branch, rarely on a short branch, with one or rarely two innovations; bracts somewhat complicate, unequally or subequally bifid, the sinus sometimes very shallow, lobe obliquely spreading, narrowly oblong, 0.4 mm. long, 0.17 mm. wide, rounded at the apex, lobule similar to lobe but sometimes obtuse at the apex, 0.35 mm. long, 0.12 mm. wide, margin crenulate from projecting cells: perianth obovoid, well exserted, 0.5 mm. long, 0.3 mm. wide, cuneate toward base, truncate or rounded at the apex and with a short broad beak, sharply five-keeled in upper part, surface papillose from convex cells: ♂ spike sometimes on a short branch, sometimes on a longer branch; bracts in two to eight pairs, imbricated, very concave, subequally bilobed, the lobes rounded or very obtuse, crenulate, postical lobe without marginal teeth; antheridia borne singly or in pairs: spores greenish with a thickened, minutely verruculose wall, angular, averaging 17 μ in diameter.

Type-locality, England.

On trees. South Carolina (Ravenel); Florida (J. D. Smith, Mrs. Russell, Underwood, Straub); Alabama (Sullivant); Mississippi (Lloyd and Tracy); Louisiana (Drummond, Langlois); Texas (Wright). Widely distributed in southern and western Europe.

EXSIC.: Musc. Amer. St. Merid. 172 (as *Jungermannia parvula*). Musc. Alleg. 276 (as *Lejeunea minutissima*). Hep. Amer. 132 *p. p.* (as *Lejeunea* (*Colo-Lej.*) *minutissima*).

The complicated synonymy of *Cololejeunea minutissima* is due largely to the fact that for many years it was not clearly distinguished in Europe from *Microlejeunea ulicina*. It is probable indeed that the original *Jungermannia minutissima* was a mixture of these two species, which frequently grow together and bear much superficial resemblance to each other. In this country *C. minutissima* has been similarly confused with *Microlejeunea bullata*. It can of course be readily distinguished from both these species by its autoicous inflorescence, geniculate stems and particularly by the entire absence of underleaves.

The species is variable, and it is not unusual to find specimens in which the lobules are poorly developed. This is even true of fruiting plants, where the stems bearing perianths tend to be crowded together in the middle of a tuft. In such cases the sterile stems around the edges are likely to be more characteristic. Of the published figures of this species, the only one which brings out clearly the marginal teeth of the lobule is that of Stephani,* illustrating a luxuriant form from Portugal. All the other figures seem to have been drawn from imperfectly developed material.

Although Lindberg recognized *Lejeunea parvula* as a distinct species he failed to give a complete description of it. He stated merely that it agreed with *L. minutissima* in being autoicous and in having no underleaves but that it differed in its spreading, semioval and plane lobules. These slight differences by themselves in so variable an organ as the lobule are hardly sufficient to separate the two species. Lindberg referred to *L. parvula* the specimens distributed by Drummond as *Jungermannia parvula* and those distributed by Sullivant as *L. minutissima*. The writer has examined both and finds that the material is not only fragmentary but badly weatherworn. It is sufficient, however, to indicate that the specimens are the same as that rather common species of the Southern States, which subsequent writers have referred, without question, to *L. minutissima*. There seems to be no reason, therefore, for trying to hold *L. parvula* distinct. It should perhaps be noted that sometimes, in American specimens, the lobe is more narrowed at the apex and less crenulate than in European plants. Both of these very slight differences, however, are inconstant. American specimens in which the lobes are just as blunt and just as crenulate as in normal European forms are also frequent, and intermediate conditions exist between the two extremes.

C. minutissima is our smallest *Cololejeunea*. It can easily be distinguished from our other three species by its relatively larger lobule and extremely rudimentary stylus. From *C. Jooriana*, with which it sometimes grows, it differs also in its autoicous inflorescence, in its total lack of hyaline cells, in the shape and in the distinctly crenulate margin of its leaf-lobes.

21. **Cololejeunea Biddlecomiae** (Aust.)

Lejeunea calcarea Sull. Musc. Alleg. 275. 1845. Not Libert.

Lejeunea echinata Aust. Hep. Bor.-Amer. 99. 1873. Not Taylor.

Lejeunea Biddlecomiae Aust.; Pearson, List of Canadian Hepaticae, 5. *pl. 5.* 1890.

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* Hedwigia, 26 : *pl. 1. f. 1.* 1887.

Pale or bright green, scattered or depressed-caespitose: stems prostrate, 0.04 mm. in diameter, irregularly pinnately branched: rhizoids somewhat abundant: leaves distant to imbricated, the lobe obliquely to widely spreading, plane or usually convex, ovate, 0.35 mm. long, 0.2 mm. wide, apex varying from rounded to acute, usually obtuse, margin crenulate or denticulate from projecting cells, antical margin arching just across axis, slightly rounded at the very short base, postical margin almost straight, forming a continuous line with keel: lobule inflated, at least near keel, ovoid to globose, 0.17 mm. long, 0.15 mm. wide, keel strongly arched, free margin curved, involute about half its length, bearing an obtuse or rounded, sometimes indistinct tooth just beyond the middle, then obliquely truncate to end of keel, with a tooth usually composed of two rounded cells midway between the blunt tooth and the end of keel; stylus mostly conspicuous, usually composed of two to ten cells in a single row, sometimes two cells broad a part of its length, in rare cases reduced to a single papilla; cells of lobe thin-walled, usually with minute trigones, averaging 10 μ in diameter at edge of lobe, 13 μ in the middle and 21 × 13 μ at base, walls on outer surface of lobe convex to conical, sometimes with a distinct thickening or wart in the middle; cells of lobule plane: inflorescence dioicous or autoicous: ♀ inflorescence borne on a leading branch, innovating on one side; bracts unequally bifid, the lobe obliquely spreading, broadly ovate, 0.35 mm. long, 0.2 mm. wide, obtuse to acute at the apex, lobule orbicular, 0.17 mm. long, margin denticulate and outer surfaces of both lobe and lobule papillose from projecting cells; perianth partly exserted, obovoid to oblong, 0.6 mm. long, 0.35 mm. wide, not compressed, rounded to truncate at the apex, with a short beak, sharply five-keeled in upper part, surface roughened from projecting cells except near the base: ♂ spikes usually borne on leading branches; bracts in two to five pairs, imbricated, similar to the leaves, but with a proportionately larger lobule; antheridia borne singly or in pairs.

Type-locality, Canada (Macoun).

On trees or rocks: Ontario (Macoun, Dearness); Massachusetts (Stone); Connecticut (Eaton, Underwood, Evans); New York (Underwood); New Jersey (Rau); District of Columbia (Coville, Maxon); Ohio (Miss Biddlecome, Beardslee, Wilcox, Werner); Florida (Miss Biddlecome); Alabama (Sullivant).

EXSIC.: Musc. Alleg. 275 (as *Lejeunea calcarea*). Hep. Bor.-Amer. 99 (as *Lejeunea echinata*). Hep. Amer. 51 (as *Lejeunea* (*Colo-Lej.*) *calcarea*. Can. Hep. 13 (as *Lejeunea calcarea*).

Cololejeunea Biddlecomiae is closely related to the European

C. calcarea (Lib.) Schiffn. In the latter species the lobes of the leaves are narrower than in *C. Biddlecomiae* and much more pointed, varying from acute to acuminate; they spread more widely from the stem and the postical margin is incurved beyond the keel; the lobule is more inflated with its free margin strongly involute, the roughness of the leaves is more pronounced, and the stylus is commonly shorter.

Although Spruce at one time tentatively accepted *C. Biddlecomiae* as a species, he afterwards regarded it as a luxuriant form of *C. calcarea*. This opinion was based on the fact that it is sometimes difficult to distinguish certain specimens of the American species from certain specimens of the European. The forms which resemble each other so closely, however, seem to be always imperfectly or abnormally developed plants in which some of the specific characters fail to show themselves in a satisfactory manner. When robust and well developed specimens are examined, there is little difficulty in distinguishing between them. *C. calcarea* grows preferably on limestone rocks, it seems to be much rarer on siliceous rocks and there are few records of its occurence on trees. *C. Biddlecomiae*, on the contrary, attains its best development on trees, particularly in cedar-swamps, and although it is not infrequent on siliceous rocks, it is often less robust in such localities. Whether it is abundant on calcareous rocks does not appear from the specimens examined. The poorly developed specimens, growing on rocks, are the ones which can scarcely be distinguished from rudimentary plants of *C. calcarea*, as for example the specimens distributed by Gottsche and Rabenborst in Hep. Eur. 323. Since however no *typical* specimens of *C. calcarea* have as yet been collected in America, it seems wisest to refer these doubtful rock-forms to *C. Biddlecomiae*.

The presence or absence of a stylus has been used as a distinguishing mark between species of *Cololejeunea*. This practice is not absolutely correct because the stylus is always present, although sometimes reduced to a unicellular papilla which early shrivels up and disappears. Where the stylus is filiform, the papilla can often be detected somewhere near its apex. Regarding the morphological value of the stylus, opinions have varied. Nees von Esenbeck and afterwards Spruce looked upon it as one of the divisions of a bifid underleaf, the other having become obsolete. Stephani calls attention to the improbability of this view. As a matter of fact the postical segments cut off from the apical cell bear no appendages whatever except the rhizoids. The stylus, on the other hand, arises from a lateral segment which normally bears a leaf, and there seems to be no reason why it should not be considered homologous with the stylus of *Frullania*, which is acknowledged to be a part of the leaf.

In a note sent by Spruce to Underwood, it is stated that a few stems of the European *Cololejeunea Rosettiana* (Massal.) Schiffn. occur mixed with Hep. Amer. 51. Apparently on the strength of this statement, Underwood has listed the species as an American plant. In the two sets of Hep. Amer. examined by the writer, no. 51, which grew on trees, is made up entirely of *C. Biddlecomiae;* and since *C. Rossettiana* has not been collected in Europe except on calcareous rocks, perhaps it would be well to omit it from our lists until its presence is more definitely proved. *C. Rossettiana* was first recoganized in Italy, but has since been detected on the British Isles and in western France. It often grows in company with *C. calcarea*, with which it was long confused. It differs from this species in its broader and even rougher lobe and in its plane lobule, which is denticulate on the margin and rough on the postical surface. Its stylus also is reduced to a unicellular papilla, which is often difficult to demonstrate.

22. **Cololejeunea Macounii** (Spruce)

PLATE 22, FIGS. 1–8

Lejeunea (*Cololejeunea*) *Macounii* Spruce; Underwood, Bull. Torrey Club, **17**: 259. 1890.

Pale green or yellowish, scattered or loosely depressed caespitose: stems prostrate, 0.08 mm. in diameter, irregularly pinnately branched: rhizoids not abundant: leaves imbricated, the lobes suberect to obliquely spreading, straight or slightly falcate, plane, oblong-obovate, on robust plants 0.7 mm. long and 0.45 mm. wide, rounded at the apex, margin entire or subcrenulate from projecting cells, antical margin not arching across axis, almost straight near base, postical margin forming an almost continuous line with keel; lobule inflated at least near keel, ovate in outline, 0.4 mm. long, 0.2 mm. wide, keel arched, free margin usually plane and appressed to lobe, bearing an acute tooth beyond the middle, then obliquely truncate to end of keel with a tooth composed of two rounded cells midway between the acute tooth and end of keel; stylus inconspicuous and soon obsolete, composed of two or rarely of three cells in a row, sometimes reduced to a one-celled papilla; cells of lobe thin-walled with small but distinct trigones and occasional intermediate thickenings averaging 10 μ in diameter at edge of lobe, 20 μ in the middle and 25 × 20 μ at the base, walls on outer surface of lobe slightly convex, each cell, except those near the base, bearing a single, large, short-cylindrical, rounded projection, representing a local thickening of the wall: inflorescence dioicous: ♀ inflorescence borne on a leading branch innovating on one side; bracts complicate, unequally bifid, the lobe similar to the leaf-lobes but narrower, 0.6 mm. long, 0.3 mm. wide, lobule ovate, 0.35 mm. long, 0.17 mm. wide, apiculate or subacuminate at apex, margin and cells of lobe as in leaves; perianth exserted, obconic in lower part, rectangular-oblong above, 0 75 mm. long, 0.3 mm. wide, slightly compressed, subtruncate at apex, sharply five-keeled, the entire surface except near the base roughened as in leaves: ♂ inflorescence unknown.

On maple bark. British Columbia (Macoun), the type-locality.

EXSIC.: Hep. Amer. 177 (as *Lejeunea* (*Colo-Lej.*) *Macounii*).

Spruce's original description of *C. Macounii*, which was published by Underwood, is so complete that very little has been added to it. In fact the characters of the perianth as stated above are taken wholly from this description, the perianths in the specimens examined by the writer being either too young or too old to show these characters clearly.

In its rough leaves *C. Macounii* resembles *C. Biddlecomiae*, but in the latter species the roughness is due mainly to the very convex or conical cell walls, while in *C. Macounii* it is due almost entirely to the globose warts on the cells. In *C. Macounii* also the lobe is rounded at the apex with its broadest part above the middle, while in *C. Biddlecomiae* the lobe is more or less sharply pointed with its broadest part below the middle. There are also differences in the marginal teeth of the lobule.

In an interesting note to Underwood, Spruce compares *C. Macounii* with two autoicous species of tropical America—*C. cardiocarpa* (Mont.) and *C. platyneura* (Spruce). Both of these species differ in their compressed perianth with a low, bluntly two-angled, postical keel, which is almost obliterated at maturity. *C.*

cardiocarpa differs also in the hyaline apex of its lobe and in its muticous lobule, while *C. platyneura* shows a very small lobule and a false nerve of elongated cells in the lobe.

23. **Cololejeunea Jooriana** (Aust.)

PLATE 22, FIGS. 9–20

Lejeunea Jooriana Aust. Bull. Torrey Club, **6**: 20. 1875.

Lejeunea (*Colo-Lejeunea*) *Jooriana* Steph. Bot. Gazette, **17**: 171. 1892.

Yellowish-green or whitish, darkening somewhat with age, scattered or loosely depressed-caespitose: stems prostrate, 0.05 mm. in diameter, irregularly pinnately branched: rhizoids somewhat abundant: leaves imbricated, the lobe widely spreading, plane, ovate, 0.5 mm. long, 0.35 mm. wide, gradually narrowed from just below the middle to the rounded, obtuse or subacute apex, margin entire or subcrenulate from projecting cells, antical margin arching across axis and rounded at the very narrow base, postical margin forming a continuous line with keel, almost straight from end of keel to apex; lobule inflated, ovoid, 0.25 mm. long, 0.15 mm. wide, keel arched, free margin involute about half its length, bearing an obtuse tooth just beyond the middle, then obliquely truncate or lunulate to end of keel, with a tooth composed of two rounded cells midway between the obtuse tooth and the end of keel: stylus inconspicuous and soon obsolete, composed of two cells in a row or reduced to a one-celled papilla; cells of lobe scarcely convex, with slightly thickened walls, very inconspicuous trigones and occasional, minute intermediate thickenings, averaging 14 μ in diameter at edge of leaf, 18 μ in the middle and 25 × 18 μ at base; hyaline cells at apex one to ten in number, radially elongated, usually in a single row, united at their basal ends but often with rounded, more or less spreading, free extremities, hyaline cells sometimes present also along a part of antical margin, sometimes absent altogether, usually becoming very indistinct with age: inflorescence synoicous and sometimes paroicous: ♀ inflorescence usually borne on a leading branch, more rarely on a short branch, innovating on one side, the innovation sometimes floriferous; bracts similar to the leaves, unequally bifid, with more or less inflated lobule and arched keel, lobe narrowly ovate, 0.5 mm. long, 0.25 mm. wide, margin slightly crenulate from projecting cells, usually with a small group of hyaline cells at apex and occasionally on antical margin, lobule ovate, 0.35 mm. long, 0.2 mm. wide, crenulate or denticulate in upper part from projecting cells and sometimes bearing one to three hyaline cells at apex, stylus sometimes three or four cells long; perianth about half exserted, broadly ovoid to obovoid, 0.55 mm. long, 0.4 mm. wide, rounded at the base and rounded, truncate or very slightly retuse at apex, with an extremely short and indistinct beak, somewhat flattened, antical face plane or with a broad low keel, lateral keels sharp to blunt, postical keel broad, obtusely two-angled, cells of perianth with thicker walls than the leaf-cells, slightly convex, especially along keels: antheridia borne singly or in pairs in the axils of the ♀ bracts and sometimes in the unmodified leaf below the innovation: spores more or less elongated, angular, greenish, with a thickened, minutely verruculose wall, averaging 14 μ in short diameter.

Type-locality, Louisiana (Joor).

On bark and on reeds. North Carolina (Johnson); Florida (J. D. Smith, Underwood). Also known from Bermuda (Howe).

Austin's original description of this interesting species is incomplete and omits several of its most essential characters. For this reason the species has not been understood, and although specimens of it have been collected several times and at various localities, they have most of them been referred to *C. minutissima*, with which they really have less in common than with either of our other species. Apparently no one except Austin studied the type-material. Underwood's description, the only one since published, is simply a translation of the original description, and Stephani states distinctly that the species is unknown to him. The original specimens were collected on reeds, but the plant grows preferably on bark.

The most remarkable feature of *C. Jooriana* is its synoicous inflorescence. A paroicous inflorescence occurs in the European *C. microscopica* (Tayl.) Schiffn. and in a few of the larger Lejeuneae and Frullaniae, but a synoicous inflorescence has not before been recorded for any member of the Jubuloideae. In fact the only genera of the leafy hepaticae in which it has been observed are the widely removed *Marsupella* and *Gymnomitrium*, belonging to the Epigoniantheae. In order to see the antheridia of *C. Jooriana*, an unfertilized flower must be examined or one in which the perianth is still very immature. As the perianth develops the antheridia, having carried out their function, shrivel up and are soon difficult to demonstrate. In most flowers antheridia occur only in the axils of the perichaetial bracts, their occurrence in the axil of the subbracteal leaf below the innovation being somewhat unusual.

It is interesting to note that the bracts or at any rate those without innovations exhibit inflated lobules, an indication of their perigonial character.

The hyaline leaf-cells of *C. Jooriana* are also a unique character among our Lejeuneae. On old leaves these cells soon become indistinct, and on poorly developed leaves they may be scanty or wanting, but it is rare to find a plant from which they are altogether absent. Hyaline marginal cells are known in a number of tropical Lejeuneae,* the majority of them being species of *Cololejeunea.* The one most closely allied to *C. Jooriana* is perhaps the autoicous *C. cardiocarpa*, in which the ♂ spike bears six to eight pairs of bracts. In this species also, according to Spruce, the lobule is plane, sublinguiform in shape, obtuse at the apex and almost parallel with the axis.

Of our own species, *C. Jooriana* bears some resemblance to *C. Biddlecomiae* and *C. Macounii.* Aside from its inflorescence and hyaline cells, it differs from both these species in its ordinary leaf-cells which are plane or very slightly convex. It differs also from *C. Biddlecomiae* in its much shorter stylus and from *C. Macounii* in the very different shape of its leaf-lobes.

EXCLUDED SPECIES

The species in the following list have all been recorded from the United States. They are now excluded either because they are imperfectly known or because there is insufficient evidence that they occur within our limits. All of these species are referred to more fully in the preceding text.

1. *Neurolejeunea catenulata* (Nees) Schiffn.
2. *Platylejeunea transversalis* (Swartz) Schiffn.
3. *Archilejeunea Auberiana* (Mont.) Steph.
4. *A. xanthocarpa* (Lehm. & Lindenb.) Steph.
5. *Lopholejeunea Sagraeana* (Mont.) Schiffn.
6. *Acrolejeunea torulosa* (Lehm. & Lindenb.) Schiffn.
7. *Euosmolejeunea trifaria* (Nees) Schiffn.
8. *Pycnolejeunea macroloba* (Mont.) Schiffn.
9. *Lejeunea Caroliniana* Aust.

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* *Cf.* Stephani, Hedwigia, **27**: 288. 1888.

10. *L. diversiloba* Spruce.
11. *L. flava* Swartz.
12. *L. laete-fusca* Aust.
13. *L. laete-virens* Mont.
14. *L. Ravenelii* Aust.
15. *L. Wrightii* Gottsche.
16. *Microlejeunea crenulifolia* Steph.
17. *M. cucullata* (R. Bl. & N.) Jack & Steph.
18. *M. erectifolia* (Spruce) Steph.
19. *M. ulicina* (Tayl.) Evans.
20. *Cololejeunea calcarea* (Lib.) Schiffn.
21. *C. Rossettiana* (Massal.) Schiffn.

YALE UNIVERSITY.

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Explanation of Plates

PLATE 16

Archilejeunea clypeata (Schwein.) Schiffn. 1. Stem with perianth, postical view, × 27. 2. Sterile stem, postical view, × 27. 3. Leaf, antical view, × 27. 4. Cells from middle of lobe, × 350. 5. Cells from antical margin of lobe, × 250. 6, 7. Apices of lobules, × 250. 8, 9. Bracts, × 40. 10. Bracteole, × 40. 11. Transverse section of perianth in upper third, × 40. The figures are all drawn from specimens collected by the writer at Woodbridge, Connecticut.

Archilejeunea Sellowiana Steph. 12. Stem with two perianths and ♂ inflorescence, postical view, × 16. 13. Leaf, antical view, × 16. 14. Cells from middle of lobe, × 350. 15. Cells from antical margin of lobe, × 250. 16. Apex of lobule, × 250. 17, 18. Bracts, × 40. 19. Bracteole, × 40. 20. Transverse section of perianth at about the middle, × 40. The figures are all drawn from specimens collected by A. Commons, at Laurel, Delaware (no. 19).

PLATE 17

Archilejeunea conchifolia Evans. 1. Stem with perianth, postical view, × 27. 2. Leaf, antical view, × 27. 3. Cells from middle of lobe, × 350. 4. Cells from antical margin of lobe, × 250. 5. Apex of lobule, × 250. 6, 7. Bracts, × 40. 8. Bracteole, × 40. 9. Transverse section of perianth at about the middle, × 40. The drawings are all made from the type specimens.

Mastigolejeunea auriculata (Wils. & Hook.) Schiffn. 10. Stem with perianth, postical view, × 27. 11. Small branch, postical view, × 27. 12. Leaf, antical view, × 40. 13. Cells from middle of lobe, × 350. 14. Cells from antical margin of lobe, × 350. 15. Apex of lobule, × 50. 16, 17. Bracts, × 40. 18. Bracteole, × 40. 19. Transverse section of perianth at about the middle, × 40. The figures are all drawn from specimens collected by L. M. Underwood in Florida; 11 and 15 came from Orange Bend (no. 1583) and the remainder from Blandton (no. 1988).

PLATE 18

Brachiolejeunea corticalis (Lehm. & Lindenb.) Schiffn. 1. Stem with perianth, postical view, × 31. 2. Leaf, postical view, × 35. 3. Cells from middle of lobe, × 310. 4. Cells from antical margin of lobe, × 220. 5. Free margin of lobule, inner portion, × 220. 6. Free margin of lobule, outer portion, × 220; both from leaf 2. 7, 8. Bracts, × 35. 9. Bracteole, × 35. 10, 11. Transverse sections of perianth, 10 from upper third, 11 from about the middle, × 35. The figures are all drawn from specimens collected at Lake Worth, Florida, by L. M. Underwood (no. 293).

Euosmolejeunea duriuscula (Nees) Evans. 12. Stem with ♀ inflorescence, postical view, × 35. 13, 14. Sterile stems, postical view, × 35. 15, 16. Cells from middle of lobe, × 310. 17. Apex of lobule, × 220. 18, 19. Bracts, × 35. 20. Bracteole from same involucre, × 35. 21–23. Bracts and bracteole from another involucre, × 35. 12, 13, 15, and 17–20 are drawn from Hep. Bor.-Amer. no. 96; 14, 16, and 21–23, from Hep. Amer. no. 97.

PLATE 19

Euosmolejeunea opaca (Gottsche) Steph. 1. Sterile stem, postical view, × 40. 2. Branch with perianth, postical view, × 40. 3. Cells from middle of lobe, × 350. 4. Cells from antical margin of lobe, × 250. 5. Apex of lobule, × 250. 6. Apex of underleaf, × 250 7. Apex of underleaf-segment, × 250. 8, 9. Bracts, × 40. 10. Bracteole, × 40. 11. Transverse section of perianth in upper third, × 40. The figures are all drawn from specimens collected at Enterprise, Florida, by E. Faxon.

Cheilolejeunea polyantha Evans. 12. Stem with perianth, postical view, × 40. 13. Stem with ♀ inflorescence, postical view, × 40. 14. Leaf, antical view, × 40. 15. Cells from middle of lobe, × 350. 16. Apex of lobule, × 250. 17. Apex of underleaf-segment, × 250. 18, 19. Bracts, × 40. 20. Bracteole, × 40. 21. Transverse section of perianth in upper third, × 40. The figures are all drawn from the type-specimens.

PLATE 20

Cheilolejeunea phyllobola (Nees & Mont.) Schiffn. 1. Stem with perianth and ♂ inflorescence, × 40. 2. Cells from middle of lobe, × 350. 3. Cells from antical margin of lobe, × 250. 4. Apex of lobule, × 250. 5. Underleaf, × 60. 6–8. Details of preceding figure 6 representing one side of base, 7 and 8 apices of segments, × 250. 9, 10. Bracts, × 40. 11, 12. Bracteoles, × 40. 13. Transverse section of perianth at about the middle, × 40. The figures are all drawn from specimens collected at Lake Worth, Florida, by L. M. Underwood (no. 301 *p.p.*).

Lejeunea Americana (Lindb.) Evans. 14. Stem with perianth and ♂ inflorescence, postical view, × 40. 15. Sterile stem (a slender form), postical view, × 40. 16. Cells from middle of lobe, × 350. 17. Apex of lobule, × 250. 18. Base of underleaf (one side), × 250. 19–22. Apices of underleaf-segments, × 250. 23, 24. Bracts, × 40. 25. Bracteole, × 40. 26. Transverse section of perianth in upper third, × 40. 2 is drawn from specimens collected by A. B. Langlois near St. Martinsville; the other figures, from specimens collected at Eustis, Florida, by L. M. Underwood (no. 11).

PLATE 21

Microlejeunea lucens (Tayl.) Evans. 1. Stem with ♀ inflorescence, postical view, × 35. 2. Sterile stem, postical view, × 35. 3. Cells from middle of lobe, × 310. 4. Antical base of lobe, × 220. 5. Apex of lobe, × 220. 6. Apex of lobule, × 220. 7. Stem underleaf, × 220. 8. Branch underleaf, × 220. 9. Bract, × 35. 10. Bracteole, × 35. 2 is drawn from the doubtful type-specimen in the Taylor herbarium (no. 147); the others are all drawn from specimens collected at Manatee, Florida, by L. M. Underwood (no. 305).

Microlejeunea Ruthii Evans. 11. Stem with ♀ inflorescence, postical view, × 35. 12. Sterile stem, antical view, × 35. 13. Cells from middle of lobe, × 310. 14. Apex of lobe, × 220. 15. Apex of lobule, × 220. 16. Underleaf, × 220. 17, 18. Bracts, × 50. 19. Bracteole, × 50. The figures are all drawn from the type-specimens.

Microlejeunea bullata (Tayl.) Evans. 20. Stem with ♀ inflorescence, postical view, × 50. 21. Sterile stem, antical view, × 50. 22. Branch of 21, antical view, × 50. 23. Cells from middle of lobe, × 310. 24. Antical base of lobe, × 220. 25. Apex of lobule, × 220. 26–28. Underleaves, × 220. 29. Bracts and bracteole, × 50. 20 is drawn from a specimen collected in Florida by J. D. Smith; the remaining figures are drawn from specimens collected at Manatee, Florida, by L. M. Underwood (no. 308).

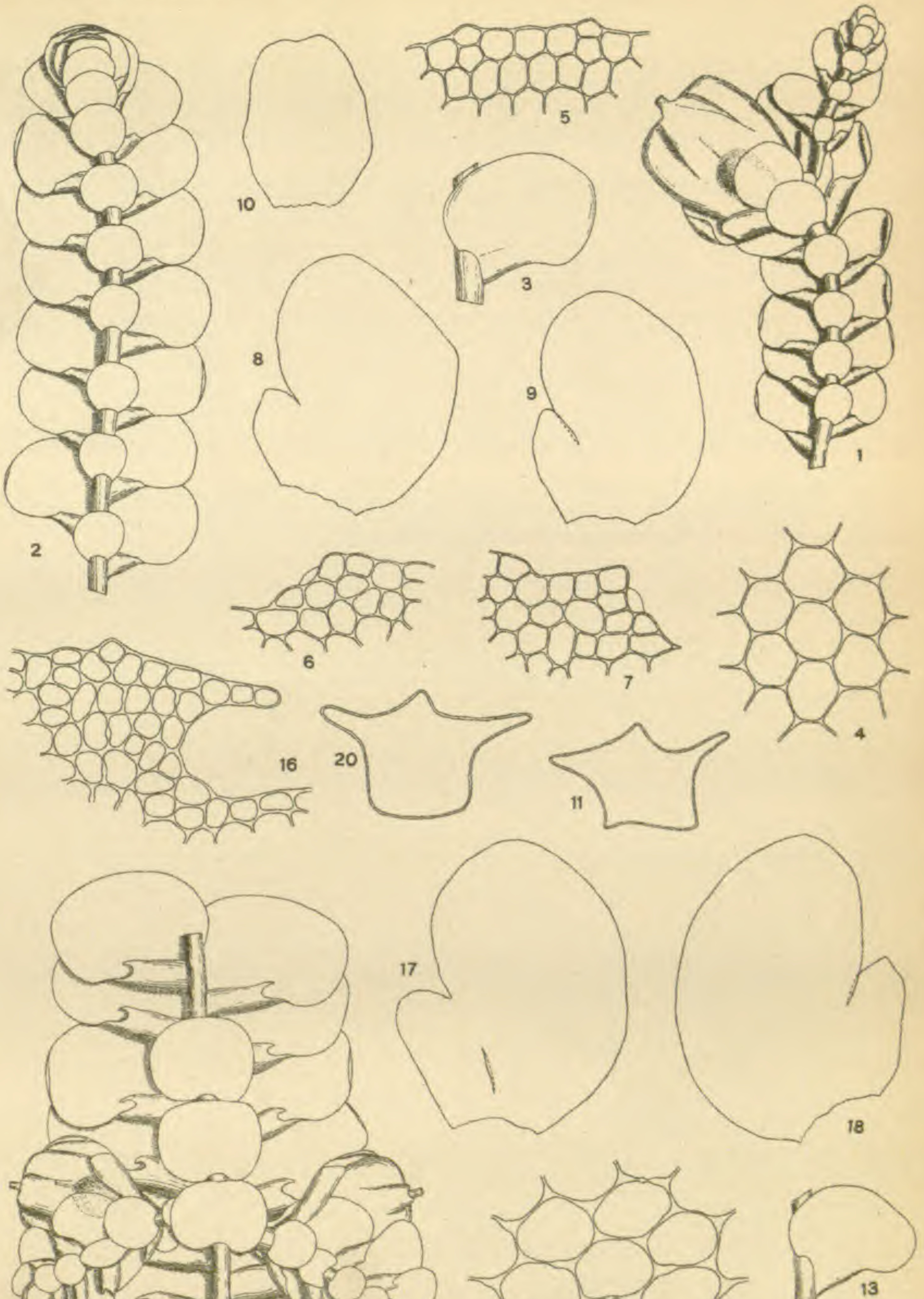
PLATE 22

Cololejeunea Macounii (Spruce) Evans. 1. Stem with very young perianth, postical view, × 40. 2. Sterile stem, postical view, × 40. 3. Cells from middle of lobe, × 350. 4. Similar cells in cross-section, × 350. 5. Cells from margin of lobe, × 250. 6. Apex of lobule, × 250. 7, 8. Bracts, × 40. The figures are all drawn from specimens collected in British Columbia by J. Macoun.

Colo ejeunea Jooriana (Aust.) Evans. 9. Stem with perianth and bisexual inflorescence, postical view, × 40. 10. Stem with perianth on a short branch, postical view, × 40. 11. Two leaves, antical view, × 40. 12. Cells from middle of lobe, × 350. 13. Cells from antical margin of lobe, × 250. 14–16. Apices of lobes, × 250. 17. Apex of lobule, × 250. 18, 19. Bracts, × 40. 20. Transverse section of perianth in upper third, × 40. The figures are all drawn from specimens collected at Lisbon Florida, by L. M. Underwood (no. 100).

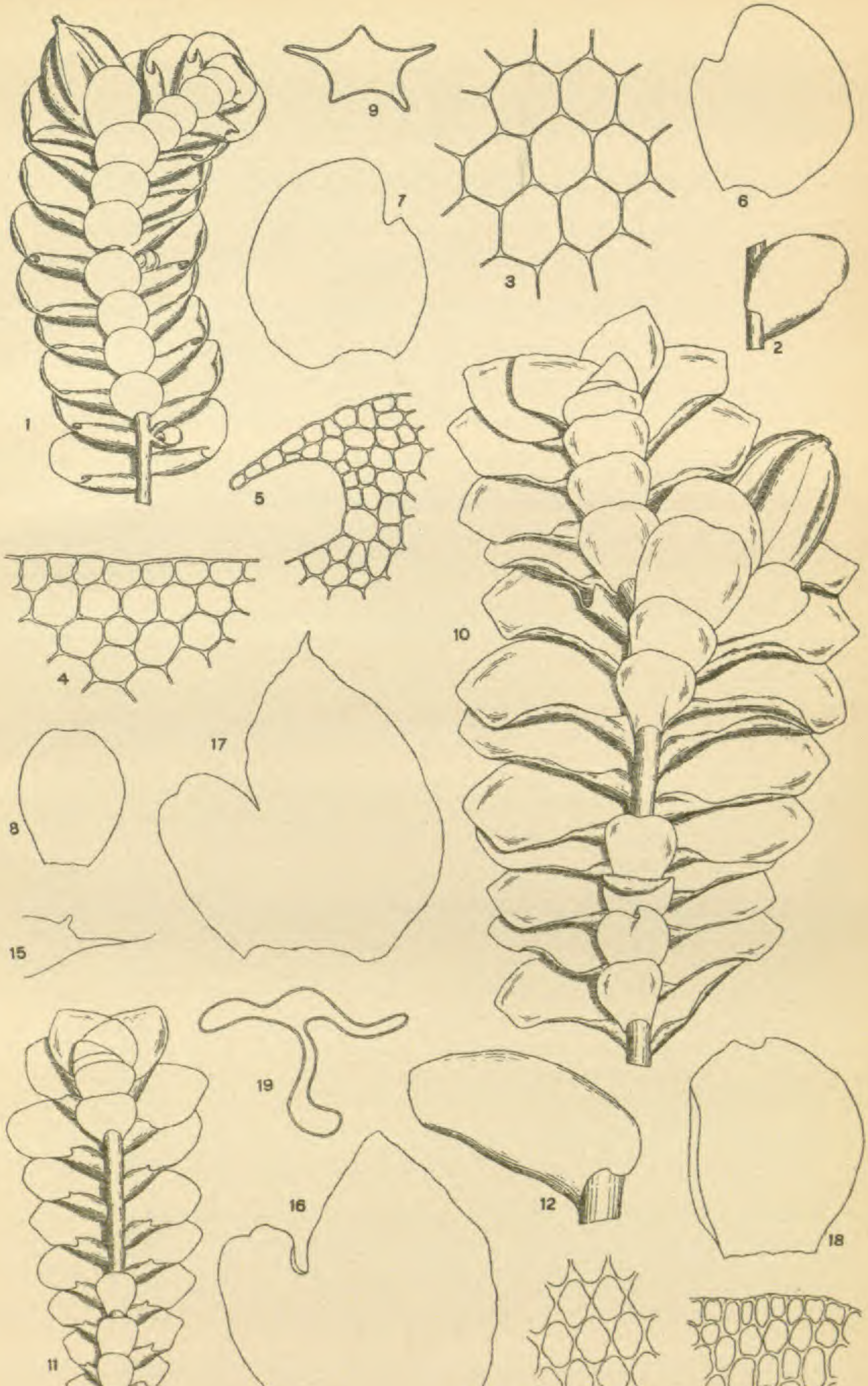
INDEX TO SPECIES

Species described are in SMALL CAPITALS, the page at which the description occurs being in full face type; species cited without description in Roman type; synonyms in *Italics.*



1-11-ARCHILEJEUNEA CLYPEATA (Schwein.) Schiffn.
12-20-ARCHILEJEUNEA SELLOWIANA Steph.

HELIOTYPE CO., BOSTON



1-9-ARCHILEJEUNEA CONCHIFOLIA Evans

10-19-MASTIGOLEJEUNEA AURICULATA (Wils. & Hook.) Schiffn.

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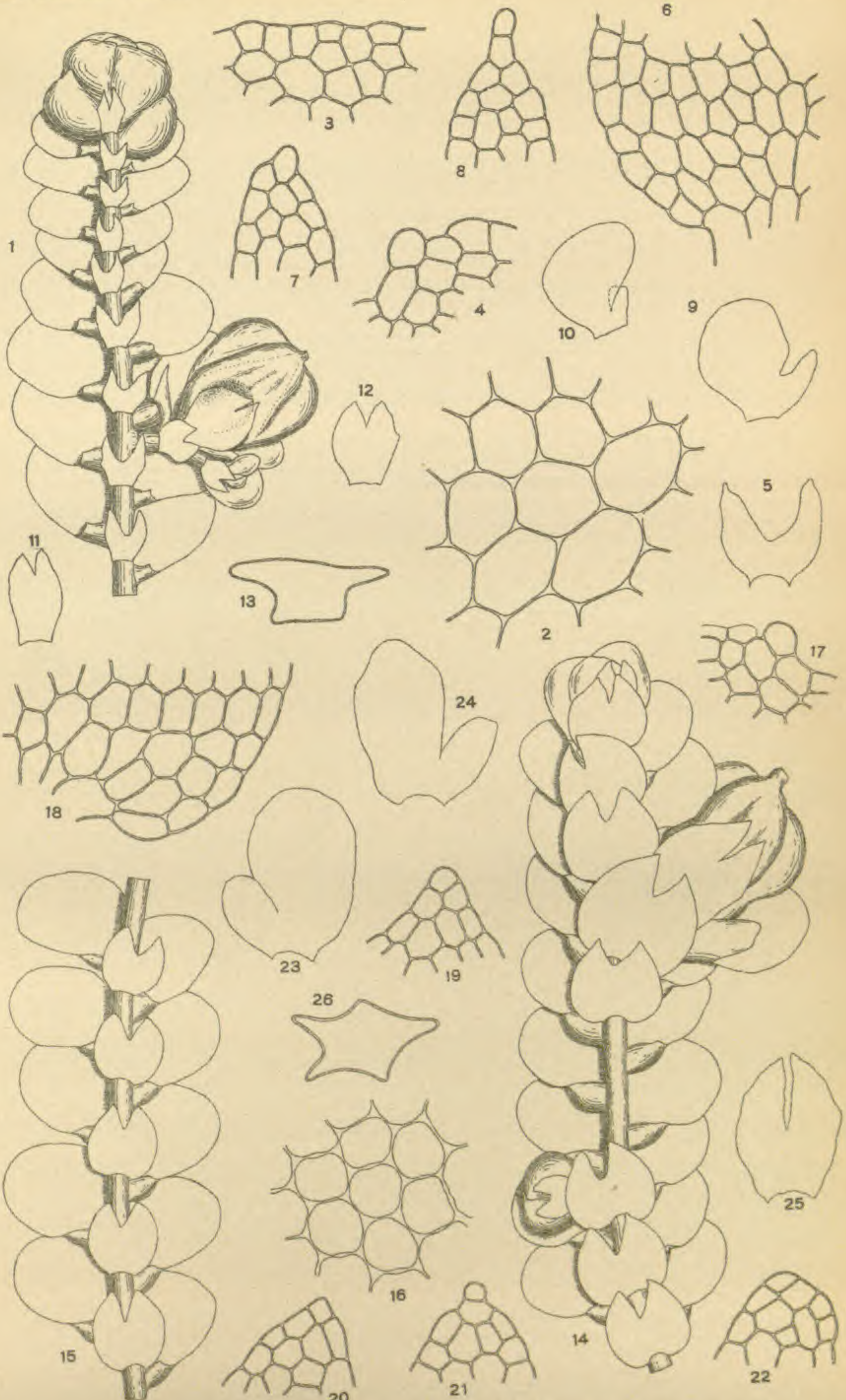
12-23-EUOSMOLEJEUNEA DURIUSCULA (Nees) Evans.

1-11-EUOSMOLEJEUNEA OPACA (Gottsche) Steph.
12-21-CHEILOLEJEUNEA POLYANTHA Evans



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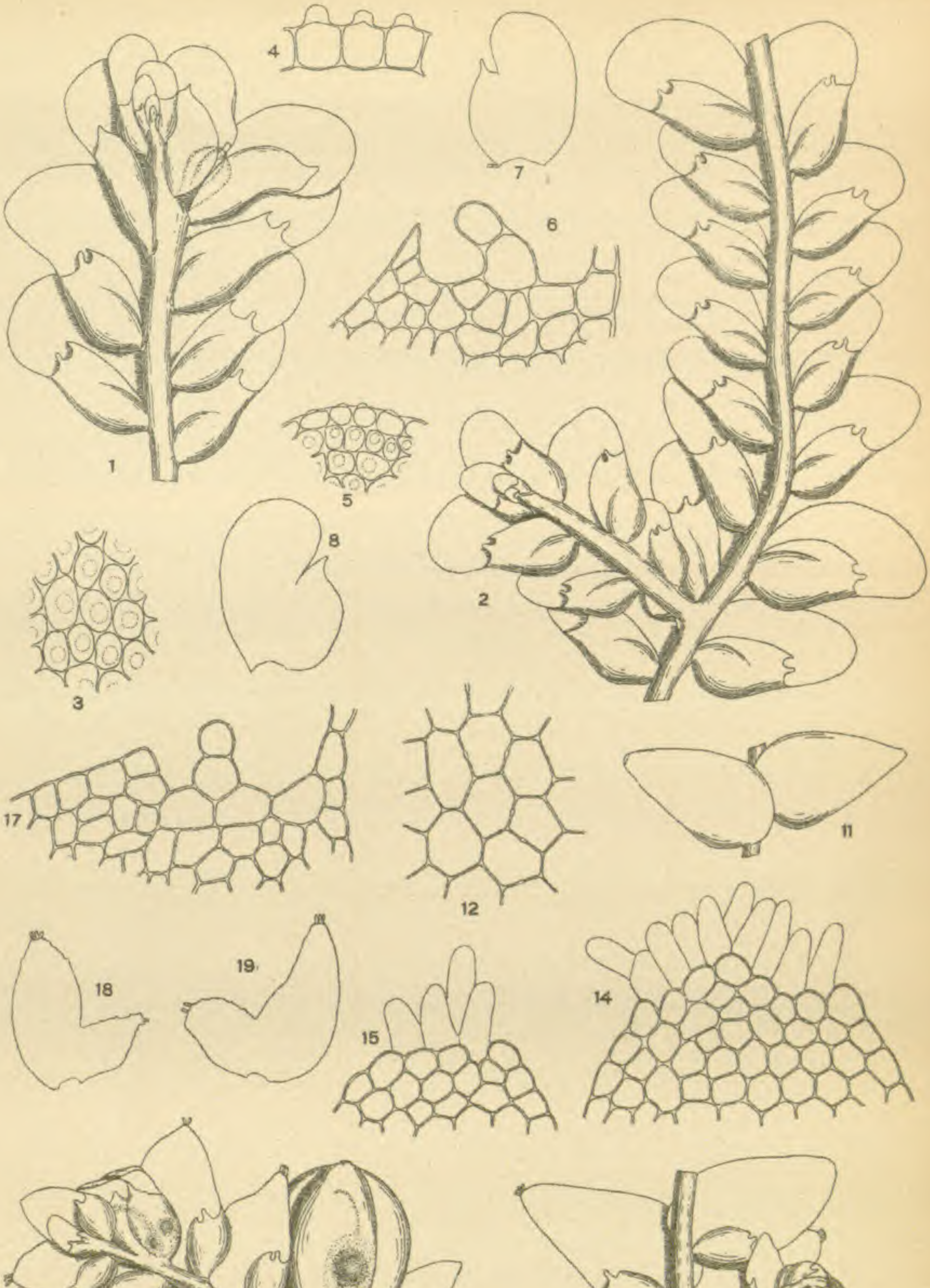
14-26-LEJEUNEA AMERICANA (Lindb.) Evans

1-10-MICROLEJEUNEA LUCENS (Tayl.) Evans
11-19-MICROLEJEUNEA RUTHII Evans
20-29-MICROLEJEUNEA BULLATA (Tayl.) Evans



1-8-COLOLEJEUNEA MACOUNII (Spruce) Evans

9-20-COLOLEJEUNEA JOORIANA (Aust.) Evans

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THE LIFE HISTORY

OF

VITTARIA LINEATA

BY

ELIZABETH G. BRITTON

AND

ALEXANDRINA TAYLOR

ISSUED 30 AUGUST 1902

The Life History of Vittaria lineata

By Elizabeth G. Britton and Alexandrina Taylor

(Plates 23-31)

At the conclusion of our studies on *Schizaea pusilla,* Mr. Tracy Hazen called our attention to the fact that Francis Wolle[*] had figured a filamentous protonema, which he suspected to belong to a fern, but had previously described as *Poterophora Donnellii.*[†] It was collected on trees in Florida by John Donnell Smith who loaned us the type from which drawings have been made, as the figures given by Wolle were found to be incorrect. The urns described by Wolle are podetia and produce spherical or cylindric gemmae which Wolle did not figure. This curious method of vegetative propagation has been figured by Goebel[‡] in a species of *Trichomanes*, but as the sporophyte is still unknown in *Poterophora* and we knew of no epiphytal species of *Trichomanes* in Florida, suspicion was aroused regarding *Vittaria lineata.* Living plants in all stages were secured from E. W. Reasoner, of Oneco, Florida, and also from Miss Abbie M. Small at Jacksonville, Florida. We have kept these plants growing in the laboratory for more than a year, and watched the stages of their development. As far as we can learn, the gametophyte of this fern has never been described ; in fact the only reference to it is in a footnote in Eaton's Ferns of North America, which states that "J. Donnell Smith and C. F. Austin found the prothalline growth of this fern very abundant on palmettos along the Caloosahatchie River, Florida." The peculiarities of its structure are remarkable, agreeing in essential particulars with those of *Vittaria elongata*, described by Goebel from specimens studied at the Botanical Gardens at Buitenzorg, Java.[§]

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[*] F. Wolle, F. W. Algae of N. A. 120. *pl. 106.* 1887.

[†] Bull. Torrey Club, **6** : 177, 188. 1877.

[‡] Goebel, Ann. Jard. Buit 7 : 78–87. *pl. 10–13.* 1888.

[§] Goebel, Ann. Jard. Buit. 7 : 95. *pl. 12, f. 60–61.*

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The systematic records of *Vittaria lineata* were also found to be very imperfect; specimens were much mixed in our collections and several other closely allied species had been mistaken for this species. The types of several of these need to be restudied microscopically before we can reach a correct knowledge of the limits and distribution of the American species. The material in American collections is necessarily incomplete, and the types are scattered through European herbaria. However, with what specimens and literature are available, we believe it will be helpful to give a brief survey of the history of *Vittaria lineata*, and to describe and figure the gametophyte of our specimens from Florida. It would be still more helpful if collectors in the West Indies would make it a point to collect the prothallia and young stages of *Vittaria*, and preserve them in condition for study.

The genus *Vittaria* is in need of revision, as there has been none made since that of Fée,* and subsequent treatment in the Synopsis Filicum has largely disregarded the results attained in his memoir. Kunze and Fée were the first to recognize the value of the spores and sporangiasters in specific distinctions, and Fée also figured the scales and sporangia, although in many species the lip cells were omitted. The venation is obscure in many species, and in consequence has been wrongly described. *Taenitis* has been combined with *Vittaria* by some authors which tends to complicate the synonymy, and *Taeniopsis* was founded on the type species of *Vittaria*.†

The most recent list given of the species is that of Salomon ‡ from which the following has been compiled, but it will be found that a number of corrections have been made after consulting the original place of publication.

CHRONOLOGICAL LIST OF THE AMERICAN SPECIES

1753. *Pteris lineata* L. Sp. Pl. 1073.
1801. *Vittaria filiformis* Cav. Praelect. 270 (671).
1803. *V. angustifrons* Michx. Flor. bor. Am. **2**: 261.
1819. *V. Schkuhrii* Raddi, Fil. Bras. 51.

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* Fée, Mem. des Foug. **3**: 1–24. 1851.

† J. Smith, Hook. Journ. Bot. **4**: 67. 1842.

‡ Salomon, Nom. Gefäss.-Krypt. 1883.

1824. *V. graminifolia* Kaulf. Enum. Fil. 192.
1837. *V. stipitata* Kze. Analect. pteridogr. 28. *pl. 18. f. 1.*
1851. *V. Gardneriana* Fée, Mem. des Foug. **3**: 15. *pl. 3. f. 1.*
1851. *V. filifolia* Fée, Mem. des Foug. **3**: 20. *pl. 3. f. 6.*
1851. *V. Ruiziana* Fée, Mem. des Foug. **3**: 16. *pl. 3. f. 3.*
1851. *V. scabrida* Klotsch; Fée, Mem. des Foug. **3**: 20.
1854. *V. remota* Fée, Mem. des Foug. **7**: 26. *pl. 20. f. 1.*
1854. *V. curvidentata* CM. Bot. Zeitung, **12**: 546. *pl. 13. f. 1.*
1854. *V. dimorpha* CM. *l. c.* 547. *pl. 13. f. 3.*
1854. *V. pachydictyon* CM. *l. c.* 547. *pl. 13. f. 4.*
1854. *V. Deppeana* CM. *l. c.* 547. *pl. 13. f. 6.*
1864. *V. Karsteniana* Mett. Ann. Sc. Nat. V. **2**: 206.
1864. *V. Moritziana* Mett. *l. c.*, 207.
1869. *V. Orbignyana* Mett. Linnaea, **36**: 67.
1869. *V. gracilis* Moritz, Linnaea, **36**: 67.
1877. *V. intramarginalis* Baker, Journ. Bot. **15**: 266.
1893. *V. longipes* Sodiro, Crypt. Vasc. Quit. 423.

Of these *V. filiformis*, *V. angustifrons*, *V. Schkuhrii* and *V. curvidentata* have been referred to *V. lineata* as synonyms, and *V. graminifolia* has been reduced to a variety of both *V. lineata* and of *V. curvidentata*. Mettenius* expressed the opinion that *V. graminifolia* and *V. filifolia* were the same species, and figured *V. filifolia* with a cross-section of the leaf. The type of *V. graminifolia* should be found either at the University of Leipzig or in the herbarium of Count du Roemer at Dresden and the type of *V. filifolia* in the Cosson herbarium at Paris. Fée says it is remarkable for its long stipe. *V. Gardneriana* and *V. remota* are too closely allied and need more study; *V. Ruiziana* is said to be a synonym of *V. Moritziana* by Mettenius and if so has priority over that species; *V. scabrida* has not been figured, and is apparently closely related to *V. dimorpha* in size; *V. Deppeana* has been referred to *V. filifolia*, by Mettenius, but is apparently distinct; *V. gracilis* and *V. intramarginalis* should be compared with *V. filifolia*; and *V. longipes* should be compared with *V. Orbignyana.*

Karl Müller† has shown that the character of the scales surrounding the base of the leaves vary in different species, and may

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*Mett. Fil. Hort. Bot. Lips. 25–27. *f. 21, 22.* 1856.

†Bot. Zeitung, **12**: 537–548. *pl. 13.* 1854.

be either entirely parenchymatic, or the cell walls may be thickened evenly, or even papillose. This character he made use of in describing six new species, but he ignored the spores and paraphyses, so that it is hard to compare his species with those described and figured by Fée. Luerssen * followed Mettenius in reducing *V. Deppeana* to *V. filifolia*, in spite of the differences of the scales as figured by Müller, and maintained *V. curvidentata* to which he referred *V. graminifolia* as a variety.

GEOGRAPHICAL DISTRIBUTION

In the following list the type locality is given first, and then the distribution as cited by Fée, the authors of the species and subsequent lists, without any attempt to verify the determinations :

V. lineata, Haiti; West Indies, North and South America, East Indies (?).

V. graminifolia, Brazil; Peru, Mexico.
V. stipitata, Peru; West Indies and South America.
V. Gardneriana, Brazil; South America and Mexico.
V. filifolia, Mexico; Central and South America, West Indies.
V. Ruiziana, Peru and South America. (*V. Moritziana*, Peru.)
V. scabrida, Brazil; Mexico.
V. remota, New Granada, South America and West Indies.
V. Karsteniana, United States of Colombia.
V. gracilis, United States of Colombia.
V. Orbignyana, Bolivia.
V. longipes, Ecuador.
V. intramarginalis, Jamaica.
V. dimorpha, Mexico.
V. curvidentata, Brazil.
V. pachydictyon, South America, Surinam.
V. Deppeana Mexico.

Leaving out of consideration the South American species, it will be found that ten of the above species have been reported from Mexico and the West Indies. Of these the Mexican species are most interesting and need revision. *V. scabrida* and *V. Deppeana* have not been seen in any American herbarium. In *V. scabrida* Fée † gives the length as 90 cm.; this is probably a mis-

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* Luerssen, Fil. Graeff. 92–94. 1871.
† Fée, Mem. des Foug. 3 : 20. 1852.

take for he says it is a small species with short fronds, and it is described in the Synopsis Filicum as two inches long, and Sodiro † says the leaves are 2–6 inches. Specimens labeled *V. dimorpha* collected by F. Müller in 1848–1855, at Orizaba, are in the Columbia University herbarium, but do not answer to the description of this species. Fournier ‡ credits *V. lineata, V. gramifolia* and *V. scabrida* to Mexico, and Fée § lists *V. filifolia* from several Mexican localities and collectors.

We have not studied the Central American species, but we find among the specimens distributed by J. Donnell Smith as *V. lineata*, that no. 811, collected by Turckheim in Guatemala is *V. filifolia* and that no. 7489 collected by H. Pittier in Costa Rica, is probably *V. graminifolia.*

Grisebach ‖ records only one species, *V. lineata,* from the West Indies, which he says occurs in Jamaica, St. Vincent and Barbadoes. Charles Wright collected in Cuba as no. 865, in 1856, two species, *V. filifolia* and *V. lineata,* which were distributed as one. No. 865, of his collection of 1865, is *V. stipitata.* Kunze ¶ records *V. graminifolia* from Cuba.

V. Gardneriana has been collected in Puerto Rico by Blauner and Sintenis, and *V. remota* has also been credited to Puerto Rico. Fée** has reported *V. filifolia* from that Island and *V. lineata* was collected by Sintenis.

Jenman †† has described *V. lineata, V. stipitata, V. remota* and *V. intramarginalis* from Jamaica: the last a new species closely allied to *V. filifolia,* judging by the description and specimens received from B. D. Gilbert; it has triangular spores, but the paraphyses have not been seen. *V. remota* is described as having the venation anastomosing once besides the normal marginal one; this does not agree with Fée's ‡‡ figures, in which the venation is oblique as in *V. Gardneriana.*

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† Sodiro, Crypt. Vasc. Quit. 423. 1893.

‡ Fournier, Miss. Scient. au Mex. et Am. Cent. 114. 1872.

§ Fée, Mem. des Foug. 3: 15. 1852; 11, 13. 1866.

‖ Grisebach, Flora of the West Indies, 674. 1864.

¶ Kunze, Syn. Plant. Crypt. Poepp., Linnaea, 9: 76, 77. 1833.

** Fée, Mem. 11: 13. 1866.

†† Jenman, Syn. List of Jamaica Ferns. Bull. Bot. Dept. Jam. 4: 212. 1897.

‡‡ Fée, Mem. 7: 26. *pl. 30. f. 1.*

Haiti is the type locality for *V. lineata*, but we have never seen a specimen of *Vittaria*, from Haiti or Santo Domingo. Specimens were distributed from Berlin, determined by Kuhn as *V. graminifolia* var. *filifolia* collected by Hahn on Martinique. *V. filifolia* has been credited by Fée to Guadeloupe collected by L'Herminier, and *V. lineata* was collected on Trinidad by Fendler. A dwarf form of *V. lineata* also occurs in the Bahamas. Mr. Britton has collected sterile specimens of *V. filifolia* on St. Kitts.

HISTORY OF THE GAMETOPHYTE

The statement has been made that the gametophyte of *Vittaria lineata* has not been described, and so far as we knew, the gametophyte was unknown in all the other American species. Professor Underwood has called our attention to a copy of Lindenberg's monograph of the Ricciaccae [*] which formerly belonged to Austin, in which Austin had written opposite the description of *Riccia reticulata*, "a species of *Vittaria*." Lindenberg had classed it among the "*Species dubiae*." *Riccia reticulata* was described by Swartz [†] as having the fronds laciniate, glabrous and reticulate. He referred to it specimens from the Island of [New ?] Providence described by Dillenius [‡] as *Lichenoides gelatinosus tenue reticulatum*. Swartz [§] stated that it grew on trees covered with mosses in the mountains of Jamaica, and described it as follows:

RICCIA ? RETICULATA. "Frons membranacea, plana, difformis, lobata, laciniata, latitudine unciales, laciniis linearibus, saepe bipartitis, pollicaribus, glabra, obscure viridis, tenuissime reticulato-venosa. Obs. Ob texturam teneriorem Hepaticis conjungere malui quam Lichenibus." The illustration given by Dillenius is simply an outline, but the figure and description given by Lindenberg agree exactly with no. 327 from St. Kitts, collected by Mr. Britton in 1901, which he also took for a hepatic. It proves to be the gametophyte of a species of *Vittaria*, probably *V. filifolia*, the leaves of which were collected in another ravine but were not

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[*] J. B. W. Lindenberg, Mon. Ricc. 501. *pl. 36. f. 1–4.* 1836.

[†] Swartz, Prod. Ind. Occ. 146. 1788.

[‡] Dillenius, Hist. Musc. 1: 138. *pl. 19. f. 21.* 1741.

[§] Sw. Fl. Ind. Occ. 3: 1883. 1806.

found with or near no. 327. This implies an independent existence for the gametophyte, which agrees with that of *V. lineata* in being proliferous by its septate gemmae and in being lobed, but it differs in the shape and size of the thallus, the shape of the lobes, and the cellular structure. However, the specimens were dried when examined, as were Lindenberg's, whose description and figures were drawn from the type of *Riccia reticulata*, belonging to Swartz, which had been collected thirty years at the time the drawings were made. The cell contents had shrunk, forming a fine mesh of the strings of protoplasm, radiating from the nucleus of each cell, which gave the dotted and reticulated appearance described by Swartz as visible with a hand lens. The gemmae also must have disappeared, for they are neither figured nor described. In the specimen from St. Kitts, they are most abundant on the truncate ends of the long, narrow lobes.

That the gametophyte of *Vittaria* maintains an indefinite and independent existence, without forming the sporophyte, seems to be an established fact. It is autoicous, the archegonia being borne mostly on the thallus, and the antheridia on the gemmae. In a climate where violent winds and heavy rains are frequent the gemmae would be liable to be detached without fertilization having taken place. Dr. Campbell reports having seen in Jamaica, enormous sterile prothallia, forming circular mats at least three inches in diameter on the trunks of palms, and resembling a liverwort. Dr. Campbell * has also described and figured a prothallium collected in the Sandwich Islands, similar to that of *Vittaria*, which he has referred to a species of *Hymenophyllum*. He states that they lived for two or three years in his laboratory. He also states that "Goebel has described in *Vittaria* a type of prothallium recalling that of *Hymenophyllum*, both in its large size and extensive branching." From our present knowledge we are inclined to believe that Campbell has mistaken the genus, and that these prothallia should be referred to *Vittaria*, probably to *V. elongata*.

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* Campbell, Mosses and Ferns, 362. *f. 187, 188.* 1895.

Synopsis of the North American Species of Vittaria*

- Stipes green ; 1–2 cm. long, margins recurved when dry.
  - Spores reniform, paraphyses enteriform ; scales papillose, serrate.
    - Leaves 30–120 cm. long, 2–3 mm. wide, pendent. *V. lineata.*
    - Leaves 10–15 cm., narrowly linear, erect. *V. graminifolia.*
  - Spores tetrahedral ; scales smooth. *V. intramarginalis.*
- Stipes green or yellow, 10–15 cm. long ; margins revolute.
  - Spores tetrahedral, paraphyses mastoid-claviform, scales smooth, entire. *V. filifolia.*
  - Spores tetrahedral ? ; paraphyses enteriform ? ; scales papillose, aristate, serrate. *V. Deppeana.*
- Stipes green, short ; leaves 4–16 cm. long.
  - Spores tetrahedral ; paraphyses cucullate ; scales dentate. *V. scabrida.*
  - Spores ? ; paraphyses ? ; scales aristate, papillose, entire. *V. dimorpha.*
- Stipes brown or black, 2–9 cm. long ; margins flat ; spores reniform.
  - Leaves 20–30 cm. long ; paraphyses cyathiform.
    - Leaves 7–9 mm. wide ; rhizome creeping. *V. Gardneriana.*
    - Leaves 6–12 mm. wide ; rhizome erect. *V. remota.*
  - Leaves 1 meter long, 3–5 mm. wide ; paraphyses pyriform. *V. stipitata.*

VITTARIA LINEATA (L.) J. E. Smith.

Lingua cervina longissimus & angustissimis foliis. Plumier Fil. Am. 123. *pl. 143.* 1705.

Phyllitis lineata, graminis folio longissimo. Pet. Fil. 126. *pl. 14.* 1712.

Pteris lineata L. Sp. Pl. 1073. 1753.

Vittaria lineata J. E. Smith, Mem. Acad. Roy. Sci. Turin. **5**: 413. 1793.

V. lineata Swartz, Schrad. Journ. **2**: 72. 1800; Syn. Fil. 109. 1806.

V. filiformis Cav. Praelect. Bot. 270, 671. 1801; Willd. Sp. Pl. **5**: 405. 1801.

V. angustifrons Michx. Flor. Bor. Am. **2**: 261. 1803; *non* Bory. Itin. **2**: 325. 1804.

V. Schkuhrii Raddi, Fil. Bras. 51. 1819.

Taeniopsis lineata J. Smith, Hook. Journ. Bot. **4**: 67. 1842.

V. lineata Sw. Fée, Mem. Fam. Foug. **3**: 17. 1851; Hook. Sp. Fil. **5**: 180. 1864; Hook. & Baker, Syn. Fil. 396. 1874; in part; Eaton, Ferns of N. Am. **1**: 289. 1879; Sodiro, Crypt. Vasc.

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* This synopsis is necessarily incomplete, owing to deficiencies in the descriptions, and lack of knowledge of the types.

Quit. 420. 1893; Jenman, Bull. Bot. Dept. Jamaica, **4**: 251. 1897.

V. curvidentata CM.? Bot. Zeitung, **12**: 546. 1854.

Linnaeus founded this species on the plate and description given by Plumier, cited Santo Domingo for the type locality, and adopted the specific name from Petiver's description, according to citations. Plumier figured the species very clearly on a large quarto plate, and described it in French and Latin; as this work is rare in America, it seems desirable to quote his description.

PLANCHE CXLIII.

"Langue de Cerf à feuilles tres longues et tres étroites. La racine de cette Langue de Cerf n'est proprement qu'un amas de plusieurs pédicules pourris mélez de plusieurs petites fibres roussatres, & toutes couvertes de mousses: elle jette quantité de feuilles tres longues & tres étroites, car elles n'ont pas plus d'une ligne & demie de large, sur environ trois pieds de longueur: elles sont fort pointuës, solides, épaisses comme du parchemin, unies, & d'un vert assez gay par devant, mais toutes traversées de biais en derriére par quantité de petites nervûres tres proches les unes des autres: outre ce elles ont aussi le bord replié en dedans, & couvrent tout le long de leur pli un nombre infini de tres petites vessies noiratres.

J'ay rencontré cette Plante en plusieurs endroits des Isles de l'Amérique, particuliérement à la Source de la Riviére Froide, vers le quartier du Port de Paix, dans l'Isle Saint Domingue."

Plumier's description agrees very well with the general acceptance of the characters of the species. It must be taken as the type of the genus, for J. E. Smith founded the genus on *Vittaria lineata;* there is no reason for taking up *Taeniopsis* of J. Smith, nor for citing Swartz as the authority for the species. It has been found that the sporophyte only has been described, and in the case of some of the synonyms, in the briefest and most superficial manner, giving only macroscopic characters. It follows that further study may reinstate some of these as species. This may be true of *V. filiformis* Cav. "foliis filiformibus, tripedalibus, glaucis." Fructification as in *V. lineata;* habitat Peru, or of *V. angustifrons* Michx. "frondibus simplicibus, integerrimis angustissime longissimeque linearibus, debilibus. Fructification linea continua sub replicato frondis margine, ab istius sinu distincta. Hab. in Florida juxta ammem Aisa-hatcha."

It is not likely that the Florida species will be found to be distinct from the West Indian, but until the gametophyte of both is known there is still this possibility. Fée has suggested it in his memoir, as he states that he has seen in Willdenow's herbarium a specimen of *V. lineata* collected in Jamaica by Swartz, which had bright amber-colored sporangiasters, with the terminal cell mastoid or elongated pyriform, and that he also had a specimen collected in Florida from Richard which has ribbon-like sporangiasters. He believed the two plants were distinct species. Yet he contradicts himself in his description of *V. lineata* which he attributes to Swartz and states that the sporangiasters are vittate, with dilated colored contorted apex. He also states, that although *V. lineata* is the oldest species, there exists the greatest vagueness and uncertainty in the descriptions and that he considers it to be exclusively American. Unfortunately, he did not figure *V. lineata*, only the variety *graminifolia* Kaulf, without stating whether he had seen the types. He also took up *Taeniopsis*, as a subgenus, and referred *V. lineata* to it; we have shown that this position is untenable. In this he was followed by the authors of the Synopsis Filicum, who also reduced *V. filifolia* and several Asiatic species to *V. lineata*. We have already shown in the key, that *V. filifolia* has the characters of a good species, but we have not studied the exotic species.

There is another character of *V. lineata* which has been overlooked, probably because only mature, fruiting specimens are generally collected. This is the first leaf stages of the plant, which are quite distinct in size and shape, as may be seen by the plate. Jenman has described similar leaves in *V. intramarginalis*, of which he says: "A small plant which much resembles seedlings of *V. lineata* from which it is readily distinguished by the distinct small barren fronds (not however present in full-grown plants)." *

As none of the descriptions have been found to be complete, we have framed one from fresh material, and have necessarily been obliged to limit it to Florida specimens.

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* Bull. Bot. Dept. Jam. 4: 213. 1897.

Gametophyte capable of indefinite growth and duration, branching irregularly or bifurcating into numerous lobes, which are proliferous by gemmae borne from podetia, usually on marginal cells; serving to propagate the plant asexually, and also rendering it autoicous by bearing antheridia; archegonia borne on the under side of the thallus.

Sporophyte forming rudimentary leaves, 1–4 cm. long, spathulate, with a single central vein ending below the apex or forming a loop in the rounded apex; rhizome short, divided, creeping, sparingly, densely covered with lanceolate, serrate, filiform-pointed scales, with papillose walled cells; leaves dark green or glaucous, two-ranked, crowded in dense compact pendent tufts, often 2–3 ft. long, 2–3 mm. wide, coriaceous, three-veined, the midvein pinnate and anastomosing with the lateral veins, with a deep sporangial groove over each lateral vein, in which the stomata are borne, paraphyses branching twice, usually forking, cylindric, the end cells curved and larger, brown; spores reniform, smooth, .027 × .054 mm.

Florida, as far north as St. Augustine; also credited to South Carolina by Fée and Hooker, but probably by mistake. Presumably the same as the West Indian species, of which the gametophyte is still undescribed, and the microscopic structure imperfectly known.

GAMETOPHYTE *

PROTHALLIUM.—(*F. 1–38*). The gametophyte of *Vittaria lineata* is an irregularly branched prothallium (*f. 1–4*), consisting of a single layer of distended cells containing chlorophyl (*f. 14, 15*). New prothallia may arise from any one of the marginal cells, or from two or more of the lamellar cells of the prothallium (*f. 5–8*). This capacity for vegetative reproduction by proliferation of the prothallus must be of great service to this species which is epiphytic on trees and much subject to the attack of small animals. Almost any fragment of the prothallus might continue growth independently.

The younger portions of the prothallia assume a horizontal position at right angles to the trunk of the tree to which they are attached, extending to a distance of 9 mm. in some instances. As the formation and growth of rhizoids proceeds successively in

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* The material on which the anatomical study is based was collected by Miss Abbie M. Small at St. Augustine, Florida, 22 Feb. 1901, on the bark of the palmetto.

these younger regions, however, the rhizoids penetrate the bark of the tree and then draw the prothallus down against it. The rhizoids may be formed in clusters (*f. 1*) from an undifferentiated cell of the prothallus, or from a proliferation consisting of a single cell. Rarely more than one rhizoid originates from a single cell. The rhizoids are long colorless structures rarely branching near the apex, and sometimes distended at the base (*f. 13*).

The prothallium is occasionally monoicous-autoicous, but more frequently pseudo-dioicous with the antheridia and archegonia produced indirectly from the same plant. In such instances the archegonia are borne on the main prothallium, which also produces gemmae from which antheridia originate.

Barrel-form or spherical sterigmata containing chlorophyl arise from the margin, apex and occasionally from the middle of the prothallus bearing gemmae in great numbers. A sterigma may give rise to one or several gemmae, and these gemmae may divide repeatedly before falling off. The gemmae may either lie on the surface of the prothallus or stand out from it after the manner described by Goebel, who found the first position assumed in *Vittaria elongata* and the second in *Monogramma paradoxa* (*f. 19–25*).* A sterigma may give rise to several sterigmata before the gemmae are produced (*f. 22*). The gemmae are very similar to those of *Vittaria elongata* as described by Goebel and are in the form of spindles composed of 5 to 11 moniliform cells (*f. 28, 29*). The terminal cells may give rise to rhizoids, but these and the antheridia may be produced from any one of the cells of the spindle (*f. 30–33*). The gemmae produce prothallia in various ways, and also may develop other gemmae, and antheridia (*f. 33–37*).

ANTHERIDIA.— The antheridia are produced either directly from one or more cells of the gemmae (*f. 39, 40*), or on the lower surface of the prothallium, the margin and occasionally on the upper surface. A prothallium sometimes bears both antheridia and archegonia (*f. 56*). The development of the antheridia is as follows : A cell in any one of the positions named sends out a protuberance containing chlorophyl which becomes club-shaped

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* Goebel, K. Morphologische and Biologische Studien. Ann. Jard. Bot. Buitenzorg, 7 : 78–107. 1888.

and then cuts off the terminal portion by a partition wall, making two cells of unequal size, the lower being much larger (*f. 40b, 41*). The apical cell becomes almost spherical, and the next wall formed in it is funnel-shaped, connecting with the wall previously formed in such manner as to separate a central cell. A third wall is now formed in the apical portion of the peripheral cell cutting off a cap cell shaped like a watch glass (*f. 43–45*). The antheridium now consists of four cells, a pedestal cell, a hemispherical central cell enclosed by a cylindrical peripheral cell, and crowned by a cap cell (*f. 42*). Further division occurs in the peripheral cell in rare instances. The first division wall in the central cell is generally longitudinal, and the second one is at right angles to it, and this sequence is followed during the formation of an indefinite number of mother cells (*f. 42, 44*).

An antherozoid is produced in each mother cell. The connecting walls of the mother cells dissolve and the antheridia lie free in the antheridium (*f. 48a*). When the antheridium is ripe the antherozoids are ejected by the swelling of the peripheral cell and of the upper contiguous portion of the pedicel (*f. 49*) which is pushed up into the antheridial cavity; the cap cell is ruptured either at the center or at one side. When the antherozoids escape from the antheridium they are enclosed by a thin membrane, which is thrown off shortly after their liberation. The antherozoids uncoil with a whip-like motion, curling and uncurling very rapidly during a few seconds, the movements of the cilia increasing in rapidity. The action of the cilia propels the antherozoid at a comparatively great speed, and they remain active for some time (*f. 50*).

Four antheridia were seen in the act of discharging the antherozoids: the latter escaped in rapid succession, although two or three came out together in some instances. It was not difficult to count the emerging antherozoids, and two antheridia were found to contain twelve and another twenty-four. One antheridium was emptied in a little more than a minute, and the antherozoids burst the enclosing membrane in forty seconds or less after emergence. The entire number (twelve) had freed themselves in this manner in less than two minutes from the time action began. A portion of the mother cell in the form of a hyaline sphere with a granulated center was carried by the antherozoids to which it was still attached forty-five minutes later.

Archegonia (*f. 57–60*).—The few archegonia that were seen occupied positions similar to those of *Vittaria elongata* as described by Goebel, being borne on the under surface of the prothallium, and also on the small lobes among the rhizoids. The archegonia have a slightly curved neck, although the number of cells shown on the concave and convex surfaces are the same, being four or five in number.

THE SPOROPHYTE

The sporophyte generally remains attached to the gametophyte for some time after its formation (*f. 89–91*).

RHIZOME.—The main axis of the sporophyte consists of a dorsiventral rhizome with short internodes bearing the tufted leaves in two ranks, the roots are very numerous and completely clothe the lower surface of the rhizome. The growing portion of the rhizome appears as a fleshy green bulbous formation with a conical apex, completely enveloped in long brownish scales (*f. 58, 59*). Glands, similar to those of the leaves and hairs, resembling those of the root are also present. The apical cell is wedge-shaped and the differentiation of the tissues follows quite closely the advance of the apical meristem (*f. 61, 62*).

In the earlier stages of development of the stelar tissues they appear as a cylinder of thin-walled elements (*f. 63*) in which the scattered groups of protoxylem soon appear (*f. 64d*). The metaxylem next appears as a complete cylinder of scalariform tracheids (*f. 65*). The metaphloëm is much more highly developed externally to the cylinder and consists of numbers of sieve cells separated from the metaphloëm and from the pericycle by parenchymatous elements. The pericycle is well defined (*f. 65a*). As the cylinder is traced upward along the stem, gaps appear where an entire segment of the fibrovascular ring is sent out into a leaf (*f. 66*). The external cortex, which is composed of extremely thin-walled elements in the younger specimens, becomes somewhat thickened and perforated in older organs. The epidermis does not participate in the thickening however.

ROOTS.—Roots are produced in great numbers from the rhizomes opposite the leaves and are usually quite advanced in development as soon as visible. Hairs are produced profusely, originating .5 mm. from the tip. The roots quickly penetrate the bark of the palmetto tree to which the plant is attached, and as they are exposed to the light in various places form chlorophyl.

The root hairs measure from 0.6–4.5 mm. in length and .0115 .0299 in width. The hairs seldom form cross walls but occasionally branch near the apex, although the branches do not attain any considerable length. The roots branch profusely: one 13 mm. long produced 6 branches and 1 branch 7 mm. long produced 3 branches (*f. 88*). The central cylinder of the root is apparently diarchic (*f. 86, 87*) and the endodermis is plainly differentiated. The cortex consists of 4–6 layers of large cells with strongly differentiated walls; the outer rows show this striation less plainly however. The outer layer immediately internal to the epidermis contains large numbers of crystalline bodies connected with their inner walls (*f. 87, 88*). The epidermal cells are large, the thin outer walls being pressed inwardly in many instances.

STERILE LEAVES. — The leaves of *Vittaria lineata* show progressive variation in form and venation (*f. 89–95*). Those which arise earliest are spatulate and have a single central vein, later they show a branching venation (*f. 89, 93*). The laminar portion of the first leaves is flattened and the cross section does not show such complete dorsiventral differentiation as may be found in the leaves arising later. They are but slightly curved when they emerge from the scales, and the curvature soon disappears. The epidermal cells are somewhat longer than broad with wavy walls (*f. 97*). Among these cells are a few elements with pointed ends and wavy walls (*f. 98a*), which are most abundant near the fibrovascular bundles. The epidermal cells generally contain chlorophyl with the exception of the hyaline border. The latter is composed of elongated elements with oblique end walls (*f. 96a*). The epidermal cells of the petioles are prosenchymatous and rarely have wavy walls. Stomata occur on the under side of the lamina but do not occur immediately external to the veins. Numbers of club-shaped bodies, composed of three cells (*f. 97a*), resembling glands, are to be found on both surfaces. Scales arise on the basal portion of the earlier leaves directly external to the bundles, while these formations occur more abundantly on leaves developing later yet they are rarely over a bundle (*f. 99*).

Leaves formed from the rhizome at a later stage of growth show a variation in form from oblanceolate to linear (*f. 94, 95*). Such leaves have a vein extending through the middle and one along each margin with numerous anastomosing branches. Glands and scales are somewhat more numerous and the epidermis contains but little chlorophyl.

The latest leaves formed show the greatest length and are ridged over the nerves on the upper surface, bearing scales between the central and marginal veins (*f. 109*). These scales, while no more numerous on the upper surface than on the lower, are frequently larger, measuring as much as 1.9 mm. in length. It is found that the regularity of arrangement of the stomata and the increase of the ridges of the leaves increases as a form approximate to that of the adult is reached (*f. 104*).

SPOROPHYLLS.—The sporophylls are long linear coriaceous leaves with a short petiole exhibiting the epinastic growth of so many ferns. The numerous scales which doubtless serve as a protection to the unrolling leaves persist in mature forms (*f. 109–111*). The dorsal surface is marked by two deep grooves immediately external to the lateral veins, and these grooves contain the stomata, glands, sporangia and accompanying paraphyses (*f. 104–109*). The two fascicles of stelar elements given off from the edges of the incomplete cylinder in the foliar gap in the rhizome do not fuse until some distance in the petiole has been traversed, and the lateral branches are given off before the fusion is complete (*f. 102, 103, 1, 6, 7*). The lateral veins and the central vein are connected by various anastomosing branches (*f. 102–106*). The central vein runs quite to the apex of the leaf (*f. 94–95*), while the lateral veins end free a short distance below the tip or terminate in an anastomosing branch (*f. 103–109*). The vascular elements of the leaves are the same as the rhizome in composition, and the bundles are enclosed in a sheath of two to six layers of cells with perforated walls (*f. 108d, f*). The mesophyll of the upper side of the leaf is closely packed and contains a large amount of chlorophyl, giving this surface a dark green color (*f. 114*). The mesophyll of the lower side is more loosely arranged and contains less chlorophyll (*f. 116*).

The epidermis is composed of elements with very thick walls except in the grooves (*f. 114–119*). A reduction in size is noticeable over the middle and lateral veins and at the margins of the leaves. Chlorophyl is to be found in the epidermal cells in the grooves but seldom elsewhere. The epidermis of the grooves is uniformly thin-walled and gives rise to stomata and glands ; the latter are also found over the entire surface of the sporophyll. A narrow band of two to six rows of cells immediately external to the bundle underlying the groove bears the sporangia and paraphyses (*f. 123c*). One to four layers of prosenchymatous cells are to be seen underneath the epidermis of the upper side of the leaf (*f. 114b*). Similar elements are to be found on the lower side of the leaf between the grooves, and these cells are somewhat larger than those of the upper surface (*f. 116b*). These hypodermal prosenchymatous elements are generally free from chlorophyl and are separated by numerous large air-spaces, giving the region a light gray color. The absence of these elements in some instances cannot be accounted for.

SCALES. — Scales are most abundant on rhizomes and least so on the leaves produced earliest (*f. 72–74*). The first leaf formed may bear but one scale while the later leaves may be covered with them. The scales are never more than one cell in thickness and nine or ten in width, attaining a length of 5 mm. and a breadth of .4–1.1 mm. The growth of these structures is long-continued and the basal cells may be in a state of division while the apical portion may be withered and brown (*f. 75–82*). The thin walls of the younger cells at the base measure 1.9 μ in thickness which later increases to as much as 19.2 μ, which is a most noticeable multiplication. This thickening is confined to the cross walls, the outer walls not participating in this increase (*f. 76a, 81, 82a*). The thickened walls show great numbers of dots or minute papillae, which are most numerous in scales borne on the stems and are not easily found in scales of the earlier leaves. Both the thickening of the walls and the formation of papillae are less marked in the marginal region of the scales.

STOMATA. — Stomata are present only in the grooves of the leaves. In the formation of these organs the upper portion of an epidermal cell is cut off by a wall having a horse-shoe shape in surface view (*f. 124b*). The newly formed cell appears to contain chlorophyl and the nucleus increases in size while the protoplasm becomes granular (*f. 125c*). This mother cell divides along a line parallel to the long axis of the epidermal cell from which it arose (*f. 126e*). The later stages of the splitting of the wall and the development of the guard cells follows in the usual manner (*f. 127*). The original epidermal cell from which the stomatal mother cell was cut off undergoes some alterations and it is difficult to distinguish it from its neighbors (*f. 121, 122*).

GLANDS. — The glands are club-shaped, measuring about .08 mm. in length and consist of three cells. These organs originate from the upper or apical end of the epidermal cells on both surfaces of the leaves and are inclined toward the apex of the leaf. The cross walls become suberized in a few cases and turn a rich golden brown (*f. 97, 110, 112, 128*).

SPORANGIA. — The sporangia and the attendant paraphyses are borne on the epidermal cells in the bottom of the two grooves on the under sides of the sporophyll (*f. 123, 129*). The margin of the leaf and the walls of the groove fold over and cover the sporangia and form a false indusium. An examination of any single sporophyll will show the presence of sporangia in all stages of development and these bodies are produced in such great profusion that many are not brought to full development. The principal features in the development of the sporangia are as follows: An epidermal cell sends out a tubular extension in which a wall soon appears parallel with the outer wall of the epidermis (*f. 130, 131, 136*) and a second wall cuts off a portion of the tube which becomes the sporangial stalk. Occasionally two or more transverse walls are formed in the basal portion of the structure before the terminal portion constituting the sporangial mother cell begins to divide (*f. 130*). Longitudinal divisions in the basal portion take place later. The sporangial mother cell first divides obliquely (*f. 130, 133b*) and then a second wall is formed at right angles to this (*f. 130, 134c*). A third and fourth division takes place resulting in the final formation of four outer cells which will constitute the wall of the sporangium and a fifth central tetrahedral spore mother cell (*f. 130, 136d*). The cells which are to form the annulus divide by parallel walls into 13–15 cells (*f. 131*) which extend from the stalk at the base of the sporangium over the back a short distance down the other side, where they join with the thin-walled cells which connect with the lip cells (*f. 133b*). When the sporangium is young, these cells have thin walls and become inflated and raised above the other cells (*f. 133a*). These cells contain chlorophyl which is often retained until the spores are fully formed.

As the sporangium ripens, the walls of the annulus thicken considerably with the exception of the dorsal wall, becoming cuticularized (*f. 134a*) and take on a golden brown color which later turns to a dull brown. The dorsal walls turn a dull yellow, and frequently bend back toward the inner walls of the cells, so that the cross walls form ridges along the annulus of the old sporangium. The other cells of the sporangium also divide. The frontal cells are generally eight in number and extend from the annulus to the pedicel at the base of the sporangium. They are composed of two kinds of cells, those whose walls do not thicken to any extent—called connective cells—and those whose walls thicken considerably forming the lips. There are four lip cells and they occupy the center of the row of seven or eight, occasionally nine (*f. 133c, 134c*). These lip cells differ greatly from the other cells of the sporangium, having a short longitudinal diameter and a very long radial one. They are connected with the annulus by one to three thinner walled cells, and with the pedicel by two (*f. 133bb, 134bb*). The two lip cells, which occupy the center of the group of four, frequently thicken their walls to a greater extent than the other two, and it is between these two cells that the sporangium opens when the spores are ripe (*f. 134*), the slit extending back generally in a straight line through the thin walls of the other cells almost to the annulus. The central tetrahedral cell of the sporangium divides by oblique walls until another tetrahedral cell has been formed inside of it (*f. 130 9f*), this inner cell dividing up into the spore mother cells and the cells between this cell and those constituting the sporangial wall form the tapetal cells (*f. 130, 9g*), which dissolve after a time so that the spore mother cells lie free in the sporangium. Each mother cell divides into four spores. These ripe spores are reniform with a smooth surface.

PEDICEL.—The pedicel is long and consists of three or more cells, though only one cell wide until near the sporangium, where the first longitudinal walls are formed (*f. 139, 9, 133e, 134e, 135, 1, 2*); here it is generally two cells in width, less often three, though at the base of the sporangium there are almost always three cells. These small cells are formed at or near the front of the sporangium (*f. 133, 134*). As the sporangium ripens all the cells of the upper part of the pedicel become inflated and throw the sporangium back (*f. 134*), so that when the split occurs, and the lip cells open by the everting of the annulus, the spores have a less interrupted access to the opening of the groove, their original position being such that did they keep it during the discharge of the spores many of them would become entangled among the branches of paraphyses from which they would be powerless to escape.

PARAPHYSES. — The paraphyses develop before and with the sporangia and frequently attain a large size while the sporangia are still very immature. They are always multicellular and branched, except when young (*f. 129*); they grow to some length as a single cell before they branch into two or three divisions (*f. 129, 136–139*), the first cell of each forming a stalk. The round branches generally branch in their turn. The cells are two or three times longer than wide, each containing a good-sized nucleus and some chlorophyl; as they grow older they become discolored and shrivel up. The branches terminate in cells which are always very long, much wider at their apex and generally curved (*f. 136, 137*).

SUMMARY

The gametophyte of *Vittaria lineata* is an irregularly branched, pseudo-dioicous prothallium, bearing the archegonia and giving rise to gemmae which bear the antheridia and also produce new prothallia.

The *antheridia* are produced in great numbers, rarely on the same prothallium with the archegonia. From twelve to twenty-four antherozoids are produced in one antheridium and the opening occurs in the center of the cap cell, or at its junction with the peripheral cells. It ruptures by the swelling of the peripheral cell or cells, and the portion of the pedicel immediately under the antheridium; this drives the wall that separates them up into the antheridial cavity, and ejects the antherozoids.

The *archegonia* occur among the rhizoids near the margin, on the under side of the older portions of the prothallium; also on specialized branches which are formed at the margin of the main prothallium. They have slightly curved necks, but the rows of cells in both the anterior and posterior sides are equal in number.

The *rhizoids* are unicellular, simple or branched, structures and are produced either directly from a cell of the prothallium or by the formation of an initial cell.

The *sporophyte* consists of a creeping, dorsiventral rhizome, bearing its leaves ordinarily in two ranks. It frequently branches and the internodes of both stem and branch are so short that the leaves appear crowded together. The growing point appears as a fleshy green bulb which is densely covered by brown scales having a structure peculiar to this genus. The *rhizome* has a wedge-shaped apical cell and a concentric, tubular bundle, with foliar-gaps associated with the leaf-bundles.

The *roots* are produced near the growing tip and are usually twice as numerous as the leaves. They have a normal root-cap and an axial diarch bundle, the two groups of xylem are generally united after a time by large tracheids. The walls of the parenchymatous cells are strongly striated and in the young roots there are crystalline substances formed against the inner walls of the cells immediately under the epidermis. The roots branch frequently and the branching appears to bear a definite relation to the original xylem groups of the diarch bundle.

There are three kinds of *leaves;* first, the rudimentary ones which are spathulate and long-petioled, usually with a single central vein; second, the young sterile leaves, which are short-petioled, oblanceolate to linear, and show all gradations of venation, from the simple central vein to the three veins which characterize the sporophyll. The sporophylls are short-petioled and linear.

The *venation* of the leaf arises from two primary bundles, each giving rise to one smaller one which become the lateral bundles of the leaf. The larger portion of the two primary bundles unite to form the central bundle; these three bundles run parallel with the long axis of the leaf and are united with each other at intervals by small strands taking an oblique apical course from the central one to each lateral one.

The *sporophyll* has two deep dorsal grooves, running parallel with the lateral bundles and just over them; in these grooves occur the stomata and glands, and in them are borne the sporangia and paraphyses. All the leaves bear scales which show a higher order of development as the leaves approach the type of the sporophyll.

The *sporangia* are long-stalked and spherical with an annulus of about fourteen cells, four lip cells and four connectives. The spores are reniform with a smooth outer coat. The smaller cells on the pedicel at the base of the sporangium become very much inflated and when the sporangium opens they tilt it back, thus aiding in the escape of the spores. The paraphyses are long-stalked, branched and multicellular; the terminal cells being longer, curved, and enlarged at the apex.

Explanation of Plates

The figures were drawn with a magnification twice that indicated and the resulting figures were reduced one half.

PLATE 23

FIG. 1. Under side of a prothallium, showing its irregular branching: *a*, rhizoids; *b*, sterigmata. × 7.

FIG. 2. A young prothallium showing sterigmata along margin. × 7.

FIG. 3. Prothallium showing manner of branching at apex. × 6.

FIG. 4. An older piece with the archegonia just forming. *a*, rhizoids; *b*, archegonia; *c*, sterigmata; *d*, young sporophyte. × 9.

FIG. 5. Margin of prothallium at apex, showing branching and *b*, sterigmata. × 25.

FIGS. 6, 7. Young prothallia starting from margin of old ones. × 120.

FIG. 8. A young prothallium, *a*, with three growing points starting from a single cell of an old prothallium. × 25.

FIG. 9. Four marginal cells of the prothallium, each one giving rise to a rhizoid. × 87.

FIG. 10. Same as Fig. 9. × 87.

FIG. 11. A rhizoid formed from an initial cell. × 87.

FIG. 12. A rhizoid formed from two cells. × 120.

FIG. 13. Rhizoid with inflated cell. × 87.

FIG. 14. Side view of portion of prothallium showing inflated cells; *a*, rhizoids; *b*, sterigmata with gemmae and also curved apex. × 25.

FIG. 15. Portion of prothallium with apex recurved; gemmae are shown at the margin. × 25.

FIG. 16. Apex of prothallium, *a*; *b*, sterigma and gemmae; *d*, filament growing from the margin; *e*, sterigmata; *f*, young prothallium with a sterigma and gemma; *g*, growing end of filament. × 87.

FIG. 17. A prothallium showing eleven growing points.

FIG. 18. A filament from a margin of a prothallium. × 45.

PLATE 24

FIGS. 19–22. Apex of prothallia showing sterigmata and gemmae. × 87.

FIG. 23. Marginal cell, sterigmata and gemmae. × 120.

FIGS. 24–26. Prothallia showing many-celled gemmae. × 25.

FIG. 27. Gemmae. × 87.

FIG. 28. Gemmae of six cells: cells *a*, *a* forming rhizoids. × 120.

FIG. 29. Same as Fig. 28, only older. × 87.

FIG. 30. A gemma of which one cell has sent out a filament of three cells and an antheridium. × 87.

FIGS. 31, 32. Gemmae with rhizoids. × 35.

FIG. 33. Gemma, with an antheridium, *a*, a rhizoid at each end and small aprothallium originating from two cells. × 45.

FIG. 34. Gemma, with rhizoids and prothallium. × 35.

FIG. 35. Gemma with a young prothallium originating from a single cell. × 87.

FIG. 36. A gemma with two withered antheridia, *a*, *a*, and a young prothallium, from the margin of which have arisen three prothallia. × 35.

FIG. 37. A gemma of five cells, bearing two rhizoids and two prothallia, the older one producing sterigmata and branching in two places. × 25.

FIG. 38. Portion of the apex of the parent prothallium with two filaments: one still growing and bearing an antheridium, *a*, and a rhizoid, *b*, and the other filament (broken) and bearing two rhizoids. × 35.

PLATE 25

FIG. 39. Gemma showing an antheridium, *a*, as a small protuberance from one of the cells; the next cell has given rise to a filament of two cells, *b*; *c*, *c*, rhizoids. × 87.

FIG. 40. Gemma with an antheridium, *a*, showing first wall, *b*; *c*, nuclei; *d*, chlorophyl. × 120. In places the gemma is more than one cell wide.

FIGS. 41–49. Stages in the development of the antheridia and antherozoids.

FIG. 41. *a*, Nuclei. × 210.

FIG. 42. *a*, Peripheral cell; *b*, cap cell; *c*, central cell dividing into the mother cells of the antherozoids. × 210.

FIGS. 43–45. Showing the different ways the walls may be formed, in tiers or obliquely; *a*, central cell. × 120.

FIGS. 46, 47. Looking down on the antheridium, showing the mother cells, *a*. × 210.

FIG. 48. A ripe antheridium with the mother cells, *a*, lying free, each one containing an antherozoid. × 210.

FIG. 49. An antheridium with two antherozoids still inside ; *a*, ruptured cap cell ; the antheridium also showing the inflated peripheral cell, and inflated upper portion of the pedicel. × 210.

FIG. 50. Three antherozoids, *a* ; *b*, cilia ; *c*, portion of mother cell. × 600.

FIGS. 51, 52. Two antheridia consisting of more than one peripheral cell. × 210.

FIG. 53. Gemma with three antheridia, one in the act of discharging the antherozoids ; *a*, rhizoid. × 88.

FIGS. 54, 55. Gemmae with antheridia, *a*, and rhizoids, *b*. × 120.

FIG. 56. An antheridium from near margin of parent prothallium ; *a*, antheridium ; *b*, pedicel. × 210.

FIG. 57. Under side of wing of prothallium showing archegonia, *a*, *b*, the four stigmatic cells. × 87.

FIG. 58. A prothallium with young sporophyte ; *a*, prothallium ; *b*, archegonia ; *c*- first leaf of young plant ; *d*, root ; *e*, root hairs ; *f*, foot, *g*, scales around the growing tip of rhizome and next leaf. × 7.

FIG. 59. Wing of a prothallium with three young archegonia, *a*, and sporophyte, *b*. × 5.

FIG. 60. *a* of Fig. 59 magnified 35 times, to show young archegonia, *b* ; *c*, foot imbedded in the calyptra ; *d*, rhizome ; *e*, root.

PLATE 26

FIG. 61. Longitudinal section of rhizome near apex, *a* ; *b*, young leaf ; *c*, scales. × 12.

FIG. 62. A portion of the same showing the differentiating tissues : *a*, apical portion ; *b*, epidermis ; *c*, cortical parenchyma ; *d*, vascular bundle ; *e*, medullary parenchyma ; *f*, young scales. × 120.

FIG. 63. Cross section of rhizome near tip, *a*, cortex ; *b*, meristem of bundle ; *c*, medullary parenchyma. × 120.

FIG. 64. The same further from tip, *a*, cortex ; *b*, medullary parenchyma ; *c*, phloëm ; *d*, xylem, the walls of the tracheids thickening. × 120.

FIG. 65. Older portion of rhizome. Marking as in Fig. 64. × 120.

FIG. 66. Cross section of the tubular bundle, *a* ; showing two root bundles, *b* and *c* ; and the two bundles of a leaf, *d*, *d* ; with a "foliar gap," *e* ; *f*, medullary parenchyma ; *g*, cortical parenchyma. × 45.

FIGS. 67–71. Diagrams showing the different aspects of the tubular bundle in cross section, *a*, leaf bundles ; *b*, "foliar gap" of leaf above ; *c*, root bundles. × 11.

FIGS. 72, 73. Outlines of scales. × 13.

FIG. 74. The same, magnified ten times to show the cells.

PLATE 27.

FIG. 75. Basal portion of scale showing the thin-walled cells. × 87.

FIG. 76. Cells from the margin half way up the scale showing the thin outer wall, *a*, and the papillae on the thickened inner walls, *b*. × 120.

FIG. 77. Portion of scale showing the framework of suberized walls, *a*. × 120

FIG. 78. The characteristic twist of the thin portion of the cross walls at margin. × 210.

FIG. 79. View of the back of the scale at base showing bend. × 25.

FIG. 80. Base of scale showing twist. × 25.

FIG. 81, 82. Apex of scales showing the wrinkling of the thin outer wall, *a*. × 87½.

FIG. 83. Longitudinal section through tip of root : *a*, root cap ; *b*, apical portion ; *c*, parenchymatous cells ; *d*, meristem of axial bundle. × 45.

FIG. 84. Tip of root showing how the cap cells often curl before being thrown off — *a* ; *b*, three cap cells still remaining attached to root.

FIG. 85. Portion of rhizome bundle showing connection of root bundle ; *a*, endodermis ; *b*, phloëm ; *c*, xylem ; *d*, cortex ; *c*, medullary parenchyma. × 120.

FIG. 86. Diarch bundle of young root : *a*, cortex ; *b*, endodermis ; *c*, *c*, phloëm ; *d*, *d*, two primary xylem groups. × 292.

FIG. 87. Cross section of young root : *a*, rhizoids ; *b*, cells containing crystalline substances ; *c*, endodermis ; *d*, the two phloëm groups ; *e*, xylem. × 38.

FIG. 88. Cross section through root and two of its branches, and a longitudinal section through a third branch at its point of attachment with the first root : 2 was given off first ; then 3 ; and then 4. Marking as in Fig. 87. × 45.

PLATE 28

FIGS. 89, 90. Prothallia and young sporophytes growing on the bark of the palmetto. × 3.

FIG. 91. A wing *a*, of the prothallium showing young sporophyte ; *b*, first leaf ; *c*, root. × 9.

FIGS. 92, 93. Rudimentary primary leaves showing variation. × 2.

FIG. 94. Variation of secondary leaf.

FIG. 95. Mature sterile leaf, the sporophyll shows the same variation with the exception that the two primary veins, *b*, are apt to run a longer distance before anastomosing ; 2 is basal portion of 1, they join at *a* ; *b* primary veins. × 2.

FIG. 96. Apex of first leaf showing epidermis of under side of hyaline border. × 87½.

FIG. 97. Portion of epidermis of same under side : *a*, gland ; *b*, stoma. × 210.

FIG. 98. Portion of epidermis showing prosenchymatic cell *a*. × 210.

FIG. 99. Scale from upper side of first leaf. × 87.

FIG. 100. Cross section of petiole showing vascular bundle with two xylem groups, *b*, in primary leaves. × 25.

PLATE 29

FIG. 101. Surface view of rhizome, with the leaves removed to show the two-ranked arrangement, and the two primary bundles. × 11.

FIG. 102. Diagram of leaf bundles: *a*, bundle of rhizome; *b*, the two primary bundles; *c*, first lateral bundle; *d*, second lateral bundle.

FIG. 103. Nine diagrams showing different cross sections of leaves with bundles. In 2, 3, 4 and 5 the thick-walled cells surrounding primary bundles have united before the formation of the lateral bundles, and shows the primary bundles anastomosing after the lateral bundles have been given off; 9 shows the apex of a leaf with one lateral bundle ending free.

FIG. 104. Diagram of middle portion of leaf: *a*, central bundle composed of parts of the two primary bundles; *b*, thick-walled cells surrounding bundle; *c*, mesophyll; *d*, band of thick-walled cells and epidermis; *e*, groove (under side of leaf); *f*, lateral bundle; *g*, denser mesophyll of upper side of leaf. × 13.

FIGS. 105, 106. Cross sections of petioles showing different degrees of thickening of the outer parenchymatous cells of the cortex. Fig. 105 is more often found in the sporophylls. 1, upper side; *a*, primary bundles. In Fig. 106 one lateral bundle is shown, *b*. × 25.

FIG. 107. Cross section of central bundle of leaf; *a*, phloëm; *b*, xylem; *c*, endodermis; *d*, thick-walled cells of the ground tissue surrounding bundle. × 120.

FIG. 108. Cross section of one of the lateral bundles. Marking as in Fig. 107. *e*, mesophyll of under side; *f*, thin-walled epidermal layer which gives rise to the sporangia. × 120.

FIG. 109. Curled apex of young sporophyll showing scales, *a*, and cut so as to show the bundles, *b*; and grooves, *c*. × 15.

FIG. 110. Side view of apex of young leaf showing curl and glands. × 13.

FIG. 111. Front view of same. × 13.

FIG. 112. Portion of epidermis from under side of young leaf; *a*, scale; *b*, gland; *c*, stoma just forming. × 87.

PLATE 30

FIG. 113. Apex of leaf. Dotted line indicates the area of the dense mesophyll cells, containing chlorophyll, under epidermis. × 87.

FIG. 114. Portion of upper side of leaf, over bundle, seen in cross section; *a*, epidermis; *b*, thick-walled cells, generally prosenchymatic, often becoming bast-like; *c*, mesophyll cells containing chlorophyl. × 87.

FIG. 115. Portion of epidermis, *a*, from under side of young frond showing first stoma, *d*. Marking as in Fig. 114.

FIG. 116. Ridge over bundle on under side. × 87.

FIG. 117. Inner margin of groove extending from ridge to ridge. Marking as in Fig. 114. × 87.

FIGS. 118, 119. Illustrate peculiar folding of the epidermal walls. Fig. 119 has been treated with potash to show the way they fit into each other.

FIG. 120. Diagram of surface of under side of leaf showing the ridge and lateral grooves, *a*, the stomata and glands. × 13.

FIG. 121. Epidermis from groove; *a*, stoma; *b*, gland. × 87.

FIG. 122. *A*, represents width of groove from edge to the sporangial layer ; *b*, stoma ; *c*, initial cell ; *d*, original epidermal cell.

FIG. 123. Cross section of groove : *a*, stoma ; *b*, epidermal cell ; *c*, air space ; *d*, thick-walled cells around bundle ; *e*, thin-walled epidermal layer giving rise to the sporangia, *f*, and paraphyses, *g*. × 120.

FIGS. 124–126. Showing origin of the stoma : *a*, original epidermal cell ; *b*, initial cell of the stoma ; *c*, the mother cell of the stoma ; *d*, longitudinal wall through mother cell, in Fig. 126, dividing it into the two guard cells, *e*, *e* ; *f*, nucleus ; *g*, chlorophyl. × 294.

FIG. 127. Mature stoma. Dotted line, *h*, represents wall of mother cell, the two guard cells being raised somewhat above the epidermis as in the cross section (Fig. 123). Marking as in Figs. 124–126. × 310.

FIG. 128. Gland. × 294.

PLATE 31

FIG. 129. A diagram of the longitudinal section of the leaf passing through center of groove : *a*, upper epidermis and band of thick-walled cells ; *b*, mesophyll ; *c*, *c*, band of thick-walled cells surrounding bundle ; *d*, lateral bundle ; *e*, thin-walled layer of epidermis giving rise to the sporangia ; *f*, sporangia here shown in all stages of development ; *g*, the paraphyses. × 25.

FIG. 130. Nine sections showing the development of the sporangium : *a*, original cell of the sporangium; *b*, first oblique wall ; *c*, second wall ; *d*, first tetrahedral cell ; *e*, peripheral cell dividing to form the sporangial wall. No. 9 shows the divisions of the tetrahedral cell, which form the mother cells of the spores and the tapetal cells, *g* ; *h*, pedicels. No. 5, surface view of very young sporangium. × 120.

FIG. 131. Nos. 1 and 2. Surface views of older sporangia : *a*, annulus ; *b*, lip cells just forming ; *c*, cells of pedicel at base of sporangium. × 120.

FIG. 132. Mother cells from a young sporangium before dividing to form the spores. × 210.

FIG. 133. Young sporangium, all the cells containing chlorophyl, except the lip cells ; *a*, annulus ; *b*, *b*, four connective cells ; *c*, the four lip cells ; *d*, thin-walled cells of sporangial wall ; *e*, pedicel. × 120.

FIG. 134. Ripe sporangium showing the way in which it opens : *f*, spores. Marking as in Fig. 133. × 120.

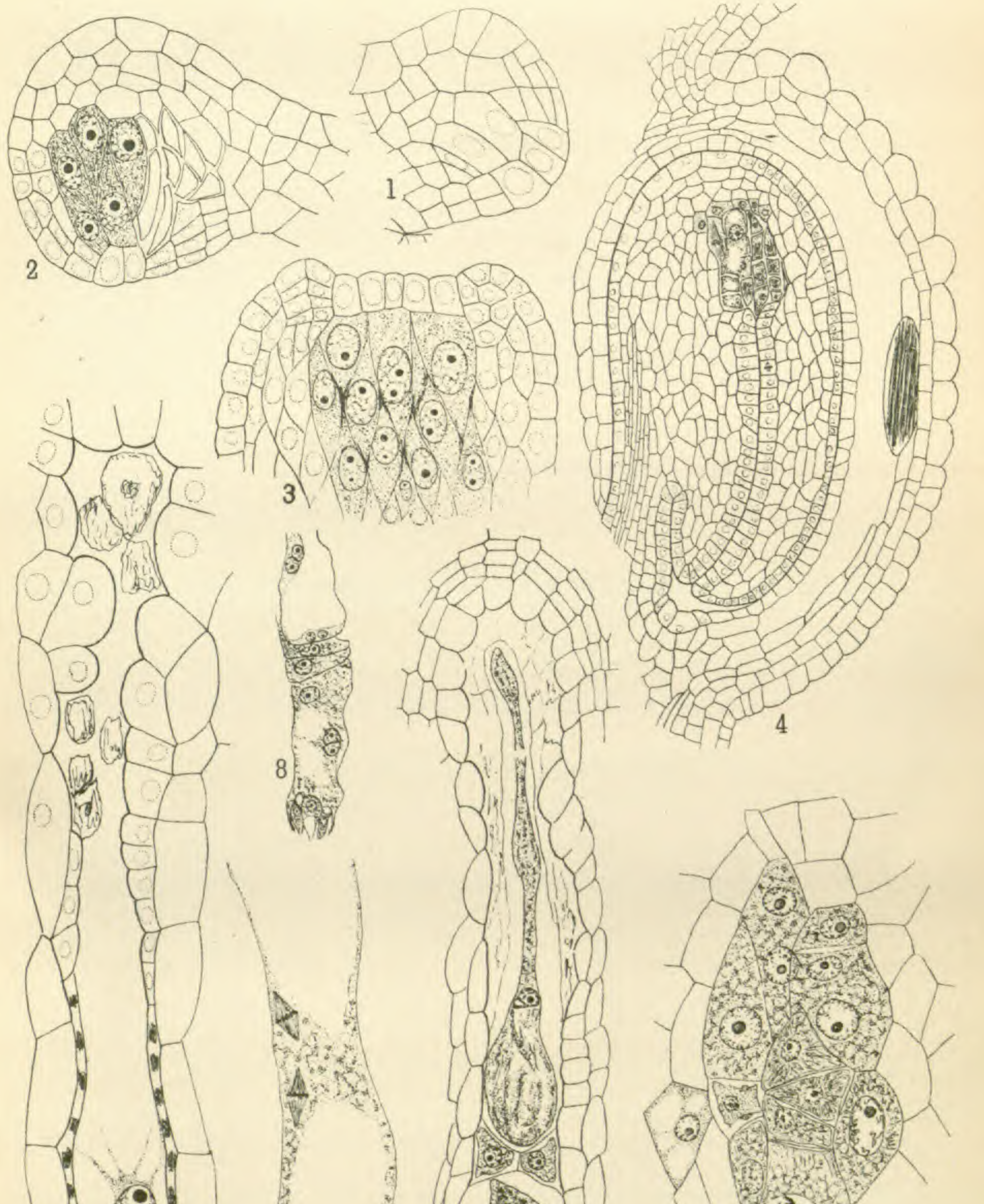
FIG. 135. Different ways in which cells of pedicel divide ; part of the basal portion of the sporangium is shown at *a* in No. 1. No. 1, × 87. No. 2, × 120.

FIG. 136. Four cells from epidermal layer, *a*, one of which has given rise to a young sporangium, *b* ; *c*, first tetrahedral cell in process of dividing (this stage is between Nos. 8 and 9 of Fig. 130) ; *d*, sporangial wall ; *e*, pedicel ; *f*, young paraphysis from adjoining cell containing a nucleus and some chlorophyl. × 120.

FIGS. 137, 138. Young paraphyses. × 120.

FIG. 139. Seven diagrams showing the branching of the paraphyses.

FIG. 140. Young sporophyte, *b*, growing from mutilated end of rhizome, the growing apex of rhizome having been removed ; *a*, base of two old sporophytes.



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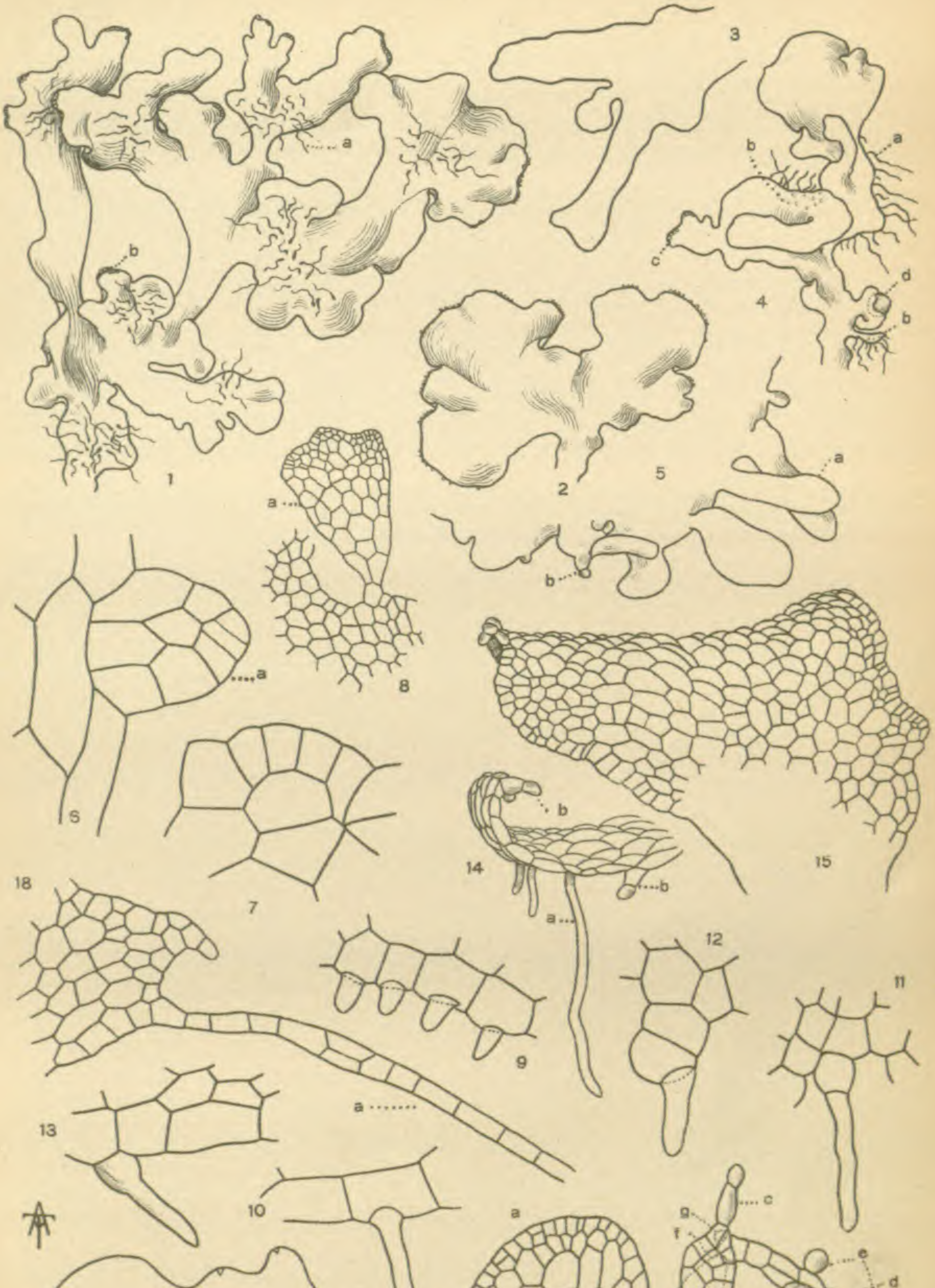

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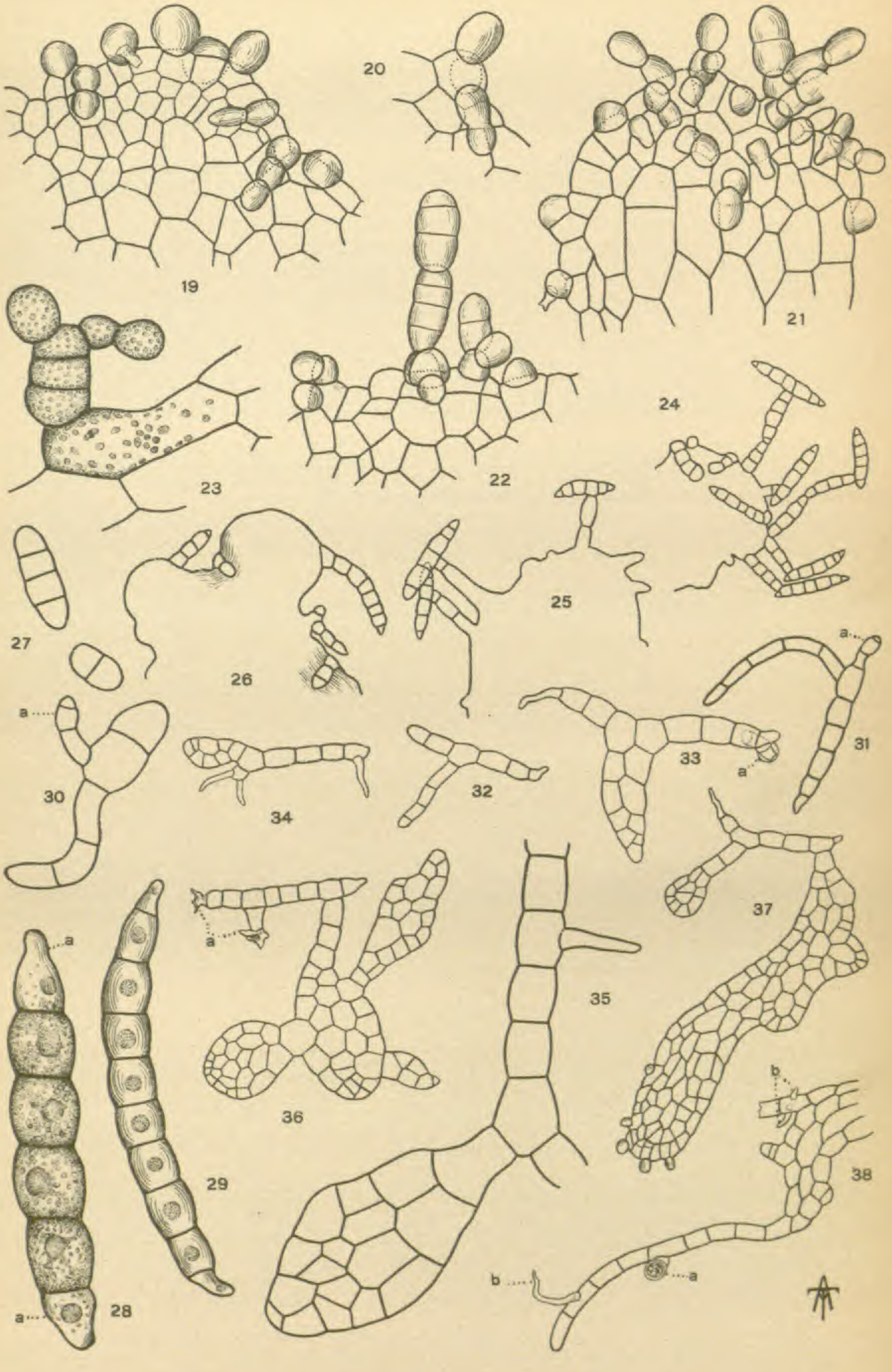

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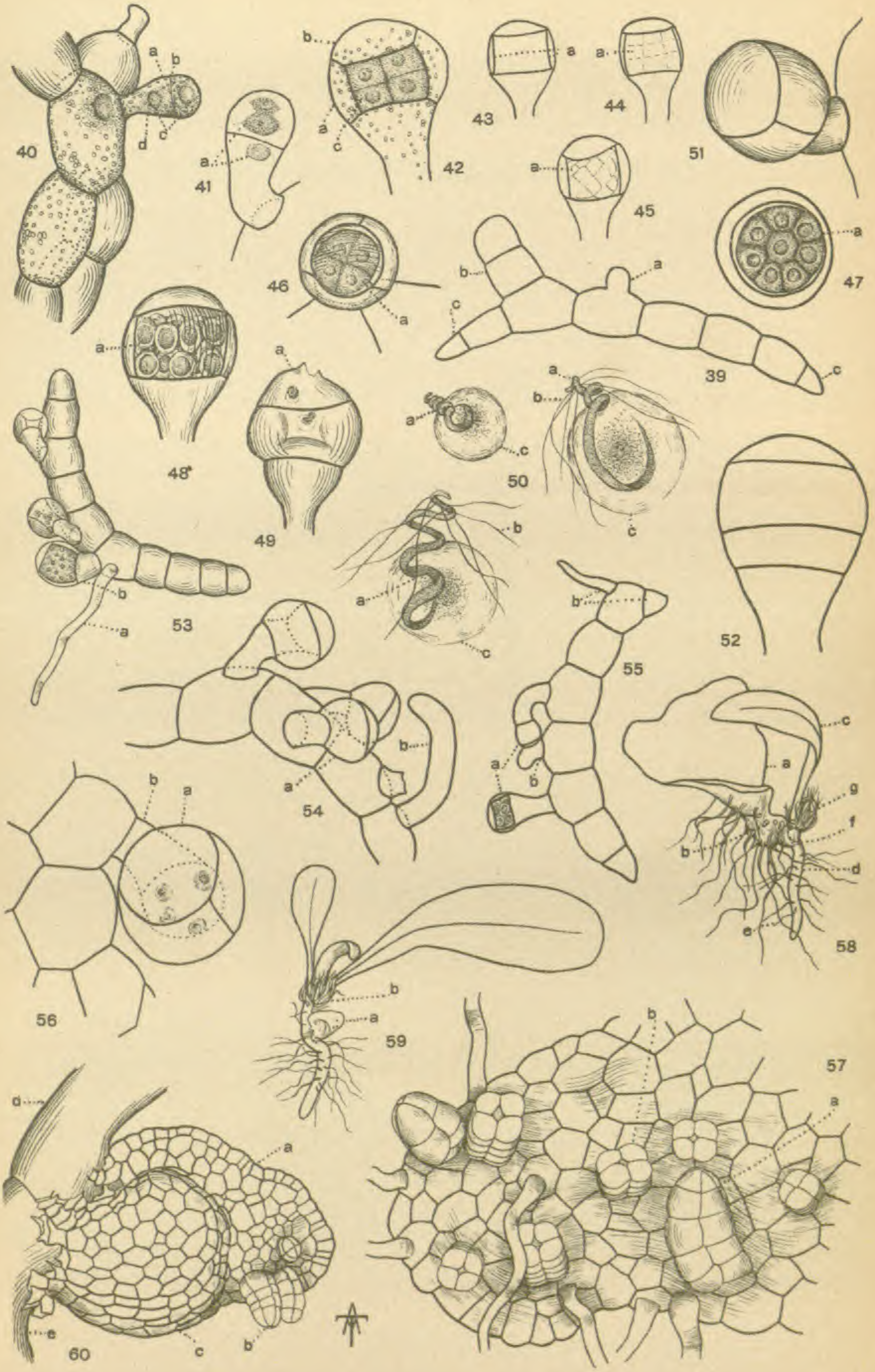

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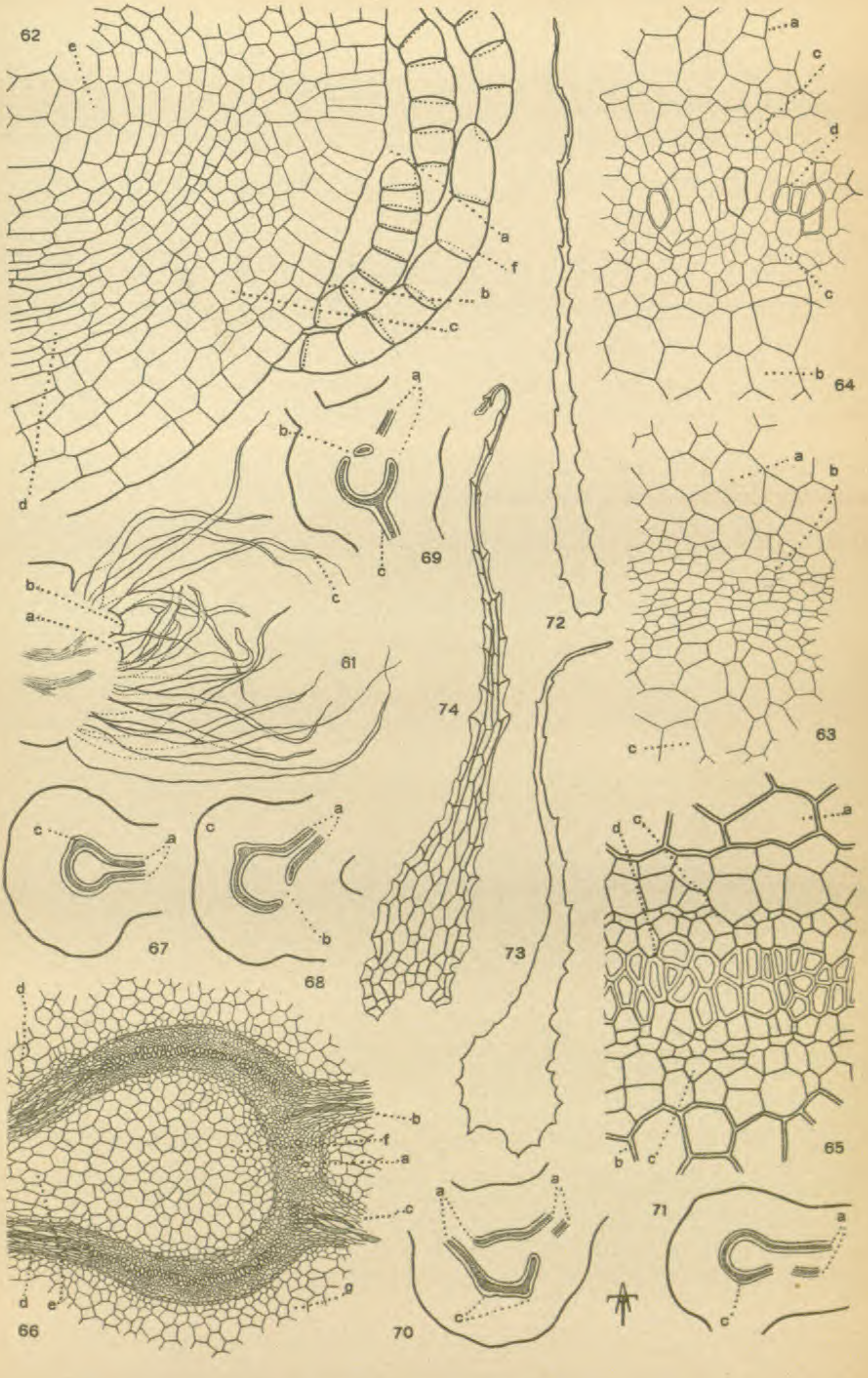

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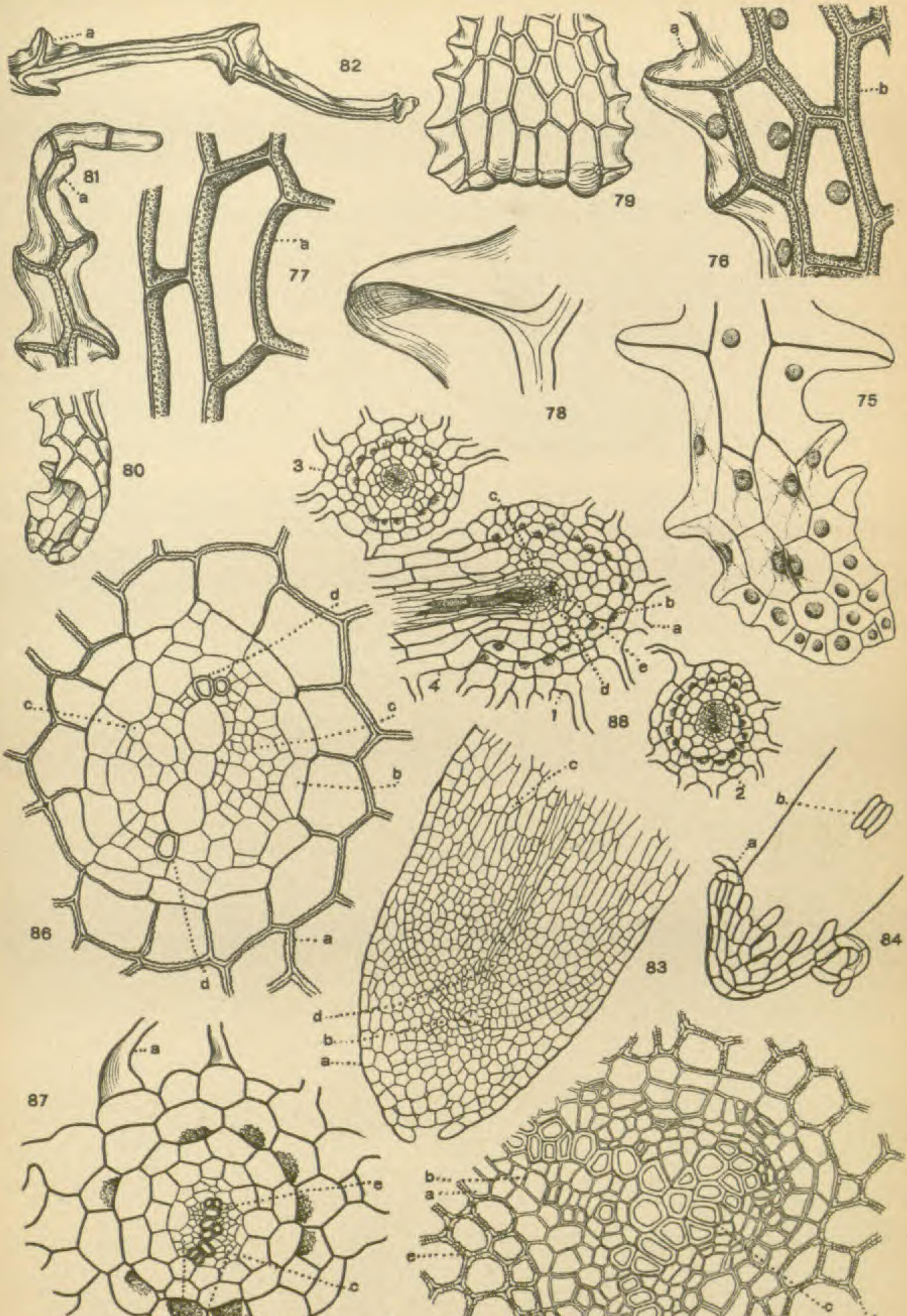

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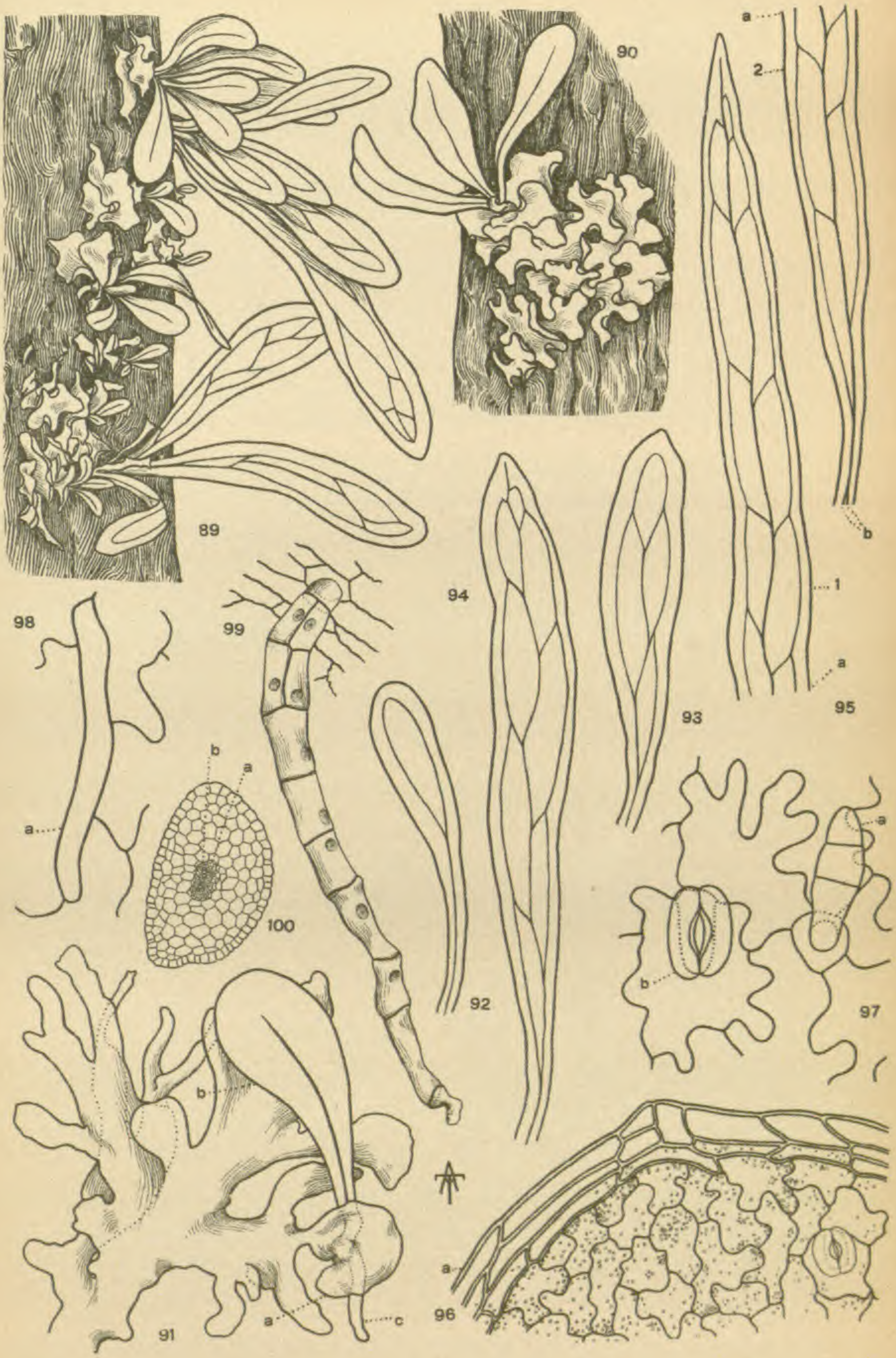

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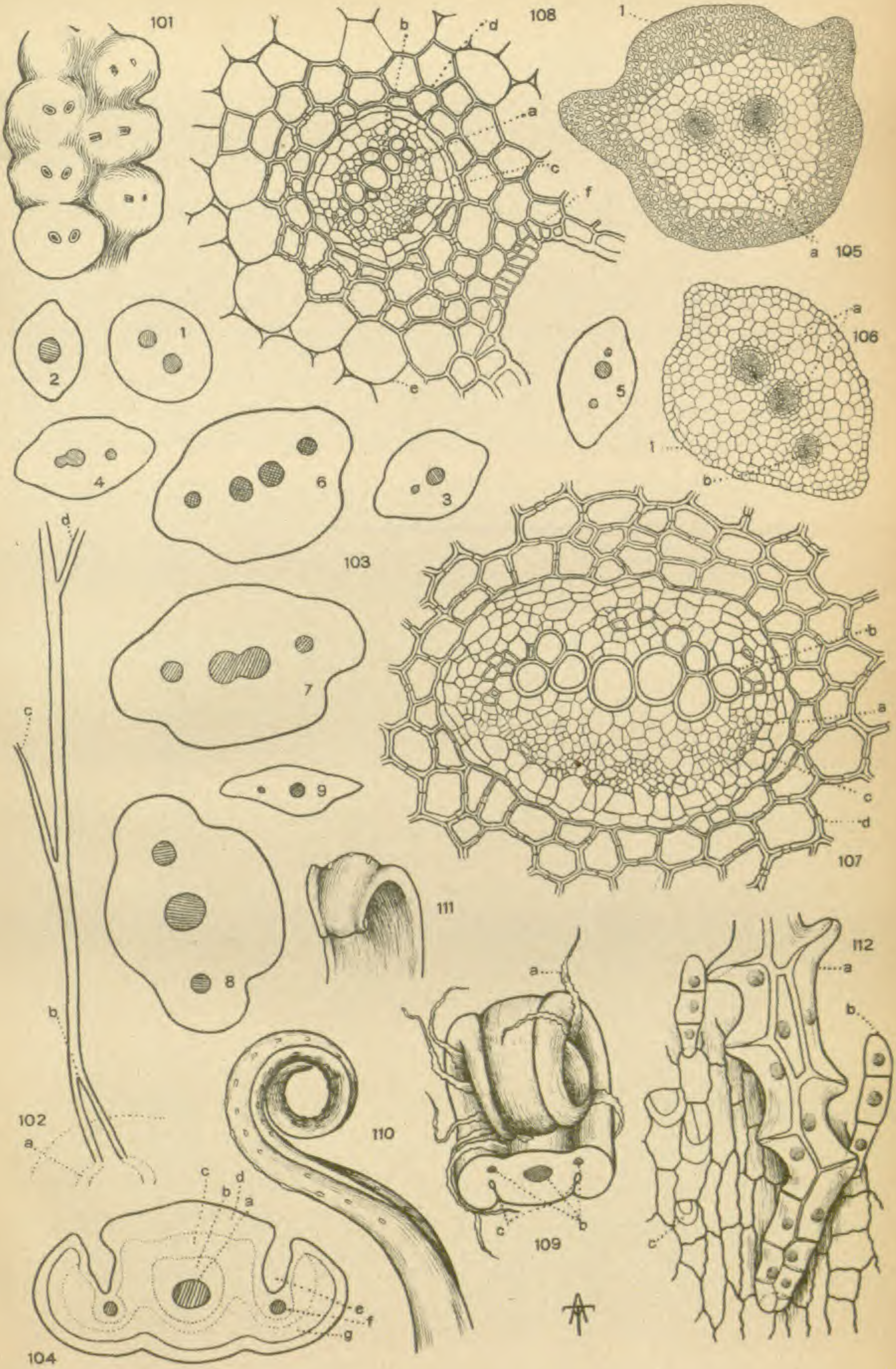

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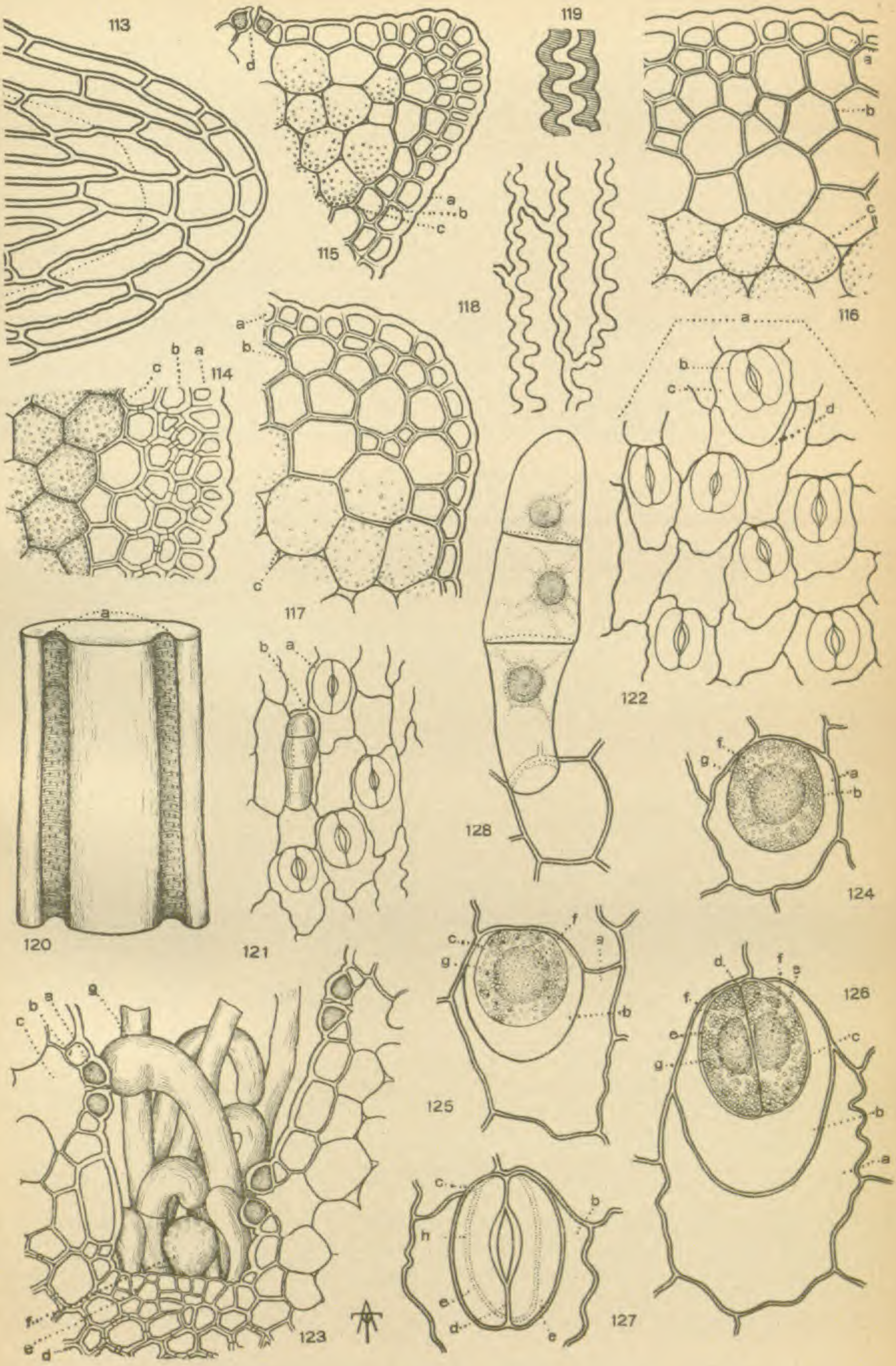

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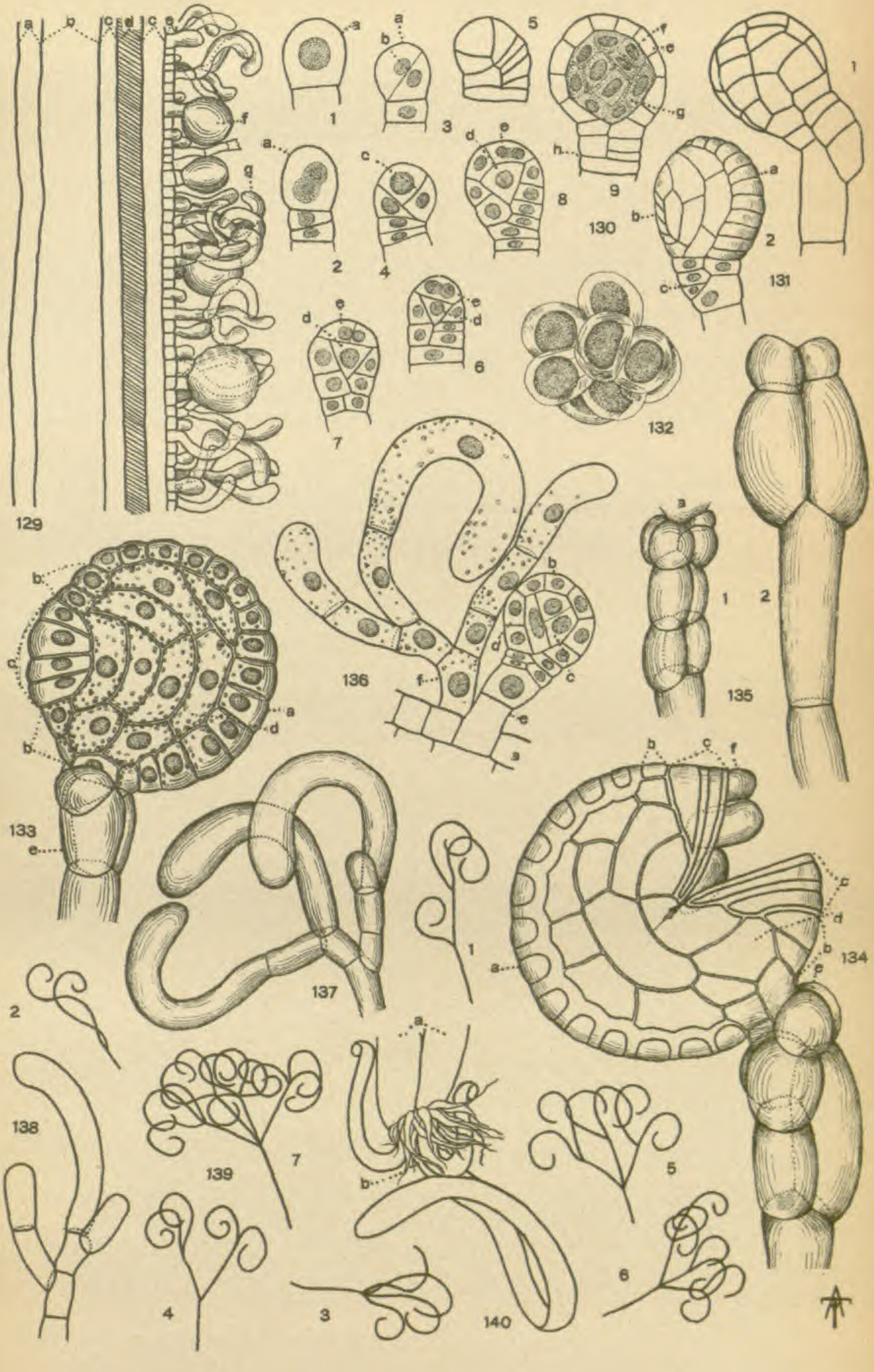

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