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EDITOR
JOHN MERLE COULTER

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P. 70, line 3 from top, for types read type.

P. 159, line 3 from top, for seem read seems.

P. 182, line 3 from bottom, for *VSW* read *VTW*.

P. 367, last line, for $\frac{FD-FG}{FG}$ read $\frac{FD}{FG}$.

P. 401, line 8 from top, for *Jungermanni* read *Jungermannia.*

P. 436, line 15 from top, for recent read ancient.

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Editor: JOHN M. COULTER

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JULY 1914

THE MORPHOLOGY AND CYTOLOGY OF THE AECIDIUM CUP

F. D. FROMME

(WITH PLATES I AND II AND EIGHT FIGURES)

Recent cytological investigations of the Uredineae have materially aided in clearing up the obscure points connected with their complex life history and development. The nature of the sexual processes involved in the transition from the gametophytic to the sporophytic (haploid to diploid) stages has received much attention, and, although the results achieved are somewhat conflicting on minor points, the general nature of the phenomena described by the different authors is quite uniform. Although examples of both the caeoma and cup types of aecidia have been studied from this standpoint, the most clear and acceptable accounts have been given for the less complicated, superficial caeomas. No comprehensive cytological account of the stages in cup-formation or of the general morphology of the aecidium has been given. Certain authors also disagree as to whether the nuclear divisions are all mitotic or in part amitotic.

So far sexuality has been reported in 13 species of rusts; 11 of these cases may be regarded as well established for the present, but the remaining 2, *Uromyces Poae* and *Puccinia Poarum*, as reported by BLACKMAN (**6**), must be considered as doubtful or at best not entirely understood, since only a few inconclusive fertilization stages were seen. Of the remaining 11 cases, 9 are forms that have aecidia or primary uredosori in their life cycles, and 2 are forms that lack aecidia. Of the first group, 2 species have aecidia of the cup type and 5 have aecidia of the caeoma type; while the remaining 2 have primary uredosori that have been shown to be functional aecidia. The 2 forms that lack aecidia are short-cycled micro-forms. Of these 11 species, 10 are autoecious and one (*Melampsora Rostrupi*) is heteroecious.

TABLE I

SUMMARY OF FERTILIZATION PHENOMENA

Species	Author	Date	Length of cycle	Type of aecidium	Method of fertilization
Phragmidium violaceum....	Blackman	1904	o, I, II, III	Caeoma	Nuclear migrations
Phragmidium speciosum....	Christman	1905	o, I, III	Caeoma	Equal cell fusions
Melampsora Rostrupi.....	Blackman and Fraser	1906	o, I, II, III	Caeoma	Equal cell fusions
Phragmidium Pot. canadensis	Christman	1907	o, II^1, II^2, III	Primary uredo	Equal cell fusions
Caeoma nitens..	Olive	1908	o, I (?)	Caeoma	Equal cell fusions
Triphragmium Ulmariae....	Olive	1908	o, II^1, II^2, III	Primary uredo	Equal cell fusions
Puccinia transformans.	Olive	1908	o, III		Equal cell fusions
Caeoma nitens..	Kurssanow	1910	o, I (?)	Caeoma	Equal cell fusions
Puccinia Falcariae....	Dittschlag	1910	o, I, III	Cup	Equal cell fusions
Endophyllum Sempervivi...	Hoffman	1912	o, I	Cup	Equal cell fusions
Melampsora Lini.........	Fromme	1912	o, I, II, III	Caeoma	Equal cell fusions
Puccinia Malvacearum	Werth and Ludwigs	1913	(o?), III		Equal cell fusions

In 10 of the cases reported the fertilization processes described are essentially of the type that involves a complete cell fusion between two equal gametes as originally described by CHRISTMAN for *Phragmidium speciosum*. In the remaining case, *Phragmidium violaceum*, as described by BLACKMAN, two cells are also involved in the fertilization, but these cells were held to be morphologically unequal and complete cell fusion was not observed. Nuclear migrations apparently similar to those described by BLACKMAN, but variously placed in the hyphae, have been reported by CHRISTMAN, KURSSANOW, OLIVE, and the writer, and were interpreted as pathological phenomena. The 10 cases of equal cell fusions are described by 7 different authors, and none of these has found true fertilizations of the type described by BLACKMAN. OLIVE (**22**), however, reports and figures cases of fertilizations in *Caeoma nitens* (*Gymnoconia interstitialis*) and *Triphragmium Ulmariae* that suggest the nuclear migrations of BLACKMAN, but are in reality, as he says, simply early stages in cell fusion in which the connecting pore is as yet small. This pore enlarges subsequently and complete union of the cells is accomplished.

A summary as to the fertilization phenomena in the 11 species where fertilization has been described to date is given in table I.

Besides the question of sexuality, there are a number of unsettled points relating to the morphology of the aecidium cup. Some of these questions were raised by DEBARY and have as yet not been completely settled. For example, does the cup enlarge by the addition of new spore chains between those previously formed, or are the new chains added at the lateral borders? Is the peridium formed from the peripheral chains only, or are the central chains also involved? Do buffer cells similar to those found in the caeomas also occur in the aecidium cup?

DEBARY (**4**) stated that the hymenium of *Aecidium Berberidis* broadens before the cup completely matures, but was unable to determine how this was brought about. He states that the peridium arises from the marginal "basidia," and the entire outer chains composed of peridial cells arched over the center of the cup to form a covering over the central spore chains. RICHARDS (**27**) found that the growth of the hymenium was largely at the periphery and that only rarely were new chains added between those already formed. He states that the peridium is formed from the apical cells of the central spore chains and from all of the cells of the peripheral chains. The peridial cells are first formed at the center, and they are successively formed on all sides of this center until a complete protective layer is formed over the entire mass of spores. OLIVE (**23**) agrees substantially with RICHARDS as to the method of formation of the peridium.

The work of RICHARDS, BLACKMAN, CHRISTMAN, OLIVE, KURSSANOW, and others has been summarized by DITTSCHLAG (**10**), HOFFMAN (**15**), MAIRE (**19**), and the author (**12**), and therefore only the more recent papers will be reviewed.

DITTSCHLAG (10) was the first to describe sexual fusions in an aecidium of the cup type. He found cell fusions at the base of the young aecidium of *Puccinia Falcariae*, but was unable to trace completely the origin of the fusing cells. A single sterile cell was sometimes found above each gamete, but was not always present. Trinucleated basal cells were found that apparently arose from the fusion of three cells, and these basal cells gave rise to chains of trinucleated aecidiospores and intercalary cells. He further described branching basal cells for the first time. The primary basal cell formed a bud on the lateral wall, and two daughter nuclei from the preceding conjugate division passed into the bud. The bud enlarged further and then the nuclei proceeded to divide and give rise to a second chain of spores. His description of the origin of the peridium agrees with that of RICHARDS.

HOFFMAN (15) studied the development of the aecidium of *Endophyllum Sempervivi*, a species that completes its life cycle with the production of a single spore form, an aecidio-teleutospore, besides the spermatia. He distinguished two kinds of tissue in the young cup. The first tissue formed disintegrated to provide room for the development of the spores, and a second tissue, the "Paarungsgewebe," was then formed at the base of the primordium. The cells of this tissue were conspicuous for their size and the density of their cytoplasm, and were borne in filaments that had their long axes parallel to the surface of the leaf. Fertilization was accomplished by the dissolution of the adjoining cell walls between two gametes and perpendicular basal cells resulted. He also found triple cell fusions and trinucleated basal cells and spore chains. He thinks that one of the nuclei in a trinucleated spore eventually disintegrates, but obtained no convincing evidence of this. He also found branching basal cells like those described by DITTSCHLAG, and states in addition that the conjugate nuclear division that precedes the formation of the branch produces two pairs of nuclei of unequal size. The smaller pair enters the branch and the larger pair remains in the original half of the basal cell. His figures of this process are not at all convincing.

The author (12) has described the nuclear development of the caeoma of *Melampsora Lini.* This form differed in structure from previously described caeomas in that two sterile cells were normally produced above each gamete. Equal cell fusions were found in abundance. A number of three and a few four-cell fusions were found, and these gave rise to chains of three and four-nucleated aecidiospores and intercalary cells. Multinucleated cells, whose origin and fate were not determined, were also found among the spore chains.

TABLE II

PLURINUCLEATED CELLS

Author	Date	Rust	No. of nuclei to a cell	Kind of cell
Sappin-Trouffy..........	1896	Ur. Betae	4	Uredospore
Blackman and Fraser...	1906	P. Malvacearum	3	Teleutospore and basal cell
Blackman and Fraser...	1906	Ur. Ficariae	3	Teleutospore
Blackman and Fraser...	1906	P. Poarum	3 and 4	Aecidiospore initial cell
Blackman..............	1904	Ph. violaceum	3	Basal cell
Olive..................	1908	P. Cirsiil-anceolati	Up to 15	Cell at base of aecidium
Dittschlag.............	1910	P. Falcariae	3	Aecidiospores and basal cells
Hoffman...............	1911	Endo. Sempervivi	3	Aecidiospores and basal cells
Fromme...............	1912	Mel. Lini	3 and 4 3, 4, and 11	Aecidiospores Basal cells

WERTH and LUDWIGS (28) studied the teleutosorus of the microform *Puccinia Malvacearum.* They found cell fusions between the tips of club-shaped hyphae. The fusing cells were usually of unequal size and the nucleus of the smaller passed over into the larger. This binucleated cell cut off two cells, the lower of which became the stalk, and the upper, after a division, the two-celled teleutospore. They occasionally found binucleated cells in the vegetative tissue and were unable to explain their presence.

The occurrence of plurinucleated cells in the rusts is of some interest, since the uninucleated and binucleated condition seems to be very constant in the gametophytic and sporophytic mycelium, respectively. A number of instances of plurinucleated cells that have been figured by various authors are tabulated in table II.

Material and methods

The aecidia included in this study were collected during the spring and summer of 1912 in the vicinity of New York City and at Woods Hole, Massachusetts. Some 20 different species of aecidia were fixed and examined, and the most favorable were selected for a more detailed study.

The 6 species treated here are *Puccinia Claytoniata* Peck on *Claytonia virginica*, *P. Violae* (Schum.) DC. on *Viola papilionacea*, *P. Hydrocotyles* (Link) Cke. on *Hydrocotyle umbellata*, *P. Eatoniae* Arthur on *Ranunculus abortivus*, *P. angustata* Peck on *Lycopus virginicus*, and *Uromyces Caladii* Farlow on *Arisaema triphyllum*. I am indebted to Dr. J. C. ARTHUR for the identification of the aecidia.

Some of these species have been previously studied from the standpoint of sexuality. The aecidium of *Ur. Caladii* has been studied by RICHARDS (27) and by CHRISTMAN (9). RICHARDS has also studied an aecidium on *Ranunculus* that probably belongs to the same species as the one studied here. So far as I have ascertained, the remaining forms have not previously been studied cytologically.

Three of these rusts, *P. Violae*, *P. Hydrocotyles*, and *Ur. Caladii*, are eu-autoecious forms, that is, all four spore forms are included in the life cycle and all are borne upon the same host. Two of the other species, *P. Eatoniae* and *P. angustata*, are eu-heteroecious forms, the former with the uredosori and teleutosori on a grass, *Sphenopolis* (*Eatonia*), and the latter with these sori on a sedge, *Scirpus*. The remaining species, *P. Claytoniata*, is autoecious, but lacks the uredo stage. It belongs to the *opsis* group of SCHROETER'S classification and to the genus *Allodus* of ARTHUR'S (1).

In 3 of the species the aecidia are borne on a mycelium that is diffused throughout the tissues of the host. In the other 3 the mycelium is localized within a rather restricted area. These two types of aecidia can usually be distinguished at a glance. The aecidia from a diffused mycelium are distributed uniformly over the leaf or stem surface at approximately equal distances apart, and all on one part of the host are usually at the same stage of development. When the mycelium is localized, the aecidia are crowded together in groups, often with an annular arrangement, and the older ones are found in the center of the group and the younger at the margins. This distinction is of some importance in collecting material for study, as it is usually necessary to make several collections of the forms from a diffused mycelium in order that all stages may be represented, while all stages may be present in a single fixation when the aecidia are from a localized mycelium.

All of the material was fixed in the field. Small segments of leaves or stems bearing aecidia were immersed immediately after removal in a small vial of fixing solution. Of a number of fixing solutions tested, weak and medium Flemming's were found to give the best results. The segments were allowed to remain in the fixative for 48 hours, after which they were washed, hardened, and imbedded in paraffin. The sections were stained for the most part with the safranin, gentian violet, and orange G combination, although iron-hematoxylin was used to some extent for comparative study.

The development of the cuplike aecidium

Puccinia Claytoniata proved to be an exceptionally favorable form for study. The cells and nuclei of the fungus are large, and the host tissue is soft and succulent and apparently permits rapid penetration of the fixing solution. The vegetative mycelium that precedes the formation of the spermogonia and aecidia is especially abundant and conspicuous. It is found in all of the leaf tissues, but is most abundant in the mesophyll near the lower epidermis. Most of the hyphae have their axis of growth in the long axis of the leaf. They are almost entirely intercellular except for the haustoria, which are short, knoblike, and usually penetrate only a short distance into the host cell. The hyphae are somewhat irregularly septate. The individual cells vary considerably in size. The average breadth is about 5 μ and the length three or four times the breadth. A single globular nucleus is located, usually, near the center of the cell; its diameter is but slightly less than the short diameter of the cell. The small nucleole stains a ruby red and is readily seen. The chromatin stains a deep blue and is distributed in small globular masses that are connected by delicate strands.

These often appear to be oriented on a point on the nuclear membrane, as OLIVE has found (**22**), but the presence of a central body was not ascertained with certainty. The hyphae branch monopodially at irregular intervals. The branch usually arises in the lateral wall near the apical end of the cell.

Binucleated cells were sometimes found in the vegetative mycelium, and continuous filaments of these were found in some cases. It is probable that the sporophytic mycelium had already established itself, and that both gametophytic and sporophytic mycelia were associated together in the same leaf tissue.

The aecidia are hypophyllous, and the first evidence of their formation is found in a conspicuous massing of hyphae between the lower epidermis and the cells of the first, second, and third layers of the mesophyll. The center of the young hyphal mass lies between the first and second cell layers. The hyphae are conspicuous on either side of this center for a distance of about two host cells. Thus the area to be occupied includes, in cross-section, 12 host cells, 4 cells broad and 3 cells deep. These host cells are gradually destroyed and replaced by the fungous hyphae.

The host cells in the center of the area are the first to disappear. The hyphae ramify between them, force them apart, and multiply in the intercellular spaces. They act as a wedge between the layers of host cells, and in forcing them apart produce a slight elevation of the epidermis. After these host cells have been completely cut off, they gradually diminish in size, and in most cases completely disappear eventually. The hyphae do not penetrate the host cells during their disintegration, and their disappearance seems to be due to the pressure brought to bear on them by the enlargement of the fungous mass. Their walls become much convoluted and infolded. The host cells are not always completely destroyed; sometimes they may be found imbedded in the tissue of an old aecidium.

In order that they may be described more clearly, the different surfaces of the hyphal mass will be designated as apical, basal, and lateral surfaces, the apical surface being that adjacent to the epidermis. This will apply to either an epiphyllous or hypophyllous aecidium. The individual filaments that make up the young hyphal mass have their direction of growth toward the center of the mass, a point that usually lies between the first and second layers of host cells. In the very young stages the direction of growth is scarcely evident, since the hyphae wind around the intervening host cells; but as the host cells are crowded out and their site filled by branches of the surrounding hyphae or by others that force their way into the mass, it becomes more apparent. Not all of the hyphae are able to reach the center of the mass. Those on its lateral surfaces are crowded out by the earlier formed hyphae within and grow toward the epidermis, encircling the surface of the hyphal mass. There are 5 or 6 layers of these encircling hyphae.

The cells that make up the hyphal mass of the young cup are shorter and broader than those of the vegetative mycelium. Their cytoplasm is more dense and stains more deeply. This is particularly true of the cells of the interior, while those on the surface of the mass are less sharply differentiated from the purely vegetative cells. As the mass increases in size with the continued destruction of host cells, the fungous cells at the center begin to disintegrate. The first evidence of their disintegration is seen in the appearance of vacuoles in their cytoplasm. This is accompanied by the disorganization of the nucleus. They become detached from the hyphae on which they are borne and round up and enlarge to two or three times their original size if sufficient space is available. Some of these cells evidently undergo complete disintegration, while others become almost entirely empty except for a few cytoplasmic shreds and the remnants of the nucleus, and remain for some time in the center of the mass. They often become closely packed together as a result of enlargement, and have the appearance of a parenchyma. Because of this condition, this tissue of sterile cells is known as the pseudoparenchyma of the young cup (text fig. 1).

The first pseudoparenchyma cells formed are the apical cells of the hyphae that converge at the center of the hyphal mass. The disintegration of the cells of these hyphae proceeds from their apices toward their bases, and the area of pseudoparenchyma is increased by the addition of further cells on its margins. The apical surface of the mass is soon reached, and the sterilization of hyphae then continues toward the lateral and basal surfaces. The hyphae that run from the basal surface of the mass to its center are on the average about 10 cells in length, while those that run from the lateral surfaces are somewhat shorter. Fig. 1 shows a section through the lateral surface of a young hyphal mass in which the sterilization of 3 or 4 of the apical cells of the hyphae has been accomplished. At the top of the figure the border of an epidermal cell, marking the apical surface of the mass, is indicated by a double line, and a cell of the mesophyll at the base of the figure indicates the basal surface. The cells beneath the pseudoparenchyma are shorter and broader than those on the lateral and basal surfaces of the mass, their nuclei are larger, with larger nucleoles, and their cytoplasm is considerably denser. Several layers of hyphae at the base of the figure that run tangentially to the curved basal surface of the mass are seen to give rise to the perpendicular hyphae that bear the differentiated, well nourished cells. The perpendicular hyphae shown in the figure average about 6 or 7 cells in length and have apparently cut off 3 or 4 sterile cells each. The sterilization process continues until only 4 or 5 cells at the bases of the perpendicular hyphae remain. The pseudoparenchyma is thus extended until it occupies about two-thirds or three-fourths of the vertical diameter of the mass. The remaining cells of the perpendicular hyphae now stand

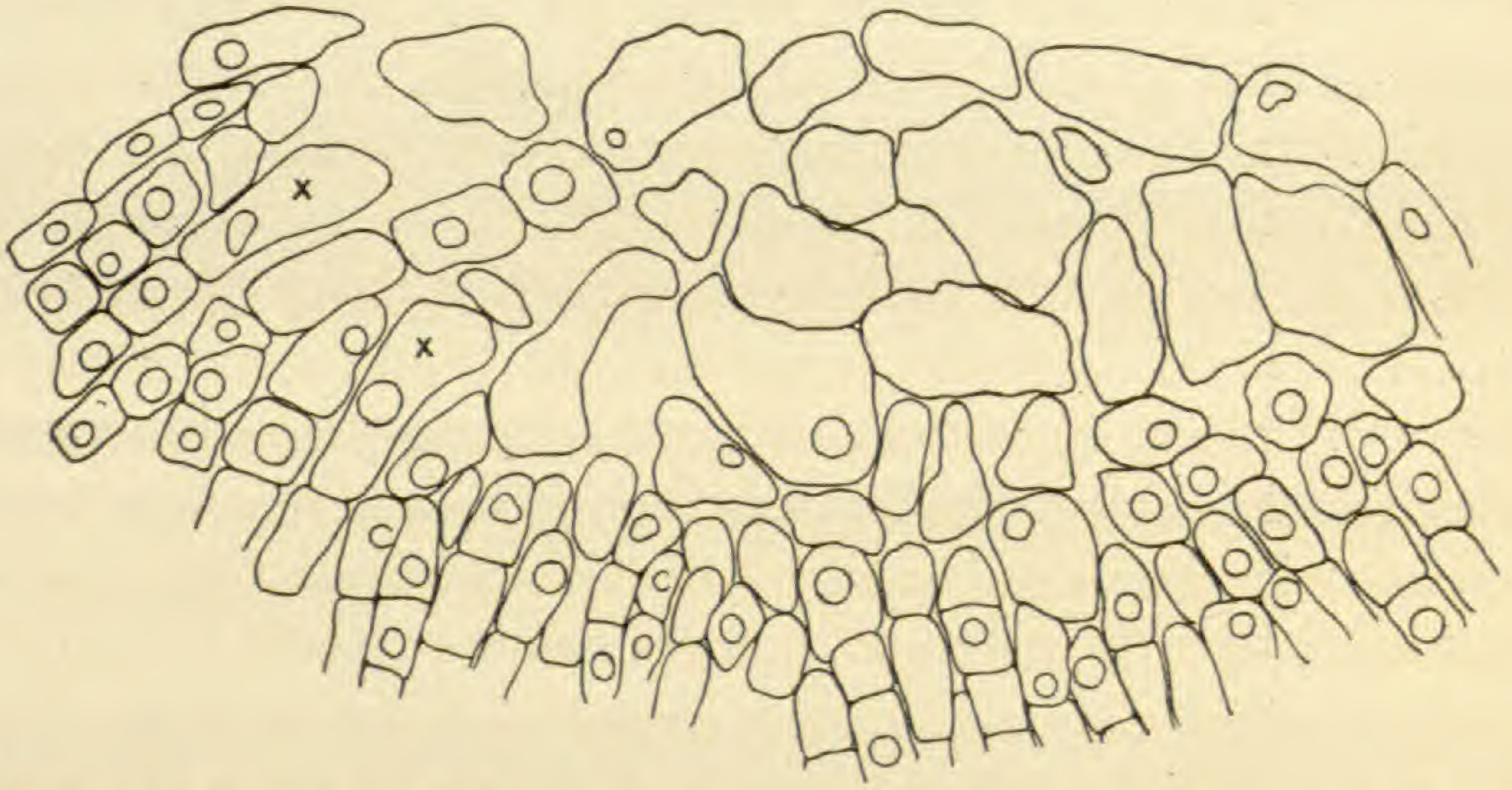

FIG. 1.—Formation of the pseudoparenchyma in the aecidium of *P. Claytoniata:* the attachment of the forming pseudoparenchyma cells (*x*) with the hyphae on which they are borne is evident.

out sharply from the pseudoparenchyma and the undifferentiated cells below them. Their cytoplasm is dense, their nuclei large, and the nucleoles especially large and prominent. They are apparently richly nourished at the expense of the cells of the underlying hyphae and vegetative mycelium. These richly nourished cells form a tissue, 2 or 3 cells in depth, that lines the inner basal surface of the young aecidium cup and extends for some distance upward on its lateral surfaces.

A comparison with the caeoma type of aecidium naturally suggests that these richly nourished cells are the gametes, and, as a matter of fact, practically all of the cells of this cup-shaped tissue may later fuse in pairs. Even though the fusion of all of them is not ultimately accomplished, the fusing pairs are distributed throughout the tissue and, before the fusions, those which are to fuse cannot be differentiated from the others.

These gametes of the aecidium cups of *P. Claytoniata* are quite comparable to the gametes of the caeomas. The aecidium of the caeomas is broad and shallow, and the gametes are produced in a single continuous layer beneath the leaf epidermis from which they are separated by a single layer of sterile cells only. They are the penultimate cells of the gametophoric hyphae. The aecidium of *P. Claytoniata* is spherical in shape and is deep-seated in the tissue of the host. The gametes form a tissue, 3 or 4 cell layers in depth, that lines the basal surface of the spherical mass. Above the gametes is found a tissue of sterile cells that has resulted from the disintegration of the upper two-thirds of the gametophoric hyphae. In the cup both the gametes and sterile cells form a tissue, while in the caeoma they form but a single layer. The sterile cells of the pseudoparenchyma and the "buffer" cells of the caeoma seem to be of similar origin and bear the same relation to the respective gametes above which they are borne. In both cases they are possibly potential gametes which have become sterile. If the sterile cells of the cup and the "buffer" cells of the caeoma are in reality homologous, BLACKMAN's conception, that the latter are morphologically trichogynes, would have to be extended to include a pluricellular type of trichogyne. It may be noted in passing that OLIVE (**22**) contends that the "buffer" cells are sometimes wanting in *Caeoma nitens* and *Triphragmium Ulmariae*, and that according to my own observations (**12**) two "buffer" cells are normally produced above each gamete in the caeoma of *Melampsora Lini*. Further, I have found cases of two gametes borne one above the other in the same hypha in this form (**12**, pl. 9, fig. 18). *Melampsora Lini* thus seems to be an intermediate form between the more simple caeomas, with but one sterile cell and gamete to each hypha, and the aecidium cup with several sterile cells and gametes. It should be mentioned in this connection that the sterile cells of the cup can scarcely be considered to function as "buffer" cells in the sense that CHRISTMAN (**7**) used the term. If any function is to be ascribed to them, it is apparently that of space making. Their disintegration provides room for the development of the spores.

Up to this point in the development of the cup no multinucleated cells were seen, nor any other large cells that could in any way be considered central cells or organs from which the gametophoric hyphae might have arisen. Careful search was made for them in all stages in all of the forms included in this work, as well as in some additional forms. My observations do not agree, therefore, with those of MASSEE (**20**) as to the presence of central organs, nor with RICHARDS' (**27**) as to the presence of a "fertile hypha," nor do I find the multinucleated cells of OLIVE (**22**). I am confident that these multinucleated cells do not normally occur in any of the forms that I have studied. It is possible that they are peculiar to certain types of aecidia only.

The conditions found in the development of the aecidia of the other species investigated up to the time of the fertilization stage are very similar to those described for *P. Claytoniata*. Excepting minor differences, such as involve the form and size of the cup, its position in the leaf tissue, the relative extent of the pseudoparenchyma, and the number and position of the gametes, the general morphological development of all is of the same nature. The same excavation of the mesophyll of the host in areas of varying size and shape, and the same sterilization of radial hyphae to form the pseudoparenchyma are found in all.

The most noticeable difference found is in the position of the gametes. *P. Violae* is more like *P. Claytoniata* in this respect, and in the general appearance of the sorus, than any of the others. The number and position of the gametes are practically the same in both. The sterile cells of *P. Violae* do not disintegrate so completely as do those of *P. Claytoniata*, and consequently form a more compact pseudoparenchyma. *P. Violae* is likewise a very favorable form for study, although the later stages do not fix so favorably as do the earlier ones.

In general appearance the early development of *Ur. Caladii* is much unlike that of the two foregoing species. The aecidium is much broader and shallower and is more superficially located in the leaf tissue. The young aecidium has the appearance of a deep-seated caeoma. The perpendicular gametophoric hyphae do not converge toward a central point in the young hyphal mass to such a noticeable degree, but run almost vertically toward the epidermis, a condition to be expected in a broad shallow sorus (text fig. 2). This condition of the gametophoric hyphae is more suitable to the study of the individual hyphae, and the sterilization of their apices and the position of the gametes are more easily seen.

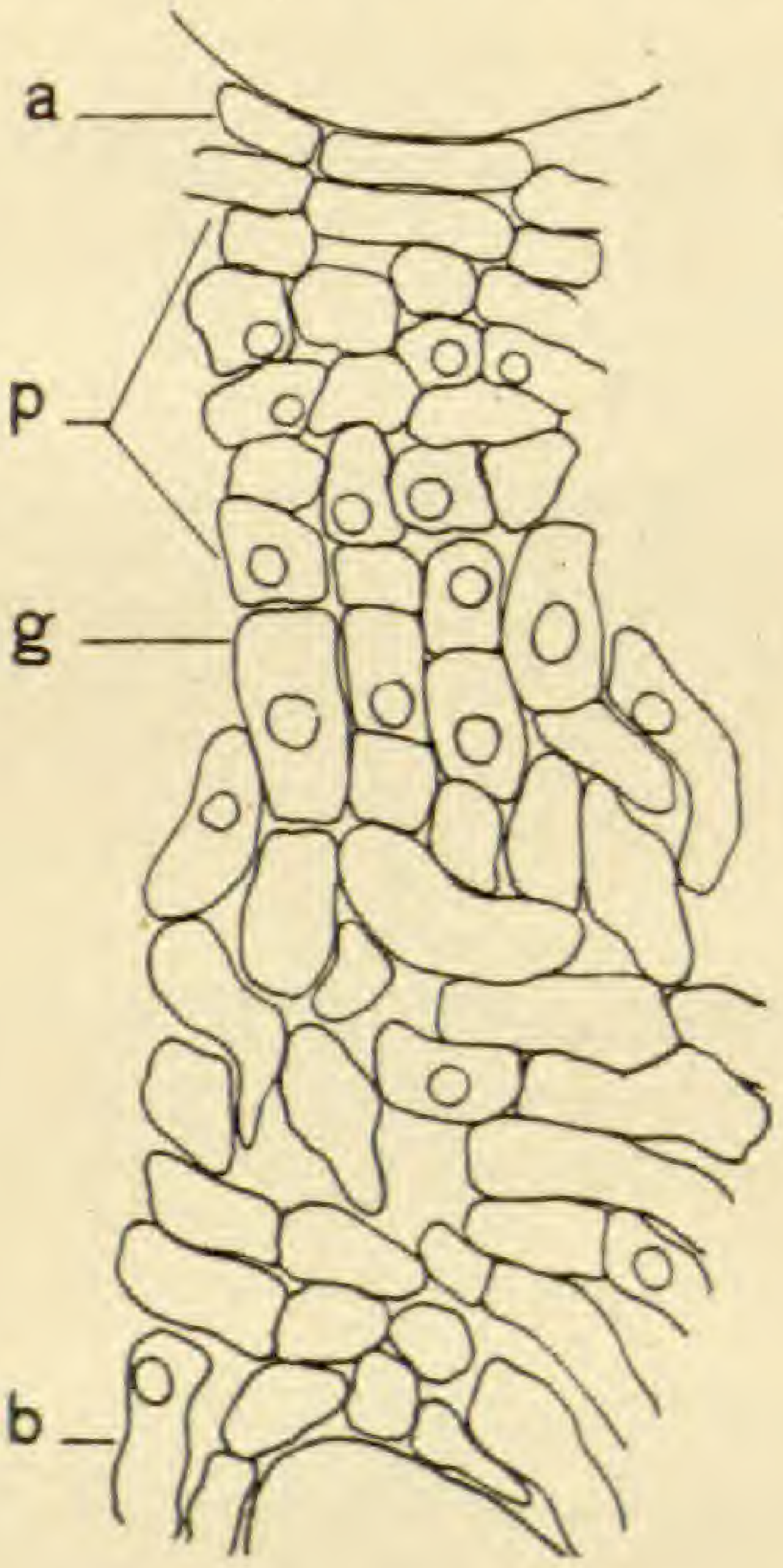

FIG. 2.—Section through the young aecidium of *Ur. Caladii*: *a*, apical surface; *b*, basal surface; *g*, gametic tissue; *p*, pseudoparenchyma.

The gametophoric hyphae consist of about 6 or 7 cells (text fig. 2). The upper 3 or 4 of these are sterilized and the remaining cells at the base are the gametes. As a rule, about two layers of gametes are formed, though in some cases there was apparently only one, and three were sometimes seen. The gametes are especially large at the time of fusion. The sterile cells do not disintegrate very completely prior to the fusions, and consequently scarcely any characteristic pseudoparenchyma appears. The aecidium is favorable for study, since both cells and nuclei are large. In comparing the sections of my material on *Arisaema* with RICHARDS' figures (**27**, figs. 1–4) of *Ur. Caladii* on *Peltandra*, it seems evident that the aecidium on

Peltandra is more spherical in form and less caeoma-like. My material of the aecidia on *Peltandra* was poorly fixed and only a few sections were cut. It is evident from these, however, that the general shape of the cup here is as RICHARDS has drawn it. A comparative study of the aecidia on these two hosts should be of interest in determining the relative influence of the host tissues on the morphology of the fungus.

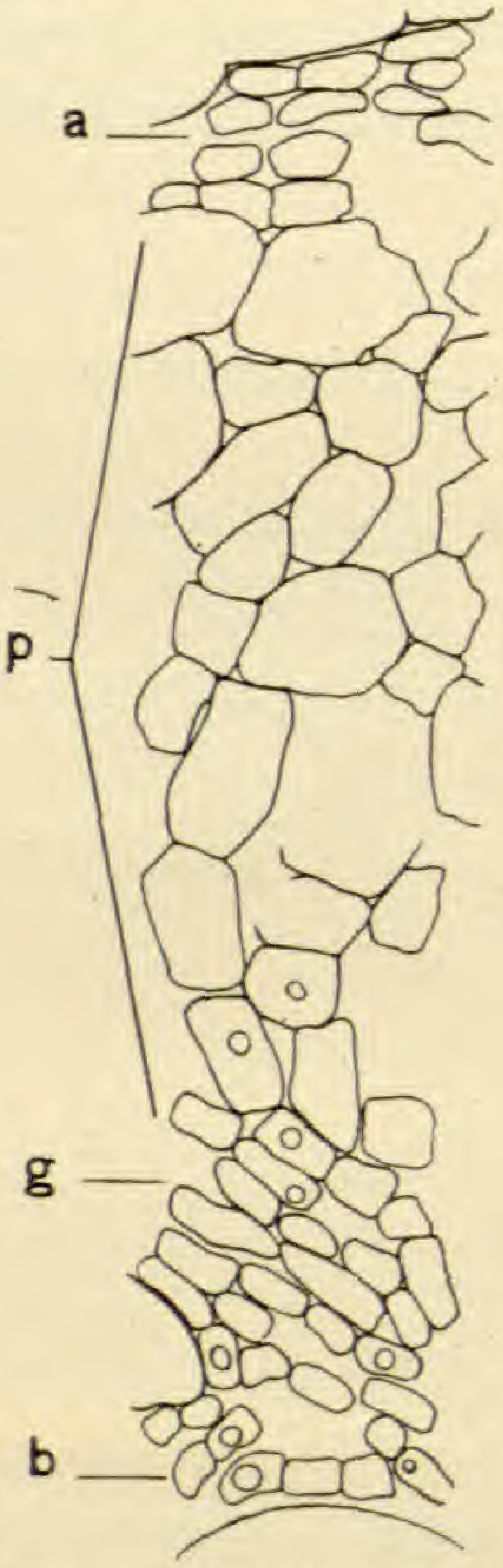

FIG. 3.—Section through the young aecidium of *P. Eatoniae*: *a*, apical surface; *b*, basal surface; *g*, gametic tissue; *p*, pseudoparenchyma.

The aecidia of *P. angustata*, *P. Hydrocotyles*, and *P. Eatoniae* are less favorable for study than any of the foregoing species. The cells of the young aecidia of these forms form a more compact hyphal mass, in which the direction of the individual hyphae is more difficult to trace. The pseudoparenchymatous tissue of all 3 forms is extensive and reaches to the lateral surfaces of the young aecidia, and to a deep point at their basal surfaces. My material of these forms was somewhat old, and the series of early stages is consequently less complete than in the case of the others. The directions of growth of the hyphae and their differentiation into the tissues of the cup are essentially similar to those described for *P. Claytoniata*. The gametes of these forms are not so sharply differentiated from the cells of the pseudoparenchyma and the underlying vegetative tissue, and often cannot be distinguished with certainty except when found fusing.

Since all my material of *P. angustata* was rather old, the gametes or fusion stages were not observed. The location of the two-legged basal cells seen (figs. 26, 27) seems to indicate that the gametes lie at the very bases of the perpendicular gametophoric hyphae. In *P. Eatoniae* the perpendicular hyphae are completely sterilized and the gametes are found in the upper two or three layers of the horizontal hyphae that line the basal surface of the hyphal mass. This condition is illustrated in text fig. 3. The general direction of the hyphae on the lower border of the figure is tangential to the curved basal surface of the mass. These horizontal hyphae are present in all forms, and, as previously stated, give rise to the perpendicular hyphae. Fusions between cells of these horizontal hyphae are sometimes found in *Ur. Caladii*, but the gametes of this species are normally borne in the perpendicular hyphae. In *P. Eatoniae*, however, the gametes seem to be normally formed in these horizontal hyphae. *P. Hydrocotyles* is more like *P. Claytoniata* in the position of the gametes (text fig. 4). About 5 or 6 cells are found in the perpendicular hyphae below the pseudoparenchyma, and apparently any of the cells in this tissue may function as gametes.

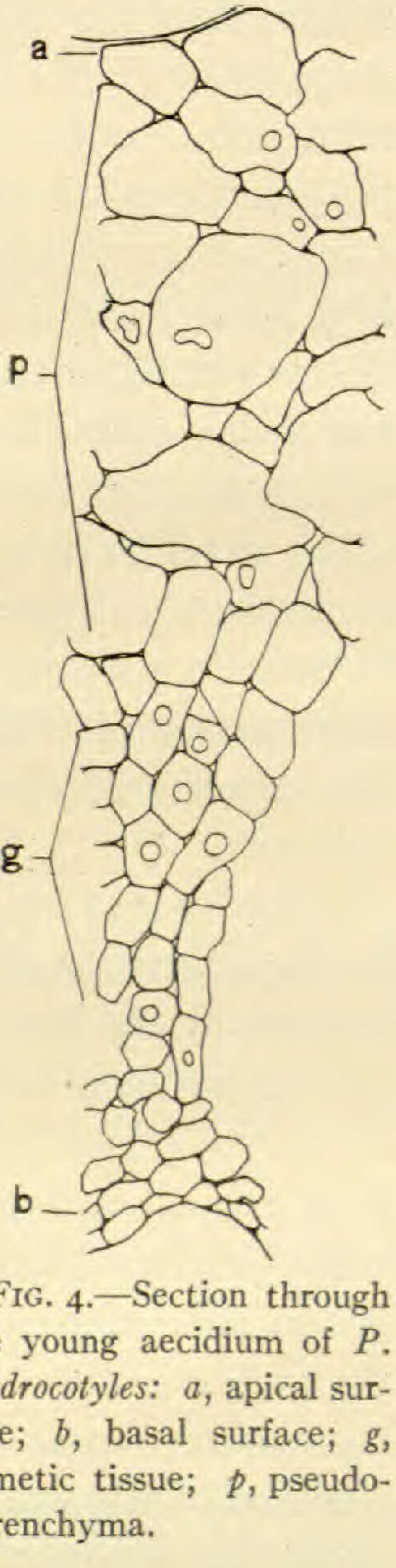

FIG. 4.—Section through the young aecidium of *P. Hydrocotyles: a*, apical surface; *b*, basal surface; *g*, gametic tissue; *p*, pseudoparenchyma.

Sexual fusions and spore-production

The fertilization in all these forms is accomplished by the fusion of two closely associated gametes that are normally equal in size and position. The first fusions are found in the central part of the gametic tissue, and the wave of fusions proceeds from this center toward the lateral borders of the aecidium. The fusions are quite abundant, and, though not so readily distinguishable as in the caeomas, many may be found in a favorable section (fig. 23). The process of fusion is identical with that found in the caeomas, and involves the dissolution of an area of the adjoining cell walls between two gametes. The gametes before the fusions are more or less differentiable by their size, the size of their nuclei, and the density of their cytoplasm. The nucleoles are especially large and conspicuous.

The dissolution of the walls may take place anywhere in the region of contact between the gametes. They usually lie in parallel hyphae with their lateral walls in contact, and when they are in this position and are of equal height, the initial point of dissolution is usually near the middle of the cells or slightly above. A small pore is first formed. Figs. 4 and 5 are of early fusion stages between gametes of *P. Claytoniata*, and fig. 20 between those of *P. Violae*. As a rule, the dissolution of the walls continues on all sides of this pore until practically all of the adjoining walls have been dissolved away. Figs. 6, 16, 17, 21–24 show this condition in various forms. Fig. 23, of *P. Hydrocotyles*, is of especial note since three fusions are shown clearly within a small area. The figure shows further that the fusing cells have no definite position in the hypha or tissue in which they are borne. The two gametes on the right lie immediately beneath the pseudoparenchyma. Those in the center are considerably deeper in the tissue and are the third and fourth cells below the pseudoparenchyma of the respective hyphae in which they are found, while the pair on the left is placed midway between the others. A binucleated basal cell lies above the left gamete of this pair.

The fusions found in *P. Eatoniae* are different from those found in the other forms in that the gametes are located in horizontal hyphae at the base of the cup. A completed fusion between two such gametes is shown in fig. 24, and just above this lies the base of a two-legged basal cell. The upper part of the basal cell has been cut off in sectioning. The right gamete of the basal cell is the adjoining cell in the same hypha with the upper gamete of the fusion cell. Four layers of horizontal hyphae are found between the fusion cell and the host cell that marks the lower boundary of the sorus. According to HOFFMAN (15), the gametes of *Endophyllum Sempervivi* are also formed in horizontal hyphae near the base of the cup, and his figs. 1, 3, and 4 are very similar to corresponding stages in *P. Eatoniae*.

When the fusion of the gametes is completed, the fusion cell elongates in the direction of the epidermis and the nuclei move up into the central part of the cell (figs. 19, 22, 25–27). In *P. Eatoniae*, where the gametes lie in a horizontal position, the elongated part of the fusion cell often turns up at a sharp angle, as in fig. 25. The cytoplasm of the fusion cells is more dense in the upper and central part and is often vacuolate in the base. For this reason it is often impossible to make out the two-legged character of an old fusion cell. Further, the fusion of the cells is often complete, and this also serves to make the detection of fusion cells more difficult in the cup aecidia than in the caeomas, where the fusion is usually between the tips of the gametes, and the bases remain distinct. After the elongation of the fusion cell, the nuclei divide conjugately in the upper central part. In the early stages of division the two spindles stand out sharply (fig. 10). They lie parallel to each other, with their poles in the long axis of the fusion cell. The process of mitosis was not studied in detail, but it seems evident, from the examination of a number of stages in both gametophytic and sporophytic cells, that the essential features are as described by OLIVE (**22**). The spindle figures in the early stages are very small. No central bodies could be differentiated at the poles and radiations were only rarely seen. Fig. 11 shows a late anaphase with the dumb-bell-shaped appearance that has been figured by many investigators of nuclear division in the rusts.

With the completion of the conjugate nuclear division, the fusion cell divides and the apical one-third, containing two daughter nuclei from separate spindles, is cut off (figs. 8, 14). This cell, the so-called aecidiospore mother cell, or, as it should more properly be termed, the aecidiospore initial cell, redivides soon afterward, producing the aecidiospore and the small intercalary cell. The basal cell meanwhile elongates and repeats the process of nuclear and cell division. Fig. 8 shows a distinctly two-legged basal cell of *P. Claytoniata*. Both the basal cell and the aecidiospore initial cell are four-nucleated as the result of conjugate division. The subsequent divisions of the basal cell and aecidiospore initial cell produce a catenulate series of alternating aecidiospores and intercalary cells.

The terms "fusion cell" and "basal cell" are not synonymous as I have used them. The fusion cell is the immediate product of the sexual cell fusion and may or may not function as a basal cell. It becomes a basal cell with the production of aecidiospores. The basal cell is a conidiophore ("basidium" of the earlier writers) from which the spores are abstricted. The term "basal cell" may with this understanding be used with reference to the conidiophore of any of the spore forms found in the rusts, while the term "fusion cell" should be restricted to indicate the cell in which the transition from the uninucleated to the binucleated condition occurs.

In addition to the normal cell fusions between two gametes a number of cases of triple cell fusions were found. Two of these are illustrated in figs. 7 and 18. Fig. 7 is of *P. Claytoniata* and fig. 18 of *Ur. Caladii.* In both of these cases the three fusing cells lie in separate hyphae. In one or two other cases found two of the gametes came from the same hypha. Similar cases have also been found in *Mel. Lini* (**12**, fig. 18). The trinucleated fusion cells resulting from a fusion of three cells may function as basal cells. In this case the three nuclei divide simultaneously (figs. 12, 13), in the same manner as those in the binucleated fusion cells, and trinucleated aecidiospores and intercalary cells are formed. In fig. 9 a trinucleated aecidiospore initial cell has been abstricted from a trinucleated basal cell. The basal cell appears two-legged, but it is probable that one of the legs has been cut off in the section. Mature trinucleated aecidiospores are quite common in *P. Claytoniata;* several are often found in one section of a mature cup. They are somewhat less common in *Ur. Caladii* and *P. Violae* and are only rarely met with in the other forms.

Quadrinucleated aecidiospores were also found, but in fewer numbers than the trinucleated ones. A chain of quadrinucleated cells is shown in fig. 14. The apical aecidiospore of the chain contains 4 nuclei, while none are visible in the intercalary cell below it. Only 3 nuclei appear in the next aecidiospore, but the subtending intercalary cell is distinctly quadrinucleated. The lowest cell of the chain is probably an undivided aecidiospore initial cell. The 4 nuclei are arranged serially in the long axis of the cell. The chain was cut off at this point in the section and could not be located in adjoining sections. While no four-cell fusions nor four-legged basal cells were found, there can be little doubt that these occur in the cupulate aecidia as well as in the caeoma of *Mel. Lini* (**12**).

Many of the fusion cells formed undoubtedly do not function as basal cells for lack of space. Those in the upper part of the gametic tissue, immediately beneath the pseudoparenchyma, are more favorably located for spore-production than those that lie more deeply in the tissue. The elongation of the fusion cell formed at the surface of the tissue is unimpeded except for the slight resistance offered by the empty, thin-walled cells of the pseudoparenchyma, while the fusion cell formed below must force its way between the closely packed gametes and fusion cells above. Sometimes they are able to do so and function as basal cells, but many were found that were apparently inhibited from so functioning by the resistance of the overlying cells.

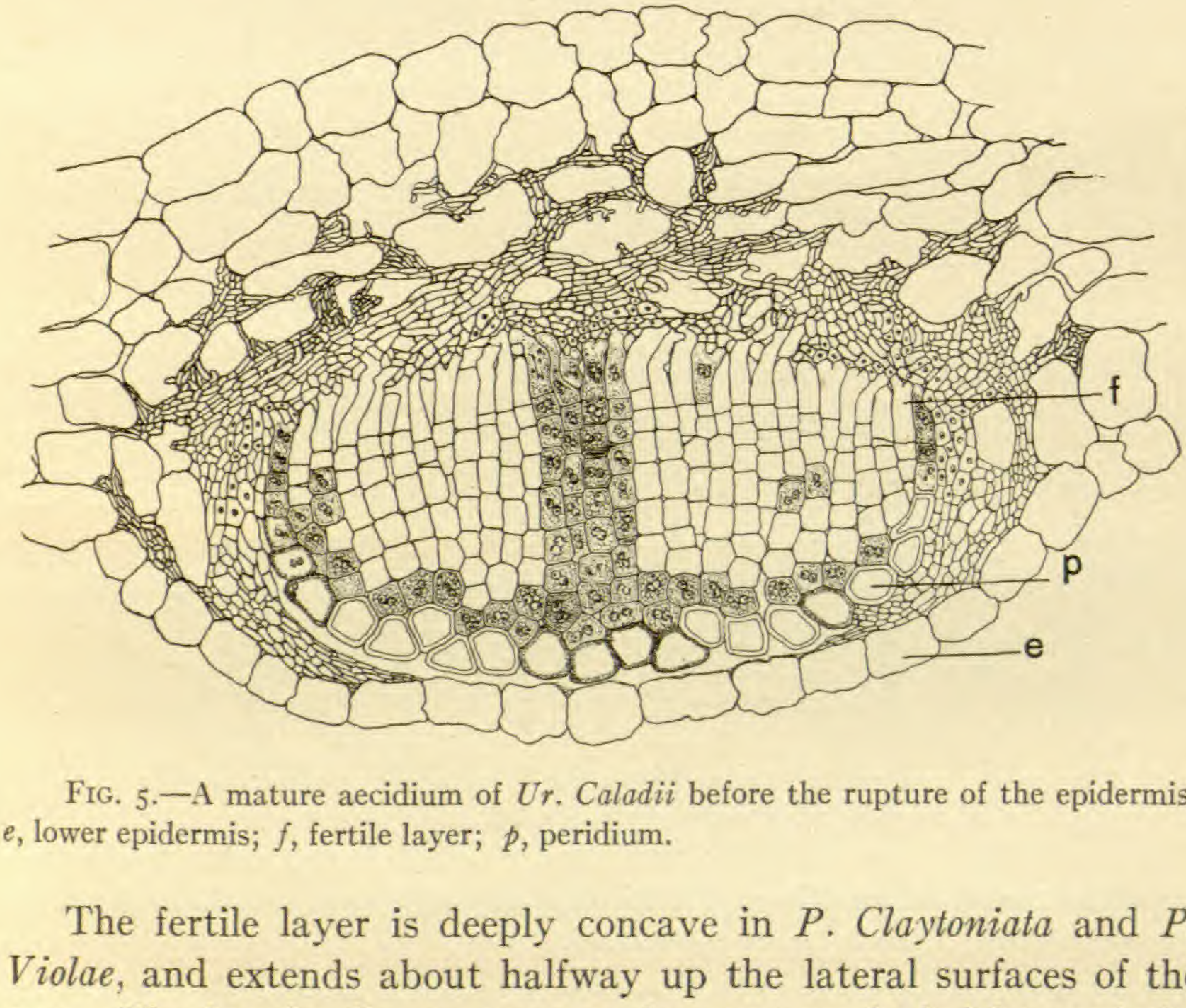

FIG. 5.—A mature aecidium of *Ur. Caladii* before the rupture of the epidermis: *e*, lower epidermis; *f*, fertile layer; *p*, peridium.

The fertile layer is deeply concave in *P. Claytoniata* and *P. Violae*, and extends about halfway up the lateral surfaces of the cup. The basal cells are more or less uneven in height, and the surface of the layer in outline has an irregular, broken appearance. The fertile layers of *Ur. Caladii* (text fig. 5) and of *P. Eatoniae* (text fig. 6) are especially broad and only slightly concave. The fertile layers of *P. Hydrocotyles* (text fig. 7) and of *P. angustata* are narrow and only slightly concave. The production of spore chains is confined to the basal surface of the cup and does not occur on the lateral surfaces. The basal cells of *P. Hydrocotyles* (text fig. 7) form quite an even palisade and their bases converge toward a central point below. This conveys the impression that they may have arisen from a common central point or area.

Spore-production follows very rapidly after the fusions. The first spores formed are from the basal cells at the center of the fertile layer in the region where the first fusions occurred. The wave of spore-production proceeds from this center toward the borders of the fertile layer and follows closely after the fusion wave. The central basal cells continue to cut off spores and have usually produced a chain of 3 or 4 when the first spores are being produced from the basal cells on the extreme lateral margins of the fertile layer. The number of spores found in any one chain at this stage is dependent on the position of the basal cell with reference to the center of the fertile layer. The number decreases gradually from 3 or 4 at the center to one at the lateral margins. The surface of the spore mass is thus dome-shaped, with the highest point of the

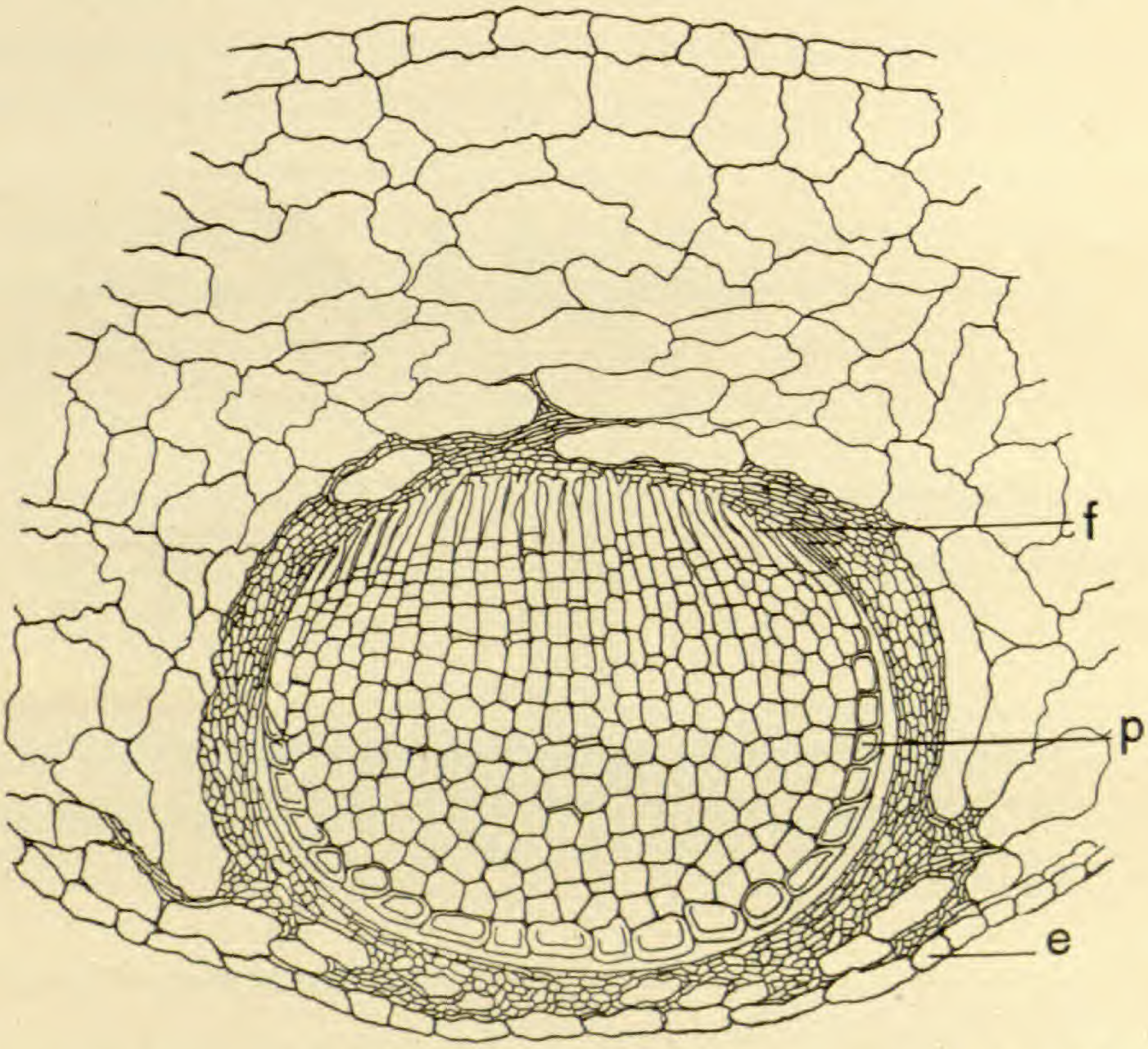

FIG. 6.—A mature aecidium of *P. Eatoniae* before the rupture of the epidermis: *e*, lower epidermis; *f*, fertile layer; *p*, peridium.

dome at the center. It is convex in vertical section, while the surface of the fertile layer is concave. The mass of spores forms an ellipse, the long axis of which is parallel to the epidermis.

The production of spores now proceeds at a uniform rate across the entire extent of the fertile layer, and the dome-shaped roof of the spore mass is elevated or pushed toward the epidermis. The thin-walled, empty cells of the pseudoparenchyma apparently offer but little resistance. They are crushed and pushed upward or to one side, and either disappear entirely or remain as a thin layer of material without cellular structure. Meanwhile the leaf epidermis has been pushed up as an arch over the developing spore mass, as the result of the pressure, and when the pseudoparenchyma has

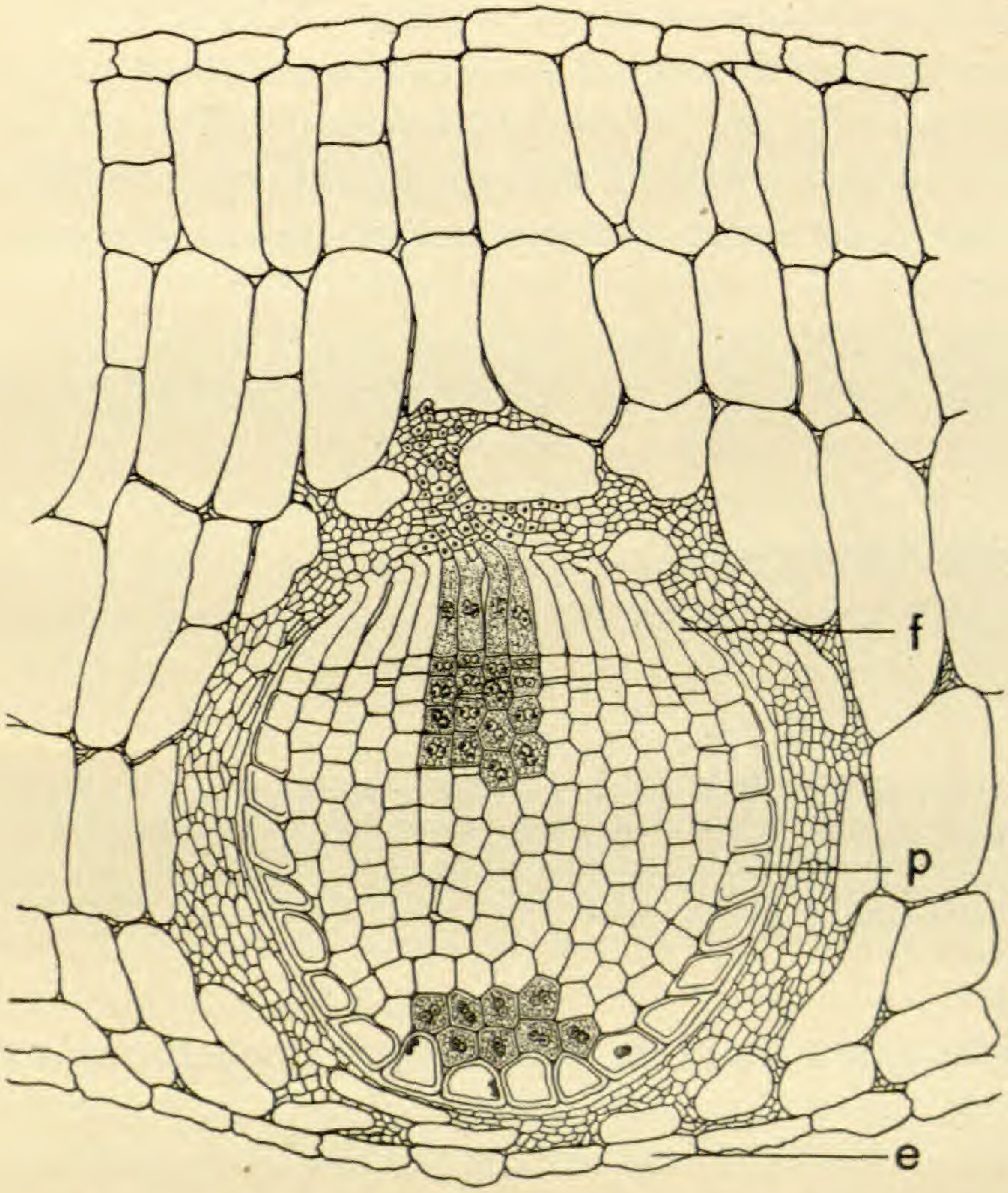

FIG. 7.—A mature aecidium of *P. Hydrocotyles* before the rupture of the epidermis: *e*, lower epidermis; *f*, fertile layer; *p*, peridium.

been entirely pushed away and the top of the spore mass presses directly on the epidermis, the arch is ruptured at the center.

Development of the peridium

The peridial cells make their appearance with the enlargement of the spore mass. The first peridial cells are seen at the apex of the dome-shaped spore mass, and are first distinguishable from the aecidiospores when the central spore chains are about 5 or 6 spores in length (text fig. 8). These first-formed peridial cells are produced by a metamorphosis of the apical aecidiospores of the central chains that involves an enlargement of the aecidiospore in all dimensions, a decrease in the density of its cytoplasm, and a marked thickening of its walls. The diameter of the mature peridial cell is about one and one-third times that of the mature aecidiospore, or more. The length of the cell is greater than the breadth, and its long axis is parallel to the axis of growth of the spore chain in which it is borne. This feature of the peridial cells is of some value in determining their point of origin, as will be seen later.

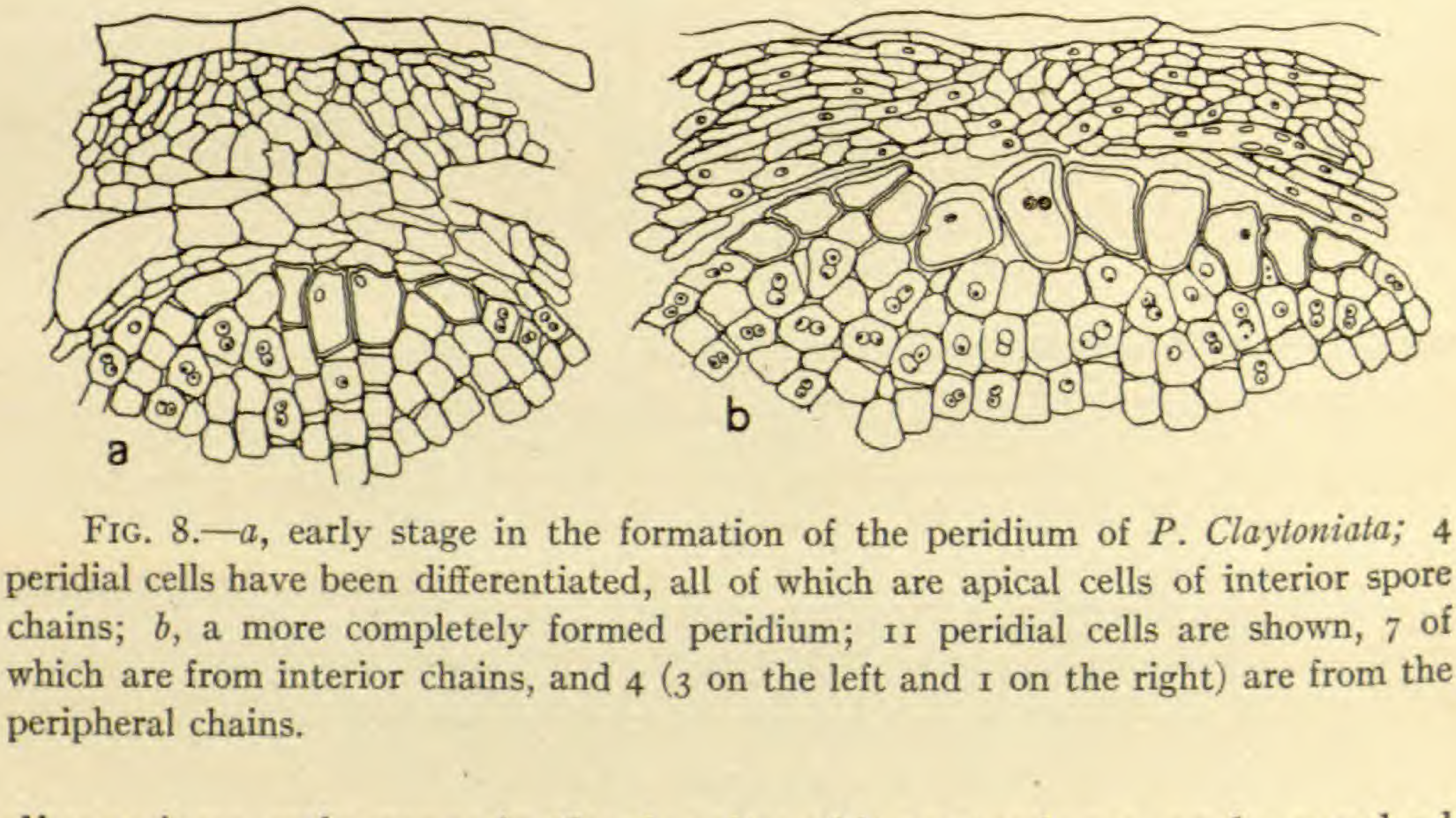

FIG. 8.—*a*, early stage in the formation of the peridium of *P. Claytoniata;* 4 peridial cells have been differentiated, all of which are apical cells of interior spore chains; *b*, a more completely formed peridium; 11 peridial cells are shown, 7 of which are from interior chains, and 4 (3 on the left and 1 on the right) are from the peripheral chains.

An early stage in the development of the peridium of *P. Claytoniata* is shown in text fig. 8, *a*. Only 4 peridial cells have been differentiated in this section. The walls of these are drawn with a double line. Three of them are apical cells of central spore chains, and the fourth is the apical cell of the fourth chain from the right-hand border. The extreme outer border chains have as yet produced no peridial cells, and it is evident that the 4 peridial cells shown in the figure could not have been produced by them. The figure shows, further, that not all of the interior spore chains produce peridial cells, since the apices of some of these do not reach to the outer surface of the spore mass. A more complete peridium at a later stage is shown in text fig. 8, *b*. Eleven peridial cells appear in this section; 7 of these have apparently been borne on interior chains, although their connection with any one chain cannot be determined with certainty. The long axes of these cells are perpendicular to the epidermis and parallel to the axis of growth of the interior chains. The other 4 peridial cells, 3 on the left and 1 on the right, are evidently borne in the peripheral chains. It is also evident from this figure that not all of the interior chains have produced peridial cells, since there are 20 interior chains and but 7 peridial cells of interior origin.

While the peridial cell is forming, its connection with the spore chain on which it is borne is evident (text fig. 8), but with its enlargement at maturity and the changes in its position brought about by the continued elevation of the spore mass, this connection is made difficult or impossible to determine.

Not all of the peridium is formed from sterilized apical aecidiospores; its lateral walls are made up of the entire peripheral spore chains (text fig. 8, *b*). The cells of these chains are distinguishable as peridial cells when they have become the third or fourth cell from the base of the chain. The cells that make up the lateral walls of the peridium are differentiable from those that form the central arch in that they are modified aecidiospore initial cells rather than aecidiospores. They do not, except perhaps in rare cases, produce intercalary cells. Both the cytokinesis and karyokinesis of these cells are apparently inhibited by the same agent that produces the metamorphosis of the cell.

The production of peridial cells proceeds from the central point of the apical surface of the spore mass outward in all directions until a complete layer is formed over the entire apical and lateral surfaces of the spore mass. The peridium of this type of aecidium is normally but one cell in thickness. It is interesting to note, however, that two or more layers of peridial cells are apparently formed regularly in certain species of *Peridermium* (3). When the peridium is completed over the entire outer surface of the spore mass, its subsequent enlargement is accomplished entirely by the basipetal addition of cells to its lateral walls from the peripheral basal cells.

The cytoplasm of the mature peridial cell is vacuolate and the nuclei are smaller and more compact than those of the aecidiospore. It is difficult to be sure whether they have decreased in size with the metamorphosis of the cell or whether they have not been completely reconstructed from the preceding mitosis. The latter explanation seems more probable and is supported by some observations that are not, however, conclusive. In size and general appearance they resemble the nuclei of the intercalary cells. They do not become disorganized; the chromatin masses and nucleoles stain deeply and are sharp and clean-cut. The walls stain with the orange, and a properly stained peridial cell is easily distinguished from an aecidiospore by the thickness of the wall as well as by the comparative emptiness of the cell and smallness of the nuclei. The outer side of the wall, the one next the pseudoparenchyma, is thicker than the inner or lateral sides (fig. 15). This was true to some extent of all of the forms I have studied. The nuclei are often located near the thickest part of the wall. The process of wall-thickening accompanies the decrease in the density of the cytoplasm, and the natural assumption is that the thickening is produced by the deposition of substances from the cytoplasm. No stratification appears in the walls. They may be variously sculptured, however, and the outer portion of the wall is usually marked by transverse striae.

The origin of the peridium is more easily followed in the broad cup of *Ur. Caladii* than in any of the other forms. The greater part of the peridium that is formed here before the rupture of the epidermis originates from interior spore chains. This is apparent even in mature cups, as shown in text fig. 5, which is a semi-diagrammatic representation of a stage before the rupture of the epidermis. Of the peridial cells shown here, 14 are in all probability of interior chain origin. There are about 29 interior chains.

It seems that in general the shape of the cup and the breadth of the hymenium determine the relative numbers of peridial cells of peripheral and interior origin. If the cup is shallow and the fertile layer broad, as in *Ur. Caladii*, the number of those of interior origin will be comparatively greater than when the cup is deep-seated and spherical and the fertile layer narrow, as in *P. Hydrocotyles* (text fig. 7).

So far as I am aware, no estimate of the approximate number of spores produced in an aecidium cup has been made. A comparatively accurate estimate of the number produced in the aecidium of *P. Eatoniae* was made as follows: The spore chains in median sections of 10 mature aecidia were counted. The average number found was 32. Since the cup is circular in cross-section, its radius would be 16 and the area of the cross-section 804.24. The average number of spores per chain (10), multiplied by the number of spore chains (804.24), gives a total production of 8042 spores. The estimate of 10 spores per chain is low, since the count was necessarily made before the opening of the cup, and the production of spores probably goes on for some time after this.

WOLF (**29**) has recently called attention to the production of internal aecidia of *P. angustata* on *Lycopus virginicus*. These were found principally in sections of stems and petioles. The cups are very deep-seated, and being unable to reach the epidermis discharge their spores into the parenchyma or the pith cavity. No internal aecidia appear in any of my sections of this species, as they are all of leaf tissue. I have found cases of internal spermogonia, however, in *P. Claytoniata*. These were buried at considerable depth in the parenchyma of the stem, but were normal in other respects. The spermatia had been discharged in some cases and were found in the intercellular spaces above the ostiole. Still more curious were several cases of intimate association between spermogonia and aecidia in which the spermogonium was borne in the center of an aecidium. None of the aecidia in these cases had reached the stage of sporulation, but the spermogonia had produced spermatia in abundance. The condition is evidently abnormal, but could have been construed as proof of a sexual relation between the spermogonium and aecidium by the older exponents of this view. It does show the similar and perhaps interchangeable nature of the mycelia that produce the two fructifications.

Discussion

From the evidence gained from the study of the 6 species of aecidia treated here, the conclusion is reached that the essential processes involved in the development of the cup and caeoma types of aecidia are similar. The gametes of the two are apparently similar in origin. They are borne, in both types of sori, in perpendicular hyphae, but those of the cup are less markedly differentiated in size from the surrounding cells than those of the caeoma. Fertilization is accomplished in the cup, as in the caeoma, by complete cytoplasmic union between two morphologically equivalent gametes and produces a double, binucleated cell that later functions as the basal cell for a chain of aecidiospores. The fertile layer of both types enlarges by centrifugal growth, the first fusions occurring at the center of the gametic tissue and the last ones at the lateral margins. The breadth of the fertile layer of the cup is determinate, being limited by the breadth of the primordium and the layers of encircling hyphae on the lateral surfaces, while that of the caeoma is somewhat indeterminate, the only apparent limiting factor being the food supply.

The development of a peridium in the cup is the only sharply distinctive feature that separates the two types of aecidia. The peridium is formed as an outer layer of sterilized, differentiated cells that covers and presumably protects the spores beneath. The origin and growth of the peridium were found to conform in all essentials to RICHARDS' descriptions (27). It is composed of metamorphosed aecidiospores and aecidiospore initial cells that are not differentiable from the others, before their metamorphosis, except by their position on the periphery of the spore mass. The central part of the arch of the peridium is formed from the modified apical aecidiospores of the interior spore chains, while the lateral walls are formed from the undivided aecidiospore initial cells of the peripheral chains. The peridium, like the fertile layer, enlarges centrifugally. The cells at the center of the arch are first differentiated and the differentiation proceeds from this point outward in all directions until a complete layer is formed over the entire mass. The subsequent enlargement of the peridium is accomplished by the basipetal growth of the lateral chains of peridium initial cells.

The "buffer" cells of the caeoma are homologous with the pseudoparenchyma cells of the cup, and represent a scanty production of pseudoparenchyma. The production of a peridium seems to be dependent on the presence of a considerable pseudoparenchyma, and this is in turn the result of the deep location of the primordium in the host tissue, and the deep location of the gametes in the primordium.

As I have elsewhere stated (**12**), in the caeoma of *Mel. Lini* the gametophoric hyphae are 3 or 4 cells long. Two sterile cells are normally produced, and though, as a rule, but one gamete is formed in each hypha, two are occasionally found. In the production of more than one sterile cell and the tendency to produce more than one gamete there is seemingly a transition toward the conditions found in the cup. The cup of *Ur. Caladii*, as found on *Arisaema*, is very much like a caeoma in appearance before the formation of the peridium. The gametophoric hyphae are 6 or 7 cells in length, and 4 or 5 of the apical cells are sterilized. If, as I have suggested, the production of a peridium is correlated with the amount of pseudoparenchyma produced, the line of separation between the aecidia without and those with a peridium should be found at some point between the caeoma of *Mel. Lini* with 2 sterile cells, and the cup of *Ur. Caladii* with 4 or 5. A careful study of the more deeply seated caeomas may perhaps reveal a more or less marked differentiation of the outermost spore layer. Those species of cupulate aecidia with evanescent peridia are perhaps most nearly like the deep caeomas.

The study of the origin of the peridium that is found in the uredosorus of certain genera should prove of considerable interest, but apparently no such study has ever been made and no data are available. According to ARTHUR's treatment of the Uredinales in the *North American flora* (**2**), 6 genera of the family Uredinaceae have uredosori with peridia: *Pucciniastrum, Melampsoridium, Hyalopsora, Uredinopsis, Melampsoropsis*, and *Cronartium*. *Melampsoropsis* has catenulate uredospores, while those of the remaining 5 genera are reported as pedicellate. A peridium of the type found in the aecidium cup is to be expected in a deep-seated uredosorus of catenulate spores, but is scarcely to be looked for in a sorus of pedicellate spores, where the supposed protective function is normally performed by paraphyses.

No central organs ("fertile hyphae") or multinucleated cells were found in any of the species of aecidia studied, and it is therefore concluded that these do not necessarily occur in aecidia of the cup type. While this by no means precludes the production of multinucleated cells in other species, it is evidence that these are not necessary for the development of the centralized structure of the cup. It is perhaps possible that the multinucleated cells found by OLIVE in certain cupulate aecidia are the result of multiple cell fusions. The presence of tricellular fusions and trinucleated and quadrinucleated aecidiospores in several of the species I have studied shows that pluricellular fusions are rather common in the cup as well as in the caeoma.

The aecidium cup, from the evidence presented here, is not to be regarded as an organ with a centralized development like that of the ascocarp, as DEBARY and others have considered it, but is seen to be merely a remarkably unified colony of individual gametophores. The presence of a central organ is no more necessary to the development of the cup than the caeoma. The existence of uredosori with catenulate spores, that arise from sporophytic mycelium and hence cannot be considered the product of central organs, is further evidence that a seemingly centralized fructification may be developed from a colony.

The presence of trinucleated spores in various rust sori has been noted by a number of investigators, and there seems to be no question that such spores, when found in the aecidium or the teleutosorus of the micro-forms, are the products of tricellular fusions. The germination of a trinucleated spore would be highly interesting to observe. HOFFMAN believes that one of the nuclei in trinucleated spores of *Endophyllum Sempervivi* degenerates, but has no convincing proof of this.

As previously noted, branching basal cells have been found in the aecidium of *P. Falcariae* by DITTSCHLAG and in the sorus of

Endo. Sempervivi by HOFFMAN. Although I have found no such cells in any of the aecidia included in this study, I have found a single case of a basal cell that seems to have given rise to a branch in the aecidium of *Aecidium Dicentrae* Trel. Only a few sections of this form have been examined, and hence no estimate can be made as to the prevalence of the condition. In the single case seen, the second basal cell seems to have arisen as a lateral branch of the primary basal cell, and the opening between the two has not been closed by wall-formation. Both basal cells have produced a chain of spores.

HOFFMAN compares these branching basal cells to the basal cell of the primary uredosorus as described by CHRISTMAN. The two cases, however, are not at all comparable. The basal cell of the primary uredosorus gives rise to successive stalked spores that originate as buds on the upper surface of the cell. The comparison is made, therefore, between a bud that produces a stalked spore in one case and a basal cell in the other. As CHRISTMAN has pointed out, the homology lies between the primary uredospore and stalk cell and the aecidiospore and intercalary cell. The homology is also extended to include the basal cells of the two sori.

According to CHRISTMAN, the basal cell is the true morphological unit, and the basal cells of the different sori are to be considered as homologous. This, however, involves the difficulty, which CHRISTMAN recognized, that the basal cells of the uredosorus and teleutosorus are not the outgrowth of fusion cells, as are those of the primary uredo and aecidium, but are borne on a mycelium of binucleated cells. The basal cell of the micro-forms is also without doubt to be homologized with that of the aecidium, since OLIVE'S work on *P. transformans* and that of WERTH and LUDWIGS on *P. Malvacearum* indicate that the basal cell of these forms is the outgrowth of a fusion cell.

The evident homology between the primary uredospore and the aecidiospore is used by CHRISTMAN as a strong argument that the eu-type of rust with catenulate aecidiospores cannot be considered as a primitive type, but is rather a highly specialized and derived type. If the homology is to be accepted, and it seems to have been very generally, the catenulate method of aecidiospore-production must have been derived from the pedicellate, and the primary uredo is therefore more primitive than the aecidium. For, as he argues, the intercalary cell is thus seen to be in reality a stalk cell that has been necessarily shortened by the catenulate method of spore-production and persists as a vestigial cell. If the aecidium, however, is considered the primitive sorus and the uredo the derived form, the intercalary cell must be considered a functionless structure that persists and is later modified into a structure of value to the organism in the stalk of the uredospore.

In view of this convincing explanation of the nature of the intercalary cell, one can scarcely agree with GROVE (13) that *Endo. Sempervivi* is to be considered as a representative of the primitive type of rusts. The fact that the spores of this species are borne in a complex aecidium-like fructification, surrounded by a peridium and accompanied by intercalary cells, makes its acceptance as a primitive type extremely difficult. To all morphological appearances the spores are aecidiospores and the sorus an aecidium. The spores, however, function as teleutospores, as HOFFMAN has conclusively shown. GROVE's acceptance of *Endophyllum* as a primitive type and his relegation of the micro-forms to the position of reduced types seem inconsistent when the relative complexity of the two types of sori are considered. It certainly seems more logical to consider *Endophyllum* a reduced form, as the gametophytic generation of a former eu-heteroecious or autoecious species that has dropped the uredo and teleuto stages, with the assumption of a teleutosporic method of germination by the aecidiospore, and to regard the micro-forms as the more primitive and ancestral. The assumption of the teleutosporic method of germination by an aecidiospore is not a difficult conception, since nothing more than the fusion of nuclei in the spore should be necessary for its accomplishment.

It is interesting to note that KUNKEL (17) has recently discovered a companion form to *Endo. Sempervivi* in the common orange rust of the blackberry, *Caeoma nitens*. The life history of the two species is practically identical, seemingly, but the sorus of the latter is a caeoma, while that of the former is an aecidium cup. *Caeoma nitens*, therefore, should offer a much better ancestral type for

GROVE's argument than *Endo. Sempervivi* because of the relative simplicity of the sorus, but the presence of intercalary cells, on the other hand, is a strong argument against its acceptance as such.

GROVE advances the perennial nature of the mycelium of *Endo. Sempervivi* as further proof of the primitive nature of the fungus. The perennial nature of the mycelium seems to me, however, a highly specialized condition. A more desirable relation from the standpoint of the continued welfare of the fungus is difficult to conceive. The fungus thus becomes independent of the chance association of hosts for its propagation. A decrease in the number of spore forms is perhaps to be expected with the increased efficiency of the perennial mode of life. The necessity for the production of resting spores is done away with, as well as the production of repeating spores for extensive propagation. A perennial mycelium is also found in certain of the short-cycled micro-forms, for example *P. fusca* and *P. Adoxae*, and it seems, therefore, that this condition cannot be advanced as proof of either a primitive or a derived condition. The efficiency of the perennial gametophytic mycelium may be one reason why the gametophyte has maintained the supremacy and these micro-forms have persisted as such.

The remarkable cases of correlation between the teleutospores of certain micro-forms and those of certain eu-heteroecious forms that have been cited by FISHER (11) and others are certainly strong evidence of a phylogenetic relation between the two groups. Further study of this phase of rust morphology will doubtless bring to light many groups of correlated species with life cycles of various lengths, and will in all probability settle many of the problems as to the origin and development of such types. The most reasonable view of the phylogeny of the rusts seems to me that of DIETEL as amplified by CHRISTMAN and OLIVE. This view regards the micro-forms as the most primitive forms, from which the brachy, opsis, and eu-forms have been derived by the lengthening of the sporophyte generation and the intercalation of aecidiospores and uredospores.

This work was conducted under the direction of Professor R. A. HARPER, to whom I am indebted for many helpful suggestions and criticisms.

Summary

1. The essential features in the development of the cup are similar to those found in the development of the caeoma. The initial hyphal mass, or primordium, is formed by hyphae growing radially toward the center of the future cup.

2. The cup is more deeply seated and produces a greater number of sterile cells and gametes to each gametophoric hypha. The gametes form a fertile layer two or more cells in thickness. The sterile cells that form the pseudoparenchyma of the cup are homologous with the "buffer" cells of the caeoma.

3. Sexual cell fusions, by the breaking down of the cell walls between two equal gametes, were found in 6 additional species of cupulate aecidia, namely *Ur. Caladii*, *P. Claytoniata*, *P. Violae*, *P. Hydrocotyles*, *P. Eatoniae*, and *P. angustata*. Although the actual fusion stages were not seen in the last named species, the presence of two-legged basal cells is evidence that the fusions are of the same type as those found in the other species. No central organs ("fertile hyphae") or multinucleated cells were found. The organization of the cup, therefore, is merely that of a remarkably unified colony of gametophores.

4. Triple cell fusions were observed in *P. Claytoniata* and *P. Violae*, and trinucleated aecidiospores were frequently found in both of these species and in *Ur. Caladii*. Several quadrinucleated aecidiospores and a chain of quadrinucleated cells were found in *P. Claytoniata*.

5. The first fusion cells are formed at the center of the gametic tissue, and the subsequent ones are formed on all sides of this center in centrifugal order, until the lateral borders of the aecidium are reached.

6. The fusing cells may have their long axes in general in the long axis of the cup, for example *P. Claytoniata*, *P. Violae*, *P. Hydrocotyles*, and *Ur. Caladii*, or tangential to its curved basal surface, for example *P. Eatoniae*.

7. The presence or absence of a peridium is a natural but not very fundamental distinction between the aecidium cup and the caeoma. The production of a peridium is correlated with the deep location of the cup and the extensive formation of sterile cells.

8. As has long been known, the peridial cells are metamorphosed aecidiospores and aecidiospore initial cells. The central arch of the peridium is formed from the apical aecidiospores of the interior spore chains and the lateral walls from entire peripheral spore chains. The first peridial cells are produced at the center of the arch and the peridium enlarges from this point centrifugally until the bases of the lateral walls are reached. Its subsequent enlargement is by the basipetal growth and sterilization of the peripheral spore chains.

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EXPLANATION OF PLATES I AND II

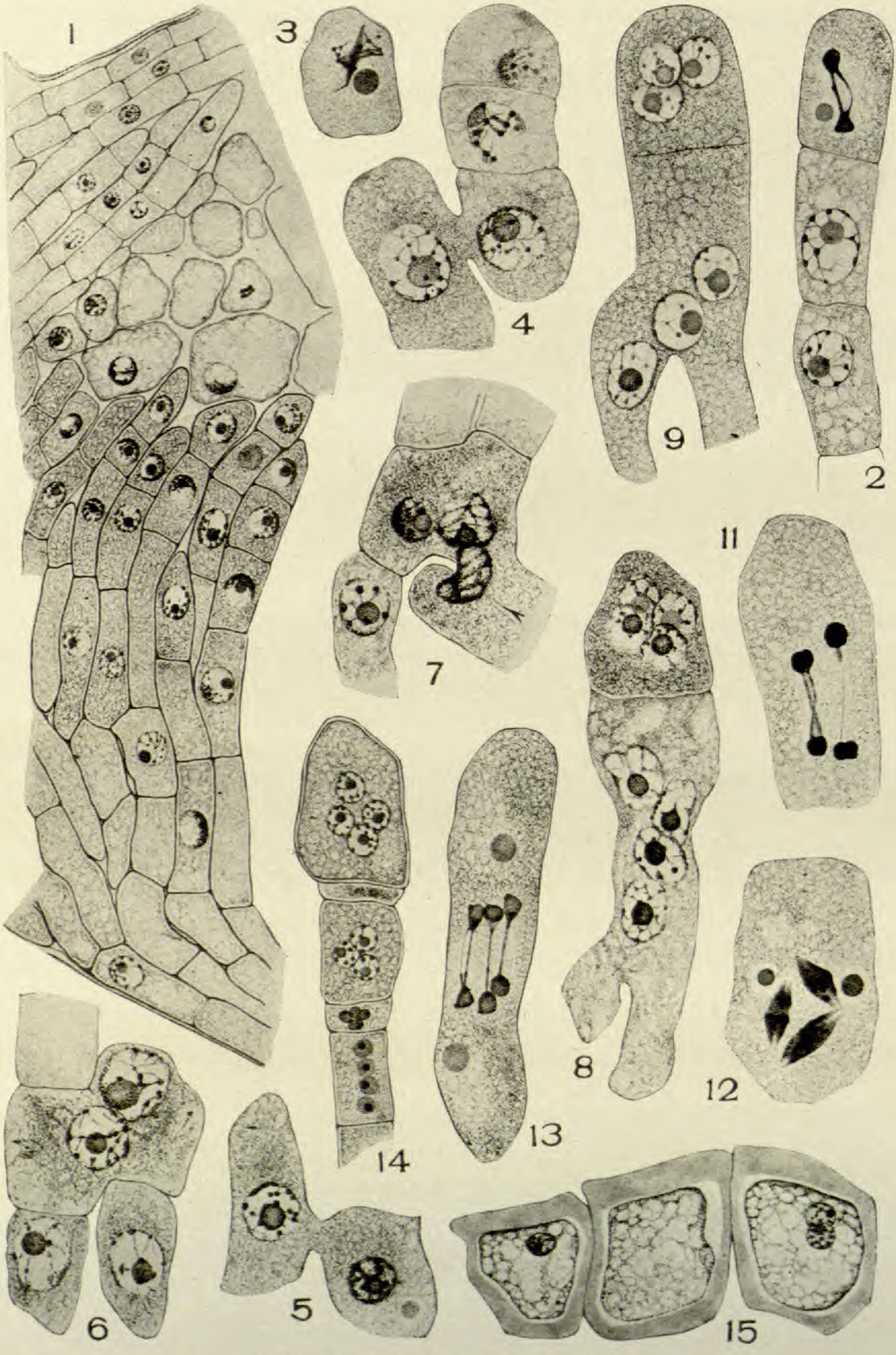
All of the figures were drawn with the aid of the camera lucida, and, except where otherwise mentioned, at a magnification of 1140 diameters. They are all placed in their natural position in the sorus, with the top of the page representing the direction of the leaf epidermis.

Puccinia Claytoniata

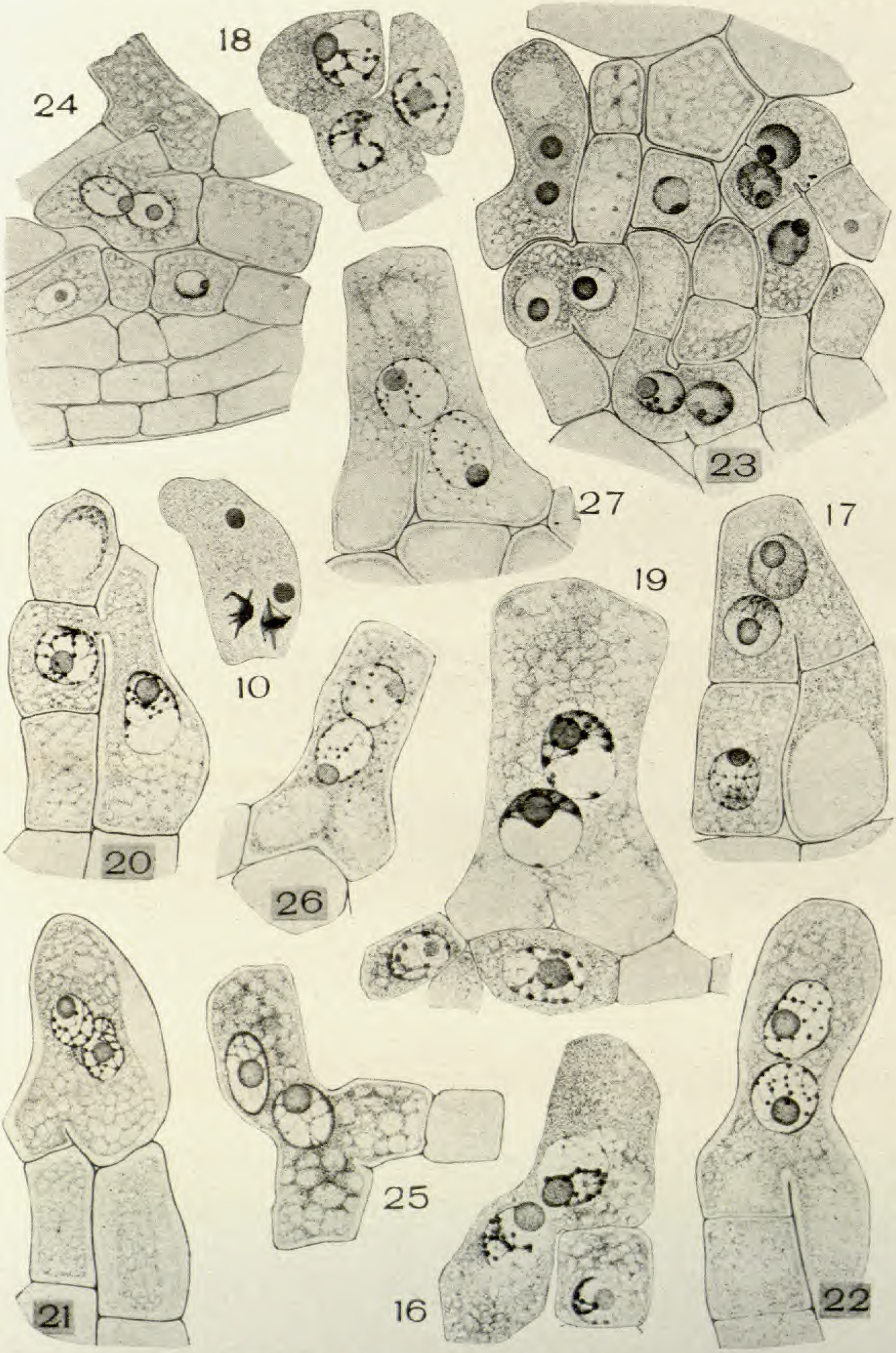
FIG. 1.—A section through the lateral border of the cup before the cell fusions; 6 layers of encircling hyphae are seen at the top, below these are the sterile cells of the pseudoparenchyma and below these the perpendicular gametophoric hyphae; all of the cells are uninucleated; ×570.

FIG. 2.—A more highly magnified view of the tip of a gametophoric hypha in a young aecidium; the nucleus of the apical cell is shown in the anaphase of mitosis.

FIG. 3.—An earlier stage of mitosis in a uninucleated cell.



FROMME on AECIDIUM CUP



FROMME on AECIDIUM CUP

FIGS. 4 and 5.—Two early stages of cell fusions.

FIG. 6.—A completed cell fusion.

FIG. 7.—A tricellular fusion.

FIG. 8.—A two-legged basal cell and above it an aecidiospore initial cell; 4 nuclei are found in both cells as the result of the preceding conjugate divisions; ×900.

FIG. 9.—A trinucleated basal cell and aecidiospore initial cell.

FIG. 10.—Early stage of conjugate mitosis in an aecidiospore initial cell.

FIG. 11.—Anaphase of conjugate mitosis in a fusion cell.

FIG. 12.—Simultaneous division of three nuclei in a fusion cell.

FIG. 13.—A later stage than the preceding; the elongated spindles lie parallel with each other and the long axis of the fusion cell.

FIG. 14.—A chain of quadrinucleated aecidiospores and intercalary cells; ×570.

FIG. 15.—Three peridial cells from the central region of the peridium; ×570.

Uromyces Caladii

FIGS. 16 and 17.—Two cases of completed cell fusions.

FIG. 18.—A tricellular fusion.

FIG. 19.—A two-legged basal cell.

Puccinia Violae

FIG. 20.—A very early stage of cell fusion in which the fusion pore is still very small.

FIG. 21.—A completed cell fusion.

FIG. 22.—A two-legged fusion cell.

Puccinia Hydrocotyles

FIG. 23.—Three cases of cell fusion within a small area; the borders of two cells of the pseudoparenchyma are shown at the top of the figure.

Puccinia Eatoniae

FIG. 24.—Fusion between two cells in horizontal lying hyphae near the base of the sorus; the base of a two-legged fusion cell lies just above the fusing gametes.

FIG. 25.—A two-legged fusion cell that has bent up at a sharp angle and elongated in the direction of the epidermis.

Puccinia angustata

FIGS. 26 and 27.—Two-legged basal cells.

INVESTIGATIONS ON THE PHYLOGENY OF THE ANGIOSPERMS

NO. 2. ANATOMICAL EVIDENCES OF REDUCTION IN CERTAIN OF THE AMENTIFERAE

IRVING W. BAILEY AND EDMUND W. SINNOTT

(WITH PLATES III–V AND THREE FIGURES)

The earlier taxonomists by systematic studies, principally of external characters, have contributed much toward a truly natural classification of the angiosperms, but the problem is such an intricate one that in searching for a satisfactory solution evidence from all fields of botanical research must be considered and harmonized.

In view of the assistance given by comparative anatomists in elucidating the phylogeny of gymnosperms and lower vascular plants, the recent hypothesis of Professor JEFFREY and his pupils, in regard to the development of "aggregate," "compound," and "multiseriate" rays in dicotyledonous angiosperms, merits careful consideration by taxonomists, since, if shown to rest on secure foundations, it is likely to produce radical changes in existing systems of classification.

The "aggregate" ray hypothesis

The salient features of this hypothesis may be summarized as follows: The angiosperms have not been derived from the Bennettitales, but from ancestors which possessed only linear or uniseriate rays, such as are a well developed feature of the Coniferales. During the warmer times of the Mesozoic, sheets of parenchymatous tissue were "built up" from congeries of uniseriate rays about the traces of leaves which persisted for a number of seasons. The influence at work in the development of this tissue was originally the demand for the storage of assimilates descending from the large leaves of these earlier angiosperms. These "foliar" rays have persisted in their very primitive "aggregate" condition (composed of congeries of small rays), and in their more advanced "compound" condition (completely parenchymatous), in primitive families of the dicotyledons. With the advent of a severe winter season and the consequent acquirement of the deciduous habit in connection with the leaves, the organization of these storage systems about the leaf traces as permanent centers was no longer advantageous or desirable. Thus in the development of the "multiseriate" type of ray which characterizes the majority of living dicotyledons, the enlarged units of the aggregating mass of foliar ray tissue have been diffused more or less uniformly throughout the stem. Besides being less unwieldy, this system of smaller rays affords equally large capacity for storage and a more convenient general relation between conducting, supporting, and storage tissue.

The principal arguments in favor of this hypothesis were first formulated in a paper presented by JEFFREY ('09) before the Botanical Society of America at Baltimore.

> One of the most striking triumphs of modern plant anatomy is to have discovered many examples of recapitulationary confirmation of the principle of evolution. To take a modern and striking example, let us consider our common and flourishing northern genus, the oak. You are all familiar with the very broad rays which constitute so ornamental a feature of the structure of oak wood. You are likewise doubtless aware that the weight of paleobotanical evidence speaks for the derivation of the oaks from ancestors resembling the chestnuts, since the older oaks approach the chestnuts both in their foliage and in their reproductive organs. The wood of the chestnut differs, however, strikingly from that of oaks by the entire absence of large rays. It has been recently discovered that certain oaks of the gold gravels (Miocene-Tertiary) of California have their large rays composed of aggregations of smaller rays. In the seedlings of certain of our existing American oaks this condition, interestingly enough, is a passing phase, which by the loss of the separating fibers in the congeries of small rays produces the characteristic large rays of the adult. This condition of development in the living oaks is all the more significant because in certain breech-fertilized or chalazogamic amentiferous trees of the present epoch, such as the alder, the hazel, and the hornbeam, such aggregated, so-called false, rays are a permanent feature of structure in the adult. From the anatomical side, in the case of the lower Amentiferae, we have accordingly at the same time an interesting example of the general law of recapitulation and a confirmation of the view expressed by TREUB and NAWASCHIN, on evidence from the gametophytic and reproductive side, that the breech-fertilized Amentiferae are relatively primitive angiosperms.

The arguments blocked out in this paper have been elaborated under JEFFREY'S direction by several students (see bibliography).

Especially significant are two collateral lines of evidence which have played an important part in amplifying the original hypothesis. The first of these is concerned with the connection between certain "aggregate" and "compound" rays and the traces of leaves, a phenomenon which is said to indicate conclusively that "aggregate" and "compound" rays were "built up" for purposes of storing the assimilates descending from the large persistent leaves of mesozoic angiosperms. The second line of evidence deals with the apparent disintegration of "foliar" rays in passing from the first formed to the mature portions of the stems of certain Ericales, Fagales, and Casuarinaceae. This ontogenetic sequence has been interpreted as indicating that the "multiseriate" type of ray originated from the diffused portions of "aggregate" or "compound" rays.

Objections to the "aggregate" ray hypothesis

In endeavoring to trace certain steps of the evolutionary history of the so-called "aggregate" and "compound" rays in the Fagales, one of the writers (BAILEY '11) discovered indications of reduction in *Castanea* and *Alnus*. Additional investigations ('12) of these genera, and of *Castanopsis*, *Ostrya*, and *Carpinus* revealed much evidence for believing that the "aggregate" and "compound" rays have disappeared or are in the process of disappearing from living species of these genera. Furthermore, GROOM ('11) has suggested that the small rays of *Quercus* may have originated by the disintegration of primitive wide multiseriate rays. It is somewhat difficult to harmonize completely these observations with the general trend of the investigations upon "wide" rays, since they introduce the possibility that the congeries of small rays (the so-called "aggregate" rays) may be in every case stages in the "breaking down" rather than in the "building up" of wide rays. This fact is particularly significant when we consider that the "aggregate" ray hypothesis derives much of its support from the theory that the chalazogamic Amentiferae are in all probability the most primitive living angiosperms, for many botanists, from comparative studies of sporophytes and gametophytes, consider that these angiosperms with unisexual flowers are reduced rather than truly primitive.

The phenomenon of chalazogamy, which was considered at first of great phylogenetic value, cannot, in view of later investigations, be considered a reliable criterion for the determination of the position of plants in a phylogenetic sequence. The paleontological evidence which has been cited cannot be considered to be entirely convincing, since "multiseriate" rays are found in middle and upper cretaceous dicotyledons, although according to the "aggregate" ray hypothesis they are the most recent development of the angiosperm ray. If "aggregate" and "compound" rays originated for purposes of storing the assimilates descending from the persistent leaves of mesozoic angiosperms, and were later replaced by "multiseriate" rays as an adaptation to the advent of a severe winter season and the consequent acquirement of the deciduous habit by the leaves, we should hardly expect to find the "multiseriate" ray well developed in cretaceous angiosperms or in families which have lived in moist, warm, tropical conditions since ancient times. It is a notable fact, therefore, that "multiseriate" rays are characteristic of such typically tropical families as the Lauraceae, Anonaceae, Ebenaceae, Rubiaceae, Myristicaceae, Apocynaceae, Myrtaceae, etc., although there is no evidence to show that these families have been exposed to a refrigerated climate since the Mesozoic. On the other hand, the "aggregate" ray, which is comparatively infrequent, characterizes the obviously reduced xerophytic Casuarinaceae and the temperate families Betulaceae, Fagaceae, and Ericaceae. Apparently, therefore, the most conclusive evidence that has been advanced in favor of the origin of the "aggregate" and, *pari passu*, of the "compound" and "multiseriate" rays must be considered to be that derived from the study of the phenomena of recapitulation.

STRUCTURE OF SEEDLINGS

We have noted above that JEFFREY places much emphasis upon the fact that the first formed rays of seedling oaks are all of the uniseriate type that occur throughout the wood of the supposedly very primitive chestnut. In white oaks with deciduous foliage (subgenus *Lepidobalanus*) this primitive condition persists until the plants have attained considerable size. These oaks, therefore, are assumed to be more primitive than oaks of the subgenus *Erythrobalanus*, since in the latter the "aggregation" and "fusion" of rays begins much earlier. Similarly, the "live" or "evergreen" oaks are regarded as more primitive than either of these types, since they possess even in the mature wood "aggregate" tissue from which the separating fibers have not been entirely eliminated.

The writers have recently examined seedlings of different species of the Fagales, and have found phenomena that are apparently of considerable interest. Especially significant are the effects of different degrees of vigor upon the development of ray structures in seedling plants. Suppressed, slow-growing, feeble plants are characterized in many cases by the retarded development of large rays. In fact, the effect of stunted growth may be so strongly marked that only uniseriate rays are formed in stems 30–50 years old. On the other hand, in plants with large, vigorous, well nourished growing points the development of large rays is often accelerated. Vigorous specimens of certain oaks, e.g., *Quercus rubra* L., may even possess wide rays (so-called compound or completely parenchymatous rays) in the first formed portion of the seedling stem (figs. 3 and 13). In the ontogeny of these rays, as in those of *Fagus grandifolia* Ehrh. and *F. sylvatica* L. (fig. 1), there are no putative stages of "aggregation" and fusion.

It is somewhat difficult to explain satisfactorily the facts of seedling anatomy in the Fagaceae, since a strict application of the doctrine of recapitulation might be considered to indicate in the case of certain seedlings that the multiseriate type of ray is primitive, whereas in other young plants it seems to show that wide rays have been "built up" phylogenetically from congeries of uniseriate rays.

The seedling or young plant has been shown in a number of cases to retain characters that are in all probability ancestral, but these phenomena have been interpreted differently by different investigators. HILL and DEFRAINE and others maintain that the seedling is very sensitive to changes in its internal or external environment and therefore of little or no value for phylogenetic purposes. Primitive structures persist only where they are of functional importance in the young plant. In opposition to this are the views of JEFFREY, who considers that HAECKEL'S doctrine of recapitulation is of "universal validity," as invariably operative as the laws of chemistry, physics, and the other cognate sciences. A more conservative working hypothesis which combines elements from each of these antagonistic extremes is held by other biologists, who believe that there are categories of predominantly conservative and of predominantly variable characters, just as there are organs or regions of the plant that are more retentive of primitive characters than others. The mere fact that certain ontogenetic characters have been found to be extremely inconstant and sensitive to physiological conditions does not necessarily invalidate the doctrine of recapitulation. Nor does the fact that the young plant has been shown in certain cases to retain ancestral features indicate that every seedling character is of phylogenetic value. The seedling may display a strong tendency toward conservatism and still be subject to environmental influences, just as the behavior of a falling body may be influenced by other forces than that of gravity. However, the fact that any character in the young plant may be subject to modification by physiological changes makes it difficult in many cases to distinguish palingenetic from cenogenetic features. Phylogenetic conclusions drawn from the study of the structure of seedlings are not conclusive unless substantiated by reliable corroborative evidence.

In view of the somewhat paradoxical behavior of wide rays in the seedling stem, the structure of other regions which are supposed to be conservative and retentive of ancestral characters has an important bearing on the problem under discussion.

THE ROOT

In a recent paper JEFFREY ('12) makes these comments upon the conservatism of the root:

> There are organs of the plant, for example, even more strongly retentive of ancestral characters than the seedling stem. Perhaps the most conservative organ is the root, which varies so little in its fundamental organization throughout the vascular plants that one formula will represent the organization of all roots.

The roots of *Fagus grandifolia* and *F. sylvatica* (fig. 2) possess even in the first formed secondary xylem multiseriate rays which radiate from the clusters of protoxylem. These wide sheets of homogeneous ray parenchyma do not arise by a process of "compounding." Similarly, the "secondary" multiseriate rays which develop as the root increases in circumference are not formed by the "aggregation" and "fusion" of small rays, but originate, as they do in the young stem and mature shoots, by the widening of a single uniseriate ray. Conditions equally significant exist in other genera of the Fagales. For example, wide multiseriate rays occur in the first formed portions of the roots of *Quercus velutina* Lam., although in the seedling stem only uniseriate rays are formed by the first activity of the cambium. On the other hand, certain species of the Betulaceae and Fagaceae possess only uniseriate rays in the first formed portions of the roots, although so-called "aggregate" or "compound" rays may develop during subsequent growth (fig. 6). In the root, as in the seedling stem, variations in vigor and other physiological conditions produce marked variations in the development of rays. Vigor usually accelerates the formation of large rays and feeble or stunted growth tends to reduce their size or retard their development.

THE REPRODUCTIVE AXIS

SCOTT in his studies of cycads was the first to point out in a convincing manner the importance of the anatomy of the reproductive axis as a possible seat of conservatism. More recently JEFFREY, working upon the comparative anatomy of gymnosperms, has reached the conclusion that this region is even more retentive of ancestral characters than is the seedling stem.

The flowering axes of many dicotyledonous plants are less favorable for the study of structures which occur in the secondary wood than are the cone axes of gymnosperms, since they often are herbaceous or possess only a narrow zone of secondary tissue. It is fortunate, therefore, that the peduncles of many species of *Quercus* and *Casuarina* have wide zones of secondary wood and well developed rays. The peduncles of the red or black oaks (subgenus *Erythrobalanus*) are particularly interesting, since they persist through two growing seasons and possess in consequence two layers of secondary tissue. The development of ray structures in these species is well illustrated by the peduncles of *Quercus coccinea* Moench. and *Q. ilicifolia* Wang. Multiseriate rays are formed by the first activity of the cambium and show no putative stages of "aggregation" and "fusion" in their ontogenetic development (fig. 15). Conditions equally significant have been observed by the writers in the peduncles of *Casuarina suberosa* Otto and Dietr., a species which possesses well developed "aggregate" rays in the seedling stem (fig. 7). The peduncles of *Quercus pedunculata* Ehrh., *Alnus maritima* (Marsh) Muhl., *A. incana* L. Moench., and *A. yasha* Matsum, are slender and possess narrower zones of secondary tissue. However, even in these peduncles biseriate and triseriate as well as uniseriate rays are often formed by the first activity of the cambium.

THE NODE

SCOTT, JEFFREY, and others have emphasized the conservatism of the leaf trace and neighboring tissues. The structure of the nodal region is therefore important in a discussion of the origin and development of "aggregate" and "compound" rays.

Throughout the Fagales there is a marked tendency for large rays to be more strongly developed in the young shoot in the vicinity of those strands of the vascular cylinder which are about to pass out to the leaves. These rays are in many cases composed of homogeneous ray parenchyma, whereas the wide rays in other radii of the stem arise apparently by a "compounding" process from congeries of uniseriate rays. Perhaps the most significant conditions are those which occur in supposedly primitive representatives of the Fagales. Among the Betulaceae, for example, vestiges of "aggregate" rays may occur in the nodal region when the internodes possess only uniseriate rays (fig. 12). Similar conditions are of frequent occurrence in the white oaks (subgenus *Lepidobalanus*). Stems of *Quercus alba* L. often possess for many years only uniseriate rays except in the vicinity of the lateral traces of the leaves (fig. 10). The root may likewise be devoid of wide sheets of ray tissue except in the vicinity of the vascular elements which pass out to the rootlets (figs. 6, 11, and 20). In this region vestiges of wide sheets of homogeneous ray parenchyma occur. Especially significant are the wide multiseriate rays which radiate from the clusters of primary elements in the hypocotyledonary region of young plants of *Quercus virginiana* Mill., a "live" or "evergreen" oak which often possesses "aggregate" rays in the mature wood of the stem.

THE FIRST ANNUAL RING

The first elements formed by the cambium or lateral growing point (the so-called first annual ring) have been considered by JEFFREY, THOMSON, and others to be conservative of ancestral characters. It has been shown in the preceding pages that the first formed portions of the seedling stem and root may possess often only uniseriate rays which later appear to "aggregate" and form wide sheets of ray tissue (figs. 4 and 6). However, in certain cases the first annual ring of vigorous shoots and roots may possess "aggregate" and "multiseriate" rays when the mature portions of these organs develop only uniseriate rays. For example, vestiges of wide multiseriate rays have been observed in very vigorous young roots of *Castanea dentata* (Marsh) Borkh. (figs. 11 and 20). These rays occurred in the vicinity of the vascular strands which supply the rootlets. Similarly, vestiges of "aggregate" rays occur in the first formed portions of vigorous shoots and roots of *Alnus mollis* Fernald, *Alnus acuminata* H.B.K., and *Ostrya virginiana* (Mill.) Koch, species which do not possess "aggregate" or "compound" rays in the normal mature wood.

The structure of vigorous mature shoots of *Quercus velutina* and *Q. rubra* is also significant. As is well known, the primary vascular bundles of the oak are not grouped about a more or less cylindrical pith (except in the peduncle and epicotyledonary region), but about one that is deeply fluted (figs. 9 and 10). In cross-section the young twigs possess, therefore, a cambium layer that is composed of ten alternating convex and concave arcs. Thus five large wedge-shaped segments of secondary xylem are formed, which include between them five narrow depressed segments with more nearly parallel sides. This condition may persist in some cases for a number of years, but usually is replaced sooner or later by a stem of cylindrical outline. Vigorous shoots of the red and black oak (fig. 19) resemble the normal stem of *Fagus grandifolia*, since the gaps which separate the numerous distinct clusters of protoxylem subtend an equal number of multiseriate rays. There is this difference, however, that in subsequent growth of the twigs not all of these so-called primary rays increase in breadth as do those of the vigorous seedling stem (fig. 3), peduncle (fig. 8), and beech (fig. 1). The multiseriate rays which occur in the first annual ring of the narrow depressed segments gradually decrease in width during the next two years' growth and become uniseriate.

The structure and development of rays in the first annual ring of mature shoots are subject, as in the seedling stem, the root, and the peduncle, to marked variations under different physiological conditions. Thus wide rays show a strong tendency to become more numerous and parenchymatous in vigorous, well nourished shoots than in feeble, stunted, or suppressed twigs.

TRAUMATIC REGIONS

JACKSON called attention to numerous cases of reversion to supposedly ancestral types of structure under abnormal growth conditions or as a result of traumatism. JEFFREY, working largely with the internal structure of the gymnosperms, has emphasized the importance of traumatic reactions in the study of phylogeny. His contribution upon recapitulations in those regions of the plant which are assumed to be conservative, such as the root and seedling, is particularly significant, since injuries in these regions are said to recall ancestral characters when reversions cannot be induced traumatically in the mature stem.

The wound reactions of the Fagales are accordingly of interest in a consideration of the "aggregate" ray hypothesis. It has been found by the writers that the stimulating and irritating effect of certain types of injuries (whether mechanical or pathological) often accelerates the development of wide rays. The results of very severe injuries which have a marked distorting effect upon the tissues subsequently formed by the cambium are in some cases very different from these. Such injuries retard the development of large rays, just as feeble or stunted growth has been shown to retard the development of wide rays in seedlings and roots.

The stimulus of certain injuries may produce "aggregate" or multiseriate rays in plants or portions of plants which normally do not possess these structures. For example, when infected with the chestnut bark disease, *Endothia parasitica* Murrill, the chestnut may form large, completely parenchymatous sheets of ray tissue (fig. 16), just as "aggregate" or false rays may be recalled in the stems and roots of Betulaceae which normally possess only uniseriate rays (fig. 12). Wide multiseriate rays may also be induced in certain of the Betulaceae by traumatic stimuli. Especially significant are the effects of injuries in seedlings, roots, and the first formed portions of the mature shoots. Injured seedlings of *Quercus velutina* show an abrupt transition from congeries of uniseriate rays to wide sheets of homogeneous ray parenchyma. Furthermore, a seedling stem or root of *Quercus alba*, which possesses only uniseriate rays, will, when injured, form wide multiseriate rays (fig. 21). These rays often develop without indication of the putative stages of "compounding" (fig. 6). Similar phenomena occur in the first formed portion of mature shoots, in those radii of the stem which do not normally possess wide rays (fig. 10).

Discussion of evidence from conservative regions

In applying HAECKEL's doctrine of recapitulation, the fact that plants develop by the activity of growing points or meristems rather than by interstitial growth has not always received sufficient consideration. Among higher animals the embryonic and very plastic stages of development are replaced by more highly organized and stereotyped conditions during early stages of ontogeny. In plants, however, the undifferentiated meristematic tissues retain much of their primitive plasticity throughout the life of the individual. This is shown by the fact that the growing points or meristems of mature plants are potentially able to reproduce the whole organism. Owing to this fact, that embryonic types of tissue are active throughout the life history of plants, phenomena of recapitulation need not be confined necessarily to the so-called seedling plant, and may be expected to be more varied than in the higher animals. Thus, there appears to be no fundamental a priori objection to the supposed natural conservatism of the first annual ring, root, node, reproductive axis, or any other particular region. However, the meristematic tissues of the developing plant are in all probability more subject to modifying environmental influences than are the embryos of the higher animals. It is therefore not at all surprising that in many cases the normal conservatism of the embryonic tissues in any region should be more or less neutralized by local physiological changes in the same way that reversions to a more primitive type of structure may be recalled by abnormal stimuli or by traumatism. Nor is it necessary to suppose that all regions of the plant will be subject simultaneously to similar modifying influences. In any given individual or group of individuals, palingenetic characters may occur in one or more regions when they have been lost or replaced by cenogenetic structures in others. It may be seen, therefore, that very misleading conclusions will undoubtedly be drawn by assuming that a given character which appears in a certain conservative region of the plant is primitive, unless reliable corroborative evidence exists. In determining the possible antiquity of a given character it is essential that its structure, development, and behavior under different environmental and physiological conditions should be studied and compared throughout each representative of a wide range of living and, if possible, of fossil forms.

The results of such investigations are in general most conclusive when concerned with categories of characters which have been termed "degradational" or "regressive," that is, characters which are being reduced or lost. JACKSON ('99), in his study of the leaves of a number of gymnosperms and angiosperms, has contributed much toward the elucidation of the behavior of these characters. He has shown that in plants which are losing foliar characters by reduction or simplification the ancestral structures are recalled on vigorous, well nourished stems, or in tissue subject to stimulating types of injury. On the other hand, stunted, feeble, senile conditions tend to hasten the process of reduction, just as on stunted or sickly mature twigs or very old specimens, of a species which has not suffered reduction; the leaves may undergo an incomplete development and revert to the seedling type through a failure in their individual ontogeny to develop full specific characters. The suppression of characters may progress in two ways. In most cases, the young plant, although more conservative in acquiring new foliar characters, is more retentive of these characters, once they become firmly fixed, than are most regions of the mature stem. On the other hand, marked changes in the environment or physiological activity of the young plant may more or less neutralize the effects of its natural conservatism. Under such conditions the seedling may develop cenogenetic characters or lose structures which are retained in mature portions of the plant. Thus JACKSON and COPE have shown that animals and plants may lose ancestral characters by "retardation of development. That is, features may appear at later and later stages in development until they finally disappear."

Internal structures appear in general to behave in regression and progression much as do external foliar characters. That vigorous or stimulated types of growth tend to recall characters which have been reduced has been illustrated, for example, by the recurrence in such types of tissue of marginal tracheids in the Cupresseae, of resin canals in the Taxodieae, and of wood parenchyma in the later Araucarieae. It also seems to be true that the influence of vigor and stimulating injuries in recalling reduced characters are most effective in regions which are supposed to be conservative, such as the first annual ring, root, node, and reproductive axis.

In the Fagales there is apparently a very complete series of species in which the successive stages of the reduction of wide multiseriate rays can be traced in detail. This process of reduction has taken place in most species by "retardation of development," accompanied by a greater or less degree of disintegration of the wide sheets of ray parenchyma. Unusually stimulating types of growth or traumatism recall the wide rays in regions from which they have disappeared or cause the cambium to form less complete stages of the disintegration process. These stimuli are often most effective in those regions of the plant which are supposed to be conservative, such as the first annual ring of roots and shoots, the seedling stem, and node. In the process of reduction the tissues near the entering traces of the leaves and rootlets and the peduncle are particularly retentive of primitive, unreduced characters. Stunted, suppressed, or poorly nourished cambiums hasten the reduction of wide rays by an incomplete development of specific characters. The sensitiveness of wide rays to changes in the environment or physiological activity of the plant might be anticipated when we consider the function of these sheets of parenchyma as storage organs. It is not surprising, therefore, that the effects of conservatism should have been neutralized in certain regions of the plant.

A brief description of the comparative anatomy of species which occur at various levels in this "regression" series and their behavior under different physiological conditions follows:

Fagus grandifolia.—This plant illustrates diagrammatically the structure of a species in which the multiseriate rays have suffered little or no reduction. The stem (fig. 1) possesses a ring of primary fibrovascular bundles which are separated by well developed gaps. Those arcs of the cambium which bridge these gaps, the so-called interfascicular cambiums, form ray parenchyma exclusively. As a result of their activity, multiseriate rays are formed which vary in height and width as do the gaps in the vascular cylinder. In subsequent secondary growth these "primary medullary rays," which are 2–5 cells wide, increase gradually in width and may eventually attain a breadth of approximately 15–25 cells. Next the pith these rays are in the form of long vertical lines of parenchymatous tissue. As the stem develops, these tall rays or lines of superimposed high rays are dissected into shallower rays, which are gradually deflected from their original vertical axes. The so-called fascicular cambiums form at first tracheary tissue and uniseriate rays. The latter are also high in tangential section and form long lines which are dissected in subsequent development into shorter rays. Certain of these later increase in width and may in time become as wide as the rays of the so-called interfascicular segments. With the increasing circumference of the stem, new rays are formed continually by the cambium to maintain the proper proportion of ray tissue in each radius. These shorter "secondary" medullary rays which do not extend to the pith are uniseriate at first, but may increase in width during subsequent development. In any annual layer of growth, therefore, there are rays one to many cells wide. In the first annual ring the widest rays occur in the vicinity of the nodes, on each side of traces which are about to enter the leaves.

The structure and development of rays in the ontogeny of secondary tissues in the seedling are fundamentally the same as in the mature stem. The root (fig. 2), which is commonly pentarch, possesses in cross-section five large rays that radiate from the five clusters of protoxylem. These rays are high and connect the traces of the rootlets. Although narrow when first formed, they widen rapidly and at the same time are dissected into shallower sheets of parenchymatous tissue. The other radii of the root possess at first only uniseriate rays, certain of which later increase in width as do some of the linear rays of the stem. Conditions such as have just been described occur in shoots and roots of normal development. The structure of wide rays is often different in suppressed, stunted, or feeble growth. Under these circumstances the first rays formed by the cambium are linear except in the vicinity of the traces which enter the leaves and rootlets, where multiseriate rays are persistent. In the stem the reduction of wide rays consists principally in the gradual narrowing of the sheets of parenchyma at their inner ends. In the root and the hypocotyledonary region, however, where the rays are often of considerable width, the reduction may be accompanied by slight indications of disintegration or dissection. If a shoot or root of this type receives a stimulating injury or develops suddenly a more normal type of vigor, an abrupt transition from uniseriate to wide multiseriate rays takes place, so that arcs of the cambium that have been forming linear rays and tracheary elements suddenly form only ray parenchyma (fig. 5). The phloem portion of the wide multiseriate rays, particularly in the stem, is characterized by a somewhat modified form of ray tissue. The cells of the rays become thick-walled and sclerenchymatous. At the same time the formation of ray cells upon the xylem side of the cambium is retarded, so that wedges of ray sclerenchyma project from the phloem into the xylem cylinder.

Quercus rubra.—The peduncle and the well nourished seedling stem or vigorous yearling twig of red oak resemble the normal twig of *Fagus grandifolia*, since the gaps which separate the numerous distinct clusters of protoxylem subtend an equal number of multiseriate rays. There is this difference, however, that in subsequent growth of the twigs not all of these rays increase in breadth, as do those of the vigorous seedling stem and peduncle. The multiseriate rays which occur in the first annual layer of growth of the narrow depressed segments (fig. 9) gradually decrease in width during the next two years' growth and become uniseriate. That these rays are vestiges of wide rays which have been reduced by the arrested development of the depressed segments is indicated by the fact that when the cambium loses its specialized lobed form and releases these segments, one or more of the rays may eventually increase in width from uniseriate to multiseriate. In addition, it is interesting to note that a stimulating type of injury causes these reduced rays to resume their multiseriate form.

The "secondary" multiseriate rays which are formed as the stem increases in circumference are wider and arise more abruptly than do those of the beech. These rays may be formed by the rapid widening of a simple uniseriate ray or may show indications of incipient retardation of development and be disintegrated slightly at their inner ends.

The reduction of multiseriate rays is conspicuous in feeble, poorly nourished seedlings or in stunted or suppressed twigs (figs. 4 and 10). Under such conditions of reduced vitality the first formed portions of the seedling plant may possess only uniseriate rays, although the outlines of the suppressed wide rays are clearly marked; for each gap between the primary vascular bundles subtends an aggregation of uniseriate rays or a band of tissue that is entirely devoid of vessels. These "trails," or so-called "false" rays, radiate outward and in turn subtend the multiseriate rays which are eventually formed during subsequent growth. The retarded development of "secondary" multiseriate rays is likewise marked by a trail of aggregated small rays and tissue devoid of tracheae. If the cambium of a feeble seedling receives a stimulating injury or suddenly increases in vigor, multiseriate rays are recalled at once and appear abruptly in those radii from which they have been lost.

The retardation of the development of wide rays in stunted or suppressed twigs is also marked by short trails of disintegrated ray parenchyma and tissue devoid of vessels. This process of reduction is least conspicuous, however, in the vicinity of the entering traces and in the five pairs of wide rays which separate the depressed segments from the wider wedge-shaped ones. It is not uncommon, therefore, to find in the cross-section of a young twig that during their first activity the so-called interfascicular arcs of the cambium have formed multiseriate rays in certain radii of the stem and disintegrated sheets of ray parenchyma or tissue devoid of vessels in others. As in the case of poorly nourished seedlings, stimulating types of injuries or increased vigor recall the multiseriate rays in those radii of the stem in which they have suffered suppression or disintegration.

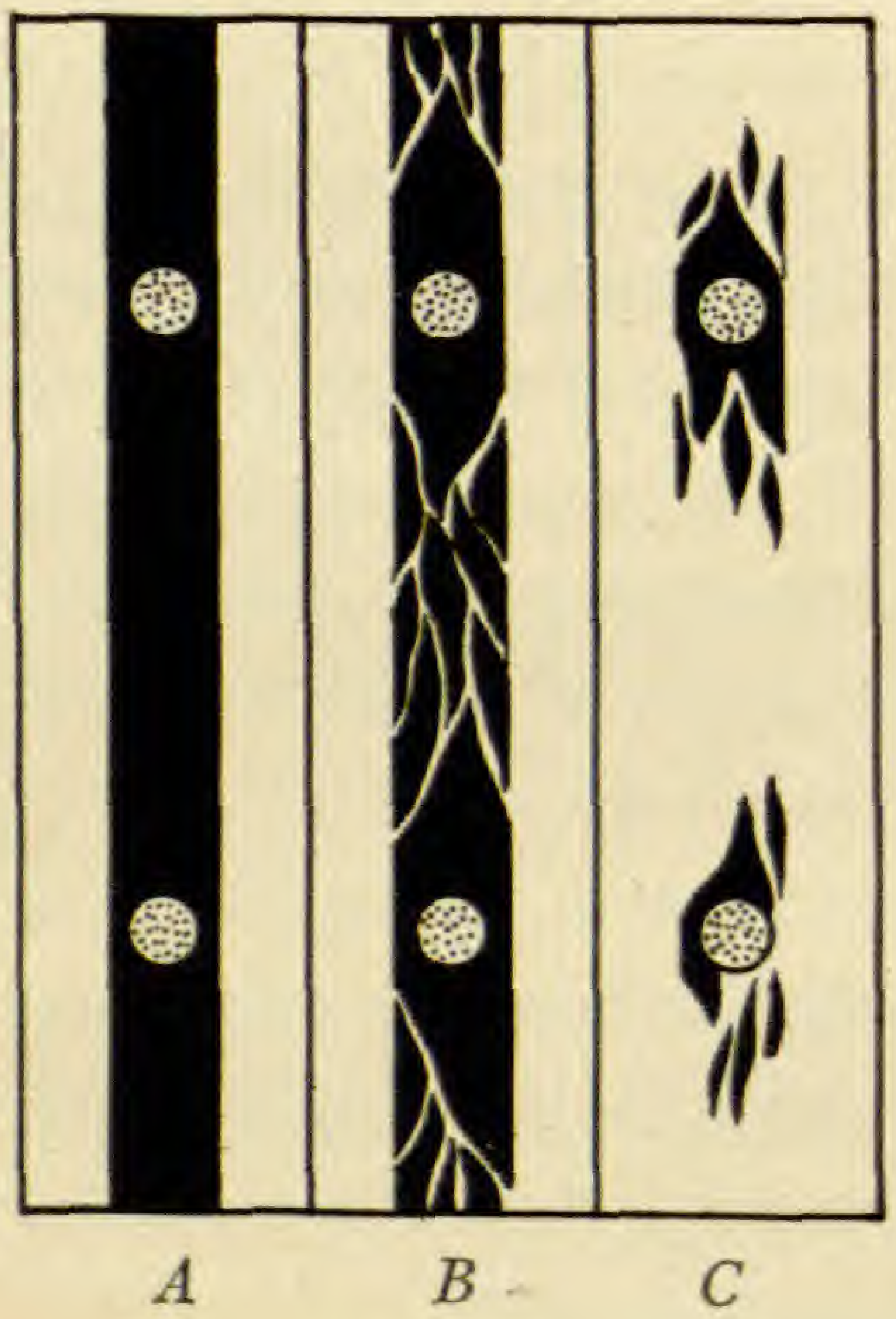


FIG. 1.—*A*, tangential section of a young root of *Fagus*, showing the vascular elements of two rootlets connected by a multiseriate ray; *B*, *Quercus* (subgenus *Erythrobalanus*), showing incipient stages of the disintegration of a wide multiseriate ray; *C*, *Quercus* (subgenus *Lepidobalanus*), showing vestiges of a multiseriate ray persisting about the vascular elements of the rootlets.

In vigorous young roots, wide multiseriate rays radiate outward from the clusters of protoxylem. These rays, as in *Fagus grandifolia*, form long vertical sheets of parenchyma which connect the traces of the outgoing rootlets (text fig. 1). Although these "primary" rays do not show well marked signs of incipient reduction, the broad alternating "secondary" multiseriate rays are in most cases considerably disintegrated at their inner ends. In less vigorous roots the primary multiseriate rays may also show evidences of reduction. However, the disintegration of these rays is most strongly shown usually at some distance from the strands of vascular tissue which supply the rootlets. Stimulating injuries or increased vitality recall the wide rays in regions of the root where their development has been retarded.

Quercus alba.—The reduction of wide multiseriate rays has progressed much farther in this oak of the subgenus *Lepidobalanus* than it has in most species of the subgenus *Erythrobalanus*, for even in vigorous, well nourished shoots and roots vestiges of wide rays persist, in the first formed secondary xylem, only in the vicinity of traces of the leaves and rootlets (fig. 6). The withdrawal of multiseriate rays from the mature shoots is accompanied by slight evidences of disintegration, but in the cotyledonary region and particularly in the root the very wide multiseriate rays are subtended by longer trails of disintegrating ray parenchyma and tissue devoid of vessels. With decreasing vigor, the multiseriate rays appear at progressively later stages in the development of the stem and root (text figs. 2 and 3), but may be recalled by stimulating injuries or improved growth conditions.

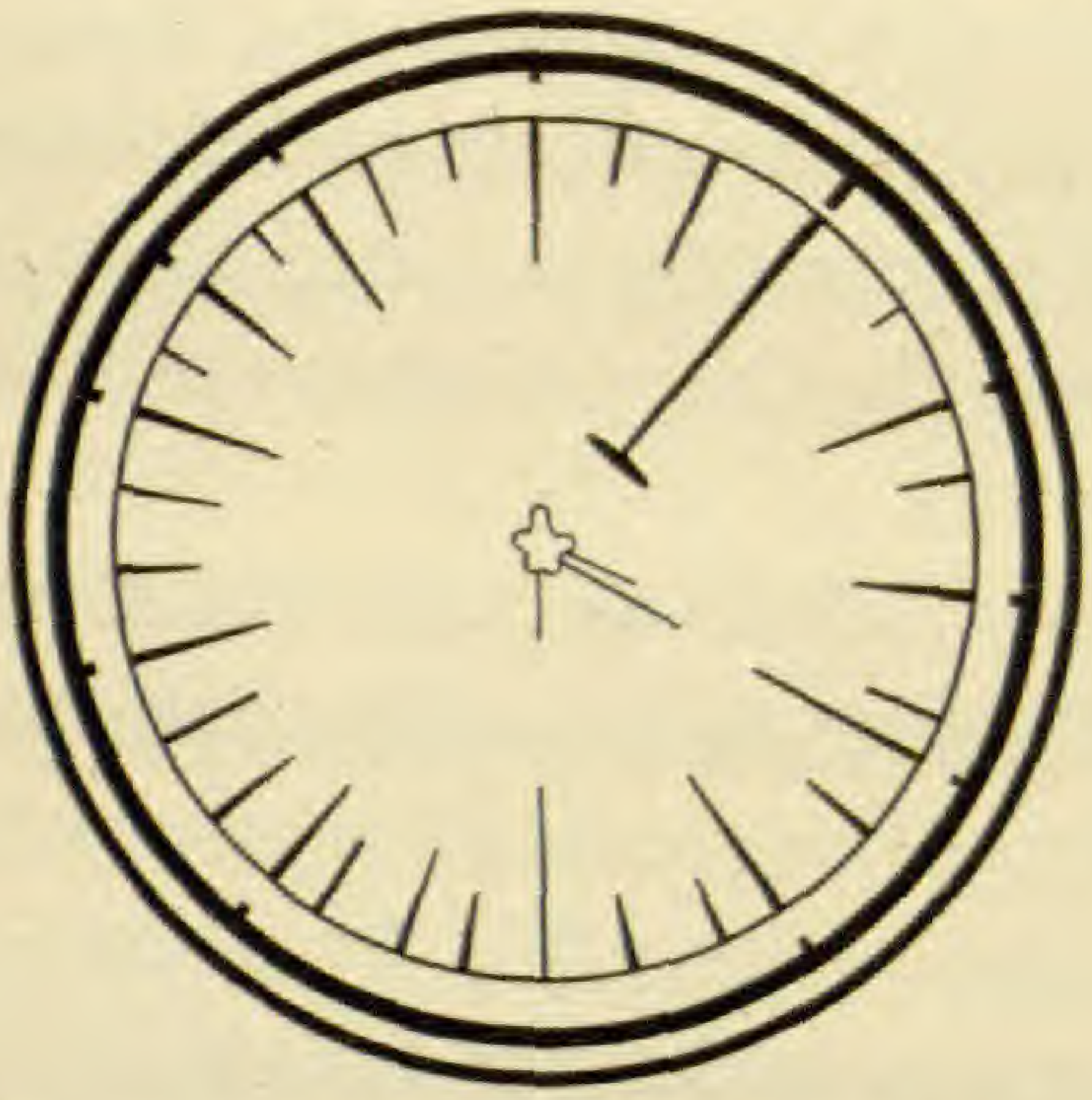


FIG 2.—Transverse section of a suppressed, forty-year-old branch of a mature specimen of *Quercus alba*, showing the retarded development of wide rays.

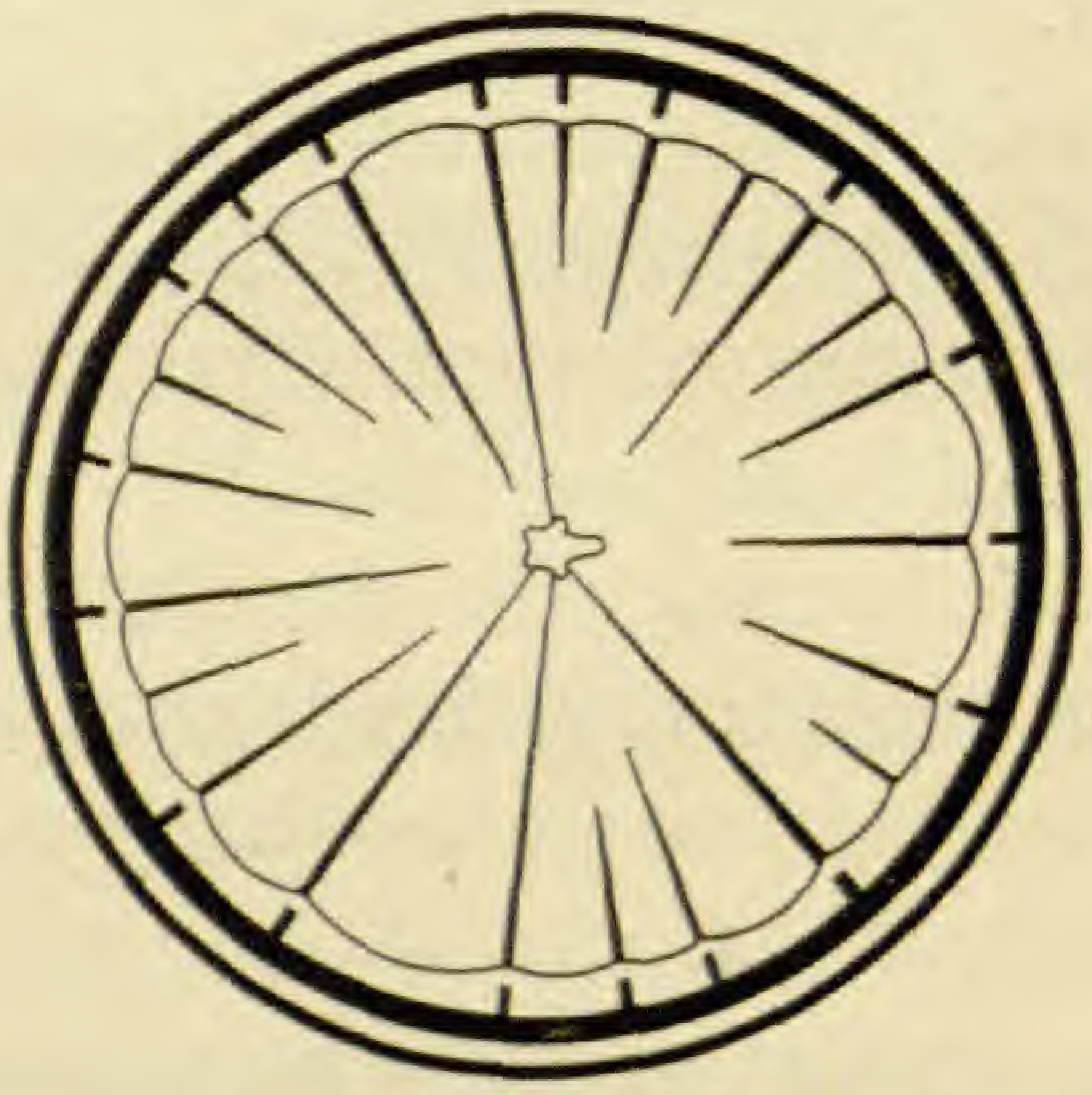


FIG. 3.—Transverse section of a vigorous, eleven-year-old shoot taken from the same tree as the suppressed branch illustrated in fig. 2.

Quercus virginiana.—In this evergreen or live oak the reduction of multiseriate rays has been carried farther than in either of the preceding species. The wide rays are commonly absent in young stems, but may be well developed in the vicinity of the vascular elements which pass out to the rootlets (fig. 17). When the wide rays appear during subsequent growth, they are much disintegrated and may persist in this dissected condition for many years, although in some cases they may finally become homogeneous ray parenchyma. This tendency for large multiseriate rays to become disintegrated not merely at their inner ends but throughout their ontogenetic development is characteristic of many tropical or subtropical species of *Quercus*. Severe, stunting types of injuries hasten the disintegration of the sheets of ray tissue, whereas stimulating or irritating injuries cause reversions to wide multiseriate rays.

Castanea dentata.—The common sweet chestnut illustrates a case in which the reduction of multiseriate rays is nearly complete. Vestiges of wide, multiseriate rays occur, however, in the first formed tissue of very vigorous roots (figs. 11 and 20) and shoots in the vicinity of the traces which pass out to the leaves and rootlets. Multiseriate rays may also be recalled by stimulating types of injuries such as are produced by the irritating effects of infections of *Endothia parasitica* (fig. 16). It is interesting to note that not only is the oak type of ray recalled but also the oak type of fiber-tracheid and leaf (fig. 18).

Betulaceae.—In the Betulaceae the reduction and disintegration of wide rays is far advanced. Typical wide multiseriate rays occur, however, somewhat sporadically in the stems of *Alnus rhombifolia* Nutt. and *A. maritima*, or may be recalled by stimulating injuries or vigorous growth in regions which do not normally possess them. In most species the rays have become entirely disintegrated except in the peduncle, where narrow multiseriate rays may be persistent. As the process of reduction is continued, these sheets of dissected ray parenchyma are replaced gradually by aggregations of multiseriate rays, and finally by bands of tissue that are merely devoid of vessels. These trails or vestiges of former multiseriate rays, so-called false rays, are frequently persistent in the vicinity of the traces of the leaves (fig. 12) and rootlets, and may remain in these regions, particularly in the first annual ring of vigorous roots and shoots, after they have disappeared from the rest of the plant. This process of reduction is accelerated by stunted, suppressed growth and retarded by vigor. The less complete stages of reduction and disintegration are recalled by stimulating injuries and unusually vigorous growth.

We have seen above that the wide multiseriate rays of the Fagales are characterized by a peculiar sclerenchymatous modification of their phloem extensions (figs. 1, 2, 7, etc.). It is significant, therefore, that these typical intruding wedges of sclerenchyma occur in the Betulaceae opposite each "false" ray of the xylem cylinder (fig. 12).

Casuarinaceae.—Successive stages of the reduction and disintegration of wide multiseriate rays, such as are found in the genus *Quercus*, occur in the shea-oaks or Casuarinas. There are several species in this family, however, in which the wide multiseriate rays are persistent in the first formed portions of the stem. In the subsequent development of these wide rays reduction and disintegration occur. These dissected sheets of smaller ray tissue become diffused through certain radii of the stem, and in this way wide multiseriate rays are replaced by narrower biseriate or triseriate ones. At the same time, certain of the uniseriate rays which occur between the wide rays widen until they become as broad as the narrow sheets of tissue which are dissected from the original wide ray. A somewhat similar phenomenon appears to have occurred in the genus *Betula*, in which narrow biseriate or triseriate rays have replaced the original wide multiseriate rays. As in the Fagales, wide multiseriate rays may be recalled in the Casuarinaceae by stimulating growth or injuries, and tend to be persistent in the peduncle and the vicinity of the traces of the leaves and rootlets.

Origin, distribution, and antiquity of multiseriate rays

Multiseriate rays of varying width are well developed in the majority of arborescent or shrubby dicotyledons and may be traced through the Tertiary to the Middle Cretaceous. These sheets of parenchyma characterize the great tropical families of woody dicotyledons, as well as those which live in a more temperate habitat. Very wide multiseriate rays occur in presumably specialized types, such as lianas, mangroves, desert plants, semi-herbaceous shrubs, etc., which are adapted to peculiar environments. The investigation of the structure and development of rays in the various families of the dicotyledons reveals much evidence that the multiseriate rays originated by the gradual widening of primitive uniseriate rays. Detailed evidence in favor of this view will be given by the writers in a subsequent paper.

Summary and conclusions

The "aggregate" ray hypothesis developed by JEFFREY and amplified by a number of students working under his direction has an important bearing upon the phylogeny of the angiosperms, since it indicates that certain of the Amentiferae are in all probability the most primitive living representatives of the phylum. There appear to be serious objections to this hypothesis, however.

OBJECTIONS TO THE "AGGREGATE" RAY HYPOTHESIS

1. The phenomenon of chalazogamy, which was considered at first of great phylogenetic value, cannot, in view of later investigations, be considered a reliable criterion for determining the phylogenetic position of plants.

2. The occurrence of so-called "aggregate" rays in the Tertiary does not appear to be significant, since "multiseriate" rays, which are considered to be a comparatively recent adaptation to the advent of a severe winter season and the consequent acquirement of the deciduous habit, are found in middle and upper cretaceous dicotyledons.

3. If "aggregate" and "compound" rays originated for the purpose of storing the assimilates descending from the persistent leaves of angiosperms in the warmer times of the Mesozoic and were later replaced by "multiseriate" rays as an adaptation to a period of refrigeration, we should hardly expect to find multiseriate rays well developed in families which have lived in tropical environments since ancient times.

4. The "aggregate" ray, which is comparatively infrequent, characterizes the obviously reduced xerophytic Casuarinaceae, and the temperate families Betulaceae, Fagaceae, and Ericaceae.

5. The "aggregate" ray hypothesis does not account for the development of "secondary" multiseriate rays nor for the origin of wide rays in the root.

6. The seedling evidence which has been advanced in favor of the origin of wide rays from congeries of uniseriate rays is invalidated by the occurrence of wide multiseriate rays in seedlings of oaks, and also in such supposedly conservative regions in this genus as the node, root, reproductive axis, and first annual ring.

"AGGREGATE" RAYS STAGES IN THE REDUCTION AND DISINTEGRATION OF WIDE MULTISERIATE RAYS

In the Fagales and Casuarinaceae there is a very complete series of form in which the progressive reduction and disintegration of wide multiseriate rays can be traced in detail. During this process of reduction the wide rays appear usually at later and later stages in ontogeny, until they finally disappear. The so-called "aggregate" rays are stages in the disintegration of wide multiseriate rays. Stimulating types of growth and injury recall the wide rays in regions where they have been lost, and are frequently most effective in those regions which are supposed to be conservative, such as the first annual ring, root, node, and seedling. Stunted, suppressed, poorly nourished types of growth, and severe distorting injuries hasten the reduction and disintegration of the wide multiseriate rays. In this process of reduction vestiges of the wide rays tend to be more persistent in the peduncle, root, and nodal regions.

THE MULTISERIATE RAY A WIDENED UNISERIATE RAY

The multiseriate ray does not appear to be of recent origin, since it is well developed in most tropical and temperate families and extends through the Tertiary at least to the Middle Cretaceous. This type of ray structure originated in all probability by the gradual increase in width of the primitive uniseriate ray.

PHYLOGENY OF THE AMENTIFERAE

One character, of course, cannot be considered conclusive evidence for assuming that a plant or group of plants is "regressive" or reduced, since all characters will not be similarly affected by changes in the environment or physiological activity, but the reduction of wide rays in the Fagales indicates that this order, as well as the Casuarinaceae, has been subjected to a strong modifying influence. This fact, taken together with the occurrence of syncarpy, epigyny, abortive ovules, and vestiges of bisexual flowers and floral envelopes, emphasizes the importance of the frequently repeated suggestion that the Amentiferae, instead of being the most primitive of angiosperms, are a group of specialized families which have reached their present more or less simple structure through reduction from earlier and usually more complicated forms.

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EXPLANATION OF PLATES III–V

FIG. 1.—Transverse section of a seedling stem of *Fagus*, illustrating the structure, development, and distribution of multiseriate rays which have not suffered reduction.

FIG. 2.—The same; young root.

FIG. 3.—Transverse section of a vigorous young seedling stem of *Quercus rubra*, showing multiseriate rays which radiate from each wide gap in the primary elements.

FIG. 4.—The same; less vigorous seedling stem, showing the disintegration and reduction of wide rays and their recurrence in tissue which has been formed under the stimulating effects of an injury.

FIG. 5.—Transverse section of a suppressed seedling of *Fagus*, showing the arrested development of wide multiseriate rays in the first formed portion of the hypocotyledonary stem and their sudden recurrence after a stimulating type of injury.

FIG. 6.—Transverse section of a young root of *Quercus* (subgenus *Lepidobalanus*), showing the reduction of multiseriate rays; "trails" of aggregated uniseriate rays mark the former position of the wide rays; in one radius vestiges of a multiseriate ray have persisted in the vicinity of the outgoing vascular elements of a rootlet; in another portion of the root a stimulating type of injury has recalled wide homogeneous sheets of ray parenchyma.

FIG. 7.—Transverse section of the seedling stem of *Casuarina suberosa*, showing the disintegration and reduction of wide rays.

FIG. 8.—Transverse section of a peduncle of the same species, showing well developed multiseriate rays.

FIG 9.—Transverse section of a vigorous young shoot of *Quercus* (subgenus *Erythrobalanus*), showing five depressed segments and multiseriate rays.

FIG. 10.—Transverse section of a stunted, slow growing branch of *Quercus* (subgenus *Erythrobalanus*), showing the reduction of multiseriate rays, their persistence on either side of the depressed segments, and their recurrence in tissue stimulated by injuries.

FIG. 11.—Transverse section of a very vigorous young root of *Castanea dentata*, showing the persistence of vestiges of wide rays in the vicinity of the vascular elements which supply the rootlets.

FIG. 12.—Transverse section of a shoot of *Alnus*, showing the persistence of "trails" of uniseriate rays about the lateral leaf-traces and their recurrence in traumatic tissue.

FIG. 13.—Transverse section of a portion of a vigorous seedling stem of *Quercus rubra;* two multiseriate rays radiate from the gaps between three clusters of primary elements; ×45.

FIG. 14.—Transverse section of a portion of a less vigorous seedling stem of *Quercus rubra*, showing the reduction and disintegration of two multiseriate rays; ×45.

FIG. 15.—Transverse section of part of a two-year-old peduncle of *Quercus coccinea*, showing multiseriate rays; ×80.

FIG. 16.—Transverse section of traumatic tissue of *Castanea dentata*, showing oaklike multiseriate rays and fibers recalled by the stimulating effects of *Endothia parasitica;* ×130.

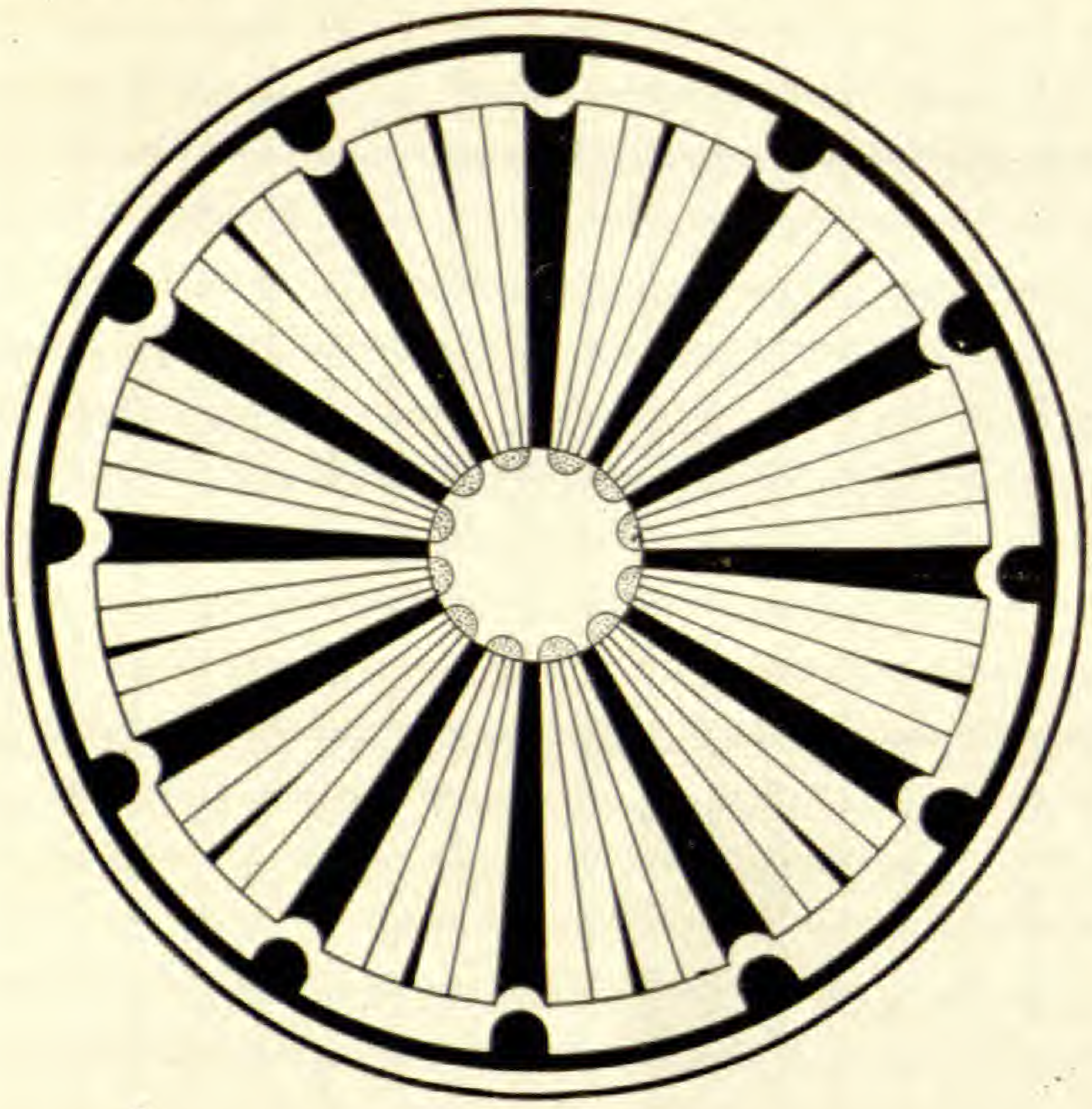
FIG. 17.—Transverse section of a portion of the hypocotyledonary stem of *Quercus virginiana*, showing wide multiseriate ray subtended by protoxylem; ×20.

FIG. 18.—Reversionary leaf of *Castanea dentata*, showing oaklike characters recalled by the stimulating effects of *Endothia parasitica;* ×$\frac{1}{2}$.

FIG. 19.—Transverse section of the first formed portion of a depressed segment of a vigorous shoot of *Quercus velutina;* multiseriate rays radiate from each gap in the primary vascular cylinder; ×45.

FIG. 20.—Transverse section of the first formed portion of a very vigorous root of *Castanea dentata*, showing vestiges of multiseriate rays; ×15.

FIG. 21.—Transverse section of the primary root of *Quercus alba*, showing the recurrence of multiseriate rays under the stimulating effects of an injury; ×5.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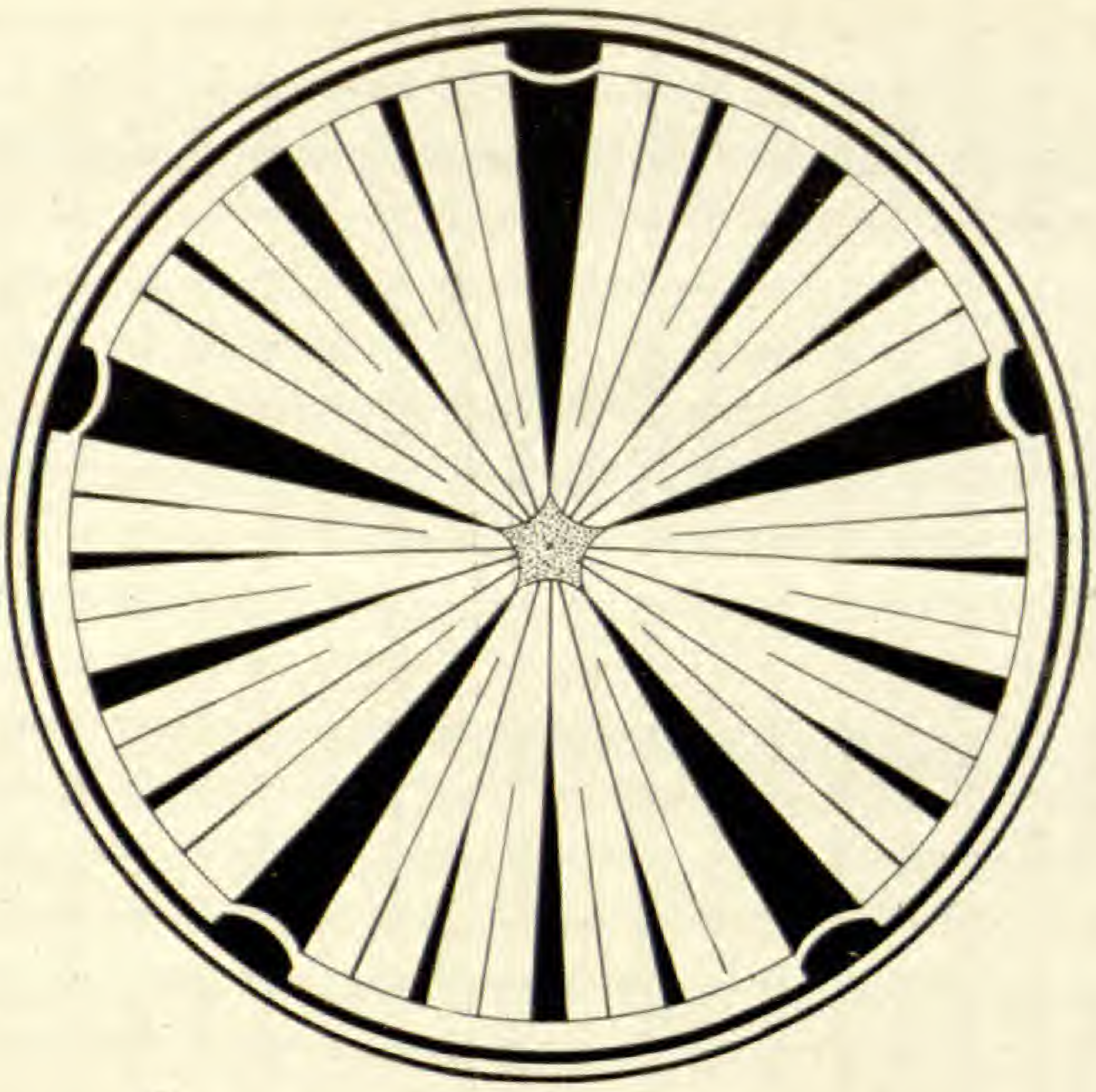
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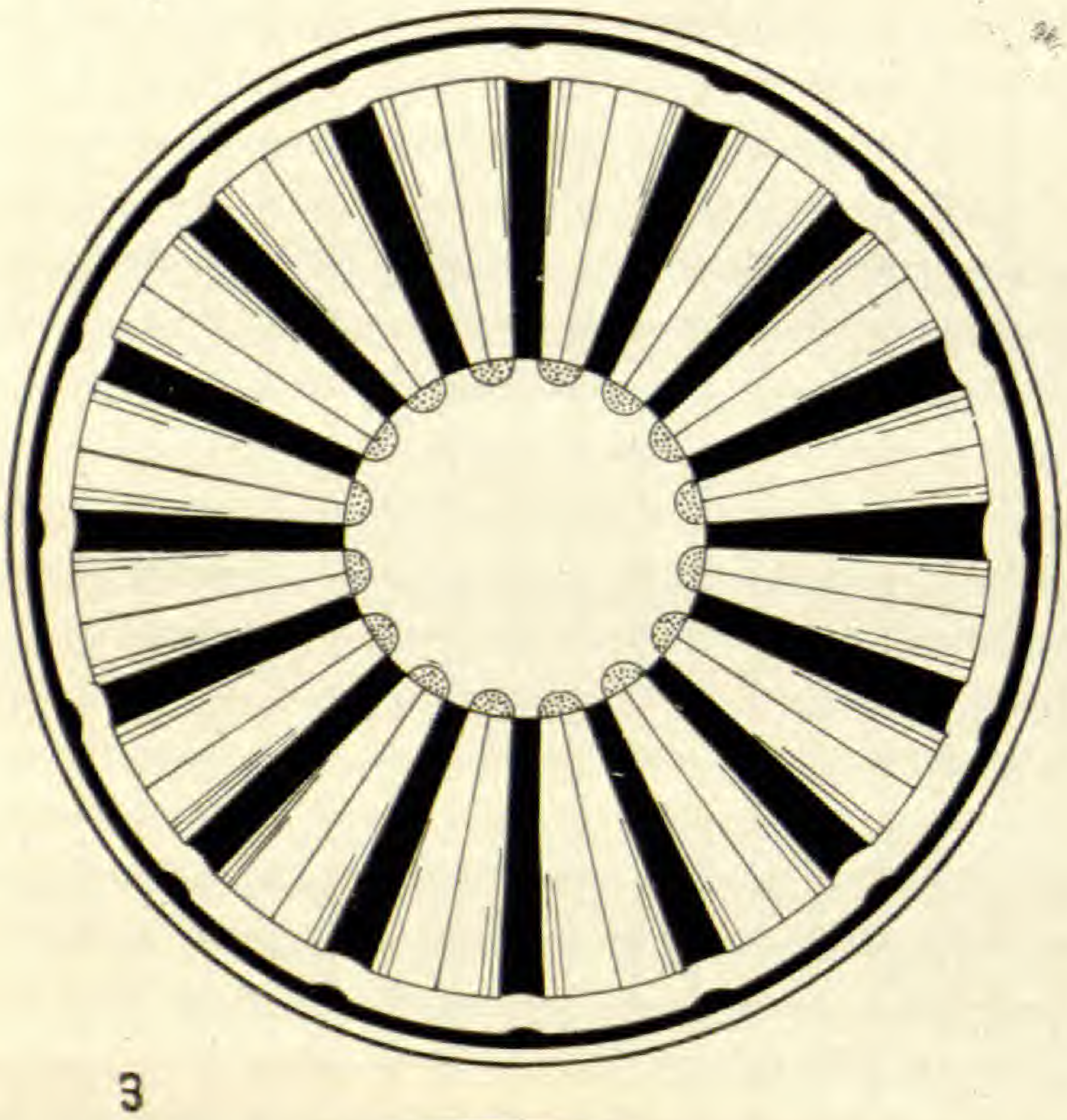
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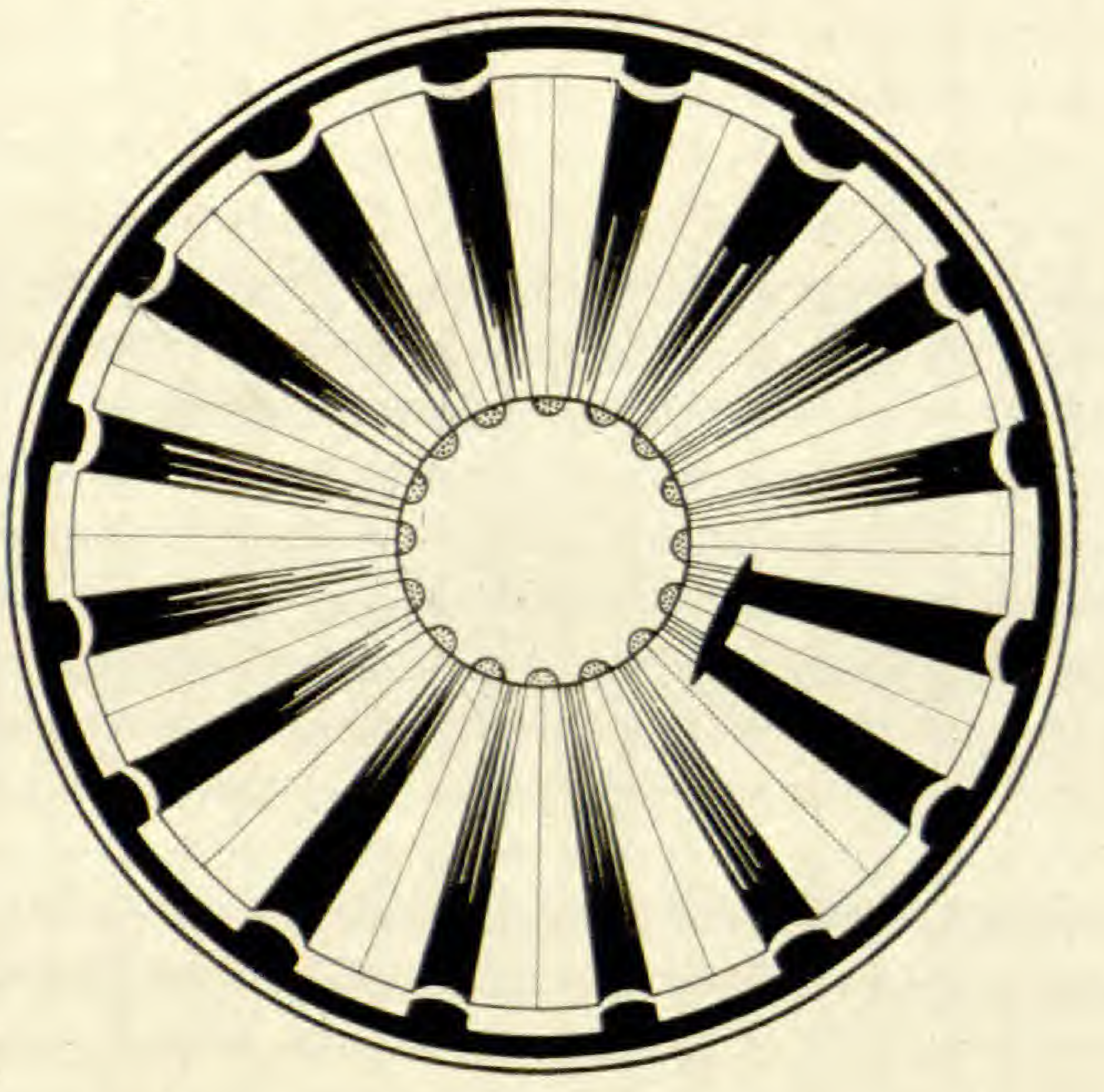
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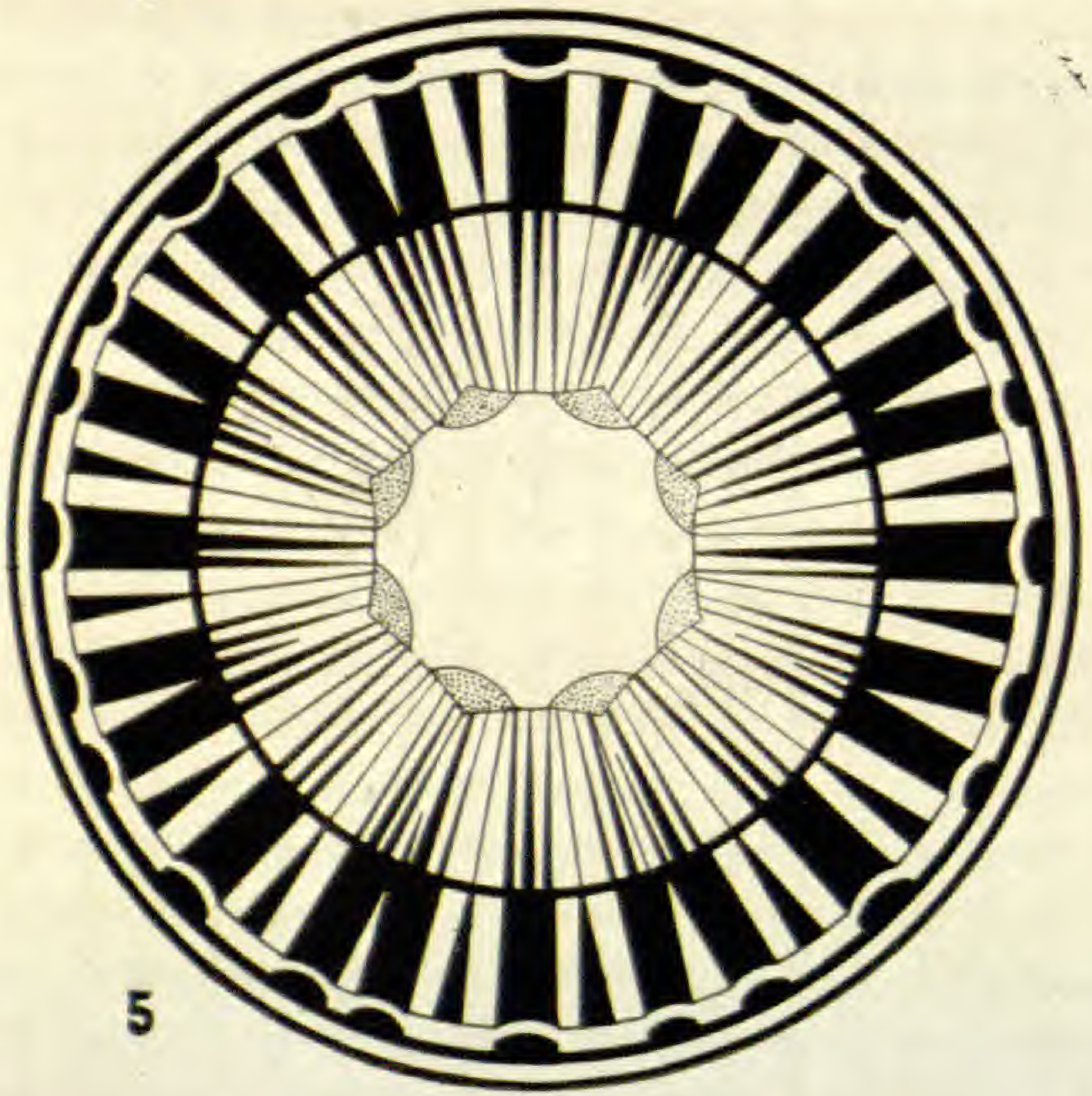
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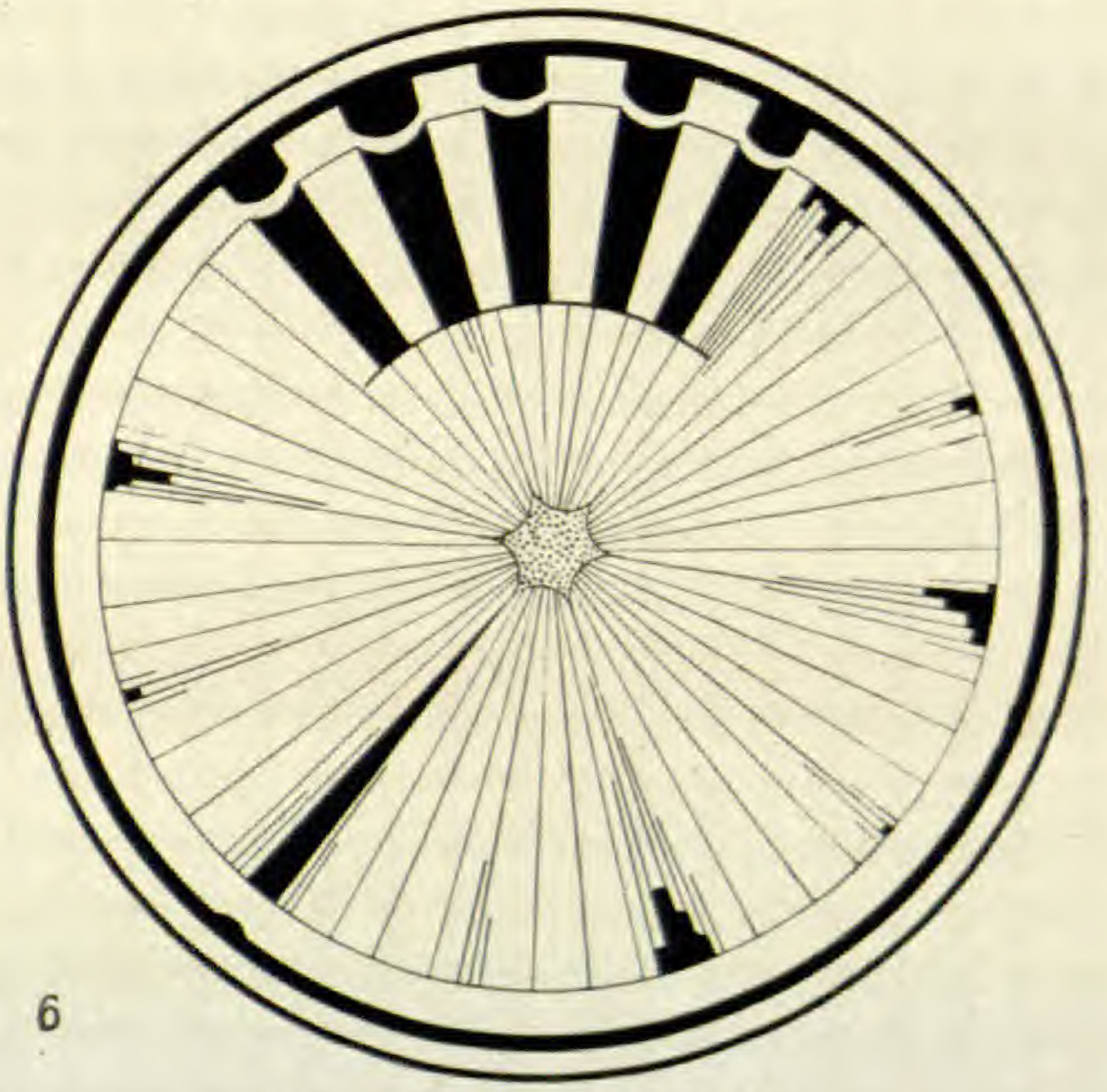
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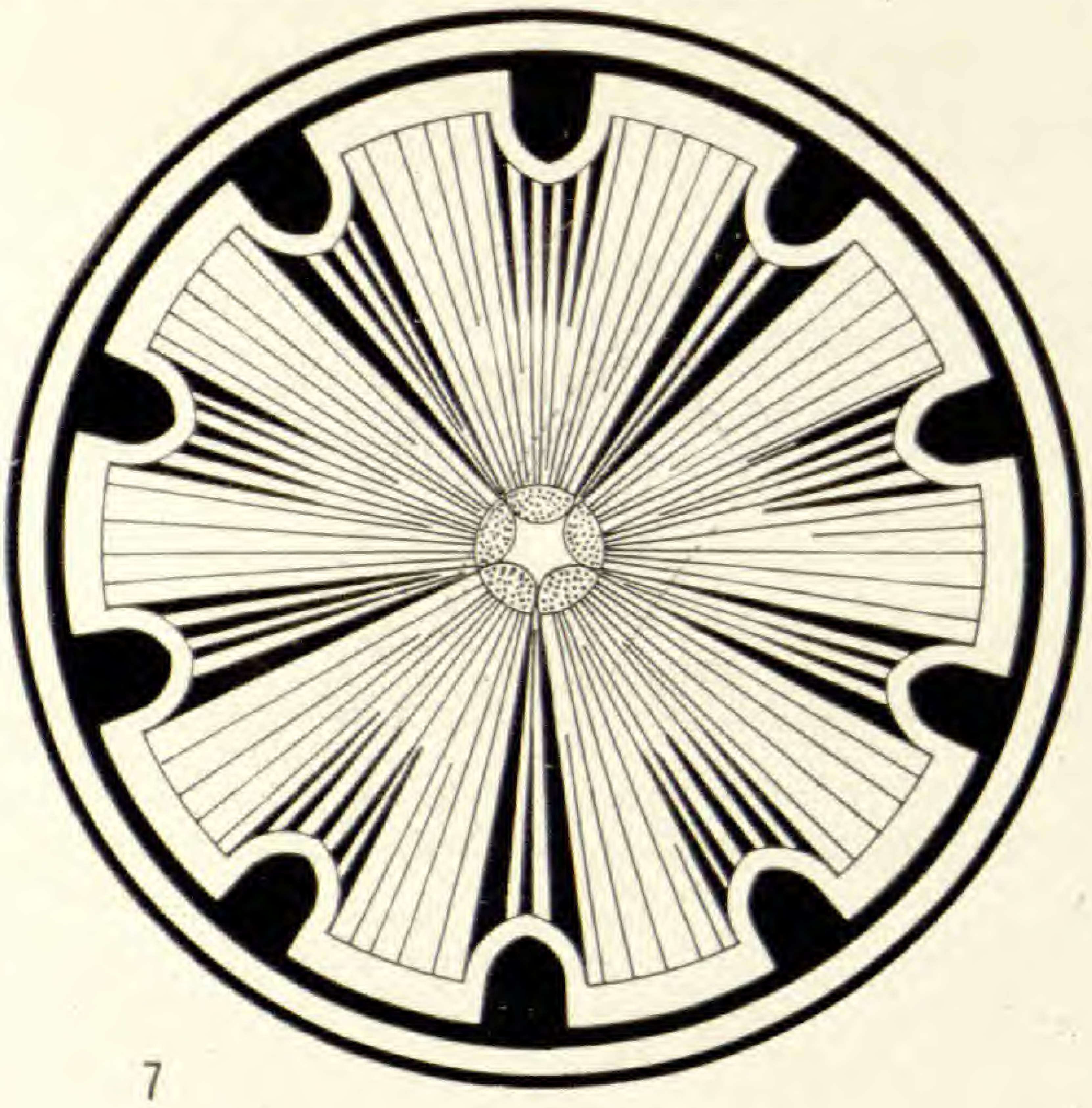
BAILEY and SINNOTT on PHYLOGENY OF ANGIOSPERMS



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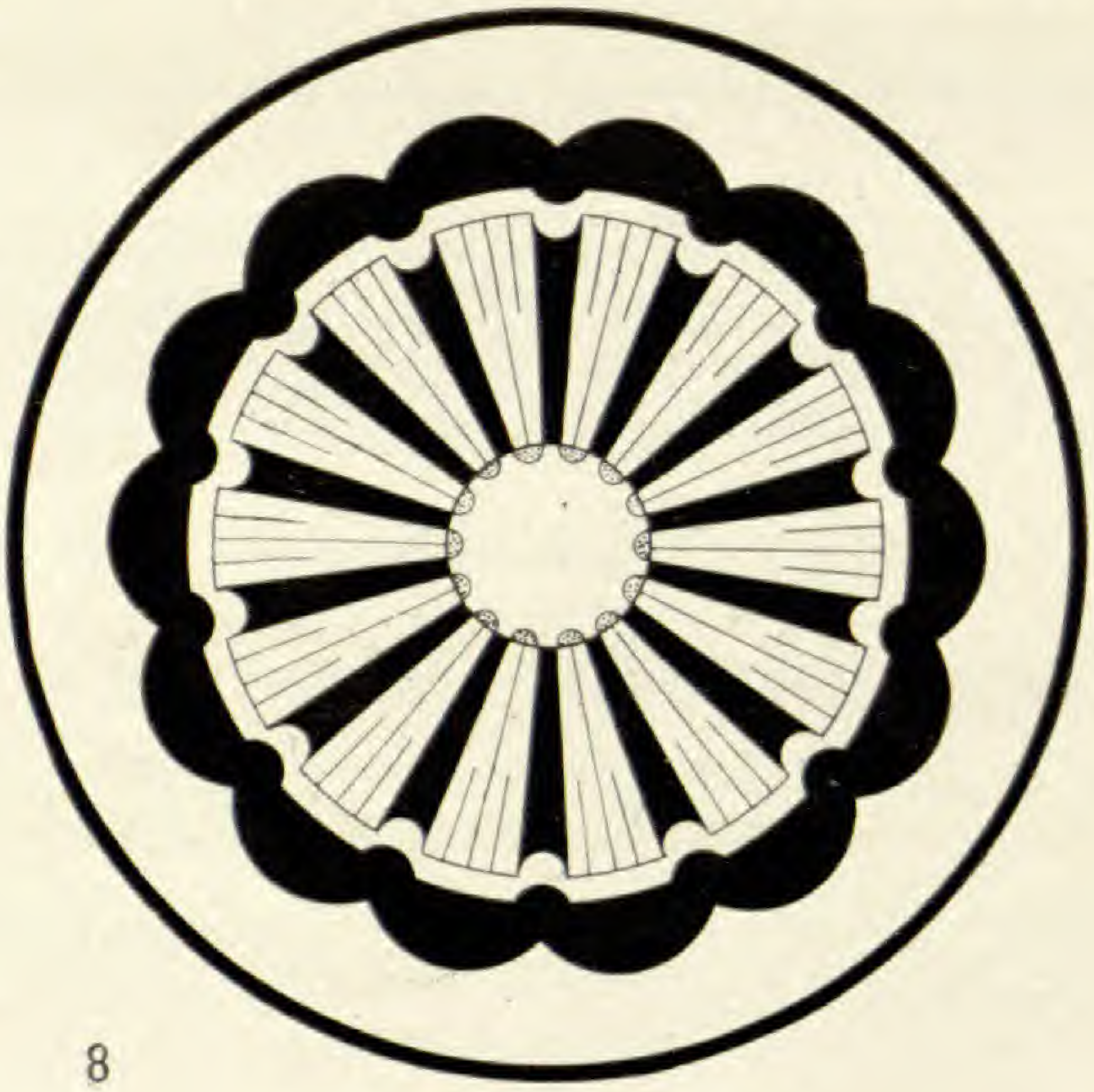

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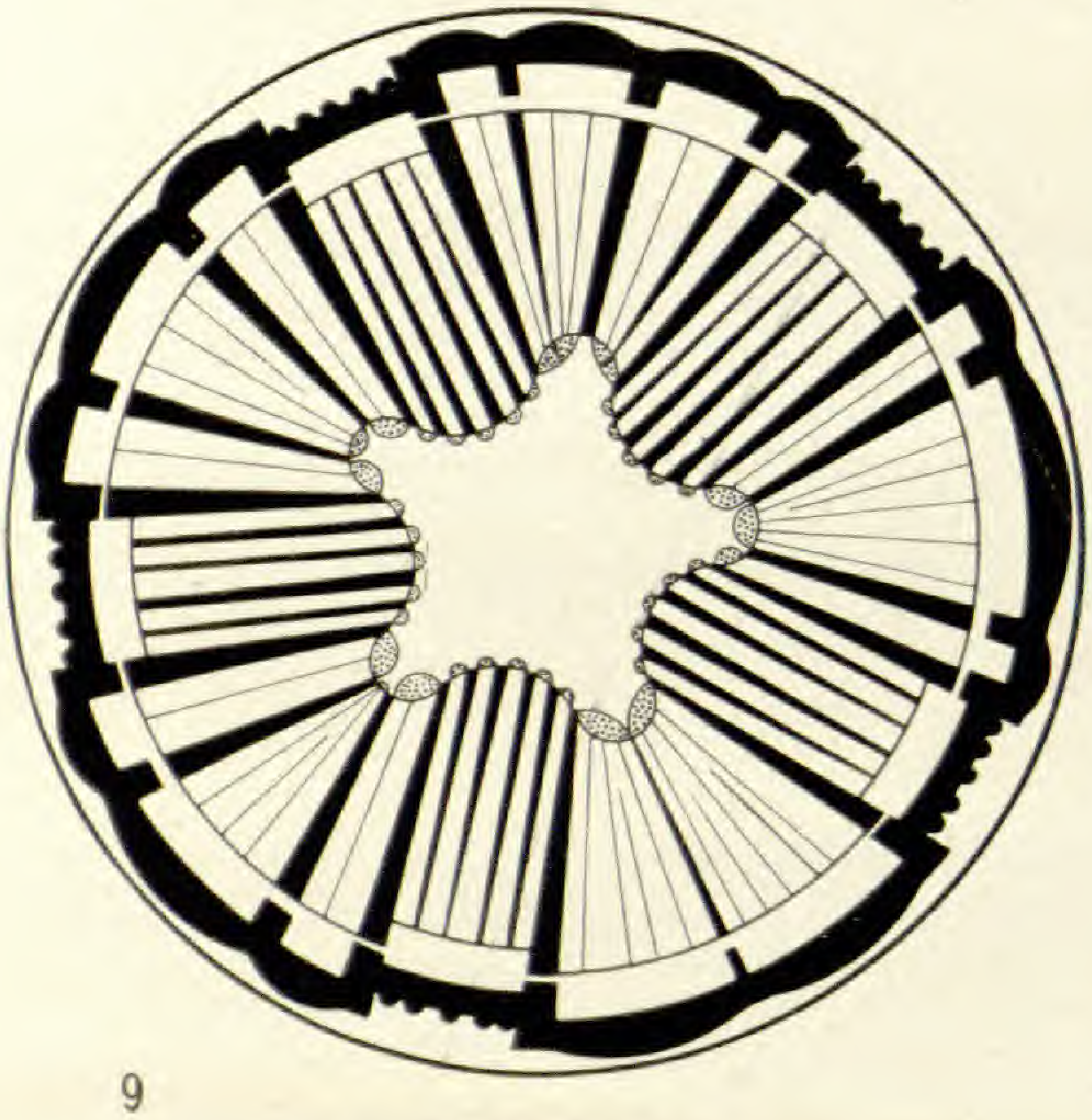

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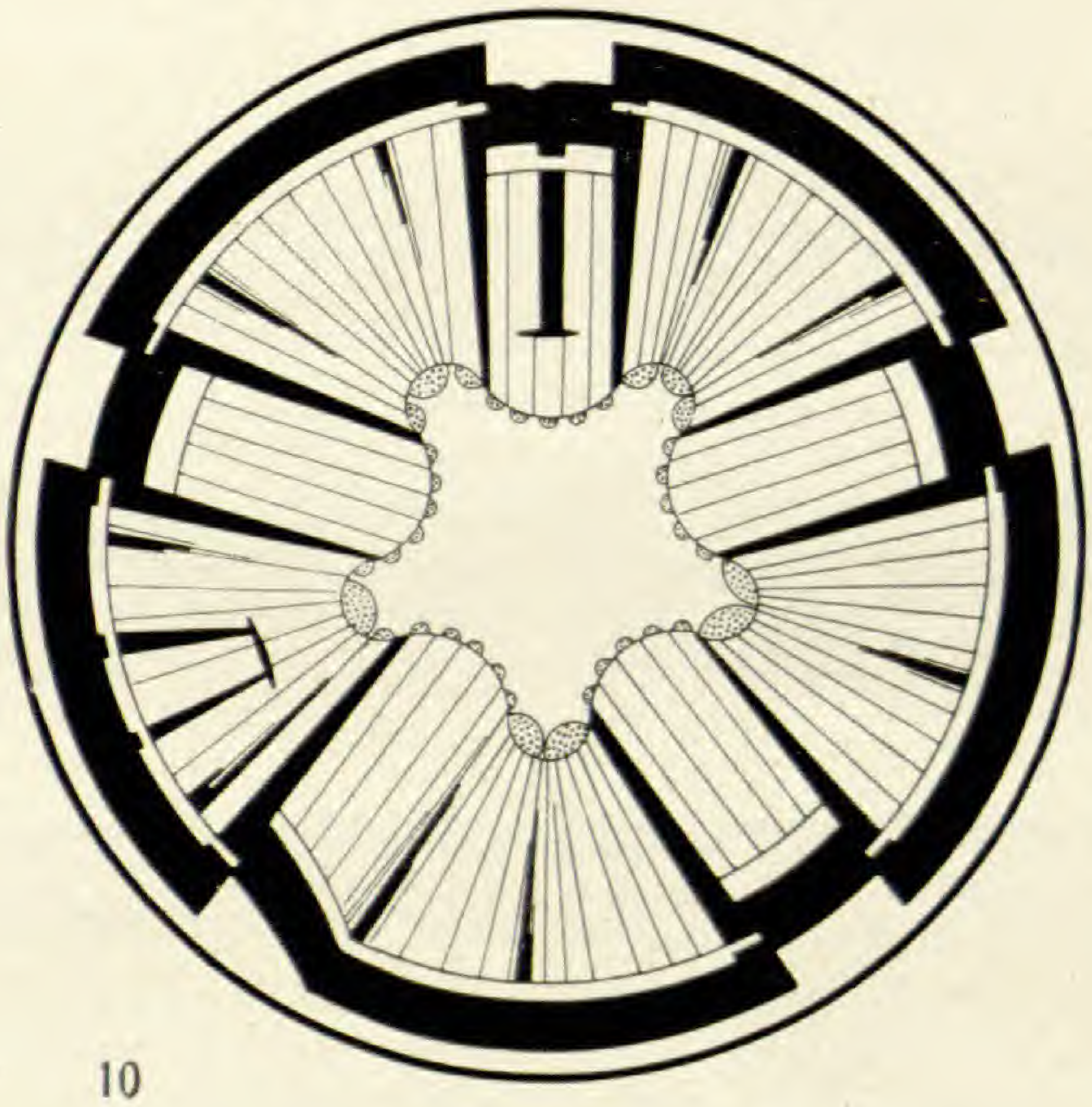

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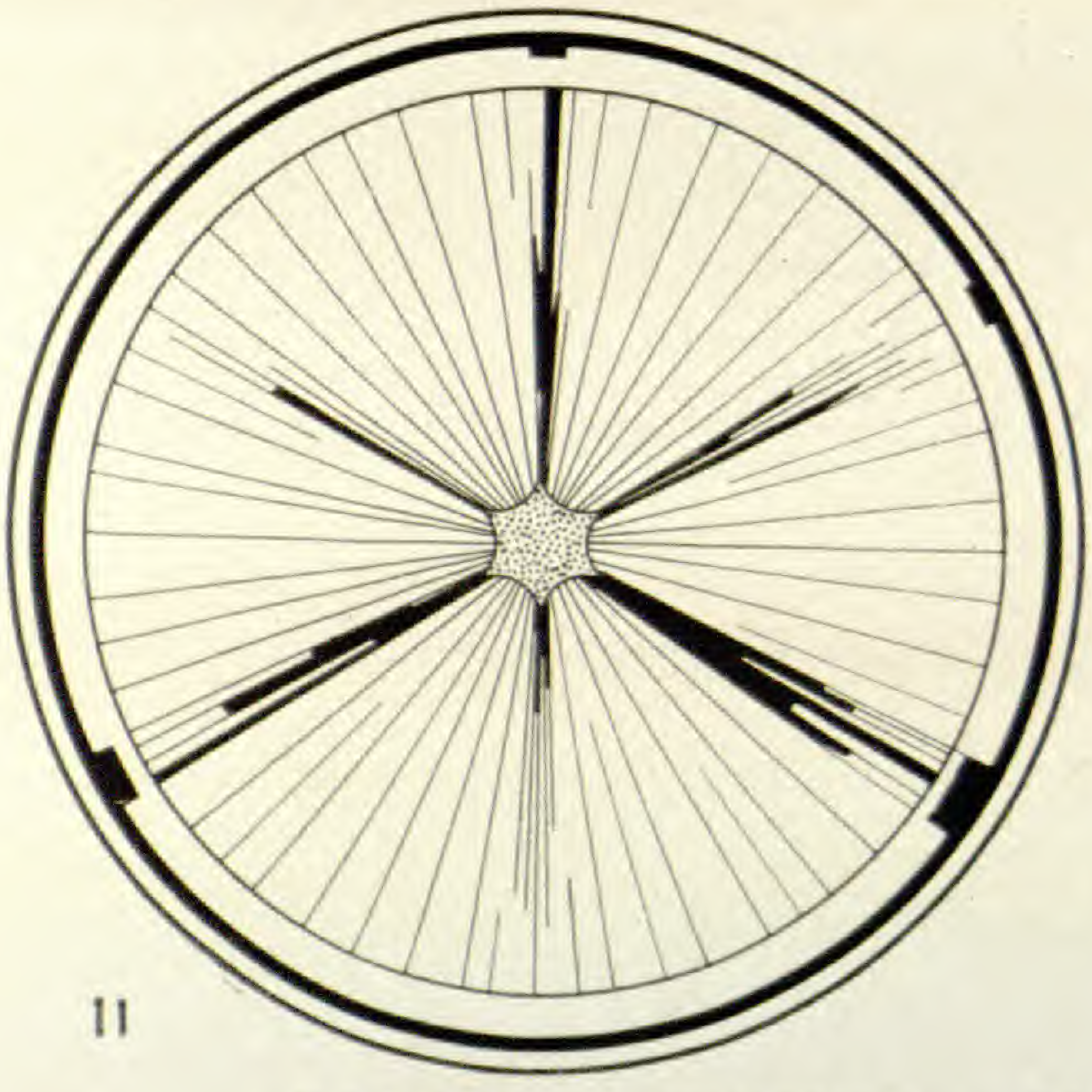

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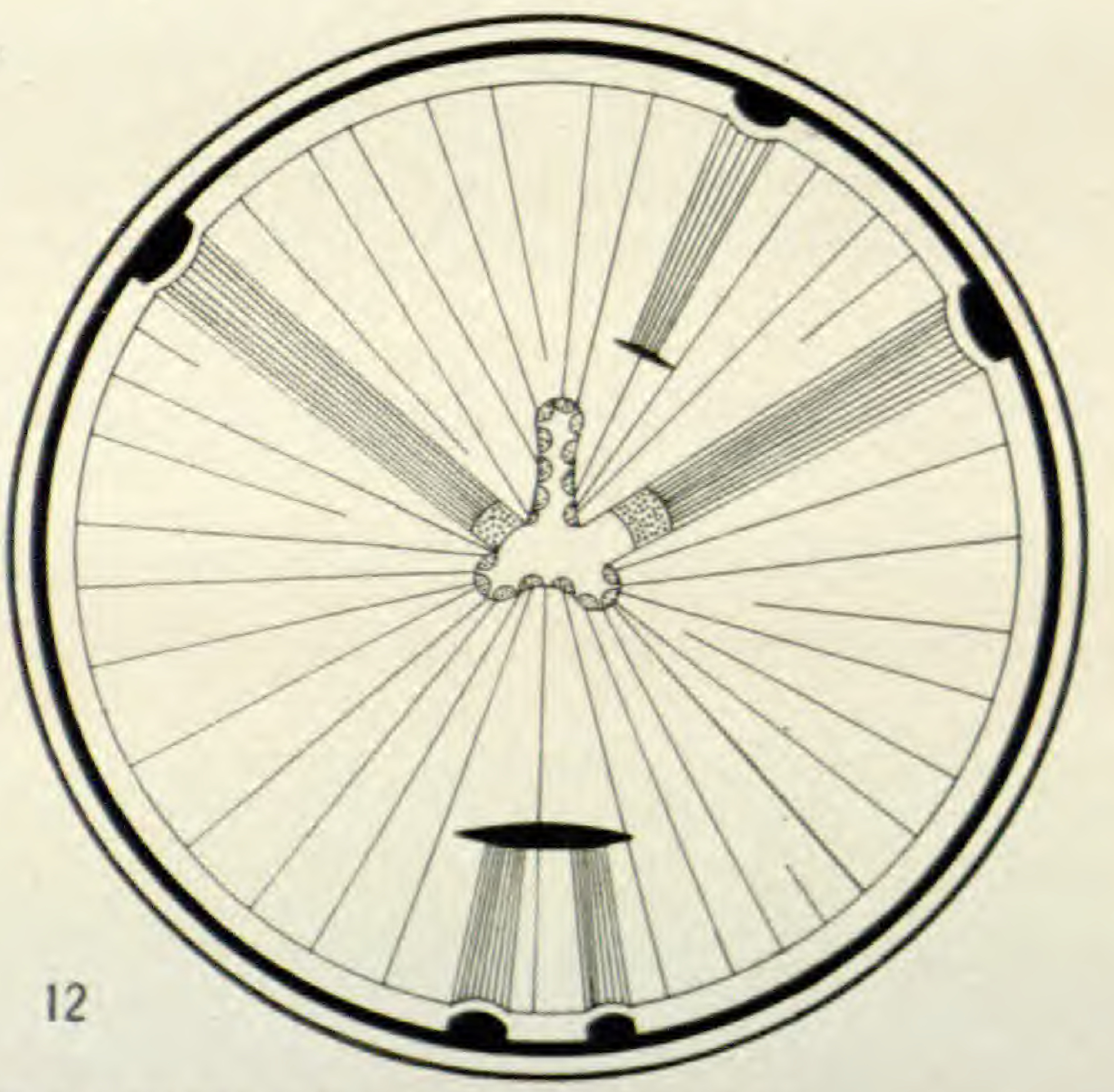

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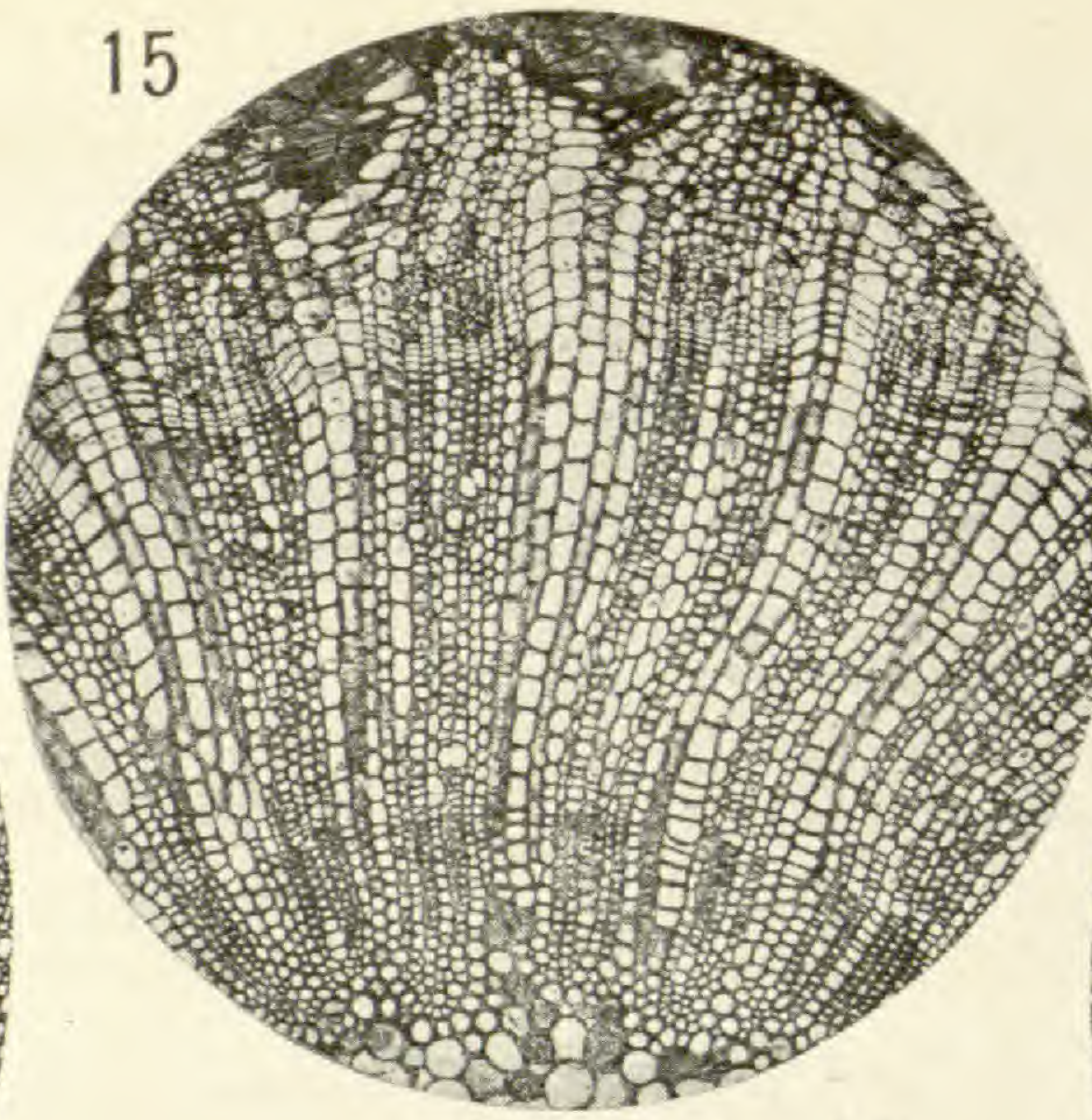

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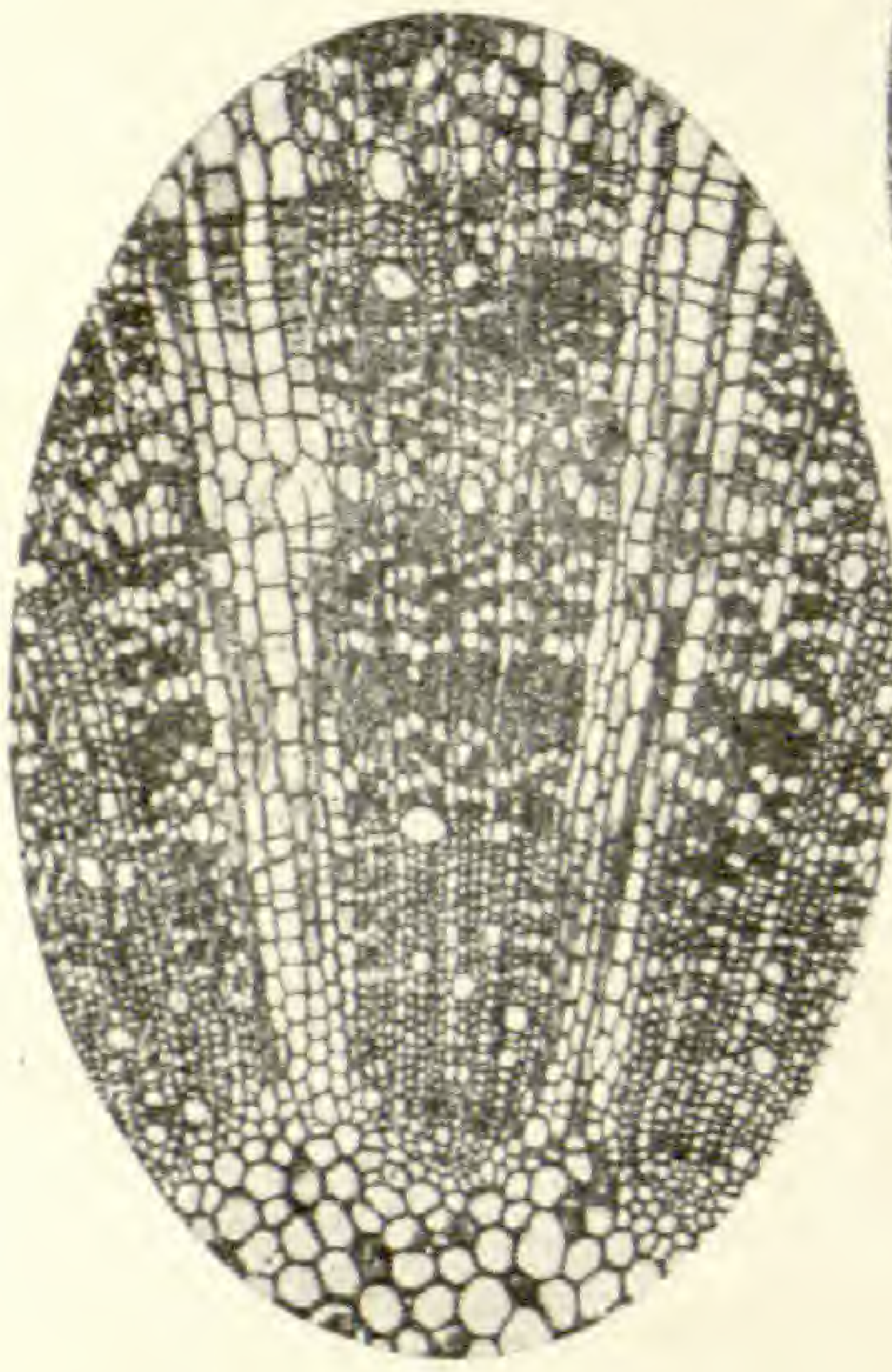

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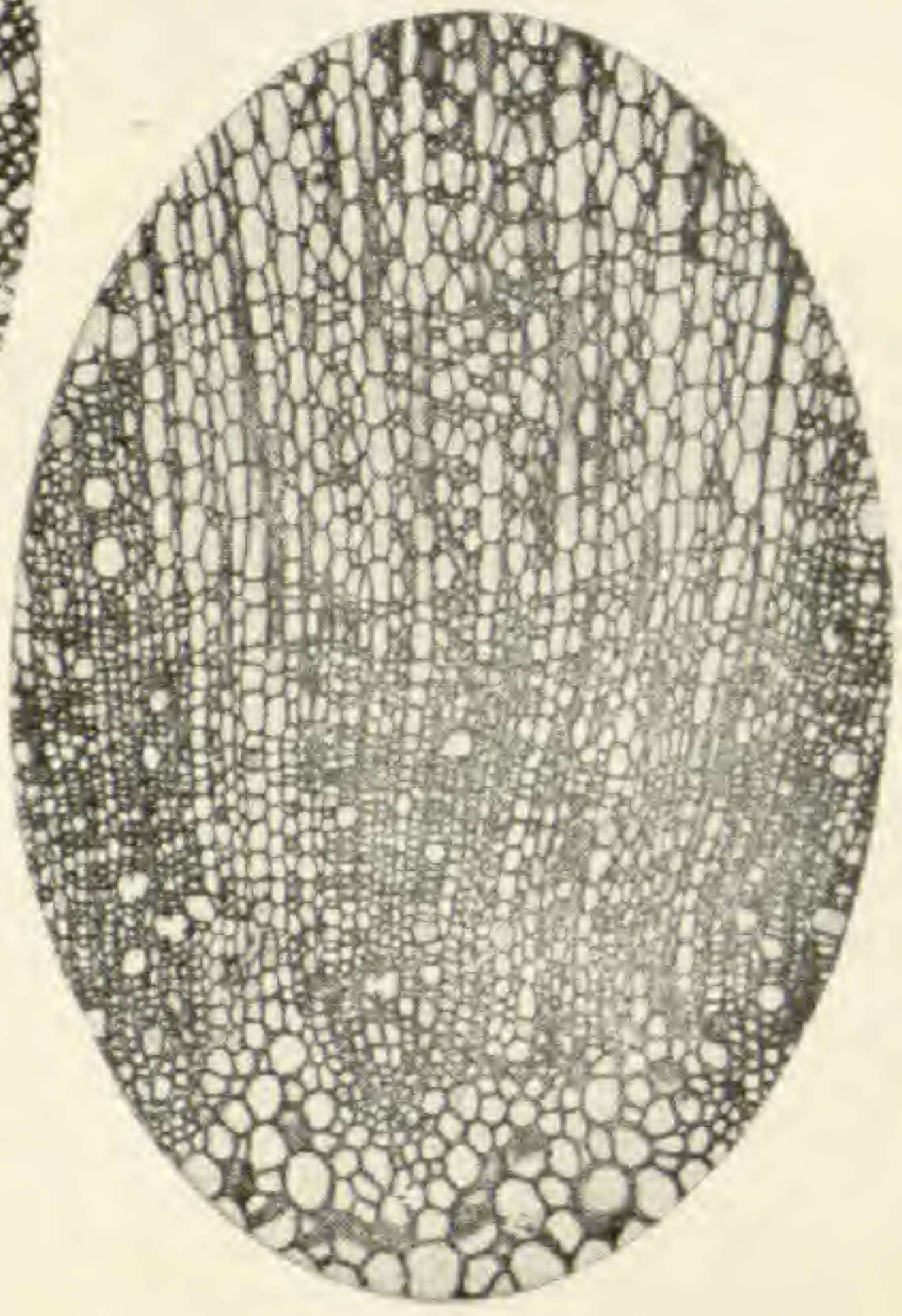

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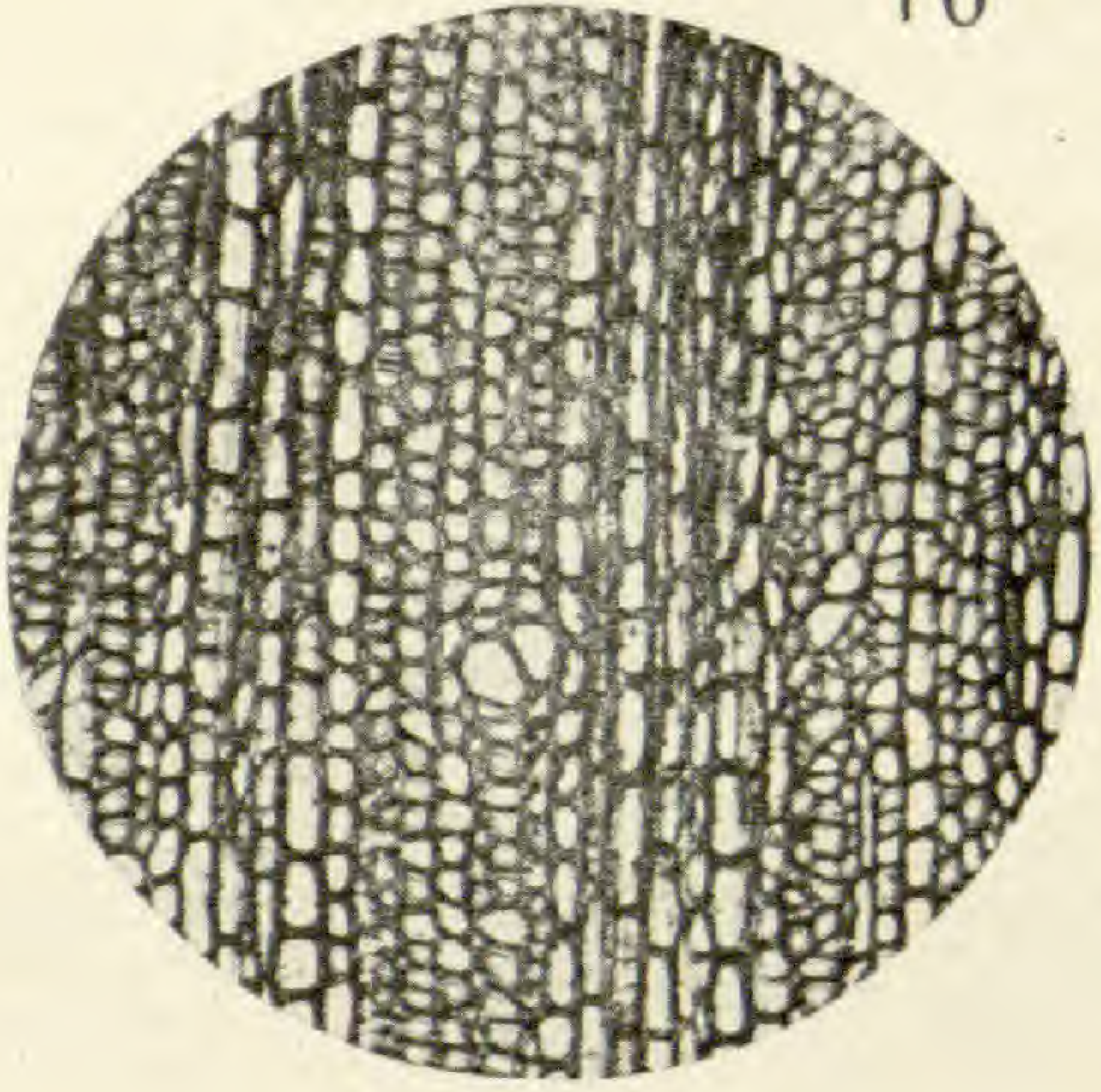

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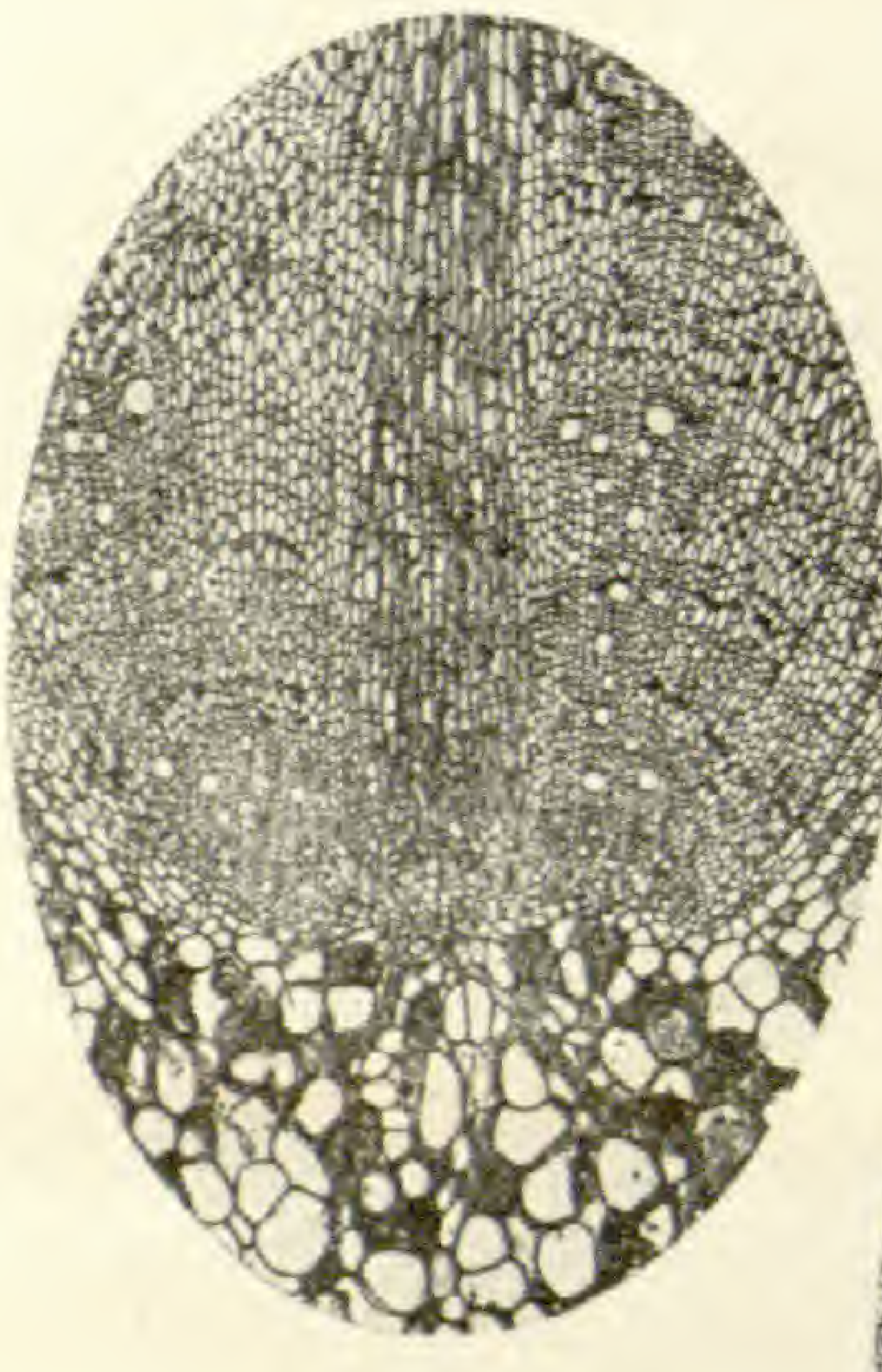

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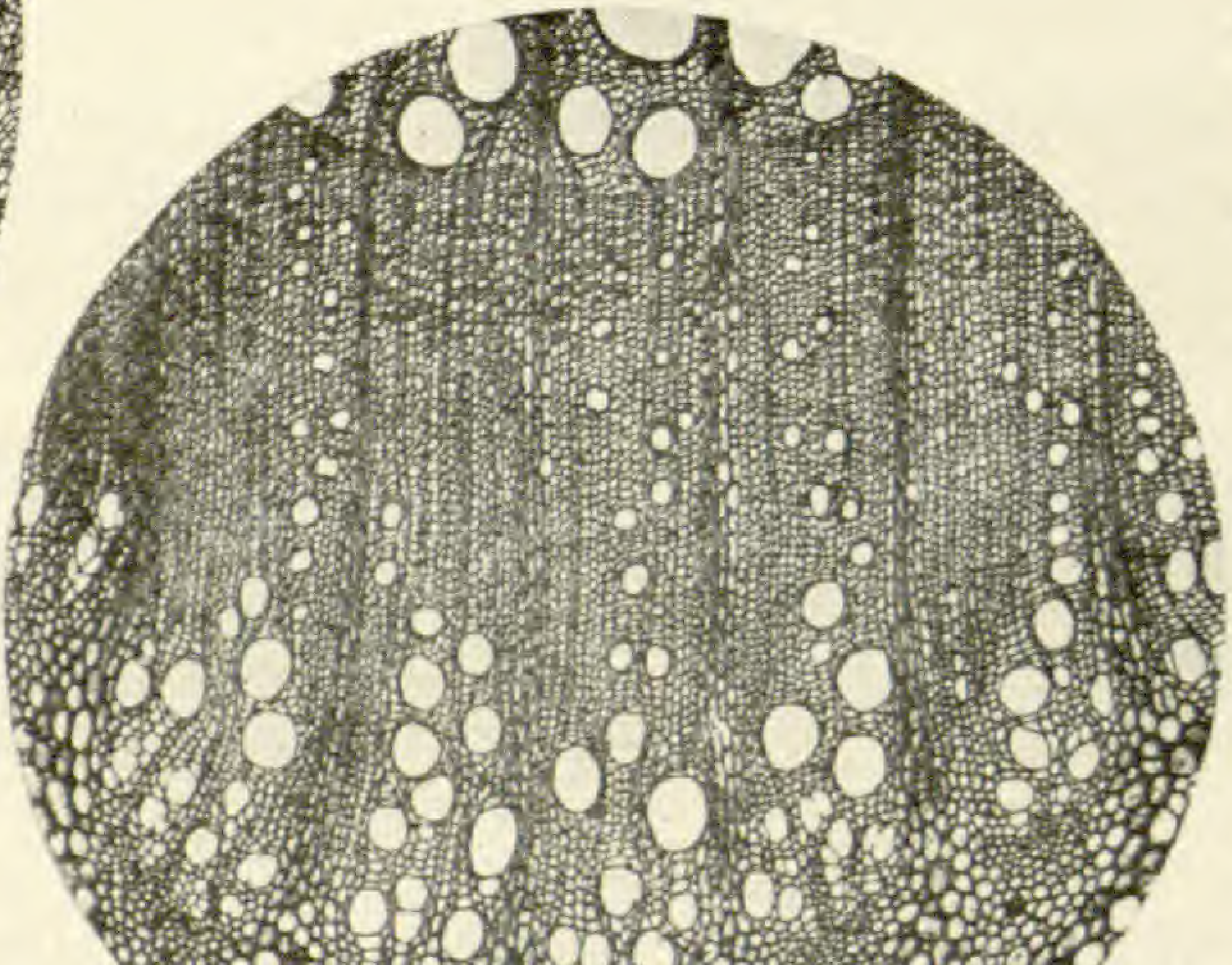

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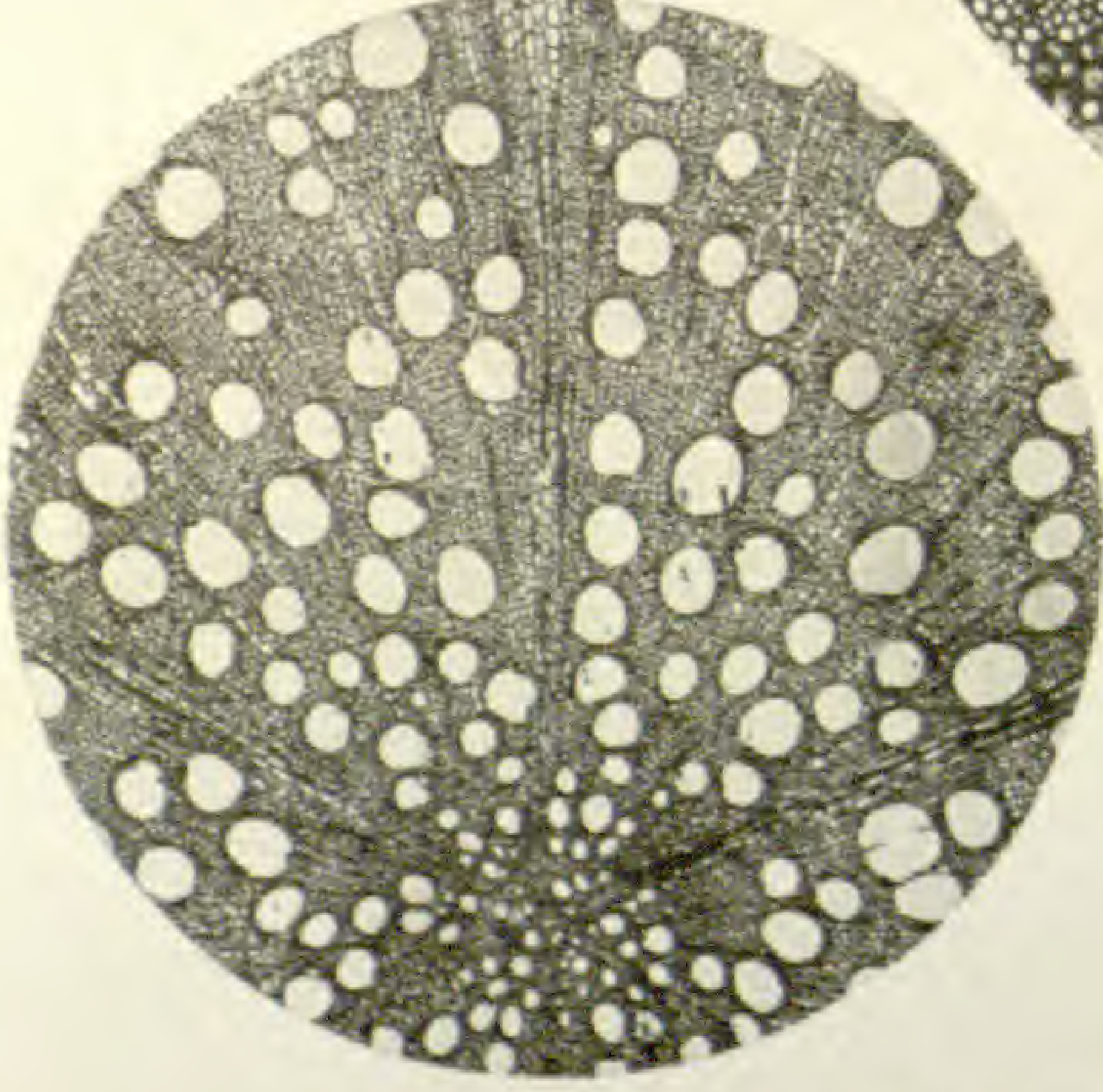

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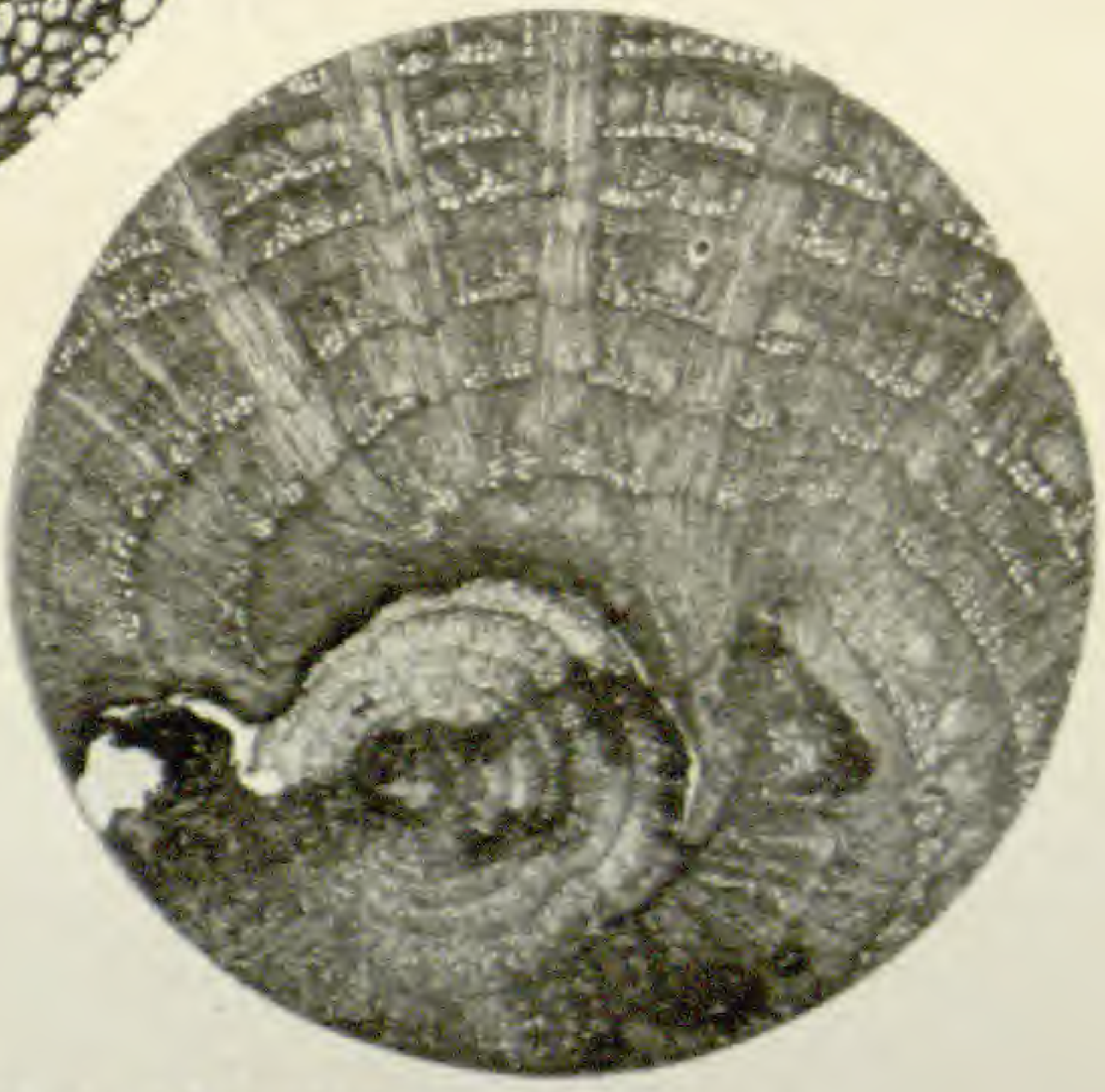


BAILEY and SINNOTT on PHYLOGENY OF ANGIOSPERMS

THE ANATOMY OF SIX EPIPHYTIC SPECIES OF LYCOPODIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 189

J. BEN HILL

(WITH TWENTY-EIGHT FIGURES)

In this investigation, six epiphytic species of *Lycopodium* were studied. Two New Zealand species, *L. Billardieri* Spring. and *L. varium* R. Br., with two South African species, *L. verticillatum* G.f. and *L. Holstii* Hieron., were furnished by Dr. CHARLES J. CHAMBERLAIN; and two forms from Samoa, *L. Phlegmaria* Linn. and *L. carinatum* Desv., were collected by Dr. W. J. G. LAND. The two species from New Zealand were identified by Dr. JESSE M. GREENMAN of the Field Museum, Chicago, and the remainder were identified by Dr. G. HIERONYMUS of Berlin. There was some doubt concerning the identity of the two forms from Samoa, since they do not correspond exactly to the descriptions of their respective species. Dr. HIERONYMUS suggests that each represents a new variety or subspecies. The species studied are described as growing epiphytic upon trees, with the short, vegetative branches more or less erect, and the long, slender, dichotomously branched strobili pendulous (fig. 1). Most of these species are rather rare, but *L. Phlegmaria* and *L. Billardieri* are mentioned in the recent literature dealing with the morphology of the group. Since these forms are not very familiar to residents of the northern hemisphere, a short general description may serve to make this account more intelligible.

L. Holstii is a very coarse plant, with short thick stems covered with large stiff leaves. The stem is 4–6 mm. in diameter, with a small stele 0.35 mm. in diameter. The leaves are about 2.5 cm. long and sharply pointed. Type material, furnished by Dr. G. HIERONYMUS, shows sporophylls with little or no modification from the vegetative leaves. They are not grouped in a definite strobilus, but are simply aggregated near the apex, much as in *L. lucidulum*.

FIG. 1.—*L. Phlegmaria:* epiphytic upon cocoanut tree; photograph of the plant in the field showing the habit of the species, by LAND.

L. verticillatum is much more delicate, with a slender stem covered with long, slender leaves. The sporophylls are arranged in definite strobili, which are regularly dichotomously branched and attain a length of 20–40 cm. The sporophylls show a slight modification from the foliage leaves, being smaller and more sharply pointed. Both leaves and sporophylls show spiral phyllotaxy.

L. Billardieri and *L. varium* resemble each other in their general appearance. Both bear long, dichotomously branched strobili with cyclic sporophylls arranged in alternating pairs, so that the outline in transverse section is square. In both species the sporophylls differ from the foliage leaves, being short and bluntly pointed. The chief gross difference in the two species is that *L. varium* is slightly coarser and the square shape of the transverse section of the strobili seems to be more definitely fixed than that of *L. Billardieri*, which produces some strobili circular in transverse section.

L. Phlegmaria is well known and needs little description. It is one of the most conspicuous examples of dimorphic leaves, the sporophylls being very small and delicate, almost membranous, while the vegetative leaves are broad and short. The strobili are very definite because of the extreme modification of the sporophylls and are circular in transverse section. Both vegetative leaves and sporophylls are sometimes cyclic in arrangement.

L. carinatum probably represents the highest specialization of any of the species studied. There is definite dimorphism of the leaves, which show the cyclic arrangement to the extent of giving even the young shoots the quadrangular appearance so characteristic of the strobili of some epiphytic lycopodiums. The strobili are also square in transverse section and dichotomously branched. The anatomical study also justifies the statement that this species represents the highest specialization of the species studied.

The material from New Zealand consisted entirely of mature stems and strobili, with no vegetative shoots. Roots were present in the material of *L. Billardieri*. The material of *L. verticillatum* consisted of several complete mature plants with both vegetative shoots and strobili, while that of *L. Holstii* was entirely vegetative.

The two species from Samoa were complete. No prothallia nor young sporophytes were present in any of the material. An investigation of the anatomical structures of the plants offered the most interesting feature of study, and this investigation was undertaken with reference to the development of the stele and its bearing upon phylogeny. The material was studied from paraffin serial sections cut 10–15 μ in thickness and stained in safranin-anilin blue and in safranin-light green. Since the material of *L. carinatum* was complete, and of such a character as to show the structures especially well, this species was selected as a basis for description and comparison.

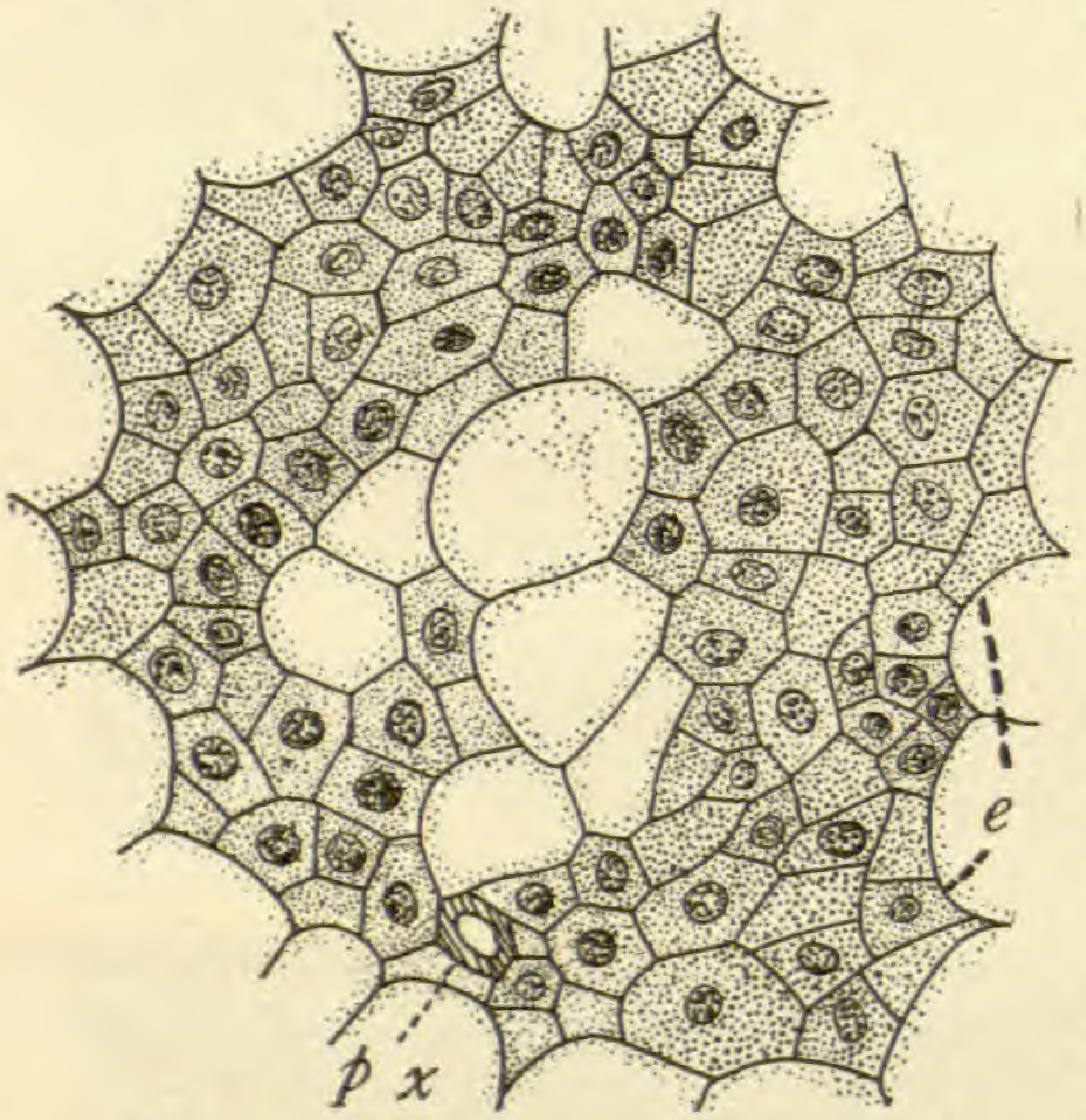


FIG. 2.—*L. carinatum:* transverse section of the stem near the apex, showing the organization of the young stele; *e*, inner wall of endodermal cells; *px*, protoxylem; large cells in center are unlignified potential metaxylem cells; ×500.

L. carinatum

In the apex of the strobilus of *L. carinatum* the outline of the transverse section of the young vascular cylinder is often almost square. Within the first millimeter of the stem, before any lignification of the protoxylem is recognizable, there is distinct differentiation of the tissues; not only is the cylinder organized as a region distinct from the cortex, but the elements of the tissues of the vascular system are differentiated. The large cells of the endodermis are discernible, inclosing a mass of smaller cells, part of which have abundant cytoplasm and conspicuous nuclei. This group of cells is to be differentiated into the vascular tissues.

At this stage of development there are two distinct systems of cells within the stele. The central region of the young cylinder is occupied by 5–10 large, thin-walled, unlignified cells with vacuolate cytoplasm, forming an irregular radiating group. These are to become lignified and form metaxylem. The angles of this radiating mass of cells and the portions of the cylinder just within the endodermis are occupied by groups of smaller cells which have relatively very large nuclei and dense cytoplasm. These smaller cells are the parenchyma of the cylinder and will give rise to both the protoxylem and the phloem elements (fig. 2).

The cylinder of the vegetative apex is more nearly circular in outline than that of the strobilus. The two show similar differentiation and differ little excepting that the cylinder of the vegetative shoot has about twice the diameter of that of the strobilus, and the extent of the group of large cells is greater, with more numerous groups of small parenchyma cells.

In the further organization of the stele, the protoxylem is the first to be differentiated. The protoxylem points arise in irregular succession in the peripheral region of the cylinder by the lignification of some of the small cells. Generally there is only one cell lignified first, and usually this cell is situated in the second layer of cells from the endodermis. This is followed by the lignification of some of the adjacent smaller cells similarly situated. This leaves a pericycle, at first one layer of cells in thickness. There are 2–4 protoxylem points differentiated in the strobilus apex, and a large number, generally 6 or 8, in the vegetative apex. These points are located at the peripheral ends of the radiating strands of the central group of unlignified cells (fig. 3). This is the regular situation in the vegetative apex, but when there are only 2 protoxylem points in the strobilus apex, the relation of the protoxylem and the

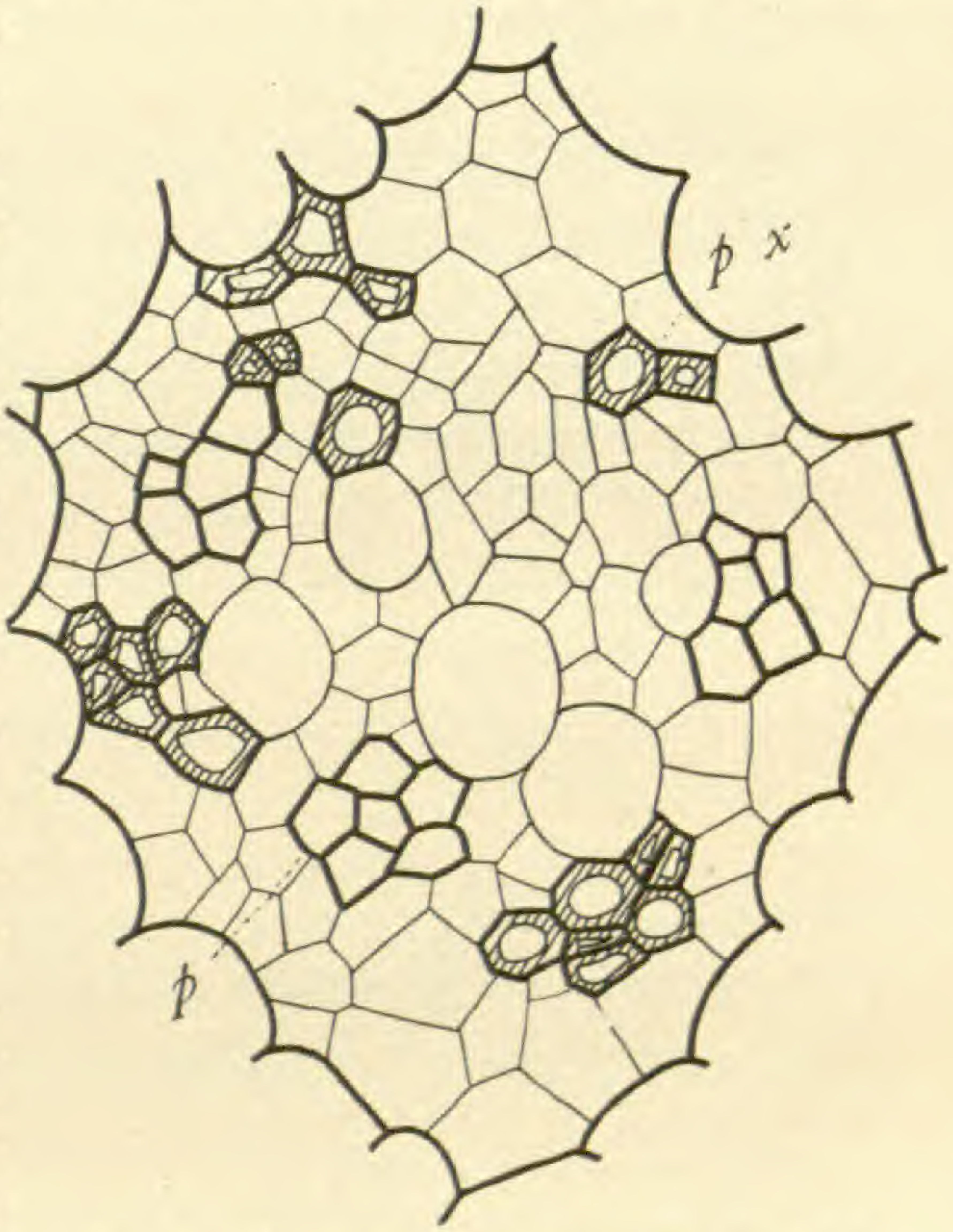
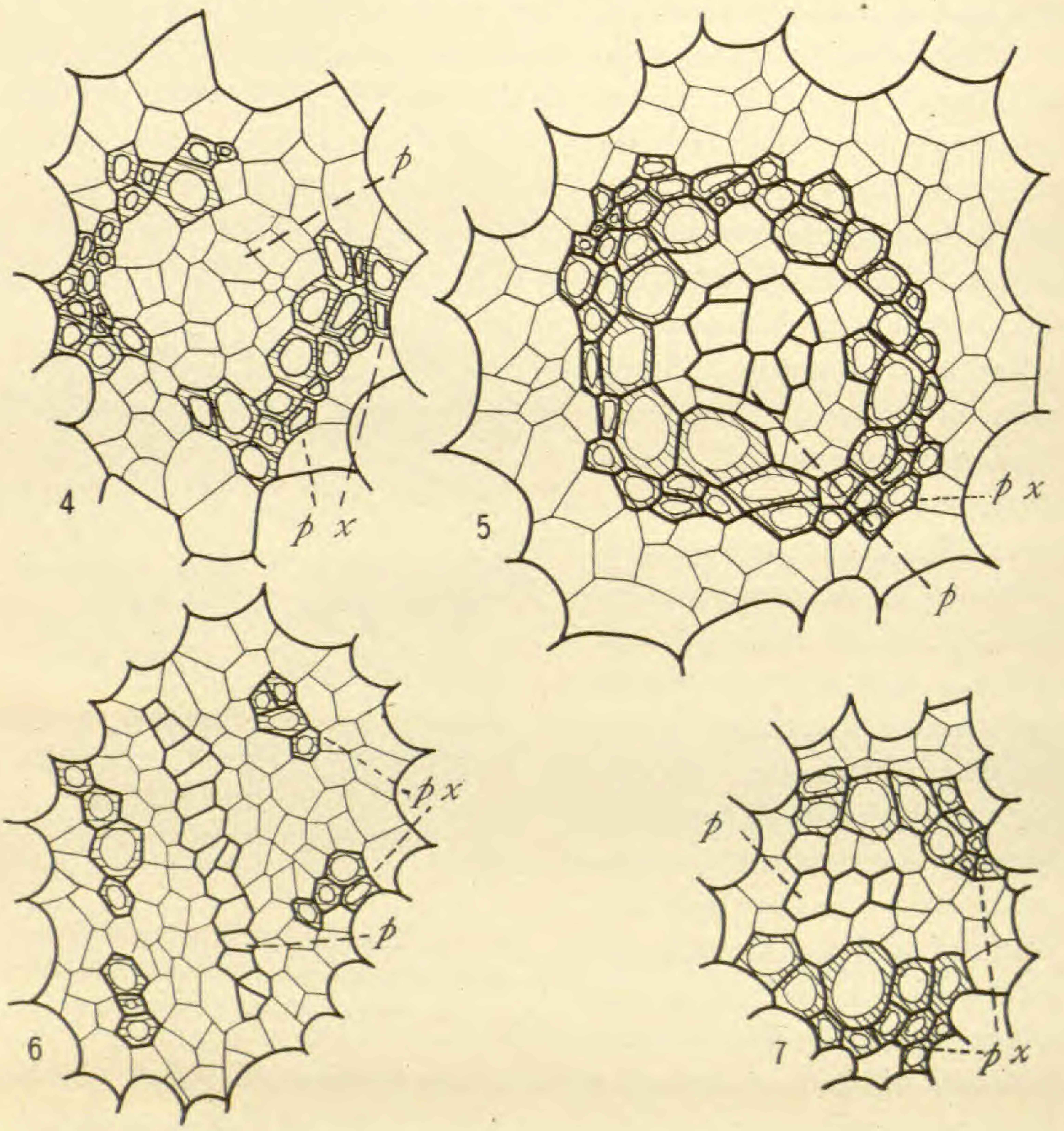


FIG. 3.—*L. carinatum:* transverse section of the strobilus axis, showing the radial arrangement; *px*, protoxylem; *p*, phloem; ×500.

unlignified cells may vary. Often the arrangement shows the protoxylem point on each side of the cylinder, with a band of unlignified cells arranged parallel to it and just inside, while the middle of the cylinder is occupied by a band of phloem extending



FIGS. 4–7.—Fig. 4, *L. carinatum:* transverse section of the strobilus apex, showing the development of the parallel-banded type; *px*, protoxylem; *p*, phloem; fig. 5, *L. carinatum:* transverse section of the stele in the strobilus axis, showing the amphivasal condition, phloem in the center inclosed by a ring of xylem; *px*, protoxylem; *p*, phloem; fig. 6, *L. Phlegmaria:* transverse section of strobilus, showing radial arrangement, with the phloem extending across the center forming a band; the same condition is also found in *L. carinatum; px*, protoxylem; *p*, phloem; fig. 7, *L. Phlegmaria:* showing the development of the parallel-banded stele; *px*, protoxylem; *p*, phloem; all ×500.

from the sides across the center (fig. 4). This gives the parallel-banded type of stele, that is, alternating parallel bands of xylem and phloem. In all of these situations there is a tendency for the protoxylem to grow around the circumference of the cylinder (figs. 8, 9), with very irregular behavior of the groups, consisting of fusions and splitting, resulting in crescent-shaped masses and even in masses completely encircling a central mass of the parenchyma and phloem, giving a type of stele resembling the amphivasal type found in monocotyledons (fig. 5).

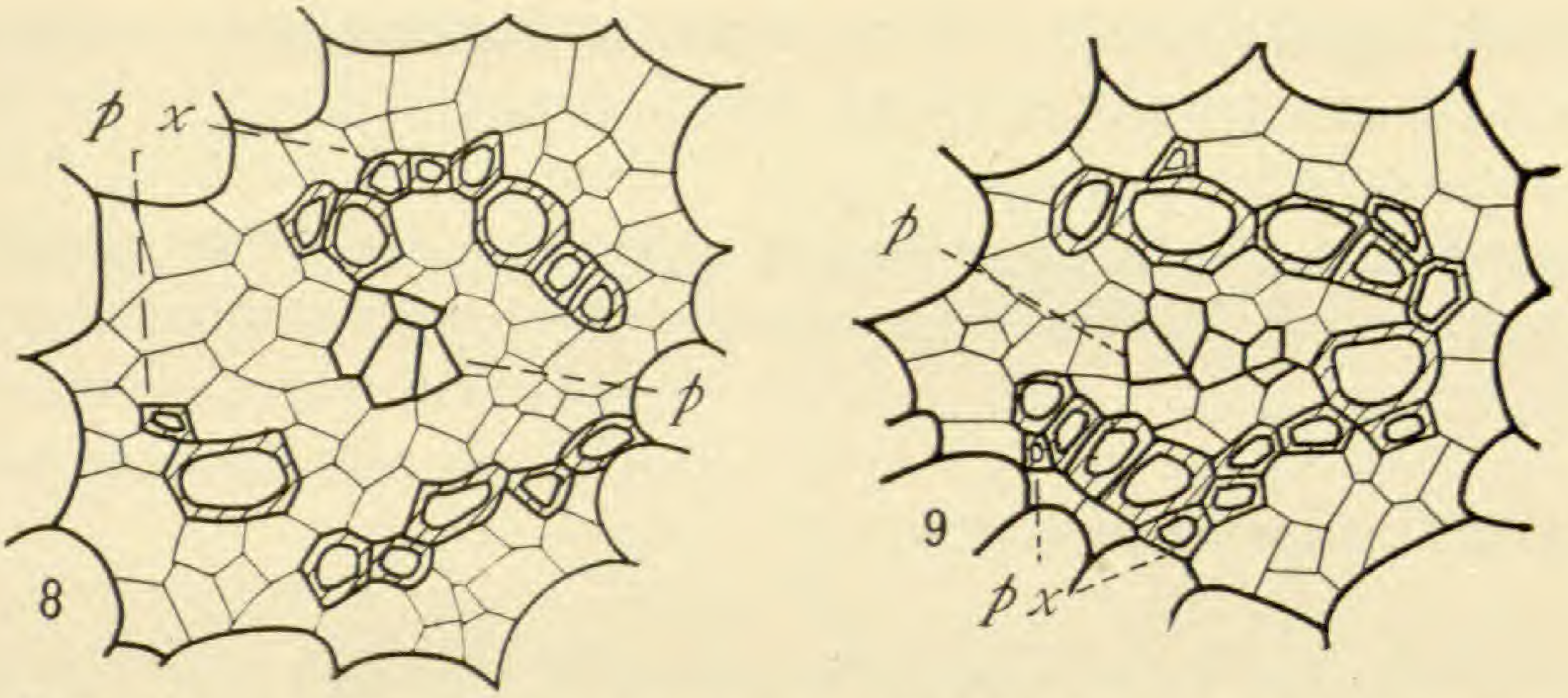
The phloem as recognizable tissue is differentiated from the parenchyma at a somewhat later period than the protoxylem. In all of the protoxylem situations described above, the phloem arises from the small parenchyma cells located on the same circumference as the protoxylem, giving a true radial stele.

The study of the strobilus in transverse serial sections shows three types of stele: radial, parallel-banded, and amphivasal, the two latter conditions being derived from the first by modifications and specialization. These changes are not connected with branching. They are the result partly of the behavior of the protoxylem groups, but chiefly of the growth and development of the metaxylem. The young stele in the apex is organized at first with a distinct radial arrangement, the protoxylem points, 2 or 3 in number, alternating with phloem groups on the same circumference (fig. 3). Lower in the stem, the sections show the protoxylem extending around the periphery of the cylinder, with the developing metaxylem organized as two parallel bands, with the phloem groups at each end, extending inward and forming a central band of phloem (fig. 4). At a slightly lower level in the young strobilus, the amphivasal arrangement is found (fig. 5). This is a further modification of the parallel-banded arrangement. It is formed by the continued peripheral growth of the xylem until a complete ring is formed inclosing the phloem. This ring remains intact only a short distance in the stem. At a lower level it appears broken up into the parallel-banded types, and this condition still lower passes into the distinctly radial arrangement. Since the parallel-banded and radial arrangements are found both above and below the amphivasal, the latter passing into the parallel-banded, and that into the radial, it is clear that these various conditions are all modifications of the radial arrangement (fig. 3). In most cases the amphivasal condition is not attained. This occurs where the xylem grows around only one end of the band of phloem, giving a crescent-shaped xylem (fig. 9). This arrangement may be either an intermediate condition between the parallel bands and the amphivasal situation, or it may represent the final development at that point and, breaking up, return to the parallel-banded type without the formation of the amphivasal. These modifications seem to be entirely confined to the strobilus cylinder. In the vegetative stems and in the vegetative part of the stem which bears the strobilus, there is no evidence of the modifications of the stele which are so characteristic of the strobilus. All vegetative parts are radial as to their stelar structure excepting where this condition is modified by branching.

At the base of the vegetative stems roots leave the stele, and pass downward through the cortex for some distance before finally passing out of the stem. These roots show a peculiar tendency to form a ring of xylem resembling the ring of xylem in the stem.

L. Phlegmaria and L. varium

Both these species greatly resemble *L. carinatum* in the tendency of the strobilus to develop the parallel-banded type of stele, by the peripheral growth of protoxylem and by the development of the metaxylem at the sides of the cylinder, leaving the central portion occupied by the phloem. This tendency to the peripheral growth of the xylem is especially marked in *L. varium*, where even in the mature stem it is sufficiently extensive to inclose one-third to one-half of the stele in certain portions for a considerable distance (fig. 15). *L. Phlegmaria* shows many crescent-shaped masses of xylem in the strobilus stele (figs. 8, 9), which nearly close, but it seldom if ever fully attains the amphivasal condition reached by *L. carinatum*. The parallel-banded type in *L. varium* is not always derived from the radial arrangement as it seems to be in *L. carinatum*. The apex shows distinctly two methods of organization of the stele. One is the radial as described for *L. carinatum* (figs. 10, 11). The other is the method in which the radial arrangement



FIGS. 8, 9.—*L. Phlegmaria:* transverse sections in the same series, showing the development of the crescent-shaped xylem mass from the parallel-banded type; the same method of development is found in *L. carinatum*, which carried farther gives the amphivasal condition; *px*, protoxylem; *p*, phloem; ×500.

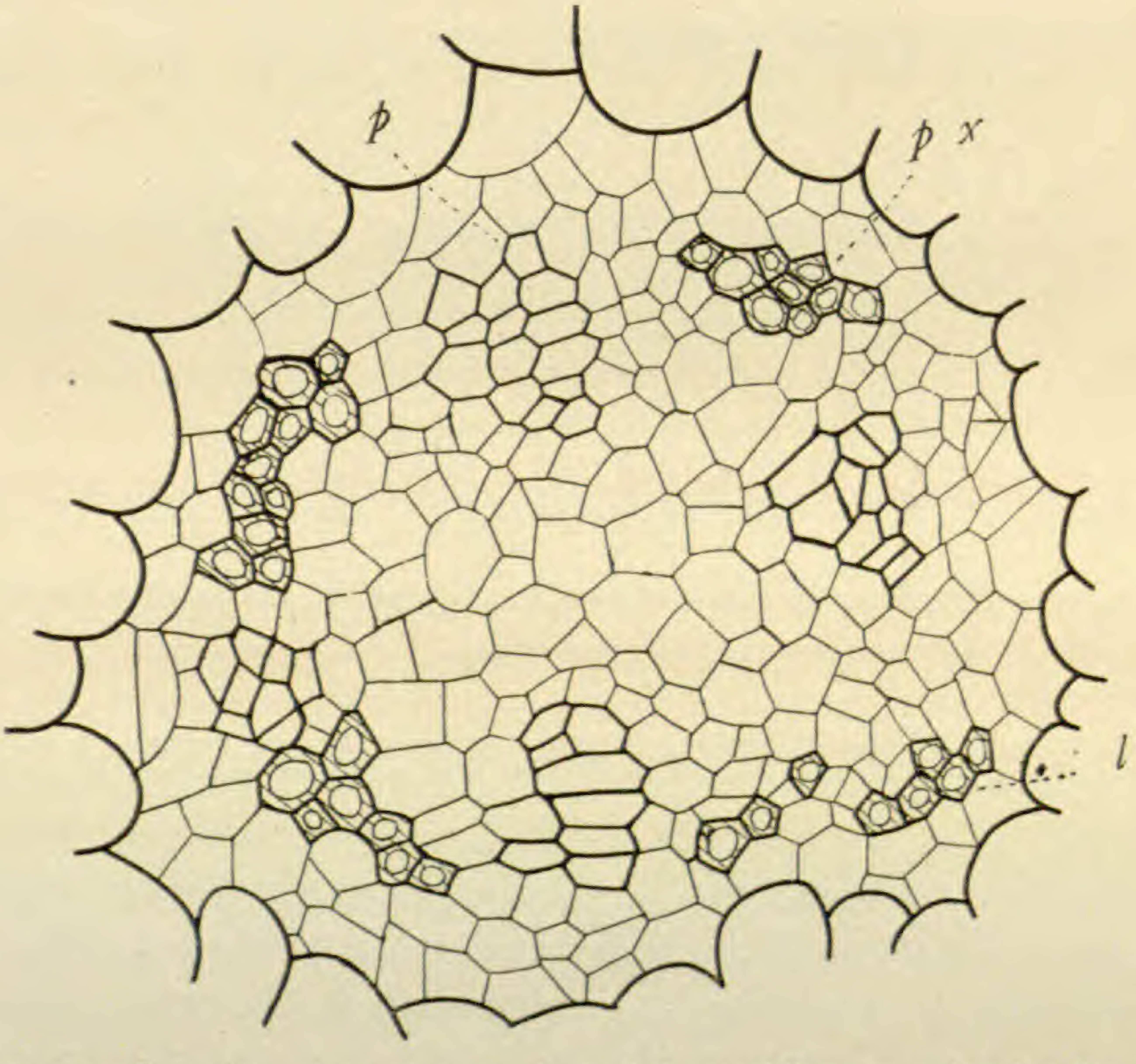


FIG. 10.—*L. varium:* transverse sections of the strobilus apex, showing the radial arrangement; *l*, leaf trace; *px*, protoxylem; *p*, phloem; ×500.

does not appear at first. There is one protoxylem point on either side with the phloem between, which develops directly into the parallel-banded types (figs. 12, 13). These parallel bands of xylem may develop into crescent-shaped xylem masses. The crescent-shaped xylem is a high development of the parallel-banded type of stele, formed, as in *L. carinatum*, by the growth of xylem around one end of the phloem (fig. 9). The mature stem and the vegetative stem of *L. Phlegmaria* are characterized by the true radial arrangement (fig. 14). The material of *L. varium* was entirely strobilus-bearing, but the vegetative portions show the radial arrangement (fig. 15). The type of the stele in all cases in these species, as in *L. carinatum*, is determined by the growth of the metaxylem.

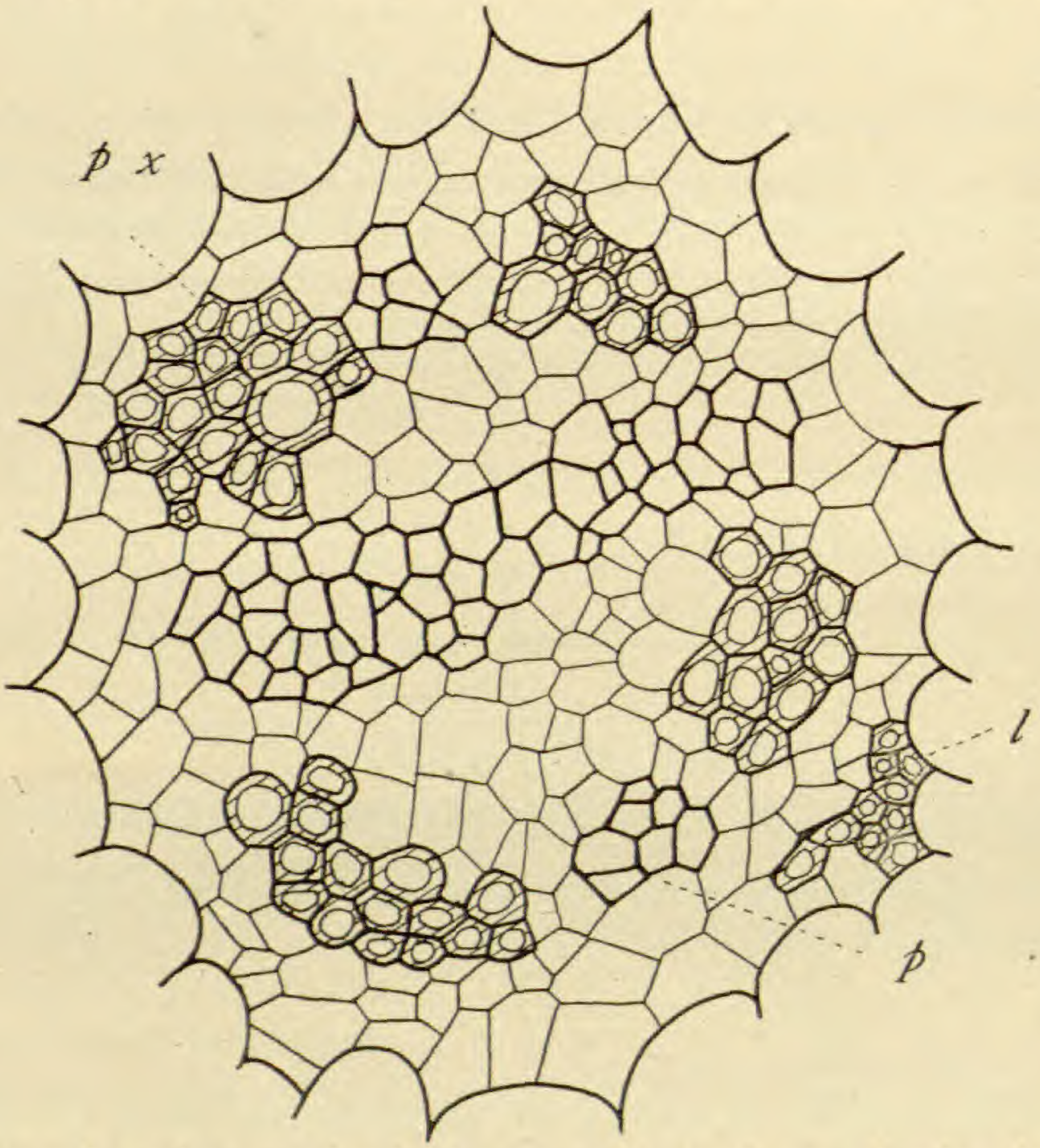
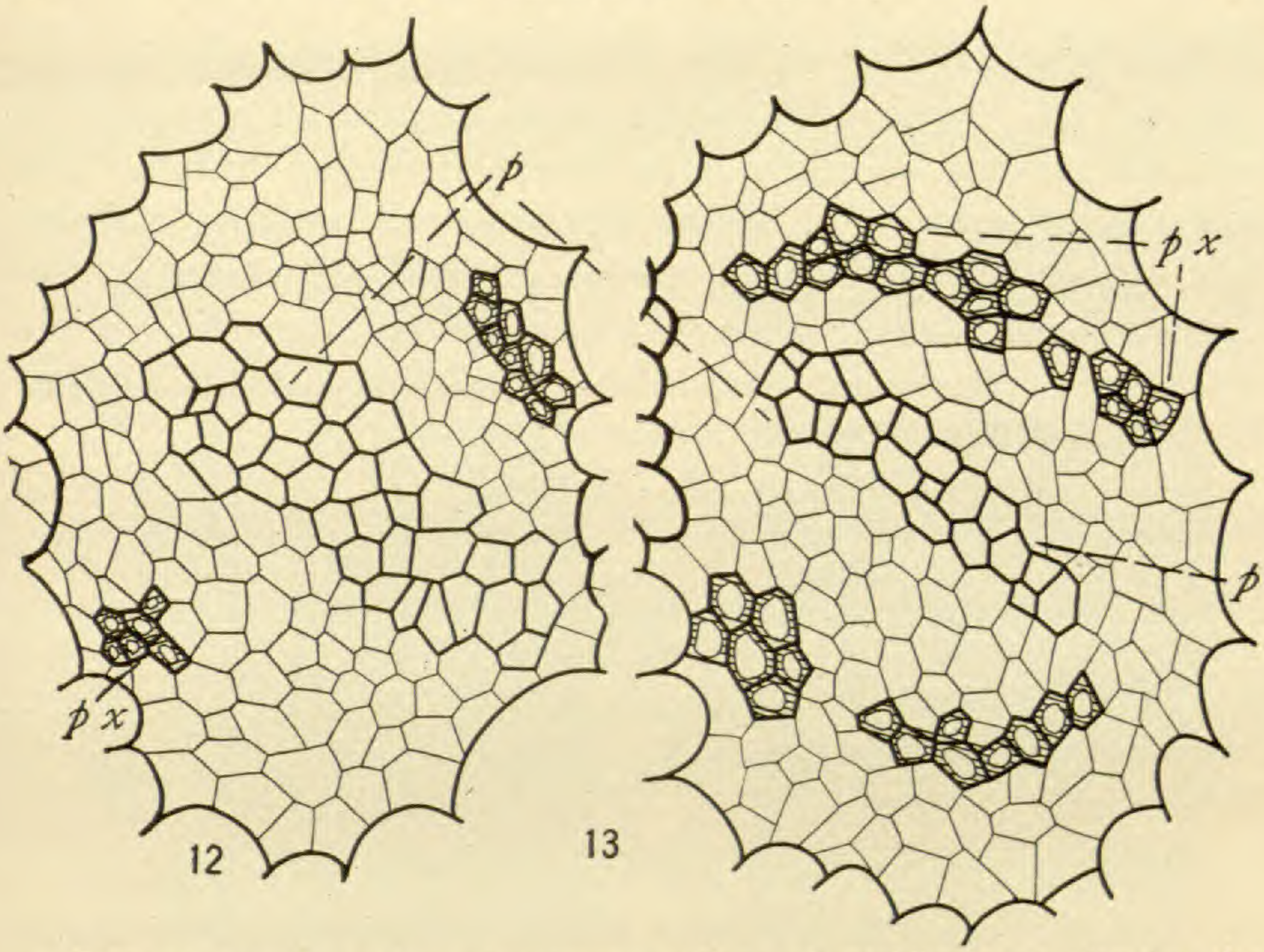


FIG. 11.—*L. varium:* section in the same series as fig. 10, showing the development of the parallel-banded type from the radial; *l*, leaf trace; *px*, protoxylem; *p*, phloem; ×500.

As an aid to a better understanding of these stems, clay models were made of the xylem portions of the steles by studying serial



FIGS. 12, 13.—*L. varium:* transverse sections of strobilus apex, showing the parallel-banded type of stele developing directly without passing through the radial arrangement; *px*, protoxylem; *p*, phloem; ×500.

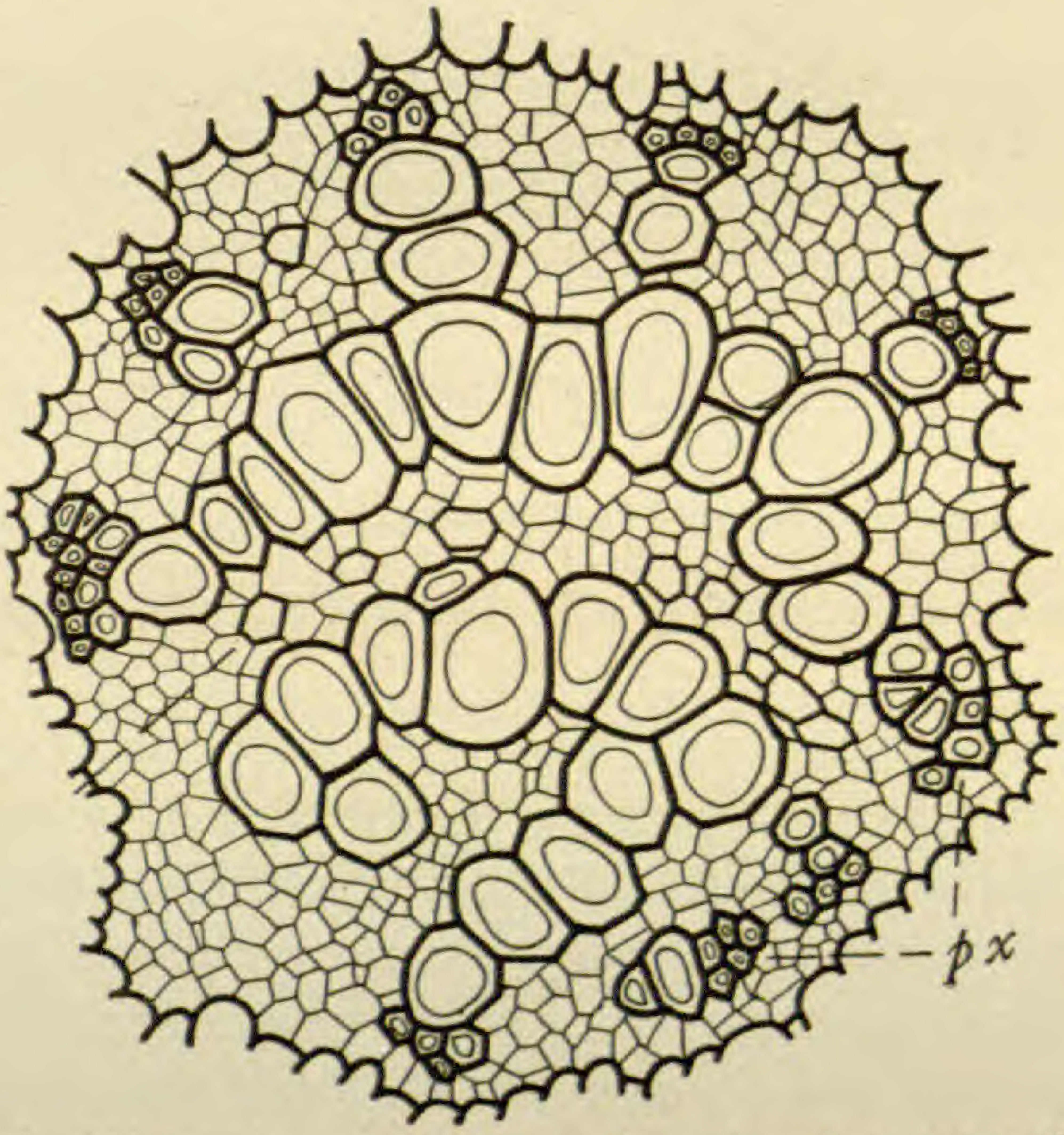


FIG. 14.—*L. Phlegmaria:* transverse section of mature vegetative stem; *px*, protoxylem; *p*, phloem; ×185.

sections and building up the corresponding structures in clay (figs. 16, 17). Vegetative portions were selected for reproduction and the method of study gave some interesting results. The model of the stele of *L. varium* was almost a complete cylinder, with occasional breaks in the peripheral shell of xylem (fig. 16). This structure is due to the growth of the xylem around the periphery. There were some indications that this growth is related to the passing out of the leaf traces, since often there would be a leaf trace at the point of meeting of two of the peripheral growths. There was too much irregularity in the matter of leaf traces to justify making any definite statements, since leaf traces pass off from the protoxylem points and from the peripheral growths also, with no apparent general relation to the growth of the xylem. The study of the clay models showed branching and fusions of the protoxylem points to be quite common. The relation of xylem

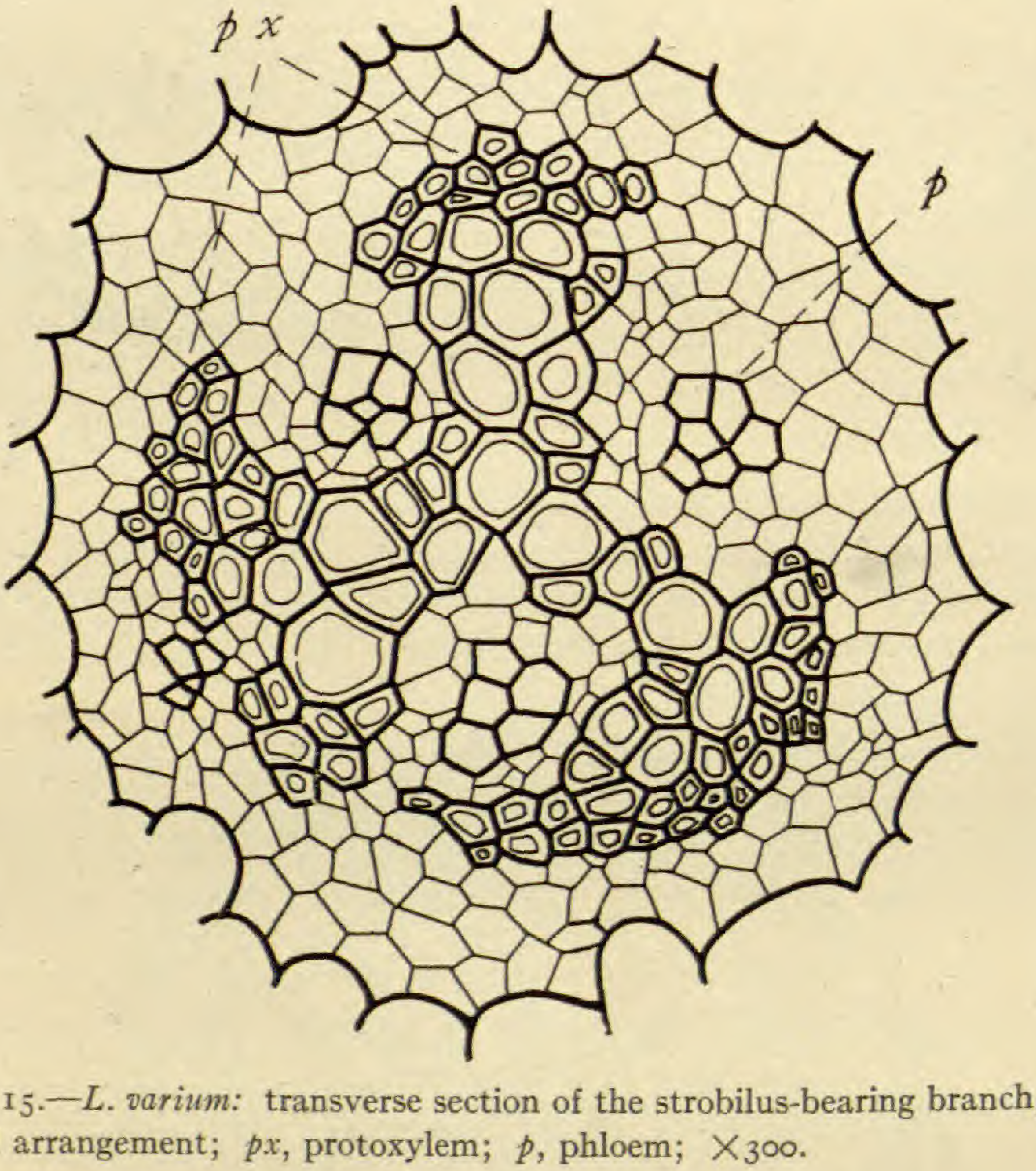


FIG. 15.—*L. varium:* transverse section of the strobilus-bearing branch, showing the radial arrangement; *px*, protoxylem; *p*, phloem; ×300.

and phloem was evident in the model; the branching of the xylem was often followed by branching of the phloem groups and xylem fusions by phloem fusions. Frequently the peripheral growth of the xylem cut off phloem on the outside of the xylem, and sometimes phloem seemed to arise outside when the xylem was indented.

FIG. 16.—*L. varium:* photographs of the clay models of the stele; the base is started at the portion of the stem represented in fig. 15; the projections represent the leaf traces which pass out indiscriminately from the stele; *l*, leaf trace.

FIG. 17.—*L. Phlegmaria:* photographs of the clay models of the stele; the ridges represent the projecting protoxylem groups which fuse and branch irregularly; leaf traces are represented by projections; *px*, protoxylem; *l*, leaf trace.

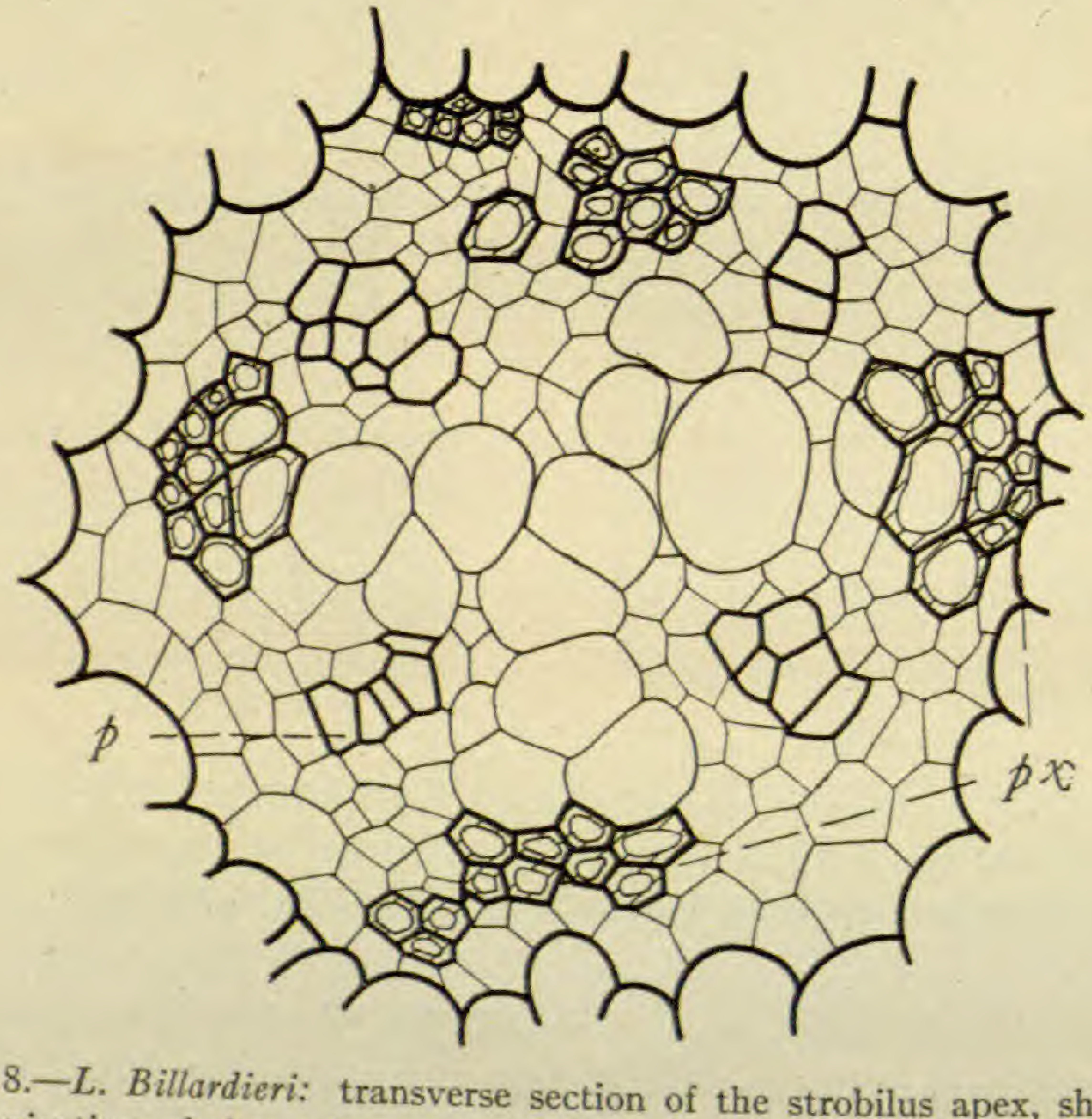


FIG. 18.—*L. Billardieri:* transverse section of the strobilus apex, showing the radial organization of the stele; protoxylem groups alternating with phloem; the center of the stele is occupied by the unlignified potential metaxylem cells; *px*, protoxylem; *p*, phloem; ×500.

L. Billardieri

The organization of the strobilus in this species is distinctly radial, and this condition was constant in all the material examined (fig. 18). The further development of the metaxylem also results in a very regular structure for the stem. This structure consists of several radiating bands of xylem with phloem groups between them. The xylem also has a great tendency to form an almost complete ring inside the stele. The center of this ring may be occupied by a single isolated strand of either phloem or xylem. The development of the ring is dependent entirely upon the behavior of the metaxylem and not upon the peripheral growth as in *L. carinatum*, for it is not peripheral to the stele, but is located inside the periphery, forming an inner ring with radiating masses of xylem which extend to the circumference of the vascular cylinder (fig. 19).

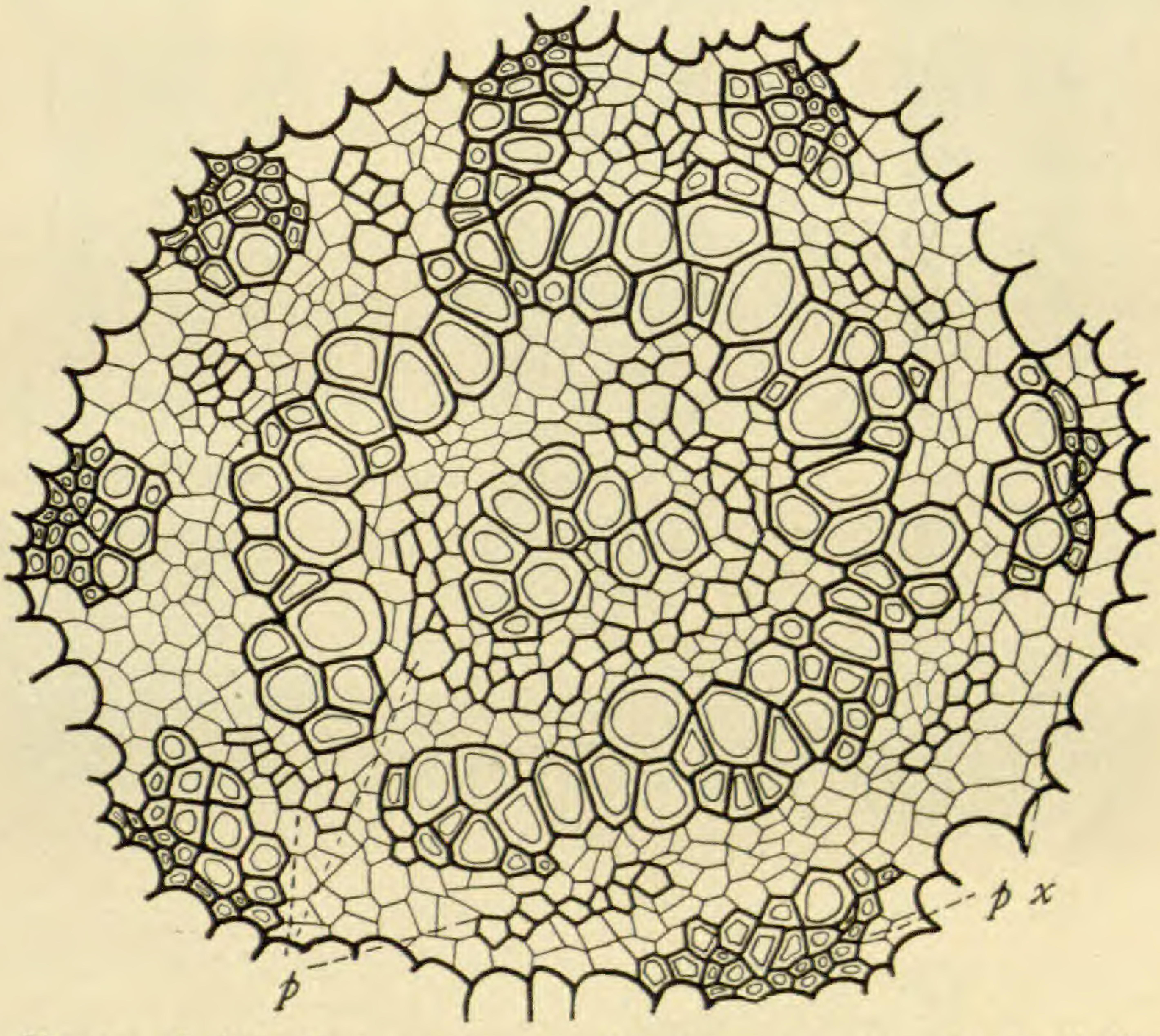


FIG. 19.—*L. Billardieri:* transverse section of a mature stem, showing the inner xylem ring; *px*, protoxylem; *p*, phloem; ×185.

FIG. 20

FIG. 20.—*L. Billardieri:* photographs of the clay model, showing the irregular behavior of the protoxylem groups and their relation to the leaf traces; the protoxylem groups here show both fusions and splitting; *l*, leaf trace.

FIG. 21

FIG. 21.—*L. Billardieri:* photograph showing an end view of the model shown in fig. 20.

This is the usual condition of the vegetative portions of the stem and can be designated as a radial arrangement. A clay model of the xylem portions of the stele was made, and it shows something of the xylem behavior in the stem (figs. 20, 21). No young vegetative shoots were present for comparison in this species, but the mature vegetative stem, bearing strobili, shows the characteristic structure of the stem (fig. 19). The phloem is distinct and is recognizable earlier than in most of the species.

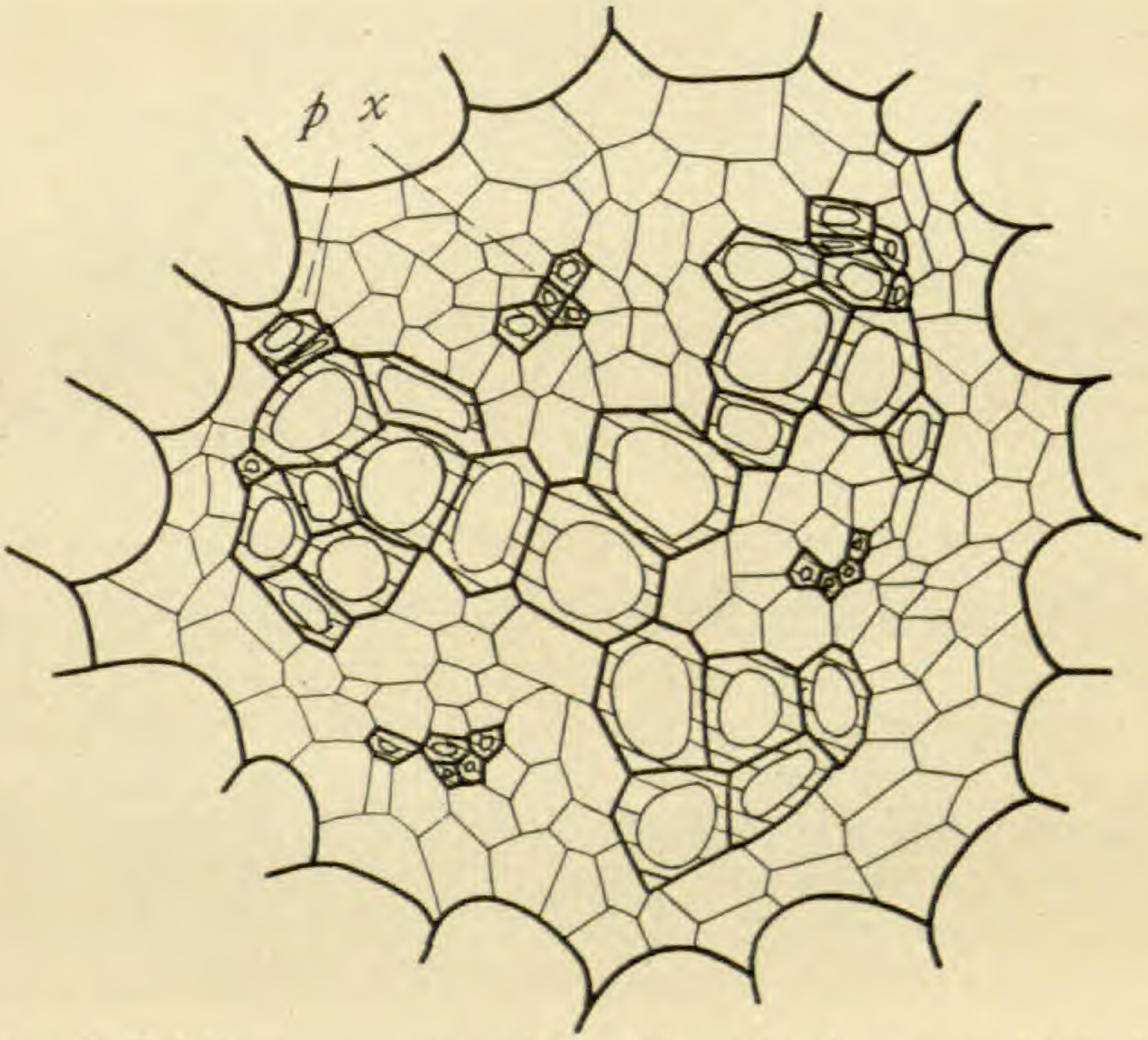


FIG. 22.—*L. Holstii:* transverse section of the stele of a young shoot, showing the radial arrangement; *px*, protoxylem; ×500.

Cortical roots occur toward the base of the stem as described in *L. carinatum*, but their structure is similar to those described for *L. pithyoides*.[1]

L. Holstii

The material of this species was entirely vegetative, and of the vegetative shoots there were very few young ones. From a study of a limited number of slides, it appears that the stele is organized with a rather large number of protoxylem points (about 8). The

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[1] STOKEY, ALMA G., The roots of *Lycopodium pithyoides*. BOT. GAZ. 44:57–63. *pls*. 5, 6. 1907.

central portion of the stele is occupied by large unlignified cells which are slowly thickened into metaxylem. The phloem seems to arise irregularly near the periphery and is not easily recognized when young. In the young shoot examined, the stele became radial toward the base (fig. 22). Here there were fewer protoxylem points also, 3 or 4 in number, and part way up the stem there was an isolated xylem strand as occurs in *L. Billardieri* (fig. 19). The distinctly radial arrangement extended to the base of the shoot where it joined the main plant.

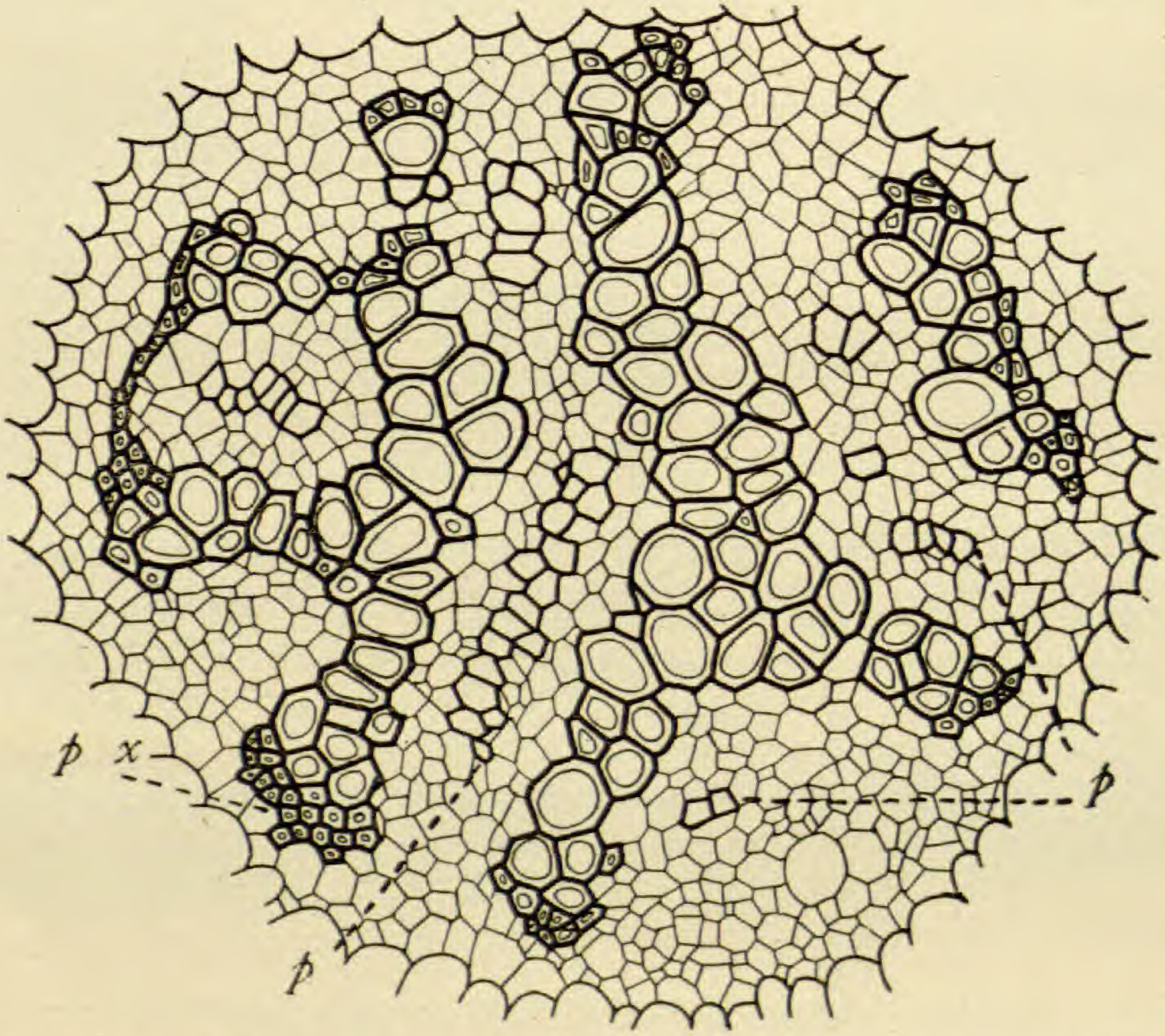
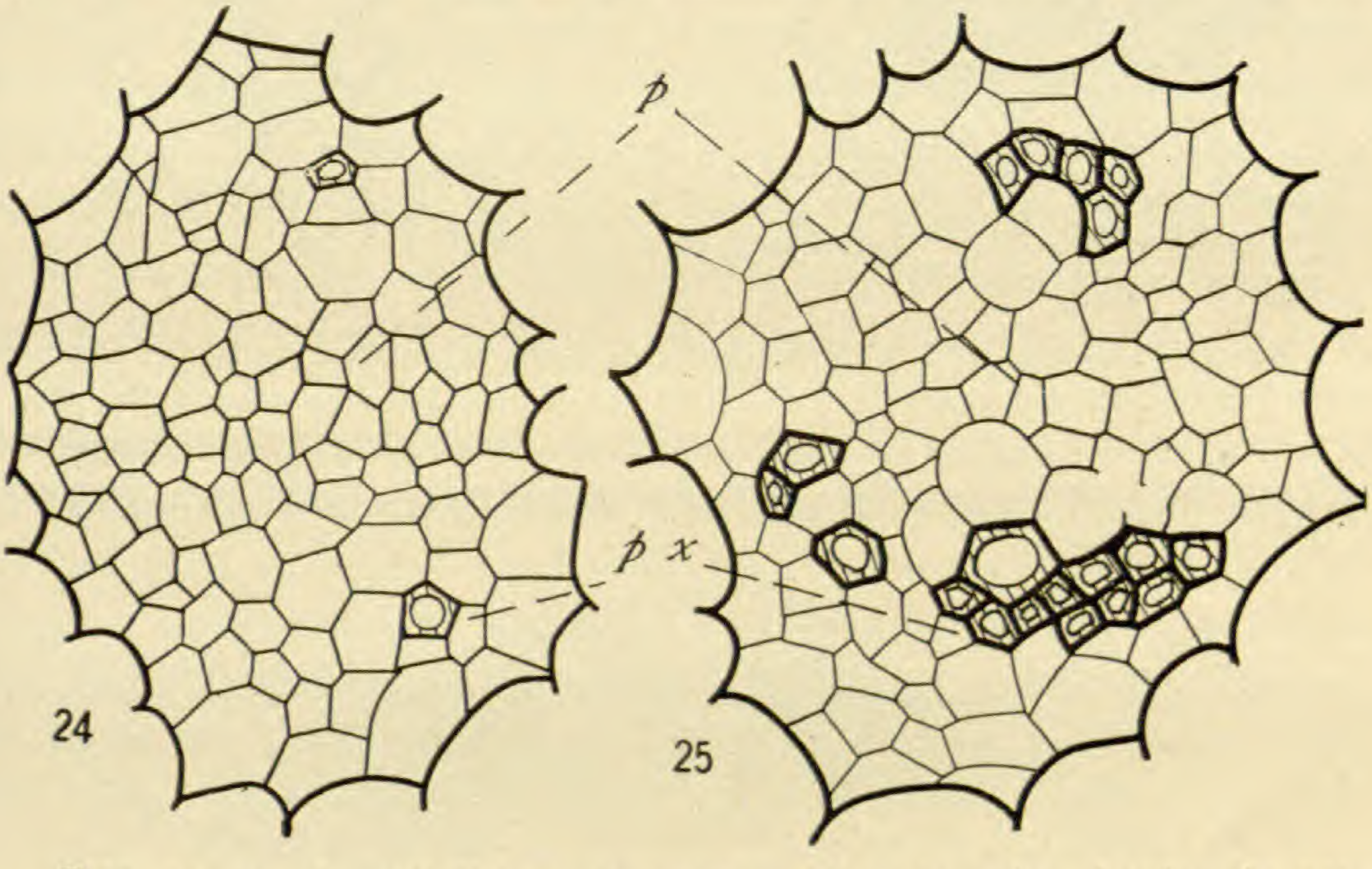


FIG. 23.—*L. Holstii:* transverse section of mature stem, showing parallel-banded type of stele; phloem scattered irregularly between the xylem bands; *px*, protoxylem; *p*, phloem; ×185.

In the fully mature vegetative stem there is an irregular parallel-banded type of stele (fig. 23) differing in appearance from that described for *L. verticillatum*, and more developed than those in the strobilus of *L. carinatum*. The phloem in the mature stele is scattered in patches throughout the parenchyma bands between the xylem groups.

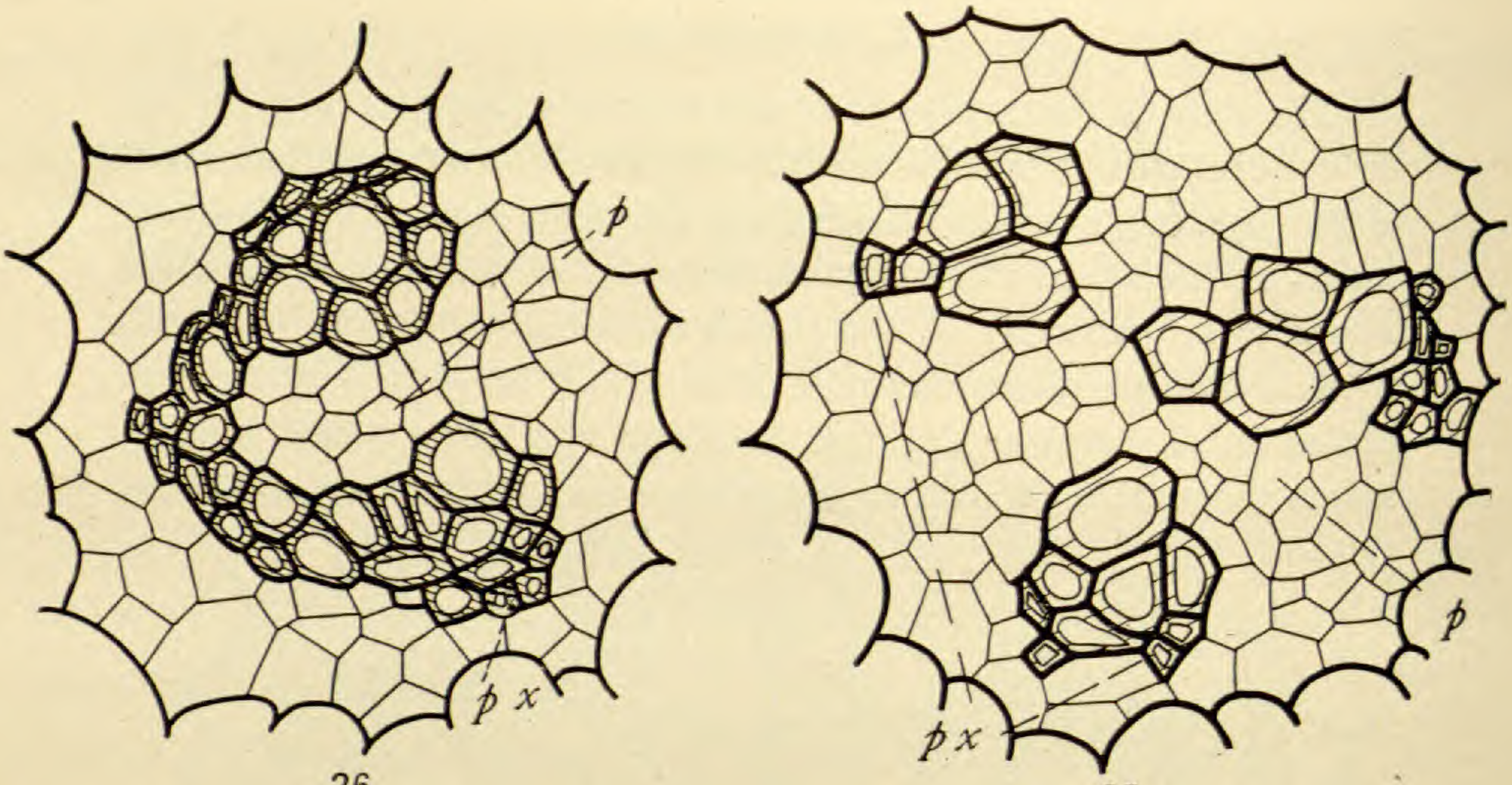
L. verticillatum

The stele of the strobilus in this species is characterized by the differentiation of very few protoxylem points, 2 or 3 groups being usual (figs. 24, 25). It differs from the other species in not being radial at the apex. The organization of the stele in the strobilus seems to be generally of the parallel-banded type from the first, with a phloem group between two xylem bands, as sometimes occurs in *L. varium*, and this develops into the crescent-shaped xylem mass with phloem in the middle, as has been described for the other species (figs. 9, 26). This crescent-shaped mass breaks up into the parallel-banded type, and then later at a lower level in the strobilus axis, the metaxylem begins to grow inward and breaks up the phloem band, forming a distinctly radial arrangement (fig. 27). The phloem in this species is very difficult to recognize, and often even in the mature stem the extent of the phloem is uncertain.



FIGS. 24, 25.—*L. verticillatum:* transverse sections in series, showing the protoxylem groups and the developing parallel bands; *px*, protoxylem; *p*, phloem; ×500.

The mature vegetative stem is of an irregular parallel-banded type with rather numerous protoxylem points. The phloem is very limited in amount, and is scattered somewhat irregularly



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FIGS. 26, 27.—Fig. 26, *L. verticillatum:* transverse section, showing the development of the crescent-shaped xylem mass from the parallel-banded arrangement; *px*, protoxylem; *p*, phloem; ×500; fig. 27, *L. verticillatum:* transverse section, showing the radial arrangement derived from the crescent-shaped xylem mass; *px*, protoxylem; *p*, phloem; ×500.

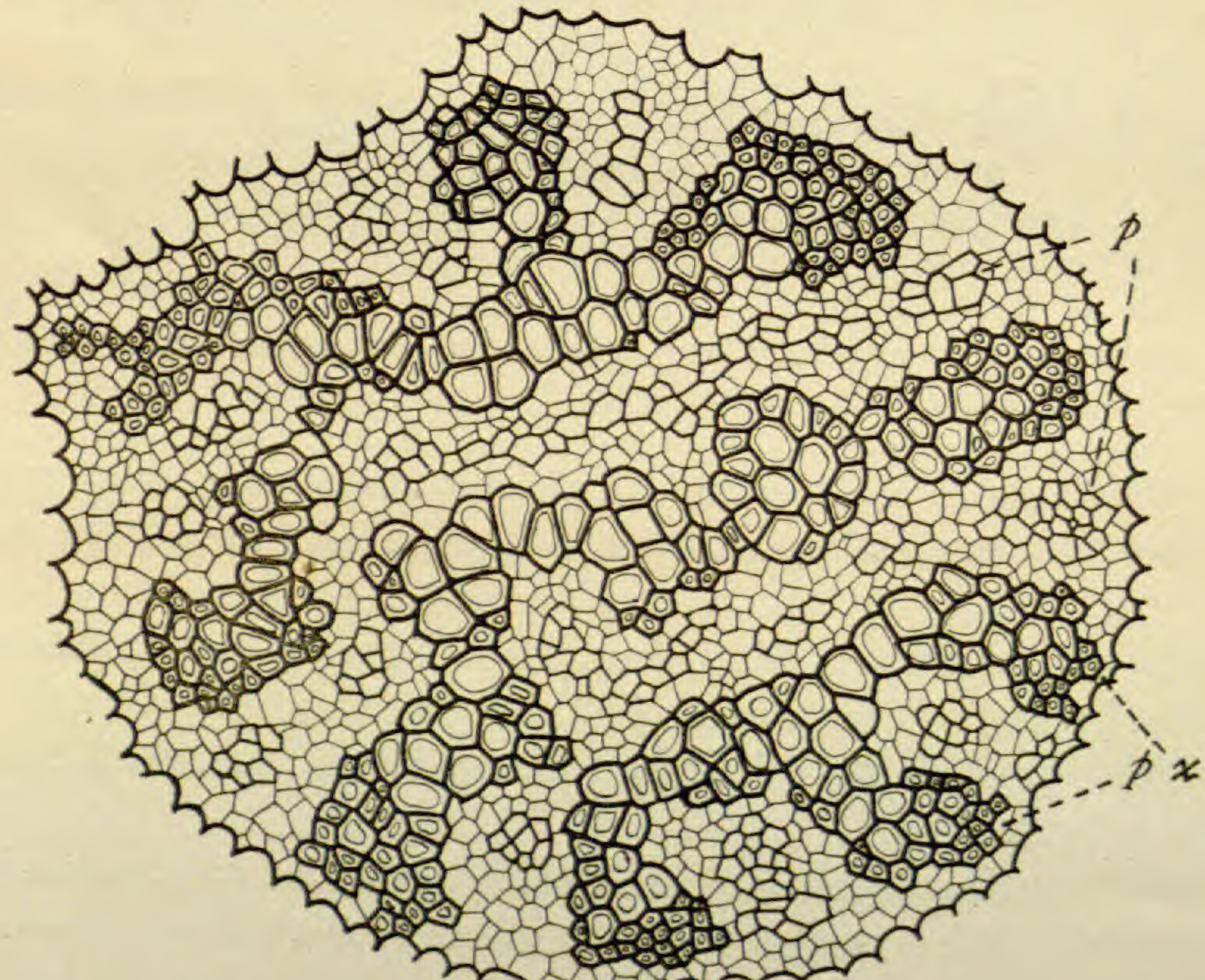

FIG. 28.—*L. verticillatum:* transverse section of the mature stem, showing the parallel-banded type of stele; *px*, protoxylem; *p*, phloem; ×185.

between the protoxylem points and between the xylem bands (fig. 28).

Discussion

JONES,[2] in an investigation of about a dozen temperate and tropical species of *Lycopodium*, found that the radial arrangement of the stele is very characteristic, especially in young plants. He says "the principal feature observed in sections of the young stem is that the vascular bundles present a triarch or tetrarch arrangement exactly similar to the structure which may be found in roots." He also states that it has always been suggested that this arrangement represents a very primitive type of stele. JONES also divides the mature stems into two categories: parallel-banded, connected with a high number of protoxylem groups; and a second type characterized by a promiscuous mixture of xylem and isolated phloem patches, which he regards as characteristic of tropical epiphytes.

HOLLOWAY,[3] in a study of the young sporophytes of six New Zealand species of *Lycopodium*, classifies them as follows in regard to the type of stele: (1) a "mixed" type, with indiscriminate mixture of xylem and phloem; (2) a radially banded type, with the radial arrangement of xylem and bands of phloem situated between the xylem radii; and (3) the parallel-banded type, with the xylem and phloem arranged in alternating bands across the cylinder. He notes that the radial and parallel-banded types are closely related and may pass into one another, and that the latter is associated with a relatively high number of protoxylem points, 5–9 he says being sufficient to give that arrangement.

WIGGLESWORTH,[4] from a study of young sporophytes of *L. complanatum* and *L. clavatum*, concludes that the radial arrangement of xylem and phloem occurring in upright forms of *Lycopodium* is the more primitive condition. In the upper part of the stem she

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[2] JONES, C. E., The morphology and anatomy of the stem of the genus *Lycopodium*. Trans. Linn. Soc. II. 7:15–35. *pls. 3–5.* 1905.

[3] HOLLOWAY, J. E., A comparative study of the anatomy of six New Zealand species of *Lycopodium*. Trans. N. Zeal. Inst. 42:356–370. *pls. 32–34.* 1909.

[4] WIGGLESWORTH, GRACE A., The young sporophytes of *Lycopodium complanatum* and *Lycopodium clavatum*. Ann. Botany 21:211–234. *pl. 22.* 1907.

found a triarch or tetrarch arrangement, with the three or four protoxylem groups connected with metaxylem, and in the base of the young plants there was a central core of xylem in the center of the stele.

BOODLE[5] investigated the stem structure of *L. volubile* and *L. salakense.* He regards the normal *Lycopodium* stele to be the parallel-banded type, as in *L. volubile. L. salakense* has the intermingling of xylem and phloem, resembling *Gleichenia.* He notes that in some cases the presence of the peripheral growth of the protoxylem forms a nearly continuous ring.

The present investigation extends the range of knowledge of the anatomical structure of *Lycopodium* by including some species not studied before, which show certain phases of stelar development to be especially emphasized. It emphasizes the fact that the radial arrangement of the stele is quite common, and that in many cases it is the original condition from which the parallel-banded type is derived. While this radial arrangement is probably the common one in *Lycopodium*, it is not the universal condition, and the great variability of the stelar structures in these epiphytic species deserves especial emphasis. It should also be kept in mind that the greater variability in structure occurs in the stele of the strobilus, while the vegetative steles remain relatively constant. The presence of a great variety of types of stele, radial, parallel-banded, crescentic, and that corresponding by definition to the amphivasal in the same plant, and even in the same stem, as occurs in *L. carinatum*, makes it clear that these types are more closely related than has been supposed.

JONES relates the parallel-banded type to the plagiotropic stems generally, but notes that there are some exceptions, as the orthotropic *L. obscurum*, which has the parallel-banded arrangement. HOLLOWAY points out that the parallel-banded arrangement is derived from the radial as a result of the branching stem. Both JONES and HOLLOWAY consider the radial arrangement characteristic of the stems of epiphytic species of *Lycopodium.*

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[5] BOODLE, L. A., On the structure of the stem in two species of *Lycopodium.* Ann. Botany 14:315–317. 1900.

The present investigation shows that not all of the epiphytic species are characterized by the radial arrangement of the stele, since *L. verticillatum* has generally the parallel-banded type. Further, it shows that not only may both radial and parallel-banded types occur in the same stem, associated with crescentic and amphivasal, but that these changes from one arrangement to another are independent of the branching of the stem, as seen in *L. carinatum, L. Phlegmaria*, and *L. varium*. Branching does induce change from radial to parallel-banded arrangement, but this change may also occur without branching.

There seems to be a general opinion, as expressed by JONES and also by HOLLOWAY, that the parallel-banded type of stele is associated with a large number of protoxylem points, and this opinion may be completely justified by evidence drawn from the study of the young sporophytes. In the mature plants, in some of the species used in this investigation, the parallel-banded arrangement occurred where there were but 2, 3, and 4 protoxylem points; and in *L. verticillatum* the parallel arrangement started with but 2 protoxylem points. In these species the parallel-banded arrangement seems to be just as definitely associated with a small number of protoxylem points as in those studied by JONES and by HOLLOWAY, where it was associated with a large number.

BOODLE regards the parallel-banded arrangement as the normal *Lycopodium* stele, but from this study it seems unsafe to regard any particular type of bundle arrangement as normal, since it will depend upon the level at which the stem is cut, or how near the section is to the point of branching as to what type of stele is found, for all the known *Lycopodium* steles may be found in the same stem excepting the so-called "mixed" stele.

Attempts have been made to connect the factors determining the stelar development with the type of stele found in the various species of *Lycopodium*. Plagiotropism has been suggested as being the factor favoring the formation of the parallel-banded type of stele, and orthotropism that favoring the development of the radial stele, but so many exceptions are to be found to these statements that they seem to lose significance. The conditions under which these epiphytic species grew are described as being about the optimum for vegetative growth. A definite structural evidence for rapid elongation in these plants is the close series in sporogenesis shown by serial transverse sections of the strobilus. It would seem then that these variations of stelar structure occur under conditions favoring rapid elongation. Whatever the conditions may be, the fact of the variations emphasizes the susceptibility of these species to conditions and the ability to modify the stelar development, which is generally regarded in most plants as rather a fixed structure.

Summary

1. From this investigation it may be concluded that the species of *Lycopodium* studied are characterized by great variability in the development and structure of the stele.

2. The radial stele may be considered as the prevailing type, and as the basis in most cases for modification to the other types found.

3. There are found radial, parallel-banded, crescentic, and amphivasal steles in the same strobilus axis in *L. carinatum*, and all types but the amphivasal in *L. Phlegmaria* and *L. varium*.

4. *L. Billardieri* is the most constant in its stelar structure, with a type of stele so characteristic as to make the species almost recognizable by the transverse section of the stem.

5. *L. verticillatum* has generally parallel-banded arrangement of stele, although the radial stele has been considered the prevailing type in epiphytic species.

6. All attempts to place the species of *Lycopodium* in definite categories based on the character of the stele are extremely uncertain, since there are exceptions in some species and even exceptions in different parts of the same stem in some species.

7. If the character of the stele is in any way dependent upon varying conditions, its use in phylogeny must recognize this fact.

8. The investigation confirms the idea that the radial arrangement of the stele, retained persistently by the root, is probably the most primitive stem arrangement, from which most known stems have departed.

This investigation was undertaken at the Hull Botanical Laboratory, University of Chicago, and was completed under the direction of the staff of that institution. The writer wishes to express his thanks to Dr. J. M. COULTER for his constant advice and criticism, and to Dr. CHARLES J. CHAMBERLAIN and Dr. W. J. G. LAND for the material furnished for the investigation and for their criticism of the preparations and aid in interpretation.

HULL BOTANICAL LABORATORY
UNIVERSITY OF CHICAGO

CURRENT LITERATURE

BOOK REVIEWS

Die Kultur der Gegenwart

During the past twenty years no botanist has appeared oftener in our "book reviews" and "notes for students" than EDUARD STRASBURGER. It is with a keen sense of loss that we write this final review.[1] In the spring of 1911 STRASBURGER wrote to the reviewer: "A year ago I felt compelled to participate in a work of great scope under the title of *Kultur der Gegenwart,* which is to present in accessible form the entire field of science. The object may be good in itself, but I have often regretted that I undertook the work and that I must devote to it, rather than to my research, the few years of scientific activity which still remain for me. I have not felt well the past winter, but nevertheless have had to work hard." About this time he wrote to TISCHLER that he was devoting eight hours a day to the work. The day before he died the manuscript was completed, and he also added the finishing touches to the manuscript for the third edition of his *Streifzüge an der Riviera.* With these two tasks out of the way, he was eagerly planning to take up his interrupted research, but his contribution to the *Kultur der Gegenwart* was destined to be his last.

The *Kultur der Gegenwart* is a work of even greater scope than STRASBURGER's letter indicated, for it embraces not only the sciences, but also philosophy, law, history, and literature. Some of the titles, like "The religion of the orient," "The history of philosophy," "The Greek language and literature," "The history of law," "Mathematics in ancient and mediaeval times," "Chemistry," "Astronomy," "The transformation of energy," "Anthropology," "Mountain structure," "The technic of war," will give some idea of the range of knowledge one should possess if he is to be regarded as a man of culture at the present time. The entire work comprises 61 volumes. The present review deals only with Vol. 2 of the fourth section of the third subdivision, or III Teil, IV Abteil, Band 2. This method of designating volumes may be very clear to the German mind, but, like the endless "Teil" and "Abteil" of the *Pflanzenfamilien,* it is confusing to the American. We should have marked the present contribution Vol. 36, which seems to be its position in the series of 61 volumes. In this volume there are two sections: "The plant cell and tissues" by STRASBURGER, and "Morphology and development of plants" by BENECKE. The two contributions will be considered separately.

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[1] Die Kultur der Gegenwart. Teil III. Abt. IV. STRASBURGER, EDUARD, Zellen und Gewebelehre; und BENECKE, W., Morphologie und Entwickelungsgeschichte. 8vo. pp. vi+338. Leipzig: Teubner. 1913. *M* 14.

THE PLANT CELL AND TISSUES.—The title is broad enough to cover most of the fields now designated as cytology and morphology. Some of the topics are: cell contents, cell membranes, nuclear and cell division, reduction of chromosomes, fertilization, alternation of generations, origin of tissues from apical cells and from meristem, differentiation of tissues, etc. Throughout the work the cell and tissues are treated not only from the standpoint of structure, development, and phylogeny, but also from the standpoint of chemical composition and function. While both vegetative and reduction mitoses are rather minutely described, little attention is given to conflicting theories. The main facts stand in bold relief, without those obscuring details which vary in different forms, or which may be present in some plants and lacking in others. In the treatment of mitosis, the chromosome is regarded as an individual organ. In the description of fertilization, the nucleus is regarded as the sole bearer of hereditary characters, so far as heredity is concerned, the cytoplasm being only the necessary medium in which the nucleus exercises its functions. Alternation of generations, of course, is regarded as antithetic; alternation is recognized in animals as well as in plants, in both cases the two generations being distinguished by the haploid and diploid number of chromosomes, a position with which the reviewer is in the heartiest accord. The origin of tissues from apical cells or meristem and the differentiation of cells into vessels, sieve tubes, sclerotic cells, glandular hairs, etc., is followed in many cases.

The work, as indicated by STRASBURGER'S own words, was not intended as a piece of research. The object was to make such a presentation of the cell and tissues as a man of culture, although not a professional botanist, might read with profit. It can be said, without the slightest hesitation, that even the professional botanist can read it with profit, for it covers most of the field of cytology and morphology, and presents the views of one who speaks from an abundance of first-hand knowledge and who has contributed more to the subject than any other man of his generation. While the reading may be rather difficult for the average man who regards himself as cultured, it is hard to see where it could have been simplified. Such a presentation was no new experience for STRASBURGER, since he had for many years given his weekly Friday lecture to the people of Bonn. These lectures brought fundamental botanical problems within the reach of those who were interested enough to attend. The style is much simpler than STRASBURGER used in publishing his researches. This is seen particularly in the shorter sentences and in the comparative scarcity of technical terms. To the cytologist, the book is full of suggestions for research.

MORPHOLOGY AND DEVELOPMENT OF PLANTS.—The field left for BENECKE'S contribution, after the broad presentation by STRASBURGER, would seem rather limited. The subject is treated under two subdivisions: (1) general, and (2) special. The first is devoted largely to a consideration of the form and function of the root, stem, and leaf, comparatively little attention being given to reproductive structures, because vegetative structures can be presented without all sorts of details, and because reproductive structures lead so easily to general questions and plant systems. Goeth's theory of metamorphosis is presented and a modified view of this theory seems to dominate the discussion. This general part occupies only 31 pages.

The second, or special part, presents the various groups from the algae up to the flowering plants, and occupies 120 pages. The reading should not be very difficult for an educated man, interested in botany, but not a professional botanist. The technical terms, especially those used in describing flowering plants, are rather numerous.—Charles J. Chamberlain.

NOTES FOR STUDENTS

Recent work on tropisms.—For orthotropic organs Fitting and others have proved that geo-excitation increases with the sine of the angle of displacement from the normal or labile rest position. Therefore, the horizontal position gives maximum stimulation, and all equal displacements below and above it equal stimulation. Noack asserts that this physiological response does not parallel any known change in the energy of gravity itself with variation of the angle, and is not capable of direct physical explanation.

Noack[2] inquires whether photo-excitation of orthotropic organs obeys the sine of angle law. Assuming constant source of unilateral light, the intensity falling on a given surface of the plant organ varies as the cosine of the angle of deviation from the perpendicular, or as the sine of the angle of deviation from the rest positions. On the basis of light intensity, therefore, one might expect the sine law to hold. Noack finds, however, that intensity of the illumination of the flank of the organ is not the sole factor, but the direction of the striking rays is important, hence the sine law does not apply. He studied chiefly the coleoptile of *Avena*. The following table shows the "Schwelle" (product of light intensity in candle-power actually falling on the illuminated surface of the organ by least time in seconds necessary to give a final response in 50 per cent of the organs) and presentation time under constant light source for the various angles of deviation from the normal rest position.

Angle	15°	30°	45°	65°	90°	105°	120°	135°	150°
Schwelle	7.3	9.5	11.9	11.18	12.2	15.8	20.3	23.7	32.4 (C.M.S.)
Presentation time	28.2	19.0	16.8	12.9	12.2	16.4	23.6	33.5	64.8

The "Schwelle" for the different angles shows the organ is more sensitive to impinging light from above than from below the horizontal, and that this sensitiveness increases continuously from the inverse to the normal rest position. This increase follows a regular law, as is shown by the fact that the product of

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[2] Noack, Konrad, Die Bedeutung der schiefen Lichtrichtung für die Helioperzeption parallelotroper Organe. Zeitschr. Bot. 6:1–79. 1914.

the supplement of the angle of deviation from the normal rest position by the "Schwelle" is a constant. These facts indicate that the organ is most excited by light striking it from directly above, though of course this produces no response. The "Schwelle" for this position is calculated at 6.7 C.M.S. Some measurements were made also on the sporangiophore of *Phycomyces* and on the mustard seedling. In the latter, as in *Avena*, the "Schwelle" decreases as the angle of impinging rays passes from the inverse to the normal rest position, while in *Phycomyces* just the reverse behavior appears. With light striking the organs at right angles, mustard has a "Schwelle" of 240 and *Phycomyces* 60, against 12 C.M.S. for oats. NOACK believes he has settled a long-contested point by establishing that the direction of the impinging ray and not the difference in light intensity on two flanks is the determining factor in phototropism. He also takes his results as evidence for the polarization conception of FITTING in conduction of the phototropic stimulus. He believes photoperception and presention are too complex to be explained as simple photochemical reactions, as some have attempted to do.

BOYSEN-JENSEN[3] repeats and confirms his earlier experiments which showed that the conduction of the phototropic stimulus in the coleoptile of *Avena* is localized in the half of the seedling not illuminated. He reasserts that FITTING'S conception of the polarization in all cells of the organ determined by the direction of the impinging rays is untenable, and finds no evidence for VAN DER WOLK'S claim of wound effects compensating for phototropism.

RISS,[4] working in JOST'S laboratory has devised a special sort of centrifuge for the purpose of studying the effect on orthotropic stems and roots of applying centrifugal force equilaterally at right angles to the longitudinal axis of these organs. Such application of centrifugal force, unlike unilaterally applied light, has no tonic effect on the plant organ. This finding is contrary to the assumption of BACH. Such equilaterally applied centrifugal force also causes no modification in the geotropic effect of unilaterally applied gravity, whether the former be applied before, during, or after the latter. In some cases the equilateral force was 20 times the unilateral. This leads to the important conclusion that WEBER'S law does not apply to geotropic discriminative sensibility. Centrifugal force acting in the longitudinal direction inhibits the geotropic effect of a right angle stimulus. The action of gravity at an oblique angle on the orthotropic organ is not a result of the right angle components alone, but the effect of the latter is inhibited by the longitudinal components. For this reason, the author concludes that the sine of angle law of FITTING and BACH does not strictly apply even between 45° and 90°, although the deviation here is slight. The horizontal position of the organ is the position

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[3] BOYSEN-JENSEN, P., Über die Leitung des phototropischen Reizes in der Avenakoleoptile. Ber. Deutsch. Bot. Gesells. **31**:559–566. 1914.

[4] RISS, MARIE-MARTHE, Über den Einfluss allseitig und in der Langsrichtung wirkender Schwerkraft auf Wurzeln. Jahrb. Wiss. Bot. **53**:157–209. 1913.

of maximum geo-stimulation both because gravity acts at right angles to the organ and because no longitudinal components are present.

DEWERS[5] has applied the PICCARD rotation method to determining the distribution of geo-sensitiveness in various plant organs.[6] In the root of *Lupinus albus* the greater sensitiveness lies in the terminal 2.5 mm. The hypocotyl of *Helianthus* always gives a permanent *S* response due to low irritability and slow conduction of the stimuli. The method does not determine the distribution of geo-sensitiveness in this organ. In *Hordeum vulgare, Panicum miliaceum*, and *Setaria italica*, the coleoptile is much more sensitive than the internode, although the internode is slightly sensitive in all these, most so in *Panicum*. The sensitiveness in the coleoptile of *Hordeum* is about equally distributed, so that when about half of the organ projects across the axis of the centrifuge an *S* response occurs which later entirely straightens out. Apparently there is about equal acropetal and basipetal conduction of the stimulus in the two directions. Whether this occurs by separate paths in the two directions is not known. The geo-irritability of the internode of *Panicum* is higher than that of *Sorghum*, while the reverse is true of photosensitiveness. In general, however, DEWERS finds that geo-conduction and photoconduction and reaction run parallel in these organs. In general, those organs that show quick perceiving power show rapid conduction, and those showing slow perceiving power show slow conduction. The coleoptile of *Hordeum* belongs to the first class, and the hypocotyl of *Helianthus* to the second. In an "Anhang" the author reports that he was unable to find a destarching agent, for the purpose of throwing some light on the statolith theory, the application of which did not greatly injure the root. He tried Al_2Cl_6 and $Al_2(SO_4)_3$ alone and in combination with Knop's solution and KH_2PO_4.

PORODKO[7] has studied chemotropic response of roots to various alkalies and alkali earth salts. The experiments consisted of a square millimeter of filter paper saturated in the salt solution applied to the side of the roots in darkened moist chambers. In lower concentrations positive chemotropic responses occurred; in higher, negative chemotropic responses; and in still higher positive, chemo-traumatic responses. PORODKO asserts that the first response is a true tropic response, for perception is localized in the tip, bending is due to growth, and the concentration producing the response is comparatively low. It is also not osmotropic, for the concentrations producing it in the various salts show great variation. The positive and probably the negative response is due to the action of ions. The effect of the ions beginning with those most effect-

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[5] DEWERS, F., Untersuchungen über die Verteilung der geotropischen Sensibilität an Wurzeln und Keimsprossen. Beih. Bot. Centralbl. **31**^{1}:309–357. 1914.

[6] For methods see BOT. GAZ. **47**:482, 483. 1909; and PFEFFER'S Plant physiol. Eng. ed. **3**:419.

[7] PORODKO, TH. M., Vergleichende Untersuchungen über die Tropismen. Ber. Deutsch. Bot. Gesells. **32**:25–35. 1914.

ive is (1) for positive response, tartrate>citr.>SO_4>acet.>ClO_3>Cl>NO_3>J >CNS; Rb>Cs>K>Li>Na; (2) for negative response, (*a*) for alkali salts, acet.>tartr.>J>Cl>Citr.>ClO_3>CNS>SO_4>NO_3; Na>Li>K>Cs>Rb; (*b*) for salts of alkali earths, J>Br>acet.>Cl.; Mg>Ca, Ba, Sr.

The bromide and perhaps the iodide of alkali earths do not produce the positive response. For negative chemotropism, salts of alkali earths are about 10 times as effective as those of the alkalies. PORODKO believes from the relative effectiveness of ions that the negative excitation involves coagulation of cell lipoids as well as proteins, and that both the positive and negative irritability are lined up with change of condition of cell colloids. Our knowledge in this field is too limited, however, to follow the parallel in any detail.—WILLIAM CROCKER.

A theory of evolution.—Lest we forget that the method of evolution remains undemonstrated, that evolution itself is somewhat of a scientific dogma, it is desirable occasionally to have our attention called to the fact that scarcely two even of the clearest-headed of our contemporary thinkers hold the same views regarding it. Read BERGSON, BUTLER, DEVRIES, SEMON, WEISMANN. Their works are lawyers' briefs, written to uphold the importance of a single possible evolutionary cause to the greater or less neglect of all others; but they are remarkable briefs for all that. Evolution is due entirely to a directive force within the organism; evolution is due wholly to imperfections in the machinery of heredity and has no directive aim whatever; evolution is due solely to external causes; it is gradual, it is discontinuous; it is continual, it is periodic. One is often led to believe that no middle ground, no combination of methods is possible; moreover, it is often the individuals that strum continually on a few notes, who force recognition of tunes labeled conspicuously with their own personalities, by loud and persistent reiteration.

The latest writer to be enrolled as an exponent of a unique cause of evolution is LOTSY.[8] The unique cause is hybridization and the author's brief has been extraordinarily well done. As the paper is introduced by the following statement, the words "unique cause" do not exaggerate the position taken:

> Toutes les théories de l'évolution, y compris celle de Lamarck, Darwin et DeVries, s'appuient sur l'hypothèse, ou sur la prétendue preuve, qu'il existe d'une façon ou d'une autre une variabilité héréditaire. Le présent travail a pour but de prouver que cette hypothèse se base sur une erreur; qu'il n'y a pas de variabilité héréditaire, sous aucune forme, mais que les expèces sont constantes.

LOTSY does not believe that Linnean species are constant, but that forms truly homozygous are constant. His outline of the growth of evolutionary belief shows this.

A. The period when it was believed that the characters of an individual were transmitted as a whole.

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[8] LOTSY, J. P., La théorie du croisement. Arch. Néerland. Sci. Exact. et Nat. III B 2:1–61. 1914.

a) The idea that Linnean species form a natural system.
  1. Belief in the constancy of Linnean species.
  2. Belief in the variability of Linnean species.

b) The idea that the elementary species of JORDAN form a natural system.

B. The period in which proof was given of the independent transmission and chance recombination of characters.
  a) Belief in the variability of JORDAN'S species: the theory of mutation.
  b) Belief in the constancy of JORDAN'S species: the theory of crossing.

LOTSY'S arguments are based upon the following assumptions, on each of which there is room for a difference of opinion: (1) that all characters obey the Mendelian law of heredity, (2) that acquired characters are never transmitted, (3) that homozygotes are absolutely constant in successive generations, (4) that there has been no proof of variation independent of crossing, and (5) that the variations observed after crossing are sufficient to account for evolution.

The first point is taken for granted, although there are certain to be many objections to it raised. Even the most ardent Mendelians have only gone so far as to assert the generality of Mendel's law in the sense that the transmission of many characters is controlled by some mechanism that is widespread in the animal and plant kingdoms, probably the chance apportionment of the chromosomes to either of the two daughter cells at the reduction division. The probability that there are many cases where such a mechanism is replaced by others can hardly be denied, though JENNINGS' recent investigations on paramecium indicate a generality of segregation hitherto unsuspected. Furthermore, even in cases where Mendel's law might be expected to be valid from other considerations, as in the Oenotheras, there appear to be independent or subsidiary laws at work which modify the results.

Perhaps most biologists admit that the inheritance of acquired characters has never been proved experimentally; on the other hand, it may be that it is impossible to prove that the hour hand moves in an experiment covering a second of time, as BUTLER very aptly puts it. Is it not justifiable, therefore, for experimentalists to assume non-inheritance of acquired characters as a practical working hypothesis for experimental biology, and just as permissible for evolutionists to assume their transmission over long periods of time, provided it is granted that this is a mere assumption? LOTSY applies the *negative* conclusions of experimental biology to evolution, a method that is always open to criticism.

The contention that homozygotes are absolutely constant in all succeeding generations is also disconcerting. The conclusion is drawn largely from JOHANNSEN'S work, yet JOHANNSEN believes in mutations. But even leaving out of account the sudden changes that have appeared in material apparently homozygous, there are those who believe that the pure line work does not show constancy in succeeding generations. CASTLE, for example, who does not come to a conclusion without due consideration, believes that selection may always modify a homozygous character. The reviewer, taking a middle ground, believes that the pure line work least subject to criticism, that on self-fertilized material, does prove homozygotes to be sufficiently constant in succeeding generations to make this constancy a basis for mathematical description, but he believes it to be unbiological to assert this constancy as absolute.

As the basis of his assertion that there has been no proof of variation independent of crossing, the author notices only the work of DeVries. Undoubtedly there is a great deal in favor of the idea that the *Oenothera* mutants are the results of segregation from crosses, though the phenomena have not been fitted into present Mendelian concepts. But that the very fine contributions of Davis and Heribert-Nilsson on this subject have clinched the matter, as Lotsy believes, would not be asserted, I venture to say, by the authors themselves. It is pointed out very clearly that both the constructive work of Gates in defense of the *Oenothera* mutations and his criticism of Heribert-Nilsson are not so conclusive as that author so confidently asserts, but this is only negative evidence. Moreover, the work of Morgan, Jennings, Bateson, and others on the occurrence of mutations in controlled cultures is complacently neglected.

Lotsy's own extensive work on specific crosses in the genera *Nicotiana*, *Petunia*, *Pisum*, and *Antirrhinum*, the constructive work of the paper, is exceedingly interesting, and his detailed accounts, which are in press, will be eagerly awaited. In brief, all the inter-specific crosses that he has undertaken have shown true Mendelian segregation. The conclusion of DeVries, drawn from the peculiar behavior of the *Oenothera* species, that inter-specific and intra-specific crosses obey different laws of heredity, is shown, therefore, not to be of general validity.—E. M. East.

Cecidology.—Among the very important contributions to European cecidology are Howard's papers on the collection in the Museum of Natural History in Paris[9] and from Western Africa,[10] all of which are taxonomic in character and well illustrated. The author uses the modern method of grouping the galls with reference to the host plants, which makes the data available to those botanists who are interested in the study of malformations of plants and in the relation of plants to other forms of life.

Roll Howard[11] presents an exceptionally good paper on the anatomy of the galls on the margins of leaves. He divides these malformations into four groups; those caused (1) by hypertrophy and hyperplasia, (2) by hyperplasia,

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[9] Howard, C., Les collections cécidologiques du laboratoire d'entomologie du muséum d'histoire naturalle de Paris: Galles de Burséracées. Marcellia **12**:57–75. 1913; also Galles d'Afrique et Asie **12**:102–117.

[10] ———, Les Galles de l'Afrique occidentale française. VI. Cécides du haut Sénégal-Niger. Marcellia **12**:76–101. 1913.

[11] Howard, Roll, Recherches anatomiques sur les Cécidies foliaires marginales. Marcellia **12**:124–144. 1913.

(3) by hypertrophy, (4) by atrophy. This paper is well illustrated and leads the thoughtful American botanist to realize the enormous amount of research work that could be carried on in this country on this one branch of cecidology or plant pathology.

The recent American literature presents a paper by PARROTT and HODGKINS[12] in which the authors describe the pathological condition caused by the false tarnished plant-bug (*Lygus invitus*). This pest attacks the fruits before they are one-half inch in diameter, causing many of them to fall. The injury is said to be quite characteristic. "As the pears grow, the outer layer of the skin about these spots becomes ruptured, and a light-yellow, mealy-appearing growth of the inner layers of skin protrudes, making more or less triangular, granular spots; or when two or more spots run together a patch or crack lined and bordered with corky tissue. The yellowish, protruding growth at first makes a marked contrast with the smooth green skin of the little pear; and later the cessation of growth at these points causes depressions and marked general deformity of the fruit. In the flesh beneath, also, hard, gritty granulations are produced, through which it is difficult to cut with a knife." This paper illustrates another broad field of plant pathology and physiology which is practically untouched by American botanists.

One of the most satisfactory pieces of scientific cecidology of recent years is TRIGGERSON'S[13] work on *Dryophanta erinacei*. The author begins his study with the well known *Acraspis erinacei* or hedgehog-gall which occurs on the white oak, and proves it to be caused by a dimorphic species of insect. The insects from this gall are agamic and oviposit on the leaf and flower buds of the same host, causing an entirely different gall giving rise to the sexual form which belongs to the genus *Dryophanta*. The author also gives the results of some very interesting studies of the parasites and inquilines, and finally some studies leading to the conclusion that the stimulus is due to a fluid secreted by the malpighian vessels of the larva. However, comparative studies indicate that this is not necessarily true in the case of other galls. The physiological side of this paper will be of great interest to those plant physiologists and pathologists who can overcome their prejudice long enough to give it careful consideration.

Another exceptionally good piece of work which is strictly botanical is by STEWART[14] and treats of the anatomy of the black knot (*Plowrightia morbosa*). The author finds that these knots may originate from spore infection from

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[12] PARROTT, P. J., and HODGKINS, H. E., A pear-deforming plant bug. New York Agricultural Experiment Station (Geneva) Bull. 368. 1913.

[13] TRIGGERSON, C. J., A study of *Dryophanta erinacei* (Mayr) and its galls. Annals Ent. Soc. America 7:1–34. *pls. 11.* 1914.

[14] STEWART, ALBAN, The anatomy of other features of the black knot. Amer Jour. Bot. 1:112–125. 1914.

mycelium spreading from old knots; the fungus during the first year penetrates nearer to the pith in the distal than the proximal end, and the greatest disturbance is in the vicinity of the leaf gaps; in the case of the choke cherry, which was the host used in these studies, the multiseriate rays become broadened, the production of xylem elements is greatly inhibited, and the production of parenchyma stimulated. There is also a stimulation of the cambium accompanied by the misplacing of certain elements. The reviewer will add that many of the data given in this paper are homologous with those derived from the study of insect cecidia. The American botanical literature is very deficient in studies of pathological tissues, and it is to be hoped that this paper will stimulate research in this long-neglected field.

COSENS[15] gives a paper which is very suggestive to botanists, in which he says: "One fundamental and far-reaching principle of gall-production by insects is that the stimulus does not endow the protoplasm of the host with power to produce new types of organs, tissues, etc. Structures are in many cases originated that are not found on the same part of the normal host, but invariably their prototypes are present on another part of the plant or nearly related species. The protoplasm is so stimulated that not only are dormant characteristics strengthened, but also in certain cases latent properties are called into activity, and thus the apparently new type of production appears in the host." The author gives evidence from the study of several galls supporting this principle.

Among other American papers which should be mentioned is a valuable key for determination of the midge galls on the hickory by FELT;[16] and a very interesting biological paper by the same author[17] on adaptations; and also several systematic papers by the same author.[18] There should also be noted three valuable taxonomic papers by BEUTENMÜLLER on the acorn galls[19] and on new species of the Cynipideae.[20]—MEL T. COOK.

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[15] COSENS, A., Insect galls. Canad. Ent. **45**:380–384. 1913.

[16] FELT, E. P., Table of hickory leaf midge galls. Bull. Brooklyn Ent. Soc. **8**:98–99. 1913.

[17] ———, Adaptation in gall midges. Canad. Ent. **45**:371–379. 1913.

[18] ———, Three new gall midges. Canad. Ent. **45**:305–308. 1913.

———, Description of gall midges. Jour. N.Y. Ent. Soc. **21**:213–219. 1913.

———, Gall midges in an aquatic or semi-aquatic environment. Jour. N.Y. Ent. Soc. **21**:62, 63. 1913.

———, The gall midge fauna of New England. Psyche **20**:133–146. 1913.

[19] BEUTENMÜLLER, WILLIAM, The North American acorn galls with descriptions of new species. Bull. Brooklyn Ent. Soc. **8**:101–105. 1913.

[20] ———, A new species of *Neuroteras* from Washington. Canad. Ent. **45**:280–282. 1913.

———, Descriptions of new Cynipidae. Trans. Amer. Ent. Soc. **39**:243–248. 1913.

Subantarctic vegetation.—Of the several antarctic regions whose vegetation has been recently studied, South Georgia seems of particular interest, both because of its isolation and on account of the character of its vegetation, being transitional between the truly antarctic type and the well developed subantarctic associations found in such regions as the Falkland Islands. As a result of visits to the island in 1902 and in 1909, SKOTTSBERG[21] gives an interesting account of the plant associations. The island is mountainous, some peaks reaching 2000 m., and is largely covered with ice in the form of glaciers moving down the valleys and reaching the sea in fiords. There is little seasonal difference in climate, the summer mean temperature being about 4° C., and the winter about $-1°$ C. Exposure is a factor of prime importance in determining the distribution of the vegetation. Only 15 species of seed plants and three ferns are found upon the island, but the moss and lichen floras are comparatively rich, with 99 and 58 species respectively, of which 46 and 24 respectively are endemic.

The principal plant associations are the tundra, the swamp and the tussock grass. The tundra has by far the most extensive development, showing all transitional forms from one rich in grasses to the moss-lichen carpet. The swampy places are dominated by Juncaceae, while the halophilous *Poa flabellata* tussock-grass association fringes the beach. It is often almost pure, the tussocks attaining a height of 1.5 m., with an equally great diameter. This association was formerly more widespread and equally important in the Falkland Islands,[22] but has been disturbed and largely destroyed by the introduction of sheep.

These islands have a comparatively mild climate of insular type. The summer mean temperature is 10° C., the winter mean 2°5 C., affording a fairly well marked periodicity, especially in the flowering of the seed plants, although the 73 cm. of precipitation are very evenly distributed. In portions of the islands there is little snow, and the soil is never frozen hard, but, apparently because of very high winds, there are no trees. Nevertheless, 47 of the 162 species of vascular plants are evergreen. The possible land connection with the mainland during the Tertiary may account for 82 per cent of the species being Magellan plants; 15 species are endemic. SKOTTSBERG decides that the vegetation, because of its close peat-forming character, is really a heath, exhibiting many characters in common with the heaths of northern Europe, and particularly with that of Faeröes, although with grasses forming a more conspicuous element. The most widespread association is that dominated by *Cortaderia* and other grasses, largely of tussock habit. It seems to occupy

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[21] SKOTTSBERG, C., The vegetation in South Georgia. Wiss. Ergeb. Schwed. Südpolar. Exped. 1901–1903. **4**: Lief. 12. pp. 36. *pl. 6* and *map*. 1912.

[22] ———, Botanische Ergebnisse der schwedischen Expedition nach Patagonium und dem Feuerlande 1907–1909. III. A botanical survey of the Falkland Islands. K. Svensk. Vetensk. Handl. **50**: 129. *pl. 13* and *map*. 1913.

much of the non-swampy ground where the subsoil is composed of finer material. Above the coarser dry soils the *Empetrum* heath association dominates with an abundance of low evergreen shrubs. In wet depressions the Falkland representative of the peat bog occurs in the *Astelia* association, where several seed plants replace *Sphagnum* and forming low absorptive cushions are largely responsible for the immense layers of peat, several meters thick, that furnish the only fuel on the islands.

The tops of the highest mountains (only 700 m.) are covered with *Empetrum* heath, but a semialpine character is given to the vegetation by the presence of many cushion plants, among which the two remarkable umbelliferous genera *Bolax* and *Azorella* are conspicuous.

The author gives interesting notes on the flowering of many species, and also classifies the plants according to the "biological types" of RAUNKIAER. He points out that the results hardly support RAUNKIAER's characterization of the islands as possessing a "chamaephyte climate," in spite of the large percentage of chamaephytes and hemicryptophytes, since both classes are evergreen in the Falklands, showing slight vegetative periodicity, simply some arrest of growth during the winter. Among the numerous other interesting facts regarding various phases of the vegetation, the presence of a very considerable number of ferns belonging to the rainy west coast of Chile and Fuegia is worthy of notice, and is made conspicuous upon the map of the author's travels.

Tierra del Fuego[23] shows the passage of the grassy heath to the steppe, a transition to deciduous forest dominated by *Nothofagus pumilio* and in higher altitudes by *N. antarctica*, while the western half is covered with an evergreen rain forest in which *N. betuloides* and *Drimys Winteri* are the chief members. The distribution of these formations is shown upon an excellent map which has been extended in a more recent publication[24] to include South America to latitude 41° S. The evergreen rain forest is shown to extend to 48° S. without striking change. Within this southern extension of rain forest, the number of species is small and the precipitation so evenly distributed that little periodicity seems to be shown. On account of the rather sudden change due to a great increase in the number of species, SKOTTSBERG has selected the parallel of 48° S. as the northern boundary of the Magellan province of the subantarctic region. North of this line, not only is the forest richer in species, but there is more periodicity on account of the more unequal distribution of the precipitation. The rain forest extends to the eastern slopes of the Andes through several

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[23] SKOTTSBERG, C., Pflanzenphysiognomische Beobachtungen aus dem Feuerlande. Wiss. Ergeb. Schwed. Südpolar Exped. 1901–1903. **4**: Lief. 9. pp. 63. *pl. 3* and *map*. 1909.

[24] SKOTTSBERG, C., Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. I. Übersicht über die wichtigsten Pflanzenformationen Südamerikas S. von 41°, ihre geographische Verbreitung und Beziehungen zum Klima. K. Svensk. Vetensk. Handl. **46**: no. 3. pp. 28. *map*. 1910.

valleys and usually passes by a transitional deciduous forest to the steppes of Patagonia.

HAUMAN-MERCK[25] has studied the northern part of this forest, and finding it quite different from the southern portion would separate the two along the parallel 46°S. into the Magellan and Valdivian forests, the latter extending to 36°S. and being distinguished by the richness of its flora as well as by the diversity of its species. At Valdivia, near the center of the area, the annual precipitation is 266 cm., well distributed. Some idea of the climate may be obtained from the fact that while peaches and grapes will not ripen, apples, plums, and potatoes grow readily, while there are also plenty of bamboos and bromeliads. While the mountainous character gives considerable diversity, the greater portion of the valleys and slopes is covered with a luxuriant evergreen forest of subtropical aspect, extremely rich in species. The different strata of the forest are well marked. Trees of the first size, 20–30 m. in height, overtopping dense stands of smaller size, represent comparatively few species, *Eucryphia cordifolia* and the largest of the evergreen beeches, *Nothofagus Dombeyi*, being most widely distributed. Quite as remarkable for their endemic character and for their local abundance are *Aextoxicum punctatum*, *Saxegothaea conspicua*, *Podocarpus nubigena*, and *Fitzroya patagonica*, the last being most important as a lumber tree. Many families are represented in the trees of second size, but none more conspicuously than the Myrtaceae, which contributes 30 species, including shrubby forms of *Eugenia*, *Myrtus*, and *Myrceugenia*. The legumes are conspicuously absent and *Drymis Winteri* is probably most abundant. The shrubs comprise many species, and like many of the trees often possess attractive flowers. Special mention should be made of the abundant bamboos, some developing the climbing habit and all belonging to the genus *Chusques*. Other climbers are fairly abundant and many, like *Hydrangea scandens*, are very beautiful when in flower. Epiphytes are abundant, but mostly limited to ferns, mosses, and lichens. At least 10 species of *Hymenophyllum* were noted. Other ferns are common among the epiphytes and dominate the herbaceous vegetation of the soil, *Blechnum*, *Dryopteris*, and *Asplenium* being prominent genera. Mosses penetrate the deepest forests, two particularly large and beautiful ones being *Polytrichum dendroide*, 30 cm. high, and *Hypopterygium Thouini*, 10 cm. high.

Of the many problems of this interesting area, the occurrence of a large deciduous beech, *Nothofagus obliqua*, in the midst of an otherwise evergreen forest, and the extension of the forest upon the eastern slopes of the Andes appear particularly fascinating. The transition of this eastern extension to the semidesert of Patagonia receives a portion of the author's attention, as does the distribution of *Librocedrus chilensis*, and the character of the alpine flora.—GEO. D. FULLER.

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[25] HAUMAN-MERCK, L., La forêt-valdivienne et ses limites. Rec. Instit. Bot. Léo Errera **9**:347–408. 1913.

Development of fern prothallia.—Working under KLEBS, ISABURO-NAGAI[26] gives further evidence, through an investigation of the physiology of fern prothallia, in support of the idea that the course of development in plants is largely dependent upon and influenced by external factors. The author divides his work into four parts, dealing respectively with the germination of the spore, the development of the prothallium, the production of rhizoids and sex organs, and the formation of adventitious branches.

The paper gives an exhaustive summary of previous investigations dealing with the prothallium in ferns, and describes also a considerable amount of original investigation carried out with a view to ascertaining the effect of external conditions upon the qualitative and quantitative courses of development of the gametophyte. By far the most interesting and significant feature of the work is the extent to which the investigator is able to induce or inhibit the formation of sex organs, the appearance of apogamy, and finally of adventive shoots. Interesting, too, but possibly of less significance, are the changes of form which he seems able to produce in the thallus.

He finds, for instance, that where the nutrient solutions on which the spores are germinated are poor in potassium, magnesium, and calcium, both antheridia and archegonia may be formed; on the other hand, while antheridia may be formed quite readily in a solution containing little or no nitrogen, the production of archegonia cannot take place. In other forms, where germination and vegetative growth go on in darkness as in light with equal facility, no antheridia are set in the former instance. The experiments further point to a direct connection between the concentration of the nutrient solution and the production of sex organs, since under scant illumination archegonia are not developed in the weaker concentrations. Still other results indicate that if the prothallium be kept under conditions favoring vegetative growth, sex organs will not appear; and the author concludes from this that sex organs are produced only on prothallia whose vegetative growth has been hampered (ameristic prothallia).

In this connection, ISABURO-NAGAI brings up the question of the distribution of sex organs, pointing out the fact that whereas the antheridia are generally scattered over the entire prothallial surface, the archegonia are restricted to the meristematic region around the notch. His explanation of this situation, however, is far from satisfactory, and will need considerable experimental backing before it is given general acceptance. Briefly, the author first remarks the difference between the egg and the sperm, in that the latter is poor in albumen, with which the former is abundantly supplied; secondly, that the cells of the apical region of the prothallium are also rich in albumen; and thirdly, that the archegonia are probably restricted to this apical region because they derive their excessive protein supply from the meristematic cells.

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[26] ISABURO-NAGAI, Physiologische Untersuchungen über Farnprothallien. Flora **106**:281–330. *figs. 18.* 1914.

If this be true, it is probably the only case on record where the actively dividing members of a meristem act as nurse cells.

One of the most striking experimental results ISABURO-NAGAI publishes concerns his control of the formation of adventive branches. While he is unable to duplicate the results of HEILBRONN[27] in inducing adventive branching by exposing the prothallia to such narcotics as ether and chloroform, he finds that plasmolysis of the cells of the gametophyte will induce luxuriant formation of the vegetative shoots. In his explanation of this fact he makes the statement that the stimulus of plasmolysis is a purely physical one, consisting probably of the withdrawal of water from the cell. The possibility of this stimulus being chemical in its nature is precluded, because plasmolytic agents of widely different chemical nature all produce the same effect. He believes, also, that this is not a traumatic response, since wounding the thallus with a fine needle will not produce or stimulate the production of adventive branches. He accepts as a solution of the question the explanation of KLEBS who claims that the normal cell growth, at first rapid, is checked by the formation in the cell sap of deleterious substances. These are either withdrawn in the plasmolysis, allowing the initiation of renewed and vigorous growth when once the cell has returned to the normal condition, or else they are rendered inactive by the concentration of the cell sap during plasmolysis. A further hypothesis is that the growth of the older cells is checked by the younger cells through the direct protoplasmic connections between the two; that plasmolysis ruptures these connections; and that, therefore, upon the return to the normal condition vigorous growth may be resumed.

The investigation is concluded with a few additional facts on the influence of light upon germination, which are of no particular significance, inasmuch as they merely add a few names each to the lists of those spores which can germinate in darkness, and those which cannot.—HERMANN B. DEUTSCH.

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[27] HEILBRONN, A., Apogamie, Bastardierung, und Erblichkeitsverhältnisse bei einigen Farnen. Flora **101**:1–42. 1910.

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This book, of general interest because of its character and authority, will naturally be of peculiar interest to residents of Chicago and the Middle West. Its importance is indicated by the fact that it is issued under the auspices of the Geographic Society of Chicago, and has been prepared by two of the best known weather experts in the country. It includes discussions of a great variety of subjects, such as temperature, precipitation, atmospheric moisture, cloudiness and sunshine, wind direction and velocity, barometric pressure, and storm tracks; and among the interesting appendixes to the book are one on the weather of holidays and another containing journal entries relative to the great Chicago Fire of 1871.

The volume contains also a remarkable series of tables with reference to temperature, precipitation, atmospheric moisture, and atmospheric pressure—one hundred and forty-seven in all, with more than one hundred figures and plates.

Of especial interest and importance to teachers in connection with *The Weather and Climate of Chicago* is the preceding Bulletin of the Geographic Society edited by Professor Cox, and by Professor J. Paul Goode of the University of Chicago. It was prepared by a committee of the Geographic Society of Chicago and is entitled *Lantern Slide Illustrations for the Teaching of Meteorology.* It will be found an admirable aid in interesting students in the phenomena of weather and climate.

Unpopular Government in the United States. By Albert M. Kales, Professor of Law in Northwestern University.

272 pages, 12mo, cloth; $1.50, postage extra (weight 1 lb. 8 oz.)

This volume by a prominent member of the Chicago bar is an especially timely book, presenting with great clearness and cogency some of the political needs of the country, particularly the necessity of the short ballot. The author defines unpopular government as one of centralized power which is able to maintain itself in the face of popular disapproval. He then points out that the establishment in the United States of state and municipal governments, according to the plan of splitting up the power of government among many separate offices and requiring the widest and most frequent use of the elective principle, has cast so great a burden upon the electorate that an intelligent citizen is reduced to a state of political ignorance inconsistent with self-government. This situation has made it possible, he thinks, for a well-organized hierarchy to acquire the real power of government and to retain it, in the face of popular disapproval, for selfish ends. Such leaders the author characterizes as "politocrats."

The first part of the volume deals with the rise of the politocrats; the second discusses various expedients for restoring the American ideal of democracy; while the third considers constructive proposals like the commission form of government for smaller cities, and the application of the principles underlying this form to larger cities and the state, and to the selection of judges.

Chicago Tribune. Albert M. Kales, Professor of Law in Northwestern University, has written a book which ought to be read wherever citizens are perplexed by the intricacies and distressed by the failures of government.

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The Nation. In this monograph [on the history of Fort Dearborn] we have one of the most careful studies in Western history that has ever been made.

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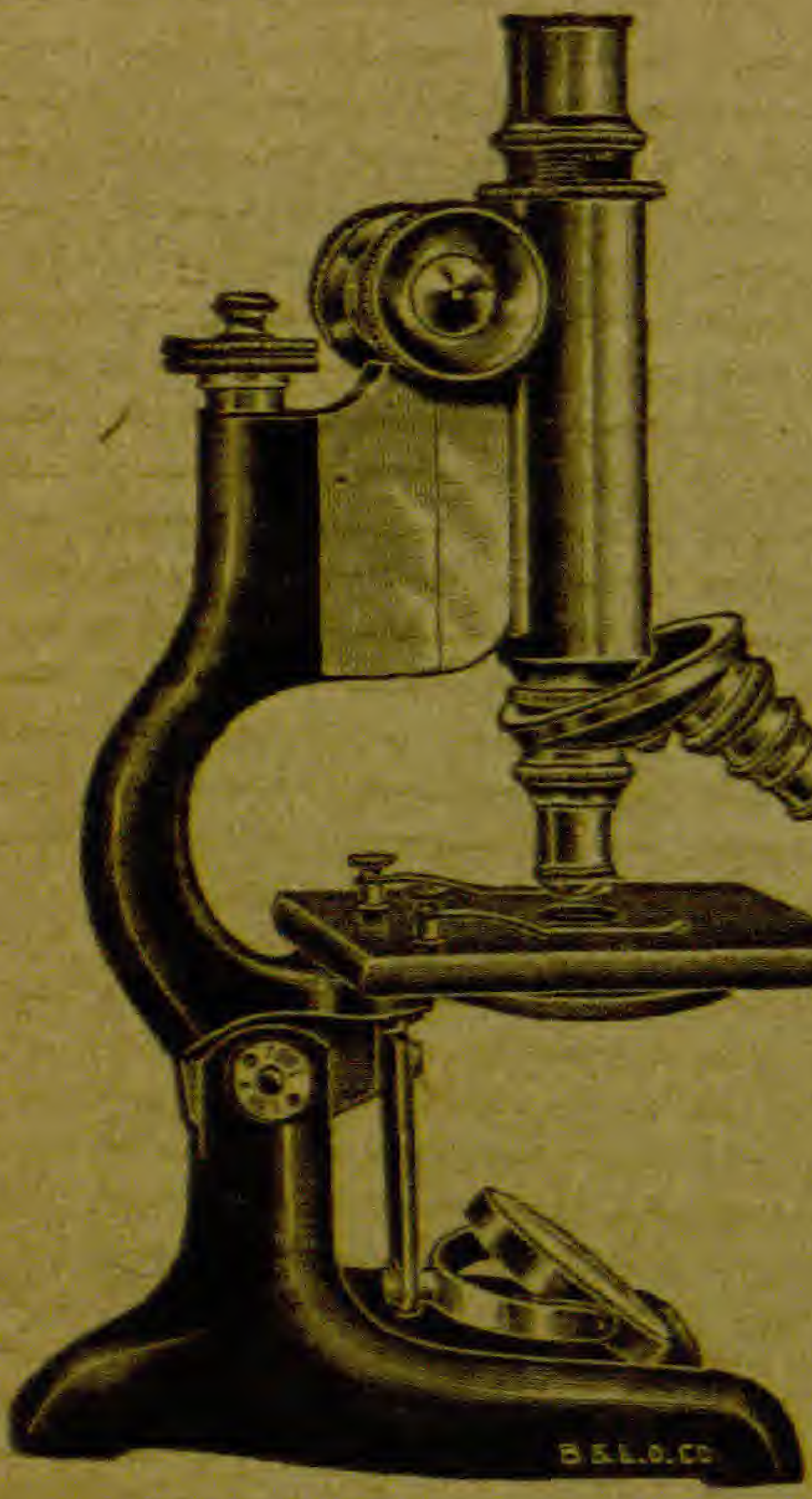
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THE
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Editor: JOHN M. COULTER

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A STUDY OF THE GERMINATING POWER OF SEEDS

MARVIN L. DARSIE, CHARLOTTE ELLIOTT, AND GEORGE J. PEIRCE

(WITH EIGHTEEN FIGURES)

Scattered throughout botanical literature are many statements regarding the length of time during which seeds may retain their germinating power or, as it is called, their viability. Some of these statements record the germination of seeds from old herbaria, others of seeds supposedly long buried in the earth, and still others of seeds which have been stored for known periods and under known conditions. Few of these records, however, bear critical examination.

Perhaps the earliest authentic records of tests of the continued vitality of air-dry seeds are those of ALPHONSE DE CANDOLLE.[1] In 1832 he first conceived the idea of testing seeds of different species which he had obtained in the harvest of 1831. He kept them all air-dry until May 1846, when he planted 20 seeds of each species. There were 368 species, representing 53 families. Of these but 5 out of 10 species of Malvaceae, 9 out of 45 species of Leguminosae, and 1 out of 30 species of Labiatae showed any power of germination.

Tests of the continued viability of buried seeds were made by DUVEL.[2] He used 109 species of 84 genera and 34 families, and,

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[1] DE CANDOLLE, A., Sur la durée relative de la faculté de germer dans des graines appartenant à diverses familles. (Première expérience.) Ann. Sci. Nat. Bot. III. **6**:373. 1846.

[2] DUVEL, J. W. T., The vitality of buried seeds. Bull. 83, Bur. Pl. Industry, U.S. Dept. Agric. 1905.

with the exception of two of his duplicate samples, they were all of the harvest of 1902. He mixed his seeds, in definite numbers, with dry clay soil in ordinary flower pots, and buried these in December 1902, to different depths, carefully covering each pot with an earthenware saucer to prevent the loss of seed and other accidents. The majority of the grains of wheat buried 6–8 inches and 36–42 inches had germinated and then decayed, while those at the medium depth of 18–22 inches were merely decayed, without indications of germination, when the pots were taken up in November 1903, eleven months after burial. Approximately all the barley at these three depths had germinated and afterward decayed during the same lapse of time. The majority of the commonly cultivated plants of field and garden could not withstand one year of burial, under the conditions which prevail in the soil outside of Washington, D.C. Many weed seeds, however, showed little deterioration within this length of time.

In 1907 BECQUEREL[3] reported the results of his examination into the germinating power of about 500 species of seeds, belonging to 30 of the more important families of the monocotyledons and dicotyledons, and varying in age from 25 to 135 years. These seeds came from the Muséum d'Histoire Naturelle in Paris. He used 10 seeds of each species, breaking off parts of the integuments of those which seemed impermeable, and, after washing them carefully in distilled water, placed them on damp cotton in crystallizing dishes and kept them at a temperature of 28° C. for more than a month. He obtained germinations in 50 species, all of which were included in four families, namely, the Leguminosae, Nelumbiaceae, Labiatae, and Malvaceae. The oldest seeds which germinated were 3 out of 10 of *Cassia bicapsularis*, one of the Leguminosae, which dated from 1819, and were therefore more than 85 years old at the time of the experiment.

In 1908 EWART[4] published the results of a similar set of tests of over 1000 species of seeds which he found locked in a cupboard in the botanical laboratory at Melbourne, Australia. They had been sent

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[3] BECQUEREL, P., Recherches sur la vie latente des graines. Ann. Sci. Nat. Bot. IX. 5:193–311. 1907.

[4] EWART, A. J., On the longevity of seeds. Proc. Roy. Soc. Victoria 21:1–210. 1908.

from Kew in 1856 for the University Gardens, but these not being ready at the time expected, the seeds had been put away in a dark dry closet and had remained there unopened for upward of 50 years. In addition, he examined some ten-year-old seeds from Sydney and Adelaide, and more from the National Herbarium, making altogether nearly 3000 tests. He first tried germinating the seeds in soil, but finding this unsatisfactory, he soaked the seeds and then placed them on moist filter paper in glass dishes and set them in a germinator. Seeds which did not swell after one or two days in water were either filed or treated for 15–90 minutes with concentrated sulphuric acid, that is, until the cuticle was dissolved away. *Adansonia*, for example, required almost 6 hours' treatment of this sort. The seeds were then washed and thereupon swelled readily. EWART adds to his own long list by including some of the results of BECQUEREL, NOBBE, DE CANDOLLE, GIRARDIN, DARWIN, DUVEL, ROMANES, PETER, BERKELEY, and others, making a list, therefore, which comprises about 4000 species. He too found that the majority of those seeds which retain their germinating power for the longest term are members of the Leguminosae, and are generally hard-shelled.

As to the physical and chemical conditions prevailing in dormant seeds there is a diversity of opinion corresponding to the paucity of knowledge. EWART, for example, states that molecular changes and rearrangements continue until finally the seeds no longer retain the power to resume active life. Whatever these molecular changes may be called, whether respiratory or other, it is obviously important, for both theoretical and practical reasons, to determine the conditions in the seeds themselves and the means of maintaining and bettering these if possible. In this paper, however, we are concerned with the results of these conditions rather than with the conditions themselves.

Until recently, so far as we know, tests of the longevity or viability of seeds have depended upon the percentages of actual germinations in prepared beds. Such tests are simple enough in the case of seeds which germinate quickly, and in these cannot be improved upon. When, however, two weeks or more must elapse, even under the most favorable conditions, before one may know the quality, that is, the germinating power, of the seeds in which one may be interested, a quicker method is desirable for every reason. Not only is the economy of time desirable, possibly for pecuniary reasons, as in the case of a seed-buyer, but also there is less danger, in briefer exposure, of injury or loss from fungous or other enemies of the seeds under examination. One of us has shown that, by using silvered Dewar flasks as calorimeters, one may quickly determine that heat is liberated in the germination of seeds, and has suggested that there may be such differences in the heats liberated by seeds of different ages that one may use these as indicators of age and germinating power or viability.[5] The following experiments were begun in order to test this idea, and they were continued with other and older seeds in order to prove its correctness.

The material used in our experiments came to us through the courtesy of Professor R. A. MOORE, of the University of Wisconsin, Professor E. J. WICKSON, of the University of California, and Professor L. H. PAMMELL, of the Agricultural College at Ames, Iowa, whom we take this opportunity of thanking for their prompt and generous response to our request for seeds of known and considerable age.

Method

The method has been described before. Some of the details, however, as applied to this particular investigation, should be described now. We used silvered Dewar flasks, some made by Burger of Berlin, others not so good, of about 250 cc. capacity. Most of the flasks were round-bottomed, but a few contained a small drainage tube opening into the bottom of the flask. There are differences in the efficiencies of the different flasks even of the same good make and pattern, but, as will appear later, there are great differences between good and bad flasks as insulators. These differences can be ascertained, without destroying the vacuum of the flask, only by using them under constant temperature.

We were fortunate enough to have a convenient constant temperature chamber. This has been sufficiently described before.[6] A maximum-minimum thermometer was taken into the room, but

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[5] PEIRCE, G. J., A new respiration calorimeter. BOT. GAZ. 46:193–202. 1908; also The liberation of heat in respiration. BOT. GAZ. 53:89–112. 1912.

[6] See PEIRCE, BOT. GAZ. 53:90, 91. 1912.

the variations in the temperature were so slight that it was not thought to be worth while to continue to record the readings. The slight variations in room temperature shown in the record given below are due mainly to the opening of the room, the presence of one or more of the experimenters, and the heat liberated by a 32 candle-power incandescent light bulb. The light was turned on only as needed, but it is obvious that if the temperature of the room is moderately low, as it was, the heat liberated from a carbon filament lamp of considerable candle-power and radiated and exhaled from the body of an adult individual of average stature, during the 10–40 minutes required for work or observation, would be considerable, and in a smaller room would make a noticeable change in the temperature. In our case the fluctuations were slight.

The thermometers were of two sorts, short and long, the one requiring to be pulled part way out of the flasks to be read, the other long enough to make this unnecessary. Both read to 0°1 C. The differences in the thermometers, flasks, and cotton plugs used to close the flasks and to hold the thermometers steadily in the necks, as well as the inevitable differences among the seeds themselves, are responsible for such lack as there may be of uniformity in the corresponding results.

The flasks were sterilized by being washed in corrosive sublimate solutions, generally saturated aqueous, and then thoroughly washed out with boiled and cooled distilled water. In many cases the seeds could not be sterilized, with the methods which we employed, without impairing their vitality. It is a matter of very considerable practical importance to find an agent which, at the same time that it is inexpensive, will effectively sterilize the surface of seeds without harming the germ within. We tried copper sulphate in various concentrations, but found it unreliable and often injurious. In most instances we used a saturated aqueous solution of corrosive sublimate. This is thoroughly efficient wherever it penetrates, but a considerable part of the surface of many, if not most, seeds is covered with a film of air, hard to dislodge, which prevents the sterilizing solution from reaching the spores or bacteria which may be adhering to the seed coats. SCHRÖDER[7] has discussed the

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[7] SCHRÖDER, H., Die Wiederstandsfähigkeit des Weizen- und Gerstenkornes gegen Gifte und ihre Bedeutung für die Sterilization. Centralbl. f. Bakt. **28**: 492. 1910.

difficulties in the way of sterilization, and suggests various methods and agents, but for our purposes the solutions of corrosive sublimate were the least objectionable. It is obviously desirable, if sterilization is to be generally practiced, to have a less powerful general poison than corrosive sublimate, at least in concentrated solutions; and experience has shown us that some seeds are so thin-walled or have walls so easily penetrated by the poison that it is only too easy to injure or even to kill them. Several of our experiments gave entirely negative results from this cause. Clover seemed to be particularly susceptible, presumably on account of the small size of the seed and its thin and permeable coat.

Experimental work

We made germination experiments, both in Dewar flasks and in seed beds, on barley, clover, corn (Cory sweet corn), hemp, oats, and wheat. The records of these are in the form of tables, graphs, and photographs. Our records will show that, other things being equal, a high temperature within a reasonable length of time is indicative of high germinating power and also of the ability to make

TABLE I

BARLEY

Date	Time	Hours elapsed	Room	Max.	Min.	1905	1911
March 8	11:00 A.M.	....	19°9 C.	....	....	17°10 C.	17°00 C.
9	10:00 A.M.	23	17.3	17°21 C.	16°22 C.	17.20	17.10
9	5:00 P.M.	30	17.2	....	....	17.30	17.35
10	9:00 A.M.	46	17.2	17.16*	16.17	17.50	17.77
10	6:00 P.M.	55	17.2	....	....	17.80	18.50
11	9:30 A.M.	70.5	17.1	17.16	16.17	18.30	19.44
11	5:00 P.M.	78	17.1	....	....	18.60	20.20
12	9:00 A.M.	94	17.2	17.16	16.06	19.20	22.20
12†	4:00 P.M.	101	17.2	....	....	19.50	22.50
12	4:05 P.M.	101	17.2	....	....	19.20	22.00
13	9:45 A.M.	118.75	17.1	17.21	16.39	20.20	22.25
13	4:30 P.M.	125	17.0	....	....	20.62	22.00
14	9:00 A.M.	142	17.0	....	....	21.40	21.40
14	3:00 P.M.	148	17.0	....	....	21.40	21.30

*This and other discrepancies between room and maximum temperatures are due to (1) the poor thermometer used to indicate the room temperature, and (2) the fact that the maximum temperatures were calculated from a Weather Bureau pattern thermometer with Fahrenheit scale.

† On the afternoon of March 12, the flasks were opened in order to determine whether any odor was present. None was detected and the contents of the flasks were not disturbed in any way. Nevertheless, the temperature in the flask containing 1911 seed fell steadily, from that time on, as the record shows.

a rapid growth of root and shoot after germination, in other words, of vigor. The following experiments furnished the grounds for this statement.

EXPERIMENT I.—Barley from the University of Wisconsin; 15 grams of the crop of 1905 and a like amount from the crop of 1911, washed with a saturated solution of copper sulphate. Experiment set up March 8, 1912. The data are in table I.

On the eighth day the flasks were opened and emptied. No infection was visible and both lots of seed had germinated freely. It is to be noted, however, that the radicles from the 1911 seed were two or three times as long as those from the 1905 seed. The accompanying graph (fig. 1), constructed from the thermometer readings of table I, indicates the evolution of heat in these two sets of seeds.

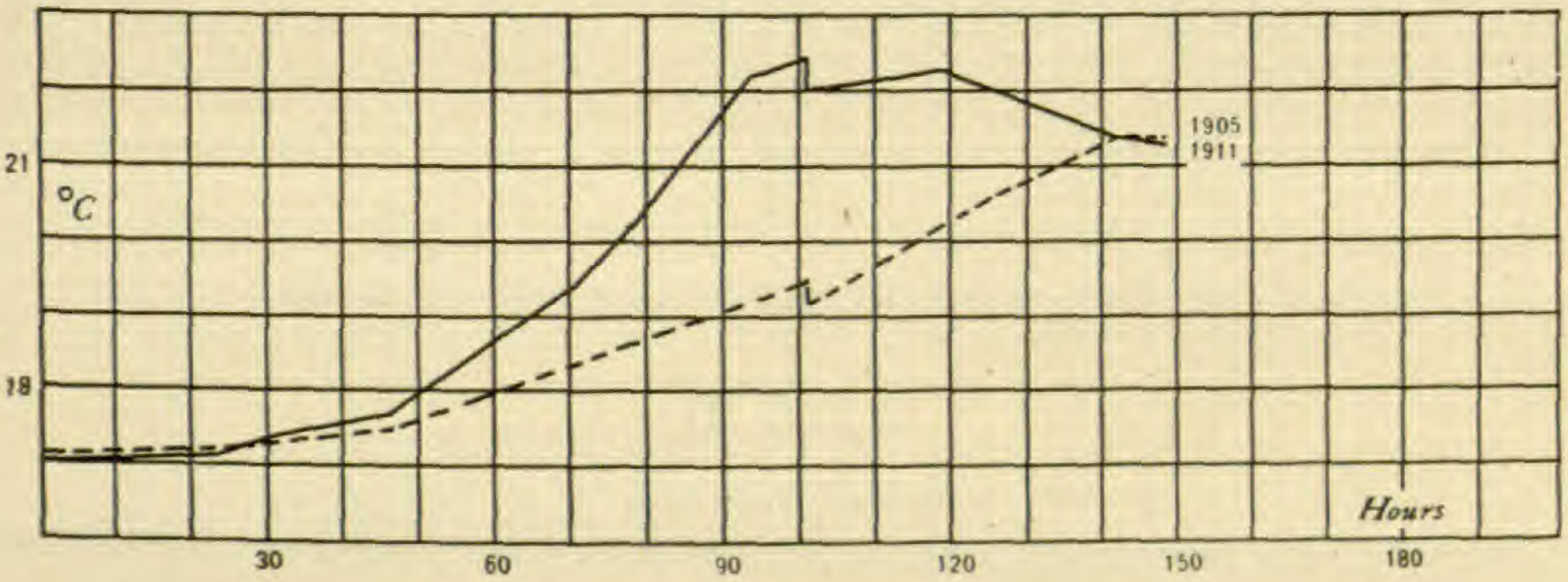

FIG. 1.—Barley (experiment I): 15 grams; broken line, 1905; solid line, 1911

EXPERIMENT II.—Barley from the University of Wisconsin and from Ames, Iowa; 10 grams of each year. On account of the hulls, no sterilization was attempted. Experiment set up as indicated in 1913. The data are in tables II and III.

The fact that the 1909 seeds were very moldy when taken from the flask accounts for the high temperature in that flask. Two other experiments were set up at the same time, but as we were not able to sterilize, the seeds were found to be covered with mold and the unusually high temperatures were not thought worth recording.

It is not of course to be expected that such seeds will show a perfectly regular decrease in heat yield with increasing age. There are too many other factors which may influence their viability. In order correctly to interpret the variations from this regular decrease, one should know the climatic conditions under which the seed was grown and harvested, and the conditions under which it was afterward stored. Immature seeds are open to the influence of environmental conditions to a far greater extent than the fully mature seed (EWART, *loc. cit.*). Even fully matured seeds, when stored under humid conditions, lose their vitality much more quickly than those stored in a dry atmosphere (DUVEL, *loc. cit.*).

TABLE II

WISCONSIN BARLEY

Date	Time	1905	1906	1907	1908	1909	1910	1911	Room
April 13	1:00 P.M.	17°.4 C.	17°.5 C.	17°.4 C.	17°.4 C.	17°.6 C.	17°.6 C.	17°.6 C.	17°.0 C.
14	8:00 A.M.	17.6	17.6	17.5	17.6	18.6	18.4	18.2	16.9
14	6:00 P.M.	17.8	17.7	17.5	17.8	19.3	19.2	18.6	16.9
15	8:00 A.M.	17.9	17.8	17.5	18.0	21.1	21.0	19.1	16.9
15	5:15 P.M.	18.0	18.0	17.6	18.2	22.9	23.0	19.6	16.9
16	8:15 A.M.	18.3	18.3	17.6	18.6	23.6	24.0	20.8	16.9
16	5:30 P.M.	18.4	18.5	17.6	18.9	23.3	23.8	20.9	16.9
17	8:00 A.M.	18.7	19.0	17.7	19.4	22.4	23.3	21.0	16.9
18	8:30 A.M.	19.4	19.3	17.9	19.7	21.3	22.7	20.5	16.9
18	6:00 P.M.	19.5	19.4	17.9	19.7	21.0	22.6	20.3	16.9
19	9:00 A.M.	19.5	19.6	18.0	19.6	20.8	22.6	20.1	16.8
19	4:30 P.M.	19.6	19.7	18.05	19.6	20.7	22.7	20.1	16.9
21	8:00 A.M.	19.9	20.5	18.4	19.6	20.6	23.4	20.1	16.9
		2°.5	3°.0	1°.0	2°.2	3°.0	5°.8	2°.5	Increase

The 1910 and 1906 seeds were moldy when taken from the flasks.

TABLE III

BARLEY NO. 202

Date	Time	1909	1910	1911	Room
April 23.....	8:30 A.M.	17°.6 C.	17°.7 C.	17°.6 C.	17°.2 C.
23.....	4:30 P.M.	17.7	17.8	17.7	17.1
24.....	8:00 A.M.	18.0	18.2	18.0	17.2
24.....	4:30 P.M.	18.1	18.4	18.1	17.2
25.....	9:30 A.M.	18.6	19.1	18.6	17.2
25.....	5:00 P.M.	18.9	19.2	18.9	17.3
26.....	12:00 M.	19.7	19.2	19.7	17.3
27.....	10:00 A.M.	20.4	19.2	20.4	17.3
28.....	8:00 A.M.	21.7	19.4	21.7	17.3
28.....	6:00 P.M.	22.5	19.6	22.5	17.3
29.....	9:00 A.M.	24.9	20.1	24.9	17.3
		7°.3	2°.4	2°.1	Increase

The foregoing records have shown that there is a decrease in the amounts of heat liberated by germinating seeds of certain sorts as the seeds increase in age. In order to ascertain whether there is any proportional relationship between the respiratory activity, as indicated by the heat yield, and the germinating power, we still further tested some of the seeds used in the foregoing experiments by setting them out to germinate. Five lots of barley, those from Wisconsin and the no. 202 above, together with three more from Ames, Iowa, were selected for the test. Fifty kernels of each year in each of the five lots were soaked for 24 hours in boiled distilled water. They were then planted in rows in shallow boxes of sand which had previously been steamed for three hours in an Arnold steam sterilizer and allowed to cool. The boxes were then set on the benches in the greenhouse awaiting germination. The date was April 22, 1913. The weather was very warm at this time. This partly accounts for the very quick response of these seeds. The data are in table IV.

TABLE IV

	YEAR	NUMBER SPROUTING APRIL				PER-CENT-AGE SPR. 28	LENGTHS OF PLUMULES IN CM. APRIL 27–28			
		25	26	27	28		Shortest	Longest	Av.	Percentage growth
No. 364...	1909	17	25	38	......	76	1.4	7.8	3.5	43
	1910	16	22	27	......	54	1.0	8.1	5.5	67
	1911	31	37	46	......	92	2.4	7.5	4.7	58
No. 294...	1909	19	27	43	......	86	1.0	7.7	5.3	65
	1910	21	25	32	......	64	1.0	8.7	6.9	8.5*
	1911	27	38	49	......	98	1.0	8.9	6.1	75
No. 304...	1909	26	29	41	......	82	1.3	8.5	6.0	74
	1910	24	24	28	......	56	0.5	7.9	6.5	80
	1911	38	45	45	......	90	1.0	9.5	6.6	81
Wisconsin.	1905	17	26	......	40	80	0.5	8.9	5.3	65
	1906	3	23	......	29	58	1.2	8.9	5.9	72
	1907	6	12	......	18	36	1.0	7.6	4.2	51
	1908	26	38	......	42	84	0.3	10.5	6.8	83†
	1909	41	46	......	49	98	3.5	10.5	8.1	100
	1910	29	41	......	47	94	2.0	9.7	6.7	82
	1911	28	39	......	42	84	2.2	8.4	6.5	80
No. 202...	1909	12	29	......	40	80	1.6	7.5	5.4	66
	1910	18	35	......	40	80	3.5	8.1	6.5	80
	1911	18	41	......	47	94	1.5	9.8	6.5	80

* Length of plumules April 27.

† Lengths measured April 28.

The first counting was made three days from the time the seeds were planted; the last, six days from that time. In almost every case the 1911 seeds show the greatest number of seedlings at the first as well as at the last counting, and here also the 1910 seeds show lowered vitality, especially when compared with 1909. In the percentage of growth of the seedlings, the same decrease with age is evident.

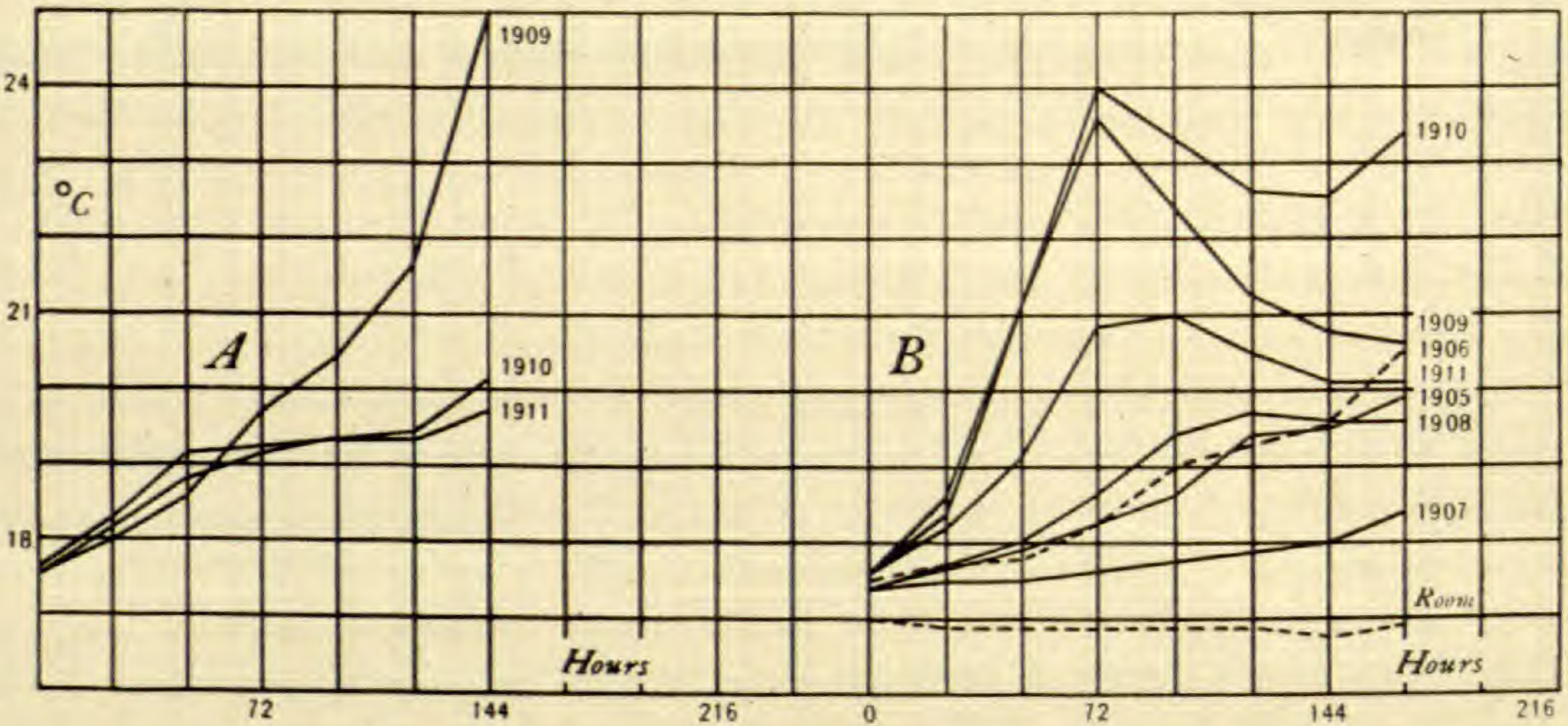

FIG. 2.—Barley in flasks (experiment II): *A*, no. 202; *B*, Wisconsin

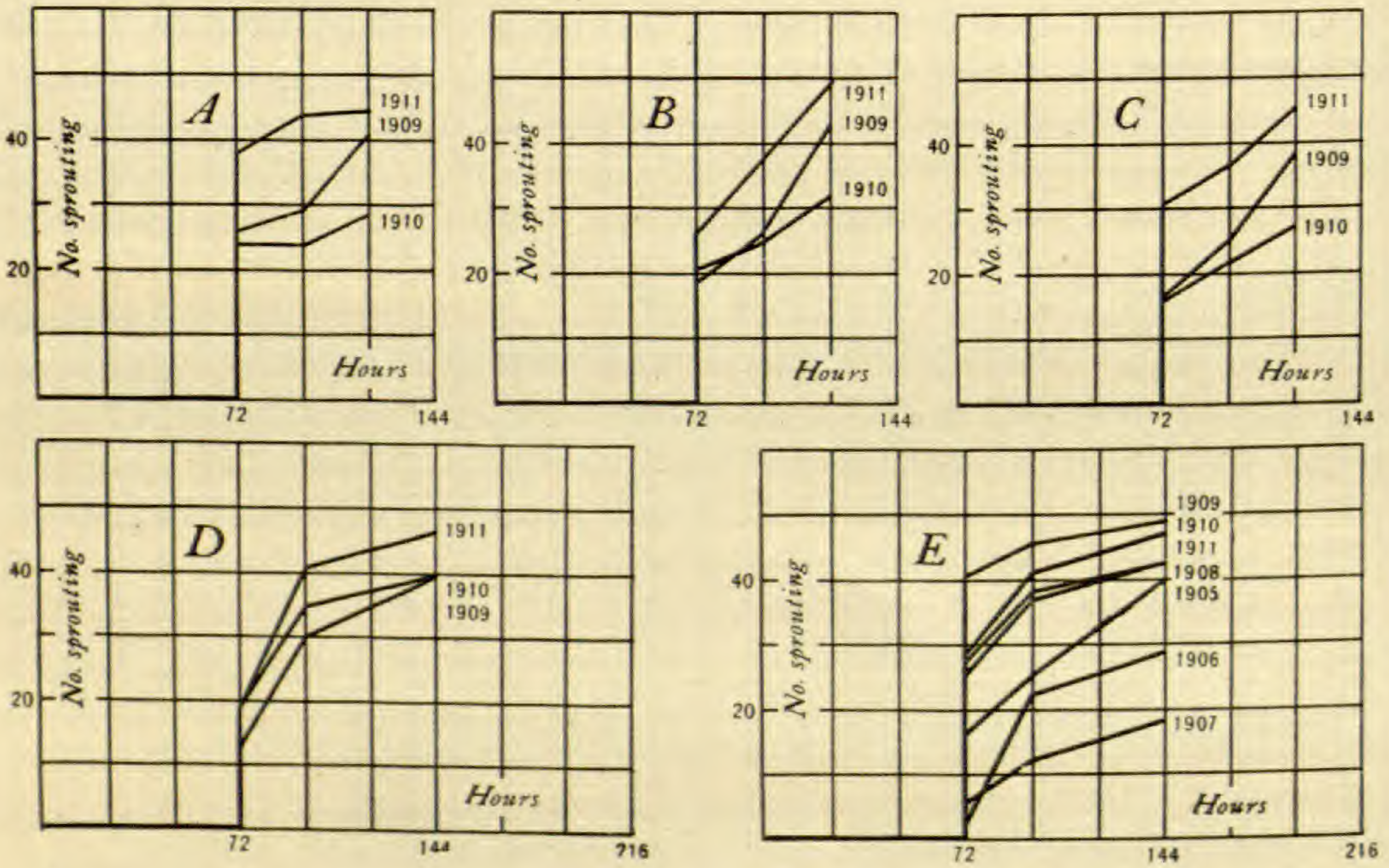

FIG. 3.—Barley in soil: *A*, no. 304; *B*, no. 294; *C*, no. 346; *D*, no. 202; *E*, Wisconsin.

For the sake of comparison, the accompanying curves are given (figs. 2, 3), but attention should be called again to the fact that, owing to the hulls, no attempt at sterilization was considered worth while, and hence there was very considerable molding in the Dewar flasks, with a corresponding rise in temperature independent of the heat yielded by the germinating barley. That this is the case will be more plainly shown in subsequent experiments and figures.

In spite of the various defects in this experiment, it is clear not only that the germinating power of seeds declines from year to year, but that this is indicated and can be tested by ascertaining the heat yield in such a good insulator as silvered Dewar flasks. Furthermore, inspection of the tables will show not only that the youngest seeds show the highest percentage of germination and the greatest heat yield, but they respond most quickly to the influence of conditions favorable to germination. They reach the maximum percentage of germination and maximum temperature sooner than older seed.

Experiment III.—Red clover (*Trifolium pratense*); 25 grams of seed from the crop of 1904 and the same amount from 1911; sterilized by washing with a concentrated aqueous solution of corrosive sublimate which was removed by repeated rinsings with boiled distilled water; placed in two sterile flasks and covered with boiled distilled water previously reduced to room temperature. At the end of 18 hours the water was poured off and the plugs carefully replaced in the necks of the flasks. The experiment was set up on February 20, 1912. The temperature record is given in table V.

TABLE V

Date	Time	Hours elapsed	Room	Max.	Min.	1904	1911
February 20	4:00 P.M.	....	17°6 C.	....	....	18°20 C.	18°10 C.
21	9:30 A.M.	17.5	17.8	17°16 C.	16°39 C.	18.10	18.20
21	4:30 P.M.	24.5	....	....	....	17.90	18.60
22	10:00 A.M.	42.0	17.6	17.05	16.50	17.80	20.20
22	5:30 P.M.	49.5	....	....	....	17.70	21.70
23	9:30 A.M.	66.5	17.7	17.16	16.39	17.70	24.50
23	5:30 P.M.	74.5	18.0	....	....	17.70	25.40
24	9:30 A.M.	91.5	17.6	17.11	16.50	18.00	26.30
24	5:30 P.M.	99.5	17.7	....	....	18.40	26.45
25	9:30 A.M.	116.0	17.7	17.16	16.50	24.70	27.40
25	3:00 P.M.	122.0	17.7	....	....	25.80	27.50

As table V shows, and as graphically displayed in fig. 4, there was a very marked difference in the heat liberated by the two sets of seeds up to the fifth day. At this time the temperature in the 1904 flask rose very rapidly. Upon opening the flasks, the cause of this sudden rise was at once seen to be the active fermentation, the odor of which was evident, and the contents of the flask were found to be covered with *Penicillium*. The accuracy with which the heat yield indicates the germinating power of the seeds is shown by fig. 5, in which the contents of the two flasks are photographed in the Petri dishes into which they were emptied for this purpose. Not more than 1 per cent of the whole quantity of 1904 seed showed any sign of germination. On the other hand, practically all of the 1911 seed had germinated and the seedlings were growing vigorously. In this flask merely a very slight trace of mold was present. I do not see that the inference that the faulty germination of the 1904 seed was due to the amount of mold and bacteria upon it is at all justified by the evidence, but rather that the sterilization had resulted in killing all but a few spores of the mold, and that some time had to elapse before these could produce any considerable amount of mycelium and liberate any considerable amount of heat.

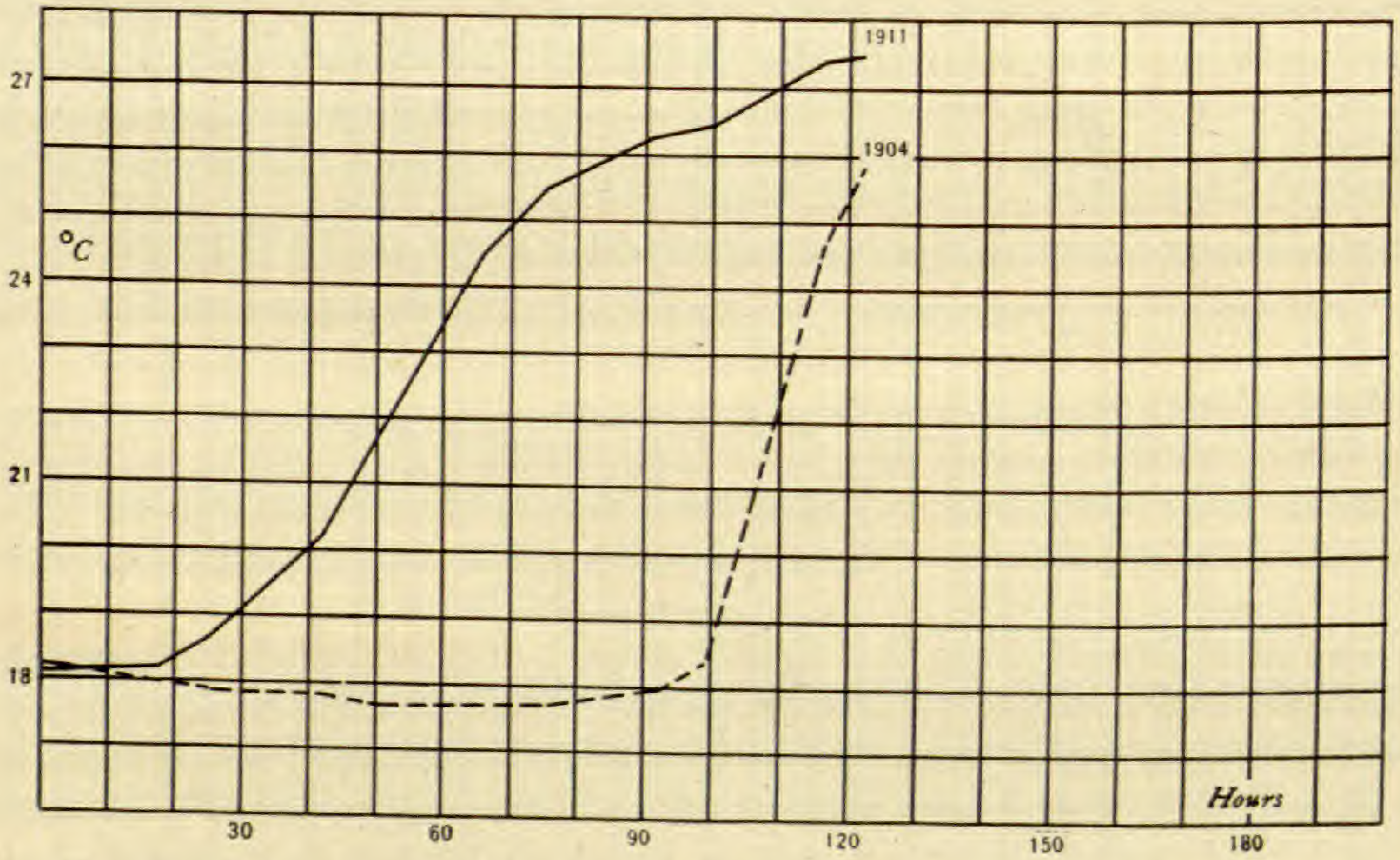

FIG. 4.—Red clover (experiment III): 25 grams; broken line, 1904; solid line, 1911.

EXPERIMENT IV.—Cory sweet corn, white cob, bought of C. C. Morse & Co., seedsmen, San Francisco, in 1908 or 1909 and 1911 or 1912, and purporting to be of the crops of 1908 and 1911, respectively; 30 grams of each, thoroughly washed in a 10 per cent aqueous solution of copper sulphate and then rinsed in boiled distilled water at room temperature, were put in silvered Dewar flasks and soaked for 24 hours in boiled distilled water. This was poured off when the first temperature reading was taken. The experiment was set up on March 15, 1912. The data are given in table VI.

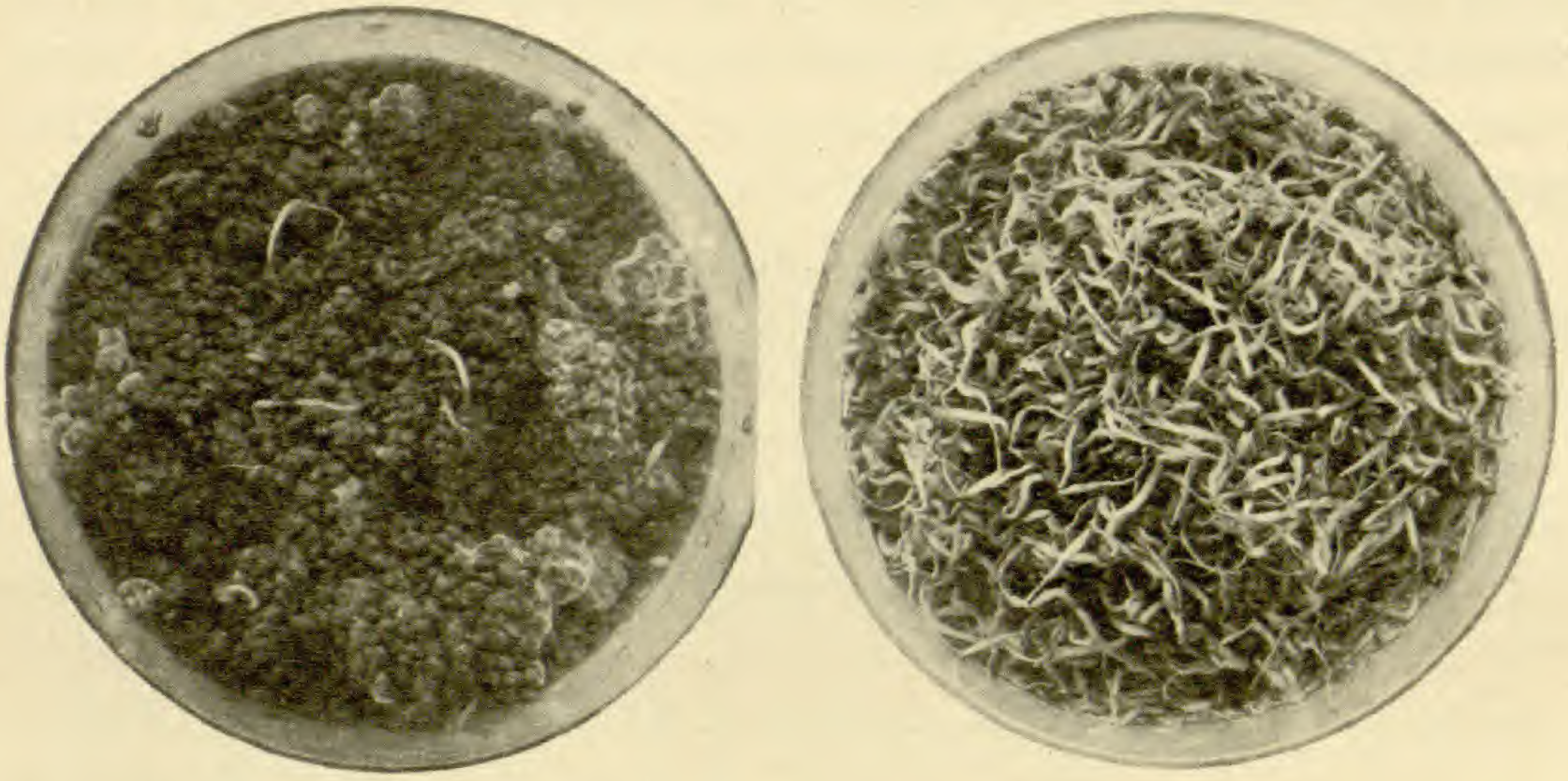

FIG. 5.—Red clover: *A*, 1904; *B*, 1911

TABLE VI

Date	Time	Hours elapsed	Room	Max.	Min.	1908	1911
March 15	12:30 P.M.	....	17°6 C.	....	....	17°00 C.	17°10 C.
16	11:30 A.M.	23	16.9	17°21 C.	16°01 C.	17.00	17.15
17	10:30 A.M.	46	17.0	17.16	16.01	16.90	18.70
18	9:30 A.M.	69	17.0	17.16	16.06	16.90	20.75
18	5:00 P.M.	76.5	17.0	....	....	17.00	21.45
19	9:00 A.M.	92.5	17.0	17.16	16.06	17.75	23.00
19	5:00 P.M.	100.5	17.0	....	....	18.25	23.70
20	9:30 A.M.	117	17.2	17.16	16.06	18.75	24.45
20	4:30 P.M.	124	17.0	....	....	18.56	24.45
21	9:00 A.M.	140	17.0	17.16	16.01	18.40	24.30

On opening the flasks, both sets of seeds were found to be infected with mold, but with more on the older seeds than on the younger ones; 24 per cent of the 1908 corn had germinated at the end of the experiment; the radicles were short as well as few. Practically 100 per cent of the 1911 corn germinated and the radicles were long and vigorous. In fig. 6 are given the curves made from the temperature data of table VI. This experiment, in addition to being very clear and striking in its indication of the deterioration which takes place on keeping seed even for the short space of three years, is of special interest because it furnishes a test of the value of commercial seed.

EXPERIMENT V.—Hemp seed, from Ames, Iowa, of the crops of 1907 and 1911, and of 1908 and 1910; 5.5 grams of each lot were washed with concentrated aqueous solution of corrosive sublimate, thoroughly rinsed with boiled distilled water, and soaked for the usual length of time. The experiment with 1907 and 1911 seed was set up on May 1, that on the 1908 and 1910 seed on May 13, 1912. The data are given in table VII.

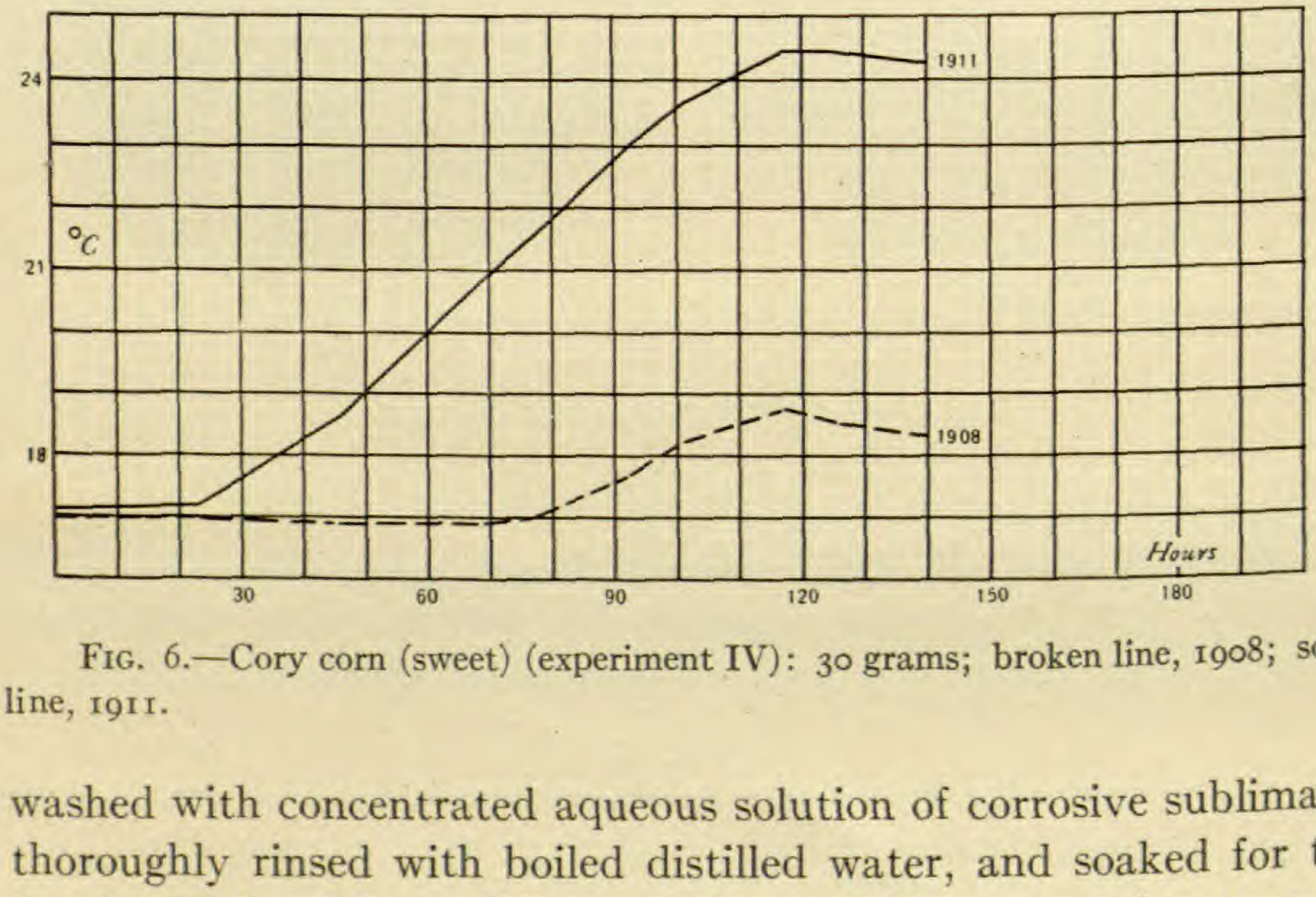

FIG. 6.—Cory corn (sweet) (experiment IV): 30 grams; broken line, 1908; solid line, 1911.

It is obvious that, because of the small amount of seed used, namely, 5.5 grams, the rise in temperature would be less than when larger quantities were used; but it is interesting and significant that only a small sample need be used to test the quality of seed, provided only that the insulator be a good one. Thus we have a rise of 5°35 C. taking place in the flask containing 1911 seed, whereas the temperature in the flask containing 1907 seed merely fluctuated with the temperature of the room. On opening the flasks a corresponding difference was revealed in the condition of the two sets of seeds. The 1911 lot had germinated very freely, and showed rather remarkable growth. Many radicles were 3–4 cm. long, and the cotyledons had emerged in nearly all the seedlings. On the other hand, only three of the 1907 seeds had germinated, less than 1 per cent. There was no mold in the 1911 seed, whereas the older seed had molded considerably. As table VII shows, the records of the 1910 and 1908 seeds are intermediate between those of the 1911 and 1907 seeds. About 95 per cent of the 1910 seeds germinated, but of the 1908 seed not over 40 per cent germinated. The seedlings of both of these latter sets were vigorous, as is shown by fig. 7. We believe that the high initial temperature to which the seeds of these two latter sets were exposed stimulated respiration in both lots, and

TABLE VII

Date	Time	Hours elapsed	Room	1907	1911	1908	1910
May 1...	4:00 P.M.	....	18°.0 C.	19°.80 C.	20°.55 C.	....	....
2...	2:30 P.M.	21.5	17.5	17.60	18.35	....	....
3...	9:30 A.M.	40.5	17.5	16.70	17.35	....	....
3...	5:30 P.M.	48.5	17.5	16.75	17.40	....	....
4...	8:00 A.M.	63.0	17.6	16.80	17.75	....	....
4...	5.30 P.M.	72.5	17.6	16.80	18.10	....	....
5...	9:30 A.M.	88.5	17.6	16.85	18.90	....	....
5...	4:30 P.M.	95.5	17.7	16.90	19.40	....	....
6...	9:30 A.M.	112.5	17.8	17.15	20.60	....	....
6...	3:30 P.M.	118.5	18.2	17.30	20.90	....	....
7...	8:30 A.M.	135.5	17.8	17.20	21.50	....	....
7...	4:30 P.M.	143.5	18.0	17.20	21.70	....	....
9...	10:00 A.M.	181.0	18.0	17.20	22.70	....	....
10...	9:30 A.M.	204.5	18.0	16.75	21.90	....	....
11...	9:30 A.M.	228.5	18.0	17.30	21.40	....	....
13...	12:00 M.	....	18.0	....	....	27°.80 C.	28°.00 C.*
14...	9:30 A.M.	21.5	18.0	....	....	21.70	20.80
14...	3:30 P.M.	27.5	18.0	....	....	18.60	17.90
15...	8:30 A.M.	44.5	18.0	....	....	17.90	17.50
16...	8:00 A.M.	68.0	18.0	....	....	17.90	17.80
16...	4:00 P.M.	76.0	18.2	....	....	18.00	18.00
17...	9:30 A.M.	93.5	18.0	....	....	18.10	19.10
17...	3:30 P.M.	99.5	18.0	....	....	18.10	19.80
18...	9:30 A.M.	117.5	18.0	....	....	18.40	22.00
20...	5:30 P.M.	173.0	18.0	....	....	19.80	21.10
22...	9:30 A.M.	214.0	18.0	....	....	20.20	20.00

* In setting up this experiment, it was necessary to prepare a fresh supply of boiled distilled water. This did not have time to cool to room temperature, and hence the high initial temperatures and the immediate drop to room temperature.

that the temperature record is somewhat higher than it would have been under perfectly normal and proper conditions.

From this experiment it is evident that a small sample of seed in a Dewar flask of good quality may be used with confidence to indicate the germinating power of a much larger quantity. At the same time that we are fortunate in knowing the ages of the seeds used in this experiment, we cannot know that the seeds were equally mature when they were harvested in the several seasons, and we can only believe that they were equally well kept. But be these things as they may, this experiment demonstrates the feasibility of ascertaining the germinating power of a given lot of seed, whatever its age and experience may have been, and, furthermore, shows that this is possible in a short time and even with small quantities of material. But on the assumption that these four lots of seed differed from one another only in age, an assumption which we cannot make with any assurance, it is noticeable that the germinating power falls abruptly; thus the germinating power of the 1911 seed in 1912 was approximately 100 per cent, of the 1910 seed approximately 95 per cent, of the 1908 seed 40 per cent, and of the 1907 seed less than 1 per cent. We did not have any 1909 seed, and we regret this. The results recorded in table VII are graphically represented in fig. 8.

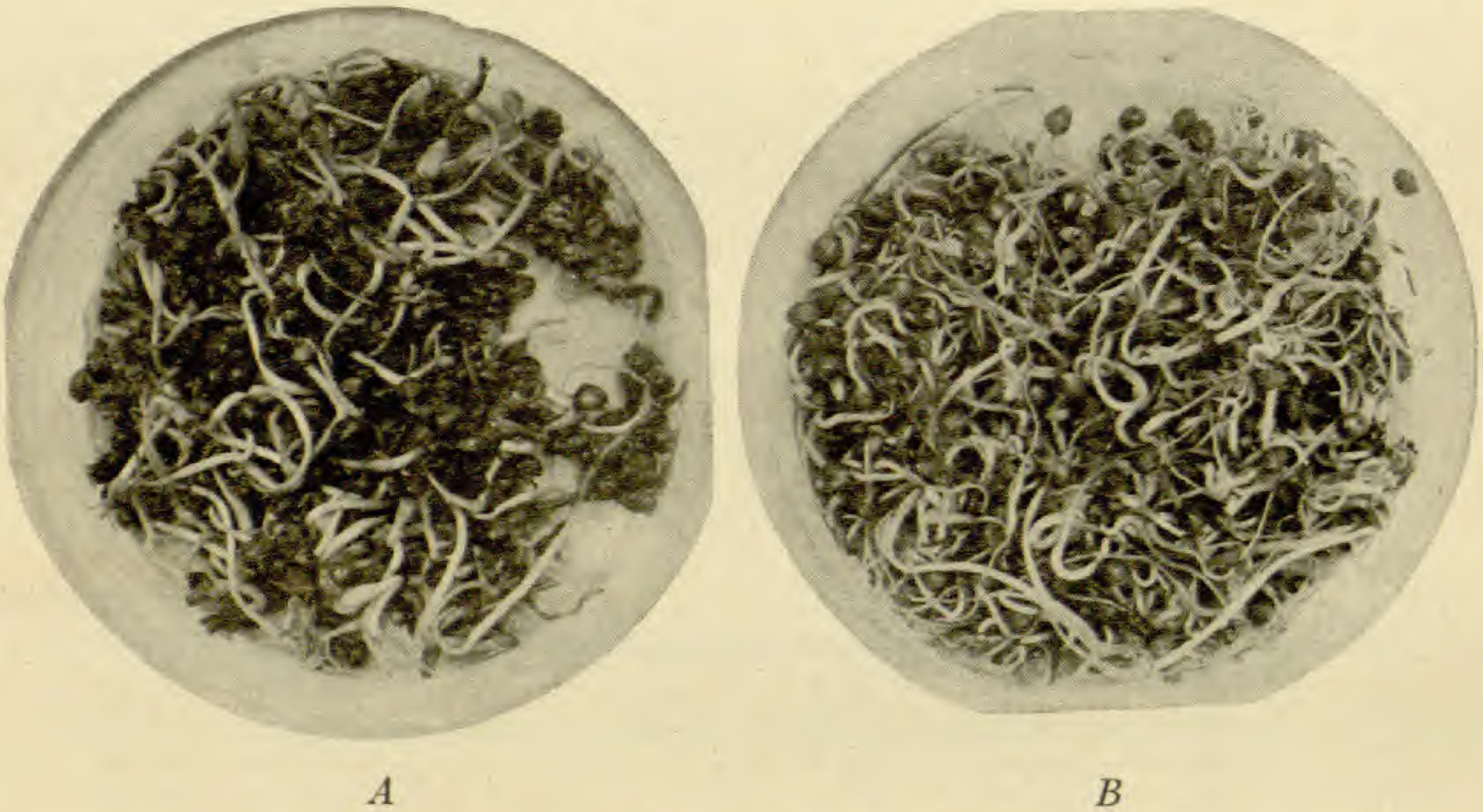

FIG. 7.—Hemp: *A*, 1908; *B*, 1910

EXPERIMENT VI.—Oats from the University of Wisconsin, from the Experimental Farm at Davis, California, under the direction of the University of California, and from Ames, Iowa, were used in different quantities, as recorded below. In our early tests we attempted to sterilize the material, but experience showed this to be futile, at least under the ordinary conditions. It is to be noted, however, that in almost every instance, the amount of fungous infection increased with the age of the seeds. This is indicated in all of our experiments. In our first test, 20 grams of oats of the crops of 1904 and of 1911 from the University of Wisconsin were washed with a concentrated aqueous solution of corrosive sublimate, rinsed with boiled distilled water, and then soaked as before in the flasks and the water presently drawn off. The data are in table VIII.

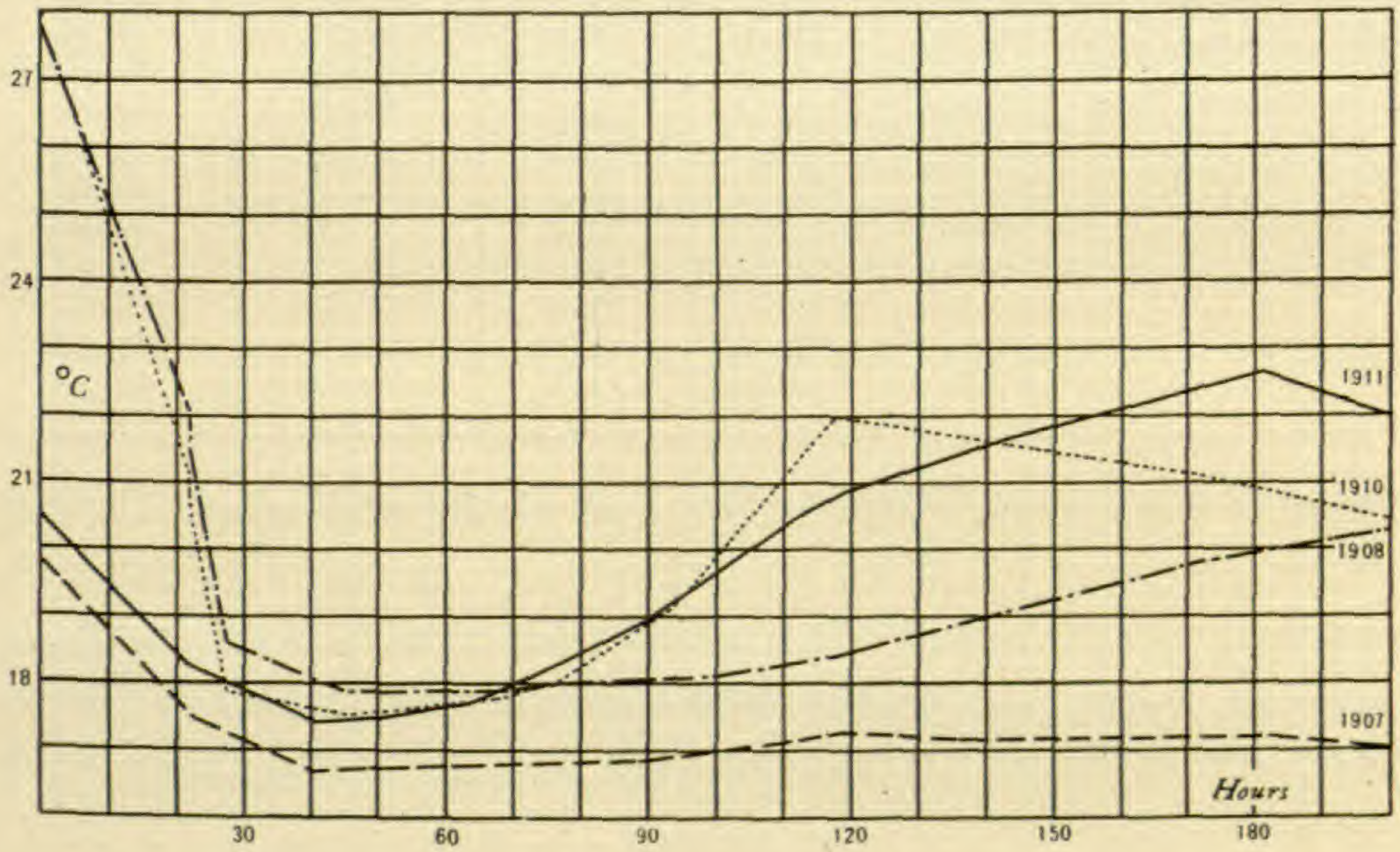

FIG. 8.—Hemp (experiment V): 5.5 grams; broken line, 1907; broken and dotted line, 1908; dotted line, 1910; solid line, 1911.

On opening the flasks recorded in table VIII, one saw that 24.4 per cent of the 1904 seed had germinated, and of these seedlings not more than 2 or 3 per cent had radicles more than 3–4 mm. in length. A trace of blue mold was present. On the other hand, practically all of the 1911 seed had germinated, the radicles were long and vigorous, and there was no evidence of infection.

For purposes of contrast, and as indicating the direct connection between the quality of the seed and the amount of heat which it will liberate on germination, the following record is given in a separate table (IX), instead of being combined, as in some of the other cases, with others. Oats of the seasons of 1907 and 1911, from Davis California, were used. Much dirt and chaff, and many broken grains were present in the lot, but these were removed as carefully as possible. The cleaned residue was then treated with corrosive sublimate solution, and washed with boiled distilled water as before. Without these extra precautions, the results would have been entirely unreliable. The thoroughness with which one of us cleaned the material is indicated by the figures in table IX, the record of 30 grams of seed from each lot.

TABLE VIII

Date	Time	Hours elapsed	Room	1904	1911
February 27.....	4:00 P.M.	....	17°8 C.	18°30 C.	18°20 C.
28.....	4:00 P.M.	24.0	17.7	17.90	17.90
29.....	9:00 A.M.	41.0	17.6	17.85	17.80
29.....	3:30 P.M.	47.5	17.6	17.85	17.80
March 1.....	10:00 A.M.	66.0	17.6	18.00	18.15
1.....	6:30 P.M.	74.5	17.8	18.05	18.40
2.....	11:00 A.M.	91.0	17.7	18.20	19.00
2.....	6:00 P.M.	98.0	17.6	18.25	19.35
3.....	9:30 A.M.	113.5	17.5	18.40	20.10
4.....	9:30 A.M.	137.5	17.4	18.70	21.40
4.....	5:30 P.M.	145.5	17.6	18.70	22.00
5.....	9:00 A.M.	162.0	17.4	19.10	23.10
5.....	4:00 P.M.	169.0	....	19.30	23.50
6.....	3:00 P.M.	192.0	17.6	20.10	24.38

TABLE IX

Date	Time	Hours elapsed	Room	1907	1911
April 3..........	3:30 P.M.	....	18°2 C.	18°30 C.	17°50 C.
4..........	4:30 P.M.	25	17.5	17.70	17.60
6..........	11:30 A.M.	68	17.6	18.00	18.50
8..........	9:30 A.M.	114	....	19.90	21.65
9..........	10:30 A.M.	139	17.6	20.70	24.75
9..........	4:30 P.M.	145	17.5	20.60	25.45
10..........	2:30 P.M.	167	17.5	20.90	27.50

In figs. 9 and 10 are shown the curves constructed on the basis of the records of tables VIII and IX. Allowing for the difference in the weights of the two samples and a correspondingly steeper curve, the difference in these two curves is indicative of the difference in the cleanliness, and the corresponding goodness of the two sets or lots of seeds. It is to be noted, also, that both sets of seeds in this latter test were badly infected with mold. Of the 1907 seeds less than half had germinated; but the 1911 seeds showed nearly 100 per cent germination.

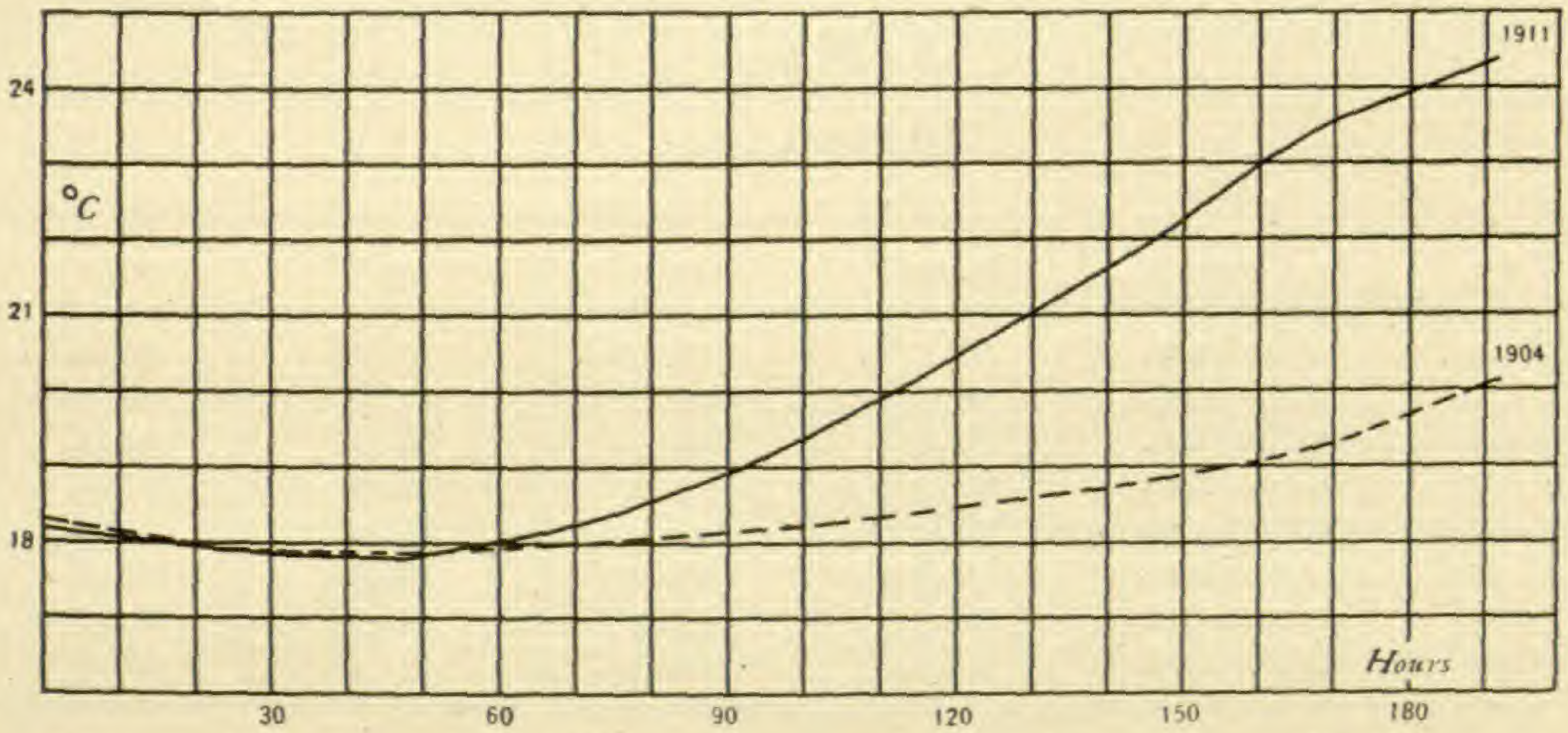

FIG. 9.—Oats (experiment VI): 20 grams; broken line, 1904; solid line, 1911

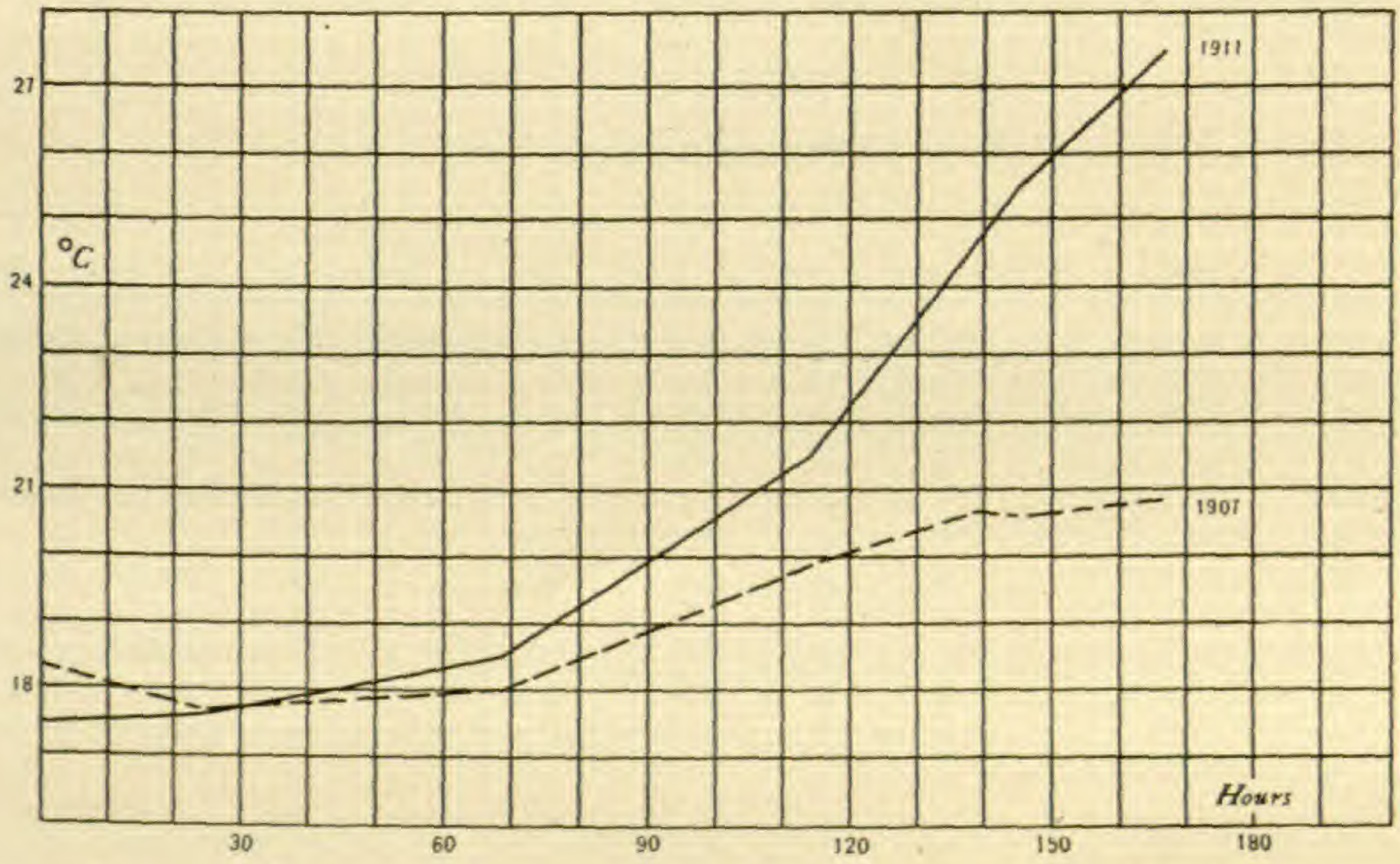

FIG. 10.—Oats (no. 339): 30 grams; broken line, 1907; solid line, 1911

With these records, which show the behavior of certain varieties of oats during the winter following the summer in which they grew, we should compare others made a year later. Except where explicitly stated otherwise, the quantities used were 10 grams of seed. These were selected as well as possible to insure soundness, hulled, washed quickly in a saturated aqueous solution of corrosive sublimate, and rinsed four times in sterile distilled water. They were then put into the Dewar flasks, which had been previously sterilized, together with the thermometers, and covered for 24 hours with sterile distilled water. At the end of this time the water was poured off. The data are given in tables X–XIV.

TABLE X

OATS NO. 444

Date	Time	Room	1909	1910	1911
March 20....	9:00 A.M.	16°5 C.	16°9 C.	17°0 C.	17°0 C.
20....	4:30 P.M.	16.4	17.8	17.6	18.0
21....	9:00 A.M.	16.4	18.7	18.3	19.4
21....	4:30 P.M.	16.4	19.3	18.6	20.5
22....	10:30 A.M.	16.4	21.9	19.9	25.0
22....	4:00 P.M.	16.3	23.0	20.4	26.1
23....	11:00 A.M.	16.3	23.3	22.5	24.7
24....	11:00 A.M.	16.2	20.3	23.3	20.7
Increase in temperature between first and highest readings................			6°4	6°3	9°1

TABLE XI

WISCONSIN OATS

Date	Time	Room	1904	1905	1906	1907	1908	1909	1910	1911
March 26..	6:00 P.M.	16°2C.	16°2C.	16°6C.	16°5C.	16°5C.	16°8C.	16°7C.	16°7C.	16°7C.
27..	9:00 A.M.	16.1	16.9	17.1	16.8	16.9	17.8	17.6	17.2	17.5
27..	4:00 P.M.	16.1	17.0	17.2	16.8	17.0	18.2	18.0	17.4	17.85
28..	9:00 A.M.	16.1	17.3	17.8	17.1	17.4	20.2	19.4	18.0	19.3
28..	4:30 P.M.	16.1	17.6	18.2	17.2	17.7	21.9	20.6	18.4	20.4
29..	9:00 A.M.	16.2	18.3	19.6	17.7	18.5	26.8	14.9	19.6	24.0
29..	6:30 P.M.	16.3	18.9	20.5	18.0	19.2	26.8	28.4	20.5	25.0
30..	11:00 A.M.	16.3	19.8	20.5	18.7	19.7	24.3	30.0	20.8	23.9
30..	7:30 P.M.	16.4	19.9	20.4	18.9	19.7	23.1	28.6	20.6	23.1
31..	9:00 A.M.	16.4	19.7	20.0	18.9	19.6	21.7	26.3	20.3	22.1
Increase in temperature between first and highest readings...............			3°3	3°9	2°4	3°2	10°0	13°3	4°2	8°3

Inspection of table XI will show that the seeds of the crops of 1909 and of 1911 gave considerably higher temperatures than the older seeds of the four years preceding, but the results are not so regular as an average of similar experiments on similar seeds of this and other sorts might give. Not knowing the maturity of the seed when harvested, the manner of its curing and storage, and various other factors which might affect its vigor, we are dependent, in all of these cases, upon the facts of age and vigor as shown by Dewar flask and seed bed. We cannot further account for the differences.

TABLE XII

OATS NO. 293

Date	Time	Room	1907	1908	1909	1910	1911
April 2........	3:00 P.M.	16°.7 C.	17°.2 C.	17°.3 C.	17°.3 C.	17°.2 C.	17°.3 C.
3........	9:00 A.M.	16.7	17.6	17.7	17.6	17.8	18.4
3........	3:00 P.M.	16.6	17.7	17.85	18.75	18.1	18.9
4........	9:00 A.M.	16.7	18.4	18.75	18.5	19.2	21.8
4........	5:00 P.M.	16.7	18.8	19.35	19.0	20.0	24.0
5........	9:30 A.M.	16.6	20.2	20.5	19.4	21.2	27.8
5........	5:00 P.M.	16.7	20.2	20.6	19.4	21.4	27.4
6........	8:00 A.M.	16.7	20.1	20.3	19.15	20.9	24.4
6........	5:00 P.M.	16.7	19.8	19.9	18.9	20.5	22.9
7........	8:00 A.M.	16.6	19.2	19.3	18.6	19.8	21.6
7........	5:00 P.M.	16.7	19.1	19.15	18.5	19.6	21.2
8........	8:00 A.M.	16.9	18.7	18.6	18.3	18.8	20.1
Increase in temperature between first and highest readings................				4°.7	5°.9	4°.2	3°.1

In this and some of the other tests, the first temperature reading in the Dewar flasks was 0°.5–0°.6 higher than the room temperature. This points to the fact that in the preliminary stages of germination, while the seeds were soaking in water, heat was also being liberated. The rate of heat liberation at different stages in germination is not uniform. This one of us will show elsewhere, for it has little to do with the special topic of this paper.

Table XIII shows irregularities which we are unable to account for, since we are unacquainted with the experience of the seeds before they came into our hands; but we include the table for the sake of completeness.

The record of the behavior of seeds of the same ages and varieties in a seed bed, that is, under the usual conditions for germination, will show how well the viability of the seeds is indicated by their heat yields within a comparatively short time after germination is started in Dewar flasks. Fifty kernels were selected from each lot, but on account of the hulls, no attempt was made to sterilize them.

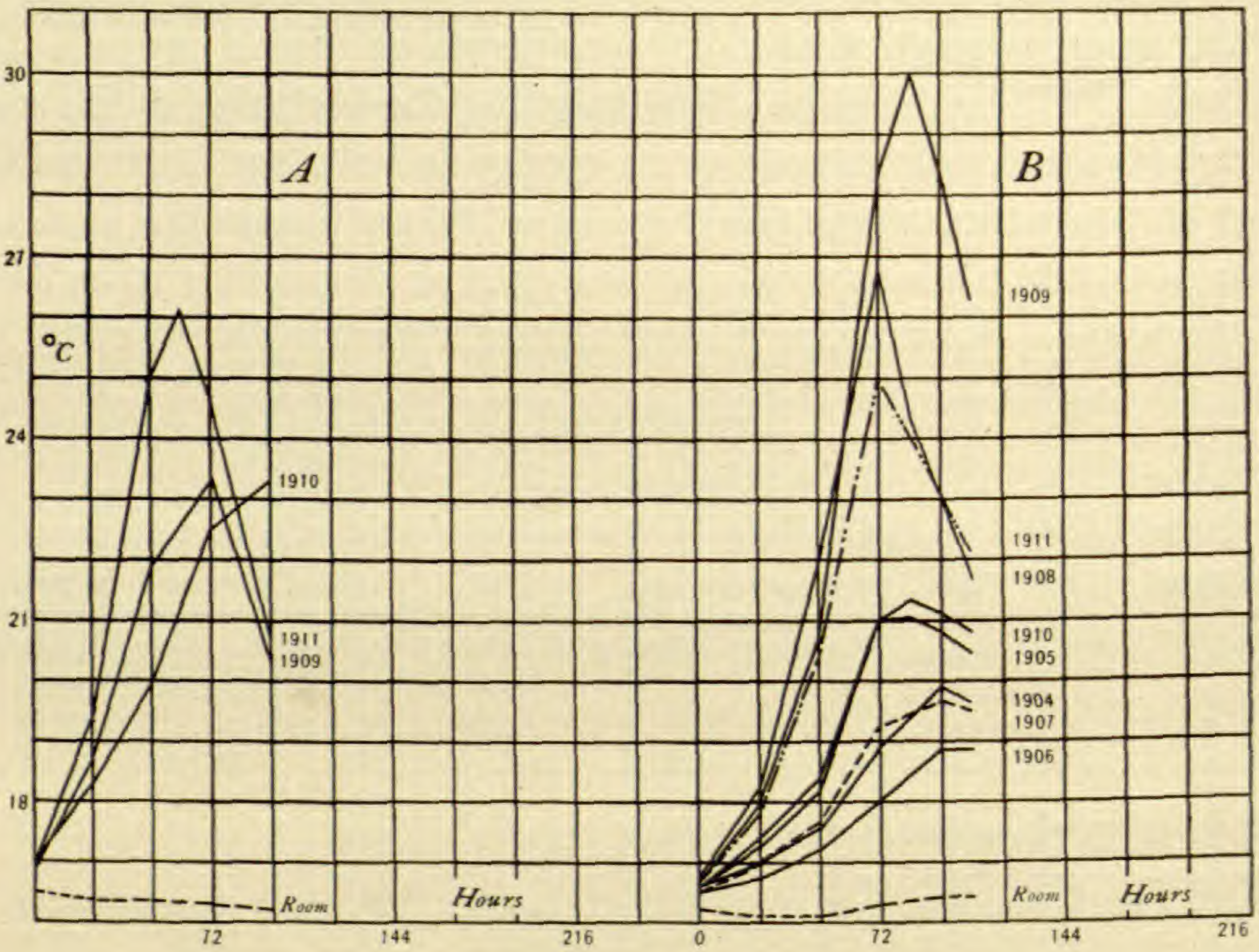

FIG. 11.—Oats in flasks: *A*, no. 444; *B*, Wisconsin

TABLE XIII

OATS NO. 339

Date	Time	Room	1907	1909	1910	1911
April 3....	3:00 P.M.	16°.6 C.	17°.2 C.	17°.2 C.	17°.3 C.	17°.2 C.
4....	9:00 A.M.	16.7	17.9	18.2	18.1	17.7
4....	5:00 P.M.	16.7	18.1	18.6	18.4	18.0
5....	9:30 A.M.	16.6	18.7	20.2	19.2	18.6
5....	5:00 P.M.	16.7	19.0	21.2	19.6	19.0
6....	8:00 A.M.	16.7	20.2	23.0	20.8	19.8
6....	5:00 P.M.	16.7	21.1	23.0	21.3	20.2
7....	8:00 A.M.	16.6	22.6	21.8	21.5	20.3
7....	5:00 P.M.	16.7	22.9	21.2	21.4	20.2
8....	8:00 A.M.	16.9	20.2	19.3	19.5	18.8
Increase in temperature between first and highest readings........			4°.7	5°.9	4°.2	3°.1

TABLE XIV

OATS	YEAR	NUMBER SPROUTING FEBRUARY				PERCENTAGE SPROUTING	LENGTHS OF PLUMULES FEB. 8–9 IN CM.			PERCENTAGE OF GROWTH
		3	4	6	8		Shortest	Longest	Average	
White Probster. . .	1872	0	0	0	0	0	....	....	....	....
	1876	0	0	0	0	0	....	....	....	....
Wisconsin. . . .	1877	0	0	0	0	0	....	....	....	....
	1904	24	38	44	48	96	2.2	12.1	9.12	75
	1905	31	39	42	42	84	1.0	11.8	8.10	67
	1906	5	27	41	46	92	3.1	11.1	7.96	66
	1907	19	27	35	39	78	1.6	11.3	8.44	70
	1908	37	49	49	49	98	8.2	11.9	10.50	87
	1909	30	43	47	48	96	3.7	12.4	9.22	76
	1910	8	25	44	44	88	3.0	12.2	8.03	66
	1911	34	46	50	50	100	7.4	13.3	11.33	94
No. 451.	1907	27	33	37	38	76	2.8	12.9	9.98	82
	1909	39	46	48	49	98	2.6	13.5	10.87	90
	1910	33	37	37	37	74	6.2	15.9	12.04	100
	1911	43	49	49	49	98	8.4	15.9	11.56	96
No. 286.	1907	25	27	28	28	56	7.6	14.6	11.29	93
	1909	34	44	45	46	92	3.9	13.5	11.08	92
	1910	30	40	40	47	82	4.7	14.5	9.60	79
	1911	38	46	47	47	94	5.8	16.0	10.55	39
No. 444.	1909	19	33	45	47	94	3.7	12.6	10.34	85
	1910	18	30	35	39	78	1.7	14.5	9.39	77
No. 293.	1907	27	40	42	44	88	3.8	13.6	9.05	75
	1911	18	37	44	50	100	2.9	14.2	10.13	84
	1908	20	33	42	43	86	5.2	16.2	11.51	95
	1909	14	36	48	49	98	6.4	15.0	10.88	90
	1910	21	40	47	47	94	5.4	16.8	10.92	90
	1911	19	40	50	50	100	6.7	16.3	11.42	94
No. 339.	1907	16	28	35	36	72	3.7	13.4	10.20	84
	1909	5	27	37	41	82	2.3	11.9	9.38	77
	1910	2	11	27	33	66	2.1	12.6	8.37	69
	1911	9	30	49	50	100	3.5	6.2	9.99	82

These were planted in boxes of sterilized sand in the greenhouse, on January 28 and 29, 1913.

Comparison of the behavior of oats of different ages as recorded in tables X–XIV is rendered somewhat easier by figs. 11–14. In these it is plainly shown that the vitality and viability of these seeds is indicated more promptly by the temperatures yielded in Dewar flasks than in seed beds, and that what may properly be called the "normal" temperature for the species is developed, other things being equal, by the youngest and freshest seed. This will come out still more plainly in the following experiment with wheat.

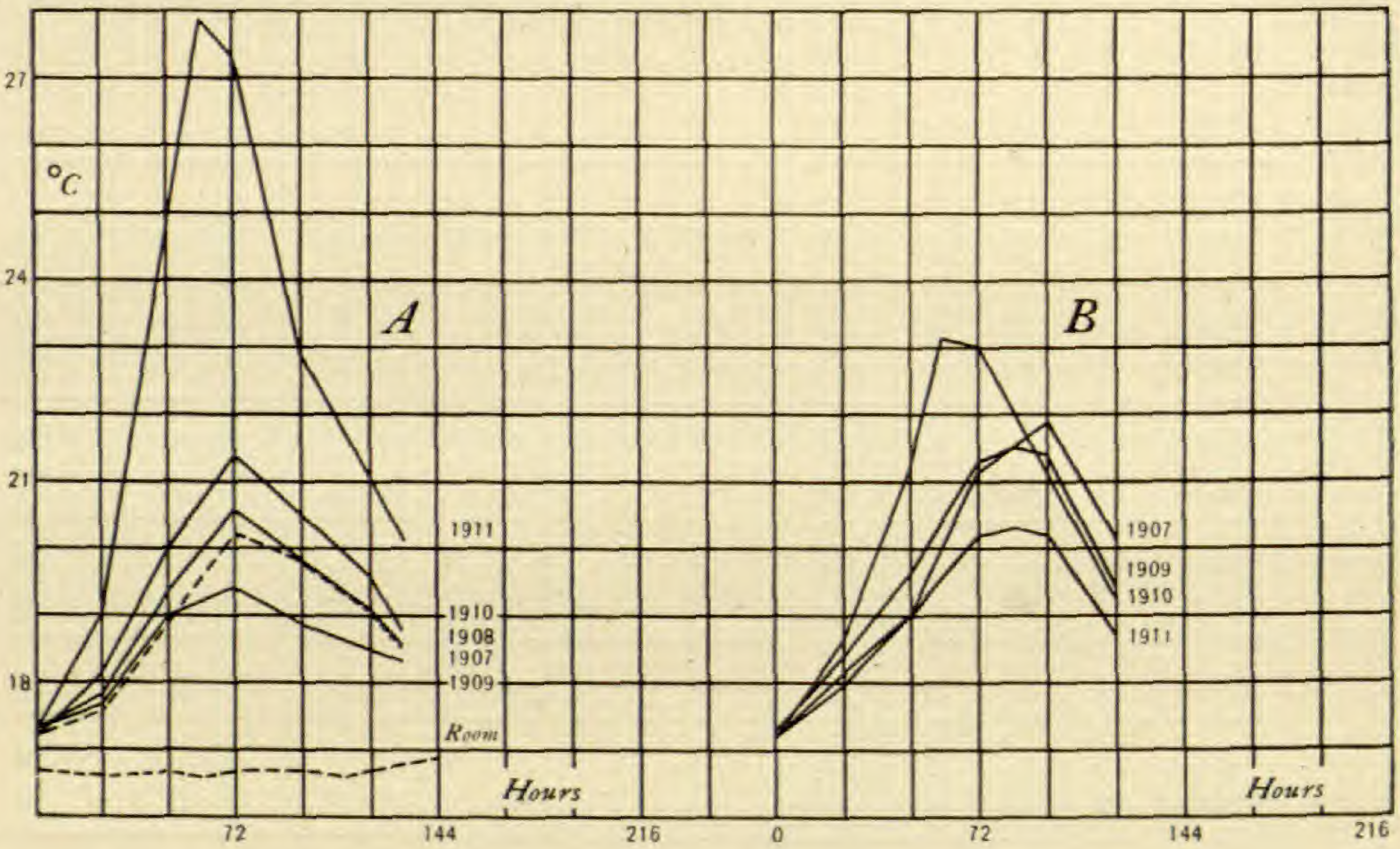

FIG. 12.—Oats in flasks: *A*, no. 293; *B*, no. 339

TABLE XV

Date	Time	Hours elapsed	Room	1907 (no. 1746)	1911
April 3......	3:30 P.M.	....	18°2 C.	16°80 C.	17°10 C.
4......	4:30 P.M.	25	17.5	16.90	17.50
6......	11:30 A.M.	68	17.6	18.60	20.50
8......	9:30 A.M.	114	....	23.80	28.15
9......	10:30 A.M.	139	17.6	26.50	28.00
9......	4:30 P.M.	145	17.5	26.35	27.70
10......	2:30 P.M.	167	17.5	25.15	27.15

EXPERIMENT VII.—Wheat, from the University of California, the University of Wisconsin, and the College of Agriculture at Ames

Iowa, was used in the various quantities recorded below and treated in the various ways there indicated. Our first test was made in April 1912, with 30 grams of seed from the Experimental Farm of the University of California, at Davis, California. The seed was not as clean and whole as one could wish, and there was too much chaff with it. The material was treated with a concen-

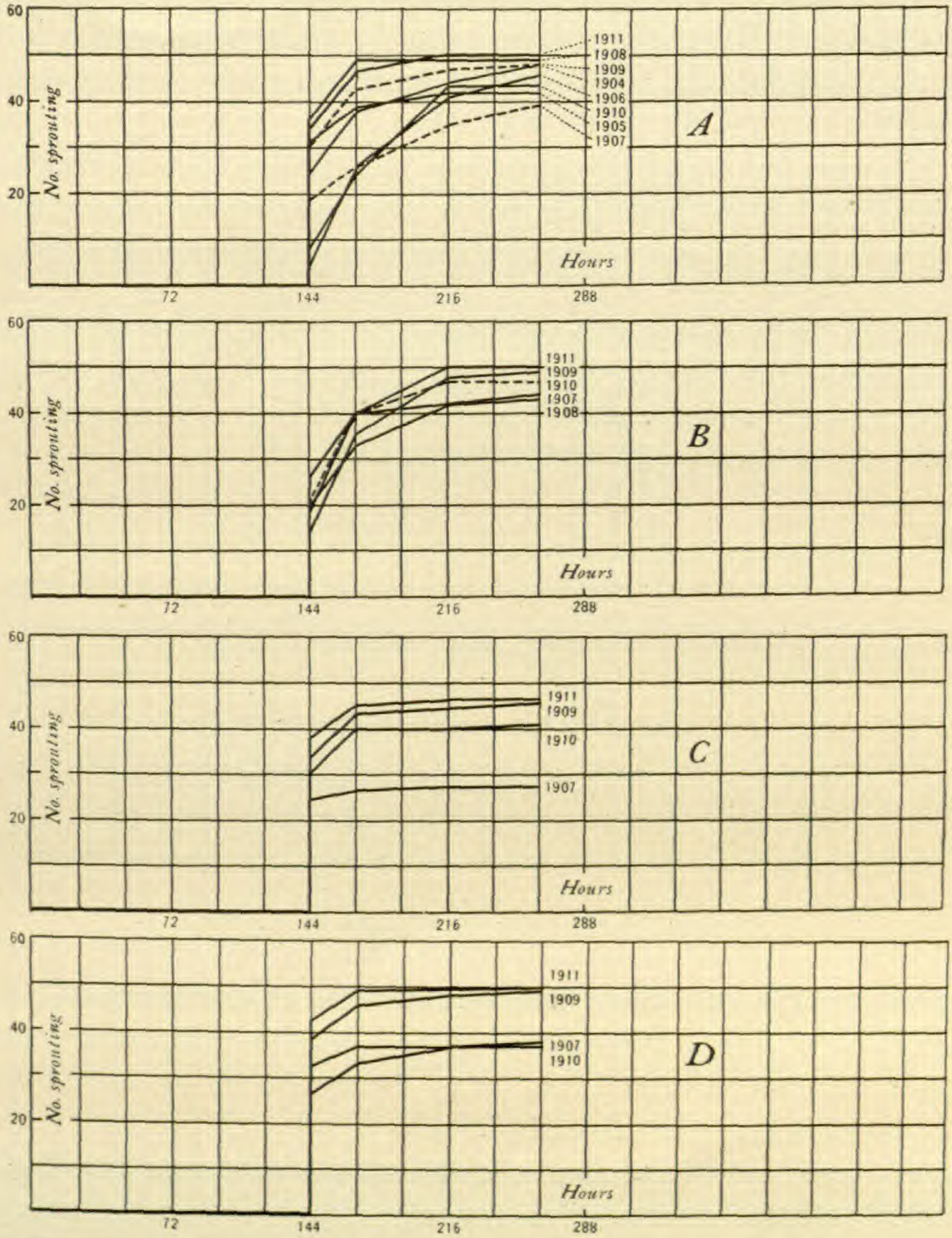

FIG. 13.—Oats in soil: *A*, Wisconsin; *B*, no. 293; *C*, no. 286; *D*, no. 451

trated aqueous solution of corrosive sublimate and then duly washed in sterile distilled water. The record is given in table XV. Upon opening the flasks, the wheat was found to be quite sweet and free from mold. The 1911 seed showed practically 100 per cent germination. The 1907 seed, on a rough estimate, showed only 60 per cent germination. Both lots of seedlings were growing vigorously.

The next test was made upon four sets of wheat seeds, from the same source as the preceding and of the same ages; 30 grams of seed were used in each lot, and all were carefully washed with an aqueous solution of copper sulphate, saturated at room temperature, and rinsed as usual with sterile water. As the results show, the copper sulphate solution was quite ineffective as an antiseptic. The record is given in table XVI.

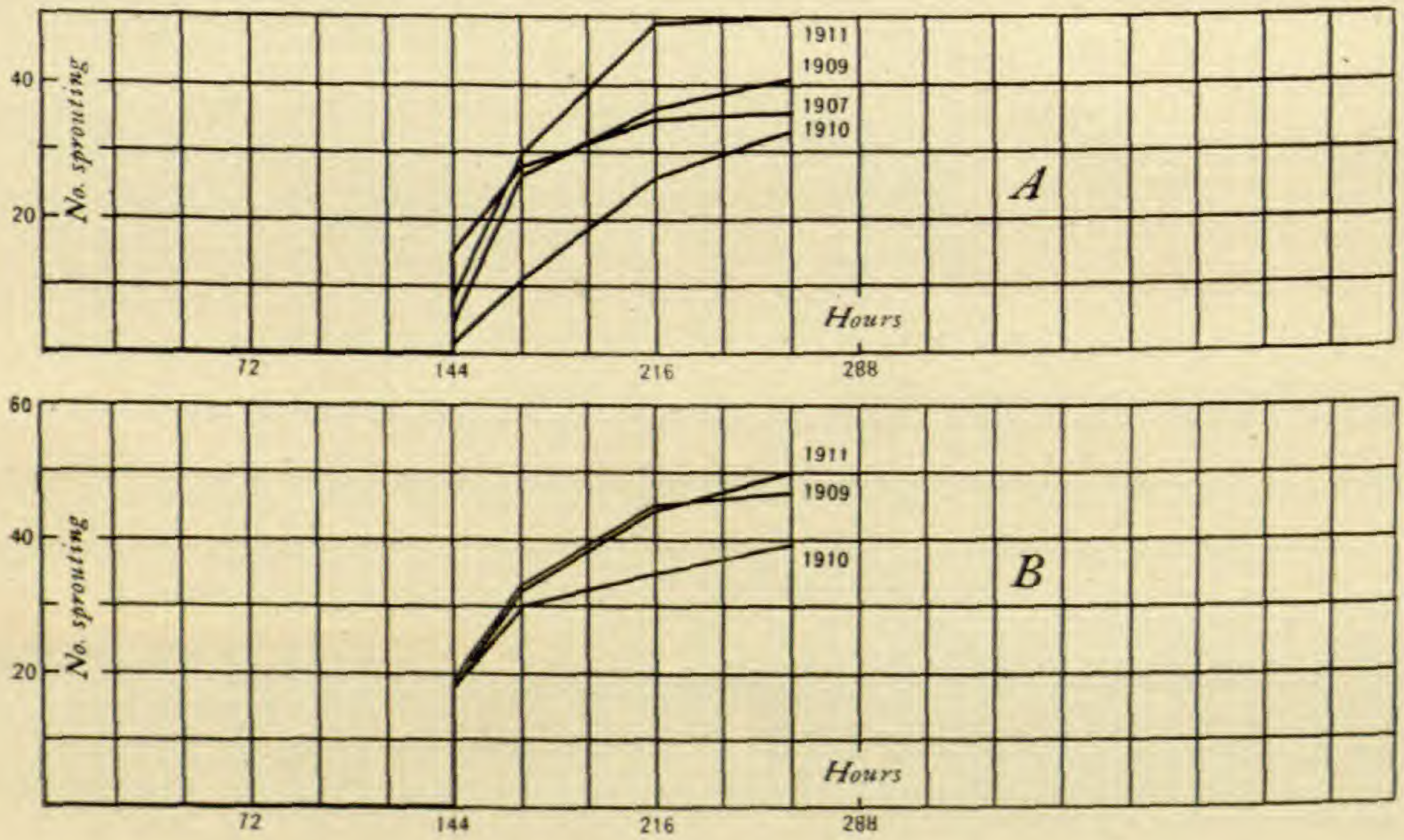

FIG. 14.—Oats in soil: *A*, no. 339; *B*, no. 444

As these last temperatures indicate, the seed was too badly infected with mold (*Mucor*) to give the experiment any other significance than this, namely, that germinating seeds, as well as the higher animals, have temperatures which may be considered "normal" or characteristic; and if the seed under test does not show this temperature, or one not far removed from it, one is justified in concluding that there is something wrong with it. If the temperature is abnormally high, this is due to other organisms also liberating heat in the insulator; if abnormally low, the seed itself is weak. In many cases, at least, this weakness is due to age.

Through the courtesy of Professor PAMMEL, of Ames, Iowa, we had a number of seeds of quite considerable age. We made preliminary germination tests of these while our Dewar flasks were in use, and found that none of the seeds which we had from the crops of 1871 to 1887, inclusive, would germinate under the conditions of our germination boxes. We cannot say that no preservative had been applied to them, but their behavior is entirely consistent with that reported by BECQUEREL and by EWART. BECQUEREL (*loc. cit.*) found that wheat only 34 years old could no longer germinate. EWART (*loc. cit.*) found that out of 750 seeds of wheat 16 years old only 8 per cent could sprout, while in other experiments wheat 12–13 years old showed no vitality. We tested, therefore, only two lots of these oldest seeds in Dewar flasks and, owing to the age and corresponding value of the material, used only small quantities; 5 grams of each of these two lots were carefully selected, cleaned, washed with a sterilizing solution, and then rinsed thoroughly with sterile water. The record is given in table XVII.

TABLE XVI

Date	Time	Hours elapsed	Room	1907 (no. 114)	1911	1907 (no. 639)	1911
April 16......	3:00 P.M.	....	18°0 C.	....	....	....	....
17......	3:00 P.M.	24	18.0	19°10 C.	19°45 C.	20°00 C.	18°60 C.
18......	2:30 P.M.	47.5	18.0	18.00	19.20	19.90	19.15
19......	12:00 M.	69.5	18.0	18.40	21.00	21.35	21.20
20......	10:30 A.M.	92	17.5	19.00	24.25	23.40	24.60
21......	10:30 A.M.	116	17.5	21.40	31.00	27.00	26.95
23......	2:00 P.M.	167.5	....	38.80	44.20	37.00	42.90

From these figures it is apparent that one can ascertain whether seeds will germinate under ordinary conditions by moistening them duly and keeping them for a time under known conditions of temperature in Dewar flasks. If, within a reasonable length of time there is no rise in temperature or a rise which does not indicate a "normal" temperature for the species concerned, one may conclude that the seed will not germinate. It goes almost without saying that the time which must elapse before such a conclusion is justified varies with the species, as does the "normal" temperature.

TABLE XVII

Date	Time	Room	Talaverra spring wheat, 1871	California white spring wheat, 1872
December 12....	11:30 A.M.	19°0 C.	18°1 C.	17°6 C.
13....	1:30 P.M.	19.0	18.1	17.6
14....	9:00 A.M.	18.75	18.1	17.6
14....	4:30 P.M.	18.75	18.1	17.6
15....	4:00 P.M.	18.5	18.1	17.6
16....	1:00 P.M.	18.5	18.0	17.6
17....	2:00 P.M.	18.5	18.0	17.5
18....	12:00 M.	18.5	17.95	17.5
20....	3:00 P.M.	19.0	17.9	17.4

Table XVIII records the temperatures developed in silvered Dewar flasks by three lots of wheat of the same variety, marked no. 791, of the crops of 1909, 1910, 1911; 10 grams of each lot were used, being washed and soaked in the usual ways. As the table shows, the rise in temperature of the 1911 seed was much more prompt and rapid than in the other lots, and more rapid in the seed of 1910 than in that of 1909. The maximum temperatures

TABLE XVIII

Date	Time	Room	1909	1910	1911
February 5..	1:30 P.M.	17°5 C.	16°7 C.	16°7 C.	16°8 C.
6..	10:00 A.M.	17.0	16.7	16.8	17.3
6..	1:30 P.M.	17.0	16.8	16.9	17.4
6..	4:30 P.M.	17.0	16.9	17.0	17.4
7..	8:30 A.M.	17.0	17.0	17.2	17.7
7..	5:30 P.M.	17.25	17.1	17.3	18.3
8..	9:30 A.M.	17.0	17.3	17.6	19.2
8..	1:30 P.M.	17.25	17.3	17.7	19.4
8..	4:30 P.M.	17.0	17.4	17.7	19.5
9..	2:00 P.M.	17.25	17.7	18.1	20.0 ✓
10..	8:30 A.M.	17.0	18.1	18.6	19.7
10..	4:00 P.M.	17.0	18.2	18.7	19.6
11..	8:30 A.M.	17.0	18.3	18.9	19.3
11..	4:30 P.M.	17.0	18.3	19.0	19.2
12..	8:30 A.M.	17.0	18.3	19.0	18.9
12..	4:30 P.M.	17.0	18.2	19.0 ✓	18.8
13..	8:30 A.M.	17.0	18.1	18.8	18.7
Increase in temperature between first and highest readings................			1°6	2°3	3°2

increased correspondingly regularly from 1909 to 1911, and the maximum is reached more than 42 hours earlier in the 1911 seed than in the other two. In this connection it should be stated that, as will be shown later, the comparative viability of the different lots of seed is indicated in the Dewar flasks within 24–48 hours, whereas the seed planted in soil showed nothing within 72 hours. Had there been older seed than that of 1909, the delay in soil would have been still greater in proportion. The data of the flask test are given in table XVIII.

The increasing heat yield, indicated in the last line of table XVIII, is quite as striking in regularity as the increasing percentage of germination for the crops of the years 1909, 1910, 1911, as recorded in the table of germinations following. This is shown again, and for another variety of wheat, in table XIX.

TABLE XIX

Date	Time	Room	1909	1910	1911
February 6..	1:30 P.M.	17°.0 C.	16°.6 C.	16°.3 C.	16°.7 C.
6..	4:30 P.M.	17	16.8	16.4	16.9
7..	8:30 A.M.	17	17.1	16.5	17.3
7..	5:30 P.M.	17.25	17.2	16.65	17.5
8..	9:30 A.M.	17	17.5	16.8	17.9
8..	1:30 P.M.	17.25	17.5	16.8	18.0
8..	4:30 P.M.	17	17.6	16.9	18.0
9..	2:00 P.M.	17.25	17.8	17.0	18.5
10..	8:30 A.M.	17	18.2	17.2	19.1
10..	4:00 P.M.	17	18.3	17.3	19.3
11..	8:30 A.M.	17	18.5	17.4	19.8
11..	4:30 P.M.	17	18.6	17.5	19.9
12..	8:30 A.M.	17	18.7	17.6	19.9
12..	4:30 P.M.	17	18.8	17.7	19.9
13..	8:30 A.M.	17	18.8	17.75	19.8
Increase in temperature between first and highest readings................			2°.2	1°.45	3°.2

Ten grams of each harvest, 1909 to 1911, inclusive, of wheat no. 98, were treated in the usual way and placed in Dewar flasks. The figures are given in table XIX.

For some unknown reason, the seeds of the 1910 lot started at a disadvantage, the temperature in the flask in which they were contained (flask no. 5) being 0°.3–0°.4 lower than in the other two. Nevertheless, the temperatures behave as in the preceding experiments, rising more rapidly and to a higher point in the flask containing the freshest seed, and the rise beginning more promptly among the freshest seed, the other seeds lagging more and more according to their ages. In 24 and 48 hours marked differences in viablility are indicated in the flasks which did not appear in the seed beds until 72 hours had elapsed.

In order to test the quality of flask no. 5, which had been used in the preceding experiment with seed not the freshest, we set up another experiment in the same way as the preceding, using another variety of wheat, no. 1746, of which we had material from 1907 to 1911, inclusive, and putting the freshest and therefore presumably the best in this flask. As before, the temperature in the flask was lower throughout this experiment than in the others. From this we can only infer the inferior quality of this particular flask. The data are given in table XX. Except for the behavior of this particular flask, this experiment conforms to the rule which the preceding tests have indicated, namely that the freshest seeds are also the most vigorous. This is confirmed still further by the germinations in the seed bed.

TABLE XX

Date	Time	Room	1907	1908	1909	1910	1911
February 15..	12:00 P.M.	17°5 C.	16°8 C.	16°8 C.	16°8 C.	16°8 C.	16°4 C.
15..	4:00 P.M.	17.1	16.9	16.9	16.9	17.0	16.5
16..	9:00 A.M.	17.1	17.0	17.1	17.2	17.3	16.7
16..	5:00 P.M.	17.1	17.1	17.2	17.3	17.5	16.8
17..	8:30 A.M.	17.1	17.3	17.3	17.6	17.9	17.0
17..	12:00 M.	17.1	17.3	17.3	17.65	18.0	17.05
17..	4:30 P.M.	17.1	17.4	17.4	17.7	18.1	17.1
18..	8:30 A.M.	17.1	17.5	17.5	18.1	18.7	17.4
18..	4:00 P.M.	17.1	17.6	17.55	18.3	19.0	17.6
19..	8:30 A.M.	17.1	17.7	17.7	18.8	19.7	18.0
19..	4:30 P.M.	17.1	17.7	17.8	19.0	20.0	18.2
20..	9:00 A.M.	17.1	17.75	18.0	19.5	20.4	18.7
20..	6:30 P.M.	17.1	17.8	18.2	19.7	20.4	18.8
21..	8:30 A.M.	17.1	17.8	18.4	19.8	20.4	18.8
21..	4:30 P.M.	17.8	18.4	18.4	19.8	20.4	18.8
22..	9:45 A.M.	17.1	17.7	18.5	19.8	20.2	18.8
Increase in temperature between first and highest readings			1°0	1°7	3°0	3°6	2°4

A series of seeds, no. 639, also including the crops of 5 years, but in flasks of uniformly better quality, is reported upon in table XXI, the quantities and the preliminary treatment of the seed being the same as before.

TABLE XXI

Date	Time	Room	1907	1908	1909	1910	1911
March 11	8:30 A.M.	17°.0 C.	17°.2 C.	17°.2 C.	17°.1 C.	17°.1 C.	17°.4 C.
11	3:00 P.M.	16.7	17.3	17.4	17.4	17.4	17.4
12	8:30 A.M.	16.5	17.4	17.5	17.7	18.1	18.2
12	4:30 P.M.	16.55	17.5	17.6	17.9	18.5	18.6
13	8:15 A.M.	16.5	17.7	17.8	18.3	19.85	19.9
13	4:30 P.M.	16.5	17.9	18.1	18.6	20.8	20.9
14	8:30 A.M.	16.5	18.2	18.8	19.6	21.3	22.5
14	4:30 P.M.	16.5	18.4	19.0	20.0	21.1	22.7
16	9:00 A.M.	16.5	18.6	19.7	20.3	20.3	21.2
17	9:00 A.M.	16.5	18.6	20.1	20.2	20.5	21.0
Increase in temperature between first and highest readings			1°.4	2°.9	3°.2	4°.2	5°.1

The high room temperature at the beginning of this test was undoubtedly due to the presence of the experimenter and to the electric light (32 candle-power, carbon filament) which was in use for some little time.

For the sake of completeness, we include also table XXII, showing the behavior of wheat no. 114, of the crops of 1907, 1909, 1910, 1911, under conditions similar to those of the foregoing tests.

TABLE XXII

Date	Time	Room	1907	1909	1910	1911
March 18	11:00 A.M.	17°.2 C.	17°.05C.	17°.1 C.	17°.1 C.	17°.1 C.
18	4:30 P.M.	16.5	17.1	17.1	17.2	17.1
19	9:00 A.M.	16.5	17.2	17.2	17.7	17.4
19	6:00 P.M.	16.5	17.3	17.3	18.0	17.6
20	9:00 A.M.	16.5	17.5	17.6	18.3	17.95
20	4:30 P.M.	16.4	17.6	17.7	18.4	18.2
21	9:00 A.M.	16.4	17.9	17.7	18.5	18.5
21	4:30 P.M.	16.4	17.9	17.7	18.5	18.5
22	10:30 A.M.	16.4	18.1	17.8	18.35	18.4
22	4:00 P.M.	16.3	18.2	17.8	18.3	18.4
23	11:00 A.M.	16.3	18.3	17.8	18.2	18.2
24	10:00 A.M.	16.2	18.5	17.6	17.9	17.9
Increase in temperature between first and highest readings			1°.45	0°.7	1°.4	1°.4

For a comparison of these respiration temperatures with the actual percentages of germination under the usual conditions, we selected 50 good kernels of the crop of each year, from 1907 to 1911, inclusive, of the different varieties which had been tested in Dewar flasks, as the preceding records show. These seeds were quickly washed in a saturated aqueous solution of corrosive sublimate and rinsed four times in boiled distilled water. They were then soaked for 24 hours in distilled water and planted, on January 16 and 17, 1913, in shallow boxes of sand. These boxes contained sand and had previously been steamed for three hours in an Arnold steam sterilizer and thereupon allowed to cool. Pending the germination of the seeds, these boxes stood on the benches in the greenhouse. In the last four columns to the right, in table XXIII, will be found the measurements and the percentage of growth of the plumules of the seedlings from the seeds of different ages. These percentages were obtained by using the longest plumules as an arbitrary standard for comparison. In addition, therefore, to the information regarding actual germination which this table gives, we have also a record of the amounts of growth in length of these seedlings. These figures show that the older seed is not only slower in germinating and that there are fewer germinating seeds the older the seed is, but also that the seedlings, when the seed does germinate, are inferior in size to those from fresher seed, even when grown under the same conditions. The temperatures developed, therefore, within a short time in such an excellent insulator as a silvered Dewar flask, indicate plainly the values of the lots of seeds sampled. It would have been interesting for us to follow the later development of these seedlings of different ages, and to compare the harvests from the different lots, but the conditions of our experiments were such that this was not at the time possible. Table XXIII, supplementing the figures of previous tables showing the results of our Dewar flask experiments, shows the percentages of germination and also the percentages of growth immediately following germination.

Inspection of table XXIII shows an almost surprisingly regular decrease in the number of seeds sprouting as the age of the seed increases. This is plainest in the varieties numbered 791 and 98. The reasons for the less regularity in the other three varieties are not known to us. We have already pointed out that the different flasks are not equally perfect insulators, and that the various conditions of harvesting and storage would also affect the results. Nevertheless, it is plain that the evidence of Dewar flask and of seed bed are quite consistent. Germination is increasingly tardy the older the seed. Furthermore, the percentages of growth, as shown by the lengths of the plumule, accord perfectly with the percentages of germination and correspond with the temperatures attained in the flasks. In varieties numbered 791 and 98, for example, there is the same regular decrease in growth as in

TABLE XXIII

WHEAT	YEAR	NO. OF KERNELS	NO. SPROUTING JANUARY		PER CENTAGE SPR. JAN. 27	LENGTHS OF PLUMULES IN CM. JANUARY 27–28			
			25	27		Shortest	Longest	Average	Percentage of growth
Talaverra spring..	1871	50	......	......	0	......	......	......	......
California white spring.........	1872	50	......	......	0	......	......	......	......
No. 791..........	1909	50	45	46	92	0.4	7.0	4.75	74
	1910	50	47	47	94	1.0	8.1	5.67	88
	1911	50	47	49	98	1.1	8.5	5.95	92
No. 98..........	1909	50	28	35	70	0.3	6.8	3.73	58
	1910	50	33	36	72	0.2	7.8	4.28	66
	1911	50	34	41	82	1.0	7.1	4.63	72
	1876	50	......	......	Jan. 30 0	......	......	......	......
No. 1746........	1907	50	27	29	58	0.7	7.3	3.62	56
	1908	50	6	6	12	1.4	8.8	6.41	100
	1909	50	36	45	90	0.3	8.5	3.46	53
	1910	50	36	38	76	0.3	8.1	2.81	43
	1911	50	39	43	86	1.3	8.5	5.35	83
No. 639.........	1907	50	26	26	52	0.2	6.2	2.66	32
	1908	50	15	18	36	0.2	3.4	1.20	18
	1909	50	26	29	58	0.3	6.5	2.49	38
	1910	50	41	42	84	0.4	7.3	2.71	42
	1911	50	50	50	100	0.2	7.4	2.41	37
No. 114.........	1907	50	34	36	72	0.2	6.2	2.75	42
	1909	50	43	44	88	0.6	6.9	3.84	59
	1910	50	42	44	88	1.0	6.0	2.94	45
	1911	50	44	44	88	0.3	8.2	3.32	51
	1876	50	......	......	0	......	......	......	......
	1876	50	......	......	0	......	......	......	......
	1876	50	......	......	0	......	......	......	......
Central Kansas I	1877	50	0	0	0	0	0	0	0
Central Kansas II	1877	50	0	0	0	0	0	0	0
Iowa white winter	1887	50	......	......	0	......	......	......	......

germination with the increasing age of the seed. The younger and more viable seeds sprout more promptly and produce a greater early growth than the older ones. The accompanying graphs (figs. 15–17) facilitate a comparison of the results as indicated in the foregoing tables.

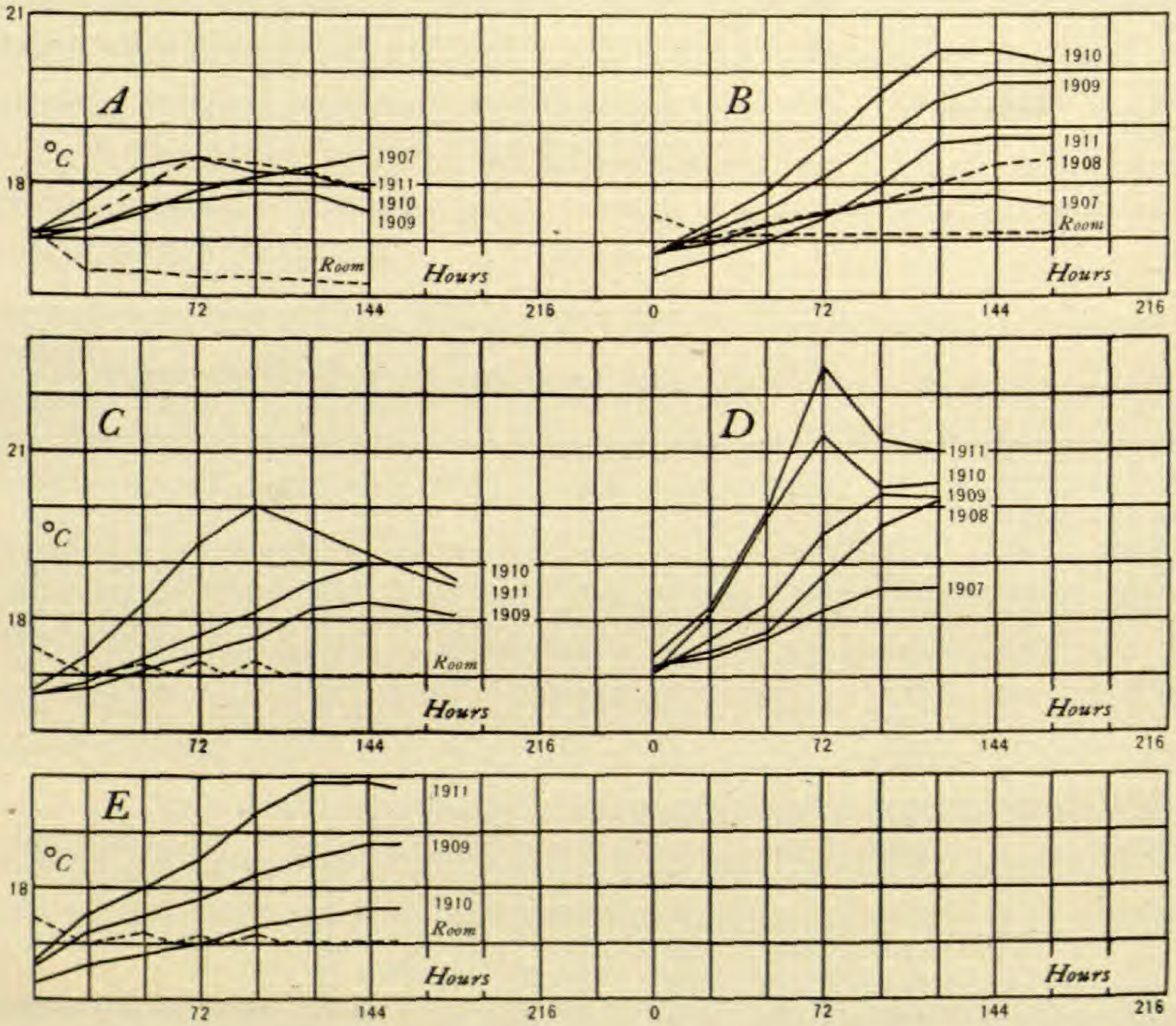

FIG. 15.—Wheat in flasks: *A*, no. 114; *B*, no. 1746; *C*, no. 791; *D*, no. 639; *E*, no. 98.

Summary

Our experiments with seeds of different known ages indicate that one may readily ascertain the quality of these seeds, that is, their germinating power or viability, and the vigor of their growth immediately following germination, by determining the temperatures which they will develop in silvered Dewar flasks under conditions suitable for germination.

Each species of plant which we have studied appears to have, like the higher animals, a "normal" temperature, departures from

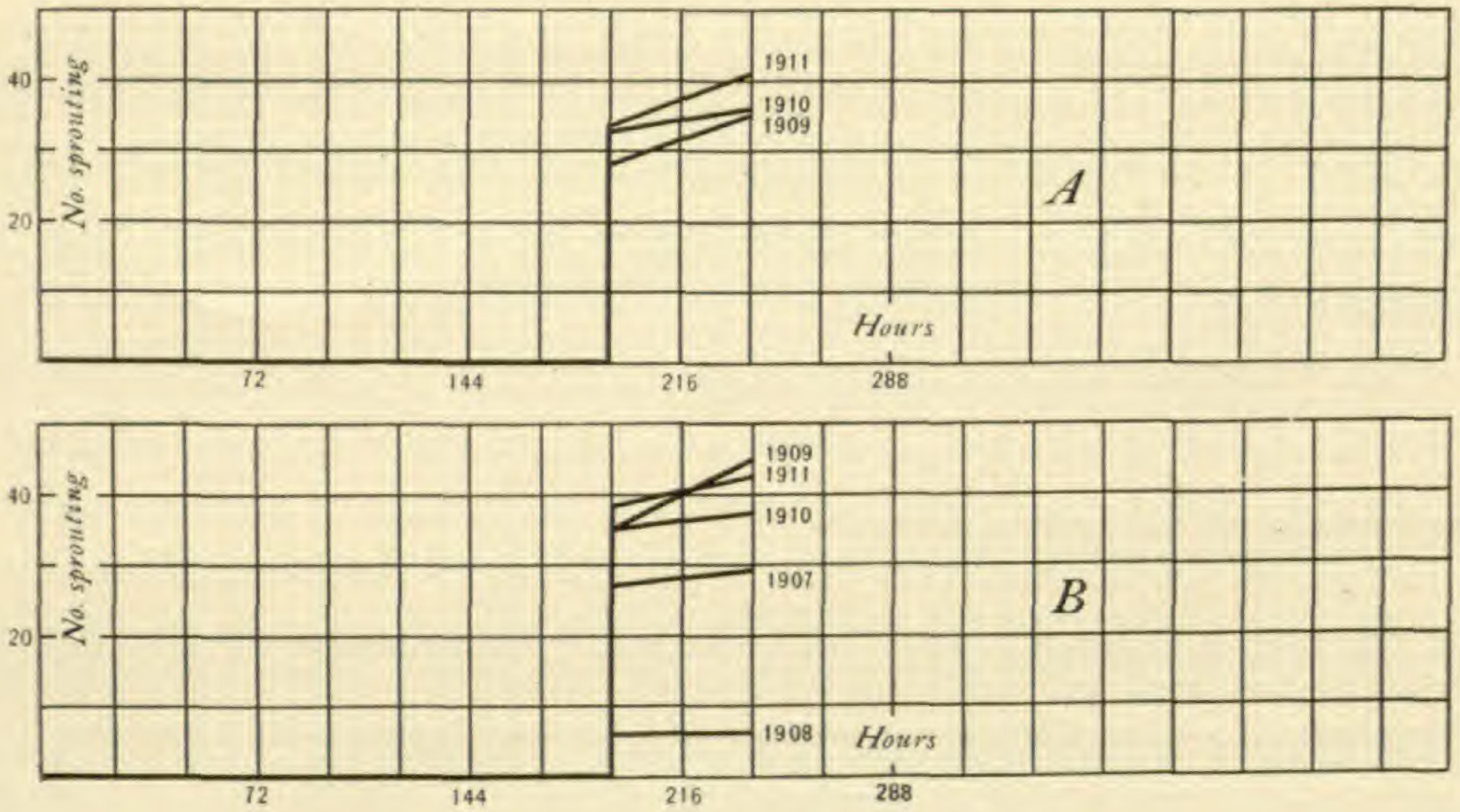

FIG. 16.—Wheat in soil: *A*, no. 98; *B*, no. 1746

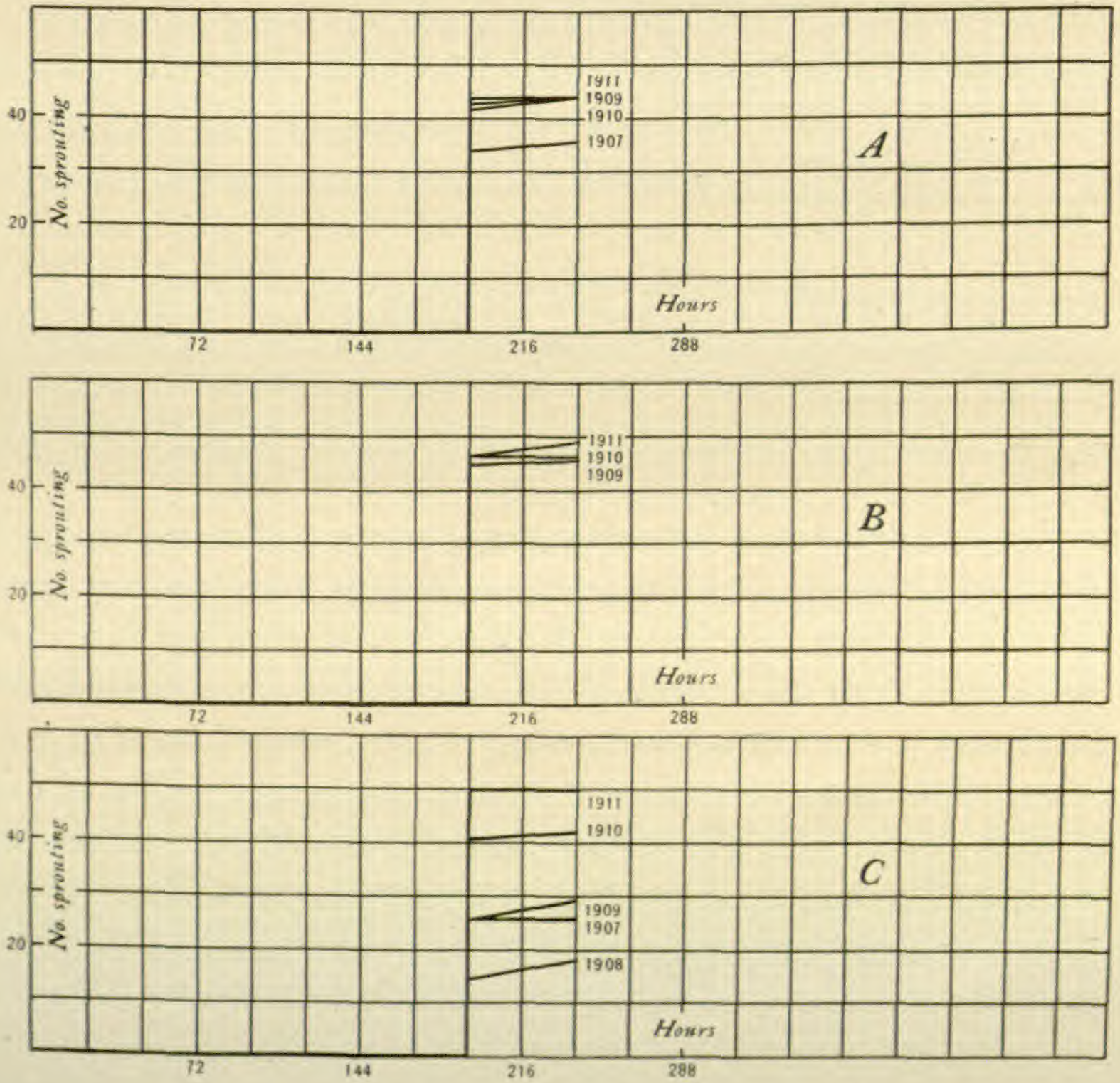

FIG. 17.—Wheat in soil: *A*, no. 114; *B*, no. 791; *C*, no. 639

which indicate departures from the best condition of the organism. A temperature in excess of the normal generally indicates an infection; a subnormal temperature, on the other hand, indicates lessened vigor. Decreased vigor is very generally due to increased age.

This "normal temperature" has been worked out graphically for some of our seeds and is shown in fig. 18, in which is indicated the average daily heat yield, in terms of 10 grams of seed of different sorts, all of them from the crop of 1911 and experimented with in the academic year 1911–1912. Inspection of the figure shows, for example, that a temperature curve indicating normal germinating power in oats would mean less than 50 per cent germination if given by an equal quantity of barley.

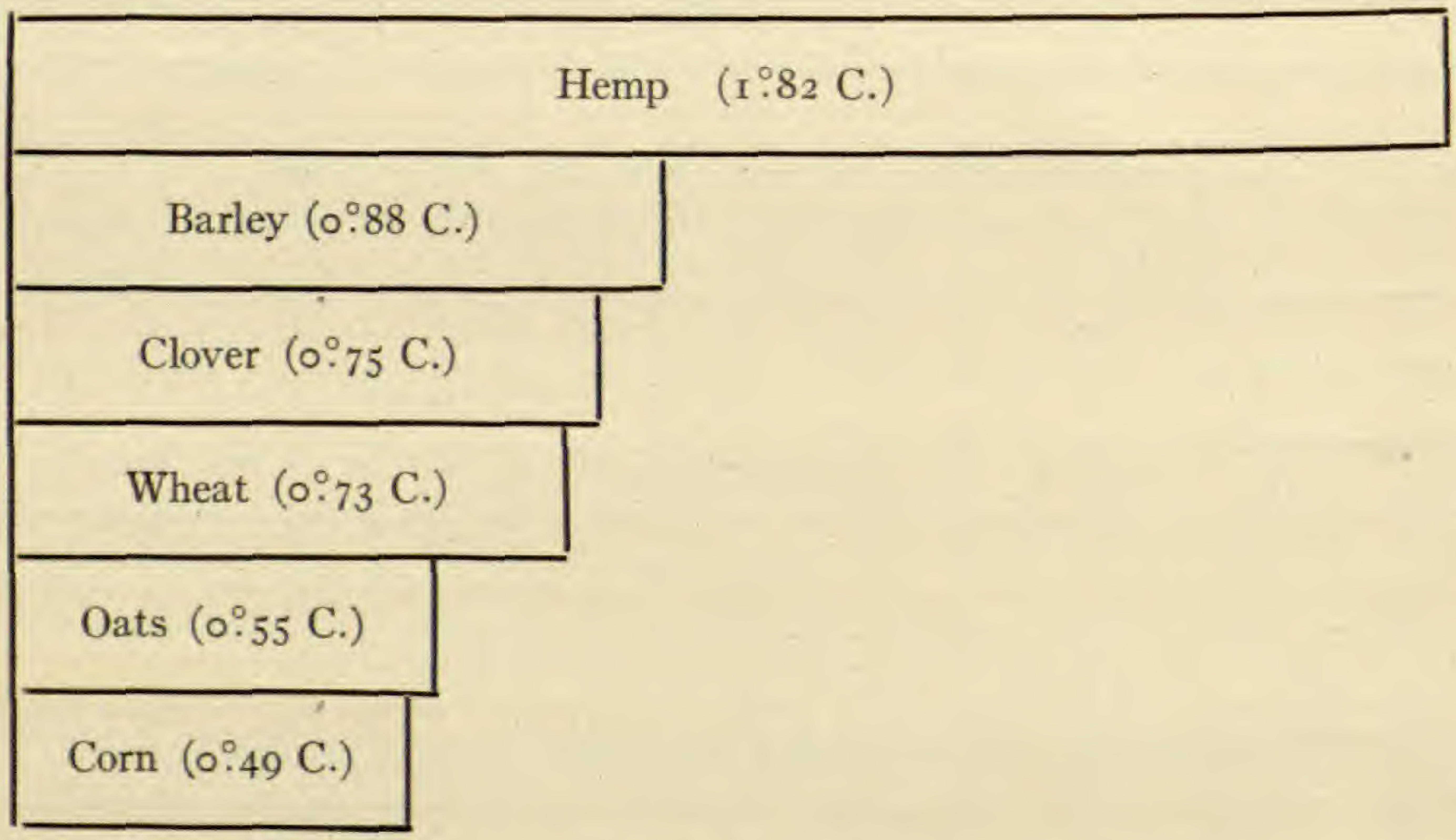

FIG. 18.—Showing the average daily heat yield in terms of 10 grams; 1911 seed

Departures from the "normal" temperatures are accompanied by differences in the amounts of growth immediately following germination. This may be true of the other stages in the life of the plant, as is the case in the higher animals, though the nature of our experiments does no more than suggest this possibility.

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THE DEVELOPMENT OF THE EMBRYO SAC IN THE CONVALLARIACEAE

F. McALLISTER

(WITH PLATES VI AND VII)

The family Convallariaceae as used by BRITTON (2) is the equivalent of the family Asparagoideae as it is used by ENGLER and PRANTL (12). GRAY'S *New manual* (20) has not made use of either of the above family names, but has distributed the 10 genera occurring within the family in the tribes Polygonateae and Parideae. In this paper I shall refer to this group of genera as the Convallariaceae.

Of the 10 genera of the Convallariaceae occurring in the northeastern part of the United States, *Clintonia* has been investigated by SMITH (23), *Convallaria* by WIEGAND (24), *Trillium grandiflorum* by ERNST (13), and *T. recurvatum* by COULTER and CHAMBERLAIN (11). I have in earlier papers reported on *Smilacina stellata* (18) and *S. racemosa* (19), and in this paper report my investigations on *Maianthemum*, *Streptopus*, *Polygonatum*, and *Medeola*. The only genera occurring within this range which have thus far not been reported upon are *Asparagus* and *Disporum*.

Much of this work on the Convallariaceae was carried on at Beloit College during the years 1907 and 1908. Material for the study of *Smilacina stellata*, *S. racemosa*, *Polygonatum commutatum*, and *Maianthemum canadense* were collected in the vicinity of Beloit, Wisconsin. Professor W. J. V. OSTERHOUT kindly supplied me with fixed material of *Smilacina sessifolia* from the vicinity of Berkeley, California, and Professor H. D. DENSMORE very generously turned over to me considerable material of *Smilacina amplexicaulis* which he had collected and fixed in California. I am indebted to Mr. R. E. WEBSTER for material of *Clintonia borealis* from the vicinity of Iron Mountain, Michigan. Flowers of *Streptopus roseus* and *Medeola virginica* were collected and fixed in the vicinity of Ithaca, New York, in the spring of 1912.

The publication of these results has been delayed from time to time, partly owing to the press of other work and partly through the hope of including other members of the group in this report.

I have reviewed in another connection (18) the scanty literature on the development of the embryo sac among members of the Convallariaceae. Two accounts of the development of the embryo sac of *Convallaria majalis* differ radically as to the fate of the first four nuclei resulting from the division of the nucleus of the mother cell. According to WIEGAND's account (24), all 4 of these nuclei enter into the structure of the mature embryo sac, while SCHNIEWIND-THIES (21) reports that but one of 4 megaspores enters into the structure of the embryo sac.

ERNST (13) reports that in *Trillium grandiflorum* the inner of the 2 cells resulting from the heterotypic division develops into the embryo sac, while CHAMBERLAIN (9) finds that in *Trillium recurvatum* the inner of 4 megaspores develops into the embryo sac. ERNST (13) also found that in *Paris quadrifolia* the inner of the first 2 cells arising from the first division of the mother cell formed the mature embryo sac by three divisions of its nucleus, as was the case in *Trillium grandiflorum*.

In the paper referred to above (18) I have shown that in *Smilacina stellata* the megaspore mother cell divides to form 4 fully separated megaspores, and that the separating membranes later disappear, forming thus a tetranucleate cell, from which, by one division of its 4 nuclei, the mature embryo sac is formed.

Since the publication of the above-mentioned paper, one other member of the family has been reported upon. According to SMITH (23), the reduction divisions of the megaspore mother cell of *Clintonia borealis* result in the formation of a tetranucleate cell, the outermost nucleus of which is plump and normal, while the remaining 3 inner nuclei are shrunken and disorganized. The outermost nucleus divides twice, and 3 of the resulting 4 nuclei organize an apparently normal egg apparatus, while the remaining nucleus serves as the single polar nucleus. I have been able to confirm SMITH's results from material collected in the vicinity of Iron Mountain, Michigan, a few sections of which I had already prepared at the time of the publication of his results.

My work on the embryo sac of *Smilacina racemosa* (**19**) has shown that in closely related species of the same genus a marked difference may exist in the origin of the nuclei entering into the structure of the embryo sac. In *S. racemosa* the mother cell divides unequally, forming a large outer and a small inner cell. Later stages show the division membrane to be permanent. From the outer cell the 8 nuclei of the mature embryo sac are formed by three divisions. Split cell membranes separate for a short time the two pairs of nuclei resulting from the division of the heterotypic daughter nuclei (figs. 28, 29). The nucleus of the small inner cell divides but once, and the 2 resulting nuclei gradually degenerate. The embryo sac in *S. racemosa* is thus formed from the 2 outer of the 4 potential megaspores. *S. stellata* (**18**), on the other hand, forms its embryo sac from 4 megaspores which become merged in one 4-nucleate cell by the disappearance of the partition membranes.

Smilacina sessifolia

As cited above, the embryo sac of *S. stellata* is formed from 4 fully separated megaspores which become merged in one cell, one further division of the 4 nuclei forming the 8-nucleate embryo sac (figs. 26, 27). Three divisions of the nucleus of the megaspore mother cell thus produce the necessary number of nuclei for the mature embryo sac, as in cases of the so-called *Lilium* type of embryo sac formation.

I have found that in *S. sessifolia* the 4 nuclei resulting from the first two divisions of the megaspore mother cell are at first separated by cell membranes, and later, owing to the disappearance of the membranes, come to occupy a large common cell precisely as in *S. stellata*.

Fig. 3 shows the 4 cells arranged bilaterally, while in fig. 4 a linear row of 4 is to be seen. The bilateral arrangement here is much the more abundant. The cell membranes of the second division, as is the case in *S. stellata*, are the first to disappear (fig. 5), forming thus 2 binucleate cells. Later the middle membrane disappears, giving rise to a tetranucleate cell (fig. 6). This cell enlarges rapidly by vacuolization (fig. 7) and its nuclei undergo another division to form the 8-nucleate embryo sac (fig. 8).

Smilacina amplexicaulis

I have also in an earlier paper (**19**) referred to the apparent identity of the embryo sac development in *S. racemosa* with that of *S. amplexicaulis.* A more careful examination of the first two divisions of the megaspore mother cell of the latter species confirms these earlier observations.

The megaspore mother cell of *S. amplexicaulis* may be hypodermal (fig. 11), or it may be one or two cell layers beneath the epidermis. Fig. 13 illustrates the unequal first division of the mother cell to form a large outer cell and a small inner one. A cell plate is formed which splits, causing the complete separation of these 2 cells. Later phases show this separation to be permanent. These heterotypic daughter nuclei divide simultaneously, and conspicuous cell plates are formed (figs. 14, 15), but I have never observed the splitting of the membranes as is the case in *S. racemosa.* In the latter species the complete separation of these homoeotypic nuclei seemed to be of short duration, and it is probable that more abundant material would show that in the case of *S. amplexicaulis* complete membranes are also formed, which, however, disappear early to form the 2 unequal binucleate cells (fig. 16).

Because of scarcity of material, I have been unable to follow the development of this embryo sac farther than the 4-celled stage. The close similarity of the two species (*S. amplexicaulis* being the Pacific Coast form of *S. racemosa*) makes it very probable that the embryo sac development is identical in the two species.

Maianthemum canadense

In *Maianthemum canadense* the first division of the nucleus of the megaspore mother cell is followed by the formation of a cell membrane which separates the 2 resulting nuclei (fig. 19). Similar membranes are formed separating the homoeotypic nuclei, so that 4 fully separated cells result (figs. 20, 21), as is the case in *Smilacina stellata* and *S. sessifolia.* As is shown in figs. 19–21, the 4 resulting megaspores are rarely arranged in an axial row, but are usually arranged more or less bilaterally. Although I was not able to identify split cell membranes between these reduction nuclei, the cell plates are nevertheless very different from "evanescent cell plates" such as are to be seen, for example, in the first divisions in the developing embryo sac of *Lilium*. In *Maianthemum* the cell membrane extends out and joins with the lateral wall of the mother cell, while all traces of the central spindle disappear. Later the partition membranes degenerate, thus giving rise to a tetranucleate cell (fig. 22). This tetranucleate cell enlarges by the formation of vacuoles in its interior (figs. 23, 24), and its nuclei undergo a further division to form the 8-nucleate embryo sac (fig. 25).

Streptopus roseus

The first division of the megaspore mother cell of *Streptopus roseus* results in the formation of 2 equal and fully separated daughter cells (fig. 30). The inner cell enlarges, gradually compressing the outer into a disorganized crescent-shaped mass (fig. 31).

Before the outer cell has been completely disorganized, the inner daughter cell divides, forming, in some cases at least, 2 fully separated daughter cells (fig. 32). In most cases, however, the partition wall is lacking, either not having been formed or having degenerated after formation (fig. 35). It is of course impossible to determine whether a partition wall is formed in all cases, but since the evidence is clear that it is frequently formed, it seems reasonable to expect that it is formed in all cases and subsequently undergoes degeneration.

Widely separated daughter cells such as are illustrated in fig. 33 are occasionally to be seen. While this wide cleft between the cells is in this case, without doubt, due to plasmolysis, such a wide separation could of course not have taken place had not the 2 cells been perfectly distinct. Whether 2 such widely separated cells can fuse to form a single binucleate cell may be doubted. Further evidence on this point is to be seen in fig. 34. Here the nuclei of 2 homoeotypic daughter cells have each divided, forming 2 distinct binucleate cells. The disorganized mass at the micropylar end of the outer cell is the remains of the outer cell of the first division. A tendency is thus shown toward the formation of an embryo sac from each of the potential megaspores arising from the inner heterotypic daughter cell.

The binucleate cell arising from the homoeotypic division in the inner (heterotypic) daughter cell enlarges greatly by vacuolization, and by two further nuclear divisions forms the 8-nucleate embryo sac (figs. 36, 37). After a period of growth, a typical egg apparatus and an antipodal group are organized. The polar nuclei fuse and the fusion nucleus takes up a position close to the egg.

Medeola virginica

The very large megaspore mother cell of *Medeola virginica* is in many cases hypodermal. Fig. 38 shows a very common condition in which the mother cell in synapsis lies in contact with the epidermis.

Although a conspicuous cell plate is formed at the time of the first division of the nucleus of the mother cell (fig. 39), it does not, so far as I can determine, result in the formation of a division membrane. It entirely disappears before the homoeotypic division.

The outer heterotypic nucleus divides slightly in advance of the inner, and temporary cell plates are formed between each pair of nuclei (fig. 40). These cell plates persist for some time, often being visible after the third division of the mother cell (fig. 43).

The daughter nuclei resulting from the division of the inner heterotypic nucleus may be equal in size (fig. 40) or they may be very unequal (fig. 41), the innermost nucleus being much smaller than the outer. In several cases, in fact, the inner nucleus appeared so shrunken and disorganized as to be very probably incapable of further division (fig. 42). Such a condition would cause embryo sacs with but 2 antipodal cells, and it seems very probable that this is occasionally the case.

Frequently the small inner nucleus divides at the time of the division of its larger sister nucleus, the result being 2 large and 2 small nuclei. One of the large nuclei is a polar nucleus, and the other, with the 2 small nuclei, forms the 3 antipodal nuclei (fig. 43). In still other cases, where the division of the inner heterotypic nucleus has been such as to form 2 nuclei of equal size, 3 uniform antipodal nuclei are formed (fig. 44).

A normal egg apparatus is formed from the 3 micropylar nuclei. In other respects as well the embryo sac seems normal.

Polygonatum commutatum

In *Polygonatum commutatum* the megaspore mother cell is frequently hypodermal (fig. 45), or it may be separated from the epidermis by one or two layers of cells (fig. 46). The mother cell divides twice to form an axial row of 4 permanently separated megaspores (figs. 47, 48). The inner spore enlarges by vacuolization, while the outer 3 gradually shrivel and disorganize (fig. 49). Three divisions of the nucleus of this functional megaspore form the 8 nuclei of the mature embryo sac (figs. 50, 51, 52). A normal embryo sac is organized from the 8 nuclei thus formed. The 2 polar nuclei fuse early, and the fusion nucleus lies in close proximity to the antipodal cells until immediately before fertilization, when it takes up a position near the egg.

This mode of embryo sac development has been called the "normal" as contrasted with the "lily type" of development. It seems clear, especially from the embryo sac behavior in the Convallariaceae, that no one type of development can be regarded as "normal."

I have shown that in the cases of *Smilacina stellata* and *S. racemosa* (**18, 19**) reduction in the number of the chromosomes takes place with the first two divisions of the megaspore mother cells. While I have been unable to make reliable countings of the chromosomes in the case of the other species studied, I have found evidences of the reduction divisions, such as the synapsis stage and double heterotypic chromosomes, in all the forms investigated, with the exception of *Streptopus roseus*, in which I was unfortunately unable to get the first division of the mother cell. In view of the indirect evidence mentioned above, it seems safe to conclude that, as with *Smilacina stellata* and *S. racemosa*, reduction in the chromosome number accompanies the first two divisions of the mother cell in the members of the group which I have studied. In *Clintonia* (**23**), *Trillium* (**11, 13**), and *Paris* (**13**), the evidence shows clearly that the first two divisions of the megaspore mother cells are reduction divisions.

Two megaspore mother cells

Among the monocotyledonous plants, 2 megaspore mother cells in the same nucellus have been reported in but few instances. In *Ornithogalum pyrenacium*, GUIGNARD (15) reports that 2 large cells ("deux grosses cellules collaterales") are often present at the apex of the nucellus. BERNARD (1) has reported 2 embryo sacs in *Lilium candidum* in the same nucellus. COULTER and CHAMBERLAIN (11) report two cases in *Lilium philadelphicum*, in one of which 3 "archesporial cells" were present in the same nucellus and in the other 5. Miss FERGUSON (14) has called attention to a single case of the occurrence of 2 mother cells separated by a layer of somatic cells in a single megasporangium of *Lilium longiflorum*. LECHMERE has also reported (16) for *Fritillaria messanensis* 2 embryo sacs which apparently have arisen from distinct mother cells side by side in a single ovule.

In the genus *Smilacina* 2 megaspore mother cells or their derivatives occur occasionally in the same nucellus. In *S. stellata* I have observed in four different cases 2 partially developed embryo sacs in the same nucellus, separated by somatic tissue (fig. 10). There can be no doubt that these have arisen from distinct mother cells. In *S. sessifolia* 2 mother cells were frequent. On one raceme, approximately one nucellus out of 4 contained either 2 mother cells or 2 developing embryo sacs. As is shown in fig. 9, they are usually separated more or less by somatic cells. In *S. racemosa* 2 mother cells or embryo sacs were in several cases observed lying side by side in the same nucellus, in some instances lying in contact and in others separated by sterile cells. In *S. amplexicaulis* 2 mother cells in the same ovule were observed on several occasions. While a complete record was not kept of all preparations showing this, I have records of five such abnormalities. As is shown in fig. 12, they are usually separated more or less by somatic cells.

In *Polygonatum commutatum* 2 mother cells in one megasporangium were occasionally observed (fig. 45). Four such cases have been recorded but others were observed. In *Maianthemum canadense* three cases were also observed of 2 megaspore mother cells in the same nucellus. As will be seen from fig. 17, the nucellus is abnormally broad and the mother cells are partially separated by disintegrating somatic cells.

It is probable that little significance is to be attached to these abnormalities. The occurrence of more than one megaspore mother cell in a nucellus is common in the dicotyledonous plants, and it has been rather remarkable that more have not been found among the monocotyledons.

As will be seen from figs. 11, 12, 17, and 18, the ovules in which 2 mother cells or 2 embryo sacs have been figured are all conspicuously broader than those containing but one mother cell. The relative proportion of the sterile tissue in the two cases is essentially the same, thus suggesting that where a normal amount of sterile tissue is present but one mother cell is formed.

Discussion

It will be seen from the foregoing that within the limits of the Convallariaceae considerable variation exists as to the origin of the embryo sac. In *Polygonatum commutatum* and in *Trillium recurvatum* (**9**) the embryo sac arises from one of an axial row of 4 megaspores. In *Clintonia borealis* (**23**) it arises from the outer of 4 megaspore nuclei, which are, however, not separated by cell walls or membranes. In *Smilacina racemosa* and in *S. amplexicaulis* it has its origin from the outer daughter cell of the first division of the mother cell; while in *Streptopus roseus, Trillium grandiflorum* (**13**), and *Paris quadrifolia* (**13**) the embryo sac arises from the corresponding inner daughter cell. In *Smilacina stellata, S. sessifolia*, and *Maianthemum canadense* 4 fully separated megaspores, by the disappearance of the partition walls, become merged in one tetranucleate cell. One division of each of these 4 nuclei forms the 8 nuclei of the complete embryo sac. The immature embryo sac of *Convallaria majalis*, according to WIEGAND (**24**), has a single cell membrane separating the inner pair of reduction nuclei from the outer pair, and in *Medeola virginica* a pronounced cell plate is developed between the daughter nuclei of the first division of the mother cell, which, however, disappears before the second division, and definite though temporary cell plates are also formed between the homoeotypic nuclei. Thus it will be seen that in this group, one, two, or four of the reduction nuclei may enter into the structure of the mature embryo sac.

In those forms in which more than one reduction nucleus enters into the structure of the embryo sac, we find various degrees of separation of these nuclei in temporary cells. In *Smilacina stellata* and *S. sessifolia* and in *Maianthemum canadense* the 4 reduction nuclei become fully separated by cell membranes, which later disappear. In *Smilacina racemosa*, whose embryo sac arises from the outer of 2 daughter cells, the homoeotypic nuclei are for a time fully separated from one another by split cell plates. In *S. amplexicaulis* definite cell plates are present between these homoeotypic nuclei, and it seems probable that an examination of sufficient material would show the splitting of these cell plates. In *Streptopus roseus*, whose embryo sac arises from the inner daughter cell of the first division, a definite cell plate is formed which, at times at least, splits, thus causing complete separation of the 2 homoeotypic nuclei. The single cell membrane in the developing embryo sac of *Convallaria majalis* (**24**) and the cell plates in *Medeola* show the tendency here toward the separation of the products of the reduction divisions into distinct cells.

There seems to be substantial agreement that in cases where one cell of an axial row of 4 develops into the embryo sac, the 4 cells are to be regarded as megaspores, and the cell from which these have arisen a megaspore mother cell. Both megaspore mother cell and megaspore are regarded as the morphological equivalents of the microspore mother cell and microspore respectively. In those cases, however, in which the embryo sac develops from one of the 2 daughter cells of the megaspore mother cell or from the undivided megaspore mother cell, in general two opposing views are prevalent. The one, elaborated by COULTER (**10**), regards reduction as a criterion by which spores or spore nuclei may be identified, and holds that even though the reduction nuclei are not separated they should nevertheless be regarded as megaspore nuclei. The other view, probably most actively supported by CAMPBELL (**6, 7**) and BROWN (**3, 4**), holds that reduction is not the "sole criterion" for distinguishing spores and gametophytes, and that the cell giving rise to the embryo sac should be regarded as a megaspore, whether it is the undivided megaspore mother cell, one of 2 daughter cells, or one of 4 daughter cells.

It seems clear that these two views are due to a difference in the usage of the terms "megaspore mother cell" and "megaspore," rather than to any misunderstanding or misinterpretation of the data. That the megaspore mother cell of *Lilium* has a function similar to that of the inner megaspore of the row of 4 in *Polygonatum* may be the case, inasmuch as both give rise to the embryo sac, but the mother cell in the first case has arisen from the tissue of the nucellus, in the same position and by almost identical cell divisions as in *Polygonatum*. Aside even from any consideration of the reduction phenomena, there would seem to be no doubt as to the strict homology of the megaspore mother cells in these two forms on the basis of their position in the nucellus, their conspicuous size, the character of their protoplasm, and the mode of their differentiation from the tissue of the nucellus. This conclusion applies equally well to the megaspore mother cells of most other angiosperms. The fact that the heterotypic division occurs in the megaspore mother cell of *Lilium* may be regarded as confirmatory evidence of its nature.

The first 4 nuclei of the lily embryo sac originate, also, by steps identical with those giving rise to the nuclei of the megaspores of *Polygonatum*. These 4 nuclei in the above-mentioned two forms are homologous, whether we call them "megaspore nuclei" or "the first 4 nuclei of the embryo sac." The increasing number of cases in which the first 4 nuclei arising from the megaspore mother cell are found to be more or less separated by temporary cell membranes suggests very strongly that the conditions in *Lilium* have arisen in a like manner, namely the loss by the 4 megaspores of their physiological individuality as spores and the subsequent disappearance of the separating membranes to form the 4-nucleate stage of the embryo sac.

In *Smilacina stellata* (18) I have shown that the 4 reduction nuclei are completely separated, the cell plate having split so that wide clefts between the cells are often present. This separation is due probably to shrinkage in fixation. The cell membranes cannot be regarded in the same light as evanescent cell plates, for here the cell plates are completely formed, after which they split to form the distinct membranes of the new cells. There can be no doubt as to the individuality of the 4 cells, and that they are the morphological equivalents of megaspores is beyond question.

In *Smilacina racemosa* (**19**), although but the 2 outer reduction nuclei enter into the structure of the embryo sac, they too are for a time fully separated by a split cell plate.

In *Streptopus roseus*, also, the cell plate which separates the 2 homoeotypic nuclei entering into the structure of the embryo sac very often splits, thus causing a complete separation of these 2 nuclei. I have referred above to evidence which suggests that at times this separation may be permanent.

No other conclusion seems possible than that 4 fully separated cells arising from a megaspore mother cell by the reduction divisions must be megaspores. That the 2 cells which in *Smilacina racemosa* and in *Streptopus roseus* fuse to form the 2-celled stage of the embryo sac are also megaspores seems equally clear.

The cell membranes separating the reduction nuclei in the megasporangia of *Smilacina sessifolia*, *S. amplexicaulis*, and *Maianthemum canadense*, although in my material showing no splitting into two distinct cell walls, are nevertheless much more complete and persistent than the evanescent cell plates such as have been reported at times for the embryo sac of *Lilium* and in other genera. These membranes extend out and join the lateral walls and all traces of a central spindle disappear. It seems very possible that an examination of sufficient stages would show that these membranes also split as is the case in *Smilacina stellata*.

The transition from forms like the foregoing, in which the division membranes persist for some time, to the lily type of embryo sac is strongly suggested by those forms in which the membranes are incomplete and evanescent, as is the case in *Medeola* and *Clintonia*. Additional evidence on this point has been contributed by BROWN and SHARP for *Epipactis* (**5**). According to their account, although the embryo sac usually arises from the inner of an axial row of 4 megaspores, it also frequently arises from the megaspore mother cell, evanescent cell membranes being formed, and it may possibly be formed from the 2 inner megaspores. Evidence on this latter point, however, was not conclusive.

The cell plates or membranes in the embryo sac of *Medeola* and of *Epipactis* are simply more fully formed and more persistent than those of *Lilium*, and a little less fully formed and less enduring than those of *Smilacina* and *Maianthemum*. The question as to the relative completeness and duration of the membranes separating the reduction nuclei in these forms is one that cannot affect the homology of the cells in question. They are all morphologically megaspores. That those reduction nuclei which are not even separated by evanescent cell plates, if such exist, are also to be regarded as megaspore nuclei would seem, on the basis of their homology with the above-mentioned forms, to be an unavoidable conclusion.

The presence or absence of temporary or evanescent cell plates between the reduction nuclei as a means of determining whether the mother cell is to be regarded as a megaspore or whether each of the reduction nuclei is to be regarded as the nucleus of a megaspore (4) seems in the light of the above evidence to be not only "inconclusive" but worthless. I have shown that the presence even of split cell membranes is no indication that such membranes will be permanent, while, on the other hand, the lack of division membranes between the reduction nuclei does not necessarily result in the lily type of embryo sac formation. In the cases of *Eichhornia* (22), *Avena* (8), *Crucianella* (17), and *Asperula* (17), although division membranes are lacking, nevertheless the functional megaspores develop exactly as though such membranes were present. In *Crucianella* all 4 megaspores may germinate, though ultimately but one embryo sac matures while the other 3 degenerate. If the lack of cell plates or membranes between the reduction nuclei really signified that the reduction divisions have been shifted so that they occur in the embryo sac, we should have upon the division of the homoeotypic nuclei in *Crucianella* an 8-nucleate embryo sac. Subsequent development shows, however, that we really have 4 embryo sacs "in tandem."

Summary

1. In the eight members of the Convallariaceae investigated by the author, the embryo sac is formed from one reduction nucleus

in *Polygonatum*, from 2 in *Smilacina racemosa*, *S. amplexicaulis*, and *Streptopus roseus*, and from 4 in *Smilacina stellata*, *S. sessifolia*, *Maianthemum canadense*, and *Medeola virginica*.

2. In all forms in which more than one reduction nucleus enters into the structure of the embryo sac, these nuclei are at first more or less completely separated by cell membranes, the degree of separation varying from split cell plates in *Smilacina stellata* to evanescent cell plates in *Medeola virginica*.

3. The difference in the degree of the separation of these cells cannot affect their morphological status; they are all megaspores.

4. In the light of this evidence it seems reasonable to conclude that all reduction nuclei arising from the nucleus of the megaspore mother cell, whether temporarily separated or not separated at all, should be regarded as megaspore nuclei.

5. Two megaspore mother cells were occasionally observed in six of the eight species investigated.

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EXPLANATION OF PLATES VI and VII

All the figures were made with the aid of a camera lucida and reduced one-third. The magnification (reduced) is about 400, with the exception of fig. 38, which has a magnification of 200. Unless otherwise indicated, the micropyle is down in the figures.

Smilacina sessifolia

FIG. 1.—Embryo sac mother cell recovering from synapsis.

FIG. 2.—First division of megaspore mother cell.

FIG. 3.—Four fully separated megaspores arranged bilaterally.

FIG. 4.—Four fully separated megaspores in an axial row.

FIG. 5.—The membranes of the homoeotypic division have disappeared, leaving only the membrane of the first division.

FIG. 6.—No traces of membranes remain; the 4-nucleate stage of the embryo sac.

FIG. 7.—A slightly older embryo sac.

FIG. 8.—An 8-nucleate embryo sac.

FIG. 9.—Two immature embryo sacs in the same nucellus.

Smilacina stellata

FIG. 10.—Cross-section of nucellus showing 2 megaspore mother cells.

Smilacina amplexicaulis

FIG. 11.—Mother cell hypodermal, in synapsis.

FIG. 12.—Two mother cells in synaptic stage in the same nucellus.

FIG. 13.—The unequal first division of the mother cell.

FIG. 14.—The second division of the mother cell; the cells of the first division completely separated.

FIG. 15.—Second division; cell plates between the homoeotypic nuclei.

FIG. 16.—The 4 reduction nuclei are now contained in 2 binucleate cells; the inner pair of nuclei are degenerating, while the outer pair, from which the embryo sac develops, are plump and normal.

Mianthemum canadense

FIG. 17.—Two megaspore mother cells in synaptic condition.

FIG. 18.—A single megaspore mother cell.

FIG. 19.—The first division of the megaspore mother cell.

FIG. 20.—Four fully separated cells arising from the megaspore mother cell; the arrangement of the 4 cells very irregular.

FIG. 21.—A similar stage, showing again 4 fully separated cells.

FIG. 22.—A later stage in which the cell membranes separating the cells have disappeared, causing the 4-nucleate stage of the embryo sac.

FIGS. 23, 24.—Stages in the vacuolization of the tetranucleate embryo sac.

FIG. 25.—An immature 8-nucleate embryo sac.

Smilacina stellata

FIG. 26.—Four megaspores fully separated by split cell plates.

FIG. 27.—The cell membranes of the second division have disappeared, but the split cell plate of the first division still persists.

Smilacina racemosa

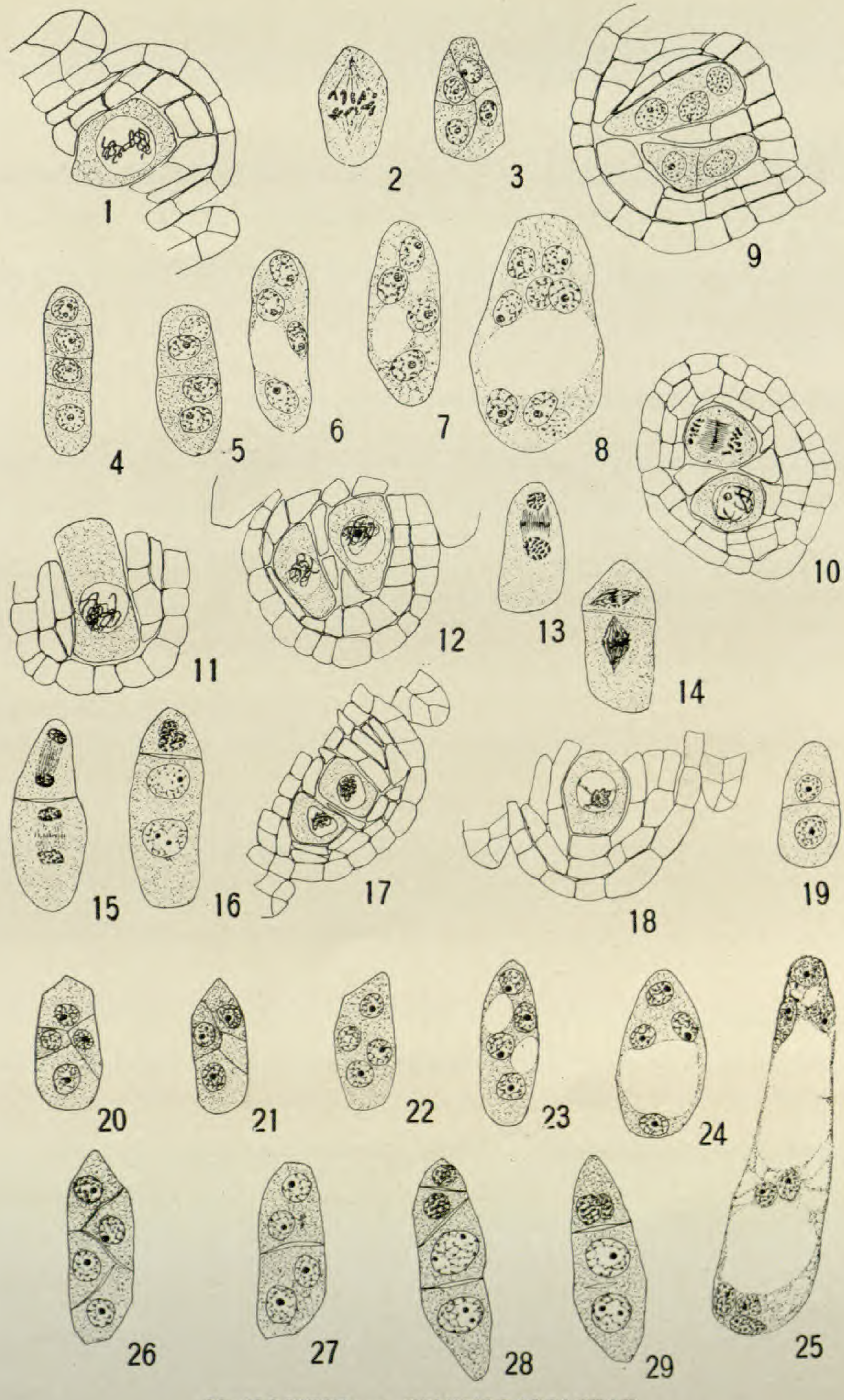
FIG. 28.—Four unequal megaspores fully separated by split cell plates.

FIG. 29.—A slightly later stage than the above, in which the cell membranes of the second division are disappearing; the inner pair of nuclei are no longer separated, while but a small part of the cell plate persists between the outer pair.

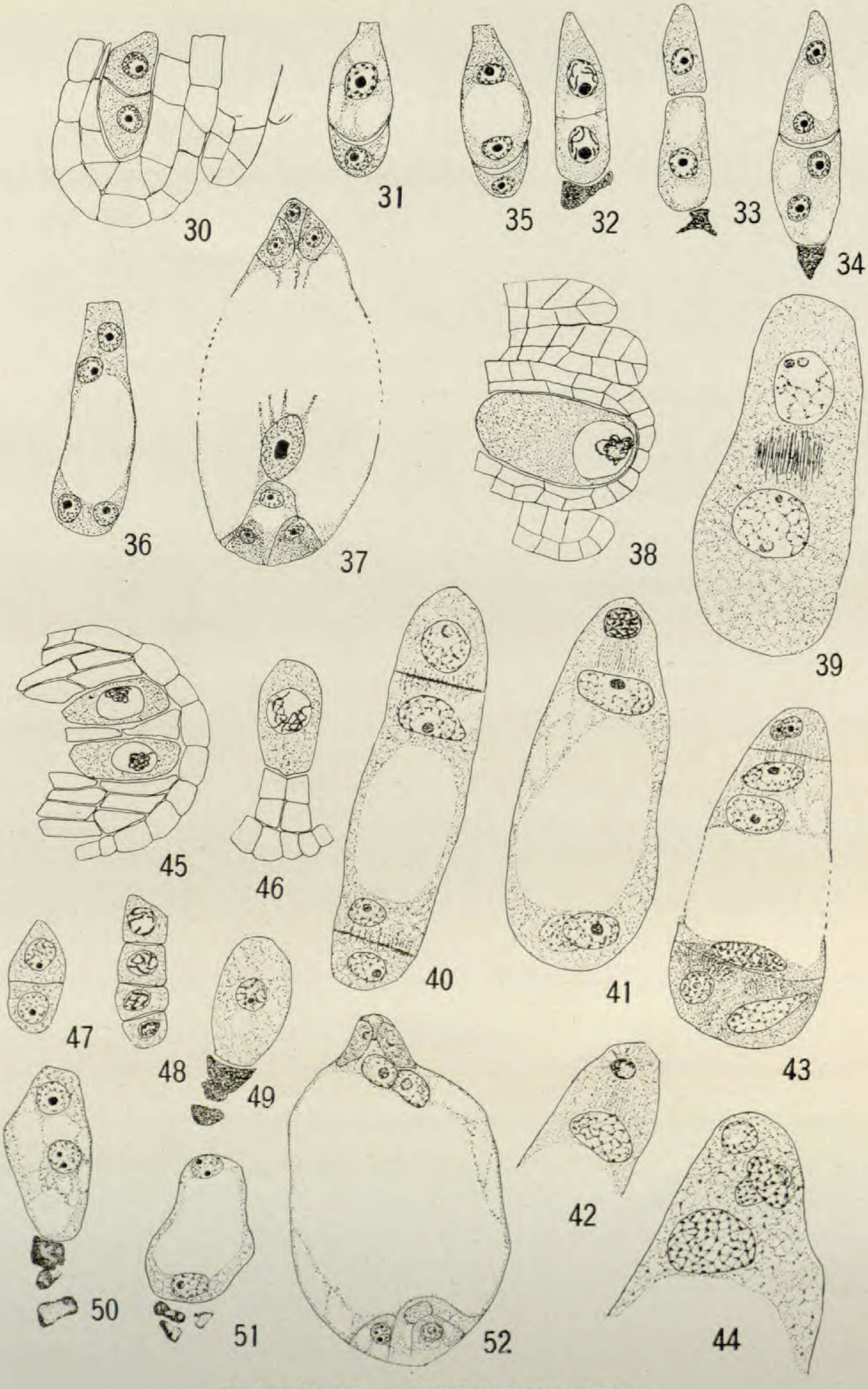
Streptopus roseus

FIG. 30.—Two fully separated daughter cells arising from the megaspore mother cell.

FIG. 31.—The inner daughter cell is enlarging at the expense of the outer.



McALLISTER on CONVALLARIACEAE



McALLISTER on CONVALLARIACEAE

FIG. 32.—The inner daughter cell has divided to form 2 cells which are separated by a definite and complete cell plate; the outer daughter cell now but a disorganized mass.

FIG. 33.—The 2 daughter cells of the second division widely separated by a split cell plate.

FIG. 34.—The nuclei of 2 fully separated inner daughter cells have divided, thus forming 2 binucleate cells; since both inner cells are to be regarded as megaspores, these 2 binucleate cells are immature female gametophytes.

FIG. 35.—A binucleate embryo sac with no trace of cell membranes.

FIG. 36.—A 4-nucleate stage of the embryo sac.

FIG. 37.—A fully formed embryo sac.

Medeola virginica

FIG. 38.—A megasporangium showing a single hypodermal megaspore mother cell, in the synaptic stage; magnification but half that of the other figures.

FIG. 39.—The first division of the mother cell; a conspicuous though incomplete cell plate is present.

FIG. 40.—The second division of the mother cell; the cell plate of the first division no longer visible; those of the second division very conspicuous but not sharply defined; the chalazal nuclei are practically equal.

FIG. 41.—A slightly earlier phase in which the inner pair of nuclei has a small inner (chalazal) nucleus and a large outer nucleus.

FIG. 42.—An embryo sac in which the inner pair of nuclei is very unequal; the inner nucleus stains deeply as though degenerating.

FIG. 43.—The third division; 2 small nuclei and 2 large ones in the antipodal end of the sac as a result of the unequal division of the antipodal nucleus in the previous division; the cell membranes of the second division still visible.

FIG. 44.—Antipodal region of the embryo sac showing 3 equal antipodal cells and the single fusion nucleus, fusion of the polar nuclei having taken place.

Polygonatum commutatum

FIG. 45.—Two hypodermal mother cells in a single nucellus.

FIG. 46.—A single mother cell showing two layers of cells between it and the epidermis.

FIG. 47.—Two daughter cells of the first division of the mother cell.

FIG. 48.—An axial row of 4 megaspores.

FIG. 49.—The enlarged inner megaspore and the disintegrated remnants of the outer three.

FIG. 50.—First division of the megaspore.

FIG. 51.—Binucleate embryo sac with a single large central vacuole.

FIG. 52.—Mature embryo sac; the polar nuclei not yet fused.

COMPARATIVE MORPHOLOGY OF SOME LEGUMINOSAE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 190

JOHN N. MARTIN

(WITH PLATES VIII–XI)

This investigation covers the development of the embryo sac, embryo, and endosperm of *Trifolium pratense, T. hybridum, T. repens, Medicago sativa,* and *Vicia americana.* The work was done at the University of Chicago and Iowa State College. I wish to express my thanks to Professor COULTER and Professor CHAMBERLAIN who supervised the work, and to Professor PAMMEL at Iowa State College for valuable suggestions.

Historical

In 1839 and 1842 SCHLEIDEN and VOGEL (**8**) described the floral development and the endosperm of the Leguminosae. They investigated the endosperm of more than 50 species well distributed through the group. They found only a little endosperm remaining in *Trifolium* and *Medicago,* and none in *Vicia.* In 1855 TULASNE (**13**) described the proembryo of *Lathyrus Aphaca;* it produced a long filamentous suspensor and a distinct terminal embryo. HOFMEISTER (**5**) in 1858 described the embryo sac and proembryo of some species of *Lotus, Tetragonolobus, Trifolium, Lupinus,* and *Lathyrus;* he found a short massive proembryo in *Trifolium.* In 1880 STRASBURGER (**10**) described a proembryo developing a long suspensor in several species of *Lupinus* and in *Orobus vernus;* the cells of the suspensor are multinucleate and often separate. In the same year HEGELMAIER (**4**) reported the results of his investigations of the embryo sac, proembryo, and endosperm in four species of *Lupinus.* He found that the cells of the filamentous suspensor are multinucleate and that ephemeral cell plates appear during the division of the endosperm nuclei. In 1881 GUIGNARD'S (**3**) work appeared, covering about 40 species of the Leguminosae, well distributed through the family. At that time the homology between microsporangium and megasporangium had not been established, and the terms "apical" and "subapical" were used to designate the primary parietal and sporogenous cells. His account shows that a one-celled archesporium prevails through the group. The archesporial cell always cuts off one parietal cell, which may remain undivided or produce a tissue varying in amount. The megaspore mother cell may produce the embryo sac directly, or form an axial row of 2, 3, or 4 cells, of which the innermost or one next to it may function. The embryo sac is always 8-celled and the antipodals are ephemeral. The fusion of the polar nuclei may occur in the center of the sac, against the inner wall, or in contact with the egg apparatus. The first division of the egg is transverse. The following divisions may result in a massive proembryo with no distinct line between the massive suspensor and embryo, or in a proembryo with a slender suspensor and a sharply defined terminal embryo. In 1907 SAXTON (7) described the embryo sac of *Cassia tomentosa*, and found one *deeply* buried megaspore mother cell. The third megaspore out of the longitudinal row of 4 functions; the polars fuse early; and the antipodals are persistent and form an absorptive tissue which fills the tubular projection in the chalazal region.

In 1912 COMPTON (1) described the seedling structure of 201 species of Leguminosae, ranging through all the regions of the vast family. He found the seedling epigeal in *Trifolium* and *Medicago*, but hypogeal in *Vicia*.

Material

Several fixing agents were tried, but chromo-acetic acid gave best results; one-half of 1 per cent strength was most satisfactory. The heads of *Trifolium* were split and entire halves run through and sectioned. Since the head is a compact raceme, this method enables one to trace the development of the embryo sac more readily, and proved to be of valuable assistance in determining the sterility of ovules. Separate flowers of *Medicago* and *Vicia* were used. The sections were stained with safranin and gentian violet.

Trifolium pratense

A more thorough study was made of this species because of its economic importance, and it was hoped that a better knowledge of its morphology would aid in controlling seed production. The discussion of *Trifolium pratense* will be somewhat detailed, and will form a basis for a comparative treatment of the other 4 species.

The ovary develops invariably 2 campylotropous ovules which are attached to a cushion-like placenta (fig. 1). The outer integument, which is barely a distinct ridge when the inner appears, soon passes the inner and forms a heavy rim about the micropyle (figs. 8, 10). The outer integument, which varies from 2 to 4 rows of cells in thickness at fertilization, except at the micropyle, thickens by periclinal divisions to many rows after fertilization, and the outer row of cells forms the peculiarly thickened and cutinized layer of the testa. The inner integument usually remains two layers in thickness until destroyed by the embryo sac. Sometimes three layers are seen in its basal region (fig. 10).

The nucellus is hemispherical at the time the archesporium can be identified, but elongates rapidly and is quite slender at the time the embryo sac is mature (fig. 12). There are usually 3 subepidermal rows (fig. 3), but often 3–6 rows are found at the base of the nucellus (fig. 12).

EMBRYO SAC.—From 1 to 4 archesporial cells were observed, and more than half of the ovules showed more than one archesporial cell. In fig. 3 there are 4 archesporial cells in a longitudinal row. In fig. 4 there are 4, but 3 are hypodermal and the other is more deeply placed. In either case, it is probable that the 4 archesporial cells have come from the division of a hypodermal cell at an early stage in the development of the nucellus. It is also probable that the cells deeper than the hypodermal layer may become sporogenous. One parietal cell is cut off (fig. 2), which usually divides transversely to form a longitudinal row of 2 or 3 cells (fig. 8), or one transverse and one longitudinal division may occur (fig. 6). No division (fig. 7) or only a longitudinal division has been observed. In fig. 5 two of the three megaspore mother cells have reached the synapsis stage, but more than one row of megaspores was not found.

So far as observed, a longitudinal row of 4 megaspores is always formed and the lower one functions (figs. 7, 8).

No chromosome counts were made, but the number is small and probably the same as in *Trifolium repens*, where it is about 12. The functioning megaspore rapidly destroys the surrounding tissue. The encroachment is at first most rapid at the chalazal end and results in a tubular sac (figs. 9, 10). As the megaspore enlarges, the tip of the nucellus thickens and with the surrounding portion of the inner integument becomes packed with starch (fig. 10). The megaspore divides in the direction of the long axis of the sac and the daughter nuclei pass to opposite poles (fig. 9). The following divisions may be parallel or transverse to the long axis of the sac (figs. 10–12). The longitudinal divisions are no doubt associated with the narrowness of the sac and occur most often in the antipodal end. As the embryo sac matures, it destroys the micropylar end of the nucellus and becomes much larger in this region (fig. 11). When the sac is mature, only the basal portion of the nucellus remains and the embryo sac lies against the inner integument (fig. 13). Sometimes the nucellus is more persistent, as shown in fig. 12.

The polar nuclei usually meet on the median line of the sac close to the egg apparatus (fig. 12), but occasionally they lie against the inner wall of the sac. Fusion awaits fertilization, but was found to occur if fertilization was prevented. Fig. 14 shows the fusion of the two polars before fertilization. In this case pollination was prevented and the ovaries were killed soon after the flowers began wilting.

The synergids often show a distinct filiform apparatus (fig. 14), which becomes more prominent if fertilization is prevented. The antipodals are ephemeral and no trace of them is left at the time of fertilization.

FERTILIZATION.—The fusion of the sex nuclei was not seen, although many flowers were pollinated and killed at various periods after pollination. The time between pollination and fertilization varies. Flowers pollinated during the high temperature of July and killed 18 hours after pollination showed pollen tubes entering, egg in first division, and 3-celled embryos. In October, when the temperature was much lower, the time of fertilization ranged from 35 to 50 hours. This difference, no doubt, is partly due to a difference in growth conditions, and partly to delayed germination of the pollen. During the cooler weather pollen placed on the stigma at 3:00 P.M. was found dormant at 9:00 A.M. on the following day. This delayed germination will cause a marked difference in the time of fertilization. The pollen tube enters around the wall or in the region of a synergid (fig. 15); its behavior with reference to the synergid was not determined.

EMBRYO.—The first divisions of the egg are transverse (fig. 17), and result in a filament of three cells (fig. 18). By vertical walls in two planes this filament is divided into tiers of 4 cells each (fig. 19). The basal tier and a part of the second tier remain less active, but later form a massive suspensor (figs. 20, 21). No distinct line between embryo and suspensor was made out. In fig. 20 the dermatogen is being differentiated, which occurs later than the octant stage.

ENDOSPERM.—The division of the endosperm nucleus usually precedes that of the egg (fig. 15), but occasionally follows it (fig. 16). In fig. 17 the fertilized egg has completed its first division, and 5 endosperm nuclei were counted. The endosperm masses about the embryo and from this mass it extends around the wall of the sac. Its later development is centripetal. Only the first division of the endosperm nucleus was seen in the many ovules studied. This fact indicates that the divisions in the endosperm nuclei are simultaneous, but this feature was not determined.

STERILITY.—The sterility of ovules is a prominent feature in *Trifolium pratense*. In the sterile ovules all the cells of the nucellus remain vegetative and hence no embryo sacs are found. All the flowers of a plant frequently develop sterile ovules only. This seems to be related to moisture conditions, but more work is necessary before a definite conclusion can be drawn as to its cause. Plants grown in the greenhouse and well watered gave 100 per cent sterile ovules. First crop heads collected from the field during wet weather showed nearly 100 per cent sterility, while first crop heads collected after two weeks of dry weather showed a large percentage of fertile ovules. But even during dry weather there is considerable variation among plants, some producing nearly all fertile ovules, and others a large percentage of sterile ones. There is a marked tendency toward sterility, which seem to be favored by moisture. This tendency, no doubt, always lowers the percentage of seed production, and in some cases reduces it almost to zero. The fact that this tendency varies among plants under similar conditions suggests that it may be partly eliminated by selection. A sterile ovule is shown in fig. 22. The flower was open and the embryo sac should have been ready for fertilization. Sterile ovules can be identified only in later stages. The cells of the subepidermal rows are usually larger and less dense in content, but it is safe to pass judgment on the earlier stages only when all the later stages of the head are sterile. No mother cells in synapsis were found in the sterile ovules, so sterility seems to be determined before this stage is reached.

PARTHENOGENESIS.—*Trifolium pratense* has been reported parthenogenetic. Flowers were run under cover and killed at various times after wilting. An examination of more than 500 ovaries showed no embryos. The ovule enlarges very rapidly for several days after the embryo sac is ready for fertilization and then begins to break down.

Trifolium hybridum

This species is so similar to *Trifolium pratense* that a few features only deserve mention. The number of ovules in an ovary is variable, ranging from 3 to 8. Fig. 23 shows the lower megaspore germinating before the others are destroyed. The embryo sac has a large central vacuole and the cytoplasm is almost entirely limited to a thin peripheral layer (fig. 24). The embryo sac becomes more curved than that of *Trifolium pratense* (fig. 27). The polars fuse in a parietal position (fig. 24). The proembryo is more slender and there is a more definite line between embryo and suspensor in the later stages (fig. 25). Fig. 25 also shows the faint walls that sometimes occur in the early development of the endosperm. Fig. 26 shows the suspensor on the hypocotyl of the embryo. The tendency toward sterility is not so pronounced in this species as it is in *Trifolium pratense.*

Trifolium repens

This species agrees very closely with *Trifolium hybridum*. Fig. 28 shows the reduction division of the mother cell; 11 chromosomes are shown, but various counts gave 11 and 12. The number is small, about 12. In fig. 29 one megaspore mother cell has produced 4 megaspores, while the other one has enlarged but has made no division. The third megaspore often functions (fig. 30). The embryo does not differ from that of *Trifolium hybridum*. The endosperm masses about the embryo in its early development, but no walls occur. Not much sterilization was observed.

Medicago sativa

In *Medicago sativa* the number of ovules in an ovary varies considerably, ranging between 12 and 18. The nucellus is more massive than that of *Trifolium*. The number of subepidermal rows ranges from 5 to 7 (figs. 31, 34). The outer integument precedes the inner as in *Trifolium*. The number of archesporial cells ranges from 1 to 6, and more than one usually occurs (fig. 31). One parietal cell is nearly always cut off, but occasionally megaspore mother cells may be found with no parietal cells (fig. 32). The parietal cell usually makes only one division, which is transverse (figs. 32, 33), but at times the transverse division is followed by one or more longitudinal ones (fig. 34). Prominent cell plates accompany the formation of the megaspores (figs. 33, 34). From 2 to 4 rows of megaspores may occur in the same nucellus (fig. 34) and often more than one megaspore starts to form an embryo sac (fig. 35), but not more than one mature sac was found. The embryo sac destroys the surrounding nucellar tissue more uniformly and does not become so tubular as in *Trifolium* (figs. 36, 37). The large central vacuole which appears during the formation of the 8 nuclei (fig. 36) disappears later, and the cytoplasm becomes compact and filled with starch (fig. 37). The 8 nuclei of the embryo sac are arranged in two groups of 4 each, separated by the large vacuole (fig. 36), and when the embryo sac is mature, 3 nuclei of each group are definitely set off at the poles in separate masses of cytoplasm, while the 2 polar nuclei occupy the median mass of cytoplasm (fig. 37). The polars meet near the middle of the sac (fig. 37) and then move to a position near the egg apparatus (fig. 38), where they fuse late, probably not until fertilization. Three antipodals are usually formed (fig. 36), but sometimes only one division occurs in the antipodal end, which results in only one antipodal cell (fig. 37). The antipodals disappear before the embryo sac is mature (fig. 38).

EMBRYO.—The egg forms a filament of 5 cells, the terminal one of which produces the embryo, while the other 4 constitute the suspensor (figs. 39, 40). The basal cell of the suspensor is quite long. All the cells have thin, granular cytoplasm and are usually multinucleate. The suspensor is still seen on the advanced embryo (fig. 41). Fig. 40 shows the embryo with dermatogen already differentiated.

ENDOSPERM.—The endosperm takes the parietal arrangement with the earlier development in the micropylar end, but does not mass about the embryo as in the clovers (fig. 40). No sterility was observed in *Medicago sativa*, but all material used, so far, was collected during rather dry periods, and further investigation is necessary to determine the effect of moisture upon its fertility.

Vicia americana

The number of ovules in *Vicia americana* has about the same range as in *Medicago sativa*. The nucellus is smaller, usually having 3 or 4 subepidermal rows. Periclinal divisions are rapid in the early stage of the nucellus, which give it a slender form. The outer integument, as in *Trifolium* and *Medicago*, precedes the inner. Fig. 42 shows 5 archesporial cells, all of which are probably not of hypodermal origin. The development of parietal tissue is variable, as shown by figs. 43–45. A row of 4 megaspores is formed (fig. 44) and the lower functions (fig. 45).

The embryo sac resembles that of *Medicago sativa* in formation, shape, and in the destruction of nucellar tissue. The antipodals are ephemeral as in the other species (figs. 46, 47), but the position of the polars is near the inner wall in the middle of the sac (fig. 47). It resembles the clover in having much starch in the inner integument and little in the sac.

EMBRYO.—The proembryo consists of a filament of three cells, of which the terminal forms the embryo, while the other two form a long suspensor of two tiers of two cells each. The cells of the suspensor have very little cytoplasm and are multinucleate (figs. 48–51).

ENDOSPERM.—The endosperm nucleus and egg divide at about the same time. The endosperm nuclei divide rapidly and simultaneously. The endosperm is parietally placed and does not mass about the proembryo in the early stages of its development (figs. 52, 53). Some sterile ovules were found, but the tendency toward sterility is not so pronounced as in the clovers.

Discussion

GUIGNARD'S account of *Trifolium* (**3**, pp. 119, 120) is limited to the development of the embryo. The fertilized egg produces a filament of 3 cells, the terminal of which develops the embryo. The other 2 cells produce a short, several-celled suspensor. In the later stages the line of separation between embryo and suspensor is indistinct. The dermatogen is differentiated in the octant stage. In the three species of *Trifolium* investigated by the writer, the suspensor is more massive and the dermatogen is differentiated later than the octant stage.

In *Medicago arborea* GUIGNARD (**3**, pp. 119, 120, *figs. 192–194*) reports a one-celled archesporium and two superimposed parietal cells. The megaspore mother cell functions directly to produce the embryo sac. The proembryo produces a long, filamentous suspensor which is distinct from the terminal embryo. The dermatogen is differentiated in the octant stage. In *Medicago sativa* there is usually a multicellular archesporium, production of megaspores, and more parietal tissue, but in other features it is similar to *Medicago arborea*. In *Vicia sepium*, GUIGNARD (**3**, p. 53, *figs. 66–70*) found one parietal cell which occasionally makes one transverse division. The single megaspore mother cell produces a longitudinal row of 3 cells, the lower 2 being megaspores, or a longitudinal row of 4 megaspores; in each case the lowest megaspore functions. The proembryo produces a long suspensor which consists of two rows of cells and is distinct from the embryo. In *Vicia americana* a multicellular archesporium usually occurs, and so far as observed a longitudinal row of 4 megaspores is always formed.

GUIGNARD gives no account of a multicellular archesporium in any of the species which he studied, but the early stages of the ovules were examined without sectioning, and it is probable that present methods would give different results. He found parietal tissue in all species studied, but the greatest amount in the Mimosoideae and Caesalpinioideae.

The following records show that a multicellular archesporium occurs in other families of the Rosales. Miss PACE (**6**) found a multicellular archesporium in *Parnassia* and *Saxifraga*. WEBB (**14**) reported the same type in *Astilbe*. SHOEMAKER (**9**) found several archesporial cells in *Hamamelis;* and COULTER and CHAMBERLAIN (**2**, pp. 58, 59) in a summary of the literature show that a multicellular archesporium prevails among the Rosaceae.

The filiform apparatus in *Trifolium pratense* differs from that described by PACE in *Parnassia* and *Saxifraga* and by STRASBURGER in *Polygonum* (**11**) and *Santalum* (**12**), in that no notch appears.

GUIGNARD (**3**, p. 142) states that the polar nuclei fuse before fertilization except in the subfamily Vicieae, and that the fusion nucleus rests on the median line of the sac in the Mimosoideae and Caesalpinioideae, and against the inner side of the sac in the Papilionoideae. In the five species treated in this paper, the fusion of the polar nuclei was found to await fertilization, and their position is median in *Medicago sativa*, but may be either median or parietal in the species of *Trifolium*, and always parietal in *Vicia americana*.

GUIGNARD (**3**, p. 141) found the antipodal cells persisting till fertilization in the Mimosoideae and Caesalpinioideae, but disappearing earlier in the Papilionoideae. SAXTON (**7**) found the antipodals persistent and functioning as haustoria in *Cassia tomentosa*.

Summary

Features common to the five species are as follows: (1) campylotropous ovules; (2) two integuments, the outer preceding the inner; (3) a multicellular archesporium; (4) one parietal cell cut off which gives rise to more or less parietal tissue; (5) the production of a row of 4 megaspores; (6) the rapid destruction of nucellar tissue which brings the embryo sac in contact with the inner integument; (7) antipodals ephemeral.

Contrasting features are as follows: (1) the number of ovules is always 2 in *Trifolium pratense*, but more than 2 and various in the other species; (2) the third megaspore sometimes functions in *T. repens;* (3) in *Trifolium* the embryo sac rapidly destroys the antipodal end of the nucellus and thus forms a long tubular sac; (4) in *Trifolium* the embryo sac remains very vacuolate, while in *Vicia* and *Medicago* the sac fills with cytoplasm; (5) polars meet on median line or on inner side of sac in *Trifolium*, but rest near the egg apparatus; in *Medicago* the polars meet near the center of the sac and rest near the egg apparatus; while in *Vicia* they meet on the inner side of the sac and remain some distance from the egg apparatus; (6) in *Trifolium* and *Vicia*, the starch appears in the micropylar end of the nucellus and in the inner integument, while the starch fills the sac in *Medicago;* (7) in *Trifolium* the proembryo is short and massive and no definite line between suspensor and embryo was made out; more evidence of the separate parts was seen in the more slender proembryos of *T. hybridum* and *T. repens;* (8) definite suspensors with multinucleate cells appear in *Medicago sativa* and *Vicia americana;* in the former species the suspensor is filamentous, but composed of two superimposed pairs of cells in the latter species; (9) sterilization is most marked in *T. pratense.*

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EXPLANATION OF PLATES VIII–XI

Trifolium pratense

FIG. 1.—Young ovary showing the two ovules and placenta; ×330.

FIG. 2.—Young nucellus showing one sporogenous and one parietal cell; ×1560.

FIG. 3.—Young nucellus with a row of 4 archesporial cells; both integuments are prominent; ×1500.

FIG. 4.—Young nucellus with 4 archesporial cells; inner integument is just beginning to show; ×1560.

FIG. 5.—Cross-section of nucellus with 3 megaspores, 2 of which are in synapsis; ×1500.

FIG. 6.—Young nucellus with one mother cell in synapsis; the integuments are well advanced; ×1200.

FIG. 7.—Nucellus with a row of 4 megaspores; two large dense cells lie in line below the megaspores; parietal cell has not divided; ×1200.

FIG. 8.—Four megaspores with lower one functioning; ×1500.

FIG. 9.—A binucleate embryo sac eating its way into the chalazal end of the nucellus; ×1560.

FIG. 10.—A 4-nucleate embryo sac; the divisions at each end have been in the direction of the long axis of the sac; integuments well advanced and outer is thickened at micropylar end; the ends of the nucellus and the inner integument are filled with starch; ×880.

FIG. 11.—An 8-nucleate sac, with linear arrangement at antipodal end; micropylar end of nucellus being destroyed; embryo sac quite vacuolate; ×920.

FIG. 12.—Polars in contact near the egg apparatus; nucellus more persistent; ×1200.

FIG. 13.—Embryo sac mature and in contact with inner integument; ×920.

FIG. 14.—Egg apparatus with synergids showing filiform apparatus; the nucleoli of the polars are fusing; ×1560.

FIG. 15.—Pollen tube in region of synergid, and egg in division; endosperm cell has made one division; ×920.

FIG. 16.—A 2-celled proembryo, while the endosperm cell is in first division; ×920.

FIG. 17.—A 2-celled proembryo; 5 endosperm nuclei were counted; ×920.

FIG. 18.—A 3-celled proembryo; ×920.

FIG. 19.—Proembryo has divided by vertical walls; ×750.

FIG. 20.—Dermatogen is cut off; ×750.

FIG. 21.—The massive proembryo with no line of separation between embryo and suspensor; ×540.

FIG. 22.—Median longitudinal section of a sterile ovule; embryo sac replaced by vegetative cells; ×1200.

Trifolium hybridum

FIG. 23.—Early germination of lower megaspore; ×1500.

FIG. 24.—An 8-nucleate embryo sac; cytoplasm of the sac forms a marginal layer around the large vacuole; polars in contact on inner side of sac; ×910.

FIG. 25.—Proembryo with cotyledons appearing; the stalk is composed of large cells, and there is an apparent line of separation between suspensor and embryo at this stage; ×540.

FIG. 26.—Remains of suspensor on the hypocotyl of the embryo; ×530.

FIG. 27.—Ovule showing the long, curved embryo sac, and proembryo in early stage; ×360.

Trifolium repens

FIG. 28.—Reduction division of mother cell; outer integument well developed; ×1500.

FIG. 29.—One row of megaspores and one enlarged mother cell; ×1500.

FIG. 30.—Third megaspore functioning; ×1200.

Medicago sativa

FIG. 31.—Young nucellus with 3 sporogenous cells, each capped by one parietal cell; ×1500.

FIG. 32.—Three mother cells in synapsis; two have no parietal cells; ×1500.

FIG. 33.—Mother cell in reduction division; parietal cell has divided transversely; ×1500.

FIG. 34.—Two rows of megaspores; ×1500.

FIG. 35.—Two embryo sacs; one is binucleate; ×1500.

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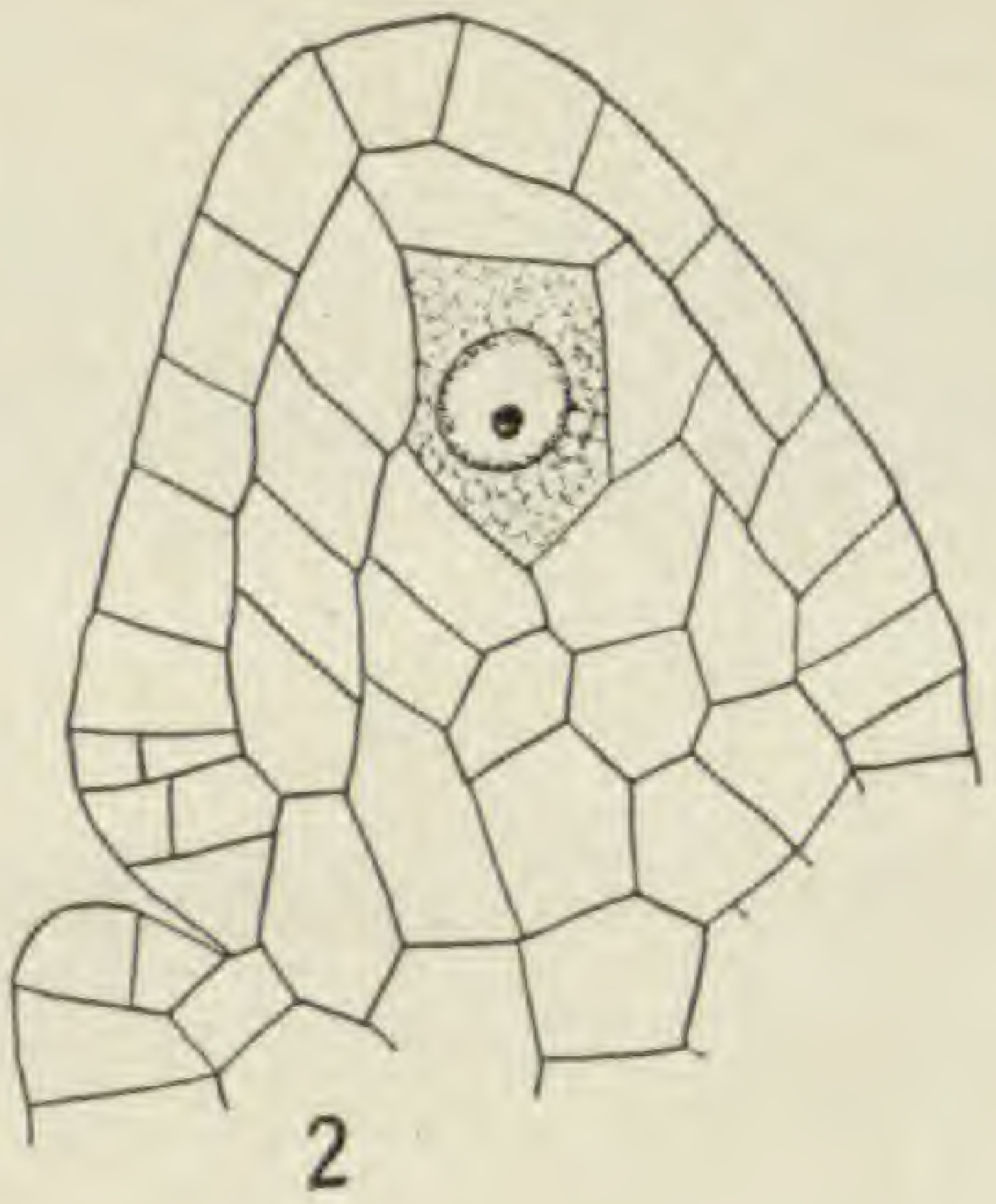

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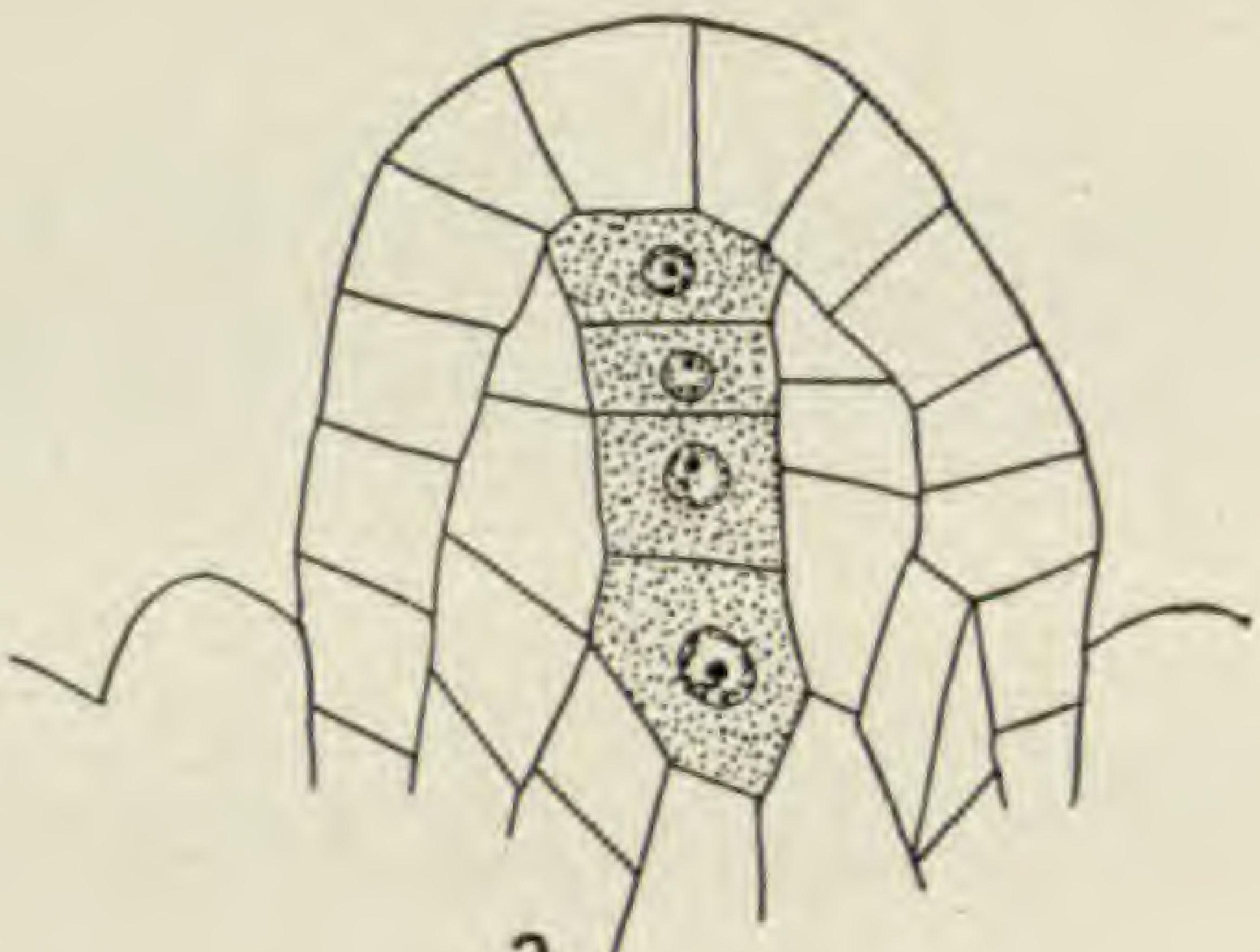

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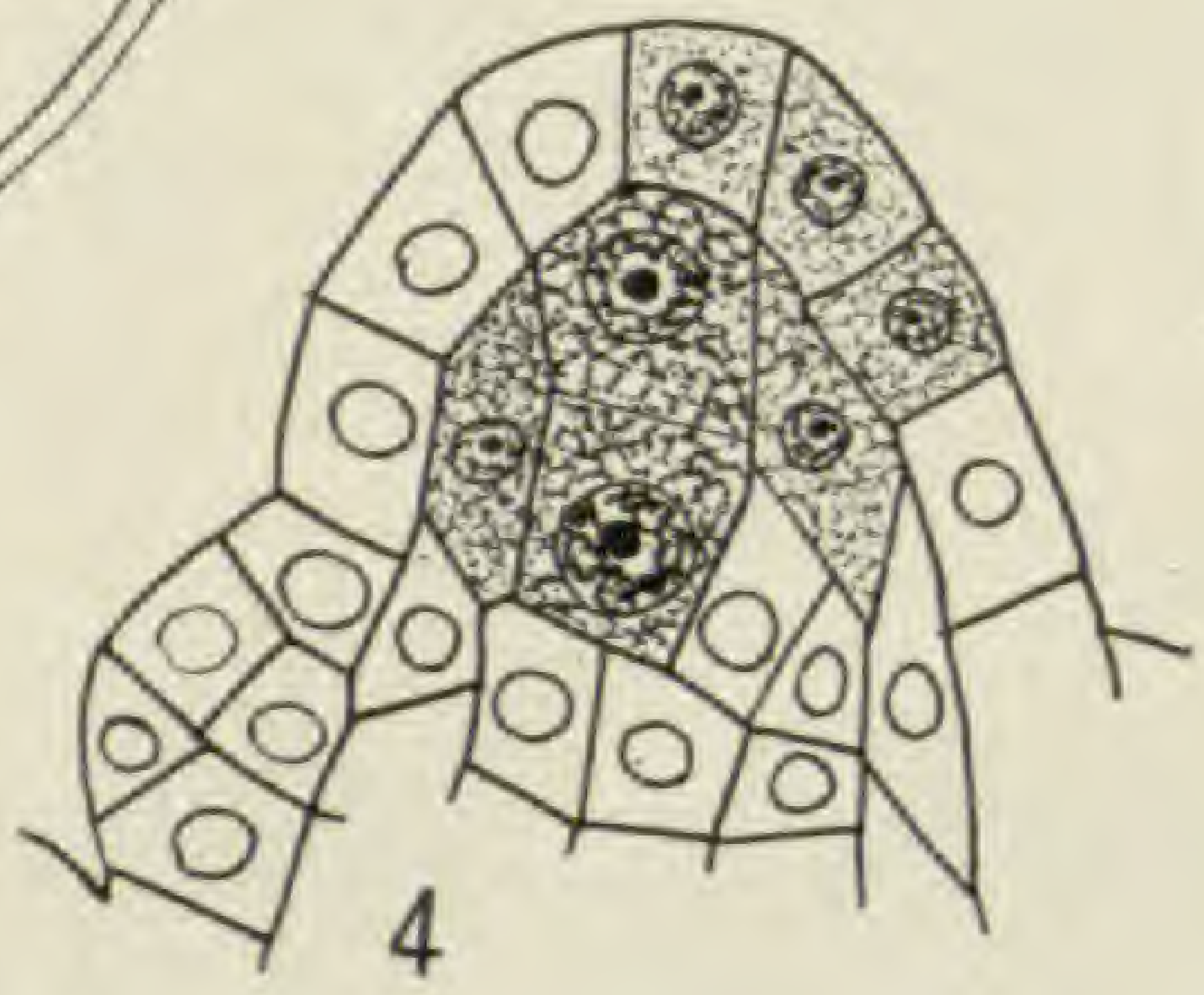

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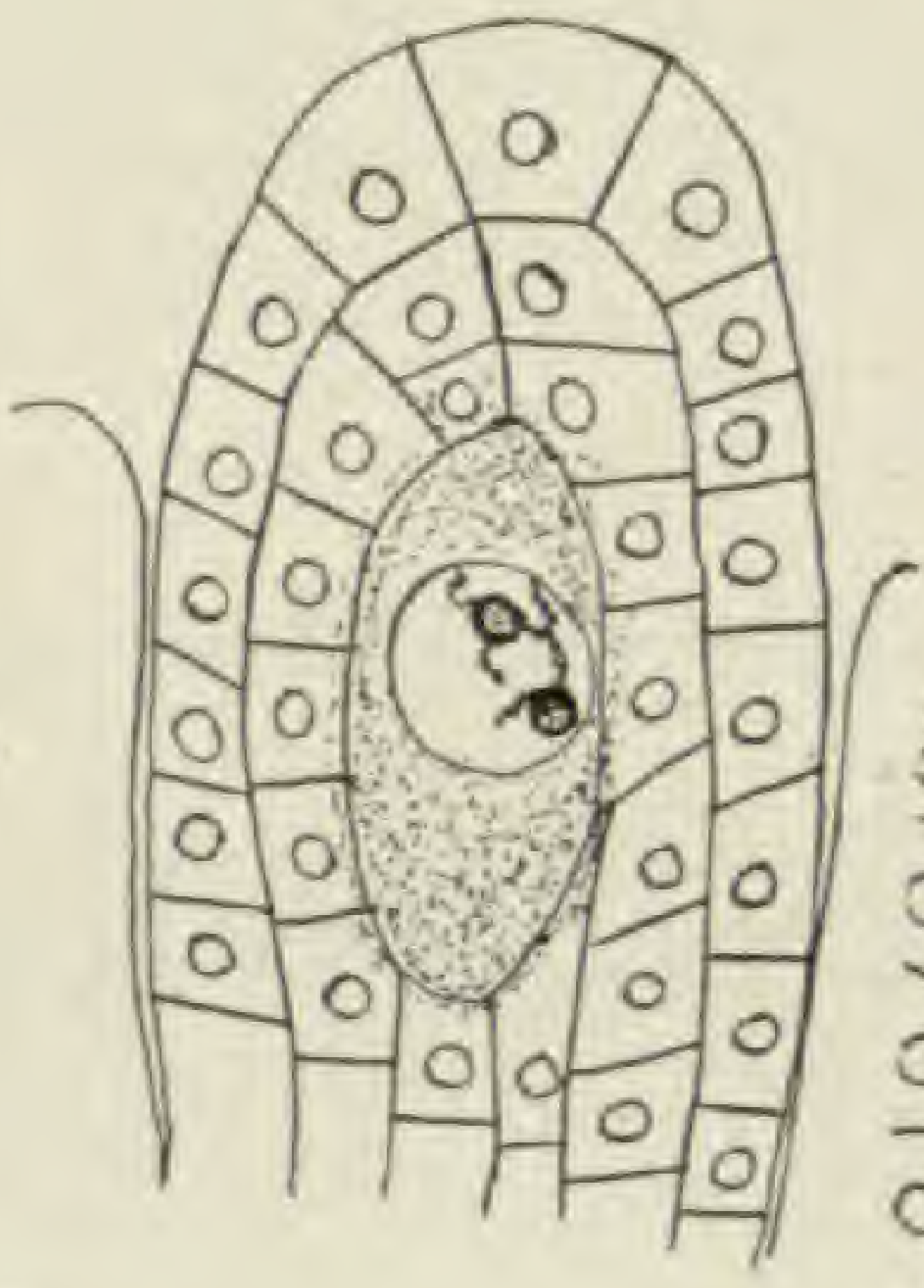

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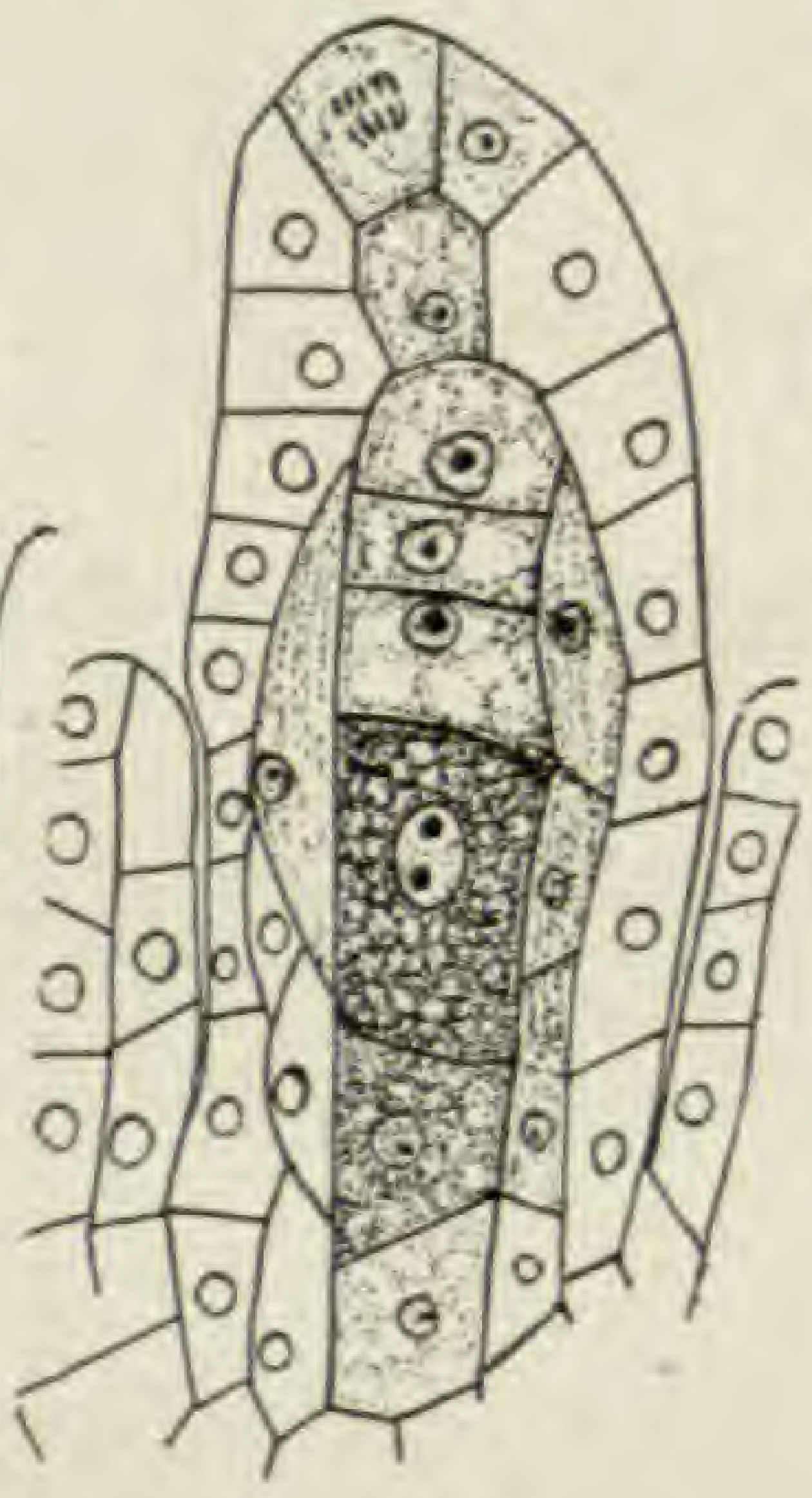

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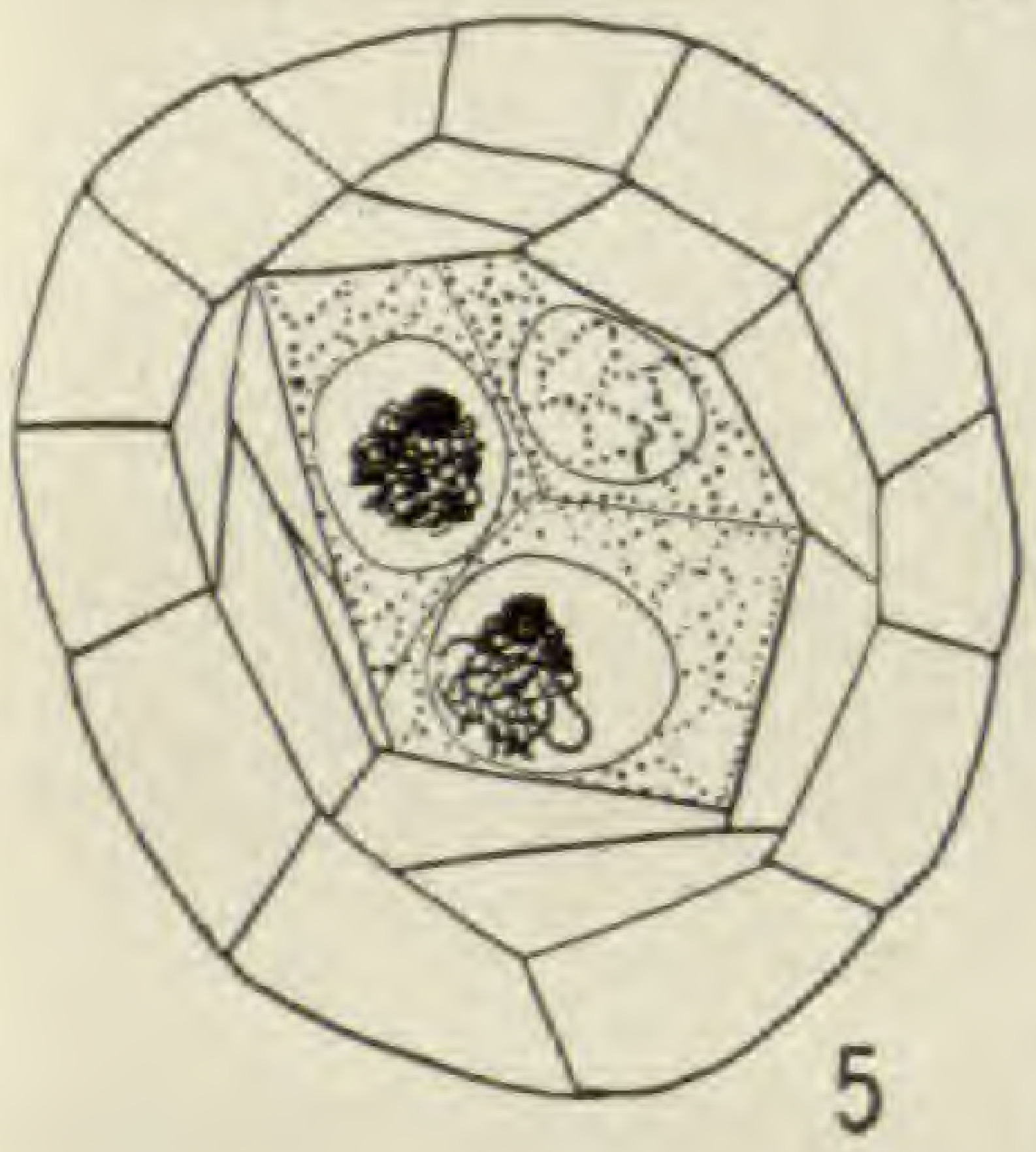

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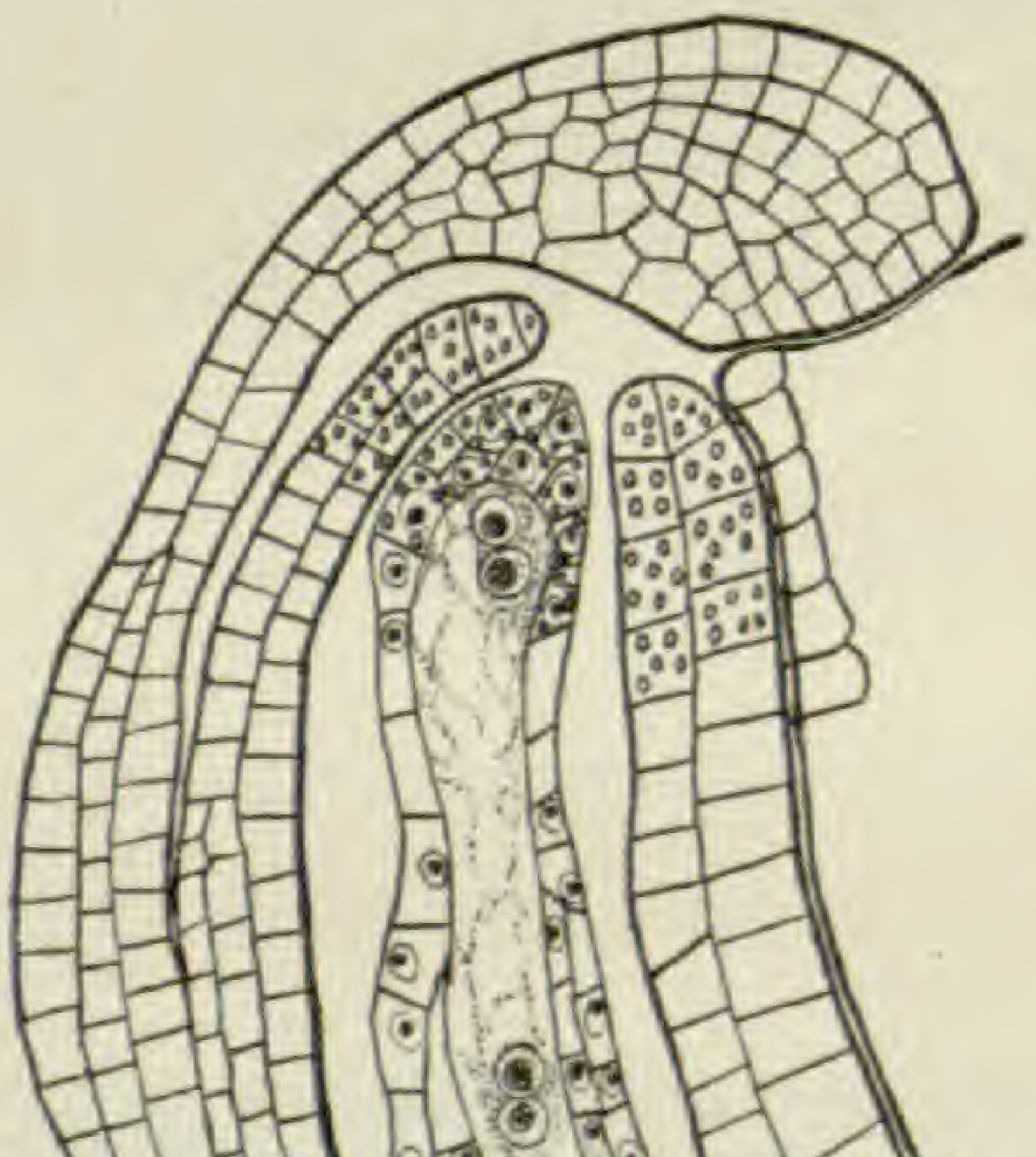

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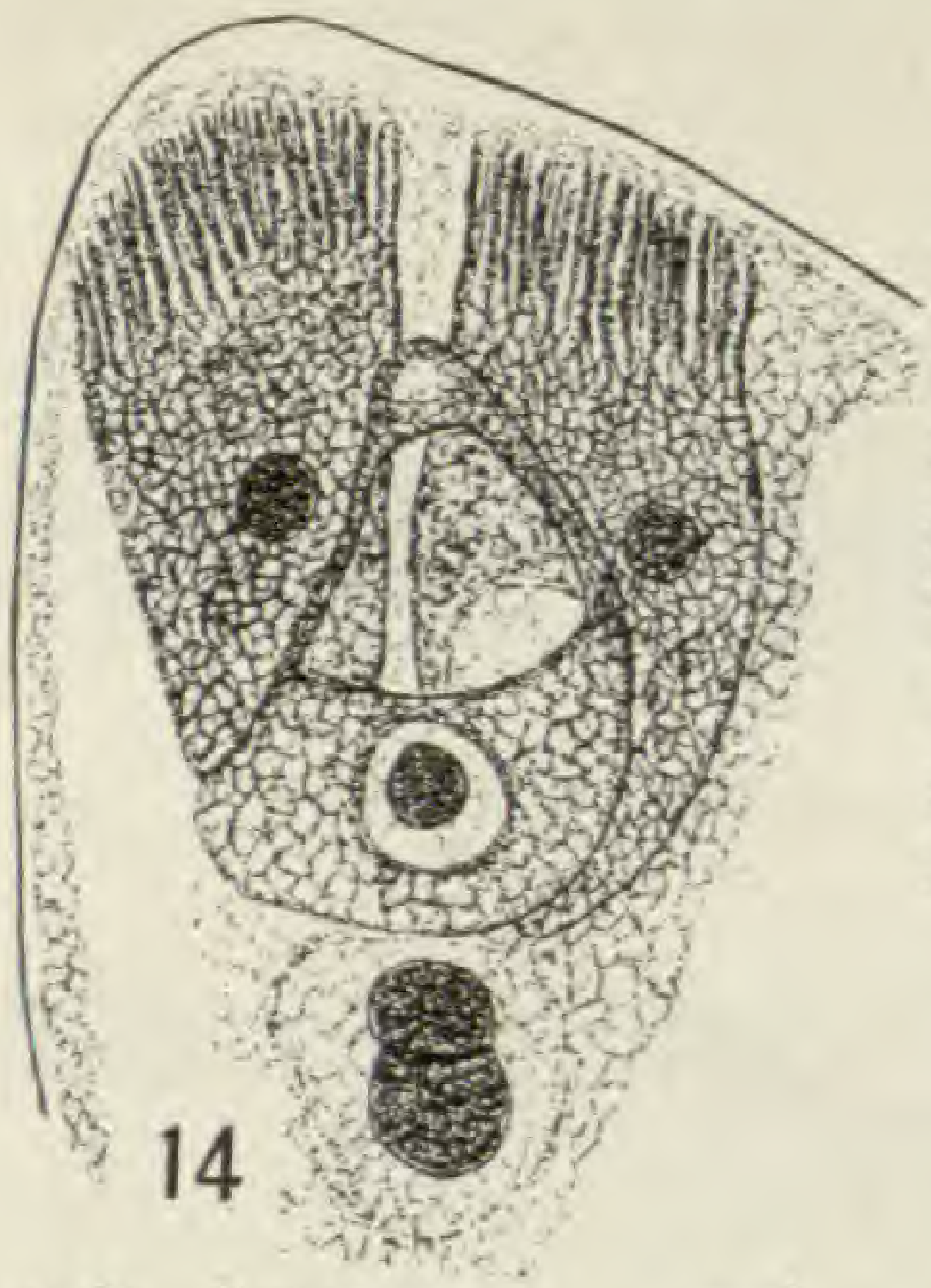
MARTIN on LEGUMINOSAE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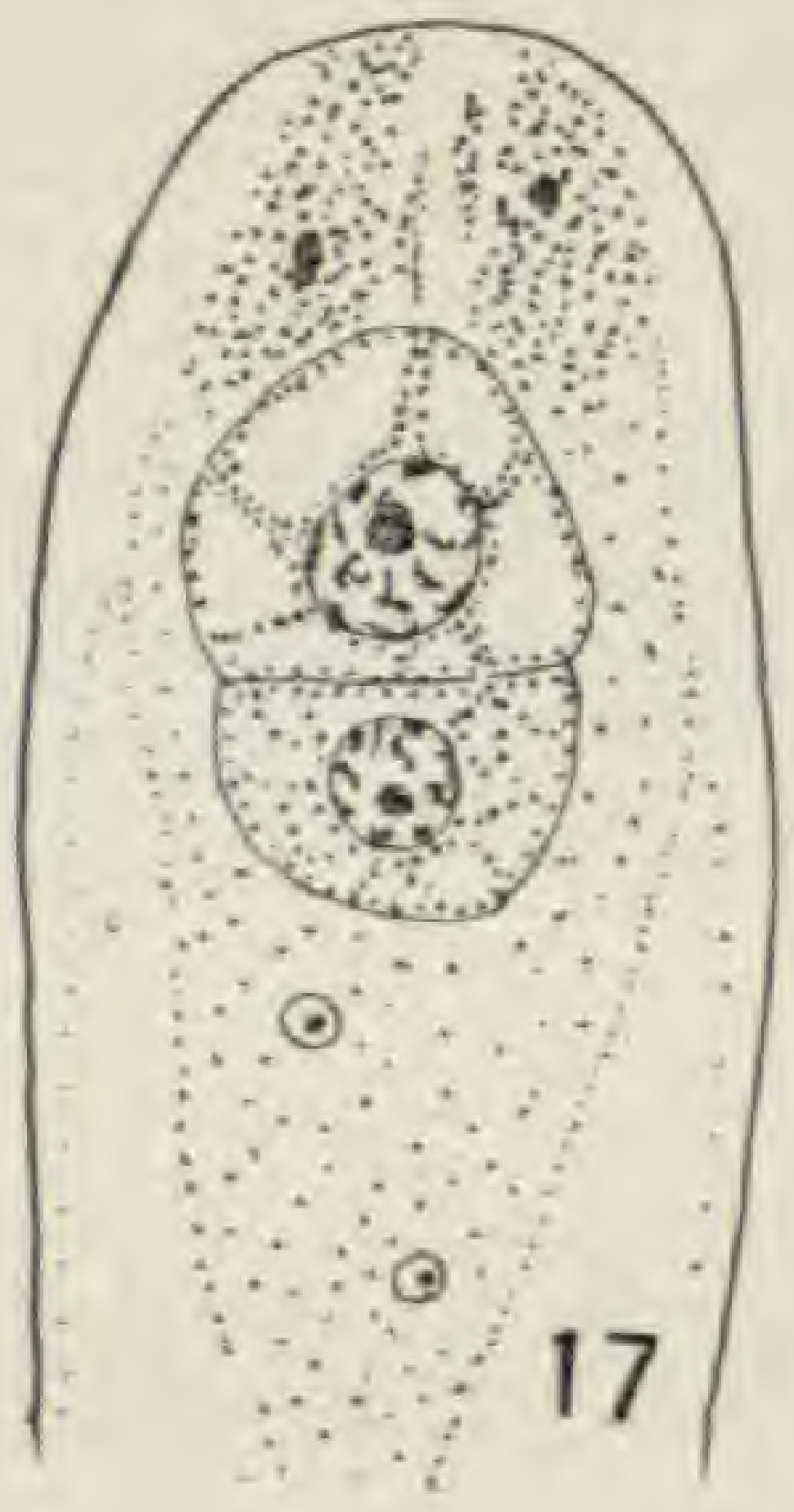
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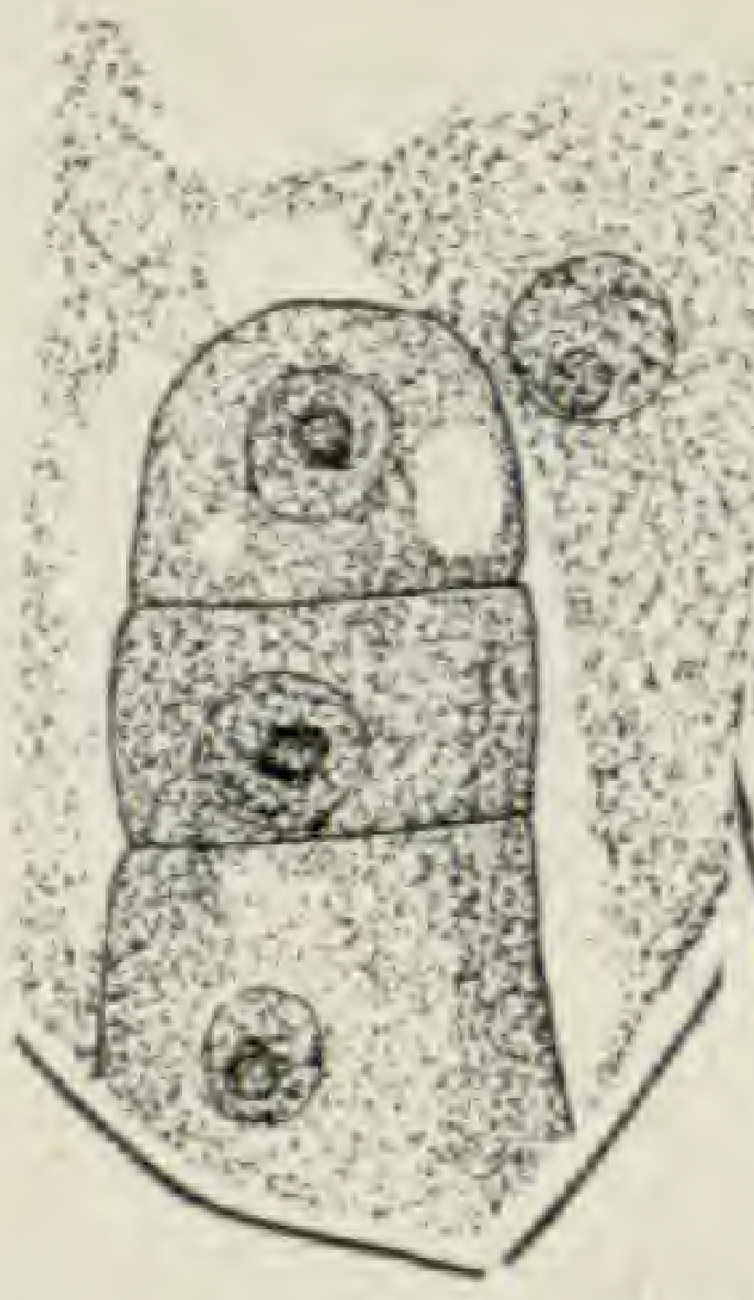
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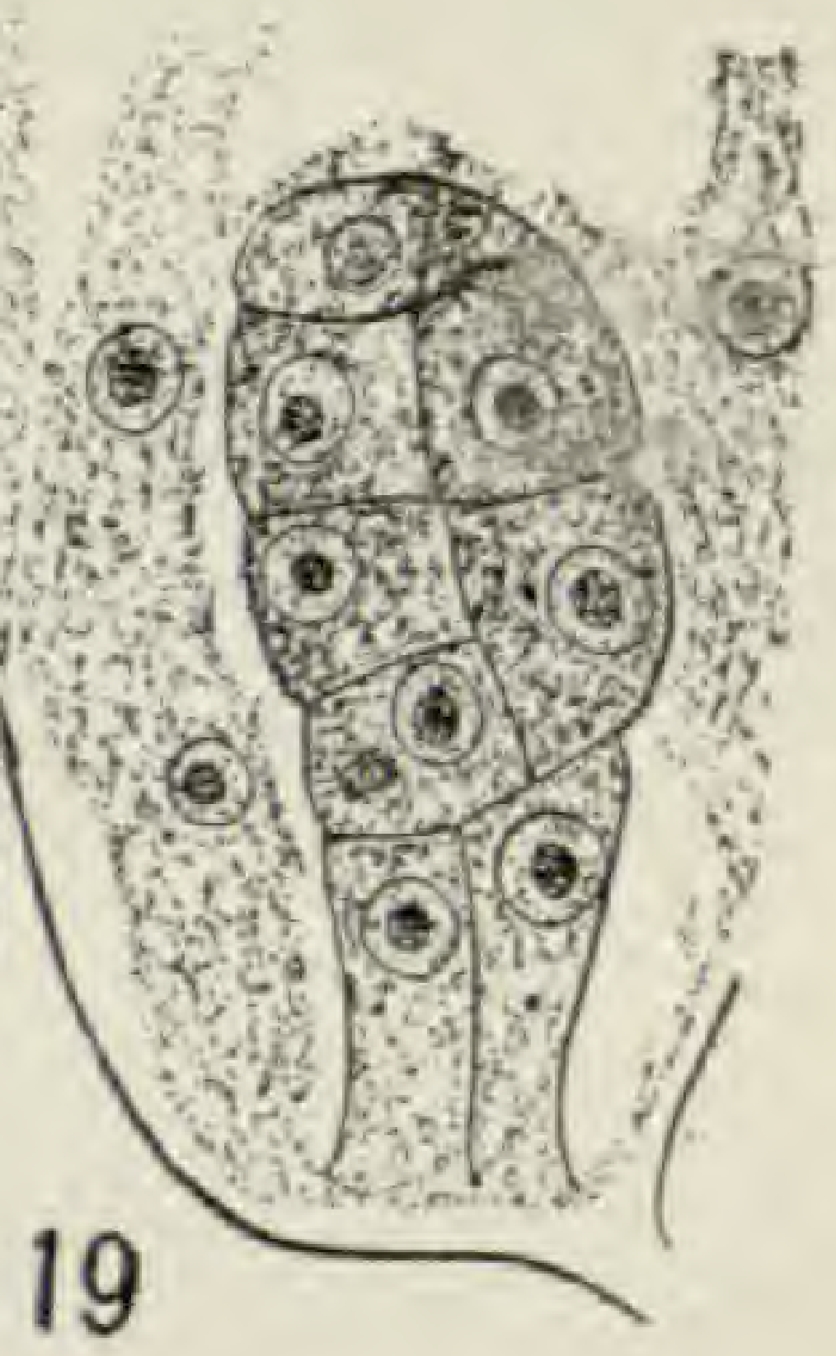
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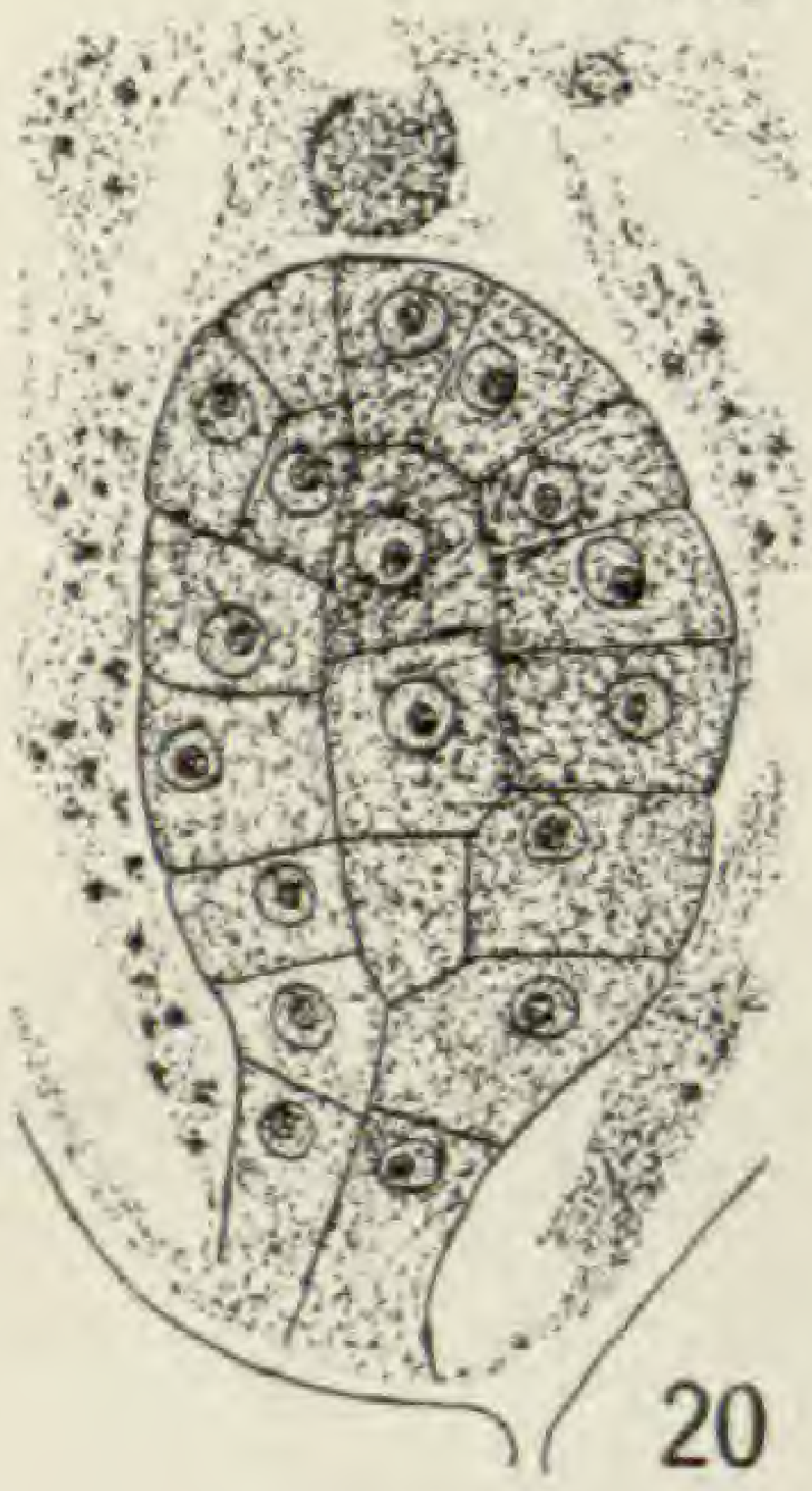
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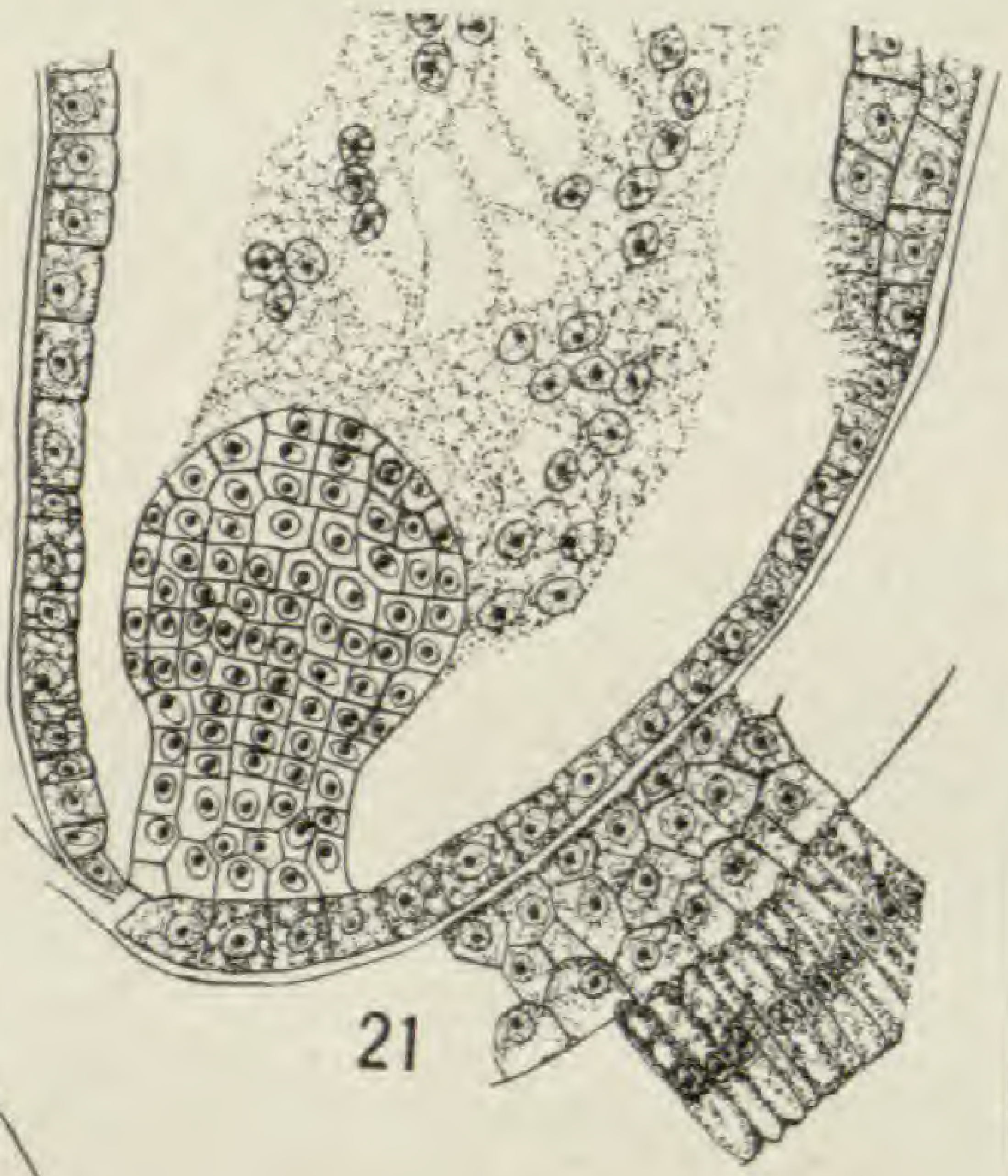
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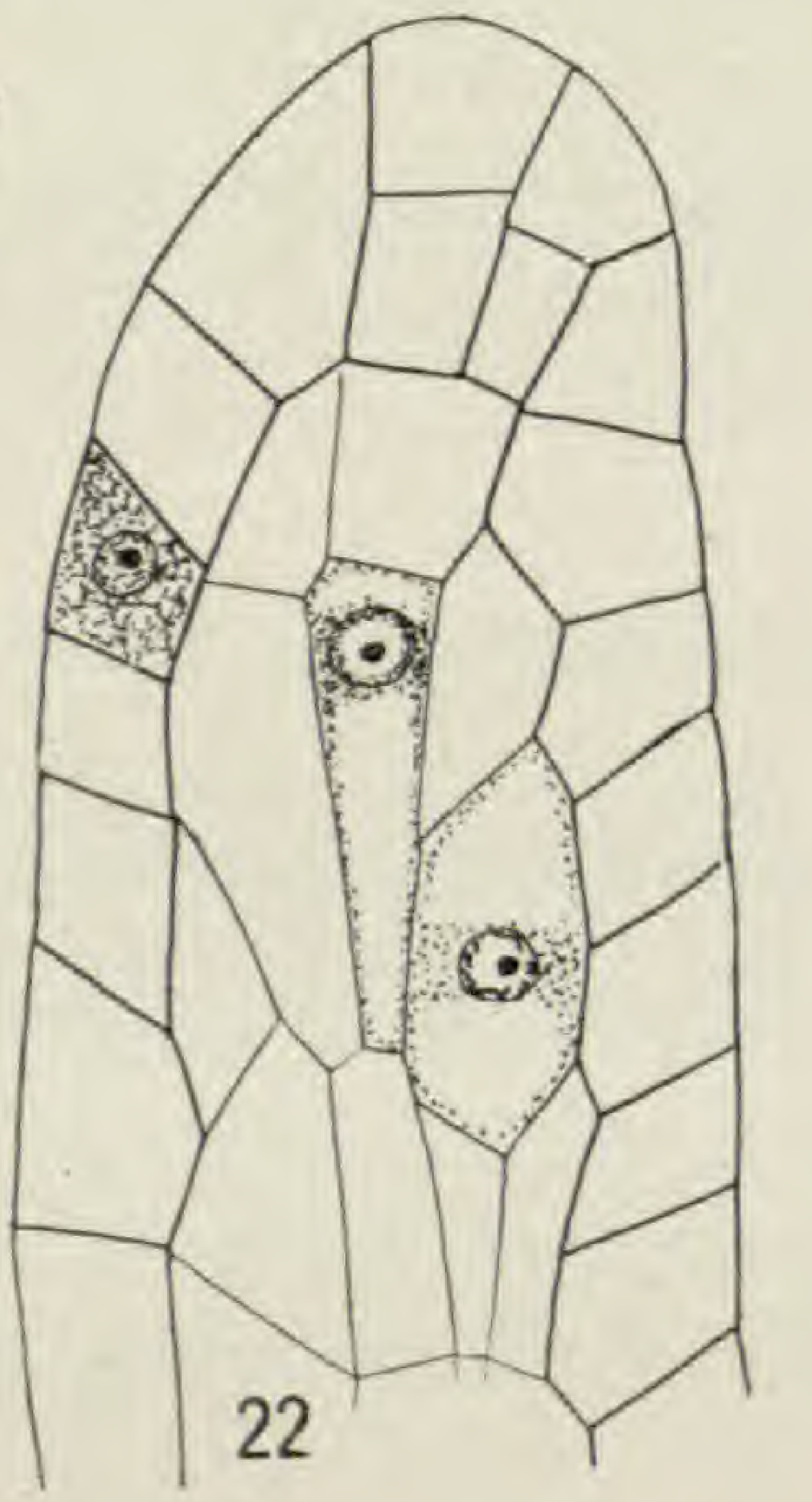
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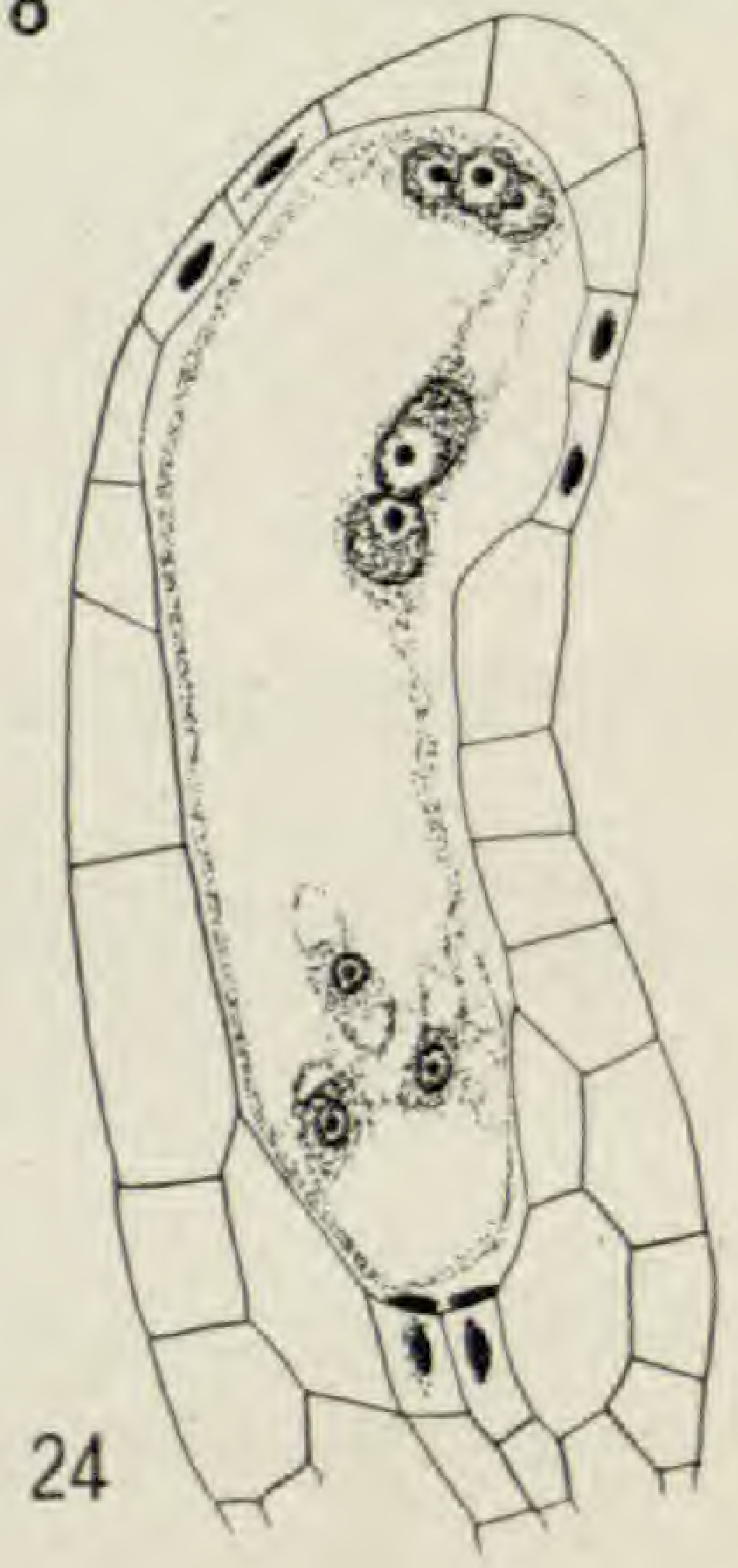
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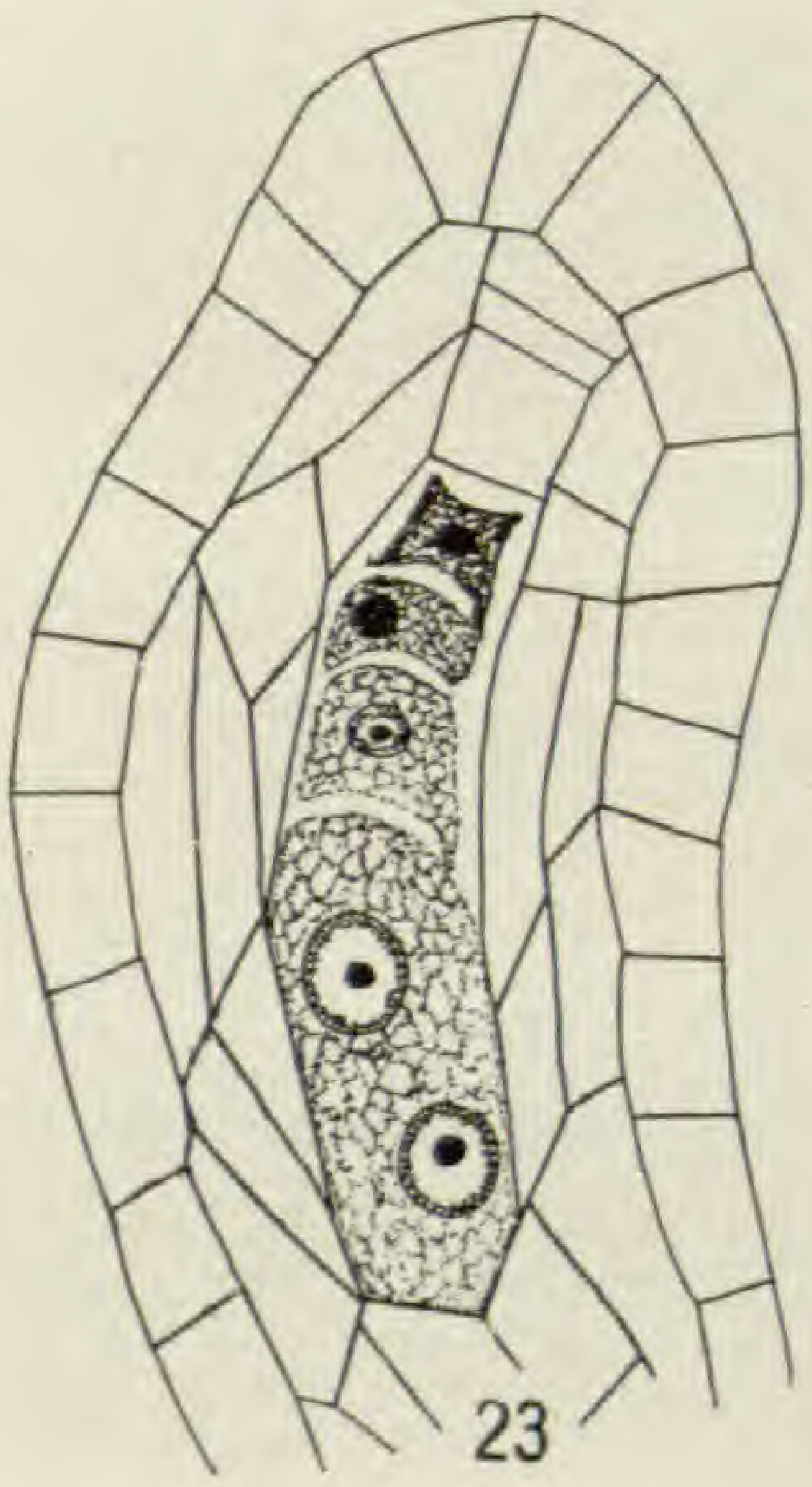
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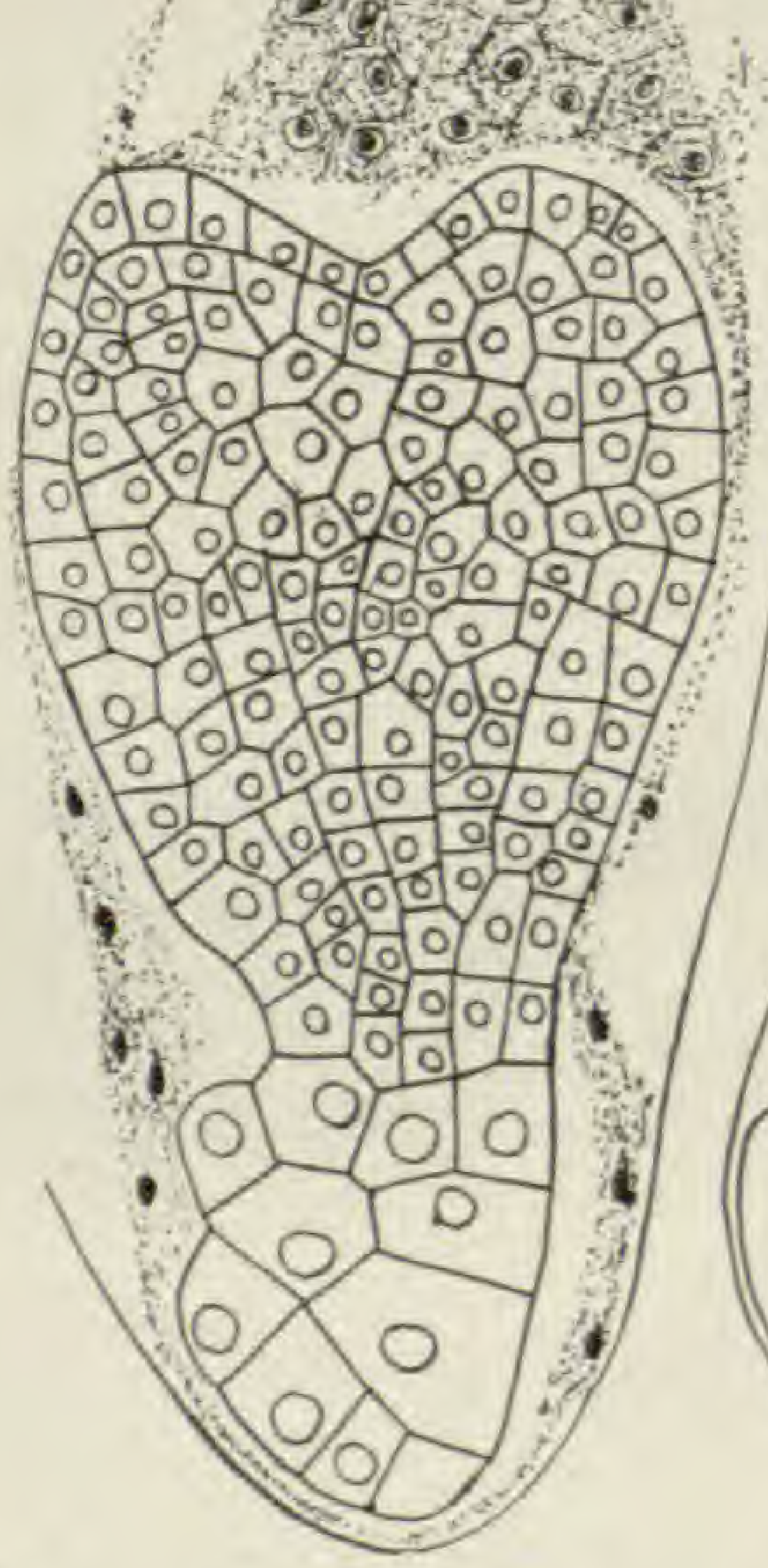
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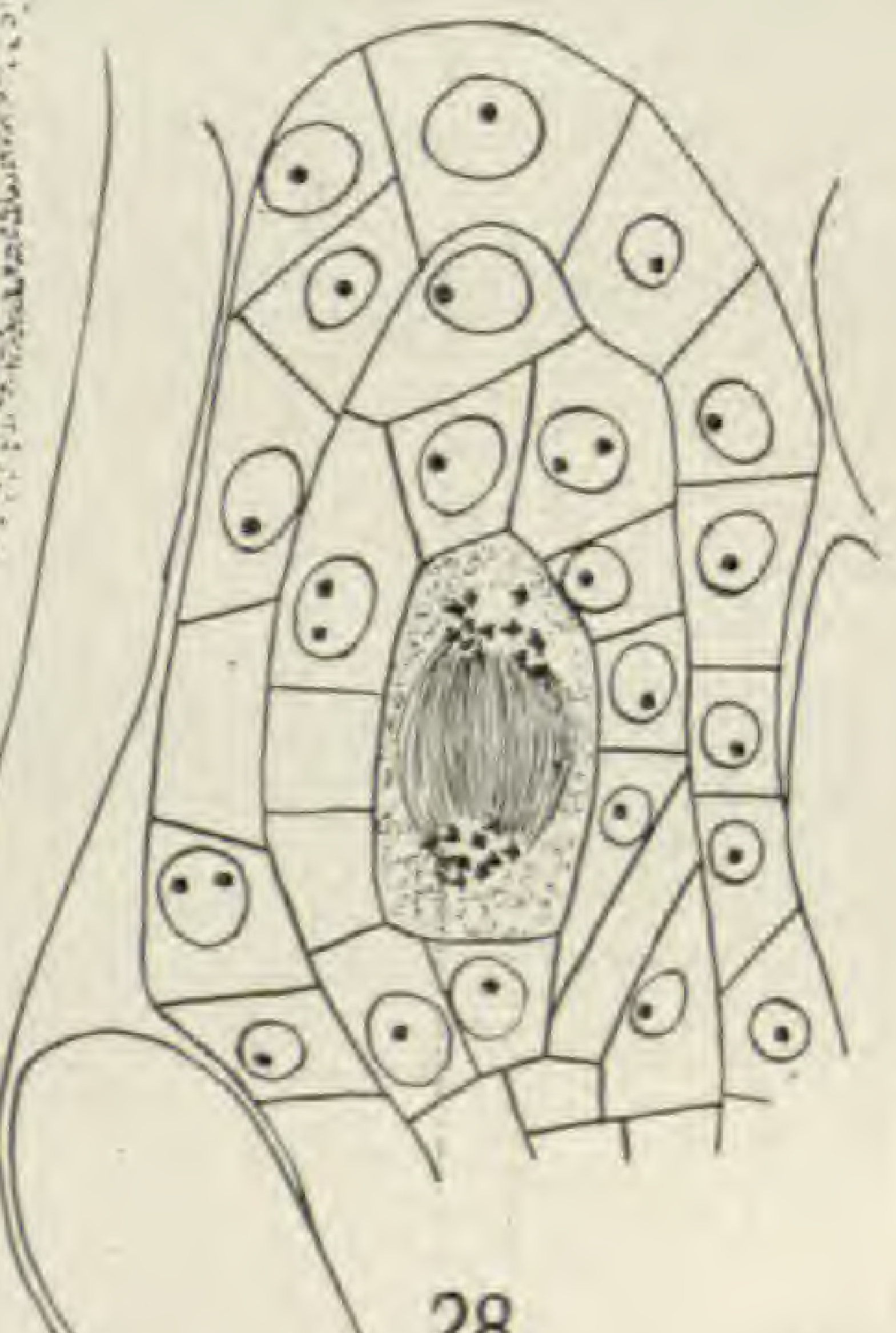
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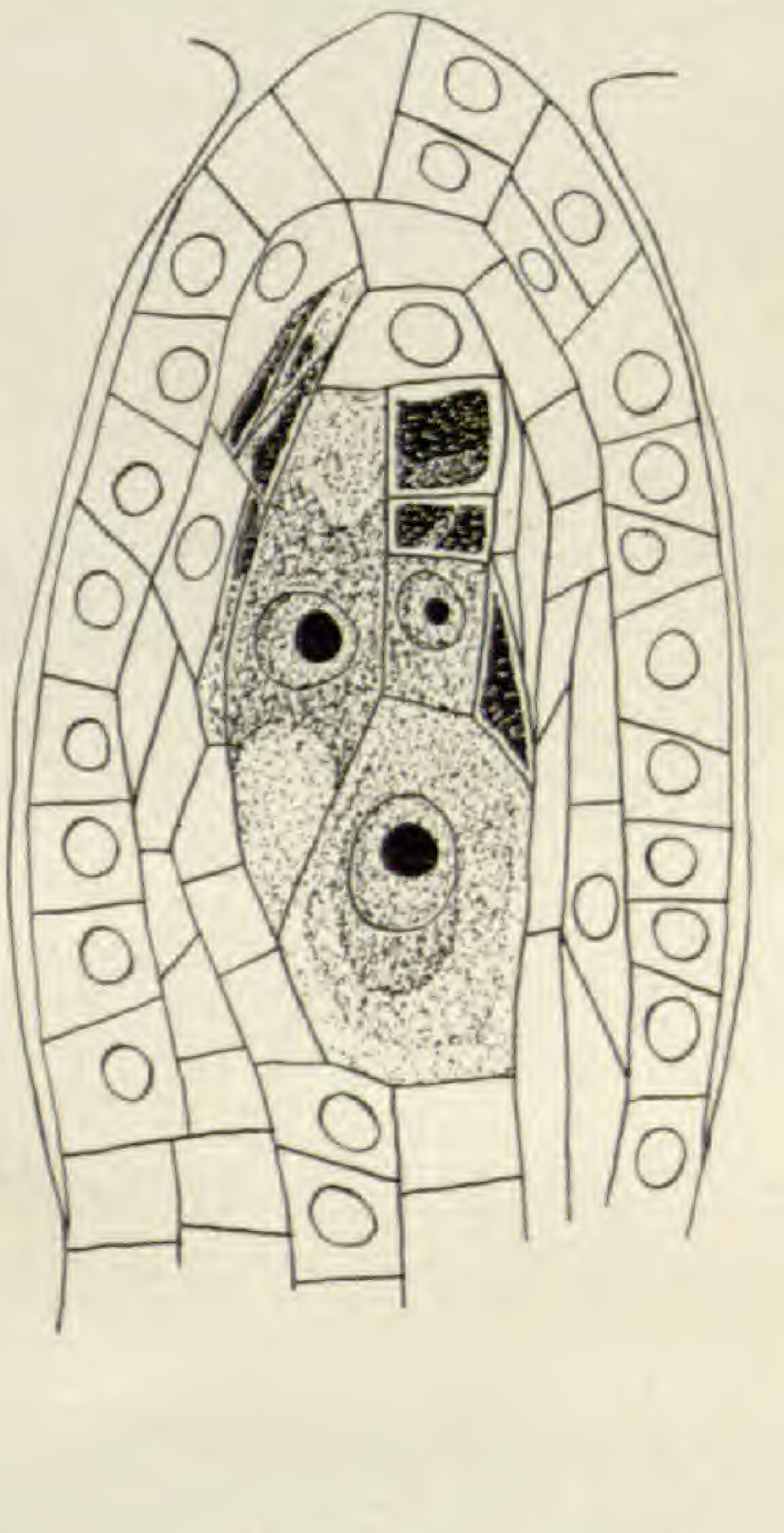
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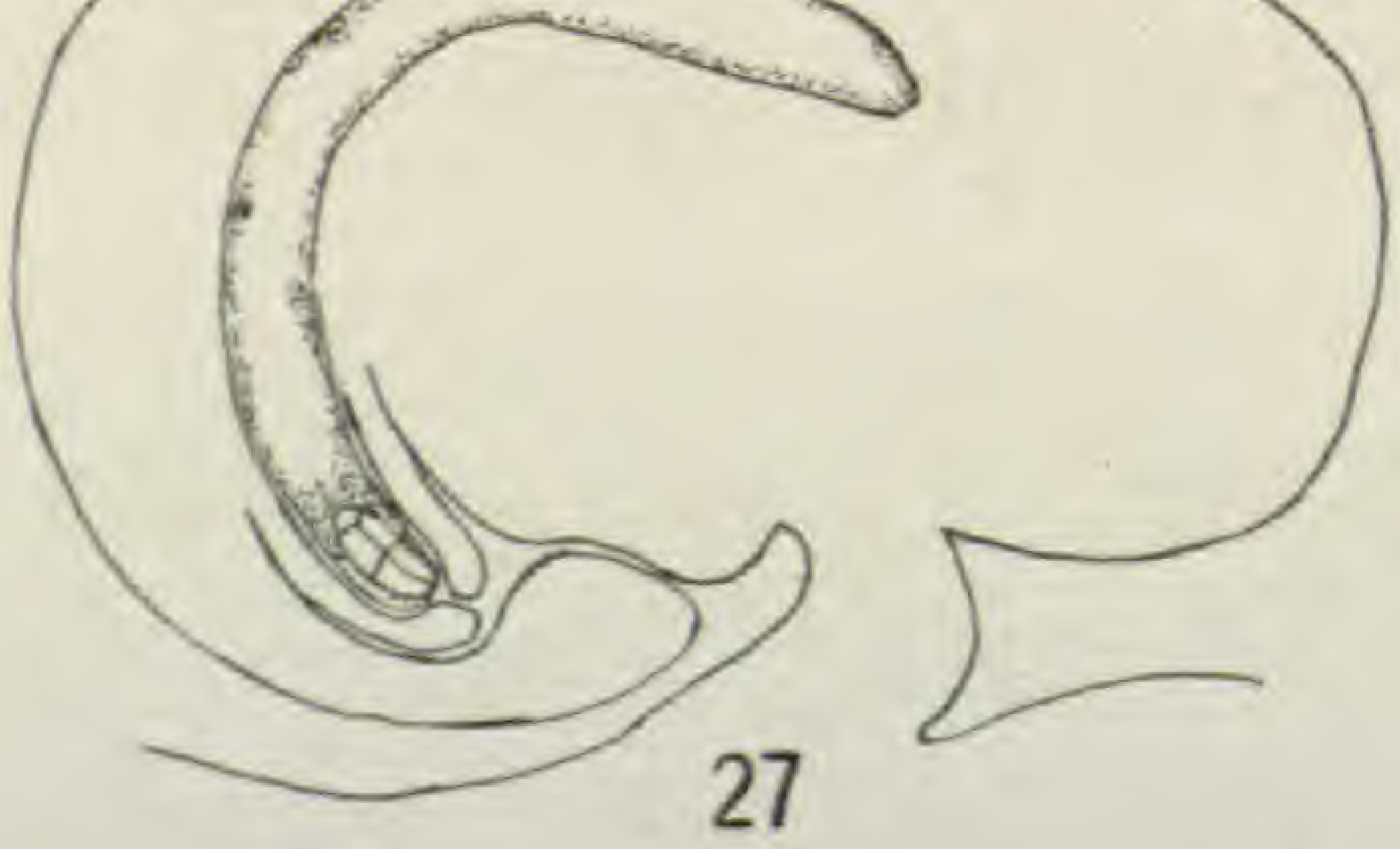
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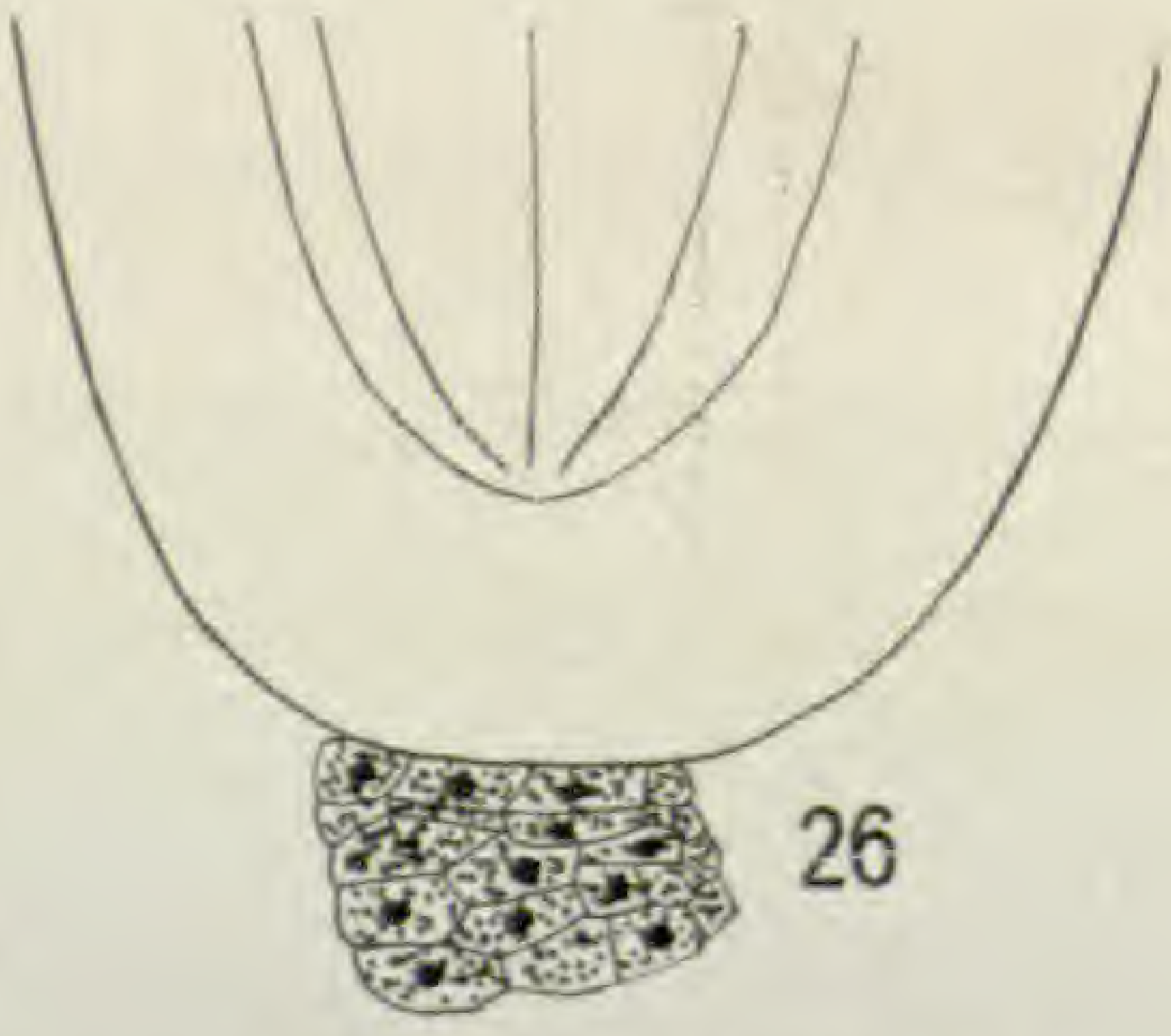
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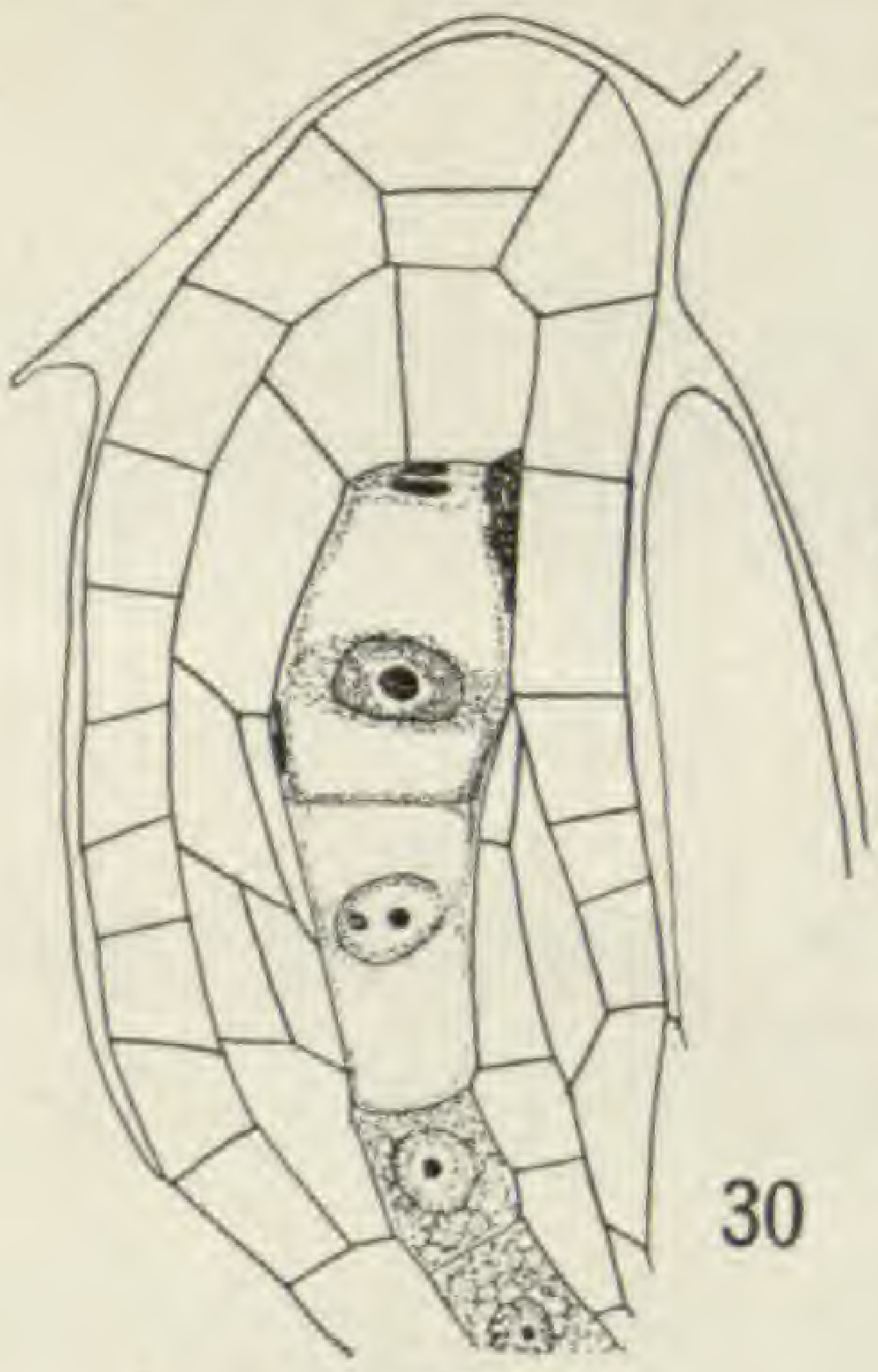
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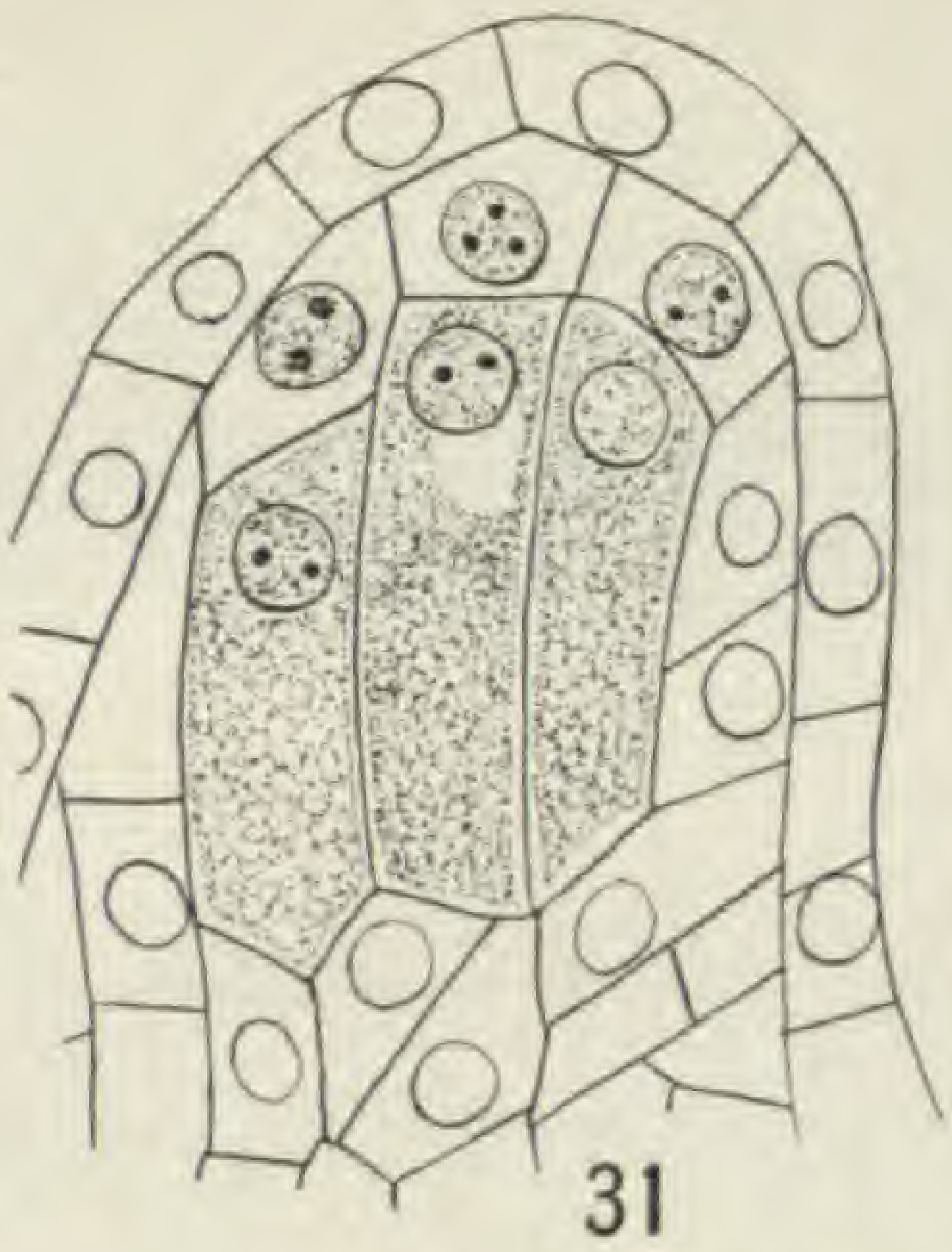
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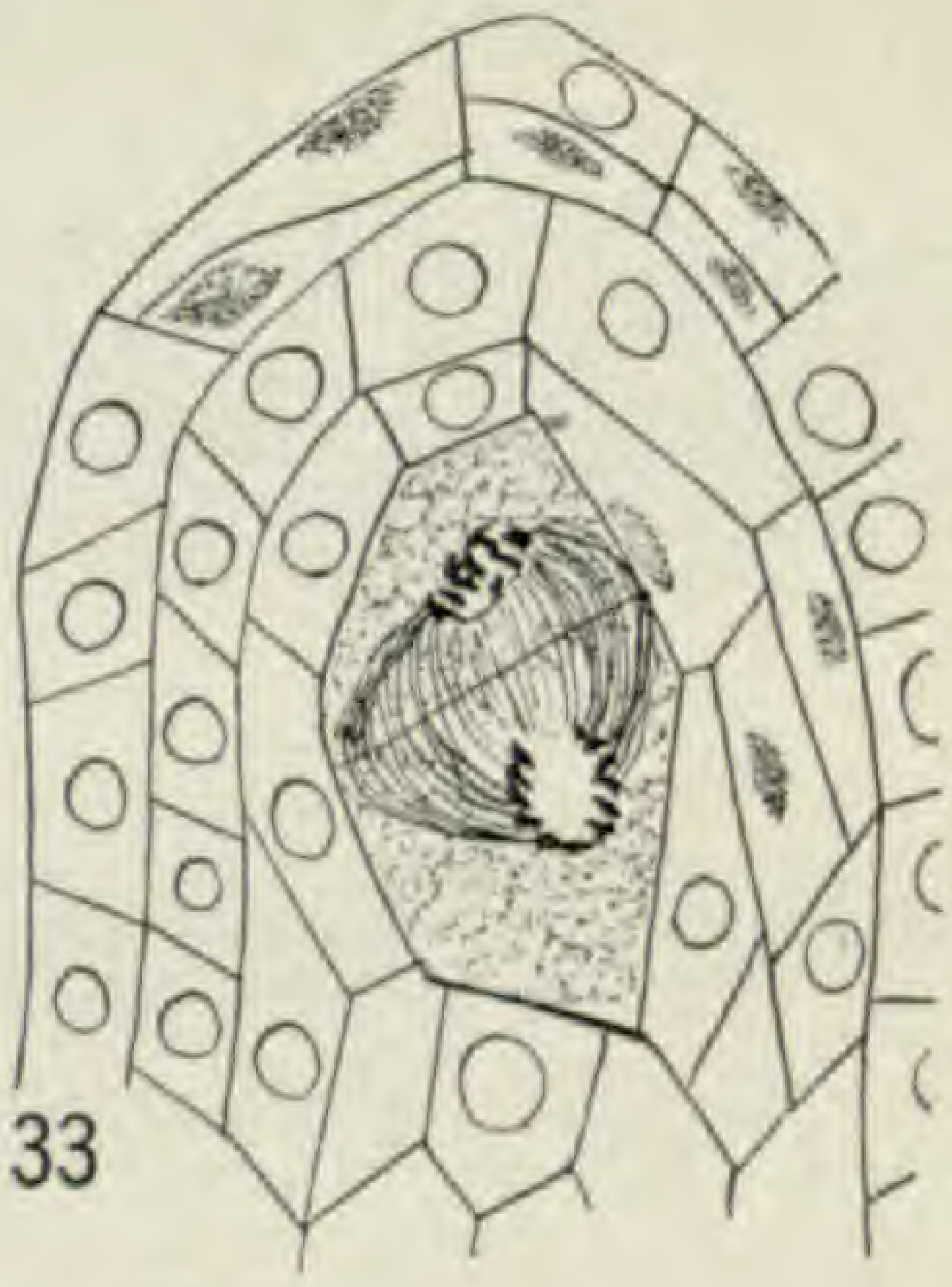
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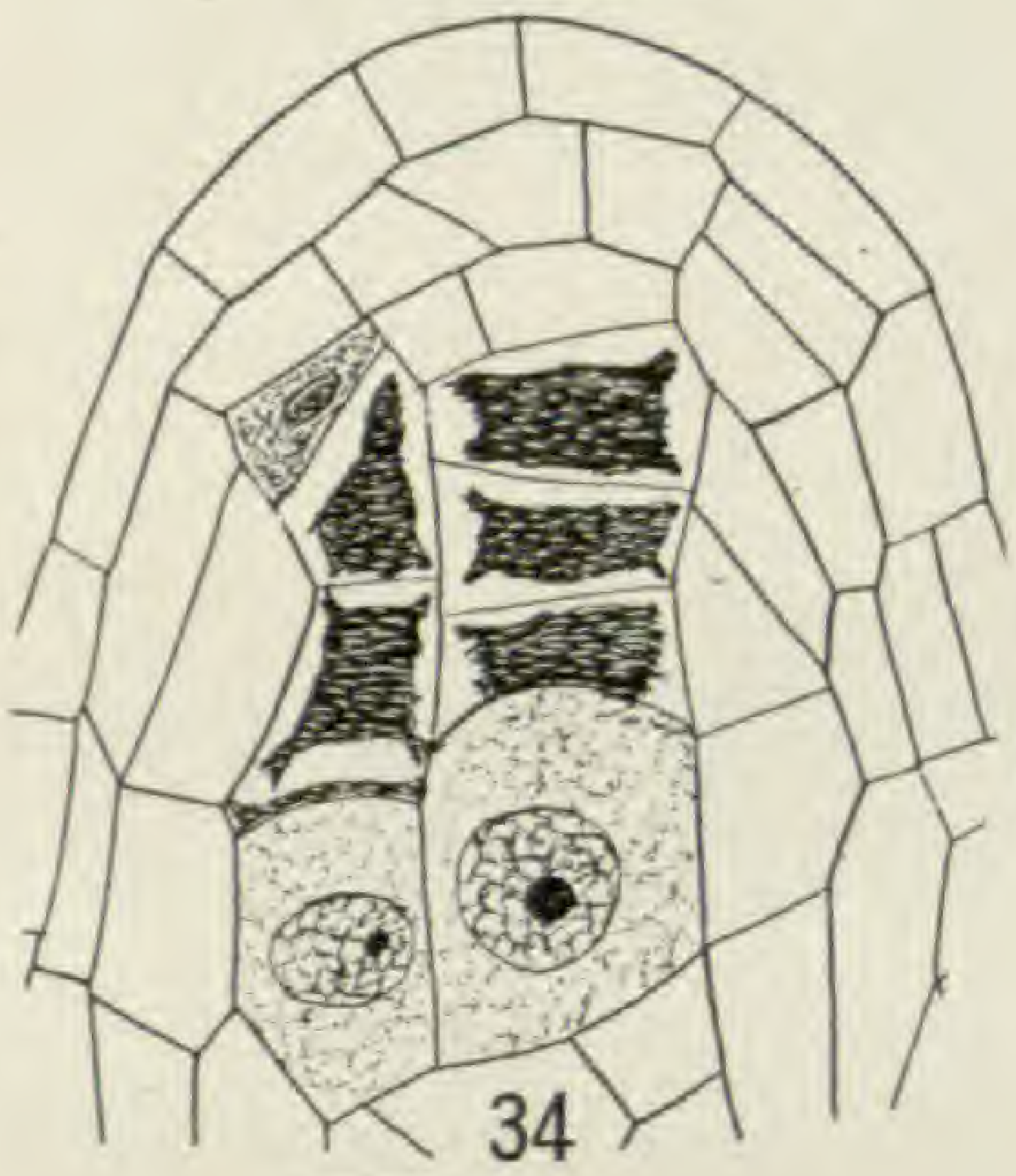
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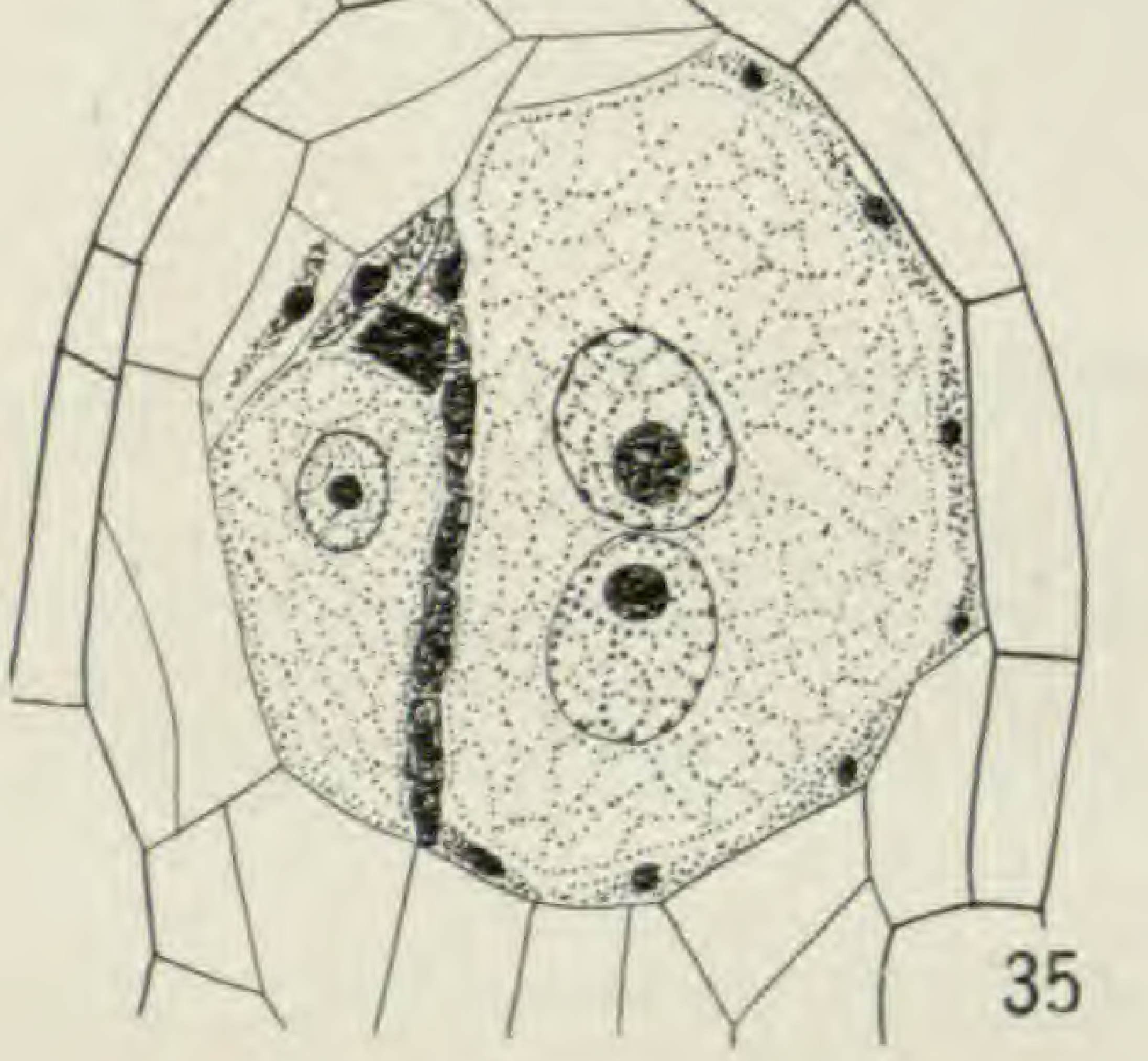
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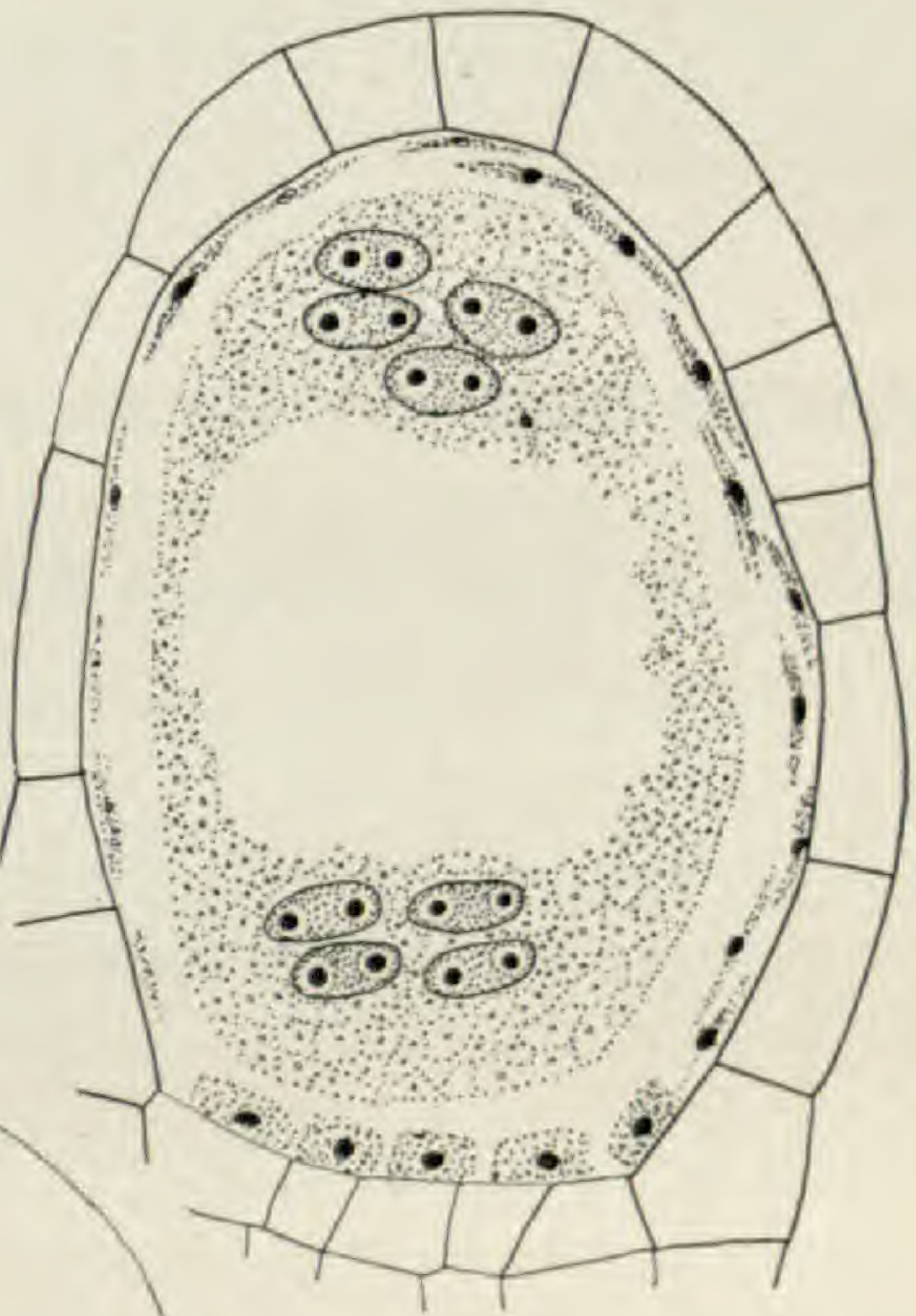
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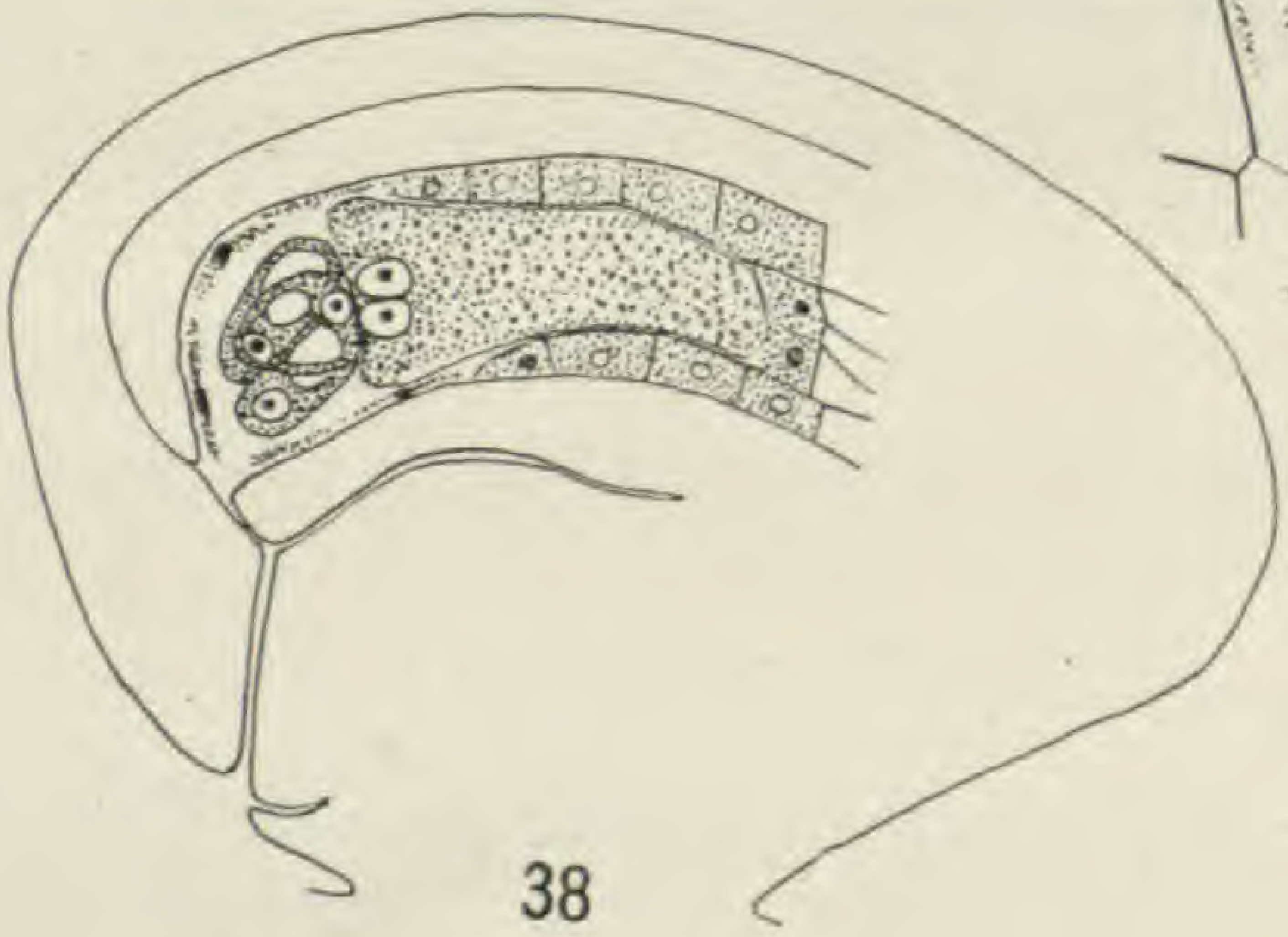
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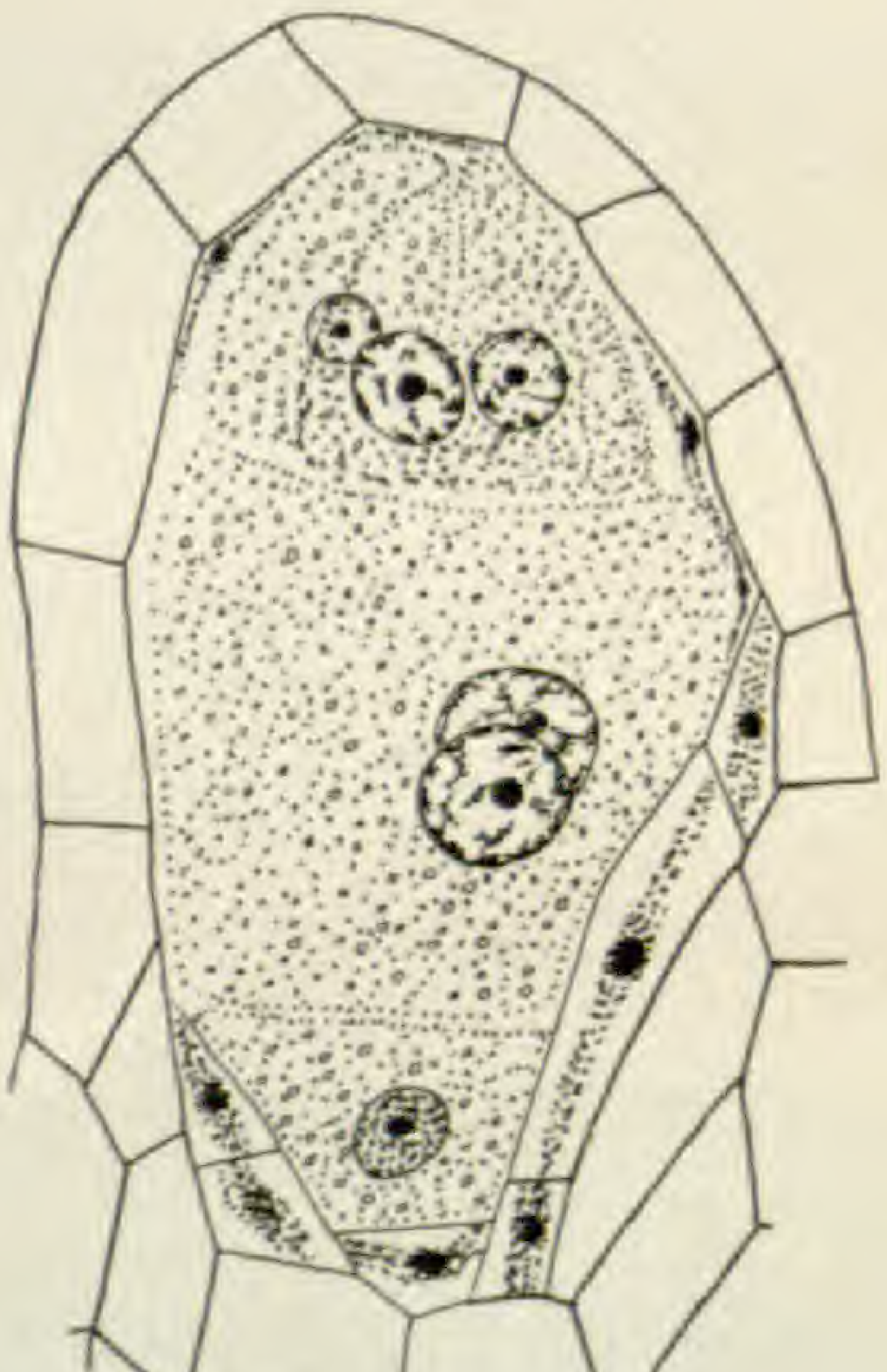
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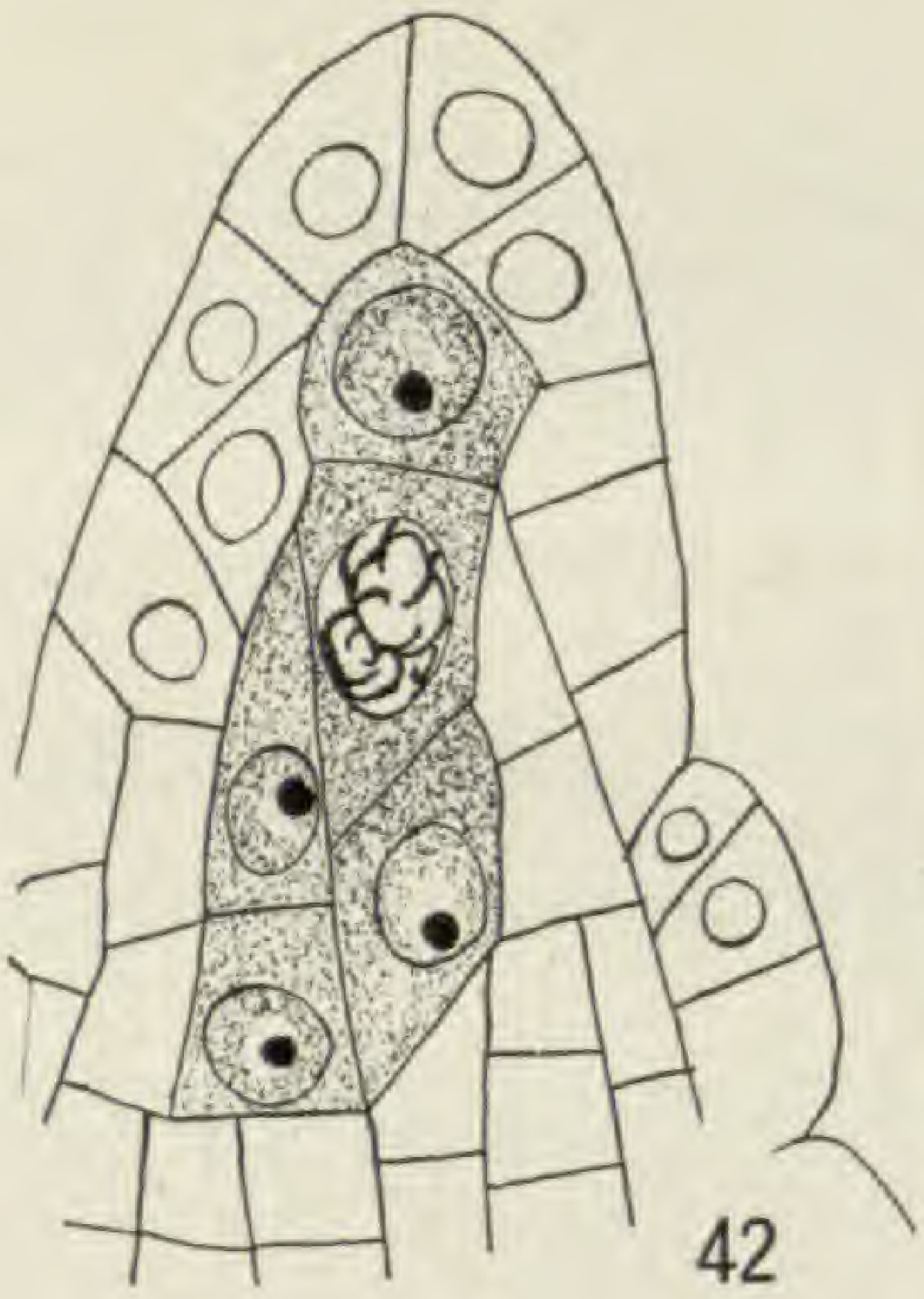

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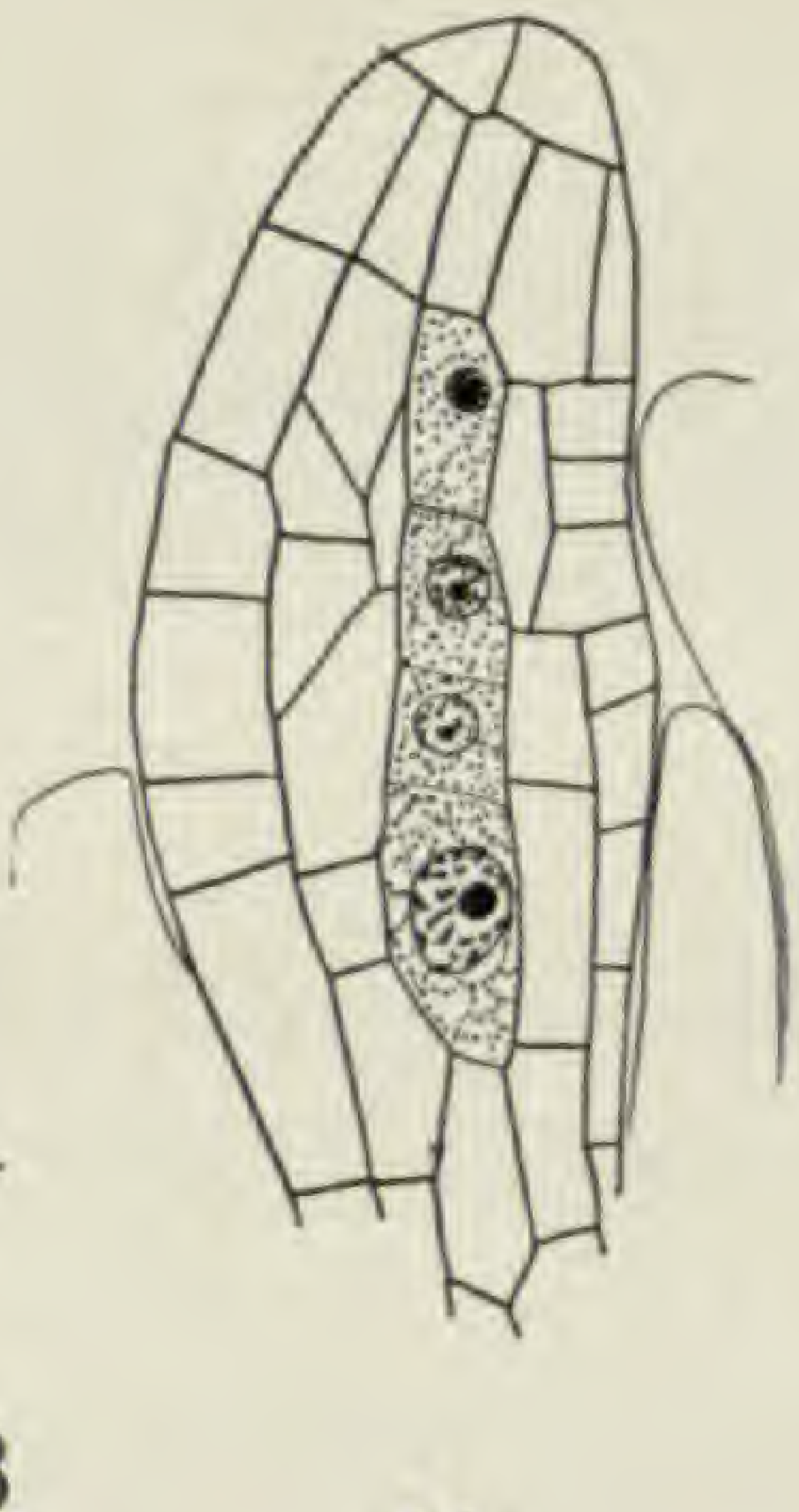

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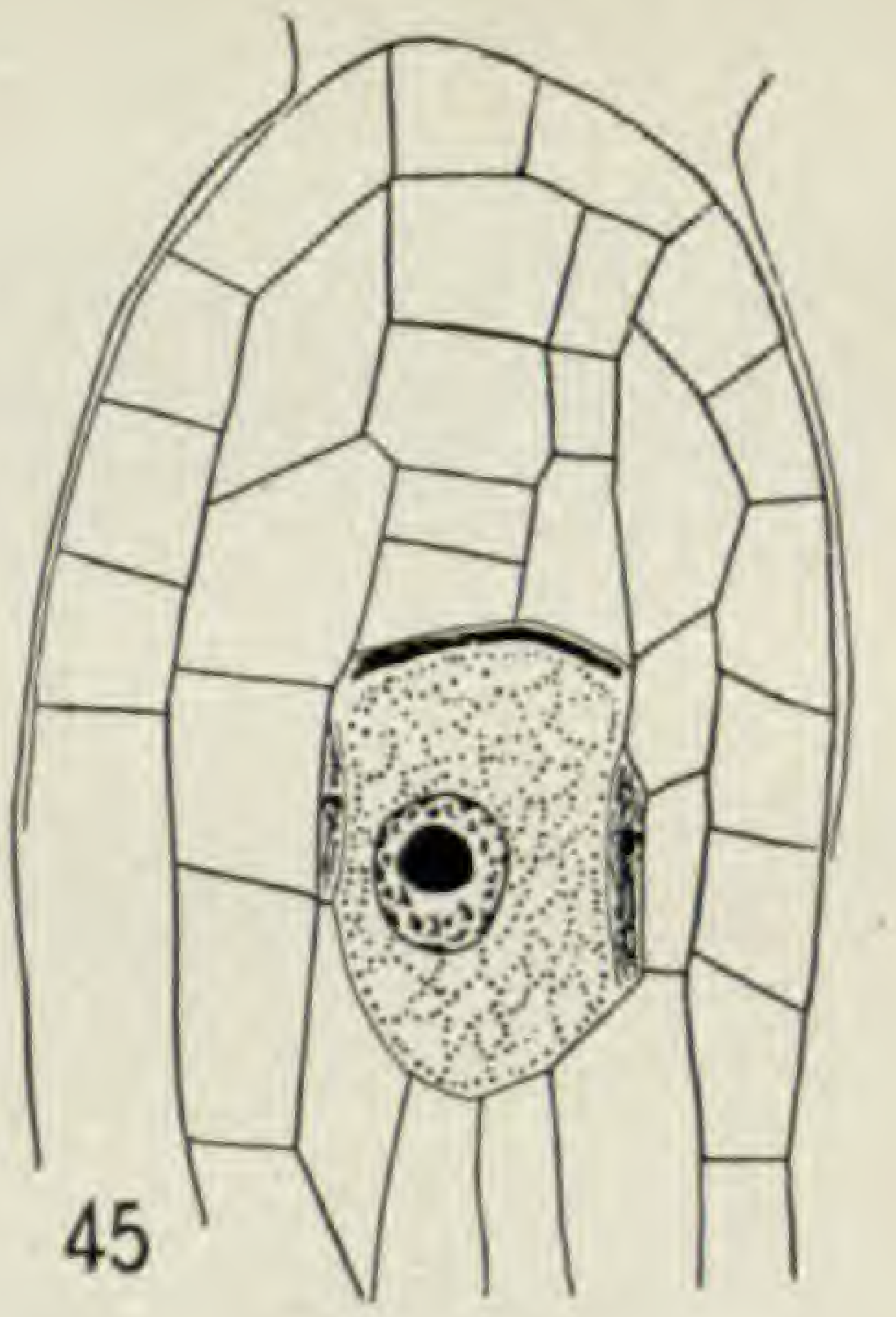

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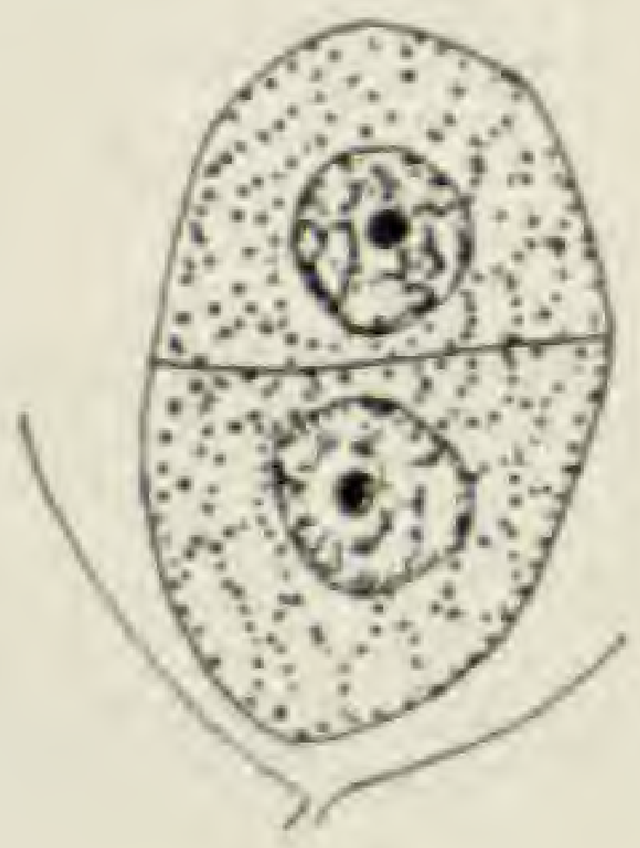

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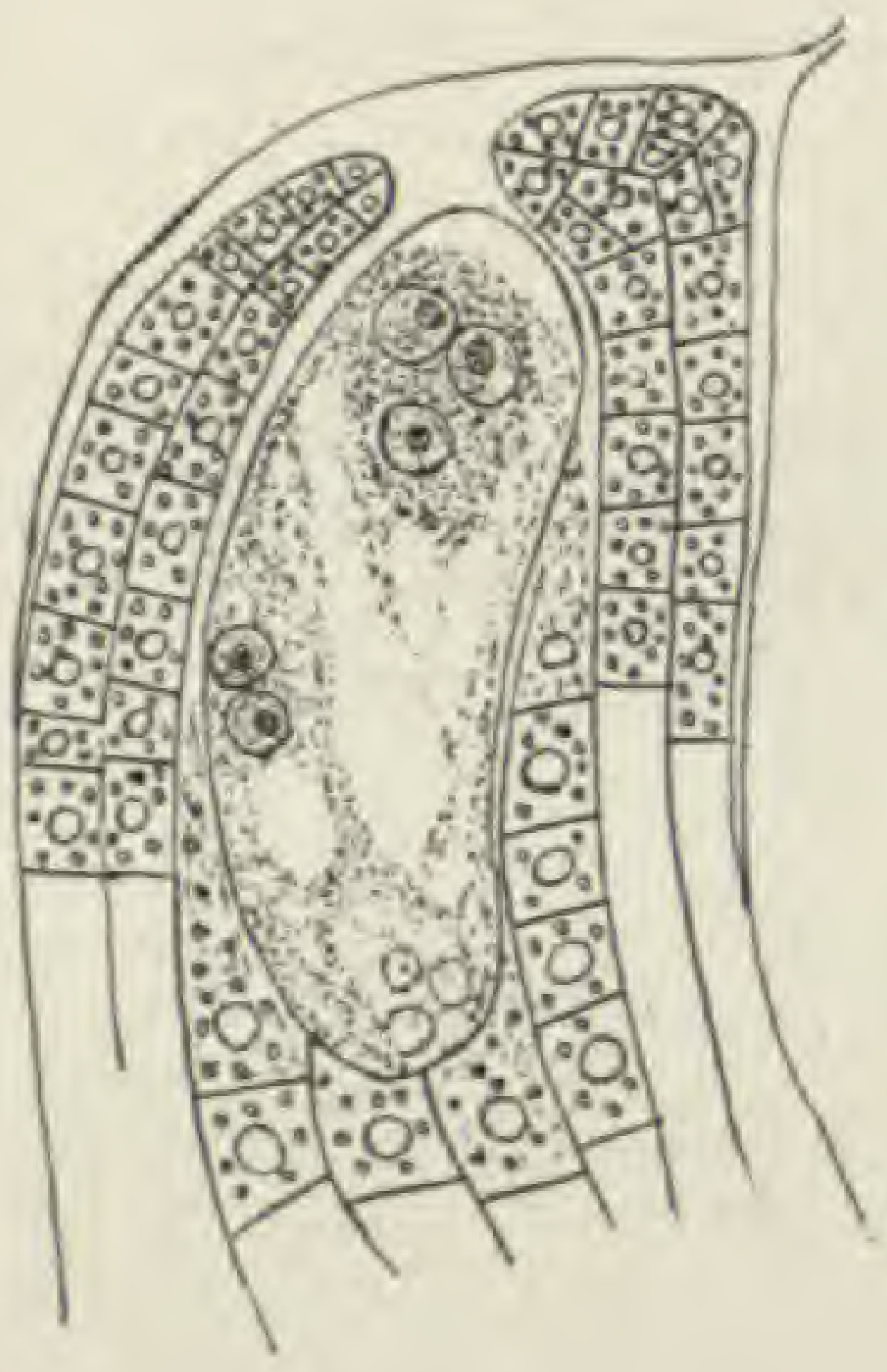

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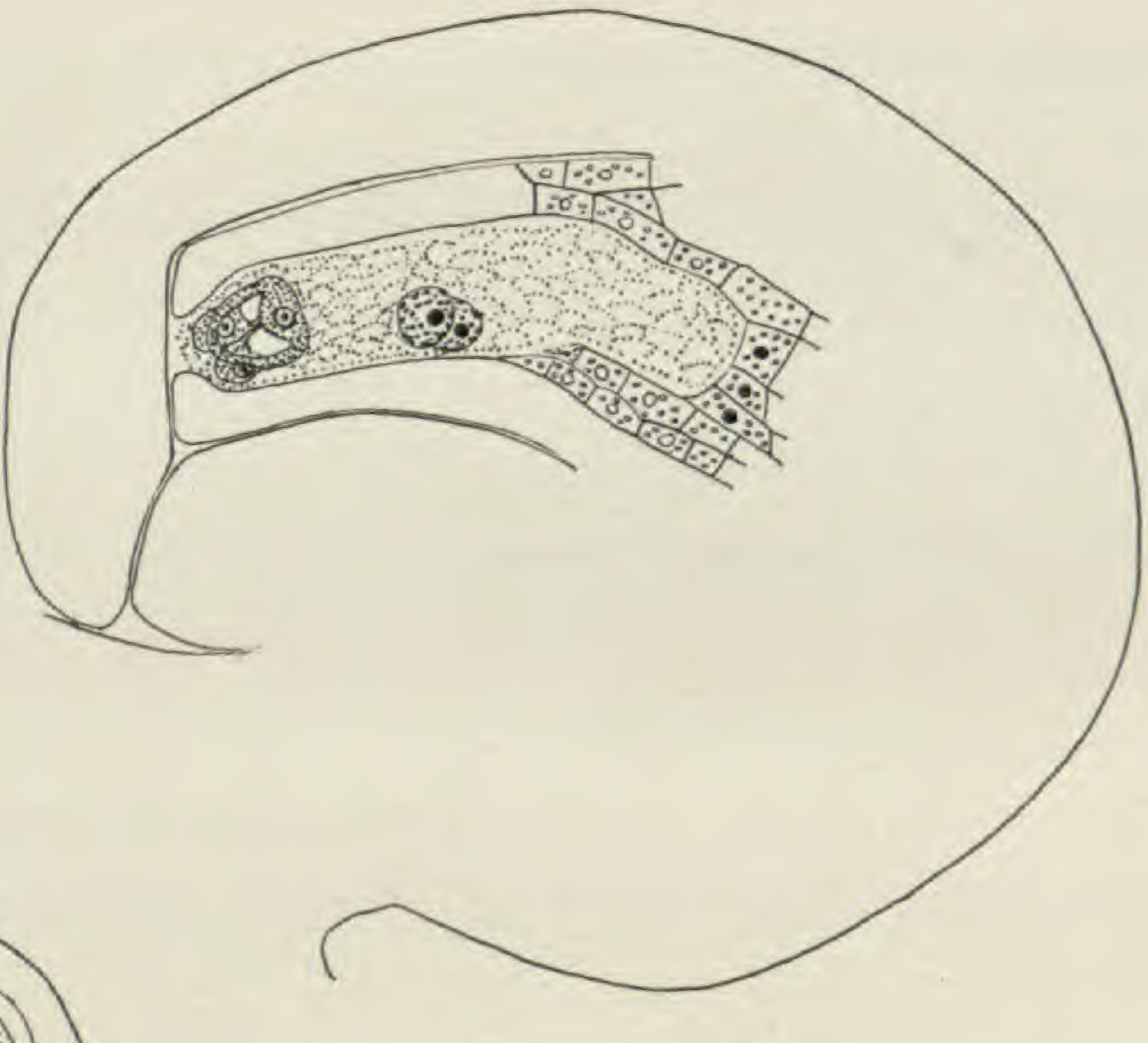

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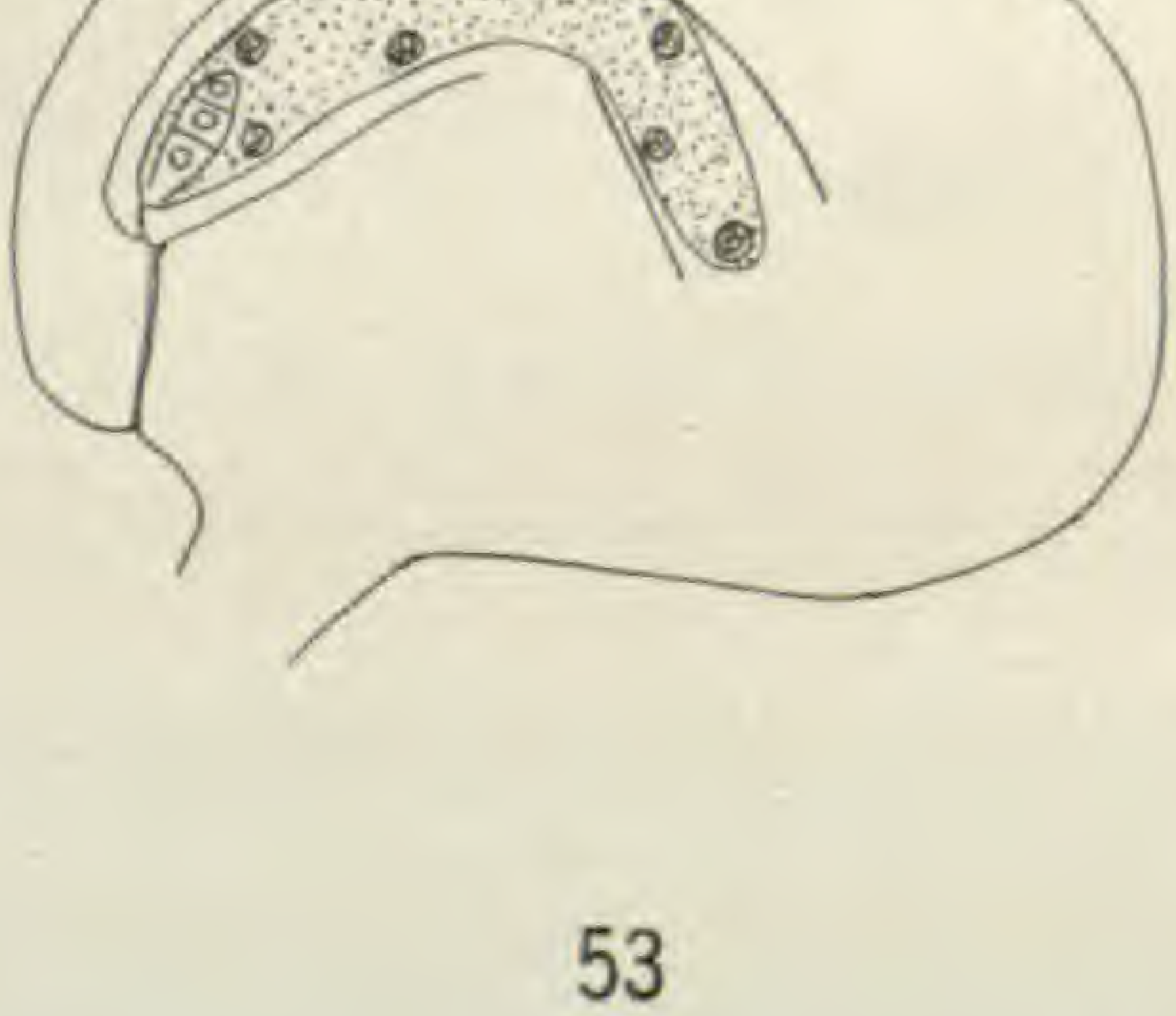

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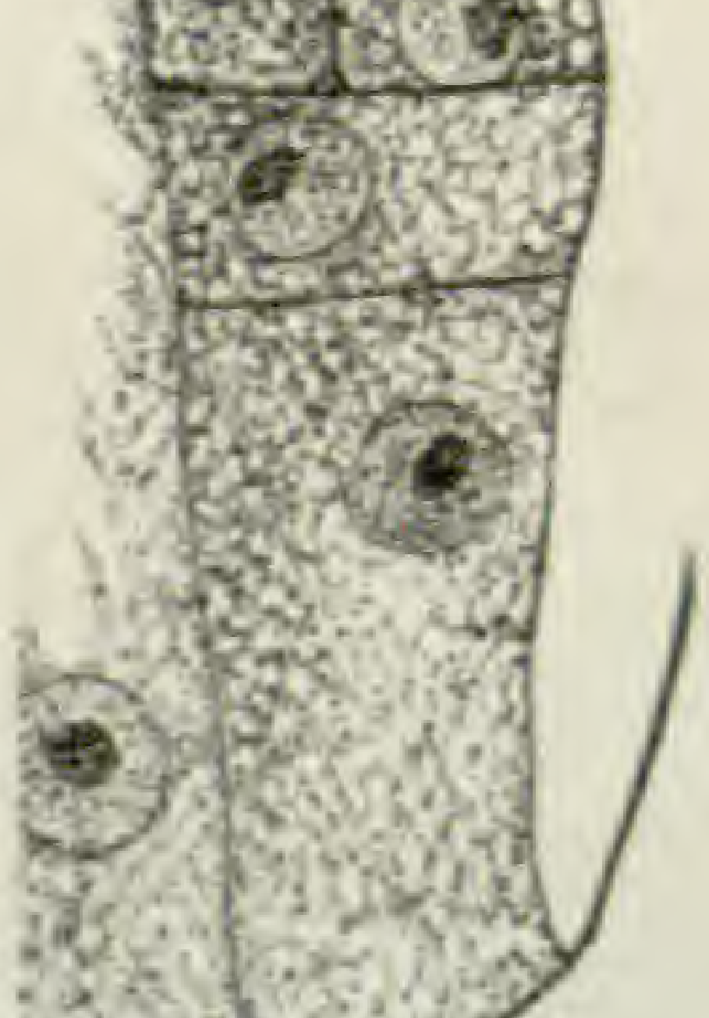

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MARTIN on LEGUMINOSAE

FIG. 36.—Embryo sac 8-nucleate, with large central vacuole and much starch; ×1500.

FIG. 37.—Vacuole in embryo sac has disappeared; polars in center of sac; sac is divided into three separate portions; only one antipodal cell; ×1500.

FIG. 38.—Mature embryo sac; polars in contact with egg apparatus; nucellus has disappeared at the micropylar end; ×360.

FIG. 39.—Proembryo with 4-celled suspensor; ×910.

FIG. 40.—Advanced stage of embryo; embryo has cut off epidermis; suspensor has thin cytoplasm and its cells are multinucleate; ×510.

FIG. 41.—Advanced embryo with suspensor showing on hypocotyl; ×360.

Vicia americana

FIG. 42.—Young nucellus with 5 archesporial cells; the integuments are appearing; ×1500.

FIG. 43.—Mother cell in synapsis; parietal cell has divided longitudinally; ×1200.

FIG. 44.—A row of 4 megaspores; ×750.

FIG. 45.—Functioning megaspore; much parietal tissue has developed; ×1500.

FIG. 46.—Mature embryo sac with nucellus eaten away; starch abundant in the inner integument and remaining portion of nucellus; polars on inner side of embryo sac and distant from egg apparatus; ×540.

FIG. 47.—The campylotropous ovule with mature embryo sac; ×330.

FIG. 48.—A 2-celled proembryo; ×1500.

FIG. 49.—A 4-celled proembryo; apical cell produces the embryo; ×900.

FIG. 50.—Proembryo in a view showing only one cell of each pair of cells composing the suspensor and the divided apical cell which produces the embryo; ×1200.

FIG. 51.—Suspensor distinct from embryo; basal cells of suspensor much elongated and multinucleate; the cells of the suspensor have very little cytoplasm; endosperm is parietally arranged; ×1200.

FIG. 52.—A 2-celled proembryo and 4 endosperm nuclei; ×360.

FIG. 53.—A 3-celled proembryo and 8 endosperm nuclei parietally placed; ×360.

CONTRIBUTIONS TO THE ANATOMY OF MESOZOIC CONIFERS

NO. 2. CRETACEOUS LIGNITES FROM CLIFFWOOD, NEW JERSEY[1]

RUTH HOLDEN

(WITH PLATES XII–XV)

Araucarioxylon

One of the most interesting and, at the same time, most disputed questions in the phylogeny of the Coniferales deals with the relative antiquity of the abietineous and araucarian lines. The general ligneous structure of the latter has led the majority of botanists to its direct affiliation with the Cordaitales. In a recent paper, Professor JEFFREY[2] has shown that this resemblance exists only in the normal mature wood, and that in the seedling stem, root, cone axis, and traumatic tissue, there are present altogether different conditions. In these regions the rays often become thick-walled and heavily pitted, there are wood parenchyma cells, and the tracheary pits, instead of being closely approximated, are scattered and opposite. Moreover, in the cone axis the pits are separated by well marked cellulose bars of Sanio. All these features are characteristic of the Abietineae, and diametrically opposed to anything found in the Cordaitales. The locality of these digressions from the *Araucarioxylon* type is of especial significance. On both the zoological and botanical sides, the law of recapitulation is regarded as one of the fundamental conceptions of evolution, and according to this law it is in the plant seedling that ancestral features should be found. Further, case after case has been recorded where these primitive conditions are retained in the root and reproductive axis, and recalled in traumatic tissue. As

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[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 63.

[2] JEFFREY, E. C., The history, comparative anatomy, and evolution of the *Araucarioxylon* type. Proc. Amer. Acad. 48:531–571. *pls. 7.* 1912.

instances of the first may be mentioned the occurrence of resin canals in the center of the root of such conifers as *Abies* and *Tsuga*, a harking back to the time when they were scattered throughout the wood, as in *Pinus;* as instances of the second, the presence of centripetal wood in the cone axis of *Equisetum;* and of the last, the ray tracheids in wounded specimens of *Abies*. It seems clear, therefore, from comparative anatomical and developmental evidence, that the Araucarineae are descended from ancestors which had thick-walled pitted rays, wood parenchyma, and scattered tracheary pits separated by bars of Sanio. These hypothetical ancestors are probably the Abietineae.

If such a conclusion is correct, we should expect to find fossil record of woods which possessed these modified araucarian structures, not only in primitive places, but also in their normal, mature growth. Recent investigation has shown such to be the case. For example, *Araucarioxylon Lindleyi* Seward, *Cormaraucarioxylon crasseradiatum* Lignier, and *Araucarioxylon noveboracense* Jeffrey have wood parenchyma; *Cormaraucarioxylon crasseradiatum* Lignier, *Protocedroxylon araucarioides* Gothan, and *Araucariopitys americana* Jeffrey have thick-walled pitted rays. Further, many of these Mesozoic araucarians have traumatic resin canals, as do *Abies*, *Cedrus*, etc. Up to the present, however, no fossil araucarian has been described with opposite pits or bars of Sanio. In an earlier paper[3] the writer has described several species of *Pityoxylon* from the Raritan Cretaceous of Cliffwood, New Jersey. These were included in a considerable amount of lignite collected by Professor JEFFREY, and turned over to the writer for investigation. In addition to the *Pityoxyla*, there were a number of *Cupressinoxyla*, and one *Araucarioxylon*. This last specimen was of especial interest in this connection, and will accordingly be described first.

The material consisted of a flattened stem about two inches in length and one in diameter. The preservation of the outer layer was but indifferent; near the center, however, it was excellent. The pith contains large masses of stone cells, similar to those of the living *Agathis*. Fig. 1 represents a radial section of the wood at

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[3] HOLDEN, RUTH, Cretaceous *Pityoxyla* from Cliffwood, New Jersey. Proc. Amer. Acad. 48:609–623. *pls. 4.* 1913.

some distance from the pith; fig. 2, the same at a higher magnification. The general araucarian nature of the specimen is vouched for by the thin rays, absence of wood parenchyma, and especially by the alternating and closely compressed tracheary pitting.

The structure next the pith is elucidated by fig. 4. At the extreme left are the ringed protoxylem and metaxylem elements, which, toward the right, are replaced by those of the secondary wood. In the first pitted tracheid the pits are uniseriate and scattered; in the second they are opposite. A careful examination of the wall between the pairs of opposite pits shows that they are separated by white lines. Fig. 5 represents these same elements at a higher magnification, and here the lines are still more conspicuous. The study of fossil *Pityoxyla*, a section of which is shown in fig. 8, has proved that the bars of Sanio in those woods are represented by similar white lines, a condition which would be expected from the cellulose nature of the bars, and the tendency of cellulose structures to disappear in the process of fossilization. That the white lines appearing in figs. 4 and 5 are also bars of Sanio seems unquestionable. The general resemblance of the pitting of this Cretaceous stem to that of the cone axis of *Araucaria Bidwillii* (fig. 7) is very striking. In the case of the latter, the cellulose composing the bars is still present, and stains a dark blue with hematoxylon, causing the bars to stand out as black lines in the photograph. In studying unstained living material, it would be possible to mistake the spirals of the primary wood for bars of Sanio. This possibility may be obviated, as JEFFREY has demonstrated, by using a double stain of hematoxylon and saffranin. The former stains the bars a deep blue and leaves the spirals untouched, while the latter stains the spirals a bright red. With fossil material, however, there is no chance for mistake. Here the protoxylem spirals, being lignified, persist, and appear as black lines (left of fig. 4); on the other hand, the bars of Sanio, being cellulose, drop out, and appear as white lines (right of fig. 4).

Fig. 3 represents a similar section from the same Cretaceous specimen. Toward the extreme left may be seen indistinctly a tracheid with metaxylem spirals; next it is one with approximately opposite pits. Near the lower limit bars of Sanio may be made out.

In the next tracheid the pitting becomes uniseriate again, and the bars of Sanio stand out with considerable clearness. Still a third case is presented in fig. 6. At the left are two spiral elements, and next them is a pitted element. Toward the upper end of the latter the pits are biseriate, with faint bars of Sanio; below they become triseriate, and then biseriate again. In the latter case they are alternate, but even here bars of Sanio are present. A similar combination of alternating pitting and bars of Sanio is shown in the tracheid at the right of fig. 7 (cone of *Araucaria Bidwillii*), and similar triseriate pitting in that at the extreme left.

This type of pitting is uniformly present in this specimen near the pith. Accordingly it seems to supply the only missing link in the chain of evidence pointing to the derivation of the Araucarineae from the Abietineae. All the araucarian features of wood structure have been previously shown to disappear in the primitive regions of extant araucarians, and now they have all been shown to disappear in the stem of extinct ones.

Brachyoxylon

Of the remainder of the Cliffwood lignites, a considerable amount belongs to the genus *Brachyoxylon*. In some cases twigs were found similar in almost every respect to such specimens as *Geinitzia Reichenbachi*, *Brachyphyllum macrocarpum*, etc., from the Cretaceous of Kreischerville, New York.[4] Figs. 9 and 10 represent transverse and longitudinal sections of one of these. The tracheids have the same combination of araucarian and abietineous pitting, the rays are smooth-walled, there is no wood parenchyma, and, furthermore, there are abundant sclerites in the pith. The particular specimen figured here is so like *Geinitzia Reichenbachi* in the shape and arrangement of stone cells that it seems safe to identify it with that species.

In other twigs, however, the arrangement of these sclerenchymatous elements is quite different. In figs. 11 and 14, for example, they are grouped to form nests, extending like plates, sometimes almost completely across the medulla. As shown in the photo-

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[4] Hollick, Arthur, and Jeffrey, E. C., Studies of cretaceous coniferous remains from Kreischerville, New York. Mem. N.Y. Bot. Garden 3:1–38. *pls. 1–29.* 1909.

graphs, the individual cells are elongated longitudinally, and filled with a dark substance. This stem was one of the few with the bark still adhering. Figs. 12 and 13 show the details of the bast, and it is evident that, although in other respects it resembles closely some of the Kreischerville material, in this respect it is quite different. In *Brachyphyllum*, *Araucariopitys*, etc., the phloem is composed entirely of sieve tubes and parenchyma cells, while here there are tangential rows of bast fibers. This alternation of hard and soft bast commonly obtains in the Cupressineae (e.g., *Juniperus* and *Thuya*), Taxodineae (e.g., *Sequoia*), and Podocarpineae (e.g., *Podocarpus* and *Dacrydium*), and adds another to the points of resemblance between the araucarians and podocarps.

In addition to these twigs, there was a considerable amount of wood showing the same structure. Representative sections are shown in figs. 17–19. It seems to conform exactly to the *Brachyoxylon* type, both normally and traumatically. A number of pieces had been severely wounded, and in every case one or more tangential rows of resin canals extended from the wound cap; in one specimen there were as many as four concentric series. As shown in figs. 15 and 16, the canals are often small and constricted at intervals, like those formed traumatically in the Abietineae.

Cupressinoxylon

In addition to the *Pityoxylon*, *Araucarioxylon*, and *Brachyoxylon* described above, there are others belonging to the genus *Cupressinoxylon* Kraus. They have the same combination of araucarian and abietineous tracheary pitting without bars of Sanio, but differ in having wood parenchyma scattered throughout the year's growth. The most abundant of the stems of this type is represented in figs. 20–24. The pith is large and composed entirely of parenchyma cells (figs. 20, 21), without the sclerites characteristic of the *Brachyoxyla*. The wood is composed of tracheids, rays, and wood parenchyma. The tracheids are small, with uniserial pits on the radial wall. Usually the pits are scattered (fig. 23); rarely they are crowded, but in neither case is there the slightest indication of bars of Sanio. The parenchyma cells are relatively large, being sometimes three or four times the diameter of the tracheids. The rays are low (figs. 23, 24), with thin unpitted walls. All the parenchyma, both radial and longitudinal, whether in pith, wood, or bark, is filled with a dense black substance. The structure of the phloem is shown in fig. 22. It consists of rays, sieve tubes, parenchyma cells, and also bast fibers. These last are usually more or less crushed, but it is not difficult to see that they occur in tangential rows, alternating with rows of soft bast, just as in the case of the *Brachyoxylon* twig described above. It is noteworthy that in the former specimen the soft bast collapsed and the hard retained its natural size, while here just the reverse is true. On account of the absence of bars of Sanio, such a wood as this, though strictly speaking a *Cupressinoxylon*, cannot be affiliated with other members of that genus, e.g., *Juniperus*, *Cupressus*, *Sequoia*, etc. On the contrary, its affiliations must be with the araucarians. The type genus *Paracedroxylon* was founded by SINNOTT[5] to include wood which is *Cedroxylon* in everything but bars of Sanio; and for similar *Cupressinoxyla* the genus *Paracupressinoxylon* was established.[6] Two species were described. The first, *Paracupressinoxylon cedroides*, resembles the Cliffwood specimen in question in absence of medullary stone cells, but differs in having thick-walled, heavily pitted rays like a *Cedroxylon*. The second, *P. cupressoides*, lacks pith and bark, but has exactly the wood structure of this Cretaceous twig from Cliffwood. It seems safe, accordingly, to include both specimens as *P. cupressoides*, in spite of the difference in horizon.

The stem just described, although the most abundant of the *Cupressinoxyla*, was the only one without stone cells in the pith. Figs. 25–28 represent a more common type. In the medulla may be seen groups of sclerites, and in the wood the scattered parenchyma cells. Fig. 27 shows the low rays and well spaced pits characteristic of the mature wood of this twig. Fig. 28 shows the structure near the pith. The pits here, instead of being distant, are fairly close, and are in several places separated by bars of Sanio.

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[5] SINNOTT, EDMUND, A. W., *Paracedroxylon*, a new type of araucarian wood. Rhodora 11:165–173. *pls. 80, 81*. 1909.

[6] HOLDEN, RUTH, Jurassic coniferous woods from Yorkshire. Ann. Botany 27:533–545. *pls. 39, 40*. 1913.

Owing to the cellulose nature of these bars, they have dropped out in the course of fossilization, and now are represented by white lines. Their occurrence near the pith of this specimen, which is clearly transitional between the Araucarineae and Abietineae, is quite in keeping with their occurrence in the cone axis of the living genus *Araucaria*, and in the first annual ring of the fossil *Araucarioxylon* described earlier in this paper. In all these cases the bars of Sanio are to be interpreted as vestiges of what was characteristic of the mature wood of their ancestors, retained only in certain conservative regions of these reduced forms. Viewed in this light, it seems evident that their presence in the first formed wood of an araucarian *Cupressinoxylon* is another indication of the derivation of the Araucarineae from the Abietineae.

This stem is representative of a considerable number which differ from each other only in slight and unimportant details. The three diagnostic features are (1) wood parenchyma scattered throughout the year's growth, (2) thin-walled ray cells, and (3) scattered pits on the radial walls of the tracheids, without bars of Sanio intervening. All these are shown in figs. 27 and 29. In such structures as arrangement and size of medullary sclerites, there is considerable divergence. For example, in the specimen represented in figs. 25 and 26, the individual stone cells are grouped in small and irregular clusters, while in the case of the twig photographed for fig. 30 they form long lines extending down the pith. There is not a little variation also in the pitting of the radial walls of the rays, though in all the horizontal and end walls are unpitted. Usually there are one to four small piceform pits to each cross-field, but in fig. 31 is shown a specimen with a single large pit. That each large pit originates from the fusion of two small pits is indicated by the occurrence of two partially fused pits, end to end. Similar stages in pit fusion were described in the case of one of the *Pityoxyla* from the same deposit. Another interesting feature of this specimen, shown in fig. 32, is the resinous exudation from the rays into the tracheids. Similar appearances are common in the living *Agathis*, and thus serve to establish another bond between these transitional Mesozoic forms and living members of the Araucarineae.

Summary

1. An *Araucarioxylon* from the Raritan Cretaceous of Cliffwood, New Jersey, shows bars of Sanio near the pith of the stem, similar to those on the cone axis of the living Araucarineae.

2. *Brachyoxyla* from the same locality are as a rule very similar to those from Kreischerville, Staten Island, differing only in such details as arrangement of medullary sclerites and structure of the bast.

3. The *Cupressinoxyla* of Cliffwood all lack cellulose bars of Sanio in the mature wood, and should on that account be placed in the new genus *Paracupressinoxylon*.

4. The occurrence of three absolutely typical *Pityoxyla*, and not a single typical *Araucarioxylon*, among these lignites seems to indicate that in tracing back the families of living conifers it is the Abietineae which remain unchanged, and the Araucarineae which become less and less like living representatives of that family. The same conclusion may be drawn from a consideration of the lignites of Staten Island.

5. The variety of structure of these Mesozoic araucarians has its bearing on the question of the monophyletic or diphyletic origin of the Coniferales. There are certain features which have been supposed to sharply differentiate the araucarians from the other families. Both fossil and comparative anatomical evidence demonstrate the fallacy of this view. As regards wood structure, every feature of the Abietineae—resin canals, bars of Sanio, thick-walled pitted rays, wood parenchyma (terminal and diffuse), even to as small and unimportant details as fusion pits in the rays and regularly alternating bands of hard and soft bast—has been found in the Araucarineae, living or extinct. As regards strobilar anatomy, EAMES[7] has shown that the stages in the reduction of the female cone are closely paralleled in various cupressineous and taxodineous genera, and the writer[8] has shown that in one Mesozoic araucarian (*Voltzia*) there was a double cone scale, like that of the living genus

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[7] EAMES, ARTHUR J., The morphology of *Agathis australis*. Ann. Botany **27**: 1–38. *pls. 1–4.* 1913.

[8] HOLDEN, RUTH. Some fossil plants from eastern Canada. Ann. Botany **27**: 243–255. *pls. 22, 23.* 1913.

Cryptomeria. In view of all the facts, it seems evident that the conifers, as a whole, are derived from the same ancestral stock, and that the Abietineae are more like that stock than the Araucarineae.

This investigation was carried on in the Phanerogamic Laboratories of Harvard University, and the sincerest thanks of the writer are due to Professor E. C. JEFFREY for the lignites from Cliffwood, for the photograph of the cone of *Araucaria Bidwillii* (fig. 7), and for many helpful suggestions in the course of the work.

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EXPLANATION OF PLATES XII–XV

FIG. 1.—*Araucarioxylon* sp.; radial section of mature wood; ×125.

FIG. 2.—Same, showing alternating and crowded pits; ×250.

FIG. 3.—Same, near the pith; toward the left, a tracheid with opposite pits and bars of Sanio; toward the right, one with uniserial pits and bars; ×500.

FIG. 4.—Same; at the left are the primary wood elements; next, a tracheid with scattered pits; and then one with opposite pits and bars of Sanio; ×250.

FIG. 5.—Same, more highly magnified; ×500.

FIG. 6.—Same, showing opposite, triseriate, and alternating pits, in every case separated by bars of Sanio; ×500.

FIG. 7.—*Araucaria Bidwillii;* radial section of cone axis in proximity to the protoxylem, showing presence of bars of Sanio; ×500.

FIG. 8.—*Pinus protoscleropitys;* radial section of mature wood showing opposite pits and bars of Sanio; ×500.

FIG. 9.—*Geinitzia Reichenbachi;* transverse section of stem, showing sclerites in pith; ×15.

FIG. 10.—Same; longitudinal section of pith; ×15.

FIG. 11.—Twig from Cliffwood; transverse section of pith, including nest of stone cells; ×15.

FIG. 12.—Same; the outer bark contains clusters of large stone cells, below which is the inner bark, consisting of alternate layers of hard and soft bast; ×40.

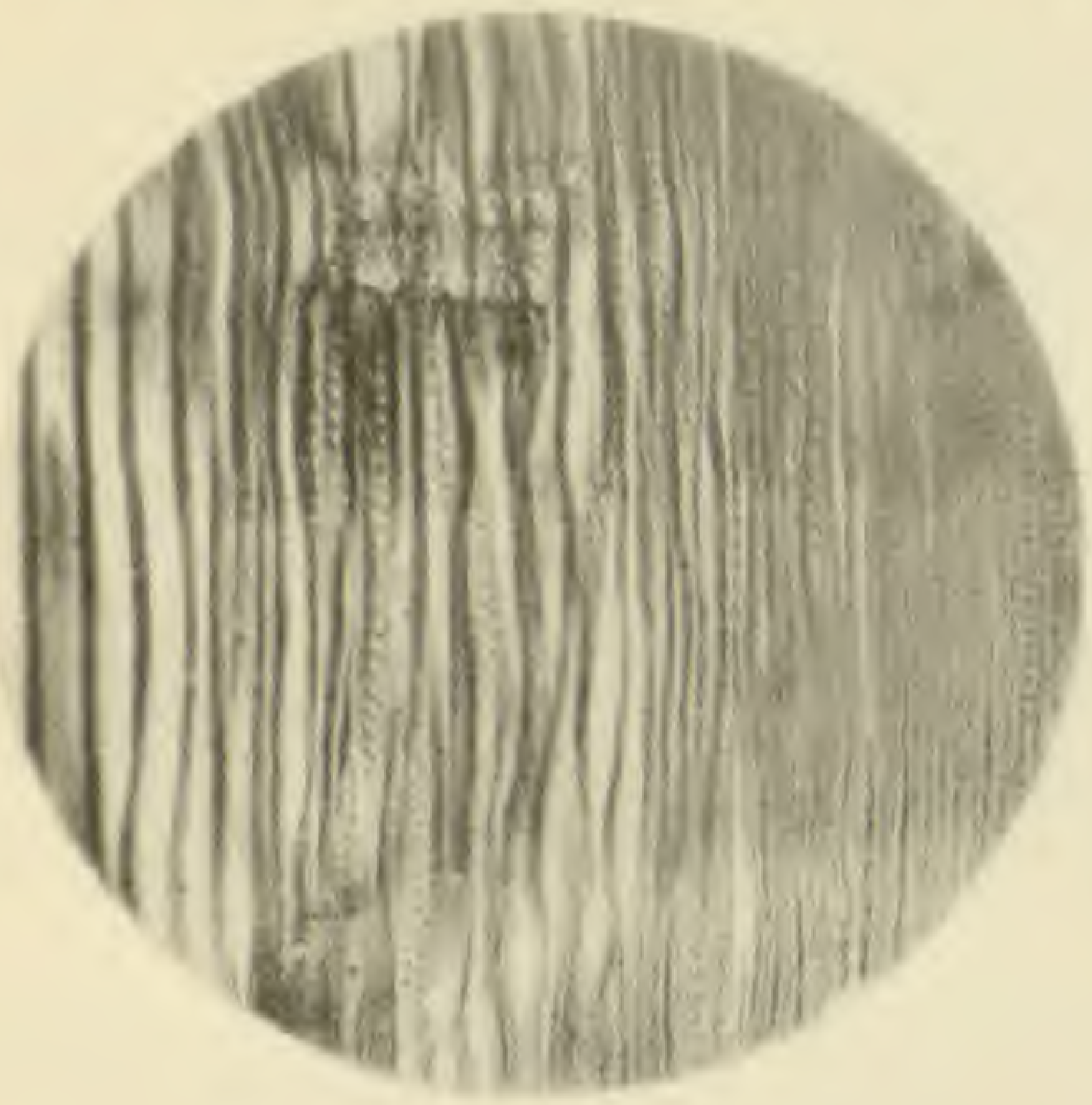
FIG. 13.—Same; longitudinal section of bark; ×40.

FIG. 14.—Same; longitudinal section of pith, showing nests of stone cells; ×15.

FIG. 15.—*Brachyoxylon* sp. including row of traumatic resin canals; ×40.

FIG. 16.—Same; longitudinal section; ×40.

FIG. 17.—*Brachyoxylon* sp.; transverse section of normal mature wood; ×90.



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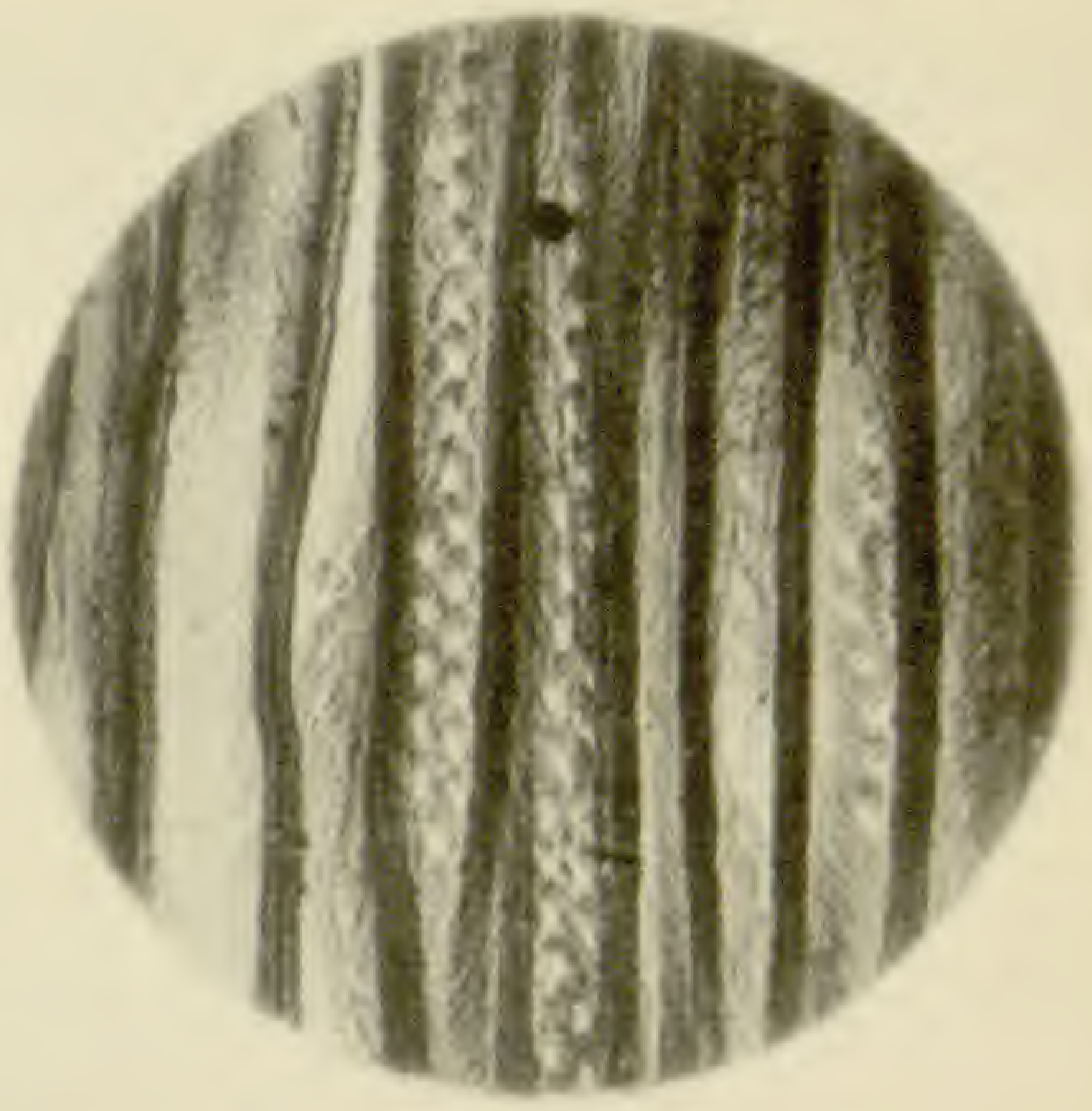

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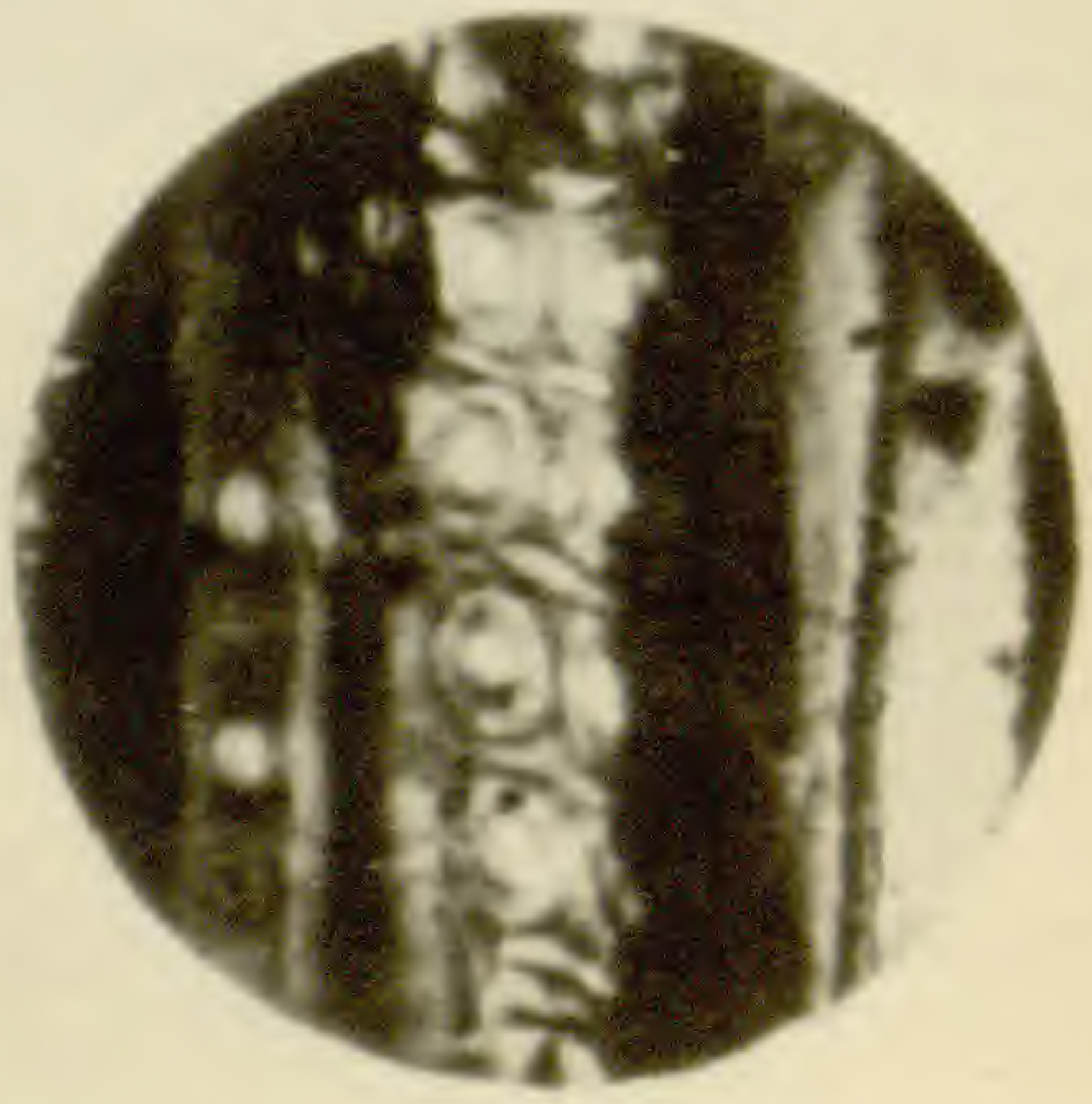

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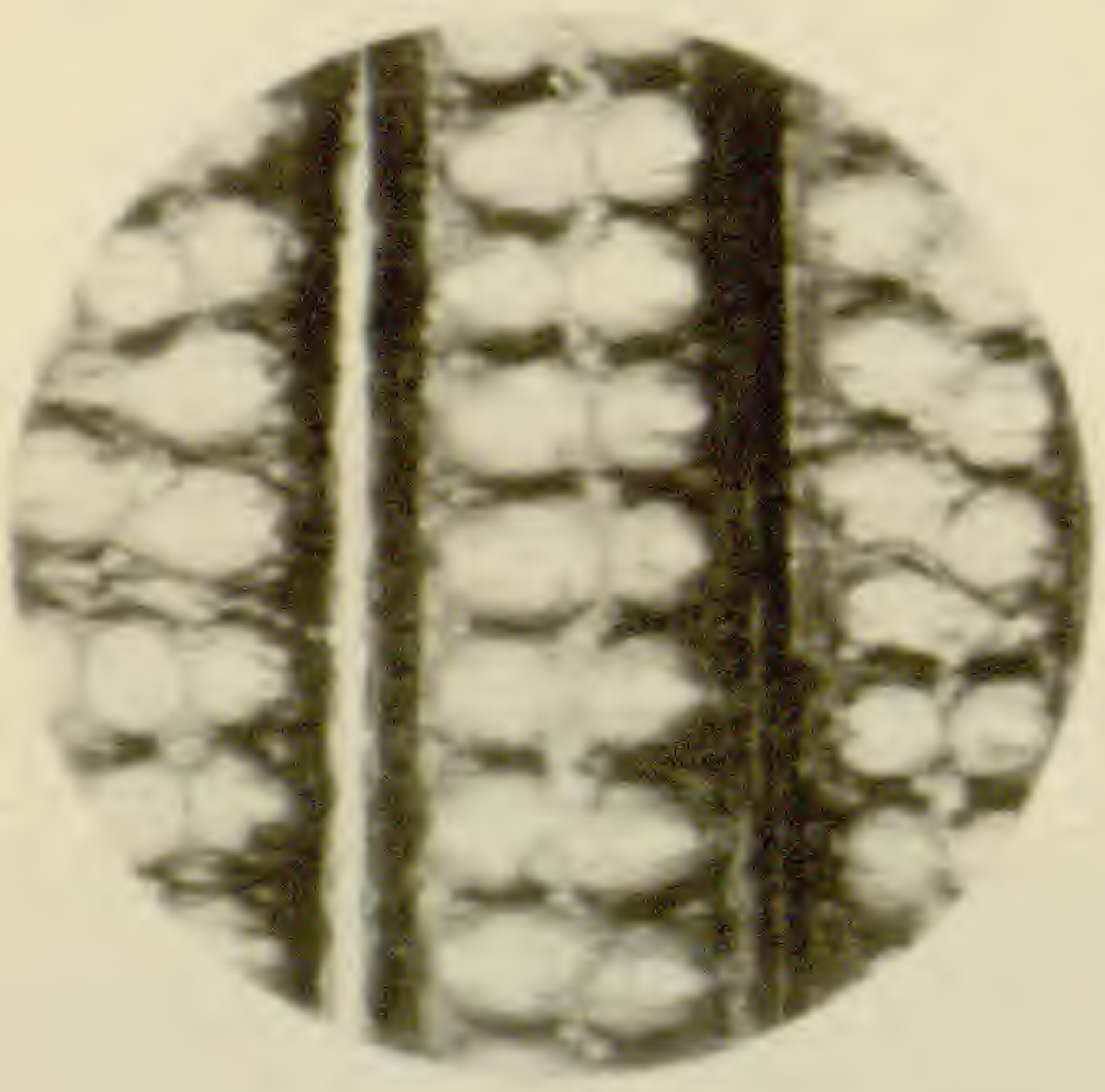

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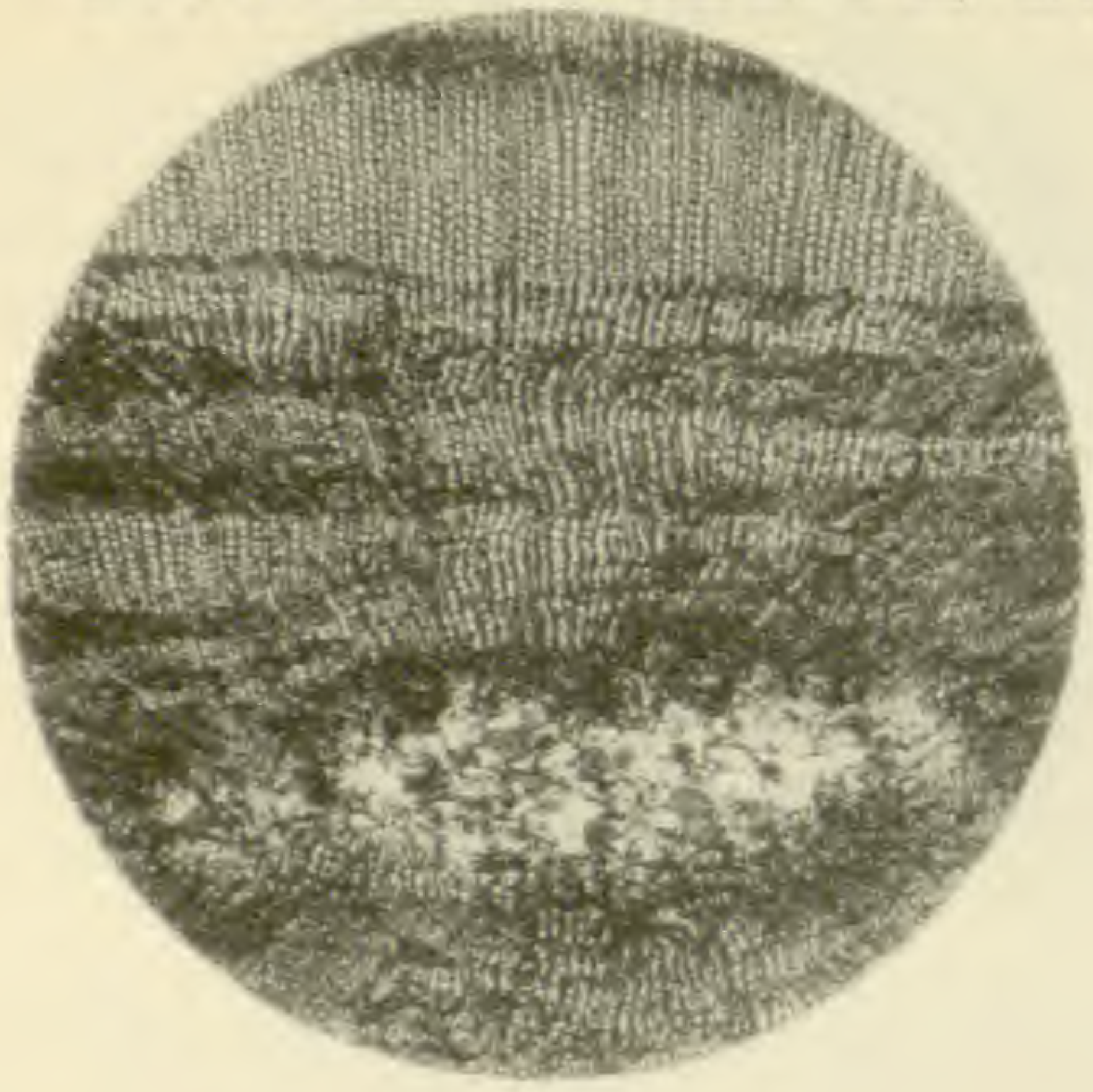
HOLDEN on CRETACEOUS LIGNITES



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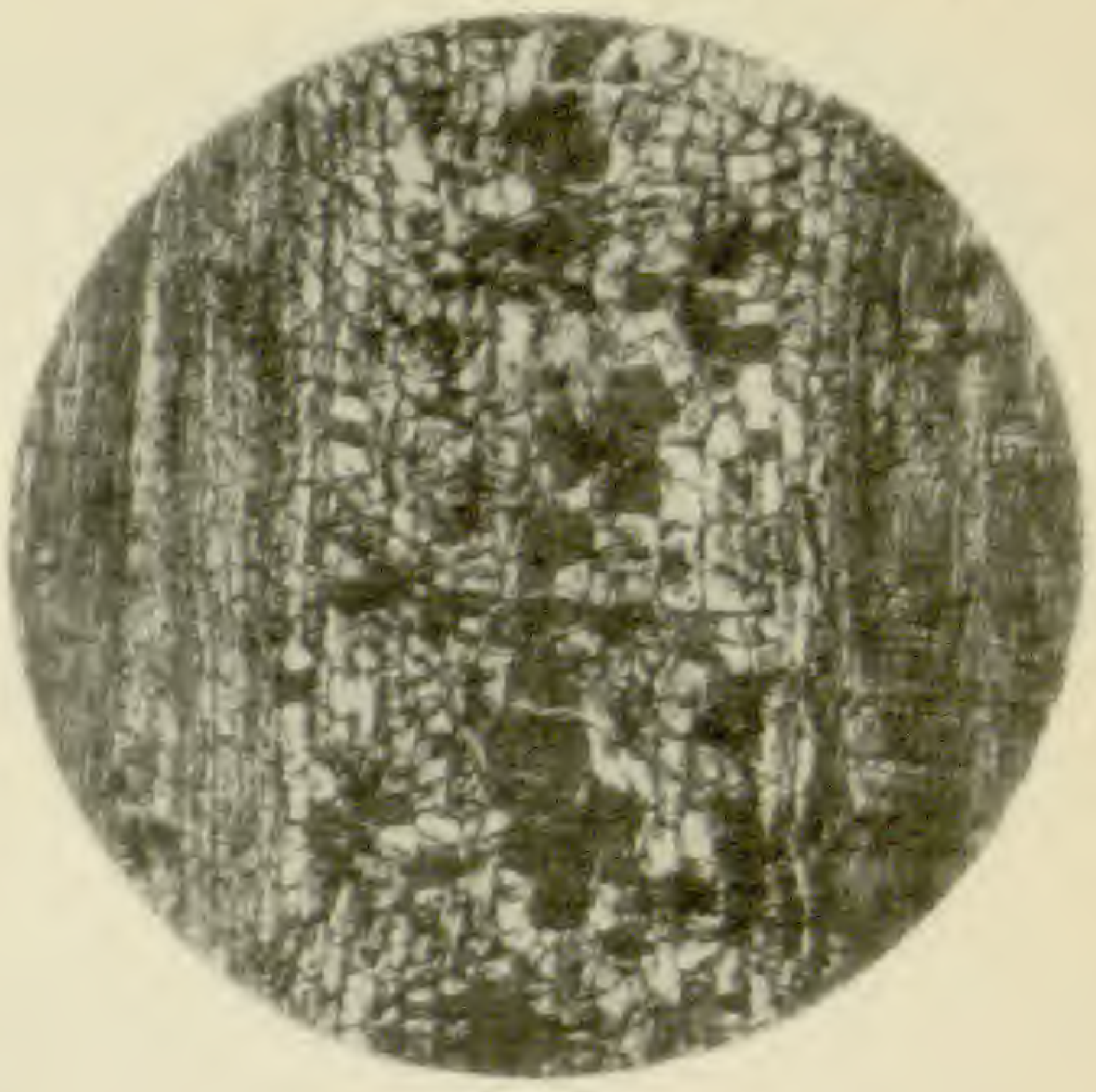

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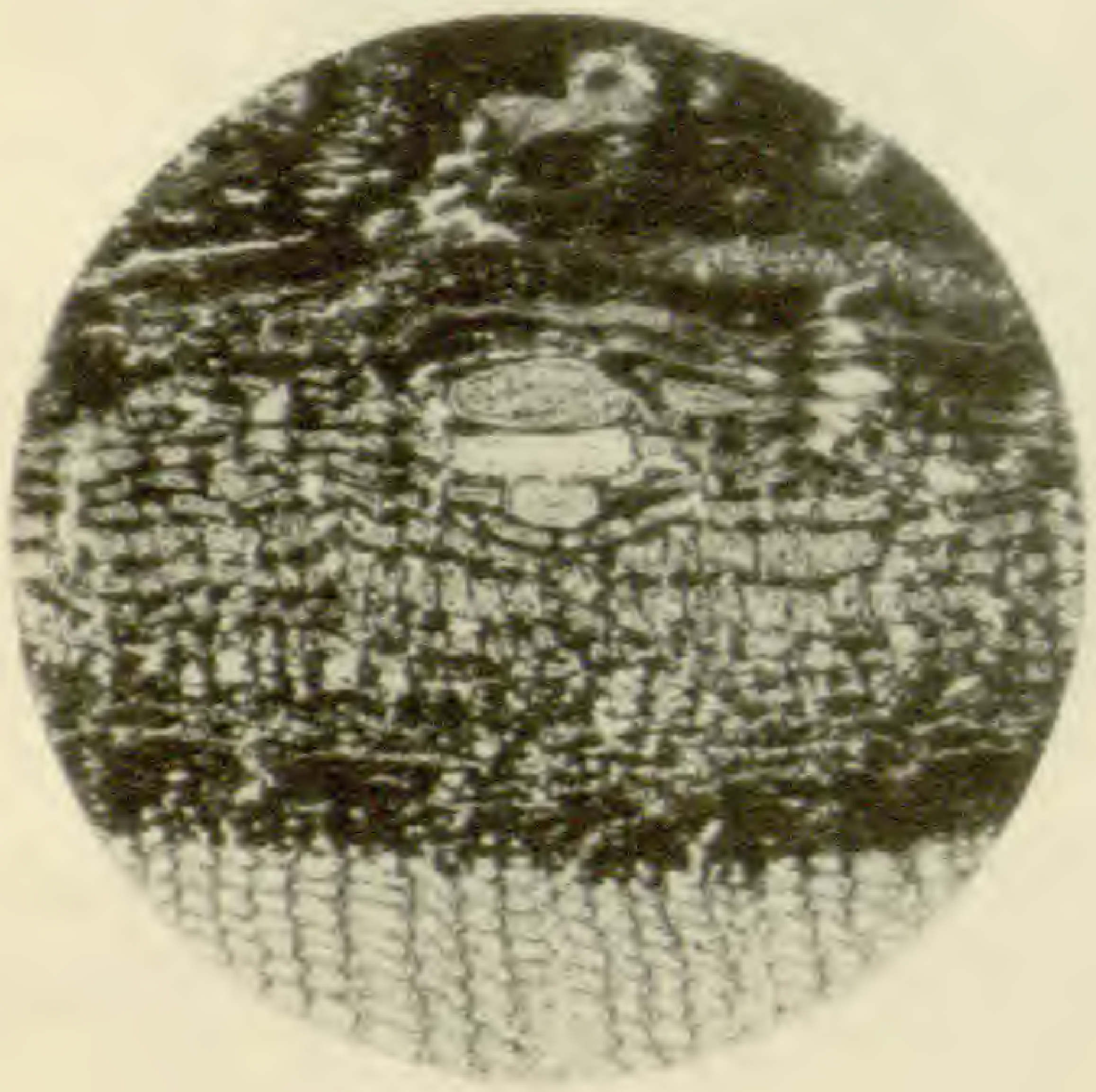

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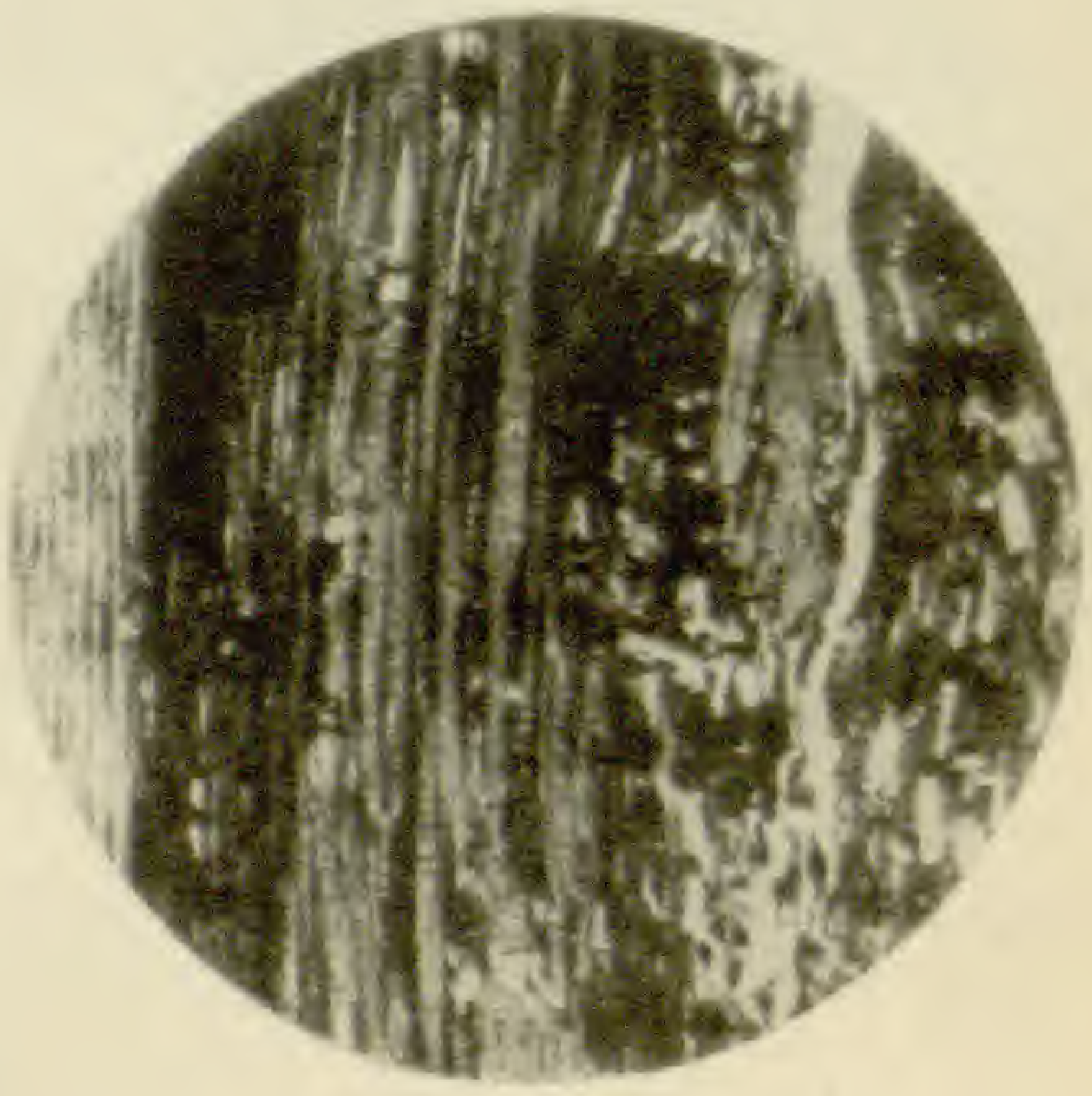

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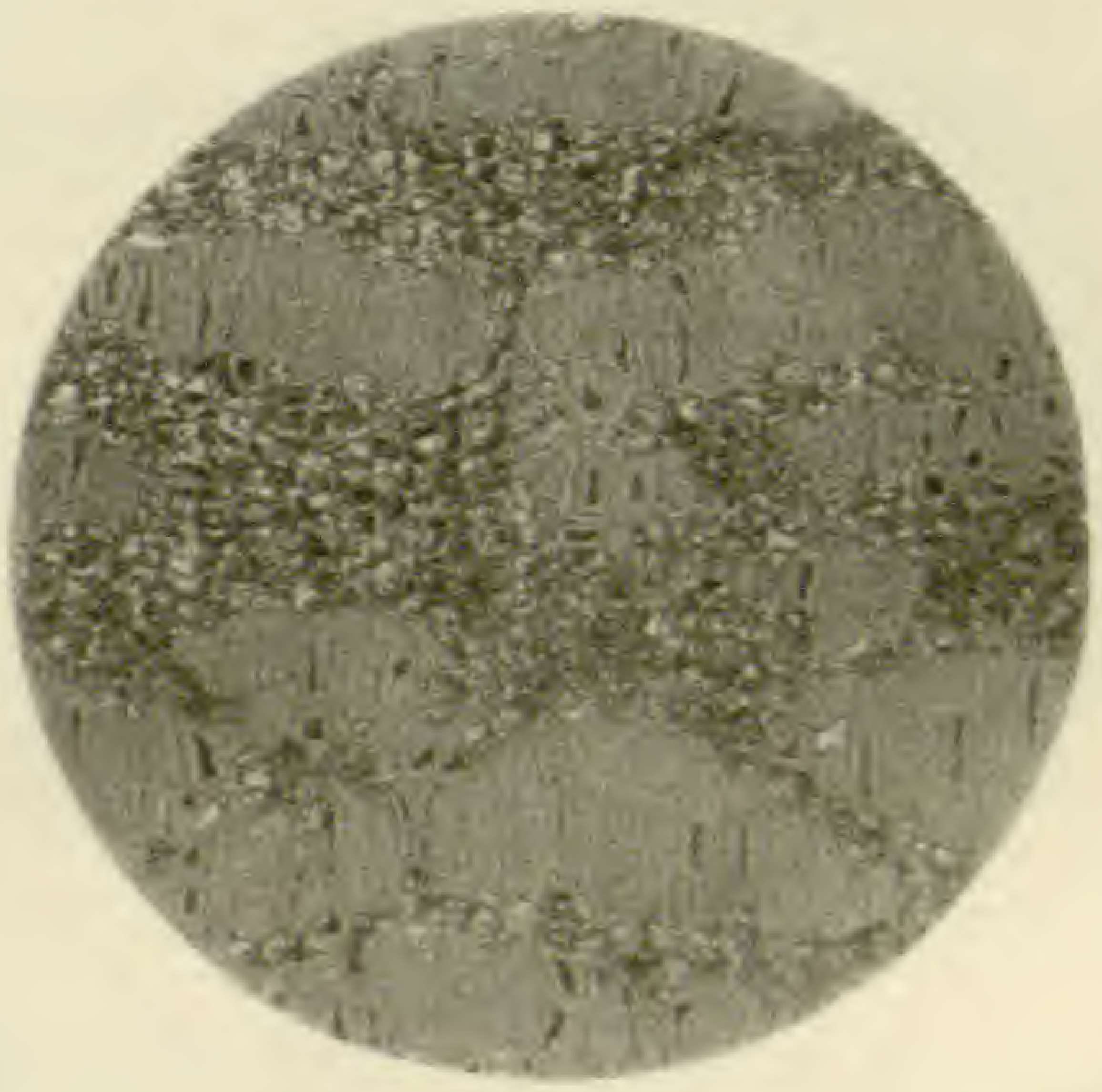

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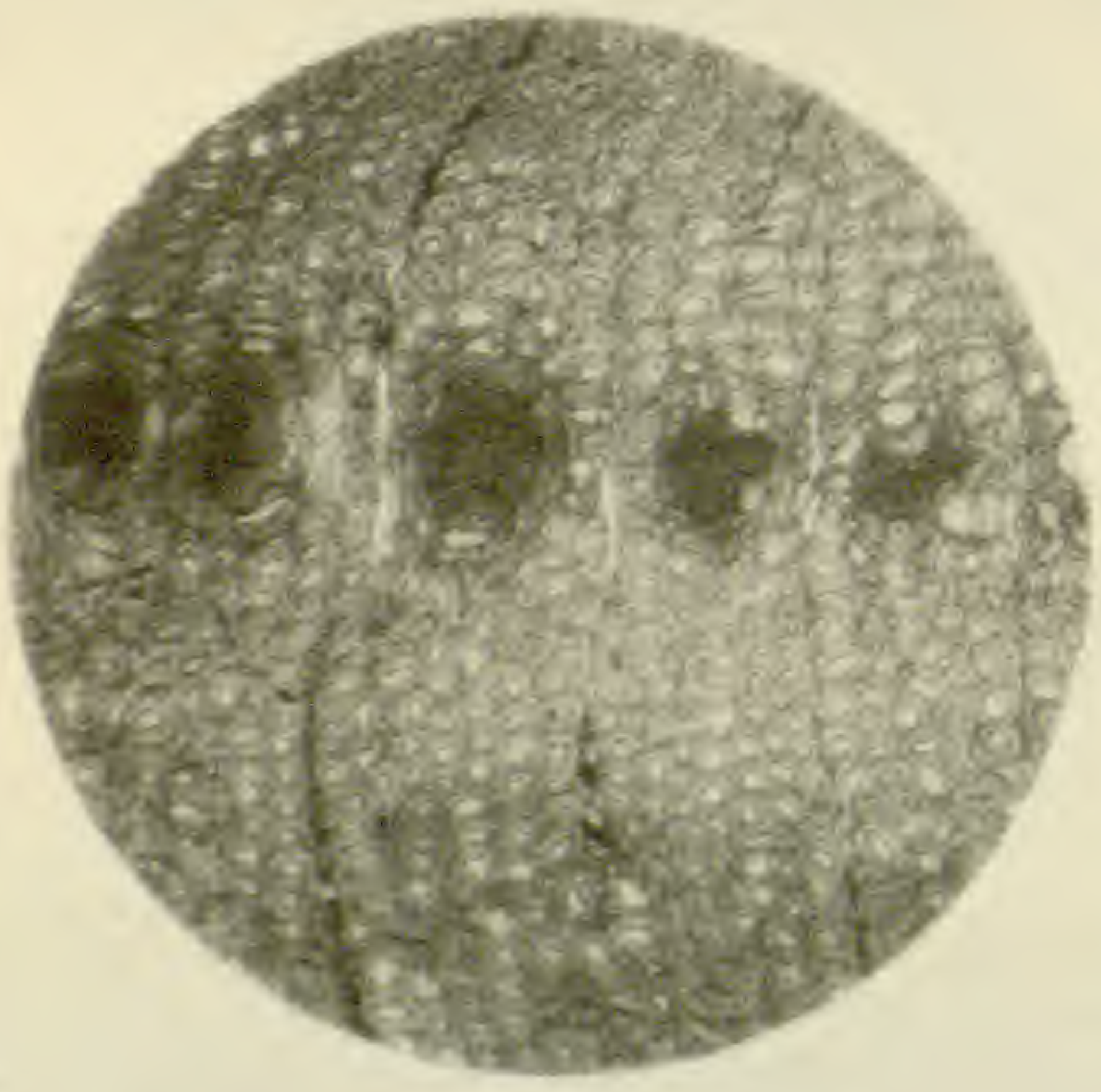

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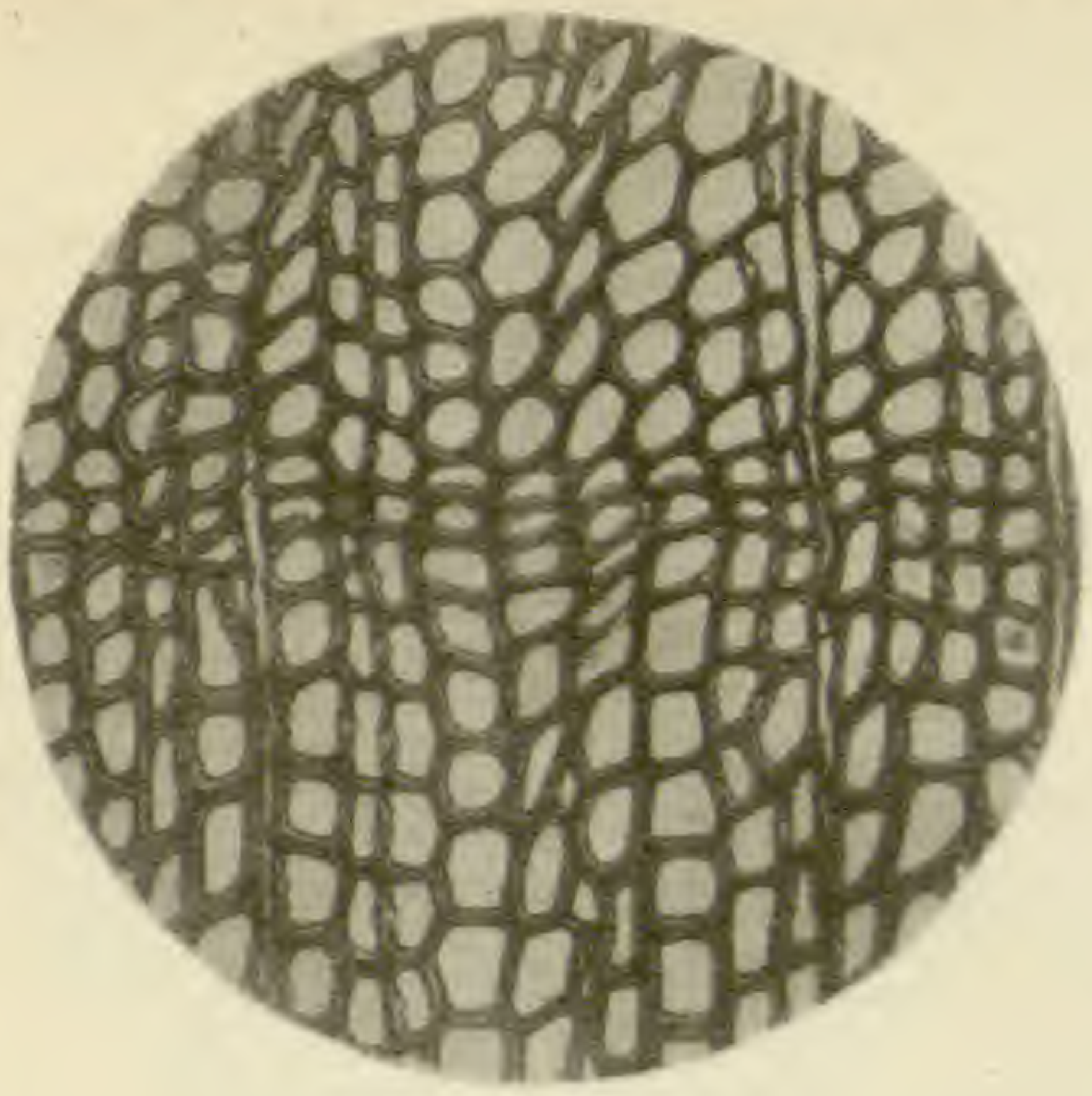

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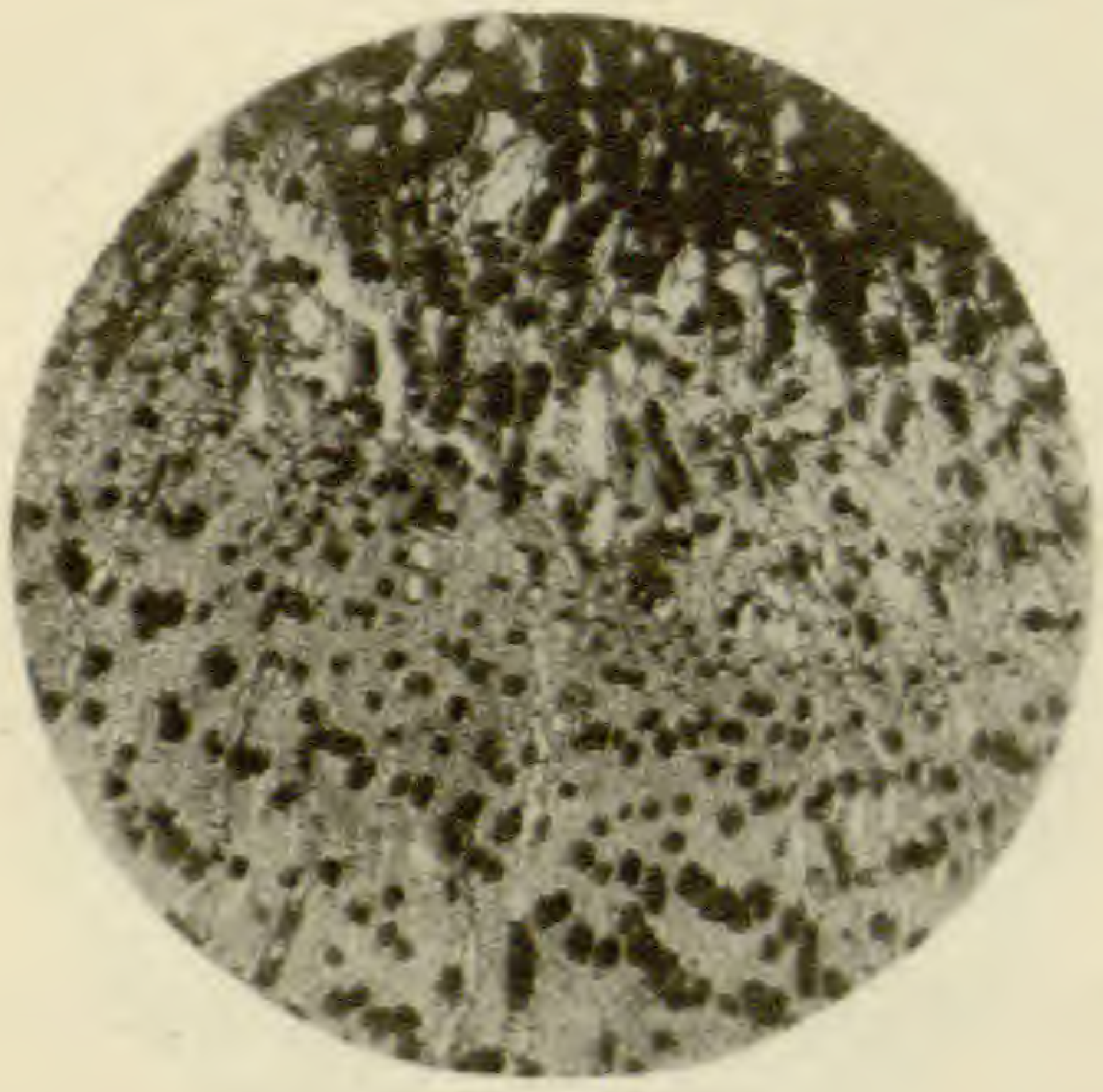

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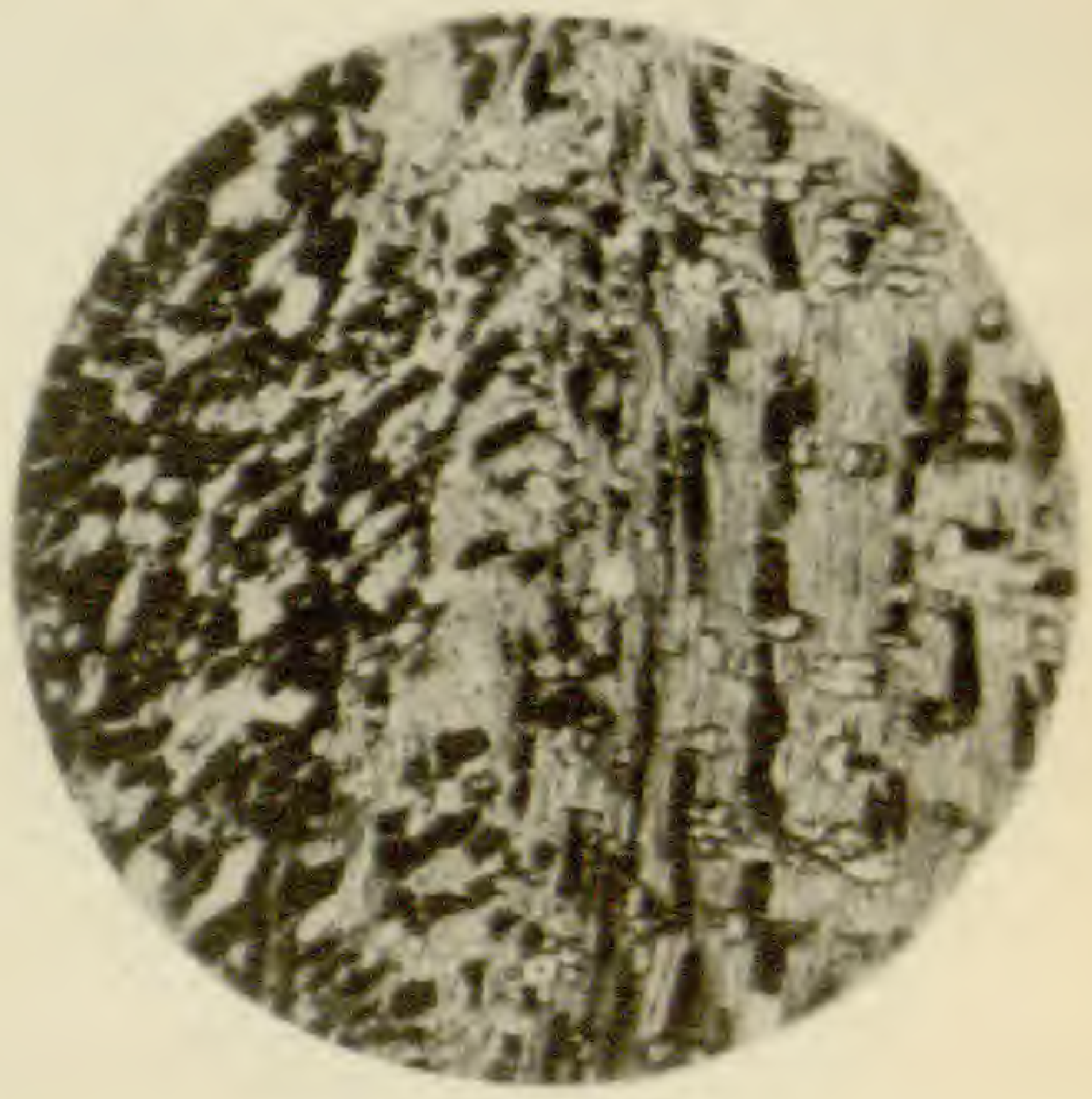

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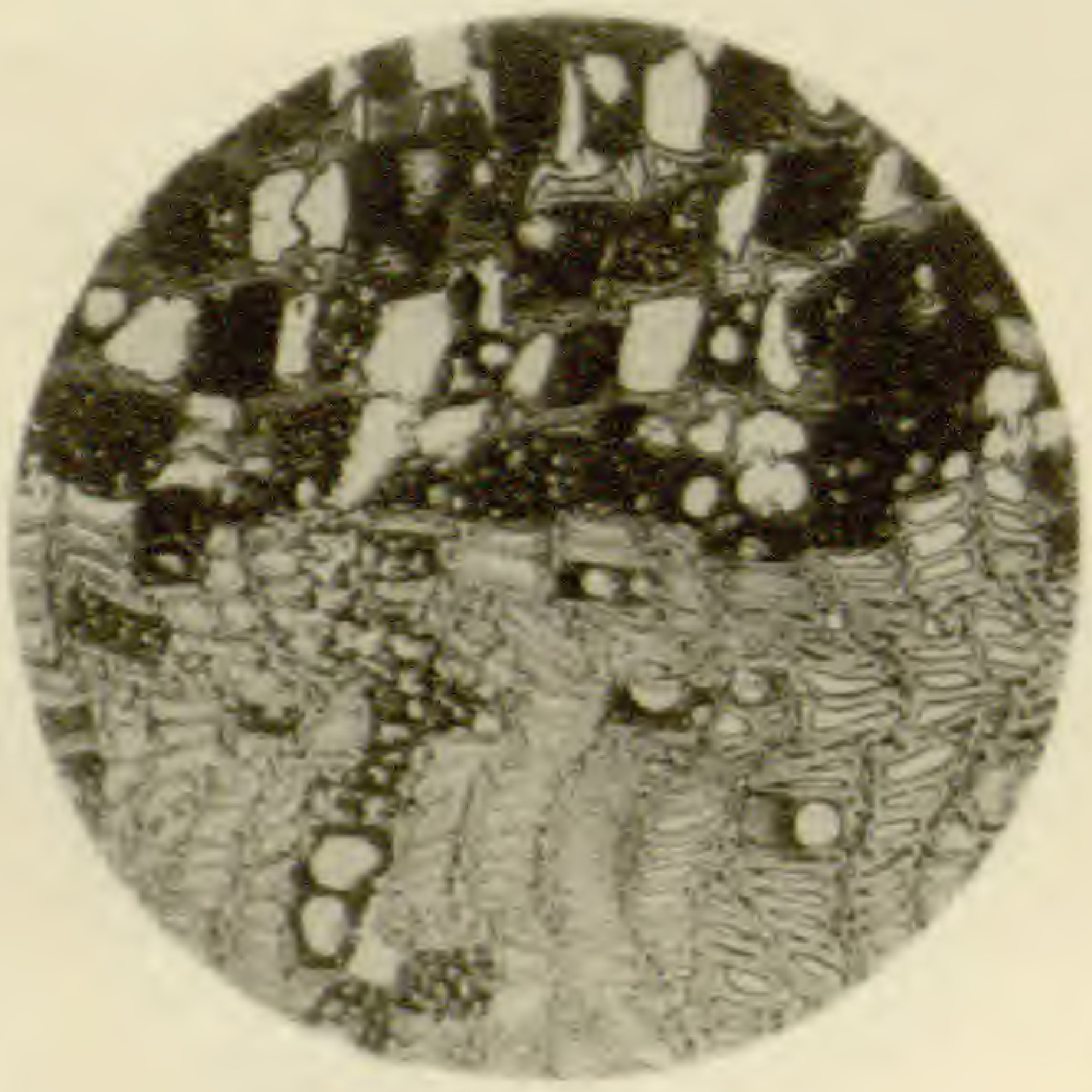

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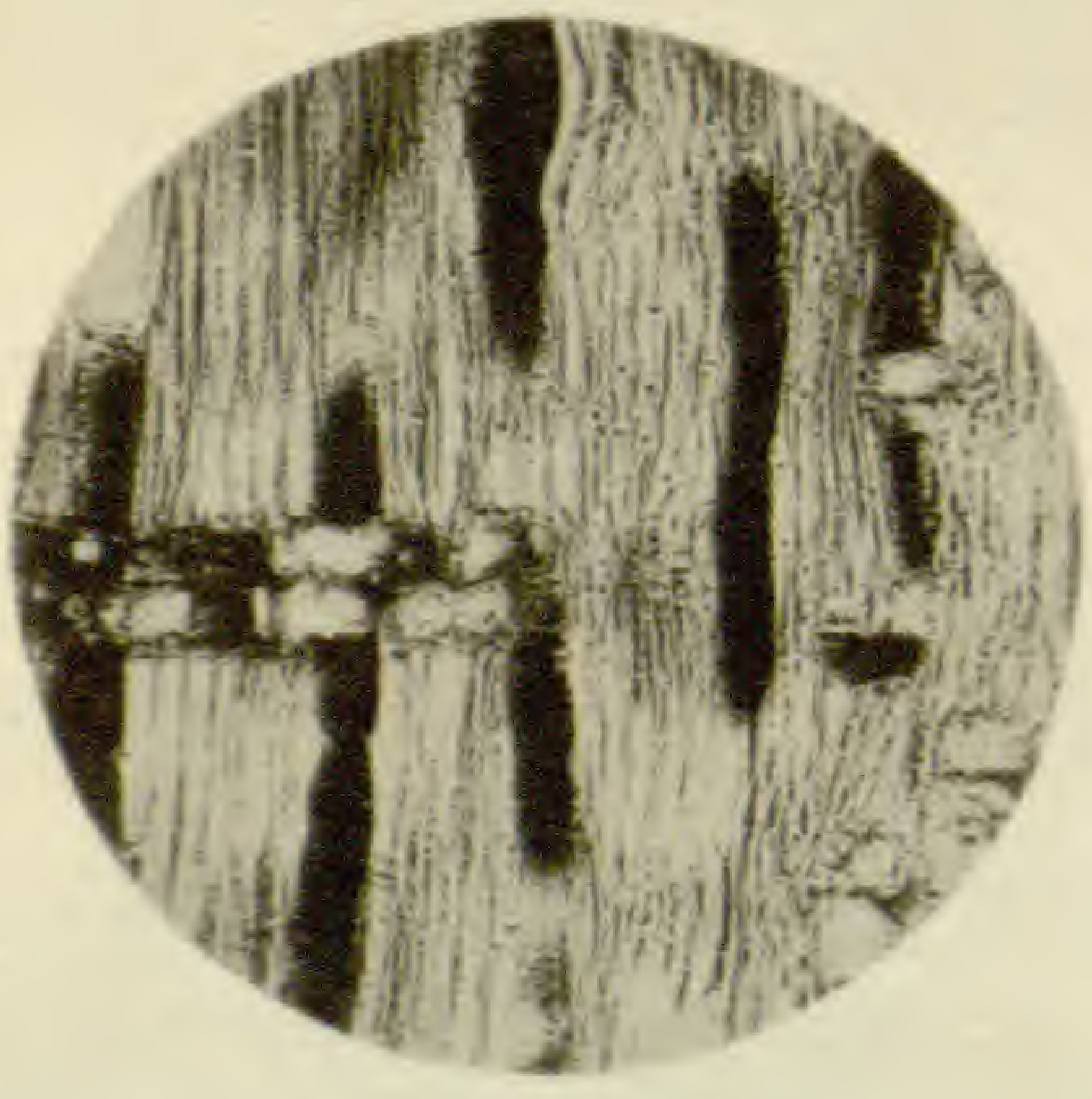

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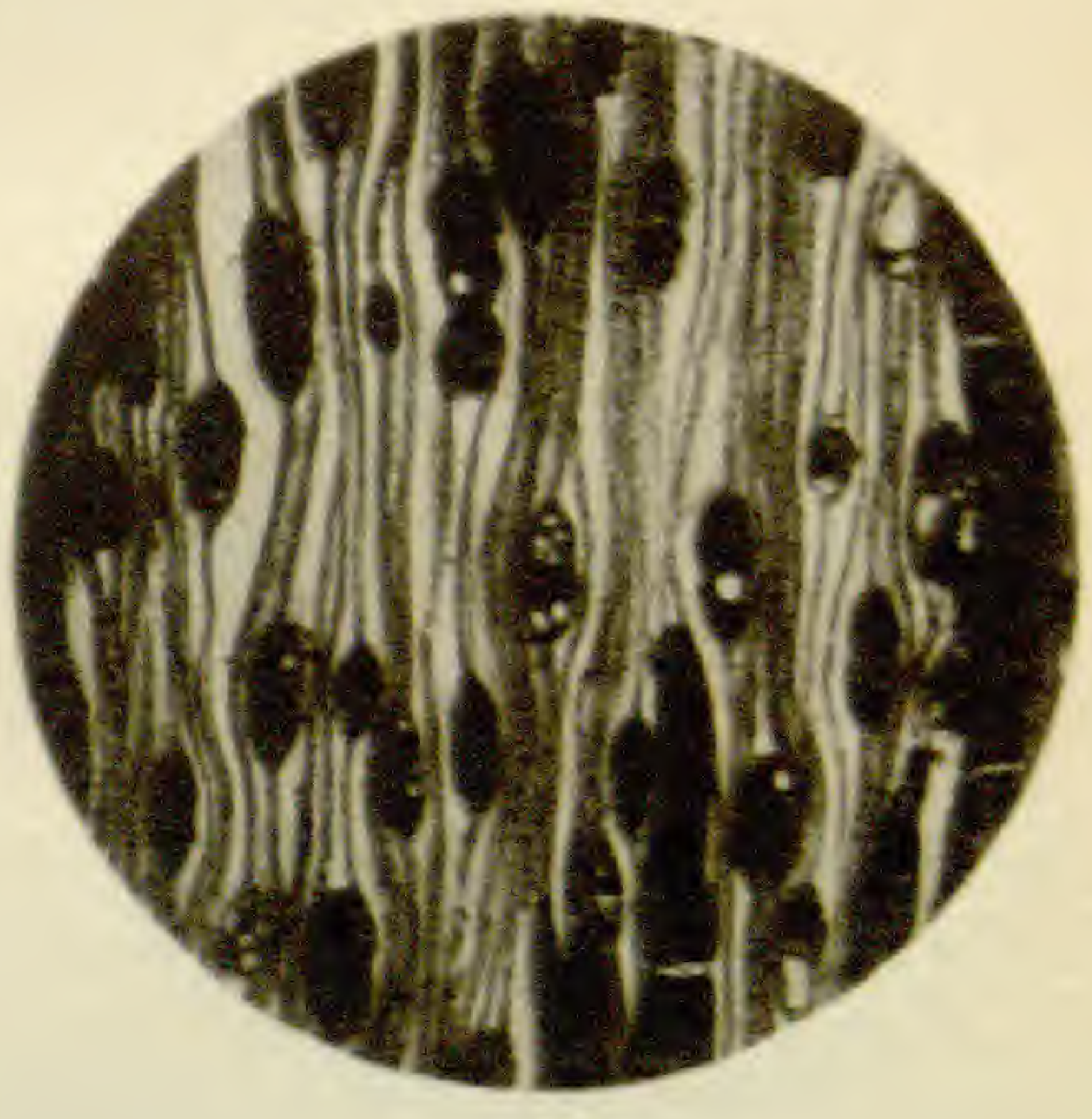

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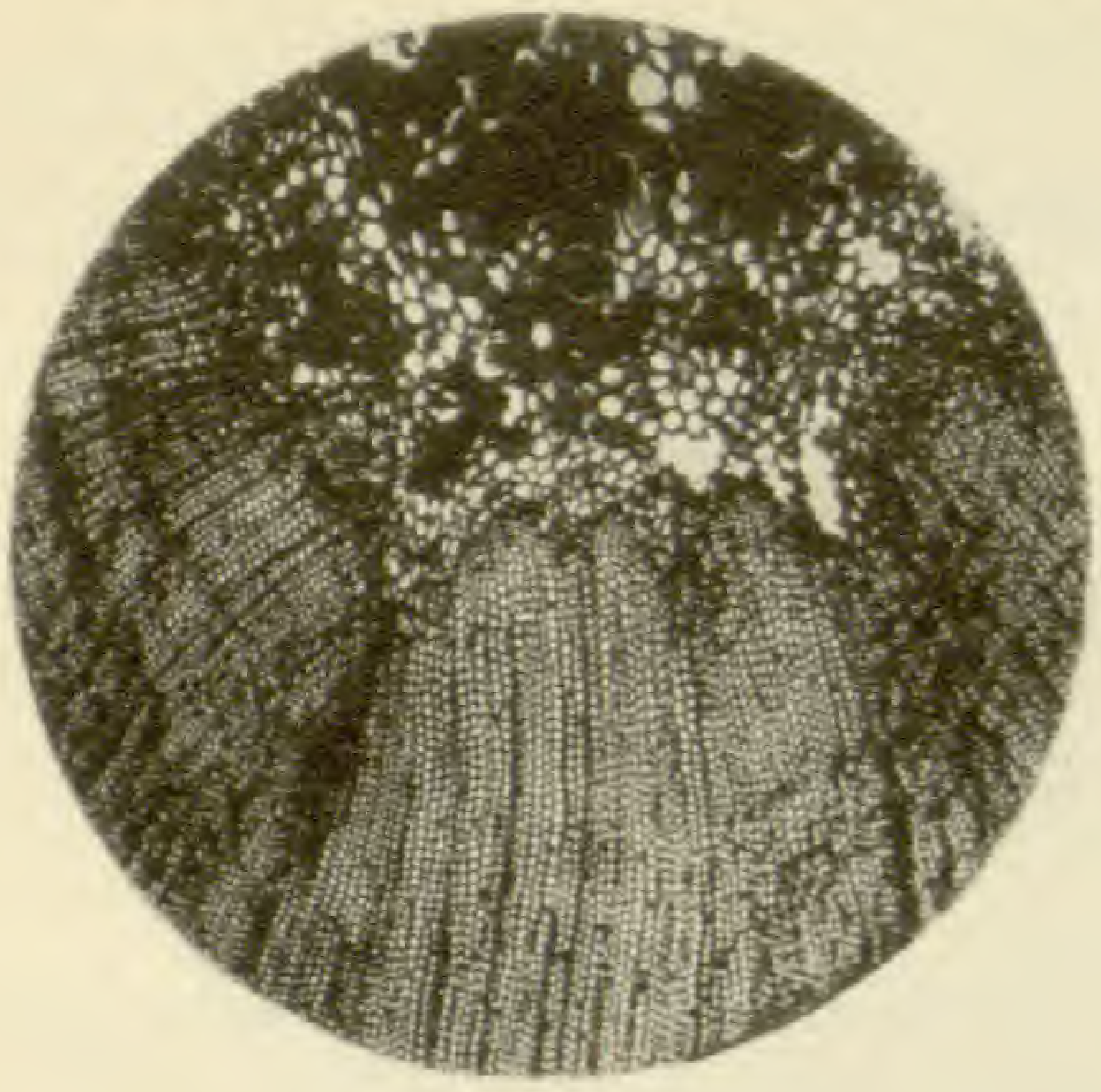

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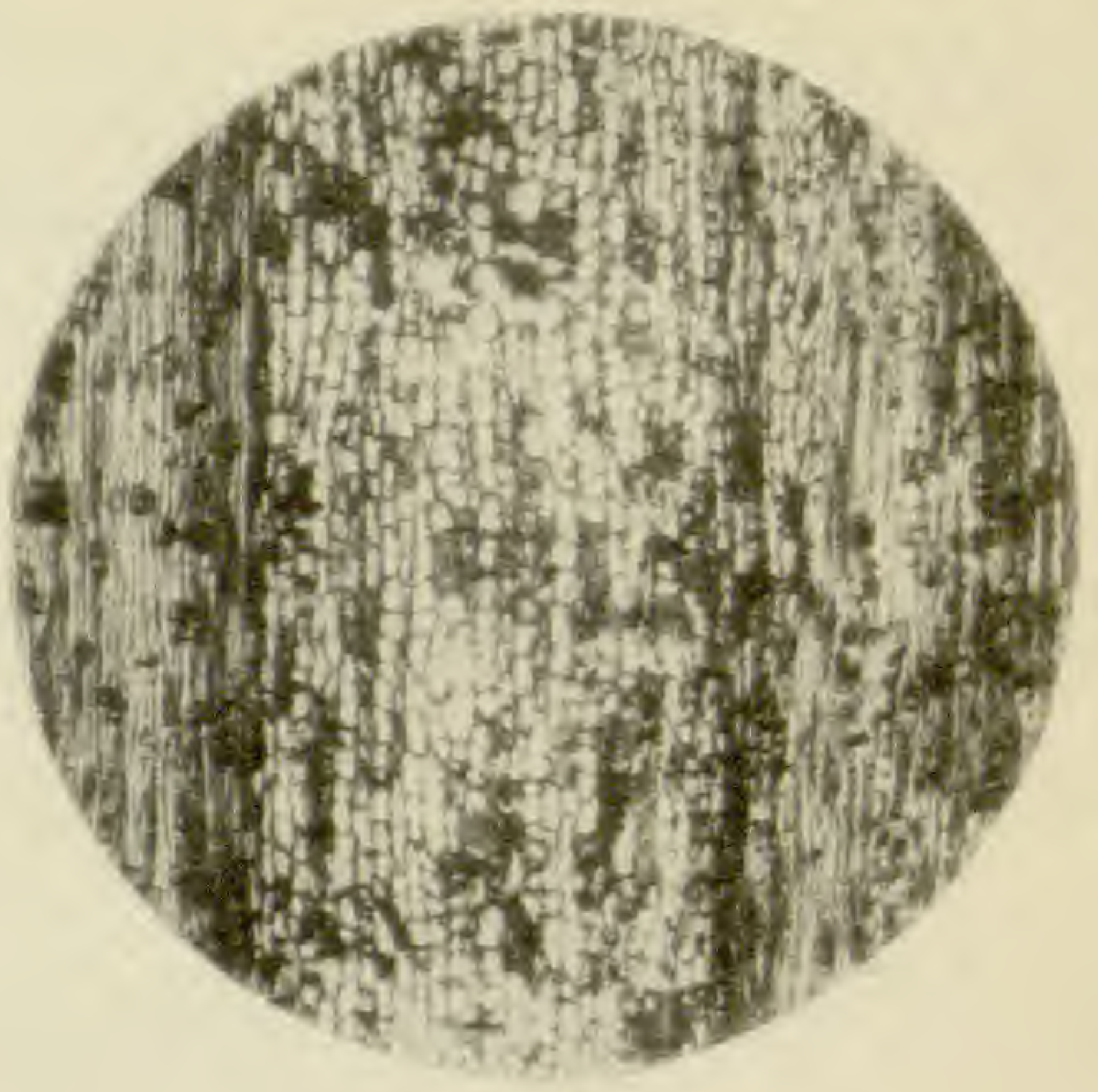

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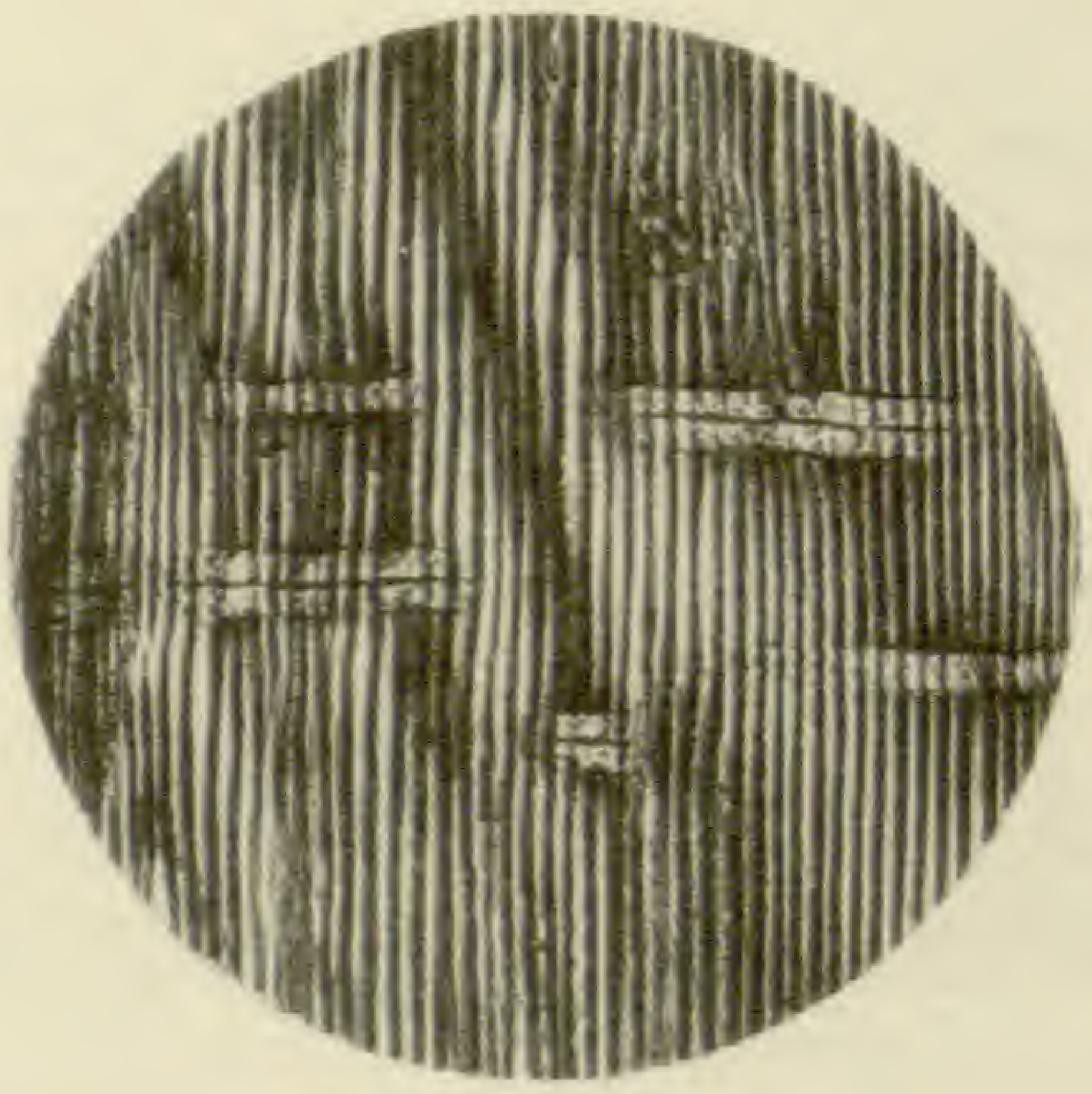

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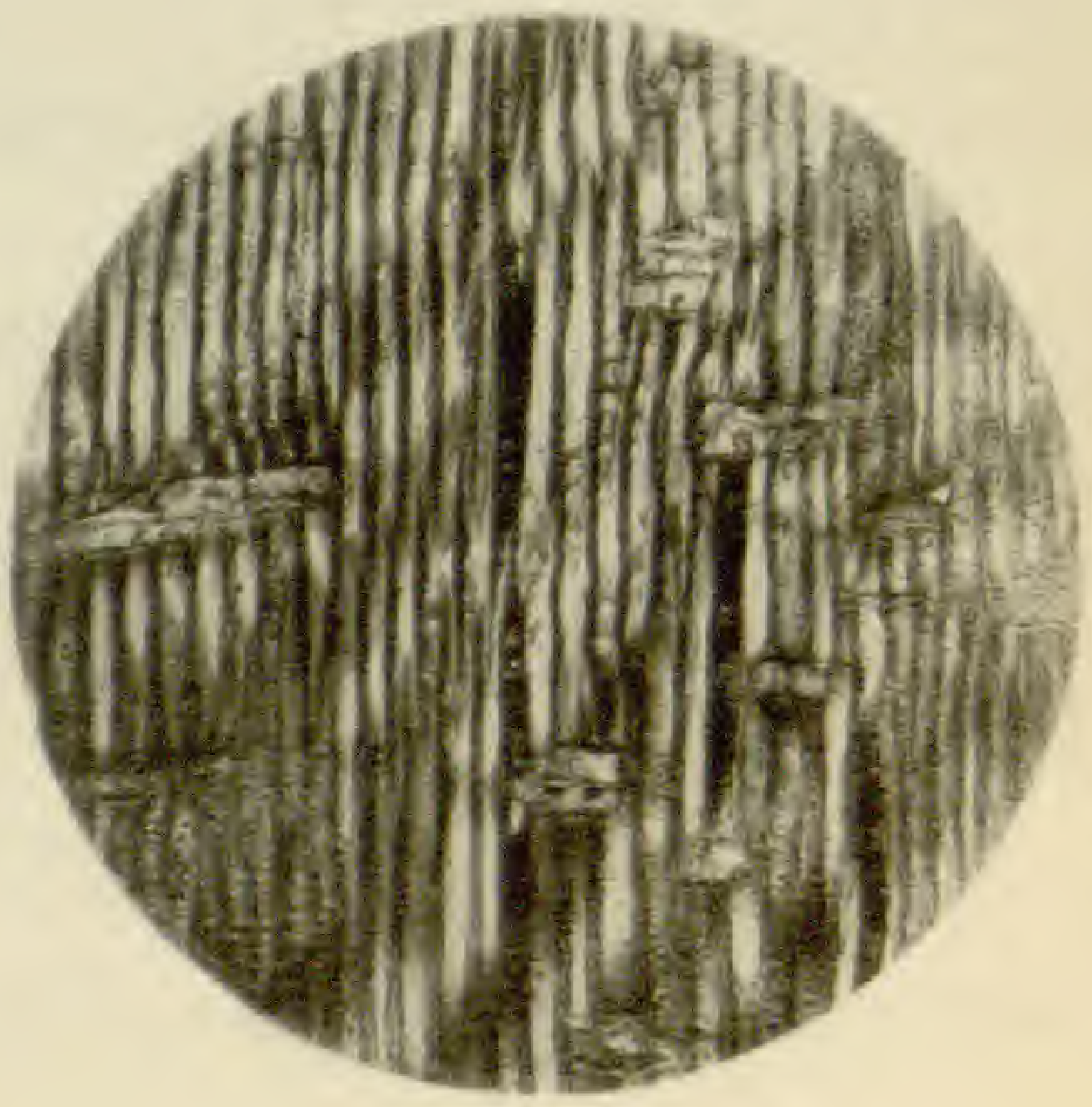

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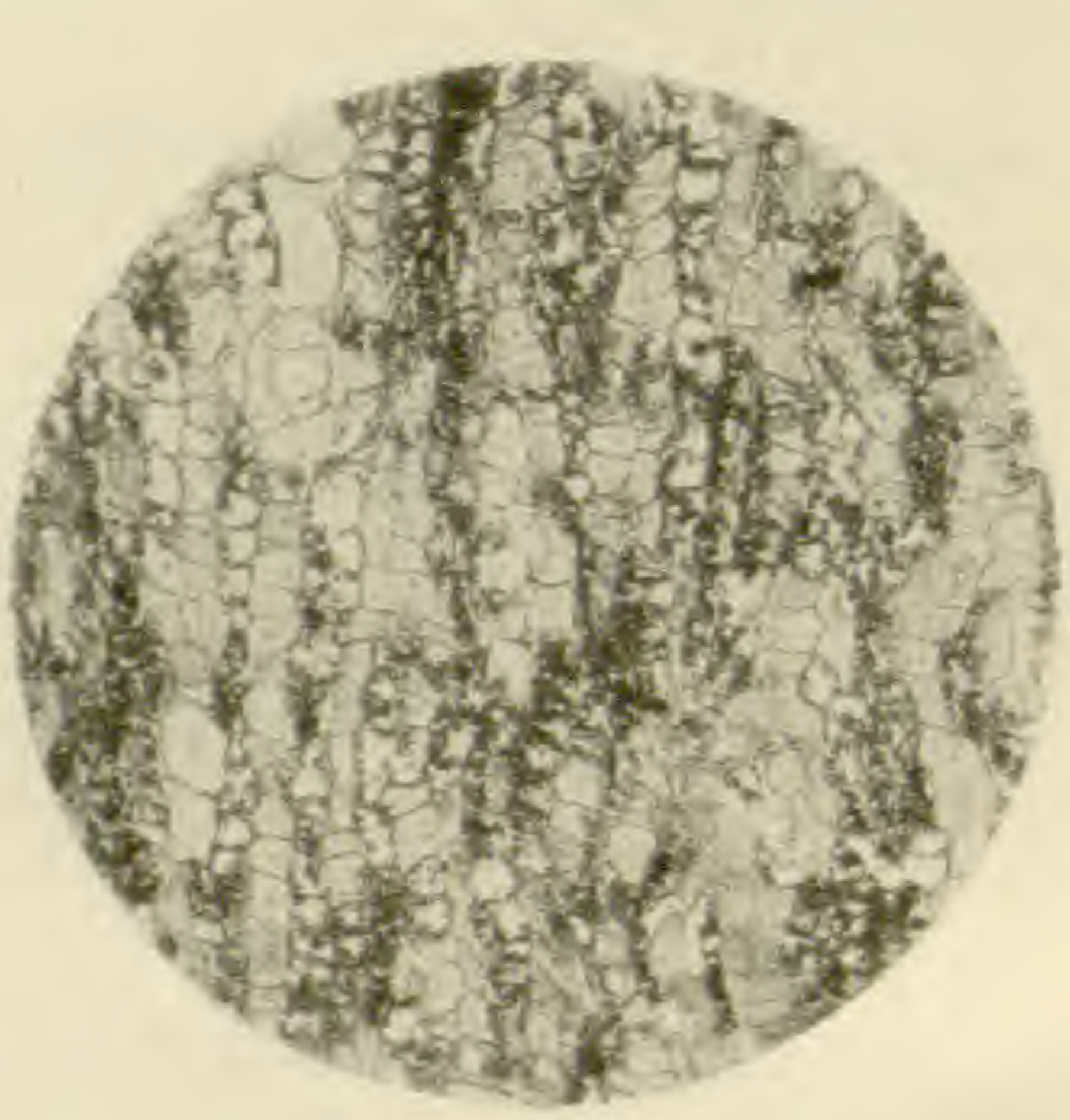

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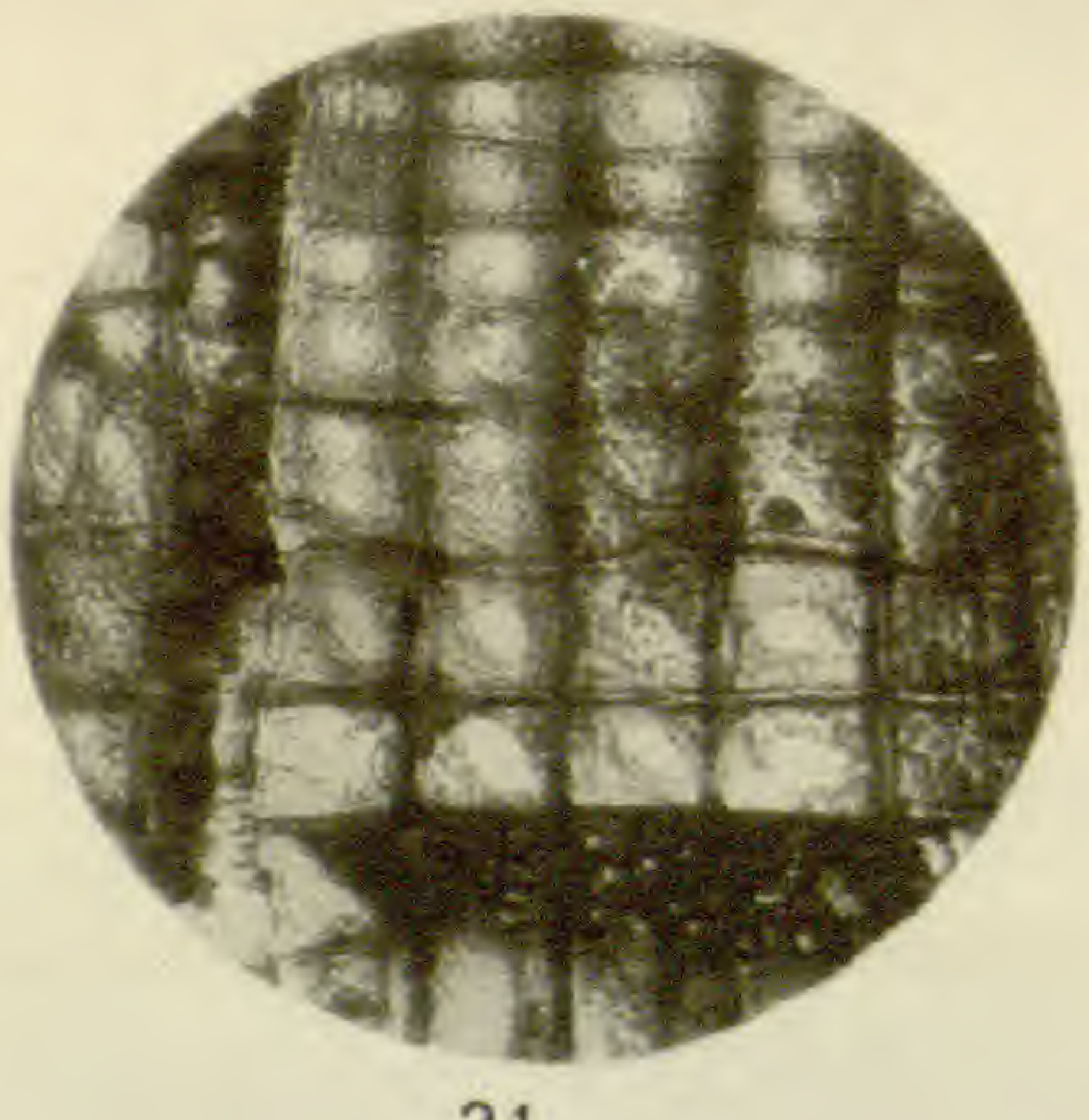

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HOLDEN on CRETACEOUS LIGNITES

FIG. 18.—Same; radial section, showing tracheary pits sometimes crowded and sometimes scattered; thin-walled rays, with numerous small pits on longitudinal wall; ×90.

FIG. 19.—Same; tangential section, showing tangential pitting; ×90.

FIG. 20.—*Paracupressinoxylon cupressoides;* transverse section near pith, showing abundance of parenchyma cells; ×15.

FIG. 21.—Same; longitudinal section; ×15.

FIG. 22.—Same; transverse section including bark and wood; in the former the large parenchyma cells and crushed fibers may be seen; ×90.

FIG. 23.—Same; radial section, showing low, resinous rays, large parenchyma cells, and scattered tracheary pits; ×90.

FIG. 24.—Same; tangential section; ×90.

FIG. 25.—*Paracupressinoxylon* sp.; transverse section, showing stone cells in the pith, and wood parenchyma; ×15.

FIG. 26.—Same; longitudinal section; ×15.

FIG. 27.—Same; radial section of mature wood; ×40.

FIG. 28.—Same; section near pith, showing bars of Sanio; ×250.

FIG. 29.—Another specimen of *Paracupressinoxylon* showing wood parenchyma, scattered tracheary pits, and thin-walled rays; ×90.

FIG. 30.—Another specimen, showing peculiar arrangement on stone cells; ×40.

FIG. 31.—Another specimen, radial section, showing fusion pits in the rays; ×150.

FIG. 32.—Same; tangential section, indicating resinous exudations in tracheids from rays; ×90.

QUANTITATIVE CRITERIA OF ANTAGONISM

W. J. V. Osterhout

(WITH FOUR FIGURES)

It is apparent from a consideration of the literature that faulty criteria of antagonism are frequently employed. It often happens that such criteria do not permit us to decide in critical cases whether antagonism exists or not.

As the study of antagonism becomes more quantitative in character it becomes necessary to have well defined standards by which antagonism may be measured. Failure to make use of such standards has led in some cases to serious misconceptions.

As an example of this the following case may be cited. Suppose a solution of a toxic salt, A, to be mixed with a solution of another salt, B, the solutions having the same molecular concentration and the same degree of toxicity. Suppose that in a mixture of 100 cc. of 0.1 M solution of A plus 100 cc. of 0.1 M solution of B, plants grow better than in either of the pure solutions. Some investigators assert that this increase of growth should not be attributed wholly to

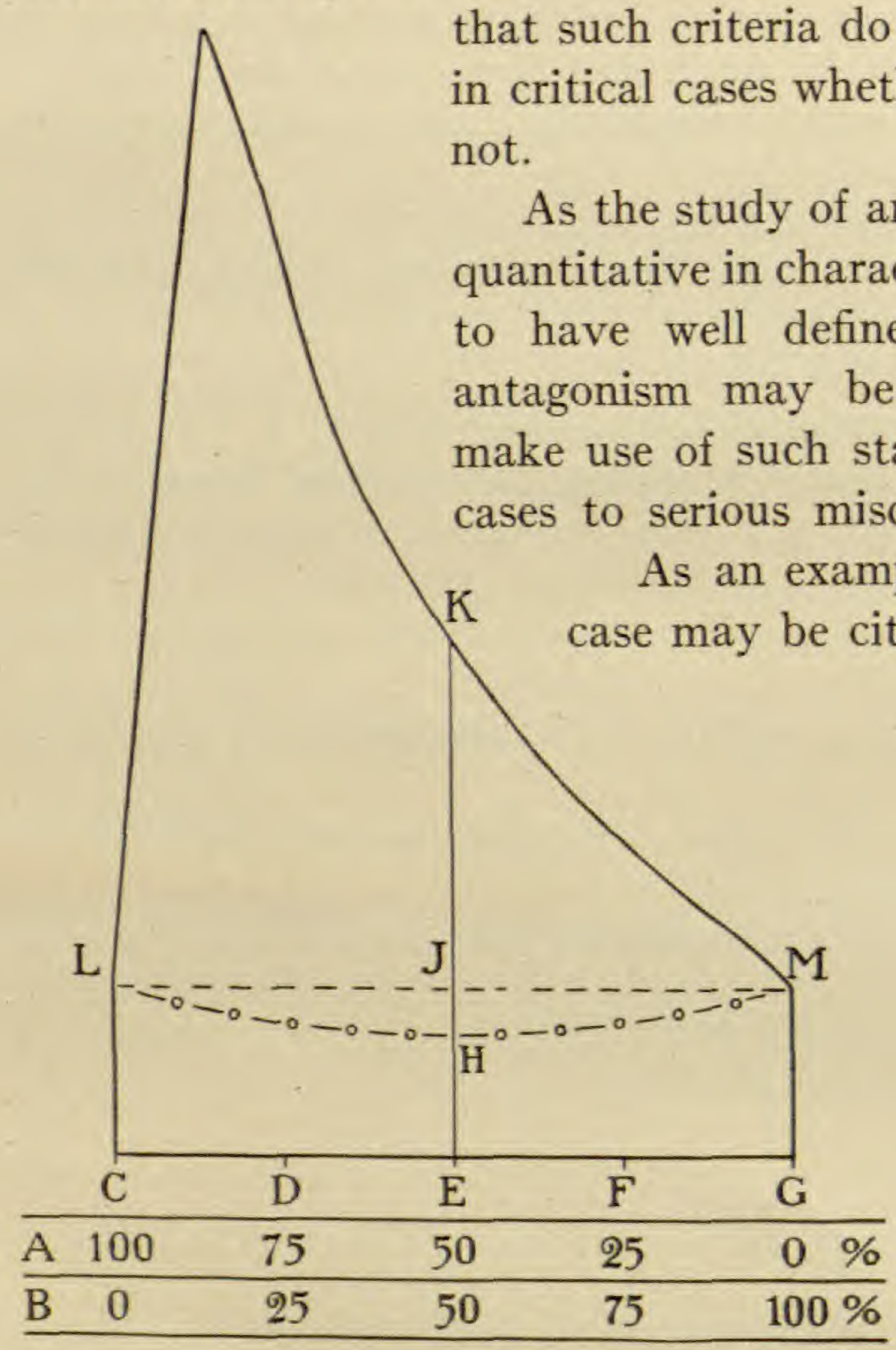

FIG. 1.—Curves showing the growth of roots in mixtures of equally toxic solutions of two salts A and B: the ordinates represent growth; the abscissas represent the composition of the mixtures, thus A 50, B 50 means a mixture in which the dissolved molecules are 50 per cent A and 50 per cent B; the horizontal dotted line (LJM) represents the growth which would occur if there were no antagonism (additive effect); LKM is the antagonism curve; LHM, curve expressing increased toxicity (opposite of antagonism); the quantitative expression of antagonism at the point E is $\frac{KJ}{JE}$.

antagonistic action, but that it is partly due to the dilution of the toxic salts, for it is evident that the concentration of each of them has been reduced from 0.1 M to 0.05 M.

It seems desirable to formulate the matter so as to obviate such misconceptions and it is clearly necessary to provide a quantitative criterion of antagonism which shall be both accurate and convenient. A graphical expression of such a criterion is seen in Fig. 1.

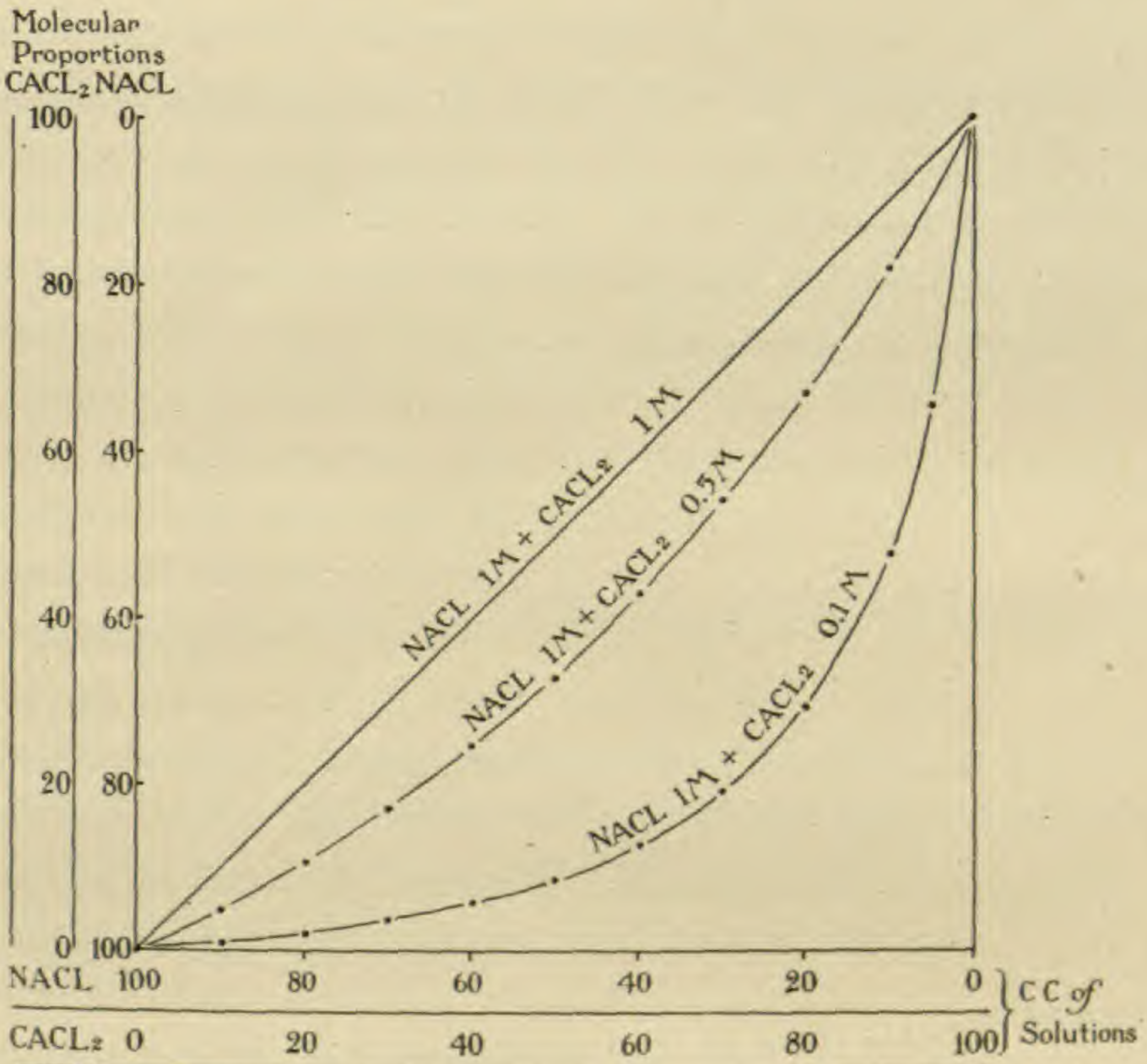

FIG. 2.—Curves showing the relation between the molecular composition of a mixture of two solutions and its composition expressed as cc. of the component solutions; see footnote 1.

In this figure the growth of the plant in a solution of the salt *A* 0.1 M is expressed by the ordinate at *C;* the growth in a solution of the salt *B* 0.1 M is expressed by the ordinate at *G;* as the ordinates are equal the solutions are equally toxic. The ordinates between *C* and *G* express the growth in various mixtures of the two solutions; thus that at *D* expresses the growth in a mixture in which 75 per cent of the dissolved molecules are *A* and 25 per cent are *B;* the ordinate at *E* expresses growth in a mixture in which 50 per cent of the dissolved molecules are *A* and 50 per cent are *B*.[1]

It is obvious that the effect of mixing two equally toxic solutions must fall into one of the following categories.

1. The toxicity is unaltered, that is, the toxic action of the two salts is *additive*. Each salt produces its own toxic effect precisely as though the other were not present. This is expressed by the horizontal dotted line *LJM*.

It is evident that we cannot get increased growth by mixing two such solutions unless the salts have an antagonistic action. The dilution of *A* from 0.1 M to 0.05 M is exactly compensated by the introduction of molecules of *B*. Or, to put it in another way, the toxic effect depends on the number of molecules present (if both kinds of molecules are equally toxic and there is no antagonism) and it makes no difference whether the solutions are pure or mixed.

If the toxic effect depends on ions, rather than on molecules, then, since the number of ions may be somewhat increased by mixing solutions, the toxicity may be correspondingly increased; but the amount of this increase would ordinarily be negligible.

2. The toxicity is diminished, that is, the effect is *antitoxic*. We then get a curve rising somewhere above the dotted line, such as the unbroken line *LKM*.

3. The toxicity is increased. We then get a curve which somewhere falls below the dotted line, such as the line interrupted by circles *LHM*.

The considerations here set forth apply in all cases where two equally toxic solutions are mixed, whether their concentration is the

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[1] In order to avoid unnecessary calculations in making up solutions with the desired molecular proportions, curves similar to those in fig. 2 serve a very useful purpose. The figures on the vertical scale denote molecular proportions, while those on the horizontal scale denote cc. of solutions. Suppose that we are mixing NaCl 1 M and $CaCl_2$ 0.5 M. If we mix 60 cc. of the NaCl with 40 cc. of the $CaCl_2$, the molecular proportions are NaCl 75 per cent+$CaCl_2$ 25 per cent. If each of the scales (vertical and horizontal) is 100 mm. long, the ordinate (measured from above downward) will in this case be 25 mm., and the abscissa (measured from right to left) 60 mm. After determining a series of such points, a curve may be drawn from which other proportions may be read off directly. Such a curve is shown in the figure (NaCl 1 M − $CaCl_2$ 0.5 M); this curve serves equally well for all solutions in which the molecular concentration of one component is twice that of the other. In the same manner the other curve NaCl 1 M − $CaCl_2$ 0.1 M applies equally well to all solutions in which the molecular concentrations of the two components are as one to ten.

same or not. Thus, if a solution of *A* 0.05 M is just as toxic as a solution of *B* 0.1 M, mixtures of the two will give a straight line (as in fig. 1) provided their effects are additive.

Emphasis should be laid upon the fact that the method of mixing two equally toxic solutions eliminates disturbances due to variations of osmotic pressure. If a molecule of *A* is twice as toxic as a molecule of *B*, a solution of *A* 0.05 M will be just as toxic as a solution of B 0.1 M, provided there are no other factors to be considered. But if the osmotic pressure of the 0.05 M solution of *A* is less than that of the 0.1 M solution of *B*, there will in many cases be better growth in the 0.05 M solution of *A*. In order to make the solution of *A* appear equally toxic with the solution of *B*, the concentration of *A* must be somewhat increased, say to 0.055 M. We thus compensate for the variation in osmotic pressure, and this compensation is not destroyed when the 0.055 M solution of *A* is mixed with the 0.1 M solution of *B*. If the effects of the salts are additive, we must therefore get a straight line, as shown in fig. 1.

It is evident that this straight line furnishes a criterion of antagonism which for quantitative purposes leaves nothing to be desired. All that is necessary is to determine what concentrations of *A* and *B* are equally toxic, mix these solutions in various proportions, and determine the amount of growth. The antagonism in any mixture may then be expressed in a very simple manner. Let the curve showing the growth in the mixtures be *LKM*. The antagonism in a mixture in which the molecules are 50 per cent *A* and 50 per cent *B* may be expressed as $\frac{KJ}{JE}$. *JE* is the growth which would have been obtained if the effect of the salts had been additive (that is, if there had been no antagonism, but each salt had produced its effect independent of the other). *KJ* is the increased growth due to antagonism; it is best expressed as percentage of *JE* or as $\frac{KJ}{JE} \times 100$.

In the same way increased toxicity (when the mixture is more toxic than either of the pure solutions) may be expressed as $\frac{JH}{JE}$. This sometimes occurs, but it is much less common than antagonism.

As an illustration of this method the results given in table I may be cited. In this case the growth in the various mixtures was in part determined directly and in part was calculated from results obtained by growing plants in mixtures having almost the same composition as the solutions given in the table.

TABLE I

MIXTURES OF EQUALLY TOXIC SOLUTIONS

Wheat (growth during 30 days) (NaCl 0.12 M + $CaCl_2$ 0.164 M)

Culture solution	Aggregate length of roots per plant in mm.	Additive effect	Antagonism
$CaCl_2$	55	55	....
75 per cent $CaCl_2$ 25 " NaCl	105	55	$\frac{105-55}{55}=0.91$
50 " $CaCl_2$ 50 " NaCl	180	55	$\frac{180-55}{55}=2.27$
25 " $CaCl_2$ 75 " NaCl	298	55	$\frac{298-55}{55}=4.42$
15 " $CaCl_2$ 85 " NaCl	370	55	$\frac{370-55}{55}=5.73$
5 " $CaCl_2$ 95 " NaCl	435	55	$\frac{435-55}{55}=6.91$
1 " $CaCl_2$ 99 " NaCl	300	55	$\frac{300-55}{55}=4.45$
NaCl	55	55	....

The percentages refer to molecular proportions; that is, 75 per cent $CaCl_2$ + 25 per cent $NaCl_2$ means a solution in which 75 per cent of the dissolved molecules are $CaCl_2$ and 25 per cent are NaCl.

We may now consider the effect of mixing two solutions which are not equally toxic. Suppose solution *A* 0.1 M to be twice as toxic as solution *B* 0.1 M. The effect of mixing these, if the effects were strictly additive, would be the same as mixing a solution of *A* 0.1 M with another solution of *A* just twice as toxic, or in other words would be the same as increasing the concentration of *A*. In this case the curve expressing purely additive effects would not be a straight line, but would assume the form of a curved line, convex to the horizontal axis, similar to *VSW* in fig. 3. This is evident from the curves given by MAGOWAN[2] showing growth in toxic solutions of various concentrations.

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[2] BOT. GAZ. 45:45. 1908.

It would be possible to determine this additive curve experimentally, and then to express antagonism quantitatively; for example, at the point *P* it would be expressed as $\frac{UT}{TP}$. But the labor would be much greater than by the method of mixing equally toxic solutions. The additive curve would be determined by growing plants, not in mixtures of *A* with *B*, but in mixtures of *A* with another solution of *A* having the same toxicity as *B*. Or we might use mixtures of *B* with another solution of *B* having the same toxicity as *A*. The two methods might not give exactly the same result. This is an additional argument in favor of using equally toxic solutions.

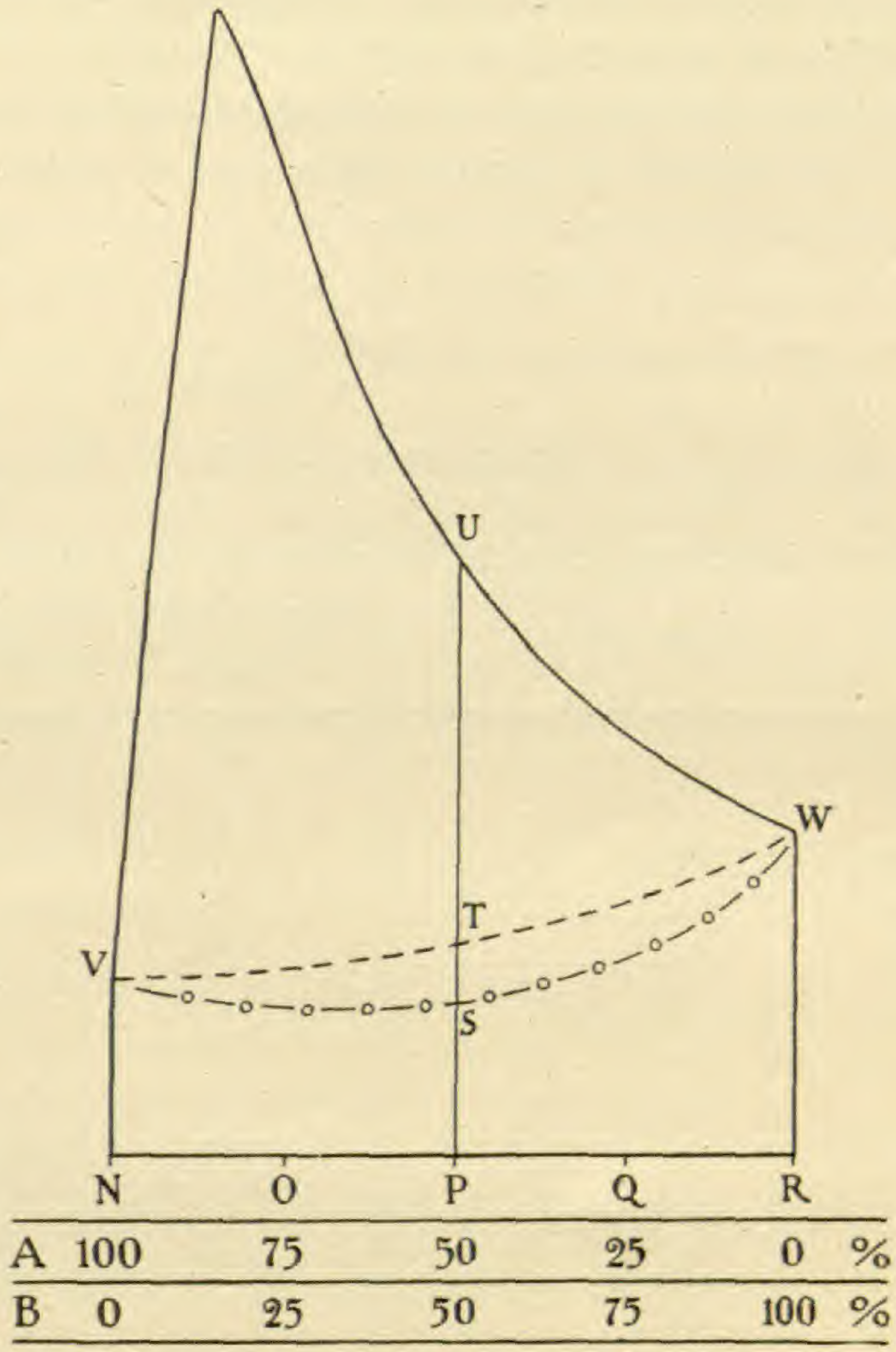

FIG. 3.—Curves showing growth in mixtures of unequally toxic solutions: the ordinates express growth; the abscissas express the composition of the mixtures as in fig. 1; the dotted line *VTW* expresses the growth which would occur if there were no antagonism (additive effect); *VUW*, antagonism curve; *VSW*, curve expressing increased toxicity (opposite of antagonism); the quantitative expression of antagonism at the point *P* is $\frac{UT}{TP}$.

An illustration of this method is found in the results given in table II. The growth in the various mixtures (additive and antagonistic) was in part determined directly and in part was calculated from results obtained by growing plants in mixtures having almost the same composition as the solutions given in the table mentioned.

For the sake of completeness it may be mentioned that other types of antagonism curves are found; for example, flat-topped curves and also curves with two maxima, as shown in fig. 4.

If instead of mixing two equally toxic solutions we keep the concentration of one salt constant while varying that of the other, it becomes very difficult to determine the additive curve, especially when variations in osmotic pressure influence the result. It is therefore difficult to obtain an accurate quantitative expression of antagonism by this method, and in critical cases it may be impossible to decide whether antagonism exists or not.

TABLE II

MIXTURES OF UNEQUALLY TOXIC SOLUTIONS

Wheat (growth during 30 days) (NaCl 0.12 M + $CaCl_2$ 0.12 M)

Culture solution	Aggregate length of roots per plant in mm.	Additive effect	Antagonism
$CaCl_2$........................	85	85	....
75 per cent $CaCl_2$............ 25 " NaCl............	125	75	$\frac{125-75}{75} = 0.67$
50 " $CaCl_2$............ 50 " NaCl............	195	66.5	$\frac{195-66.5}{66.5} = 1.93$
25 " $CaCl_2$............ 75 " NaCl............	310	60	$\frac{310-60}{60} = 4.17$
15 " $CaCl_2$............ 85 " NaCl............	380	58	$\frac{380-58}{58} = 5.55$
5 " $CaCl_2$............ 95 " NaCl............	438	56	$\frac{438-56}{56} = 6.82$
1 " $CaCl_2$............ 99 " NaCl............	300	55	$\frac{300-55}{55} - 4.45$
NaCl........................	55	55	....

The percentages refer to molecular proportions; that is, 75 per cent $CaCl_2$+25 per cent NaCl means a solution in which 75 per cent of the dissolved molecules are $CaCl_2$ and 25 per cent are NaCl.

Emphasis should be laid on the fact that the growth of parts not in immediate contact with the solution does not furnish a trustworthy criterion of antagonism. Thus the leaves of wheat (which are not in contact with the solution) often grow well at the start in solutions of copper salts, while the roots (which are immersed in the solution) do not grow at all. The reason is that as the solution passes through the roots to the leaves a great part of the copper is removed either by adsorption or by chemical combination.[3]

Finally, it may be noted that quantitative results are more reliable and much more easily obtained when uniform material is used. "Pure line" wheat and other seeds may now be obtained and should be used whenever possible. When they are not obtainable the following method (suggested by Professor JOHANNSEN) may be employed. Several heads of wheat are taken. One grain of wheat from each is placed in each solution (and these grains should resemble each other as much as possible). In this way each solution receives the same kinds of wheat, and an average of the growth of all the plants in any solution may be safely used for comparison with the average in any other solution. It is desirable to employ this method even when pure line seeds are used.

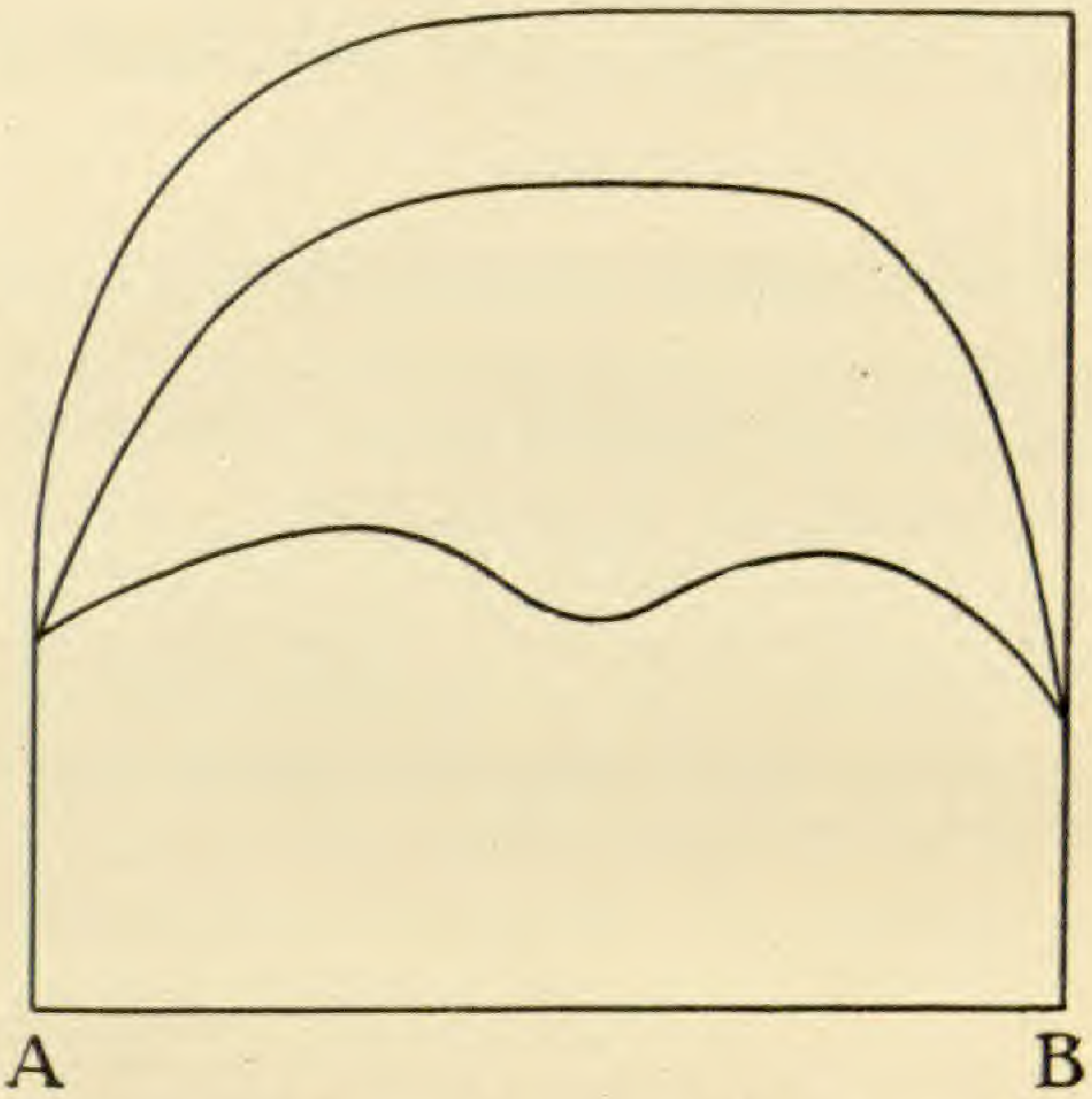

FIG. 4.—Types of antagonism curves: the ordinates express growth; the abscissas express the composition of the mixtures as in fig. 1.

Summary

The method of mixing equally toxic solutions furnishes the best criterion of antagonism, since we know at the outset just what effect each mixture must have provided there is no antagonism.

Mixtures of two equally toxic solutions must have precisely the same effect on growth as the pure solutions themselves, provided that the effects of the salts are additive. If antagonism exists there

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[3] Cf. BOT. GAZ. 44:268. 1907.

is an increased growth in the mixtures. The amount of this increase, expressed as percentage of the growth obtained in the pure solutions, is the most satisfactory measure of antagonism.

The most reliable results are obtained by the use of uniform material and by taking for measurement only such parts as come into immediate contact with the solution.

HARVARD UNIVERSITY

CURRENT LITERATURE

BOOK REVIEWS

The British rusts

A volume dealing with the British Uredinales is very welcome, since it organizes in convenient form a widely scattered literature.[1] The descriptions are based upon those of SYDOW'S *Monographia Uredinearum*, and all the species of which British specimens could be procured have been revised. The nomenclature of course presents unusual difficulties, but the principle of priority has been followed, subject to two conditions: (1) names given to varieties need not be adopted, and (2) names given to imperfect stages are not to be preferred, but the earliest name given to the perfect stage. Both of these conditions have been provided for by international agreements.

There are six introductory chapters dealing with general topics before the systematic presentation. The first chapter uses *Puccinia Caricis* as a typical "uredine" in giving an account of the life history of a rust. The reason given for dislodging *P. graminis* from this usual position is that its aecidium is now very rarely found in England, while that of *P. Caricis* (on nettle) is common.

The second chapter discusses the sexuality of the Uredinales and reaches the usual conclusion that there is a definite alternation of n and $2n$ generations. In the third chapter the multitudinous spore forms are discussed, with the various elisions in the life history, and the terminology arising from them.

The fourth chapter contains accounts of the life histories of certain representative Uredinales: *Puccinia graminis, P. Poarum, P. Malvacearum, Gymnosporangium clavariaeforme, Endophyllum Sempervivi, Cronartium ribicola, Melampsora pinitorqua,* and *Calyptospora Goeppertiana.* These life histories were selected to show the variations in life cycles, so far as could be done from British species.

The fifth chapter deals with specialization, including immunity; while the sixth discusses classification and phylogeny. The Uredinales are regarded as monophyletic, arising possibly from the Rhodophyceae. According to the diagrammatic scheme, the Fungi offshoot from Red Algae soon forked into two divergent branches, one ending in the Ascomycetes, and on the way giving rise to the Basidiomycetes; while the other branch resulted in Uredinales and Ustilaginales. There is also presented a scheme starting with the "primitive uredine" and resulting in the various families of the Uredinales.

The systematic part of the volume (306 pp.), with its full descriptions and numerous illustrations, makes the recognition of the British rusts as easy as

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[1] GROVE, W. B., The British rust fungi (Uredinales); their biology and classification. 8vo. pp. xii+412. *figs. 290.* Cambridge University Press. 1913. 14s.

such a group can be. The number of species included is about 250, presented under five families.—J. M. C.

Forestry in New England

The increased attention that is being devoted to the question of forest preservation and forest restoration is being fostered and given intelligent direction by a number of publications appealing to the landowner who would make his forest-lands more valuable to himself and to the community. One of the best of these[2] deals somewhat specifically with the forestry problems of New England. Such problems appeal especially to many residents of towns and cities who own wooded land in the country, both because they often have a broader view of the economic principles involved and because intelligent forest management requires less constant attention than almost any sort of agriculture. To these and other intelligent owners of woodlands the present volume makes a direct appeal, although it may also be used with advantage by students in forestry schools.

The volume is arranged in two parts, the first dealing with such general principles of forestry as may be indicated by the chapter-headings: Silvics; Silvicultural systems; Silvicultural characteristics of New England trees; Forest planting; Forest insects and fungi; Forest fires; and Growth of trees and forests. The second part deals in some detail with the different forest regions of New England and the forest administration in the different states. A couple of maps show the distribution of the various forest regions of the New England states, while the appendix contains forest fire statistics, foresters' tables, and a bibliography.

The various topics appear to be handled with scientific accuracy, and still in a sufficiently non-technical manner to appeal to the intelligent layman; in fact, it seems to the reviewer that the mission of the book lies in such an appeal rather than in any use that may be made of it in the classroom. This would in no way lessen its usefulness, for one of the most important things in promoting the advance of forestry is the education of the general public to a conception of the problems involved, and an appreciation of the efforts that are being made for this solution. The book is well printed and attractively illustrated.—GEO. D. FULLER.

MINOR NOTICES

Rubber.—LOCK[3] has brought the subject of rubber-planting within reach of a large audience. He has combined an account of the scientific side of the subject with a certain amount of practical information that will be of service

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[2] HAWLEY, R. C., and HAWES, A. F., Forestry in New England. 8vo. pp. xv+479. *figs. 140*. New York: John Wiley & Sons. 1912. $3.50.

[3] LOCK, R. H., Rubber and rubber-planting. 8vo. pp. xii+245. *figs. 22. pls. 10.* Cambridge University Press. 1913.

to the prospective planter. The science and practice of rubber-planting are both new, and important developments in both are to be expected. Some of the topics treated in the eleven chapters indicate the scope of the work: The history of the use and cultivation of rubber; The botanical sources of rubber; The physiology of latex production; Planting and harvesting operations; the pests and diseases of *Hevea;* The chemistry of India rubber.

Anyone who is familiar with LOCK's *Recent progress in the study of variation, heredity, and evolution* will know the accuracy and clearness with which the present subject is presented.—J. M. C.

The genus Sabicea.—WERNHAM[4] has published in book form a monograph of *Sabicea,* which is the first of a series of monographs on Rubiaceae. The genus belongs to tropical Africa and America, a large majority of the species being "scrambling shrubs." The number of species reaches 105, and 62 of these are described as new. This is an indication of the harvest of new species the tropics will yield when investigated. The monograph is more than a description of species, for it includes a discussion and graphic illustrations of their interrelationships.—J. M. C.

Weeds.—With the increasing demand for practical lessons for children, it is of interest to note the appearance of a booklet on weeds, by R. LLOYD PRAEGER,[5] as one of the "Cambridge Nature Study Series." The titles of the chapters suggest the contents: What weeds are; The life of a plant; On weeds in general; Seeds and their ways; The war against weeds; Some common weeds.—J. M. C.

The fresh-water flora of Germany, Austria, and Switzerland.—This very compact and well illustrated manual of the fresh-water flora of its region was planned to appear in 13 small volumes, 5 of which have appeared and have been noticed in this journal. Part 6 has now appeared,[6] dealing with three orders of the Chlorophyceae, and prepared by HEERING of Hamburg.—J. M. C.

NOTES FOR STUDENTS

Antarctic vegetation.—The activity in the south polar explorations during the past decade and a half has added somewhat to the botanical knowledge of a remarkably poor flora. In agreement with SKOTTSBERG and others, BROWN[7]

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[4] WERNHAM, H. F., A monograph on the genus *Sabicea.* 8vo. pp. 82. *pls. 12.* Published by the British Museum (Natural History). 1914.

[5] PRAEGER, R. LLOYD, Weeds; simple lessons for children. 8vo. pp. x+108. *figs. 45.* Cambridge University Press. 1913. 1*s.* 6*d.* net.

[6] PASCHER, A., Die Süsswasser-Flora, Deutschlands, Österreichs, und der Schweiz. Part VI. Chlorophyceae. 3 (Ulothricales, Microsporales, Oedogoniales) by W. HEERING. pp. 250. *figs. 384.* Jena: Gustav Fischer. 1914.

[7] BROWN, R. N. R., The problems of antarctic botany. Scottish National Antarctic Expedition 3:Bot. 3–20. Edinburgh. 1912.

accepts parallel 60° S. as a more or less natural limit for the antarctic region. Compared with the arctic flora, the antarctic is very poor, including only two species of seed plants (*Deschampsia antarctica* and *Colobanthus crassifolius*), in contrast with about 400 species in corresponding northern areas. The author finds this poverty of vegetation due not so much to the isolation of the land areas in this portion of the Southern Hemisphere as in unfavorable climatic conditions, and chiefly to the very low summer mean temperature, usually below 0° C., while in corresponding arctic regions it is well above this point. SKOTTSBERG considers that the remarkably high winds of the antarctic region must also be considered detrimental to the existence of higher plants. A second adverse factor is found in the immense number of penguins that inhabit during their nesting season every bare spot of land, thus preempting the areas with the best soil conditions for seed plants.

There are no antarctic ferns, but the mosses are represented by 52 species, of which 24 are endemic, 16 northern, and 12 southern. The fact that 16 moss species are common to antarctic and Fuegian lands is perhaps the strongest argument for the Fuegian origin of the antarctic flora. Vegetative reproduction seems the rule among these mosses, very few (6 only) being found with well developed sporophytes.

Only 6 species of hepatics have been found and but a single fungus, *Sclereotium antarcticum*, growing among *Deschampsia* on Danco Island. On the contrary, antarctic vegetation is rich in lichen display, DARBISHIRE[8] recording 106 species, of which 67 are endemic, 25 found also in New Zealand, and 32 in America, these last affording additional evidence of the probability of a migration from Fuegian lands as the origin of the antarctic flora.

SKOTTSBERG'S[9] account of the vegetation of Graham Land, including the South Shetland Islands, is quite in accord with BROWN'S. The mean summer temperature during the warmest months was $-2^{\circ}.14$ C., although the uppermost layers of soil usually thawed for a few hours about midday. The best areas for plant life were the islands and the somewhat elevated rocks which the winds kept comparatively free from snow. Here were considerable areas of moss tundra, consisting of species of *Polytrichum*, *Pogonatum*, and *Brachythecium*, thick mats dominated by *Andreaea* and *Grimmia* upon rock surfaces, and a fairly abundant lichen flora, in which species of *Placodium*, *Lecanora*, *Buellia*, and *Neuropogon* were conspicuous. SKOTTSBERG thinks that the present flora is of post-glacial age, but that it also represents the last relic of a vegetation that was formerly somewhat more abundant.—GEO. D. FULLER.

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[8] DARBISHIRE, O. V., The lichens of the Swedish Antarctic Expedition. Wiss. Ergebn. Schwed. Südpolar Exped. 1901–1903. 4: Lief. 11. 1912.

[9] SKOTTSBERG, CARL, Einige Bemerkungen über die Vegetationsverhältniss des Graham Landes. Wiss. Ergebn. Schwed. Südpolar Exped. 1901–1903. 4: Lief. 13. pp. 16. *pl. 3* and *map*. 1912.

Crosses of Oenothera.—GATES[10] reports the results of various crosses between *Oenothera grandiflora* and a variant of *Oenothera rubrinervis* of DEVRIES which he has described previously under the name *Oenothera rubricalyx*. He finds *rubricalyx* pigmentation (R) dominant to the type of pigmentation found in *rubrinervis* (r), and he believes this difference to be due to a single Mendelian factor, though his proof does not seem convincing to the reviewer. Assuming this to be the case, however, the discovery that various F_1 individuals produce F_2 ratios running from 3:1 to nearly 10:1 is very interesting, particularly as the same phenomenon appeared in the segregation of tallness from dwarfness. The author says these results are "inexplicable on a Mendelian basis," and reverts to that familiar piece of biological sarcasm, the word "prepotency," as an explanation. Unquestionably there is a chance that these odd ratios may lead to a distinct genetic advance when they are finally worked out, but the word "inexplicable" is a little hasty, since it may be pointed out that some of DEVRIES' dwarf mutants (*O. nanella*) have been shown to be infected with a micrococcus.

The crucial proof that mutation is independent of hybridization, which the author feels he has obtained, came from four aberrant plants which occurred among the hybrids. Two combined characters of the DeVriesian mutant *semilata* with characters of *grandiflora*, and two combined features of *lata* with features of *rubricalyx*. One plant out of the four was examined cytologically, and its cells were found to contain 15 instead of 14 chromosomes. This furnishes definite proof, it is said, that the *lata* (or *semilata*) foliage and habit results from the presence of an extra chromosome.

A large portion of the paper is taken up with general Mendelian criticism of a very acrimonious character. It is somewhat reminiscent of the windmill tourney of a certain Spanish cavalier, for obstacles are erected, labeled "Beliefs of Mendelians," of course without any citations whatever, and tilted at with great gusto and satisfaction.—E. M. EAST.

Cruciate-flowered Oenotheras.—BARTLETT[11] has discussed certain species of the much studied genus *Oenothera*. NUTTALL named *O. cruciata* from its linear petals, and thus the character of linear or narrowly oblong petals in the genus, as contrasted with broadly obovate petals, has come to be known as "cruciateness." The origin of this character is under discussion, and BARTLETT believes that it has originated in several lines of descent. As a consequence, he regards *O. cruciata*, as it has been ordinarily interpreted, as an aggregate, which should be resolved. After determining the real type of *O. cruciata*, he

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[10] GATES, R. R., Breeding experiments which show that hybridization and mutation are independent phenomena. Zeitschr. Ind. Abst. u. Vererbungslehre 11:209–279. 1914.

[11] BARTLETT, H. H., An account of the cruciate-flowered Oenotheras of the subgenus *Onagra*. Amer. Jour. Bot. 1:226–243. *figs. 2. pls. 19–21.* 1914.

adds three new cruciate species: *O. atrovirens*, *O. venosa*, and *O. stenomeres*, the first two being published in collaboration with SHULL. In connection with the segregation of these species, the cultures of the author have opened some very interesting questions that will be discussed later. For example, a new mutation was secured, which is called *O. stenopetala* mut. *lasiopetala*, and which is reserved for further discussion until its seeds have produced new plants. BARTLETT proposes a trinomial system of nomenclature, shown by the name of this mutation, for mutations of garden origin, "in order to set them clearly apart from forms of which cognizance must be taken in floras."—J. M. C.

A drought-resistant citrous fruit.—The search for hardy races of valuable plants has discovered a genus of drought-resistant citrous fruits from Australia, which SWINGLE[12] has concluded to be a new genus, to which he has given the name *Eremocitrus*. It is the Australian desert kumquat, now commonly called *Atalantia glauca* (Lindl.) Benth. It is the only member of the orange group that shows marked adaptation to desert climates, and has the general aspect of "sagebrush." It is under investigation in this country, having been sent to a number of localities for trial, so that within a year or two the limitations of its culture in the United States will be known.—J. M. C.

Pith of Osmunda.—GWYNNE-VAUGHAN[13] has described a stem of *Osmunda regalis* whose pith contains scattered tracheae. Such a "mixed pith" was described by KIDSTON and GWYNNE-VAUGHAN (1910) for the fossil *Osmundites Kolbei*. This same situation in an anomalous specimen of *Osmunda regalis* is regarded as further supporting the theory that the pith of the Osmundaceae "is phylogenetically stelar and not cortical, and that it arose by the progressive conversion of the central tracheae of a solid xylem strand into parenchyma." J. M. C.

Flora of southeastern Washington.—PIPER and BEATTIE[14] have published a manual of the vascular plants of a very interesting region, being an extension of their *Flora of the Palouse region*, published in 1901. The region covered is said to embrace the richest wheat lands of the northwest, the principal drainage systems being those of the Snake and Spokane rivers. The manual is handsomely printed, and includes descriptions of 1139 species, distributed as follows: 20 pteridophytes, 11 gymnosperms, 270 monocotyledons, and 838 dicotyledons.—J. M. C.

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[12] SWINGLE, WALTER T., *Eremocitrus*, a new genus of hardy, drought-resistant citrous fruits from Australia. Jour. Agric. Research **2**:85–100. *figs. 7. pl. 8.* 1914.

[13] GWYNNE-VAUGNAH, D. T., On a "mixed pith" in an anomalous stem of *Osmunda regalis*. Ann. Botany **28**:351–354. *pl. 21.* 1914.

[14] PIPER, CHARLES V., and BEATTIE, R. KENT, Flora of southeastern Washington and adjacent Idaho. 8vo. pp. xi+296. Pullman: State College of Washington. 1914. Paper, $1.00; cloth, $1.20.

Recent Publications

OF

The University of Chicago Press

The Weather and Climate of Chicago. (*Bulletin No. 4, Geographic Society of Chicago.*) *By Henry J. Cox, Professor of Meteorology, United States Weather Bureau, and John H. Armington, Local Forecaster, United States Weather Bureau.*

396 pages, 8vo, cloth; $3.00, postage extra (weight 3 lbs. 1 oz.)

This book, of general interest because of its character and authority, will naturally be of peculiar interest to residents of Chicago and the Middle West. Its importance is indicated by the fact that it is issued under the auspices of the Geographic Society of Chicago, and has been prepared by two of the best known weather experts in the country. It includes discussions of a great variety of subjects, such as temperature, precipitation, atmospheric moisture, cloudiness and sunshine, wind direction and velocity, barometric pressure, and storm tracks; and among the interesting appendixes to the book are one on the weather of holidays and another containing journal entries relative to the great Chicago Fire of 1871.

The volume contains also a remarkable series of tables with reference to temperature, precipitation, atmospheric moisture, and atmospheric pressure—one hundred and forty-seven in all, with more than one hundred figures and plates.

Of especial interest and importance to teachers in connection with *The Weather and Climate of Chicago* is the preceding Bulletin of the Geographic Society edited by Professor Cox, and by Professor J. Paul Goode of the University of Chicago. It was prepared by a committee of the Geographic Society of Chicago and is entitled *Lantern Slide Illustrations for the Teaching of Meteorology.* It will be found an admirable aid in interesting students in the phenomena of weather and climate.

Unpopular Government in the United States. By Albert M. Kales, Professor of Law in Northwestern University.

272 pages, 12mo, cloth; $1.50, postage extra (weight 1 lb. 8 oz.)

This volume by a prominent member of the Chicago bar is an especially timely book, presenting with great clearness and cogency some of the political needs of the country, particularly the necessity of the short ballot. The author defines unpopular government as one of centralized power which is able to maintain itself in the face of popular disapproval. He then points out that the establishment in the United States of state and municipal governments, according to the plan of splitting up the power of government among many separate offices and requiring the widest and most frequent use of the elective principle, has cast so great a burden upon the electorate that an intelligent citizen is reduced to a state of political ignorance inconsistent with self-government. This situation has made it possible, he thinks, for a well-organized hierarchy to acquire the real power of government and to retain it, in the face of popular disapproval, for selfish ends. Such leaders the author characterizes as "politocrats."

The first part of the volume deals with the rise of the politocrats; the second discusses various expedients for restoring the American ideal of democracy; while the third considers constructive proposals like the commission form of government for smaller cities, and the application of the principles underlying this form to larger cities and the state, and to the selection of judges.

Chicago Tribune. Albert M. Kales, Professor of Law in Northwestern University, has written a book which ought to be read wherever citizens are perplexed by the intricacies and distressed by the failures of government.

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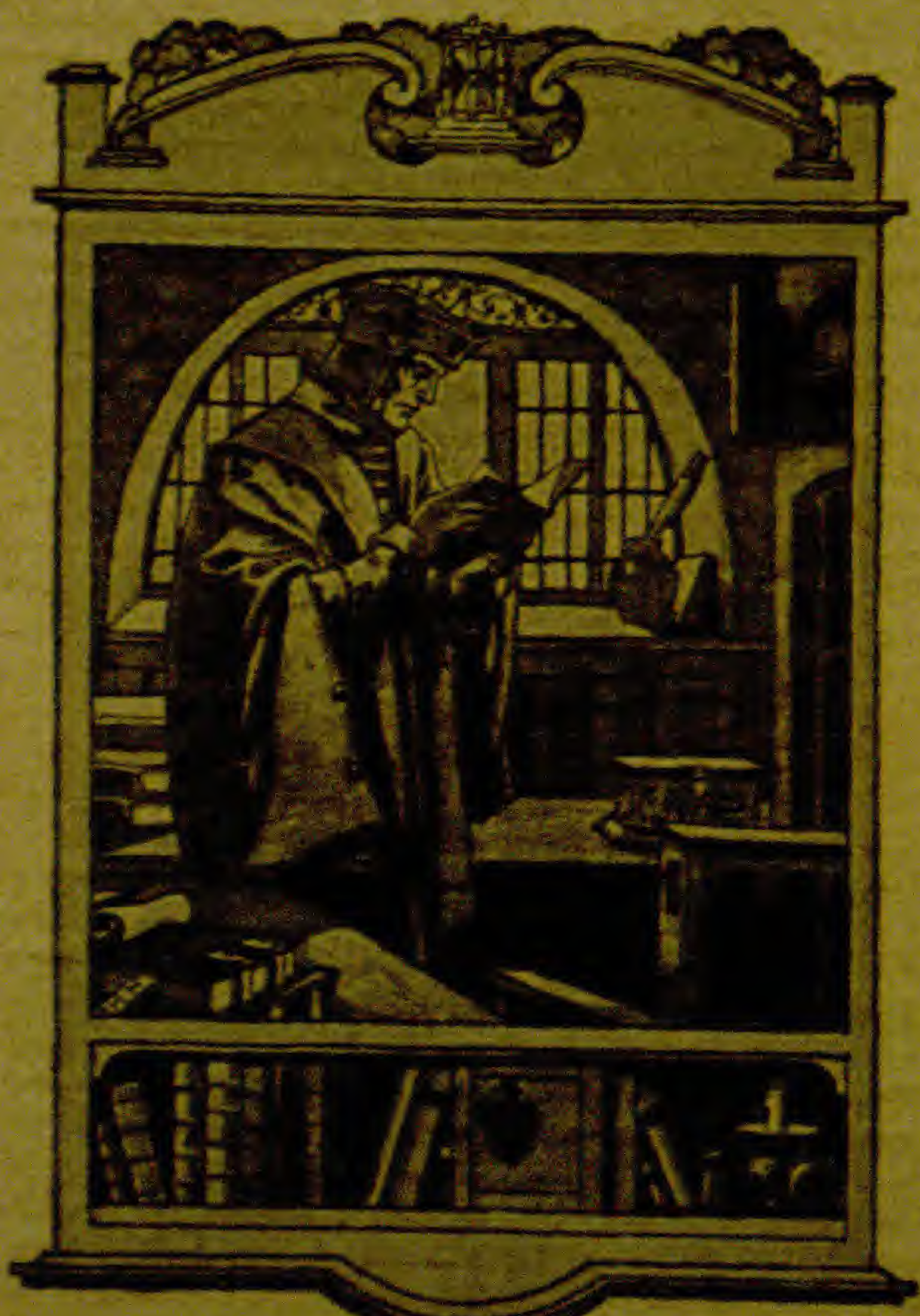


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Editor: JOHN M. COULTER

SEPTEMBER 1914

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THE

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SEPTEMBER 1914

EVAPORATION AND SOIL MOISTURE IN RELATION TO THE SUCCESSION OF PLANT ASSOCIATIONS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 191

GEORGE DAMON FULLER

(WITH TWENTY-SEVEN FIGURES)

I. Evaporation

The water conditions of plants have long been recognized by ecologists to be matters of the highest importance, but unfortunately it has seldom been possible to describe these conditions in other than the most general qualitative terms. The only factor affording quantitative data has been precipitation, and this is only indirectly related to plant production on account of the many irregular variations that exist between the amount of rainfall and the quantity of water available for plant growth. In a general way, and especially in dealing with large areas, a fairly close relationship may be established, but within the different habitats of a single region no such connection can be recognized.

In a study of water conditions, two phases of the subject are of importance. They are the direct source and amount of the supply and the region and cause of the loss. The latter is a climatic, the former largely an edaphic, problem, for it is evident that plants derive their moisture from the soil and lose it into the air, and for the quantitative solution of these problems it is necessary to measure the power of the air to extract water from the plant; in other words, the evaporating power of the air, and the amount of moisture in the soil available for the use of plants. Such measurements have been carried on in certain parts in the Chicago region in an effort to establish a relation between the moisture conditions and the succession of plant associations.

The researches of LIVINGSTON (1) and others have shown that the evaporating power of the air is a rather satisfactory summation of all the atmospheric factors that determine and limit the growth of plants, since it indicates the power of the atmosphere to extract water from their aerial parts, and has been shown in general to vary almost directly with their rate of transpiration. He has also devised the porous cup atmometer and shown that it is able to measure this power with a very considerable degree of accuracy during the growing season, or rather during that portion of the year free from frost, which in the Chicago region is practically the same as the growing season. Hence, during the three seasons of 1910–1912 stations with these atmometers were established and maintained in six distinct plant associations in the Chicago region. Since nowhere in this region is a succession of associations more clearly marked or more easily determined than upon the sand dunes immediately south of Lake Michigan, it seemed that a large number of the determinations should be made within this area. This vegetation has been described by COWLES (2), who has shown that the forest succession consists principally of associations dominated by cottonwood, pine, black oak, white and red oak, and beech and maple, in the order named. These represent a continuous series extending from pioneer trees to the mesophytic climax forest of the region. The physiographic factors, the detailed composition of the associations, the variety of the transitional forms, and the frequency of retrogression have been so well explained by COWLES that further detailed discussion at present seems unnecessary. While all the associations mentioned occur upon the sand dunes in the order indicated, it was found to be impossible to obtain easy access to the two final stages of the succession upon sand, and hence the oak-hickory and beech-maple forests were upon clay soil. Objections may be urged against such a selection, and many are recognized by the writer, but it is maintained that the comparisons that have been made in this investigation are quite legitimate ones, and, further, it is hoped that future studies may supply the lacking data for these associations upon a sandy soil. In addition to this successional series of associations, through the cooperation of some of the writer's students, data were obtained from the edaphic prairie characteristic of the Chicago region.

The period of investigation was during 1910, from May 6 to October 31 (178 days); during 1911, from May 1 to October 28 (180 days); and during 1912, from May 3 to October 22 (172 days), the records for the oak-hickory forest and the edaphic prairie being for the seasons of 1911 and 1912 only. Weekly visits were made to all stations throughout this period, except to those of the beech-maple forest, which were visited once in two weeks. A preliminary report of much of the data obtained during the first season has already appeared.[1]

INSTRUMENTS AND METHODS

The instruments employed were mostly the porous cup atmometer devised by LIVINGSTON, although during the first season a few of the type described by TRANSEAU (3) were also used. The atmometers were mounted in wide-mouthed bottles, having a capacity of 500 cc., closed with tightly fitting cork stoppers that were perforated for the atmometer tubes and for bent capillary glass tubes which served to equalize the atmospheric pressure within the bottles with that of the exterior air, without causing any loss by evaporation or permitting rainwater to enter the reservoir. The bottles were sunk in the soil about two-thirds of their height, so that the evaporating surface of the instruments was 25–20 cm. above the surface of the soil. Except where otherwise specified, the readings were made weekly by filling the bottles from a graduated burette to a file scratch on the neck. The small area of the water surface at this point made the probable error in readings less than 0.5 cc., and this could have had no appreciable effect upon the results. The instruments were all standardized to the same unit before being used, restandardized at intervals of 6–8 weeks during the season, a revolving table being used for the purpose similar to

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[1] BOT. GAZ. 52:193–208. 1911.

that described by NICHOLS (4), and a final correction made on their being collected in the autumn. By the coefficients thus obtained, all readings were reduced to the standard adopted by LIVINGSTON (5), the directions he gives being so closely followed that it is unnecessary to detail further the methods used in operating the instruments. Three or more stations were always maintained in each association, the mean of the various readings being taken as giving the true measure of the evaporating power of the air for that association.

In most instances no correction has been made for errors caused by rainfall, although during showers some water undoubtedly passes into the porous cup and into the reservoir, because it was thought that the amount of variation thus produced would be the same for all stations within so limited an area, and hence the comparative relation of results would remain unchanged. This assumption has been largely verified by BROWN (6), using an atmometer with a rain-correcting valve, and also by the experience of the writer by maintaining control instruments with the valves. The record for the prairie association for 1911 was wholly, and that for the oak-hickory forest for 1912 was partially, made with rain-correcting atmometers.

In order to facilitate comparisons between the various stations, and to exhibit the progress of the evaporation rate during the entire season, the average water-loss per day between the weekly readings has been calculated, and the results expressed in graphs, with ordinates representing the number of cubic centimeters lost per day by a standard atmometer, the abscissas being the intervals between the weekly readings. The readings included within each calendar month are indicated at the top of the diagram. For convenience of reference, the stations are numbered consecutively, beginning with those of the association of lowest rank, that is with those of the cottonwood dune.

PLANT ASSOCIATIONS AND STATIONS

The stations established in the plant associations upon the sand dunes were all upon an area of dunes lying between the little village of Miller, Indiana, and the southern shore of Lake Michigan. The shore at this point is gradually encroaching upon the lake because of the material being deposited off shore. This being swept inward by the waves and wind forms increasing areas of dunes, at first quite bare, but with forests soon advancing upon them. Grasses and shrubs constitute the first vegetation, but in the moist depressions the seeds of the cottonwood (*Populus deltoides*) germinate, and some of the seedlings are able to maintain themselves. A more detailed account of their establishment has been given elsewhere by the writer (**7**), and it is sufficient here to note that they surmount the moving dunes and at a distance of 100–200 meters from the shore establish the pioneer tree association that may be designated the cottonwood dune association, or more briefly the "cottonwood dune." This persists upon more or less actively moving sand, forming dunes varying in size up to 20 or even 30 meters or more in height, until from various causes, among which the vegetation is the most important, movement is checked and the dunes become fixed. It is an association of a single tree species and a paucity of shrubs and herbs, all having strongly xerophytic structures. Among the prominent species are *Salix glaucophylla*, *S. syrticola*, *Prunus pumila*, *Cornus stolonifera*, *Calamovilfa longifolia*, *Ammophila arenaria*, and a very few annual and perennial herbaceous plants.

In this association, upon dunes that had become almost completely fixed (fig. 1), four stations were established, each with at least one atmometer. These stations were about 200 meters from the lake shore, some 100 meters apart, and about 12 meters above the level of the waters of Lake Michigan. Three of these stations were upon comparatively level areas, surrounded by the usual open stand of cottonwoods and willows (fig. 2). At all stations the atmometers received a small amount of shade for a few hours of the day, and on account of the open nature of the association were little sheltered from the wind, the cups receiving a rather sharp sand blast during high winds. The differences of exposure to winds probably caused some of the variations in the records of the different stations, but affected very slightly the average rate for the season. Station 4 was upon the leeward slope of a very slowly advancing dune, and was further sheltered by a good stand of *Cornus stolonifera*. It was about 3 meters below the crest of the dune upon an eastern exposure. This station was maintained only during the season of 1910. A detailed report of the atmometer readings for the four stations during the season of 1910 is shown in fig. 3, where in addition to the evaporation records the weekly rainfall in centimeters at Chicago during the summer months is plotted. As it has been possible to establish no direct relationship between rate evaporation and the occurrence and amount of precipitation, rainfall data are omitted from the remaining diagrams.

FIG. 1.—Sand dunes with *Populus deltoides* or the cottonwood dune association still moving slowly over an area with *Pinus Banksiana*, *P. Strobus*, etc.; Miller, Ind.

An examination of these graphs will at once show that the rate of evaporation was high and subject to sudden and considerable changes. There was no great divergence in the rate at stations 1, 2, and 3, but the rate at station 4 was decidedly lower, showing the modifying influence of the shrub cover in creating less extreme conditions, which permit the entrance and establishment of species of less xerophytic nature, which eventually form the succeeding association. Thus not only does the nature of the vegetation control to a great extent the evaporation beneath it, as pointed out by GLEASON (8) and others, but the evaporation thus controlled and changed is one of the principal factors in causing the development of a different vegetation, or, in other words, the decreased rate of evaporation caused by the heavier vegetation is the direct cause of succession between different associations. It seems surprising that GLEASON has reached an opposite conclusion from somewhat similar data.

An average of the records of stations 1, 2, and 3 is plotted for comparison with similar records from the other associations (fig. 4).

FIG. 2.—Dune with *Populus deltoides* and *Salix syrticola;* station 3; Miller, Ind.

Here it will be seen that the maximum average evaporation for any week of 1910 was just above 32 cc. per day, and the minimum only once fell below 12 cc. per day. The average for the entire season of 178 days was 21.1 cc. per day. In 1911 several days in May, with a temperature above 90° F., caused a remarkable maximum of 47 cc. per day in that month (fig. 5), and serves to emphasize the importance of records extending through several seasons. The midsummer maximum was 42 cc. per day, the minimum 11.5 cc., and the average 24.6 cc. per day. The season of 1912, on the

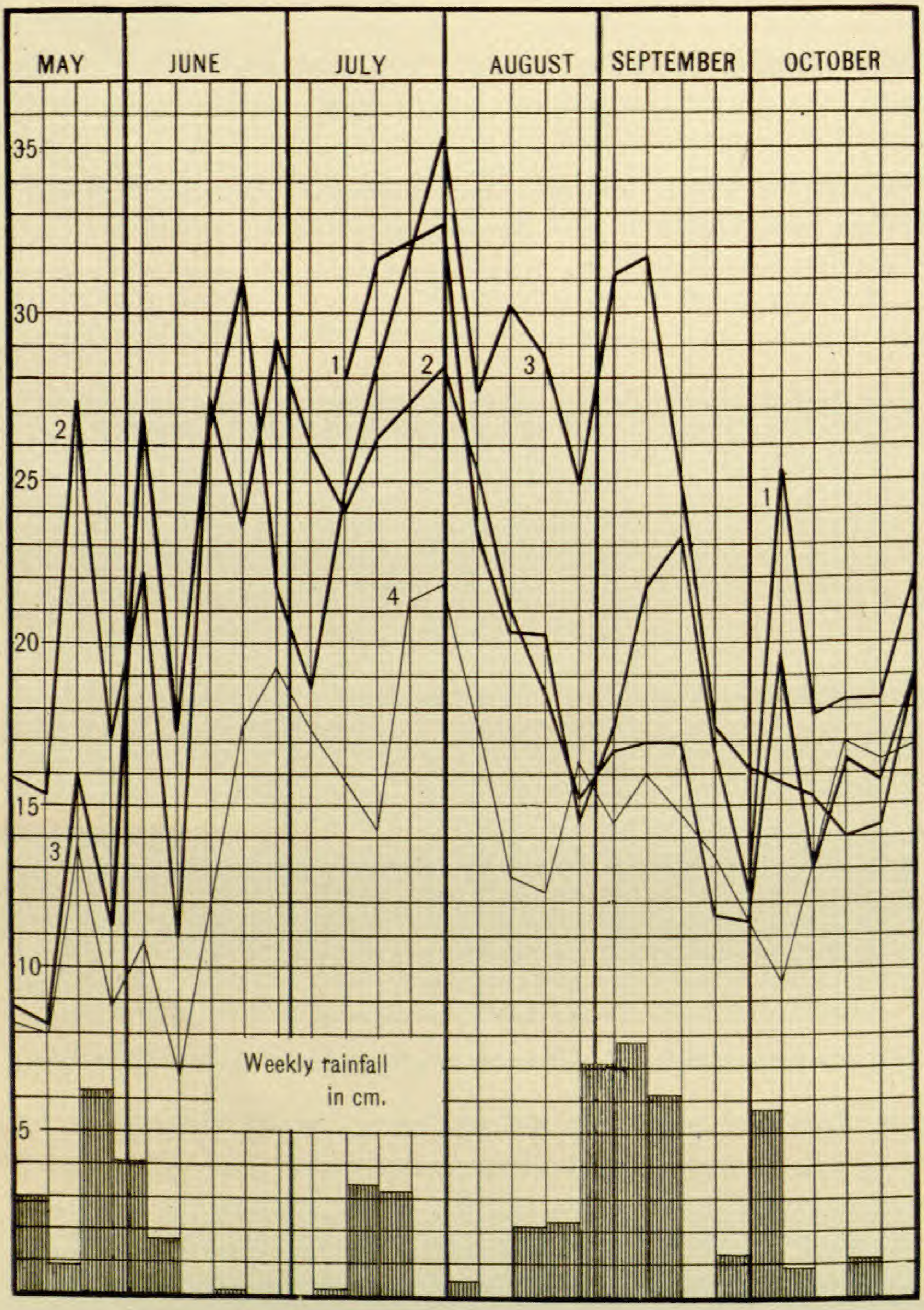

FIG. 3.—Daily evaporation rates in the cottonwood dune association at stations 1, 2, 3, and 4, during the season 1910.

contrary, was one of less extremes (fig. 6), giving a maximum evaporation rate of only 31 cc. per day and a minimum of 12.2 cc., while

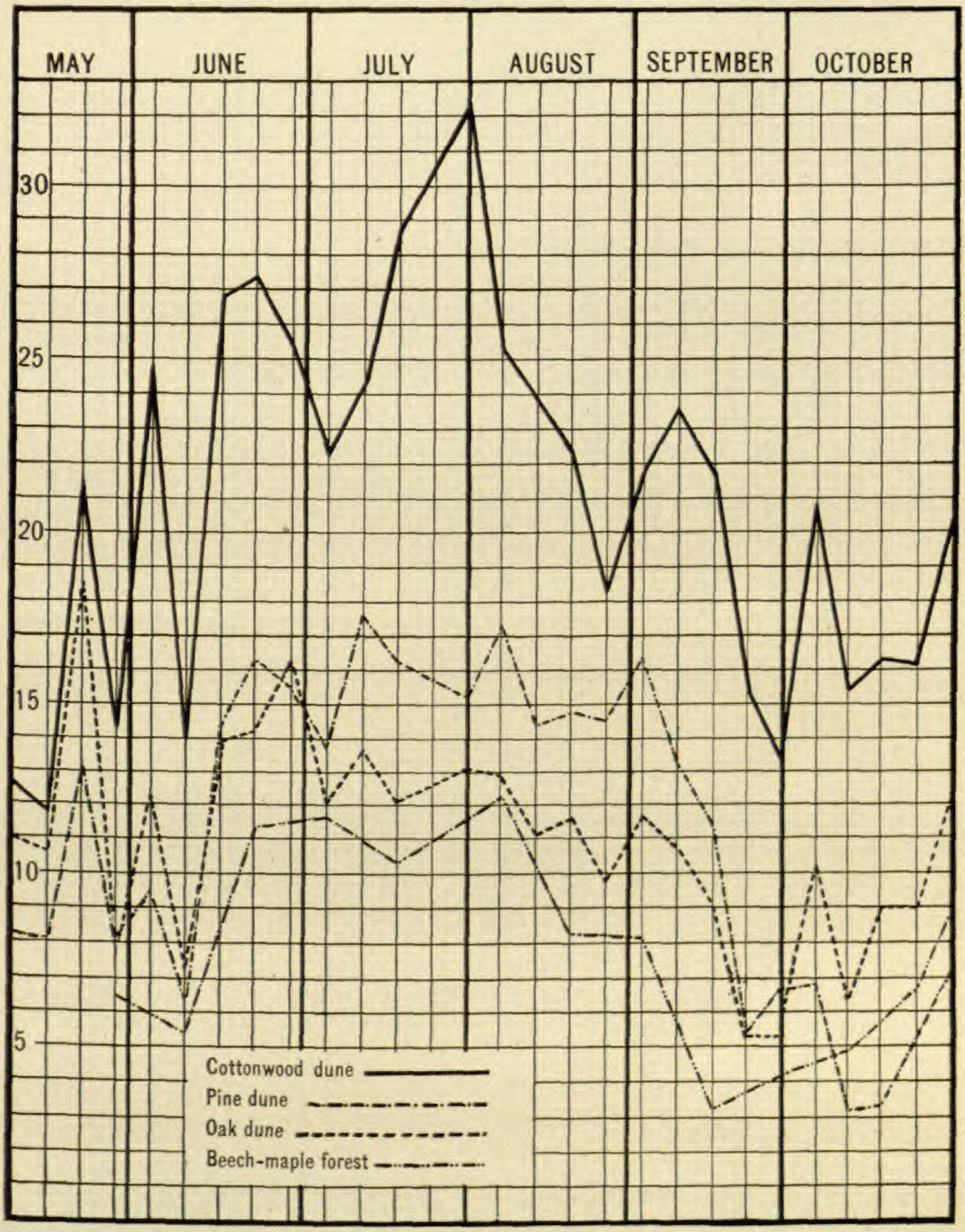

Fig. 4.—Mean daily evaporation rates in the different associations during the season 1910.

the average was almost identical with that of the first year, amounting to 21.3 cc. per day. Here the general results of the three

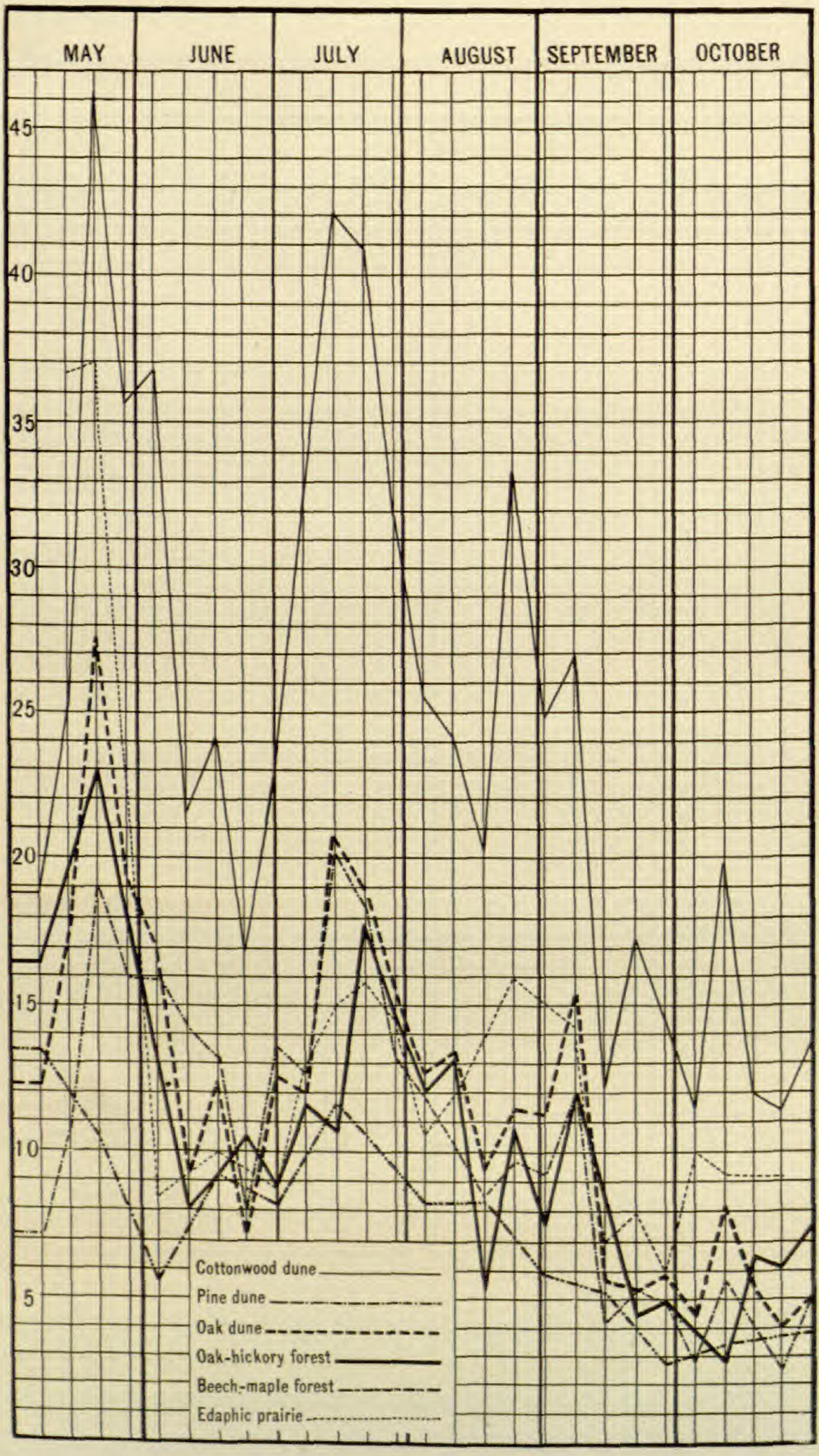

FIG. 5.—Mean daily evaporation rates in the different associations during the season 1911.

seasons investigated are seen to be consistent, and to indicate that not only is the cottonwood dune an association with a very high

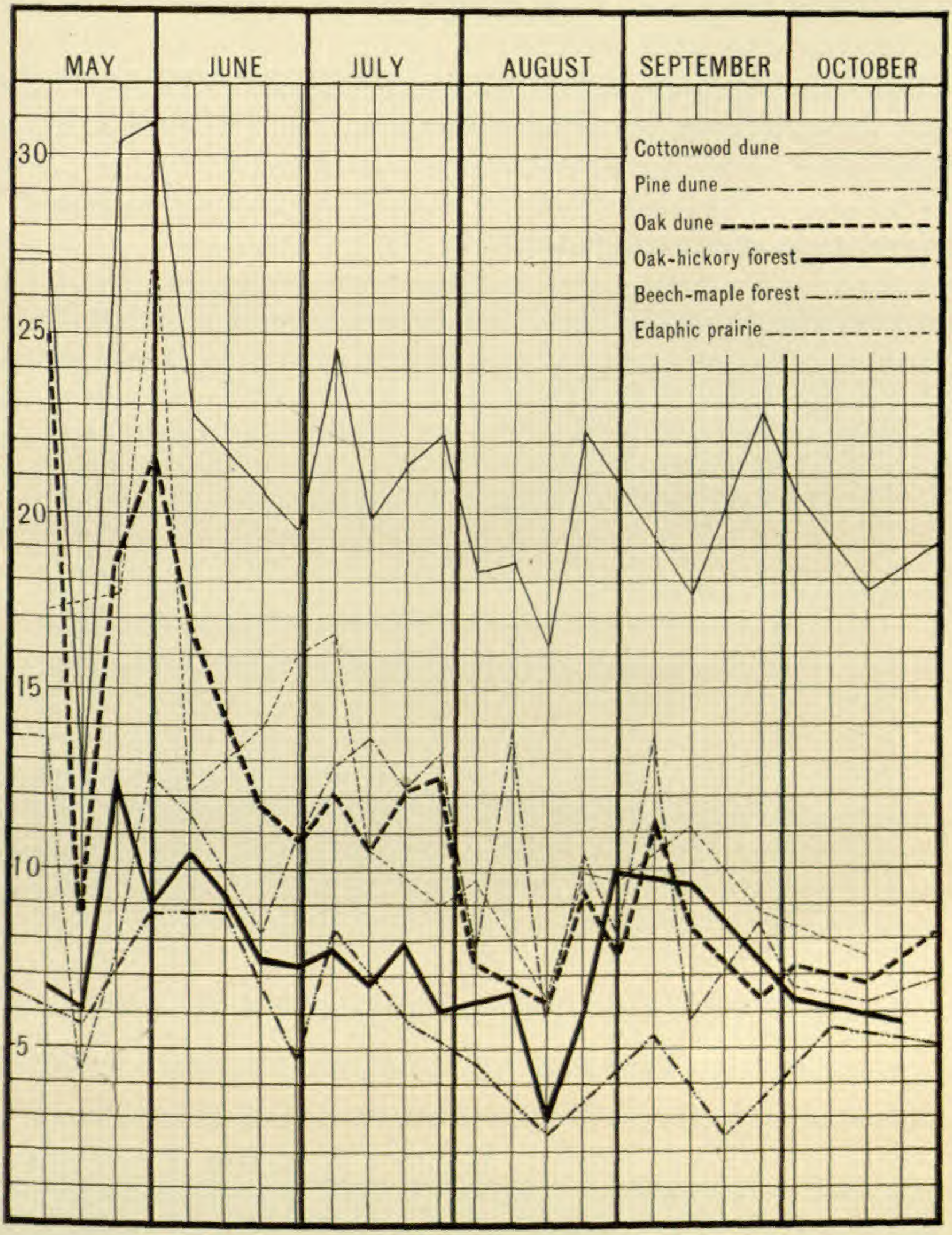

FIG. 6.—Mean daily evaporation rates in the different associations during the season 1912.

rate of evaporation, but also that it is subject to excessive variation. This is very noticeable during May and June, and prevails to a less extent during the remainder of the season, the fluctuations being markedly greater than in the other associations.

With the fixation of dunes and the increase of grasses and other herbaceous vegetation, seedlings of conifers develop and give rise to an evergreen forest association succeeding the cottonwood, and here designated the pine dune association (fig. 7). This association varies somewhat in composition in different localities, but in the area under consideration is dominated by *Pinus Banksiana*, associated with *Juniperus virginiana*, *J. communis*, and in older portions with *Pinus Strobus*. In the undergrowth *Arctostaphylos Uva-ursi* is conspicuous, associated with *Rhus canadensis*, *R. toxicodendron*, *Prunus virginiana*, *Celastrus scandens*, seedlings of *Quercus velutina*, *Smilacina stellata*, *Asclepias tuberosa*, *Monarda punctata*, and other woody and herbaceous plants. It is evident that this association is unique in the dominance of evergreens, while its limited extent shows that it is comparatively short-lived, a

FIG. 7.—Dune with *Pinus Banksiana*, *P. Strobus*, *Juniperus communis*, etc.; station 6; Miller, Ind.

fact that is emphasized by the presence, very early in its history, of seedlings of *Quercus velutina*, the dominant tree of the succeeding association.

In this association, stations 5, 6, and 7 were placed at spots of medium density of growth, about 100 meters south and east of the cottonwood dune series. The averages of the readings from the three stations are plotted for comparison with similar data from the other associations (figs. 4, 5, 6). Compared with that of the preceding association, the rate of evaporation is seen to be much lower and subject to less violent fluctuations. The maxima and minima are nearly synchronous with the preceding and succeeding associations, the most remarkable feature being the very low comparative rate during the weeks of May and October, when the deciduous associations are largely without foliage. The maximum for 1910 (fig. 4) was 17.5 cc. per day, the minimum fell below 4 cc., and the average rate for the season was 11.3 cc. daily.

The next season the maximum rate was 20.2 cc. per day (fig. 5), the minimum 2.5 cc. per day, and the average 10.3 cc.; while in 1912 (fig. 6) the maximum was only 13.7 cc. per day, the minimum rose to 4 cc. per day, but the average was reduced to 9.7 cc. per day, again demonstrating the fact that 1912 was a season of moderate climatic conditions.

Proceeding inland from the lake shore, the pines gradually decrease in number, and the black oak (*Quercus velutina*) becomes more plentiful, until at a distance of about 500 meters south of the last group of stations it forms an almost pure stand, with only occasional trees of white oak (*Quercus alba*). The shrubby under-growth consists principally of *Prunus virginiana*, *Rosa blanda*, *Viburnum acerifolium*, *Vaccinium pennsylvanicum*, *Ceanothus americanus*, and seedlings of *Quercus velutina* and *Q. alba*. Among the herbaceous members of the association are *Smilacina stellata*, *Lupinus perennis*, *Tephrosia virginiana*, *Lithospermum canescens*, *Asclepias tuberosa*, *Helianthemum canadense*, *Polygonella articulata*, and *Aster linariifolius*. In this oak dune association four stations were placed: nos. 8, 9, and 10 in the stands of average density (fig. 8), and no. 11 in one of the very characteristic openings sparsely covered by xerophytic grasses, together with such plants as *Monarda punctata*, *Asclepias tuberosa*, and *Opuntia Rafinesquii.* This last station was maintained only during the seasons of 1910–1911, and, owing to a series of accidents, its record was by no means continuous, especially during the latter season. During 1910 (fig. 9) its rate of evaporation was decidedly in excess of that of the other stations, especially in June and July. The records of the other stations are quite comparable and their average appears in fig. 4.

FIG. 8.—Dune covered with open forest of *Quercus velutina;* station 10; Miller, Ind.

In 1910 (fig. 4) a maximum of nearly 19 cc. per day occurred in May, before the trees were in full foliage, and similar high rates at the same season of the year were seen in 1911 (fig. 5), when it rose to the surprising height of 27.5 cc. per day; while in 1912 (fig. 6) it was 21.5 cc. per day. This could hardly be a critical period for vegetation, on account of the abundant supply of water in the soil (see second part of this paper), although it might be decisive for many young seedlings, and it may therefore be disregarded in the general discussion.

Midsummer afforded maxima of 16 cc. in 1910, 18.9 cc. in 1911, and 12.5 cc. in 1912, the minima for these years being respectively

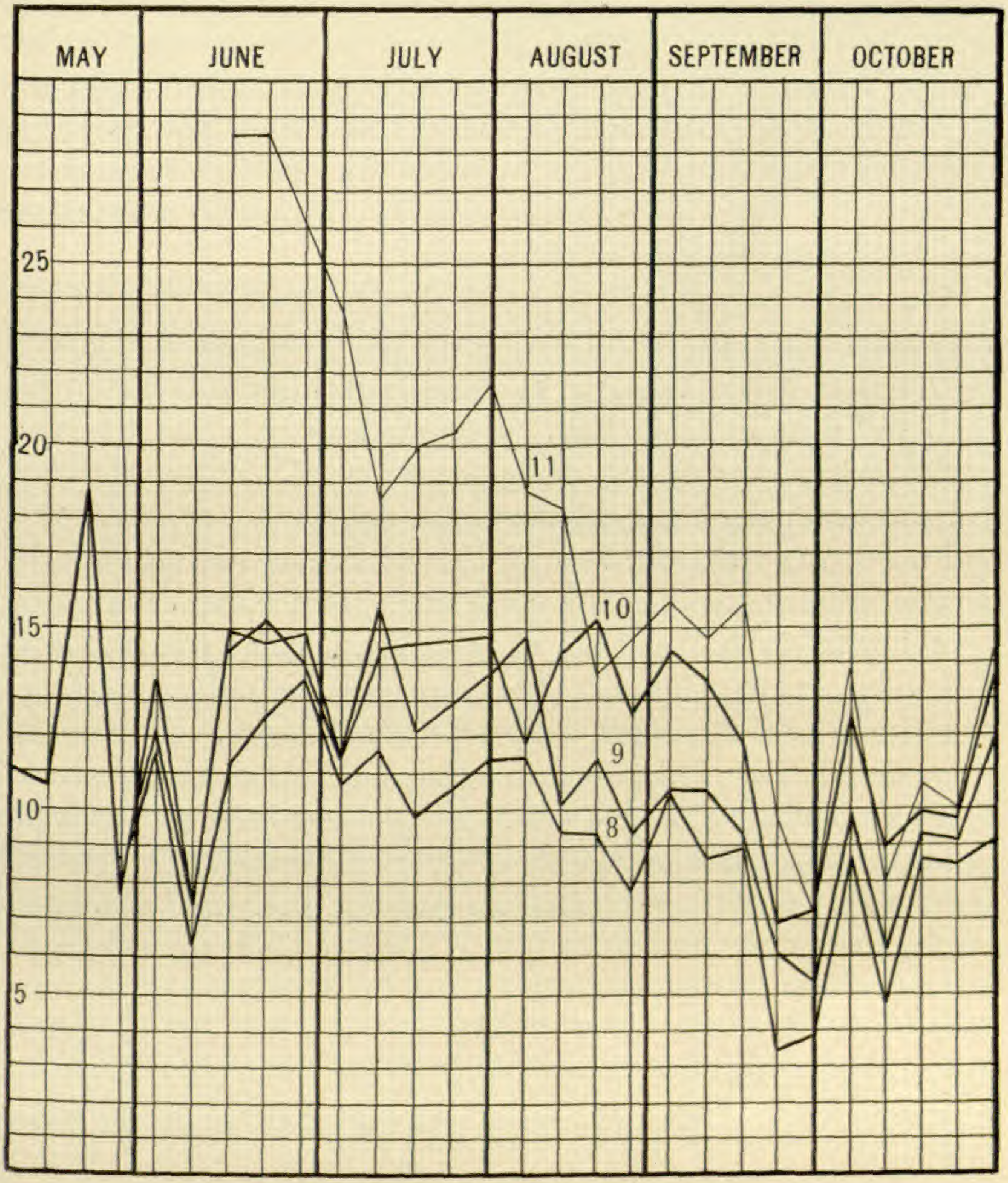

FIG. 9.—Daily evaporation rates in the oak dune association; stations 8, 9, 10, and 11 during the season 1910.

5 cc., 4 cc., and 6.3 cc. per day, while the averages for the seasons were 10.3 cc., 11.8 cc., 10.9 cc. daily (figs. 4, 5, 6).

The forest association dominated by *Quercus velutina* is rather persistent upon the dunes, but is gradually changed by the invasion of other more mesophytic trees, notably the red and white oaks (*Q. rubra* and *Q. alba*) and one or two species of *Carya*, eventually giving rise to a fairly mesophytic association, commonly designated the oak-hickory forest. Although rather abundant in the Chicago region, it does not seem desirable to enter here upon any discussion of its occurrence or composition, especially as it has been excellently described by COWLES (**9**). Similar reasons are sufficient for very brief descriptions of the other associations included within the scope of this paper.

The most accessible, comparatively undisturbed area of this association near the city of Chicago is found about 15 miles southwest of Miller, Indiana, at Palos Park, Illinois, where it has developed upon morainic clay. Here stations 12, 13, and 14 were established in 1911 by one of my students, Mr. WADE MCNUTT, in the typical upland mesophytic forest, and station 15 in a depression which was really the floor of a broad shallow ravine and comparable in most respects to a floodplain. In the depression there were, in addition to the trees of the upland, such typically floodplain species as the white ash (*Fraxinus americana*), the elm (*Ulmus americana*), and the black walnut (*Juglans nigra*). A more detailed description of the forest and an analysis of the results of 1911 have already appeared (**10**). In this year there was an average midsummer maximum rate of 17.5 cc. per day (fig. 5) from stations 12, 13, and 14; a minimum rate of 2.7 cc.; and an average for the season of 180 days of 9.8 cc. per day. In 1912 the midsummer maximum was 10 cc. daily (fig. 6), the minimum the same as the preceding year, while the average was reduced to 7.8 cc. daily. Comparing this rate with that exhibited by the mesophytic floodplain forest of the depression, we find that the latter had a maximum of 16.2 cc. daily in 1911, a minimum of 1.7 cc., and an average of 8.3 cc. daily (**10**). In 1912 the maximum was reduced to 8 cc. daily, the minimum to 1.5 cc., and the average rate was only 4.2 cc. daily (fig. 10).

The climax of mesophytic conditions in the northern United States appears to be a forest in which the beech (*Fagus grandifolia*) and the maple (*Acer saccharum*) are conspicuous members. The succession upon the sand dunes is found to attain this climax, a good instance being seen at Sawyer, Michigan, but unfortunately for the purposes of our investigation no such area was available nearer Chicago, and hence recourse was had to a good tract of beech-maple forest at Otis, Indiana, about 20 miles east of the stations at Miller. In this forest, in addition to the two dominant trees, there were a few individuals of *Tilia americana*, *Prunus serotina*, and *Liriodendron Tulipifera*, while notable in the undergrowth were seedlings of the principal trees, together with *Asimina triloba*, *Sambucus racemosa*, *Evonymus americanus*, and such herbaceous species as *Dicentra canadensis*, *Trillium grandiflorum*, *Adiantum pedatum*, *Polystichum acrostichoides*, *Viola rostrata*, and *Erigenia bulbosa*.

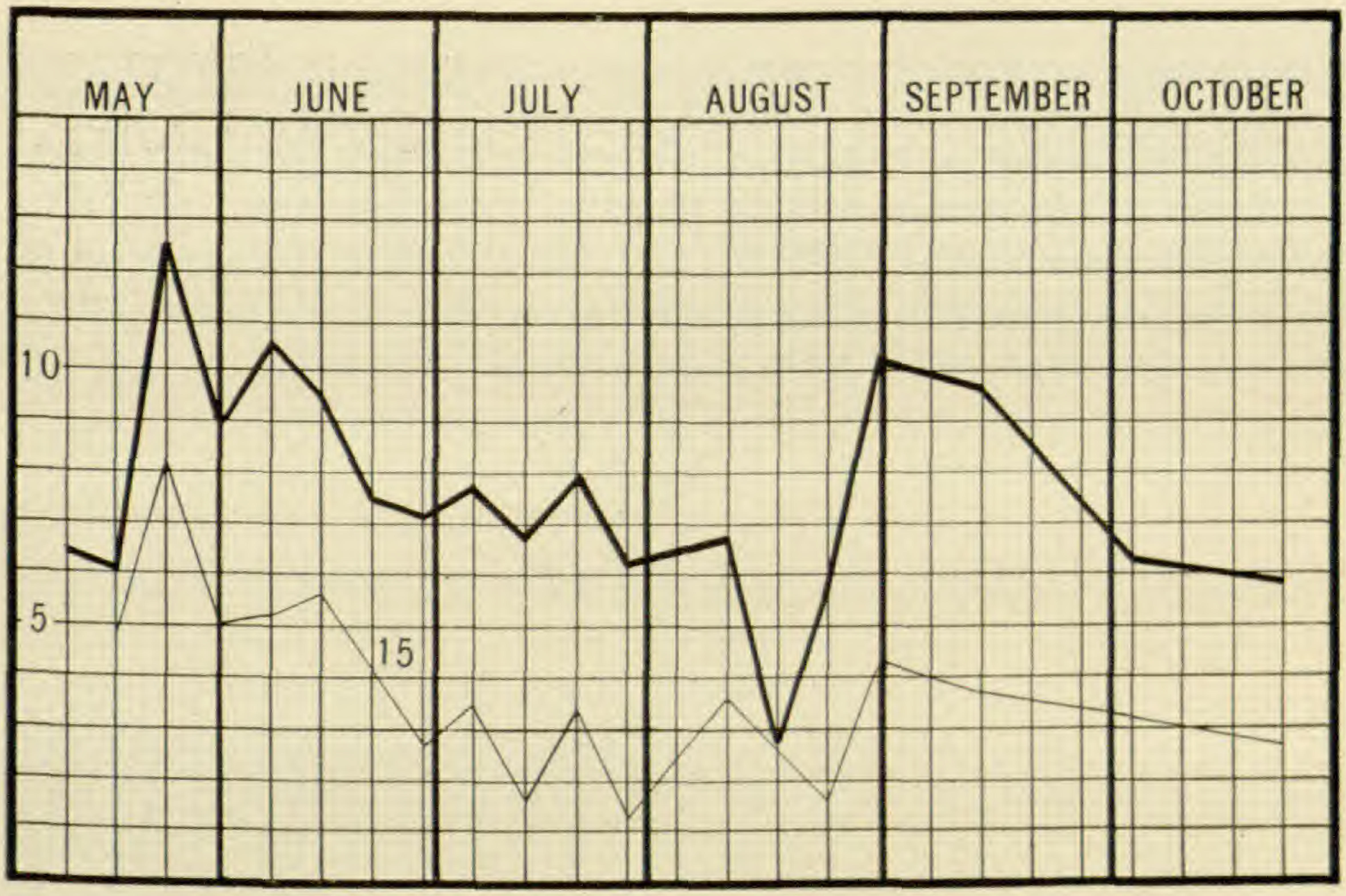

FIG. 10.—Daily evaporation rates in the oak-hickory forest for the season 1912; heavy line representing the mean rate for stations 12, 13, and 14, and light line that for station 15.

In this beech-maple forest, stations 16 (fig. 11), 17, and 18 were placed about 100 meters apart, upon the floor of the forest, station 19 in a rather narrow ravine (fig. 12) about 4 meters below the level of the others, while at station 20 the atmometer was attached to the branch of a tree 2 meters above the surface of the soil. The last station yielded a very broken record during 1910; its record during 1911 has already been published (11), and at the end of that year it was discontinued, as other studies upon the evaporation rates in different strata were planned and in progress.

A comparison of the records of the five stations during 1911 will be found interesting and instructive (fig. 13). Stations 16, 17, and 18, upon the floor of the forest, show graphs of considerable regularity, differing but little from each other. Their combined average for the season was 7.4 cc. daily, and if this be compared with the average rate from station 20, of 13.5 cc. daily, and from station 19, of 5.9 cc. daily, the proportional evaporating power of the air in the three strata will be found to be very nearly 1.84:100:0.80.

FIG. 11.—Beech-maple forest; station 16; Otis, Ind.

The average rates from the three stations upon the floor of the forest for the three seasons (figs. 4, 5, 6) gave maxima of 12.2 cc., 11.6 cc., and 8.1 cc. daily; minima of 3 cc., 2.8 cc., and 3.5 cc. daily; and seasonal averages of 8.1 cc., 7.4 cc., and 5.6 cc. per day respectively for the years 1910–1912.

It is interesting here to note the close correspondence between the records for this beech-maple forest and those obtained by

TRANSEAU (**12**) in a mesophytic forest containing a small percentage of beech, and situated on Long Island, New York, where for the period of observation from June 5 to July 2, 1907, the evaporation rate averaged 8.5 cm. daily, compared with 8.4 cm. daily during the month of June 1910, in the Otis, Indiana, forest, and 8 cc daily as the mean average rate for the midsummer weeks of the years 1910–1912 (table II). While it is not safe to draw any very definite conclusions from records covering but a single month, it may be assumed that the two associations differ very little in the amount of mesophytism developed. It is to be regretted that similar comparisons cannot be made between the writer's results and those of GLEASON (**8**), but unfortunately the latter were not made with standard atmometers.

FIG. 12.—Ravine in beech-maple forest; station 19 about two-thirds down the right hand slope; Otis, Ind.

The edaphic prairie is a characteristic plant association of the Chicago region, and while it does not lie in the successional series with which this investigation is most particularly concerned, it was thought that it would be profitable to compare it with the various forest associations. It seemed all the more urgent that it should be investigated because, with the growth of the city and the advance of agriculture, it is rapidly disappearing. Consequently, in 1911 the attention of Mr. E. M. HARVEY was directed to this portion of the problem and the range of evaporation and of soil moisture as determined, and the results have been published (13), but

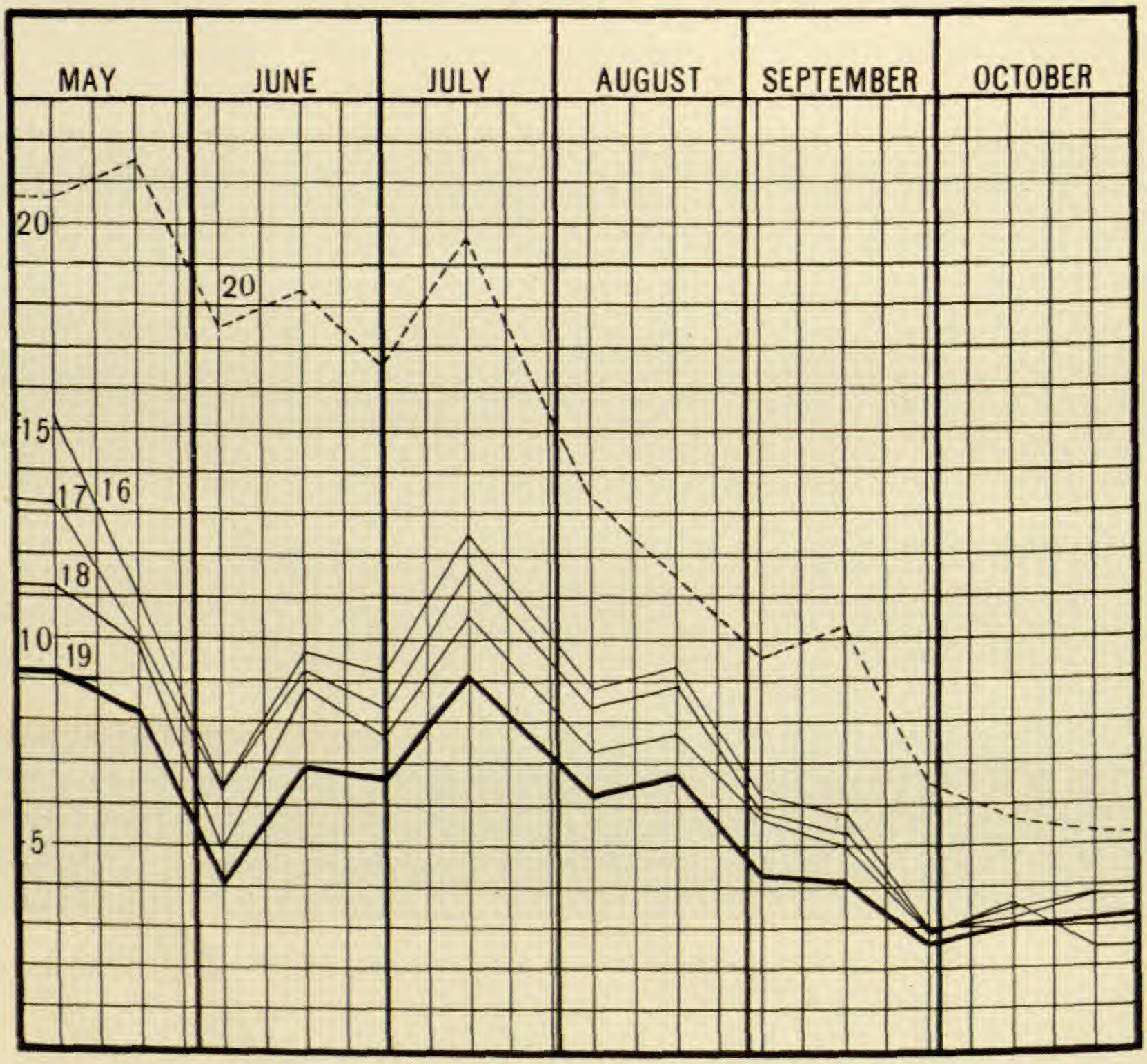

FIG. 13.—Daily evaporation rates in the beech-maple forest at stations 16, 17, 18, 19, and 20 during the season 1911.

through the courtesy of HARVEY, the averages for the year are included in fig. 5. The floristic composition of the prairie vegetation has been discussed by COWLES (9) and by HARVEY, and needs no further reference at present. This association seems to be the most usual stage in succession following the sedges in the filling up of shallow ponds and lakes formerly abundant in the Chicago region.

For the season of 1912 the prairie stations were under the efficient charge of Miss L. NEWLON, to whom the writer is indebted for the results here presented. During both seasons the range of the evaporation rate was great (figs. 5, 6), the vernal maxima being 37 cc. and 27 cc. daily, the midsummer maxima 16 cc. and 16.5 cc. daily; the minima 5.9 cc. and 6.1 cc.; while the average for each of the two seasons was 12.5 cc. per day.

GENERAL CONCLUSIONS

Several methods may be employed for comparing the data from the various associations. Perhaps the best is by means of the charts upon which the daily average rate by weeks for all the associations are plotted together (figs. 4, 5, 6). Here the characteristics of the different rates are represented graphically, and may be seen at a glance. Throughout the entire series the maxima and minima are generally coincident in time and proportionate in amount. Minor irregularities appear that it would be useless to attempt to explain. The different years show characteristically different curves. Thus, 1910 comes nearest to the commonly accepted ideas, with a somewhat regular curve increasing rather regularly from the beginning of the growing season, reaching a marked maximum about midsummer, and falling rather sharply with the humid weather of late August and September. The following year there are excessively high rates of evaporation in May (fig. 5), which will be found to correspond to a period of unusual weather conditions. The month had the highest temperature record for May experienced since the establishment of the Chicago Weather Bureau in 1871. The average temperature was 10° above normal, and for six days it reached or exceeded 90° F. The percentage of sunshine (79 per cent) was also greater than observed during any previous May. Moderate temperature conditions at midsummer, and a relative humidity slightly above the average, together with the percentage of sunshine below the normal mean are reflected in the general course of the evaporation graphs. The year 1912 is marked by a very moderate summer, the wind record of the weather bureau showing comparatively light air movement, while throughout July, August, and September the temperature and sunshine records were considerably below the average. These weather conditions have resulted in very moderate and equable evaporation rates throughout all the associations and particularly in the more mesophytic (fig. 6). A further study of these diagrams in comparison with the data of the Chicago Weather Bureau would prove even more conclusively the assertion that the evaporating of the air represents a rather accurate summation of all the atmospheric factors that may be related to the water content of the aerial parts of plants. The differences in the records for the various years also prove the necessity of continued observation and extended records before definite conclusions are reached.

The records of 1911 and 1912 serve to give greater emphasis to some of the facts recorded and to the tentative conclusions arrived at during 1910 and published in the preliminary report[2] of these investigations. Thus, the evaporation rate of the cottonwood dune is farthest removed from the other associations, and by it there is exhibited not only a very great evaporating power, but also excessive and rapid variation, an increase or decrease of 50–100 per cent between the rates for consecutive weeks being not uncommon. This cannot but denote extremely rigorous conditions for the development of seedlings of ordinary herbaceous plants. The high midsummer maximum, apart from the question of soil moisture, would likewise prove an efficient factor in excluding all mesophytic plants.

Such graphs seem to depict rather well a habitat of atmospheric extremes, making large demands upon all available water, and naturally and necessarily resulting in a xerophytic plant association with a very limited undergrowth and an almost entire absence of herbaceous plants and seedlings. Perhaps nowhere could an association be found more entirely dependent upon vegetative reproduction for its maintenance, since almost without exception any increase in vegetation is the result of subterranean branches.

The records for this association, when considered in relation to the character of its vegetation and compared with those of the other associations, is believed to emphasize the fact that, although these data are for the lower stratum of the vegetation only, they are

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[2] Bot. Gaz. 52:193–208. 1911.

for the critical one, especially in forest associations. Within this stratum develop all the seedlings, and upon their death or survival depends the character of the succeeding vegetation. Therefore, if the vegetation of an association so affects the evaporation rate of this stratum that it permits the survival of seedlings of more mesophytic species, it is evident that a more mesophytic association will develop and succession will be accomplished.

Any individuality in the graphs from the pine dune is plainly due to the evergreen character of the association, and is seen in the low rates in May and October, which are always decidedly below those of the succeeding oak dune association, and are often even lower than those of the oak-hickory and beech-maple forests. That this association is very close to the succeeding one may be seen by referring to table I. Here it will be seen that the mean evaporation rates were during two of the three years slightly less than those of the succeeding association. The same is true for the average of the rates, but if the comparison be made for the 10 weeks of summer, from the last week of June to the first of September, as shown in table II, the comparative rates are reversed, and the pine dune association has a slightly higher average. This is believed to represent the actual condition during the weeks of greatest stress of moisture conditions.

TABLE I

MEAN WEEKLY EVAPORATION RATES IN CC. FROM A STANDARD ATMOMETER FOR THREE SEASONS UNDER INVESTIGATION

Association	1910	1911	1912	Average	Comparative rates
Cottonwood dune	21.1	24.6	21.3	22.3	319
Pine dune	11.3	10.3	9.7	10.4	149
Oak dune	10.3	11.8	10.9	11.0	157
Oak-hickory forest	....	9.8	7.8	8.8	126
Beech-maple forest	8.1	7.4	5.6	7.0	100
Edaphic prairie	....	12.5	12.5	12.5	179

The graphs of the oak-hickory and beech-maple forests seem to be without any special features other than that they depict the moderate conditions of truly mesophytic associations, while those of the edaphic prairie express the condition of an association abounding in extremes and fluctuations inferior only to those of the pioneer association dominated by the cottonwood. As might be expected, there is a similarity between the evaporation rate of the prairie and that of the open areas of the oak dune (fig 9).

TABLE II

MEAN WEEKLY EVAPORATION RATES IN CC. FROM A STANDARD ATMOMETER DURING THE 10 MIDSUMMER WEEKS OF THE THREE YEARS UNDER INVESTIGATION

Association	1910	1911	1912	Average	Comparative rates
Cottonwood dune	25.0	30.2	20.3	25.2	315
Pine dune	14.1	12.6	10.3	12.3	154
Oak dune	12.1	13.4	10.1	11.9	149
Oak-hickory forest	....	11.6	6.7	9.2	115
Beech-maple forest	10.2	8.5	5.3	8.0	100
Edaphic prairie	....	15.1	12.4	13.7	171

It is interesting to note that comparative evaporation rates for all the associations, with the exception noted in the case of the pine dune, remain substantially the same whether the comparison is based upon the averages for the entire seasons (table I) or for the weeks of misdummer (table II) only. The comparison is perhaps more striking when the data are represented graphically, either for the individual seasons (fig. 14) or when the data for the three years are combined (fig. 15), when, if it be true that water conditions are the most important factors affecting the establishment of different plant associations, there can be no reasonable doubt that the progressive increase of the moisture content of the habitats indicated by the progressive decrease in the evaporation rates causes a corresponding progressive increase in the mesophytism of the plant associations as a whole, a change which we are accustomed to term *succession*.

As recommended in the writer's preliminary report (*loc. cit.*), the beech-maple forest is taken as the unit of comparison, and the evaporation rates in the other associations are expressed in terms of this unit. Thus, the beech-maple forest being represented by 100, the comparative evaporation rates for the midsummer weeks (table II) in the associations which precede it in the succession are respectively 115, 149, 154, and 315, showing a striking and progressive increase in the humidity of this stratum of the vegetation as the succession advanced from the pioneer cottonwood to the climax beech-maple association.

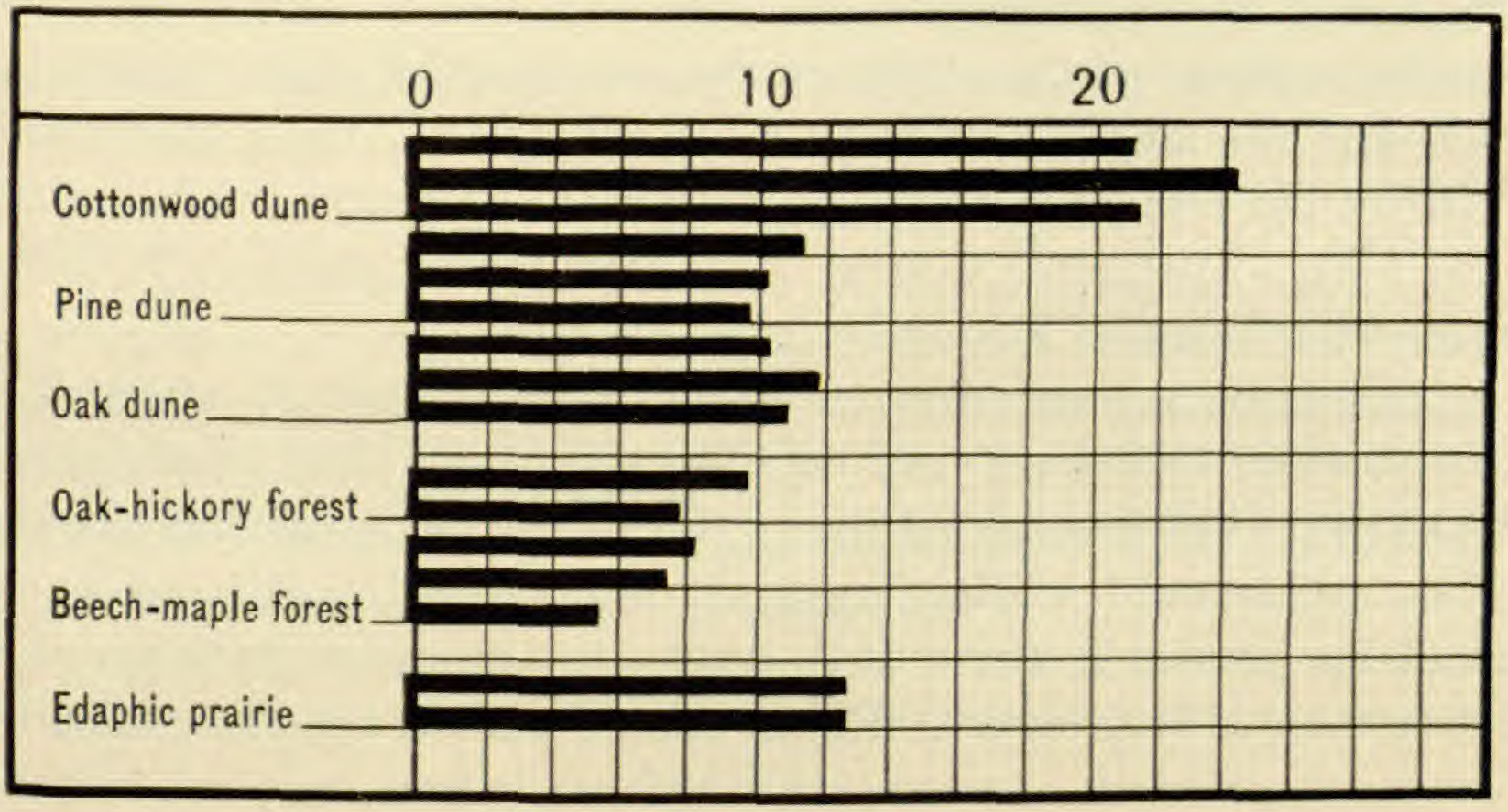

FIG. 14.—Diagram showing the comparative average daily evaporation rates in different associations for the seasons of 1910, 1911, and 1912.

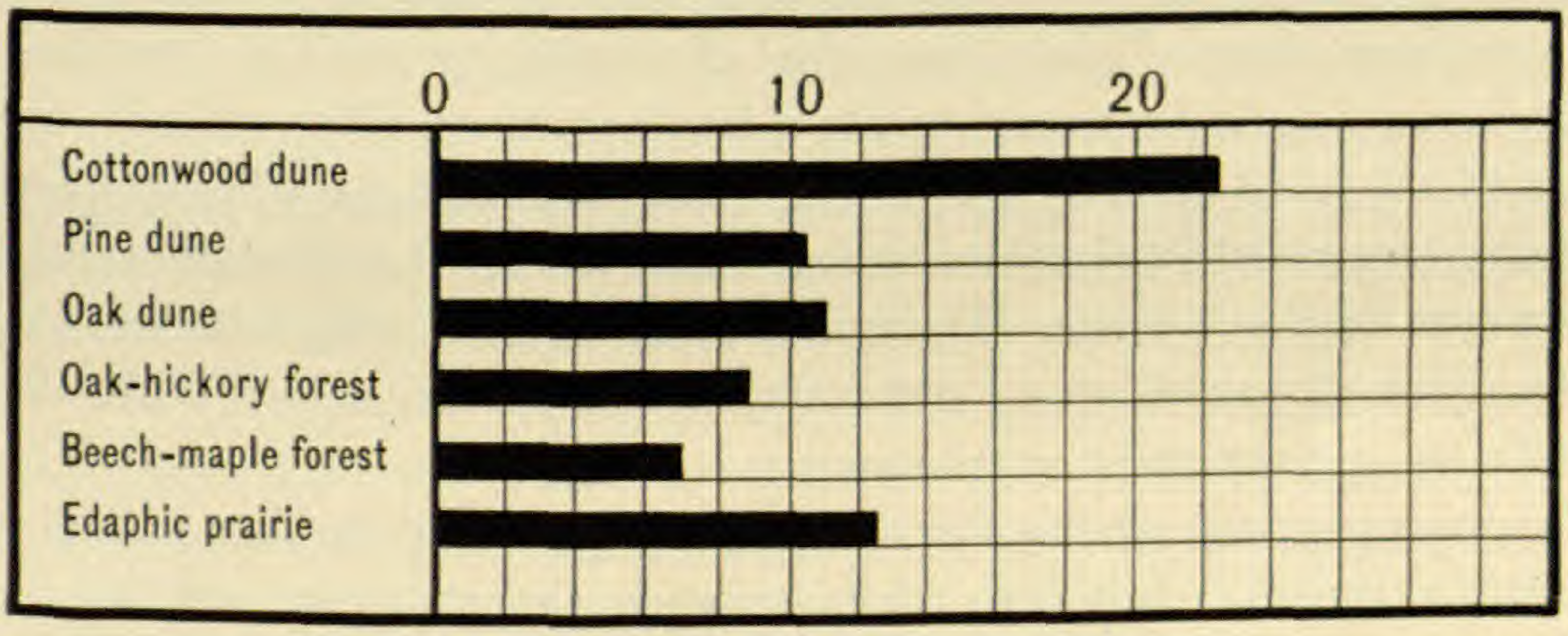

FIG. 15.—Diagram showing the comparative mean average daily evaporation rates in the different associations for the three seasons investigated.

II. Soil moisture

The direct source of the water supply of plants being the moisture in the soil, the amount of this moisture is evidently of the highest importance to vegetation. This has been recognized by many leading ecologists and phytogeographers, but very few data have been made available as to the effects of definite quantitative amounts upon vegetation, or of the amount and range of the soil moisture in different plant associations. This has been largely due to the difficulty in relating the amount of moisture actually present in the soil to the production of vegetation. It is clear that there can be no direct relation between the percentage of water present in soils and the amount available for plant growth, for a sandy soil with 15 per cent of moisture is at or near saturation, while a stiff clay with 15 per cent of water is so dry that all plants wilt in it, even with a humid atmosphere.

Efforts have been made to establish a standard by which the actual water content of soils could be related to plant production. CLEMENTS (14) determined the amount of water remaining in soils when pronounced wilting occurred, and regarding this as non-available termed it the *echard*, while the difference between the amount actually present in the soil and the echard was the available water, or *chresard*. LIVINGSTON (15) recognized that the water-holding capacity of soils varied and had a fairly constant relation to the soil moisture conditions. Then BRIGGS and MCLANE (16) determined the *moisture equivalent* of soils by the application of a centrifugal force of 1000 times that of gravity, providing a method of measuring and comparing the retentiveness of different soils for moisture acted upon by a definite force. This had the advantage of being measured in absolute terms and of being reproducible within narrow limits of error. It remained for BRIGGS and SHANTZ (17) to refine the methods of determining the percentage of water in soils when permanent wilting occurs in such a plant as the standard Kubanka wheat, giving the *wilting coefficient*, and further to show that a constant relation exists between the moisture equivalent and the wilting coefficient; that is, $\frac{\text{moisture equivalent}}{1.84} = \text{wilting}$ coefficient.

They also clearly demonstrated the fact that plants continue to take water from the soil long after the wilting coefficient is reached. The writer, believing that none of the water absorbed from soil whose moisture content is below the wilting coefficient is used for the growth of the organism, has used *growth-water* (18) for the soil moisture in excess of the wilting coefficient.

That the water content of the soil at the time of wilting, or, in other words, the magnitude of the wilting coefficient, is affected by excessive evaporation rates, causing very high transpiration rates, has been shown by BROWN (**19**) and by CALDWELL (**20**), although their work also goes to show that it holds perfectly within certain limits differing but slightly from those obtaining in ordinary mesophytic or semi-mesophytic habitats. Although the validity of these objections to the wilting coefficient in extreme conditions is recognized, it is nevertheless believed that it is, especially when determined by the indirect method of BRIGGS and SHANTZ, an efficient means of relating the range of soil moisture to the production of vegetation and an important addition to the equipment of ecological and agricultural investigators.

METHODS

The soil moisture determinations here reported were made in the plant associations described in the previous part of this paper during the years 1911–1912, and for the same months as the atmometer records. In making the determinations, weekly samples, each consisting of 200 to 250 grams of soil, were taken in each of the associations at depths of 7.5 cm. and 25 cm. In order to provide against unnecessary error, each sample consisted of two portions of some 100 grams each, taken from spots several meters apart, care also being taken that no soil was taken nearer than a meter to holes where previous samples had been dug. The soil was placed in wide-mouthed jars, tightly sealed, brought to the laboratory, weighed and dried at a temperature of 100° to 104° C. until it reached a constant weight (about 5–7 days). The percentage of water to the dry weight of the soil was then calculated.

The wilting coefficients of the same soils were determined by both the direct and the indirect methods of BRIGGS and SHANTZ (**17**). The results from the two methods agreed within the limits of experimental error, which appeared to be much greater in the direct method. This was particularly noticeable in the sandy soil of the dunes, where the wilting coefficient approximates 1 per cent. All the wilting coefficients are the averages of at least 10 determinations.

Those of the clay soils made by the centrifuge, using the formula

$$\frac{\text{moisture equivalent}}{1.84} = \text{wilting coefficient},$$

the moisture equivalent being the amount of water which the soil retains against a centrifugal force of 1000 times gravity, showed very constant results.

The results are represented graphically, the wilting coefficients being represented by broken lines and the range of soil moisture in percentages of the dry weight of the soil by graphs with the weekly intervals as abscissas; while the ordinates represent the percentage of soil moisture present at the weekly determinations. Throughout the diagrams the vertical scale is denoted by figures at the left; and heavy lines are used for the determinations at 7.5 cm., and light lines for 25 cm. depth. The intervals between the graphs and the line denoting the wilting coefficient give the amount of the growth-water.

RANGE IN THE DIFFERENT ASSOCIATIONS

An examination of the accompanying diagrams will show at a glance some of the peculiarities of the water supply of the various associations. The results for the cottonwood dune association for 1911 have already been published (**18**), and show rather surprising results (fig. 16). The water content is rather constant, but seldom more than 5 per cent, a decidedly small amount. However, the wilting coefficient was here found to be less than 1 per cent, the average for many determinations by the indirect method being 0.8 per cent at both depths, the absence of humus and the instability of the soil accounting for the same coefficient at both depths. Considered in relation to this wilting coefficient, the soil moisture is seen to be continually at least twice the amount of water necessary for the growth of such a plant as wheat. This is in striking contrast to the desert-like aspect of this association, due to the almost complete absence of herbaceous undergrowth. Doubtless this constancy in soil moisture is largely due to the conserving action of a dry mulch of 3 to 5 cm. thickness maintained by the action of the wind upon the sand and to the small quantities withdrawn by the sparse vegetation. The record for 1912 (fig. 17) differs in no important particular from that of the previous year, an unfailing supply of growth-water being maintained, although its average amount during the weeks of midsummer is slightly less.

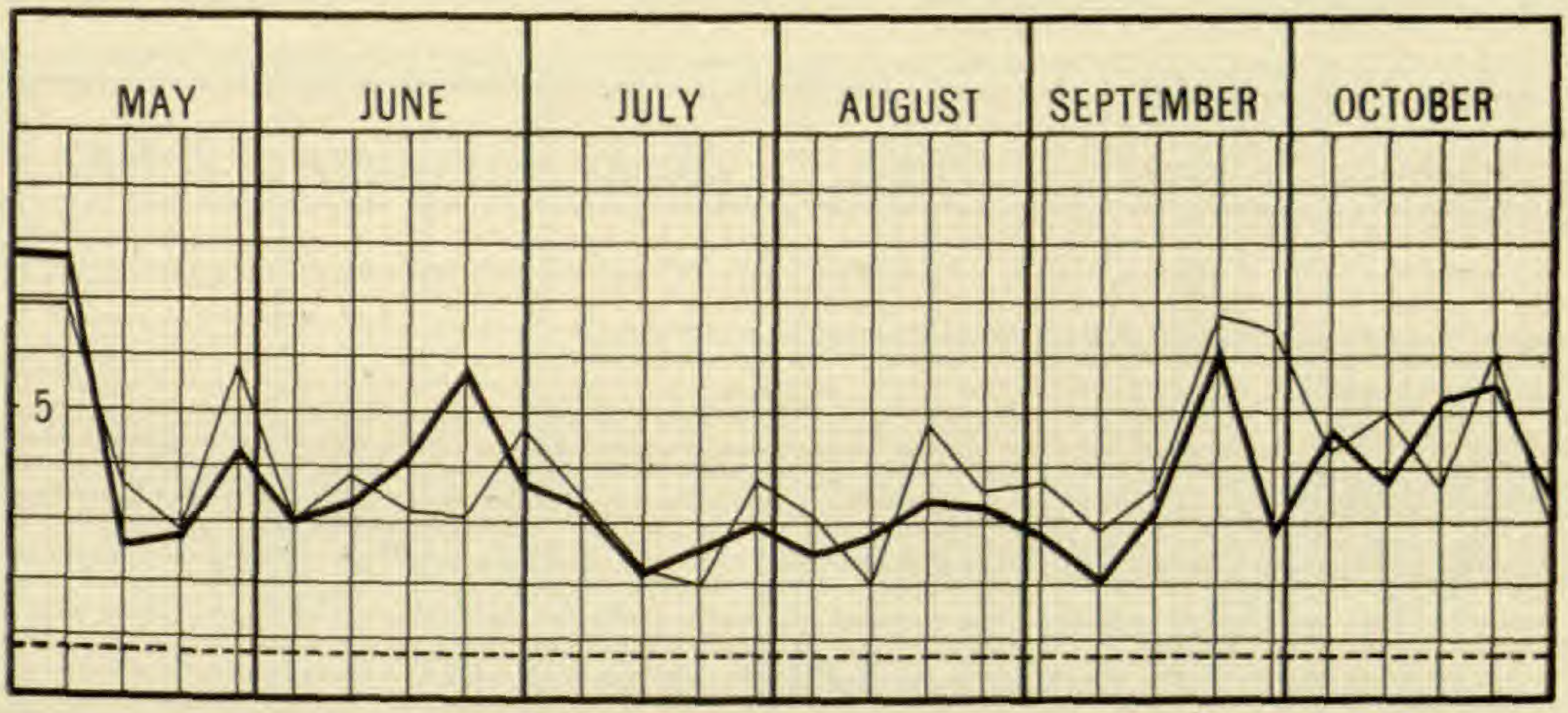

FIG. 16.—Graphs showing the range of soil moisture in the cottonwood dune for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by a broken line.

In the next association, the pine dune, the accumulation of humus increases the wilting coefficient to 1.1 per cent at 7.5 cm., and to 1.0 per cent at 25 cm. The range of the moisture throughout both 1911 (fig. 18) and 1912 (fig. 19) is more irregular than in the previous association, especially in the upper stratum, and what

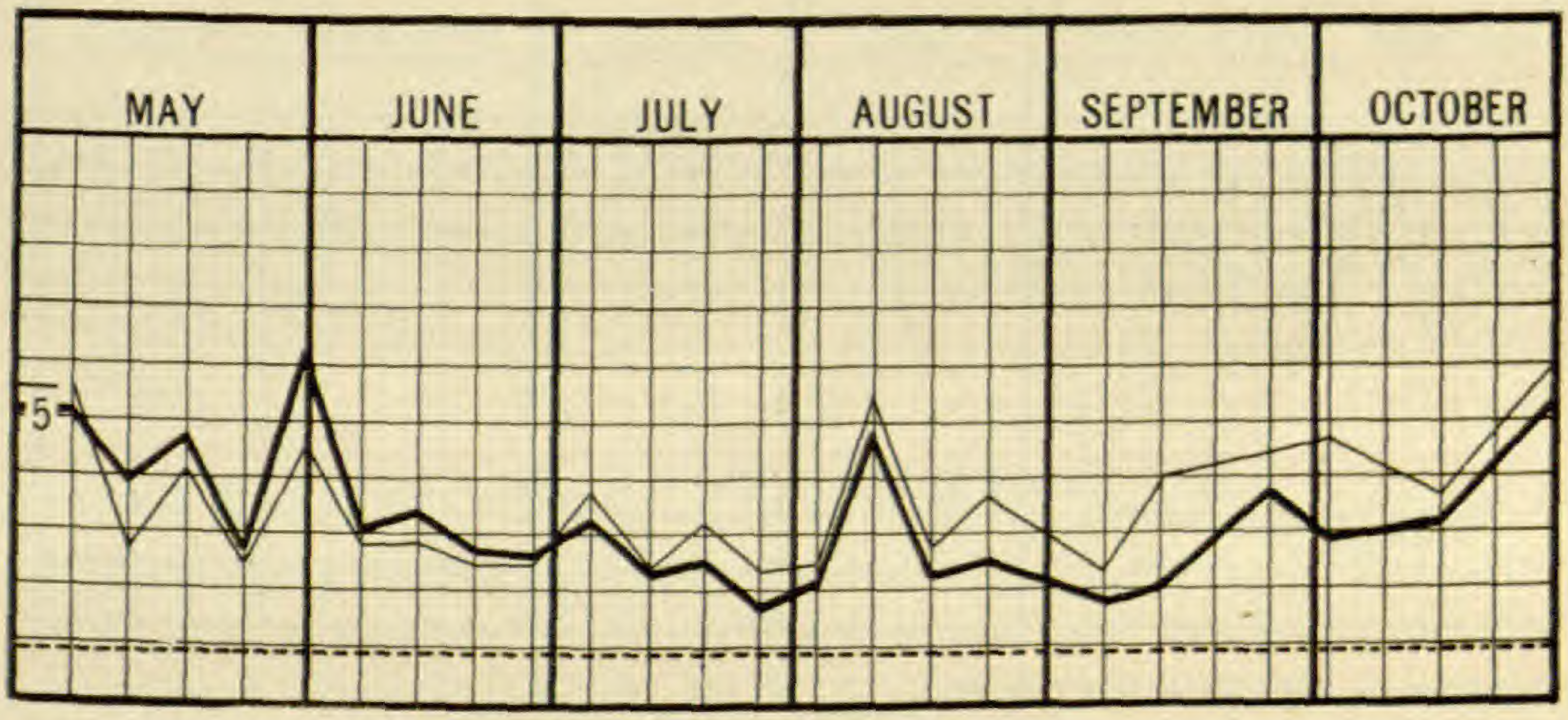

FIG. 17.—Graphs showing the range of soil moisture in the cottonwood dune for 1912; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by a broken line.

is more important, during three different weeks of each year the supply falls almost to or actually below the wilting coefficient. It is thus an association in which the growth-water fails repeatedly, and consequently with respect to its water supply is decidedly more xerophytic than the cottonwood dune. Reasons for the failure of the water supply may be found in the comparative absence of the conserving mulch of dry non-conducting soil, and in the much larger demands made by the denser stand of vegetation. The plentiful

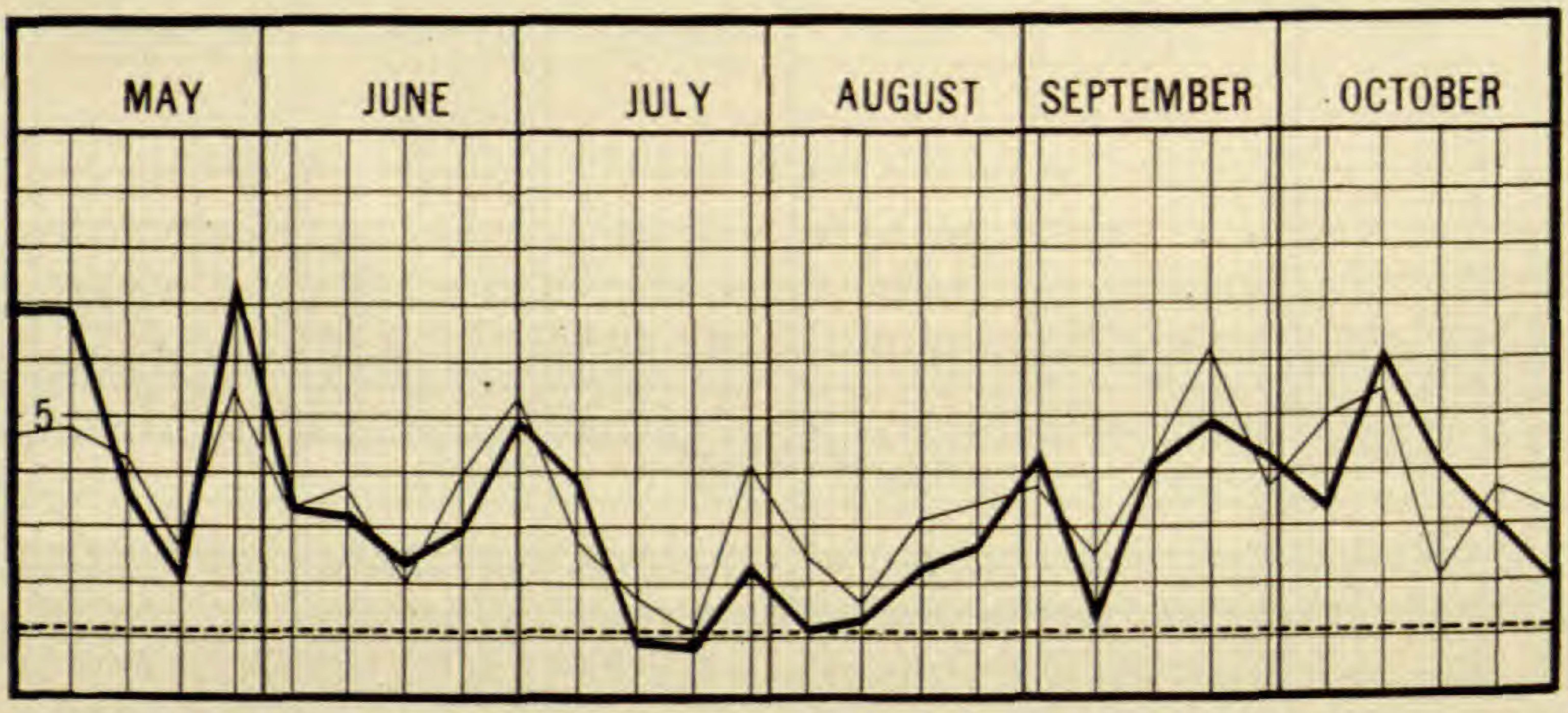

FIG. 18.—Graphs showing the range of soil moisture in the pine dune for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by broken lines.

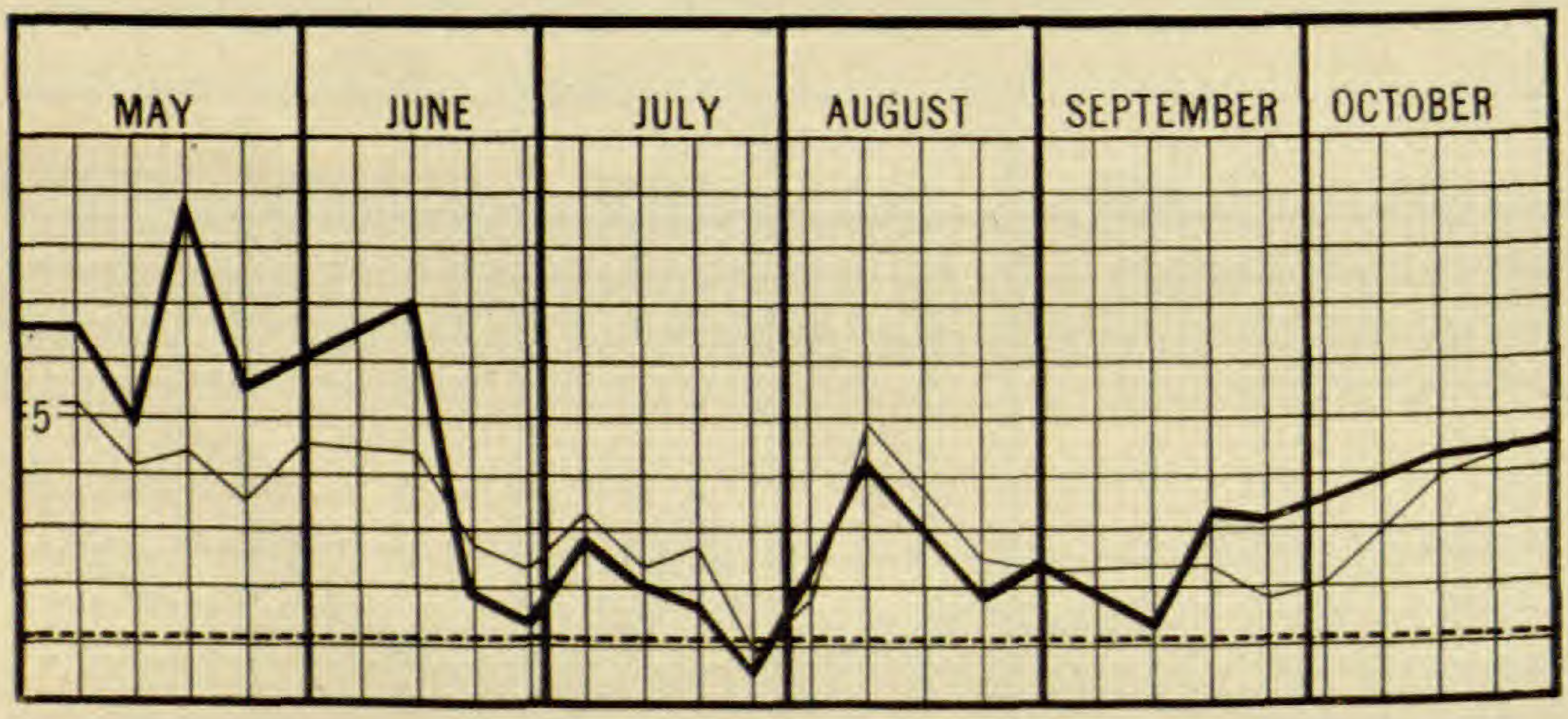

FIG. 19.—Graphs showing the range of soil moisture in the pine dune for 1912; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by broken lines.

supply during the weeks of spring permits the growth of a mesophytic herbaceous spring flora.

The open character of the forest on the oak dunes has brought no increase of humus, as indicated by wilting coefficients of 1.1 per cent and 0.9 per cent respectively for the 7.5 cm. and 25 cm. strata. The seasonal range of soil moisture is irregular (figs. 20, 21), and several times each season it approximates or falls below the wilting coefficients. The graphs indicate comparatively xerophytic

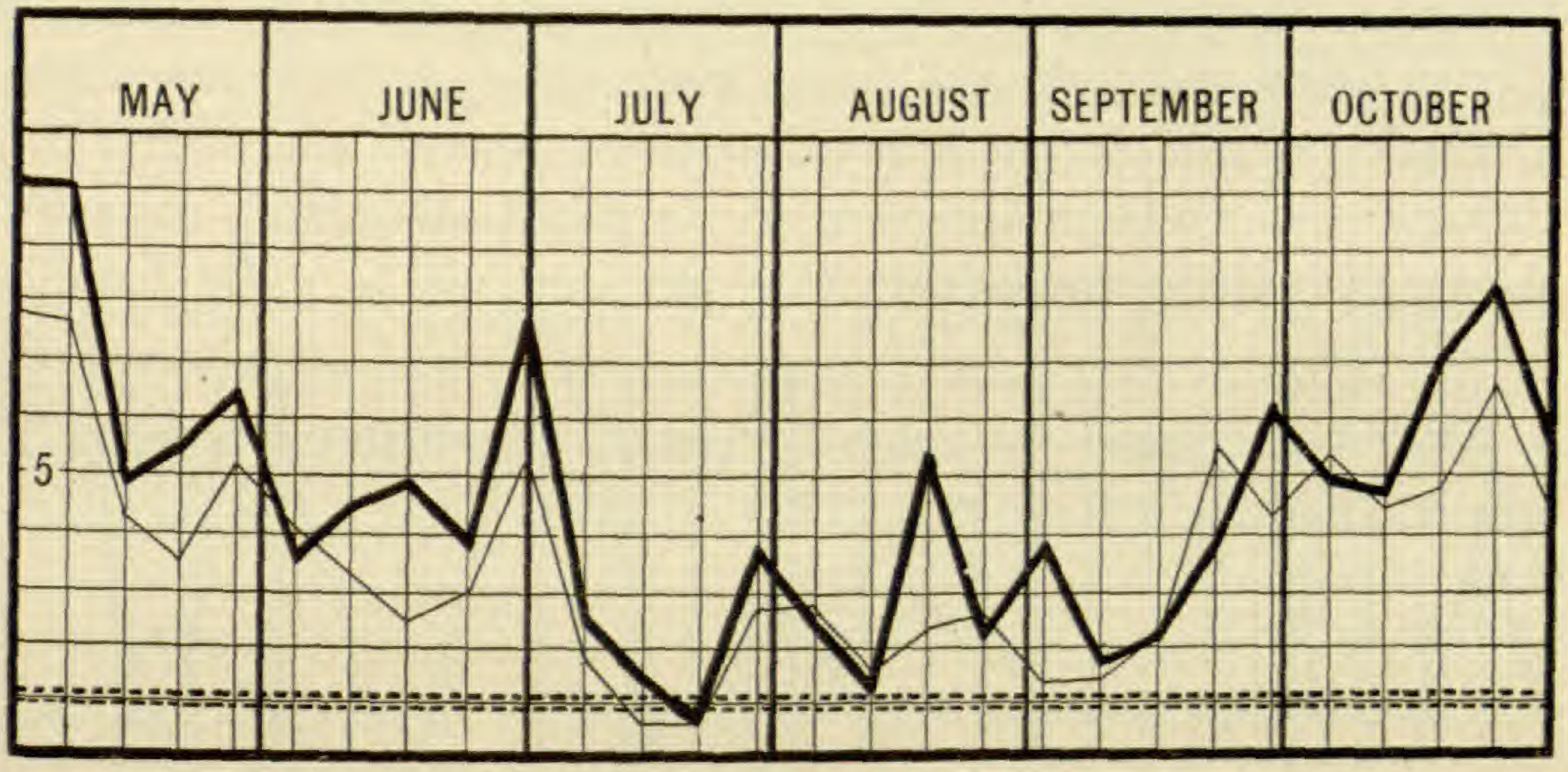

FIG. 20.—Graphs showing the range of soil moisture in the oak dune for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

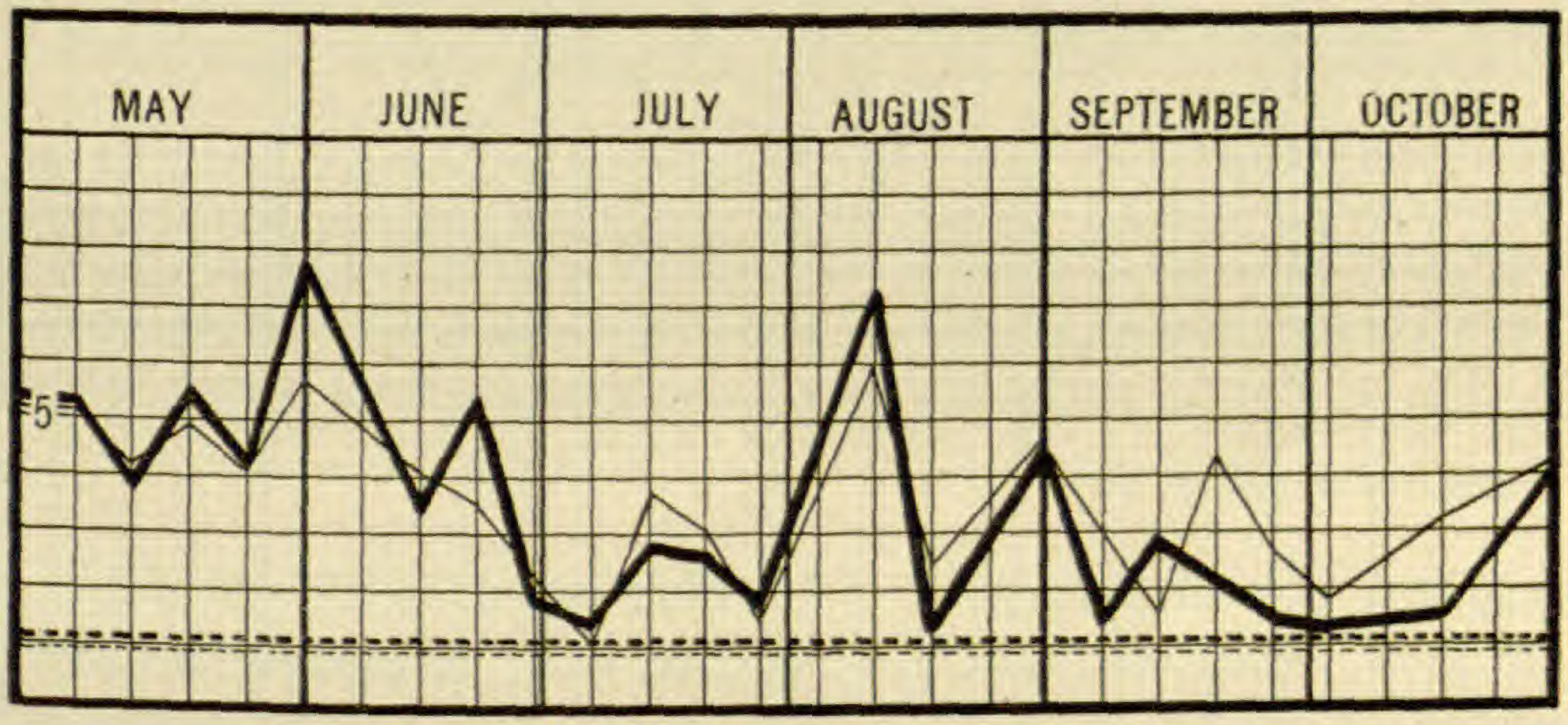

FIG. 21.—Graphs showing the range of soil moisture in the oak dune for 1912; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

soil conditions approximately similar to those of the preceding association.

The results for the oak-hickory forest for 1911 have already been published (**10**), but are reproduced here for the sake of completeness, especially since the record for 1912, owing to a series of interruptions and accidents, is too fragmentary to be of any value. The soil here is a clay with an admixture of gravel, and differs in a striking manner from the sand in its moisture-holding capacity, shown by wilting coefficients of 9 per cent and 9.5 per cent at depths of 7.5 cm. and 25 cm. The fluctuations in the soil moisture are great, particularly at 7.5 cm. (fig. 22). Although the water content of the soil at 35 cm. once falls below the wilting coefficient, the average amount of growth-water for the midsummer weeks is considerable (table III), much greater in fact than in any preceding association, indicating decidedly more mesophytic soil conditions.

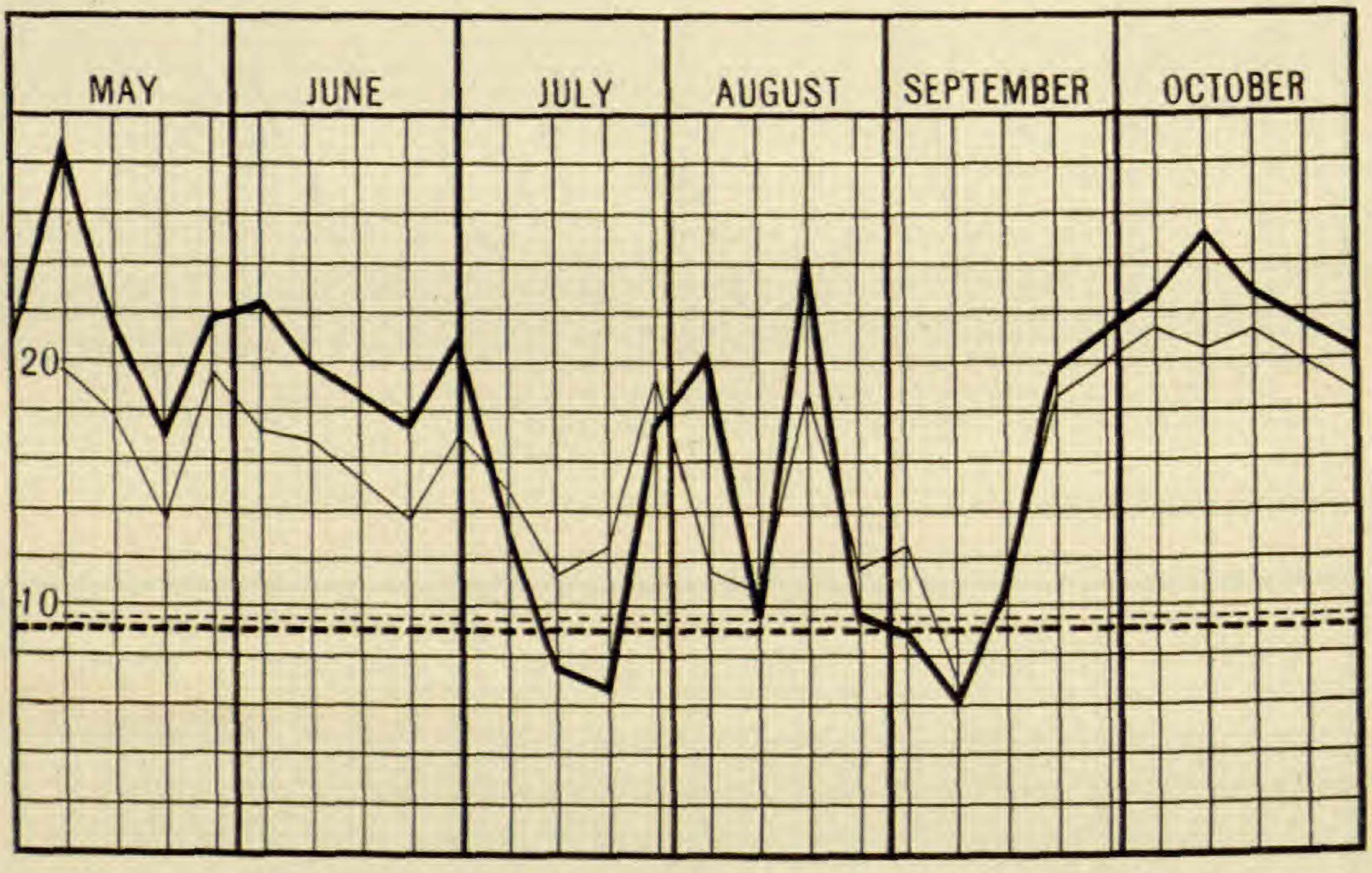

FIG. 22.—Graphs showing the range of soil moisture in the oak-hickory forest for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

It may be noted that the wilting coefficients now given for this and the succeeding association differ slightly from those formerly published. This is due to their redetermination by more careful methods, particularly to the use of the indirect method.

The ravine of the oak-hickory forest, with its abundance of humus, gave wilting coefficients of 16.3 per cent and 12.2 per cent respectively for the soil at depths of 7.5 cm. and 25 cm. The graphs (fig. 23) show the presence of a constant and abundant supply of growth-water throughout the season. This would quite agree with

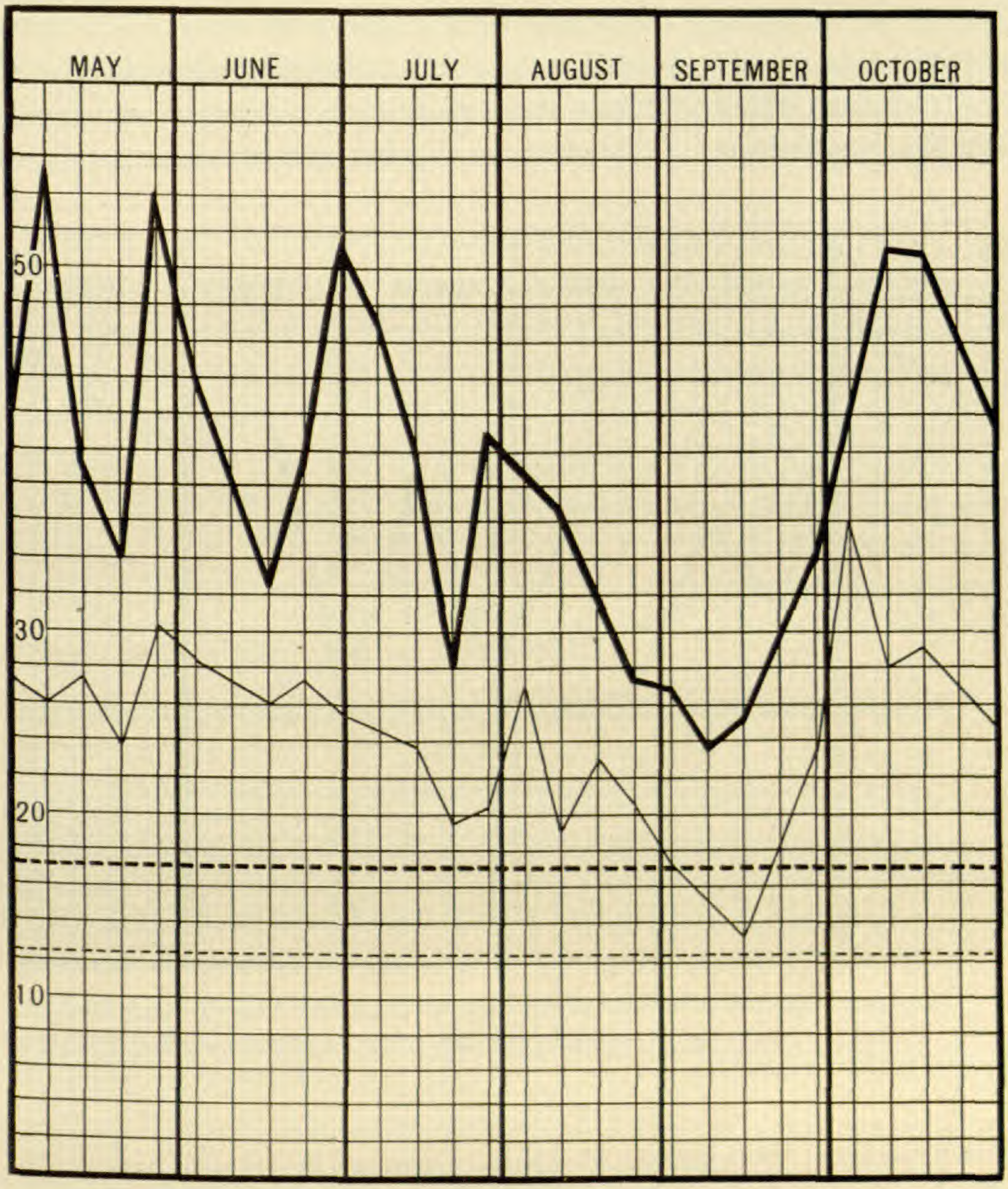

FIG. 23.—Graphs showing the range of soil moisture in the ravine of the oak-hickory forest for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by broken lines.

the hyper-mesophytism of rich floodplains, of which this may be regarded as a type.

The climax beech-maple forest shows the accumulation of humus in its wilting coefficient of 9.5 per cent at 25 cm., being increased to 13.5 per cent at 7.5 cm. In this association the soil moisture determinations were made only every second week, but the graphs (figs. 24, 25) show a constant and generous supply of growth-water, indicative of truly mesophytic conditions. The supply of growth-water is unfailing. As in the other associations, the upper stratum shows the larger amount of variation. A comparison of the two seasons will show that, while the averages are about the same, the year 1912 shows a much greater uniformity in the range of the moisture supply.

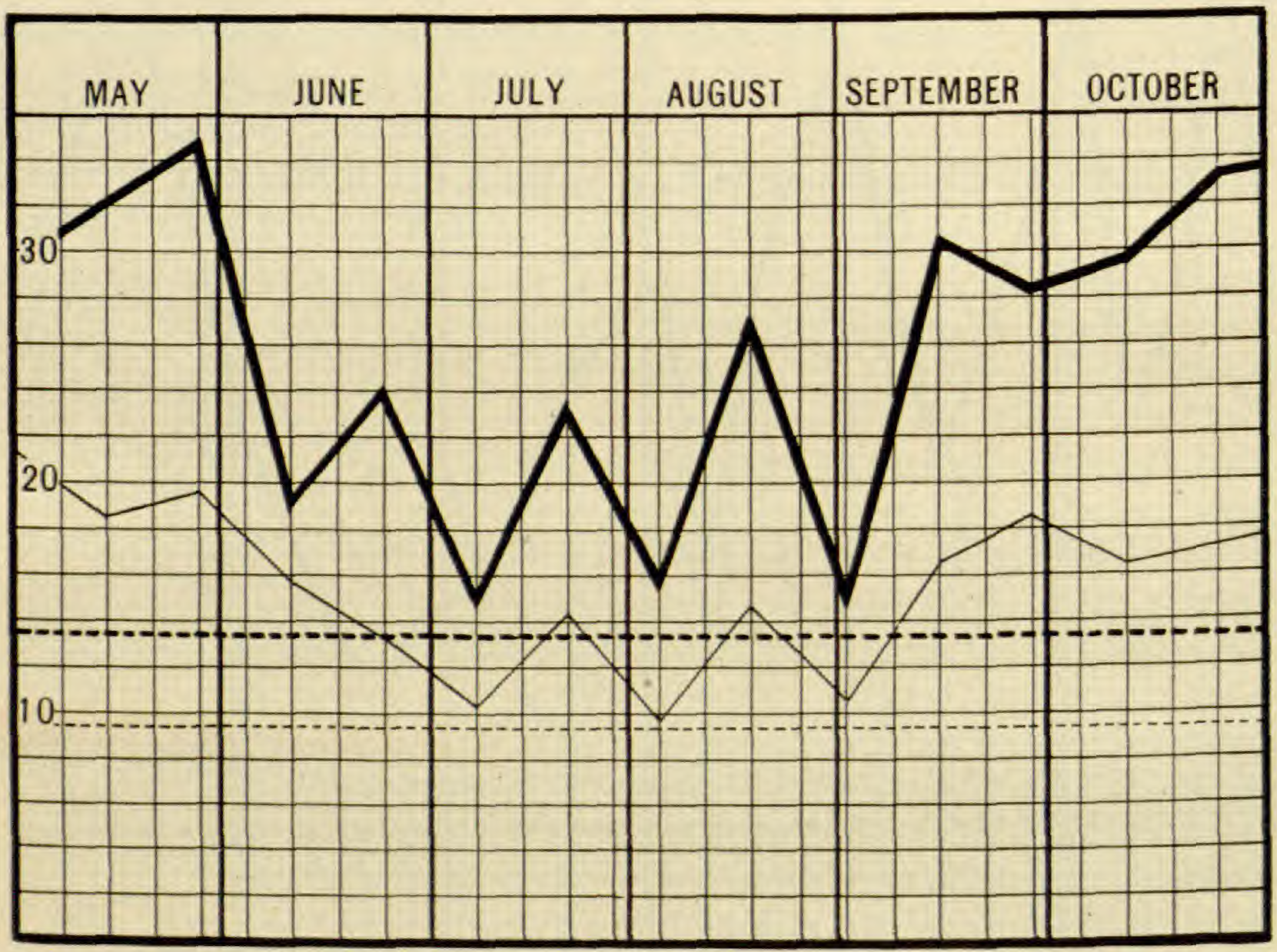

FIG. 24.—Graphs showing the range of soil moisture in the beech-maple forest for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

The results for the prairie association are more difficult to interpret. The range plotted in fig. 26 is the mean of the two stations reported by HARVEY (13) for the season of 1911, while fig. 27 gives the results obtained by Miss NEWLON in 1912. The wilting coefficients of 24 per cent at 7.5 cm. and 21 per cent at 25 cm. indicate soil with a high water-retaining capacity. This soil is at or near saturation point early in the spring, just as the growing season begins (figs. 26, 27); in fact it seems probable that the amount of water present is not only in excess of all requirements of the vegetation, but even in such abundance as to prove detrimental to many plants. Late in the fall the supply is also very large. In striking contrast is the small and irregular supply during midsummer, when the wilting coefficient is more than once reached or approximated. In general the habitat is shown to be one of extreme fluctuations in respect to its moisture supply, conditions which may help to account for the absence of trees. It is particularly xerophytic during late summer.

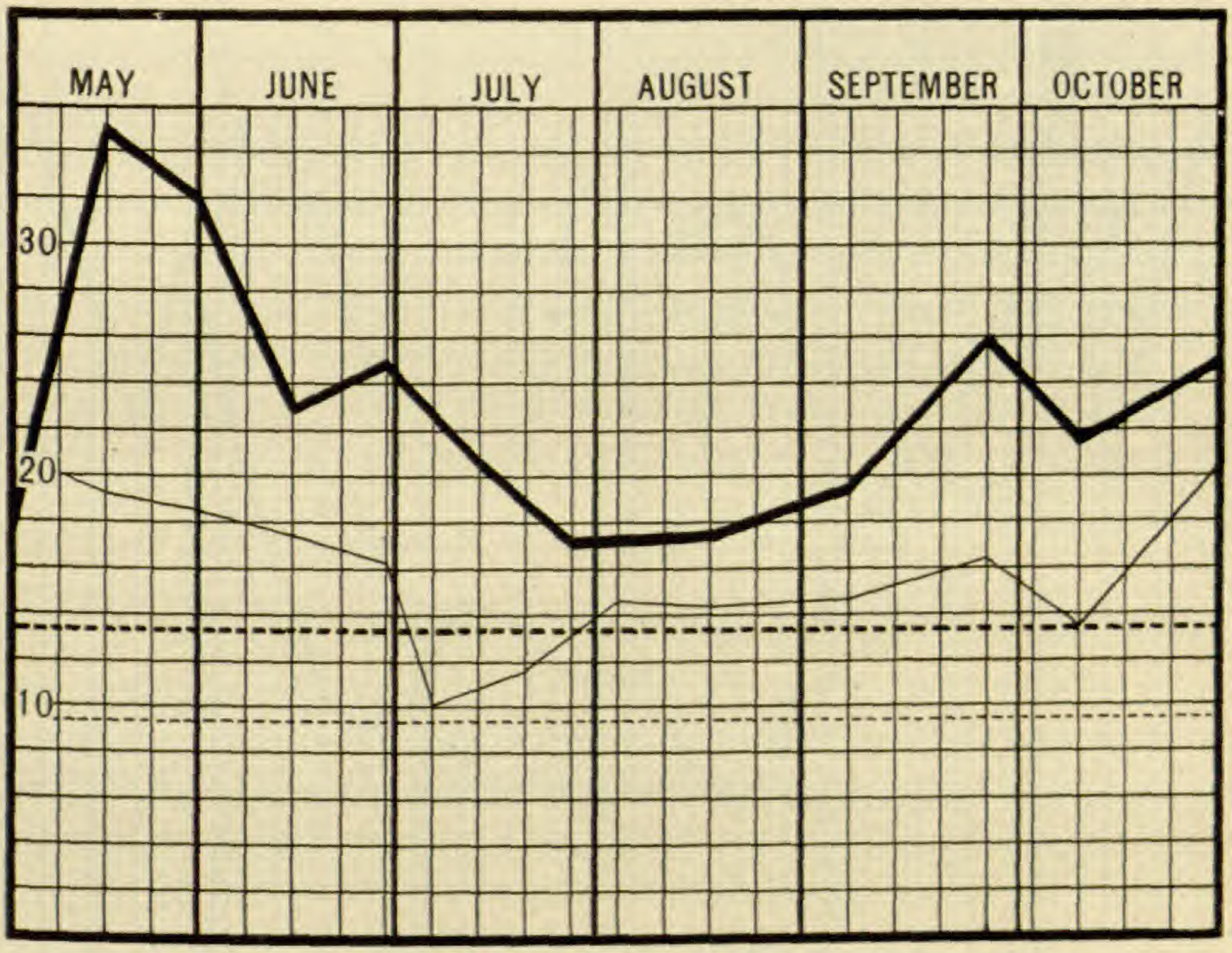

FIG. 25.—Graphs showing the range of soil moisture in the beech-maple forest for 1912; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

GENERAL CONCLUSIONS

An examination of all the graphs showing the range of soil moisture, as well as a general consideration of the conditions of growth in these associations, indicates that only during midsummer is there any scarcity in the supply in any of the habitats. It has seemed desirable, therefore, and even more necessary than in the evapora-

FIG. 26.—Graphs showing the average range of the soil moisture in the edaphic prairie for 1911; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines (after HARVEY).

tion studies, to limit our comparisons to this period of stress, and to establish the rather arbitrary limit of the 10 weeks from the last of June to the first of September. A summary for these weeks appears in table III.

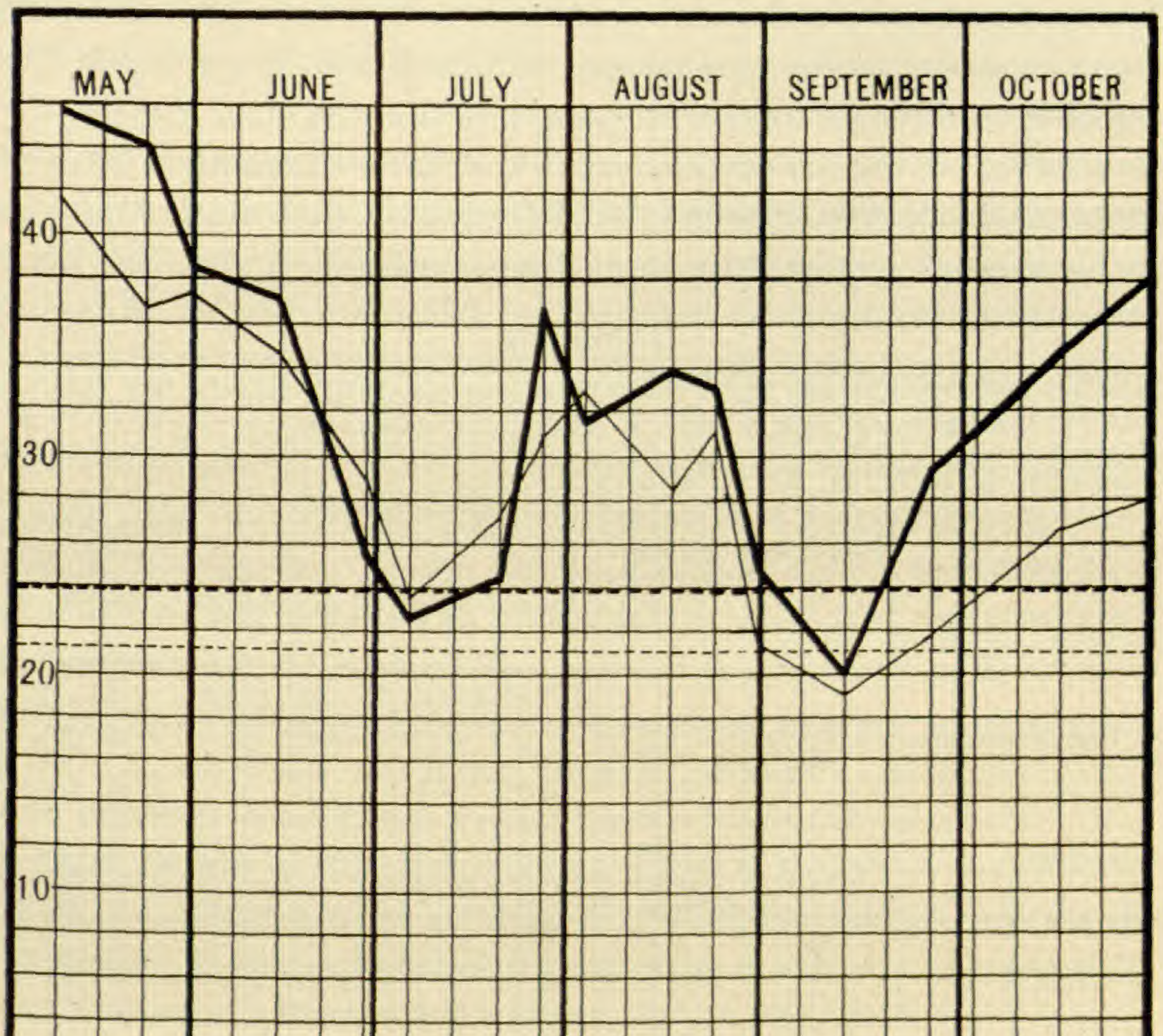

FIG. 27.—Graphs showing the range of soil moisture in the edaphic prairie for 1912; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficients represented by broken lines.

No one can realize more fully than does the writer the limitations of the data or the desirability of having them supplemented by more numerous determinations, especially from deeper strata. These limitations will make the conclusions more or less provisional and subject to modification and correction in the future. The most interesting and profitable comparisons are doubtless those to be made from a consideration of the growth-water data shown in table III, and especially as expressed in the sixth and seventh columns, which contain the mean percentages of growth-water and the comparative amounts, the beech-maple forest being taken as a standard and its mean growth-water represented by 100. In the five associations that form the succession, the mean growth-water for midsummer of the two seasons will be found, if we except the cottonwood dune, to form a progressive series, the most mesophytic association having the largest amount. This was exactly what was supposed to be the situation, but hitherto no quantitative data of such moisture relationships have been available, and it has been impossible to tell how much an association differs in its water conditions from the preceding or succeeding association. As has already been stated, the cottonwood dune, with a larger and more constant water supply than the two succeeding associations, must owe its surplus to the conserving power of its dust mulch and to the small outgo due to the paucity of its vegetation.

TABLE III

WILTING COEFFICIENTS AND MEAN PERCENTAGES OF GROWTH-WATER IN THE VARIOUS ASSOCIATIONS DURING THE 10 MIDSUMMER WEEKS OF 1911–1912

ASSOCIATION	DEPTH IN CM.	WILTING COEFFICIENT	GROWTH-WATER				RATIO BETWEEN EVAPORATION AND GROWTH-WATER
			1911	1912	Mean	Comparative am'ts	
			per cent	per cent	per cent	per cent	
Cottonwood dune..	7.5	0.80	2.2	1.8	2.15	49	11.7
	25.0	0.80	2.6	2.0			
Pine dune........	7.5	1.10	0.9	0.7	1.15	26	10.7
	25.0	1.00	1.7	1.3			
Oak dune........	7.5	1.10	1.4	1.4	1.27	29	9.37
	25.0	0.90	0.8	1.5			
Oak-hickory......	7.5	9.0	3.2	......	3.3	75	2.78
	25.0	9.5	3.3	......			
Beech-maple......	7.5	13.5	5.5	5.0	4.4	100	1.81
	25.0	9.5	3.0	4.0			
Prairie...........	7.5	24.0	4.0	4.0	4.7	107	2.91
	25.0	21.0	4.9	5.9			

The comparative amounts of growth-water indicate even more clearly the relationship existing between the available water supply of the associations, and should serve to emphasize the fact that the progressive increase in the water-retaining power of the soil, due largely to its increased humus content, must play no inconsiderable rôle in causing the succession here culminating in the mesophytic beech-maple forest. Little need be said concerning the rank of the prairie, in respect to its soil moisture in comparison with the other associations under consideration, further than to point out that its soil has a very great water capacity, and that over against its large amount of growth-water should be placed the fact that the supply completely fails at intervals. More investigation must be made before more definite comparisons can be made.

Another and still more important comparison may be instituted among the associations under investigation by considering the ratio between the average mean weekly evaporation rates for the 10 midsummer weeks of the years 1910–1912 and the mean growth-water for the same period. These ratios are expressed in the final column of table III. In determining these ratios it is recognized that the units of measurement in the case of the evaporation rates and the soil moisture are not directly comparable. Still it is thought that the comparison is a legitimate one, and institutes a quantitative summation of the mesophytism of the habitats which is valuable and exceeds in accuracy anything hitherto attained. It is true that these habitats are limited to the lower stratum of the aerial and the upper strata of the subterranean vegetation, but, as previously pointed out, these are the portions of the habitat that are of critical importance in the establishment and maintenance of the associations, because in them the seedlings, both woody and herbaceous, develop. An extension of the habitats by the addition of the higher strata of the air and the lower strata of the soil containing all the aerial and subterranean portions of the vegetation would doubtless modify and perhaps decrease the steepness of the gradient between the various ratios. The ratios may either be compared directly, remembering that the mesophytism of the various habitats varies in inverse ratio with the numbers expressing these ratios, or the beech-maple forest may again be taken as the standard and represented by 100, when the direct ratio of the mesophytism of the corresponding portions of the oak-hickory forest, the oak dune, the pine dune, and the cottonwood dune will be respectively 65, 20, 17, and 15. The prairie expressed in similar terms will be 62. These comparative values of the moisture factors show such a surprising rate of increase as one proceeds from the pioneer to the climax associations that it cannot be doubted that such a change in water conditions must be one of the chief factors, if not the most important cause, of the succession of associations from the more xerophytic to the more mesophytic.

Summary

1. These data represent the evaporation rates in the lower aerial stratum and the range of soil moisture in the upper subterranean strata of the vegetation of the various associations, but these must be regarded as critical regions, since within them develop the seedlings which determine the character of succeeding vegetation.

2. Evaporation at different stations in the same plant association exhibits variations similar in character and degree.

3. The rate of evaporation in the cottonwood dune association, both by its great amount and by its excessive variation, seems a quite sufficient cause for the xerophytic character of the vegetation and for the absence of undergrowth, in spite of the constant presence of growth-water.

4. The pine and oak dune associations resemble one another closely both in their mean evaporation rates and in their supply of growth-water. The former is slightly more xerophytic during the midsummer weeks.

5. The vernal vegetation of the pine dune is quite as mesophytic as that of the succeeding association, thus agreeing with its lower evaporation rate during that portion of the year.

6. The evaporation rates and the amount of growth-water in the various associations vary directly with the order of their occurrence in the succession, the pioneer being the most xerophytic in both respects.

7. The ratios between evaporation and growth-water in the beech-maple forest, oak-hickory forest, oak dune, pine dune, and cottonwood dune associations have been shown to have comparative values of 100, 65, 20, 17, and 15 respectively, and the differences thus indicated are sufficient to be efficient factors in causing suc-

cession. The corresponding value of this ratio in the prairie association is 62.

8. The midsummer conditions of the prairie association seem to be decidedly xerophytic.

Grateful acknowledgment is made of the cooperation and advice given by Professor HENRY C. COWLES, under whose direction the investigation has been conducted, and of the assistance of Messrs. WADE MCNUTT, E. M. HARVEY, C. SHIRK, and Miss L. NEWLON in collecting data.

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ON CERTAIN PECULIAR FUNGUS-PARASITES OF LIVING INSECTS[1]

ROLAND THAXTER

(WITH PLATES XVI–XIX)

During the past ten years the writer has examined many thousands of freshly collected insects of various sorts preserved in alcohol, which have come from various parts of the world, especially from tropical regions, and in looking them over for fungus-parasites, the possibility of encountering forms which might throw some light on the origin of the Laboulbeniales, yet not members of this group, has been constantly in mind. Although the hope of meeting with forms of this nature has not been realized, and nothing remotely related to these plants has been seen, apart from many genera and species which are entirely typical of the group, a certain number of wholly unrelated fungi have been observed, which appear to be as peculiar in their mode of life on living insects as are the Laboulbeniales themselves. Although few in numbers, these parasites belong to several quite unrelated groups, and seem to have adjusted themselves successfully to the uncertain conditions of life and propagation on rapidly moving living hosts. The apparent rarity of most of them seems quite remarkable, however, in view of the fact that any such exist; since, if a certain small number of insects furnish favorable conditions for such development, it is difficult to understand why hosts of other similar insects have not also been similarly parasitized, and why an extensive flora of this nature, or at least one comparable in numerical importance to that of the Laboulbeniales, has not been developed.

What may be called the idiosyncracies of such parasitism are well illustrated by equally inexplicable host relations or rather lack of host relations, between certain groups of insects and the Laboulbeniales. The ants, for example, would seem from their

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[1] Contributions from the Cryptogamic Laboratories of Harvard University, LXXIV.

enormous numbers, gregarious habits, wide distribution, overlapping generations, and usual habitats, to offer the most favorable conditions for the development of a very large flora, but as yet only two forms of Laboulbeniales have been found on them. Their habit of cleaning themselves evidently does not interfere with the successful propagation of such parasites, since several typical genera and species are thus successfully attacked. That they rarely become hosts, however, seems to be indicated by the fact that, among the many that have been examined both by the writer and by Professor WHEELER, whose attention has been called to this matter for some years past, none have been found which appear to be hosts for any forms except the common *Laboulbenia formicarum* of America, and the apparently equally common *Rickia Wasmanni* of Europe. On the other hand, the most nondescript type among those described below is an ant-parasite; although its characteristics are not such as would have been expected to makes its parasitism successful on any type of insect.

Of the five genera herewith enumerated, three, including the form on ants just mentioned, are very closely allied to well known genera of Hyphomycetes, the species of which are either saprophytes or parasites on other plants; and did they not occur on living hosts, might have been regarded as accidental saprophytes which had developed after death; dead insect remains being, as is well known, a very prolific source of such forms. Since, however, all the insects examined in the present connection were collected while living, directly into alcohol, and some were examined by the writer while still alive, there can, it would seem, be no question as to the true nature of the relation in these instances. Of the two remaining genera, one comprises species also belonging to the Hyphomycetes, but not closely related to any described types, while the other seems to be more nearly related to the Chytridiales than to other known organisms.

In comparing the miscellaneous assemblage of forms which are now known to live as external parasites on living insects, it is of interest to note that a great majority, at least, possess one characteristic in common, namely a more or less clearly defined, blackened footlike structure which serves both as an organ of attachment to the host and a means of absorbing such materials as are necessary for growth. In other words, the foot is also a haustorium. Among the Laboulbeniales, those forms which, like *Dimeromyces rhizophorus*, perforate the host's integument, may be assumed to derive their nutriment directly from the fluid materials which surround their deeply penetrating rhizoids; in fact this conclusion seems unavoidable. But that a very closely allied species like *D. coarctatus*, which possesses a typical foot and does not penetrate, although it grows under identical conditions on a soft-bodied host, should use materials which are either of a different nature or derived from a different source, seems not at all probable. In the opinion of the writer, even those forms which grow on spines or hairs or thin wing-membranes obtain their food supply from the same source as do the penetrating forms, namely from the circulatory system, which by diffusion or otherwise supplies the structures mentioned in the living insect. There seem certainly to be no differences in the vegetative characteristics or in the peculiar fatty cell contents in any of the Laboulbeniales which would suggest that the nutrition of these plants is not the same in all cases. The assumption that the food material is obtained directly from the circulation seems further supported by the fact that individuals which grow nearer the circulatory centers, as for example about the bases of the two anterior pairs of legs, or along the chief circulatory channels, are usually larger and more luxuriant. That any considerable portion of their food is derived from the integument itself seems quite improbable in view of the host-relations of the penetrating forms. An examination of the accompanying plates will show the presence, in most instances, of a blackened footlike structure similar in a general way to that of the Laboulbeniales, and in the writers' opinion these plants, also, may be assumed to obtain their food materials from the circulatory system through the medium of this haustorium.

Among entomogenous Fungi Imperfecti, one other type has been observed on living insects, which is not herewith included; for the reason that, as yet, no definite spore-formation has been seen in any of the several species examined. These plants consist of colorless, septate, copiously branching filaments, which grow on various parts of small silphids, especially, and on the wings of certain flies in the tropics. They may produce conspicuous and dense tufts, and in some instances correspond very closely in external form to types of *Cladophora*. No characteristic foot is developed and no definite spores have been seen, propagation being effected, as far as can be determined, solely by fragmentation.

Hormiscium myrmecophilum, nov. sp.—Plate XIX, figs. 22–25

Filaments nearly hyaline becoming brownish, darker near the base, closely septate, the cells often as broad as, or broader than long, undifferentiated, distally bluntly rounded, erect or curved upward, rigid, simple, less frequently sparingly branched, tapering but slightly if at all, one to several arising from a deeply blackened foot of variable size and shape. Maximum length about 280 μ by 7–8 μ in width.

On various parts of *Pseudomyrmex* sp., Amazon (MANN).

This plant was received from Mr. W. H. MANN, who found it growing on a majority of the individuals taken from a nest of *Pseudomyrmex*, while he was acting as entomologist of the Leland Stanford Expedition to Brazil in 1911. It is sufficiently large to be readily visible as it projects from the surface of the host, and, although it is such an insignificant type, possesses sufficient individuality to distinguish it. It produces no definite spores or differentiated cell-groups, as far as has been observed, and appears to propagate itself by fragmentation only, the filaments proliferating, as indicated in the figures, after a terminal portion has been broken off. The opaque and somewhat variable "foot," by which the individuals are attached to the surface of the host, appears to correspond to such a small fragment broken from a hypha, which, adhering laterally, becomes blackened and indurated, and gives rise to new filaments, while at the same time it serves the office of attachment as well as of food absorption. It is not, however, so firmly fixed as is the case with most of the Laboulbeniales, and might be easily removed by its host from portions of the body which can be reached by the mouth. When one considers the habits of cleanliness which characterize most ants, it seems singular that a type like the present should be able to establish itself successfully. It is possible that an examination of fresh specimens might show the presence of some more or less viscous secretion from the hyphae, which enables them to adhere readily and firmly to any surface with which they may come in contact, but there seems to be no indication that such is the case in the alcoholic material.

It may here be mentioned that several other imperfect forms have been seen on ants. Among them one has been found by the writer in the vicinity of Cambridge, which forms blackish incrustations on various parts of the host and gives rise to a few short, colorless, erect branches. It has not been possible, however, to determine the nature of this plant. Another form has recently been mentioned by Dr. BISCHOFF (Berl. Ent. Zeitschr. 57:(2), 1912), as occurring on living ants at Potsdam, which possesses brown hyphae and grows on various parts of the host in tufts. No further details as to its structure are given, and it is uncertain whether it is related to the present form.

Muiogone, nov. gen.

Entomophilous; pulvinate. Sporophores short, simple, hyaline, crowded. Spores terminal, solitary, dark, muriform, the cells of the mid-region distinguished from those of the basal and terminal portions, which bear more or less conspicuous median processes or spines.

Muiogone Chromopteri, nov. sp.—Plate XVI, figs. 1–3

Sporophores short, slender, several-septate, crowded so that the spores form a compact spreading pulvinate mass on the surface of the host. Spores irregularly oblong or piriform, usually broader distally and tapering slightly at the base; the cells very numerous and arranged in about twelve tiers which are regular, except distally; four or five of the middle tiers remaining subhyaline or variably suffused with dirty brownish yellow; contrasting, though not abruptly, with the nearly opaque blackish brown basal and terminal regions; the cells of the latter more prominent, forming a sort of cap; all of them, especially the upper which are slightly irregular, usually slightly flattened distally, and bearing a spinelike process, straight or curved, sometimes stouter and distally perforate, sometimes obsolete: the cells of the basal tiers similarly modified, less prominent, flattened; the spinous process minute or obsolete. The whole sporiferous pustule, in the type, 330 μ in diameter by 210 μ deep. Spores 62–77×32 μ, the stalk (broken) about 25×7 μ.

On the inferior surface of the abdomen of *Chromopterus delicatulum* Beck., Kamerun, West Africa.

A single specimen of the apparently rare host, bearing this very peculiar fungus on its abdomen, was found in a collection of flies sent me by the Rev. GEORGE SCHWAB, to whom I am very greatly indebted for this as well as for numerous similar favors, and to whom I owe the remaining forms from Kamerun described below. Since there is but a single specimen, I have been unwilling to destroy it in order to determine the exact relation of the fungus to its host, and have merely removed a certain number of spores with a needle point from the general mass, which is firmly adherent to the soft integument of the inferior surface of the abdomen. This mass is somewhat diagrammatically illustrated in fig. 1, where it is shown *in situ* on the insect's body; but whether the vegetative hyphae penetrate the integument, or merely adhere firmly to its surface, cannot be determined in its present condition. The spores (fig. 2), which are in different stages of development in different parts of the mass, the younger ones mostly near the edges close to the substratum, are easily detached, and carry with them a portion of the slender stalk, which is probably somewhat longer than is represented in the figures. The cap-cells of the spore are distinctly different from those of the paler mid-region, and their terminal processes vary greatly in development. In some instances (fig. 3) they are much stouter, and seem certainly to be distally perforate; although in others this is quite evidently not the case, and it is barely possible that they may be associated with some viscous secretion which might aid the spore in attaching itself to a new host. No such secretion, however, can be detected in the present condition of the material; although, as in the case of the *Hormiscium* just described, as well as in the species of the following genus, it is difficult to imagine how the parasitism of such forms can be successful in the absence of some contrivance to insure adherence to a moving host. The cells of the lower tiers of the spore, though more prominent than the smaller ones of the middle region, are distinctly flattened, and the minute apical projection, when present, can only be distinguished along the margin.

The genus is perhaps too near *Sporidesmium*, and I have had some hesitation in separating it under a new name. The differentiation of its spores, however, into specialized distal, basal, and middle regions, of which the last is probably the functional portion, corresponds in a general way to that seen in the spores of the following genus, and, taken in connection with its entomogenous habit, may perhaps be considered as sufficient reason for regarding it as distinct. It seems not improbable that the sporiferous pustule arises from the multiple germination of the paler mid-region of the spore, which must include nearly one hundred cells, in some cases.

Muiaria, nov. gen.

Entomophilous, more or less deeply suffused throughout, growing in dense, more or less isolated tufts, or rarely repent, each tuft attached by a blackened base in which the vegetative hyphae may be indistinguishable; the tufts consisting of fertile, or both sterile and fertile elements; the sterile, when present, simple and not clearly distinguished from the sporophores; the latter bearing terminally solitary spores which are not abjointed, or, as a rule, clearly differentiated from them. Spores at first transversely septate, consisting of a slender terminal portion and a broader main body in which two flat central cells are distinguished that become several times longitudinally divided, after usually dividing once transversely; the cells adjacent to these four central tiers often showing occasional longitudinal or slightly oblique divisions; the stalk and distal prolongation sometimes producing a short but characteristic spurlike process.

This genus, which inhabits living flies in the tropics, so closely resembles certain types of *Macrosporium* that, as in the case of *Muiogone*, I have hesitated to give it a new name. It seems, however, to possess certain peculiarities, in addition to its very different habit of life, which are sufficiently distinctive to render a generic separation desirable. In only one species, *M. repens*, does it assume a repent habit, such as is illustrated in fig. 6, and in this instance only on the host's wing. This may be due in part to the less nutritious character of the substratum; yet other species, when they occur in the same situation, retain their isolated tuft-like habit, which is also characteristic of this species when it occurs on the body or legs of its host (fig. 8).

The spores, which always resemble those of *Alternaria* in general form, differ from those of *Macrosporium* in being inseparable from the sporophore, a portion of which breaks off with them, and in the characteristic differentiation of the central portion, which consists of two similar flattened cells; which, in all the species except *M. repens*, become divided once transversely before the appearance of a few longitudinal septa. The four tiers of small cells which result are usually clearly distinguishable, as is indicated in fig. 4; and with the exception of *M. repens*, the vegetative portion is hardly developed; a tuft of more or less divergent elements being attached by a compact blackened base, which may or may not be associated with slight rhizoid-like outgrowths. The body of the spore is flattened, so that when it is viewed edgewise, it is often hardly broader than the stalk and tip. Both the spores and their stalks are brittle, and it seems probable from the appearance of very small plants which are sometimes found growing on hairs or spines, that propagation may be effected by small detached fragments as well as by whole spores, from which the larger groups appear to arise; although in the latter case, it is seldom possible to determine definitely that a portion of the general blackened base is made up of the old spore body. The spurlike processes which may arise in some species (figs. 9), either from the stalk just below the spore, or from the slender termination of the latter, sometimes in both positions (figs. 4 and 5), are characteristic, but are not present invariably or in all the species.

The body of the spore, sometimes also its termination and the whole or a portion of the stalk and sterile elements, if they are present, are irregularly mottled or lined by a somewhat darker incrustation which gives the surface a somewhat roughened appearance. This superficial modification tends to obliterate the longitudinal divisions of the cells when they occur, so that they often cannot be clearly distinguished without the use of an immersion.

It is evident from an examination of the sporophores, that after a spore has matured and has broken off, the portion of the stalk which remains proliferates distally and produces a new spore. Since this may be repeated several times, the spore-formation in a given tuft may be more or less continuous, even if new sporophores are not produced.

Although the species of this genus, all of which occur on living individuals of small flies, are so unlike other entomogenous types, they appear to be similarly limited to definite hosts. This seems to be very distinctly the case, for example, in *M. repens*, which has been seen on numerous individuals all belonging to a single species, apparently, of the genus *Clasiopa*, while no others among the very numerous and often closely related flies, which were collected with them in the same locality, are thus parasitized.

In addition to the species described below, a few others are known, but from lack of sufficient material these are not herewith included.

Muiaria gracilis, nov. sp.—Plate XVII, figs. 12–13

Olivaceous, forming a tuft attached by a compact, footlike, blackened base. Spores and sporophores very long and slender; the body of the spore not abruptly distinguished from its long terminal portion, or from the sporophore; the cells of the four central tiers very small; the adjacent cells above and below usually undivided by longitudinal septa; the whole rather inconspicuously marked by more or less elongated darker areas separated by lighter somewhat labyrinthine lines, this modification involving the upper portion of the sporophore and the lower two-thirds, or more, of the slender spore-termination; the spore outline even, with hardly indicated indentations at the septa or with none. Total length of spore and stalk 300–480 μ, the stalk about 7 μ in diameter, the body of the spore 14–17 μ in diameter.

On the legs and inferior surface of the abdomen of *Leucophenga* sp., no. 2299, Kamerun, West Africa (SCHWAB).

This species is well distinguished by its very slender form and the great length of its spores and sporophores. In one or two of the tufts it seems possible to distinguish the body of the spores, from the middle segments of which they seem to have arisen, lying flat against the substratum.

Muiara Lonchaeana, nov. sp.—Plate XVII, figs. 10–11

Scaly-punctate throughout, or almost hirsute. Sterile and fertile elements relatively rather short and stout, densely crowded; the sterile elements numerous. Basal cell of the spore usually rather abruptly distinguished from the sporophore, which is often shorter than the spore itself; the body of which is irregular, its basal and distal cells variably inflated and constricted at the septa, rarely divided longitudinally. Spores $100–140 \times 15–18\ \mu$, the stalk $35–70 \times 8\ \mu$.

On the abdomen, legs, and antennae of *Lonchaea* sp., no. 2298, Kamerun, West Africa (SCHWAB).

This species is characterized by its dense habit of growth, dark color, conspicuously and coarsely scaly-punctate spores, which are more irregular in outline than those of the other species, and are borne on relatively short stalks. The sterile elements are more than usually numerous and are roughened much like the spores. In certain instances small groups have been observed which seem certainly not to have sprung from entire spores, but rather from small fragments. Two specimens of the host were found to be parasitized.

Muiaria armata, nov. sp.—Plate XVI, figs. 4–5

Forming a compact tuft with narrow base. The stalk and spore-termination pale, relatively slender and rather abruptly distinguished from the body of the spore; which is relatively broad, rather rich brown, the four middle tiers clearly distinguished; the cells immediately above and below divided by occasional longitudinal septa; the outline comparatively even, and streaked in a somewhat labyrinthine fashion by darker crustlike areas, which are wholly absent on the stalk and distal portion of the spore; either or both of which may be furnished with a simple, usually somewhat recurved spurlike outgrowth which may, however, be wholly wanting. The sterile elements scanty. Total length of stalk and spore 210—260 μ; average length of spore to tip 120 μ; body of spore 60×18–24 μ, the termination 3.5–4 μ broad. Spur from spore-tip about 20×4 μ, that from the stalk somewhat longer.

On the legs of *Drosophila* sp., no. 2178, Sarawak, Borneo.

This very distinct form was found among material for which I am greatly indebted to the kindness of Mr. J. C. MOULTON, and has been seen on a single specimen only of its host. It is clearly distinguished by the relatively broad and evenly curved outline of the body of its spores, their characteristic markings, relatively slender termination, and by the peculiar spurlike processes, which may arise from the latter, as well as distally from the sporophore, or may be wholly absent.

Muiaria repens, nov. sp.—Plate XVII, figs. 6–9

Repent on the wings or growing in tufts on other parts of the host; brown, concolorous. Repent form producing rather closely septate, somewhat tortuous hyphae, tending to run in straight lines, sparingly branched, bearing solitary spores here and there, or small groups of spores along the anterior wing margins or along the larger veins. The spores in both types rather short and stout; the two middle tiers not transversely divided; the cells above and below them similar, or hardly distinguishable, and showing several longitudinal septa; the stalks somewhat shorter than the spore, as a rule, and usually bearing a subterminal spurlike process. Sterile elements not distinguished. Spores 60–70×15 μ, those on the wings somewhat smaller. Total length including stalk 70–100 μ.

On the wings and abdomen of *Clasiopa* sp., no. 2283, Kamerun, West Africa (SCHWAB).

This species is unlike those previously described from the fact that the four tiers of small cells, usually present in the middle of the spore body, are replaced by two tiers of relatively larger cells, which are often so similar to the cells immediately above and below, that they are hardly differentiated from them. This appears to be due to the fact that the two median flattened cells from which these tiers are formed do not divide transversely, as in the other species, before the longitudinal septa appear. In one group, a portion of which is represented in fig. 8, the spores have begun to germinate *in situ*, and it is noticeable that the rhizoid-like germ tubes all arise from cells of the middle region. Although other species have been found growing on the wings of flies, it is only in the present instance that a creeping series of hyphae is produced, in place of the usual compact tuft. This repent habit seems therefore to be specific. The species seems to be distinctly limited to a single host, of which perhaps two dozen have been found infested, and here it may be remarked that the species of *Stigmatomyces*, which inhabits the same insect, was found to occur much more rarely. It is thus evident that, however unsuited such a form as the present may seem to its parasitic habit, it is actually quite as successful as the *Stigmatomyces*, which is so peculiarly adjusted to this mode of life.

Two other forms very closely allied and perhaps identical with this species, but less definitely repent and differing in minor points, have been examined on species of *Clasiopa* from Sarawak and from Trinidad; but sufficient material is not available for a definite determination in either case.

Chantransiopsis, nov. gen.

Entomophilous. Filaments firm, elastic, persistent, thick-walled, colorless, septate, growing in variably developed tufts attached to the body of the host by an opaque black base, or foot; variably branched; the terminal branches sterile or fertile, and bearing solitary terminal simple spores successively abjointed.

This type was first found growing on living specimens of the staphylinid beetle *Xantholinus* near Fresh Pond, in Cambridge, where scanty material, largely sterile, was obtained in the autumn of 1900 and 1902. Later, among a number of Javan beetles sent in alcohol by the late F. ROUYER, two more genera of staphylinids were found to be similarly infested, as well as a third species belonging to the Hydrophilidae. Although it has been sought for on thousands of other insects belonging to these families which have been examined, this type has not again been seen, and must thus be assumed to be very rare or local. Having in mind their possible floridean derivation, it was at first thought that this type might prove to be connected with some genus of the Laboulbeniales, and to represent a form corresponding in some manner to the monospore-producing *Chantransia*-forms among the Rhodophyceae, the general habit of the plant and its spores suggesting a resemblance of this nature. There seems to be not the most remote possibility, however, that such is actually the case. These plants are not associated with any forms of Laboulbeniales which might by any chance form part of their life cycle, and they have no inherent characteristics, except their similar habitat, which would point to such a connection.

The spores are, as a rule, rather sparingly produced, and at maturity the outer wall appears to be somewhat viscous or gelatinous, so that they may perhaps more readily adhere after being abjointed. In many instances, as is indicated in figs. 19 and 21, a collar is present below the developing spore, which seems to indicate that the usually somewhat smaller terminal cell of the fertile branch is proliferous, and continues to abjoint spores after the first has been separated. In this process the terminal cell enlarges, pushing upward, and soon divides by a partition coincident with the plane of separation of the first spore, which is indicated by a slight ridge or collar. The upper of these two cells becomes the new spore, and after it has been separated, the lower, renewing its activity, produces a third spore in a similar fashion, and so on.

The filaments are quite colorless and appear white on the living host. They may be simple, or several times branched, varying considerably in this respect. In one Javan species, not herein included, since it is sterile, a copious development of mostly unilateral branchlets takes place; some of the longer branchlets being elongate and attenuated, as well as spirally coiled at the tips. The filaments are also apt to be beset by masses of bacteria, and in some cases by attached infusoria. The spores usually contain one or more large fatty masses, and the contents of the cells are rather coarsely granular-reticulate. The deep black foot is usually small and clearly distinguished. In *C. stipatus*, however, it forms a more extensive black crust, a portion of which, only, is shown in fig. 17, from which the crowded filaments arise in a mass. Three species are here distinguished, and there are one or two other Javan forms in the material at hand, which may prove to be distinct, and another from the Philippines.

Chantransiopsis decumbens, nov. sp.—Plate XVIII, figs. 19–21

Filaments divergent or decumbent, flexed or reflexed, colorless, rather scanty, long and slender, simple or once to several times branched, rather closely septate below the terminal sterile branchlets; which are more remotely septate and taper slightly to their blunt tips, which are very rarely more attenuated and slightly spiral. Spores long-elliptical or subpiriform, 30–35×9–11 μ. Total length of branches about 230 μ, the longest 350 μ, with an average diameter of about 6 μ.

On the inferior surface of an undetermined staphylinid beetle, Malang, Java (ROUYER).

This species differs from the others which have been examined by its more or less decumbent habit, some of the filaments lying in contact with the surface of the host. Its large spores are somewhat broader than those of the following species, from which it also differs in its small foot and spreading flexed and stouter filaments. The spores seem to be more frequently produced than in the other species.

Chantransiopsis stipatus, nov. sp.—Plate XVIII, figs 17–18

Filaments densely crowded; erect, straight, or but slightly flexed, rigid, hardly tapering, closely septate, usually once branched near the base; arising from a spreading opaque blackened insertion. Spores elongate, distally rounded, nearly isodiametric, or slightly broader in the middle, 25–32×8 μ. Filaments about 110×5 μ.

On the inferior surface of a staphylinid beetle allied to *Tachinus*, no. 1401, Java (ROYER).

This species differs from the preceding in its densely crowded, erect, nearly straight filaments, which seldom branch, except close to the base, and in its somewhat smaller, narrower spores. Its insertion is an opaque black crustlike structure, from which large numbers of filaments arise in a dense tuft. Only a portion of this crust is shown in the figure.

Chantransiopsis Xantholini, nov. sp.—Plate XVIII, figs. 14–16

Filaments somewhat densely tufted, sometimes rather copiously branched; erect, slightly flexed, arising from a small and well defined opaque black foot. Spores relatively small, ovoid to oblong, 10–18×5–6 μ. Filaments 70–175×5–7 μ.

On the inferior surface of the thorax of *Xantholinus obsidianus*, Fresh Pond, Cambridge.

This species is smaller in all respects than the two preceding forms. The outline of the successive cells tends to become slightly convex, and the spores are rather short and stout. The species has been collected but twice, in October 1900, and again in 1902 in the same locality; but although it has been repeatedly sought for elsewhere, it has not again been met with, and may be regarded as very rare.

A small tuft of a different species has also been observed on a species of *Xantholinus* from the Philippine Islands, but the specimen is not sufficient for description.

Amphoromorpha, nov. gen.

Entomophilous; consisting of two superposed cells surrounded by a firm common envelope, which becomes perforate at the apex for the escape of numerous naked amoeboid(?) spores into which the upper cell becomes completely divided; the base attached to the host by a well developed blackened foot.

The position of this genus is quite uncertain. It is known only in its fully mature condition, the characteristics of which seem to correspond more closely to those of some of the Mycochytridineae than of any other organisms. The spores, into which the upper of the two cells appears to divide *in toto*, seem to possess no walls, and their irregular outline suggests that they may be amoeboid in character. No appearance has been seen which would suggest the presence of cilia. The lower cell is surrounded by a very thin membrane which, in a few specimens, is made visible through the shrinkage of the protoplasm; but no indication of this division can be seen in the general envelope, which is continuous from base to summit like that of the Laboulbeniales.

All the individuals examined are, as has been mentioned, quite mature, and the distal region is filled in every case with closely packed spores, except in the individual represented in fig. 28, from which the contents has for the most part escaped through a rupture at the base. It is therefore not possible to determine what the course of development is; whether, after the discharge has taken place the basal cell enlarges so as to fill the cavity, and again cuts off a terminal cell which divides as before, or whether there is but one such period of sporulation in the history of an individual. It is evident, however, from a comparison of different individuals, that the relative space occupied by the spore-mass and by the basal cell varies greatly, and it is not impossible that the original spore-mass may be pushed slowly out by pressure from the enlarging basal cell which, after it has filled the whole cavity, cuts off an upper portion which divides into spores that are again pushed out by the further growth of the cell below. Such a process would correspond very closely to that described, for example, in *Cladochytrium Alismatis* by CLINTON, in which, however, the successive sporangia empty completely through the swarming of the zoospores at the moment of maturity. Unless the spores of the present type are actively amoeboid, some mechanical means for emptying the sporangium, like that above suggested, seems necessary, since there is no indication that the spores are furnished with cilia.

In addition to the organism herewith described, several others have been noticed that appear to be similar in their general characters. One of these is clavate in shape, much smaller than the present form, and is found occasionally on Carabidae or on Laboulbeniae growing on these hosts in New England, but of this no material is at the moment available. A second type occurs commonly on a variety of insects and rarely on Laboulbeniae infesting them, and is represented in figs. 30–31. That these organisms belong to the same category seems very probable; but since their development has not as yet been satisfactorily followed out, these figures are given merely to call attention to their existence. They usually grow on the bristles, antennae, or legs of their hosts, and closely resemble germinating spores of Laboulbeniales, or might be mistaken, when mature, for male individuals of Amorphomyces or Dimeromyces. There is no reason to believe, however, that they have any connection whatever with the Laboulbeniales. The individuals, which always terminate in a more slender necklike portion, consist of a basal cell attached by a black foot, above which two other cells appear to be, as a rule, obliquely related. Of these the upper appears either to abjoint or become divided into small spermatium-like bodies, which pass out through a terminal pore. Until their development has been more carefully examined, however, it has seemed best not to give names to such species as are in the possession of the writer. Of the forms illustrated, fig. 31 occurs on *Labia minor*, the others on Staphylinidae.

Amphoromorpha entomophila, nov. sp.—Plate XIX, figs. 26, 27

Pale yellowish brown, translucent, amphora-shaped, the body long elliptical or tapering below to the narrow base, abruptly contracted distally below the well defined subcylindrical terminal neck, the apex of which is slightly compressed and truncate; the foot relatively large, pointed below, somewhat spreading, black. Total length 110–130 μ, the body 70–105×28–31 μ, the neck 14–17×7.5–8 μ; spores about 4 μ; foot 35×17 μ.

On the bristles of *Diochus conicollis* Motsch., and species of two other genera of Staphylinidae; also on a species of (?) *Labia*, Manila, Philippines.

The hosts bearing this curious plant were found among a number of miscellaneous insects which Mr. C. S. BANKS of the Bureau of Science was so kind as to have collected for the writer. The individuals are solitary, and occur in small numbers projecting at an acute angle from the bristles of the legs, or of other portions of the body. Being much larger than many Laboulbeniales, they are readily seen, but no other insects have been found which bear them, with the exception of a small bug, also from the Philippines, on two specimens of which a closely allied or perhaps identical form (fig. 29) was obtained, but not in sufficient numbers for description. It differs in its smaller size and broader blunt discharge tube.

HARVARD UNIVERSITY

EXPLANATION OF PLATES XVI–XIX

The figures are reduced from camera drawings made with Zeiss dry objectives and eye-pieces and the Leitz water immersion as indicated.

Muiogone Chromopteri Thaxter

FIG. 1.—Abdomen of host showing a pustule of the fungus growing on the under surface; A4.

FIG. 2.—Two detached spores with broken stalks; D12.

FIG. 3.—Tip of a spore greatly magnified, some of the spines distally perforate; water im. 12.

Muiaria armata Thaxter

FIG. 4.—A tuft of the fungus growing on the host's leg; D4.

FIG. 5.—Two spores showing the scaly modification of the surface; D4.

Muiaria repens Thaxter

FIG. 6.—General habit of repent form on the hosts wing; A4.

FIG. 7.—Small portion of the same enlarged.

FIG. 8.—Portion of a tuft growing on the abdomen in which the spores are germinating; D4.

FIG. 9.—Surface view of single spore with basal spur and below it the ring indicating proliferation; D4.

Muiaria Lonchaeana Thaxter

FIG. 10.—Tuft of the fungus from abdomen of host showing scurfy character of the surface and rhizoidal outgrowth from base; D4.

FIG. 11.—Single spore in optical section; D4.

Muiaria gracilis Thaxter

FIG. 12.—Tuft of the fungus growing on leg of host; D2.

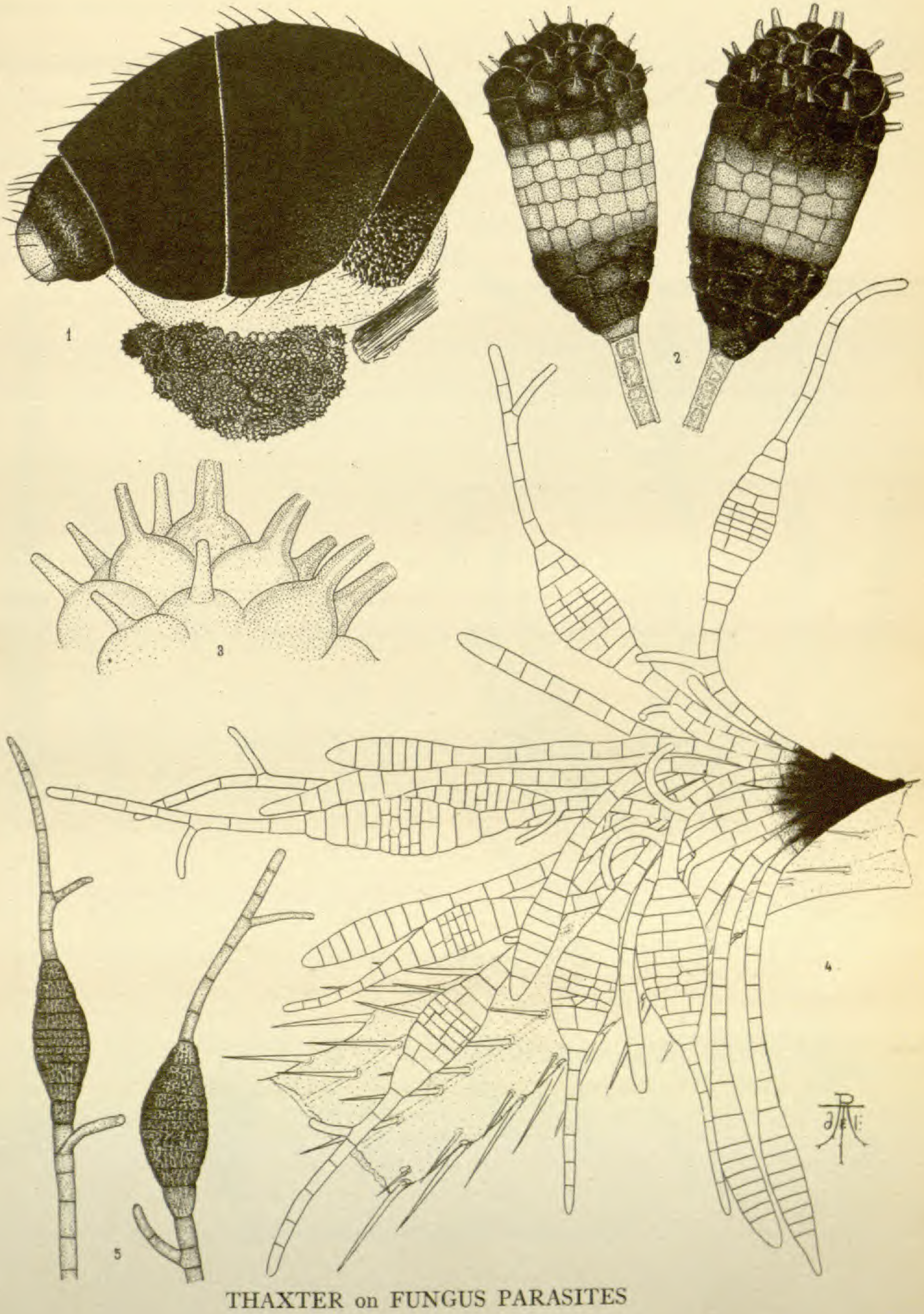
FIG. 13.—Single spore showing character of surface; D4.

Chantransiopsis Xantholini Thaxter

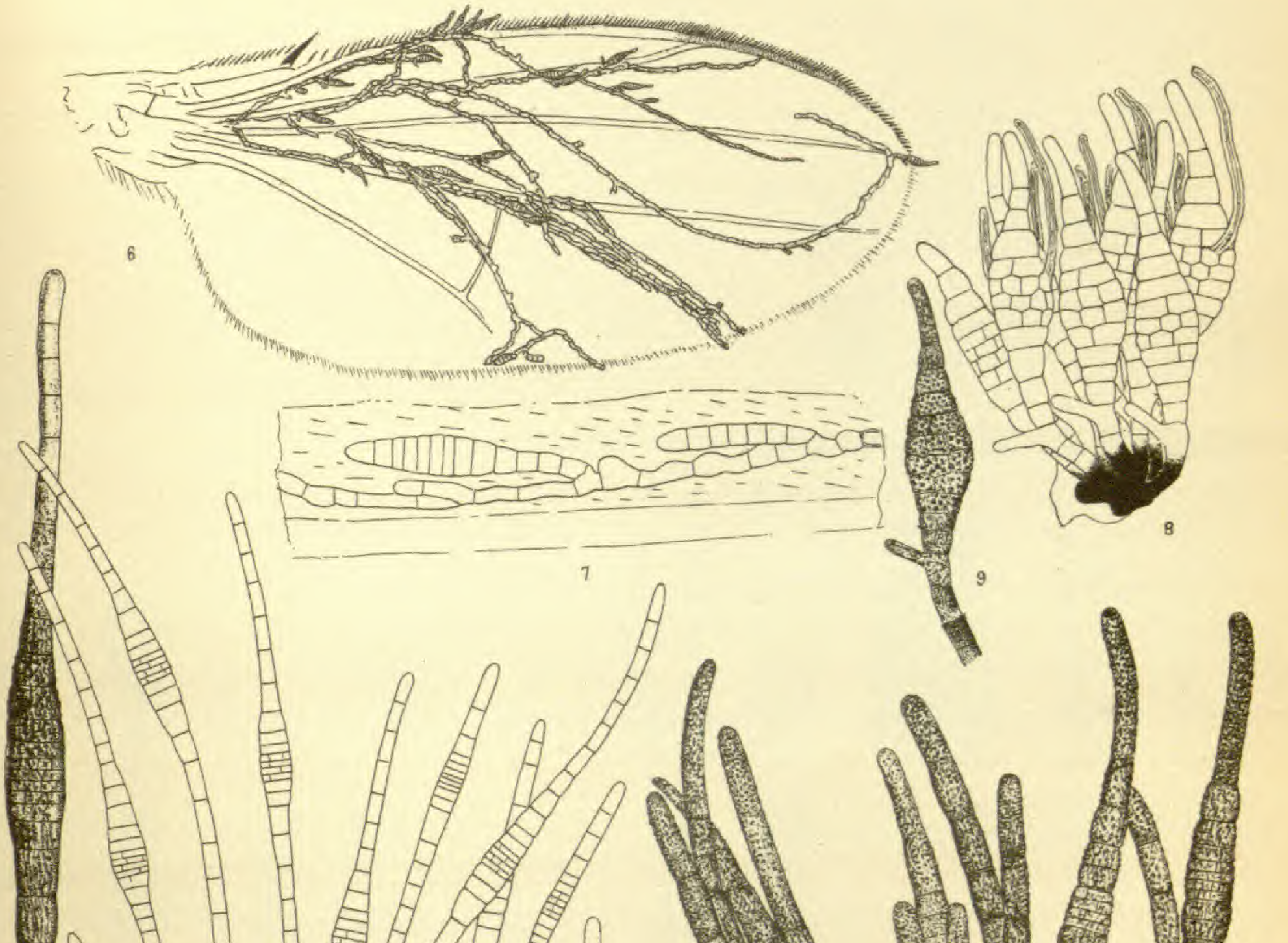
FIG. 14.—Rather large tuft with numerous spores; D4.

FIG. 15.—Tips of two sporiferous branchlets; water im. 4.

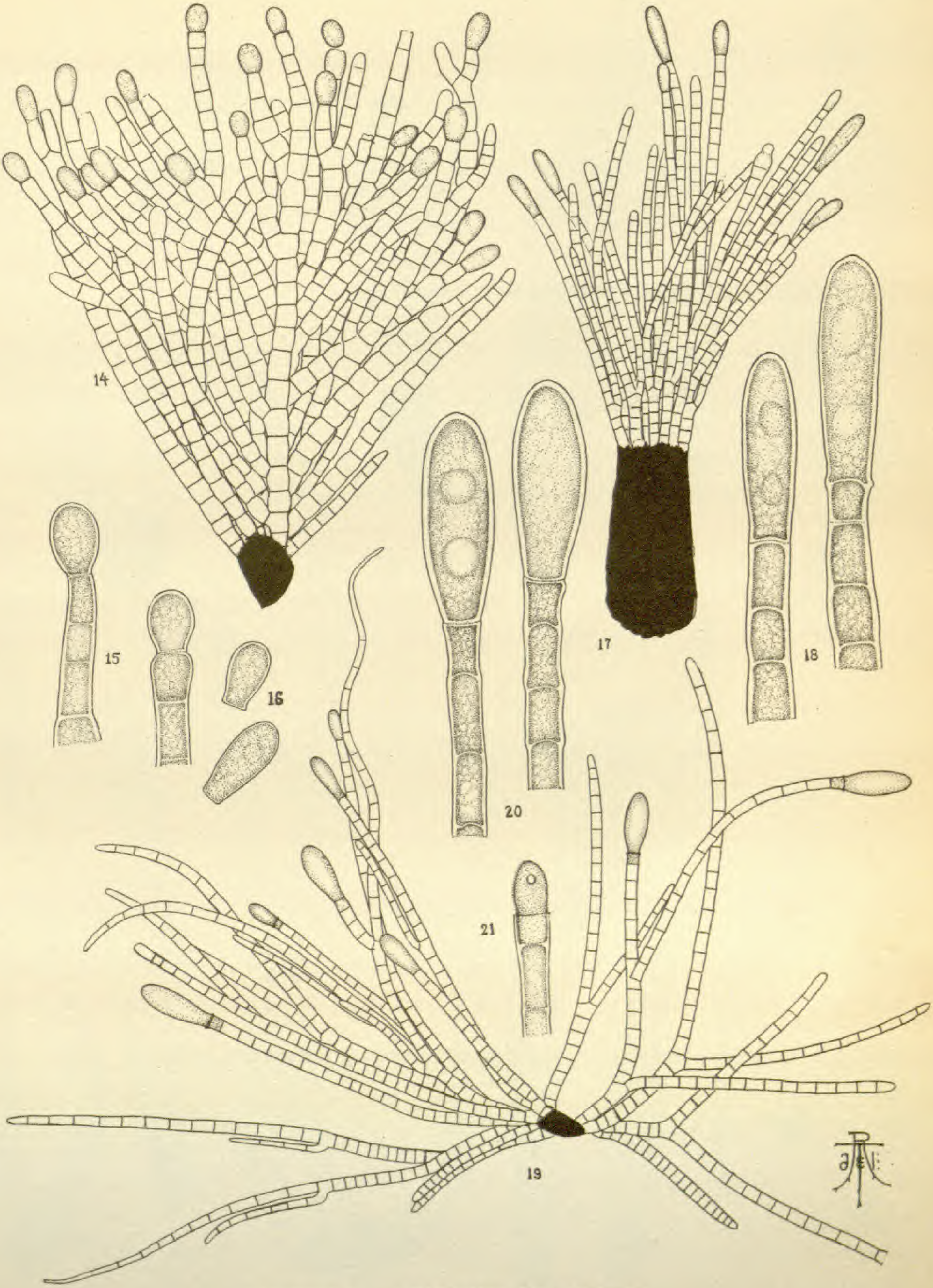
FIG. 16.—Two spores; water im. 4.



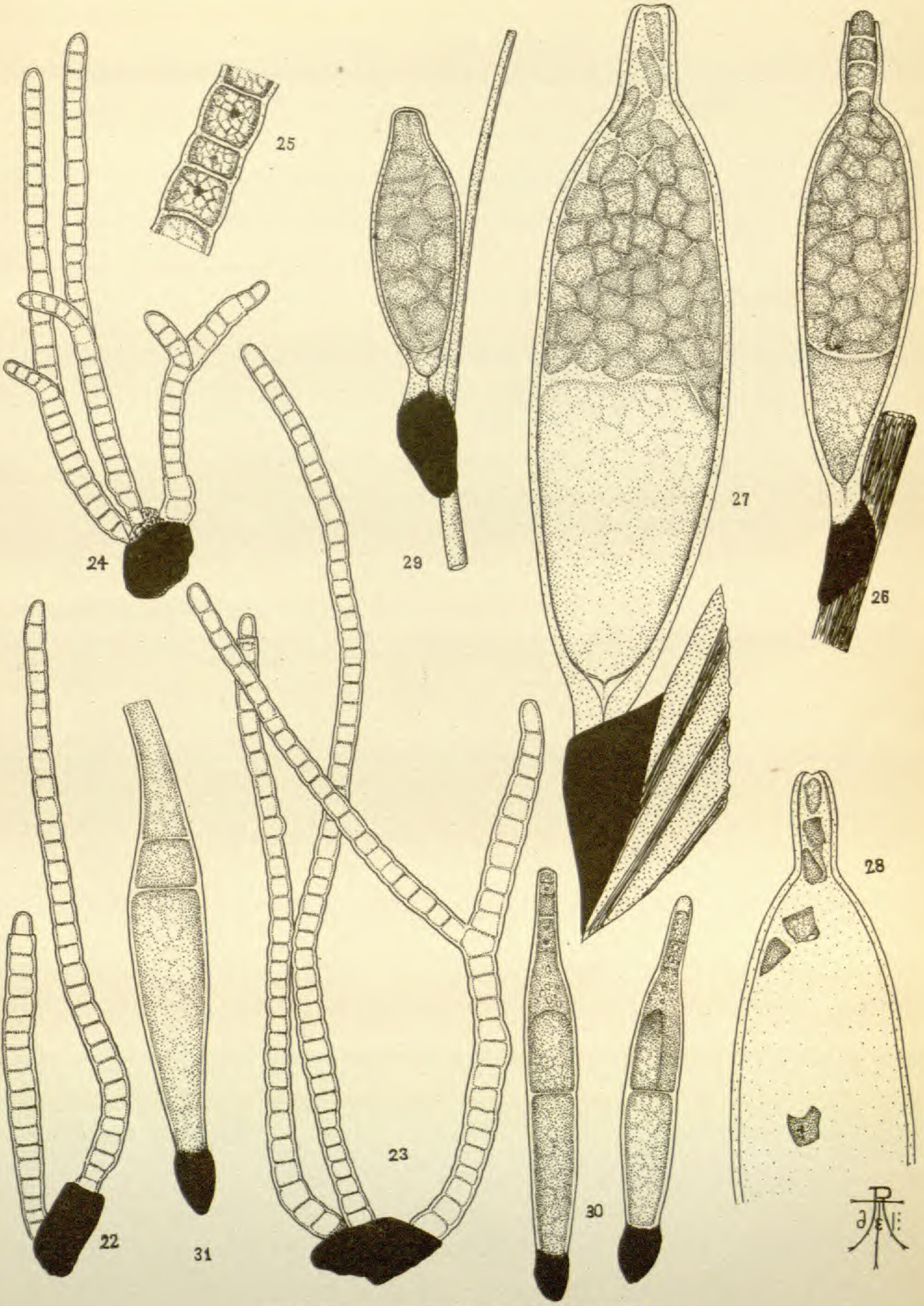
THAXTER on FUNGUS PARASITES



THAXTER on FUNGUS PARASITES



THAXTER on FUNGUS PARASITES



THAXTER on FUNGUS PARASITES

Chantransiopsis stipatus Thaxter

FIG. 17.—Portion of a much larger tuft, arising from an extensive blackened base; D2.

FIG. 18.—Tips of two sporiferous branchlets; water im. 4.

Chantransiopsis decumbens Thaxter

FIG. 19.—A whole plant showing characteristic habit; D2.

FIG. 20.—Tips of two sporiferous branchlets; water im. 4.

FIG. 21.—Tip of sporiferous branchlet showing secondary spore-formation by proliferation; water im. 4.

Hormiscium myrmecophilum Thaxter

FIGS. 22–24.—Characteristic habits of entire plants; D4.

FIG. 25.—Small portion of a filament enlarged; water im. 4.

Amphoromorpha entomophila Thaxter

FIGS. 26–27.—Two individuals *in situ;* water im. 4.

FIG. 28.—Upper portion of broken individual with isolated spores; water im. 4.

Amphoromorpha sp.

FIG. 29.—Individual from small Philippine bug; water im. 4.

FIG. 30.—A related organism from staphylinid beetles; water im. 4.

FIG. 31.—A species similar to the last from *Labia minor;* water im. 4.

THERMOTROPISM OF ROOTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 192

SOPHIA ECKERSON

(WITH SIX FIGURES)

I. The thermotropic curvatures of certain roots at temperatures from 10° to 40° C.

II. The changes in permeability of these roots caused by change in temperature from 10° to 40° C.

Introduction

Our knowledge of thermotropism is in a somewhat confused state. We know little about the thermotropic response of stems. A few scattered observations have been made, indicating that stem tips turn toward the source of heat at low temperatures and away from it at high temperatures. More exact investigations have been made of the thermotropic curvatures of roots, but here there seems to be no uniformity of behavior. Under the influence of unequal temperature on two sides, the roots of different species react differently. Some roots give positive curvatures at low temperatures and negative at high temperatures; others show only positive curvatures, and still others give only negative curvatures. It was with the purpose of clearing up these apparent discrepancies and the hope of finding the physical mechanism of the curvatures that the present investigation was undertaken.

Thermotropic curvatures of roots

LITERATURE

The two important papers on thermotropism of roots are WORTMANN'S (10) and KLERCKER'S (2). WORTMANN investigated four species: *Ervum lens, Pisum sativum, Zea Mays,* and *Phaseolus multiflorus.* He concluded that roots have positive thermotropism at low temperatures and negative at high temperatures, that is, above 35° or 40° C. The one exception he found was *Phaseolus multiflorus*, which gave negative curvatures from 22° to 50° C., but no curvature below 22°. The secondary roots of *P. multiflorus* reacted positively at low and negatively at high temperatures. WORTMANN thought, therefore, that the primary roots must have a positive thermotropism, although he was not able to demonstrate it.

AF KLERCKER studied *Pisum sativum*, *Helianthus annuus*, *Faba vulgaris*, and *Sinapis alba*. In the first three species he observed only negative thermotropism; while *Sinapis alba* gave positive curvatures from 14° to 29° C., and no curvatures at the higher temperatures. PORODKO (7) studied the thermotropic curvatures of roots at temperatures from 40° to 70° C. He obtained negative curvatures and thought therefore that roots have only negative thermotropism.[1]

INVESTIGATION

Method.—The apparatus used is a modification of GANONG'S differential thermostat.[2] A zinc trough, 20 inches long, having a zinc box attached at each end, was heated at one end by an electric coil and cooled at the other end by a freezing mixture. This gives a fairly even gradation from 58° to 5° C. The electric coil has low, medium, and high adjustment, so that the temperature gradient in the trough can be increased or diminished as desired. Three such thermostats were in use at one time.

The seedlings chosen for this study were *Raphanus sativus* and *Pisum sativum*. The trough was filled with sterilized *Sphagnum* This was found to be the best medium, since in it the roots grow perfectly straight. Seeds were sown in the trough at definitely spaced intervals. When the roots were 1.5–2 cm. long, the thermostat was brought to the desired temperatures and the response

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[1] In work described in a very recent article, HOOKER (HOOKER, HENRY D., Thermotropism in roots, Plant World **17**:135–153. 1914) obtained no reaction in roots set in 1.25 per cent agar. He concluded, therefore, that the curvatures of roots when grown in sawdust, as in the work of WORTMANN and KLERCKER, are due to hydrotropism. The methods of experimentation used are subject to criticism and the conclusions are erroneous.

[2] GANONG, W., Plant physiology, p. 207. 1908.

of the roots observed. In another series of experiments, seedlings grown at 20° C. were put directly into the heated thermostat.

Curvatures.—When seedlings of *Raphanus sativus* have been in the thermostat 2 hours, the roots show the following reactions:

Positive	No curvature	Positive	Negative
7–15° C.	16–23° C.	24–36° C.	38–51° C.

At the higher temperatures the curvature occurs very quickly. Roots grown at 20° C., when put into the thermostat at 45° C., give a positive curvature in 5 minutes. This quickly goes over into a negative curvature, so that within 20 minutes there is a strong negative curvature. The explanation of this double curvature, of course, is that as the temperature of the root rises to 38° C. there is a positive curvature; when the root temperature has reached 45° C., a negative curvature begins. It should be remembered that the side of the root toward the hot end of the thermostat is always at a slightly higher temperature than the opposite side. At the lower temperatures the roots react less rapidly, requiring 1.5–2 hours for complete reaction at 7–15° C.

TABLE I

THERMOTROPIC CURVATURES OF ROOTS

	Positive	No curvature	Positive	Negative
1. Raphanus sativus........	7–15° C.	16–23° C.	24–36° C.	38–51° C.
2. Pisum sativum..........	8–15° C.	17–29° C.	....	34–50° C.
——— (WORTMANN)....	8.5–31° C.	....	....	34–50° C.
3. Sinapis alba (KLERCKER)	14–29° C.	....	....	None
4. Helianthus annuus (KLERCKER)..........	None	....	....	15–40° C.
5. Phaseolus multiflorus primary roots (WORTMANN)...............	None	8–22° C.	....	22–50° C.
6. ———, secondary roots (WORTMANN)........	10–?° C.*	....	....	?–40° C.*

* WORTMANN obtained positive curvatures at 10° C. and negative curvatures at 40° C., but made no investigations at the intermediate temperatures.

The roots of *Pisum sativum* are less sensitive to temperature changes than those of *Raphanus sativus*. After one hour in the thermostat all the roots at temperatures from 34° to 50° C. showed negative curvatures; and in 2.5 hours 80 per cent of those at temperatures from 8° to 15° C. gave positive curvatures. At the temperatures from 17° to 29° C. there were no curvatures even after 9 hours.

Table I gives the thermotropic curvatures of five species, selected to show the various "types" of reaction. Where the data have been obtained by other workers, the name is given in parentheses.

In attempting to locate the mechanism of thermotropic curvatures, one must bear in mind the various possibilities, or "types" of reaction, shown in the table. The rapidity of the reaction indicates that it is not a growth phenomenon. It is known that the permeability of protoplasm increases with increase of temperature. The range of permeability change was not known, nor was it known whether there is such great variation with species as would be necessary to explain the curvatures given in table I. However, permeability changes and consequent turgor changes were considered a possible factor; accordingly the permeability of the roots at temperatures from 10° to 40° C. was determined for the five species.

II. Permeability

EFFECT OF TEMPERATURE ON PERMEABILITY

In 1902 RYSSELBERGHE (8) found that the permeability of the protoplasm of epidermal cells of *Tradescantia discolor* to dissolved substances (glycerine, potassium nitrate, and urea) increases with the temperature from 0° to 30° C. In 1905 LEPESCHKIN (3) found that the volume of liquid extruded by hairs on the leaves of *Phaseolus multiflorus* increases from 0° to 20° C., and decreases from 20° to 35° C. During the extrusion the osmotic pressure of the cell sap decreases, indicating an increased permeability to solutes as well as to water. In 1908 LEPESCHKIN (4, 5, 6) established the fact that pulvinal movements of leaves are due to the effect of light on the permeability of the protoplasm of the pulvinal cells. Light increases the permeability, with consequent decreased turgor pressure (decrease of volume). Darkening decreases the permeability, with consequent increase of turgor pressure (increase of volume). In 1910 TRÖNDLE (9) found that the leaves of *Buxus sempervirens* are more permeable to sodium chloride in light than in darkness;

also with a 32 C.-P. electric lamp as light source, he found an increase of permeability up to a certain light intensity (50 cm. from the lamp), and then a decrease at the higher intensities (35–10 cm. from the lamp).

METHOD

The method for determining permeability is essentially that of LEPESCHKIN (6). This method is based on the fact that the permeability of protoplasm to sucrose does not change under varying conditions, while the permeability to potassium nitrate does change. That is, with increasing permeability, higher concentrations of potassium nitrate are required to produce plasmolysis.

Weight molecular solutions were used throughout; the percentages in any series varied by 0.02 mol. The tests of permeability at the temperatures from 20° to 50° C. were carried on in a constant temperature oven, electrically controlled; those below 20° C., in an ice chest. Of course, all were in darkness. Seeds were germinated on filter paper in large Petri dishes. When the roots were about 1.5 cm. long, they were put in covered watch glasses containing the solutions and left for 20 minutes. Then they were put on a slide in a drop of the solution and observed as quickly as possible.

Repeated examination of sections of roots plasmolyzed at various temperatures showed that the degree of plasmolysis of the root hairs is an exact indication of the degree of plasmolysis of the cortical cells of the root. When the protoplasm is slightly drawn back from the tip of the root hair, the outer two rows of cortical cells are slightly plasmolyzed. When the protoplasm of the younger root hair is beginning to break up into several parts, the walls of all the cortical cells of the corresponding part of the root are slightly shrunken. In complete plasmolysis the protoplasm of the root hairs is rounded up into three or four parts, and the cortical cells are plasmolyzed. The criterion then for slight plasmolysis of the root is that condition of the root hair in which the protoplasm is slightly drawn back from the tip.

DATA

The effect of temperature on permeability is shown in the accompanying figures. The ordinates give the percentage weight-molecular solution which produces slight plasmolysis. The increase or decrease of permeability with change of temperature is shown by the increase or decrease of these concentrations, the plasmolyzing concentration of sucrose remaining constant.

The permeability of roots of *Raphanus sativus* (fig. 1) increases from 10° to 18° C.; does not change from 18° to 24° C.; increases from 24° to 40° C., and then decreases. The turning point in permeability to glucose is at 42° C. The drop in the sucrose curve above 42° C. suggests a decreased osmotic pressure due to exosmosis. To test this, roots were put in distilled water at 45° C.; after 20 minutes the water gave a sugar test with Fehling's solution. Thus at 42° C. there is an increased permeability, in all probability caused by coagulation of the protoplasm.

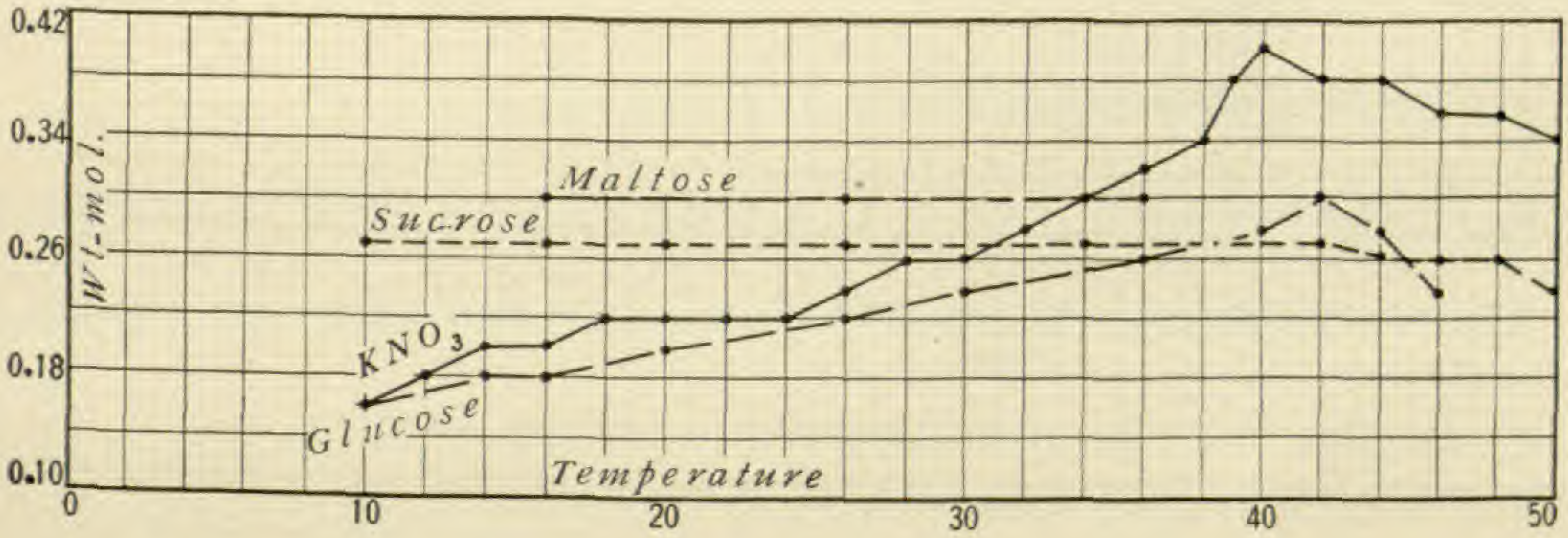

FIG. 1.—*Raphanus sativus:* curves showing the effect of temperature on the permeability of roots to potassium nitrate and glucose; ordinates indicate the percentage wt.-mol. solutions producing slight plasmolysis; dots indicate temperatures at which determinations of plasmolysis were made.

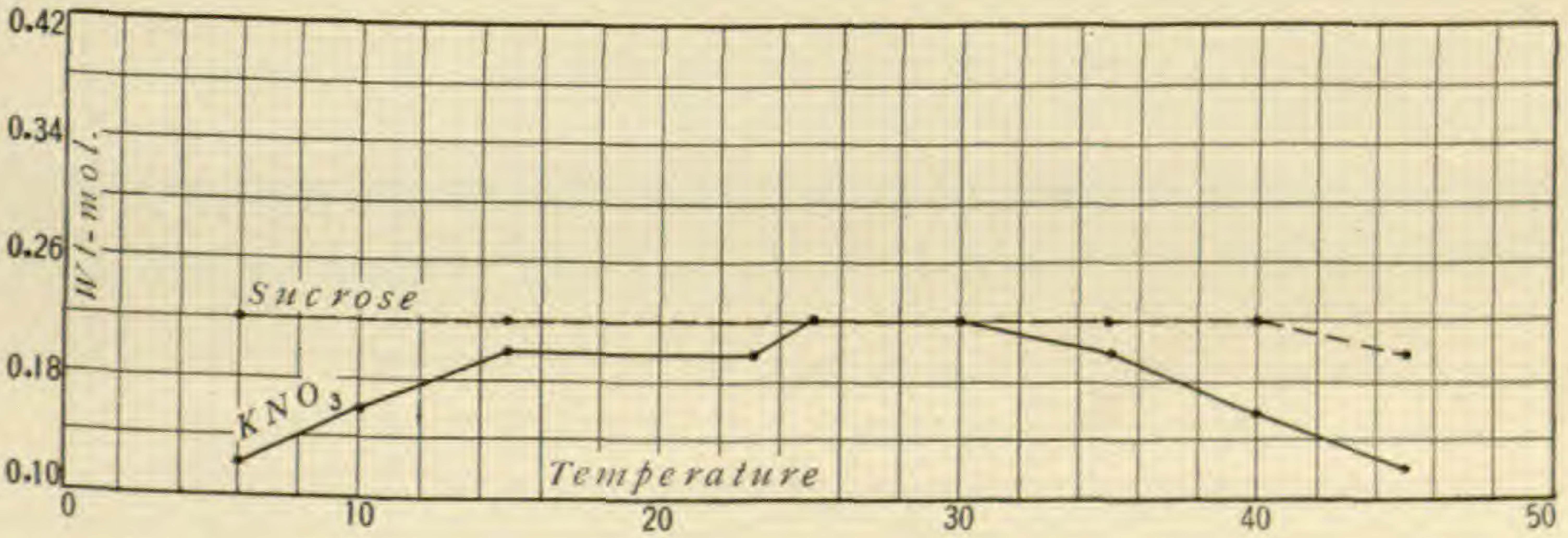

FIG. 2.—*Pisum sativum:* the potassium nitrate and sucrose curves are identical from 25° to 30° C.

The permeability of roots of *Pisum sativum* (fig. 2) to potassium nitrate increases from 6° to 15° C.; does not change from 15° to 23° C.; and decreases from 30° to 40° C. The sucrose curve shows that the osmotic pressure is lower at 45° C. than at 40° C.

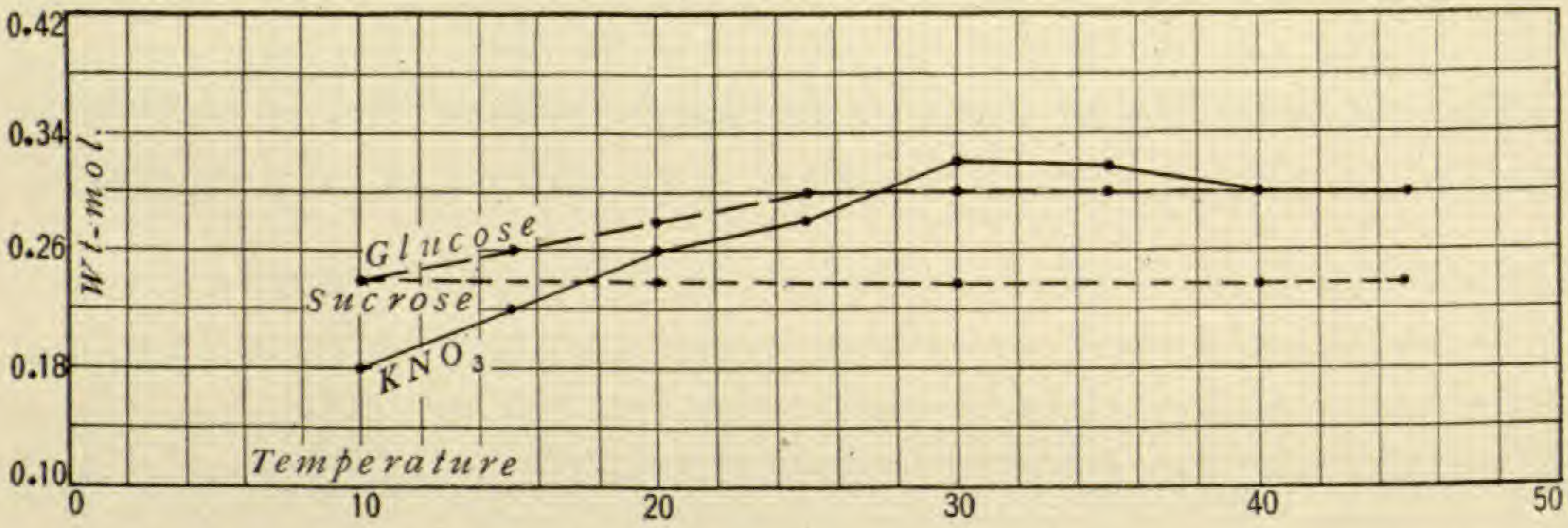

FIG. 3.—*Sinapis alba:* the potassium nitrate and glucose curves are identical from 40° to 45° C.

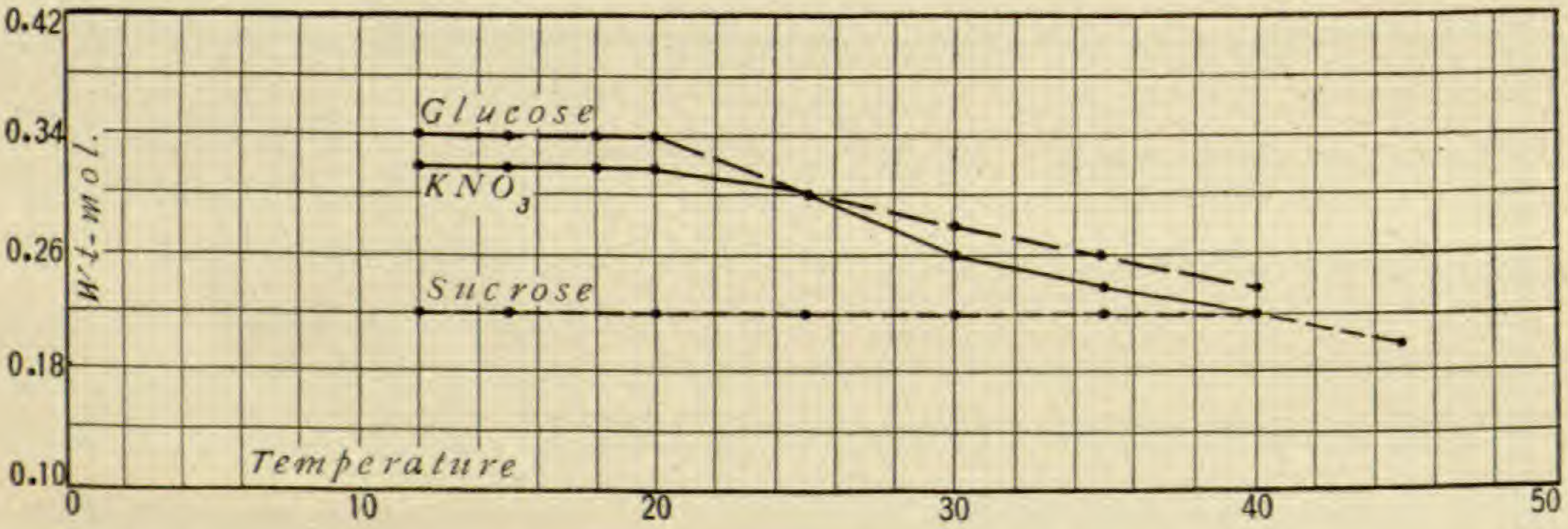

FIG. 4.—*Helianthus annuus:* the potassium nitrate and glucose curves are identical from 40° to 45° C.

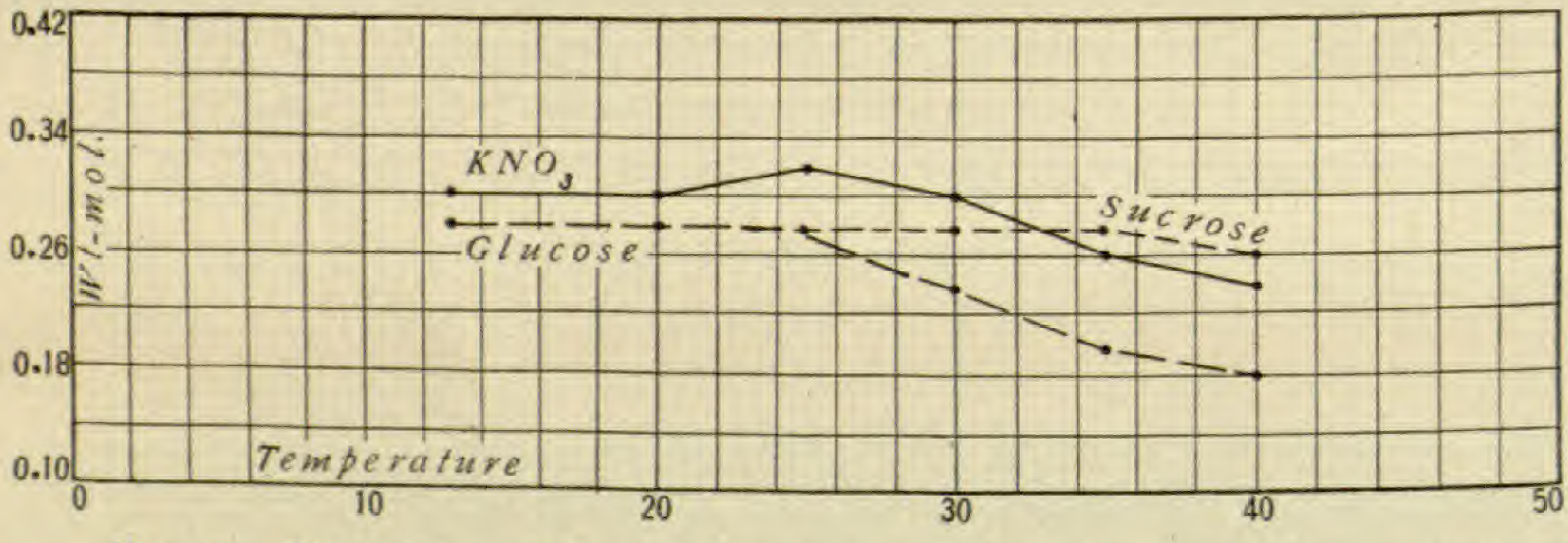

FIG. 5.—*Phaseolus multiflorus:* primary roots; the sucrose and glucose curves are identical from 15° to 25° C.

The permeability of *Sinapis alba* (fig. 3) increases from 10° to 25 or 30° C., then remains practically constant to 45° C.

Helianthus annuus (fig. 4) shows no increase in permeability with increase of temperature, but a decrease from 20° to 40° C.

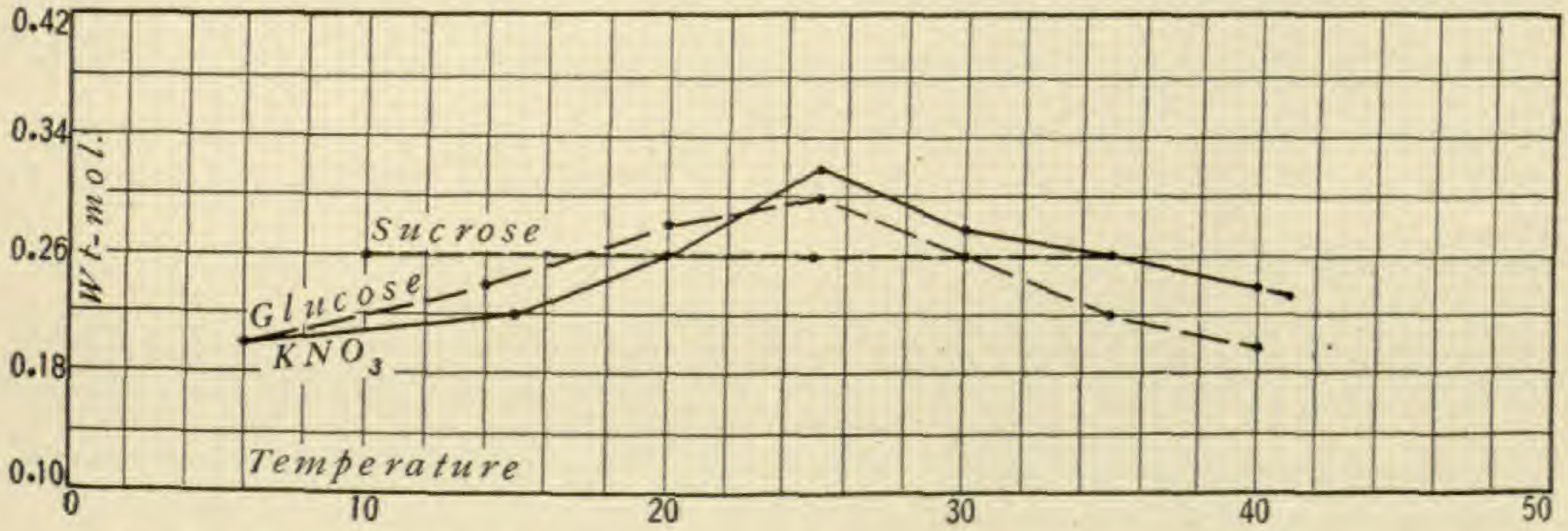

FIG. 6.—*Phaseolus multiflorus:* secondary roots; the potassium nitrate and sucrose curves are identical from 35° to 40° C.

The primary roots of *Phaseolus multiflorus* (fig. 5) show no increase in permeability from 13° to 25° C.; while in the secondary roots (fig. 6) the permeability increases from 6° to 25° C. Both have a decreasing permeability from 25° to 35° C.

COMPARISON OF THERMOTROPIC CURVATURES AND PERMEABILITY CHANGES

To show the relation between thermotropic curvatures and permeability changes, the data given in table I are given in table II

TABLE II

THERMOTROPIC CURVATURES AND PERMEABILITY VARIATIONS OF ROOTS

		+	o	+	−
1. Raphanus sativus. . .	Curvatures	7–15° C.	16–23° C.	24–36° C.	38–51° C.
	Permeability	10–14° C.	18–24° C.	24–40° C.	40–50° C.
2. Pisum sativum.	Curvatures	8–15° C.	17–29° C.	. . . .	34–50° C.
	Permeability	6–15° C.	15–35° C.	. . . .	35–45° C.
3. Sinapis alba.	Curvatures (K)	14–29° C.	. . . .	. . . .	None
	Permeability	10–30° C.	30–45° C.	. . . .	None
4. Helianthus annuus. .	Curvatures (K)	None	. . . .	. . . .	15–40° C.
	Permeability	None	12–20° C.	. . . .	20–40° C.
5. Phaseolus multiflorus (primary roots). . .	Curvatures (W)	None	8–22° C.	. . . .	22–50° C.
	Permeability	None	13–20° C.	. . . .	25–40° C.
6. ——— (secondary roots).	Curvatures (W)	10– ?° C.	. . . .	. . . .	?–40° C.
	Permeability	6–25° C.	. . . .	. . . .	25–40° C.

together with the temperatures at which there is increasing or decreasing permeability, for each species. In the table, + indicates positive curvatures and increasing permeability; o indicates no curvatures and no change in permeability; – indicates negative curvatures and decreasing permeability.

The data show that the permeability increase or decrease parallels almost exactly the positive or negative curvatures. In every case, at those temperatures which cause positive curvatures there is increasing permeability; where there are no curvatures, there is no change in the permeability; and at temperatures causing negative curvatures there is decreasing permeability. The slight differences in temperature at the turning point are well within the range of experimental error.

Conclusions

WORTMANN'S inability to obtain positive thermotropic curvatures in the primary roots of *Phaseolus multiflorus* is explained by the fact that there is no increase in permeability. In the secondary roots, however, where he found positive curvatures, there is an increasing permeability. KLERCKER obtained no negative thermotropic curvatures in *Sinapis alba;* there is no decreasing permeability. Also, KLERCKER obtained only negative curvatures in *Helianthus annuus;* there is no increasing permeability, therefore no positive curvatures.

The permeability of the cells of the root to potassium nitrate and to glucose increases or decreases with increase of temperature according to the species, and for a given species according to the temperature.

With unequal temperature on opposite sides of a root, a curvature is produced only when the cells of the root are more permeable at one of the temperatures than at the other. Those cells which are subjected to a temperature at which they are more permeable to dissolved substances are consequently less turgid. This results in a shrinking of the tissues on that side of the root and a consequent mechanical curvature. Always the more permeable side of the root becomes concave.

Summary

1. Thermotropic curvatures of roots vary with the temperature and with the species.

2. Permeability of the cells of the root to dissolved substances varies with the same factors.

3. In every case the greater permeability is in the concave side of the root; where the thermotropic reaction of the root changes, the permeability also changes.

4. The parallelism between the permeability and thermotropic reaction is exact; turgor change produced by permeability change offers a mechanical explanation of the curvature.

5. Heat does not act as a stimulus, but by affecting permeability as a direct factor producing curvature; hence, thermotropism is not a tropism, but is a turgor movement.

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OOGENESIS IN HORMOSIRA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 193

M. R. GETMAN

(WITH PLATE XX AND SEVEN FIGURES)

The genus *Hormosira* is placed by OLTMANNS (7) under the Fucaceae and classified with *Notheia* in the family Anomalae, characterized by him as a group of small and perhaps reduced forms. The genus is fully described and illustrated by HARVEY (giving DECAISNE as authority) in his *Phycologia Australica* (3). The larger plant he names *H. Banksii* var. *Labillardieri* or *Billardieri* (fig. 1), and the smaller, *H. Banksii* var. *Sieberi* or *obconica* (figs. 2 and 3). HOOKER (quoting ENDLICHER) in the *Handbook of New Zealand flora* (4) describes the same forms, naming the first *H. Billardieri* var. *Labillardieri*, and the second, var. *Sieberi*.

The material used in this study was collected by Dr. C. J. CHAMBERLAIN at Avoca, near Sydney, on the eastern coast of Australia. It occurs in the tide pools and on rocks where it is constantly exposed to the dashing of salt spray.

The plant varies in color from an orange-brown to an olive-green. It has no differentiation into parts, but is merely a chain or "necklace" of swollen vesicles or bladders which bear the conceptacles. HOOKER refers to the plant as a series of internodes (the inflated portions) alternating with smaller narrower parts (the nodes). The development, according to GRUBER (2), is from four apical cells. Branching commonly occurs at the internodes, but it may take place at the nodes. It is usually dichotomous, but cases of trichotomy are common, and even polychotomy has been observed. Each internode, excepting the one at the base, contains a central cavity. In fresh material threads may be seen extending from the base to the top of this cavity. The internode consists of an external mucilaginous layer varying in thickness depending upon the age of the plant and the position of the internode. This epidermis or outer layer BOWER (1) prefers to call limiting tissue. Underneath lies the cortex, and beneath this a thick mass of anastomosing filaments, termed irregular tissue by

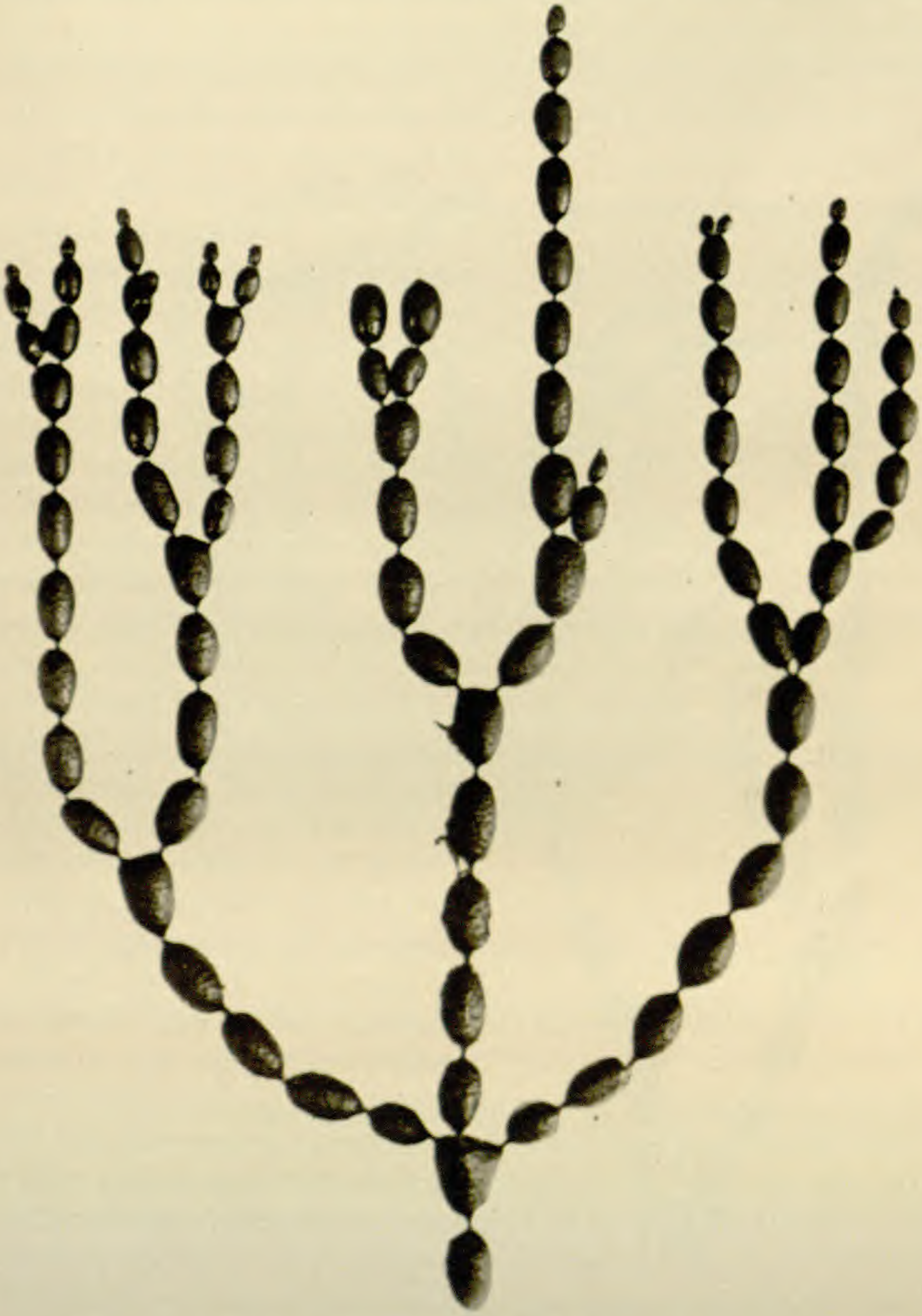

FIG. 1.—*Hormosira Banksii* var. *Labillardieri*

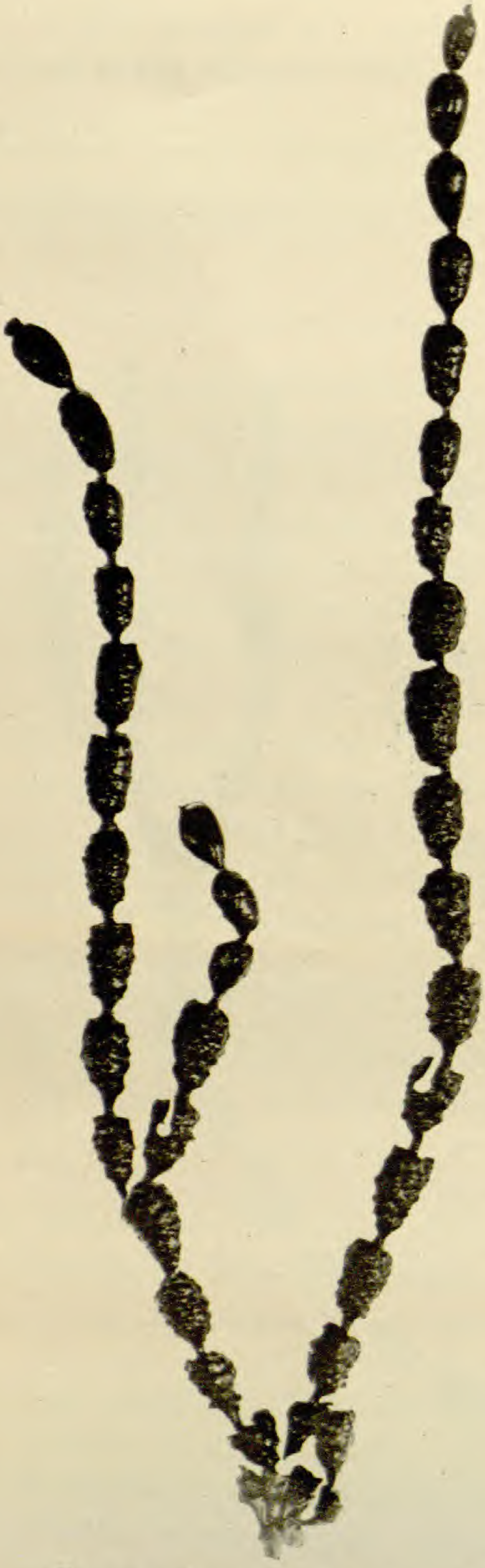

Fig. 2.—*Hormosira Banksii* var. *Sieberi:* mature oogonial plant.

Mollet (**6**). These cells are very gelatinous and are limited below by a layer of parallel cells (fig. 4).

There is no cavity in the node. An epidermis and cortical layer are both present, and its center is made up of parallel cells, which divide into two strands as they pass into the internode below. At the distal end of the node there seems to be a decrease in parallel cells as they merge into the anastomosing filaments (fig. 5).

The plant is dioecious. The antheridial plants are readily recognizable on account of the bright orange color. The conceptacles are flask-shaped, and are sunken in the outer tissues of the internode. From the few observations made of the conceptacle, the development seems to tally with Bower's account (**1**) of its development in the Fucaceae, where the basal cell (*b*) and adjoining cells contribute to the growth of the conceptacle. In the figure, Bower's "initial cell" shows a nucleate stage (fig. 6). A later stage of the conceptacle furnishes characteristic paraphyses (fig. 7), a few of which may persist in the mature oogonial conceptacle, but whose place is taken almost entirely by hairs of a different nature.

It will be recalled that the several genera of the Fucaceae, in their oogenesis, present an interesting illustration of recapitulation. Of the members of this family which have been investigated, all except *Sargassum* show three mitoses in the oogonium, resulting in the formation of eight nuclei. In the genus *Fucus*, all the nuclei are centers for the formation of the eggs. In another genus, *Ascophyllum*, OLTMANNS found four functional eggs. In *Pelvetia* he found that only two eggs mature and that the other six nuclei abort. In *Himanthalia*, OLTMANNS (8) found only one egg, and YAMANOUCHI has observed the same condition in *Cystosira*. In both cases the other seven nuclei degenerate. In *Sargassum filipendulum*, Miss SIMONS (9) finds no mitosis after the formation of the oocyst, and therefore the $2x$ number of chromosomes should

FIG. 3.—*Hormosira Banksii* var. *Sieberi:* young plants

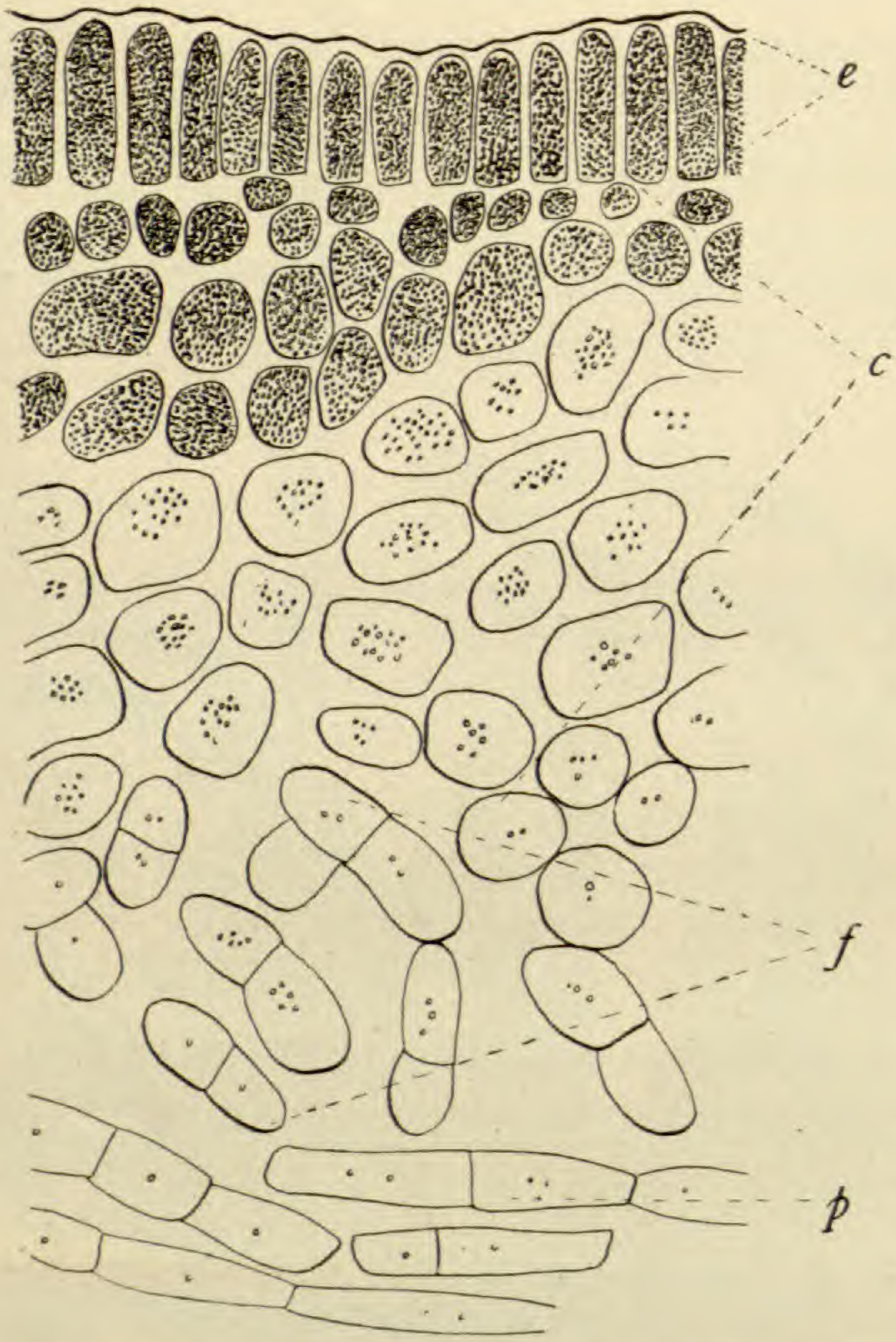

FIG. 4.—Portion of an internode: *e*, limiting tissue or epidermis; *c*, cortex; , anastomosing filaments; *p*, parallel tissue; ×250.

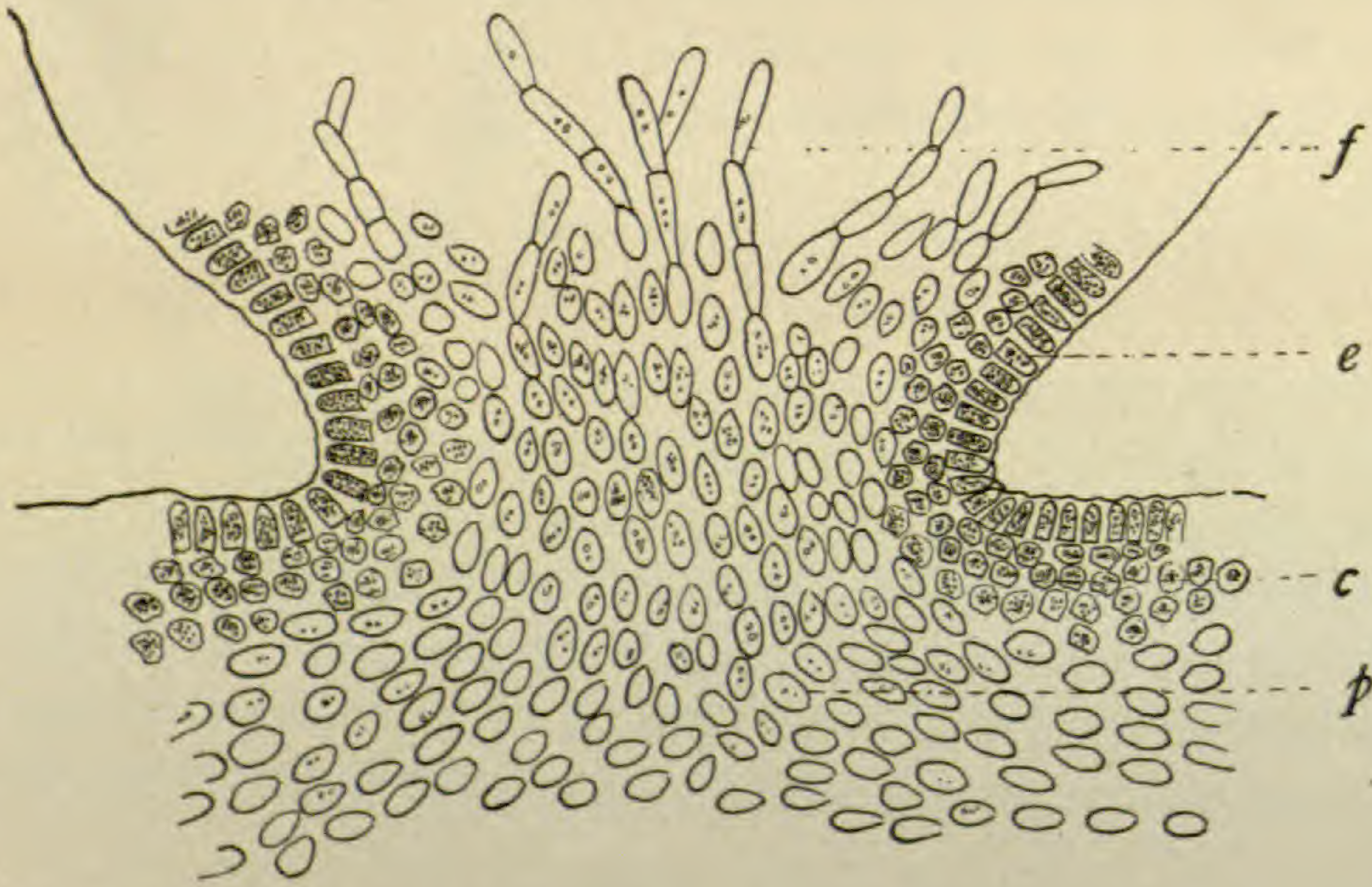

FIG. 5.—Structure of a node: *e*, epidermis; *c*, cortex; *f*, anastomosing filaments; *p*, parallel tissue; ×85.

be present in the egg. Since there has been no reduction division, the three mitoses characteristic of oogenesis in *Fucus* have been suppressed in *Sargassum*. However, out of the large number of conceptacles examined in this form, one oogonium was found which contained two eggs and two oogonia that contained eight; this was regarded as a rare reversion to the *Fucus* type. The above instances in oogenesis form a series beginning with the eight eggs of *Fucus* and ending with the parthenogenetically developed egg of *Sargassum*. Oogenesis in *Fucus* is regarded as the primitive type and the others as reductions from it.

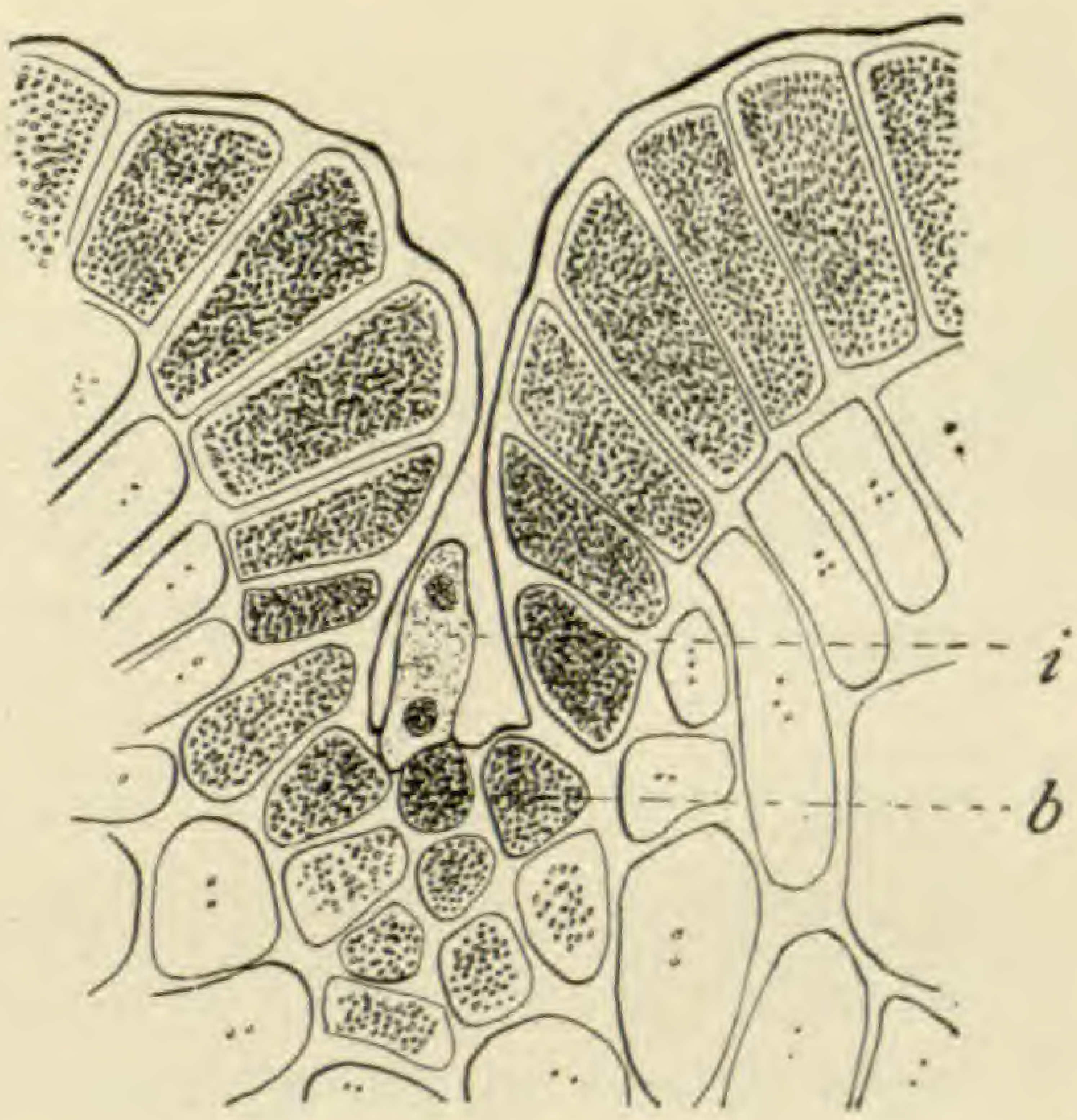

Fig. 6.—Conceptacle: *a*, Bower's "initial"; *b*, "basal" cell; ×480.

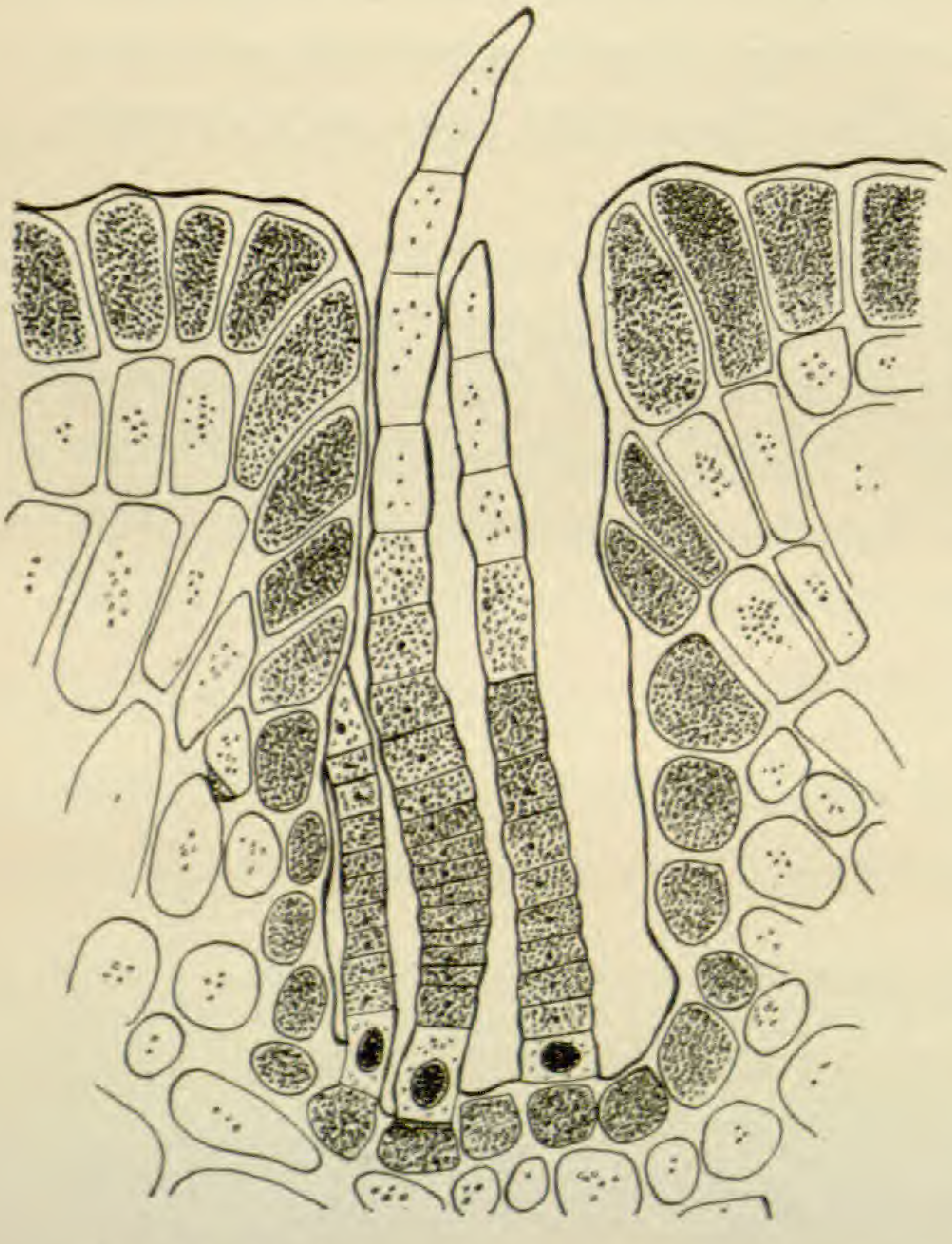

Fig. 7.—Conceptacle: first formed paraphyses; ×410.

Oltmanns, Kutzing, and Gruber have all mentioned the ultimate formation of four eggs in *Hormosira*, but no investigation has been made of the conditions of oogenesis.

The material was fixed in Flemming's weaker solution with the osmic acid a little weaker than the formula requires. As in Oltmanns' account of *Ascophyllum*, simultaneous free nuclear division takes place, resulting in 2-nucleate, 4-nucleate, and 8-nucleate stages (figs.

8–10). Thus far, the conditions seem the same as for *Ascophyllum*. After this the account differs, for the coming in of walls was observed in many cases. For instance, a rather unusual case is the occurrence of seven nuclei, and the division into three parts by two horizontal walls (fig. 11). The coming in of a vertical wall after the formation of a single horizontal one is also found (fig. 12). The most usual situation seems to be a blocking out by walls of the nuclei and the plastids (fig. 13). Here six such characteristic groups can be seen and also a seventh nucleus. Rarely (fig. 14) four eggs are formed and eight nuclei are present. This may be a situation immediately preceding that presented in fig. 15, or the walls shown in fig. 13 may have disintegrated, leaving only the primary walls. No spindles were seen to account for the formation of the walls. They may have been formed by cleavage as does happen among certain of the algae and fungi.

While the details of oogenesis remain to be investigated in several genera of the Fucaceae, it seems certain that the 8-nucleate condition followed by eight functioning eggs is primitive, and that most of the genera which form less than eight eggs pass through this stage.

This study of *Hormosira* shows that not only are eight nuclei formed, but eight eggs begin to develop, so that the final 4-nucleate condition is reached by the breaking down of four immature eggs rather than of four free nuclei. Such a condition is safely interpreted as less removed from the *Fucus* condition than forms in which the 4-nucleate stage is reached by the breaking down of free nuclei.

I am very much indebted to Dr. C. J. CHAMBERLAIN under whose direction the work was done, and to Dr. W. J. G. LAND for the photographs in the text.

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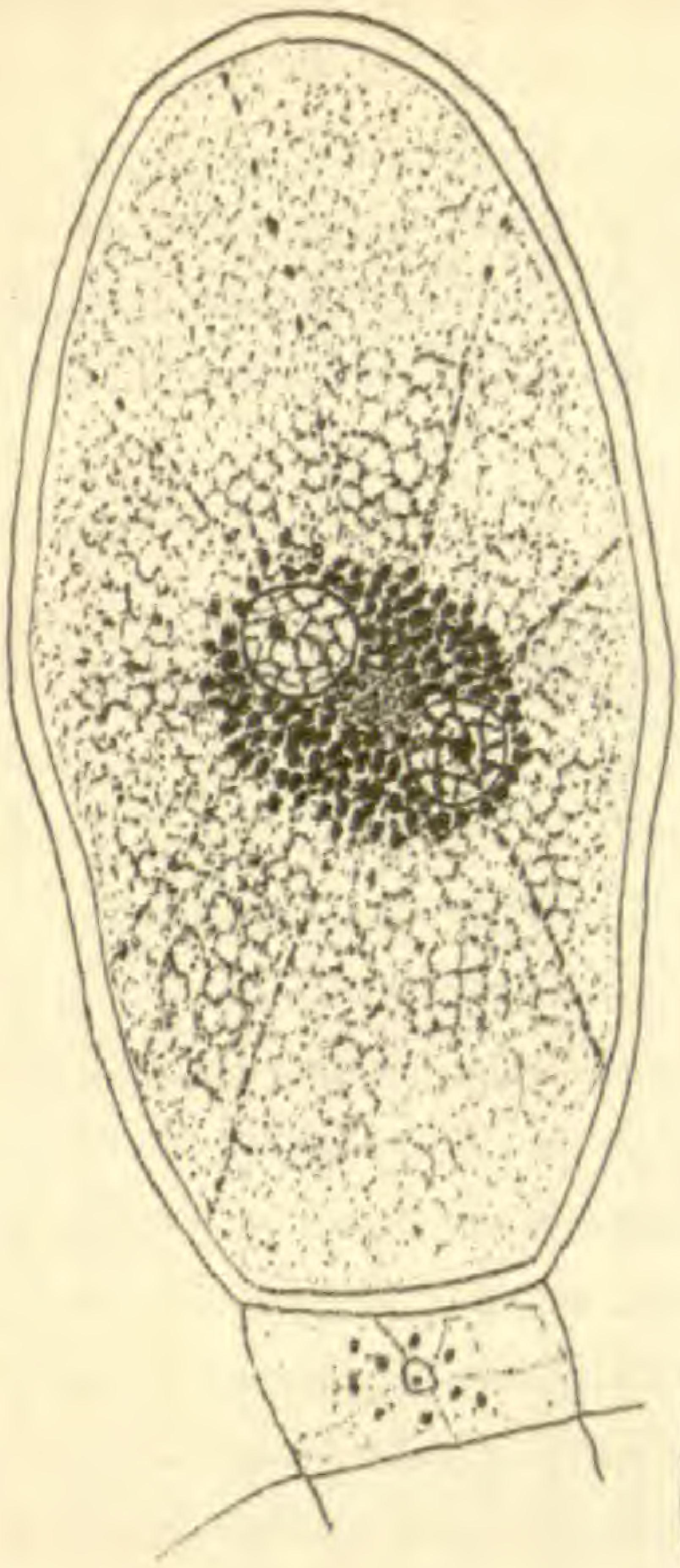

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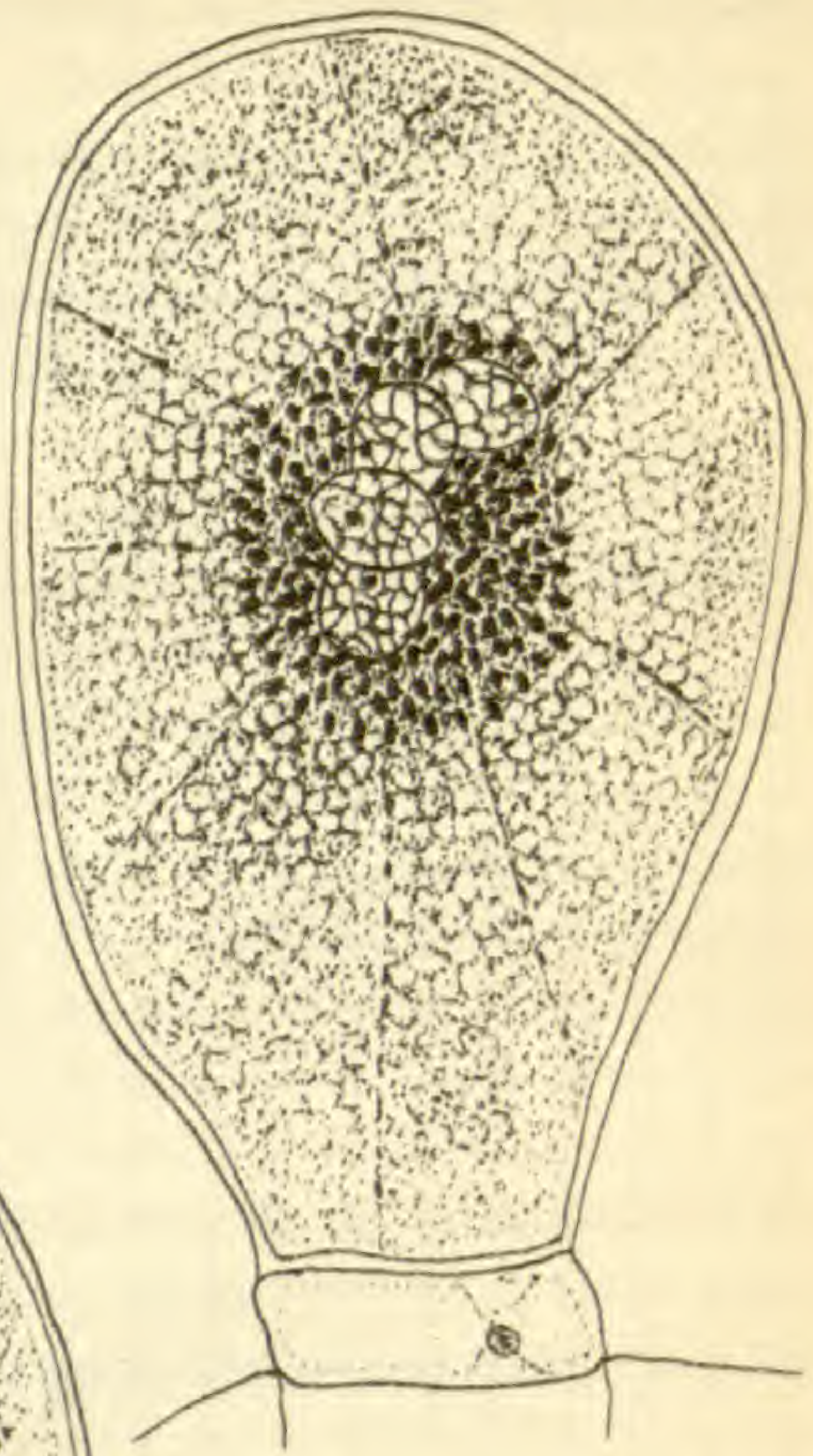

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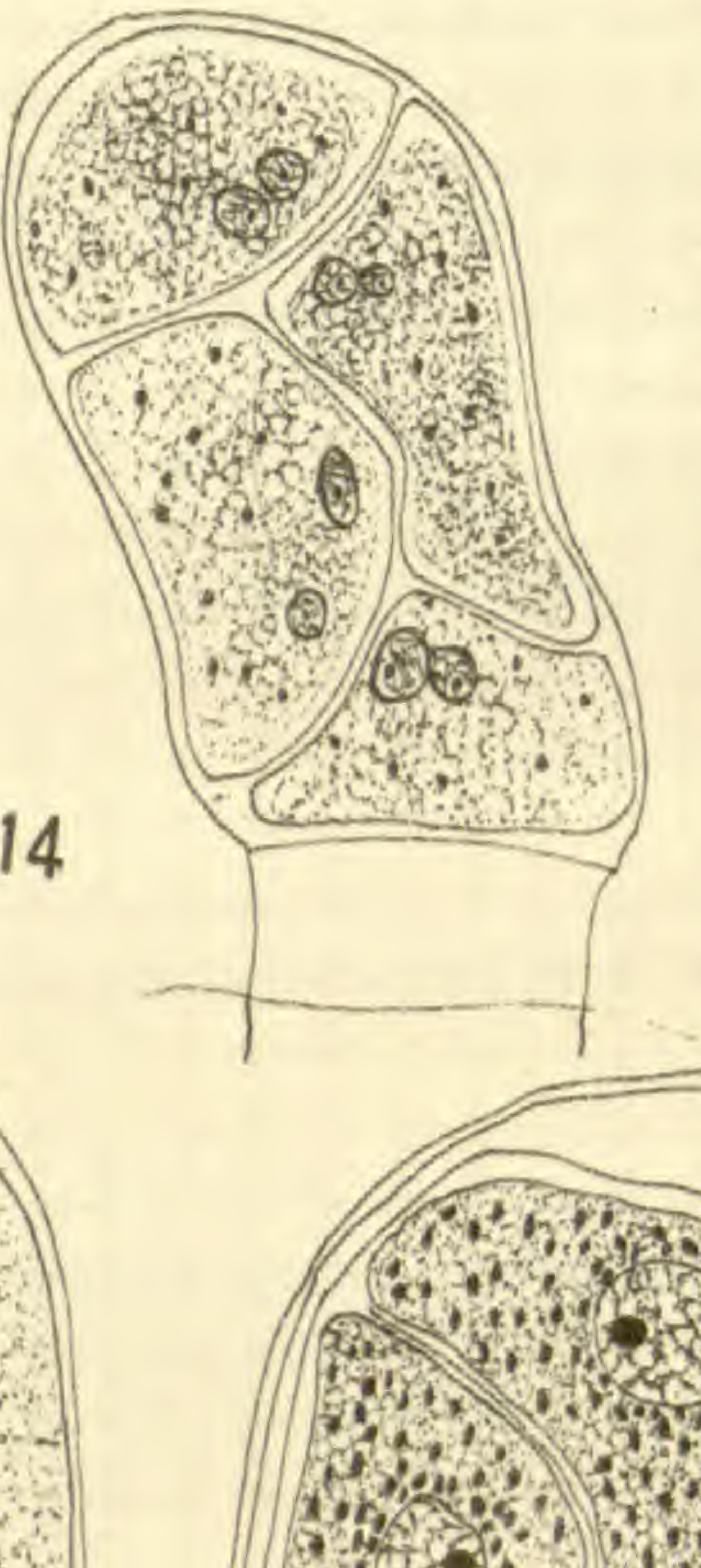

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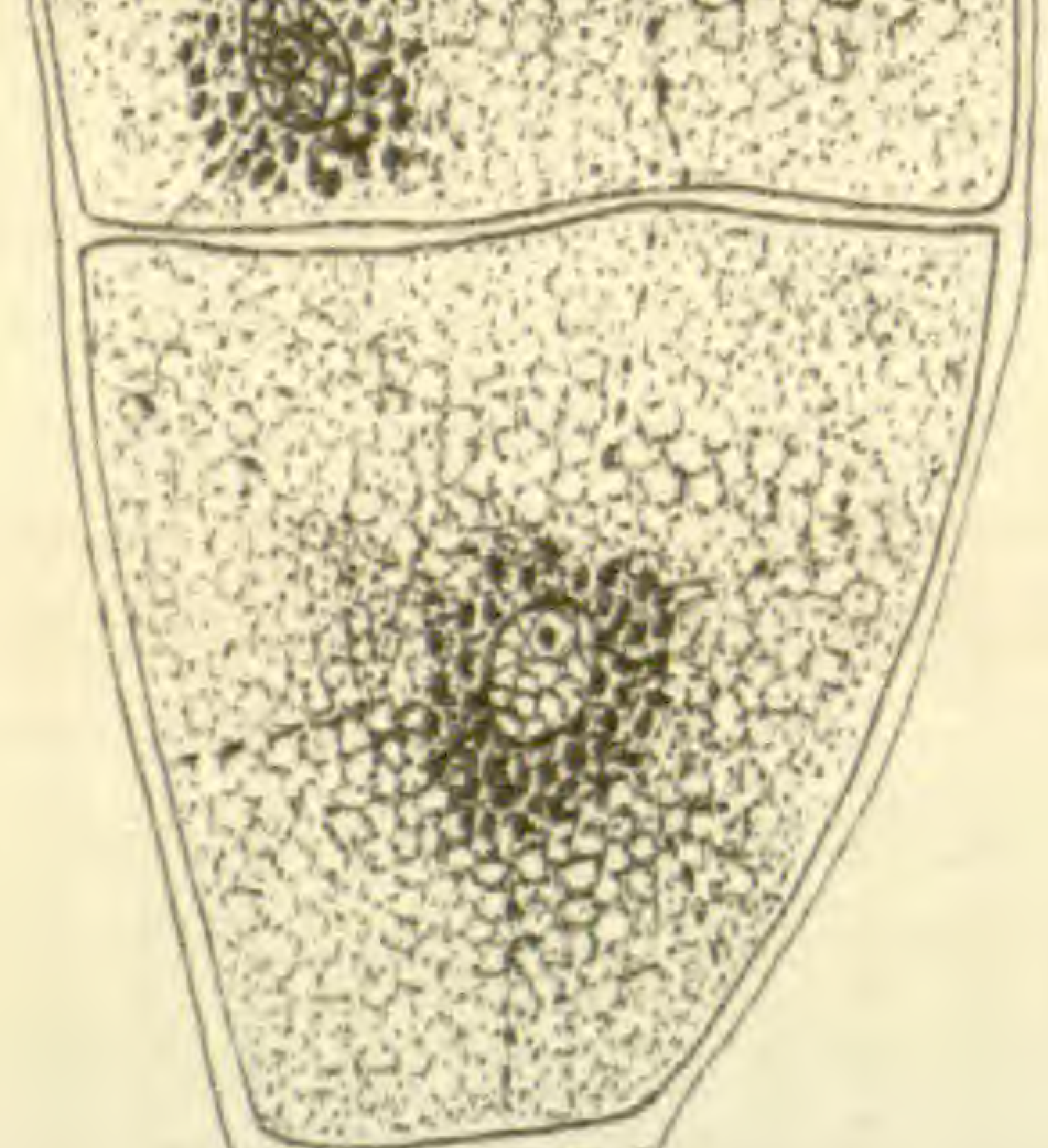

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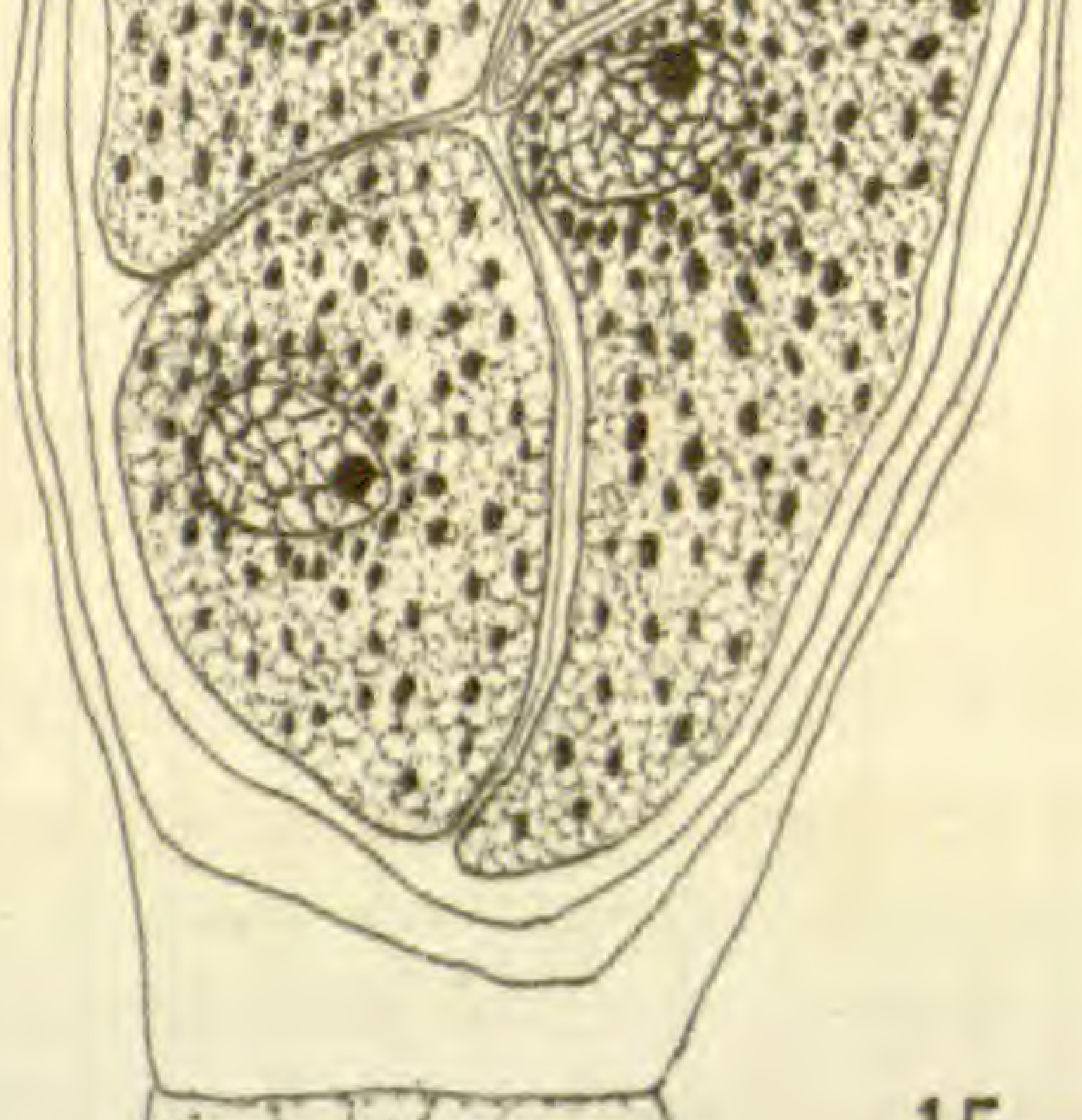

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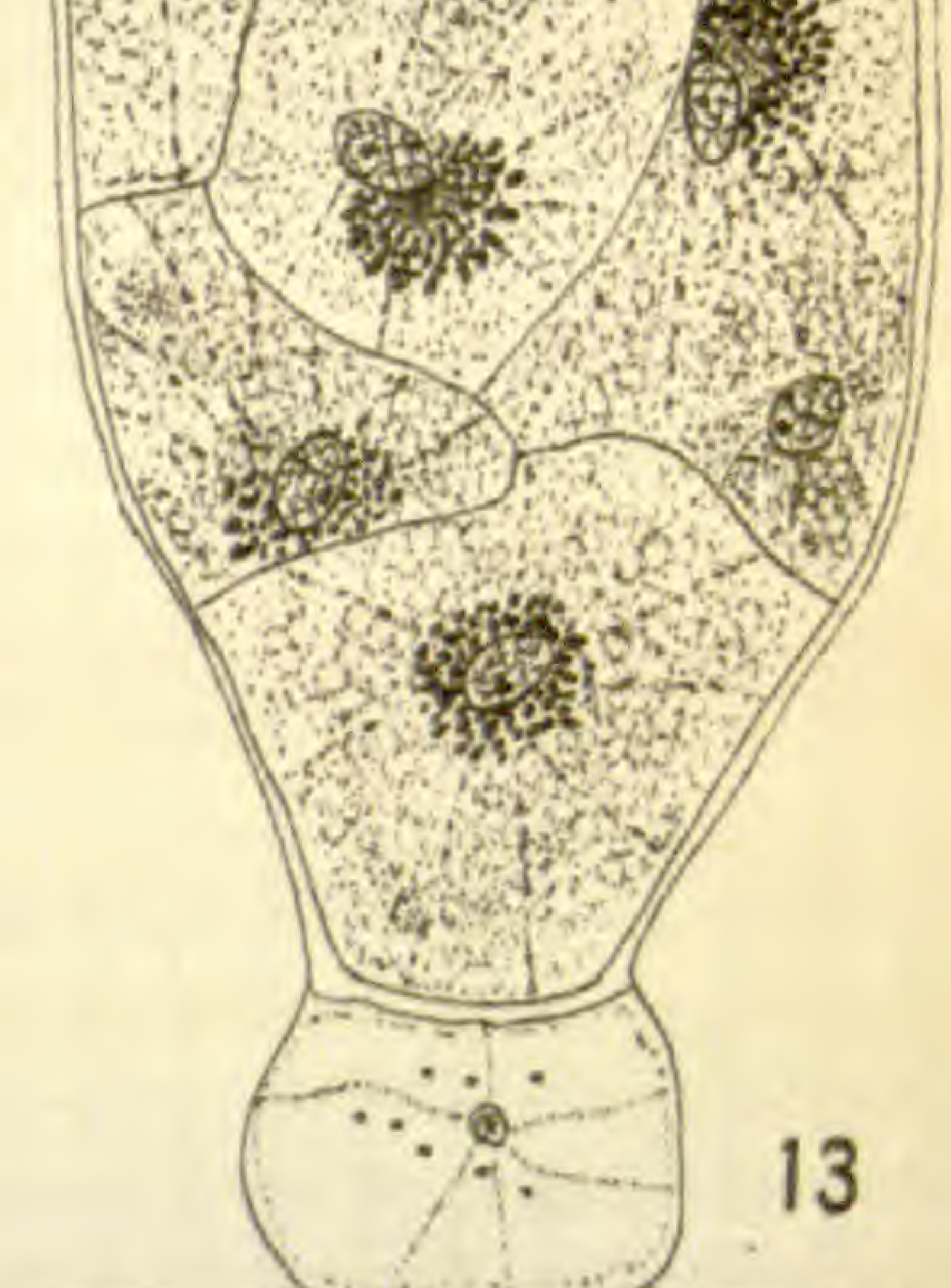

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Minnie R. Getman del.

GETMAN on HORMOSIRA

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EXPLANATION OF PLATE XX

FIGS. 1–7 are text cuts. All figs. of the plate ×480.

FIGS. 8–10.—Free-nucleate condition.

FIGS. 11, 12.—Development of walls.

FIG. 13.—Blocking out of six eggs; a seventh nucleus showing.

FIG. 14.—Four eggs and eight nuclei; the four other eggs have degenerated.

FIG. 15.—Four mature eggs.

THE MEASUREMENT OF ANTAGONISM

W. J. V. OSTERHOUT

(WITH THREE FIGURES)

Attention has been called to the need of a quantitative criterion of antagonism, and it has been shown that such a criterion is easily secured by mixing equally toxic solutions. In this paper[1] mixtures of more than two components were not considered. In order to clear up more fully the confusion which still exists in regard to the measurement of antagonism, it seems advisable to point out the special advantages of this method for mixtures containing three or more components.

The chief advantages lie in the fact that when equally toxic solutions are mixed, the additive effect remains unaltered, no matter how many components are used.[2] (By the additive effect is meant the effect produced when each salt acts independently of every other, when its toxicity is neither augmented nor diminished by the presence of other salts.) If antagonism exists, there will be better growth in the mixtures than in the pure solutions. The increase of growth over what would be expected if the effect were purely additive is the best measure of antagonism. It is best expressed as percentage of the additive effect.[1]

The determination of the additive effect is of first importance for quantitative results. The best method is that which permits us to make this determination most readily and exactly. As has been said, the method of mixing equally toxic solutions makes this determination simple and accurate, no matter how many components are used. Other methods permit this determination for binary solutions, but they involve much more labor, and as the number of components increases, the difficulty of determining the

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[1] OSTERHOUT, W. J. V., Quantitative criteria of antagonism. BOT. GAZ. 58:178. 1914.

[2] When the toxic effect depends on ions, it may increase somewhat as the result of mixing the solutions because the ionization is increased. But this effect is usually small and it may be calculated without difficulty.

additive effect increases very rapidly. These methods usually consist in mixing unequally toxic solutions or in keeping the concentration of some salt or salts constant while varying that of the others.

The method of mixing equally toxic solutions also has a great advantage when the results are to be expressed graphically. As an illustration of this we may take mixtures of NaCl+KCl+CaCl$_2$. In the case of wheat it was found that the roots grew equally well in solutions of NaCl 0.12 M, KCl 0.13 M, and CaCl$_2$ 0.164 M. Mixtures of these solutions were prepared and the growth of the roots in these mixtures was measured after a period of 30 days. In order to show the results graphically, the composition of the solutions may be conveniently expressed by means of a triangular diagram as drawn in fig. 1.[3]

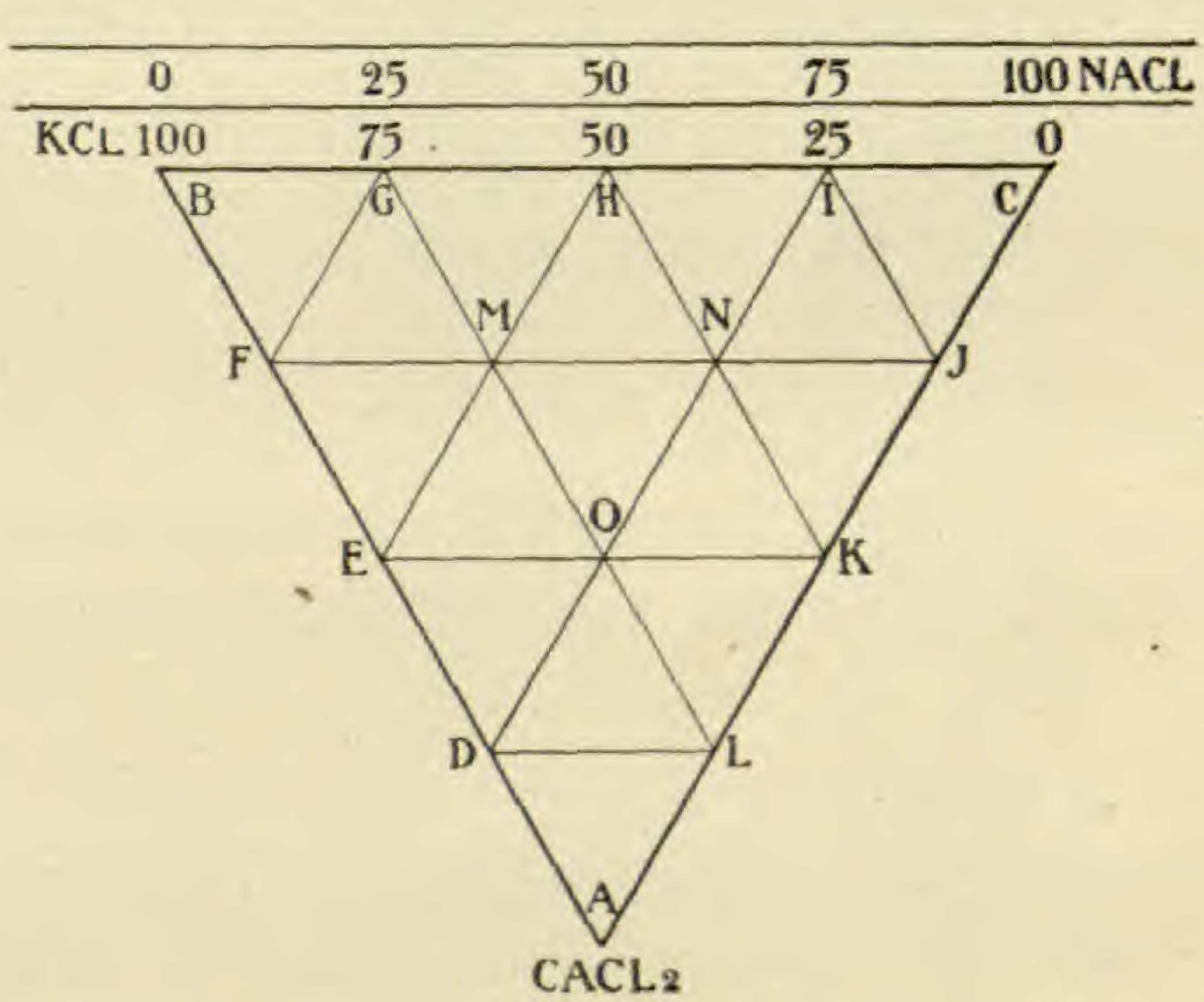

FIG. 1.—Diagram representing the composition of various mixtures of KCl+NaCl+CaCl$_2$: this serves as the base of the solid model shown in fig. 2.

The diagram consists of an equilateral triangle, the apices of which represent equally toxic pure solutions. Thus the point *A* represents pure CaCl$_2$ (0.164 M), *B* represents pure KCl (0.13 M), and *C* represents pure NaCl (0.12 M). All points on the sides of the triangle represent mixtures of two solutions only, the composition depending on the position of the point. Thus the point *H* represents a solution made by mixing the equally toxic solutions NaCl 0.12 M and KCl 0.13 M in such proportions that in the mixture 50 per cent of the dissolved molecules are NaCl and 50 per cent are

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[3] These diagrams are employed in physical chemistry and have been used by SCHREINER and SKINNER in plant physiology (BOT. GAZ. **50**:1. 1910). Finely ruled diagrams may be purchased from the Cornell Cooperative Society.

KCl. In the same way *G* represents a solution in which the molecular proportions are NaCl 25 per cent+KCl 75 per cent; *I* represents NaCl 75 per cent+KCl 25 per cent; *E* represents KCl 50 per cent+$CaCl_2$ 50 per cent; *K* represents NaCl 50 per cent+ $CaCl_2$ 50 per cent.

All points in the interior of the triangle represent mixtures of the three equally toxic solutions NaCl 0.12 M, KCl 0.13 M, and $CaCl_2$ 0.164 M. Along the line *FJ* are represented mixtures in which the dissolved molecules are 25 per cent $CaCl_2$; the line *EK* represents mixtures in which the dissolved molecules are 50 per cent $CaCl_2$; the line *DL* mixtures in which the dissolved molecules are 75 per cent $CaCl_2$. In the same way *FG* means 75 per cent KCl; *EH*, 50 per cent KCl; *DI*, 25 per cent KCl; *GL*, 25 per cent NaCl; *HK*, 50 per cent NaCl; and *IJ*, 75 per cent NaCl.

The point *M* is on the line *FJ*, meaning 25 per cent $CaCl_2$; it is also on the line *EH*, meaning 50 per cent KCl; and likewise on the line *GL*, meaning 25 per cent NaCl. It therefore represents a mixture of the three equally toxic solutions, NaCl 0.12 M, KCl 0.13 M, and $CaCl_2$ 0.164 M, in which the dissolved molecules are 25 per cent $CaCl_2$+50 per cent KCl+25 per cent NaCl. In the same way the point *O* represents a mixture in which the dissolved molecules are 50 per cent $CaCl_2$+25 per cent KCl+25 per cent NaCl.

It is obvious that the composition of any solution can be represented by selecting a suitable point on the diagram. At any such point an ordinate may be erected expressing the growth of the plant in that solution. When this has been done for a sufficient number of points, a solid model may be constructed which gives a complete description of the growth of the plant in all the solutions. Such a model is shown in fig. 2. The ordinates represent the aggregate length of roots per plant of wheat at the end of 30 days. The ordinates in the pure solutions are all equal (55 mm.), showing that the solutions are equally toxic. The ordinates were in part determined directly by experiment and in part calculated from data obtained by growing plants in solutions of approximately the same composition as those represented.[4]

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[4] The data from which this model was constructed will appear in a subsequent publication.

From such a model the antagonism in any solution may be determined at once by measuring with calipers the height of the ordinate at the required point, subtracting 55 which is the amount of growth in the pure solutions, and in this case (since all the pure solutions are equally toxic) the amount of growth which would occur if the toxic actions of the salts were additive (that is, if each salt exerted its own toxic effect independently of the other salts); the result should then be divided by 55.[5]

In this case the additive effect is represented by a plane surface parallel to the plane which forms the base of the model. The height of this plane is indicated by the shading in the figure.

Other methods (as mixing unequally toxic solutions or keeping the concentration of one salt constant while varying that of the others) will give for the additive effect a curved surface very difficult to determine and not easily represented or measured on the model.

With solutions of more than three components the results cannot be expressed in a solid model; but a graphical expression may easily be obtained in the following way. Let us suppose that equally toxic solutions of *A*, *B*, *C*, and *D* are to be mixed. A mixture of the first three may be made and called solution 1 (different mixtures may be called solution 2, etc.). To solution 1 various amounts of *D*

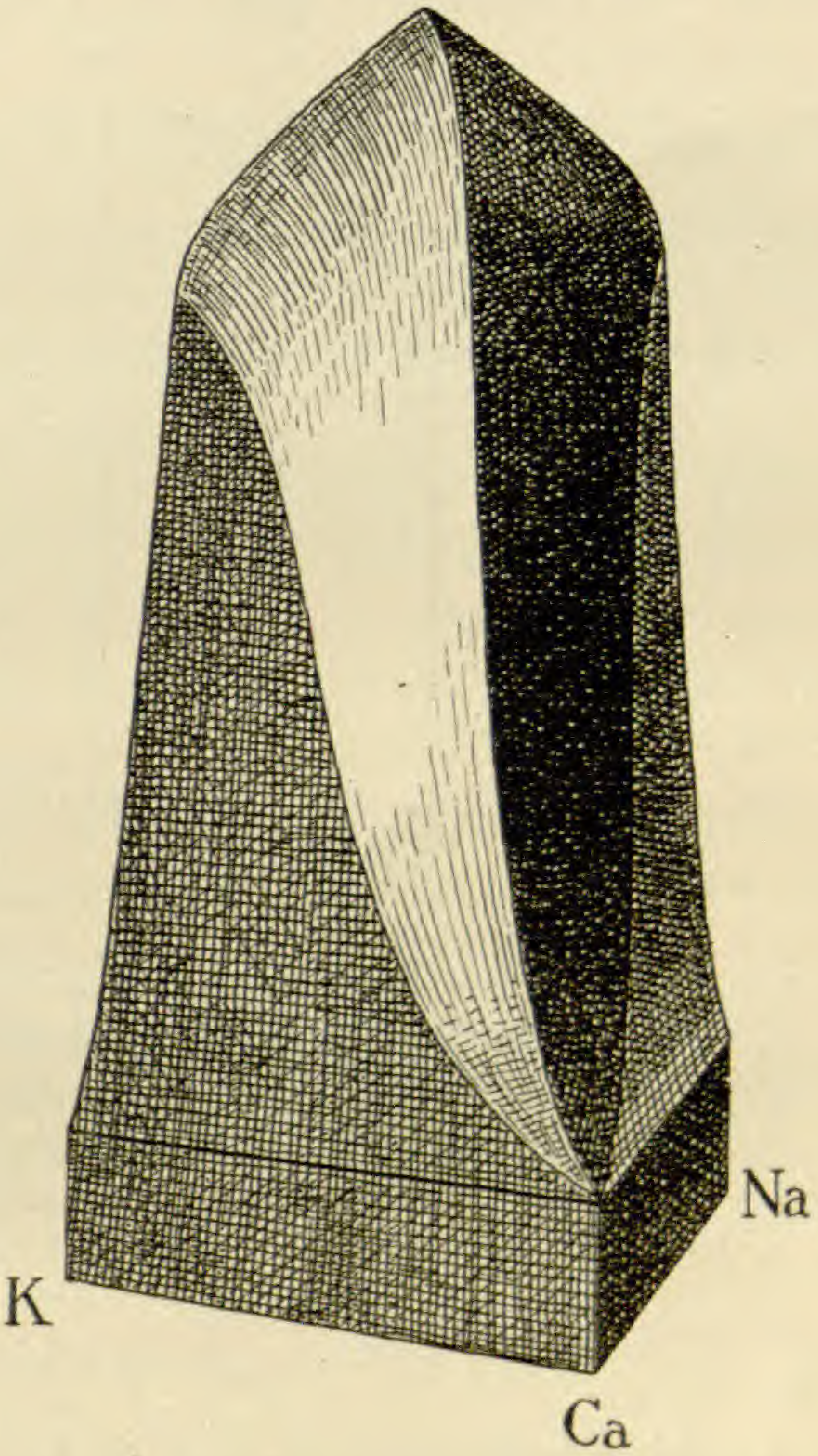

FIG. 2.—Solid model showing the forms of the antagonism curves in all possible mixtures of NaCl 0.12 M, KCl 0.13 M, and $CaCl_2$ 0.164 M.

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[5] For a fuller discussion see BOT. GAZ. **58**:178. 1914.

may be added and the results plotted as shown in fig. 3, in which the additive effect is expressed by the dotted line and the growth in the mixtures by the unbroken line. Antagonism at any point may be easily expressed. For example, the antagonism at the point M is $\frac{MO-MN}{MN}$.

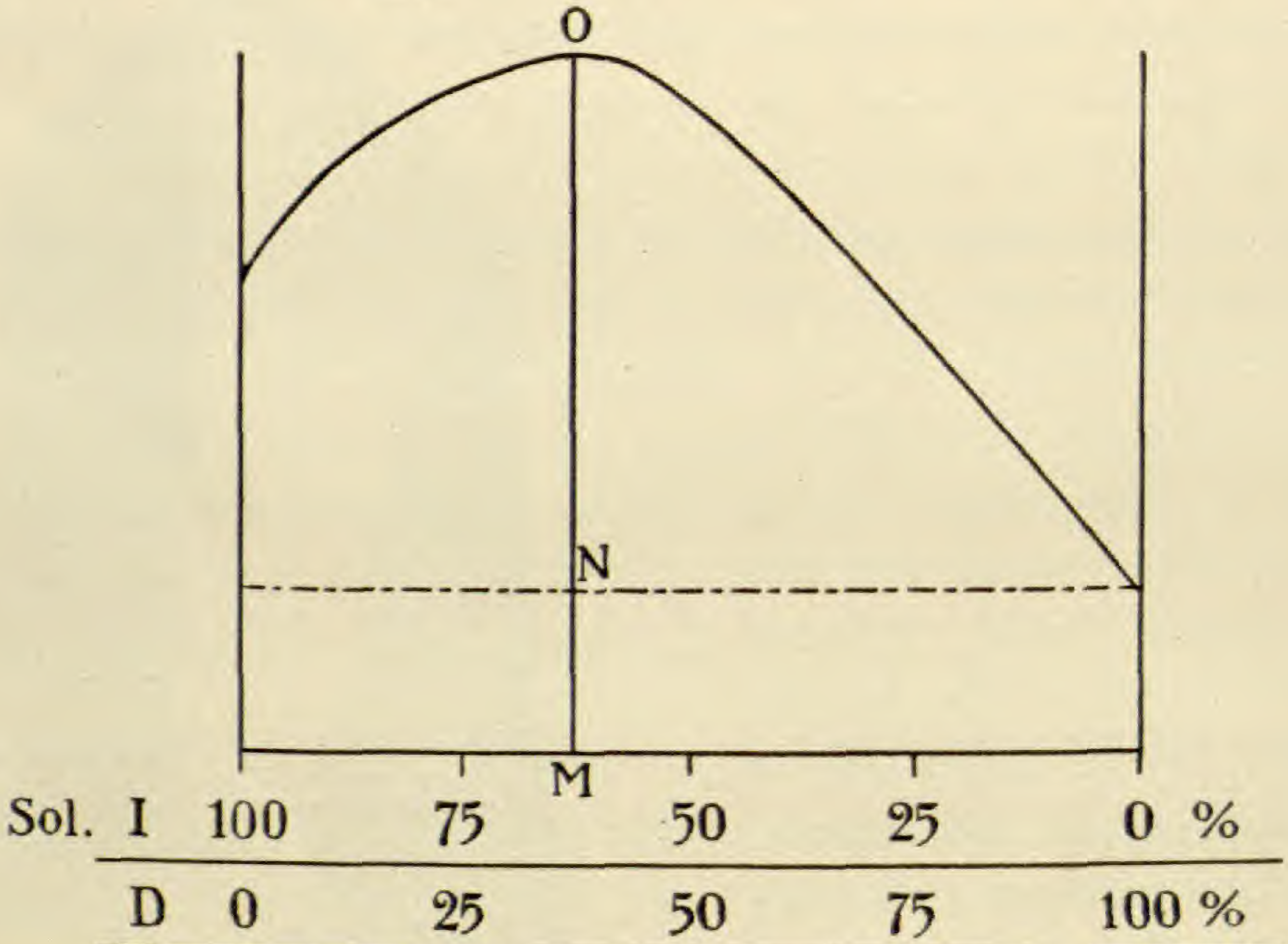

FIG. 3.—Method of expressing antagonism in mixtures containing more than three components: three of the components (A, B, and C) are combined into solution 1 and various amounts of the fourth component (D) are added; the ordinates represent growth; the abscissas represent the composition of the mixtures; thus at the point M the mixture contains 62.5 cc. of solution 1 to each 37.5 cc. of solution D, the antagonism at M is $\frac{ON}{MN}$.

By the method of mixing unequally toxic, pure solutions or by the method of keeping the concentration of one salt constant while varying that of the others, the dotted line would become a curved one.

Summary

The measurement of antagonism in solutions containing more than two components presents no difficulty as long as we pursue the method of mixing equally toxic pure solutions.

Methods are suggested for the graphical expression of antagonism in mixtures of three or more components.

HARVARD UNIVERSITY

FIELD NOTES ON THE CLIMBING BAMBOOS OF PORTO RICO

AGNES CHASE

(WITH PLATE XXI)

In two months spent in the study and collection of grasses in Porto Rico in the fall of 1913, the writer became acquainted with the habits and field aspect of the beautiful and interesting climbing bamboos of the island. The botanical descriptions published, having been drawn from herbarium material, fail to give much idea of the appearance of the living plants.

The climbing bamboos, with the tree ferns and mountain palms, are characteristic of the mountain regions from 2000 feet altitude upward to the summits. At present four species are known: *Arthrostylidium multispicatum* Pilg., *A. sarmentosum* Pilg., *A. angustifolium* Nash, and *Chusquea abietifolia* Griseb. Sterile plants of the last were collected by Dr. F. L. STEVENS and Mr. W. E. HESS on Monte Alegrillo in November 1913, but this species was not found by the writer. The three species of *Arthrostylidium* have much the same habit, climbing high, repeatedly branching, and in their greatest development swinging down in great curtains from the trees overhanging trails or streamlets. They love the glints of sunlight along the trails or water courses and are very rarely found in deep shade. On mature culms two sorts of branches are produced, short leafy ones in whorls at the nodes, and elongated ones which bear whorls of short leafy branches and branch again, the process being repeated until at times a slope for several yards is bound together in a tangled mass.

Arthrostylidium angustifolium, a species very closely related to the Cuban *A. capillifolium* Griseb., I found only once near a cataract at some 3000 feet or more in Indiera Fria. This has linear blades, 2 to 4 mm. wide and as much as 30 cm. long, crowded on short sterile branchlets which are arranged in dense whorls at the distant nodes of the slender culms. These culms hang straight 20 or 30 feet from trees 40 or 50 feet high, or festoon themselves over lower growth, the dense masses of foliage like great pompons strung along the stems at distant intervals. From these whorls occasionally spring slender, divaricate, elongated branches bearing leafy tufts like those of the main culms, but less dense and with shorter blades, the ultimate branches almost capillary and bearing but a single leaf at a node.

Arthrostylidium multispicatum occurs on most of the wet higher mountains. The slender naked growing ends of the culms and branches are beset with very short, sharp-pointed retrorse prickles. These ends, from 5 to 12 feet or more long, swing in the breeze like whip lashes until they strike a place to take hold. Only after attaching themselves to some support do the leaves and branches develop from the clusters of short, sharp, radiating, scale-covered branch buds. The prickles later fall off, the old culms being smooth. These long grappling branches are freely produced, resulting in an inextricably tangled mass that draws blood at every foot of one's progress through it. The short leafy branches are rather less densely whorled than in either of the other species, there being from few to about 20 at a node. The lanceolate, not crowded, blades are 6–8 cm. long and 10–12 mm. wide, or, on vigorous shoots in rich spots, 10 cm. long and 2.5 cm. wide.

The most beautiful and interesting of the climbing bamboos is *Arthrostylidium sarmentosum*. This I found on nearly every wet high mountain, having collections from ten stations. It had been collected before in but three stations and was unknown in flower, the original description having been drawn from sterile specimens. Among mountain palms on the forested north slope of El Yunque (ascending from Rio Grande), at about 3000 feet altitude, it was found in abundant bloom December 2, 1913 (CHASE no. 6730). This is the only time it has been known to flower. The conditions here, so far as could be seen, were in no way different from those under which it grew elsewhere and failed to bloom. Fifty herbarium specimens were prepared and several have since been distributed to herbaria in this country and in Europe. The inflorescence consists of short-exserted, terminal and axillary, strongly zigzag racemes of 2–5 spikelets, the rachis joints flat on one side, minutely ciliate on the edges, a strong pulvillus at the base of each joint forcing it to bend back at right angles to the joint below.

CHASE on ARTHROSTYLIDIUM

Spikelets sessile, 12–20 mm. long, slender, the slender, clavate rachilla joints zigzag, 3–5 mm. long; glumes 3 or 4, approximate (the lower internodes of the rachilla about 0.1 mm.), the strong midnerves hispidulous toward the summit, the lowermost glume acuminate or setaceous, 2.5–3 mm. long, the uppermost acute, 4–4.5 mm. long, about equaling the rachilla joint; florets 2 or 3, nearly terete, 6–8 mm. long, distant, one-third to one-quarter longer than their rachilla joints; lemma lanceolate, acuminate, pubescent, with three strong nerves and one or two pairs of faint intermediate nerves; palea membranaceous, slightly shorter than its lemma, broad, obtuse, deeply folded between the ciliate keels; stamens 3; stigmas 2, plumose.

From my observations, I think this species forms an exception in the bamboos in that the culms are not perennial but herbaceous, dying down each year. When first seen along the Rio Maricao, the middle of October, there were numerous young culms, from a foot or two to six or eight feet long, crawling on the ground or beginning to climb. Hanging in the trees overhead were quantities of frayed dead stems falling to pieces when touched. By the last of December this species was high in the trees and hanging down like the other two species. There are no strong culms as in other bamboos or in *Lasiacis;* the largest found is but 3 mm. in diameter. The culms are not more woody in texture than are those of some of our species of *Panicum* or *Andropogon.* Since there is neither winter nor dry season, there seems to be no reason why the plants should die down, but apparently they do die down like ordinary grasses that are perennial by underground parts only. It is a most airy, graceful, delicately beautiful species, the long, slender, vinelike culms with their clusters of pale green foliage festooning the trees or hanging free from the long limbs above a trail or rivulet and suggesting a lacy veil. The foliage becomes glaucous in drying, but in the growing plants is a light but not grayish green.

BUREAU OF PLANT INDUSTRY
WASHINGTON, D.C.

EXPLANATION OF PLATE XXI

Arthrostylidium sarmentosum Pilg.: *a*, portion of culm with inflorescence, ×$\frac{1}{2}$; *b*, spikelet with portion of rachilla, ×3.

CURRENT LITERATURE

NOTES FOR STUDENTS

The wilting coefficient.—The importance in ecological work of some method of determining what portion of the soil moisture is available for the growth of plants caused ecologists to welcome the "wilting coefficient" of BRIGGS and SHANTZ[1] as an important constant for the investigation of plant associations. The general conclusion that for any given soil the wilting coefficient is largely independent of the kind of plant or of the external conditions under which the plant grew and wilted was directly at variance with the ideas of plant physiologists and was soon questioned. Unfortunately, in the extensive and careful experiments of BRIGGS and SHANTZ there was no exact quantitative description of the atmospheric factors under which the experiments were carried out. Limiting these factors rather definitely, CALDWELL[2] found that only when wilting was slowly brought about under rather moist conditions was the wilting coefficient, or "the ratio of soil moisture content at permanent wilting," the same as that determined by BRIGGS and SHANTZ. Similar plants placed under the high transpiration condition of the desert atmosphere at Tucson wilted with a soil moisture content 30–40 per cent in excess of the wilting coefficient for the humid aerial conditions, the difference being greatest in soils with a low saturation capacity, although under a given set of atmospheric conditions the wilting coefficient was approximately a constant for each of the soils used. In order that the wilting coefficient may be determined solely by soil conditions, therefore, it is only necessary that the evaporating power of the air shall not exceed a certain limit, but where this limit lies, beyond which this coefficient is decidedly greater than that determined by BRIGGS and SHANTZ, was not determined.

BLACKMAN[3] has recently reviewed the situation, including CRUMP'S[4] new method of expressing the soil moisture (coefficient of humidity) and has aptly pointed out what appears to be some of the important related ecological problems of the water relations of plants urgently requiring investigation. They are (1) the confirmation of the results of BRIGGS and McLANE (on the moisture equivalent of soils), and of BRIGGS and SHANTZ; and (2) how far the formula

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[1] See BOT. GAZ. **53**:20–37, 229–235. 1912.

[2] CALDWELL, J. S., The relation of environmental conditions to the phenomenon of permanent wilting in plants. Physiol. Res. **1**:1–56. 1913.

[3] BLACKMAN, V. H., The wilting coefficient of the soil. Jour. Ecol. **2**:43–50. 1914.

[4] See review in BOT. GAZ. **57**:85. 1914.

devised by BRIGGS and SHANTZ to express the wilting coefficient in terms of soil composition is capable of simple modification for higher rates of transpiration. As there seems to be no reason at all to doubt the experimental accuracy of the work of BRIGGS and SHANTZ, especially when their extensive character is taken into consideration, the second of these problems would seem to offer a favorable field for further experimentation, with a strong probability of results that would be useful in many phases of ecological study. Indeed, the most recent paper upon the subject by SHIVE and LIVINGSTON[5] makes an unsuccessful attempt at a determination of the limits within which the formula of BRIGGS and SHANTZ does apply. It confirms the results of CALDWELL, further emphasis being given to the fact that for the soils of high water-holding powers the wilting coefficient, or the "soil moisture residue at permanent wilting" as SHIVE and LIVINGSTON prefer to call it, even with high evaporating power of the air, is but little above, in fact, in some instances, is slightly below that obtained by the direct methods of BRIGGS and SHANTZ. This paper also contains an attempt to express by an algebraic equation the relation of the wilting coefficient to the evaporation intensity under which wilting was brought about, but the results are so diverse that only a rather wide approximation is obtained. The general conclusion seems to be that the formula of BRIGGS and SHANTZ holds within certain limits, as yet undetermined, but doubtless within atmospheric conditions of comparatively low evaporation intensity.—GEO. D. FULLER.

Ecology of fresh-water algae.—COMERE[6] has published a general account of the ecology of the fresh-water algae. The paper itself is so nearly a summary of the results of investigations by the author and other European limnologists, that it is difficult to condense the matter further. The paper is divided in three parts, the first of which considers the classification and nomenclature of aquatic formations, the separation of these formations into characteristic regions, and the arrangement and terminology of the "florules" corresponding to these regions. This part is especially useful because of its concise definitions and citations of synonyms. Algal habitats are primarily divided into aquatic and subaerial. The former are further separated into permanent and transient groups. The algal formations are first divided into those of large lakes, small lakes, and streams. In these there may be further recognized the littoral, planctonic, and bottom regions, each with its corresponding florule. The subdivisions are too numerous to mention here, but this will suffice to show that

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[5] SHIVE, J. W., and LIVINGSTON, B. E., The relation of atmospheric evaporating power to soil moisture content at permanent wilting in plants. Plant World **17**:81–121. 1914.

[6] COMERE, JOSEPH, De l'action du milieu considérée dans ses rapports avec la distribution générale des Algues d'eau douce. Mém. 25, Bull. Soc. Bot. France **16**: 1–96. 1913.

the basis of classification is essentially static, and ignores the genetic relationships of both the habitats and the formations. Consequently, proximity in the resulting scheme of classification does not necessarily imply near relationship, nor wide separation a lack of connection.

The second part contains a summary of observations on the influence of the various ecological factors. These include the usual factors classified as climatic, physical and chemical, and biotic.

The means of dispersal, the geographic distribution of the various families of algae, the algal populations of various formations, and the periodicity of the algal flora form the topics of the last division of the memoir. The discussion of periodicity is largely drawn from COMERE's previous paper on this subject. The division of the algal flora into vernal, estival, autumnal, and hyemal groups, it should be noted, is really a characterization of the seasons by means of algal reproduction, rather than a classification of algae on the basis of their seasonal phenomena. With regard to the concentration of natural waters, the usual assumption is made that there exists an inverse relation between the height of the water level and the concentration. This leaves out of account the removal of solutes by the adsorption and subsequent settling of the solid particles in these waters, which it seems is much more important in determining concentration than changes in volume. But these points to which exception may be taken are few compared with the great number of topics discussed. —E. N. TRANSEAU.

British North Borneo.—Miss GIBBS[7] has published a notable contribution dealing with the flora of North Borneo. The first part deals with the ecological features of a most interesting region. The general character of the country is discussed, as to its orography and meteorology, and also the general plant-formations under the titles "secondary formations" and "primary forest." A very full itinerary makes the aspects of the flora vivid; and there is a special description of the plant formations on Mt. Kinabalu, the highest mountain of the Malay Archipelago, which was first ascended in 1851 by a botanist, Sir HUGH LOW, then colonial secretary of Labuan.

In the systematic account (184 pp.) of the remarkably large collection of plants made in January to March 1910, Miss GIBBS has had the assistance of several specialists. The collections include plants of all groups from algae to seed plants. Descriptions of about 85 new species, well distributed throughout the families of seed plants, are published, including the following new genera: *Phyllocrater* and *Cowiea* (Rubiaceae), *Sigmatochilus* (Orchidaceae), and *Lophoschoenus* (Cyperaceae). As might be expected, Orchidaceae secure the largest representation of new species, 21 in number. *Elatostema* illustrates how a

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[7] GIBBS, LILIAN S., A contribution to the flora and plant formations of Mount Kinabalu and the Highlands of British North Borneo. Jour. Linn. Soc. Bot. 42:1–240. *figs. 8. pls. 1–8.* 1914.

genus now and then becomes enriched suddenly in a new region, 7 new species being added to its list. Among the new species is a *Dacrydium*, which means more than a new angiospermous species. The ratio of increase in the number of species as the flora of the tropics becomes known is so great that a new census of the plant kingdom is called for, as the old enumerations, so often quoted in textbooks, are wide of the mark.—J. M. C.

Syncotyly and schizocotyly.—COMPTON[8] has made a somewhat extensive investigation of dicotyledonous seedlings with a single cotyledon, and also of those with more than two cotyledons. The terminology of the title indicates his belief that the single cotyledon of a dicotyledonous seedling is the equivalent of two fused cotyledons; and that extra cotyledons represent a splitting of cotyledons.

The conclusions in reference to syncotyly are in substance as follows: syncotyly occurs in a great number of species, normally or "teratologically"; in species with albuminous seeds syncotyly usually gives rise to a symmetrical cotyledonary tube, the reason probably being "the homogeneity of the surroundings of the embryo before germination"; in species with exalbuminous seeds syncotyly is usually asymmetrical, the cotyledons uniting along one edge only, the suggested reason being "the asymmetry of its [embryo] environment, which produces accumbency and other irregularities."

The study of schizocotyly is made the basis of a discussion as to the primitive condition of cotyledony. Arguments have been advanced for both dicotyledony and polycotyledony as the primitive condition. The author's judgment inclines to dicotyledony as the primitive condition. If this historical question must be settled, it will probably have to await the discovery of the embryos of Cycadofilicales.—J. M. C.

Tyloses.—The extensive collections of the Forest Products Laboratory have enabled Miss GERRY to undertake a survey of the occurrence of tyloses.[9] Of the 45 genera of hardwoods examined, 24 are found to contain tyloses. These proliferous growths into the vessels naturally reach their most marked development in ring-porous woods, such as oak, although in this genus black oaks rarely show tyloses, while white oaks show abundant evidences. Woods in which parenchyma surrounds the vessels show the best development of tyloses, though the proximity of medullary rays to vessels is also a factor. Contrary to previous accounts, Miss GERRY finds tyloses in the sap wood of all species in which they occur in the heart wood, and she produces photographs of hickory which illustrate the point. With respect to soft woods, *Pinus* is the only genus in which true tyloses have been found, and here they are held

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[8] COMPTON, R. H., An anatomical study of syncotyly and schizocotyly. Ann. Botany **27**:793–821. *figs. 41.* 1913.

[9] GERRY, E., Tyloses; their occurrence and practical significance in some American woods. Jour. Agric. Research **1**:445–470. *pls. 52–59.* 1914.

to be of normal occurrence (contrary to RAATZ, but agreeing with the reviewer). They are found to be better developed in spring wood than in summer wood, and more numerous in sap wood than in heart wood. The effect of tyloses on penetration of wood by preservatives is also discussed.—M. A. CHRYSLER.

The Congo flora.—WILDEMAN[10] has published a list of the recorded plants from the state of Congo, which adds much to our knowledge of the African flora. In addition to the vascular plants, the list includes the fungi, of which 145 species are enumerated. The new species of fungi number 16, and the following new genera are described: *Volutellopsis* and *Gilletia* (Mucedinaceae). The ferns enumerated are 35, and among them is a new species of *Dryopteris*. About 130 monocotyledons are enumerated, and 63 of these are grasses. The dicotyledons, of course, are far the most numerous, about 700 species being listed. Among them 25 new species are described, but 15 of these belong to the leguminous genus *Geissaspis*, an addition that doubles the number of its species. A student in the north temperate regions expects the Compositae to be the dominant dicotyledonous family; but in the Congo region the Leguminosae are dominant, being represented in this list by 176 species, while the Compositae reach only 62 species.—J. M. C.

Embryogeny of Ranunculaceae and Cruciferae.—In continuing his studies of the embryo of Ranunculaceae, SOUÈGES[11] has attacked the genus *Ranunculus*, recording every stage in the embryogeny with great detail and excellent illustrations. The same investigator[12] has also made a preliminary announcement of additional details observed in the embryogeny of crucifers.—J. M. C.

South African mosses.—South Africa is beginning to yield its quota of new mosses, as is evidenced by a publication from WAGER[13] of the Transvaal University College, Pretoria. Ten new species are described, representing ten genera. The author promises an early publication of a list of all the mosses recorded from South Africa.—J. M. C.

New orchids of the oriental tropics.—As the vegetation of the tropics is investigated more intensively, the number of new species discovered is always surprising. In a recent contribution, SMITH[14] has described 26 new species of orchids from the Malay Archipelago, and 40 new species from Papua.—J. M. C.

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[10] WILDEMAN, E. DE, Additions á la flore du Congo. Bull. Jard. Bot. Bruxelles **4**:1–241. 1914.

[11] SOUÈGES, R., Recherches sur l'embryogénie des Renonculacées. Bull. Soc. Bot. France **60**:506–514, 542–549. *figs. 354–427*. 1913.

[12] ———, Nouvelles observations sur l'embryogénie des Crucifères. Compt. Rend. **158**:1356. 1914.

[13] WAGER, HORACE A., Some new South African mosses. Trans. Roy. Soc. South Africa **4**:1–6. *pls. 1, 2*. 1914.

[14] SMITH, J. J., Bull. Jard. Bot. Buitenzorg. II. no. 13. pp. 77. 1914.

Recent Publications
OF
The University of Chicago Press

The Weather and Climate of Chicago. (*Bulletin No. 4, Geographic Society of Chicago.*) *By Henry J. Cox, Professor of Meteorology, United States Weather Bureau, and John H. Armington, Local Forecaster, United States Weather Bureau.*

396 pages, 8vo, cloth; $3.00, postage extra (weight 3 lbs. 1 oz.)

This book, of general interest because of its character and authority, will naturally be of peculiar interest to residents of Chicago and the Middle West. Its importance is indicated by the fact that it is issued under the auspices of the Geographic Society of Chicago, and has been prepared by two of the best known weather experts in the country. It includes discussions of a great variety of subjects, such as temperature, precipitation, atmospheric moisture, cloudiness and sunshine, wind direction and velocity, barometric pressure, and storm tracks; and among the interesting appendixes to the book are one on the weather of holidays and another containing journal entries relative to the great Chicago Fire of 1871.

The volume contains also a remarkable series of tables with reference to temperature, precipitation, atmospheric moisture, and atmospheric pressure—one hundred and forty-seven in all, with more than one hundred figures and plates.

Of especial interest and importance to teachers in connection with *The Weather and Climate of Chicago* is the preceding Bulletin of the Geographic Society edited by Professor Cox, and by Professor J. Paul Goode of the University of Chicago. It was prepared by a committee of the Geographic Society of Chicago and is entitled *Lantern Slide Illustrations for the Teaching of Meteorology.* It will be found an admirable aid in interesting students in the phenomena of weather and climate.

The Evolution of Early Christianity. By Shirley Jackson Case, Associate Professor of New Testament Literature in the University of Chicago.

390 pages, 12mo, cloth; $2.25, postage extra (weight 1 lb. 11 oz.)

The beginnings of the Christian movement are here studied from a wholly new point of view. By examining the actual religious situation in which the Christians of the first century lived, the author is able to shed fresh light on many parts of the New Testament. Some of the subjects discussed are Christianity's developmental nature, the importance of environment for Christian origins, the early believers' Jewish connections and the causes of their break with Judaism, their contact with various gentile religions such as emperor worship, Stoicism and oriental mystery cults, and the ultimate triumph of Christianity.

Problems of Boyhood. A Course in Ethics for Boys of High-School Age. By Franklin W. Johnson.

152 pages, 12mo, cloth; $1.00, postage extra (weight 1 lb. 1 oz.)

This book, prepared by the laboratory method, is the result of the experience of a teacher of boys in the high school, a leader of high-school boys in the Sunday school, and of work with boys of a similar age in Young Men's Christian Association groups. The author is the principal of the University of Chicago High School. Such topics as Keeping Clean, Habits, Gambling, Betting, Clean Speech, Right Thinking, Sex, Loyalty, Self-Control, and other themes of equal importance are discussed informally and in such a way as to arouse the keenest interest on the part of boys. This long-needed book will be useful, not only in the Sunday school, but in day-school and Association classes. It is the first book in the field to start with a recognition of the boy's point of view.

Unpopular Government in the United States. By Albert M. Kales, Professor of Law in Northwestern University.

270 pages, 12mo, cloth; $1.50, postage extra (weight 1 lb. 8 oz.)

An epecially timely book, presenting with great clearness and cogency some of the political needs of the country, particularly the necessity of the short ballot. The author discusses various expedients for restoring the American ideal of democracy. The book has already attracted wide attention and discussion.

FORTHCOMING BOOKS

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Water Reptiles of the Past and Present. By SAMUEL WENDELL WILLISTON.

The Lincoln and Douglas Debates. By HORACE WHITE. (Publications of the Chicago Historical Society.)

THE UNIVERSITY OF CHICAGO PRESS

The Origin and Teachings of the New Testament Books. By ERNEST D. BURTON and FRED MERRIFIELD.

William James and Henri Bergson. By HORACE M. KALLEN.

Papers of the Bibliographical Society of America. Vol. VIII. Edited by A. C. VON NOÉ.

A Historical Examination of Some Non-Markan Elements in Luke. By ERNEST WILLIAM PARSONS. (Vol. II, Part 6, Second Series, Historical and Linguistic Studies.)

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The Evolution of Sex in Plants. By JOHN MERLE COULTER, Head of the Department of Botany in the University of Chicago.

The Origin of the Earth. By THOMAS C. CHAMBERLIN, Head of the Department of Geology in the University of Chicago.

The Isolation and Measurement of the Electron. By ROBERT A. MILLIKAN, Professor of Physics in the University of Chicago.

The Theory of Collineation Groups. By HANS F. BLICHFELDT, Professor of Mathematics in Leland Stanford Junior University.

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- *I. Catalogue of Authors (1800–1883).* Twelve volumes. Cloth or half morocco. Prices on request.
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Tables for Statisticians and Biometricians. Edited by KARL PEARSON. 228 pages, quarto, bound in boards; $2.50, postpaid.

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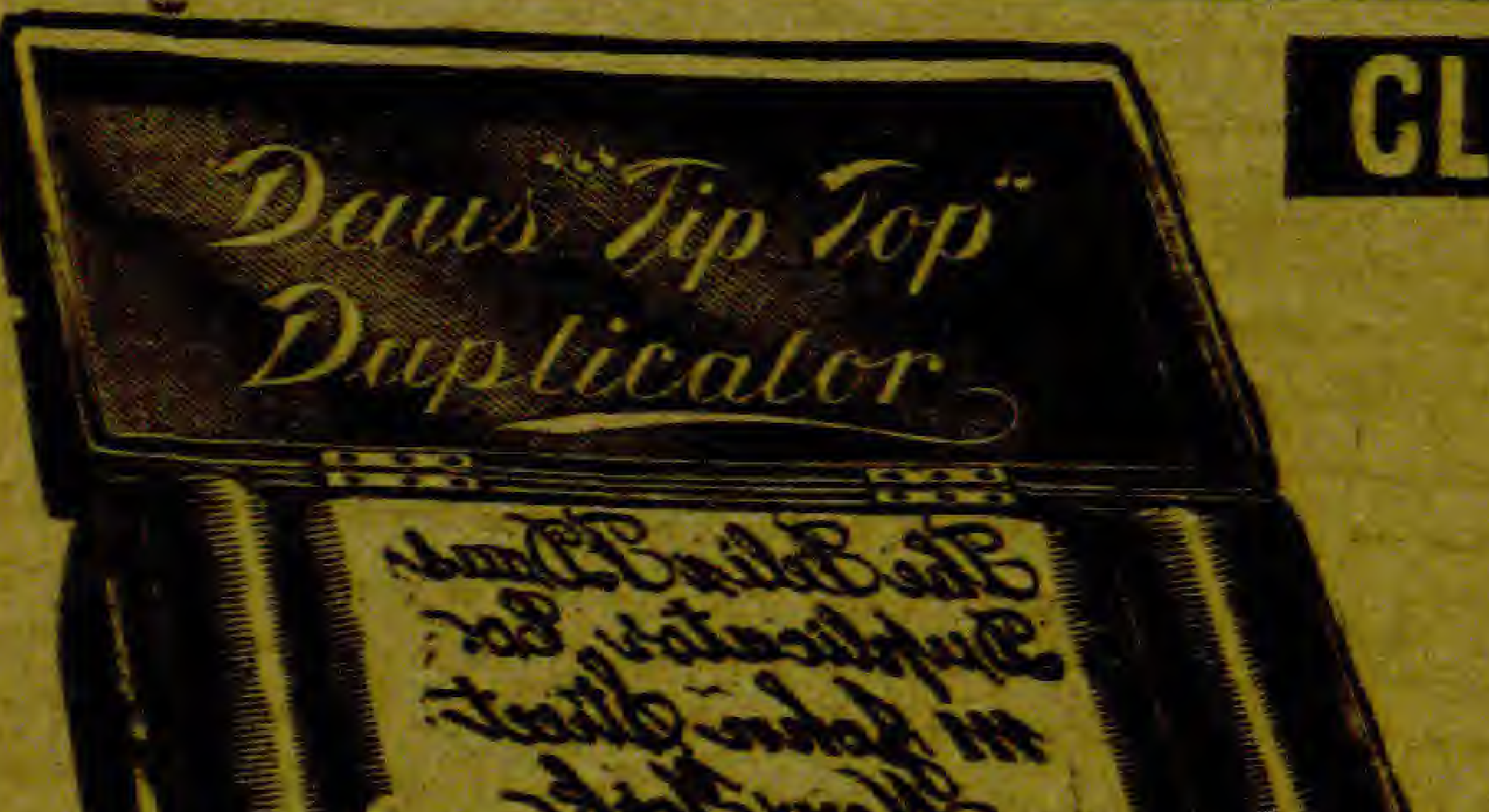
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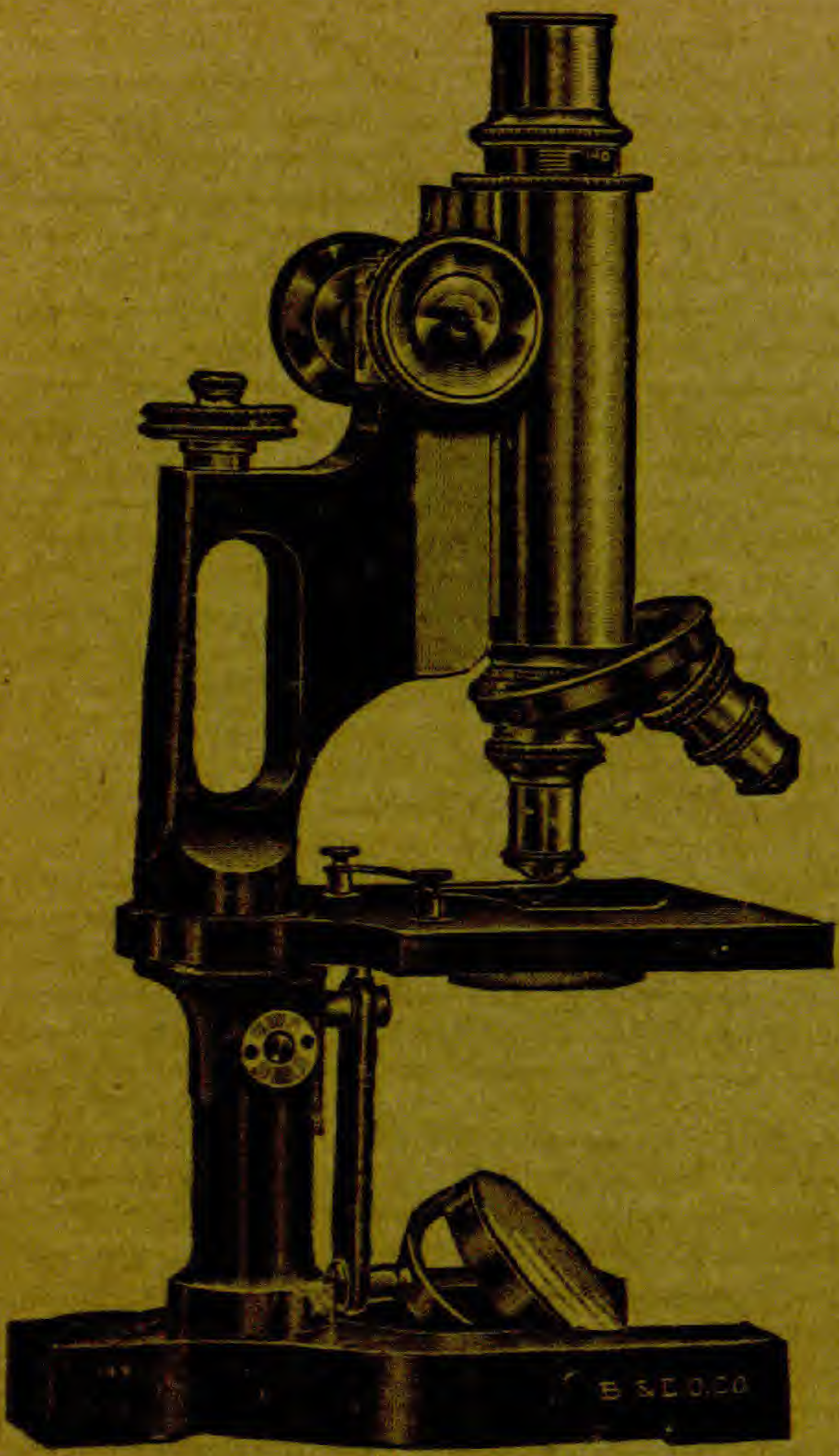


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Contributors are requested to write scientific and proper names with particular care, to use the metric system of weights and measures, and in citations to follow the form shown in the pages of the **Botanical Gazette.**

Papers in excess of thirty-two printed pages are not accepted unless the author is willing to pay the cost of the additional pages, in which case the number of pages in the volume is correspondingly increased.

Illustrations are furnished without cost to author only when suitable originals are supplied. A copy of the suggestions made in the January number, 1907, will be sent on application. It is advisable to confer with the editors as to illustrations required in any article to be offered.

Separates, if desired, must be ordered in advance of publication. Twenty-five separates of original articles without covers will be supplied gratis. A table showing approximate cost of additional separates is printed on an order blank which accompanies the proof; a copy will be sent on request.

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VOLUME LVIII NUMBER 4

THE

BOTANICAL GAZETTE

OCTOBER 1914

DELAYED GERMINATION IN SEED OF ALISMA PLANTAGO

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WILLIAM CROCKER AND WILMER E. DAVIS

(WITH EIGHT FIGURES)

I. Introduction

The cause of delay in the germination of seeds of various water plants has been the subject of considerable discussion and some experimentation. MÜLLER (23) early found that seeds of *Eichhornia* and *Heteranthera* do not germinate without first being desiccated, and LUDWIG (26) demonstrated this for seeds of *Mayaca fluviatilis.* PFEFFER (23) says, "nor is it certain whether BROWN and MÜLLER are correct in assuming that previous drying is essential for the further development of *Chlamydomonas* or for the germination of the seeds mentioned." A. FISCHER (12) found that acids and bases arouse many seeds of water plants from their dormancy, and attributes the action of these reagents to an embryo rather than a coat effect. The following species were studied by FISCHER: *Alisma Plantago, Potamogeton lucens, P. pectinatus, Hippurus vulgaris, Polygonum amphibium, Scirpus lacustris, S. maritimus, Sagittaria platyphylla, S. sagittifolia,* and *Sparganium ramosum.*

Somewhat later, CROCKER (6) cast doubt upon FISCHER'S conclusion that the acids and bases are effective through their action on the embryos. It was found that the seeds of various water plants (*Alisma*, *Sagittaria*, *Eichhornia*, etc.) germinate readily in distilled water frequently changed, provided the seed coats are broken or removed with care not to injure the embryo. From this it would seem that the embryos are not dormant if the limiting effects of the coats are not present. EWART (**11**) confirms these results by finding that the seeds of *Sagittaria* germinate readily after abrasion with sandpaper. He also points out the fact that the effect of the acid or the base is not counteracted by the application of a sufficient amount of the other to neutralize it. This criticism is especially significant in the light of the finding reported later in this paper, that the coat is largely composed of pectic substances.

It is evident that the dormancy in the seeds of water plants is of a different type from that in the seeds of the haw (**9, 10**), apple, peach, etc. In these forms the naked embryos do not grow when they are supplied with all ordinary germinative conditions if they are not first after-ripened. OSTENFELD (**22**) finds, confirmatory of the much earlier work of GUPPY (**15**), that the passage through the alimentary canals of birds greatly improves the germination of various water seeds. He considers further work necessary to justify the conclusion of either FISCHER or CROCKER. This statement seems to be fully justifiable, for it is possible that the reagents used by FISCHER have their total effect through their joint action on coats and embryos, although the latter when coat-free are certainly not dormant. It is for the purpose of throwing more light on this question that the following experiments are reported. Up to date the work has been entirely limited to a study of the seeds of *Alisma Plantago*. Of forcing agents, hydrochloric acid mainly has been studied.

II. Material

The ripened fruit of *Alisma Plantago* as it is shed from the plant is an akene, from which the pericarp can be removed by slight rubbing of the fruit between the fingers. This structure seems to play no rôle in water-intake or delay in germination, hence, for convenience in detecting the quality of the seed and for avoiding errors due to the large inert mass, the fruits worked with were always freed from this structure, leaving only the seed proper. A single harvest of seeds thus prepared shows much variation between the individuals both in appearance and in physiological behavior. In color the seeds vary from a deep reddish brown to a light pink. As a general rule the intact dark seeds absorb water less rapidly and to much slighter total amount than the light-colored ones. With the coats broken or removed, they also show far less vigor in water absorption and in growth rate. For this reason, in the experiments here reported, light-colored seeds of plump appearance were selected chiefly. Even with this precaution to remove less vigorous ones, the seeds showed great variation in rate of water absorption and of growth.

The air-dry seeds freed from the pericarp retain a relatively large percentage of water. The amount approximates 16 per cent, varying with the humidity of the air and with the seed. The large percentage of water retained in contrast to many fatty seeds is probably related to the richness of the embryo in starch and of its walls in pectic substances, and to the high pectic content of the relatively thick coat.

When seeds were to be used with coats broken or partly removed, it was at first done by inserting a thin knife blade between the two arms of the embryo. This method did not prove desirable, for it left many coats intact, only splitting the two layers lying against the embryo from each other but not breaking them. It also often cracked the embryos at the arch. It was soon found that slight pressure of a knife blade at the micropyle end removed a quite definite cap of the coat from that end of the embryo. The break occurs at thin regions well shown in fig. 1. In some experiments, the coats were also removed by similar means from the end of the embryo adjacent to the micropyle. In this case the breaking was somewhat more irregular, and the size of the pieces showed more variation, although at this end of the embryo the coat shows very definite thinner places at the position of the cross-walls, as is the case at the micropyle end. The feature just described also accounts for the method by which the embryo breaks the coat after the seed is treated with an acid or a base. In this case the same sort of cap is pushed off the micropyle end of the coat by the lengthening embryo. Before embryos from which a portion of the coat was removed were used, they were examined with the microscope to see that no injury was incurred in the process.

All the cultures were made under water or other solutions mentioned. The seeds will not grow normally between filter papers or on wet absorbent cotton, probably owing to insufficient water supply.

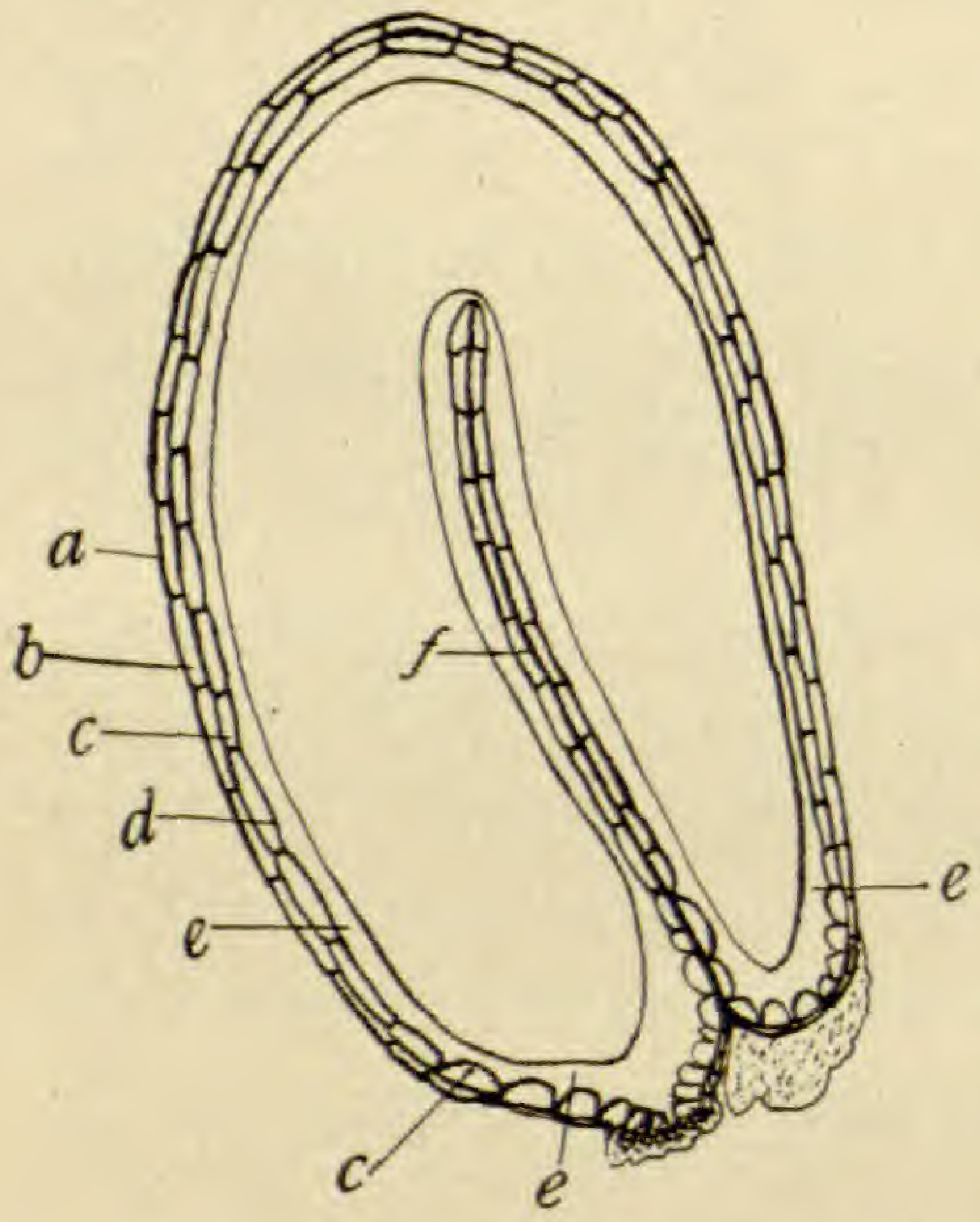

FIG. 1.—Camera drawing of a longitudinal section of the seed coat of *Alisma Plantago: a*, outer wall of the outer layer of cells, pectic substances swelling up and slowly dissolving in water; *b*, contents and cross-walls of the outer layer of cells, largely pectic material; *c*, contents and cross-walls of the inner layer of cells, largely pectic material; *d*, inner wall of inner layer of cells slightly suberized; *e*, acellular inner layer of coat, possibly originating from the endosperm, a mixture of pectic substance and hemicellulose.

III. Experiments

A number of experiments showed that the embryos themselves have no period of dormancy or need of after-ripening, for fruits just gathered from the plants gave prompt germination when the seed coats were ruptured and the seeds placed in water. Likewise, acid or base-treated seeds never showed as high percentage of germination (within 10–30 per cent) as seeds from which a portion of the coat was carefully removed. In short, there is no evidence of stimulation by the acid and base; they are simply more or less efficient agents for removing an obstruction to germination, never equaling in efficiency the mechanical method.

Intact seeds that have been soaked in water for 12 hours and then transferred to 2 mol. sodium chloride solution show rapid shrinkage, reaching a constant weight which they maintain as long as they are in the solution. These determinations are subject to rather large errors owing to the great surface represented by the 400 small seeds used in each test and the error of drying this surface to the same degree before each weighing. The permanent shrinkage in salt solution may be due to a semipermeable membrane in the seed coat or to a change in the water-imbibing power of the colloids of the coats and perhaps of the embryo owing to the presence of the salt. A. FISCHER found that the intact fruits of *Sagittaria* were not at all injured by five days' soaking in mol. copper sulphate solution. We find that one month's soaking of intact seeds of *Alisma* (1 mol. $CuSO_4$) does not injure their germination, if they are thoroughly washed and the coats opened before they are germinated. The opened seeds grow better in 0.000001 mol. $CuSO_4$ than in distilled water, but very little in 0.001 mol. $CuSO_4$. Soaking of the intact seeds in 10 per cent $AgNO_3$ for 24 hours kills all of them. From these facts it seems probable that in *Alisma* and *Sagittaria* the seed coats bear semipermeable membranes akin to those found in *Xanthium* (**29**) and various grasses (**5**, **28**).

1. STRUCTURE AND MICHROCHEMISTRY OF THE SEED COAT.—As the later experiments will show, the study of the structure and the microchemistry of the coat is much to the point. Fig. 1 is a camera drawing of a median longitudinal section of the coat. In the main the coat consists of two layers of cells: the outer yellow, red, or brown layer (*b*), and the inner colorless layer (*c*). At the micropyle end there is usually only one layer of cells. In the region where the two arms of the seed lie together, the two adjoining outer layers form a collapsed mass (*f*), while the cells of the inner layer are distinct. The single layer of cells at the micropyle end have deep indentations from the inner face at the cross-walls. As a consequence, the inner face in this region has a very undulating appearance. When the seeds germinate after acid treatment or when one picks off the coat at the micropyle end, a rather definite cap is removed. The cap seems to result from the breaking at one of the more outer of these indentations. Inside the cellular portion of the coat is an acellular lining mass of material consisting of a mixture of hemicellulose and pectic material. This layer is rather thick at the micropyle end of the embryo, and as thick or thicker at the opposite adjacent end of the embryo. In this connection it should be stated that it is common to find seeds with the outer layer of cells largely abraded lying in water in the dormant

condition. This shows that it is largely, if not entirely, the inner layer of cells of the coat, with perhaps the acellular layer, that is responsible for the failure to grow.

The methods given by TUNMANN (31) in his late work were followed in the microchemical tests. The following reactions justify the conclusions given in the description of fig. 1. After treating sections of the coat 48 hours with cuprammonia and then staining with ruthenium red, *a*, *c*, *e*, and part of *b* became red. Treatment for 48 hours with cuprammonia followed by 2 per cent ammonia dissolved all the section except *d* and part of *b*. Sudan III stained only the inner wall of the inner layer of cells. Chlorzinc iodide stained *a* violet and *e* blue. Chromic acid in 10 minutes dissolves everything except *d*, but after 16 hours *d* still remains intact. One half-hour's heating in 5 per cent hydrochloric acid dissolves a considerable part of *e*, especially at the hilum end and the small adjacent end of the coat. One-half hour's heating in 2.5 per cent sulphuric acid followed by treatment with IKI stains *e* blue; IKI alone gives no reaction in any part. Treatment with copper sulphate for 48 hours, followed by 2 per cent ammonia, dissolved the greater part of *c;* 2 per cent ammonia alone brings about no visible changes. Sections in water for 10 days showed the contents and most of the cross-walls in *c* dissolved, and the plano-convex cells at the large end swollen to about twice their former size.

These tests indicate that there is no cellulose in the coat. The blue coloration of *e* with chlorzinc iodide is probably due to the presence of hemicellulose rather than cellulose, as indicated by its insolubility in cuprammonia, its ease of dissolution by 5 per cent hydrochloric acid, and its ready transformation to amyloid by 2.5 per cent sulphuric acid.

It is evident that the coat is largely composed of pectic substances, with a suberized wall at *d* and an admixture of hemicellulose in *e*. The dissolution or marked swelling of *a*, the contents and cross-walls of *c*, and the plano-convex cells at the large end of the embryo, indicate that these are made of the type of pectic substances included under the terms pectic, parapectic, and parapectosic acids. Slight chemical transformation of these substances may easily weaken the coat, so that the imbibing embryo can rupture it, for we shall see later that the evidence is strong that the delay is due to the swelling force of the embryo being unable to break the restraining coat. We must bear in mind also that without any chemical decomposition acids and bases may increase greatly the water-absorbing power of the hydrophilous pectic and hemicellulose substances of the seed coats, but undoubtedly chemical transformations as well as physical are brought about in the acid and base-sensitive substances of the seed coat.

Heating the seeds to 99–100° C. for 0.5 hr. in 2 per cent HCl, followed by 0.5 hr. in 2 per cent NaOH, the usual method of dissolving out the middle lamella of cell walls, dissolves away most of the coat at the large end of the embryo and causes the embryo to break the coat and elongate 200–400 per cent. All regions of the coat were modified; in some cases the walls were apparently largely dissolved away, leaving a thin lamella, and in others gelatinized and greatly swollen. Some color dissolved out of the wall in the acid, but immediately upon transfer to the base the latter took on a deep red color. Heating to 99–100° in 2 per cent NaOH for 0.5 hr. gave similar results, and 0.5 per cent NaOH was almost as effective. Even at room temperatures, similar but less marked changes appeared in 2 per cent NaOH, and at this temperature 0.5 per cent caused noticeable exosmose of coat pigments and decomposition of the coats within a half-hour.

It is found that seeds treated with 0.3 N HCl for 1 hr. at 40° C. give 30–50 per cent germination in distilled water; much poorer germination in 0.000001 mol. $CuSO_4$, and none at all in 0.001 mol. $CuSO_4$. As has been pointed out, the embryos with coats partly removed germinate better in 0.000001 mol. $CuSO_4$ than in distilled water. It seems that the copper is rather readily absorbed by the gel-like coat and the consistency of the latter changed. The absorption is evidenced by the coat turning a dark dull brown rather rapidly in the stronger solution and slowly in the weaker. The rather plastic gel of the coat becomes hard and brittle and is easily cracked under the pressure of a scalpel. The hardening takes place to a more marked degree in untreated seeds soaked in water. Apparently this hardening of the coat gel increases the resistance of the coat to the enlarging embryo, and thereby prevents germination, even in the treated seeds. The facts reported in this paragraph show the danger of applying reagents to intact seeds and drawing conclusions from the results as to the effects the reagents have on the embryos.

2. WATER RELATIONS OF THE EMBRYO AND COAT.—In considering the water relations of the embryo and coat we will first examine the rate of absorption of water by the seeds under three different conditions: (1) seeds with the coats removed from the micropyle end of the embryo; (2) intact seeds untreated; (3) intact seeds treated with solutions of 0.2 N HCl for various periods. Of the six experiments performed only two will be given, since they represent the trend of the results. Table I gives the data for the first of these, and fig. 2 presents the results in the form of curves.

TABLE I

Showing percentage of increase over air-dry weight of *Alisma* seeds treated as follows: I, 400 seeds in water, coats broken; II, 400 seeds in water, coats intact; III, 400 seeds, coats intact, in 0.2 N HCl for 2 hours then transferred to water. Temperature 20° C.

No. of hours soaked	Percentage of increase on basis of air-dry weight		
	I	II	III
1	40	31.6	34
2	65	40	48
3	65	40	48
4	68	40	52
18	73	50	52
23	180	50	52

Table II gives the data for the second experiment, and fig. 3 gives the results in the form of curves.

Only the general features of the curves in these experiments are of value, because of the necessary errors involved in the experiment. The seeds are very small, and the 400 used in each culture have a large specific surface. Any variation in degree of drying before weighing gives considerable error. Another variation that appeared in these experiments was the promptness with which the acid treatment became effective. This accounts for the curve for intake by the acid treatment running close to the untreated ones in the first experiment and falling between the other two curves in the second experiment. In the first experiment very few of the embryos had broken the coat previous to the 43d hour, while

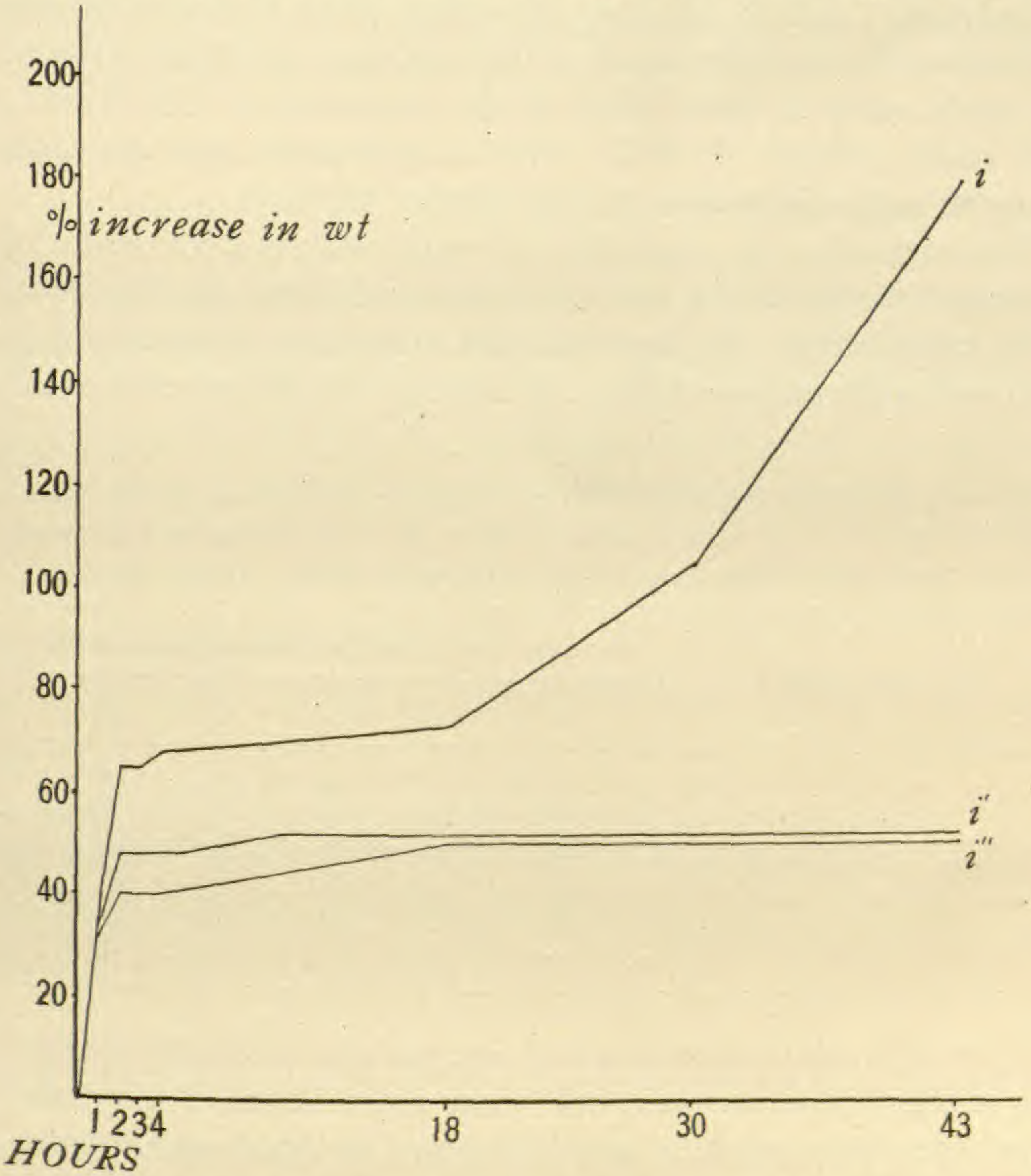

FIG. 2.—Rate of water absorption (percentage of increase over air-dry weight) by *Alisma* seeds with pericarp removed: temperature 20° C.; *i*, 400 seeds, coats broken and seeds soaked in water; *i′*, 400 seeds, coats intact, first two hours in 0.2 N HCl and rest of the time in water; *i″*, 400 seeds, coats intact and soaked in distilled water.

more than 30 per cent of them did so within 50 hours. In the second many of the embryos had broken the coats after 10 hours, and about half had broken the coats within 43 hours. The difference in the promptness of the action of the acid in these two experiments may be explained in part by the difference in temperature. When FISCHER used 0.2 or 0.3 N HCl with one or two hours' exposure as a forcing agent, he found 40° C. a very effective temperature. Individual seeds also show great variation in the readiness with which they swell to the maximum and begin growth. Old seeds, such as those used in the experiments with $CuSO_4$, seem more resistant to HCl. This is prominent even in cases where the coats are broken, as later results will show.

The curves for the absorption of water with the coats broken correspond closely in the two experiments reported, as they do in all the experiments. In these seeds the absorption of water is very rapid during the first 2–4 hours, amounting to 65–80 per cent of the air-dry weight, or to approximately 100 per cent of the dry weight. This is followed by a period of 10 or more hours of very slow water absorption, which in turn is followed by rapid water absorption. The first period of rapid water intake is largely a matter of imbibition and osmosis. The slow water absorption lying between these marks the interval between imbibitional and growth enlargement.

TABLE II

Showing percentage absorption of water (figured on the basis of air-dry weight) by *Alisma* seeds: I, coats broken, seeds in water; II, coats intact, seeds in water; III, coats intact, seeds 2 hours in 0.2 N HCl and then in water. Temperature 25° C.

No. of hours soaked	Percentage of water absorbed on basis of air-dry weight		
	I	II	III
1	32.5	23	45
2	55	33	52
6	80	45	53
9	80	45	61
21	101	51	....
32	160	51	73
52	....	....	96

With the untreated intact seeds the water absorption essentially all occurs within 2–4 hours, and approximates 45 per cent of air-dry weight, or about 70 per cent of dry weight. The imbibitional and osmotic capacity of the coat and embryo for water is not nearly satisfied, for, as is shown above, when the coat is broken water absorption is increased by about 50 per cent. From these facts, together with the structure of the seed, as well as from facts to be given later, one might be led to conclude that the embryo is hindered from swelling before its imbibitional forces are satisfied, because these forces are not sufficient to rupture the coat. The initial rate of water intake by both the intact seeds and the seeds with the coats broken equals that of the rapidly imbibing seeds of

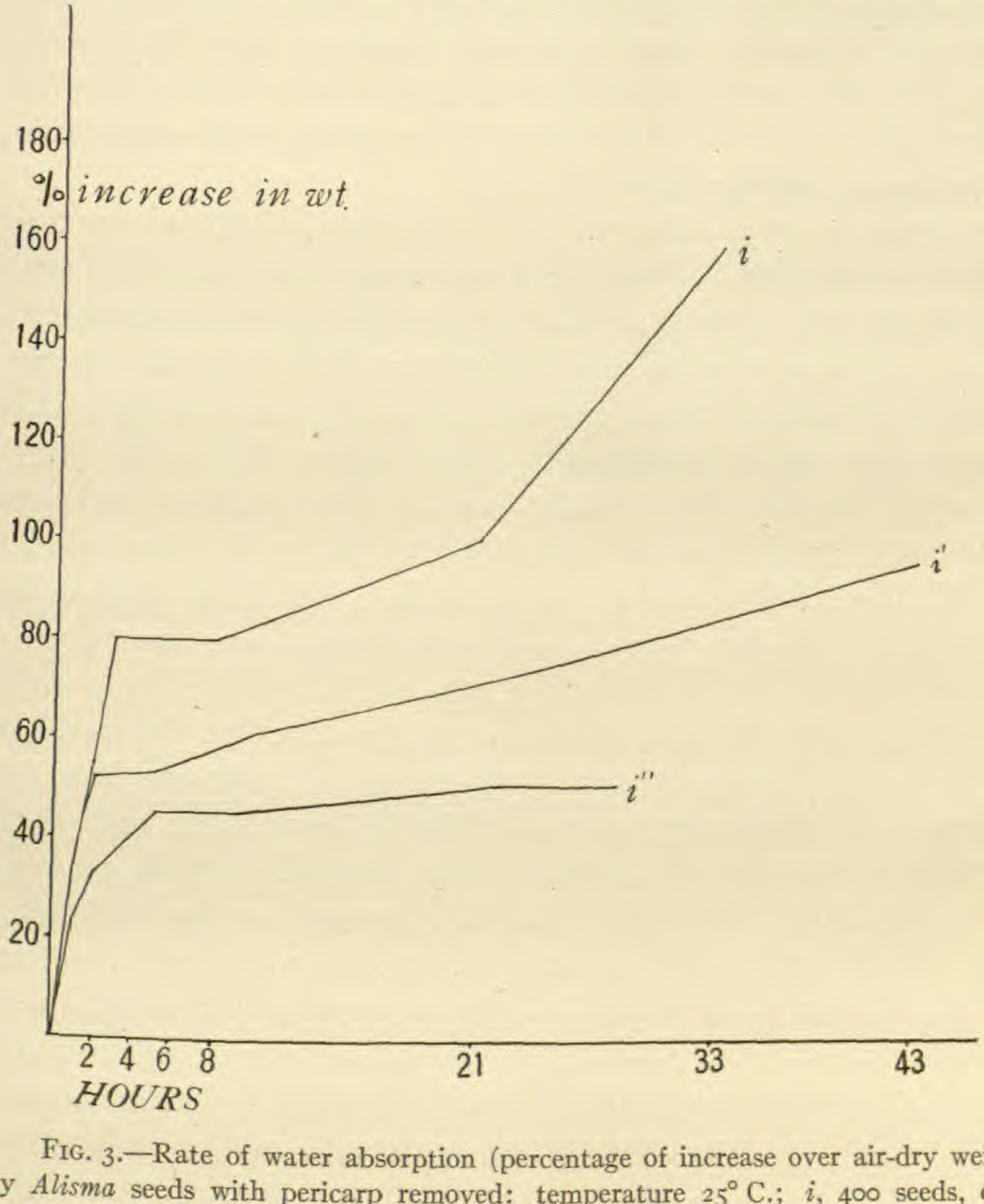

FIG. 3.—Rate of water absorption (percentage of increase over air-dry weight) by *Alisma* seeds with pericarp removed: temperature 25° C.; *i*, 400 seeds, coats broken and seeds soaked in water; *i'*, 400 seeds, coats intact, first two hours in 0.2 N HCl and rest of the time in water; *i''*, 400 seeds, coats intact and soaked in distilled water.

Xanthium as shown by SHULL (29), and far exceeds that of the slow imbibing seeds of the grasses as found by SCHRÖDER (28). In turn this rate of water intake is considerably exceeded by some of the Cucurbitaceae (32) (*Cucurbita argyrosperma*), where, however, the intake is largely due to a spongy capillary layer in the coat itself. On the other hand, we do not know to what degree the water intake in intact *Alisma* seeds is due to the coats; it is certainly due to this to a very large extent.

3. EFFECT OF ACIDS UPON RATE OF WATER INTAKE BY THE EMBRYOS.—MARTIN FISCHER (13) has found that bases and acids increase the rate as well as total amount of water absorption by colloids. BOROWIKOW (4) has shown that acids increase the rate of growth, or at least the rate of elongation of roots in water; while PROMSY (25) and ECKERSON (10) have shown that acids hasten the rate of germination of many seeds. These workers attribute the effect of the acids, at least in part, to the fact that they further the hydration of the colloids—in the case of the plant organs, the cell colloids. It will suggest itself immediately that the effect of the acids on the germination of water seeds may be due to their increasing of the imbibition force of the embryo, thereby enabling the embryo to rupture the coat. If this proves to be the case, the interesting situation appears that while the coat is the real cause of the delay, the effect of the acid is upon the embryo itself, increasing its imbibition power and enabling it to rupture the restraining coat. To determine this point experiments were made to find the rate of elongation of the embryo in water and in solutions of hydrochloric acid and sodium hydrate of various concentrations. In order to allow free access of the acid solutions and water to the embryo, the coat was removed at both ends of the embryo as described under "material." Only embryos that remained uninjured after the removal of the coats were used in the experiments. The first experiment was run with water, 0.01 N HCl, and 0.001 N HCl. Table III shows the rate of elongation of 20 embryos placed in water and measured at suitable intervals for 96 hours.

A great variation in the rate of elongation of the various embryos is shown. This seems to be characteristic of every crop gathered. Nos. 6, 13, and 20 are individuals showing low rate of elongation

TABLE III

EMBRYO	LENGTH OF EMBRYO	TIME IN WATER AND LENGTH OF EMBRYO (COATS BROKEN)						
	Dry	1 hr.	3 hrs.	6⅓ hrs.	23 hrs.	31 hrs.	50 hrs.	96 hrs.
1........	95.5	104	112	117	140	140.5	145	360
2........	100	115	121	125	138	141	152	396
3........	95	105	117	126	146	146	148	230
4........	97	103	117	121	121	122	124	161
5........	87	96	114	128	142	142	148	200
6........	96	101	114	128	141	138	146	147
7........	99	117	127	132	151	151	157	800
8........	99	109	118	129	168	199	230	430
9........	89	107	111	124	137	134	134	360
10........	85.5	89	99	107	113	113	116	165
11........	90	104	118	116	116	115	120	230
12........	94	101	117	129	143	143	170	560
13........	86	106	116	119	143	144	146	144
14........	93	95	118	124	134	140	157	570
15........	84	114	122	121	121	123	124	430
16........	82	89	101	103	114	136	139	180
17........	74	88	97	106	118	116	120	270
18........	100	111	125	141	185	210	276	540
19........	83	190	116	124	132	132	136	400
20........	95	111	122	124	132	134	136	140

TABLE IV

EMBRYO	LENGTH OF EMBRYO	TIME IN 0.01 N HCL AND LENGTH OF EMBRYO (COATS BROKEN)						
	Dry	1 hr.	3 hrs.	6⅓ hrs.	23 hrs.	31 hrs.	50 hrs.	96 hrs.
1........	92	114	114	112	120	....	122	....
2........	84.5	110	115	124	124	....	129	....
3........	103	106	113	121	120	....	123	....
4........	95.5	117	116	129	124	....	134	....
5........	91.5	104	112	124	126	....	126	....
6........	102	115	120	135	130	....	162	....
7........	91	100	102	112	112	....	111	....
8........	77.5	96	106	109	108	....	108	....
9........	75.5	98	95	106	106	....	105	....
10........	102	103	120	130	131	....	131	....
11........	89.5	97	105	115	116	....	126	....
12........	102	125	129	134	134	....	134	....
13........	93	110	116	120	135	....	130	....
14........	86	95	103	127	122	....	122	....
15........	86	96	105	111	115	....	112	....
16........	102	113	121	137	132	....	132	....
17........	91	110	115	125	124	....	127	....
18........	101	111	93	120	117	....	135	....
19........	106	111	121	139	132	....	138	....
20........	100.5	105	112	121	119	....	122	....

TABLE V

EMBRYO	LENGTH OF EMBRYO	TIME IN 0.001 N HCL AND LENGTH OF EMBRYO (COATS BROKEN)						
	Dry	1 hr.	3 hrs.	6⅓ hrs.	23 hrs.	31 hrs.	50 hrs.	96 hrs.
1........	83	99	100	108	103	....	106	106
2........	108.5	188	132	140	149	....	256	350
3........	85.5	103	108	112	127	....	129	145
4........	101	96	118	131	150	....	160	180
5........	92	109	120	125	120	....	122	125
6........	104.5	125	129	134	134	....	141	157
7........	98.5	107	115	122	130	....	130	144
8........	81	98	101	109	112	....	111	111
9........	87	101	109	120	125	....	125	125
10........	96.5	110	110	118	118	....	118	121
11........	98	125	127	132	131	....	132	137
12........	93	101	115	126	131	....	131	129
13........	90	112	125	129	126	....	128	125
14........	98	105	115	134	136	....	235	290
15........	87.5	98	114	110	114	....	119	110
16........	112	122	134	145	148	....	156	192
17........	85.5	95	111	119	122	....	122	156
18........	105	115	125	135	134	....	149	200
19........	96	101	114	123	120	....	121	127
20........	75.5	84	95	104	98	....	98	98

TABLE VI

Showing the elongation of 20 *Alisma* embryos each in water, 0.01 N HCl, and 0.001 N HCl. Coats removed at both ends of the embryo. Temperature 25° C.

Condition of the embryos	Total length of embryos	Average length of embryos	Percentage of increase over dry length
Air dry........................	1834.5	91.7	....
1 hour in water..............	2073.5	103.6	13.1
3 hours " "	2312.5	115.6	26.1
6⅓ " " "	2470.0	123.5	34.7
23 " " "	2759.5	137.9	50.4
31 " " "	2832.0	141.6	54.3
50 " " "	3025.0	151.2	64.9
96 " " "	6720.0	336.0	266.0
Air dry........................	1876.0	93.8	....
1 hour in 0.01 N HCl.........	2104.0	105.2	12.2
1 hour in 0.001 N HCl........	2257.5	112.9	20.3
6⅓ " " " "	2471.0	123.5	31.2+
23 " " " "	2462.0	123.1	31.2
50 " " " "	2512.0	125.6	33.9
	No further elongation		
Air dry........................	1878.0	93.9	....
1 hour in 0.001 N HCl........	2131.0	106.5	13.4
3 hours " " "	2319.0	116.0	23.5
6⅓ " " " "	2474.0	123.7	31.7
23 " " " "	2515.0	125.7	33.9
51 " " " "	2789.5	139.5	48.5
96 " " " "	3139.0	156.9	67.1

and a low total at the end of 96 hours, while nos. 7, 22, and 14 show both a high rate and a high total. Table IV shows the elongation of 20 embryos in 0.01 N HCl; and table V the elongation of 20 embryos in 0.001 N HCl.

Table VI summarizes the results for the 20 seeds each in water, 0.01 N HCl, and 0.001 N HCl, and fig. 4 presents the results in the form of curves. The percentage of elongation is platted on the abscissa and the time on the ordinate. It is evident from these

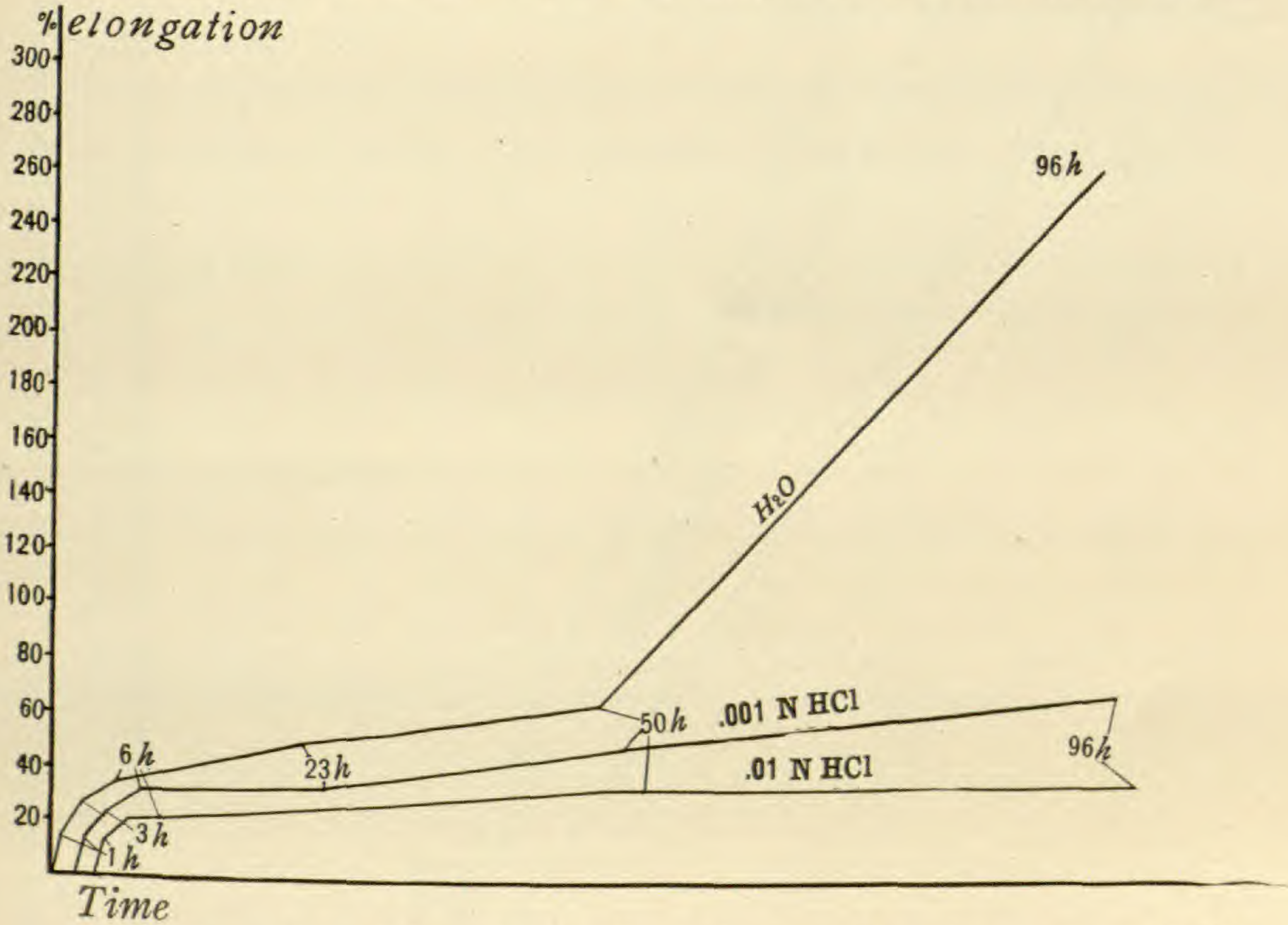

FIG. 4.—Rate of elongation of *Alisma Plantago* embryos in water, 0.01 N HCl, and 0.001 N HCl.

curves that the rate of elongation in water equals or exceeds that in either solution at all times, and shows a great advantage over both from 50 hours on. In the 0.001 N HCl cultures, the rate of elongation and the total elongation stands between that of water cultures and the 0.01 N HCl cultures.

A second experiment was performed using water, N/3000, and N/6000 HCl. These results are summarized in table VII and put in the form of curves in fig. 5. In this case the N/3000 HCl at

FIG. 5.—Rate of elongation of *Alisma Plantago* embryos in water, 1/3000 mol. HCl, and 1/6000 mol. HCl

first slightly leads water in rate of elongation, but falls behind it later. This slight early advantage can well be accounted for by the variation in the embryos from employment of so few, while the later falling behind water is undoubtedly related to injurious effects of the acid. The N/6000 HCl at first kept pace with water but later fell behind it.

TABLE VII

Showing the elongation of *Alisma Plantago* embryos in water, 1/3000 mol. HCl, and 1/6000 mol. HCl.

Condition of the embryos	Total length	Average length	Percentage of increase over air-dry length
Air dry	811	101.4	....
1 hour in water	899	112.5	10.5
3 hours " "	996	124.5	22.8
6 " " "	1080	135.0	33.2
24 " " "	1208	151.0	49.0
72 " " "	1967	246.0	142.5
Air dry	817	102.0	....
1 hour in N/3000 HCl	918	114.7	12.3
3 hours " " "	1035	117.0	26.6
6 " " " "	1102	137.7	35.0
24 " " " "	1193	148.9	45.3
72 " " " "	1788	223.5	119.0
Air dry	1005	100.5	....
1 hour in N/6000 HCl	1114	111.4	10.8
3 hours " " "	1222	122.2	21.5
6 " " " "	1312	131.2	30.5
24 " " " "	1449	144.9	44.1
72 " " " "	2107	210.7	109.0

Table VII A summarizes two other sets of measurements on the effect of N/3000 and N/6000 HCl on the rate of elongation.

TABLE VII A

Average percentage elongation for 10 embryos each in water and the HCl solution mentioned.

	1 hr.	2 hrs.	3 hrs.	4 hrs.	5 hrs.
N/3000 HCl	10.1	16.9	24.7	28.9	32.0
N/6000 HCl	10.8	16.9	23.0	27.0	30.0
Water	9.1	16.2	21.9	27.5	30.6
N/3000 HCl	11.0	20.0	26.0	29.0	32.0
Water	10.0	16.8	24.7	28.7	31.0

From all these measurements it seems barely possible that acid solutions hasten somewhat the rate of elongation of the embryo, and that the maximum effect appears at about N/3000 in a 5-hour period, but the effect is not great.

Table VII B shows the effect of various concentrations of NaOH on the rate of elongation of embryos. The solutions were protected from CO_2 of the air, but of course were continually being transformed to carbonates by the CO_2 from the respiring seedlings, so the concentration of the hydrate was falling from the beginning of the experiments.

TABLE VII B

Average percentage of elongation for 10 embryos each in water and the NaOH solutions mentioned.

	1 hr.	2 hrs.	3 hrs.	4 hrs.	5 hrs.	20 hrs.
0.01 N NaOH	12.9	17.8	23.5	28.2	30.5	43.0
0.001 N NaOH	12.7	19.2	24.9	32.6	35.7	49.0
Water	10.2	16.5	22.6	27.0	30.3	42.9
0.0001 N NaOH	11.9	18.9	25.0	30.7	34.7	46.9
N/3000 NaOH	11.9	18.0	24.2	27.6	30.4	40.3
Water	10.4	17.3	23.2	28.0	30.1	39.0

In each case the results in the various solutions should be compared only with their corresponding checks in water; also the checks in water are not comparable with each other, because the various experiments were not run at the same temperatures.

The base seems to increase imbibition rate very noticeably in contrast to acid, and there seems to be a distinct optimum concentration which for a 20-hour period lies in the region of 0.001 N NaOH. Such an optimum appears for the swelling of various colloid gels in the case of both acids and bases.

There is then doubtful evidence for acids causing increased rate of elongation of the embryo, and very certain evidence for bases doing so. It is probable, but by no means established, that along with such an increase in rate of elongation there goes an increase in force of elongation. If this be so, the base and perhaps the acid may further the breaking of the coat in part by an effect on the embryo.

4. TURGOR IMBIBITION AND GROWTH ELONGATION OF THE EMBRYOS.—The object of the experiments reported in this section

is to see to what extent the elongation of the embryos in water is a matter of imbibition and osmosis, and to what extent a matter of growth. Embryos with the seed coats removed at both ends were measured and placed in water for various lengths of time and the elongation determined. They were then transferred to plasmolytic agents and the amount of shrinkage determined. Cane sugar was finally chosen as the water-absorbing agent, for it produced permanent shrinkage and showed relatively low toxicity. Embryos which have been soaked in water for 12 hours and then transferred to 2 volume mol. cane sugar for 24 hours are still capable of normal growth when transferred to water. On the other hand, lithium chloride, which in saturated solution has great water-absorbing power, proved unsatisfactory both because of its toxicity and the variation in results.

Table VIII shows the average change in length caused in 8 embryos by soaking them 2.5 hours in water and then transferring them to 2 volume mol. sugar solution for 40 hours.

TABLE VIII

Elongation of 8 *Alisma* embryos soaked 2.5 hours in water, then transferred to 2 volume mol. cane sugar solution. Seed coats removed from both ends of the embryo. Temperature 25° C.

Treatment of embryos	Total length of embryos	Average length of embryos	Percentage of elongation
Air dry	814.0	101.8	
2.5 hours in water	969.5	121.2	19.1
5 " " sugar solution	866.0	108.2	6.4
25 " " " "	856.0	107.0	5.2
40 " " " "	840.0	105.0	3.7
50 " " " "	840.0	105.0	3.7
Extreme individuals—		Length of embryo	
1. Dry		109	
2.5 hours in water		139	27.5
40 " " sugar solution		111	1.9
2. Dry		96	
2.5 hours in water		108	12.5
25 " " sugar solution		98	2.0
40 " " " "		98	2.0

Two and one-half hours in water gives an elongation of 19 per cent of the air-dry length, while the transfer to the sugar solution shrinks the embryos back to within 3.7 per cent of the air-dry length. The two extreme individuals are also given in the table. One showed elongation in water of 27.5 per cent and shrinkage in the sugar solution back to 1.9 per cent; the other extreme individual showed an elongation of 12.5 per cent in water and shrinkage back to 2 per cent in the sugar solution. In all the measurements of this section we find great variation between the individual embryos.

Table IX shows the elongation of 10 air-dry embryos, freed from the seed coats at both ends, when they are placed in 2 volume mol. cane sugar.

TABLE IX

Elongation of 10 *Alisma* embryos placed in 2 mol. cane sugar solution for 52 hours. Seed coats removed at both ends of the embryos.

Treatment of embryos	Total length of embryos	Average length of embryos	Percentage of elongation
Air dry	1080.0	108.0	....
5 hours in sugar solution	1093.0	109.3−	1.2+
20 " " " "	1109.7	111.0−	2.7+
40 " " " "	1113.5	111.3+	3.1
52 " " " "	1114.5	111.4+	3.2

After 52 hours these embryos showed an average elongation of 3.2 per cent. Allowing for considerable variation in individuals, it is evident that about the same final elongation results whether air-dry embryos are soaked directly in 2 mol. cane sugar or whether they are first soaked in water for 2.5 hours and then transferred to the sugar solution. The 19 per cent elongation of the embryo which occurs in water in the course of 2.5 hours is all a matter of imbibition and turgor. The intact seed itself, as we shall see in the next section, elongates on the average 10 per cent when it is soaked in water for a similar period. It is probable that the embryo in the intact seed thus soaked elongates far less than 10 per cent, for the acellular mass at both ends of the embryo and at the arch show much swelling in water, as do the other layers of the coats. Were the embryos in the intact seed allowed to carry on their imbibitional and osmotic intake of water freely and break off the coat cap at the large end of the embryo, within 2.5 hours the embryos would extend 10 per cent of their total length beyond the coat. Since the embryo has two arms of about equal length, the imbibitional and osmotic swelling would cause the embryo to extend 20 per cent the length of the seed beyond the limits of the coat. The rapid elongation of the freed embryos is brought about in part by the rapid swelling of the pectic walls. *These facts force one to believe that delay in germination in the Alisma seed is caused by the seed coat preventing the complete imbibitional and osmotic elongation of the embryo.* If one assumes that, on the average, the embryo in the soaked intact seed has elongated only 3–4 per cent of its air-dry length, and this is probably not far from correct, one sees that in the soaked condition of the seed the embryo is in water equilibrium with 2 volume mol. cane sugar solution. Such a solution has an osmotic pressure exceeding 100 atmospheres according to later estimates (**24, 27**). This probably gives a rough estimate of the force with which the embryo is pressing against the coat in the intact seed lying in water.

TABLE X

Elongation of 8 *Alisma* embryos soaked in water 5 hours and then transferred to 2 volume mol. cane sugar solution. Seed coats removed from both ends of the embryo. Temperature 25° C.

Treatment of embryos	Total length of embryos	Average length of embryos	Percentage of elongation
Air dry	803	100.4	...
5 hours in water	1050	131.2	30.8
5 hours in sugar solution	879	109.9	9.5
25 " " " "	861	107.6	7.2
40 " " " "	863	107.9	7.5
Extreme individuals—		Length of embryo	
1. Air dry	...	97.0	...
5 hours in water	...	131.2	40.2
5 " " sugar solution	...	116.0	19.5
25 " " " "	...	114.0	17.5
2. Air dry	...	103.0	...
5 hours in water	...	128.0	24.2
5 " " sugar solution	...	110.0	6.8
25 " " " "	...	111.0	7.7

Table X shows the changes in length brought about in 8 embryos by soaking them 5 hours in water and then transferring them to 2 volume mol. cane sugar for 40 hours. Five hours in water gives an average elongation of 30.8 per cent, and in the extreme individuals

40.2 per cent and 24.2 per cent. Transfer to the sugar solution caused an average shrinkage back to 7.2 per cent elongation.

In the extreme individuals the shrinkage was back to 17.5 per cent and 7.7 per cent elongation. It is evident that permanent elongation or growth has set in to a slight but measurable degree at the end of 5 hours. In one of the extreme individuals the growth was considerable. This is another example of the great individual variation that is always evident. Fig. 6 shows these results in the form of curves.

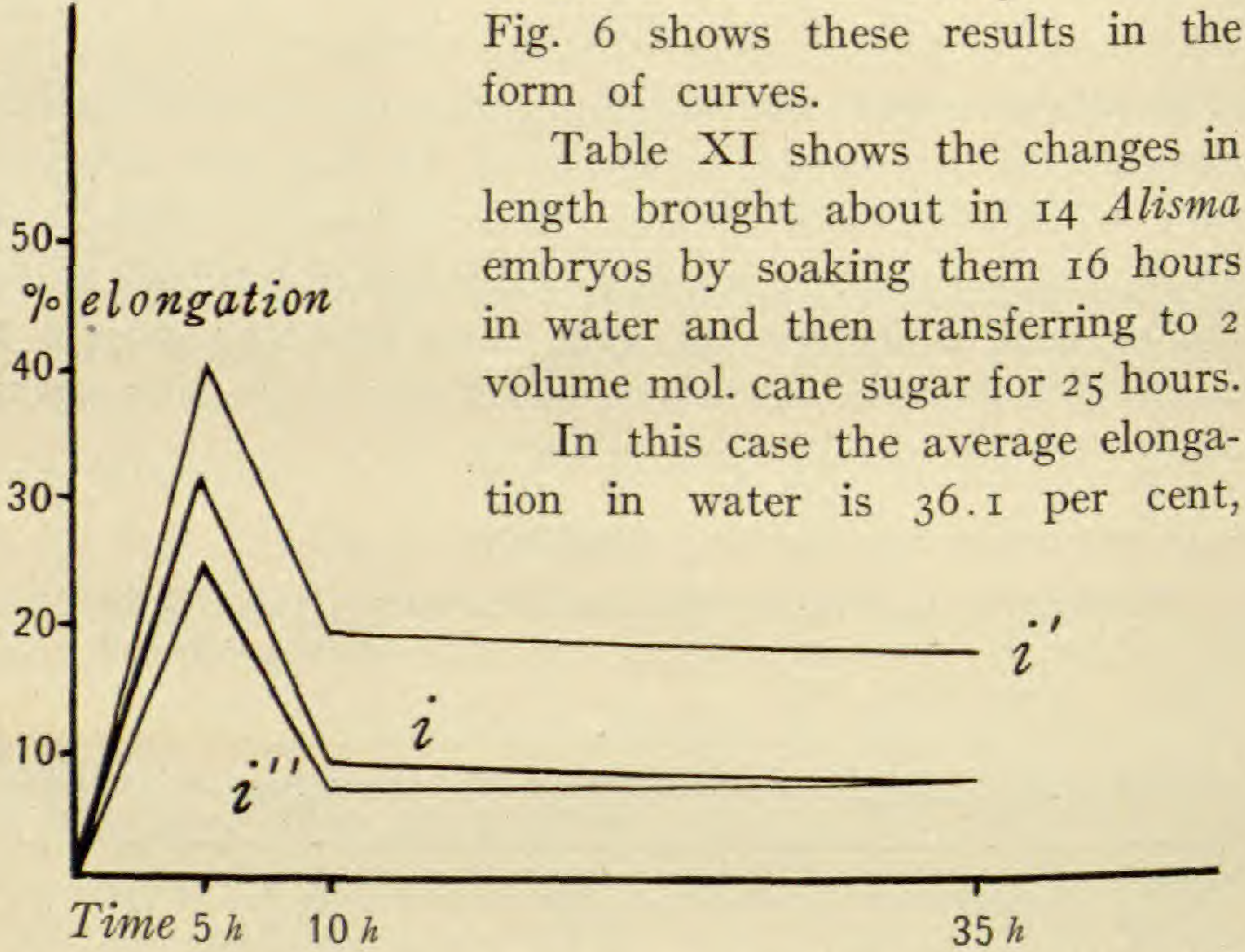

FIG. 6.—Percentage of elongation of *Alisma* embryos (seed coat removed at both ends) soaked in water 5 hours, then placed in 2 mol. cane sugar solution: measurements were made on dry embryos, after 5 hours in water, and after 5 and 30 hours in the sugar solution; *i*, curve for the 8 embryos studied; *i'*, curve for the individual showing the greatest swelling; *i''*, curve for the individual showing least swelling.

Table XI shows the changes in length brought about in 14 *Alisma* embryos by soaking them 16 hours in water and then transferring to 2 volume mol. cane sugar for 25 hours.

In this case the average elongation in water is 36.1 per cent, while the sugar causes a shrinkage back to 11 or 12 per cent elongation. The behavior of the extreme individuals is also shown in this table. Greater permanent elongation is evident than in the embryos in water for 5 hours. Here also there is some evidence of a slight permeability to sugar as shown by a slight swelling from 5 hours to 10 hours. Fig. 7 shows these data in the form of curves.

TABLE XI

Elongation of 14 *Alisma* embryos soaked in water 16 hours and then transferred to 2 volume mol. cane sugar solution. Seed coats removed from both ends of the embryos. Temperature 25° C.

Treatment of embryos	Total length of embryos	Average length of embryos	Percentage of elongation
Air dry	1378	98.4	...
16 hours in water	1876	134.0	36.1
5 “ “ sugar solution	1536	109.6	11.3
25 “ “ “ “	1543	110.2	11.9
Extreme individuals—		Length of embryo	
1. Air dry	...	98.5	...
16 hours in water	...	149.0	51.0
5 “ “ sugar solution	...	115.0	16.7
25 “ “ “ “	...	115.0	16.7
2. Air dry	...	102.0	...
16 hours in water	...	129.0	26.4
5 “ “ sugar solution	...	105.0	3.0
25 “ “ “ “	...	108.0	5.0

Table XII shows the behavior of 13 *Alisma* embryos kept in water 16 hours and then transferred to 1 volume mol. cane sugar.

TABLE XII

Elongation of 13 *Alisma* embryos placed in water 16 hours and then transferred to 1 volume mol. cane sugar for 25 hours. Seed coats removed from both ends of the embryo. Temperature 25° C.

Treatment of embryos	Total length of embryos	Average length of embryos	Percentage of elongation
Air dry	1283.0	98.7	...
16 hours in water	1716.0	132.0	33.7
5 “ “ sugar solution	1535.0	118.0	19.0
25 “ “ “ “	1565.5	120.4	22.0
Extreme individuals—		Length of embryo	
1. Air dry	...	87.0	...
16 hours in water	...	138.0	58.5
2 “ “ sugar solution	...	109.0	25.3
2. Air dry	...	94.0	...
16 hours in water	...	115.0	22.3
25 “ “ sugar solution	...	109.0	16.0

The 1 mol. cane sugar shows far less shrinkage than the 2 mol. Fig. 8 shows these data in the form of curves.

This series of experiments shows that the imbibition and osmotic forces alone cause an average elongation of about 20 per cent in the embryos partly freed from the coat. The elongation all occurs within 2.5 hours when the temperature is maintained at 25° C. This elongation of the embryo is probably three to five times that taking place when the intact seed is soaked for the same time or even for months. It is probable that the swelling of the embryo in thickness is inhibited to quite as large a percentage by the coat, for when one observes the embryo protruding from the coat, owing to the removal of the cap at either end, he sees a marked constriction at the line of the broken edge of the coat. The much swollen acellular layer seems to restrict greatly the swelling of the portion of the embryo within it. Growth begins within five hours on the average when partly naked embryos are placed in water at 25° C. Even 16 hours in water at this temperature shows rather slight growth, although the average elongation is about 36 per cent. This all emphasizes the main rôle of osmosis and imbibition in the early very rapid elongation of

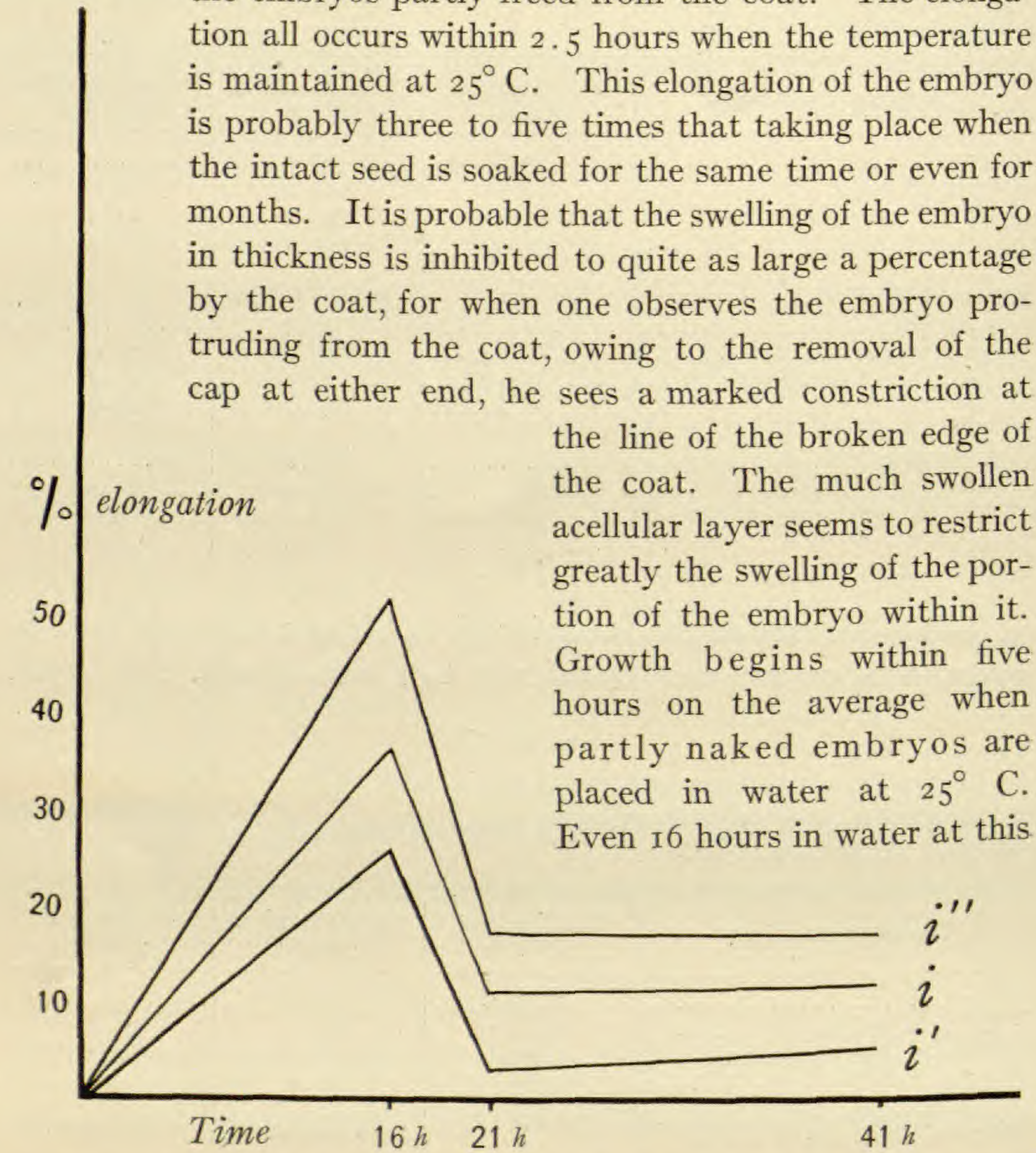

FIG. 7.—Percentage of elongation of 14 *Alisma* embryos with seed coats removed at both ends, soaked 16 hours in water, then placed in 2 mol. cane sugar solution for 25 hours: *i*, curve for the 14 embryos studied; *i'*, curve for the embryo showing the greatest swelling; i'', curve for the embryo showing least swelling.

the embryo. The great elasticity of the embryo as compared with that of the intact seed is also noteworthy. The results of this section enable one to approximate the force (imbibitional osmotic) with which the embryo of *Alisma* in the saturated condition is pressing against the coat; this approximates 100 atmospheres (**24, 27**).

ATKINS (**34**) finds in certain legume seeds that only imbibitional forces are at work taking up water until growth actually begins; that is, a plasmolytic agent (KNO_3) does not inhibit the rate or final total amount of water taken up. In *Alisma* seeds, whether the coats are intact or not, as is seen from the experiments in this and previous sections, semipermeable membranes are functional from the beginning. With the coats broken, it is very likely protoplasmic membranes that are functional. It is evident that ATKINS' findings are not of universal application.

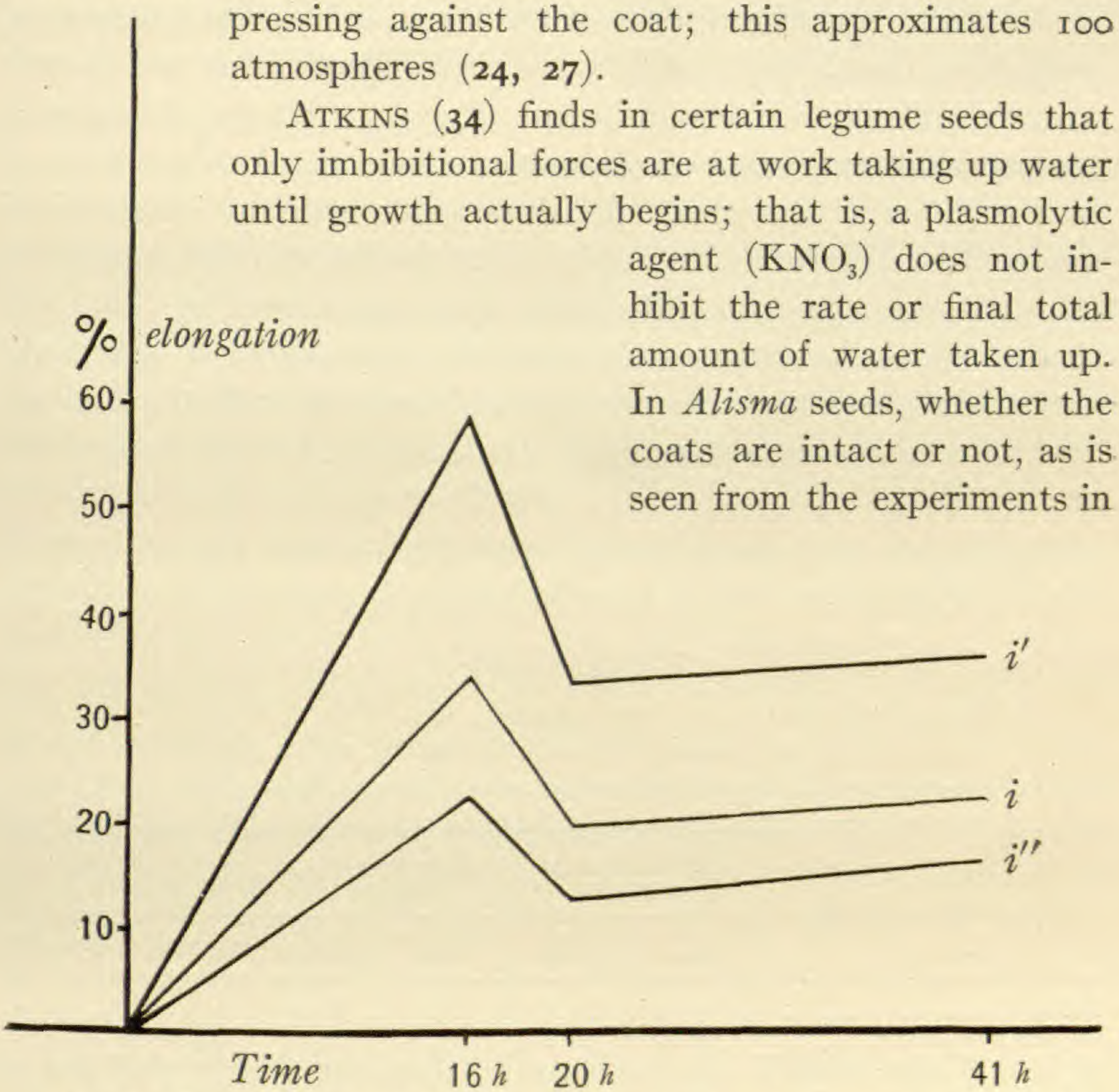

FIG. 8.—Percentage of elongation of 13 *Alisma* embryos (coats removed at both ends) placed in water for 16 hours, then transferred to mol. cane sugar solution for 25 hours: measurements made on dry embryos, after 16 hours in water, and after 5 and 25 hours in the sugar solution; *i*, curve for the 13 embryos studied; *i'*, curve for the individual showing most swelling; *i''*, curve for the individual showing least swelling.

5. Elasticity of the seed coat.—An attempt was made to determine the elasticity of the seed coat of *Alisma*. Thirteen good seeds freed from the ovary wall were selected and the length measured from the crown of the arch to the tip of the big arm and the width across the middle of the two arms. The seeds were soaked one day in water and remeasured and placed in 2 mol. cane sugar solution and measured after 15 and 24 hours. They were then transferred to water for one day and measured; then followed four days in dry air with the final measurement. Table XIII shows the modifications brought about in the two dimensions by the various treatments. The slight shrinkage caused by the transfer from water to cane sugar is especially noticeable. It shows the very slight elasticity of the seed coat as compared with the embryo. The total elongation of the intact seed, which is reached after two or three hours and becomes no greater even after months, is also slight (10 per cent) as compared with the embryo (19 per cent in 2.5 hours, 30.8 per cent in 5 hours, and 36.1 per cent in 16 hours).

TABLE XIII

Thirteen *Alisma* seeds, ovary wall removed, seed coats intact, soaked in water, followed by 2 volume mol. sugar solution, followed by water, and finally dried in air to get an estimate of the elasticity of the coats. Temperature 25° C.

Treatment of the seeds	Width in scale lengths		Length in scale lengths		Percentage of increase over dry size	
	Total	Average	Total	Average	In width	In length
Air dry................	334.0	25.7	905.8	69.7	....	....
1 day in water.........	494.0	38.0	993.5	76.4	14.0	9.8
15 hours in sugar solution	481.0	37.0	963.0	74.1	11.0	6.3
24 " " " "	478.0	36.8	952.0	73.2	10.0	5.3
1 day " water.......	508.0	39.6	996.5	76.6	17.0	10.0
4 days " air..........	447.5	34.4	931.0	71.6	3.0	3.0

6. Oxygen pressure in relation to the growth of Alisma seeds and seedlings.—We have already shown that the failure of *Alisma* embryos to break the coats, as well as their dormancy, is due to the fact that their possible imbibitional and osmotic swelling can be only in small part consummated in the intact seed. It has long been established (Nobbe, *Samenkunde*. 1876) that the swelling of seeds is merely a mechanical process which goes on

independently of oxygen supply. It is evident, therefore, that lack of oxygen cannot be the cause of dormancy in these seeds. MAZÉ (20) finds that seeds of most land plants will not germinate under water, and that storage under water in otherwise good germinative condition soon leads to loss of vitality. Good aeration of the water or addition of hydrogen peroxide to it will lead to germination under water. In contrast to this, GUPPY (15), FISCHER (12), and others have shown that seeds of many water plants may lie in water for years without germinating and still retain their vitality. This in itself suggests that the seeds of water plants are very different from land plants in their behavior toward a deficiency in oxygen. In *Alisma* we have shown that the embryo in the intact imbibed seed lacks much of being fully saturated with water. This probably holds for the seeds of many water plants, as one of us (6) has pointed out, and may in part account for the lack of injury from long storage under water. So far as investigated, seeds of water plants have extremely low minimum oxygen pressures for germination, if indeed any free oxygen is necessary for the process. The fact that their physiological processes can go on normally under water probably accounts in part for the capacity for water storage. One of the authors (6) has already pointed out this fact for seeds of several water plants.

During this investigation we have made a large number of experiments determining the relation of the amount of oxygen pressure to the growth rate, course of development, and chlorophyll formation in *Alisma* seeds and seedlings. We need mention only a few of the data and general results.

In all the experiments with the effect of various oxygen pressures on germination and development, the embryos used were partially freed from the coats and in an uninjured condition. Part of the experiments were run *in vacuo* and part by the displacement of air by hydrogen. In general, the cultures in hydrogen did not do as well as those *in vacuo*. This may be due to a slight toxicity of hydrogen itself or to some impurity in it. The hydrogen was derived from the electrolytic dissociation of water and freed from oxygen by passing it through a quartz tube filled with small copper disks and heated white hot with a blast flame. The hydrogen proved to be essentially free from oxygen, as shown by its failure to color potassium pyrogallate. The experiments *in vacuo* were performed as follows. The seeds freed from coat cap and soaked in water at 0° C. for 12 hours were placed in 30 cc. distilling flask bearing about 20 cc. of distilled water. The main neck of the distilling flask was sealed off just above the side neck, and the side neck reduced to a capillary tube at one region. A Geryk air pump (capable of exhaustion to less than 0.1 mm.), protected by a drying system with great water-absorbing capacity, was attached to the side neck and the flask exhausted. The flask was then placed under water at 35° C. for one-half hour and the exhaustion continued. During the process the water generally boiled down to 5 or 10 cc., depending upon the bore of the capillary region. While still maintaining the boiling and exhaustion, the capillary was carefully sealed off.

Since toxicity entered into the results with hydrogen, we will report only experiments *in vacuo*, and of these only 2 of the 30 or more cultures need to be given. In these experiments 10 seeds were used in each culture. The controls were in Stender dishes bearing 0.5 cm. column of distilled water. The cultures were run in total darkness at a temperature of 21° C. for 21 days.

TABLE XIV

Length of the seedlings *in vacuo*		Length of the seedlings in full air pressure	
I	II	I	II
40 mm.	35 mm.	70 mm.	70 mm.
30	35	60	60
30	35	60	60
30	40	50	60
40	40	50	60
25	30	45	55
25	30	45	55
25	30	40	50
32	30	40	50
25	15	40	50
Av. length. . 30 mm.	32 mm.	50 mm.	57 mm.

The imbibed embryo in the intact seed is approximately 2.5 mm. long, so that the total elongation in the vacuum cultures equals

28–30 mm., 1120–1200 per cent; while in full air pressure, other conditions the same, an elongation of 48–55 mm., or 1820–2200 per cent, occurs. In these conditions only the stored food of the embryo is available for growth. It is evident that there is a much more economical use of the food in the presence of oxygen than in its absence, and still the growth is very considerable in its absence. It is possible that the use of nutrient solutions would have induced much greater growth, for it is certain that much leaching (35) of the salts of the embryos must have occurred in these experiments.

Even in light, no leaf branches are ever formed in the seedling grown *in vacuo*, nor does any chlorophyll develop. In weak diffuse light at 25° C., the seedling did not develop chlorophyll even after a month, if the air pressure was less than 5 mm. If the air pressure exceeded 5 mm., chlorophyll generally developed in these conditions. This shows that the oxygen pressure demanded for greening is rather slight though easily measurable. Seedlings in darkness under full air pressure all develop one or more leaves. If the air pressure is reduced much below 5 cm., no leaf branches develop even after two months. If the air pressure is more than 15 cm., there is an abundant formation of leaf branches. The development of a primary root also seems to be dependent upon oxygen pressure. Nearly every seedling growing in a drop culture in a Van Tieghem cell shows the early development of a primary root, as do seedlings growing on the water surface. Fewer seedlings developing at the bottom of a considerable layer of water show primary roots, and none in cultures with air pressure reduced much below 5 cm. The growth of water seeds and seedlings *in vacuo* stands in contrast to the facts found by SHULL (30), BECKER (2), and ATWOOD (1) for the seeds of land plants, where definite oxygen minima exist.

IV. General discussion

Work to date has shown that delayed germination of seeds is secured in a variety of ways: by almost absolute exclusion of water by seed coats, as in the "hard-seeded" legumes and species of several other families; by limiting the degree of swelling of the embryo by surrounding structures, as in *Alisma* and probably in seeds of a large number of water plants; by reduction of oxygen supply below the minimum necessary for germination by means of seed or fruit coats or other structures, as is the case in *Xanthium* (30) and a number of other Compositae (2), in *Chloris ciliata* (14) and other grasses, and in *Datura Stramonium;* and finally, perhaps, by deficiency in salts. To these must be added delays due to embryo characters, as slowness of acid development in the hypocotyl of the haw, apple, peach, and perhaps other Rosaceae. The investigation of the mechanics of delayed germination in any particular seed should consider all of these possibilities, and not assume, under the incubus of the overworked stimulus conception with its indefiniteness and implied inscrutability, that the cause must lie in the embryo. The German investigators, with few exceptions, have been especially prone to the stimulus view and its implication that in characters of the embryo alone dormancy is determined. They of course except the seeds that are known as "hard-coated." This inclination to the stimulus conception is evident in FISCHER'S (12) interpretation of his results with seeds of water plants. We find BEHRENS (3) assuming that the pricking of intact seeds has its effect only through stimulus action, and not implying at all the possibility of greater oxygen admission or mechanical weakening of the coats. The same can be said of KIESSLING (17) working with various grasses, and KINZEL (18) with the "light-hardened" seeds of *Nigella*.

Again, in their work with light-sensitive seeds, with the single exception of GASSNER (14) on *Chloris ciliata*, the German investigators have assumed that the light has its effect always upon the embryo and never upon the coat. One must remember that the coat is most strongly exposed, and that it reduces the light intensity greatly before it reaches the embryo, at least in heavy coated seeds like *Phacelia tanacetifolia*. It is quite as possible that photochemical changes are occurring in the coat as in the embryo. NEUBERG has found that about every group of organic substances, polysaccharides, fats, proteins, etc., is hydrolized, and often the completely hydrolized products are further transformed by light, if iron, manganese, or certain other salts are present. These decompositions occur in non-living substances, so there is no reason for assuming that photochemical transformations are limited to the embryo and are not occurring in the more highly illuminated surrounding structures. Again, it is well established that light increases the permeability of protoplasmic membranes to various solutes. The possibility appears that it may likewise increase the permeability of non-living semipermeable membranes of the coat to oxygen or perhaps other materials needed for germination. Likewise, they have failed to see that the fixation of the carbon dioxide released in respiration may in some cases supply the oxygen needed for germination. It is strange that these workers have never done the evident thing of experimenting with naked embryos to see what their needs are in the way of germinative conditions. In seeds like *Viscum album* it is evident that the demand for light cannot be related to the seed coats, but in most light-sensitive seeds the conclusion is not evident.

It is established, however, that not all cases of delayed germination are due to coat characters acting in conjunction with embryo characters, but there are some embryos, or rather organs of some embryos, that are dormant when entirely naked. But even here it is probable that the explanation of the action of forcing agents will not need to be veiled under such an indefinite term as stimulus. ECKERSON (10) has shown that the hypocotyls of haw and apple seeds are dormant because of slowness in developing acidity, a condition necessary for proper water absorption for growth and for the formation and action of digestive and perhaps respiratory enzymes. The acid development begins even during swelling in all organs of most seeds, as it does in the cotyledons of the haw and apple, but the hypocotyls in the latter seeds remain slightly basic or neutral for a long period. It has been shown (9, 10) that temperature and water and oxygen supply determine to a great degree the speed of acid development in the hypocotyls mentioned. Likewise, the seed coats and carpel walls play an important rôle here, so far as they affect these factors. Acids are good forcing agents for dormant hypocotyls; apparently, they have their significance in this fundamental relation to water absorption and to the formation and activity of enzymes. LEHMANN (19) has suggested that light and agents and conditions that substitute for light in light-demanding seeds have their effect in bringing about hydrolysis of proteins. His evidence is hardly conclusive. It is quite possible, however, that dormancy in an embryo may be due to the abeyance of some single simple process under a given set of conditions. If so, it may be any one of several aside from protein hydrolysis. If such cases exist, they stand more or less in contrast with the case worked out by ECKERSON (10).

FISCHER found phosphoric and certain organic acids more effective as forcing agents for *Alisma* than their dissociation would insure on the basis of hydrogen ions. This we are unable to explain. Of course FISCHER worked with chaffy fruit coats intact, and it is possible that organic acid had its main function in acting as a culture medium in the carpel wall, so that fungi and bacteria could get a hold on the seed coats. The seed coats seem to form excellent media for the growth of fungi and bacteria. Both layers of cells are very rich in reducing substances. If cultures were started in the carpel wall, they would probably thrive on the seed coats. In contrast to the seed coats, the embryos are very resistant to the attack of fungi and bacteria. As FISCHER points out, one gets good germination in putrefying cultures. This we are quite confident is not due to acid formation, but is rather due to an organism actually decomposing the coats. At 25° C., 0.001 N hydrochloric acid will not cause the rupture of the coats in *Alisma* even after many days' soaking, and this concentration of acid permits but little growth in the naked embryo. It is evident then that the acid could not be strong enough to cause the swelling of the embryo to break the coat and still allow the embryo to grow after it had broken the coat. FISCHER had the preconceived notion that the embryo was dormant, and therefore neglected the possibilities that have proved to be much more to the point. This makes it probable that in putrefying waters in nature the germination is brought about by the direct attack of the seed coats by the organisms, and not through the action of acids formed by the organisms. In the face of the fact that he could soak *Sagittaria* seeds in 1 mol. copper sulphate for 5 days and later secure their germination by treating with acids and placing in water, FISCHER comes to the conclusion that the seed coats are very permeable to solutes in general:

This has been a standing assumption for a long time, but an assumption not backed by evidence. The claim has received lately most telling counter-evidence by the work of Brown (**5**), Schröder (**28**), and Shull (**29**), from which it appears that semipermeable membranes are of rather common occurrence in seed coats. We have already given evidence for a sodium chloride excluding membrane in the coat of *Alisma*. We find likewise that while the intact seed is not injured by many days' soaking in 1 mol. copper sulphate, the naked embryo will not grow markedly in a 0.001 mol. solution of the same salt.

The conclusions drawn in this paper must be applied only to *Alisma* seeds, but it will be surprising if they do not hold for the very similar seeds of *Sagittaria*, and for the less similar seed of *Eichhornia*, and perhaps for the seeds of many water plants.

The power of acids to hasten the germination of the haw must not be identified with the forcing effects in *Alisma*. In the first case, the effect is on the dormant hypocotyl itself, and in the second, on the coat in the main. In the first case it is hardly necessary to confuse the matter by calling the effect a stimulus, and in the second such an explanation is quite aside from the point.

The peculiar effect of copper sulphate solutions on the germination of acid-treated intact seeds shows the danger of assuming that such effects of salts are on the embryos rather than the coats when intact seeds are used.

We wish to express our gratitude to Dr. Sophia Eckerson for most of the microchemical determinations reported in this paper.

V. Summary

1. Dormancy in the akenes of *Alisma Plantago* is due to the mechanical restraint of the seed coat. This restraint enables the seed to be in water for years without germination.

2. The chaffy carpel wall plays no part in the dormancy. Of the three layers of the seed coat (the outer single layer of reddish-brown cells, the inner single layer of white cells, and the lining acellular pectic hemicellulose material), the outer seems to play no

part in the delay. The effect must be attributed to one or both of the inner layers.

3. As the intact fruit lies in water in the saturated condition, the embryo itself does not half (probably not more than one-fourth or one-fifth) consummate its possible imbibitional and osmotic swelling. The embryo only partly swollen thus lies for years in water, restrained in its swelling by the seed coat, against which it must be exerting a pressure of approximately 100 atmospheres.

4. The air-dry seed (freed from the carpel wall) when placed in water swells rapidly. It increases 40 per cent of its air-dry weight in the course of two hours. From this time on it shows a slow increase to 50 per cent of its air-dry weight, which is maintained constant even after long periods of soaking. A large part of the water absorption is due to the hydrophilous pectic and hemicellulose substances of the seed coat, especially the inner acellular layer.

5. When the coat cap is removed from the large end of the embryo, thus leaving the embryo more free to continue its imbibitional and osmotic swelling, the seed swells even much more rapidly, reaching about 60 per cent of its air-dry weight in two hours and more than 100 per cent after 20 hours. The imbibitional and osmotic swelling gradually passes into growth enlargement.

6. With the coat cap removed from both ends of the embryo and the seed placed in water, the embryo elongates 19 per cent of its air-dry length in 2.5 hours. This would extend the embryo at least 20 per cent the length of the swollen seed beyond the limits of the seed coats. This elongation is all imbibitional and osmotic, involving no growth. Five hours' soaking gives an elongation of 30 per cent of the air-dry length of the embryo. This is only in very small part due to growth. Sixteen hours' soaking gives 36 per cent elongation, which involves considerable growth. Imbibitional and osmotic swelling alone would extend the embryo of *Alisma* far beyond the limits of the swollen seeds.

7. The seed coat is composed almost entirely of pectic substances which are very easily transformed by weak acids and bases. Besides bringing about chemical changes in these substances, acids and bases change their water relations as is true of hydrophilous colloids in general.

8. There is some evidence that acid increases the imbibitional force of the embryo. If such is the case, the increase is very slight. Bases increase greatly the rate of elongation of embryo.

9. It seems that the effect of acids and bases on the germination of *Alisma* seeds is largely to be explained by a weakening of the seed coats, so that the imbibitional and osmotic swelling of the embryo is capable of breaking away the coat cap at the large end of the embryo. It is possible that they are also in part effective by increasing the force of the imbibitional and osmotic swelling.

10. This gives a chemical-physical explanation which displaces the vague implications of the term "stimulus."

11. The seeds of *Alisma*, as of the seeds of water plants in general, are capable of lying in water for years in the imbibed condition without losing their vitality. In contrast to this, seeds of land plants will withstand such storage for a relatively short time.

12. The embryo of *Alisma*, at the expense of its stored foods alone, is capable of more than 120 per cent elongation in total absence of oxygen. For various other phases of its development (greening, branching, development of primary root) it requires some free oxygen. The greening requires at least 5 mm. of air pressure, the branching more than 5 cm. of air pressure, and the general development of primary roots still more.

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SPORE CONDITIONS IN HYBRIDS AND THE MUTATION HYPOTHESIS OF DE VRIES[1]

EDWARD C. JEFFREY

(WITH PLATES XXII–XXV)

At the end of the sixteenth century CHARLES DE L'ECLUSE became professor of botany in the University of Leyden. He brought with him from Vienna to his new abode plants of the tulip, which had been introduced from Turkey into southeastern Europe. These formal plants he cultivated with great success in his own garden, and was fortunate in arousing a keen and even commercial interest among the phlegmatic Dutch; so much so that when the excitement was at its height, his garden was invaded and many of his choicest varieties stolen. Thus arose the famous "Tulipomania," which has been immortalized by DUMAS. Three hundred years later another Dutch botanist has become the author of another botanical sensation, which will doubtless also live in history. Professor DE VRIES has initiated the investigations on the genus *Oenothera* in connection with the hypothesis of mutation or saltatory origin of species. His discovery first that *Oenothera Lamarckiana* and subsequently that other species of the genus are capable of producing distinct so-called elementary species when cultivated on a large scale has very properly attracted a great deal of attention, particularly in the continent of North America, which prides itself, not altogether without reason, on its openness to new ideas. Thus it has come about that the genus *Oenothera,* and in particular *O. Lamarckiana,* has become the battleground of the mutation hypothesis on the botanical side. We have had during the past decade a veritable "Oenotheromania" comparable to the "Tulipomania" of three centuries ago.

There have been many objections raised to the mutation hypothesis of DE VRIES, particularly on the part of geneticists of

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[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 70.

standing. The Englishman BATESON was apparently the first of these to record the opinion that *Oenothera Lamarckiana* was a hybrid, and he has been followed in this expression of opinion by many American scientific students of plant breeding. The greatest difficulties which have arisen in connection with *Oenothera Lamarckiana*, as studied by geneticists, have been in connection with its origin, and all herbaria, which could be supposed in any way to throw light on its original much discussed appearance, have been ransacked, without apparently a final or decisive result. The antecedents of this much disputed species, however, are now of less importance in view of the fact that other and possibly all species of *Oenothera* are likewise "mutating." The question of mutation, so far as it depends for its resolution on the study of *Oenothera*, has fortunately at the moment a much wider basis than the conditions found in any individual species of the genus, concerning the origin of which there may be serious doubt. As will be shown later in the present article, many of the species of *Oenothera*, if not all, are in the same peculiar and obviously extremely significant state as is *Oenothera Lamarckiana*. Attempts have been made to synthesize *O. Lamarckiana* from other American species, but this line of attack seems to lose some of its importance from the fact that almost any wild American *Oenothera* has apparently the same genetical peculiarities and the same power of "mutating" as has *Oenothera Lamarckiana* itself.

It has long been recognized on the part of scientific students of plant breeding that spore infertility is an important characteristic of hybrids. This view, originally expressed well on to a century ago, has lost none of its force in the intervening years. It is further recognized quite generally that relatively fixed hybrids may be produced. The opinion is at the present moment rapidly gaining ground, both on the zoological and on the botanical sides, that many of our wild species of plants and animals are in reality more or less fixed hybrids. In the case of plants we have peculiar advantages in connection with the recognition of this fact. We owe the most important results which have yet been produced on this continent, in this direction, to the studies of BRAINERD upon spontaneous hybrids of the violets and Rosaceae, for the most part published in *Rhodora*. BRAINERD'S line of attack has been from the systematic, and, to a less extent, from the genetical side. It is the purpose of the present and succeeding articles to demonstrate evidence from the morphological side that hybridism is extremely widespread in nature, among the higher or angiospermous plants in particular, and that there is every reason to suppose that it has been an agency of great importance in *multiplying* species, although it is logically inconceivable in the present state of our biological knowledge that it could have presided at their *origin*.

In the following paragraphs the general conditions of sporogeny, so far as they are related to the matters under consideration, will be discussed and compared in the main groups of the embryophytes.

Beginning with the liverworts, the writer has examined a number of examples from the Marchantiales, Anthocerotales, and Jungermanniales (both acrogynous and anacrogynous), with the result that in no case which has come under his observation are there present any abnormal products in connection with spore-formation, unless the elaters can be considered abnormal structures in this respect. These elements, although undoubtedly derived from potential spore mother cells, are perfectly normal and have no significance in relation to a possible genetical impurity, any more than have the abortive spores and spore mothers found in the case of heterospory. In *Boschia*, as is shown in LEITGEB'S classic monograph, the elaters are represented by sterile cells without tracheary thickenings. In *Sphaerocarpus* the multinucleate condition of the elateriform cells clearly reveals their morphological derivation from spore mother cells. Fig. 1 illustrates the condition of the spores in *Marchantia polymorpha*, as an example of the liverworts. The elaters and spores are clearly seen, the former as spirally thickened bands, and the latter as dark or lighter spherical bodies. Where the spores are light in hue, the plane of section does not include the protoplasmic contents. Whether light or dark, the spores are of equal size and unshrunken.

An examination has been made of the sporogonia of a considerable number of the leafy mosses, with results, as far as they have gone, similar to those presented by the liverworts. The only genus examined which showed imperfect or abortive spores was

Sphagnum. As is well known, this genus is extremely variable, and the species are often difficult to distinguish. It appears accordingly not improbable that the abortion of spores sometimes found here may be correlated with hybridism in nature. Fig. 2 shows the homogeneous character of the spores in the common species *Polytrichum commune*. As is the case in the leafy mosses or Phyllobrya in general, there are no elaters present.

Numerous representatives of the Lycopodiales, heterosporous and homosporous, were examined and abortive spores were seen to be characteristically absent. Five species of *Lycopodium*, as well as *Phylloglossum*, *Psilotum*, *Tmesipteris*, *Selaginella*, *Isoetes*, *Lepidodendron*, *Spencerites*, etc., all yielded uniform results.

One species of *Equisetum* has long been recognized to be of hybrid origin, namely *E. littorale*, which from its anatomical and external features is a hybrid between *E. arvense* and *E. limosum*. It is one of the few conventionally recognized hybrid species, and is characterized by the large number of abortive spores which are found in its sporangia. Miss HOLDEN has recently published in *Science* an interesting account of abortive sporogeny, accompanied by blended anatomical features, in *Equisetum variegatum* var. *Jesupi*. It appears beyond question, from Miss HOLDEN'S work, that this variety is the result of a cross between *E. hiemale* and *E. variegatum*. It is further probable from her work that other recognized varieties of species of *Equisetum* are likewise hybrids in their origin. Fig. 3 represents a section through part of a sporangium in *E. hiemale*. Although all of the spores are not equally in the plane of section, it is clear that they are normal and unmingled with abortive individuals. In fig. 4 is shown a view of a section through a sporangium of *E. variegatum* var. *Jesupi*. Here there are practically no sound spores, unless one to the right of the figure can be considered sound. Even the spores of relatively large size and dark (protoplasmic) contents are abnormal. The smaller and abortive spores, which enormously predominate in the figure, have very scanty protoplasmic contents or none at all. Contrary to statements usually made in regard to abortive spores of *Equisetum*, the elaters are present, although not normally developed. They can be seen as circles bounding the spore proper at an interval. They do not ordinarily separate into the usual bands, which is doubtless the reason their presence has not been heretofore recognized in the case of abortive *Equisetum* spores. Examination has been made of a number of sporangia of *Calamites*, and here, as in the living *Equisetum*, when uncontaminated by species crossing, the spores are perfect, although without the elaters, which appear likewise to have been absent in the mesozoic *Neocalamites*.

The ferns may next be considered, and for the purpose of the present investigation they may be divided into the Polypodiaceae and the remaining ferns. Taking the latter first, no evidence of hybridization in the recognized older groups of ferns has been found in this connection. Fig. 5 illustrates in section a sporangium of *Angiopteris evecta*. The spores are obviously all perfect. Examination of the genus *Marattia* has led to similar results. Other representatives of the Marattiaceae were not available. The Ophioglossaceae, as represented by the three genera *Ophioglossum*, *Botrychium*, and *Helminthostachys*, were studied and no evidence of abortive spores found in the sporangia. Representatives of the Gleicheniaceae and Schizaeaceae yielded similar results. *Osmunda regalis*, *O. cinnamomea*, and *O. Claytoniana* have strikingly perfect spores. *Todea barbara* showed similar conditions. Hymenophyllaceae, as represented by *Hymenophyllum* and *Trichomanes*, and the Cyathaceae by *Alsophila* and *Dicksonia*, yielded the same results. Of the heterosporous ferns, *Marsilia* and *Pilularia* were available, and these showed uniform spores. *Azolla* of the Salviniaceae has uniform spores.

Numerous cases of hybridism among the Polypodiaceae, accompanied by greater or less spore abortion, are known. The writer has personally examined only one hybrid fern of this group, namely the so-called *Adiantum hybridum* of gardeners. The spores here are apparently completely abortive, at any rate in greenhouse specimens. It will be unnecessary to enlarge upon the hybridism of the Polypodiaceae further, because recently an admirable statement has been published by BENEDICT,[2] in which he discusses the subject fully. He reports 11 natural hybrids for the eastern

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[2] BENEDICT, R. C., Bull. Torr. Bot. Club **36**: 1909.

states, representing three genera. The status of some of these hybrids is beyond question because the cross has been repeated experimentally. Spore sterility is a marked feature in such cases. A large number of examinations of normal species has been made in the Polypodiaceae in the present connection, and uniformity of spore-formation has been found in such cases.

The Cycadales are of considerable interest from the evolutionary standpoint. The writer has been unable to find evidence of imperfection in the mature output of the sporangium. Two species of *Zamia*, as well as *Cycas revoluta*, *Stangeria paradoxa*, *Bowenia* sp., and *Microcycas*, were all examined with unvarying results. Fig. 6 shows part of a section through the microsporangium of *Zamia floridana*. The spores appear round where seen in face view, and somewhat crescentic when examined in profile. Both views may be seen in the illustration.

The monotypic *Ginkgo*, the sole survivor of a group once abundant in the Northern Hemisphere, has pollen which, in the large number of cases in which I have examined it, has proved to be singularly free from variation in size in the same sporangium. I have yet to see an imperfect microspore of *Ginkgo*. Fig. 7 shows the pollen as seen in a transverse section of the microsporangium. It will be noticed that the pollen grains present different appearances according to the plane of section and to the angle of incidence. The fact that the pollen in this interesting genus is winged as in *Pinus* can already be seen with the magnification employed in fig. 7. Fig. 8 presents a much more enlarged view, and the wings can be clearly discerned. It is curious that this striking feature of the pollen appears to have escaped notice. The wings bear the same relation to the cells of the microgametophyte within the pollen as they do in the Abietineae, and the number of prothallial cells in *Ginkgo* corresponds with that found in the Abietineae and not with the conditions found in the cycads, with which they are usually more nearly associated. A contribution from this laboratory dealing with the extremely striking features of resemblance between the Ginkgoales and the Abietineae will appear very shortly. The resemblance extends to nearly all the more important details of the reproductive and vegetative organs of the two groups.

The writer has had the opportunity of examining large quantities of coniferous material of all the subtribes, since his own studies have been particularly in this group. The Abietineae, Araucarineae, Podocarpineae, Taxineae, and Cupressineae in the broad sense, have all been studied in most of their genera, and in the case of the larger genera in a number of species. Perfection of pollen development was found to be characteristic of the microsporangia of this important group. The only case of pollen abortion which has come to light during the present investigation is that furnished by one species of *Abies*, to be described later. Fig. 9 illustrates the pollen conditions in *Araucaria Cooki*, cultivated in a greenhouse. It will be seen that the grains are all perfect, the difference of size being due to their greater or less inclusion in the plane of section. The greenhouse conditions have obviously not affected the morphological perfection of the pollen. Fig. 10 shows part of the same section under a higher degree of magnification. The numerous prothallial cells, which are a feature of the organization of the gametophyte produced in the pollen grains of the Araucarineae, can be seen.

The Gnetales have been studied in all their three surviving genera. *Welwitschia* has entirely perfect grains. The same statement holds for the three or four species of *Gnetum* which I have examined in this connection. Two species of *Ephedra* were examined, with the result that the pollen appeared to be without tendency to abortion. It is perhaps of interest to record, in this connection, that the pollen of *Ephedra* and *Welwitschia* are strikingly alike externally, both being characterized by spiral striation of the external coat of the oval grains. This feature was not found in the case of *Gnetum*. It has not been thought necessary to introduce an illustration of the microspores of the Gnetales, although several were prepared for this purpose.

The Monocotyledons may next be considered. Fig. 11 shows the pollen conditions in a wild species, *Iris versicolor*. The pollen is obviously perfect in development. Many hybrids of the various species of *Iris* are grown in gardens, in fact most of the more attractive cultivated irises are the result of hybridization. Fig. 12 illustrates the pollen conditions in a hybrid improvement of *Iris germanica*. The species of *Iris* are usually quite free from any indication of hybrid contamination, with the possible exception of *Iris Hookeri*, which has not been fully studied. In fig. 12, the pollen is largely abortive and is reduced in amount, as is frequently the case in hybrids of all kinds.

Fig. 13 shows the pollen conditions in *Lilium canadense*. The grains are here quite perfect. Similar observations were made on *Lilium philadelphicum* and the common Easter lily. Fig. 14 illustrates the pollen abortion which is the usual condition in our cultivated *Narcissus*, nearly all of which are known to be of hybrid origin. The shriveled and abortive condition of a large number of the grains is quite evident. Fig. 15 pictures the condition of the pollen in *Lachenalia Nelsoni*, a plant very frequently grown in greenhouses in winter. This hybrid between two natural South African species of the genus was made by an English clergyman, in window culture, many years ago. Most of our garden tulips show their hybrid origin by large quantities of abortive pollen. A very large number of observations has been made upon monocotyledonous cultivated hybrids, with the unvarying result that hybridism was characteristically connected with a considerable amount of pollen degeneracy. On the other hand, monocotyledons grown in the greenhouse under obviously somewhat unnatural conditions, where of pure specific origin, showed, in all cases examined, good pollen. This was the case, for example, in species of *Gasteria*, *Agave*, etc.

We now advantageously turn our attention to the very large natural group of Dicotyledons. Here hybridization both natural and resulting from the intervention of man is extremely common. We may first consider with advantage the Rosaceae, in view of BRAINERD's very interesting studies on this family. This investigator has shown that a great many natural hybrids of *Rosa* and *Rubus* occur in nature. The morphological observations made in this family entirely confirm BRAINERD's results, and extend them in an apparently very interesting way, which will be summarized here, a fuller account being reserved for future publication. Not only are certain of the Rosaceae recognizable as hybrids, on account of their transitional external features of organization, Mendelian phenomena, etc., but certain others, which have not revealed themselves as hybrids in these ways, are clearly such, as a result of the study of their spores. As an example let us take our mountain ashes (*Rosa* or *Rubus* furnish just as good illustrations, or in fact almost any of the larger genera of the Rosaceae in the Northern Hemisphere). In Europe and Asia it is generally recognized that the valid species of *Sorbus* have between them a number of natural hybrids. In the eastern and northern region of North America, we have two common species of mountain ash, *Sorbus americana* and *Sorbus sambucifolia*. These have been shown in connection with the present investigations to have pollen which is to a considerable degree abortive. The same observation has been made in regard to the European *Sorbus aucuparia*. In fact, the only species of *Sorbus* yet examined in this connection with perfect pollen is one growing in Japan. Or turning to another genus, *Prunus*, most of the species examined had imperfect pollen. Of the common species in New England investigated, the only one with perfect pollen was *Prunus serotina*, which flowers somewhat later than the others and is consequently phenologically isolated, just as is the case geographically with the Japanese *Sorbus* mentioned above. Illustrations of a similar nature could be given to an almost unlimited extent from studies on the Rosaceae, which are as yet far from complete. We have consequently to distinguish in the case of the Rosaceae, if the morphological features are taken into account as well as the data of systematic botany, three kinds of individuals, namely pure species, recognized species which from the condition of their pollen are in reality concealed hybrids or crypthybrids, and recognized hybrids. In some genera the multiplication of species through hybridization is very large; for example, over 4000 species of *Rubus* have been described in Europe, and in this country SARGENT and others have described a very large number of species of *Crataegus*.

Nearly all our common garden herbaceous dicotyledons, which from the nature of things are capable of hybridization, are hybridized. For example, we may take the carnations, the petunias, the phloxes, the chrysanthemums, the calceolarias, certain primroses, etc. Without concerning ourselves further with the dicotyledonous cases of hybridization, we may now advantageously turn our attention to the consideration of the Onagraceae, the family which has supplied the famous case of *Oenothera Lamarckiana*. We may conveniently begin with our common garden fuchsias, which are known to be of hybrid derivation from *Fuchsia magellanica*, an inhabitant of southern South America. Fig. 19 shows the interesting pollen conditions found in certain cases in the cultivated *Fuchsia*. Many of the grains are shriveled and empty. In other instances still less pollen perfection was observed; in fact in some flowers there is practically no functional pollen and the anther sacs do not open, but dry up without dehiscence. In still other cases the pollen does not definitely shrivel up, but the grains are of very unequal size and contain a very scanty supply of protoplasm.

Let us now turn to the genus *Epilobium*. Our common fireweed, which inhabits somewhat generally the Northern Hemisphere, is illustrated in fig. 16. The figure includes all four anthers, which are laid open in the plane of section. It will be observed that the pollen in their cavities is perfect. The illustration is purposely made to show a large amount of pollen to demonstrate how normal the pollen development is in *Epilobium angustifolium*, the common willow herb, or fireweed. Fig. 17 shows a similar section of the flower of *Epilobium hirsutum*, the giant willow herb, which occurs near ballast heaps and is not uncommonly cultivated in New England. Even with the low magnification used, it becomes at once clear that the pollen development is abnormal, some of the grains being smaller and without protoplasmic contents. Fig. 18 shows a higher magnification of two of the anther cavities in this species, and on the left may be seen two sound grains and five abortive ones. On the right only abortive grains appear. The pollen in certain species of *Epilobium* occurs in tetrads, and in a smaller number of others it is quite separate at maturity. Those with the latter condition of the microspores are quite commonly put under the genus *Chamaenerion*. *Epilobium hirsutum* consequently shows evidence of hybridism in the presence of abortive spores in its anther cavities. For comparison with this type, the pollen development of the genus *Rhododendron* in the Ericaceae was examined. In a pure species, such as *Rhododendron catawbiense*, all the grains are alike and all the tetrads are similar to one another. There are a number of hybrid derivatives of this species in cultivation. Two of these, named *R. Metternichi* and *R.* Mrs. H. W. Sargent, have been examined in this connection. The conditions found are exactly like those presented by *Epilobium* in the stricter sense. Some of the tetrads of pollen are entirely abortive, some only partially so, and in still others all the grains are perfectly developed. An extremely interesting fact in the present connection is the statement in standard European works on the genus *Epilobium* that its species all hybridize naturally with one another. In our specimen of *Epilobium hirsutum*, we obviously have to do with one of these hybrid conditions.

We are now, without further consideration of the Onagraceae, which would take us beyond the scope of the present article, in a position to consider advantageously the genus *Oenothera*. In fig. 20 is shown a portion of the anther contents of *Oenothera Lamarckiana*. Obviously the pollen is largely abortive. In fact, in his *Mutationstheorie*, DE VRIES does not conceal the fact that about one-third of the pollen of this species is shriveled and non-functional. Not only is this true of the species, but it is likewise true of its so-called mutants, some of the weaker of these, such as *O. nanella* and *O. lata*, having almost no good pollen. But it is not in *O. Lamarckiana* alone that one finds imperfect pollen. All of the numerous species of the genus which I have examined in this connection show more or less the same state of affairs. Fig. 21 illustrates the conditions in one of our commonest oenotheras, namely *O. biennis*. Even with the low magnification used, it is easy to see that the contents of the eight anthers shown photographically are far from normal. Fig. 22 shows the conditions as they appear under a higher magnification. Obviously here, as in *O. Lamarckiana*, a large amount of the pollen is sterile. All that can be said is that the genus *Oenothera* is in general, judging from its morphological condition, in a state of high genetical impurity. Fig. 23 shows a rather low magnification of several of the anthers of *O. Lamarckiana*. *O. grandiflora* is illustrated under the same degree of magnification in fig. 24. In this species the number of abortive pollen grains present is very small, and it is in fact the least characterized by shriveled microspores of any species which I have yet had the opportunity to examine. It would seem consequently that it has either largely recovered from the effects of previous hybridization or else that the hybridizing ancestors have been less incompatible than those of, for example, *O. biennis*.

It is obvious that in the Onagraceae we have a peculiar condition, which is likewise present in other families of the angiosperms. Taking the Rosaceae as an illustration, there are in the various genera of this family numerous forms which are generally recognized on external characters as hybrids. Some of these conditions have recently been described by BRAINERD. In addition to admitted hybrids in the Rosaceae, there are a number of forms which very generally are admitted as good species on account of their relative constancy and the absence of observed intergrading types. In many of these recognized species, however, the morphological conditions, found in connection with the formation of the reproductive elements, are clearly those of hybrids. In view of the common occurrence of admitted hybridism in the family, these may properly be regarded as concealed or crypthybrids. The value of internal structure in the case of hybrids, as a key to the conditions involved, has not been sufficiently regarded in the past. It is obviously of the greatest importance in the Rosaceae. A further group of forms is found in the Rosaceae, where the reproductive structures are those of normal species elsewhere. That is to say, the pollen, the more readily investigated of the reproductive elements, is quite sound. This condition, for example, is characteristic of monotypic genera or genera with few well marked species (for example, *Kerria*, *Rhodotypus*, *Cydonia*, etc.). In genera with numerous species, contamination is very likely to be present, except in cases where the species are very distinct, or are isolated phenologically or geographically. For example, *Rosa* or *Sorbus*, geographically isolated in a mountainous or insular habitat, is genetically pure; while *Rosa* or *Sorbus* of continental or lowland origin is very likely to be genetically impure.

The principles cited above in the case of the Rosaceae have an obvious bearing on the conditions found in the Onagraceae.

Here, as in the larger family Rosaceae, we have the occurrence of admitted hybrids in certain genera (*Epilobium* and *Fuchsia*), side by side with recognized species. In other cases the recognized species have for the most part the same pollen conditions as those characteristic of hybrids. This state of affairs is found to a very large and striking degree in the genus *Oenothera*. Since the species of *Oenothera* to a very considerable extent, particularly those which have been used in investigations of a mutational or genetical nature (*O. Lamarckiana*, *O. biennis*, etc.), are under the strongest possible suspicion of hybrid origin, it follows that any conclusions drawn from their genetical behavior, in connection with the vexed problem of the origin of species, must be subject to a large degree of reserve. So far as the conduct of *O. Lamarckiana* and other species of the genus throws any light at all upon the species problem, it is in connection with the *multiplication* of species by hybridization, a very different matter indeed from the actual *origin* of species.

The relation of hybridization to "mutation" has recently been strongly emphasized for animals by GEROULD.[3] The reader is referred to this highly interesting and important contribution on the zoological side, for an expression of views very similar to the conclusions reached in the present article in the case of plants. In plants we have the great advantage of being able to a very large extent to supplement genetical and taxonomic data by the examination of internal organization.

The writer[4] has previously made a general statement on the questions here involved. GATES[5] has recently published an article in which he attempts to show that mutation and hybridization are independent phenomena. His conclusions seem to be fatally invalidated by the fact that his experiments were carried on upon *Oenothera* species and "mutants." The situation is apparently the same as would present itself if a chemist worked with impure chemicals or a physicist with mixed radiations.

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[3] Species-making by hybridization and mutation. Amer. Nat. **48**: no. 570.

[4] The mutation myth. Science N.S. **39**:488–491. 1914.

[5] Breeding experiments which show that hybridization and mutation are independent phenomena. Zeitschr. Induktive Abst. und Vererb. **2**: Heft 4.

Summary

1. Spontaneous hybridization is comparatively rare among lower plants, but very common in the angiosperms.

2. A long recognized criterion of hybridism is sterility, partial or complete, of the reproductive cells. In plants this is recognized with particular ease in the case of the pollen.

3. In forms which are ordinarily recognized taxonomically as species, pollen infertility frequently indicates past genetical contamination.

4. In families such as the Rosaceae and the Onagraceae, we find grading into each other recognized species and recognized hybrids, having in common the character of partial or complete reproductive sterility, most easily recognized in the organization of the pollen.

5. This situation points inevitably to the hybrid origin of these abnormal species.

6. Species of this type may conveniently be called crypthybrids.

7. The species of *Oenothera* and many of those of *Epilobium* and probably those of *Fuchsia* as well are crypthybrids.

8. This condition must be clearly recognized in connection with any investigation in regard to the origin of species based on material of this sort, that is, on crypthybrids such as *Oenothera Lamarckiana*, *O. biennis*, etc.

9. Although there appears to be good evidence that hybridism has been an important cause of the multiplication of species, there seems to be no logical support for the view that it has to do with their actual origin.

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EXPLANATION OF PLATES XXII–XXV

PLATE XXII

FIG. 1.—Spores and elaters of *Marchantia polymorpha;* ×250.

FIG. 2.—Spores of *Polytrichum commune;* ×250.

FIG. 3.—Spores of *Equisetum hiemale;* ×200.

FIG. 4.—Spores of *E. variegatum*, var. *Jesupi*, a hybrid; ×200.

FIG. 5.—Spores of *Angiopteris evecta;* ×200.

FIG. 6.—Pollen of *Zamia floridana;* ×250.

PLATE XXIII

FIG. 7.—Pollen of *Ginkgo biloba;* ×250.

FIG. 8.—Pollen of the same; ×700.

FIG. 9.—Pollen of *Araucaria Cooki;* ×200.

FIG. 10.—Pollen of the same; ×400.

FIG. 11.—Pollen of *Iris versicolor;* ×150.

FIG. 12.—Pollen of *Iris germanica* hybrid; ×150.

PLATE XXIV

FIG. 13.—Pollen of *Lilium canadense;* ×125.

FIG. 14.—Pollen of *Narcissus* hybrid; ×250.

FIG. 15.—Pollen of *Lachenialia Nelsoni*, cultivated hybrid; ×250.

FIG. 16.—Central portion of flower of *Chamaenerion angustifolium;* ×25.

FIG. 17.—Part of flower of *Epilobium hirsutum;* ×25.

FIG. 18.—Anther of the same; ×125.

PLATE XXV

FIG. 19.—Part of anther of garden *Fuchsia* (hybrid of *F. magellanica*); ×200.

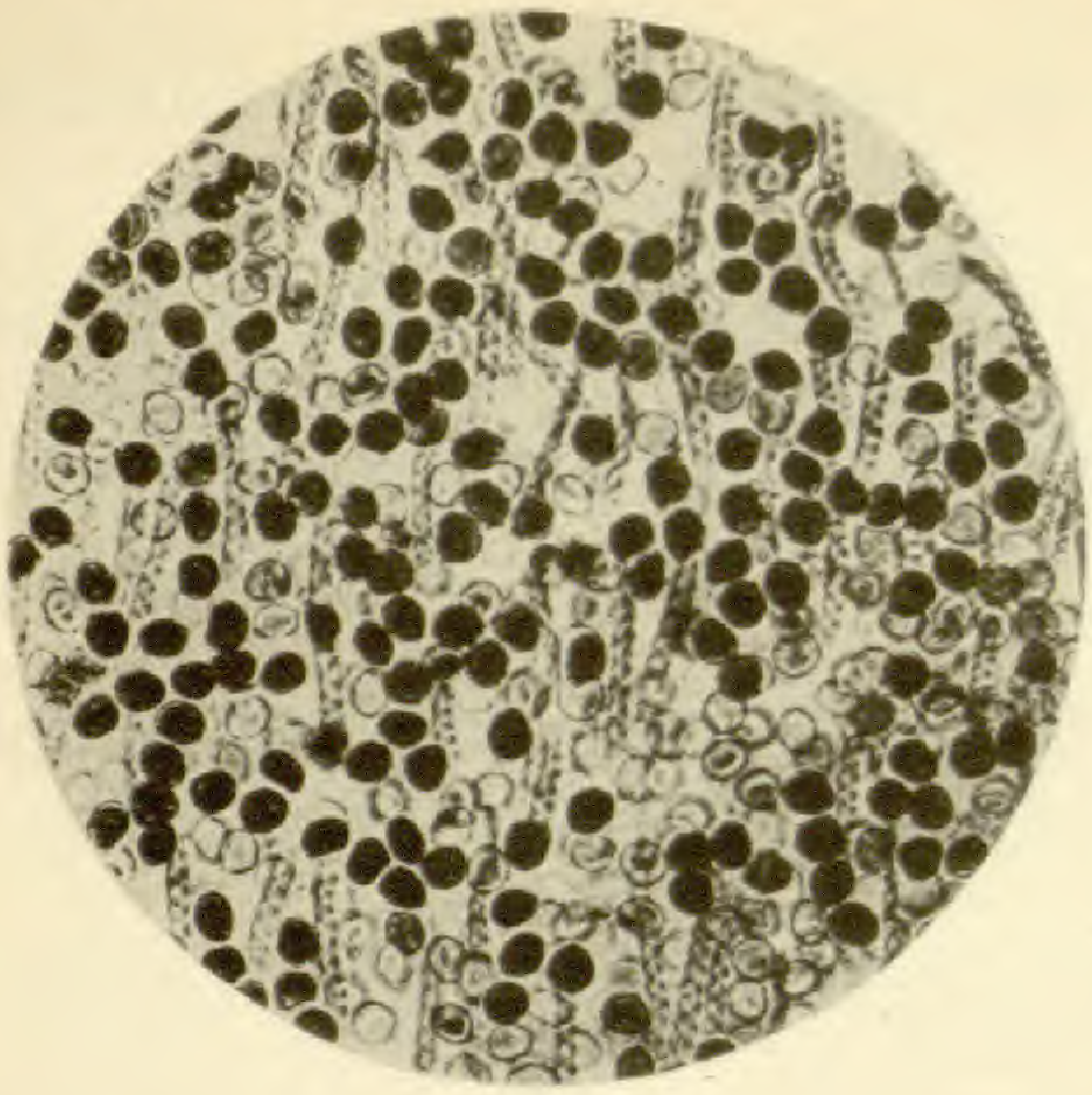
FIG. 20.—Part of anther of *Oenothera Lamarckiana;* ×200.

FIG. 21.—Flower of *O. biennis;* ×25.

FIG. 22.—Anther of *O. biennis;* ×200.

FIG. 23.—Anthers of *O. Lamarckiana;* ×50.

FIG. 24.—Anthers of *O. grandiflora;* ×50.



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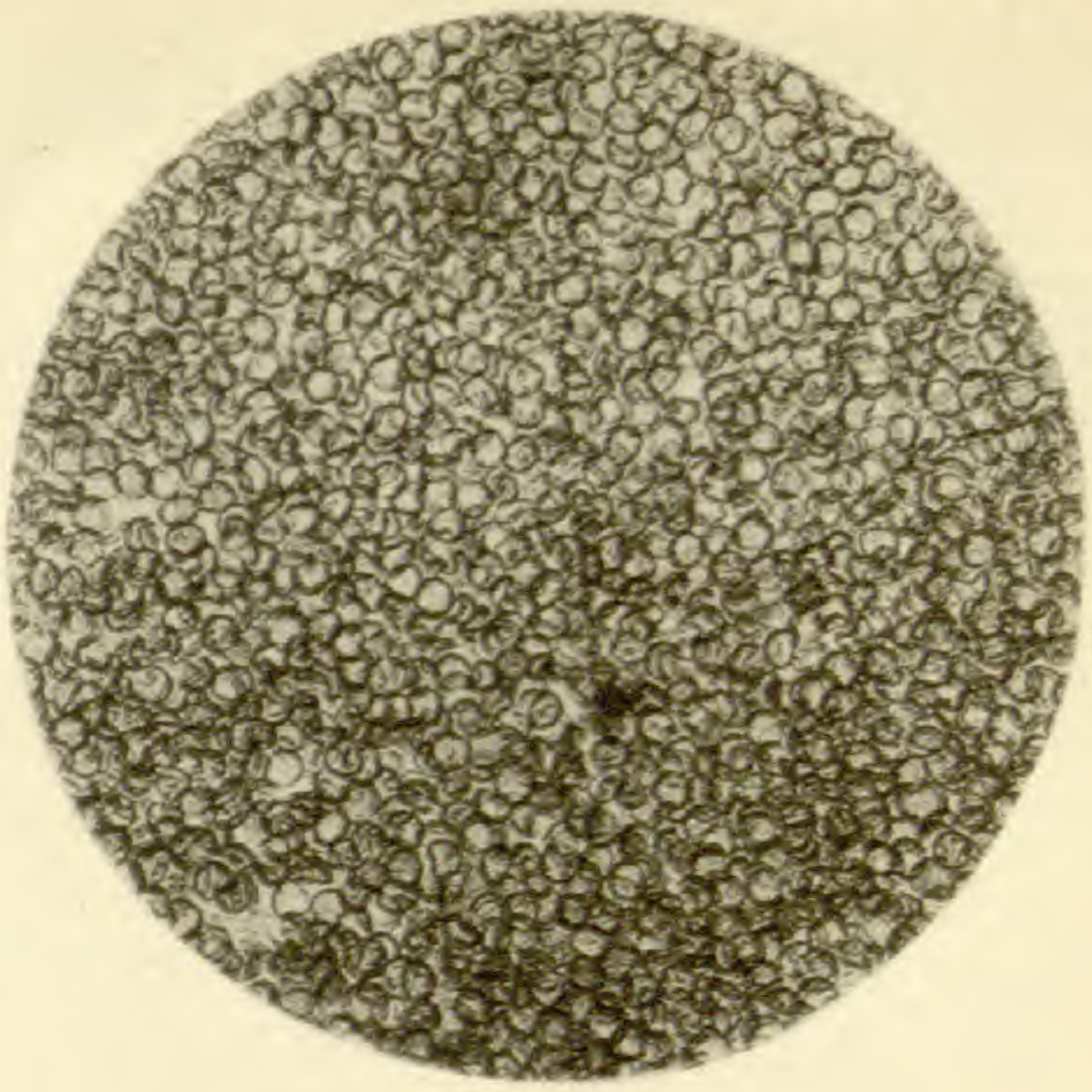

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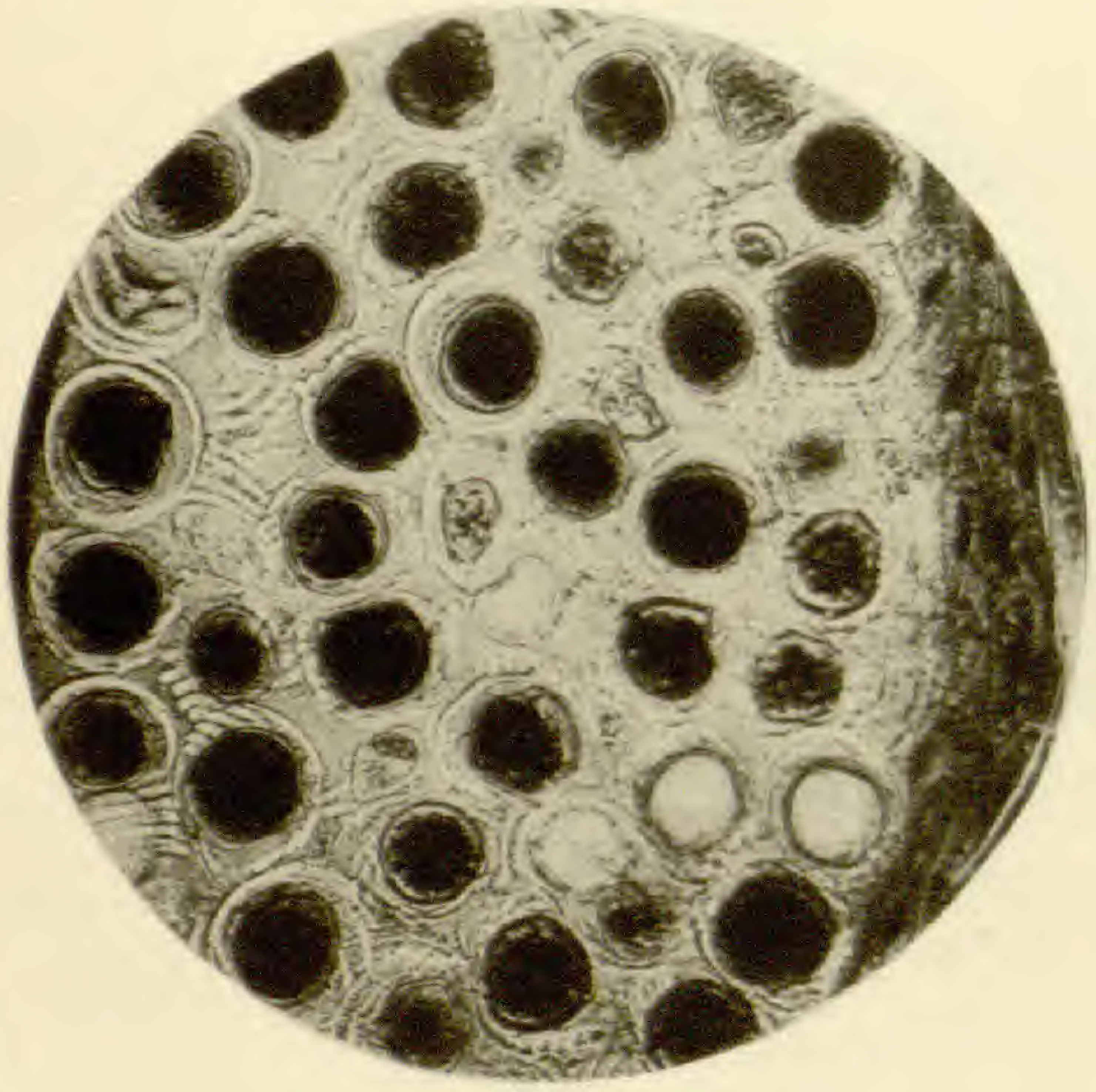

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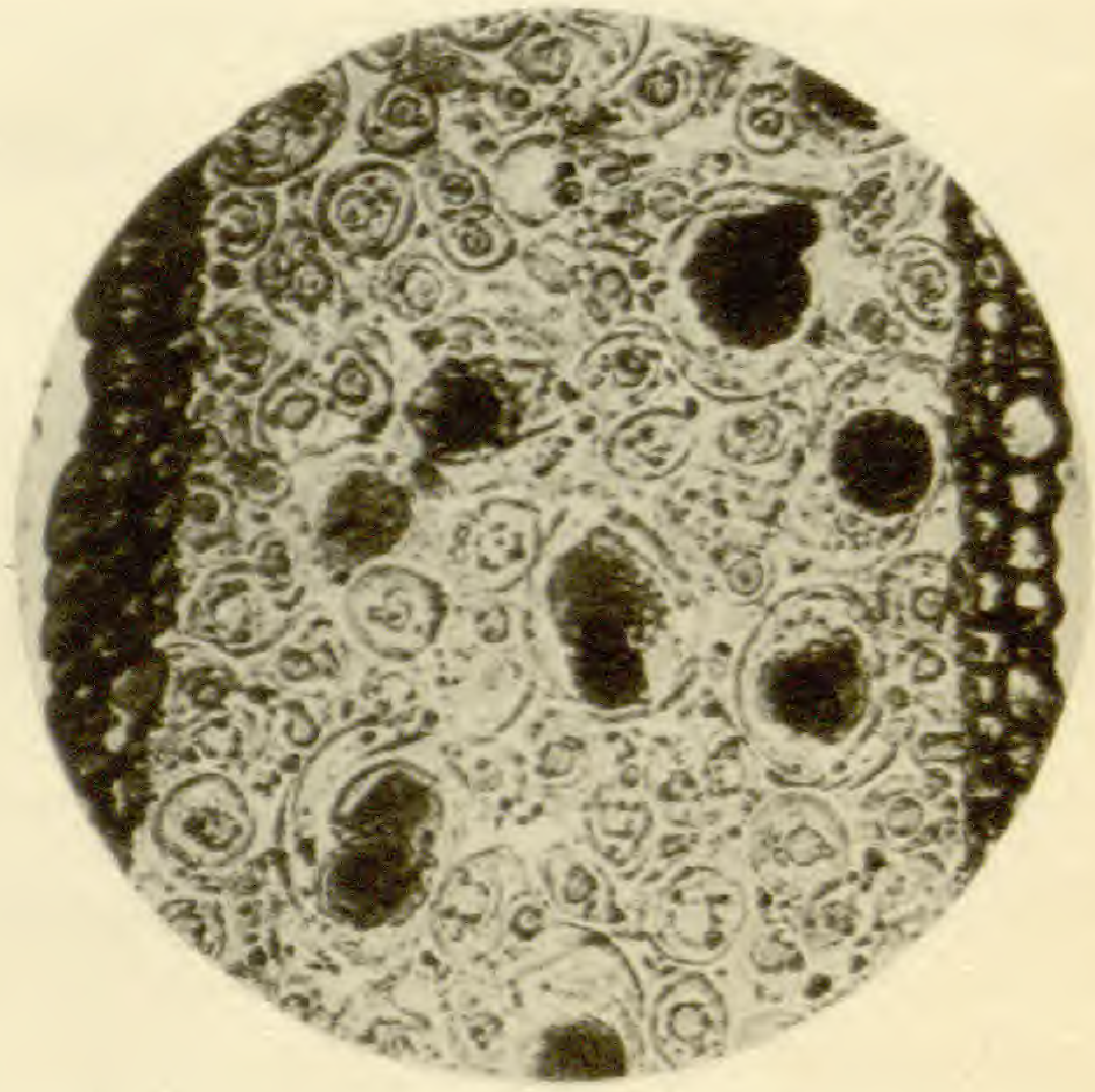

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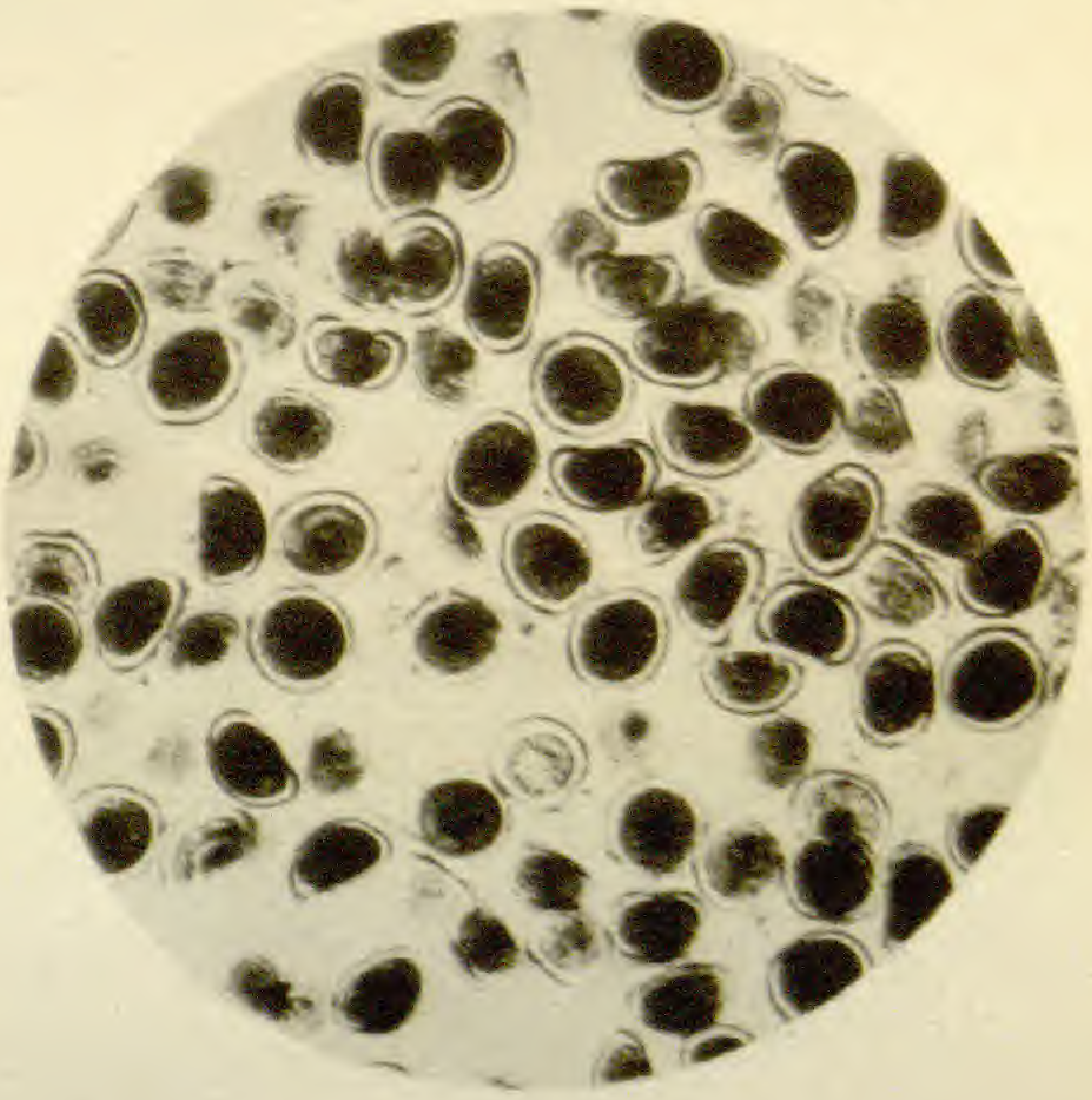

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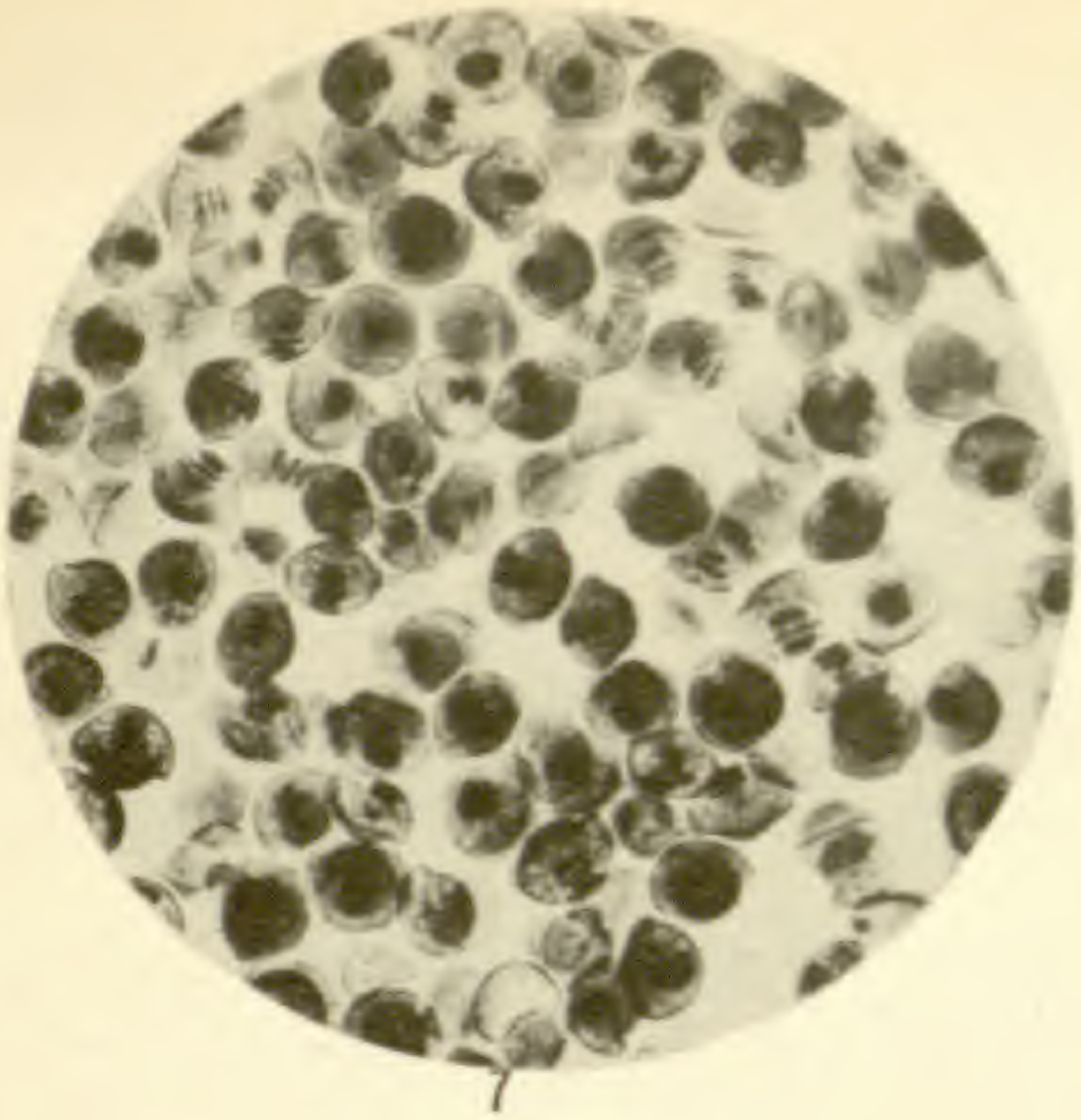
JEFFREY on SPORE CONDITIONS



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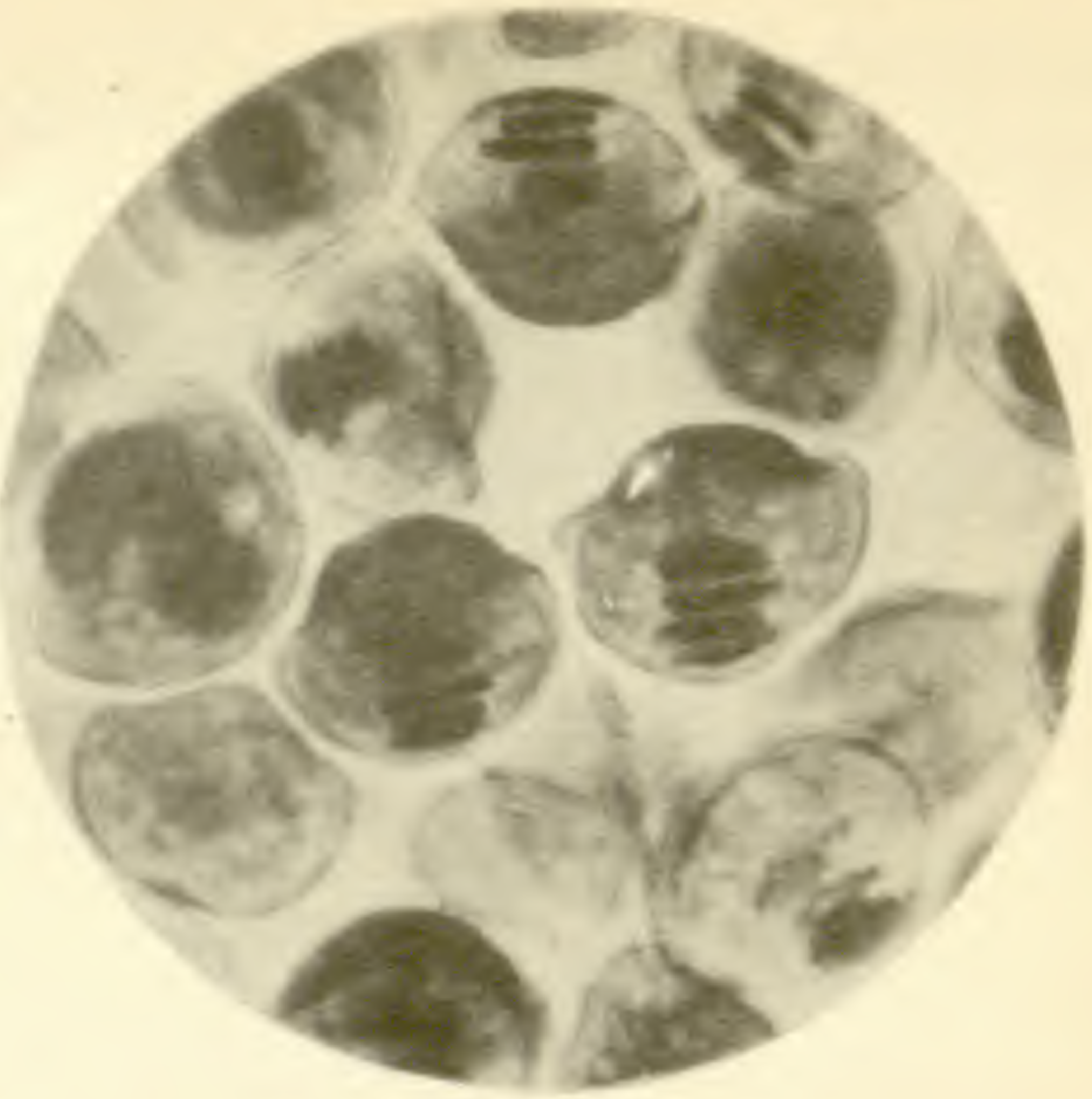

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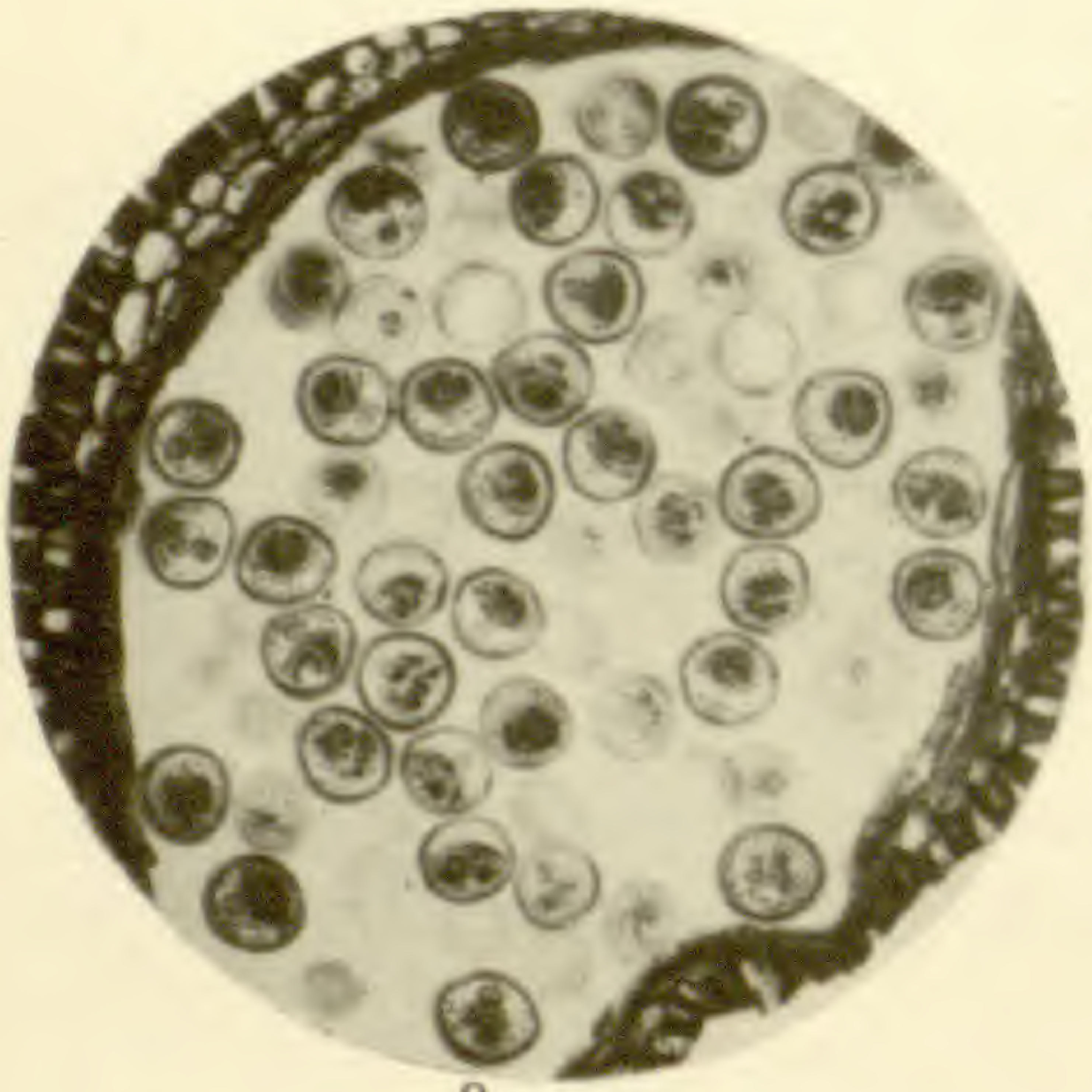

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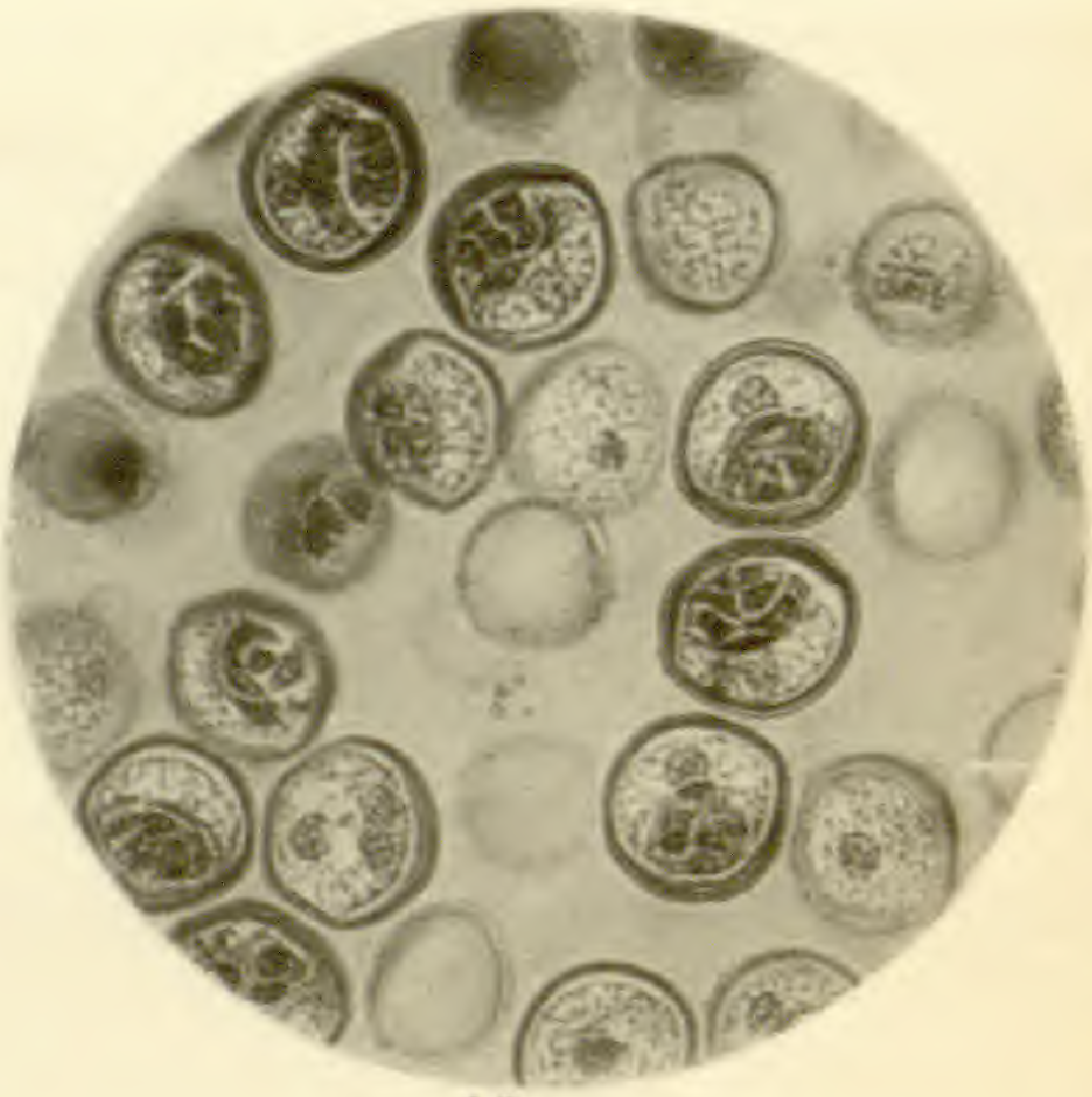

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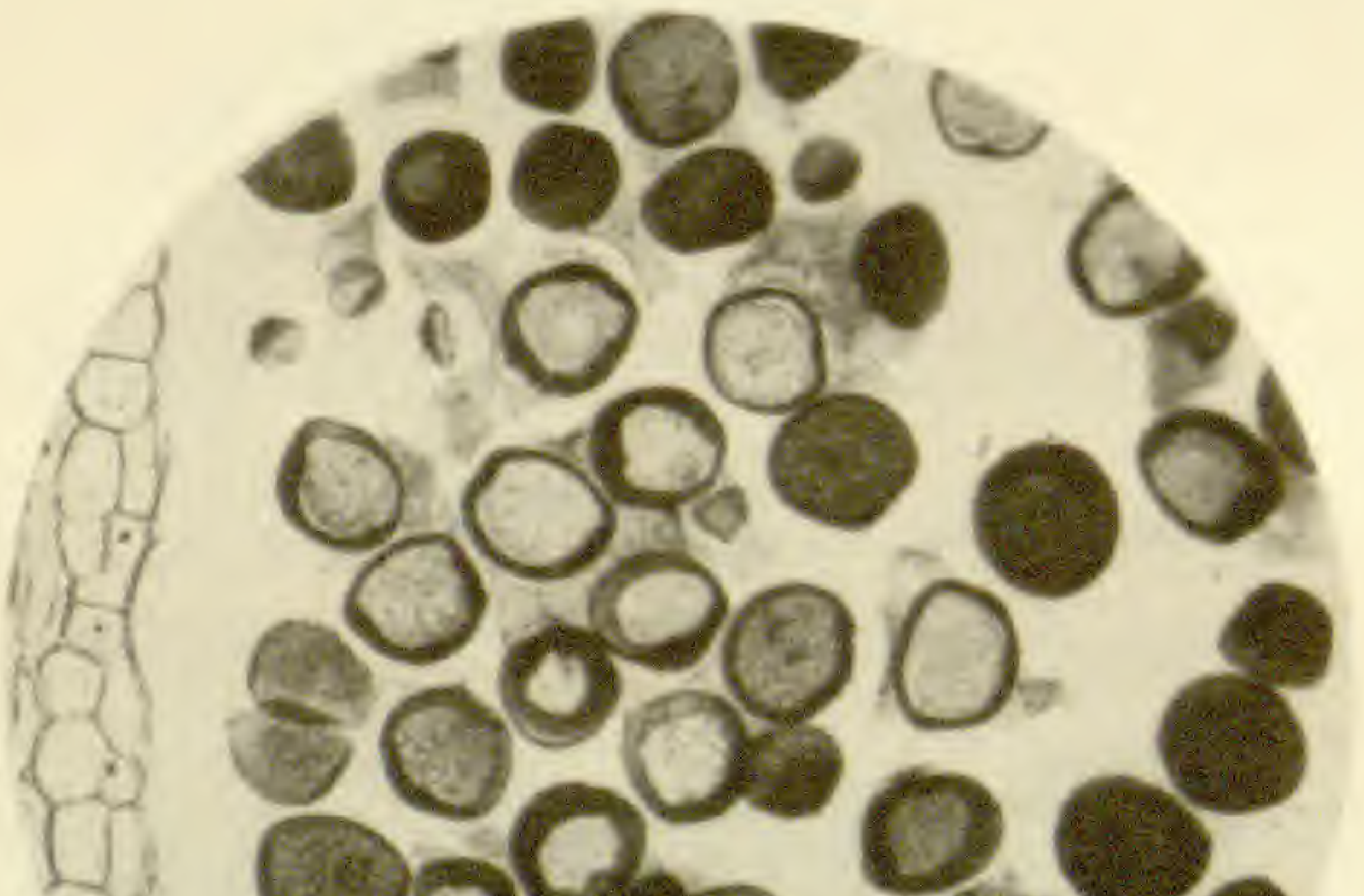

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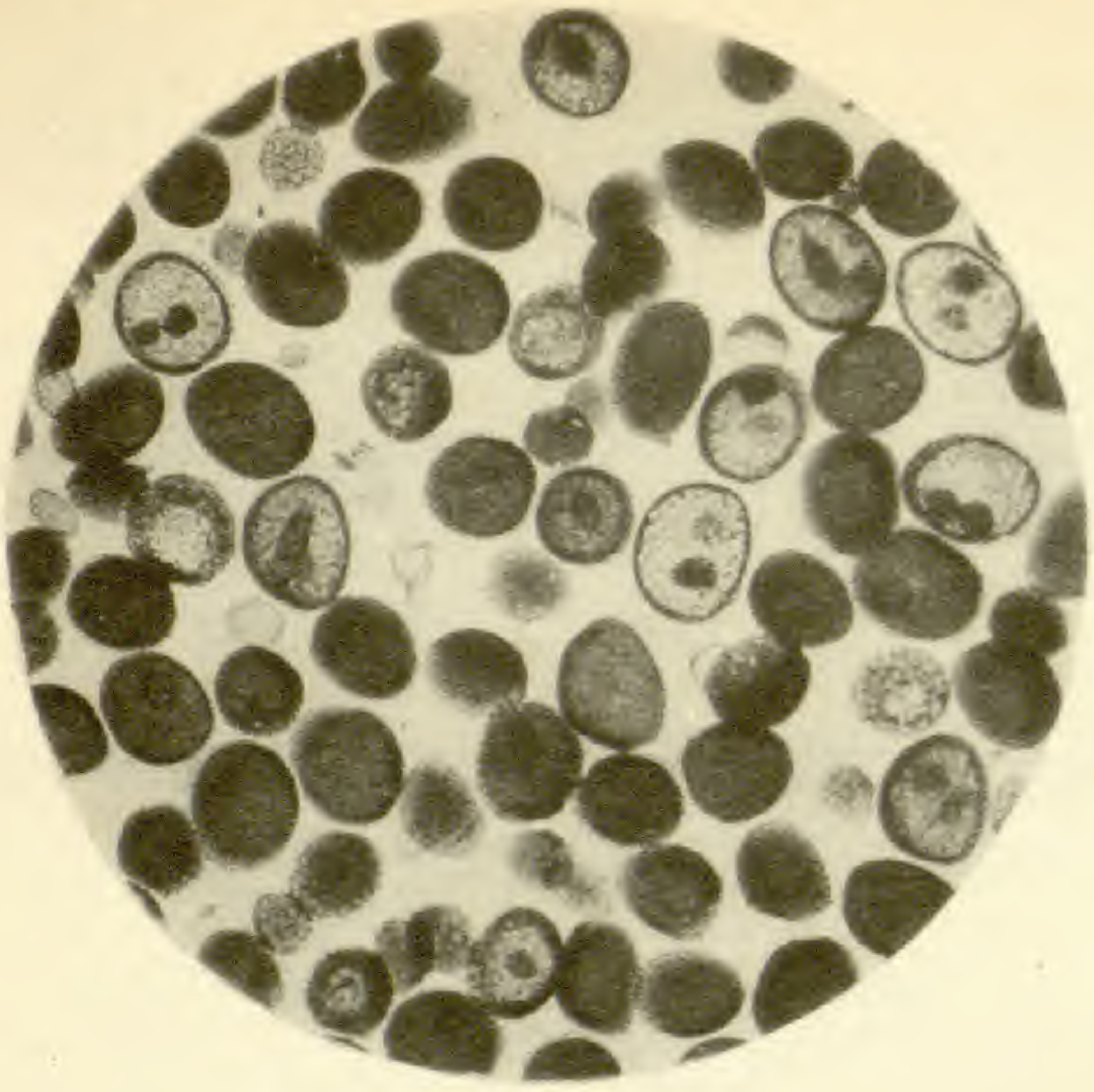
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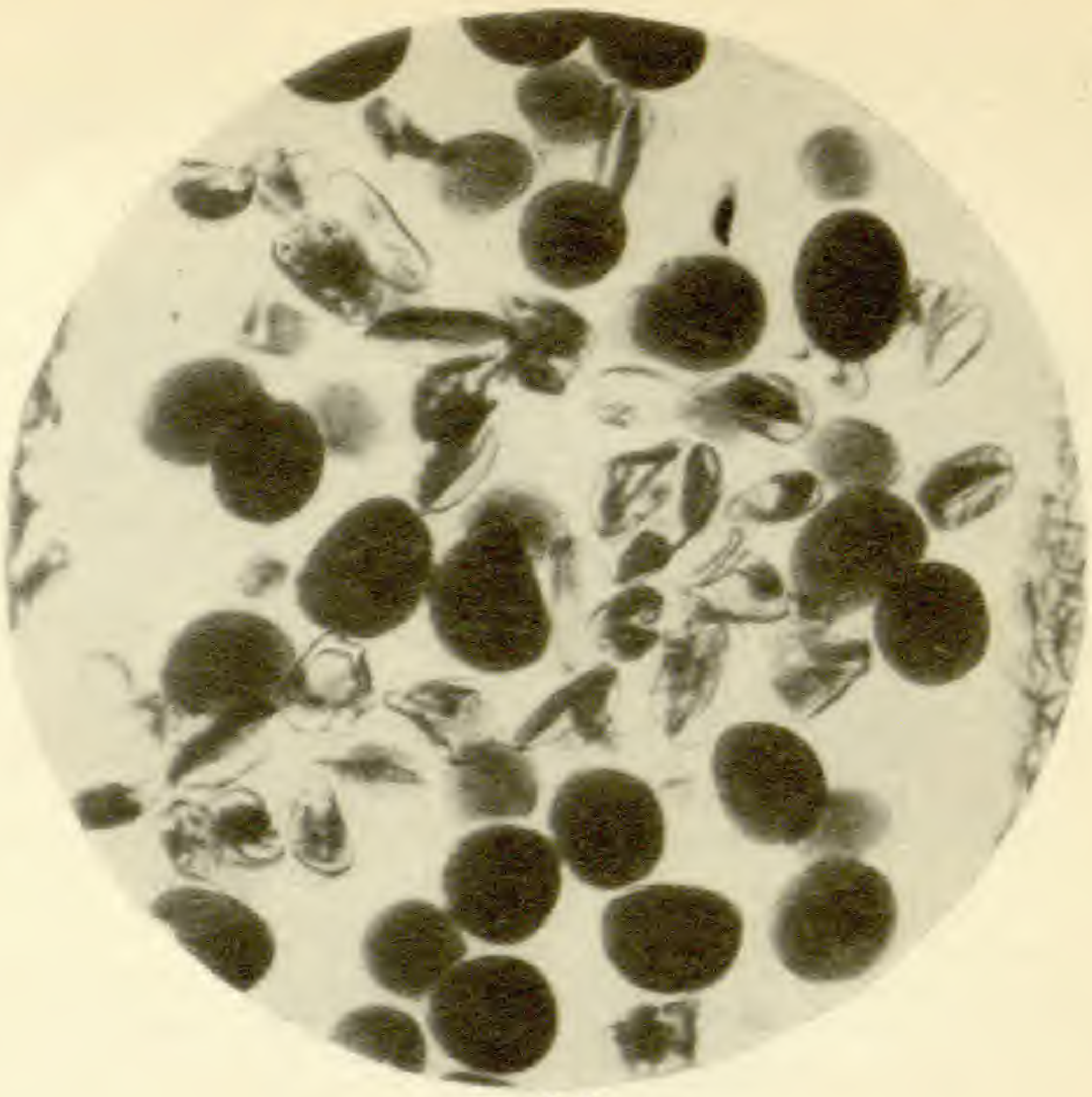
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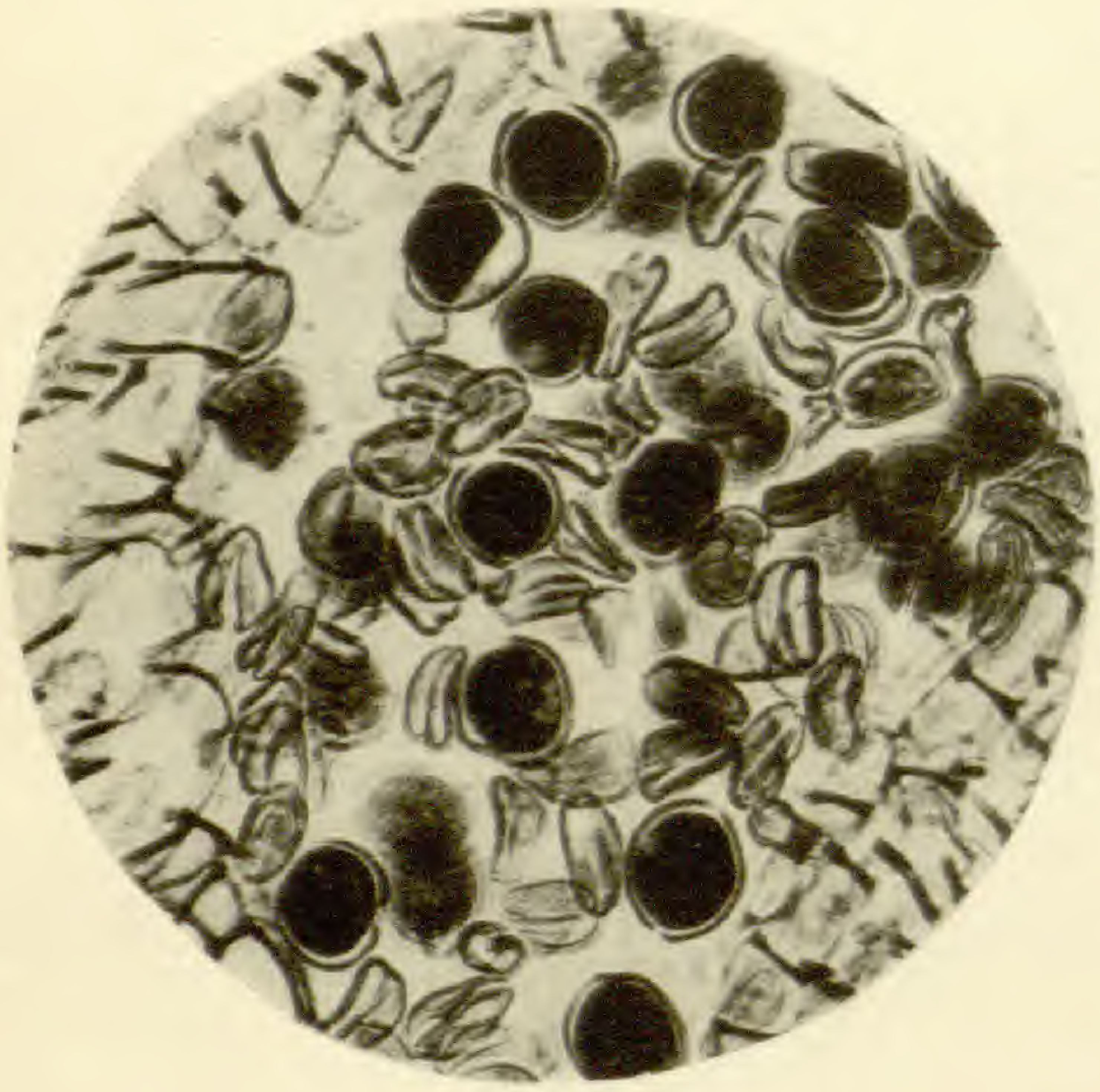
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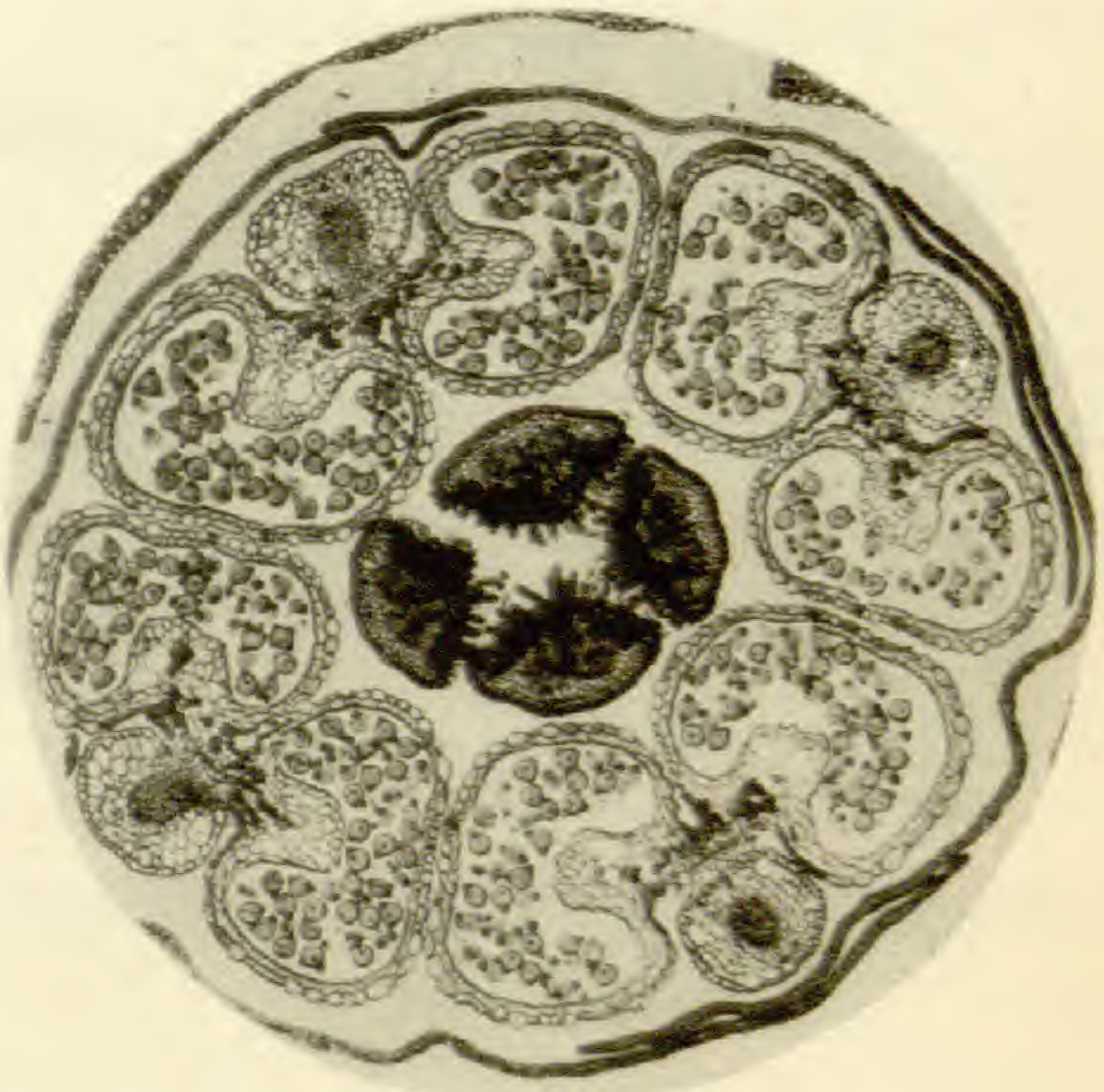
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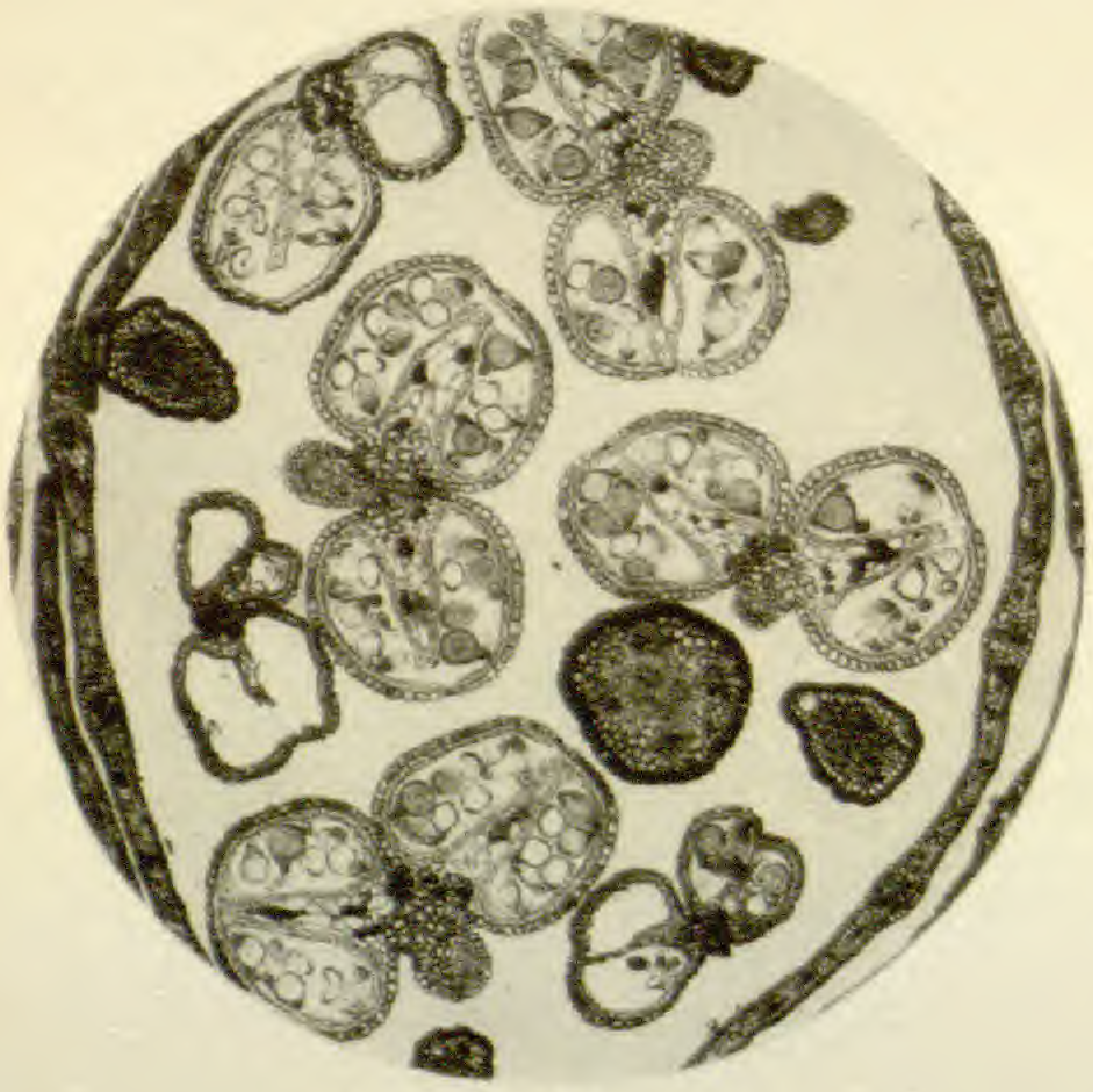
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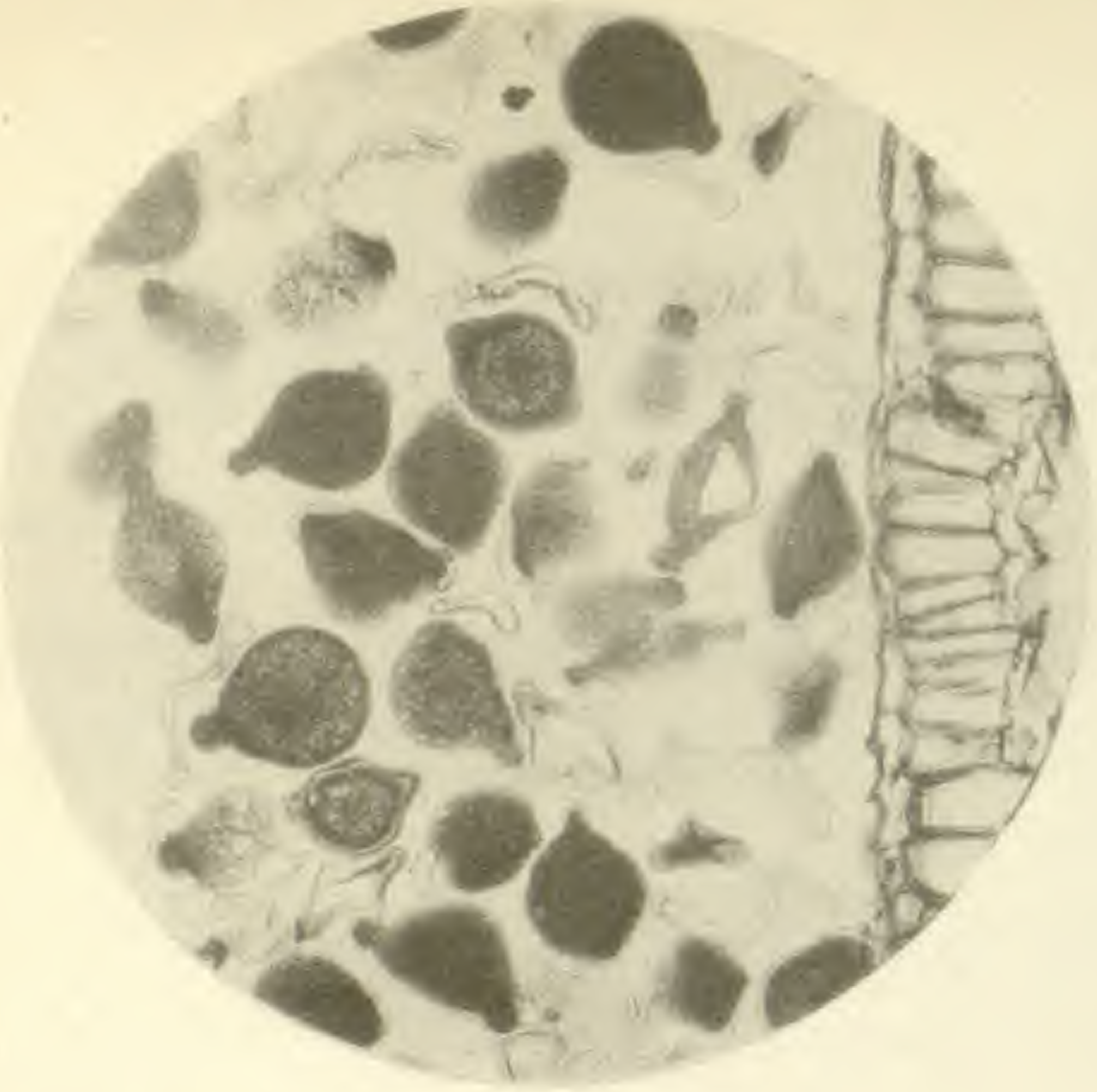

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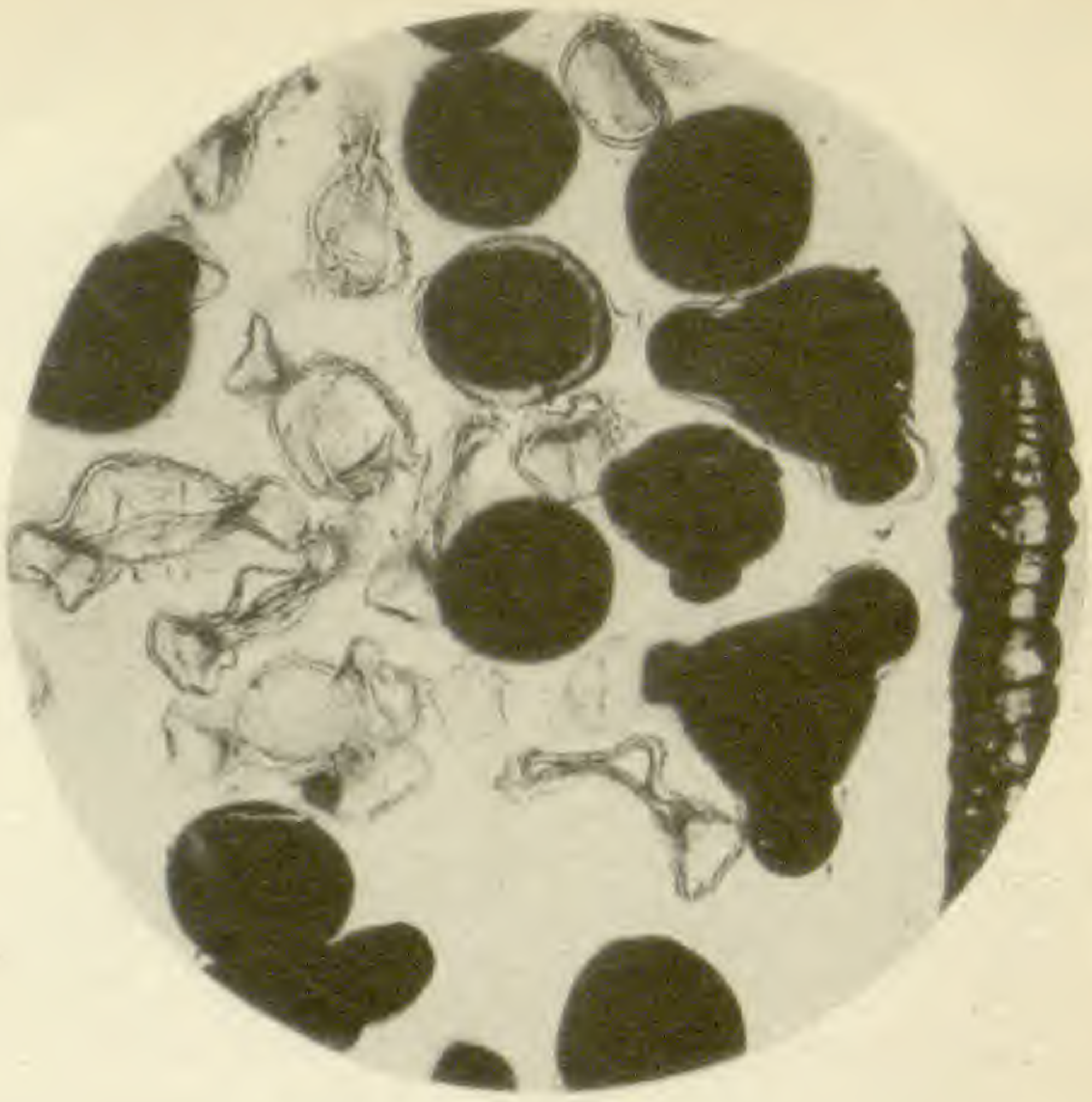

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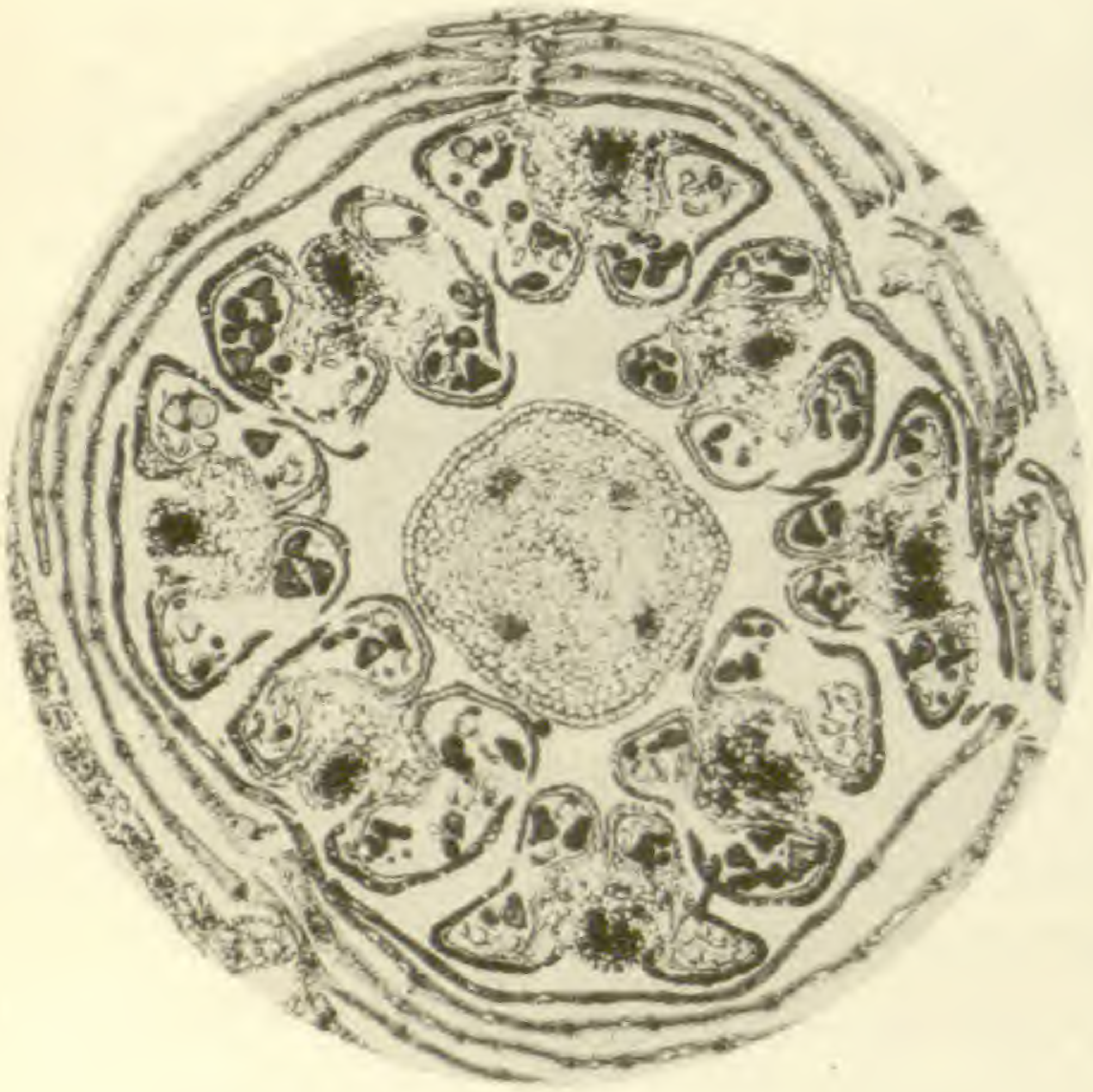

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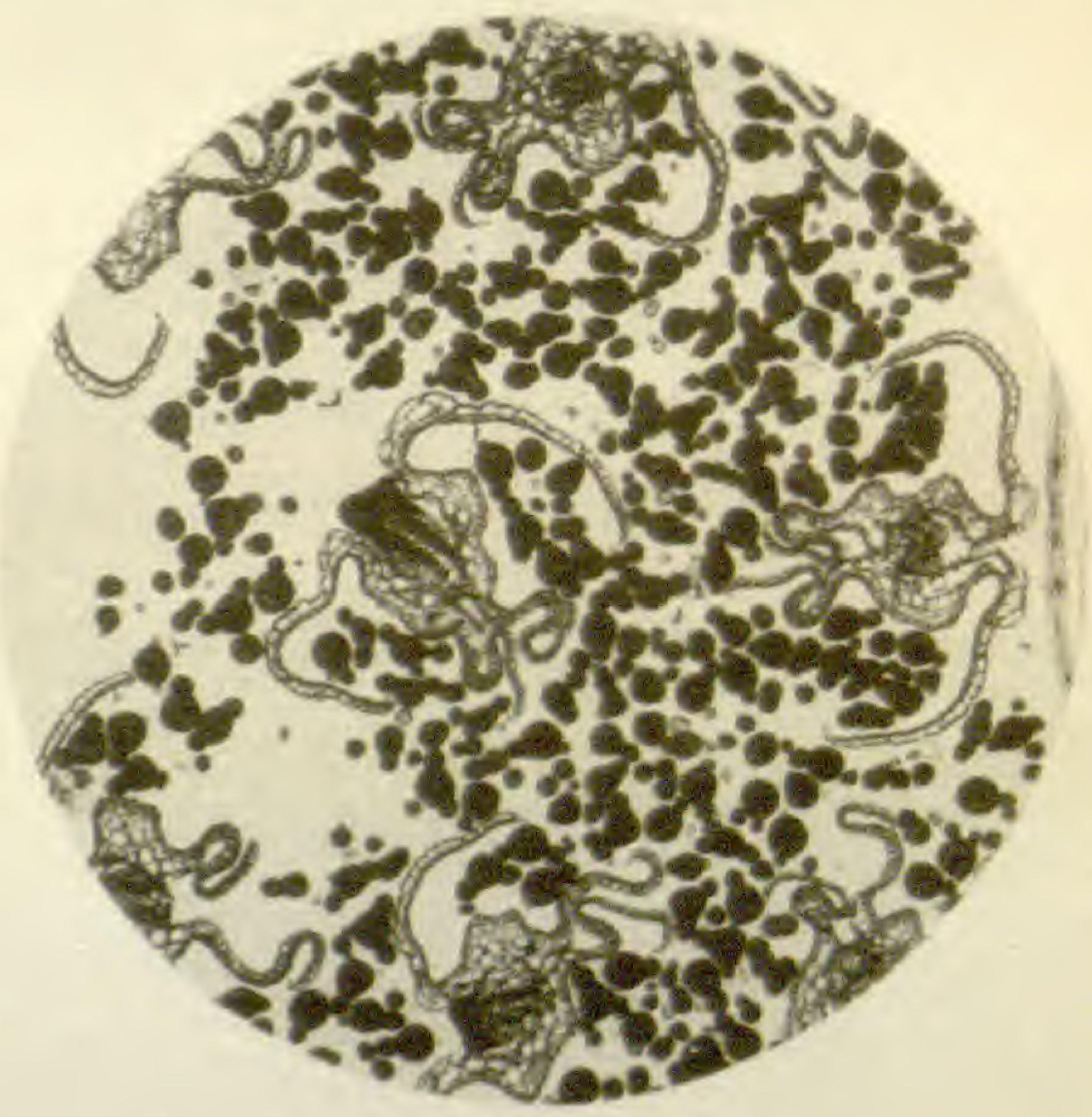

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JEFFREY on SPORE CONDITIONS

REPRODUCTION IN PLANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 195

JOHN M. COULTER

In connection with the vast accumulation of facts concerning reproduction, our morphological categories are in danger of becoming too rigid. Emphasis is laid upon secondary features, and the fundamental features common to all reproduction escape attention. An extensive terminology further enforces rigidity of classification, because terminology makes exact definitions necessary. As a consequence, the various so-called "types" of asexual and sexual reproduction are pigeon-holed in our texts as though they had nothing in common. It is the purpose of the present paper to attempt a tentative analysis of the phenomena of reproduction as observed in plants, to eliminate the secondary features that make for too great rigidity of conception, and to discover the facts which are common to all reproduction, which underlie all superficial differences, and which, therefore, relate naturally the various "types." It is hoped that such an analysis may serve, not only to soften morphological distinctions, but also to suggest research that will deal with fundamentals more than with superficial details. In such a presentation it would be impossible and confusing to pay attention to all of the variations recorded. Only the general situations can be included, so that the conclusions reached will not seem to satisfy every case, but the point of view will be indicated which can eventually adjust all details.

The use of the term "reproduction" in this paper must be defined. Any cell that produces another one is performing the function of reproduction, but the result may be merely the growth of an individual, the restoration of wasted tissue, or the healing of a wound. Reproduction will be used as meaning the production of new and independent individuals, which is the current understanding of the word.

Vegetative multiplication

In one-celled plants the individual and the cell are identical. Among the varied activities of the protoplast, the power of self-division is one, and in such plants this division results in two new individuals. In other words, this is reproduction, and the conclusion is that the fundamental mechanism of reproduction is cell-division. There is nothing more in the machinery of reproduction than this phenomenon of cell-division, whether it be sexual or asexual reproduction. If the essential machinery of reproduction is provided for in cell-division, it follows that the cell-fusion connected with the sex act must be regarded as an addition to the fundamental process of reproduction, an added preliminary process, not necessary to reproduction, but securing something in connection with it. In fact, the extent to which asexual reproduction occurs among plants is not fully appreciated. It is probably true, taking the plant kingdom as a whole, that the multiplication of individuals is greater by asexual than by sexual methods. The abundant asexual reproduction even among angiosperms testifies to the fact that asexual reproduction is not even a declining method. What may be called the first stage in the evolution of asexual reproduction, therefore, is represented by those one-celled plants whose only method is ordinary cell-division, which is a function exercised by any protoplast under appropriate conditions.

Reproduction by spores

Among many-celled plants, ordinary cell-division usually does not result in new individuals, but in the growth of the individual. This transition from cell-division resulting in new individuals to cell-division resulting in growth is associated with the establishment of a new form of asexual reproduction. So long as protoplasts are held together by their walls in the continuous framework of an individual, there can be no production of new individuals. There must be detachment from the parent stock as a preliminary to the series of cell-divisions that are to result in the new individual. Among the lower algae this is accomplished in a very simple way. The protoplast detaches itself from the cell wall and escapes into the surrounding medium. The escaped protoplast (spore) is nothing more than a protoplast acting independently of its wall and of its parent plant. No new powers seem to belong to the escaped protoplast; it begins a series of divisions, but being free from the parent form, the divisions result in a new individual. The difference between such a spore, therefore, and any other protoplast belonging to the parent body is not a difference of power but of opportunity.

Ordinarily the spore-forming protoplast begins a series of divisions before escape, resulting in several spores; but it is obvious that the series of cell divisions is responsible for reproduction, whether the protoplast divides before it escapes, or escapes before it divides. In many fungi the detachment of spores is secured, not by the discharge of protoplasts, but by the abstriction of walled cells from special branches. This "pinching off" a part of the body is merely a detail of separation. The essential fact is that a spore means a protoplast separated from one individual, and capable of producing another individual. The multitude of names applied to spores on the basis of secondary characters has obscured the fundamental idea that belongs to all of them, the idea of a detached protoplast.

It would be interesting to know what conditions determine the separation of a protoplast from its wall and its abandonment of the structure it has made and kept in condition. A possible suggestion may be obtained from the occasional behavior of protoplasts at the inception of conditions unfavorable to vegetative activity. Just as in spore-formation, the protoplasts become freed from the wall, round off, and are entirely detached from the general life of the individual which has produced them. The experimental control of spore-formation in many algae and fungi shows that conditions can be supplied which inhibit spore-formation indefinitely, and other conditions can be supplied which stimulate abundant spore-formation. In general, whatever diminishes vegetative activity favors spore-formation, so that it is the physiological condition of the protoplast that determines whether it continues to do vegetative work, or becomes a spore. It is certainly suggested that the favorable condition for spore-formation in nature is the waning activity of the protoplast. The conclusion is that spore-formation is a response to relatively unfavorable conditions on the part of plants whose activity extends through a period long enough to encounter varying conditions. This would make spore-formation possible among one-celled plants, as well as among many-celled plants.

One of the problems of reproduction, perhaps to be regarded as the most fundamental one, has been suggested by the previous statements. When protoplasts are detached from a parent plant, whether it be a single protoplast called a spore, or a group of protoplasts, as in the case of a propagating bud, the whole structure of the parent is reproduced. Of course the essential separation is physiological, which may take place although complete structural separation has not been effected. When one considers the reproductive power in a group of active cells isolated from the parent stock, such as gemmae, propagating branches, buds, tubers, bulbs, cuttings, isolated nodes, and even leaf fragments, it becomes evident that reproduction is a function of every active cell, and that it can express itself when certain conditions are supplied. The conspicuous condition seems to be detachment from the parent stock. It is really a restoration of lost parts, and therefore is a form of regeneration, differing in degree but not in kind from what is ordinarily called regeneration. From this point of view, a spore is to be regarded not so much as a specialized reproductive cell, differing in power from other protoplasts, but as a single detached protoplast rather than a group of them, and therefore regenerating all the structures of the body. What induces these detached protoplasts, whether single or in groups, to produce a new individual is no more clear than what induces a fertilized egg to produce a similar structure, but both seem to belong to the same category, and that is, a series of divisions that result in a definite structure.

A further stage in the evolution of spore-formation is the differentiation of sporangia, which needs no discussion in this connection. Sporangia are formed under the conditions that favor spore-formation, and not during maximum vegetative activity. They are not formed as parts of the body, awaiting appropriate conditions for spore-formation. The fundamental difference between plants without and with distinct sporangia is that in the former all protoplasts may respond to the conditions for spore-formation, while in the latter only a restricted number of protoplasts respond. What determines the selection is a question that remains for physiology to answer. When the differentiation of sporangia first takes place, the vegetative cells have either lost the power of spore-formation once common to all vegetative cells, or are inhibited from expressing it. Spore-formation by cells ordinarily vegetative occurs often enough to assure us that spore-formation is only inhibited in such vegetative cells.

A summary of what may be called three stages in the history of asexual reproduction, as given above, may be stated as follows. The first stage is represented by cell-division, which belongs to cell-activity in general; in other words, it is a process as natural to all protoplasts as any work. The second stage is represented by spore-formation, in which ordinary vegetative cells under certain conditions produce spores. In this case the activities of a cell are differentiated by varying conditions, and are not differentiated permanently. The third stage is represented by the reproduction of spores by special cells which are differentiated in function permanently from the ordinary vegetative cells. This specialization of certain cells is accompanied by the inhibition of the spore-producing power of cells in general.

The origin of sex

If all plants were sexual, the origin of sex would be as obscure a problem as is the origin of life. Fortunately for this problem, the most primitive plants are sexless, and the gametes are seen to be as definitely related to previous structures as are any other features of evolutionary progress. What is ordinarily referred to as the "origin of sex," however, is simply the morphological origin of gametes, the visible structures associated with sex. The use made of *Ulothrix* as an illustration in this connection is familiar to all botanists. The gradations from zoospores to gametes are complete, so that it seems to be clear that in this case gametes are morphologically spores greatly reduced in size, and usually incapable of functioning as spores. It is a temptation to infer that the difference in size means simply a difference in the nutritive capacity, but further consideration shows this to be a hasty conclusion.

The important difference between the spores and gametes of *Ulothrix* is that the latter pair and fuse and the former do not. To obtain any suggestion as to the cause of this difference it is necessary to recall the conditions of spore-formation and gamete-formation. When the conditions favor maximum vegetative activity, neither spores nor gametes are produced. When the conditions are less favorable for vegetative activity, spores are produced; and when the plant is approaching the end of its activity, gametes are produced. It has been found possible to control experimentally the conditions that determine these various activities. The distribution of these functions in the ordinary life history of the plant is naturally related to its changing environment. The production of gametes in the simple plant we are considering is the last act in the life of the plant, an act induced by conditions that are bringing the activity of the plant to its close.

But why do gametes pair and fuse? It is obvious that more important differences than a difference in size have been developed in connection with the derivation of gametes from spores. The difference in size is visible, but in connection with it there develops a very different set of physiological conditions. This first stage of gamete production has been called "isogamy," but the name is only optically true. The same idea is expressed when such plants are said to be "unisexual." Exception may be taken to both of these terms. The gametes are alike in appearance, but that they are not alike in fact is evidenced by their pairing and mutual attraction. Morphological likeness may justify the term "isogamy," but for the term unisexual there is no excuse whatever. Sexuality, with its pairing sexual cells, implies two sexes, whether they can be distinguished or not. All sexual plants must be bisexual to be sexual at all.

The result of the sex act in these primitive sexual plants deserves attention. The zygote produced has the powers of an ordinary spore, in that it can produce a new individual, but the notable difference is that it does not germinate immediately. It is produced under conditions unfavorable to vegetative activity, and therefore unfavorable for the production of a new individual. The conditions that favor zygote-formation inhibit zygote-activity, and it responds with its heavy wall and dormant protoplast. Even when this zygote germinates, it may not produce a new individual, but the protoplast may divide at once to form spores. In other words, the protoplast of a zygote may function directly as a spore-forming protoplast. The inference is that the production of a vegetatively active individual or the production of spores depends upon the conditions for vegetative activity. If these conditions favor maximum vegetative activity, a vegetative individual will be produced; but if they do not favor maximum vegetative activity, spores will be produced. The succession of conditions at the opening of a growing season is just the reverse of the succession at the ending of a growing season. In the latter case there is a gradually waning activity, resulting in spore-formation following great vegetative activity; while at the opening of a season there is gradually increasing activity, the conditions first favoring spore-formation, and then vegetative activity.

The seasonal relation between spores and gametes lies at the basis of the changes which gradually established a definite alternation of generations. Spores are always as essential a feature of the life history as gametes, and in plants sexual reproduction is never the whole of reproduction.

A summary of the important facts in reference to the "origin of sex" may be stated as follows: (1) gametes have been derived from zoospores which have become so reduced by succcessive divisions as to be incapable of functioning as spores; (2) when first recognized by their behavior, gametes are alike in every visible feature, so that there is no evident distinction of sex; (3) a physiological differentiation of gametes is indicated by their mutual attraction in pairing, so that two sexes are present, although not distinguishable; (4) gametes are formed under conditions relatively unfavorable to either vegetative activity or spore-formation, representing the closing activity of a plant; (5) gametes therefore appear in response to unfavorable conditions that arise in the life history of a plant which is long enough to extend over a considerable range of varying conditions; (6) the sex act results in a zygote which is formed under conditions unfavorable to vegetative activity, and therefore passes into a protected dormant condition; in other words, the conditions which favor the formation of a zygote inhibit its germination; (7) a zygote may function as an ordinary spore, producing a new individual, or it may produce spores, functioning like an ordinary protoplast; (8) the physiological changes involved by the introduction of the sex act are very great and far-reaching, for they include the mutual attraction of gametes, the organization into a single cell of the contributions of two cells, a provision for reducing the number of chromosomes which the sexual fusion has doubled, and the appearance of two kinds of individuals produced by spores and zygotes.

The differentiation of sex

The differentiation of sex usually discussed is morphological differentiation, which means in this case a visible difference in the size and activity of gametes, so that they can be recognized as male and female. The increase in bulk of one of the pairing gametes is observed to be due chiefly to the increased bulk of cytoplasm, and on this account the egg is said to have much greater nutritive capacity than its mate. This is probably not the only function of the cytoplasm of the egg in connection with the sex act, but whatever the functions may include, they are evidently as subsidiary to the act as are swimming appendages and mutually attractive substances.

Among the heterogamous plants, the variable gamete in appearance is the sperm, and its variability has to do chiefly with its swimming appendages, its form, and its amount of cytoplasm. From algae to gymnosperms, the apparatus for locomotion is developed in a variety of ways, reaching a high degree of specialization in such groups as the ferns and cycads. But among the angiosperms and higher gymnosperms a very different situation has developed, for motility has disappeared, even in its simplest expression. It follows that all the elaborate specialization of the sperm of ferns and cycads has to do with their motility, and not at all with their function as gametes. It is evident also that even the simple cilia of the primitive gametes are no essential part of a sexual cell. The need for emphasizing this is apparent when it is realized that this secondary feature of a sperm has been regarded as its essential feature by those who demand rigid categories. When motile sperms were first discovered among gymnosperms, they were hailed as the only sperms in seed plants. In other words, the sperms of most seed plants were not regarded as sperms because they cannot swim.

Another rigid conception in reference to the sperms of angiosperms needs attention. Ciliated sperms are produced and discharged by the mother cell. This has led to so rigid a definition of a sperm that if the sperm generation is omitted it is concluded that there are no sperms. The usual formula for describing this situation has been to say that "the mother cell functions directly as a sperm," implying that in fact there is no sperm, but that the mother cell behaves like one. Since the test of a gamete through all its history is its behavior, it is difficult to understand such a statement, except that a secondary feature has been substituted for the essential one. It is obvious that if organization and discharge of a sperm by a mother cell are essential to secure freedom of approach to the egg, when another method of approach is secured, the necessity for discharge disappears. The protoplast within the mother cell and the discharged sperm are the same protoplast. The sperm mother cell of angiosperms behaves like a sperm because it is a sperm.

The obvious conclusion is that a sperm is a protoplast which fuses with another one to form a zygote; that in visible features it differs originally in no essential way from any other protoplast; that eventually it becomes less bulky than its mate on account of a difference in the amount of cytoplasm; that it often develops an elaborate swimming mechanism as a secondary feature; and that the swimming apparatus is eliminated when the necessity for swimming disappears.

The phenomenon of "double fertilization" in angiosperms introduces a situation that is suggestive. In this case a sperm fuses with another cell, so that there is the same mutual attraction as between egg and sperm, leading to contact and fusion, but there is no production of a new individual. The inference is that the mutual attraction and fusion of two protoplasts is not all that is necessary for reproduction, and that mutual attraction is as much a secondary feature of sexual reproduction as is motility, and simply directs motility. There must be some fundamental difference between an ordinary cell, therefore, and one that has matured as an egg, but at the same time probably any protoplast may mature as an egg. It seems fairly well established that whatever of significance there may be in the sex act is found in the fusion of nuclei. When two protoplasts fuse, therefore, and do not produce a new individual, their nuclei must differ in some way from those of functioning sperms and eggs. One may imagine the adjustment of one nucleus to another before fusion can result in reproduction, and this mutual adjustment probably lies at the basis of sex-reproduction. It also probably explains the fact that sperms and eggs vary in their ability to fuse, and in the results of fusion.

Sexually differentiated individuals

The appearance of male and female individuals may be regarded as the extreme expression of sexual differentiation, which involves much more than the differentiation of male and female gametophytes, with their different sex organs. It is not necessary to present illustrations of the various situations this differentiation includes, for such a presentation would be merely a recital of life histories very familiar to morphologists. When the life histories of sexual plants are considered, ranging from the algae to the angiosperms, the following tentative conclusions are suggested:

Gametes are necessarily differentiated physiologically, and whatever explains this differentiation will explain the sexual differentiation of individuals. It seems to be a differentiation in chemical and physical constitution, which may or may not express itself in bodies visible in the sexual cells.

Whatever may be the cause of sexual differentiation, it is capable of being transmitted through generations of vegetative cells, until conditions favor its expression in the form of gametes and their associated structures. The implication of this statement is that sexuality does not arise *de novo* when gametes appear, but that what may be called for convenience "sex-determiners" are always present in the plant body. These determiners are conceived of as representing substances that under appropriate conditions react in such a way as to determine the formation and character of the sexual cells.

Along with sex-determiners there must be sex-inhibitors, for it seems clear that every protoplast contains both determiners, but gamete-forming protoplasts produce only one kind of gamete. It seems probable, therefore, that every gamete-forming protoplast is equipped with two determiners and one inhibitor.

In the early history of sex the protoplasts of an individual differ as to this equipment, so that the individual is bisexual so far as gamete-formation is concerned. Later, all the protoplasts of an individual are alike in sexual equipment, and as a consequence individuals are sexually differentiated. Finally, with the appearance of heterospory, sexual individuals are permanently differentiated.

Apparently the amount of available nutrition holds no relation to the differentiation of sex, except as it inhibits the production of highly nutritive eggs by a body of small nutritive capacity, and at the same time permits the production of sperms. In other words, nutrition does not determine sex, but sometimes determines the opportunity for the expression of sex.

All the sporophytes contain both sex-determiners, and in sporogenesis they are transmitted to the spores, which may produce bisexual gametophytes or unisexual gametophytes, dependent upon the distribution of the inhibitors.

All fertilized eggs contain both sex-determiners and inhibitors, and may transmit them all to the sporophyte, in which case the sporophyte would produce spores functioning alike, or two kinds of spores differing in their inhibitors.

In the case of the monosporangiate sporophyte of seed plants, the fertilized egg transmits to the sporophyte only one inhibitor, which determines whether it produces megaspores or microspores.

The presence of sex-determiners and inhibitors determines not only the character of the gametes produced, but also the character of the sexual structures associated with them; and, in the case of monosporangiate sporophytes, determines the development of a much wider range of structures than the appropriate sex organs.

Parthenogenesis

A strict application of the term parthenogenesis to the germination of an unfertilized egg is intended here. The facts that have accumulated in reference to parthenogenesis among plants seem to justify the following conclusions:

An egg may function as a spore in that it may germinate without fertilization. It seems evident, however, that an egg so differs from a spore in constitution that it needs a different kind of stimulus for germination. Usually this stimulus is applied in connection with the act of fertilization, but it may be applied in some other way.

The peculiar organization of the egg for fertilization is determined at the reduction division. If the reduction division does not occur, parthenogenesis is more likely to occur, and the egg is probably incapable of fertilization.

If spores are eliminated from the life history, as in animals and some plants, reduction occurs in connection with gamete-formation.

An egg necessarily produces a sporophyte, and a spore a gametophyte, but vegetative protoplasts of either generation may be organized to produce either generation; that is, they may function as eggs or spores, dependent upon the determiners they have received.

In general, therefore, parthenogenesis differs from reproduction by other protoplasts only in requiring a more specific stimulus, a fact which ordinarily prevents eggs from germinating unless fertilized.

Some conclusions concerning sexuality

Any general survey of the facts connected with sexual reproduction shows them to be very numerous and in some instances apparently contradictory, but they are all consistent with some general situation that determines sexuality. A review of the more prominent facts referred to in the preceding pages may suggest a working hypothesis. There are three features belonging to the most primitive gametes that deserve attention: they are motile, small, and pairing cells.

It is evident that motility is not an essential feature of sexual cells, for early in the evolution of plants, one of the pairing gametes becomes passive, and finally both are non-motile. Motility, therefore, is a secondary feature common to both gametes at first, retained with remarkable persistence by the male gamete, but dispensed with entirely in most seed plants.

It is equally evident that the small size of the primitive gametes, as compared with the spores of the same plant, is not an essential feature of sexual cells. In other words, they are not gametes simply because they are smaller than the spores. Later in the history of plants, one of the pairing gametes becomes much larger than the spores, and still it is a gamete. The difference in size is due chiefly to the varying bulk of the cytoplasm, and in some seed plants the sperm is a naked nucleus. The conclusion is that the amount of cytoplasm is also a secondary feature of sexual cells. It is certainly true that the activity of the cytoplasm of the egg is intimately related to the act of fertilization, not only as a source of nutrition, but also as the source of an activating substance, which LILLIE has called "fertilizin," which determines the physiological moment of fertilization. It should be recognized, however, that even this activating substance is not an essential feature of sexuality, but belongs to the category of secondary features which aid in making the sex act possible.

The pairing of the primitive gametes is certainly a feature that belongs to all gametes, and yet there are pairing and fusing cells that are not gametes. If pairing and fusing are not peculiar to gametes, they do not represent the essential features of sexuality. Pairing seems to be a secondary feature, just as are motility and cytoplasm, and represents a mutual attraction that makes the sex act possible, just as motility is a mechanism that makes pairing possible.

It is certainly true, however, that the primitive gametes differ from the spores with which they are clearly associated in pairing and fusing, and this difference should be accounted for first. Since spores are formed in conditions of greater vegetative activity than gametes, it is reasonable to suppose that the difference between spores and gametes is due to a difference in the activities of the protoplast in the two cases, a difference associated with declining vigor. Under such conditions, the products of metabolism will differ, and substances will be produced that do not appear when the protoplast is in full activity. This means that gametes will contain substances that spores do not, and among these substances are those that determine the mutual attraction that results in pairing. If this is true, it follows that different substances differentiate gametes into two kinds that are mutually attractive. These characteristic substances which appear later in the vegetative history of protoplasts may be regarded as among the products of waning metabolism. The appearance of different substances under such conditions is familiar in the case of the autumnal coloration of leaves.

It does not follow that these substances which characterize gametes appear only when the vegetative vigor of the plant as a whole is declining. This is generally true of such plants as the filamentous algae, but in more complex plants this decline of metabolic activity may occur in a region of the plant body, rather than in the body as a whole. For example, it is usually stated that the developing sex organs of mosses check the growth of the axis. It is a fair question to ask whether the sex organs do not appear because for some other reason growth has been checked. A checked growth indicates declining vegetative vigor, and this favors gamete-formation. Another illustration of the same fact may be obtained from the appearance of the sex organs of ferns. When a fern spore germinates, metabolism begins in a relatively feeble way, and during this early period antheridia are formed. Later, when the development of the gametophyte becomes more vigorous, sperm-formation may cease. The so-called "inhibitor" of sperms in this case, therefore, is the disappearance of the characteristic substances that belong to gametes, on account of the increasing vegetative activity of the protoplasts. In this case only such gametes can be formed as are characterized by a small amount of cytoplasm. Later in the history of the fern gametophyte, after it has developed a well nourished body, cells in the apical region become checked in vegetative activity, the substances characteristic of gametes appear again, and eggs are produced.

We still face the fact that there are cell fusions, even pairing and fusing cells, which show the presence of the mutually attractive substances characteristic of gametes, but which do not represent the sex act. All such cases may be explained as evidences of declining vigor of the protoplast concerned, but if pairing and fusing are not peculiar to gametes, although universally displayed by them, what is the esssential feature of gametes, or, in other words, of the sex act? The only answer that can be made is that gametes are pairing cells whose fusion results in the production of a new individual. This means that in addition to possessing mutually attractive substances formed in connection with declining metabolism, gametes possess nuclei so constructed that when the two fuse, a new individual is produced. This does not mean that neither gamete can produce a new individual alone, for parthenogenesis would contradict this. It means ordinarily that a new individual can be produced only after the nuclei have fused. In other words, the essential feature of sexuality must lie in the peculiar structure of the nuclei of the sexual cells. Whether this peculiar structure is chemical or physical, or both, must be a matter of opinion based on no direct evidence. Nor can it be true that gametes are peculiar in containing the factors of heredity, for these must have been handed down through all the cell generations leading to the gametes. Gametes furnish the opportunity for heredity to express itself, but so do spores, and so does vegetative multiplication.

If gametes are peculiar in the construction of their nuclei, how do they develop this peculiarity? The available evidence seems to make it clear that this gametic peculiarity, whatever it may be, is developed in connection with the reduction division. Among plants this division occurs generally in connection with spore-formation, and when there are no spores, as in *Fucus*, it occurs in connection with gamete-formation. In case the reduction division fails in connection with spore-formation, it has been observed that the resulting $2x$ egg is unable to fuse with the sperm. In any event, the reduction division determines the sexual condition, and the peculiarity of this division, as compared with ordinary division, is related to the peculiar constitution of the nuclei of gametes as compared with other nuclei. If gametes have any structural peculiarity, it must be developed in connection with this peculiar nuclear division.

In well balanced alternation of generations, as in bryophytes and pteridophytes, there are many cell generations between spores and gametes and how the peculiarities of the gametes are transmitted through the cell generations of the gametophyte is a subject of speculation, but certainly something maintains a continuity between spores and gametes. In heterosporous plants, chiefly the seed plants, the cell generations between spore and gamete become fewer and fewer, until finally sperms are reached in two successive cell divisions, and the eggs are reached in one to three successive divisions. The next advance would be the elimination of spores entirely and the occurrence of reduction in connection with gamete-formation, as in animals.

In conclusion, the impression one obtains of sexuality as a method of reproduction is that it represents protoplasts engaged in reproduction under peculiar difficulties, that do not obtain in reproduction by spores or by vegetative multiplication, and that its significance lies in the fact that it makes organic evolution more rapid and far more varied.

UNIVERSITY OF CHICAGO

NEW OR PECULIAR ZYGOMYCETES. 3: BLAKESLEA, DISSOPHORA, AND HAPLOSPORANGIUM, NOVA GENERA[1]

ROLAND THAXTER

(WITH PLATES XXVI–XXIX)

Blakeslea, nov. gen.

Mycelium copious, cottony; hyphae very irregular in diameter, the copious branches often rhizoidal and contorted and producing numerous intercalary chlamydospores. Sporangia of two types with numerous intergrading variations: larger solitary sporangia like those of *Choanephora*, with columella and dark appendiculate sporangiospores; and sporangiola without columella, containing few dark appendiculate spores and covering the surface of large spherical sporangioliferous heads to which they are attached by a vesicular basal piece; the heads solitary on the ends of erect fertile hyphae or produced in clusters from the numerous ultimate branchlets which may result from the successive branching of the latter.

Blakeslea trispora, nov. sp.—Plates XXVI and XXVII.

Mycelium colorless to bright orange. Fertile hyphae stout, erect, arising laterally or terminally, very variable in size. Sporangia spherical, nodding or circinate, very variable; the larger spherical with a rough granular wall, the columella from hemispherical to more elongate; the smaller more conspicuously and coarsely roughened, as is often the distal end or more rarely the whole of the sporangiophore, with spores often distinctly larger and the columella frequently obsolete. Sporangioliferous heads solitary, with fewer, twelve or more, sporangiola; or typically in groups of ten or more each bearing forty or more sporangiola and terminating branchlets of the subdichotomously branched extremity of the fertile hypha, the branches and branchlets of which are

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[1] Contributions from the Cryptogamic Laboratories of Harvard University, LXXV.

marked by irregular successive constrictions; the sporangiola typically three-spored, rarely four or six-spored, broadly elliptical, falling from the small nearly spherical vesicle which bears them, or, if not fully matured, carrying the latter with them. Spores from all types of sporangia purplish to reddish brown, marked by sub-labyrinthine longitudinal ridges and furrows, oval or long-elliptical, those from the sporangiola at first somewhat three-sided from pressure, bearing a group of straight fine radiating appendages from either pole. Spores very variable; those of the larger sporangia 8–10×4 μ; from smaller sporangia 10–13×5–8 μ; from sporangiola, average 12×5 μ. Larger sporangia 40–50 μ; smaller to 16 μ; sporangiola, average 11–12×13–14 μ; the vesicle 3–3.5 μ. Chlamydospores very variable, average 17–24×8–18 μ.

This interesting type, which has been named in honor of Professor A. F. BLAKESLEE in recognition of his brilliant researches on the Mucorales, appeared as an impurity in a transfer of *Botrytis Rileyi* which was kindly sent me several years ago, together with specimens of the affected larvae, by Professor FAWCETT. The larvae attacked by the *Botrytis* were found on cowpeas at Gainesville, Florida, and it seems probable that the spores of the present fungus, which may have been growing on the faded flowers of this plant, were accidentally transferred to the diseased insect.

The fungus fruits readily on various agar media and does not appear to lose its power of spore production, like species of *Choanephora*, after continued cultivation on nutrients. When first cultivated, the fatty protoplasm of the hyphae was usually bright orange yellow, so that the mycelium as a whole was strikingly colored; but after continuous culture for several years on potato agar, this characteristic has disappeared, or the mycelium retains only a slightly yellowish tint. The mycelium grows very rapidly, and in two or three days the sporangiola begin to be produced in abundance, each fertile hypha bearing from one to a dozen sporangioliferous heads, which under a hand lens resemble exactly in color and appearance the ordinary "conidial" fructifications of *Choanephora*. Instead, however, of producing a primary head from the surface of which the conidial heads arise, as in the last mentioned genus, the fertile hypha branches repeatedly in an irregularly dichotomous fashion, the outline of the branches and branchlets being characteristically corrugated through the presence of successive constrictions, the ultimate divisions bearing the sporangioliferous heads. From the whole surface of the latter buds arise, distributed without great regularity, which as they develop become distinguished into two parts: a short stout basal stalk which later assumes the form of a nearly spherical vesicle, and a terminal rounded portion which becomes transformed into the broadly elliptical sporangiolum (figs. 3 and 4). In each sporangiolum three spores are normally produced by longitudinal radiate cleavage, but even in typical sporangiola instances occur in which one or all of these spores may divide before maturing, so that there may be four to six in the mature sporangiolum (figs. 5 and 7). In such cases the spores are more irregular in form, size, and arrangement. When fully mature, each sporangium becomes separated from its vesicle (fig. 6); or, if not quite matured, may be separated with the vesicle coherent, as in figs. 5 and 7. Ordinarily the vesicles are left attached to the sporangioliferous heads as is shown in figs. 2 and 3. The normal spores (fig. 9) are somewhat bean-shaped at first, tending to assume a more rounded form after they are freed from the sporangiolum, rather rich purplish brown in color, marked by longitudinal depressions which appear as fine dark lines, more or less parallel and slightly labyrinthine, which, when the spores are freshly discharged in water, are sufficiently conspicuous, although they become faint after swelling or mounting in glycerine. When viewed end on, as in fig. 8, the furrows give the margin a finely corrugated outline. From either pole in all the spores a variable number of very fine and hardly visible, irregularly divergent appendages radiate, which seem to be formed from an intersporal substance and converge to a more or less distinct cap or small mass of viscous material, which sometimes forms a distinct dark spot. These appendages are straight and very fine, seldom much longer than the spore, and are readily seen only in freshly separated spores and with considerable magnification. They seem to be entirely similar to the corresponding structures which are found on the sporangiospores of *Choanephora*. The spores germinate rapidly in nutrients by producing a terminal or lateral germ-tube which grows directly to a mycelium.

Under ordinary conditions sporangiola of the type just described are formed almost to the exclusion of other forms of sporangia; but, especially when the culture is made in a saturated atmosphere, typical sporangia appear, associated with them, having the normal structure of the ordinary sporangia of the Mucoraceae, and similar to those which occur in *Choanephora*. These sporangia, however, are subject to very great variation, and almost every imaginable intermediate condition between a form such as is represented in fig. 16, and the three-spored sporangiolum may be met with. These single sporangia when well developed, as in the instance just referred to, possess a typical columella, and contain very numerous spores, which are more uniform and usually smaller than such as occur in smaller sporangia. Their characters are in general similar to those of the spores formed in the sporangiola; they possess the same appendages, which are perhaps slightly longer and are similarly though less distinctly marked. Their color is often more reddish brown, but is variable. They may rarely be borne almost erect, but are usually nodding or strongly circinate, the termination of the sporangiophore in many cases being coiled in a more or less irregular spiral. Such large forms with small spores are far less frequent than smaller sporangia which show the greatest variability in size (figs. 13–15 and 17), some of which may be hardly larger than the typical sporangiola and like them may possess no columella (fig. 14). On the other hand, abnormalities or more simple conditions of the sporangiolum type of fructification occur which, like that illustrated in fig. 12, serve to break down any clean-cut distinction between the two types. The spores of the smaller sporangia are likely to be larger than those of better developed examples (figs. 13–15), and the walls are more coarsely roughened. The wall of the sporangiophore, and even sometimes of hyphae which bear sporangiola, may be roughened by a scaly incrustation, sometimes confined to the summit, sometimes extending to the base.

Chlamydospores are produced usually in enormous numbers, especially under unfavorable conditions, and vary considerably in form, from cylindrical to nearly spherical.

Although no "conidia" appear to be produced by this species, it is evident that it must be regarded as very closely related to

Choanephora, the peculiar characteristics of its sporangiospores being in themselves sufficient evidence of this relationship. But the chief interest which attaches to it rests upon the fact that the conidia so characteristic of Choanephorae are here replaced by sporangiola similarly related to large spherical heads; and further that these sporangiola, in the life history of one and the same species, pass by almost insensible gradations to large typical solitary sporangia such as are produced normally by a species of *Choanephora*. If, however, one compares the conidial fructification of *C. cucurbitarum*, for example, with the sporangiolate fructification of the present type, one is unavoidably impressed by the close correspondence between them, both in the form, peculiar color, and ornamentation of the spores, and in the similar origin of conidia and sporangiola from large spherical heads. The conclusion seems almost inevitable that in the conidia of *Choanephora* we are dealing with a condition in which the sporangiola of the present type are replaced by single spores which have been called conidia, but which should in all probability be regarded as monosporous sporangiola. On this supposition it might even be questioned whether the two types should be separated generically.

The writer has been unsuccessful in attempting to separate mechanically an outer thin wall from the colored and ornamented wall of the conidia in *C. cucurbitarum;* but that such a thin wall, corresponding to the sporangiolum wall, may actually be present is suggested by the fact that sometimes in normal heads, but more often in those in which the spore formation has been arrested or is in some way abnormal, one finds a condition like that represented in fig. 18*A*. In such instances the contents of the "conidium" has contracted away from the base of the thin colorless mother cell wall, and has surrounded itself with the characteristic purple "conidial" wall, which is clearly distinguished from the empty space below it, as is indicated in the figure cited. No indication has been seen, however, of the formation of more than one spore in this supposed sporangiolum. In all the species of *Choanephora*, moreover, the conidial heads when not primary arise from a primary head, not from a subdichotomously branched hypha-termination as in the present instance, and the distinction between sporangia and monosporic sporangiola, if we may so call them, is wide and abrupt.

In the type represented by *Cunninghamella* it has been assumed that sporangia of the normal type are wholly lacking; but although none has been seen by persons who have cultivated any of the three described species of this genus, it by no means follows that they may not exist. In *Choanephora*, where they are known to occur, it is often extremely difficult to obtain them, unless under special conditions of cultivation; and in the case of *C. cucurbitarum*, for example, one might continue cultures under ordinary conditions for an indefinite period without ever obtaining any but the conidial form. On the other hand, at least one species of *Choanephora* is known to the writer, which was isolated by BLAKESLEE during his investigations on the Mucorales, and has never been seen to produce anything but normal sporangia with the typical appendiculate spores of this genus, although it was kept in cultivation for a period of years. As in this instance it cannot be assumed that "conidia" do not exist, so also in the case of *Cunninghamella* it remains to be determined whether sporangia of some sort are not occasionally produced under special conditions. In whatever way this question may be settled by further investigation, it is evident that the "conidia" of this genus, which are also borne on heads having the characteristics of the form-genus *Oedocephalum*, may, like those of *Choanephora*, and with equal plausibility, be considered homologous with the sporangiola of the form under consideration.

In a recent paper on the reproduction of the Mucorales, MOREAU (Le Botaniste **13**: nos. 1–3) has advanced the view that heads of the *Oedocephalum* type represent sporangia which have, as it were, been turned inside out; and that the sporangiospores thus exogenously produced are to be regarded as conidia. He would then trace to the sporangium thus metamorphosed all *Oedocephalum* conditions, isolated instances of which are known to occur among the higher fungi, *Polyporus annosus*, *Corticium effuscatum* in the Basidiomycetes, and species of *Aleuria* among the Discomycetes. The spores endogenously formed in the clavate or cylindrical bodies, which in *Syncephalastrum* replace the single spores of *Cunninghamella*, MOREAU also regards as conidia, and not as sporangial spores, comparing them to the phaeophragmic spores of *Thielavia basicola*, in which the endospore may become more or less separable from the exospore before the disunion of the spore-segments. To the writer such an explanation seems highly improbable, nor does the presence of the *Oedocephalum* type in diverse and scattered instances among the higher fungi seem in the least significant in this connection; but rather as an indication that this simple and effective method of economizing space and raising a large number of spores above the substratum is a convenient type, which has been used independently by various unrelated groups, even by the Peronosporales.

The spores of *Syncephalastrum* appear to arise by internal, not always transverse, cleavage, rather than by transverse septation as in the phragmospores of *Thielavia basicola*, and the bodies which contain them are in the writer's opinion true sporangiola, from which it is a very short step to the "conidia" of *Cunninghamella*, which, as has been suggested, might be regarded as monosporic sporangiola. That monosporic sporangia are not an anomaly in the Mucorales is shown by the characters of the genus described below as *Haplosporangium*. This opinion seems further substantiated by the comparison already made between *Choanephora* and the present genus, the sporangiola of which are, as has been pointed out, but a short step from the "conidia" of the former, and are clearly shown to be sporangial in their nature, not only through the presence of intermediate forms, but by reason of their peculiar appendages so characteristic of sporangiospores in the Choanephorae.

In a majority of the other "Cephalideae" the conditions are superficially, though not fundamentally, different from those seen in *Syncephalastrum*, owing to a different arrangement for spore-dissemination. An intersporal substance is here present which causes the sporangiospores to cohere at first, and to separate only when this substance together with the sporangium wall becomes transformed to a somewhat viscous fluid; which, as in species of *Syncephalis*, causes all the spores formed on a given head to become united in a large viscous droplet, which adheres to small Drosophilidae and other insects frequenting the substrata on which they grow. In *Syncephalastrum*, on the other hand, the spore-mass when ripe is quite dry, and spore-dissemination is probably for the most part accomplished by air currents. It is hardly necessary to mention that both these methods of dissemination occur, and may be associated, in other genera of the Mucorales, like *Mucor* and *Mortierella*.

In this connection it may be mentioned that since the publication of the writer's note on *Choanephora* (Rhodora 5:97) the common *C. cucurbitarum* has been cultivated in the Harvard Laboratories from Cuba, Porto Rico, Venezuela, and other localities, and that the culture, formerly mentioned as having been brought by the writer from La Plata, Argentina, which seemed to correspond to this species, has been contrasted with the plus and minus strains separated by BLAKESLEE from New England material of this species. As a result, the Argentine form produced abundant conjugations, forming perfect zygospores, which left no doubt as to its identity. The normal sporangia were also obtained by subjecting these forms to special conditions of moisture and nutrition, and were found to agree in all essentials with the figures and description given by MOLLER of his *C. americana*. Since, therefore, the ranges of the two overlap, and there seem to be no essential differences between them, the synonymy suggested in the *Rhodora* note may be regarded as finally established.

In addition to *C. cucurbitarum*, the writer has had in cultivation for some years two other American species. One of these was first obtained on *Hibiscus* flowers in the park at Palermo near Buenos Aires, and appears to correspond to *C. infundibulifera*, the secondary heads of which, unlike those of *C. cucurbitarum*, are persistent and become cupulate after the spores, which are smooth, have been shed. This species is very common on *Hibiscus* flowers in the West Indies, and is everywhere abundant in Grenada and Trinidad during the rainy season, where it was often seen by the writer fruiting abundantly on flowers which were still attached to the host plant, or even on buds that had apparently been hindered from opening by its growth. It has also been cultivated on material received from British Honduras and from Guatemala.

A third species, unlike either of the two just mentioned, was also found on flowers of Cucurbitaceae near Buenos Aires and was kept in cultivation for eight years. Unfortunately, the culture ran out during the writer's absence in the West Indies. Although allied to C. *cucurbitarum*, this species differs in possessing smooth spores of a lighter red-brown color.

Dissophora, nov. gen.

Fertile hyphae abruptly differentiated from slender creeping vegetative filaments, stout, of indeterminate growth, and producing sporangiophores which arise as buds, continuously produced, behind its advancing apex. Sporangia and sporangiophores as in *Mortierella.*

Dissophora decumbens, nov. sp.—Plate XXVIII

Primary fertile hypha at first erect, then decumbent, stout, creeping over the substratum indefinitely, rarely septate, sometimes producing short branches; the sporangiophores arising irregularly from all sides immediately behind its growing apex, tapering somewhat at the base and apex, often septate when mature, rarely branched. Sporangia spherical, columella none, spores spherical or irregularly somewhat angular from pressure; the whole clear white at first, the sporangia becoming slightly yellowish. Primary fertile hyphae up to 10 mm. or more in length, 10–16 μ in diameter. Sporangiophores 100–150×8 μ. Sporangia 17–23 μ. Spores about 4 μ.

On dung of wood mouse from vicinity of Cambridge.

This species was cultivated for several years, but like the two succeeding forms was unfortunately lost during the writer's absence from Cambridge, so that the accompanying figures and description have been made from mounts and dried material. Although very closely allied to *Mortierella*, the peculiarities of the primary fertile hypha, which is unlike that of any others of the Mucorales, has seemed sufficient basis for generic separation. The fructification is pure white and easily distinguished among other fungi with which it may be growing. At first it is erect, but soon becomes decumbent, the older prostrate axis being left behind by the constantly advancing apex (figs. 19 and 26), and reaches a considerable and more or less indefinite length. Immediately behind the blunt stout apex scattered buds arise (fig. 26), which soon become clavate branches, slightly divergent or even appressed, and as one traces these branches backward from the tip a gradual transition is seen from the first buds to the fully matured sporangiophores (figs. 19 and 20), and when the older portions of the axis are reached, the old sporangiophores alone are found from which the sporangia have disappeared (fig. 21). In a few instances the sporangiophores have been seen to be replaced by a branch on which two or several sporangiophores may be borne. As the latter become fully mature, and when the spores are ripe, one or more septa usually make their appearance and may also occur in the older parts of the fertile axis at considerable intervals. The latter originates from very slender hyphae running on the substratum and are very abruptly distinguished from them (fig. 25). Whether the mycelium is parasitic as it grows in nature has not been determined, but it develops very readily on potato agar without the presence of any host.

Haplosporangium, nov. gen.

Mycelium of slender branching filaments forming a felted layer on the surface of which numerous intercalary or terminal portions become differentiated, forming a superficial network of stout, often septate, segments, or series of segments, of variable length; from which sporangiophores are radiately produced, of characteristic form, broad at the base and attenuated distally to a threadlike termination which bears the primary sporangium and may be subtended by one, rarely two, threadlike secondary sporangiophores. Sporangia monosporous or bisporous.

The species of this genus differ from those of *Mortierella*, to which they are closely allied, in the presence of highly differentiated often very long segments, from which arise peculiar sporangiophores bearing threadlike terminations or lateral branches, on which are produced minute sporangia containing usually only one, sometimes two, spores. The sporangiferous segments are very characteristic and variable, forming a network on the surface of the mycelial weft, crossing it in all directions, and lying parallel to the substratum; sometimes a mere swelling from which a single sporangiophore is produced, but often elongate and bearing large numbers of the latter which arise from all sides without regularity.

The genus resembles *Dissophora* in possessing specialized structures from which the sporangiophores arise, but is clearly distinguished from the fact that these structures are intercalary and determinate, as well as by its peculiar sporangia. In general appearance, and in its habit of producing its sporangiophores in a radiate fashion from the segments of repent filaments, it closely resembles certain hyphomycetous forms like *Hyalopus* or *Cephalosporium*, and it was at first mistaken for an imperfect fungus of this nature when examined with a hand lens. The sporangia are very minute, even when they contain two spores, and the plant would hardly be taken for one of the Mucorales unless examined with some care. The presence of numerous septa in the sporangiferous segments also serves to render the general appearance of the fungus deceptive.

Both the species described below have been cultivated on nutrient agar, one of them for nearly twenty years; but, as has been previously mentioned, both were recently lost, and the material now available consists of dried specimens and glycerine mounts. In the accompanying figures no attempt has been made to represent the general appearance of the mesh of sporangiophoric segments which, though very striking in appearance, is too intricate for satisfactory drawing. The segments illustrated are small, but many occur which may reach a millimeter or more in length, with more or less clearly marked constrictions where septa occur. They are rigid and usually very straight, tapering off at the ends to fine filaments which may at once pass into another segment, or branch and run for a considerable distance before this occurs.

Haplosporangium bisporale, nov. sp.—Plate XXIX

Clear white becoming yellowish with age, forming a dense cobweb-like layer on the substratum, composed of slender filaments connecting the fertile segments which form the greater portion of the layer and may be very short, producing only a single sporangiophore, or may reach more than a millimeter in length and produce large numbers of the latter developed at right angles and in all directions. Sporangiophores simple or rarely furcate, the abruptly attenuated extremity usually straight or but slightly bent, and bearing the primary sporangium; one, or less often two, secondary sporangia borne on short straight fine branchlets which project at right angles, or may be bent slightly downward, and are opposite when two are present. Primary and secondary sporangia minute, spherical, smooth; containing one spherical spore, or less frequently two, which are subhemispherical in shape, becoming somewhat rounded. The spores hyaline, often, but not always, distinctly roughened. Bisporous sporangia 11–12 μ; monosporous 8 μ. Sporangiophores, average, 48–55×5 μ. Hyphae 1–3 μ, segments to 6.5 μ in diameter.

This form was first found on pig dung at Burbank, E. Tennessee, more than twenty years since, and has since been observed at Kittery Point, Maine, on dung of skunk and of field mice, and also at Intervale, New Hampshire, on dung of squirrels.

The species appears to be not very rare, and has probably escaped notice from its resemblance to some very insignificant hyphomycetes of the *Hyalopus* type. Although all the strains examined produce two-spored sporangia, which are in some cultures very abundant, in one instance at least they are very rare, and may be found only after long-continued search among the predominant one-spored type. Both the primary and secondary sporangia may produce two spores without regularity and on the same sporangiophore; a one-spored primary sporangium may even be associated with a two-spored secondary one. Both this and the succeeding species grow readily on rat-dung agar, fruiting abundantly.

Haplosporangium decipiens, nov. sp.—Plate XXIX

Similar to the last. The sporangiophores on the average constantly somewhat larger, the sporangia always one-spored and nodding, the sporangium wall roughened by minute folds, the spores spherical and smooth. Sporangiophores, average 60–65 μ. Sporangia 8–10 μ.

This species, although it has been cultivated from the original material, has been seen but once and was found on dung of the curious cave-dwelling

Selenodon from Hayti. It seems sufficiently well distinguished from the preceding species by its roughened nodding sporangia, smooth spores, which are always solitary in the strain examined, and its slightly larger dimensions. It is not impossible, however, that strains may occur in which two spores may be produced in single sporangia, as in *H. bisporale*.

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EXPLANATION OF PLATES XXVI–XXIX

The figures have been drawn with a camera lucida and reduced in reproduction. The objectives used, Zeiss dry and Leitz water immersion, are indicated in each case, and also the eyepiece numbers.

PLATES XXVI AND XXVII

Blakeslea trispora Thaxter

FIG. 1.—Habit of moderately well developed group of heads bearing sporangiola, showing a portion of the fertile hypha and its origin; D2.

FIG. 2.—Group of heads denuded of sporangiola; D2.

FIG. 3.—Single head with five sporangiola attached, showing corrugation of branchlets below heads; water im. 4.

FIG. 4.—The same in optical section, much younger; the spores not yet mature in the sporangiola; water im. 4.

FIG. 5.—Sporangiolum mature, with adherent basal piece and containing six spores; water im. 4.

FIG. 6.—Normal three-spored sporangiolum; water im. 4.

FIG. 7.—Sporangiolum with four spores, the basal piece adherent; water im. 4.

FIG. 8.—Three-spored sporangiolum seen in optical section from above; water im. 4.

FIG. 9.—Four spores from sporangiola; water im. 12.

FIG. 10.—Chlamydospores; D4.

FIG. 11.—Fertile hyphae from the irregularly swollen end of which five small sporangia were produced intermediate in character between sporangiola and small normal sporangia; water im. 4.

FIG. 12.—Fertile hypha with single head bearing more normal sporangiola; water im. 4.

FIGS. 13–17.—Different variations seen in normal sporangia; water im. 4.

FIG. 18.—Sporangial spores from the sporangium shown in fig. 16; water im. 12.

Choanephora cucurbitarum

FIG. 18*A*.—Two "conidia" showing thin membrane inclosing space below the single spore and suggesting a monosporangiolum; water im. 12.

PLATE XXVIII

Dissophora decumbens

FIG. 19.—Terminal portion of a fertile hypha in two parts, showing origin and progressive development of sporangiophores; A4.

FIG. 20.—Portion of a fertile hypha bearing mature sporangiophores, in which septa have begun to appear; D4.

FIG. 21.—Older portion of same bearing naked septate sporangiophores; D4.

FIG. 22.—Termination of sporangiophore from which sporangium has disappeared; water im. 12.

FIG. 23.—The same bearing a mature sporangium; water im. 12.

FIG. 24.—Sporangiospores; water im. 12.

FIG. 25.—Origin of fertile hypha from vegetative hypha; D4.

FIG. 26.—Terminal portion of fertile hypha showing origin of sporangiophores behind growing apex; D4.

PLATE XXIX

Haplosporangium bisporale

FIG. 27.—Sporangiferous segments, small and of moderate length, bearing sporangiophores or just budding to form them; D4.

FIG. 28.—Small segments each giving rise to one or two sporangiophores and connected by slender isthmuses; D4.

FIGS. 29–32. Sporangiophores bearing one, two, or three one- or two-spored sporangia; water im. 4.

FIG. 33.—Mature bisporangium; water im. 12.

FIG. 34.—Two spores from a bisporangium still adherent; water im. 12.

FIG. 35.—The same separated; water im. 12.

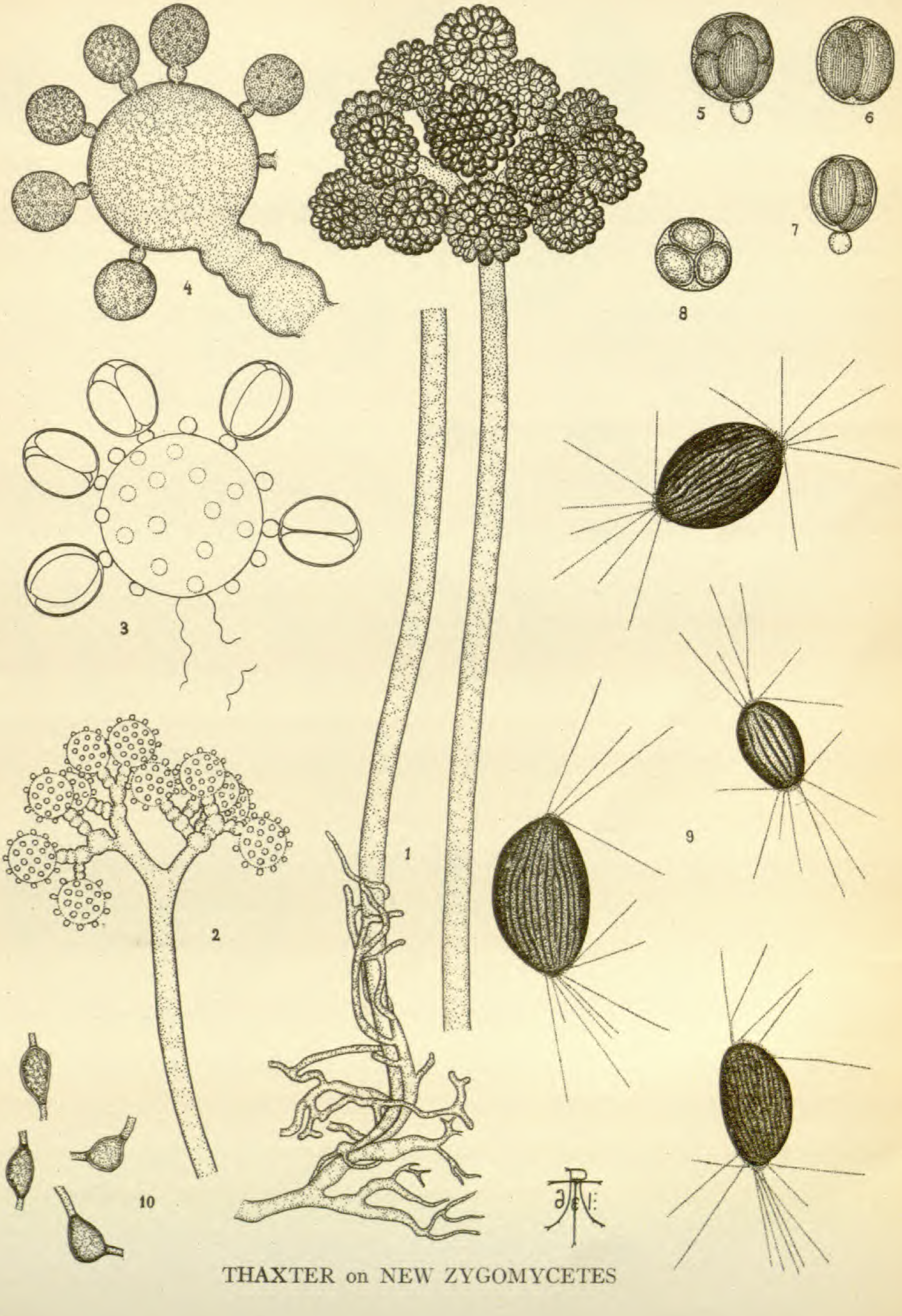
FIG. 36.—Spore from monosporangium; water im. 12.

Haplosporangium decipiens

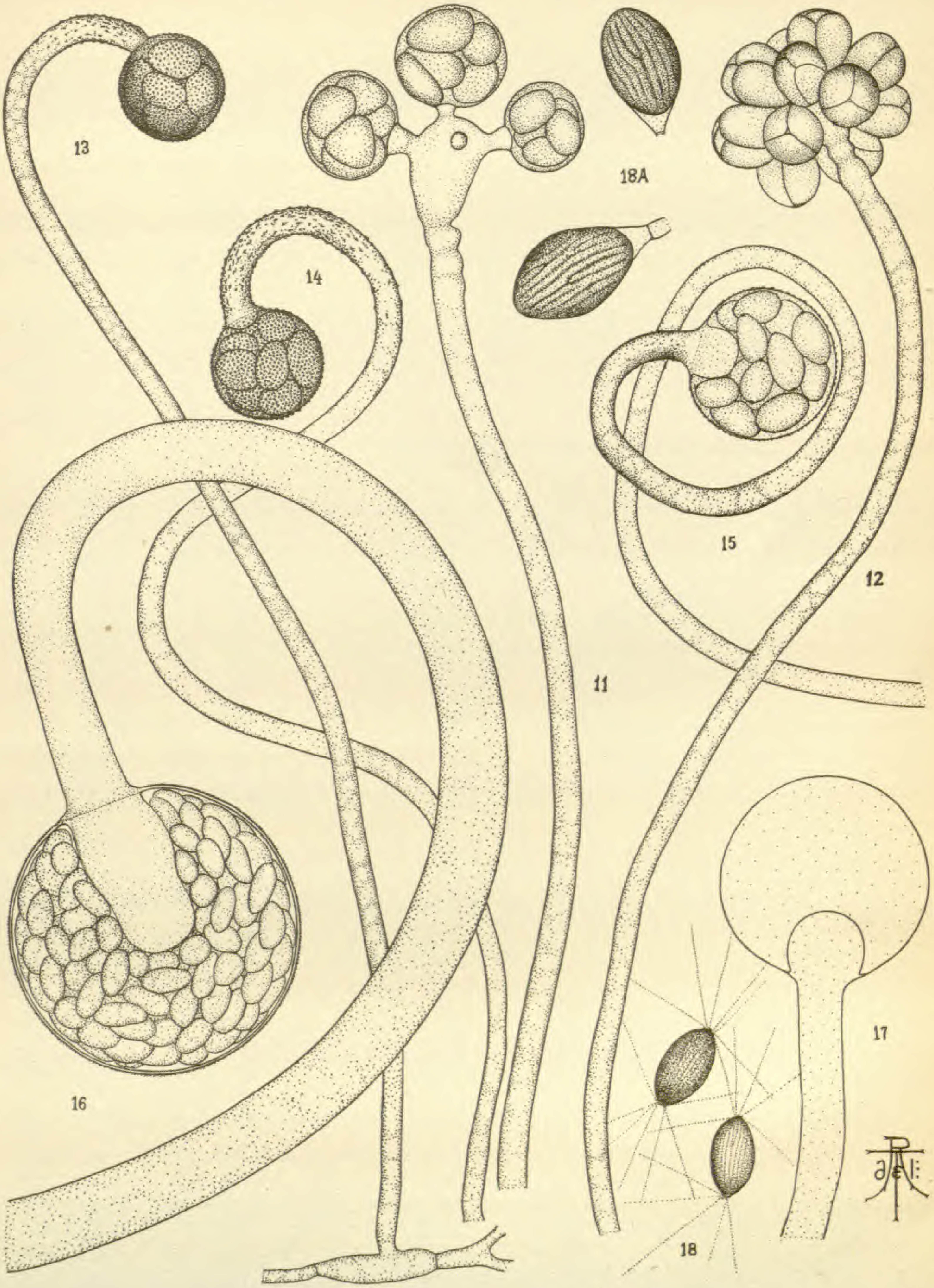
FIG. 37.—Small segments bearing sporangiophores; water im. 4.

FIG. 38.—Sporangiophores; water im. 4.

FIG. 39.—Monosporangium with its single spore; water im. 12.



THAXTER on NEW ZYGOMYCETES



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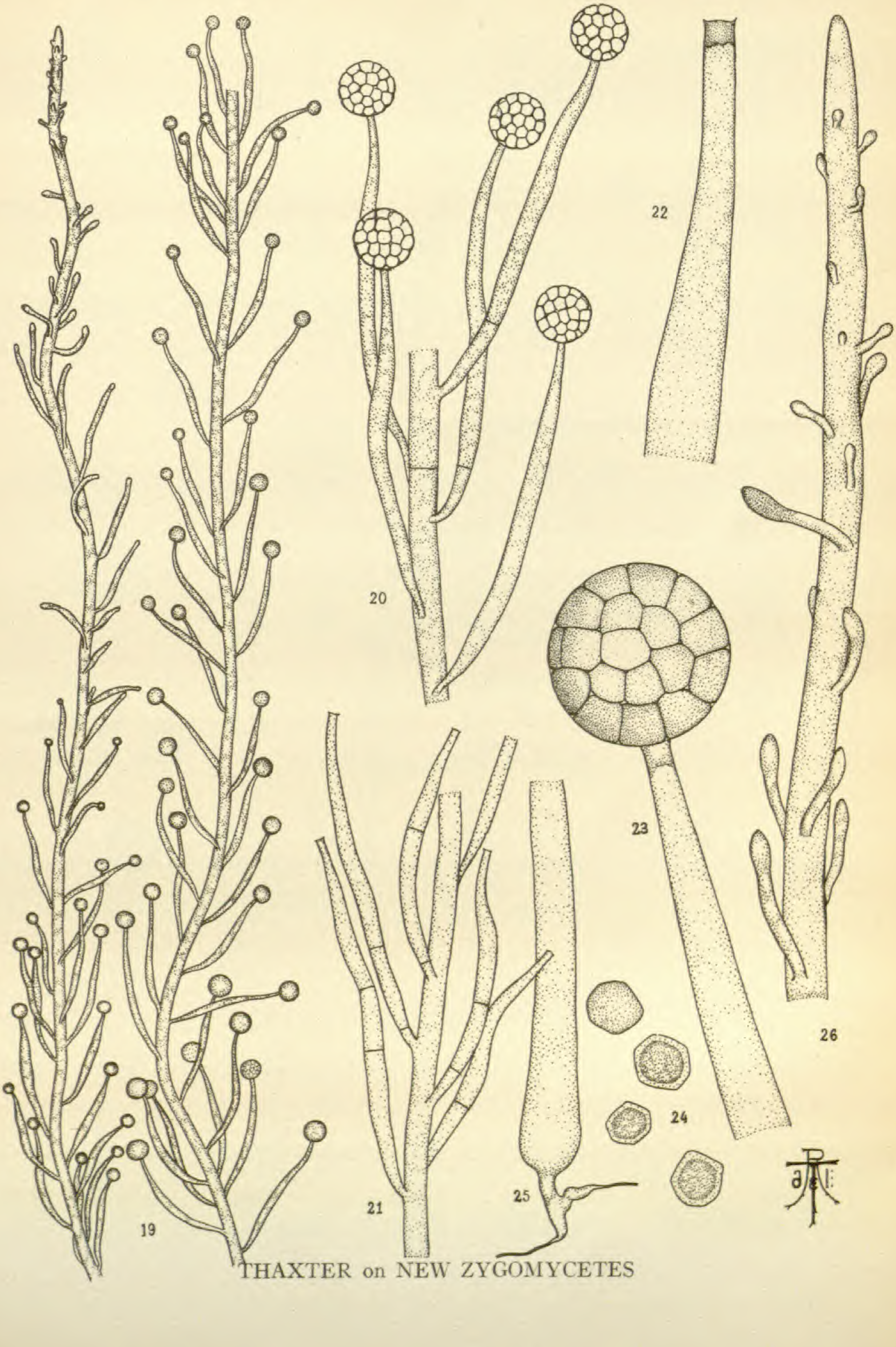

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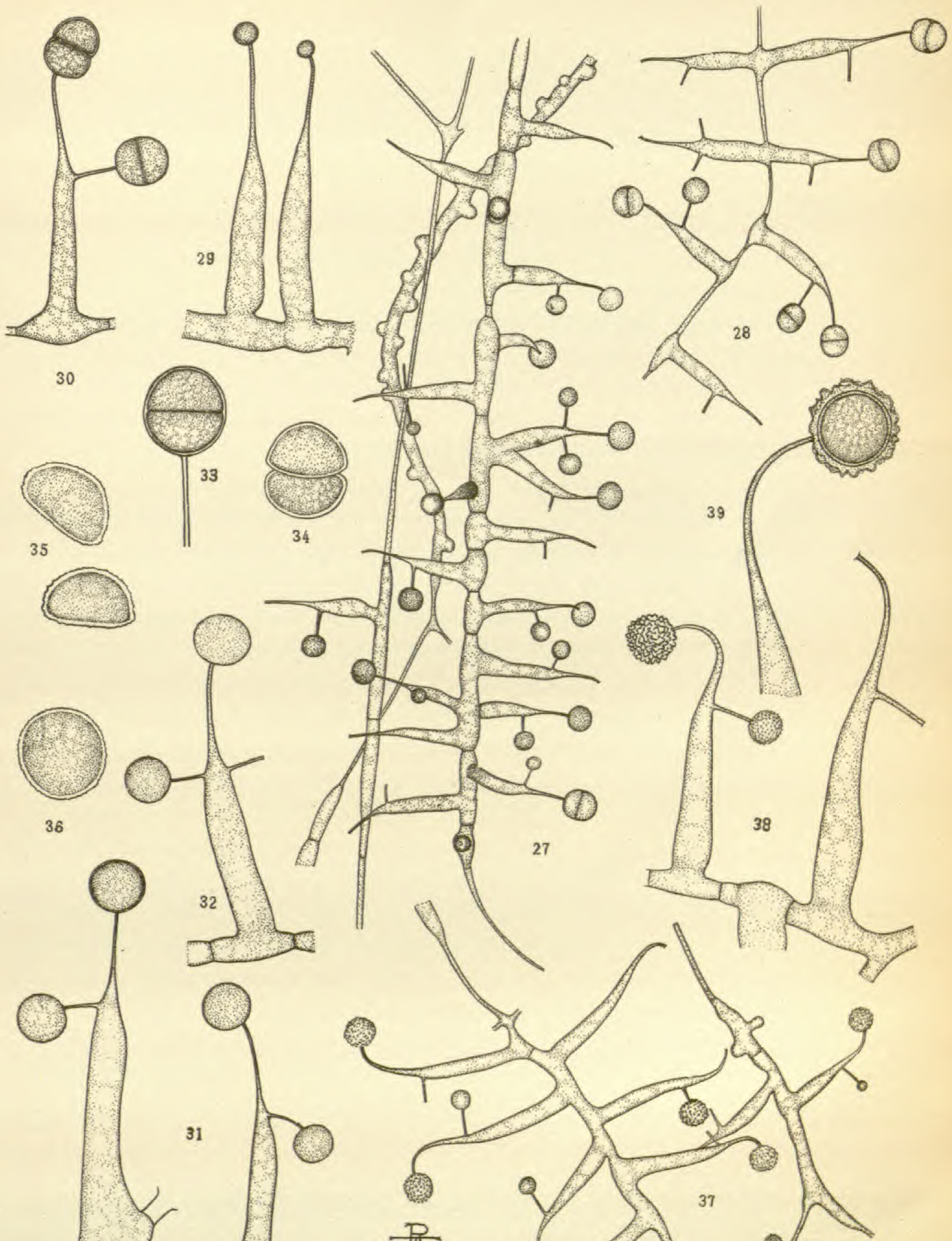

THAXTER on NEW ZYGOMYCETES

THE FORMS OF ANTAGONISM CURVES AS AFFECTED BY CONCENTRATION

W. J. V. OSTERHOUT

(WITH THREE FIGURES)

A study of the literature shows that the effect of concentration on the form of the antagonism curve is not fully appreciated. The alterations in the form of the curve are very marked when solutions are diluted to one-half strength. The writer has found this to be the case with antagonism curves of different types obtained by using a great variety of solutions. The purpose of this paper is not to give the results of these experiments, but merely to state some general principles in the hope that they may be of use to those who have occasion to make quantitative studies on antagonism.

For this purpose curves have been prepared which are diagrammatic composites of the curves obtained by the use of several pairs of salts; these composite curves are shown in fig. 1. For the sake of simplicity they are represented as having been obtained by the use of one pair of salts, which are designated as *A* and *B*. The curve *CDE*, therefore, represents diagrammatically the growth of roots in mixtures of equally toxic solutions of two salts, *A* and *B*. The abscissas represent molecular proportions; thus the point *G* represents a mixture in which the dissolved molecules are 75 per cent *A* and 25 per cent *B;* the point *H* a mixture in which the dissolved molecules are 50 per cent *A* and 50 per cent *B*. The ordinates represent the growth of roots in the various mixtures.

The antagonism at any point is the total growth minus the growth which would have taken place if no antagonism existed.[1] This antagonism is best expressed as percentage of the growth which would have taken place in the absence of antagonism. Hence the antagonism at the point *G* is expressed as $\frac{FD-FG}{FG}\times 100$.

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[1] This latter amount of growth is called the additive effect and is expressed by the horizontal dotted line *CE*. Cf. BOT. GAZ. 58:178. 1914.

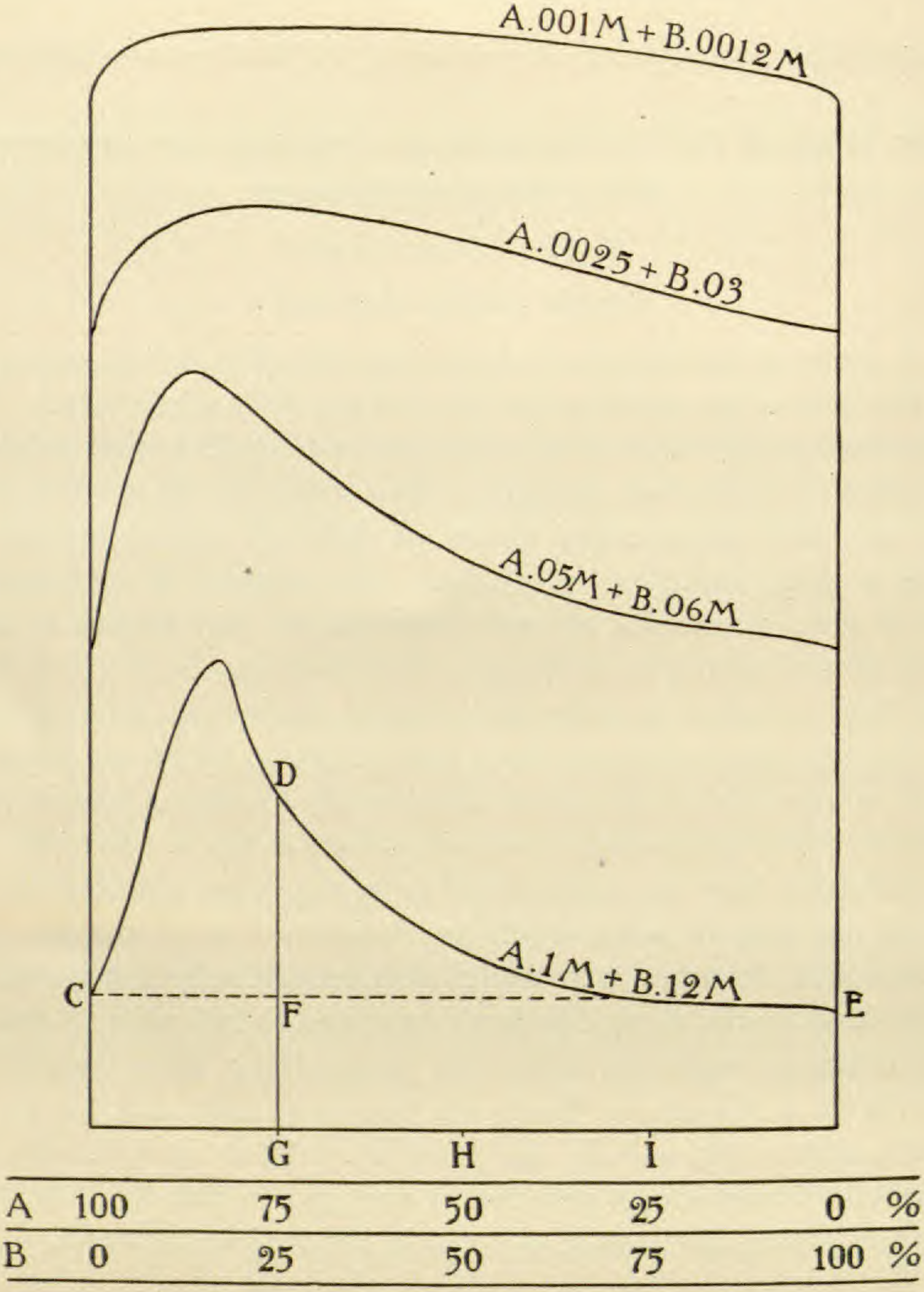

FIG. 1.—Effect of dilution on the forms of antagonism curves: the ordinates represent the growth of roots in solutions, the composition of which is represented by the abscissas; for example, on the curve *CDE* the ordinate at *G* represents growth in a mixture of *A* 0.1 M and *B* 0.12 M in such proportions that 75 per cent of the dissolved molecules are *A* and 25 per cent are *B;* on the curve which lies immediately above *CDE* the ordinate at *G* represents growth in a mixture of *A* 0.05 M and *B* 0.06 M in such proportions that 75 per cent of the dissolved molecules are *A* and 25 per cent are *B.*

The figure shows in a diagrammatic way the effect of dilution on the form of an antagonism curve. The lowest curve *CDE* shows the effect on growth of various mixtures of two equally toxic solutions *A* 0.1 M+*B* 0.12 M. The next curve shows the form of the antagonism curve when all of these mixtures were diluted by the addition of an equal volume of water (*A* 0.05 M+*B* 0.06 M). The next curve was produced by growing plants in mixtures of *A* 0.0025 M+*B* 0.03 M. The topmost curve was obtained with mixtures of *A* 0.001 M+*B* 0.0012 M.

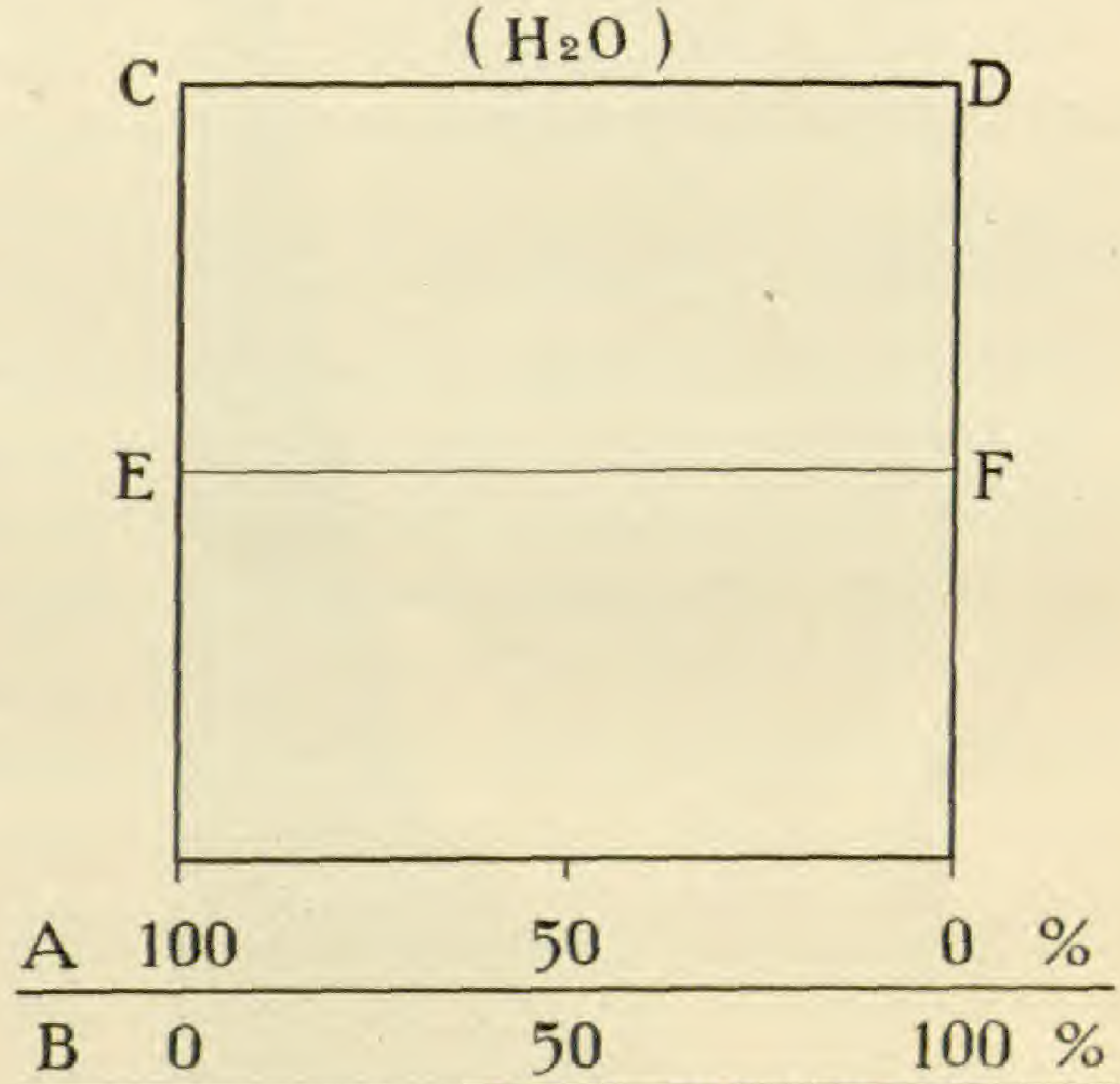

FIG. 2.—Diagram representing the composition of solutions (this serves as the base of the solid model shown in fig. 3): the lowest line represents various mixtures of solutions of two salts, *A* and *B;* the line *EF* represents the same mixtures diluted with equal volume of water; any line drawn parallel to *EF* will express the same mixtures diluted to a degree corresponding to the position of the line, the nearer it approaches to *CD* the greater the dilution; on the line *CD* all points represent distilled water.

The pairs of pure solutions were in each case equally toxic, as is shown by the fact that the two ordinates at the ends of each curve are equal in height.

It will be observed that as the solutions become more dilute, the antagonism curve becomes flatter, and it is evident that at still greater dilutions it must tend to become a horizontal straight line.

In order to give a complete description of the changes in the antagonism curve as dilution increases, it is necessary to construct a solid model. This might have as its base a triangular diagram as described in a previous paper.[2] The apices of the triangle would in that case represent *A*, *B*, and H_2O.

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[2] BOT. GAZ. 58:178. 1914.

It is more suitable for our present purpose to employ a square as the base and to represent the composition of the solutions according to the scheme shown in fig. 2. In this figure the abscissas have the same significance as in fig. 1, while the ordinates represent various dilutions of the mixtures. Thus all points on the line *CD* represent distilled water, while a point such as *E*, halfway between *A* and *C*, represents a mixture containing equal quantities of distilled water and of *A* 0.1 M. The points on the line *EF*, therefore, represent the same mixtures as the corresponding points on the lowest line, except that the concentrations are in all cases just one-half as great as those represented on the base line. It is evident that the growth in any concentration may be expressed by erecting at the proper point a line perpendicular to the plane of the paper. In this way we may obtain a solid model which gives a complete description of the changes in growth produced

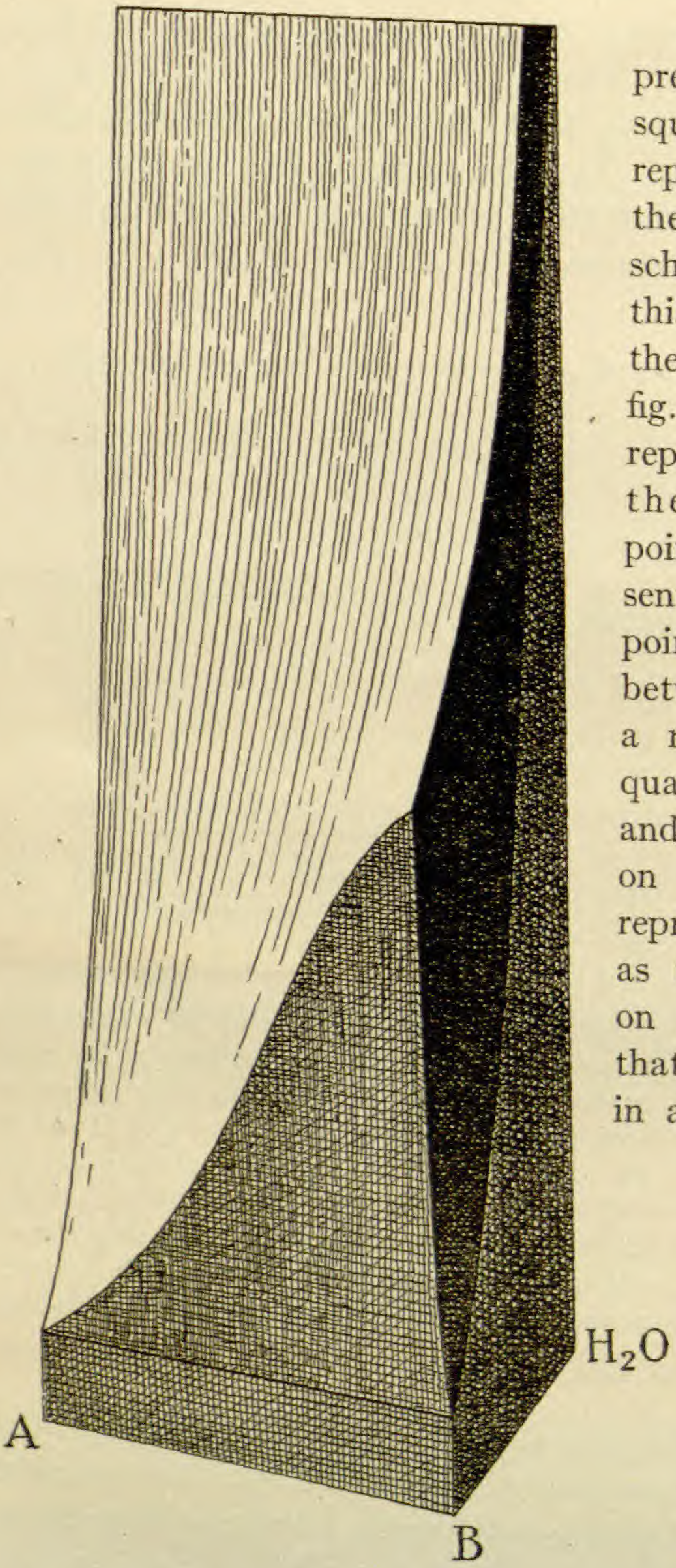

FIG. 3.—A solid model which gives a complete description of the changes produced in the form of the antagonism curve by altering the concentrations of the solutions.

by diluting the various mixtures. Such a model is shown in fig. 3.

It may be desirable to add something concerning the comparative amount of growth in distilled water and in balanced solutions. When dilute solutions are employed, the maximum growth obtained in a fully balanced solution may be greater than that in distilled water, owing to the nutrient action of the solution. But when strong solutions are employed, this is not the case, for the osmotic pressure of the strong balanced solution will inhibit growth.

In general, growth in strong solutions furnishes a much more satisfactory criterion of antagonism than growth in weak solutions. The inhibition of growth due to the osmotic pressure of the strong solutions does not noticeably affect the form of the antagonism curve, since it makes itself felt in the pure solutions to about the same degree as in the mixtures. When we employ the method of mixing equally toxic solutions, the osmotic disturbances are compensated in a manner which has been previously discussed.[3]

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[3] BOT. GAZ. 58:178. 1914.

CURRENT LITERATURE

NOTES FOR STUDENTS

Mitosis in Vicia.—SAKAMURA[1] has studied the somatic and maturation mitoses in *Vicia Cracca* L. In the somatic cells of the young flower organs he has made the following observations. At anaphase the 12 chromosomes, which vary in size, pass to the poles without splitting. After being tightly pressed together, they separate and become vacuolate chiefly along the center, which results in the appearance several writers have erroneously interpreted as a telophasic split. Contrary to the opinion of FRASER and SNELL, the anastomoses are thought to play no important part in the transformation of the chromosomes. The chromosomes can be distinguished as alveolar bands very late, but are no longer visible when the resting stage is fully reached. The resting reticulum is finely uniform, with neither prochromosomes nor other conspicuous chromatic aggregations. In prophase the reticulum gives rise to chromatic bands which have the same arrangement as those in the preceding telophase. This persistence of polarity is believed to favor the theory of the individuality of the chromosomes. There are no chromomeres, no tetrad structure such as Miss MERRIMAN has described, and no continuous spirem either at telophase or at prophase. The split occurs in the very early prophases and remains until the metaphase.

In the pollen mother cells the reticulum is somewhat looser than in the somatic cells. The chromatic granules appear to be more numerous, but there are no prochromosomes. As synizesis approaches, the granules form many small clumps along the linin threads and the whole network contracts into a tight ball. Although a parallel arrangement of threads was not seen before or during the contraction, the author believes such a side-by-side conjugation occurs, since double threads are seen projecting from the knot and in the immediately following stages. As the spirem loosens up, the two halves are distinguishable only in places, but later become very distinct. When the "hollow spirem" is formed they fuse, but soon split apart again. A second contraction occurs, during which the 6 bivalent chromosomes are formed by the simple cross segmentation of the double spirem.

At diakinesis the gemini, 2 of them larger than the other 4, sometimes show a secondary split, thus forming "Längstetraden" such as other authors have described. At metaphase of the first maturation mitosis, the members of each pair appear to be wholly fused. As they separate during the anaphase, the split which is to take effect in the second mitosis appears. At telophase there

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[1] SAKAMURA, T., Über die Kernteilung bei *Vicia Cracca* L. Bot. Mag. Tokyo 28:131–147. *pl. 2.* 1914.

is a partial alveolization and anastomosing of the chromosomes, but no complete resting stage. The second or homeotypic division follows very quickly.

Extranuclear nucleoli appear about the time of the second contraction, and are seen at all subsequent stages with the exception of the metaphases of the two mitoses. It is thus held to be not improbable that there is some connection between the substance in these bodies and that of the spindle.

The foregoing results are of interest in connection with the observations which the reviewer[2] has made on the nearly related *Vicia Faba*. In this species there is a very clear conjugation of leptonema threads before synizesis, many more stages in the somatic prophase, and a much more definite size difference in the chromosomes, both in somatic and in maturation mitoses, than SAKAMURA has shown in *Vicia Cracca*. These facts have led the reviewer to believe either that the latter species is not so favorable as an object for study as *Vicia Faba*, or that there are to be made out many more details than SAKAMURA has represented in his rather inadequate series of figures.—L. W. SHARP.

Sporogenesis in Equisetum.—In the third of a series of studies in spore development, BEER[3] gives an account of sporogenesis in *Equisetum arvense*. In the premeiotic cells the spirem, discontinuous from the first, arises from the reticulum by condensation and the breaking down of anastomoses along certain lines. The spirem segments appear to be unsplit until they become arranged on the spindle in the form of definite chromosomes. At telophase the chromosomes develop a reticulum by the formation of numerous anastomoses, but without internal vacuolation.

In the spore mother cell the discontinuous spirem is formed from the reticulum during synizesis. A longitudinal split visible during the early stages disappears as the spirem thickens. In a former note, BEER held this to represent parasynapsis, but as a result of the present study he has altered his opinion with regard to the origin of the heterotypic chromosomes. He now takes the view of FARMER, and believes they arise by the folding together of pairs of somatic chromosomes placed end to end in the spirem, the folding occurring at the time of the second contraction. During this period the nucleolus gives off material which appears to contribute to the growth of the chromatic threads.

The spindle is formed in the manner described by OSTERHOUT, with no centrosomes. The two maturation divisions occur as usual, but with an intervening resting stage. After the second division the resting reticulum is developed in the same manner as in somatic cells.—L. W. SHARP.

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[2] SHARP, L. W., Somatic chromosomes in *Vicia*. La Cellule **29**:297–331. *pls. 2*. 1913.

———, Maturation in *Vicia*. (Prelim. note.) BOT. GAZ. **57**:531. 1914.

[3] BEER, R., Studies in spore development. III. The premeiotic and meiotic nuclear divisions of *Equisetum arvense*. Ann. Botany **27**:643–661. *pls. 51–53*. 1913.

Coal Measure plants.—Our knowledge of the flora of the British Coal Measures has been enriched by recent contributions from KIDSTON[4] and ARBER.[5] The former paper is devoted to a description of the plants secured from the beds cited in the title. Among the forms referred to the ferns, 20 genera are included, represented by about 60 species. New species are described under *Sphenopteris*, *Pecopteris*, and *Neuropteris;* while a new sporangium genus (*Coseleya*) is proposed, which may represent the microsporangium of one of the Cycadofilicales. Among the Equisetales, 7 genera are included, represented by 25 species, among which is a new species of *Palaeostachya*. The Lycopodiales are represented by 12 genera, including 34 species, among which are new species of *Sigillaria* and *Lepidocarpon*. There is also a new *Sphenophyllum*. The Cordaitales are represented by 9 species. Eight new seeds are described under *Samaropsis*, *Tripterospermum* (2), *Polypterospermum*, *Lagenostoma* (2), *Rhabdocarpus*, and *Hexagonocarpus*. A new species of *Whittleseya*, a genus usually referred to Ginkgoales, calls forth the opinion of the author that it is more related to Cycadales.

ARBER's paper, as its title implies, is more concerned with the geology of the beds investigated, but it lists a large number of the plants that are made the basis of conclusions as to comparative stratigraphy. Among them two new species of *Sigillaria* are described.—J. M. C.

The embryo sac of Peperomia.—FISHER[6] has extended our knowledge of the embryo sac situation in *Peperomia* by a study of additional species, chiefly from Jamaica. The investigation included 8 species of *Peperomia* and also *Piper tuberculatum*. In all the species of *Peperomia* the mature sac is 16-nucleate, one nucleus maturing as the egg nucleus, another one as a synergid, 6–9 fusing to form the primary endosperm nucleus, and the remainder cut off individually by walls and later degenerating. In connection with the first two divisions of the mother cell, evanescent walls appear and reduction occurs, the conclusion being clear that the first 4 nuclei of the sac are megaspore nuclei. In *Piper* the mature sac is 8-nucleate, and is developed directly from the mother cell.

The author reaches the general conclusion that all of the peculiarities of the sac are derived, and that therefore the embryo sac of *Peperomia* does not represent a primitive condition.—J. M. C.

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[4] KIDSTON, R., On the fossil flora of Staffordshire coal fields. III. The fossil flora of the Westphalian series of the South Staffordshire coal fields. Trans. Roy. Soc. Edinburgh **50**:73–190. *pls. 5–16.* 1914.

[5] ARBER, A. E. NEWELL, On the fossil floras of the Wyre Forest, with special reference to the geology of the coal field and its relationships to the neighboring Coal Measure areas. Phil. Trans. Roy. Soc. London B **204**:363–445. *pls. 26–29.* 1914.

[6] FISHER, G. CLYDE, Seed development in the genus *Peperomia*. Bull. Torr. Bot. Club **41**:137–156, 221–241. *pls. 3–6.* 1914.

Fertilization of synergids.—Occasional anomalies have been noted even in 8-nucleate embryo sacs developed from a single megaspore. PERSIDSKI[7] describes additional cases in *Delphinium elatum*. Usually the development of the sac is normal, the egg having a vacuole at its micropylar end, while the synergids have the vacuole at the opposite end. In some cases the position of the vacuoles is reversed, so that the synergids have the organization of eggs and the egg has the appearance of a synergid. One case is figured in which the two male nuclei are fusing with the nuclei of two such synergids. It will be remembered that GUIGNARD figured two embryos of *Naias major* which may have arisen in this way. PERSIDSKI also figures an egg apparatus of five cells; three eggs and two synergids. This emphasizes what most of us have long believed, that the various nuclei of the sac are homologous and may replace each other in function.—CHARLES J. CHAMBERLAIN.

A new Araucarioxylon.—Dr. STOPES[8] has described a new *Araucarioxylon* (*A. novae-zelandii*) from the Cretaceous of New Zealand. It is described as new because it differs greatly from the more imperfect specimens of fossil araucarians hitherto recorded from that region. Its chief differential feature is the extreme development of the rows of thickened tracheids on either side of the rays, which are filled with large "resin-spools." By "resin-spools" is meant deposits of resin in the form of large disks opposite the middle of the pith rays, the lateral extensions of these disks running up and down the containing wall for some distance. The new species has also much more regular and strongly marked annual rings than usual among araucarians, which is held to be good evidence that New Zealand had well marked seasons during the Middle Cretaceous.—J. M. C.

Cases of suspended vitality.—BULLER and CAMERON[9] have recorded some remarkable cases of suspended vitality. They have shown that the "fruit bodies" of *Daedalea bicolor* can retain their vitality when dried, kept in the dark, and exposed to ordinary air at room temperatures, for at least seven and a half years; while those of *Schizophyllum commune* endured the same treatment for at least five years and seven months. The fruit bodies of the latter fungus, after previous drying by exposure to phosphorus pentoxide *in vacuo*, retained their vitality after being kept for 16.5 months in a vacuum at a pressure of not more than 0.1 mm. of mercury, in the dark at room temperatures;

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[7] PERSIDSKI, D., Einige Fälle anomaler Bildung des Embryosackes bei *Delphinium elatum*. Mém. Soc. Nat. Kiew **23**:97–112. *figs. 6.* 1914.

[8] STOPES, MARIE C., A new *Araucarioxylon* from New Zealand. Ann. Bot. **28**: 341–350. *figs. 3. pl. 20.* 1914.

[9] BULLER, A. H. REGINALD, and CAMERON, A. T., On the temporary suspension of vitality in the fruit bodies of certain Hymenomycetes. Trans. Roy. Soc. Canada 6:73–78. 1912.

and these same fruit bodies were found to retain their vitality when dried, kept *in vacuo*, and at a temperature of liquid air for three weeks.—J. M. C.

Seedling anatomy.—In continuing his investigations of the seedling anatomy of Sympetalae, LEE[10] has published an account of the Compositae, having examined about 50 species, well distributed through the tribes. The general conclusions are as follows: all seedlings are either diarch or tetrarch; variations in vascular anatomy occur not only in nearly related species, but in different individuals of the same species, the inference being that seedling anatomy "is of no value in questions of affinity"; the evolution of the vascular structures of seedlings is probably not an extremely slow process; tetrarchy and diarchy have probably been "interchanged" several times during the evolution of angiosperms; physiological factors are probably not sufficient to account for all the structures found in seedlings.—J. M. C.

The origin of Ascomycetes.—In a paper which reviews all the available data, approximately 100 papers being cited, DODGE[11] discusses the relationships of the red algae and the Ascomycetes. It is a very useful summary of our knowledge of the reproductive structures of these two groups, as well as a clearly presented argument in favor of the view that the Ascomycetes are a monophyletic group and have been derived from the red algae. The reproductive structures of the two groups are compared in detail, and the interesting transitions shown by *Collema* and *Ascobolus* are described.—J. M. C.

Flora of Panama.—STANDLEY[12] has issued the first of a series of papers preliminary to a flora of Panama. The present paper contains descriptions of some 40 new species from tropical America, which are distributed among 18 genera belonging to the Cyperaceae, Leguminosae, Gentianaceae, and Rubiaceae. Two new generic names are proposed, namely *Nothophlebia* and *Geocardia* (*Geophila* D. Don, not Berg.) of the Rubiaceae, and the following genera have been revised: *Sommera* (5), *Watsonamra* (11), and *Cobaea* (18).—J. M. GREENMAN.

Variation in Oenothera ovata.—Mrs. BRANDEGEE[13] has discovered that this Californian species of *Oenothera* has a remarkable range of variation. Apparently it is a plexus of "elementary species" quite as numerous as have been found in *O. Lamarckiana* and *O. biennis*.—J. M. C.

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[10] LEE, E., Observations on the seedling anatomy of certain Sympetalae. II. Compositae. Ann. Botany **28**:303–329. *figs. 2*. 1914.

[11] DODGE, B. O., The morphological relationships of the Florideae and the Ascomycetes. Bull. Torr. Bot. Club **41**:157–202. *figs. 13*. 1914.

[12] STANDLEY, PAUL C., Studies of tropical American Phanerogams, no. 1. Contrib. U.S. Nat. Herb. **17**:427–458, *pls. 24–31*. 1914.

[13] BRANDEGEE, KATHARINE L., Variation in *Oenothera ovata*. Univ. Calif. Publ. Bot. **6**:41–50. *pls. 8, 9*. 1914.

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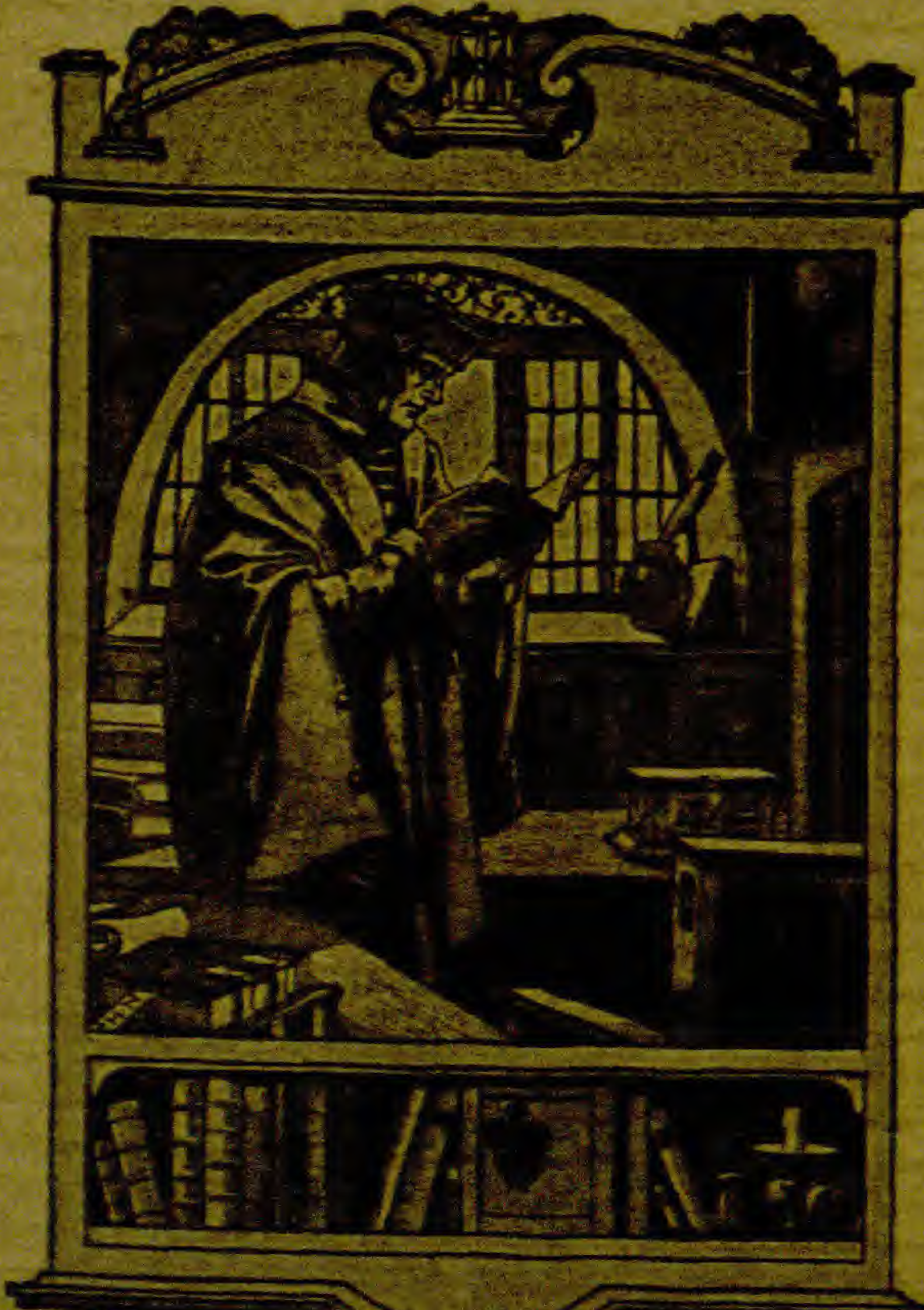

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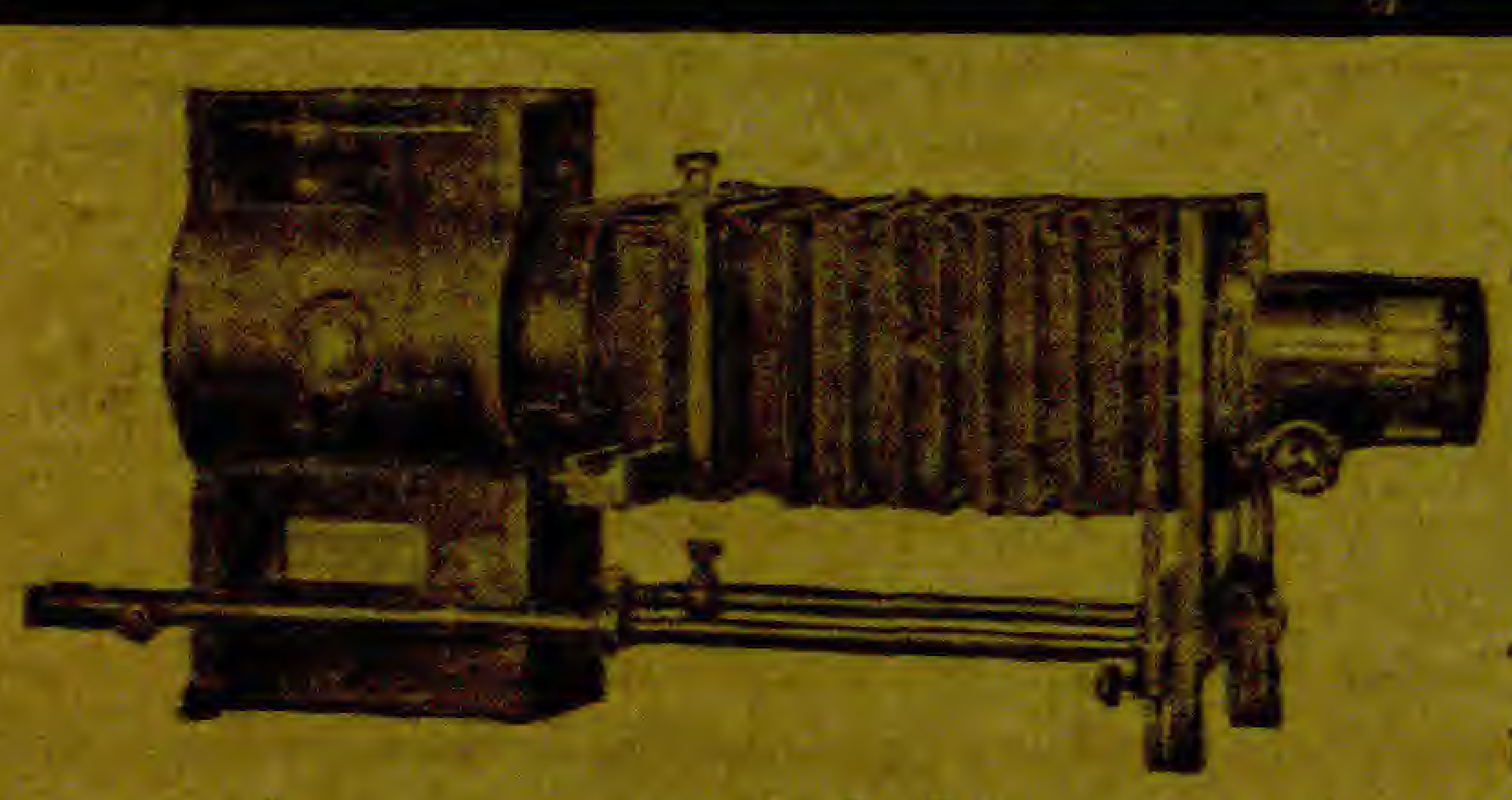

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THE
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PRAIRIE VEGETATION OF A MOUNTAIN-FRONT AREA IN COLORADO

ARTHUR G. VESTAL

(WITH NINE FIGURES)

This account is based on a study, during the past three seasons, of plant associations in the Great Plains region and of their modifications along the mountain-front. These are caused by climatic, physiographic, and vegetational differences which are of influence immediately adjoining the foothills, and to a less degree within a "mesa" belt extending eastward for several miles from the mountains. The study was carried on chiefly in the neighborhood of Boulder, Colorado. The area under particular consideration may be seen in the map (fig. 1). The mesas at Colorado Springs, slightly more arid than those at Boulder, have been studied by SHANTZ (17). A mountain-front area in New Mexico has recently been described by WATSON (20). Vegetation of the open plains has been studied principally by POUND and CLEMENTS (13), and by SHANTZ (18).

The region

The structure of the Great Plains is well described by JOHNSON (10, especially pp. 627, 628). They are essentially a structural rock slope, covered by débris from the Rocky Mountains. Near the mountains the débris apron is a mixture of rock fragments of all sizes; it has been removed in places by erosion, exposing the shales or sandstones beneath, with their residual soils. The

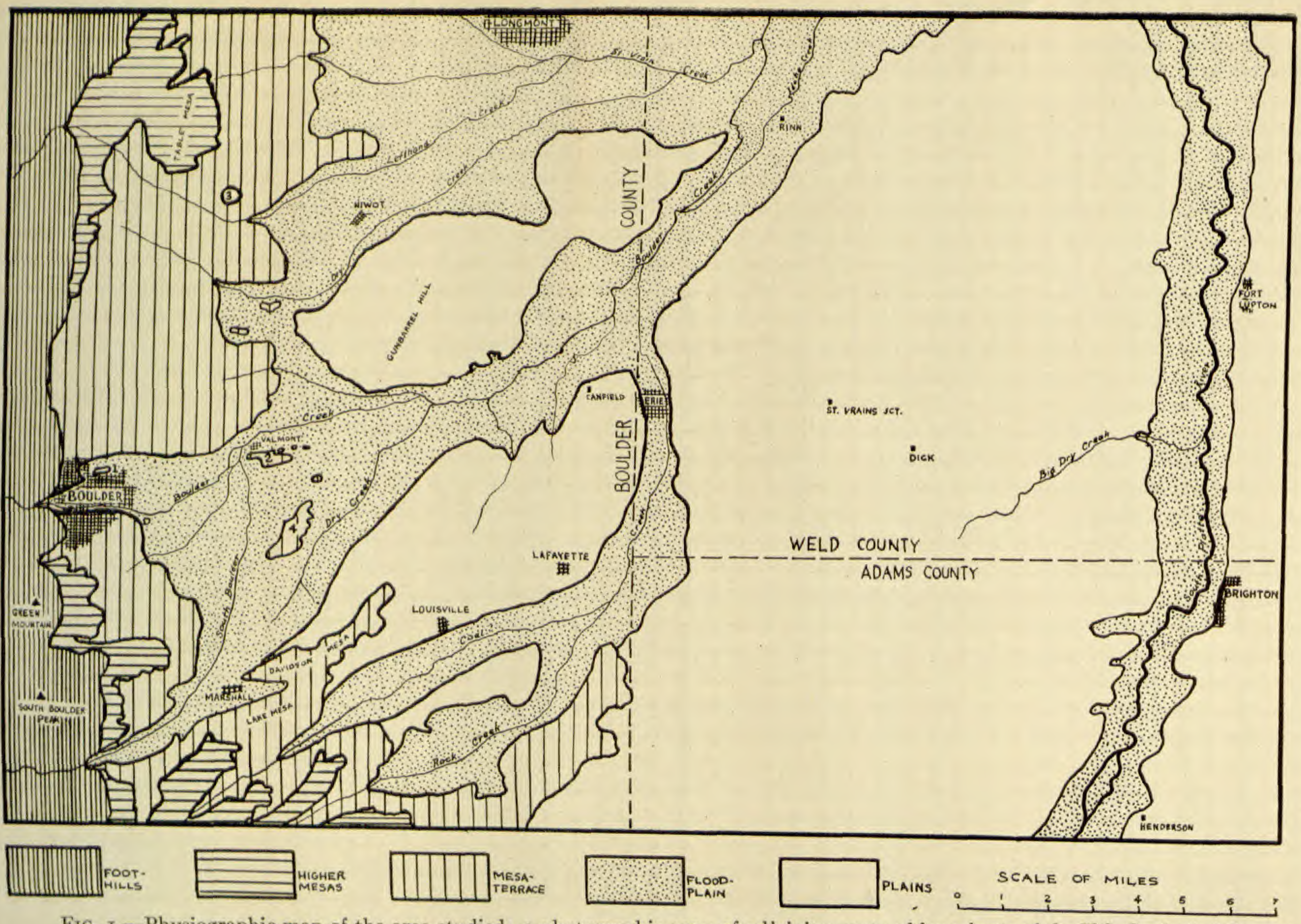

FIG. 1.—Physiographic map of the area studied: a photographic copy of adjoining parts of four sheets of the U.S. Geological Survey topographic atlas was used as a base; the high mesa areas north of Boulder Creek, and those extending east along the lower border of the map, are not exact physiographic counterparts of those between Boulder and South Boulder creeks; they are also drier, and the vegetation is that of the mesa-terrace.

uneroded areas are left as elevated benches, locally called mesas, which have been described by LEE (11) and which are discussed also by FENNEMAN (4) and by DODDS (3). The physiographic divisions of the region are shown in the map (fig. 1); they are as follows:

1. The foothills, with their hogback ridges and upturned crags, locally quite variable in soil, exposure, slope, etc.

FIG. 2.—Green Mountain and its mesas: in the foreground the mesa-terrace level occupied by a modified short-grass growth; next the floodplain of South Boulder Creek; next a continuation of the mesa-terrace; above that the higher mesa level, interrupted, with long slopes, and graded tops partly covered with pines; October 1913.

2. The mesas of the older and higher level, not continuous along the mountain-front.

3. The mesa-terrace, a more extensive, lower, and more recently graded surface.

4. The floodplain, of the present and still lower stream grade, generally débris-covered as the two mesa levels.

5. The plains proper, usually separated from the mountain-front, and with generally fine soil, residual or aeolian.

The first four divisions may be distinguished in fig. 2.

A mesa may abut at its head upon the higher slopes of the foothills or of a mesa of a higher level, or it may be isolated, cut off by erosion. Vegetation of cut-off mesas more closely approximates that of open plains. The physiographic parts of a mesa are four:

1. The mesa-top, flat, slightly inclined (at the angle of the stream gradient), and covered with unassorted rock waste. An exposure of the detritus cap is shown in fig. 3.

2. The mesa-crest, either abrupt, with loosely strewn surface rocks, and coarse, dry, unstable surface soil; or gently rounded, with soil conditions as on the mesa-top.

FIG. 3.—Vertical exposure of the detritus cap of a remnant of mesa-terrace four miles east of Boulder: the layer of mixed soil is about twelve feet deep; the surface layer is darker; the substratum is Fort Pierre shale; 1912.

3. The side-slope, either actively eroding or stable. If the slope has been lowered below the bottom of the mesa-cap, the soil of the slope is usually derived from the substratum, with only a few surface rocks. Otherwise, soil conditions are similar to those of the mesa-top. Seepage areas just below the crest are infrequent.

4. Valleys or draws, originating on the side-slope, usually broad and shallow. Gullies are infrequent. V-shaped ravines, with intermittent streams, are present in the higher mesas. Surface soil is usually fine grained.

Climatic influences within the region have been studied by RAMALEY (14) and ROBBINS (15). Only a brief summary from these two papers is given. Climatic variation from east to west is probably very abrupt at the mountain-front, although actual data are extremely scanty. The mean annual rainfall at Boulder is 18.46 inches. At Brighton (see map) the annual rainfall is about 4 inches less; on the upper mesa level it is higher than at Boulder. The months of greatest precipitation are April and May. Evaporation is on the whole rapid, less so at the foothills. The mean annual temperature at Boulder is 51° F. Temperature variations are more extreme on the mesa-terrace than on the higher mesas, the plains having a still more severe climate. Temperature inversion is a local factor in reducing diurnal temperature variations in the mesas. The growing season is thus longer at the mountain-front; spring plants appear here several weeks earlier than on the plains some miles to the east.

Diverse character of the vegetation

In the open plains, as discussed by SHANTZ (18), the plant associations are well defined, and their relations to soil and topography have been clearly distinguished. Near the mountains, however, associations are more numerous, are variable, mixed in character, not definite. The following conditions are suggested as tending to complicate the character of the vegetation:

1. Climatic conditions undergo a transition at the meeting line of plains and mountain regions. The average climate for the mesa zone, if such a term can be used, is thus intermediate in character.

2. Annual fluctuations in climate are here unusually great, favoring alternately mountain and plains vegetation.

3. Rainfall during April and May is adequate for mesophytic prairie-grass vegetation, while the latter part of the summer is usually dry. Less xerophytic foothill plants are conspicuous in the mesa areas during the vernal period; later, xerophytes of plains and dry prairie-grass predominate.

4. Variability of soil conditions (soil texture, moisture content, run-off, and absorption) is considerable and is extremely local, the usual mesa soil being composed of unsorted rock fragments of all sizes. Mesophytes can grow immediately beside and from under surface bowlders. Local and extreme variability in character of vegetation is thus possible. Radically different plants, as regards growth-form and physiological constitution, occur frequently in the same growth.

5. Topography is considerably and very locally diversified.

6. Opportunity for invasion by mountain plants is very good.

7. Environmental conditions are on the whole severe; the vegetation is in large part open. Open associations are less definite in plant composition than closed associations, in which plant competition has exercised more of a selective influence (cf. footnote below). Different associations are thus as likely to intergrade as to alternate sharply, the more so since environments frequently pass gradually one into another.

8. Present tendencies toward stabilization of mesa vegetation are more or less obscured by artificial factors, chief of which is grazing.

The principal effect of these complicating agencies is the presence of mixed growths of all grades. Mixed associations are frequent, in which plants normally dominating different associations occur together. The various secondary species also are not so regularly associated with particular dominants as would be expected from the study of more nearly typical representations of these same associations in other parts of the prairie region. At present an arrangement of the minor growths and variations of associations must be tentative. The associations are characterized partly from their occurrence and composition in other parts of the prairie province, and while certain growths in the mesa area are typical in composition, the best that can be done at present with certain growths within the area is to regard them as mixtures of two certain associations, or as a representative of one association varying in the direction of another, or with an added plant element from some particular source. On the other hand, certain appearances of some of the associations[1] are quite definite in composition, quite regular and uniform in occurrence in different stations of the mountain-

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[1] Definitions of terms applied to plant growths of different rank, as herein used, may conduce to accuracy. The unit of vegetation is taken to be the *plant association*, meaning an essentially uniform assemblage of plants living together in an area essentially uniform in environmental conditions. No interrelationship of different plants is necessarily implied, nor is uniformity taken to exclude internal *local* variability of either environment or vegetation. Those who have worked principally with closed vegetation in the humid eastern states are likely to formulate certain attributes of plant associations which will not apply to open growth in the less favorable environments of semi-arid regions, or to primitive stages in development of vegetation, or to mixed growths in habitats internally variable. In areas of vegetation permanently or temporarily open, plant competition is usually not an important limiting factor; there is no competition for light as in forest, and very little for above-ground space as in closed grassland; root competition is perhaps not so general as accommodation of root systems, so that different plant species derive moisture from different soil depths. Physical conditions may thus exert more direct control upon plant indi-

front, and often definitely to be correlated with particular environmental features.

Synopsis of the associations

The following associations, with the exception of several of the local growths, are typical within, and usually restricted to, the generally treeless interior region of North America, which is characterized by low winter rainfall and grassland vegetation (*Prairie Province*, POUND and CLEMENTS 12; GLEASON 5, p. 43). Practically all the associations are considerably variable in composition over their range, which in most cases is extended. No single criterion has been depended upon in classifying the associations.[2]

Associations of extended and general distribution within the area of the province; established vegetation, relatively stable or permanent, occupying the more extensive habitats provided by climate and physiography (Climatic or Major Prairie Associations).

- Growth dominated by surface-rooted grasses, extensive in the more arid western part of the province, or Great Plains region.
  - Dominant plants of low mat form (the short-grass growth-form of grama-grass and buffalo-grass). *Short-Grass Association*
  - Dominant plants taller (wheat-grass); growth extensive in northern parts of the plains region, and extending southward locally along the mountain front. *Wheat-Grass Association*

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viduals. It seems advisable at present to make our concept of the plant association quite broad, and to recognize that there are different types of associations.

A *consocies*, as here used, refers to an appearance or representation of an association characterized by one or several of its *dominant* species. English ecologists use *facies* in the sense that consocies is here used. A *society* of an association is taken to mean a representation of an association distinguished by abundance of one or several *secondary* species, using the word secondary to include "principal" and "secondary" species. Certain ecologists would use *society* in the sense that consocies is here used, preferring to use consocies as synonymous with association, reserving the latter term for referring generically to plant growths in general. The writer prefers to distinguish between growths characterized by dominant species and those named for secondary species, by calling the first a consocies, the second a society. It is apparent that there are a number of different kinds of societies. The present use of consocies is that of GLEASON (5), who gives criteria (p. 38) for determining whether two growths represent distinct associations or two consocies of the same association.

[2] The associations within a particular region form a complex, which may be classified in different ways, according to the purpose of the study. Bases of classification have been discussed by the writer (Local distribution of grasshoppers in relation to plant associations. Biol. Bull. 25:150. 1913).

Growth dominated by usually deep-rooted grasses; more extensively developed in the less arid central and eastern parts of the province, or Prairie region, and of local distribution along the mountain-front.

Dominant plants of tuft growth-form (of the *Andropogon* type); many of the secondary species pronounced xerophytes; growth most extensively developed in the central part of the prairie region.

Bunch-Grass Association

Dominant plants close-growing mesophytic grasses, usually sod-formers (of the nature of *Poa pratensis*); secondary species composed of a larger proportion of mesophytes; most extensively developed in the eastern part of the prairie region, particularly along the forest border.

Prairie-Grass Association

Associations of local, though commonly wide, distribution within the area of the province; either established or primitive stages of vegetation; frequently not restricted to the area of the province (Minor Associations).

Associations typical of habitats representing extreme conditions within the area of the province, in which *local* physical conditions, not being in accord with climatic conditions, determine the character of the vegetation to a large extent. The growth is thus as stable and permanent as the physical environment (Local or Edaphic Associations).

Associations of rock or of non-alkaline soils.

Growth of rock surfaces; well developed only in the foothills.

Lichen Association

Associations of dry soil.

In stony or gravelly habitats, as buttes, rock ridges, and exposed mesa-crests.

In the most extremely xerophytic and stony habitats; dominant plants cespitose, prostrate.

Mat Association

In less extreme habitats of coarse or loose soil; dominant plants xerophytic grasses.

Stipa-Aristida Association

In sandy soil; not well represented within the area studied.

Sand-Hills Mixed Association

Associations of soils of high water content.

In moist soils, usually bordering depressions.

Hordeum jubatum Association

In wet or submerged soils.

Swamp Associations, etc.[3]

Associations of saline or alkaline soils.

In deep dry alkaline soil, frequently sandy; growth dominated by tall xerophytic shrubs.

Chrysothamnus-Sarcobatus Association

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[3] Swamp associations, dominated by species of *Typha*, *Scirpus*, *Calamagrostis*, *Spartina*, etc., are about the same within the region studied as in other parts of the United States, and are not here discussed.

In clay or loam, sometimes subjected to flooding (margins of reservoirs, alkali flats).
Salt-Grass Association

Associations not typical of particular habitats, but scatteringly distributed chiefly because they are *primitive growths;* early stages in development of vegetation; growths typical of recently denuded or broken surfaces, or of physiographically new environments. Vegetation temporary in character; usually tending to change more rapidly than physical environments (Primitive Associations).

Growth dominated by annuals; short-lived growths typical in recently disturbed areas.
Plains Ruderal Association

Growths dominated by perennials; frequently preceded by a ruderal stage; usually less temporary in character.

Dominant plants xerophytic bunch-grasses.
Primitive Bunch-Grass Association

Dominant plants bushy xerophytes, deep-rooted, not grasses.
Gutierrezia-Artemisia Association[4]

Descriptions of the associations

The descriptions of associations are necessarily brief. Only the very important variations of each association are mentioned, and only dominant or very characteristic plant species receive notice. References to the same growths, or different representations of these same growths, as described by various authors, are given. It is the opinion of the writer that the time has come for correlation of associations in different parts of the same region, in cases in which the region is fairly well known. Effort has been made to select the more important references to prairie associations, but not to make a complete synonymy of the various growths.

THE SHORT-GRASS ASSOCIATION

Buffalo-grass formation.—POUND and CLEMENTS 13, p. 350.
Bouteloua (grama-grass) formation.—SHANTZ 17, p. 26.

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[4] The *Gutierrezia-Artemisia* association, while most frequent in gravelly mesa-tops, is a primitive growth rather than an association of this particular habitat. In such situations the growth normally develops into short-grass. On the other hand, certain appearances of the *Stipa-Aristida* association (the wire-grass association of SHANTZ, see p. 394), may be, following conditions of disturbance, a primitive association. Local associations, or growths relatively permanent in extreme habitats, may become primitive or temporary associations in the less extreme habitats in which climatic associations are dominant except for a short time after disturbance. Though primitive and local associations cannot always be rigidly separated, it seems helpful to distinguish the two groups.

Grasslands of the high plains.—BRAY 1, p. 91.

Grama-buffalo-grass association.—SHANTZ 18, p. 24.

Grama-grass association.—SHANTZ 18, p. 21.

Grama-grass formation.—HARSHBERGER 7, p. 537 (after POUND and CLEMENTS).

Buffalo-grass formation.—HARSHBERGER 7, p. 528 (after POUND and CLEMENTS).

The short-grass association in its typical form (*Bouteloua-Buchloe* consocies), as developed on the open plains, has been well described by SHANTZ (18). The eastern half of the Boulder region is covered principally by this growth. Near the mountains the buffalo-grass (*Buchloe dactyloides* [Nutt.] Engelm.; *Bulbilis dactyloides* [Nutt.] Raf.) is very scantily represented, as also in the northern part of the plains region. Its scarcity is made up by increased abundance of the grama-grass (*Bouteloua oligostachya* [Nutt.] Torr.), which dominates much of the area. It forms either a pure or nearly pure growth (*Bouteloua* consocies), or, in the coarse soil of the mesa-terrace, enters into a mixed growth (*Bouteloua* mixed consocies). This growth is characterized by abundance of the deeper-rooted perennial plants of the plains region, as *Euphorbia robusta* (Engelm.) Small, *Psoralea tenuiflora* Pursh, *Aragallus Lambertii* (Pursh) Greene, and *Grindelia squarrosa* (Pursh) Dunal; and usually there are additional vegetational and floristic elements: (1) some few deeper-rooted grasses; (2) tall composites, legumes, etc., typical in the more xerophytic prairie-grass just east of the plains region; and (3) less xerophytic plants from the foothills (species of *Pentstemon* and *Mertensia*, *Eriogonum umbellatum* Torr., *Geranium Parryi* [Engelm.] Heller, etc.). Certain of these, as the last two, are rarely found except at the base of surface rocks. Here also are found occasional bunch-grasses, and shrubs from the foothills, as *Ceanothus*, *Prunus*, *Oreobatus*, marking invasion of foothill shrub associations. The vegetation of the mesa near Colorado Springs, described by SHANTZ (17) is in large part to be assigned to the *Bouteloua* mixed consocies. A rather dry representation of this growth is seen in the foreground of fig. 2.

The different growths dominated principally by *Bouteloua* are considered to be parts of the same association, rather than different associations, for the resemblances appear to be more constant and striking than the differences. The *Bouteloua* mixed consocies, presenting the most radical departure from the typical short-grass growth, is different mainly in the possession of a derived element. Local patches of pure short-grass are still present, and the mesophytic plants are found in very local spots differing in moisture conditions, due to the extreme mixture of all sizes of soil constituents.

FIG. 4.—Wheat-grass, with *Artemisia aromatica* (the dark plant) in fine-grained soil of the mesa-terrace just south of Boulder; June 1913.

THE WHEAT-GRASS ASSOCIATION

Wheat-grass association.—SHANTZ **18**, pp. 21, 48.
Agropyron formation.—POUND and CLEMENTS **13**, p. 383.
Agropyron occidentale consocies.—SHANTZ **17**, p. 36.
Agropyron growth of prairie crests.—HARVEY **8**, p. 279.

The wheat-grass (*Agropyron Smithii* Rydb.; *Agropyron occidentale* Scribn.) is established in rather looser clay soil than that in which the short-grasses dominate. The typical habitat is the deposition area at the base of side-slopes of mesas, with fine soil washed down from above. Recently disturbed clay and what appear to be areas of wind deposition are also occupied by wheat-grass. Invasion by grama-grass is often initiated, and the intermediate growth in which *Agropyron* and *Bouteloua* occur together is frequently seen. In the pure wheat-grass, *Astragalus goniatus* Nutt. and *Artemisia gnaphalodes* Nutt. together form one very definite society, while *Tium Drummondii* (Dougl.) Rydb. (*Astragalus Drummondii* Dougl.) characterizes a second. A third (fig. 4) is marked by *Artemisia aromatica* A. Nels. *Carex stenophylla* Wahlenb. and *C. pennsylvanica* Lam. dominate very small areas, usually within the wheat-grass association.

The wheat-grass association has very general distribution in northern parts of the Great Plains region, extending locally southward along the foothills. These interrupted growths would probably occupy a much larger area but for the influence of grazing, which appears to favor succession of wheat-grass by grama-grass.

THE BUNCH-GRASS ASSOCIATION

Bunch-grass association.—SHANTZ **18**, p. 54. Eastern Colorado.

High prairie.—HALL **6**, pp. 30–35, in part. Eastern Kansas.

Andropogon-Sorghastrum growth.—HITCHCOCK **9**, p. 64. Eastern Kansas.

Bunch-grass formation.—POUND and CLEMENTS **13**, p. 354. Nebraska.

Grasslands of the semi-humid black-soil prairies.—BRAY **1**, p. 86, in part. Texas.

Andropogon growth of ridges, etc.—HARVEY **8**, pp. 287, 288. South Dakota.

Bunch-grass association.—GLEASON **5**, p. 47, in part. Illinois.

Dry prairies of the prairie-grass formation.—HARSHBERGER **7**, p. 523 (after BRENDEL **2**, p. 34). Central Illinois.

Bunch-grass formation.—HARSHBERGER **7**, 532 (after POUND and CLEMENTS). Nebraska.

The bunch-grass association, though occupying a very small part of the area studied, appears to be similar in composition to bunch-grass growths over the extent of the prairie province. It is best seen near the outer ends of the tops of the higher mesas south of Boulder (mixed bunch-grass consocies). The soil is gravelly, the growth somewhat open, about 35 per cent of bare surface being exposed. A number of species dominate together, in about the following order of importance: *Andropogon scoparius* Michx., *Koeleria cristata* (L.) Pers., *Andropogon furcatus* Muhl., *Sorghastrum nutans* (L.) Nash, *Muhlenbergia gracilis* Trin., *Atheropogon curti-*

pendulus (Michx.) Fourn. (*Bouteloua curtipendula* [Michx.] Torr.). Secondary species include other grasses, rather xerophytic prairie perennials, as *Liatris punctata* Hook., *Gaillardia aristata* Pursh, *Psoralea tenuiflora* Pursh, *Aster Porteri* Gray, and *Chrysopsis villosa* Nutt. The growth is shown in fig. 5.

The bunch-grass association depends upon a constant water supply which endures through the latter part of the summer. As available soil moisture is constantly present in mesa-terrace soils only till the middle of July, the association is limited to moist slopes, the higher mesa-tops, and small depressions. Scattered bunch-grasses occur beside surface rocks in the mesa-terrace.

FIG. 5.—Bunch-grass at the south crest of Horse Mesa (of the higher level): *Andropogon*, *Sorghastrum*, *Artemisia*, *Carduus;* next to the large rock a shrub of poison ivy; on rock surfaces, lichens; September 1913.

The *Andropogon furcatus* consocies is a pure or nearly pure growth of the big blue-stem. It is found in local areas of coarse soil. There is also the *Andropogon scoparius* consocies, which is synonymous with the bunch-grass association of SHANTZ (**18**, p. 54). The occurrence of a practically closed bunch-grass growth, made up of *Andropogon furcatus* and *Sorghastrum nutans*, in fine-grained moist soil of stream bottoms in the floodplain, should also be noted.[5] It probably formerly occupied considerable areas.

THE PRAIRIE-GRASS ASSOCIATION

Prairie-grass formation.—POUND and CLEMENTS **13**, p. 348, in part.
Prairie-grass formation.—SHANTZ **18**, p. 23, in part.
Prairie-grass formation.—HARVEY **8**, in part.
Prairie-grass formation.—HARSHBERGER **7**, pp. 522, 527, in part.
Prairie-grass associations.—VESTAL **19**, pp. 354, 355.

The prairie-grass growth within the region is mesophytic, meadow-like, in spring, becoming quite dry in late summer, most of the plants being then dead. It is typically developed in rich black soil of fine texture, of high moisture content in spring and early summer. Such soil is regularly found in alluvial lower slopes of foothills and higher mesas.

The *Poa-Koeleria* consocies is dominated by *Poa Buckleyana* Nash and by *Koeleria cristata* (L.) Pers. *Stipa viridula* Trin., *Poa pratensis* L., *Agropyron violaceum* (Hornem.) Vasey, and *Agropyron Smithii* Rydb. are occasionally present. The growth is tall and close. In alluvial fans at the base of certain slopes, facing to the north usually, the *Arnica* society of the prairie-grass growth is developed (fig. 6). It is characterized by abundance of *Arnica monocephala* Rydb. (*Arnica fulgens* Pursh, in part). The *Delphinium-Cerastium* society is a growth in which *Delphinium Nelsonii* Greene and *Cerastium campestre* Greene are very conspicuous. There are several other well defined societies.

The *Stipa viridula* consocies is dominated by *Stipa viridula* Trin., with occasional other grasses. It is usually on the outer

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[5] The occurrence of bunch-grass in such different habitats as its mesa and floodplain stations bears out the view that the plant growth itself, rather than the habitat, should be used in delimitation of associations within even such a small area as the one studied. The resultant conditions essential to the plant growth, that is, continually available moisture, are fulfilled in both situations. SHANTZ has shown (**18**, p. 55) that the *Andropogon scoparius* consocies is found in gravelly soil near the mountains, in sand and loose loam in eastern Colorado, in Fort Pierre clays in South Dakota, and in loam soil in the eastern part of the prairie region. Probably the vegetation itself is a very good expression of the *resultant* of climatic, local, and historic factors; the *complete* environment.

slopes of the foothills. Narrow zones of this growth are frequently found bordering *Symphoricarpos* and *Prunus* shrub associations of the foothills, which appear to be increasing in area on the slopes, at the expense of the grassland. In such meadow-like zones are seen *Frasera speciosa* Griseb., *Thermopsis divaricarpa* A. Nels., *Achillea lanulosa* Nutt., and *Aster Geyeri* (Gray) Howell, with other conspicuous mesophytes. Such meadow-like zones border scrub oak associations farther south, at Castle Rock, Perry Park, near Larkspur, and at Palmer Lake.

FIG. 6.—Society of *Arnica*, in a prairie-grass growth of moist alluvium at the base of a steeper slope, south of Boulder; dominant plants are *Poa* and *Koeleria*; May 1913.

The prairie-grass locally found west of the plains belt has many features in common with eastern black-soil prairie as represented along the border of the eastern deciduous forest. The secondary species, however, are mostly different, and the growth found along the mountain-front would probably be considered a separate association, which may be called the western mesophytic prairie-grass association. It may perhaps intergrade with the prairie-grass of the middle part of the prairie region. The growth on what is called the Middle Mesa (fig. 7) is intermediate between short-grass and prairie-grass; it is floristically quite like the South Dakota prairie-grass described by HARVEY (**8**). This similarity is more evident in late summer, xerophytic prairie-grass species like *Solidago rigida* L., *Sideranthus spinulosus* (Pursh) Sweet, *Helianthus*, *Petalostemon*, and *Aster* spp. being very conspicuous. The dominant grasses are the same in both Colorado and South Dakota areas. The dry prairies in east and west show considerable similarity; the more mesophytic prairies of east and west show considerable divergence, so far as species composition is concerned.

FIG. 7.—Mixed growth of the Middle Mesa, on the outskirts of Boulder: *Koeleria*, *Stipa*, *Helianthus*, *Senecio* (the flat-topped heads), *Erysimum*, *Aragallus*, *Eriogonum alatum* (the tall dead stalk), *Eriogonum umbellatum;* in the middle ground, the valley of Boulder Creek (the trees are planted in the town); above, the foothills, generally grass covered, with scattered rock pines, which are more abundant on the rocky ridges; June 1, 1913.

THE LICHEN ASSOCIATION

Lichen formation.—SHANTZ **17**, p. 188.
Lichen formation.—SHANTZ **18**, pp. 22, 62.

The lichen growth on rock surfaces contributes an element to the vegetation of detrital soils of the higher mesa and mesa-terrace levels within the region. Surface rocks are present on practically all the mesa-tops. The dominant species, as given by SHANTZ (**17**, **18**) are *Parmelia conspersa* (Ehrh.) Ach., *Rinodina oreina* (Ach.) Mass., *Lecanora calcarea* (L.) Nyl., and *Lecanora subfusca allophana* Ach.

THE MAT ASSOCIATION

Mat formation of buttes and cliffs.—POUND and CLEMENTS **13**, p. 376.
Mat formation of buttes and cliffs.—HARSHBERGER **7**, 535 (after POUND and CLEMENTS).

The open growth of dwarfed perennials which occupies sterile gravelly stations should perhaps not be regarded as a separate association; it is, however, distinctive in growth-form, and is frequent and well defined on buttes and hogbacks of northeastern Colorado, eastern Wyoming, and western Nebraska. It is physiologically similar to the *Bouteloua hirsuta* growth, and to the *Artemisia frigida* consocies, sometimes being found with these (fig. 8), not, however, in extreme conditions of coarse soil and exposure to sun and wind, as on certain abrupt mesa-crests. A number of the species are found also in gravel slide growths of the mountains. These growths have been studied by CLEMENTS, and by SCHNEIDER (**16**), and are akin to the mat growths of stony habitats of the plains, in several respects.

Distinctive plants of the mat association are: *Townsendia exscapa* (Rich.) Porter, *Orophaca tridactylica* (Gray) Rydb. (*Astragalus tridactylicus* Gray), *Lesquerella montana* (Gray) Wats., *Paronychia Jamesii* T. and G., *Hymenopappus filifolius* Hook., *Gilia pinnatifida* Nutt. Several species of *Chrysopsis*, *Geranium Parryi* (Engelm.) Heller, *Oreocarya virgata* (Porter) Greene, and *Phacelia heterophylla* Pursh are frequently present.

THE STIPA-ARISTIDA ASSOCIATION

Stipa formation of high prairies.—POUND and CLEMENTS **13**, p. 381.
Wire-grass association.—SHANTZ **18**, p. 48.

The dominant plants of this growth are xerophytic grasses of tuft growth-form, with moderately deep roots. They are found usually in coarse sterile soil, more commonly on south-facing slopes and crests.

FIG. 8.—Primitive grassland on a gravelly terrace left by Gregory Creek, which lies across the picture in a slanting position, and is marked by the large tree, a narrowleaf cottonwood; the growth consists of *Bouteloua hirsuta*, *Artemisia frigida*, and a few mat plants, and is very open; July 1913.

The *Stipa comata* consocies, dominated by *Stipa comata* Trin. and Rupr., occurs in the region on gravelly slopes and on windswept tops and crests of mesas. In it are occasionally found *Chrysopsis villosa* Nutt., *Psoralea tenuiflora* Pursh, *Helianthus pumilus* Nutt., *Aristida longiseta* Steud., and *Sitanion brevifolium* J. G. Smith. A pure growth of *Stipa* has been seen on a pebbly railroad embankment.

The *Aristida longiseta* consocies is dominated by the wire-grass (*Aristida longiseta*). It is important (in sandy loam and broken soils) in parts of eastern Colorado and west-central Kansas and Nebraska (SHANTZ **18**, p. 48). In the mesa area *Aristida* does not occur except in association with other grasses, chiefly *Stipa comata*. For the present the two growths have been considered together, on account of similar habitat preference, similarity of secondary species, and regularity of occurrence in association, at least in the region studied. More extended study may show the two growths to be representatives of different associations, which intergrade within the region.

THE SAND-HILLS MIXED ASSOCIATION

Sand-hill formations.—POUND and CLEMENTS **13**, p. 352, in part.
Sand-hills mixed association.—SHANTZ **18**, p. 58.

Within the region studied no truly sandy areas of any extent have been found. Local areas of sandy soil occur with sandstone outcrops and in certain dry stream beds of the plains. The sand-hills mixed association is perhaps not typically developed within the area, though well shown on sandy bluffs of the South Platte at Globeville, on the outskirts of Denver; the usual growth may be referred either to a variation of the short-grass mixed association, or to a primitive open growth made up chiefly of plant species abundant in sand-hills. Sandy soil may be recognized by the presence, often in abundance, of *Mentzelia nuda* (Pursh) T. and G., *Abronia fragrans* Nutt., *Cleome serrulata* Pursh, and *Artemisia filifolia* Torr. *Yucca glauca* Nutt. is often extremely abundant in sandy soil.

THE HORDEUM JUBATUM ASSOCIATION

A pure growth of the squirrel-tail grass (*Hordeum jubatum* L.) typically occupies moist soil of depressions, or a zone of moist soil, of variable width, surrounding swampy areas or standing water, or bordering gently sloping ditch banks. The growth appears to be native in such situations, and geographically widespread.

THE CHRYSOTHAMNUS-SARCOBATUS ASSOCIATION

Chrysothamnus growth of the sage-brush formation.—POUND and CLEMENTS **13**, p. 372.

Greasewood-white sage formation.—POUND and CLEMENTS **13**, p. 374.
Chrysothamnus graveolens society.—SHANTZ **17**, pp. 41, 47.
Bigelovia association.—WATSON **20**, p. 200, in part.
Greasewood society of the *Bigelovia* association.—WATSON **20**, p. 202.

This growth occurs in deep alkaline soil which is usually more or less loose or sandy. *Chrysothamnus graveolens* (Nutt.) Greene (rabbit brush) is more abundant in loam; *Sarcobatus vermiculatus* (Hook.) Torr. (greasewood) is more abundant in sandy loam or sand; the two often dominate together. The lower slopes of the two Table Mountains at Golden are covered with a *Chrysothamnus* growth. *Sarcobatus*, with or without *Chrysothamnus*, is abundant in sandy stream bottoms farther south in the valley of the Arkansas River. With *Chrysothamnus graveolens* are often found *Eurotia lanata* (Pursh) Moq. and *Chrysothamnus plattensis* Greene. An open growth of the latter, usually mixed with the short-grass cover, is frequent in low ground of draws, in which the soil is fine-grained and with a high proportion of soluble salts, or on level alkaline loose clay.

Within the Boulder area these growths are local, and not particularly well developed. They range locally through the plains region, and with similar growths, through the southwestern United States. The present arrangement in one association of the particular growths seen is tentative.

THE SALT-GRASS ASSOCIATION[6]

Salt-grass *Orache* formation.—POUND and CLEMENTS **13**, p. 388, in part.

Two grasses, *Sporobolus asperifolius* (Nees and Mey.) Thurb. and *Distichlis spicata* (L.) Greene, either together or singly, are dominant plants in flats which are sometimes white with alkali. Within the region such flats occur on gently sloping margins of floodplain lakes and irrigation reservoirs, and in restricted stream bottom areas. Irrigation, as at present practised, tends to increase their number and extent. The soil may be clay or loam, is compact, often trampled by cattle, and frequently subject to occasional flooding.

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[6] Vegetation of saline basins in the prairie region is discussed by J. H. SCHAFFNER in Notes on the salt-marsh plants of northern Kansas, BOT. GAZ. **25**:255–260. 1898.

The sea blite (*Suaeda diffusa* Wats.) is occasionally found in similar habitats, though usually the clay is dry and loose. It may represent a distinct association of strongly alkaline or saline habitats, or perhaps a primitive growth of alkaline soil.

THE PLAINS RUDERAL ASSOCIATION

Open waste formation.—POUND and CLEMENTS 13, p. 412.
Plains ruderal formation.—SHANTZ 17, p. 182.

The first plants to invade disturbed ground in the area studied are annuals, practically all of the plains region. The more important species are *Argemone intermedia* Sweet, *Euphorbia marginata* Pursh, *Solanum rostratum* Dunal, *Festuca octoflora* Walt., *Lappula occidentalis* (Wats.) Greene, *Plantago Purshii* R. and S., *Ambrosia psilostachya* DC., *Boebera papposa* (Vent.) Rydb., *Helianthus petiolaris* Nutt. *Ambrosia trifida integrifolia* (Muhl.) T. and G. is a very conspicuous ruderal in moist soil.

Toward the mountains, and in all except the driest soils, the sweet clover (*Melilotus alba* Desv.) is becoming very frequent in disturbed situations. In such habitats, as in the eastern part of the prairie, it is apparently more successful than native ruderals. The Russian thistle (*Salsola Tragus* L.) behaves as if it were a successful native ruderal, having become thoroughly established.

THE PRIMITIVE BUNCH-GRASS ASSOCIATION

Calamovilfa longifolia consocies.—SHANTZ 17, p. 46.
Sporobolus cryptandrus (growth).—SHANTZ 17, p. 46.

Certain of the grasses of the prairie region are very abundant in new growths or in open or sterile situations, as contrasted with other grasses which are found only in more permanent, closed associations, or in mesophytic stations or in soils of considerable humus content. Among these xerophytic grasses distinctive in primitive growths are *Elymus canadensis* L., *Eriocoma cuspidata* Nutt., *Calamovilfa longifolia* (Hook.) Hack., *Sporobolus cryptandrus* (Torr.) Gray, and *Panicum virgatum* L. *Stipa Vaseyi* Scribn., though infrequent in the immediate area, occupies many similar situations throughout the Colorado mountain-front. All of these can grow in coarse soil, being deep-rooted; some of them build temporary dunes on the sand-hills and on the shores of the Great Lakes. Each species occurs in places alone, but mixed growths of several of these grasses, are about as frequent, and since they are very similar in growth-form, in physiology, and in distribution, they are for the present considered as members of one variable association.

Within the region these growths occur in scattered patches in disturbed situations, frequently in railroad rights-of-way, and usually in loose or sandy soil. Extremely local growths are found on the higher mesas and foothill slopes.

FIG. 9.—*Gutierrezia-Artemisia* growth of a mesa four miles east of Boulder: this end of the mesa differs from the rest of it in that it is not at present pastured, and in that *Gutierrezia* is scarce; *Eriogonum effusum* is conspicuous, though not so in the photograph; September 1912.

THE GUTIERREZIA-ARTEMISIA ASSOCIATION

Gutierrezia-Artemisia association.—SHANTZ **18**, p. 60.
Undershrub formation.—POUND and CLEMENTS **13**, p. 371, in part.
Artemisia frigida society.—SHANTZ **17**, p. 37.
Gutierrezia Sarothrae society.—SHANTZ **17**, p. 37.
Gutierrezia formation.—WATSON **20**, p. 202.

The *Gutierrezia-Artemisia* association, described by SHANTZ (18), is typically developed in the plains areas of the region studied. *Gutierrezia Sarothrae* (Pursh) B. and R. is more abundant in the southern part of the plains region, and is not common in the foothills or even in the mesa-terrace. *Artemisia frigida* Willd. ranges far to the north, and forms an important primitive growth in the mountains to as high as 10,000 feet. The *Artemisia frigida* consocies, therefore, is the important growth of the mountain-front, being quite frequent on talus slopes and gravel slides of the foothills. *Bouteloua hirsuta* Lag. is often associated with *Artemisia;* this growth may represent a separate association.

The *Gutierrezia-Artemisia* growth in the plains of the region contains *Eriogonum effusum* Nutt. and *Grindelia squarrosa* (Pursh) Dunal, sometimes abundantly. There are indications that relative abundance of *Gutierrezia* and *Artemisia* is materially influenced by grazing animals, *Gutierrezia* being apparently more resistant.

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A STUDY OF SYMPHYOGYNA ASPERA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 196

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(WITH PLATES XXX–XXXII)

The species of *Symphyogyna* are tropical and semitropical liverworts. They grow best in abundant moisture, and especially well in dripping water, but do not thrive in standing water. As a genus distinct from the other genera of Hepaticae, it was first described by NEES AB ESENBECK and MONTAGNE (9) in 1836, and four species were described: *S. brasiliensis*, *S. Hockstettii*, *S. difformis*, and *S. circinata*. Up to this time the first three species had been included in *Jungermanni*. The fourth species was evidently a new one. Additional forms were discovered, and later GOTTSCHE, LINDENBERG, and NEES AB ESENBECK (18) listed 24 species. SCHIFFNER (31), in his census of 1909, reports 27 species.

Symphyogyna is closely related to *Pallavicinia*, which is well known in our flora. These two genera have an interesting parallel series of plant bodies, ranging from the entire ribbon-like form to the deeply dissected and leaflike thallus which closely resembles a fern. While many of the species of *Symphyogyna* are distinctly anacrogynous in form, others with their leaflike lobes are strikingly like the acrogynous Jungermanniales, so that the genus as a whole holds a high rank among the Jungermanniales. Moreover, in the development of the sporophyte and the late differentiation of its sporogenous tissue, it almost approaches the condition of the mosses. STEPHANI (33) considers *Treubia insignis*, with its acrogynous characters, more closely related to *Symphyogyna* than to any other genus, and SCHIFFNER (31) places *Monoclea*, whose position among Jungermanniales has been severely contested by others, especially JOHNSON (22), close to *Symphyogyna*. These two relationships, whether real or imaginary, give some indication of the range of habit of the genus.

Comparatively little is known of the morphology of *Symphyogyna*. LEITGEB (26) gives a general survey of the genus and emphasizes in particular *S. sinuata*, *S. subsimplex*, and *S. rhizoloba*. He discusses the thallus, including the central strands of smaller cells, the apical cell, and the branches on the ventral side of the thallus. He passes over briefly the sex organs, giving no figures of the antheridia and few of the archegonia. He illustrates a close series of stages of the young sporophyte, but states that the later details in the development of the sporogenous tissue into spore mother cells and elaters remained dark to him. The only observations which he makes concerning the older sporophyte are that the apex of the sporophyte undergoes secondary divisions, to which is due the beaklike form of the tip of the capsule; that the differentiation into elaters and mother cells occurs relatively late; that the former are arranged in a direction parallel to the embryo axis and that they are uniformly distributed throughout the capsule. TANSLEY and CHICK (34) discuss more fully the structure of the central strand of the thallus. No other papers bearing directly on the morphology of the genus have been published, and only occasional references in connection with other liverworts have been made.

The highly developed conducting tissue of the gametophyte and the mosslike development of the sporophyte make the genus peculiarly interesting. It was hoped that a complete life history of the species might be secured, but many stages are lacking. While little is added to LEITGEB'S account, a few facts concerning a genus about which so little is known may be of interest.

Material

The material was collected in the vicinity of Xalapa and Texolo, Mexico, by Dr. W. J. G. LAND and Dr. CHARLES R. BARNES in the autumns of 1906 and 1908, and by Dr. LAND in the autumn of 1910. It was killed in the field in 6 per cent formalin made up with 50 per cent alcohol. Excepting for the young embryos, this killing agent was found to be satisfactory, and in fact it is almost a necessary one when time and light baggage are to be considered. From the alcohol-formalin solution the material was transferred to 50 per cent alcohol, and the process of dehydration was carried on through series of absolute alcohol and xylol into pure xylol, was imbedded in paraffin and cut, usually, 5 μ thick. Safranin and gentian violet, safranin and lichtgrün, and Haidenhain's iron-alum hematoxylin were the stains used.

Thallus

Symphyogyna aspera (figs. 1 and 2) has a rhizome-like portion which closely adheres to the soil, and from this rhizome arise somewhat inclined aerial branches. GOEBEL (15), in his description of *S. sinuata*, states that the winged shoots can again decrease at the apex and become stolons, but usually they conclude their growth after reaching a definite medium size, and then at their base they form a ventral lateral shoot which continues the growth as a stolon, subsequently rises above the substratum, broadens out, again forms a dorsiventral shoot, and so on. His illustration of *S. sinuata* shows a chain of five such generations. In *S. aspera* no indications were noted that the apex of the thallus may act as a stolon, but growth by a basal stolon is characteristic of this species also.

Rhizoids are very abundant, forming thick mats upon the ventral surface of the rhizome and parts of the aerial branches in contact with the soil. As has been previously noted, especially by BOLLETER (2) in *Fegatella conica* and by CLAPP (7) in *Aneura pinguis*, the ends of the rhizoids are curiously branched, twisted, and often greatly enlarged (figs. 3 and 4). The branched ends often tightly surround particles of foreign material. If there are cross-walls near the ends of the rhizoids they must be quite rare, for none were observed in the material examined.

Fungi are abundant, especially in the rhizoids (figs. 5 and 6). A favorable view gave indications that the fungus had penetrated the tip of the rhizoid (fig. 6). The fungous species could not be determined from the preserved material, but evidently more than one species is present. Some hyphae are large and abundantly septate (fig. 5), and other hyphae are quite small, so that the septations, if present, could not be distinguished. Fungi have been frequently reported among liverworts, especially by LEITGEB (26), KNY and BOTTGER (24), J. PEKLO (30), GOLENKIN (16), NĚMEC (28 and 29), CAVERS (5), JANSE (21), GARJEANNE (13 and 14), and CLAPP (7). GARJEANNE has done an extensive piece of work in having examined over 30 species, and he concludes that the fungi neither do harm nor good to the host plant.

In transverse section, the rhizome of *S. aspera* is somewhat irregularly oblong (fig. 7). The cells are undifferentiated except in the central region, where there is a group of small, thick-walled cells which stand out in sharp contrast with the much larger, thinner-walled cells surrounding them. In longitudinal section they appear as very narrow, greatly elongated cells, whose pointed ends dovetail into each other (fig. 8). LEITGEB (**26**, p. 69) gives the length of the cells in *S. sinuata* as 0.3 mm. and the breadth 0.009 mm. In *S. aspera* the cells are 0.537 mm. long and 0.008 mm. in diameter.

The aerial part of the thallus has the same general structure as the rhizome (fig. 9). There is a central region of small, thick-walled cells surrounded by broader, thin-walled cells, which together form the midrib of the thallus. From the midrib the thallus narrows abruptly into winglike extensions consisting of one layer of cells. By treating the thallus, either the rhizome or aerial parts, with Schulze's macerating solution, the cells of the central area can be separated entire, and by staining them with Delafield's hematoxylin, the structure of the cell walls may be seen distinctly (fig. 10). This treatment enables one to get a more accurate measurement of their length, and it is also interesting to know that they remain intact after the action of this reagent. The cells of the wing are disintegrated, but some cells surrounding the central strand may remain intact provided the action of the reagent is not too long (fig. 8). These long, narrow cells, with their thick walls and spirally arranged pores, make *Pallavicinia*, *Hymenophyton*, and *Symphyogyna* peculiarly interesting. They were discovered by Sir WILLIAM HOOKER in 1816 in *Pallavicinia Lyellii*. In 1864 GOTTSCHE (**17**) described them in *S. sinuata*. LEITGEB (**26**, p. 69) describes the cells with their spirally arranged pores, but he has no illustrations. FARMER (**10**) adds little to LEITGEB'S account, though he gives a good drawing of the transverse section of the rhizome, and also one showing the lack of continuity between the strand of the main part of the thallus and that of the ventral branch. TANSLEY and CHICK (**34**) discuss fully the strands in *Pallavicinia*, *Hymenophyton*, and *Symphyogyna*, and they have demonstrated with eosin that in *Pallavicinia Lyellii* the strands conduct water. Their detailed drawing of part of a cell showing pores (*pl. 1. fig. 4*) is representative of the pores in *Symphyogyna*, with the probable exception that in *S. aspera* the pores are more regularly arranged and more obliquely spiral. Sections of the thallus treated with acidulated alcohol and stained with methylene blue, following Mayer's method given by HAAS and HILL (**19**), gave the test for pectose by showing the middle lamella stained a deeper blue (fig. 11). The pores are so narrow that except in very thin sections they are readily overlooked in transverse sections.

In the species of *Symphyogyna* which he examined, LEITGEB found the dolabrate apical cell like that in *Pallavicinia*, etc., though for *S. sinuata* he makes the statement that at first glance one might think the apical cell like that in *Pellia calycina*, *Blasia*, etc., which is the well known wedge-shaped cell. However, he considers that such a view is an erroneous one, and that the apical cells of all the species of *Symphyogyna* are alike. *S. aspera* has two types of apical cell, the dolabrate and the wedge. STEPHANI identified the species and grateful acknowledgments are due him. However, in the material sent to him, the part collected at Texolo, Mexico has the wedge-shaped apical cell, and that collected at Xalapa has the dolabrate apical cell. Moreover, the thallus of the material collected at Texolo is slightly broader and less deeply lobed than the material collected at Xalapa. The last two characters may be overlooked as due to a difference in environment; but when to them is added a difference in the apical cell, one may be justified in considering the material as representing different species, especially since species are often separated for less convincing reasons. If both forms belong to the same species, then there is the interesting situation of two types of apical cell in mature plants of the same species (figs. 12–16). However, CAMPBELL (**3**) reports two types of apical cell in *Calycularia radiculosa*.

In the dolabrate cell a segment is cut off alternately to the right and left. The primary segments on both sides are divided longitudinally, and from the middle secondary segment in each side can be traced the one-layered winglike extensions of the thallus (fig. 17).

From the nature of the dolabrate apical cell there cannot be true dichotomy, if by the term "true dichotomy" is meant the division of the apical cell into two segments alike in shape and size and also like the original apical cell. This seems to be the only standard for the determination of true dichotomy; but frequently the organization of the apical cell of the branch occurs so close to the apical cell of the main branch that the mature thallus has the appearance of true dichotomy. In the liverworts which have a wedge-shaped apical cell true dichotomy is the probable form of branching; for a cell of this form can be divided into two cells which are alike in size and shape and also like the parent cell; although it is possible that segments near the apical cell may organize a new apical cell.

Two-celled mucilage hairs are organized from segments close to the apical cell, and these occur on both the dorsal and the ventral sides. These mucilage hairs at first project over the apical region of the thallus; but as the thallus grows new ones are formed and the older ones, apparently in good condition, can be seen far back from the apex. LEITGEB (**26**, p. 73) states that they are more abundant on the ventral than on the dorsal side of the thallus, and this statement seems to be true also for *S. aspera*. The mucilage hairs are formed only in the immediate vicinity of the apex.

Branching on the ventral side of the thallus of *S. aspera* is quite common. LEITGEB discusses rather extensively the situation, and traces the branches close to the apical cell.

Sex organs

Symphyogyna is dioicous, the plants bearing antheridia usually being more slender than those bearing archegonia.

ARCHEGONIA

The archegonia are borne in groups in the dorsal side of the thallus. Each group is surrounded by a deeply dissected involucre, which is attached on one side to the thallus. Usually there is a group at the place of forking of the thallus, but they are not restricted to that region, and often there are several groups close together on one branch. The archegonia have their origin close to the apical cell (fig. 18), and in this particular thallus the initial shown is the only one of the group which had made its appearance. Moreover, a cell which would have been actively involved in the development of the involucre is in the second row to the left of the initial. Since similarly shaped cells may be distinguished in several sections, it seems probable that the involucre has its origin from a row of meristematic cells. As the archegonia (figs. 19–25) develop, the thallus below them becomes meristematic, so that the archegonia come to be arranged on a pad, as is common among the anacrogynous Jungermanniales.

The earliest stage of an archegonium might readily be mistaken for a young mucilage hair; but a mucilage hair may be distinguished by the bend which it makes very early toward the apical cell. By transverse divisions the archegonial initial is divided into a tier of three cells, and the outermost cell by three longitudinal walls is divided, in the usual way, into four cells, an inner cell surrounded by three outer cells (fig. 21). The neck of the archegonium is long, and the neck cells are spirally arranged, as in the mosses (fig. 6). There were counted 13 neck canal cells in one archegonium, and in another archegonium the neck canal row was in part double (fig. 28). The egg is small, and in that respect it resembles the egg of mosses. An undoubted case of fertilization was not seen, though fig. 22 27 represents an archegonium which may be interpreted as showing fertilization. The withered neck cells and the presence of young embryos in the same cluster add weight to this interpretation.

ANTHERIDIA

The antheridia are grouped in compact masses on the midrib on the dorsal side of the thallus, and each antheridium is surrounded by a small involucre somewhat similar to the one which surrounds each group of archegonia. (SPRUCE **32**, *pl. 30*), in a diagrammatic way, illustrates the antheridial scales of *S. trivittata.* More than one group of antheridia may occur on the same thallus, indicating a cessation followed by a renewal of activity in the production of antheridia. This feature LEITGEB observed in the species which he investigated (**26**, p. 74). No plants bearing antheridia were found in the material which gave the young stages of archegonia, and though many antheridial plants were mixed with the plants bearing sporophytes, the antheridia with few exceptions had discharged their sperms and fallen off. The few antheridia that were found seem to have been delayed ones. No very young stages were obtained, but the older ones indicate the method of development usual in the Jungermanniales (figs. 29–31). The body of the antheridium is nearly spherical, and the stalk is short and slender.

Sporophyte

The fertilized egg is divided into two cells by a transverse wall (fig. 32), and a third cell is cut off by a wall parallel to the first. In the material studied karyokinetic figures were entirely lacking in the young embryos, so that it is impossible to state with certainty whether it is the epibasal or hypobasal cell that divides. LEITGEB mentions that in *S. rhizoloba* it is the inner cell which remains undivided, and that this cell can be recognized in well developed embryos. He gives a close series of stages for this species, and apparently after the row of three cells is formed there is some variation in the subsequent walls. However, he states that the outermost cell is divided by an oblique wall. This may also be true for *S. aspera* (fig. 33). This oblique wall is the beginning of the apical growth which LEITGEB emphasizes very strongly for *S. rhizoloba*, and in fact later stages of *S. aspera* (figs. 35–37), with their marked segmentation, seem to verify this method of development.

The young embryo is slender, and it is early shown that the uppermost part is the region most actively involved in cell division, and that part is also marked by a denser cell contents. The middle part is concerned with elongation, and there the cells lengthen, with little activity in cell division (fig. 37). The cell contents in this part is less dense than in the upper part, and it is also greatly vacuolate. The innermost cell of the embryo may very early divide, as shown in fig. 34, but, judging from the general contour of the young embryos and without the aid of figures, it seems probable that cell multiplication in this part of the embryo is restricted to very few divisions. Periclinal walls are formed separating the amphithecium from the endothecium. Three wall layers are formed, the middle layer being apparently cut off from the outer layer (fig. 38). The walls of the outermost layer of cells thicken as the sporophyte matures, and the two inner layers do not entirely disappear, so that the mature capsule wall is not one layer thick, as has been reported for some species of *Symphyogyna* (1). Plastids are quite numerous in the cells of the capsule wall. The beaklike extension of the apex of the capsule is prominent, as LEITGEB noted in the species which he studied (fig. 38). The foot of the mature embryo is often somewhat anchor-shaped, but more frequently there is a gradual narrowing toward the tip of the foot, which is always bent over in a mosslike manner (fig. 39). The cells of the thallus surrounding the sporophyte become greatly disintegrated, and the foot of the mature sporophyte is imbedded in a mucilaginous mass. The pad upon which the archegonia stand elongates as the embryo grows, and the non-functioning archegonia are carried up to the apex of the calyptra. Five young embryos were found in one group, and it is quite common to find two or three together. The potentially sporogenous cells are sharply delimited from the beginning by their denser cell contents, larger nuclei, and active cell division.

SPORE MOTHER CELLS

The subsequent history of the sporogenous part of the embryo is interesting and important, for there must be a fundamental process which lies back of the formation of the curiously lobed spore mother cell so uniformly characteristic of the Jungermanniales. In the Marchiantiales it is a simple matter to dismiss the formation of the spore mother cells with the familiar expression that they "round up"; but the formation of a lobed mother cell demands more consideration. However, the stages immediately preceding the rounding up of the mother cells in the one group, and the lobing of the mother cells in the other group, are fundamentally the same. These stages in permanent mounts show the sporogenous cells irregular in shape, and bearing every indication that they were plasmolyzed in the fixation or imbedding. As mentioned above, LEITGEB frankly admits that he did not understand the processes leading up to the formation of the spore mother cells and elaters; and KIENITZ-GERLOFF (23), in discussing the Jungermanniales, adds nothing of importance. While a great deal has been written on the mitoses in the spore mother cell, literature on the formation of the mother cell is strikingly scanty. LECLERC DU SABLON (25) has made some important observations. He carefully investigated the development of the sporophyte of *Frullania dilata*, and with that species he compared *Scapania compacta*, *Pellia epiphylla*, *Aneura pinguis*, *Targionia hypophylla*, and *Sphaerocarpus terrestris*. He emphasizes some important points, namely, that there is an early differentiation between elaters and spore-producing tissue; that the elater is the equivalent of a row of mother cells; and that the walls between spore mother cells and elaters early become gelatinized. In the following statement he considers the irregularity of the potential spore mother cells, but does not seem to consider this feature of any importance.

> Tandis que certaines masses protoplasmic (*s*) destinées à devenir cellules-mères de spores s'accroissent régulièrement sur tout leur pourtour et présentent l'aspect d'amibes à peu près isodiamétriques d'autres (*el*) s'allongent exclusivement dans une direction, et acquièrent la forme se produit cet accroissment rapide, si c'est par formation de cellules nouvelles, ou par l'elongation des cellules déjà existantes.

Again he says (25, p. 169):

> Les cellules-mères continent a s'accroitre pendant longtemps encore, puis on voit apparaître à leur surface de petits sillons, premier indice d'une division en quatre spores. Pendant que ces sillons se creusent et accusent ainsi de plus en plus la forme de tétrade que prend la cellule, le noyau se divise en quatre, puis le protoplasma se divise de même, et à partir de ce moment on peut dire que la division de la cellule-mère en quatre spores est consommée, les phénomènes qu'on observe ensuite étant d'un ordre tout a fait accessoire.

CAMPBELL (4, p. 111) does not agree with LECLERC DU SABLON'S observations on the disappearance of the walls in the sporogenous tissue, and in this connection he makes the following statement:

> A great many carefully stained microtome sections of a large number of liverworts belonging to all the principal groups have been examined by me and invariably the presence of a definite cell wall could be demonstrated at all stages.

Again, he says (4, p. 34) in regard to the Ricciaceae:

> As the sporogonium increases in diameter, the central cells begin to separate and round off. Their walls become partially mucilaginous and in microtome sections stain strongly with Bismarck-brown or other reagents that stain mucilaginous membranes. With this disintegration of the division walls the cells separate more and more until they lie free within the cavity of the sporogonium.

FARMER (10), in discussing *Pellia epiphylla*, says in regard to the spore mother cell:

> At first more or less irregularly spherical, it soon becomes four-lobed, and these lobes increase in size, chiefly owing to radial extension, so that the spore mother cell ultimately comes to consist of four large sacs whose cavities communicate with each other by means of a small central space common to them all.

In a later paper (11), in summing up the characteristics of the sporogenous tissue of the Hepaticae, he says:

> A third feature of some interest, and which in practice is especially noticeable, is that just at the period of the spore-formation it becomes exceedingly difficult to fix the cells without some contraction. This is the more remarkable since the nuclei, which may happen to be dividing in either earlier or later stages, present not the slightest difficulty. Moreover, the cytoplasm also stains deeply with most nuclear stains, and everything points to the conclusion that there is something going on in the cell during this so-called reduction division which is not met with at any other period, whether in resting or dividing cells.

WILSON (34), in regard to *Mnium hornum*, says:

> FARMER has already noted that at the reduction division the spore mother cells of the Hepaticae can only be fixed with great difficulty. This is especially the case in the Muscineae.

Of the spore mother cell of *Pallavicinia decipiens*, FARMER (10) says:

> The mother cell becomes tetrahedrally lobed, and the cell walls at their inner angles grow into the cell cavity towards the nucleus.

These citations are representative of the literature on spore-formation in the Hepaticae.

While the spore mother cells of *Symphyogyna* are comparatively small, the large amount of sporogenous tissue in each sporophyte and the deep lobing of the mother cells make it a favorable species for study. A young sporophyte, such as is represented in part by fig. 40, shows no differentiation in the sporogenous tissue, though some of the longer cells may be considered as potential elaters. In an older sporophyte (fig. 41) the elaters by their elongation are in sharp contrast with the cells which will produce spore mother cells. In such a sporophyte the protoplasts have contracted slightly from the cell walls, which are still distinctly seen, and the intervening spaces are filled with a mucilaginous substance which stains a faint yellow in gold orange. The protoplasts show no difference in their staining, and excepting the difference in shape are alike in general structure. In older sporophytes (fig. 42) the elaters have assumed their characteristic shape, and their protoplasts are undergoing the peculiar changes incident to the formation of the spiral thickenings. The walls between the cells are still distinct, but they have lost some of their sharpness, and the mucilaginous substance stands out more distinctly when stained with gold orange. The pronounced irregularity of the shape of the cells which are to produce spore mother cells is a striking feature, and this irregularity continues until the lobed mother cell is fully mature. From the beginning of the differentiation of elater-producing cells and sporogenous cells (fig. 43), the division of the sporogenous cells continues, and frequently lobed mother cells and sporogenous cells still in division are seen in the same capsule.

Since living material of *Symphyogyna* could not be obtained to verify the observations made from prepared slides, *Pellia epiphylla*, *Aneura pinguis*, *Pallavicinia Lyellii*, *Cephalozia bicuspidata*, and *Porella platyphylla* were studied. The sporogenous tissue was separated from the walls of the sporophyte and mounted in water, and also other material was studied in the crushed sporogonium without the addition of any reagent whatever. The living cells were immediately examined under the microscope, and they were found to show the same irregular amoeboid forms which had been noted in the permanent mounts. Sporophytes from the same material were killed in different strengths of chromo-acetic, with and without osmic acid, and in Benda's solution, and in each case the results showed the same irregularity of the sporogenous cells (figs. 56–60). Moreover, in the laboratory all slides of sporophytes of liverworts belonging to the Marchantiales, Jungermanniales, and Anthocerotales, in the stages preceding the maturity of the spore mother cell, show the same situation. These slides are the accumulation of years and have been made by different people. On account of the lobing of the mother cell, the Jungermanniales show the irregularity to a more marked degree and for a longer time, but before the rounding up of the mother cell in the other groups, similar irregularity in shape and peculiarity in staining may be seen. From the observations made, it may be a reasonable interpretation that during the development of the tissue which eventually gives rise to spore mother cells, the protoplasts assume amoeboid forms, and the walls undergo a change. Older stages of the sporophyte (figs. 42–44) show increase in the accumulation of the mucilaginous substance and also the reducing of the cell walls into a substance of that nature. HOFMEISTER (**20**, p. 81) notes that the walls become considerably thicker, and that the substance of these walls is converted into a substance which swells extensively in water. There are striations which readily could be mistaken for walls, but any mucilaginous substance may give that effect.

Development of the spore mother cells in an individual sporophyte is not simultaneous, as may be seen in fig. 44, which shows the beginning of the lobing of one mother cell and other sporogenous cells still dividing. As the mother cell begins to become lobed, the extensions of the protoplast become more marked and vacuoles seem to play an important part in the process of lobing. A characteristic stage (fig. 45) shows the orientation of the four lobes and in each lobe there is a large vacuole. Later (figs. 46 and 47) the large vacuoles are broken up into smaller ones and the cytoplasm is uniformly distributed throughout each lobe. Apparently the nucleus always occupies the central position of the mother cell.

DAVIS (**8**), in discussing the spore mother cell of *Anthoceros*, asks the question whether the cytoplasm could be intrusted with so important a task as the preparation of a chloroplast for each of the four nuclei. A similar question may be asked in regard to the lobing of the mother cells. In the lobing of the mother cells it seems as if there are two alternatives: either the nucleus, long before it shows any visible signs of activity, affects the cytoplasm to such a degree that the four lobes are organized in advance of the reduction division of the nucleus; or the cytoplasm, in addition to the nucleus, is an important factor in the reduction division.

The quadripolar spindle may be distinctly seen at the beginning of the reduction division (fig. 51); but the later stages (figs. 52 and 53) verify MOORE'S interpretation (**27**) rather than the interpretation of FARMER (**10**). The chromosomes are very short and thick (fig. 48).

The four young spores gradually separate (fig. 51). At this stage of the sporophyte the greatly elongated nuclei of the elaters, with their strong bands of chromatin and prominent nucleoli, are very striking. The mature spore (fig. 55) measures about 18.3 μ in diameter. The echinations are short but very sharp, and a surface view (fig. 53) shows them distinctly reticulate. Spores with two nuclei (fig. 54) are not very common, but enough were found to lead one to think that there is a feeble tendency toward intrasporal germination. The mature elaters (fig. 55) have two very prominent spirals.

Summary

1. The thallus of *Symphyogyna aspera* has a central strand of greatly elongated cells which taper at both ends. The walls of these cells have narrow pores which are spirally arrañged.

2. Like the other species of the genus, *S. aspera* is dioicous. The plants bearing antheridia are more slender and less freely branched than the plants bearing archegonia.

3. The antheridia are scattered over the thickened part of the thallus on the dorsal side. Each antheridium is surrounded by a scale.

4. The archegonia are in groups on the dorsal side of the thallus. Each group is on a padlike extension of the thallus and is surrounded by an involucre.

5. More than one embryo may be formed in a group, but so far only one has been found to reach maturity.

6. As the embryo elongates, the calyptra and pad also elongate and the old archegonia are left in the tip of the calyptra.

7. The young embryo develops by segmentation similar to that formed by a dolabrate apical cell.

8. The sporogenous tissue is differentiated relatively late in the history of the sporophyte.

9. The cells which are to form elaters may early be distinguished from the cells which are ultimately to give rise to the spore mother cells. The former cells elongate without further division, while the latter cells undergo several divisions.

10. The walls of the sporogenous mass of cells become gelatinized, and the protoplasts are potentially free in the gelatinous substance.

11. The spore mother cells attain their lobing by a slow amoeboid change of the protoplast, and in this movement vacuoles seem to play an important part. The examination of the living sporogenous tissue of other Jungermanniales verifies the occurrence of this phase in them also.

12. Spores with two nuclei have been found, though this is not a usual condition.

Grateful acknowledgments are due Professor JOHN M. COULTER for advice and criticism, and to Dr. W. J. G. LAND, who supplied all the material and to whose help and encouragement the completion of the paper is due.

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EXPLANATION OF PLATES XXX-XXXII

Symphyogyna aspera

FIG. 1.—Thallus with antheridia; ×2.

FIG. 2.—Thallus with sporophytes; ×2.

FIGS. 3, 4.—Ends of rhizoids; ×700.

FIG. 5.—Rhizoid containing a septate fungus; ×700.

FIG. 6.—Tip of rhizoid showing a fungus; ×1600.

FIG. 7.—Transverse section of rhizome; ×70.

FIG. 8.—Outline of a longitudinal view of a cell from the central region and three adjoining cells; ×180.

FIGS. 9, 10.—Cells of thallus adjoining cells of central region; ×180.

FIG. 11.—Transverse section of aerial part of thallus; ×170.

FIG. 12.—Part of cell of central region showing pores; ×2300.

FIG. 13.—Transverse section of cells of central region; ×1300.

FIG. 14.—End view of apical cell; ×645.

FIG. 15.—Section of apical cell parallel with the surface of the thallus; ×645.

FIG. 16.—Median longitudinal section of apical cell; ×645.

FIG. 17.—Median longitudinal section of wedge-shaped apical cell; ×645.

FIG. 18.—Transverse section of wedge-shaped apical cell; ×645.

FIG. 19.—End view of apical cell showing segment from which the wing has its origin; ×645.

FIGS. 20–22.—Stages in the development of the antheridium; ×700.

FIG. 23.—Median longitudinal section of thallus showing apical cell, initial of archegonium, beginning of involucre, and beginning of development of central cells; ×645.

FIGS. 24–30.—Stages in the development of the archegonium; ×645.

FIG. 31.—Archegonium showing spiral arrangement of neck cells; ×140.

FIG. 32.—Archegonium showing probable fertilization; ×1300.

FIG. 33.—Archegonium showing a doubling of the neck canal cells in one part; ×645.

FIGS. 34–38.—Stages in the development of the embryo; ×645.

FIG. 39.—Older stage of embryo; ×450.

FIG. 40.—Another view of the basal part of the embryo shown in fig. 39; ×450.

FIG. 41.—Tip of mature sporophyte; ×180.

FIG. 42.—Foot of mature sporophyte; ×180.

FIG. 43.—Part of young embryo showing sporogenous tissue and walls, and length of sporogenous tissue; ×860.

FIG. 44.—Part of sporogenous tissue showing the beginning of contraction of protoplasts; ×860.

FIGS. 45–47.—Stages in development of sporogenous tissue; ×860.

FIG. 48.—Early stage of lobing of mother cell; ×1600.

FIG. 49.—Late stage of lobing of mother cell; ×1600.

FIG. 50.—Mature spore mother cell; ×1600.

FIG. 51.—Mature spore mother cell just before reduction division; ×1600.

FIG. 52.—Spore mother cell during reduction division; ×1600.

FIG. 53.—Homotypic division of spore mother cell; ×1600.

FIG. 54.—Young spores nearly separated; ×1600.

FIG. 55.—Surface view of echinations of spore coat; ×1600.

FIG. 56.—Mature spore; ×1600.

FIG. 57.—Mature spore with two nuclei; ×1600.

FIG. 58.—Mature elater; ×1600.

Pellia epiphylla

FIG. 59.—Outline of spore mother cell from living material; ×1300.

Aneura pinguis

FIGS. 60–64.—Outlines of sporogenous cells from living material; ×1300.

FIGS. 65–67.—Outlines of sporogenous cells from preserved material; ×1600.

Pallavicinia Lyellii

FIGS. 68–75.—Outlines of sporogenous cells from living material; ×1300.

FIGS. 76–83.—Outlines of sporogenous cells from preserved material; ×1600.

Cephalozia bicuspidata

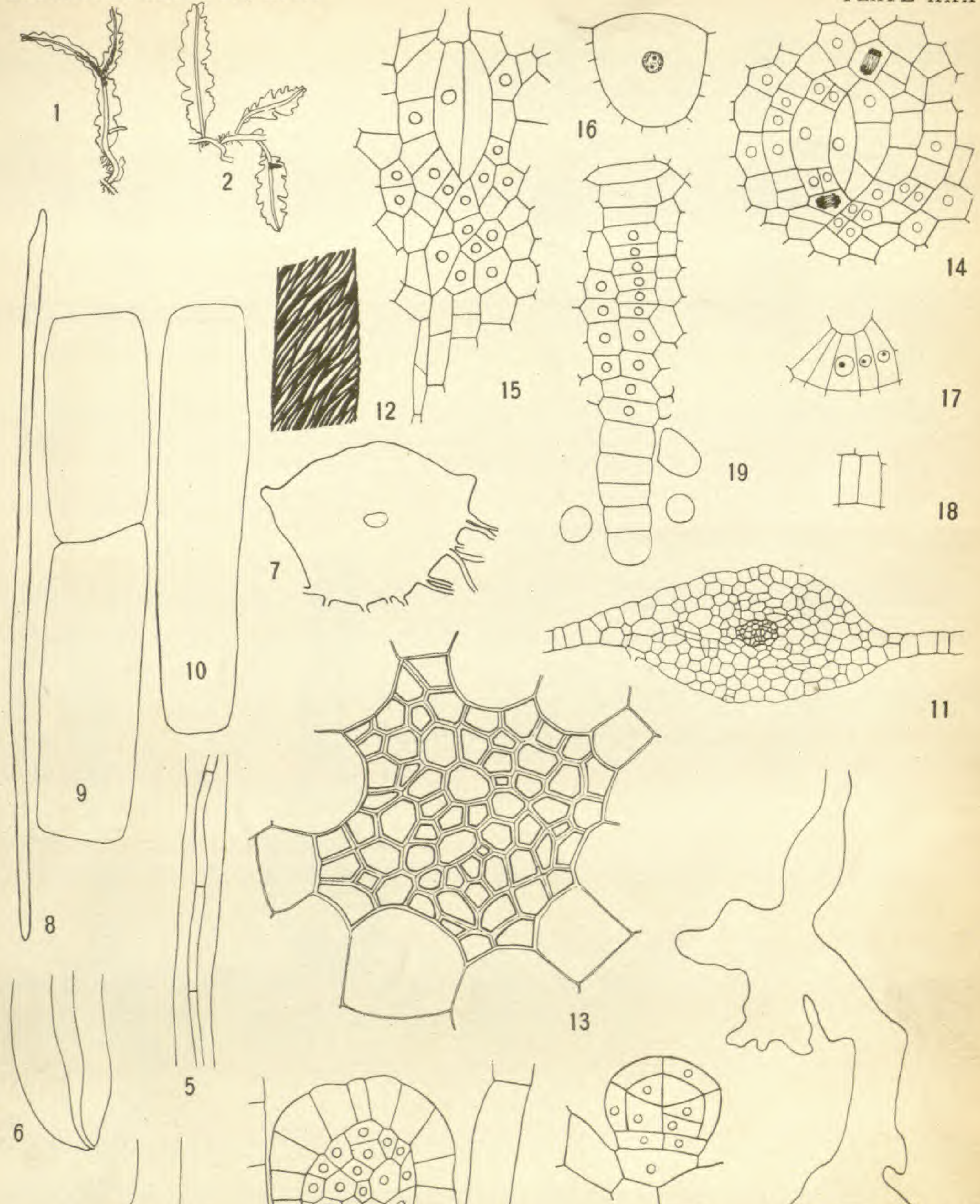
FIGS. 84–87.—Outlines of spore mother cells from living material; ×1300.

FIGS. 88–93.—Outlines of spore mother cells from preserved material; ×1600.

Porella platyphylla

FIGS. 94–99.—Outlines of spore mother cells from living material; ×1300.

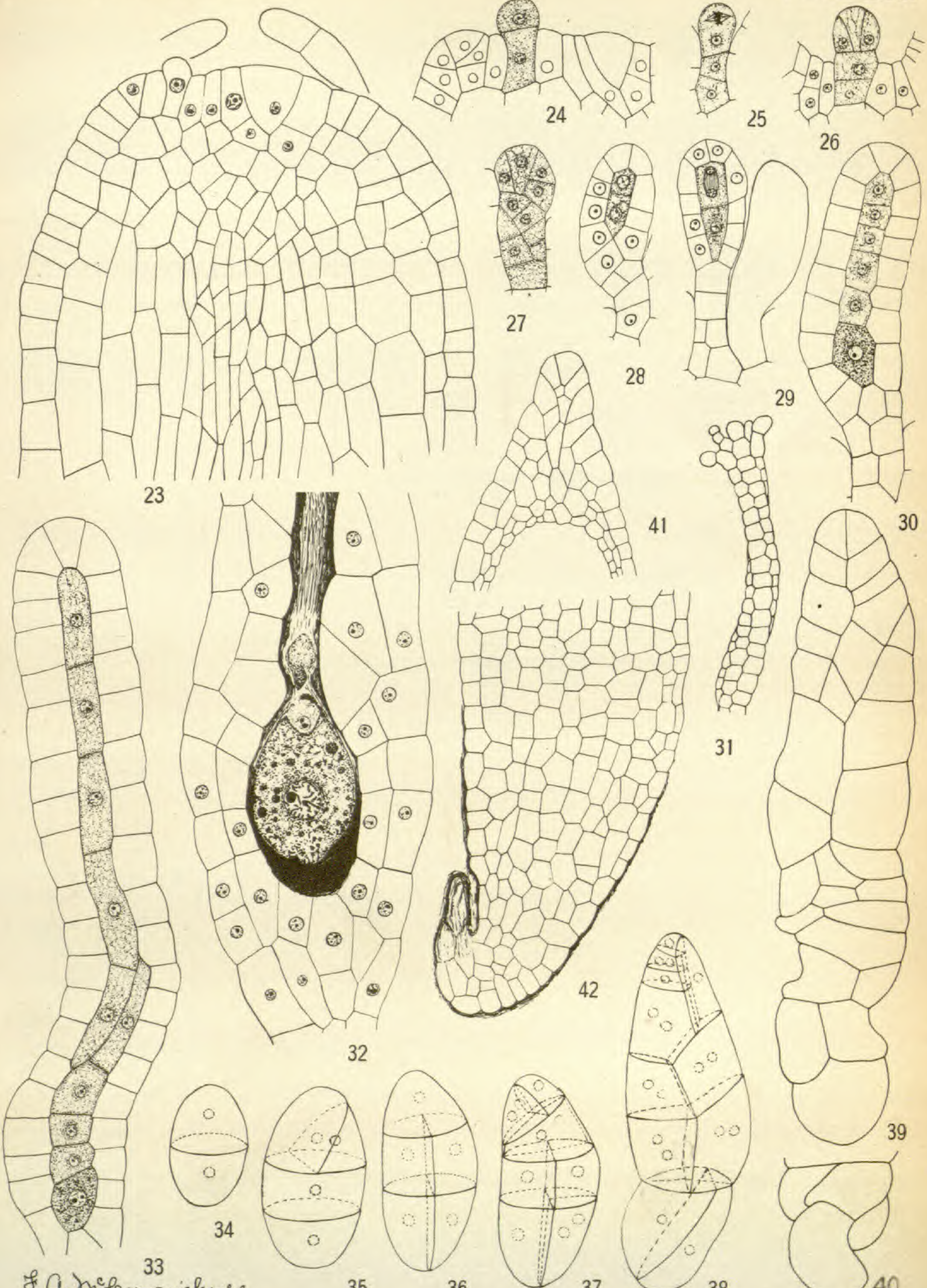
FIGS. 100–102.—Outlines of spore mother cells from preserved material; ×1600.



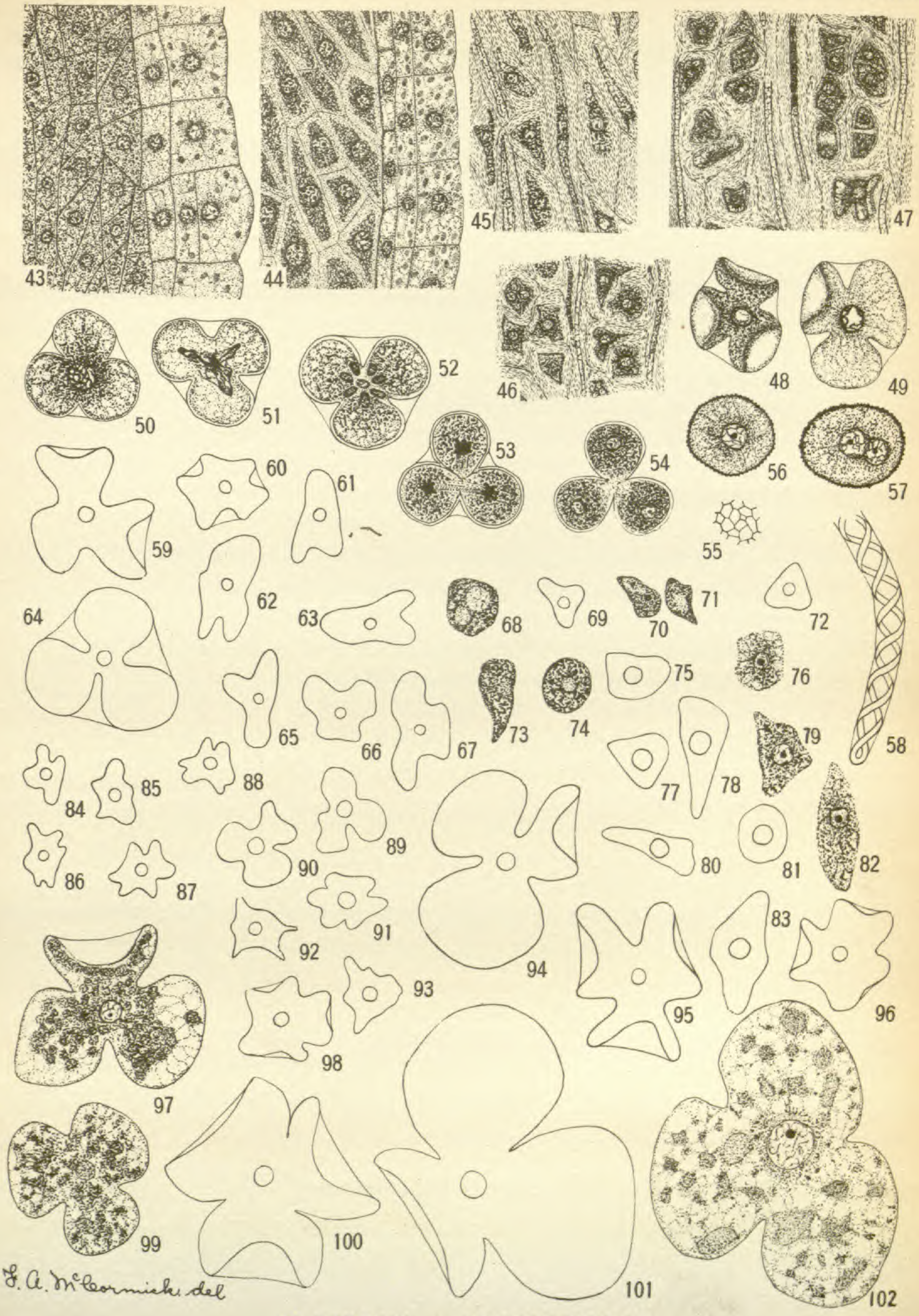
F. A. McCormick, del.

McCORMICK on SYMPHYOGYNA

PLATE XXXI



McCORMICK on SYMPHYOGYNA



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McCORMICK on SYMPHYOGYNA

SPERMATOGENESIS IN MARSILIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 197

LESTER W. SHARP

(WITH PLATES XXXIII AND XXXIV)

Introduction

In 1912 the writer (6) published the results of an investigation of spermatogenesis in *Equisetum*. The principal conclusion was that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are derived ontogenetically or phylogenetically from centrosomes. The basis for this conclusion was found in the behavior of true centrosomes and cilia-bearing organs in plants and certain animals, special emphasis being laid upon the remarkable centrosome-like activity of the blepharoplast of *Equisetum*.

The behavior of the blepharoplast of *Marsilia*, as described by SHAW (7) and by BELAJEFF (3) in 1898 and 1899, was also used as a strong argument for the centrosome nature of the blepharoplast. Since these accounts show incompleteness and uncertainty with regard to several points, and since the two writers reached contrary theoretical conclusions, it was deemed advisable to examine certain material[1] at hand with a view toward establishing the true state of affairs in *Marsilia*.

An extensive historical résumé of researches on centrosomes and cilia-bearing structures in plants was presented in the writer's paper on *Equisetum* and will not be repeated here. To the list of papers given should be added those of ALLEN (1) and WALKER (8) on *Polytrichum*. In the present work only those dealing with *Marsilia* need to be reviewed.

The early papers of CAMPBELL (4, 5) on *M. aegyptiaca* and *M. vestita* show the general topography of the male gametophyte. The sequence of wall-formation was not determined in the former species, and great irregularity was reported in the latter. CAMPBELL made out none of the cytological details of spermatogenesis.

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[1] The writer is indebted to Dr. C. J. CHAMBERLAIN for a portion of the material used.

In 1898 BELAJEFF (2) described the development of the male prothallium in several Hydropteridineae. In *Marsilia elata* he worked out carefully the exact sequence of walls, which, it will be seen, resembles rather closely that in *M. quadrifolia* as described below. In the latter species BELAJEFF did not figure a developmental series.

SHAW (7) in the same year gave an account of the blepharoplast in *M. vestita*. According to this investigator, a small granule or "blepharoplastoid" appears near each daughter nucleus at the telophase of the second spermatogenous mitosis. During the prophases of the third mitosis it divides and then degenerates in the cytoplasm, while a blepharoplast appears near each spindle pole at metaphase. In the following cell generation (spermatid mother cell) the blepharoplast divides to two which occupy positions near the spindle poles through the fourth or final mitosis. Each spermatid thus receives a blepharoplast. The latter soon shows a small internal granule which multiplies and forms a band; this elongates in close union with the nucleus and bears the cilia. In these facts SHAW found no grounds for the homology of the blepharoplast and the centrosome.

In the following year BELAJEFF (3) reported the results of his researches on *M. macra* and *M. vestita*. He found centrosomes, which he did not hesitate to call them, at the spindle poles in the last three spermatogenous divisions. With regard to the first division he was uncertain; the figure which he gave as possibly representing the first mitosis almost certainly represents the second. He was inclined to identify the centrosome of the second mitosis with the "blepharoplastoid" of SHAW, but believed it to be continuous from the time of its origin, dividing after each mitosis in preparation for the next, and in the spermatid performing the function of a blepharoplast. BELAJEFF regarded this as a strong confirmation of his previously stated theory that the blepharoplast and the centrosome are homologous structures.

In the present paper an attempt will be made to clear up the points left in doubt by these earlier workers, and to add new details which will make it possible to decide between their divergent views concerning the morphological nature of the blepharoplast.

Material and methods

Sporocarps of *Marsilia quadrifolia* were cut open and placed in water at room temperature. Sori were fixed at short intervals until sperms were seen swimming in large numbers, a period of 10 or 12 hours.

Several fixing reagents were employed, including those of Flemming and Benda. The best results were obtained in preparations stained with Haidenhain's iron alum-hematoxylin after the following fixing fluid: 1 per cent chromic acid 25 cc., water 75 cc., glacial acetic acid 1 cc., 2 per cent osmic acid 14 drops.

Description

THE MALE GAMETOPHYTE

A comparison of figs. 1–7 with fig. 8 will do more than a written description to make clear the development of the male gametophyte.

At the time when the gelatinous ring bearing the sori escapes from the sporocarp, the microspore has in section the appearance shown in fig. 1. The nucleus occupies a central position, and large starch grains lie scattered throughout the cytoplasm. These very soon move to the periphery, leaving the nucleus surrounded by a zone of granular cytoplasm. The nucleus then passes to the side of the spore, usually the side opposite the point where the spore met the others of the tetrad, and cuts off a small prothallial cell (wall 1, figs. 2, 3). No "basal cell," such as BELAJEFF (2) figures above the prothallial cell in *M. quadrifolia*, was found in our material.

The next wall (wall 2, fig. 4) passes through the center of the spore. The two hemispherical cells so formed behave alike, each producing an antheridium in the following manner. A curved wall (wall 3, fig. 5) cuts off a large wall cell. A small sterile cell is next formed in the angle between walls 2 and 3 (wall 4, fig. 6). Wall 5 then cuts off a peripheral cell (fig. 7) which completes the wall of the antheridium and defines the limits of the primary spermatogenous cell. There are no centrosomes in any of these mitoses.

Each primary spermatogenous cell by four successive divisions gives rise to a group of 16 spermatids (figs. 9–12). Since the two spermatogenous masses formed in the two hemispheres are entirely separated from each other by the sterile cells cut off by the walls numbered 4, it seems reasonable to hold with BELAJEFF that the microspore develops two symmetrically placed antheridia separated by wall 2. The prothallial cell degenerates during the later antheridial divisions.

The foregoing account agrees in its essential features with that given by BELAJEFF (2) for *M. elata*, but in that form the development in the two hemispheres is not so symmetrical. In a very few cases we have seen wall 3 in the upper hemisphere strike the spore wall rather than wall 2, which results in a condition more like that in *M. elata*.

SPERMATOGENESIS

As stated above, each primary spermatogenous cell gives rise, by four successive divisions, to 16 spermatids. In these mitoses the chromosomes behave as in ordinary vegetative mitoses, and in view of the purpose of the present study do not require special description. Attention will therefore be directed wholly to the centrosomes and associated structures.

First spermatogenous mitosis.—The primary spermatogenous cell shows nothing which can be called a centrosome. The cytoplasm is dense and contains many small granules, but it is evident that no significant rôle can be attributed to them. The spindle forms without the agency of any visible kinetic center. At late prophase and metaphase it ends rather indefinitely at the poles (fig. 13), but during anaphase these regions appear denser (fig. 14). A little later long and very distinct radiations develop about each pole; at their focus there is a dense and finely granular appearance (fig. 15), but no distinct body is formed. At telophase these polar achromatic structures disappear; in fig. 16 their last remnants may still be seen.

Second spermatogenous mitosis.—In the prophases the second mitosis is similar to the first. The spindle at first ends indefinitely (fig. 17), but during early anaphase it rapidly becomes pointed. Long radiations develop as in the preceding mitosis, and at each pole a very minute and intensely staining granule appears (fig. 18). This is the centrosome. On account of its extremely small size it is practically impossible to make out the exact manner of its origin;

whether it is single from the first or is formed by the union of several granules such as are seen at the poles of the previous mitosis (fig. 15) is a question which must remain in doubt. The cell shown in fig. 18 seems to favor the latter interpretation; at the upper pole there appears to be a small group of granules, while at the lower pole the centrosome is larger and distinctly single.

The centrosomes increase rapidly in size. At very late anaphase they are very conspicuous, and the surrounding radiations form a striking system extending through the greater part of the cell (fig. 19). At telophase the rays become short and faint. The centrosomes are still growing, and in some cases may already show indications of division (fig. 20, upper centrosome).

Third spermatogenous mitosis.—There are now 4 cells in each spermatogenous group, and conspicuous in the cytoplasm of each cell (fig. 21) is the centrosome formed during the anaphase of the preceding mitosis. This centrosome undergoes division at once (figs. 22, 23), in fact this process is often seen beginning during the previous telophase (fig. 20). The two daughter centrosomes rarely diverge from one another. In two or three cells they had moved apart to a distance equal to several times their own diameter, and in one uncertain case they appeared to have reached approximately polar positions. As a rule, however, they degenerate in the cytoplasm without performing any further function. At late prophase and metaphase they can often be made out in the cell (fig. 24), but they bear no relation to the spindle poles, which are at first rather indefinite, as in the first and second mitoses. The persistence of faint radiations about them helps to make their identification sure. During anaphase they usually lie in the cytoplasm at the side of the spindle (fig. 25). The cell shown in fig. 26 contains two pairs of minute granules with very faint rays; since this was the only case of the kind observed, it is impossible to say what it may mean, but it is probable that the two centrosomes which ordinarily degenerate at once have here moved apart and divided again. This renders more certain the interpretation placed upon the paired bodies in figs. 24 and 25. They are doubtless to be identified with the "blepharoplastoid" of SHAW, and are in reality the non-functioning centrosomes.

During anaphase a new centrosome appears at each spindle pole, exactly as in the second mitosis, and behaves in a wholly similar fashion in the subsequent stages. When first discernible it is extremely minute (fig. 25), but very rapidly becomes larger (fig. 26). This formation of new centrosomes after the failure of the old ones is a feature of considerable interest, and will be touched upon again in the discussion.

The division of the centrosome occurs during the telophases, but not always at exactly the same stage, as figs. 27 and 28 show. In fig. 27 the lower centrosome is elongating and the upper one beginning to constrict. In fig. 28 the lower one is still spherical, while the upper one is almost completely divided.

Fourth spermatogenous mitosis.—In the interval between the third and fourth mitoses the centrosomes gradually move apart (figs. 29–31). In view of the rôle which they are to play, they may now be called the blepharoplasts. As they diverge, a delicate central spindle remains between them. The radiations on the side toward the nucleus become stronger, and at the stage shown in fig. 31 form two conspicuous cones of spindle fibers with the blepharoplasts at their apices. The rays extending in other directions are not so well developed as in the previous mitoses.

A marked change now begins in the blepharoplasts. They enlarge, develop one or more internal vacuoles, and become irregular in outline (figs. 31, 32). At late anaphase this process has gone on still farther (fig. 33), and at telophase they may be seen breaking up to several irregular pieces (fig. 34).

Metamorphosis of the spermatid.—The transformation of the spermatid into the spermatozoid seems to take place rather rapidly. The fragmentation of the blepharoplast, begun during the telophase of the last mitosis, continues until a considerable group of pieces has accumulated (fig. 35). These soon take the form of an irregular, lumpy rod, which lies close to the nucleus or against it (fig. 36). A later stage is shown in fig. 37; in this cell, which is noticeably larger than those of figs. 35 and 36, the nucleus has begun to undergo a change in shape which will finally result in the spiral form of the sperm, and the blepharoplast, in close union with it, has formed nearly one complete turn.

As the blepharoplast grows in length it gradually becomes more uniform in thickness without passing through such a regular beaded stage as is seen in *Equisetum*. Our preparations did not permit a more detailed study of this growth, nor was the time of the first appearance of the cilia determined. The blepharoplast often shows a double structure (fig. 37), traces of which are visible in the mature sperm (fig. 42, at middle). SHAW (7) believed this to be an appearance due to the U-shaped cross-section, an idea which is not supported by the present study.

A more advanced stage in the spiral growth of the nucleus and the blepharoplast is shown in side view and in cross-section in figs. 38 and 39. The blepharoplast grows out freely beyond one end of the crescentic nucleus, a feature again clearly brought out in fig. 40, which represents a cell in which the metamorphosis is about half completed. Cilia are easily made out at this stage. As the transformation continues the nucleus and blepharoplast become more closely compacted and are soon very difficult to distinguish.

When the sperm escapes from the spore the coils, about 8 in number, are rather closely wound (fig. 41). The first three or four anterior coils are made up of blepharoplast only and bear no cilia. The remaining coils are composed of both blepharoplast and nucleus and bear cilia upon all but the most posterior regions. The large vesicle, held in the posterior coils, contains the cytoplasm of the spermatid with its inclusions, such as an occasional starch grain and other disorganized material of undetermined nature (figs. 37–41).

As the sperm swims about, it enlarges through the absorption of water, and when it reaches a denser medium, such as the gelatinous material about the megaspore, the coils become more widely separated from each other. Such a sperm, fixed over osmic fumes, is shown in fig. 42. It has a length of 50 μ, while the newly escaped sperm shown in fig. 41 measures but 15.3 μ.

Discussion

The subject of the morphological nature of the blepharoplast was discussed fully in the writer's paper on *Equisetum* (SHARP **6**), to which the reader is referred. Two extracts will suffice to make clear the conclusions reached.

> Although limited to a single mitosis in the antheridium, the blepharoplast [of *Equisetum*] retains in its activities the most unmistakable evidences of a centrosome nature, and at the same time shows a metamorphosis strikingly like that in the cycads. In thus combining the main characteristics of true centrosomes with the peculiar features of the most advanced blepharoplasts, it reveals in its ontogeny an outline of the phylogeny of the blepharoplast as it is seen developing through bryophytes, pteridophytes, and gymnosperms, from a functional centrosome to a highly differentiated cilia-bearing organ with very few centrosome resemblances [p. 107].
>
> The activities of the blepharoplast in *Equisetum*, taken together with the behavior of recognized true centrosomes in plants and analogous phenomena in animals, are believed to constitute conclusive evidence in favor of the theory that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are derived ontogenetically or phylogenetically from centrosomes [p. 113].

Let us now turn to the case of *Marsilia*. We have seen that a centrosome first appears at each spindle pole during the anaphase of the second spermatogenous mitosis, and later divides only to degenerate without performing any further function. A new centrosome then appears in the same manner at each pole during the anaphase of the third mitosis, divides, and occupies the spindle poles through the fourth mitosis, and in the spermatid functions as the blepharoplast. This corresponds in the main with SHAW'S (7) description, but that writer failed entirely to see the extensive achromatic structures and the intimate relation they bear to the body in question. Had he done so, it is difficult to understand how he could have failed to recognize the homology of the centrosome and the blepharoplast.

The foregoing features constitute the strongest arguments in favor of the centrosome nature of the blepharoplast. We have as yet found no other case in plants where they are emphasized in so striking a fashion. The body divides at each mitosis and forms the center of an achromatic system unmistakably the same as that accompanying true centrosomes in alga and animal cells. The theory that this is more than mere resemblance and is due to homology surely has a better basis in observed fact and is far simpler than the assumption that a special cilia-bearing organ has taken on characters corresponding in all details to those of centrosomes and has extended itself to three cell generations.

To the present writer it seems clear that we are here dealing with an organ which is gradually passing out of the life history. The farther we pass back from the last spermatogenous mitosis the more indefinite its behavior becomes. The centrosome appearing in the third mitosis is intimately concerned in the formation of the achromatic figure for the fourth mitosis, and before the latter is complete the centrosome has already begun to undergo the peculiar transformation of the blepharoplast. The centrosome appearing at the second mitosis later divides, but only occasionally goes farther. In the first mitosis there seems to be still an abortive start in the formation of a centrosome at anaphase (fig. 15), but no definite body is organized. Even in the earlier mitoses of the male gametophyte a system of rays suggests the presence of a dynamic center at each spindle pole, though no centrosome is present (fig. 4).

These considerations, taken together with other instances in which centrosomes have been reported in several generations of spermatogenous cells (bryophytes), and the large number of cases in which they are limited to the last mitosis (*Equisetum*, *Nephrodium*, cycads), have only served to strengthen our formerly expressed opinion that centrosomes have been partially or wholly eliminated from the early spermatogenous cells, and are retained in so many forms only at the end of the series because of the very important biological function they there perform—the bearing of cilia. They are finally lost altogether when the change from motile to non-motile sperms occurs. Just such a progression as this is seen in passing upward through the bryophytes, pteridophytes, and gymnosperms, and *Marsilia* shows a very instructive stage in the process.

A feature of special interest is the degeneration of the *Marsilia* centrosome just before the third spermatogenous mitosis, and the formation of a new one at each spindle pole. This was also reported by SHAW (7), while BELAJEFF (3) thought there was no break in its continuity after the time of its first appearance. As stated in the description, our material shows at this point some variability, and it is of a sort which tends to reconcile the two earlier accounts. In the majority of cases degeneration begins directly after the centrosome has divided. In some cases, however, the daughter centrosomes diverge somewhat, and very rarely they may reach polar positions. Although we have observed no metaphase figure of the third mitosis with undoubted centrosomes at the poles, it is nevertheless probable that further search would reveal such cases. It is thus possible that both SHAW and BELAJEFF were correct in their interpretations, that they were dealing with two lots of material showing different behavior at this point.

This is apparently a stage in the life history where the centrosome may be seen in the act of dropping out through failure to carry out its function. A new one forms at each spindle pole for the same reasons that one is developed at the preceding mitosis, where it has been entirely lost from the earlier phases, though as yet it is impossible to determine the nature of these reasons. Since the variable behavior indicates that the organ in question is in all probability a disappearing one, and since there is no organ other than a centrosome which we should expect to see being eliminated from spermatogenous cells, the lack of continuity, if it argues at all, argues for the centrosome nature of the blepharoplast rather than against it.

The conclusions reached as the result of the present investigation are necessarily the same as those stated in the writer's paper of 1912 and cited at the beginning of this discussion. *Marsilia* is even more convincing than *Equisetum* in showing the direct derivation of an advanced cilia-bearing organ from a functional centrosome. Since there is every reason to believe that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are homologous structures, it follows that they are all "ontogenetically or phylogenetically centrosomes."

Summary

1. In the first spermatogenous mitosis there is present at each spindle pole a dense region with radiations, but no centrosome.

2. During anaphase of the second mitosis a centrosome develops at each spindle pole and at telophase divides to two daughter centrosomes. These only rarely develop farther; they usually degenerate at once in the cytoplasm.

3. In the third mitosis a centrosome develops at each spindle pole at anaphase exactly as in the second mitosis, and during telophase or later divides to two daughter centrosomes.

4. These daughter centrosomes, which may now be called blepharoplasts, move apart and occupy the spindle poles through the fourth or final mitosis.

5. The centrosomes are at all times accompanied by extensive radiations, which in the fourth mitosis give rise to the achromatic figure. When the centrosome divides there is present a central spindle and amphiaster as in animal cells.

6. Before the fourth mitosis is completed the blepharoplast becomes vacuolate and breaks up to a number of fragments. In the spermatid these form a band which elongates spirally in close union with the nucleus and bears the cilia.

7. The evidence afforded by *Marsilia*, together with that gained from other plants and certain animals, is believed to show conclusively that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are derived ontogenetically or phylogenetically from centrosomes.

The writer is greatly indebted to Professor JOHN M. COULTER for placing at his disposal the facilities of the Hull Botanical Laboratory.

UNIVERSITY OF CHICAGO

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A full list of papers dealing with the subject may be found in the writer's paper on *Equisetum*, cited below.

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EXPLANATION OF PLATES XXXIII AND XXXIV

All figures were drawn at the level of the stage with the aid of an Abbé camera lucida, figs. 1–11 under a Spencer achromatic objective 2 mm. N.A. 1.30 with Zeiss compensating ocular 4, and figs. 13–42 under a Zeiss apochromatic objective 2 mm. N.A. 1.40 with compensating ocular 18. They have been reduced one-half in reproduction, and now show magnifications as follows: figs. 1–11, ×368; figs. 13–42, ×1400.

PLATE XXXIII

FIG. 1.—Microspore at time of liberation from sporocarp: starch grains in cytoplasm.

FIG. 2.—First mitosis in microspore, cutting off prothallial cell (wall 1).

FIG. 3.—Prothallial cell completed.

FIG. 4.—Second mitosis in microspore, forming wall 2 (fig. 8).

FIG. 5.—Third mitosis in microspore, forming walls 3.

FIG. 6.—Fourth mitosis in microspore, forming walls 4.

FIG. 7.—Fifth mitosis in microspore, forming walls 5.

FIG. 8.—Diagram to show sequence of wall formation: the two primary spermatogenous cells marked with nuclei.

FIG. 9.—Two primary spermatogenous cells enlarged.

FIG. 10.—Two-celled stage.

FIG. 11.—Eight-celled stage.

FIG. 12.—Sixteen-celled stage (spermatids).

FIG. 13.—*First spermatogenous mitosis:* late prophase; spindle poles indefinite.

FIG. 14.—Anaphase: cytoplasm denser about poles.

FIG. 15.—Late anaphase: dense regions and radiations present at poles, but no definite centrosomes.

FIG. 16.—Telophase: remnants of polar radiations visible.

FIG. 17.—*Second spermatogenous mitosis:* late prophase; cytoplasm becoming dense and granular at poles of spindle.

FIG. 18.—Anaphase: centrosomes present.

FIG. 19.—Late anaphase: centrosomes and radiations prominent.

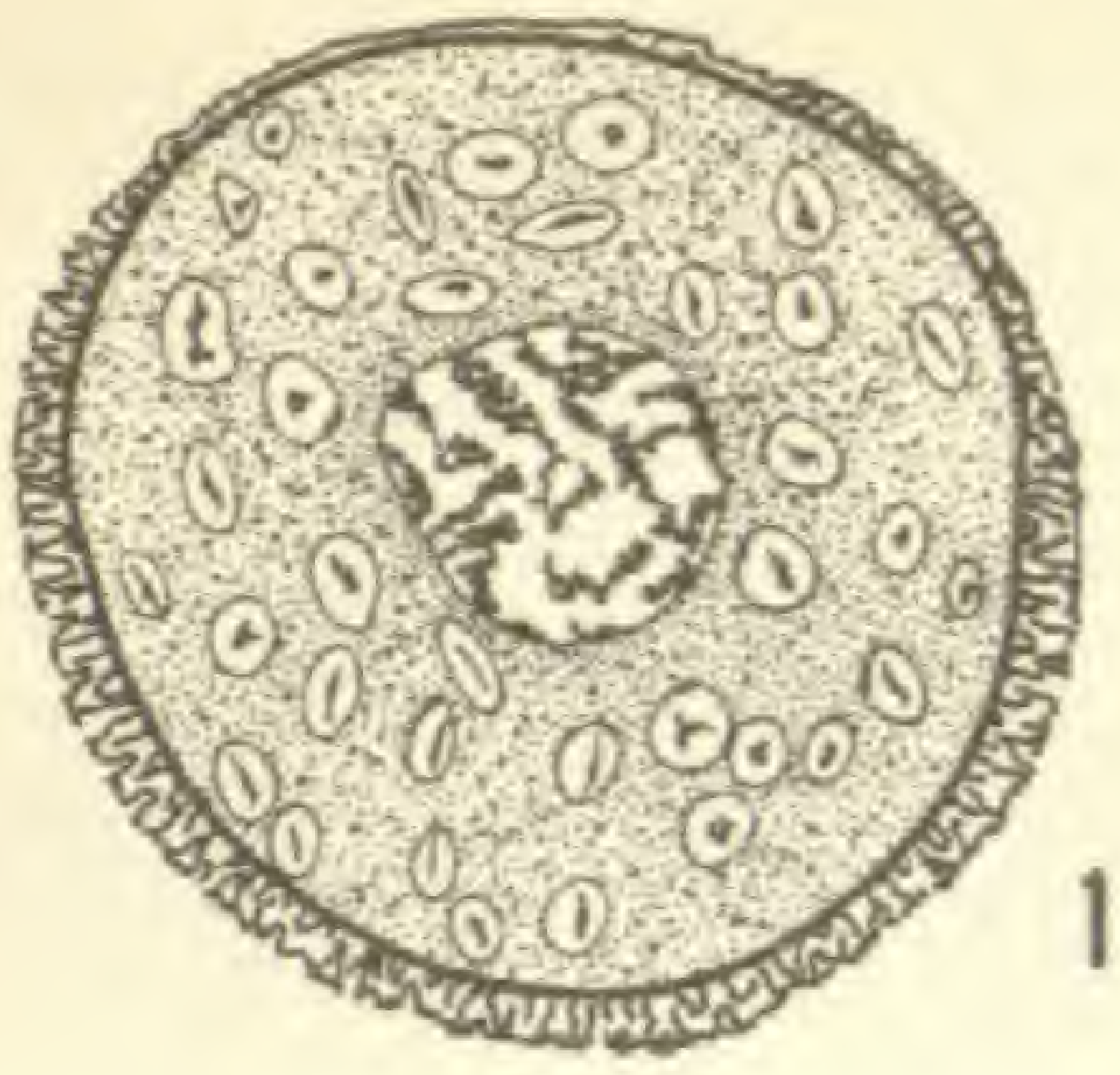
FIG. 20.—Telophase: centrosome at upper pole beginning to divide.

PLATE XXXIV

FIG. 21.—Cell of four-celled stage: centrosome undivided.

FIG. 22.—The same: centrosome divided.

PLATE XXXIII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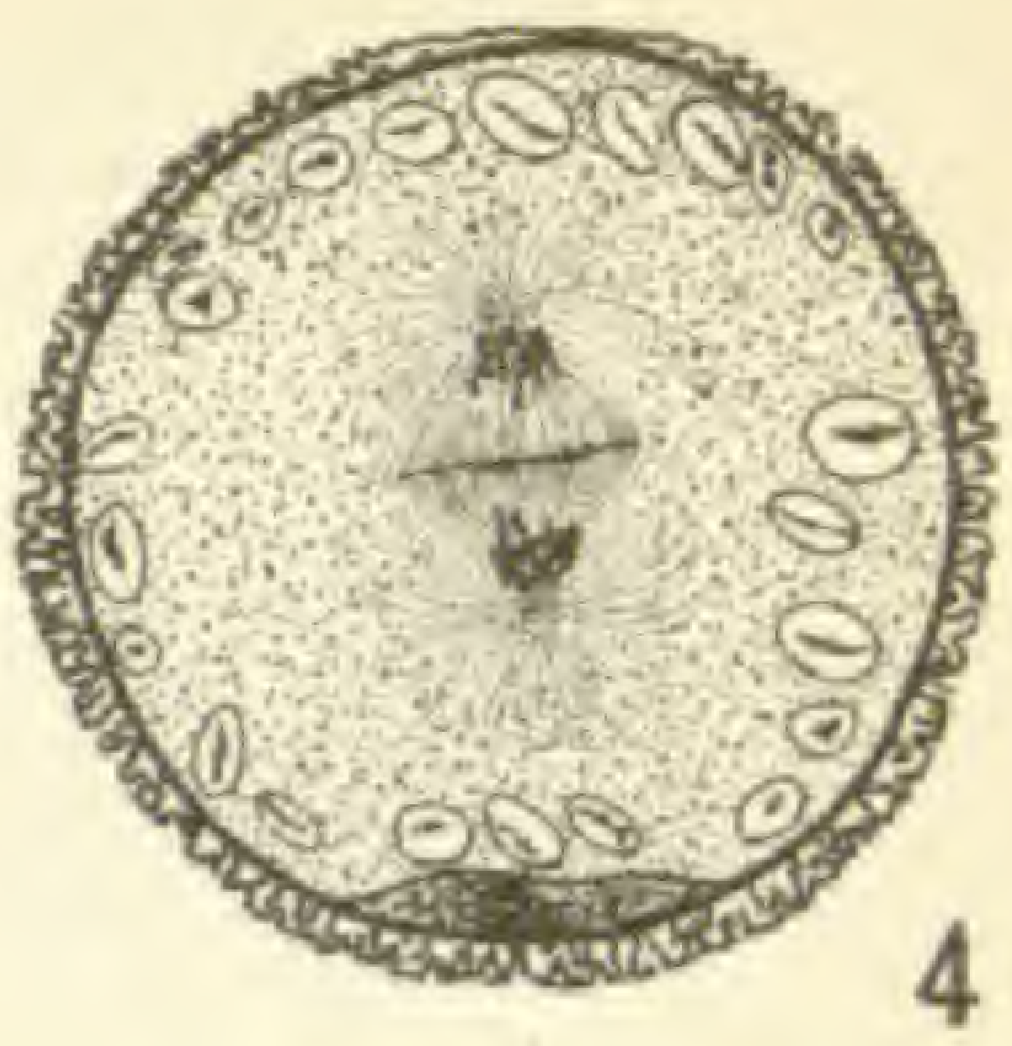
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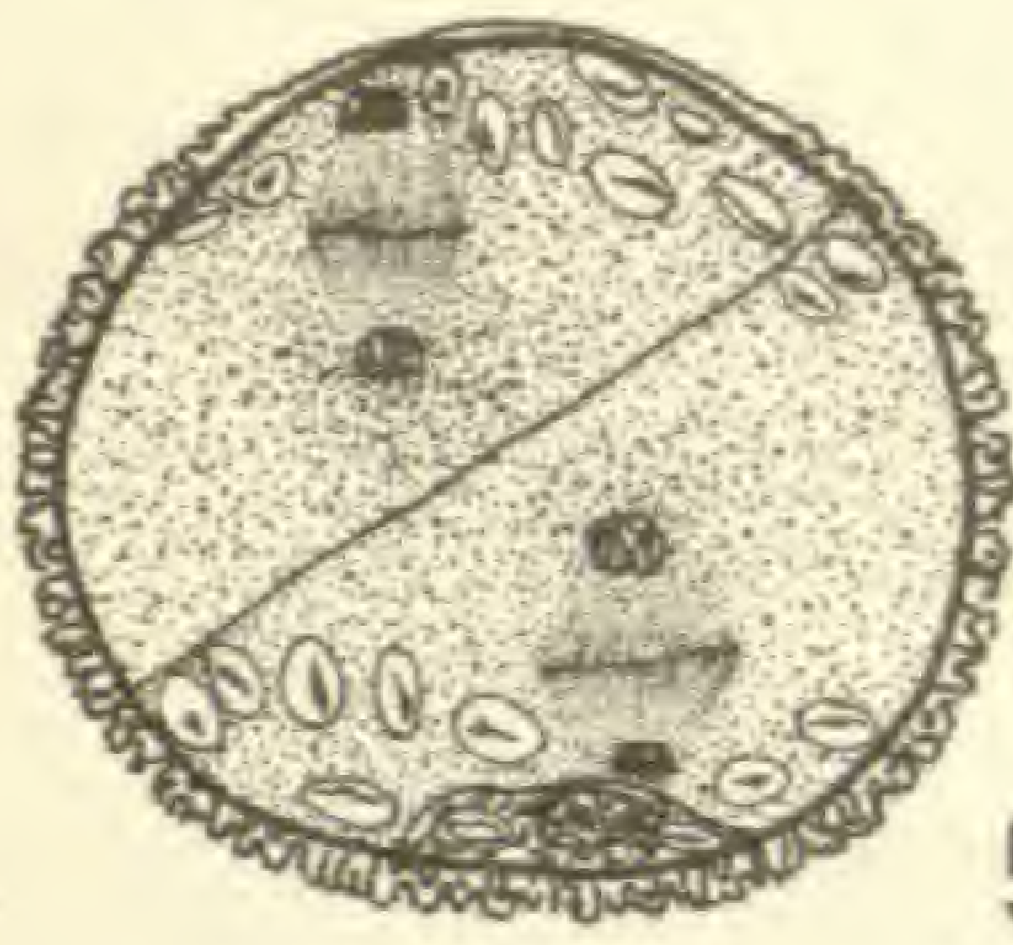
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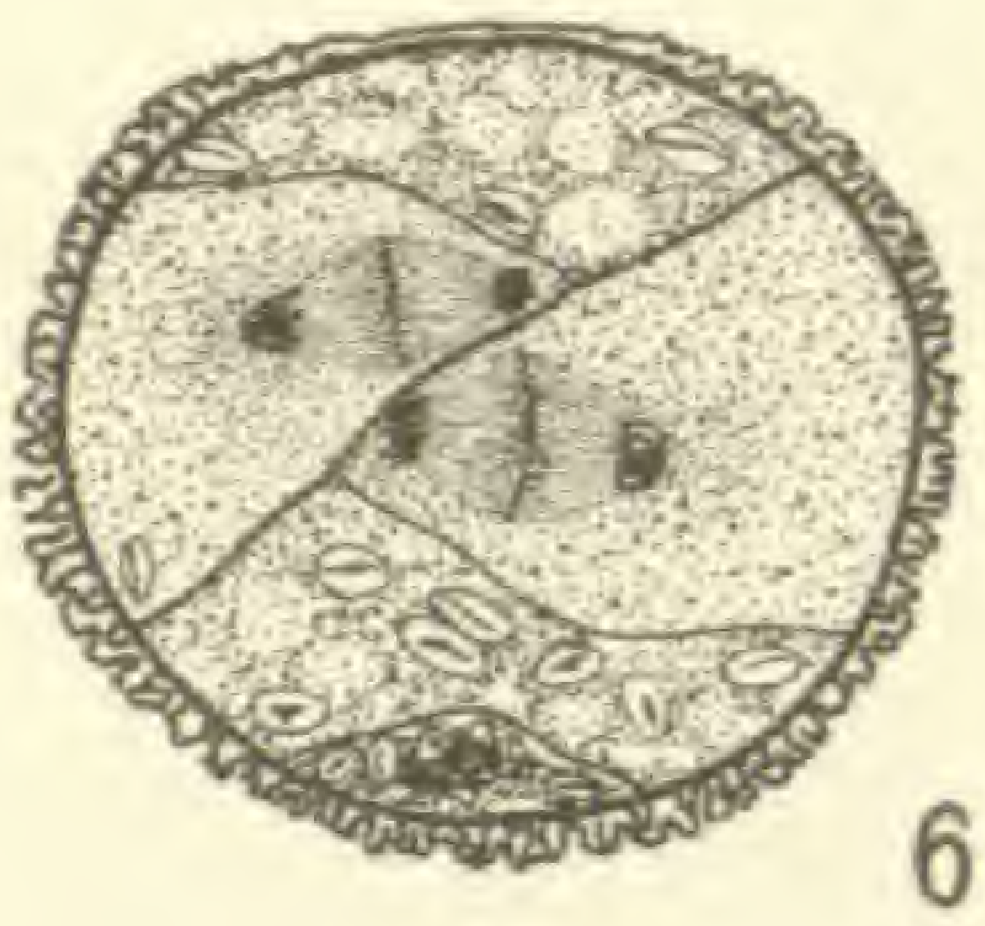
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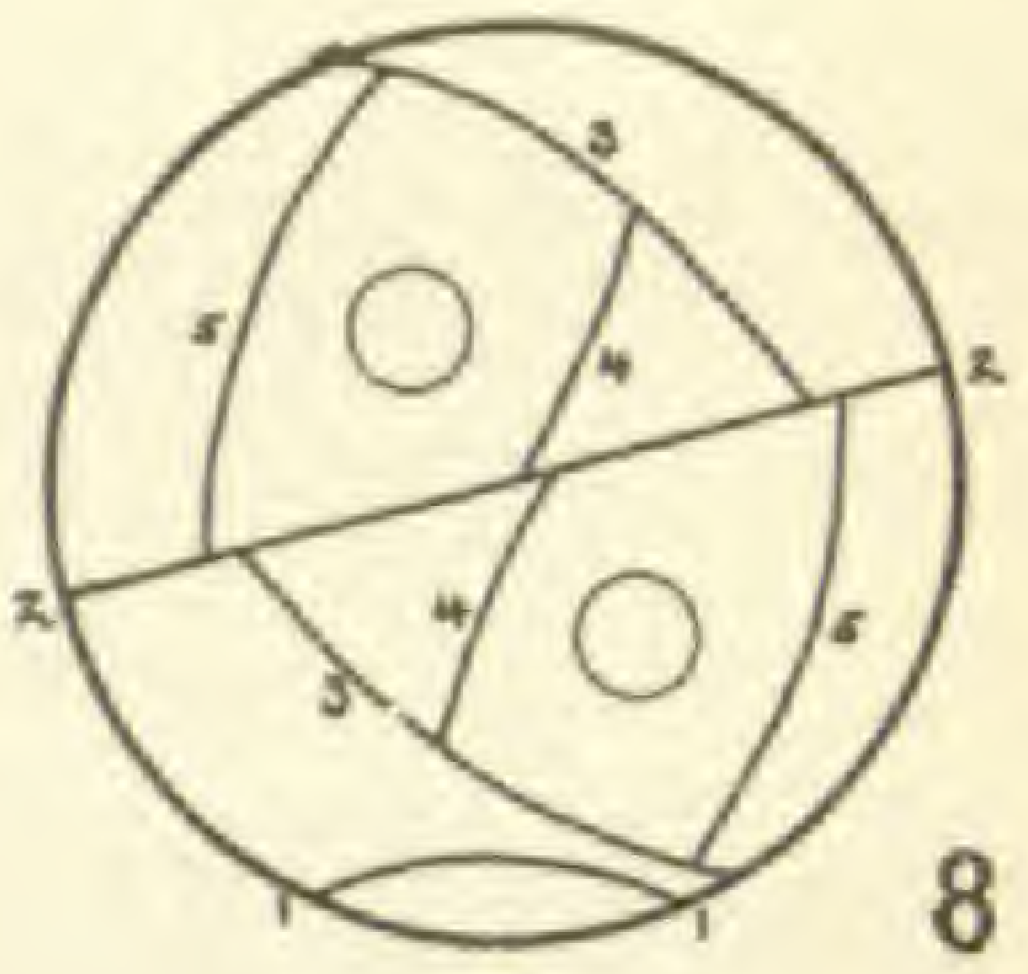
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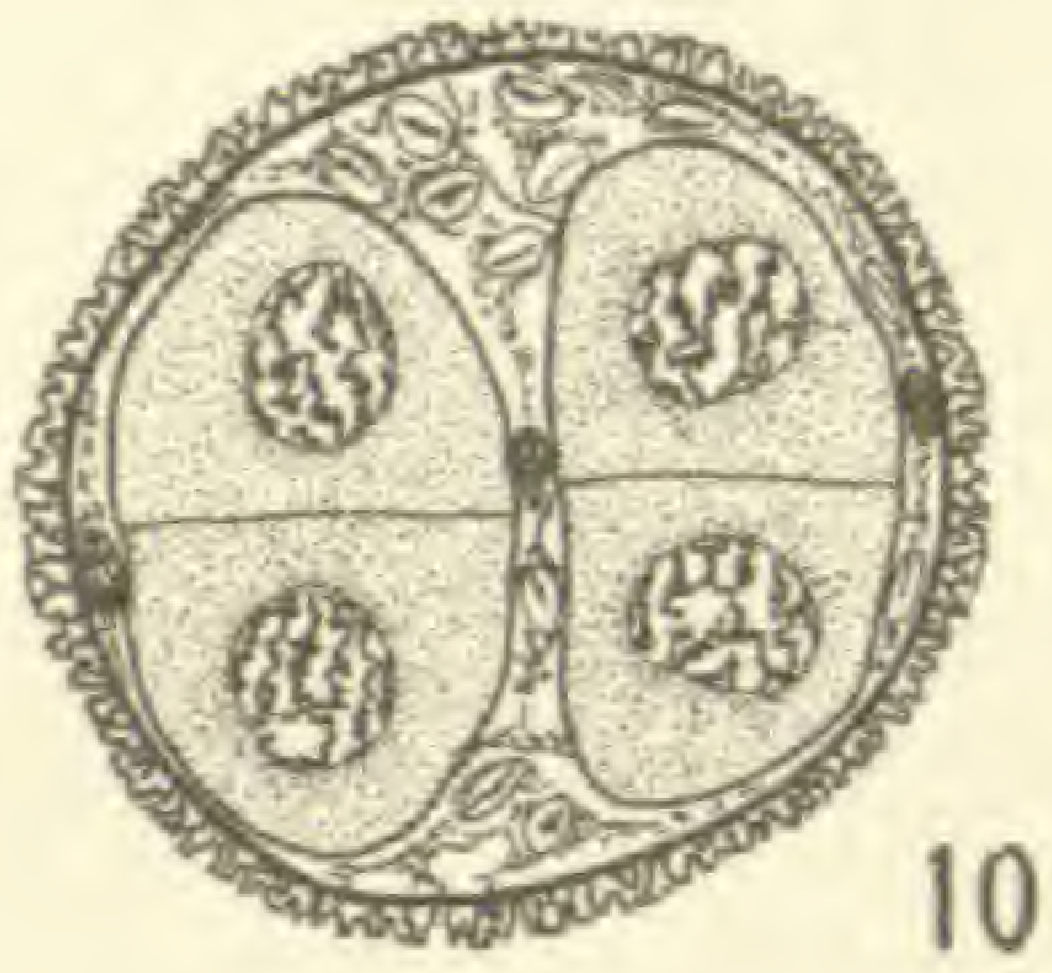
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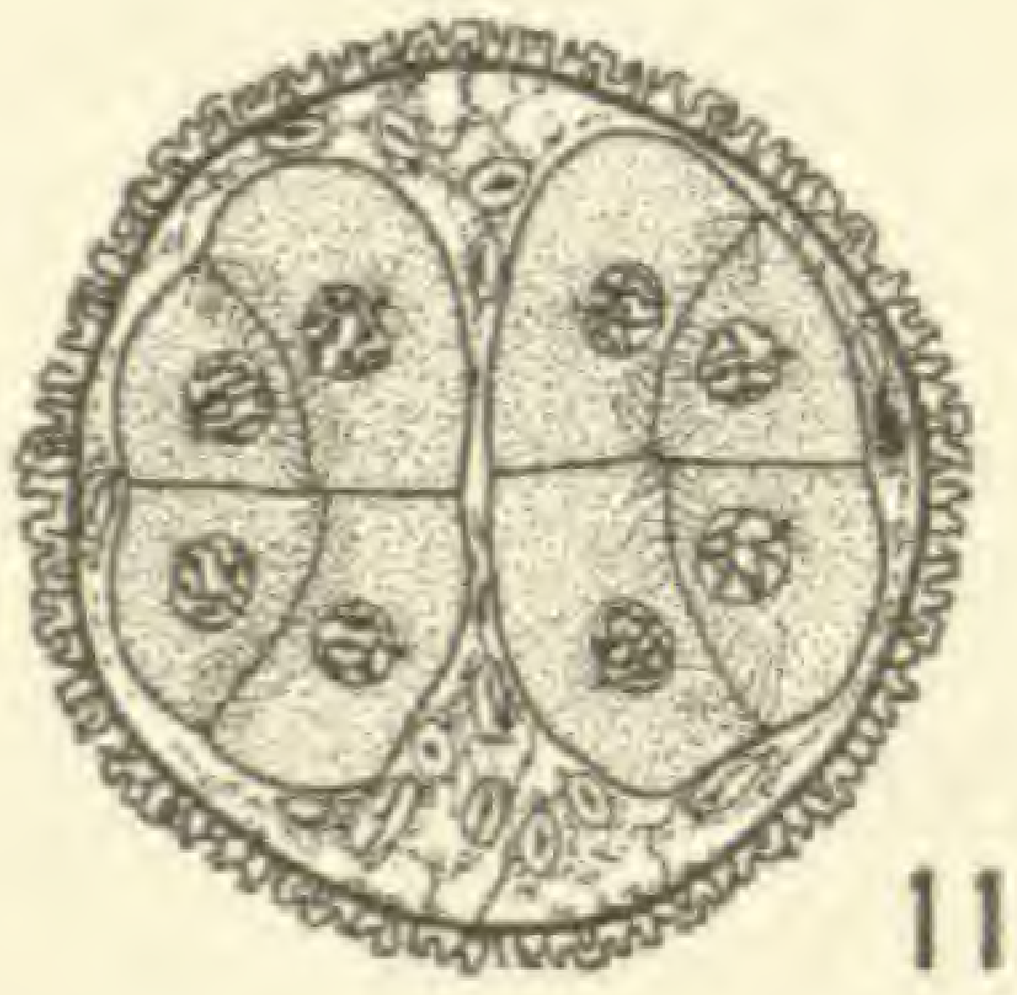
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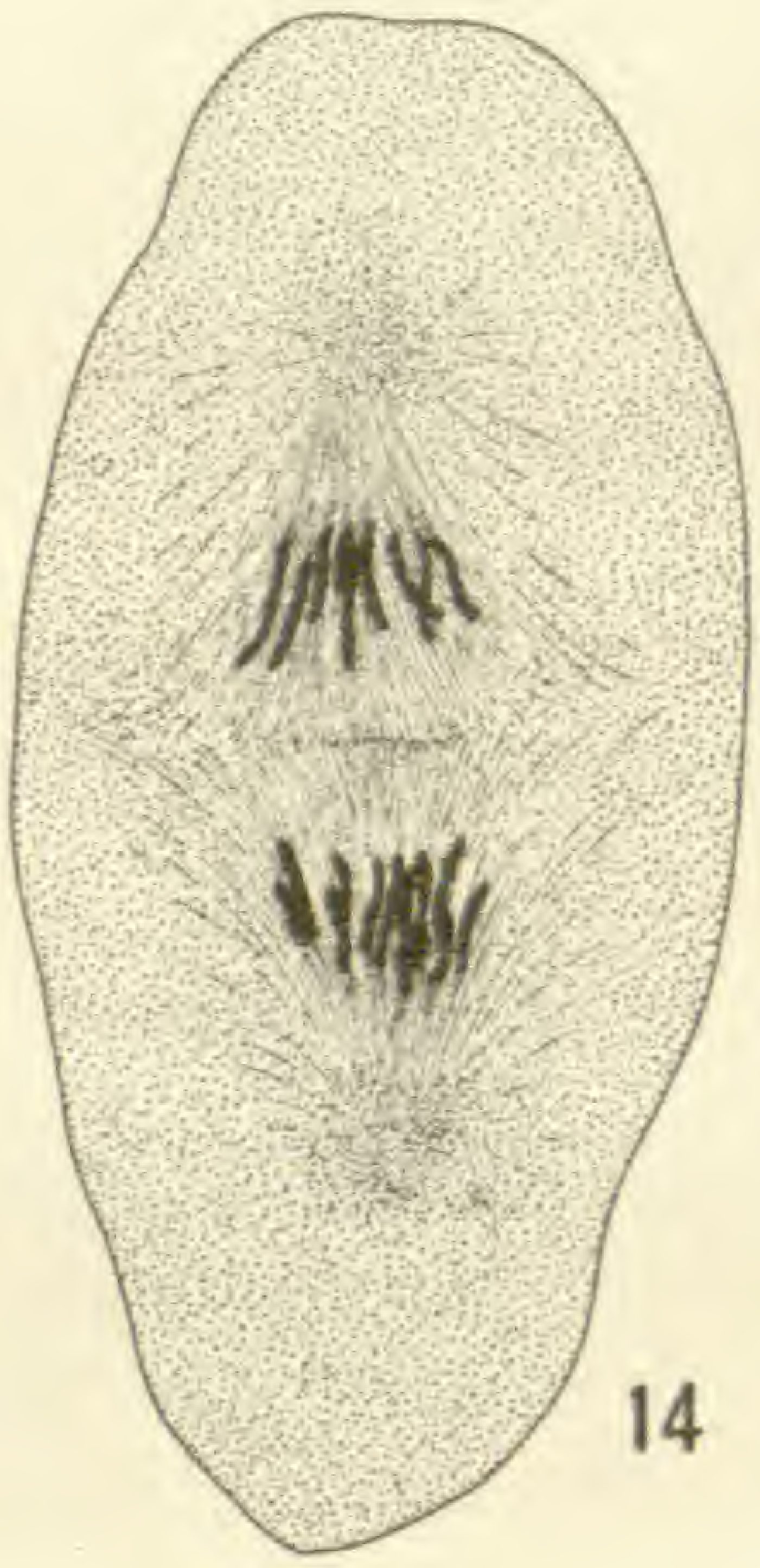
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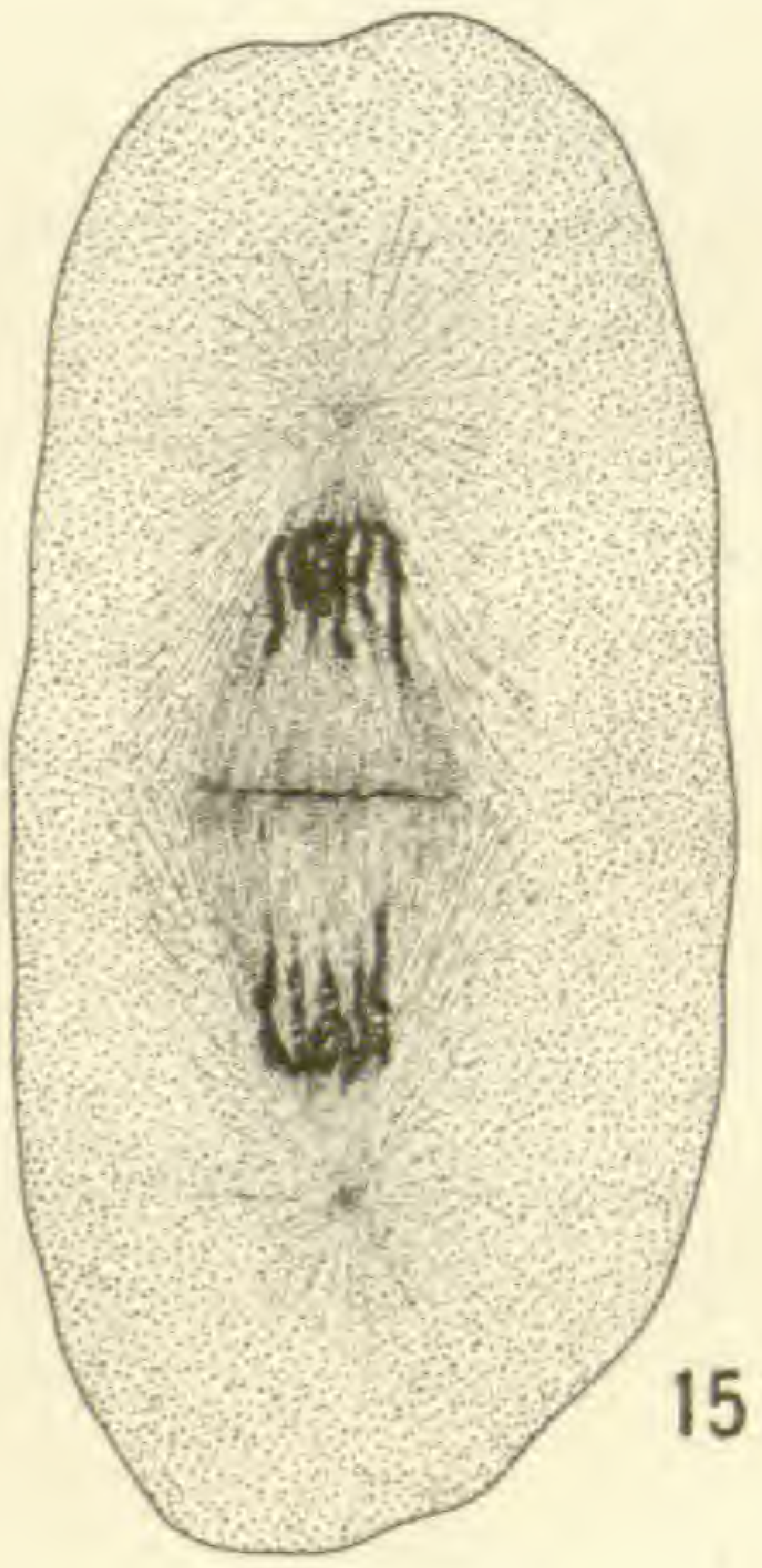
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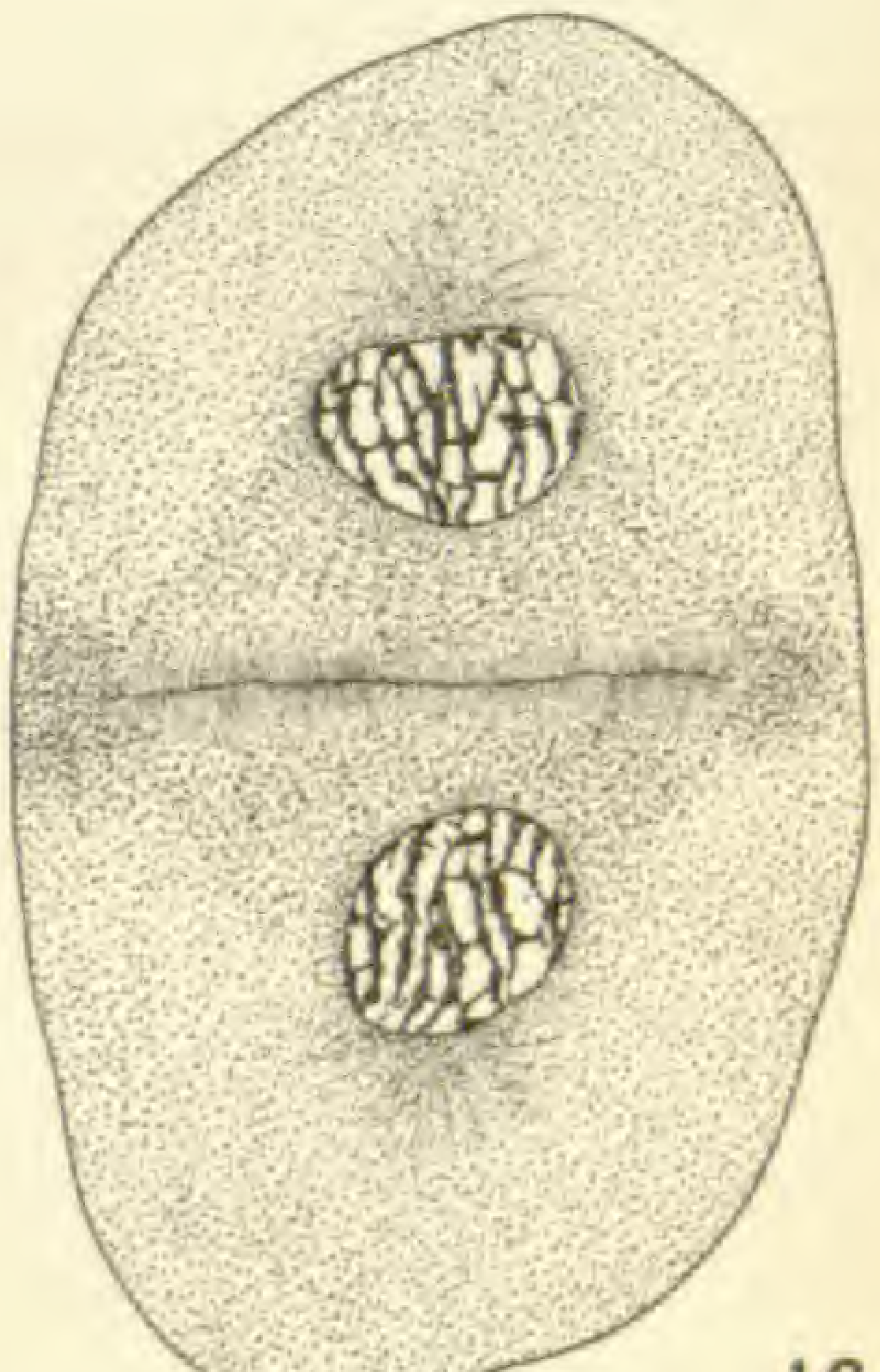
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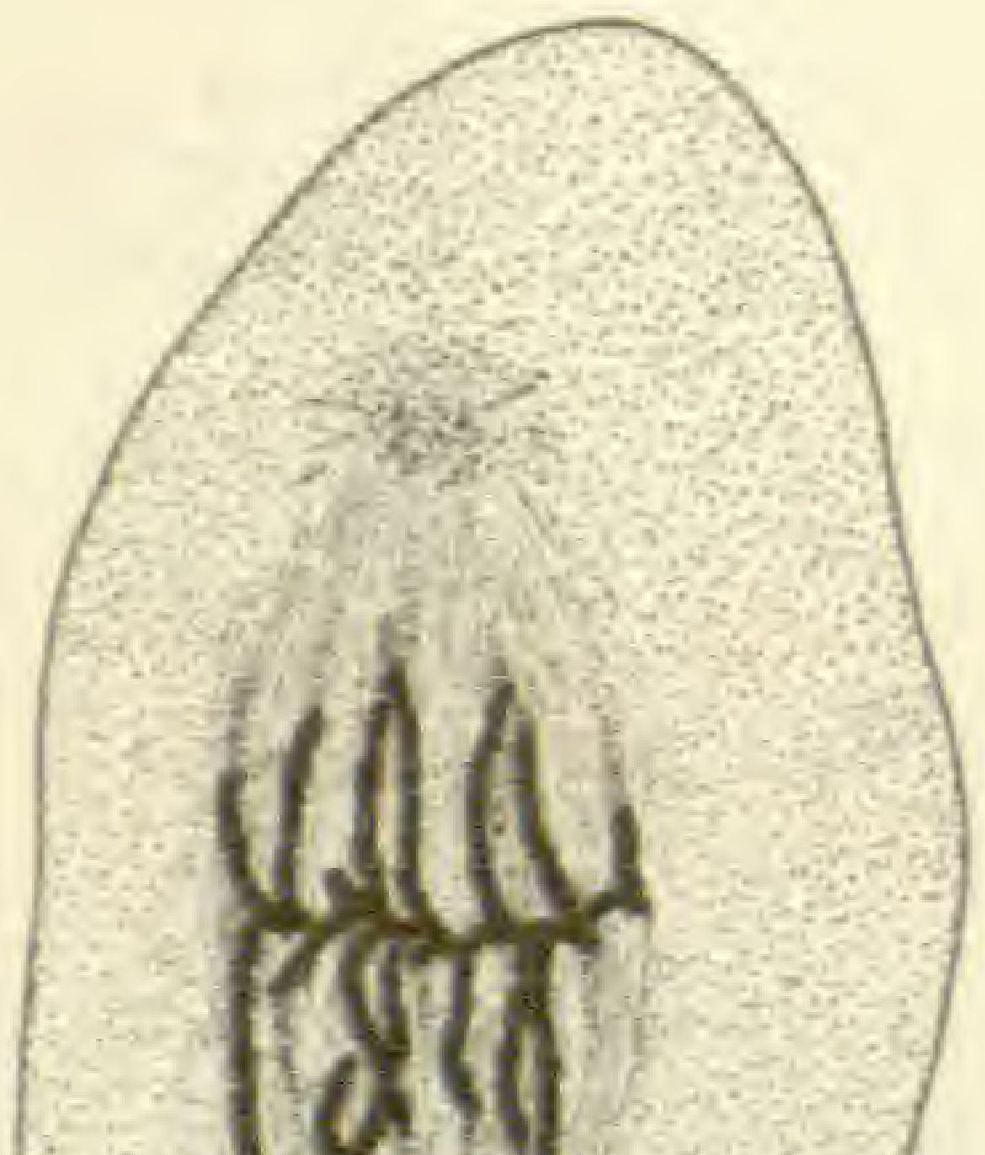
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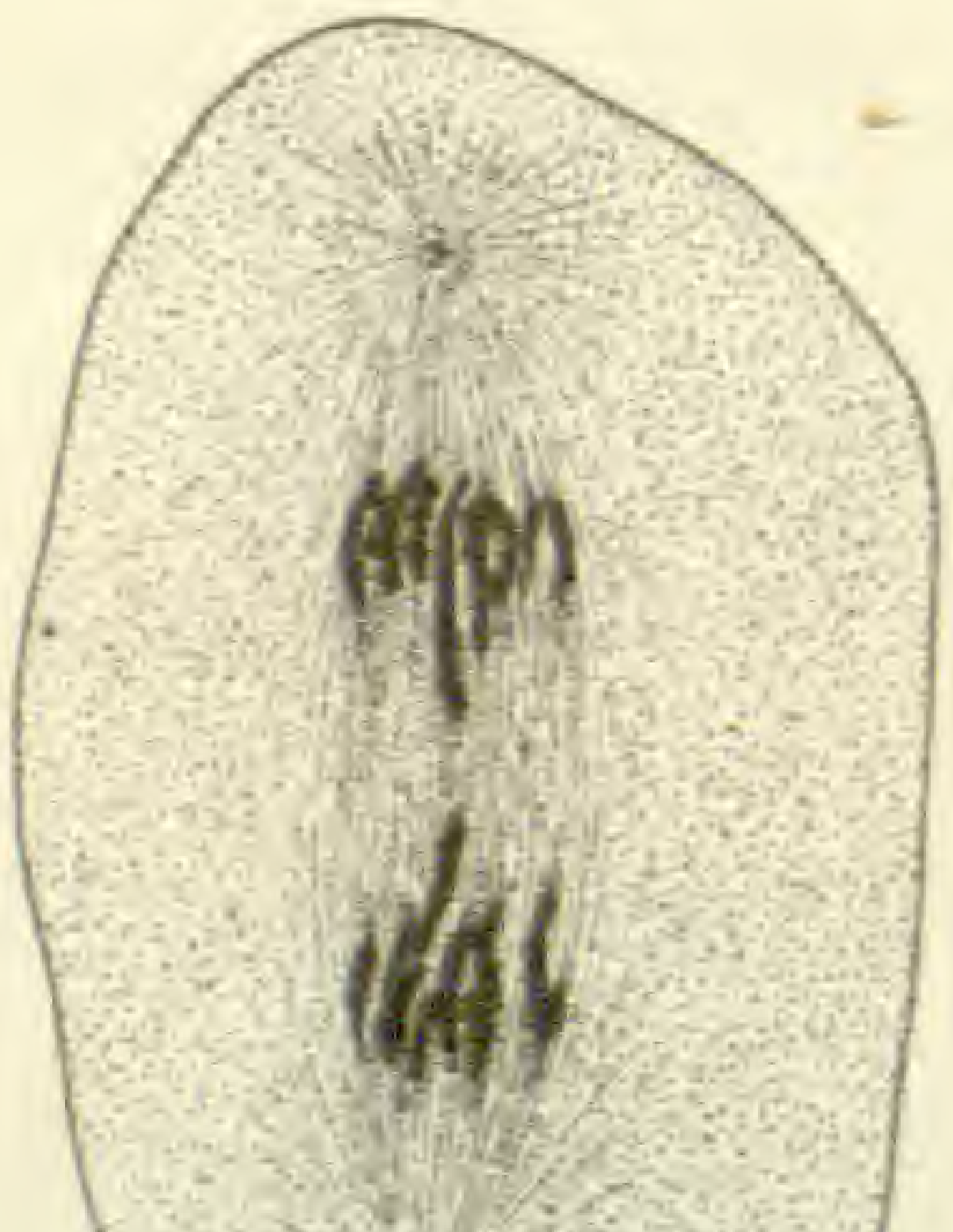
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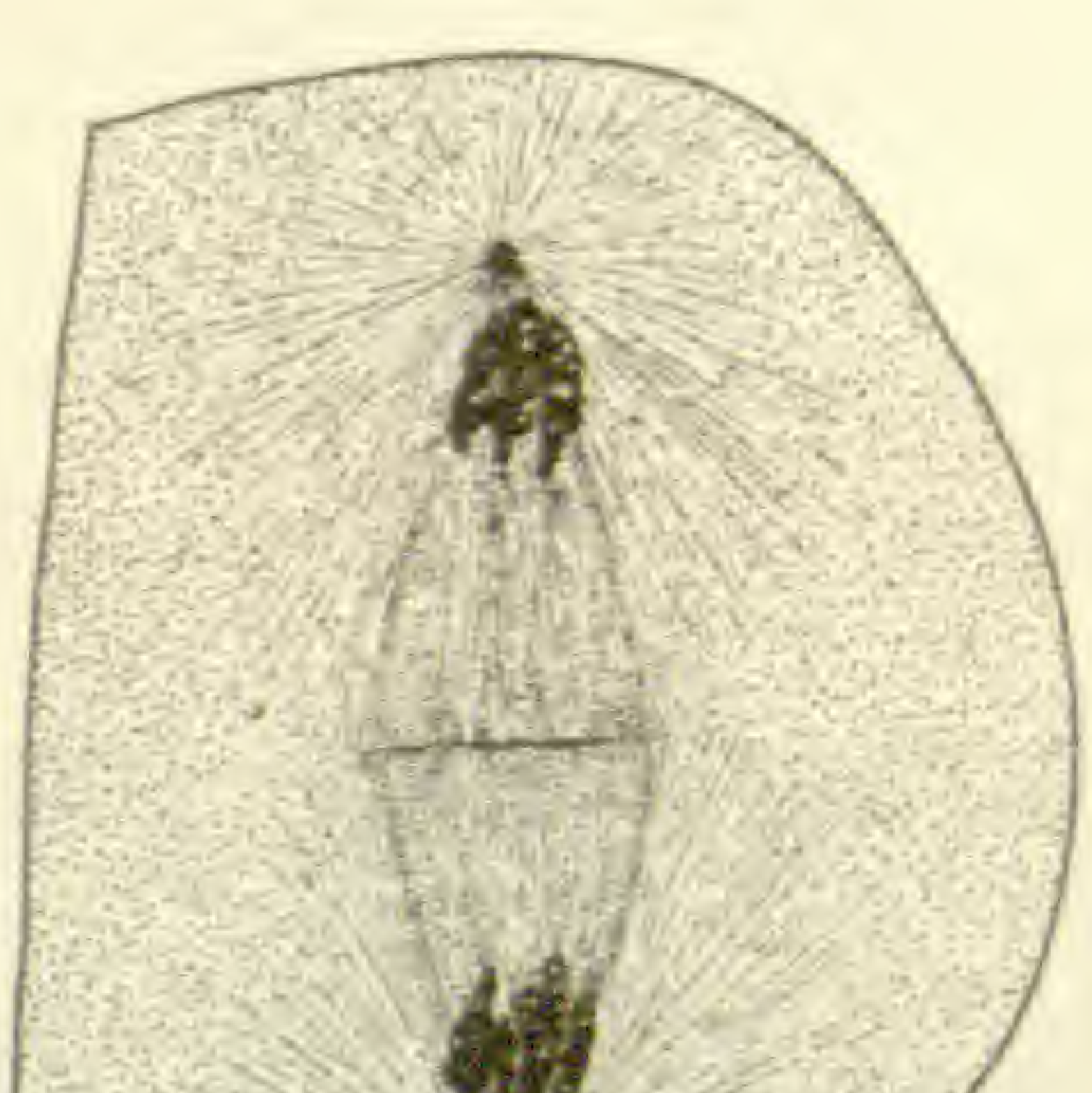
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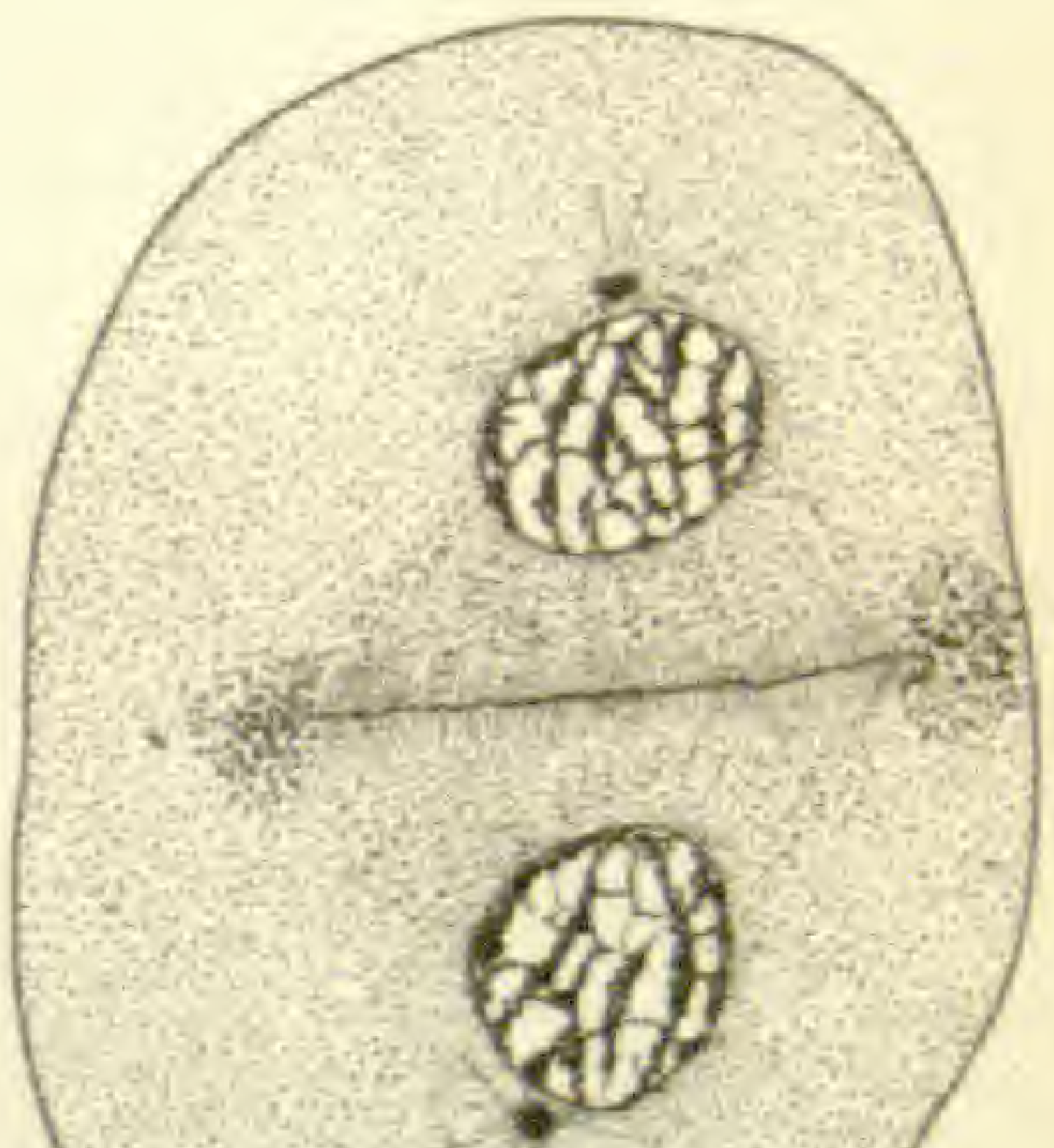
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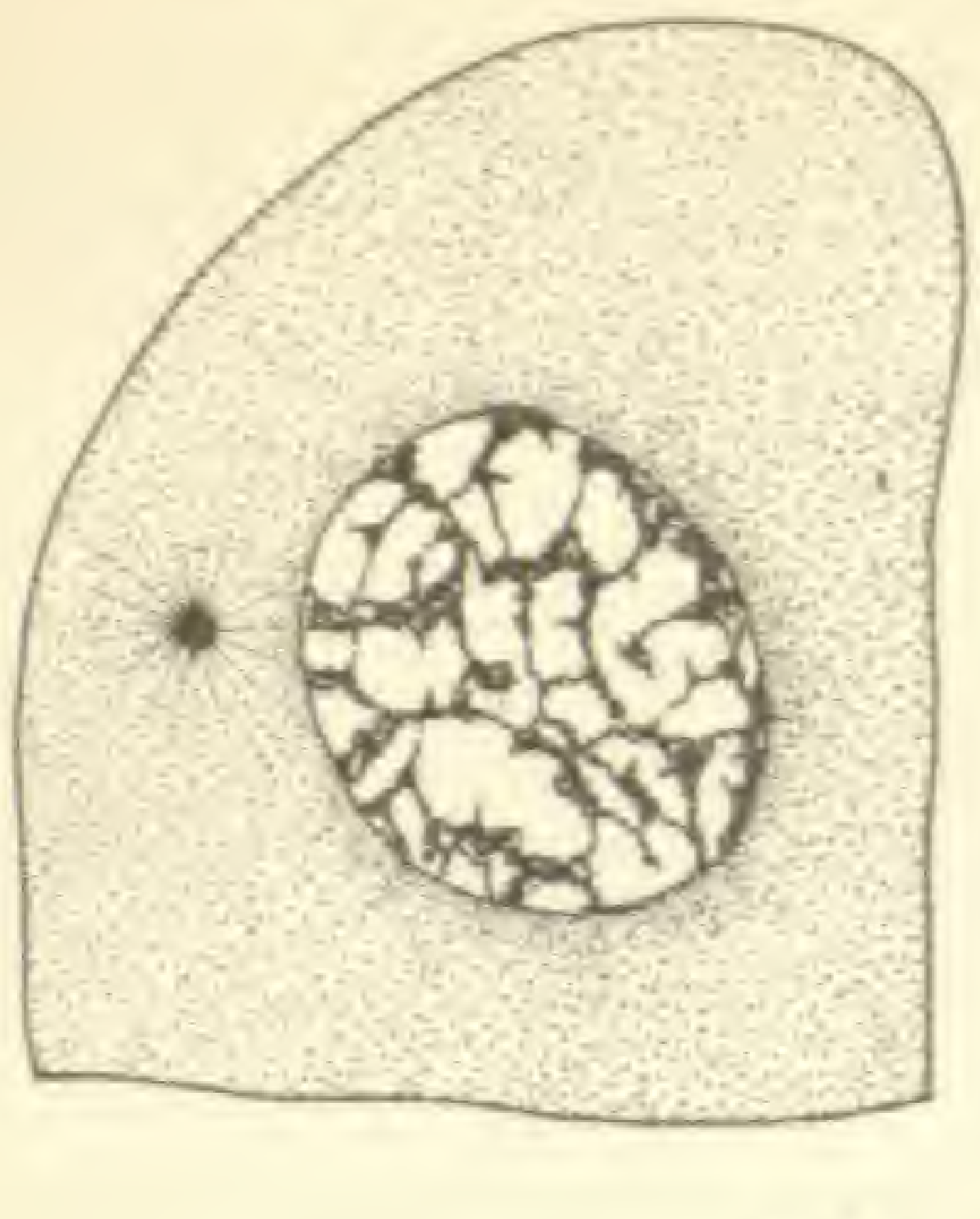
SHARP on MARSILIA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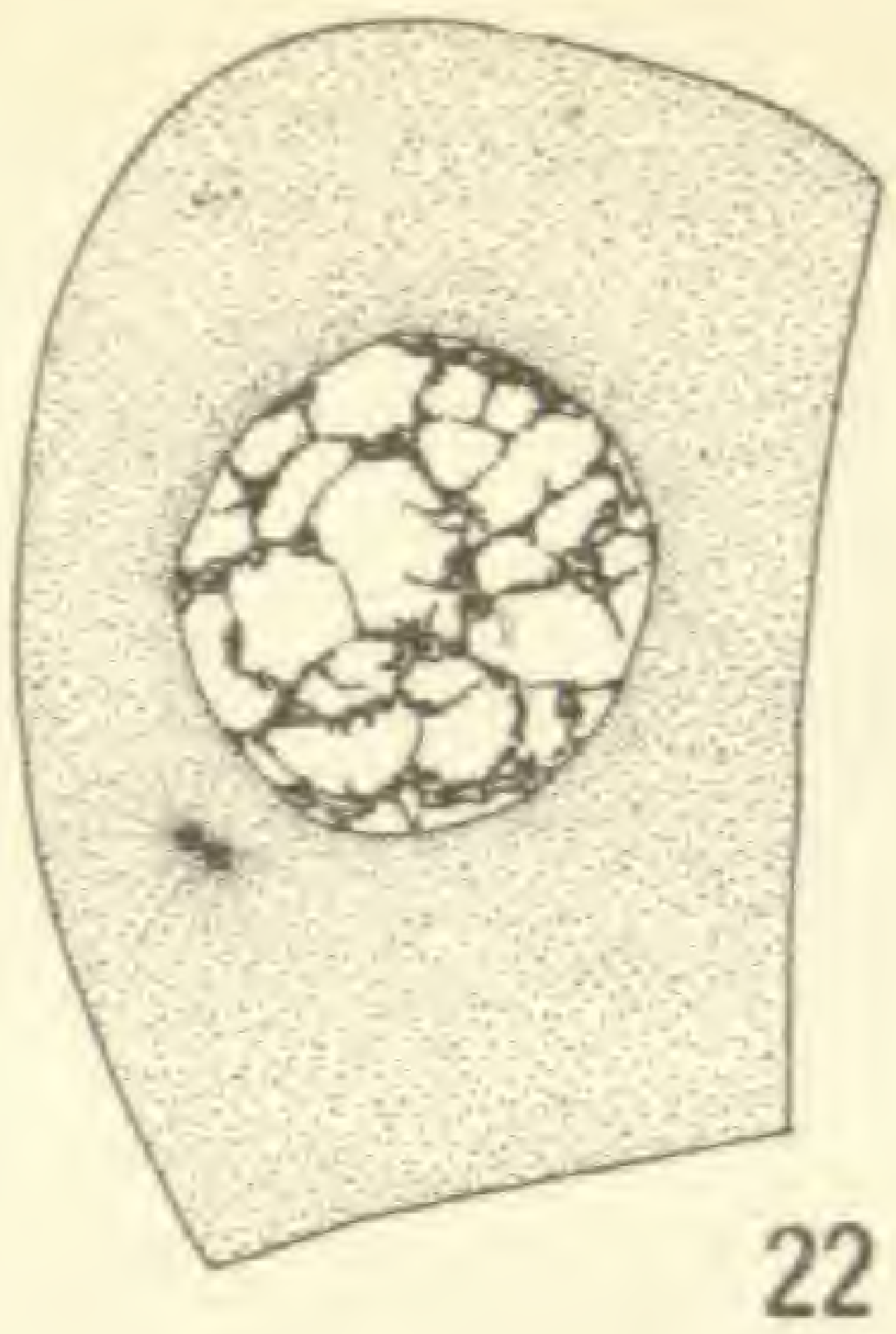
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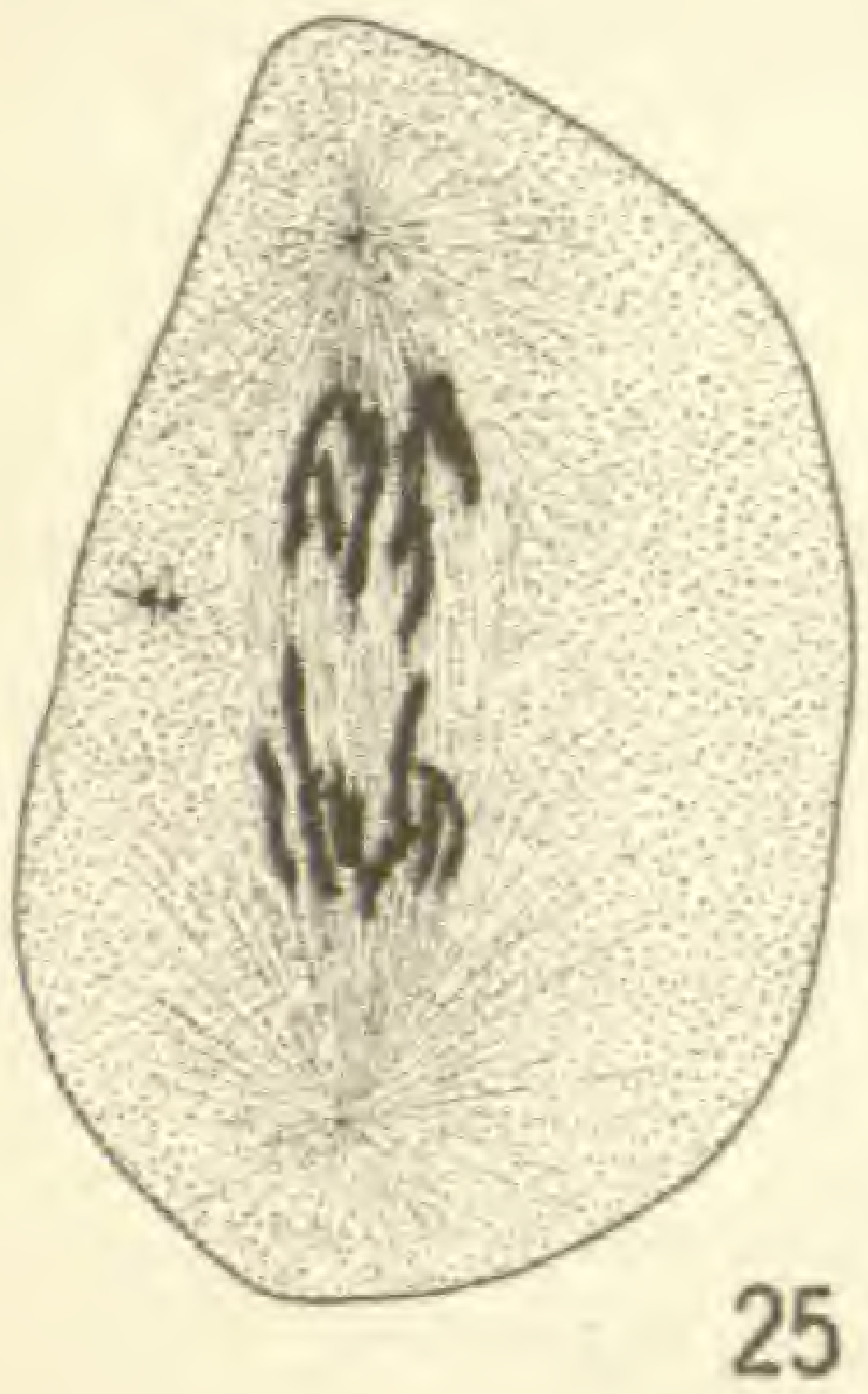
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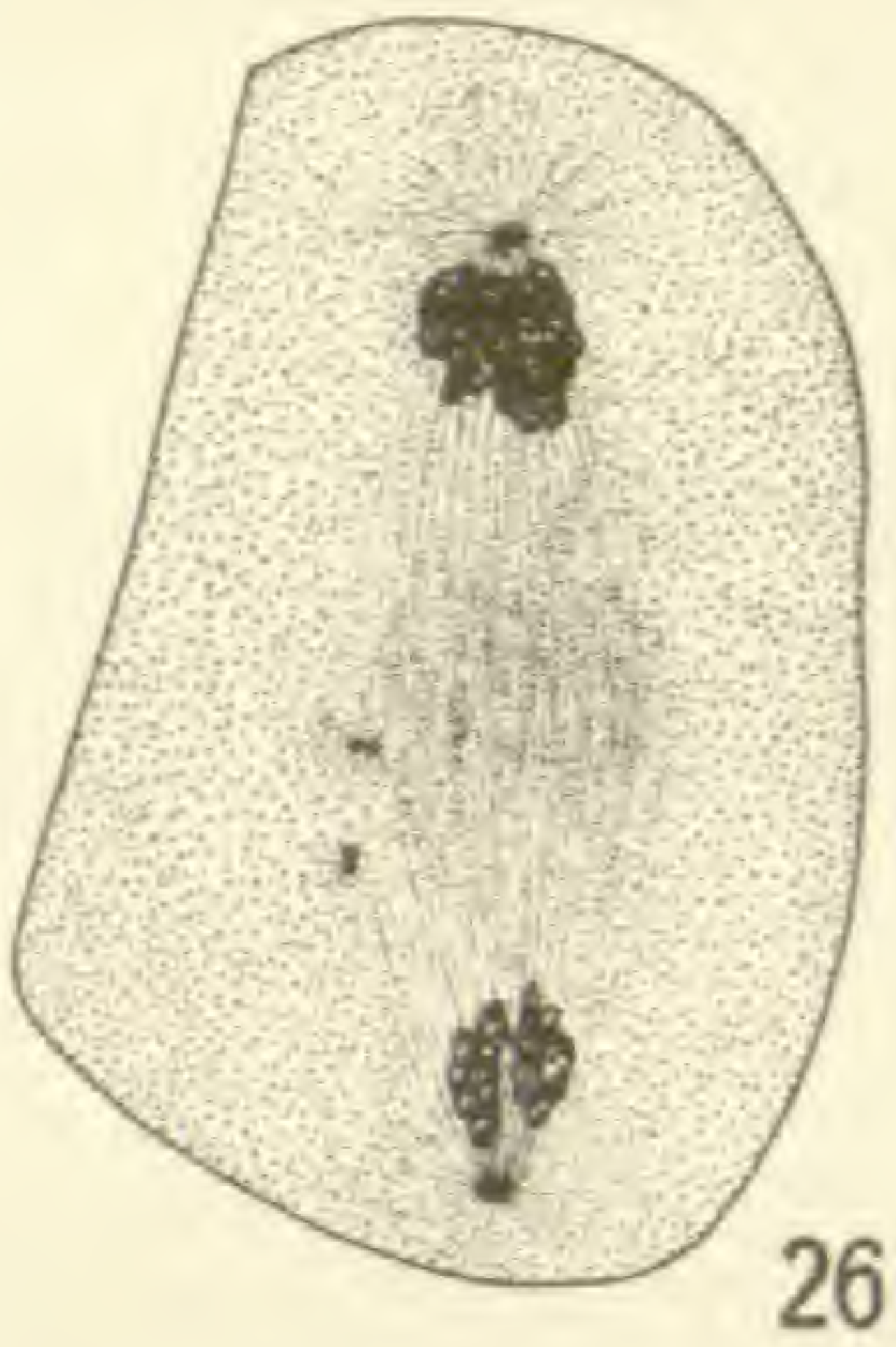
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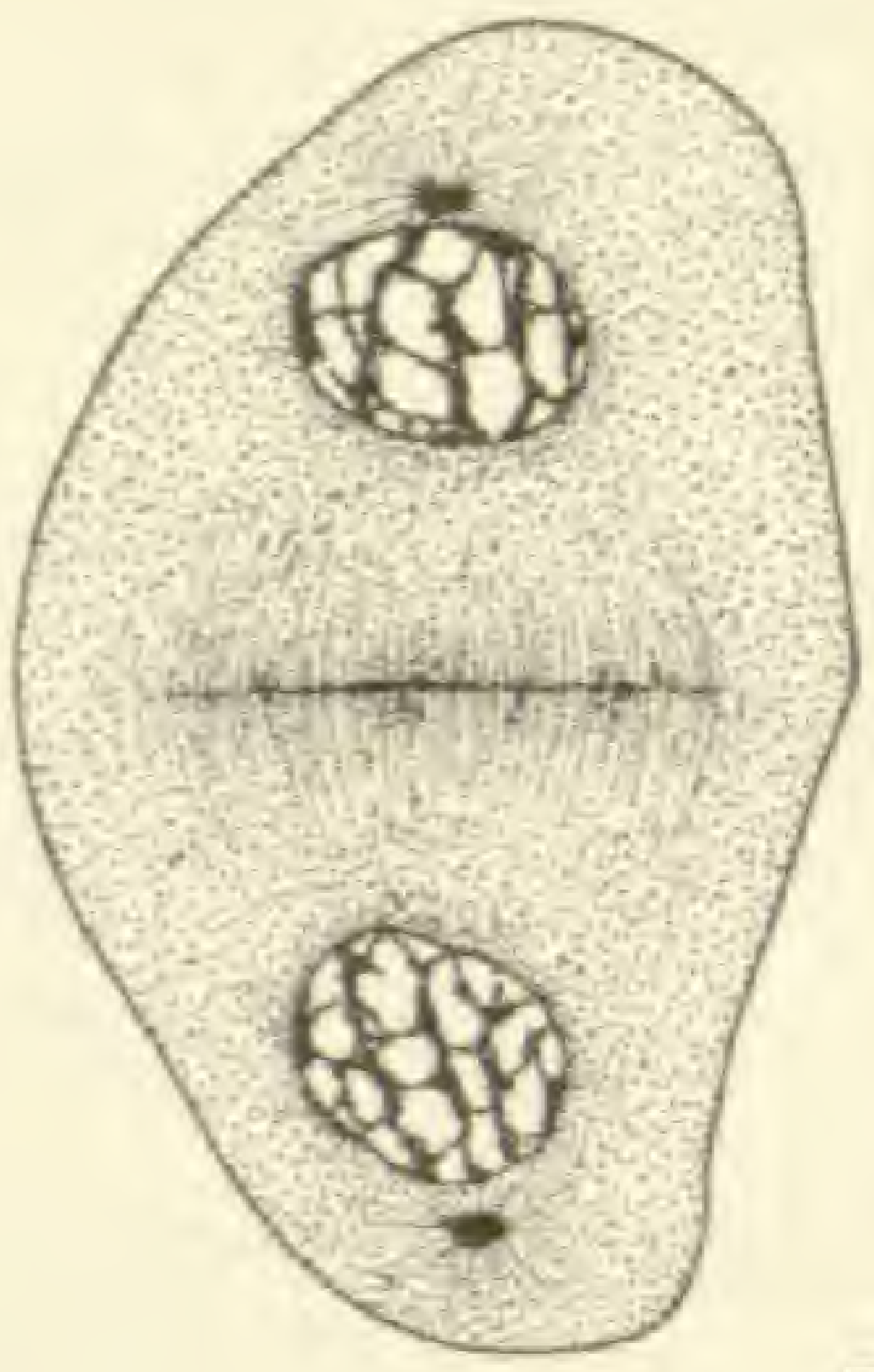
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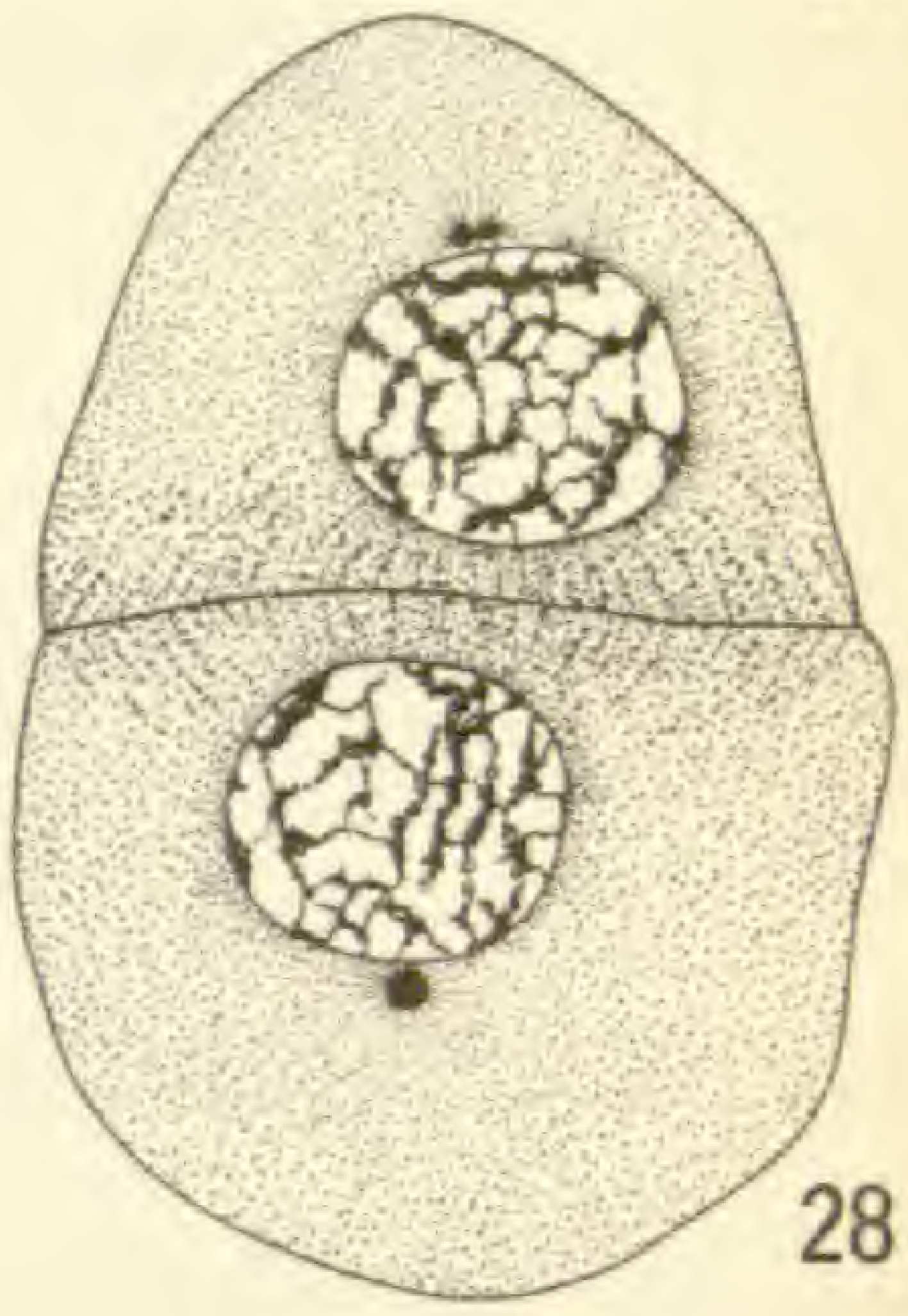
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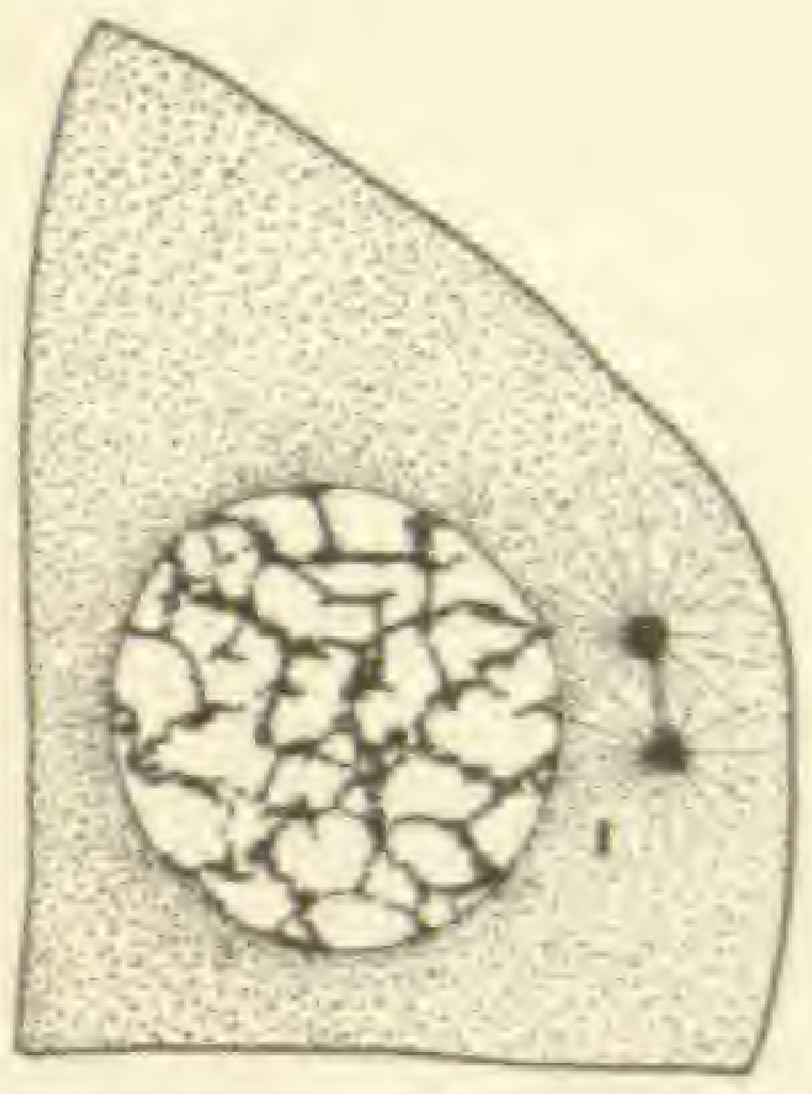
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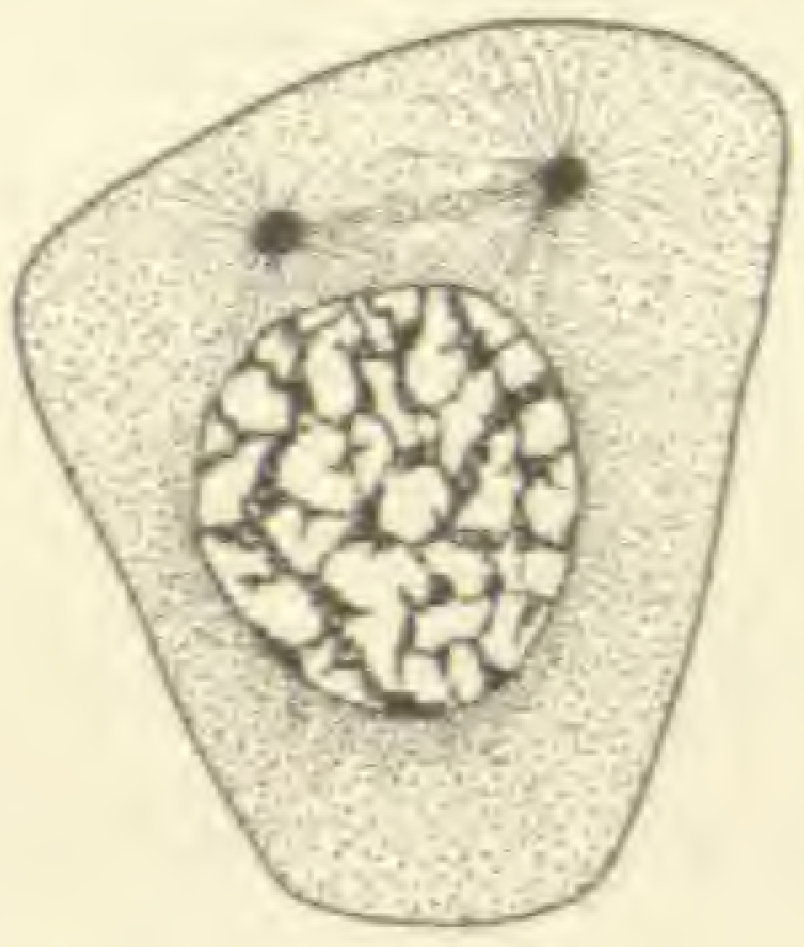
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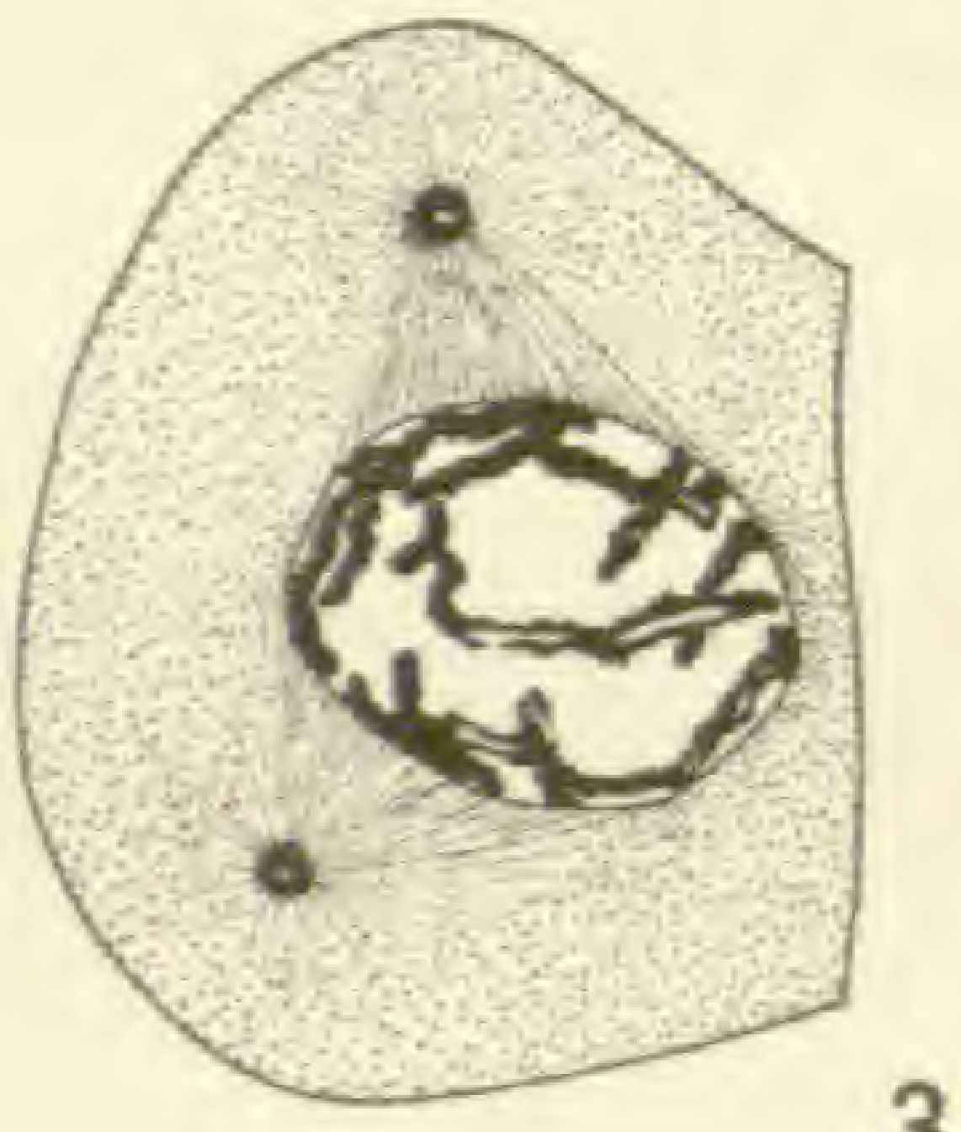
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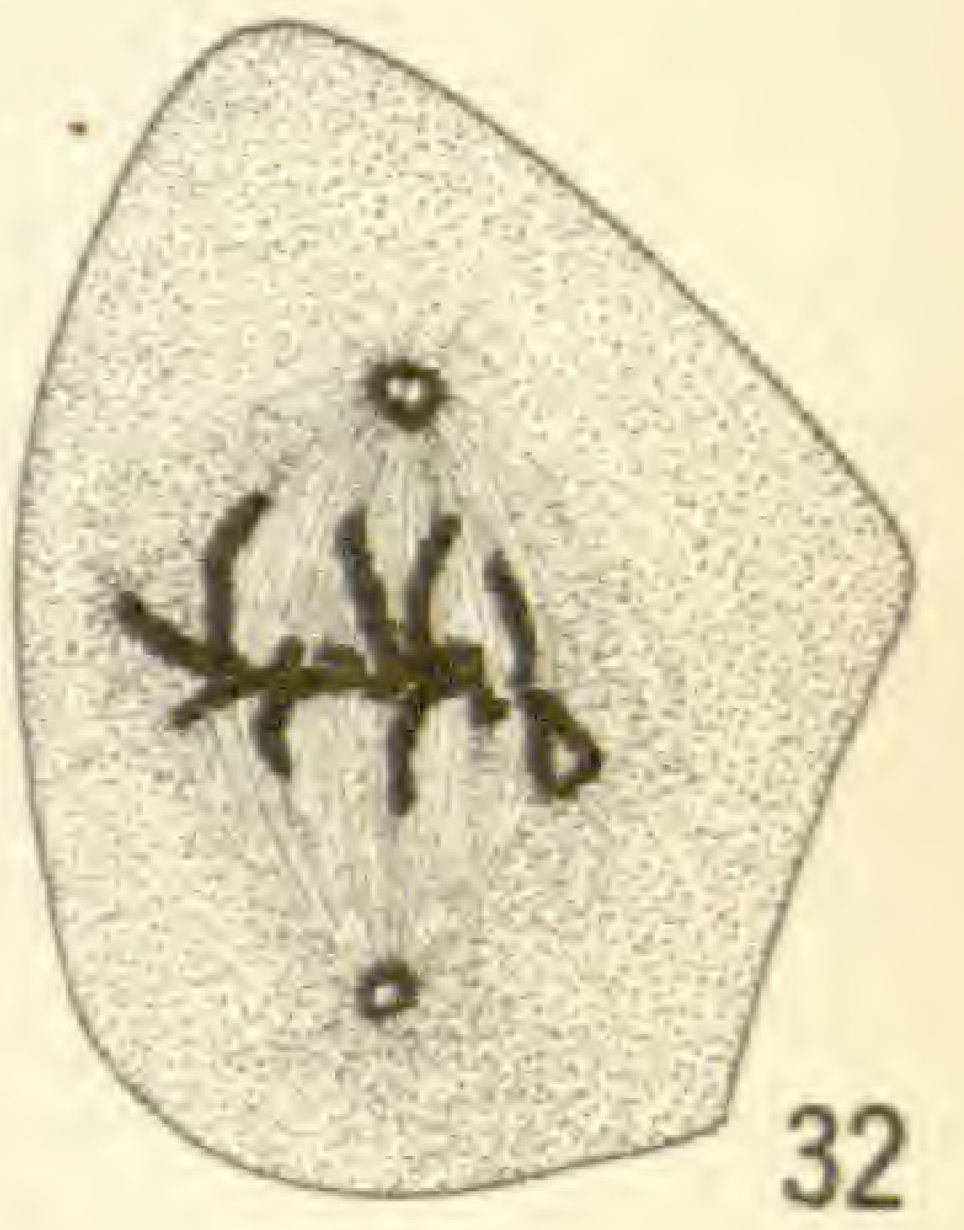
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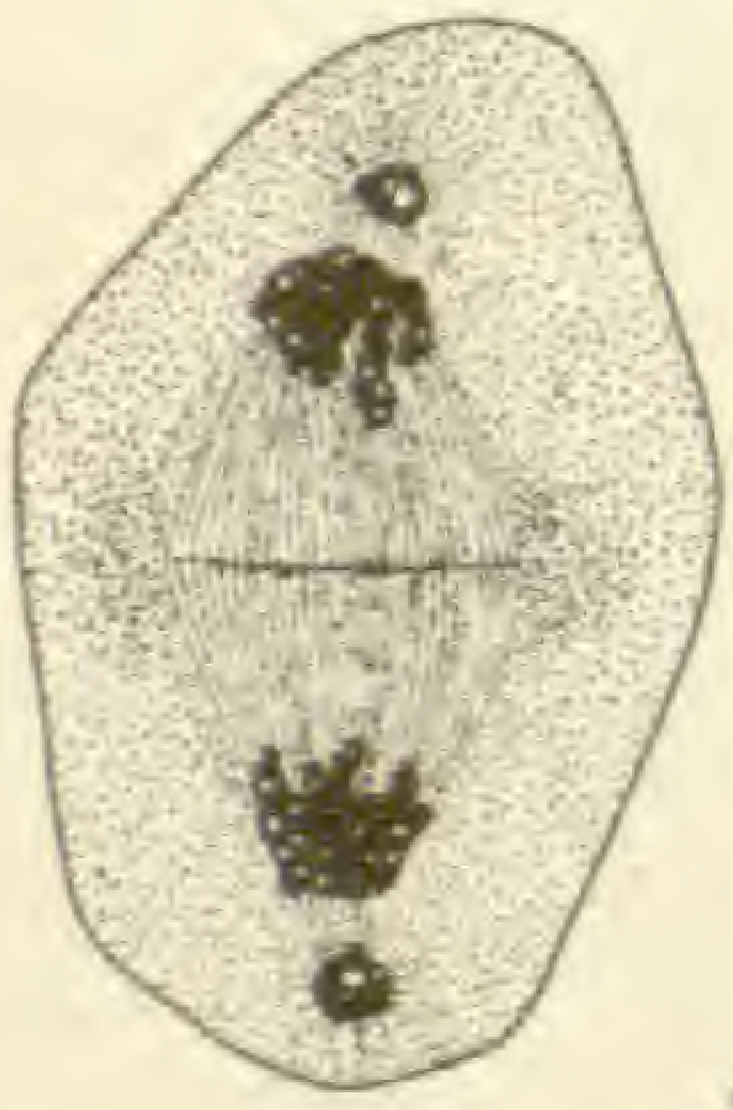
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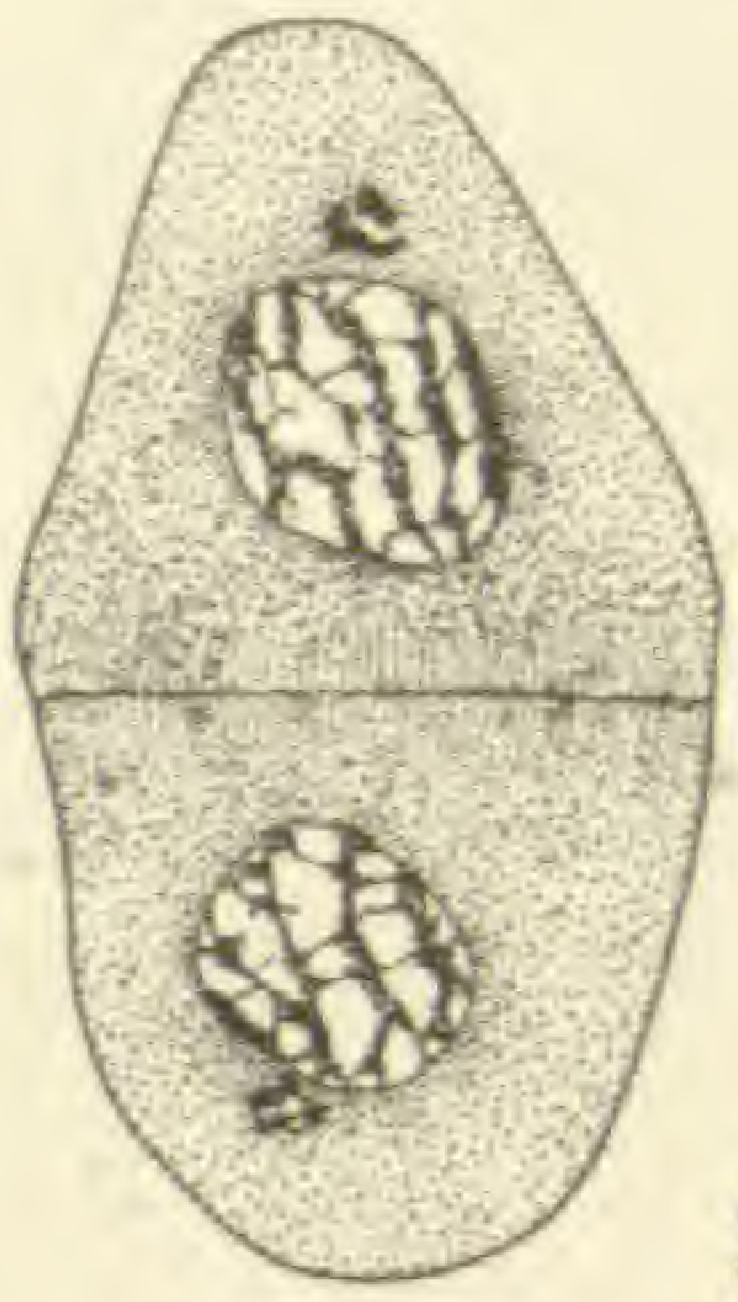
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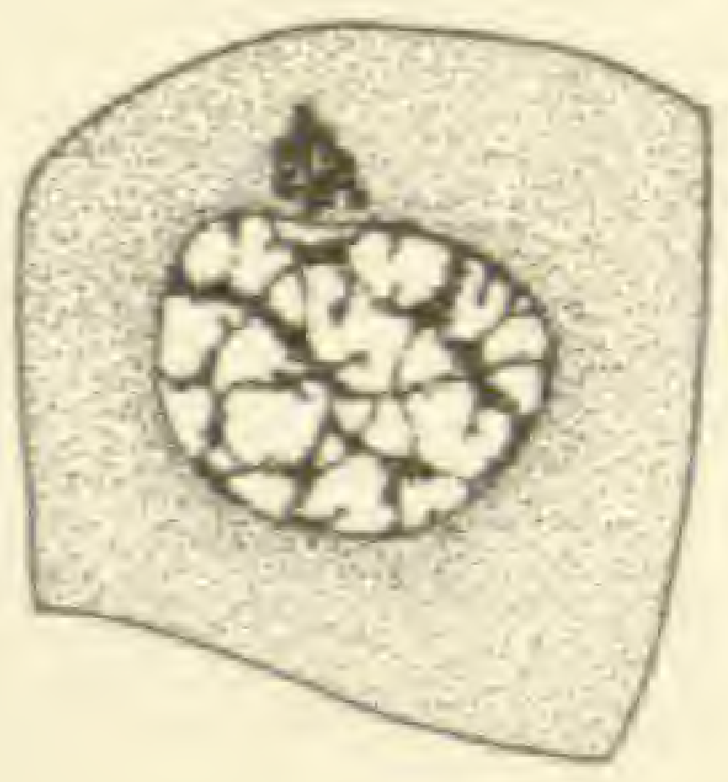
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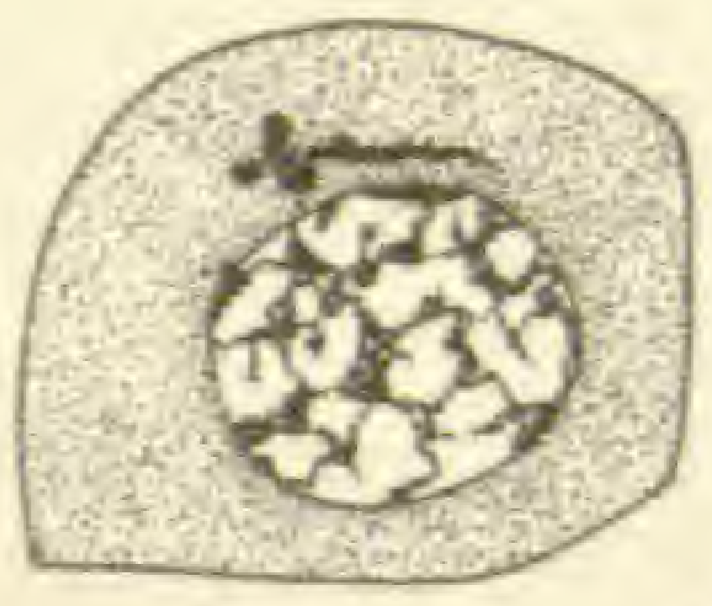
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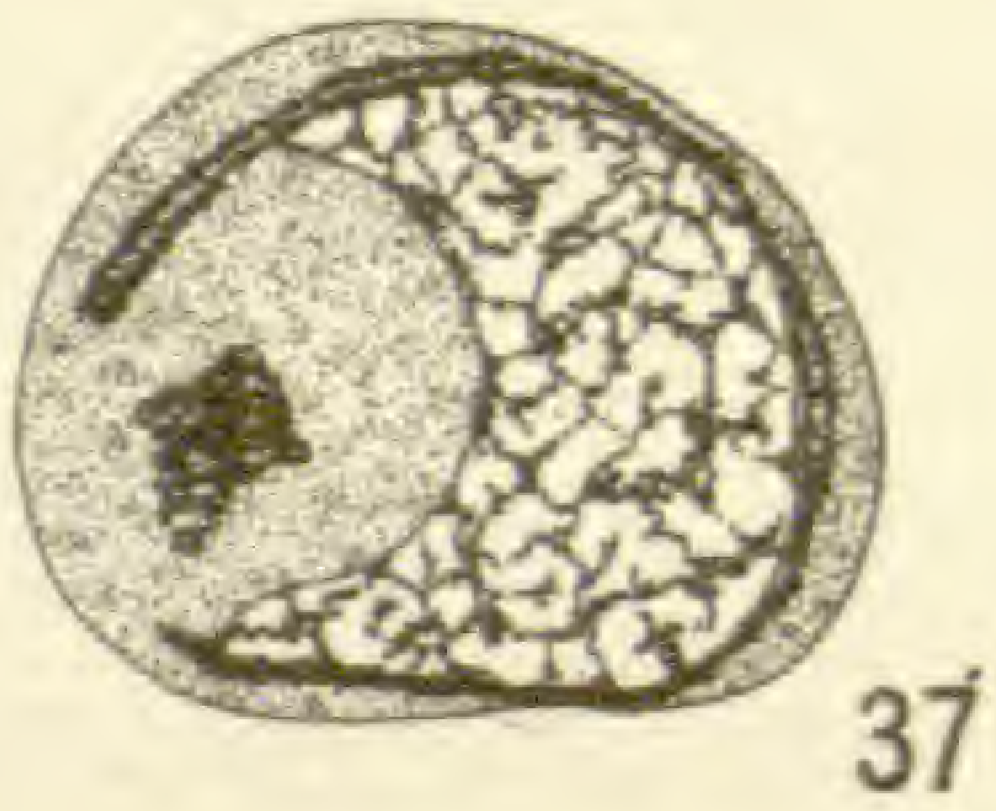
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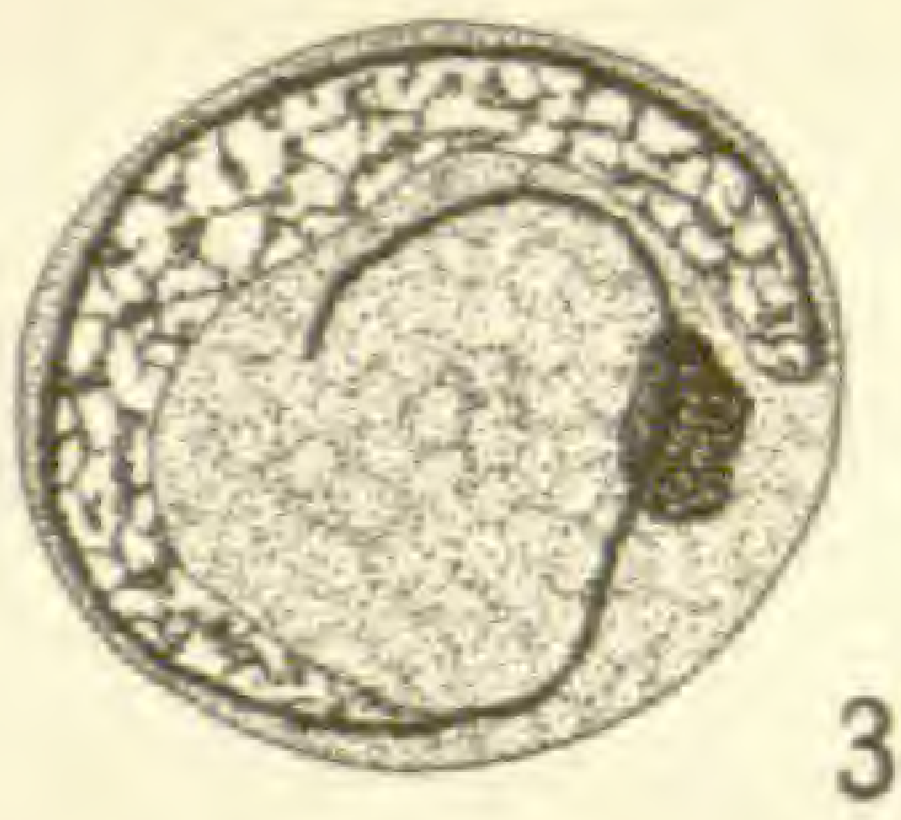
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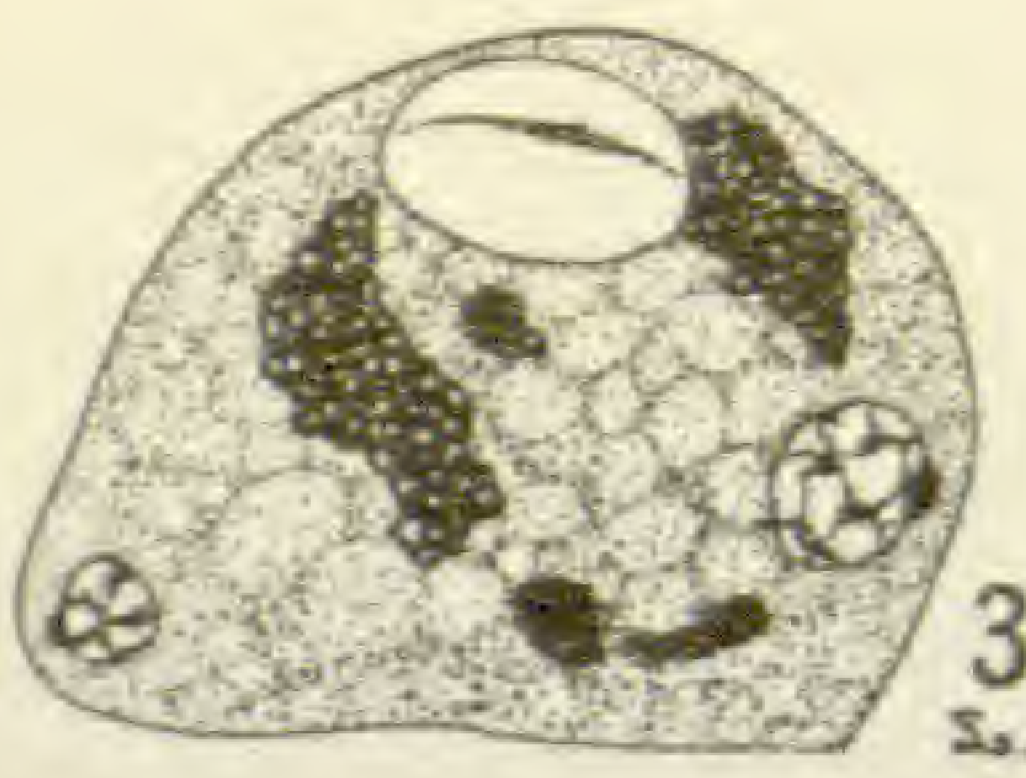
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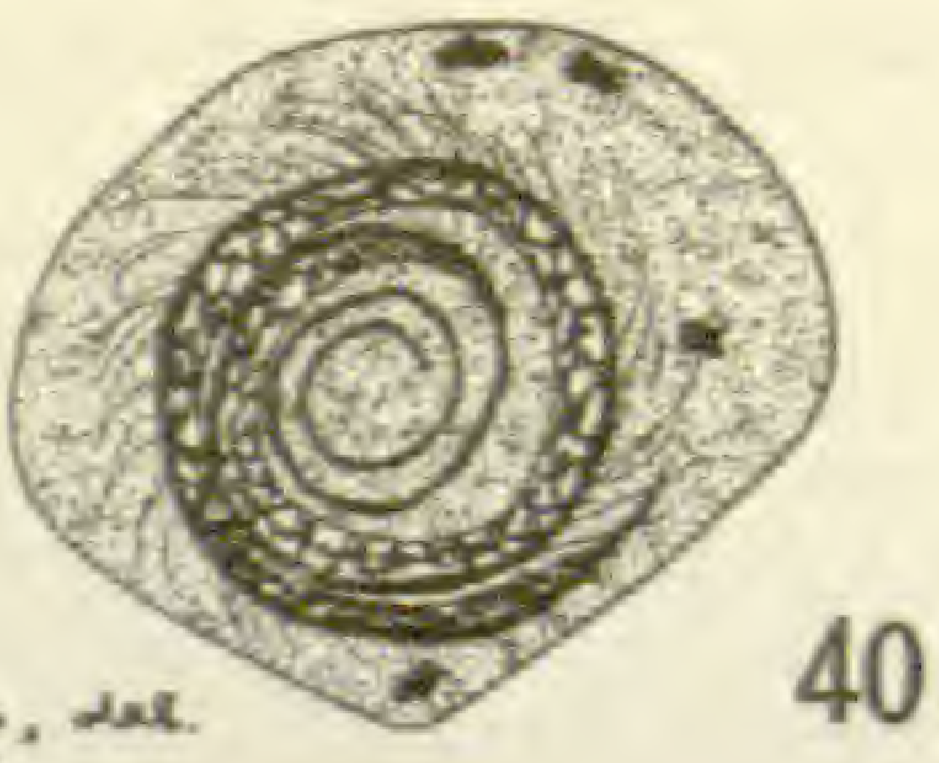
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SHARP on MARSILIA

FIG. 23.—*Third spermatogenous mitosis:* prophase.

FIG. 24.—Late prophase: centrosomes disorganizing in cytoplasm.

FIG. 25.—Anaphase: old centrosomes disorganizing; newly formed centrosomes at poles.

FIG. 26.—"Tassement polaire" stage: old centrosomes have undergone division; new centrosomes greatly enlarged.

FIG. 27.—Telophase: centrosomes beginning to divide.

FIG. 28.—Telophase: division of upper centrosome nearly completed; lower one undivided.

FIG. 29.—Cell of eight-celled stage: centrosomes (blepharoplasts) moving apart.

FIG. 30.—The same, more advanced.

FIG. 31.—*Fourth spermatogenous mitosis:* prophase; spindle forming from radiations; blepharoplast becoming vacuolate.

FIG. 32.—Late prophase: blepharoplast more irregular.

FIG. 33.—Late anaphase.

FIG. 34.—Telophase: blepharoplast breaking up.

FIGS. 35, 36.—Spermatids: blepharoplast has fragmented further and is beginning to form band.

FIG. 37.—Early stage of metamorphosis of spermatid: blepharoplast shows double structure in certain parts.

FIG. 38.—Later stage: blepharoplast grows out freely beyond one end of nucleus.

FIG. 39.—Cross-section of cell in same stage: sections of nucleus with closely appressed blepharoplast at right and left; starch and other disorganized material in cytoplasm.

FIG. 40.—More advanced stage: cilia growing out from blepharoplast.

FIG. 41.—Spermatozoid shortly after escape from microspore: cilia only on middle coils; length 15.3 μ.

FIG. 42.—Spermatozoid in gelatinous material about megaspore, fixed over osmic fumes; length 50 μ.

THE PLANT SUCCESSIONS OF THE HOLYOKE RANGE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 198

EDITH A. ROBERTS

(WITH MAP)

Introduction

The Holyoke Range lies well within the eastern deciduous forest region with the climatic plant formation of the mesophytic deciduous climax type made up of *Acer saccharum* (sugar maple), *Fagus grandifolia* (beech), and *Tsuga canadensis* (hemlock). The range is located nearly in the center of the Connecticut valley, which crosses the state of Massachusetts from north to south and varies from 100 to 1200 feet in elevation. The many topographical features offer opportunity for the study of the development of the vegetative cycles terminating in the climax forest of central Massachusetts.

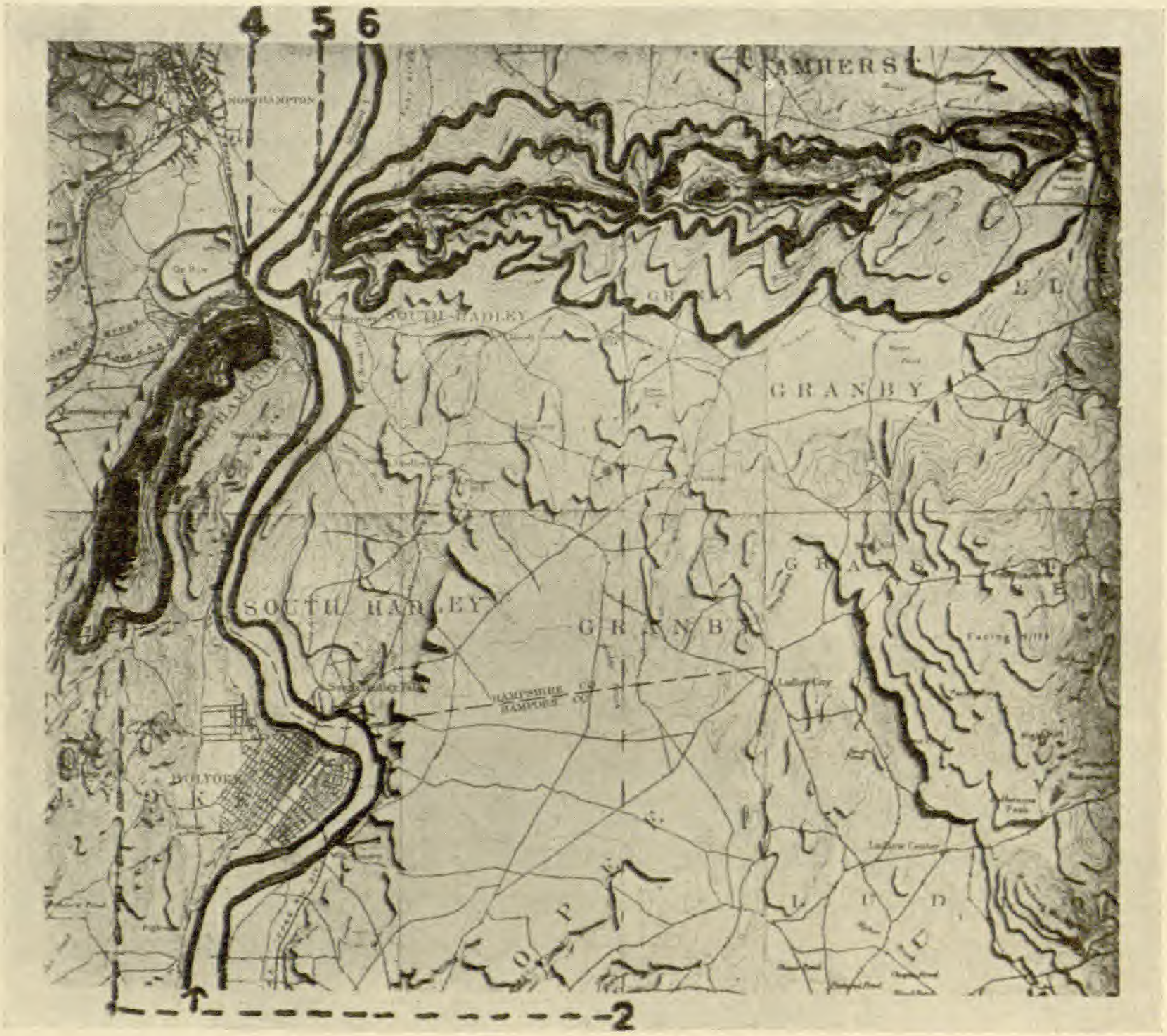
A few isolated portions which have been uncut for over 250 years furnish evidence as to the climax, while the repeated cutting in other places gives excellent opportunity to study the development of the so-called "secondary succession" (1), a study which will of necessity be more valuable as the work of reforesting increases, especially in the New England states, where the future forests will for the most part be of that type.

The purpose of the work is to determine the varying lines of biotic successions leading to the present climax in this region, and in a later paper to determine the relationship of the factors which are influencing these successions.

The region is typical of the central portion of the state and the range represents a natural unit which, owing to its direction (see map), offers opportunity to study north, south, east, and west slopes, with their variations in succession.

The work was begun at the suggestion of Dr. HENRY C. COWLES, of the University of Chicago, and I wish to express my thanks for his suggestions and interest in the work. I wish to thank Miss MIGNON TALBOT, of Mount Holyoke College, for the material on the topography and physiography of the region, and Miss Sarah J. Agard, of the botany department, for identification of uncertain species.

The nomenclature of the pteridophytes and spermatophytes is that of the seventh edition of Gray's *Manual*.



Map.—1, Mount Tom Range; 2, Mount Holyoke Range; 3, Holyoke Range; 4, Nonotuck; 5, Titan's Pier; 6, Connecticut River.

Topography and physiographic history

The Holyoke Range is situated in the western central part of Massachusetts in lat. 42° N., long. 70°30′ W., in an old river valley. The range varies in elevation from 100 feet to 1200 feet and is 10 miles in length.

The valley was carved out by stream erosion upon a great thickness of sandstone, conglomerates, and shales with interbedded lavas; the main sheet of which, and the one which caps the ridges, is the Holyoke diabase. These Triassic rocks were later subjected to tilting, warping, and faulting, and these processes, together with stream erosion, resulted in the formation of the "trap" ridges which stand above the valley floor with steep cliffs facing the west or the north, as the case may be, and more gentle slopes on the east and the south, slopes that are practically that of the dip of the rocks. These cliffs are in places 600 feet high and in others are almost buried by the accumulation of talus and glacial débris. There are numerous faults running north and south, in general crossing the Holyoke Range at right angles and running almost parallel with the Mount Tom Range.

During the ice age the ice sheet passed over the region and left much glacial material on the north side of the range. As the ice retreated north a lake was formed here and another one on the south side. The one north of the range was called the Hadley Lake and the one south, the Springfield Lake.

The Hadley Lake found an outlet between Nonotuck and Titan's Pier (see map). Today the area is drained by the Connecticut River, which doubtless has occupied different portions of the lake bed, but now is cutting close to the east side of the Mount Tom Range (see map).

The region is being acted upon but little by stream erosion, as the streams are of small size. On the south side of the Mount Holyoke Range there formerly were 20 streams originating at an elevation of 400–500 feet, while on the north side there were 6 at that height. The many streams on the south side of the range were doing active erosion work along the fault lines, but the frequent deforestation has been instrumental in exhausting the streams, and as a result there are many ravines, young topographically but quite old floristically.

On the north side of the Mount Holyoke Range there are wide crevices in the cliff face due to the presence of faults, but below the cliff face the mountain side presents a uniform mass of talus and glacial débris. Along the talus below the wide crevices there is always a greater amount of moisture, where more of the "run off" on the north side of the range sinks into the talus than along the talus at the foot of the unbroken cliff face.

There is little bare rock exposed except on the cliff faces and at the edges of the highest peaks; there weathering is playing an active part. Small and large flakes of the trap rock are being split from the face. A great many of them pile up at the top of the talus slope and furnish splendid agents for catching the finer material which is washed down.

The vegetation is playing an active part in changing the physiographic features of the region.

Classification of successions

The initial biotic vegetative cycles are so determined by the original xerophytic and hydrophytic habitats, that I have classified the xerarch (1) and hydrarch successions in topographic terms as follows:

I. Xerarch successions: (1) trap slope successions; (2) trap cliff successions; (3) talus successions.

II. Hydrarch successions: (1) ravine successions; (2) brook successions.

All the region except the brooks has passed through several of the successions leading to the climax forest, and a small area is now in the beech-maple climax, which is the culminating stage of the region, while a little to the west of the range the hemlock forms the climax. There is, however, in this region some indication of the hemlock coming in as a climax type.

It is doubtful if there is any climax representing that of the so-called primary succession, which might well be called the initial succession. The region represents a third or fourth attempt to develop a climax forest, as do most of the New England forest areas. These successions have been called secondary successions, but might better be called repetitive successions, because the deforestation causes the area to revert to an aspect which is a combination of a former succession with the successions which ordinarily follow it. The term "secondary" does not carry with it the idea of more than one attempt at repetition, while "repetitive" indicates no limit in the number of attempts.

Mount Tom has been a state reservation for 10 years, and since then has been free from the retarding and retrogressing factor, man.

This biotic influence has interrupted successions on every topographic type, chiefly in the following ways: cutting, with or without burning, followed by cultivation, pasturing, or permitting the area to become of economic value without assistance from man.

This always retards the development of the area temporarily, although it soon assumes the aspect of some previously established type, modified by the interpolation of certain species, and it retains, unless burned over, remnants of the previously established types, especially among the herbs. These are of aid in the determination of the history of the region in regard to the activities of men and plants.

The plants are listed here under the great groups, making it possible to bear out NICHOLS' (3) statement that "species in groups of comparatively recent evolutionary derivation are far more restricted in range than species in groups of more recent origin." The spermatophytes are again divided into trees, shrubs, and herbs, to indicate more clearly the difference in biotic influence.

Xerarch successions

TRAP SLOPE

There is an east face and a south face; the former belongs to the Mount Tom Range, which has been a state reservation for 10 years, and which, it is hoped, will some day afford an opportunity of seeing in this region a climax forest of some extent.

There is no difference in the two slopes aside from the presence on the south face of more ravines; in these ravines cutting has ceased, as deforestation followed by fire has caused the drying up of streams, leaving the ravines young topographically. The entire region has been cut over within the last 25 years. At the top the vegetation is again getting a foothold on the rock outcrop, except at the edge, along the fault lines; here there is young tree growth, in which can be found old stumps of red oak three feet in diameter, indicating how far the region had progressed in its development.

On the rock outcrop are found the following:

Spermatophyta: Herbs.—*Carex rosea*, *Aquilegia canadensis*, *Corydalis sempervirens*, *Arabis Drummondi*, *Saxifraga virginiensis*, *Arctostaphylos Uva-ursi*, *Cardamine parviflora*.

Pteridophyta: *Woodsia Ilvensis*, *Selaginella rupestris*.

Bryophyta: *Umbilicaria* sp., *Ceratodon purpurea*, *Physcia* sp.

A few feet below the rock outcrop are found the following:

Spermatophyta: Trees.—*Juniperus virginiana*, *Carya alba*, *C. ovata*, *Quercus alba*, *Q. rubra*, *Q. Prinus*. Shrubs.—*Quercus prinoides*, *Amelanchier canadensis*, *Pyrus arbutifolia*, *Cornus circinata*, *Vaccinium stamineum*, *V. cassinoides*. Herbs.—*Maianthemum canadense*, *Polygonatum biflorum*, *Hypoxis hirsuta*. New ferns are *Aspidium marginale*, *Polypodium vulgare*, and *Polystichum acrostichoides*.

Where the faults are at right angles to the range, the rock cliff has been worn away and the edges take on a rounded form. Here the trees have been established longer and are about three inches in diameter. There is found the same grouping as is found a hundred feet below the top of the trap rock slope, with the addition of *Castanea dentata* and *Acer saccharum* as seedlings. The new shrubs are *Diervilla Lonicera* and *Viburnum acerifolium*, while the spermatophytic herbs are *Uvularia perfoliata*, *Thalictrum dioicum*, *Hepatica triloba*, *Anemone quinquefolia*, and *Aralia nudicaulis*. The ferns are *Pteris aquilina*, *Asplenium Trichomanes*, and *Cystopteris bulbifera*.

The lower half of the slope, though cut at the same time, has advanced much more rapidly. Wherever there is a trap rock outcrop the bryophyte and pteridophyte vegetation is found, and about it the spermatophytes just mentioned, but the trees are larger and the following additional species have come in: *Fagus grandifolia* as a seedling, with occasional plants of *Tilia americana* and *Fraxinus americana*. The shrubs are *Hamamelis virginiana*, *Dirca palustris*, *Cornus florida*, and *Viburnum dentatum*. Characteristic spermatophytic herbs are *Arisaema triphyllum*, *Habenaria Hookeri*, *Habenaria bracteata*, *Actaea rubra*, *Pyrola elliptica*, *Lysimachia quadrifolia*, *Orobanche uniflora*. The ferns are *Pteris aquilina*, *Polystichum acrostichoides*, *Dicksonia punctilobula*, and *Asplenium acrostichoides*.

The base of the trap slope has now on it every type of repetitive succession except that of cut-over beech forests. Places untouched for the longest time show the dominance of chestnut. Red oak and white oak stumps 4 feet and 5.5 feet in diameter indicate that the region was allowed to pass at least through the oak succession, and chestnut 2 feet in diameter with hard maple 1 inch in diameter show that it is the day of the chestnut with the promise of hard maple later. Old landmarks of hard maple and chestnut give evidence of a previous attainment of that stage of succession, which appears to be the temporary climax of the east and south slopes.

TRAP CLIFF

The cliff is of greater height on the west side of Mount Tom than on the north side of Mount Holyoke. The numerous faults on Mount Holyoke run at right angles to the range, and the more active erosion along the fault lines increases the amount of talus. This, in addition to the glacial drift deposited on the north side, accounts for the talus reaching the top of the mountain and burying the cliff face, except for short spaces between the fault lines. On Mount Tom the faults are fewer and run parallel with the cliff face, and the glacier left no deposit except at the Nonotuck end (see map).

A lichen flora, yet undetermined, is established on most of the cliff, *Umbilicaria* playing a conspicuous part. The rock flakes off so rapidly that it is doubtful if any later vegetation is established. Often before the lichens are established the rock flakes off and is added to the talus below. The talus is made up of large flakes with or without lichens upon them.

The crevices and shelves afford a more permanent foothold and conifers have become established here, so that from a distance the mountain side appears to be rather well covered with trees.

The following species are found in crevices, and on shelves of the east-facing cliff: Spermatophyta: Trees.—*Juniperus virginiana, Pinus Strobus, Pinus resinosa, Tsuga canadensis.* Herbs.—*Saxifraga virginiensis, Corydalis sempervirens, Campanula rotundifolia.* Pteridophyta: *Woodsia Ilvensis, Asplenium Ruta-muraria.* Bryophyta: *Hedwigia albicans, Grimmia apocarpa.*

The cliff represents, if do any of the regions, the first of the initial successions. The first stages in the group of initial successions on the north face and the east face are the same, but the second stages are different. The many shelves found on the east side offer a place for more rapid accumulation of soil; junipers, pines, and grey birches come in, while on the north face *Tsuga canadensis* gets a foothold in the crevices.

The pines and the hemlock seem to represent a temporary climax until the edaphic situation becomes altered.

TALUS SUCCESSION

At the west side of the Mount Tom Range the talus is made up of trap flakes alone, while on the north side of the Mount Holyoke Range it is composed of trap and glacial drift. In each case trees and undergrowth are established on the entire talus except where patches of rapidly weathering rock have covered all but tree growth; in such places birch or butternut may be seen growing in the midst of an island of trap chips. At the base of Mount Holyoke, where the glacial drift is associated with trap chips, the soil is far more stable and is covered with herbaceous forms.

Shrubs and vines advance up the slope at the base of the cliff, with the assistance of a little lichen or moss growth. At the top of the talus, which is made up of clean trap chips, an interesting advance is made by the plants with creeping stems and rootstocks, *Rhus Toxicodendron*, *Psedera quinquefolia*, and *Vitis aestivalis*.

The talus on the north side of Mount Holyoke presents an almost unbroken slope except at the top. As the fault lines extend across the trap face, short ravines have been formed at the head of the ravines of the trap slope. Here the drainage divides to the north and south and the north face receives more moisture below these short ravines. This unequal amount of moisture together with the greater amount of shade, due to the projecting sides of the trap ravines, affects the vegetation for about 50 feet along each fault, and below this the talus assumes a uniform aspect.

In a short ravine facing north are found: Spermatophyta: trees over a foot and a half in diameter, *Tsuga canadensis*, *Betula alba*, *B. lutea*, and *B. lenta;* trees about an inch in diameter, *Ostrya virginiana*, *Quercus rubra*, *Q. alba*, and *Carya ovata;* there are a few seedlings of *Acer saccharum;* and scattering shrubs of *Hamamelis virginiana*, *Acer spicatum*, and *Viburnum acerifolium* are found. The spermatophytic herbs are *Maianthemum canadense*, *Senecio aureus*, *Polygonatum commutatum*, *Aralia nudicaulis*, and *Mitchella repens*. The Pteridophyta are *Adiantum pedatum* and *Lycopodium lucidulum*.

Where the slope is uniform are found: *Betula lenta*, *B. alba*, *Juglans cinerea*, *Fraxinus americana*, *Quercus rubra*, *Q. alba*, *Q. Prinus*, *Carya alba*, and *Castanea dentata*, all over a foot in diameter. Old stumps of *Tsuga canadensis* and isolated specimens of *Pinus rigida* and *Pinus Strobus* tell of the history of the slope. *Acer saccharum* of small size prophesies the future of the slope if it is left to itself. The following shrubs, *Kalmia latifolia*, *Acer spicatum*, *Cornus florida*, evidence better conditions for growth, as do also the herbs *Uvularia perfoliata*, *Trientalis americana*, *Trillium erectum*, and *Maianthemum canadense*. The Pteridophyta are represented by *Adiantum pedatum*, *Osmunda cinnamomea*, *Dicksonia punctilobula*, and *Polystichum acrostichoides*.

The chestnut–red oak–white oak–hickory stages seem to be telescoped (2) on the north side, while on the south face the stages are distinct.

The talus on the north side below this grouping has much hard maple and many young beech trees 10 inches or more in diameter. Whether it is or is not a question of more frequent deforestation on the one side than on the other, it is true that the beech is far more common on the north side. In some places there are beech trees three feet in diameter with an undergrowth of young beech and hemlock; while on the east-facing talus and on the south-facing trap rock, as well as on the north, old stumps of hard maple and chestnut three feet in diameter are common, but there is no indication of beech coming in other than occasional one-inch saplings.

Herbs show a quicker reaction to environment and are more rapid indicators of changing conditions than trees. The spermatophytic herbs found near the base of the slope are *Uvularia perfoliata*, *Erythronium americanum*, *Trillium sessile*, *T. erectum*, *T. cernuum*, *Orchis spectabilis*, *Habenaria bracteata*, *Epipactis repens*, *Actaea rubra*, *Dicentra Cucullaria;* and the Pteridophyta, *Phegopteris Dryopteris*, *P. polypodioides*, *P. hexagonoptera*, *Adiantum pedatum*, *Aspidium spinulosum*, *Cystopteris fragilis*, and *Botrychium virginianum*.

There is an indication of the hemlock coming in twice in the succession, first in the early stages of the ravines as a temporary climax, and later at the climatic climax of the region as shown in the successions on the north talus slope. The white pine does much the same thing, forming a temporary climax on the east-facing cliffs and a temporary climax on the lake bottom sands, which are at the foot of the talus slope. There are many places just south of the range along the old lake shore where the pine remains established for some time. It looks as if the region had reached the pine stage many times; now conditions are such that the region is advancing a stage and oaks and chestnut are beginning to get a foothold. The accompanying diagram in a general way indicates the natural successions and the effect of repeated deforestation.

Hydrarch successions

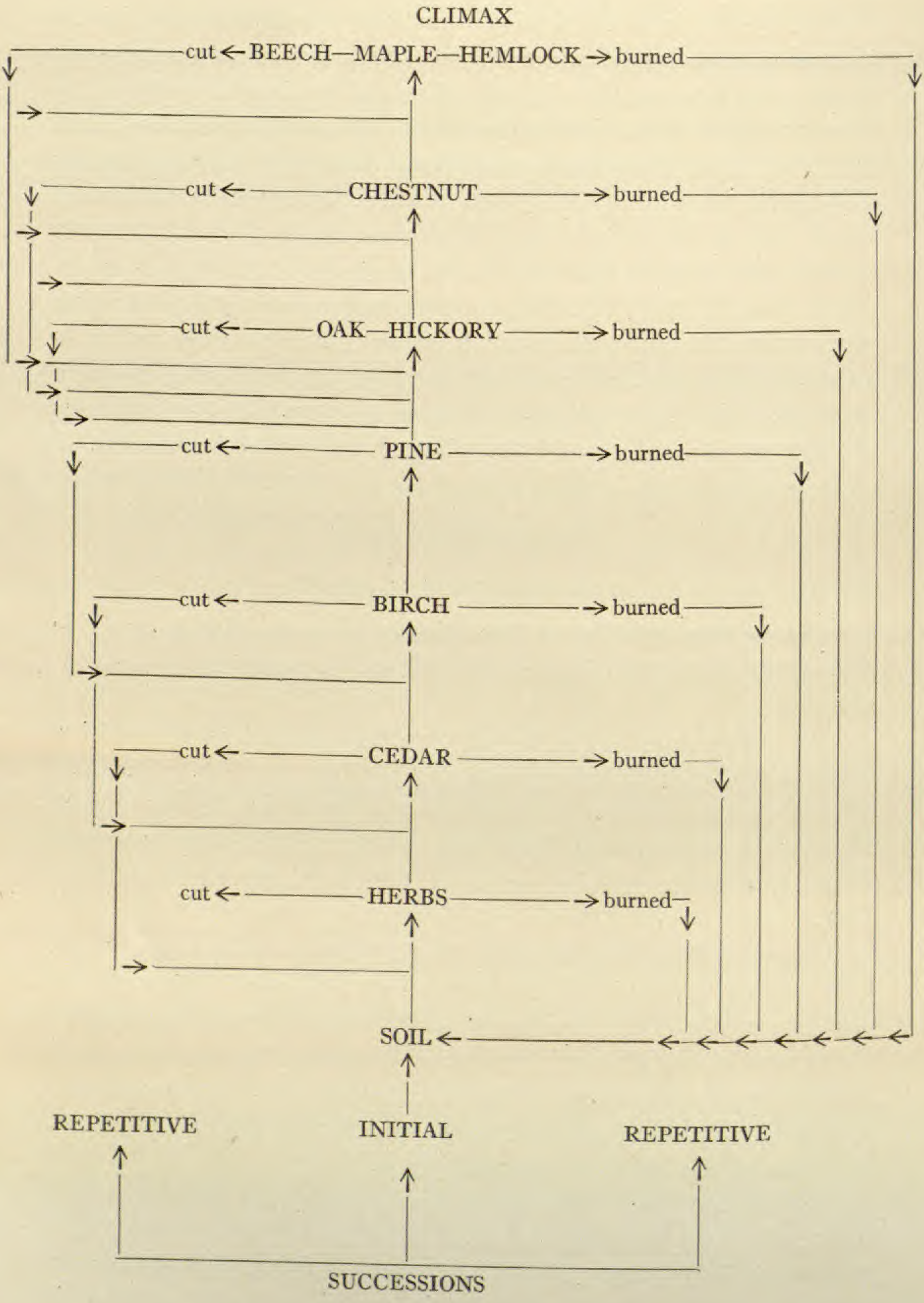
RAVINE SUCCESSIONS

The ravines parallel to the Mount Holyoke Range and the ravines on the south trap face of Mount Holyoke are to be considered.

The parallel ravines on Mount Tom have been formed by differential weathering and never had any streams in them. The rock sides are perpendicular and have no vegetation but lichens, except for a few crevice plants. The base of the ravine is covered with trap chips among which vines and a few shrubs are getting a foothold.

The ravines on the trap slope are no longer being actively cut. The rapidly repeated deforestation has exhausted many of the streams, so that there are found many ravines young topographically but old floristically. In the early spring the melting snows drain down these ravines. Other ravines are older topographically and have wide sides, which are the same floristically as the adjoining slope of the range at the same level.

In a ravine from which water has recently been withdrawn can be found *Tsuga canadensis*, *Pinus Strobus*, *Juglans einerea*, *Tilia americana*, *Betula lenta*, *B. lutea*, *Castanea dentata*, *Acer saccharum*, and some very young *Fagus grandifolia*. Time enough apparently


CLIMAX
cut
BEECH—MAPLE—HEMLOCK
burned
cut
CHESTNUT
burned
cut
OAK—HICKORY
burned
cut
PINE
burned
cut
BIRCH
burned
cut
CEDAR
burned
cut
HERBS
burned
SOIL
REPETITIVE
INITIAL
REPETITIVE
SUCCESSIONS

has passed in the ravine formation to permit the passing of the succession to *Fagus grandifolia.*

A young ravine on the south side in which cutting has long since ceased contains many of the same forms showing a slow succession.

THE BROOK

The brooks are fast passing out of existence in the vicinity of the range, so that mention is made only of the plants found in the brook and on its immediate banks. The trees are *Ulmus americana* and *Acer rubrum;* the shrubs, *Alnus incana, Benzoin aestivale, Ilex verticillata, Vitis Labrusca, Cornus stolonifera,* and *Dirca palustris;* the herbs, *Thaspium aureum, Caltha palustris,* and *Symphoricarpus foetidus.* This is soon followed by a heavy growth of *Carpinus caroliniana,* with *Betula lutea, B. lenta,* and *Fraxinus americana.* These pave the way for oaks and hickories.

Summary

1. The region is a mountain range of trap rock.

2. The climax forest of the region is of the beech-maple-hemlock type.

3. The successions may be classified as:

I. Xerarch successions: (1) trap slope successions; (2) trap cliff successions; (3) talus successions.

II. Hydrarch successions: (1) ravine successions; (2) brook successions.

4. The terms initial and repetitive seem to be better than primary and secondary in conveying the idea of often-repeated successions such as are found in a frequently deforested area.

5. The east-facing and the south-facing trap slopes have the same successions. *Castanea dentata* seems to present a temporary climax.

6. The trap cliff doubtless presents an initial succession in which the east and north cliffs have similar first stages, but the second stage on the east is *Pinus Strobus* and *Pinus resinosa,* while on the north it is *Tsuga canadensis.*

7. The combination of weathered rock with glacial drift on the north talus slope affords a better opportunity for the climax formation than does rock alone on the talus east of Mount Tom.

8. Repeated deforestation has prevented all. but a small area from reaching the climax.

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MOUNT HOLYOKE COLLEGE

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3. NICHOLS, G. F., The vegetation of Connecticut. Torreya **13**:89–112. 1913.

HISTOLOGY OF FLAX FRUIT

KATE BARBER WINTON

(WITH FOUR FIGURES)

Flax (*Linum usitatissimum* L.), although grown throughout the temperate zone for its fiber, is valuable as well for its seed, which yields the well known linseed oil, the residue being used as a cattle food. The chaff from the threshing of the seeds, consisting of broken pods and stems with varying amounts of immature and broken seeds, has of late come into the cattle food market under the name "flax bran."

The histology of the fiber is described by VON HÖHNEL,[1] HANAUSEK,[2] and other technical microscopists, and that of the seed by writers on the microscopy of foods and drugs,[3] but the elements of the pericarp appear to have escaped attention except for brief mention by COLLIN and PERROT,[4] with whom the present writer does not entirely agree.

FIG. 1.—Dehiscing fruit with sepals; × 2.

The yellowish pods (fig. 1), 8 mm. in length, are slightly broader than long, with five pointed sepals and a slender pedicel. Each of the five locules is incompletely halved by a false dissepiment, making a 10-celled fruit which dehisces at maturity into ten valves. Each cell contains a single flattened, shining, brown, mucilaginous seed.

CALYX.—The *outer epidermis* consists of longitudinally elongated cells with wavy walls and simple stomata. The cuticle has faint longitudinal striations.

Mesophyll.—Several layers of simple parenchyma cells, through which runs a network of small bundles, form the mesophyll.

The *inner epidermis* is similar to the outer.

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[1] Die Mikroskopie der Technisch Verwendeten Faserstoffe. Wien, 2 Aufl. 1905. p. 42.

[2] Microscopy of technical products. Trans. by WINTON. New York. 1907.

[3] See bibliography in WINTON, Microscopy of vegetable foods. New York. 1906. p. 204.

[4] Les résidues industriels. Paris. 1904. p. 202.

PEDICEL.—The *epidermis* is made up of longitudinally elongated rectangular cells with straight, pitted walls. Occasional simple stomata are present.

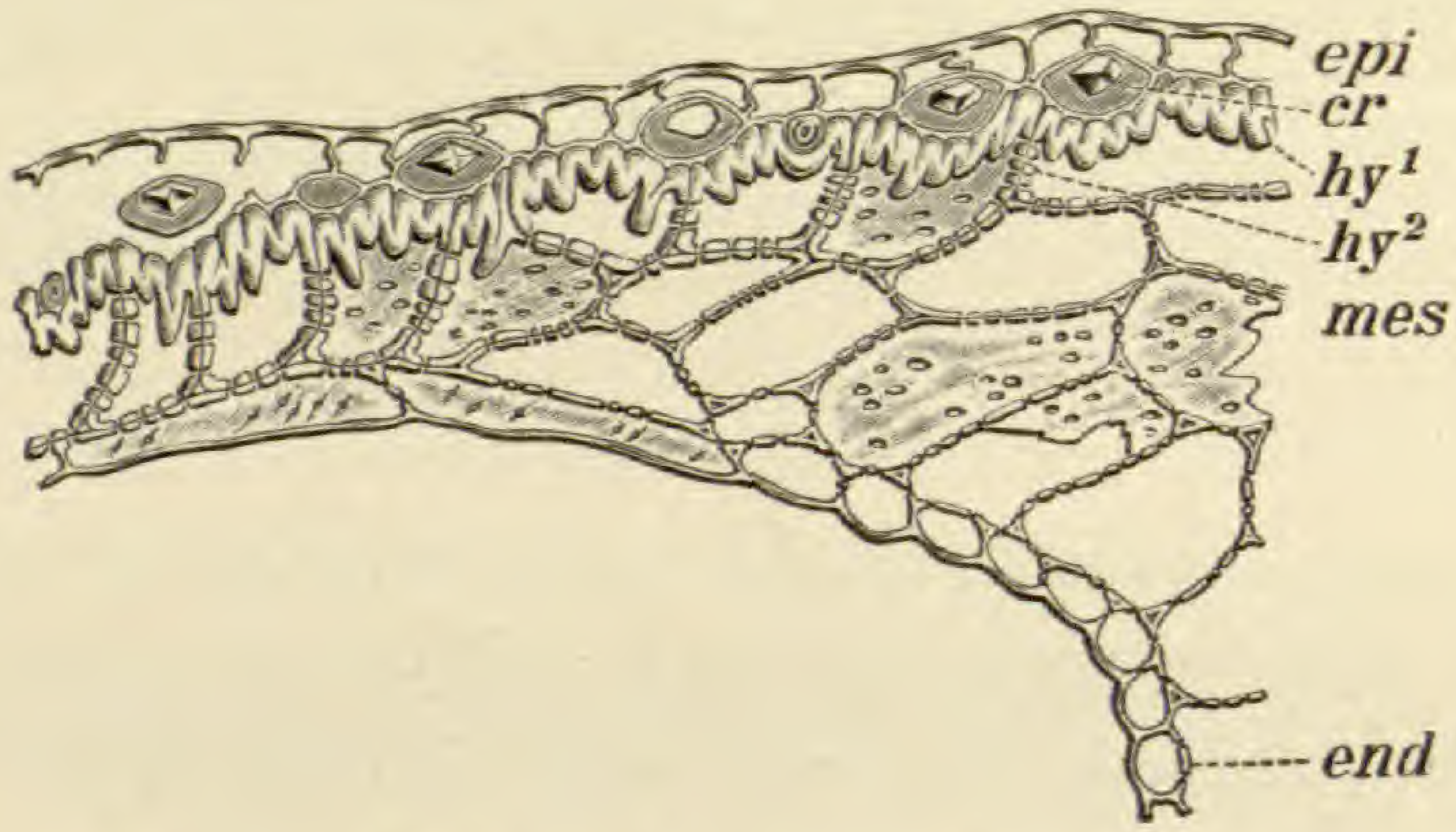

FIG. 2.—Pericarp in cross-section: *epi*, epicarp; *cr*, crystal cells; hy^1, projections of hypoderm; hy^2, hypoderm; *mes*, mesocarp; *end*, endocarp; ×160.

Subepidermis.—A few layers of small thin-walled parenchyma form this tissue.

Bast.—The conspicuous elements constituting the bulk of the pedicel are the bast fibers. They are greatly elongated thick-walled cells with occasional characteristic cross-striations resembling joints, and conform in general structure to the bast fibers of the stem, which yield the linen of commerce.

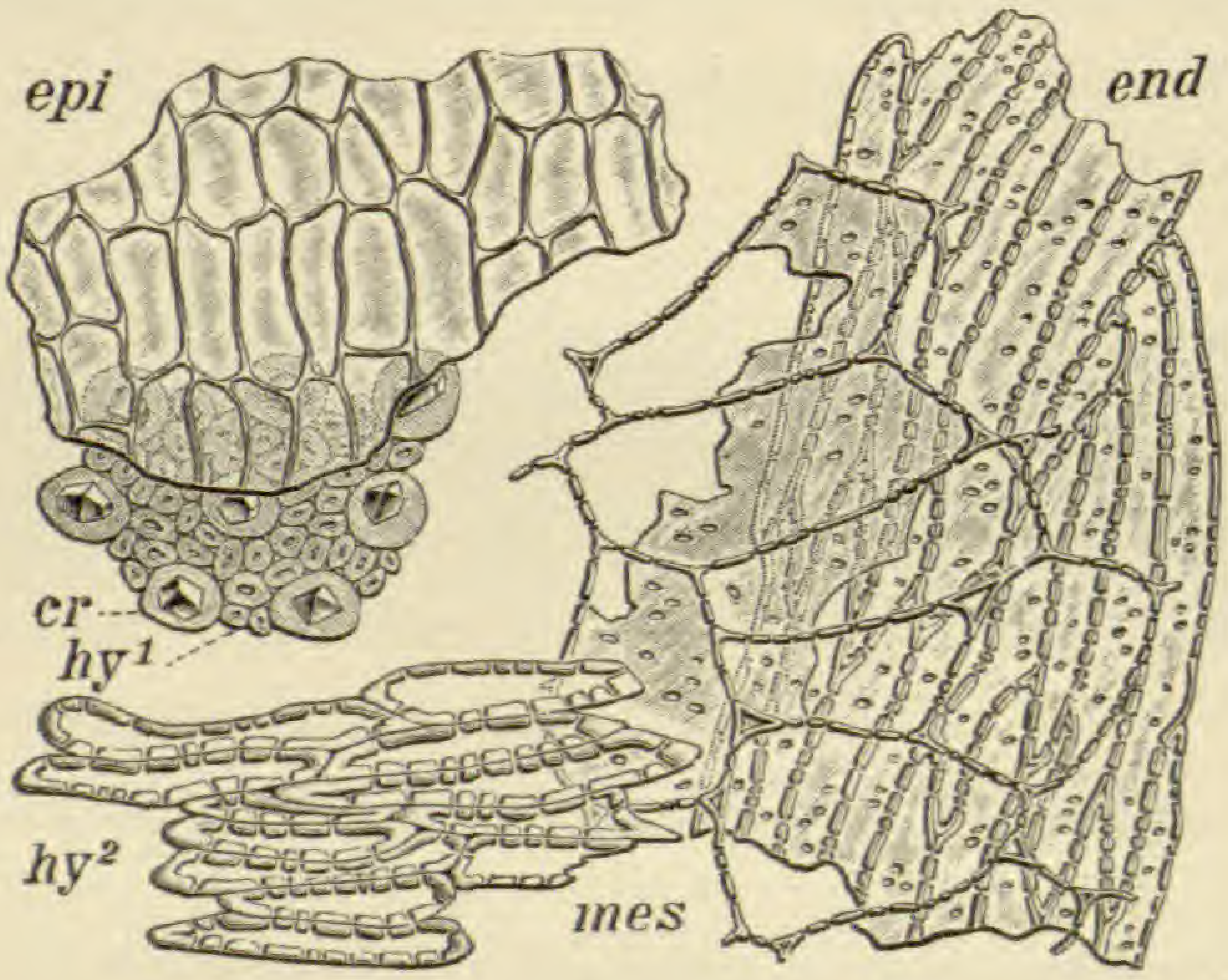

FIG. 3.—Elements of pericarp in surface view: *epi*, epicarp; *cr*, crystal cells; hy^1, projections of hypoderm; hy^2, hypoderm; *mes*, mesocarp; *end*, endocarp; ×160.

The *xylem* contains spiral and pitted vessels, wood fibers, and parenchyma cells without distinctive features.

None of the tissues of the calyx and pedicel is of especial diagnostic importance.

PERICARP (figs. 2 and 3).—The *epicarp* (*epi*) consists of a single layer of collapsed cells whose outlines are found most easily in surface view. They are frequently longitudinally elongated to about twice their width, have straight thin walls, and occasionally yellowish contents which harden at maturity, retaining the shape of the confining cell walls. COLLIN and

PERROT (*loc. cit.*) describe crystals in this layer, but the writer finds them in an interesting tissue below the epicarp.

Crystal cells (*cr*).—Resting on the hypoderm and more or less separated by its projections is a strikingly characteristic tissue one cell in thickness, consisting of isolated compressed spherical or lens-shaped cells arranged in indistinctly longitudinal rows. The light brown inner and side cell walls are so thickened that the cell contents, consisting of a single monoclinic crystal (about 13 μ), completely fill the lumen. On sectioning, the crystal usually escapes through the thin outer wall.

The *hypoderm* (*hy*^{1} and *hy*^{2}) is yellowish in color, pitted, and greatly thickened, with numerous projections of the outer wall pushing up under and between the isolated crystal cells. In tangential sections through the outer walls these projections (fig. 3, *hy*^{1}) appear like another layer of small, more or less spherical cells. The cells are transversely elongated over the greater part of the valve, changing abruptly to a longitudinal arrangement at the sutures.

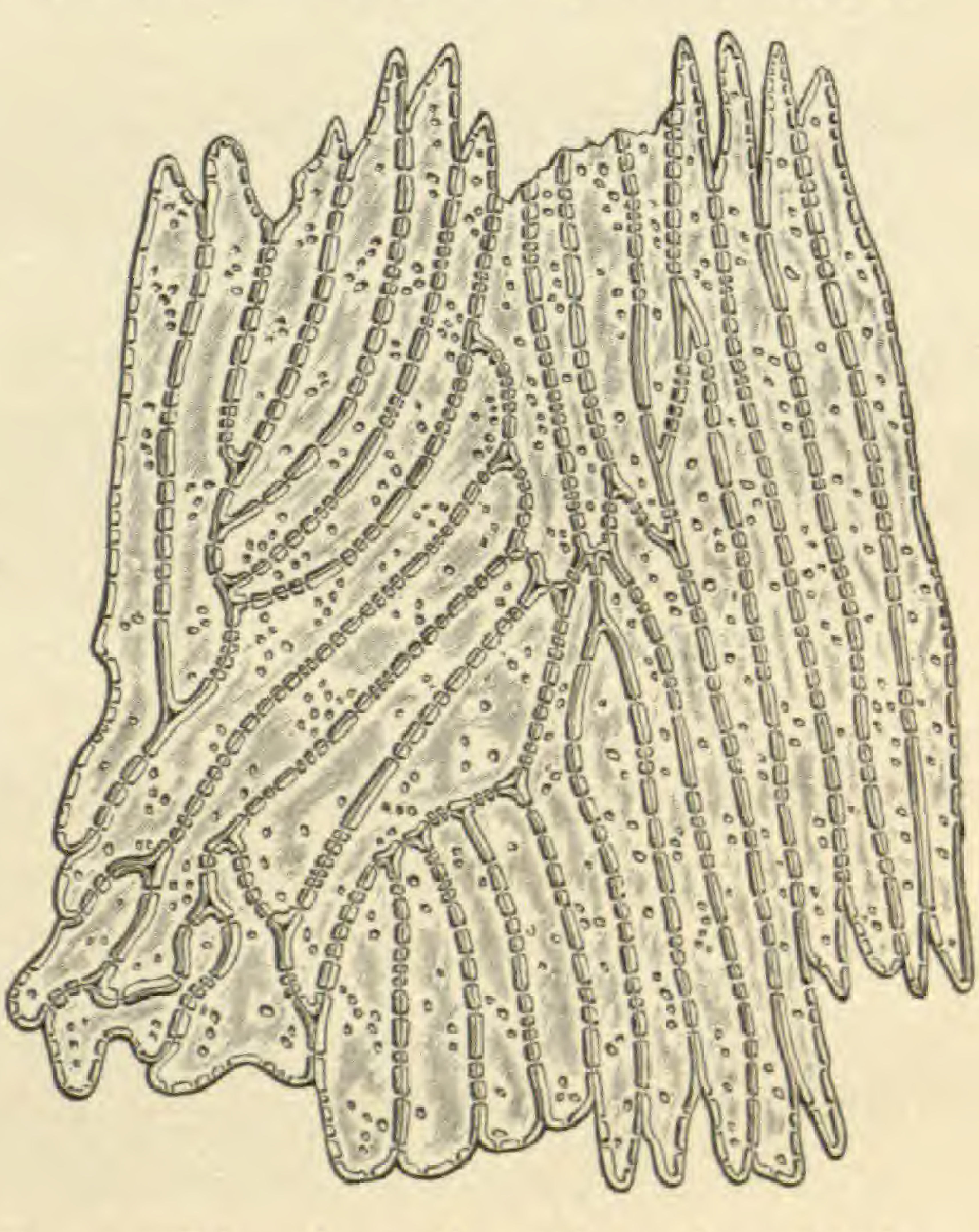

FIG. 4.—Dissepiment in surface view; × 160

The *mesocarp* (*mes*) varies greatly in thickness. At the thin center of the valve it is frequently lacking, but becomes a thick mass of cells along the juncture with the dissepiment. The cells have slightly thickened pitted walls, except those adjoining the hypoderm, which may be thicker. Cell contents are usually lacking though occasionally small starch grains are present indicating slight immaturity.

Endocarp (*end*).—The single layer of pitted, strongly elongated cells, arranged side by side in groups, is similar to the epidermis of the dissepiment, with which it forms one continuous tissue, the only noticeable difference being that the cells are somewhat smaller.

DISSEPIMENT (fig. 4).—This transparent papery tissue at once attracts attention, being made up of two parquetry-like epidermal layers of elongated, pitted cells between which is an inconspicuous empty parenchyma. The cells of one epidermis frequently cross those of the other, which at once distinguishes the dissepiment from the endocarp. The walls are approximately straight except at the free edge of the dissepiment, where they become sinuous, acquiring beautiful irregular shapes. The contour of the cell varies greatly with the focus, owing to irregularities of the end walls.

CHARACTERISTIC ELEMENTS.—The tissues which are of chief value in the identification of flax fruit in ground products, such as mixed cattle feed, are the elongated, thick-walled cells of the hypoderm with projections (figs. 2 and 3, hy^1), the accompanying cells each containing a single crystal (*cr*), and the transparent dissepiments with elongated cells (fig. 4), those of the two epidermal layers often crossing at an angle.

All of these tissues are quite different from the elements of any other material likely to be encountered.

WASHINGTON, D.C.

CURRENT LITERATURE

BOOK REVIEWS

The vegetation of Lake Constance

An admirable illustration of the intensive study inspired in his students by SCHRÖTER is found in the elaborate and thorough monograph on the vegetation of the Untersee by BAUMANN.[1] The Untersee is one of the lower arms of Lake Constance on the border of Germany and Switzerland, it being through this arm that the Rhine leaves the lake. After an account of the geology, geography, and hydrography, BAUMANN gives a most interesting account of the different sorts of calcareous deposits, which here take an unusually important part in soil formation, as noted years ago by HONSELL. Calcareous tuffs are formed in extensive amount through the agency of algae. These organisms withdraw carbon dioxide from the calcium bicarbonate in the waters, and the remaining calcium monocarbonate is deposited about the algae as a crust. Later the plants die, leaving only the incrusting masses. In time these processes result in the formation of extensive banks, of which the inner layers are dead, whereas the outer layers contain living algae; these banks, therefore, are precisely comparable to coral reefs. At times the calcareous deposits are in grains, each grain representing the stratified calcareous accumulations about an alga. The Island of Langerain has been formed mostly in this manner. It is thought that these calcareous deposits have been accumulating continuously since the ice age, and they are still accumulating.

The great body of the work is devoted to a detailed study of the species ecology of the characteristic plants. This represents a vast amount of valuable work, which will be of first importance to all students of the vegetation of lakes and swamps. A chapter is devoted to the plant associations, which are of the usual sort for such habitats. Only the larger plants are discussed here, the plankton and the profundal benthos being omitted. The associations are considered under three main heads: the littoral benthos ("Uferflora"), the pleuston, and the "Grenzflora" (that is, the flora between low and high water). These main divisions are of course subdivided. The subdivisions of the littoral benthos from deep to shallow water (also in the successional order) are the Characetum, the Potametum, the Nupharetum, the Scirpetum, and the Phragmitetum. It is of interest to note that these associations are still almost entirely natural, in spite of the many centuries of human occupation of the region. The work closes with a short floristic chapter.—H. C. COWLES.

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[1] BAUMANN, EUGEN, Die Vegetation des Untersees (Bodensee), eine floristisch-kritische Studie. pp. v+554. *pls. 15. figs. 31.* Stuttgart: E. Schweizerbartsche Verlagsbuchhandlung. 1911.

MINOR NOTICES

North American Flora.[2]—The first part of volume 10 presents 10 genera of the white-spored series of the tribe Agariceae. The species number 281, of which 39 are new. The largest genus is *Melanoleuca*, with 119 species, 24 of which are new, and 65 transferred from other genera, chiefly *Agaricus* and *Tricholoma*. The other large genera are *Lepiota*, with 88 species, 10 of which are new, and *Venenarius*, with 26 species, 2 of which are new. There are also 3 new species in *Cortinellus*.

The first part of volume 29 presents five of the eight families of Ericales, 281 species being recognized, 50 of which are new. New genera are described in Monotropaceae (*Pityopus*) and Ericaceae (*Therorhodion*, *Oreocallis*, and *Ornithostaphylos*). New species are also described in *Clethra* (7), *Hypopitys* (1), *Pleuricospora* (1), *Newberrya* (1), *Pyrola* (2), *Ramischia* (1), *Chimaphila* (6), *Ledum* (1), *Azalea* (1), *Kalmia* (1), *Kalmiella* (1), *Cassiope* (1), *Andromeda* (1), *Xolisma* (5), *Gaultheria* (10), *Arbutus* (1), *Comarostaphylis* (6), and *Arctous* (1). The large genera of Ericaceae, as now organized, are *Xolisma* (24 spp., mostly from *Lyonia*), *Gaultheria* (24 spp.), *Uva-ursi* (24 spp., mostly transfers), and *Comarostaphylis* (22 spp., mostly from *Arctostaphylos*).—J. M. C.

Icones Bogorienses.—The fourth volume of this work, dealing chiefly with plants of Java and Borneo, is completed by the fourth fascicle,[3] which presents 3 species of Zingiberaceae, one each of Burmanniaceae, Euphorbiaceae, and Ericaceae, and 19 species of Rubiaceae, each species illustrated by a plate. New species are described in *Burmannia* (1), *Antidesma* (1), *Rhododendron* (1), *Lerchea* (1), *Argostema* (3), *Andina* (1), and *Acranthera* (8).—J. M. C.

NOTES FOR STUDENTS

The xeromorphy of marsh plants.—A study of great interest and thoroughness is reported by YAPP,[4] who has for some years been investigating the ecology of marsh plants. He has made an intensive study of the species ecology of *Spiraea Ulmaria*, carrying on many experiments, as well as making many field observations. The fundamental importance of carrying on many such studies cannot be emphasized too strongly. In this species all leaves formed during the first year are glabrous; on older plants the leaves become

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[2] North American Flora **10**: part 1. pp. 76, Agaricaceae (pars), by W. A. MERRILL; and **29**: part 1. pp. 102, Ericales, by J. K. SMALL; Clethraceae, by N. L. BRITTON; Lennoaceae and Pyrolaceae, by P. A. RYDBERG; Monotropaceae and Ericaceae, by J. K. SMALL (*Uva-ursi* by LEROY ABRAMS). New York Botanical Garden, 1914.

[3] Icones Bogorienses **4**:239–294. *pls. 376–400.* Leide: Jardin Botanique de l'État. 1914.

[4] YAPP, R. H., *Spiraea Ulmaria* L., and its bearing on the problem of xeromorphy in marsh plants. Ann. Botany **26**:815–870. *pls. 3. figs. 11.* 1912.

progressively hairy from the base to the top. On non-flowering shoots, however, the later leaves, like the earlier, are glabrous. On partially hairy leaves the terminal leaflet is invariably the most hairy, and there is a regular decrease in hairiness downward. Although it is more conspicuous in *Spiraea Ulmaria*, this seasonal periodicity in hair formation was found in many other plants. The lower glabrous leaves have the structure of shade leaves, whereas the upper leaves may be called sun leaves. While the xeromorphic upper leaves have more stomata per unit area, the size of the aperture is less. Correspondence is found between hair production and evaporation curves, both seasonally and in height above the soil. *Spiraea* is found to be less plastic, however, in respect to hairiness than are various plants previously reported (e.g. *Mentha aquatica* and *Polygonum amphibium*). It was found impossible to make the early leaves hairy or the later leaves smooth. The first parts to wither are those that are hairy. As to cause, hair production may be related to heredity, individual variation, or external factors. Of the latter it is believed that a diminished water supply is the most important. YAPP believes that *Spiraea Ulmaria* is becoming fixed as to the presence or absence of hairs; already the glabrous condition of the early leaves is a fixed character, and the hairiness of the later leaves is tending to become fixed. He concludes that xeromorphy is of physiological utility to those bog and marsh plants which exhibit it, but that no one factor can be singled out as of sole importance in determining xeromorphy. The physiological dryness of the soil is important, but it does not explain everything. For example, the presence of hygrophytic and xerophytic species side by side is likely to be explained by differences in transpiration, the xerophytic species generally being more exposed to severe transpiration.—H. C. COWLES.

Low temperature and plant tissues.—CHANDLER[5] has treated in considerable detail the killing of plant tissues by low temperature. He discusses the nature of injury by low temperature, giving a good summary of the literature relating to this subject. In his experiments he has shown that the killing temperature of many plant tissues may be reduced by means which increase the sap density; for example, intake of potassium chloride, glycerine, etc., or partial withholding of water. Rapidity of thawing had little effect on the amount of killing at a given temperature in case of all tissues experimented upon except that of ripe fruit of apple and pear. Previous exposures to low temperatures lowered the death point. In case of hardy winter buds and wood, a rapid fall of temperature increased the severity of injury. In fruit trees during early winter the wood at the base of the trunk and at the crotches of rapidly growing branches was found most susceptible to injury. At the stage of most complete maturity, the pith cells and fruit buds were most tender of all the above ground tissues. The hardiness of root tissue was found in general

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[5] CHANDLER, W. H., The killing of plant tissues by low temperature. Research Bull. Agric. Exper. Sta. Univ. Mo. no. 8. pp. 143–309. *figs. 3.* 1913.

to vary indirectly with the distance from the crown. Roots of French crab, so extensively used in America as stock, are less hardy than roots from scions of an average variety of apple. It is of considerable interest to note that heavy dormant pruning, thinning of fruit, and application of nitrate fertilizers prolonged the growth period, lengthened the rest period, and consequently reduced the early forcing of growth in spring with subsequent injury by late frosts. The selection of trees with long rest period also helps to obviate the latter injury. Of apple blossom tissue, the pollen was found most resistant to low temperature.

The work presented in this bulletin is of such a character as to be of great interest alike to those engaged in "pure" science and to those whose chief interest is in the applied side.—L. I. KNIGHT.

Mitosis in Tetraspora.—In the green alga *Tetraspora lubrica*, MCALLISTER[6] finds that mitosis, so far as can be made out from the very small nuclei, corresponds in its essential features with that in higher plants. In the cell which is to give rise to 8 gametes, the resting nucleus contains a reticulum with net knots and a nucleolus. During the prophases, the reticulum develops chromatic bodies which apparently become arranged in a row to form a spirem thread. The nucleolus takes no part in this process. The spirem segments to about 13 chromosomes, which divide and pass to opposite poles. Details of spindle-formation were not made out, but there was found no reason to believe that *Tetraspora* differs from higher plants in this respect. Centrosomes or centrospheres, which might be expected on account of their reported presence in the gamete-forming cells of certain bryophytes, were not found. Cell-division is brought about by the splitting of a granular cell plate formed by the central spindle. The splitting takes place from the center outward.

The second and third mitoses follow quickly, but in each case the daughter nuclei enter the resting stage. The single pyrenoid of the original cell remains unchanged through the three divisions, so that it comes to lie in only one of the 8 gamete cells. In each of the other 7 cells one appears to arise *de novo* from the cytoplasm. The entire pyrenoid is said to fragment to form several starch bodies.

Since *Tetraspora* and other green algae resemble higher plants so closely in mitosis and differ so widely from the Euglenidae, the theory that the Chlamydomonadaceae, to which *Tetraspora* is held to be so closely related, have arisen from the Euglenidae is believed by MCALLISTER to be excluded.—L. W. SHARP.

Mitosis in Preissia.—In many papers dealing with mitosis in liverworts, attention has been focused chiefly upon the centrosome and related structures.

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[6] MCALLISTER, F., Nuclear division in *Tetraspora lubrica*. Ann. Botany 27: 681–697. *pl. 56.* 1913.

In a study of *Preissia commutata*, Miss Graham[7] has emphasized the behavior of the chromatin. In the vegetative cells of the gametophyte, the earliest prophase is marked by an elongation of the nucleus and the appearance of large chromatin masses on the linin strands. These strands thicken, forming a spirem upon which the chromatin is borne in the form of chromomeres. The spirem shows a temporary contraction, after which it segments to form 8 chromosomes. The disappearance of the nucleolus is sudden and coincident with the appearance of the central spindle fibers, which suggests a material relationship between these structures. At telophase the chromosomes elongate to slender threads which lose their individuality in the reticulum of the daughter nuclei.

In the spore mother cell the reticulum gives rise to a leptonema spirem. Many threads lie side by side, but whether this represents a parallel conjugation or is without special meaning was not determined. Synizesis ensues. After the knot loosens up, the spirem thickens and for a time the chromomeres become more prominent. During a second contraction the spirem splits longitudinally and soon segments to form the bivalent chromosomes. The further behavior presents no unusual features.

In both somatic and heterotypic prophases there are hyaline caps at the poles of the nucleus, and in them, at least in the former case, the spindle fibers are formed. Centrosomes or centrospheres were not found at any stage.—L. W. SHARP.

Plant breeding in Sweden.—On account of the important practical results obtained at the Svälof Institute, as well as because of contributions to the science of heredity resulting from the extensive and exact investigations carried on at this station, an authentic account of its history, ideals, and methods coming from an authoritative source is especially welcome. The present director, NILSSON,[8] sketches briefly the origin of the organization, emphasizing the object, which was to arrive at absolutely practical results, and giving in some detail the sources of its income. In the development of methods, attention is directed to the comparatively small results coming from "selection in mass" as practiced up to 1891, when "pedigree culture" was introduced. Thus the method of isolating and studying pure lines derived from a single individual was practiced at the Svälof station for ten years before it was advocated by DE VRIES in his *Die Mutationstheorie* in 1901. With the adoption of this radically new method, results have been more abundant. NILSSON emphasizes the fact that the isolation of elementary species is only a preparatory auxiliary for getting out properly the material to be utilized, the essential thing being testing the practical value of the material and making the best selections. To

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[7] GRAHAM, MARGARET, Studies in nuclear division of *Preissia commutata*. Ann. Botany **27**:661–681. *pls. 54, 55.* 1913.

[8] NILSSON, H. HJALMAR, Plant breeding in Sweden. Jour. Hered. **5**:281–296. 1914.

accomplish this specialists have been allowed to concentrate their attention on a limited field of one or two cereals. The importance of practical trials, the use of hybridization, and some of the practical results are noted, as well as the fact that mutations do appear in cultivated plants; but the main point of the paper is the contribution made to the science of plant breeding by the method of pedigree culture originated at the Svälof station.—GEO. D. FULLER.

The case of Oenothera.—Probably no genus of plants has ever been the subject and the cause of so much investigation as *Oenothera*. It has become a storm center, and it is to be hoped that the result will be the clearing of an atmosphere which has become heavy with discussion. The latest contribution to this field of controversy is by SHULL,[9] who suggests that *Oenothera* itself may be the occasion of the trouble, since "fundamental difficulties are encountered whenever attempts are made to apply to the Oenotheras rules of genetic behavior which are readily demonstrated in other groups of organisms." He concludes, for example, that *Oenothera* must have a hereditary mechanism fundamentally different from that which distributes the Mendelian unit characters.

In connection with the results of breeding experiments reported on in the present contribution, SHULL is convinced that certain conclusions reached by GATES regarding the origin and genetic nature of the *rubricalyx* character are erroneous, a character which the former has found behaving in various perplexing ways. The conclusions objected to are that the character represents a purely quantitative difference from *O. rubrinervis;* that it differs from the latter species in a single monohybrid Mendelian unit; and that the nature of a character itself, instead of the nature of the inheriting-mechanism to which it is related, determines the manner of inheritance of that character.—J. M. C.

Chromosomes and sex.—DONCASTER[10] has continued his breeding experiments in the study of sex-inheritance in the currant moth. In a previous paper he had described a strain which in each generation produced females only and showed that the oogonia of this strain had 55 chromosomes instead of 56, the normal number in the species. The more recent studies confirm the results previously announced and add further interesting data. It is found that the tendency to produce only females "varies in intensity," ranging from equality of the sexes to complete absence of males. It was discovered that the eggs of females with 55 chromosomes in the oogonia have 28 in one polar equatorial plate and 27 in the other. The facts as a whole make it clear that eggs which eliminate the 28th chromosome produce females, while those which

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[9] SHULL, GEORGE HARRISON, A peculiar negative correlation in *Oenothera* hybrids. Jour. Genetics 4:83–102. *pls. 5, 6.* 1914.

[10] DONCASTER, L., On the relations between chromosomes, sex-limited transmission, and sex-determination in *Abraxas grossulariata*. Jour. Genetics 4:1–21. *pls. 1–3.* 1914.

retain it produce males. The author calls attention to the fact that this condition is "the converse of that described in most other insects."

The problem of the relation of chromosomes to sex-inheritance naturally becomes more complex as the facts accumulate, and the rather definite results obtained from the study of a few forms must be checked by the more general situation.—J. M. C.

Immunity as a physiological test.—VAVILOV[11] has suggested an interesting application of the specific relation that so often exists between a parasitic fungus and its host. He concludes that it has been demonstrated that immunity does not depend upon the anatomical peculiarities of plants, but upon their physiological peculiarities. Of course there is every evidence that in many cases there is some specific relation between a parasitic fungus and the metabolism of its host. The author suggests that "narrowly specialized" fungi may be used as a physiological test for the recognition of the species and races "in systematic and genetic studies of plants." He illustrates the possibilities in connection with a classification of the races of cereals, claiming that in this way he has been able to detect unsuspected races of wheat and oats. This coupling of the reactions of parasitic fungi with the genetic relationships of their hosts will be more of a promise than a performance until more exact knowledge has developed as to the metabolism of the fungi and of the hosts they are able to infect.—J. M. C.

A Welsh sand dune area.—Sand dunes historically interesting on account of their position over the site of the castle and buried city of Kenfig have been studied ecologically by ORR,[12] who has just made a preliminary report of the conditions and development of the principal plant associations. The area fringes the Glamorgan coast for 15 miles from Swansea. The pioneer association is, as usual, one of the Marram grass, followed by *Salix repens*. The efficiency of *Ammophila arenaria* as a sand binder seems to have been recognized here as early as 1330, when Kenfig made provisions for its protection and preservation. Upon the fixed dunes the final stage in the succession seems to be an association dominated by *Pteris aquilina* covering considerable areas. A more exact analysis of the factors concerned and a careful delimitation of the associations is promised in a future paper.—GEO. D. FULLER.

Cordaitean wood from the Devonian.—Miss ELKINS and Dr. WIELAND[13] have described wood of Cordaitales from the black shale of Indiana. The specimens from which the sections were made rested on black shale, and were large

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[11] VAVILOV, N. I., Immunity to fungous diseases as a physiological test in genetics and systematics, exemplified in cereals. Jour. Genetics **4**:49–65. 1914.

[12] ORR, M. Y., Kenfig burrows; an ecological study. Trans. Bot. Soc. Edinburgh **26**:79–88. 1913.

[13] ELKINS, M. G., and WIELAND, G. R., Cordaitean wood from the Indiana black shale. Amer. Jour. Sci. **38**:65–78. *pls. 1, 2. figs. 11.* 1914.

trees, all of them being silicified. The species described is called *Callixylon Owenii*, a genus recently established by ZALESSKY. Formerly it would have been called *Cordaites*, the new species being closely related to *Cordaites Newberryi*. The details of structure are very complete, and are perhaps more numerous and definite than have been obtained from any Devonian wood heretofore. What WIELAND calls its "advanced structural type" indicates great antiquity for the coniferophyte phylum.—J. M. C.

Some new Chlorophyceae.—TRANSEAU[14] has published some new species of green algae discovered in connection with his study of the periodicity of occurrence and reproduction of the algae of eastern Illinois. Thirteen new species are described in the following genera: *Zygnema* (1), *Spirogyra* (7), *Mougeotia* (1), and *Oedogonium* (4). In *Spirogyra*, 5 new varieties are also described. This is probably an illustration of the additional species of algae that will be discovered in connection with any intensive study of a region.—J. M. C.

Plants of Ohio.—SCHAFFNER[15] has published a catalogue of the vascular plants of Ohio, based on specimens in the state herbarium of the Ohio State University. The catalogue enumerates 2065 species, not including varieties, about one-fourth of which are introduced. The last preceding catalogue of Ohio plants was published by KELLERMAN in 1899. The present catalogue is really a check list of the collection of Ohio plants at the State University, and the serial numbers are the record numbers of the material.—J. M. C.

New plants from Mexico.—BRANDEGEE[16] has published a sixth fascicle of new Mexican plants collected by PURPUS, included in collections made chiefly in Chiapas in 1913. The following new genera are described: *Allophyton* and *Amalophyllon* (Scrophulariaceae), *Otocalyx*, *Plocaniophyllon*, *Stylosiphonia*, and *Pinarophyllon* (Rubiaceae), *Pterosicyos* (Cucurbitaceae), and *Tonalanthus* (Heliantheae). In addition to these new genera, 66 new species are described, distributed among 51 genera.—J. M. C.

The orchids of Java.—In presenting the fourth instalment of his studies of orchids of Java, SMITH[17] describes 48 species, included in 25 genera, 13 species being new. A new genus (*Abdominea*) is described, the excuse for the name being that the rostellum resembles the abdomen of an insect. The study of tropical vegetation is making large additions to our taxonomic lists.—J. M. C.

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[14] TRANSEAU, E. N., New species of green algae. Amer. Jour. Bot. **1**:289–301. *pls. 25–29.* 1914.

[15] SCHAFFNER, J. H., Catalog of Ohio vascular plants. Ohio State Univ. Bull. **18**:131–247. 1914.

[16] BRANDEGEE, T. S., Plantae Mexicanae Purpusianae, VI. Univ. Calif. Publ. Bot. **6**:51–77. 1914.

[17] SMITH, J. J., Die Orchideen von Java. Bull. Jard. Bot. Buitenzorg II. no. 14. pp. 56. 1914.

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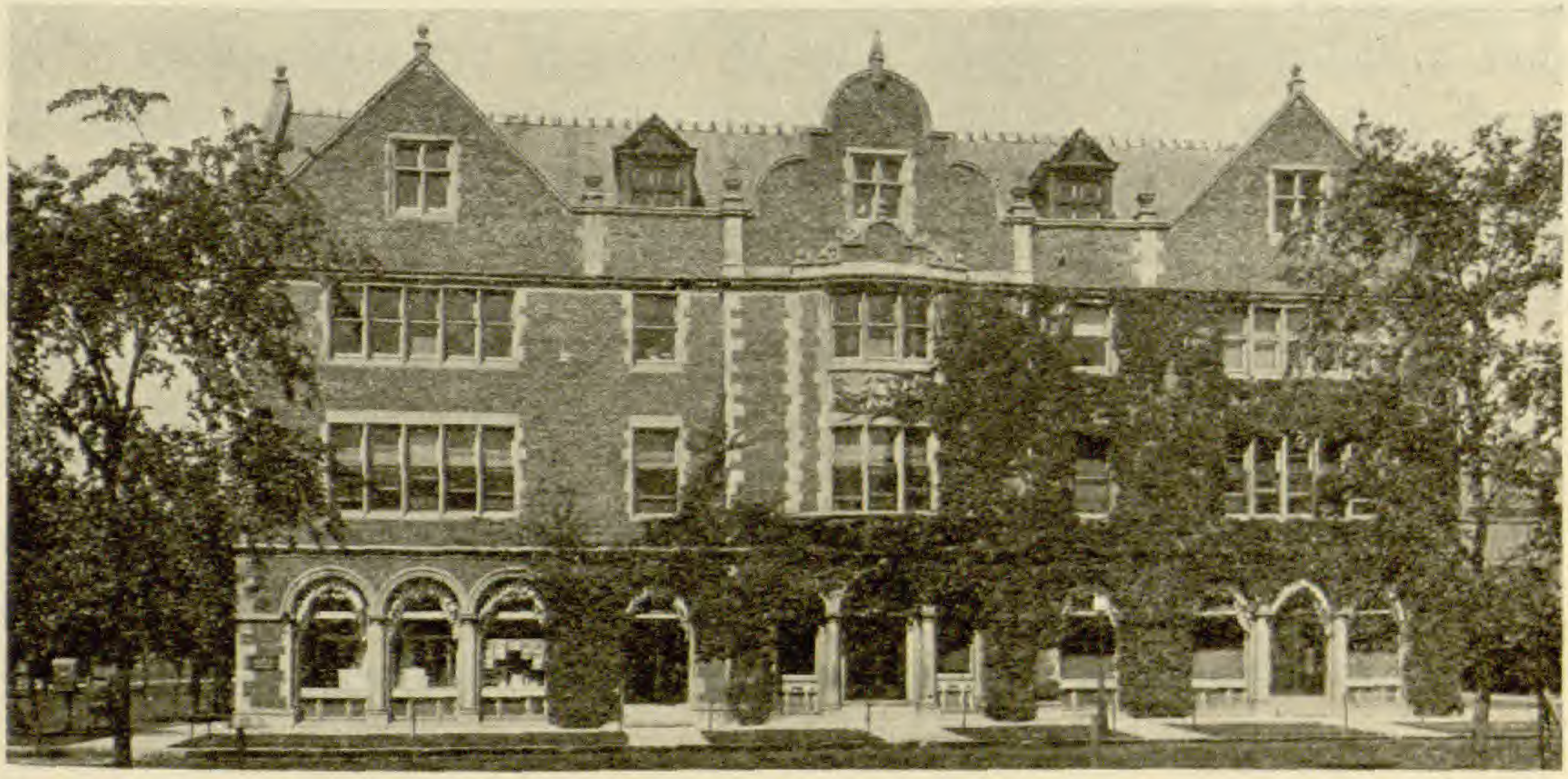

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THE TRANSPIRATION OF EMERSED WATER PLANTS: ITS MEASUREMENT AND ITS RELATIONSHIPS[1]

CHARLES HERBERT OTIS

(WITH THREE FIGURES AND FOURTEEN CHARTS)

Introduction

The evaporation taking place from free water surfaces has been the subject of much experimentation during the past century, and the laws governing this phenomenon have been quite definitely stated. The matter of transpiration of plants, a special kind of water evaporation, has also been the subject of a great deal of theoretical and experimental investigation, and we know the quantity of water transpired by certain plants in various situations and some of the factors which influence it. But, although the subject is of great importance in regions of small rainfall and scant water supply, especially where immense irrigation and water supply projects are involved, practically no investigation of any importance has been conducted to determine the effect of emersed water plants on the evaporation from a water surface.

It has been a matter of common belief that emersed water plants transpire large amounts of water, although there seems to be little evidence in support of such belief. FANNING (**6**) says, "Marshy margins of ponds are profligate dispensers of vapor to the atmosphere, usually exceeding in this respect the water surfaces themselves." Such statements as this, unsupported by experimental

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[1] Contribution no. 143 from the Botanical Department of the University of Michigan.

evidence, are of only passing interest, yet they constitute all of the scanty literature on the subject.

This investigation was undertaken to secure experimental data leading to a better knowledge of the quantity of water transpired by emersed water plants, its relationships, and some of the factors which influence it.

Relation between the amount of water transpired and the amount of water absorbed by the roots

WOODWARD (13) in the latter part of the seventeenth century measured the amount of water absorbed by the roots, and considered this amount to be a measure of the quantity transpired. BESSEY and WOODS (1), in criticism of this method, pointed out that such observations are misleading, that the amount of water absorbed is not necessarily proportional to the amount transpired. Two years later, criticizing a similar mode of reasoning by SCHNEIDER (10), WOODS (12) says, "first of all he has made a very great mistake in assuming that the amount of water absorbed by the roots of a plant represents the amount transpired," and quotes in support of his argument the investigations of EBERDT, BURGERSTEIN, VINES, and GOODALE. WOODS also points out that "transpiration is not something which protoplasm *does* but something which it *resists*. It is not a physiological function or activity of protoplasm, although it may have a physiological relation to the normal development of certain plants or parts of plants. Transpiration is nothing more than evaporation."

BURGERSTEIN (2) reports that VESQUE, using a 0.35 per cent nutritive solution in which bean plants were grown for a period of 56 days, found a water intake of 92.65 gm. and a water outgo of 82.105 gm. He cites also the work of KRÖBER with leafy branches of *Asclepias incarnata*, and shows by the results given in table I that the amount of water taken up by the cut surfaces differs from the amount given off by transpiration.

EWART and REES (5), working with trees, make the statement that "The rate of evaporation per sq. m. of leaf surface from cut branches, whether placed in water or not, is always less than from a plant rooted in the soil, under otherwise similar conditions."

Other recent investigators, among them Clements (4) and Gates (7), have come to the same conclusion. Kröber's results may be criticized, then, on the basis that cut stems and not naturally growing plants were used. It is to be noted, however, that, during the period of the experiment, the amount of water absorbed and the amount transpired were not greatly different, being 38.32 cc. in the one and 36.29 cc. in the other, showing a difference of 2.03 cc. for 42 hours. Eberdt's results with *Helianthus annuus*, as reported by Burgerstein, show even a smaller difference, his figures for a period of 24 hours being as given in table II.

TABLE I

	Absorption	Transpiration	cc.
9:15 A.M.–6:25 P.M.	11.30	12.80	+1.5
6:25 P.M.–9:50 A.M.	8.05	6.48	−1.57
9:50 A.M.–7:05 P.M.	11.30	11.80	+0.5
7:05 P.M.–7:25 A.M.	7.67	5.21	−2.46

TABLE II

Time	Evaporation of water in cc.	Absorption of water in gm.
7:15 P.M.– 8:45 A.M.	16.67	15.55
8:45 A.M.–11:45 A.M.	4.95	5.53
11:45 A.M.– 3:00 P.M.	5.50	7.40
3:00 P.M.– 7:15 P.M.	6.45	5.50
7:15 P.M.– 7:15 P.M.	33.57	33.98

Eberdt's results, employing the potometer method, are not entirely satisfactory for the reasons stated above. Summarizing the results of these investigations, however, Burgerstein states that if experiments are conducted for periods of 24 hours or longer, using plants that are healthy and under normal conditions for growth and transpiration, and only approximate values are desired, there may be assumed a certain proportionality between water intake and water outgo.

Vesque (11), experimenting with whole plants subjected to varying physical conditions, comes to the conclusions (1) that the two functions, absorption and transpiration, are not necessarily proportional; (2) that the absorption is equal to the transpiration when the plant is growing under average and fairly constant conditions, as in diffuse light and in average humidity; (3) that when a plant growing under normal conditions is placed in a dry atmosphere, transpiration is greater than absorption; (4) that when a plant growing under normal conditions is exposed to a saturated atmosphere, the absorption, in obedience to the vacuum already existing, is greater than the transpiration; and (5) that when a plant lacks water, the suction produced by transpiration is not lost, but it accumulates to act immediately when the roots come in contact with water, when absorption .is much more energetic than transpiration.

CLEMENTS (4) experimented with potted plants of *Helianthus annuus* and found by careful weighing of the amount of water absorbed by the roots and the amount transpired by the stem and leaves that at the end of 5 days the one equaled the other. His results were as shown in table III.

TABLE III

	Wt. of pot and dry soil	Wt. of pot and wet soil		Total H_2O	H_2O left	H_2O absorbed	H_2O transpired
		I	II				
I.....	1846.0 gm.	2218.0 gm.	2174.3 gm.	372.0 gm.	328.3 gm.	43.7 gm.	43.7 gm.
II....	1886.7 gm.	2253.2 gm.	2221.6 gm.	366.5 gm.	334.9 gm.	31.6 gm.	31.6 gm.

To sum up the conclusions of these investigators, the results indicate for land plants growing under natural conditions:

1. That there may be slight discrepancies between the amounts absorbed and transpired if the periods between measurements are separated by a few hours only.

2. That for a longer interval of time between measurements the amount transpired is essentially equal to the amount absorbed.

Hence the amount of water absorbed may be taken as a measure of the amount of water transpired, certainly in view of the fact that any slight error can be scarcely larger than that of any other method applicable to the field. One such error which is known to exist, but which is insignificant when one is dealing with relatively short periods of time, is the small amount of absorbed water which is used in the building up of plant tissue and also that which becomes a part of the cell sap. Further, since the roots of emersed water plants are constantly in contact with saturated soil, no matter what the transpiration demands, they are never temporarily deprived of water, as may be the case with land plants during periods of excessive transpiration; nor are water plants ordinarily subjected to as great extremes of temperature, relative humidity, and other external factors as are land plants. It is to be concluded, then, that the relations between absorption and transpiration stated above will hold equally well for even short intervals of time, as for 3–4 hours. In the experiments which follow, however, longer periods than this have been chosen, usually of about 12 hours.

Apparatus[2]

The apparatus which was finally adopted consisted essentially of nine large tanks supported in the water by two pontoons. Each tank was equipped with a simple device for measuring the evaporation from the tank. A recording thermometer was housed in a small shelter about 2 m. from the pontoons. Relative humidity was ascertained by means of a cog or "egg-beater" psychrometer (4), which was in each case rested on a support about midway of the vertical height of the growing plants. A barometer of the United States Weather Bureau pattern, but graduated in the metric system, was maintained on shore and read at intervals for the air pressure. Centigrade thermometers for ascertaining the temperature of the water both within and outside the tanks, and graduates of various capacities for measuring the amount of water evaporated were employed. In the experiments conducted on the Huron River at Ann Arbor, a Green's recording anemometer making electrical contact every tenth mile was employed in addition to the apparatus just mentioned. The cups of the anemometer revolved in a plane about 5 dm. above the surface of the water.

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[2] An excellent summary describing instruments adapted to the measurement of evaporation from water surfaces is contained in C. F. MARVIN's Methods and apparatus for the study of evaporation. II. Instruments (9).

The tanks, which were specially constructed for the experiments, were 76 cm. in diameter and 81 cm. in depth, inside measurements (fig. 1). Both cylinder and bottom were constructed of heavy galvanized iron, all joints being well riveted and soldered. A heavy iron band was riveted to the rim, through which were bored four holes, allowing the tank to be supported by spikes driven into the framework of the pontoons. Lighter iron bands were placed at intervals along the length of the tank, to which were riveted internal iron braces, one of which is shown at *a*, fig. 1. The lower edge of the tanks projected about 10 cm. below the bottom. Pieces of wood 5 cm. by 10 cm. in cross-section were fitted into this space and spiked to the projecting sides, as shown in fig. 2. This construction made a tank of great stiffness, which was not easily deformed by rough handling or the tilting caused by wave action, and which produced a solid surface to which the measuring device was secured. The foregoing features were essential, since any deformation of the tank during the progress of the experiments would cause a corresponding change in the volume of the tank and a similar error in the reading.

FIG. 1

The measuring device was a modification of the well known Hooke gauge, and was unique in its simplicity and in the accuracy with which readings could be made. A brass tube of about 6 mm. inside diameter was supported vertically in the center of the tank. The lower end of the tube was threaded and screwed into a socket which was riveted and soldered to the bottom of the tank, while the upper end terminated in a heavy brass collar. This collar was provided with a socket into which was slipped a solid brass rod, or point, pointed at its upper end. The points were first turned up in a lathe, after which they were placed in a form and ground on an oil stone until a microscopical test showed them all to be of the same angle and of a uniform degree of sharpness. The angle of the cone thus formed was 45°, which was found experimentally to give the best results. Screwed into the sides of the collar at angles of 120° with each other were three iron radius rods terminating in the heavy iron band at the rim. The outer extremity of the rods was threaded for a considerable distance, so that by means of lock-nuts and rubber gaskets on either side of the heavy band the point could be centered with ease and accuracy. It was essential that the point should be in the exact center of the tank, since only in this position could accurate readings be made in case the tank were tilted slightly from the vertical. The points in all the tanks were set at a distance of 4.5 cm. below the level of the rim.

FIG. 2

The pontoons which supported the tanks in the water were at first constructed of rough hemlock lumber and covered with a good grade of asphalt roofing felt. They consisted of two boxes

4.26 m. long, 3 dm. wide, and 3.5 dm. deep. The boxes were left open on the upper side for a greater part of their length to allow a ballast of rocks to be placed to sink the tanks to the required depth. Any water which might enter the pontoons could also be removed through the same opening. It was found to be an advantage to have these pontoons extra large in order that the work of filling the tanks with soil and the placing of plants might be done from the pontoons rather than from a less stable boat. Cross-timbers 5 cm. by 10 cm. in cross-section held the pontoons rigidly in place and provided a support for the tanks. It was found necessary to place poultry netting of 5 cm. mesh around the finished raft to a height of 3 dm., and in the horizontal spaces between the tanks, to exclude the turtles which infested the water at this place and which proved rather troublesome. These first pontoons proved to be too frail, since they were easily damaged, with consequent submersion of the entire apparatus. They were replaced the following year by more substantial pontoons with solid tops. The interior of these was subdivided by four water-tight partitions into five compartments. Through holes in the top provided with corks water could be placed in or taken from the compartments, and it was by this means that the proper level of the tanks was

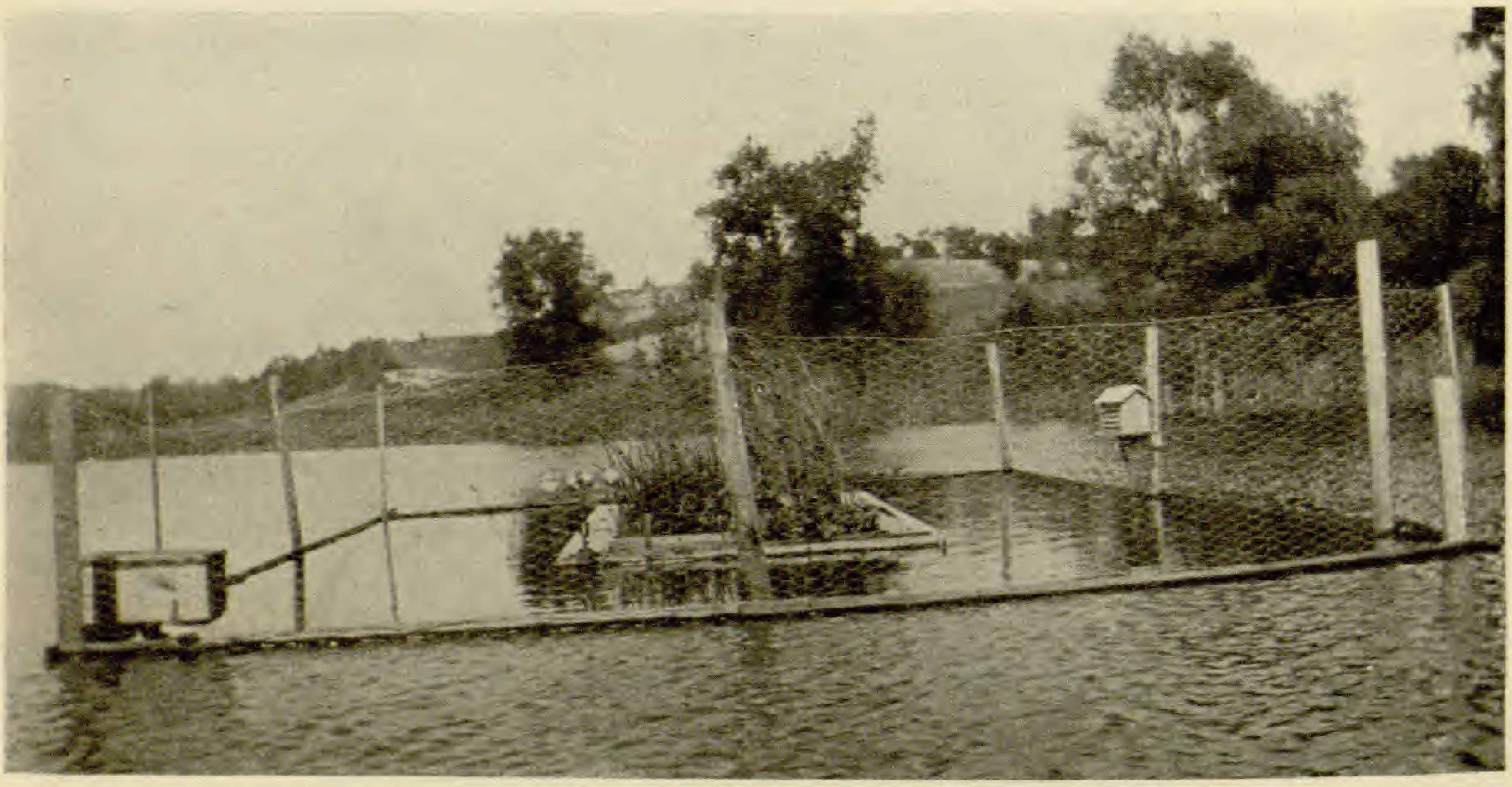


FIG. 3

maintained. The wire netting was also removed from the raft, and a netting 1.5 m. high was substituted at a distance of 1.5–2 m. from, but inclosing, the raft, since turtles were not abundant. The relations of the various instruments and the pontoons is shown in fig. 3.

Methods

Readings were regularly made early in the morning and late in the afternoon or early evening, since at these times the water was usually quite still and the light conditions best for accurate readings. A boat was necessary at all times, all work being done from it as soon as observations were begun. Measurements made at the station included wet and dry bulb temperatures as indicated by the psychrometer. Temperatures of the water in the tanks and of the water surrounding the tanks were ascertained and recorded both at the surface and at a depth of 76 cm. beneath the surface. Continuous records of air temperature and wind were made by the recording instruments. The amount of water taken up by the plants or evaporated from the water surface was ascertained by measuring the quantities of water it was necessary to place in the tanks to bring the water to the standard level, as indicated by the height of the point of the brass rod. Water taken from the lake or river surface adjacent to the tanks was always used, since it was of the same temperature and had other characteristics in common with the water in the tanks. Once a week the tanks were filled to overflowing with several bucketfuls of water rapidly applied to remove any scum or refuse matter which might accumulate and which would influence the evaporation therefrom.

The best way to ascertain accurately the amount of water to be added to a tank in each case was found to consist in adding a little more water than was necessary to cover the point. On placing the eye close to the level of the water a point could be found where the entire surface of the water in the tank appeared like a bright mirror. Then, with the eye directed toward the center of the surface, a small quantity of water was removed. As soon as the surface became still, an examination was made for the appearance of the point. If it did not show, more water was removed, until finally a minute black spot was distinguishable in the center of the mirrored surface. (If, at this stage, more water is removed, the minute spot rapidly enlarges, spreading out in a circle around the exposed point.) A very small quantity of water was then added, just enough to obliterate entirely the dark spot. Usually the finger was applied to the point at this stage, a slight rubbing serving to clean the point and to break the surface film of the water over the point. The point was shown to be just beneath the surface, as, on lightly touching the water with the finger, a tiny wave would be sent across the surface, and the point would appear momentarily to be immediately obliterated. This phenomenon was most readily observed when the light was somewhat diminished. At midday the sun on a cloudless day was so intense that the eye was flooded with the light reflected from the water surface, making it difficult to see the dark spot. Repeated observations under varying conditions carried out with a test tank showed that on the average a change in water height produced by the addition or subtraction of 25 cc. of water could be detected. Since the area of water surface in the tank approximated 4,575 sq. cm., this volume would give a theoretical difference in height, or minimum error due to observation, of 0.05 mm.

Experiments

Experimental stations were established and maintained during the summers of 1910 and 1911. The first was located in a bay of about 12 hectares' extent in Portage Lake, situated 27 km. northwest of Ann Arbor, Michigan. A long, narrow peninsula covered with a scrubby growth of trees and shrubs separated the bay from the lake proper and protected the station from the prevailing westerly winds. It was subsequently found necessary to establish a boom of floating logs on the south and east as a protection against occasional winds from these directions.

Two tanks at the diagonal corners of the raft contained neither soil nor plants and were used to ascertain the evaporation from the free water surface. The other tanks were supplied with lake mud, the depth depending upon the plants placed therein. Plants from the immediate vicinity were planted in these tanks, the depth of the water being in all cases identical with the depth of the water where the plants were naturally growing. Care was also taken to set the plants as nearly as possible in the same density of stand as naturally growing plants in the lake. Where there was any tendency for the plants to work their way out of the soil, which was of common occurrence among the larger kinds, on account of their natural buoyancy and the extreme looseness of the newly placed soil, stones were used freely to press down the roots and hold them in place. The plants used during 1910 were *Scirpus validus* and *S. americanus*, *Sagittaria latifolia*, *Castalia odorata*, *Pontederia cordata*, *Typha latifolia*, *Zizania aquatica*, and *Eichhornia speciosa*. The two latter were discontinued before the measurements were begun, as the *Zizania* was twice completely destroyed by water animals and the *Eichhornia* floated away the first time the raft sank. The plants, after transplanting, were allowed to remain undisturbed for a period of two weeks, during which time they became well established.

At the beginning of the experiment measurements were made of the area of leaf and stem surfaces exposed to the action of the air. These measurements were made in the following manner. In the case of those species having petioles and expanded blades (as *Sagittaria* and *Pontederia*), a tracing was made of every leaf blade or portion of a leaf blade above the standard water level, and the upper and lower diameters and length of the petioles above water were recorded separately. Subsequently the area of blade surface was ascertained by use of a planimeter and the area of petiole surface was calculated as the area of the frustum of a cone. In the case of *Scirpus validus* the height of the culm above the water and its basal diameter were recorded, its surface being calculated as the surface of a cone having the dimensions recorded. With *Scirpus americanus* similar measurements were made, the surface being treated as the surface of a pyramid whose base is an equilateral triangle. The leaves of *Typha* were measured for the length exposed to the air (not the height above the water) and the width of the corresponding base, the surface exposed being calculated by treating each leaf as a triangle whose base is the width and whose altitude is the length given. Finally, a photograph of the surface of the tank containing *Castalia* was made from a point exactly above the center of the tank, since leaf tracings of the floating leaves could not be made without injuring them. By means of the planimeter and a simple proportion the surface of the leaves exposed was approximated. During the course of the experiment, when leaves or parts of plants were for any reason removed, the parts were measured and a record was made of the date of removal. At the end of the experimental period all parts above water were again measured and calculated in the same manner as outlined above. In making calculations the slide rule was resorted to wherever practicable.

A second station was established in the summer of 1911 in the Huron River near Ann Arbor. The river at this place is about 60 m. wide. There is little or no natural protection on any side, and it was necessary to inclose the entire station by a stationary boom. The plants were in this case taken from the river near by. They included *Scirpus validus*, *Typha latifolia*, *Castalia odorata*, and *Pontederia cordata* used the first year, together with *Sparganium eurycarpum* and *Acorus Calamus*. Owing to the withdrawal of the water for a period of several weeks, while repairs were being made on a near-by dam, the *Sagittaria latifolia* was all but destroyed and could not be used. Consequently only eight tanks were used. Two tanks were used as controls and the preliminary treatment of the plants was the same as at the Portage Lake station. The plants were not measured, however, and the surface area exposed to the air was not ascertained.

Just before measuring observations were begun, pontoons and tanks were sunk to such a depth that the water in the tanks and the water of the lake were in the same horizontal plane, which was 4.5 cm. below the level of the rim.

Ecological and physiological aspects of plants used

1. *Scirpus validus* Vahl. (great bulrush) inhabits the still water at the margins of lakes, ponds, and quiet streams, or covers shallow shoals in lakes, often forming thick stands of large extent. The maximum depth of water in which good growth occurs is about a meter, while the denser stands are found in depths of 3–6 dm. The culms are stout, terete, attaining a height of 2.5 m. under

favorable conditions, and rising stiffly above the water or bending in graceful curves. The leaves are reduced to basal sheaths. Seed is usually abundant, while vegetative propagation is secured by perennial, creeping rootstocks.

2. *Scirpus americanus* Pers. (three-square or chair-maker's rush) inhabits the borders of lakes, ponds, and streams, usually in water somewhat shallower than the great bulrush. It does not form thick stands, as does the latter, but is sparingly placed here and there. The culms are sharply three-angled throughout, with concave sides, growing straight upward, sometimes twisted or curved, to a height of a meter. The leaves are basal, narrowly linear, 1–3 dm. long, usually not appearing above the water. The rootstocks are long, stout, perennial.

3. *Pontederia cordata* L. (pickerel-weed) inhabits the shallow water of lakes, ponds, and quiet streams, making its best growth in depths of 2–3 dm. The plants usually stand in clumps, sending up several erect, long-petioled leaves and spikes of showy, blue flowers to a height of 6–12 dm. The leaf blades are ovate to cordate-sagittate, 1–2 dm. long, and about one-half as wide at the base. Stomata occur plentifully on the petioles and both sides of the leaves, but they are somewhat more numerous on the lower than on the upper sides of the blades. Propagation is secured by an abundance of seed, but chiefly by thick, creeping, perennial rootstocks.

4. *Sagittaria latifolia* Willd. (arrow-head) inhabits only the shallowest water and muddy banks of lakes, ponds, and rivers, usually in solitary clumps and seldom covering any considerable area. The leaves are basal, long-petioled, arising from tuberous or fibrous rootstocks to a height of 6 dm. or more. The leaf blades vary greatly in size and shape, but they are nearly always sagittate. Stomata occur sparingly on the upper surface of the blade and on the petiole, but are only moderately abundant beneath.

5. *Acorus Calamus* L. (sweet flag) is rather infrequently found along the margins of streams in water as much as 4–6 dm. in depth. The narrow, sweet-scented, swordlike leaves arise from the thick,

creeping rootstocks to a height of 6 dm. to a meter or more, often forming dense stands over small areas.

6. *Sparganium eurycarpum* Engelm. (bur-reed) inhabits water 4–6 dm. in depth on the borders of ponds, lakes, and rivers, rising to a height of 8–15 dm. The leaves are linear, mostly flat. While propagation is provided vegetatively by perennial, creeping rootstocks, solid stands of any considerable area are exceptional, growth in small groups being usual.

7. *Typha latifolia* L. (common cat-tail) inhabits the marshy banks and shallow water of marshes, lakes, and rivers. The leaves are linear, flat, sheathing at the base, commonly growing to a height of 1–2 m. The plants usually stand in close clumps and sometimes predominate over a considerable area. Stomata are abundant on both sides of the leaves. Propagation is by perennial, creeping rootstocks.

8. *Castalia odorata* (Ait.) Woodville and Wood (sweet-scented water lily) inhabits water of varying depths, covering large areas in shallow ponds and the still water of lakes and slow streams, or mingling freely with open-growing forms of water plants, even occupying the deeper water to the exclusion of other plants when crowded out by competition. The large rootstocks creep through the soft mud, sending up large leaves at the end of long petioles and large, showy, white flowers. The leaves are 0.5–2 dm. wide, orbicular, and float on the surface of the water, frequently partly covering one another in the struggle for space. Stomata occur on the upper side only, but here they are very numerous and their openings are relatively wide. The stomata are kept free from water in the following manner. KERNER (**8**) states that the leaves are slightly raised where they join the petiole and the margins are somewhat undulating up and down, so that any water which may find itself thereon will roll down from the center of the leaf to the edge on the slightest rocking movement, where it coalesces with the water on which the leaves float. The under side of the leaves is often colored purple by anthocyanin, by virtue of which the temperature of the leaves is said to be raised somewhat above that of the water, tending to increase the transpiration therefrom.

Results

EVAPORATION FROM A FREE WATER SURFACE AND FROM A WATER SURFACE OCCUPIED BY EMERSED WATER PLANTS

A compilation of the data collected during the summers of 1910 and 1911 shows a number of features of interest concerning the evaporation from water surfaces. As would be expected from a consideration of the various plants used, their differences of growth, habit, and structure, together with the varying physical factors, the results show considerable diversity in total and relative amounts of evaporation. A vast amount of data has been recorded throughout the course of the investigation, all of which it is impossible to include in this paper. The statistical tables and graphs which are published here for the most part summarize the more detailed data. The results fall naturally into several groups, which will be taken up successively.

(*a*) *Total amount of water evaporated*

Tables IV and V give in tabular form the amount of water added to each tank, which represents the amount of water evaporated by water and plant surfaces during any period, for successive intervals. It will be noted that the total amount of water added varies over a considerable range for the different tanks. If the average of the two control tanks be accepted as the amount of evaporation from a free water surface, to which a value of 1 is assigned, then the plants used in 1910 would stand in order of evaporating power thus: pickerel-weed:cat-tail:arrow-head:great bulrush:three-square rush:water lily as 1.98:1.88:1.55:1.19:1.12:0.86. Using the plant combination indicated in table V, the ratio would appear as follows: cat-tail:sweet flag:bur-reed:pickerel-weed:great bulrush:water lily as 3.05:2.36:2.26:2.08:1.20:0.89. The values for water lily (0.86 and 0.89) and for great bulrush (1.19 and 1.20) are nearly the same for the two years. The other values are much higher for 1911, thought to be due in part to the somewhat drier season and more exposed situation and in part to a more luxuriant growth. The evaporation from the water lily tank was in both years much less than that from the control tanks. This might be expected from the fact that the lily leaves floated on the water, forming a partial cover and reducing the area of water surface exposed to the air. Moreover, lying in a plane only slightly above that of the water surface itself, the lily leaves were constantly bathed by the very humid atmosphere which is commonly present a short distance above the water surface. It is also probable that the amounts assigned to the taller-growing plants are somewhat lower than the actual, since dew collected heavily on the cooler and broader leaf surfaces during foggy nights and, running down the veins and petioles, found its way into the tanks, thus making the observed measurement too small. The water lily was the only plant found to diminish the evaporation from a water surface. All other plants, especially those with a large leaf and petiole surface exposed to the air, increased the evaporation, in one case as much as three times (for example, cat-tail, table V).

(*b*) *Periodicity of evaporation*

Referring again to tables IV and V of comparative evaporation, it will be noticed that a comparison of successive day and night records for any one tank usually shows a period of high rate of evaporation during the day, followed by a relatively low rate of evaporation during the succeeding night. This phenomenon is most conspicuous in the cat-tail, sweet flag, pickerel-weed, and others exposing a large transpiration surface to the air, and least evident in the rushes and water lily.

The amounts of evaporation from the various tanks given in tables IV and V have been incorporated for the sake of convenience and ready comparison in charts I–XIV, the standard of comparison being the rate of evaporation in cubic centimeters per hour. Charts I and VIII show the rate from the control tanks, and the mean value has been taken to represent the rate of evaporation from a free water surface. These values are plotted in the graphs of charts II–VII and IX–XIV with a heavy broken line. The heavy solid line represents the rate from the tanks containing emersed water plants, that is, the evaporation from the water surface of the tank plus the evaporation from the plant surfaces. The vertical distance between the horizontal lines representing the evaporation from the free water surface and that from the water surface and plant surface together represents the evaporation due to the plant surfaces alone.

TABLE IV

COMPARATIVE EVAPORATION IN 1910

DATE	APPROX. TIME INTERVAL IN HRS.	CONDITIONS	AMOUNTS OF EVAPORATION FROM THE TANKS (CC. OF WATER ADDED)							
			Arrow-head	Three-square rush	Pickerel-weed	Cat-tail	Water lily	Great bulrush	Control no. 5	Control no. 2
Aug. 10..	6	Day	834	519	1400	1200	470	550	450	400
10..	18	Day and night	1650	1400	1715	1750	1015	1425	1150	1375
11..	12	Day	1750	1250	2400	2250	1215	1250	1300	1100
11..	12	Night	1150	1030	987	1053	750	1090	975	1100
12..	10	Day	1600	975	2585	2650	900	1080	1140	750
12..	14	Night	1500	1575	1300	1250	990	1550	1225	1570
13..	11	Day	1770	975	2490	2385	975	1150	790	660
13..	13	Night	988	940	1000	1193	630	1000	910	1120
14..	10	Day	1730	995	2425	2445	905	1090	835	762
14..	14	Night	745	750	887	820	475	730	715	767
15..	8	Day	1145	500	1845	1840	575	673	500	407
16..	9	Day	940	553	1247	1245	450	610	452	425
16..	14	Night	650	553	654	650	420	600	500	500
17..	10	Day	1495	815	2060	1785	630	863	580	678
19..	11	Day	2070	1317	2890	2673	1185	1550	1340	1130
19..	13	Night	1305	1300	1398	1358	863	1327	1228	1250
20..	11	Day	2058	1235	2670	2565	970	1405	1000	1063
20..	23	Night and day	2950	2150	3728	3378	1435	2063	1837	1913
21..	12	Night	783	685	890	900	395	785	655	595
26..	25	Day and night	2920	2075	3470	3255	1675	2175	1725	1918
27..	7	Day	1042	575	1590	1500	555	805	543	460
27..	13	Night	955	950	925	865	590	850	860	990
28..	25	Day and night	2755	2070	3660	3375	1587	2180	2100	1395
29..	10	Day	2267	1443	3040	2587	810	1550	958	1040
29..	13	Night	1080	975	1305	1235	650	1055	1045	905
Totals for an approximate period of 324 hours (cc. of water added)...............			38,132	27,605	48,561	46,207	21,115	29,406	24,813	24,273

In most instances the evaporation during the night was found to be in excess of that from the free water surface, indicating that emersed water plants transpire during the night. An exception is the case of the water lily, in which the evaporation was usually less than from the free water surface. We are led, then, to the conclusion that transpiration from these plant surfaces occurs both by day and by night, but that the day transpiration is greatly in excess of that taking place at night. These observations are in accordance with the results obtained by CLAPP (3) and others with land plants, in which it has been found that land plants transpire principally during the day and only feebly if at all at night.

TABLE V

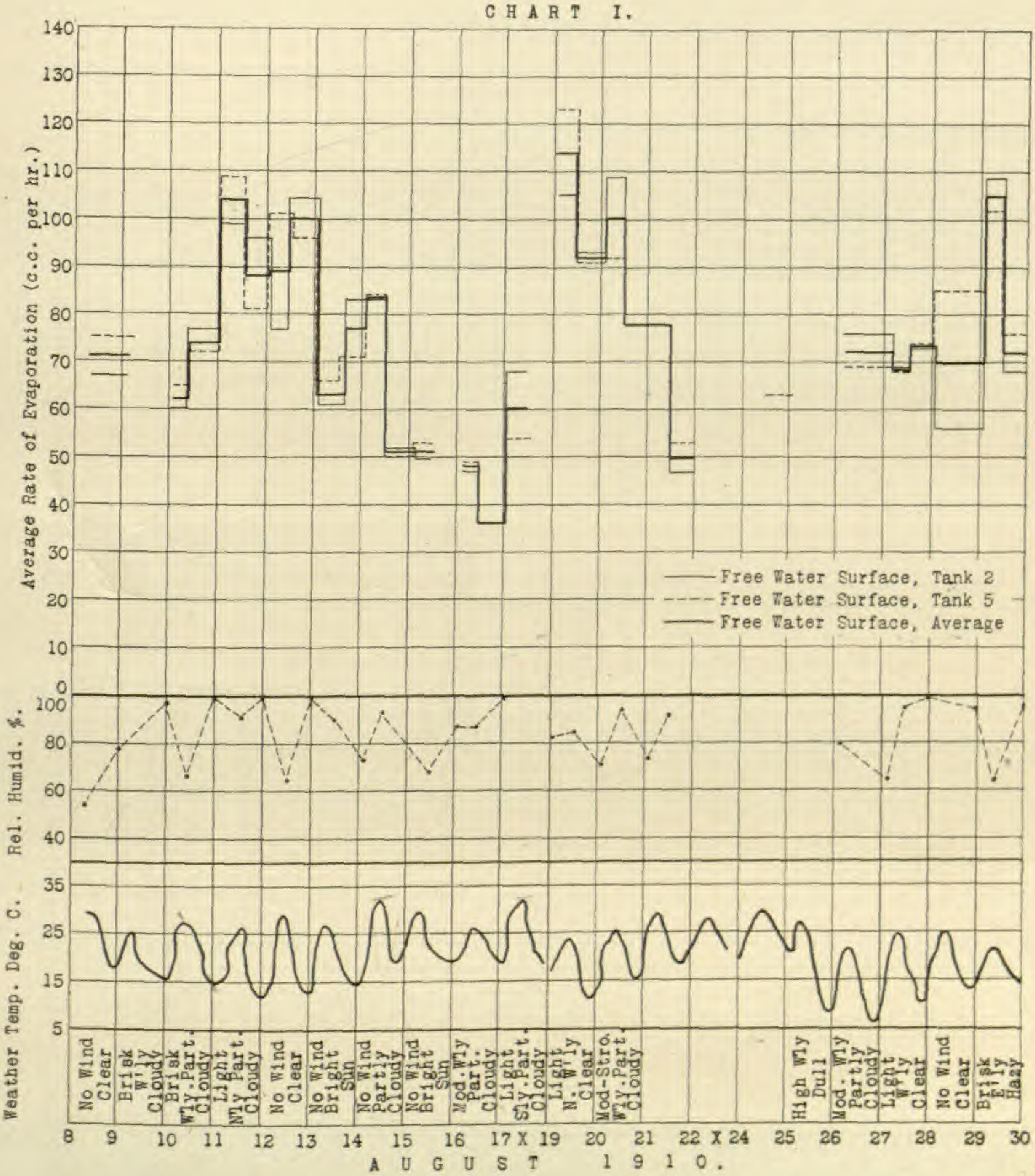
COMPARATIVE EVAPORATION IN 1911

Date	Approx. time interval in hrs.	Conditions	Amounts of evaporation from the tanks (cc. of water added)							
			Cat-tail	Sweet flag	Pickerel-weed	Bur-reed	Great bulrush	Water lily	Control no. 8	Control no. 1
Aug. 30..	12	Day	4160	3590	2860	3085	1630	1175	1095	1420
30..	12	Night	1000	780	680	1145	680	620	600	615
31..	12	Day	3050	2405	1905	2100	745	490	585	510
31..	12	Night	600	540	560	520	595	520	575	575
Sept. 1..	11	Day	5110	3410	3200	3360	1300	790	950	835
1..	13	Night	925	860	870	800	660	455	575	655
2..	24	Day and night	7560	5730	5075	5725	3120	2310	2780	2880
3..	12	Day	4850	4300	3090	3945	1960	1415	1545	1690
3..	12	Night	1050	935	920	975	1030	830	830	1030
4..	11	Day	5680	4200	4060	3540	1880	1345	1270	1550
4..	12	Night	780	730	640	725	710	630	655	720
8..	8	Day	1885	1495	1885	1250	400	265	255	265
8..	14	Night	440	375	340	380	240	210	225	250
9..	10	Day	3240	2285	1915	2250	580	350	360	350
9..	13	Night	640	580	400	530	510	465	510	600
10..	9	Day	3030	2025	1735	1940	535	300	365	345
10..	15	Night	550	460	210	440	270	175	220	240
13..	11	Day	4640	3620	2800	3450	1700	1130	1180	1390
13..	13	Night	1430	1240	1220	1280	1195	1030	1050	1180
15..	8	Day	3880	2275	2425	2570	700	485	530	440
15..	13	Night	700	655	575	740	510	430	380	470
19..	13	Night	1500	1360	1285	1250	1350	1120	1200	1330
Totals for an approximate period of 270 hours (cc. of water added)................			56,700	43,850	38,650	42,000	22,300	16,540	17,735	19,340

(*c*) *Relation of transpiration to transpiring surface*

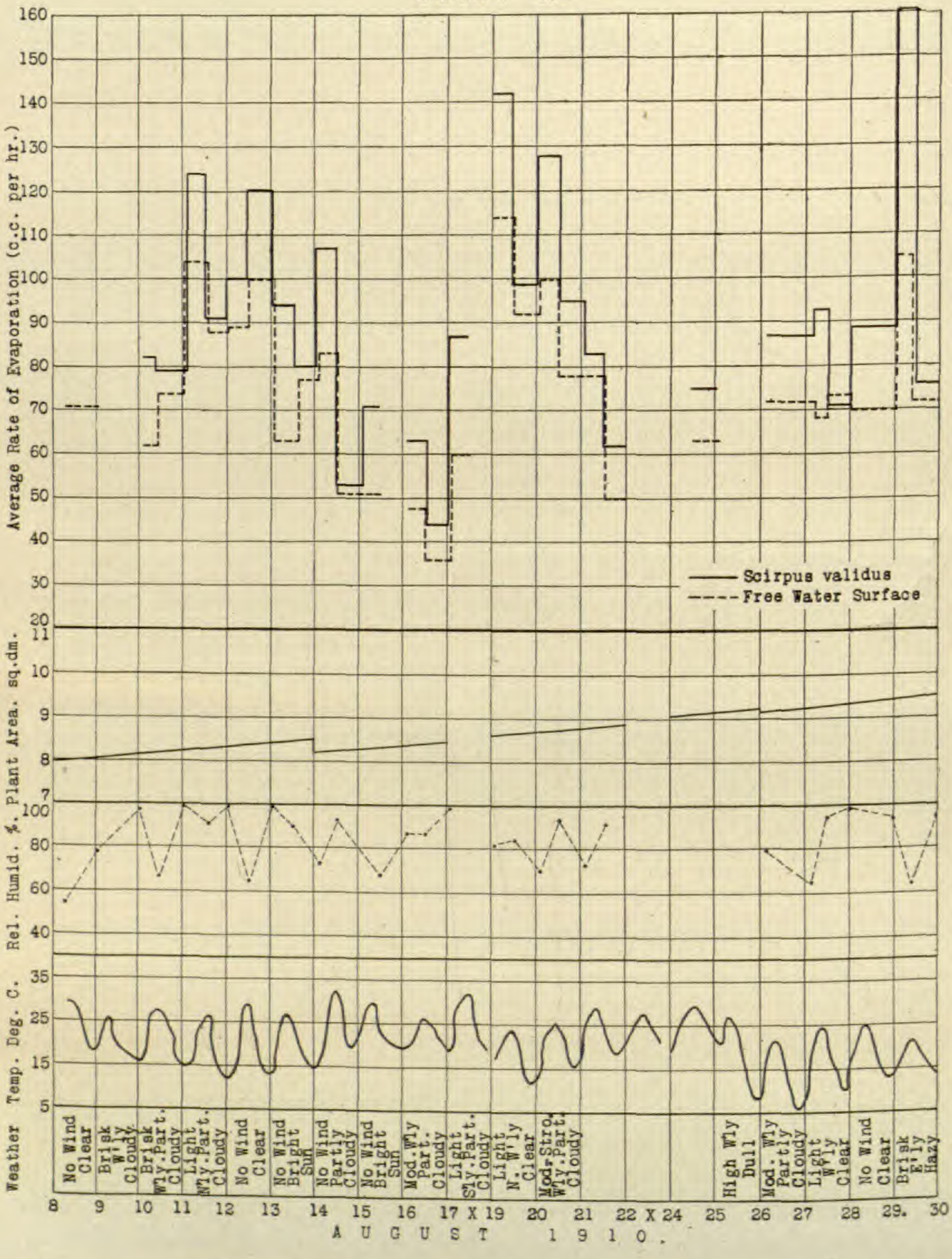
It has been commonly held, for land plants at least, that with plants of different species, or even with different plants of the same species, there is no relation between the amount of water transpired and the area of the transpiring surface exposed to the air. Dealing collectively with a number of plants of the same species, so that an average transpiration rate overcoming individual differences was obtained, this fact was borne out in the experiments of 1910. Utilizing the data on the amount of plant surface exposed

CHART I.



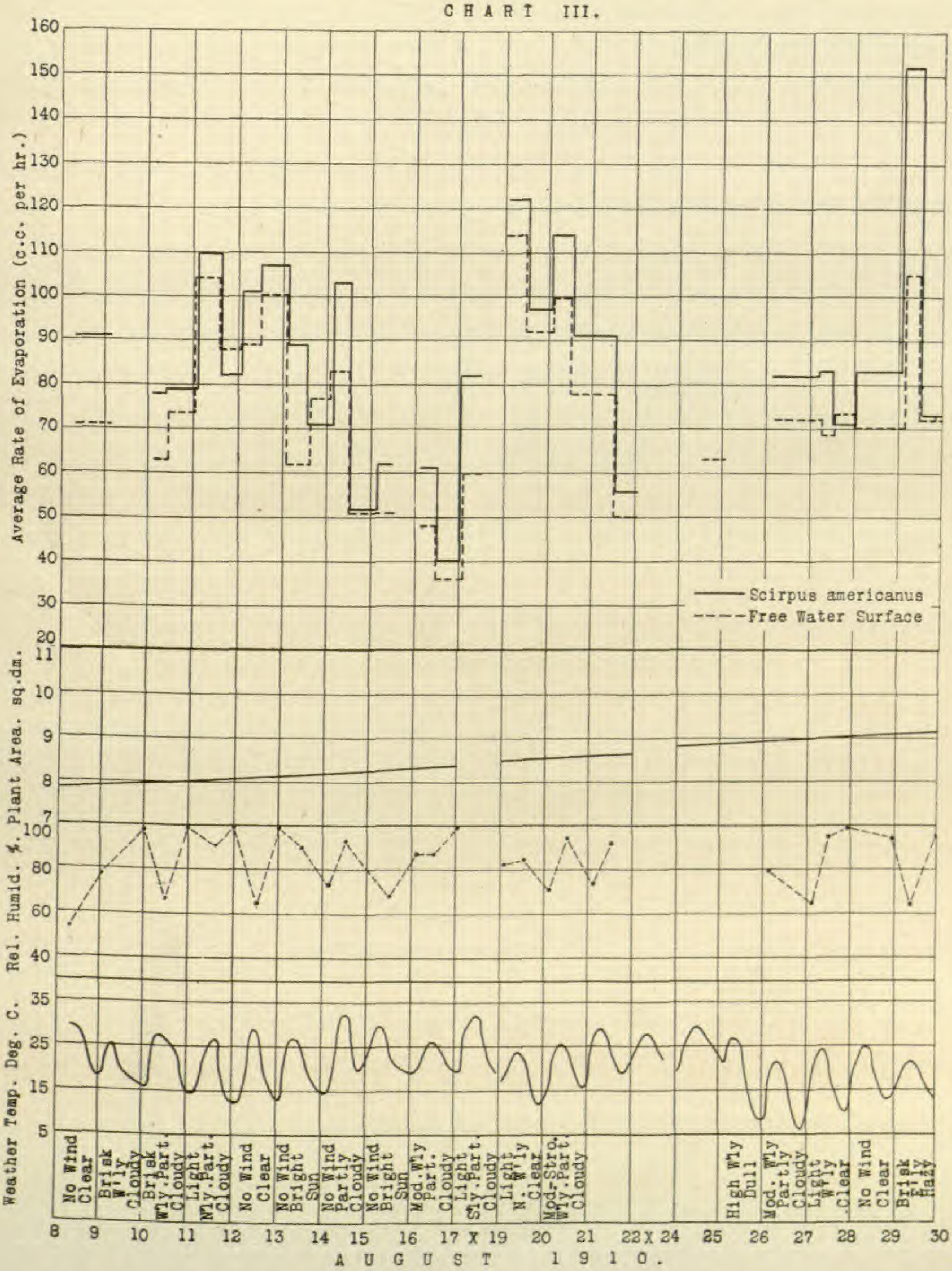
to the air, described under the heading "Experiments," the growth curves of charts II–VII were constructed as a working basis for

CHART II.



the transpiring surface. Growth in area was assumed to be uniform from the time of starting the readings to the date of final measurement, making due allowance for the loss of surface occasioned by the removal of the various parts from time to time. This was thought to approximate very nearly growth under normal

CHART III.



conditions of development. Both sides of the leaf blades, with the exception of those of the water lily, which contain stomata on the upper side only, and those portions of the petioles or culms above the level of the water surface were taken as a basis for transpiring surface, since these surfaces all contained stomata in greater or lesser numbers. The unit of surface selected was, for convenience, the square decimeter.

Table VI shows the rate of transpiration in cc. per hour per sq. dm. of total plant surface. Several things are brought out. The rate during the day is usually much higher than the night rate. This is not so apparent in the case of the water lily, for in this instance the difference between day and night rates is not so great as in the other cases. This is remarkable when it is considered that the lily leaves float on the surface of the water in a very humid atmosphere, especially at night, whereas the taller-growing plants are in a relatively less humid layer of air. This may be accounted for in part by the fact that the lily leaves, because of their contact with the water, are warmer at night than those leaves which project into the air, which is much cooler than the water during most of the nights.

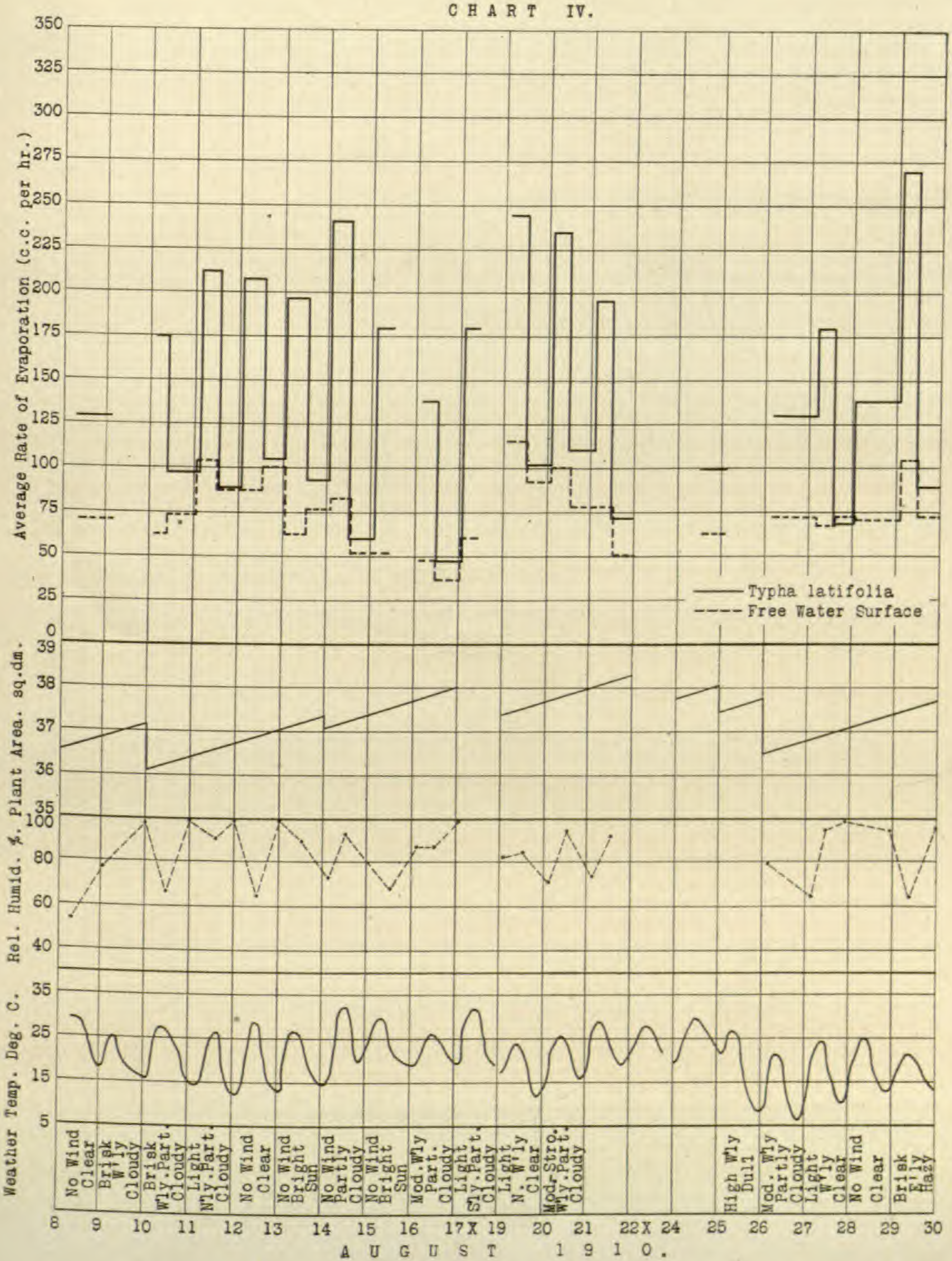
TABLE VI

RATE OF TRANSPIRATION PER AREA OF SURFACE

DATE 1910	CONDITIONS	TRANSPIRATION IN CC. PER HOUR PER SQ. DM. OF TOTAL PLANT SURFACE						
		Pickerel-weed	Cat-tail	Arrow-head	Great bulrush	Three-square rush	Water lily	Free water
Aug. 10..	Day	1.758	1.565	0.718	2.463	2.007	1.704	1.359
10..	Day and night	0.274	0.332	0.224	0.616	0.627	1.184	1.623
11..	Day	1.654	1.483	0.501	2.439	0.750	2.280	2.281
11..	Night	....	0.000	0.044	0.366	....	1.125	1.929
12..	Day	1.603	1.608	0.827	1.325	1.481	1.799	1.952
12..	Night	0.060	0.054	0.056	2.409	0.864	1.428	2.193
13..	Day	1.696	1.797	1.045	3.690	3.198	2.017	1.381
13..	Night	0.012	0.216	....	0.357	....	0.811	1.688
14..	Day	1.812	2.129	1.050	2.927	2.439	2.119	1.820
14..	Night	0.140	0.108	0.011	0.244	0.122	0.579	1.118
15..	Day	1.665	1.885	0.920	2.409	1.333	1.647	1.118
16..	Day	0.872	1.194	0.613	1.789	1.566	1.083	1.053
16..	Night	0.172	0.146	0.120	0.954	0.482	0.605	0.789
17..	Day	1.670	1.566	0.982	3.187	2.631	1.407	1.316

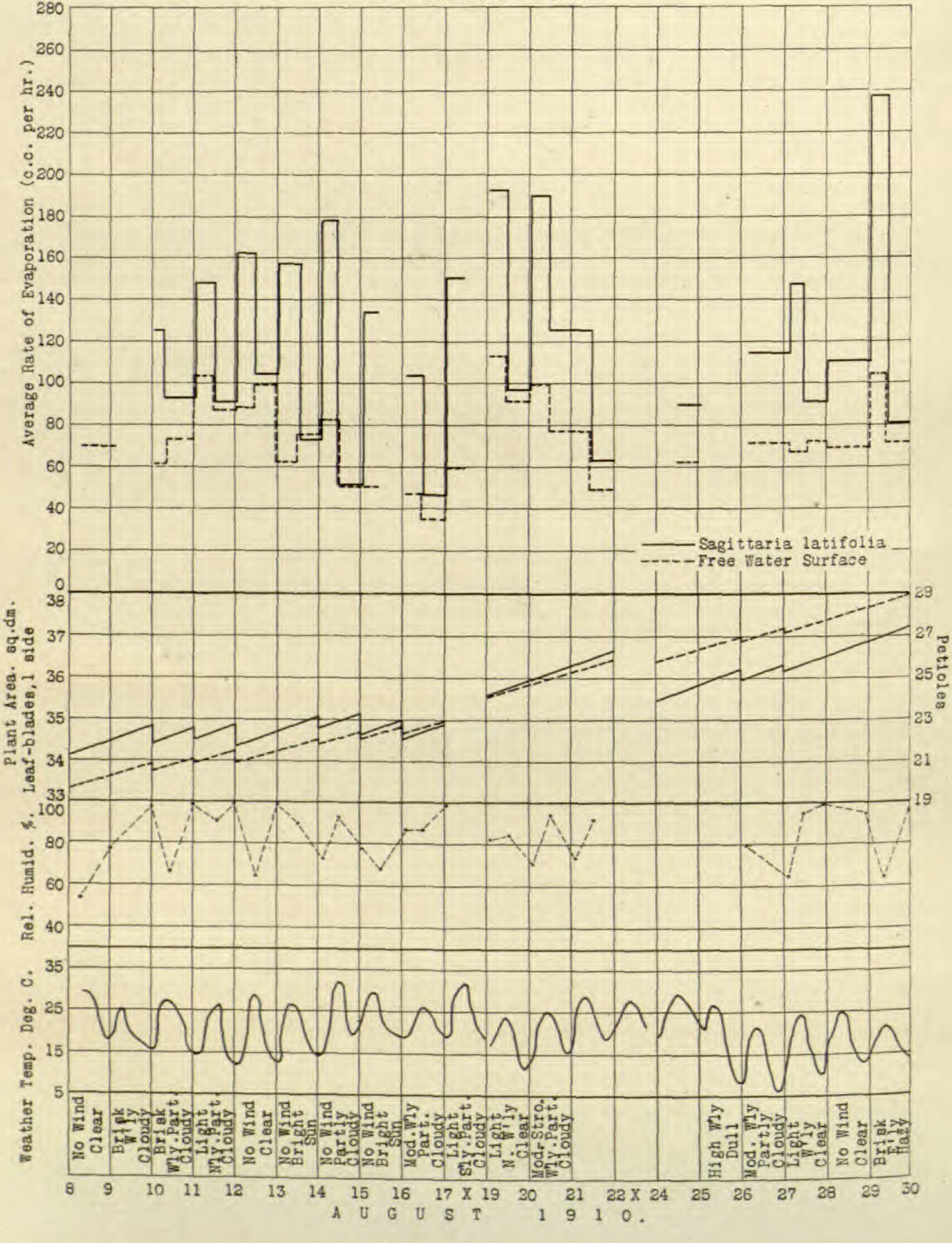
Aside from these differences between day and night rates of transpiration, there is also a great difference between the rates from different species during the same time period. Again, the difference is not so marked in the case of the night readings, but is conspicuous during the day. On a basis of surface exposed, the

CHART IV.



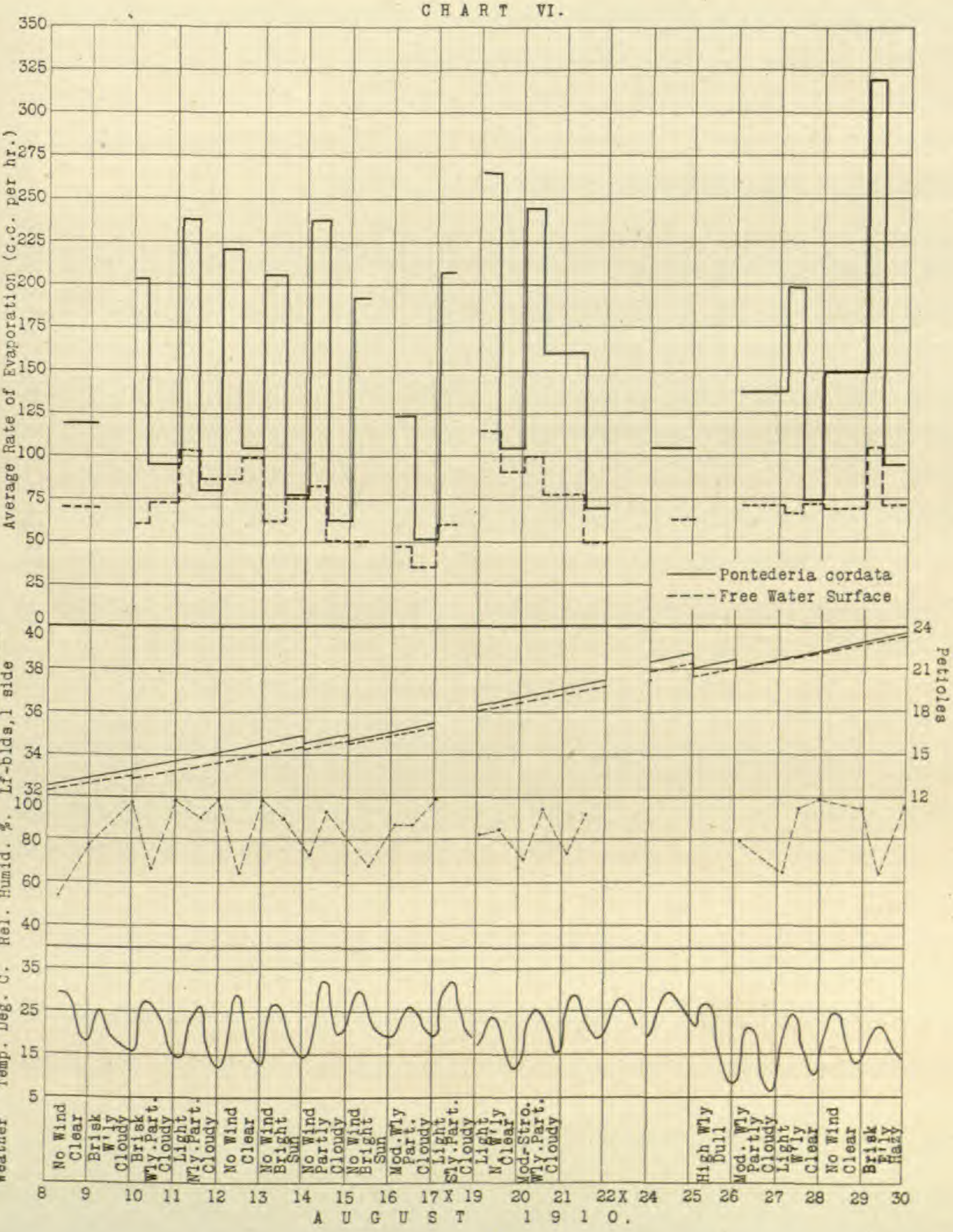
arrow-head would seem to be the least effective from the standpoint of water dispersal, the rushes and water lily showing greatest efficiency, with the pickerel-weed and cat-tail occupying an intermediate position. GATES (7), with a temperature of 26° C. and a relative humidity of 69 per cent, reports that cuttings of *Sagittaria*

CHART V.



latifolia had a rate of water conductivity of 49 cm. per hour, while cuttings of *Typha latifolia* had a rate of 114 cm. per hour. It should be remembered, too, that in the case of the cat-tail all of the stomatal surface is not equally effective, owing to the sheathing habit and consequent crowding of the leaves, while in the pickerelweed and arrow-head a similar decrease in transpiration is caused

CHART VI.



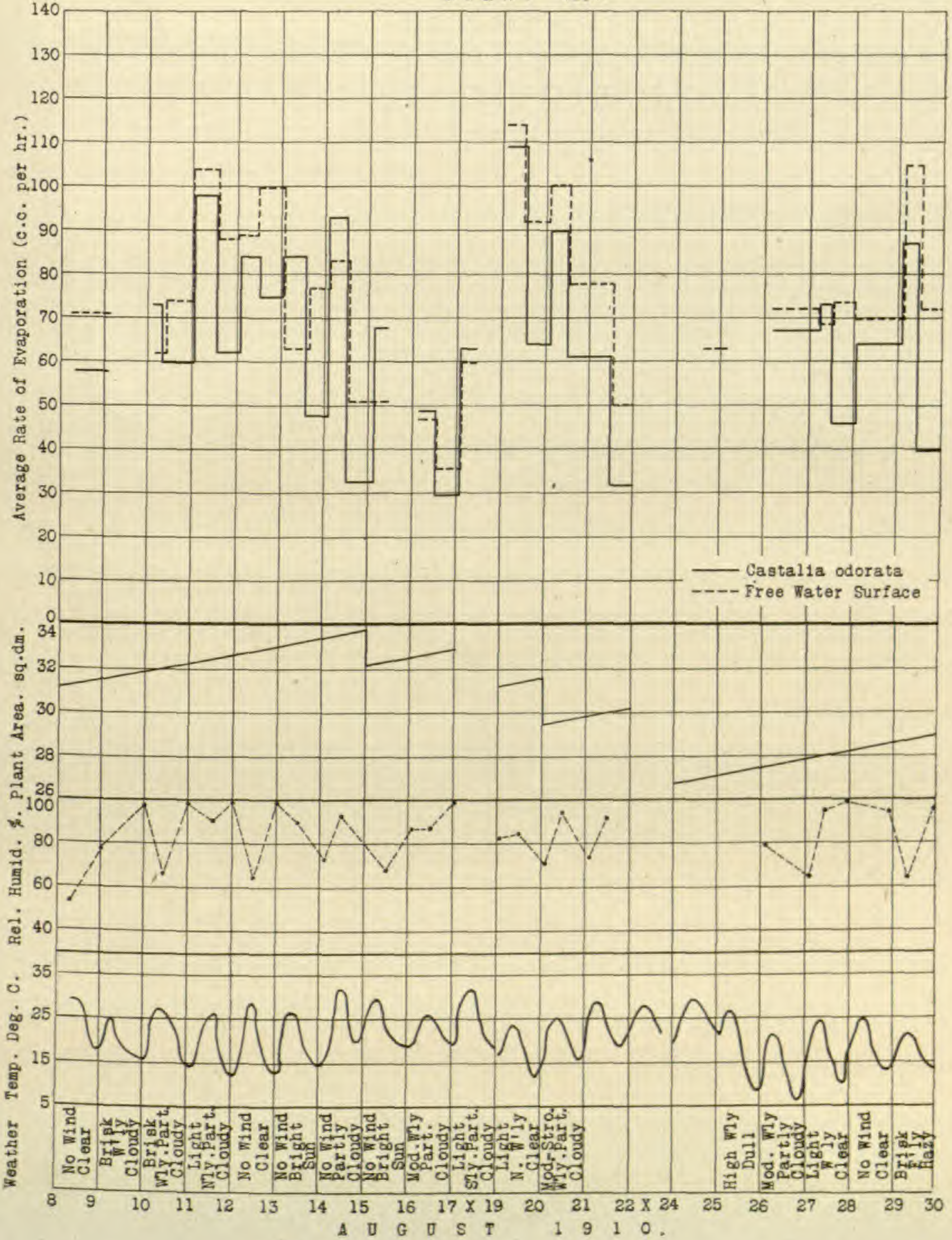
by shading and by hindrance to air movements by the closely growing leaves and petioles. This might explain in a measure, or at least have some influence on, the differences in transpiration rates for different species.

(*d*) *Comparative evaporation from a plant surface and from a free water surface*

Table VI, referred to above, is interesting from the standpoint of a comparison of equivalent areas of plant surface and the surface of free water. It has been commonly held that the transpiring surface of a land plant is normally unable to evaporate as great a quantity of water as is evaporated from a free water surface of the same area and exposed to the same external conditions. GATES (7), experimenting with potted bog plants, makes the statement that three to five times as much water is evaporated from a free water surface as is evaporated from an equivalent area of leaf surface during a hot summer day. This would seem reasonable in view of the fact that the stomatal openings, being widely scattered and not continuous, even when very numerous, do not even approximate the amount of space above a water surface. It should be remembered in this connection, however, that the tissues of water plants are in general very thin, as is evidenced by their early collapse on removing them from the water, and the epidermis shows little or no cuticularization. It is probable, then, that the amount of cuticular transpiration from water plants is greater than is popularly supposed, and that it may compensate to a greater or lesser extent the insufficiency of stomatal openings. In view of these facts the data of table VI show rather interesting results.

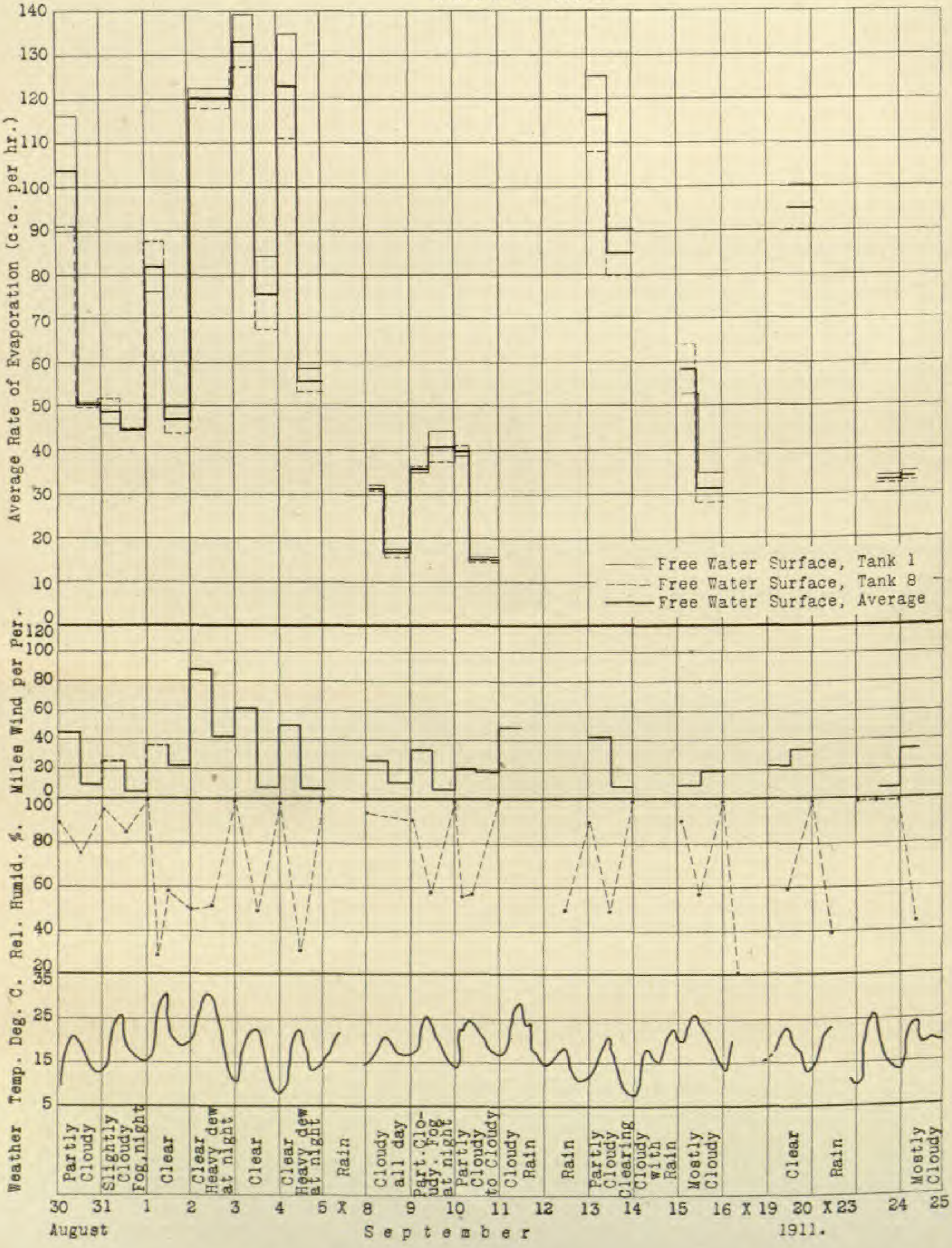
Leaving out the case of the arrow-head for the present, it will be seen that in a majority of the day readings the rate of evaporation from the plant surfaces nearly equals the rate from the free water surface, and in some cases even exceeds this rate. Thus, on August 10, 13, 15, and 17, all of the day rates from the plant surfaces exceeded that from the free water surface; on August 14 and 16 all but one showed a greater rate, pickerel-weed in both instances being deficient; but on August 11 there was only one, and on August 12 there were no plant surfaces with a rate greater than that from free water. The transpiration rates at night from the plant surfaces are low compared with those from the free water surface. The one exception is the water lily, whose transpiration rate at night was relatively high compared with that of the other plants, although in no case recorded did it equal that from the free water surface. Just what is the cause of these variations is not clear, since a survey of the weather conditions for these days gives

CHART VII.



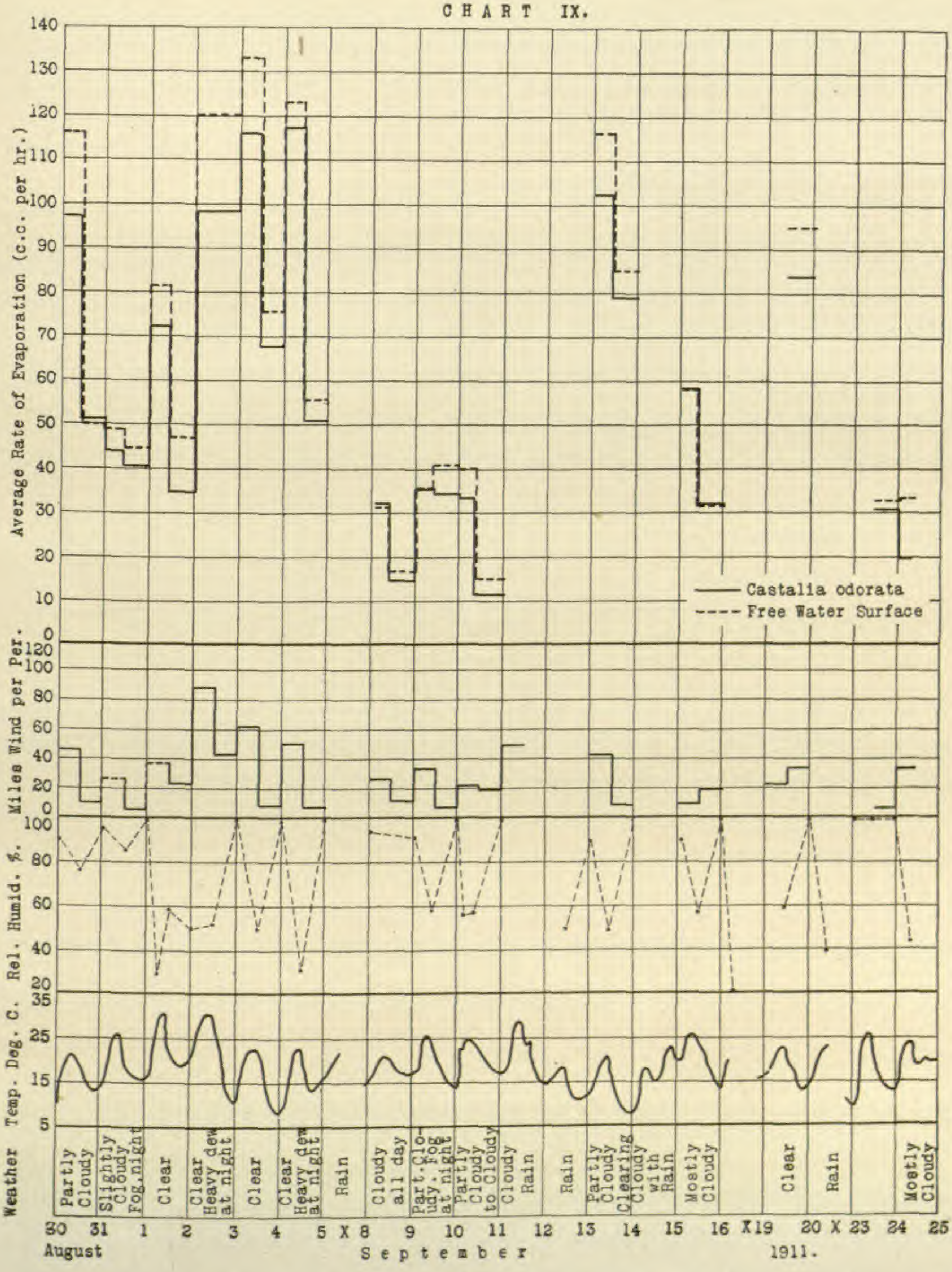
no indication of the controlling factors. The fact, however, that the majority of the day rates is greater than that from free water, while all of the night rates are less, leads to the supposition that the factor, or combination of factors, responsible for the difference acts differently or with different intensities at night than during the day.

CHART VIII.



Among the plants used the water lily offers perhaps the fairest comparison, since the floating leaves are but slightly elevated above the water surface and physical conditions are thus nearly equal for leaf and water surfaces. It is said (8) that the purple coloring matter of the lower side of the lily leaves absorbs the sun's rays and in this way tends to increase the internal temperature of the leaves and hence the transpiration. Experimental evidence seems to be lacking on this point, and it is the belief of the writer that, assuming any slight changes in temperature to be probable, they would be

CHART IX.



counteracted or even destroyed by convection currents in the water surrounding the leaf. It is not thought, then, that the increase in transpiration in the water lily is due to temperature differences, but to other causes. The arrow-head is a transition plant, growing, with some modifications, on land, as well as in water, and it is interesting to note that this plant, even when growing in a hydrophytic habitat, behaves more like a typical land plant in the matter of its transpiration.

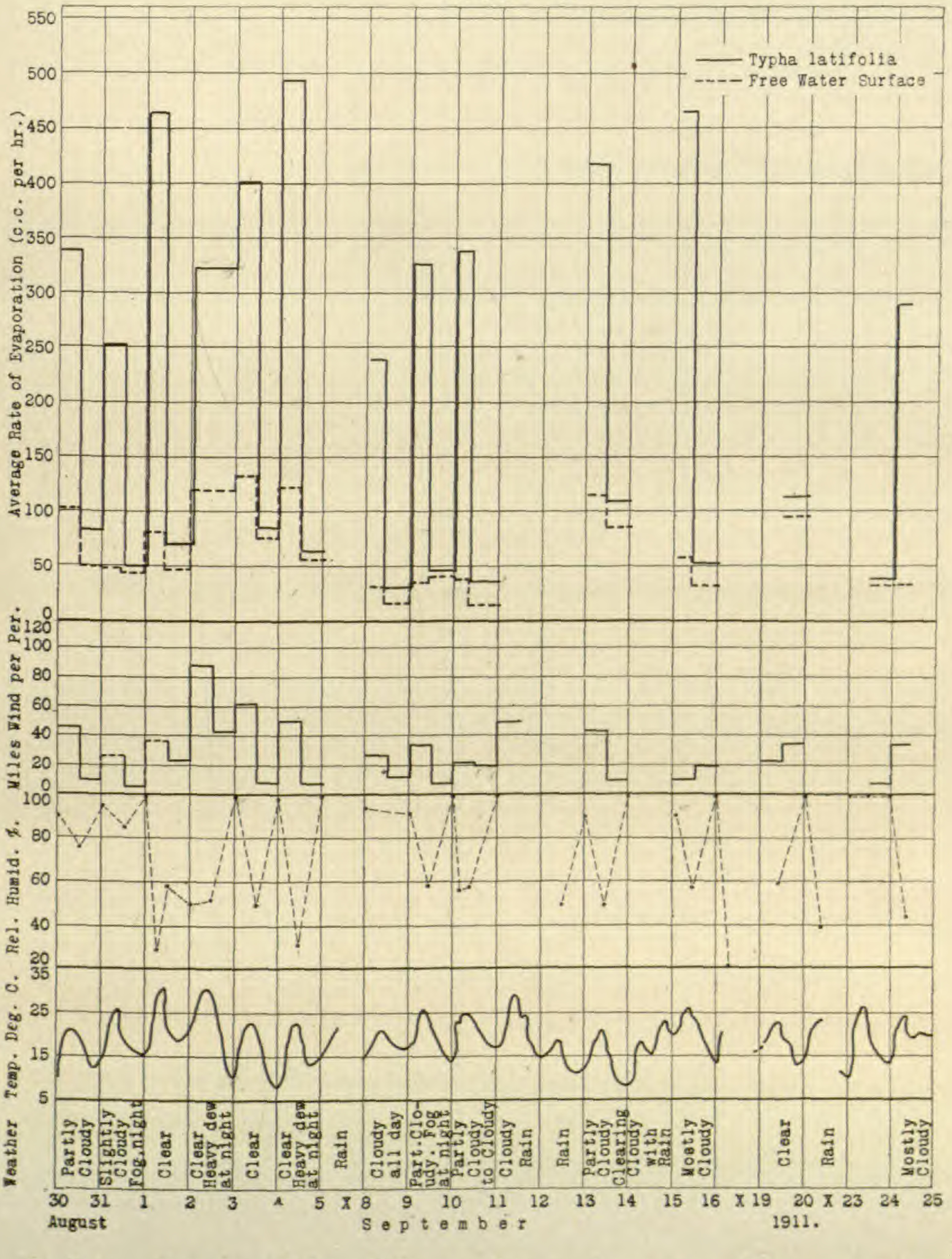
(*e*) *Relation of certain physical factors to transpiration*

An inquiry into the various external factors which exert an influence on transpiration leads to some interesting conclusions. It is not our purpose to consider all of the possible factors which may or may not affect transpiration, nor to consider every factor separately, but rather to consider the combined effect of the more important factors as they occur under natural conditions in the field. Relative humidity, temperature, and wind are quite generally recognized as the principal factors affecting evaporation from an open water surface. In so far as plant transpiration is largely a physical process, omitting, therefore, the phenomena of root pressure, increased protoplasmic activity, and other purely physiological mechanisms, it would be expected that these three factors would be of principal importance in plant transpiration.

1. TEMPERATURE.—The graphs of transpiration shown in charts VIII–XIV show the effect of temperature on the rate of transpiration. With few exceptions the temperature during the night was much less than that during the day. The transpiration graphs show this same relationship as between night and day, the rate during the day being high and correspondingly low during the night. That temperature is not the only factor is shown by the fact that the highest rate of transpiration recorded for most of the plants occurred during the day of September 4, at which time the day temperature was somewhat low. Likewise, during the periods of highest day temperature, that is, September 1, 2, and 15, the transpiration was only moderate. Moreover, on the nights of August 31 and September 3 and 4 the wind velocity was very nearly constant, from 3–5 miles for the period, and the percentage

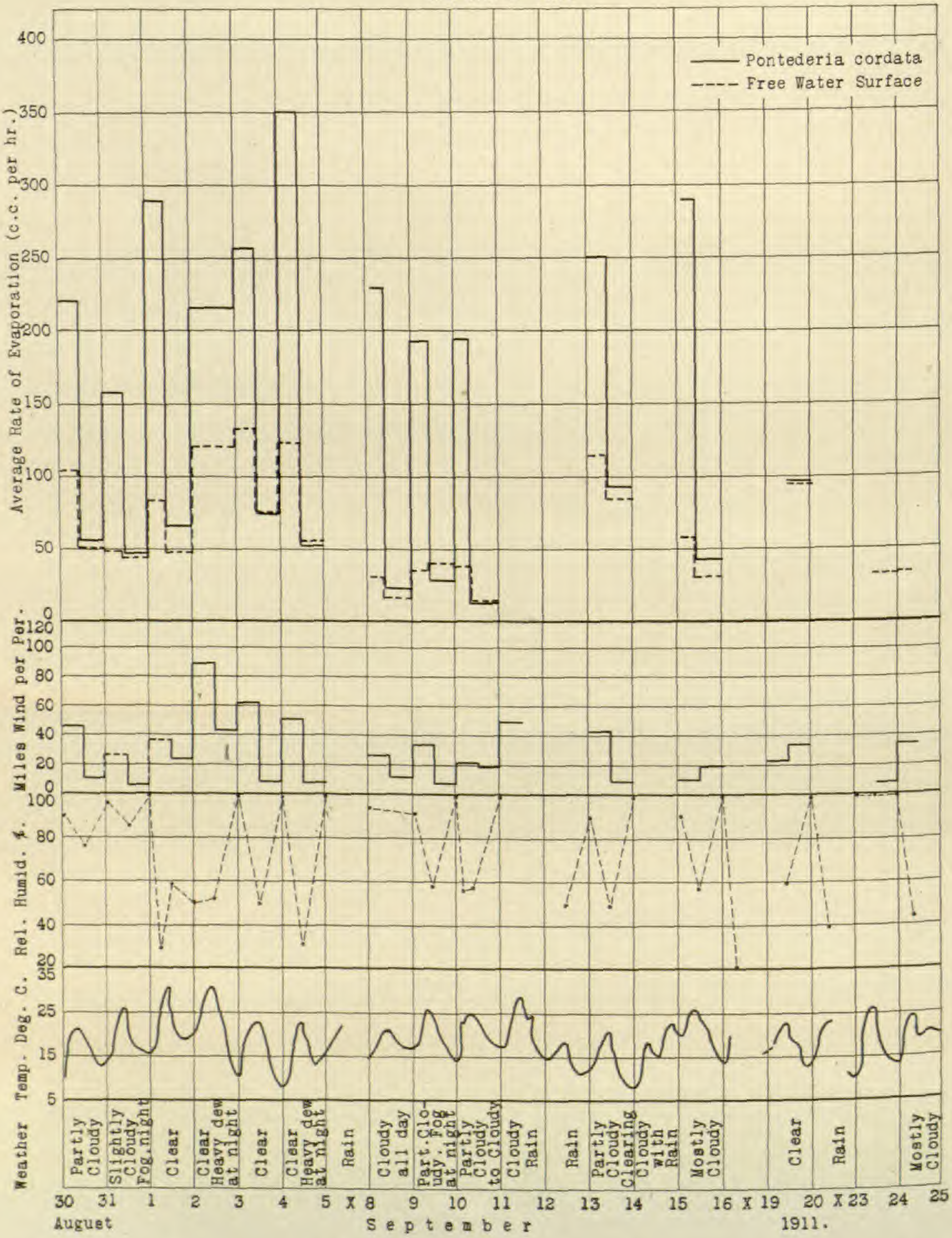
of relative humidity was about the same. The temperatures on the nights of August 31 and September 4 were nearly equal, and for most of the plants the rates of evaporation were correspondingly similar. On the night of September 3, however, the temperature was much lower than in the other two cases, but the rate of evaporation was higher.

CHART X.



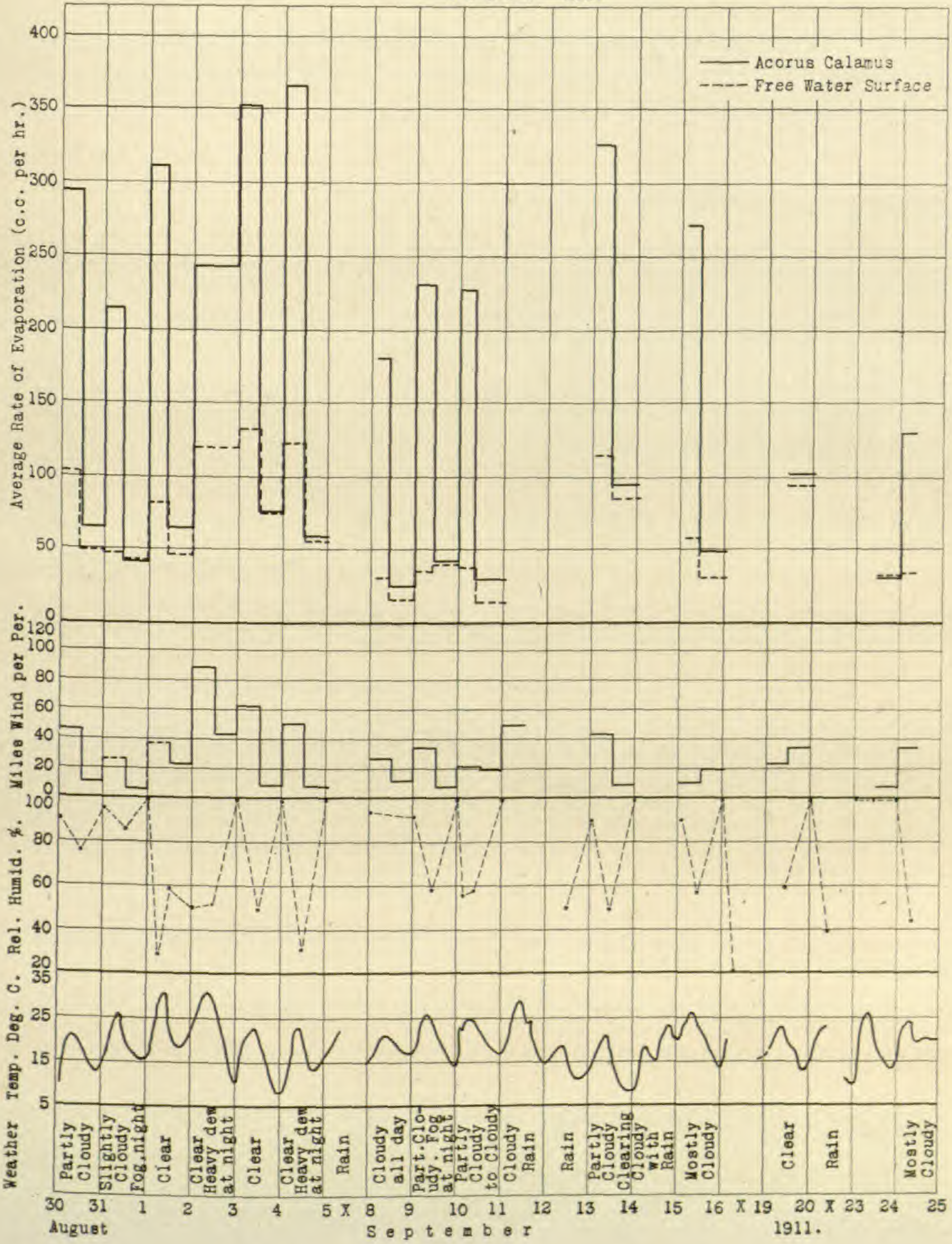
2. Relative humidity.—The records of relative humidity are more or less incomplete, owing to the lack of readings during the day; and it is probable that the day humidity was often less than indicated, although it is thought that these readings are relative. However, it was generally true that the humidity was very high

CHART XI.



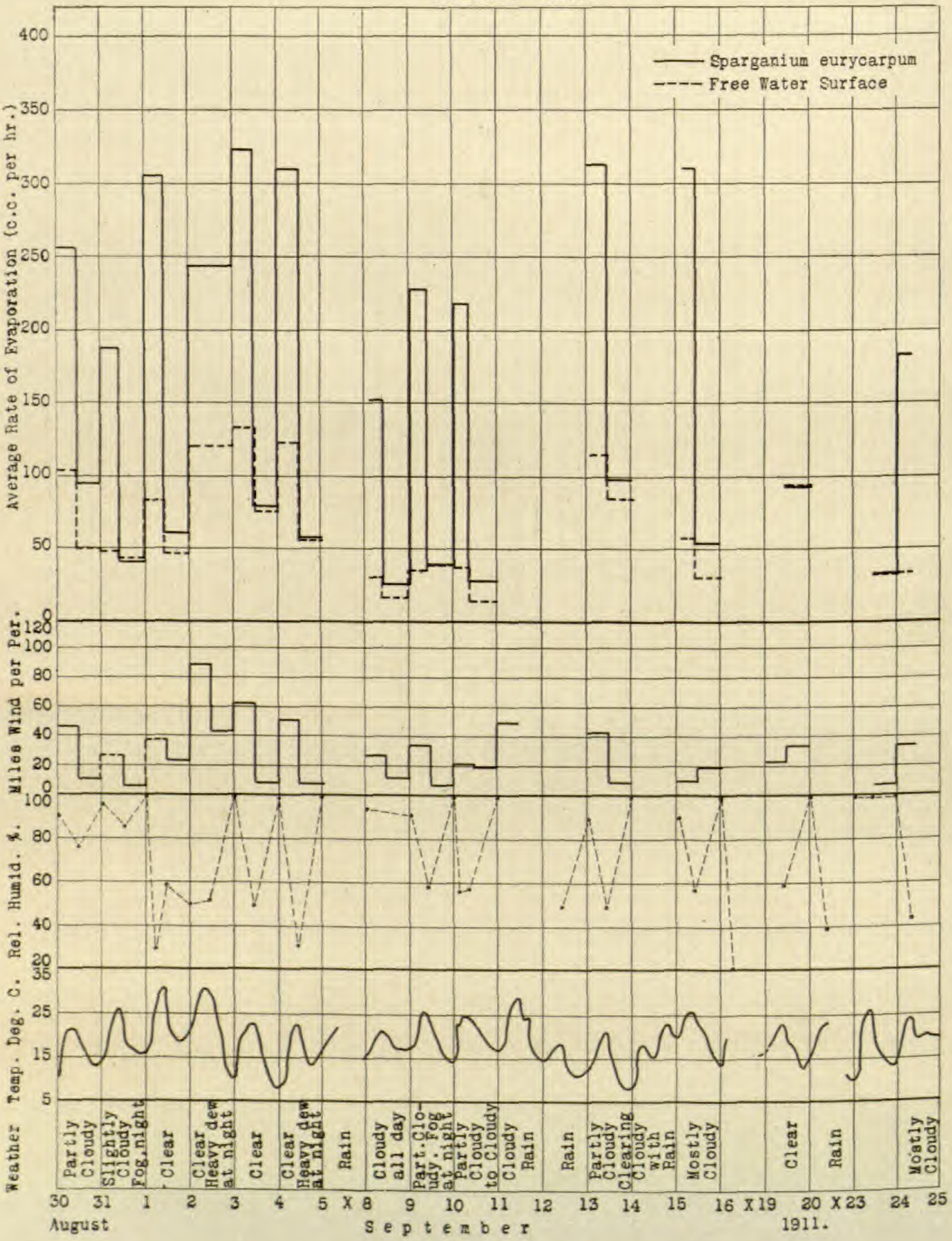
during the night, almost reaching the point of saturation in several instances. Probably this extreme limit was reached in most cases

CHART XII.



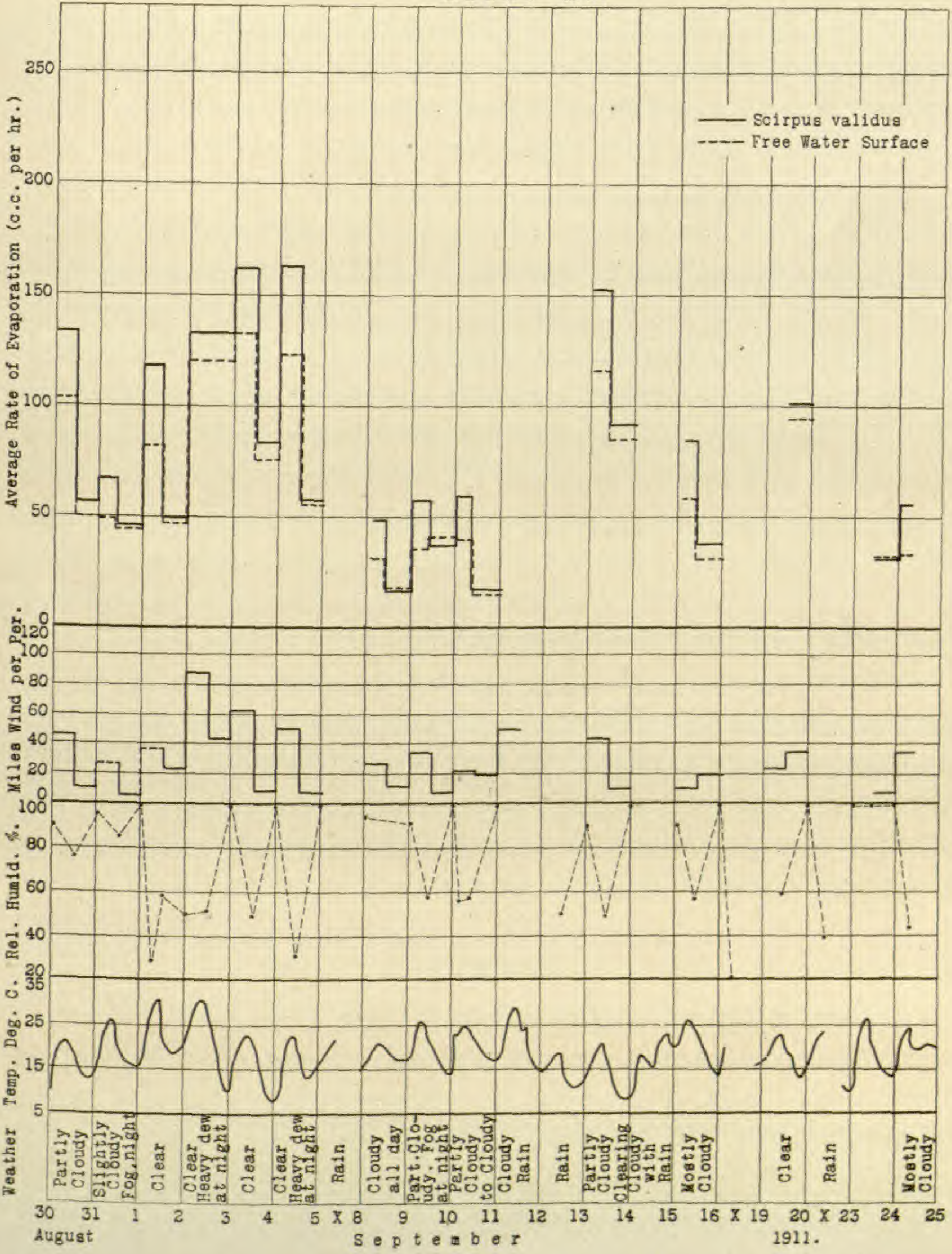
between 4 and 6 o'clock in the morning, when the temperature was at its lowest point. Referring again to charts VIII–XIV, it will be observed that periods of high humidity are accompanied by a low transpiration rate. Also interesting are the results for September 10, when the wind velocity was practically uniform for day and night, and temperature varied through a small range; transpiration was high while humidity was low, with a reversal of positions when the humidity became high.

CHART XIII.



3. **Wind** is undoubtedly an important factor in plant transpiration, at least up to a certain point, that is, to a point at which the

CHART XIV.



wind is strong enough to carry away the moisture as fast as it forms on the surfaces of the plants. It is doubtful, however, if transpiration is materially increased with winds in excess of this amount.

The effect of wind was shown clearly on September 8 (charts VIII–XIV), where relative humidity and temperature did not vary much, but the miles of wind were greater during the day than during the night; the rate of transpiration was greater during the period of greater wind. That wind is a minor factor is shown by the fact that the periods of highest wind velocity are not in all cases periods of highest transpiration rates.

Whether transpiration from plant surfaces is due to one factor more than to another, we are not prepared to say from an examination of the data at hand. Indeed, considering the intimate relation existing between temperature and humidity, it would be impossible to determine the exact influence of the one without being able to maintain the other constant, a state of rare occurrence in nature. And, after all, we are not greatly concerned with these various factors individually, since not one of them of itself is capable of exerting its greatest influence without the accompanying influence of the others. Whether the factors which influence plant transpiration are identical with those which influence evaporation from water surfaces, it is clearly brought out in these experiments that the effects produced on the one and the effects produced on the other are profoundly different in their intensities, and we are led in consequence to the opinion that plant transpiration is not a strictly physical process, but a physiological process as well. The data for 1910 contained in charts I–VII, while not mentioned in detail here, confirm the same conclusions.

Summary

1. Emersed water plants transpire large amounts of water.

2. With one exception (water lily), the evaporation taking place from a water surface occupied by emersed water plants is much greater than that which takes place from a free water surface of the same area and subjected to the same external conditions.

3. The amount of evaporation from a water surface on which water lilies are growing is less than that which takes place from a free water surface of the same area and subjected to the same external conditions.

4. The amount of evaporation from a water surface occupied by emersed water plants depends upon the following factors: (*a*) the species of plant; (*b*) the density of plant stand; (*c*) the amount of plant surface exposed to the evaporating power of the air; (*d*) the height of the plant growth above the level of the water; (*e*) external factors (physical factors, like wind, temperature, relative humidity, etc.); (*f*) internal factors (chemical and physiological phenomena within the plant).

5. Transpiration from emersed water plant surfaces occurs both by day and by night, but transpiration by day is greatly in excess of that by night.

6. For different species there is no constant ratio between rate of transpiration and the area of surface exposed.

7. The rate of evaporation from the transpiring surface of an emersed water plant during the day may equal, and in some cases may exceed, that from a free water surface of the same area; but at night the evaporation from a free water surface is usually greatly in excess of that from a transpiring plant surface.

8. Wind, temperature, and relative humidity undoubtedly have a great influence on the rate of transpiration of emersed water plants, but these factors alone do not explain the great difference existing between transpiration of emersed water plants and the evaporation from a free water surface.

9. These data are of economic importance in indicating what plants should be grown in and what plants should be excluded from storage reservoirs in regions of small rainfall and scant water supply.

In conclusion I desire to extend my hearty thanks to Professor F. C. NEWCOMBE, who has directed this work throughout and who has been a constant inspiration and help, and to Mr. GARDNER S. WILLIAMS and the Eastern Michigan Edison Company for their aid in furnishing the tanks and pontoons and for their suggestions on methods of construction.

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CONTRIBUTIONS TO THE KNOWLEDGE OF THE DIAPHRAGMS OF WATER PLANTS

I. SCIRPUS VALIDUS

LAETITIA M. SNOW

(WITH SIXTEEN FIGURES)

I. Introduction

The form and structure of water plants have been studied by botanists for many years and much has been written on the subject. Many of these investigators, however, have not mentioned the presence or absence of diaphragms in the plants which they have studied, and the reports of those who have considered these structures are often contradictory. The aim of the present paper is to organize these numerous and conflicting reports and to present certain results, which have been obtained chiefly from a study of *Scirpus validus* Vahl. The other forms which have been studied will be referred to as occasion demands. The work has been carried on at Wellesley College and Wood's Hole.

II. Definition of the term "diaphragm"

LEITGEB (18) evidently considers a diaphragm as any partition which breaks the continuity of the air passage, for he speaks of them as being present at the nodes of *Hippuris*. DUVAL-JOUVE (7), DEBARY (6), and SCHENCK (29) deny the presence of diaphragms in *Hippuris*, but GOEBEL (13) uses this form as an example of a water plant with diaphragms. MEYEN (20) states that the hollow stems of the umbellifers and grasses have no cross-walls, but are interrupted at the nodes by masses of tissue. COURCHET (4), however, considers that diaphragms are present at the nodes of the umbellifers, and HACKEL (11*c*) mentions diaphragms of thick tissue at the nodes of grasses. MEYEN (20, 21) states that the canals in the leaves of *Ceratophyllum* and in the stem of *Myriophyllum spicatum* end blindly in thick tissue. According to DUVAL-JOUVE (7) no diaphragms are found in *Myriophyllum verticillatum*, but they are present in the leaves of *Ceratophyllum;* while DEBARY (**6**) denies their presence in both genera.

It is evident, therefore, that some writers consider as diaphragms the thick masses of parenchyma at the nodes of certain plants, while others do not. The loose use of the word has led to much confusion, and it is necessary to define the term. The word "diaphragm" should be reserved for the perforated structures, one to several layers thick, which cross at intervals the air passages of plants. This definition excludes from consideration the woody partitions occurring in the pith of certain trees (*Juglans*, etc.), because they are not only relatively massive, but have been proved by WIESNER and MOLISCH (**36**) to be impervious to air. Owing to the uncertainty as to the exact meaning of the term, unless perforated diaphragms are distinctly mentioned, one can never be sure that such structures are present in the plant under consideration. In the discussion of the distribution of diaphragms among plants, no effort has been made to distinguish the reports of "perforated diaphragms" from those of "partitions," because many references to diaphragms are without descriptions or figures.

III. Occurrence of diaphragms

A. DISTRIBUTION IN THE VARIOUS PLANT GROUPS

From a study of the outline given under the heading above (see p. 514), it is evident that among the angiosperms the great majority of families in which diaphragms have been found are monocotyledons. It cannot be said, however, that they are restricted to this class, or that they are characteristic of certain genera. I have examined representatives of various families of dicotyledons with the result that diaphragms were found in one species only, *Myriophyllum tenellum*. In this species beautiful perforated diaphragms are present at the nodes, while a second species, *Myriophyllum humile,* and a specimen believed to be another species of the same genus show masses of tissue at these points. Further investigations along this line are in progress.

B. IN PLANT PARTS

Diaphragms have been reported for all parts of plants except flowers and fruits, and in the following order as to abundance:

leaves (especially the blade), upright stems, flower stalks, roots, and rhizomes. Only three instances of the presence of perforated diaphragms in roots have been reported: *Enhalus acoroides* (CUNNINGTON **5**), *Hydrocharis morsus-ranae* (SAUVAGEAU **23**), and *Limnobium Boscii* (MONTESANTO **22**). It is possible, however, that the partitions noted in the roots of *Eriocaulon* and a few species of *Paepalanthus* by HACKEL (*11c*) may prove to be true diaphragms. Only one reference (DUVAL-JOUVE **7**) has been made to the presence of diaphragms in rhizomes.

C. UNDER VARYING CONDITIONS OF SOIL MOISTURE

LEITGEB (**18**) states that diaphragms are found "especially in leaves of swamp and water plants." DUVAL-JOUVE (**10**), in his study of partly submerged grasses, found air spaces and diaphragms present in the immersed parts only. SOLEREDER (**32**), on the other hand, reports their presence in the aerial as well as the submerged parts of the leaves of *Stratiotes*. DUVAL-JOUVE (**9**) found no diaphragms in the leaves of *Iris germanica* growing in a dry habitat, but found them in *I. pseudacorus* and *I. foetidissima* growing in water or wet places. He did not, however, test the same species in the two habitats.

My work upon *Scirpus validus* has shown no apparent difference, as to the presence or structure of diaphragms, between the immersed and the aerial parts. Experiments are at present in progress to test the possibility of growing this species in drained soil, and to investigate any structural changes which may take place under drier conditions.

IV. Structure

A. OF DIAPHRAGMS

In accordance with the reports for various plants, the diaphragms of *Scirpus validus* are one to several layers thick. Commonly in old stems the greater extent of the diaphragm is composed of one layer of cells, which increases to several layers around the cross-bundle (fig. 7). As a rule, a diaphragm extends over one air space, but DUVAL-JOUVE (**9**) states that those of *Cyperus Papyrus*, *Thalia dealbata*, *Butomus umbellatus*, and *Sagittaria* *lancifolia* may extend over several spaces; and SCHWENDENER (30) finds the same to be true for *Papyrus antiquorum*. Only in rare instances do the diaphragms of *S. validus* extend over more than one space.

The shape of the cells varies, with the species studied, from polygonal cells with tiny air spaces at the corners, to stellate cells with very much elongated arms. A study of *S. validus*, taken in connection with the reports of DUVAL-JOUVE (9) for *S. lacustris*, *S. littoralis*, and *S. triquetrii*, and of DEBARY (6) and MEYEN (21) for *S. lacustris*, suggests "scirpus type" as an appropriate term by which to designate diaphragms showing the peculiar arrangement of cells characteristic of these species. In this type the cells are elongated and have very short arms. These long narrow cells occur in groups of two, three, four, or five, the usual number being four. While the cells in a single group are all elongated in the same direction, the different groups (with certain exceptions to be noted later) have their axes of elongation pointing in different directions. DUVAL-JOUVE (9) states that *Sagittaria lancifolia* has this type of diaphragm, except that the cells are in groups of two (his figure, however, does not agree with the statement), and that *S. sagittifolia* and *Alisma Plantago* resemble *S. lancifolia*. In another paper (10) he states that the diaphragms in "certain species of grasses" have cells in groups of four. A study (as yet incomplete) of the different species of *Scirpus* leads to the conclusion that some species of the genus may possess more than one type of diaphragm. It has not yet been determined whether any correlation

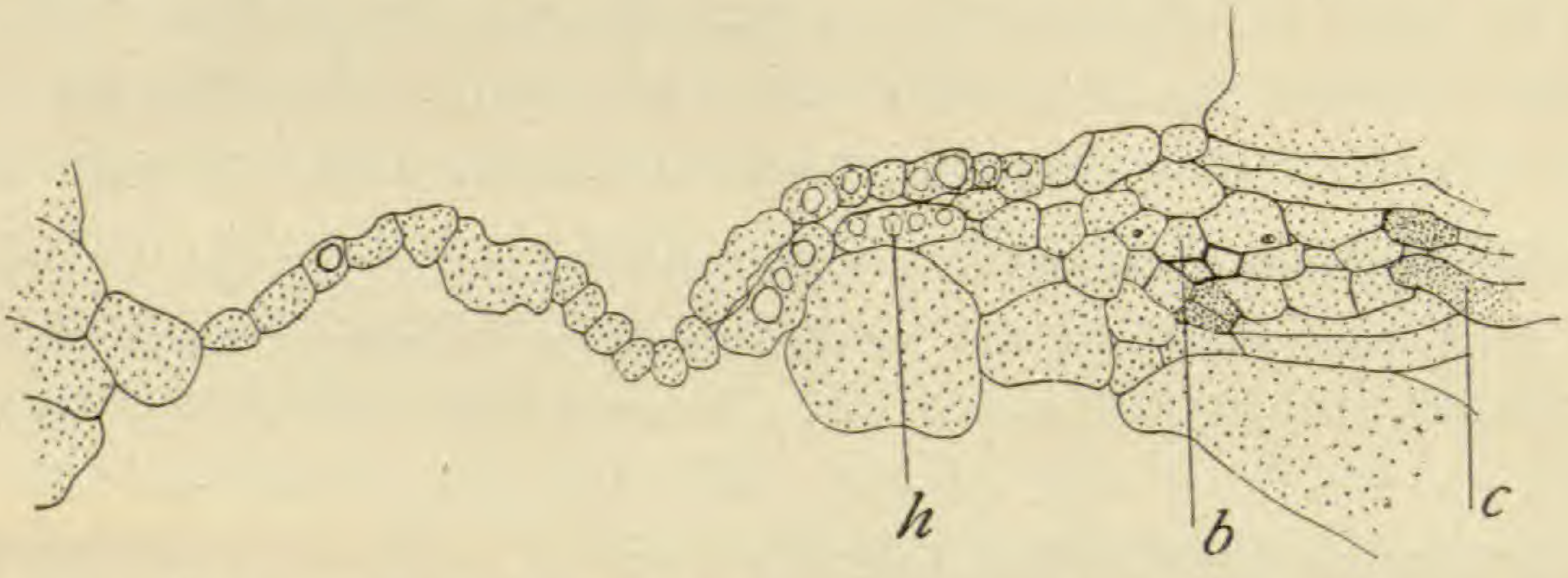

FIG. 1.—Flax seedling: longitudinal section through hypocotyl: *c*, ordinary cortical cells; cells are elongating in the direction of food current passing to meristem beyond ~~h; b, young bundle; ×110~~.
m; ×100.

exists between the different types of diaphragm and the presence or absence of cross-bundles.

Although both vascular and non-vascular diaphragms are mentioned by writers, the former so far outnumber the latter that some authorities consider the chief function of diaphragms to be the support of the cross-bundles. In *Scirpus validus* the presence of cross-bundles is so nearly universal that the relatively few instances where they cannot be found lead one to suspect that in these cases the material has been broken or a section or two lost at the critical point.

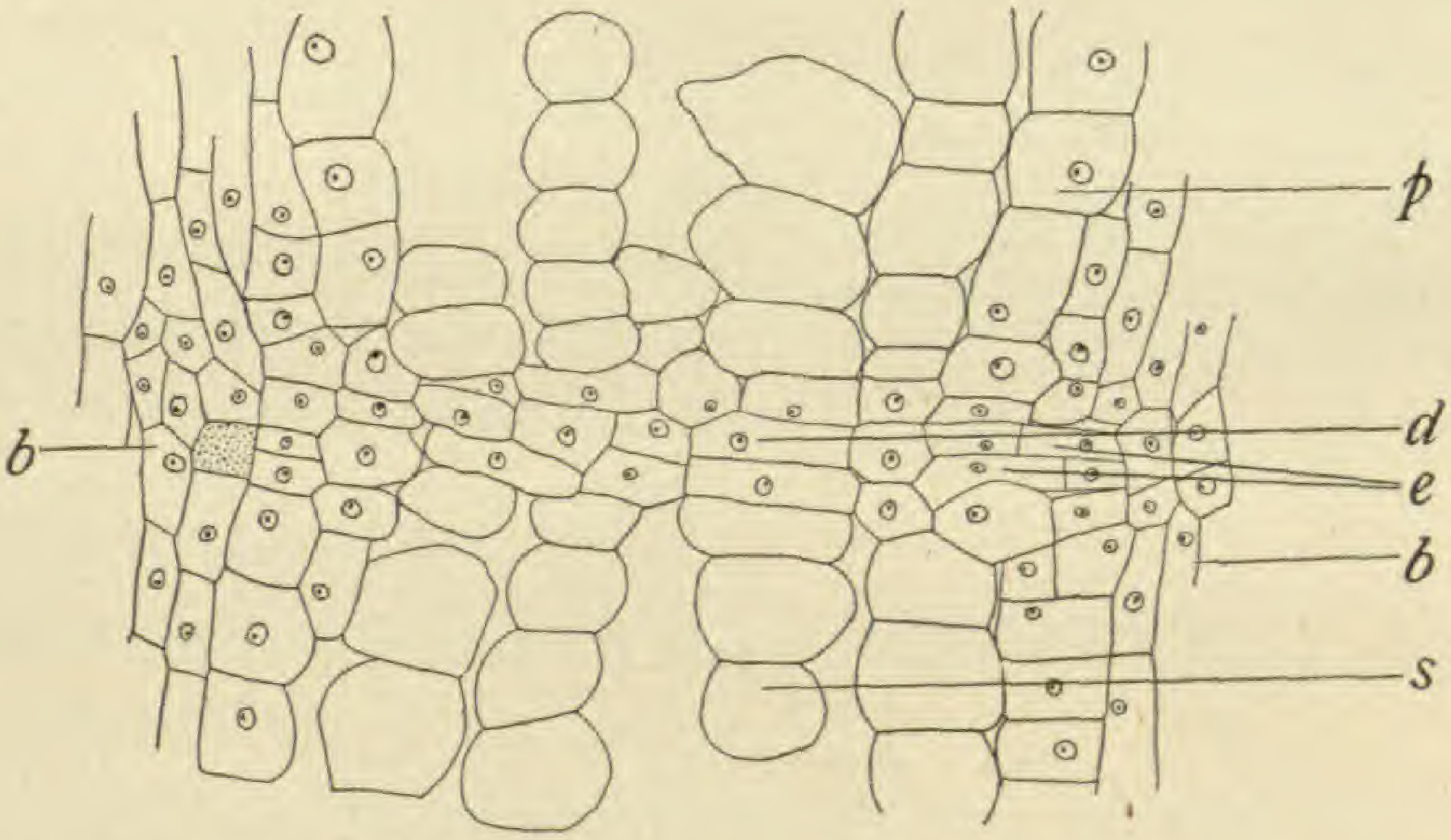

FIG. 2.—*Scirpus validus:* longitudinal section of very young stem: diaphragm cells elongating to form cross-bundle; nuclei indicate the greater density of protoplasmic contents of cells of diaphragm and partition walls of spaces; some nuclei were not demonstrable but were placed arbitrarily; *p*, partition cells; *d*, diaphragm cells; *b*, young longitudinal bundle; *s*, cells of space; *e*, elongating cells; ×175.

B. OF CROSS-BUNDLES

DUVAL-JOUVE (**9**) describes the cross-bundles of *Musa paradisiaca* as containing large spiral vessels; those of *Butomus umbellatus, Alisma Plantago, Sagittaria lancifolia,* and *S. sagittifolia* as bundles of tracheae. He states in one report (**8**) that the cross-bundles connect with the outer part of the longitudinal bundles. In his next paper (**9**) he describes a cross-bundle as articulating itself with the side of the longitudinal bundle, a little back of the large vessels and opposite the interior region of tracheids and small vessels. A figure in a third paper (**10**) shows a cross-bundle uniting with the phloem.

A study of the cross-bundles of *Scirpus validus* leads to the conclusion that both conditions occur, and are dependent upon the age of the diaphragm. In the very young stem the cells of the cross-bundle are similar to those of the diaphragm and connect with the phloem (figs. 2 and 12). Later the cells greatly elongate, some of those in the center of the bundle become transformed into tracheids with very indistinct spiral (?) markings, and a secondary connection with the xylem of the longitudinal bundle is established (figs. 3 and 4).

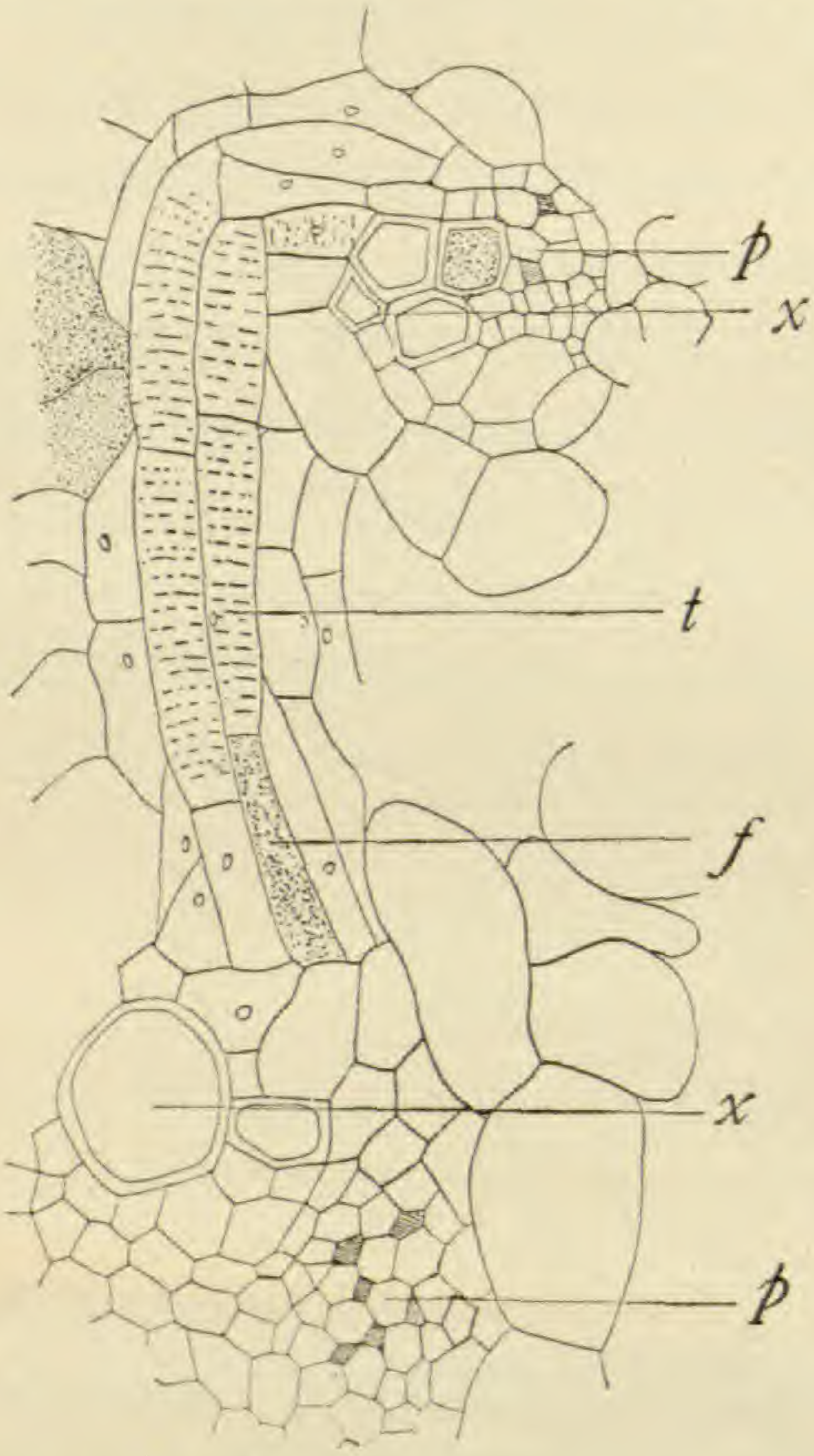

FIG. 3.—*Scirpus validus:* cross-section of stem: two longitudinal bundles connected by a cross-bundle; connection originally with phloem (*p*); tracheids (*t*) have formed and made secondary connection with xylem (*x*); the connection is not yet established with larger bundle; this bundle lies near the edge of a space, but is not connected with a diaphragm; *f*, food storage cells; ×175.

DUVAL-JOUVE (**9**) mentions the fact that in *Sagittaria lancifolia* the bundles do not run on the diaphragms but in them, thus implying that the reverse is usually the case. The diaphragms of *Scirpus validus* run in the diaphragms, as is shown in fig. 5.

V. Origin

A. OF THE STELLATE PARENCHYMA

The canals of many water plants are filled with a network of stellate cells. In the case of *Scirpus validus* the cells on the upper and lower surfaces of the diaphragms connect directly with these stellate cells, and in some places have been seen to grade into them. It is necessary, therefore, to inquire into the origin of the stellate tissue.

SCHACHT (**28**) states that the arms of the stellate cells are caused by greater growth, due to a greater amount of nourishment, at certain points. LEITGEB (**18**) discusses the development of this tissue at some length, and considers the star-shape to be a result of adhesion at certain points, combined with the growth of the surrounding tissue and the "pressure of the secreted air." That the growth of the surrounding tissue causes a pulling out of the cell is indicated by the "diminishing cell body." He adds that the arms, after having been formed, increase in size (presumably by growth). DUVAL-JOUVE (**7**) considers that the body of the cell does not increase in size, but that the arms grow out as rays; the presence of apparently bifurcated rays indicates a pulling out of the body. In another paper (**10**) he speaks of the pulling out of the cells from the points of contact. SCHWENDENER (**30**) believes stellate cells to be due, not directly to a pull, but to growth under a tension caused by the faster growth of the surrounding tissue. DEBARY (**6**) speaks of cells growing into long arms. LE BLANC (**17**) gives the same explanation as LEITGEB (whose paper he has apparently not seen), and proves the existence of tension in stellate tissue by an experiment. By bursting one of the stellate cells in a diaphragm, he found that a round hole resulted, which was larger than the original cell, and which was caused by a retraction of the surrounding cells.

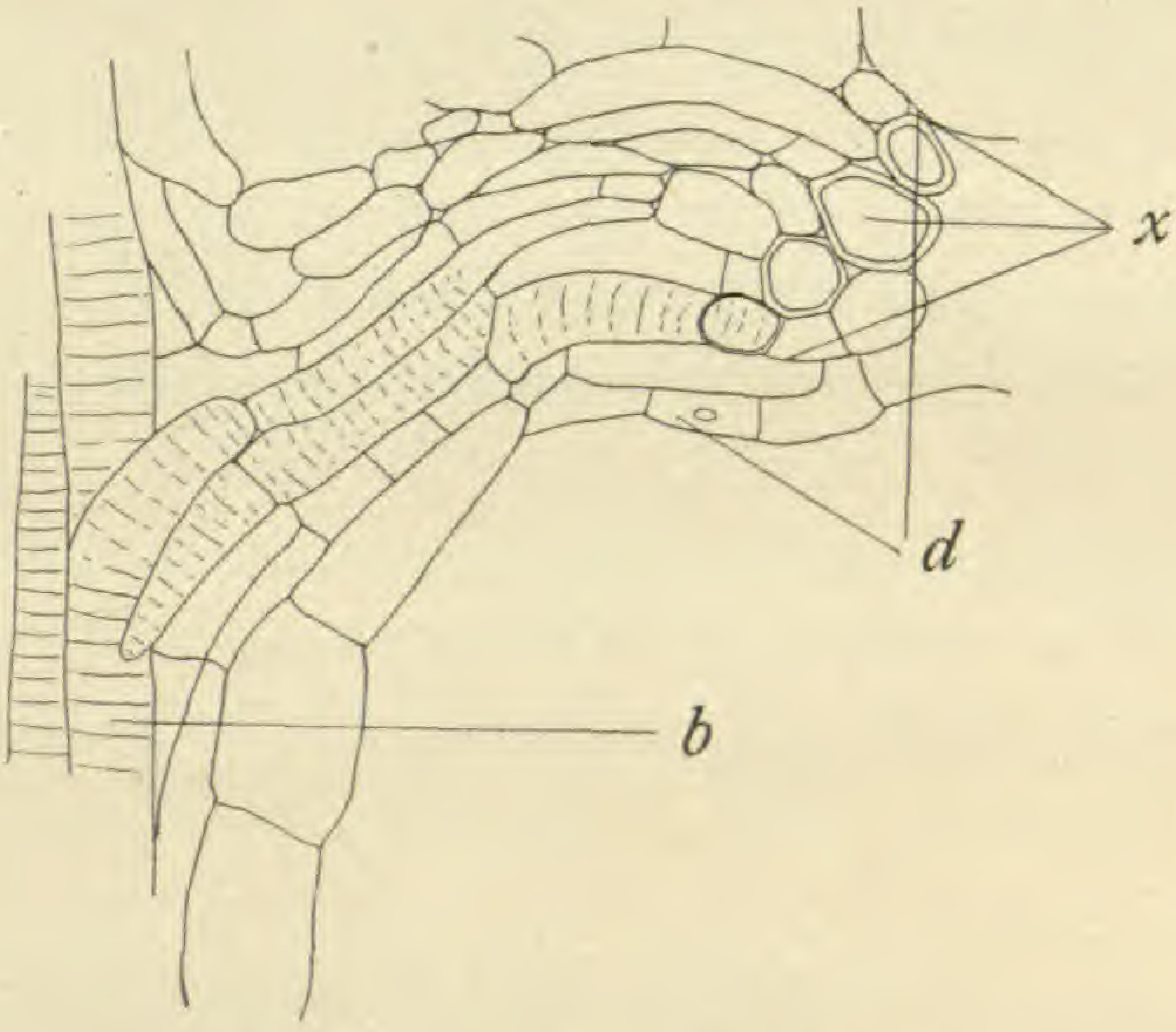

FIG. 4.—*Scirpus validus:* longitudinal section of stem: cross-bundle curving, part in cross-section (*x*) and part in longitudinal section; xylem making connection with xylem of longitudinal bundle (*b*); ×175.

LEITGEB (**18**) does not explain the formation of the intercellular spaces otherwise than by the pressure of the secreted air. TSCHIRCH (**34**) thinks that intercellular spaces are formed by a splitting of the primary membrane, because the spaces are covered with a substance giving the same reaction as the primary membrane. GOEBEL

(13), in his study of aerenchyma, came to the conclusion that the cells adhere by the thickenings of the walls, while the pits remain free. MANGIN (19) believes the split to be due to a gelatinization of pectates in the wall, which substances, in consequence, line the intercellular space thus formed.

A study of the stellate parenchyma of *Juncus effusus* leads me to the conclusion that SCHWENDENER has given the correct explanation of the origin of this type of cells. All cells pass through a curve of growth. The center is the oldest part of the pith and reaches the mode of the curve first. As the growth in this region becomes slower, the outer parts are approaching the mode of the curve.

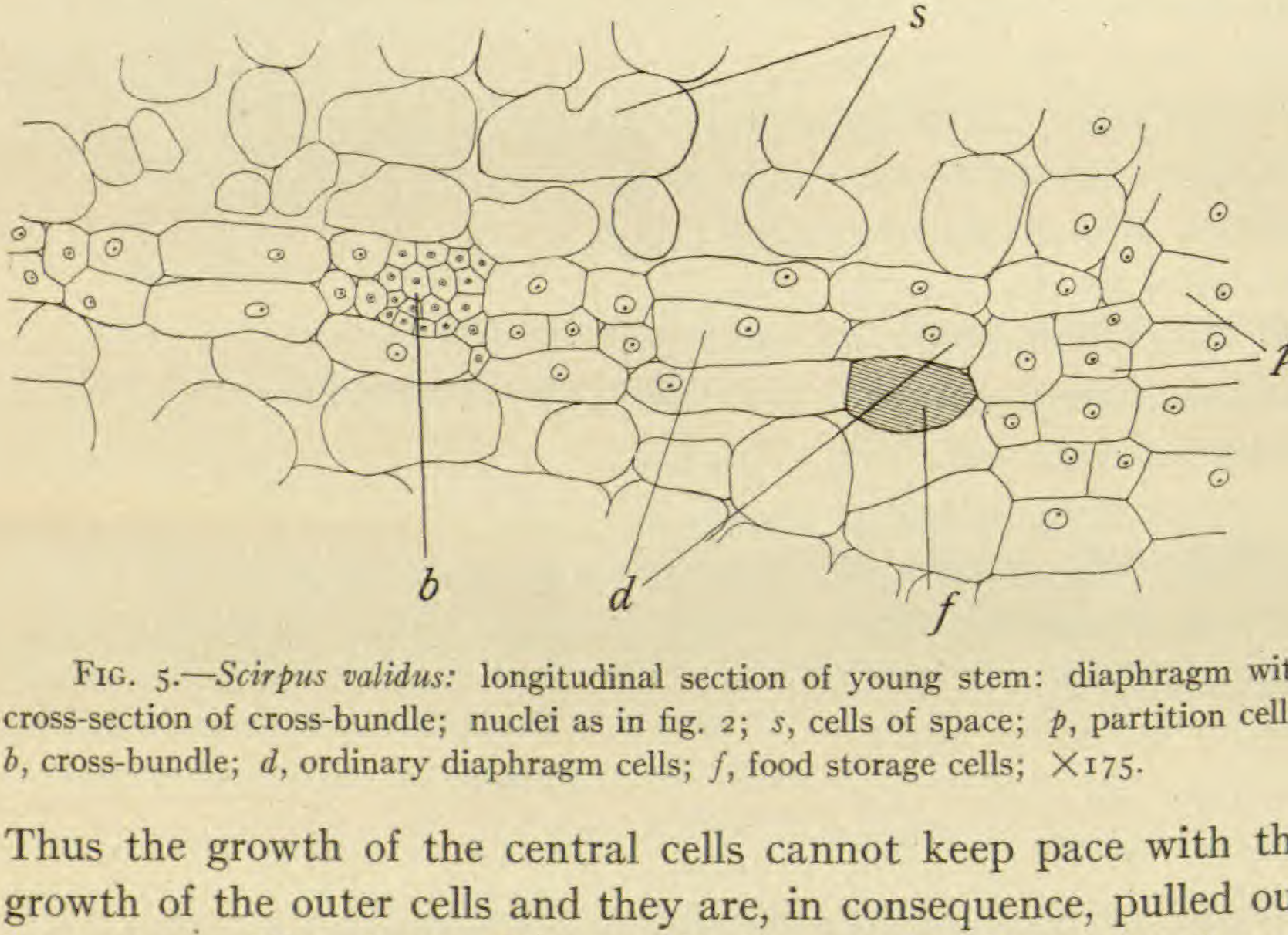

FIG. 5.—*Scirpus validus:* longitudinal section of young stem: diaphragm with cross-section of cross-bundle; nuclei as in fig. 2; *s*, cells of space; *p*, partition cells; *b*, cross-bundle; *d*, ordinary diaphragm cells; *f*, food storage cells; ×175.

Thus the growth of the central cells cannot keep pace with the growth of the outer cells and they are, in consequence, pulled out into arms. The slower the growth the greater the proportion of pull, and consequently very old cells have quite long, slender arms. By taking an average of the longest and the shortest diameters of the bodies of many pith cells at the same stage of development, and comparing it with similar averages for pith cells at different stages, it was found that the cell body passed from 25.6 μ at the tip of the stem, to 21.5 μ a little farther back, and to 17.1 μ still farther back. In any one section the cells at the center are at a much later stage of development than those toward the outside of the stem (fig. 16).

B. OF DIAPHRAGMS

LEITGEB (18) states that he cannot account for the fact that some cells do not pull out, but remain as diaphragms. MEYEN (21), studying *Scirpus lacustris*, and FALKENBERG (12), studying *Typha* leaves, state that diaphragms result from stellate parenchyma by a separation of this tissue into layers. CUNNINGTON (5) finds that the diaphragms in the leaves of *Enhalus acoroides* arise from small cells cut off from the original mesophyll cells. These small cells increase in one plane and form plates separating the other mesophyll cells, which elongate in a plane perpendicular to these plates and thus separate them by spaces.

In *Scirpus validus* there are no special cells which give rise to diaphragms. In *Juncus effusus* the parenchyma splits into layers which retain an occasional vertical connection (fig. 15). In longitudinal sections of *Scirpus* a similar layering may be observed. The cells of some of the layers retain their meristematic character and continue to divide and to keep pace with the growth of the surrounding tissues, thus forming diaphragms. The other cells become stellate by the process already described (figs. 2, 5, 12, 13).

C. OF THE GROUPS OF CELLS IN THE DIAPHRAGMS

Several writers have noted or figured the diaphragm cells in groups of four. DUVAL-JOUVE (9) reports this arrangement for several species of plants, but offers no explanation as to the origin of the groups. DEBARY (6) believes each group of cells in the diaphragms of *Scirpus lacustris* to originate from one mother cell.

From a comparison of figs. 12 and 13, it seems evident that such an origin as that suggested by DEBARY is reasonably probable. The number, however, is not invariably four, but groups of three and five also appear (fig. 6). The reason for the formation of two, three, or four walls parallel to the long axis of the cell is not easily explained in terms of cytological mechanics. It was suggested to me that a study of the adventitious buds of flax seedlings might throw light upon the subject. Flax seedlings were grown, therefore, until the cotyledons had opened, and were then decapitated. After about a week or ten days small swellings (adventitious buds) appeared on the hypocotyl. It is found, upon studying longitudinal sections of these hypocotyls, that the meristem of the bud is composed of small cubical cells which have arisen, by division, from the epidermis and outer cortical cells. Deeper cortical cells, however, are found to be elongating and apparently dividing parallel to their long axes, that is, in the direction of the current of food materials passing to the growing meristem (fig. 1).

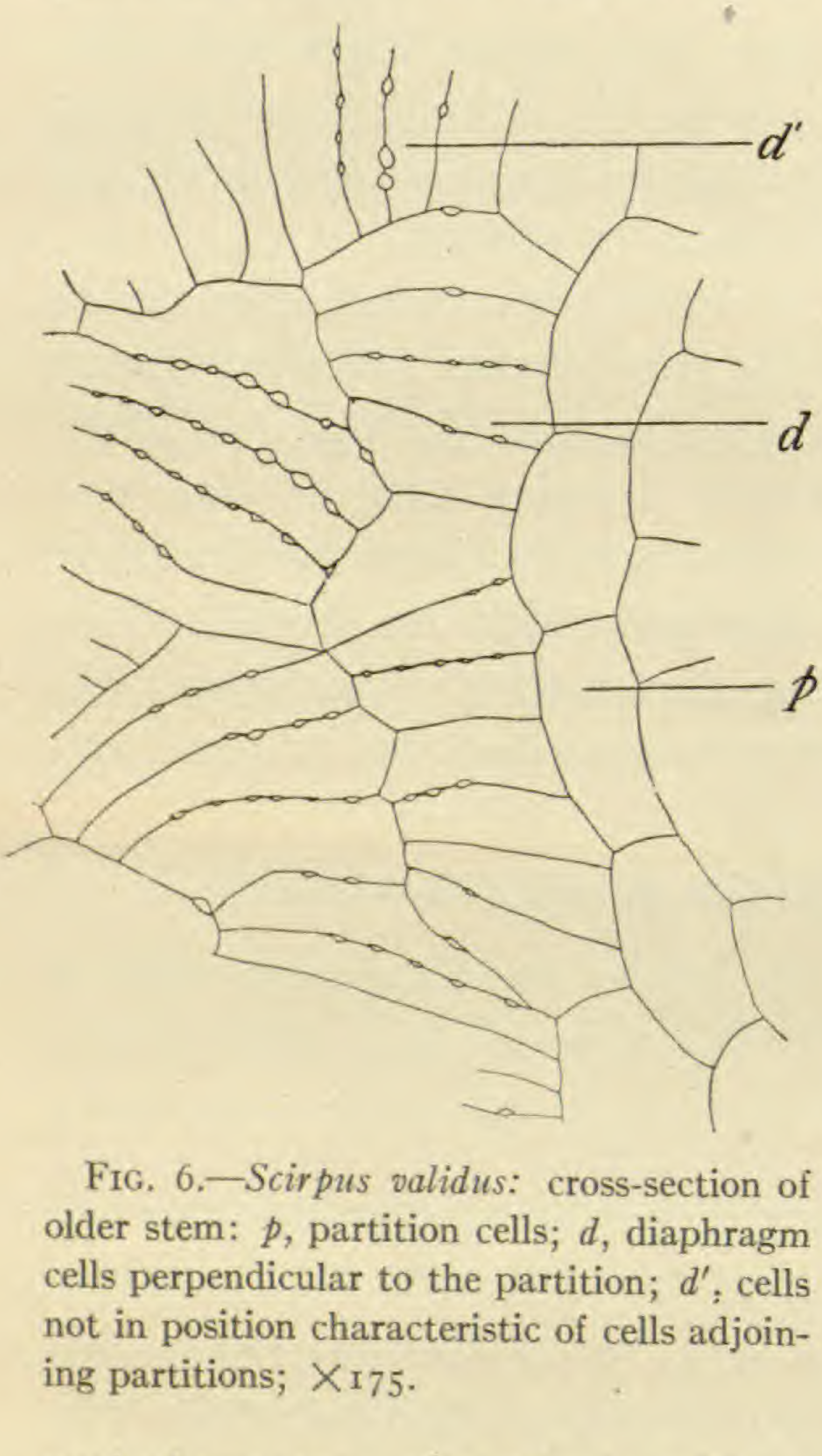

FIG. 6.—*Scirpus validus:* cross-section of older stem: *p*, partition cells; *d*, diaphragm cells perpendicular to the partition; *d'*, cells not in position characteristic of cells adjoining partitions; ×175.

It is well known that HABERLANDT (**15**) correlates the shape of the palisade cells with the transportation of the products of photosynthesis. A similar elongation of cells for the purpose of conduction is found in the secondary transfusion tissue of *Cycas*, where, according to WORSDELL (**38**), the ordinary mesophyll cells become modified in order to supply water to the parts of the leaf which are distant from the bundle. From GOEBEL'S study of adventitious buds (**14**) it is seen that the bundle becomes differentiated first in the leaf and afterward extends itself backward, until it reaches and becomes connected with a bundle in the stem. This elongation of cells to continue the bundle may be interpreted as a result of the current of food materials passing to and from the growing leaf. In a similar way the current of food materials from the cross-bundle to the partition walls of the air space may determine the direction of the walls of the groups of cells in the diaphragms.

VI. Function of diaphragms

A. MECHANICAL

1. *To resist strain.*—SCHWENDENER (**30**) considers diaphragms to be girders; HABERLANDT (**15**) and LE BLANC (**17**) agree with him, but believe strengthening to be only one of their functions. This is probably true. If certain species of *Juncus* with nodose stems and leaves be compared, it will be seen that those forms having firm, stiff outer walls have a smaller number of cross-partitions than have those with softer walls.

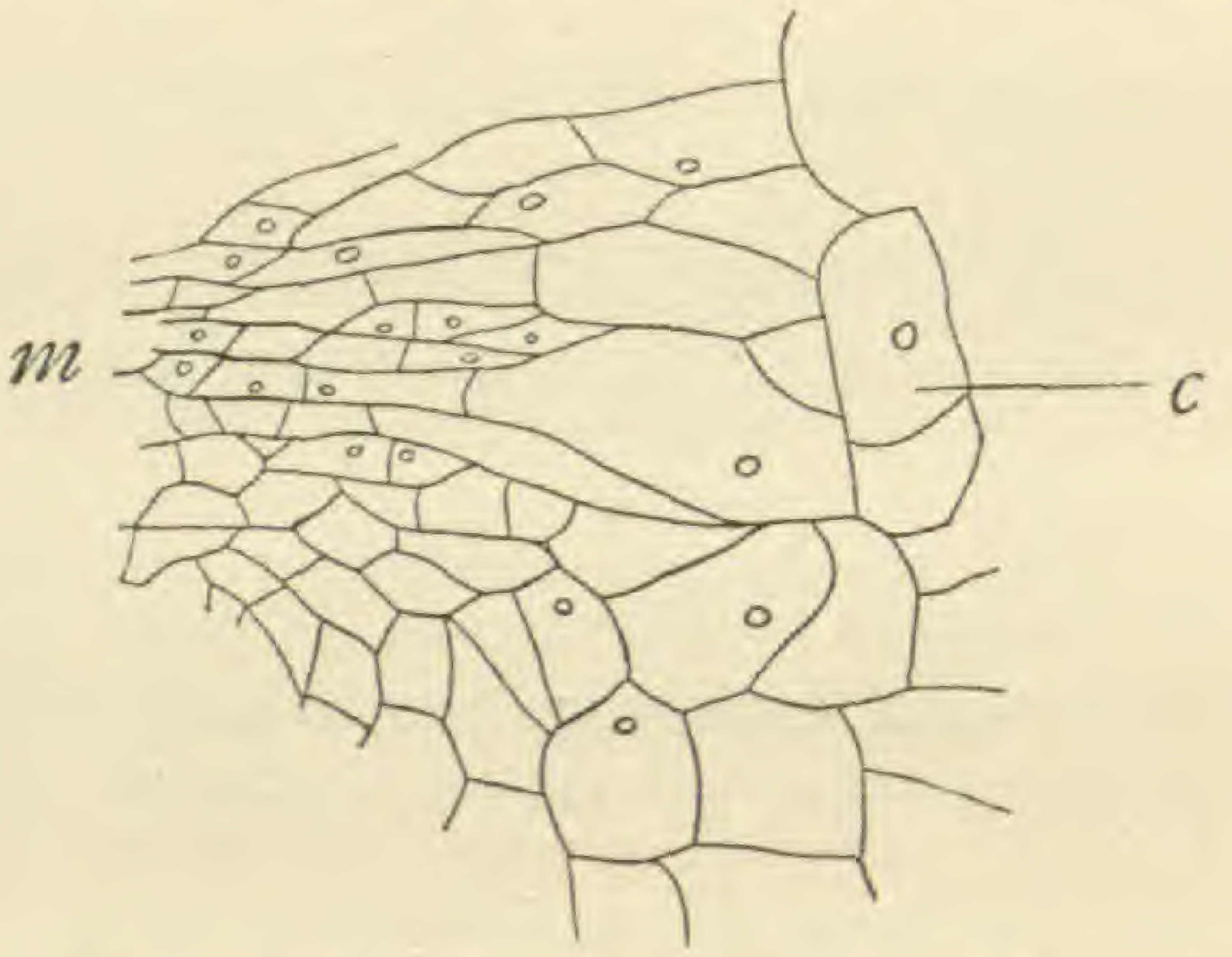

FIG. 7.—*Scirpus validus:* longitudinal section of stem: diaphragm varying in thickness; cross-bundle (b) at edge of diaphragm establishing connection (c) with a longitudinal bundle beyond section; cells stippled to distinguish from spaces; h, cut arms of cells; × 100.

2. *Support of cross-bundles.*—LEITGEB (**18**), DUVAL-JOUVE (**9**), DEBARY (**6**), and SAUVAGEAU (**25**) definitely state that diaphragms are for the support of cross-bundles. LE BLANC (**17**) assigns it as one of their functions. Where cross-bundles occur there can be no doubt as to the value of such support. It cannot be assigned as a function of all diaphragms, however, because non-vascular diaphragms appear to be characteristic of certain plants.

B. TO PREVENT THE ENTRANCE OF WATER

GOEBEL (**13**) believes that diaphragms are of use in keeping water from entering broken parts, stating that it takes great pressure to infiltrate the air passages. It is quite probable that the small size of the perforations in the diaphragms prevents the entrance of water against the pressure of the contained air. The fact that, in order to force killing fluids into the tissues of plants with diaphragms or with small intercellular spaces, it is necessary to exhaust the air with a pump indicates the difficulty with which water penetrates small openings against air pressure. This difficulty might be increased by the presence of cutin on the walls of the diaphragm cells, but the walls of these cells in *Scirpus validus* give the cellulose reaction only.

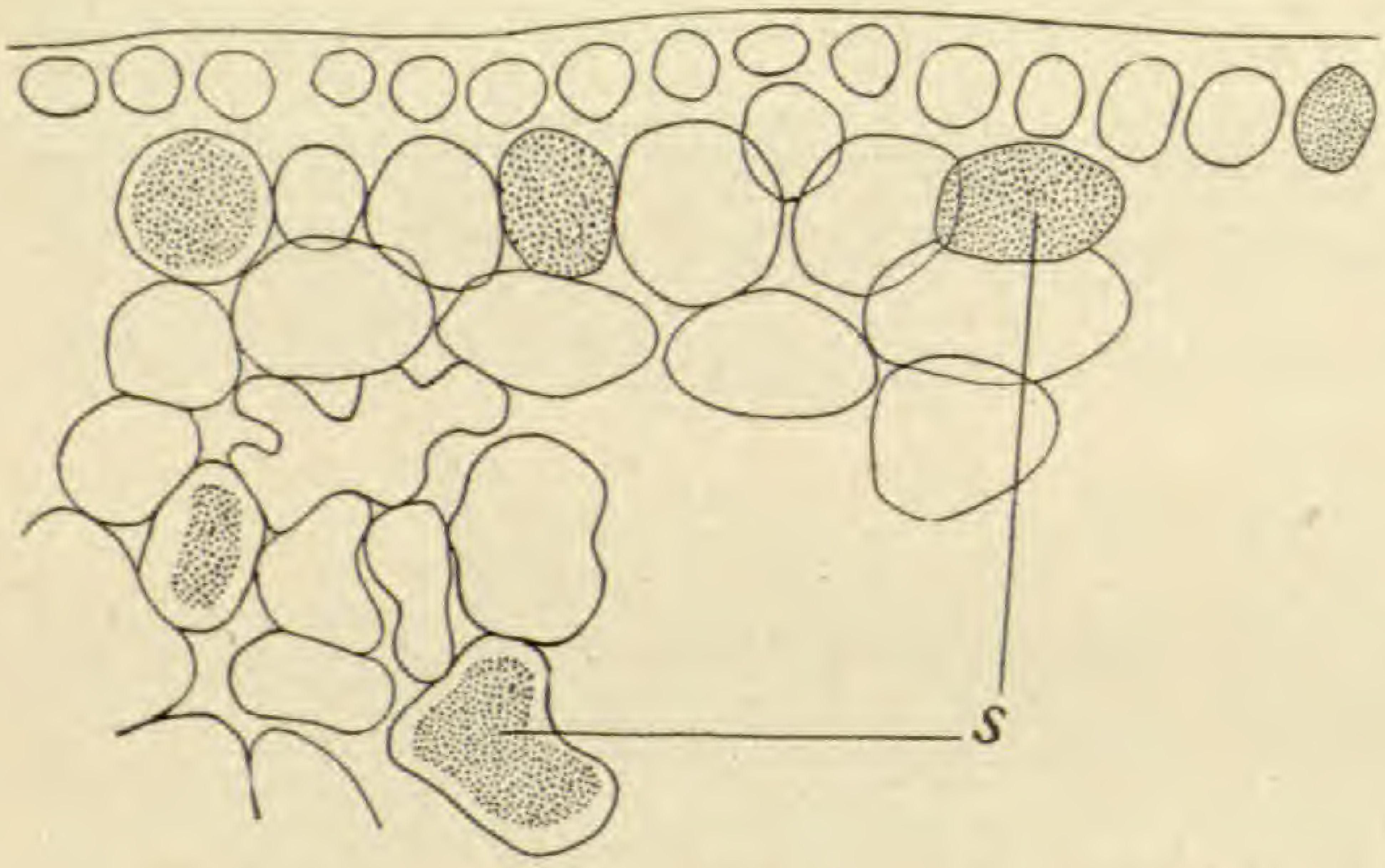

FIG. 8.—*Scirpus validus:* a few cells from cross-section of leaf of young bud: epidermis, parenchyma, and spongy tissue of air space shown; section treated with Fehling's solution; strong reaction indicated by stippling (*s*); merely size, position, and shape of cells indicated; ×175.

SAUVAGEAU (27) found that after injecting the stem with water, some of the canals were suberized, and concluded that suberization takes place after contact with water, to prevent infiltration of the surrounding tissues. As he offers no direct proof of suberization following contact with water, definite conclusions cannot be derived from this work.

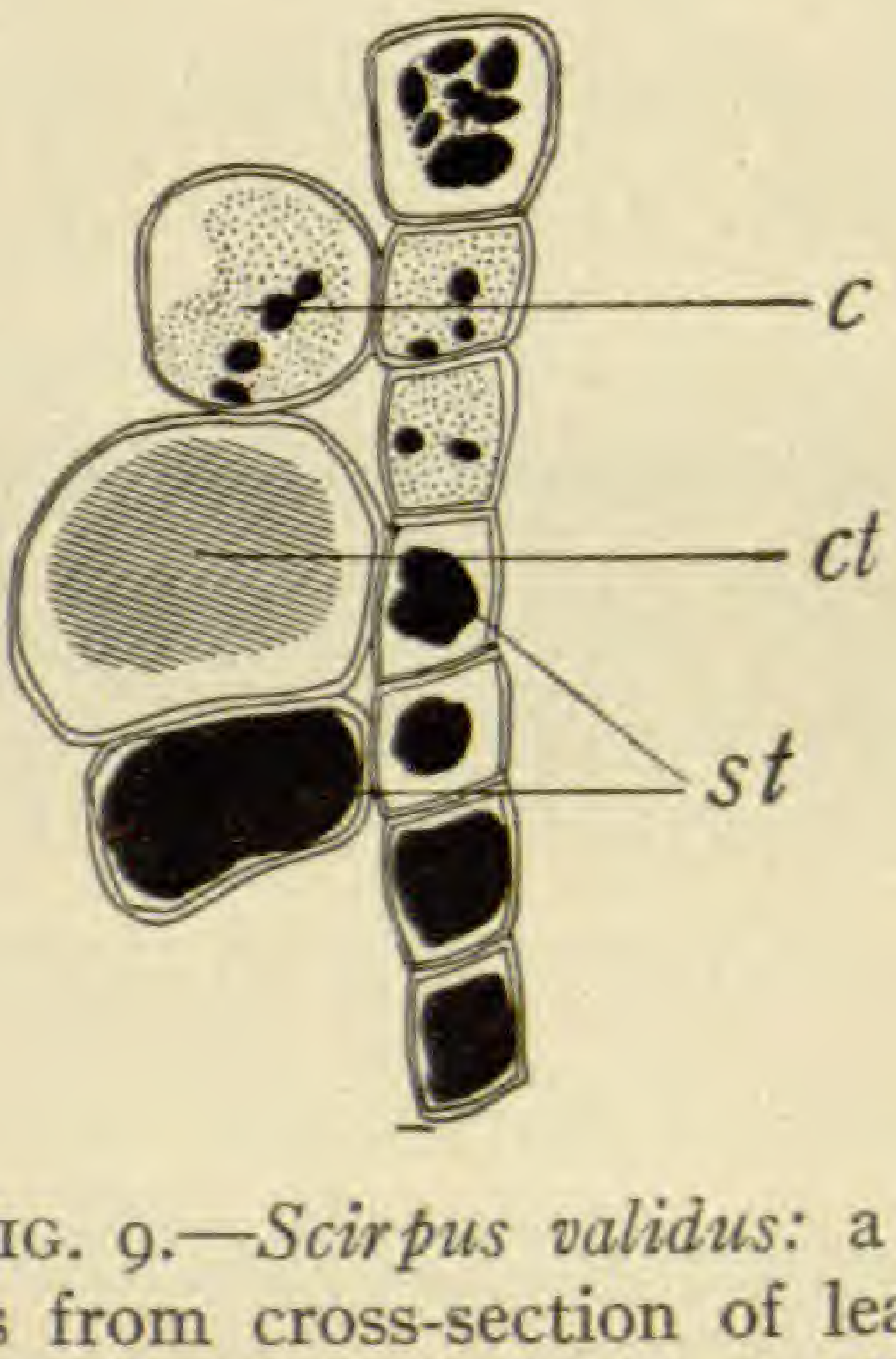

FIG. 9.—*Scirpus validus:* a few cells from cross-section of leaf of young bud: treated with Fehling's solution, I in KI, and $K_2Cr_2O_7$; *c*, cell showing cytoplasm and scattered starch grains; *ct*, cell with contents plasmolyzed, starch grains not distinguishable; *st*, cell which has reduced Fehling's solution and given tannin test with $K_2Cr_2O_7$; ×175.

C. TO AID IN CIRCULATION OF AIR

HABERLANDT (15) and LE BLANC (17) include this among the functions of diaphragms. It seems evident that, given partitions, it is advantageous to have them perforated, to allow circulation of air. The statement made by GOEBEL (13) that non-perforated diaphragms in *Pontederia crassipes* (*Eichhornia*) allow circulation of air needs proof.

D. NUTRITION

LE BLANC (17) supports CHATIN[1] in believing nutrition to be one of

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[1] CHATIN, ADOLPHE, Anatomie comparée des végéteaux. Paris. 1856–1862. I have not been able to obtain this publication.

the functions of diaphragms. Food manufacture undoubtedly takes place, to some extent, in very young diaphragms of *Scirpus validus* which are close to the exterior. As the stem grows larger and the diaphragms are removed from the exterior by the growth of the outer tissues, they lose their chlorophyll and appear glistening white.

E. STORAGE

That food (or waste) is stored in diaphragm cells is evident at a glance (figs. 12 and 13), but the nature of the stored material has not been definitely determined. SAUVAGEAU (**24–27**) notes secretory cells in various forms of water plants, and in certain places definitely calls the contents tannin. SOLEREDER (**31**) records the presence of tannin-bearing cells in the diaphragms and the walls of air spaces of the Hydrocharitaceae. He tested with vanillin and concentrated hydrochloric acid, as suggested by HARTWICH and WINCKEL (**16**), and obtained the phloroglucin reaction. He obtained the same result with HCl alone, which showed that an aldehyde, similar in action to vanillin, was present. He found in *Vallisneria* that the contents of certain cells gave the tannin reaction with iron, while other cells were filled with a clear oil-like material.

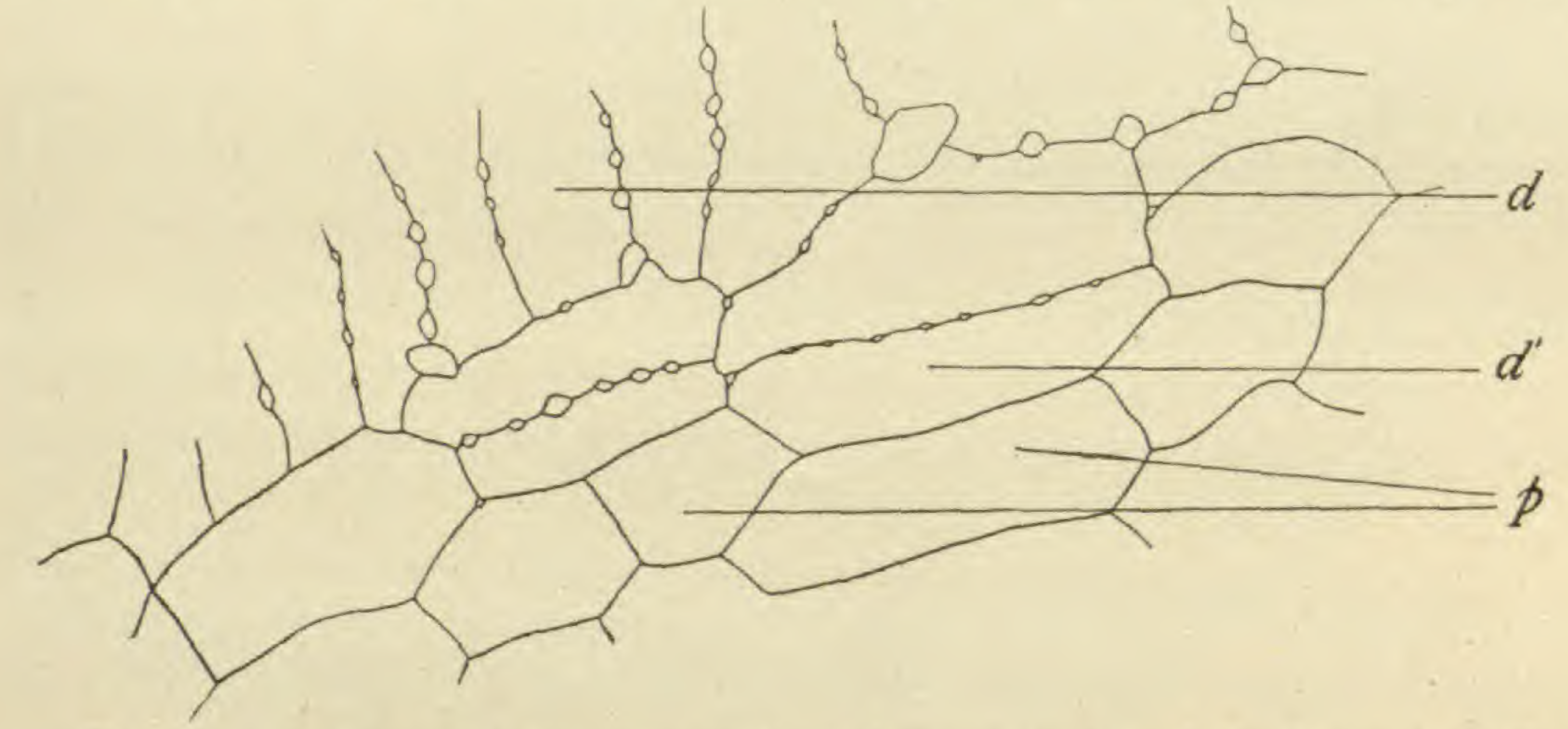

FIG. 10.—*Scirpus validus:* cross-section of stem at edge of diaphragm: *d*, diaphragm cells in position characteristic for cells adjoining a partition; *d'*, cells of partition which have assumed the character of diaphragm cells and are therefore not in the characteristic position; *p*, partition cells; ×175.

In material of *Scirpus validus* killed with chromacetic acid, many brown storage cells appear. An investigation of the chemical nature of the storage material led to the following results. Fresh sections after having been boiled in Fehling's solution showed many red-brown cells (fig. 8). The sections were then washed in water and treated with a solution of iodine in potassium iodide. These "sugar cells" remained red-brown, while the others gave a strong starch reaction. The sections were again washed in water and then treated with potassium bichromate, and the reddish cells turned very dark brown. Fig. 9 shows a portion of a section at this stage. Tested with ferric chloride these "sugar cells" gave the characteristic tannin reaction. TRIMBLE (33) states that glucose is frequently present with tannin, and also that tannin will reduce Fehling's solution; consequently the reactions described above may be due to tannin and glucose or to tannin alone. TRIMBLE also found that in the rhizome of *Acorus Calamus*, the tannin-bearing cells were quite distinct from the starch-bearing cells.

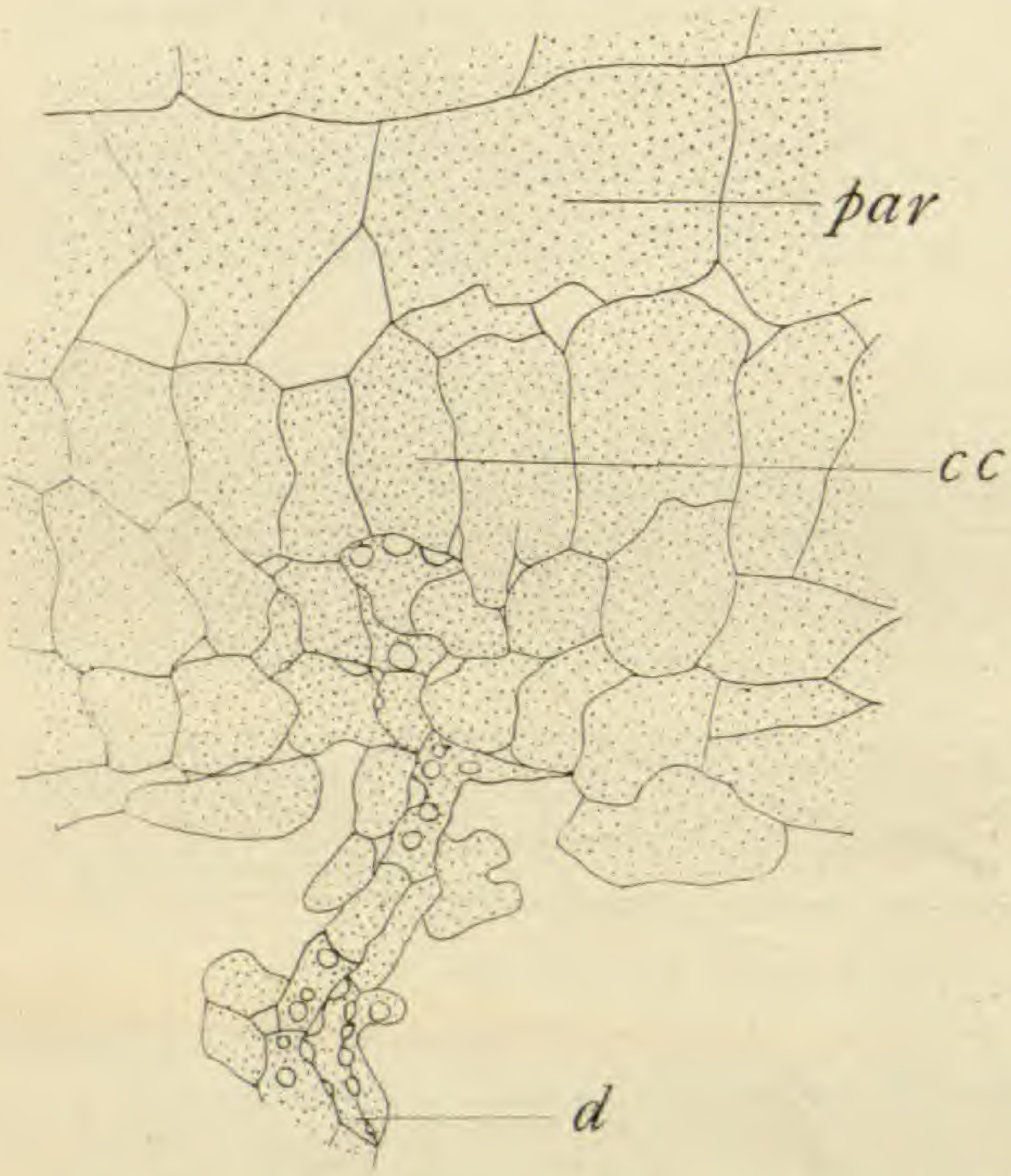

FIG. 11.—*Scirpus validus:* longitudinal section of stem: *d*, diaphragm extending into partition; *par*, ordinary, polygonal, partition cells; *cc*, partition cells elongated for conductive function; circles in cells indicate cut arms; stippling to distinguish cells from spaces; ×110.

When fresh specimens of *Scirpus validus* were tested with vanillin and concentrated HCl, according to the method described by HARTWICH and WINCKEL (16), it was found that numerous cells turned ruby red. This reaction showed the presence of phloroglucin or some related tannoid. The reaction did not take place with HCl alone, therefore the necessary aldehyde was not present in the cells. Washing the sections in water caused the red color to disappear, and subsequent treatment with $K_2Cr_2O_7$ brought out strongly the tannin reaction. This took place at once, instead of slowly, as before the phloroglucin test.

To ascertain if gallic acid was present, fresh sections were treated with potassium cyanide (TRIMBLE 33). The majority of the sections gave no reaction, but one or two showed a faint diffuse pinkish tint at one corner where there was a mass of very dark brown sclerenchyma cells. Left over night, many cells turned a very pale brown, thus showing the presence of tannin rather than gallic acid. When the sections, which had been washed after the phloroglucin test, were treated with KCN, many cells (presumably those which had responded to the previous test) immediately turned dark brown. It is thus seen that after the phloroglucin test the tannin reaction takes place with great rapidity and clearness.

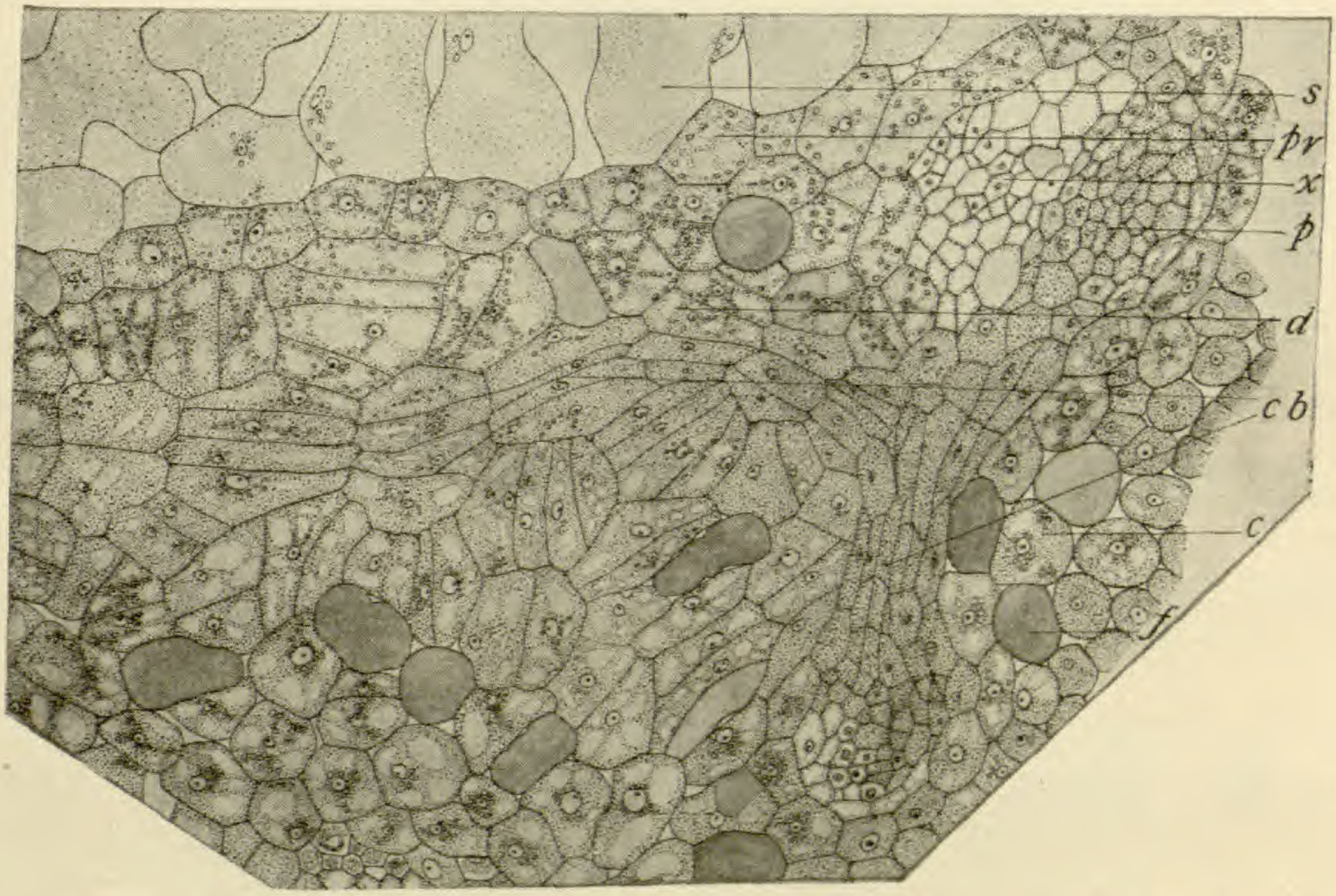

FIG. 12.—*Scirpus validus:* cross-section of tip of very young stem: two longitudinal bundles and connecting cross-bundles (*cb*); the latter runs in a diaphragm (*d*); cross-bundles connect with phloem (*p*); diaphragm cells starting to form groups; note similarity between cells of diaphragm and of cross-bundles; *c*, cortical parenchyma; *pr*, partition wall separating two spaces; *s*, cells of space; *x*, xylem; *f*, food storage cells; ×175.

Since the fresh cells give the tannin reaction with $K_2Cr_2O_7$ and $FeCl_3$, and also the phloroglucin reaction, it is possible that the food is stored as some tannin compound containing the phloroglucin radical. I am not sufficiently familiar with the chemistry of the tannin compounds to make any further suggestions as to the nature of the stored material.

Storage cells are very abundant in the diaphragms and in the parenchyma of the stems of *Scirpus validus*, but are also present in the scales of young buds, the spongy parenchyma of the rhizome, and in both longitudinal and cross-bundles. They have not been observed in the young roots of this species.

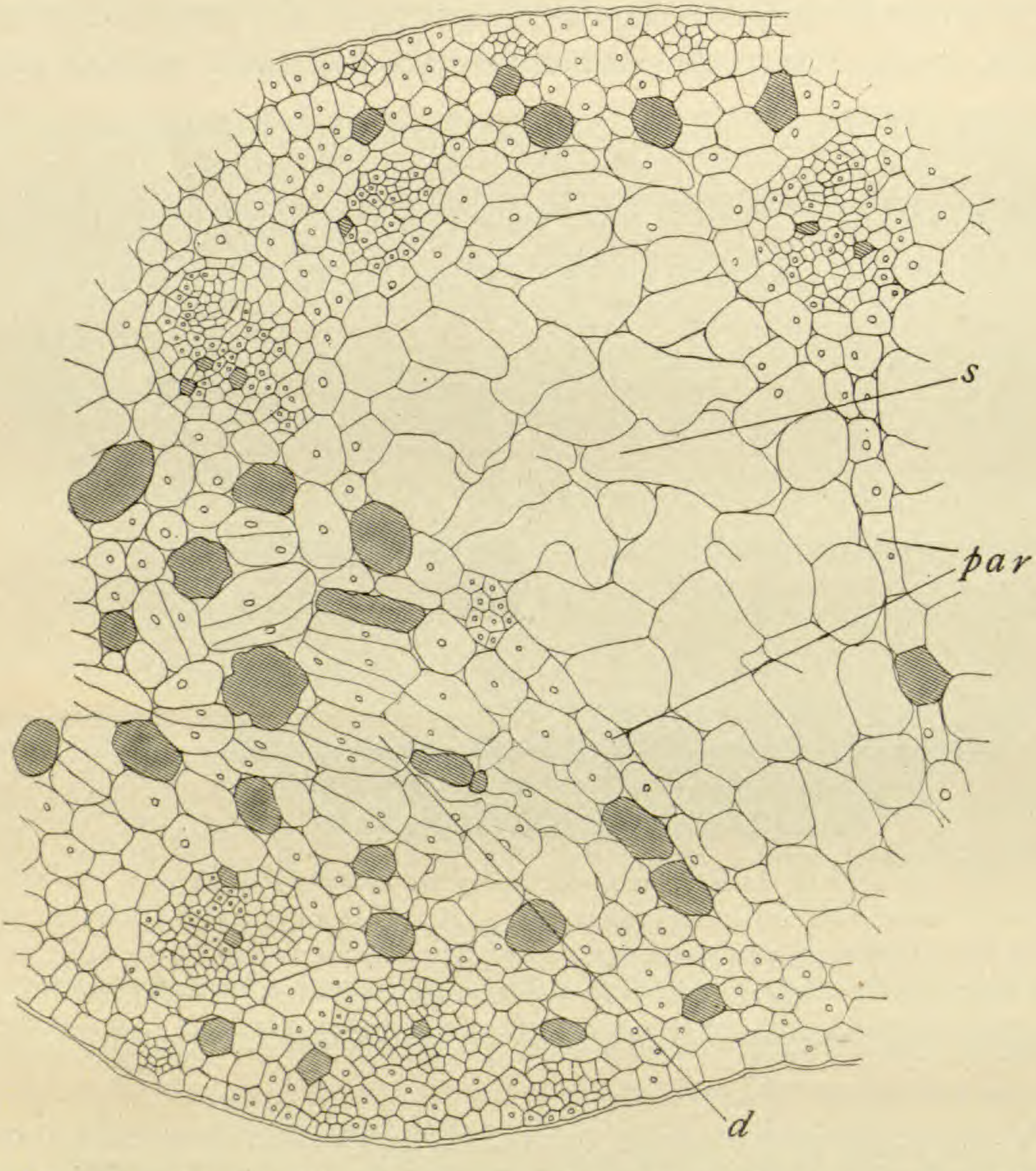

FIG. 13.—*Scirpus validus:* cross-section of tip of very young stem: *par*, partitions separating three spaces; *s*, cells of space which will become stellate; *d*, young diaphragm; note great number of food storage cells in diaphragm; ×110.

F. CONDUCTION

To the above-mentioned functions may be added that of conduction. An examination of figs. 6, 10, and 12 will show that the groups of cells adjoining the cross-bundle and the partition walls of the air spaces have their long axes perpendicular to the bundle and the walls respectively. This is an almost universal condition; where

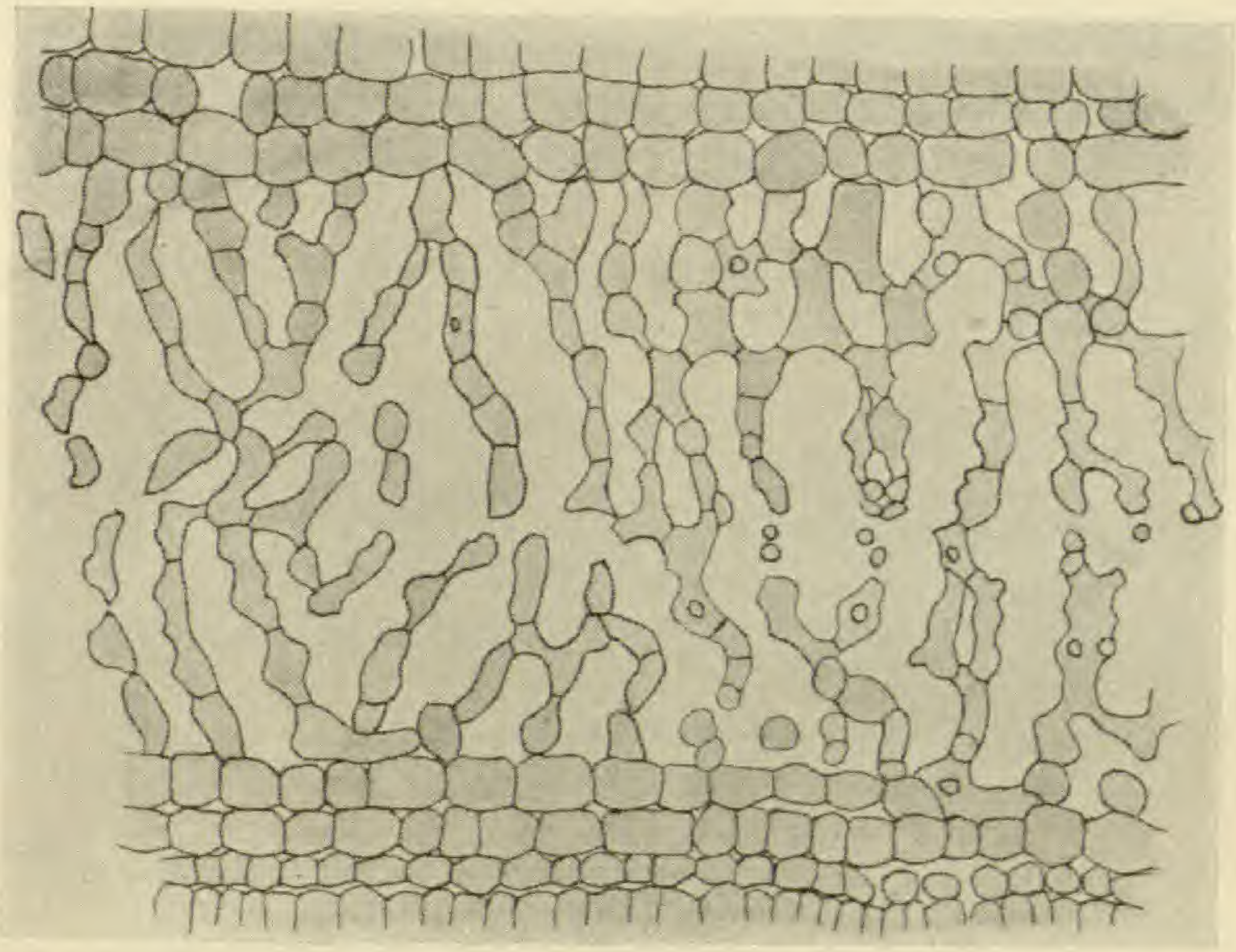

FIG. 14.—*Juncus effusus:* a few cells from cross-section of stem, showing transition from rounded cells on outer edge of pith to stellate cells nearer the center; ×110.

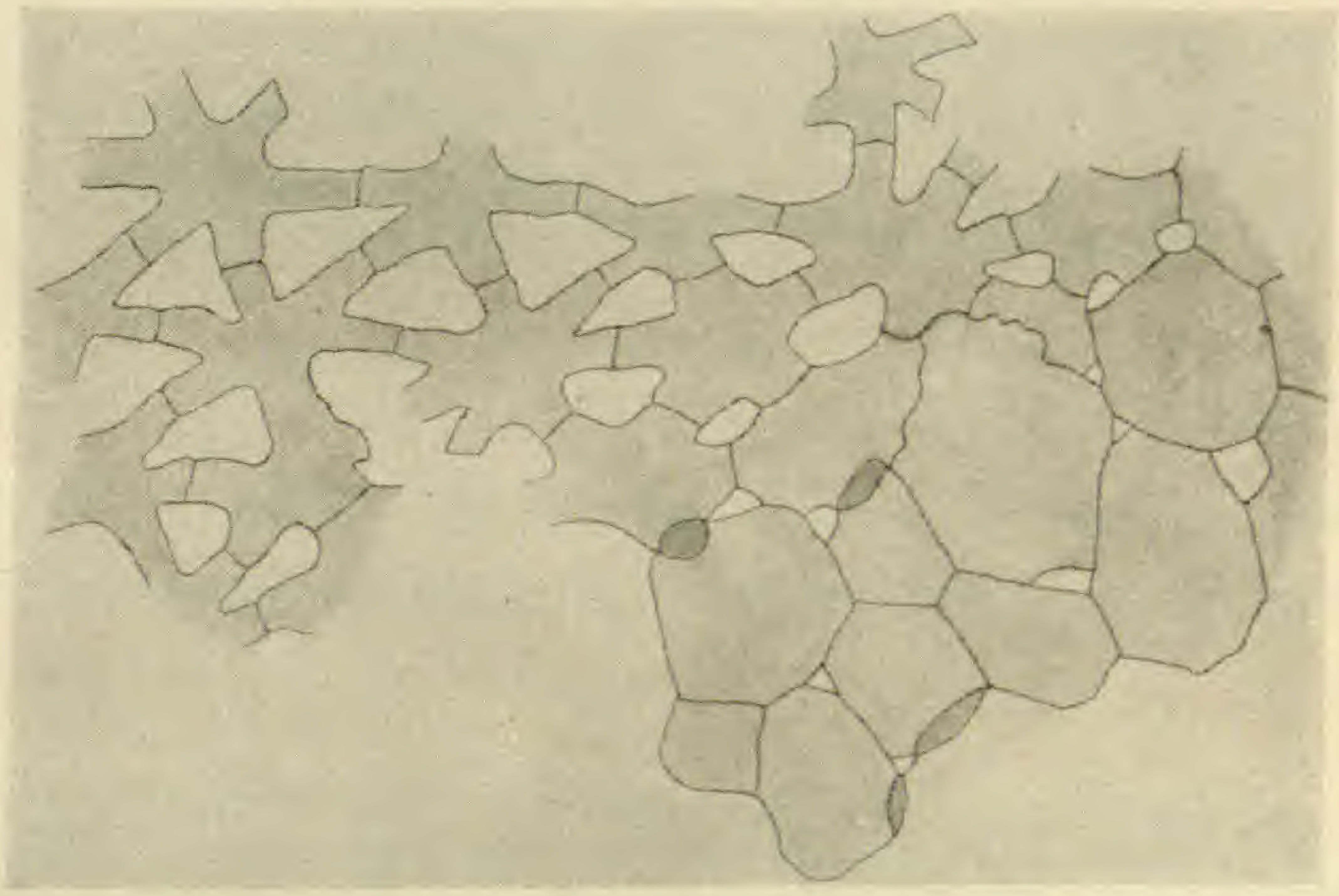

FIG. 15.—*Juncus effusus solutus:* longitudinal section of stem showing formation of cross-layers in stellate parenchyma; ×35.

Figures appearing on this page should be interchanged; the legends should remain as printed.

there are exceptions, some at least can be shown to be partition cells which have secondarily assumed the character of diaphragm cells (fig. 10). Around storage cells the diaphragm cells frequently assume a rosette arrangement (fig. 16), apparently for conductive purposes. The fact that the first connection of the cross-bundle with the longitudinal bundle is with the phloem also lends weight to this suggestion. Longitudinal sections show that the diaphragm cells extend a short distance into the partitions, and that the ordinary polygonal partition cells become elongated and slope toward the diaphragm, thus suggesting a conductive function (fig. 11). From these conditions it seems reasonable to conclude that conduction is one function of the diaphragms of *Scirpus validus*.

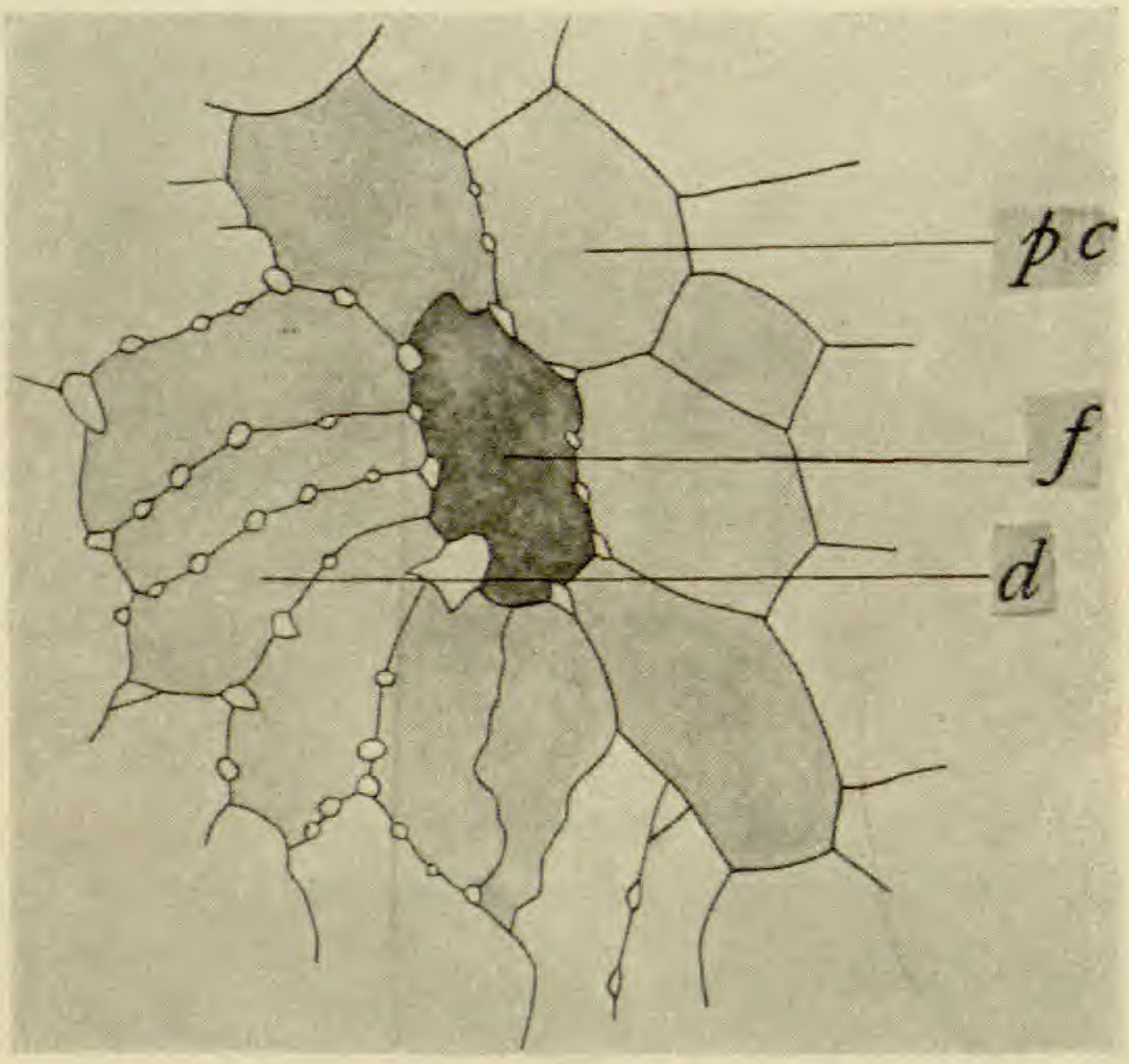

FIG. 16.—*Scirpus validus:* a few cells at edge of diaphragm: *f*, food storage cell; *d*, diaphragm cells leading to or from storage cell; *pc*, cortical parenchyma; ×175.

Summary

1. Diaphragms, although present in many monocotyledons, are not restricted to that group. The present state of our knowledge, however, does not allow us to make definite statements as to their distribution.

2. Diaphragms are especially characteristic of leaves, but have been reported for all parts of plants except flowers and fruits.

3. Diaphragms have been found in immersed and in aerial parts of plants.

4. Diaphragms appear to be characteristic of plants growing in water or very wet places.

5. The structure of diaphragms varies: (*a*) they may be one to several layers thick; (*b*) the cells vary from polygonal to stellate; in the "scirpus type" the cells are in groups (usually of four) and are long and narrow, with short arms; (*c*) the presence of cross-bundles appears to vary with the form studied. In *Scirpus validus* nearly all the diaphragms have bundles in them.

6. The cross-bundle is made up of xylem and phloem. At first the connection with the longitudinal bundles is with the phloem, but later a secondary connection is made with the xylem.

7. The stellate cells originate from ordinary parenchyma cells by the differential growth of the cells from the inside outward.

8. Diaphragms in *Scirpus validus* arise by a division of the parenchyma into layers, some of which retain their meristematic character, while the remaining cells gradually cease growing and become the slender stellate cells of the air spaces.

9. Each group of four cells of the diaphragm of *Scirpus* spp. arises from a mother cell. The formation of dividing walls parallel to the long axes of the cells is probably determined by the current of food materials passing from the cross-bundle to the partition walls of the space.

10. Diaphragms have the following functions: (*a*) to resist strains and keep the spaces open; (*b*) to support cross-bundles; (*c*) to prevent entrance of water by the small size of the perforation; (*d*) perforations permit air to circulate; (*e*) while young and green, to manufacture carbohydrates; (*f*) to store food: (i) this is possibly in the form of some tannin compound containing the phloroglucin radical, and may or may not be associated with glucose; (ii) this substance is stored in special cells which are distinct from the starch-bearing cells; (*g*) to conduct food materials from the cross-bundle to the partition walls of the space.

My thanks are due Professor KARL M. WIEGAND for his kindly assistance in the identification of the species studied, and

to Professor B. M. DUGGAR for helpful suggestions during that part of the investigation which was conducted at Wood's Hole.

WELLESLEY COLLEGE

THE DISTRIBUTION OF DIAPHRAGMS IN THE VARIOUS GROUPS OF PLANTS

1. PTERIDOPHYTES.—They are reported for ferns and *Equisetum* by LEITGEB (18), but are not mentioned by COSTANTIN (3) in his report on *Equisetum*.

2. SPERMATOPHYTES.—

a) No mention has been made of the presence of diaphragms in the gymnosperms.

b) Diaphragms have been observed in the following families of angiosperms:

(1) *Dicotyledons:*

In Nymphaeaceae by LEITGEB (18), SOLEREDER (31), and LE BLANC (17). Their presence in *Nelumbium* (*Nelumbo*) is denied by DEBARY (6).

In Ceratophyllaceae by DUVAL-JOUVE (7), but their presence is denied by MEYEN (20, 21), DEBARY (6), and SCHENCK (29).

In Haloragidaceae by LEITGEB (18) and GOEBEL (13), but their presence is denied by MEYEN (20, 21), DUVAL-JOUVE (7), DEBARY (6), and SCHENCK (29).

In Gentianaceae by DUVAL-JOUVE (9), but their presence in *Limnanthemum nymphoides* is denied by DEBARY (6).

In Rubiaceae by UNGER (35) for *Richardia aethiopica* (authority not noted). In ENGLER and PRANTL *Richardsonia* is given as a synonym for *Richardia*, but the species *aethiopica* does not appear, and it is not safe to conclude from this report that diaphragms occur in this family.

In Umbelliferae by LEITGEB (18) and (at nodes) by COURCHET (4), but their presence is denied by MEYEN (20).

In Compositae by LEITGEB (18).

COSTANTIN (3) made an extended study of water plants, including many families, the greater number of which were dicotyledons, but he does not mention the presence of diaphragms. LE BLANC (17) states that they occur only in monocotyledons and the related Nymphaeaceae.

(2) *Monocotyledons:*

In Typhaceae by LEITGEB (18), DUVAL-JOUVE (7, 9), and FALKENBERG (12).

In Pandanaceae by MEYEN (20).

In Sparganiaceae by DUVAL-JOUVE (7, 9).

In Potamogetonaceae by DUVAL-JOUVE (9), SAUVAGEAU (25, 26, 27), and MEYEN (21). Their presence is denied in *Zostera* and *Posidonia caulini* by DEBARY (6). SAUVAGEAU (25) reports them for *Zostera*, but does not consider the thin partitions extending from epidermis to epidermis in the leaves of *Posidonia caulini* and *Cymodocea antarctica* to be diaphragms. He does not mention diaphragms in his reports on *Phyllospadix* (26) and *Ruppia* (27).

In Najadaceae by LEITGEB (18).

In Hydrocharitaceae by MEYEN (20), SAUVAGEAU (23, 24, 25), SOLEREDER (32), MONTESANTOS (22), and CUNNINGTON (5). BALFOUR (1) states that the canals of *Halophila* end at the nodes in thick tissue, and CASPARY (2) makes the same statement for the Hydrilleae. SAUVAGEAU (24) does not mention diaphragms in his report on *Halophila*.

In Aponogetonaceae by DUVAL-JOUVE (9) and in ENGLER and PRANTL (11*c*).

In Juncaginaceae in ENGLER and PRANTL (11*c*).

In Alismaceae in ENGLER and PRANTL (11*c*), by DUVAL-JOUVE (9), and MEYEN (20).

In Butomaceae in ENGLER and PRANTL (11*c*) and by DUVAL-JOUVE (9). No mention of diaphragms is made by COSTANTIN (3) in his report on *Butomus*.

In Gramineae by LEITGEB (18), DUVAL-JOUVE (7, 8, 9, 10), and MEYEN (20).

In Cyperaceae in ENGLER and PRANTL (11*c*), by MEYEN (20, 21), LEITGEB (18), DUVAL-JOUVE (7, 9), SCHWENDENER (30), FALKENBERG (12), and DE-BARY (6).

In Araceae by MEYEN (21), LEITGEB (18), DUVAL-JOUVE (9), and WEISS (37).

In Eriocaulaceae (?) in ENGLER and PRANTL (11*c*).

In Mayacaceae. The description of the leaves in ENGLER and PRANTL (11*c*) suggests the presence of diaphragms.

In Pontederiaceae in ENGLER and PRANTL (11*c*), by MEYEN (20), DUVAL-JOUVE (7, 9), and GOEBEL (13).

In Juncaceae in ENGLER and PRANTL (11*c*), by DUVAL-JOUVE (7, 8, 9), and SCHWENDENER (30).

In Liliaceae by MEYEN (20) and DUVAL-JOUVE (9).

In Iridaceae by DUVAL-JOUVE (9).

In Musaceae in ENGLER and PRANTL (11*c*), by MEYEN (20), and DUVAL-JOUVE (9).

In Cannaceae by MEYEN (20) and LEITGEB (18).

In Marantaceae in ENGLER and PRANTL (11*c*) and by DUVAL-JOUVE (9).

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FASCIATION

M. A. Brannon

(WITH SEVEN FIGURES)

During the spring of 1910, while an examination of a tree claim near Larimore, North Dakota, was being made, there were discovered some pronounced cases of fasciation. The tree claim had been planted to cottonwoods and willows in 1885. During the winter of 1909 the owner had taken considerable fuel from the northern portion of this grove of vigorous trees. In the summer of 1909 a large number of sprouts came from the stumps of the trees which had been removed (fig. 1). The number of sprouts was variable on different stumps, but in all cases the growth was pronounced and occasionally it was extreme, some of the sprouts having reached a height of two or three meters. On all of the stumps of the cottonwoods and on some of those of the willows one or more fasciated sprouts appeared. The flattening was particularly marked near the outer extremities of the stem, and was accompanied generally by profuse branching and forking of the fasciated specimens. The most superficial markings on the

FIG. 1.—A portion of the original timber claim and three years' growth of the cut-over region adjoining.

fasciated sprouts were prominent cortex ridges along the whole axis of the young plant. Fig. 2 shows the relative size and the shape of the cortex ridges and also the flattened xylem and pith in a transverse section of modified cottonwood stem. This section shows that pith, xylem, phloem, and cortex maintain the same relative positions in the abnormal specimens that they have in the normal cottonwood stem. The two exaggerated features of these flattened stems are the huge cortex ridges and the modification of radial symmetry.

FIG. 2.—Transverse section of a fasciated cottonwood stem one year old; ×8; the notable cortex ridges and change of symmetry in the cross-section of the stem are well illustrated by these sections.

The phenomenon of fasciation is not rare among plants, though it is not often reported for those having woody stems. Manifestly, the disturbing features, whatever they may be, which produced "banding" or "bundling" must have been considerably more pronounced in the wooded stems of cottonwoods, ash, willow, and other woody plants than they are in herbaceous stems of seedlings of pumpkin, young stems of thistles, floral axes of coxcomb, stems of asparagus, and other fasciated herbs.

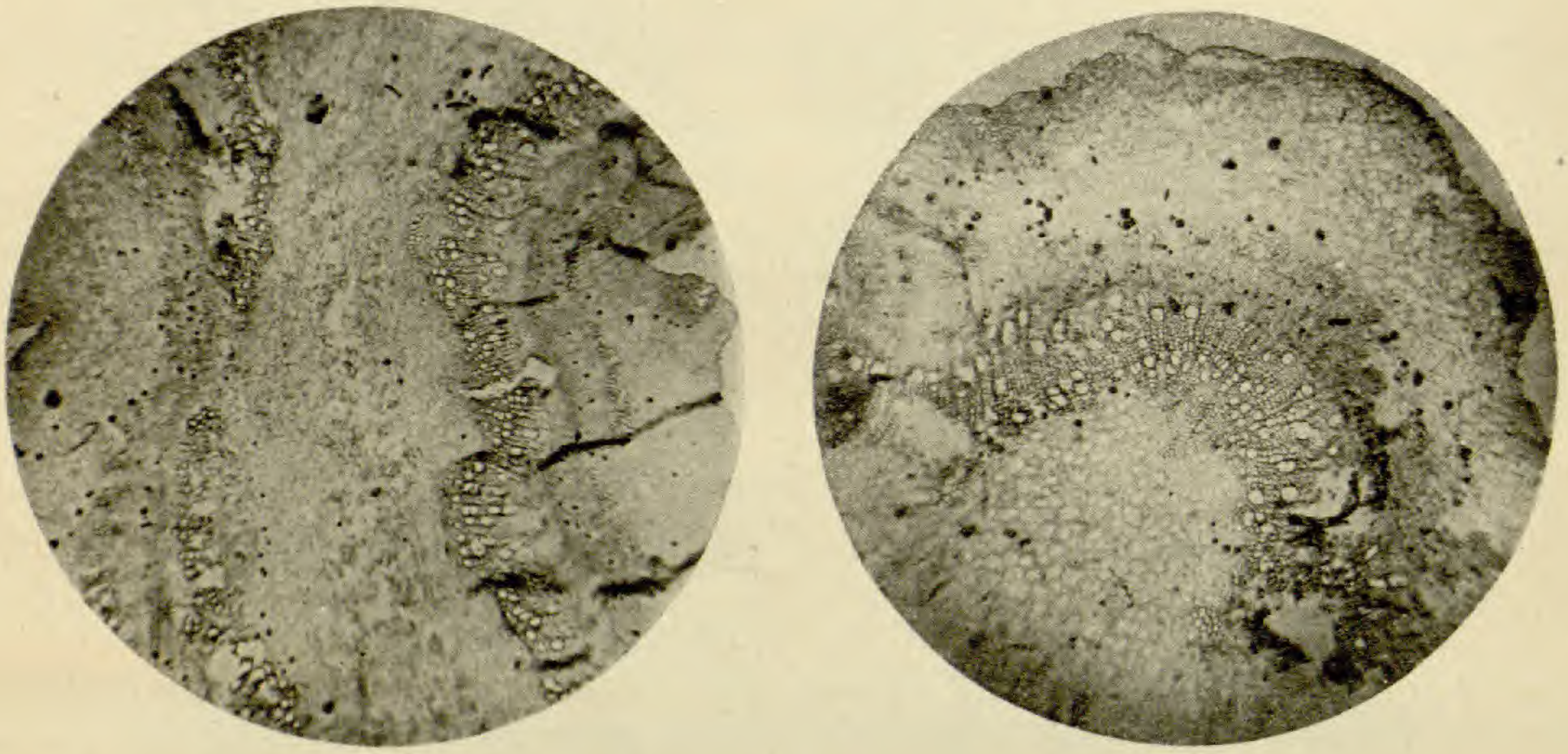

FIG. 3 FIG. 4

FIGS. 3, 4.—Parts of the stem section showing the relation of the cortex ridges with phloem, xylem, and pith; ×13; fig. 4, section showing more clearly the relation indicated in fig. 3; ×25.

The number of atmospheres of pressure requisite for the flattening of a wooded stem corresponding to the cottonwood shown in the accompanying section (figs. 3 and 4) has not been determined. It is evident, however, that an enormous molecular disturbance would be required in order to change the molecular arrangement which caused the disturbance of radial symmetry of these woody stems. In seeking for the cause of the energy release which was expressed by this modification of symmetry, one naturally inquires into the chemical and physical factors involved. With reference to the chemical factors it seems evident that the stumps of the cut-away trees did not contain other compounds than those which had been moving freely through the tissues of the tree while it was standing. There might have been larger quantities of various chemical substances per unit of living tissue, but hardly a different quality than that present in the uncut cottonwoods and willows. The soil had not been disturbed; there had been no change in drainage, and no great variation of precipitation during the latter months when the trees were standing and during the time that the fasciated sprouts had been developed. This seemed to indicate that, so far as the causes of fasciation in the stems of cottonwood and willow were concerned, it was necessary to seek them among physical rather than among chemical factors. From the list of physical factors such as light, gravity, and turgor it was easily possible to select turgor as the one which would be variable in the meristematic tissue near the exposed surface of the tree stumps out of which numerous sprouts developed. Root pressure of the cottonwood and willow plants was apparently in full operation during the early spring months after the trees had been cut away. The full flow of sap was directed into the meristematic tissues of the stumps from which a few buds developed in the early spring. This seemed the probable cause in the production of the phenomenon of cottonwood and willow fasciation.

Traumatism may have been involved in the changes registered in the young, rapidly growing sprouts. However, this seemed improbable, inasmuch as numerous sprouts were wholly free from fasciation, notwithstanding the fact that some of the more pronouncedly fasciated sprouts came from the same stumps on which normal sprouts were growing. Transition from the abnormally fasciated to the normal radial symmetry was evidenced by the most strongly fasciated sprouts after three seasons of growth. Figs. 5 and 6 show the bases of cottonwood saplings which had sprouted from the stumps four years before. The wide scar near the base of each fasciated specimen clearly indicated the location of a ruptured cortex which took place in the deeply furrowed fasciated specimen during its second season's growth. The dimensions of the cross-section of the base of the specimen shown in fig. 5 were 6 by 4.5 cm. Fig. 6 shows the base of a fasciated stem whose cross-section 15 cm. from the ground was 6.5 by 5 cm.

Fig. 7 shows a stem whose cross-section 25 cm. from the ground was 11×9.5 cm. These variations in symmetry were gradually lost, and practically disappeared in fasciating sprouts at the end of three years' growth. Nearly all of the specimens which had such manifest banding and bundling during their first three years

FIG. 5

FIG. 6

FIG. 7

FIGS. 5–7.—Basal lateral views of the sprouts three years after the beginning of fasciation, illustrating separation of cortex from woody cylinder and consequent exposure of wood to weather.

of growth had changed to symmetrical cylinders having practically no evidences of fasciation beyond the terminal portion of the third season's growth. The uniform diameter in all parts of the stem produced during the fourth year, together with its smooth, firm bark, presented a great contrast to the unsymmetrical, fluted cortex produced during the three previous seasons. Seemingly the distribution of stress and the physical and chemical factors had reached stages similar to those which prevail in the production of normal cylindrical stems.

HUS[1] states that fasciation may be produced experimentally in annuals (*Phaseolus multiflorus* and *Vicia Faba*). The stems of these annuals fasciated when they were cut off directly above the cotyledons, and the roots fasciated when the tips were amputated or split. HUS also showed in work carried on at the Missouri Botanical Garden that plants with an indeterminate inflorescence would fasciate when treated as follows:

> About the time of the appearance of the first flowers the plant is kept as dry as possible, only enough water being given to prevent wilting. As a result, the flowering period will be comparatively short, and, in an indeterminate inflorescence, the buds near the end of the spike remain undeveloped. If at that time the plants are daily abundantly irrigated, occasionally with manure water, numerous fasciations will make their appearance, but it must be remembered that this result is usually reached only with plants which throughout their existence have been well nourished and well cared for generally. For no apparent reason, one plant will fasciate, while the next one belonging to the same species remains normal.

From this and other experiments, HUS concludes that GOEBEL is correct when he affirms that fasciation results from the rapid introduction of sap into stems which would not normally have fasciated. This conclusion was further supported by experiments carried on at Berkeley, California, in September 1904. Within a week after a heavy rainfall a very large number of teratological cases appeared. They were represented by fasciations, by torsions of the stem, petalody of the stamens, phyllody of the pistils, and prolongations of the axis through the center of the flower, known as frondiferous diaphysis. HUS further cites the experiences of

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[1] Mo. Bot. Gard. Report, 1906, pp. 147–152.

some asparagus growers in California, who testified that there was a greater percentage of fasciated shoots in their beds of asparagus during the period when the first stems pierce the soil, especially after a cold winter.

DEVRIES conducted experiments[2] in his garden at Amsterdam, and minutely studied fasciated plants in their natural conditions. From the experiments and observations he agrees heartily with GOEBEL that fasciation is due to internal stimuli, notably increasing pressure of cell sap.

The whole question of monstrosities might be ignored but for the light their study throws upon numerous morphological structures among plants. To illustrate some of these morphological problems the lists of floral parts which are closely united have been cited. In the whorl of microsporophylls one often finds a complete union of the filaments, also the fusion of megasporophylls in the formation of compound ovaries; the fusion of the petals in the gamopetalous corolla, as for instance in the orchids; the fusion of seed coats in cycads; the fusion of nucellus and integuments in some of the other gymnosperms; the fusion of the bract with the axillary flowering stock in basswood (*Tilia americana*); and the union of the calyx with the ovary as in the apple and other pomaceous fruits. This group of morphological modifications was classified as negative by WORSDELL.[3] The same author classifies as positive congenital increase of parts the following: the pappus or the sepals in the Compositae; twin embryos which develop from a single egg that divides vertically perhaps instead of transversely; and twin flowers which arise by the modifications of the apical region of growth.

WORSDELL holds that, in addition to these congenital fusion problems, there are those which may be called post-genital; for example, the plantain with twin spikes of flowers at the summit of the stem, the *Campanula* with four flowers borne at the apex of an abnormal stem, the leaves of the *Oxalis* sometimes individual instead of being in three parts as is customary, the fusion of the flowers in *Crocus*, and lastly fasciation itself. In support of his view that the various monstrosities in plants are sometimes con-

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[2] Die Mutationtheorie 2:541. 1903.

[3] New Phytol. 4:55–74. 1905.

genital and sometimes post-genital, he has recourse to a theory of CHURCH, who holds that "growth is distributed at the apex of a shoot in such a manner that its transverse component may be expressed by a plane, circular construction around a circular point (the growth center), and the circular section of the vast majority of plant axes is evidently the outcome of such a regular and symmetrical distribution from the growing point." WORSDELL approves of CHURCH's theory that central distribution is distributed around several points instead of about one center of growth. He holds that some growth centers are weaker than others, hence develop less in diameter and elongate more slowly, and this produces torsion, which is an almost invariable component of fasciation. Having developed this theory of centers of growth in different radii of the apical region of a stem, he holds that any force which upsets the equilibrium of the organism will tend to bring about a reversal to ancestral conditions. In other words, cylindrical woods like those of our cottonwood and ash, upon losing their balance, will repeat the long-past experience of lycopods, ferns, and algae, where branching primarily is probably in one plane.

WORSDELL furthermore treats of plant monstrosities as a possible pathological condition. He refers to it as a subtle diseased condition brought about by superabundant nutrition that destroys the balance of the organism and produces hypertrophy of parts. It is pointed out that the crested form of *Celosia argentea* is not produced abundantly without manuring the potted plants. WORSDELL's conclusion is that there are morphogenetic principles underlying the phenomenon of fasciation. He holds that fasciation is to be explained as a resultant of the more or less equal conflict waged between two opposing tendencies or forces, one of which induces integrity of parts of a plant and the other induces plurality of parts.

In a recent discussion, WHITE[4] reviews interesting genetic studies based upon a fasciated variety of *Nicotiana Tabacum*. The race of these fasciated specimens was obtained from the self-fed seed of a mutant found growing in a field of Cuban tobacco. He

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[4] WHITE, O. E., The bearing of teratological development in *Nicotiana* on theories of heredity. Amer. Nat. 47:216–228. 1913.

suggests that these studies indicate that "the gene for fasciation appears to me to lie deeper in sporogenesis than the chromosome." "The abnormal character development appears most easily interpreted from a physiological standpoint." Whether or not his contention is correct that "physiological" factors rather than chromosomes control the continuous fasciation through the chain of alternation of generations, there can be no question, however, regarding the fact that some physiological factor, notably sap pressure, is intimately associated with the control of the fasciation of ash, willow, and cottonwood on stems found on tree stumps in the North Dakota tree claim.

The examples of fasciation presented in this paper have been noted because of the bearing which the study of abnormal structures may have upon the study of normal morphological structures; and also because of the possible interesting physiological relation existing between increased sap pressure and the disturbed balance of forces which are believed to be responsible for cottonwoods and willows undergoing a change from radial to more or less bilateral symmetry of stem during their first three seasons of growth.

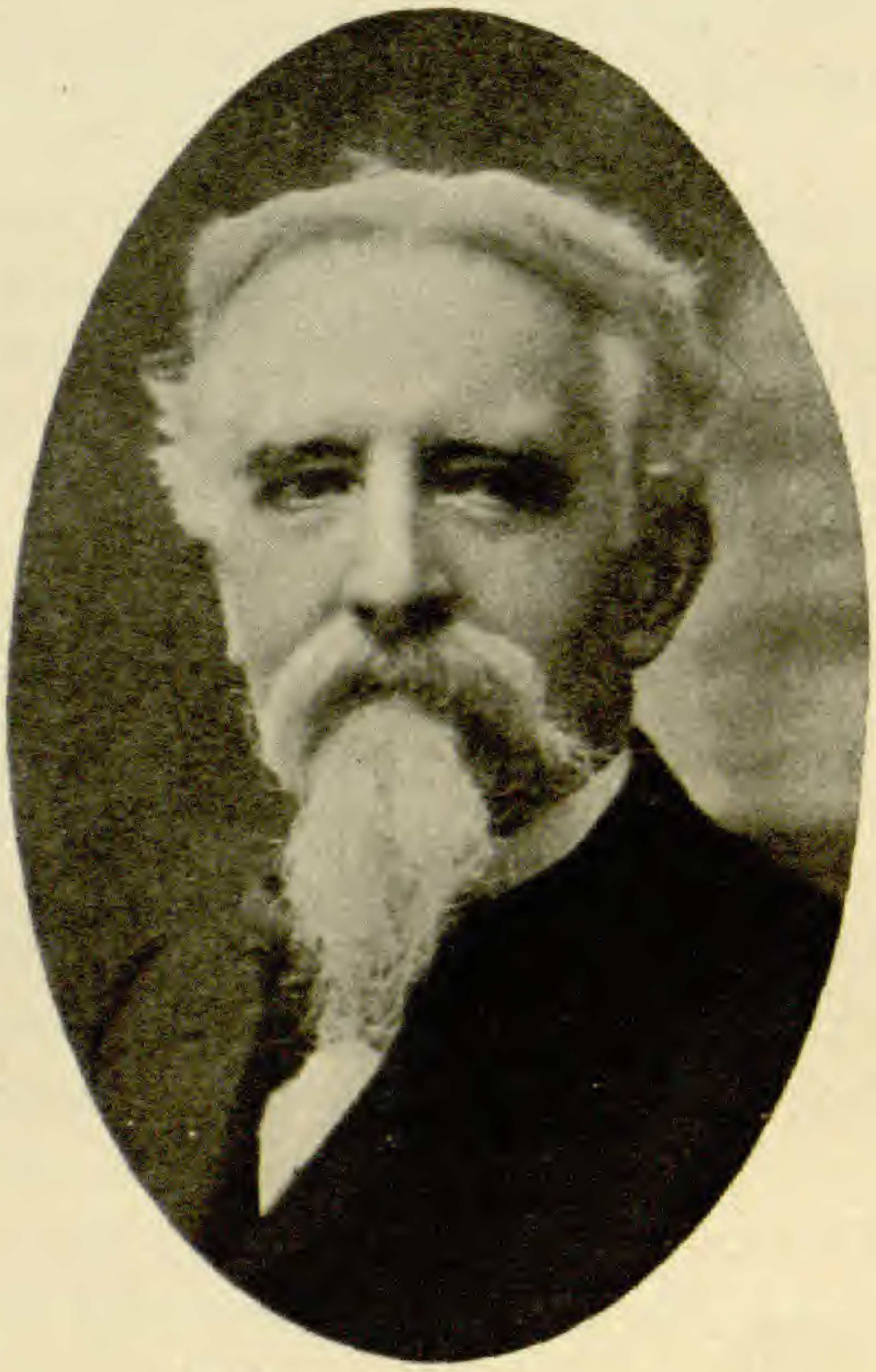
UNIVERSITY OF IDAHO
MOSCOW, IDAHO

BRIEFER ARTICLES

PHILIPPE EDOUARD LEON VAN TIEGHEM

(WITH PORTRAIT)

The younger generation of botanists perhaps does not realize the important part played by van Tieghem in the progress of botany. In recent years his publications, chiefly in the *Annales des Sciences Naturelles,* have had to do with the anatomical details of various families. Such work attracts very little attention in these days. In 1886, however, when van Tieghem and Douliot published the paper entitled "Sur la polystélie," a new epoch in the history of anatomy was introduced. It was the first formal statement of the stelar theory, as we have had it ever since. Before that time the section of a stem was described as consisting of "fundamental tissue" which vascular strands traversed in various ways. In other words, pith, medullary rays, and cortex were all regarded as regions of the same tissue. It may be said in passing that this old conception is still current in certain texts. It was van Tieghem's good fortune to present first the fact that the stele is an entity, quite distinct from the cortex. Curiously enough, the conception of the polystele presented in the original thesis has disappeared, and the rest of the stelar terminology of van Tieghem has been set aside, but the conception remains.



Ph. van Tieghem

Van Tieghem was born in 1839 at Bailleul. In 1879 he was appointed Professor of Botany at the Museum of Natural History (Paris), and from that time until his death, on April 28, 1914, he held the most commanding botanical position in France. His influence upon the botany of France, on account of the peculiarly intimate official relations of French universities, was greater than that of mere reputation as a botanist. He became botanical editor of the *Annales des Sciences Naturelles* in 1882, succeeding DECAISNE in that position. Perhaps his most extensive and most used volume was the *Traité de botanique*, published in 1884, but most referred to in connection with the second edition, published in 1891.—J. M. C.

RETENTION OF CHLOROPHYLL THROUGH THE PARAFFIN PROCESS

In order to study the chloroplasts in corn plants showing various types of reduction of chlorophyll content, the following method was devised to retain the chlorophyll through the paraffin process. The material is fixed in a saturated solution of barium hydrate for 12–24 hours, washed with water, dehydrated with alcohol, dealcoholized with xylol, and imbedded in paraffin. The material should be kept in the dark and dehydrated rather rapidly. This method may also be used for imbedding in celloidin. The details of the methods as stated here are purely arbitrary, and may no doubt be modified with advantage. If a weaker fixing solution is used, it must be handled with great care, as barium hydrate precipitates readily as barium carbonate on exposure to carbon dioxide. If a stronger solution is desired, barium hydrate may be dissolved in an ammonium chloride solution.

Acknowledgments are due Professor R. A. EMERSON, of Cornell University, at whose suggestion the investigation was undertaken.—E. G. ANDERSON, *University of Nebraska.*

CURRENT LITERATURE

BOOK REVIEWS

Bacteriology

The Book of Books somewhere states that a man is not to be heard for his much speaking; inferentially, one surmises that quality is to be more highly esteemed than quantity, and doubtless this may be regarded as holding equally true in the making of books. In the book under review,[1] Professor REED has done well, very well, in this respect, without brevity in the least way marring the quality of the subject-matter presented to his readers.

The preface to a book may frequently be regarded as a mirror of the mind of an author, for therein is displayed the purpose that prompts the writing of the book. So it was with pleasure that the reviewer noted the following phrase: "Wherever possible the experiments are planned to give quantitative results, to the end that vagueness of statement and uncertain thinking may disappear." Were this idea more frequently found expressed and acted upon in "books for students," fewer puny guides to wisdom would be found in the hands of students in our laboratories.

The manual is divided into 16 sections, and in addition 16 appendices. The sections deal with the form and occurrence of bacteria; the nutrition of bacteria; sterilization of culture media; relation of bacteria to factors of physical environment; relation of bacteria to biological factors; methods of culture, isolation, staining, and routine study of bacteria; qualitative and quantitative studies of bacteria of water and sewage, of soil, and of milk; the bacterial diseases of man and animals, and of plants; and fermentation studies. The appendices are framed with the idea of presenting in a handy fashion important matter that otherwise would be scattered in various places throughout the text. Therein are noted descriptions of the most recent methods and applications of sterilization, handling of stock cultures, making of permanent museum preparations, of titration, of chemical determinations of ammonia, nitrate, nitrite, of total nitrogen, of reducing sugars; conversion tables; alcohol computation tables; and the like. In appropriate places throughout the exercises are references to textbooks, monographs, and papers in the current literature of the subjects under discussion, a most important feature not infrequently omitted by authors.

Excellent as the presentation is in most respects, the reviewer does not find himself in perfect accord with the author in certain instances; for example,

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[1] REED, HOWARD S., A manual of bacteriology for agricultural and general science students. 8vo. pp. 179. *figs. 46.* Boston: Ginn & Co. 1914.

in the section allotted to diseases of man and animals the impression is produced in section 132 that the use of mercuric chloride is too lavishly recommended. It has its place, but would it not be better to advocate the sterilization of such cultures as those of anthrax and tuberculosis by means of the autoclave? Then, too, it would have been well to have inserted some special admonitory warnings in introducing the student to the study of anthrax and tuberculosis.

Attention might be directed to an error in the description of carrying out the technic of WELCH's capsule stain (p. 36); water in no instance ought to be allowed to come in contact with the film, all washing should be done with 0.85 per cent sodium chloride solution. In exercise no. 27, the presentation of the formula of ELSNER'S potato gelatine medium would appear to be misleading, inasmuch as this medium is not one suitable for the growth of bacteria in general; in fact, the reverse is true, as ELSNER introduced it in 1896 for the purpose of providing a selective medium for the typhoid bacillus and preventing the growth of other bacteria associated with it in such materials as feces, urine, water, etc. The reaction as given is evidently a misprint for "plus 0.25." An unfortunate error is given prominence in Appendix E, wherein it is stated in paragraphs five and six that the term "plus(+)1.0 is equivalent to 1.0 cc. of normal hydrochloric acid per *liter*"; on the contrary, it should read 1.0 cc. *per cent* (see *Standard methods of water analysis*, 2d ed., 1912, p. 126).

Apart from the foregoing criticisms, and judged upon its merits, the manual is admirably adapted, not alone for students of agriculture and of the technical sciences, but for students of any institution where bacteriology is worthily taught in its broader and more fundamental aspects. The book is of a handy size, well printed, attractively bound, and adequately illustrated.—N. MACL. HARRIS.

The marine algae of Iceland

The Danish botanists, largely through the inspiration of WARMING, having completed in satisfactory form the botanical investigation of the Faeröes, have turned attention to Iceland, as the Danish dependency now most in need of study. The first paper of the Iceland series is the work of Dr. HELGI JÓNSSON[2] of Reykjavik, Iceland, and it gives an elaborate account of the marine algae which are so richly represented on the coast of that far northern island. There are 200 species listed, of which 76 are reds, 67 browns, and 51 greens. In the chapter on life-conditions, the subjects treated are the nature of the coast; the movements, temperature, and salinity of the water; atmospheric temperature and humidity; precipitation; wind; and light. As usual elsewhere, the algae are best developed on rocky coasts. The practical upper limit of algae is reached at the flood level of neap tides.

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[2] ROSENVINGE, KOLDERUP, L., and WARMING, E., The botany of Iceland. I. The marine algal vegetation by HELGI JÓNSSON. pp. 186. *figs*. 7. Copenhagen: J. Frimodt. London: John Wheldon & Co. 1912.

The body of the work deals with the horizontal and vertical distribution of the species. Of the 200 species, 11 only are rated as arctic, whereas 81 are termed subarctic, and 108 boreal; of the last, 12 are even warm boreal species extending south to the Mediterranean. In considering the vertical distribution, JÓNSSON terms the upper part of the shore, from the upper limit of algal growth to the low-water mark of neap tide (almost coinciding with the lower limit of the Fucaceae), the upper littoral zone. The lower littoral zone extends from here to the usual low-water mark of spring tide. Then begins the vegetation that is constantly submerged. In the upper littoral zone there are 18 reds, 18 browns, 36 greens, and 6 blue-greens; the great bulk of the vegetation, however, is composed of browns. Furthermore, 13 of the reds in the upper littoral zone occur in shaded clefts, being proper to lower zones. In the lower littoral zone there are 39 reds, 37 browns, and 17 greens; the relationship of these is much closer to the submerged species than to the upper littoral species. Of the submerged or sublittoral species, 39 are reds, 22 browns, and 3 greens. It is possible that algae may occur as far down as 80 meters, but they are not abundant below 60 meters. A third of the work is devoted to a detailed account of the numerous algal associations of the three zones noted above, the littoral associations being subdivided into those of the light and of the shade.

This valuable treatise closes with some notes on the duration of algae and periodical changes. The perennial algae, such as *Fucus* and *Laminaria*, have only a very short period of rest, in spite of the long winter; some species hardly rest at all. *Pelvetia caniculata* vegetates and fruits the year around.—H. C. COWLES.

Postglacial changes in German vegetation

HAUSRATH,[3] professor of forestry at Carlsruhe, has issued an extremely useful little book, which gives in compact form a summary of our knowledge regarding landscape and vegetation changes in Germany since the Ice age. One of the author's chief objects is to explain the present landscapes in terms of past conditions. To give proper orientation to the reader, HAUSRATH presents in brief fashion the ordinary fundamentals of phytogeography, noting the various factors and formations that are in evidence in Germany. It is interesting to note that nearly half the land of Germany is cultivated, one-quarter forest-covered, and one-sixth pasture and meadow. The various views concerning the climate of the Ice age and of subsequent times from the Ice age to the days of the Romans are well set forth, as are the probable stages in the re-establishment of vegetation immediately following the retreat of the glaciers. A chapter is devoted to changes subsequent to Roman occupation,

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[3] HAUSRATH, HANS, Pflanzengeographische Wandlungen der deutschen Landschaft. Wissenschaft und Hypothese XIII. pp. vi+274. Leipzig: B. G. Teubner. 1911. *M* 5.

and there are here depicted the early periods of forest destruction, the fluctuations in forest area associated with peace and war, and the growth of the ideas of conservation and afforestation. The closing chapters consider changes in the composition of forests and the problems of heaths and moors, which are discussed from the viewpoint of origin, of destiny if left to themselves, and of utilization by man. The great merit of this volume lies in its strongly dynamic attitude, an attitude that cannot be too highly commended in all phytogeographic work.—H. C. COWLES.

The trees of Belgium

MASSART[4] has issued a profusely illustrated little book on the trees of Belgium, his object being to present the subject so as to interest intelligent lovers of the woods, rather than to make a manual for botanists or foresters. The book is in no sense designed as a manual of identification, but rather it presents the interesting problems about which the nature-lover is likely to inquire. In the first portion of the book MASSART considers wood structure and tree architecture. Then follows a section on the relation between trees and soil, and a similar section on the relation between trees and the atmosphere. The final section presents the life-history of trees, dealing with birth, competition, decrepitude, and death. In the chapter on tree architecture, the author discusses deliquescent and excurrent trees, regeneration of injured terminal and lateral branches, the influence of isolation on the shape of the crown, and enlarged trunk bases. The section on soil relations considers the distribution of trees (an excellent detailed map of the Belgian woodlands accompanies this), the influence of the soil on trees, and the influence of trees on the soil; among the topics treated under the latter heading are rock disintegration, fixation of dune sand, and chemical changes in the soil. In the final section much attention is paid to tree diseases and insect pests. It is a pity that we do not have many similar books to accommodate the rapidly increasing army of nature-lovers.—H. C. COWLES.

NOTES FOR STUDENTS

The vegetation of the Nebraska sandhills.—The average traveler regards the prairies and plains as regions of extreme monotony; particularly is this true if his way takes him through a region of sandhills. The total incorrectness of this view is admirably illustrated by the publication of POOL's researches in the Nebraska sandhills.[5] From an earlier and semipopular presentation

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[4] MASSART, J., Nos arbres. pp. viii+214. *figs. 238. map 1.* Brussels: Henri Lamertin. 1911.

[5] POOL, RAYMOND J., A study of the vegetation of the sandhills of Nebraska. Minn. Bot. Studies, III. 4:189–312. *pls. 15. figs. 16. map 1.* 1914.

by the same author[6] we had learned to know something of the fascination and scientific interest of these dynamic landscapes, and now we have his detailed results.

The Nebraska sandhill country covers an area of about 18,000 square miles, that is, nearly one-fourth of the area of the state. There are similar but smaller areas of sandhills in Kansas, Colorado, and the Dakotas. The soil is composed of dune sand, probably derived from the Loup Fork (Tertiary) beds. These hills seem to have been formed largely at some previous epoch and to have become stabilized and occupied by vegetation. Through the influence of man, mostly on account of prairie fires and overgrazing, many of these ancient dunes have become rejuvenated to the detriment of those responsible for it.

After giving the results of his careful measurements of wind, rainfall, evaporation, temperature, and other ecological factors, POOL takes up in detail the vegetation of the region. It is a pleasure to note the author's caution in using the word "formation." He rightly believes in using this term only for large units, referring the "formations" of many authors to associations. The characteristic upland formation is the prairie-grass formation, which is contrasted sharply with the short-grass formation of the plains, the two embracing most of the great climatic grasslands between our eastern forests and the mountains. These two great formations have similar physiognomy but different component species; the limiting factors are the available water and competition, and not temperature, as supposed by MERRIAM. The chief association is the bunch-grass association, dominated especially by *Andropogon scoparius;* this is the vegetation that prevailed generally before the advent of the white man, and is regarded as the temporary climax of the region. The vegetation of this association is open, the grasses occurring in tufts or bunches, but it is supposed that ultimately some closed prairie-grass association will prevail. There is evidence of this in the spear-grass association (dominated by *Stipa comata* and *Koeleria cristata*), and farther west in the grama buffalo-grass association (dominated by *Bouteloua* and *Bulbilis*).

Doubtless the most interesting features of the sandhills are the blow-outs. These are retrogressive features and are due, as noted above, especially to prairie fires and overgrazing. At first, through the death of the plants there are small patches of bare sand. Later the sand is scooped out by the wind, forming conical or crateriform depressions, known as blow-outs. As the sand is scooped out, more sand falls in from the sides, so that the blow-out is increased in circumference, as well as in depth. Extreme cases are recorded where the depth may be as much as 100 feet and the circumference 600 feet. When wind erosion becomes checked, vegetation again gets a foothold, the chief

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[6] POOL, RAYMOND, J., Glimpses of the Great American Desert. Pop. Sci. Monthly **80**: *209–235. figs. 17.* 1912.

pioneers being *Calamovilfa longifolia*, *Psoralea lanceolata*, and *Redfieldia flexuosa*. After a time these pioneers are followed by the bunch-brass association; after this vegetational changes are much less rapid. One of the chief features of interest in the woodland formations along the streams is the overlap of the deciduous eastern forest and the yellow pine (*Pinus ponderosa scopulorum*) forest of the west. The lowland formations are much like those elsewhere both as to content and succession, except that a meadow type represents the temporary climax; probably one of the more eastern of the prairie-grass associations represents a more ultimate condition.—H. C. COWLES.

The water-balance of desert succulents.—The Sonoran desert is very rich in succulents which carry a large water-balance. Some of the most striking of these have been studied in detail for some years at the Desert Laboratory.[7] Mrs. SPALDING had previously shown that the stems of *Cereus giganteus* expand and contract in a most remarkable manner, as water is accumulated or lost.[8] These movements are readily measured by noting the variations in distance between the ridges from time to time. Mrs. SPALDING, as her part of the contribution, reports greatly extended experiments along this line on the same and on additional species. The earlier work has been confirmed in practically all respects. In addition to the influence of soil water in changing the plant form, insolation is found to be an important secondary factor; for example, the furrows on the south sides of stems are narrower than those on the north sides. The behavior of *Echinocactus Wislizeni* is much like that of *Cereus giganteus*, but in *Opuntia* the behavior is simpler, consisting merely of the swelling and shrinking of the stem segments.

MACDOUGAL's part of the work consisted of a study of variations in the water-balance, due to seasonal moisture fluctuations and other causes. The remarkable ability of these desert succulents to tide over long periods of drought is brought out in striking fashion in the case of plants of *Cereus giganteus*, in which branches have remained alive and even have bloomed a year after the main trunk bearing them has died. More efficient even than the cacti is *Ibervillea sonorae*, a plant whose stem base is tuberized. For ten years tubers of this species have remained alive, without a renewal of water supply, sending up short green stems each summer; during this time but half of the original weight had been lost. In the general conclusions attention is called to great differences in individual behavior under similar experimental conditions. The

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[7] MACDOUGAL, D. T., and SPALDING, E. S., The water-balance of succulent plants. Carnegie Institution of Washington, Publication 141. *pp.* 77. *pls.* 8. 1910. See also MACDOUGAL, D. T., The water-balance of desert plants. Ann. Botany **26**:71–93. *pls.* 5. 1912.

[8] SPALDING, E. S., Mechanical adjustment of the Sahuaro (*Cereus giganteus*) to varying amounts of stored water. Bull. Torr. Bot. Club **32**:57–68. 1905; see BOT. GAZ. **40**:396. 1905.

decline in evaporation each year in plants whose water supply is not replenished is attributed in part to increasing concentration of the cell sap; in the cacti this increase was from 1 to 3 per cent. From 60 to 70 per cent of the maximum water-balance may be lost by cacti without impairing the power of recovery and subsequent growth. It is suggested that a detailed chemical study of these plants is needed, it being felt that their high osmotic activity and their great acidity resulting from modified photosynthesis are insufficient to explain the origination of the habit of accumulating and retaining large water-balances.—H. C. COWLES.

English woodlands.—As would be expected, very few of the English woodlands are primeval. Such woodlands may still be found, however, near the upper forest limits in mountainous regions.[9] Most English woodlands are to be regarded as semi-natural, that is, the trees are felled somewhat regularly, but the reproduction, either from seeds or suckers, is natural. New forest plantations are distinguishable from natural or semi-natural woodlands by the presence at times of exotic tree species, and almost always by the absence of a representative woodland ground flora. Three main series of woodlands are recognized, the alder-willow series of wet soils, the oak-birch series of siliceous soils, and the beech-ash series of calcareous soils. The series are further divided into associations.

ADAMSON has made an intensive study of Gamlingay Wood in western Cambridgeshire, one of the semi-natural woodlands noted above.[10] The wood is on bowlder clay, part of which is calcareous and part non-calcareous; the trees on the former are oak and ash, while the ash is absent on the latter. Although it is noted that there are intergradations, it is observed that the herbage in the two woodland types is different; the dominant forms in the siliceous woodland are *Pteris aquilina* and *Holcus mollis*, whereas those of the calcareous woodland are *Spiraea Ulmaria*, *Mercurialis perennis*, *Deschampsia caespitosa*, and *Fragaria vesca*. Little attention is paid to successional features. It is believed by the reviewer that more thorough successional studies would tend to break down some of the distinction between calcareous and siliceous woodlands, as recognized by English ecologists; it seems almost certain that an original underlying soil must more and more lose its influence on vegetation, as humus accumulates. Careful studies were made by ADAMSON of evaporation, soil moisture, and other factors.

In connection with the above it may be noted that TANSLEY and ADAMSON[11] have given an account of some observations made in some Gloucestershire

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[9] MOSS, C. E., RANKIN, W. M., and TANSLEY, A. G., The woodlands of England. New Phytol. 9:113–149. 1910.

[10] ADAMSON, R. S., An ecological study of a Cambridgeshire woodland. Jour. Linn. Soc. Bot. 40:339–387. *pls. 6.* 1912.

[11] TANSLEY, A. G., and ADAMSON, R. S., Reconnaissance in the Cotteswolds and the Forest of Dean. Jour. Ecol. 1:81–89. 1913.

woodlands. One of the most interesting features is a wood composed largely of box (*Buxus sempervirens*), possibly native to Britain.—H. C. COWLES.

Jurassic Osmundaceae.—SINNOTT[12] has investigated the structure of petrified stems of *Osmundites Dunlopi* from the Jurassic of New Zealand. They are characterized by a parenchymatous pith, with no internal phloem or endodermis, and leaf gaps are invariably present. In one specimen typical diarch roots, with a definite cortex, were observed in the pith, and it is concluded that the xylem elements described as forming part of a "mixed pith" in *O. Kolbei* probably represent root bundles. It is thought that the relationship between Zygopterideae and Osmundaceae cannot be close, since the anatomy of the leaf trace and foliar bundle in the two groups is so widely different. It seems evident that there were both protostelic and siphonostelic Osmundaceae during the Mesozoic, and there is no evidence that the protostelic forms have given rise to the siphonostelic ones.—J. M. C.

Welwitschia.—CHURCH[13] has made a detailed study of the strobili of *Welwitschia*, supplying facts and new illustrations that were much needed. The "flowers" having clearly been originally bisporangiate, much attention is given to reduction phenomena, such as dicliny, the diminished number of members, etc. A good deal is made of "minimum construction" associated with a xerophytic type, observed in the perianth, the androecium, and gynoecium; but the statement is emphasized that "a minimum construction does not imply any phylogenetic relationship to other minimum types." The author finds no indication of any relation to the flowers of angiosperms.—J. M. C.

Relationships of Fagaceae.—Miss BERRIDGE[14] has investigated the flowers of certain Fagaceae, especially those of *Castanopsis chrysophylla*, comparing them with those of *Castanea vulgaris*, *Fagus sylvatica*, *Quercus Robur*, and *Juglans regia*. She takes issue with the common conclusion that the Amentiferae are an isolated group, with no obvious relationship to other angiosperms. She shows that the flower differs in no essential from other epigynous types of flowers, and compares in detail the flowers of Rosaceae and Cupuliferae, claiming that in all probability the epigynous Rosaceae are most nearly related to the ancestors of the Fagaceae.—J. M. C.

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[12] SINNOTT, E. W., Some Jurassic Osmundaceae from New Zealand. Ann. Botany **28**:471–479. *pl. 37.* 1914.

[13] CHURCH, A. H., On the floral mechanism of *Welwitschia mirabilis* (Hooker). Phil. Trans. Roy. Soc. London B **205**:115–151. *pls. 9–13.* 1914.

[14] BERRIDGE, E. M., The structure of the flower of Fagaceae, and its bearing on the affinities of the group. Ann. Botany **28**:509–526. *figs. 9.* 1914.

GENERAL INDEX

Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic.*

Recent Publications

OF

The University of Chicago Press

Artificial Parthenogenesis and Fertilization. By Jacques Loeb, Member of the Rockefeller Institute for Medical Research.

x + 312 pages, 12mo, cloth; $2.50, postage extra (weight 2 lbs. 4 oz.)

This new work presents the first complete treatment of the subject of artificial parthenogenesis in English. Professor Loeb published four years ago a book in German under the title *Die chemische Entwicklungserregung des tierischen Eies.* Mr. W. O. R. King, of the University of Leeds, England, translated the book into English, and the translation has been revised, enlarged, and brought up to date by Professor Loeb. It gives, as the author says in the preface, an account of the various methods by which unfertilized eggs can be caused to develop by physicochemical means, and the conclusions which can be drawn from them concerning the mechanism by which the spermatozoön induces development. Since the problem of fertilization is intimately connected with so many different problems of physiology and pathology, the bearing of the facts recorded and discussed in the book goes beyond the special problem indicated by the title.

British Medical Journal. The author has gained a world-wide reputation for his achievements in artificial fertilization, and this work shows how, according to his observations, the action of well-known chemical and physical agencies may be substituted for that of the living spermatozoön.

Animal Communities in Temperate America. A Study in Animal Ecology. (Bulletins of the Geographic Society of Chicago.) By Victor Ernest Shelford, Assistant Professor of Zoölogy in the University of Illinois.

xiv + 362 pages, 8vo, cloth; $3.00, postage extra (weight 2 lbs. 12 oz.)

This volume by Dr. Shelford presents the principles of field ecology, illustrated by the more widely distributed animal habitats of the eastern half of temperate North America, and

the aquatic habitats of a much larger territory. Six chapters deal with general principles.

In several chapters animal communities of lakes, streams, swamps, forests, prairies, and various soils and topographic situations are considered from the point of view of modern dynamic ecology. A very valuable feature of the book is the three hundred figures of widely distributed animals chosen to represent the chief types of animal communities and their characteristic modes of life.

Bulletin of the American Geographical Society. This book is unique in that it is a pioneer of its sort and the first serious attempt to treat of the physiology of organisms and of animal communities in such shape as to serve as an adequate text and reference work for students.

Water Reptiles of the Past and Present. By Samuel Wendell Williston, Professor of Paleontology in the University of Chicago.

viii+252 pages, royal 8vo, cloth; $3.00, postage extra (weight 2 lbs. 8 oz.)

Professor Williston, who is widely known as a student of extinct reptiles and as the author of *American Permian Vertebrates*, which has now become a recognized authority, presents in this new volume a summary, divested as far as possible of unnecessary scientific details, of our present knowledge concerning the reptiles of the seas, lakes, and rivers of past and present times. While no attempt has been made, save incidentally, to discuss the strictly terrestrial reptiles, twelve of the fourteen orders of the class recognized by the author are treated more or less fully —their structure, habits, geological distribution, etc. Unlike most of the works for the general reader treating of "ancient monsters," the present work is by an author who has spent many years in the field and laboratory in the collection and study of extinct reptiles, upon which he has an international reputation as an authority.

The numerous illustrations, in large part from the pen or brush of the author himself, include not only living types and twenty-four restorations of extinct forms, but also many figures elucidating the structure and habits of the animals.

THE UNIVERSITY OF CHICAGO PRESS

The Weather and Climate of Chicago. (Bulletins of the Geographic Society of Chicago.) By Henry J. Cox, Professor of Meteorology, United States Weather Bureau, and John H. Armington, Local Forecaster, United States Weather Bureau.

xxvi + 376 pages, 8vo, cloth; $3.00, postage extra (weight 3 lbs. 1 oz.)

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