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JOHN MERLE COULTER AND CHARLES REID BARNES

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DATES OF PUBLICATION

No. 1, July 23; No. 2, August 22; No. 3, September 22; No. 4, October 17; No. 5, November 16; No. 6, December 30.

ERRATA

P. 43, footnote 2, for KARSTEN, H., read KARSTEN, G.
P. 52, Tradescantia zebrina optimum, for .990 read .966.
P. 88, in table under Mean chresard, for 14.7% read 14.1%.
P. 109, line 2 from top, omit hyphen.
P. 111, line 8 from bottom, for semioribcularibus read semiorbicularibus.
P. 113, line 13 from bottom, for punctulata read punctulato.
P. 115, line 10 from bottom, before minore insert folio.
P. 116, line 10 from bottom, for bimellemetrali read bimillemetrali.
P. 116, line 3 from bottom, for pedunculos implice read pedunculo simplice.
P. 117, line 13 from top, for longa read longo.
P. 124, line 5 below Table III, for 0.004^{gm} read 0.0004^{gm}.
P. 131, line 18 from top, for 1883 read 1833.
P. 147, line 4 from top, for WILLIAM read EDWARD.
P. 154, line 16 from top and footnote 15, for SARGENT read SARGANT.
P. 156, line 19 from top, for cell read cells.
P. 193, under title, for PIERCE read PEIRCE.
Pp. 195, 197, 199, 201, in folio, for PIERCE read PEIRCE.
P. 206, line 21 from top, for *edule* read *edulis.*
P. 256, line 16 from top, for mere read near.
P. 323, in legend, for "*lucidum*" read "*lucidus.*"
Pp. 323, 325, in legend, for *pseudoboletum* read *pseudoboletus.*
P. 330, line 19 from top, for vörtiga read vårtiga.
P. 334, line 24 from top, for PSEUDOBOLETUM read PSEUDOBOLETUS.
P. 335, line 2 from top, for *tusgae* read *tsugae.*
P. 335, lines 3 and 5 from bottom, for pseudoboletum read pseudoboletus.
P. 336, line 3 from top, for pseudoboletum read pseudoboletus.
P. 336, line 5 from top, for 21007 read 21077.
P. 338, lines 1, 7, 22, for *pseudoboletum* read *pseudoboletus.*

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BOTANICAL GAZETTE

JULY 1908

A STUDY OF REDUCTION IN *OENOTHERA RUBRINERVIS*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **111**

REGINALD RUGGLES GATES

(WITH PLATES I–III)

The present contribution is a statement of some of the results obtained in the cytological study of *Oenothera Lamarckiana* and its mutants. Since these results have a more or less direct bearing on a wide range of fact and theory in various fields, their full discussion is reserved for a future time. The facts presented in this communication will be taken almost wholly from the study of *O. rubrinervis*, one of the most vigorous of the mutants. Other papers will be presented later, giving the further evidence upon which the conclusions of this paper rest, and attempting to indicate their bearing on the general problems of cytology and variation involved.

Material

The plants from which the material for these studies was obtained were grown from pedigreed seeds of DEVRIES, the purity of these cultures being further proven, in some cases, by carrying on the pedigree for another generation before collections were made. The results of these cultures, which are still being carried forward to later generations, will be published at another time in connection with an account of other studies on variation and hybridization in Oenothera. In this way it is hoped, if possible, to correlate the cytological data with the work in hybridization and variation. It seems to the writer that only by thus combining cytological with experimental studies is an explanation of the peculiar and remarkable phenomena of variation exhibited by the Oenotheras to be reached.

The cytological studies presented here will be confined chiefly to the phenomena of synapsis and reduction in the pollen mother cell. Various forms have been studied, a complete series of stages being obtained in some forms and a partial series or only a few stages being examined in others. The forms investigated include (1) *O. rubrinervis*, (2) *O. Lamarckiana*, (3) *O. gigas*, (4) *O. nanella*, (5) *O. biennis cruciata*, a variety of the European *O. biennis*, (6) both *O. lata* (see **12**) and *O. Lamarckiana* from the F_1 of *O. lata*×*O. Lamarckiana*, and (7) plants resembling *O. gigas*, from the F_1 of *O. lata*×*O. gigas*. Preliminary reports have already been made upon some of these studies, in various connections (**11, 12, 13, 14, 15**). Reference will be made to some of these results later.

The material from each individual was collected separately in nearly all cases, in order to observe possible individual differences in the same race, either in the number of chromosomes or in other cytological features. I am indebted to Mr. C. H. SHATTUCK for making a number of these collections. The material for the study of *O. rubrinervis* was obtained from a number of individuals grown in two different seasons and representing several strains derived from the same original pedigree. Sections were cut from six of these, and it may be stated here that in *O. rubrinervis* no individual differences were discovered, either in the number of chromosomes, which was 14 in all cases, or in any other features. In some of the other mutants, also, a number of individuals were examined. It was found necessary to reserve the account of *O. gigas*, which presents several features of special interest, for a separate paper. A preliminary report on this form has already been made (**14, 15**).

For various reasons, *O. rubrinervis* was chosen as the most favorable form for a thorough study of synapsis and reduction. The nuclei and chromosomes of Oenothera are small, and for this reason the selection of the most favorable type for study is a matter of some importance. In *O. rubrinervis* the pollen mother cells, although they vary much in size, are usually considerably larger than in *O. Lamarckiana*, the nuclei being also proportionately larger. The reason for this will be explained later. The chromosome number being low in most of the forms ($2x=14$, $x=7$), they can be counted without any difficulty, notwithstanding their small size. Another notable advantage in comparing this with other studies in reduction is in the shape of the chromosomes, which are globular or somewhat oblong or cylindrical in most stages of mitosis, and are never greatly elongated or looped. For this reason it is a comparatively easy matter to obtain accurate counts of the chromosomes in the pollen mother cells of any of the forms. This shape is also found to be very advantageous in a study of the events of reduction following synapsis. The appearances are clear and easily interpreted, in striking contrast to the forms with long twisted chromosomes, such as have been made the basis of many of the studies on reduction in plants.

On the other hand, the somatic nuclei and chromosomes are very much smaller, and in metaphase the latter are elongated and looped, making it impossible to count them with the same degree of accuracy. Some of these appearances have already been described elsewhere (**12**, p. 19). Thus while it was found that the chromosomes could be counted almost equally well in pollen mother cells of all the forms studied, *O. rubrinervis* was found to be especially favorable for the investigation of reduction phenomena, especially the events of synapsis and the prophases of the heterotypic mitosis. The account given here will refer throughout to *O. rubrinervis*, with occasional comparisons with other forms. Later papers will take up these other forms in detail, in so far as this is necessary after the account presented here. Special attention will be given at that time, in particular, to the later stages, beginning with the telophase of the heterotypic mitosis, and also to the interesting conditions in some of the hybrids. The detailed account in *O. rubrinervis* will not be carried farther than the metaphase of the heterotypic mitosis, at which time the essential events have already taken place.

Methods

The usual methods of cytological technique were employed, various chrom-acetic and chrom-osmo-acetic solutions being tried until satisfactory fixation was obtained. The thickness of the sections varied from 4 to 10 μ. The latter thickness was found most favorable for counting chromosomes, because it is somewhat greater than the diameter of the nuclei, many of which in such sections were therefore uncut. It is possible to determine easily whether a nucleus has been cut by the knife by examining it in low and high focus. The chromosomes in such uncut nuclei can then be counted with absolute accuracy, either in the prophase of the heterotypic mitosis before the disappearance of the nuclear membrane, or in the telophase after the walls of the daughter nuclei are formed. In nearly every individual examined, large numbers of such cases, all yielding the same result, were counted before the number was finally determined upon. The chromosomes could also be counted in certain positions on the spindle, particularly in anaphases, but in metaphase they were usually too closely grouped to allow of satisfactory counting.

In the second division, particularly in the forms having seven chromosomes as the gametophytic number, the chromosomes could be counted with certainty in almost any stage of mitosis. The thinner sections were used chiefly in the study of spirem and synapsis stages, although here also the comparatively short length of the thickened spirem frequently made it advantageous to study uncut nuclei in which the spirem could be followed throughout its length.

Of the various stains Heidenhain's iron-hematoxylin was found to be superior for chromosome counting and for clear differentiation of chromatic structures in nearly all stages of synapsis and reduction, safranin-gentian being used occasionally for comparison or for differentiating particular cytoplasmic structures. Orange G was also used with the iron-alum stain for bringing out clearly certain special features, particularly the protoplasmic connections between mother cells, which will be described later.

Description

EARLY STAGES

Some of the very early stages of the anthers, previous to the formation of mother cells, have been studied particularly with the purpose of tracing the origin of the bodies which were called heterochromosomes in my first paper. The provisional use of the name was based on the very close resemblance of these bodies to the chromosomes in appearance, and their frequent presence close by, or in some cases apparently attached to, the heterotypic spindle. They were not stated to pass undivided into one of the daughter nuclei, as misquoted by TISCHLER (32), but to remain outside in the cytoplasm where they gradually disappear. The study of their early history shows that no line of distinction can be drawn between them and the large body readily recognized as the nucleolus. They are then smaller nucleoli, not differing essentially in origin from the single larger body which is almost constantly present in the mother cell during synapsis and prophase, but diverging from the latter somewhat in their later history.

In the earliest stages studied, the young meristematic cells of the anther primordia are very small (*figs. 1, 2*), and the tissues are wholly undifferentiated, except the epidermal layer. Usually several smaller nucleoli are present in each nucleus of the meristematic cells, in addition to the larger nucleolus. Compared with the cells of the anther wall when they are no longer meristematic, the smaller nucleoli of the former are about the size of the nucleoli of the latter, which are approximately equal in size. There is nothing in the latter corresponding to the larger nucleolus of the meristematic cells. Probably afterward one of these nucleoli enlarges as the cell increases in size, or it is possible that the nuclei of meristematic cells are always derived from previous ones which already possess a large nucleolus.

Chromatic staining bodies are also found closely appressed to the nuclear membrane in all the meristematic cells (*figs. 1, 2*). This tendency for chromatic material to accumulate on the nuclear walls gives these nuclei a characteristic appearance. These bodies often appear like a thickening of the membrane itself.

At the next stage studied many cell divisions have taken place, and the sporogenous, tapetal, and wall tissues have been differentiated. The sporogenous cells have increased enormously in size, and form a single row in longitudinal section down the center of the anther, the walls of these cells being especially thickened and distinct (*fig. 3*). The cells of the surrounding tapetal layer have also increased greatly in size and are distinctly marked off from the sporogenous row. In the sporogenous cells the nuclei (*fig. 4*), though much increased in size, have not increased in proportion to the cytoplasm. The large nucleolus, much larger than in the earlier stage, is now a conspicuous object in the nucleus. Smaller nucleolar bodies are almost invariably present, but masses are no longer found attached to the nuclear membrane. (The characteristic masses, however, may remain for some time attached to the nuclear walls of the tapetal cells).

Figs. 5–10 are from drawings of other nuclei at this stage of development. In the majority of cases one or two smaller nucleoli occur in addition to a single large one, but rarely (*fig. 6*) two large nucleoli of equal size may be found; and very frequently the number of small bodies, of equal or unequal size, may be greater, reaching as many as five or six. *Figs. 5, 7, 8, 9* show these in various stages of fusion with each other and with the large nucleolus.[1] They are thus not in any sense autonomous bodies. It appears that usually these fusions take place until only one large nucleolus and one or two smaller ones are present during synapsis and diakinesis. But occasionally the fusions do not take place, and several of these bodies may then be present in the later stages. The number of these nucleoli finally present depends, then, largely upon the amount of fusion which has previously taken place between them. In the later stages one large nucleolus is almost invariably present and usually a smaller one bearing a certain proportion to the larger in size, though the latter may vary in size and number as already stated. There is usually a clear area around the large nucleolus, as in the earlier stage, and threads of the reticulum may or may not cross this and appear to be attached to the nucleolus (*fig. 4*). The reticulum of the cytoplasm usually stains rather more deeply at this time than that of the nucleus. It may as well be stated at this time that in the resting nuclei of the pollen tetrad and in the nuclei of the nearly mature pollen grains of Oenothera one finds (*fig. 11*) the same condition of the nucleoli as in the mother cells, namely, usually one large and one small nucleolus bearing a rather definite size relation to each other, with sometimes additional small ones.

The sporogenous rows are differentiated from the tapetum by the greater growth of the cells, nuclei, and nucleoli of the former. At the same time they are distinctly marked off by the formation of a continuous thickened wall between tapetum and archesporium (*fig. 3*). It is obvious that as the cells and nuclei increase in size, the nucleolus grows also. Up to the time of synapsis the mother cells usually form a compact tissue, but about this time the cells begin to

[1] Miss NICHOLS (21) figures what are in all probability stages of fusion of large and small nucleoli in Sarracenia pollen mother cells, but interprets them as a budding-off of small bodies from the nucleolus. The budlike attachments to the nucleolus frequently observed by other authors are doubtless to be explained in like manner.

break apart at the corners where they meet, and before diakinesis is reached they are completely rounded off and independent, or they frequently remain connected with other mother cells only at the ends. In the meantime the cavity of the loculus grows rapidly, so that the mother cells, in normal development, usually lie loose in the cavity.

The events of synapsis and reduction usually go forward simultaneously throughout a flower, with comparatively little variation in the different parts of the same loculus or in the different anthers of a flower. In one flower, however, wide variation was found in different anthers, but comparative constancy in the loculus. One anther of this flower was in synapsis, another in diakinesis, another in metaphase of the heterotypic mitosis, and in still another some of the mother cells had completed the second mitosis. No abnormalities in the cytological condition of this flower were observed.

SYNAPSIS

After the stage described in *fig. 4*, the nucleus increases greatly in size, but without an appreciable increase in the size of the cell. The single row of sporogenous cells divides, so that there are usually two rows of pollen mother cells. Occasionally three or more mother cells are found in the cross-section of a loculus. In general there are fewer divisions than in the other forms, and this is at least one of the reasons why the mother cells are on the average larger than, for example, in *O. Lamarckiana*.

The resting nucleus of the pollen mother cell increases in size and begins to show signs of approaching synapsis. *Figs. 12, 13, 14* show stages in the beginning of this process. A number of these stages were found—although they are uncommon—in the same sections with regular synapsis stages. In some cases they occurred side by side with mother cells in which the synaptic knot had already been formed. A complete series of stages may be found in the same section, from the beginning of contraction to the formation of a close synaptic ball. The cytoplasm in these cells shows no contraction whatever, but is perfectly fixed. For this and other reasons there can be no doubt that this is a real contraction stage, leading to synapsis, and not a result of imperfect fixation, as one might judge on first examination.

That these nuclei are going into synapsis and not coming out is shown by several features: (1) the extremely delicate character of the threads, like those of the resting nucleus; (2) the fact that the periphery of the reticulum as it contracts frequently preserves perfectly the curved outline of the nuclear wall (*fig. 12*); (3) immediately after synapsis the thread is somewhat shorter and thicker than previously and appears to be continuous, while in the earlier contraction stages we still have the appearance of a reticulum (*fig. 13*).[2] As the contraction progresses, the threads are gradually rearranged from an anastomosing reticulum to a very long and continuous delicate thread. The exact manner of this rearrangement could not be observed, but one finds many transitions (*fig. 14*) from the anastomosing reticulum of the resting nucleus to the closely coiled and apparently continuous spirem of the synaptic knot (*fig. 15*). The contraction may take place from one side of the nucleus, leaving the reticulum attached for a time to the nuclear membrane at one point (*fig. 13*), or it may take place simultaneously from all sides (*fig. 12*). A few threads of the reticulum usually remain attached for a time to the nuclear membrane while the contraction is going on. These are drawn in finally as the synaptic ball becomes more compact.

The small number of these intermediate stages found indicates that they are passed through rather rapidly, the frequency of the occurrence of synapsis stages indicating, on the other hand, that this condition is of considerable duration.

No indication of a doubling or pairing of the threads during these intermediate contraction stages could be observed, though they were carefully searched for. Moreover, in the earliest stages of the synaptic ball the thread appears to be as thin and delicate as in the reticulum, which does not favor the view that a pairing has taken place. The evidence, then, so far as it goes, is decidedly not in favor of a pairing.

During these stages the nuclear membrane is often indistinct, making it difficult to define accurately the limits of the nucleus. The

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[2] This explanation assumes, of course, that the synapsis stages themselves are normal and not due to artifact, as I presume all cytologists will now agree, although SCHAFFNER (29) apparently still entertains some doubt on the subject. The regularly coiled arrangement of the thread in the synaptic ball appears to me to be one of the best arguments against this stage being an artifact. Evidently a rearrangement of the threads is going on as contraction proceeds.

same condition is observed during synapsis, which is found in the same sections. In places the nuclear membrane has either disappeared or is too delicate to be observed. The cytoplasm, however, retains the original outline of the nucleus. Mottier (**20**) has apparently observed similar conditions of the nuclear membrane at this time. In some cases it is ruptured and a portion of it is actually carried inward with the nuclear reticulum at the beginning of the contraction (*fig. 12*). One is tempted to explain this as an artifact; but that this is not the explanation is shown by the considerations already mentioned. The explanation appears to be that as contraction proceeds a portion of the nuclear membrane may be torn away and carried inward attached to the threads. Frequently in these stages one finds the nuclear membrane present on one side of the nucleus but invisible elsewhere. This is the case in *fig. 12*, although the membrane was drawn as though complete. Observations of other nuclei bear out this interpretation, the nuclear membrane being clearly visible in some cases attached to portions of the reticulum which have contracted far away from the original position of the nuclear wall. In the late prophase, when the definitive chromosomes are formed, a distinct and perfect nuclear membrane is invariably present, so it would appear that in such cases as those just described a new membrane is afterward formed.

Mention must now be made of the chromatic staining material of the nucleus during these stages. The nucleolus is frequently, though not always, included within the synaptic knot. There is a tendency for other dark-staining bodies to accumulate near the periphery of the nucleus (*figs. 12, 14*); as contraction proceeds these are swept in by the reticulum. The exact relation they bear to the threads is not known. In some cases they appear, in the later stages of contraction at least, to form a part of the threads themselves, in other cases they appear to be merely inclusions in its coils. These bodies show no constancy in number, size, or shape. As the spirem takes on the appearance of the synaptic knot, they are still found in its meshes, and portions of the thread itself may also stain darkly, suggesting a solution of a part of their substance and its transfer into the thread. Even when the greater part of the spirem is completely decolorized certain portions of it retain the stain. This appears to be partly due to the denser aggregation of the spirem in these regions, but in some cases it is evidently due to the presence of bodies which retain the stain and appear to be giving up the stainable part of their substance to the spirem. These bodies are evidently not the prochromosomes found by OVERTON (**22**) in certain dicotyledons, nor are they the gamosomes of STRASBURGER (**30, 31**).

Just the relation these bodies sustain to the spirem is not easy to determine. From *figs. 12* and *14* it is evident that they are at first small "nucleoli" caught in the contracting reticulum, but quite independent of it. Later they appear to give up a portion at least of their material to the spirem, finally disappearing as independent bodies. Usually, however, at least one of these bodies remains independent, and appears in synapsis and diakinesis as a small nucleolus bearing a definite relation to the size of the large nucleolus, being about the size of a chromosome. These bodies are usually free in the nuclear cavity (*fig. 15*). A certain depth of stain is required for demonstrating them during synapsis, for they usually decolorize more quickly than the large nucleolus. With a favorable stain they are found to be of strikingly uniform occurrence at this time. A plasma stain such as orange G may be used with advantage to demonstrate their presence. The uniformity in their occurrence is so great that for some time they were thought to be constant in size and number. With the demonstration of their inconstancy and their origin we have chosen to call them merely small nucleoli, as there appears to be no sufficient reason for another name. The (large) nucleolus disappears with great promptness immediately after the nuclear membrane breaks down, only persisting for a time in a few rare instances. In no case has fragmentation of the nucleolus, previous to its disappearance, been observed, although the presence of deeply staining globular bodies occasionally found near the periphery of the cytoplasm might be accounted for in this way. The mass of the latter, however, is sometimes greater than that of the nucleoli. The smaller nucleoli persist and are frequently found close by the heterotypic spindle. They may also be found on the homotypic spindle (*fig. 41*). Apparently they never reenter a nucleus, but remain in the cytoplasm until they finally disappear. These bodies have been found showing the same behavior in all the forms studied.

POST-SYNAPTIC STAGES

Synapsis lasts for a comparatively long time, as shown by the frequency of its occurrence in the material sectioned. During this time the spirem shortens and thickens and then begins to arrange itself more loosely in the nuclear cavity. This shortening and thickening is progressive (*figs. 16–18*) and apparently continues for some time. During these stages the thickness of the spirem may be nearly uniform throughout, or it may vary greatly, giving a moniliform appearance, or the spirem may appear irregularly constricted at varying intervals. In other cases, with a certain depth of stain it is seen to be composed of lighter and darker areas more or less regularly alternating. Portions of the thread may appear homogeneous or may show the lighter and darker areas, according to the depth of stain (*fig. 17*). In more deeply stained nuclei, such as *fig. 16*, the thread appears homogeneous throughout. These darker areas are the chromatin discs or chromomeres of various authors; and they give the thread a very characteristic appearance. During this well-defined stage the greatly thickened spirem is loosely distributed in the nuclear cavity. Deeply staining bodies still appear attached to or enmeshed in the coils of the thread.

At this time one finds undoubted indications of parallel threads. When represented by camera drawings in one plane the evidence for this is not so satisfactory as in the original preparation, but there is no doubt of their occurrence. As already stated, in the earlier stages previous to and during synapsis, parallel threads could not be observed, and it has not been determined whether they were really absent or whether the failure to observe them was due to their extreme delicacy. Hence it cannot now be stated whether they have arisen through an approximation of spirems at an earlier period, or through a split in the single continuous spirem. This matter will be discussed later.

Following this stage a second well-marked contraction takes place (*figs. 18, 20, 21*), apparently quite as typical and constant in its occurrence as the first contraction stage, which is ordinarily identified as synapsis. This contraction is of much shorter duration, however, and entirely different in appearance, owing to changes which the thread has undergone since synapsis, resulting in a great amount of shortening and thickening of the spirem. MOTTIER (**20**) has recognized this second contraction stage in Podophyllum, Lilium, and

Tradescantia, though he formerly thought it resulted from bad fixation; and it appears to have been observed also by FARMER and SHOVE (**10**). MOTTIER states that in these forms there is but little shortening of the spirem between synapsis and segmentation into chromosomes. In Oenothera, on the contrary, as is evident from a comparison of *figs. 15* or *16* with *22*, a very considerable amount of shortening as well as thickening of the spirem takes place during this interval. During the second contraction the paired threads apparently fuse, and further shortening of the (from now single) thread results in an enormous amount of thickening of the spirem, so that when it uncoils from this second contraction it has approximately the thickness of a chromosome and exhibits only a few loops. It can then frequently be traced through nearly its whole length. At this time there is a great amount of variation in the thickness of different parts of the spirem, as seen in *figs. 22* and *23*. *Fig. 19* is a portion of the spirem at this period, drawn with a higher magnification. It shows the chromatic bodies, which vary in size, imbedded in the linin substratum. As to how far two different substances are represented, I am at present unprepared to say.

DIAKINESIS

The single thick thread now segments transversely into 14 chromosomes, the sporophyte or $2x$ number. At this time there is no indication whatever of a longitudinal split in the thread. Even when greatly washed out, the material of the chromosomes appears perfectly homogeneous, or if a granular structure is observable there is in its arrangement no indication of the previous split. At the time of this second contraction a pair of chromosomes is frequently observed separated from the spirem and apparently always lying with their long axes parallel and connected at one end (*figs. 20, 22*). This condition occurs very commonly, although in other cases the spirem is continuous throughout (*fig. 21*). In no case has more than one pair of chromosomes been observed to be thus precociously cut off in *O. rubrinervis*, though two such pairs have been observed in *O. lata* (see **11**, *fig. 19*). In no case has a single chromosome been observed to be cut off in this manner, and apparently they are invariably cut off in pairs, that is, bivalent chromosomes are detached.

What significance this early separation of chromosome pairs may have is not known, but it appears that the later history of these pairs on the spindle can be traced. In the paper just cited (**11**), the writer wrongly identified them with the smaller nucleoli which persist by the heterotypic spindle. These chromosome pairs are frequently so closely approximated at the end opposite the end of actual connection as to give the appearance of a ring. It was thought that these rings by condensation (which actually takes place) were reduced to the size of these nucleolar bodies. The latter had the size and shape of chromosomes, and with a certain depth of stain invariably appeared hollow. These pairs are not condensed to rings, however, but to chromosome pairs of the ordinary Oenothera type.

The spirem at this time varies greatly in thickness in different parts, exhibiting constrictions and dilatations which indicate more or less clearly where segmentation into chromosomes will take place. This segmentation may happen while the spirem is still in the contracted condition (*fig. 25*), or after it has again uncoiled and distributed itself in the nuclear cavity (*figs. 24, 26, 28*), or before this uncoiling is completed. The segmentation appears to be in some cases nearly simultaneous (*fig. 24*); in other cases the segmentation is successive, as in *fig. 23*, where the spirem is clearly divided into three portions and the constrictions for the formation of the chromosomes are so far advanced that the number of chromosomes to be formed by each segment can already be foretold with practical certainty. The segmentation at this time is into 14 chromosomes, the sporophyte number. A large number of counts made at this time demonstrate the absolute constancy of this number in all the individuals of *O. rubrinervis* examined. It is possible, however, that individuals of this race may be found whose chromosome number differs from this number by one. This matter will be discussed later.

In every single case where the count could be determined with certainty it was shown to be 14. These counts were all made from sections 10 μ thick, and from nuclei which were uncut by the knife. The less numerous counts made in the multipolar stage of the heterotypic spindle gave invariably the same number. In this case all in a given cell were obtained by examining the adjacent sections. In all, hundreds of counts were made. In such nuclei as *figs. 26, 29, 30, 31* there can be no possible doubt of the number of chromosomes present.

As already shown (*fig. 20*), one or in some cases more pairs of chromosomes may be cut off from the spirem before it undergoes segmentation, and frequently while it is still in the second contraction period. The exact method of origin of these pairs has not been observed, but they invariably, so far as observed, lie with their long axes parallel and connected at one end, from which it would appear that they were successive chromosomes on the spirem. In later stages, when the spirem has constricted into a chain of chromosomes arranged near the periphery of the nucleus, one or more pairs of chromosomes are found separated from the rest. Some of these have doubtless had the origin shown in *fig. 20*. Others appear to have originated later, as indicated in some of the figures, by successive chromosomes on the chain swinging around parallel to each other and thus pairing. Usually in diakinesis one or two such pairs are found, though occasionally there is no evidence of pairing. The highest number of pairs observed at this stage was five, with indications of pairing among the others (*fig. 29*); which is unusual. Later, in the multipolar spindle stage two distinct pairs are usually found in varying stages of conjugation (*figs. 35, 36*). A single case was observed (*fig. 37*) in which the fourteen chromosomes were all paired.

As the figures indicate, constriction of the spirem at regular intervals proceeds progressively until a chain of chromosomes is formed. When this has taken place, the chromosomes are at first several times longer than broad, and their margins have a very irregular, sinuous outline, like that of the spirem just previous to segmentation. They are not so long, however, that they can be twisted and looped in the confusing manner of many heterotypic chromosomes of plants. This is very gratifying in the study of these stages, since it permits a clearness of interpretation which would otherwise be unattainable. *Figs. 22* and *23* show the beginning of contraction, which has proceeded farther in *fig. 24*, leaving only the so-called linin connection between the chromosomes. The constrictions are all equivalent and the spirem thus segments into the sporophyte number of chromosomes and not into the reduced number of chromosome pairs. If successive chromosomes on the spirem are really the members of a pair, there is nothing in the manner of segmentation of the spirem to indicate this. However, it is clear enough that one chromosome frequently swings around, as already mentioned, and pairs with its neighbor on the spirem. We do not really have, then, a transverse division of chromosome bivalents, but a separation of whole (somatic) chromosomes. Nothing has been found in the earlier stages which would correspond to the gamosomes and zygosomes of STRASBURGER, and even should a pairing of parallel threads during synapsis occur (a possibility which will be discussed later), the final pairing is between chromosome bodies which were lying end to end on a single spirem thread.

The linin connections during diakinesis appear to be merely the more finely drawn out portion of the spirem between the chromosomes. As condensation and contraction of the chromosomes progress, these linin connections become longer and more delicate (*figs. 31, 33*). The chromosomes become more dense and compact, being at first oblong-cylindrical (*figs. 24, 26*) and then more nearly globular or pear-shaped (*fig. 31*). Certain chromosomes sometimes undergo this contraction more quickly than others, as in *fig. 29*, and the different stages of this condensation may occasionally all be found in the same nucleus. In other cases the globular appearance is due to the position in which certain chromosomes happen to be lying (*fig. 34*).

HETEROTYPIC MITOSIS

During the prophase stages last outlined the cytoplasm usually possesses a more or less obscurely radiate appearance. A felt-work of fibrillae finally appears around the nuclear membrane. Later these fibrillae come to run tangentially to the latter, terminating in the cytoplasm, and by their aggregation in certain regions the multipolar spindle is formed. From this stage the fibers are rearranged to form the bipolar spindle, passing through conditions in which the spindle appears quadripolar or tripolar in section. In the meantime the nuclear membrane has dissolved and the chromosomes are found at first in a cavity surrounded by fibers which preserve the outline of the nuclear wall. Later they come in and become attached to the chromosomes. Usually the large nucleolus has vanished before this time, but occasionally it may still be seen (*fig. 35*). In *fig. 37* the small nucleolus is shown, which can very frequently be seen at this time. *Figs. 36* and *37* are merely sketches of the spindle fibers to indicate their general direction. *Fig. 35* is an unusual case. A cone of fibers appears to have been formed on one side only of the nucleus. The fibers are coming in and finding attachment to the chromosomes. The large nucleolus is still present, as well as two smaller ones.

The most critical stages of reduction have now been described and the remaining stages will be taken up with less detail at this time, but will be presented in full in a later paper. The chromosomes are at first irregularly arranged on the heterotypic spindle. As already seen, during spindle formation many of the chromosomes are frequently separate and unpaired. The attraction between the chromosomes which leads to pairing is evidently weak, so that it is doubtful if any pairing takes place at metaphase between chromosomes which had not previously paired. On the other hand, chromosomes which have once paired, no matter how early, appear to remain together until their separation in the metaphase of the heterotypic mitosis. Hence probably in many cases the chromosomes pass to the poles of the heterotypic spindle without having previously paired with each other, that is, they were merely lying loosely in the equatorial region of the spindle in metaphase, so that it was largely a matter of chance which pole any particular chromosome went to. This is believed to be a matter of prime importance in determining the final result of the reduction divisions in Oenothera, and the nature of the distribution of chromatin elements which takes place. Its possible significance will be pointed out in the discussion. *Fig. 38* shows the chromosomes just being drawn into the equatorial plate of the heterotypic spindle. In the examination of thousands of spindles in about this stage, one usually finds the chromosomes spread out in several planes along the long axis of the spindle. Of course some of these are early anaphase stages in which the chromosomes have begun their journey to the poles, but the condition is seldom found where the chromosomes are arranged regularly in pairs on the spindle. The daughter chromosomes seldom advance toward the pole in a single plane, as is the case in so many forms, but are more or less irregularly strung out along the spindle in their passage to the poles. This is in striking contrast with their behavior in the homotypic mitosis.

Usually in the early anaphase of the heterotypic mitosis a longitudinal split appears in the daughter chromosomes. This split does not stop short of one end, giving a V-shaped body as in many plant chromosomes, but usually passes right through, forming two independent bodies, which, however, remain paired in the telophase and occupy a great variety of positions in regard to each other. The homotypic chromosomes thus assume many of the characteristic shapes which are usually observed in the heterotypic chromosomes of other forms, such as X, Y, V, H, etc. The failure of the heterotypic bivalents to form these shapes is due partly to the weaker attraction between the members of a pair, but largely to a difference in their shape, each member of a pair being usually more rounded in the heterotypic and more elongated and rodlike during the stages between the two mitoses.

The telophase of the heterotypic mitosis is one of the best stages for counting the chromosomes, as they are distributed at equal intervals around the periphery of the nucleus, no two ever being in contact and the halves of each (bivalent) chromosome rarely separating. The chromosomes now evidently repel each other, while the halves of each chromosome attract each other rather strongly. The halves of these bivalent chromosomes are usually short rods, but they may be dumb-bell or hour-glass shaped, or nearly globular, as previously mentioned (**12**). Sometimes, however, this split fails completely to occur in the anaphase, the daughter chromosomes remaining single and globular or somewhat elongated (*fig. 39*). These telophase stages and the prophases of the homotypic mitosis will be taken up in detail in a paper dealing with different forms. These results, therefore, will not be duplicated here, but a brief statement of the events of the second mitosis will be given.

HOMOTYPIC MITOSIS

In the telophase of the heterotypic mitosis the nuclei never pass into the resting condition and the chromosomes never lose their identity completely, though they spread out and anastomose with each other more or less. Nucleoli are formed, as previously described (**11**). These stages between the two mitoses last for some time, but the events of the second mitosis are passed through very quickly. The two homotypic spindles are formed simultaneously and their axes are at various angles to each other. Spindle formation is the same as for the heterotypic mitosis, except that the spindles are smaller. In regard to the chromatin, suffice it at present to say that the chromosomes of the homotypic prophase show the same general types and are often identical in appearance with those of the heterotypic telophase. There can be no doubt that the bivalent bodies which appear on the homotypic spindle are the same bodies that were present in the telophase of the heterotypic. *Fig. 41* shows an early anaphase of the second mitosis, the members of each pair having just separated. One of the small nucleoli appears by one of the spindles.

IRREGULARITIES

In *fig. 39* spindle fibers are seen in the cytoplasm by the side of the spindle in anaphase. This may be connected with a condition which is illustrated in *fig. 40*. Six such cases were observed in which a regular spindle occurred at the side of the mother cell instead of between the daughter nuclei, after the partial or complete disappearance of the heterotypic spindle. Some of these cases were in the telophase of the heterotypic spindle (*fig. 40*); others were in the prophase of the homotypic. In these cases the spindles were regularly formed and rather sharp-pointed and occupied the same position at the side of the cell; of course they contained no chromosomes. The method of their origin is unknown, but it seems probable that they are connected with the condition observed in *fig. 39*. Mother cells which probably indicate an intermediate condition, in which irregularly arranged fibers were found at the side of the cell, were occasionally observed. They may merely indicate a persistence of the kinoplasm of the heterotypic spindle after its function has ceased, but their structure appeared remarkably definite in most of the cases observed.

A single case of extra nuclei in the pollen tetrad was observed in *O. rubrinervis*. These have been previously described in *O. lata* (11), where they are common occurrences in connection with pollen degeneration. The single case observed in *O. rubrinervis* is sketched in *fig. 42*. Two small nuclei are present in addition to the four larger ones composing the tetrad. The nuclei had passed too far into the resting condition to count the chromosomes in each nucleus.

POLLEN DEGENERATION

The general question of pollen degeneration in Oenothera is an interesting one. It reaches its extreme expression in *O. lata,* which is usually completely sterile in this regard, and in which I have already shown (**11**) that irregularities occur during the reduction divisions similar to those found in sterile hybrids. The question of sterility is evidently, as TISCHLER (**32**) suggests, a relative one.

In *O. rubrinervis* one is led from a gross examination to judge that the pollen production is copious and probably equal to that of *O. Lamarckiana* itself, but in reality many of the pollen mother cells fail to complete their divisions. From an examination of sections of anthers of *O. rubrinervis* it is found that in some loculi a large number or perhaps nearly all the mother cells may be degenerating in the synapsis stage. Frequently the cells are flattened and distorted, appearing pressed together for lack of space in the loculus. The chromatic contents of such cells often form a dense irregular mass, or their nuclei may be in normal synapsis or mitosis, notwithstanding the distorted shape of the cell; while still other cells of the same loculus may be entirely normal. Even earlier, in the archesporial stage, the tapetal cells in many sections were found to be breaking down, as in *O. lata* (**11**). No indications of degeneration have yet been observed in mother cells of *O. Lamarckiana,* and very few in the tapetum.

The percentage of mother cells which thus degenerate in *O. rubrinervis* was not determined. TISCHLER (**32**) suggests that the causes of sterility in mutants are the same as those in hybrids and in plants under cultivation. This general cause he designates as a disturbance or derangement of the constitution of the idioplasm, which he thinks has taken place in the production of mutants as well as in hybrids and under the conditions of cultivation.

PROTOPLASMIC CONNECTIONS

It is an interesting fact that large and rather conspicuous protoplasmic connections are found between the pollen mother cells in *O. rubrinervis.* They are usually quite easily seen and it is probable that they are always present. They consist of delicate strings or threads of cytoplasm connecting adjacent mother cells. In size they vary greatly, from the delicacy of a spindle fiber to a coarse thread or strand connecting the cells (*figs. 45, 46*). When the cytoplasm has shrunken slightly away from the cell wall they are particularly clearly observable. These connections appear to be in all cases between mother cells, and in no case have they been observed between the mother cells and the tapetum. Generally one such strand is seen connecting two cells, but not infrequently there are two or three or occasionally even more. There is no constriction or change in the nature of the connective as it passes through the cell wall. These connections are even larger and more conspicuous in *O. gigas*, where the mother cells are also much larger. They have not been observed in *O. Lamarckiana* or the other forms, but they doubtless occur in all, being probably smaller and more inconspicuous in some.

Discussion

The method of reduction described in this paper at once raises a number of questions of prime importance from the cytological standpoint, as well as from that of the relation subsisting between hereditary and cytological phenomena. A discussion of all these features will not be attempted at this time, the intention of the writer being merely to indicate the general directions in which the facts point and the possible bearing which these data may be found to have on the problems connected with the phenomena of mutation in Oenothera. A fuller discussion of these subjects is reserved for a future time, after the presentation of further data. In the present communication reference will be made only to the most recent papers on reduction in plants, the purpose not being a review of the literature, or a discussion of present views, except in so far as they bear directly on the matter in hand.

The recent accounts of reduction in plants, given by BERGHS (**3, 4, 5, 6**), GRÉGOIRE (**16**), STRASBURGER (**31**), ALLEN (**1, 2**), MIYAKE (**18**), OVERTON (**22**), ROSENBERG (**25**), YAMANOUCHI (**33**), and others, have agreed in so far as the following general course of events is concerned: In synapsis a pairing of homologous maternal and paternal elements occurs either in the form of gamosomes (STRASBURGER and MIYAKE), prochromosomes (OVERTON), or parallel threads (ALLEN, ROSENBERG, GRÉGOIRE, BERGHS, CARDIFF **7**, and YAMANOUCHI). In every case two parallel threads result, which unite more or less intimately about the time of synapsis or later. After the events of synapsis, a longitudinal split reappears in the thickened spirem threads, this split representing the line of approximation of the two original spirems. Transverse segmentation into pairs of chromosomes, which are believed to be homologous somatic chromosomes of maternal and paternal origin, then takes place. The halves of these bivalent chromosomes, which lie side by side, are then distributed in the heterotypic mitosis, which is thus a reduction division. In the anaphase of the heterotypic mitosis a longitudinal split appears in the daughter chromosomes, which is regarded as a premature split for the homotypic mitosis, the latter being thus an equation division. The persistency with which this general account has been given, notwithstanding differences in detail, particularly preceding and during synapsis, leads the writer to the belief that it is probably correct in its main outlines, at least in many of the forms described. This being judged to be the case, every effort was made to bring the account in Oenothera into harmony with this general course of events but without success, for Oenothera is found to deviate in some important particulars, as is already evident from the description.

Another general account of reduction in plants, which was adhered to by STRASBURGER as late as 1904 (**30**), and has been held notably by FARMER and MOORE (**8, 9**), FARMER and SHOVE (**10**), SCHAFFNER (**28**), MOTTIER (**19, 20**), and others, to mention only a few of the recent papers, is in general as follows: The split in the spirem which occurs at about the time of synapsis is a true split, such as may occur in the prophase of somatic mitoses, and is not preceded by a pairing of parallel threads, but the thread is single from the beginning. This split afterward closes up as the thread shortens and thickens after synapsis, and the single spirem so formed segments usually into the reduced number of chromosomes, which are thus arranged successively end to end. Each such bivalent chromosome thus consists of two halves arranged end to end, not side by side, and the heterotypic mitosis thus separates successive whole chromosomes on the spirem, being therefore, as in the other account, a reduction division. The split which appears in the anaphase of this mitosis is interpreted as a reappearance of the earlier longitudinal split of the spirem. The homotypic mitosis is therefore an equation or longitudinal division.

There are of course minor differences in these accounts, SCHAFFNER (**28**) stating, for example, that in *Lilium tigrinum* there is a splitting of granules in the spirem, but the linin thread remains single. Differences of opinion are also expressed regarding the arrangement of the loops of the spirem before segmentation, and their relation to the chromosomes formed.

These two general schemes agree that the heterotypic mitosis is a reduction division separating whole somatic chromosomes, while the second division is longitudinal. The essence of the distinction is that the first view regards the chromosome bivalents as formed by a side-by-side union of homologous chromosomes through the medium of parallel threads, while the second view holds to an end-to-end union. It will be seen that, omitting the points which are left undetermined, the account in Oenothera corresponds more nearly with the latter scheme than with the former, though differing in some respects from both. ROSENBERG (**25**), from a comparison of forms having long and short chromosomes, has attempted to harmonize the latter view with the former. He examined Listera, Tanacetum, Drosera, and Arum, and found that, for example in Drosera, which has short definitive chromosomes much like those of Oenothera, the spirem first segmented into long twisted chromosomes lying in pairs with their long axes parallel. Later, as they condensed into the short, rounded definitive chromosomes, they frequently swung around end to end, so that an observer seeing only the later stage would conclude that they had been arranged tandem on the spirem at the time of their origin. Similar conditions were sometimes observed in Listera. I think my *figs. 22–28* make it evident that this explanation will not apply to Oenothera. The chromosomes in Oenothera do not undergo any such great amount of condensation, but are already thick, heavy bodies when first formed from segmentation of the spirem (*fig. 24*). Their diameter at this time is about the same as that of the spirem just previous to segmentation, as is shown by comparing *figs. 22* and *23* with *figs. 24* and *26*. The fact that as many as eight or more chromosomes may be found forming a single connected chain (*fig. 26*) also renders this explanation impossible.

MIYAKE (**18**) finds that after the pairing of elements in synapsis (the exact method of this pairing need not be entered into here) in

Galtonia and Tradescantia, a longitudinal split appears in the thickened thread, and the double spirem thus formed breaks transversely into the reduced number of chromosome pairs. Later, in these forms, a secondary union between the chromosomes is claimed to take place, forming a single connected chain of chromosomes (as in Oenothera). Sometimes a pair of chromosomes lies free by itself at this time. Then by further shortening the chromosomes of Galtonia again fall apart into pairs, though in Tradescantia they frequently remain connected even after spindle formation. The apparent similarity of the chromosome chain thus described by MIYAKE in Galtonia to the condition in Oenothera, led the writer to make an endeavor to harmonize the two accounts. But instead of this, all the evidence obtained from a critical study of the stages concerned shows that in Oenothera a single very thick spirem breaks transversely into the sporophyte number of chromosomes. A critical examination of *figs. 22–28* will make it clear, I think, that we are following the progressive segmentation of a single spirem, and there is no room for stages between, in which a double spirem breaks into two parallel series of chromosomes. Moreover, it is hardly likely that secondary fusions between chromosomes would take place to such an extent as is shown in *figs. 23* and *24*. In nuclei such as *fig. 20*, in which a pair of chromosomes is cut off prematurely from the spirem while still in the second contraction, they are invariably connected at one end and rarely, if ever, at the other (though sometimes the close approximation of the latter ends may give the false appearance of a ring). This would not be the case if they came from separate paired threads merely lying side by side, so that this connection shows them to have been really successive on the spirem. From this evidence the writer cannot see how anything except a distortion of the facts can lead to the assumption in Oenothera of two parallel threads breaking into chromosomes. Hence the conclusion is that the double threads appearing in the stage represented by *fig. 17* have united to form a single thread, which then breaks transversely into the sporophyte number of chromosomes.

This corresponds fairly well with STRASBURGER'S 1904 (**30**) account of the post-synaptic stages in Galtonia, and suggests to the writer that perhaps after all the earlier account may be nearer the facts, so far as the points here under discussion are concerned, than the paper of 1905 (**31**). The close similarity of the conditions in Galtonia and Tradescantia during diakinesis to those in Oenothera suggests that they may be found finally to conform to Oenothera in these later stages. Whether or not this will be found to be the case, we must conclude that in Oenothera the longitudinal fission in the spirem (however it originated) closes up, and that after the second contraction, or during it, the thick thread segments into the sporophyte number of chromosomes. Since this diverges in important respects from nearly all the recent accounts of reduction in plants, the conclusion is that reduction probably takes place differently in different plants. Whether or not the results are different from the standpoint of a qualitative distribution will not be discussed now. The writer believes the above conclusions to be necessary, despite the fact that authors have reached different conclusions in regard to the same plant, particularly in such cases as Lilium and Podophyllum.

The next important point which requires discussion and which was left undecided in the statement of observations, is in regard to whether the double thread observed after synapsis arises from an approximation of parallel filaments or through a primary split in the thread. It may be well to examine the results which follow from either assumption. The writer hopes later to determine more definitely this difficult matter. On the first assumption of a lateral approximation in synapsis of two spirems representing respectively the maternal and paternal chromosomes, we should expect the double thread so formed to segment into the *reduced* number of chromosome pairs, in order to conform to the current account in forms in which there is a pairing of spirems, for example ALLEN (**1**), GRÉGOIRE (**16**), and YAMANOUCHI (**33**). Instead, however, the spirem segments into the unreduced number of bodies. We may still assume that each of these bodies consists of maternal and paternal longitudinal halves still closely held together and resulting from a previous approximation. According to this view the first mitosis would separate bodies which were arranged successively on the spirem, while the second mitosis would separate the maternal and paternal halves of these bodies. The reason for such a result would be that the maternal and paternal spirems remained closely fused after pairing, so that their elements were separated in the second mitosis instead of the first. This view is scarcely admissible for several reasons. In the first place, on this hypothesis transverse segmentation of the spirem must have taken place not only between the (bivalent) chromosomes but also in the middle of each chromosome, in order to give a chain of fourteen bodies. Such a segmentation seems unlikely. Another possible explanation would be that the chromosomes have lost their identity during synapsis, and that the bodies we are dealing with now are new arrangements of the chromatic material, irrespective of the somatic chromosomes. Many considerations, however, strongly support the belief that these bodies really represent the somatic chromosomes. The facts so far educed in Oenothera, in the opinion of the writer, all favor the hypothesis of the separate existence and genetic continuity of the chromosomes from one generation to another. In this connection may be cited certain plants from the F_1 of *O. lata* ×*O. gigas*, which as stated elsewhere (**14**) have 21 chromosomes as somatic number, 10 of which regularly go to one pole of the heterotypic spindle and 11 to the other. Occasionally, however, the segregated numbers of chromosomes are 12 and 9, one chromosome having gone to the wrong pole of the spindle. In this hybrid 7 of the chromosomes are maternal and 14 paternal. If in this case there were a pairing of maternal and paternal spirems, it is difficult to see how it could be accomplished and result in the distribution of chromosomes in the heterotypic mitosis already stated.

It will be instructive to compare the chromosome history in this cross with the often-quoted condition found by ROSENBERG (**23, 24**) in *Drosera longifolia*×*D. rotundifolia*. *D. rotundifolia* has 10 chromosomes and *D. longifolia* 20, as the gametophyte number. The hybrid naturally has 30 chromosomes in its sporophyte tissues, but in diakinesis 20 chromosome bodies appear, 10 of which are double, consisting of a larger and a smaller half, while the remaining 10 are the unpaired (smaller) *longifolia* chromosomes. The larger and smaller halves of the 10 bivalents separate and pass regularly to the poles of the heterotypic spindle, but the unpaired chromosomes are irregularly distributed or left out of the daughter nuclei. Later the pollen deteriorates. This result is strikingly different from that in the Oenothera hybrid, and, while perfectly in harmony with the idea of the pairing of threads in synapsis in Drosera, makes it highly probable, and in fact necessary, that the method of reduction in the Oenothera hybrid be different. This is a strong argument not only against pairing of maternal and paternal spirems in Oenothera, but in favor of the probability that reduction takes place in diverse ways in the two genera. A considerable amount of time has already been devoted to the study of reduction in this Oenothera hybrid, and an account will be published later. So far as observed it shows no differences in method from the account given here for the pure races.

The hypothesis of the pairing of parental spirems in synapsis in Oenothera being thus rejected, the other alternative remains, namely, that the double spirem results from a split; and this appears to satisfy all the facts. The observations have already shown that the spirem segments into a single chain of chromosomes. The description of events in Oenothera from synapsis on thus agrees in outline with the 1904 account of STRASBURGER (**30**) in Galtonia, and in general also with that of FARMER and MOORE (**9**) in Lilium, Osmunda, Psilotum, and Aneura, FARMER and SHOVE (**10**) in Tradescantia, and MOTTIER (**19**, **20**) in Lilium, Podophyllum, and Tradescantia. The belief of the writer is that some of these forms will be found to correspond more nearly with the account which involves a pairing of threads, and some with the account involving only a split.

Another important matter which requires mention at this time is the nature of the chromosome distribution which takes place on the heterotypic spindle in Oenothera. As already observed, the chromosomes even during spindle formation are frequently unpaired. This appears to be due to the weakness of the mutual attraction which ordinarily leads to pairing. Granting that homologous maternal and paternal chromosomes unite when pairing takes place, what are the possibilities regarding the unpaired chromosomes? Pairing insures ordinarily that the members of the pair will proceed to opposite poles of the spindle, and hence that the homologous maternal and paternal elements will enter different nuclei. There is no such certainty in the distribution of the unpaired chromosomes, so that it might be expected that in certain cases both members of a pair would enter the same daughter nucleus. It is important to note that this result is entirely independent of the origin of these chromosome pairs, whether from an end-to-end or side-by-side union of somatic chromosomes, or in any other manner, so that this question holds no necessary relation to the method of reduction. On the common cytological assumption that the chromosomes are qualitatively different (which has apparently been shown to be a fact in certain well-known cases in animals, that need not be cited), germ cells would occasionally arise lacking both members of a pair, and hence lacking the possibility of developing certain qualities. In this manner it is conceivable that a series of types might arise from the parent *O. Lamarckiana*, each lacking the possibility of developing a certain group of characters possessed by *O. Lamarckiana*.

On this view, which is suggested merely as a tentative hypothesis, we would have in the mutations of *O. Lamarckiana* an analytical process in which a series of types arises from the parent form, each lacking in a different group of qualities or capacities which the parent form possessed. This does not apply to *O. gigas*, however, which will be taken up at another time. The further bearings of this hypothesis on the mutation theory of DEVRIES will not be followed up in this discussion, but it may be pointed out here that such a hypothesis accounts for the absence of reversions of the mutants to *O. Lamarckiana*, and it may also account for some of the peculiarities of hybridization among the Oenothera mutants. I should therefore suggest that there may be a relation between the type of reduction in any organism and its variation and hybridization phenomena.

In Galtonia and probably also in Tradescantia there are apparently the same possibilities that both chromosomes of a pair may occasionally enter the same daughter nucleus. In other plant forms studied the attraction between chromosomes seems to be strong enough to keep the members of a pair together until their separation in the anaphase of the heterotypic mitosis. The segregation of the members of a pair into separate germ cells is thus insured. In cases where, as in Oenothera, the members of a pair do not always remain in contact, but are loosely arranged on the spindle, such a result as already suggested seems certain to occur in certain instances.

It has already been mentioned that occasionally one chromosome goes to the wrong pole of the heterotypic spindle. This is found to be the case particularly in the hybrids, for example, in the *O. Lamarcki-*

ana plants from the F_1 of *O. lata*×*O. Lamarckiana* (**13**), in which sometimes eight chromosomes pass to one pole and six to the other; but it may also occur rarely in the pure races. This matter was briefly discussed elsewhere (**14**). Assuming that the 14 chromosomes are in two similar sets of 7 each, and that homologous members of these sets conjugate except when there is a failure to pair, then when 8 chromosomes go to one pole and 6 to the other, both members of one of the pairs must have gone to the same pole. This probably takes place in cases where such members were unconjugated, for the purpose, or at any rate, the result of the pairing is in ordinary cases that one member of every pair shall be distributed to each pole. If, while two members of one pair thus go to one pole, the second member of another pair goes to the other pole, we should have an equal numerical distribution of chromosomes, but one daughter group would be lacking both members of one pair and the other would be lacking both members of another pair. It is highly probable that such a distribution occasionally takes place, though it would be less common than the case, already proved, where the members of a single pair are unilaterally distributed. It should be borne in mind that such cases are most likely to occur, not when the members of a pair are conjugated, but when they lie separately in diakinesis and on the spindle.

Miss Lutz (**17**), from an examination of root tips, states that she has observed several individuals belonging to different strains having 15 chromosomes instead of 14. This is to be anticipated from the irregularities in chromosome distribution in reduction already mentioned. I have observed one such case in *O. lata*×*O. gigas* (**14**)—a certain plant having 20 chromosomes instead of 21. All the plants of *O. lata* (**12**) and *O. nanella* (**13**) thus far examined by me had 14 chromosomes, while Miss Lutz (**17**) finds in root tips some *O. lata* plants with 14 and also some with 15 or she thinks possibly 16 chromosomes. She reports finding two *O. nanella* plants with 14 chromosomes and one with 15. Two *O. albida* seedlings are said to have 15 chromosomes and two *O. oblonga* plants 15, while a third has 14. Disregarding the possibility that these results might be due to the well-known variation in chromosome numbers in root tips, they are such as would be likely to arise in different individuals from the cytological irregularities I have already described. Whether there are external differences between the plants having 14 chromosomes and those of the same race having 15, is as yet unknown. But it is quite conceivable that no such differences will be found, for if the sporophyte chromosomes consist of two complete sets (and for a variety of reasons this seems the only tenable view at the present time if we assume qualitative differences at all), the presence of an additional chromosome, which is already present in duplicate, would scarcely be expected visibly to affect the plant.

ROSENBERG (**26**) has found an analogous situation in Hieracium. For example, *H. excellens*×*H. Pilosella* gives hybrids with different numbers of chromosomes. This he ascribes to the fact that the eggs of *H. excellens* differ in their numbers of chromosomes, which he finds is due to irregularities in chromosome distribution during the reduction divisions. The writer has pointed out elsewhere (**12**) certain similarities between the hybridization phenomena in Hieracium and Oenothera, and this seems to be a further similarity between the two genera.

ROSENBERG (**27**) has since shown that *H. excellens* produces three kinds of embryo sacs: (1) Normal embryo sacs which require fertilization for their development. These are presumably the only ones which can be hybridized. The egg cells in these sacs vary in their number of chromosomes owing to the fact that some of the chromosomes, lacking in "affinity," remain univalent (that is, fail to pair) during the heterotypic mitosis and are irregularly distributed. It is evident that this lack of affinity between chromosomes is similar to that in Oenothera. (2) In rare cases apogamous embryo sacs are formed after a single division of the megaspore mother cell, and without reduction. (3) More frequently the condition occurs which ROSENBERG calls apospory, in which tetrad formation takes place and then an adjacent cell of the nucellus enlarges, displaces the tetrad, and forms an embryo sac without reduction.

Summary

In conclusion a brief summary of the facts and considerations here presented will be useful.

1. In Oenothera the heterotypic mitosis is a reduction division, separating whole chromosomes which lie successively on the spirem. The homotypic mitosis is an equation division, separating the longi-

tudinal halves of the daughter chromosomes of the heterotypic mitosis. Whether an approximation of threads or a split in a single thread occurs in synapsis was not determined with certainty from the observations, but various considerations lead to the belief that in Oenothera the doubling is due to a split which closes up later, rather than to an approximation of separate spirems.

2. The conclusion that the method of reduction probably differs in different genera is based on two considerations: (1) the fact that in most of the recent accounts of synapsis and reduction in plants a side-by-side pairing of chromosomes from maternal and paternal spirems is described, while in Oenothera the members of a pair are arranged end to end on a single spirem; and (2) on differences in chromosome distribution during reduction in certain hybrids of Drosera and of Oenothera (see p. 25). If reduction took place in the same manner in both genera, the chromosome distribution during reduction in these hybrids with reference to the parental chromosome numbers should be the same in both, but this is not the case.

3. Pairing between the definitive chromosomes during diakinesis and the prophase of the heterotypic mitosis does not always take place, owing to a weak attraction between the chromosomes. This allows irregularities of distribution in the heterotypic mitosis, so that both (unpaired) chromosomes belonging to one pair will *occasionally* enter the same daughter nucleus (see p. 26). Germ cells will thus arise, from which both members of a given pair of chromosomes are absent.

4. If we assume qualitative differences between the chromosomes or parts of them, various types would be expected to originate in this manner, each of them lacking the ability to develop certain qualities possessed by the parent form. On this view the mutations of *Oenothera Lamarckiana* are an instance of a process of analysis by which from the parent form arises a series of types, each lacking in certain characters or capacities possessed by the parent. This hypothesis would account for the absence of reversions among Oenothera mutants, and perhaps also for some of the peculiarities of hybridization in Oenothera. This matter will be considered at another time. This explanation does not apply to all the mutants, however; for example, *O. gigas*.

5. It is suggested that there is probably a direct relation between the events of reduction in a given genus and its variation, as well as its hybridization phenomena.

I desire to express my thanks to Professors JOHN M. COULTER and CHARLES R. BARNES for valuable suggestions and adequate facilities in connection with this work.

THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES I–III

The figures were drawn with the aid of a Bausch & Lomb camera lucida. All except *figs. 1* and *19* were drawn under a Zeiss apochromatic objective 2^{mm} ap. 1.30, with a Zeiss compensating ocular 18. The figures are reduced one-fourth in reproduction, giving a magnification of nearly 3000 diameters. *Fig. 1* was drawn under a 2^{mm} objective and compensating ocular 6; *fig. 19* under B. & L. objective $\frac{1}{16}$ N. A. 1.32 and Zeiss ocular 18.

PLATE I

FIGS. 1, 2.—Young meristematic cells of anther primordium showing one large nucleolus and several smaller ones, and chromatic masses adherent to the nuclear membrane.

FIG. 3.—Longitudinal section of anther, showing size relations of nucleoli in sporogenous, tapetal, and wall cells.

FIG. 4.—One sporogenous cell from stage of *fig. 3*, previous to synapsis; cytoplasm somewhat vacuolate.

FIGS. 5, 7–9.—Nuclei at same stage, showing fusions of nucleoli.

FIG. 6.—Two nucleoli of equal size; an unusual condition.

FIG. 10.—Several small nucleoli, and no indication of fusion.

FIG. 11.—Nucleoli of young pollen grain nucleus.

FIG. 12.—Beginning of synaptic contraction; the reticulum has contracted from the nuclear membrane on all sides, leaving several loops attached to the membrane; on the side on which the reticulum retains the curved outline of the nuclear membrane the latter has been drawn inward attached to the threads; on the rest of the circumference, between the loops, the nuclear membrane remains *in situ;* the cytoplasm is perfectly fixed.

FIG. 13.—Another contraction stage, showing loops attached to the nuclear membrane, which is intact.

FIG. 14.—A slightly later stage of contraction, in which the rearrangement of threads is taking place.

FIG. 15.—Synapsis; dark-staining bodies are still held in the meshes of the spirem; a small nucleolus, usually about the size of a chromosome, is generally present in addition to the large nucleolus.

FIG. 16.—After synapsis; the thread thicker and shorter and loosely coiled.

FIG. 17.—Slightly later stage than *fig. 16*, and less deeply stained; thread shows the characteristic light and dark areas; indications of parallel threads in two places; edge of thread may be even or moniliform.—5 μ.

FIG. 18.—Later stage; thread much shortened and greatly thickened and entering upon second contraction phase; nucleus uncut.—10 μ.

FIG. 19.—Higher magnification of a portion of the thread in *figs. 20* and *21*.

PLATE II

FIG. 20.—Second contraction stage; a pair of chromosomes cut off from spirem; nucleus uncut.—10 μ.

FIG. 21.—Second contraction stage; nucleus uncut.

FIG. 22.—Uncoiling from second contraction stage; pair of chromosomes detached; nucleus uncut.

FIG. 23.—Spirem segmented in three places, each segment showing constrictions which will form the chromosomes; certain chromosomes already detached; nucleus uncut.

FIG. 24.—Constriction of spirem has proceeded farther, the chromosomes being elongated bodies with irregular margins like the spirem, and connected by rather

thick "linin" bands; pair of chromosomes detached earlier lies at side of nucleus; *n*, small nucleolus; nucleus cut.

FIG. 25.—Spirem more or less completely segmented into chromosomes while still in the second contraction stage; preparation considerably destained; 13 chromosomes in view.

FIG. 26.—Spirem segmented, showing chain of eight chromosomes and three pairs; nucleus uncut.

FIG. 27.—Chain of six chromosomes, and probably four pairs; linin connections between members of a pair not always visible; nucleus uncut.

FIG. 28.—Fourteen chromosomes; several small nucleoli; nucleus uncut.

FIG. 29.—Fourteen chromosomes, including five pairs more or less closely associated; linin connections not visible; one pair of chromosomes has already contracted into the globular shape.

FIG. 30.—Fourteen chromosomes, several in pairs; apparent inequalities in size due to positions in which some of the chromosomes are lying.

FIG. 31.—Slightly later stage; the fourteen chromosomes contracted into the globular or pear-shaped definitive form; linin connections longer and extremely delicate; nucleus uncut.

FIGS. 32–34.—Other groups in diakinesis, showing various peculiarities of chromosomes.

FIG. 35.—Peculiar case of spindle formation; three nucleoli present and fourteen chromosomes, including three or four pairs.

FIG. 36.—Multipolar stage of heterotypic spindle; two more or less closely united pairs of chromosomes present.

PLATE III

FIG. 37.—Same as *fig. 36;* an unusual case in which all the chromosomes are closely joined in pairs; seven such pairs present and a small nucleolus.

FIG. 38.—Heterotypic spindle in metaphase; spindle has usually more mantle fibers than in *O. Lamarckiana;* chromosomes usually loosely arranged in equatorial region of spindle.

FIG. 39.—Late anaphase; an uncommon case; daughter chromosomes have failed to divide, and fibrillae are scattered in cytoplasm at side of cell; chromatic staining material also present.

FIG. 40.—Telophase of heterotypic mitosis; exceptional case, in which a rather sharp pointed spindle is formed at side of cell; it probably originated from the fibrillae shown in *fig. 39*.

FIG. 41.—Early anaphase of homotypic mitosis; small nucleolus having the characteristic appearance, present on one of the spindles.

FIG. 42.—The single case of extra nuclei observed in *O. rubrinervis* pollen mother cells.

FIGS. 43, 44.—Nuclei from telophase of second mitosis, passing into resting condition.

FIGS. 45, 46.—Protoplasmic connections between mother cells.

GATES on REDUCTION in OENOTHERA

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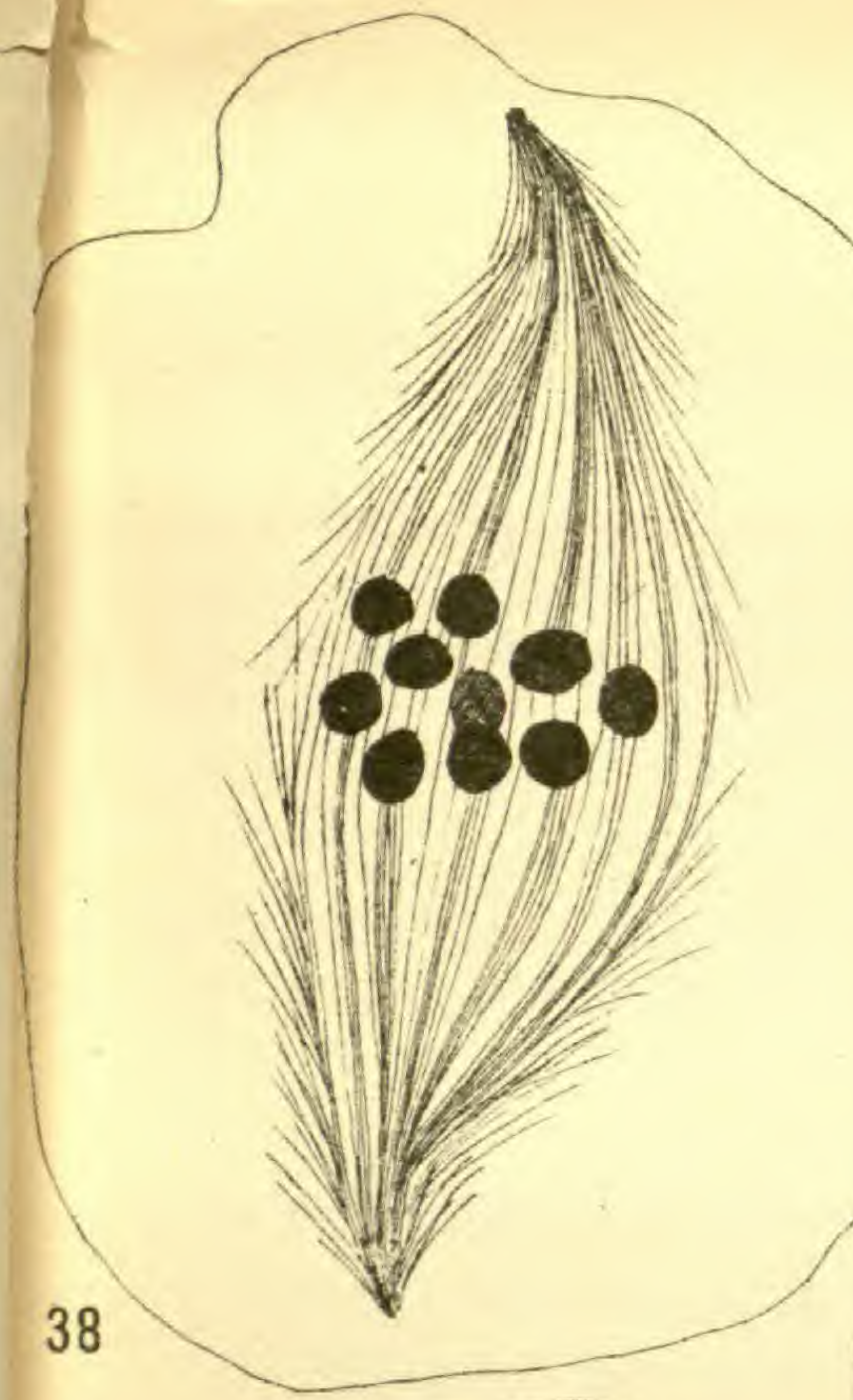
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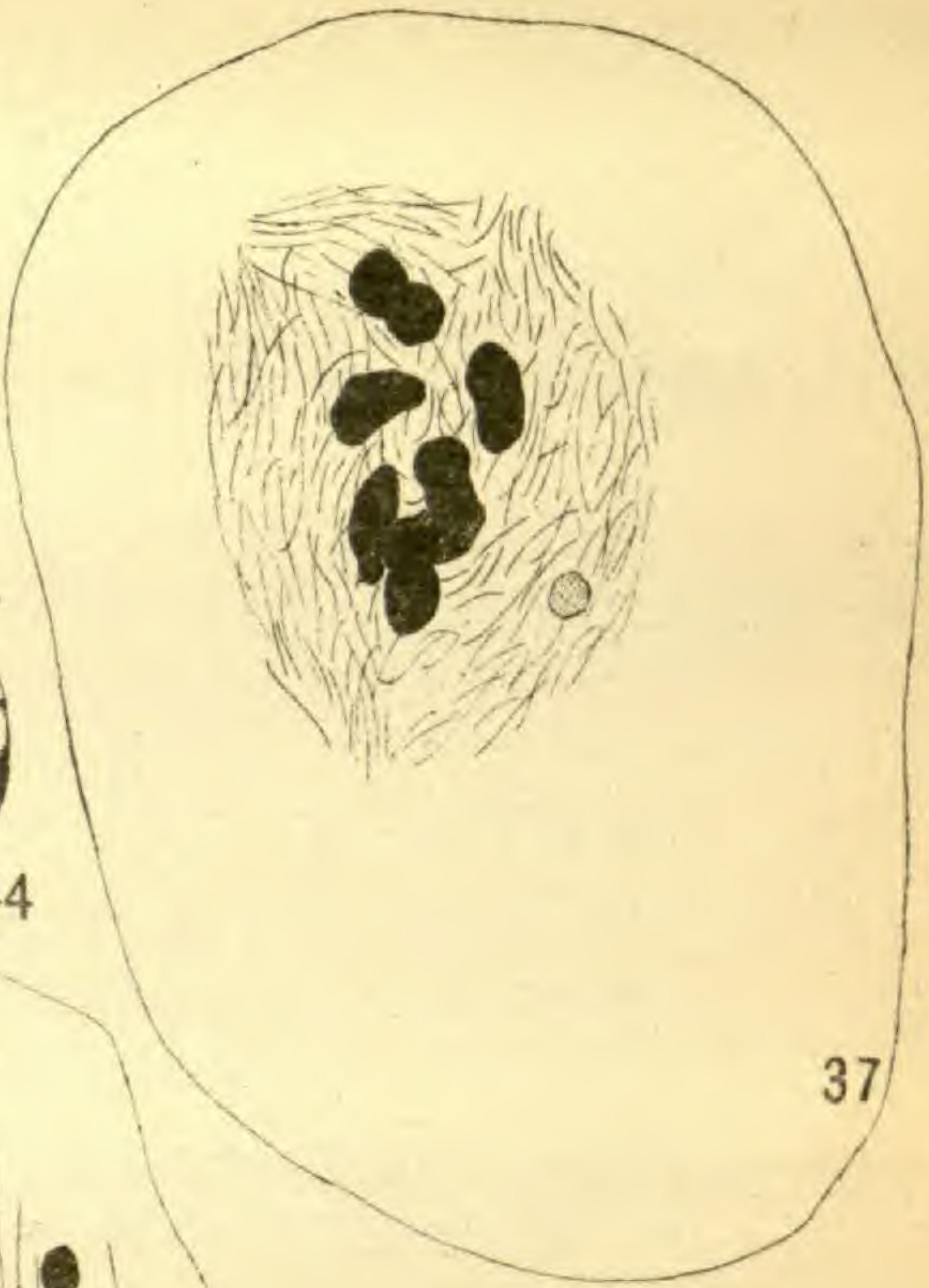
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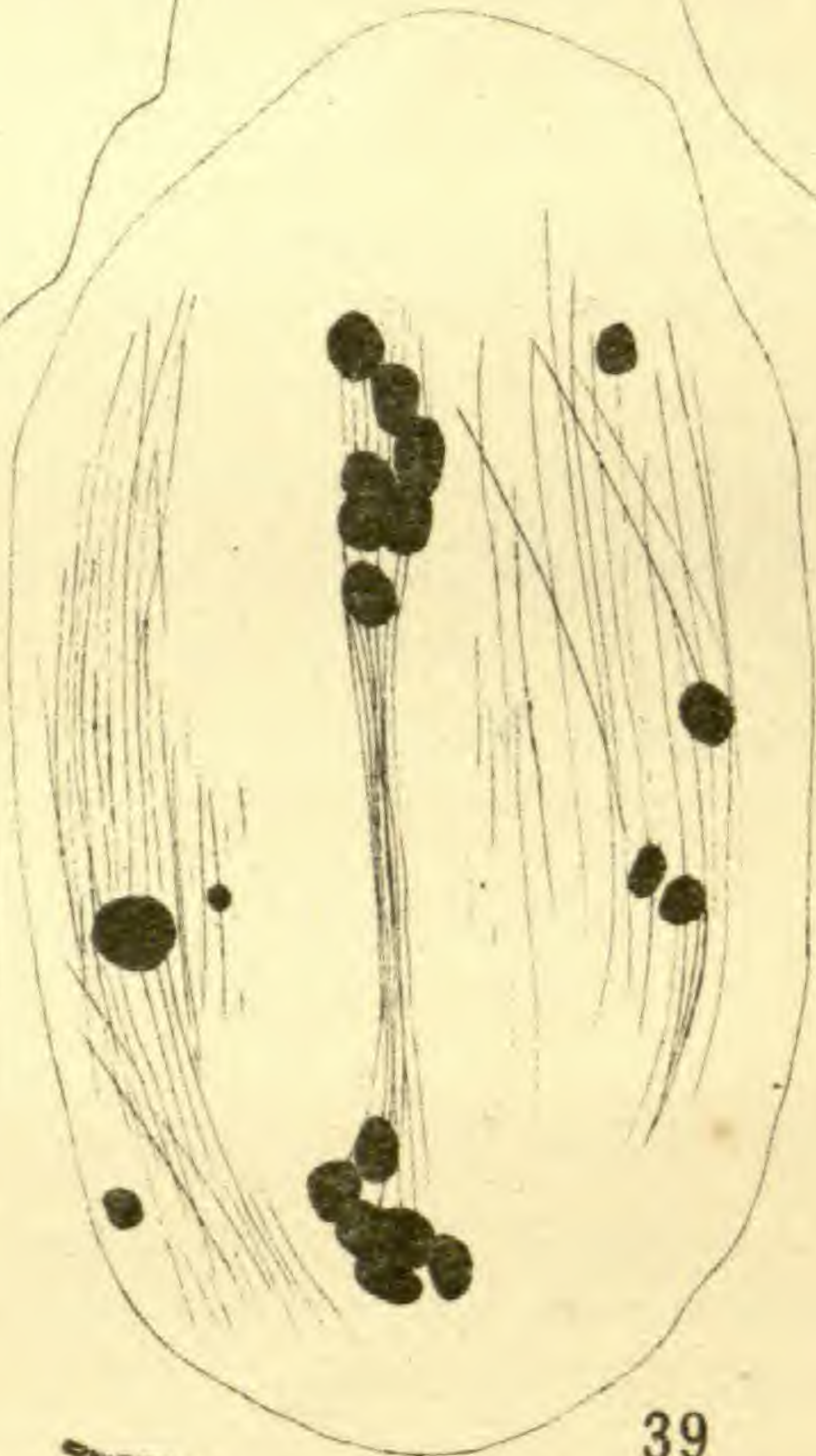
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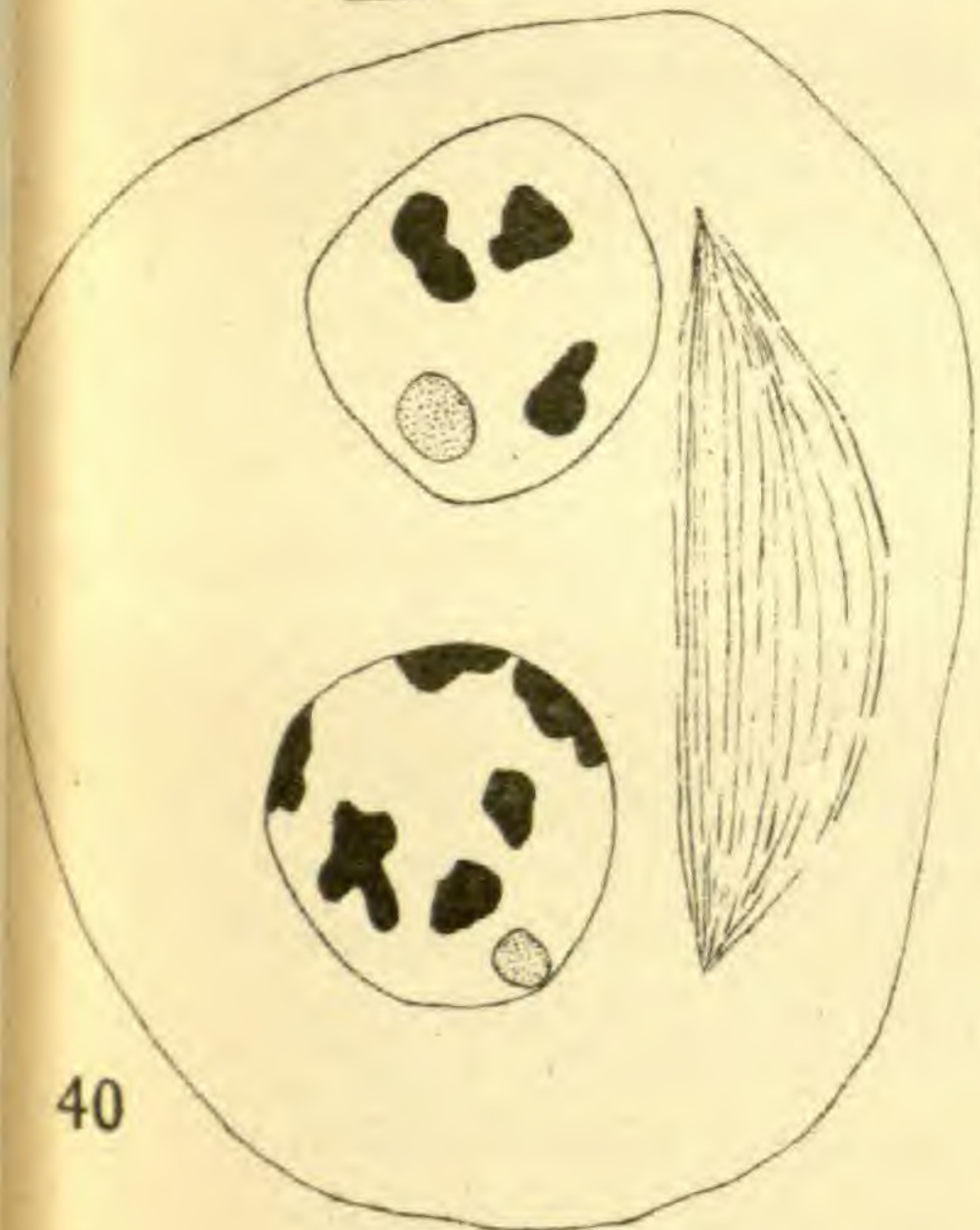
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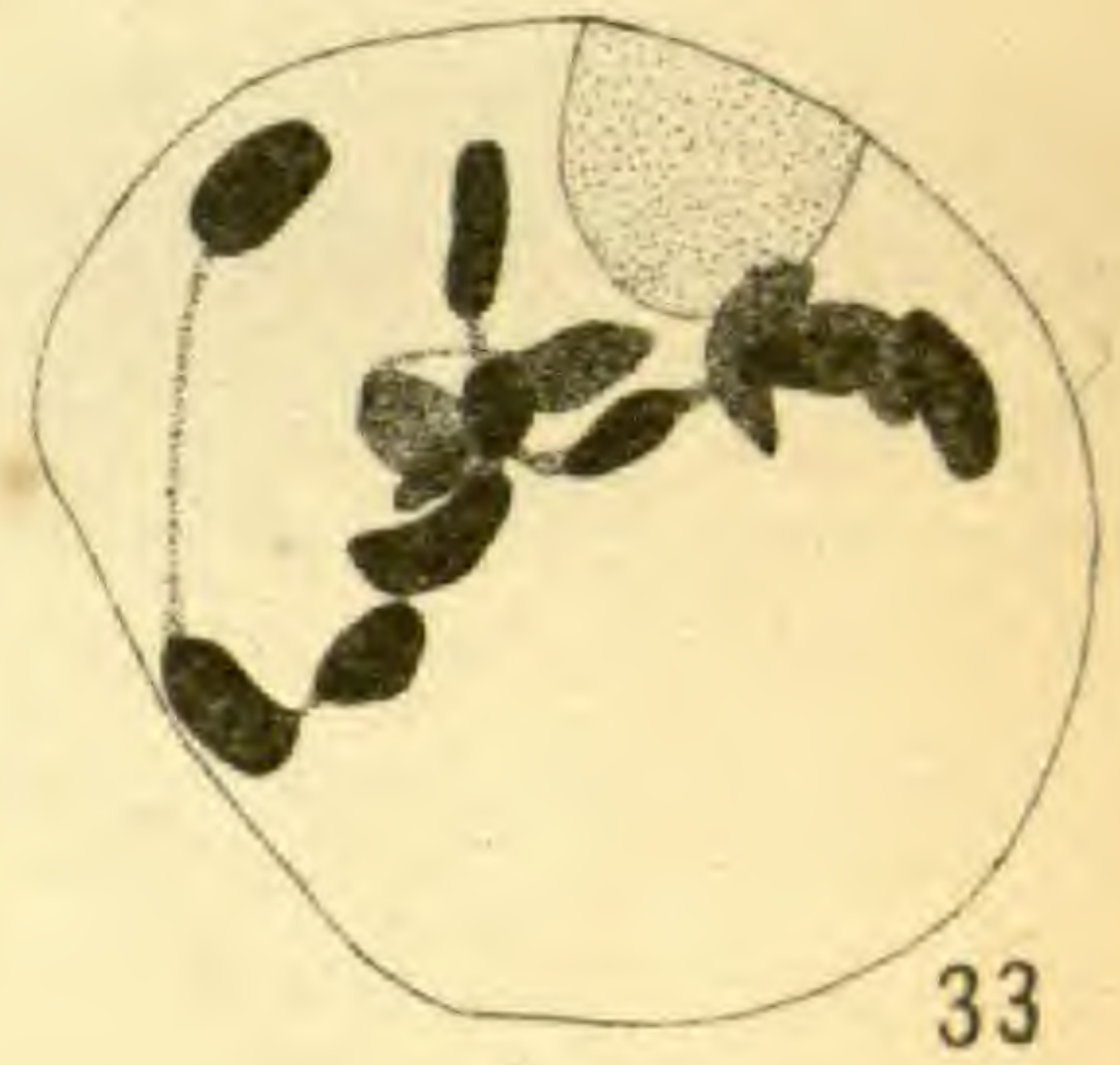
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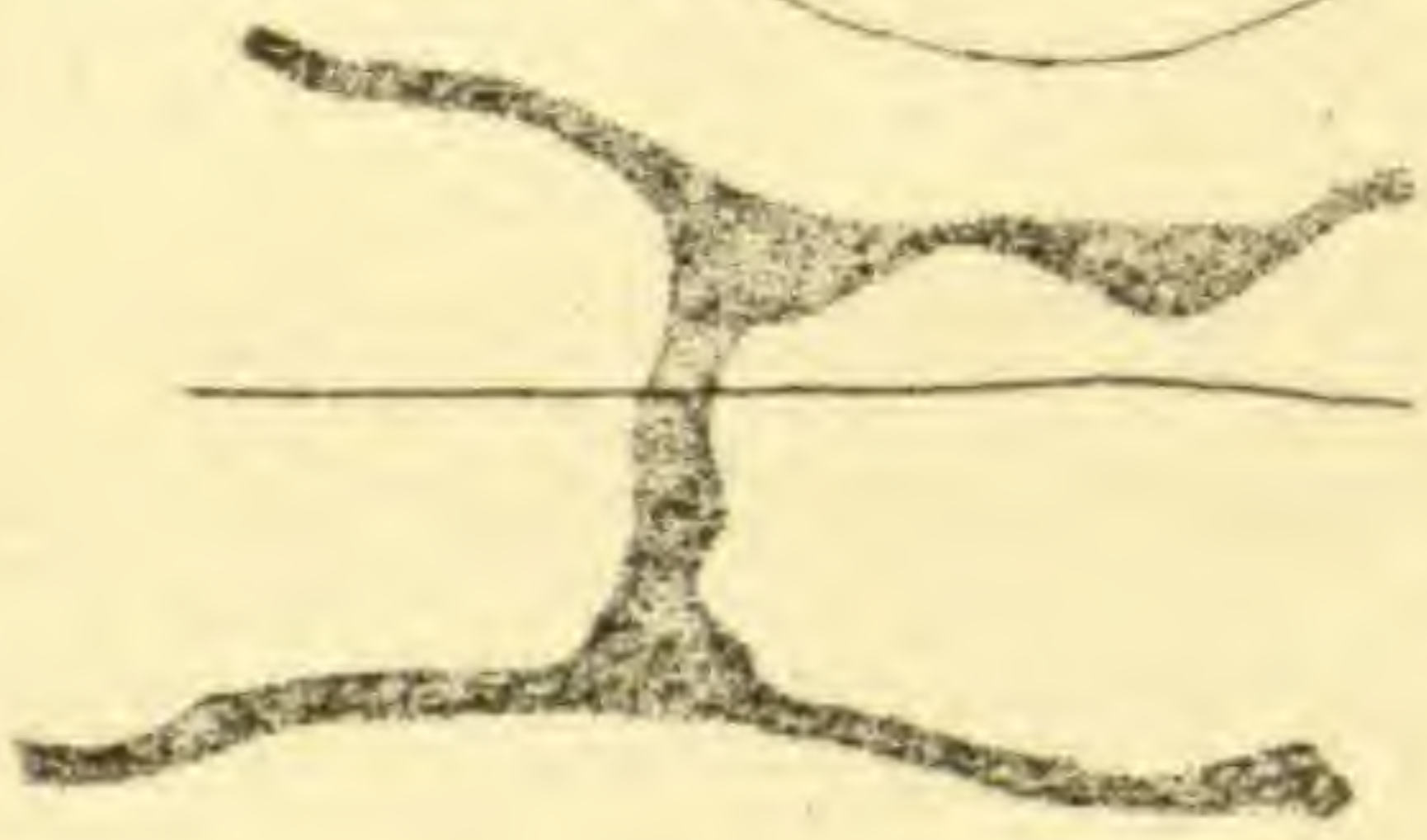
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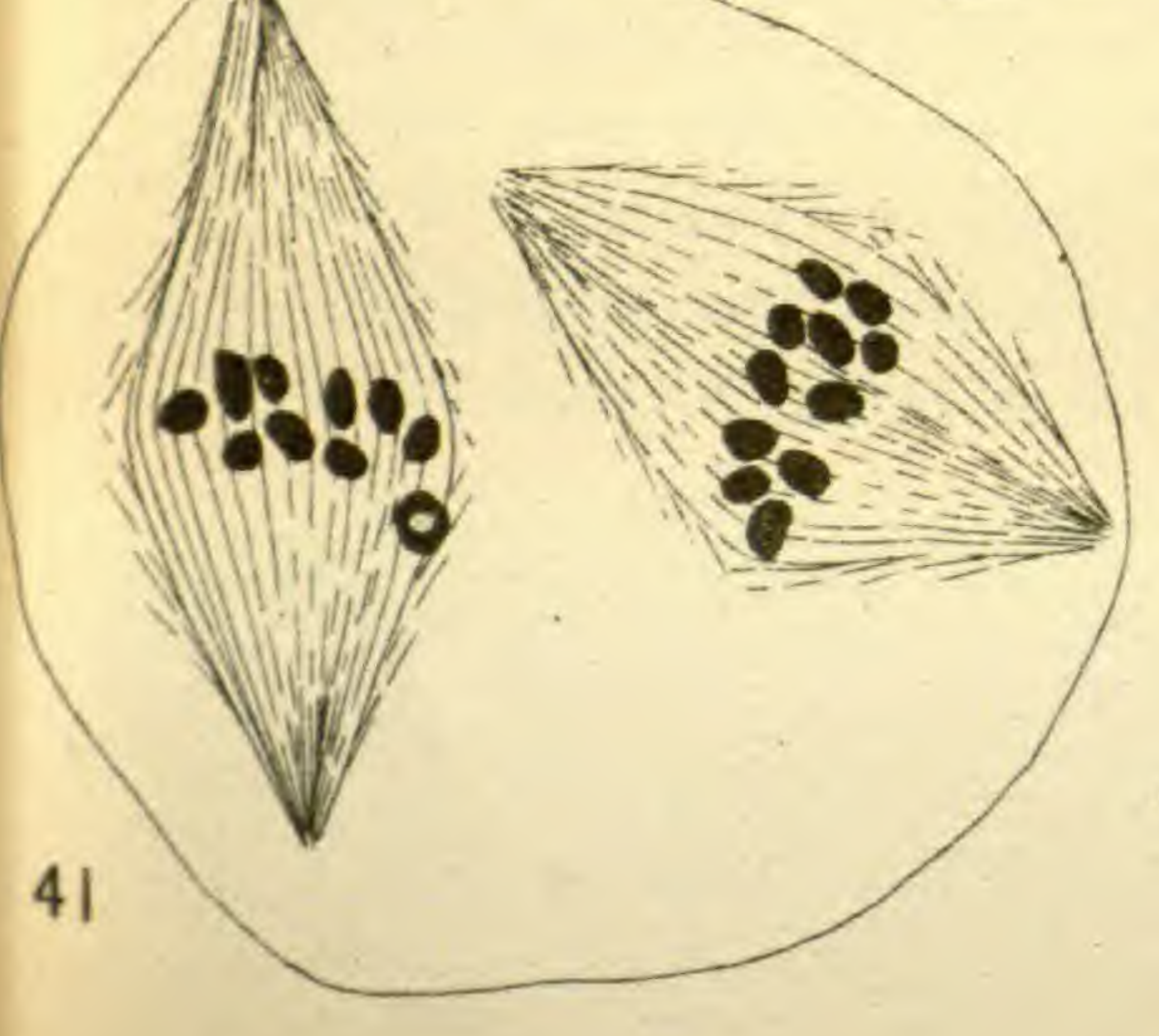
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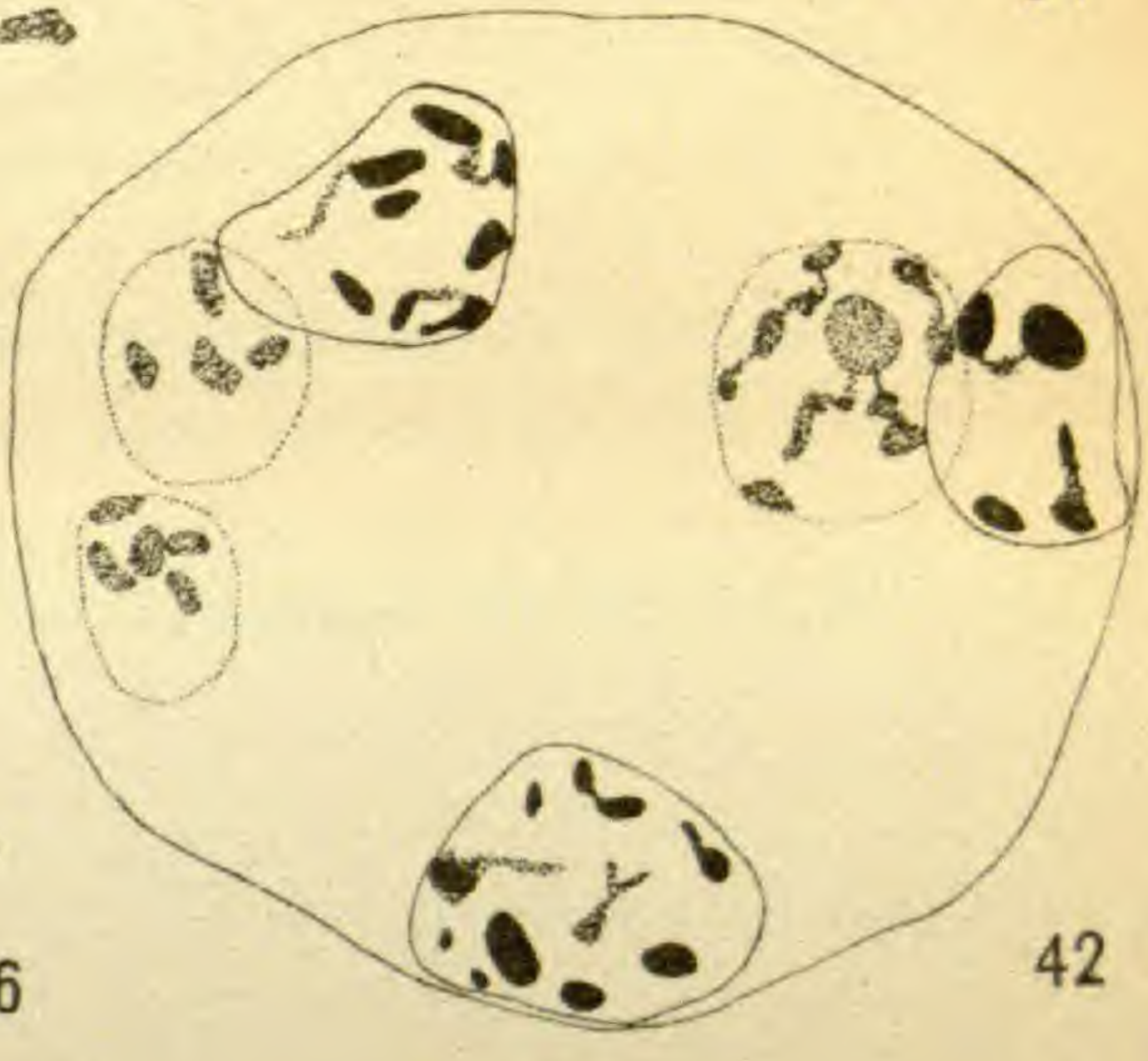
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GATES on REDUCTION in OENOTHERA

STUDIES IN ARACEAE

JAMES ELLIS GOW

(WITH PLATES IV–VI)

I. NEPHTHYTIS GRAVENREUTHII

In the fall of 1906 the writer enjoyed the privilege of examining the extensive collection of tropical aroids in the greenhouses of the New York Botanical Gardens, and of collecting material for an investigation of the embryo sac and embryo. Among other species, *Nephthytis Gravenreuthii* was selected for this purpose. A considerable amount of material was obtained, illustrating stages from the archesporium to the mature embryo.

OVARY.—The genus is characterized by a single simple carpel which shows a tendency toward a slightly unsymmetrical development, the stylar canal never being in the axis of the carpel (*fig. 2*). The carpel is short and thick, the stylar canal very short, funnel-shaped, and lined with viscid conducting cells. On the interior of the carpel the conducting cells reach a considerable length and come in contact with the ovule on all sides, sometimes reaching quite to the micropyle.

OVULE.—The ovary contains a single, basal, anatropous, cauline ovule. Probably the single, basal, orthotropous ovule is the most primitive kind, and in Arisaema we find an orthotropous ovule, but there are typically four ovules; and while they are cauline in origin they occur as lateral outgrowths of a suppressed placenta, the ill-defined point of the placenta representing the axis of the flower. The single axial ovule, even though it be anatropous, is no doubt a simpler type than this; and when we compare it with such a form as Dieffenbachia, in which each ovule, arising from the partially suppressed placenta, is surrounded by a separate carpel, its primitive character becomes yet more apparent.

In general, the ovule of the species now under discussion is peculiar for its massive integuments and for the poor development of the nucellus. The latter consists at first of a single row of cells surrounded by an epidermal layer (*fig. 1*). The hypodermal archesporial cell usually gives rise to two sporogenous cells; and one case of three sporogenous cells was discovered. In every case when observation was possible, the outer sporogenous cell developed the embryo sac. At the same time, the epidermal cells at the tip of the nucellus divide periclinally. No evidence was found to indicate that a primary parietal cell is ever cut off by the archesporium.

EMBRYO SAC.—As the ovule develops, the funiculus increases greatly in length, and this is accompanied by a corresponding lengthening of the outer integument (*fig. 2*). At the same time the integuments thicken considerably, and leave a narrow space between the nucellus and the inner integument. The embryo sac lengthens downward and encroaches somewhat on the chalaza (*fig. 3*). Preparations of sacs were obtained containing two, four, and eight nuclei. In the preparation represented in *fig. 3* (three sections of a single sac) there were eight active nuclei, but also traces of several degenerate nuclei, apparently indicating that more than eight nuclei had been formed. In *fig. 3a* there appears to the left a small nucleus with feebly defined boundary, but abundant chromatin contents; two similar but smaller nuclear fragments appear in *fig. 3b*. All this perhaps indicates the presence of ten or twelve nuclei in the embryo sac, some of which break down.

Three of the eight active nuclei form the egg-apparatus (*fig. 4*). Fusion of the polar nuclei was not demonstrated, nor were any of the phases of fertilization well shown except in one case (*fig. 12*).

The number of antipodals is variable; for example, there are three in *fig. 5*, two in *fig. 6*, and four in *fig. 11*.

ENDOSPERM.—The endosperm begins with free nuclear division. Whether it originates from a single endosperm nucleus, or by direct divisions of six of the eight nuclei previously figured could not be satisfactorily determined. In *fig. 5* walls are beginning to appear between the free nuclei and it seems that the wall-formation begins at the middle of the sac and proceeds toward the ends.

The walls of the endosperm cells soon become heavy (*figs. 6, 7, 8*). When the embryo reaches the stage shown in *fig. 8*, the thickening of the endosperm walls is complete, and the nuclei begin to show a tendency to disintegrate.

EMBRYO.—The first divisions of the fertilized egg were not found. The earliest stage observed is shown in *figs. 6* and *8*, showing a spherical proembryo without a suspensor. The proembryo is usually at the upper extremity of the sac, but its position is extremely variable. *Fig. 9* represents a somewhat older embryo, a slight notch beginning to show on one side, which at later stages becomes more pronounced (*fig. 10*). At the same time the endosperm is gradually destroyed, and the embryo finally assumes the form shown in *fig. 11*, the endosperm having disappeared completely.

POLYEMBRYONY.—The sections shown in *figs. 6, 7*, and *8* were cut from the same sac. *Fig. 6* shows the embryo developed from the fertilized egg, and also a synergid; while in *fig. 8* another embryo is shown. These two sections cannot be different sections of the same embryo, for there are several intervening sections which show endosperm only, one of which is represented in *fig. 7*. It should be noted also that the second embryo (*fig. 8*) is not lower down in the sac than the one shown in *fig. 6;* in fact, the two lie side by side. All of the sac lying above the embryo in *fig. 8* represents a lateral upward extension of the sac not shown in *fig. 6*. This would suggest that the second embryo may have been derived from a synergid.

2. DIEFFENBACHIA DARAQUINIANA

In the material collected in the greenhouses of the New York Botanical Gardens, some was obtained from specimens labeled *Dieffenbachia daraquiniana*. This specific name is recognized neither by SCHOTT nor ENDER, and the species is probably identical with the one listed by the latter as *D. baraquini*.[1] The genus is notable in that the spadix is adherent along one side to the broad spathe, in which it is more or less tightly inclosed, the flowers occurring on the opposite side of the spadix. In the species under discussion the flowers were found scattered irregularly over the free surface of the spadix, crowded in places, but usually standing far apart and showing between them bits of the surface of the spadix. The male flowers occupy the upper part of the spadix, the female flowers the lower, the latter consisting only of an ovary. No traces of floral envelopes

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[1] ENDER, Index Aroidearum 43. Berlin. 1864.

are present, but many staminodia are inserted near the base of the ovaries.

OVARY.—In the youngest material examined, the beginning of the flower appears as a slight protuberance on the surface of the spadix. A transverse crease soon appears, dividing this into two ill-defined lobes (*fig. 13*) which are destined to develop into the two carpels, and between the carpels appears the placenta, representing the axis of the flower (*fig. 14*). The carpels rapidly increase in size and overtop the placenta (*figs. 15, 16*). At the same time the ovules appear as lateral outgrowths of the placenta, filling the two cavities formed by the growth of the carpels (*fig. 15*). The continued growth of the carpels causes them to approach each other until there is left between them only a narrow canal, which divides over the apex of the placenta in such a way that the two branches lead down into the cavities of the carpels (*fig. 17*). On the upper and inner surface of each carpel, and leading down to the stylar canal, occurs a circular patch of somewhat viscid stigmatic cells (*fig. 17*).

OVULE.—The ovule first appears as a dome-shaped mass of undifferentiated cells projecting laterally into the carpellary cavity (*fig. 15*). The inner integument soon appears as an ill-defined ring about the upper portion of the ovule, and by the time the carpel has partially covered the placenta, the integument has grown out even with the apex of the nucellus, and the outer integument has begun to appear (*fig. 16*). At this stage the ovule is orthotropous. The lower surface now ceases to develop, while the upper continues to grow, thus finally making the ovule anatropous. At the same time, the integuments lengthen greatly, the outer one much exceeding the inner one (*fig. 17*).

ARCHESPORIUM.—Before the ovule becomes anatropous, the archesporial cell may be recognized by its greater size and by its nucleus (*fig. 19*). Before the first division of the archesporium the overlying epidermal cells usually divide once (*fig. 20*). The archesporial cell, which in this case is the mother cell, gives rise to four megaspores (*fig. 21*), the outermost one of which produces the embryo sac.

EMBRYO SAC.—The functioning megaspore increases greatly in size, destroying as usual the other megaspores and some of the adjacent tissue. When the outer integument has closed over the nucellus, the first nuclear division in the embryo sac usually occurs (*fig. 22*). This is followed by the usual divisions (*figs. 23, 24, 25*), until eight nuclei are formed, which assume the usual positions. In this case the polar fusion was observed (*figs. 24, 25*). Before the embryo sac is complete, the lateral tissue of the nucellus has usually disappeared, only the tissue at the tip remaining.

FERTILIZATION.—Although the material was at the proper stage to show fertilization, good preparations were very difficult to obtain. The best are shown in *figs. 26, 27, 28*, and double fertilization is evident.

ENDOSPERM.—Before the first division of the fertilized egg takes place, the embryo sac has increased greatly in size and has become almost completely filled with endosperm. The endosperm begins with free nuclear division, which continues until numerous nuclei are distributed through the sac. Later wall-formation occurs (*fig. 28*) and the sac is filled with tissue.

EMBRYO.—At the close of the free nuclear stage of the endosperm the fertilized egg divides transversely (*figs. 29, 30*); then longitudinal and transverse divisions follow in no definite sequence until the spherical proembryo is produced (*fig. 28*).

CHROMOSOMES.—The preparations of Dieffenbachia were unusually favorable for a definite count of chromosomes, and the alternating numbers were found to be eight and sixteen.

3. AGLAONEMA VERSICOLOR

Flowering material of this East Indian species was also obtained from the New York Botanical Gardens. The earlier stages of the microsporangium were not found, but quite a complete series was obtained showing the development of the megasporangium.

MICROSPORANGIUM.—In the youngest material examined the tapetum and middle wall layers had disappeared, leaving only the distinct endothecium overlaid by the epidermis. At this stage the mother cells have rounded off and are forming the tetrads. In older material the division into tube and generative nuclei was observed and eight chromosomes were counted (the reduced number).

MEGASPORANGIUM.—Aglaonema has one carpel containing a single anatropous ovule, which is cauline, although its lateral position at maturity might suggest that it is carpellary in origin (*fig. 33*). The stigmatic surface is prominent, and the cavity of the stylar canal is partially filled by a mass of similar cells, and long conducting cells extend downward on either side of the ovule, reaching the vicinity of the micropyle. At an early period the inner integument closes over the tip of the nucellus, but the outer integument does not close over the inner (*fig. 33*).

The earliest satisfactory preparations of the embryo sac show the first division (*fig. 36*) and the second (*fig. 37*). The final stages show great irregularity. *Fig. 38* shows a group of three cells (to the right) which suggests the egg apparatus; the two cells at the extreme left are certainly antipodals; while the two in the middle are evidently fusing polar nuclei. The solitary cell to the left suggests the third antipodal, but a male cell appears to be fusing with it. The ninth cell may be the other male nucleus. The embryo sac represented in *fig. 39* contains only five cells, two of which are clearly fusing polar nuclei.

The number of antipodals varies from two to eleven, and it is quite possible that they may sometimes be even more numerous (*figs. 33, 34, 35, 40*).

ENDOSPERM.—In Aglaonema the endosperm does not begin with free nuclear division, as in Dieffenbachia, Nephthytis, and Arisaema, but wall-formation begins at once. The growing endosperm first lines the side of the embryo sac which is toward the funiculus, but later fills the cavity and completely surrounds the embryo (*figs. 33, 40, 41, 42*).

EMBRYO.—The embryo much resembles that of *Lysichiton kamschatcense* as figured by CAMPBELL.[2] *Fig. 41* represents the position in which the proembryo was most frequently found, but in many cases it appears at the micropylar extremity of the sac. It appears quite as frequently adhering to the surface opposite the growing endosperm, and in at least one case was found resting on the antipodals. There was no evidence of displacement by sectioning, so that this variable position is probably due to the fact that the egg may lie in any part of the embryo sac.

BLAIRSTOWN, N. J.

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[2] CAMPBELL, D. H., Notes on the structure of the embryo sac in Sparganium and Lysichiton. BOT. GAZETTE 27:153–166. 1899.

EXPLANATION OF PLATES IV–VI

PLATE IV

Nephthytis Gravenreuthii

FIG. 1.—Section of tip of ovule, showing massive integuments, small nucellus, and two sporogenous cells.

FIG. 2.—Ovary at somewhat later stage.

FIG. 3.—Three adjoining sections of the same embryo sac, showing eight vigorous nuclei and traces of two or three others.

FIG. 4.—Egg-apparatus.

FIG. 5.—Antipodals, and endosperm nuclei with incipient wall-formation.

FIG. 6.—Endosperm at a later stage, proembryo (*e*), and a persistent synergid (*s*).

FIG. 7.—Endosperm.

FIG. 8.—Second proembryo in same sac shown in *fig. 6*.

FIG. 9.—Proembryo.

FIG. 10.—Embryo showing notch.

FIG. 11.—Mature embryo.

FIG. 12.—Fertilization, showing pollen tube (*p*), egg (*o*), male cell (*m*), and synergid (*s*).

PLATE V

Dieffenbachia daraquiniana

FIG. 13.—First appearance of carpels.

FIG. 14.—Later stage.

FIG. 15.—First appearance of ovule.

FIG. 16.—Later stage, showing nucellus (*n*) and integuments (*i, o*).

FIG. 17.—Section of ovary, showing stigmatic surface (*st*), stylar canal (*s*), and the anatropous ovules.

FIG. 18.—Section of ovule showing an embryo sac containing endosperm nuclei (*e*); the other structures are evident.

FIG. 19.—The archesporial cell.

FIG. 20.—Division of epidermal cells.

FIG. 21.—The linear tetrad, the outermost megaspore (*m*) functional.

FIGS. 22–25.—Stages in the development of the sac.

FIG. 26.—Fertilization of egg.

FIG. 27.—Fusion of male cell with endosperm nucleus.

FIG. 28.—Free endosperm nuclei.

FIG. 29.—Endosperm at later stage, and proembryo.

FIGS. 30–32.—Early divisions in proembryo-formation.

PLATE VI

Aglaonema versicolor

FIG. 33.—Ovary with the solitary ovule; embryo sac containing embryo (*e*), endosperm (*n*), and antipodals (*a*).

FIG. 34.—Group of eleven antipodals.

FIG. 35.—Group of three antipodals.

FIG. 36.—First nuclear division in embryo sac.

FIG. 37.—Four-nucleate sac.

FIG. 38.—Eight-nucleate sac and two male cells (one fusing with a cell).

FIG. 39.—Fusion of polar nuclei.

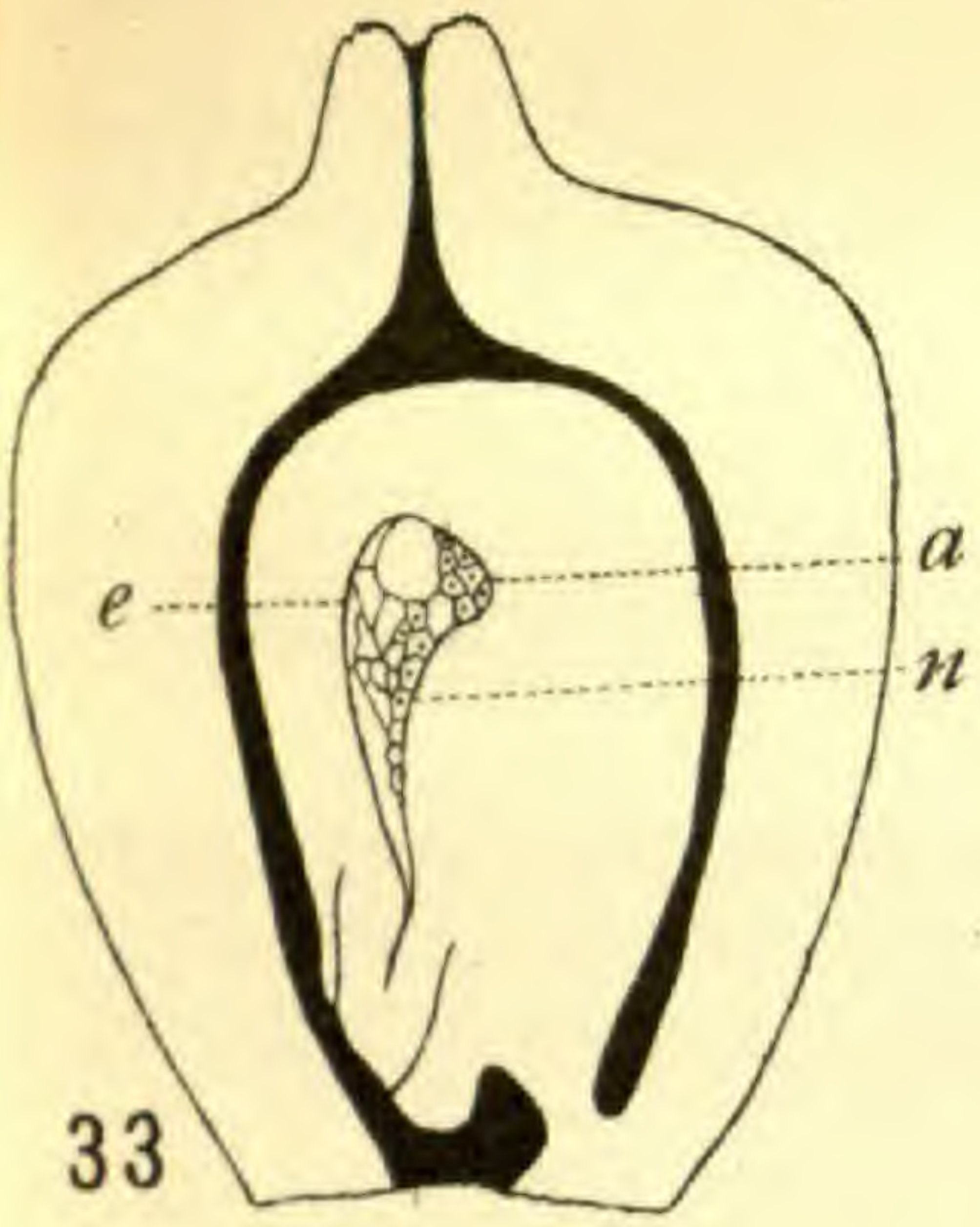
FIG. 40.—Older sac, showing endosperm (*n*) and antipodals (*a*).

FIG. 41.—Sac showing endosperm (*s*) and proembryo (*e*).

FIG. 42.—Diagram showing later development of embryo (*n*) and endosperm (*e*).

GOW on ARACEAE

GOW on ARACEAE



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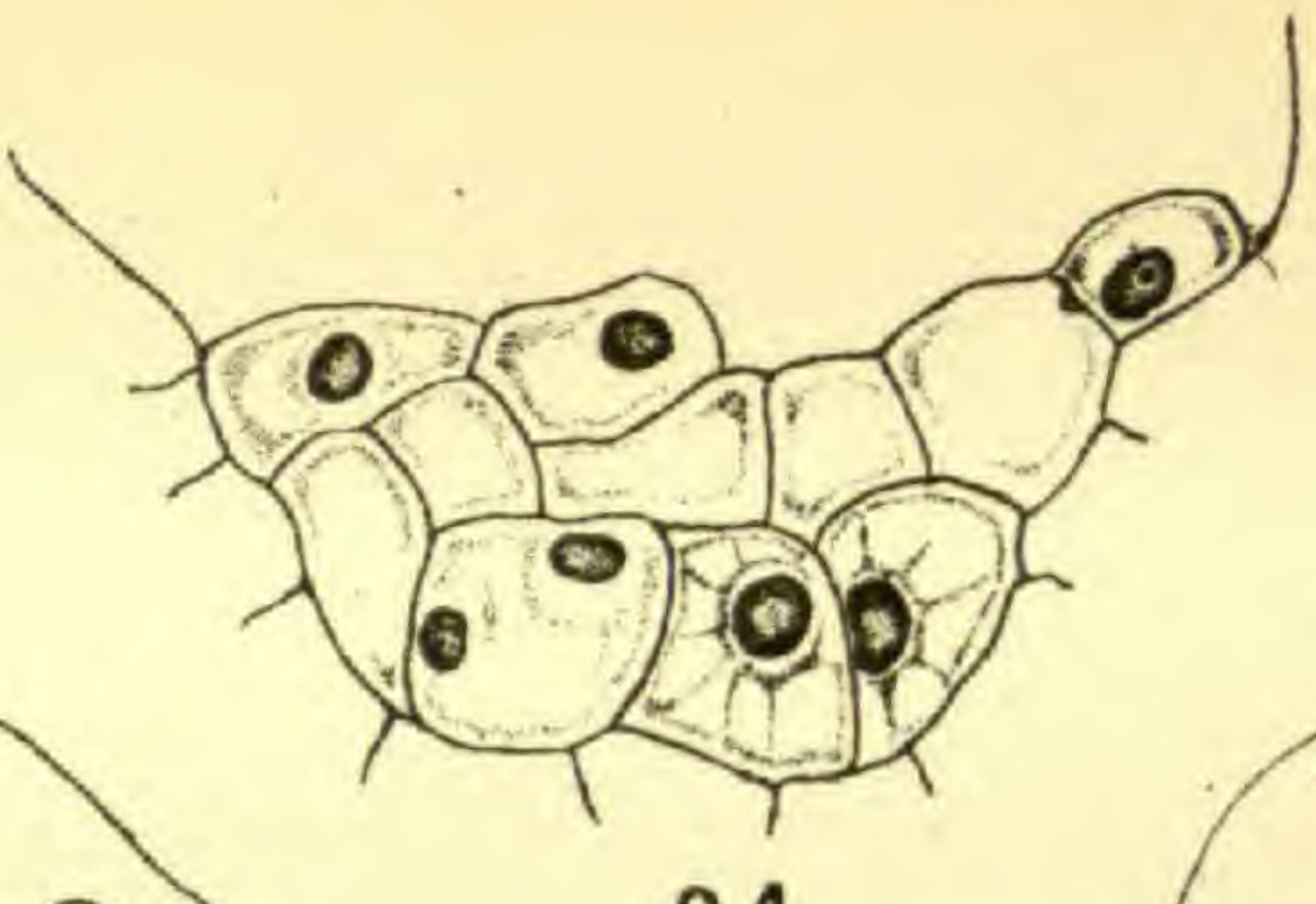

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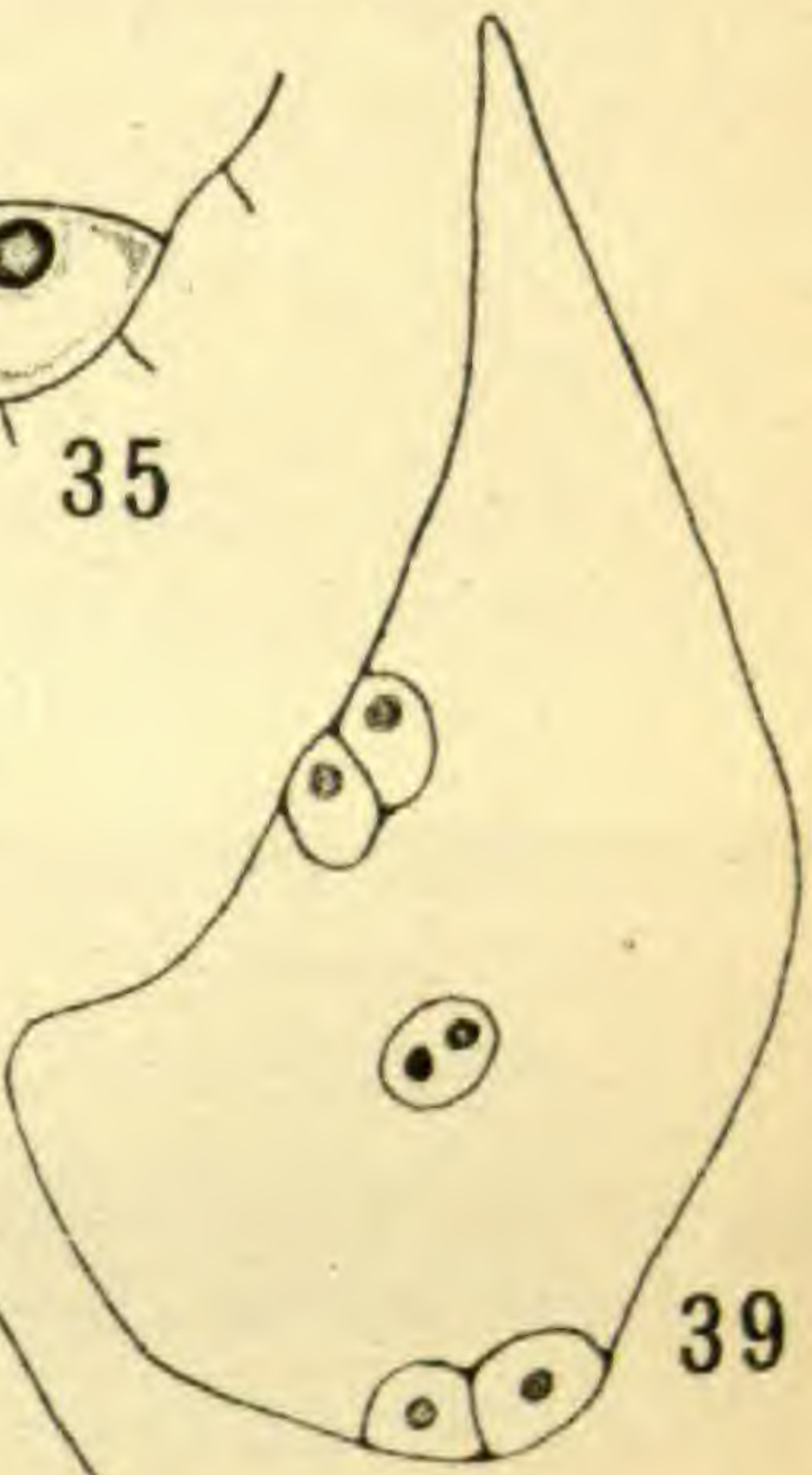

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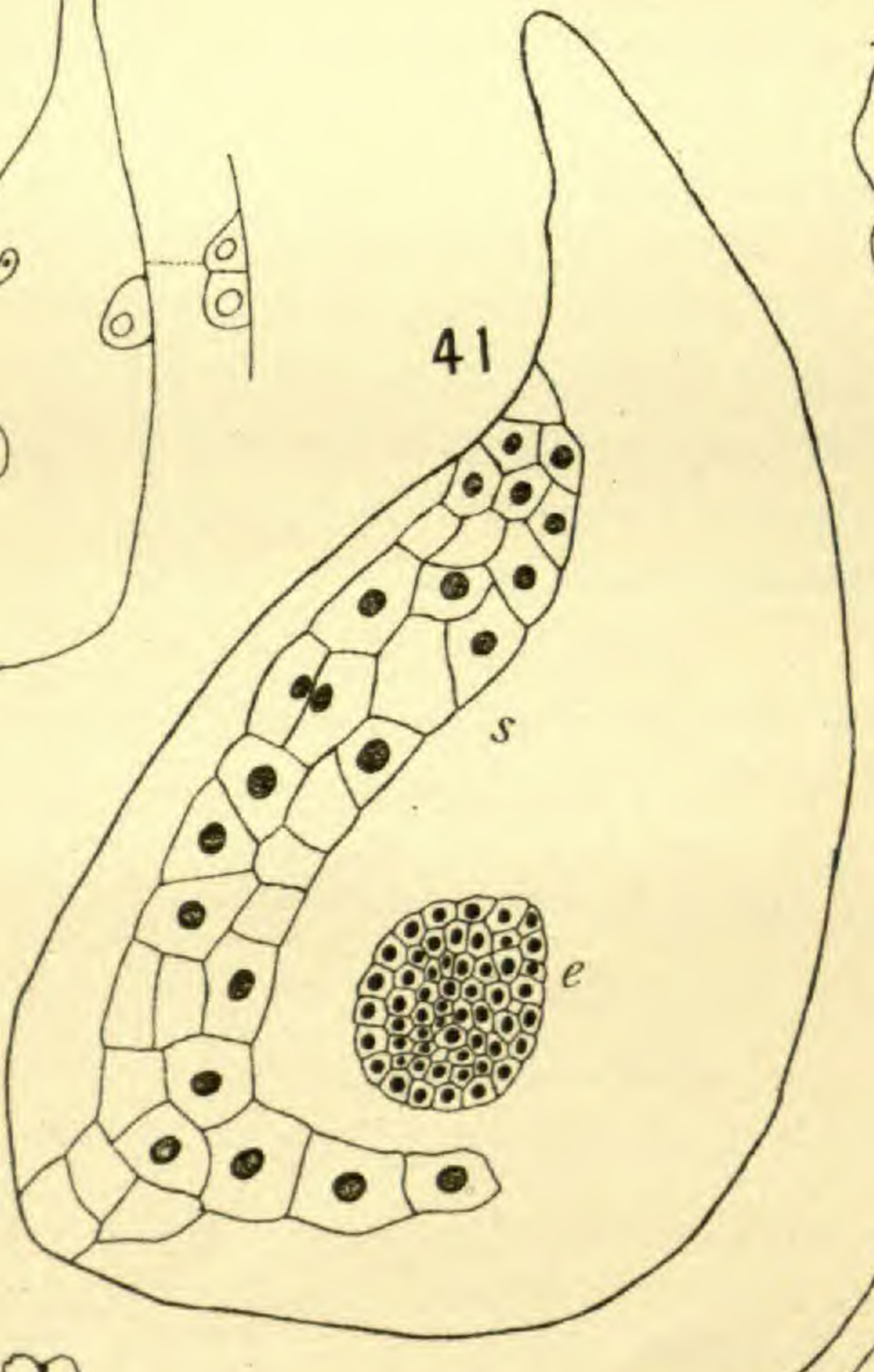

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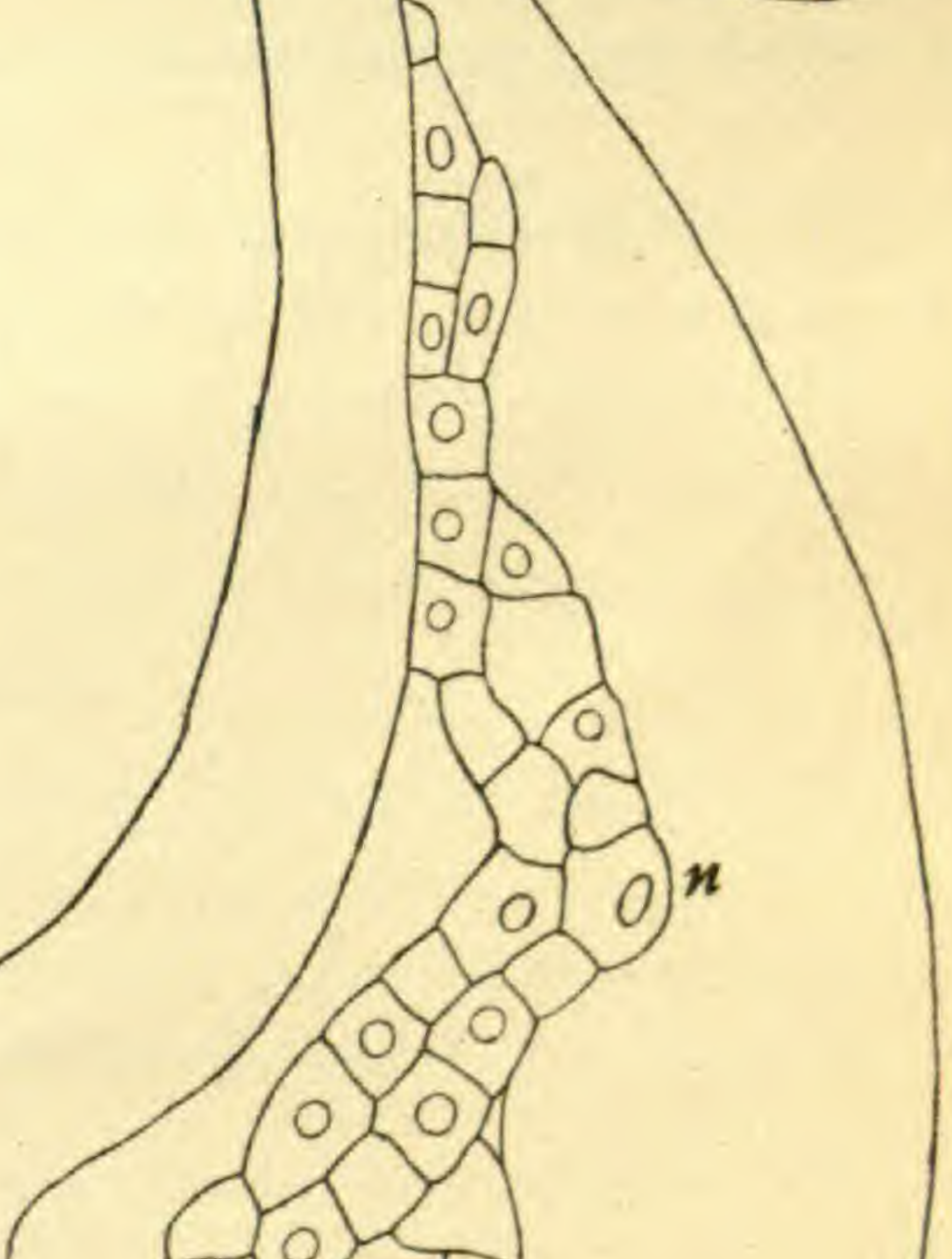

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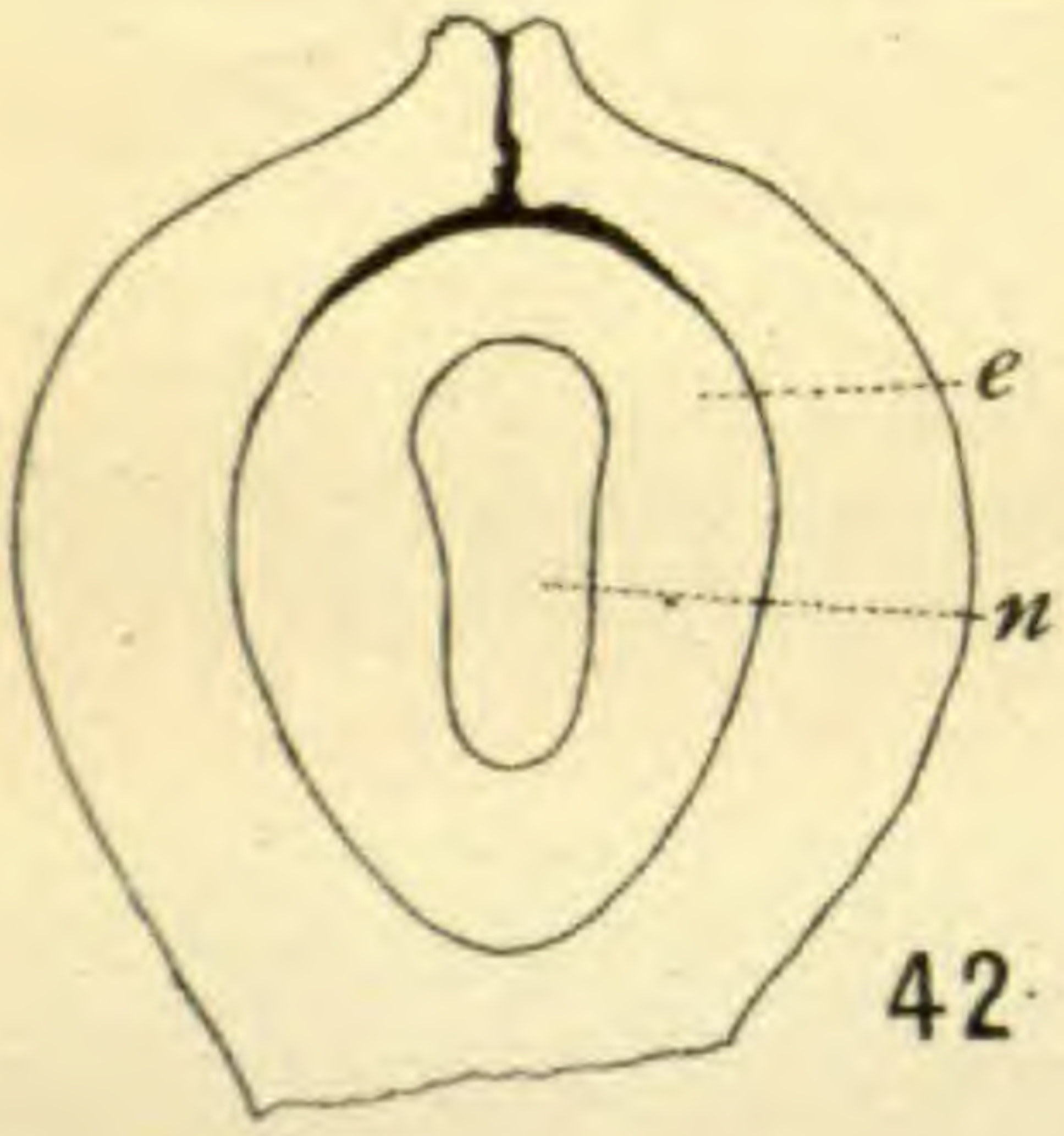

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GOW on ARACEAE

THE EMBRYO SAC AND EMBRYO OF *GNETUM GNEMON*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 112

JOHN M. COULTER

(WITH PLATE VII)

Gnetum Gnemon has been made conspicuous among the other species of Gnetum chiefly by the investigation of LOTSY published in 1899.[1] The structures described were of such interest that it seemed desirable to supplement the somewhat incomplete account by a further examination. Accordingly material was obtained from the Philippine Islands and from British Guiana; the former from Dr. H. N. WHITFORD, and the latter from Mr. A. W. BARTLETT, director of the Botanic Garden at Georgetown. This material was first assembled by Dr. W. J. G. LAND, of this laboratory, in connection with his investigation of Ephedra; and he has kindly turned it over to me for separate study. The preparations and drawings were made by Dr. SHIGÉO YAMANOUCHI, of this laboratory, and to his technical skill the results are largely due.

The material included stages from two successive seasons, but unfortunately many intervening stages were not represented, so that no continuous account can be given. However, certain facts have been discovered that supplement and correct the previous accounts.

EMBRYO SAC

LOTSY described the embryo sac of *G. Gnemon* as showing an interesting deviation from those found by KARSTEN[2] in other species of Gnetum. Instead of containing only free nuclei at the fertilization stage, the embryo sac of *G. Gnemon* was described as containing

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[1] LOTSY, J. P., Contributions to the life history of the genus Gnetum. Ann. Jard. Bot. Buitenzorg II. 1:46–114. *pls. 2–11.* 1899.

[2] KARSTEN, H., Bot. Zeit. **50**:205–215, 221–231, 237–246. *pls. 5, 6.* 1892; Ann. Jard. Bot. Buitenzorg 11:195–218. *pls. 17–19.* 1893; Cohn's Beitr. Biol. Pflanzen **6**: 337–382. *pls. 8–11.* 1893.

a compact antipodal tissue, sharply distinct from the micropylar chamber with its free nuclei. As a consequence, the embryo sac of *G. Gnemon* has been used ever since as illustrating a female gametophyte intermediate in structure between the tissue-filled sacs of Ephedra and Tumboa on the one hand, and the sacs of other species of Gnetum, which contain only free nuclei. Later the same investigator in reporting parthenogenesis in *G. Ula*[3] described the embryo sac of that species as being of the *G. Gnemon* type.

Our material of *G. Gnemon* does not confirm this account. At an early stage of the embryo sac, eight nuclei are observed grouped near the center (*fig. 1*), the sac being invested by the loose tissue of the nucellus. At a somewhat later stage the nucellar cells at the chalazal end of the sac are strikingly differentiated (*fig. 2*), becoming more and more compactly arranged, gradually obliterating the intercellular spaces, and taking on the appearance of glandular cells. The relation of this tissue in its early stage to the embryo sac is shown in *fig. 2a*. As vacuolation proceeds in the sac and the free nuclei become parietally placed, this "pavement tissue" becomes more compact and extends deeper into the chalaza (*figs. 3, 3a*). Still later it spreads laterally below, until it becomes fan-shaped in section (*figs. 4, 4a*), but it is always very distinct in contour and sharply marked off from the surrounding nucellar tissue. At the fertilization stage (*figs. 4, 5*) the sac contains only free nuclei, which become somewhat grouped at the antipodal end (*fig. 5*), but there is no walled tissue. Spreading below the sac, however, the mass of nucellar pavement tissue shows a definite contour, which might be merged in imagination with that of the sac and thus mistaken for a compact tissue within the antipodal end of the sac. LOTSY'S figures show the real contour of the sac, and his antipodal tissue is clearly this glandular pavement tissue developed in the chalaza. So far as the sac of *G. Gnemon* is concerned, therefore, its fertilization stage is that described for other species of Gnetum. It will be noted that after the fertilization stage is reached (*fig. 5*) the pavement tissue begins to lose its glandular character; and later it is destroyed entirely by the growing endosperm.

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[3] LOTSY, J. P., Parthenogenesis bei *Gnetum Ula* Brongn. Flora 92:397–404. *pls. 9, 10.* 1903.

ENDOSPERM

A year later, the endosperm has destroyed all of the nucellar tissue except a very small amount at the tip (*figs. 6, 6a, 7a*), and it is clearly differentiated into a central region of smaller, more compact cells, and a more extensive peripheral region of larger and looser cells. In destroying the nucellar beak, a curious result is observed. The central region of the endosperm advances into the beak and then spreads laterally (*fig. 6*). In the meantime the peripheral region advances more slowly toward the beak, and as a consequence a ring of nucellar tissue is pinched between two growing masses of endosperm. The growth of the endosperm into the chalazal region also results in pressure toward the beak, so that the pinched nucellar tissue is under considerable pressure and becomes completely disorganized. Under this pressure some of the adjacent endosperm cells also become disorganized.

In ovules of the preceding year, at the fertilization stage of the embryo sac, a curious disorganization of some of the cells of the nucellar beak was observed (*fig. 5a*). Two transverse rings of cells, several layers beneath the epidermis, begin to disorganize; later the epidermis becomes involuted between the disorganized rings, resulting in a deep groove around the nucellus. The epidermal cells remain very vigorous in appearance, and when the endosperm develops into this region the groove disappears. The cause and the significance of this disorganization and of the temporary involution of the epidermis cannot be suggested.

EMBRYO

LOTSY has described the entrance of pollen tubes into the embryo sac, the fertilization of the free eggs, the excessive elongation of the fertilized eggs to form suspensors, and the cutting-off of the embryonal cells at the tip of the suspensor. Later stages in the development of the embryo have been described by BOWER,[4] but the intermediate stages have not been observed. Fortunately our material from the Philippines contained them, and revealed an unexpected situation.

When the endosperm has become fully developed, its peripheral

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[4] BOWER, F. O., The germination and embryology of *Gnetum Gnemon*. Quart. Jour. Micr. Sci. 22:278–298. *pl. 25*. 1882.

region contains a tangle of long, tortuous, and branching suspensors (*figs. 6, 7*), which are difficult to trace. During the formation of a suspensor by a fertilized egg, free nuclear division occurs, resulting in a few nuclei (four in *fig. 7*) distributed along the suspensor. Usually between these nuclei transverse walls are formed by the development of a cleavage plate from the wall of the suspensor. A cell at the tip of the suspensor is cut off in the same way, and contains one of the free nuclei, which becomes associated with numerous starch grains (*fig. 7*).

In this terminal embryonal cell free nuclear division continues (*figs. 8, 9, 10*), accompanied by cleavage walls, until a multicellular embryo is formed. In *figs. 9* and *10* it will be observed that this cleavage apparently continues until uninucleate cells are produced; and in our material this stage is reached first by a group of cells on one side of the embryo. It could not be determined whether this group holds any relation to a body region or not.

It has been supposed that in the embryogeny of Gnetum the preliminary stage of free nuclear division, common to other gymnosperms, had been eliminated; and that the first nuclear division was accompanied by wall formation, as in angiosperms. In *Gnetum Gnemon*, however, free nuclear division not only characterizes the proembryo, but also the early stages of the embryo. The case may be compared to that of Ephedra,[5] in which free nuclear division within the fertilized egg results in eight independent proembryonal cells, each of which continues free nuclear division and develops as a suspensor, which by a cleavage wall cuts off the terminal embryonal cell. In Gnetum the suspensor is formed by the fertilized egg instead of by a proembryonal cell, but the number of free nuclei formed by the egg in each case is approximately the same.

INTEGUMENTS

The mature seed of *Gnetum Gnemon* gives an opportunity to compare the integument and testa with those of other gymnosperms. *Fig. 6a* shows the seed slightly stalked within the so-called "perianth," which is fleshy. Two integuments are evident, and they develop in

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[5] LAND, W. J. G., Fertilization and embryogeny in *Ephedra trifurca*. BOT. GAZETTE 44:273–292. *pls. 20–22*. 1907.

basipetal succession. The inner one extends above to form the elongated micropylar tube, and at the maturity of the seed completely invests the nucellus (at this time replaced by the endosperm) as a papery layer. The outer integument becomes differentiated into an outer fleshy layer (white in the figure) and an inner stony layer (black in the figure), the latter completely investing the seed, the former being chiefly developed in the region of the nucellar beak. Two sets of vascular strands are present, the outer set traversing the fleshy layer of the outer integument, the inner set traversing the inner integument.

In Cycadophytes, Ginkgoales, and Coniferales, a single integument becomes differentiated into a testa of three layers: outer fleshy, stony, and inner fleshy. In Gnetum the same three layers are present, but the inner fleshy one has become differentiated in ontogeny as a separate integument. In all cases, this innermost layer finally forms a papery lining of the stony layer. Among the Pinaceae the outer fleshy layer is present in the integument, but it does not develop into the extensive pulpy investment that characterizes the Cycadales, Ginkgoales, and Taxaceae, a fact which is probably associated with the close investment of the seeds by the scales.

The variation in the distribution of the vascular strands among these layers is interesting. Among the more primitive Cycadofilicales and Cordaitales, in which the nucellus is relatively free from the integument, the outer set of strands traverses the outer fleshy layer and the inner traverses the peripheral tissue of the nucellus. In other Cycadofilicales and Cordaitales, however, and in Cycadales in which the nucellus and integument are free only in the region of the nucellar beak, the inner set of vascular strands traverses the inner fleshy layer of the integument; and this is the condition in Gnetum, except that this layer has become differentiated as an inner integument. In Ginkgoales the outer set of strands (belonging to the outer fleshy layer) is suppressed; in Taxaceae the inner set (belonging to the inner fleshy layer) is suppressed; and in Pinaceae both are suppressed.

MALE GAMETOPHYTE

It was a disappointment that the development of the male gametophyte was not secured, for it is only known among Gnetales in Ephedra, in which it has been described by LAND.[6] The development of the tetrad was observed; and although the early anaphase of the first mitosis was not available for the counting of chromosomes, the late prophase of this mitosis and the anaphase of the second mitosis showed clearly that the chromosome numbers are 12 and 24.

SUMMARY

1. The "antipodal tissue" described by LOTSY as occurring in *Gnetum Gnemon* at the fertilization stage is a sharply differentiated nutritive tissue developed in the nucellus beneath the embryo sac, which at this stage contains only free nuclei, as described for other species of Gnetum.

2. Embryo formation begins with an excessive, suspensor-like elongation of the fertilized egg, accompanied by free nuclear division and cleavage walls; and the continuation of free nuclear divisions and cleavage walls in the embryonal cell until a multicellular embryo is formed.

3. The endosperm encroaches upon the tissue of the nucellar beak with some irregularity, an irregularity which reaches its extreme expression in Torreya, with its so-called "ruminated" seeds.

4. The inner integument of the ovule is the morphological equivalent of the "inner fleshy layer" of the single integument of other gymnosperms; and the occurrence of two sets of vascular strands is a relatively primitive condition, which has been departed from by Ginkgoales and Coniferales.

5. The chromosome numbers are 12 and 24.

THE UNIVERSITY OF CHICAGO

EXPLANATION OF PLATE VII

FIG. 1.—Embryo sac at an early stage, with centrally placed group of eight free nuclei; the cell above, with a large nucleus, is another embryo sac. ×500.

FIG. 2.—Somewhat later stage of embryo sac (all the nuclei not included), showing the beginning of the formation of the pavement tissue; a second embryo sac is also shown. ×500.

FIG. 2*a*.—An ovule at an early stage, showing the two integuments and the relation of the pavement tissue and embryo sac to the nucellus at the stage shown in *fig. 2*. ×40.

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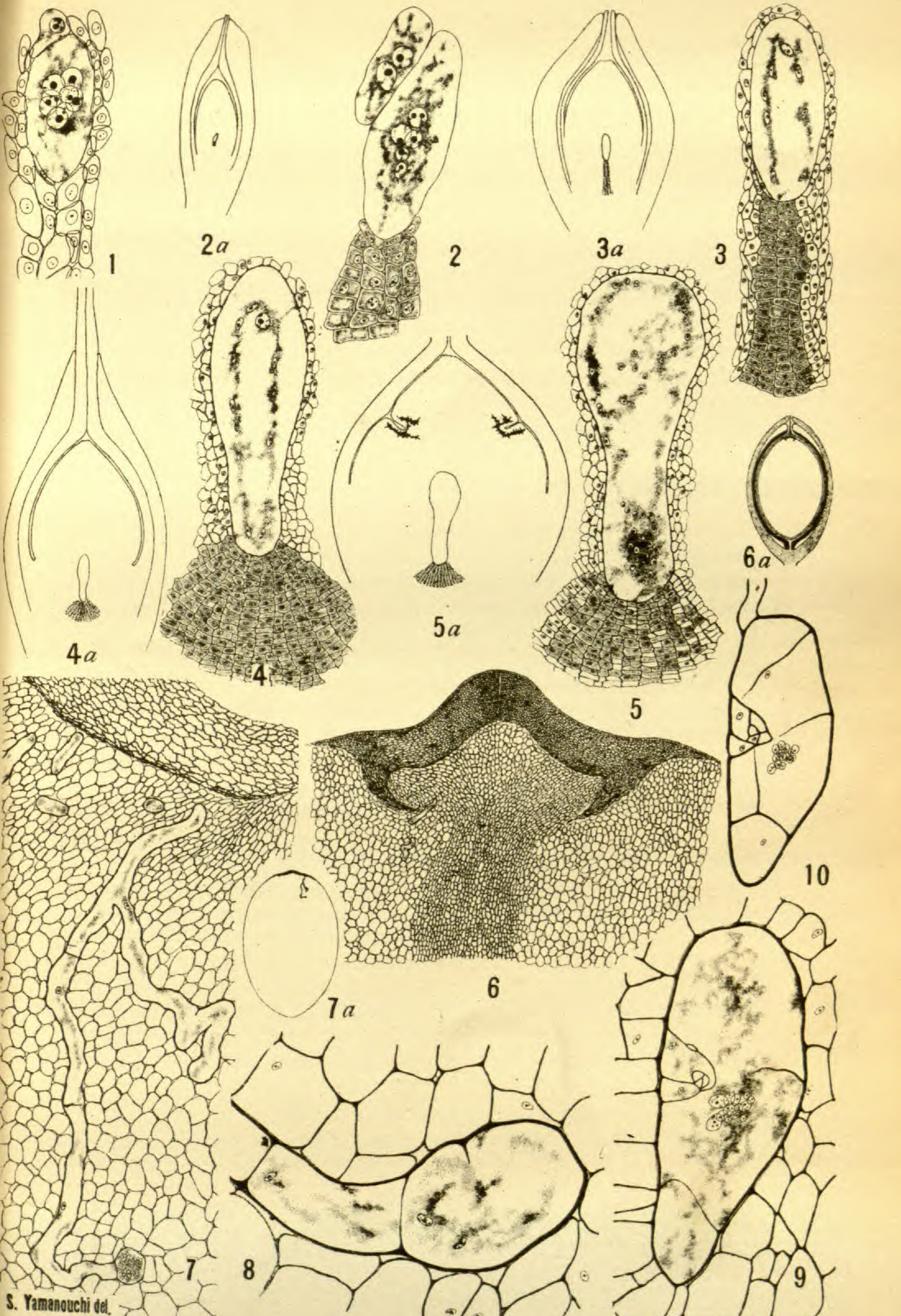
[6] LAND, W. J. G., Spermatogenesis and oogenesis in *Ephedra trifurca*. BOT. GAZETTE 38:1–18. *pls. 1–5*. 1904.



S. Yamanouchi del.

COULTER on GNETUM

FIG. 3.—Further development of pavement tissue; vacuolation of the sac. ×250.

FIG. 3*a*.—An ovule, showing general relation of regions shown in *fig. 3;* the tip of the nucellus has broken down (the only indication of a pollen chamber). ×40.

FIG. 4.—Further development of pavement tissue and embryo sac (probably fertilization stage). ×220.

FIG. 4*a*.—An ovule, showing relation of regions shown in *fig. 4.* ×40.

FIG. 5.—Later stage of embryo sac (possibly still in fertilization stage), with grouping of nuclei in the antipodal region, where tissue formation probably begins; beginning of disorganization of pavement tissue. ×210.

FIG. 5*a*.—An ovule, showing relation of regions shown in *fig. 5;* also the curious disorganization of cells and infolding of the epidermis in the nucellar beak. ×40.

FIG. 6.—Tip of seed; small amount of tissue of nucellar beak not destroyed by endosperm; differentiation of central and peripheral regions of endosperm, the former having advanced into the center of the nucellar beak and spread laterally, resulting in crushing nucellar tissue against the encroaching peripheral region of endosperm; sections of two suspensors shown. ×40.

FIG. 6*a*.—Mature seed invested by the fleshy "perianth;" outer integument differentiated into outer fleshy (white) and stony (black) layers; inner integument forming the micropylar tube; at apex of nucellus is indicated the remains of the nucellar tissue (shown with greater magnification in *fig. 6*). ×2.

FIG. 7.—A proembryo, showing the branching, suspensor-like elongation of the egg, with free nuclei and cleavage walls; also the embryonal cell containing a nucleus and numerous starch grains; sections of other suspensors shown, and also a small portion of the undestroyed tip of the nucellus. ×40.

FIG. 7*a*.—Outline to show the relation of parts illustrated by *fig. 7.* ×3.

FIG. 8.—Beginning of embryo formation by the embryonal cell, showing free nuclei and the beginning of a cleavage wall; a cleavage wall in the suspensor also shown. ×250.

FIG. 9.—Section of later stage of embryo, showing free nuclei, cleavage walls, and the beginning of small-celled tissue at one side. ×210.

FIG. 10.—An embryo reconstructed from serial sections, showing free nuclei, cleavage walls, and the beginning of uninucleate cells. ×140.

BRIEFER ARTICLES

THE OCCURRENCE AND RATE OF PROTOPLASMIC STREAMING IN GREENHOUSE PLANTS

In the Botanical Laboratory of Smith College, under the direction of Professor Ganong, various lines of investigation are in progress to determine which plants of those available during the school and college year are best adapted for educational work in each of the principal physiological processes. The results are appearing from time to time in the Botanical Gazette.[1] The object of the present inquiry is to discover which of such plants show protoplasmic movement, in which the streaming is most active, and at what temperatures.

The development and sum of our knowledge of protoplasmic streaming may be traced through Pfeffer's *Plant physiology*, which needs to be supplemented, however, by the references under "Protoplasmabewegung" in Just's *Jahresbericht*, and by the admirable new work of Ewart, *On the physics and physiology of protoplasmic streaming in plants* (Oxford, Clarendon Press, 1903). Streaming has been found in a great number of plants of the most diverse groups, from fungi to phanerogams, and in the most different structures, including the exposed cells of algae (where it reaches its finest display), emergences and hairs on various organs (notably stamens), root hairs (where it has been found in at least sixty-five families), plasmodia of myxomycetes, mycelia of molds, pollen tubes, the bark, young wood, and medullary rays of various trees, stamens, petals, and other parts. The rate of the streaming has been measured by several observers in different plants, and ranges from zero up to an extreme of 10^{mm} per minute, but in each plant the rate is dependent upon temperature and rises from a minimum of no movement up to an optimum of greatest movement, whence it sinks to a maximum of no movement, which cardinal points vary with the species but approximate in a general way to 5°, 35°, and 45°. The significance of the streaming is not known, and the explanatory guesses range all the way from "pathological," through "incidental," to "ecological," the most reasonable of the latter (especially in view of its greater activity in large cells) being that it is a mechanical aid to diffusion.

Protoplasmic streaming is a striking and perhaps a fundamentally important phenomenon, well worth demonstration to elementary classes

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[1] 40:302. 1905; 45:50. 1908; and 45:254. 1908.

and measurement by advanced ones. Of the plants available for the purpose in winter, namely, those which are or may readily be grown or kept in greenhouses or houses, the best known heretofore are as follows: species of Chara and Nitella, which may be kept over winter in tubs under the greenhouse benches; Elodea and Vallisneria, responsive to the same treatment; *Tradescantia zebrina* or wandering Jew, very commonly grown, and *T. virginica* (or *pilosa*) which can be kept part of the winter if planted on a greenhouse bench and cut back until July or August; squash or tomato, which can be grown from seed in two or three weeks; root hairs of mustard and other plants, which can be grown to perfection in wet, covered flower-pot saucers; heliotrope and pelargonium.

The brevity of this list in plants presenting material ready at all times led me to undertake a systematic search for others through a range of educational greenhouses, and I was successful in finding the considerable number of new cases marked by the asterisks in the table below.[2] I also undertook to determine, upon a uniform system, the rate of movement, both for these and for the other common forms, at the two temperatures practically most important, namely 20° (approximately ordinary room temperature) and the optimum; and the results are recorded in the table. For the control of temperature I used GANONG's temperature stage, with the method, including standardized ocular micrometer and metronome, described in his *Laboratory course in plant physiology.* The figures in the table are averages of two or more determinations from different specimens except in a few cases of the optimum, where only one measurement was made.

GREENHOUSE PLANTS SHOWING PROTOPLASMIC STREAMING, WITH ITS RATE

NAME OF PLANT	PARTS OBSERVED	RATE (mm. per min.)	
		@ 20°	Optimum
*Abutilon striatum hyb.	unicellular hair from surface of ovary	.161	.773@32°
	hair from calyx	.016	
*Ampelopsis Veitchii (Boston ivy)	unicellular hair from under side of midrib	.138	.368@36°
Avena sativa (oat)	root hair of seedling	.322	
*Azalea sinensis	cell of hair from leaf blade	.138	.322@34°
Brassica alba (white mustard)	root hair	.322	

*Those marked by an asterisk are here recorded for the first time.

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[2] As concerns outdoor plants for this same purpose there is a paper entitled "Subjects for protoplasmic movements," by B. D. HALSTED, in Bull. Bot. Depart. Iowa State Agric. Coll. **1888**:578. It enumerates ten common plants.

NAME OF PLANT	PARTS OBSERVED	RATE (mm. per min.)	
		@ 20°	Optimum
*Campanula glomerata (bell flower)	unicellular hair from leaf blade or petiole	.258	.644@38°
*Capsella Bursa-pastoris (shepherd's purse)	unicellular hair from flower stalk	.215	.483@32°
*Cestrum elegans	unicellular hair from stem or veins on under side of leaf	.161	.428@35°
*Coleus Blumei Verschaffeltii	cell of hair from stem at node or edge of petiole	.276	.892@35°
Cucurbita maxima (squash)	cell of hair from petiole	.258	.859@32°
*Cuphea hyssopifolia	cell of hair from stem	.121	.258@34°
*Cuphea ignea (cigar plant)	cell of hair from stem	.048	.215@36°
Elodea canadensis	cell near midrib of leaf	.604	.966@36°
*Fuchsia speciosa	unicellular hair from flower stalk	.175	.322@34°
*Gaillardia grandiflora	cell of hair from petiole	.227	.703@36°
*Gloxinia speciosa	cell of hair from stem or petiole	.322	1.054@36°
	cell of hair from leaf blade	.351	1.088@36°
*Helianthus annuus (common sunflower)	cell of hair from edge of petiole	.175	.429@35°
	cell of hair from midrib	.081	
Heliotropium peruvianum (common heliotrope)	unicellular hair from stem, surface of leaf, or under side of midrib	.121	.386@34°
*Hibiscus Cooperi (rose mallow)	unicellular hair from petiole or under side of midrib	.175	.773@35°
*Isoloma hirsutum	cell of hair from stem	.193	.515@34°
*Lavandula vera (lavender)	cell of hair from stem	.242	.508@35°
*Lobelia Erinus	unicellular hair from leaf edge, petiole, or stem	.297	1.073@37°
*Lopezia albiflora	unicellular hair from stem	.193	.483@30°
	unicellular hair from leaf	.322	.858@30°
	epidermal cell from under side of midrib	.121	.322@32°
Nitella (common species)	young cells	1.610	2.840@34°
Pelargonium quercifolium (oakleaf pelargonium)	cell of conical hair from petiole or surface of leaf	.322	.552@33°
Lycopersicum esculentum (common tomato)	cell of hair from stem, leaf edge, or vein	.386	1.288@34°
*Oxalis Bowiei	cell of hair from leaf-edge	.242	.575@34°
*Primula obçonica (primrose)	cell of hair from stem or leaf	.276	.805@30°
*Saxifraga cotyledon palmata (saxifrage, rockfoil)	cell of hair from edge of leaf	.176	.859@37°
*Saxifraga sarmentosa (beefsteak saxifrage)	cell of hair from flower stalk	.322	.859@35°
*Senecio cruentus (cineraria)	cell of hair from under surface of leaf	.193	.386@31°
*Streptosolen Jamesonii	cell of hair from stem or leaf blade	.183	.428@37°
Tradescantia virginica (spiderwort)	cell of stamen hair	.242	.644@33°
Tradescantia zebrina (wandering Jew)	cell of stamen hair	.386	.990@32°
*Vinca major (periwinkle)	cell of hair from leaf edge	.107	.322@35°
*Whitlavia grandiflora	unicellular hair from petiole or calyx	.242	.644@38°
	" " " leaf blade	.193	
	cell of glandular hair from leaf blade	.138	

* Those marked by an asterisk are here recorded for the first time.

This table shows that suitable material can easily be obtained in winter for the demonstration of protoplasmic streaming. Of the plants studied, I should recommend Nitella and Elodea as good examples of rotation; *Gloxinia speciosa*, *Tradescantia zebrina* and *virginica*, *Abutilon striatum* (hyb.), *Lycopersicum esculentum*, *Whitlavia grandiflora*, *Cucurbita maxima*, *Lobelia Erinus*, and *Saxifraga cotyledon palmata* for circulation. *Gloxinia speciosa* is especially good, as the entire hair cell can be brought within the range of vision, and a constant change observed in the arrangement of the strands, circulation passing into rotation as the temperature rises. Campanula, Lobelia, Vinca, Streptosolen, Capsella, and Ampelopsis have markings on the cell wall which obscure the view of the protoplasm to some extent.

A complete study of the streaming involves the measurement of its rate at various temperatures from minimum through optimum to maximum. Results of such study, expressed in a graph, are available for Chara, Elodea, and Vallisneria in DAVENPORT'S *Experimental morphology* (**1**:226), and for a common Nitella in GANONG'S *Laboratory course in plant physiology* (p. 19). My own graph for Tradescantia shows a curve much flatter than that above mentioned for Nitella, though otherwise somewhat similar to it.—GRACE L. BUSHEE, *Smith College, Northampton, Mass.*

ON PLASMOLYSIS

According to the conception of plasmolysis developed by DE VRIES and PFEFFER, the contents of a cell contract and round up when it is placed in a solution whose osmotic pressure exceeds that of the cell sap. This is explained by supposing the outer layers of protoplasm to be impermeable to the substances in solution which produce the osmotic pressure. If the protoplasm is permeable to these substances, either wholly or in part, deviations from the rule given above will occur. Deviations have in fact been described by several authors and explained by supposing the protoplasm to be more or less permeable to the substances in solution, which enter the cell sap and increase its osmotic pressure.

I propose in this paper to describe deviations which range from those which are very slight to those which are of extraordinary intensity, the explanation of whose nature is entirely different from the one mentioned above.

My attention was first called to these deviations some three years ago by the results of some of my experiments on the rôle of osmotic pressure[1]

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[1] A brief account of these investigations appeared in Univ. Calif. Publ. Bot. 2:227, 229. 1906.

in marine plants. I then experimented on fresh-water plants and found even more striking results.

In order to make clear the nature of these results I will describe an experiment with Vaucheria. Zoospores which had attached themselves to slides were allowed to germinate and produce short tubes. The slides were then transferred to 0.0937 *m* NaCl solution. In the course of a few minutes the protoplasm began to contract away from the cell wall. The solution was apparently strong enough to produce plasmolysis and I prepared weaker ones. These, however, produced the same effect, taking more time to do so in proportion as they were weaker. It then occurred to me that the effect was not due to osmotic pressure but to a *contraction of the protoplasm due to the chemical action of the salt.*

In order to test this idea I endeavored to determine how dilute the solution could be made and still produce this effect. I found that even 0.0001 *m* solution produced it, though usually only after a day or so. The experiments are repeated several times with Kahlbaum's C. P. sodium chloride which I had recrystallized six times. The result remained the same.[2]

I then tried to do away with this effect. This is easily accomplished by adding a little $CaCl_2$. The addition of $CaCl_2$ in solid form increases the osmotic pressure of the solution, but in spite of this it prevents the contraction of the protoplasm away from the cell wall. If one molecule of $CaCl_2$ is present for every hundred molecules of NaCl, the algae endure solutions of 0.1 *m* (that is to say, solutions with a thousand times greater osmotic pressure) without any contraction or apparent plasmolysis.

I have since experimented with a great variety of salts and combinations of salts which produce effects similar to those just described. I have found that all the plants with which I have experimented (algae, fungi, mosses, liverworts, Equisetum, flowering plants) give similar results, though most of them are much less sensitive than Vaucheria.

After these experiments I was in no way surprised when I found that water distilled from a metal still could produce apparent plasmolysis within a few minutes, and that this could be prevented by the addition of various substances.

In what way is the contraction just described distinguishable from true plasmolysis? In many cases it cannot be so distinguished at all[3] by its

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[2] Vaucheria from other localities and especially in later stages proved less sensitive to the action of NaCl. Cf. Jour. Biol. Chem. 1:363. 1906.

[3] It is possible that the results described by DUGGAR (Trans. St. Louis Acad. Sci. 16:473. 1906, and TAKEUCHI (Bull. Coll. Agri. Imp. Tokyo Univ. 7:623. 1908) are explicable on this basis.

appearance, but only by comparison with other (especially non-toxic or balanced) solutions, or by determination of the freezing-point of the cell sap. The protoplasm rounds up just as in true plasmolysis, and may even subsequently recover and expand in characteristic fashion when transferred to distilled water.

It may happen that a contraction is caused by true plasmolysis, but the subsequent chemical action of the salt renders the protoplasm unable to recover and expand when the cell is transferred to distilled water. Such recovery cannot therefore be used as a means of distinguishing true plasmolysis from a contraction due to chemical action.[4] In some cases the contraction may be distinguished from true plasmolysis by the irregular outline of the contracted protoplasm.

On looking over the literature it becomes evident that such precautions as are necessary to distinguish this contraction from true plasmolysis have not been generally observed in making plasmolytic determinations, and a revision of such determinations is necessary. Determination of the freezing-point of the cell sap will certainly be needed in many cases if an accurate result is desired.

In conclusion I would call attention to the importance of this discovery in respect to one of the most prominent biological problems, the question whether salts are able to penetrate the protoplasm or not. Far-reaching conclusions have been drawn from the fact that when a cell is placed in a solution of a certain substance the protoplasm contracts and does not subsequently expand if left in contact with the solution. This has been interpreted to mean that the substance in solution is unable to penetrate the protoplasm. I find, however, in many cases, that the true interpretation is exactly the opposite. The permanent contraction of the protoplasm is caused by the *penetration of the substance in question* which produces chemical effects upon the protoplasm, wholly different from those produced by a substance whose action is purely osmotic.

In view of this we cannot give credence to certain very important conclusions and theoretical considerations which have been based on this criterion of penetrability. These points will receive fuller discussion in a subsequent paper.—W. J. V. OSTERHOUT, *University of California.*

[4] The expression chemical action is here used in a very broad sense to include effects which are not osmotic in character.

CURRENT LITERATURE

BOOK REVIEWS

The origin of a land flora

Under this title Professor Bower has written a volume[1] which must be regarded as the culmination of his important studies during the last twenty years. It is a formal and amplified statement of the views advanced in his series of five papers entitled "Studies in the morphology of spore-producing members," published between 1894 and 1903.

The scope of the volume is very broad and its spirit is admirable. The author recognizes that his thesis is not proved; that in the very nature of the case it never can be; and that there are many possible alternatives. However, he presents so strong a case that the truth of the theory would not come to anyone as a surprise. Naturally the book is speculative, and the author's frequent insistence that this is the case should be respected by those who follow its doctrine. The human mind seems to be so constituted that when a view is distinctly formulated it thereby seems to gain additional proof.

There is a strong tincture of teleology at every turn, the elimination of which would have strengthened the discussion. This gives it a flavor of unreal "otherworldliness" that is becoming unscientific. That a certain structure would be useful to a plant and therefore it grows, is hardly acceptable as an explanation of origins.

The thesis of the volume is the origin of the sporophyte as an antithetic generation, which has become fixed and amplified by the invasion of the land. In developing this doctrine, the author presents first a statement of the working hypothesis (pp. 254), then a detailed statement of facts (pp. 403), and finally the general comparisons and conclusions (pp. 60). In a brief review it is impossible to present the suggestions that fill these three parts. The second part—the statement of facts—is wisely separated from the other two, and in this form it represents an admirable treatment of the morphology of bryophytes and pteridophytes, especially the latter. Much new material is included here, and especially helpful is the massing of the morphological, anatomical, and paleobotanical evidence. These three points of view are too often kept separate, when they should serve as checks upon one another.

The two theoretical parts also contain much more detail than can be presented. However, the broad outlines of the working hypothesis and some of the more important conclusions may be indicated.

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[1] Bower, F. O., The origin of a land flora: a theory based upon the facts of alternation. 8vo. pp. xii+727. *figs. 361*. London: Macmillan and Co. 1908. $5.50.

Running throughout the hypothesis is the assumption that the most critical and hence controlling fact in the life of any organism is the relation existing between environment and fertilization. Perhaps the most fundamental conception is that the "Archegoniatae" are amphibious. (It may not be out of place here to suggest that the group name "Archegoniatae" has about outlived its usefulness. To associate the widely separated bryophytes and pteridophytes in this way, and to include or exclude part of the gymnosperms, is a grouping too unnatural and misleading to be continued.) That the gametophyte of "Archegoniatae" is amphibious means that it is just as aquatic as an alga, and shows this in its delicate structure, lack of intercellular spaces, lack of a water-conducting system, and the possibility of fertilization only in the presence of water. "The gametophyte proclaims its ultimate dependence on external fluid water as thoroughly as an alga." On the other hand, the sporophyte is characteristically an aerial body, with its more robust habit, "ventilating" system, vascular strands, and spores adapted for dryness.

Attention is called to the fact that the "Archegoniatae" retain with remarkable pertinacity this "awkward and embarrassing" method of fertilization; but that with the advent of the seed plants this becomes modified, and the higher seed plants at last become completely terrestrial.

A general outline of the steps by which the sporophyte was established and amplified as a terrestrial structure may be stated as follows: The gametophyte was the previously existing phase, and the initial step in the appearance of the sporophyte was the "post-sexual divisions, giving rise to a plurality of germs," such as is observed in the life-histories of certain green algae. In plants exposed to changing conditions of moisture and drought the fixing of such a generation would be assured, according to the following logic: external water would be occasional rather than constant; hence the sexual act would be occasional; hence there would be less dependence upon the sexual act for multiplying individuals; hence a "premium would be put upon" the other method of propagation suitable for drier conditions. Thus the sporophyte is to be recognized as a body originating as an adaptation to terrestrial life.

In amplifying the sporophyte, it is assumed that the first and also the final office of the sporophyte is to produce spores, and that the larger the number of spores (in homosporous forms) the better the chance of survival; therefore the increase in number of spores is "encouraged." But to protect spores when young and to nourish them during development presupposes some vegetative system.

The process for developing this vegetative system is the familiar theory of progressive sterilization, so well traced by the author among bryophytes. Among bryophytes, however, there are certain limits imposed by mechanical and physiological conditions; while among vascular plants there is greater freedom for progress, chiefly by the segregation of the sporogenous tissue into distinct sporangia and the formation of "appendicular organs." As a result of this progressive sterilization and organization of vegetative tissues, the fertile tissue appears later and later in ontogeny, until what was first in phylogeny comes to be last in ontogeny. This disposition of the recapitulation theory appears in various places throughout the volume, and it is evident that the author regards it as reliable only within certain limits, when it agrees with other evidence.

From among the general conclusions the following may be selected as of most general interest. The author concludes that no definite algal form now living can be held to have been a direct progenitor of any known archegoniate type; but that certain algae suggest in their post-sexual phase how the initiation of the sporophyte may have occurred. Also the liverworts and mosses may be held to be "blind branches of descent;" but they illustrate changes that suggest the origin of sterile tissues from those potentially fertile, and the final establishment of a self-nourishing system in the sporophyte.

The gametophyte of early pteridophytes was probably a relatively massive green structure, with deeply sunk sexual organs; and the sporophyte was the strobiloid type of body illustrated by *Lycopodium Selago* and its allies (the author's well-known "theory of the strobilus"). This reconstruction of the most primitive vascular body is obtained by converging all the known pteridophyte lines, and the result is a body which arose from no one knows what, but which does not suggest any known bryophyte or alga.

This is a very meager outline of the contents of a large volume, crowded with facts and suggestions. Such speculation brings perspective and stimulus, and its only danger is a confusion of theory with fact, for which the author in this case could not be held responsible. Perhaps the most serious charge that could be brought against him, in this connection, is his great command of picturesque statements, which are highly figurative but contain perilous suggestions for the unwary. For example, that "encouragement was given" to a multiplication of spores; that the method of fertilization in archegoniates is "awkward and embarrassing;" that "a premium was put upon" aerial spores, etc., are extremely telling forms of statement, but they are more rhetorical than exact, suggesting far more than was intended.

At all events, the volume is a monument to the research power and philosophical insight of its distinguished author.—J. M. C.

Electro-physiology

Two years ago plant physiologists were rather taken aback by a large volume of researches on plant response from the pen of a contributor previously unknown in this field. It is not often that so brilliant a display marks the advent of a new scientific luminary, and it was impossible at once to determine whether he was a meteor, whose light would flash and disappear, or a star of the first magnitude. There were not wanting, indeed, signs that he was erratic. This work[2] conspicuously lacked relation to the present state of knowledge and showed scant acquaint-

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[2] BOSE, J. C., Plant response as a means of physiological investigation. See review in BOTANICAL GAZETTE **42**:148. 1906.

ance with the researches of others; while the naïveté with which some of the most recondite problems were attacked and dismissed as solved awakened amused incredulity. At the same time the author's ingenuity in devising and adapting self-registering methods to the mechanical and electrical responses of plants, as well as the suggestiveness of some of his results, made the book possibly an epochal one, since it struck out a rather new path for most important investigations.

So far, however, nothing has come of it. Its reception has been apathetic, not to say cold, and to all appearances it has fallen dead because of its faults and in spite of its manifest virtues. No researches have followed it up; no investigator has used its methods. That volume on *Plant response* was the second of a series of three (the first on *Response in the living and non-living*), of which the third has just made its appearance under the title *Comparative electro-physiology*.[3]

The author herein shows the same peculiarities as in the preceding volume. There is the same naïve interest in well-known phenomena, as though they were quite novel; there is the same lack of effort to connect his work with that of others, so far, at least, as citing their researches or results is concerned. It is doubtful if in this book of over 800 pages, dealing with a very special topic on which there must be a legion of workers, there are a dozen citations of original sources. There is much repetition of the earlier volume; the same tilting at windmills—vigorous attacks on vitalism and on the contrast between animals and plants, and between "sensitive plants" and others, till one is tempted to inquire with Sairey Gamp, "Who denyges of it, Betsey, who denyges of it?"

This volume maintains the same simple thesis as its predecessor—as simple as the faith of Islam, "Allah is great and Muhamed is his prophet"—contraction is universal and negativity is its sign. The direct response to every stimulus is "contraction," the indirect one (at a little distance) is "expansion." The former is said to be *accompanied by* reduction and the latter by increase of turgidity, with corresponding electric variations. The expression of contraction in movement, "suction" (ascent of sap), growth, "torsion" (in climbing plants), death, and electric variation, constitutes the theme of the two volumes. This much needs to be said: There are reasons for expecting some universal fundamental reaction in all responses; it may be that BOSE has hit upon it in what he miscalls "contraction" (for this is really nothing but a reduction in turgidity); but his work is not convincing.

This book shares with its predecessor, also, the confusion between energy and stimulus, a confusion that is possible because we know so little of plant energetics. This reaches its absurd climax in the conception of the author as to the function of plant nerve. He gravely tells us that the ramification of the "nerves" in a leaf provides a "virtual catchment basin for the reception of stimulus," whence it is transmitted to the body of the plant, there to be stored and

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[3] BOSE, J. C., Comparative electro-physiology, a physico-physiological study. 8vo. pp. xliv+760. *figs. 406*. New York: Longmans, Green & Co. 1908. $5.75.

used later in responses. All this is quite apart from the question of the energy fixed in photosynthesis.

This suggests another fault. BOSE seems to ignore, if he is not ignorant of, the anatomy of the parts with which he is dealing. Skin is skin, whether it be the skin of plant or animal. Stomach of Gecko and pitcher of Nepenthes (an open stomach of a primitive type, he calls it) are all one to him; they behave alike, in spite of their extraordinary differences of structure. Nerves of animal and nerves of plants, which have been identified by their behavior as the vascular bundles of plants, are physiologically the same. Digestion being a "diphasic process," that is, consisting of secretion first and absorption afterward, roots, which secrete substances that dissolve their mineral "food" and then absorb it, must be another kind of open stomach; and besides, they behave electrically as stomachs do! Now if these things are so, it argues that the responses with which BOSE is dealing are either extremely superficial or extremely fundamental, inhering in all living matter; and in either case they would be of little significance.

The situation seems to be most peculiar. BOSE, we judge, is a brilliant experimentalist, trained first as a physicist, but inadequately equipped with knowledge of what has been done in the field of plant irritability. This has been at once an advantage and a snare. It has left him free to present his researches untrammeled by the conventional view, but it has exposed him to mistakes which a little more knowledge would have avoided. It has given him courage to attack the most knotty problems, but it has led him to satisfaction with inadequate conclusions. Apparently, too, he has become possessed by a theory as to the nature of response, and under the yoke of that theory he makes all his captive facts to pass.

Out of these books we look for some one to rescue many good observations, now apparently gone awry; and by his methods and apparatus in the hands of real physiologists we hope soon to see made important advances in the knowledge of *Reizphysiologie*.—C. R. B.

Conference on Genetics

The report[4] of the Third International Conference on Genetics held under the auspices of the Royal Horticultural Society, July 30 to August 3, 1906, is a veritable treasure-trove for students of heredity, hybridization, and plant-breeding, both in their theoretical and practical aspects. Besides giving a minute account of the doings of the Conference, there is a brief but excellent sketch by the secretary, Rev. W. WILKS, of the life and work of GREGOR MENDEL, illustrated by three good portraits, a fine view of the Abbey at Brünn, and a facsimile letter written to NÄGELI. Excellent portraits are also given of some of the more

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[4] Report of the Third International Conference, 1906, on Genetics; hybridization (the cross-breeding of genera or species), the cross-breeding of varieties, and general plant-breeding. Edited by the Rev. W. WILKS. 8vo. pp. 496. *figs. 131.* London. 1907.

prominent participants in the Conference, as LAWRENCE, WILKS, BATESON, JOHANNSEN, TSCHERMAK, WITTMACK, HURST, Miss SAUNDERS, and the VILMORIN brothers.

Besides the address of the chairman, Prof. BATESON, upon "The progress of genetic research," there are a number of important contributions to Mendelian inheritance, by HURST, DARBISHIRE, DAVENPORT, Miss SAUNDERS, TSCHERMAK, and BIFFEN; two papers upon orchid hybrids by ROLFE, and CRAWSHAY; and several papers upon the occurrence of natural hybrids, the most comprehensive of which by E. G. CAMUS is not printed in full because it was sufficiently voluminous to make a separate book. This paper deals with the spontaneous hybrids of the European flora. A lengthy list of natural hybrids is also given by LYNCH, Curator of the Botanic Garden, Cambridge. PFITZER deals briefly with hybridization and the systematic arrangement of orchids, and a valuable posthumous paper by the same author discusses the probability of the origin of the Orchidaceae from the Amaryllidaceae. OSTENFELD describes some castration experiments with Hieracium, and ROSENBERG reports briefly his work upon the cytology of Drosera, and also on Hieracium hybrids. In some of the latter he has found considerable differences in the number of chromosomes carried by different eggs of the same plant. BUNYARD reviews the question of xenia, stating that after an extensive search for evidence of this phenomenon he knows of but a single instance, this being an apple cross made by him ("Sandringham" × "Bismarck"). J. H. WILSON describes a considerable number of infertile hybrids, which he has studied with some care.

Dealing with plant breeding from the more practical point of view are the following: E. F. SMITH outlines the plant-breeding operations of the U. S. Department of Agriculture; the improvement of sugar cane is discussed at length by Sir DANIEL MORRIS; papers by ZAVITZ, P. DE VILMORIN, C. E. SAUNDERS, and BIFFEN describe results in breeding improved races of wheat and other small grains; HANSEN tells of his work in breeding cold-resistant fruits; RIVERS and LAXTON also give some of their results in hybridizing fruits, particularly peach × nectarines, apple hybrids, and plum hybrids; LAXTON draws some conclusions from the work with peas for which his family is justly famous; WARD gives a finely illustrated description of some of his excellent work on carnations, explaining among other things his method of keeping pedigree records; VAN TUBERGEN, of Haarlem, discusses hybrids among bulbous plants; PAUL gives the derivation of a number of fine hybrid roses of recent production; H. H. GROFF, the specialist in Gladiolus, discusses plant-breeding from the point of view gained by work with these plants, and emphasizes the idea that the plant-breeder has much to learn from the animal-breeder. There are several shorter papers by other authors.

Many of the articles are illustrated with fine halftones and the press work is up to the high standard for which the reports of the Royal Horticultural Society are well known.—GEORGE H. SHULL.

North American trees

Three years ago this journal[5] noticed the appearance of SARGENT'S excellent *Manual of the trees of North America*, which brings into a convenient volume the information that is much more elaborated in his great *Silva*. Now another manual of the trees has appeared, bearing the title *North American trees*, and written by BRITTON and SHAFER.[6] The very handsome volume is made bulky by the heavy paper, so that it will have to be used more as a standard dictionary than as a handy manual.

The distinct mission of the volume, however, is to present the trees in language so free from technical terminology, and by illustrations so characteristic, that they may be recognized by "any person of ordinary information." This will certainly meet and stimulate the growing interest in trees, a purpose that is worth while. The authors are in an exceptionally favorable position to make such a book accurate rather than merely popular, and it is a good thing now and then for men who have the facts to give to the public something that can be relied upon. The identification of trees should now be as easy as the long popular identification of birds. The characters are drawn from foliage, flowers, and fruit, and they are presented in the free style of ordinary description, rather than in the compact style of taxonomy. The illustrations are from excellent sketches and photographs, and really illustrate. The economic value of the various trees is included, so that when the name of a tree is discovered, the inquirer is in a position to obtain much useful and interesting information concerning it. Of course any definition of a tree must be arbitrary, but the authors have liberally included all species known to become trees in habit (with "single erect stem or trunk"), even if they are almost always shrubs.—J. M. C.

MINOR NOTICES

Physiology of stomata.—LLOYD has given us a careful study of the behavior of the stomata in two desert plants, *Fouquieria splendens* and *Verbena ciliata*, made at the Desert Botanical Laboratory of the Carnegie Institution.[7] He addressed himself particularly to the question of the regulation of transpiration by stomatal movements, and furnishes conclusive evidence that the stomata in these plants, where there are no complications in the way of pits, plugs, or other contrivances, are not able to adjust the transpiration to the "needs" of the plants. Wide variation in the rate of transpiration is found, quite independent of the

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[5] BOT. GAZETTE 39:301. 1905.

[6] BRITTON, NATHANIEL LORD, and SHAFER, JOHN ADOLPH, North American trees; being descriptions and illustrations of the trees growing independently of cultivation in North America, north of Mexico and the West Indies. Imp. 8vo. pp. x+894. *figs. 781*. New York: Henry Holt and Company. 1908. $7.00.

[7] LLOYD, F. E., The physiology of stomata. Imp. 8vo. pp. 142. *pls. 14. figs. 39.* Washington: The Carnegie Institution, Publication 82. 1908.

position of the guard cells, the maximum diffusion capacity of the pore being seldom (if ever) utilized. A rhythmic variation in the transpiration rate was found to be independent of the stomatal rhythm. As to the latter, LLOYD finds that, aside from the indirect effect of high relative humidity in reducing the water loss and so favoring the opening of the stomata, there is no relation between the humidity and the position of the guard cells. He finds no closure of the stomata in anticipation of wilting, but during wilting a slow closure, without the preliminary opening attributed to them by FRANCIS DARWIN.

LLOYD also attacked an interesting problem in the supposed photosynthetic activity of the guard cells. He finds evidence of amyloplastic but none of chloroplastic activity, and concludes that the movements of the guard cells are related to their accumulation and dissolution of starch derived from the chlorenchyma, rather than to any photosynthetic products of the guard cells themselves.

This is a careful and thorough piece of work, highly creditable to the laboratory from which it comes. The experimental evidence is now at hand supporting conclusions which have been held by some physiologists for some years as highly probable on purely physical grounds.—C. R. B.

The timbers of commerce.—A second edition of BOULGER'S *Wood*, revised and enlarged, has appeared.[8] It deals with 1000 kinds of wood, and includes most of those known in general commerce. The first part (pp. 121) discusses wood in general, under such topics as origin, structure, development, classification, defects, selection, uses, supplies, and tests. The second part presents the woods of commerce, giving in each case the source, character, and use. The 48 plates are from photomicrographs of sections, and are intended to show the distinctive microscopic features. Such a book is encyclopedic, and therefore for its purpose it is extremely useful. The demand for a second edition speaks well for the favorable reception of the first.—J. M. C.

Knuth's Handbook.—The second volume of DAVIS' English translation of this encyclopedic work has just been issued by the Clarendon Press.[9] The original volumes and the first volume of the translation were reviewed in this journal,[10] so that the general scope and character of the work have been noted. The present volume includes observations on flower pollination made in Europe and in the arctic regions, and is a great mass of observations upon species ranging through the natural orders, from "Ranunculaceae to Stylidieae." Such a book cannot be reviewed, for it is an encyclopedia. It can only be announced, and

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[8] BOULGER, G. S., Wood, a manual of the natural history and industrial applications of the timbers of commerce. 8vo. pp. xi+348. *pls. 48*. London: Edward Arnold. 1908. $4.20.

[9] KNUTH, PAUL, Handbook of flower pollination. Translated by J. R. AINSWORTH DAVIS. Volume II. 8vo. pp. viii+703. *figs. 210*. Oxford: Clarendon Press. 1908. Half morocco 35*s*.; cloth 31*s*. 6*d*.

[10] BOT. GAZETTE **28**:280. 1899; **28**:432. 1899; **42**:494. 1906.

this translation should greatly stimulate observation in a field too much neglected by American botanists.—J. M. C.

Flora of Manchuria.—Komarov[11] has completed his *Flora of Manchuria* with the appearance of the second part of the third volume. The whole work contains 853 pages, and the last part includes the Sympetalae from Labiatae to Compositae. It is interesting to note that in presenting 18 families, 130 genera, and 336 species, only two new species are described—one a Scutellaria, the other a Saussurea. An appendix contains descriptions of two new species of Anemone. In this part much the largest families are Compositae (164 spp.), Labiatae (48 spp.), and Scrophulariaceae (43 spp.)—J. M. C.

Grasses of Louisiana.—R. S. Cocks,[12] Tulane University, has published a list of the grasses of Louisiana, based upon collections made during each season since 1897. The catalogue contains 290 species, which is said to represent 12 per cent. of the flora of the state. It is interesting to note that 11 species are known to find their northern limit in Louisiana; 9 species their southern limit; 10 species their western limit; and 10 species their eastern limit; while 5 species are given as occurring only in Louisiana so far as the United States is concerned.—J. M. C.

The western willows.—Jones[13] has published an account of the western Salicaceae, recognizing 53 species of Salix, with numerous varieties, and 8 species of Populus. The species have been studied in the field and the descriptions are compact and clear; so that the willows are presented as they actually appear in nature. A key to the species makes their recognition very direct, and the characters used are very obvious ones. Willows have been difficult to identify, and this presentation should be of much service.—J. M. C.

North American Flora.—The second part of Volume IX concludes Polyporaceae, by W. A. Murrill, 32 genera being presented, 16 of which have recently been described by the author. In various genera 36 new species are described.—J. M. C.

NOTES FOR STUDENTS

Biometrical studies.—The close interrelation between fluctuations and the environment, especially those factors of the environment which in any way affect nutrition, has been recognized by many authors and overlooked or ignored by others. Several valuable contributions have been made to this subject. In a

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[11] Komarov, V., Flora Manchuriae. Acta Hort. Petrop. 25^2:335–853. *pls. 4–16.* 1907.

[12] Cocks, R. S., Annotated catalogue of grasses growing without cultivation in Louisiana. Bull. 10. Gulf Biologic Station, Cameron, La.

[13] Jones, Marcus E., The willow family of the Great Plateau. pp. 32. Salt Lake City, Utah.

paper read before the third Flemish Natural History Congress at Antwerp in 1899, MACLEOD[14] shows that in *Centaurea Cyanus* the mean numbers of rays and disk-florets are highest in heads which bloom earliest and that they fall continually as the flowering season progresses, the change in disk-florets being the greater. When individuals are considered, the terminal heads have the highest numbers, and each successive bud-generation has a less number than the preceding. Three series of cultures under different conditions of soil led to the conclusion that the first heads of each plant behave like the terminal heads of well-nourished plants; and that the last heads of each plant and of the season resemble the terminal heads of poorly nourished plants. There is no indication in this species that the Fibonacci numbers tend to predominate. This paper is not listed in DAVENPORT'S rather comprehensive bibliography, and was unfortunately unknown to me when I was investigating the seasonal variability in *Aster prenanthoides*. The conclusions reached for Centaurea are the same as those reached by me about a year later in Aster.

More recently MACLEOD and BURVENICH[15] have made an experimental study of the variability in the number of rays of *Chrysanthemum carinatum* and find essentially the same condition as in Centaurea, except that, unlike that species, *Chrysanthemum carinatum* shows the modes on the Fibonacci numbers, and as the mean number changes with the change of nutrition, the prominence of one mode is lessened as the neighboring one increases. The variation goes by steps or leaps from one favored value to the next. In discussing these "variation-steps" (*Varietietrappen*), three types of behavior are recognized: first, that in which the modes, whether one or several, agree with the terms of the relevant series, e. g., *Chrysanthemum carinatum*, 13 and 21; second, that in which the number of parts is constant or but very slightly variable and the values are those of the terms of the series, e. g., *Senecio Jacobaea*, 13, *S. nemorensis*, 5, *S. nemorensis octoglossus*, 8, etc.; third, the condition found in *Centaurea Cyanus* and in Aster in which the mode may fall upon any of the values lying between the terms of the series and in which as the mean values rise or fall the mode passes gradually through all the successive values. Seven variation-scales or series are recognized as fully demonstrated for one or more plant-characters; viz., (1) the Fibonacci series, 3, 5, 8, 13, 21, 34; (2) 5, 10, 15, 20 (carpels of Geranium); (3) 3, 5, 7 (leaflets of Trifolium); (4) 3, 6, 9 (flowers of Lonicera); (5) 2, 5, 8, 11 (flowers of *Cardamine pratense*); (6) 4, 8, 12, 16 (flowers of *Cornus mas*); (7) 4, 8, 16, 32, 64 (peristome of mosses). The author gives a lucid explanation of the cause for the existence of such series by referring them back to the period in

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[14] MACLEOD, J., Over de veranderlijkeid van het aantal randbloemen en het aantal schijfbloemen bij de korenbloem (*Centaurea Cyanus*) en over correlatieverschijnselen. Botanisch Jaarboek **12**:40–74. 1900.

[15] MACLEOD, J., and BURVENICH, J. V., Over den invloed der levensvoorwaarden op het aantal randbloemen bij *Chrysanthemum carinatum* en over de trappen der veranderlijkheid. Botanisch Jaarboek **12**:77–170. 1907.

development when a single additional cell-division will determine the leap from one stage to the next. The causes which incite cell-division may proceed gradually and continually but not until they have increased to a certain required degree will the additional cell-division take place, so that the effect is more or less discontinuous, though the combination of causes may be continuous.

It is also shown by MACLEOD in the paper just mentioned and by DE BRUYKER,[16] both working with *Chrysanthemum carinatum*, that the usual rule, according to which the earliest heads have the highest numbers, may be reversed by increasing the nutrition after the earliest heads are blocked out, thus fully demonstrating that the normal change which takes place from the beginning to the end of the flowering season is dependent upon the regular decline in the nutritional conditions. This seasonal periodicity is strongly emphasized in another paper by DE BRUYKER.[17] He finds that the number of flowers in the umbels of *Primula elatior* follows the same law of seasonal change as that followed by Centaurea, Aster, and Chrysanthemum above mentioned, and now known to hold for a number of species. Specimens of Primula growing in dry places had a lower mean number of flowers in the umbels than plants growing in moister places. The variation-curves for this character differ under different conditions and at different times, but always display modes on the Fibonacci numbers, 3, 5, 8, and 13. Evidence is given to show that these multimodal curves are not due to the presence of heterogeneity in the race, but are referable to the fact that development proceeds by more or less discontinuous stages, whose value in any particular instance depends upon the external and internal environment.

The complete dependence of the values of fluctuating characters upon the environment has also been well shown by KLEBS[18] in a comprehensive investigation of variation in the floral organs of *Sedum spectabile*. To avoid the possibility of dealing with mixed races, KLEBS has confined his studies to groups of individuals formed by taking cuttings from a single original plant. Growing these in several different habitats, he finds that for the stamens there is a different type of variation-curve in each habitat, which remains fairly constant so long as the habitat remains unchanged. Stamens of Sedum show the first of MACLEOD's three types of behavior, with 5 and 10 as the favored classes. The various habitats produce curves ranging from a monomodal curve with 5 as the mode and with very slight variability, through a bimodal curve with different relative values of modes 5 and 10, to monomodal curves with 10 as the mode. It is shown

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[16] DE BRUYKER, C., De gevoelige periode van den invloed der voeding op het aantal randbloemen van het eindhoofdje bij *Chrysanthemum carinatum*. Handel. 10de Vlaamsch Nat. u. Gen. Cong., Brugge, S. 1906. pp. 6.

[17] ———, De polymorphe variatiecurve van het aantal bloemen bij *Primula elatior* Jacq.; hare beteekenis en hare beinvloeding door uitwedige factoren. Handel. 10de Vlaamsch Nat. u. Gen. Cong., Brugge, S. 1906. pp. 29. *figs. 2.*

[18] KLEBS, G., Studien über Variation. Roux's Arch. **24**:29–113. *figs. 15.* Jy. 1907.

that not only variability itself, but the nature of the variation-curve and all of its "constants" are the product of the environment, and are a measure of the uniformity or lack of uniformity of environmental conditions. He concludes that there is no such thing as absolutely constant characters, and that the most constant may become quite variable under special conditions. There is no real distinction between continuous and discontinuous variability, if the question of heredity is left out of account, as both of these as well as transitions between them may be induced by changes of the environment. The applicability of QUETELET'S law, which seems to indicate that variability is due to chance, depends upon the fact that the different values of the variable characters are determined by the coordinate action of several independently variable environmental factors. In an attempt to analyze the effective factors in the environment it is shown that the values of variable characters of Sedum increase directly as the quantity of carbohydrates increases and inversely as the quantities of available water and of salts increase. Chemical analysis of plants grown in the different habitats are presented in support of this view.

PEARL[19] has studied the variability of *Chilomonas paramecium* and *Paramecium caudatum* living under favorable and unfavorable conditions. He finds that the types of the two populations are significantly different, that of the less favored culture being smaller and relatively more slender. The variability was the same in the two cultures; but the curve of the well-fed culture was positively skew, while the poorly fed presented a nearly normal variation-curve. There is a correlation of 0.6 between length and thickness, and also a significant correlation between size and form, which is recognized as opposing DRIESCH'S statement that proportionality is absolutely independent of size. In Paramecium, PEARL[20] also finds that there is a high degree of correlation or "assortative mating" between the two members of a pair of conjugating Paramecium, the coefficient ranging from 0.43 to 0.79 in respect to length, and 0.217 to 0.349 in respect to breadth. This strong tendency for like to mate with like is attributed to the inability of two individuals to unite successfully unless the mouths are of approximately the same size, the length of the mouth being closely correlated with other dimensional relations of the animal, particularly with the length. It is also found that the conjugants are differentiated as a class from the non-conjugating population, the former being smaller and less variable. From this the author concludes that conjugation tends to restrict rather than increase variability, and that the conjugant type bears much the same relation to the non-conjugants as that borne by the germ-cells of a metazoan to its soma. All evolutionary progress must rest upon changes in the conjugant type.

Of interest for the purely methodological side of biometry is a brief paper

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[19] PEARL, R., Variation in Chilomonas under favorable and unfavorable conditions. 5:33–72. *figs.* 7. O. 1906.

[20] PEARL, R., A biometrical study of conjugation in Paramecium. Biometrika 5:213–297. *figs.* 9. F. 1907.

by DE BRUYKER,[21] in which it is shown that the means and quartiles, and indeed all the ordinates, of the ogive, when calculated according to the methods of GALTON, are a half-unit too low, due to the fact that GALTON constructs his curve on the extremity of the classes instead of on their mid-values. The suggested correction brings a very close agreement between the median and the arithmetical mean. DARBISHIRE[22] gives an interesting popular discussion of correlation of the kind dealt with by biometers, using as his basis the dice-throwing experiment of WELDON, in which the relation between two successive throws of dice are the correlated quantities considered, when a certain number of dice from the first throw are left on the table to influence the result of the second. When none of the dice are left, the two throws are totally unrelated and the correlation is zero; and when all are left, so that the second entry is an exact repetition of the first, correlation is complete. Tables are given showing the actual results of throwing 12 dice in this way under every possible condition as to the number of dice left back to influence the second throw, thus beautifully illustrating the different degrees of correlation between zero and unity.—GEORGE H. SHULL.

Symbiosis.—A recent paper by KEEBLE of Reading and GAMBLE of Manchester, England, continues the investigations of these two naturalists into the subject of the symbiosis of plants and animals.[23] Of late years these two men have been almost the only ones continuing this study, which, as the literature shows, was being actively pursued fifteen or more years ago.

Convoluta roskoffensis is a simple flat-worm living between the tide-marks on the northern coasts of Europe. It is usually green, owing to the presence in its tissue of chlorophyll-containing cells, which have been diagnosed as one of the Chlamydomonadeae. They resemble the members of the genus Carteria, but for certain reason KEEBLE, the botanical collaborator, hesitates to place them positively in this genus. The life-history of both components of the association has been worked out. From this study it is clear that the flat-worm begins its existence free from green cells. There is no transmission of green cells or even of rudimentary chromatophores (plastids) from parent to egg. The green cells appear to be chemotactically attracted to the eggs and egg-cases. Pure cultures of the alga may often be obtained from egg-cases which have attracted and become partly filled with the green motile cells. By carefully washing in sea-water free from the alga, colorless Convolutas can also be obtained. These will remain colorless or will turn green according to subsequent treatment. If kept in sea-

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[21] DE BRUYKER, C., Bemerkingen aangaande de Galton'sche curve. Handel. 10de Vlaamsch Nat. u. Gen. Cong., S. 1906. pp. 6. *figs. 2.*

[22] DARBISHIRE, A. D., Some tables for for illustrating statistical correlation. Mem. and Proc. Manchester Lit. and Phil. Soc. 51:no. 16. pp. 21. diagrams 12. *1 dbl. pl.* 28 Je 1907.

[23] KEEBLE AND GAMBLE, The origin and nature of the green cells of *Convoluta roskoffensis.* Quart. Jour. Micros. Sci. 51:167–219. *pls. 13, 14.* 1907.

water passed through a Pasteur-Chamberland filter, they will remain colorless; if kept in such filtered water to which a loopful of a pure culture of the alga has been added, they will turn green as completely as if they were kept in unfiltered sea-water. Apparently the young animals cannot be infected by cells removed from the bodies of older green Convolutas.

The green cells are reported to undergo degeneration in the tissues of the animal, especially as regards their nuclei, and to this is attributed the inability of the green cells to maintain an independent existence, or to thrive in cultures, or to infect young Convolutas, when removed from the bodies of older green ones. Whether under suitable conditions of culture, the algal cells may be able to complete themselves, to restore or to regenerate the deficient nucleus, to become rejuvenated, is not determined by these experiments.

The functions of the alga in the body of its host have been experimentally studied. The authors conclude that the alga, photosynthesizing sugar, is osmotically relieved of a considerable portion of this food. It must diffuse, if it remain unchanged, to adjacent cells containing less; but if the sugar be converted into starch,the animal cannot digest and absorb it so long as the algal cells themselves live. Soon after infection with the alga, the animal ceases to excrete its nitrogenous wastes, and these, absorbed by the alga, are converted by it into higher organic compounds, into nitrogenous foods. As many of these as are soluble also diffuse into adjacent animal cells. At this stage it would appear that both animal and plant profit by their association, the animal gaining a supply of sugar and of soluble nitrogenous food, the plant obtaining a steady supply of partly elaborated organic nitrogenous food-material. Later on, however, the animal ceases to ingest solid food, and there being no other source of nitrogenous food than the algal cells themselves, the animal proceeds to devour them in its own tissue. Thus it destroys its source of food and ultimately itself, but before this it breeds.

This association, therefore, is similar to that of fungus and alga in lichens, where the fungus component, incapable of photosynthesis, is forced to obtain non-nitrogenous food, saprophytically or parasitically. The excreta of the dependent component may manure the green plants, but if they do, the benefit is a dubious one, since it leads to destruction without issue.

A word may well be added to commend the ingenuity of the experiments, the care and thoroughness with which they seem to have been carried out, and the caution with which inferences have been drawn from them and stated.—G. J. PEIRCE.

Plant diseases.—A root disease of sugar cane, first described from Java in 1895 by WAKKER is the subject of a bulletin by FULTON.[24] It is characterized by canes of reduced size and weight, and by reduced leaf system. A large percentage of

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[24] FULTON, H. R., The root disease of sugar cane. Bull. 100, La. Agric. Exp. Sta. Jan. 1908.

affected stalks die. These effects are traceable to deficiency in the root system. The lower leaf sheaths of affected canes do not fall away as they normally do, but remain cemented together by the whitish mycelium of a fungus, *Marasmius plicatus*, which occurs saprophytically upon decaying vegetable matter, and is also able to attack living tissues of low vigor and thus to become a parasite. The conditions favoring attack are summarized as follows: "Slowness of germination and early growth; improper cultural procedures; unsuitable soil; bad drainage; unfavorable seasonal conditions; the stubble crop." Preventive measures are: "careful cultivation; selection and disinfection of seed cane; resistant varieties; destruction of infected trash; resting land from cane."

A second bulletin by the same author treats diseases of pepper and beans.[25] He mentions a wilt of pepper caused by a non-sporing sclerotial fungus; the bean anthracnose due to *Colletotrichum lindemuthianum;* the bacterial blight due to *Pseudomonas Phaseoli;* and a disease caused by Rhizoctonia.

EUSTACE[26] has been experimenting on fruit rots. Tests were made of the ability of fungi to produce decay in cold storage. On March 9 several varieties of apples were inoculated with bitter rot (*Glomerella rufomaculans*), black rot (*Sphaeropsis malorum*), blue mold (*Penicillium glaucum*), brown rot (*Sclerotinia fructigena*), pink rot (*Cephalothecium roseum*), and Alternaria. The fruit was then placed in cold storage at a temperature of 31° F. When removed and examined on May 9, it was found that the only fungus which had caused decay was *Penicillium glaucum.* When removed to warmer temperature, all the other species developed and caused decay. Decay was not entirely prevented by a temperature from 35 to 56° F., and decay proceeded rapidly at a temperature of 48° to 69° F. *Sclerotinia fructigena* on the peach developed decay slightly in two weeks at a temperature of 32° F., when inoculated by puncture. Fruits inoculated by contact merely showed no decay at the end of two weeks under these conditions. Experiments were made to determine whether sulfur fumigation (1 oz. of sulfur to 25 cubic feet of space) would kill the spores of rot producing fungus. It was found that the spores of *Penicillium glaucum* can be killed this way, but that injury is caused to the apples themselves by the sulfur fumes. Careful notes were made concerning the development of apple scab, and it was ascertained that the scab of the apple can increase even when the scab in question is completely covered with a coating of the Bordeaux mixture.

Apple leaf spots have long perplexed the plant pathologist. One of them has at last been definitely proved to be caused by *Sphaeropsis malorum.*[27]. The disease in question is characterized by circular or irregular reddish-brown spots

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[25] FULTON, H. R., Diseases of pepper and beans. Bull. 101, La. Agric. Exper. Sta. Jan. 1908.

[26] EUSTACE, H. J., Investigations on some fruit diseases. Bull. 297, N. Y. Agric. Exp. Station, Geneva, N. Y. Feb. 1908.

[27] SCOTT, W. M., and RORER, J. B., Apple leaf spot caused by *Sphaeropsis malorum.* U. S. Dept. Agric., Bur. Plant. Ind. Bull. 121, part 5. March 1908.

with slightly raised purplish margins, which attain a diameter of 3.5 to 13^{mm}. The mature spots are usually circular, but may become irregular. This disease has been variously attributed to Phyllosticta, Coniothyrium, and other causes. The present authors obtained pure cultures of *Sphaeropsis malorum* from all young spots which were studied. From older spots other fungi were obtained. Inoculations with this Sphaeropsis produced typical disease in 5–20 days upon leaves. The fungus causing the leaf spot in nature is probably derived from cankers on the branches which are frequently abundantly infested.—F. L. STEVENS.

Peat.—From the Geological Survey of Michigan there has recently appeared a volume on peat.[28] The work consists of three separate essays under the following titles: The ecology of peat formation in Michigan; The formation, character, and distribution of peat bogs in the northern peninsula of Michigan; Economics of peat. The author presents a classification of the Michigan peat deposits based upon (*a*) form of land surface, (*b*) method of development, and (*c*) surface vegetation, in which he seems to follow previous authors. The place taken by plants in peat formation depends directly upon their specific ecological demands, hence the floristic diversity which appears in the formation of peat in shallow depressions, upon flat areas and raised surfaces. Applying this principle, a thorough study is made of Mud Lake, which lies in the southern peninsula, and the successions are well traced out. The conclusion is reached that light is the principal factor controlling the development of peat through its limiting influence on the growth of plants, both below and above the water level. Physical and chemical characters of the substratum, temperature, aeration, mechanical and physiological effects of the wind, and competition are considered cooperating but secondary factors influencing peat development.

In the second essay the northern peninsula is made the basis of study, and the vegetation of a large number of lakes and ponds is described in some detail, and the conclusions reached from the study of the southern peninsula substantiated. A comparison of the conditions found in the two peninsulas leads to the statement that the noted variety of the sedge zone in the north is to be related to the fact "that in the cooler, more humid climate of the north, the shrubs mentioned are able to grow better in the water than they can in the south." From a study of "Algal Lake," a type of peat hitherto unrecognized, in this country at least, must be added to those which were known before, namely, algal peat, formed almost entirely of the remains of one-celled or few-celled plants.

To part I is appended a detail map of the original swamp area of the southern peninsula; while part II is likewise accompanied by a map of the original vegetation of the upper peninsula. These maps should prove of great service, both in this field and as a permanent record of a vegetation too fast suffering destruction.

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[28] DAVIS, C. A., Peat. From the report of the Geological Survey for 1906. pp. 95–395. Lansing. 1907.

It is to be regretted that fuller credit for most of the apparently new ideas is not assigned. One looks in vain for acknowledgment of the works of FRÜH and SCHRÖTER, GANONG, and TRANSEAU, whose studies have partially covered the significant results of DAVIS. The mention of these works in their proper places would relieve the book of much that might appear to be an original contribution. The greatest value of the book to the ecologist lies in its careful descriptions of various types of swamps and the detailed record of the distribution of peat-forming species. A complete index makes this material readily available. —LEROY H. HARVEY.

Endodermis of ferns.—The sporadic occurrence of the endodermis and the modifications it shows have been frequently remarked. A comprehensive study of this layer in the fern stem and leaf has been made by BÄSECKE,[29] whose contribution may be considered a companion paper to that of RUMPF[30] on the fern root.

Following this writer, BÄSECKE distinguishes (1) the primary endodermis, characterized by Caspary's band, and (2) the secondary endodermis, in which the cell walls are more or less thickened and suberized. The leaves of the eusporangiate ferns lack an endodermis, while those of Osmundaceae show only a primary layer; but most of the leptosporangiate ferns are well provided throughout the length of the leaf with a secondary layer. Anatomical and physiological studies show that food manufactured in a fertile leaf first supplies the sporangia, and any excess passes out through the vascular bundles. In rhizomes devoted to storage, only a primary endodermis is found, and in those which are active in propagating the plant a more or less impenetrable layer extends nearly to the growing point; hence the view is maintained that the secondary endodermis serves to prevent the escape of food from the vascular bundles while it is in process of transport.

The second part of the paper describes a reinvestigation of the question as to the occurrence of cork in the ferns, and the conclusion is reached that true cork is never present, but that substitutes are frequent, such as "metacutinized" walls of the outer cell layers. In this respect the ferns are less differentiated than the angiosperms. As to shedding of leaves, the author distinguishes three sorts of absciss layers, in contrast to earlier workers who were unable to find special structures connected with leaf fall. A classification of the various mechanical tissues of ferns concludes the paper.—M. A. CHRYSLER.

Protection from light.—BAUMERT reviews very fully[31] the many suggestions that appear in literature as to the function of various structures in protecting

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[29] BÄSECKE, PAUL, Bieträge zur Kenntniss der physiologischen Scheiden der Achsen und Wedel der Filicinen, sowie über den Ersatz des Korkes bei dieser Pflanzengruppe. Bot. Zeit. **66**:25–87. *pls. 2–4.* 1908.

[30] RUMPF, G., Rhizodermis, Hypodermis, und Endodermis der Farnwurzel. Bibl. Botan. **62**:1904.

[31] BAUMERT, K., Experimentelle Untersuchungen über Lichtschutzeinrichtungen an grünen Blättern. Beitr. Biol. Pfl. **9**:83–162. *figs. 6.* 1907.

mesophyll cells from excessive light, and made exact measurements as to the efficiency of some of them. Light from a lamp, concentrated by a reflector, was allowed to fall upon the experimental leaves at an angle of 45° in a suitable moist chamber, and the differences measured by means of a thermocouple of needle form, inserted between two pieces of the leaf, and connected with a galvanometer. The cooling by evaporation as a source of error during the exposure (10–15 min.) could not be wholly avoided, but was assumed to be nearly uniform in the control and the experimental leaves.

The results show that hairy, scaly, shining, and glaucous leaves become less heated than the same leaves deprived of protection. A thick white coating of hairs, as in *Centaurea candidissima*, reduces the heating effect 37.5 per cent., shininess up to 30 per cent., and wax coating up to 13.6 per cent. A layer of water reduces it 19.2 per cent.; but this result seems more open to objection on the score of cooling by evaporation than the others, though the author takes it to be as valid as the rest. Reflection is held to be due in some Bromeliaceae to the inner epidermal wall, the cell acting like a concave lens, while epidermal cells that contain brown contents act as shades. The special value of the paper is in its application for the first time of quantitative methods, instead of deductive reasoning.—C. R. B.

Turgor and curvature.—The old problem has been again attacked by KERSTAN,[32] namely the question whether, under tropistic stimulation, there first occurs a variation in turgor that causes the curvature, both in growing parts and in motor organs. The evidence accumulating has been all against the idea, so far as concerns growth curvatures, and PFEFFER'S result with Hordeum has stood almost alone. KERSTAN adds his testimony that in most cases there is no acceleration of geotropic and heliotropic growth movements by a heightened turgor, and often the cells of the convex side become less turgid. When such curvatures are mechanically prevented, no one-sided or opposed turgor changes occur. Only in the nodes of some grasses does turgor rise on the convex side by 0.5–2 per cent. KNO_3. This is partly due to the interference with growth, partly to geotropic induction. But the growth reaction occurs in 2.5 hours, and the turgor reaction only after 15. Hence the turgor change does not cause the growth reaction. The geotropic movements by motor organs, as has already been sufficiently proved, are due wholly to turgor. The movements coincide in time with the turgor reaction, which appears to be produced by the migration of soluble materials from the concave to the convex side. The turgor differences do not appear on the clinostat, but turgor increases on all sides. In Marantaceae, however, a very slightly heightened turgor was found in curved petioles, and none could be observed in the imperfect organs of Malvaceae.—C. R. B.

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[32] KERSTAN, K., Ueber den Einfluss des geotropischen und heliotropischen Reizes auf den Turgordruck in den Geweben. Beitr. Biol. Pfl. 9:163–213. 1907.

Mendel's law in violet hybrids.—BRAINERD[33] has given an interesting account of the offspring of supposed violet hybrids which show that certain characteristics behave according to MENDEL'S law. The characteristics observed were the color of the capsule, purple vs. green; and the color of seeds, brown vs. buff. The parents of his plants were supposed to be hybrids between *Viola hirsutula* and *V. papilionacea*. With respect to the two characters considered, the supposed hybrids should be di-hybrids. The number of F_2 offspring was only twenty-one, but all four of the possible combinations were present and the larger number showed the two dominant characteristics, purple capsules and brown seeds. Several F_3 families further demonstrated the Mendelian nature of these characteristics. The writer points out that Mendelian behavior in the offspring of the supposed hybrids demonstrates their hybrid character.—G. H. SHULL.

Age of Hepaticae.—CAMPBELL contends[34] that both the Hepaticae and Musci are old types, the perishability of their tissues and insufficient search accounting for the lack of known fossil remains. He finds in the wide distribution of certain genera of Marchantiales and Anacrogynae, and the cosmopolitan distribution of many of their species, evidence of the relative antiquity of the groups, since these plants are not adapted to rapid distribution. In proof of the latter he cites a few experiments, the character of the spores, and the fact that no Hepaticae have been found on Krakatau since the eruption, though Java with an abundant hepatic flora is in sight. Analogy from pteridophyte and spermatophyte distribution is adduced in support of this conception of the significance of bryophyte distribution. The weakness of the case is evident enough, but certainly it is as good as any, if one must speculate.—C. R. B.

Klinostats.—VAN HARREVELD finds[35] by chronographic tests that the klinostats in use at present are all defective in that they do not secure uniform rotation, especially when the axis of rotation is inclined or horizontal and the load is not exactly centered. The modern motor-driven forms are the least objectionable. This inequality of pace leads to definite and unexpectedly large geotropic responses and should therefore be eliminated. To obviate these difficulties, he has constructed an instrument upon new principles. It is driven by a weight automatically raised, and it is released under pendulum control by a rachet actuated by an electromagnet. The intermittent shock of stopping is reduced by vanes and a wheel train. Photographs and drawings are given and a full description is promised when the instrument has been exhaustively tested.—C. R. B.

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[33] BRAINERD, E., Mendel's law of dominance in the hybrids of Viola. Rhodora **9**:211–216. *figs. 2.* 1907.

[34] CAMPBELL, D. H., On the distribution of the Hepaticae and its significance. New Phytol. **6**:203–212. 1907.

[35] HARREVELD, PH. VAN, Die Unzulänglichkeit der heutigen Klinostaten für reizphysiologische Untersuchungen. Recueil Trav. Bot. Néerl. **3**:173 ff. (pp. 144). *pls. 3.* 1907.

Cytology of the ascocarp.—According to FRASER,[36] *Humaria rutilans* (*Peziza rutilans*) shows some interesting features in the origin and development of the ascus. The ascocarp originates as a tangle of hyphae without any differentiated sex organs, but nuclei fuse in pairs and the cells containing the fusion nuclei form ascogenous hyphae. Nuclear divisions in the hyphae show sixteen chromosomes, as do also the first and second divisions in the ascus. These two divisions have the characters of the heterotype and homotype mitoses. The third division in the ascus has eight chromosomes. During the first mitosis in the ascus the two nuclei of the ascus fuse. The spores are delimited by radiations passing from the centrosome, but near the base of the spore vacuoles may take part in the process.—CHARLES J. CHAMBERLAIN.

Fossil cycadophytes.—WIELAND[37] has published a short preliminary account of his examination of some of the most famous specimens of the Mesozoic cycadophytes preserved in European collections. The specimens described are those of *Cycadeoidea etrusca*, *C. Reichenbachiana*, *Williamsonia gigas*, and *Anomozamites minor*. With his long training in the American forms, the author was able to detect features which had escaped previous notice, confirming his results as to the bisporangiate strobilus, the synangial microsporangia, the branching habit, etc. Of special interest are Williamsonia, which links up the Mesozoic with the modern cycadophytes, and Anomozamites, with its slender branching stem, small bladelike leaves, and small strobili, which is more suggestive of the dicotyledons than any known cycadophyte.—J. M. C.

Plant remains in Scottish peat bogs.—In continuing his studies of the Scottish peat bogs, LEWIS[38] has published the results of his investigations in the Scottish Highlands and in the Shetland Islands. Most interesting details are given in reference to the different zones, and the author summarizes the situation in the following statement: "All the Scottish peat mosses [bogs] show a definite succession of plant remains. The oldest, in the south of Scotland and the Shetland Islands, have an arctic plant bed at the base. This is succeeded by a forest of birch, hazel, and alder containing the temperate plants. A second arctic plant bed occurs above the 'lower forest,' and is overlaid in all districts (except the Hebrides and the Shetland Islands) by an 'upper forest' covered by several feet of peat bog plants."—J. M. C.

Blepharoplast and centrosome of Marchantia.—ESCOYEZ[39] has studied mitoses in the spermatogenous tissue of *Marchantia polymorpha* and *Fegatella*

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[36] FRASER, H. C. I., Contributions to the cytology of *Humaria rutilans*. Annals of Botany **22**:35–55. *pls. 4, 5.* 1908.

[37] WIELAND, G. R., Historic fossil cycads. Am. Jour. Sci. IV. **25**:93–101. 1908.

[38] LEWIS, FRANCIS J., The plant remains in the Scottish peat mosses. Part III. The Scottish Highlands and the Shetland Islands. Trans. Roy. Soc. Edinburgh **46**:33–70. *pls. 4.* 1907.

[39] ESCOYEZ, EUD., Blépharoplaste et centrosome dans le *Marchantia polymorpha*. La Cellule **24**:247–256. *pl. 1.* 1907.

conica. The results are different from those of IKENO in regard to the blepharoplast and centrosome. He finds no centrosome in the mitoses preceding the mother cell of the spermatid, and believes that his failure to find one is due to the absence of such a structure and not to any defect in technique. Two blepharoplasts were observed first in the mother cell of the spermatid near the plasma membrane, far from the nucleus. ESCOYEZ does not consider the blepharoplast to be a true centrosome; yet he has not traced its origin, and whether it comes from within the nucleus or from a certain region of the cytoplasm is not settled. —S. YAMANOUCHI.

Sorus of Dipteris.—Miss ARMOUR[40] has studied material of Dipteris that included the younger stages of the sporangium. *D. bifurcata* showed simultaneous development of sporangia in the sorus, and *D. conjugata* sporangia of different ages. The former, therefore, conforms to BOWER'S "Simplices," and the latter to his "Mixtae." The three species seem to make a series in the form of the leaf, with *D. bifurcata* as the most primitive, and *D. quinquefurcata* in an intermediate position; parallel with this is the division of sori, leading to increase in their number and decrease in the number of sporangia in a sorus; and finally there is the progression from the "Simplices" type to the "Mixtae" type. This series is thought to have progressed from such a type as Matonia.—J. M. C.

Morphology of Symplocarpus.—ROSENDAHL has investigated the embryo sac and embryo of Symplocarpus, and an abstract of his results has been published.[41] The primordia of the flowers appear eighteen to twenty months before anthesis, the ovules being "formed" in the season (autumn) preceding pollination. The proembryo is of the massive type characteristic of the aroids, in this case becoming ovoid in form. There is a short suspensor, and the stem tip is organized in a groove of the proembryo which develops near the suspensor. The endosperm encroaches upon both integuments and even into the chalazal tissue; and in turn the massive proembryo ("protocorm") destroys the endosperm, so that finally the embryo is freely exposed in the cavity of the ovary.—J. M. C.

Proteases.—VINES, in his fifth paper on this subject,[42] reports that oily seeds, those of hemp in particular, contain proteolytic enzymes which act vigorously without restraint from the oil present. He succeeded in isolating, for the first time from plant tissues, "a protease that is essentially peptic in its properties, digesting fibrin to albumose or peptone, but not acting on albumose or peptone, whether produced by its own digestion of fibrin or added as Witte-peptone. The facts justify the conclusion that the hemp seed contains two proteases, the one a

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[40] ARMOUR, HELEN M., On the sorus of Dipteris. New Phytologist **6**:238–244. *figs. 11–14.* 1907.

[41] ROSENDAHL, C. O., Embryo sac development and embryology of *Symplocarpus foetidus.* Science, N. S. **27**:209. 1908.

[42] VINES, S. H., The proteases of plants. V. Annals of Botany **22**:103–113. 1908.

peptase, the other an ereptase. He hopes soon to arrive at a general conclusion as to the nature of "vegetable trypsin," which by his admirable researches so far seems resolvable into a peptase and an ereptase.—C. R. B.

Structure of chloroplasts.—This has long been in doubt, the current doctrine being that the ordinary chloroplast consists of a stongy stroma in whose meshes the chlorophyll is held as a green fluid. PRIESTLEY and IRVING show[43] that in the large chloroplasts of *Chlorophytum elatum*, *Selaginella Kraussiana*, and *S. Martensii* the chlorophyll is restricted to a peripheral zone, probably less than 1μ thick, where it is held in the meshes of a spongy stroma. This agrees with the arrangement theoretically best according to TIMIRIAZEFF. The authors also confirm the neglected observations of NÄGELI and TIMIRIAZEFF on the splitting of the chloroplasts in solutions of low osmotic pressure.—C. R. B.

Morphology of wheat.—ARTHUR H. DUDLEY,[44] in a presidential address before the Liverpool Microscopical Society, presented an account of floral development, sporogenesis, and embryogeny in wheat. A summary of his results is as follows: the archesporium of the microsporangium is a single row of cells, two or three divisions occurring before the mother-cell stage is reached; the archesporial cell of the megasporangium does not cut off a parietal cell, but produces directly the linear tetrad, the reduction number of chromosomes being eight; a large development of antipodal tissue occurs; and the embryo is said to be derived from the "apical cell only" of the proembryo.—J. M. C.

Scion and stock.—GUIGNARD has made another attempt to settle the question whether compounds peculiar to either scion or stock are able to migrate past the point of grafting.[45] When a plant which contains an HCN-glucoside is grafted on a plant which contains none, or conversely (GUINARD used *Phaseolus lunatus*, *Photinia serrulata*, and five species of Cotoneaster), there is no transfer of this glucoside in either direction. This adds one more bit to the negative evidence that is accumulating against the uncertain positive claims of such migration. The paper contains a good history of the question.—C. R. B.

Tolerance for salts.—Continuing their work on the relation between alkali soils and vegetation, KEARNEY and HARTER, testing pure solutions of various salts, find[46] that different species and even different varieties of the same species differ considerably in resistance to the action of magnesium and sodium salts.

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[43] PRIESTLEY, J. H., and IRVING, ANNIE A., The structure of the chloroplast considered in relation to its function. Annals of Botany **21**:407–413. *figs. 2.* 1907.

[44] DUDLEY, ARTHUR H., Floral development and embryogeny in wheat. Report Liverpool Micros. Soc. 1908 1–19. *pls. 1, 2.*

[45] GUIGNARD, L., Recherches physiologiques sur la greffe des plants à acide cyanhydrique. Ann. Sci. Nat. Bot. IX. **6**:261–305. *figs. 9.* 1907.

[46] KEARNEY, T. H., and HARTER, L. L., The comparative tolerance of various plants for the salts common in alkali soils. U. S. Dept. Agric., Bur. Pl. Ind., Bull. 113. pp. 22. 1907.

Seedlings grown from fresh seed are much more resistant than those from older seed. By different experimentation they confirm the findings of other observers as to the power of calcium salts (they speak of sulfate) to offset the toxic action of magnesium and sodium salts.—C. R. B.

Edwin James.—Students of taxonomy will be interested in a recent paper by PAMMEL,[47] which gives an account of Dr. JAMES, whose name is so intimately associated with the early explorations of the Rocky Mountain region. Not only numerous plants, but also a mountain peak bears his name, though the latter is now better known as Pike's Peak. Through papers found in the Parry herbarium, local biographical sketches, and information obtained directly from relatives, a very satisfactory account has been prepared, and the personality of JAMES is thus rescued for botanists.—J. M. C.

Conifers of China.—The late MAXWELL T. MASTERS left a paper on the distribution of conifers in China, which has just been published.[48] The total number of species known from China at the time of writing (June 20, 1907), inclusive of Formosa, was 87, distributed among 23 genera. In one table China and Japan are compared; the former containing 87 species, of which 42 are peculiar; the latter 48 species, of which 15 are peculiar. A large table shows the distribution of all the native species of China in the various regions of the empire as well as in neighboring countries.—J. M. C.

Nuclear division in Basidiobolus.—OLIVE[49] has studied nuclear and cell division both in the beaks and in the vegetative cells of Basidiobolus. The spindle is broad, cylindrical, barrel-shaped, and intranuclear. At the equatorial plate stage it shows three darkly staining regions, the chromatin plate at the center and two pole plates at the ends. The wall is formed as a ring, which begins at the periphery of the cell and closes in like an iris diaphragm, as in many algae, a mode of growth quite different from that described by FAIRCHILD in 1897.—CHARLES J. CHAMBERLAIN.

Variegation and infectious chlorosis.—Those who are interested in these problems will find useful an extensive paper by LINDEMUTH,[50] which embodies a precise and comprehensive exposition of the results of his studies on variegation, which go back as far as 1870, and have been continued with more or less vigor to

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[47] PAMMEL, L. H., Dr. Edwin James. Annals of Iowa **8**:161–185, 277–295. 1908. Also distributed as a separate.

[48] MASTERS, MAXWELL T., On the distribution of the species of conifers in the several districts of China, and on the occurrence of the same species in neighboring countries. Jour. Linn. Soc. Bot. **38**:198–205. 1908.

[49] OLIVE, E. W., Cell and nuclear division in Basidiobolus. Annales Mycol. **5**:404–418. *pl. 10.* 1907.

[50] LINDEMUTH, H., Studien über die sogenannte Panaschüre und über einige begleitende Erscheinungen. Landw. Jahrb. **36**:807–862. *pls. 8, 9. figs. 16.* 1907.

the present time. The paper includes a summary of many scattered contributions, and makes it clear that he had recognized, much earlier than BAUR, the infectious character of certain forms of variegation. He contends, rightfully, that chlorosis is an inept term.—C. R. B.

Sap rot of red gum.—VON SCHRENK[51] describes diseases due to fungi which infect the sapwood of red gum (Liquidambar) when the logs lie in the forest while wet, and continue to spread, to the destruction of the lumber when cut. *Polyporus adustus*, *Polystictus hirsutus*, and *Poria subacida* are the most frequent enemies, but there are a number of others. Sap rot may be prevented by hastening the drying or by coating the ends of the logs as soon as cut with hot coal tar. Similar diseases injure the heartwood of red gum and also affect the swamp oak and maple.—C. R. B.

Cytology of Microsphaera.—SANDS[52] has shown that during all stages in the life-history of Microsphaera a central body is differentiated as a permanent nuclear structure, which serves as a point of attachment for the chromatin. It is always extranuclear, never intranuclear, as claimed by MAIRE and GUILLIERMOND. The delimitation of spores is accomplished by the astral rays persisting from the third mitosis in the ascus. The work in this respect supports the conclusions of HARPER rather than those of FAULL.—CHARLES J. CHAMBERLAIN.

Morphology of Cornus florida.—MORSE[53] has investigated *Cornus florida* and found the following facts: the male gametophyte passes the winter in the two-celled stage; no walls separate the nuclei of the linear megaspore tetrad; the embryo sac probably passes the winter in the eight-nucleate stage, which persists until the last of May, when pollination occurs; the synergids are slender cones projecting far into the micropyle; the endosperm tissue is formed first in the micropylar end of the sac, and by the middle of July completely fills the sac.—J. M. C.

Fossil flora of Florissant.—COCKERELL[54] has enumerated the known flora of the Florissant shales (Miocene), including 106 genera, 45 of which occur in Colorado today. Of the genera not occurring now in Colorado, 36 occur in our eastern and southern states, the conclusion being reached that a flora similar to that of the Carolinian region occupied the Rocky Mountains during the Miocene. About 50 new species are described, including a Chara, a fungus, four ferns, and two gymnosperms.—J. M. C.

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[51] VON SCHRENK, H., Sap rot and other diseases of the red gum. U. S. Dept. Agric., Bur. Pl. Ind., Bull. 114. pp. 32. *pls. 8.* 1907.

[52] SANDS, M. C., Nuclear structure and spore formation in *Microsphaera alni.* Trans. Wis. Acad. Sci. 15:733–752. *pl. 46.* 1907.

[53] MORSE, WILLIAM CLIFFORD, Contribution to the life history of *Cornus florida.* Ohio Naturalist 8:197–204. *pl. 14.* 1907.

[54] COCKERELL, T. D. A., The fossil flora of Florissant, Colorado. Bull. Amer. Mus. Nat. Hist. 24:71–110. *pls. 6–10.* 1908.

Trees and shrubs.—The second part of the second volume has followed[55] the first part promptly, and is devoted to species of Crataegus and Viburnum. SARGENT describes 10 new species of Crataegus, 7 of which are from Missouri; while REHDER presents and illustrates 13 species of Viburnum from China and Japan, 3 of which are new. The species of Viburnum are followed by a synopsis of the genus as displayed in eastern Asia, 65 species being recognized under 9 sections, and 9 of these species are new.—J. M. C.

Cytology of geotropism.—GEORGEVITCH contributes little that is new by his study of the cytology of roots of *Lupinus albus* when stimulated by gravity.[56] He correlates, much as NĚMEC did, though with differences in detail, the aggregation of the protoplasm and the position of the nucleus with geotropic stimulation, and so practically settles the fact that there are observable differences in the cell contents of normal and stimulated roots. It is not possible, however, to say what these mean.—C. R. B.

Sexuality in Ceratiomyxa.—OLIVE[57] has shown that the cleavage of the plasmodium of Ceratiomyxa to form spores is progressive and not simultaneous, as claimed by FAMINTZIN and WORONIN. Toward the close of the cleavage stage there is a fusion of nuclei in pairs, followed almost immediately by synapsis and two rapidly succeeding divisions, which are regarded by the author as reduction divisions, and give rise to four-nucleate spores.—CHARLES J. CHAMBERLAIN.

Dumortiera autoicous.—ERNST reports in a preliminary paper[58] that Javanese material of *Dumortiera trichocephala* (commonly) and *D. velutina* (sparingly) have both antheridia and archegonia on the same receptacle, though on different lobes. A single instance of the same thing has been observed (hitherto unpublished) by Dr. W. J. G. LAND, of the University of Chicago, in Mexican material of *D. hirsuta* collected at Xalapa, V. C.—C. R. B.

Anatomy of Isopyrum.—HOLM[59] has added *Isopyrum biternatum* to his anatomical records, including with the anatomical details a discussion of geographical distribution and generic limitations.—J. M. C.

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[55] SARGENT, C. S., Trees and shrubs. Illustrations of new or little known ligneous plants, prepared chiefly from material at the Arnold Arboretum of Harvard University. Vol. II. Part. II. pp. 57–116. *pls. 126–150.* Boston and New York: Houghton, Mifflin, & Co. 1908. $5.00.

[56] GEORGEVITCH, PETER M., Cytologische Studien an den geotropisch gereizten Wurzeln von *Lupinus albus*. Beihefte Bot. Cent. **22**^{1}:1–20. *pl. 1.* 1907.

[57] OLIVE, EDGAR W., Cytological studies on Ceratiomyxa. Trans. Wis. Acad. Sci. **15**:753–773. *pl. 47.* 1907.

[58] ERNST, A., Ueber androgyne Inflorescenzen bei Dumortiera. Ber. Deutsch. Bot. Gesells. **25**:455–464. *pl. 13.* 1907.

[59] HOLM, THEO., *Isopyrum biternatum* T. & G.; an anatomical study. Am. Jour. Sci. IV. **25**:133–140. *figs. 3.* 1908.

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CONTENTS

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AUGUST 1908

FLORAL SUCCESSION IN THE PRAIRIE-GRASS FORMATION OF SOUTHEASTERN SOUTH DAKOTA

THE PREVERNAL, VERNAL, AND ESTIVAL ASPECTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 113

LEROY HARRIS HARVEY

(WITH THREE FIGURES)

The western part of Iowa, the eastern and northeastern counties of Nebraska, and southeastern South Dakota lie in the drainage basin of the Missouri. This tri-state area is well within the prairie region of that vast and far-reaching prairie province of the middle west. This area is only a part of the Ponca District of POUND and CLEMENTS,[1] being more strictly Dakotan than Nebraskan, and may be considered as representing a transition between the more mesophytic eastern areas of Iowa and those dominantly xerophytic somewhat to the west, with which it shows the closer floristic agreement. Its composition is thus twofold, pointing to the primitive and more xerophytic stages of the past and at the same time prophetic of the mesophytic stages to come. This aberrant character links it strongly to the xerophytic prairie to the west and southwest, from which it is genetically descended, and the prophetic character links it to the more mesophytic prairie of western Iowa, which has encroached ever westward. Under this migration tension from the southeast and east the primitive prairie has retreated, civilization always being a potent factor in this succession.

Study began in this tri-state region in the fall of 1903 at Sioux City, Iowa, and was carried on during that fall and the next summer

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[1] POUND, R., and CLEMENTS, F. E., Phytogeography of Nebraska. 1900.

in the contiguous portions of Iowa, Nebraska, and South Dakota. In the fall of 1904, Yankton, South Dakota, became the base station, and for the next three seasons (1904–1907) the work was carried on from that point. During this period the greater part of South Dakota east of the Missouri was visited, and repeated trips were made into contiguous Nebraska and into Iowa, while at the same time detailed study of a restricted area was being prosecuted. This local area upon which study has been focused lies in the township of Yankton and embraces about 49 hectares, being a rectangular strip 1210^{m} north and south by 405^{m} east and west. The topography is uneven and comprises a series of prairie knolls and slopes, separated into two groups by a gentle drainage valley which traverses it in a southwest and northeast direction. The knolls are low and their slopes gentle, scarcely higher than 10 or 15^{m}, with a gradient never exceeding 30 or 40°. The entire area is largely underlaid by glacial gravel and clayey till. The former mainly constitutes the knolls—the humus is here the most shallow, averaging only about 15 to 20^{cm} in depth. Off from the knolls on the level the humus caps the deposit of clayey till. On the lower erosion slopes (25 to 30^{cm}) and in the drainage valley (60^{cm} plus) the humus has accumulated to a greater depth, sufficient in the latter to bury the till beyond the zone of root activity. The humus is in all cases till or gravel modified by atmospheric, organic, and biotic agencies.

To insure uniformity the nomenclature of BRITTON and BROWN'S *Illustrated flora* has been followed, except where it has conflicted with the verification of grasses made for me through the United States Department of Agriculture by Mr. PERCY L. RICKER and Mr. D. A. BRODIE, to whom I am greatly indebted for this courtesy.

This problem has been carried on under the direction of Dr. HENRY C. COWLES, to whom I wish to acknowledge my indebtedness for many valuable suggestions and criticisms during the progress of the investigation.

Geology and topography

To appreciate fully existing conditions, an epitome of the post-Cretaceous geological development of the region is necessary. The Cretaceous was terminated by that great uplift and crustal movement which formed the Rocky Mountains and gave birth to the major features of the Missouri valley drainage. This movement particularly affected this region by elevating it from an estuary condition to a point considerably above sea-level, and even probably many feet above its present level. This uplift inaugurated a period of vast erosion, and before the advent of the ice the Missouri had cut its present great valley at least 20 to 25^m below its present level.

With the Pleistocene came the glaciers. While doubtless there were five periods of glacial advance and recession in the region, we need concern ourselves now only with the second, the Kansan, which spread from the Keewatin center and deposited over this entire region the Kansan drift sheet, obliterating the questionable pre-Kansan. The Illinois, Iowan, and Wisconsin epochs followed successively, only the latter reaching into southern South Dakota, where a lobe of the Altamont moraine pushed down between the Big Sioux and Missouri Rivers, reaching approximately to Vermillion, South Dakota.

The Kansan must have seriously interfered with the established preglacial drainage, greatly rejuvenating it, at least along minor lines. It seems probable also that subsequent erosion mainly sought out previous lines, largely reestablishing the post-Pliocene drainage system. The Wisconsin likewise disturbed and caused a readjustment of this drainage system, which could have differed but little from that previously worked out in the Kansan. Upon this readjustment of the post-glacial Wisconsin drainage topography, there followed the deposition of that much mooted deposit, the loess.

The region divides itself naturally into two great topographic types, the rolling upland prairie and the flood plain, which cuts the prairie in a general northwest and southeast direction. On either side the flood plain is limited by the escarpments of the Missouri. From this flood plain extend the minor flood plains of its tributaries, further dissecting the upland. The vast valley is cut out from 25 to 50^m deep in the upland and presents a flood plain varying from a narrow terrace to frequently 10^{km} in width.

The upland now presents an almost perfectly developed erosion topography, predetermined in the Kansas drift sheet and subsequently veneered by the Wisconsin drift and loess deposit. The latter, which frequently has a depth of 50^m to the south of the Wisconsin drift area, thins out northward. The escarpment bluffs are steep and high, but pass back into a complex of gently rounded, semi-detached hills, which present a sinuate or undulating sky line of jumbled peaks; it is a vast mountain system in miniature. Back a few miles from the bluffs these hills pass imperceptibly into the low, rolling prairie hills, which extend with scarcely a variation in either direction. So perfectly is this tributary drainage system established that upon the prairie swamps and "sloughs" rarely occur. The small streams which have threaded the upland are characterized by ravines of depth and precipitousness, especially in the loess, where they usually end abruptly in a bluff, again dividing the upland into a series of ridges, intricately related, which pass back into the low, rolling hills of gentle profile.

Origin of the prairie

The uplift of the Rocky Mountains, which terminated the Cretaceous, introduced a modifying element which exercised an ever-increasing influence upon the climate of the Great Plains region. Intercepting the eastward-moving moisture-laden winds from the Pacific, a decrease in the annual precipitation to the east of the range must of necessity have followed. The greatest reduction would have been nearest the mountains, decreasing to the eastward. When this interior continental land was finally left by the interior sea and opened to migration, invasion must have been in large degree controlled by this graduated distribution of rainfall. The subsequent origin of the Cascades could have served only to accentuate this distributional difference and reduction in precipitation. Under such conditions the Tertiary phytogeographical distribution of this central region must have been adjusted. Whatever the source, it would seem highly probable that while the entire Mississippi valley was occupied by the rich Tertiary forest, the region lying to the west and bounded by the Rocky Mountains and extending northward into Assinaboia was, on account of the low precipitation, denied to tree invasion and came to be occupied by a prairie formation, increasing in its xerophytism westward just as it does today.

Toward the close of the Tertiary (late Pliocene) fossil evidence points conclusively to climatic change. A retrogressive succession of floral waves swept southward under the influence of the gradually falling temperature of the Pleistocene. In this glacial movement, the plains region, unable to support tree growth, acted as an entering wedge, causing an east and west divergence. One wing of the migration, dominantly coniferous, followed the Rocky Mountains southward; the other, typically deciduous, sought the Mississippi and its tributary valleys as a migration track; while the prairie moved directly toward the Gulf. At the time of maximum ice advance the descendants of the Tertiary forest were mobilized in the southern Appalachians about the Chattanooga region as a center (ADAMS **:02**), while the prairie formation concentrated in the southwestern United States, with a possible center in the region of northeastern Texas and eastern Oklahoma and southern Kansas.

With final glacial retreat from this region and subsidence of the glacial sea, migration tension was removed and distribution tension became active. The life waves now in succession rolled northward. The content of our flora demands a consideration of the third wave only. A study of the floristics shows indisputably the commingling of forms of diverse geographical affinity. An unmistakable floristic relation, in many cases specific, exists with a southwestern and southeastern center of post-glacial dispersal.[2] To the east and southeast the deciduous forest type becomes increasingly characteristic, while to the west and southwest the plain or prairie type gradually predominates; the region thus lies in the western border of the tension zone in which migration from these two competing centers of distribution meet. From the southeast the dispersal route has been up the Missouri valley; while the northwestern migration has spread diagonally across natural drainage lines, following the upland plains.

Forest invasion of the prairie

When the arborescent elements of the southeastern biota, migrating up the valleys of the Mississippi and of the Missouri and its tribu-

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[2] BESSEY (**'99**, p. 82) says: "There are 66 or 67 species of native trees in Nebraska, and 56 or 57 have advanced to the state from the southeast." MACMILLAN (**'92**, pp. 653, 721) has shown that 66 per cent. of genera indigenous to the Minnesota Valley are eastern and 62 per cent. southern, while 32.5 per cent. of the total species are of southeastern origin. Of the native trees of South Dakota at least 75 per cent. show indubitable southeastern affinities. The presence of such genera as Opuntia, Cactus, Yucca, Mentzelia, Croton, Bouteloua, Bulbilis, Lygodesmia, and Aplopappus strongly bespeaks the southwestern alliance.

taries, reached the prairie region they were unable to occupy the high lands, but occupied the flood plains and adjacent slopes. There is no evidence to indicate that the then existing topographical and climatic conditions differed radically from those of today. Again these elements have today their most widespread distribution, a condition at once intelligible when related to physiographic development in the working-back of streams and the increase of flood plain. Two salient points may now be noted: the initial and the continuous subsequent preemption of the upland by the prairie formation, and secondly the continuation of initial climatic conditions. The initial causes which operated to restrict tree invasion and ecesis upon these prairie-covered uplands would thus seem to have their duplication in those natural factors which operate to that end at the present time.

Under the discussion of ecological factors of the region it will be shown that there is a coincidence of factors operating most antagonistically against tree growth upon the upland. The almost entire absence of fungi upon the prairie cannot but be significant. The roots of most of these deciduous trees are obligatively provided with symbiotic mycorhiza and the absence of their specific fungus would preclude advance. Hence fungal infection of the prairie soil must precede or at least accompany forest encroachment. Again, the difficulty of seed germination, almost impossible either because of a dense sod or a lack of soil moisture, successfully checks invasion. In consideration of these precarious climatic factors, peculiar edaphic conditions, and the fact that if planted upon the prairie trees thrive, I am led to the view that the question of non-invasion upon the prairie proper is primarily and initially one of pre-occupation and the inability of seedlings successfully to withstand the extremely severe conditions of the first winter's exposure. In the positive and coincident interaction of unfavorable biological and climatic conditions may be found a cause sufficient to account for tree absence upon the prairie and the slow migration of tree species into this region.

While these causes are all sufficient, yet we must not disregard a secondary and artificial though highly cooperative factor, which in recent times must have served in many places to prevent tree establishment. I refer to prairie fires; yet even in the absence of prairie fires for half a century the prairie stands uninvaded except in cases of physiographic development (BESSEY '99). And again, as the prairie existed as a climatic formation long before these fires, either of Indian or Caucasian origin, swept the prairies, it would appear that this fire factor has been overestimated by many and is in no sense to be regarded as the fundamental factor. That there is, nevertheless, an extremely slow advance of the forest usually through the medium of its forerunner, the shrub association, whose pioneer *Symphoricarpus occidentalis* is followed by *Rhus glabra*, is very evident.

While the above factors are seemingly adequate to account for tree absence upon the western upland prairie, yet in light of the prairie as a natural climatic formation it would seem more proper to make the problem one accounting for the occasional presence rather than the general absence of trees. A future paper is planned to discuss the factors controlling this encroachment.

The period of growth resumption

Not until about the first week in March are climatological conditions at all favorable to an awakening of vegetation, and then only on infrequent days; but the month as a whole is marked by the opening of flower and leaf buds of trees and the beginning of the germination of prevernal annuals and the formation of the basal rosettes of the perennials, though some tide over from the previous season. The prevernal bloomers naturally make most rapid progress, aided by their geophytic habit. Not infrequently the temperature falls below freezing and killing frosts ordinarily result. Light snow storms, which rarely occur, may temporarily retard growth. The conditions become progressively more favorable and pass insensibly into the period of the prevernal flowers.

The usual snows and rains of the early part of the month assure abundant moisture. The chresard, which is about 18 to 20 per cent. in the early days of the month, decreases to about 14 per cent. at the middle, and to about 12 per cent. toward the last of the month, thus giving an average chresard of some 15 per cent. The different exposures of the prairie hills, knolls, and ravines progressively recover from the effects of winter in the following order: southeast to southwest, southwest to northwest, northeast to southeast, and northwest to northeast. The frost clings to the northern exposure in ravines, only leaving toward the latter part of the month, particularly when this exposure is forested. On March 16 on a northwest exposure of a prairie knoll the frost was recorded at the following depths: at base of slope 13.97^{cm}, at middle of slope 30.48^{cm}, at crest considerably below 35^{cm}. Thus the base of the exposure recovers much more slowly than the crest, a condition holding equally true for all exposures; hence vegetation starts earlier upon the upper slopes. However, the chresard increases toward the base of the slope. On March 16 the slope in question showed a chresard at the crest of 7.1 per cent., at the middle of 14.1 per cent., and at the base of 18.2 per cent., the differences being more pronounced and the chresard greater than in any subsequent aspect.

The physical conditions of the period are shown in the adjacent table.

TEMPERATURE*			WIND*			RAIN*			LIGHT*			SOIL§			Mean relative humidity†	Relative evaporation‡
Maximum	Minimum	Mean	Prevailing direction	Total movement	Hourly velocity	Days	Mean daily	Total	Relative¶ intensity	Mean cloudiness	Sunshine per cent.	Mean holard	Mean echard**	Mean chresard		
22° C.	−17 C.	2° C.	N. W.	7666	10.3	8	.11cm	3.35cm	.459	5.2	51	21.3%	7.2%	14.7%	75.2	.510

* Data from Yankton, United States Weather Bureau, being the means of ten years (1894–1904). The nearness of the station to the field makes the data very representative.

† Data from Sioux City, United States Weather Bureau, being the mean of 8 A. M. and 8 P. M. observations from July 1, 1889, to December 31, 1903. The station is about 30 miles south of Yankton.

‡ Relative evaporation is determined by the formula: R.E. = saturation deficit × average hourly wind velocity × mean temperature centigrade ÷ 1000. It is recognized that such a result is by no means quantitative, yet it may well serve relatively as an index, invaluable in contrasting the floral aspects.

§ Soil data all from station B, Solidago slope, N. W. exposure. For technique see CLEMENTS, Research methods in Ecology. 1905.

¶ Relative light intensity equals sunshine per cent. of theoretical maximum light intensity as determined for Yankton by method of sun's altitude.

** Determined from an experiment on the Windsor bean. It will be used as an index of the non-available water. The chresard is then directly computed from the holard.

Prevernal floral aspect

Floral activity begins only in the first week of April, and is characterized by the slow and progressive flowering of six forms, extending up to the last week in April, when an apparent break in floral continuity occurs, no forms flowering for a week or ten days. This break very naturally segregates the prevernal floral aspect.

In addition to the floral forms this aspect is conspicuous as the time of appearance of the rosettes of the vernal, serotinal, and autumnal perennials, and seedling annuals of these same aspects. No facies is established, and the tone of the formation is that of winter and early spring, mainly produced by the standing brown stalks of *Solidago rigida*, *Helianthus scaberrimus*, and *Verbena stricta* of the autumnal aspect, which gives everything a brownish cast, enlivened here and there by the mats of *Antennaria campestris* and *A. neodioica*, and at the base of slopes and in depressions by the green of *Poa pratensis* sod. At the base of slopes now and then are to be seen clumps of green produced by the unfolding leaves of colonies of *Symphoricarpus occidentalis*. To complete the aspect, dotted here and there are the floral forms which characterize it. Ruderal species are noticeably absent.

The pertinent climatological conditions of the prevernal floral aspect may be obtained directly from the adjacent table. On only 63 per cent. of the days does the mean average temperature rise above 6° C., with a range between −6° and 29° C. Coupling this with an average soil temperature of 13° C., growth conditions are seen to be far from favorable. The prevailing wind direction is northwest and with a mean

PREVERNAL CLIMATOLOGY

TEMPERATURE			WIND			RAIN			LIGHT			SOIL			MEAN RELATIVE HUMIDITY	RELATIVE EVAPORATION
Maximum	Minimum	Mean	Prevailing direction	Total movement	Hourly velocity	Days	Mean daily	Total	Relative intensity	Mean cloudiness	Sunshine per cent.	Mean holard	Mean echard	Mean chresard		
29 C.	−6° C.	11° C.	N. W.	7919	11	10	.26cm	7.87cm	.547	4.7	63	20%	7.2%	12.8%	63.7	4.392

hourly velocity of 11 miles, which is not exceeded during the other aspects. Precipitation is slight (7.87^{cm}) and falls on only about 33 per cent. of the days. The average cloudiness of the sky (4.7) is low, and the sunshine (63 per cent.) is correspondingly higher, resulting in a low light intensity (0.547). The saturation deficit is here not at its maximum (36.3), but, augmented by the high wind velocity, evaporation, which must necessarily serve as a rough comparative index of transpiration, is rising in amount. While far more favorable for vegetation, it becomes progressively more so, the last half of the aspect presenting conditions in soil and air noticeably more congenial to growth. The chresard decreases steadily during the aspect from 14.8 per cent. on April 17 to 12.2 per cent. on April 25, and a marked difference in holard was evident at crest (15.8 per cent.), slope (18.4 per cent.), and base (22.6 per cent.) on April 18. The average chresard is 12.8 per cent.

SPECIES OF THE PREVERNAL ASPECT

FACIES.—None.

PRINCIPAL SPECIES.—Antennaria campestris,† Carex pennsylvanica,† Peucedanum nudicaule,† Pulsatilla hirsutissima.*†

SECONDARY SPECIES.—Astragalus crassicarpus,† Peucedanum foeniculaceum,* Draba micrantha, Ranunculus ovalis.

* Not occurring in area proper but in vicinity. † Forming associations.

The earliest flowering form is Pulsatilla and occurs copiously to subcopiously and characteristically upon the upper slopes of the prairie hills. It appears several days earlier upon the south to southwest exposure, which holds equally true for the other prevernal bloomers. The early warming-up of this exposure accounts for the above phenological precocity. But the greatest abundance of these prevernal forms occurs on the north to northeast exposure. Maturation follows close upon anthesis, which likewise holds for all prevernal flowering species.

Pulsatilla is followed by the blooming, during the first week of April, of *Peucedanum foeniculaceum* and *P. nudicaule*. The former with its umbel of yellow flowers is of rare occurrence; but the latter with its umbel of white flowers appears even copiously in restricted plats, and in its distribution occurs mainly upon the upper xerophytic slopes of prairie knolls where the grasses are bunched and the association more or less open, though rarely seen at the crests; it thus not infrequently exerts a subtone effect at short range. It is perennial by means of its geophytic root. With the elongation of its peduncle and spreading of its umbel in maturation during the last week of the aspect, it becomes more conspicuous and persists thus far into the vernal aspect.

The beginning of the second week of the prevernal aspect sees *Carex pennsylvanica* in full bloom. It occurs copiously, extending well up to the crests of knolls, but more abundantly on lower slopes, yet never influences the tone of the aspect. In places Carex may assume almost facial rank, but always maintains a bunchy or isolated distribution, which, however, is quite general. The peculiar yellowish-green shade of its leaves and its yellow staminate spikes which appear after the stigmas make it conspicuous. It is a perennial of xerophytic tendencies, propagating itself by rootstocks and stolons.

Carex is shortly followed by the flowering of *Antennaria campestris*, and with its white tomentose leaves, scapes, and papillate heads, it gives a characteristic local tone to this floral aspect, even from a distance. It occurs usually gregariously, being one of the two mat-forming species of the formation, and is very generally distributed throughout, facilitated by its perfect adaptation to wind dispersal. The mats themselves may be isolated or gregarious, as many as twenty having been noted in a plat of $64^{\mathrm{sq\,m}}$, yet single mats frequently cover $16^{\mathrm{sq\,m}}$, averaging about 1000 plants to the square meter. Propagation is by stolons and migration is centrifugal, with a slow but positive occupation. Mats unite and take complete possession of extensive plats, yet it yields before *Poa pratensis*, in no way being able to hold its own against this sod-forming mesophyte.

The prevernal floral aspect of the formation is terminated by the appearance of *Ranunculus ovalis*, *Astragalus crassicarpus*, and *Draba micrantha* toward the end of the third week of April. They appear in bloom almost simultaneously, but in no way contribute equally to the aspect. Draba occurs only where the soil is exposed and the grass is bunched, hence on upper xerophytic slopes, and appears to be forced out whenever a close association is formed. It is an annual of marked xerophytic tendencies, its leaves being basal and heavily pubescent with stellate hairs. It is scarce and its small white flower inconspicuous, so in no respect does it influence the floral tone. Ranunculus is even more restricted, occurring sparsely on lowest slopes and in depressions on the higher slopes, and is apparently related to a high water content of the soil. Its yellow petals soon fall, and its presence might easily be overlooked in a casual survey of the formation. It is a perennial and is an index of mesophytic conditions. Astragalus, with its racemes of violet-purple flowers, is easily marked in the formation. While generally distributed, its abundance is sparse to subcopious, yet frequently it assumes a gregarious habit. It is a perennial of thickened tap roots which branch above and eventually fragment behind, establishing new individuals. Its migration is slow; dispersal is effected mainly by gophers, which store the fruits for winter consumption. However, ecesis is very certain.

Vernal floral aspect

Toward the last of the first or the beginning of the second week in May there is a floral outburst inaugurated by the blooming of *Nothocalais cuspidata* and *Lithospermum angustifolium*, closely followed by *Castilleja sessiliflora*, *Lithospermum canescens*, *Viola pedatifida*, and *Oxalis violacea*, which marks the inception of the vernal floral aspect. Forms are now progressively added up to about the first week of June, when the aspect is distinctly terminated by the general blooming of certain sod-formers. *Astragalus crassicarpus* and *Ranunculus ovalis* have extended over into this aspect, the former reaching its maximum flowering about the second week in May, thus entering conspicuously into the vernal period. The fruiting scapes of *Peucedanum nudicaule* enter into the tone, while *Antennaria campestris* with its white fruiting heads is now more noticeable than earlier. The deadened brown tone of the prevernal aspect is at last relieved and replaced by the green of the grassy sod, which is rendered somewhat bizarre by the very general distribution of some twenty-eight flowering forms, the largest number occurring in any aspect. No floral facies is developed except in the case of *Poa pratensis* at the base of slopes, and then only in the later part of the aspect. Most of the prairie annuals have by the later part of the aspect appeared and those of the following aspect are now all ready to bloom. Much growth has taken place in the summer perennials and they have apparently outstripped the autumnal forms. Together they overtop the majority of the vernal group, and toward the end of the aspect the large cauline leaves of Solidago and Helianthus of the autumnal aspect render many of the low-statured bloomers quite hidden, except in the very open associations on the highest slopes and crests. Four ruderals bloom in this aspect but have little influence on the formation.

The summary clearly indicates the significant climatological facts. Physiological activity ensues practically throughout the aspect; the temperature range of 31° C. to 2° C., with a mean of 16° C., rarely inhibiting growth. The wind is dominantly from the south and east quarters. It reaches during this aspect a less total movement and so a less mean hourly velocity than in the prevernal, but the atmosphere has a much lower relative humidity; the relative evaporation is thus nearly twice as great. Couple this with the highest light intensity (.704) and the beneficial results of 8.19^{cm} of precipitation on twelve days are much reduced. The chresard shows a marked decrease from 14.1 per cent. on May 10 to 7.4 per cent. on May 22, though the average chresard for the aspect is 10.7 per cent. The base (12.7 per cent.), slope (14.6 per cent.), and crest (8.8 per cent.) on May 22 still showed a gradation in holard, though the distinction of position is less marked than in the prevernal aspect.

VERNAL CLIMATOLOGY

TEMPERATURE			WIND			RAIN			LIGHT			SOIL			MEAN RELATIVE HUMIDITY	RELATIVE EVAPORATION
Maximum	Minimum	Mean	Prevailing direction	Total movement	Hourly velocity	Days	Mean daily	Total	Mean cloudiness	Sunshine per cent.	Relative intensity	Mean holard	Mean echard	Mean chresard		
31 C.	2 C.	16 C.	E.	6877	9.2	12	$.26^{cm}$	8.19^{cm}	5.2	73	.704	17.9%	7.2%	10.7%	51.7	7.109

SPECIES OF THE VERNAL FLORAL ASPECT

FACIES.—Poa pratensis† (base of slopes and in depressions).

PRINCIPAL SPECIES.—Spiesia Lamberti sericea, Sisyrinchium angustifolium†, Antennaria campestris,*† Spiesia Lamberti, Castilleja sessiliflora.†

SECONDARY SPECIES.—Viola pedatifida,† Oxalis violacea,† Lithospermum canescens, Carex Meadii,† Meriolix serrulata, Hedeoma hispida, Plantago Purshii,† Antennaria neodioica,† Lithospermum angustifolium, Oxalis stricta, Carex festucacea,† Polygala alba, Poa compressa,† Astragalus crassicarpus.*†

TERTIARY SPECIES.—Pentstemon gracilis, Nothocalais cuspidata, Linum rigidum, Lappula texana, Astragalus plattensis, Gaura coccinea, Senecio plattensis, Psoralea esculenta, Vicia linearis, Osmodium molle, Astragalus hypoglottis, Viola cucullata.

RUDERAL SPECIES.—Lepidium virginicum, Melilotus officinalis,† Melilotus alba,† Lappula Lappula.

* From earlier aspect. † Forming associations.

The first week in May is marked by the flowering of *Nothocalais cuspidata* and *Lithospermum angustifolium.* The solitary yellow head of the false calais, frequently 5^{cm} in width terminating a long (20 to 30^{cm}) naked scape, makes it very conspicuous, though it is never more than sparse to subcopious. It is largely confined to loosely sodded ridges and high slopes, and is pronouncedly of xerophytic tendencies. It is perennial by an excessively thickened root. The achenes are heavily provided with pappus, assuring a wide dissemination.

Nothocalais has scarcely bloomed before the puccoons are in flower, *L. angustifolium* appearing several days before the hoary puccoon (*L. canescens*). The former with its terminal leafy racemes of light-yellow flowers and its sparse occurrence remains an inconspicuous element. The hoary puccoon occurs throughout with the other, but more abundantly. Its orange-yellow flowers in a compact leafless umbel make it perhaps the most conspicuous though it is not the most abundant element in the vernal aspect. Both of the puccoons are abundantly pubescent and in their structure and distribution show marked xerophytic tendencies. They are perennials by deep thick roots. The smooth nutlets preclude all but a very limited migration.

Castilleja sessiliflora, Viola pedatifida, Oxalis violacea, Sisyrinchium angustifolium, and *Spiesia Lamberti sericea* bloom progressively during the second week of the aspect, and together produce a very noticeable change in the floral tone, a change which is further accentuated by the forms that occur later. The yellow tone given by the puccoon becomes dotted here and there by yellow, blue, violet, white, and purple, and a bizarre tone is the result. Castilleja occurs rarely and of a very restricted distribution, being confined to associations upon upper slopes, where its pale-yellow flowers render it always inconspicuous. The thickened perennial roots are parasitic upon the roots of other plants. Many flowering stalks may arise from one root, thus assuming a bunch habit. The high immobility of the seeds, resulting in a very restricted distribution, accounts for its gregarious habit and local occurrence upon the prairie.

Viola pedatifida with its bright-blue flowers and unrestricted distribution and sparse to subcopious abundance exerts a characteristic effect on the vernal tone. The prairie violet is a perennial from a fleshy short rootstock.

Oxalis violacea seems somewhat restricted to middle and lower slopes, where it may occur densely in open, matlike patches, resulting from a slow centrifugal migration through bulb formation coupled with a positive ecesis. Though acaulescent and of low stature, its gregarious habit and rose-purple flowers, with their green background of palmately trifoliate leaves, make it in restricted plots of primary floral importance in the aspect. It likewise occurs sparsely but generally distributed over all parts of the formation, with the exception of crests and Poa sod, where it exerts only a minor effect. The shallow scaly brown bulbs indicate its perennial nature. Dissemination is by propulsion, the few seeds formed being not distantly ejected from the pentalocular ovary by the recurving of the loculicidally dehiscing carpels. In this we have a still further explanation of its gregarious tendency.

Characterized by a general distribution, a subcopious abundance, and the "bunch-habit" of growth which aggregates its many blue and white flowers, *Sisyrinchium angustifolium* becomes of first prominence in the vernal floral aspct. It is perennial by short fibrous rootstocks. It is abundantly fertile, and the smooth ovoid seeds are discharged but weakly by the loculicidally dehiscing tricarpellate capsule.

The stemless loco-weeds, *S. Lamberti* and its somewhat earlier flowering and more abundant silky variety, *S. Lamberti sericea*, are acaulescent perennial herbs from thick deep roots. Their dense spikes of dark-purplish flowers borne on long peduncles, a restricted though subcopious distribution upon the higher slopes, and silky pubescence make them very conspicuous, easily dominating in the aspect. The middle of the aspect is controlled by the variety, but the type, which flowers some ten days later, holds the floral dominance for the remainder of the vernal aspect. The type is decidedly more mesophytic in its structure and distribution, and it seems evident that the variety is very possibly a xerophytic mutant of *S. Lamberti*. Propagation occurs through fragmentation of the perennial root, producing as in Astragalus a gregarious habit. A limited seed dispersal furthers this patchy distribution.

Noteworthy on account of their rarity in the aspect are *Astragalus plattensis*, *A. hypoglottis*, and *Viola cucullata*, all flowering toward the end of the second week in May. The Astragali occur only in open association toward the crest and are strikingly inconspicuous. They are both decumbent and perennial. The two-valved pod of *A. plattensis* is fleshy and dehiscent and its seed dispersal is accomplished through limited propulsion. *Viola cucullata* is noteworthy, as only a single individual has been recorded in the area and that on the middle slope of a northwest exposure, doubtless the result of fortuitous distribution.

The third week is characterized by the blooming of *Antennaria neodioica*, *Carex Meadii*, *C. festucacea*, *Vicia linearis*, *Senecio plattensis*, and *Pentstemon gracilis*. Early in the third week *Antennaria neodioica* flowers; it appears to be more mesophytic than *A. campestris*, occupying the lower slopes, and it occurs less abundantly, but with the fruiting scapes of the earlier species the antennarias are scarcely second to any forms in conspicuousness. *A. neodioica* is a stoloniferous perennial and forms mats, its rosettes living over winter. It is easily distinguished even at a distance by its large and lighter-colored mats, and by the fact that it flowers while the other species is undergoing maturation and distribution.

The carices appear at about the same time toward the last of the week. *C. Meadii*, however, is earlier and occurs sparsely on lower slopes and is found inclusive in Poa sods. *C. festucacea* occurs likewise on lower slopes, but more abundantly and assumes the "bunch-habit" of growth. Both the carices perennate and propagate vegetatively by rhizomes. They contribute little if any to the floral tone of the aspect.

Florally associated with the carices, as just noted, are *Vicia linearis*, *Senecio plattensis*, and *Pentstemon gracilis*, to which are soon added *Lappula texana* and *Plantago Purshii.* Vicia occurs rarely, is confined to lower slopes, and exerts no tone effect; it is a perennial form and is pollinated by bees. Senecio, also of rare occurrence, seems to be confined to mesophytic portions of the formation. It is conspicuous on account of its numerous yellow heads and ray flowers. But for its limited occurrence it might easily dominate the tone, and in the vicinity of Sioux City it was recorded as controlling the aspect. The achenes are provided with a copious pappus and a wide distribution is assured. It is a perennial, and its scarcity seems to indicate that it is of decidedly mesophytic tendencies; it may be considered prophetic in our area. *Pentstemon gracilis*, though rarely a component in any plot, is an interesting form. It is confined to the mesophytic portions of the prairie and has been noted as abundant in western Iowa. Its rarity in our area is explained as in the case of Senecio; it is a perennial, and its smooth though numerous seeds are limited in their distribution. *Lappula texana*, the hairy stick-seed, is also a minor element, occurring mainly on lower slopes in sparse abundance. It is much branched and its numerous small blue flowers exert but a restricted effect. It is an annual and very fertile, producing numerous nutlets whose margins are each bordered by a single row of bristles with recurved tips; distribution is entirely by aid of animals. It continues to bloom well into the estival aspect. The prairie plantain, *P. Purshii*, is a woolly annual whose indeterminate spikes rise some 20^{cm}. Of copious abundance and of gregarious habit, it frequently becomes conspicuous at short distances. Its flowers bloom progressively up the spike, reaching the maximum in the early estival aspect and continuing well into July. Its highly immobile seeds prevent other than a limited distribution, thus readily accounting for its gregarious habit.

The fourth week of the aspect, about the last week in May, is remarkable for the general flowering of *Poa pratensis*. *P. compressa* is associated, but occurs sparsely and principally upon the upper slopes. The relative place of these two forms has been hard to determine, but it seems that *P. compressa* occurs as a forerunner of the bluegrass. In its distribution *P. pratensis* is confined to depressions and lower slopes, and is always indicative of the highest soil-water content, the most favorable exposure, and richest humus. In these situations it forms a dense sod, frequently exclusive, which is constantly pushing up the slopes replacing the bunch-grasses, outlying individuals frequently reaching the higher slopes. It is perhaps one of the most mesophytic of prairie forms, and is almost invariably the forerunner of the prairie shrubs, *Symphoricarpus occidentalis* and *Rhus glabra*. It reaches its highest development on the northwest exposure, and it is up this exposure that the flood-plain and ravine forest of this region has made its greatest advance upon the prairie. Poa is the first facies to bloom, but as noted above is of restricted distribution. It is a perennial and propagation is rapid by the abundant rootstocks, which leads to dense sod.

With the bluegrass are successively added *Oxalis stricta*, *Linum rigidum*, and *Polygala alba*. Never very abundant and of low stature, they add but little to the tone of the aspect, as they are overtopped by the oncoming facies of later aspects. Oxalis appears on lower slopes, possessing frequently a gregarious distribution. It may be either annual or perennial. The few seeds are restrictedly dispersed by the dehiscing capsules. Linum is a decidedly xerophytic annual, being a relict of earlier stages. It appears in the open association on the upper slopes and along prairie crests. It is never common and its fugacious petals prevent all but entire inconspicuousness. Its seeds are few and their mobility little. Polygala is sparingly distributed over the lower slopes of prairie knolls, always working up to higher positions with the increase of mesophytic conditions, but it never remains in the Poa sod. It is perhaps one of the best indices of progressive mesophytism among the prairie species. It is a perennial from woody rootstocks. Seeds are borne two in a capsule and migration is very slow.

As the vernal floral aspect is drawing to a close, several minor elements bloom, extending vernal floral activity over into the first few days of June. *Gaura coccinea*, *Meriolix serrulata*, *Psoralea esculenta*, *Hedeoma hispida*, and *Osmodium mollė* now progressively appear. Though flowering during the transition from vernal to estival aspect, these forms reach their maximum display during the early estival; particularly is this true of Meriolix, Hedeoma, and Osmodium. They should be considered transitional species, which appear during the unsettled climatological conditions between the vernal and estival periods, and are not specially indicative of either. Of subcopious occurrence and largely overtopped by leafy stalks of autumnal forms they must be ranked as almost neutral in the floral aspect. *Gaura coccinea* is a relict of more xerophytic stages and occurs primarily though sparsely in the open association of upper slopes and crests. It is an annual and a low and obscure element. It bears a few-seeded indehiscent nut of little mobility. Meriolix may also be considered as a relict of the xerophytic stages of the prairie, having its present distribution limited to the open association along crests and upper slopes, where it frequently occurs subcopiously. Its large yellow flowers make it conspicuous, but only at short range, as low stature relegates it to a sublayer. It is a slightly shrubby perennial from a woody root, producing numerous seeds which are strikingly immobile. It continues blooming up into the autumnal floral aspect, but reaches its maximum in the early estival. Psoralea is rare and of solitary occurrence on middle slopes; add to this its inconspicuous fading-blue flowers and it is scarcely seen upon the prairie by the casual observer. It is a perennial from a large edible farinaceous tuberous root. In the autumnal aspect, breaking off close to the ground, it becomes a tumble-weed. Its rarity is problematical. Hedeoma, a low annual, scarcely ever more than 20^{cm} high, occurs subcopiously and not infrequently copiously upon middle slopes. Its low stature and leafy branches completely hide its abundant small blue flowers, rendering it ever inconspicuous. Osmodium occurs sparsely though quite generally over the whole formation, with the exception of the very crests. It is a perennial with several stalks, terminated by leafy, pendent, scorpioid racemes of greenish flowers, arising from a thick root. It is also quite unnoticeable. The smooth nutlets possess limited mobility.

The estival floral aspect

Marked by a conspicuous decrease of the vernal floral display, a decided climatological change, the flowering of certain sod-formers initiated by *Panicum Scribnerianum* and followed by *Koeleria cristata* and *Stipa spartea*, and the rapid addition of several prominent estival flowers, which all results in a complete shift of the floral tone, the estival floral aspect begins toward the last of the second week in June and extends well up into middle July, when it is terminated by a climatological and floral change even more pronounced.

Toward the end of the vernal aspect the leafy stalks of oncoming facies render the floral tone weak and in places drown it in a sea of dark green; however, the estival forms like Erigeron, Delphinium, Brauneria, Ratibida, Kuhnistera, and others seem to push rapidly above these, forming a higher floral stratum than the vernal, but to be overtopped later on by the still higher stratum of autumnal forms.

With the shifting of climatological conditions, which is very generally appreciated, comes the blooming of *Rosa arkansana, Erigeron ramosus, Delphinium carolinianum*, and *Brauneria pallida*, which with the sod-formers noted above are always indicative of the inception of the estival aspect. The physical factors of the soil have become less contrasting on the various slopes and between different positions on the same slope; still the south exposure seems slightly earlier. The middle and base of slopes closely approach in absolute water content and are less separated from the crests in this respect than in earlier aspects. Correspondingly there appears a more uniform plant-covering at this time. It is to be noted that the holard is markedly much lower than in the vernal aspect.

During this time Solidago, Helianthus, and Aster have become vegetatively of primary importance and give the general tone of dark green to the aspect. Extending over from the vernal aspect and largely occurring on the upper slopes are *Polygala alba*, which on account of its indeterminate inflorescence blossoms through the entire estival aspect, Meriolix, and *Gaura coccinea*. Hedeoma and *Oxalis stricta* continue blooming on the middle slopes. The dominating species added in this aspect are *Koeleria cristata, Ratibida columnaris, Symphoricarpus occidentalis*, and *Verbena stricta*. The floral forms added in this aspect are twenty-one in number, nine less than appeared in the vernal aspect. It should also be noted that six new ruderals are added. *Panicum capillare* and *Hordeum jubatum* not infrequently attain no small significance. The latter frequently establishes in waste situations exclusive associations. Its permobile awned spikelets being readily carried by wind or animal, its migration is rapid. In the autumnal aspect *P. capillare* becomes detached at the surface, and the large and profusely branched panicles go tumbling over the prairie until lodgment stops the distribution.

In addition to the floral delineation of the estival from the vernal aspect, it is strongly set off by a change in the climatological conditions. With the introduction of hot dry days and prevailing southern winds the estival aspect begins. The precipitation is slightly higher than in the vernal aspect, but its effect is strongly offset by an average mean temperature some 5° higher than in the vernal. The average hourly wind velocity is 0.9 less and the relative humidity 3.4 lower, the lowest of any aspect. Coupled with these conditions is the fact that the relative evaporation is 1.6 higher, the greatest evaporation of any aspect occurring in the estival.

The holard has a slight rise in the aspect due to the heaviest mean daily rainfall of the season. The chresard thus rises to 11 per cent. on June 6 to fall to 8.9 per cent. on June 22 and 6.5 per cent. on July 7. On June 22 distinction of position seemed nearly eliminated, the base, slope, and crest registering a holard of 15.9, 16.1, and 16.6 per cent.

ESTIVAL CLIMATOLOGY

TEMPERATURE			WIND			RAIN			LIGHT			SOIL			MEAN RELATIVE HUMIDITY	RELATIVE EVAPORATION
Maximum	Minimum	Mean	Prevailing direction	Total movement	Hourly velocity	Days	Mean daily	Total	Mean cloudiness	Sunshine per cent.	Relative intensity	Mean holard	Mean echard	Mean chresard		
35° C.	6° C.	21° C.	S. to E.	5839	8.1	13	.31$^{\text{cm}}$	9.29$^{\text{cm}}$	4.7	56	.551	16%	7.2%	8.8%	48.3	8.794

respectively. Yet the average chresard for the aspect (8.8 per cent.) shows a steady decrease from that of the vernal (10.7 per cent.).

SPECIES OF THE ESTIVAL FLORAL ASPECT

FACIES.—Koeleria cristata,† Poa pratensis.*†

PRINCIPAL SPECIES.—Ratibida columnaris,† Amorpha canescens,† Erigeron ramosus,† Symphoricarpus occidentalis,† Verbena stricta,† Festuca octoflora.†

SECONDARY SPECIES.—Brauneria pallida, Delphinium carolinianum, Rosa arkansana, Linum sulcatum, Panicum Scribnerianum, Meriolix serrulata,* Euphorbia marginata, Potentilla hippiana, Plantago Purshii,* Hedeoma hispida,* Polygala alba,* Hedeoma hispida.*

TERTIARY SPECIES.—Stipa spartea, Aristida purpurea, Allionia linearis, Acerates viridiflora linearis, Osmodium molle,* Anemone cylindrica, Physalis heterophylla, Gaura parviflora, Gaura coccinea.*

RUDERAL SPECIES.—Hordeum jubatum, Ixophorus viridis, Panicum capillare, Melilotus alba,* Lappula Lappula,* Verbena bracteosa, Allionia nyctaginea, Potentilla monspeliensis, Melilotus officinalis,* Lepidium virginicum.*

* From earlier aspect. † Forming associations.

Koeleria cristata is a perennial bunch-grass and a very important sod-former, and may be considered one of the forerunners of the blue-grass. It occurs generally distributed higher up the slopes, where not infrequently it may reach facial rank. Above it seems to be encroaching upon the grama and buffalo grasses and so is quite lacking at the crests. *Panicum Scribnerianum* is likewise a perennial of the bunch habit and is closely associated with Koeleria in distribution, but never appears so abundantly as to become a facies. It is evidently more of a mesophyte than the latter and follows it up the slopes. In the formation studied it is mostly confined to the lower part of the middle slopes. It blossoms slightly before Koeleria. *Stipa spartea* is likewise a bunch-grass and the most xerophytic of these three grasses. It is sparsely distributed upon the uppermost slopes and crests and never forms a facies. It must be rated as an unimportant element in sod-establishment in the formation.

Almost coincident with the sod-formers listed above, blooms the prairie rose, *Rosa arkansana*. It is the first woody perennial to bloom and is distributed over upper slopes and crests where in the latter habitat it commonly becomes copiogregarious. Its abundance, large pink flowers, general anthesis, and height make it always one of the most conspicuous elements of the early estival aspect. Its prominence, however, is of passing duration, as the petals fall after several days and it passes into obscurity. Mobility is limited, resulting largely in the gregarious distribution. With Rosa, blooms *Delphinium carolinianum.* It is a perennial with a thick heavy rootstock, and occurs sparsely as a xerophyte in the open association upon upper slopes and crests. It is closely associated ecologically with the bunch-grasses and invariably seems to follow them. Its single erect stalk, some 6 to 8^{dm} high, bears a large terminal raceme of conspicuous white flowers. Rising thus so conspicuously, these plants seem like sentinels of the prairie and a few individuals are noticeable at some distance. Many seeds are produced, but mobility is slight.

The anthesis of *Erigeron ramosus* usually precedes that of Delphinium but follows that of Rosa, only a day or two separating them. Erigeron is a perennial or annual occurring along upper slopes, where it assumes a copiogregarious habit of growth. It seems quite restricted, few scattering individuals being noted. It is some 7 or 8^{dm} high, with several stalks rising from a single root, which are terminated by spreading corymbs bearing numerous flowers with yellow disks and abundant white rays; thus it is very conspicuous. The achenes are provided with a double pappus, but mobility would seem limited, judging from the gregarious tendency of distribution. Brauneria, though occurring sparsely upon the highest slopes and crests, is one of the most conspicuous early estival bloomers. It is a xerophytic perennial with a large thick root. A single stalk, some 7 or 8^{dm} high, is terminated by a single large head of flowers frequently 5^{cm} across. The numerous long pinkish ligulate ray-flowers surround a large reddish-brown hemispheric head bristling with abundant roughish chaff; in all a very prominent structure. The achenes are crowned with a short-toothed pappus, thus insuring mobility, though of a low degree. It is to be noted that Brauneria has a blooming period of nearly two months, so it remains a conspicuous element even into the following aspect.

Scarcely have these forms flowered, when two species of secondary importance begin to make their contribution to the floral aspect, blooming progressively during the earlier part of the third week of June. They are *Anemone cylindrica* and *Physalis heterophylla.*

These two perennials add little or nothing to the tone of the aspect, as they are of sparse occurrence and decidedly inconspicuous. Anemone occurs rarely though widely on upper and middle slopes. Physalis is of rare occurrence on lower slopes, but would be noticeable except for the pendent inflorescence which hides the yellow flowers beneath the leaves. The former rises some 50 to 60^{cm}, with its exposed cylindrical head of numerous woolly achenes, which are subject to wide dispersal. The immobile fruit of the latter and its ventral position cooperate to insure a very restricted dissemination.

The last days of the third week and early part of the fourth are marked by the general flowering of three forms, *Ratibida columnaris*, *Symphoricarpus occidentalis*, and *Verbena stricta*, all of primary importance. *Gaura parviflora*, *Linum sulcatum*, and *Allionia linearis*, three flowering forms of minor significance, are added at about the same time. Linum is an annual some 40^{cm} high, occurring sparsely upon the lower slopes. Its humble place in the floral tone is largely due to its limited occurrence, for its yellow flowers (1.5^{cm} in diameter) would otherwise make it a notable element. Gaura is noteworthy mainly as a matter of record, a few specimens only being noted on the middle slope of a northwest exposure. It is an annual and frequently reaches a height of 1^{m} or more. Allionia is a perennial occurring rarely upon middle slopes. The straw-colored involucre incloses one to three small purplish flowers and it is always of minor prominence. The anthocarpous fruit has little mobility. About this time are also added two sod-forming species, *Festuca octoflora* and *Aristida purpurea*. Aristida is of rare occurrence and contributes little to the floral aspect or plant covering. Festuca, on the other hand, is a sod-former of some significance upon lower and middle slopes, being easily replaced however by Poa, which seems to follow it. It is apparently a pioneer form, taking rapid possession of available ground in the open association by means of its heavy, thick, matlike sod.

In Ratibida the long yellow ligulate ray-flowers first spread about June 20, but it is not until several days later that there is a general display and the tube flowers of the columnar disk begin to open. They flower first in a band at the base of the indeterminate head, progressing up at the rate of about 3 to 5^{mm} a day. The plants are some 7.5^{dm} high, and each of the branches is terminated by a very striking head; yellow drooping rays, 6 to 9 in number and frequently 3^{cm} long, surround a deep-brownish columnar head some 4^{cm} high. The prairie cone-flower occurs copiously upon lower and middle slopes, extending crestward (*fig. 1*). In the former locations it frequently assumes almost facial rank and gives a bright-yellow tone to the entire floral aspect. It is a prolific and continuous bloomer, dominating the aspect through the month of July and the greater part of August, and extending up to the middle of September. Ratibida is a perennial from a thick root. The achenes are provided with a diminutive pappus of one or two teeth, and so lack of mobility and great fertility result in its copious abundance in restricted localities. It should be recorded that a few specimens with reddish-brown rays having yellow tips and bases have been noted.

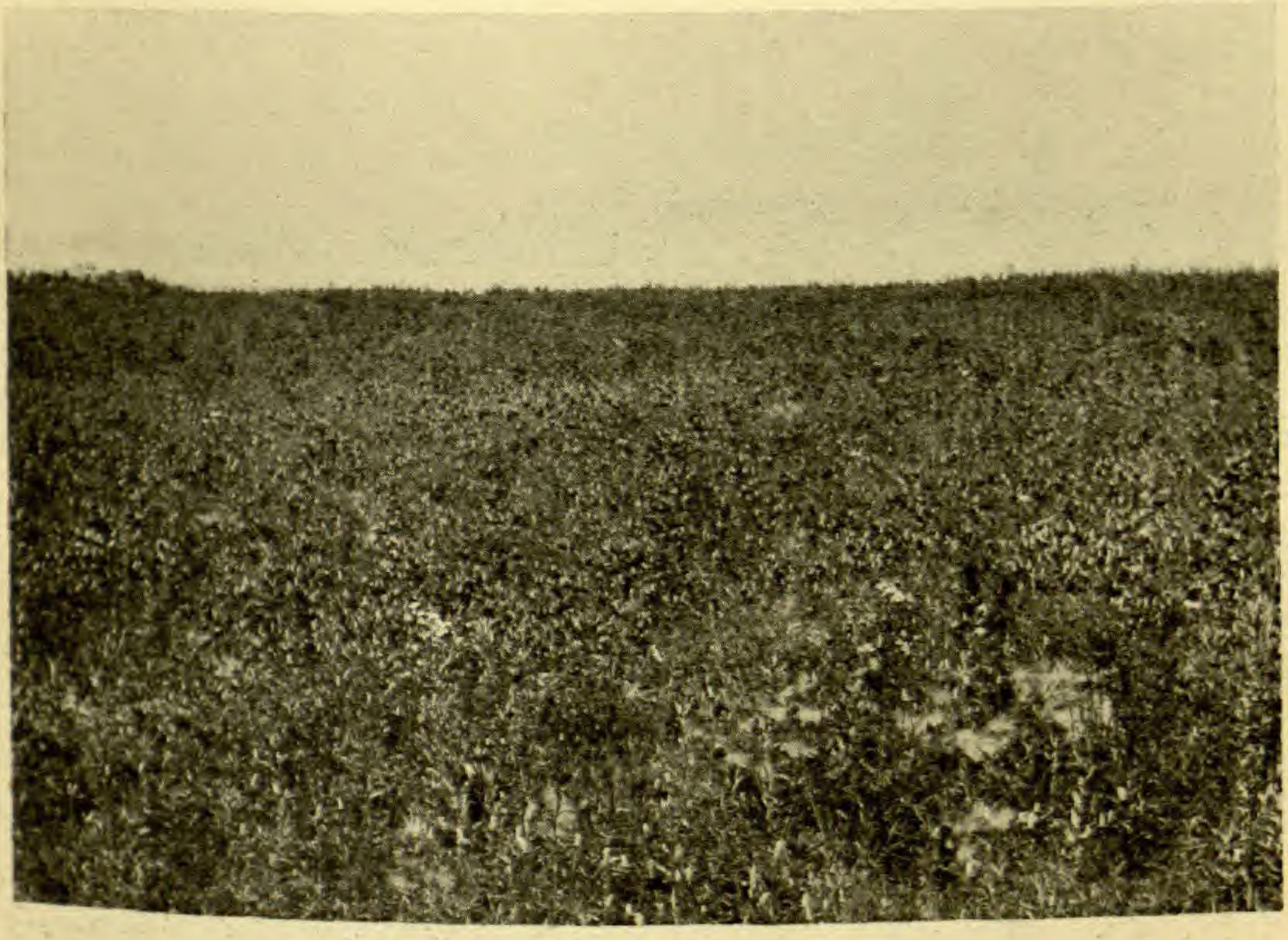

FIG. 1.—Late estival aspect; *Ratibida columnaris* upon a middle slope; the ruderal *Hordeum jubatum* in right foreground.

At about the time Ratibida is spreading its neutral ray-flowers the earlier flowers of Symphoricarpus appear, reaching their maximum flowering two or three weeks later. The wolfberry is of restricted distribution, occurring gregariously at the base of slopes and in mesophytic depressions; frequently outlying individuals are found. In the former situations it ranks not infrequently as a facies. It is the largest of the woody perennials of our area, being a profusely branched shrub frequently 1 to 1.25^{m} tall. It is characteristically associated with the Poa sod, which it follows in the latter's advance upon the prairie; the most advanced occupation is upon the north to northwest exposures, where it also first appears (*fig. 2*). It is the forerunner of *Rhus glabra*, which in other parts of the prairie follows it closely, together making up the shrub stage, which is succeeded by the *Quercus macrocarpa* and *Ulmus fulva* association as the forest pushes out upon the prairie. While the numerous axillary clusters of pink flowers are not conspicuous from a distance, the masses of dark-green leaves make the Symphoricarpus association very noticeable. Very few seeds are borne in the white globular berries;

FIG. 2.—Late estival aspect; Symphoricarpus association in a depression of a northwest exposure; Poa sod in foreground.

immobility and high ecological demands result in its gregarious habit. The berries are persistent and birds may help somewhat in dispersal.

The last of this group to bloom is *Verbena stricta.* About June 25 the purplish-blue flowers make their appearance at the base of the long ($15-30^{cm}$) indeterminate terminal spikes in a narrow band, which moves upward day by day at the rate of about 1 to 2^{cm}. The maximum flowering, however, seems to be reached about July 10 to 20.

FIG. 3.—Late estival aspect; *Verbena stricta* determining the tone of a lower slope; the white patches are the ruderal *Hordeum jubatum.*

Like Ratibida and for the same reason, it flowers abundantly through July and August and into September. It has a copious and general distribution and not infrequently assumes a dominating influence upon lower (*fig. 3*) and upper slopes as well as crests. It is a perennial from a heavy root and several stalks from the same root give it not infrequently a "bunch" appearance.

During the last days of June and the first days of July, several forms appear to complete the estival floral aspect. In order of flowering they are *Acerates viridiflora linearis, Potentilla hippiana, Euphorbia marginata,* and *Amorpha canescens.* All assume local importance except Acerates, reaching their maximum display in the serotinal aspect. Acerates appears rarely and as a solitary xerophyte upon the higher slopes and along crests. It is a perennial with numerous permobile comose seeds, yet its abundance is always low. Its solitary umbel of greenish flowers, which blend with the foliage of the prairie, renders its detection difficult. Potentilla possesses a copiogregarious or a solitary distribution along the middle and lower slopes. It rises 50 to 70^{cm}, with the erect stems terminating in loose cymes of numerous yellow flowers. It thus exercises a local effect in the floral aspect. Through its numerous annual rosettes it also contributes in a limited degree to the plant covering. It is a perennial from a thick root. The numerous achenes are highly immobile, resulting in a limited distribution and the gregarious habit. The white-margined spurge, *Euphorbia marginata*, is an annual which occurs subcopiously on lower slopes and rises erect to a height of 50 to 75^{cm}. The stems bear abundant bright-green leaves and are terminated by three-rayed umbels whose greenish-white flowers are subtended by involucres of numerous white-margined bracts, making the entire umbel a very conspicuous object. *Amorpha canescens* is a prominent perennial shrub (50 to 90^{cm} high) exerting a controlling influence. It is a marked xerophyte and may rise to primary rank upon the crests in a sub-copiogregarious distribution, but rarely occurs upon the lower mesophytic slopes. Its gregarious habit and its abundant and densely white canescent leaflets and densely clustered terminal spikes of dark-blue flowers make it a very striking object, especially when it occurs in such abundance. With sod-establishment it gradually disappears, being a characteristic component of the bunch-grass stage. The indehiscent one-seeded pod is highly immobile.

THE UNIVERSITY OF CHICAGO

UNDESCRIBED PLANTS FROM GUATEMALA AND OTHER CENTRAL AMERICAN REPUBLICS XXX[1]

JOHN DONNELL SMITH

CURATELLA AMERICANA L., var. **pentagyna** Donn. Sm.—Gynaecium e carpellis 5-compositum.

Paniculae saltem in exemplis suppetentibus solitariae vel paucifasciculatae laxiflorae.

Salamá, Depart. Baja Verapaz, Guatemala, alt. 900$^{\mathrm{m}}$, Mart. 1907, *W. A. Kellerman* (n. 6499).

Capparis (§ CAPPARIDASTRUM DC.; Eichl.) **Tuerckheimii** Donn. Sm.—Omnibus in partibus glabra. Folia oblongo-lanceolata longe incurvo-acuminata infra medium angustata ima basi obtusiuscula petiolis plerumque bis terve longiora. Pedicelli gracillimi. Sepala paene sejuncta petalis 4–5-plo breviora. Discus 4-glandularis. Gymnophorium petalis 3-plo fere longius. Ovarium cylindrico-ellipsoideum uniloculare.

Frutex inermis. Folia pergamentacea nitida 7–15$^{\mathrm{cm}}$ longa 3–5$^{\mathrm{cm}}$ lata, juniora subtus flavescentia costa nervisque rubiginosa venis pellucida, petiolis longitudine multum variis 2–9$^{\mathrm{cm}}$ longis ad apicem versus incrassatis, stipulis sicut eae bracteolarum elongato-triangularibus aegre 1.5$^{\mathrm{mm}}$ longis margine albidis. Racemus corymbosus, rhachi 2–3$^{\mathrm{cm}}$ longa, pedicellis 5–13 circa 5–6.5$^{\mathrm{cm}}$ longis apice tetragono-incrassatis. Sepala ovata obtusa 3–3.5$^{\mathrm{mm}}$ longa retroflexa. Disci glandulae carnosae. Petala lutea elliptica 14–15$^{\mathrm{mm}}$ longa 8$^{\mathrm{mm}}$ lata. Stamina numerosa 28$^{\mathrm{mm}}$ longa, antheris oblongo-ellipticis 3$^{\mathrm{mm}}$ longis. Gynophorium 4–4.5$^{\mathrm{cm}}$ longum, ovario 5$^{\mathrm{mm}}$ longo spurie 3–5-loculari. Baccae deficiunt.

Inter rupes prope Panzal, Depart. Baja Verapaz, Guatemala, alt. 1200$^{\mathrm{m}}$, Apr. 1907, *H. von Tuerckheim* (n. II. 1746).

Eurya (§ FREZIERA Szysz.) **guatemalensis** Donn. Sm.—Folia supra lucida subtus ferrugineo-tomentosa integerrima oblonga vel lanceolato-oblonga acuminata basi inaequali acuta vel subacuta, nervis lateralibus creberrimis. Flores pedicellati in fasciculam pedunculatam aggregati. Petala glabra porrecta ovata apice obtuso patula sepalis tomentulosis bis longiora. Ovarium elongato-conicum.

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[1] Continued from BOT. GAZETTE 44:117. 1907.

Arbor, ramulis subflexuosis, novellis sicut petioli et inflorescentiae ferrugineo-tomentulosis. Folia subcoriacea 10–17^{cm} longa 3–5^{cm} lata supra in sicco laete flavovirentia, costa nervisque supra impressis subtus prominentibus, his inter se 4–8^{mm} distantibus cum intermedio tenuiore brevioreque alternantibus, petiolis 12–14^{mm} longis marginato-canaliculatis inflorescentias paulo superantibus. Pedunculi crassi deciduo-bracteosi 4–7^{mm} longi, pedicellis 5–7 circiter 4^{mm} longis basi bracteola fultis, floribus 8^{mm} longis. Sepala cum bracteolis paulo minoribus suborbicularia concava ferrugineo-tomentulosa. Petala vix cohaerentia 7^{mm} longa basi 4^{mm} lata. Stamina glabra numerosa. Floris masculini filamenta antheras aequantia vel eis paulo longiora, ovarium rudimentarium depresso-pyramidatum stigmatibus carens. Floris feminini filamenta antheris plus minus breviora, ovarium glabrum triloculare petalis bis brevius in stylum 3-fidum sensim attenuatum. Bacca nondum satis matura conica stylum subulatum aequans.—*E. sericeae* Szysz. proxima.

Collium in declivibus aridis prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1350^{m}, Jun. 1907, *H. von Tuerckheim* (n. II. 1824).

Picramnia brachybotryosa Donn. Sm.—Foliola 11–15 plus minus dissociata praeter nervos subtus puberulos glabra obtuse contracto-acuminata, superioribus oblongo-ovatis, inferioribus ovatis, terminali lanceolato-elliptico. Racemi foliis breviores, masculini brevissimi, floribus apetalis tetrameris nonnunquam trimeris glabris.

Fruticulus (e scheda Tuerckheimiana), ramulis petiolis racemis leviter pubescentibus. Foliola per paria deorsum decrescentia petiolo communi 16–24^{cm} longo instructa exmucronulata, superiora 7–9^{cm} longa basi inaequali obtusa, infima 3–4.5^{cm} longa basi subtruncata, terminale remotum basi acutum, petiolulis lateralibus 2–3^{mm} longis. Pedunculus masculinus lateralis 2^{cm} longus racemos binos 9–10^{cm} longos ferens, pedicellis fasciculatis 1–2^{mm} longis glabris, calycis segmentis 3–4 ovalibus 1.5^{mm} longis, staminibus 3–4 calyce bis longioribus. Racemi feminini terminales bini 16–18^{cm} longi, pedicellis solitariis remotiusculis 3–6^{mm} longis glabris, calycis segmentis 3–4 triangularibus vix 1^{mm} longis, ovario ellipsoideo 1.5–2^{mm} longo digyno. Bacca ignota.—Haec a ceteris speciebus tetrameris adhuc cognitis est secernenda, differt enim a *P. tetramera* Turcz. (ex charactere nimis brevi) saltem foliolis inflorescentia calycibus, a *P. quaternaria* Donn. Sm. imprimis floribus apetalis.

In silvis prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1550^{m}, Jun. 1907, *H. von Tuerckheim* (n. II. 1801).

PACHYRHIZUS ANGULATUS Rich., var. **integrifolius** Donn. Sm. —Foliola integerrima subrhomboidea vel inaequilateraliter subrhomboidea sursum acutissime incurvo-elongata infra medium in angulum fere rectum sensim angustata subtus appresse pilosa nervis ferruginea.

Foliolum terminale 63–84^{mm} longum 38–52^{mm} latum, lateralia 55–71^{mm} longa 28–40^{mm} lata.

Cobán, Depart. Alta Verapaz, Guatemala, alt. 1350^{m}, Mart. 1907, *H. von Tuerckheim* (n. II. 1671).

Dalbergia (§ SISSOA Benth.) **tucurensis** Donn. Sm.—Foliola 11–15 oblongo-ovata vel ovata apice acuta et mucronulata basi acuta vel obtusa subtus pallida et minutissime fusco-reticulata. Paniculae axillares foliis bis breviores laxe ramosae. Calycis lobi 4 superiores rotundati infimo acuto bis superati. Stamina 9 monadelpha. Ovarium pilosum.

Arbor, ramulis junioribus petiolis foliis paniculis calycibus fusco-pubescentibus. Folii petiolus communis 21–30^{cm} longus, foliola remote alterna 62–105^{mm} longa 40–48^{mm} lata, petiolulis 3^{mm} longis. Paniculae subpyramidatae pedunculus 3–4^{cm} longus, rami 5–7 remoti, inferiores ramulis computatis 4–5^{cm} longi, pedicellis 1–2^{mm} longis, floribus 6–7^{mm} longis. Calyx 5^{mm} longus usque ad medium lobatus, lobis 2 summis alte connatis quam ceteri bis latioribus, infimo lanceolato tubum superante. Petala calyce paulo longiora, vexillo obovato-orbiculari. Stamen vexillare constanter deficiens. Ovarii stipes stylo bis longior.

Concepción prope Tucurú, Depart. Alta Verapaz, Guatemala, alt. 1000^{m}, Apr. 1907, *H. von Tuerckheim* (n. II. 1712).

Miconia (§ EUMICONIA Naud.; *Glomeratiflorae* Naud.) **oligocephala** Donn. Sm.—Folia satis disparia lanceolata utrinque acuta supra glabra et albido-punctulata subtus cano- et stellato-tomentulosa 3–5-plinervia calloso-denticulata. Paniculae rami simplices in apice vel prope apicem 1- aut 3-capituliferi, floribus tribracteolatis.

Ramuli novelli paniculae calyces ferrugineo- et stellato-tomentulosi. Folium in eodem jugo majus 10–19^{cm} longum paulo infra medium 3–4^{cm} latum alterum triente usque ad bis superans, petiolis 8–18^{mm} longis. Panicula pyramidalis foliis brevior, ramis superioribus unicapituliferis, infimis quaternis prope apicem capitula 2 adjecta sessilia ferentibus, capitulis semiglobosis 5–8-floris, bracteolis ellipticis 3^{mm} longis, floribus 5–6-meris 9^{mm} longis. Calyx companulatus 5^{mm} altus, lobis semioribcularibus scariosis tuberculo 1^{mm} longo extus appendiculatis. Petala obovato-oblonga 4^{mm} longa. Stamina 6^{mm} longa, antheris uniporosis. Bacca depresso-globosa 3^{mm} longa.

Cobán, Depart. Alta Verapaz, Guatemala, alt. 1550^{m}, Aug. 1904, *H. von Tuerckheim*, n. 8686 ex Pl. Guat. etc. quas ed. Donn. Sm. (sub *Conostegia lanceolata* Cogn. olim distributa): Maj. 1907, *H. von Tuerckheim* (n. II. 1781).

Miconia (§ CREMANIUM Benth. et Hook.) **purulensis** Donn Sm.—Simpliciter furfuracea. Folia oblongo-elliptica incurvo-acuminata basi acuta integra 5-nervia supra glabra subtus nervis furfuracea. Flores pedicellati 5-meri glabri. Antherae biporosae.

Ramuli obtuse tetragoni cum petiolis foliorum subtus nervis panicula fulvo-furfuracei. Folia chartacea plerumque satis disparia 11–20^{cm} longa medio 5–9^{cm} lata nervo utrinque arcte submarginali tenui computato 5-nervia, petiolis 3–7^{cm} longis. Panicula late pyramidalis pedunculo 2.5^{cm} longo adjecto 11–14^{cm} longa congestiflora, ramis ramulisque 2–4-nis, pedicellis 0.5–1.5^{mm} longis, floribus confertis 4.5^{mm} longis. Calyx hemisphaericis 1.5^{mm} altus, dentibus obtuse deltoideis tuberculo punctatis. Petala orbicularia 1.5^{mm}-diametralia. Stamina 3^{mm} longa, antheris rectis oblongo-cuneatis 1^{mm} longis, connectivo infra loculos non producto supra medium geniculato. Stylus in floribus scrutatis nullus. Bacca desideratur.

In silvis circa Purulá, Depart. Baja Verapaz, Guatemala, alt. 1800^{m}, Apr. 1907, *H. von Tuerckheim* (n. II. 1718).

Clidemia (§ SAGRAEA Cogn.) **diffusa** Donn. Sm.—Folia oblongo-ovata incurvo-acuminata basi leviter cordata vel rotundata 5-nervia subintegerrima setuloso-ciliolata. Thyrsi longissimi, ramis remotis uti pedunculus rhachisque filiformibus et ramulis divaricatis, pedicellis brevibus, floribus 5-meris. Calyx campanulatus glaber, dentibus externis minutis.

Ramuli teretes et thyrsi sparsim patenterque pilosi purpurascentes. Folia membranacea in eodem jugo leviter inaequalia 85–125^{mm} longa 35–60^{mm} lata, petiolis supra pubescentibus 25–50^{mm} longis. Thyrsi ex una axilla orti dependentes pedunculo 4–5^{cm} longo adjecto 16–19^{cm} longi ter quaterve trichotomi, rhachis internodiis 35–55^{mm} longis, axibus secundariis inferioribus 20–25^{mm} longis, tertiariis 5–6^{mm} longis, pedicellis 1–3^{mm} longis, floribus 6^{mm} longis. Calycis rubiginosi tubus 2.5^{mm} longus, dentibus deltoideis denticulo 0.5^{mm} longo appendiculatis. Petala flava obovata 3^{mm} longa staminibus paulo longiora. Ovarium vertice conicum, stylo 4^{mm} longo. Bacca globosa 3^{mm}-diametralis.—In sectione floribus constanter 5-meris anormalis.

In monte silvestri prope Purulá, Depart. Baja Verapaz, Guatemala, alt. 1800^{m}, Apr. 1907, *H. von Tuerckheim* (n. II. 1717).

Centropogon (§ SYPHOCAMPYLOIDES Benth. et Hook.) **calochlamys** Donn. Sm.—Glabra. Folia lanceolato-elliptica utrinque longe acuminata argute subcalloso-denticulata. Inflorescentia foliis superata, pedunculis racemoso-confertis paucis. Calycis lobi lanceolato-ovati tubo 4–5-plo longiores corollae tubo aliquantulum breviores. Antherae totae excepto vertice inferiorum nudae.

Fruticulus simplex 22–35^{cm} altus. Folia membranacea 9–16^{cm} longa medio 3–5.5^{cm} lata apice contracto-acuminata basi aequali in petiolum complanatum

10–22^{mm} longum attenuata costa nervis margine subtus sicut petiolus purpurascentia. Pedunculi terminales 2–5 subfasciculati nonnunquam ex axillis superioribus orti 3.5–6^{cm} longi bracteis foliaceis lineari-lanceolati 2^{cm} longis denticulatis fulti. Calycis tubus late hemisphaericus 3–5^{mm} altus, lobi 16–21^{mm} longi 10^{mm} lati denticulati monente cl. repertore in vivo intense violacei etiam in sicco saturato-colorati. Corollae dilute purpurascentis tubus extus glaber intus puberulus 22–25^{mm} longus, laciniae 15–21^{mm} longae. Tubus staminalis pubescens 32^{mm} longus, antheris 7–8^{mm} longis, minoribus apice barbatis, omnibus ceterum glabris. Stigmata semiorbicularia 3^{mm} lata. Bacca semilibera depresso- et compresso-globosa 6^{mm} longa 9^{mm} lata profunde bisulcata styli reliquis apiculata.—*C. Guatemalensi* Robinson proximus differt insigniter calycis lobis permagnis et coloratis.

In monte silvoso prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1650^{m}, Aug. 1907, *H. von Tuerckheim* (n. II. 1893).

Ardisia (§ ICACOREA Pax; Mez.) **verapazensis** Donn. Sm.—Glabra. Folia obovato-oblonga obtuse acuminata in petiolum brevem marginatum attenuata integra coriacea pellucido- et subtus rubro-punctulata. Pedicelli subumbellato-corymbosi gracillimi, floribus inter maximos 5-meris. Sepala extus punctulata intus infra medium lepidotula margine scariosa et nuda. Corollae lobi imbricati epunctati. Filamenta antheris aequalia.

Arbor. Folia 25^{cm} longa 7^{cm} lata, nervis lateralibus primariis utrinsecus 11–15, areolis in utraque pagina obscuris. Panicula corymbiformis 15^{cm} longa 20^{cm} lata, axibus robustis, pedicellis 4–6-nis 12–20^{mm} longis, floribus ebracteolatis. Sepala paene sejuncta dextrorsum tegentia oblongo-ovata 6^{mm} longa obtusa crassa. Corolla ante anthesin 11^{mm} longa vix ultra quartam connata purpurea, tubo 3^{mm} longo intus supra medium perdense aureo-punctulata, lobis orbiculari-ovatis. Stamina medio tubi corollini affixa 6^{mm} longa, filamentis liberis, antheris elongato-triangularibus dorso concoloribus. Ovarium epunctatum ovatum stylo 7^{mm} longo computato 10^{mm} longum. Bacca ignota.—Haec magnitudine florum ceteras species praeter *A. paschalem* Donn. Sm. superat.

In monte silvoso prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1600^{m}, Jan. 1908, *H. von Tuerckheim* (n. II. 2093).

Stylogyne phaenostemona Donn. Sm.—Folia inter minora lanceolata e medio utrinque acuminata coriacea glabra immaculata. Inflorescentia terminalis, floribus 5-meris. Sepala membranacea integra punctulata. Corolla ad usque medium connata, lobis ovalibus punctulatis. Stamina medio tubo inserta cum stylo bene exserta, antheris minutis.

Arbor, ramulis verrucosis, novellis et paniculis fusco-velutinis rubro-punctulatis. Folia 75–90^{mm} longa 28–33^{mm} lata apice basique ipsis obtusiuscula integra utrinque minute areolata, costa supra immersa subtus prominente, petiolis marginatis 4–5^{mm} longis. Paniculae pyramidales 50–65^{mm} longae tripinnatim compositae, saepe ramulos axillares brevissimos terminantes et pseudoaxillares, pedicellis ad apicem versus ramulorum subcorymbosis 3–5^{mm} longis, bracteolis minutis deciduis. Sepala fere sejuncta late ovata 1^{mm} longa margine scariosa et minutissime ciliolata. Corolla 2^{mm} longa, lobis apice rotundatis cum sepalis rubro-punctulatis. Stamina 3^{mm} longa, filamentis liberis antheras ovatas pluries superantibus. Ovarium globosum 1^{mm}-diametrale, stylo 2^{mm} longo, stigmate punctiformi, ovulis circiter 5 in placenta globosa absconditis. Fructus ignotus.—Secundum methodum cl. Mez juxta *S. orinocensem* Mez inserenda.

Cobán, Depart. Alta Verapez, Guatemala, alt. 1350^{m}, Jun. 1907, *H. von Tuerckheim* (n. II. 1814).

Gonolobus (§ DISTEMMA K. Schum.) **prasinanthus** Donn. Sm.—Folia oblongo-ovata incurvo-acuminata sinu obtuso latoque leviter cordāta bulboso-pilosiuscula vel glabrescentia. Cymae subumbelliformes, pedicellis pedunculum subaequantibus. Segmenta corollina oblonga calycinis linearibus dimidio longiora. Corona exterior membranacea integra a gynostegio brevissimo libera.

Rami cum inflorescentiis pubescentes vel glabrescentes. Folia supra fere glabra 54–81^{mm} longa 30–39^{mm} lata supra ad ortum limbi glandulis 2 conicis munita, petiolis pubescentibus 30–35^{mm} longis. Pendunculi 15–22^{mm} longi, pedicellis plerumque 4–6 arcte approximatis 12–20^{mm} longis, floribus 18–22^{mm}-diametralibus, perianthio herbacei coloris patente extus puberulo. Calycis partiti segmenta 5–6^{mm} longa a basi 1.5^{mm} lata sensim angustata obtusa, sinubus 1-glanduliferis. Corollae tubus brevissimus, segmenta 8–9^{mm} longa a basi 4^{mm} lata in apicem obtusum scariosum retroflexum sensim angustata nervosa. Corona exterior 0.5^{mm} lata glabra, interior stigma parallele marginans 1^{mm} lata. Gynostegium 1^{mm} longum, stigmate 4^{mm} lato. Folliculi nondum maturi solum visi laeves.—*G. martinicensi* Decne. proximus. Ad *G. fraternum* Schlecht. foliis et perianthio accedens recedit tamen inter alia pedicellis arctius approximatis et corona duplice.

Cubilquitz, Depart. Alta Verapaz, Guatemala, alt. 350^{m}, Jun. 1904, *H. von Tuerckheim*, n. 8711 ex. Pl. Guat. etc. quas ed. Donn. Sm.

Solenophora Tuerckheimiana Donn. Sm.—Pube moniliformi furfuracea. Folia ovato- vel obovato-elliptica acuminata ad basin obtusam altero lato excisa supra tuberculato-furfuracea subtus praeter nervos furfuraceos glabra. Cymae dependentes longissimae semel bis terve 2–3-chotomae, pedunculis axibusque capillaceis elongatis.

Ramuli subtetragoni purpurascentes cum petiolis inflorescentiis floribus plus minus furfuraceo-pubescentes. Folia membranacea plerumque parum interdum valde disparia 125–150^{mm} longa 68–75^{mm} lata nervis et margine purpurascentia, petiolis 45–65^{mm} longis. Cymae pedunculo 40–60^{mm} longo adjecto floribus autem exemptis 70–115^{mm} longae, bracteolis linearibus 6–10^{mm} longis, pedicellis 18–27^{mm} longis. Calycis purpurascentis tubus oblongo-obconicus 14^{mm} longus tertia parte ovario adhaerens, lobi deltoidei 4^{mm} longi dentati. Corollae totae aurantiaceae tubus tubuloso-infundibularis 30^{mm} longus, lobi semiorbiculares 7^{mm} longi integri. Antherae exsertae in quadram 4^{mm} longam atque latam cohaerentes. Glandula disci 2^{mm} crassa integra. Capsula nondum satis matura 10^{mm} longa calyci accrescenti usque ad medium adnata.

In sylva profunda uliginosa ad montem prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1600^{m}, Dec. 1907, *H. von Tuerckheim* (n. II. 2028).

DAPHNOPSIS RADIATA Donn. Sm. in BOT. GAZ. **14**:30. 1889.—Diagnosi adde charactera e specimine fructifero hactenus ignoto sumpta:—Fructus sessilis ovoideus 7^{mm} longus perianthii tubo accrescente marcido supra basin circumcisso inclusus in stylum 2^{mm} longum subabrupte dessinens, pericarpio carnoso.—Arborea.

Cobán, Depart. Alta Verapaz, Guatemala, alt. 1350^{m}, Maj. 1907, *H. von Tuerckheim* (n. II. 1874).

Pilea (§ HETEROPHYLLAE Wedd.) **purulensis** Donn. Sm.—Glabra. Folia inaequilateraliter subovato-lanceolata tenuiter acuteque elongata basi rotundata vel obtusa serrata trinervia, cujusque paris alterum petiolatum altero conformi sessili 3–4-plo majus. Dioica. Cymae masculinae in globum maximum graciliter pedunculatum glomerulatae. Cymae femininae petiolo multum breviores.

Folia tenuiter membranacea supra minute lineolata subtus cystolithis destituta toto margine crenulis antrorsis apiculatis serrata usque ad apicem trinervia venulis tantum subtus manifestis reticulata, basi saepe altero latere rotundata altero acuta, in eodem jugo folio majore 100–150^{mm} longo paulo infra medium 40–55^{mm} lato, petiolis 16–23^{mm} longis, minore 25–50^{mm} longo. Glomerulum masculinum 10–15^{mm}-diametrale pedunculo 18–30^{mm} longo suffultum, pedicellis 2–3^{mm} longis, perigonio 2^{mm} longo glabro scarioso, segmentis apice herbaceis. Cymae femininae 8–10^{mm} longae, pedicellis confertis flores subaequantibus, perigonio rubro-punctulato 1.5^{mm} longo, segmento intermedio cucullato ceteris longiore achenium ovale aequante.

In monte silvoso prope Purulá, Depart. Baja Verapaz, Guatemala, alt. 1800^{m}, Apr. 1907, *H. von Tuerckheim* (n. II. 1707).

Pilea (§ HETEROPHYLLAE Wedd.) **ecbolophylla** Donn. Sm.—Folia quam maxime disparia, alterum obovato-ellipticum vel -lanceolatum caudato-acuminatum basi acutum crenato-serratum tri- aut tripli-nervium altero conformi abortivo 12–15-plo majus. Dioica. Cymae femininae petiolis bis breviores.

Caules a rhizomate repente ascendentes 3^{dm} longi simplices. Glabra. Folium in quoque jugo majus pergamentaceum opacum tantum in pagina superiore lineolatum $100–115^{mm}$ longum supra medium $30–42^{mm}$ latum in caudam $15–18^{mm}$ longam serrulatam subabrupte acuminatum triente inferiore integrum, nervo utroque basali paulo infra caudam evanescente, folium alterum nanum $7–8^{mm}$ longum. Cymae femininae solum visae latiores quam longiores patenter dichotomae lineolatae, perianthii segmentis lanceolatis pedicellos subaequantibus achenio ovali 0.75^{mm} longo bis brevioribus.—Ad *P. rhizobolam* Miq. et *P. pansamalanam* Donn. Sm. folio quasi rudimentario accedit.

Ad ripas fluminis *Dolores* dicti, Depart. Alta Verapaz, Guatemala, alt. 350^{m}, Jul. 1901, *H. von Tuerckheim*, n. 7983 ex. Pl. Guat. etc. quas ed. Donn. Sm. (Sub *P. pansamalana* Donn. Sm. olim distributa.)

Pilea (§ Dentatae; *Glabrae; Brevipedunculatae* Wedd.) **Tuerckheimii** Donn. Sm.—Folia lineari- vel elliptico-lanceolata sensim tenuiterque falcato-elongata basi acuta vel leviter emarginata triente inferiore integra triplinervia supra manifeste subtus subtile lineolata longiuscule petiolata. Dioica. Cymae masculinae petiolos subaequantes recurvae pluries laxe patenterque dichotomae, floribus dissitis pedicellatis.

Caulis a basi oblique radicante erecta ramosa. Folia membranacea leviter disparia $100–160^{mm}$ longa plerumque $25–30^{mm}$ interdum 60^{mm} lata, serraturis antrorsis parvis apiculatis saepe ad callos reductis, nervo utroque basali paulo infra apicem limbi evanescente, lateralibus pellucidis anastomosantibus, petiolis longitudine multum variis $15–43^{mm}$ longis. Cymae masculinae solum visae ad nodos plerumque quaternae $25–45^{mm}$ longae, pedunculo $3–6^{mm}$ longo et ramis complanatis, perigonio bimellemetrali pedicellum circiter bis superante, segmentis lanceolatis minute cucullatis lineolatis, filamentis rubro-punctulatis, antheris exsertis ovatis, connectivo rubicundo.

In monte silvoso haud procul a Cobán, Depart. Alta Verapaz, Guatemala, alt. 1550^{m}, Jun. 1907, *H. von Tuerckheim* (n. II. 1835).

Pilea riparia Donn. Sm. in Bot. Gaz. **19**:11.—Monoica vel dioica. Cymae unisexuales, masculinae adhuc descriptione carentes ex axillis inferioribus ortae singulae aut binae pedunculos implice vel furcato petiolum aequante suffultae pluries dichotomae congestiflorae, pedicellis gracilibus, perigonii segmentis omnibus cucullatis.

Folia usque ad 12–14$^{\mathrm{cm}}$ longa 5$^{\mathrm{cm}}$ lata, petiolis 15–20$^{\mathrm{mm}}$ longis. Cymae masculinae pedunculo computato 40–45$^{\mathrm{mm}}$ longae, pedicellis demum 4–5$^{\mathrm{mm}}$ longis, perigonio 3$^{\mathrm{mm}}$ longo rubro-punctulato.

Ad ripas rivulorum prope Panzal, Depart. Baja Verapaz, Guatemala, alt. 1000$^{\mathrm{m}}$, Apr. 1907, *H. von Tuerckheim* (n. II. 1708).

Myriocarpa obovata Donn. Sm.—Folia glabra oblongo-obovata subabrupte cuspidata basi acuta calloso-subdenticulata inordinate lineolata vix ultra medium tri- aut tripli-nervia. Dioica. Spicae femininae foliis multum breviores pluries dichotomae laxiflorae, floribus singulis vel fasciculatis.

Ramuli glabrescentes verrucosi epidermide in sicco ferruginei. Stipulae lanceolato-ovatae 5$^{\mathrm{mm}}$ longae pilosae cito deciduae. Folia pergamentacea opaca 10–16$^{\mathrm{cm}}$ longa supra medium 3.5–6$^{\mathrm{cm}}$ lata cuspide 8–10$^{\mathrm{mm}}$ longa acuminata infra medium integra utrinque praesertim supra cystolithis haud radiatim dispositis conspersa, nervis lateralibus primariis utrinsecus 2–3 arcuatis, venis reticulatis, petiolis 6–13$^{\mathrm{mm}}$ longis. Spicae femininae solum visae ad nodos superiores defoliatos solitariae filiformes pedunculo 2–3$^{\mathrm{cm}}$ longo computato 6–8$^{\mathrm{cm}}$ longae pilosae, floribus ciliatis uti fasciculi pauciflori sparsis, his saepe breviter pedicellatis, calyculo diphyllo aegre 0.5$^{\mathrm{mm}}$ longo stipitem paulo superante. Ovarium lanceolatum 1$^{\mathrm{mm}}$ longum in stylum attenuatum. Stigma ramo brevi semilunatum.

In silvis profundis prope San Pedro Sula, Depart. Santa Bárbara, Honduras, alt. 800$^{\mathrm{m}}$, Jan. 1887, *Carl Thieme*, n. 5500 ex. Pl. Guat. etc. quas ed. Donn. Sm.

BALTIMORE, MARYLAND

A METHOD FOR THE QUANTITATIVE DETERMINATION OF TRANSPIRATION IN PLANTS

GEO. F. FREEMAN

(WITH ONE FIGURE)

In plant-breeding work, which has engaged my attention for several years, a pressing need has been felt for some means of measuring the drought-resisting quality of individual plants. Morphological characters, such as small leaves, small and few stomata, pubescence, and thick epidermis, are characters which may be assumed to be correlated with drought resistance in that they tend to reduce transpiration and are characteristic of xerophytic plants in general. Moreover, it may be assumed that, other characters of two plants being equal, the one having the lower rate of transpiration per unit of leaf surface would be more suited to the drier portions of the plains region or to withstanding long periods of drought in the more humid districts. Some direct method of measuring the transpiration of plants growing in the field would be of great value therefore to the breeder in selecting for the quality of drought resistance.

At the beginning of our work in alfalfa breeding at the Kansas Experiment Station, no method was known to me which seemed to meet all of the requirements for securing data concerning transpiration for plant-breeding work. It was desired to use the plants selected as mother plants. Therefore they could not be taken up and planted, and the rate of loss of moisture determined by weight. Furthermore, on account of the very long tap roots of alfalfa, it would be impracticable to use a pot large enough to accommodate them without such pruning as would endanger the life of the plant, or at least make them little other than cut stems.

Although it is known that the cut stems of the plant when placed in water do not transpire normally, an attempt was first made to see if the differences sought could be revealed by this method. As a preliminary study and in order to ascertain the effectiveness of the potometer method in determining these individual differences in the transpiration rate as compared with the same plants growing in the soil, four species were selected which seemed to promise a large range of difference in transpiration. Accordingly, two individuals of each of the following species were selected from young potted plants in the greenhouse: *Coleus Blumei*, *Chrysanthemum leucanthemum*, *Pelargonium* sp., and *Portulaca oleracea*. The plants to be used on their own roots were repotted into glass tumblers of suitable size. This was done without disturbing the root system. Evaporation from the soil was prevented by covering the tops of the glasses with a good quality of dental rubber.

For the potometers the plants were cut from the pots at the surface of the soil, one or two of the lower leaves removed, and the stems inserted, through holes in the cork, into bottles containing tap water. The whole stopper was then carefully sealed with paraffin. Each potometer was placed by the side of its corresponding potted plant and the whole series left on a table in a well-lighted room.

During the investigation, which lasted approximately sixty hours, the transpiration rate was found by weighings made at intervals of about one hour during the day. In Table I the average transpiration rate for each plant during the whole of the experiment is shown, and the transpiration rate of the plants on their own roots (normal) is compared with that of the plants in the potometer by reducing the latter to percentages of the former.

TABLE I

	Potted plants on own roots; transpiration in mg. per sq. cm. of leaf surface per hr.	Cut stems in potometer; transpiration in mg. per sq. cm. of leaf surface per hr.	Cut stems in potometer; per cent. of normal transpiration
Daisy	7.21	1.44	20.
Coleus	2.77	0.37	13.3
Portulaca	1.72	0.47	27.3
Geranium	0.65	0.65	100.

It will thus be noted that there is a great difference between the average transpiration rate of a plant on its own roots and that of a cut stem of the same plant placed in water. Moreover, roughly speaking, this difference is greatest in those plants having the highest normal transpiration. This difference, however, may vanish altogether in plants with a low normal rate, as in the case of the geranium. A close scrutiny of Table I is sufficient to demonstrate that although the potometer will give some idea of the purely relative rates in different plants, it cannot be depended upon to give results which are at all comparable with their normal absolute transpiration rates. Thus if we arranged the plants according to their normal transpiration rates, they would stand from highest to lowest thus: daisy, coleus, portulaca, geranium; but if a similar arrangement were made from the results of the potometer experiment they would fall into the following order: daisy, geranium, portulaca, coleus. It was necessary therefore to find some other method for measuring transpiration whereby the plant could be kept on its own roots in the soil and in as nearly normal condition as possible.

As at least a partial solution of this problem, I would suggest the following method for measuring directly the transpiration of plants on their own roots, a method which provides at the same time for supplying them with a constant and uniform current of air. The method is based upon the well-known affinity of phosphorus pentoxid for water, whereby the two are combined and phosphoric acid formed. This compound has long been used as a drying agent and as a means of separating from air or other gases their water-vapor content, for the purpose of measurement. To this end known quantities of air are drawn through U-tubes containing P_2O_5.

Fig. 1 will show the method of setting up the apparatus. The apparatus consists essentially of a glass cylinder of suitable size to be used as a transpiration chamber, two U-tubes for P_2O_5, and an aspirator of known capacity. These are connected by rubber tubing, so that as the water flows from the aspirator a known quantity of air may be drawn through the cylinder and the pentoxid tubes. The cork in the top of the transpiration cylinder has two holes, one for the insertion of a thermometer and the other for the connecting tube to the pentoxid series. The cork for the bottom of the cylinder has two holes; through one is passed a short bent tube serving as an intake for the outside air; the other is to accommodate the stem of the plant. The cork is cut in halves, so that it may be fitted around the plant before inserting in the cylinder. If the stem be not large enough to fill the hole in the cork completely, this may be made close by packing with vaselined absorbent cotton. The phosphorus pentoxid tubes used were 21^{cm} long and were fitted with glass stop-cocks and with suitable intake and outlet side tubes. The P_2O_5 was arranged in layers held apart by glass wool, so that the air could pass through it freely. Graduated aspirators fitted with stop-cocks at the base, and rubber stoppers at the top, would of course be more suitable, but in the experiments I conducted 19.5 liter bottles, fitted with two-holed rubber stoppers, for the intake tube and the outflow water syphon, were used with satisfactory results.

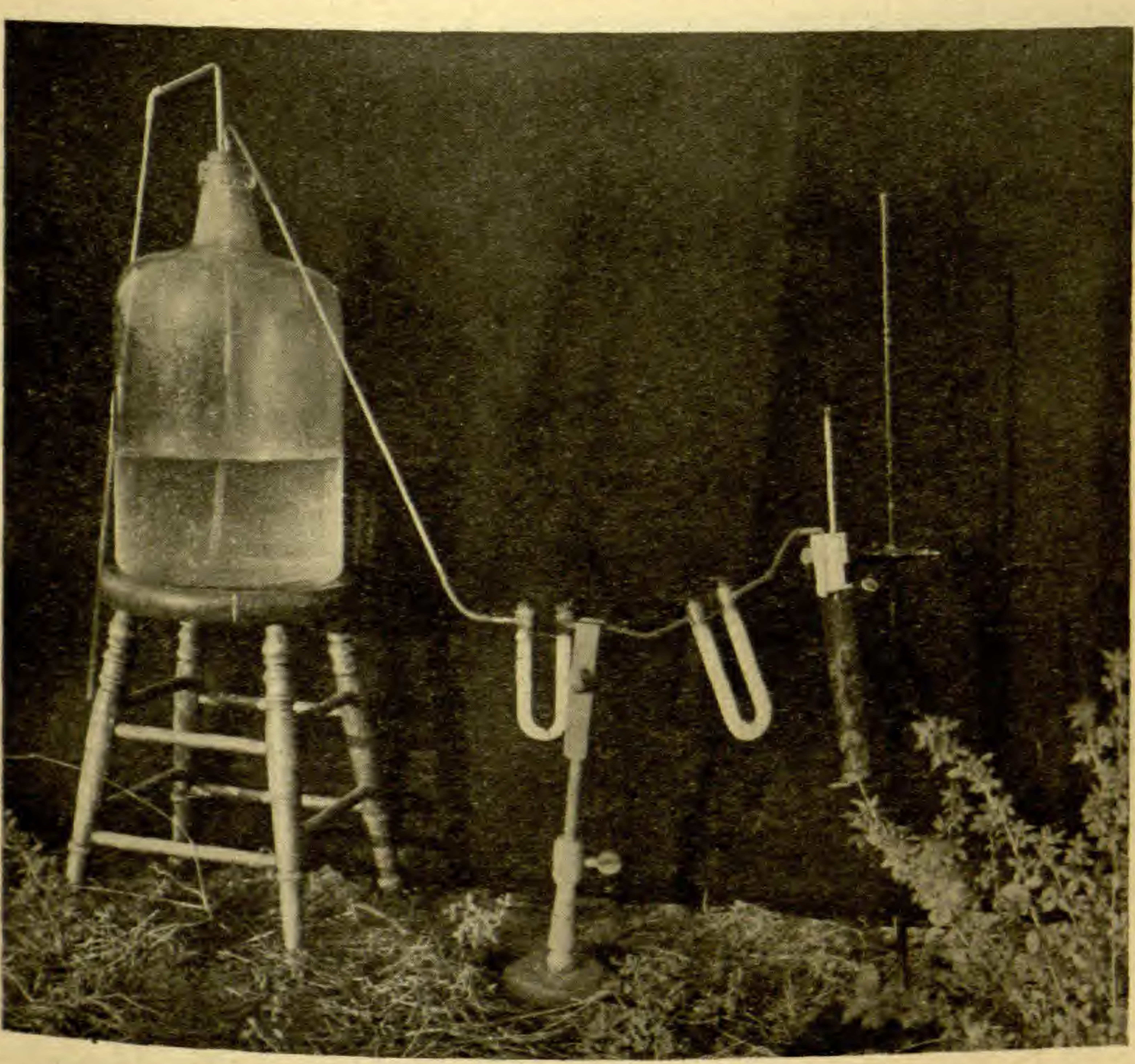

FIG. 1

For use the U-tubes are filled with P_2O_5, numbered and carefully weighed; the aspirator is filled with water and the whole apparatus set up, care being taken that all the connections are properly made and the joints air tight. The stop-cocks in the U-tubes are turned off, so that no moisture may reach the P_2O_5 between the time of weighing and the beginning of the experiment. The last operation is the insertion of the stem of the plant into the cylinder. This should be done as quickly as possible and the exact time noted. The stop-cocks in the U-tubes are then turned so as to allow free passage of air, and the water is started running from the aspirator. As the water flows from the aspirator, a steady current of air is thereby drawn into the transpiration cylinder, where it passes over the leaves, out through the outflow tube at the top, thence through the pentoxid tubes, where both the moisture of the normal air and that given off by the plant is absorbed. One tube is usually quite sufficient if it is fresh, but since I used the same tube a number of times without refilling, it was thought best to use a second tube as a guard, and as a means of indicating the exhaustion of the water-absorbing capacity of the first tube. The flow of water from the aspirator was so regulated that each experiment lasted approximately an hour. The area of leaf surface, the cubic contents of the transpiration cylinder, and the capacity of the aspirator in the experiments made were approximately in the proportion of 1:5:500. Of course the leaf surface varied considerably in the different experiments, since it was impossible to obtain the same amount each time. It will thus be seen that the air in the transpiration cylinder was changed 100 times in 60 minutes, or once in every 36 seconds. The rise in humidity in the cylinder due to transpiration of the plant can therefore easily be controlled by regulating the rapidity of the flow of air through the cylinder or by changing the amount of leaf surface inclosed. The exact time when the water ceases to flow from the aspirator is noted, the stop-cocks in the U-tubes are cut off, and the plant severed from the parent stem at the point where it enters the cylinder. The plant may be kept in the transpiration cylinder until ready to be weighed. When the flow of air through the cylinder ceases, the contained air soon reaches the saturation point and the plant is thus kept fresh until ready for weighing and for putting the leaves in the press for area determination.

The increase in weight in the pentoxid tubes gives the sum of the amounts of water transpired by the plant in the given time, plus the water present in the quantity of air used; therefore it becomes necessary to know the exact water content of the air. This may be found by use of the sling psychrometer, the wet and dry bulb thermometer, or by passing a given quantity of the normal air at the time of the experiment over phosphorus pentoxid in U-tubes in the same manner as in the case of the transpiration experiment itself. I prefer the latter method, as it is more direct and accurate, corrections are not required for altitude, barometric pressure, etc., and it calls for little extra labor to set up the additional apparatus and to run it simultaneously with the other. If all of the aspirators be of the same size, it will simply be necessary to subtract the increase in weight of the tubes used for the normal air from the increase in weight of those used in the plant series to find the actual amount of water vapor transpired by the plant in the given time. By dividing this amount by the product of the area of the leaves and the duration of the experiment expressed in minutes, and then multiplying this quotient by 60, the transpiration rate per hour per unit area is obtained.

The degree of accuracy of this method may be measured by checking it against the transpiration of a cut stem in a potometer or of a plant in a sealed pot. In my experiments I used the cut stem of an alfalfa plant. The leaves were removed from a few inches of the lower part of the stem, which was then inserted in a bottle of water through an opening in the cork which was thoroughly sealed over and around the stem with paraffin. By making several weighings of this plant before and after its use in the transpiration apparatus, its rate of loss of water was determined for the time before, during, and after its inclosure in the cylinder. The net increase in weight in the P_2O_5 tubes, after the weight of water present in the amount of normal air used has been subtracted from their total increase, should of course equal the loss in weight of the potometer during its inclosure in the cylinder. This method of checking was repeated three times with highly favorable results, details of which are shown in Tables II and III.

It will be noted from Table II that the last weighing of the potometer was made at 3:10, or two minutes before it was placed in the cylinder, and that the first weighing thereafter was made at 4:18, or five minutes after the air ceased to pass over the P_2O_5 tubes. The amount of water transpired during these intervals must be subtracted from the total of 0.150 grams as shown in Table II before comparing it with the net gain of the P_2O_5 tubes. Again referring to Table II, it

TABLE II

POTOMETER WEIGHINGS

Time	Total weight: grams	Number of minutes since last weighing	Loss: grams	Loss per min.: grams	Remarks
2:46 P. M.	108.890	....	......	......	
3:10 P. M.	108.775	24	0.115	0.0048	The rate in normal air before the experiment
4:18 P. M.	108.625	68	0.150	0.0022	Includes the period during which the plant was inclosed
4:48 P. M.	108.540	30	0.085	0.0028	The rate in normal air after the experiment

TABLE III

Plant placed in cylinder 3:12 P. M.
Water stopped flowing from aspirator 4:13 P. M.
Duration of experiment 61 minutes.

Total gain in weight of P_2O_5 tubes	0.343 grams.
Amount of water in air used	0.217 grams.
Net gain of P_2O_5 tubes	0.126 grams.

will be seen that for the first of these intervals the rate was 0.0048$^{\text{gm}}$ for two minutes or 0.0096$^{\text{gm}}$; and for the second, 0.0028$^{\text{gm}}$ for five minutes or 0.0140$^{\text{gm}}$, making a total of 0.0236$^{\text{gm}}$. Now, $0.1500 - 0.0236 = 0.1264$; it is thus seen that the two methods check within 0.004$^{\text{gm}}$ for a one hour's run.

It would be useless to give the details of the other two check experiments, since they were carried on in exactly the same manner and extended through approximately the same length of time. It will suffice simply to show the results of the three experiments, corrected for time, as follows:

TABLE IV

	Transpiration as recorded by potometer	Transpiration as shown by P_2O_5 tubes	Difference
1st experiment	0.1264$^{\text{gm}}$	0.1260$^{\text{gm}}$	0.0004$^{\text{gm}}$
2nd experiment	0.0690	0.0660	0.0030
3rd experiment	0.0614	0.0624	0.0011

It will be noted again from Table II that the transpiration rate was greatly reduced during the time the plant was in the cylinder. This was of course due to the increase in relative humidity in the air, owing to the transpiration from the leaves. It may be suggested, therefore, that the plant was thus shown to be under abnormal conditions. However, the normal air in the room was at a temperature of 27° C. and contained 10.9^{mg} water per liter. According to the Smithsonian tables, such air at saturation contains 25.4^{mg} per liter; the relative humidity of the normal air was therefore 42.5 per cent. Since 19.5 liters of air were drawn through the transpiration cylinder, from which the P_2O_5 collected 343^{mg} of water, the air in the cylinder contained 17.5^{mg} per liter. This would give a relative humidity of 68.8 per cent. The change in relative humidity from the outside air to that inside the cylinder was thus seen to be from 42.5 per cent. to 68.8 per cent. This cannot be termed abnormal, since much greater changes in the outside air take place from day to day, and the range in a given day is very often even wider. Since the air was completely changed in the cylinder every thirty-six seconds, this condition of humidity must have been reached during that time, and have remained constant for the remainder of the hour. Owing to changes in temperature and light a plant in the open will vary much more in the transpiration rate in the course of a few hours than did the alfalfa plant when placed inside the cylinder. Until the exact effect of light, humidity, and temperature are known, therefore, and reduced to formulae whereby, the conditions of the given transpiration experiment being known, the transpiration constant for that plant can be estimated, all comparative transpiration experiments must be made at the same time, and under conditions as nearly identical as possible. The results of such experiments are moreover valuable only in proportion to the degree in which identical conditions are approached.

In order to test the practicability of this method in the field, I selected two alfalfa plants, growing within about 12^{dm} of each other, which showed marked differences in form and texture of the leaves. They had been previously cut at the same time and the stems were therefore of the same age and stage of growth, that is, just beginning to bloom. Three simultaneous comparative experiments were made on these two plants, in order to ascertain whether any constant difference could be shown to exist in their transpiration rates per sq. cm. of leaf surface. The following table gives the details of this work. The column marked "check" contains the data derived from the apparatus set up to measure the quantity of water in the normal air.

An examination of Table V shows a constantly higher rate for no. 64 over that of no. 67; the rate of difference, however, was very variable. Unfortunately a larger leaf area was taken each time for no. 67, so much so that the relative humidity in its cylinder was higher than that of no. 64 in the first two experiments. This fact would place no. 67 at a disadvantage in these two experiments, since the higher relative humidity would retard to a greater degree its transpiration rate. Had it not been for the third experiment, therefore, in which, notwithstanding the greater leaf area of no. 67, the total transpiration of no. 64 was greater, thereby causing a higher relative humidity within its cylinder, the series would have been inconclusive. This third experiment, however, confirms the results of the other two, by showing that plant no. 64 may even overcome the disadvantage of a higher relative humidity and still transpire nearly twice as much per sq. cm. of leaf surface as the other.

It may be well to add here several suggestive details for those who wish to use this method. On account of the strong affinity of P_2O_5 for water, it must be kept very tightly sealed. Moreover, it is a difficult substance to handle, especially to transfer to the mouth of a small U-tube. I have found it very convenient to keep it in such a flask as is made especially for holding anhydrous copper oxid. This has a small neck out of which the P_2O_5 can readily be poured into the test tube, is fitted with a good ground-glass stopper within, and a ground-glass cap without. I have found that phosphorus pentoxid keeps perfectly dry in this form of bottle; the stopper does not stick fast, and it is ready for use at any time.

In filling the U-tubes it is well to push a bit of glass wool into the tube with a glass rod, pour on this about 0.5^{gm} of P_2O_5, then more wool and more P_2O_5, until the tube is filled. A bunch of glass wool is put on the top, so that in handling the tubes the P_2O_5 will not get into and clog the intake and outflow tubes while they are being handled, between the times of weighing and setting up the apparatus.

TABLE V

FIRST EXPERIMENT

Plant no.	Date September	Experiment began	Experiment ended	Total gain in P_2O_5 tubes: mg.	Amount of air used: liters	Mg. of water in air used	Net gain of P_2O_5 tubes: mg.	Time: duration of experim't in minutes	Total number of leaves	Total area of leaves: sq. cm.	Loss mg. per hour per sq. cm. leaf surface	Relative humidity of air in cylinder	Relative humidity of external air	Temperature inside of cylinder	Temperature of external air
		P. M.	P. M.									%	%		
64.........	21	3:50	4:50	375	19.5	130	245	60	33	22.282	10.9	77.5	28.7	26°.5 C.	25° C.
67.........	21	3:51	4:55	418	19.5	130	288	64	14	32.457	8.3	86.4	28.7	26°.5 C.	25 C.
Check.....	21	3:48	4:51	130	19.5	....	....	63	....	......	....	....	....	.....	.....

SECOND EXPERIMENT

Plant no.	Date September	Experiment began	Experiment ended	Total gain in P_2O_5 tubes: mg.	Amount of air used: liters	Mg. of water in air used	Net gain of P_2O_5 tubes: mg.	Time: duration of experim't in minutes	Total number of leaves	Total area of leaves: sq. cm.	Loss mg. per hour per sq. cm. leaf surface	Relative humidity of air in cylinder	Relative humidity of external air	Temperature inside of cylinder	Temperature of external air
		A. M.	A. M.												
64.........	23	10:16	11:26	324	19.5	148	175	70	12	17.130	8.7	59.8	28.	28°.5 C.	28 C.
67.........	23	10:22	11:29	353	19.5	148	205	67	14	41.981	4.3	65.3	28.	28°.5 C.	28 C.
Check.....	23	10:14	11:15	148	19.5	....	....	61	....	......	....	....	....	.....	....

THIRD EXPERIMENT

Plant no.	Date September	Experiment began	Experiment ended	Total gain in P_2O_5 tubes: mg.	Amount of air used: liters	Mg. of water in air used	Net gain of P_2O_5 tubes: mg.	Time: duration of experim't in minutes	Total number of leaves	Total area of leaves: sq. cm.	Loss mg. per hour per sq. cm. leaf surface	Relative humidity of air in cylinder	Relative humidity of external air	Temperature inside of cylinder	Temperature of external air
		P. M.	P. M.												
64.........	23	4:13	5:29	422	19.5	126	295	77	29	21.252	10.9	80.4	25.3	28 C.	27° C.
67.........	23	4:16	5:40	415	19.5	126	289	84	11	33.810	6.1	79.1	25.3	28 C.	27° C.
Check.....	23	4:10	5:14	126	19.5	....	....	68	....	......	....	....	....	.....	.....

It is advisable to have a number of tubes already filled where work is being done in the field, in order that several parallel experiments may be run before returning to the laboratory for making weighings. The same tube may be used repeatedly so long as there is a part of it filled with dry P_2O_5. Care should be taken, however, to set up the tube in the same way each time, that is, to have the air enter and pass out of the tube in the same direction. The reason for this is that the phosphoric acid, after being formed from P_2O_5 plus water, will itself take up water. If now the tube be turned so that perfectly dry air in leaving the tube passes over the phosphoric acid, which has previously taken up an excess of water, it will itself take up water from the acid and the tube will lose weight.

It requires some experience to know how much leaf area to include in the cylinder for each experiment. After a few trials, however, one will learn to estimate sufficiently closely the capacity of the apparatus so as not to overcrowd it. Overfilling is indicated by the collection of moisture drops on the side of the cylinder, showing that the air inside has reached the saturation point. This may be remedied either by reducing the amount of leaf surface inclosed, or by increasing the rate of flow of the water through the aspirator.

This method of measuring transpiration may be said to be only a modification and a new adaptation of the methods used by LAMARLIÈRE[1] and E. and J. VERSCHAFFELT,[2] in that air is drawn over the plant in the same manner, and the transpired moisture collected in U-tubes containing hygroscopic substances which are not contained in the vessel with the plant, but are connected in the same aspirating series, so that the air, after passing through the evaporation cylinder, next passes through the U-tubes. However, a different absorbent is used and the apparatus, moreover, is adapted for measuring the transpiration of plants on their own roots. The essential point of difference, nevertheless, lies in the condition of the air as supplied to

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[1] GANEAU DE LAMARLIÈRE, L., Recherches physiologiques sur les feuilles, developpées à l'ombre et au soleil. VI. Transpiration. Rev. Gén. Botanique 4:529. 1892.

[2] VERSCHAFFELT, E. en J., De transpiratie der planten in koolzuurorije lucht. Botanisch Jaarboek (uitgegeven door het kruidkundig genootschap "Dodonaea" te Gent) 2:305. 1890.

the plant. While in my method normal air is supplied, both of the above investigators first completely dried the air before allowing it to reach the plant. This is detrimental, for as BURGERSTEIN[3] says: "In Gegensatze zur zweiten hat die dritte Methode, bei welcher die evaporierte Wassermenge aus der Gewichtszunahme hygroskopische Substanzen in Erfahrung gebracht wird, den Nachteil das sich die Pflanze in einer zu trockenen Luft befindet."

SUMMARY

1. In plant breeding and in physiological and ecological work, it is very necessary to have some accurate and practical method of measuring the transpiration of plants.

2. The potometer method does not give the normal transpiration rate of a plant, neither can it be depended upon to give a rate which is even comparative as between different plants.

3. By the method herein described the transpiration of a plant under known and constant conditions may be accurately measured.

4. It is possible by this method to demonstrate individual differences in the transpiration rates in different plants of the same species.

5. By the use of this apparatus, data may be secured to serve as a basis for plant selection and breeding.

MANHATTAN, KANSAS

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[3] BURGERSTEIN, ALFRED, Die Transpiration der Pflanzen 12. 1904.

THE TOXIC PROPERTY OF BOG WATER AND BOG SOIL

ALFRED DACHNOWSKI

(WITH SIX FIGURES)

The publication of recent work on the existence of injurious substances excreted from roots of plants (**19, 12, 16,**) has necessarily resulted in disclosing to ecologists some overlooked data. Repeatedly it has been shown that the commonly accepted environmental factors are not always sufficient to explain certain important problems of association among plants. It must be admitted, therefore, that there is a problem to be solved not only regarding the relation of one field crop to another, but also with reference to the succession of one plant society by another.

In the study of the structural adaptations of bog plants and the causes of their occurrence in bog areas, various theories have been brought forward. The idea generally current among workers in the ecology of bogs is that the geographical distribution of bogs and the local differences in the flora of bog areas and swamps have probably come about chiefly through post-glacial migrations and changes in the physiography of the habitat. The cause determining the structural characteristics of bog plants is generally understood to lie in the "physiological dryness" of the habitat. But while some writers lay stress upon low temperature of the bog substratum and the presence of drying winds as the prominent factors (**11, 7, 8**), others emphasize humous acids in the soil, abundance of soluble salts, and alkalies (**15**). More recently the effect has been correlated with low temperature and lack of aeration of the subsoil rather than with acidity (**6, 17**).

In 1904, while at work on the ecology of ravines near Ann Arbor, Mich., the writer became convinced that the reactions of plants on their habitat were equally as great and profound, in some cases, as the influence of edaphic and climatic factors. In various places the decomposed remains of an earlier vegetation led to mechanical and chemical changes in the soil, the extent of which was more effective toward breaking up the flora into a heterogeneous formation, accompanied by a frequent replacement of one dominant group by another (3). These reactions of plants seemed still more pronounced in bog societies. During the past year a grant obtained from the Emerson McMillin Research Fund afforded an opportunity to test by physiological methods the nature of plant reactions. The investigation here reported forms a part of a more extended study on the ecology of Buckeye Lake. This brief report is merely intended to reveal the toxic character of bog water and bog soil. A more detailed account, together with data obtained from an inquiry on the possible isolation and identification of the toxic bodies by a method of fractional distillation, will appear later.

Buckeye Lake is situated 40^{km} east of Columbus, Ohio, in a region free from limestone. It is an extensive body of water about 16^{km} long and 1.6^{km} wide, and was formerly known as the Licking reservoir. The reservoir was originally a lake in the glacial drift. Its chief supply today is the south branch of the Licking River. In 1883 and again in 1834 its water surface was raised by forming a dike around the west end. Near the northern bank, and midway between the small towns of Lakeside and Avondale, is a bog island, approximately one-tenth the dimensions of the lake. Soundings which were made to determine the character of the peat gave $9–12^{m}$ as the depth of the island. With its surface vegetation of distinctly northern forms, the island is virtually a water culture on a large scale. The plants are not dependent for any important part of their food on the soil; rooting in the soil at such depth is not possible here. The vegetation presents two well-marked zones: a central one consisting of sphagnum, several species of Carex, Menyanthes trifoliata, Dulichium arundinaceum, Scheuchzeria palustris, Eriophorum, Oxyzoccus, Drosera, Rhus vernix, Aronia nigra, and others; and a marginal zone which includes besides various forms of Salix, Alnus incana, A. rugosa, Ilex verticillata, Cornus canadensis, etc., a few small oaks, and Acer rubrum as the dominant form. Mycorhiza is quite common in both zones. Many plants are strictly hydrophilous, and such plants of the cultivated variety as are grown in either zone for experimental purposes show marked difficulties of absorption, soon become stunted, and often take on xerophilous characters. In the following account these zones are spoken of as the *central zone* and the *maple-alder zone* respectively. The bog water and bog soil used in the experiments were brought every month to the laboratory in glazed earthen-ware jugs from stations which remained identical throughout the period of investigation.

To ascertain the osmotic pressure of the bog water, determinations of the freezing-point were made. As compared with the freezing-point of pure distilled water the average lowering in the various determinations is 0°007 and 0°009 for the central station and the maple-alder station respectively. Compared with similar determinations for Michigan bogs (**13**) the bog water of Buckeye Lake has no higher concentration.

Data on temperature deviations in the bog substratum are omitted here as having no particular significance in the problem at hand in this region. They do not seem adequate to account for the differences, since plants growing in soil, nutrient solutions, or bog water are equally affected. If there is any property of bog water which prevents rapid and successful invasion of plants, this inhibiting influence must rest not in the physical character of the habitat alone, but in some chemical quality as well.

A study of the acidity of the bog water under examination gave results differing but little from those obtained in the Michigan bogs (**13**). Titrations were made with a *n*/100 KOH solution. The bog water from both zones is alkaline to methyl orange and acid to phenolphthalein. A comparison of the acidity figures shows that the bog water of the central station is uniformly less acid than that of the maple-alder zone. Boiling, however, greatly reduces the acidity of the bog water in the latter station. This is due to the escape of carbonic acid. In the light of the results here brought out, the presence of the toxic bodies is not necessarily to be correlated with high acidity.

To determine the presence and possible nature of the injurious substances affecting plants through their toxic effects, the following experiments were planned. Familiarity with the behavior and the conditions of development of *Marchantia polymorpha* (**4**) suggested marchantia gemmae of known history as an indicator for preliminary observations. A large number of gemmae were placed in crystallizing dishes (9.5×4^{cm}) containing 100^{cc} of bog water. Cultures were prepared, containing respectively the untreated bog water from each zone and spring water. The gemmae were allowed to float on the surface of the solutions. An additional series of test conditions was arranged at the same time from the bog water of each zone variously treated. In the table given below, culture medium no. 3 is bog water aerated daily by means of a rubber bulb; no. 4 is prepared by mixing with the bog water dry calcium carbonate and then filtering off the solution; no. 5 is treated by shaking the bog water with carbon (lampblack) and then filtering off the solution; no. 6 is a culture medium obtained by growing in distilled water in battery jars a set of representative plants from each zone. The attempt is made here to simulate undrained bog conditions and to test the water for excretions of roots. To discover whether the effects of poisons were also manifest in the bog substratum, a relatively concentrated aqueous extract was prepared. Quantities of the subsoil from each station were taken from a layer 30^{cm} below the surface vegetation and dried in an oven at a temperature varying between 52° and 60° C. One gram of the material was then mixed with 100^{cc} of distilled water and left standing for several days. The soil solution thus obtained was used as culture medium no. 1. There were thus produced six conditions for each zone in which it was possible to test the bog soils, the excretions of bog plants, the effect of aeration, and toxic ingredients of bog water. The following Table I shows the results of growth in length of marchantia gemmae during a period of twelve and twenty-five days.

It will be noticed that the gemmae made scarcely any growth in the bog soil solution, while in the untreated bog water a fairly good growth occurred. An inhibiting action of these solutions is plainly marked. Evidence of this is further obtained from a microscopic study. For the first five or six days the gemmae made some growth, but after ten days development ceased. Only in the untreated bog water the two opposite growing points of the gemmae were thrifty in appearance. They gradually gave rise to narrow threadlike filaments, which at the end of the twentieth day began to broaden at the tip. In all solutions growth was greatly increased after treatment. Exceptions were noted only when the bog water used was collected just following

TABLE I

MARCHANTIA POLYMORPHA

Culture solution	Growth in 12 days Length in mm.	Growth in 25 days Length in mm.	Remarks
I. Central zone:			
1. Bog soil extract..........	1 and less	......	dead after 8 days
2. Bog water untreated.....	1 –1.5	1.5– 2	filamentous outgrowths
3. Bog water aerated.......	4 –6	6 – 8	
4. Bog water neutral.......	5 –5.5	6 – 7.5	
5. Bog water filtered.......	7.5–8	11 –12	
6. Bog plant water.........	2	5	
7. Spring water............	3 –4	4 – 5	
II. Maple-alder zone:			
1. Bog soil extract..........	1	1 – 2	larger number dead after 12 days
2. Bog water untreated.....	6 –7.5	11	
3. Bog water aerated.......	6 –8	12	
4. Bog water neutral.......	6	10.5–14	
5. Bog water filtered.......	5 –8	10 –11	
6. Bog plant water.........	5 –6	10 –12	

a period of heavy rains, or when the vessels containing the bog water were left uncorked. The differences in growth in the various solutions were less marked, showing that the degree of toxicity at one concentration was entirely different at another. The same is to be said of solution no. 6; its toxic character became more marked with increase in the time during which the bog plants were under cultivation.

Briefly summarized, the data thus far agree in showing (1) that the contrasts in the relative growth of plants in solutions from the maple-alder zone were less marked than those in the solutions from the central zone; (2) that the inhibiting factors of bog conditions are in part due to the presence of injurious water-soluble substances; (3) that the central zone possesses these toxic bodies more decidedly than the maple-alder zone; and (4) that in both zones the toxicity can be corrected by a method of aeration and by the use of calcium carbonate and carbon black.

A series of experiments was next made in the form of bog water cultures with various cultivated plants. Half-liter glass jars of the Mason pattern were used, and prepared in the conventional way. The seeds were germinated in sawdust. Germination in quartz sand and in paraffin-coated disks of galvanized iron wire was found less satisfactory. Transplanting was done when the plants had attained a height of 5–6^{cm}. The culture media used were prepared as indicated for marchantia. From two to six plants were used for 400^{cc} of solution. Each experiment was continued for 7 to 10 days according to the amount of water transpired before renewing the culture solution. The different cultures always stood side by side in the university greenhouse, so as to give uniform environment. The light conditions were the same also; direct sunlight was avoided by cloth screens. In place of temperature and moisture readings, measurements of the evaporation power of the air were obtained from

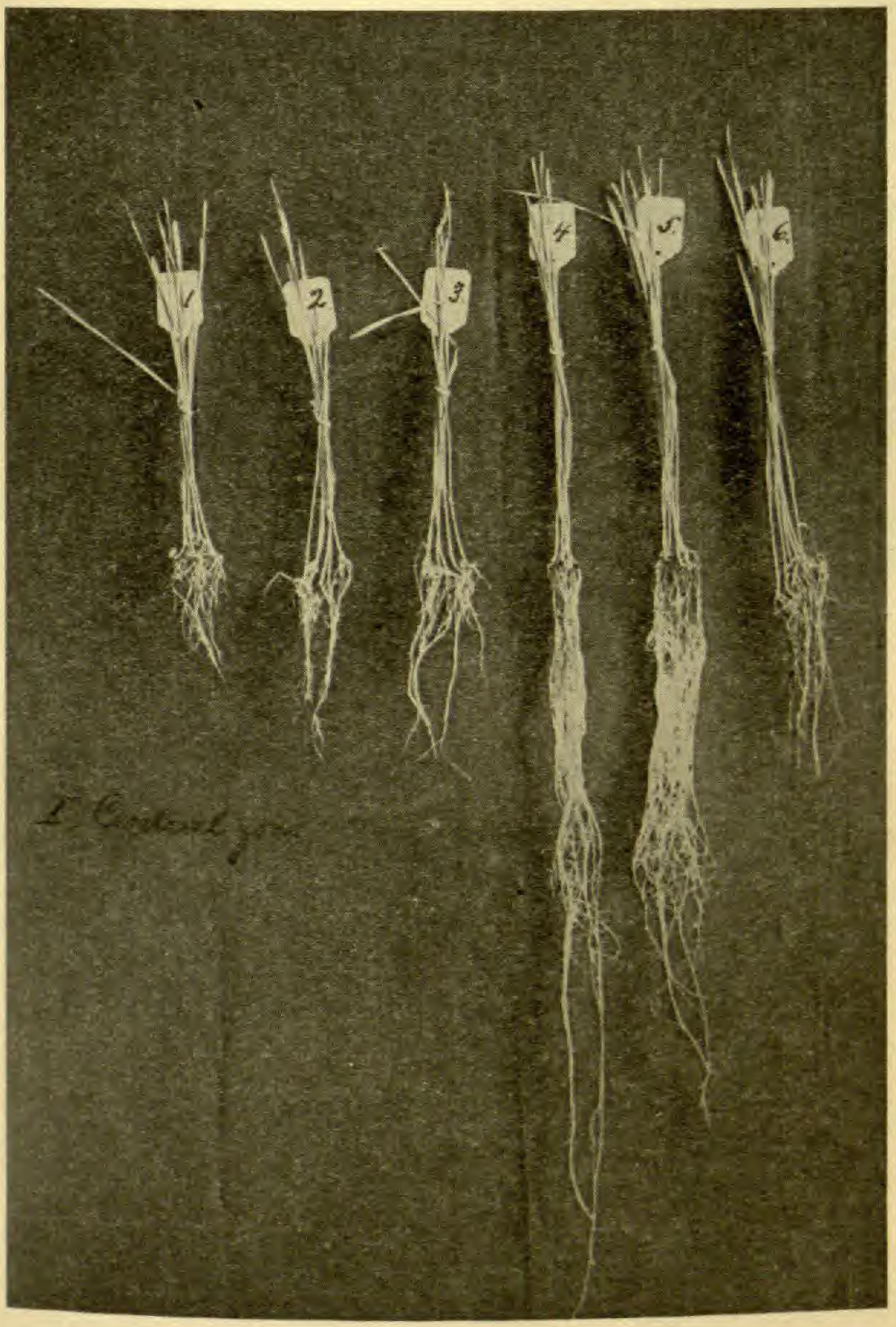

FIG. 1.—Wheat plants from various cultures of bog water and bog soil. Numbers as in the text, p. 133. Six plants from each solution.

the records of two atmometers. The instruments were prepared on a scale as given by LIVINGSTON (**14**). The integration of humidity, temperature, and air-current data given in a weekly rate varied between 200 and 270^{cc}.

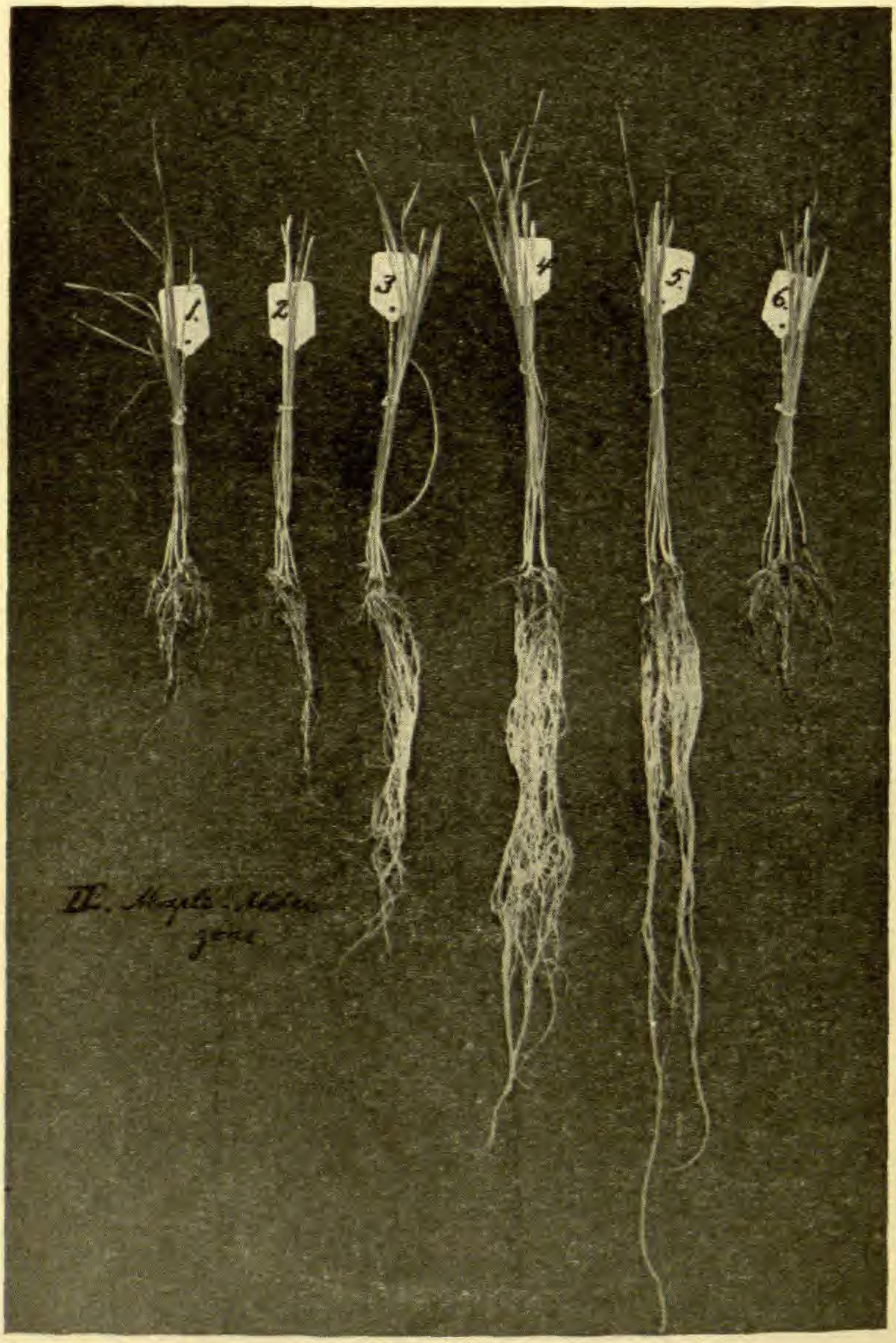

FIG. 2.—Wheat plants from various cultures of bog water and bog soil. Numbers as in the text, p. 133. Six plants from each solution.

As an aid for comparing the rate of growth of similar plants in different media various criteria were used. The main emphasis, however, is placed upon the total transpiration for a definite period of growth, since the difference between the amounts of water lost has been shown to be equivalent to the difference between the physiological value of the solutions (19). Other criteria employed were the condition of the roots, green and dry weight of plants, length and anatomical structure of roots, stem, and leaves. None of these alone can be regarded as accurate measures of plant activity, but taken together they generally agree in indicating the relative value of the results. Without dwelling here at length upon the exact data derived from these experiments, only the results in transpiration-increase are given below in tabular form. The percentage increase in transpiration is calculated for the larger number of the plants upon the basis of the quantities for the bog soil solution considering it as unity.

TABLE II

Percentage increase in transpiration

Culture solution	Wheat	Corn	Phaseolus	*Vicia faba*	Elm	Buckeye	Cowpea	Oats	Tradescantia
I. Central zone:									
1. Bog soil extract*......	0	0	0	0	0				0
2. Bog water untreated...	19	16	113	22	68	0	0		9.8
3. Bog water aerated.....	55	27	201	...	...	1.3	20		...
4. Bog water neutral.....	209	91	...	100	...	...	...		8.6
5. Bog water filtered.....	245	52	225	215	94	38.8	42		24.7
6. Bog plant water.......	54	22	184	...	...	...			
II. Maple-alder zone:									
1. Bog soil extract*......	0	0	0					0	
2. Bog water untreated...	38	65	287					90	
3. Bog water aerated.....	164	71	...					44	
4. Bog water neutral.....	298	136	335					148	
5. Bog water filtered.....	256	76	...					...	
6. Bog plant water.......	11	40	178					113	

*4^{gm} of bog soil and 400^{cc} distilled water.

An increase in the dry weight of roots and tops was obtained in all plants growing in the solutions treated with $CaCO_3$ and carbon black. For the corn and wheat respectively the increase in the dry matter produced varied from 20 per cent. to 50 per cent. during the time of the experiment.

It will be observed that the evidence derived from wheat, corn, bean, elm, and buckeye seedlings (two years old), and other plants yields results and conclusions similar to those pointed out for marchantia. The plants grown in the bog soil extract and in the untreated bog water show stunting clearly in the roots. The tops of the plants are more nearly alike, except in the stronger solutions. Marked differences in the degree of sensitiveness to toxicity or of the oxidizing power of roots are noticeable for the various plants. Phaseolus and *Vicia faba* proved thus far to be the most plastic plants. In the solutions filtered with $CaCO_3$ and carbon black the tops surpass in development the growth of roots. The plants show marked variations in the internal structure of leaf and stem. Those grown in the bog soil extracts show distinct xerophilous characters. The leaves are reduced in area, thicker, of a deeper green, and with revolute

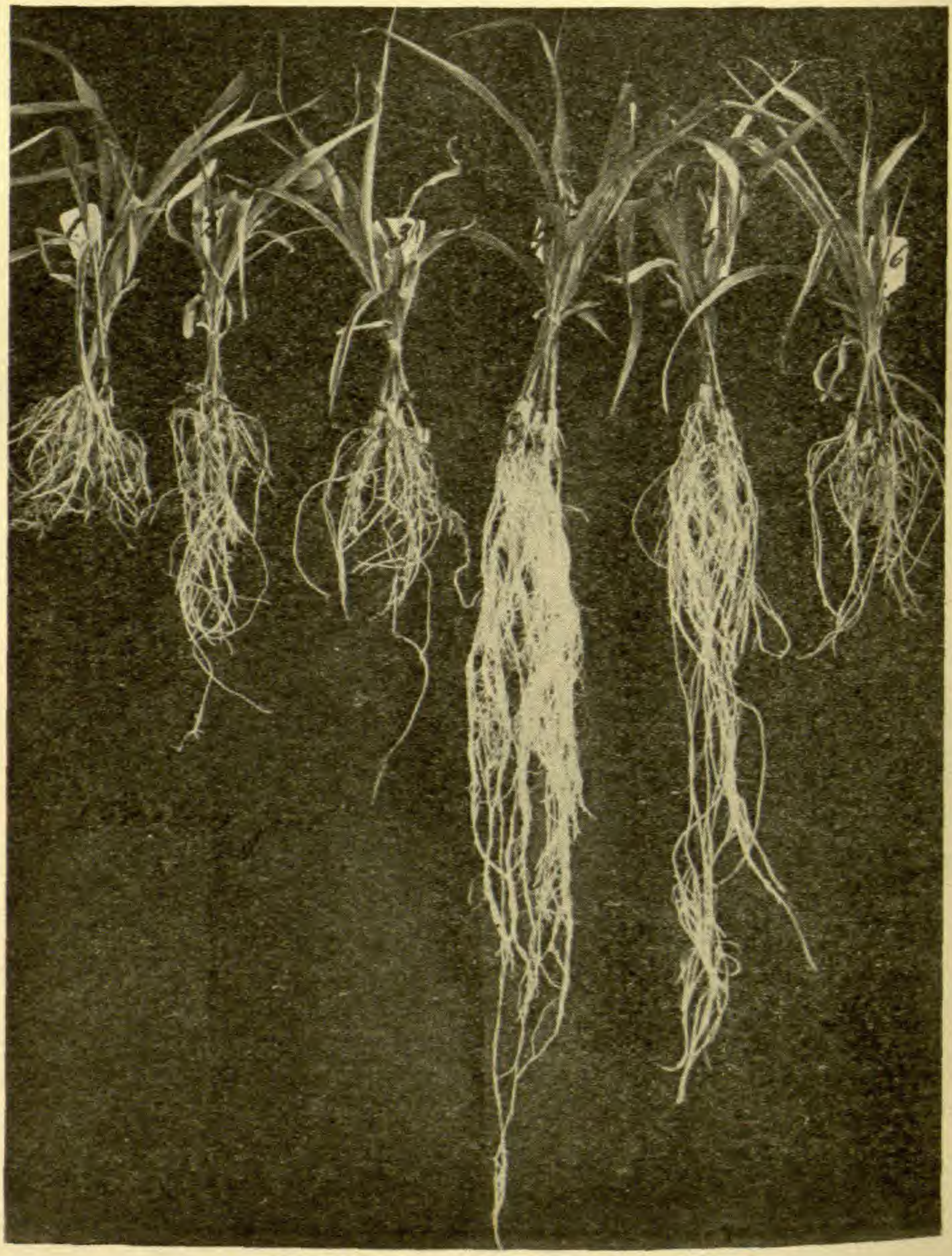

FIG. 3.—Corn plants from the various cultures of bog water and bog soil. Numbers as in the text, p. 133. Four plants from each solution.

margins; responses which cannot be attributed to light but to a reduced transpiration current (**18**) consequent upon the toxicity of the habitat (*figs. 1–6*).

It is worthy of note in this connection that when grown in a 0.01 per cent. solution of strychnin sulfate, atropin sulfate, or other toxic body of a similar nature and with a high reducing power, the same dwarfing effects are obtained with Phaseolus. When treated with $CaCO_3$ and carbon black the solutions become highly beneficial. The accelerated growth and transpiration are no doubt due to the

FIG. 4.—Corn plants from the various cultures of bog water and bog soil. Numbers as in the text, p. 133. Four plants from each solution.

presence of these substances in small amounts, and the behavior of the plants is very much like those grown in a 0.0001 per cent. solution of strychnin or atropin sulfate.

The striking agreement of results obtained from such a variety of material seems sufficient proof that the factors inhibiting plant growth and plant association and succession are at least in part due to the plants themselves. Carbon black and calcium carbonate add no soluble matter to the solutions (**2**), hence it becomes certain that the beneficial effects cannot be due to the introduction of nutrient material but to the taking up, i. e., the adsorption of injurious substances present. This would indicate, therefore, that the changes in the soil conditions are produced by noxious substances formed in the absence of O_2. They may be products of decomposition, perhaps they are in part plant excreta, but whatever their nature, they are water-soluble toxic bodies which retard oxidation in the tissues and decrease transpiration, thus causing xerophily, stunting, and even death.

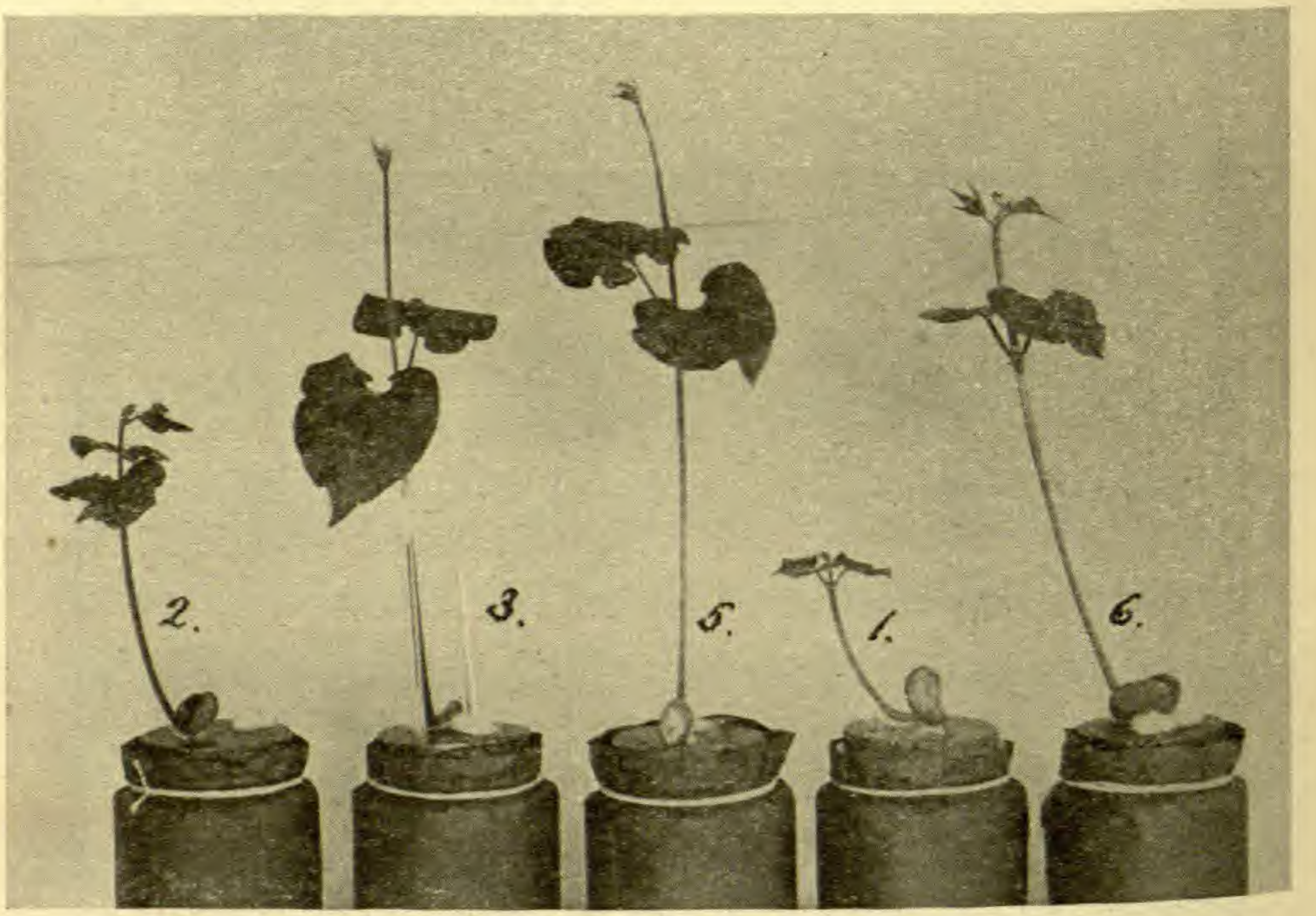

FIG. 5.—Average plants of *Phaseolus multiflorus*, showing effect of bog water variously treated. Numbers as in the text, p. 133.

It may be readily questioned whether part of the response arises from a deficiency of oxygen in the soil. The evidence obtained by

BENNETT (1) is against aerotropism in roots. It follows, therefore, that results reported as due to lack of aeration in the bog substratum are really due to toxicity. Under natural conditions the inhibiting effect is eliminated by aeration, a slow process of oxidation preventing the accumulation of injurious plant excreta in the soil. However, on account of the great demand for oxygen, the process can be carried on efficiently only near the surface. Beneath, the active bodies are more plentiful in the dead material than in the plants themselves. An undrained peat substratum, therefore, must necessarily cause more marked deterioration in development and permit a different association and succession of plants than a drained habitat.

FIG. 6.—*Vicia faba* from cultures of the central zone. Numbers as in text, p. 133. Transpiration data and photograph by Miss FREDA DETMERS.

That the response to toxic bodies when present in small amounts may lead to acceleration of growth has become evident also in connection with a biometric study on the annual wood-increment in *Acer rubrum* (**5**). Measurements upon such trees from the outermost edge of the maple-alder zone as were nearly the same in size, age, concentric growth of wood, and general environment, as similar forms found in woodlots near the shore gave the following differences in the frequencies of rings:

Width of rings in mm	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5
Frequencies in bog-habitat	16	10	23	20	27	12	20	5	7	5
Frequencies in woodlots	26	30	31	9	6					
Width of rings in mm		6	6.5	7	7.5	8	8.5	9	9.5	10
Frequencies in bog-habitat		5	5	6	1	2	0	1	0	2
Frequencies in woodlots										

The mode and the variation constants derived from them are equally interesting:

Habitat	Bog	Woodlots
Mode	3 mm	2 mm
Mean	3.425±0.098	1.701±0.038
Standard deviation	1.870±0.069	0.566±0.027
Coefficient of variability	54.60±2.55	33.28±2.46

We have here the type and the place-habit from two distinct edaphic conditions. The differences in the soil habitat have led to physiological variations which changed not only the type, but the variability and even the sign of the skewness. Quantity and quality of the wood have been affected; as products of the environment they are a measure of environmental conditions.

To attempt to correlate the data with the work of previous authors on toxic action is obviously impossible. Definite knowledge of the chemistry of bog water and bog soils is lacking at present. There are always present a great variety of chemical and biological agents, and products of decomposition, which may react collectively. Hence definite conclusions cannot be based upon the results obtained here. The limited extent to which these experiments have been carried, gives no more than a suggestion of the possibilities.

OHIO STATE UNIVERSITY
Columbus

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BRIEFER ARTICLES

THE FLOWERS OF WASHINGTONIA

(WITH FIVE FIGURES)

While my paper on the genus Washingtonia[1] was passing through the press, I had the pleasure of receiving from Dr. BECCARI a copy of his recent monograph of the Coryphine palms of America.[2] In his treatment of Washingtonia this distinguished palmographer gives much weight to certain floral characters which have been heretofore overlooked, and it seems desirable that these should be brought to the attention of American botanists, in order that their value may be tested by field studies.

These distinctions relate to the characters of the filaments, the stigma, and the summit of the ovary. In the flowers of Washingtonia the filaments of the stamens opposite the lobes of the petals are consolidated with them for nearly one-third their length, and are much thicker than the free filaments opposite the sinuses.

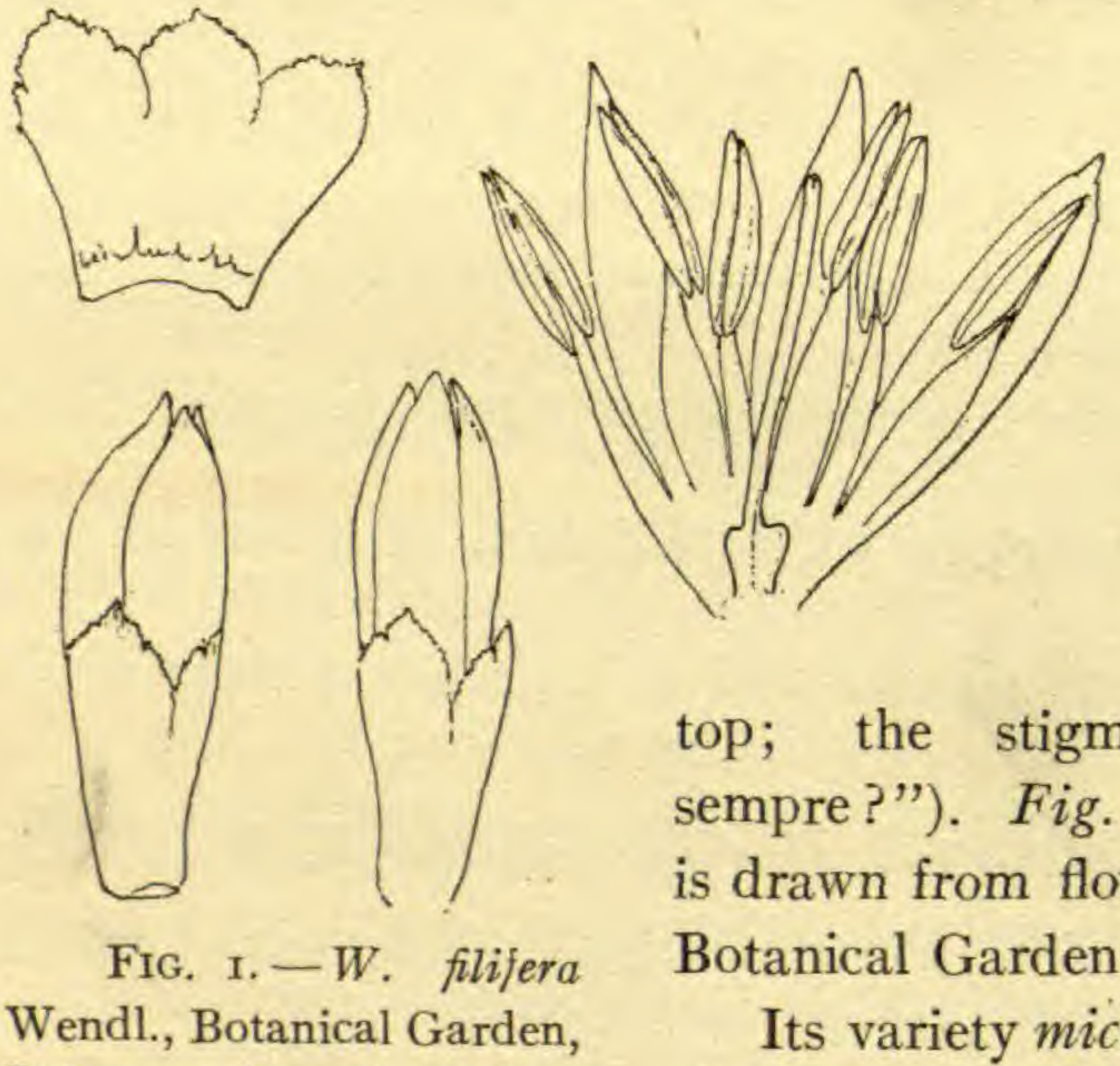

FIG. 1.—*W. filifera* Wendl., Botanical Garden, Palermo, August, 1906.—O. BECCARI. ×3.5.

Washingtonia filifera Wendl. is defined as having the lobal filaments thickened-fusiform; the ovary turbinate, 3-lobed, and strongly gibbous at top; the stigma undivided ("puntiforme, sempre?"). *Fig. 1* represents this species, and is drawn from flowers of a tree growing in the Botanical Garden at Palermo, Italy.

Its variety *microsperma* Beccari differs in its slightly less strongly fusiform lobal filaments, but mostly in its somewhat smaller flowers and decidedly smaller seeds. *Fig. 2* shows the variety, drawn from flowers of a tree in the Garden Ricasoli, Port Ercole, Tuscany.

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[1] PARISH, S. B., A contribution toward a knowledge of the genus Washingtonia. BOT. GAZETTE 44:408–434. *figs. 12.* Dec. 1907. I take this opportunity to correct two errors: Page 409, line 18, for "eleven" read "fifteen;" page 415, line 3 from bottom, for "the trees" read "most of the trees."

[2] BECCARI, ODOARDO, Le Palme Americane della tribú Corypheae. Estratto dalla Webbia 2:pp. 343. Oct. 1907. Firenze.

The rank of species and variety seems here assigned somewhat arbitrarily, and it may be of interest to give the history of the trees which have been taken as their respective types. The palm accepted as typical *W. filifera* is a certain tree in the Garabaldi Garden, at Palermo, Italy, which was raised from seed at the Botanical Garden in the same city, in 1874, and which began to flower in 1892. The source of the seed is not known.

Five or six living plants of the *Prichardia filifera* of his trade catalogue were exhibited by LINDEN at the international exhibition at Florence, in May, 1873. Three of these exhibition plants are now large trees, producing flowers and fruit, and these are taken by BECCARI as the types of his *W. filifera microsperma*. As these palms are directly traced to LINDEN, and were exhibited by him as *Prichardia filifera*, it would seem probable that they are about as near as we are likely to get to authentic representatives of WENDLAND'S first published species.

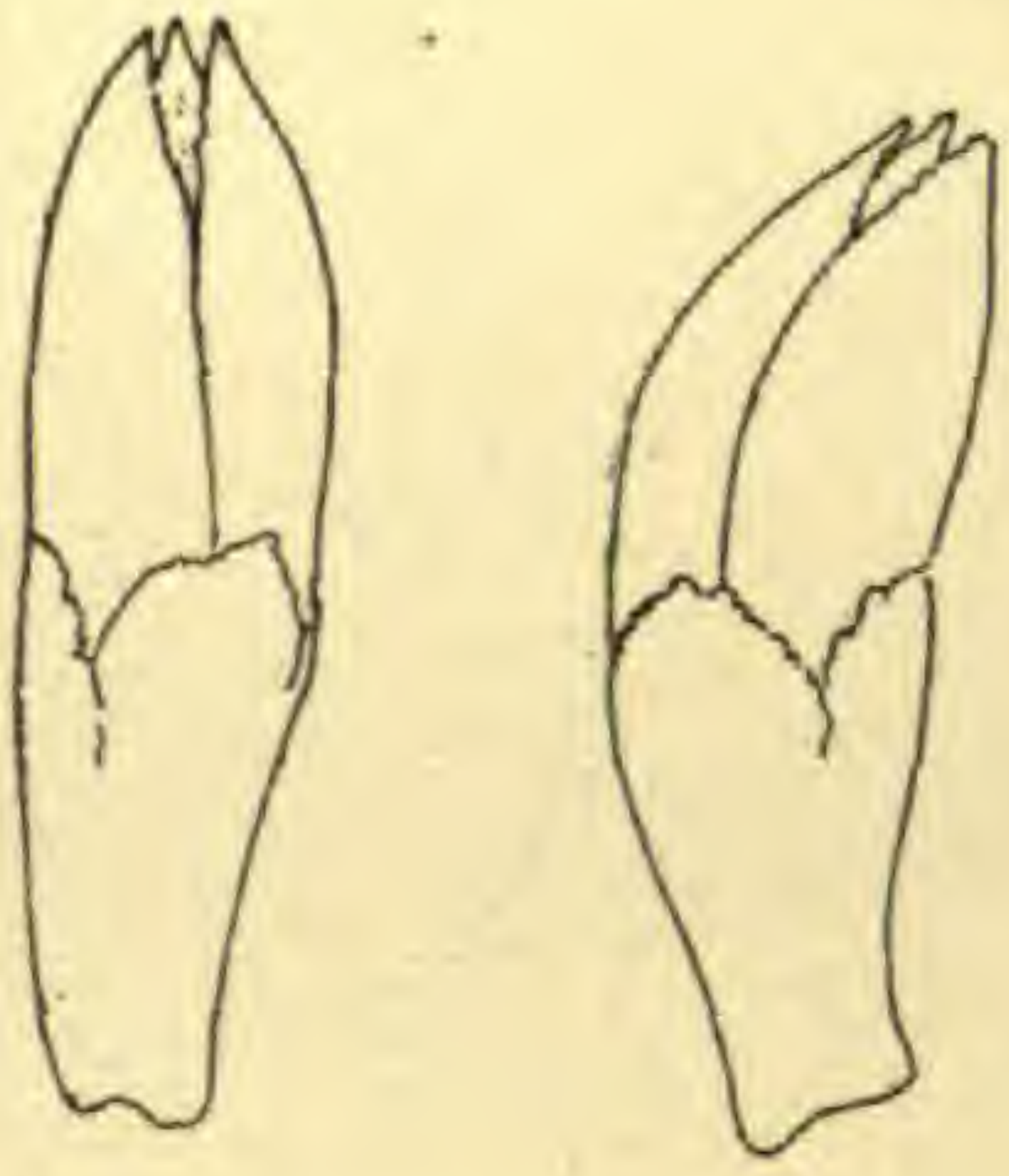

FIG. 2.—*W. filifera microsperma* Becc., Garden Ricasoli, Port Ercole, Tuscany, August, 1906.—O. BECCARI. ×3.5.

The flowers of *W. robusta* Wendl. are described as having the lobal filaments tuberculately enlarged at the coherent base, and abruptly subulate above; stigma bilabiately 3-parted into three short lobes; ovary turbinate at summit, but neither excavated nor gibbous. On these grounds BECCARI sustains the specific rank of this palm; and should they prove constant, it may be desirable to follow this disposition. *Fig. 3* is from a flower of a tree in the Botanical Garden at Palermo. Its historical identification with the Wendlandian plants is not related. The first two characters hold in the flowers of Californian trees which have been referred here, so far as concerns the few specimens I have examined. The ovarian character is less satisfactory.

W. gracilis Parish has flowers very near those of the last, except that the summit of the turbinate ovary is very distinctly 3-lobulate. *Fig. 4* was drawn from a flower taken from Mr. McLEOD'S tree, a panicle of which is the subject of *fig. 10* of my previous paper. BECCARI regards this palm as a variety of *W. robusta*. It would be possible, although in my opinion undesirable, to regard all the Washingtonias as varieties of a single polymorphous species, but the one now under consideration would of all be the least capable of such comprehension. Without question floral characters are of greater diagnostic value than those drawn from foliage or habit; but when the latter are of marked distinction, and apparently constant, they cannot be refused great weight.

FIG. 3.—*W. robusta* Wendl., Botanical Garden, Palermo, August, 1906.—O. BECCARI. ×3.5.

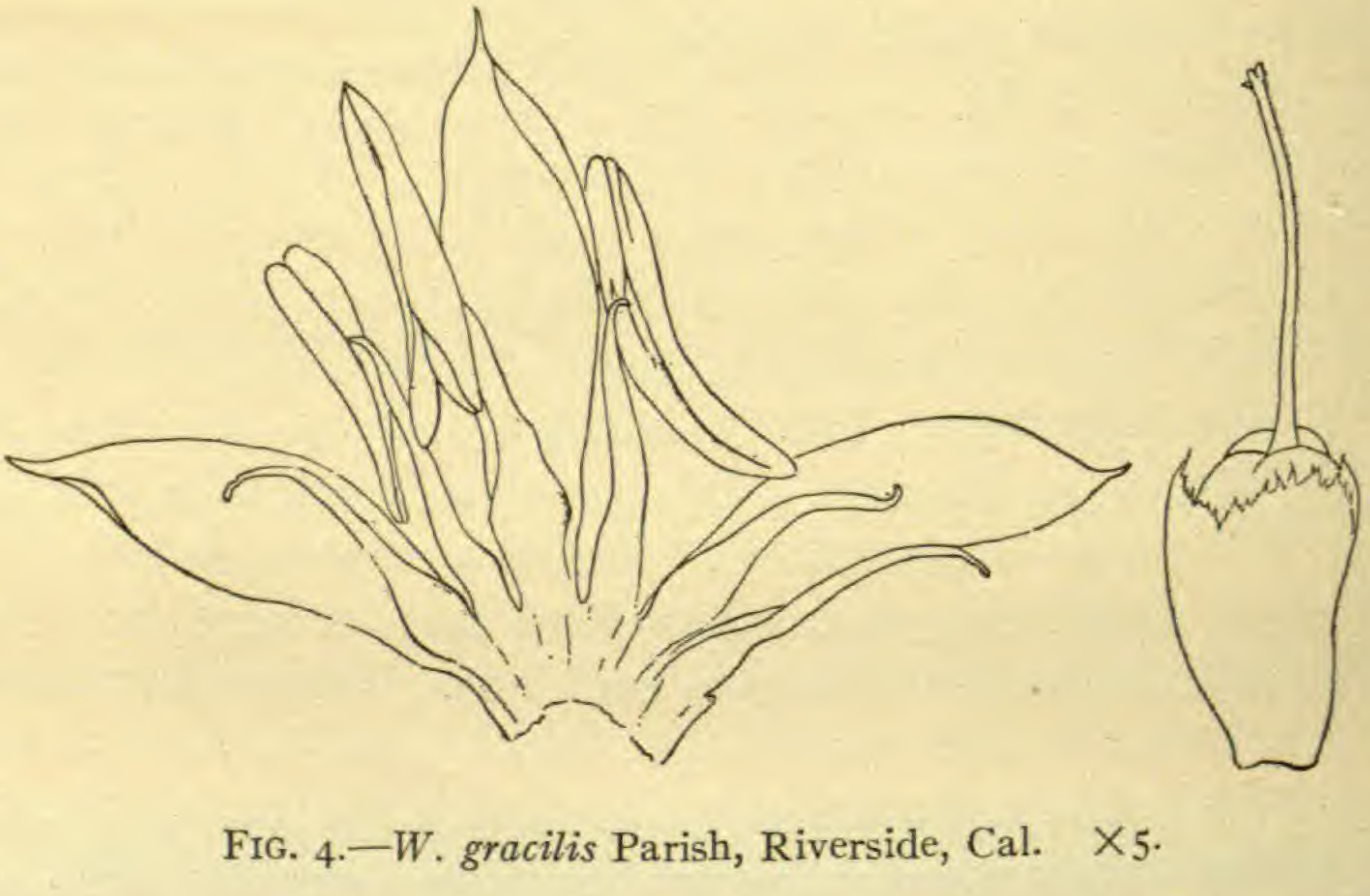

FIG. 4.—*W. gracilis* Parish, Riverside, Cal. ×5.

BECCARI had not had an opportunity of examining flowers of *W. sonorae* S. Watson, and he regards it as a doubtful species, which may be a variety of *W. robusta*, suspecting that the obtusely triangular insertion of the petiole in the leaf blade may not prove a constant character. Through the kindness of Dr. B. L. ROBINSON, of the Gray Herbarium, I have received a few flowers taken from the type specimen of this species, collected by WILLIAM PALMER at Guaymas, Mexico. One of these is represented in *fig. 5*, the anthers being omitted, as all had fallen from the flowers. It will be seen that this has the characters assigned to *W. filifera* so far as the filaments are concerned, the character of *W. robusta* as to the divided tip of the stigma, and the markedly lobate ovary of *W. gracilis*. Such a combination of characters throws a shadow of uncertainty on their value. It must be remembered, however, that they are drawn from a study of too few individuals. What is now desirable is that the proposed characters, both those drawn from the flower and fruit, and from the foliage and habit, should be put to the test by the examination of numerous examples, growing under varying conditions. Especially is it to be hoped that botanists who may have the opportunity should study carefully the groves near Guaymas, and those reported to exist on the seacoast of northern Lower California. Until such extended studies shall be made it cannot be considered that we stand on altogether firm ground in the discrimination of the various indicated species and varieties of Washingtonia.

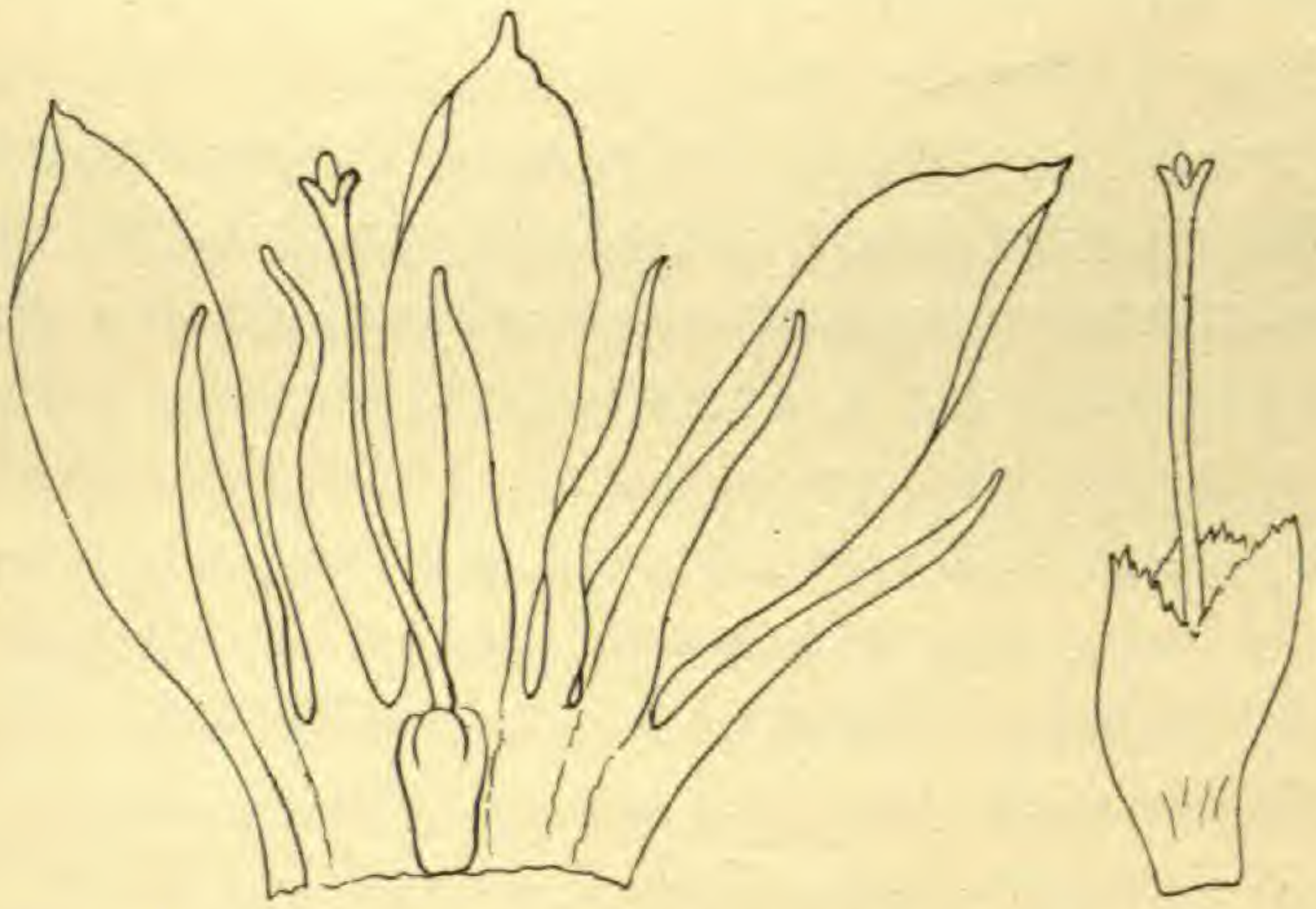

FIG. 5.—*W. sonorae* S. Watson. From PALMER'S type, Guaymas, Mexico. ×5.

For the drawings from which *figs. 1, 2,* and *3* are reproduced I am indebted to the kindness of Dr. BECCARI. They are enlarged seven diameters. *Figs. 4* and *5* are from drawings by Mrs. CHARLOTTE M. WILDER, and are enlarged ten diameters. All the drawings are reduced one-half in the reproduction.—S. B. PARISH, *San Bernardino, California.*

CURRENT LITERATURE

BOOK REVIEWS

The question of sex

The determination and inheritance of sex have presented problems of peculiar interest and also of peculiar difficulty. CORRENS[1] has grappled with them from a new point of view and has gained some surprising results. His point of attack is through the hybridization of plants having different sex characteristics, as for example the crossing of a dioecious species with a hermaphrodite or monoecious species. His most important conclusions are that each germ cell of the forms he has used carries a progamic sex tendency, but that the actual determination of sex is syngamic, that is, it results from the chance that brings together two germ cells having particular sex tendencies. In *Bryonia dioica* he shows that the female germ cells carry always the same sex tendency, namely to produce females; while the male germ cells are of two kinds, half bearing the female tendency and half the male. The male tendency dominates over the female, so that when the eggs are fertilized by these two kinds of sperms, those which receive sperms bearing the female tendency produce females, and those which are fertilized by sperms bearing the male tendency produce males. The females are homozygous (♀+♀) with respect to sex and the males are heterozygous (♀+♂). Evidence is presented that the same condition exists in *Melandrium album*, as shown by crossing with *Silene viscosa*, and he considers it very probable that all dioecious plants are similarly constituted. The author is properly cautious in discussing the applicability of these results to other classes of organisms than those with which he has dealt, and especially to animals, but he discusses WILSON'S noteworthy studies upon the idiochromosomes of the Hemiptera,[2] and points out how readily these can be interpreted on the basis of a sex relation similar to that discovered in higher plants.

An epigamic modification of sex through the influence of nutrition or other external conditions is not deemed to be wholly excluded, owing to the fact that one sex may carry the other in a recessive or latent condition, and it is at least conceivable that such latency may be to some extent modifiable by external factors.

In respect to the sex of hermaphrodite and monoecious plants, it is noted that in all cases of "mosaic" inheritance which have been sufficiently investigated

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[1] CORRENS, C., Die Bestimmung und Vererbung des Geschlechtes nach neuen Versuchen mit höheren Pflanzen. pp. 81. *figs. 9.* 1907. Berlin: Gebrüder Borntraeger.

[2] WILSON, E. B., Studies on chromosomes. III. The sexual differences of the chromosome groups in Hemiptera, with some considerations on the determination and inheritance of sex. Jour. Exp. Zool. **3**:1. 1906.

there is a distinct factor present for the mosaic condition, so that the sex of such plants is not to be looked upon as due to the presence of the male- and female-producing units alone, but to the presence of a factor determining the tendency to be hermaphrodite or monoecious respectively.

The field for investigation which has thus been thrown open is a very inviting one, and it is to be hoped that other dioecious species which have nearly related hermaphrodite or monoecious species among both plants and animals will be made to yield whatever support they may for the generalizations CORRENS has made.—GEORGE H. SHULL.

Plankton of Illinois River

Four years ago, this journal reviewed the first part (1903) of KOFOID'S *Plankton of the Illinois River*,[3] which dealt with the quantitative investigations and general results. There has just appeared the second part, which deals with the organisms of the plankton and their seasonal distribution.[4] The character of the work, with its mass of statistics, forbids an adequate review. As was stated in the preceding review, this series forms the most important contribution yet made to the subject of river plankton, and the work has been carried on with the most painstaking care. In the discussion of species, plants occupy 45 pages, and animals 230. The plant groups considered are Bacteriaceae, Schizophyceae, Chlorophyceae, Bacillariaceae, Conjugatae, and certain seed plants. Some general conclusions in reference to the seasonal changes are stated, conclusions that are promised detailed discussion in a later paper. For example, each month is characterized by certain plankton features, dependent upon a certain range of hydrographic, thermal, and chemical conditions, and of illumination. There is a certain range of component species, and a range of numbers of individuals, the proportions varying from month to month, and constituting one of the main elements in the seasonal changes of the plankton. Transitions from month to month are most profound at seasons of greatest environmental changes, as at the times of vernal increase and autumnal decline in temperatures. In general two types of plankton were found, the summer and the winter, the vernal and autumnal types being only transitions between the two when organisms from both are present. The winter plankton is characterized by a small number of species peculiar to that season, and a number of perennial forms; the summer by a larger number of summer organisms with the perennial forms.

In reference to the question whether the plankton of streams differs from that of lakes and ponds, the author states that it may be distinguished from them in being a mixed plankton (due to the mingling of planktons from all sources in the

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[3] BOT. GAZETTE 37:472. 1904.

[4] KOFOID, C. A., The plankton of the Illinois River, 1894–1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part II. Constituent organisms and their seasonal distribution. Bull. Ill. State Lab. Nat. Hist. 8:Article I. pp. vii+360. 1908.

drainage basin), in being subject to extreme fluctuations in quantity and constitution, and in containing no species peculiar to it.—J. M. C.

Floral mechanism

Such is the title of a work whose first part has just appeared.[5] In this part twelve types of common spring flowers are selected, all of which are readily cultivated and may thus be kept under continued observation. In the case of each one of these flowers there is a full account of all the details of structure and the problems presented. A definite scheme of work is elaborated, so that in due order all questions are raised and answered. The work is intended for botanical students, teachers of elementary botany, "lovers of flowers," and candidates for examination.

A single example, selected at random, will illustrate the scheme. Under *Viola odorata* the following topics are presented: history, distribution, nomenclature, description, variations, floral diagram, sectional elevation, development, special mechanism, pollination, cleistogamy, monstrosities, fruit and seed, comparison of allied types, theoretical considerations, and note on Fibonacci phyllotaxis systems. All this is illustrated by five plates, three of them colored.

The large page and handsome type are exceedingly attractive, and the colored plates are as fine as we have seen. In short, the whole appearance of the book is ornate. But still, we wonder at its purpose. The author explains this as follows: "The general idea has been the provision of a methodical framework for the inclusion of all facts of observation and experiment, which may serve as an introductory scheme admitting of progressive elaboration and perfection with the attainment of new information." This sounds as if there was a pedagogical motive; but if it is for the teaching of botany, the tremendous emphasis laid upon a few "type" flowers is something new or something very old; at least it holds no relation to botany as at present developed. If it is a scientific treatise, which the author disclaims, it is too simple and diffuse. If it is for ornament, it is a great success. If it is to give opportunity for the display of admirable printing and three-color work, we have seen nothing better.—J. M. C.

MINOR NOTICES

Kew Index.—The third supplement to this invaluable work has appeared,[6] including names and synonyms of all genera and species from the beginning of 1901 to the end of 1905. The second supplement, which appeared in 1904, and included names through 1900, was under the direction of W. T. THISELTON-

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[5] CHURCH, ARTHUR HARRY, Types of floral mechanism; a selection of diagrams and descriptions of common flowers, arranged as an introduction to the systematic study of angiosperms. I. Types I–XII (Jan. to April). Royal 4to. pp. vii+211, with 39 colored plates and numerous figs. Oxford: Clarendon Press. 1908. $6.75.

[6] Index Kewensis plantarum phanerogamarum. Supplementum tertium. pp. 193. Oxford: Clarendon Press. 1907. 28*s*.

DYER. The third supplement appears under the direction of D. PRAIN, the new director of the Kew Gardens. The supplement is a record of the remarkable activity in taxonomy during the five years covered, and critical judgment in reference to this great volume of work is becoming increasingly difficult. In fact, the list is a record of publication rather than an expression of opinion. For example, 476 acknowledged species of Crataegus are recorded for the five years, and Rubus is not far behind. To review such a work is impossible. It is only necessary to announce its appearance.—J. M. C.

North American Flora.—The third part of volume 22 has just been issued. It contains Grossulariaceae by F. V. COVILLE and N. L. BRITTON, 43 species (2 new) being referred to Ribes and 40 (4 new) to Grossularia; Platanaceae (6 spp.) by H. A. GLEASON; Crossosomataceae (4 spp., 1 new) by J. H. SMALL; Connaraceae (3 genera, 9 spp.) by N. L. BRITTON; Calycanthaceae (4 spp.) by C. L. POTTER; and the beginning of Rosaceae by P. A. RYDBERG, the key recognizing 18 tribes, 6 of which are completed and the seventh (Potentilleae) begun. Among the 19 genera of Rosaceae presented, Horkeliella (3 spp.) is new; and 29 new species are described, being distributed among Opulaster (4), Spiraea (5), Petrophytum, Aruncus (3), Chamaebatiaria, Lindleyella, Vauquelinia, Sericotheca (6), Horkelia (6), and Ivesia.—J. M. C.

Marine algae of Sweden.—KYLIN[7] has published a monograph of the algal flora of the west coast of Sweden. The species of the four following groups are first presented: Chlorophyceae (12 fams., 26 gen., 71 spp.), Fucoideae (16 fams., 51 gen., 105 spp.), Bangiales (5 gen., 11 spp.), Florideae (16 fams., 55 gen., 107 spp.). One new genus (*Acrothrix*) of Fucoideae is described. The second part of the contribution (80 pp.) presents the ecological factors and analyses the geographical distribution. At the conclusion of the discussion, the 105 species of Fucoideae and the 118 species of Florideae (incl. Bangiales) are distributed into arctic, subarctic, boreal-arctic, cold-boreal, and warm-boreal groups. The paper concludes with "biological" notes, a full bibliography, and an adequate index.—J. M. C.

Das Pflanzenreich.[8]—Part 33 contains the 9 genera of Aloineae (Liliaceae) by A. BERGER, *Chortolirion* being a new genus with 4 species. Altogether, 370 species are presented, many of them with numerous cultivated forms and entering into hybrids. The large genera are Aloe (178 spp., 14 new), Kniphofia (67 spp., 2 new), Haworthia (60 spp.), and Gasteria (43 spp.).

Part 34 contains the Sarraceniaceae by J. M. MACFARLANE, who gives an interesting account (in English) of the structure of the vegetative organs and the

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[7] KYLIN, HARALD, Studien über die Algenflora der schwedischen Westküste. pp. 288. *pls.* 7. Upsala. 1907. (Inaugural dissertation.)

[8] ENGLER, A., Das Pflanzenreich. Heft 33, Liliaceae-Asphodeloideae-Aloineae von A. BERGER. pp. 347. *figs. 141 (817)*. *M*17.60. Heft 34, Sarraceniaceae von J. M. MACFARLANE. pp. 39. *figs. 10 (43)*. *M*2.40. Leipzig: Wilhemn Engelmann. 1908.

insect relations of this remarkable family. Heliamphora and Darlingtonia are still recognized as monotypic, but a new species of Sarracenia (*S. Sledgei*, from the Gulf states) is described, 7 in all being recognized.—J. M. C.

Lactarius and Russula.—BATTAILLE[9] has published a monograph of these genera, to which he gives the group name Astérosporés, on account of their echinulate or granulate spores. He describes all of the European species, adding personal observations to the diagnoses of the various authors. The keys are admirably constructed to lead easily to the species. For Lactarius the author has adopted the classification of QUÉLET. For Russula the two grand divisions (Leucosporae and Xanthosporae) of QUÉLET are continued, but a number of subsections are defined and named. At the same time, it is shown, that the color of the spores is not a very reliable character, and the principal groups must be defined by a varying combination of characters.—J. M. C.

Grout's Mosses.—The fourth part of this work,[10] issued in April last, maintains the reputation of its predecessors and brings the author's task within sight of completion. Part V, the final one, is announced for 1909, to contain some plates and text missing from this part, together with an index and other useful adjuncts.

Part IV completes the Leskeaceae and contains a good part of the Hypnaceae, with the usual excellent reproductions of illustrations from the *Bryologia Europaea* and SULLIVANT'S *Icones*, and some characteristic details which are original.—C. R. B.

Index of desmids.—A supplement to NORDSTEDT'S *Index Desmidiacearum*, which was published in 1896, has just appeared.[11] The interval of over ten years has witnessed such an accumulation of material that a large supplement became necessary. The new bibliography included bears testimony to the great activity of the students of the group during this period, about 500 titles being enumerated, under 120 authors. To examine this vast amount of material and to organize it for the purpose of the index has called for an amount of labor that the students of desmids are sure to appreciate.—J. M. C.

Flora of Greece.—The last fascicle of Halácsy's *Conspectus Florae Graecae* was published in 1904, and now a supplement has been issued.[12] The first fas-

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[9] BATAILLE, FRÉDÉRIC, Flore monographique des Astérosporées (Lactaires et Russules). pp. 100. Besançon (route de Vesoul, 18): The author. 1908. *fr.*3.

[10] GROUT, A. J., Mosses with hand lens and microscope. A non-technical handbook of the more common mosses of the northeastern United States. Part IV. Imp. 8vo. pp. 247–318. *pls. 56–75. figs. 134–165.* Brooklyn: The Author, 360 Lenox Road, Flatbush. 1908. $1.25.

[11] NORDSTEDT, C. F. O., Index Desmidiacearum citationibus locupletissimus atque bibliographia. Supplementum. pp. 150. Berlin: Gebrüder Borntraeger. 1908.

[12] HALÁCSY, E. DE, Conspectus Florae Graecae. Supplementum. pp. 132. Leipzig: Wilhelm Engelmann. 1908.

cicle appeared in 1900, so that four to eight years have elapsed since the various parts appeared. During this period the author says that local and visiting botanists have been extremely active in exploration, discovering new stations, plants new to Greece, and new species. All these additions have been brought together in this supplement, so that the *Conspectus* may be regarded as fairly complete again.—J. M. C.

Anatomy of dicotyledons.—The translation of the SOLEREDER'S *Systematische Anatomie der Dicotyledonen*[13] into English gave the author opportunity to revise the work and to add much supplementary matter. This has now been brought together at the instance of the German publisher for the benefit of those who have the original. This large *Erganzungsband* will be desirable for all those libraries that have the first two volumes, for it contains an immense amount of material. Besides the additional data, the concluding remarks have necessarily been revised. —C. R. B.

NOTES FOR STUDENTS

Sieve tubes in Laminariales.—Miss SYKES[14] has investigated the anatomy and histology of Macrocystis and Laminaria, chiefly *M. pyrifera* and *L. saccharina*. A few other species, such as *Sacchariza bulbosa*, *Laminaria digitata*, *Alaria esculenta*, and *Nereocystis Luetkeana*, were also examined to supplement the main results. Chief attention was paid to the morphological nature of the trumpet hyphae and of the true sieve tubes, the presence or absence of protoplasmic connecting threads, the development of sieve plates, and the nature of callus.

Some of the conclusions may be summarized as follows: (1) The trumpet hyphae in *M. pyrifera* and *L. saccharina* are to be looked upon as true sieve tubes. They represent the original central cells of the thallus modified, and may be termed primary pith filaments. Though they differ as to their degree of development, they are certainly homologous with the secondary sieve tubes of Macrocystis, which are similarly derived from the modified primary cortex of the young thallus. (2) It is believed that the histology of the sieve plates in the primary pith filaments and secondary sieve tubes is essentially the same. Threads are formed traversing the young sieve plates, and each gives rise in the older plate, apparently by means of ferment action, to a slime string inclosed in a rod of callus. In Macrocystis each original thread first divides to form a group, and each thread of a group forms its own callus rod, but finally, by fusion, only one slime string is produced from each group. The older sieve plates are obliterated by the deposition of a large mass of callus over their surface, and callus is also formed throughout the length of the old sieve tubes. (3) The callus is to be looked upon as a

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[13] SOLEREDER, H., Systematische Anatomie der Dicotyledonen. Ein Handbuch für Laboratorien der wissenschaftlichen und angewandten Botanik. Erganzungsband. Imp. 8vo. pp. viii+422. Stuttgart: Ferdinand Enke. 1908.

[14] SYKES, M. G., Anatomy and histology of *Macrocystis pyrifera* and *Laminaria saccharina*. Annals of Botany **22**:291–325. *pls. 19–21*. 1908.

hydrated form of cellulose, and is found in *L. saccharina* and *L. digitata* in various states of hydration. It appears to be produced in the young sieve plates by the action of a ferment on the already formed cell wall, but is afterward accumulated by deposition from the protoplasm, both on the surface of the sieve plate and on the lateral walls of the tube. (4) The histology of the sieve tubes agrees with that of spermatophytes. The only contrast between the method of obliteration of the sieve tubes in Laminariaceae and Pinus is that in the latter the heads of the slime strings are still visible on the free edge of the callus cushions, and the path of the slime strings can be traced throughout the callus mass; while in Macrocystis and Laminaria the callus is laid down by the protoplasm of the sieve tubes over the heads of the slime strings, so that they are buried by the overlying callus and no perforations can be traced through the rod. (5) The protoplasmic connecting threads throughout the tissue of *M. pyrifera* and *L. saccharina* were demonstrated, but it is impossible to be certain of their formation in case of secondary attachment.—S. YAMANOUCHI.

Primitive angiosperms.—Miss SARGENT has developed more fully her view as to the origin of the monocotyledons,[15] which was stated formally in 1903. The present paper of course deals with the characters of primitive angiosperms, but this is a necessary corollary to the recently developed phylogenetic position of monocotyledons. It is an abstract of a course of eight lectures delivered for the London University about a year ago, and even then leaves the discussion of the origin of the flower to the recent paper by ARBER and PARKIN.[16] It is impossible to discuss the numerous lines of evidence presented and the inferences drawn from them. In general it may be said that facts are treated with a free hand and not always critically, that they are often related to one another with great boldness, and that the conclusions are in some cases more evident than the proofs.

Reasons for believing in the monophyletic origin of angiosperms are first presented, and with the recent development of our knowledge of vascular anatomy, it is questionable whether there exists today any serious objection to this view. And yet, perhaps it is well to have the situation summarized for us.

The reconstruction of the primitive race of angiosperms is based chiefly upon floral structure, stem anatomy, and number of cotyledons. The outcome is a plant with a strobiloid flower (as Magnolia), with a cambium, and with two cotyledons. A comparative study of pteridophytes, gymnosperms, and angiosperms would seem to make the last two conclusions inevitable, and the first at least partially true.

The real contention of the author, however, is the origin of the monocotyledonous condition. There is a very full discussion of all possible alternatives,

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[15] SARGENT, ETHEL, The reconstruction of a race of primitive angiosperms. Annals of Botany **22**:121–186. *figs. 21.* 1908.

[16] ARBER, E. A. N., and PARKIN, J., On the origin of angiosperms. Jour. Linn. Soc. Bot. **38**:29–80. 1907. See BOT. GAZETTE **44**:389. 1907.

and the conclusion reached is that the fusion hypothesis is the most tenable; that is, the two lateral cotyledons of primitive angiosperms have become phylogenetically fused in monocotyledons, and the result appears as a terminal member. The anatomical proofs of this position are fairly well known and seem cogent. The final question asked is as to the cause of fusion, and the answer is, the geophilous habit of the primitive monocotyledons. The author recognizes the fact that there are other distinctive features of monocotyledons which geophily cannot be called upon to explain, but these are "departures from the primitive type."

To boil it all down: the angiosperms are monophyletic; the monocotyledons are derived from the primitive dicotyledonous stock; the terminal "cotyledon" is a historical fusion of two lateral cotyledons, which was induced by geophily; and the other characters of monocotyledons remain to be explained.—J. M. C.

Polar conjugation in angiosperms.—Recently[17] PORSCH attempted to explain the embryo sac and double fertilization in angiosperms. He holds that the two synergids are homologous with the neck canal cells of the gymnosperm archegonium (as to what gymnosperm has two neck canal cells, we are left in doubt); that the oospheres of gymnosperms and angiosperms are homologous; that the upper polar nucleus is homologous with the ventral canal cell of the gymnosperm archegonium; and that the antipodal end of the angiosperm sac is the equivalent of the micropylar end. The triple fusion results from the essentially female character of the polars.

It is with considerable surprise that we find an observer so acute as SCHAFFNER[18] writing that the view of PORSCH in regard to these homologies has much in its favor, and that his interpretation of the triple fusion seems correct. That the eggs of gymnosperms and angiosperms are homologous, no one denies; but the other homologies are so inaccurate that to note them at all seems useless. In following the reduction of the archegonium, one notes in the bryophytes a shortening of the neck and a diminution in the number of neck canal cells. In the lower Filicineae there are two neck canal cells separated by a wall; in the higher Filicineae there is one binucleate neck canal cell, the wall always failing to develop. In the Hydropteridineae even the nuclear division fails to take place and there is only one small, uninucleate neck canal cell; while in the gymnosperms there is no neck canal cell at all. In some gymnosperms there is a ventral canal cell, separated from the egg by a wall; but in more cases there is only a nuclear division without the formation of a wall, and in Torreya even the nuclear division is suppressed. In the Gnetales we note the disappearance of even the archegonium. Recalling such a series, it is difficult to understand how anyone could propose such homologies as those suggested by PORSCH.—CHARLES J. CHAMBERLAIN.

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[17] PORSCH, OTTO, Versuch einer phylogenetischen Erklärung des Embryosackes und der doppelten Befruchtung der Angiospermen. Jena: Gustav Fischer. 1907.

[18] SCHAFFNER, JOHN H., On the origin of polar conjugation in the angiosperms. Ohio Naturalist 8:255–258. 1908.

Gametophytes and embryo of Cunninghamia.—This monotypic Chino-Japanese genus has been investigated by MIYAKE, who has just published a preliminary notice[19] of his results. The male gametophyte has no prothallial cells, and at pollination it consists of two nuclei (generative and tube). These two nuclei enter the pollen tube, in which the generative nucleus soon divides, one of the daughter nulcei entering into the structure of the rapidly enlarging body cell, and the stalk nucleus remaining free in the cytoplasm of the tube. Pollination occurs early in April, and the tube reaches the archegonial complex about the end of June. There is a solitary megaspore mother cell, which divides about the time of pollination. The embryo sac is invested by a distinct tapetal zone, and before the end of June is full of tissue. The archegonium initials appear early and the development of archegonia is rapid, the complex being fully formed by the end of June. This complex is singular in that the group of archegonia (15 in the case illustrated) surrounds a central mass of sterile tissue. The cutting-off of a ventral nucleus and its rapid disorganization were observed, this division being promptly followed by fertilization during the first week of July. The fusion nucleus soon divides, and the two daughter nuclei pass to the base of the egg. Walls appear after eight nuclei are formed, which is apparently true for Pinaceae without exception. The proembryo comprises three tiers of cell, with the usual functions.—J. M. C.

The ancestor of Pinus.—JEFFREY concludes that Prepinus, a name which he gives to an abietineous form from the Middle Cretaceous of Staten Island (N. Y.), is the direct ancestor of Pinus.[20] It is characterized by deciduous dwarf-shoots, which bore numerous spirally arranged leaves, and it is the structure of these leaves that forms the basis of the claim mentioned. They have paired resin canals continuous to the very base; possess a well-marked centripetal xylem; and about the vascular bundles there is a complicated double sheath of transfusion tissue closely related to the centripetal wood and resembling that found in some of the Cordaitales. It is also shown that many of the true pines of the Middle Cretaceous had the same double "transfusionary foliar sheath," but lacked the centripetal wood. The tissue on the ventral side of the protoxylem in existing coniferous leaves, which has been described by WORSDELL as representing centripetal xylem, JEFFREY regards as a relic of the inner transfusion sheath. In this way he has connected Pinus with the Cordaitales through Prepinus; and has shown that the Mesozoic pines display transition characters between Prepinus and the pines of today. His conclusion is that the Abietineae are the oldest tribe of Coniferales, and that Pinus is its oldest living representative.—J. M. C.

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[19] MIYAKE, KIICHI, The development of gametophytes and embryogeny of Cunninghamia (Preliminary note). Bot. Mag. Tokyo **22**:45–50. *figs. 14.* 1908.

[20] JEFFREY, EDWARD C., On the structure of the leaf in Cretaceous pines. Annals of Botany **22**:207–220. *pls. 13, 14.* 1908.

Aerotropism.—POLOWZOW has taken up the question of the response of plant organs to gases.[21] Reserving the usual term aerotropism for sensitiveness to the mixture of gases that compose the air, he proposes the term *aeroidotropism* for sensitiveness to pure gases. This seems an unnecessary refinement of terms. Very properly he criticizes the use of roots as subjects for experiments with gases, since the organ is under wholly unnatural conditions, and uses stems, which SAMMET tried with negative results. POLOWZOW finds *Brassica Napus*, *B. Rapa*, *Vicia sativa*, *V. Faba*, *Pisum sativum*, *Lupinus albus*, *Phaseolus multiflorus*, and *Helianthus annuus* sensitive to O_2 and CO_2, but unaffected by H and N_2. The grasses studied were all indifferent. At the beginning there is a positive curvature, which becomes more rapid, slows, ceases; shortly a negative curvature sets in, gradually increasing. When stimulation ceases, curvature slows, stops, and then the recovery of the normal position takes place. The active region may be a centimeter or more distant from the perceptive region, which may even be in the part of the stem that has ceased growing, showing that perceptive capacity persists longer than capacity for the curvature reaction. The perception time was found to be 0.5 sec. with 0.01^{cc} of CO_2 and periods of stimulation and rest in the ratio 1:3. The reaction time was found to be not much more than in various tactic responses; POLOWZOW thinks because the movements in both cases were examined by the microscope, and he pleads for the use of the more refined methods of the animal physiologists. There is certainly nothing to prevent; BOSE has blazed the path. We hope that in the full paper to which this is preliminary the author will give us such records and discuss more fully some general questions he raises.—C. R. B.

Seed production in Pinus.—Under this title HAYDON[22] presents the results of an extended field study supplemented by cytological work. The cytological conditions found in both microsporangiate and megasporangiate cones at various seasons are noted in detail. The staminate cone, in the vicinity of Liverpool, passes the winter in the spore mother cell stage. The megaspore mother cell appears about the end of May, but its origin was not determined. Occasionally large ventral canal cells are formed, and in a few cases the first mitosis in the egg was observed when there were no traces of pollen tubes or other evidences of fertilization. HAYDON believes this supports the suggestion of the reviewer[23] that a large ventral canal nucleus might fertilize the egg. The simultaneous divisions at the base of the egg by which the proembryo passes from the 8-celled stage to the 12-celled stage is sometimes in the lower tier instead of in the upper tier, as is usually the case. Theoretically, the ovulate cone might produce some

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[21] POLOWZOW, W., Experimentelle Untersuchungen über die Reizerscheinungen der Pflanzen, mit besonderer Berücksichtigung der Einwirkung von Gasen. Vorläufige Mitteilung. Ber. Deutsch. Bot. Gesells. **26a**:50–69. 1908.

[22] HAYDON, WALTER T., The seed production of *Pinus sylvestris*. (Inaugural address.) Proc. and Trans. Liverpool Biol. Soc. **22**:1–32. *figs. 16.* 1907.

[23] BOT. GAZETTE. **42**:349. 1906.

1500 proembryos, but actually it produces only 10 to 20 seeds. The factors responsible for the difference between the theoretical and the actual output are considered, both in the field study and in the cytological work.—Charles J. Chamberlain.

Geotropic curvature.—Porodko, reinvestigating the statement of Kohl that "the geotropic curvature extends also to parts of the stem in which growth can no longer be demonstrated," comes to the contrary conclusion, though he does not discover the source of Kohl's error, unless in the fact that he did not use the microscope in his measurements.[24]

Bach's conclusion that the presentation and reaction times for geotropic curvatures are not affected by shaking and jarring, has been welcomed by opponents of the statolith theory of geoperception as depriving it of an important support, though Bach himself does not so use his data. Haberlandt, whose experiments in shaking and jarring led him to quite the opposite conclusion, reexamines Bach's data, criticizes his methods somewhat, and interprets some of his experiments as showing the very thing which Bach thought they did not show.[25] Haberlandt also pays his compliments to Linsbauer, who raised a theoretical objection to the value of the jarring experiments. The statolith theory has a watchful champion, ready to meet all comers.—C. R. B.

A lycopod with a seedlike structure.—Miss Benson's abstract of her paper on Miadesmia was noticed in this journal.[26] The full paper has now appeared,[27] and the fuller description and plates make the situation more evident. The discovery of the sporophylls of this minute, herbaceous, paleozoic lycopod, has shown a clear relationship to the ligulate Lycopodiaceae, especially Selaginella. The megasporangium produces a single, thin-walled spore, which germinates *in situ*. An integument is developed around the sporangium, leaving a micropyle; and from the surface of the integument numerous long processes develop, giving quite a fringed look to the apparatus. At maturity the sporophyll is shed, the whole structure resembling a winged and fringed seed. The relation of this "integument" to the "velum" of other groups is vague and apparently hardly worth considering; but another case of integumented sporangium, to be added to the previously described Lepidocarpon, is quite worth while.—J. M. C.

Dwarf male prothallia.—Boodle[28] has observed that if *Todea Fraseri*, a filmy species, be kept in a sufficiently damp atmosphere, the sporangia do not

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[24] Porodko, T., Nimmt die ausgewachsene Region des orthotropen Stengels an der geotropischen Krümmung teil? Ber. Deutsch. Bot. Gesells. **26a**:3–14. 1908.

[25] Haberlandt, G., Ueber die Einfluss des Schüttelns auf die Perception des geotropischen Reizes. Ber. Deutsch. Bot. Gesells. **26a**:22–28. 1908.

[26] Bot. Gazette **44**:318. 1907.

[27] Benson, Margaret *Miadesmia membranacea* Bertrand; a new palaeozoic lycopod with a seed-like structure. Phil. Trans. Roy. Soc. London B. **199**:409–425. *pls. 33–37*. 1908.

[28] Boodle, L. A., On the production of dwarf male prothalli in sporangia of Todea. Annals of Botany **22**:231–243. *pl. 16*. 1908.

dehisce, and spores germinate in the closed sporangia. As a result, dwarf male prothallia are produced, antheridia sometimes appearing at the three- or four-celled stage. Free spores under the same conditions never produce such prothallia, not having developed sexual organs at the conclusion of the experiment. The dwarf males do not burst through the wall of the sporangium, and ultimately die. It was found also that both free spores and those inclosed in sporangia germinate in darkness. The suggested explanation of the formation of the dwarf male prothallia under the conditions described has no foundation in experimental work. It is to be hoped that the day of imaginary "explanations" is about over.—J. M. C.

Periodicity of algae.—BROWN[29] has studied the appearance and disappearance of algae in selected ponds and streams in the vicinity of Bloomington, Indiana. In this region, an alga growing under "steady normal conditions" remains in a healthy vegetative state throughout the year. A sudden change in external conditions checks this vegetative growth, and induces a resting stage or sexual reproduction. In reference to specific plants, *Spirogyra nitida* is the most abundant of the Conjugatae in the region studied, and *S. varians* is the most widely distributed alga, conjugating at all seasons of the year when exposed to hard conditions (as the drying-up of a pond); Chaetophora thrives best in slightly stagnant water at a temperature between 5° and 25° C.; Draparnaldia finds its most congenial conditions in flowing surface water between 1° and 15° C.—J. M. C.

Cytology of Synchytrium.—GRIGGS[30] has continued an investigation on *S. decipiens* begun by F. L. STEVENS, to whom he is indebted for material. There are 500 to 800 free nuclei in the cyst when cell walls begin to appear; but most of the study was upon cysts with 100 to 300 free nuclei. While no centrosomes were found in the metaphase and anaphase, in the telophase there are large asters with centrosomes at the center, whose origin has not yet been determined. As the nuclear vacuole forms about the chromosomes, the coarse rays of the aster bend about it and become transformed into the thick nuclear membrane characteristic of the genus. It is hoped that a further study will throw some light upon systematic relations.—CHARLES J. CHAMBERLAIN.

Sporangia of Lycopodiaceae.—As a result of her study of the sporangium-bearing organs of the Lycopodiaceae, Miss SYKES[31] has arranged the different species of Lycopodium in a continuous series based on the shape and structure of the sporophyll, the position of the sporangium, and the position of the line of dehiscence. The evidence adduced seems scarcely sufficient to warrant the con-

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[29] BROWN, HARRY B., Algal periodicity in certain ponds and streams. Bull. Torr Bot. Club 35:223–248. 1908.

[30] GRIGGS, ROBT. F., On the cytology of Synchytrium. Ohio Naturalist 8:277–286. *pl. 20.* 1908.

[31] SYKES, M. G., Notes on the morphology of the sporangium-bearing organs of the Lycopodiaceae. New Phytol. 7:41–60. *pls. 2, 3.* 1908.

clusion that the genus Lycopodium should be interpreted as a reduction series, or to afford a basis for the supposition that the sporangium-bearing organ of the Lycopodiaceae has been "derived from a branch structure which had the morphological value of an axillary bud."—ALMA G. STOKEY.

Embryo and endosperm of Potamogeton.—COOK[32] has investigated material of *P. lucens* obtained from Cuba. The embryo was found to resemble closely that of Alisma in its development. In endosperm formation a transverse wall chambers the sac at the first division; in the micropylar chamber the endosperm formation proceeds as a series of free nuclear divisions, usually with parietal placing; the antipodal chamber develops as a haustorial extension of the sac into the chalaza, and during this development the second daughter nucleus of the primary endosperm nucleus seems to be very active, but does not divide.—J. M. C.

Ophioglossum simplex.—This rare Sumatran species has been collected again, and these new specimens show to BOWER[33] an outgrowth which, evidently single, represents a sterile blade, of which there was no such indication in the specimen he had examined previously. The fact is important because of the difference of opinion as to the phylogenetic position of Ophioglossum. CAMPBELL has regarded *O. simplex* as the most primitive known member of the genus, while BOWER has claimed it to be a reduction form. The evidence just reported would seem to justify the latter contention.—J. M. C.

Anthocyan and chlorophyll.—An interesting bit on the function of anthocyan is the observation by MOLÉR[34] that the red leaves of a species uniformly contain less chlorophyll than the green leaves. The ratio runs between 1.08 and 1.27. This seems to be difficult to reconcile with TISCHLER's hypothesis that anthocyan enables the plant to nourish itself better and so to stand a more severe climate. —C. R. B.

Radioactivity.—ACQUA reports[35] that salts of uranium and thorium, even in very dilute solutions, injure seedlings of wheat by reducing the development of the primary root. Germination was also retarded. His experiments supplement those on radium and other radioactive substances by other investigators.—C. R. B.

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[32] COOK, MELVILLE THURSTON, The development of the embryo sac and embryo of *Potamogeton lucens*. Bull. Torr. Bot. Club **35**:209–218. *pls. 9, 10.* 1908.

[33] BOWER, F. O., Note on *Ophioglossum simplex* Ridley. Annals of Botany **22**: 327, 328. 1908.

[34] MOLÉR, T., Ueber den Chlorophyllgehalt anthocyanführender Blätter (Vorläufige Mitteilung). Bot. Notiser **1908**:49–53. 1908.

[35] ACQUA, C., Sull'azione dei sali radioattivi di uranio e di torio nella vegetazione. Annali di Botanica **6**:387–401. 1908.

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THE STAMINATE CONE AND MALE GAMETOPHYTE OF PODOCARPUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 114

L. LANCELOT BURLINGAME

(WITH NINE FIGURES AND PLATES VIII AND IX)

Knowledge of the gametophytes of the Podocarpineae is at the present time limited to that contained in three brief papers. In 1902 COKER (**3**) published an account of two species of Podocarpus; in June 1907 JEFFREY and CHRYSLER (**5**) added some new facts concerning Podocarpus and Dacrydium; and in September of the same year Miss YOUNG (**14**) gave an excellent résumé of the subject of the male gametophyte and added several new and interesting details for Dacrydium. COKER records that in *Podocarpus coriacea* there are produced two primary prothallial cells, both of which may divide amitotically; a tube nucleus; and a primary spermatogenous cell, which gives rise to a stalk cell and a body cell. The body cell undergoes nuclear division and one of the nuclei is then extruded from the cytoplasm, leaving a single functional male cell. JEFFREY and CHRYSLER add to this the interesting details that from the two primary prothallial cells there may arise by subsequent division as many as eight prothallial cells. Of still greater interest is the record of the "proliferation" of the primary spermatogenous cell, whereby there arise three cells placed transversely, the middle one of which is considerably larger than either of the others. Miss YOUNG reports that in Dacrydium one or both of the primary prothallial cells may divide once. From the primary spermatogenous cell arise two cells, one of which is usually sterile, the other of which functions as the body cell. The interesting observation is made that there is a tendency for both derivatives of the primary spermatogenous cell to function as body cells.

The material for the present study was secured through the kindness of Dr. L. COCKAYNE of Christchurch, New Zealand, and Miss INEZ FRANCES STEBBINS of the Huguenot College at Wellington, Cape Colony, South Africa. To both are due our thanks for their kindness in obtaining the material at no inconsiderable personal inconvenience. Though the collections were necessarily few, yet they include a considerable range of developmental stages in each of the species. The material was fixed in a 5 per cent. solution of commercial formalin in 70 per cent. alcohol. The fixation has proved unexpectedly good, except for stages from the rounding-up of the mother cells to the time when the microspores have a good firm wall and abundant contents. The shrinkage and general distortion within the limits just mentioned have rendered necessary the omission of a number of what appear to be rather interesting and perhaps important details. Some of these will be mentioned briefly in the general account. It is hoped that other material so killed and fixed as to show details of cytological structure will be in hand within the near future. The preparations have been imbedded in 54° paraffin, cut 3–5 μ, and stained in Haidenhain's iron alum hematoxylin stain, alone or counterstained with various aqueous stains such as orange G, Bismarck brown, erythrosin, etc., and with the saffranin gentian-violet combination. Three species have been examined, though not covering exactly the same ground.

Observations

The cones of *P. totarra Hallii* are of a generally oval shape, varying from 3 or 4 to 15 or 20^{mm} in length, and from 2 to 4^{mm} in diameter. They are usually in pairs, one being large and one small. The base of the cones is surrounded by several closely appressed, rigid, scalelike bracts. The peduncle is quite short or almost lacking. The cones of *P. nivalis* are somewhat shorter, not paired, and decidedly slenderer. The cones of the third species (the label of which was lost in transit) are similar in shape to the first ones, but are smaller. In other respects the cones are very similar. *P. totarra* is one of the tallest of forest trees and *P. nivalis* a very small shrub, sometimes creeping. The third species may be *P. elongata*, a common forest tree of the South African region. This is a mere inference from its abundance in the region from which this material

FIG. A.—Group of *P. dacrydioides* in remnant of taxad forest, N. Z.—Photograph by J. CROSBY SMITH.

was received, and from the fact that I have received other material from the same source belonging to this species.[1]

In cross-section a staminate cone shows about ten to twelve sporophylls, each with two sporangial cavities (*fig. 1*). The vascular system seems to be rather weakly developed, but shows a distinct endarch collateral bundle (*fig. 3*) corresponding to each sporophyll. Just outside of the bundle there usually is found a resin canal (*fig. 1*).

FIG. B.—Buttressed base of *P. dacrydioides*, in ancient forest of Canterbury Plain, N. Z.—Photograph by L. COCKAYNE.

The resin canals contain little material of any sort in the preparations available for study. The distinctly glandular cells lining them (*fig. 2*) suggest, however, that they are functional. The number varies in different strobili, but in those examined did not fall below six nor exceed eighteen or twenty.

The sporophylls as seen from the upper surface are somewhat spatulate, with a rather pointed apex. *Fig. 4* presents an outline

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[1] We have received from Dr. COCKAYNE two excellent photographs of *P. dacrydioides*, which are reproduced on account of their general interest (*figs. A* and *B*).

of a longitudinal section somewhat to one side of the middle, and will give an idea of the side view, as well as the relation of the sporangial cavity to the sterile portion of the leaf. *Fig. 6* shows a cross-section of a sporophyll near the middle of the sporangium. The sporangia are somewhat less prominently exposed on the under side than those of Pinus, for example. A single weakly defined vascular bundle (*fig. 6*) traverses the upper part of the central sterile septum and is sometimes accompanied by a resin canal lying below it and between the sporangia. The wall of the sporangium varies in thickness somewhat, but in general on the freely exposed part it is about four or five cells thick (*fig. 5*). One or two of the inner layers are slightly differentiated as a tapetum. This is not very evident and does not occur until the sporogenous tissue has nearly reached the mother cell stage. The tapetum does not long persist, but disappears as a functional tissue about the time the young spores have formed a thick wall and wings. All of the wall proper, except the outermost layer of thickened cells, may break down before the spores are shed.

The earliest stages of the sporogenous tissue observed (in *P.* sp.) lacked one or two divisions of the mother cell stage. *Fig. 7* will serve as a typical representative cell of the sporogenous tissue at this stage. The walls are thin and delicate, as is usually the case, and the cytoplasm stains somewhat more densely than that of the wall cells. It was possible to secure very good preparations of this, considering the nature of the killing and fixing agent. The cells were slightly shrunken, so as to have pulled away in many places from one another or from their own walls. *Fig. 7* will show the principal facts. The cytoplasm does not seem to present either a typically reticulated or a foam structure, but rather resembles a sort of flocculent precipitate scattered more or less irregularly through the cell. These flocculent masses may assume a sort of feathery, filamentous, more or less branched form, or they may appear as scattered masses of irregular shape. The filaments and other masses do not seem to be connected in any definite manner, but to be distributed through the cell by chance. No stored food can be detected microscopically in the cytoplasm at this time, though the parenchymatous cells of the axial portion of the strobilus contain considerable quantities of large starch grains. The wall cells of the sporangium do not at this time, as in some sporangia (Ophioglossum, for example), contain starch, but are relatively poor in cytoplasm and cytoplasmic inclusions. There is relatively little change in the cytoplasm of the sporogenous tissue as growth advances, except that it grows gradually less dense until at the time of the formation of the young spores there is almost no stainable substance left.

The nuclei of the sporogenous cells (*fig. 7*) previous to the mother cell stage show a structure that is very like that of the cytoplasm just described, except that it is denser and there is more of a tendency to aggregate itself into disconnected masses. There are one or more large nucleoli present in the nucleus at this stage, as there seem to be in the resting nuclei of all the stages of all the tissues examined.

As the nucleus approaches division, the nuclear substance begins gradually to arrange itself into filaments or strands (*fig. 8*) which may end freely or anastomose with other filaments or masses. About the same time the hitherto nearly uniformly staining material begins to stain differentially, so that filaments seem to link together knots of more deeply staining material. Whether this indicates a difference of substance, as some think, or merely a difference in the state of aggregation, as has been recently maintained by several authors, cannot be said with certainty. However, the gradual derivation of this structure from the preceding one, in which everything seems homogeneous, would certainly point to the latter interpretation as the correct one. During this time the nucleolus (or nucleoli) gradually loses its density, as shown by the staining reactions. It continues to do so until it finally does not stain at all or has disappeared entirely. *Fig. 9* shows a surface view of a nucleus in which the filaments have become more regular and somewhat thicker. In *fig. 10* is shown a spirem, into which the filamentous stage gradually passes, in which the deeply staining knots on the spirem are unusually prominent. The figure shows nearly all of the spirem that was included in a 3-μ section; therefore it probably contains one-third to one-half of the entire spirem, since the nucleus is about $7 \times 10\ \mu$. In some cases the spirem consists of darkly stained masses connected by much smaller threads, and in others, as shown in *fig. 10*, by broader strands which seem to be of different material because of the considerable difference in depth of staining.

The spirem gradually becomes denser and ramifies all through the nucleus (*fig. 11*), the nucleolus disappears, and finally the spirem breaks into elongated loops, which arrange themselves into a tangled mass at the equatorial plate. The exact method of division was not made out owing to the close tangling of the long chromosomes. In the anaphase the chromosomes appear as twenty-four straight elongated rods of about half the length of those entering the mitosis (*fig. 12*).

As the chromosomes approach the poles, the polar ends draw together and the others spread out, so that the daughter nucleus usually has a concavity on the polar side. The chromosomes gradually lose their density and put out processes on one side or the other to fuse with those put out by neighboring ones, thus establishing a sort of reticulate structure (*fig. 13*). This gradually passes back into the stage shown in *fig. 7*. In the reorganizing nucleus one large nucleolus may appear or several small ones, but I did not attempt to discover the origin of them or their relation to one another.

When the cells have reached the mother cell stage, they break loose from one another and round up in the usual manner. As already remarked, the mother cells killed and fixed very poorly, so that only a very meager and perhaps uncertain account of them can be given. About the time the mother cells round up many of them begin to abort; this abortion seemingly may occur as late as the young spores. Up to this time and on to the time of the divisions in the young microspores the development of the sporogenous tissue seems to be nearly simultaneous.

After the mother cells have rounded up, the nucleus soon passes into a condition in which its contents stain so nearly uniformly that it has not proved possible to disentangle its separate constituents. If stained deeply, it appears absolutely uniform, and if the stain be then slowly and gradually drawn, the homogeneous appearance gives way to a sort of pebbled one. Sometimes it looks as if this might be due to the parts of a large and long spirem being crowded closely together. This interpretation is strengthened by the fact that in some cases one can see what looks like the end of a loop pushing out the nuclear membrane. In other cases the appearance is more that of a great many lumps of some plastic substance thrown into a tight mass. Whether these appearances are normal or not I cannot say. That they represent the only appearances that the present material shows is certain. In the face of the numerous and fairly uniform accounts of sporogenesis in which no such phenomena have been recorded, it is certainly entirely proper at present to ascribe these unusual phenomena to the effects of the reagents. Nothing any more nearly resembling synapsis was seen. It should be noted that of some hundred strobili cut only five showed cells in this stage. However, three of these strobili are the only ones that have shown the reduction divisions. A few sporangia had cells like those shown in *fig. 14*, where the chromosomes are beginning to appear, being almost completely concealed in a mass of granular matter. In the figure the difference in intensity of stain between the chromosomes and the imbedding substance has been greatly exaggerated for the sake of clearness. One gets two views of these developing chromosomes, one in which the chromosomes are mostly seen in cross-section and one in which they lie lengthwise. In some fashion (which the density and abundance of the imbedding substance prevent being made out clearly) out of this comes a rather sharply pointed spindle at whose equator are arranged the short apparently bivalent chromosomes (*fig. 15*). Some preparations seemed to favor the idea that these apparently bivalent chromosomes then split longitudinally. After passing to the poles (*fig. 16*) they became surrounded by a nuclear membrane, but did not, in the few preparations of this stage observed, lose their identity in a resting nucleus. A very few cases of the homotypic mitosis are shown in the preparations and all of these are in the telophase, as shown in *fig. 17*. Walls are not formed till after second division.

Beyond the telophase of the second division the preparations show nothing until after the formation of the wall around the young spores. These are so badly shrunken and distorted that no attempt has been made to figure them. It is observable, however, that the nucleus is at first rather small and oval and lies to one side of the spore cavity, most of which is occupied by an enormous vacuole. *Fig. 18* shows a microspore after the contents have become more abundant. At this time starch may or may not be present; later it becomes abundant and occurs in relatively large grains (*figs. 30, 31*). The wall has a thick exine much roughened on the outer surface and a distinct intine. The spore coat is usually much thinner on the side away from the point where the prothallial cells will later lie. The external appearance of the pollen grain bears a considerable resemblance to that of Pinus, except that it is smaller, rarely reaching more than 35 μ in the greatest diameter (exclusive of the wings).

The microspore nucleus is large (*fig. 18*) and contains apparently two sorts of material. There is a more deeply staining substance distributed in irregular masses through a very fine ground substance. As the nucleus prepares for division, the amount and density of the more deeply staining substance increases in amount, assumes a more definitely reticulated structure, and finally passes into a rather thick and comparatively short spirem (*fig. 29*). This spirem breaks up into the chromosomes (*fig. 28*), which often still show the distinct segmentation into lighter and darker segments that has already been referred to in discussing the sporogenous tissue. This segmentation is not always found in the chromosomes or even in the spirem. It might be supposed that the different appearance is due to differences in the depth of stain, but this does not seem to be true. The chromosomes are rather long and considerably twisted at the metaphase, but in dividing and passing to the poles they apparently shorten up (*fig. 31*). What has been said of the first division applies equally well to the next, so far as the few mitoses observed show.

One or two prothallial cells are cut off and then the antheridial initial divides to produce the tube nucleus and the primary spermatogenous cell (*fig. 32*). In *P. nivalis* two primary prothallial cells, which do not subsequently divide, seem to be the rule, though one example of the division of the first prothallial was observed. The pollen in the same sporangium varies in the stage of development from microspores to the stage shown in *fig. 32*. These sporangia were, in some cases at least, shedding their spores.

In *P. totarra Hallii* one primary prothallial cell may be cut off, after which the free nucleus divides to form the primary spermatogenous cell and the tube nucleus (*fig. 21*); or two primary prothallial cells may be cut off before the tube nucleus is separated from the primary spermatogenous cell (*figs. 20, 22*). When only a single primary prothallial cell is cut off, it may (*fig. 19*) or may not (*fig. 21*) divide again. Far more frequently it does divide anticlinally. No case in either species has been observed where either prothallial cell divides periclinally. In case two prothallial cells are cut off, both usually divide anticlinally (*figs. 23, 26, 27*), although the division may be long delayed or fail wholly (*text fig. 4*). The first one may remain undivided, or in rare cases may divide twice, so that the first tier of prothallial cells contains four cells. The second one almost always divides once and usually twice. Thus there may be one, three, four, six, or eight prothallial cells; six is much the commonest number, and one or eight the rarest. In case only one prothallial cell is cut off, its nucleus

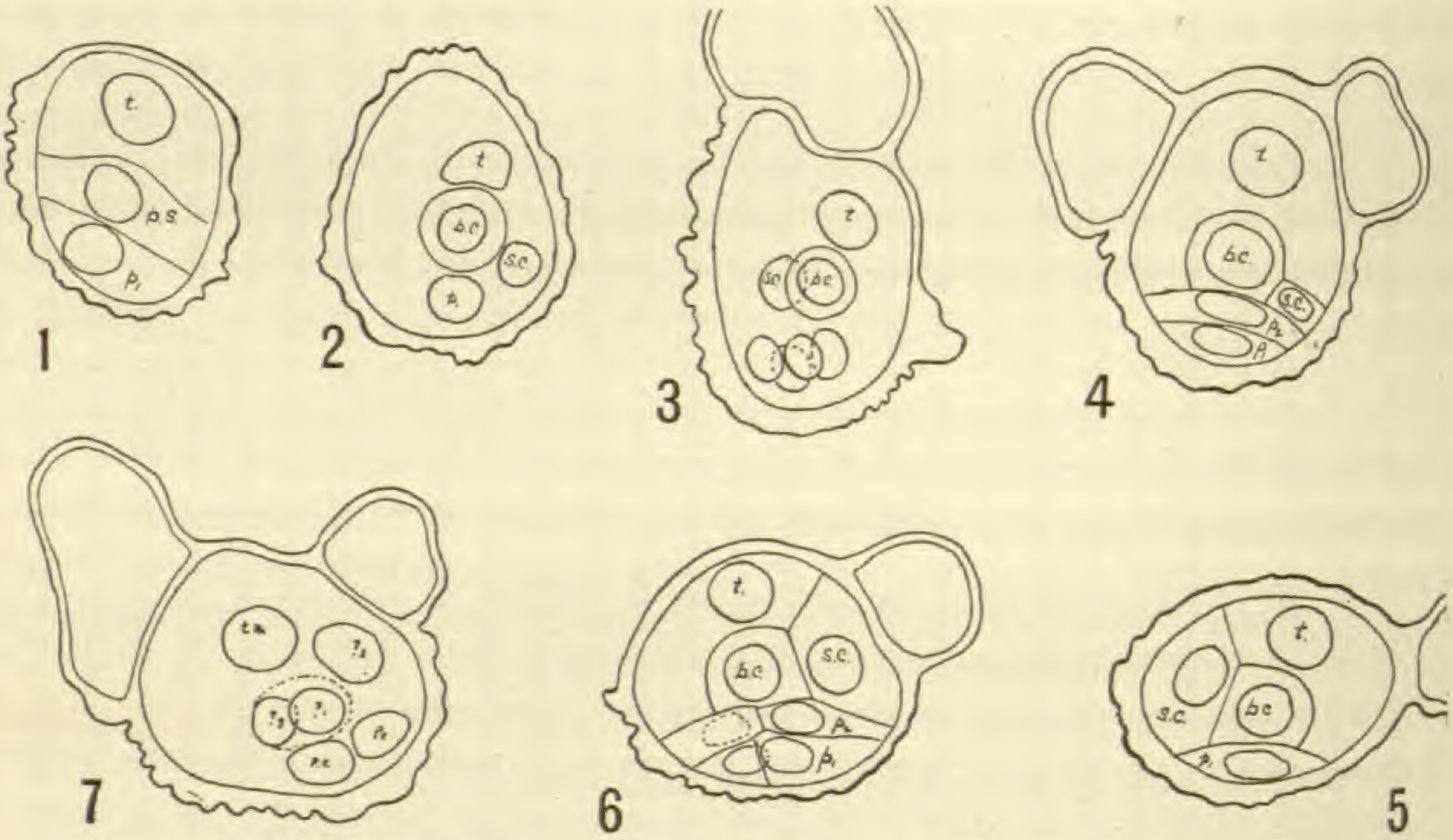

FIG. 1. Transverse section of a male gametophyte consisting of one prothallial cell (p_1), the primary spermatogenous cell (ps), and the tube nucleus (t).—FIG. 2. Male gametophyte in which the primary spermatogenous cell has divided into the body cell (bc) and the stalk cell (sc), and in which all the gametophytic walls have broken down.—FIG. 3. Same as the preceding except that there are four prothallial nuclei instead of one; it is uncertain whether they have been derived from one or two primary prothallial cells.—FIG. 4. A gametophyte with two primary prothallial cells (p_1, p_2) which have not divided, though the pollen is presumably ready for shedding.—FIG. 5. A gametophyte with a large stalk cell placed transversely to the axis of the body cell.—FIG. 6. Same as preceding except that there are four derivatives of the primary prothallial cell.—FIG. 7. A gametophyte in which the origin of the free nuclei is not easily traced; see text for discussion.

remains large and the cell itself is often much larger than when two are cut off (*text fig. 1*). Sometimes the three resulting nuclei then lie in a row across the spore (*text fig. 1*) and differ but little from one another in appearance. The walls separating them then run nearly straight across, and it is only by courtesy that the tube nucleus can be said to be free in the spore cytoplasm. To all intents and purposes it is as much walled-off into a cell of its own as the prothallial nucleus, for both eventually are freed in a common cytoplasm (*text fig. 2*). Further, it is to be noted that in this case the prothallial cell does not have a fixed position with respect to the wings, as in the ordinary course of events.

After the tube nucleus has been cut off, the primary spermatogenous cell divides transversely, giving rise to two cells (*fig. 25*). Usually these cells differ markedly in size, the smaller lying to one side and the larger lying nearly in the center of the pollen grain (*fig. 26*). In this case one may safely use the usual terms for them and speak of the larger as the body cell and the smaller as the stalk cell. It not infrequently happens that the two derivatives of the generative cell are about equal in size (*figs. 24, 27; text figs. 5, 6*), though even then one is centrally placed and the other laterally. Before the division of the generative cell, the second primary prothallial cell has usually divided at least once. In this case the generative cell often sinks down among its derivatives (*figs. 23, 27*). The stalk cell is sometimes placed transversely to the body cell (*text figs. 5, 6*). Whether these large stalk cells will produce male cells or not can only be conjectured, though the fact that some of them seem to retain their cytoplasmic envelope, almost as distinct from the cytoplasm as the body cell itself, up to a certain early stage, would lead one to suppose that in some cases they might do so. *Text fig. 7* may show three derivatives of the generative cell and two prothallial cells in addition to the tube nucleus. One of the three derivatives of the generative cell has no cytoplasmic sheath and is probably a stalk nucleus; the two lying close together are ensheathed, though I have been unable to ascertain definitely whether each has a distinct sheath or whether both lie in a common sheath, or whether perhaps one of them is not merely beneath the cytoplasmic sheath of the other. If either the first or second supposition is true, there still remains the question whether the two cells are body cells or male cells. If the third supposition is true then there are four prothallial nuclei, a generative cell, and the tube nucleus.

In a number of preparations there seemed to be a cell on the side of the body cell opposite the stalk cell (*fig. 27*), but in no case could I satisfy myself of the presence of a nucleus; though in view of the figures published by JEFFREY and CHRYSLER it was diligently looked for. In *fig. 27* is shown a mass at one end of this "cell," which may stand for a degenerating nucleus, although I think not. It is very indistinct and may very well be a mere aggregation of slightly denser cytoplasm. By constructing a model of the cell complex, where the body cell has sunk down between the cells of the second tier of the prothallus, and then cutting it so that the section will pass about centrally through stalk and body cell and include most of one-half of them and take a slice off the prothallial cells lying beyond them, it is possible to get preparations which show cell walls in the position shown in the figure. Hence it is not certain that in this species there are two lateral derivatives of the generative cell, as seems to be the case in the species mentioned by JEFFREY and CHRYSLER (4).

The dividing nuclei of the species of Podocarpus here investigated show uniformly twelve chromosomes in cases where they could be certainly counted (*figs. 14, 27, 32*), and twenty-four were counted several times, with less certainty, in the sporogenous tissue of *P.* sp. In this it conforms to the count for all other gymnosperms so far as known except Taxus, with eight and sixteen (STRASBURGER 12), and Sequoia, with sixteen and thirty-two (LAWSON 7).

It is not possible to speak with certainty concerning the stage at which the pollen is shed without knowing over how long a time shedding continues, and without actually having gathered pollen as it is shed naturally. But from cones that were apparently ready to shed their pollen, stages were obtained in *P. nivalis* running from the microspore to gametophytes with two prothallial cells, generative cell, and tube nucleus. It often happens that both extremes may be found in the same sporangium. In *P.* sp. no cones were apparently old enough to shed their pollen, though the oldest had essentially the same structure as those of the species just mentioned. In the cones of *P. totarra Hallii* the range appears to be still wider, for the oldest stages shown in the plates (*figs. 26, 27; text fig. 7*) occurred along with the youngest. In some cases the cell walls were still intact, while in other pollen grains not more advanced, the nuclei and body cell were free in the common cytoplasm (*text figs. 1, 3, 7*).

Discussion

The facts presented in the preceding account are in the main confirmatory of those already reported by COKER and by JEFFREY and CHRYSLER for other species of Podocarpus; hence their main value is that they offer additional evidence that the phenomena described by these authors are not limited to the species studied by them. These authors and others as well have called attention to the resemblances to the Abietineae in the winged pollen, thick sporangium wall, and general similarity of the staminate strobilus.

The main interest centers about the development of the male gametophyte. COKER (**2**) reported two primary prothallial cells in *P. coriacea*, which divide amitotically. JEFFREY and CHRYSLER (**5**) have recorded as many as eight in the species studied by them. Miss YOUNG (**14**) has also recorded as many as four in species of Dacrydium. THOMPSON (**13**) has found 30 to 40 prothallial cells in Agathis; and LOPRIORE (**8**) has reported a cell complex in Araucaria that reaches about 15 in number before the walls break down, when the freed nuclei may then further divide until as many as 44 may be found in the pollen tube. He interprets these as spermatogenous cells and cites the case of Cupressus as analogous. CHAMBERLAIN (**2**) has already called attention to the fact that the drawings seem to indicate that these nuclei are really prothallial and that there is only one body cell. In this view Miss YOUNG (**14**) has concurred, as it would seem most students of gymnosperms must. RENAULT (**10, 11**) and OLIVER (**9**) have described the multicellular pollen grains of the Cordaitales and Stephanospermum, where as many as 20 cells are found in the male gametophyte; whether they are prothallial or spermatogenous is uncertain.

CALDWELL (**1**) has reported as many as nine or ten body cells in Microcycas, along with a single stalk and single prothallial cell. CHAMBERLAIN in a forthcoming paper reports that Ceratozamia occasionally has four sperms. JUEL (**6**) found a variable number of sperm cells (it is not clear whether he means body cells or male cells) in *Cupressus goweniana.*

It thus seems to be an established fact that more than two prothallial cells and more than two sperms occur in widely unrelated gymnosperms. Though we may all be willing, perhaps, to accept this statement of facts, there is no such unanimity of opinion as to the interpretation of them. It is obvious that one may adopt either of two views: (1) One or two prothallial cells were found in the primitive gymnosperms and in some cases these have divided to form a complex. This would be JEFFREY'S (**5**) "coenogenetic proliferation." In support of this view he has urged that a multiplication of prothallial cells is correlated with "protosiphonogamic" fertilization in the Araucarineae, "since the length of the pollen tube, in the absence of any special conductive tissue, such as is found in angiosperms, calls for a greater development of prothallial tissue." This line of reasoning could hardly be extended to Podocarpus or to any other case now known. If one could find some physical cause applicable to all cases, he might believe that this multiplication of cells is a thing of recent origin in each case. Furthermore, the idea that a multiplication of cells would be forthcoming just when needed is more teleological than accords with modern physiological teaching. If we do not accept this explanation, as I think we cannot, we may turn to the other possibility. (2) Primitive gymnosperms had a multicellular prothallial tissue, and not unlikely a spermatogenous complex of several cells. The evidence for this view is of two sorts, historical and theoretical. Historically we know that the pollen grains of certain Cordaitales (**10**) and Cycadofilicales (**9, 10, 11**) had a considerable tissue of some sort. Whether it was spermatogenous or prothallial is not very material, since this view assumes that both sorts existed somewhere in the ancestry of living gymnosperms and that by a gradual reduction each sort has been reduced to one or two cells. It is of interest to note that all the heterosporous pteridophytes show the same tendency, each of the living genera having a single prothallial cell and in some cases producing as few as four sperms. This assumption makes it easy to account for the facts already related. We have but to suppose that in these cases the forms showing these peculiarities have merely retained their primitive characters or, in cases where they occur only occasionally, that it is a reversion to ancestral conditions. JUEL (6) has already suggested this explanation for the case of Cupressus, and has even gone so far as to suggest a possible sequence in the reduction. At this point one must be on guard against supposing that types which illustrate this reduction series necessarily, or even probably, stand in the same series phylogenetically. It seems to the writer that if this fundamental principle be firmly grasped, it is entirely unnecessary to suppose that because Podocarpus and Pinus are clearly related and because Pinus is older historically, therefore the multiplication of prothallial cells in Podocarpus must be coenogenetic. One need but assume that both are derived from a common ancestral stock and that one has retained the prothallial complex and the other has lost it. Of course if one believes that Podocarpineae have come directly out of living Abietineae, this explanation would not hold. While it is true that the latter are known as far back as the Carboniferous (4) and the former are not known to be nearly so old, it is equally undeniable that we know but little of the plant remains of those parts of the world in which their remains would be most likely to be found.

Summary

1. There are in the species of Podocarpus studied two prothallial cells which may or may not divide. There may be as many as eight prothallial cells in two tiers derived from the two primary ones.
2. Division in the prothallial tissue is mitotic and the prothallial cells do not degenerate.
3. There is a stalk cell and a body cell, sometimes differing very little from one another in appearance; whether both may produce male cells is yet uncertain.
4. The number of chromosomes is twelve and twenty-four.
5. There may be a variable number of cells or free nuclei in the pollen grain at the time it is shed.

Acknowledgments are due to Professors JOHN M. COULTER and CHARLES J. CHAMBERLAIN of this laboratory for valuable advice and criticism during the progress of this investigation.

THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES VIII AND IX

The drawings were made with a Bausch and Lomb camera lucida and Zeiss apochromatic lenses and compensating oculars. The plates have been reduced one-half in reproduction.

PLATE VIII

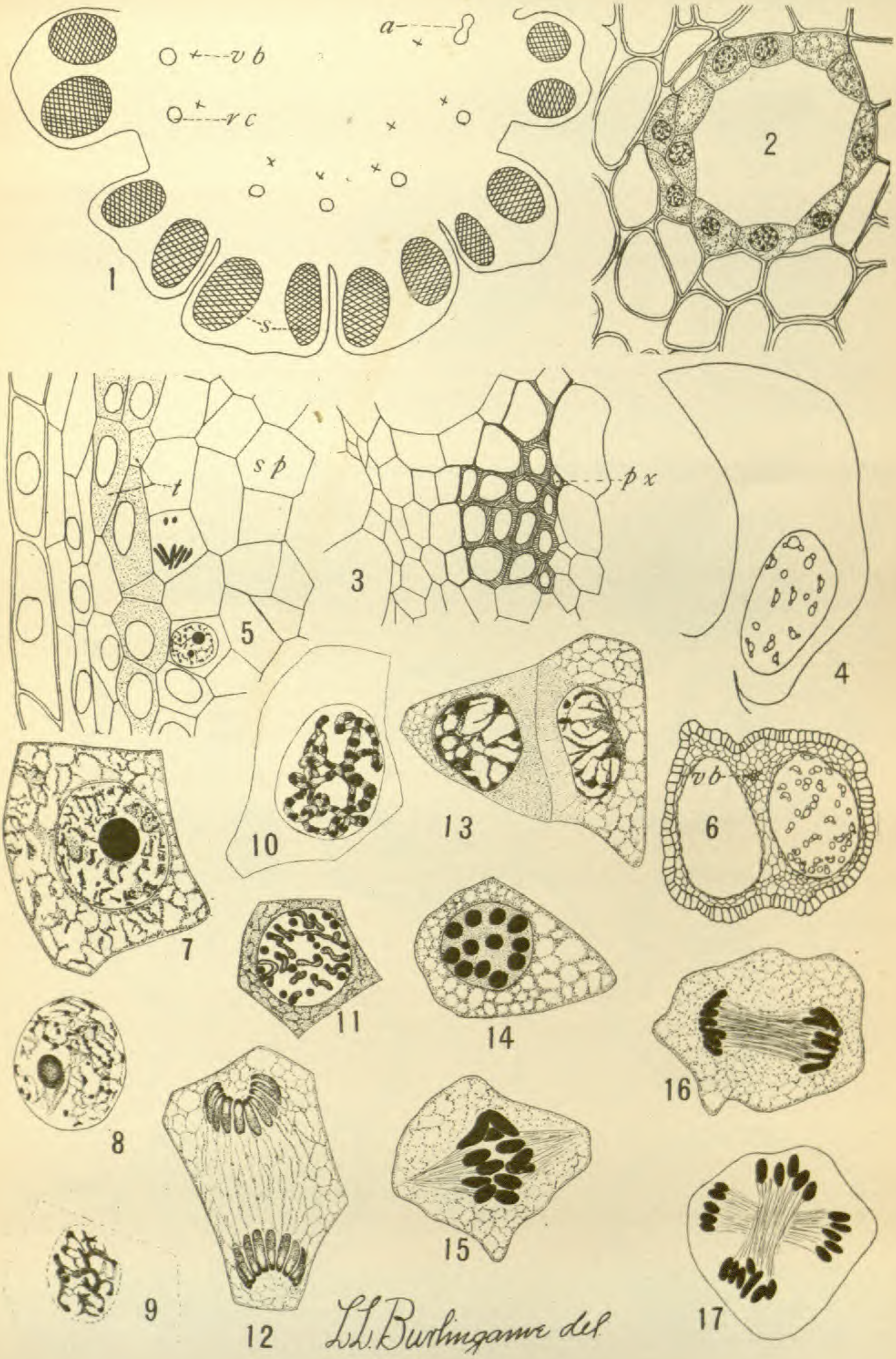
(*Figs. 1, 2, 5, 7–17* are *P.* sp.; *figs. 3, 4, 6* are *P. totarra Hallii*)

FIG. 1.—Cross-section through the middle region of a staminate cone, showing the relative position of sporophylls and sporangia (*s*), vascular bundles (*vb*), and resin canals (*rc*); the canals sometimes branch as shown at *a*.

FIG. 2.—Cross-section of resin canal.

FIG. 3.—Cross-section of vascular bundle from strobilus; *px* shows position of protoxylem.

FIG. 4.—Longitudinal section of a sporophyll, and one sporangium of a young cone about 3^{mm} in length.



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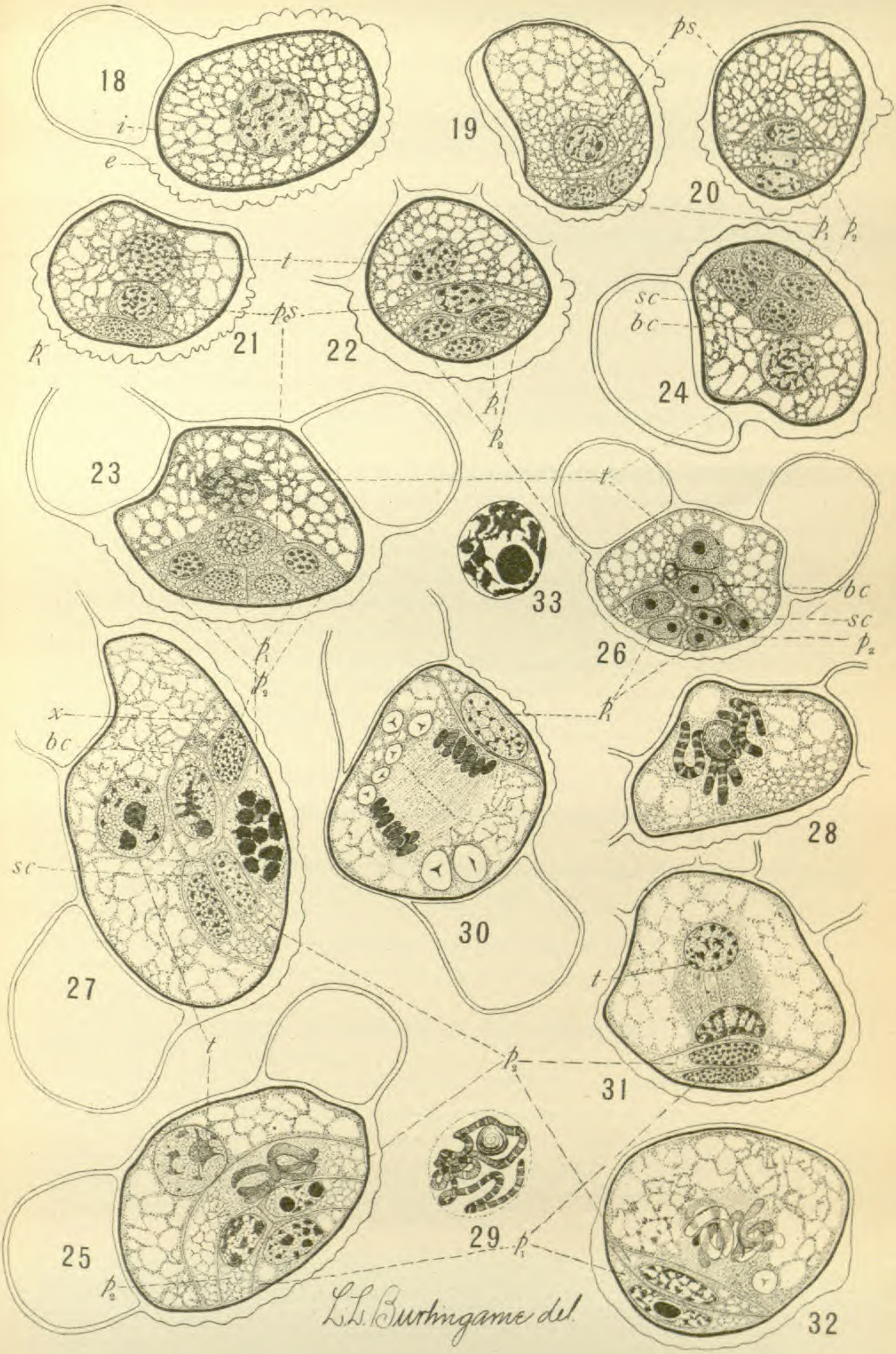
BURLINGAME on PODOCARPUS



BURLINGAME on PODOCARPUS

FIG. 5.—Detail of sporangium of same age as preceding, showing relations of wall, tapetum (*t*), and sporogenous tissue (*sp*).

FIG. 6.—Cross-section through sporangia; *vb*, vascular bundle.

FIG. 7.—Cell of the sporogenous tissue about one division short of the mother cell stage.

FIG. 6.—Detail of a nucleus a little later than preceding, showing the nuclear materials beginning to arrange themselves into threads with here and there deeply staining chromatin knots.

FIG. 9.—Surface view of a still older nucleus showing the strands more distinct and larger.

FIG. 10.—The definitely organized spirem with unusually distinct chromatic knots; the spirem is usually more homogeneous and stains more evenly.

FIG. 11.—A very thin section of a nucleus whose spirem is beginning to segment into chromosomes; compared with *fig. 7*, it shows the variation in size and shape of the sporogenous cells.

FIG. 12.—Longitudinal section of a cell in telophase showing about half of each group of chromosomes; the spindle is curved with the concavity toward the observer.

FIG. 13.—Showing the reconstruction of the daughter nuclei.

FIG. 14.—Mother cell showing the emergence of the chromosomes from the granular mass out of which the spindle arises; the granular materials are actually much denser than shown in this figure and nearly conceal the chromosomes.

FIG. 15.—Longitudinal section of the heterotypic spindle.

FIG. 16.—Late anaphase of the heterotypic mitosis.

FIG. 17.—The homotypic mitosis.

PLATE IX

(*Figs. 18–27, 33* are *P. totarra Hallii; figs. 28–32* are *P. nivalis*)

FIG. 18.—Section of microspore slightly oblique to the wings; *i*, intine; *e*, exine.

FIG. 19.—Male gametophyte showing first prothallial cell (p_1) divided, no second prothallial (p_2) cell, primary spermatogenous cell (*ps*), and in next section the tube nucleus (*t*).

FIG. 20.—Same stage as preceding except that there are here two primary prothallial cells (p_2), the second of which has divided (only one, p_2, of the segments shown).

FIG. 21.—Same as *fig. 19* except that the single primary prothallial cell (p_1) has not divided; *t*, tube nucleus.

FIG. 22.—Male gametophyte showing first prothallial (p_1) undivided, second $(p)_2$ divided once, primary spermatogenous cell (*ps*), and tube nucleus (*t*).

FIG. 23.—Same as preceding except that first prothallial cell (*p*) has also divided and the primary spermatogenous cell (*ps*) has sunk down between the derivatives of the second prothallial cell (p_2); adjacent sections show that there are here four derivatives of the second prothallial cell.

FIG. 24.—Showing the stalk (*sc*) and body (*bc*) cells as well as prothallial cells (p_1, p_2) and tube nucleus (*t*).

FIG. 25.—The mitosis giving rise to stalk and body cells from the primary spermatogenous cell.

FIG. 26.—A usual type of mature gametophyte, having four derivatives of the first primary prothallial cell (p_1), four of the second (p_2), stalk (*sc*), and body (*bc*) cells, and tube nucleus (*t*); nine cells also usual (two p_1, four p_2, stalk, body, tube).

FIG. 27.—Showing the prophase of the division of the first prothallial cell (p_1) and what appears to be a "cell" (*x*) on the side of the body cell opposite to the stalk cell (*sc*); no nucleus could be discovered in this "cell;" see text for further details.

FIG. 28.—Division of the microspore nucleus in *P. nivalis*; a peculiar segmented appearance of the spirem, which has about completed segmentation into chromosomes, is shown.

FIG. 29.—A similar but younger spirem which has not yet begun to segment as the preceding one has done.

FIG. 30.—Anaphase of the division resulting in second prothallial cell (p_2) and antheridium initial.

FIG. 31.—Late telophase of division of antheridium initial into primary spermatogenous cell and tube nucleus; this is the usual shedding stage of this species, with prothallials undivided.

FIG. 32.—Metaphase of division of antheridium initial showing the twelve gametophytic chromosomes; see also *fig. 27*.

FIG. 33.—Details of nucleus of primary spermatogenous cell of *P. totarra Hallii*.

SISYRINCHIUM: ANATOMICAL STUDIES OF NORTH AMERICAN SPECIES

THEO. HOLM

(WITH PLATES X, XI, XI A)

Before the genus Sisyrinchium becomes entirely lost in segregates and in new species, which in late years have accumulated very rapidly, it might be appropriate to present some notes to demonstrate the characteristics of the genus as represented within our own boundaries.

Three sections are recognized by BENTHAM and HOOKER: BERMUDIANA Adans., ECHTHRONEMA Herb. (HYDASTYLUS Salisb.), and ERIPHILEMA Herb., based on floral structure, and especially whether the filaments are connate for their entire length or only partly so. In his work on the *Botany of California* WATSON reached the same conclusion, and considered these floral characters as being merely of sectional importance. But in late years some American writers have raised these sections to generic rank, though with the preference of Sisyrinchium for Bermudiana, and Hydastylus for Echthronema, and without having invented any other distinctive characters than the floral, already described by BENTHAM and HOOKER, and by WATSON. In fact the habit of these plants is very much alike; and strikingly so when compared with Iris, in which genus the floral structure exhibits no small modification, and besides, the habit is extremely variable; nevertheless Iris has not yet suffered the same dissolution as Sisyrinchium.

The internal structure of the Irideae has already been studied by some authors, but not very extensively, since only the leaves have been examined. ROSS,[1] and CHODAT and BALICKA-IWANOWSKA[2] have published some very interesting anatomical papers dealing with the foliar structure of a large number of genera, but very little has been written in regard to our genus Sisyrinchium. The following notes may thus be considered as supplemental to these papers, but I have included the structure of the stem and root for the sake of

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[1] Anatomia comparata delle foglie delle Iridee. Malpighia 6:1892; and 7:1893.

[2] La feuille des Iridées. Jour. de Botanique. 1892.

making the anatomical diagnosis a little more complete. Moreover, I believe that the internal characters observed in representatives of the three sections mentioned above will strengthen the former view of considering Sisyrinchium as one genus, and a very natural one.

The material examined consists of *S. anceps* Cavan., which is very frequent in sandy soil among rocks on the Potomac shore (D. C.); *S. angustifolium* Mill., from sandy hills near Brookland (D. C.); *S. montanum* Greene, from gravelly soil along creeks on Long's Peak (Colorado), at an elevation of about 9000 feet; *S. xerophyllum* Greene, which I found quite abundant in low pine barrens near Eustis (Florida); *S. grandiflorum* Dougl., from dry hillsides in Oregon; and *S. californicum* Ait. f. from swamps at Bodega (Cal.). The last two species were kindly sent to me by Miss ALICE EASTWOOD and Mr. THOMAS HOWELL. To these may be added the tuberous-rooted *S. alatum* Hook. from lava fields above Cuernavaca, Morelos, Mexico, at an elevation of 8500 feet, collected by Mr. C. G. PRINGLE.

As stated above, the general habit of these species is very much the same, especially the inflorescence. This represents in our species of Sisyrinchium a rhipidium,[3] and this type of monochasium is frequent among the Irideae. Whether the inflorescence is single and terminal or accompanied by a lateral, the flowers are always surrounded by green, leaflike bracts (L, L^1, and L^2, *fig. 2*); a membranaceous foreleaf occurs at the base of the lateral inflorescence (P, *fig. 2*) and at the base of the axillary flowers (P^1–P^3, *fig. 6*). The successive development of the flowers may be seen in the diagram (*fig. 6*), where five flowers (*1–5*) are situated in the same plane, and where *1* is the terminal, the earliest developed. The various stages of these flowers are shown in *figs. 3–5*, but the two bracts (L^1, L^2) are only indicated. The stamens, especially the anthers (*St*, *figs. 4, 5*), are much farther advanced than the outer (P^1) and inner perianth leaves (P^2). I have found no deviation from this type of inflorescence in any of the three sections, but the relative length of the green bracts (L–L^2, *fig. 2*) varies very much, and is considered as a specific character, with no good reason, however. Bracts and

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[3] Compare EICHER, Blüthendiagramme 39. *fig. 20A.*

foreleaves, as we know, are very frequently subject to variation, sometimes in accordance with the surroundings

The rhizome is usually very short and cespitose, but in some species, S. *californicum* for instance, the rhizome is horizontally creeping, with the internodes quite distinct. The leaves are two-ranked, equitant, and the aerial stems strongly compressed, except in S. *grandiflorum*, in which leaves and stems are almost cylindric. It would be interesting to know whether the species of these three sections germinate in the same way, but so far this point does not seem to have been studied. For this reason I have followed S. *angustifolium*, which is so very frequent in the vicinity of Brookland, from seedling to mature plant, and the structure of the seedling is as follows. The cotyledon (*Cot, fig. 1*) is epigeic and consists of a sheathing base and a long filiform blade, the apex of which remains inclosed within the seed for some time, as shown in the accompanying drawing. Three leaves (L^1–L^3) are developed from the plumule during the first season, and the structure of these leaves agrees with that of the later ones, being ensiform and green. The primary root (*R*) grows and remains active during the first season, and becomes ramified; secondary roots (*r*) develop also, and these proceed from the base of the cotyledon. It requires several years for the plant to reach the flowering stage, and until then the small rhizome remains as a monopodium similar to Iris. This method of germination represents KLEBS' type 5,[4] and corresponds, to some extent, with that most frequent among the dicotyledons where the seed leaves are epigeic. It is characteristic of several Liliaceae (Allium, Bowiea, Asphodelus, etc.) and of Agave, but not of Iris; in *I. Pseudacorus*, for instance, the apex of the cotyledon remains inclosed within the seed, and does not become free as in Sisyrinchium. So far as the external structure of the various members of the three sections mentioned above is concerned, there seems no plausible reason for dividing the genus, and we shall see that the internal structure also does not warrant any such segregation. Whatever distinctive characters have been observed are merely sectional, and it is hardly necessary to call attention to the fact that much more pronounced deviations in struc-

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[4] Beiträge zur Morphologie und Biologie der Keimung. Untersuch. Bot. Inst. Tübingen 1:572. 1881–1885.

ture are known in many other genera, which so far have been left intact.

Anatomically our genus is not a very interesting one, but the structure has never been studied, and I thought that the following discussion of the vegetative organs might be of some interest from a comparative point of view. Some knowledge of the structure, especially since the material came from widely separated stations, may be of interest to students of plant societies, for it seems to me that many of the conclusions reached in the name of ecology are too superficial, so long as the plants themselves have not been studied thoroughly.

ROOTS

In our native species of Sisyrinchium the secondary roots are slender; they are soft and of a whitish color in *S. californicum*, but quite strong, and yellowish brown in the other species. In *S. xerophyllum* and *S. grandiflorum* the roots are almost villous from the dense covering of root hairs, while in the other species the roots are much less hairy. The epidermis is thin-walled, and inside this is an exodermis of a single stratum, whose cells are mostly pentagonal in cross-sections, and thin-walled in all the species except *S. xerophyllum*, in which the exodermis is very distinctly thickened. The cortical parenchyma contains no stereids, and is composed of a compact, but thin-walled tissue; in *S. montanum* the cortex collapses tangentially, but remains solid in the other species, and contains deposits of starch except in *S. californicum*. The endodermis shows a very pronounced thickening of the inner cell walls, thus representing a U-endodermis, but is thin-walled in *S. californicum*.

The pericambium consists generally of a single layer of thin-walled cells (*P*, *fig. 8*), and is continuous; however, the following exceptions were noticed. In *S. montanum* (*fig. 9*) there is frequently a second stratum of pericambium to be observed outside some of the hadrome rays and this same condition occurs also in *S. xerophyllum* (*fig. 10*). Sometimes the pericambium becomes thick-walled, as may be seen from *fig. 11*, which is of *S. xerophyllum*, and in which the cells outside the leptome are quite thickened in contrast to those outside the hadrome. In these same figures of *S. xerophyllum* (*figs. 10, 11*) we notice also that the pericambium is not continuous, but interrupted by the protohadrome vessels. This interruption of the pericambium was observed only in this species (*S. xerophyllum*), in all the roots examined, but not in any of the roots of the other species.

The hadrome is very conspicuous in all the roots, and there may be as many as twelve rays with two or three protohadrome vessels in each ray; the leptome, on the other hand, consists of very narrow strands, in which the protoleptome cell is readily visible (*PL, figs. 8–11*). Although the rays of the hadrome extend to the center of the root, the conjunctive tissue, nevertheless, is very conspicuous, and is mostly thin-walled except in *S. xerophyllum* and in some of the roots of *S. anceps.*

This structure seems to be characteristic of the slender secondary roots of mature specimens of this genus. In the corresponding roots of the seedling of *S. angustifolium* no exodermis is developed and the cortical parenchyma is very thin-walled; the endodermis, on the other hand, is very thick-walled, representing a typical U-endodermis. In these young roots the pericambium is continuous, and the stele contains only two hadromatic rays alternating with two small groups of leptome. In regard to the structure of the stele, the pericambium, and the mestome, the thin lateral roots of mature specimens agree with that observed in the secondary ones of the seedling; but the endodermis is different, being thin-walled and showing the Casparyan spots very plainly (*End, fig. 16*).

The structure of the roots of these species is thus very uniform, and the only distinction seems to depend upon the structure of the pericambium, which sometimes consists of more than one stratum, and which may be interrupted by the protohadrome, as observed in *S. xerophyllum* from subtropical Florida.

In the tuberous roots of the Central American *S. alatum* Hook. the cortical parenchyma represents a very large parenchyma filled with starch, and with the cell walls thickened; but otherwise the structure of epidermis, exodermis, endodermis, and pericambium, which is continuous, is identical with that of the species described above. The number of hadromatic rays averages about twelve, and the leptome occurs as exceedingly narrow strands in these tuberous roots.

RHIZOME

S. californicum is the only species examined that possesses a horizontally creeping rhizome with the internodes distinct. The structure is rather weak when compared with that of the rhizomes of the monocotyledons in general, since no stereome is developed. The epidermis is thin-walled and covers a cortex of broad, compact parenchyma; the endodermis is thin-walled, and the cells somewhat irregular in shape. Inside the endodermis is a large, thin-walled pith, in which the numerous mestome strands are located, but without being arranged in bands; most of these mestome bundles were observed to be leptocentric, the leptome being more or less completely surrounded by the hadrome.

STEM ABOVE GROUND

With exception of *S. grandiflorum* the stem is ancipital, simple, or sometimes branched above; the wings vary somewhat in breadth, but the central portion of the stem is always cylindric, and of a very firm structure, due to the presence of a solid sheath of thick-walled stereome. The cuticle is frequently thick and wrinkled, and cell walls of the epidermis are prominently thickened, especially the outer, and very often extended into short papillae, but not in *S. californicum.* In the body of the stem as well as in the wings the cortex is composed of palisades and represents a very compact tissue, but in *S. californicum* the cortical parenchyma is more open and the cells very short, almost roundish in transverse sections. There is no hypodermal collenchyma or stereome in any of these species, and the stereome constitutes, as stated above, a closed sheath of several strata located on the inner face of the cortex in the cylindric portion of the stem; in the wings the stereome accompanies the larger mestome strands as small groups on the leptome side. The mestome bundles are arranged in two concentric bands in the cylindric part of the stem, but in a single plane in the wings. They are collateral, and those of the peripheral band are very small, and contain mostly leptome; they are located in the cortex, but their hadrome touches the stereomatic sheath. Those of the inner band are much larger and are located directly inside the stereome cylinder, with their hadrome bordering on the pith. The innermost part of the cylinder is occupied by a pith, which is frequently somewhat thick-walled and solid. In the wings the mestome strands are few, and they show mostly the same position of the hadrome, which is turned toward the center of the stem; it is only the marginal mestome strands that differ in this respect, the leptome and hadrome being vertical on the surface of the wings, instead of parallel.

In *S. grandiflorum* the structure of the stem is somewhat different; the outline is less compressed and there are many deep furrows. These furrows contain cortical parenchyma, and the peripheral band of small mestome bundles is located in the ridges, thus imbedded in the cortex and removed from the stereomatic sheath. The inner band of mestome bundles, on the other hand, is located inside the stereome, as in the other species described above.

The structure of the stem is thus very uniform in these species of Sisyrinchium, and it seems characteristic of the genus that no hypodermal mechanical tissue is developed; that there is a strong sheath of stereome separating two concentric bands of mestome bundles, of which the peripheral are of the same size and much smaller than the inner ones; furthermore, the winged stem of most of these species constitutes also a very conspicuous feature.

LEAVES

The foreleaves are membranaceous, almost destitute of chlorophyll, and strongly compressed from side to side; they are frequently scabrous from thick-walled papillae (*fig. 12*), but only on the dorsal face. The cuticle is smooth, and the epidermis is moderately thick-walled on the dorsal face, but thin-walled on the ventral. There is only chlorenchyma in the middle portion of these leaves, and it consists of roundish cells throughout, with very little chlorophyll; the broad and very thin margins of the foreleaves consist only of epidermis, that of the dorsal face. The stereome is very poorly represented; it occurs as two very small, hypodermal strands, one on each side of the ventral sinus above the midrib, and the veins have a few layers of this tissue on the hadrome side. There are several mestome strands in these leaves (3 to 8) and the midrib is usually a little thicker than the others; the mestome strands are collateral, and surrounded by parenchyma sheaths. While the leptome is well developed in all the veins, the hadrome is frequently absent, except in the midrib.

The green leaves are sheathing, and provided with a long, strongly compressed blade, the structure of which is very markedly isolateral. By examining the anatomical structure of the blade one gets the impression that the peculiar position of the leptome and hadrome in the veins is due to a concrescence of the two halves of the leaf-blade, resulting in a more or less complete suppression of the morphologically ventral face of the blade.

However, the development of the ensiform leaf of Irideae, as described by GOEBEL,[5] teaches us something very different. According to this author the singular shape and structure of the blade is caused not by a concrescence of the wo halves of the blade, but by the peculiar growth of the leaf-primordium. The young leaf becomes laterally compressed at a very early stage of its development, and it so happens that its dorsal face shows this flattened growth much more than the ventral. The real growing-point soon ceases to be active, while a new point takes its place and this is located on the extreme back of the primordium, and somewhat lower than the original. The leaf thus shows two apices, and the secondary of these grows out into a long bladelike organ, which consequently has no ventral face, and in which the arrangement and structure of the veins must follow other laws than in a normally developed leaf-blade. The real apex of the leaf is thus to be found at the upper part of the open sheath, while the bladelike organ represents merely a secondary growing-point, which has surpassed the primary one.

In the species of the section BERMUDIANA the leaf-sheath is usually much shorter than the ensiform blade; in the section ECHTHRONEMA, on the other hand, the sheath may be traced to very near the apex of the blade; and finally, in the section ERIPHILEMA the blade is less compressed and often much shorter than the open, sheathing portion of the leaf. It is interesting to see that although the leaves are ensiform in all these species, the internal structure nevertheless exhibits two types so far as concerns the disposition of the mestome strands, which are in a single plane, as in BERMUDIANA, or in two parallel planes, as in the two other sections. But otherwise the

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[5] In SCHENK's Handbuch der Botanik 219. Breslau. 1884.

structure is rather uniform, and the few distinctions which I have observed seem to be of merely specific importance.

Beginning with section BERMUDIANA, the leaf-blade is smooth in *S. anceps*, but furrowed longitudinally in several of the other species, as *S. angustifolium*, *S. bellum*, etc. The surface varies from perfectly glabrous to very prominently scabrous, and it deserves notice that the leaves may exhibit both structures when examined at different places. The apex may be very scabrous, for instance, in contrast with the lower parts of the blade, or sometimes *vice-versa;* or some of the earliest developed leaves may be more glabrous than the succeeding. I mention this since the characters "glabrous" and "scabrous" figure so very conspicuously in the recently published diagnoses of "new species of Sisyrinchium."

The cuticle is thick and distinctly wrinkled. The epidermis is frequently thick-walled, especially the outer walls (*figs. 13, 15, 20, 21*), and, as stated above, the extension of epidermis into papillae of various forms, pointed or obtuse, is common to several members of the genus (*fig. 21*).

The stomata are arranged in longitudinal lines on both sides of the blade, and they are sunk (*fig. 13*). It is interesting to notice that in the subtropical *S. xerophyllum* (from Eustis, Florida) the thickness of epidermis reaches its maximum (*fig. 15*); the cell walls are extremely thick and porous, but no papillae were observed in this species.

In regard to the chlorenchyma, we have in this section a more or less typical and compact palisade tissue of several layers, the innermost of which forms circular bands around the mestome bundles, with the cells radiating toward the center; while in the peripheral (hypodermal) strata the palisade cells are vertical to the epidermis. In some species, for instance *S. anceps* and *S. xerophyllum*, the chlorenchyma breaks down and forms lacunes between the veins, especially in the latter species. The mechanical tissue in the genus is only represented by stereome, which accompanies the mestome bundles as a small cover on the leptome and hadrome side; but it is not very thick-walled except in *S. xerophyllum*, and it does not occur as isolated, hypodermal groups in any part of the leaf. It occupies the somewhat unusual position of being located inside the thin-walled, chlorophyll-bearing parenchyma sheath, which surrounds each of the mestome strands. However, this parenchyma sheath differed from similar sheaths in other monocotyledons by showing no resistance when treated with concentrated sulfuric acid.

The arrangement of the mestome strands is very peculiar, and especially the disposition of leptome and hadrome. From the fact that the blade is not a blade in the proper sense of the word, but an outgrowth of the dorsal face, hence with no ventral face developed, the course of the veins is different from that of leaves in general. If we examine a cross-section of the blade we notice at once that all the mestome strands occupy a single plane, extending from the one margin of the blade to the other; also that the mestome strands show a different position of leptome and hadrome in relation to the periphery of the section. Those near the center of the blade are the largest, and in these the leptome turns alternately with the hadrome to the right or left of the longitudinal axis of the leaf; in this way, by examining the two sides of the leaf, we find in one mestome strand the leptome turned toward the right, in the next toward the left, etc.; and the same alternating position is of course also occupied by the hadrome. But the small strands, which are located in the thin margins of the blade, show almost constantly the leptome turning toward the edge of the leaf, and the hadrome, on the contrary, toward the center. In other words, the structure of the blade looks as if the two halves had grown together, but we know from the development of the leaf-primordium that no such concrescence has taken place. The mestome bundles are collateral and show the ordinary structure; anastomoses are not infrequent, and they form very acute angles with the larger veins, as in Eriocaulon for instance. The leaf structure is thus very uniform in this section, and the most conspicuous variation seems to depend upon the thickness of the epidermis, and upon whether the chlorenchyma forms typical palisades (*fig. 20*), or consists of short, almost roundish cells, as in *S. anceps* (*fig. 21*).

In *S. grandiflorum* (section ERIPHILEMA) the leaf structure differs very conspicuously from that of the former section, and resembles much more the structure of a stem than of a foliar organ. In this species the leaf is less compressed; the mestome strands constitute a narrow elliptical band, instead of being located in a single plane;

also the central portion of the leaf contains a thin-walled, colorless tissue very much resembling the pith of a stem, and is frequently hollow. Otherwise the structure of the tissues is identical with that of several species of the former section (BERMUDIANA). The cuticle is thick, but smooth; the epidermis is papillose, moderately thick-walled, and the chlorenchyma is composed of palisades, which are vertical to the epidermis but very open from wide intercellular spaces. The stereome is rather thin-walled, and shows the same distribution as in BERMUDIANA. The leaf is very distinctly furrowed longitudinally, and the mestome strands, which are of two sizes, are arranged alternately so that the smaller are in the furrows and the larger in the ridges. All the mestome strands turn the leptome toward the periphery of the blade, while the hadrome borders on the thin-walled parenchyma, which fills the innermost portion of the blade, thus resembling a pith in respect to structure and position.

In the section ECHTHRONEMA the principal structure of the blade agrees better with that of ERIPHILEMA than of BERMUDIANA; because the mestome strands are here also in a very narrow elliptical band with the hadrome turned inward and bordering on a central, thin-walled parenchyma. In *S. californicum* the cuticle is thin and smooth; the epidermis is relatively thin-walled and perfectly glabrous. The chlorenchyma (*fig. 18*) shows no palisades, but is composed of a homogeneous tissue of oblong to roundish cells (in cross-section); however, a superficial section of the blade (*fig. 17*) shows the cells of the chlorenchyma very distinctly stretched and lobed, not parallel with the longitudinal axis of the leaf, but vertical to it. In this way the chlorenchyma shows actually the structure of a pneumatic tissue, as this is developed in the dorsal portion of leaves; the central part of the chlorenchyma in this species is also a colorless, thin-walled parenchyma. No stereome was observed, and the mestome bundles are in a narrow elliptical band; they are collateral and surrounded by thin-walled parenchyma sheaths.

This is in brief the anatomical structure of these species of Sisyrinchium, and bearing in mind that representatives of each of the three sections have been examined, it appears to me that the genus is a very natural one, and that it ought not to be divided. In regard to the morphological structure of the shoot, I have not been able to detect any character that seems peculiar to these sections; on the contrary, the rhizome, the leaves, and the inflorescence are very uniformly developed, and the only distinction depends upon the floral structures which were mentioned in the introduction. If these floral structures were accompanied by differences in the development of the shoot, and also by peculiarities in the internal structure, there might have been some reason for dividing the genus. There are several very peculiar looking species in Mexico, and these ought to be examined anatomically from fresh material. Until then it seems most advisable to leave the genus intact.

Finally, I wish to add a few words in reference to the structure of the chlorenchyma in other genera of the Irideae. We have seen the chlorenchyma in the sections BERMUDIANA (*fig. 19*) and ERIPHILEMA is more or less differentiated as palisades, while in ECHTHRONEMA this tissue is composed of oblong cells parallel with epidermis; moreover, that the cells in ECHTHRONEMA are lobed, resembling those of a pneumatic tissue. These structures occur also in other genera, and for the sake of making a comparison I examined some of them. In Iris, for instance, we find in *I. cristata* Ait. (*fig. 22*) a structure of the chlorenchyma which corresponds well with that of *Sisyrinchium californicum*, but the cells of which are branched rather than lobed, thus representing a typical pneumatic tissue. In *Iris verna* L. and *I. fulva* Ker., on the other hand, there are typical palisades, which, however, show the same direction, being parallel with the epidermis and vertical to the longitudinal axis of the blade; in *I. xiphioides* Ehrh. the palisades are vertical to the epidermis. A structure that corresponds with that of *Iris verna* is furthermore characteristic of *Tapeinia magellanica* Juss., *Freesia refracta* Klatt., and *Tritonia* sp. In *Belamcanda chinensis* Adans. the chlorenchyma has a very irregular structure, the cells varying from oblong and entire to more or less deeply lobed. We have thus in Iris as varied a development of the chlorenchyma as was observed in Sisyrinchium.

I have also pointed out the somewhat peculiar arrangement of the mestome strands in Sisyrinchium (the single plane in BERMUDIANA, and the narrow elliptical band in ERIPHILEMA and ECHTHRONEMA). That such variation in the position of the mestome bundles is also observable in other Irideae may be seen from the descriptions and figures in the work of Ross cited above. It is really surprising to see the polymorphic structure possessed by Iris. In *I. alata* Poir. the leaves are perfectly open, not ensiform, and the veins show exactly the same position as in a typical linear leaf of grasses, for instance; in species with ensiform leaves we notice in *I. foetidissima* L. the mestome strands forming a narrow ellipse; in *I. juncea* Desf. they are arranged in an almost circular band; in *I. reticulata* M. B. the band is quadrangular; and finally in *I. japonica* Thunb. the structure is like that of section BERMUDIANA. A very striking variation occurs in Gladiolus, where the outline of the section varies from linear to cross-shaped with a corresponding variable position of the mestome strands. These modifications in structure are very striking, and moreover they are in several cases accompanied by distinct external characters, floral or vegetative; nevertheless they are not looked upon as being of anything but specific importance, an opinion which no doubt is the most natural.

In regard to the almost untold number of recently described "species" of Sisyrinchium, I have examined the internal structure of some of these, but so far have failed to detect any character that might appear specific; and moreover it seems very evident, when the diagnoses of the majority of these are read, that they deal not with "species" but merely with "local forms."

BROOKLAND, D. C.

EXPLANATION OF PLATES X, XI, XI A

PLATE X

FIG. 1.—*S. angustifolium:* seedling, showing cotyledon (*Cot*) with seed still attached; *R*, primary root; *r*, secondary roots; L^1–L^3, the first leaves succeeding the cotyledon. Natural size.

FIG. 2.—*S. anceps:* young inflorescence; L–L^2, green bracts; *P*, foreleaf of axillary inflorescence. Natural size.

FIG. 3.—*S. anceps:* inflorescence, the terminal of *fig. 2;* P^1–P^2, foreleaves; L^1–L^2, green bracts. Magnified.

FIGS. 4, 5.—*S. anceps:* two youngest flowers of same inflorescence; P^1, outer, P^2, inner perianth; *st*, stamens. Magnified.

FIG. 6.—*S. anceps:* diagram of a five-flowered inflorescence; *1–5*, the flowers, of which *1* is the first developed; the other letters as above.

FIG. 7.—*S. alatum:* cross-section of root; *C*, cortex; *End*, endodermis; *P*, pericambium; three rays of hadrome and two strands of leptome are figured. ×320.

PLATE XI

FIG. 8.—*S. anceps:* cross-section of root; *PH*, protohadrome; *PL*, protoleptome; the other letters as in *fig. 7*. ×496.

FIG. 9.—*S. montanum:* cross-section of root stele; letters as above. ×496.

FIG. 10.—*S. xerophyllum:* cross-section of root stele; letters as above. ×496.

FIG. 11.—*S. xerophyllum:* cross-section of root stele; *V*, vessels; the other letters as above; many of the pericambium cells are thick-walled. ×496.

FIG. 12.—*S. angustifolium:* epidermal projection from the foreleaf. ×240.

FIG. 13.—*S. angustifolium:* cross-section of the stoma from the leaf. ×496.

FIG. 14.—*S. angustifolium:* a stoma seen from above. ×496.

FIG. 15.—*S. xerophyllum:* cross-section of leaf; *C*, cuticle; *Ep*, epidermis. ×496.

PLATE XIA

FIG. 16.—*S. montanum:* cross-section of a thin lateral root; letters as above. ×496.

FIG. 17.—*S. californicum:* chlorenchyma of leaf, seen from above.

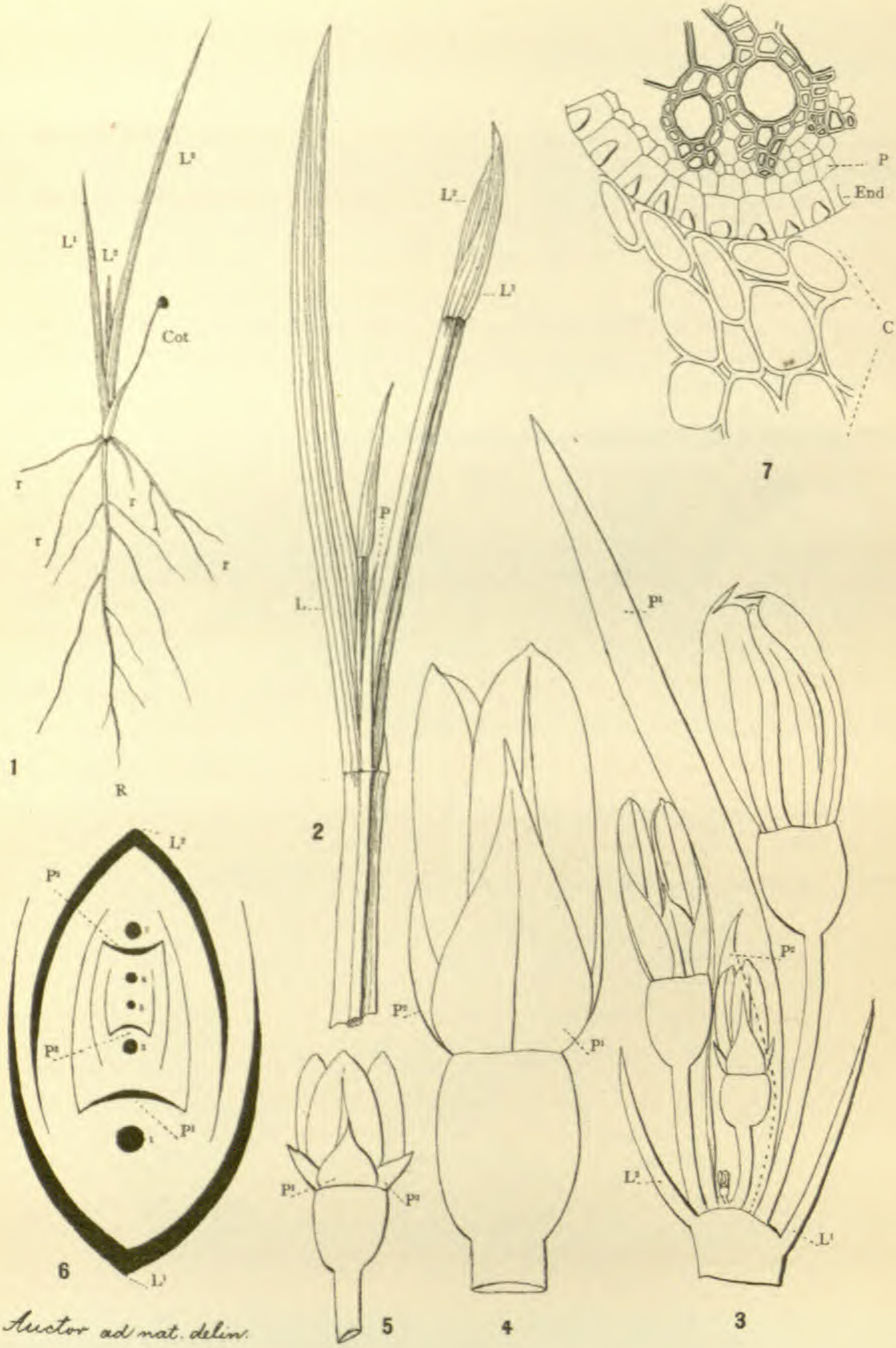
FIG. 18.—*S. californicum:* cross-section of part of leaf; *Ep*, epidermis; *PS*, parenchyma sheath of mestome strand.

FIG. 19.—*S. montanum:* chlorenchyma of leaf, seen from above. ×240.

FIG. 20.—*S. montanum:* cross-section of part of leaf; *St*, two stomata with their air chambers (*A*); the other letters as in *fig. 18*. ×320.

FIG. 21.—*S. anceps:* cross-section of part of leaf; *Ep*, epidermis; both leptome and hadrome have a support of stereome. ×496.

FIG. 22.—*Iris cristata:* chlorenchyma of leaf, seen from above. ×240.



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HOLM on SISYRINCHIUM

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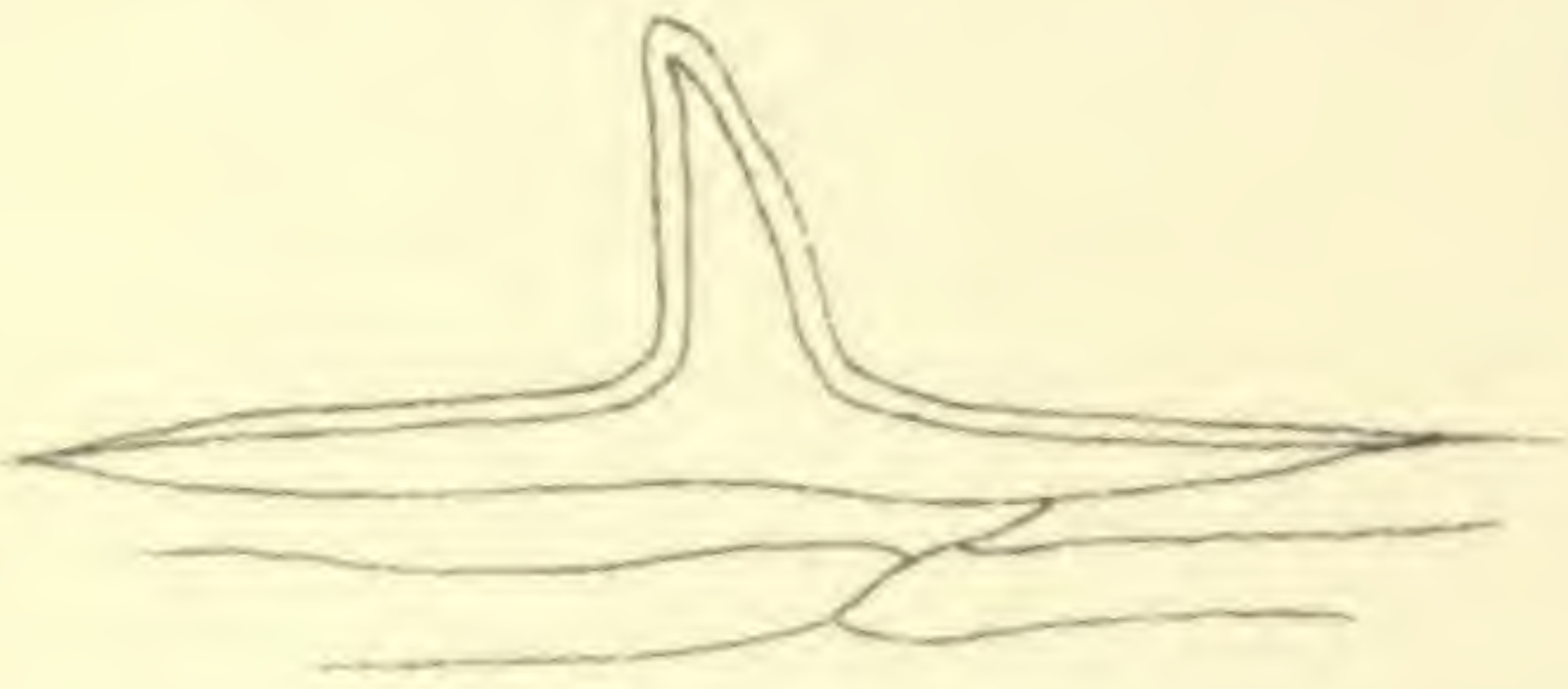

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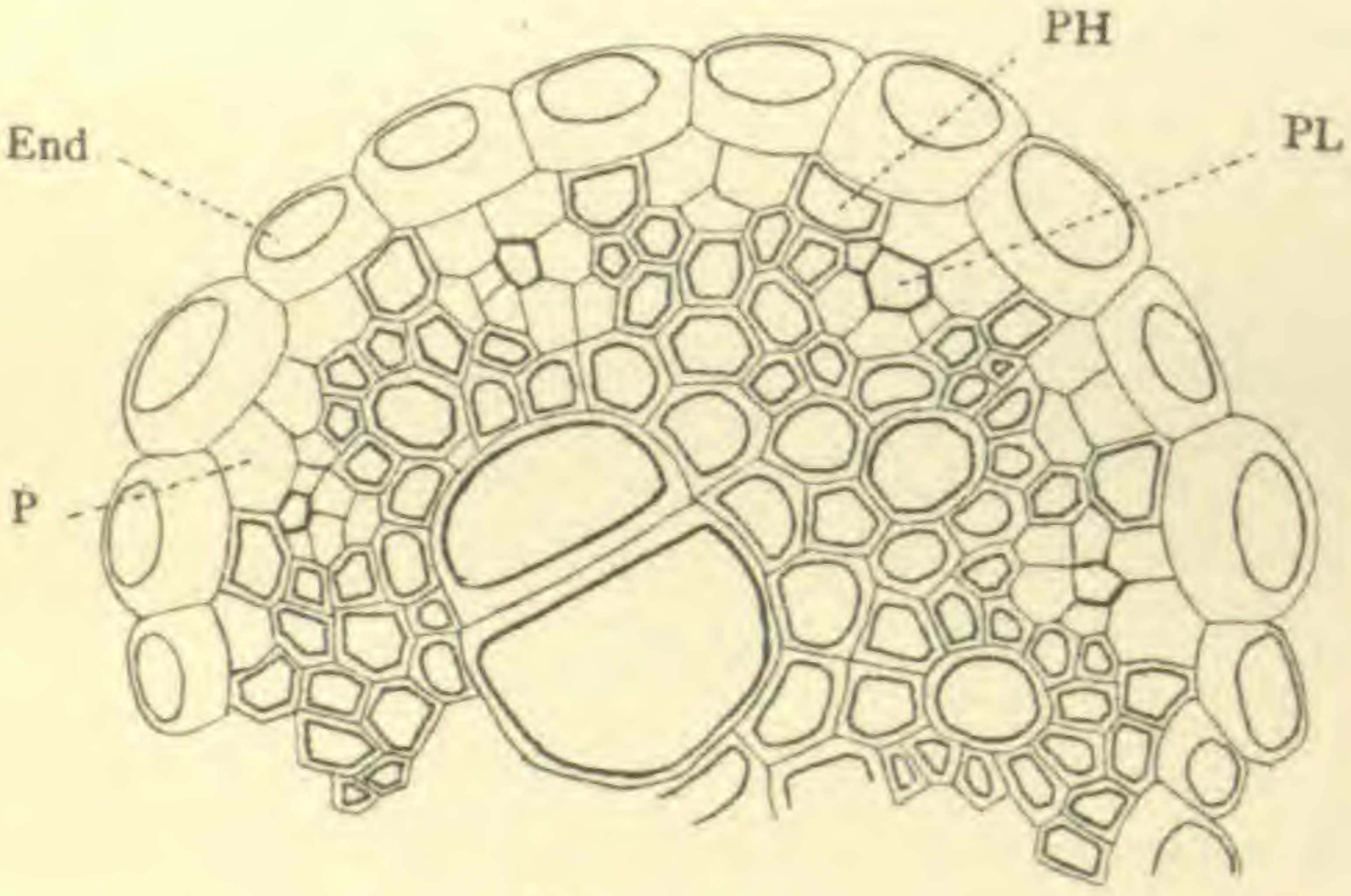

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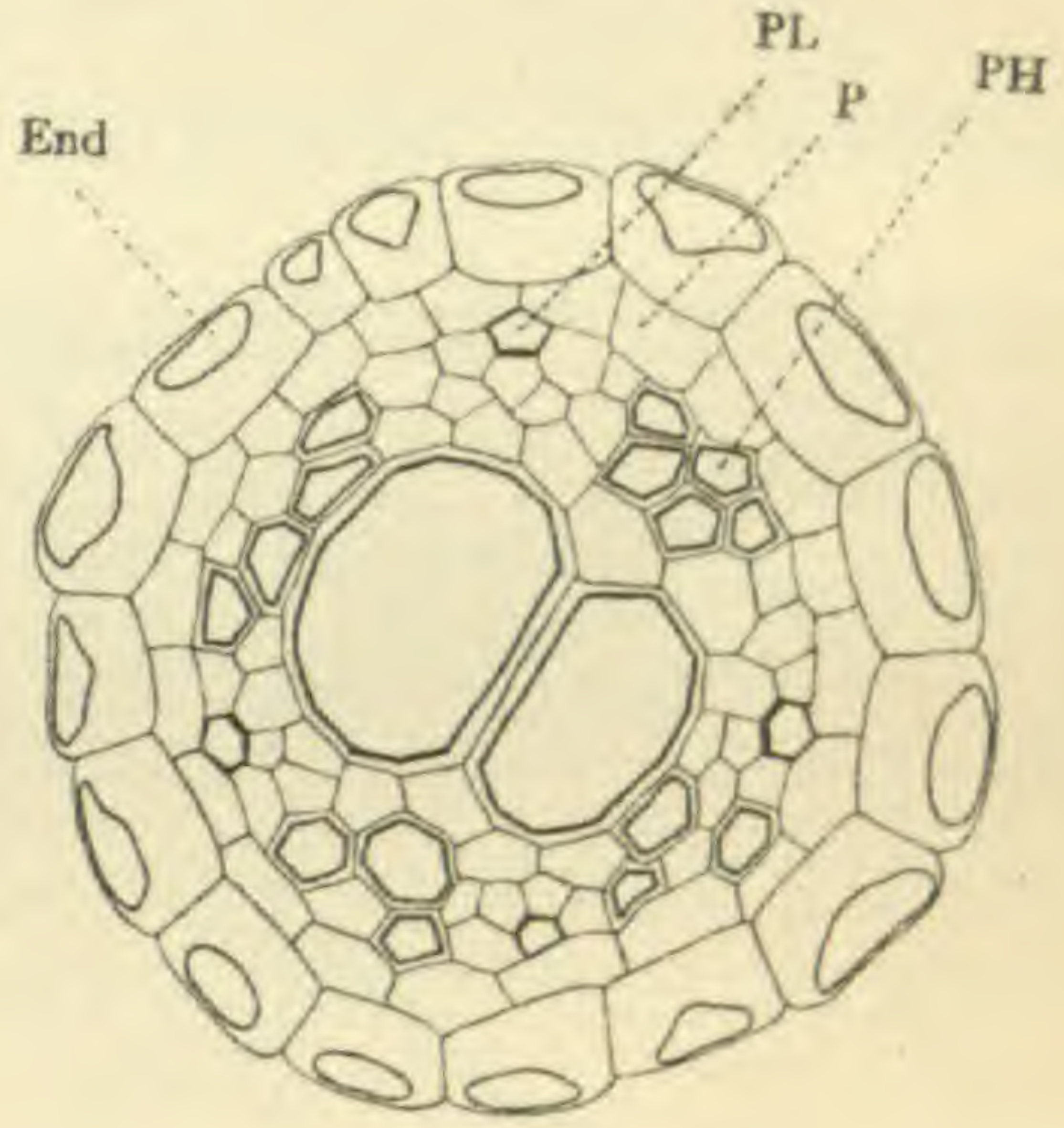

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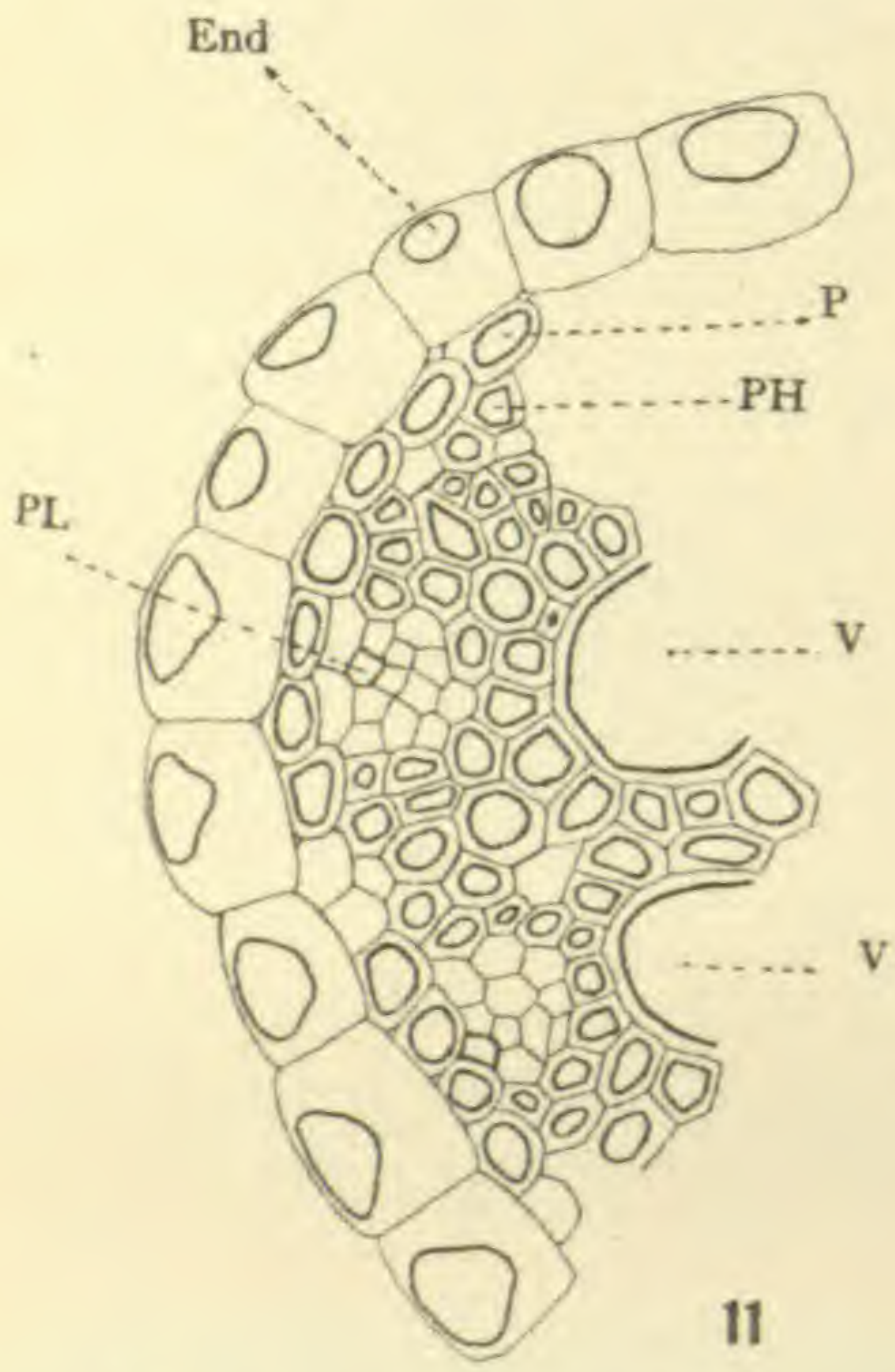

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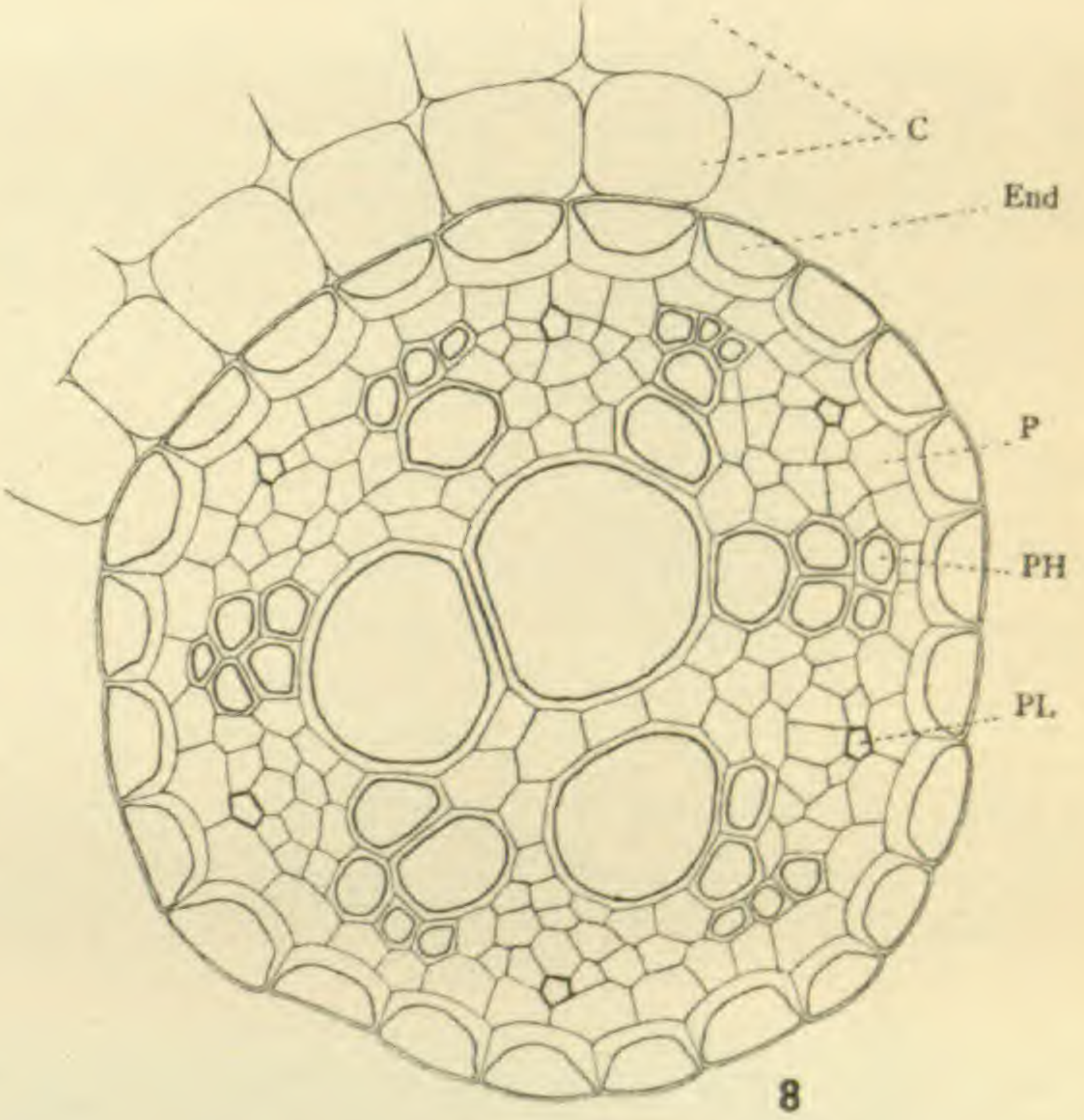
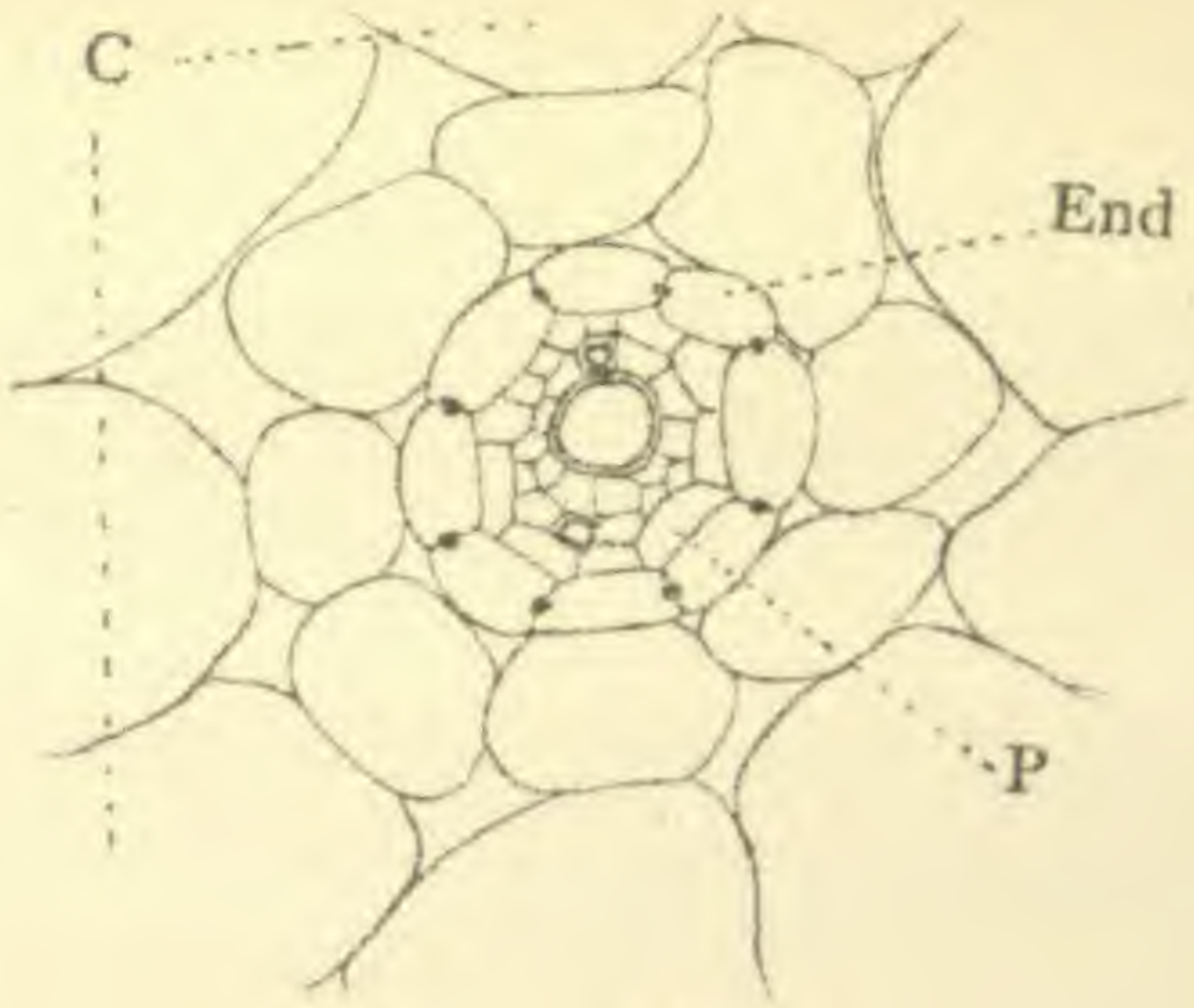


8

Auctor ad nat. delin.

HOLM on SISYRINCHIUM

19



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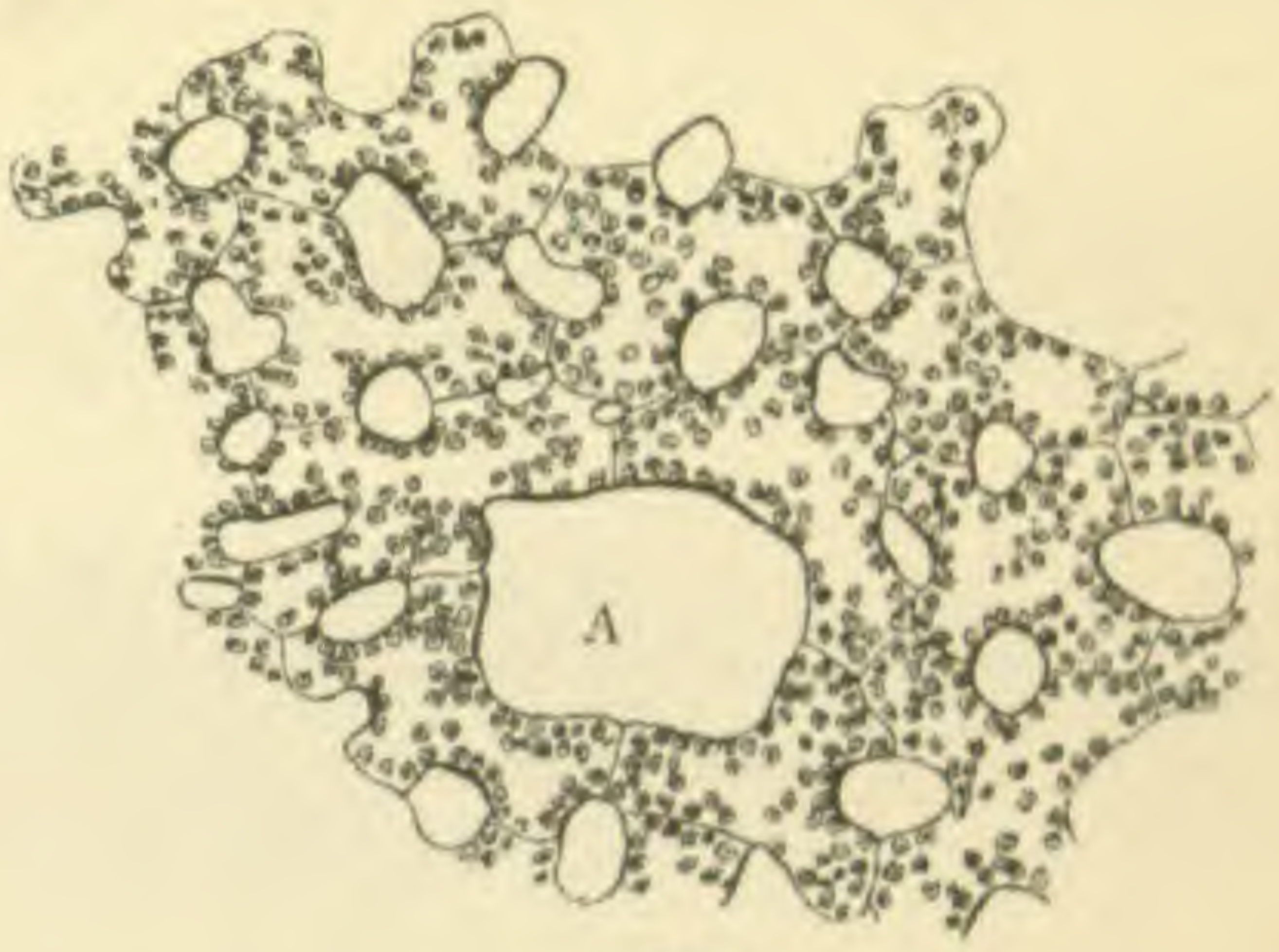

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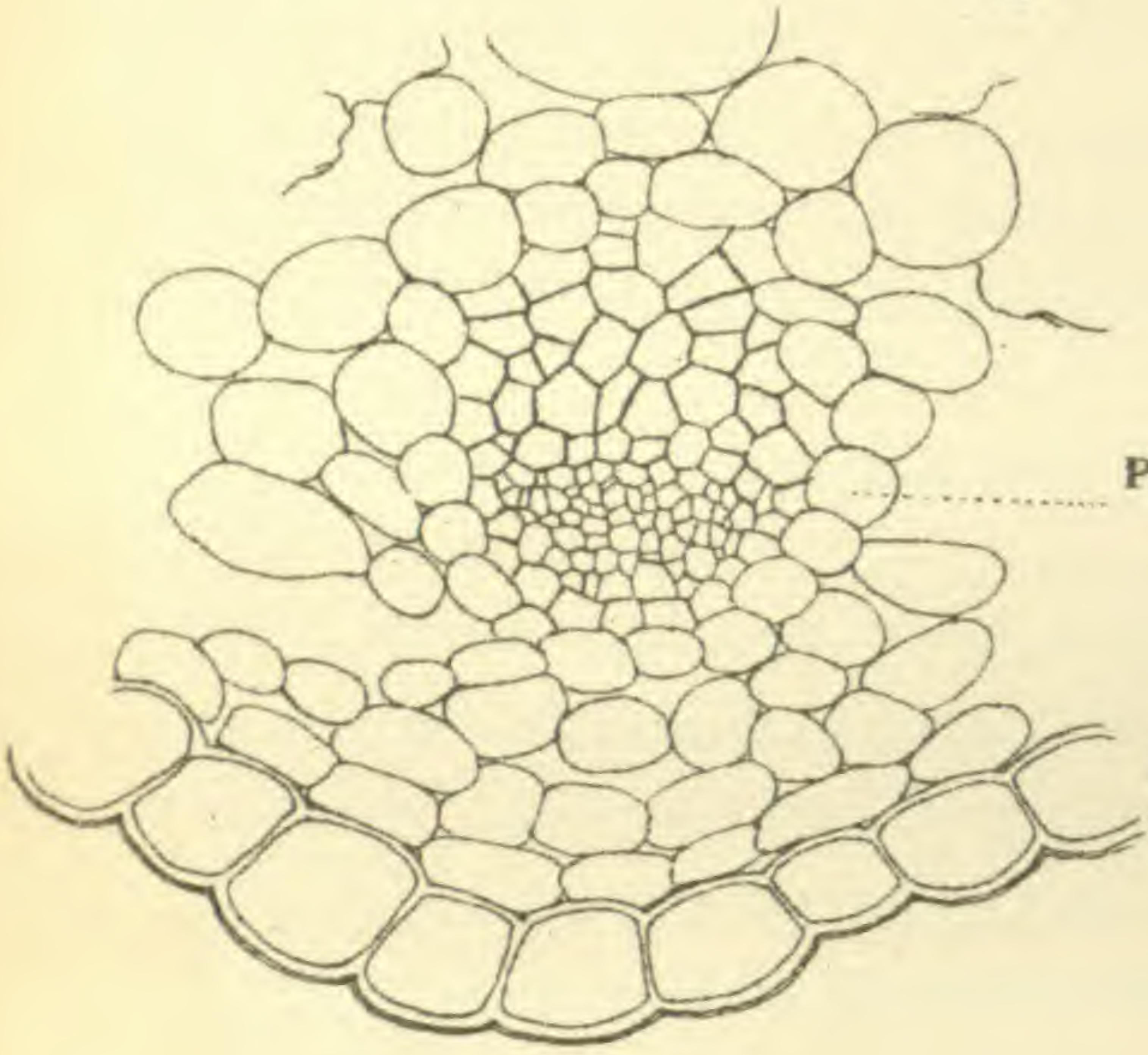

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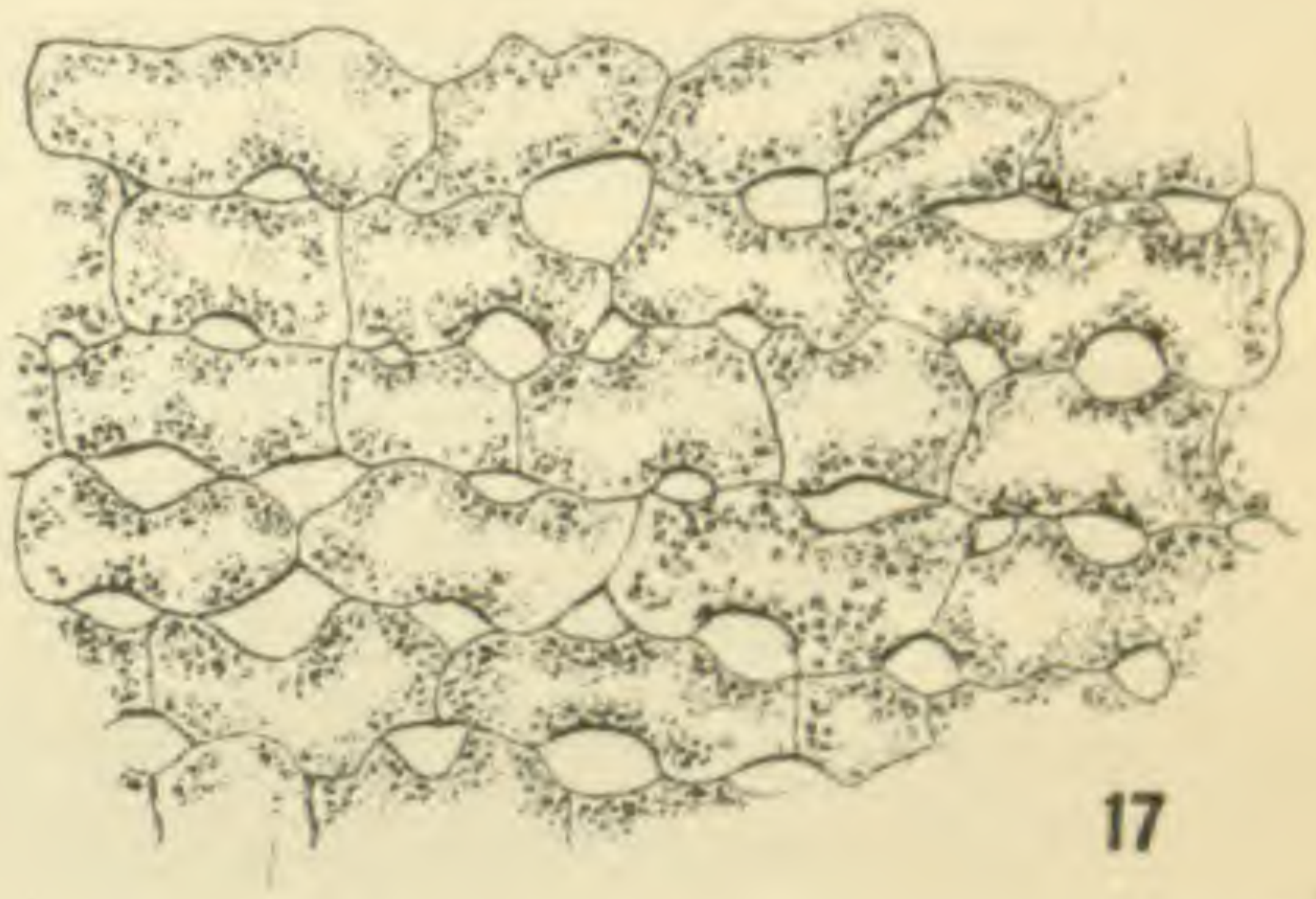

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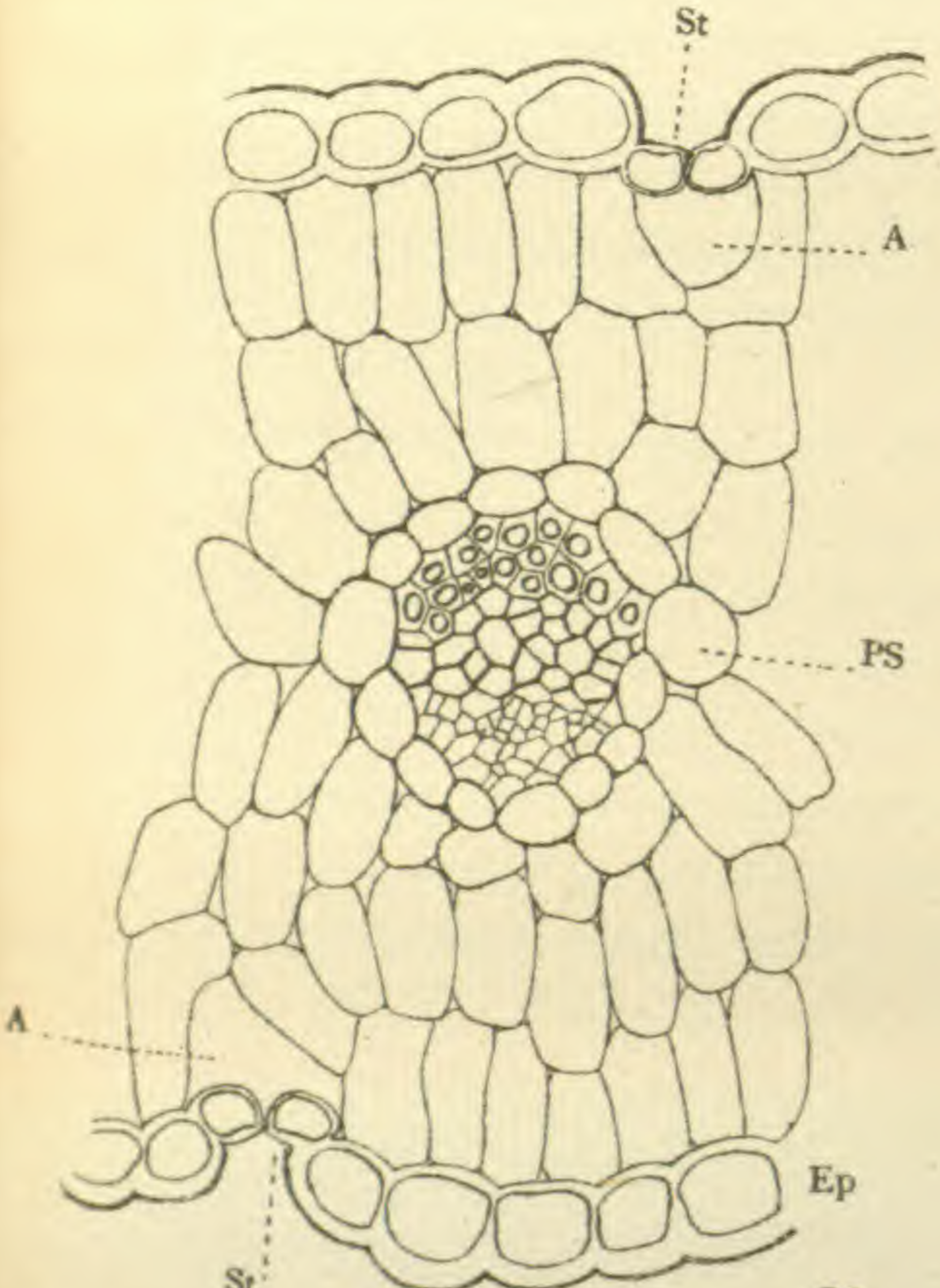

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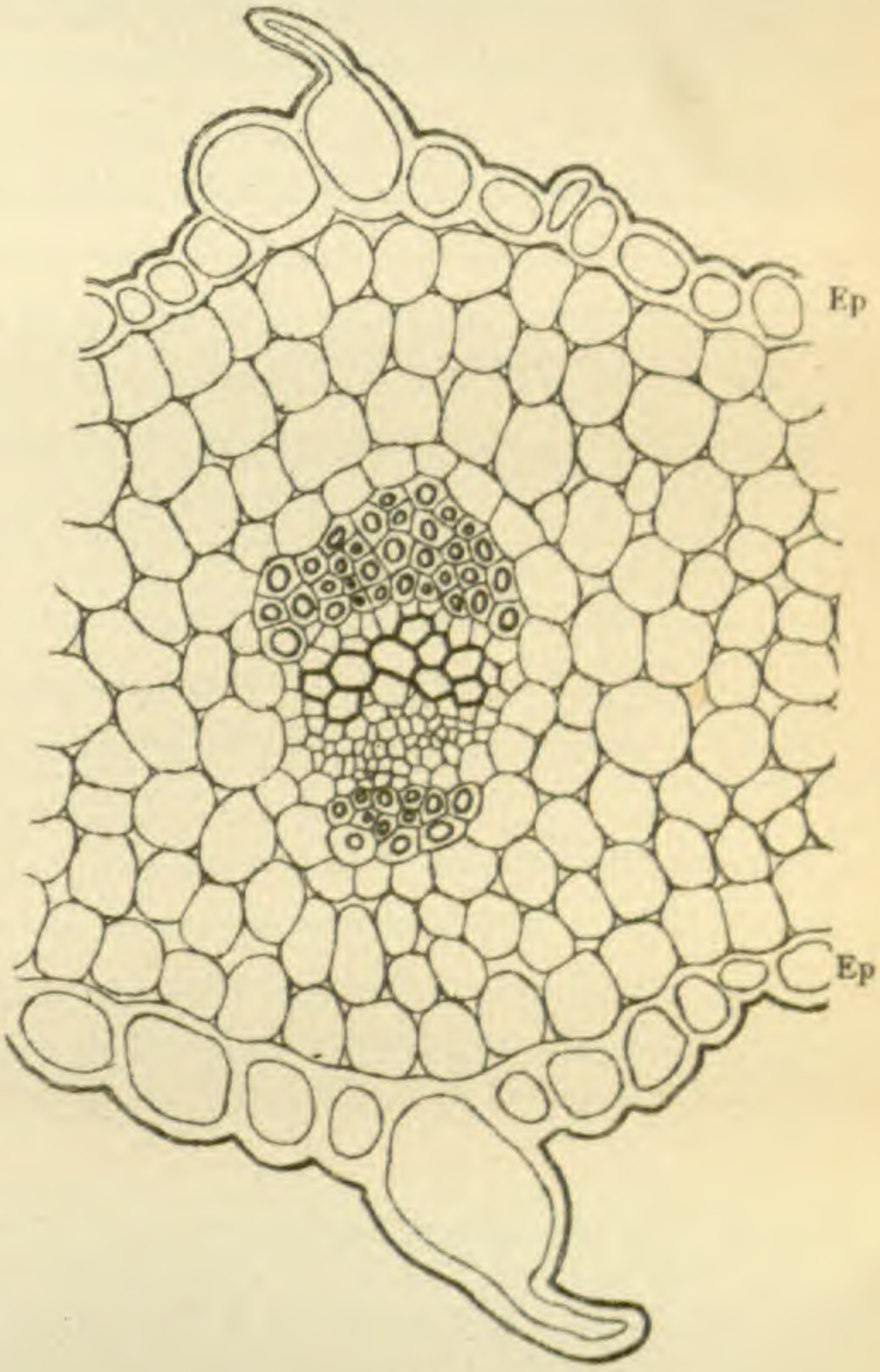

21

Auctor ad nat. delin.

HOLM on SISYRINCHIUM.

A NEW RESPIRATION CALORIMETER

GEORGE J. PIERCE

It is generally known that heat is liberated, often in great quantity, whenever germination or fermentation takes place under such conditions that only a small proportion of the heat liberated is lost by radiation. For example, in the malting of barley, it is necessary to take precautions lest the temperature of the germinating grain rise too high; and California wine-makers have repeatedly told me that they are obliged to watch the temperature of the must very carefully lest the fermentation go too fast and "the yeast burn." Brewers and distillers are aware of the same fact. Botanists generally lecture about the liberation of heat in the spathes of aroids, but how many of us have seen an experiment demonstrating this phenomenon? I, for one, do not recall ever having seen one. I find that a considerable number of naturalists associate these various instances of heat liberation with rapid growth, and in some laboratory manuals of plant physiology the liberation of heat is treated in connection with growth phenomena. These same naturalists, and a good many others, think of respiration not only as involving an intake of oxygen (which is not always the case, as for example in anaerobic respiration), but also an outgo of carbon dioxid. This latter is by no means always the case, as the respiration of the sulphur, iron, and certain nitrogen bacteria shows.

The intake of oxygen and the outgo of carbon dioxid are the easiest features of the process of respiration to demonstrate in the organisms ordinarily studied in those biological laboratories in which any attention whatever is paid to live plants or animals. It is easy enough for us all to go on thinking of respiration as a sort of ventilating process, in which a poisonous waste product of the living organism is displaced or replaced by a useful gas. We do not necessarily realize how this latter gas is useful, except as it takes the place of another which is poisonous. Whether carbon dioxid is itself poisonous is, I suppose, open to dispute. At any rate, it is ordinarily of no use to the organism.

It can be used only as a food material, only by chlorophyll-containing cells, and by these only in the light.

The other features of the process of respiration are hard to demonstrate, hard even to study. The chemistry of respiration is scarcely less difficult than the chemistry of photosynthesis.[1] Whatever the reactions may be in the chain which connects the free oxygen of the air with the oxygen combined with carbon or iron or sulphur, etc., it is clear, on theoretical grounds, that the oxidation or oxidations which take place must liberate heat. The demonstration of this fact, with reasonably small quantities of living organisms, has hitherto been nearly impossible. For this reason, it has been almost useless for the teacher to insist that the liberation of heat, the setting-free of energy, and not the material products, is the essential end, the fundamental characteristic of respiration.[2]

The apparatus of BONNIER,[3] which has furnished the most satisfactory results so far in the study of the heat-yield, is too elaborate and too costly for most botanical laboratories. On the other hand, the simple appliances described and figured in the laboratory manuals are useless, for they do not illustrate the subject, but mislead the student. Using the ordinary apparatus and the usual quantities of live and dead peas, for example, one obtains, with good luck, a difference of 0°.5 C. between the live and dead peas in the course of twenty-four hours, or perhaps a whole degree, or, best of all, 1°.5! This is mortifying enough, but if the temperature of the laboratory fall much, so that all the peas are chilled, there will be practically no difference at all. The evidence of the experiments, therefore, is all against the teacher who would have it that respiration is the means of supplying the living thing with the energy it needs to do its work. Evidently the trouble is with the insulation of the vessels in which the respiring and the dead plants or parts are contained; for if radiation and absorption were reduced to a minimum, the live and respiring peas would certainly grow warmer, while the dead peas would remain at the same temperature or grow slightly cooler.

[1] See BARNES, C. R., The theory of respiration. BOT. GAZETTE 39:81–98. 1905.

[2] See, for example, PEIRCE, G. J., Textbook of plant physiology, chap. 2.

[3] BONNIER, G., Recherches sur la chaleur végétale. Ann. Sci. Nat. Bot. VII 18: 1893.

Convinced of this, as well as thoroughly dissatisfied with the insulating appliances which I had or could make in the laboratory, I went to my friends in the chemical laboratory of this university, told them of my difficulty, and asked for suggestions. Professor YOUNG, professor of physical chemistry, suggested trying some Dewar flasks. I take this opportunity to acknowledge my indebtedness, and to express my gratitude to Mr. YOUNG, for his suggestion is one which will be appreciated by any physiologist who tries the apparatus for this purpose.

Dewar glassware is made in several shapes—cylinders, cups, and flasks. The flasks are made either tubulated or with closed round bottoms. The Dewar apparatus is made also silvered or unsilvered. The principle is simple—double-walled vessels with the air between the two walls exhausted. Thus there is a receptacle surrounded more or less completely by a vacuum. Across this vacuum radiation or absorption will take place at a rate inversely proportioned to the perfection of the vacuum. If the walls of the vessel are silvered on the surfaces bounding the vacuum, the efficiency of the insulation will be greatly increased. The apparatus was devised for liquid-air experiments and is named for the inventor, the famous chemist at the Royal Institution in London. This double-walled glassware has now come into commerce and may be bought, under the name of "thermal bottles," in drug stores and of the dealers in automobilists' and campers' supplies. It is used for keeping food or drink warm or cold, as may be desired, for many hours. Thus soup, milk, coffee, ice-water, etc., can be maintained at the desired temperature for astonishing lengths of time. The commercial bottles are protected against breakage by cases of metal or basketry, but since these do not improve the insulation materially, they are unnecessary in the laboratory, and the thinner-walled scientific apparatus is much cheaper, besides being obtainable in a greater variety of shapes.

In the experiments which I am about to describe, I used silvered Dewar flasks of about 250^{cc} capacity, which were supplied by EIMER and AMEND of New York for \$2.40 each. If imported duty free, as they would have been had I not been impatient to use them, they would have cost decidedly less. There should be at least two such flasks, for it is desirable to use always a lot of dead or other check material for comparison; but it is naturally better to set up the experiment in duplicate and thereby reduce the sources of error. In many instances I used three flasks of live material and one of dead. Since the efficiency of each flask as an insulator depends upon the completeness of the evacuation of the space between the walls and upon the silvering it is evident that the flasks themselves will not be exactly alike, and that an average result is likely to be better than any single one. If proper pains are taken, the efficiency of each flask can be determined in advance; but unless the experiments are conducted in a constant temperature, as they should be, there is little use in doing this.

Miss BERTHA A. WILTZ, a graduate student and assistant in physiology in this university, did most of the actual work of setting up and recording the results of these experiments; but as we have worked constantly together, the experiments are ours rather than the work of either one of us. As the work progressed, experience showed us how the experiments should be improved in method, but the reasons for these improvements will be more evident if I describe one.

Experiment 1.—An unweighed quantity of dry peas was soaked for 24 hours in tap-water. They were then rinsed in boiled distilled water two or three times and divided into two unequal lots, the smaller of which was then covered with a fairly concentrated aqueous solution of corrosive sublimate for at least half an hour in order to kill these peas. The other lot was divided into equal parts, which were poured into two Dewar flasks of about 250^{cc} capacity, the one silvered, the other unsilvered. The dead peas were poured into another silvered flask of the same size. The flasks were cotton-plugged and suspended on strings (not wire), in such a manner that they would not touch any object, metallic or other. This was done to avoid the changes in temperature which might otherwise result. A thermometer reading only to degrees was pushed through the cotton so that the bulb was as nearly as possible in the center of each mass of peas. The data will be found in the accompanying table (p. 197).

Various things are evident in this first rough experiment. It was continued for nearly nine days and, in spite of the fluctuating temperature of the room, the temperature in the silvered flask containing live peas rose until the last day very steadily. Comparing this with the temperatures recorded for the unsilvered flask, containing live peas, and with the silvered flask into which dead (killed) peas had been placed, one sees at once the superiority of the silvered flask as an insulator, and also that there was liberated and retained in the silvered flask containing live peas a very substantial amount of energy in the form of heat, even within the first twenty-four hours. Even the unsilvered flask gave a result better than I had ever been able to obtain with the ordinary insulators available in the laboratory.

Date	Temp. live peas silvered	Temp. dead peas silvered	Temp. live peas unsilvered	Room temp.
Feb. 26, 4:30 P.M.	17	17	17	....
27, 8:15 A.M.	19	16	13	....
12:15 P.M.	20	16	16	....
4:00 P.M.	23	17.5	19	....
28, 9:20 A.M.	32	15.5	15.5	16
12:00 P.M.	33	16	....	....
5:00 P.M.	36	16	20	....
29, 9:20 A.M.	38	15	15	15.5
12:30 P.M.	39	15	17.5	18
3:30 P.M.	40	15.5	19	17
Mar. 1, 10:30 A.M.	42.5	15	17.5	16.5
2, 10:20 A.M.	45	14	15	16
1:30 P.M.	47.5	14	18	19
5:00 P.M.	49	14.5	20	19
3, 9:25 A.M.	53	14	15	16
1:00 P.M.	54	15	19	....
4:15 P.M.	54+	15.5	22	22
4, —— A.M.	54.5	15	14	14.5
4, 2:30 P.M.	55+	15	23	18
4:30 P.M.	56	15.5	23	19
5, 9:15 A.M.	54	14.5	14	13
12:30 P.M.	54	....	....	....
6, 10:00 A.M.	50	14	14	....

When the experiment was stopped on the ninth day, because the temperature had begun to fall, it was at once evident that fermentation had been very active for some time. It was inevitable that this should be so, for I had not taken the slightest pains to sterilize anything. But in fermentation and decay heat is liberated, for these are processes in which respiration, as well as nutrition, takes place. We have here, then, the heat liberated in the respiration of the peas and of the other organisms in the flask. The obvious thing to do in succeeding experiments is to sterilize the peas and everything else used in the experiment, and to make similar experiments to determine the heat liberated by various ferment organisms. This I have done, to a very limited extent and only as a preliminary, with Fleischman's "compressed yeast," as will be shown later.

This first experiment, with all its roughness, seemed of sufficient importance to repeat several times in order to be quite sure that there was no mistake about it. The results were similar in every respect, and I do not need to record them here. The following experiment shows the effect of some of the improvements suggested by the preceding.

Experiment 2.—Into each of six Dewar flasks of approximately equal capacity, which had been sterilized by being washed with a saturated aqueous solution of corrosive sublimate and rinsed with boiled distilled water (sterile), 80^{gm} of air-dry peas were put. The peas and the flasks were then sterilized by shaking the peas very thoroughly in the flasks with a 1:500 aqueous solution of corrosive sublimate, and this was rinsed off with two wash-waters, both sterilized. Fresh sterilized distilled water was then poured into the flasks and the peas soaked in them for twenty-four hours at a temperature which ranged from 20 to 22° in the oven in which I had placed the flasks. I did not take the temperatures in the flasks during this time, as my apparatus was not then so arranged as to make that possible. However, I shall repeat the experiment under constant temperature and with readings from the beginning. The data will be found in the accompanying table (p. 199).

In this experiment fermentation and decay were reduced very greatly, though perhaps not as completely as possible. Therefore we have a very fair index of the amount of energy in the form of heat which 80^{gm} of peas (weighed air-dry) can liberate in something less than three days. We also see that, in all probability, the efficiency of the individual Dewar flasks varies considerably. The efficiency of each flask should be determined and recorded. I have not done this because it would be useless unless pains were also taken to conduct the experiments in a constant temperature, and this I was not able to do at that time. I shall repeat the experiment under uniform conditions as soon as possible to arrange it. The thermometers used in this experiment were good ones, reading to tenths of a degree, loaned to me by the department of physiology of this university, and I take pleasure in thanking my friend Professor

Date	Time	Flask 1	2	3	4	5 dead*	6	Room temp.	Max.	Min.
Apr. 29.....	6:00 P.M.	22°.7 C.	21°.6	22°.1	22°.4	22°.0	22°.3	19°.5		
Apr. 30.....	8:15 A.M.	23.7	22.3	23.8	23.8	18.2	23.0			
	12:15 P.M.	24.2	23.1	24.8	24.5	18.3	24.0	20.5		
	5:30 P.M.	27.0	25.7	27.3	27.4	19.6	26.5	21.0		
May 1......	8:15 A.M.	31.1	31.7	32.4	32.4	17.4	31.3	14.5		
	12:30 P.M.	32.3	33.5	33.9	33.8	17.7	33.0	18.2		
	eve.	33.4	35.1	35.3	35.0	18.2	34.5	19.0	27°.5	14°.4
May 2......	8:45 A.M.	35.7	38.4	39.0	37.5	17.6	37.5			
	12:30 P.M.	36.2	39.5	40.2	38.5	18.0	39.0			
	3:50 P.M.	36.8	40.5	41.4	38.8	18.4	40.0	18.3	26.2	16.1

Experiment stopped at 3:50 P.M., May 2.

	Flask 1	2	3	4	5	6	
No. peas decayed†.	3	2	4	2	0	3	Radicles 2.5–3^{cm} long.

Some of the sprouted peas planted in soil all grew normally.

* The peas marked *dead* were killed as in experiment 1.

† These decayed peas were without exception weevily, and because of the boreholes of the weevils could not be sterilized. Since the weevils close the outer ends of the holes, it is impossible to detect all the weevily peas when working with considerable quantities.

MACFARLAND for his help in this particular respect as well as in others. Owing to the position of the thermometers, making uniform sighting impossible, I do not record the attempt to read to fractions of tenths of degrees.

To see whether the heat liberated by a small amount of yeast in a small volume of a fermentable solution could be measured by the method described in the foregoing pages, I carried on some experiments, only one of which I need to report now. The yeast used was "Golden Gate compressed yeast," which is, I believe, only one of the many local names for what passes in the east under the name of Fleischman's compressed yeast. Four flasks were sterilized by being washed thoroughly with a saturated aqueous solution of corrosive sublimate. They were subsequently rinsed twice with sterilized water and plugged with cotton. Into each of these flasks 250^{cc} of 10 per cent. solution of cane sugar were poured as quickly as possible. The solution had previously been sterilized in four cotton-plugged flasks, from each of which it was poured into a Dewar flask. Since the yeast to be added is by no means a pure culture, I thought this sufficient care to exercise with the solution. To three of these Dewar flasks approximately 4.5^{gm} of a yeast cake were added, to the fourth flask nothing. The yeast had been quickly rubbed up in a sterilized mortar, with a sterilized pestle, in a small quantity of the sterile sugar solution. Thus, on shaking the flask after adding the yeast, I hoped to mix the yeast thoroughly with the whole volume of fermentable liquid. The fourth flask contained, then, only sterilized sugar solution, which had been exposed to the air for only a moment in transferring it from one sterilized vessel to another. The data follow.

Date	Time	Flask 1	2	3	4	Room temp.
					(no yeast)	
April 8.......	6:00 P.M.	19°1 C.	18°6	18°6	17°8	
April 9.......	9:15 A.M.	22.1	20.5	21.1	17.5	
	5:30 P.M.	23.3	21.5	22.3	17.7	20°0
April 10.......	8:00 A.M.	24.2	20.6	23.0	17.2	15.3
	12:30 P.M.	24.5	20.8	23.4	17.2	19.5
April 11.......	8:15 A.M.	25.0	20.6	24.0	17.3	
	12:30 P.M.	25.1	20.7	24.2	17.4	20.0

At this point, two days and eighteen hours after the experiment was started, it was ended and the flasks opened. The odor and flavor of the solutions were pleasant. I used the same thermometers as in the preceding experiment, but for the reasons previously given record here nothing less than tenths of degrees. Of course the thermometers were sterilized, by standing in saturated corrosive sublimate solution, and afterward washed in sterile water, before being introduced into the flasks. The efficiency of a good Dewar flask as an insulator is indicated by flask 4 in this experiment; for although the temperature of the room varied at least 5° C., as the record shows, the temperature within this flask varied only 0°6 C., according to the readings taken at the same times. Whether flask 2 was a poor one, or whether the yeast was poor, or what the trouble was, I do not know. In the other two flasks the mercury rose to a degree which surprised me, considering the small amount of yeast sown in each of the three flasks and the small volume of fermentable liquid. This rise in temperature indicates the liberation of considerable energy in the form of heat.

In connection with these experiments on the respiration of healthy plants I made one experiment, purely preliminary like the others, on wounded plants. RICHARDS reported in 1896 and 1897,[4] as a result of his experiments, that plants develop fever on wounding, as animals do. This increase in temperature is due to increased respiration in both sets of organisms. RICHARDS' methods are excellent, but unless an efficient insulator is used or the experiments are carried on in a constant temperature, they are not absolutely exact. I determined, therefore, to try Dewar flasks in a simple experiment of this sort. Two lots of onion sets (seedling onions) were carefully skinned, thus removing much if not all of the dead tissue by which these young bulbs are surrounded. Each lot was found to weigh 111^{gm} after skinning. One lot was put whole into a sterilized flask (no. 2), care being taken that the onions were not scratched or bruised in being put into the flask. The other lot was cut into irregular pieces, each onion into four to eight pieces, with an ordinary and fairly dull knife and put into another flask (no. 1). The temperature record follows.

Date	Time	Temp. no. 1 (chopped)	Temp. no. 2 (whole)	Room temp.
April 26............	2:00 P.M.	17°5 C.	17°50	17°0
April 27............	10:20 A.M.	23.25	18.50	19.0
	1:30 P.M.	25.00	19.50	....
	5:00 P.M.	27.00	20.25	20.0
April 28............	12:15 P.M.	38.00	20.50	....

The experiment was stopped at noon, when it had run nearly two days, and the contents of each flask turned out upon the table. Both lots of onions appeared to be in perfectly normal condition. In some cases the edges of the cuts of the wounded onions were a little dry. The material looked as if the experiment could have been continued for twice this length of time without decay or other disturbance setting in. It would seem, therefore, that these flasks can be used for such experiments on wounded plants.

In the experiments here reported, temperatures are given as the evidence that energy (heat) is liberated in respiration. Although these temperatures are interesting, they do not give us any idea of the

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[4] RICHARDS, H. M., Respiration of wounded plants. Annals of Botany 10:1896; 11:1897.

amount of heat liberated by a given organism or part. Because of the roughness of these preliminary experiments, and of my lack of the apparatus for carrying on the experiments under constant conditions, I have made as yet no effort to ascertain the number of calories liberated by a given weight of germinating peas. I hope to do this presently, not only for peas, but also for other things; but I do not wish this statement to be taken as suggesting that I wish to keep this method at present for my own use.

Dewar flasks seem to me to offer to the physiologist, both animal and plant, a convenient means of testing the yield of heat by respiration, testing in the case of an animal the calorific value of its food, testing in plants and plant parts the liberation of heat at various stages and under various conditions. Since the Dewar glassware is obtainable in various forms, and can be made in others if desired, it can be used for all the purposes of BONNIER'S experiments and for many others. For example, I see no reason why it would not be possible to ascertain the respiratory curve of any particular plant, from the beginning of the germination of its seeds until it had attained considerable size; to ascertain more exactly than we now know the relation of respiratory activity to the other activities or to the stages of development of the plant. These flasks, or cylinders, can be used also for demonstration experiments, on the lecture-table for example, proving at once to a class that respiration is really a process in which energy is released, and that it is the chief process by which the living organism obtains the energy which it constantly needs and uses.

STANFORD UNIVERSITY
California

THE SEEDLING OF CERATOZAMIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 115

HELEN A. DORETY

(WITH TWO FIGURES AND PLATES XII–XVI)

The vascular anatomy of adult cycad stems is likely to be obscured by two sets of complications. One, called anomalous thickening, described by VON MOHL (14) in 1832 in species of Encephalartos, is limited to certain forms; the other, the phenomenon of girdling, was described by KARSTEN (5) in *Zamia muricata* Willd. in 1856, and by METTENIUS (8) in Cycas, Encephalartos, and Dioon in 1860. Since then it has been found in the three other genera investigated. In the seedling these complications are either absent altogether or are just being initiated, hence the selection of juvenile forms is probably even more important in the anatomical study of cycads than in that of any of the other vascular plants. Anatomists have recognized this and have given us numerous descriptions, only the more pertinent of which need be cited here.

In 1856 KARSTEN (5), in the work mentioned above, found that each of the cotyledons of Zamia receives only one bundle, which may branch; that the central cylinder is broken up by parenchymatous communication between pith and cortex; and that in older stems, with the increase in the number of cauline strands, there is a corresponding increase in the number of bundles entering the leaves, because every bundle of the central cylinder contributes a trace. He also observed the frequent anastomosing of the leaf traces reported by VON MOHL, as well as the occurrence of girdling.

In 1884 BOWER (1) wrote a few descriptive notes on the seedling of *Cycas Seemanni* Al. Braun. He found the two cotyledons unequal in size and dissimilar in vascular anatomy. He says that while in some there is a median bundle which extends the whole length of the cotyledon without branching, in others there are two equal bundles near the center.

In 1887 GREGG (4) reported anomalous thickenings in the root of this species.

In 1896 WORSDELL (**16**) discovered them in the adult stem of *Macrozamia Fraseri* Miq., giving it an appearance which recalled to his mind the stem of the Medullosae.

In 1897 the same author (**17**) gave the name "transfusion tissue" to certain short, scattered tracheids with reticulate markings on their transverse walls, found in lateral communication with the bundles in the green parts of some gymnosperms. He considers this tissue a "direct derivative of the centripetal xylem" in the vascular bundles of fossils. Later in the same year (**18**) he recorded its occurrence in the cotyledons of *Cycas revoluta* Thunb. and in the leaf traces of *Stangeria paradoxa* T. Moore. He found that in each of the two cotyledons of *Cycas revoluta*, there are three collateral bundles, which may increase to five; that there may be some centrifugal wood near the base of the cotyledon, but none farther out; that the root may be tetrarch or triarch; that girdling had not yet begun in the young seedling he was investigating; and that anomalous thickenings were conspicuous. In *Stangeria paradoxa*, the two cotyledons have a common stalk, each is multifascicular, and the bundles are said to be concentric near the base. The root is triarch, changing to diarch near the tip. In the same paper, the two cotyledons of *Macrozamia spiralis* Miq. are said to be like those of *Cycas revoluta*.

The author calls attention to the absence of anomalous thickenings in this species of Macrozamia in contrast with the mature stem of *M. Fraseri* previously studied by him. In all three seedlings WORSDELL missed the transition from stem to root.

In 1898 the seedling of *Bowenia spectabilis* Hook. was described by PEARSON (**9**). He says that each of the two cotyledons has four to seven bundles derived from one, and that these bundles are all collateral with normal orientation. He is emphatic as to the collateral nature of the bundles, even after having examined a preparation of WORSDELL'S in which the latter considered them concentric. In the leaves the bundles are oriented normally, and the centripetal wood, scanty at the base, becomes more and more abundant farther up the petiole; but the centrifugal wood does not disappear even in the pinnae. The root is tetrach or pentarch, but may reduce to triarch. In the young material at his disposal, PEARSON found no anomalous thickenings in the root, but they were discovered later in presumably older plants by WORSDELL (**19**), who seized the occasion to emphasize the similarity to the Medullosae.

In 1904 MATTE (**6**) published his masterly thesis, which in the third part treats of the seedlings of *Dioon edule* Lindl., *Cycas siamensis* Miq., and *Encephalartos Barteri* Carruth. Of his two seedlings of *Dioon edule* one proved abnormal, one cotyledon being partly aborted. The cotyledonary bundles are mesarch near the base, but the protoxylem moves quickly outward, so that the bundles are exarch throughout most of their course. The axis is considered as an aggregation of leaf bases, and the girdling is explained as being due to intense intercalary growth produced under the influence of the developing leaf within. The four root poles are inserted upon the cotyledonary bundles, the median bundles furnishing insertion for two diagonally opposite poles, and each lateral trace uniting with its mate of the other cotyledon to furnish insertion for the other two poles. Mucilage canals are reported in the root, for the first time in a cycad. The root of *Cycas siamensis* is diarch; its two poles are inserted upon the median bundles of the cotyledons, the lateral bundles dying out in the cortex. Anomalous thickenings or cortical vascular strands are conspicuous; MATTE's demonstration that these are not abnormal, but merely remnants of an ancestral character, justifies his objection to the term "anomalous" used to describe them.

In Encephalartos the root is pentarch, and the cotyledonary bundles—a single, ringlike trace from each of the three cotyledons—fuse with the leaf traces at different levels before entering the central cylinder. This cylinder is polystelic, as in *Medullosa anglica* Scott. In considering this feature, MATTE indorses WORSDELL'S view that it helps to relate the Cycadales to ancient forms like Medullosa rather than to monostelic forms like Heterangium as SCOTT suggests. He regards the root of cycads as a "new organ" inserted upon the lower extremity of the hypocotyl, and not merely an extension of that organ.

The main facts discovered by these investigations, and agreeing, so far as they relate to *Dioon edule*, Cycas, and Zamia, with unpublished studies made in this laboratory by LAND, THIESSEN, and others, may be classified as follows:

Characteristic features.—Under this heading may be placed the occurrence of two cotyledons, the hypogean character of germination, the thick tap root, centripetal wood in the cotyledons and leaves, girdling, and numerous mucilage ducts.

Character upon which the seedlings may be divided into two groups.—This is the presence or absence of anomalous thickenings or cortical vascular strands. They occur in Cycas, Bowenia, and Encephalartos; they are said to be absent in Zamia, Dioon, Macrozamia, and Ceratozamia, though they were found in the mature stem of *Macrozamia Fraseri* by WORSDELL. Microcycas remains to be reported upon.

Features peculiar to certain genera.—We may place here the single cotyledon reported for Ceratozamia, the three cotyledons of Encephalartos, concentric bundles in the base of the cotyledon of Stangeria, the polystele in the earliest formed part of the axis of Encephalartos, and mucilage ducts in the root of Dioon.

The present series of studies aims in the first part to add to the list a detailed account of Ceratozamia, Microcycas, *Dioon spinulosum*, and species of Zamia; and in the second part to extend the investigation to the conifers by examining some juveniles of each of the great groups. Podocarpus, Keteleeria, Cunninghamia, *Pinus edule*, *P. Banksiana*, and a few others, as well as the cycads mentioned, are well under way.

Ceratozamia

In 1846 BRONGNIART (2) gave the generic and specific names to *Ceratozamia mexicana*, a "new cycad from Mexico." He described the adult forms and the ovulate and staminate strobili. In 1870 WARMING (15) reported the monocotyledonous character of the embryo. In 1872 VAN TIEGHEM (13) examined four seedlings and found a thick scale enclosed by the sheathing base of the single cotyledon, and, in turn, enclosing a hairy foliage leaf with circinate vernation. One of the four seedlings was suspected by him of having the rudiment of a second cotyledon. He describes the root after the xylem and phloem have reached their final position, and gives the number and derivation of the cotyledonary strands and early leaf traces; but in these respects, no two of the seedlings agree. A piece of mature stem, examined by SOLMS-LAUBACH (12) in 1890, was found to have a single cylinder, but peduncular strands occurred in the pith, an observation which was corroborated later by WORSDELL (16). In the work previously mentioned (6) MATTE made a careful study of the ovulate cone and the mature leaf, with a few observations on younger leaves. He found terminal teeth on some of the pinnae of the younger plants, and at the bases of the petioles stipules with a bundle in each. He says that the meriphyte of the leaves has a modified Ω-shape in cross-section, with an anterior system, and shows that in this as well as in other cycad petioles the so-called fusions of the traces are often only approximations (*accolements*).

MATERIAL AND METHODS

The seedlings of Ceratozamia and *Dioon spinulosum* were grown from seeds provided by Professor CHARLES J. CHAMBERLAIN; the Microcycas seedlings were given to me by Professor OTIS W. CALDWELL, and later some were grown from seeds secured by Professor CHAMBERLAIN. The Zamia seedlings were furnished by Dr. W. J. G. LAND.

Having in mind the danger of drawing conclusions from a few specimens, I have used freely the wealth of material at my disposal. The chief part of the investigation was made from material fixed in picro-acetic-alcohol, stained with safranin and anilin blue, and cut in serial sections. *Figs. 21, 22,* and *23* are diagrams of wax models constructed from serial sections.

GENERAL DESCRIPTION OF EMBRYO AND SEEDLING

The seeds of Ceratozamia are about 2.5^{cm} long and 1.5^{cm} thick, that is, about the same size as those of *Dioon edule*, and intermediate between *Dioon spinulosum* on the one hand and Zamia on the other. Like most cycad seeds, they are flattened on two or three sides by the pressure of growth within the cone, and it is not unimportant to remember that during the whole period of embryonal development —the longest known for a cycad—the seed lies upon whatever side it happens to fall. The single cotyledon begins to be differentiated in November, and early in December its appearance is like that represented in *fig. 1*. Later it begins to surround the axis (*fig. 2*), and finally the two edges meet (*fig. 3*). In these early stages, the coleorhiza is proportionally long; but later elongation of the cotyledons forces the base of the embryo backward, so that both coleorhiza and suspensor are crushed little by little to a flat, brown disk (*figs. 4, 5*). Further elongation forces the base of the embryo through the softer, micropylar portion of the seed coat; *figs. 6, 7, 8* show this and the two succeeding stages. In *fig. 7* the base of the cotyledon is curved downward, and the plumule is seen issuing from between its opened edges; and it may be observed that this method of development has thrown the first leaf out of alignment. The edges close in again, and remain adhering the full length of the cotyledon (*fig. 13*). The tip is sometimes lobed (*figs. 14, 15*).

The cotyledon always develops on the lower side of the embryo as the seed lies during germination. In seedlings which were turned after the cotyledon had begun to develop, the plumule has not succeeded after a year in emerging from underneath the cotyledonary sheath with which it is hampered.

Fig. 8 shows the appearance of the tardy root, which has made its way through the brown cap formed from the remains of the disorganized coleorhiza and suspensor. When the root pierces the soil, the starch is transferred to it from the endosperm, and the root thickens into a tap root. By its further penetration into the soil, it often draws the upper portion further down, imbedding the seed, and possibly giving to the first series of lateral roots their initial upward slant. The lateral roots almost always appear in threes, whether the root be tetrarch or triarch. *Fig. 9* represents a seedling toward the close of this period of its activity. The extreme shortness of the hypocotyl may be conjectured from the small distance between the base of the cotyledon and the insertion of the first whorl of lateral roots. The plumule is composed in this case of two brownish, hairy scales, enclosing a foliage leaf with circinate vernation (*fig. 10*). Each scale is terminated by a sharp, curved point. The number of scale leaves varies in different seedlings; some have only one, and in some few observed the first organ was a perfect foliage leaf. The base of both scale leaf and foliage leaf is furnished with broad, winglike expansions which enclose the next leaf. The petiole of the first leaves reaches a length of 15–20^{cm}, and bears one or two pairs of pinnae inserted near the adaxial face. Between the two terminal pinnae there is a tiny, sharp spine, which has its counterpart in the apical point of the scale leaves. At irregular intervals along the petiole are other, even smaller points. The first leaves are opposite, but the later ones assume the spiral phyllotaxy represented in *fig. 12*.

ANATOMY

As was above noted, the edges of the cotyledon close in after the exit of the plumule, the two halves of the adaxial face meeting in a plane represented by the line *ad* in *fig. 13*. Three bundles enter the cotyledon from the vascular plate, and each dichotomizes again and again (*fig. 16*), the median one being no more a "double" bundle than any of the others. The number of traces may be increased to fifteen toward the upper portion, but is gradually reduced again toward the tip, some bundles approximating in pairs, others dying out. Those in the lobes disappear lower down than the others (*fig. 15*). The bundles are collateral throughout the cotyledon, and their orientation is normal, as seen in *figs. 13, 14, 15*, where the xylem faces the line *ad*. The wood is mesarch (*fig. 17*), with the protoxylem gradually moving out toward the phloem as it ascends. In the upper portion centrifugal elements are wanting, that is the wood is exarch (*fig. 18*). The vascular system of the cotyledon is differentiated relatively early in the development of the seedling. In that from which *fig. 19* was drawn, in which no root has yet appeared, the vessels are fully matured. WORSDELL'S transfusion tissue was frequently observed in direct continuation with the centripetal xylem (*fig. 18, tr*).

Mucilage canals are numerous in the lower part, and seem to bear no definite relation to the strands (*figs. 30, 31*); farther up they usually number one more than the strands and alternate with them; higher still they die out irregularly; in some cotyledons they are absent altogether.

The vascular plate of the hypocotyl axis is irregularly four-sided as seen in cross-section; all the xylem is in the center, sometimes in a solid mass, sometimes interspersed with pith cells. The protoxylem points are clearly distinguishable. In the plant from which *fig. 20* was drawn, the protostelic condition persisted through a vertical distance of 1.6^{mm}. Above this the pith cells occupy the central region, so that a siphonostele replaces the protostele (*fig. 28*). About

1^{mm} above the upper terminus of the protostele, the xylem is grouped sometimes in four conspicuous mesarch lobes, but oftener in three prominent ones and a fourth weaker one (*D*, *fig. 29*). From this weaker lobe a very small strand passes out (*D*, *figs. 21–24, 26, 30*), and in some cases it branches, but is lost in the cortex. From the lobe diametrically opposite, the median strand of the cotyledon (*C*, *figs. 21, 24, 25, 29, 30*) enters that organ; and from each of the other two angles or lobes a strand passes out (*A*, *B*) and branches, one member in each case bending tangentially (*b*, *b′*) to form the lateral trace of the cotyledon, the other, a very small strand (*a*, *a′*), either fusing with the leaf traces or dying out in the cortex. This cotyledonary node is represented in cross-section in the diagram (*fig. 24*).

Comparison with the same node in Zamia, Cycas, *Dioon edule*, and Microcycas suggested that the smaller bundles (*D*, *a*, *a′*) were the mates of the larger ones on the side of the cotyledon (*C*, *b*, *b′*), and that the second cotyledon was suppressed. The cause of the suppression was indicated by the long-continued one-sided presentation to gravity during germination, and the fact that the cotyledon is always on the under side. It was with the intention of testing these surmises that the experimental work already recorded (3) was undertaken. *Fig. 25* represents the cotyledonary node in Ceratozamia embryos developed on the clinostat, and *fig. 13a* a transverse section of their cotyledons.

Although the stem contains several layers of extrafascicular cambium (*cb*, *fig. 32*), I have not been able to find in two-year-old plants any anomalous thickenings except the solitary bundle (*fig. 33*) whose position in the base of the cotyledon is indicated in *fig. 30* at *z*. This bundle has its origin in a small group of cells (*cb″*, *fig. 32*) in the outermost layer of cambium. It is about 0.4^{mm} long and approximately vertical. Its tracheids have only spiral thickenings.

The foliar bundles (*fb*) may occur in four groups alternating with the cotyledonary bundles (*figs. 21–23, 26, 30*); but oftener there are only three groups, because of the fusion of two of them or the entire elimination of one, on the side of the suppressed cotyledon, when the main bundle (*D*) is slight or entirely wanting (*fig. 26*). At first they are all vertical; higher up they branch, and a strand from each group is sent to the first leaf (*fig. 22*). As previously noted, this organ, whether scale leaf or foliage leaf, is displaced laterally by the peculiarities of its development. All the traces which enter it are likewise distorted, giving rise to a pseudo-girdling condition which is apparent in very young seedlings (*figs. 22, 27, 31*). The two traces which enter from the groups nearest the leaf (*e, e′*) take first a radial, and then a tangential course to reach a position in the middle of the leaf (*figs. 22, 31*), showing on the way a tendency to branch. The traces (*d, d′*) supplied from the groups farther away take a tangential course, each giving off vertical branches, which in turn branch again. The remaining traces of the original four foliar bundles ascend vertically (*fig. 25*), and branch and anastomose freely. Only a limited number, in most cases four or five, remain (*fb, figs. 24, 31*). Before reaching the leaf base, each of these divides, one member entering it (*t, fig. 23*), the other, which remains small, being directed toward the growing point of the stem (*u, figs. 23, 27*). *Fig. 23* represents the branching and anastomosing of these strands. It should be noted that the vertical scale of the three diagrams (*figs. 21–23*) is magnified considerably.

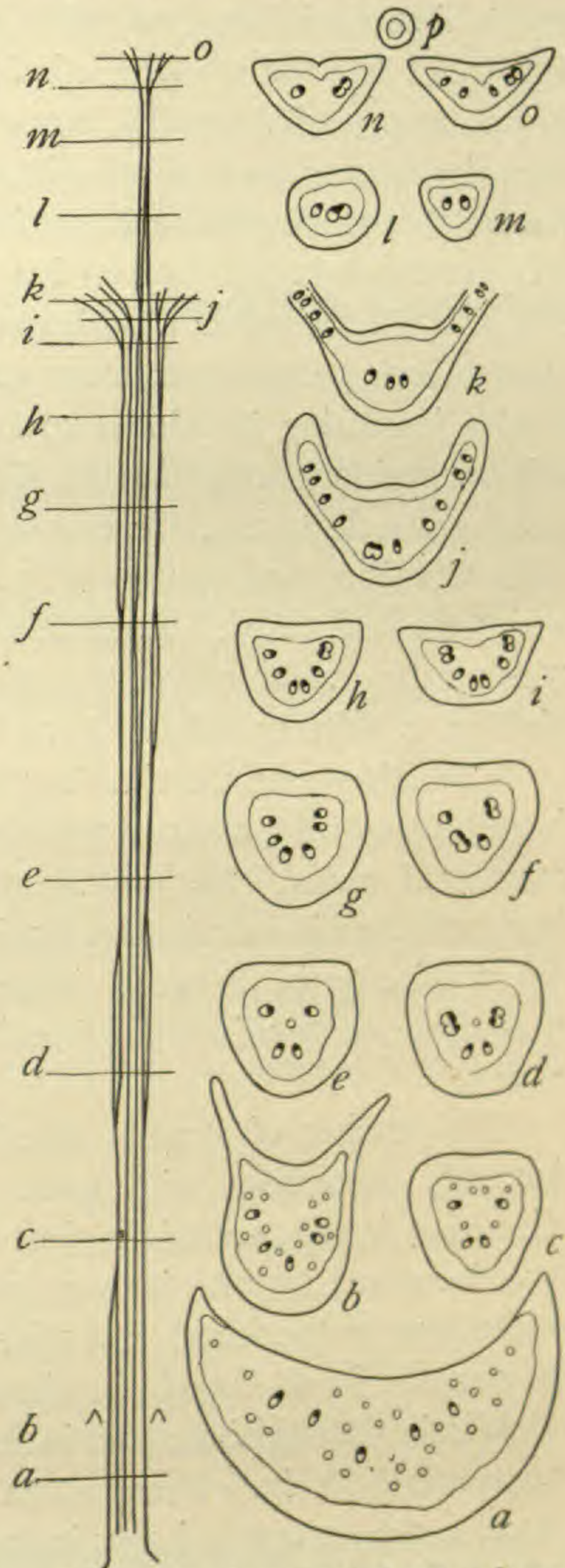

FIG. 1.—Study of foliage leaf from base (*a*) to apex (*p*); for explanation see text.

In the younger stages there is no attempt at girdling on the part of the leaf traces, except that which has been referred to in the first leaf as pseudo-girdling, whose cause is to be sought in the accident of its development. When the inner face of a leaf encloses a mass whose diameter is less than 3^{mm} (fourth leaf in *fig. 12*), the vascular bundles of that leaf are all vertical; but when the enclosed mass, by its enormous radial growth, has reached a diameter of $5–8^{mm}$ and comprises two or more developing leaves (second leaf in *fig. 12*) the base of the enclosing leaf enlarges its inner face accordingly. The first stage in the enlargement consists in an increase in the number of cells, but the second in a horizontal elongation of these (*text fig. 1*). While this is going on the older part of the central vascular cylinder is also increasing its diameter, separating farther and farther the original positions of the bundles of the leaf. As a result, the marginal traces gradually elongate as they are drawn more and more from the vertical position, and their upper parts stretch outward in the direction which the leaf takes. These facts have been observed repeatedly; whether they are an adequate solution of the problem of the cause of girdling, as MATTE thinks, I am unable to say.

In seedlings with three or four leaves, the stem bundles (*u, fig. 19*) branch repeatedly, and many of the branches reunite to form a small number of traces. Each of the remaining ones now forks once, the larger member in each instance going to the leaf as before, the smaller one continuing in the axis. Thus, even at this early stage, there is present the sympodial stem described by Miss SMITH (**11**) for older plants.

The number of strands entering successive leaves was seen to increase, sometimes with great regularity. In the plant whose dissection is represented in *figs. 11* and *12*, the number of traces was increased by one in each successive leaf, from the cotyledon with three, to the fourth leaf with seven; but the increment was not so constant in all the plants observed.

Within the leaf base and in the petiole, the bundles branch and anastomose freely. There is no real Ω in these first leaves; the bundles are arranged simply in an open arch. *Text fig. 2* is a study of a foliage leaf which was the second lateral organ of the plumule, that is, it was preceded by only one scale leaf. The scale leaf had four bundles; this leaf has five (*a, b*); but just above the stipules the number is reduced to four by the approximation of two of them (*c*).

Other changes occur as the meriphyte ascends the petiole (*c, d*). Just below the first pair of pinnae the branching is rapid, and at the level where the blade is seen exteriorly to separate from the petiole, there are four strands provided for it (*j*). In the rachis another approximation takes place (*l*), and the number of bundles is reduced to two (*m*). Each enters a pinna and branches continuously (*n, o*). The growing point terminating the rachis has no vascular trace in this leaf, in this respect agreeing with the young leaf represented in *fig. 10a*. As the plant increases in age, the meristem of this point retains its activity longer, producing a greater number of pinnae, as in the seed plants.

The wood in all the leaf traces is endarch in the central cylinder (*fig. 26*), but it soon becomes mesarch, with the protoxylem moving outward by almost imperceptible degrees. It never reaches the exarch condition, however; even in the tips of the pinnae there are always two or three elements of centrifugal wood. Here and there may be seen a few elements of transfusion tissue.

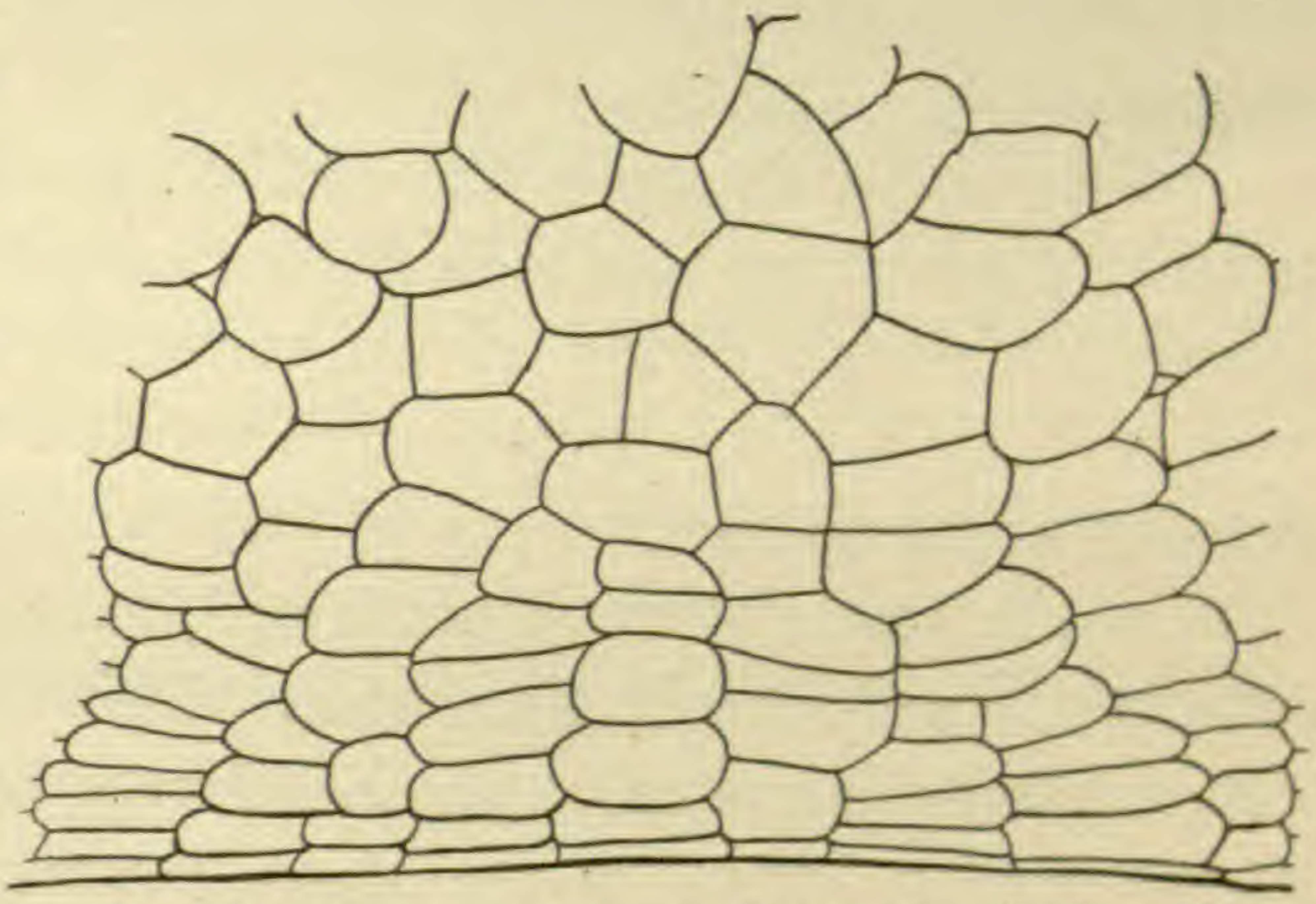

FIG. 2.—Cross-section of flattened cells from inner face of petiole near the base.

Mucilage canals are numerous in the leaf bases (*figs. 30, 31*), but they have no more definite arrangement there than in the base of the cotyledon. Throughout the region of the stipules there is a gradual decrease in number, which is not altogether due to fusing. Toward the upper levels of this region they are sometimes arranged in two series, an adaxial row and an abaxial one, with a definite relation to the bundles (*text fig. 2b*). About 1^{cm} above the base, there is left only one centrally located canal (*d*), which persists for half the length of the petiole (*e*).

The bases of the leaves as well as of the cotyledons are covered by a thick layer of cork. As was seen externally, the hypocotyl is extremely short, the transition from stem to root taking place in an almost horizontal plane (*fig. 30*). In the absence of cauline bundles, the root poles are inserted upon the cotyledonary strands (*A, B, C, D, figs. 34, 35*). There is no rotation of the protoxylem, but the phloem and metaxylem separate opposite the protoxylem groups (*Bn, Cn, fig. 36*), the cambium proliferating to fill the breach in the metaxylem, and the cortex invading the space left vacant by the phloem. The resulting halves swing, the one to the right, the other to the left, giving the appearance of a double fan of phloem and metaxylem connected by a single group of protoxylem. The right half of the phloem of one pole joins the left half of that of the next, and the cambium layer is thus curved inward (*cb, figs. 37, 38*). One result of this complicated process is that the entire xylem system of the root is bordered peripherally by cambium.

The medulla throughout the root is extremely meristematic, and its activity sometimes results in a displacement of one or more of the protoxylem groups, giving an unsymmetrical appearance in cross-section. This activity is indicated by the thin walls (*o, fig. 38*) showing recent division.

In all the plants I have investigated, the number of poles remains constant throughout any given root. This number may be three or four, depending seemingly upon the degree of development attained by the median bundle of the aborted cotyledon. *Figs. 26* and *34* will serve to illustrate this point. They represent the same level in two different plants. In the former the median bundle (*D*) was very weak, and there were but three root poles; in the latter this bundle was well developed and the root was tetrarch.

Fig. 39 represents the condition of the root tip in the region of the differentiation of protoxylem. The connective tissue is clearly defined, but there is no xylem plate connecting the poles. Examination of longitudinal sections of the root tip furnishes nothing that could be added to the description of REINKE (**10**). One initial group produces plerome, another periblem. There is no calyptrogen or dermatogen, but the outermost layers of the periblem become loosened at the tip and form the root cap (*k, fig. 42*).

There is no distinct endodermis, and the pericycle is several-layered, making it impossible to distinguish with absolute certainty any line of demarkation between phloeoterma and stelar tissue.

There are no anomalous thickenings in the roots of plants two years old.

In general, mucilage ducts extend but a slight distance into the root, usually about 8^{mm}, but in one specimen they were beginning to be formed in the plerome, immediately behind the region of its differentiation (*md, fig. 42*).

The lateral roots are diarch. *Fig. 40* represents a transverse section of a secondary root and the exit of a tertiary one. The uppermost lateral roots become ageotropic at a very early stage, and show symptoms of bacterial infection; and in some of the two-year-old plants, these roots present the characteristic "coralloid" appearance indicative of algal infection.

The root, as was seen above, is late in developing. *Fig. 27* represents the position and form of the meristematic plate, which has given rise to stem above, but is yet inactive below. *Fig. 19* shows the beginning of the activity which produces the root; the central portion of the active region in this figure is sketched in greater detail in *fig. 41*. In the stage represented in *fig. 42*, the root cap is developed and the plerome and periblem initial groups are easily distinguishable, but the plerome has not yet differentiated any xylem elements.

While in older seedlings the vascular systems of stem and root seem to be continuous, one sometimes finds sections which indicate a certain amount of interruption. Such a case is shown in *fig. 43*.[1]

Discussion

The result of the experimental work on Ceratozamia places this genus in line with the other cycads with reference to the dicotyledonous

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[1] When this investigation was completed, MATTE (7) published a preliminary note on the same subject. He says that the petiolary bundles have the Ω arrangement, that there is an anterior fascicular system in the region of insertion of the rachis, and that the pinna has terminal teeth. These features do not appear in any of my seedlings. Speaking of the root, he says it is tetrarch, and that he has observed a progressive reduction of poles, to three and even to two. As I have observed, no reduction occurred in the roots of any of the seedlings I sectioned, and the root is triarch as often as it is tetrarch. He has also found the abnormal thickenings strongly developed; but he does not give the age of the seedlings which manifest them.

character. The proof of the abortion of the second cotyledon and the discovery of the manner in which that abortion was brought about naturally revive the question of the monocotyledonous nature of certain dicotyledons. It is possible that in some cases this condition may be caused by the same factor which produces it in the embryo of Ceratozamia, but this is not so in all cases; the experimental work now in progress upon these forms shows that other factors are involved.

The lobing at the tip of the cotyledon is suggestive of a primitive condition, which will be discussed in connection with *Dioon spinulosum.*

It would be interesting to compare the cotyledonary node in all cycads, in order to determine whether they are modifications of the same type or whether there are different types; but it is a matter of regret that all investigators have not considered it of sufficient importance. MATTE has described it fully for *Dioon edule* and *Cycas siamensis.* The latter is clearly a modification of the type which may be represented by the former. The present paper shows that Ceratozamia conforms to this type, and it may be in place here to say that Microcycas and the species of Zamia I am investigating are the same. WORSDELL'S *Cycas revoluta* and *Macrozamia spiralis* are doubtless similar. *Encephalartos Barteri* according to MATTE'S description, *Zamia muricata* according to KARSTEN'S, and *Bowenia spectabilis* according to PEARSON'S seem to differ from this type, in receiving only one bundle from the central cylinder; but there are two facts which conspire to make us consider that the seedling of Encephalartos described by MATTE was an unusual one: the presence of three cotyledons, and the union of the cotyledonary strands with the central cylinder at different levels.

That cycads, especially such fernlike ones as Stangeria and Bowenia, should be found to have an occasional concentric bundle is only to be expected from the nature of their fern origin. WORSDELL'S announcement, then, of such bundles in the base of the cotyledon of Stangeria was not a surprise, even though his drawings were not convincing. But the emphatic statement of PEARSON that he could not be convinced of it in WORSDELL'S preparation of Bowenia raises the doubt whether he would have recognized it in Stangeria. Of course the whole question resolves itself into the possibility of determining phloem in the absence of sieve plates.

In the feature of anomalous thickenings, as in so many other features, Ceratozamia appears to hold an intermediate position. The extrafascicular cambium is clear and distinct, yet in plants with two scale leaves, two expanded foliage leaves, and two or three leaves developing, the secondary fascicular systems are entirely wanting. The failure or delay of this cambium to function indicates that it is a vestigial character. I have seen it in Zamia as clear and distinct, though not so abundant, as in Ceratozamia.

There seems to be great variation in the number of root poles throughout the whole group of cycads and even in individual roots. This variation, taken in conjunction with the fact that in Ceratozamia the number depends upon the degree of development of the median bundle of the aborted cotyledon, indicates that this character is not to be depended upon as a phylogenetic one.

Summary

1. Ceratozamia is dicotyledonous, the second cotyledon being aborted by gravity.

2. The cotyledon is often lobed at the tip. It is multifascicular, and all the bundles are derived from three. The wood is mesarch at the base and exarch in the upper portion. Mucilage ducts usually alternate with the bundles.

3. The leaf traces are at first vertical; girdling follows upon increase in radial growth of the enclosed leaves and stem apex. The wood of the leaf traces is endarch in the central cylinder, but becomes mesarch in the leaf base and remains so to the tips of the pinnae.

4. The scale leaves are aborted foliage leaves.

5. The first-formed portion of the central vascular cylinder may be a protostele.

6. The stem is a sympodium.

7. There are several layers of extrafascicular cambium, but in seedlings two years old only the slightest trace of anomalous thickening.

8. The root is a delayed organ, and its four poles are inserted upon the cotyledonary bundles.

9. The entire xylem system of the root is bordered peripherally by cambium.

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THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES XII–XVI

All the drawings except *figs. 6–11, 16, 21–25* were made with the aid of a camera lucida. The abbreviations used are as follows: *A*, *B*, *C*, *D*, the four main cotyledonary bundles; *An*, *Bn*, *Cn*, *Dn*, the corresponding root poles; *C*, median bundle of developed cotyledon; *D*, median bundle of aborted one; *a*, *a′*, lateral bundles of aborted cotyledon; *b*, *b′*, lateral bundles of developed one; *ad*, adaxial face of cotyledon; *c*, cotyledon; *cb*, cambium; *cb′*, *cb″*, extrafascicular cambium; *cl*, coleorhiza; *ct*, connective tissue of root; *cx*, cortex; *cfx*, centrifugal xylem; *cpx*, centripetal xylem; *d*, *d′*, lateral traces of first leaf; *e*, *e′*, middle traces of same; *f*, foliar bundles; f^1, f^2, f^3, f^4, four principal groups of foliar bundles; *g*, cotyledonary trace; *h*, vascular system of hypocotyl; *i*, vascular system of root; *imd*, initiation of mucilage duct; *j*, sclerenchyma; *k*, root cap; *l*, leaf; *m*, meristematic plate; *md*, mucilage duct; *n*, medulla; *o*, indices of radial cell division in medulla; *p*, plumule; *ph*, phloem; *pph*, protophloem; *px*, protoxylem; *px′*, rupture of tissues caused by protoxylem; *q*, plerome; *r*, root; *s*, suspensor; *t*, leaf trace; *tr*, transfusion tissue; *u*, stem bundles; *v*, periblem; *w*, stipules; *x*, xylem; *y*, cork; *z*, anomalous thickening.

FIGS. 1–5.—Stages in intraseminal development showing single lateral cotyledon and gradual enlargement of its base to encompass axis. ×5.

FIG. 6.—Rupture of micropylar end of seed coat and protrusion of base of embryo. ×½.

FIG. 7.—Bending of base of embryo and exit of plumule. ×½.

FIG. 8.—Appearance of root. ×½.

FIGS. 9, 10.—Young seedlings. ×½.

FIG. 10*a*.—Longitudinal section through tip of unfolding leaf. ×5.

FIG. 11.—Dissection of aerial portion of two-year-old seedling. Nat. size.

FIG. 12.—Diagram showing spiral phyllotaxy of later leaves. Nat. size.

FIG. 13.—Transverse section of cotyledon. ×8.

FIG. 13*a*.—Transverse section of cotyledons of embryo developed on clinostat. ×8.

FIG. 14.—Transverse section of upper portion of cotyledon showing tendency to lobe. ×8.

FIG. 15.—Transverse section of same cotyledon nearer tip. ×8.

FIG. 16.—Diagram to show venation of cotyledon.

FIG 17.—Mesarch bundle from lower portion of cotyledon. ×380.

FIG. 18.—Exarch bundle from the middle region of cotyledon. ×380.

FIG. 19.—Longitudinal section of lower part of embryo emerging from seed. ×8.

FIG. 20.—Transverse section of the vascular plate of hypocotyl. ×225.

FIG. 21.—Diagram representing rise of cotyledonary bundles from vascular plate.

FIG. 22.—Diagram showing origin and course of first leaf traces.

FIG. 23.—Diagram showing origin and behavior of traces of second leaf.

FIG. 24.—Horizontal diagram of cotyledonary node.

FIG. 25.—Same node in plants developed on clinostat.

FIG. 26.—Transverse section slightly above cotyledonary node showing the four main cotyledonary bundles and the three groups of foliar bundles. ×60.

FIG. 27.—Longitudinal section of embryo somewhat less developed than the one represented in *fig. 19*. ×10.

FIG. 28.—Transverse section of stele of hypocotyl 2^{mm} above the section represented in *fig. 20*. ×225.

FIG. 29.—Transverse section of stele of hypocotyl immediately below cotyledonary node. ×225.

FIG. 30.—Transverse section of plant with median bundle of aborted cotyledon fairly well developed. Same level as *fig. 26*. ×8.

FIG. 31.—Section of same plant 140 μ above that represented in *fig. 30*. ×8.

FIG. 32.—Detail of portion of axis 0.2^{mm} below *fig. 30*, between the cotyledonary bundle *B* and the phellogen; shows group of cambium cells which gave rise to anomalous strand *z*. ×75.

FIG. 33.—Transverse section of the anomalous strand represented in base of cotyledon in *fig. 30*. ×135.

FIG. 34.—Cotyledonary node of plant with median bundle of aborted cotyledon well developed. ×150.

FIG. 35.—Stele of hypocotyl 0.36^{mm} below *fig. 34*; xylem and phloem collected in ring. ×150.

FIG. 36.—Section of stele of same plant 0.16^{mm} below *fig. 35*; shows breaking apart of phloem opposite the protoxylem. ×150.

FIG. 37.—Same, 0.2^{mm} below the previous section; separation of metaxylem. ×150.

FIG. 38.—Section of root stele between the third and fourth whorls of lateral roots. ×179.

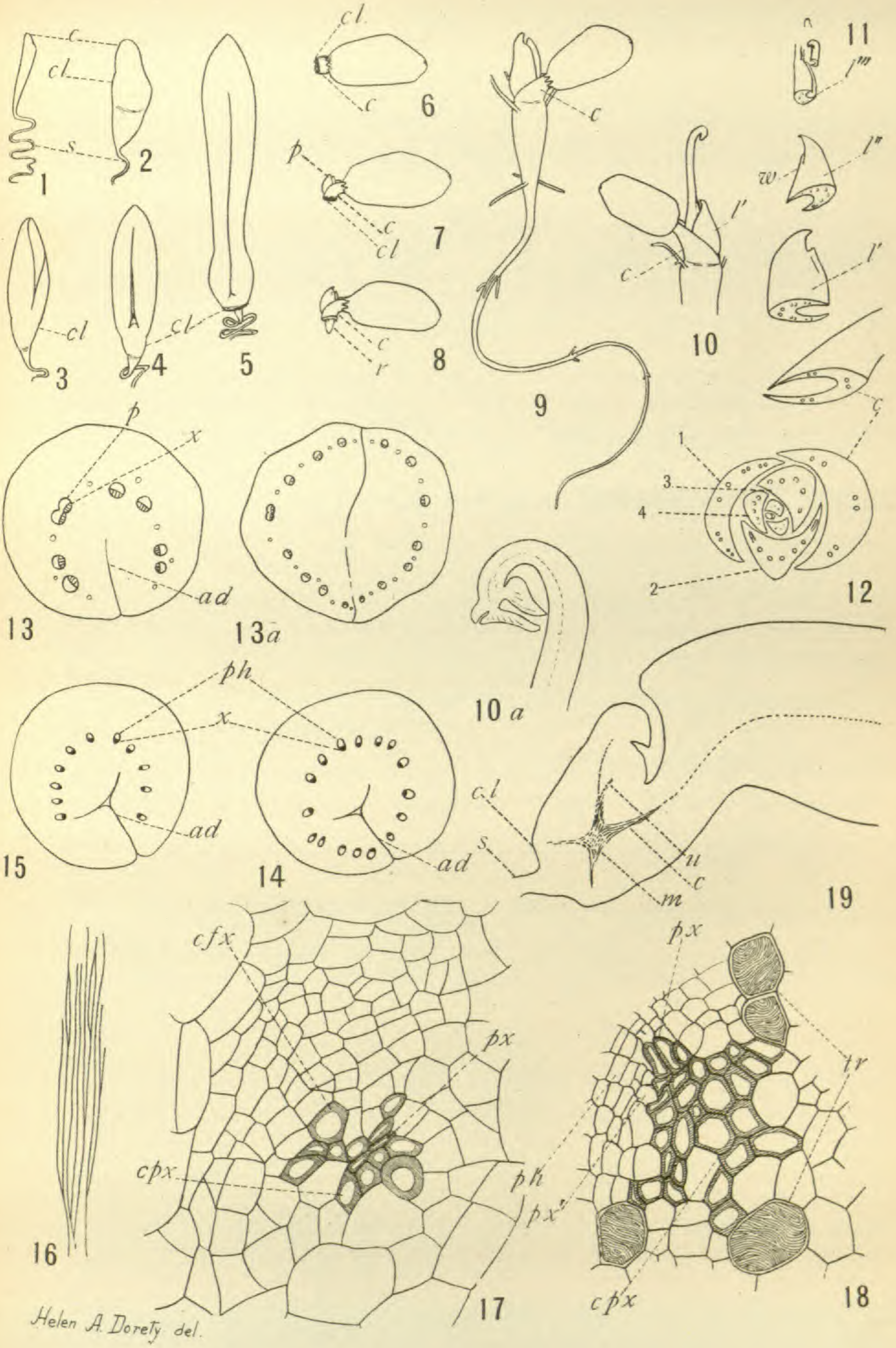
FIG. 39.—Section of stele near root tip at beginning of differentiation of xylem. ×225.

FIG. 40.—Transverse section of stele of lateral root showing exit of a tertiary root. ×225.

FIG. 41.—Longitudinal section of seedling showing beginning of root formation. ×10.

FIG. 42.—Detail of beginning of root formation. ×60.

FIG. 43.—Detail showing interruption between vascular tissues of hypocotyl and root. ×120.



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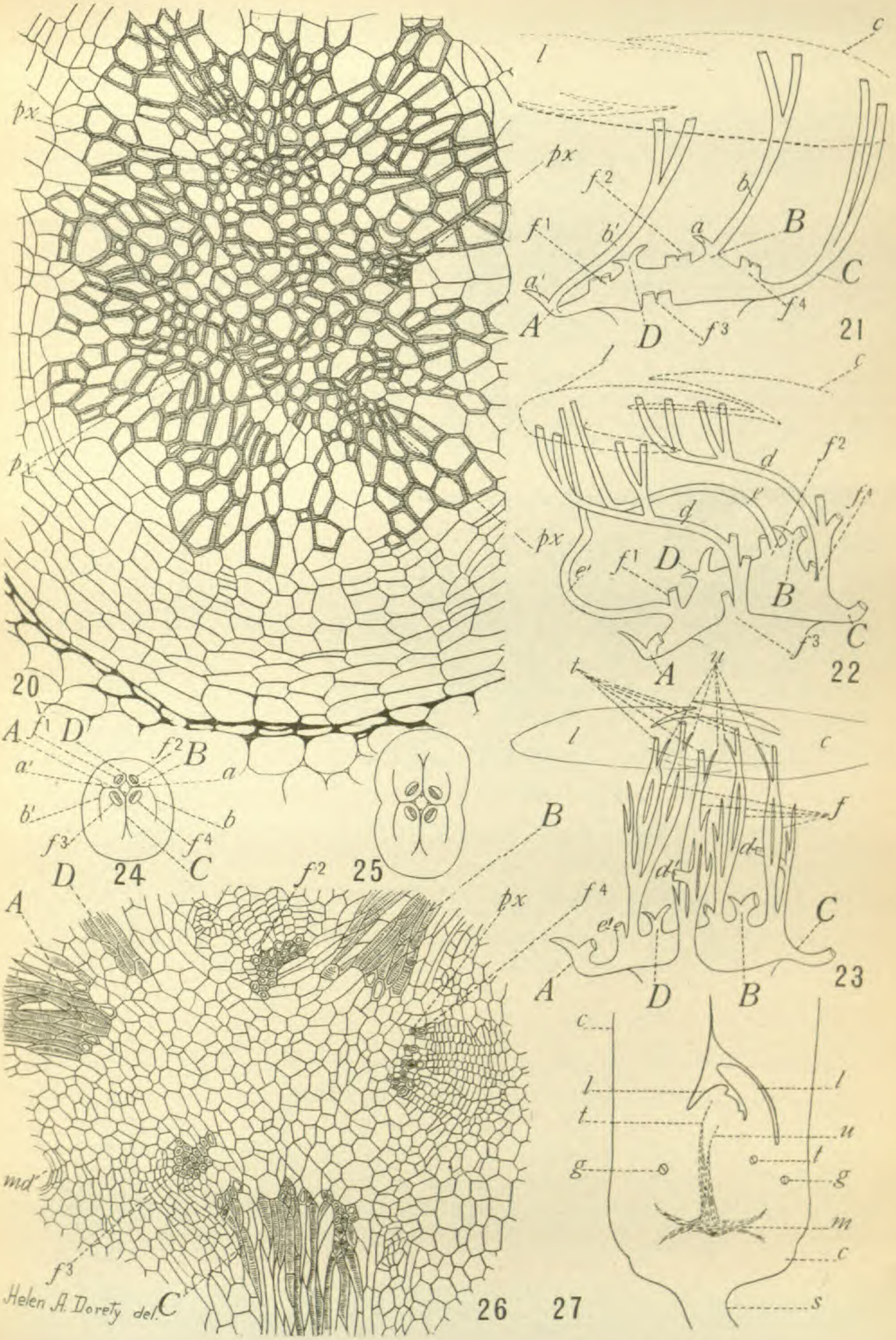
DORETY on CERATOZAMIA



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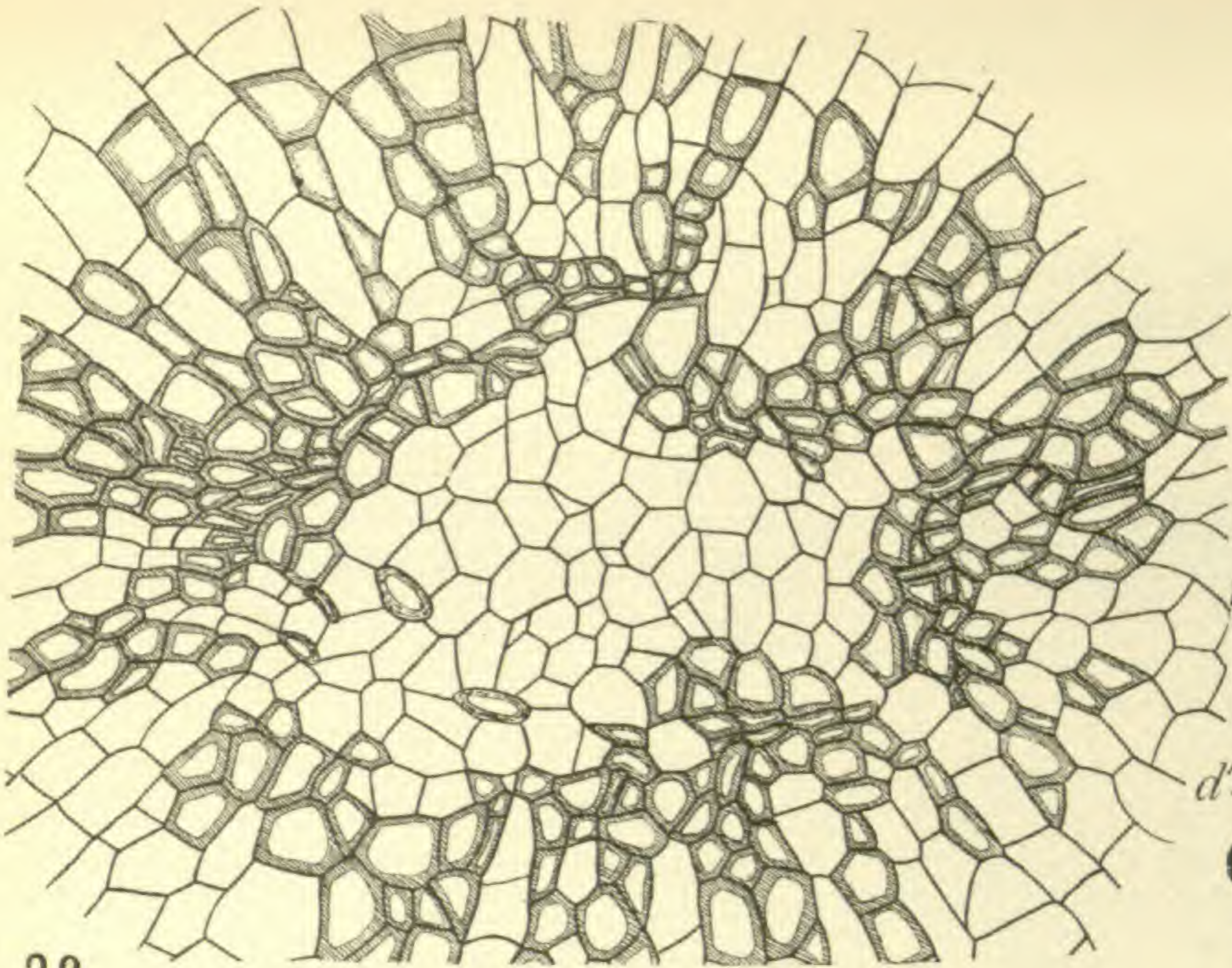

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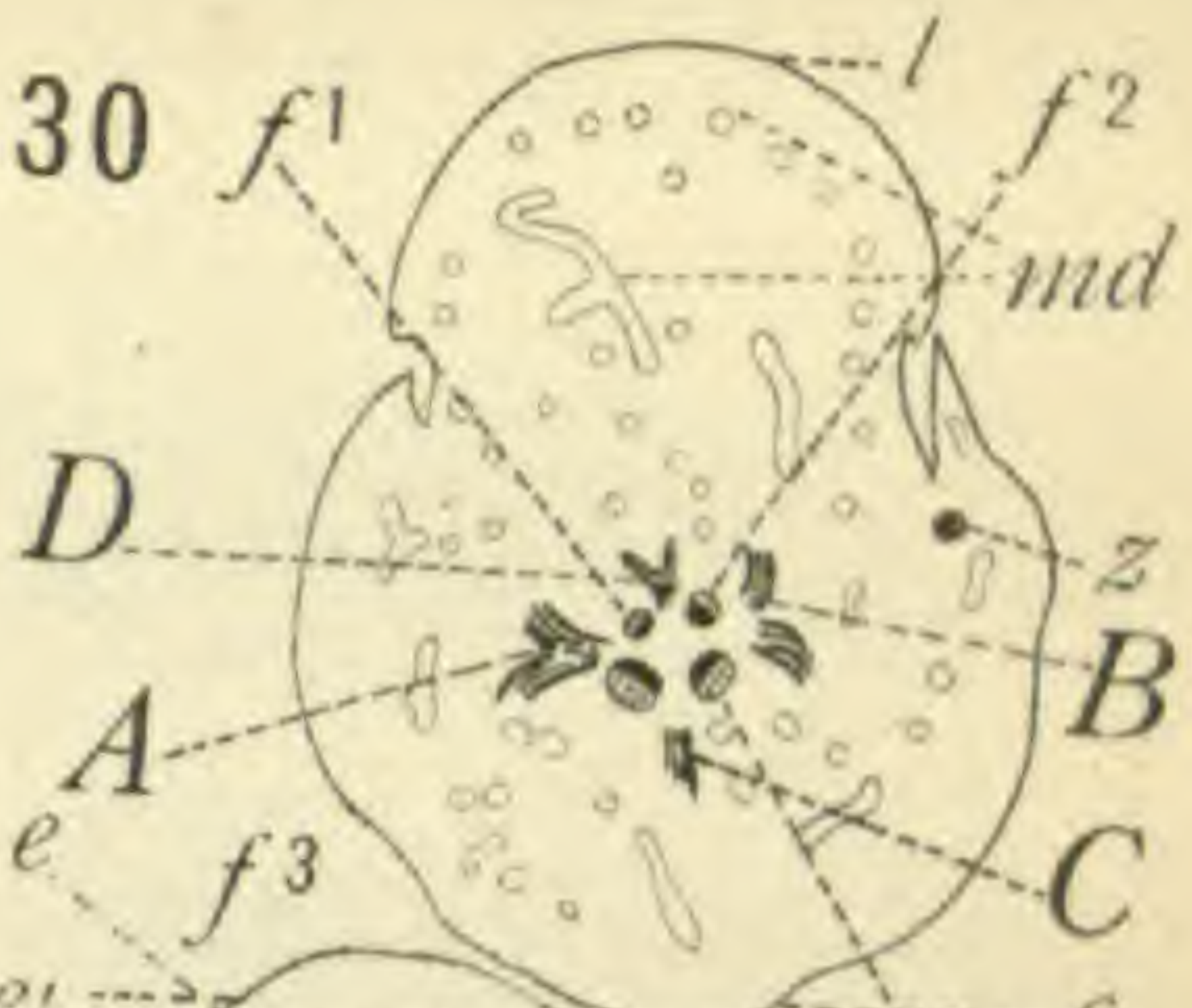

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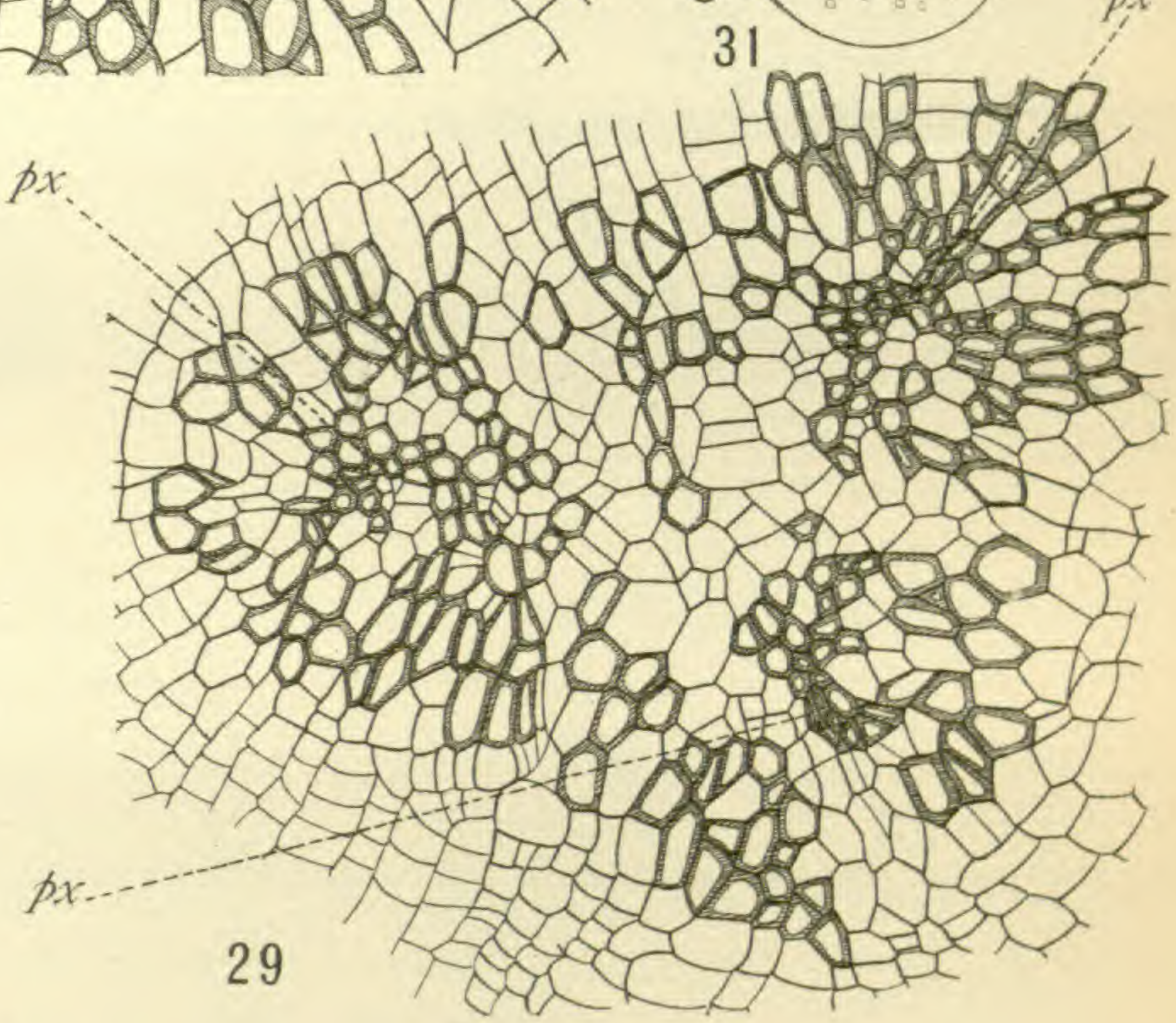

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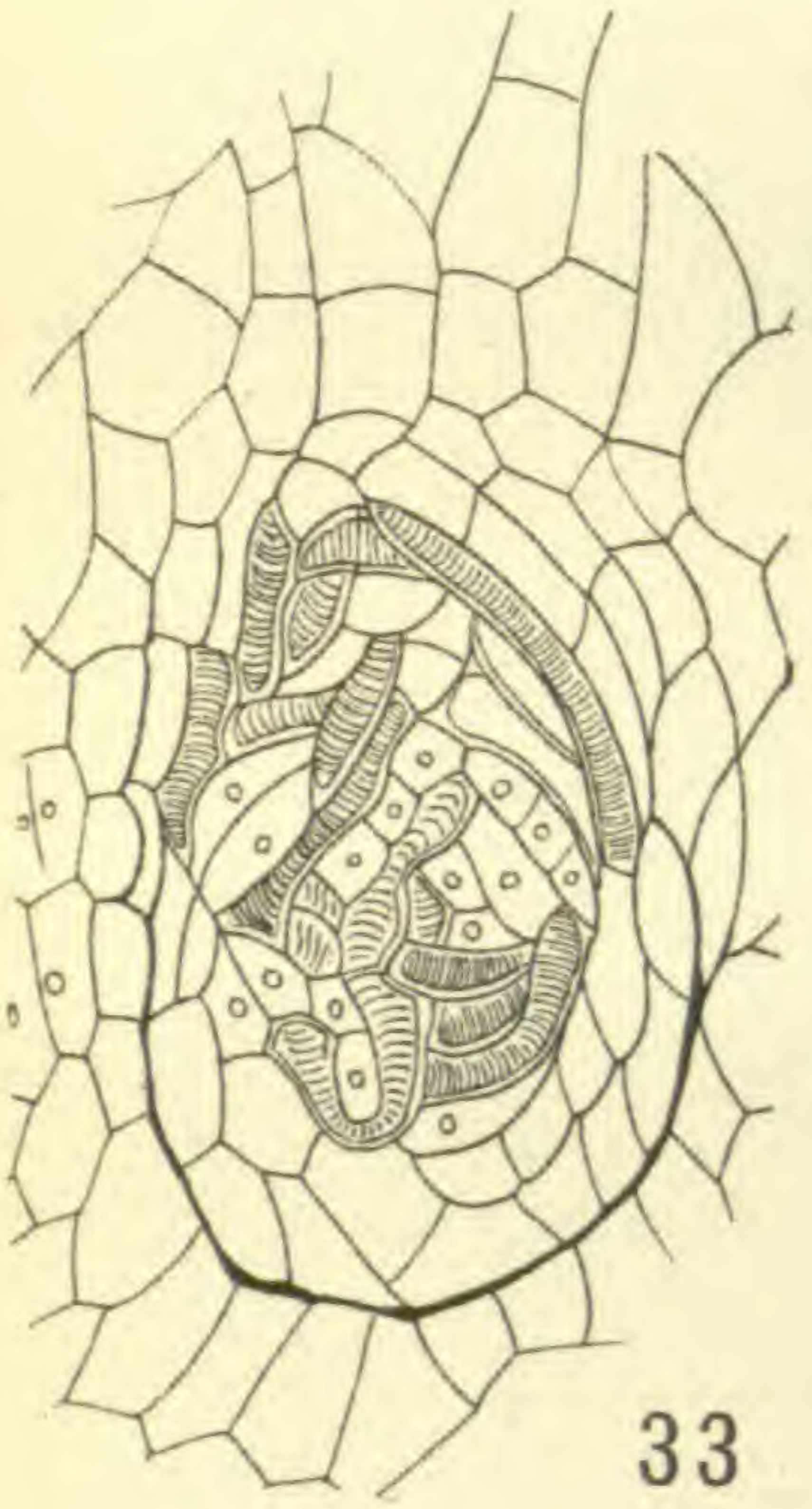

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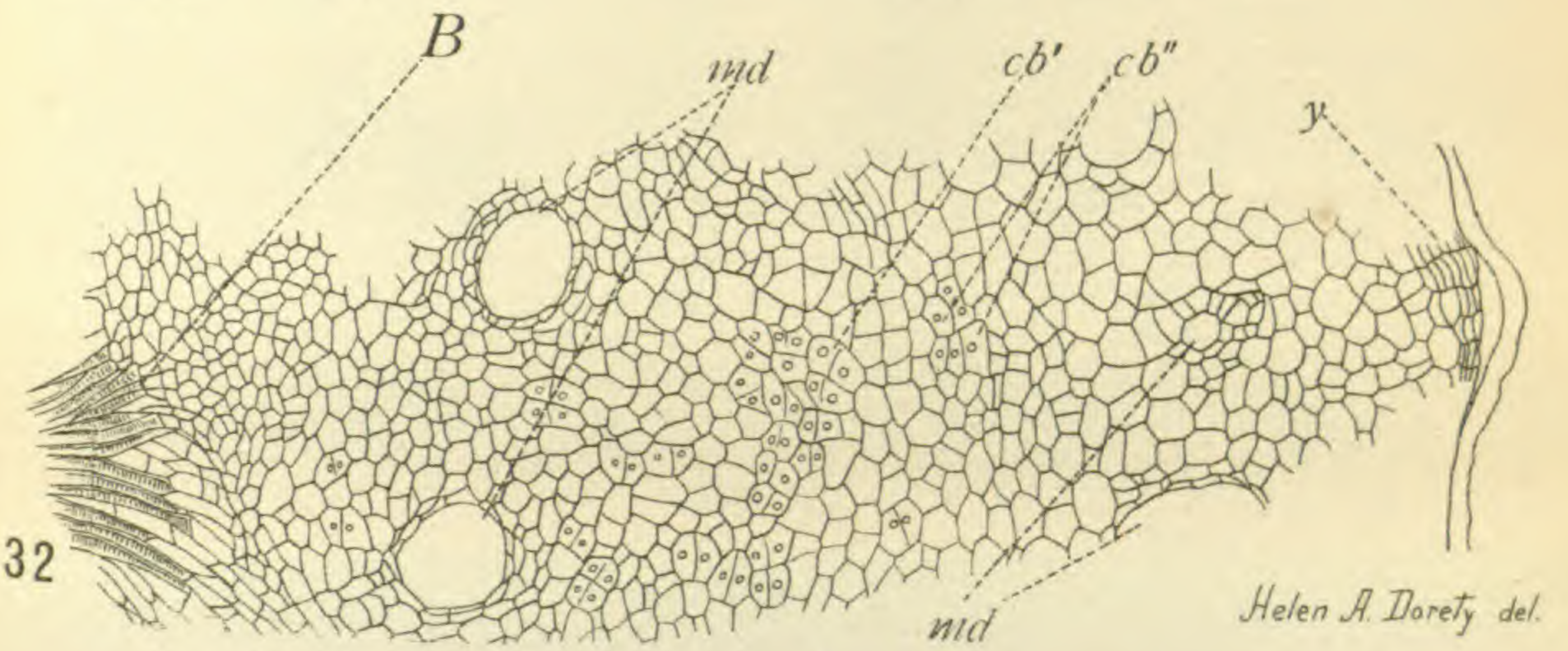

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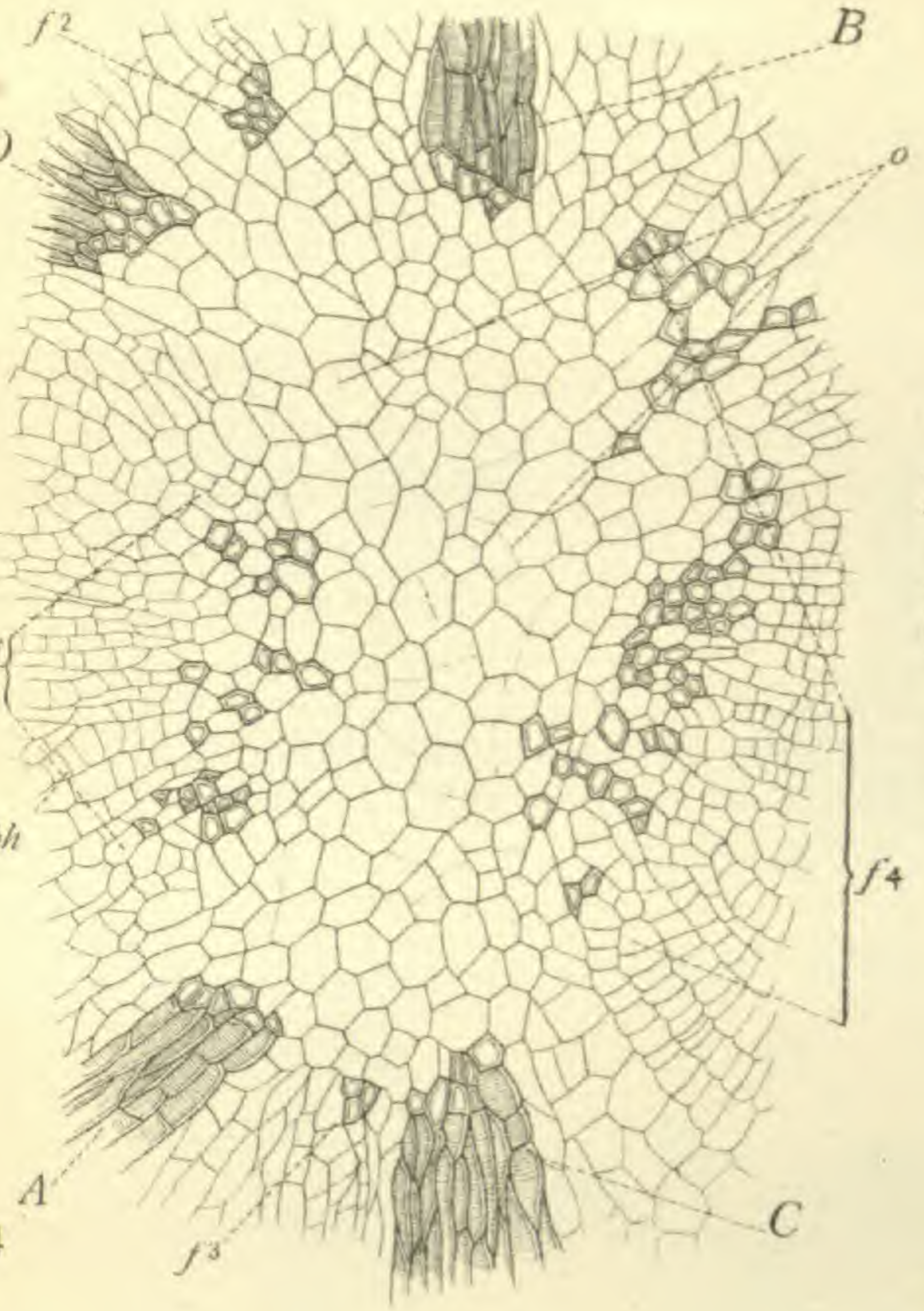

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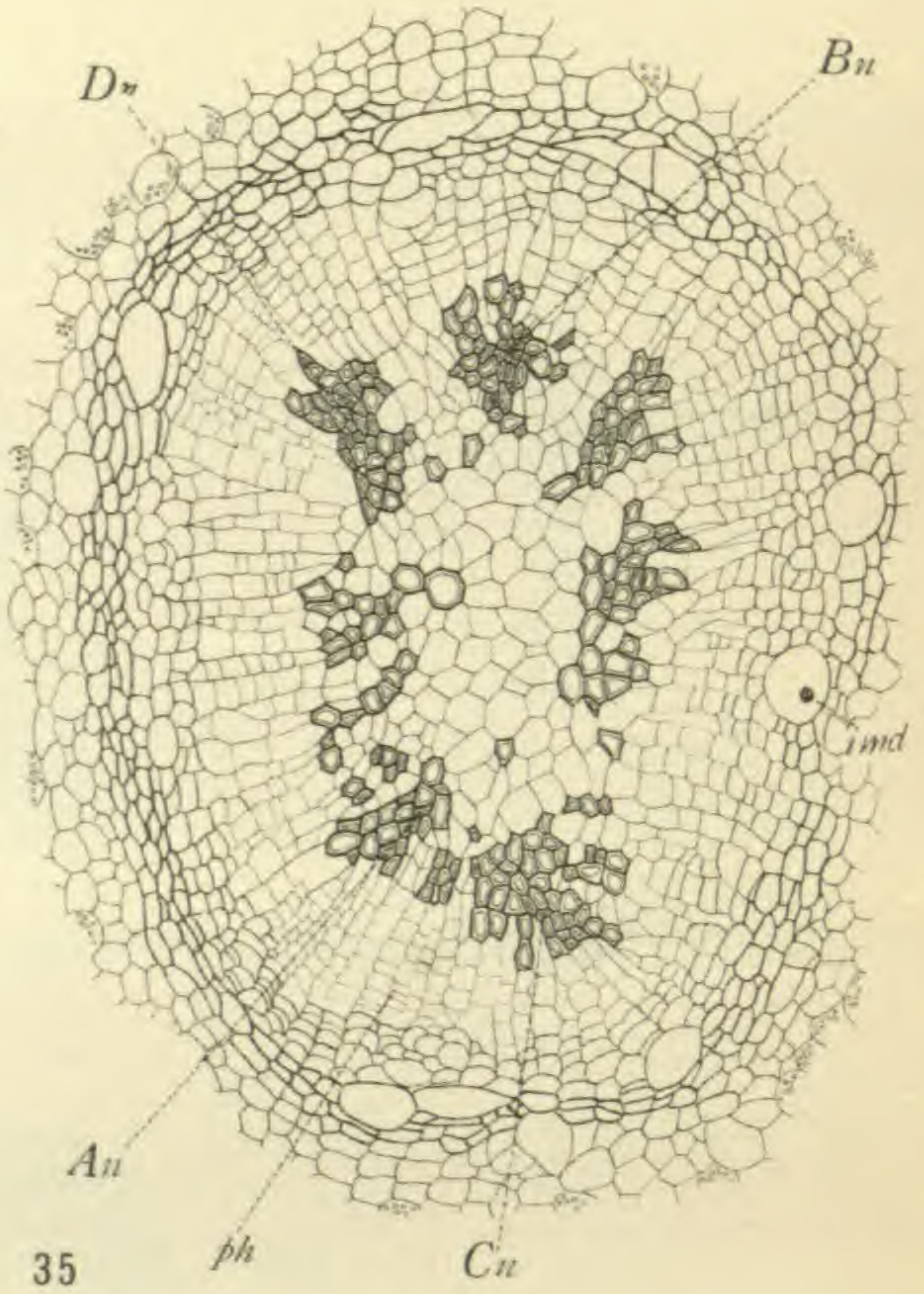

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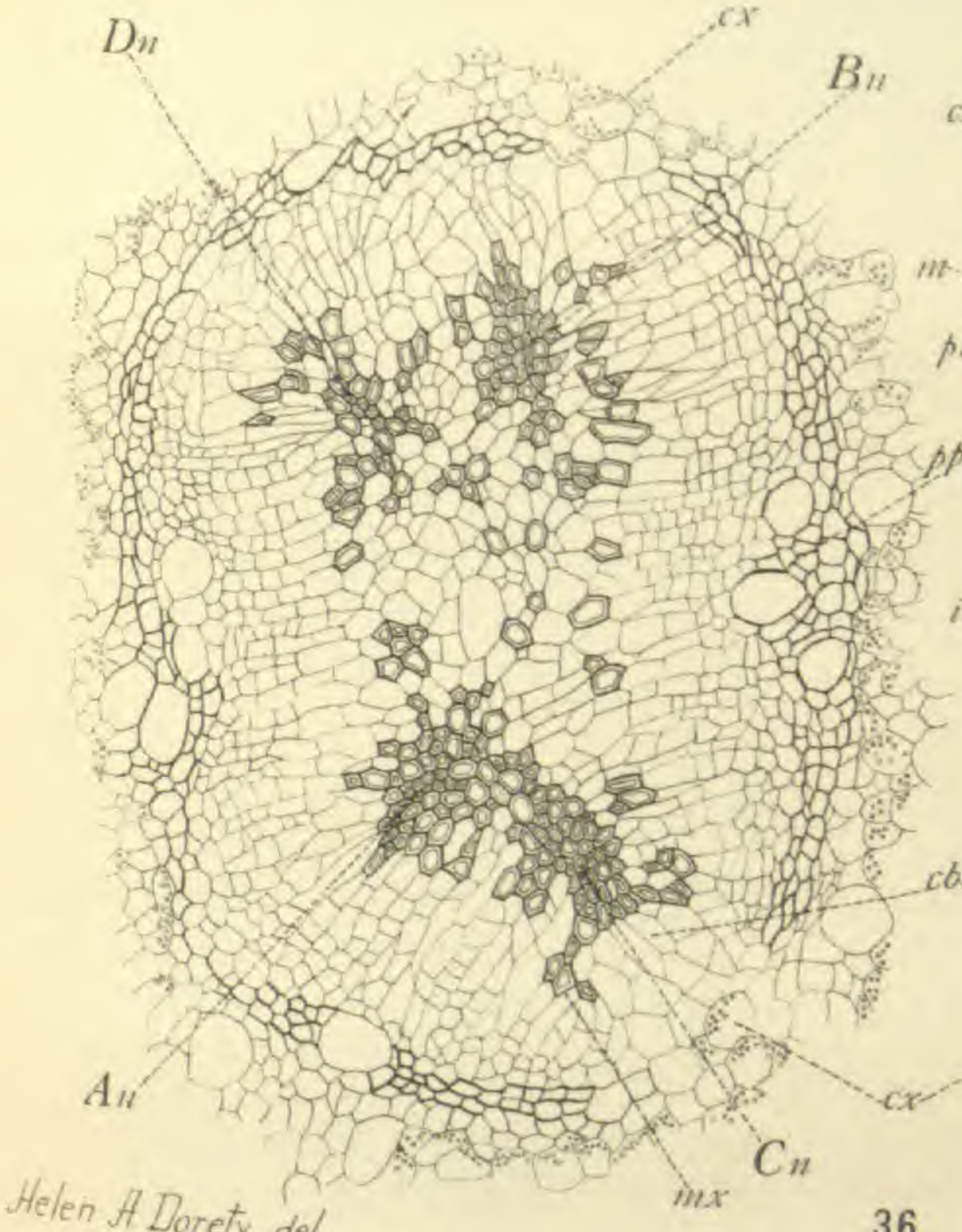

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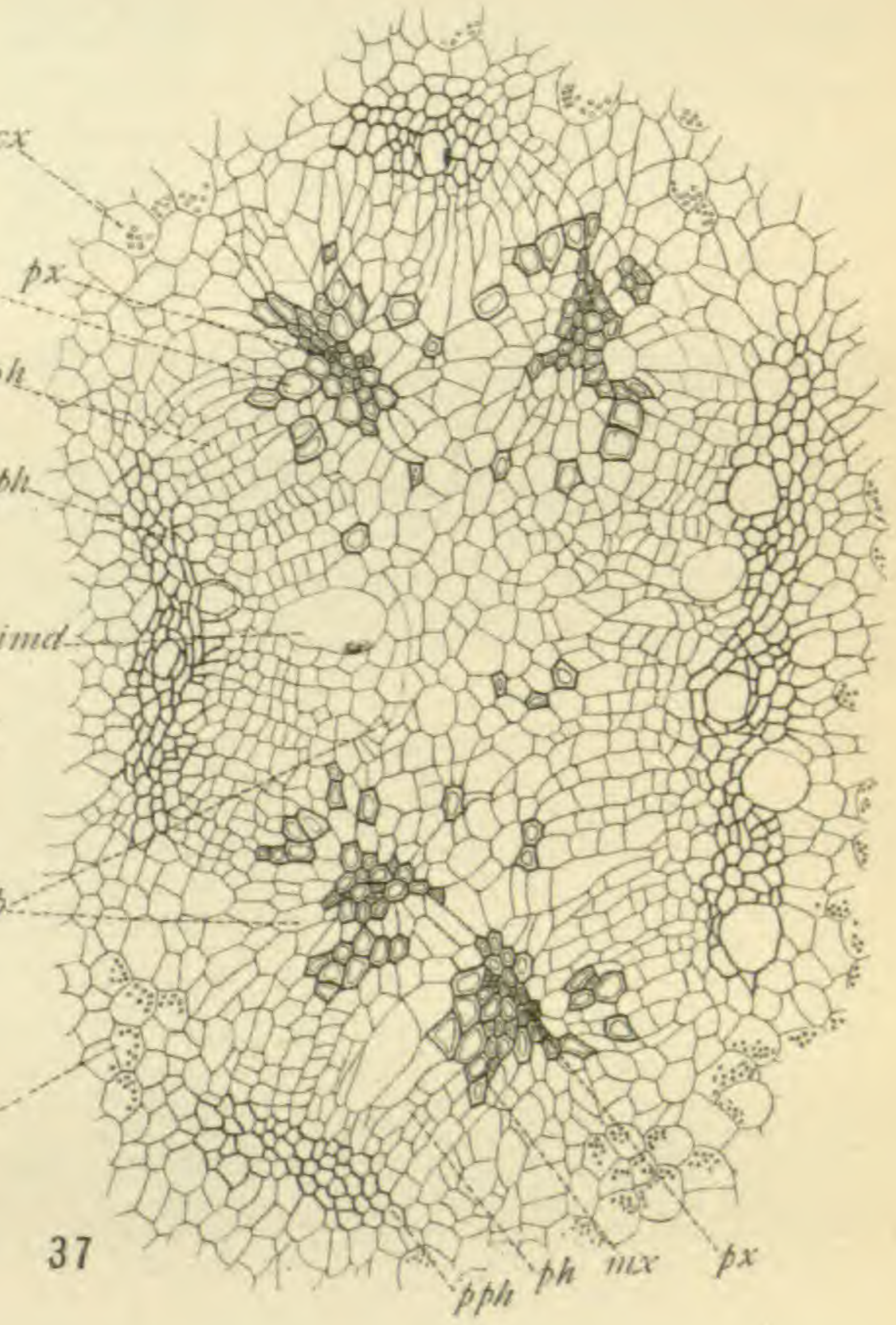

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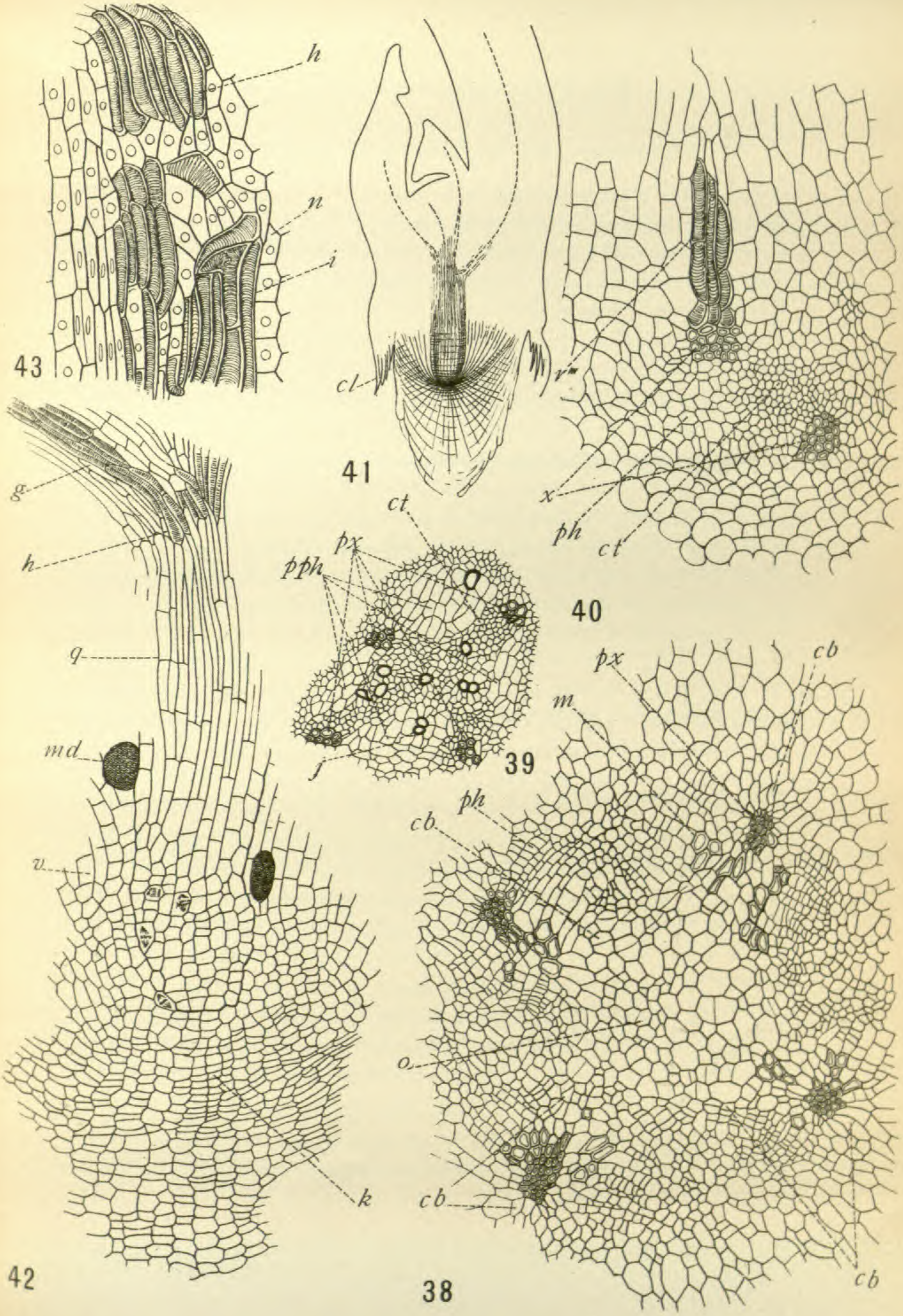
DORETY on CERATOZAMIA



DORETY on CERATOZAMIA

BRIEFER ARTICLES

THE NUMBER AND SIZE OF THE STOMATA

For some educational purposes it is needful to know which plants possess the largest, the most numerous, the most readily observable, or the most definitely distributed stomata, and what quantities are involved in each of these features. The most important work upon the subject thus far is by WEISS,[1] but he includes only a few of those plants used for laboratory study in this country, namely, the common greenhouse plants and those readily raised in greenhouses from seed. Accordingly, in continuation of similar studies upon other topics as already described in this journal,[2] I have undertaken to obtain exact data upon this subject, with results recorded below. The study was begun, and carried well along, by Miss ALICE T. MITCHELL, while a senior student in Smith College, but she was unable to bring it into final form. I undertook at first simply to complete her work, but later I found it better, in order that all the results might represent a single method of treatment, to work over the entire subject from the beginning. The work has been done in the laboratory of plant physiology in Smith College, and has had the criticism and advice of Professor W. F. GANONG.

My method of study, in general, was that developed by LLOYD in his recent investigations[3] on the stomata of desert plants. I removed pieces of the epidermis from different parts of full-grown representative leaves, and dropped the pieces immediately into absolute alcohol. In order to test the possible effect of any shrinkage of the epidermis upon the numerical results, I made many comparisons of the data yielded by the epidermis alone with those yielded by untreated leaves; but I found no appreciable differences. I used throughout the same microscope and combination (Zeiss, objective DD, ocular 1 with cross hairs as an aid to counting). In counting the stomata, I adopted WEISS's method of counting all those falling within the field of vision, the area of which is easily calculated and reduced to square millimeters. For every species I counted the stomata, and calculated the mean, from thirty different fields selected at random from epidermis taken from three different plants (or, in two cases only, from different

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[1] Jahrb. Wiss. Bot. **4**:123, 196. 1865–1866.

[2] BOT. GAZETTE **40**:302. 1905; **45**:50. 1908; **45**:254. 1908; **46**:50. 1908.

[3] LLOYD, F. E., The physiology of stomata. Publ. Carnegie Institution. 1908.

shoots of the same plant), this precaution being observed in order to minimize any possible abnormalities of single plants.

In order to measure the size of the stomata, which involves the length and breadth of the guard cell apparatus when closed, and the length and breadth of the pore when most widely open, the same general method was used, except that, in order to prevent the closure of the pore through any possible wilting of the leaf, the epidermis was removed while the leaves were still attached to the plants. The pores of the stomata were found as a rule to be widest open at about 10 A. M., and accordingly the material was taken at that time. The measurements were made with an ocular micrometer, carefully valued by comparison with a stage micrometer. As in the case of the countings, thirty measurements were made upon material practically taken at random from three plants, and the figures in the table represent the mean of these. Only the linear dimensions of the pore are given in the table, but the area can very easily be determined by treating the opening as an ellipse,[4] though it is to be remembered, as BROWN and ESCOMB have shown,[5] that in the passage of gases through stomata, it is the linear dimensions, and not the area, which is important.

The data of the accompanying table may be summarized as follows. The stomata of our common greenhouse plants occur chiefly upon the under surfaces of the leaves, only about two-fifths (43 per cent.) having any upon the upper surface, and those almost invariably far less numerous than those upon the under. The most numerous stomata occur (in order of abundance) in Abutilon, *Ficus repens*, *Phaseolus vulgaris*, *Cucurbita Pepo*, and *Salvia involucrata*. The largest occur (in order of size) in *Triticum sativum*, Tulipa, *Avena sativa*, *Primula sinensis*, *Chrysanthemum frutescens*, and *Tradescantia zebrina*. In a general way, there is an inverse proportion between number and size of stomata. Taking all of the plants collectively, the number of stomata ranges from 0 through a mean of 121 to 484 per square millimeter, or, in general terms, they average over 100 to the square millimeter. The mean size of the open pores is $17.7 \times 6.7\ \mu$, and the mean area is 92 square μ. The total pore area for a square millimeter of leaf, therefore, is 11,132 square μ (121×92), which means that when the pores are open, one-ninetieth (or in round numbers over one-hundredth) of the epidermal surface is open.

Some other points worthy of mention in connection with the practical study of stomata in the laboratory are the following:

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[4] Area of an ellipse $= \frac{\text{length}}{2} \times \frac{\text{breadth}}{2} \times \pi$.

[5] Nature **62**:212.

The epidermis may readily be stripped in large pieces from the majority of greenhouse plants, notably from *Chrysanthemum frutescens*, *Cyclamen latifolium*, *Pelargonium zonale*, *Helianthus annuus*, Tulipa, *Vicia Faba*, and *Tradescantia zebrina*. It can be removed, though with difficulty, from some others, such as Abutilon, *Cestrum elegans*, and *Coleus Blumei*, while in some, e. g., *Ficus elastica* and *Hedera Helix*, it can be removed only by tangential sectioning with a razor.

STOMATA-QUANTITIES IN GREENHOUSE PLANTS

	NUMBER Minimum, mean, maximum in 1 square millimeter		SIZE Length and breadth in microns			
			Upper surface		Lower surface	
	Upper surface	Lower surface	Guard cells closed	Pore open	Guard cells closed	Pore open
Abutilon	0	198–**333**–484	0	0	17×15	6× 3
Avena sativa	13–**25**–39	13– **23**–30	64×32	31× 7	70×36	38× 8
Begonia coccinea	0	22– **40**– 53	0	0	42×29	21× 8
Cestrum elegans	0	92–**146**–224	0	0	34×25	14× 7
Chrysanthemum frutescens	4–**15**–35	22– **34**– 61	57×31	31×11	58×31	33×11
Cineraria cruenta	0	39– **55**– 88	0	0	40×27	25× 8
Coleus Blumei	0	105–**141**–211	0	0	24×19	10× 5
Cucurbita Pepo	6–**28**–68	175–**269**–368	21×14	5× 2	20×16	6× 3
Cyclamen latifolium	0	44– **68**– 96	0	0	45×33	21× 7
Euphorbia pulcherrima	0	176–**233**–365	0	0	26×19	11× 7
Fagopyrum esculentum	17–**45**–66	127–**152**–184	27×20	10× 5	27×21	12× 6
Ficus elastica	0	83–**117**–180	0	0	40×36	19× 6
Ficus repens	0	228–**282**–365	0	0	21×17	5× 3
Fuchsia speciosa	0	52–**121**–193	0	0	39×28	19× 7
Hedera Helix	0	123–**158**–193	0	0	29×26	11× 4
Helianthus annuus	52–**85**–118	96–**156**–268	33×21	18× 8	36×21	22× 8
Heliotropium peruvianum	0	118–**149**–176	0	0	21×17	9× 5
Impatiens Sultani	0	118–**208**–396	0	0	26×18	9× 6
Lycopersicum esculentum	0–**12**–87	79–**130**–202	27×20	10× 5	33×23	13× 6
Oxalis Bowiei	0	52– **77**–118	0	0	28×21	11× 4
Pelargonium domesticum	8–**19**–35	39– **59**– 88	47×34	23× 8	45×32	24× 9
Pelargonium peltatum	4–**11**–22	13– **28**– 48	46×31	20× 6	45×30	22× 7
Pelargonium zonale	8–**22**–39	83–**118**–171	37×26	16× 9	37×25	19×12
Phaseolus vulgaris	13–**40**–96	184–**281**–356	25×14	8× 3	21×13	7× 3
Primula obconica	0	26– **47**– 70	0	0	39×34	17× 6
Primula sinensis	0	22– **31**– 48	0	0	59×46	30× 9
Ricinus communis	39–**64**–96	140–**176**–224	30×16	8× 4	30×20	10× 4
Salvia involucrata	0	211–**263**–330	0	0	20×16	9× 3
Senecio mikanioides	0	83–**114**–158	0	0	30×24	10× 7
Senecio Petasitis	0	66–**106**–149	0	0	44×32	23×10
Tradescantia zebrina	0	8– **14**– 22	0	0	55×33	31×12
Triticum sativum	22–**33**–44	8– **14**– 26	79×37	40× 7	84×35	38× 7
Tropaeolum majus	0	92–**130**–171	0	0	27×17	12× 6
Tulipa hybrid	22–**40**–57	35– **47**– 66	56×35	18× 7	72×35	32×10
Vicia Faba	35–**48**–66	39– **52**– 70	44×27	19× 8	46×28	20× 8
Vicia Faba equina	17–**34**–52	30– **48**– 61	42×26	18× 8	43×28	19× 8
Zea Mais	39–**52**–79	52– **68**– 88	47×36	19× 4	45×36	19× 5

Counting or measuring the stomata *in situ* on the leaf is possible with a few plants, notably *Begonia coccinea*, *Chrysanthemum frutescens*, *Fuchsia speciosa*, *Impatiens Sultani*, *Primula obconica*, *Pelargonium zonale*, *Tradescantia zebrina*, and *Vicia Faba*. In some others the condition of the pore can thus be observed, though the outlines of the guard cells are not clear: this is true in *Senecio Petasitis*, *Helianthus annuus*, *Cyclamen latifolium*, *Coleus Blumei*, *Cestrum elegans*, and *Phaseolus vulgaris*.

Marked variations in number and size of stomata occur, not only in different varieties of the same species, but in the same varieties grown under different external conditions. So far as my observation goes, however, the variation is greater in number than in size. Furthermore, while in most leaves the stomata are fairly evenly distributed over the surfaces containing them, in some, especially in oblong leaves (e. g., *Fuchsia speciosa*, *Helianthus annuus*, and *Impatiens Sultani*), the stomata are much more numerous near the base than near the tip (more than twice as many), and near the midrib than near the margin. For this reason very different figures might be given for the same leaf by different observers.

The opening and closing of the stomata of greenhouse plants is correlated closely with the time of day, and secondarily with the weather. As already noted, they are, as a rule, as wide open as they can be about 10 A. M.—this, of course, in well-watered plants. In favorable weather they remain wide open until about 2.30 P. M., when they begin to close, and they are mostly completely closed by 5 P. M., though some may remain open until 6. On hot days in the spring they may close as early as 12 M., probably because of incipient wilting of the leaf. If the stomata are closed by wilting, they may be made to open, partially at least, by immersion of the leaf in water.

The best plants for general laboratory study, taking account of ease of removing the epidermis, size and clearness of stomata, and commonness of occurrence in greenhouses, are, in order of excellence, *Chrysanthemum frutescens*, *Tradescantia zebrina*, *Pelargonium zonale*, *Fuchsia speciosa*, *Helianthus annuus*, and *Vicia Faba*.—SOPHIA H. ECKERSON, *Smith College, Northampton, Mass.*

THE ABSORPTIVE POWER OF A CULTIVATED SOIL

(WITH THREE FIGURES)

In the winter of 1908 we undertook a study of the absorptive power of a certain soil from one of the fields of the Michigan Agricultural College. In addition to the purely analytical methods which have been exclusively employed up to the present time in investigations of this kind, it was decided to approach the problem in a somewhat different way. If the absorptive power of the soil is a factor of real importance, so far as plant life is concerned, it would be reasonable to expect that a concentration of a given salt solution which has proved to be detrimental for a given kind of plant when grown in soil extract would be beneficial or at least do no harm to the same kind of plant when grown in the soil itself.

With this idea in mind, we undertook (1) to determine the maximum tolerance of wheat seedlings to concentrations of certain salts when grown in soil extract to which known quantities of the salt in question were added; (2) to grow the same kind of plants in paraffined wire baskets,[1] using the same kind of soil, making it up to the proper moisture content, and watering the plants with solutions of the same salts, of concentrations equal to and higher than the maximum tolerance determined for the extract by cultures.

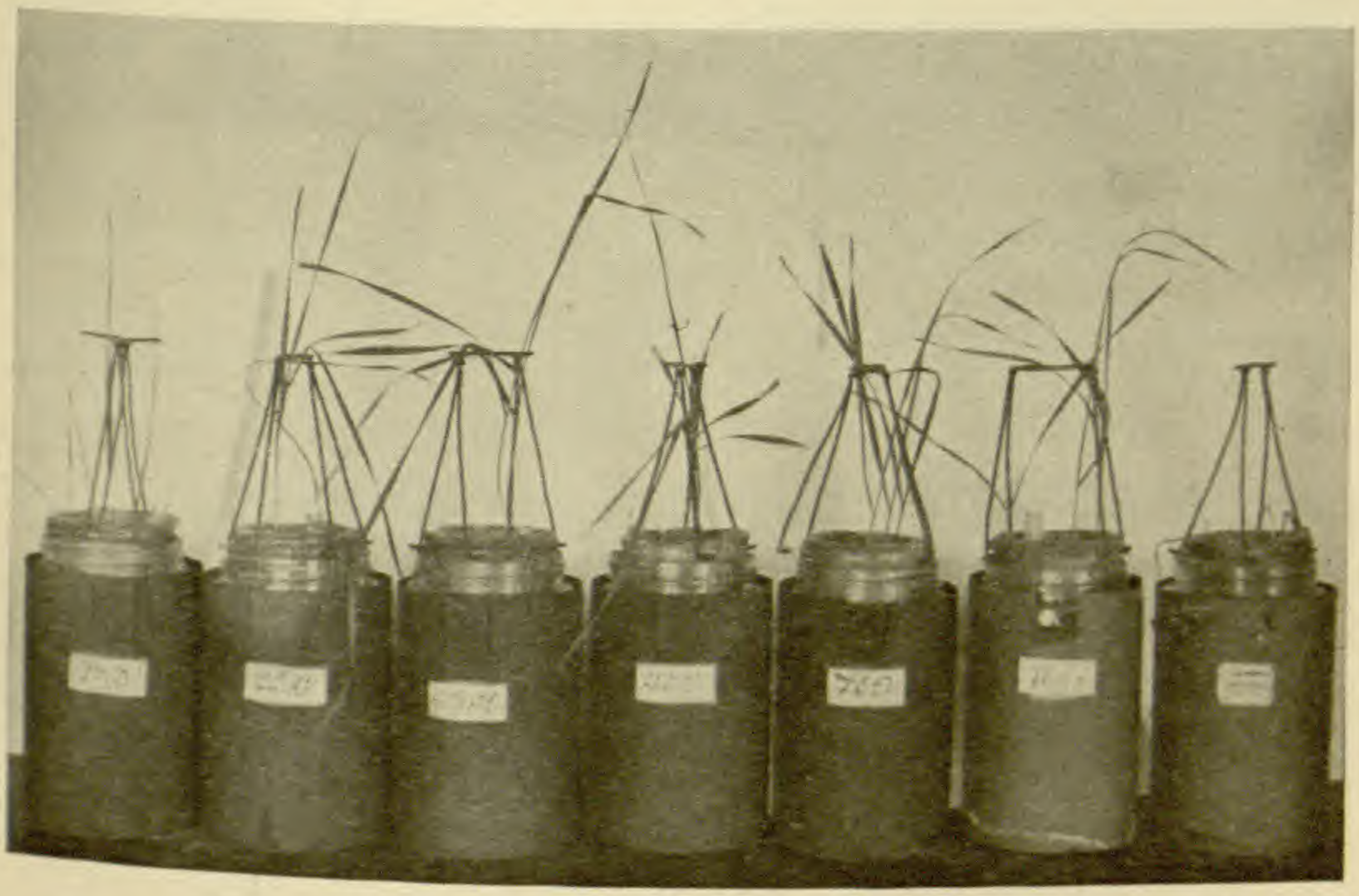

FIG. 1.—Tolerance of wheat seedlings to solutions of Na_2HPO_4; roots immersed in the solution: *1*, distilled water; *2*, soil extract (2:1); *3*, extract + 300^{ppm} P_2O_5; *4*, same + 500^{ppm}; *5*, same + 700^{ppm}; *6*, same + 1000^{ppm}; *7*, same + 2000^{ppm}.

Na_2HPO_4, KCl, and $NaNO_3$ were selected for use, separately and in various combinations. Some of the results obtained with the phosphate salt are given here. The extract was prepared by mixing a known quantity of air-dry soil with twice its weight of distilled water, leaving the mixture, with occasional stirring, for 48 hours, and filtering off the liquid. Portions

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[1] The method devised by the Bureau of Soils, U. S. Dept. Agric. (see Bull. 23 and others of the Bureau).

of this extract were then made up to contain 300, 500, 700, 1000, and 2000 parts per million of P_2O_5 in the form of Na_2HPO_4.

The plants were set in small wire baskets (paraffined along the sides only) containing some sterile quartz sand, and the baskets placed in jars containing the proper extract, as shown in *figs. 1* and *2*. One set of plants was prepared with the roots immersed in the liquid, another with roots remaining in the sand The cultures were aerated by pouring the liquid from one jar into another and the losses by evaporation and transpiration were made up daily with the corresponding extracts. The effect is seen from the photographs. Up to the 700^{ppm}[2] concentration there was no marked difference between the two lots of plants. But while 700^{ppm} immersed plants had a decidedly sickly appearance, the non-immersed ones looked quite healthy even in the 1000^{ppm} extract. The 2000^{ppm} of the non-immersed lot kept on struggling along even after three weeks from planting; while the immersed ones were killed in less than ten days.

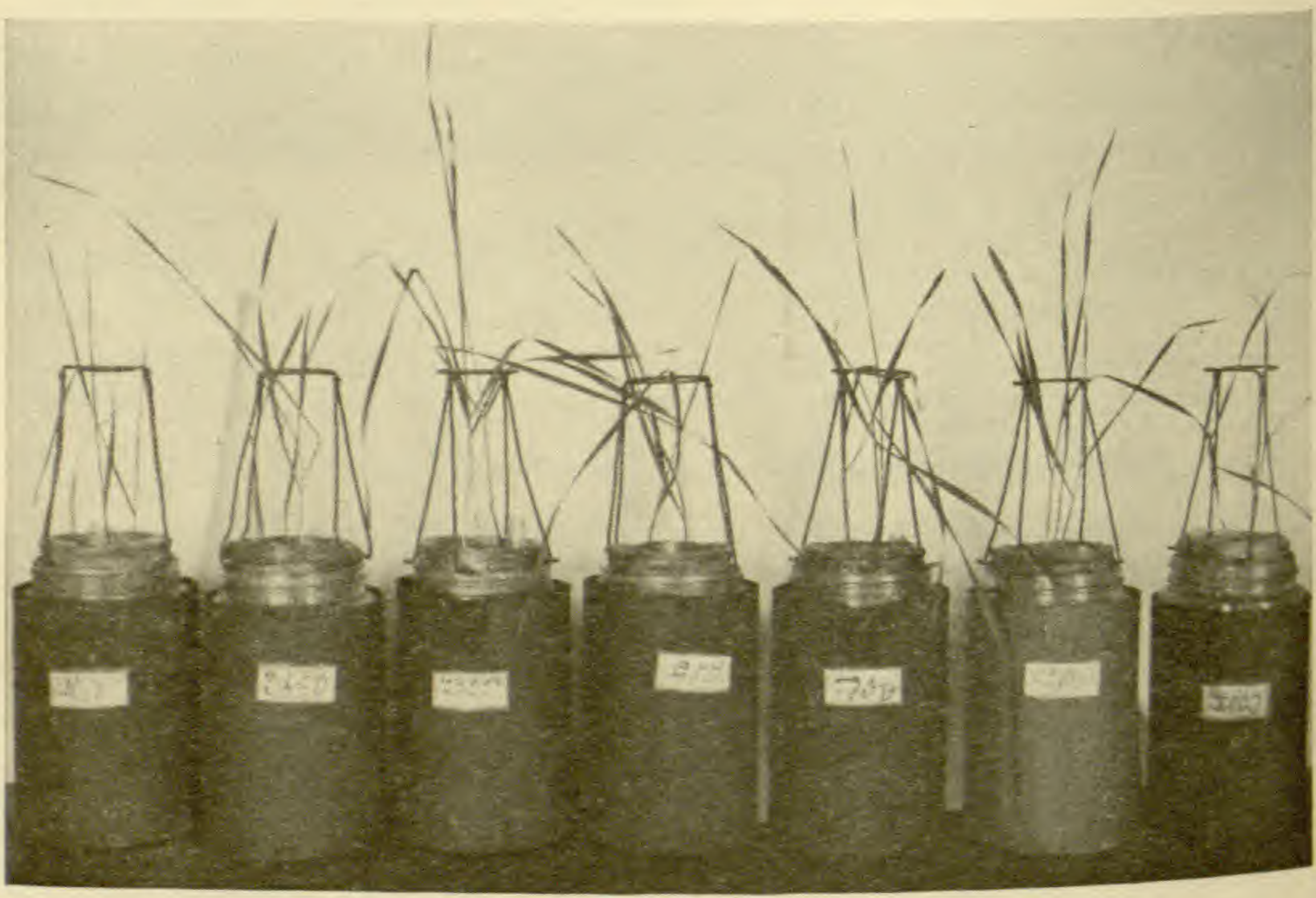

FIG. 2.—Tolerance of wheat seedlings to solutions of Na_2HPO_4 in soil extract; roots kept in sand of the baskets: *1*, distilled water; *2*, soil extract (2 water: 1 soil); *3*, extract + 100^{ppm} P_2O_5; *4*, same + 500^{ppm}; *5*, same + 700^{ppm}; *6*, same + 1000^{ppm}; *7*, same + 2000^{ppm}.

It is thus seen that even the sterile quartz enables the plants to resist higher concentrations of the phosphates. The actual amount of salt

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[2] Parts per million.

absorbed by the quartz was found to be about 10 per cent. in ppm of the original quantity. It was determined in the following way. The basket with the sand was removed from the jar. A sample was immediately taken to determine the water content; at the same time another portion of the same sand was washed with distilled water in ten successive portions. The washings were then evaporated to the volume calculated from the results obtained with the first sample (per centage of moisture in the sand) and the phosphates in the liquid determined. The phosphates in the extract contained in the jar from which the basket was removed were also determined, and the difference between these determinations taken as the amount of phosphates absorbed by the sand.

FIG. 3.—Wheat seedlings in unmanured soil: upper row, left to right, all watered for last 7 days with P_2O_5 solution (*1*, 10,000$^{\text{ppm}}$; *2*, 7000$^{\text{ppm}}$; *3*, 6000$^{\text{ppm}}$); middle row, left to right, watered in same way (*1*, 5000$^{\text{ppm}}$; *2*, 4000$^{\text{ppm}}$; *3*, 3000$^{\text{ppm}}$); lower row, left to right, watered during all 29 days (*1*, 2000$^{\text{ppm}}$; *2*, 1000$^{\text{ppm}}$; *3*, distilled water).

The tolerance of the wheat seedlings to concentrations of the phosphate was very much increased when grown in the soil proper, as shown in *fig. 3*. Even concentrations of 6000$^{\text{ppm}}$, as seen also from the columns of "green" and "air-dry" weights in Table A, had no injurious effect on the plants. Only a concentration of 10,000$^{\text{ppm}}$ was distinctly harmful.

The addition to the soil of unsterilized, fairly well-rotted cow manure, in the ratio of 1:250, enabled the plants to resist still higher concentrations, as seen from the same table.

TABLE A

COMPARATIVE RESULTS AT THE END OF 30 DAYS

Treatment		Soil not manured				Manure not sterilized			
		No. of basket	Transpiration	Green weight	Air-dry weight	No. of basket	Transpiration	Green weight	Air-dry weight
During the entire 30 days	Dist. H_2O.........	27	224	3.00	0.41	16	220	3.5	0.48
	1000ppm Na_2HPO_4	9	152	3.05	0.45	6	160	3.8	0.50
	2000 " "	12	146	3.00	0.48	18	143	4.0	0.60
During the last 7 days	*3000 " "	10	122	3.20	0.54	13	138	3.55	0.56
	4000 " "	11	135	3.10	0.42	17	143	3.5	0.58
	5000 " "	8	186	3.10	0.42	5	180	3.5	0.55
	6000 " "	7	178	3.20	0.41	4	187	3.8	0.58
	7000 " "	26	190	2.90	0.38	15	195	3.7	0.54
	10000 " "	25	180	2.20	0.34	14	184	3.5	0.52

* Up to the last 7 days the even numbers of the following set were watered with a 2000ppm and the odd ones with a 1000ppm solution.

That the increased tolerance of the wheat seedlings to the concentration of the salt is actually due, at least to a very great extent, to the absorptive power of the soil is sustained by the following facts:

(1) The analytical studies show that the soil actually removes large quantities of the phosphoric acid from the solution, as seen by the following table:

TABLE B

ABSORPTION OF PHOSPHATE BY THE SOIL

P.p.m. of P_2O_5 in original solution	Method	Soil not manured		Soil manured	
		Ppm. P_2O_5 in filtrate or percolate	Per cent. of P_2O_5 in Ppm. absorbed	Ppm. P_2O_5 in filtrate or percolate	Per cent. of P_2O_5 in Ppm. absorbed
1000	A*	795	20.5	745	25.5
1000	B†	728	27.2	698	30.2
2000	A*	1740	26.0	1700	30.0
2000	B†	1690	31.0	1674	32.6

* METHOD A.—25gm of the soil mixed with 50cc of the corresponding solution left with occasional shaking for 48 hours, filtered and the filtrate analyzed for phosphates.

† METHOD B.—200gm of the soil placed in a wire basket (paraffined along the sides only) and 400cc of the corresponding solution allowed to percolate through the soil; the percolate analyzed for phosphates.

(2) In the case of a nitrate salt, where the absorption is a negligible quantity, the tolerance of the immersed and non-immersed plants, as will

be more fully demonstrated in a later communication, is practically the same.

(3) The tolerance increases with the increase of the absorptive power; both factors being lower in the quartz, higher in the unmanured soil, and still higher in the manured soil.—JOSEPH ROSEN and CHARLES HELLER, *Agricultural College, Michigan.*

CURRENT LITERATURE

BOOK REVIEWS

Biologic types

In a recently published work Professor WARMING[1] has offered a valuable contribution to the knowledge of biologic types as these occur among plants. The subject is treated with rare skill, and although not a new one, the characterization of the types is carried out in such a way that many new points have been brought together and explained by the author in accordance with his own views, and embodying many of the most important results from his long experience.

The existence of biologic types was recognized many years ago. ALBERTUS MAGNUS and PORTA knew of them, but only vaguely. When therefore the author discusses the history of these types, he begins with ALEXANDER HUMBOLDT as the founder of plant-geography and physiognomy, so excellently outlined in his *Essai sur la geographie des plantes* and *Ideen zu einer Physiognomik der Gewächse.* It is interesting to follow the course of development of this science, so very greatly influenced by the Darwinian era. Since then we have witnessed the publication of an enormous literature dealing with biology, biologic types, and plant societies, all more or less combined under the modern term ecology.

A biologic type, according to the author, is the form which the vegetative organs have acquired in conformity with the surroundings; the particular structures, external and internal, which we find in stems and leaves, also in the complete shoot, but not in the flowers and fruits, which to a certain extent are independent of the surroundings. The vegetative organs owe their various modes of development and structure to climate and soil, as related to the associations known as hydrophytes, mesophytes, and xerophytes. As understood by WARMING the biologic types comprise two large groups, *heterophytes* and *autophytes.* The former of these include *holosaprophytes* and *parasites.* The autophytes are divided into five classes: aquatic plants, lichenoid plants, muscoid plants, lianas, and autonomic land plants. The sixth class comprises five subclasses: hapaxanthic plants, redivive herbs, rosette plants, creeping plants, and erect plants with long shoots persisting through many seasons.

The following examples may illustrate these subclasses. Among the hapaxanthic plants are those which are annual, biennial, and perennial, and which bloom only once. The redivive plants (*Stands* of the Germans) are those which die down to the ground at the end of the season, but which are provided with persistent subterranean organs (rhizomes, tubers, bulbs, etc.). The rosette plants form a familiar type, from the mountains especially; it may be dicyclic or pleiocyclic, and the leaves may be long and narrow, or roundish. In the creep-

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[1] WARMING, E., Om Planterigets Livsformer. Copenhagen: G. E. C. Gad. 1908.

ing plants the organ that creeps may be either the stem, the stolons, or the roots. Finally, the fifth subclass contains species with the shoots elongated, which are able to persist for many years, for instance, the herbaceous *Arabis alpina*, also Armeria, Androsace, Eritrichium, etc.; and among the woody forms, Bambuseae, Coniferae, the dicotyledonous trees, etc.

An interesting chapter is devoted to the leaves and leafy shoots. The author recognizes three factors as being the direct cause of the shape of the leaf: (1) its function as an organ of assimilation; (2) the medium in which it lives (air or water); (3) the particular structure (outline especially) which belongs to the species, thus constituting a specific and very marked character developed through relationship. But the author makes no mention of the position of the leaf upon the shoot as having any bearing upon its form, although this seems an important factor when one remembers the great variation in leaves from seedling to mature plant, so profusely illustrated in North American plants especially.

The arrangement of plants according to their biologic character is a most difficult task, if really possible. To arrange plants in accordance with their vitality, as for example annuals, biennials, and perennials, gives no satisfaction; yet the question of age is of no small importance in classification. The characterization of biologic types, when comprising the structure of the shoot, leads us into perplexing difficulties, on account of the enormous number of intergrading forms that exist, of rhizomes for instance. It appears to the reviewer that the autonomic land plants have been classified less successfully than the others. However, we know of no system published, so far, where the classification of this particular group of plants has been outlined in any way clearer than the one suggested by WARMING. Much would be gained if the ecologists would follow his example and study the plants in the field, and not merely in the laboratory. It seems very strange that modern botanists pay so little attention to the study of organography, which actually is one of the bases of ecology; and plant-geography is indeed of no less importance. WARMING'S paper contains in itself an excellent guide to future workers in this line, and we hope that translations may follow soon, so as to make the paper more accessible to foreigners.—THEO. HOLM.

A text-book of botany and pharmacognosy

A second edition of KRAEMER'S *Text-book* has appeared,[2] designed primarily for students of pharmacy, for pharmacists, and for food and drug analysts. Perhaps it is not the province of a botanist to review it, but it certainly is an interesting illustration of the kind of botany required of students of pharmacy; besides, some of the introductory chapters deal with botany in the ordinary sense. The first impression is that of a mass of details, without any thread of continuity, which makes a book of reference rather than a textbook, a book to consult rather than to read.

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[2] KRAEMER, HENRY, A text-book of botany and pharmacognosy. pp. vi+840. *pls. 321* (*figs. 1500*). Philadelphia and London: J. B. Lippincott Co. 1907.

The first chapter describes the "principal groups of plants," in which types are selected to represent the groups. The descriptions are systematic in form, encyclopedic in content, and entirely unrelated. Just what the student is expected to do with this part is not clear. There follow chapters on the "outer morphology of angiosperms" and "the inner morphology of the higher plants." This old breaking-up of a subject that cannot be broken is artificial in the highest degree. The confusion is increased by referring to the first topic as "the anatomy or outer structure of the angiosperms;" and to the second as "the inner structure or histology of the higher plants." This may be what students of pharmacy need, but it is not modern botany.

The remaining chapters deal with the professional details of pharmacy; although under Part I, which bears the title "Botany," there appear chapters on the "classification of angiosperms yielding vegetable drugs," and "cultivation of medicinal plants." Part II is entitled "Pharmacognosy" and contains chapters on crude drugs, powdered drugs, and foods. Part III is devoted to "reagents and microscopical technique."—J. M. C.

NOTES FOR STUDENTS

Synapsis.—GRÉGOIRE has published[3] an interpretation of synapsis opposing HERTWIG'S new theory and confirming his own earlier view. He states that the nucleus in synapsis passes through three principal states (*leptotènes*, *pachytènes*, *strepsitènes*), and that synapsis represents a primary state of heterotypic prophase. He says that cytologists diverge into two schools: one believing that the pre-reduction of chromosomes occurs in the zygonema stage, the bivalent chromosomes in the strepsinema stage representing the paired true chromosomes in heterotypic mitosis; the other believing that the pre-reduction is effected by a folding back, in the strepsinema stage, of a chromosome which is believed to be composed of two somatic chromosomes attached end to end. However, they all agree in considering synapsis as a stage in the development of the heterotypic chromosomes.

Taking WOLTERECK'S conception, R. HERTWIG proposed an entirely new interpretation of synapsis, deduced from his theory of nucleoplasmic relation. The gist of the theory is this: increase of protoplasm cannot continue without an intervention of nuclear division which may or may not be followed by cell division. After cell division, the increase of protoplasm and of nucleus cannot proceed equally, the former generally being ahead of the latter; so the nucleoplasmic quotient (K/P) tends to diminish. HERTWIG designates the state of equilibrium as "nucleoplasmic tension." This tension causes a sudden and considerable increase of the nucleus, which results in the increase of chromatin. The increase of protoplasm and consequent increase of chromatin can be brought back to equilibrium only by nuclear division. Applying the theory to the nuclear division in tetradogeneses (sporogenesis, spermatogenesis, and ovogenesis), he

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[3] GRÉGOIRE, VICTOR, Les phénomènes de l'étape synaptique représentent-ils une caryocinèse avortée? La Cellule 25:87–99. 1908.

found an objection, especially where a considerable increase of the ovocyte is not followed directly by nuclear division. For the sake of harmonizing the theory with the phenomena, he suggested that synapsis is really an abortive division. This theory of synapsis naturally tends to interpret synapsis not as a stage preparing for the heterotypic chromosomes, but only as an abortive form of nuclear division. The work of POPOFF on ovogenesis of Paludina is the material on which the theory is based. POPOFF apparently considers the bivalent chromosomes after synapsis and before the growth period in ovogenesis of Paludina as tetrads. These chromosomes completely disorganize in the diplonema stage, and the heterotypic chromosomes which appear after the growth period are a new formation, without any connection with the chromosomes that emerged from synapsis. Moreover, WASSILEIFF considers that in spermatogenesis of Blatta there occurs a pulverization of chromosomes during synapsis, and he believes that it is a trace of abortive nuclear division.

GRÉGOIRE remarks, under the headings spermatogenesis, sporogenesis, and ovogenesis, that such an interpretation cannot be in harmony with the vast majority of cases of synapsis, which are believed to be an important stage in the preparation of heterotypic chromosomes. In conclusion, he emphasizes synapsis as a fundamental stage, which constitutes a primary state of heterotypic prophase and not as an abortive kinesis.—SHIGÉO YAMANOUCHI.

Soil fertility.—The Bureau of Soils is doing an excellent work in seeking the explanation of the differences in productiveness of soils along the lines of a rational physiology. In spite of various attacks upon the principles which they are developing, the work commends itself to the unprejudiced as consonant with the modern phases of physics and physiology. Two recent bulletins contain valuable reports of research. CAMERON and GALLAGHER have shown[4] that when water has been added to a given soil in such proportion that it is in its most favorable condition for working and for plant development (as determined by expert gardeners), this is also the condition when to a pointed instrument it is physically most penetrable. This "optimum" water content varies with different soils from 4 per cent. (sandy) to 120 per cent. (muck). The apparent specific gravity or volume, the rate of evaporation, and some other physical features are also definitely related to the moisture content, changing in a marked way as the optimum water content is passed. It is also shown that the optimum moisture does not vary with the plant, but what is best for one plant is best for another in a given soil. Probably the penetrability of the soil is the important factor, since roots are thus able to reach their maximum development, and so to offer the largest possible surface for the admission of water.

Another bulletin, by GARDNER,[5] reports a vast number of experiments on

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[4] CAMERON, F. K., and GALLAGHER, F. E., Moisture content and physical condition of soils. U. S. Dept. Agric., Bureau of Soils, Bull. 50. pp. 70. *figs. 33.* January 31, 1908.

[5] GARDNER, F. D., Fertility of soils as affected by manures. *Idem*, Bull. 48. pp. 59. *figs. 5.* March 21, 1908.

the effects of various fertilizers, including stable and green manures, upon wheat seedlings grown in pots. These were checked by field experiments, the results being mainly concordant. Here is presented the largest number of experiments yet made under uniform conditions, and while the conditions are still too complex for full analysis, the trend of the results is clear. Though in certain cases the composition of the soil as modified by the fertilizer is an important factor, it is rarely so important as the physical change. In very many cases, indeed, the crop yield can be as greatly increased by proper manipulation of the soil as by adding any sort of fertilizer. The experiments also indicate that the fertilizing of a particular field or region is a local problem, since even the same soil "types" from different localities show different results with the same fertilizer. (This may also be taken to indicate that the basis of classification of soils used by the Bureau is unnatural.)

Everyone who is interested in the growth of plants, either theoretically or practically, should read and reflect on these bulletins.—C. R. B.

Reduction and fertilization in Polytrichum.—The mosses have received practically no attention from cytologists. The small nuclei and some difficulties in technique are doubtless responsible for this neglect. A paper by the Drs. VAN LEEUWEN-REIJNVAAN[6] presents the results of an extended investigation of *Polytrichum piliferum*, *P. juniperinum*, *P. formosum*, and *P. commune*.

In spermatogenous tissue the nucleus contains a large deeply staining mass from which the chromosomes arise. From this mass there is cut off a small body which passes out of the nucleus into the cytoplasm and divides to form two centrosomes. These behave like typical centrosomes, and in the telophase are included within the nuclear membrane. At the last mitosis they remain in the cytoplasm and become blepharoplasts. At the same time a large piece of chromatin, which may be called a *Nebenkern*, is cut off and cast out into the cytoplasm, where it gradually degenerates.

In the sporogonium the mitoses show 12 chromosomes, 4 long, 4 short, and 4 medium. In the gametophyte there are 6 chromosomes, of which 2 are long, 2 short, and 2 medium. At the last spermatogenous division the 6 chromosomes unite in pairs, fusing longitudinally, so that one counts 3 chromosomes. Hence, the sperm contains 3 chromosomes, one long, one short, and one medium. At the division of the central cell of the archegonium, the ventral canal cell and egg cell each contain 3 chromosomes, one long, one short, and one medium. These two cells fuse with each other, and the egg, formed in this manner, is fertilized by two sperms. The fertilized egg contains 12 chromosomes, 3 from the egg proper, 3 from the ventral canal cell, and 3 from each of the two sperms. The

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[6] VAN LEEUWEN-REIJNVAAN, J. and W., Ueber eine zweifache Reduktion bei der Bildung der Geschlechtszellen und darauf folgende Befruchtung mittels zwei Spermatozoiden und über die Individualität der Chromosomen bei einigen Polytrichum-arten. Recueil Trav. Bot. Neerl. **4**: (pp. 44. *pls. 2*). 1907.

writers believe that this behavior of the chromatin in Polytrichum supports the theory of the individuality of the chromosomes.

Commenting upon the above results from the standpoint of one not personally familiar with mitotic figures in mosses, abundant confirmation is needed before the account as a whole can be accepted. We are inclined to believe that the observations are largely correct and that the situation is extremely interesting, but that the final interpretation will not be so widely divergent from current notions of reduction and fertilization as the one proposed.—CHARLES J. CHAMBERLAIN.

Ginkgo.—Under the broad title *Ginkgo biloba* SPRECHER[7] gives a rather full account of the genus, arranged according to the following outline: embryo, young plant, leaf, secondary structure, flowers, pollen and fertilization, geographical distribution, uses and culture, fossils, and conclusions. Instead of giving a historical résumé followed by his own investigations, he has simply followed the above outline, using the available accounts and illustrations, and then filling in the gaps from his own investigations. With so large a subject and so many gaps to fill, an exhaustive investigation of any particular feature could hardly be expected. Most of the original work deals with floral development, leaf development, and anatomy. While the author has studied the gametophyte, it is in this field that he is most indebted to previous investigators. A large number of abnormalities in ovules, stamens, and sporophylls are recorded.

Of course there must be a guess at the phylogeny. While the sperms and certain characters of the ovules resemble those of cycads, in most respects Gingko is nearer the Taxaceae. Both Ginkgo and the Taxaceae have come from a Filicales stock which has given rise to the Cycadophytes and also to the Cordaitales and Ginkgoales, the point of departure being in the neighborhood of the fossil Botryopteridaceae.

The book will be useful for reference. It should be regarded as a compilation, supplemented by extensive personal observations, rather than as a work in which research is the predominant feature.—CHARLES J. CHAMBERLAIN.

SHAW[8] has investigated the vascular anatomy of the ovulate strobilus of Ginkgo, chiefly with reference to the morphological nature of the "collar." From aberrant material, which seems to appear abundantly enough under Japanese cultivation, it has been inferred that this collar is a much reduced megasporophyll. From this current view SHAW dissents, on the basis of testimony obtained from the vascular anatomy. The vascular tissue of the collar is "inverted," and a comparison with Lagenostoma shows a similar situation in that seed. The author therefore suggests that the collar of the Ginkgo ovule is a vestige of the well-developed cupule found investing the seeds of many of the Cycadofilicales. —J. M. C.

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[7] SPRECHER, ANDREAS, Le *Ginkgo biloba* L. pp. 208. *figs. 225*. Genève. 1907.

[8] SHAW, F. J. F., A contribution to the anatomy of *Ginkgo biloba*. New Phytol. 7:85–92. *figs. 16–18*. 1908.

Heliotropic tone.—PRINGSHEIM discusses in a long and rather technical paper the influence of illumination upon heliotropic tone.[9] By heliotropic tone he means that internal condition of responsiveness which determines the position of the cardinal points of reaction—the liminal and optimal illumination both for positive and negative response, and the indifferent zone. He shows that the reaction time of heliotropic plants diminishes with increasing intensity of light, rapidly at first, then more slowly and finally becomes constant. Beyond this a false optimum (really temporary indifference) is reached, but only in plants grown in the dark. If such plants, however, after being taken from the dark are rotated for a time in a light to which they will later react, the indifference disappears and the reaction, contrary to the earlier statements, is actually accelerated. This reaction, by a plant attuned to a certain light, is indeed the speediest possible at that intensity. In fact during the first part of the illumination of a plant of low heliotropic tone, the direction of the light is of no significance; for whether rotated or even illuminated from the opposite direction, it reacts just as quickly as though continuously illuminated from one side. The same is true in plants of high tone with stimuli of low intensity. During this first period the plant is merely adjusting its tone to the illumination. This alteration of tone is to be considered as an effect upon the excitable structure itself, produced either by a like or an unlike stimulus. One must distinguish between accommodation or adjustment to a given illumination and *Umschaltung* which determines whether the reaction is to be positive, negative, or none. This *Umschaltung* is dependent on the difference between the existing tone and that corresponding to the intensity of the illumination. If a low-toned plant be brightly lighted it reacts negatively; if weakly, the response is positive. If a high-toned plant is brightly illuminated, it reacts positively; with weak light, it does not respond at all until the tone has fallen far enough, when a positive reaction occurs. The tone in both cases follows the intensity of the illumination, but rises more quickly than it falls. All hypotheses which predicate heliotropic tone as a constant are faulty. The phenomena line up with those already known in certain other organisms and in the human retina, whence it seems probable that they are part of a general physiological law as to light perception.—C. R. B.

Geotropism and heliotropism.—The mutual effect of geotropic and heliotropic stimulation has been the subject of several papers, notably those by WIESNER, NOLL, and CZAPEK. VON GUTTENBERG, working in PFEFFER'S laboratory, has lately attacked the problem whether or not when they operate simultaneously on parallelotropic organs an alteration of geotropic tone occurs.[10] He concludes, contrary to other interpretations, that it does not, finding it possible by choosing

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[9] PRINGSHEIM, ERNST, JR., Einfluss der Beleuchtung auf die heliotropische Stimmung. Beitr. Biol. Pfl. 9:263–306. 1907.

[10] VON GUTTENBERG, H. RITTER VON, Ueber das Zusammenwirken von Geotropismus und Heliotropismus in parallelotropen Pflanzenteilen. Jahrb. Wiss. Bot. 45:193–231. 1907.

an appropriate intensity of light in each case to balance the gravity stimulus without any effect on geotropic sensitiveness itself. Thus in the coleoptile of *Avena sativa* light of about 55 meter-candles, in the hypocotyls of *Brassica Napus*, *Lepidium sativum*, and *Agrostemma Githago* respectively 525, 666, 1026 m.-c., compensates gravity when each stimulus acts at 90°. When equivalent light acts at right angles to gravity (plants vertical, light horizontal) the parallelotropic organs take a resultant position, departing about 45° from the direction of each. On the elimination of the one-sided action of gravity by the clinostat, however, they become parallel to the light rays; but even in the final position of rest they have not lost their sensitiveness to gravity.

The geotropic series of reactions is quicker than the heliotropic, when the light is reduced to the compensating point; consequently, when light and gravity act antagonistically, the geotropic curvature appears first, and the maximum of heliotropic stimulation does not appear until much later. While these results are strictly true only for the plants observed, yet the principle is probably valid for others.—C. R. B.

Development of Juniperus.—Two preliminary accounts of fertilization in Juniperus were noted in this journal (**40**:318. 1907). The two accounts differed mainly in regard to time relations, NORÉN stating that the interval between pollination and fertilization was over a year, while SLUDSKY claimed that the development from megaspore to embryo occupies only a single summer. The present account[11] shows that NORÉN was right, SLUDSKY having made a mistake in estimating the age of the cones. The pollen grain in the uninucleate condition reaches the nucellus the middle of June and soon divides into a tube cell and generative cell, the latter remaining undivided until the following May, when it forms the stalk and body cells. Early in July the body cell gives rise to two equal male cells. In the nucellus there are several sporogenous cells, only one of which divides to form megaspores, the others becoming a nutritive jacket about the functioning megaspore. Usually only three cells of the tetrad are formed. In the archegonium there are four neck cells; and a ventral canal nucleus is formed, but never becomes separated from the egg by a wall. Fertilization occurs about the middle of July and the fusion nucleus passes to the bottom of the egg, where three mitoses give rise to eight free nuclei which become arranged in two zones. Walls now appear and the cells of the upper zone divide to form the rosette and suspensor.

The account is very full, cytological details of reduction and fertilization being figured and described.—CHARLES J. CHAMBERLAIN.

Hygroscopic movements of living leaves.—The leaves of some species of Rhododendron exhibit variation movements which follow the recurrence of freezing and thawing weather. The usual position of the leaves is horizontal, with the blade expanded. At freezing temperatures the edges of the leaves curl

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[11] NORÉN, C. O., Zur Entwickelungsgeschichte des *Juniperus communis*. Uppsala Universitets Årsskrift **1907**:1–64. *pls. 4*.

under and the petioles allow drooping to occur. With the recurrence of thawing weather the blades expand and the leaf resumes its horizontal position. HANNIG[12] has found that the rolling of the leaf is due to a loss of imbibition water by the cell walls, and especially by the walls of the spongy parenchyma. The movements may be artificially induced by conditions which cause the cell walls to lose water and so allow a contraction of the walls to occur. The formation of ice, excessive transpiration, etc. are such conditions. The author is inclined to regard this as the first known instance of hygroscopic movements by living leaves. To the reviewer it seems that he has made a closer analysis of the cause of the movements, and his discovery consists in showing that while turgor variation is a prominent and accompanying feature, the real cause is the fluctuation in the content of imbibition water in the cell walls. It seems likely that many of the leaf movements which have hitherto been regarded as due to turgor changes may later be found to be caused by swelling and shrinkage of the cell walls. The author has not overlooked the fact that some leaves whose structure is apparently as well adapted to such movements as those of Rhododendron do not exhibit them.—RAYMOND H. POND.

Embryo sac of Nymphaea advena.—Miss SEATON[13] has examined the embryo sac of this species, giving an account of its earlier stages. Abundant material has enabled her to fill in some desirable details. The archesporium is distinguishable before the integuments begin to develop; and by division of the parietal cell and the epidermal cells the functioning megaspore becomes covered by a sterile nucellar cap six to ten cells deep. The sac develops a conspicuous tubular prolongation into the chalaza, and the fusion nucleus rests in the narrow connection between this chalazal haustorium and the broader micropylar portion of the sac. At the first division of this nucleus there is no wall (contrary to previous observation), and one of the daughter nuclei passes to the end of the chalazal tube. As before reported for the family, the proembryo is spherical and almost completely invested by endosperm. The monocotyledonous character of Nymphaeaceae is inferred, but no new evidence for it is advanced. This claim, which habitually accompanies the recent studies of Nymphaeaceae, is founded upon certain rigid preconceptions as to what constitutes a monocotyledon. It might be well for investigators of this group to try the effect of their work upon the rigidity of the old definitions.—J. M. C.

Araucarians of the Atlantic coastal plain.—BERRY[14] has called attention anew to the wide distribution of araucarians in the Mesozoic, especially as contrasted with their present very restricted range. A Mesozoic distribution of the

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[12] HANNIG, E., Ueber hygroskopische Bewegungen lebender Blätter bei Eintritt von Frost und Tauwetter. Ber. Deutsch. Bot. Gesells. **26a:** 151–166. 1908.

[13] SEATON, SARA, The development of the embryo sac of *Nymphaea advena*. Bull. Torr. Bot. Club **35:** 283–289. *pls. 18, 19.* 1908.

[14] BERRY, EDWARD W., Some araucarian remains from the Atlantic coastal plain. Bull. Torr. Bot. Club **35:** 249–260. *pls. 11–16.* 1908.

group from Greenland to Patagonia in the western hemisphere and from Spitzbergen to Cape Colony in the eastern is to be contrasted with its present occurrence in South America and the Australasian region. This means that araucarians have disappeared from North America, Europe, Africa, and practically all of Asia. Recent investigations in the Atlantic coastal plain show that the group not merely occurred in that region during the Mesozoic, but was abundant, perhaps the most abundant coniferous type of the older Mesozoic. From this region BERRY describes three new species: *Araucarites Zeilleri*, from New Jersey; *Araucaria bladenensis*, from North Carolina to Alabama; and *Araucaria Jeffreyi*, from North Carolina.—J. M. C.

Embryo sac and embryo of Urticaceae.—MODILEWSKY[15] has examined twelve genera of Urticaceae (Urtica, Elatostema, Laportea, Urera, Parietaria, Fleurya, Boehmeria, Dorstenia, Morus, Celtis, Cannabis, and Humulus), and finds that the embryo sac and embryo are in general of the ordinary dicotyledonous type. *Elatostema sessile, Dorstenia drakeana*, and *D. contrayerva* are said to be parthenogenetic, and *Celtis occidentalis* is chalazogamic. In the species of Dorstenia and in *Urtica cannabina* the antipodals multiply, but finally disappear. The polar nuclei fuse very early, and in Elatostema endosperm formation occurs without polar fusion. In *Urtica cannabina* a conspicuous antipodal haustorium is developed, and a much smaller one appears in *U. urens*. Many other details are recorded, but they are of no special significance.—J. M. C.

Black rot.—The black rot of the grape is the subject of a recent bulletin by REDDICK and WILSON,[16] which is mainly popular in nature, and is well illustrated and clear. The spores germinate on the vines only in the presence of water. Infection is noticeable after a period of twelve to twenty days, or upon the berry in eight to fourteen days. After discussing the control, it is stated that four acres, well sprayed, made a gain of 1662 pounds, equalling a saving of $32.95 per acre. It is recommended that mummied fruit be picked to avoid the spread of the disease, that the ground be turned over as completely as possible, to bury rotted berries, and that the vines be sprayed with Bordeaux mixture, as has been recommended heretofore.—F. L. STEVENS.

Leaves in autumn.—TSWETT summarizes the knowledge regarding the emptying of leaves in autumn thus.[17] It may be considered as settled that the nitrogenous compounds diminish and are carried back, proteolysis simplifying the proteins to this end; results as to phosphorus compounds are more contradict-

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[15] MODILEWSKY, JAKOB, Zur Samenentwicklung einigen Urticifloren. Flora **98**: 423–470. *figs. 71.* 1908.

[16] REDDICK, DONALD, and WILSON, C. S., The black rot of the grape, and its control. Cornell Univ. Agric. Exp. Sta., Bull. **253**:367–388. April 1908.

[17] TSWETT, M., Ueber die Verfärbung und die Entleerung des absterbenden Laubes. Ber. Deutsch. Bot. Gesells. **26a**:88–93. 1908.

ory, with the weight of evidence in favor of their recovery; the removal of salts needs thorough investigation.

As to the autumnal pigments, he reports[18] that the yellows are due to a new pigment or group of pigments, which he proposes to call autumnal xanthophyll. He regards it as probably a decomposition product of the "normal xanthophylls, perhaps also of the carotin."—C. R. B.

Torreya in the Cretaceous.—BERRY[19] has described a new species of Torreya (*Tumion carolinianum*) from the Cretaceous of North Carolina, based on leaf-bearing branches, the leaves showing the distribution and character of the stomata. The genus exists today as isolated species, which are widely separated geographically, and this fact alone would suggest an ancient type. The discovery of intermediate stations will bring a knowledge of the time of general distribution and help settle the question of relative antiquity.—J. M. C.

Phylogeny of pteridophytes.—Lady ISABEL BROWNE[20] has begun a series of papers intended to bring together the large volume of recent work on the vascular anatomy of pteridophytes, and apply it to a consideration of the phylogeny and interrelationships of the group. This is a very useful service, for it organizes the scattered facts in convenient form, whether one accepts all the inferences or not. In the first two papers, the Sphenophyllales and Equisetales are presented and Lycepodiales begun.—J. M. C.

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[18] TSWETT, M., Ueber das Pigment des herbstlich vergilbten Laubes. Ber. Deutsch. Bot. Gesells. **26a**:94–101. 1908.

[19] BERRY, EDWARD W., A mid-Cretaceous species of Torreya. Am. Jour. Sci. **25**:382–386. 1908.

[20] BROWNE, ISABEL, The phylogeny and interrelationships of the Pteridophyta. A critical résumé. New Phytol. **7**:93–113, 150–166. 1908.

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OCTOBER 1908

ARE THERE FOLIAR GAPS IN THE LYCOPSIDA?[1]

EDWARD C. JEFFREY

(WITH PLATES XVII AND XVIII)

Six years ago the present writer published an account of his studies on the stem of the pteridophytes and gymnosperms.[2] In the conclusions not only these large groups were considered, but also the remaining vascular plants, which had been the subject of earlier investigations. The general result was reached "that there are two phylogenetic types of tubular central cylinder, namely, that in which only ramular gaps are present, and that in which both ramular and foliar gaps occur." Further it was stated: "The use of these constant and characteristic anatomical features results in the division of the Vasculares into two great primitive stocks—the Lycopsida, which are cladosiphonic and palingenetically microphyllous, and the Pteropsida, which are phyllosiphonic and palingenetically megaphyllous. The Lycopsida include the Lycopodiales and Equisetales. The Pteropsida include the Filicales, Gymnospermae, and Angiospermae." The opinion was expressed that the Lycopsida and Pteropsida "appear to have been separate back to the beginning of the period when the paleontological record begins." Since the publication of that memoir, the writer has been busily engaged in other directions, and his time has been fully taken up. In the interval a great deal of literature has appeared, especially in European countries, on the anatomy and phylogeny of vascular plants, and not unnaturally the writer's hypothesis has been subjected to the criticism which is the fate of every scientific hypothesis. The most vigorous objections to

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[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 14.

[2] Phil. Trans. Roy. Soc. London B. 195:119–146. 1902.

the hypothesis, as might be expected, have been raised by those whose published views are prejudicially affected by its validity. In spite of all that has been written on the subject, however, the author has seen no reason to modify his standpoint in any essential feature. It is proposed in the present article to deal with some of the objections, mainly resulting from a misapprehension of the author's statements or an unfamiliarity with the anatomical field, which have been raised against the Lycopsida. In a subsequent article the Pteropsida will receive consideration.

It will perhaps be well at the beginning to define the Lycopsida and Pteropsida in a comprehensive way and to include external characters as well as anatomical ones.

LYCOPSIDA.—Palingenetically microphyllous vascular plants, with ventrisporangiate sporophylls (sporangia adaxial), the tubular central cylinder when present characterized by the entire absence of gaps or interruptions in the fibrovascular tissue immediately above the outgoing leaf-traces.—Lycopodiales, Psilotales, Equisetales, Sphenophyllales.

PTEROPSIDA.—Palingenetically megaphyllous vascular plants, with dorsisporangiate sporophylls (sporangia abaxial), the tubular central cylinder when present characterized by foliar gaps or interruptions in the fibrovascular tissues immediately above the outgoing foliar traces.—Filicales, Gymnospermae, Angiospermae.

It is necessary to define very clearly, on account of numerous misconceptions and misunderstandings, the nature of a foliar gap, for the writer's critics have shown considerable versatility of misunderstanding in regard to this important feature. In one of the more simply organized ferns (Ophioglossum, Osmunda, Schizaea, Mohria, Adiantum, etc.), wherever a leaf passes off from the surface of the stem, it carries with it a fibrovascular strand, the leaf-trace. The foliar trace is derived from the tubular central cylinder of the stem, and as it bends away from the surface of the stele in its outward and upward course, it causes immediately above it, in the stelar wall, an interruption of the fibrovascular tissues, known as the leaf gap. The foliar gap may be distinguished from other gaps in the wall of the fibrovascular hollow cylinder by the fact that it occurs immediately above a leaf-trace. A true foliar gap, moreover, is always related to but a single leaf-trace. If several traces appear in relation to a stelar gap, and especially if they are related to the *sides* of the gap, it may be concluded at once that no true foliar gap is present. It may be added for the benefit of inexperienced anatomists that not all gaps in the wall of the central cylinder are foliar gaps. Where the fibrovascular tissues are much reduced in amount, as is not unfrequently the case, they often break up into a loose meshwork, which has no necessary relation to the vascular supply of the leaves or the branches.

LEPIDODENDREAE AND SIGILLARIAE

In the memoir cited above, the writer has called attention to the fact that in the Lepidodendreae, which are among the oldest of the Lycopsida, there are no foliar gaps in the tubular central cylinder, when present. *Fig. 9* illustrates this feature in *Lepidophloios Harcourti.* Below in the figure is to be seen the woody cylinder, showing inferiorly some of the thin-walled tissue of the pith. The cylinder is dentate on its outer surface, and the teeth are composed to some extent of small-celled protoxylem. Outside the wood may be seen nests of small cells, which mainly lie in the intervals between the dentations. These are the foliar traces. It is clear that there are no gaps or interruptions in the central cylinder corresponding to these. Consequently it may be stated that there are no foliar gaps in the species figured. An examination of a considerable number of sections of lepidodendrid stems has made it clear that foliar gaps are absent in the group.

In the older Sigillariae the primary wood in the stem ordinarily formed a continuous cylinder, and there were, as in Lepidodendron, no gaps of any kind except for the outgoing strands of branches. In more modern Sigillarias, however, the woody cylinder was frequently entirely or partially broken up into separate strands. *Sigillaria elegans* from the Lower Coal Measures had the continuous type of woody cylinder, while *S. Menardi* from the Permian had separate strands of wood constituting its tubular stele.[3] The leaf-traces in both types of Sigillaria stem, however, passed off without leaving any foliar gaps in the central cylinder, for in the Sigillarias of the more

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[3] KIDSTON, R. Internal structure of *Sigillaria elegans*. Trans. Roy. Soc. Edinburgh 41:533–550. 1905.

modern type, with the cylinder broken up into numerous bundles, the gaps between the strands were not subtended by the leaf-traces, which took their origin from the face of the fibrovascular bundles. This fact it is very important to keep in mind, in view of the conditions to be found in some of the reduced Lycopsida to be described later. It is further of interest to note that these arboreous lycopods, in which the leaves were sometimes a meter in length, offer no exception in their anatomical structure to the writer's definition of the Lycopsida.

LYCOPODIACEAE

Under this heading Lycopodium itself need not be considered, as it has a solid protostelic central cylinder. Phylloglossum, however, has a tubular stele, which in the lower tuberous portion of the stem constitutes in cross-section an almost continuous horseshoe of xylem, without foliar gaps for the relatively large radical leaves (protophylls). The opening in the horseshoe corresponds to the outgoing strand which passes into the resting tuber, forming the next year's plant. Above the tuber the stem of Phylloglossum passes into the slender peduncle of the cone. In this region of the stem the fibrovascular tissues separate into a number of distinct strands, comparable to those found in the axis of the less ancient Sigillarias. *Fig. 8* is a copy of a figure by BERTRAND,[4] showing the manner in which these isolated peduncular strands give rise to the traces of the lower sporophylls of the cone. It will be noted on the lower side of the figure that the bundles are much elongated radially. In such cases they are about to give off sporophyll traces. In the upper part of the figure three outgoing traces are seen, in different degrees of detachment from their corresponding peduncular strands. On the left, one of the traces has turned obliquely after leaving the peduncular strand, so that it nearly subtends the hiatus between two peduncular strands. An inattentive observer might readily interpret the hiatus as a real foliar gap. Only a consideration of the mode of origin of the trace from the peduncular strand makes the real condition of affairs apparent. There are clearly no foliar gaps present, else the peduncular strands would fork above the outgoing traces. The conditions in the upper part of the stem of Phylloglossum are clearly similar to those obtain-

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[4] Phylloglossum. Archives Bot. du Nord de la France 1885:112. *fig. 102.*

ing in a Sigillaria with separate fibrovascular strands. In the cone of Phylloglossum individual sections often present an appearance still more misleading. In *fig. 10* is shown such a condition. A horseshoe-shaped fibrovascular mass appears in the center, and opposite its opening a sporophyll trace. To the right and left below are two other foliar traces. An inexperienced anatomist might readily conclude that the gap opposite the uppermost trace was a true foliar gap. *Fig. 11* shows a section from another cone, with two such apparent foliar gaps, one on each side, each apparently subtended by its corresponding leaf-trace. *Fig. 12* shows another section from the same cone, a small fraction of a millimeter lower down. It is here to be noted that the foliar trace on the right in the preceding figure joins the *face* of the large cauline fibrovascular strand, forming the same radially elongated mass as is characteristic of the outgoing sporophyll traces shown in *fig. 8* from the peduncle. Still lower down, as was learned from the study of serial sections, the foliar strand on the left joined the outside of its cauline strand in a similar manner. A study of the cone of Phylloglossum has shown that the traces for the sporophylls invariably pass off from the outer surface of the central cylinder without leaving any real foliar gaps. Sometimes two or even three traces may originate along the margins of the same hiatus in the stele. The interruptions in the central cylinder or stele are no more to be regarded as foliar gaps than are the corresponding ones in certain Sigillarias. It is obviously impossible with any clear eye to anatomical relations to regard the perforations which exist in the upper part of the fibrovascular system of the stem in Phylloglossum as being of the nature of foliar gaps. Miss SYKES has recently reached the conclusion that the living Lycopodiaceae originated in all probability by reduction from the more complex arboreous lycopods of the Paleozoic period.[5] Without presuming to indorse this view, it may be pointed out that it stands in the way of presumably reduced modern lycopodineous forms in any case possessing the foliar gaps which were denied to their supposed Paleozoic ancestors, which possessed very much larger leaves.

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[5] Morphology of the sporangium-bearing organs in the Lycopodiaceae. New Phytologist 7:41–60. 1908.

PSILOTACEAE

Fig. 6 shows a magnified view of the stem of *Tmesipteris tannensis*, as viewed in transverse section. On the lower left side is a blunt projection from the surface of the stem, the base of a sporophyll.[6] At the top of the figure is another sharper projection, which is the basal portion of a foliage leaf. Subtending each of the projections from the surface of the stem noted above is a fibrovascular strand, which has recently come off from the central cylinder. *Fig. 7* shows part of the foregoing more highly magnified, to make clear the relations of the outgoing traces to the stele of the stem. With the greater magnification an additional trace can be seen emerging from the central cylinder on the lower right hand. In passing out none of these three traces subtends a gap in the central cylinder, which in this region is a continuous fibrovascular tube. In the upper region of the stem, particularly where it gives rise to sporophylls, as BERTRAND has pointed out,[7] the central cylinder breaks up into separate strands, much as happens in the upper part of the axis of Phylloglossum. In isolated transverse sections one often sees appearances such as are represented in *figs. 10* and *11* of the present article. On the strength of such evidence Miss SYKES[8] has asserted that there are foliar gaps in Tmesipteris. Her own figures, however, cannot be reconciled with this statement. On page 71 she represents sections taken at various heights through a portion of the stem, and makes a diagram of the bundle arrangement in this region. According to her figures the gaps are mainly on one side of the central cylinder or stele, and no less than three traces are related to one of these, that is, they are derived from the fibrovascular strands along its *lateral* margins. Three other traces originate near smaller stelar lacunae and one comes off remote from any gap. A greater inconstancy in the mode of origin of traces could scarcely be imagined. A general acquaintance with fibrovascular anatomy should make it clear that true foliar gaps in the same region of the stem should be nearly of a size and should occur immediately *above a single* leaf-trace. This state of affairs is

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[6] Miss SYKES prefers to regard this as a *fertile branch*.

[7] Recherches sur les Tmesipteridées. Archiv. Bot. du Nord de la France 30:—. 1882.

[8] Anatomy and morphology of Tmesipteris. Annals of Botany 22:63–89. 1908.

very far from being realized in Tmesipteris as described by Miss SYKES. The conditions are in fact the same as those found in the corresponding region of the stem in Phylloglossum. Miss SYKES has been so good as to loan her sections, and the series, although not complete, vouch for the general accuracy of her figures. One fact of importance appears, however, to have escaped her notice, although it is clearly indicated in the sections, namely, that in every case the outgoing strands of appendages originated *opposite* the strands of the central cylinder and did not subtend any gap *at their point of origin*, although some of them by a subsequent oblique course, as in Phylloglossum, seemed to subtend the stelar gaps. Appearances of this kind have been brought to the attention of Professor BOWER, and he figures one such section on page 420 and again on page 487 of his recent work.[9] He expresses the opinion that his figure overthrows the hypothesis of JEFFREY on the lycopsid side. He further adds in a footnote: "The Botryopterideae are not phyllosiphonic; thus the anatomical distinction of JEFFREY breaks down on both sides." In this added statement he is even less happy than in the original one, for he is apparently unaware that ferns with a protostelic central cylinder cannot possibly be phyllosiphonic, that is, possess foliar gaps. In all of the Botryopterideae in which the origin of the foliar strands has yet been described the central cylinder is protostelic. Professor BOWER is in general not entirely at home in discussing anatomical facts. As a further example of this, may be cited his statement that *Alsophila excelsa*, as described by GWYNNE-VAUGHAN, shows a "transition from the cladosiphonic to the phyllosiphonic" condition in the young plant. Professor TANSLEY in a review of Professor BOWER's book[10] very properly criticizes this singular misunderstanding in the following words: "Mr. GWYNNE-VAUGHAN will be probably surprised to learn that he has shown a 'transition from the cladosiphonic to the phyllosiphonic' state in *Alsophila excelsa*. What really exists, of course, is a transition from protostely to siphonostely, and protostely is not a monopoly of the microphyllous forms, but is found equally among the primitive ferns." It cannot be too strongly emphasized that, especially in difficult cases,

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[9] The origin of a land flora. London. 1908.

[10] New Phytologist 7:126. 1908.

like those occurring in the reduced Lycopsida, thin serial sections are necessary to a proper understanding of the real anatomical relations. It may be stated in conclusion that there are no real foliar gaps in Tmesipteris and that statements as to their presence depend on errors of observation and interpretation.

In Psilotum leaf-traces are absent in the case of the vegetative leaves, but as the angles of the stellate central cylinder subtend the ridges of the stem from which the leaves take their origin, there can be no question of the presence of foliar lacunae in this genus. Traces are present in the case of the sporophylls, but as these in general occur on the smaller terminal branches, where the stele is solid, they do not serve to elucidate the subject. It is of particular interest that the leaf-traces should sometimes disappear altogether in the case of the small-leaved forms (the Lycopsida). The writer has called attention to this condition as occurring in the case of the basal foliar sheaths of the smaller branches of Equisetum.[11]

EQUISETALES

It is in regard to the supposed existence of foliar gaps in the equisetal series that the writer has received the most weighty criticism. Dr. SCOTT in his masterly treatment of Paleozoic botany in *Progressus rei botanicae,* adopting the present author's division of vascular plants into two phyla, the Lycopsida and Pteropsida, states that it is "open to much criticism; the general grouping however has sufficient claims to be a natural one, to afford at any rate a basis for the discussion of affinities." The only feature "open to criticism" upon which Dr. SCOTT lifts the veil is in regard to the absence of foliar gaps in Equisetum. His words are as follows: "The absence of foliar gaps, upon which JEFFREY lays stress, may hold good in the case of Archeocalamites, but if I rightly interpret the structure, they are present in the Calamariaceae as well as in the recent genus." It will be the writer's task to show that not only are foliar gaps absent in the older genera of the Equisetales, but that they also do not occur in the living genus Equisetum.

Professor CAMPBELL'S criticism of the present writer's work on

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[11] Structure, development, and affinities of Equisetum. Boston Soc. Nat. Hist. Memoirs 5: no. 5. p. 176.

Equisetum[12] carries less weight on account of his lack of first-hand familiarity with the extinct members of the Equisetales, a necessary basis for the discussion of a group which has its history so largely in the past. His first objection is that the vascular system of Equisetum is, on the basis of growing point development, of cortical origin and consequently cannot belong to the central cylinder, a term which in this case, according to Professor CAMPBELL, must be restricted to the pith, since it alone takes its origin from the sacrosanct region of the plerome. It is perhaps too late to discuss conclusions drawn from growing point morphology; they often lead rather to a *reductio ad absurdum* than to any useful or logical results. Professor BOWER has set a very good example in his recent book in throwing the growing point theory and the octant theory overboard.[13] Professor CAMPBELL sees no reason why there should be an attempt to reduce the vascular system of Equisetales to either of the types found in the other phyla of the pteridophytes. He further adds that the equisetal series presents resemblances which "indicate a real although extremely remote relationship with the lower ferns," thus committing the very error he previously condemned. Professor CAMPBELL also attaches a good deal of importance to the presence of multiciliate antherozoids as an indication of affinities, and regards this feature both in the Equisetales and Isoetaceae as indicative of filicinean affinities. His views in both instances are at variance with those of modern paleobotanists.

It will be well in our discussion of the Equisetales to begin with the living genus and thence go backward, for only in the living form is it possible to study the anatomical relations with necessary completeness. The reproductive axis of Equisetum will also afford a better starting-point than the vegetative, since it is a well-established principle of the new morphology that the reproductive structures are more likely to retain ancestral characters than the vegetative ones. *Fig. 3* shows a longitudinal section through one of the fibrovascular strands of the cone of *Equisetum telemateia*, at a region where a trace is being given off to a sporophyll. It will be noticed that the sporophyll trace passing off on the left of the figure goes outward and

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[12] Affinities of the genus Equisetum. Amer. Nat. 39:273–285. 1905.

[13] Origin of a land flora, chaps. 14 and 42.

upward, without causing any break in the continuity of the fibrovascular strand of the axis from which it is derived. On the inner side of the axial strand is to be seen a longitudinal space, the protoxylem lacuna. This is continuous through the nodal region in the cone, although in the vegetative axis, as will appear below, the lacuna is interrupted below each so-called zone of nodal wood. The condition of continuity through the nodal region presented by the protoxylem lacuna in the cone of Equisetum is paralleled by similar conditions described by WILLIAMSON in the nodal region of Calamites. *Fig. 2* represents a transverse section through the cone of the same species of Equisetum which makes clear the topography of the sporophyll trace and its corresponding axial strand as seen in this plane. There is no indication of any gap in the strand of the axis corresponding to the outgoing leaf-trace, which exactly subtends it. The examination of a large number of sections has convinced the author that foliar gaps do not in any case occur in the cone axis of Equisetum in connection with the passing-off of the traces of the sporophylls. The sporophyll trace is only about one-third to one-fourth the magnitude of the axial strand from which it arises, and consequently if any indication of a gap were present it would be clearly recognizable. *Fig. 1* shows a general view of a cross-section of the cone of *Equisetum telemateia*, indicating the relation of several sporophyll traces to their corresponding axial bundles. In the cone the foliar traces are vertically somewhat displaced on account of the crowded arrangement of the peltate sporophylls, so that even in accurately transverse sections all of them are not cut at the same level. On the left of the figure a trace has recently left its corresponding axial strand. The next foliar trace to the right is much farther out in the cortex than the first. The interval, corresponding to the next axial strand, does not show a trace, as this is not in the plane of section for the reason indicated above. In the case of the fourth trace the conditions are much as they are in the second; while the fifth trace is just leaving its axial strand. It will be seen by inspection of the whole figure that in each case where a sporophyll trace is present, it subtends the axial bundle from which it was derived in the lower part of its course. There is accordingly no foliar gap present. These micro-anatomical results only serve to confirm the statement made by the author, in his memoir on Equisetum, concerning the frequent failure to alternate at the nodes, which is characteristic of the strobilar strands of that genus. This feature is illustrated photographically in *pl. 30, fig. 3*, of the memoir. The author's critics do not appear to have found this evidence sufficient. It is important to insist on the correspondence of the micro-anatomical absence of leaf gaps in the cone of Equisetum with the non-alternation of the axial strands of the cone at the nodes, because in some of the fossil forms we have only the latter evidence to go upon. It is perhaps a wise conservatism on the part of Dr. SCOTT to reject the evidence based on the frequent lack of alternation at the nodes, as seen in preparations of the bundle course in the cone of Equisetum. He can scarcely fail to be convinced by the microscopic demonstration of the absence of foliar gaps which has been given above and as represented in *figs. 1, 2*, and *3*. If it is reasonable to define a foliar gap as a gap in the wall of the stele, or one of its component strands in case the stele is not a continuous hollow cylinder, immediately above a leaf-trace, there are certainly no foliar gaps in the cone of Equisetum. The writer has satisfied himself that foliar gaps do not occur even when there is more or less complete alternation of the strands in the cone. *E. telemateia* has been chosen for illustration on account of the large size of the structures present. Similar results in every way are shown by *E. arvense* and *E. hiemale*.

It is now possible to turn with advantage to the examination of the outgoing foliar traces of the vegetative branches of Equisetum. As is well known, the internodal bundles of one segment of the stem in Equisetum alternate with those of the next, in this respect presenting a contrast to the condition of the strands in the cone and in the more ancient extinct genera of the phylum. The internodal strands of successive segments of the stem are joined in the region of the nodes by the so-called "nodal wood," which consists of a dense mass of short reticulated tracheids forming a completely closed ring. *Fig. 5* shows a longitudinal section through an outgoing leaf-trace and its corresponding cauline bundle. A large lacuna, the protoxylem cavity, is seen on the right of the axial strand. This disappears below the so-called "nodal wood." The outward course of the foliar trace is steeply upward, in contrast to that of the sporophyll trace. Its tracheids obviously take their origin in the region of the protoxylem lacuna and below the "nodal wood." If the usual definition of a node be accepted, as marked by the outgoing leaf-traces, the so-called "nodal wood" of Equisetum in reality is above the node. *Fig. 4* shows a transverse section through a part of the "nodal wood" intervening between the bases of two branches. The leaf-trace lies just outside the mass of reticulated tracheids which compose the wood of the "node." It is obvious that there is no break in the mass of tracheids corresponding to the leaf-trace. Above the incorrectly designated "nodal wood" are the internodal bundles of the next segment of the stem, and between these are parenchymatous gaps, which on account of the alternation of the internodal bundles in different segments are above the leaf-traces, since the latter take their origin from the bundles of the lower internode. Professor CAMPBELL and Dr. SCOTT regard these as foliar gaps. They lack, however, one important feature of foliar gaps, for they do not occur *immediately above the traces*, as should be the case with true foliar gaps. All other foliar gaps with which we are acquainted show this feature. The *onus* of proving that the internodal lacunae of Equisetum are really foliar gaps appears consequently to lie upon the investigators who claim that they are to be regarded as such. It will be clear from the anatomical facts described above that in view of the relation of the leaf-traces to the so-called "nodal wood" it is quite incorrect to designate the ring of tracheids which lies *above* the outgoing leaf-traces as "nodal wood." It can only be called accurately supranodal wood. This distinction is a very important one to make, moreover, on phylogenetic grounds.

As a sequel to the description of the actual anatomical relations of the outgoing leaf-traces of the vegetative stem of Equisetum, it is natural to proceed to the discussion of the evolutionary or phylogenetic significance of the observed facts. The following citation from the memoir on Equisetum may appropriately be introduced at this point: "But STUR has shown that in the Ostrau beds, passing from the lower to the higher strata, a series of forms, *Calamites ramifer* Stur, *C. cistiformis* Stur, *C. approximatiformis* Stur, and *C. ostraviensis* Stur, represents transitions from the bundle arrangement of Archeocalamites, represented in *pl. 1, fig. 15*, to that of Equisetum, represented in *pl. 1, fig. 16.*" It is obvious from the data of STUR, which have never been called in question, that the older Calamites were without the alternation of the strands in the region of the nodes which is characteristic of the more modern Calamites and the stem of the living Equisetum. It will be clear from the description of the anatomical conditions present in the cone of Equisetum that absence of alternation brings with it the complete absence of foliar gaps. The writer in his memoir has suggested that the explanation of the peculiar features of the foliar traces in the vegetative stem of Equisetum is to be found in the past history of the phylum to which it belongs. Dr. SCOTT would probably agree to the soundness of this proposition, for example, in the case of the older living gymnosperms. There appears to be no reason to make an exception in a group which has at least so long a past as the Gymnospermae. In the non-alternating arrangement of the internodal strands, characteristic of the stems of the older Calamites (which is still largely represented in the cone axis of the living genus), there were no foliar gaps immediately above the outgoing foliar traces. As the relations of the internodal strands of one internode to those of the next became changed in the progression from the archeocalamital to the equisetal mode of arrangement, the leaf-traces naturally came to lie opposite the gaps between the internodal strands of the next higher segment of the stem. But with the conservatism which is one of the most interesting characters of leaf-traces in general, they retained in Equisetum their old anatomical relations to the central cylinder of the stem. That is, they still pass off in the vegetative stem of Equisetum without leaving any true foliar gaps. The lacunae in the internodes cannot be regarded as foliar gaps, since they are not *immediately* above the foliar traces, but are separated from them by the depth of the so-called "nodal" wood! The explanation offered is a reasonable one in view of the past history of the group, and on those who do not accept it is placed the burden of some other more reasonable elucidation of the peculiar anatomical relations of the leaf-traces in the genus Equisetum.

The writer is credibly informed that Dr. SCOTT is of the opinion that the internodal gaps in the genus under discussion are *de facto* foliar gaps. This is a somewhat surprising opinion on the part of one whose brilliant investigations on the anatomy of the cycadean peduncle have put the whole subject of the affinities of the cycads with the lower extinct gymnosperms in a new light. Dr. SCOTT from his discovery of centripetal xylem in the peduncles of the reproductive axes of certain living cycads reached the conclusion that their ancestors with strong probability possessed similar bundles in their vegetative stem. This condition is in fact realized in certain of the Pteridospermeae, particularly in Lyginodendron, which Dr. SCOTT regards as a probable ancestor of the cycads. There can be no question that Archeocalamites and Calamites are very much more nearly related to Equisetum than is Lygindodendron or any similar form to the living cycads. It follows that the reproductive axis of Equisetum is much more likely to perpetuate the ancestral characters of its stock than is the cycadean cone. It appears to have been shown above beyond any doubt that the equisetaceous strobilus perpetuates both the non-alternating strands and the complete absence of foliar gaps of the oldest calamitean forms. In the light of these facts there can be no reasonable doubt that the peculiar anatomical relations of the vegetative foliar traces of Equisetum are likewise persistently retained indications of the ancestral condition, for although the shifting of the internodal strands in the course of evolution has caused them to subtend the gaps between the strands of the next upper internodes, they still leave the central cylinder without giving rise to true foliar lacunae, and are moreover separated from their apparent gaps by the whole depth of the supranodal wood. Collateral evidence of the correctness of this view of an even more cogent kind has been discovered, but is reserved for a subsequent communication.

The older members of the equisetal alliance may now be considered. WEISS in one of his superb and classic monographs on the Carboniferous Calamites[14] has published a number of illustrations of calamitean cones. On *pls. 1* and *2* are figures of the genus Stachannularia, which show clearly the phenomenon of non-alternation at the nodes of the cone. *Pls. 3* and *4* show the same phenomenon in the well-known genus Calamostachys. In *pl. 9* a similar condi-

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[14] Steinhohlen-Calimarien, Atlas zu denAbhandlungen Gelog. Specialkarte V. Preussen 2[1]: Berlin. 1871.

tion is figured in the cones of the remarkable genus Cingularia. Our information on the subject of the strobilus of the important calamitean genus Palaeostachya has recently been materially increased by the important investigations of HICKLING.[15] This author states: "From an examination of the numerous sections cut more or less transversely through the node, I feel little doubt that no regular pectination occurred; while on the other hand one or two sections showed features which seemed explicable only on the assumption that an occasional communication (probably irregular) did occur between adjacent bundles." The conditions in this genus of calamitean cone would seem accordingly to have approximated very closely those existing in the strobilus of the modern Equisetum, so far as the course of the bundles in relation to the nodes was concerned. This resemblance is all the more striking because, lower down on the same page, the author states that the sporophyll trace left the axial strand without giving rise to any foliar gap. His words are "*no gap is left in the main bundle*." The italics are those of the present writer. "The main bundle" here means the bundle of the axis from which the sporophyll trace was derived. It will be readily inferred from the various citations given above that, in spite of the conviction expressed by Dr. SCOTT that foliar gaps occurred in the vegetative stem of the Calamites, they must have been generally absent in the cones of the more important calamitean types. There seems accordingly little reason to doubt, when the foliar relations of the more modern Calamites are fully worked out, since the course of their internodal strands resembled that found in Equisetum, that they will prove to be very similar to those of the living genus; and, in view of the similarity shown above in the fibrovascular arrangements of the cone, will be susceptible of a similar interpretation. This follows all the more certainly because so distinguished an authority as Dr. SCOTT himself states, in his *Studies in fossil botany:* "Thus the calamite, so far as anatomy goes, is simply an Equisetum with secondary thickening."

The conditions in Archeocalamites, the oldest calamitean genus, are particularly significant. In this form one of the most characteristic features was the failure of the primary fibrovascular strands of the vegetative stem to alternate at the nodes, as they do in the more

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[15] Anatomy of *Palaeostachya vera*. Annals of Botany **21**:375. 1908.

modern Calamites and in Equisetum. It follows that there could have been no foliar gaps in this genus, if the general anatomical conditions were like those found in the rest of the calamitean stock, as has already been indicated by the present writer in the memoir on Equisetum. Our knowledge of the cone of Archeocalamites is very incomplete and nothing is known of its anatomical structure.

It may be stated with some confidence, if credence is to be attached to the doctrine of descent and to the general principles of modern plant anatomy, that the equisetal stock entirely lacks foliar gaps immediately above the outgoing leaf-traces. Dr. SCOTT's statement that in respect to their vascular anatomy the Equisetales "reach the level of the simpler gymnosperms or dicotyledons" (*Progressus rei botanicae*, p. 157) will apparently, as a consequence, need some revision. There further seems to be no reason to doubt that the Equisetales are quite typical Lycopsida in the sense defined in the writer's two memoirs, and are as a consequence far removed from any mere affinity with any of the pteropsid series.

It may be added that there seems to be no reason at the present time, on anatomical grounds at any rate, to suppose that the Pteropsida had a sphenophylloid or ophioglossaceous origin from the Lycopsida. Neither Pseudobornia, of the reproductive organs of which we know little and of the anatomical structure of which we are entirely ignorant, nor Ophioglossum, of which the characters anatomical and reproductive are entirely filicinean, can serve as a phylogenetic link between the primitively small-leaved ventrisporangiate (adaxial) forms (Lycopsida) and the palingenetically large-leaved dorsisporangiate (abaxial) forms (Pteropsida). As Professor TANSLEY has recently put it in a review of Professor BOWER'S *Origin of a land flora*,[16] "on the general point of the relation of the 'microphyll' to the 'megaphyll,' there is no evidence of any capacity of the microphyll to evolve the megaphyll."

Summary

1. True foliar gaps occur *immediately above* their corresponding leaf-traces and are not *lateral* to the leaf-traces.

2. Foliar gaps are absent in Phylloglossum, although a super-

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[16] New Phytologist 7:125. 1908.

ficial examination of the anatomy of this genus might lead to the conclusion that the perforations in the tubular stele, which are sometimes *lateral* to the outgoing leaf-traces, are to be regarded as true foliar lacunae.

3. Foliar gaps are likewise absent in Tmesipteris, and recent statements as to their presence are based on misinterpretation or misconception. Perforations in the stele are here also found sometimes *lateral* to one or *more* leaf-traces, but these cannot be regarded as true foliar gaps.

4. Foliar gaps are absent in the Lepidodendreae and the Sigillariae, but in the more modern species of the latter perforations of the tubular central cylinder are sometimes found, which have the same relations and are susceptible of the same explanation as are the similar perforations in Phylloglossum and Tmesipteris.

5. Foliar gaps are unquestionably absent in the cone axis of Equisetum, and on the basis of comparative anatomy are absent also in the vegetative stem. Similar statements apply to the reproductive and vegetative axes of Calamites. Archeocalamites has no foliar gaps in its vegetative stem.

6. The Lycopsida as defined by the author are clearly marked off from other plants by a palingenetically microphyllous habit, the absence of foliar gaps in the tubular stele, and by the possession of sporophylls with adaxial sporangia. They constitute a great natural phylum.

In conclusion the writer wishes to express his thanks to Miss SYKES, Professor A. A. LAWSON, Professor G. J. PIERCE, Dr. HOLMAN (Stanford University), and Mr. L. A. BOODLE for material which they have kindly put at his disposal.

HARVARD UNIVERSITY

EXPLANATION OF PLATES

PLATE XVII

FIG. 1.—Transverse section of part of the cone of *Equisetum telemateia*. ×15.

FIG. 2.—Transverse section showing the axial bundle and its outgoing foliar trace of the cone of *E. telemateia*. ×25.

FIG. 3.—Longitudinal section of the same. ×25.

FIG. 4.—Transverse section through the supranodal wood of the vegetative

axis of the same species of Equisetum, showing the absence of a foliar gap corresponding to the leaf-trace which lies in the cortex. ×25.

FIG. 5.—Longitudinal section through a vegetative node of the same species of Equisetum, showing the departure of the leaf-trace without causing any gap in the supranodal wood. ×25.

PLATE XVIII

FIG. 6.—Transverse section of the stem of *Tmesipteris tannensis*. ×15.

FIG. 7.—Tranverse section of the same, showing the relation of the outgoing traces to the central cylinder. ×30.

FIG. 8.—Copy of a figure from BERTRAND, showing the departure of the traces of the lower sporophylls from the upper region of the peduncular strands in Phylloglossum.

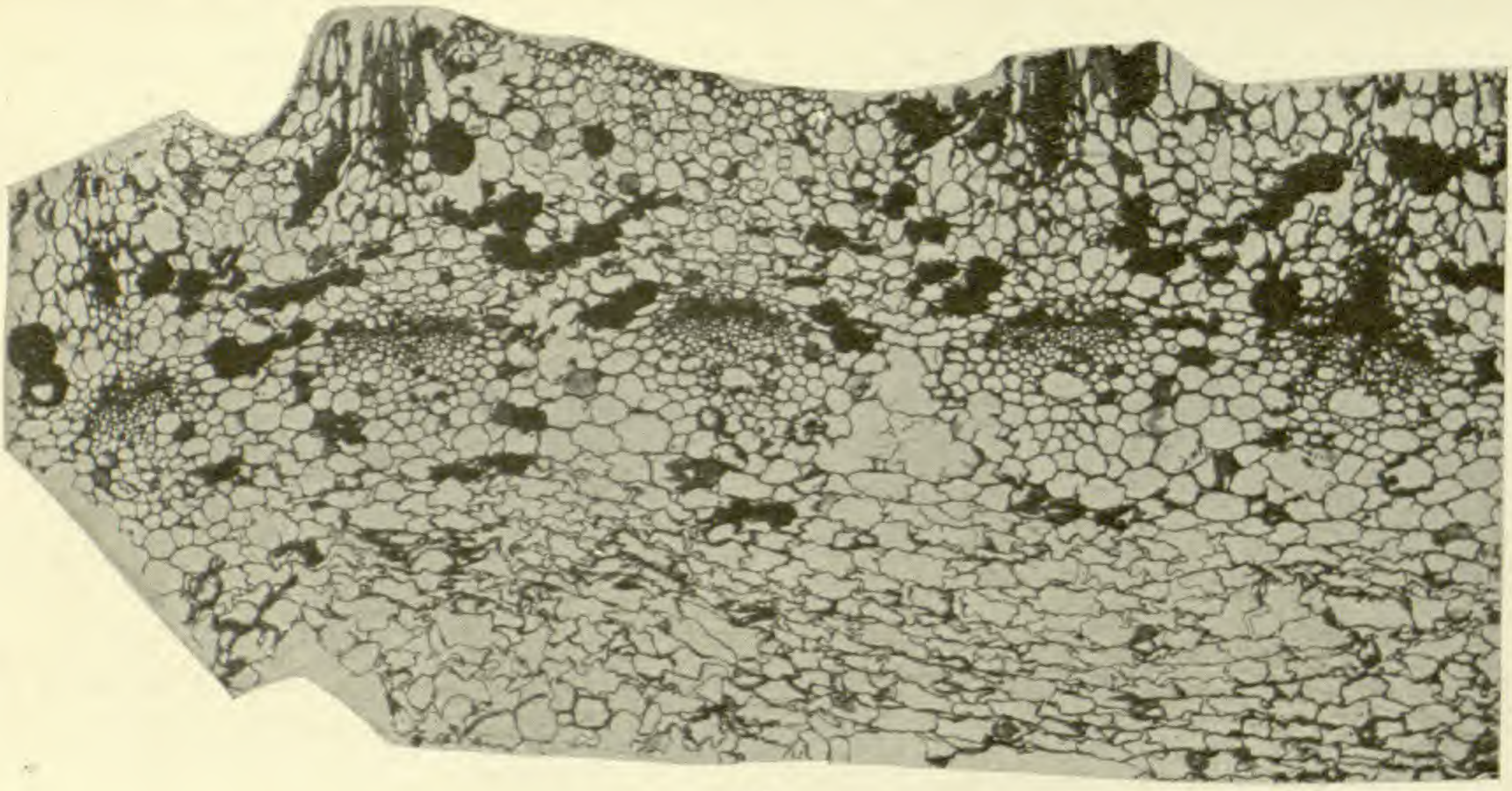
FIG. 9.—Transverse section of part of the central cylinder of *Lepidophloios Harcourti*.

FIG. 10.—Transverse section through the middle region of the cone in Phylloglossum, showing the relation of the leaf traces to the central cylinder. ×60.

FIG. 11.—Transverse section through the central region of the cone in another example of Phylloglossum, showing two apparent "foliar gaps." ×60.

FIG. 12.—Transverse section through the same cone slightly lower down, showing the connection of the foliar strand with the side of the apparent foliar gap. ×60.

NOTE.—*Figs. 10, 11, 12* are all made from herbarium specimens. In *fig. 12* the action of caustic alkali has not quite restored the size of the cells in the gap on the right of the central cylinder; it should appear the same size as that shown on the right of *fig. 11*.



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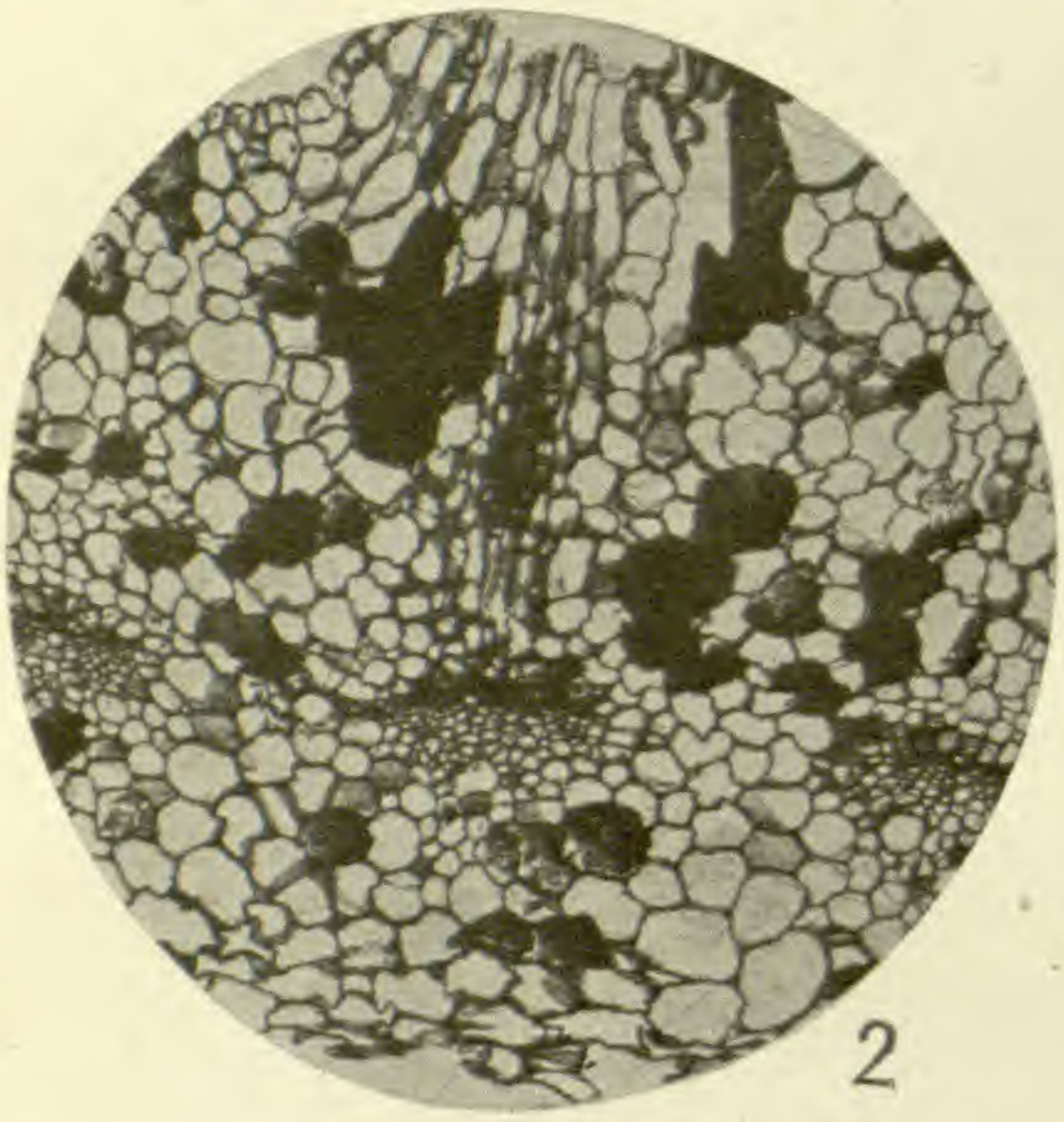

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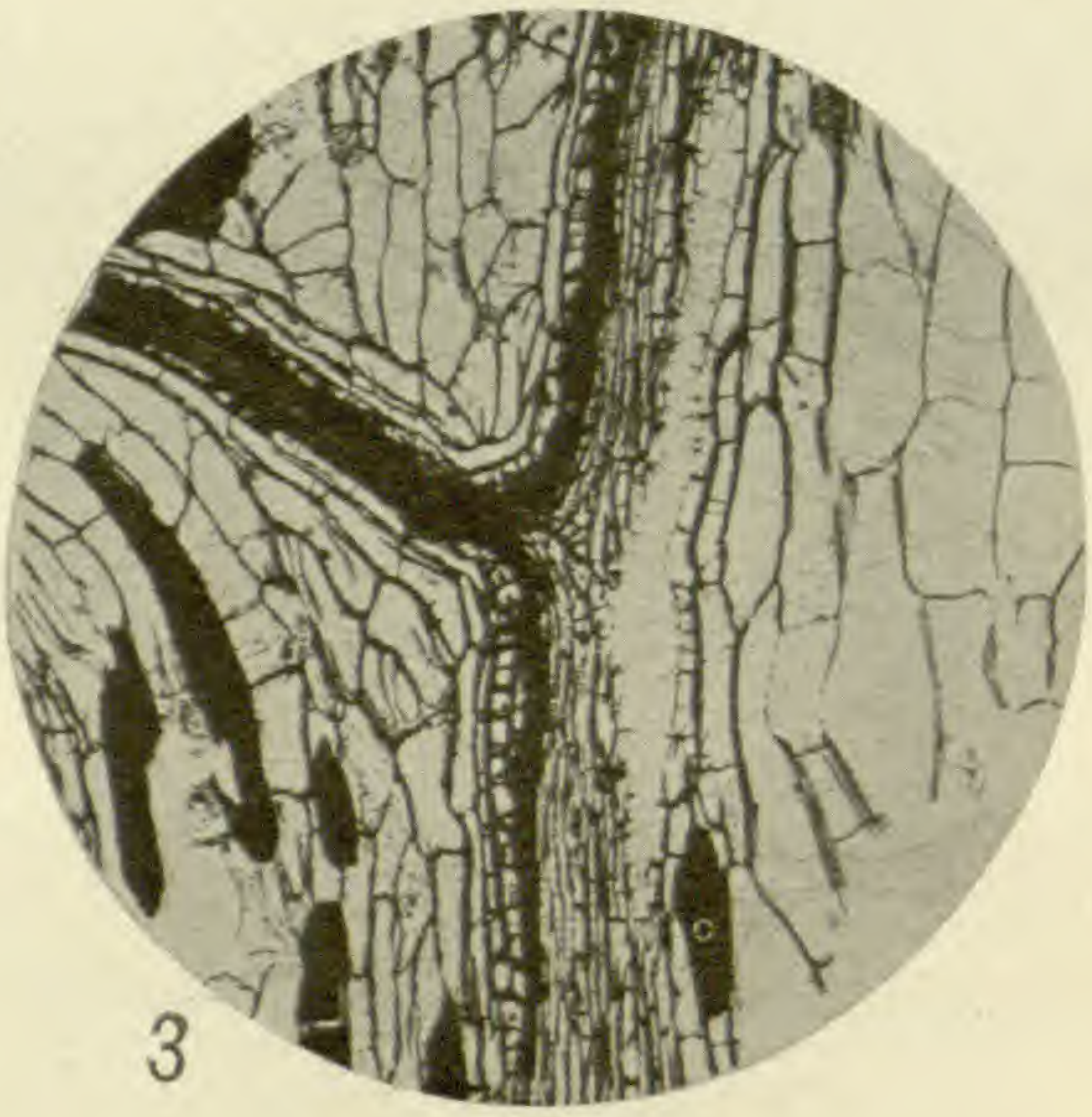

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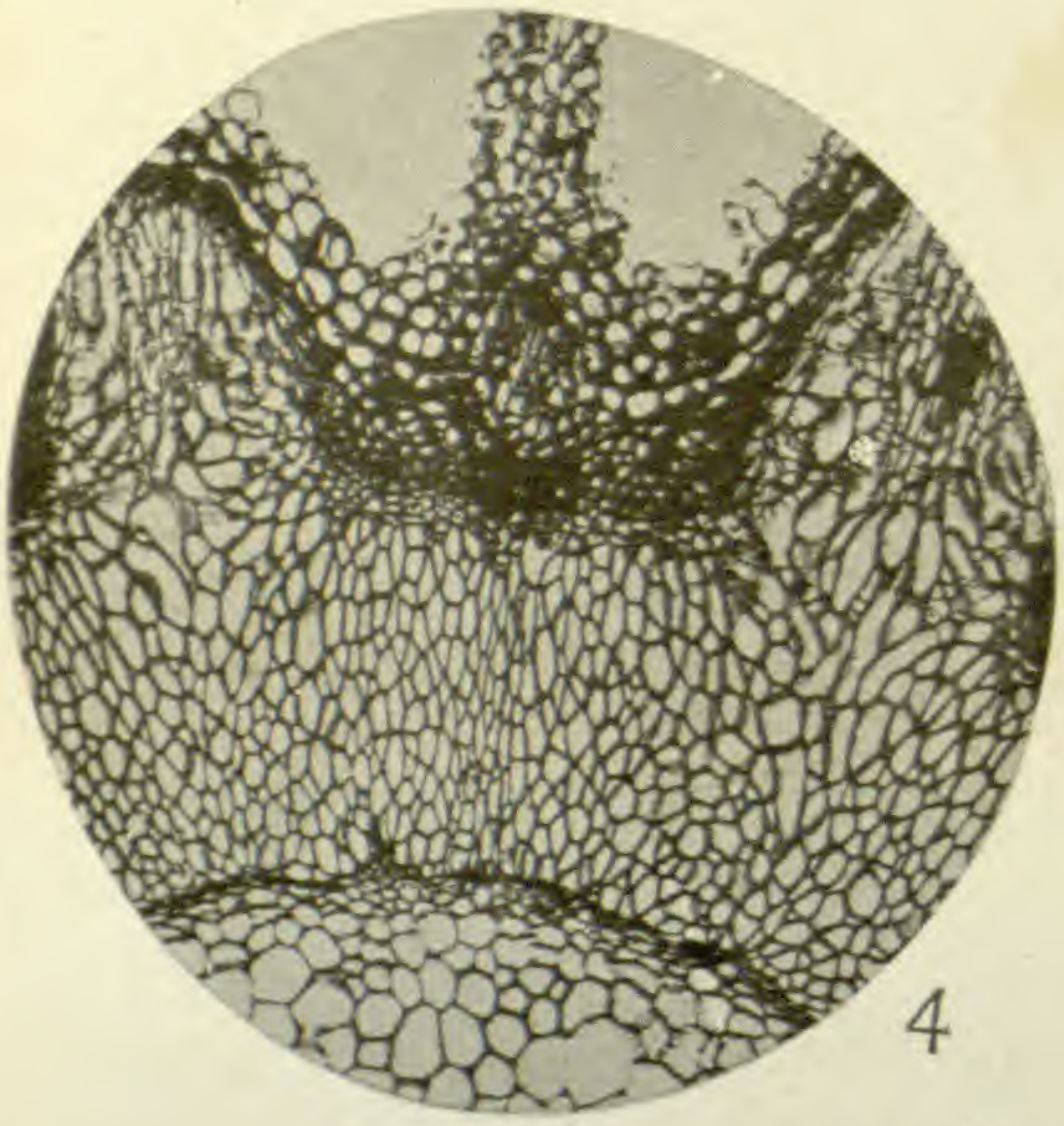

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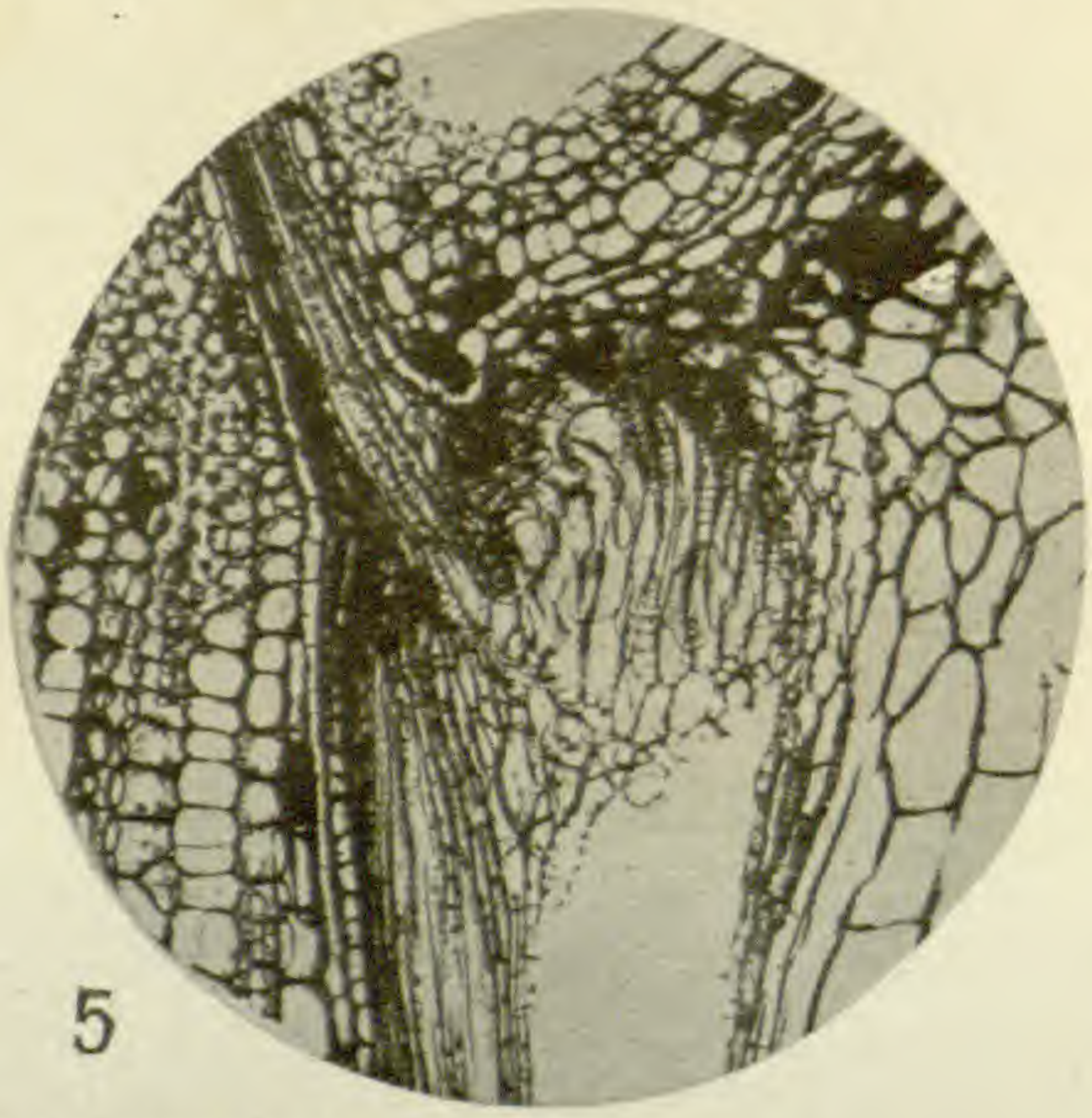

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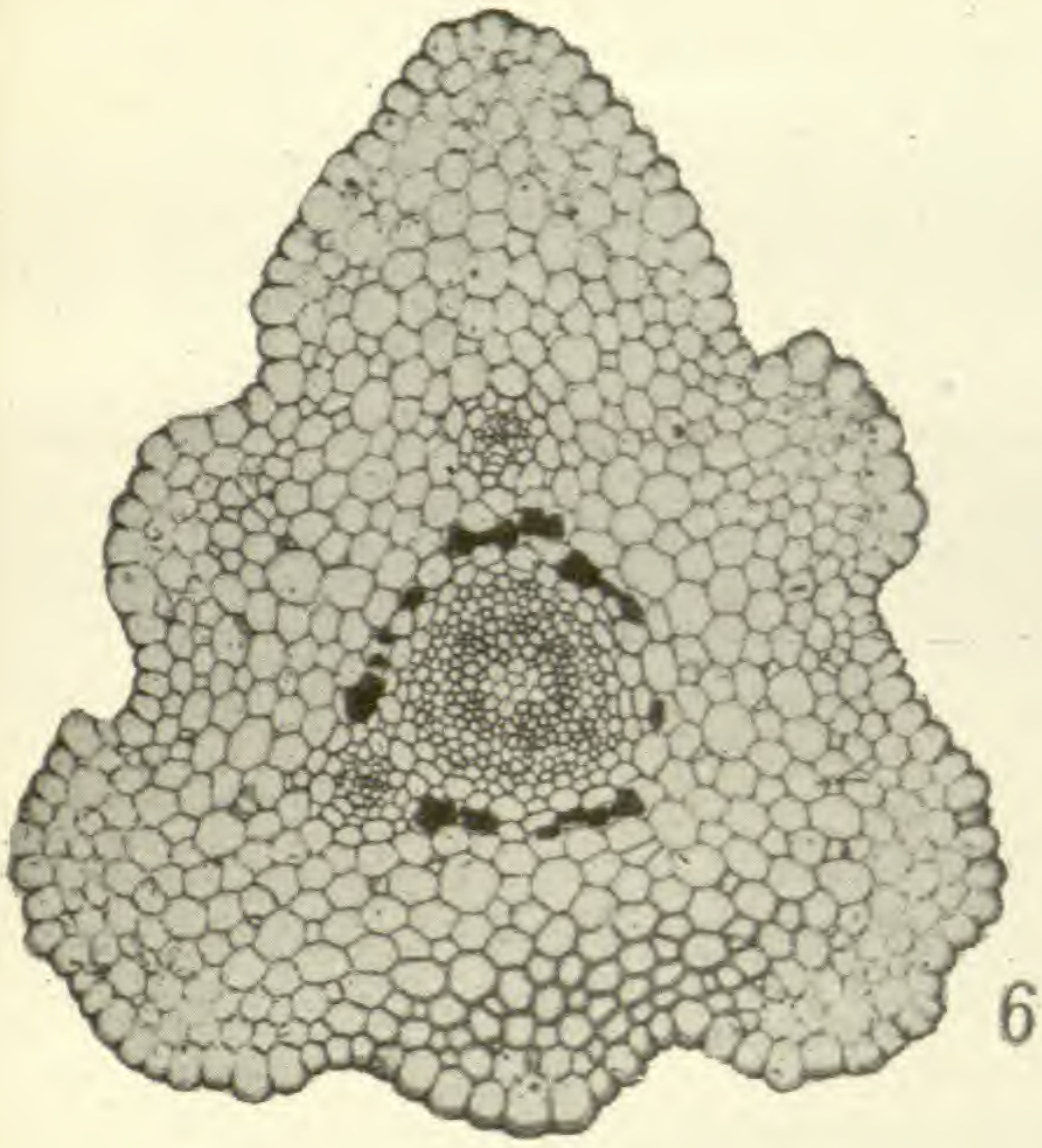
JEFFREY on LYCOPSIDA



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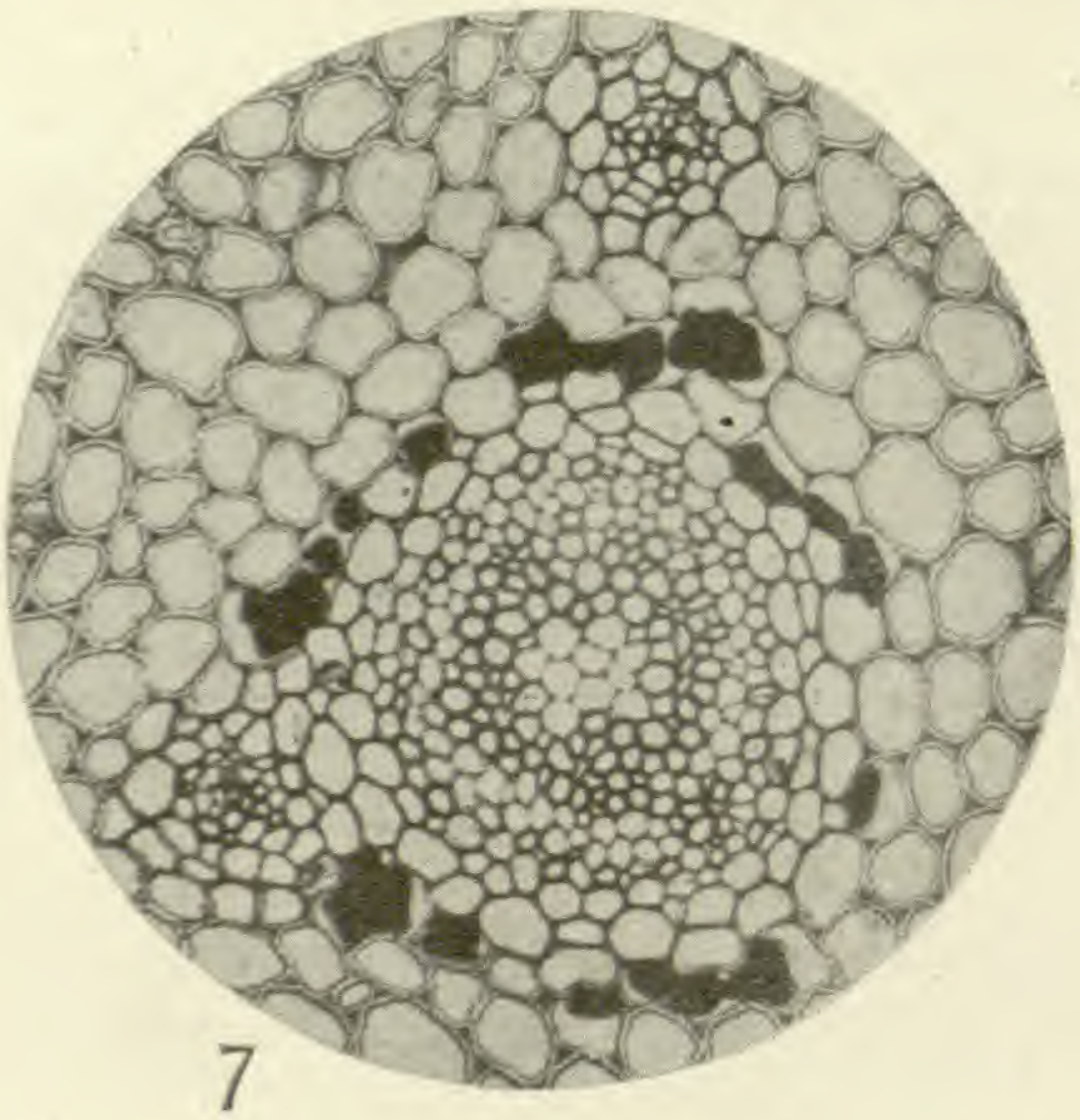

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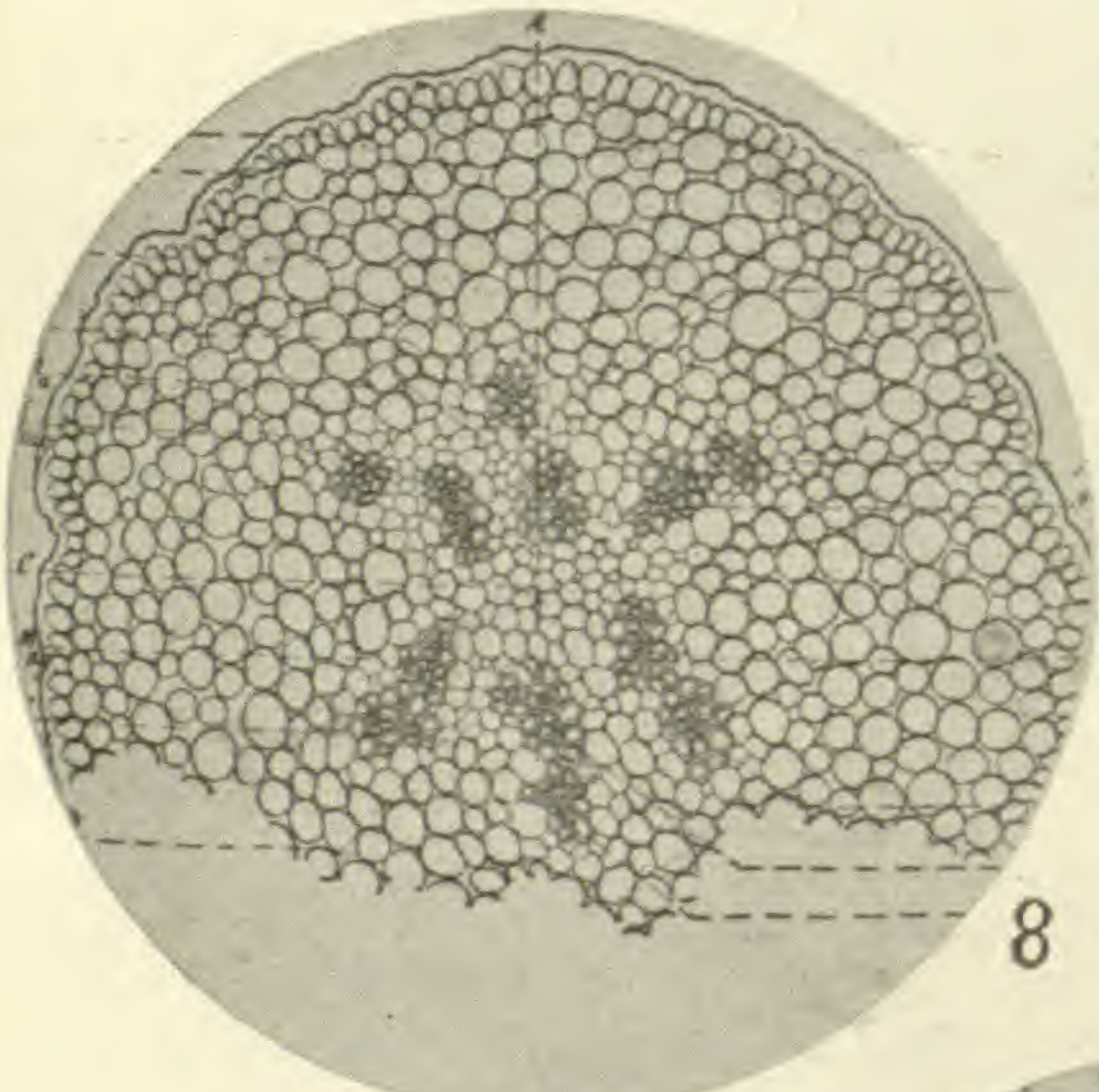

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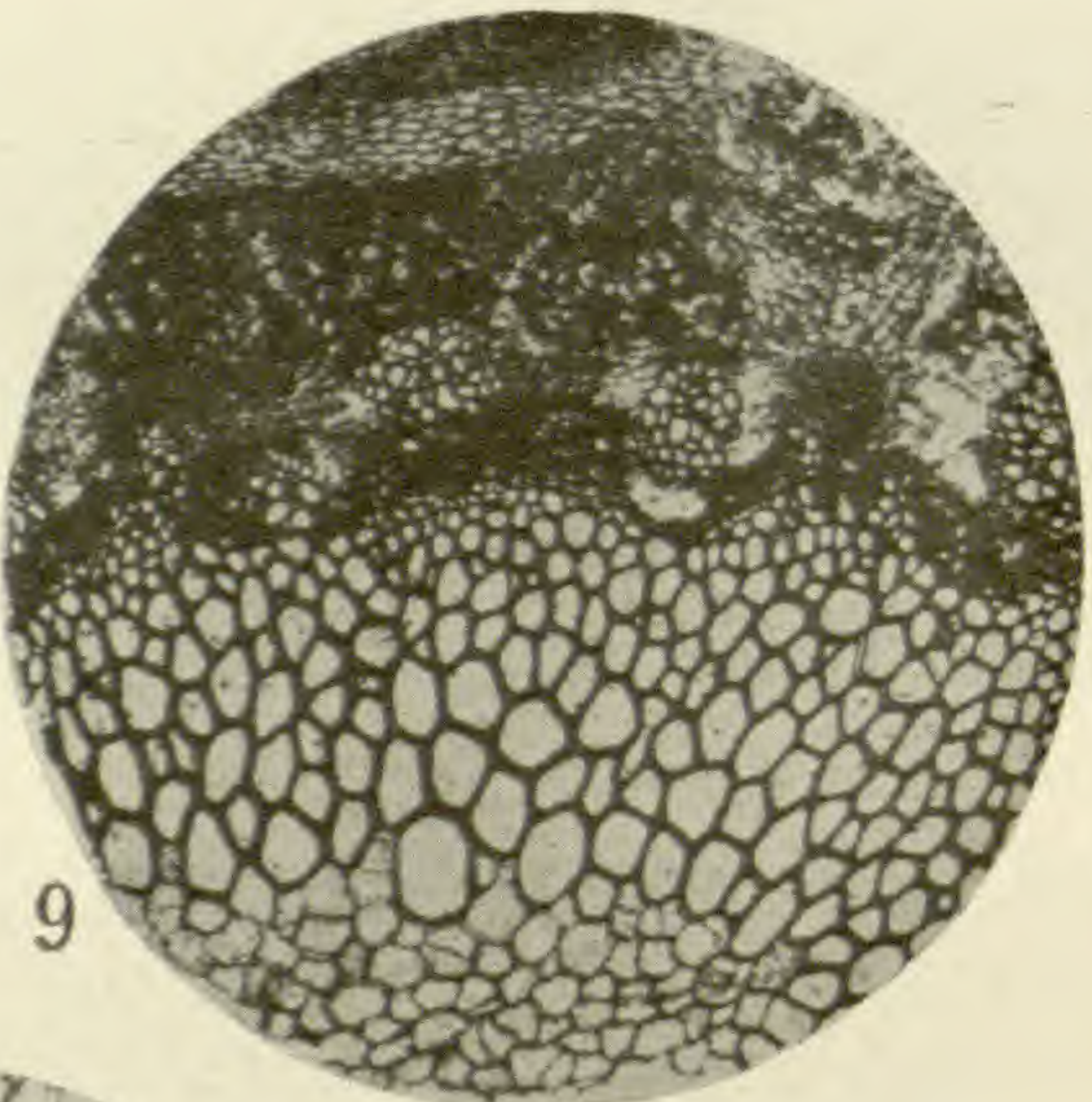

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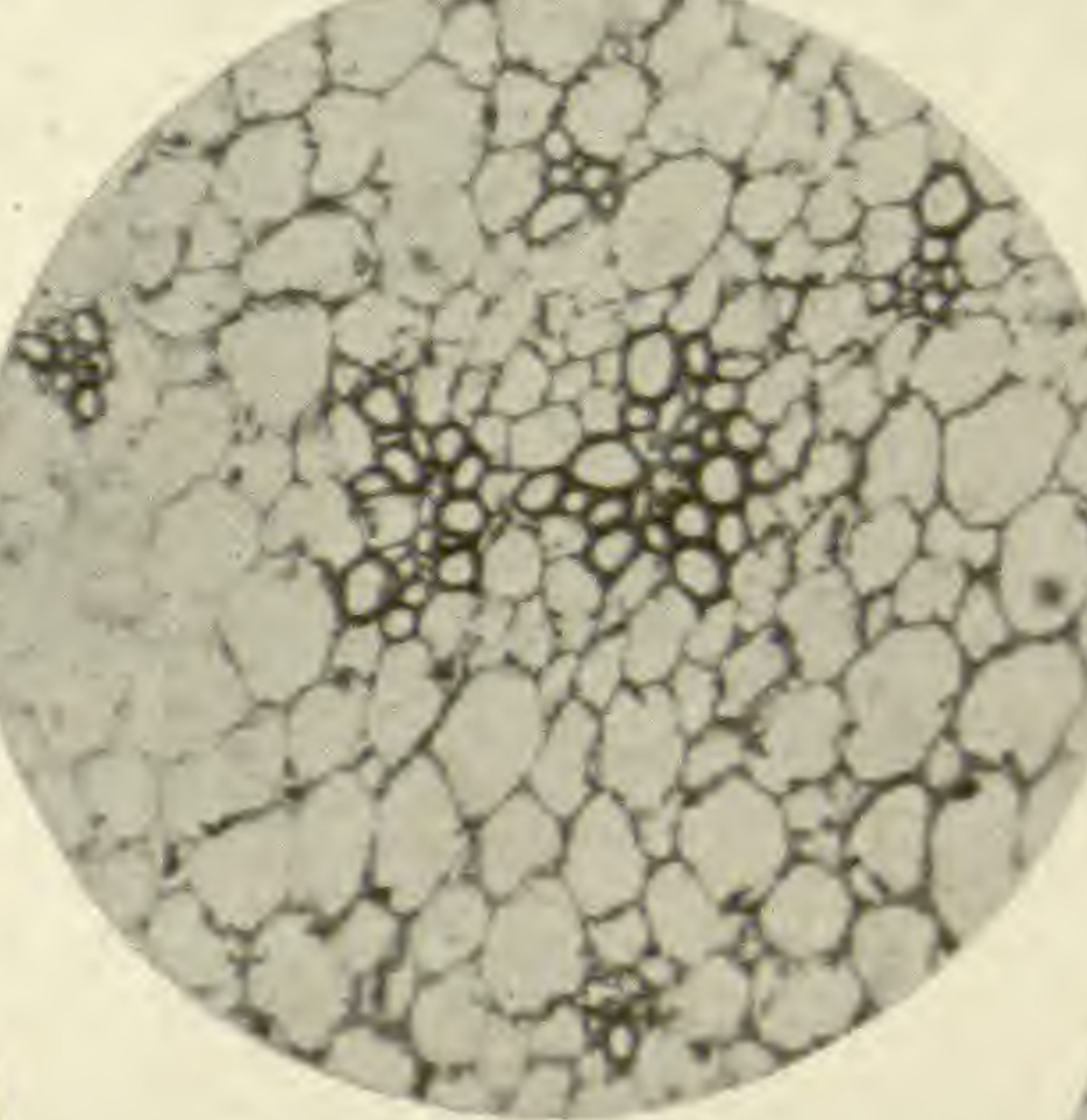

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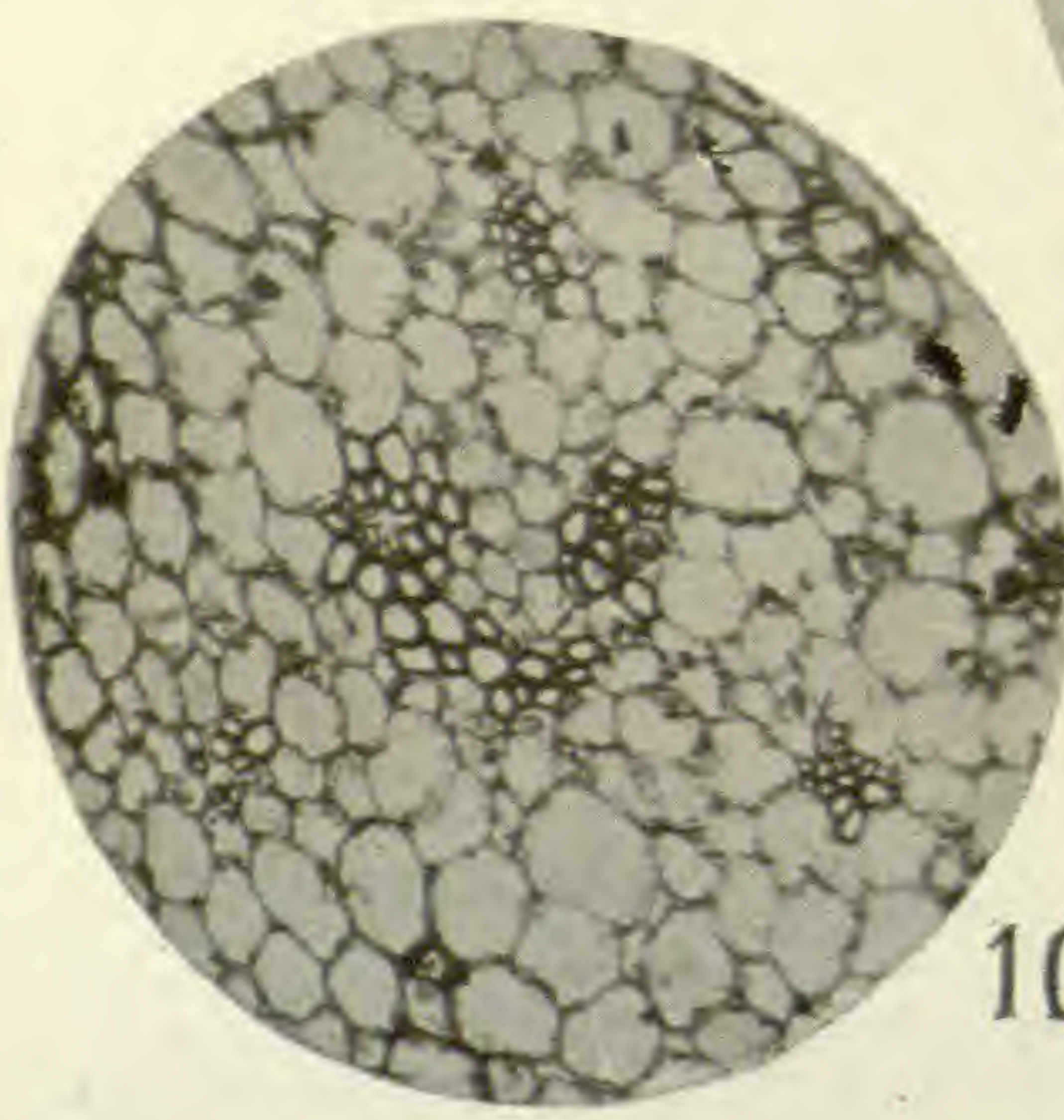

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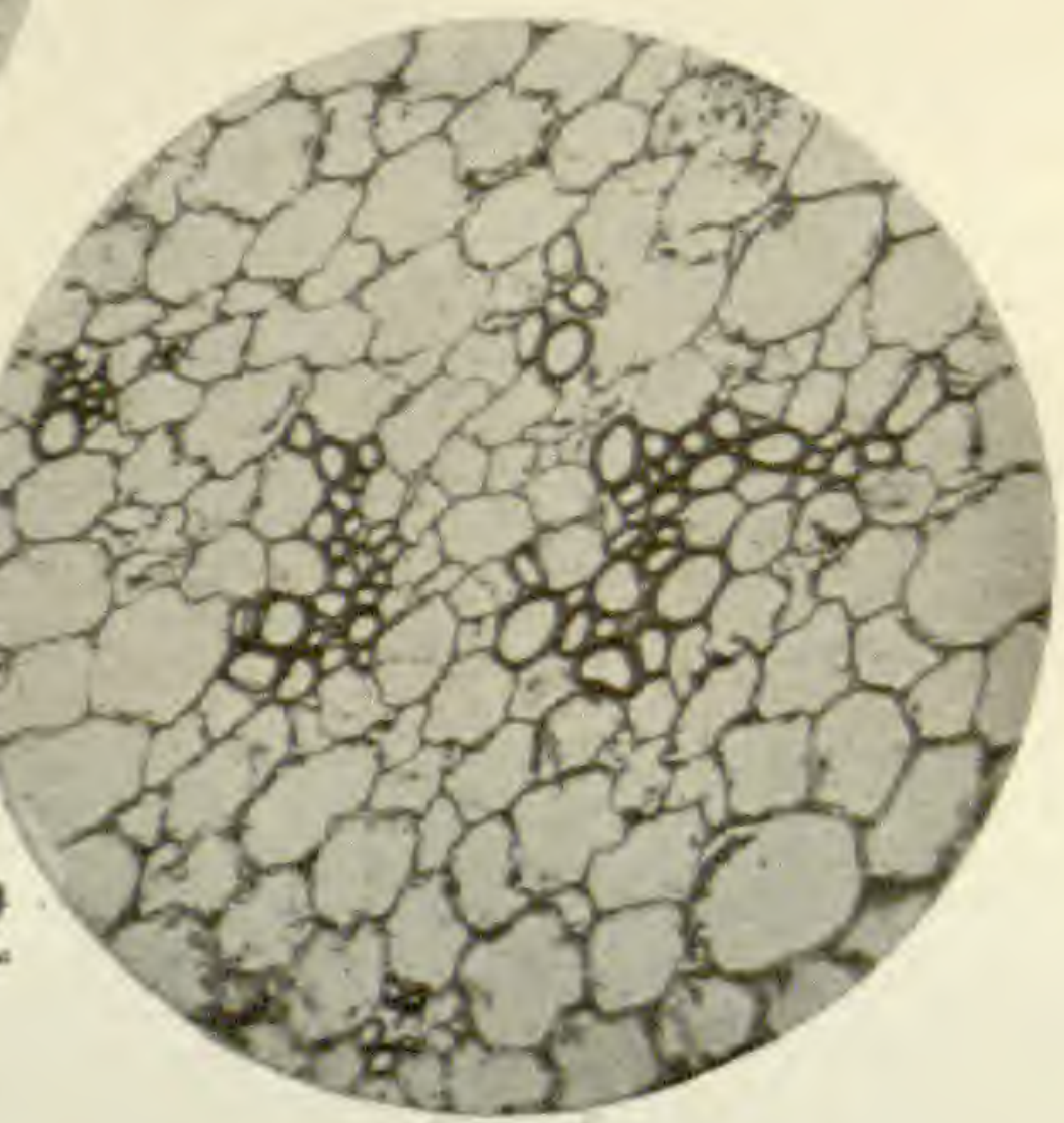

12

JEFFREY on LYCOPSIDA

EFFECT OF ILLUMINATING GAS AND ETHYLENE UPON FLOWERING CARNATIONS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 116

WILLIAM CROCKER AND LEE I. KNIGHT

(WITH FOUR FIGURES)

1. Historical

As early as 1864 observations were recorded on the effect of illuminating gas on vegetation. GIRARDIN (1) called attention to the phenomena of gas injury to trees as reported from various places in Rouen, Berlin, Hamburg, Hanover, etc. He especially investigated injury done to Italian poplars which had come into use as shade trees along the highways. He made a chemical analysis of samples of soil taken three feet from leaks in the gas pipes, and found inflammable oil as well as sulfur and ammonia compounds present. R. VIRCHOW (2) expressed an opinion that coal gas is especially injurious to vegetation. KNY (3) was one of the first to test the injury experimentally. He used three sound trees in the Berlin Botanical Garden, each about twenty years old—one maple and two lindens. Gas pipes were carefully laid 84^{cm} deep and the gas used was freed of sulfuretted hydrogen. The two pipes were laid in a circle about the maple, and four burners were attached at a distance of 118^{cm} from the trunk. Near each linden tree were two burners, 110^{cm} from the trunks. The gas escape was measured daily.

(1) Maple received daily....................	12.9 cubic meters
(2) First linden...........................	11.7 cubic meters
(3) Second linden.........................	1.6 cubic meters

The experiment was begun July 7 and lasted for (1) and (2) a half-year, for (3) a full year. First a Euonymus (*E. europea*) near the maple died, then the maple lost its leaves (September 1). At the same time an elm near by showed injury. September 30 the first linden showed signs of injury. On October 12 the first linden lost its leaves, and on October 19 the second, while other lindens in the garden were yet green. An examination of roots one-half inch in diameter showed a blue coloration extending out from the middle toward the periphery. The following spring the maple, elm, and Euonymus bush showed no signs of life. The lindens produced foliage, but the leaves were bleached and smaller than usual. Dried cambium and a rich growth of fungi were further indications of injury.

Similar investigations were carried on by SPÄTH and MEYER (4). In one case during the summer a little less than $1^{\mathrm{cu.m}}$ of gas diffused daily through $17.8^{\mathrm{cu.m}}$ of soil in a wooded plot. The roots of all the trees were killed within a few days. During four winter months the same amount of gas was allowed to escape into a wooded plat of twice the above area. In this case Platanus, silver poplar, American walnut, and Ailanthus were killed; the maple and horse chestnut were greatly injured; while the linden showed no injury. In another experiment $0.0185^{\mathrm{cu.m}}$ of gas was daily distributed equally among seventeen trees. The experiment lasted from April 11 to June 27. Before May 30 six of the more sensitive trees had died. By June 21 all the others, with the exception of the rough-fruited maple, had slackened their growth. The leaves of the injured trees were a pale green or yellow, and most of the younger roots were dead. According to the statement of the gas inspectors, their methods were not capable of detecting such light leaks as are shown in this experiment. These investigators found that when the surface of the soil is compact, the gas may travel long distances before reaching the surface. An instance is cited of gas traveling from a leak on one side of a street to a cellar on the opposite side, where it became evident by an unbearable smell. These investigators concluded that trees are far less sensitive to gas leaks during the winter than during the growth period. They also found much more rapid injury where the surface of the soil was packed. The small quantity of gas necessary to kill and the great distance that gas travels through the soil serve to emphasize the danger to which trees are exposed.

H. EULENBERG (5), besides summarizing the results given in previous literature, adds the birch to the list of less sensitive trees.

J. BÖHM (6) grew slips of water willow in water through which gas was passed. He found that they produced only short roots and that these soon died, as did also the buds. The twigs themselves remained alive for about three months, until, as he believes, the reserve food had been exhausted. In another experiment he found that soil impregnated with gas was very poisonous to plants, for seeds put to germinate in it started, but their roots soon died. A Dracaena planted in such soil died in ten days. Far less injury was shown when a given quantity of gas was in contact with the portions of the plant above the ground than when the same quantity came in contact with the roots by being passed into the soil. The roots, he concludes, are most sensitive to gas injury. He found potted plants of Fuchsia and Salvia only moderately sensitive to illuminating gas that was allowed to bubble through the soil.

LACKNER (**7**) states that camelias, azalias, cacti, and ivy are much injured if kept in rooms where illuminating gas is burned; while palms, dracaenas (*Acuba japonica*), and many other plants escape uninjured. He asserts that it remains to be determined whether it is escaping portions of unburned gas or products of incomplete combustion that produce the injury.

C. WEHMER (**8**) calls attention to a severe case of gas poisoning in Hanover. Thirteen elm trees along a street showed injuries varying with the distance they stood from a leak in a gas pipe. In late winter a number of them showed brown discoloration of the inner bark, and a falling-off of bark in large patches extending up the trunk six feet from the ground. No blue discoloration of the roots appeared as was reported by KNY and other observers. The author asserts that the area of the injury was especially great because of the hard-packed street above the leak.

MOLISCH (**9**) found that illuminating gas is more injurious to the roots of plants than chlorin or carbonic acid. Growth in length is retarded by 0.005 per cent. of illuminating gas. If uninjured and decapitated roots of corn are grown in illuminating gas, the former are remarkably bent and retarded in their growth in length, while the latter grow almost straight and are comparatively vigorous. Under the influence of the gas the growth in thickness of the roots is increased, the greatest thickening occurring where the bending is sharpest. When a 10–20 per cent. mixture of illuminating gas exerts a stimulus from one side, the roots respond negatively.

NELJUBOW (**10**) notes some very interesting effects of illuminating gas upon the etiolated seedlings of peas and other legumes. WIESNER had already reported a horizontal nutation of these seedlings, which he explained as autonomic. RIMMER later explained this horizontal growth as a response to unfavorable conditions, especially lack of moisture in the air. NELJUBOW found that while this response always occurred in the dark in the laboratory air, it did not occur in the dark in a greenhouse or in the outside air. After determining that temperature and moisture were not factors, he sought the explanation in impurities of the laboratory air. He found that laboratory air passed through KOH, $Ba(OH)_2$, $CaCl_2$, red hot CuO, and finally through $Ba(OH)_2$ gave vertical seedlings; while similar treatment with the CuO unheated gave seedlings with the horizontal placement. This proved that some impurities (probably some of the constituents of illuminating gas) of the laboratory air, which were oxidized by glowing CuO, caused this peculiar horizontal placement. He later produced the effect with mixtures of illuminating gas. He likewise tested a number of the constituents of illuminating gas. Acetylene produced this nutation, but was difficult to work with, because, on the one hand, a slight increase in concentration killed, and on the other, it rapidly disappeared because of its high solubility in water. One part of ethylene in 1,000,000 of air gave the response, while one part in 4000 killed the majority of the seedlings. He likewise mentions the fact that various other constituents (benzene, sulfur dioxid, hydrogen sulfid, and carbon bisulfid) of illuminating gas are highly toxic. He makes no attempt, however, to determine the toxic limits of the several constituents, or to learn whether one or several determine the toxic limit of illuminating gas.

SHONNARD (11) mentions several manifestations of the injury of illuminating gas to trees, and describes an experiment with a potted lemon tree exposed to a flow of $1.07^{\text{cu.ft}}$ of gas per hour. After eight days he notes the exudation of sap in considerable quantity from trunk and branches, as well as the discoloration and falling-off of the leaves.

RICHARDS and MACDOUGAL (12) tested the effect of carbon monoxid and illuminating gas upon various seedlings. Carbon monoxid, heretofore considered neutral, was shown to be toxic. It was not so effective as illuminating gas, however, in modifying the rate and amount of growth of root and shoot, in retarding the differentiation of the primary tissue, and in hindering the formation of chlorophyll. Gametophytes of certain mosses were found to be very resistant, suffering very little injury in high concentrations of these gases for three months. A more delicate moss, presumably *Mnium undulatum*, however, showed deleterious effects earlier. In Elodea and Nitella older cells were most injured, and the injury was shown by plasmolysis of the cells. A considerable part of their experimentation with illuminating gas serves to confirm the results obtained by MOLISCH, NELJUBOW, BÖHM, and others. The conclusion that "illuminating gas affords, in addition to the action of carbon monoxid, the results of the action of other substances deleterious to plants" seems to indicate that the work of NELJUBOW and others was entirely overlooked.

STONE (**13**) calls attention to the fact that very small leaks (2–$3^{\text{cu. ft}}$ per day) of gas may cause local injury to trees. Among manifestations of gas-killing in trees, he notes the early appearance of an abundant growth of fungi in contrast to the relatively late appearance on other dead trees. In speaking of the distance gas may travel he says: "In gravelly soils we have known gas to travel 2000 feet without difficulty, when the ground is frozen, and escape into the cellar of a house; whereas in heavier soils gas is more likely to be restricted to smaller areas."

RICHTER (**14**) and other investigators have pointed out a number of effects of impurities of laboratory air upon the responses of seedlings. RICHTER believes that in a number of cases the negative geotropism of hypocotyls is greatly weakened by these impurities. He points out that a one-sided illumination will produce far more nearly a horizontal position with than without these impurities. He likewise asserts that in many species the degree of horizontality from one-sided illumination indicates the degree of impurity of the air. He found great variation, however, in sensitiveness in different species even of the same genus.

2. Scope, method, and preparation of material

It is quite commonly asserted that plants do poorly in houses lighted with gas and especially is the flowering interfered with. Various inquiries have come to us from carnation growers as to the effect of illuminating gas upon the flowering carnation. These growers claimed to have had heavy losses from gas that seeped from defective pipes through the ground into the greenhouses. In some cases it is claimed that the losses occurred during cold weather, when little ventilation was possible and when the ground was frozen, so that upward diffusion from the defective pipes was hindered and thereby lateral diffusion fostered. In all these cases it is claimed that the injuries ceased with the repair or removal of the pipes.

Upon looking up the literature it was found that no accurate determinations were made upon the effects of illuminating gas and its constituents upon flowers, and that in no case have the toxic limits and relative toxicity of the several main constituents been determined. In short, it is not known in any case whether the toxic limit of the gas is determined by the action of one constituent or by the combined action of several. To answer these questions is the purpose of the investigation here reported.

This paper will deal entirely with the buds and flowers of the carnation, describing in detail the effects and toxic limits of illuminating gas and ethylene. A later paper will give in detail similar data for the other main constituents of illuminating gas, as well as describe the effects of illuminating gas and all its main constituents upon the vegetation of the carnation. The work naturally falls into these two divisions, for, as will be shown by experiments described later, the flowers are far more sensitive to illuminating gas than is the vegetation, and the toxic limit of the gas on the flowers seems (from all the evidence of our experiments) to be entirely determined by the ethylene it contains.

To determine the relative sensitiveness of buds and flowers on the one hand, and the vegetation on the other, as well as the relative sensitiveness of buds and flowers of different ages, one series of experiments was carried on by exposing entire potted plants to an atmosphere containing small proportions of gas. This was done by setting the plants into an air-tight greenhouse within the laboratory greenhouse, and then running desired quantities of gas into the air-tight greenhouse. This sort of experiment has some serious faults. It does not determine whether the flower is affected directly by the gas contained in the air about it, or whether the effect is indirect by injury to the plant through the absorption of gas by the soil and later by the roots. Also no definite determination of the toxic limit of the gas can be made, for the amount absorbed by the soil is not determinable.

To avoid such sources of error the buds and flowers still intact were exposed individually to the desired concentrations of the gases. This was accomplished by the use of the apparatus shown in *fig. 1*.

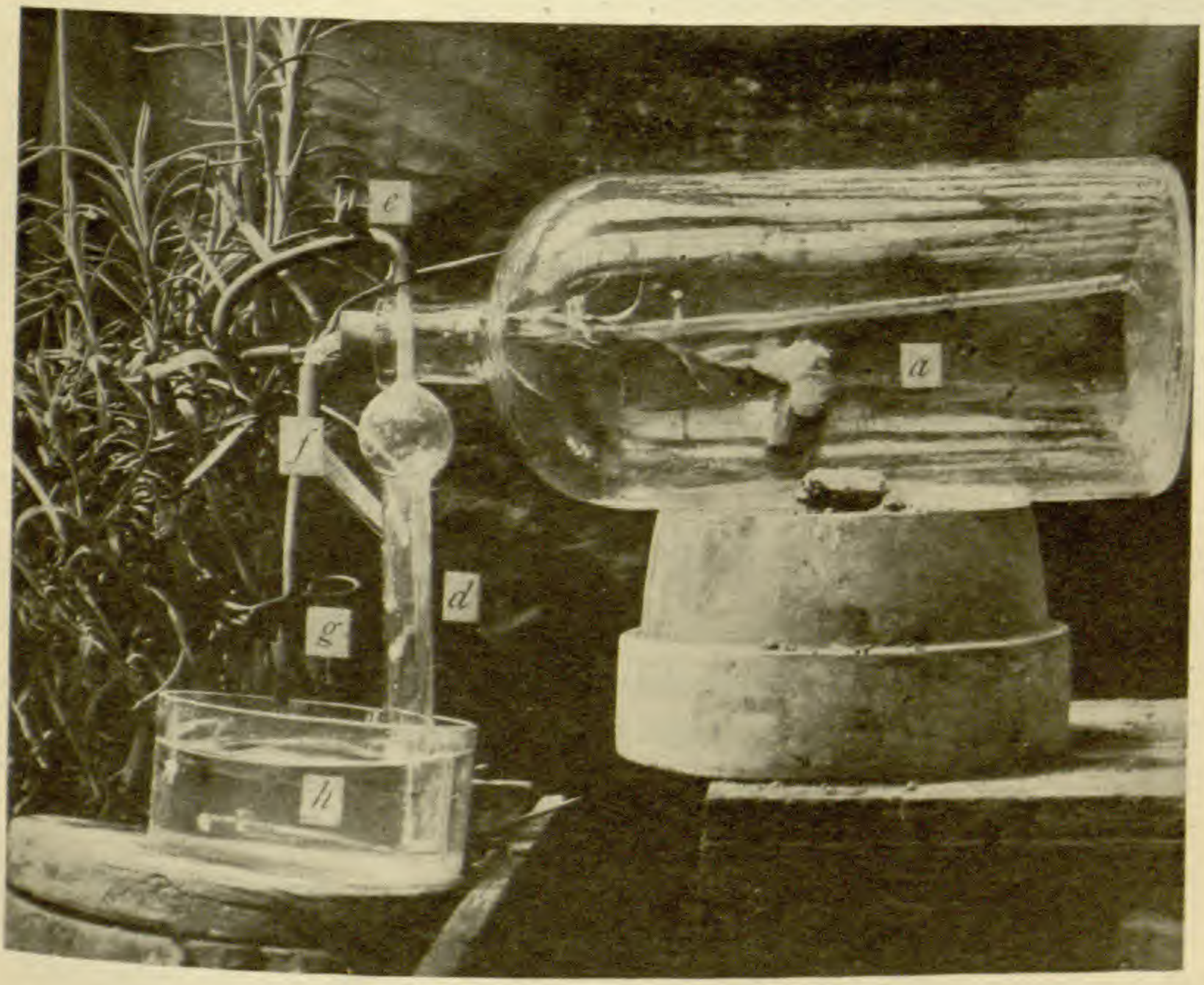

FIG. 1.—For description see text.

The bottle *a* is furnished with a three-holed rubber stopper. In one hole of the stopper is a straight glass tube reaching nearly to the bottom of the bottle. A calcium chlorid tube (*d*) is attached to the projecting end of this tube by means of a rubber tube furnished with a pinchcock (*e*). In the second hole of the stopper is a short bent glass tube (*f*), the outer end of which is furnished with a rubber tube and pinchcock (*g*). The third hole in the stopper is small and is capable of having the stem of the carnation inserted from the side by a split, which reaches from the hole to the margin of the cork. In setting up the experiment the cork is placed on the stem of the carnation by opening the cork at the split and inserting the stem. The flower or bud and the long tube are put into the nozzle of the bottle and the cork forced in until the whole apparatus is air-tight. The free end of the calcium chlorid tube is placed into a dish (*h*) of water or (with gases highly soluble in water) mercury; both pinchcocks (*e* and *g*) are opened; and suction applied to the tube *f* until the liquid rises to the small portion of the calcium chlorid tube, at which time pinchcock *g* is closed. The desired quantity of gas which is now poured into the wide end of the calcium chlorid tube rises to the top of the liquid. A one-holed rubber stopper, furnished with a tube and attached to a column of the same liquid as is contained in the dish, is now inserted into the free end of the calcium chlorid tube (*d*), and the pressure of the column allowed to force the liquid to the inner end of the long tube. This forces the gas into the end of the bottle farthest from the flower and allows a gradual distribution by diffusion. For ethylene and illuminating gas water was always used as the forcing liquid.

In determining the toxic limits of illuminating gas and ethylene, 20-liter carboys were used; while smaller bottles were employed in some of the earlier experiments with these gases, as well as with all the determinations of the least toxic gases. The question of the effect of corking a bud or flower in a closed chamber of this kind naturally arises, and suggests a criticism upon the method. It was found that flowers opened without any apparent injury when corked in flasks of only one liter capacity. In all checks and in all cases where the concentration of the injurious gas was below the toxic limit, the flowers bloomed normally while yet in the bottles. To avoid undue rise of temperature within the chambers basket-covered carboys were used. The experiments were carried on in the laboratory greenhouse during the months of May to September. The temperature in the experiments reported varied from 20°–28°, and within this range no noticeable variation in toxicity appeared.

Two varieties of carnations were used—the Boston Market and the pink Lawson. The two varieties vary so little in their sensitiveness and reaction to ethylene and illuminating gas that a description of the responses of one applies equally well to the other.

To make sure that the effect produced by ethylene was not due to some impurity contained by it, parallel experiments were run with ethylene derived by two different methods: (1) by heating concentrated sulfuric acid with absolute alcohol, and (2) by dropping absolute alcohol upon phosphorous pentoxid heated to 200° C. and later raised to 240° C. The ethylene derived from sulfuric acid was washed by the ordinary gas burette and pipette, as described by HEMPEL (**15**: 34–95); first in concentrated sulfuric acid (sp. gr. 1.84) to remove the aldehyde, and later in 33 per cent. potassium hydrate to remove the sulfur dioxid. In each case the washing was continued until no further absorption occurred. The ethylene derived from phosphorous pentoxid was washed similarly, and in addition in copper sulfate (sulfuric acid solution described by HEMPEL, p. 316) for absorption of phosphene, if any should be present. Various samples of the ethylene derived in this way were analyzed. Bromin and fuming sulfuric acid absorbed 96–98 per cent. The unabsorbed portion proved to be air, coming from the generator chamber. The gases thus derived were diluted with air to form mixtures containing 2 per cent. ethylene. The toxicity of the two mixtures was equal.

In discussing the composition of illuminating gas we can hardly do better than quote a paragraph from SMITH's (**16**) *General chemistry for colleges:*

> The illuminating gas in Europe, and in many of the smaller cities of the United States, is usually coal gas; while in the larger cities of America it is almost always made from water gas. Coal gas is obtained by the destructive distillation of soft coal, and is freed from ammonia and tar by washing and cooling, and from hydrogen sulfid and carbon dioxid by passage through layers of slaked lime. The water gas, made by the action of steam upon anthracite or coke, being composed of carbon monoxid and hydrogen, has no illuminating power. It is therefore "carburetted," that is, mixed with hvdrocarbons, by passage through a cylindrical structure filled with white-hot firebrick, upon which falls a small stream of high-boiling petroleum. The relatively involatile hydrocarbons of which the oil consists are thus decomposed ("cracked"), and gaseous substances of high illuminating power are produced. The following table shows the composition of each of these kinds of gas, together with that of oil gas (Pintsch's) which is composed entirely of the products from "cracking" oil:

Components	Coal gas	Water gas	Oil gas
Illuminants	5.0	16.6	45.0
Heating gases:			
Methane	34.5	19.8	35.8
Hydrogen	49.0	32.1	14.6
Carbon monoxid	7.2	26.1	....
Impurities:			
Nitrogen	3.2	2.4	1.1
Carbon dioxid	1.1	3.0	....
Candle power	17.5	25.0	65.0

These are average numbers, and considerable variations from these proportions are often met with. The illuminants are unsaturated hydrocarbons, such as ethylene and acetylene, and the value of the gas for illuminating purposes depends on the amount of these particular components.

The illuminating gas used in our experiments was water gas of the People's Gas Light and Coke Company, drawn from a tap in the Botanical Laboratory. In numerous analyses of samples of this gas (see HEMPEL, p. 282) absolute alcohol absorbed 0.2–0.6 per cent., and fuming sulfuric acid 11–14 per cent. Absolute alcohol absorbs the so-called hydrocarbon vapors (mostly benzene); and fuming sulfuric acid the heavy hydrocarbons, including acetylene, ethylene, and their higher homologues. Bromin is often used as an absorbent of ethylene. Besides ethylene, however, it absorbs several other constituents of illuminating gas. In a number of analyses this reagent absorbed 9–13 per cent. A more definite determination of ethylene will be given in the experimental portion.

At first the illuminating gas used was washed through 33 per cent. potassium hydrate to absorb any traces of sulfur dioxid and hydrogen sulfid it might contain. This was found not to modify the toxicity, and hence the unwashed gas was used thereafter. The methods of deriving and purifying the other constituents (of illuminating gas) worked with will be described in the later paper, which gives their effects.

3. Experimental

ILLUMINATING GAS

As a later paper will deal fully with the effects and toxic limits of the constituents other than ethylene, we need make only a general statement concerning them here. A number of experiments were run to determine the toxic limits of methane, carbon monoxid, acetylene, hydrogen, carbon bisulfid, and benzene to the buds and flowers. As would be expected, hydrogen was perfectly neutral when it completely displaced the nitrogen of the air. In all the other constituents here mentioned, the toxicity was such that in the least amount of illuminating gas necessary to kill the bud no one is concentrated enough to reach $\frac{1}{50}$ of its toxic limit. It is very probable, therefore, that these constituents play no part in determining the toxic limit of illuminating gas. It has already been stated that the absorption of hydrogen sulfid and sulfur dioxid does not modify the toxicity of the gas. This leaves, then, ethylene, the higher homologues of ethylene and acetylene, and certain aromatic sulfur compounds to account for the toxicity of the gas. All these substances except ethylene exist in very small percentages in illuminating gas. All evidence in the following experiments also points to the conclusion that there is enough ethylene in the gas to account for its toxicity.

The small greenhouse in which entire potted plants were exposed to the action of gas had a capacity of $1.69^{\text{cu. m}}$. In order to make comparisons easy between buds of the same size on the plants exposed and on the checks, corresponding buds were tagged with the same numbers. We need describe only one of these experiments. Potted plants of the Boston Market were put into the small greenhouse in the evening and 2 liters of gas were run in at the end opposite the plants, allowing a gradual distribution by diffusion. The plants were taken out the next morning to prevent injury by high temperature. The following evening the plants were returned to the enclosure and left for 60 hours (the following two days being cloudy). At the time they were put in, 4 liters of gas were run in, and the same amount was added 48 hours later, there being at that time no perceptible smell of gas in the chamber. This experiment served to show (1) that the vegetation is far less sensitive to gas injury than the buds, for there was no apparent injury to the vegetation; (2) plants remained vigorous, put out new buds, and later produced other flowers. The oldest buds (those showing color and just ready to open) and the youngest buds (those less than 0.6^{cm} in diameter) were the ones most injured. Many of the medium-sized buds, however, escaped death, although retarded considerably in their growth. The older buds showed a slight growth of the petals, but never opened. Later they shriveled and turned yellow.

FIG. 2.—*a*, result of treating a bud, just beginning to show the petals, for three days with 1 part of illuminating gas in 20,000; *b*, result of the treatment of a similar bud, for the same length of time, with 1 part of ethylene in 500,000.

Our experiments in which individual buds were enclosed and exposed to illuminating gas began with liter flasks in which as much as 25^{cc} of gas was used. The time of exposure was usually three days, starting when the petals were just beginning to show. A gradual reduction of the concentration by reducing the amount of gas used and by increasing the size of the enclosure finally located the toxic limit. The highest concentration did no apparent injury to the vegetation; but the effect upon the buds was made apparent by a failure to open, by a discoloration and withering of the petals, and by the projection of the stigmas. When using 1^{cc} of illuminating gas to $20,000^{cc}$, the stigmas still project as shown in *fig. 2, a;* 0.5^{cc} of illuminating gas did not sufficiently retard the growth of the petals to cause projection of the stigmas, yet the buds never opened farther than shown in *fig. 3*, although the petals remained fresh for several days. Very young buds were also exposed to the last concentration of the gas (1 part in 40,000, or 0.0025 per cent.) for a period of three days. The injury was not apparent at first, and the buds remained green for several days, but finally turned brown and withered.

FIG. 3.—Result of treating a bud, just beginning to show the petals, for three days with 1 part of ethylene in 1,000,000.

A series of exposures was also made on the open flowers. We selected for this work those that had just opened, in order to be sure that any change produced was due to the toxicity of the gas rather than to the natural death of the flower. Here as well as in all the other experiments checks were kept. *Fig. 4, a* shows a flower before being corked in a 20-liter carboy; *b*, the same after being corked in a 20-liter carboy (containing air only) for 24 hours; *c*, a flower before being corked in a 20-liter carboy; and *d*, the same after being corked in 12 hours with 0.5^{cc} of illuminating gas. This shows that 0.5^{cc} of illuminating gas per 20,000 (1 part in 40,000) causes the complete closing of the flower in 12 hours or less. Higher concentrations caused a more rapid closing and a marked inrolling of the petals. With 0.5^{cc} per 20,000 and less the inrolling is not conspicuous. Even 0.2^{cc} per 20,000 causes considerable closing in 12 hours, though not as marked as 0.5^{cc}.

The effect of duration of exposure was also tested. No injury was done to a bud just ready to open upon one day's exposure to 2^{cc}

FIG. 4.—*a*, a flower that has just opened; *b*, the same after being corked in a 20-liter flask of air for 24 hours; *c*, a flower that has just opened; *d*, the same after being exposed 12 hours to 1 part of illuminating gas in 40,000; *e*, result of treating a flower that just opened for 12 hours with 1 part of ethylene in 2,000,000.

of gas per 20,000 (four times killing concentration for three days' exposure). On a similar bud 5^{cc} for one day was considerably more injurious than 0.5^{cc} for three days. The stigmas did not project, but the petals were markedly discolored.

During the entire period of experimentation there was no very marked variation in the toxicity of the gas used.[1]

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[1] In determining the toxic limits we located a concentration that produced the effect while one-half that concentration did not. It is clear that this permits considerable variation without detection. It is not possible to locate the toxic limits more closely, due to the variation in the flowers. It is clear, however, that this gives a very good idea of the magnitude of toxicity.

ETHYLENE

The experiments with ethylene were begun by exposing buds just beginning to show the petals to 1, $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, and $\frac{1}{16}{}^{cc}$ of ethylene in 20 liters.

In each of these concentrations the buds were killed on three days' exposure. The usual signs of gas poisoning were noted; petals turned yellow and withered, and the stigmas projected. Since it was evident that these concentrations were far above the toxic limit, we resorted to the use of a 2 per cent. mixture of ethylene with air. Various amounts of this were used, until the toxic limits were definitely located. With 2^{cc} of this 2 per cent. mixture in 20,000 (1 part in 500,000), the results were similar to that obtaining with 1^{cc} of gas per 20,000 (1 part in 20,000). In *fig. 2, b* is a bud just showing the petals exposed to this concentration of ethylene for three days. Also 1^{cc} of 2 per cent. ethylene per 20,000 (1 part in 1,000,000) gives results similar to that shown by 0.5^{cc} of illuminating gas per 20,000 (1 part in 40,000). *Fig. 3* shows the results of such an exposure for three days on a bud just showing the petals. The growth of the petals is not sufficiently retarded to make the stigmas conspicuous; the petals remain fresh for several days but never open farther. Where much less than 1^{cc} of 2 per cent. ethylene per 20,000 was used with similar buds, three days' exposure did not prevent their opening.

When open flowers were exposed to the ethylene, it was found that 0.5^{cc} of the 2 per cent. mixture in 20,000 (i e., 1 part in 2,000,000) caused the closing within twelve hours. The result of such an experiment is shown in *fig. 4, e*.

It is seen from the data given above that ethylene must form approximately 4 per cent. of illuminating gas to be the constituent that determines the toxicity of the latter. It becomes necessary now to get an estimate of the fraction of the illuminating gas used that is ethylene. We have already stated that no absorbent used in gas analysis absorbs ethylene alone. In a special absorption chamber, packed in ice, 50 or more grams of bromin with 150^{cc} of water were placed, and measured quantities of illuminating gas passed through. When the bromin water was partially discolored, showing an almost complete exhaustion of the bromin, the resulting oil (a mixture of ethylene dibromid and other compounds resulting from the reaction of the gas constituents with bromin) was separated, washed with a weak solution of potassium hydrate, and later with distilled water. This oil was then dried with fused calcium chlorid and later fractionated. In the first distillation all the portion boiling between 129° and 134° C. was saved. This was later redistilled and the fraction boiling between 103° and 132° C. saved as representing the ethylene dibromid, since this compound boils at 131° C. About 3 per cent. of the dried material absorbed by bromin boiled between 130° and 132° C.; a small portion boiled at 129° C. or below. From this it rose up quickly to 131° C., where it again gave a considerable fraction. Then it rose rapidly to 139° C., where a considerable fraction distilled. In one trial, 208 liters of gas at 27° C. and under pressure of 745.5^{mm} of mercury gave 130^{gm} of dried oil; of this 44.2^{gm} boiled between 130° and 132° C. After correcting for pressure and temperature the following equation equals the percentage volume of gas that is ethylene:

$$\frac{22.4 \times 760 \times 44.2 \times 300}{208 \times 745.5 \times 178 \times 273} = 2.9+ \text{ per cent.}$$

In a second determination 138 liters of gas at 27° C. and 745.5^{mm} pressure gave 31.6^{gm} of oil boiling between 130° and 132°. Correcting for temperature and pressure, the following equation gives the percentage volume of ethylene in this case:

$$\frac{22.4 \times 760 \times 31.6 \times 300}{138 \times 745.4 \times 178 \times 273} = 3.2 \text{ per cent.}$$

It must be stated, however, that according to WINKLER (**17**) the absorption of ethylene by bromin is not complete, and farther that considerable ethylene dibromid is necessarily lost in washing, drying, and distilling, so that the percentage is probably considerably higher than here obtained. It must be urged also that the presence of other oils with boiling points rather near that of the ethylene bromid tends to make this fractionation less accurate.

4. General

It is of great interest to know that the most delicate chemical test for illuminating gas in the atmosphere falls far short of detecting amounts that work havoc with the flowers of the carnation. The tests for carbon monoxid are those used for detecting illuminating gas. The most delicate application of the blood test (see HEMPEL, p. 225) will detect 1 part of carbon monoxid per 40,000. The iodine pentoxid test (see HEMPEL, p. 226) is of equal delicacy. If carbon monoxid forms 25 per cent. of illuminating gas, these tests will detect 1 part of illuminating gas in 10,000. Upon three days' exposure 1 part of illuminating gas in 40,000 kills the young buds and the petals of the flowers just beginning to open; while 1 part in 80,000 causes open flowers to close upon an exposure of twelve hours.

The so-called "sleep" or closing of the carnation is a source of considerable loss to growers and dealers, for flowers that once close never again open. This "sleep" is especially likely to occur with cut flowers brought into city markets. Some varieties are so disposed to react in this way that their cultivation has almost entirely ceased. We know several homes lighted with gas where cut carnations can be kept only a few hours without "going to sleep." In one instance the displacement of gas lights by electric lights entirely overcame this difficulty. Our experiments show clearly that one cause of this sleep is traces of illuminating gas (ethylene) in the surrounding atmosphere.

STONE (**13**), WEHMER (**8**), and others have shown that illuminating gas diffuses great distances through the soil, especially if there is a hard-packed or frozen crust over the top. This paper shows the extreme sensitiveness of the carnation to this substance. From these facts it is evident that carnation growers whose greenhouses are in the region of gas pipes must take great precautions against losses from this source. It would be interesting to know whether solid cement walls set into the ground for some depth on the side next the pipes would furnish sufficient protection against leaks of this kind. It is clear that, if (as our results seem to indicate) the group of illuminants, or more accurately if one constituent of this group (ethylene) determines the toxicity of illuminating gas, coal gas is considerably less toxic than water gas, while oil gas is more toxic than either of the others; also the toxicity reported by the German investigators who used coal gas is less than that shown by the gas of the great American cities.

While it seems probable that the limit of toxicity of illuminating gas on the flower of the carnation is determined by the ethylene it contains, it does not follow that such is the case with all parts of plants or even with the flowers of all plants. It would be interesting to know the effects and toxic limits of illuminating gas and its constituents upon various double as well as single flowers. Similar data for the foliage of various plants such as Coleus, which is supposed to be especially sensitive to illuminating gas, would likewise be of interest.

5. Summary

1. The flowers of the carnation are extremely sensitive to traces of illuminating gas in the air.

2. With the Boston Market and pink Lawson three days' exposure to 1 part in 40,000 kills the young buds and prevents the opening of those already showing the petals. The buds of medium age are considerably more resistant.

3. In the same varieties 1 part in 80,000 causes the closing of the open flowers upon twelve hours' exposure.

4. This injury takes place directly on the bud or flower exposed and not indirectly through absorption by the roots.

5. No chemical test is delicate enough to detect the least trace of illuminating gas that will cause serious injury to carnations.

6. The "sleep" of the carnation is probably often caused by traces of illuminating gas in the air.

7. Ethylene is even more fatal to the flowers of the carnation.

8. Three days' exposure to 1 part in 1,000,000 prevents the opening of buds just showing the petals.

9. Twelve hours' exposure to 1 part in 2,000,000 causes the closing of flowers already open.

10. There is much evidence that indicates that the toxic limit of illuminating gas upon these flowers is determined by the ethylene it contains.

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FLORAL SUCCESSION IN THE PRAIRIE-GRASS FORMATION OF SOUTHEASTERN SOUTH DAKOTA

SEROTINAL AND AUTUMNAL FLORAL ASPECTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 117

LEROY HARRIS HARVEY

(WITH FOUR FIGURES)

Serotinal floral aspect

Climatologically and florally the serotinal is perhaps the most distinctly demarked of the aspects. The climatological changes which set it off from the estival are quite generally appreciated, while the general blooming of the pioneer sod-formers during the early part of July with the accompanying serotinal bloomers no less distinctly marks it in a floral way.

One records now less dissimilarity in aspect and tone on crest, slope, and base; the more open association, however, still marks the crest. The tone is determined by the dull-greenish vegetative stalks of *Solidago rigida* and *Helianthus Scaberrimus*, which occur copiously throughout the formation. It is relieved locally on lower slopes by the yellow of *Ratibida columnaris* and on upper slopes by the blue of *Verbena stricta* and the canescence of Amorpha; while *Meriolix serrulata, Brauneria pallida, Potentilla Hippiana, Erigeron ramosus, Polygala alba*, and *Euphorbia marginata*, all of which extend over from the estival, are less influential. A few conspicuous forms are added in this aspect, but never of sufficient abundance to strongly variegate the dull green of the tone given by the leafy stems of Solidago and Helianthus.

The general flowering of *Agropyron occidentale, Bulbilis dactyloides*, and the Boutelouas, together with *Kuhnistera purpurea* and *K. candida*, distinctly marks the inception of the serotinal aspect, which is characterized by the gradual appearance of few but conspicuous bloomers and the attainment of maximum flowering of late estival forms, rather than by the addition of numerous forms as in the

SEROTINAL CLIMATOLOGY

TEMPERATURE			WIND			RAIN			LIGHT			SOIL			MEAN RELATIVE HUMIDITY	RELATIVE EVAPORATION
Maximum	Minimum	Mean	Prevailing direction	Total movement	Hourly velocity	Days	Mean daily	Total	Mean cloudiness	Sunshine per cent.	Relative intensity	Mean holard	Mean echard	Mean chresard		
37° C.	11 C.	24 C.	S.	5682	7.7	10	.25$^{\text{cm}}$	7.95$^{\text{cm}}$	3.8	62	.604	12.4%	7.2%	5.2%	56.8	7.983

vernal and estival aspects, only thirteen new forms appearing during the aspect. It is moreover the aspect of the sod-formers, "floral" forms being represented by only six species. Several ruderals make their floral appearance in the formation during this aspect but, with the exception of *Cassia chamaecrista*, attain no conspicuousness.

The serotinal is markedly a period of extremes, bringing about a change to which one is generally sensible. During the early days of July the weather settles and there is a long succession of long and intensely hot and dry days, which condition characterizes the entire serotinal aspect. Relative evaporation (table) is at an extreme, though slightly less (0.81) than in the estival, finding its explanation in the lower (0.4) hourly wind velocity and higher (8.5) relative humidity; the hot dry winds from the south and southeast are now coexistent with the highest mean temperature, the lowest mean daily precipitation, a low relative humidity, and a high light intensity. Thus evaporation and transpiration are augmented to a precarious degree.

The chresard shows a continued decrease from the estival, being 6.5 per cent. on July 6 and 4 per cent. on July 24; while the average chresard is 5.2 per cent., the lowest yet reached. The holard of crest (8.2 per cent.), slope (12 per cent.), and base (12.2 per cent.) are now (July 28) more nearly approximate than in earlier aspects.

Relative evaporation at a maximum and

the chresard at a minimum are thus the ecological conditions which strongly mark the serotinal floral aspect.

SPECIES OF THE SEROTINAL FLORAL ASPECT

FACIES.—Bouteloua oligostachya,† B. hirsuta,† B. curtipendula,† Bulbilis dactyloides.*†

PRIMARY SPECIES.—Kuhnistera purpurea,† Verbena stricta,*† Ratibida columnaris,*† Kuhnistera candida,† Symphoricarpus occidentalis,*† Amorpha canescens.*†

SECONDARY SPECIES.—Agropyron occidentale, Carduus undulatus,* Euphorbia marginata,* Hymenopappus filifolius, Calamovilfa longifolia, Polygala alba.*

TERTIARY SPECIES.—Lygodesmia juncea, Lacinaria squarrosa, Brauneria pallida,* Meriolix serrulata,* Eriocarpum spinulosum, Erigeron ramosus,* Potentilla Hippiana.*

RUDERAL SPECIES.—Cassia chamaecrista, Onagra biennis, Amaranthus graecizans, Melilotus alba,* Chenopodium album, Lactuca canadensis, Apocynum cannabinum.

*From previous aspect. †Forming associations.

Agropyron occidentale is the first of the serotinal grasses to bloom. It is a xerophytic bunch-grass and occupies prairie crests, where it occurs copiously, rarely even of facial rank. It is one of the pioneers of the bunch-grass stage and is associated with the Andropogons, passing with these forms as they give place to the Boutelouas and being entirely absent in the older and more mesophytic prairie. In transitional stages from the bunch-grass open association to the less xerophytic closed sod association, Agropyron remains not infrequently in subcopious abundance as a relict of the earlier condition. The rootstock is here an efficient mode of propagation.

The three grama grasses, *Bouteloua hirsuta*, *B. oligostachya*, and *B. curtipendula*, which head out during the early days of July, enter upon anthesis almost simultaneously with the beginning of the second week of July, as does also the buffalo grass, *Bulbilis dactyloides*. The Boutelouas are pioneer sod-formers, following only the buffalo grass, which as the pioneer sod-former encroaches upon the bunch-grasses, replacing them and preparing the way for the Boutelouas which invariably follow closely. To the west, where the rainfall is much less, Bulbilis is the prominent sod-former and is the fodder grass of the great cattle ranges west of the Missouri. In our region it occurs along the xerophytic exposures of the bluff line, and as a xerophytic relict along the crest of prairie knolls, where it mingles with the gramas as they advance upon the bunch-grass stage, yet usually as a secondary element among these sod-formers. In our area, however, it is lacking.

Bouteloua hirsuta seems to be the pioneer of the gramas as they encroach upon Bulbilis, or upon the bunch-grasses where Bulbilis is absent, as is the case in our formation. It is in turn apparently followed by *B. oligostachya*, which seems to occur more abundantly and to occupy the most prominent place of the sod-formers. Frequently it alone encroaches upon the bunch-grasses, *B. hirsuta* being absent. Next comes *B. curtipendula* (*fig. 1*), which also contributes largely to the early prairie sod. In many places the Poa sod is the next to follow. The gramas are thus largely confined to the crests, decreasing in abundance downward, where they not infrequently rise to facial prominence. Contrary to the serotinal floral forms, the Boutelouas are of low stature, *B. curtipendula* alone rising above

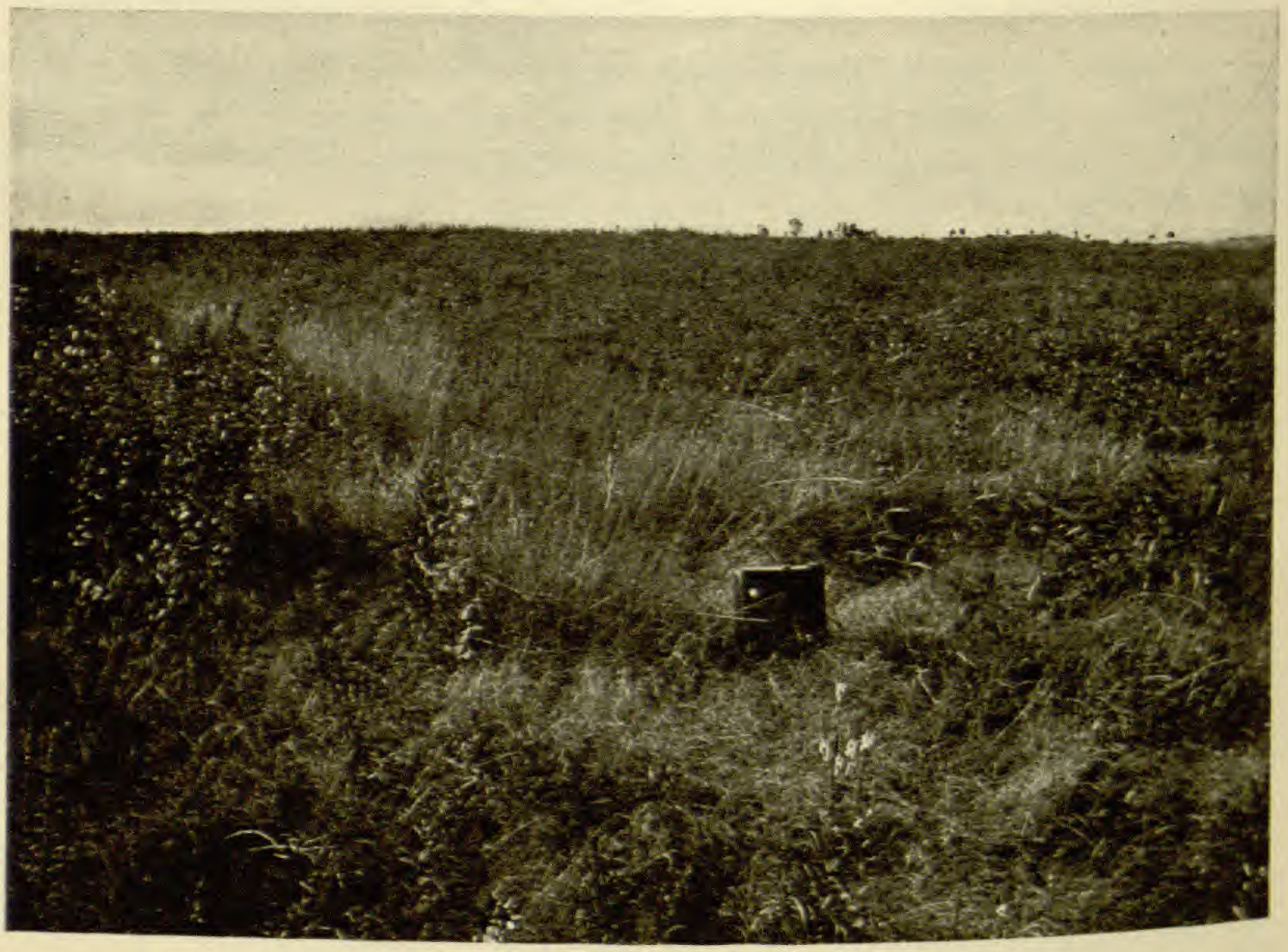

FIG. 1.—Serotinal aspect: *Bouteloua curtipendula* sod on upper slope; *Solidago rigida* to the left; *Helianthus scaberrimus* to the right; admixture in the background.

45^{cm}, which however may frequently reach 60 to 80^{cm}, and is the only species which becomes at all conspicuous. These species as they enter the open bunch-grass association form mats, which fusing form sod, finally resulting in the replacement of the bunch-grasses. The gramas are all perennial by means of the enlarged rootstocks.

Coincident with the flowering of the grasses is that of *Kuhnistera purpurea*, which seems to precede that of its related species *K. candida* by only a few days. The purple Kuhnistera is from its distribution and structure more xerophytic than the white-flowered species. The former occurs most abundantly on the higher slopes, decreasing in abundance downward; while the latter reaches its maximum abundance on the lower slopes, decreasing in the number of individuals per unit area upward. Along middle slopes the abundance of the two species approaches equality. Its distribution seems clearly related to the chresard of these various habitats. CLEMENTS (**'05**, pp. 233) in light of these facts has suggested the monophyletic origin of these two species from an ancestral form which became split up into *purpurea* and *candida* under the influence of and adaptation to a low and high chresard, a xerophytic and mesophytic habitat respectively, and has instituted experiments to test this theory. In their respective positions of maximum abundance each may rise to dominance, which, however, never occurs in the plot under study; the advanced condition of the prairie seemingly precludes such abundance in the closed association. However, they are the most conspicuous elements of the early part of the aspect. Their branching stalks rise 60 to 80^{cm} and are terminated by cylindrical spikes (some 8 or 9^{cm} long) of white flowers in *K. candida* and (some 5^{cm} long) of violet flowers in *K. purpurea*. They are perennials from thick and deep roots. The seeds are immobile, which with the perennial root accounts for their somewhat even distribution in the formation.

With the prairie clovers appear *Eriocarpum spinulosum* and *Lygodesmia juncea*. Eriocarpum is perennial from a deep woody root, whose much-branched stems rise about 30 to 40^{cm}, terminate in 1 to 25 heads fringed with yellow rays and 2.5^{cm} in diameter. In all it is very striking, but its rare occurrence along upper slopes and crests precludes more than a minor influence upon the tone. It seems to demand only a low chresard, and upon more xerophytic crests than occur in our formation, where it holds its own, it appears copiously and not infrequently determines the tone of the open association. The wind-distribution is facilitated by a copious pappus. Perhaps no plant of our formation has the remarkable degree of adaptability possessed by *Lygodesmia juncea*. The first plant to appear upon the bare exposed soil of bluffs, it persists into a well-formed mesophytic sod with even a marked abundance. It is to be reckoned as a xerophytic relict in our plot, occurring most abundantly along the crest, but at most only sparsely. It is a perennial from a heavy woody root, which interprets its persistence in the formation, and this with its reduced scalelike leaves contributes to its fitness as a pioneer xerophyte. The much-branched stems (45^{cm} high) end in solitary pink-rayed flowers, whose small size and ephemeral duration never render them florally conspicuous. Distribution is very general and wide; the achenes are provided with a copious pappus.

During the last days of the second week and early in the third week of July the prairie thistle, *Carduus undulatus*, enters upon anthesis and florally characterizes this part of the aspect. Its densely white tomentose and much-branched stems rise some 90^{cm} and terminate in large (5^{cm} in diameter) solitary heads of numerous purplish flowers. It also assumes a gregarious habit, and patches occur here and there from base to crest of prairie slopes. Thus it is a most conspicuous form, but reaches its maximum flowering only in early August. Wherever the prairie sod has been disturbed it becomes almost exclusive in its occupancy. It is a biennial of slightly mesophytic tendencies and so appears more commonly on lower slopes. Its high fertility and copious pappus insure a wide distribution, easily explaining its very general occurrence.

The last form to be added in the aspect is *Lacinaria squarrosa*, which appears here and there upon upper slopes and crests. It is very xerophytic in nature, occupying a prominent place in the early stages of the bluff line succession, and is in our plot to be considered as a relict. It is not conspicuous and adds little to the tone, which is at this time rendered bizarre by several of the earlier forms now in their greatest floral display. Lacinaria is an erect (50^{cm}) perennial herb from a tuberous structure, terminating in a spike bearing numerous heads of purplish flowers. The abundant plumose pappus assures a widespread distribution.

Autumnal floral aspect

No marked climatological change is to be noted in passing from the serotinal to the autumnal aspect, but simply one of gradually decreasing favorableness. Hence the latter has been set off partly for convenience of discussion, though it seems more or less distinctly characterized by definite floral activity; yet possibly it might be more accurately designated as late serotinal. Beginning in early August and marked by the estivation of such very conspicuous forms as *Helianthus scaberrimus*, *Solidago rigida*, and the bunch-grasses (*Andropogon furcatus* and *A. scoparius*), it extends into early October, when vegetative activity comes to an end. Its floral activity is terminated, however, in middle September by the flowering of *Gentiana puberula* and *Solidago rigidiuscula*, while florally the aspect is at its best during late August and early September, when the prairie is a sea of yellow from the Solidagos, mainly *S. rigida*, dotted here and there by the blue of Asters. Rising sentinel-like along higher slopes and crests are the rose-purple spikes of the blazing-stars, while on isolated knolls associations of *Aster sericeus* with their purplish flowers and white tomentose leaves relieve the sea of yellow. The bunch-grasses impart a very characteristic tone to the higher and more xerophytic knolls.

In earlier aspects marked restriction of forms was noted, less apparent in the serotinal it is here scarcely evident. On the other hand there is a marked identity of the controlling species on base, slope, and crest, the entire formation presenting an unbroken and identical covering, undoubtedly to be associated with the noticeable equality of the chresard throughout these various situations.

Eighteen of the twenty-two forms (82 per cent.) are composites, and all but one of these (*Kuhnistera villosa*) are wind-distributed. Like the prevernals the autumnals are pronouncedly xerophytic, fitting into uncertain, that is unfavorable, ecological conditions, the former at the initiation, the latter at the decline of floral activity. Just as prevernals have come to possess the spring period of not

AUTUMNAL CLIMATOLOGY

TEMPERATURE			WIND			RAIN			LIGHT			SOIL			MEAN RELATIVE HUMIDITY	RELATIVE EVAPORATION
Maximum	Minimum	Mean	Prevailing direction	Total movement	Hourly velocity	Days	Mean daily	Total	Mean cloudiness	Sunshine per cent.	Relative intensity	Mean holard	Mean echard	Mean chresard		
36 C.	4 C.	20 C.	E. & N.W.	5771	7.8	15	.26$^{\mathrm{cm}}$	15.9$^{\mathrm{cm}}$	4.0	63	.607	10.5%	7.2%	3.3%	55.4	4.671

over-favorable conditions, in the same degree the autumnals claim possession of that less suitable period during the closing days of vegetative activity, and for similar reasons. Each group has been able on account of peculiar characteristics to work into and occupy these periods unsuited for plants of less xerophytic tendencies, as their periods of growth and reproduction fitted into these seasons of the year, extremes in each case, where the great majority of forms could not succeed. As floral activity is more definitely restricted than vegetative, which is largely accomplished in earlier periods, it is also evident that the problems of pollination and seed dissemination must have been no small factor in working out through selection the floral restriction of these forms.

The following species extend over from the serotinal aspect, but are rendered inconspicuous by the overtopping layer of a few autumnal species: *Verbena stricta*, *Carduus undulatus*, *Ratibida columnaris*, *Meriolix serrulata*, *Polygala alba*, and *Lygodesmia juncea*. They become less and less conspicuous as the period advances.

As ruderals we may note *Melilotus alba*, coming over from earlier aspects, *Lactuca canadensis*, and *Salsola tragus*.

Conditions here are but the continuation and accentuation, during the early part of the aspect at least, of those of the serotinal. The maximum conditions there noted become less pronounced toward early September, and toward the middle of the month pass gradually into those more settled conditions of early fall in which maturation is so largely accomplished. However, the climatological conditions (table) of this aspect bear to its floral activity a relation analogous to that existing in the prevernal, and the forms here occurring seem in no less degree peculiarly adapted to the late seasonal conditions.

In August the wind is dominantly from the south and east, but in early September begins to swing to the northeast quadrant, where it remains until the prevernal, then swinging round again to the southeast. The average daily rainfall (0.26^{cm}) remains about the same as in the preceding aspect, though it falls on only 25 per cent. of the days, while in the serotinal it falls on 33 per cent. of the days. Relative humidity, sunshine per cent., and relative light intensity are noticeably similar in these two aspects, while relative evaporation has decreased almost a third. In the fact that the hourly wind velocity has increased only a tenth, and in the 4° C. fall in the mean temperature must be sought an explanation of this lowered evaporation.

SPECIES OF THE AUTUMNAL FLORAL ASPECT

FACIES.—Andropogon furcatus,† A. scoparius.†

PRINCIPAL SPECIES.—Solidago rigida,† Aster sericeus,† Helianthus scaberrimus,† Sporobolus brevifolius.†

SECONDARY SPECIES.—Solidago rigidiuscula,† S. missouriensis, S. nemoralis, Ratibida columnaris,*† Aster multiflorus, Artemisia gnaphaloides,* Verbena stricta,*† Carduus undulatus.*†

TERTIARY SPECIES.—Aster oblongifolius, Solidago canadensis,† Kuhnia glutinosa, Lacinaria scariola, Nabalus asper, Lygodesmia juncea,* Polygala alba,* Dysodia papposa, Grindelia squarrosa, Kuhnia eupatorioides, Lacinaria punctata, Gentiana puberula, Kuhnistera villosa, Meriolix serrulata.*

RUDERAL SPECIES.—Salsola tragus, Meliotus alba,* Lactuca canadensis.*

*From earlier aspect. †Forming associations.

During the early days of August four forms, destined later to become very conspicuous, make their floral appearance in the following order: *Solidago missouriensis*, *Helianthus scaberrimus*, *Solidago nemoralis*, and *S. rigida*. *S. missouriensis*, the first of the autumnal bloomers, occurs in subcopious abundance and most abundantly in the open association of the upper slopes and crests, where it is quite noticeable, though it never becomes a prominent feature of the tone because of its low stature and small panicles. It is distinctly xerophytic, as is evident both by its structure and distribution, and, as might be inferred, passes as the open formation gradually becomes closed, never being present in a compact sod at the base of the slope.

Appearing with *S. missouriensis* comes *H. scaberrimus.* It occurs both more frequently and abundantly than the former and is distinctly less xerophytic, reaching its greatest abundance upon middle and upper slopes. Its rigid, rough, and little-branched shoots, rising some 1.5^{m} and terminated by a spreading corymb bearing few conspicuous heads (3 to 5^{cm} wide) with numerous yellow rays, make it a conspicuous element of the early autumnal aspect, but it soon blends in the sea of yellow of *Solidago rigida,* which shortly comes on, completely dominating the floral tone. Helianthus (*fig. 2*) rarely holds its own along the tension line where the Poa sod is encroaching, but with other open association forms yields to its advancement, though it occurs inclusively in the less compact sods higher up the slopes, in which places it frequently assumes a copio-gregarious habit. The stiff sunflower is perennial by a thick root-

FIG. 2.—Late serotinal aspect: *Solidago rigida* and *Helianthus scaberrimus* on upper slope.

stock. A very limited pappus of two to four scalelike awns provides only a restricted distribution, easily accounting for its gregarious tendency.

About a week or ten days later *S. rigida* begins its blooming, but only reaches its maximum about the last of the month, at this time solely characterizing the floral tone and maintaining a sea of yellow for some three weeks, when the tone begins to pale as fruiting advances and completely gives way during the third week of September, the bright-yellow floral tone yielding to the dull-green foliage. The stiff goldenrod occurs ubiquitously, but reaches its greatest abundance upon middle slopes, where it is frequently copious. The single stout stem (frequently several), from the perennial rootstock, rises somewhat over a meter, terminating in a flat dense cyme bearing numerous yellow-rayed flowers, frequently 20 to 25^{cm} across, which with its abundance and frequency makes *S. rigida* the most striking and dominating in its floral tone of any single species of the formation. Following the latter species by only a few days *S. nemoralis* comes into bloom. Overtopped by and much less abundant than the former, it never is conspicuous, though frequently it adds to the dominant yellow tone of the aspect. It reaches its greatest abundance on slopes, occasionally entering the open association of the crests, but is rarely included in the compact sod of lower slopes.

The three goldenrods just noted are alike perennial from a thickened rootstock, with a tendency toward the formation of perennial basal rosettes, and are widely wind-disseminated through the efficiency of the well-developed parachute.

Almost coincident with the blooming of these four forms is that of the bunch-grasses, *Andropogon furcatus* and *A. scoparius*. Though these two grasses during the last two aspects have been vegetatively conspicuous upon the higher crests and most xerophytic slopes, where they contribute the characteristic dull tone to the bunch-grass association, they flower only during the early part of August, thereby adding but little to their already established prominence. They are accompanied by *Sporobolus brevifolius*, which occurs less abundantly, but like the beard-grasses assumes the bunch habit upon higher crests and ridges. In these situations the Andropogons assume facial rank, *A. furcatus* (*fig. 3*) being the taller and on account of its invariable bunch habit far the more conspicuous. *A. scoparius* (*fig. 4*) seems to form a very loose sod between the bunches of the former and extends lower down upon the slope, where in places it yields to the Boutelouas or rarely to Poa. In succession these forms seem to precede the Boutelouas. With a reduction of drainage and introduction of these sod-formers, the bunch-grasses yield, and in those portions of the prairie where succession has progressed most rapidly, for example the northwestern exposure, the Andropogons and the "bunch-habit" are conditions of the past. With *Agropyron occidentale*, the Andropogons and Sporobolus must be ranked as the pioneer grasses of the prairie, and as such hold a most important ecological relation in the structure and development of the formation. *A. furcatus* yields first, giving way to *A. scoparius*, which in places assumes facial abundance and frequently persists in a somewhat anomalous way in the more mesophytic associations. These grasses

FIG. 3.—Autumnal aspect: the bunch-grass, *Andropogon furcatus*, with intervening spaces occupied by Bouteloua sod near crest of prairie knoll.

are wind-distributed, to which end the hairy awned spikelets contribute. Being perennials from heavy resistant rootstocks, they are well adapted to the precarious pioneer position they occupy in the formation.

Two composites, taking a minor place in the formation, must be mentioned. While belonging to the formation proper, they function mainly as ruderals. *Dysodia papposa*, which blooms at the beginning of the autumnal aspect and often earlier, occurs everywhere along roadsides and on wastes, where it attains its greatest size and abundance. Frequently on the most xerophytic of prairie hills and bluffs it assumes a very marked prominence. In our area it occurs subcopiously along crests and ridges, in fact anywhere that the association may be open, though it is usually depauperate in such cases. The fetid marigold is an annual, and its ubiquity finds cause in the ease and abundance of its dispersal through an efficient pappus, and in the period of its germination falling at the time when the majority of forms have long since germinated and the formation is thinning off its early annuals and prevernal and vernal perennials. To these

FIG. 4.—Autumnal aspect: an Andropogon sod, mainly *A. scoparius*, upon crest of knoll; scattered individuals of Solidago, Helianthus, and Aster are present.

reasons must further be added its high degree of adaptability for germinating under these less favorable serotinal conditions.

The other form here included is *Grindelia squarrosa*, which occurs only sparsely and then almost entirely along lower slopes and frequently included in the Poa sods. On account of its scattered distribution, the gum plant usually grows about 50^{cm} high and branches much and more or less symmetrically, so that with its many heads of yellow ray-flowers it becomes quite noticeable in early September. Grindelia is a perennial from a heavy rootstock. The few awned achenes are inclosed in a glutinous head, consequently distribution is restricted, and correspondingly a gregarious tendency is to be noted.

During the last two weeks of August several forms of secondary prominence in the floral tone progressively bloom. They are *Solidago canadensis*, *Lacinaria scariosa*, *L. punctata*, *Artemisia gnaphaloides*, *Kuhnia glutinosa*, and *K. eupatorioides*. *Solidago canadensis*, the most mesophytic of our goldenrods, seems to be confined exclusively to Poa sods in valleys and at the base of slopes. It is here gregarious in tendency, occurring in isolated patches or clumps. Also upon disturbed soil around coyote burrows it usually establishes itself in dense patches. It rises about a meter, with several shoots from the same large perennial rootstock, branches profusely, bearing numerous heads in dense panicles, and in all is most conspicuous along with Grindelia at the base of slopes and in valleys. Its distribution by well-developed pappus is extensive, though its demands for the highest ecological conditions greatly restrict its establishment.

The two button-snakeroots, *Lacinaria scariosa* and *L. punctata*, bloom about the beginning of the last week of August, and though sparse in their distribution, being confined to crests, ridges, and the open association of upper slopes, they rise like sentinels of the prairie, relieving the blaze of yellow by touches of purple. *L. scariosa* seems more mesophytic than *L. punctata*, blooming usually a few days later and upon upper slopes mainly. It is also much taller and the heads are larger than in the latter and so more prominent. The numerous short-peduncled heads of purplish flowers, borne upon the erect unbranched and usually solitary stem from a prominent tuber, give these forms a most striking appearance. Copious pappus assures a wide wind-distribution.

The prairie mugwort, *Artemisia gnaphaloides*, is gregarious upon upper slopes. Here it forms dense patches, and these, on account of the white tomentosity of its stems and leaves, which are frequently 50^{cm} high, are conspicuous in the dominant tone of yellow. It bears to the autumnal quite the relation that the Antennarias hold to the prevernal and vernal tone. Perennial from a tuber-like root, it is also xerophytic in tendency. In its pappate achenes and root-propagation are found the causes of its gregarious habit.

The closing days of August are marked by the estivation of the two false bonesets, *Kuhnia eupatorioides* and *K. glutinosa*. They both occur but rarely and then mainly upon upper slopes and crests. They form little clumps (several shoots from the same perennial root) and are tall (50 to 75^{cm}) and much branched, but on account of their small few-flowered heads of creamy-white color and their only occasional frequence, they never attain any prominence. However, they become much more noticeable when the rich white pappus spreads in maturation, during the second week of September. *K. eupatorioides* is more mesophytic and so occurs more frequently over the formation. *K. glutinosa*, however, is pronouncedly xerophytic, and is restricted in its distribution to the open association along crests and higher slopes. The abundant barbulate pappus assures prolific invasion, though establishment seems to be very limited, doubtless due to the apparently low degree of adaptability possessed by these forms.

The Kuhnias are accompanied by *Nabalus asper*, which is restricted to lower slopes, is of rare occurrence and thus always a minor element. Though it is of the upper layer and bears numerous heads of pale-yellow flowers, it blends into inconspicuousness in the general tone. It is a perennial from a tuberous root. A well-developed parachute insures wide dissemination, but high ecological demands preclude more than a rare establishment upon the prairie.

The early days of September are well marked by the blooming of four forms which occasionally attain more or less restricted prominence: *Aster sericeus*, *A. multiflorus*, *A. oblongifolius*, and *Kuhnistera villosa*. They are all of evident xerophytic tendencies and occur mainly upon the upper slopes and crests. Appearing at a time when there is an apparent decline in the dominance of the earlier tone, and occurring in the open association, the Asters become quite noticeable though they are all of a lower layer than *S. rigida.* The silky Aster, *A. sericeus,* usually of low abundance and general occurrence, frequently becomes copious on bunch-grass knolls, there forming very distinct associations. Rising some 50^{cm}, with numerous spreading branches terminating in prominent heads (2 to 3^{cm} in diameter) with numerous violet rays, and bearing abundant leaves which are densely covered above and below with a silvery-white silky pubescence, this Aster is always a conspicuous element of the middle and late autumnal aspect. Its achenes are equipped with a medium pappus. It is a perennial from a thickened rootstock.

The two other Asters are similar in frequency and abundance to *A. sericeus,* but never attain its prominence. Of these *A. oblongifolius* always occurs with *A. sericeus* in the open association. With us it always remains depauperate. Seldom more than 30^{cm} high, it is ever inconspicuous, though its bluish rays make it noticeable at short range, since it is usually overshadowed by *A. sericeus.* It is a perennial and is wind-distributed; a copious pappus serves to bring about a general invasion, which, as in the other Asters, seems to be coupled with a high percentage of establishment, especially in the open xerophytic associations of the formation. The dense-flowered aster, *A. multiflorus,* occurs perhaps more frequently but less abundantly than the former, and is similarly a xerophyte of the open association, in which situations it never reaches other than a reduced stature. However, its bushy spreading branches, thickly beset with numerous small white heads, invariably make it more prominent than *A. oblongifolius,* particularly when it occurs in patches. It seems to work down upon the lower slopes, here attaining a greater stature and abundance as well as a greater prominence in anthesis.

All the Asters are perennial from rootstocks and form small basal rosettes, and are wind-disseminated.

The hairy prairie clover, *Kuhnistera villosa,* is a perennial from a deep tuberous root. Densely silky pubescent, abundantly branched, and terminating in cylindrical clustered spikes (3 to 6^{cm} long) of rose-purplish flowers, it is in itself quite conspicuous, but its restricted frequency and rare abundance make it rarely a tonal component in the formation. In the bunch-grass formation it becomes, with *Amorpha* *canescens*, more abundant but never controlling. It is distinctly xerophytic, and while largely of the open association, it may work down slopes into more favorable habitats.

During the middle days of September the last two forms of the prairie-grass association present their flowers, *Gentiana puberula* blooming a few days before *Solidago rigidiuscula*, the last form to bloom. The downy gentian occurs rarely and is largely restricted to middle and lower slopes, rarely if ever occurring along the xerophytic crests and ridges. Its terminal group of few large light-blue flowers are rendered unimportant as the plant is of short stature (30 to 40^{cm}) and so hidden. It is perennial from thickened roots, and wind-distributed, the seeds being widely winged. Its rarity therefore lies no doubt in its high ecological requirements, being somewhat mesophytic in its nature.

The last form of the prairie to bloom is *Solidago rigidiuscula*. Flowering as it does when *S. rigida* is passing into fruit, of copious abundance and high frequency upon upper slopes, occurring gregariously at times with several stalks (5 to 15) arising from the same perennial root, it is rightly named the "showy" goldenrod. It persists nearly to the middle of October, and is one of the last forms to pass into fruit, though accompanying it are the later flowers of Meriolix, Ratibida, Carduus, Polygala, and Lacinaria. It is widely wind-dispersed and establishment is quite general.

Post-floral aspect

By the second or third week in October the prairie forms of the autumnal floral aspect have all passed into seed, and the gorgeous yellow of *Solidago rigida* has given way to the somber brown of frosted leaves and stalks. While seed maturation and distribution in species of earlier aspects have been in progress during the subsequent aspects, the post-floral aspect, extending up into late November, is particularly characterized by this phase of plant life, yet dispersal may and does continue, but in a much more limited degree even during the winter season. The little fall of snow leaves the prairie bare the greater part of the winter, its tone being in no way modified; the post-autumnal appearance remains to characterize the prairie throughout the non-flowering period, and, as has already been pointed out, extends up to and even dominates the prevernal and vernal floral aspects.

Summary of the structure of the formation

The formation is strictly of the prairie-grass type, its facies being determined mainly by six species: *Bouteloua oligostachya*, *B. curtipendula*, *B. hirsuta*, *Koeleria cristata*, *Andropogon furcatus*, and *A. scoparius*, to which must be added *Poa pratensis* in valleys and on lower slopes. The Andropogons are the main sod-formers of crests and ridges, while the Boutelouas characterize the higher slopes, working up to the crest and ridges. Koeleria seems to be more closely associated with the Boutelouas, occurring on middle slopes mainly. With these are associated three sedges and seven other grasses, which are all important as cooperating sod-formers, some of them ranking as primary species in the formation. We may mention *Carex pennsylvanica*, *C. festucacea*, and *Sporobolus brevifolius* as perhaps the more important of these. It is to be remarked that the sedges are all pre-estival, while the grasses are all estival or post-estival in their floral activity; the first facies to bloom is Koeleria in the estival aspect, while the Boutelouas are serotinal and the Andropogons autumnal.

Upon this facial background of grasses there progressively appear several conspicuous flowered forms of primary importance, which with numerous secondary and tertiary species serve to impart a bizarre aspect to the formation when considered as a whole and a kaleidoscopic shift with seasonal succession. In passing it is well to note that species primary in their own floral aspect may be of only secondary or tertiary importance when the formation is considered as a unit. Among these primary species we may note the ubiquitous *Antennaria campestris*; the Spesias and Sisyrinchium of middle slopes; *Amorpha canescens* upon upper slopes and ridges; Ratibida upon lower, and Verbena and *Erigeron ramosus* upon upper slopes; Symphoricarpus in valleys and on lowest slopes; the Kuhnisteras upon slopes, *K. purpurea* occupying the upper slopes, while *K. candida* extends downward upon lower slopes; *Solidago rigida* and *Helianthus scaberrimus* of great frequency and abundance; and finally *Aster sericeus* upon isolated knolls.

Among the more important of the secondary species may be mentioned *Viola pedatifida* and *Oxalis violacea* of middle and lower slopes; *Meriolix serrulata* of higher slopes; the Lithospermums of the more xerophytic portions of the formation; *Plantago Purshii* of middle slopes; *Linum rigidum* in the open association; *Potentilla Hippiana*, *Carduus undulatus*, and *Polygala alba*, which occur on middle and lower slopes; *Solidago rigidiuscula* and *S. nemoralis* upon lower and middle slopes, and *S. missouriensis* upon upper slopes mainly; and finally *Aster multiflorus* and *A. oblongifolia.*

Considering the ground association, the open association prevails over ridges and crests and extends down somewhat on slopes, passing gradually through a transitional condition into the closed association which occupies the valleys, depressions, and base of slopes, working always up or outward, displacing the open association. *Poa pratensis* establishes the most dense association, but the Boutelouas, Koeleria, and Festuca exert perhaps a more extensive influence in reducing the open association. In this connection it should be noted that the Andropogons are *par excellence* the pioneers, breaking up the xerophytic open association upon the highest and most xerophytic crests, preparing the way for the Boutelouas. It may be possible that in some cases the Andropogon bunch-grass stage was not the pioneer society, but that on account of more favorable soil moisture conditions, largely a question of drainage, the Boutelouas were the initial sod-formers. However, upon crests and ridges of excessive drainage the Andropogons have invariably preceded the Boutelouas and Koeleria. Occurring rarely in the open association is an undetermined xerophytic moss, while two species of the Basidiomycetes have been noted in the more mesophytic portions of the formation.

The enumeration of species includes 90 forms belonging to the formation proper and some 18 ruderals which work into the formation from the contiguous cultivated regions. The most abundant and prominent of the latter are *Cassia chamaecrista*, two species of Melilotus, *Hordeum jubatum* on lower slopes and moist soil; *Panicum capillare*, *Verbena bracteosa*, and *Amaranthus graecizans* of the more open associations; *Onagra biennis* of general occurrence; Salsola of the open association; and finally *Lepidium virginicum*, which not infrequently becomes quite abundant in the open association of higher slopes. These ruderals are characteristically confined to marginal invasion, though they are frequently found wherever the open association makes possible their establishment. Onagra, however, is able to establish itself in the closed formation, as is *Potentilla monspeliensis*. Hordeum especially makes advance where some artificial agency has destroyed the equilibrium in rich moist stations; frequently in such cases it assumes even facial rank.

The 90 prairie elements proper have a most interesting taxonomic distribution. The composites with 29 species (32.2 per cent.) form the dominating family, comprising nearly a third of the total forms. The Gramineae number 15 species (16.6 per cent.), and though not leading in species they rank first in number of individuals. The third important family is the Leguminosae with 11 species (12.2 per cent.). Thus these three families provide 61 per cent. of the prairie elements and perhaps over 90 per cent. of the individuals. The remaining 35 species (39 per cent.) are conspicuous on account of their diverse affinities, belonging as they do to 22 different families, 14 of which have only a single representative in the formation. The families are as follows: Borraginaceae (4), Ranunculaceae (3), Cyperaceae (3), Onagraceae (3), Scrophulariaceae (2), Linaceae (2), Rosaceae (2), Oxalidaceae (2); and the following with one species each: Nyctaginaceae, Cruciferae, Umbelliferae, Iridaceae, Violaceae, Euphorbiaceae, Caprifoliaceae, Solanaceae, Labiatae, Plantaginaceae, Gentianaceae, Verbenaceae, and Polygalaceae.

The life conditions of the formation are by no means equable, and in this relation it is significant to record that only 11 per cent. of the species are annual, the majority of which produce abundant seeds and are provided with efficient means of distribution and occur mainly in the xerophytic open associations. Of the remaining 89 per cent. which are perennials, 96.2 per cent. are geophytic; Rosa, Symphoricarpus, and Amorpha alone are woody.

In a region characterized by strong prevailing winds it is to be noted that a high percentage of the species is wind-distributed. An analysis of this point shows that about 90 per cent. are so disseminated, some 55 per cent. showing especial facilities to this end. The great range of specific forms and their marked frequency in the formation finds an explanation in this permobility of reproductive organs possessed by such a large percentage of its components.

As to pollination, 20 per cent. of the forms are wind-pollinated, while 80 per cent. have their pollen transferred by insects, the sedges and grasses comprising the former group.

Conclusions

1. The formation is a part of the Niobrara Prairie Region of CLEMENTS. In composition it is transitional. More truly a part of the prairie to the west, yet it contains several pioneer forms from the more mesophytic prairies to the south and east.

2. These two groups of elements during post-glacial migration have entered along two distinct lines of advance. The former migrated northwestward from a southwestern center of dispersal, while the latter followed a northwestern track up the Mississippi and Missouri valleys.

3. The prairie is pre-glacial in origin and is descended from the climatic prairie of Tertiary times, which arose in response to reduced precipitation caused by the upheaval of the Rocky Mountains at the close of the Cretaceous.

4. The climate is typically a prairie climate. A relatively dry resting season from October to March, in which only 16 per cent. (10.4^{cm}) of the total precipitation falls, and a moist growing season from March to September, in which 83 per cent. (49.31^{cm}) of the precipitation is distributed over sixty days, with 25 per cent. concentrated in April and May, insures a prairie formation. On the other hand, the annual low relative humidity, the dry and high winter winds accompanying high temperature, low winter rainfall, absence of a snow blanket, and the hot, dry summer of low precipitation are inimical to tree growth.

5. The absence of trees upon the prairie is primarily to be explained upon historical lines. The prairie was climatically determined and successfully and successively maintains itself against tree invasion from the edaphically determined arboreal fringes along flood plains and in ravines.

6. The northern slopes are the last to recover from winter, but are most mesophytic. It is up these slopes that the Poa sod and the

shrub association of Symphoricarpus and later *Rhus glabra* advance, preparing the way for the bur oak–slippery elm association, which likewise makes its greatest progress up these slopes from ravines and flood plains.

7. The floral activity of the formation may be approximately recorded in the following five aspects, set off by marked climatic and floral changes: prevernal, April 1 to April 25, 6 species; vernal, May 3 to May 31, 28 species; estival, June 1 to July 7, 21 species; serotinal, July 7 to August 7, 13 species; autumnal, August 7 to September 21, 22 species.

8. The prairie elements show a marked grouping into vertical layers, which correspond approximately with the floral aspects. Overtopped by the autumnal layer the sub-layers are successively those of the serotinal, estival, vernal, and prevernal.

9. There is a marked distinction in the chresard of base, slope, and crest in the prevernal, which becomes less marked in the subsequent aspects, approaching equality in the autumnal. As a result, the floral covering shows a corresponding difference upon base, slope, and crest in earlier aspects; the influence of position gradually declines, the floral covering presenting a striking similarity over the entire formation in the autumnal.

THE UNIVERSITY OF CHICAGO

BRIEFER ARTICLES

A PARASITIC ALGA, *RHODOCHYTRIUM SPILANTHIDIS* LAGERHEIM, IN NORTH AMERICA

During February, 1908, Dr. F. L. STEVENS, of the North Carolina Agricultural College, sent me a few dried leaves of the common ragweed, *Ambrosia artemisiaefolia*, which contained a very interesting parasite. Externally it suggested the appearance of a Synchytrium, because of the numerous minute red dots distributed beneath the surface on the petioles and veins of the leaf and on the stem, although there was no gall formation similar to that caused by species of the Synchytriaceae. A section of the host, however, showed clearly that it was very different from any of the members of this family. Maceration or teasing of the host tissue revealed the presence of a mycelium, and the crowded condition of the fruit bodies suggested the genus Cladochytrium. Further study proved, however, that it was a unique type, very different from members of this genus. Since the material received was dead, it was impossible to obtain the zoospores, and Dr. STEVENS kindly promised to have fresh material sent me at stated times during the summer.

Beginning in the month of June, material was collected by Mr. J. G. HALL, assistant in botany at the North Carolina Agricultural College, and mailed once a week. Entire plants were collected, the roots were washed, and then packed mostly in pasteboard boxes with wet sphagnum. In this way they reached me in two or three days after shipment in very good condition, so that some of the parasitized ragweed plants were transplanted in the open and others in pots where they continued to grow.

From a study of this material I have been able to obtain the zoospores from the temporary zoosporangia and to work out certain stages in the life-history of the parasite. While searching the literature for unique forms of plant parasites, I discovered that this plant had been described fifteen years ago.

This remarkable parasite is *Rhodochytrium spilanthidis* Lagerheim.[1] It was first discovered by LAGERHEIM in 1889 near Quito, Ecuador, and later was observed by him in other provinces of Ecuador. In Ecuador it is parasitic on the stems and leaves of a species of Spilanthes, one of the

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[1] LAGERHEIM, G. DE, Rhodochytrium, nov. gen., eine Uebergangsform von den Protococcaceen zu den Chytridiaceen. Bot. Zeit. 51:43–53. *pl. 2.* 1893.

Compositae. LAGERHEIM searched diligently but in vain to find it on other genera of plants. Its discovery in North Carolina, therefore, is a matter of considerable interest, not only because it naturally occurs on a different host, but because of its existence in the north temperate zone as well as the temperate section (mountain regions) of the tropics. Its North American host, *Ambrosia artemisiaefolia*, is not very distantly related to the South American host Spilanthes, the former belonging to the section Heliantheae-Ambrosiinae, while the latter belongs to the section Heliantheae-Verbesininae.[2] The question of its distribution becomes an interesting one, as to whether it is distributed over the intervening territory of Mexico, Central America, Panama, and other tropical countries; or whether it has been by chance imported from one country to the other through commerce; or finally whether ages ago, when the territory from the southern United States to Ecuador may have had a different climate, the parasite might have existed throughout this range, but now is separated by a tropical belt. I hope that collectors may be on the lookout for it in other parts of the United States and also in the intervening tropical region. I should be very glad to receive material in order to obtain further information as to its distribution.

The form of the plant may be briefly described as follows: When mature it may be likened to a miniature flask with a long slender tortuous neck; while from the base, or from the sides or both, rhizoid-like processes extend, which branch profusely in a very peculiar and characteristic manner. In general its form might be likened to that of a giant Entophlyctis, one of the chytridiaceous endobiotic parasites of the algae. In its development the zoospore, at rest on the epidermis, germinates, the germ tube enters between the cells and moves on toward a fibrovascular bundle where it branches, the branches making their way between the cells parallel with the bundles, so that on the stem the mycelium extends both upward and downward. On the leaves the parasite is also confined to the vascular bundles. The entire mycelium at certain stages of development is crowded with a reddish-yellow oil, which at maturity of the temporary zoosporangia, or of the resting sporangia, is withdrawn along with the protoplasm into the main body of the plant. The zoosporangium rests within or on a fibrovascular bundle and arises by a swelling of the mycelium at the point where the entering germ tube branches. The sporangia vary greatly in shape. They are oval, subtriangular, elliptical, etc., and vary from 50 μ in diameter (the smaller ones on the leaf) to 200–300 μ. The terminal mycelium is provided with numerous short haustoria, many of which are applied very closely to the spiral ducts. In the resting sporangia the wall

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[2] See HOFFMAN in ENGLER AND PRANTL, Pflanzenfamilien 4^5: 220 and 226.

of the mycelium next to the fruit bodies becomes very thick, also that of the entering germ-tube, while the wall of the zoospore in all of the plants remains as a small trumpet-shaped expansion of the end of the tube on the surface of the host. Starch grains are abundant in the larger portions of the mycelium and in the sporangia. The wall of the resting sporangium consists of three layers, the inner being laid down by the protoplasm after its accumulation in the main part of the plant body, and is thus not continuous with the mycelium which, however, usually becomes plugged after the withdrawal of the protoplasm. The walls of the resting sporangia are yellow at maturity, while the content is dark red.

The temporary zoosporangia have a thinner wall than that of the resting sporangia, and at maturity develop a stout exit tube, the end of which opens by a pore, the margin of which grows inward by invagination. The zoospores when swimming rapidly are elliptical in form, with the red oil in minute drops at the forward end, where are the two cilia. As they slow down they become rounded and are 8–10 μ in diameter.

LAGERHEIM considered this plant to be an alga devoid of chlorophyll, though LINDAU[3] says that on account of the lack of chlorophyll it cannot be classed with the algae.

The alga to which Rhodochytrium appears most closely related, according to LAGERHEIM, is Phyllobium, discovered by KLEBS[4] (*Phyllobium dimorphum* in leaves of *Lysimachia nummularia* and more rarely in *Ajuga reptans*, *Chlora serotina*, and *Erythraea centaurium; Phyllobium incertum* in dead Carex leaves). It is an intercellular parasite and *P. dimorphum* has also a definite relation to the vascular bundles. In this species the enlarged portion of the plant body contains chlorophyll in the protoplasm, as well as a reddish-yellow oil and starch. The branched rhizoid processes are devoid of chlorophyll. Resting spores only are known. They are packed with the reddish-yellow or orange-red oil and starch and possess a thick wall with several layers. The zoospores are biciliate.

A more extended paper is in preparation, dealing fully with the question of development, morphology, physiology, and cytology of this remarkable plant. This note is published in the hope that it will stimulate a search upon the ragweed and other possible hosts for this parasite, and I should consider it a great favor to receive material from different observers in case it is found.—GEO. F. ATKINSON, *Cornell University*.

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[3] ENGLER AND PRANTL, Pflanzenfamilien 1[1]**:528. 1900.

[4] KLEBS, G., Beiträge zur Kenntniss niederer Algen formen. Bot. Zeit. 39:249–257, 265–272, 281–290, 297–308, 313–319, 329–336. *pls. 3, 4.* 1881.

NOTE ON BALANCED SOLUTIONS

Some statements by Professor W. J. V. Osterhout in the February number (p. 125) of the Botanical Gazette in reference to balanced solutions require correction.

1. Balanced solutions, which are *not* complete culture solutions, were constructed and described[1] by me in 1892.

2. A balanced solution, which is at the same time a complete culture solution, is the solution of Knop, proposed about sixty years ago. The "confusion" supposed by Osterhout does not exist in this particular.

3. Osterhout claims to have discovered an antagonistic action of potassium to magnesium. But I observed long ago that secondary potassium phosphate can retard the poisonous action of magnesium sulfate;[1] and also that another potassium salt—the monopotassium phosphate—*accelerates* the poisonous action of magnesium sulfate.

4. Osterhout claims to have discovered a poisonous action of potassium salts. But I have observed Spirogyra alive for three weeks in a 0.3 per cent. solution of KCl[2], and alive for ten weeks in a 0.1 per cent. solution. In a 0.3 per cent. solution of K_2SO_4, the alga cells remained alive for over four weeks. The definition of Osterhout, therefore, must be restricted to certain conditions. I have deprived young barley plants of endosperm, and kept them alive in 300^{cc} of a 0.5 per cent. solution of K_2SO_4 for over two months. Is it possible that here the small amount of magnesia in the plants has counteracted the "poisonous" action of the large amount of potassium salt?

5. A pupil of Osterhout claimed recently to have discovered a poisonous action of calcium salts. This is not in accordance with my observation that Spirogyra can remain alive for over sixty days in a 1 per cent. solution of KCl. "Poisonous," however, is a relative and elastic term. The favorable effect of lime upon the development of root hairs, mentioned by that author, I observed long ago.[3]

6. I cannot agree with the opinion that the antagonistic relation of potassium to magnesium has the same cause as that of calcium to magnesium. I suggested an explanation of the poisonous action of magnesium sulfate, and also of the antagonistic action of calcium salts, in 1892.[4]

[1] Flora 75:382. 1892.

[2] Loew, O., and Aso, K., On physiologically balanced solutions. Bull. Coll. Agric. Tokyo 7:no. 3. 1907.

[3] Flora 75:384. 1892; Bull. Bureau Pl. Industry, no. 45, pp. 51, 52.

[4] Flora 75:376, 383. 1892; Bull. Bureau Pl. Industry, no. 45. My explanation has been adopted by one author, from somewhat similar observations, but without giving credit.

Since my views hold good also for the animal body, it gave me great satisfaction when MELTZER and AUER[5] published recently a series of wonderful experiments on the living animal, from which they inferred that "the continuation of the studies led up finally to the discovery that *calcium is rather the strongest antagonist to the inhibitory effects of magnesium.*" This is exactly what I have claimed for plants!—OSCAR LOEW, *Munich, Germany.*

FORMATION OF ADVENTITIOUS ROOTS IN THE UMBRELLA CHINA TREE

(WITH TWO FIGURES)

A curious case of "self-eating" may occasionally be found in hollow and decaying trunks of the umbrella China tree (*Melia Azedarach umbraculifera*). During a heavy storm in July, 1908, several large trees of this kind were blown down, the breaks occurring at the point where the main

FIG. 1

FIG. 2

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[5] Amer. Jour. Physiol. 21:403. May 1908. Communication from the Rockefeller Institute, New York. These brilliant investigations obscure all others made with such salts on animals.

trunk had been sawed off many years previously. Adventitious sprouts had grown out at the top and around the edges of the stump, and had formed a complete circle of stout limbs. In time these limbs will completely heal over the cut surface so as almost to obliterate the wound. The wood of the stump soon decays, however, and into this decaying mass there project dense mats of adventitious roots which spring from the point of origin of the limbs. These roots descend through the decaying materials and often, upon reaching the harder, less decayed wood of the lower part of the stump, turn sharply back and grow upward even to the point of origin. Fine fibrous roots may be found working down into the harder portions. *Fig. 1* shows a portion of a tree which had broken off about six feet from the ground; the roots shown are about two feet long. *Fig. 2* shows a limb that had broken off from a stump. The bent roots in the center were originally so sharply bent as to bring the parts parallel, but were separated for photographing. It will also be seen from this photograph that adventitious roots may arise from any part of the inner wall of the decaying stump.—O. M. BALL, *College Station, Texas.*

CURRENT LITERATURE

BOOK REVIEWS

The Bonn Textbook

A new English edition[1] of this well-known textbook may be made the occasion to refer to the contrast between German and American instruction in botany. It is perhaps safe to say that the *Bonn textbook* is the most extensively used text in Germany, and that in its English translation it dominates in American colleges. And yet, from the American standpoint it is more a book of reference than a textbook in the usual sense. Its organization and its demands are peculiar to the German mind and the German system of education. To divide a book into "general botany" and "special botany," and especially to discover that these titles are arbitrary rather than significant, suggest some rigid, old-fashioned curriculum rather than a logical presentation. "General botany" that includes no contact with the great groups, no basis for the evolution of the plant kingdom, no large conception of any kind, is surely a misnomer. It is made to include "morphology," a morphology that does not consider the development of groups, which means a long-abandoned morphology. Then this morphology (170 pp.) is divided into "external morphology" and "internal morphology" (subtitle "histology and morphology"). The "external morphology" is really the old type, when "flowering plants" furnished almost the only material of botany. It is not a question as to the accuracy of the facts, or to their importance, but simply a question of organization. Such an organization does not represent the development of botanical science today, and it does harm if it leads the student to a misconception of the content of the great divisions of botany. Nor is the organization and presentation of this so-called "morphology" its only antique flavor; for when one finds in the textbook sections on the "metamorphosis" of shoots, of leaves, of roots, he wonders why this point of view has never been changed.

The section on physiology (153 pp.) by the late Dr. NOLL is in the main an excellent and well-ordered presentation of the facts, though here and there it has not been revised to date. Thus, the fable of the ant plants still appears with all its frills (p. 235), and the physics of absorption is decidedly antique. The peculiarity of this section most open to criticism is the remarkably vitalistic attitude of the author. To say that "any attempt to explain vital phenomena solely by chemical and physical laws could only be induced by a false conception

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[1] STRASBURGER, E., NOLL, F., SCHENCK, H., KARSTEN, G., A text-book of botany. Third English edition, revised with the eighth German edition, by W. H. LANG. pp. x+746. *figs.* 779. London: Macmillan & Co. 1908.

of their real significance and must lead to fruitless results," is to decry all investigation; for that is just what every physiologist in the twentieth century is doing. That "physical attributes . . . . can never explain qualities like nutrition" is a bold prophecy and a most discouraging one, though we be yet far from that goal. "Strictly physical and chemical processes" are contrasted with "strictly vital" ones, in that with the latter it "becomes impossible to predict what effect a particular cause will produce." True; but only because we do not know enough. NOLL disclaims "vital force" in terms, but constantly writes as though it were a necessary assumption.

The second part, entitled "Special botany," is doubtless the part of the book that gives it its deserved rank among texts. It is really and dominantly modern morphology as to facts, but not in spirit. It is a well-selected thesaurus of morphological information, in using which one feels a certain measure of confidence, and this is what has made the book indispensable. But the controlling spirit of morphology is lacking, because there is no conception of continuity in the plant kingdom. To an American teacher of botany this means that the facts are dumped down in piles, with no attempt to use them in the organization of a structure. It is good science, but poor teaching; and that seems to be the general method of instruction in German universities. This is not intended as a criticism, but merely as the statement of a distinction.

"Special botany" comprises "Crytogams" and "Phanerogamia." Note the incongruous forms of the two names, and the perpetuation of the old notion that a great chasm is fixed between cryptogams and seed-plants. Through the cryptogams and gymnosperms and the introductory part of angiosperms one breathes, for the most part, the atmosphere of modern morphology; but after that there are 170 pages dealing with the details of the classification of "Monocotylae" and "Dicotylae." And here comes a demand on the German student that fills the American teacher with amazement. It simply means that students in medicine and pharmacy are driven into these courses in botany; that it is supposed to be good for them to digest this encyclopedic information about groups of plants; that the German professor of botany cannot dispense with the fees of these students; and that all German textbooks on botany must contain this dreary waste of pages. We would suggest that this German educational necessity should not appear in the English translations, for it needlessly enlarges the book for American use.—J. M. C. and C. R. B.

Plant anatomy

Under this title STEVENS has written a book[2] which deals with the development and functions of plant tissues. Structure and function are so intermixed, and rightly, that there is no anatomical part of the book as distinct from the

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[2] STEVENS, WILLIAM CHASE, Plant anatomy, from the standpoint of the development and functions of the tissues, and handbook of micro-technic. pp. xii+348. *figs. 136*. Philadelphia: P. Blakiston's Son & Co. 1907. $2.

physiological. In a review, however, the description of structures and of their functions may be mentioned separately.

In the days of the SACH'S régime, introduced into this country by BESSEY, the detailed study of tissues was a prominent feature of botanical instruction. It was gradually eliminated because of the growing demand for details that were thought to be significant in the evolutionary history of plants. A fact without a suggestive and large meaning came to be regarded as not worth while in elementary teaching. Doubtless this elimination of the study of tissues as such went too far, and a generation of botanists has been developed with too little knowledge of this kind. Then came the wonderful modern revival of anatomy so far as the vascular system is concerned, but this revival had to do with the evolution of vascular plants. STEVENS has carried us back again into the old atmosphere of tissues, but he has sought to avoid the old deadness of the subject by relating tissues to their functions. The spirit that animates the "skeleton," therefore, is physiological and ecological, and not the conception of evolution. The tissues are well described and illustrated, for STEVENS is an excellent teacher; and the text and drawings have been prepared in large measure directly from material under observation. It is to be regretted, however, that no trace of the modern vascular anatomy appears. For example, the remarkable development of knowledge in reference to the relation between the vascular anatomy of monocotyledons and dicotyledons would seem to have deserved mention. It may be claimed that relationship is not being considered, but this particular relationship has to do with previous misconceptions as to the actual structure of the vascular anatomy of monocotyledons.

Remembering that this is a book on physiological anatomy and not a textbook of plant physiology, we may properly commend the presentation of such topics as come within its scope. That is far less comprehensive than the well-known work of HABERLANDT, and the matter is far more elementary. The topics presented are chiefly those of entry and exit of materials, their movement in the plant body, and the processes of nutrition in the broadest sense. These are presented simply, clearly, and in the main accurately. Clever diagrams have been freely used, and they fulfil well the author's design of rendering more real the processes described. If they have any fault it is perhaps in tending to make conceptions too formal. Growth movement and the extensive phenomena of irritability do not come within the author's plan.

One unfortunate conception, embodied in chapter headings, and wrought into the text, is that of "circulation" of water and foods in "circulatory tissues." This idea dies hard, and we are sorry it has a new lease of life in this book.

The final chapters deal with the preparation of sections, use of the microscope, reagents and processes, the michrochemistry of plant products (not always reliable), and the detection of adulterations (too short to be really useful).—J. M. C. and C. R. B.

Bokorny's Textbook

BOKORNY has published a textbook of botany[3] that meets the official requirements for instruction in the *Oberrealschulen* and *Realschulen* of Bavaria. It appears in two parts and is thoroughly well printed and illustrated. The authorship of the book is a guarantee of its accuracy, and therefore the chief interest lies in discovering the kind of botanical material that is thought appropriate for the German student who is approximately the equivalent of our students from the third year of high school through the second year of college. In short, the purpose of the book would be about the same as that of most of our texts for high schools, which are announced for high schools, but are really suitable for colleges.

It is evident at first glance that the demand is for a general survey of the whole domain of botany. The first section (145 pp.) deals with "flowering plants," and is introduced by studies of common garden forms, the first contact being with rape and the various cabbage types. In this way a knowledge of the gross morphology of angiosperms is developed; to which is appended what would seem to be a few useless pages of cryptogams. The second section (15 pp.) deals with "inner morphology," which is explained to be "plant anatomy" or "histology." Yeast, pine needles, starch grains, chloroplasts, growing points, vascular elements, root-hairs, etc., form the usual débris under such a caption. The third section (197 pp.) is a presentation of the classification of the plant kingdom, that amazing impossibility that rides every German text like the old man of the sea. It is like inserting a dictionary of the language into the midst of a course on literature. We presume that the German boy must submit to it, but we wonder at his docility. This closes the first volume.

The second volume includes four sections. The first (20 pp.) is really a presentation of plant symmetry, but it is not long enough to hurt; the second (104 pp.) deals with physiology and anatomy, relating structure to function; the third (90 pp.) is entitled "biology," which we include under the broader term ecology, and it looks quite modern and interesting; the fourth (17 pp.) is a brief outline of plant geography, being chiefly an enumeration of zones, provinces, etc.

The general structure of the book would not be so very different from that of the corresponding American texts, were the 200 pages of classification omitted. —J. M. C.

MINOR NOTICES

Bibliographia Linnaeana.—This work[4] represents the most complete bibliography of the numerous Linnaean publications ever compiled. The different works of LINNAEUS and the publications of other authors directly relating thereto are arranged chronologically, beginning with the *Dissertatio botanica de planta*

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[3] BOKORNY, TH., Lehrbuch der Botanik für Oberrealschulen und Realschulen. Teil I, pp. vi+366, $M4$. Teil II, pp. 233, $M3$. Leipzig: Wilhelm Engelmann. 1908.

[4] HULTH, J. M., Bibliographia Linnaeana: Matériaux pour servir a une bibliographie Linnéenne. Partie 1, Livrasion 1, 8vo. pp. 170. *pls. 1–3, 5–9, 11.* Uppsala: Librairie de l'Université, C. J. Lundström. Berlin: R. Friedländer & Sohn. 1907.

*Sceptrum Carolinum dicta, quam * * * praeside Laurentio Robergio * * * ventilandam sistit auctor Johannes Olavus Rudbeck Ol. Fil. * * * 1731.* After mentioning the original edition of the respective works, subsequent editions, reissues, and translations are accurately recorded; and in each instance the usual information is given as to place and time of publication, as well as the form, number of pages of text and index, and other details. In those works consisting of more than one volume the subjects treated in each volume and the number of pages devoted to each subject are indicated briefly in tabulated form. Reference is also made to contemporary notices and reviews.

The volume is amply provided with cross-references, and the subject-matter on the pages is well differentiated by judicious spacing and a careful selection of type, thus making the work attractive in appearance and of easy reference. Several facsimile reproductions of title-pages and frontispieces of the rarer Linnaean works are appended, which add to the interest of the volume. It is a book which will serve as a most useful guide to the Linnaean literature.—J. M. GREENMAN.

The flora of Styria.—VON HAYEK[5] has begun a systematic treatment of the ferns and flowering plants of Styria. The first number of this work contains a key to the main groups and sub-groups, which are clearly defined, and a second key leading directly to the families. The enumeration of species follows a natural sequence, beginning with *Ophioglossum vulgatum* L. and continuing through the three parts to *Chenopodium album* L. A concise description of each species is given in German, and associated with it one finds a fairly complete synonomy and bibliography. Careful attention has been given to habitat and distribution. Text figures are introduced to illustrate certain groups, but the illustrations lack clearness and detail. The nomenclature is in accordance with the Vienna Rules adopted at the last International Botanical Congress.

On the whole the work thus far happily combines a semipopular presentation and a degree of scientific accuracy which will make it useful to the local botanist and to the general systematist.—J. M. GREENMAN.

Flowering plants and ferns.—Under this title WILLIS published the first edition of his manual and dictionary in 1897. A second edition appeared in 1904, and now a third[6] has come to hand. The purpose of the book is "to supply, within a reasonable compass, a summary of useful and scientific information about the plants met with in a botanical garden or museum, or in the field." The result is a very convenient book of reference. The first part presents an

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[5] VON HAYEK, AUGUST, Flora von Steiermark. Eine systematische Bearbeitung der im Herzogtum Steiermark wildwachsenden oder im Grossen gebauten Farn- und Blütenpflanzen nebst einer pflanzengeographischen Schilderung des Landes. Vol. I. Parts 1–3. 8vo. pp. 240. Berlin: Gebrüder Borntraeger. 1908.

[6] WILLIS, J. C., A manual and dictionary of the flowering plants and ferns. Third edition. pp. xii+712. Cambridge: The University Press. 1908. New York: G. P. Putnam's Sons. $2.75.

outline of the morphology, natural history, classification, geographical distribution, and economic uses of the flowering plants and ferns. The second part, to a great extent rewritten, is a dictionary of the classes, cohorts, families, and chief genera, alphabetically arranged. The third part, to which much has been added, is a glossarial index of English names, economic products, technical terms, specific names, etc. Altogether the volume is a most convenient one for any botanist or botanical laboratory.—J. M. C.

Library of John Donnell Smith.—In 1905 JOHN DONNELL SMITH presented to the Smithsonian Institution his herbarium, containing over 100,000 mounted specimens, and his botanical library, containing about 1600 bound volumes. The herbarium has been placed in the U. S. National Museum; but for the present the library is to remain in Baltimore. The collection of books is chiefly taxonomic, and is especially rich in the literature of the floras of Mexico and Central America. This valuable collection has been placed freely at the disposal of botanists, and a very complete and handsome author catalogue has been issued by the Smithsonian Institution as a special publication,[7] in addition to the regular edition (Contrib. Nat. Herb. Vol. XII. part 1). This disposition of his exceedingly valuable herbarium and library emphasizes not only the generosity but also the scientific spirit of the donor.—J. M. C.

Cryptogamic flora of Brandenburg.[8]—The third part of the volume on Algae by LEMMERMANN has just appeared. It is devoted entirely to the Flagellatae, all of the recognized seven "orders" excepting the last (Euglenineae) being presented, and that one is begun.—J. M. C.

NOTES FOR STUDENTS

Paleobotanical notes.—NATHORST has begun the publication of an important series of paleobotanical memoirs.[9] The first deals with Pseudocycas, a new genus from the Cenomanian Cretaceous of Greenland. It has generally been considered that leaves of the Cycadeae made their appearance first in the Triassic, and thus considerably antedated the true Zamieae, which are known earliest from the Tertiary deposits. The author shows that leaves from Cretaceous deposits, which have been described by various authors as belonging to Cycadites or even to the living Cycas, are in reality not to be included in these genera at all, since they differ from the existing Cycas in that each leaf pinnule has a *double* midrib and is attached to the rachis by a broad instead of an attenuated base. On account of these divergences, the author sets up a new genus, Pseudocycas.

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[7] Catalogue of the botanical library of JOHN DONNELL SMITH, presented in 1905 to the Smithsonian Institution. Compiled by ALICE CARY ATWOOD. Special publication, Smithsonian Institution. pp. 94. July 1908.

[8] LEMMERMANN, E., Kryptogamenflora der Mark Brandenburg. Band 3, Heft 3, Algen, 305–496. Leipzig: Gebrüder Borntraeger. 1908.

[9] Kung. Svenska Vetensk. Akad. Handl. **42**:no. 5. 1907; **43**:no. 3. 1908; **43**: no. 6. 1908.

The discovery of the duplicate character of the midrib is due to the microscopic examination of leaf pinnules. Four species are described under the new genus.

The second memoir is on the cuticle of *Dictyozamites Johnstrupi* Nath. By the microscopic study of the cuticle of this species, bleached with *eau de Javelle* and mounted in glycerin jelly, the author shows its close affinity with Otozamites as described by SCHENK.

The third memoir is devoted to the study of a lycopodineous cone from the Rhaetic of Schonen, which the author earlier described, with some reserve, as being of cycadaceous affinities, under the name *Androstrobus Scotti*. A microscopic examination of the cone in question, with the aid of *eau de Javelle* and other bleaching reagents, revealed the fact that it was of lycopodineous affinities, and the name is accordingly changed to *Lycostrobus Scotti*. The cone is attached to an apparently herbaceous peduncle about 2^{cm} in diameter and is about 12^{cm} in length. The minute structure of megasporangia and megasporophylls could not be made out. The megaspores were over 0.5^{mm} in diameter and were characterized by appendages along the triradiate ridges. The rest of the surface was covered with minute spines. The microspores, occurring in distinct clusters, were found in the upper part of the cone, were bifacial as in Isoetes, and were 30 to 50 μ in diameter. The author comes to the conclusion that Lycostrobus is more nearly allied to Isoetes than any living lycopod. This cone is of great interest from two standpoints. It illustrates how extremely unsafe conclusions as to affinities based on mere superficial characters must be, since *as an impression* the fossil was considered as belonging to the Cycadophyta. Also it goes a long way toward demonstrating that Isoetes is a true lycopod, and not an appendage of the fern series, as has been suggested by VINES, FARMER, and CAMPBELL.

The fourth memoir deals with the microscopic investigation of cuticles of fossil leaves, sporangia, spores, etc. Perhaps the most interesting result under this head is the demonstration that ARBER'S *Carpolithus Nathorsti* (1908) is in reality not a seed of a pteridosperm at all, as is supposed by that author, since the supposed seminal organs were shown by maceration to be microsporangia. Numerous abietineous winged pollen grains were found in material from the Trias of Hör. The author comes to the general conclusion: "die Gattung Pinus schon gegen das Ende der Triasperiode, in den nördlicheren Teilen der Erde ausgebildet war." This result appears not to be without significance in connection with present discussions in regard to the antiquity of Pinus. Smaller winged microspores were also found, which the author does not attempt to refer to any existing coniferous genus. It appears not improbable that they represent the microspores of certain of the Brachyphylloideae, a new subtribe of araucarian conifers described by Dr. HOLLICK and the reviewer.

In the fifth memoir the author throws additional light on *Nathorstia* Heer, first described as Daneites from the older Cretaceous of Greenland. By means of maceration he has been able to show that the fossil in question is allied to the living marattiaceous genus Kaulfussia, but differs from it in having the ringlike sorus of sporangia multiseriate instead of simple.

In the sixth memoir *Antholithus Zeilleri* Nath. is discussed, which has been regarded as the staminate inflorescence of Baiera. It is shown that the fossils in question consist of dichotomously divided, dorsiventral organs, the ultimate divisions of which bore eight sporangia. Consequently they do not resemble the staminate flowers of the living Ginkgo.

Throughout the author gives paramount importance to the microscopic examination of his material, and suggests many ingenious and some novel devices for the preparation of the objects for the microscope.—E. C. JEFFREY.

Anatomy of Veronica and Gratiola.—The internal structure of the stem and leaf of about 60 species of Veronica and of *Gratiola officinalis* has been studied by HUCHEDÉ,[10] and his results constitute a very important and interesting contribution to the knowledge of the structure of these genera, especially of the former. The material examined consisted of species from Europe, Asia, Australia, and New Zealand, thus comprising both herbaceous and suffrutescent forms. So far as concerns the leaf and stem, the author has demonstrated that a considerable variation in structure exists in Veronica, in regard to epidermis, chlorenchyma, hairs, endodermis, and pith, and the petiole also offers several good characters for distinguishing a number of species. The species from New Zealand differ in a marked way from the European; for instance in regard to the chlorenchyma, which is mostly composed of palisades, unless it is bifacial; furthermore, by the veins (circular in cross-section) being imbedded in the chlorenchyma and supported by stereome or collenchyma. The stem of the New Zealand species contains but little pericyclic stereome, while the pith is frequently sclerotic. It is quite interesting to see that the author has observed some anatomical characters sufficient for distinguishing *V. virginica* L. from *V. sibirica* L., and *V. saxatilis* Scop. from *V. fruticulosa* L., which by many authors have been regarded as synonyms. Very few species are considered of any importance as medicinal plants, and our *V. virginica* (NUTTALL'S *Leptandra virginica*) is actually the only one which is recognized as such and is still in use (the rhizome).

The paper contains well-written anatomical diagnoses of these species, accompanied by a number of very fine drawings, showing their anatomical characteristics. It is only to be regretted that the root has not been considered, for there is no doubt that the structure of this organ must show variations of no small importance, when we bear in mind that among these species of Veronica are both terrestrial and aquatic types, annual and perennial, herbaceous and suffrutescent. The fact that the primary root persists in some of them, and that it becomes replaced by secondary roots in others, might also deserve notice.

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[10] HUCHEDÉ, J., Veroniques et Gratiole. Etude histologique et pharmacologique. Travaux Lab. Mat. Medic. Ecole Sup. Pharm. Paris 5:137. 1907.

However, we admit that it is often very difficult to obtain material so well represented as to include the root-system, especially of herbarium specimens.—THEO. HOLM.

Anatomy of the leaves of Ranunculaceae.—GOFFART[11] has described the leaf structure of species representing 23 genera of Ranunculaceae, nearly all from the old world. The paper is illustrated by about 400 excellent figures of the leaf outline and the internal structure. So many anatomical details are recorded that an abstract in brief space is impossible.

The author has followed the method suggested by his teacher, the distinguished anatomist A. GRAVIS, to examine the leaf at very many places and at various stages of its development, and to give due consideration to the course of the mestome strands from stem to petiole and throughout the blade. In this way one obtains a most complete idea of the structural peculiarities, and such are highly welcome to students of affinities, expressed not only by floral structures but also by internal organization. Much has been written about the validity of several of these genera, considered from a systematic point of view, especially judging from the floral characters. It is therefore interesting to learn from this paper that, so far as concerns the leaf structure, Hepatica is not distinct from Anemone, and the same seems to be the case with Nigella-Garidella, Actaea-Cimicifuga, and Ficaria-Oxygraphis-Ranunculus. However, in respect to Oxygraphis, the author has examined only *O. Cymbalaria*, which in the reviewer's opinion is no true Oxygraphis, but a Ranunculus. An examination of *O. glacialis*, for instance, would no doubt have led to a different conclusion. On the other hand, Pulsatilla appears to be generically distinct from Anemone, and Batrachium from Ranunculus. Future investigations, for instance, of the singular North American representatives of Ranuculus constituting the section Crymodes, Cyrtorhyncha, and Pseudaphanostemma might lead to the segregation of these from Ranunculus altogether. For such a purpose GOFFERT'S contribution is a very important one; and it might be stated at the same time that the same family has been treated by other pupils of GRAVIS in regard to the structure of the pericarp and spermoderm, the embryo and seedlings, etc., the result of which have appeared in the *Archives* since 1897.—THEO. HOLM.

Prothallia of Kaulfussia and Gleichenia.—One of the results of CAMPBELL'S recent visit to Java is the publication of an account[12] of the prothallia of the oriental and monotypic Kaulfussia and of Gleichenia. The account fills in an important gap in our knowledge of the prothallia and sex organs of Filicineae; and it is of interest to note that the account satisfies the desire for completeness rather than the desire for new things.

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[11] GOFFART, JULES, Recherche sur l'anatomie des feuilles dans les Renonculacées. Arch. Inst. Bot. Univ. Liège III. pp. 187. *pls. 14*. 1901. The editors feel justified in calling attention to so old a publication in view of the fact that it has an important bearing upon the current taxonomic study of the family.

[12] CAMPBELL, D. H., The prothallium of Kaulfussia and Gleichenia. Ann. Jard. Bot. Buitenzorg II. 7:69–102. *pls. 7–14*. 1908.

The prothallium of Kaulfussia is said to be the largest among Marattiaceae, a very large one reaching 2.5×1.75^{cm}; but the usual adult size is 1^{cm} or more in length and nearly as broad. An endophytic fungus is always present. The antheridia and archegonia, restricted to the ventral surface, are also of ususual size. CAMPBELL thinks that probably all the organs of the embryo of Marattiaceae, except the foot, are of epibasal origin, and he finds confirmation of this in Kaulfussia. As in other members of the family, the shoot pierces through the prothallium and emerges from the dorsal surface.

The prothallia of Gleichenia are also of the "massive-midrib" type, more or less lobed, and with an endophytic fungus. The antheridia are restricted to the ventral surface in all species except *G. laevigata*, in which they occur upon both surfaces. In the species examined they are larger and more complex than recorded in the species examined by RAUWENHOFF, the wall cells being much more numerous, several hundred sperm mother cells sometimes being produced, and an opercular cell probably always being present. The archegonia are more numerous upon the flanks of the "midrib" than upon its middle region; the necks are very long; and the neck canal cell (except in *G. polypodioides*) usually divides into two cells. The embryo, so far as the material permitted comparison, resembles that of the Polypodiaceae. The characteristic protostelic condition was observed in sporelings, but it was not discovered whether it persists in the adult form in all species.—J. M. C.

Sexual reproduction in the rusts.—During the last three or four years BLACKMAN and CHRISTMAN have described a process of sexual reproduction in the rusts. Their accounts are not in entire agreement, and so the ground has been traversed by OLIVE,[13] with an unusual wealth of material. About forty species were examined, and the most favorable form for the study undertaken proved to be *Triphragmium ulmariae* (Schum.) Link, on *Ulmaria rubra* Hill, a caeoma form similar to the species of Phragmidium studied by BLACKMAN and CHRISTMAN. The two fusing cells ("gametes"), as well as their nuclei, were found to be approximately equal, but for reasons given in detail it is concluded that they differ somewhat in time of development. The equality and sexual character of both the fusing cells are statements opposed to those of BLACKMAN. It is also concluded that the sterile cell (at the tip) is not an abortive trichogyne, but merely a "buffer cell" of the gametophyte. Conjugation takes place through a perforation developed in the contact-walls. It may begin through a very small conjugation pore (observed by BLACKMAN), but this is regarded as only the beginning of a larger perforation. In the study of the various vegetative nuclear divisions it was discovered that they are all mitotic, each nucleus during the conjugate divisions acting independently. These nuclear divisions, conducted with the aid of centrosomes, are described in detail; and in Triphragmium it was ascertained that the chromosomes are probably eight in number. The occur-

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[13] OLIVE, EDGAR W., Sexual cell fusions and vegetative nuclear divisions in the rusts. Annals of Botany **22**:331–360. *pl. 22.* 1908.

rence of one or more multinucleate cells at the base of certain young aecidia is considered, and the conclusion is reached "that they are sporophytic structures, and that they result from the stimulated growth which follows the sexual cell fusions." This is opposed to the idea (CHRISTMAN) that the "fusion cell" functions at once as a "basal cell" at the bottom of each row of spores.—J. M. C.

Gnetales and Angiosperms.—Last year ARBER and PARKIN announced[14] their "strobilus theory of angiospermous descent;" and now they have applied it to the interpretation of the relationships of Gnetales.[15] There is much to commend their general view, without conceding all the details cited; in fact the reviewer has long since reached the same conclusions as to the character of the strobilus of Gnetales, and has remarked upon its similarity to such inflorescences as those of the Amentiferae. The authors do not regard the Gnetales as a modern group, although at present unknown as fossils. The three survivors of this ancient group have "pro-anthostrobili,"[16] evident in the staminate "flower" of Tumboa and reduced in the other "flowers" of the group by the suppression of one set of sporangia. To the authors the strobilus of this group is the so-called "flower;" and the strobilus of current terminology is an aggregate of strobili. Based upon this strobilus situation, the authors regard Gnetales as a phylum of gymnosperms having a common ancestry with angiosperms in the hypothetical "hemiangiosperms," and in many respects following parallel lines of development.—J. M. C.

Origin of angiosperms.—LIGNIER[17] has discussed the recent paper by ARBER and PARKIN,[18] in which the origin of the angiosperm flower (of the Ranales type) is traced to the bisporangiate strobilus of Bennettitales. From this view LIGNIER dissents, as he regards the strobilus in question as representing an inflorescence rather than a flower. To him the intraseminal scales are not sterile carpels or sterile lobes of carpels, but bracts in whose axils the ovuliferous stalks appear. This strobilus, therefore, is a compound one, as are the ovulate strobili of many of the Coniferales and both strobili of the Gnetales. LIGNIER agrees to the idea that the Ranales type of flower is the most primitive, but he would derive it from

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[14] Review in BOT. GAZETTE 44:389. 1907.

[15] ARBER, E. A. NEWELL, AND PARKIN, JOHN, Studies in the evolution of the angiosperms. The relationship of the angiosperms to the Gnetales. Annals of Botany 22:489–515. 1908.

[16] An "anthostrobilus" is an axis bearing microsporophylls and megasporophylls, with the latter above the former. A "pro-anthostrobilus" is the variety in which the pollen reaches the ovules (gymnosperm), the strobilus of Bennettitales being an example; while a "eu-anthostrobilus" is the variety in which the pollen is received by the megasporophyll (angiosperm).

[17] LIGNIER, O., Le fruit des Bennettitées et l'ascendance des Angiospermes. Bull. Soc. Bot. France IV. 8:1–17. 1908.

[18] BOT. GAZETTE 44:389. 1907.

the earlier cycadophyte stock. Accordingly he introduces before ARBER and PARKIN'S "pro-anthostrobilus" an evolutionary stage characterized by the grouping of filicinean microsporophylls and megasporophylls in monosporangiate strobili, and to this hypothetical stage he gives the name "pteridostrobilus." This stage was temporarily a common one for the general cycad and angiosperm phyla; and at this stage the cycads practically stopped, with reduction of sporophylls; while the angiosperm phylum proceeded to the establishment of the bisporangiate condition, the evolution of angiospermy, the transformation of the habit of the vegetative body, etc. According to LIGNIER, the Bennettitales represent a different phylum, which branched from the cycadophyte phylum after the angiosperms, but still at the pteridostrobilus stage.—J. M. C.

Nitrogen fixing bacteria.—In a short preliminary paper[19] BREDEMANN summarizes the conclusions deduced from his study of nitrogen fixing bacteria of the Clostridium type. Eleven cultures of the so-called "species" of various authors were compared with sixteen types isolated by himself. These types were from many sources, particularly soil from different parts of the world. A comparison of these forms cultivated under proper conditions for considerable periods has convinced him that all must be considered as a single species, the *Bacillus amylobacter* A. M. et Bredemann. Some characters, such as size of spores, motility, and development on culture media, are quite constant; others, as the ability to ferment nitrogen free solutions, are variable. Indeed, the variability of subcultures from a single stock may be made, by appropriate methods, to exceed the differences among the various so-called species and races. Most important, perhaps, are his conclusions relative to variation in nitrogen fixing power. Old cultures which had completely lost this capacity regained it when grown for a time in soil properly sterilized. This ability to fix nitrogen is closely correlated with that of fermenting nitrogen free solutions, and varies as greatly among various subcultures from a single stock as among those types that have been described as different species. Continued cultivation brings loss of power to fix nitrogen, but this power may be regained by appropriate culture methods. —R. E. BUCHANAN.

Variations of sexual organs of Saprolegnia.—KAUFFMAN[20] has obtained some extremely interesting results from some unusually guarded cultures of the Saprolegniaceae. He has found it possible to isolate species of Saprolegnia quickly by means of a single zoospore, and such pure cultures were used in his experiments. A great variety of solutions was used, but the best substances to

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[19] BREDEMANN, G., Regeneration der Fähigkeit zur Assimilation von freien Stickstoff des *Bacillus amylobacter* A. M. et Bredemann und der zu dieser Spezies gehörenden bisher als Granulobacter, Clostridium usw, bezeichnete anaeroben Bakterien (Vorläufige Mitteilung). Ber. Deutsch. Bot. Gesell. **26a**:362–368. 1908.

[20] KAUFFMAN, C. H., A contribution to the physiology of the Saprolegniaceae, with special reference to the variations of the sexual organs. Annals of Botany **22**: 361–388. *pl. 23.* 1908.

effect the production of sexual organs were haemoglobin and leucin, as found also by KLEBS. The effect of nutrition upon the differentiation of reproductive and vegetative processes was amply confirmed; but not all species produce sexual organs under the same conditions, showing a physiological as well as a morphological distinction. *S. hypogyna*, in which true antheridia do not develop, was made to develop antheridia under proper nutrient conditions. The variations induced were so extensive as to include all the characters used for diagnostic purposes, and the author makes the suggestion that a species can be defined in terms of its behavior in an established standard culture. The conclusion is reached that there are a great many entirely distinct forms, physiologically so at least, which may be regarded as elementary species in the sense of DEVRIES. The whole tendency of the investigation is to confirm the doctrine that sex in plants is determined by external conditions.—J. M. C.

The sporangiophore.—Miss BENSON[21] has emphasized the morphological importance of the sporangiophore, and has extended its application. Originally applied in Sphenophyllales, Equisetales, and Psilotales, she would extend its application to all pteridophytes. Objection is made to BOWER'S application of the term in Ophioglossales to the "fertile spike." In the Filicales the sorus (or synangium) is the sporangiophore; while in Lycopodiales it appears in a "reduced" form as the subarchesporial pad. Primarily it is a unit structure that appears on the axis, but may be "taken up on to" the leaf, as in all known ferns and many Lycopsida. The definition suggested is that "a sporangiophore is a structure characteristic of the sporophyte of Pteridophyta, and consists of a central, generally pedicellate mass of sterile tissue, with sporogenous regions occupying one or more sporangia, which may be terminal, lateral, or basal." It is further suggested that even Cordaitales and Taxineae may be forms whose sporangiophores have never been "taken up" on leaves. All this means a monophyletic origin for pteridophytes, with the sporangiophore (as now defined) as a fundamental and unifying structure of the sporophyte. Such a hypothesis is worth thinking about, and it has enough facts to support it to make it seductive.—J. M. C.

Schizostely in Gramineae.—Schizostely has been seldom observed among the flowering plants, the recorded cases being in certain representatives of Alismaceae, Nymphaeaceae, Cabombaceae, and Ranunculaceae. Recently VAN TIEGHEM[22] has discovered this singular structure in *Sorghum halepense* Pers. So far only the monostelic structure has been observed in the aerial and subterranean stems of the numerous Gramineae examined. While the aerial stem of this Sorghum is monostelic, the rhizome possesses a large number of meristeles

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[21] BENSON, M., The sporangiophore—a unit of structure in the Pteridophyta. New Phytol. 7:143–149. 1908.

[22] VAN TIEGHEM, PH., Une graminée à tige shizostélique. Ann. Sci. Nat. Bot. IX. 5:371. 1907.

in the cortex, which are of a very different size, but each is surrounded by a special and very plainly differentiated endodermis, in which the Casparyan spots are readily noticeable. The structure of the mestome strand in each is typical, and does not differ from that known so well from the Gramineae in general. The fact that the endodermis is differentiated at a very early stage, and that the inner cell walls become thickened long before the vessels and the adjoining tissues become lignified, makes this schizostelic structure plainly visible in the young rhizome, in the internodes, and partly also in the nodes. It would be interesting to know whether the structure is not to be found in other grasses.—THEO. HOLM.

Morphology of Podostemaceae.—WENT[23] has made some remarkable observations on the ovule of Podostemaceae. He has obtained abundant material and finds the several species studied very consistent with one another and very inconsistent with other Angiosperms. A future more extensive paper is promised, which will deal with all the features of the family.

The outer integument develops first and forms the micropyle. Later the inner integument develops, but never incloses the embryo sac region of the nucellus. The hypodermal megaspore mother cell caps an axial row of cells, which first elongate and then disorganize, resulting in a pseudo-embryo sac inclosed by the inner integument. The true embryo sac enlarges but little, and the embryo grows into and occupies the pseudo-sac. After the first division of the megaspore nucleus, the primary antipodal nucleus degenerates promptly, so that there are no antipodal cells and no antipodal polar nucleus. The four micropylar nuclei form as usual, but the micropylar polar degenerates promptly, so that there is no "double fertilization" and no endosperm. It is to be regretted that alcoholic material and scattered stages did not permit absolute certainty on many points.—J. M. C.

Tracheae of ferns.—GWYNNE-VAUGHAN[24] has investigated the xylem of some of the recent ferns, and concludes that the current statement that the metaxylem of Filicales consists for the most part of scalariform tracheids is "thoroughly misleading," and that "a return must be made to the views held by the earlier anatomists (DIPPEL, SACHS, WEISS), who believed that the xylem elements of the ferns in general were true vessels and not tracheids at all." The investigation was induced by studies of certain fossil Osmundaceae, in collaboration with KIDSTON. The conclusions are that the xylem elements of pteridophytes are mostly vessels with true perforations in their longitudinal as well as in their terminal walls. In the Osmundaceae, *Nephrodium Filix-mas*, and probably others, a special type of vessel occurs which is characterized by the complete disappearance of the primary tracheal wall at certain points, so that the cavities of the pits are vertically continuous in the middle of the wall. It is probable that

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[23] WENT, F. A. F. C., The development of the ovule, embryo sac, and egg in Podostemaceae. Recueil Trav. Bot. Néerland. 5:1–16. *pl. 1.* 1908.

[24] GWYNNE-VAUGHAN, D. T., On the real nature of the tracheae in the ferns. Annals of Botany 22:517–523. *pl. 28.* 1908.

more or less rounded pits preceded the transversely elongated pits of the scalariform type in the Filicales.—J. M. C.

Origin of Sphenophyllales.—In 1903 LIGNIER[25] published his view that the Equisetales and Sphenophyllales are of filicinean origin. Recently this disposition of the Sphenophyllales has been opposed, especially by SCOTT, and by the anatomical work of Miss SYKES. LIGNIER has now resumed the discussion[26] and reaffirms his former position, with additional argument. He claims that the "fertile leaves" of Sphenophyllum cannot be homologized with the sporangiferous structures of Tmesipteris; but that their "sterile pinnules" are comparable with those Archaeopteris. The "fertile pinnules," at the same time, are of the same type as those of the Primofilices. Therefore, LIGNIER concludes that the Sphenophyllales ought to be "attached" to the Primofilices and not to the Lycopodiales. A number of secondary characters also are used to strengthen this view.—J. M. C.

Sieve tubes.—An elaborate histological investigation of the details of development in sieve tubes of angiosperms has been made by HILL.[27] It appears that the young cell wall which is to form a sieve plate, is at first pitted, the pit-floor being penetrated by one or a group of fine protoplasmic threads, which, after some change of the adjacent cell wall, "begin to be bored out to form slime strings, apparently by a ferment." These slime strings enlarge and merge, so that finally one large slime string occupies the place of the group. This is always inclosed in a protoplasmic tube, which lines each pore of the plate, and the pore itself has a callus lining covering the cellulose part of the wall. Many further details are given and the usual teleological causes assigned for the processes. The paper contains an excellent historical summary.—C. R. B.

Hygroscopic movements.—STEINBRINCK and SCHINZ, by studies on some desert plants, support further the view that the internal structure of the thickened walls, as well as differences in the tissues, are the cause of the warping movements of fruits and other parts.[28] They find that lignified walls really swell and shrink more than cellulose walls, and they attribute to differences in structure the unlike polarization phenomena observed in the walls of different layers of cells in the bending organ. Incidentally they establish the "true" Jericho rose as *Anastatica hierochuntica* L., and not *Odontospermum pygmaeum* (DC.) Benth. & Hook.—C. R. B.

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[25] LIGNIER, O., Equisétales et Sphenophyllales. Leur origine filicinéene commune. Bull. Sci. Linn. Normandie V. 7:93. 1903.

[26] LIGNIER, O., Sur l'origine des Sphénophyllées. Bull. Soc. Bot. France IV. 8:278–288. 1908.

[27] HILL, A. W., The histology of the sieve tubes of angiosperms. Annals of Botany 22:245–290. *pls. 17, 18. figs. 13.* 1908.

[28] STEINBRINCK, C., and SCHINZ, H., Ueber die anatomische Ursache der hygrochastischen Bewegungen der sog. Jérichorosen und einiger anderer Wüstenpflanzen. Flora 98:471–500. 1908.

Biology of diatoms.—Cell division is described by BERGON[29] for Biddulphia, but the nuclear details are not shown. No centrosomes are figured. The principal point of interest in the formation of auxospores is that not one, but two are formed in each cell. Spores (the so-called microspores) have been described and the observations have been disputed. Although the existence of such spores might safely be conceded, this paper describes the development of sporangia and spores so clearly that there can be no doubt either as to their existence or the mode of their formation.—CHARLES J. CHAMBERLAIN.

Sterile anthers of Ribes.—JANCZEWSKI[30] has discovered an interesting situation in the pollen of Ribes. In the genus there is every stage between entirely fertile and absolutely sterile anthers. Certain subgenera and a few hybrids habitually develop perfect pollen. Most common among the hybrids, however, is a mixture of sterile and fertile pollen grains, in varying proportion. In certain hybrids and in the subgenus Parilla the pollen is persistently inert. Degeneration generally occurs after tetrad formation, but sometimes in the mother cell stage.—J. M. C.

Protoplasmic rotation.—BIERBERG[31] concludes that rotation and streaming is neither a widespread nor usually a normal phenomenon, but he does not accept Miss KELLER's view that it is a symptom of dying. On the contrary, he finds that it accelerates the transfer of materials more than threefold over diffusion alone. His attempts to account teleologically for the existence of these movements in water plants, according as they have or have not conducting tissues, or are or are not permeable in all parts, are less valuable than his experimental work.—C. R. B.

Rusts.—OLIVE[32] has published a popular account of cereal rusts and their life-histories. He confesses that "the problem of the prevention of rusts is such a difficult one that many points still remain to be solved;" and states that "the main thing which can be done at present is simply to record the present status of our knowledge as to the nature of these complicated organisms, and to awaken interest in a knowledge of their habits."—F. L. STEVENS.

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[29] BERGON, P., Biologie des Diatomées.—Les processus de division, de rajeunissement de la cellule et de sporulation chez le *Biddulphia mobilensis* Bailey. Rev. Gén. Botanique IV. **7**:327–358. *pls. 5–8.* 1907.

[30] JANCZEWSKI, ED., Sur les anthères stériles des groseilliers. Bull. Acad. Sci. Cracovie **1908**: 587–596. *pl. 24.*

[31] BIERBERG, W., Die Bedeutung der Protoplasmarotation für den Hofftransport in den Pflanzen. Flora **99**:52–80. 1908.

[32] OLIVE, E. W., Rusts of cereals and other plants. S. Dak. Agric. Exp. Sta. Bull. 109. June 1908.

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Editors: JOHN M. COULTER and CHARLES R. BARNES

CONTENTS

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NOVEMBER 1908

OBSERVATIONS ON *POLYPORUS LUCIDUS* LEYS. AND SOME OF ITS ALLIES FROM EUROPE AND NORTH AMERICA[1]

GEORGE F. ATKINSON

(WITH FIVE FIGURES AND PLATE XIX)

The close relationship between the fungus flora of Europe and North America has long been recognized. There are many species which are common to both countries. This in a large measure is due to the same general conditions which have long been recognized in explaining the similarity between the spermatophytic floras of the two countries, namely, the strong evidence presented by certain geologic periods that many centuries ago the two floras were contiguous in the arctic regions, at a time when the climate there was mild enough to permit the growth of those species and genera, contributing through their progeny the present representatives, which have survived the climatic and edaphic rigors to which they were subjected during the subsequent glaciation of the arctics, and the shifting glacial movement farther to the south. The fungus flora of a country bears a very close and important ecological relation to other plants, especially to the spermatophytic flora, whether as parasitic, humus-dwelling, or wood-destroying species. They are "camp followers" of the higher plants. Because of this symbiotic and metabiotic relation of the fungi to other plants, in a great measure their lodging and migration is coincident with that of their hosts. In the case of the forest fungi there are some interesting examples of tenacious adherence to specific hosts, or to descendant species which have become separated in the migratory movement from the parent

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[1] Contribution from the Department of Botany, Cornell University, No. 130.

stock. There are also interesting examples of a shift from one host to a host of another related genus, instead of to a species of the same genus, where in the migration the specific hosts are not evenly distributed over the area of general migration from a given region. *Pleurotus ulmarius* Bull., while occurring on other frondose trees, is more common on the elm both in Europe and North America, although our native species of elm is different specifically from the European elm. *Annularia fenzlii* Schulz. was first collected in Hungary on *Tilia europaea* and does not seem to be common or widely distributed in other parts of Europe. It has been collected once at Ithaca, N. Y., on our native species of basswood, *Tilia americana. Fomes fraxineus* (Bull.) Fr. seems to be confined to the ash, occurring on the European ash in Europe and on our native species in the United States. *Fistulina hepatica* (Huds.) Fr. occurs in Europe especially on the oak, but sometimes on beech and chestnut. In North America it occurs most commonly on the chestnut, but is reported also on the oak, European species of oak not occurring naturally in this country. Many other similar examples might be enumerated. In a number of cases the fungus species seems to have undergone little or no change, although now separated for centuries on two different continents and subjected often to widely different environmental conditions. In other cases the North American representative of European species seems to have undergone a change, whether gradual or sudden we cannot say, so that it presents certain constant characters worthy often of specific separation, while resembling in a striking way the European species.

One of these interesting problems is presented by *Polyporus lucidus* Fr.[2] (*Boletus lucidus* Leys.[3]). My first acquaintance with what appears to be the typical form of *P. lucidus* in Europe was in the autumn of 1903, when I collected a specimen growing from the root of a dead frondose tree in the Bois de Boulogne, Paris. Two years later, while visiting M. E. BOUDIER at Montmorency, near Paris, he gave me a fresh young specimen which had been sent him from one of his numerous correspondents in France. It is a large and handsome fungus, varying considerably in size and form. The typical forms are stipitate, with a lateral pileus. In these forms

[2] Flora Halensis 300. 1783.

[3] Syst. Myc. 1:353. 1821.

the stipe is usually quite fully developed before the formation of the pileus, the latter developing gradually as a lateral extension of the free end of the stipe and becoming dimidiate, reniform, or flabelliform, usually with an entire margin, but sometimes more or less crenate or rarely somewhat lobed. Sometimes the pileus is nearly sessile, the stipe being reduced to a stout tubercle, especially when the plants grow directly on the side of a log. The plants occur singly or in clusters, and sometimes imbricated. One of the striking characters, which is also a peculiarity of a number of other species,

FIG. 1.—*Ganoderma pseudoboletum* (Jacq.) Murrill (*Polyporus "lucidum"* Leys.) (natural size), from France.

is the formation of a colored viscous substance on the surface of the stem and pileus which dries and hardens into a smooth, hard, thin, lustrous crust or "skin," which gives the plants a varnished appearance. In typical forms of *P. lucidus* this is a reddish chestnut, or *marron* color, varying to darker colors or even blackish in some forms of the species. The surface of the pileus is often marked by concentric rings and furrows, usually not very pronounced, and usually toward or on the margin where the rings are often close together. The surface is often radiately rugose. The pileus varies from 2–25^{cm} or more in diameter and 1–4^{cm} thick behind. The stipe varies greatly in length, and from 0.5–4^{cm} in diameter. The tubes are long and slender, brown within, the mouths circular, angular, white or yellowish, finally yellowish brown, with the dissepiments thin and acute. The trama or context of the pileus is pallid to brown, the portion next the tubes being darker brown, about the same color as the tubes, while it is paler to almost white next the varnished crust. The context of the stem is brown, with more or less distinct transverse concentric zones, which are also found to some extent in the pileus, and there is a distinct radiating fibrous structure extending into the pileus. The context is also soft and "punky."

Before the plant is mature, and while it is in different stages of development, the growing end of the stipe and the growing margin of the pileus are whitish, then changing to reddish yellow and finally chestnut as the varnishing becomes complete.[4] BULLIARD[5] and GILLET[6] figure young plants showing the lighter-colored margin. This condition is different from the yellowish unvarnished condition of the pileus of *P. curtisii* Berk.[7] from the southern United States, with which MURRILL[8] compared BULLIARD's and GILLET's figure.

The fact that the typical form of *P. lucidus* occurs in Europe on frondose trees lends additional interest to the most common form of this species in the United States, which occurs on the hemlock-

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[4] See EDGERTON, C. W., The rate and period of growth of *Polyporus lucidus.* Torreya 7:89–97. 1907.

[5] *Boletus obliquatus* Bulliard. Herb. de la France. *pl. 7, fig. A, pl. 459, figs. B, C.* 1880–1890?

[6] *Polyporus lucidus* Fr. Gillet. Champignons de la France 666.

[7] *Polyporus curtisii* Berkeley. Hook. Jour. Bot. 1:101. 1849.

[8] Bull. Torr. Bot. Club 29:604. 1902.

spruce (*Tsuga canadensis*). This form can be distinguished from the typical form on frondose trees in Europe only by the fact that it grows on a conifer, the hemlock-spruce, rather than on frondose trees, and perhaps by its somewhat softer and perhaps slightly lighter-

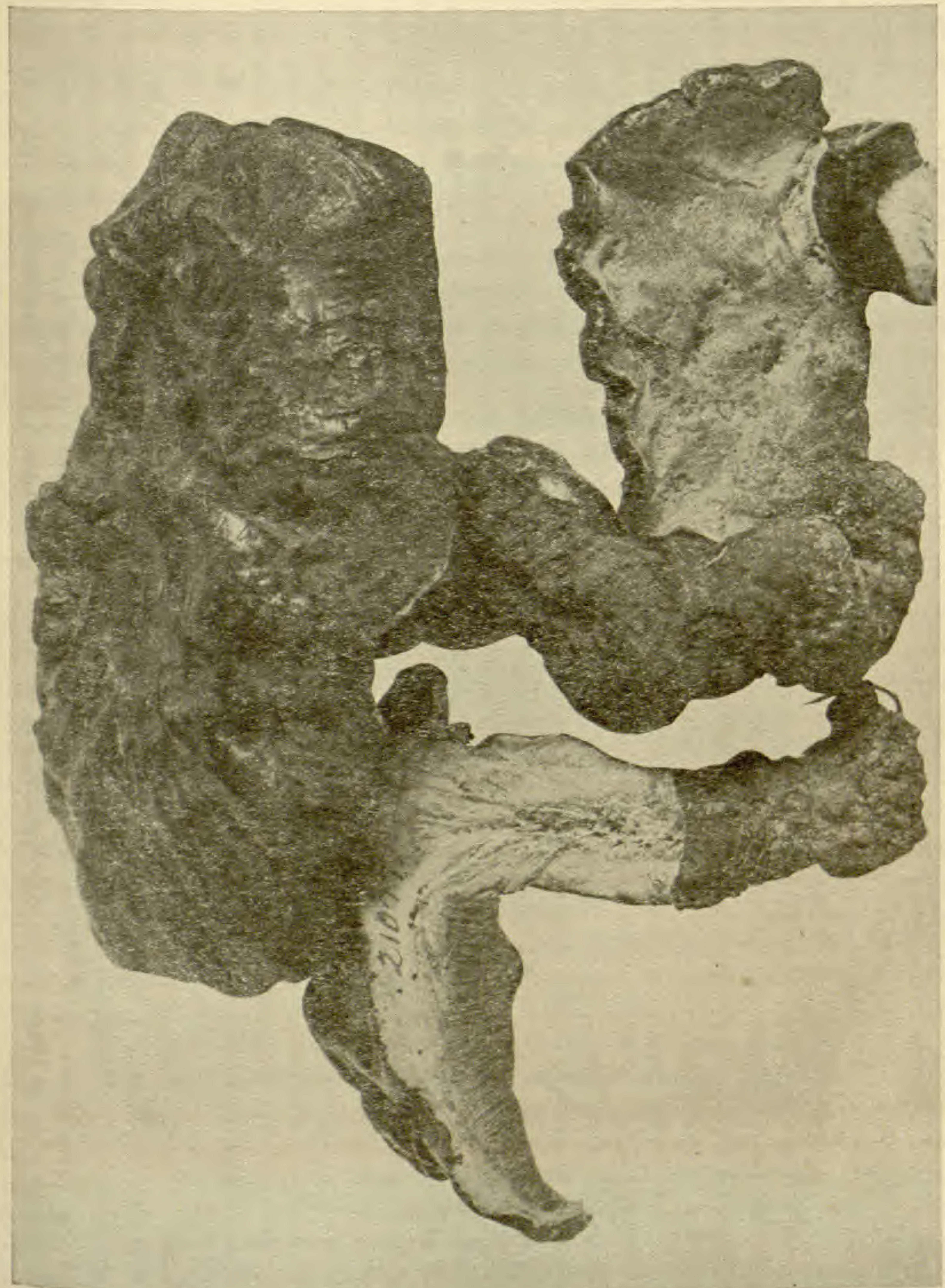

FIG. 2.—*Ganoderma pseudoboletum* forma *montanum* Atkinson (×⅘), on dead spruce, Jura Mts., France.

colored context, and the longer persistence of the individuals of the European form, since this usually does not disintegrate so soon. But these characters vary in individual plants and seem to mark our form on the hemlock-spruce merely as a physiological or biological form of the European species, rather than as a distant species as it is regarded by MURRILL[9] (p. 606).

P. lucidus is rarely reported on conifers in Europe, though it probably is common enough in certain of the mountainous regions. KARSTEN[10] reports it on *Abies excelsa* in Finland. In 1905 I found it quite common in the Jura Mountains[11] near Pontarlier and Boujeailles, Province Doubs, France, on dead stumps and logs of the common fir (*sapin*) of that region. These plants, while showing great variation in form, do not depart in this respect from the typical form. The stem varies from lateral to central in some individuals. There is, however, a marked difference in color, the Jura specimens on the fir having the varnished surface darker in color than those which I have seen from frondose trees in Europe, but also darker than our form on the hemlock-spruce, the color being a dark mahogany red, finally becoming nearly black. The color of the context is brownish like that of the typical form. So far as I could observe, I could see no evidence that this form is perennial, nor have I seen perennial specimens of the typical form. I sent specimens of these plants collected on the fir in the Jura Mountains to M. E. BOUDIER, of Montmorency, and at the same time some of the American form collected on the hemlock-spruce. The latter he pronounced a typical form of *P. lucidus*, while the former he regarded merely as a black form of the same species, which he says grows in the Vosges and Jura in France and Germany. The spores are identical in structure and size in all the above-mentioned forms.

The form in the southern United States on roots, stumps, etc., of frondose trees, seems to be distinct enough to be regarded as a distinct species. BERKELEY so regarded it and described it as *P.*

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[9] *Ganoderma tsugae* Murrill. The Polyporaceae of N. Am. I. The genus Ganoderma. Bull. Torr. Bot. Club 29:599–608. 1902; N. Am. Flora 9^2:118. 1908.

[10] KARSTEN, P. A., Myc. Fenn. pars tertia, Basidiomycetes, in Bidrag till Kännedom af Finlands Natur Och Folk 25:254. 1876.

[11] The collection and study of this material, with many other European fungi, was made possible because of a grant from the Botanical Society of America.

FIG. 3.—*Ganoderma curtisii* (Berk.) Murrill; central plant from Texas, others from North Carolina.

curtisii.[12] The general form of the plant is the same as that of *P. lucidus*, but the pileus is rarely and then only slightly varnished, and is yellowish in color, or with reddish-yellow spots and zones. The stem is exactly like that of *P. lucidus* and is varnished, reddish chestnut in color. In the extreme south forms with a central stem are more common, and then the pileus is more or less depressed in the center, as in *fig. 2*, which represents a specimen collected in Texas by A. M. FERGUSON. The surface is often zonate, faintly or strongly sulcate, and sometimes radiately rugose or corrugated toward the margin. While MURRILL first considered this as merely a geographical form[13] of *P. lucidus* (*Ganoderma pseudoboletus* Murr.), he now treats it as a distinct species[14] (*G. curtisii* [Berk.] Murr.).

Another form which has come under my observation was sent me by Mr. M. E. HARD, of Chillicothe, Ohio, who collected it from dead buried roots of oak, growing among *Datura stramonium*. These plants (*fig. 5*) resemble the typical European form in color and consistency. These individual specimens were not fully grown, and therefore the margin is lighter colored. The pileus as well as the stem is laccate or varnished. There are some differences in the spores which will be discussed below.

Another interesting form was received from E. R. LAKE, of Corvallis, Oregon, in January, 1905. It is a large stipitate plant with a lateral pileus, the pileus measuring 14^{cm} long by 12^{cm} broad and 5.5^{cm} thick. The pileus is tumid and covered with a thin crust, which is brittle, dark reddish brown, and laccate, similar to the crust of the stem. The context of the stem is also white and shows a fibrous structure which radiates out into the pileus. The tubes are slender, cinnamon brown, and $2\text{–}5^{cm}$ long. The plant was growing apparently on burnt ground from a root, probably of some conifer. In this specimen the varnished crust of the pileus extends over the under side of the margin and over the hymenophore for a distance of $0.5\text{–}1^{cm}$, and a new stratum of tubes 4^{mm} in length is deposited over the remaining portion of the hymenophore. In sections of the hymenophore this stratum tends to break away rather easily from its

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[12] *Polyporus curtisii* Berk. Hook. Jour. Bot. **1**:101. 1849.

[13] Bull. Torr. Bot. Club **29**:602. 1902.

[14] N. Am. Flora **9**²:120. 1908.

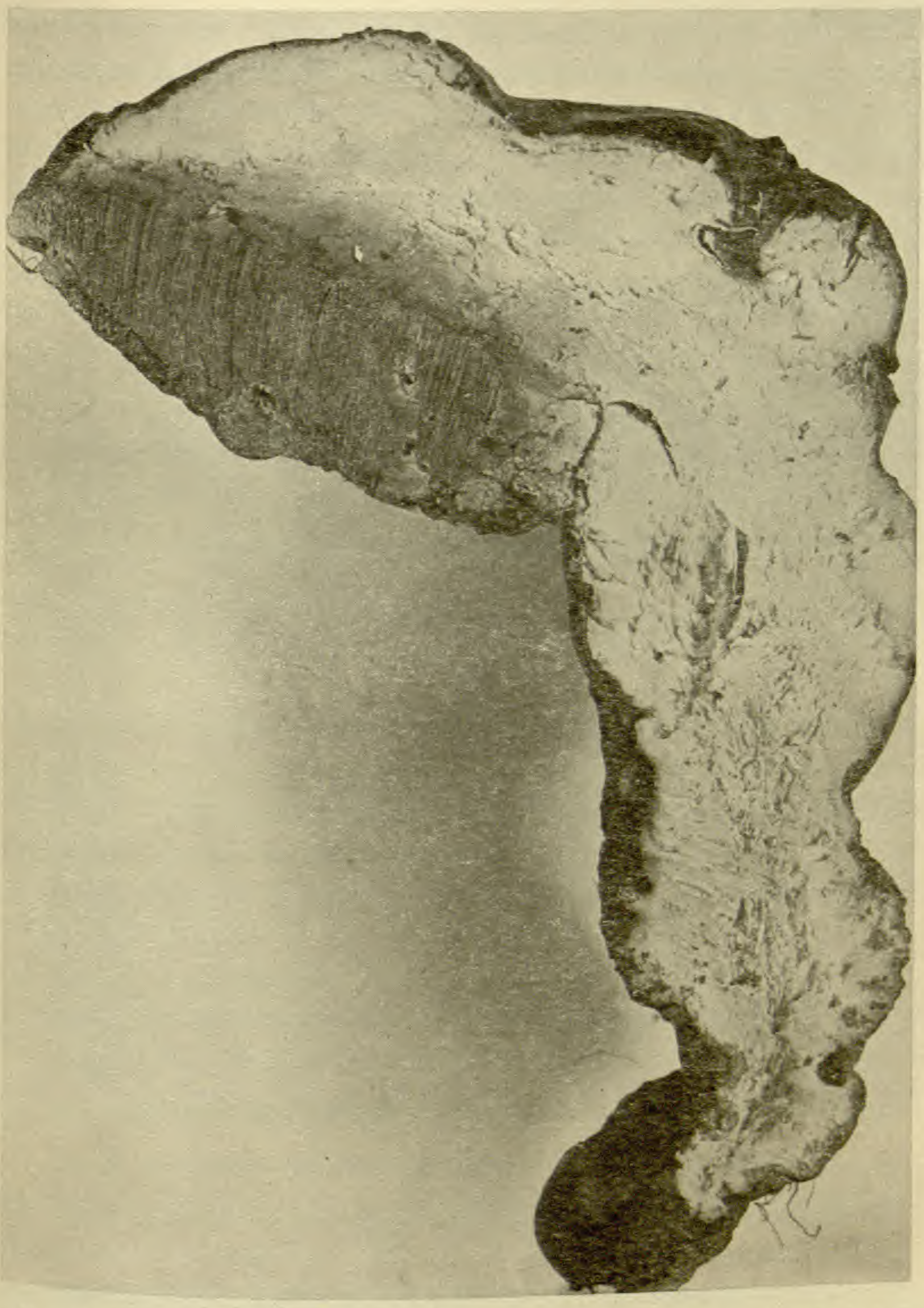

FIG. 4.—*Ganoderma oregonense* Murrill, from Corvallis, Oregon (natural size).

point of attachment with the older portion. There is also a faint stratification of the main portion of the hymenophore, but whether this is due to successive annual layers is doubtful, and can be determined only by observation of individual plants from year to year. They appear more likely to be the result of periodic variations in a single season's growth, like some of the similar strata in *Fomes fomentarius*. The plant has the appearance of being normally an annual, which under certain conditions may persist for a second season and develop a second depauperate layer of tubes; or this layer may be developed at the close of the first season, often some unfavorable condition inhibiting the growth for a longer period than usual. It appears to be specifically identical with *Ganoderma oregonense* Murrill,[15] recently described from Oregon as growing on a log of *Picea sitkensis*.

The spores of the species discussed in this paper present some very remarkable peculiarities in form and markings, which seem to have been misinterpreted by all those who have attempted to describe them up to the present time. During the past autumn and winter I have made a critical examination of the spores of the species mentioned above, and have not been able to confirm the descriptions thus far given. KARSTEN in 1889[16] says the spores are warty (sporerna äggrunda eller elliptiska, förtiga, gulbrunaktiga). PATOUILLARD in 1887[17] describes and figures the spores of the genus Ganoderma as verrucose (verruqueuses) and cites *Ganoderma lucidum* as one of the typical species. Later[18] (p. 66) this is repeated where he places *Ganoderma lucidum* in the section of Ganoderma having verrucose spores (spores verruqueuses). SACCARDO[19] says that the spores of this species are slightly verrucose (forma typica sporis ovoides, leviter verrucosis), and BRESADOLA states that they are verrucose.[20] MURRILL in 1902[21] and again in 1908[22] describes them

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[15] N. Am. Flora 9²: 119. 1908.

[16] Kritisk Ofversigt af Finl. Basidsv. 327. 1889.

[17] Les Hyménomycètes d'Europe 142. *pl. 3. fig. 21.* 1887.

[18] Le genre Ganoderma. Bull. Soc. Myc. France 5:63–83. *pls. 10, 11.* 1889; see also PATOUILLARD, N., Essai taxonomique sur les familles et les genres des Hyménomycètes 105. *fig. 58, 3b.* 1900.

[19] Sylloge Fung. 6:157. 1888.

[20] Hymenomycetes Hungarici Kmetiani. Atti Acad. Sci. III. 3:73. 1897.

[21] Bull. Torr. Bot. Club 29:601. 1902.

[22] N. Am. Flora 9²: 118. 1908.

as verrucose in several species (*Ganoderma tsugae* Murrill, *G. lucidum* [Leys.] Karsten, *G. curtisii* [Berk.] Murrill, and others).

In studying the spores of these species I have been surprised to find that they are not echinulate or roughened. The spore wall is *smooth*, that is, there are no elevated or projecting portions of the surface. But the spores have a very peculiar structure, which requires very careful examination to interpret properly, and sometimes the use of the oil immersion lens is necessary to resolve clearly the characteristic structure of the wall. On a first examination of the spores with the dry objective, they appear warty or roughened; but the appearance is so peculiar that I wàs not content with this definition and sought to determine more accurately the nature of the peculiar structure. When the upper or lower surface of the spore is in the focal plane, the wall of the spore presents the appearance of

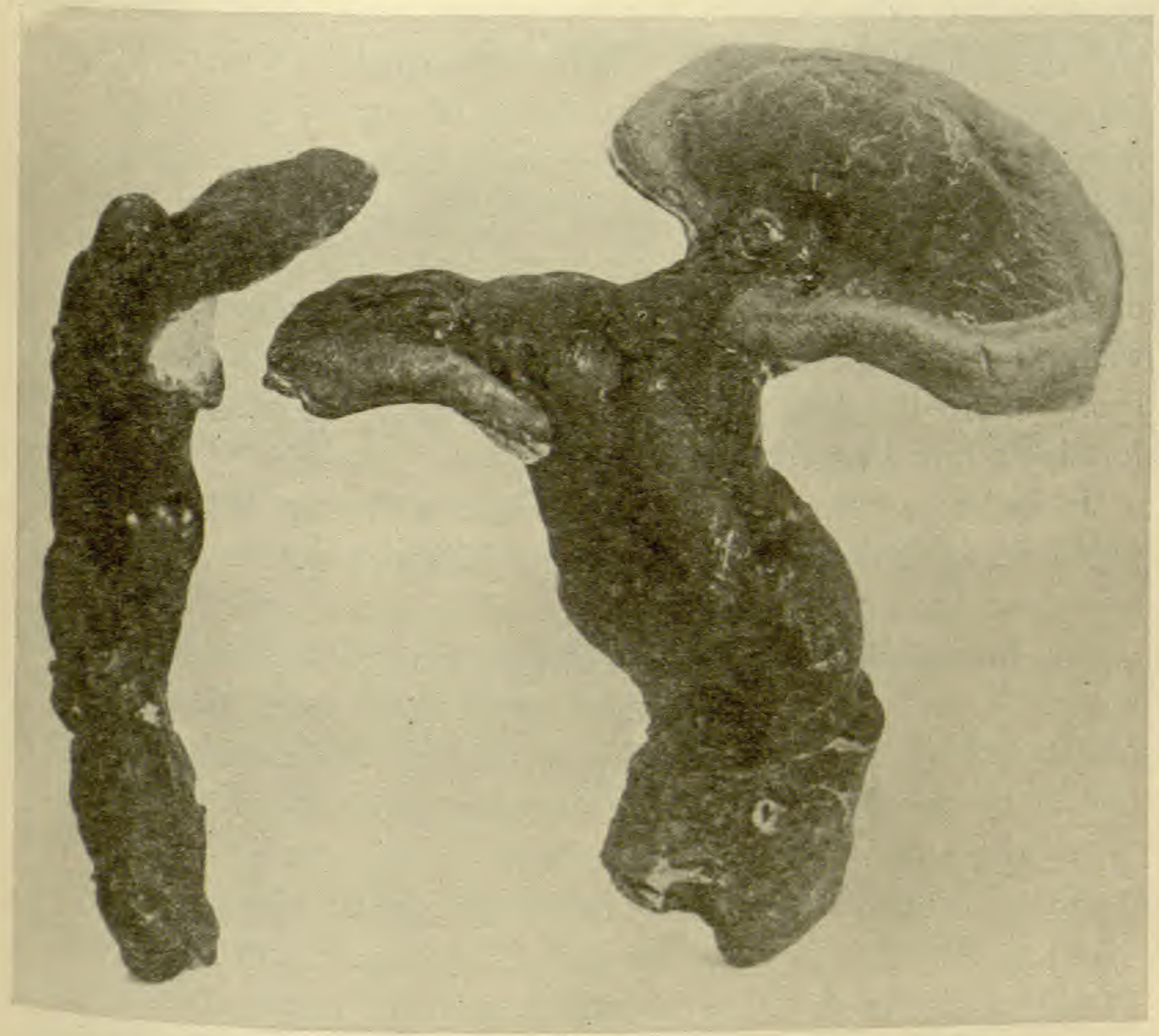

FIG. 5.—*Ganoderma subperforatum* Atkinson, from Ohio (natural size).

being verrucose from the presence of numerous brownish or yellowish-brown points; but when one examines the wall at the middle focal plane, these colored dots are seen not to project beyond the outer surface of the wall, though both above and below the middle focal plane they do appear as echinulations. The structure seemed to be so puzzling that I was led to employ the oil immersion lens (Zeiss apochromatic homogeneous immersion lens, equivalent focus 1.5^{mm} and compensation ocular 6). This revealed the true structure of the spore wall. It is hyaline or nearly so, and is perforated with numerous slender rodlike extensions of a brown or yellowish-brown substance, which appear as if they might be projections of the colored content of the spore. These do not extend beyond the outer surface of the wall, and they radiate from the endospore through the hyaline wall. They are especially prominent at the smaller end of the oval spore where the hyaline wall is considerably thicker, sometimes forming a broad conelike cap to the spore.

In order to demonstrate this peculiar structure beyond doubt, photomicrographs were made of four different species and forms, and these are reproduced in *pl. 19.* The spores which were lying so that the middle plane was in focus show very clearly that the wall is smooth, and that it is perforated with these short, dark-colored, rodlike extensions. These are very evident all around the spore, but are remarkably prominent at the apex, especially in those spores where the broad conelike hyaline cap is still intact. Where the middle plane of the spore is not in the focal plane, the spores appear "warty," but this is only an optical illusion. This is especially striking in *pl. fig. 6,* where the middle plane of nearly all the spores was out of focus. For the species from which these photomicrographs were made the reader is referred to the description of figures. The fact that the spore wall is hyaline or subhyaline, and perforated with dark lines, gives such prominence to the latter that they are apt to be taken for warts or echinulations when the examination is hasty. The hyaline portion of the spore wall appears also to be of a less firm consistency than the colored perforations or lines, and if the spores dry at a certain age, perhaps before they are quite mature, the hyaline portion of the wall appears often to shrink or collapse somewhat, thus making the colored points stand out as echinulations, but a careful examination with the oil immersion lens reveals their true structure.

Besides the markings of the spores of these species, there is another peculiarity which has been erroneously interpreted by those who have tried to describe them. This peculiarity relates to the form of the spore. PATOUILLARD[23] in 1889 describes them as truncate and emarginate at the base (tronquées et echancrées à la base) and in 1900[24] simply as truncate at the base. BRESADOLA[25] says the spores in *Ganoderma lucidum* are obovate, at length truncate at the base (sporae obovatae, demum basi truncatae). MURRILL[26] describes them in several species as follows: "Spores ovoid, obtuse at the summit, attenuate and truncate at the base." But a careful study of the spores shows that exactly the reverse is true. The base of the spore is the broadly rounded end, while the apex is the narrowed, "truncate" end. In *Ganoderma lucidum* (Leys.) Karsten from Europe, including the forms collected by myself on the fir in the Jura Mountains, in *G. tsugae* Murrill and *G. curtisii* (Berk.) Murrill, both from the United States, the spores are all similar and practically identical. They are ovate in form, and when they are lying so that they can be seen in side view, they are seen to be more or less inequilateral, that is, one side is more convex than the other. The place where the spore was attached to the sterigma is at the side of the broad rounded end opposite the convex side. Sometimes a minute angle can be seen here where the sterigma was attached. Boiling the spores in a weak solution of potassium hydrate brings out the entire structure more clearly, and at this point, where the sterigma was attached, the spore wall is very thin, there being a slender channel extending from the endospore almost through the epispore to the point where the sterigma was attached. The treatment with potash, however, is not necessary in order to demonstrate the characteristic structure of the spores described above in these species. An examination of the spores in the plate will show several in which the very thick wall at the apex is still intact and forms a broad conelike cap

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[23] Bull. Soc. Bot. France 5:66. 1889.

[24] Essai taxonomique sur les familles et les genres de Hyménomycètes 105. 1900.

[25] Hymenomycetes Hungarici Kmetiani. Atti Acad. Sci. III. 3:73. 1897.

[26] Bull. Torr. Bot. Club 29:601. 1902; N. Am. Flora 9^2:118, 120. 1908.

on the spore. As the spore matures and dries, this cap in most cases either collapses or breaks off, leaving a" truncate" or "emarginate" end.

The spores of *P. applanatus* of both Europe and the United States have exactly the same general structure as those of *Ganoderma lucidum* described above, as I shall explain in another paper.

The spores of *Ganoderma oregonense* Murrill have the same structure, but the wall is thinner and the structure is not quite so easy to make out. The form of the spores is also somewhat different, being more nearly elliptical in form, though some are obovate, and they are slightly larger. In the spores from Ganoderma received from Mr. HARD, mentioned above as growing on roots of an oak, the peculiarities in the structure of the wall described above for *G. lucidum* and some other species are not well developed, and are demonstrated with difficulty. After several examinations, even with the use of the oil immersion lens, I had nearly come to the conclusion that this species was an exception; but after boiling the spores in a weak solution of potassium hydrate, the brownish perforations of the wall were faintly visible. With some other differences in spore character this species seems to be different from the others. In order to present my interpretation of the different species employed in this study of specimens from Europe and the United States, I will add the following diagnoses.

GANODERMA PSEUDOBOLETUM (Jacq.) Murrill,[27] Bull. Torr. Bot. Club **29**:602. 1902.

Agaricus pseudoboletus Jacq. Flor. Austr. **1**:26–27. *pl. 41.* 1773.
Boletus rugosus Jacq. Flor. Austr. **2**:44. *pl. 169.* 1774.
Boletus lucidus Leys. Flora Halensis 300. 1783.
Boletus obliquatus Bull. Herb. France. *pl. 7.* 1780; *pl. 459.* 1790.
Polyporus lucidus Fries, Syst. Myc. **1**:353. 1821.
Polyporus laccatus Pers. Myc. Eur. **2**:54. 1825.

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[27] In Jour. Myc. **9**:94. 1903, MURRILL uses the combination *Ganoderma flabelliforme* (Scop.) Murrill (*Boletus flabelliformis* Scopoli, Fl. Carnolica **2**:466. 1772). It is impossible from SCOPOLI's description to say to what species he referred. SCOPOLI cites *fig. A, plate 37*, of BATARRA (Fung. Agri. Armin. Hist. 1755). There are several of BATARRA's figures which resemble *P. lucidus* more closely than the one which SCOPOLI cites. BATARRA in turn cites *Agaricum flabelliforme* Micheli (Nov. Plant. Gen. 118. 1729), which from his own and MICHELI's description evidently applies to some other plant.

Ganoderma lucidum Karsten, Rev. Myc. 3:no. 9, p. 17. 1881.
Ganoderma tusgae Murrill, Bull. Torr. Bot. Club 29:601. 1902; North American Flora 9^2:118. 1908.

Sporophore large, usually stipitate, rarely sessile, annual, rarely perennial, convex above, concave or plane below; pileus dimidiate, reniform, or rarely circular, margin plane or broadly crenate to lobed; surface smooth, sometimes coarsely radiately rugose, incrusted with a reddish or blackish substance shining like varnish, sulcate, the shallow concentric furrows marking off zones which are often narrow and crowded on the margin; trama or context punky, often quite firm and hard especially next the hymenophore, brown to pallid whitish, whitish above, brown next the hymenophore, zonate especially next the stem, though sometimes faintly; stem when present lateral or excentric or rarely central, long or short, sometimes forked, 0.5–4^{cm} in diameter, even or irregular, sometimes enlarged below, varnished and colored like the pileus, context colored like that of the pileus or somewhat darker; hymenophore of long slender tubes, brown within, 3–5 to a mm., mouths circular angular, white or yellowish, finally brown, dissepiments entire, obtuse, thin, acute; spores ovoid to ovate, rounded at the base and slightly inequilateral in side view; wall hyaline, smooth, thickened at the apex into a broad conelike cap which usually collapses, leaving the apex truncate or even depressed, everywhere perforate with numerous slender dark-colored lines which radiate from the endospore through the epispore, 9–11 × 5–8 μ. *Fig. 1.*

A large and attractive plant, very conspicuous because of its brilliant varnished appearance. Common on decaying stumps and trunks of frondose and coniferous trees. There appear to be forms or physiological species in this species. In Europe the form more commonly collected is on frondose trees, and is regarded as typical. The usual color of these is a reddish chestnut.

The forms cannot be well separated into species, though some of them may be regarded as elementary or physiological species or forms. Among these may be mentioned the following:

G. PSEUDOBOLETUM TYPICUM.—On trunks and roots of frondose trees in Europe (also in N. A.?); color reddish chestnut.

G. PSEUDOBOLETUM TSUGAE (Murrill) Atkinson.—On hemlock-spruce (*Tsuga canadensis*) in the United States and British America. Since the form does not grow on wood of frondose trees in America it may be regarded as a physiological species. In color and other characters it differs but slightly if at all from the typical form.

G. PSEUDOBOLETUM MONTANUM Atkinson.—On dead trunks of Abies in the Jura Mountains. This form is very dark, almost black, much darker than the typical form. Type specimens No. 21007 in herb. Cornell University, and a specimen of the same collection deposited in herb. Museum of Paris. *Fig. 2.*

GANODERMA CURTISII (Berk.) Murrill, North American Flora 9^2:120. 1908.

Polyporus curtisii Berk. Hooker's Jour. Bot. **1**:101. 1849.
Fomes curtisii Sacc. Syll. Fung. **6**:158. 1888.
Ganoderma pseudoboletus Murr. p. p. Bull. Torr. Bot. Club **29**:603. 1903.
Ganoderma flabelliforme Murr. p. p. Jour. Myc. **9**:94. 1903.

Fruit bodies large, corky to woody (sometimes perennial?), stipitate or nearly sessile, stipe lateral, excentric, or central; pileus reniform, or circular when the stipe is central, convex or depressed, 0.5–3^{cm} thick at base, with a thin hard crust, margin obtuse; surface zonate, faintly or quite strongly sulcate, sometimes radiately rugose or corrugated toward the margin, smooth, yellowish or reddish yellow, often with reddish spots or zones, not or rarely varnished (laccate); trama or context punky to woody, softer above, harder below next the hymenophore, pallid to pale brownish, light colored next the upper surface; margin sometimes sterile for a short distance on the under side; hymenophore of slender tubes 0.5–1^{cm} long (or longer), brown in section, pore surface grayish white becoming reddish brown where bruised, tubes 3–7 to a mm., mouths rotund, minute, dissepiments thin, edge obtuse, entire; spores ovoid to ovate, rounded at base and slightly inequilateral in side view; wall hyaline, smooth, thickened at apex into a broad conelike cap, which usually collapses, leaving the apex truncate or even depressed, everywhere perforate with numerous slender dark-colored lines which radiate from the endospore through the epispore, $9–11 \times 5–8\ \mu$; stem 1–15^{cm} long, 1–3^{cm} thick, nearly cylindrical but variable, surface laccate with a reddish-chestnut varnish on the crust, context brown, nearly the same color as the tubes or context of the pileus next the tubes. *Fig. 3.*

On dead roots, stumps, etc. of frondose trees in the southern United States.

GANODERMA OREGONENSE Murrill, North American Flora 9^2:119. 1908.—Sporophore large, stipitate; pileum 14–17^{cm} long, 12^{cm} broad, 5.5^{cm} thick, tumid, upper surface rather strongly convex, hymenophore slightly convex or plane; surface smooth, with a thin brittle crust, shining as if varnished (laccate), dark reddish brown (seal brown to clove brown, *R* with reddish tinge), sulcate, rings distant on the surface, crowded at the margin, more or less rugose; trama white, cinnamon next the hymenophore, very soft, punky, and yielding like chamois skin, the cinnamon-colored portion firmer; hymenophore of long slender tubes, up to 2–5^{cm} long, often with a stratified appearance, the strata 3–4^{mm} and marked off by faint lighter lines, brown, near cinnamon to Mars brown (*R*), firm, woody, tubes angular, 4–5 to a mm., dissepiments thin, entire; spores elliptical to subovate, rounded at the broader end, in age truncate at the smaller end, attached one side of the broader end, wall perforated by numerous short lines of a brownish substance, giving a verrucose appearance to the spore which is really smooth, 11–15×7–8 μ; stem stout, 1–15^{cm} ×3–6^{cm}, irregular, surface like that of the pileus; trama white, soft like the white part of the pileus, with a radiate, fibrous growth from the middle line and continuing into trama of the pileus. *Fig. 4.*

On dead *Picea sitkensis* near Seaside, and on dead root (of conifer?), Corvallis, Oregon.

Ganoderma subperforatum Atkinson, n. sp.—Sporophore medium size, stipitate. Pileus lateral, simple or lobed, subcircular to reniform, convex, brick red to bay, vinaceous cinnamon toward margin, and the margin lighter color when young, laccate, broadly sulcate; spores ovate-cuneate, content brownish, wall thin, very faintly perforate with slender dark lines, which are seen with difficulty, 8–12× 5–8 μ. *Fig. 5.*

(Sporophorum stipitatum. Pileo suberoso lignoso, sulcato-rugoso stipiteque laterali, laccato, rubro-castaneo; sporae ovato-cuneatae, membraneo leviter perforato ab lineis brunneis, 8–12×5–8 μ.)

On dead oak wood, Chillicothe, Ohio. Type specimen no. 19560 in herb. Cornell University.

CORNELL UNIVERSITY

EXPLANATION OF PLATE XIX

Photomicrographs of spores of several species of Ganoderma, ocular 12, objective 1.5^{mm} oil immersion, Zeiss microscope, plate-holder 370^{mm} from object. The photomicrographs were made by the author. The photographs from which the text figures were produced were made by E. J. PETRY under the author's direction.

FIG. 1.—*Ganoderma pseudoboletum* forma *montanum* Atkinson, from plant on fir, Jura Mts., France; some of the spores show the entire conical, hyaline cap at apex; note the dark lines perforating the hyaline wall; the upper right-hand spore is in side view, showing at the lower corner a point where the spore was attached to the sterigma; lower spore slightly out of median focal plane, surface appearing roughened or echinulate.

FIG. 2.—*Ganoderma pseudoboletum* forma *tsugae* (Murr.) Atkinson, from plant on hemlock-spruce, Ithaca, N. Y.; a few of the spores show the entire conical cap at the apex; one of the spores of the group in the left is in side view, showing the inequilateral form, and the point where attached to sterigma; note the perforating dark lines in the hyaline wall of the spores; one spore at extreme left slightly out of median focal plane, and these lines appear as echinulations.

FIG. 3.—*Ganoderma curtisii* (Berk.) Murrill; one of the spores at the lower side shows the entire conical cap at apex; this and another one at the left are in side view, showing the inequilateral form; note the perforating dark lines in the hyaline wall; North Carolina plants.

FIG. 4.—*Ganoderma oregonense* Murrill; showing elliptical form of spores, thinner wall, dark perforating lines in wall of spores.

FIG. 5.—*Ganoderma subperforatum* Atkinson, from Ohio; showing cuneate form of spores and faint dark lines in the spore wall, only brought out by boiling in potash solution.

FIG. 6.—*Ganoderma pseudoboletum* typicum, from plant collected in Bois de Boulogne, Paris; most of the spores are out of focus; the dark lines perforating the walls appearing as warts or echinulations, but the spores are really smooth.

ATKINSON on POLYPORUS LUCIDUS

THE MORPHOLOGY OF *PHYLLOCLADUS ALPINUS*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 118

N. JOHANNA KILDAHL

(WITH PLATES XX–XXII)

The only account of the morphology of Phyllocladus is that of Miss AGNES ROBERTSON (18) in 1906, and this deals exclusively with the anatomical structures and with the affinities of the genus.

The material for the present study was collected by Dr. L. COCKAYNE of New Zealand. It consisted of two collections: one of ovulate and staminate strobili, collected November 1, 1906; the other of ovulate strobili, collected December 11, 1906, from cultivated trees. Unfortunately, the two collections did not afford a very close series, and it was impossible to get at some of the most important points, as the development of the microsporangia, microspores, pollen tubes, female gametophyte, archegonial neck cells, ventral cell or nucleus, and embryo. Dr. COCKAYNE is making collections of the lacking stages at the present time, and it is hoped that a complete description can be presented later. Some material was also obtained from Cambridge, Mass., through the kindness of Dr. B. L. ROBINSON, consisting of three ovulate cones, taken from the Gray Herbarium and collected on the Wilkes expedition in 1838–1842. At what time of the year these cones were collected is not known, but they showed somewhat later stages than those of the last collection made by Dr. COCKAYNE on December 11. It is needless to say that this herbarium material was very much shrunken, and it was impossible to obtain from it any definite structure.

Dr. COCKAYNE'S material was killed and fixed in the field, in 70 per cent. alcohol and formalin; cut 5 μ and 7 μ thick; and stained part in safranin and gentian violet, and part in iron alum.

Staminate strobilus

The staminate strobili are formed laterally, in clusters of 2–8 at the tips of the lateral branches. Miss ROBERTSON (18) reports one staminate strobilus bearing an ovule at its base, which may indicate that the ancestral condition was bisporangiate. The sporophyll resembles that of Pinus, although it is comparatively shorter and broader, and has two abaxial sporangia (*fig. 1*). Whether it has any aborted sporangia, as reported in the Taxineae, could not be determined. At least when mature it has fewer sporangia than any of the Taxineae; *Taxus baccata* having seven, *Torreya taxifolia* four, Cephalotaxus four to two, and Phyllocladus two.

Male gametophyte

Material collected November 1 showed the microspores shed and the sporangia wide open along the whole line of dehiscence. Only three or four sporangia retained a few spores, and therefore the sections did not show many stages.

The youngest stage found in the development of the microspore was the uninucleate stage (*fig. 3*), with the wings fully developed. The microspores contain no starch; COULTER and LAND (**9**) found the microspores of *Torreya taxifolia* rich in starch; Miss YOUNG (**20**) found starch in the spores of Dacrydium; the body cell of *Cryptomeria japonica* contains starch grains, according to LAWSON (**16**); COKER (**7**) found the spores of Podocarpus, during all of the divisions, packed with starch, which disappears just before shedding; CHAMBERLAIN (**6**) found starch in the spores of *Pinus Laricio*, and Miss FERGUSON (**12**) in the spores of the species of pine studied by her.

The first division of the microspore cuts off a prothallial cell, which usually lies against the wall, and which immediately begins to disorganize (*fig. 6*). Soon a second prothallial cell is cut off. These two prothallial cells are at first surrounded by delicate walls which very soon disappear, so that when the spore is mature all the four nuclei lie free in the common cytoplasm. The first prothallial cell is commonly evanescent and its nucleus soon disintegrates (*figs. 9, 10*); in two mature spores it was still recognizable (*fig. 11*). The second prothallial cell always persists, in which respect Phyllocladus is similar to Ginkgo.

Prothallial cells have heretofore not been reported in any of the Coniferales except Podocarpineae and Abietineae. COKER (**7**) reports two prothallial cells in Podocarpus, one of which develops further, while the other slowly degenerates. In *Podocarpus Totarra*

Hallii BURLINGAME (4) finds two prothallial cells, both of which divide and form a tissue, consisting generally of six cells; a similar condition was found in Dacrydium by MISS YOUNG (16). Two more divisions follow, so that the mature spore commonly contains four free nuclei—prothallial, tube, stalk, and body nuclei.

On November 1 the four-nucleate microspores are mostly found lodged on top of the nucellus (*fig. 15*); how much earlier they reach it and how long they remain there is not known, as no material previous to this date was available. In exceptional instances pollen tubes had been formed and had penetrated the nucellus (*fig. 18*); but at this date the tube contained only the four nuclei of the mature spore. On December 11 the nucellus was in most cases entirely honeycombed with pollen tubes, and very much disintegrated (*fig. 19*). The pollen tubes do not pass deviously through the nucellus to any great extent, nor branch, but pass almost in a straight line to the embryo sac. As many as fifteen tubes were found in one ovule (*fig. 19*).

Before the pollen tube enters the embryo sac the body cell divides into two equal and optically similar male cells; it was impossible to observe this division, but it takes place some time after the tube has penetrated the nucellus and before it enters the embryo sac (*figs. 20, 31b*). The entire contents of the pollen tube (five naked nuclei) enter the egg (*fig. 20*). ARNOLDI (1) also finds that in Cephalotaxus the contents of the pollen tube are emptied into the embryo sac, the contents in this case, however, consisting of only four nuclei; a similar condition has been found in Pinus, where nearly the whole of the contents of the tube is emptied into the cytoplasm of the egg (COULTER and CHAMBERLAIN 10, and FERGUSON 12); according to COKER (8) this may also take place in Taxodium (8) and in Podocarpus (7); and COULTER and LAND (9) report it for *Torreya taxifolia.* In Cryptomeria LAWSON (16) finds that only one male cell enters the archegonium; and JÄGER (13) reports the same in *Taxus baccata.* In Phyllocladus it is not uncommon to find the entire contents of pollen tubes within the embryo sac after fertilization has taken place, and even after the eight-nucleate proembryo stage (*fig. 30*); this is no doubt due to the unusual open condition of the archegonia, the greatly disintegrated nucellus (which seems to be of a very mucilaginous consistency), and the large number of pollen tubes.

When the two male cells are equal, it is commonly inferred that both function. So far as could be determined, only one male cell functions in Phyllocladus, and the second male cell, together with the other three nuclei discharged into the egg cell from the pollen tube, disintegrate as the proembryo develops, as shown in *fig. 26*. ARNOLDI (1) finds in Cephalotaxus that the second male cell remains in the upper end of the egg and later goes through a mitotic division.

The Taxineae are equally divided in regard to the size of the male cells. In *Torreya taxifolia* they are unequal (COULTER and LAND **9**); they are also reported unequal in Taxus by BELAJEFF (**3**), and by JÄGER (**13**); ARNOLDI reports them of the same size in Cephalotaxus (**1**); and they are equal in Phyllocladus. Outside of the Taxineae they are equal in *Juniperus communis* (NORÉN **17**), Thuja (LAND **15**), Sequoia (ARNOLDI **2**), *Pinus Banksiana* (COULTER **11**), and *Pinus Laricio* (CHAMBERLAIN **6**). Miss FERGUSON (**12**) finds them unequal in *Pinus Strobus;* and one functioning male cell is reported in Podocarpus by COKER (**7**). LAND (**13**) finds in *Ephedra trifurca* that the male cells are equal, both enter the egg, but only one functions.

Ovulate strobilus

The ovulate strobilus occurs on the side of the phylloclad (in the axil of a scale leaf) near its base (*fig. 12*). It usually occurs singly, but frequently in pairs; never more than one pair was seen upon a single phylloclad. The strobilus consists of six to eight rather fleshy scales, each scale bearing a single ovule in its axis.

The ovule has two integuments, entirely free from the nucellus to the very base. The inner one is very thick and consists of three layers: an inner fleshy, a middle stony, and an outer fleshy consisting of only two layers of cells. The stony layer begins to develop at the micropylar end and extends toward the base. At first it consists of only one layer of cells, but later it becomes much thicker and extends all the way around the base of the ovule, where, however, it remains much thinner than at the micropylar end. The inner fleshy layer is somewhat crowded out by the growth of the stony layer; and the outer fleshy layer is finally sloughed off. The integument contains no vascular strands; these end at the base of the ovule (*fig. 15*); it contains a number of resin ducts, shown in the cross-section in *fig. 16*.

The second integument, called an arillus, arises quite late outside of the heavy integument; on November 1 it appears merely as a small papilla in longitudinal section (*fig. 15*). It grows very rapidly, inclosing the ovule like a cup; the ovule, however, grows up through it, and by December 11 it is merely a light, leathery sheath around the base of the ovule, reaching about half-way to its tip (*fig. 14*).

Female gametophyte

It was impossible from the material in hand to ascertain the development of the female gametophyte, as the formation of walls was in most cases well advanced on November 1. In a few instances it was still in the free nuclear stage (*fig. 18*); and one preparation showed archegonia already formed. The endosperm is of the "ruminating" type, this feature being especially pronounced in the early stages.

The development of archegonia could not be observed, as no stage before fertilization was available. It is impossible, therefore, to state definitely whether neck cells are formed or not. Some indefinite remains of cells, in a few sections, indicate that they exist; and comparing Phyllocladus with the Taxineae, and taking into consideration that neck cells are often destroyed very early by the pushing-in of the pollen tube or the growth of the central cell, the probability is that a two-celled neck exists in the early stages of the archegonium (*fig. 32b*), although nothing was found upon which a definite statement can be based. In *Torreya taxifolia* COULTER and LAND (9) found two neck cells; ARNOLDI (1) also found two in *Cephalotaxus Fortunei;* JÄGER (13) reports two in *Taxus baccata.* From such a condition as that shown in *figs. 19, 31, 32,* it may be inferred that the presence or absence of neck cells would make very little difference. The whole structure of nucellus and gametophyte is of a very mucilaginous composition, and this, together with the prodigality of pollen tubes and male cells, presents a very loose and disintegrated condition. The archegonium in every case, whether located near the surface of the gametophyte or deeper in the tissue, presents an opening as large as the width of the sac. The pollen tube penetrates the tissue, digesting it very readily, and seems to break through the layer of jacket cells surrounding the embryo sac as though no obstacle were in its way. No instance was found, at the stage of fertilization, where the archegonium had not been smashed into, either from the top or from the side, by the pollen tube.

The embryo sac is surrounded by a layer of jacket cells with very large nuclei, and many of the cells are multinucleate. JÄGER (13) also pictures a very heavy jacket layer of uninucleate cells in *Taxus baccata;* none are reported in Torreya or Cephalotaxus, although the drawings of the latter by ARNOLDI (1) suggest a jacket layer. The archegonia are one to four in number.

No ventral cell or nucleus could be demonstrated, although the probability is that a ventral nucleus is formed; the chromatin in the egg nucleus (*fig. 32b*) before fertilization indicates that it is getting ready to divide. ARNOLDI (1) says that in *Cephalotaxus Fortunei* the egg nucleus, shortly before fertilization, cuts off a ventral canal nucleus, which together with a mass of the upper part of the egg destroys the neck cells and passes out of the embryo sac. JÄGER (13) does not mention nor picture a ventral nucleus in Taxus; COULTER and LAND (9) did not find a ventral cell or nucleus in *Torreya taxifolia;* Miss ROBERTSON (1) interpreted a spindle in the central cell of *Torreya californica* as the forming of a ventral nucleus.

Fertilization

At the time of fertilization the egg becomes rich in food vacuoles in the basal end (*figs. 25, 26, 28*). The egg nucleus may be situated near the upper end of the egg (*figs. 22, 23*), or near the basal end (*fig. 28*). The fusion nucleus (*figs. 22, 24*) is partially surrounded by the finely granular cytoplasmic sheath of the male nucleus. This cytoplasmic sheath has been observed in Taxodium by COKER (8), in *Torreya taxifolia* by COULTER and LAND (9), and in *T. californica* by Miss ROBERTSON (19). The non-functional male cell (*figs. 22, 23*), which has begun to disorganize, shows the cytoplasmic sheath very distinctly.

Embryo

The first division of the oospore could not be obtained. Free nuclear division was observed to the eight-nucleate stage. As this was the oldest stage available, it is impossible to say whether more free nuclei are formed or not before the formation of walls. ARNOLDI (1) figures ten free nuclei in one section of *Cephalotaxus Fortunei,* and states that there are eight to sixteen free nuclei. Jäger (**13**) found sixteen free nuclei in the proembryo of *Taxus baccata;* and Coulter and Land (**9**) found four free nuclei in *Torreya taxifolia.* One of the older ovules showed a long suspensor and an embryo of a few cells buried near the base of the gametophyte (*fig. 33*), but it was impossible to make out its structure.

Summary

The microsporophyll has two abaxial sporangia and the microspores are shed on November 1 or before.

Two prothallial cells are formed, the first of which is generally evanescent; sometimes both persist as free nuclei, the walls of both being evanescent.

The mature microspore has usually four free nuclei, and occasionally five.

The ovulate strobilus is borne on the phylloclad, and bears two to eight ovules.

The ovule has two integuments; one thick and fleshy, the other (arillus) thin and leathery and persistent only at the base. They are free from the nucellus to its base, and contain no vascular strands.

Microspores are found resting on the top of the nucellus on November 1, and occasionally pollen tubes and archegonia are formed at this date.

Pollen tubes are very numerous and pass in a comparatively straight line through the nucellus to the archegonium. They smash the neck cells, if there are any, and empty their entire contents into the egg; the contents of one or more pollen tubes were found in an egg after the eight-nucleate stage of the proembryo.

The body cell divides into two equal male cells just before discharge into the egg; and only one male cell functions.

The archegonium is surrounded by a heavy jacket layer, consisting of multinucleate cells with large nuclei. Two neck cells are probably formed. No ventral cell or nucleus was found, but the material does not justify a definite statement as to its occurrence or not.

The male cell is surrounded by a cytoplasmic sheath which, partly at least, surrounds the fusion nucleus.

At least eight free nuclei are formed by the proembryo before cell walls are formed; and a long suspensor is developed.

This work was carried on under the direction of Professor JOHN M. COULTER; and my acknowledgments are also due to Dr. C. J. CHAMBERLAIN and Dr. W. J. G. LAND, for kindly assistance.

THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES XX–XXII

With the exception of *figs. 1* and *2* all the figures were drawn with the aid of a camera lucida and reduced one-half. Index letters are as follows: *e*, endosperm; *p*, perisperm; *n*, nucellus; *if*, inner fleshy layer; *s*, stony layer; *of*, outer fleshy layer; *a*, arillus; *fs*, fleshy scale.

PLATE XX

FIG. 1.—Abaxial view of microsporophyll, showing the empty sporangia.

FIG. 2.—Side view of microsporophyll.

FIG. 3.—Microspore. ×1850.

FIG. 4.—First division of microspore. ×1850.

FIG. 5.—Two-nucleate stage. ×1850.

FIG. 6.—Second division; first prothallial cell against upper wall. ×1850.

FIG. 7.—Three-nucleate stage, showing form of wings. ×3000.

FIG. 8.—Evanescent walls of the two prothallial cells. ×3000.

FIG. 9.—First evanescent prothallial cell lying outside of the cytoplasm of the spore. ×1850.

FIG. 10.—Mature microspore. ×1850.

FIG. 11.—Microspore with both prothallial cells retained. ×3000.

FIG. 12.—Phylloclad with ovulate strobilus.

FIG. 13.—Outer view of fleshy scale with ovule.

FIG. 14.—Inner view of fleshy scale with ovule, showing arillus.

FIG. 15.—Longitudinal section of ovulate strobilus, showing ovules with integuments, fleshy scales, and position of vascular system, November 1. ×40.

FIG. 16.—Cross-section of ovule; archegonia in the center of the endosperm; November 1. ×40.

FIG. 17.—Longitudinal section of the ovule with fleshy scales; micropyle not yet formed; arillus covering the ovule; November 1. ×40.

PLATE XXI

FIG. 18.—Part of nucellus on November 1, showing pollen tubes and part of the female gametophyte in the free nuclear stage; archegonia not yet formed; body cell not yet divided. ×850.

FIG. 19.—Nucellus showing numerous pollen tubes and open archegonia; nearly all the body cells have divided; December 11. ×180.

FIG. 20.—Pollen tube, containing two male nuclei, the stalk and tube nuclei, and one prothallial nucleus, entering the archegonium. ×1850.

FIG. 21.—Archegonial jacket cells. ×3000; *fig. 21a*, same.

FIG. 22. Fertilization: the fusing nuclei are partially surrounded by the cytoplasmic sheath; the second male nucleus lies above the fusing nuclei and has begun to degenerate. ×3000.

FIG. 23.—A later stage in fertilization. ×3000.

FIG. 24.—Fusing nuclei with cytoplasmic sheath. ×1850.

FIG. 25.—Second division of proembryo. ×3000.

FIG. 26.—Four-nucleate stage of proembryo; the other four nuclei degenerating. ×3000.

FIG. 27.—Section through thick integument showing inner fleshy layer, the row of heavy-walled cells (containing crystals) which becomes the stony layer, and the outer fleshy layer of two rows of cells. ×1850.

PLATE XXII

FIG. 28.—Basal end of egg, showing egg nucleus, pollen tube with two male nuclei and one other nucleus, and food vacuoles. ×1850.

FIG. 28*b*.—The archegonium of *fig. 28*, showing position of egg nucleus and pollen tube in the egg. ×100.

FIG. 29.—Basal end of embryo sac, showing four nuclei of the proembryo, remains of the pollen tube, and the non-functional male cell. ×1850.

FIG. 29*b*.—Same as *fig. 29*, showing whole length of embryo sac. ×100.

FIG. 30.—Eight free nuclei of proembryo in basal end of sac, with pollen tube above containing normal contents. ×1850.

FIG. 30*b*.—Same as *fig. 30*, showing top of embryo sac. ×100.

FIG. 31.—Female gametophyte, showing disintegration by pollen tube; the pollen tube is entering the egg from the side. ×100.

FIG. 31*b*.—Same as *fig. 31*. ×1850.

FIG. 32.—This figure shows the straight path usually made by the pollen tubes through the nucellus to the archegonia. ×100.

FIG. 32*b*.—Same as *fig. 32*, showing the two probable neck cells; the loose structure of the chromatin of the egg nucleus intimates that it may form a ventral nucleus; body cell not yet divided. ×1850.

FIG. 33.—Long suspensor, with embryo buried deep in the female gametophyte. ×100.

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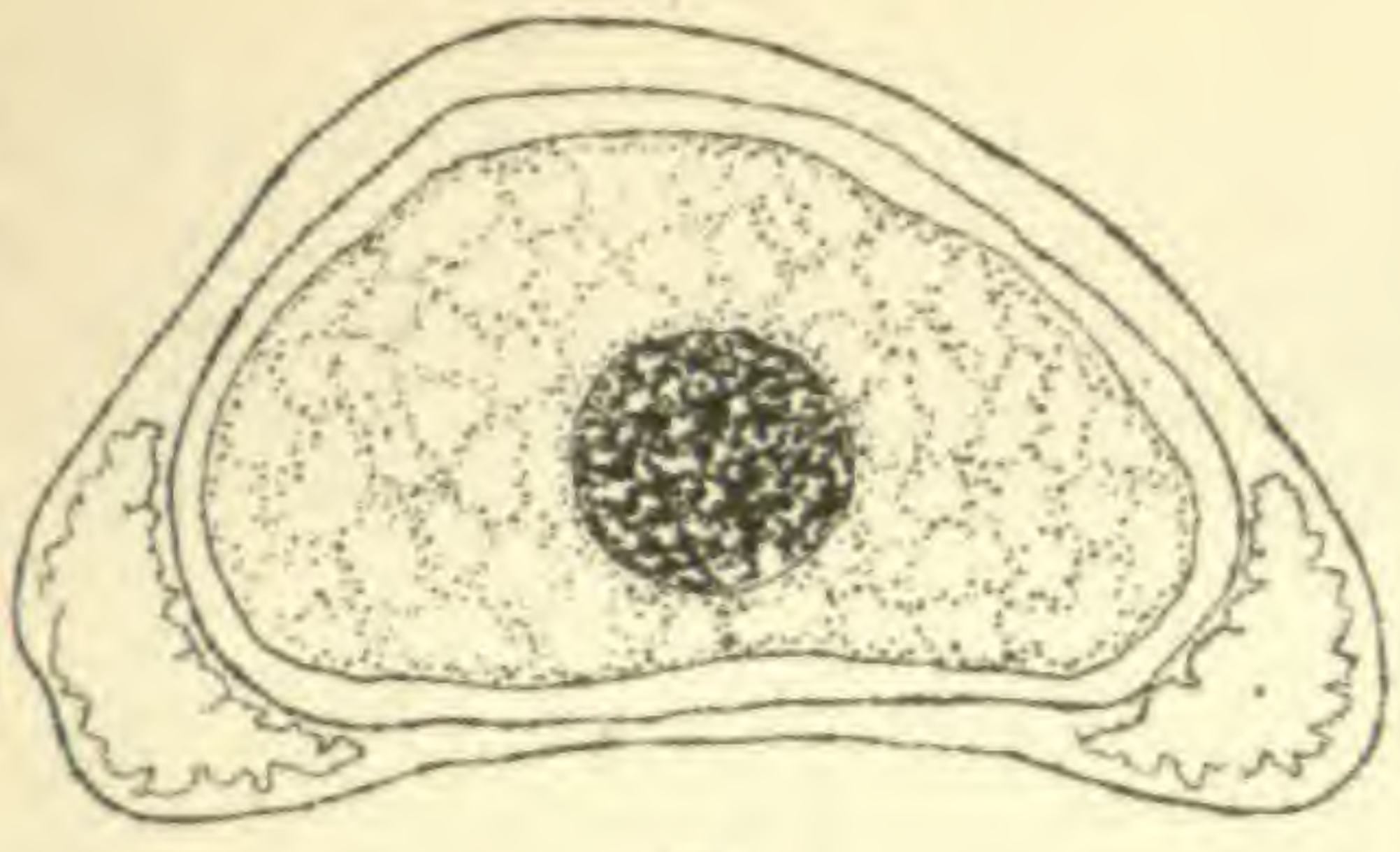

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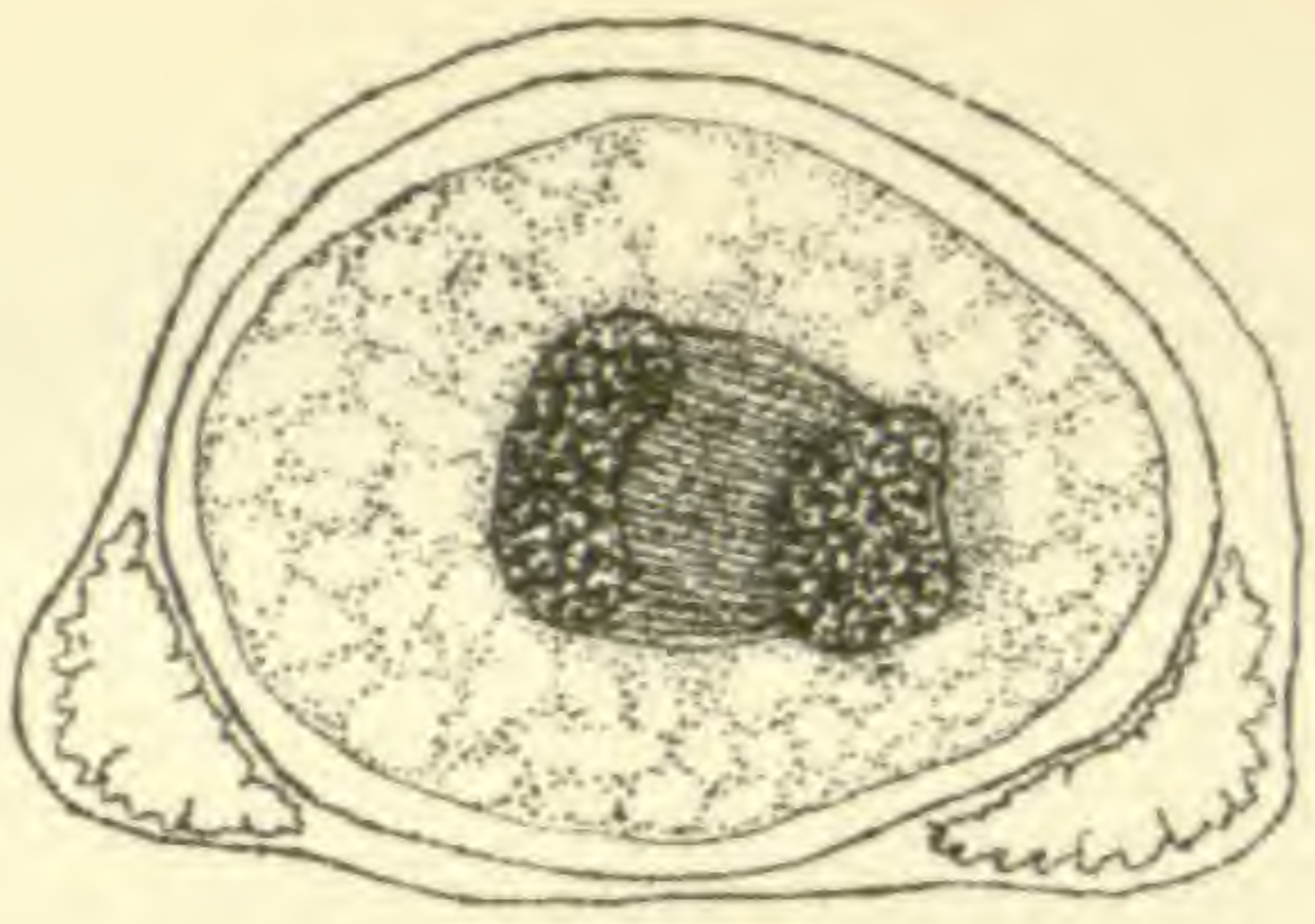

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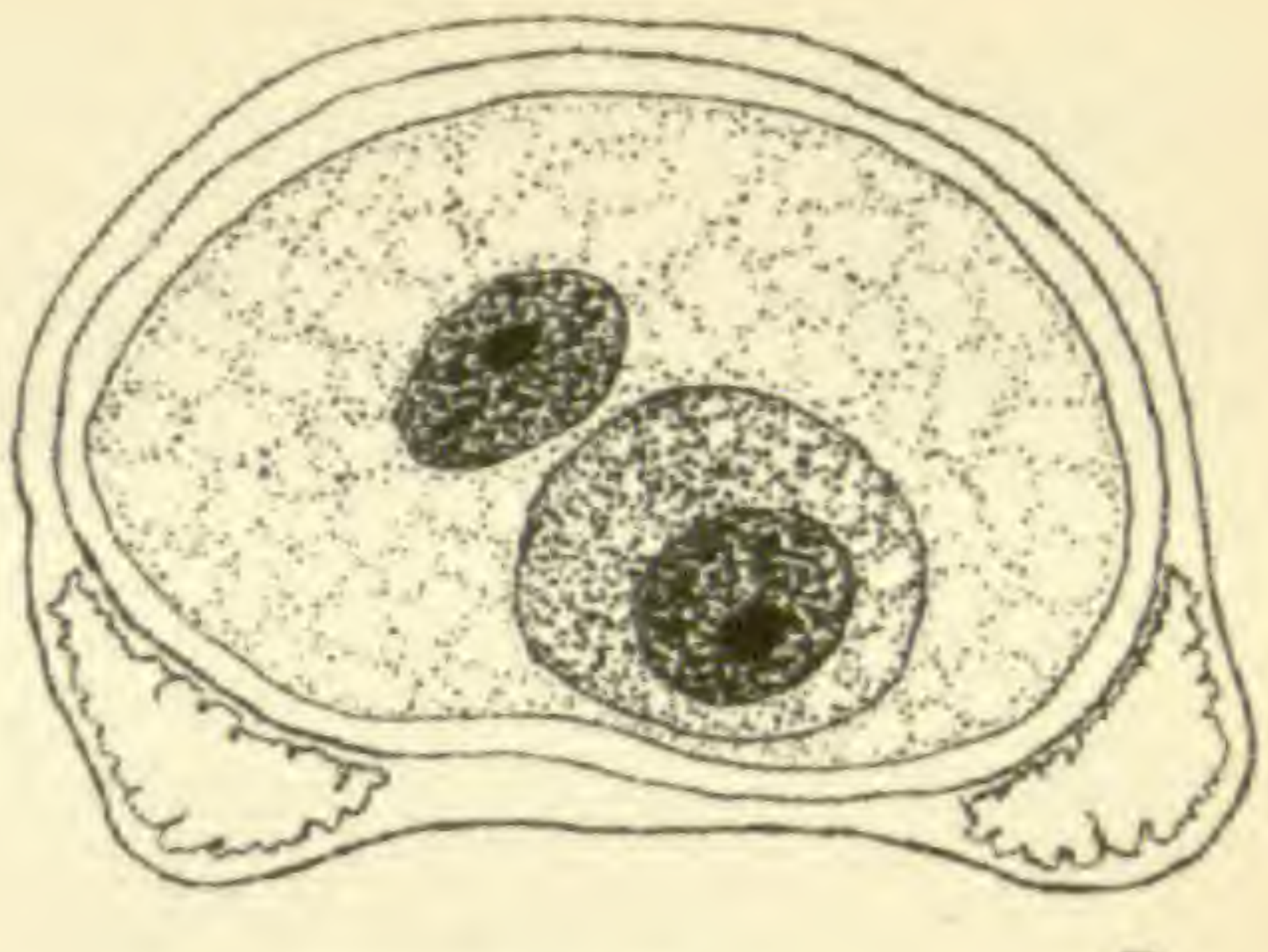

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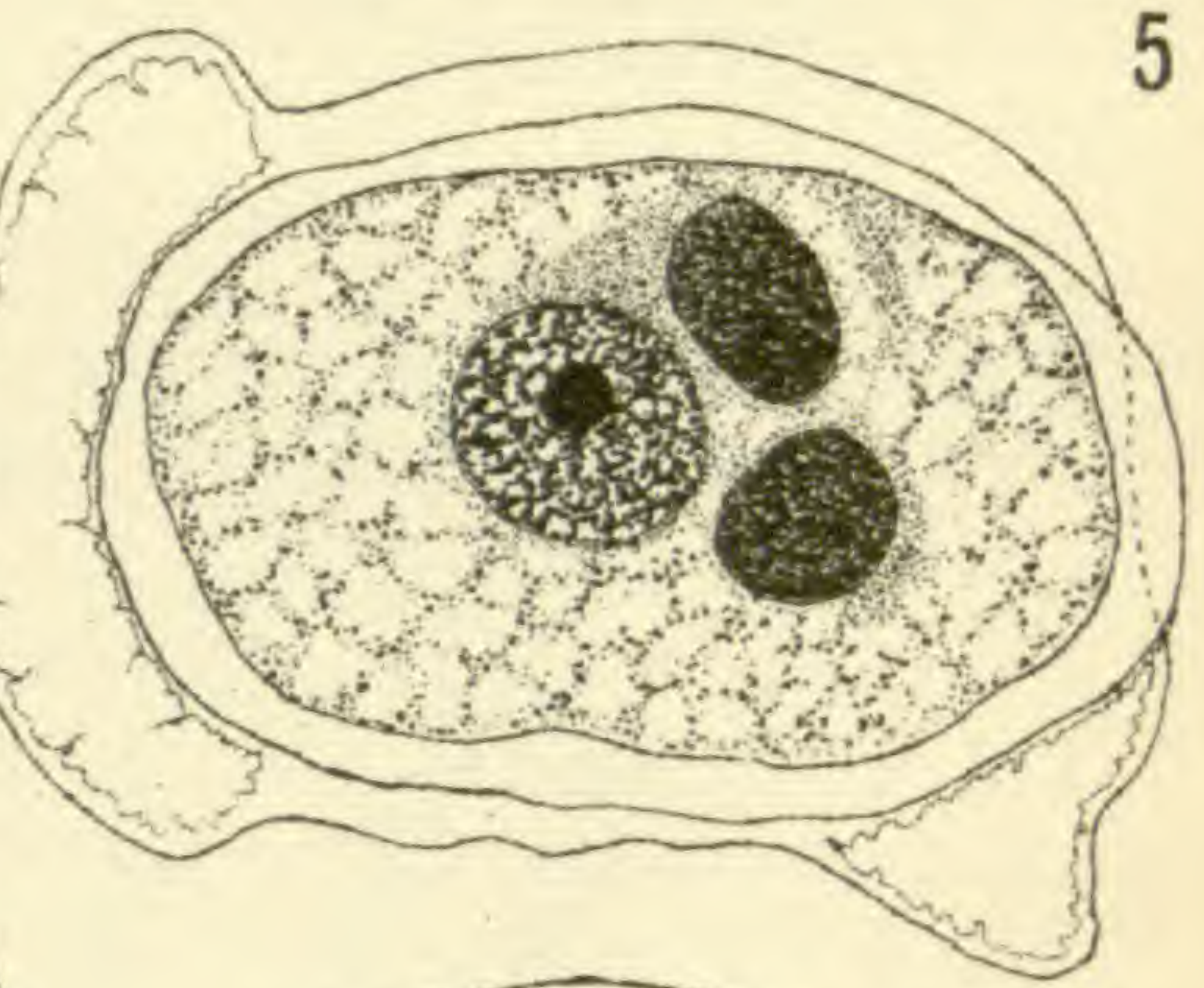

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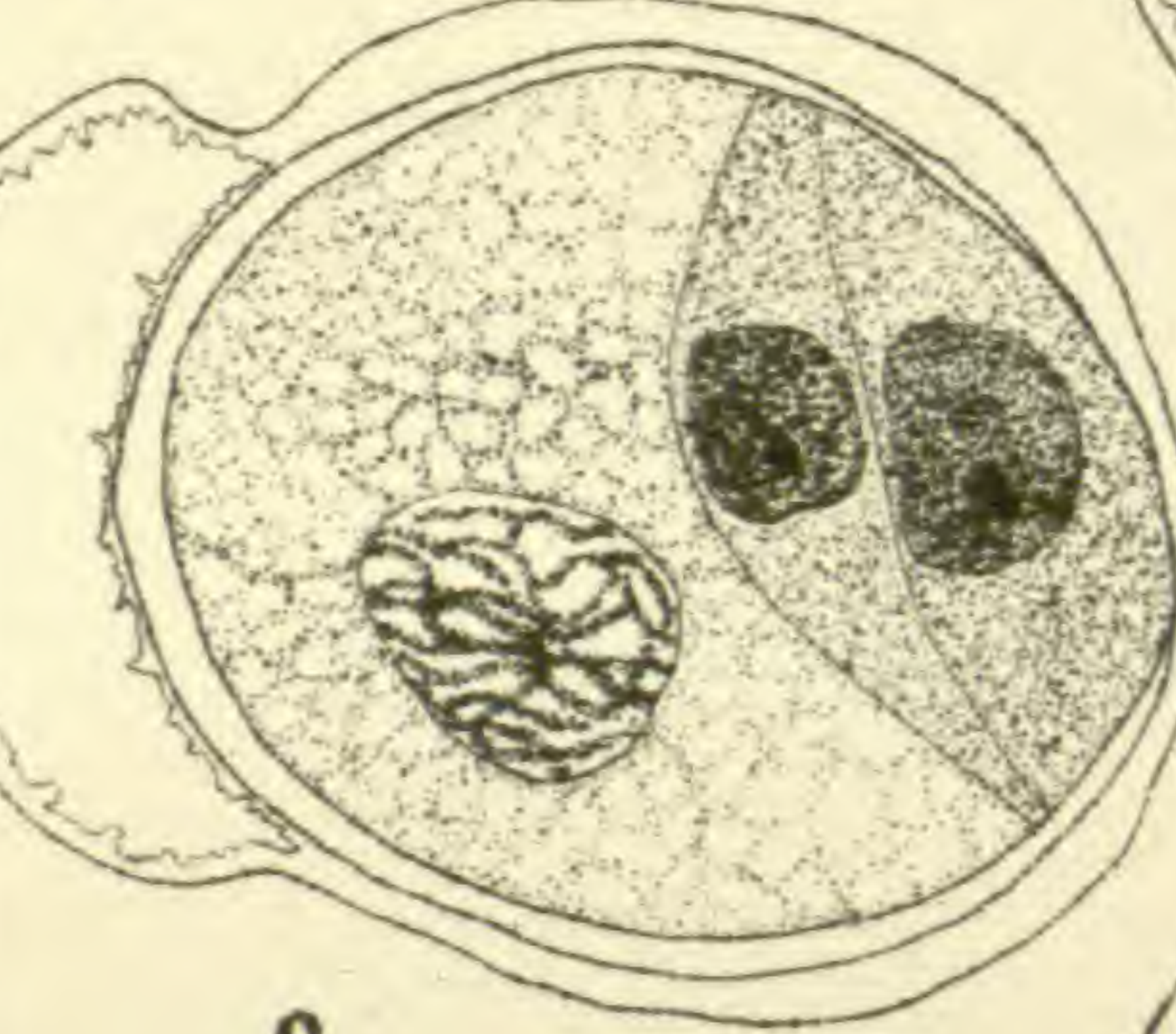

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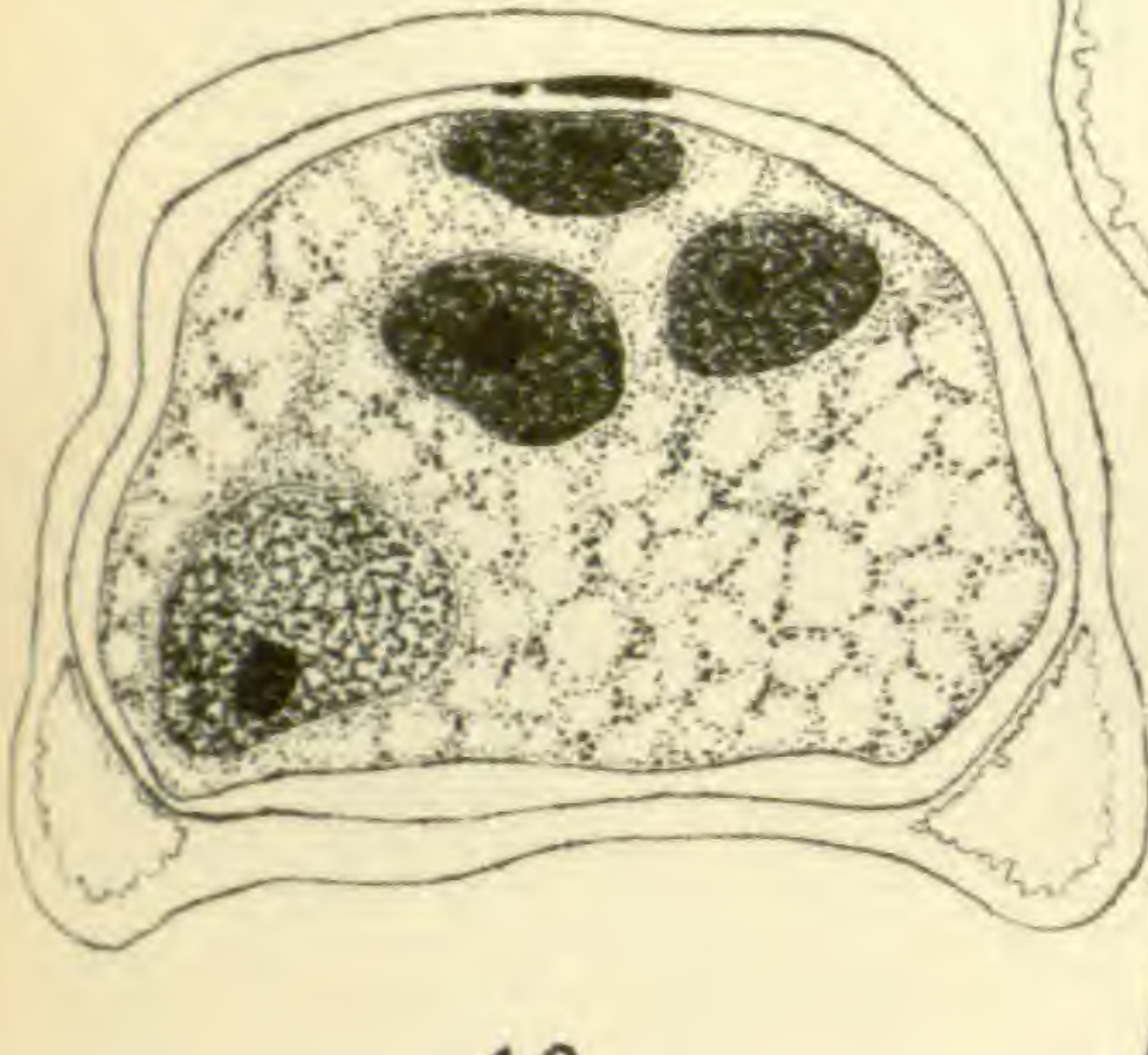

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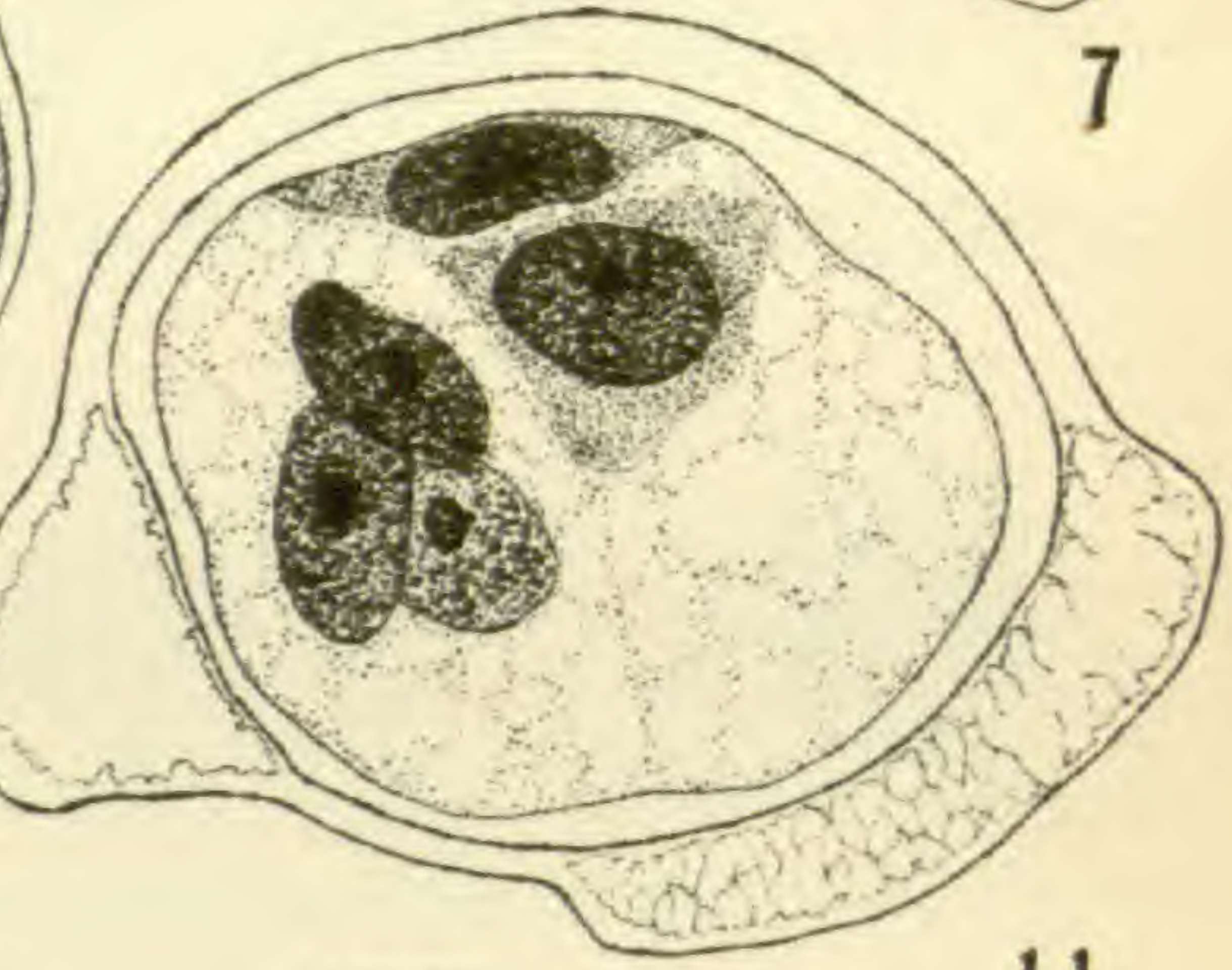

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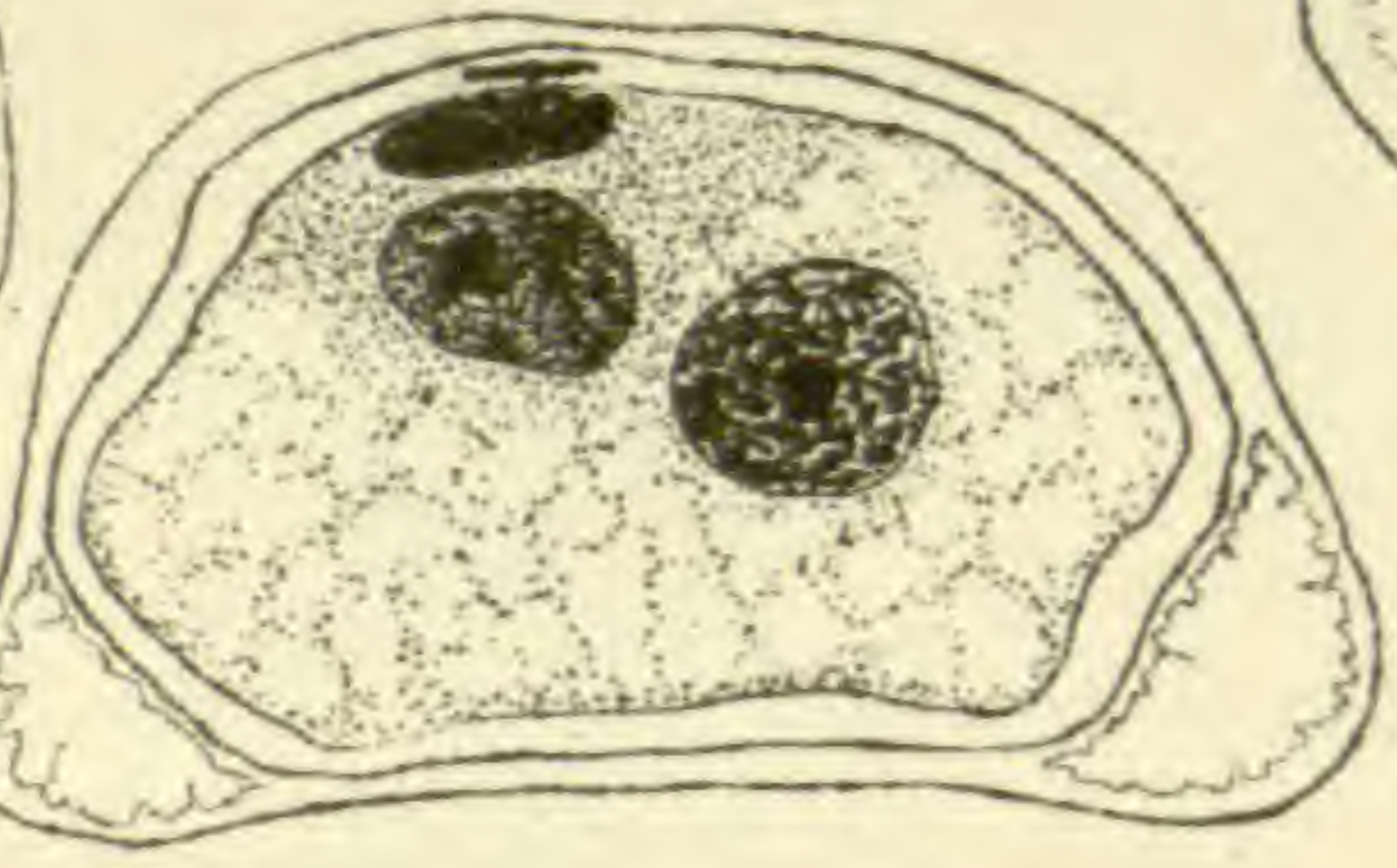

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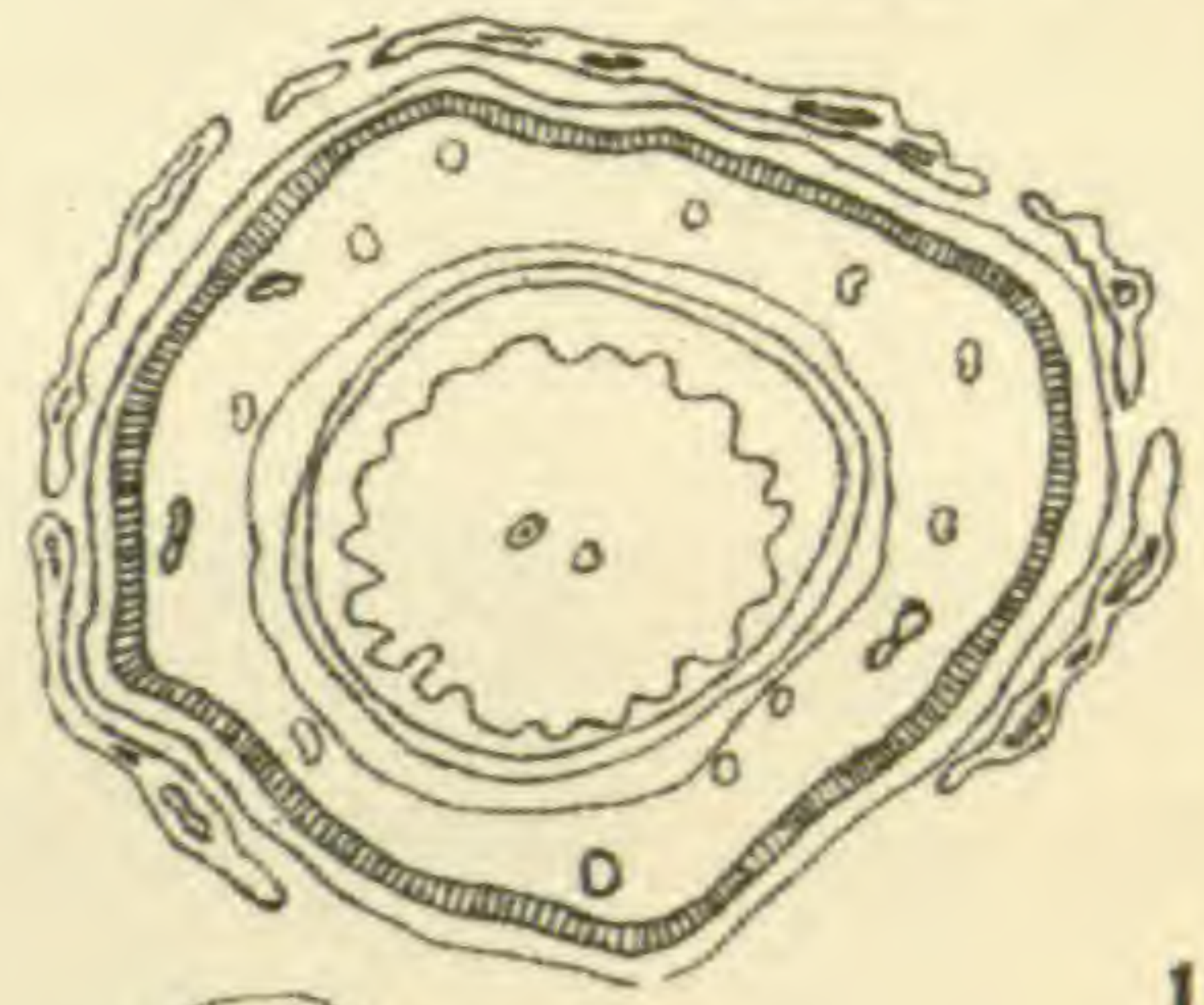

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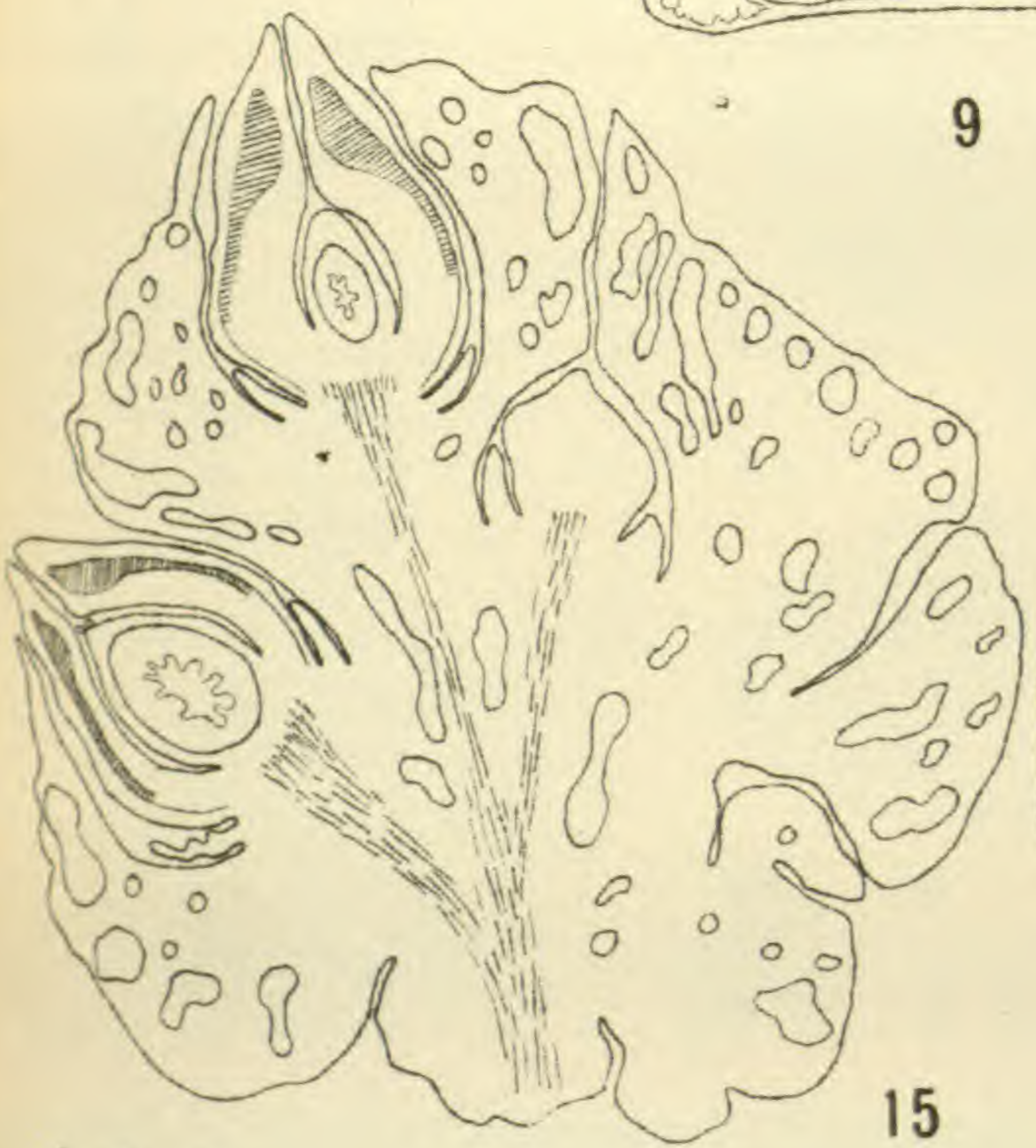

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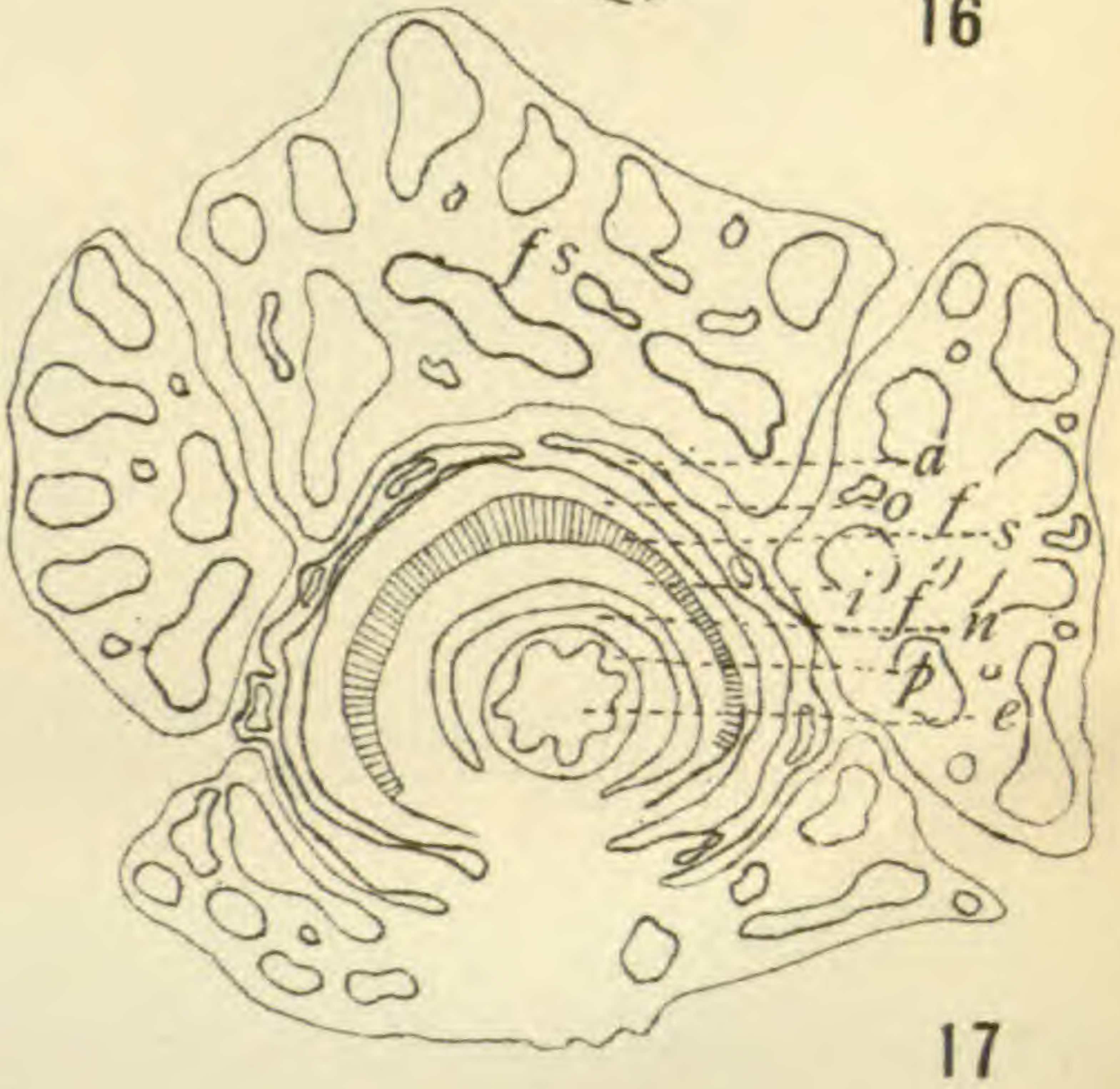

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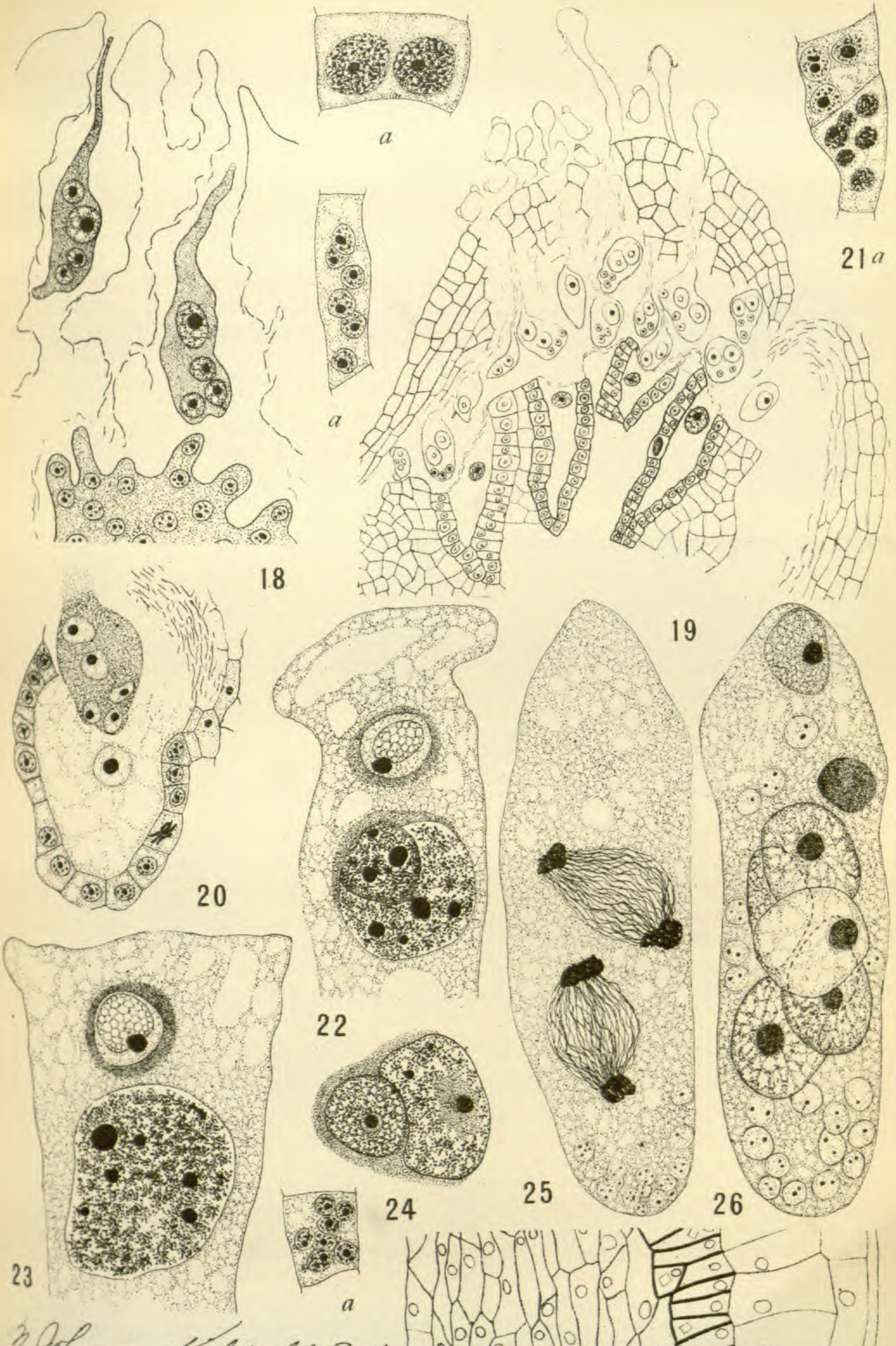
N. Johanna Kildahl Del.

KILDAHL on PHYLLOCLADUS



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KILDAHL on PHYLLOCLADUS

KILDAHL on PHYLLOCLADUS

NOTES ON NUMERICAL VARIATION IN THE DAISY

C. H. DANFORTH

Numerous observers, both in this country and in Germany, have given attention to numerical variations in the ray florets of the Compositae. For the investigation of the subject the common daisy, perhaps, has been most frequently used. The usual method of study has been simply to count and tabulate the ray florets for a number of heads collected from some prescribed locality. The results of such observations seem to show that the number of ray florets in the daisy is subject to a considerable amount of variation; but when a frequency curve is plotted, more or less definite modes become evident, one on the 21-ray line being especially prominent.

With a view to getting more data, I examined 4000 heads during the summer of 1905, from which I obtained results that agree in general with those previously obtained by TOWER, and by PEARSON and YULE from a much smaller number of heads, except that their data do not demonstrate the presence of a mode on 34, as do my own observations and those of LUDWIG (**3**). For the investigation in question I collected 1300 heads from the vicinity of Tufts College, Medford, Mass.; as many more from Norway, Oxford County, Maine; and 1400 from Dennis, Cape Cod, Mass. In these lots 12 was the lowest number of rays found in any one head and 40 was the highest. The total number of rays produced by the whole lot was

TABLE I

DISTRIBUTION OF RAYS FOR 4000 HEADS COLLECTED AT MEDFORD, NORWAY, AND DENNIS

Rays	Heads
12	1
13	9
14	4
15	9
16	12
17	12
18	25
19	49
20	135
21	423
22	370
23	295
24	278
25	216
26	204
27	176
28	191
29	192
30	184
31	224
32	218
33	266
34	303
35	115
36	47
37	27
38	9
39	3
40	3

107,464, which gives a mean of 26.866 to the head. The distribution of these rays is indicated in Table I. It will be observed that were these figures plotted the result would be a two-humped curve, indicating modes on 21 and 34.

If I combine with my own figures those given by TOWER (**6**) and by PEARSON and YULE (**4**), the resulting table (Table II) will be based on a total of 140,988 ray florets from 5585 heads, collected from five different localities by several different observers. It may be observed that this table indicates modes on 21 and 34. The mean number of rays to the head for this set is 25.242+. These results coincide with those which have been obtained in Germany in that modes are evident on 21 and 34; but differ from them in that no modes appear on 13 or 8, the next lower terms of the Fibonacci series. In fact, out of the whole number only 6 heads had less than 13 rays and none had less than 11. On the whole, then, observations seem to show that the daisy of this country has prevailingly more rays than the European plant, but that the numbers produced fall around the same modes which have the same relative prominence, except that no obvious modes occur on 13 or 8 in the American material so far examined.

TABLE II

DISTRIBUTION OF RAYS FOR 5585 HEADS, BASED ON DATA OBTAINED BY TOWER, PEARSON AND YULE, AND DANFORTH

Rays	Heads
11	1
12	5
13	40
14	43
15	51
16	67
17	67
18	110
19	141
20	313
21	752
22	536
23	390
24	342
25	279
26	252
27	212
28	217
29	219
30	201
31	254
32	242
33	307
34	325
35	122
36	53
37	27
38	9
39	5
40	3

Such facts have generally been construed as indicating that no essential alteration has taken place in the flowers of our daisy since its introduction into this country, but FERNALD (**2**) has lately called attention to the fact that the common American form is not the typical *Chrysanthemum Leucanthemum* L., but a variety (*pinnatifidum* Lecoq and Lamatte) not usually met with in Germany. Consequently the probablity is that all German data are based on the typical *Chrysanthemum Leucanthemum*, while all American data are doubtless based on var. *pinnatifidum*. In view of this fact the value of comparisons between the two forms may at first seem doubtful, but a slight further consideration of the character of numerical variations of the present kind may throw some light on the way in which such variations should be regarded.

SHULL (5), working with Aster, concluded that there is no tendency for all the flowers of the same plant to fall in the same mode, but that those that blossom first have the greatest amount of nourishment and therefore show the highest modes. TOWER (6) likewise thought that in the daisy the higher modes are met with early in the season, the lower modes later. In other words, it would seem that these authors are inclined not to regard the several modes as indicative of incipient species. My own observations, I think, fully substantiate their views in this particular. A comparison of Tables III and IV will show clearly a change in the predominant mode from 34 in the material collected between May 27 and June 14, to 21 in material collected between July 3 and July 15. Although this comparison may not be taken as certain evidence, inasmuch as the two lots were from different localities, nevertheless there is a strong suggestion here of a connection between mode and season.

TABLE III

DISTRIBUTION OF RAYS FOR 1300 HEADS COLLECTED IN MEDFORD BETWEEN MAY 27 AND JUNE 14, 1905

Rays	Heads
12	
13	1
14	
15	1
16	
17	
18	3
19	5
20	19
21	78
22	95
23	80
24	84
25	58
26	58
27	72
28	64
29	65
30	68
31	79
32	83
33	121
34	154
35	63
36	20
37	18
38	7
39	3
40	1

Two pairs of tables, one based on material collected at Norway, Maine, the other on material collected at Dennis, Mass., give much clearer evidence of the relation between mode and environment.

The collections from Norway were taken on June 22, 1905, from the two sides of a private road, about 12 feet wide, which several years previously had been run through an open field. The ground slopes in such a manner that the north side of the road receives practically all of the drainage, while the south side is drier and less favorably supplied. Noticing an apparent difference in the daisies of the two sides of the road, I marked a starting point and picked every head within about two feet of the road, till 150 had been collected from each side. The table (Table V) based on the counts shows clearly a tendency for the heads growing on the north side of the road to have a large number of rays, and for those on the south side to have a much smaller number. This difference between the two lots, it seems to me, may be regarded as clearly indicating a relationship between the amount of moisture or nutrition and the number of ray florets.

TABLE IV

DISTRIBUTION OF RAYS FOR 1300 HEADS COLLECTED IN DENNIS BETWEEN JULY 3 AND JULY 15, 1905

Rays	Heads
12	1
13	8
14	4
15	6
16	9
17	5
18	16
19	32
20	62
21	176
22	139
23	99
24	84
25	72
26	75
27	43
28	52
29	66
30	52
31	66
32	64
33	68
34	75
35	14
36	7
37	2
38	2
39	
40	

Very similar results were obtained from two lots of 250 heads, each collected at Dennis, July 13 and 14. One of these lots (Table VI, *B*) was from a rosebush tangle near the sea; the other (Table VI, *A*), was from a dry field near by. These lots likewise show clearly a tendency for plants growing in more moist and richer soil to have a higher number of rays.

These various observations seem to indicate that the number of ray florets in the daisy is in part conditioned by two general factors: an external factor, nutrition; and another, which might possibly be termed internal, namely, the tendency which gives rise to modes. A slight investigation of the latter has led me to believe that the explanation of the modes is to be sought in an explanation of phyllotaxis. As is well known, this is a subject which has given rise to a great deal of speculation. Although, perhaps, there is even now no satisfactory explanation of the rules of phyllotaxis, the facts themselves are familiar and only a brief reference need be made to one or two simple conditions.

As has been frequently pointed out, five-ranked leaves may be regarded as arranged on the stem according to any one of several different schemes. In one light they may be imagined as situated regularly along a line coiled spirally around the stem in such a way that the sixth leaf falls very nearly above the first. In this case, if the line is considered as running around the stem in one direction, it encircles it twice in passing from the first to the sixth leaf; if in the other direction, it encircles it three times in passing between the same two points. On changing the point of view slightly, the leaves may be imagined as all arranged along two parallel spiral lines running in one direction, or along three similar lines running in the opposite direction, in which case either spiral embraces five leaves in each revolution. This is equivalent to regarding the leaves as though they were placed at the points of intersection of two opposite sets of spirals, one composed of two lines, the other of three. Once more, the leaves may be regarded as placed along five nearly vertical but still slightly spiral lines. Of course these are merely different ways of regarding one and the same thing.

TABLE V

DISTRIBUTION OF RAYS IN TWO LOTS OF 150 HEADS EACH; MATERIAL COLLECTED AT NORWAY, JUNE 22, 1905; LOT *A* FROM SOUTH SIDE OF ROAD; LOT *B* FROM NORTH SIDE OF SAME ROAD

Rays	Heads	
	A	*B*
16	1	
17	4	
18	2	
19	4	
20	20	
21	37	2
22	26	5
23	15	7
24	8	8
25	3	8
26	2	10
27	4	5
28	6	8
29	5	8
30	4	6
31	4	13
32	2	14
33	1	17
34	1	17
35		10
36	1	5
37		5
38		
39		
40		2

While these conditions, on the whole, are quite constant, nevertheless when the stem is increased in diameter or shortened, thereby bringing the leaves or their morphological equivalents closer together, the parts not infrequently become arranged according to an apparently different scheme. Thus in the umbels of the wild carrot (*Daucus Carota*) peduncles are usually so arranged that they seem to be placed at the intersections of what appear to be lines arranged in the form of logarithmic spirals (see CHURCH 1), eight running in one direction and five in the other; or, if the umbel is large, eight in one direction and thirteen in the other. This arrangement might be considered as differing from the arrangement of five-ranked leaves only in the greater number of intersecting spirals. The point of chief interest in the present connection is that the number of spirals is confined rather constantly to the lower members of the logarithmic series 1, 2, 3, 5, 8, 13, 21, 34, etc.

TABLE VI

DISTRIBUTION OF RAYS FOR TWO LOTS OF 250 HEADS EACH; MATERIAL COLLECTED AT DENNIS, JULY 13 AND 14, 1905; LOT *A* FROM A DRY FIELD; LOT *B* FROM A ROSEBUSH TANGLE NEAR BY

Rays	Heads	
	A	*B*
12	1	
13	6	
14	3	
15	2	
16	6	1
17	3	1
18	7	2
19	12	7
20	22	9
21	55	27
22	27	12
23	23	14
24	12	12
25	16	12
26	13	18
27	4	4
28	3	11
29	7	18
30	5	15
31	7	28
32	5	16
33	5	16
34	6	21
35		2
36		2
37		1
38		1

If now a daisy head be examined carefully, it will generally (perhaps always) be found that the disk florets are so arranged that they appear to be placed at the intersections of two sets of spirals; or perhaps they might be more conveniently regarded as arranged in either of two opposed sets of spirals running from the periphery to the center of the head. I shall speak of the disk florets, therefore, as though they were arranged in two sets of spirals, although each of these sets (which one depending on the point of view assumed) embraces all the florets. There are usually 21 spirals running one way and 13, 21, or 34 running the other way. The set of 21 spirals may be either left-handed or right-handed in direction; but in either case the direction of the spiral is apparently correlated with the arrangement of the leaves. Only 100 plants were examined to determine this relationship, but among these specimens, which were collected at Norway in June, 1908, I found no exception to the rule that the direction of a set of 21 spirals in the disk is similar to the direction of the shortest line that can be drawn from any leaf on the stem to the next succeeding leaf. That is to say, if a stem was so held that any given leaf faced the observer, and it was seen that the next higher leaf on the stem was toward the left rather than toward the right, then a set of 21 left-handed spirals was invariably found in the disk. Of the 100 heads examined, the 21 spirals were found to be left-handed in 47 cases and right-handed in the remaining 53 cases. Of course the direction of the leaf spirals varied accordingly. There can hardly be any indication of incipient species here, for the arrangement on the branches of large plants is, as frequently as otherwise, reversed in reference to the arrangement on the main stem. I have been unable to trace the transition from the placing of the leaves to that of the flowers, except to notice the above-mentioned correlation.

The ray florets are placed, as one might expect, at the peripheral ends of these spirals. Each of the spirals in the set of 21 generally has a ray floret at its end; and frequently there are no other rays, especially if the other set consists of 13 or 21 spirals. When there are 34 spirals in one set, however, and the head is large, the number of ray florets is frequently increased, when each of the 34 spirals may be terminated by a ray. This case, though common, is less frequent than the other. Instances frequently occur where rays do not develop at the ends of some of the spirals, or (less commonly) where two rays develop on the same spiral. Heads that show more than 34 rays are of this class. In some of the Compositae, for example in Erigeron, where the disk florets are arranged in no more spirals than we find in the daisy, there are many rays; but in such cases several flowers of each spiral develop as rays, while in the daisy there seems to be but slight tendency for more than one flower to so develop.

If the typical *Chrysanthemum Leucanthemum* shows as much tendency for developing more than one ray on some of the spirals as does the var. *pinnatifidum*, it would seem hazardous to regard any comparison between the numbers of ray florets so far recorded as of taxonomic importance, inasmuch as the variations seem to be merely equivalent to variations in size.

In short, the conclusions these observations seem to warrant are: (1) that the florets in the heads of *Chrysanthemum Leucanthemum pinnatifidum* may be regarded as arranged in either of two sets of spiral lines; or, what amounts to the same thing, in the intersections of these two sets of spirals; (2) that the number of lines in each set is a term of the Fibonacci series; (3) that the number is influenced by external conditions, i. e., the conditions of nutrition affecting size; (4) that one set is composed of 21 spirals, which are in some way correlated in their arrangement with the arrangement of the leaves; (5) that each of the 21 spirals and frequently each of the spirals in the other set tends to have a ray developed at its end—hence the modes noted by various observers; and (6) that these facts supply few if any data of taxonomic value.

TUFTS COLLEGE, MASS.

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THE VASCULAR ANATOMY OF THE SEEDLING OF *DIOON EDULE*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 119

REINHARDT THIESSEN

(WITH PLATES XXIII–XXIX)

This investigation was begun during the winter of 1906, the original purpose being to clear up the confusing statements in reference to the so-called girdling habit of the leaf trace. As the work progressed, its scope became extended, until finally it included all of those anatomical features of the seedling that have a bearing upon the relationship of the Cycadales to the Cycadofilicales and Filicales.

I wish to express my appreciation of the constant encouragement received at all times from Dr. JOHN M. COULTER, under whose direction the work was carried on; I also wish to thank Dr. C. J. CHAMBERLAIN for kindly furnishing the material.

Historical

The first work on *Dioon edule* was by METTENIUS (4), who compared it with *Cycas revoluta*, which was the special form investigated. The methods of those days (1861) did not permit tracing the various vascular bundles throughout their course. Sections were cut only here and there, and the large number of bundles presented only a very incomplete and vague idea to the investigator, resulting in complete misapprehension.

The picture of the leaf trace girdle as METTENIUS drew it is in the main as follows. A bundle in its course toward a leaf divides soon after leaving the central cylinder, the two branches in turn soon dividing. These branches and branchlets, in the main retaining their radially ascending direction, but running at various angles, anastomose with one another and with branches of neighboring bundles, and finally unite with bundles which girdle the vascular cylinder. This girdle lies closest to the ring at a point diametrically opposite the leaf base which its ends enter, each of which therefore traverses the cortex through an arc of about 90°, gradually separating farther from it and finally entering the leaf base. There is such a girdle for every leaf, and every girdle must cut, on account of its course and location, every other like girdle in two places. Every girdle receives on its inner edge branches from the central vascular bundles which leave the vascular cylinder at various places, and sends out branches from its outer edge to other girdles. From this vague conception, which does not at all agree with the drawings of METTENIUS, the current textbook accounts have been drawn. These accounts, however, do not really interpret METTENIUS, but are as far from his interpretation as that was from the true situation.

In his description of the structure of the bundles METTENIUS was more fortunate, and made a very important contribution. He says that those bundles which are to leave the vascular cylinder are marked off by broad medullary rays and are more definitely bounded than those which continue in the cylinder; that on the inner edge they are provided with spiral vessels (protoxylem), while the others are provided with reticulated cells in the same relative position. At the region of the outward bend of the trace the vascular elements are grouped with the spiral elements on the inner or upper side, immediately bordering the reticulated elements beneath; and this structure the girdle retains in encompassing the stem. Before entering the leaf, however, a change in structure begins to occur, and is completed in the lower part of the petiole; after which the bundle remains unchanged up to the pinnae. The first indication of this change is the appearance of thin-walled cells in the vicinity of the spiral (protoxylem) elements, separating them from the reticulate elements. During the further course of the bundle the spiral (protoxylem) elements gradually move farther within, and the wood is now divided into two parts by the thin-walled cells; the inner part developing its elementary constituents centripetally, and the outer part centrifugally. Finally the spiral (protoxylem) elements are found in the outer part of the bundle, and the centrifugal part is still more reduced, while the centripetal part has reached its maximum development. This structure of the bundle is retained in its further course in the petiole until in the pinnae, where in *Dioon edule* the centrifugal wood is lost altogether. Such is a very brief statement of the description of the transition from centrifugal to centripetal xylem in the leaf traces, as given by METTENIUS. It was the first correct statement of the facts, but their meaning was probably not understood until an interpretation of the situation was given in 1886 by BERTRAND and RENAULT (**5**).

The second paper upon the vascular anatomy of Dioon is that of MATTE (**6**), a brief description of the anatomy of two seedlings being given. In one of them, a very young seedling, the cotyledons were unequal, the larger having four vascular bundles, and the smaller having two small bundles, but with two other very small strands at the very base, one on each side of the other bundles. The bundles continue in a vertically descending course until where the foliar bundles, after being arranged in a circle, have been reduced to four large bundles, separated by medullary rays. The six cotyledonary strands turn now abruptly toward the three poles (protoxylem groups) of the root, converge, and unite two by two in front of them, effecting an entrance through the medullary rays separating the foliar bundles, and unite their phloem with the phloem of the stem. Their secondary xylem unites laterally with that of the stem, while the primary xylem seems to be in direct continuity with the tracheal poles (protoxylem groups) of the root. The centripetal xylem disappears in the passage across the medullary rays.

In the description of the older seedling MATTE found in each cotyledon four bundles of equal size. Their course and method of union is comparable with that found in the other seedling, and they still unite two by two in converging toward the poles (protoxylem groups), but these poles are four in number.

MATTE touches also upon the girdling habit, ascribing it to an intercalary growth produced under the influence of the development of new interior leaves. The vascular strands of the youngest leaves pursue a vertical course, but those of the older ones an oblique course, a comparison of leaves of different ages showing that this departure from a direct course is due to intercalary growth.

Methods

Embryos were removed from mature seeds and killed in chromoacetic acid, imbedded in paraffin according to the usual methods, cut with a rotary Minot microtome, and mounted in series, much care being taken that no sections were lost or misplaced. When only the location or outline of the bundle was wanted, the cross-sections were cut 20 to 30 μ thick; in other cases they were cut 10 μ thick. Longitudinal sections were cut at right angles to the inner surfaces of the cotyledons, as well as parallel to that plane; these were cut 10 μ thick. Staining was done on the slide with safranin and Delafield's hematoxylin, or safranin and anilin blue. Other stains were tried, but these two combinations gave by far the best results. A few specimens were killed by the general picro-mercuric-chlorid method, but no advantage was gained.

Where seedlings were required, the hard coats of the seeds were cut partly open at the micropylar end, and the seeds placed on one side, partially pressed into moist earth, in a flower pot, and put in a warm moist place in the greenhouse and kept well watered. A good many seeds had been planted three years before and had grown to considerable size, some of them having a stem 100^{mm} in length and 25^{mm} in diameter, and bearing several leaves. These were treated about as the embryos, except that all the specimens were cut into lengths of 15 to 20^{mm}. Of course the greater the size of the plant the more slowly the processes of killing, washing, embedding, etc., were conducted. Especial care had to be taken in imbedding the larger specimens, the best results being obtained when they were carried through the process of penetration with paraffin for a whole month. After this time they could be cut with an ordinary Minot rotary microtome with perfect ease, and the sections could be held in complete ribbons. After this precaution, ribbons were obtained from specimens 26^{mm} in diameter and cut 10 μ thick. Staining was done as before with safranin and Delafield's hematoxylin, or safranin and anilin blue, the former combination giving the most satisfactory results. An enormous amount of labor is necessary and also much care to keep sections of entire plants in serial order, both in cross and longitudinal sectioning, but it is the only satisfactory method.

In order to obtain the details or to follow up the leaf trace courses, every section was examined, from the first to the last, and camera drawings made of every second or third section. These were carefully numbered and kept in series and later compared, and reconstructions were based upon them.

Observations

THE EMBRYO

EXTERNAL STRUCTURE.—In the mature seed the cylindrical embryo is fully two-thirds as long as the endosperm, averaging 20^{mm} in length and about 4^{mm} in diameter. The hypocotyl (*fig. 1*) is comparatively very short, being about 5^{mm} long, ends abruptly (very often is even concave), and in the center is still attached the slender, very much twisted and coiled suspensor (*s*). The cotyledons are free for the upper four-fifths of their length, the lower fifth forming a tubular sheath (*sh*) inclosing the leaf primordia (*figs. 2, 3*). One of the cotyledons is slightly larger than the other, and is inserted a little lower on the axis, slightly enfolding the smaller one. There are generally two leaf primordia, but sometimes three. The broad base of the outer or older one (L_1) embraces the inner and next younger one (L_2), which in turn often embraces a third (L_3); and finally beneath them all is the stem tip (*st*). On the oldest leaf primordia are all the rudiments of the pinnae (*pn*) of the future leaf quite well advanced; while no indication of them can be detected on the younger primordia.

To understand certain features to be described later, it is necessary to note the arrangement of the earlier leaves. An older plant (*fig. 7*) may be used as an illustration, and both scales and foliage leaves will be spoken of as leaves and numbered from *1* to *9* according to age. The cotyledons (*cot*) are apparently exactly opposite; *1* and *2* are approximately opposite, but close observation shows that they are not exactly so; also *1* and *2* are approximately at right angles to the cotyledons (also *fig. 2*). The sheathing leaf base of *1* is a little longer and more slender on the side toward which the spiral turns, and folds around the inner leaf or scale a little farther than it does on the other side. Leaf *3* lacks still more of being opposite *2;* also the corresponding edge of the sheathing base of *2* is more slender and folds over *3* more than its fellow. Leaf *4* lacks still more of being opposite *3*, and again the sheathing base is more slender and folds around the next inner leaves more on that side toward which the spiral turns. In the rest of the series the spiral is uniform, and the overlapping more conspicuous.

INTERNAL STRUCTURE.—The bulk of the embryo is of course parenchymatous, and the general structure is shown in *figs. 2–6, 8, 9, 29–35.*

The epidermis (*ep*) consists of large, regular, isodiametric cells with large nuclei. That of the cotyledons is abundantly supplied with stomata on the exterior surface of the tubular part and a small portion of the lobes. No stomata occur on the part of the cotyledons remaining in the endosperm, on the interior surface of the cotyledons, or on the primordia. The epidermis of the petioles and bases of the leaf primordia is covered densely with long, unicellular hairs, with well-defined nuclei (*figs. 28, 29*).

The ground tissue is composed of long, regular, prismatic cells, much longer than wide in the cotyledons, but shorter and more isodiametric in the stem proper (*figs. 3, 8*). At the lower extremity of the embryo the cells lose their nuclei, become filled with a dense material, and form a hard capping tissue (*cp, figs. 3, 28, 29*). Distributed irregularly in all parts of the ground tissue are many cells, cavities, and canals filled with mucilage (*m, fig. 8;* black spots in *figs. 28–35*). The cavities are found most abundantly in the cotyledons and are formed by the disorganization of several neighboring cells. The canals, which are formed by the disorganization of the cells end to end, forming tubes of limited length, are most abundant in the petioles of both cotyledons and leaves.

The vascular cylinder is very short, the length being much less than the diameter, and hence it is usually called the vascular plate (*vp*). It is squarish, one diagonal diameter being approximately at right angles to the inner faces of the cotyledons, and the other parallel with them. The xylem (*figs. 32, 33, x*), consisting at this stage probably of protoxylem only, is surrounded by a zone of phloem (*ph*). The xylem is compact and well developed where it borders the phloem, but toward the center it is gradually mixed more and more with pith cells, till in the center the xylem elements lie scattered among the pith cells, these scattered cells being very short and irregular. This condition varies in different specimens, in some the xylem being quite compact to the center, while in others it is entirely wanting in this region (*fig. 32*).

The protoxylem groups.—At each corner of the squarish vascular plate there is a group of protoxylem elements (*px*), which in cross-section is irregularly oval. These four groups extend downward for a short distance, where they form the protoxylem of the primary root (*a, figs. 4, 5, 8*).

The potential vascular tissue.—Above the vascular plate there is a conical or dome-shaped mass of tissue terminating in the growing point of the stem, sharply marked off from cortex and pith, and consisting of long, irregular cells with dense protoplasm and prominent nuclei. The frequent occurrence of mitotic figures shows it to be the most active meristematic region of the stem, being the tissue in which the vascular strands are developed, and therefore the procambium (*pc, figs. 8, 34, 35*).

The pith in the vascular plate contains scattered and short xylem elements (*x, fig. 8*), as stated above. Above the plate it is conical and terminates in a tier of cells against the epidermis (*pt, fig. 8*); in this region the cells are thin-walled and very irregular. In all the pith mucilage cells and cavities are abundant.

The vascular strands.—All the vascular bundles are collateral, except in the upper part of the cotyledons, where they may be regarded as concentric. In the leaf strands the collateral bundle is surrounded by a sheath, which is not well-defined. In the younger strands the few elements are protoxylem, and new elements are added centrifugally (endarch), centripetally (exarch), or in all directions (mesarch). The bulk of the bundle is as yet procambial tissue (compare *figs. 10–15* and *16–21* with *figs. 22–25*). In the older strands it is difficult, if not impossible, to determine where protoxylem ends and metaxylem begins.

The vascular strands of the cotyledons (*figs. 4–6*).—From each of the four protoxylem groups in the vascular plate (*px*) a strand runs outward for a short distance and then branches, the branches separating at wide angles and continuing outwardly in a horizontal plane until well under the bases of the cotyledons, where they turn abruptly upward into the cotyledons, thus giving four strands to each cotyledon, and in such a way that each of the opposite protoxylem groups on the diagonal perpendicular to the inner faces of the cotyledons gives rise to the two inner strands of each of the cotyledons; while each of the other two protoxylem groups gives rise to the outer strands of the cotyledons in opposite edges, that is, one branch goes into the edge of the cotyledon on one side, and the other branch from the same protoxylem group into the corresponding edge of the other cotyledon. This may be stated in another way. In tracing downward, the four strands of each of the petioles of the cotyledons may be said to join two by two. Just before reaching the central cylinder the inner strands of each fuse, and the outer strands of the one fuse with the outer strands of the other, the four strands thus formed giving rise to the four protoxylem groups. This is shown semi-diagrammatically in *figs. 4–6*. Tracing these strands farther upward, they are found to branch once more, so that in the upper part of each cotyledon there may be as many as eight strands; but before reaching the tips of the cotyledons they reunite into one concentric bundle (*fig. 15*), which abuts immediately against the epidermis, thus coming into very close contact with the gametophyte. At this place the tissue of the gametophyte is so closely attached to that of the cotyledons that it is difficult to separate them.

The vascular strands of the leaf primordia.—For each leaf or leaf primordium four strands leave the vascular cylinder or vascular plate, at points not definitely located, but quite well distributed, and generally in such a way that approximately one strand for each leaf or primordium leaves on each side of the squarish central vascular cylinder; also those strands belonging to the first leaves have their origin either in the neighborhood of or in the protoxylem groups of the plate. Two strands leave the cylinder approximately on the same side as that on which the leaf for which they are destined is located, and run more or less directly through the cortex into the ventral part of the petiole without further branching; while the other two strands leave the central cylinder approximately on the opposite side and describe a curve around it (the one in one direction and the other in the opposite direction) through the cortex, through the sheathing leaf base, and finally into the dorsal or adaxial part of the petiole, where they branch and rebranch (*figs. 4–6*). It should be emphasized that the point of origin is not at all definite, and that any particular girdle does not describe an arc of any definite extent, but that the length of the arc depends upon the place of origin of the girdle and the position of the leaf to which it belongs.

It has been said that that edge of the leaf base toward which the spiral turns is more slender and folds over the next inner leaf more than does its mate (*fig. 7*). It will be observed that the girdle which is destined for that side of the leaf generally describes a longer curve through the cortex than the one destined for the other side. The phenomenon of girdling will become clearer when illustrated by a specific case. In *fig. 6*, taken from a young seedling, L_1, L_2, L_3, and L_4 represent the first, second, third, and fourth leaves or primordia; L_1^1, L_1^2, L_1^3, L_1^4, the four strands of the first leaf; L_2^1, L_2^2, L_2^3, L_2^4, the strands of the second primordium. L_1^1 is the longest girdle of the first leaf and has its origin at the protoxylem group px^1, on the side directly opposite the leaf to which it belongs, ascends for a short distance, then turns outwardly into the cortex and describes a wide horizontal curve, enters the longer and more slender edge of the leaf base, and ascends in the petiole in the dorsal left-hand portion, branching repeatedly in its further course. Trace L_1^4 leaves the central cylinder near the protoxylem group px^4, ascends a short distance, runs upwardly and outwardly into the cortex, describes a horizontal curve in the opposite direction, enters that side of the leaf having the shorter sheathing base, and ascends in the dorsal or adaxial portion of the petiole, where it branches repeatedly in its further upward course. From this it will be seen that the leaf trace L_1^1 pursues a longer course than trace L_1^4. Trace L_1^2 has its origin near the protoxylem group px^3, to the left, ascends for a short distance, runs out into the cortex, makes a very slight horizontal curve (almost direct) into the leaf base, running outwardly, and then ascends on the ventral or abaxial left-hand portion of the petiole without further branching. Trace L_1^3 has its origin near the protoxylem group px^4, ascends for a short distance, runs outwardly (gradually ascending) with a slight curve into the leaf base, and finally ascends in the ventral or abaxial right-hand portion of the petiole without further branching. It will be seen that in the case of the two inner strands L_1^3 makes a girdle of about 90°, while trace L_1^2 is approximately direct.

About the same condition occurs in the traces of the second leaf. Trace L_2^1 has its origin to the left and near the protoxylem group px^3, ascends vertically for a short distance (but farther than the strands of L_1), runs a short distance outwardly into the cortex and then makes a wide horizontal sweep, enters the leaf base on that side which ensheaths the younger primordium with its more slender edge, ascends in the petioles on the inner or dorsal portion, and branches repeatedly. Trace L_1 has its origin near and to the right of the protoxylem group px^2, describes a girdle of approximately the same magnitude as girdle L_1^4, and runs into the base of the leaf on the right hand. Traces L_2^2 and L_2^3 have their origin respectively on the right and left of the protoxylem group px^1 (quite close to it), and after ascending for a short distance run directly into the outer or ventral portion of the leaf, where they ascend without further branching.

These facts seem to indicate that there is some relationship between the protoxylem groups of the vascular plate and the origin of the trace of the first leaves. The traces of the third leaf (L_3) are followed with some difficulty, but the same condition noted for the first and second leaves is clear. When a fourth leaf is far enough advanced, exactly the same conditions are also presented. The girdling habit of the very young strands is already marked out; but their origin appears no longer to be restricted to the neighborhood of the protoxylem groups, but may occur anywhere in the plate, from which they now ascend vertically for a longer distance before turning out into the cortex. It is very difficult, however, to follow the younger strands while they are still in the potential vascular tissue, since no xylem elements have as yet been formed; but in their passage through the cortex into the primordium their path may be made out clearly, and it shows that the girdle is already established at this stage. Even in the absence of xylem elements, the bundle is clearly marked off by the character and arrangement of its cells (*figs. 26, 27*).

Although the specific case described represents the general state of affairs, many variations are found in the place of origin of the traces. Of the many specimens examined probably no two traces were found to be exactly alike in this respect; also anastomoses between adjoining traces were found here and there. The strands thus ascending vertically for a short distance into the procambial tissue above the vascular plate are the first to assume specific characters. Although the young cylinder is made up of separate traces, it must be observed that these are in the procambial tissue, which is very different from that which surrounds the procambium.

The transition from endarch to exarch xylem.—When a cotyledonary strand leaves the vascular cylinder it is endarch (*fig. 10*). As it passes upward and outward, the protoxylem elements recede from the endarch position and are buried more and more in metaxylem, that is, centripetal wood has appeared. When well up in the tubular portion of the petioles of the cotyledons, the protoxylem is surrounded equally on all sides by metaxylem, the xylem being typically mesarch (*figs. 11–13*). From this point on the protoxylem approaches more and more an exarch position, but the xylem does not become completely exarch. Before the end of the bundle has been reached it has become quite concentric, and it becomes very difficult to determine which element was the first to appear (*fig. 15*). Where the bundle leaves the central cylinder the total xylem elements so far as developed are at the innermost part of the bundle, and as the bundle is traced upward they recede from that position and occupy one farther inward, until in the upper extremity of the cotyledon they occupy a position central to the whole bundle. Thus the transposition of the total xylem holds the same relation to the procambium as the protoxylem holds to the metaxylem (*fig. 9, a*).

The leaf traces also when leaving the vascular cylinder are endarch (*fig. 16*), and in passing outward and upward the protoxylem elements recede from the inner edge and are buried deeper and deeper in the metaxylem; and well up in the leaf bases the xylem has become mesarch (*figs. 18, 19*). Afterward the protoxylem approaches more and more an exarch position, until at the transition between petiole and leaf base the xylem has become completely exarch, with the protoxylem lying immediately against the procambium (*figs. 20, 21*). There is at this stage no centrifugal wood above this point; and there is no secondary wood anywhere. The transition may be said to occur, therefore, between the central cylinder and the leaf base, from which point upward the strands are all exarch. It must be taken into consideration that none of the leaves are as yet fully developed, only the first leaf showing plainly the different regions (*fig. 3*). *Fig. 9, a* represents the situation diagrammatically.

It will be observed that only a very small part of the procambium has been developed into xylem tissue in the whole length of the petioles (*figs. 16, 17*). Cross-sections of foliar strands at a low region show, besides the protoxylem and centrifugal metaxylem elements, a procambium stretching more than half-way across the bundle, the boundary being marked by a thicker-walled tissue, the protophloem. Higher up in the bundle the centrifugal procambium decreases proportionally as the protoxylem moves outward. *Figs. 4, a* and *21* show the situation more clearly; both are taken from very young primordia, the latter much younger and higher up than the former. In *fig. 21* the xylem elements are approximately in the center of the bundle, but there is still considerable procambium between them and the protophloem. The cambium appears to be developed later, just inside the protophloem, and develops tissue actively toward the phloem side only.

THE SEEDLING

EXTERNAL STRUCTURE.—When the seed of Dioon germinates, the hypocotyl pushes through the micropylar end of the seed, where there is at this time an area in the testa, about the diameter of the embryo, which softens readily and is easily penetrated by water. If left to itself, this process takes from a week to a month, and sometimes longer; but if the area referred to is cut away, the hypocotyl pushes through in a few days. During germination the whole of the hypocotyl and the lower part of the cotyledons lengthen.

As soon as the hypocotyl reaches the soil a tap root is sent deep into the ground, and before any leaves appear the root may have penetrated the soil 8 to 12^{cm}, and the diameter of the hypocotyl may have increased to about 1^{cm}. After a long period (which in the greenhouse was about four weeks in case the micropylar end was cut away, but many months if it was not) the first leaf appears between the cleft of the cotyledons, in direct continuation of the axis. As the natural position of the seed during germination is horizontal, and the hypocotyl bends down approximately at right angles, the leaf pushes forth where the cotyledons make a sharp bend. The cotyledons remain in the seed, and in seedlings three or four years old the seed may be seen still attached to the plant. At this time also lateral roots appear in four rows along the primary root, corresponding to the four protoxylem groups.

A second leaf does not appear until perhaps a year later, and about another year elapses before a third appears. A plant of this age has developed about nine or ten leaf primordia, but only about one-third have developed into leaves.

INTERNAL STRUCTURE.—During germination, in connection with the development of the primary root, not all of the tissue of the tip of the plantlet resumes growth, but only the plerome and a limited portion of the periblem or cortex surrounding it becomes meristematic and pushes through the hard and caplike tissue at the tip of the embryo. The cortex which does not resume growth, as well as the caplike tissue, frays off (*fig. 9, fr*). Also, as growth progresses, the outer layers of the newly formed root, some distance back of the root tip, keeps on fraying off; and underneath a phellogen soon appears and a layer of cork several cells thick is formed. Along each of the four protoxylem strands of the root, continuous from the vascular plate, lateral roots have their origin at definite intervals, being arranged in four rows. Certain cells among and near the protoxylem elements become meristematic, and form the tip of the lateral root, which pushes through the cortex.

The vascular cylinder increases in dimensions uniformly with the growth of the seedling as a whole. New bundles are inserted as new leaf primordia appear, and gradually fill in more and more the vacant spaces between the original strands, so that immediately above the original plate the vascular cylinder is quite compact, while beyond this it continues to be represented by separated strands in the potential vascular tissue.

The vascular strands of the cotyledons.—Not much need be added to the statements in reference to the cotyledonary strands. The transition from endarch to exarch xylem is very much more gradual and the mesarch stage is located relatively much farther up. This is due to the fact that most of the growth of the cotyledon in length occurs at its lower extremity. No secondary wood is developed in cotyledons. The phloem also has increased in bulk, but mature sieve tubes are never developed.

The leaves and scales.—As said above, not all the primordia develop into leaves, most of them remaining abortive and forming scales. Although about one-third of the primordia develop leaves, it does not follow that every third primordium becomes a leaf in regular succession. It sometimes happens that two leaves are developed from consecutive primordia. Evidences indicate that a scale is not predetermined, but remains abortive through some variable cause. The primordia, whether developing scales or leaves, show the same structure in every particular.

The leaf traces.—The course of the leaf traces in the seedling are the same in general plan as those described for the embryo, but the girdling in the older leaves and scales is much more marked. The internal growth and the appearance of new organs has crowded the older parts farther and farther outward. The circumference of the cortex has increased materially, and also the length of the vascular strands running through it. In the older scales and fully developed leaves these are all of about the same extent, and almost horizontal; but from these, through the younger leaves and scales to the youngest primordia, the sweep of the girdle diminishes; but the girdles are already established in the very youngest of the primordia (*figs. 34, 35, ltg.*)

Although in the strands of the youngest leaf primordia no xylem elements are present, the courses of the bundles may be made out readily because of the arrangement, the staining qualities, and shape of the cells, which have denser protoplasm and larger nuclei, and are longer than the adjacent cells (*figs. 26, 27*). The strands of the very youngest primordia which have their origin on the opposite side of the central cylinder show the girdling habit in the same manner as those of the older leaves, but on a smaller scale. The girdle does not always take the horizontal direction, but may be more oblique at the beginning (*figs. 4, 5, 34, 35*). *Fig. 35* shows this clearly, in which *pc* is the procambium and ltg^1 the girdle of the youngest primordium. So long as such a strand is outside of the procambium it can be followed easily, but is lost after it has entered it.

In the oldest plant examined (three or four years old), the first, second, third, and fourth leaves displayed exactly the same condition as was shown in the young leaves of the embryo and seedling. But in the older leaves, outside of these, it is impossible to determine whether the described order is retained, because of the difficulty in following up strands of such size; but it is certain that anastomoses are more frequent, due to the close proximity of crossing bundles.

The transition of the xylem.—The strands of the older leaves have a larger development of metaxylem; also secondary wood may have developed in the lower extremities, so that the transition from endarch to exarch has become more prominent and can be made out with greater clearness. The secondary wood accompanies the bundle as yet only for a short distance, and ceases long before the transition from endarch to exarch is complete. As the secondary xylem and centrifugal metaxylem diminish, the centripetal xylem (which of course is all primary) increases in bulk (*fig. 9, a*). In a plant three years old no other secondary wood was present (*figs. 22, 23*). Even in the oldest leaves of quite old plants the secondary wood, which at the origin of the strand is quite massive, decreases very rapidly, and in the petiole just above the leaf base has thinned out to a few elements (*fig. 24*), remaining quite uniform to the rachis, where it disappears still more; while in the pinna no secondary wood whatever is present, all the xylem being primary and centripetal. Although in the transition region the secondary wood diminishes in the same ratio in which the primary wood increases, it must be noticed that the centrifugal wood is not restricted to the secondary wood alone, as was shown in the younger bundles of the embryo, where the transition is clearly carried out in the protoxylem and metaxylem alone. Thus in the seedlings the transition from centrifugal to centripetal wood is carried on after the appearance of secondary wood, and is completed in the primary wood.

In the older strands where secondary wood has been developed, a considerable amount of the centrifugal wood therefore is metaxylem. This is shown by the amount of procambium that has been developed into centrifugal xylem; as may be seen by comparing the younger strands in *figs. 21, 4, a*, for example, where there is a certain amount of centrifugal procambium, the amount depending upon the distance from the point of egress from the central cylinder, with the older strands in *fig. 24*. Sometimes all of the centrifugal procambium has become xylem; more often, however, patches of procambium or isolated cells of it are never lignified and retain their nuclei, and are then referred to as the thin-walled cells. These thin-walled cells do not necessarily lie against the secondary wood, though they most often do, and become most evident in the upper extremities of the transition. A series of cross-sections of a maturer leaf of a seedling clearly shows the transition from endarch, through mesarch, to exarch, and shows that it is quite independent of secondary wood. The transition begins at the point where the strand leaves the central cylinder, and in the seedling progresses uniformly and is completed in the petiole; but in the old plant the larger proportion of the transition is completed in the lower part of the petiole, where only a few strands of secondary xylem remain and continue uniform until the bundles enter the pinna, when the transition is completed (*fig. 25*).

The cause of girdling.—No particular cause has been assigned for this phenomenon. If such a leaf primordium as is represented in *figs. 3*, L_2, and *8*, L, be selected, it is possible by careful staining to detect four strands which are ultimately developed into vascular bundles. The outer (abaxial) ones pursue a more or less direct course, but in following them from the stem up, their course at first, after leaving the procambium, is vertical; but in the base of the primordium they turn inward to a considerable extent (*fig. 3*, L_2). The two inner or adaxial strands after leaving the procambial cone pursue quite a vertical course, but on reaching a region at the level of the base of the primordium, they begin to turn toward it, one on each side, in some cases ascending rather obliquely, but generally horizontal from the start. *Figs. 34, 35*, ltg^1 shows the girdling of quite a young primordium, the youngest one in that specimen. It is plain, therefore, that the girdle is established very early in the development of the leaf to which it belongs.

Tracheae.—In examining older plants, the oldest one being three or four years old, a singular phenomenon is noticed. Between the various bundles of the stem, which at this time do not yet make a complete ring, vertical connections are found, consisting of irregular, reticulated elements, branching and anastomosing, but forming continuous vessels. In the upper part of the plant, where they are developing, long and narrow cells are found winding and crowding through between the parenchymatous cells. A little farther down in older parts of the stem, these cells are found to be multinucleate, with only here and there an ill-defined cross-wall. A little farther down still the nuclei disappear, and soon lignification appears, developing finally into well-defined reticulated tracheae. These wind in a very tortuous way vertically through the parenchymatous cells from one bundle to another. They are in all senses true reticulated vessels, without cross-walls, establishing a connection between the bundles of the vascular system.

Discussion

In the embryo of *Dioon edule* the vascular cylinder is a protostele, which in some specimens contains a solid xylem mass. From this solid cylinder all gradations are found to the siphonostele. The cells of the pith are actively meristematic, as shown by the mitotic figures, and often in older specimens xylem elements are found in the central part at the level of the vascular plate. The xylem cylinder also continually increases in size, new elements being added to it constantly between bundles already existing, as well as by the cambium.

It should be emphasized that the vascular cylinder in the embryo and seedling does not consist of the short xylem cylinder only, but is continuous in a tissue, very different from the cortex outside and the pith within, which gives rise to strands of procambial tissue running into the leaf primordia. The pith is also a well-defined tissue from the vascular plate to the stem tip, and nowhere suggests that it arises from an intrusion of the cortex through the leaf gaps. An inspection of *fig. 8* shows that it has its beginning at the very tip of the growing point, where it is seen to consist of a single row of cells or a tier of a few cells, gradually expanding as the stem grows into the large pith found in the older part.

The transition of the protoxylem from the endarch to the exarch position was first described by METTENIUS (4), who also suggested the descriptive terms centripetal and centrifugal xylem. The situation was interpreted by BERTRAND and RENAULT (5), who also established that the centripetal wood is in the same relative position throughout its whole length; that it increases in bulk toward its upper end; and that the centrifugal elements are reduced more and more. They say that the centripetal wood is intercalated between the pole and the outer face. It is regarded as the primary wood (developed from the procambium), while the centrifugal wood is regarded as secondary (developed from the cambium).

The present investigation shows that this statement needs modification. While all centripetal wood is primary, all primary wood is not centripetal, as one would interpret from the treatise cited. It has been shown that the transition from endarch to exarch is carried through in the metaxylem, both centripetal and centrifugal wood occurring long before secondary wood is developed. It is very hard to tell where protoxylem ends and metaxylem begins, and where metaxylem ends and secondary wood begins. The separation of metaxylem from secondary wood by means of the thin-walled parenchymatous cells is not a safe guide in the region of transition, and only becomes well marked above this region, where the separation of secondary from primary wood is well marked by the thin-walled parenchymatous cells, as noted by many authors. The metaxylem above this point gets to be relatively very bulky, while the secondary wood is represented merely by a few elements. These were the few pitted cells which presented to VON MOHL (1) a situation without a counterpart, now known to be the herald of the secondary wood which has gradually crept up into the petiole, a transformation begun in its early ancestry, according to SCOTT, the "new wood" driving out "the old," the former being the only wood present in the higher gymnosperms and angiosperms.

MATTE (6) argues in very much the same way as does METTENIUS, an argument which would hold good if the protoxylem and a large part of the metaxylem were left out of account. MATTE says that the bundles of the cotyledons have centripetal wood throughout, centrifugal wood only below the upper region of the petioles, and centripetal and centrifugal wood equally well developed at the bases of the petioles. In the present investigation it has been pointed out that there is no centripetal wood at first, and that it gradually increases; while the centrifugal wood diminishes in bulk to the upper extremities, where it is less than the centripetal but does not disappear entirely.

MATTE further says that what has been said of the cotyledonary traces applies equally well to the foliar traces, except that there is no trace of centrifugal xylem in the youngest leaves. It can be shown that as soon as there are enough xylem elements to show the direction of development the centrifugal wood is present, but gradually disappears, and the centripetal wood increases in the same ratio, until in the upper extremities there is only centripetal wood. This also agrees with BERTRAND and RENAULT, except that their statement that centripetal wood is primary and centrifugal wood secondary does not hold true, a mistake apparently shared by MATTE. It has been shown that protoxylem and metaxylem may have both centripetal and centrifugal elements. This is very well seen in cross-sections at a low level of a young strand, where only a few xylem elements are developed. In such a section the protoxylem lies against the inner edge of the bundle, and the procambium can be seen to occupy considerably more than half of the bundle; the boundary of the procambium and the protophloem is distinctly recognizable, the protophloem forming only about one-third of the bundle. In the upper extremities of the petiole, also, there may be seen at an early stage a considerable amount of procambium outside the protoxylem; as these usually fail to develop xylem, thin-walled cells occur between the primary and secondary wood in the upper extremities (*fig. 21*).

The girdling habit was first noticed and described by KARSTEN (2) in *Zamia muricata*, without, however, giving the definite number of traces. LESTIBOUDOIS (3) adds nothing new except that the traces branch and anastomose. METTENIUS (4) next misinterpreted the situation, as described in the historical introduction (p. 357).

In the embryo and young seedling, at least, the leaf traces pursue definite and well-defined courses and constitute a definite system. Four traces are invariably found to leave the vascular cylinder for each leaf. A few anastomoses occur here and there, but these are always reducible to four strands. On two occasions only five strands were found in one of the cotyledons. In the older seedlings anastomoses are more abundant, but so far as observed these can be reduced to the system found in the young seedling.

When KARSTEN (2) described the girdling habit, he suggested a cause for it in saying that the bundles are formed very early in the young leaf, and that the originally narrow curves are later crowded far out by subsequent growth and the appearance of new organs. METTENIUS (4) also gives a reason for girdling as follows: "In the developmental stage the traces of the youngest leaves lie in the region of the vegetative point, and at first ascend in an almost perpendicular direction, but during the further growth assume gradually an almost horizontal position, and with subsequent growth are lengthened and the expanse is increased." MATTE (**6**) assigns almost exactly the same cause.

A definite cause for the girdling cannot be given at present, for it seems to be deeper seated than at first suspected. The even distribution of the four strands of each leaf in the vascular cylinder appears to be the dominating factor. When the primordium appears on the stem tip, its distance from the potential vascular cylinder is very short, and the same conditions that determine cell division in the development of the leaf, cause the differentiation of cells along certain paths that run from definite points in the procambium to definite places into the developing leaf. After the traces have been started, they continue to develop with the further growth of all the tissues; new organs appear and intercalary growth continues; thus the strands are lengthened more and more and their curves are widened to keep pace with the ever increasing growth of the plant.

Summary

1. The vascular cylinder of the embryo is a protostele, but becomes a siphonostele in the seedling. It is very short and squarish in cross-section, one of the diagonals of the section being at right angles to the inner faces of the cotyledons, and the other parallel with them. Near each of the four corners is a group of protoxylem cells, the long diameter of whose section extends along the diagonal.

2. The four protoxylem groups extend downward to form the protoxylem of the root.

3. From each protoxylem group a foliar strand runs outward for a short distance and then branches, the branches separating at a wide angle and continuing outward until under the cotyledon, when they ascend it; the result is four strands for each cotyledon. The two protoxylem groups on the diagonal perpendicular to the inner faces of the cotyledons give rise to the two inner strands of each cotyledon; while the two protoxylem groups on the diagonal parallel with the inner faces of the cotyledons give rise to the two outer strands of the cotyledons, that is, one branch runs into the outer edge of the one and the other branch (from the same group) runs into the edge of the other cotyledon (opposite the first).

4. For each leaf or scale four strands leave the vascular cylinder

at points not definitely located but well-distributed; two strands of each organ leave the cylinder approximately on the same side as the leaf for which they are destined, and run more or less directly through the cortex into the central or abaxial part of the petiole without branching; while the other two strands of each organ leave the cylinder approximately on the opposite side and describe a wide curve around it, the one in one direction and the other in the other, and finally ascend in the dorsal or adaxial part of the petiole, branching repeatedly. The girdle on the side toward which the spiral may be said to turn is generally the longer one.

5. When the cotyledonary vascular strands leave the vascular cylinder they are endarch, gradually become mesarch in their upward course, and finally approach the exarch condition.

6. The foliar vascular strands also are endarch at their separation from the vascular cylinder, and in their upward course become mesarch and finally exarch. In the very young leaf this transition extends through the whole base and petiole uniformly; but in the adult leaf it is comparatively rapid through the base up to the lower part of the petiole, where only a few centrifugal elements remain, and which remain uniform until in the rachis, where the transition is completed, so that in the pinna only centripetal xylem is left.

7. In the lower stretches of the foliar strands a considerable amount of the centrifugal wood is primary xylem.

8. In the foliar strands of the embryo and seedling, the xylem tissue, so far as developed, from below upward passes from an inner to a central position in reference to the whole bundle.

9. The girdle is established very early, and is horizontal from the beginning.

United States Geological Survey
Washington, D. C.

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EXPLANATION OF PLATES XXIII–XXIX

PLATE XXIII

FIG. 1.—Embryo in mature seed: *cot*, cotyledon; *sh*, tubular sheath of cotyledons; *st*, stem proper; *r*, hypocotyl; *s*, suspensor.

FIG. 2.—Cross-section of embryo just above stem tip: *cot*, tubular part of colytedons; L_1, first leaf; L_1^1, L_1^2, L_1^3, L_1^4, vascular strands of first leaf; L_2, second leaf; L_2^1, L_2^2, L_2^3, L_2^4, vascular strands of second leaf; L_3, third leaf.

FIG. 3.—Median longitudinal section of lower part of embryo, parallel with inner faces of cotyledons: *cot*, cotyledon; L_1, L_2, first and second leaves; *pn*, pinna; *ls*, foliar strand; *st*, stem tip; *p*, pith; *cs*, cotyledonary strand; *vp*, vascular plate; *pl*, plerome; *cp*, caplike tissue; *sp*, suspensor.

FIG. 4.—Semi-diagrammatic reconstruction of part of vascular system of embryo; *cot*, cotyledon; *tb*, tubular part of cotyledons; *cs*, cotyledonary strands; $L_1^1-L_1^4$, foliar strands of first leaf; $L_2^1-L_2^4$, foliar strands of second leaf; *vp*, vascular plate; *a*, protoxylem elements continuing downward into the hypocotyl.

FIG. 4*a*.—Cross-section of a vascular bundle in upper extremity of young leaf; *x*, xylem elements; *a*, cells losing their contents during lignification; *pc*, procambium; *pph*, protophloem; *b*, line showing boundary between protoxylem and protophloem.

PLATE XXIV

FIG. 5.—Semi-diagrammatic reconstruction of part of vascular system of embryo, to show especially the girdling: L_1, L_2, traces of first and second leaves; *vp*, vascular plate; *px*, protoxylem groups; *a*, xylem elements continuing down from protoxylem groups to form the protoxylem of the primary root.

FIG. 6.—Diagram giving bird's-eye view of vascular system, to show origin and girdling of foliar strands: *cot*, tubular part of cotyledons; *cs*, cotyledonary traces, one group for each cotyledon; L_1, L_2, L_3, L_4, first, second, third, and fourth leaves; L_1^1, L_1^2, L_1^3, L_1^4, traces of first leaf; L_2^1, L_2^2, L_2^3, L_2^4, traces of second leaf; *px*, protoxylem groups.

FIG. 7.—Outline of cross-section just above stem tip of seedling three or four years old, to show phyllotaxy; *cot*, cotyledons; *1–8*, leaves in order of age.

FIG. 7*a* (1).—Stem tip from germinating embryo with leaf primordium (*L*) developing on the side.

FIG. 7*a* (2).—Stem tip from rapidly growing seedling, showing growing point (*st*) in the middle and a leaf primordium (*L*) on each side; this section showed numerous spindles in growing point and primordia.

PLATE XXV

FIG. 8.—Details of central region of embryo in median longitudinal section: *L*, youngest leaf; *st*, stem tip; *ep*, epidermis; *pt*, pith terminating in stem tip; *pc*, procambium; *vp*, vascular plate; *ph*, phloem; *a*, continuation of protoxylem into the root; *p*, pith; *pl*, plerome; *m*, mucilage cells.

FIG. 9.—Median longitudinal section of lower part of germinating embryo, showing lengthening of plerome, development of primary root, and fraying-off of epidermis and outer part of cortex (*f*).

FIG. 9*a*.—Diagram to show transition of protoxylem in the metaxylem, and transition of primary xylem from an inner to a central position in a young bundle: *aa'*, inner, and *gg'*, outer limits of bundle; shaded portion (*ab*, *cd*), xylem tissue, *ad*, protoxylem; unshaded portion in *aa'* (*cf*), procambium; *cf* (*gg'*), protophloem; dotted line *cf*, boundary between procambium and protophloem.

PLATE XXVI

FIGS. 10–15.—Series of cross-sections of cotyledonary traces: *fig. 10*, just before joining vascular cylinder; *fig. 15*, after the several bundles have reunited in upper extremity of cotyledon; *px*, protoxylem. ×850.

PLATE XXVII

FIGS. 16–21.—Series of cross-sections of leaf traces: *fig. 16*, just before joining vascular cylinder; *figs. 17–20*, at considerable intervals above each other; *fig. 21*, younger trace; shaded portion protophloem. ×850.

PLATE XXVIII

FIG. 22.—Cross-section at low level of foliar trace of a three-year-old plant: *px*, protoxylem (endarch); *x*, xylem, of which probably the larger portion is centrifugal metaxylem and only a small portion is secondary xylem; *ph*, phloem; *pph*, protophloem. ×425.

FIG. 23.—Section from the same strand as *fig. 22*, but considerably higher up; *px*, protoxylem (mesarch). ×425.

FIG. 24.—Section of bundle from old leaf of quite a large plant just below rachis: *px*, protoxylem (exarch); *mx*, metaxylem (centripetal); *tc*, thin-walled cells; *sx*, secondary xylem; *ph*, phloem; *pph*, protophloem. ×425.

FIG. 25.—Cross-section of bundle in pinna: lettering as in *fig. 24*; note absence of secondary xylem. ×425.

FIG. 26.—Median longitudinal section of very young leaf trace, showing shape and arrangement of cells; shaded portion, earliest procambium. ×1200.

FIG. 27.—Cross-section of the same bundle as in *fig. 26*.

PLATE XXIX

FIG. 28.—Median longitudinal section of embryo at right angles to inner faces of cotyledons. ×11.

FIG. 29.—Median longitudinal section similar to *fig. 28: ct*, cotyledonary traces; *cp*, caplike tissue; *s*, suspensor. ×30.

FIG. 30.—Cross-section of young seedling at region of union of cotyledonary trace with vascular cylinder: *ct*, cotyledonary traces belonging to one cotyledon. ×16.

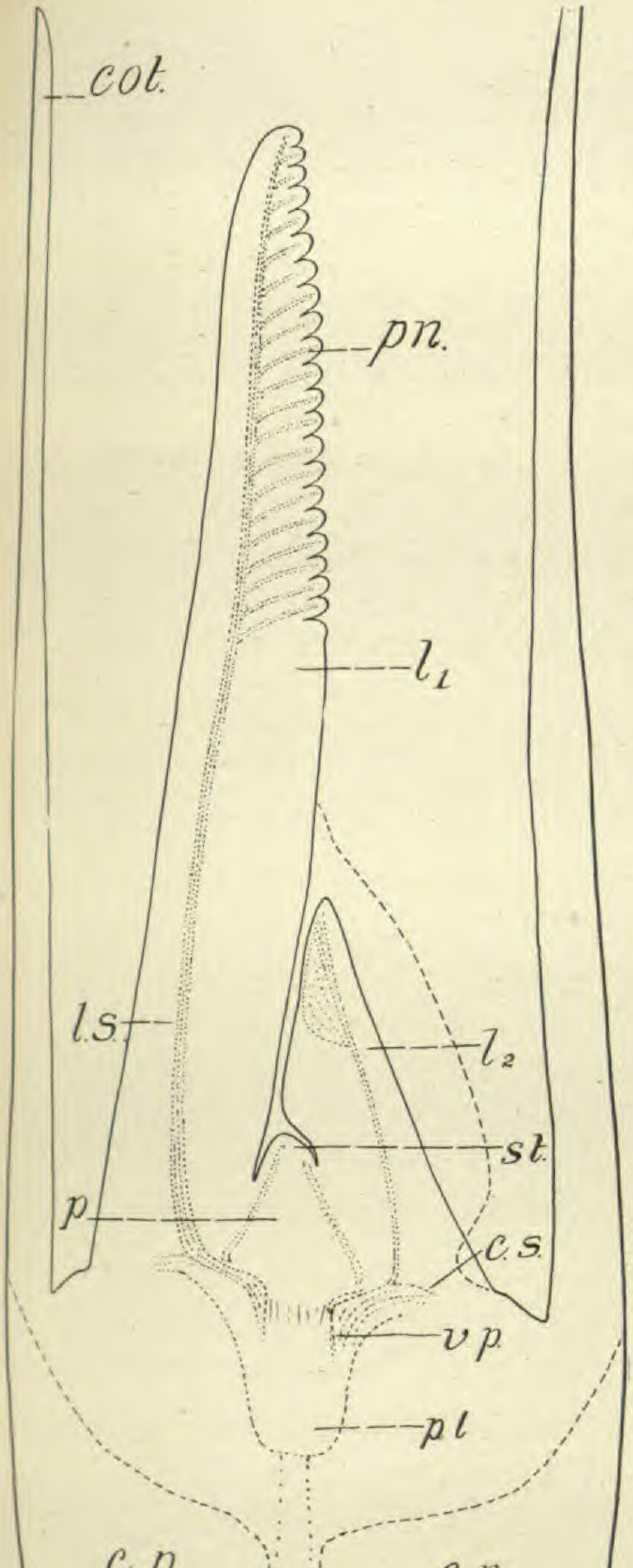
FIG. 31.—Section of same further up to show girdling: L_2^1, outer long girdle; L_2^4, outer shorter girdle; L_2^2, L_2^3, inner girdles; all of second leaf. ×16.

FIGS. 32, 33.—Cross-sections of embryo at region of vascular plate (*vp*); *px*, protoxylem; *x*, xylem; *ph*, phloem; union of cotyledonary traces two by two, and union of resultants with vascular plate at protoxylem groups. ×30.

FIG. 34.—Median longitudinal section of seedling three years old: *pc*, procambium; *ltg*, girdle; *lt*, trace; *lg*, leaf gap. ×30.

FIG. 35.—Cross-section of embryo to show early appearance of girdle; *pc*, procambium; ltg^1, girdle of very young leaf; ltg^2, girdle of next older leaf. ×30.

The black spots in all the photographs are mucilage cavities or cells.



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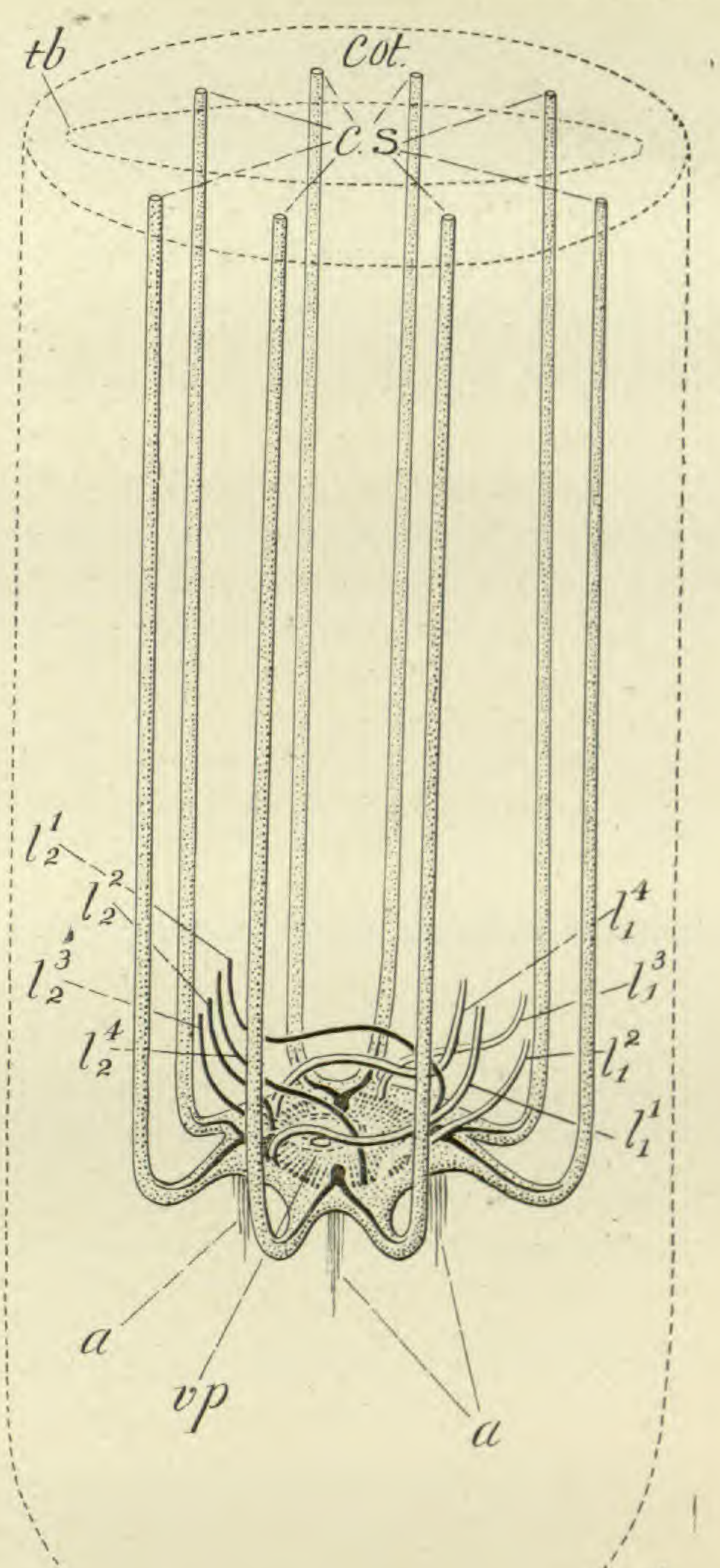

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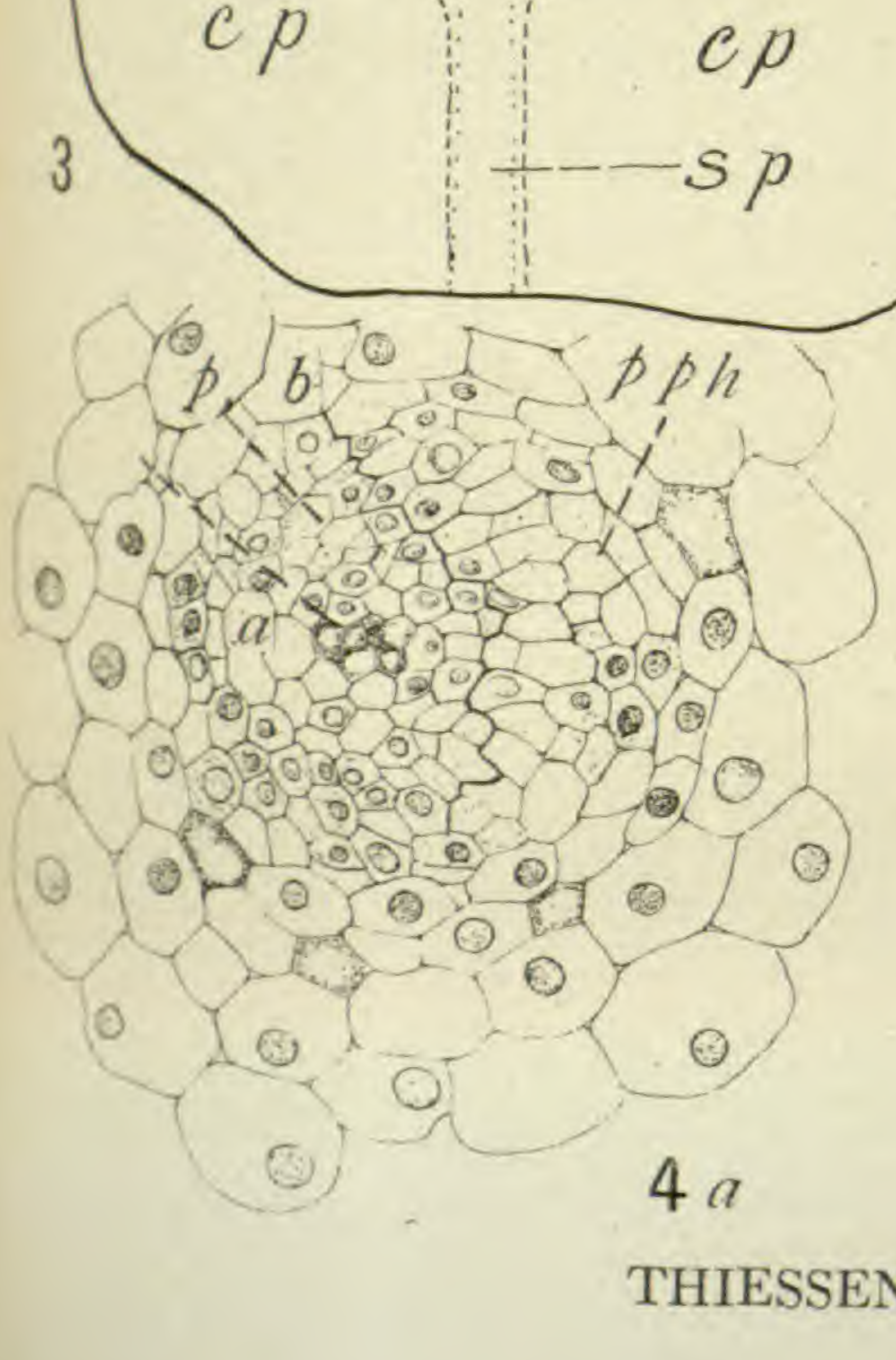

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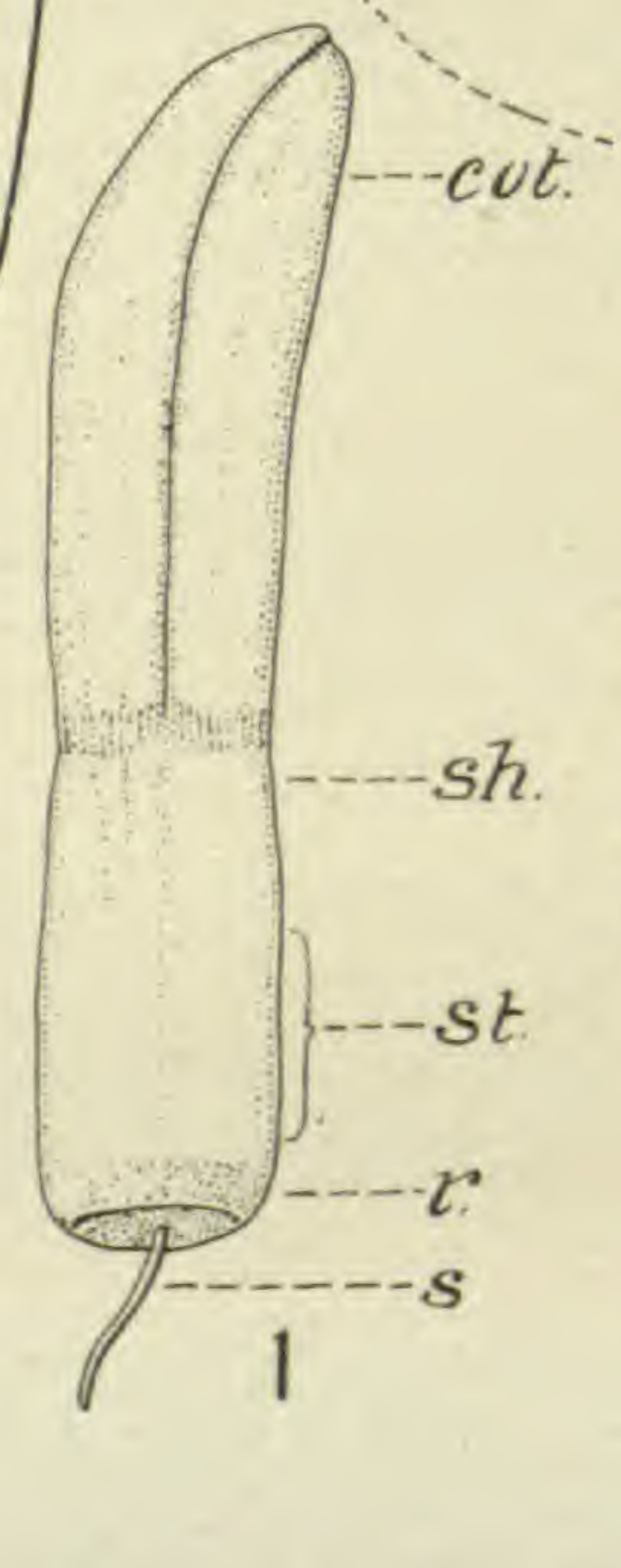

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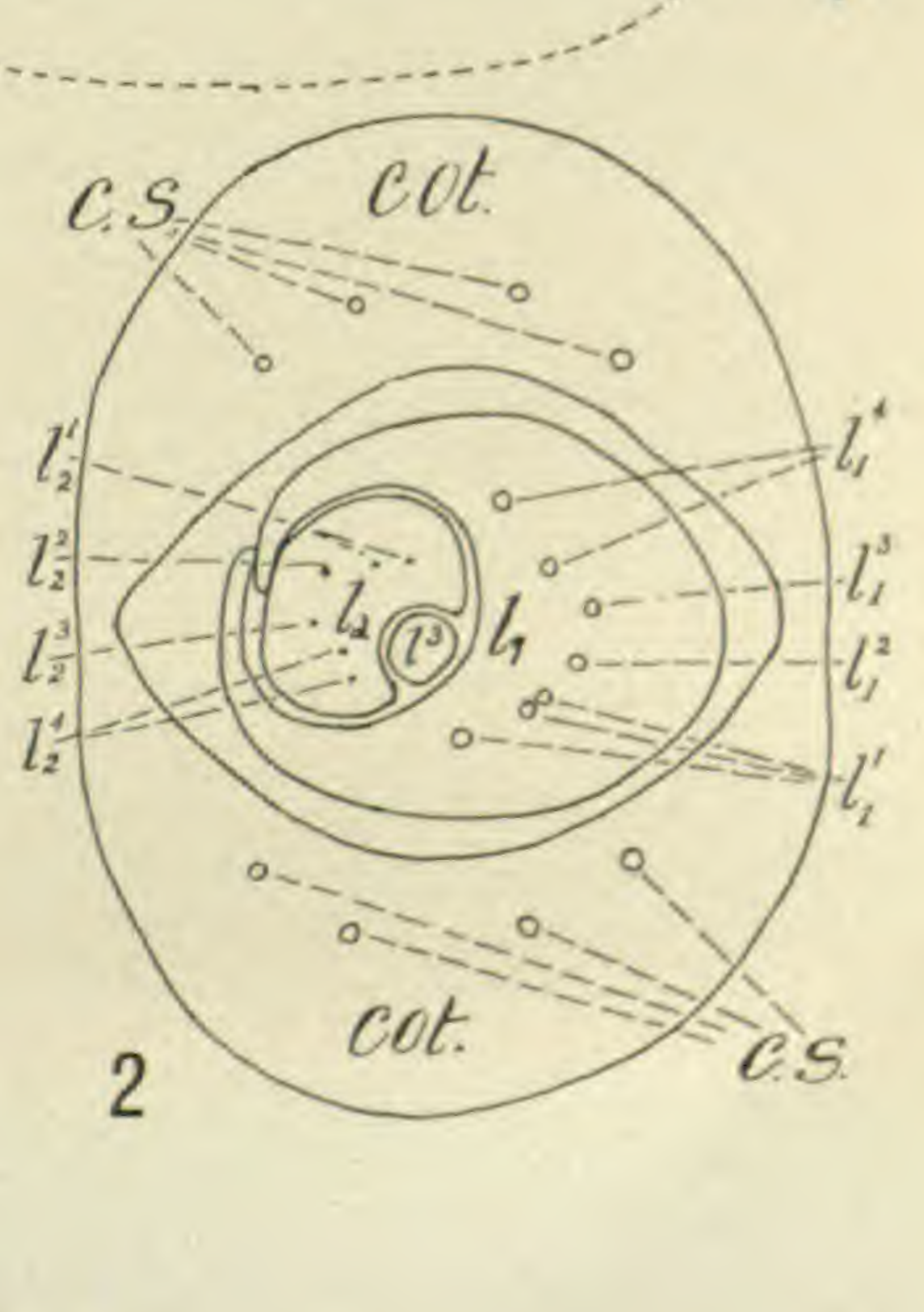

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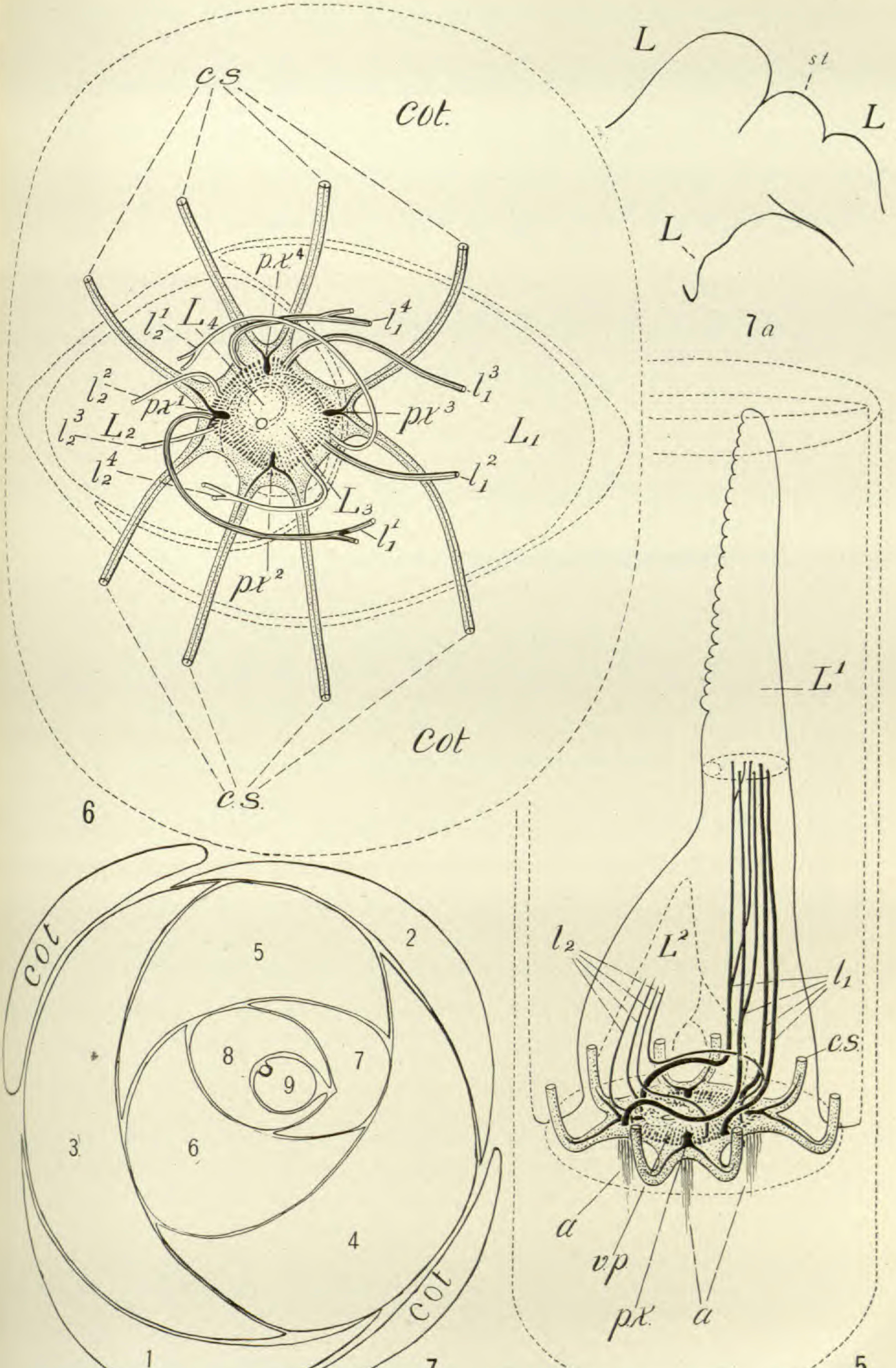

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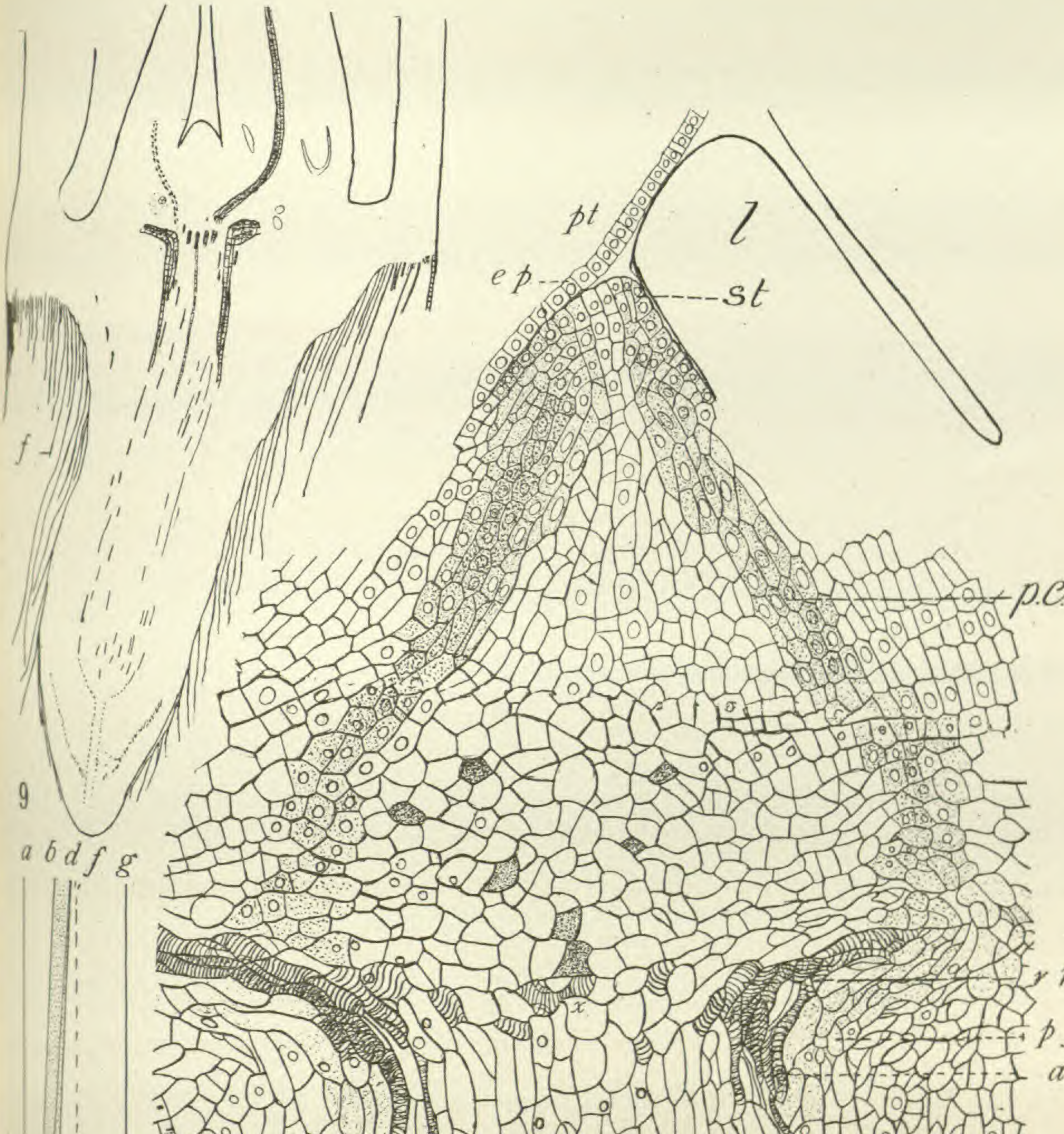

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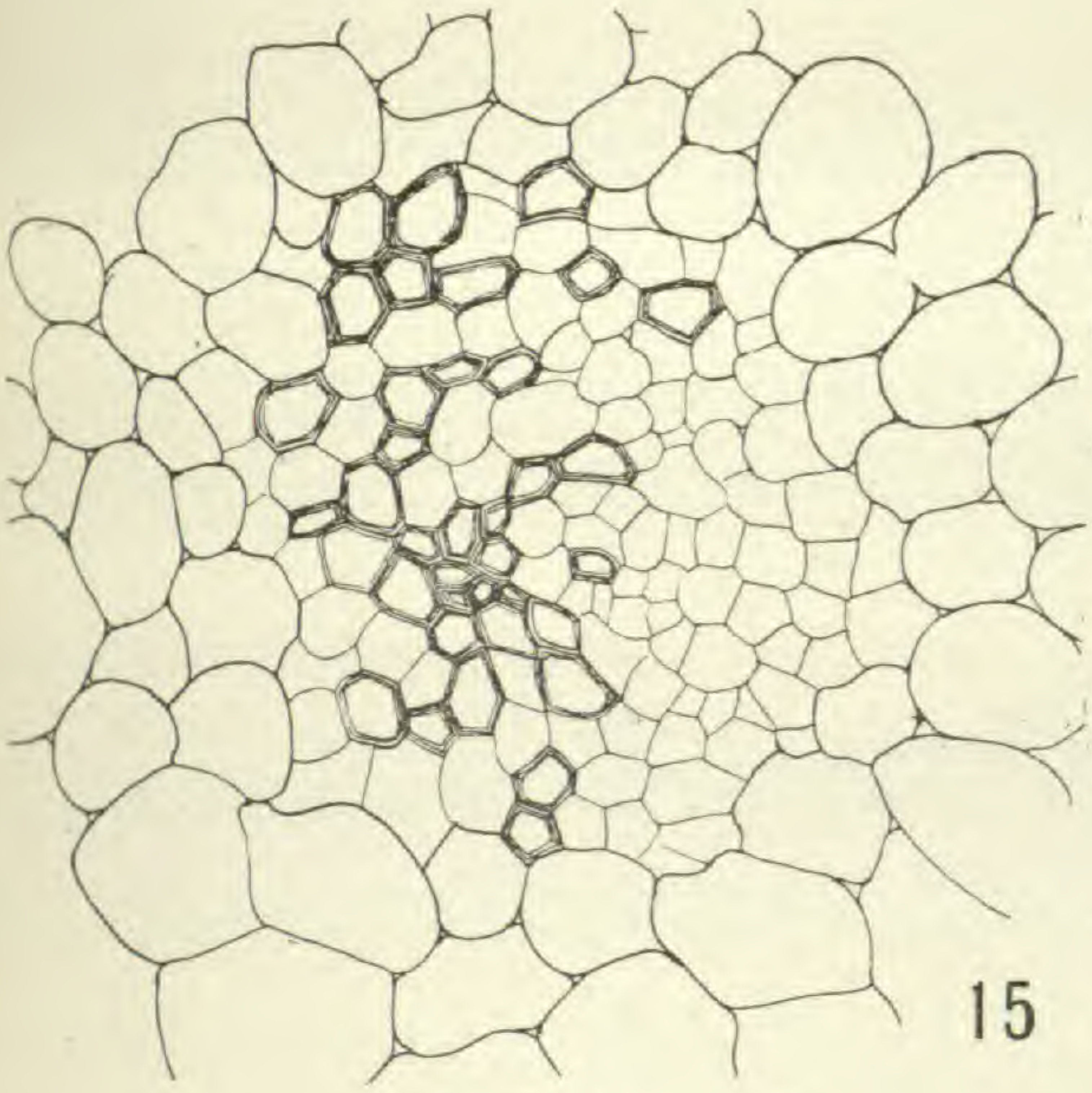
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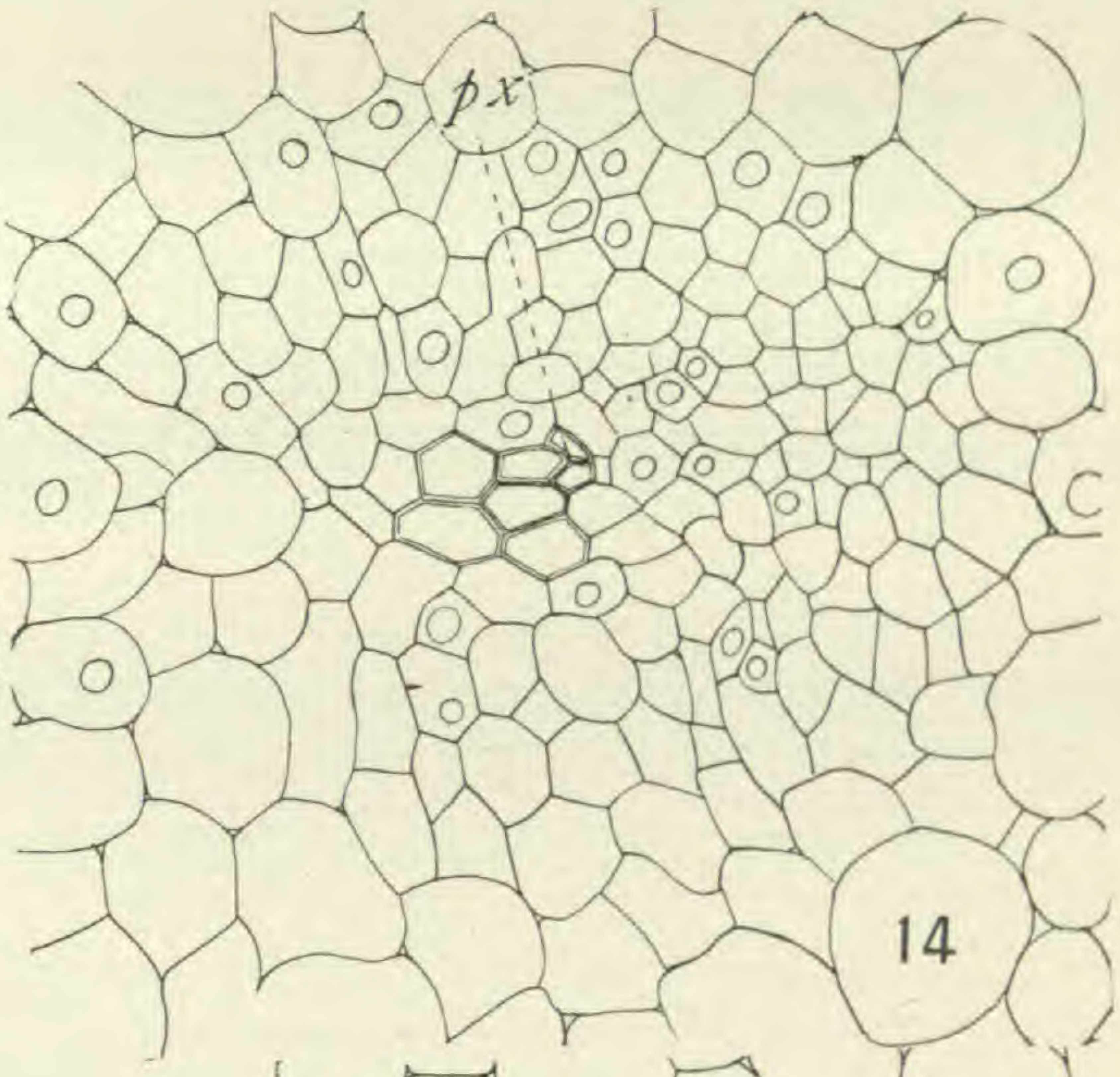

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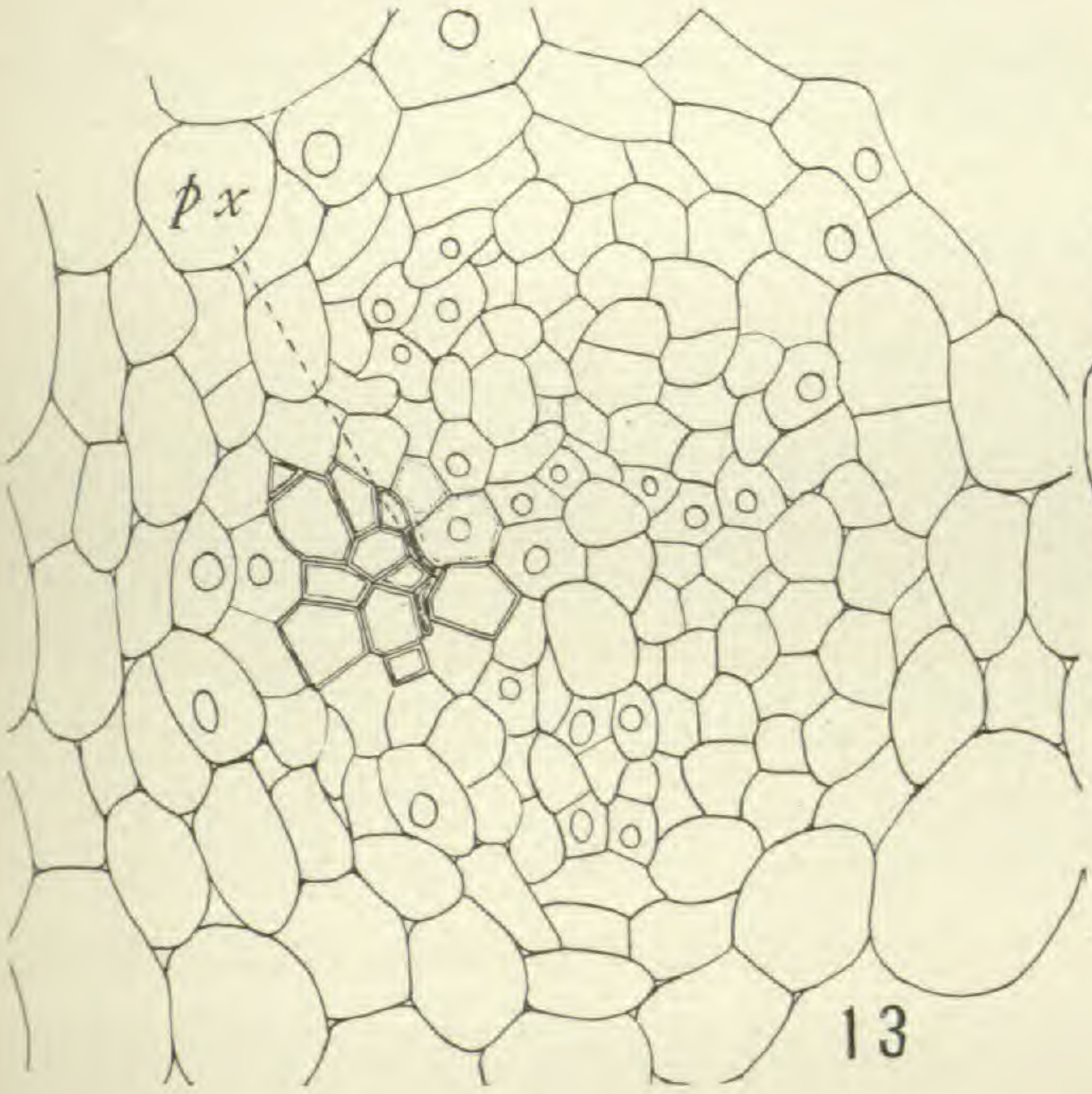

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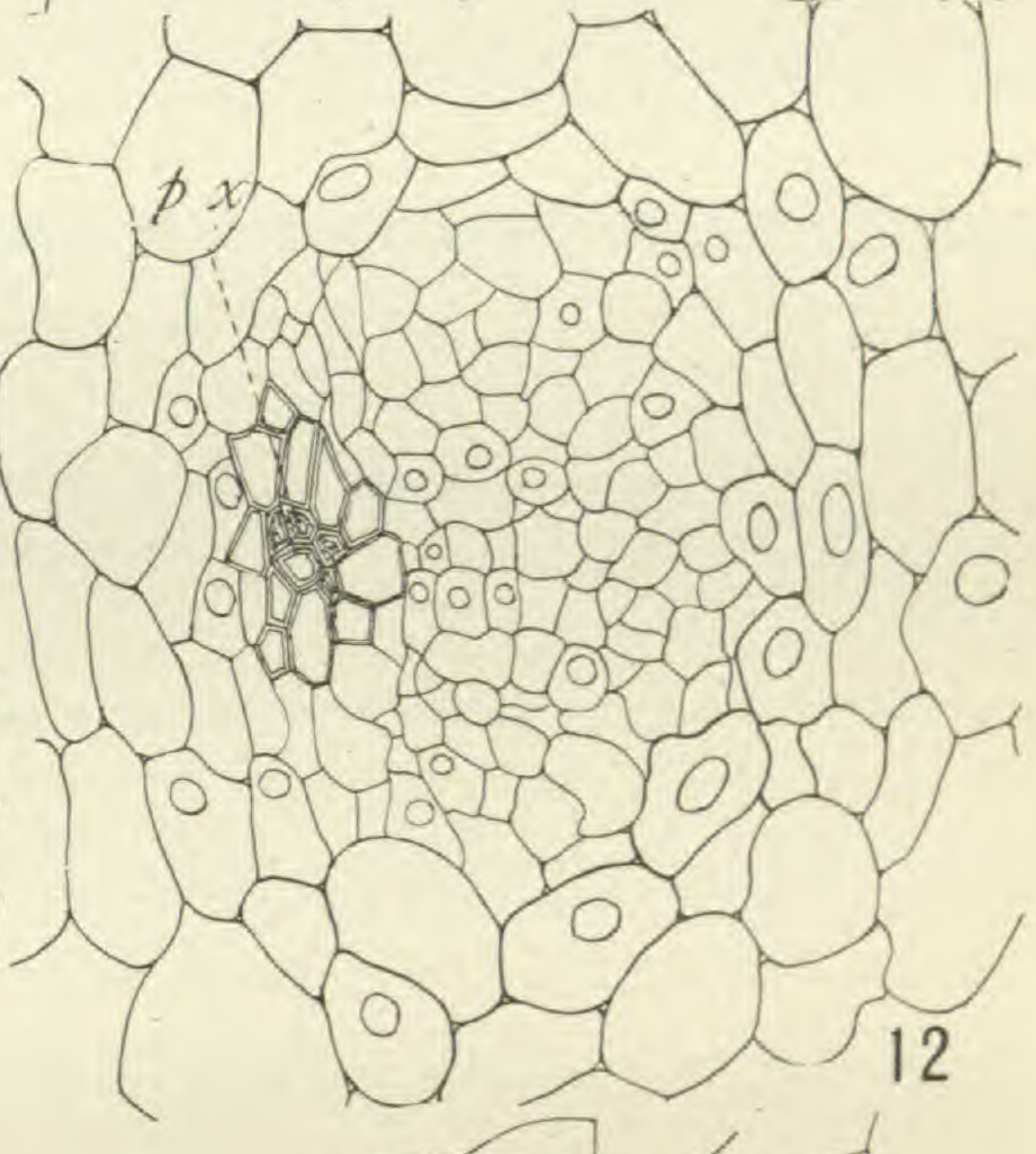

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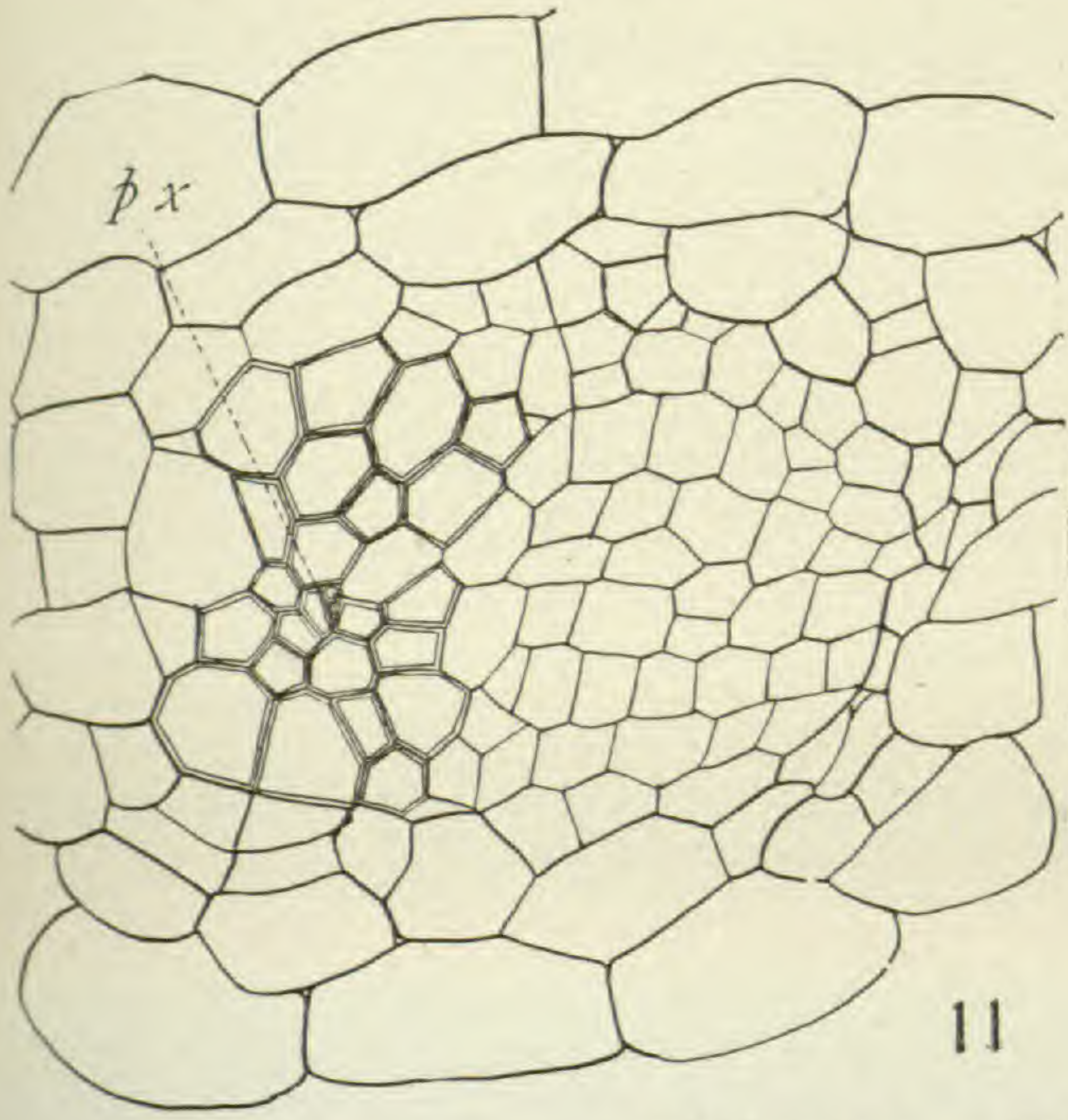

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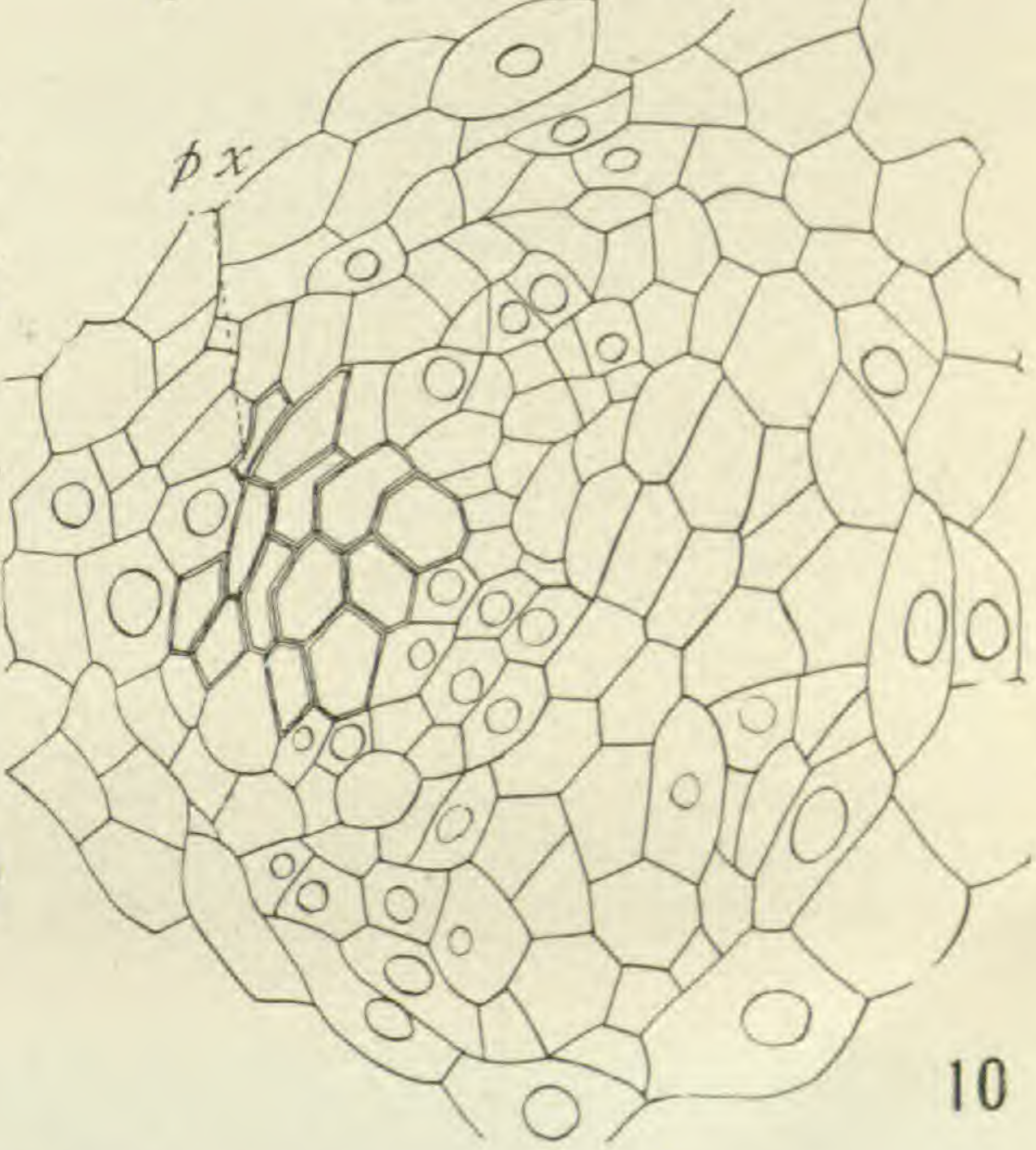

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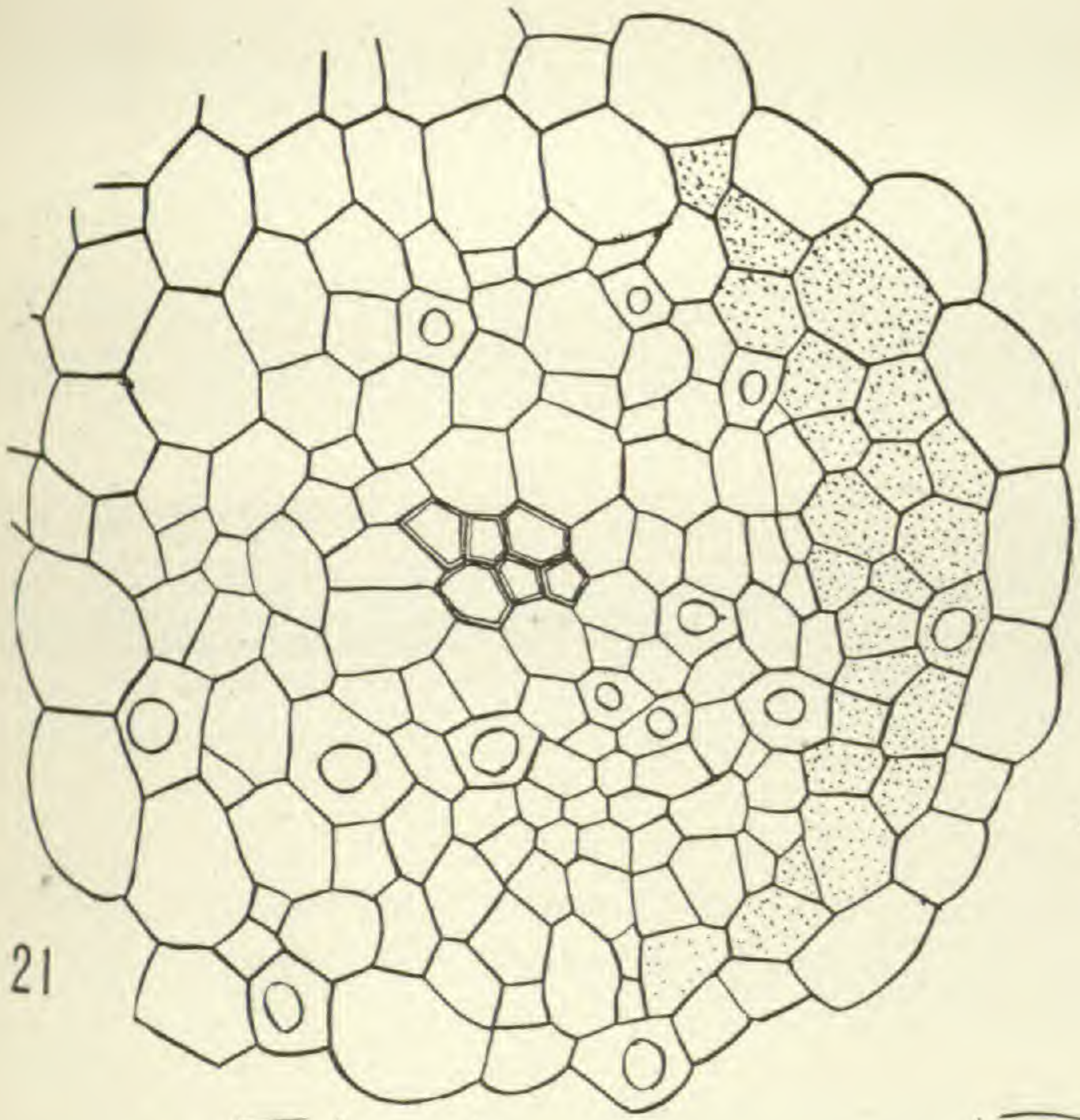
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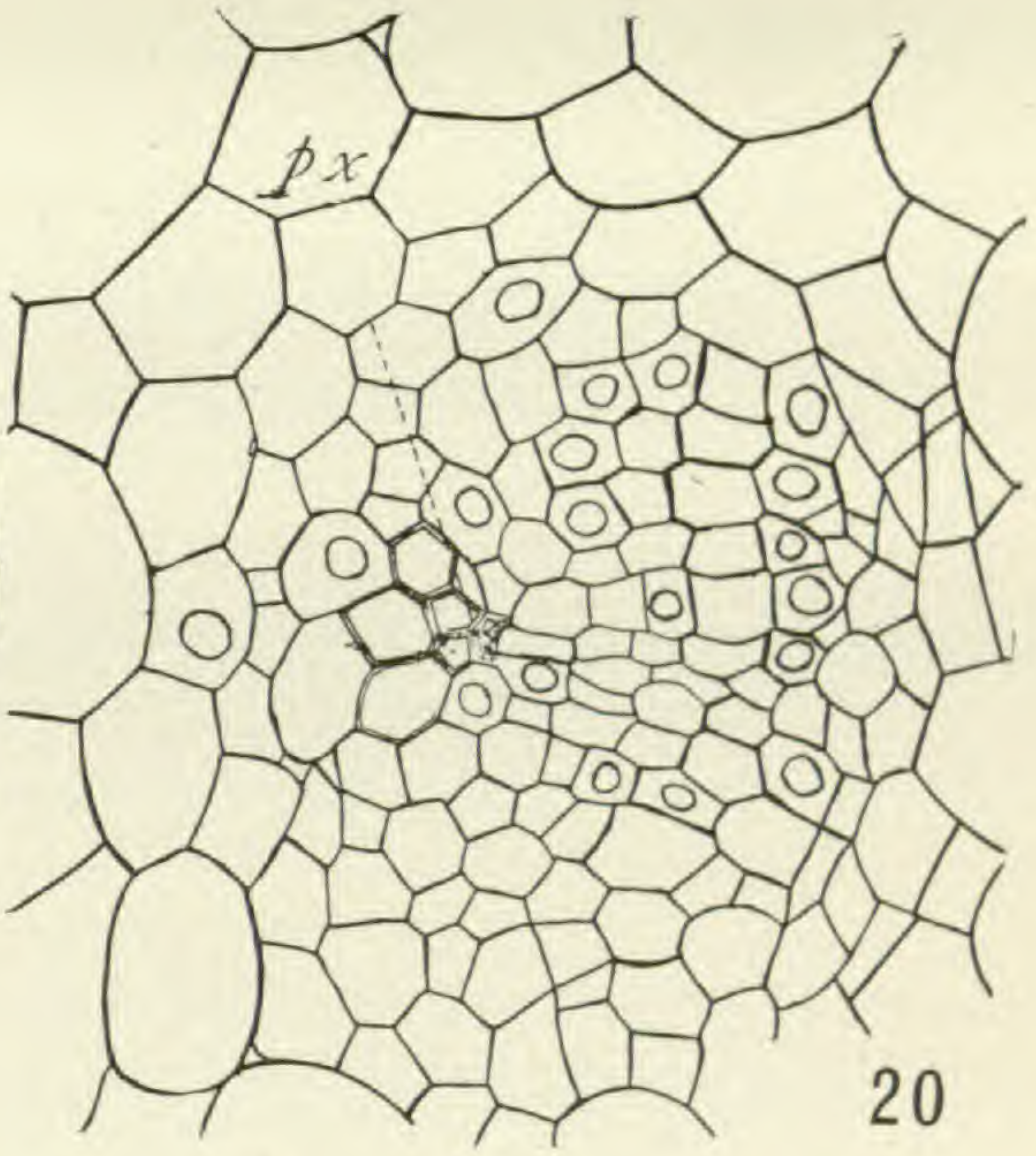

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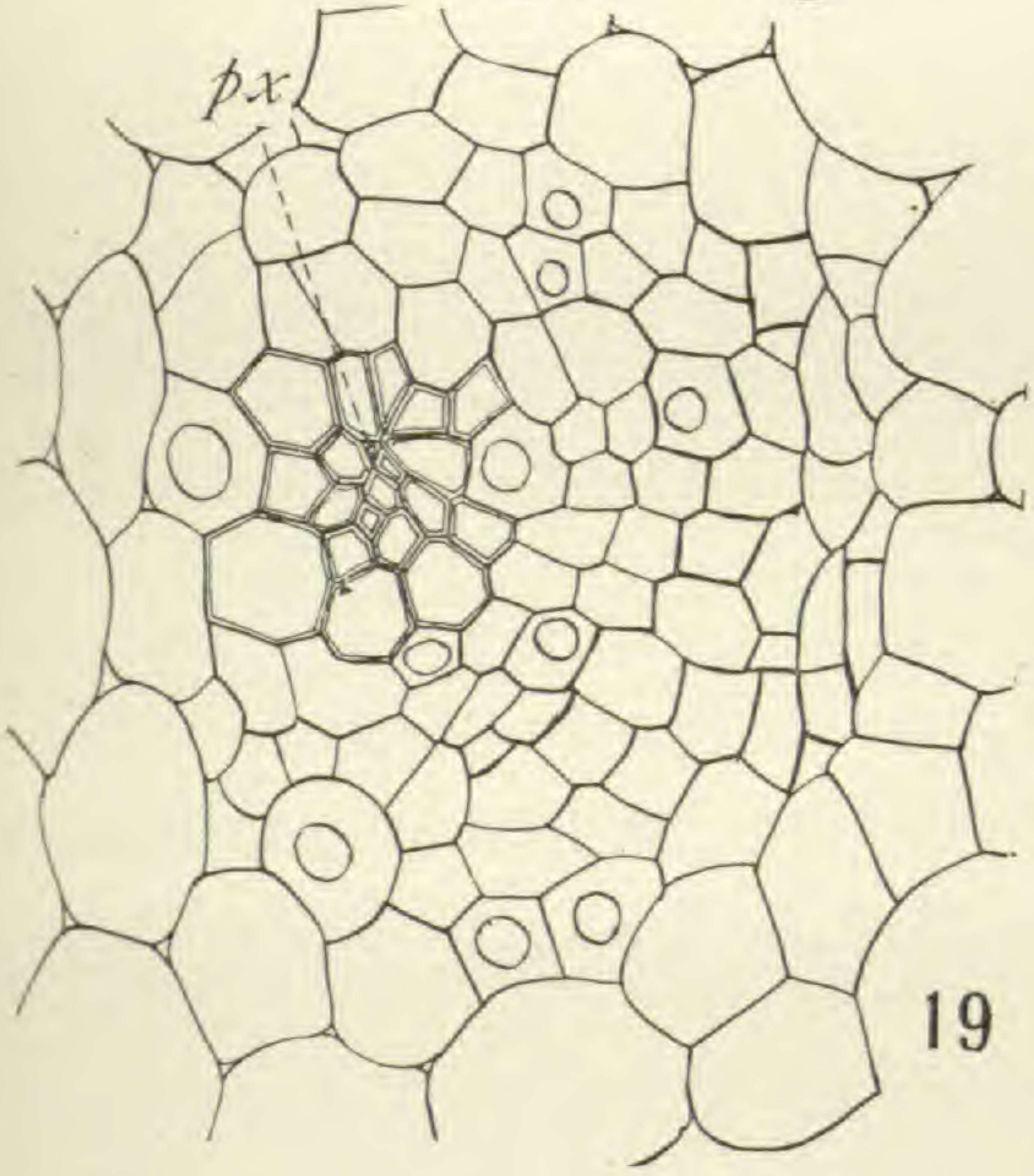

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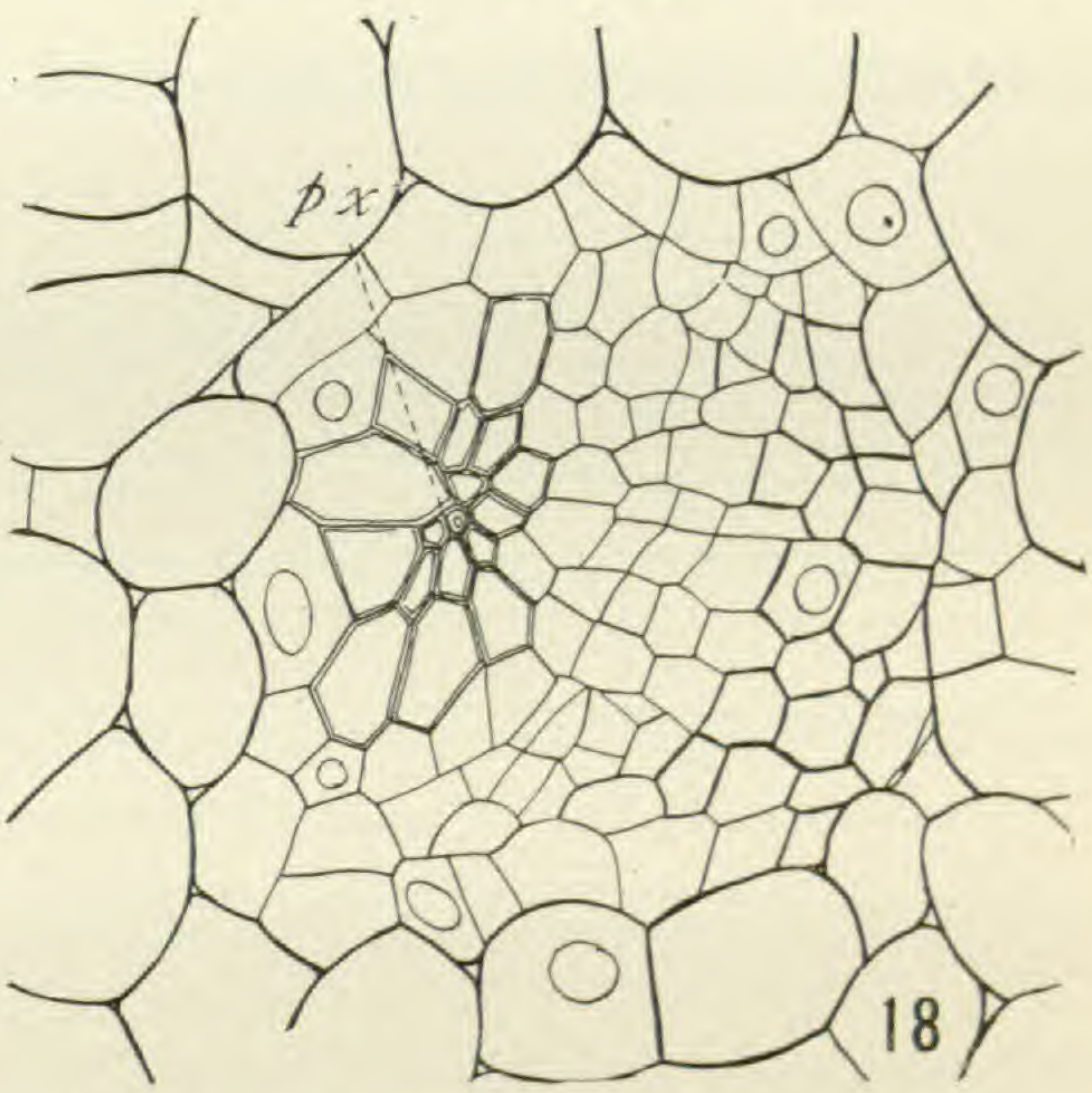

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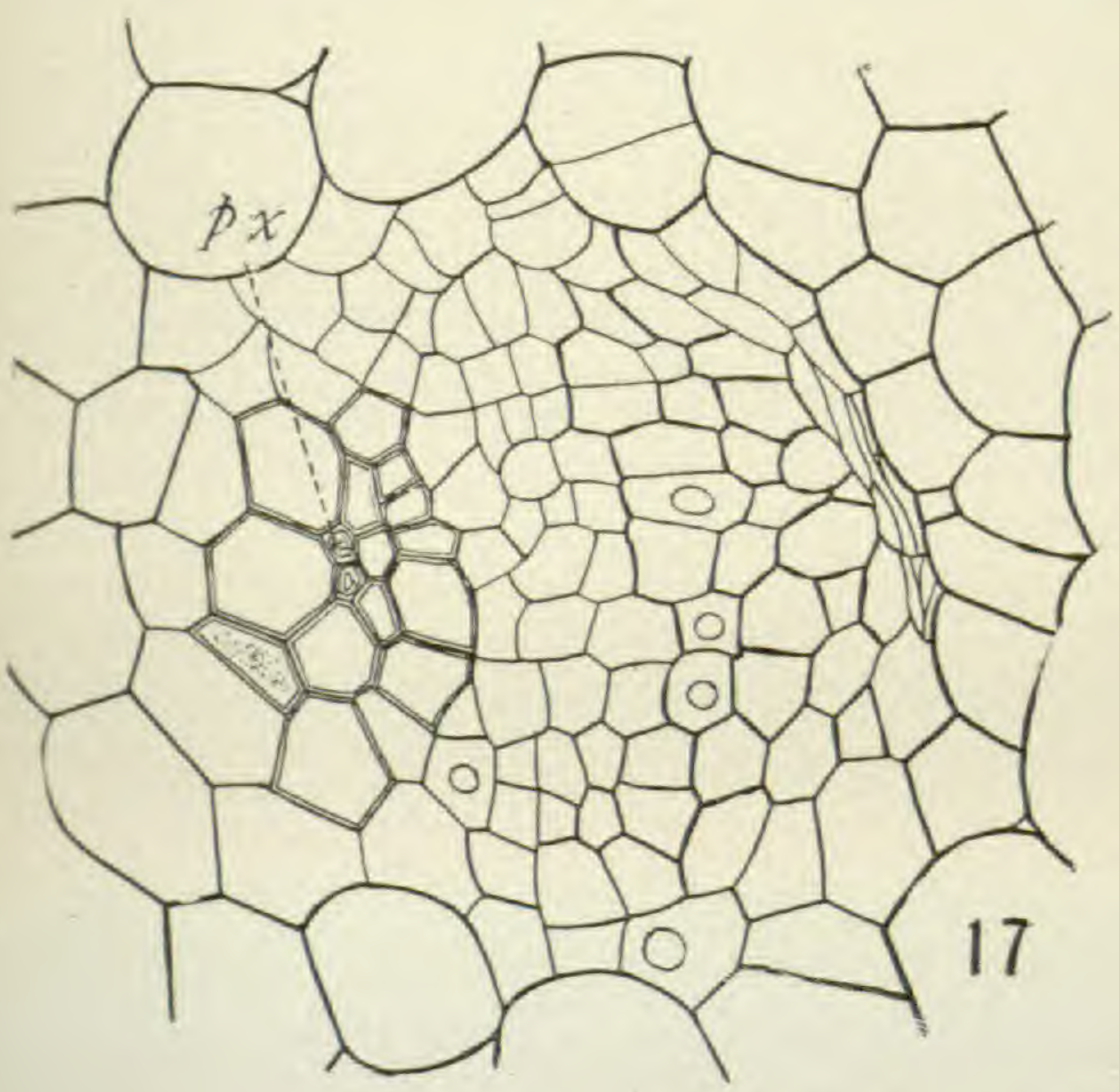

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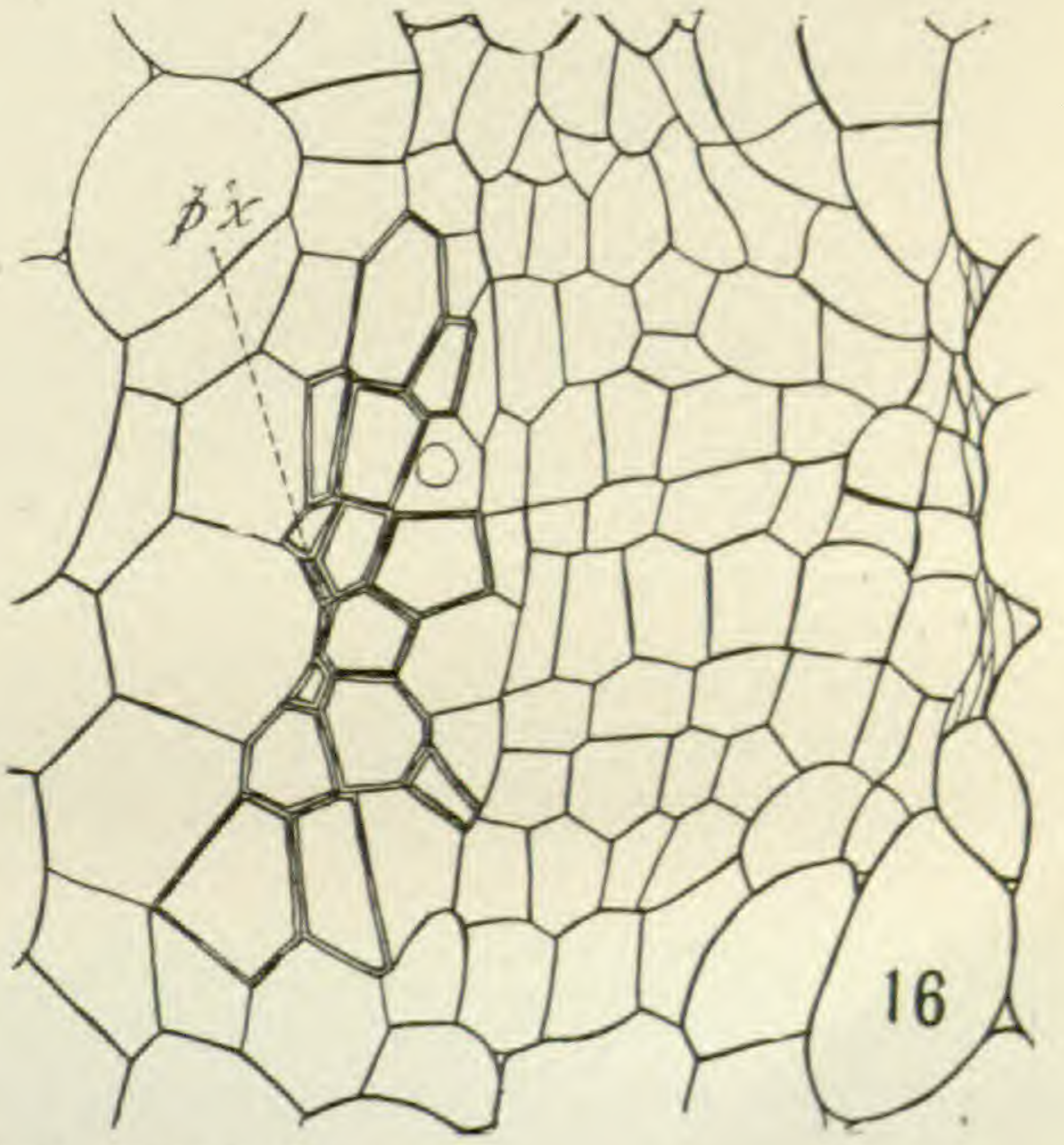

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THIESSEN on DIOON EDULE

THIESSEN on DIOON EDULE

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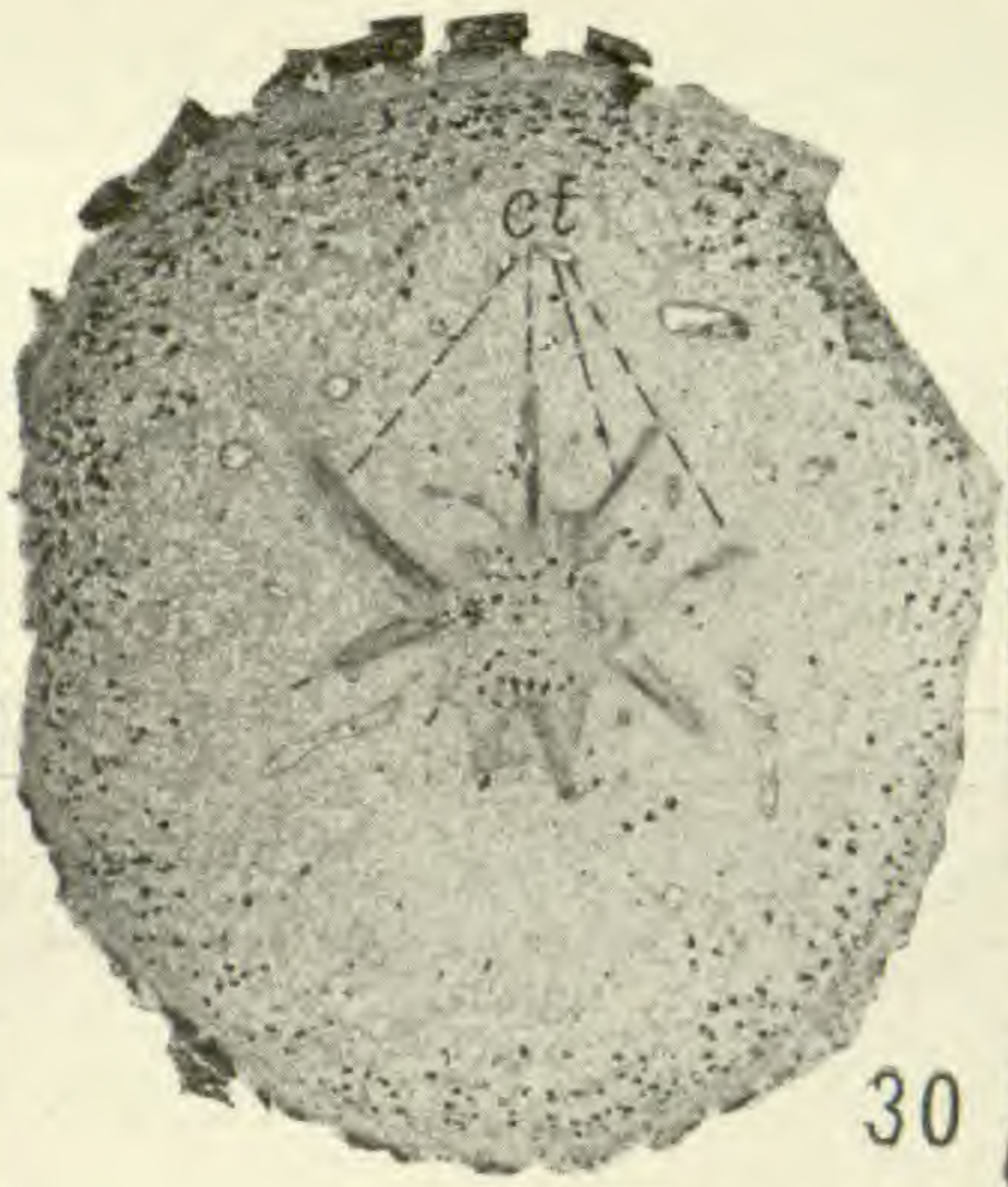

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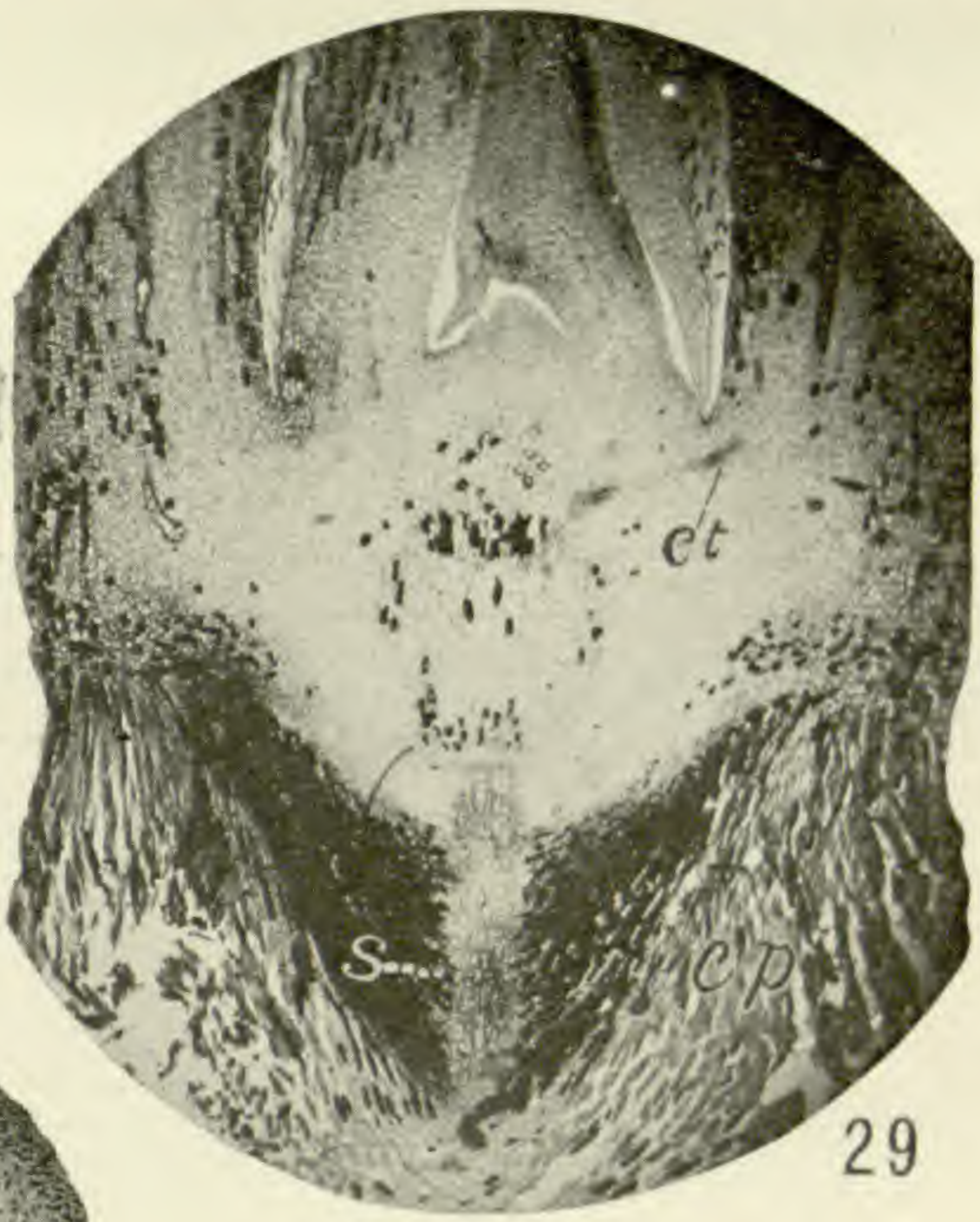

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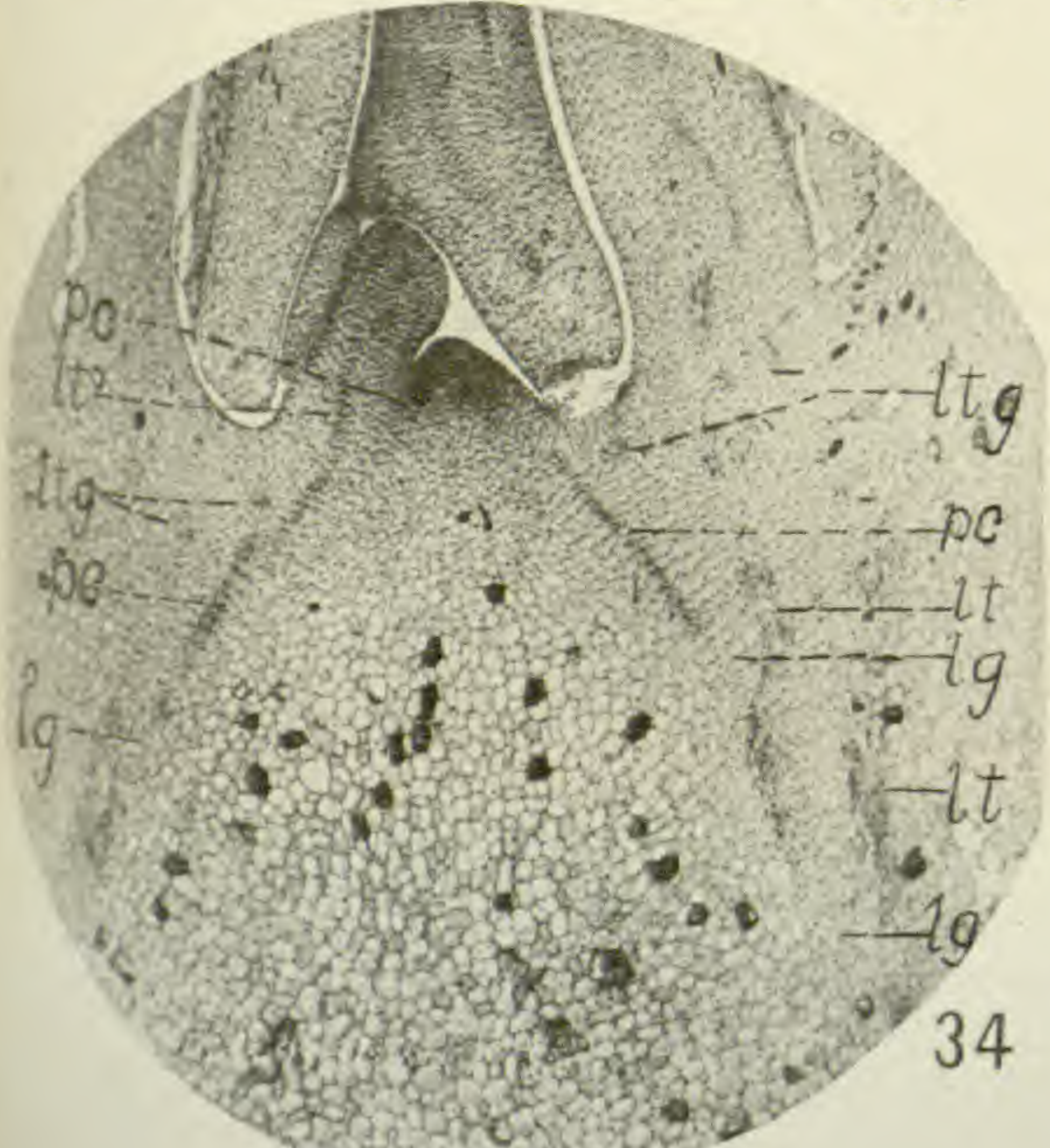

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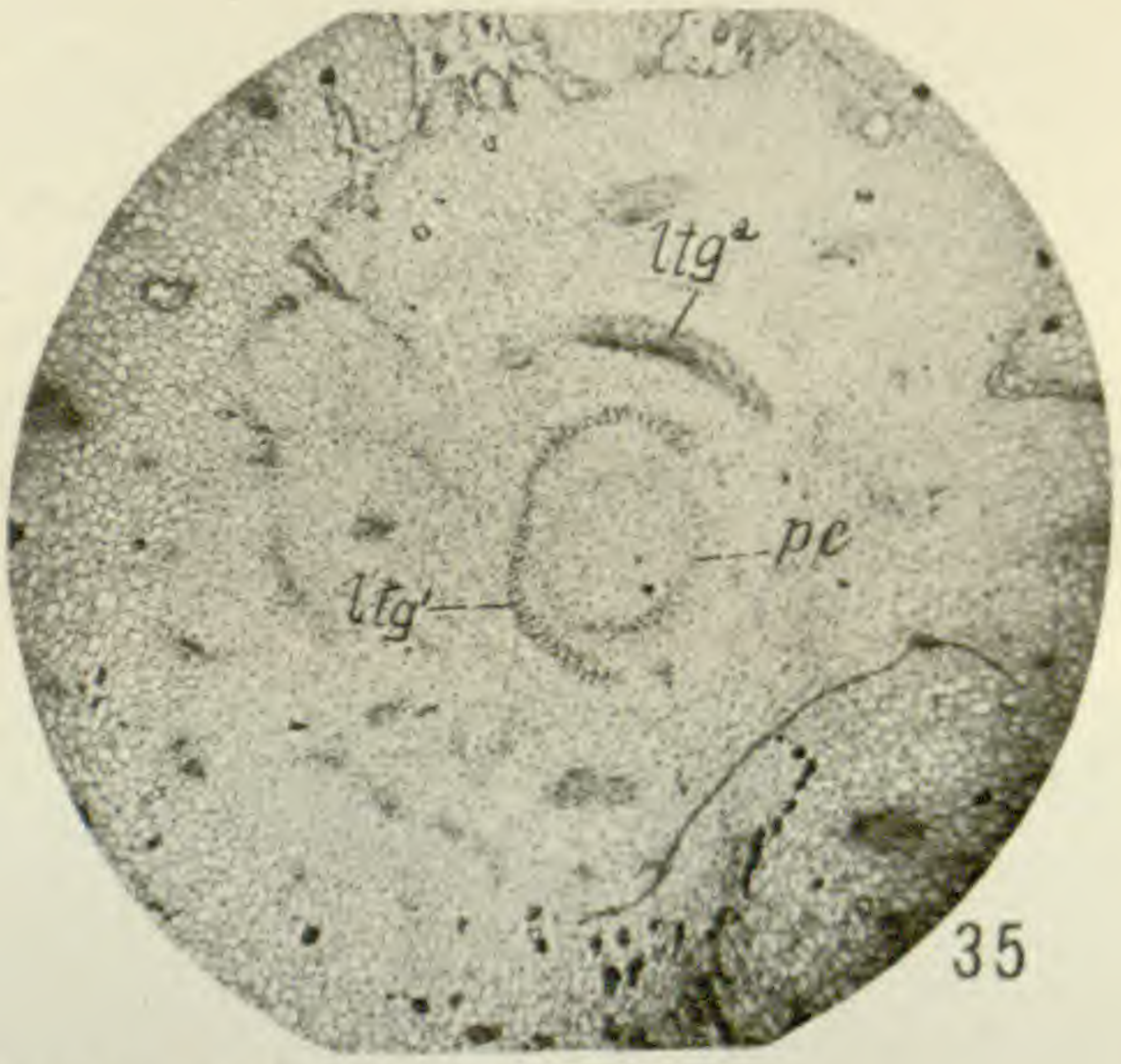

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THIESSEN on DIOON EDULE

BRIEFER ARTICLES

NEW COLORADO SPECIES OF CRATAEGUS

(WITH TWO FIGURES)

During the past three years the writer, together with Messrs. G. S. DODDS and W. W. ROBBINS, has been making ecological studies of mesa and gulch plants in the vicinity of Boulder, Colorado. In tracing out the distribution of Crataegus it became apparent that there were present some undescribed species. Full and complete collections were made therefore by Mr. DODDS and the writer during the present season from marked trees, in order that there could be no confusion in regard to the specimens. Very complete notes of abundance, occurrence in different drainage areas, etc., were made. Fruits were preserved in alcohol as well as by drying.

It was expected at the beginning of the study that the new forms would be found to be hybrids between previously described species. This, however, is not the case. The distribution of *C. Doddsii*, in particular, shows that it is a true species. Isolated thickets of *C. Doddsii* have been found as far as five or ten miles away from any trees of other species of Crataegus. Various other considerations which will be noted elsewhere lead to the belief that the Colorado species of Crataegus do not hybridize.

A paper by my colleague, Professor T. D. A. COCKERELL,[1] gives a full account of the species described for Colorado up to the present time. I am much indebted to this paper and to suggestions from its author.

The following species have the characters of TOMENTOSAE of SARGENT and should be placed in that group. The first might almost as well be placed with COCCINEAE.

Crataegus Doddsii, sp. nov.—*Arbor* parva, vel frutex; ramis cineraciis, spinescentibus; ramulis junioribus glabris vel paululum pubescentibus, colore castaneato. *Folia* lucida; glabrata, sed nerviis infra pubescentibus; obovata, saepe ad apicem truncata, margine serrata, et superne obscure lobata. *Petiolus* longe $\frac{1}{4}$–$\frac{1}{2}$ laminae; superne margine angusta glandulosa. *Flores* conspicui; corymbis compositis; pedicellis glabris vel majus minusve pubescentibus; staminibus 10 vel minus; antheris albis. *Fructus* durus, cum pilis raris, late pyriformis; longe 9^{mm}, in longitudinem costatus;

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[1] Univ. of Colorado Studies 5:41–45. Dec. 1907.

colore ruber sanguineusve; autumno maturans; nucellis osseis, 2–3.—*Fig. 1.*

Hab. in Colorado, U. S. A.

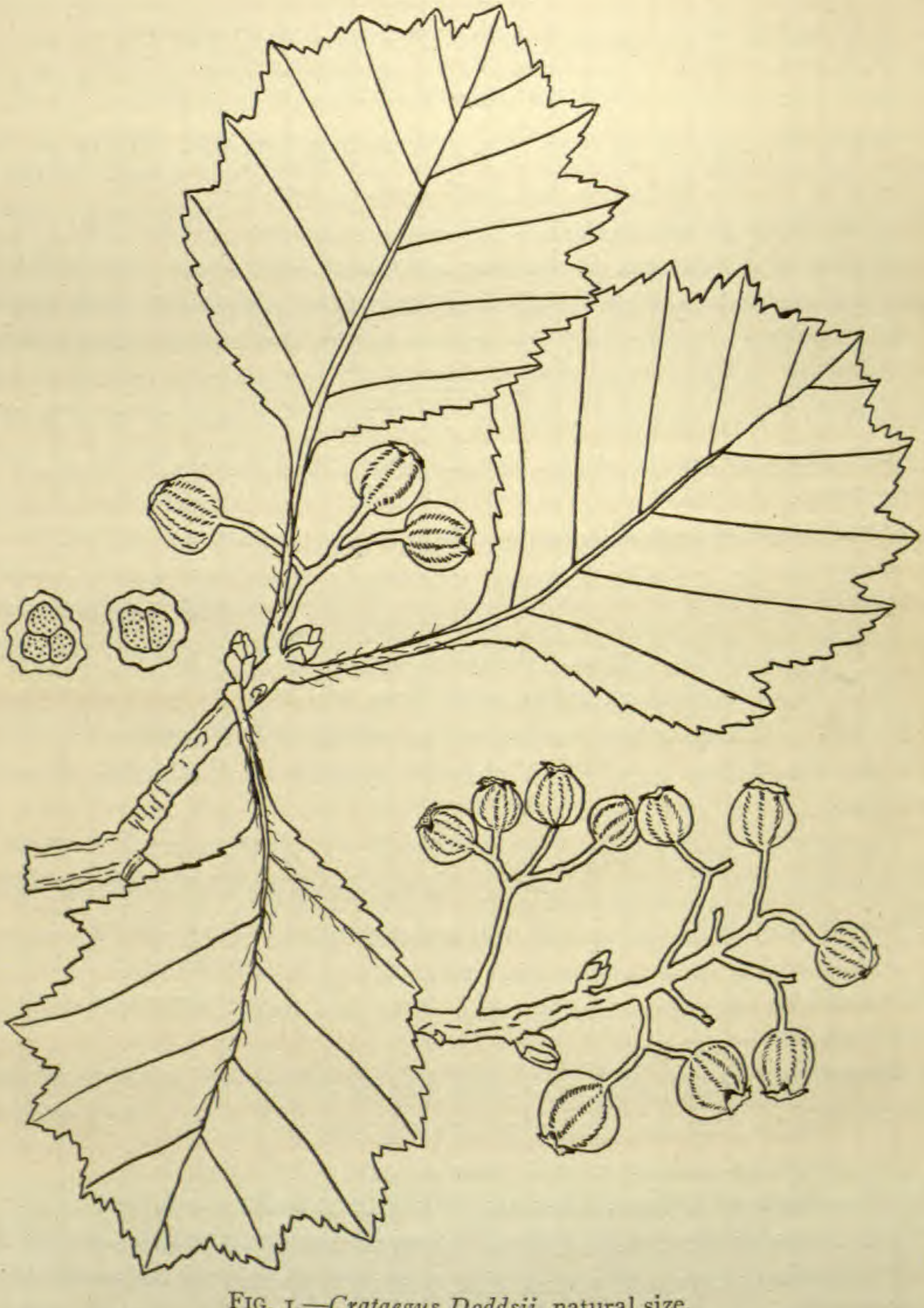

FIG. 1.—*Crataegus Doddsii*, natural size.

This species is nearest related to *C. erythropoda*, from which it differs in having the anthers white (not pink), in having less shiny leaves, in the presence of more pronounced ridges in the fruit, and in the lighter color of the fruit (that of *C. erythropoda* is mahogany brown).

Type specimen: *Ramaley* and *Dodds* 6181, Pole Canyon near Boulder, Colorado, Sept. 19, 1908. Type in University of Colorado Herbarium; cotype in Rocky Mountain Herbarium, Laramie, Wyoming. Material is at hand from various localities in Boulder County, 5000–8000ft altitude.

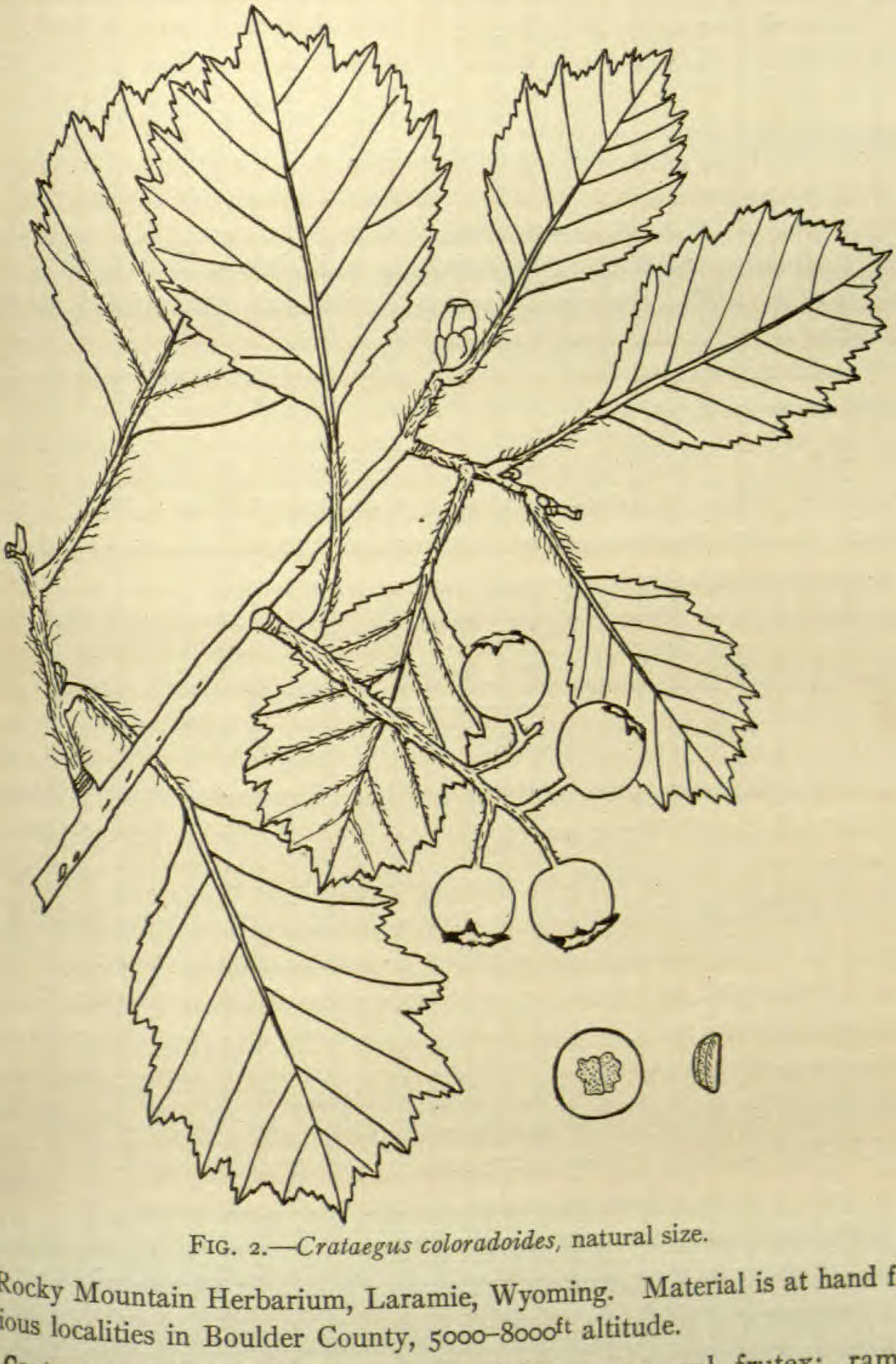

FIG. 2.—*Crataegus coloradoides,* natural size.

Crataegus coloradoides, sp. nov.—*Arbor* parva, vel frutex: ramulis junioribus pubescentibus; ramis spinescentibus. *Folia* supra cyaneo-virida, lucidula, infra glauca; obovata; margine serrata et parve lobata;

nerviis infra pubescentibus. *Petiolus* pubescens, longe $\frac{1}{3}$–$\frac{1}{2}$ laminae. *Flores* conspicui; corymbis compositis; pedicellis pubescentibus; staminibus 10 vel minus; antheris albis. *Fructus* autumno maturans; mollis, dulcis, ruber vel puniceus, globosus (9^{mm}), levis non costatus, cum pilis raris; nucellis osseis, 2–3.—*Fig. 2.*

Hab. in Colorado, U. S. A.

This species is nearest to *C. occidentalis* Britt., but has much longer petioles, smaller, shiny leaves, not dull, somewhat smaller fruit, which is globose, not broader than long as in *C. occidentalis.* The tree is also less gnarled and there are no persistent bud-scales at flowering time.

Type specimen: *Ramaley* and *Dodds* 6184, Pole Canyon near Boulder, Colorado, Sept. 19, 1908. Type in University of Colorado Herbarium; cotype in Rocky Mountain Herbarium at Laramie, Wyoming.

The species grows in gulches in the lower foothills from 5500 to 7000^{ft} altitude; mostly about 6000^{ft}.

It may be of interest to students of Crataegus to point out that the fluting of the fruits, as in *C. Doddsii,* is a character which has apparently not been used by other observers. In alcoholic material and in well-dried specimens this character is very noticeable. Attention is called to the cross-section of the fruit shown in the drawing (*fig. 1*).—FRANCIS RAMALEY, *University of Colorado, Boulder, Colorado.*

SEXUAL CONDITION IN FEGATELLA

Until the last few years, nothing has been known in regard to the sexual differentiation in the sporophytic stage of dioecious bryophytes. In connection with a discussion of the germination of the zygotes of certain dioecious molds, the writer[1] first pointed out this lack of knowledge on the subject and raised the question whether a capsule of a dioecious bryophyte contains both male and female spores or spores of but a single sex. The question so far has been settled by the writer[2] for the single hepatic *Marchantia polymorpha,* and by the MARCHALS[3] for the three mosses *Barbula unguiculata, Bryum argenteum,* and *Ceratodon purpureus.* In all these forms, as well as in the germinating mold Phycomyces, a single sporangium was found to contain both male and female spores as judged by the thalli they produced when sown in pure cultures.

The purpose of the present brief notice is to add the dioecious hepatic

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[1] Zygospore germinations in the Mucorineae. Annales Mycologici 4:25. 1906.

[2] Differentiation of sex in thallus, gametophyte, and sporophyte. BOT. GAZETTE 42:161–178. 1906.

[3] Recherches expérimentales sur la sexualité des spores chez les Mousses dioïques. Mém. couronnés Cl. Sc. Ac. Roy. Belgique 2^{1}:1–50. 1906.

Fegatella conica to the list of bryophytes already investigated, and to give increased weight to the opinion that the type of sexual differentiation in the forms so far studied is at least the predominant if not the universal type among the bryophytes.

April 22, 1906, Fegatella was found by the writer abundantly fruiting in the large pot holes in the Gletschergarten at Lucerne. The capsules for the most part were not yet opened. Two days later, in the Botanical Laboratory at Halle, unopened sporangia were carefully dissected out, and after a microscopic examination to make certain that no spores from other sporangia had adhered to their outer surfaces, they were preserved separately in small sterile paper envelopes. Spores from one of these single sporangia were sown May 10 in several Petri dishes in 0.1 per cent. Knop's solution. By June 19, the germinations from the spores had grown to sufficient size to be readily handled, and accordingly 128 from a single Petri-dish culture were transplanted to earth in regular rows in large shallow pots. They had reached a considerable size but were not sufficiently matured to produce their sexual organs when it became necessary in the latter part of July to leave them in the care of the *Diener* of the laboratory. The coming November a number of the plants were shipped to the writer packed in parchment paper with damp sphagnum moss. Fegatella does not multiply non-sexually by gemmae as does Marchantia, and there is practically no danger of infection in the earth cultures from thalli of the same species. Of the plants shipped, twelve survived the two weeks' journey and were sown in separate pots in the Harvard Botanic Gardens, where they have since been kept growing. Three of the cultures by the character of the sexual organs produced have shown themselves to be female and eight to be male. A single capsule of Fegatella, therefore, contains both male and female unisexual spores. The other cells of the sporophyte, undoubtedly, are hermaphroditic in character, although attempts to demonstrate this by regenerations from the stalk or wall of the sporangia were entire failures. One of the twelve pots, presumably with only the growth from a single spore, showed both antheridia and archegonia, but it was not possible to find that the lobes producing these different sexual organs were connected. It is possible that the differentiation of sex is not always complete in the capsule of Fegatella, and that hermaphroditic spores are in fact occasionally produced, as is the case in the mold Phycomyces; but it seems more likely that a fragment of a thallus of the other sex became accidentally mixed with the growth planted in this particular pot.—A. F. BLAKESLEE, *Connecticut Agricultural College, Storrs, Conn.*

A NEW CHARACTERISTIC OF ENGELMANN SPRUCE

In 1907 near Bernice, Mont., the writer observed a specimen of Engelmann spruce (*Picea Engelmanni* Engelm.) with resin vesicles in the bark, which are so typical of the genus Abies. They are not mentioned in any of the descriptions of Engelmann spruce, and the character appears to have been entirely overlooked by botanists. It is therefore desired to direct attention to this noteworthy feature and place it on record. Since 1907 it has been observed at several places in Colorado, and is probably found everywhere on this species of spruce. The vesicles or "blisters" are not so abundant or conspicuous as in the genus Abies. In a few instances they were found to be well developed and closely resembled the balsam blisters. Commonly, even when of large size, they were rendered obscure by being deeper in the bark.

The only genus besides Abies previously described as having these vesicles is Pseudotsuga, in which they are less conspicuous than in Abies. To these two genera must now be added at least one species of the genus Picea, which shows this common character in many individuals, though it is rarely prominent.—E. R. HODSON, *Washington, D. C.*

CURRENT LITERATURE

BOOK REVIEWS

The Wiesner Festschrift

As a testimonial of esteem and affection, the friends and pupils of Julius Wiesner, the distinguished director of the plant-physiological institute of the University of Vienna, prepared for his seventieth birthday (January 20, 1908) a volume[1] containing more than forty papers, which are of course predominantly physiological. Only one is from this country: Trelease gives an account of variegation in the Agaveae, with many illustrations. It is only possible to give an idea of the scientific contents by stating most briefly the drift of each paper.

Tschirch opens the volume with a brief sketch of some ideas on the relationships and origins of the resins and gums, as to whose chemistry light is breaking. Molisch shows that *Xylaria Hypoxylon*, *X. Cookei*, *Trametes Pini*, *Polyporus sulfureus*, and *Collybia cirrhata* are to be stricken from the list of luminous fungi. Strasburger discusses nuclear division in the Characeae, with special reference to the so-called amitosis, which he holds is not a senile process. Von Hohnel and Litschauer present a synopsis of Austrian Corticeae, including 131 species, of which 5 are new. Möbius figures and describes the siliceous accretions in the stem and leaf cells of the tropical American *Callisia repens* (Commelinaceae). Czapek discusses the relation of geotropism to certain features of plant form, especially to the position of branches both of stems and roots. Burgerstein gives a synoptical key to the genera of Coniferae, based on the anatomical characters of the wood. Von Portheim and Samec report less dissimilation ("respiration") in seedlings of pea grown in Ca-free solutions than in those grown in Knop's solution. Darwin shows by various methods that the perceptive region for gravity and light is in the cotyledon of Sorghum, thus disposing of objections that have been raised to this view.

Hanausek gives a further account of the "carbon-layer" of the pericarp of certain Compositae. Goebel finds the relations of symmetry in a considerable number of flowers and inflorescences examined to be explicable neither by pressure nor purpose, but rather by "nutritive relations" (not more exactly analyzed). Richter declares (on results derived from the usual but inconclusive culture methods) that calcium is a necessary food element for a colorless diatom, probably *Nitschia putrida*. Senft demonstrates the occurrence of physcion and parietin in lichens, and the methods of recognizing them microchemically.

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[1] Wiesner-Festschrift. Ed. by K. Linsbauer. 8vo. pp. viii+548. *pls.* 23. *figs.* 56. Wien: Verlagsbuchhandlung Carl Konegen. 1908. *Kr.* 24, geb. 28.80.

Ambronn indicates the chemical and physical alterations which the cellulose of textile fibers undergoes when impregnated with zinc sulfid. Nestler has extended MacDougal's studies on the skin poison of *Cypripedium spectabile* secreted by the glandular hairs. Němec writes briefly on his experiments upon regeneration with the roots of Taraxacum. Stoklasa declares unequivocally that in anaerobic and in aerobic respiration the formation of lactic acid, alcohol, and CO_2 (and in addition acetic and formic acids in aerobic respiration) is due solely to enzymes. Kammerer describes a case of symbiosis between *Oedogonium undulatum* and aquatic larvae of *Aeschna cyanea*. Grafe furnishes an appropriate study of the gum-ferment whose action Wiesner first correctly described.

Heinricher adds to his two previous papers on the effect of light upon germination of seeds a general discussion of the subject, with some new experiments and a valuable summary. Mikosch finds that the scion of Epiphyllum grafted upon Peireskia as a stock, exercises a definite effect in giving rise in its cells to the bodies peculiar to Epiphyllum. Figdor reports exact determinations of the phototropic sensitiveness of certain plants in relation to the zone of indifference (which seems not to exist in some). Koorders again describes and figures his Javanese genus *Wiesneromyces*. Zikes has a further account of his *Bacterium polychromicum* and its pigment production. Von Wettstein observed a saltatory rise of the fertility (at first small or none) of the pollen in two undoubted bastards of Sempervivum, and suggests that here may be an important factor in the origin of new forms. Von Weinzirl contributes data on the mechanical functions of the various organs of the embryo of cereals in their escape from investing structures. K. Linsbauer reports propagation of the excitation in the primary petiole of Mimosa at a rate of $100^{\text{mm-sec}}$, and a reaction time averaging 0.09 to 0.35^{sec}, with minimum 0.07 and maximum 0.80^{sec}.

Fritsch describes cystoliths of *Klugia zeylanica*. Raciborski recognizes in *Coreopsis tinctoria prolifica* "an undoubted mutation." L. Linsbauer gives an account of "photochemical induction" in the formation of anthocyan in the etiolated seedlings of buckwheat. Krasser makes a critical synopsis of the lower Lias flora of the Austrian Alps. Schiffner presents an ecological study of so-called *Knieholzwiesen* of the Iser Mountains. Wegschneider states that the fats are really saponified by stages and the reaction is only apparently bimolecular. Skraup writes briefly on the leucin of proteins. Strohmer gives an account of the accumulation and migration of saccharose in the sugar beet. Karzel shows some interesting peculiarities in the lignification and cutinization of the walls of the stomata in cycads. Przibram notes the renewed growth from stumps of red wood, familiar to Californians. Wilhelm figures a remarkable distortion of the tips of a fir. Lopriore writes on twin-roots in Zea and Vicia.

Besides the papers listed, there are several on more general topics, historical or philosophical, that are omitted for lack of space. The volume is a worthy memorial and gives evidence of the inspirational force of a great investigator.—C. R. B.

MINOR NOTICES

Botany and Pharmacognosy.—A third edition of KRAEMER'S *Textbook*[2] has appeared with great promptness after the publication of the second.[3] The changes made have to do chiefly with the illustrations, fifty unsatisfactory half-tones being replaced by line drawings, and several new illustrations being introduced, especially of solanaceous drugs and plants.—J. M. C.

NOTES FOR STUDENTS

Chlorophyll and assimilation.—LUBIMENKO, who has been devoting his attention to the influence of light upon various processes, has endeavored to solve these questions: Is the intensity most favorable for the decomposition of H_2CO_3 likewise the most favorable for the production of dry matter? What is the optimum illumination which will produce the most dry matter in different green plants? How is this optimum related to the various quantity of chlorophyll in the leaves? He reports[4] that the production of dry matter is determined by the light energy absorbed, which in turn varies with the illumination and the quantity of chlorophyll in the leaves. The latter is not constant, but varies with the illumination. In nature the minimal quantity of chlorophyll in all species studied corresponds to the normal daylight undiminished. As the light is weakened the quantity is rapidly increased until it attains a maximum; then it diminishes with still weaker light. In any species the maximum is reached with weaker light as the temperature rises. As to this matter, two classes of plants may be distinguished: those that produce little chlorophyll, whatever the external conditions, and those that accumulate a good deal. In the former the quantitative variations in chlorophyll due to illumination and temperature are smaller than in the latter, which also for the production of a maximum quantity require a more feeble light than the former. In general the maximum of pigment corresponds to a light sensibly weaker than that required for a maximal production of dry matter. From which it would appear that light, as inferred for other reasons, has a special action in the formation of chlorophyll.

The production of dry matter increases with the light absorbed, up to a maximum, then diminishes. This optimal light is constant with the same species at constant temperature, but diminishes as the latter increases. [This indicates that the energy optimum is a constant.] The optimal intensity for the production of dry matter varies according to the quantity of chlorophyll, augmenting as the pigment diminishes, and *vice versa*. In nature the maximal production in plants poor in chlorophyll corresponds to the normal daylight, but in those

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[2] KRAEMER, HENRY, A textbook of botany and pharmacognosy. Third edition. pp. viii+850. *figs. 328*. Philadelphia and London: J. B. Lippincott Co. 1908.

[3] Reviewed in BOT. GAZETTE 46:231. 1908.

[4] LUBIMENKO, W., Production de la substance sèche et de la chlorophylle chez les végétaux supérieures aux différents intensités lumineuses. Ann. Sci. Nat. Bot. IX. 7:321–415. 1908.

rich in pigment it corresponds to a greatly weakened light. In general the development of the plant is proportional to the dry matter produced; but growth is not exactly proportional thereto, for it is more feeble in strong light and more vigorous in weak light than it would seem if it were measured by the augmentation of the dry weight. The root and stem are unequally affected; the former grows more and the latter less as the illumination increases; but too strong a light reduces the rate of growth of both because less food is produced. The development of the leaf blades generally increases to a maximum with decreasing light, but diminishes with further enfeeblement. With some exceptions transpiration does not have any sensible effect on the total production of dry matter, though the quantity in proportion to the fresh weight generally diminishes with the diminished light.

All the green plants are capable of regulating the quantity of light absorbed, and so partly avoiding the injurious effect on production of dry matter, by altering the quantity of chlorophyll produced. These adaptations are limited in plants poor in chlorophyll; but those rich in pigment can adjust themselves to a relatively very weak illumination. Biologically the massing of plants ought to be an advantage by reducing the illumination. Physiologically the action of light is not limited to the reduction of H_2CO_3, for it affects also the speed of incorporation [assimilation] of carbohydrates. The former demands a stronger light than the latter, for which there is an optimum, and below and above this it rapidly diminishes in rate. It is by this retarding action of bright light upon the incorporation of carbohydrates and a consequent considerable accumulation of foods in the green tissues that the diminution in the production of dry matter is explicable when the illumination passes a certain limit. [This explanation does not explain and surely needs further consideration.] If the chemical transformations which constitute the incorporation of carbohydrates are of enzymic nature, it is probable that they are affected by the action of light on the formation and destruction of enzymes. [Is not the fate of the greater part of the carbohydrates to be sought rather in protein synthesis than in "incorporation;" and is there any evidence of enzymic action in this process?]—C. R. B.

Self-digestion and endospermic respiration.—The long effort to settle the question of the vitality of the endosperm, which was begun by GRIS and VAN TIEGHEM, was practically abandoned after the culminating researches of BROWN and ESCOMBE, PURIEWITSCH, and BROWN and MORRIS. Since that time very little indeed has been contributed to the subject. Perhaps one reason was that the results of somewhat related investigations so modified our knowledge of enzymes and respiration that self-digestion as a test of vitality was no longer regarded as valid. Altogether disregarding such opinions, BRUSCHI[5] takes up the problem practically as it was first attractive fifty years ago, "to solve the

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[5] BRUSCHI, DIANA, Researches on the vitality and self-digestion of the endosperm of some Graminaceae. Annals of Botany **22**:449–463. 1908.

question whether the reserve material contained in the endosperm of amyliferous seeds is exclusively digested by enzymes secreted during germination, or whether the endosperm cells renew their vital activity and themselves dissolve their own food material."

The endosperms of maize, wheat, rye, and barley were tested. The seeds were allowed to soak 48 hours before removal of the embryo and scutellum in some instances, and in the other tests no statement is made on this point. No controls are mentioned; in fact the experimental data are so meager that the reader is compelled to reject the results simply because the author leaves him too ignorant to judge. In the digestion tests no controls are mentioned. The simple statement that aseptic conditions were maintained is altogether insufficient. We read that chloroform water was used, but whether it was saturated or half saturated or something else the reader cannot know. The general trend of the conclusions is that all of the endosperms mentioned are more or less capable of self-digestion, and that such activity is independent of vitality. The endosperm of rye is pronounced dead, but in maize, barley, and wheat there is more or less vitality in some of the amyliferous cells.

STOWARD[6] has found that the pure endosperms of Hordeum and Zea under appropriate conditions manifest a gaseous exchange of respiratory character. He also regards similar behavior on the part of the aleurone layer as strengthening the evidence that the cells of that tissue possess vitality. The paper is presumably an initial effort, because (*a*) the introduction as such is unnecessarily tedious, and as a digest of the literature is deficient in so far as a judicial analysis is concerned, and is not as comprehensive as others already published; (*b*) after about ten pages of tabulated data a new subject is at once begun with no discussion or consideration of the significance of the experimental results recorded. This *pot-pourri* style of composition is more or less reflected in the impression one receives of the author's tendency to think of several matters without analysis and correlation. On the other hand, all the experimental procedure is very carefully described and the reader can analyze the results. In spite of the fact that the respiration tubes were "tarred" instead of tared, one is inclined to accept the results as reliable and the conclusions as sound.—RAYMOND H. POND.

Plant diseases.—The last annual report (21st) of the Agricultural Experiment Station of the University of Nebraska, issued January 29, 1908, contains the following papers of interest in reference to plant diseases.

POOL[7] discusses several diseases of tomatoes. Black rot, due to *Alternaria fasciculata* (C. & E.) Jones & Grout, occurs on the ripe fruit at the blossom end. The cavities within the diseased tissue are lined with the fluffy mycelium of the fungus. It was isolated and inoculations were made upon both ripe and green

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[6] STOWARD, FREDERICK, On endospermic respiration in certain seeds. Annals of Botany **22**:415–448. 1908.

[7] POOL, V. W., Some tomato fruit rots during 1907.

fruit. Five days after inoculation the rotted area of the ripe fruit was 1.2^{cm} in diameter. No infection occurred in the green fruit. Culture characteristics are discussed. Rhizoctonia on the tomato is also discussed, the disease being marked by a chocolate-colored, wrinkled epidermis. The fungus penetrates the cells in all directions, and no conidia are formed. It was isolated and tomatoes were inoculated, resulting in their complete decay in two weeks, both ripe and green fruit. The ripe rot due to *Colletotrichum lycopersici* was studied. The fungus was isolated and inoculations were made, producing four days after infection a diseased area 0.6^{cm} in diameter on either ripe or green fruit. Fusarium of undetermined species and also *F. Solani* Mart. were isolated, used in inoculations, and the culture characters determined.

Miss WALKER[8] discusses and describes a form of Sphaeropsis differing from the ordinary form principally in the size of the spore, the size and thickness of pycnidium, and the absence of the ostiole. The new form seems to be more vigorous as a rot-producer that the old one. Inoculated into apples in every case it produced the characteristic black rot. The author suggests that possibly the variation in size of the spore may be due to the nature of the fruit upon which it is growing.

HEALD[9] briefly describes the various types of barley smuts, with notes on experiments as to the best mode of treatment for their prevention. The following treatments were used: formalin steep, modified formalin steep, hot water treatment, corrosive sublimate steep, copper sulfate steep. The percentage of germination was lessened by all the treatments except the hot water, being reduced 40 per cent. by formalin 1/10, and 70 per cent. by 1/15. The author recommends as the formalin steep one pint to 20–25 gallons of water.

WOLF[10] found *Pestalozzia uvicola* on ripe grapes. It was isolated in pure culture and inoculations made upon the grape, resulting in numerous pustules after proper incubation period. Sections of these pustules showed the characteristic spore, but, contrary to the usual mode of Pestalozzia, the spores were borne in what the author regards as well-defined pycnidia, which structure would be entirely out of accord with the genus or with any of the Melanconiaceae. It is unfortunate that the drawing (p. 71) leads one to infer that the spores are not borne in the true pycnidium, as the author describes, but rather in the cavity resulting from hypertrophy of the surrounding host tissues.—F. L. STEVENS.

Mold of maple syrup.—This mold, frequently observed during the past few years, has been ascertained by HEALD and POOL[11] to be *Torula saccharina* and was grown in pure culture on media of varying composition. They conclude that the concentration of the sugar solution in which the fungus was growing

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[8] WALKER, LEVA BELL, A new form of Sphaeropsis on apples.

[9] HEALD, F. D., Seed treatment for the smuts of winter barley.

[10] WOLF, F. A., A rot of grapes due to *Pestalozzia uvicola* Spegaz.

[11] HEALD, F. D., AND POOL, V. W., The mold of maple syrup. 21st Ann. Rep. Univ. Neb. Agric. Exp. Sta. 54. 1908.

had little effect on the size of the spores or hyphae; and that ammonium nitrate can be used to a limited extent as a source of nitrogen, but that it is rather poorer than ammonium tartrate.—F. L. STEVENS.

The vegetative activity of chromatin.—DERSCHAU'S[12] results and theoretical views on the vegetative activity of chromatin are interesting. Many granular chromatin substances thrown out of the nucleus into the cytoplasm increase in size, assume spherical forms, and then, becoming oriented at the poles of spindle figure, function as centrosomes. This is regarded as the vegetative activity of the chromatin. His studies cover several forms of higher vascular plants, such as *Fritillaria imperialis*, *Iris germanica*, *Vicia Faba*, *Lilium Martagon*, *Funkia sieboldiana*, and *Osmunda regalis*. From his investigation of the pollen mother cell and meristematic tissue of these forms, he concludes that there exist central bodies in the mitotic figure of the fern and flowering plants which are of nuclear origin and are analogous to blepharophlasts.

The following is a brief summary of his account. In very young mother cells of Lilium, Funkia, and Osmunda, chromatin is observed escaping from the nucleus in various spots. Outside the nucleus the chromatin substances increase in size and assume spherical forms. The spherical chromatin substances refract light and close examination of them seems to show a reticulated structure. With stains they react like chromatin and linin. While the chromatin is escaping the nucleolus remains within, which shows that the substances thrown out are not nucleolar. In late prophase the spherical chromatin or "Sphaere" seems loosened and differentiated into two structures, one the center and the other a single heavy beaded fiber. Some of these centers make their way toward the *Hautschicht* during a later phase of mitosis and furnish the anchoring-place for the spindle; some lie scattered in the cytoplasm; and still others remain near the nuclear periphery. To each of these centers there is attached a single heavy beaded fiber, from which there seem to be spun out fine spindle fibers. Generally the spindle figures start as multipolar polyarch, then become bipolar, but remain in the polyarch condition until telophase; and therefore several centers persist without fusion at each pole, each spindle cone being associated with a single center. In rare cases some of these centers fuse together to form a kinoplasmic plate, which is connected by beaded heavy fibers with other centers that remain separate. In telophase the central and mantle spindles again take on a beaded structure. The centers and fibers, instead of entering into the constitution of the organizing daughter nucleus, remain in the cytoplasm and undergo certain changes in the structure. These centers at the pole of the spindle, DERSCHAU thinks, control the mechanism of mitosis. He states further that the centers may be structures allied to the blepharophlast, and are to be regarded as analogous with it, if not homologous; both lie near the nucleus, increase in volume, and mark the starting-point of fibers—one of cilia and the other of spindle fibers.—SHIGÉO YAMANOUCHI.

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[12] DERSCHAU, M. v., Beiträge zur pflanzlichen Mitose, Centren, Blepharophlasten. Jahrb. Wiss. Bot. 46:103–118. *pl. 6.* 1908.

Cytology of Ascomycetes.—Miss FRASER and Miss WELSFORD have recently added another contribution[13] to their important series on the cytology of the Ascomycetes. The present investigation deals with two additional Discomycetes—*Otidea aurantia* and *Peziza vesiculosa.* The authors have studied principally the triple reducing divisions in the ascus, and their observations accord in the main with those of HARPER on Phyllactinia. They find in these two species, however, intermediate conditions between the early pairing of the chromosomes in Phyllactinia and their complete independence during the stages preceding reduction in Humaria, as described in an earlier paper by Dr. FRASER. In Otidea, for example, the chromosomes do not pair till the prophases of the third (or brachymeiotic) division; whereas in *Peziza vesiculosa* they unite during the prophases of the second division in the ascus. This variation in the time of chromosome union, as described for these species, is compared in tabular form with the conditions which obtain in Humaria, Galactinia, and Phyllactinia.

The authors describe two phases of the reduction processes—the meiotic phase, embracing the first and second divisions in the ascus, distinguished in Otidea by four chromosomes and in *Peziza vesiculosa* by eight chromosomes; and brachymeiosis, involving the second reduction, when the two sets of post-meiotic chromosomes become separated during the third division, thus resulting in two chromosomes in Otidea, and four in Peziza. A definite synaptic contraction occurs in connection with meiosis, similar to that first described by HARPER in Phyllactinia; but, unlike the case in Phyllactinia and in Humaria, a second contraction takes place in the two forms studied at the beginning of brachymeiosis. The authors regard the presence of both meiosis and brachymeiosis as evidence of the occurrence of two fusions in the life-history of these forms; although in neither form were the first, "presumably pseudapagamous," fusions found. Further confirmation of HARPER's account of spore-formation is presented in that the authors find the spores delimited by the astral radiations. But they incline to the view that the rays represent, not active contractile fibers, but rather the paths of activity of an enzyme which is generated at the centrosome and which flows out equally all around the center, delimiting the spore by the chemical changes thus produced.—E. W. OLIVE.

Mitosis in Funkia.—An account of nuclear division in Funkia is given by Miss SYKES in two short papers,[14] one dealing with the reduction division in the pollen mother cell, and the other with the somatic division as it occurs in the archesporial cells and in the ovary wall.

The results may be summarized as follows: (1) The nuclear reticulum in

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[13] FRASER, H. C. I. AND WELSFORD, E. J., Further contributions to the cytology of the Ascomycetes. Annals of Botany 22:465–477. *pls. 26, 27.* 1908.

[14] SYKES, M. G., Nuclear division in Funkia. Archiv für Zellforschung 1:380–398. *pls. 8, 9. fig. 1.* 1908.

———, Note on the number of the somatic chromosomes. *Idem* 1:525–527. *pl. 16.* 1908.

the resting stages of the mother cell is composed of a number of knots connected by filaments. The pairing of the reticulum appears at a very early stage. The number of pairs of knots, though it is impossible to make an accurate count, far exceeds the number of pairs of chromosomes. She concludes that in Funkia it is inadvisable to call the knots prochromosomes. (2) Occasional contact between the pairs of knots is observed in synapsis, but they do not constitute clear cases of fusion. (3) The double thread is formed from the reticulum during synapsis due to the paired arrangement of the constituents of the nucleus. (4) The double thread fuses into a single spirem, but at the time of segmentation into chromosomes it splits along the line of fusion (thus an element of each bivalent chromosome is not one-half resulting from the division of a single spirem, but an entire piece of the double thread which fused to form a single spirem). (5) Heterotypic division of chromosomes takes place along this fission, so that there is a true reduction division. (6) In each of the daughter chromosomes a new second split occurs longitudinally. (7) The reticulum and knots in the nucleus of the pollen grain are unpaired throughout, but a double structure is found in the prophase of the somatic nucleus. (8) The number of chromosomes in the somatic nucleus of *Funkia ovata* and *F. sieboldiana* seems to vary from 36 to 48, probably is 48, the reduced number being near 24.—S. YAMANOUCHI.

Fossil Osmundaceae.—KIDSTON and GWYNNE-VAUGHAN have recently published a second contribution[15] on the extinct Osmundaceae, which deals anatomically with two species of a new genus (*Zalesskya*) from the Permian of the Ural. *Z. gracilis* and *Z. diploxylon* are characterized by a central cylinder, which the authors infer to be protostelic from the manner of exit of the leaf traces. Unfortunately in one species the center of the fibrovascular tissues of the stem has disappeared through maceration, correlated with fossilization, and in the other by the crumbling away of the stony matrix. The authors admit that the general anatomy of the fossils is not distinctively osmundaceous. They place great diagnostic importance in this connection, however, on the minute structure of the xylem tracheids, which are characterized by multiseriate pits and vessel-like perforations of the pit membranes of the terminal walls. The authors seem to attach a somewhat exaggerated importance to these features, however, since both have long been known to occur in ferns not related to the Osmundaceae. They infer that their fossils make it "clear *that the central ground tissue of the recent Osmundaceae must be regarded as phylogenetically derived by modification from the central xylem of a solid* (sic) *protostele and that primitively it had no relation with the cortex whatever.*" This statement appears to have scarcely a better basis in logic or fact than their contention in the first article that foliar gaps are primitively absent in the Osmundaceae. Even if it be admitted that the authors' species are osmundaceous, which is very far from being certain, the conclusion reached appears hardly in accordance with sound reasoning. The

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[15] KIDSTON, R., AND GWYNNE-VAUGHAN, D. T., On the fossil Osmundaceae. II. Trans. Roy. Soc. Edinburgh 46^{2}: 213–232. *pls. 1–4.* 1908.

fact that a protostelic genus Lygodium occurs among the living Schizaeaceae, throws no light on the morphological nature of the pith in the central cylinder of the other schizaeaceous genera Schizaea, Aneimia, and Mohria.—E. C. JEFFREY.

Mitosis in Cynomorium.—BACCARINI[16] has published an account of vegetative mitosis in *Cynomorium coccineum* (Balanophoraceae). From a study of the nucleus in meristem of the roots and in parenchyma of the stem, he finds the following stages: (1) *Prophase:* (*a*) chromatin granules are uniformly distributed throughout the fundamental mass of the nucleus, with or without still larger chromatin knots or joints, the chromocenters; (*b*) the chromatic granules, separating from the faintly staining fundamental mass of the nucleus, aggregate gradually into a distinct number of larger masses, the chromocenters; (*c*) these chromocenters unite to form larger masses, more compact and lengthened, which constitute the prochromosomes; (*d*) some prochromosomes fuse together by their ends into a chain, which finally results in filaments of the spirem; the spirem by this time is homogeneous in structure, but it is uncertain whether it is a single continuous thread; (*e*) the filaments of the spirem segment into a definite number of chromosomes, which seem to be more numerous than the prochromosomes. (2) *Metaphase:* The chromosomes become arranged in the equatorial plate, where they divide and the daughter chromosomes separate. (3) *Anaphase:* The chromosomes accumulate in a convergent bundle at the pole. (4) *Telophase:* The chromosomes dissolve and form the fundamental nuclear mass with its chromatin granules.—SHIGÉO YAMANOUCHI.

Riella.—In the twelfth of the *Archegoniatienstudien*, which he announces to be the last, so far at least as concerns the liverworts, GOEBEL describes the brood buds of *Riella helicophylla*, *R. cossoniana*, and *R. Battandieri.*[17] These organs were first found by UNDERWOOD and HOWE in *R. americana*, and have not yet been observed in *R. Clausonis.* They consist of an unequally two-lobed disk attached by a single stalk cell somewhat excentrically placed on the upper surface. GOEBEL holds these gemmae to be "modified slime papillae," as in Marchantia, an effort at homologizing which seems to us strained. The smaller lobe is loaded with food and therefore heavier; so the gemma sinks in the water with this end down and from it rhizoids arise. The larger lobe, which he calls the germ disk, grows, and especially the meristematic tissue between the two, parting them by a rather long stalk. From the germ disk two plants are produced directly when well nourished, and otherwise one indirectly, that is, only after proliferation of the germ disk. GOEBEL also discusses the systematic position of the genus, concluding on rather doubtful grounds, it seems, that it should

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[16] BACCARINI, P., Sulle cinesi vegétative del *Cynomorium coccineum* L. Nuovo Giorn. Bot. Ital. **15**:189–203. *pl.* 7. 1 08.

[17] GOEBEL, K., Archegoniatenstudien. XII. Ueber die Brutknospenbildung und über die systematische Stellung von Riella. Flora **98**:308–323. *figs.* 11. 1908.

form a fourth family of the order Marchantiales: Ricciaceae, Corsiniaceae, Riellaceae, Marchantiaceae, rather than be placed as an aberrant family in the Jungermanniales anacrogynae.—C. R. B.

Cleistogamy.—The examination of a large number of cleistogamous flowers of monocotyls and dicotyls showed HELENE RITZEROW[18] that all are reductions from the chasmogamous forms, and that the reductions follow a definite direction determined by the normal development of the chasmogamous form. The mode of reduction in the various floral parts is described in detail. The pollen grains of many forms germinate within the anther, the pollen tubes emerging in various ways. Chasmogamous flowers are generally so situated upon the plant that they receive better nourishment than the cleistomagous. So many forms are described that the work will be good for reference.

TUZSON[19] has observed for six years two trees of *Robinia Pseudo-Acacia*, 30 to 40 years old, and has found them producing only cleistogamous flowers. Adventitious shoots, six years old, from these trees also produce only cleistogamous flowers. The author believes that in this case the cleistogamy is entirely independent of external conditions and due rather to inner causes.—CHARLES J. CHAMBERLAIN.

Fossil polar plants.—NATHORST,[20] in connection with the publication of the results of the Russian Polar Expedition of 1900–1903, has given an account of the Triassic and Jurassic plants from the Island of Kotelny. Schizoneura is the only Triassic plant. Among the most interesting Jurassic remains are the leaves and cone scales of a pinelike conifer. As the affinity of these is not absolutely certain in the absence of structural evidence, they are denominated Pityophyllum and Pityolepis respectively. The scales present a remarkable appearance, for broadening from the base they narrow abruptly to an isthmus about the middle, to expand again at their upper ends. The question naturally suggests itself, whether the upper region does not correspond to the apophysis of modern pines. The reviewer has found somewhat similar cone scales in the Lower Cretaceous. The author takes occasion to criticize the erroneous reference of probable pine needles to the problematical Jurassic genus Cyclopitys (Sciadopitys). The latter he does not consider to form properly an element of the flora of the Mesozoic as it occurs in the northern hemisphere.—E. C. JEFFREY.

Phylogeny of Archegoniatae and Characeae.—SCHENCK[21] regards the bryophytes, pteridophytes, and Characeae as unrelated groups, the first two having

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[18] RITZEROW, HELENE, Ueber Bau und Befruchtung kleistogamer Blüthen. Flora **98**:163–212. *figs. 36.* 1907.

[19] TUZSON, JOHANN, Ueber einen neuen Fall der Kleistogamie. Bot. Jahrb. Systematik, Pflanzengeschichte, und Pflanzengeographie **40**:1–14. *pls. 1, 2.* 1907.

[20] NATHORST, A. G., Mém. Acad. Imp. Sci. St. Petersbourg VIII. **21**: no. 2. 1907.

[21] SCHENCK, HEINRICH, Ueber die Phylogenie der Archegoniaten und Characeen. Engler's Bot. Jarhb. **42**:1–37. 1908.

come from the brown algae, and even the Characeae showing more resemblance to the brown algae than to other green algae. The origin of antheridia and archegonia from a plurilocular sporangium is developed along the lines already presented by DAVIS and HOLFERTY. To some of us, it would seem better to derive antheridia and archegonia from plurilocular sporangia of some hypothetical green alga than to refer them directly to the plurilocular sporangia of brown algae. The spore mother cells of archegoniates are compared with the unilocular sporangia of the brown algae, and the sporophyte of archegoniates with the thallus of brown algae. SCHENCK does not believe the sporophyte of pteridophytes can be derived from that of bryophytes. Even the complicated antheridium of the Characeae is referred to the plurilocular sporangium of the brown algae.—CHARLES J. CHAMBERLAIN.

Translocation in green tissues.—RYWOSCH points out[22] that translocation must depend upon the concentration gradient from the peripheral cells to the vascular bundle. This gradient is due in part to the excess of food made in the cells best illuminated, and also to the fact that transpiration cooperates doubly, by reducing the amount of water and by determining the movement of water. Thus those cells next the bundle are first to receive the water supply and those nearer the periphery are driest. He shows that the emptying of leaf tissues is not simultaneous, peripheral ones being emptied first, and that the whole process is greatly retarded when transpiration is checked. [Yet it must not be forgotten that there are plants in which transpiration cannot be invoked as an aid to translocation, since it is practically non-existent for weeks or months at a stretch.] The concentration is also kept low in the inner cells by the making of starch in them. RYWOSCH also adds a note on the function of the starch sheath, holding that its character as a reserve is very doubtful.—C. R. B.

Hygroscopic living leaves.—HANNIG[23] reports what he says is the first recorded instance of the movement of living leaves produced by variations in the water-content of the cell walls. The leaves of various hardy species of Rhododendron rise and fall, roll and unroll, according as they are subject to freezing and thawing weather respectively, though the same movements may be produced by other conditions which reduce or increase the water-content of the cell walls. Turgor is not concerned, HANNIG says, because dead or live, narcotized or unnarcotized, leaves exhibit movements equal in extent and kind. HANNIG'S argument is not convincing, and it seems unlikely that this conclusion is sound. In fact, too little is known of the physics of water and cell contents under the conditions described to make it possible to state accurately the precise relations involved.—C. R. B.

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[22] RYWOSCH, S., Sur Stoffwanderung im Chlorophyllgewebe. Bot. Zeit. 66¹: 121–130. *figs. 2.* 1908.

[23] HANNIG, E., Ueber hygroskopische Bewegungen lebender Blätter bei Eintritt von Frost und Tauwetter. Ber. Deutsch. Bot. Gessells. **26a:**151–166. 1908.

Development of Ulva.—The development and conjugation of gametes and also the germination of the zygote are described by SCHILLER[24] for both living and fixed materials. Three kinds of gametes are found in Ulva and also in Enteromorpha: (1) *megagametes* or giant gametes, which do not conjugate and are incapable of development; (2) *parthenogametes*, of medium size, which germinate into normal plants without any conjugation; and (3) *microgametes*, which are smaller than the parthenogametes and which produce new plants only after conjugation. The relation between the nucleus and the protoplasmic mass in the various gametes is believed to be the reason for the differences in behavior.—CHARLES J. CHAMBERLAIN.

Paleobotanical technique.—The veteran and distinguished Swedish paleobotanist NATHORST has contributed remarkably to the technique as well as to the facts of that science. His most recent contribution to technique is in connection with the use of collodion impressions of the surface of fossil plants for microscopic study.[25] With the article are published photomicrographs made from such films, illustrating the structure of fossil fern sporangia, the epidermis of the leaves of ferns, and gymnosperms and angiosperms in a fossil condition. Even a Cupressinoxylon yields results with this method.—E. C. JEFFREY.

A Paleocene flora.—M. PIERRE MARTY of the Royal Belgian Museum of Natural History has published a memoir[26] on the Paleocene flora of Trieu de Leval. Perhaps the most interesting feature of this publication is the discussion of the phylogeny of the important genus Quercus, à propos of the new species *Dryophyllum levalense*. The latter has chestnut-like leaves and the author concludes that among the living oaks it has its nearest affinities in those ancestral forms persisting in India, Japan, and the East Indies. The flora as a whole, with the above exception, presents a marked resemblance to that at present existing in northern South America.—E. C. JEFFREY.

Algae and Fungi of Iowa.—BUCHANAN[27] has brought together in convenient form, with keys, a list of the algae reported from Iowa, based upon the study of numerous recent collections. The list includes 180 species, and the bibliography of "Iowa Algae" includes nine titles.

The same thing has been done for the Erysiphaceae of Iowa by ANDERSON,[28] including of course a complete list of hosts. The recognized species and varieties number 28, involving 35 synonymns; while the hosts reported number 187.—J. M. C.

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[24] SCHILLER, DR. JOSEF, Beiträge zur Kenntniss der Entwickelung der Gattung Ulva. Sitzungsb r. Kaiserl. Acad. Wiss. Wien 116:1–26. *pls. 1, 2.* 1907.

[25] NATHORST, A. G., Ueber die Anwendung von Kollodiumabdruecken bei der Untersuchung fossiler Pflanzen. Arkiv för Botanik 7:no. 4. 1907.

[26] MARTY, PIERRE, Mém. Musée Roy. d'Hist. Nat. Belgigique 5:1–51. 1908.

[27] BUCHANAN, ROBERT EARLE, Notes on the algae of Iowa. Proc. Iowa Acad. Sci. 14:pp. 40 (repaged). 1908.

[28] ANDERSON, J. P., Iowa Erysiphaceae. *Idem* 14:pp. 34 (repa ed). 1908.

Spermatogenesis in mosses.—The VAN LEEUWEN-REIJNVAANS add a few details to their former paper and announce their abandonment of this field of research,[29] after a brief excursion into it with rather startling results.[30] Now they report centrosomes in the antheridial cells of *Fegatella conica* (contrary to BOLLETER) and in *Pellia epiphylla* (contrary to IKENO). In Mnium (sp. ?) they find (as in Polytrichum) in the last division from 8 to 4 chromosomes, 2 long and 2 short, which is a transverse (not diagonal) reduction.—C. R. B.

Acorus Calamus.—This species was introduced into Europe in the middle of the sixteenth century, and it has always been known that the European plant produces no seeds. A study of the development of the pollen and embryo sac by MÜCKE[31] shows that both are so defective that the production of seeds is impossible. The reason for the sterility is supposed to be unfavorable climatic conditions.—CHARLES J. CHAMBERLAIN.

Germination of zoospores.—Continuing his studies upon the spores of algae, SAUVAGEAU[32] describes the germination of the zoospores of Cladostephus, Algaozonia, and Cutleria. Methods of making cultures of zoospores are also discussed.—CHARLES J. CHAMBERLAIN.

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[29] VAN LEEUWEN-REIJNVAAN, W. AND J., Ueber die Spermatogenese der Moose, speziell mit Berücksichtigung der Zentrosomen- und Reduktionsteilungsfragen. Ber. Deutsch. Bot. Gesells. **26a**:301–309. *pl.* 5. 1908.

[30] Cf. BOT. GAZETTE **45**:358. 1908; **46**:234. 1908.

[31] MÜCKE, M., Ueber den Bau und die Entwickelung der Früchte und über die Herkunft von *Acorus Calamus* L. Bot. Zeit. **66**:1–23. *pl. 1.* 1908.

[32] SAUVAGEAU, CAMILLE, Nouvelles observations sur la germination du *Cladostephus verticillatus*. Sur la germination des zoospores de l'*Aglaozonia melanoidea*. Sur la germination parthénogénetique du *Cutleria adspersa*. Sur les cultures cellulaires d'Algues. Compt. Rend. **63**:698–704. 1908.

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DECEMBER 1908

BRYOLOGICAL PAPERS

II. THE ORIGIN OF THE CUPULE OF MARCHANTIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 120

CHARLES R. BARNES AND W. J. G. LAND

(WITH FOURTEEN FIGURES)

The study of the cupule of Marchantia has evidently been confined to the later stages of its development, and especially to the origin of the gemmae and the order of cell division in them. Nowhere have we been able to find any account of the origin of the cupule, and the earlier stages of its development seem to have escaped observation. Its homology with other structures in the upper part of the thallus has apparently been a matter of speculation rather than of investigation. Thus, CAMPBELL casually remarks[1] that the gemma cup is apparently a specially developed air chamber, but gives no details and adduces no evidence therefor.

Although Marchantia has been much investigated and indeed has been long a favorite subject for instruction in laboratories, KNY seems to have been the first to examine any of the early stages of development of the cupule itself. This he did for the purpose of illustrating the development of Marchantia on his charts and describing the same in the accompanying text.[2] But he does not show or describe the origin of the cupule; the earliest stage referred to corresponds roughly to our *fig. 10*, when it has become a rather deep pit.

Our studies upon the origin of the air chambers in Marchantiales[3] suggested to us an inquiry into the origin of the cupule, to determine

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[1] CAMPBELL, D. H., Mosses and ferns, 2d ed. 44. 1905.

[2] KNY, L., Wandtafeln. Ser. III, *pl. 84*, text p. 366.

[3] BARNES AND LAND, The origin of air chambers. BOT. GAZETTE 44:197–213. 1907.

whether it could possibly be homologous with an air chamber. From an a-priori consideration of the general character of the cupule and the air chamber this idea commended itself to us both. The walls of the cup, especially the thin, lobed margin, seemed to correspond very well with the epidermal roof of the air chamber, opened wide instead of having only a narrow orifice. The gemmae, borne upon a single cell arising from the floor of the cup, might well be only a modified form of the chlorophyllose filaments of the air chamber. So natural and neat did the homology appear, that the brief prior statement of it by CAMPBELL (*l. c.*) was discovered with a distinct sense of disappointment when we began to look into the literature. But evidence for this homology could not be found therein, and against it was to be put the fewness of the cupules, their limitation to the median line, where the air chambers are least developed, and the fact that the gemmiparous region covers many times the area of an air chamber. The matter evidently needed examination. Actual observation of the origin of the cupule speedily dissipated all

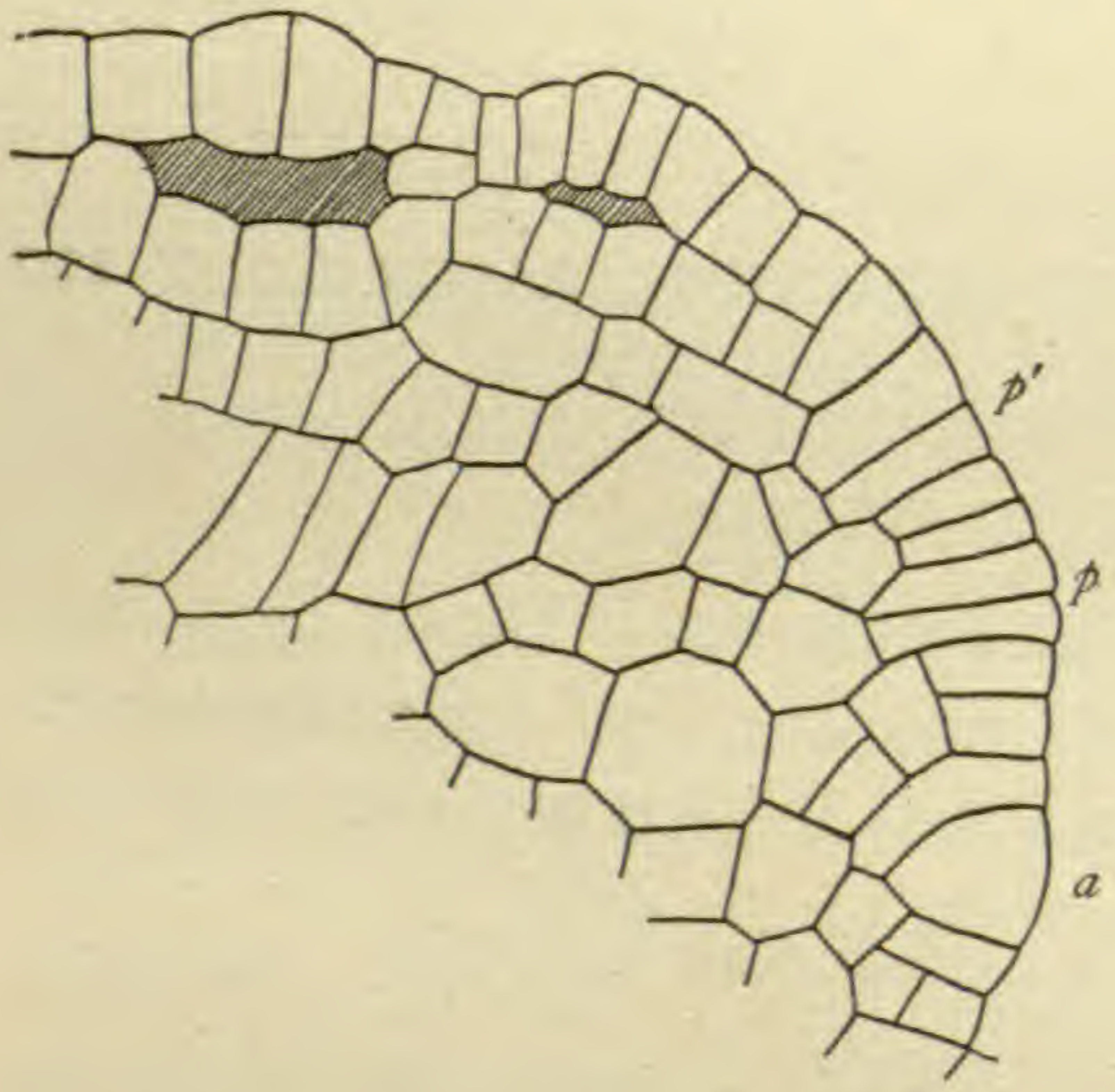

FIG. 1.—Early stage of cupule; *p*, *p'*, undivided cells, primordia of two (?) gemmiparous areas; *a*, apical cell; air chambers shaded.

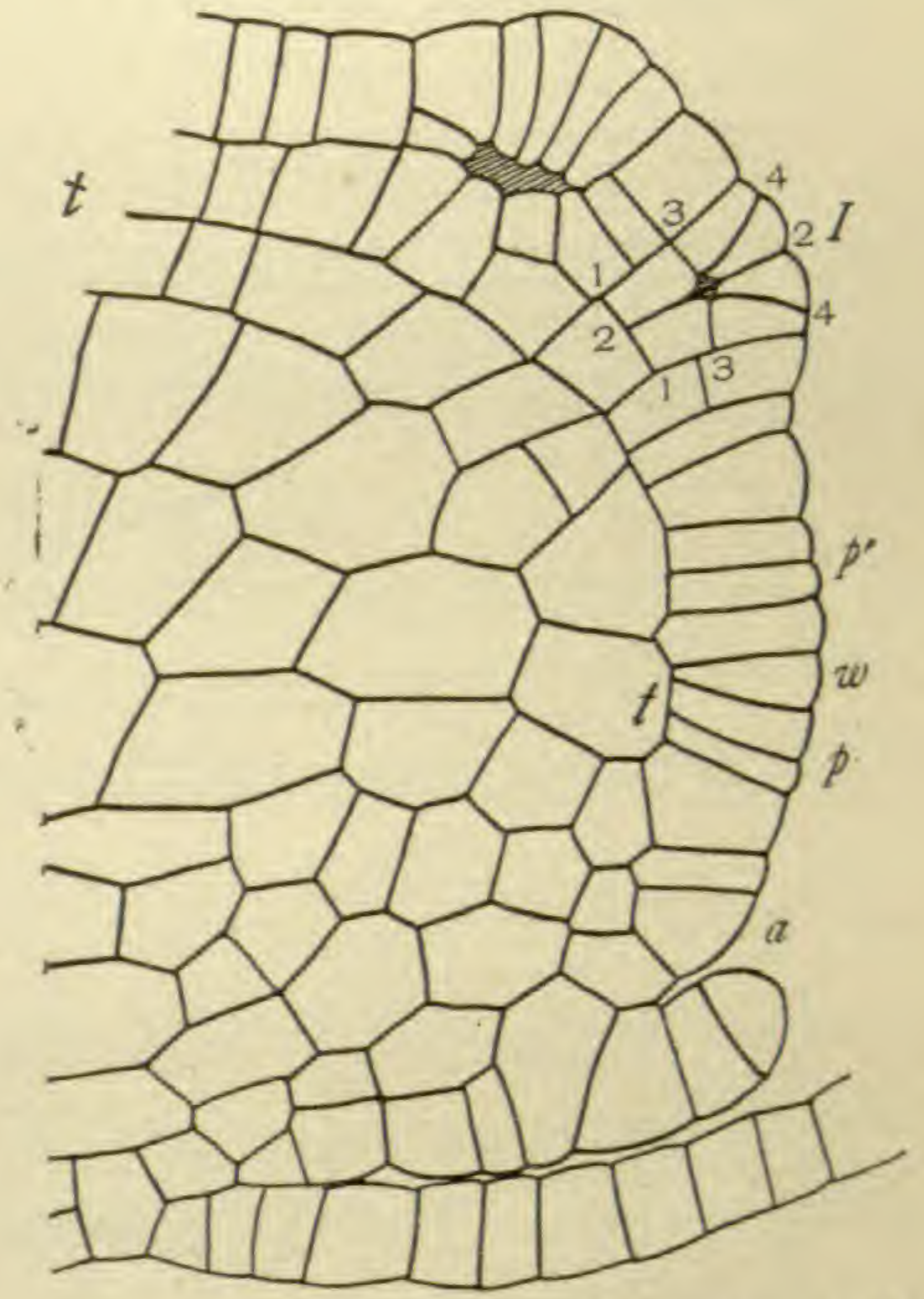

FIG. 2.—Early stage of cupule; *p*, *p'*, as in *fig. 1*; *w*, probably a rim cell between two gemmiparous areas; *a*, apical cell; *t*, *t*, line showing tissues of thallus involved in a cupule.

notions of its homology with an air chamber, as we now proceed to show.

Abundant fresh material was at hand from thrifty plants of *Marchantia polymorpha*, grown under glass by Mr. JOHN COOK, the skilful gardener of the department, who has taken much pains with the cultivation of Hepaticae. Being transferred directly from the cultures to the fixing fluids, the material was in exceptionally good condition.

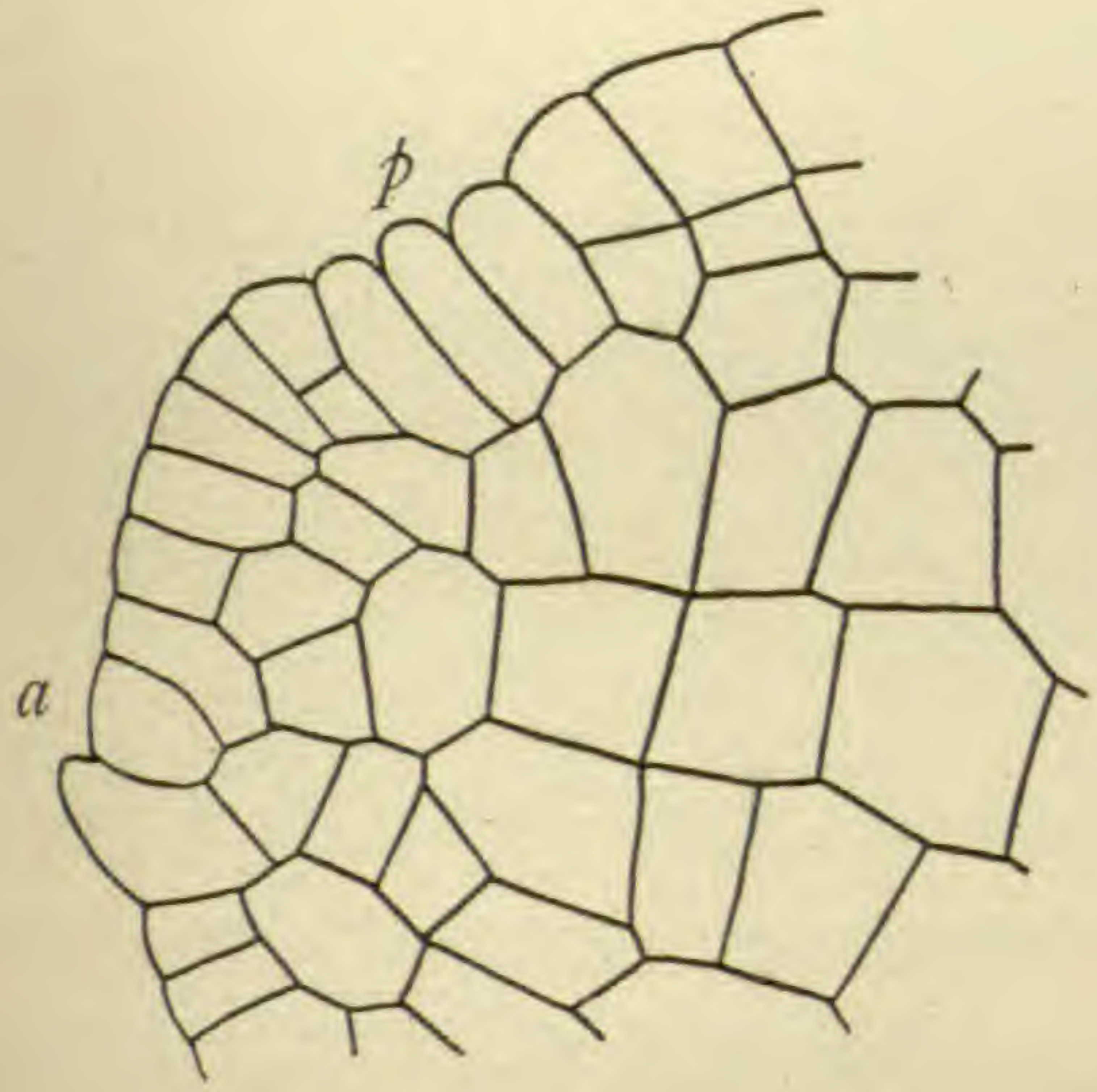

FIG. 3.—Gemmiparous area (*p*) outgrown by adjacent tissues.

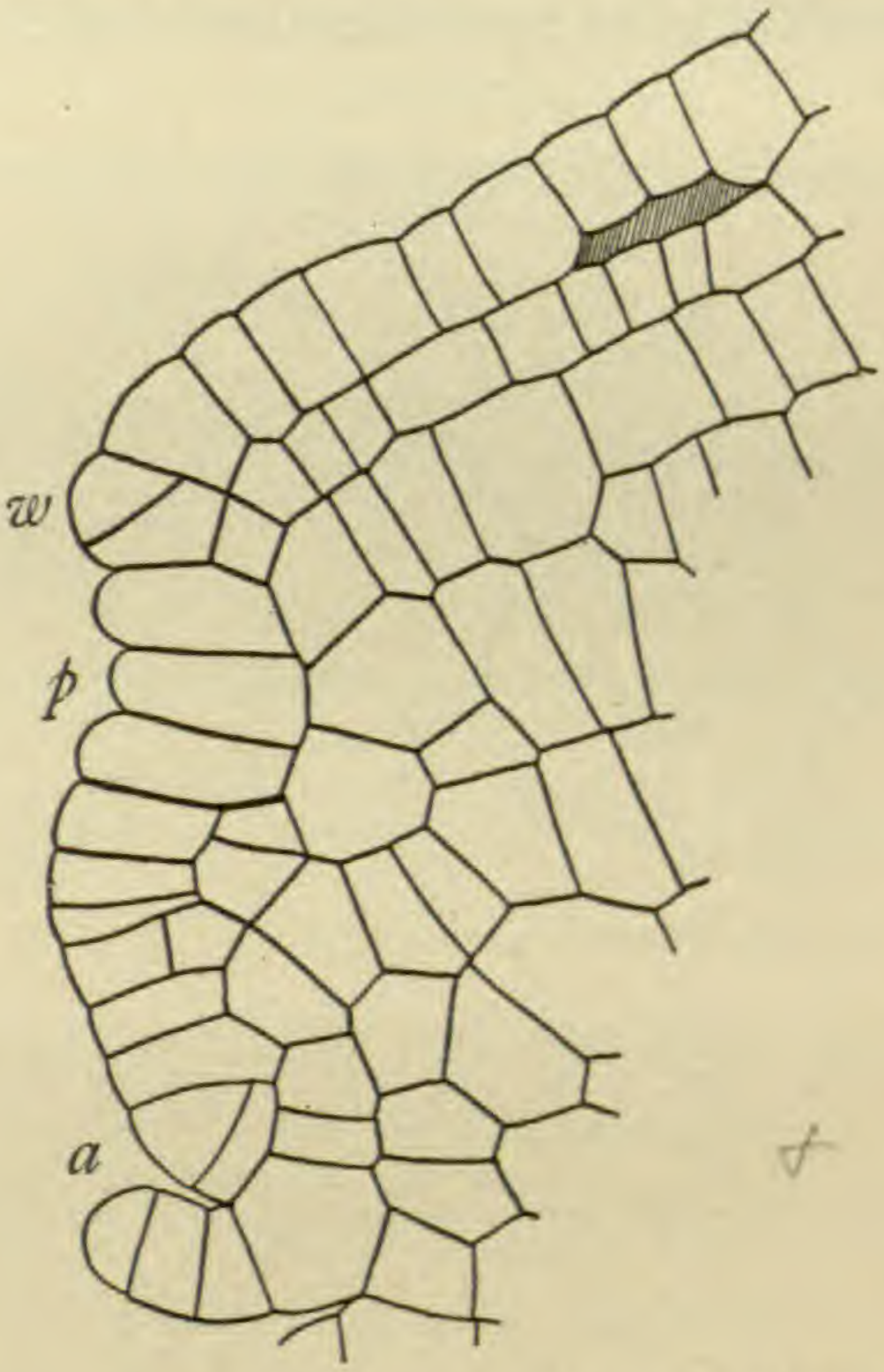

FIG. 4.—Stage nearly as in *fig. 3*; *w*, a rim cell cutting off the primordium of a lobe of the cupule.

Our figures show usually only the cell walls, the perfectly preserved contents being omitted for the sake of clearness. Mitotic figures were common, showing that the cells were in active growth. The figures are of longitudinal sections, except *fig. 13*, are all drawn to the same scale, and having been reduced one-half are now magnified about 625 diameters.

Longitudinal sections through the apex of gemmiferous plants show, as near to the apical cell as the third segment, a differentiation in the cells which are to form the gemmiparous area. Instead of dividing by several successive periclinal walls, as most of the segments promptly do, the superficial parts remain for some time conspicuously undivided (*p*, *p'*, *fig. 1*), and so are distinguishable by their depth. In particular it is the final periclinal divisions that fail. This will be more evident by following the usual segmentation of the mother cell of an air chamber. In *fig. 2*, the young air chamber *I* originated as usual in a cell which underwent one periclinal division, forming the wall *1, 1;* then an anticlinal one (*2, 2*); these two surface cells each divided periclinally (*3, 3*), and cleavage occurred at the junction of walls *2* and *3*. (The curved anticlinal walls, *4, 4,* succeeded the cleavage.) It is the divisions *1, 1,* and *3, 3,* or only the latter, which do not appear in the gemmiparous areas (*p, p'*).

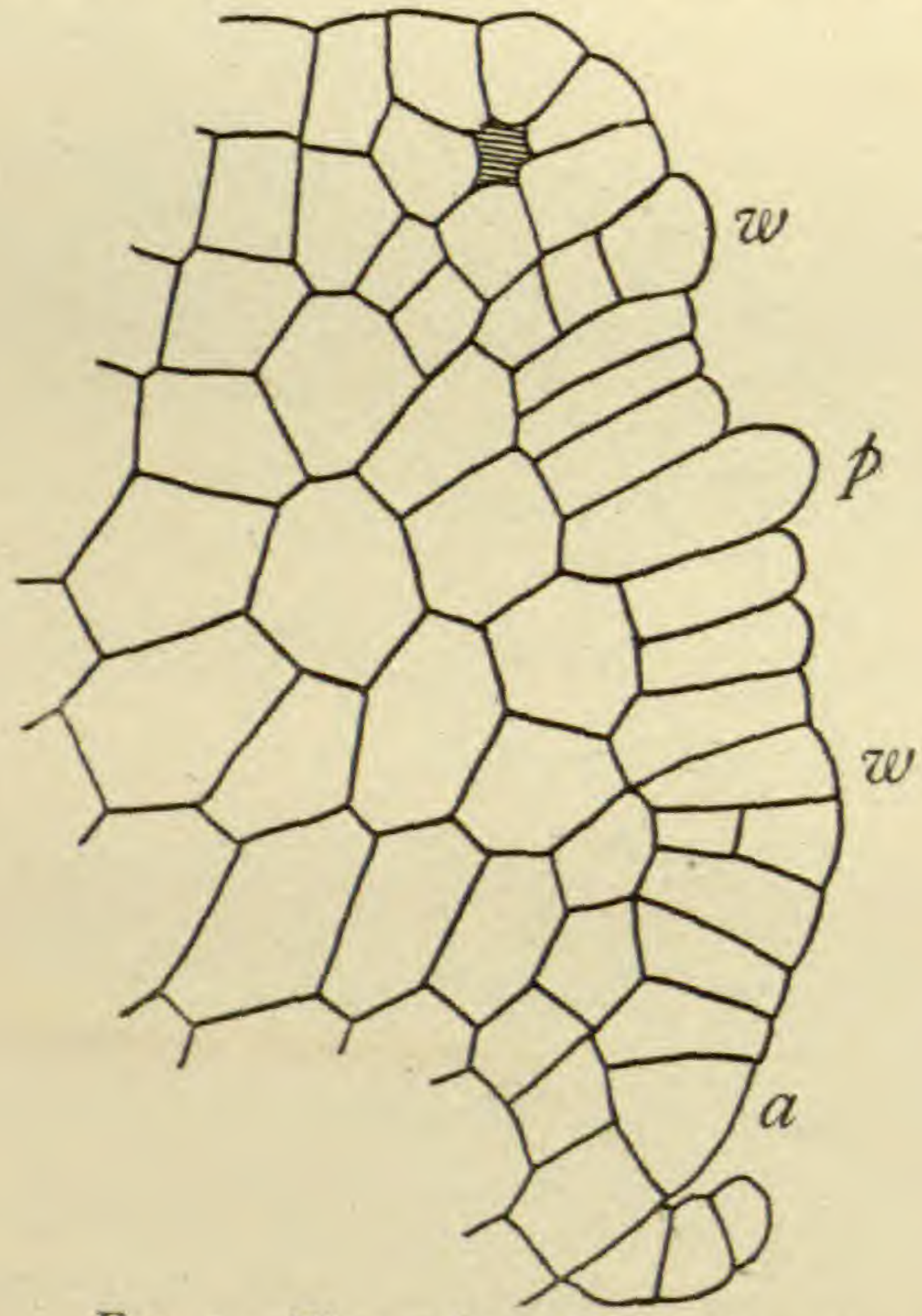

FIG. 5.—Elongation of a single gemmiparous cell (*p*); *w*, rim cells, the posterior oldest and most advanced in division.

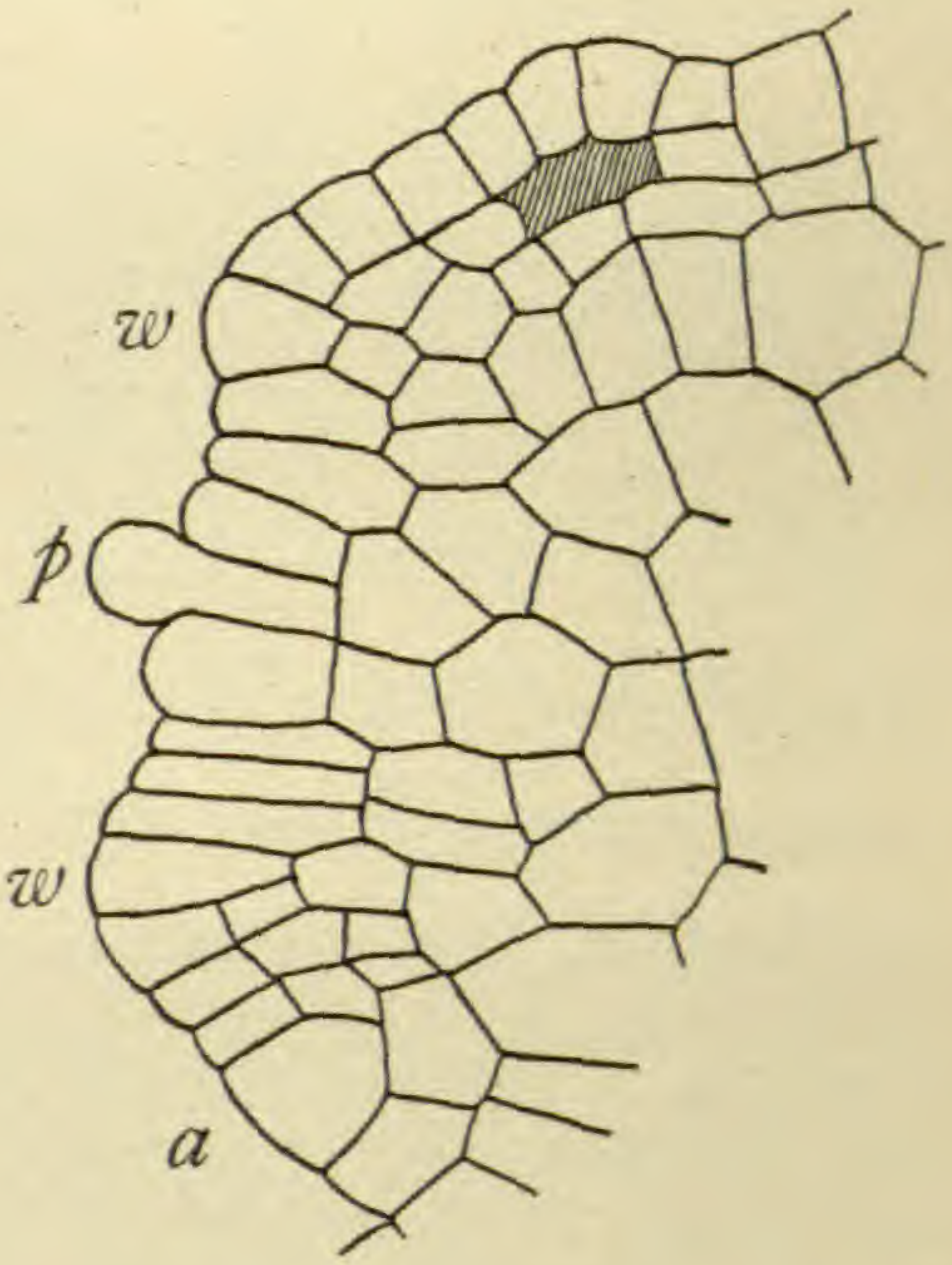

FIG. 6.—A somewhat later stage than *fig. 5*.

The relative extent of the area which these undivided cells cover, and the occurrence of somewhat different cells (*w*) between them, make it not unlikely that in *figs. 1* and *2* the primordia of two cupules are laid down in close succession; but of this we cannot be sure.

The failure of the gemmiparous cells to divide allows their neighbors to outgrow them, so that they can soon be located by the depression of the surface, as well as by their form and size (*p*, *fig. 3*). The depression, however, is not always well marked at this stage (cf. *fig. 5*). The contents, too, are sometimes distinctive, a glandular appearance being not infrequently noticeable; but as all the cells thereabouts are rich in protoplasm, this feature is not very striking.

The next step in development is the prolongation of one or more of the gemmiparous cells into papillae (*p*, *figs. 5, 6*), and simultaneously the further upgrowth of the cells at the rim of the depression, and first on the posterior margin (*w*, *figs. 4, 5, 6*). The free ends of the papillose extensions quickly enlarge (*figs. 7, 8*) and doubtless secrete some of the mucus in which the whole apical region is enveloped. Certain of the cells that form the rim divide obliquely (*w*, *figs. 4, 8*). Probably the cells thus cut off are the primordia of the thin lobes, which are so marked a feature of the mature cupule; for even in this early condition the rim becomes scalloped.

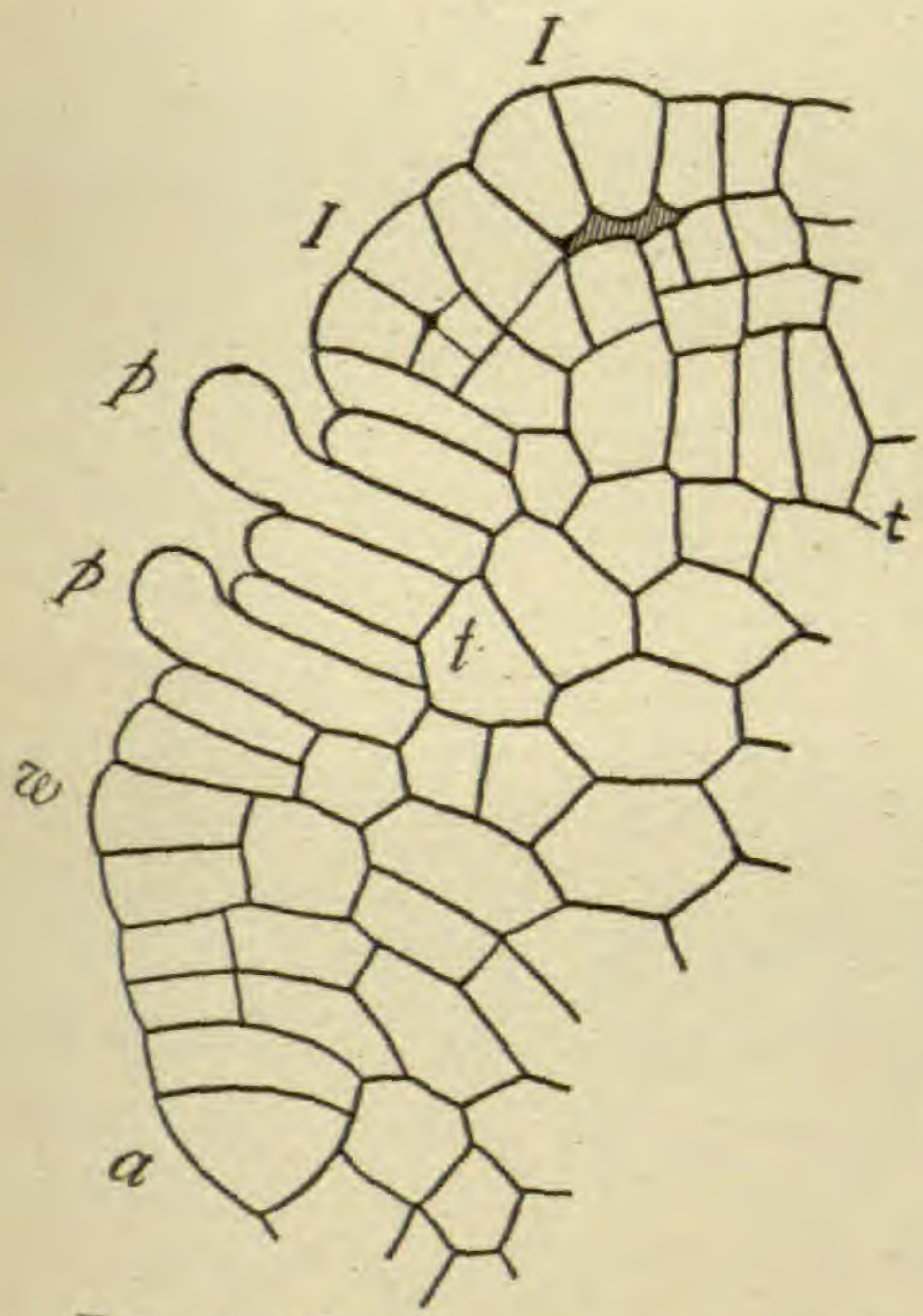

FIG. 7.—Two gemmiparous cells elongated; *I*, young air chambers; *t*, *t*, as in *fig. 2*.

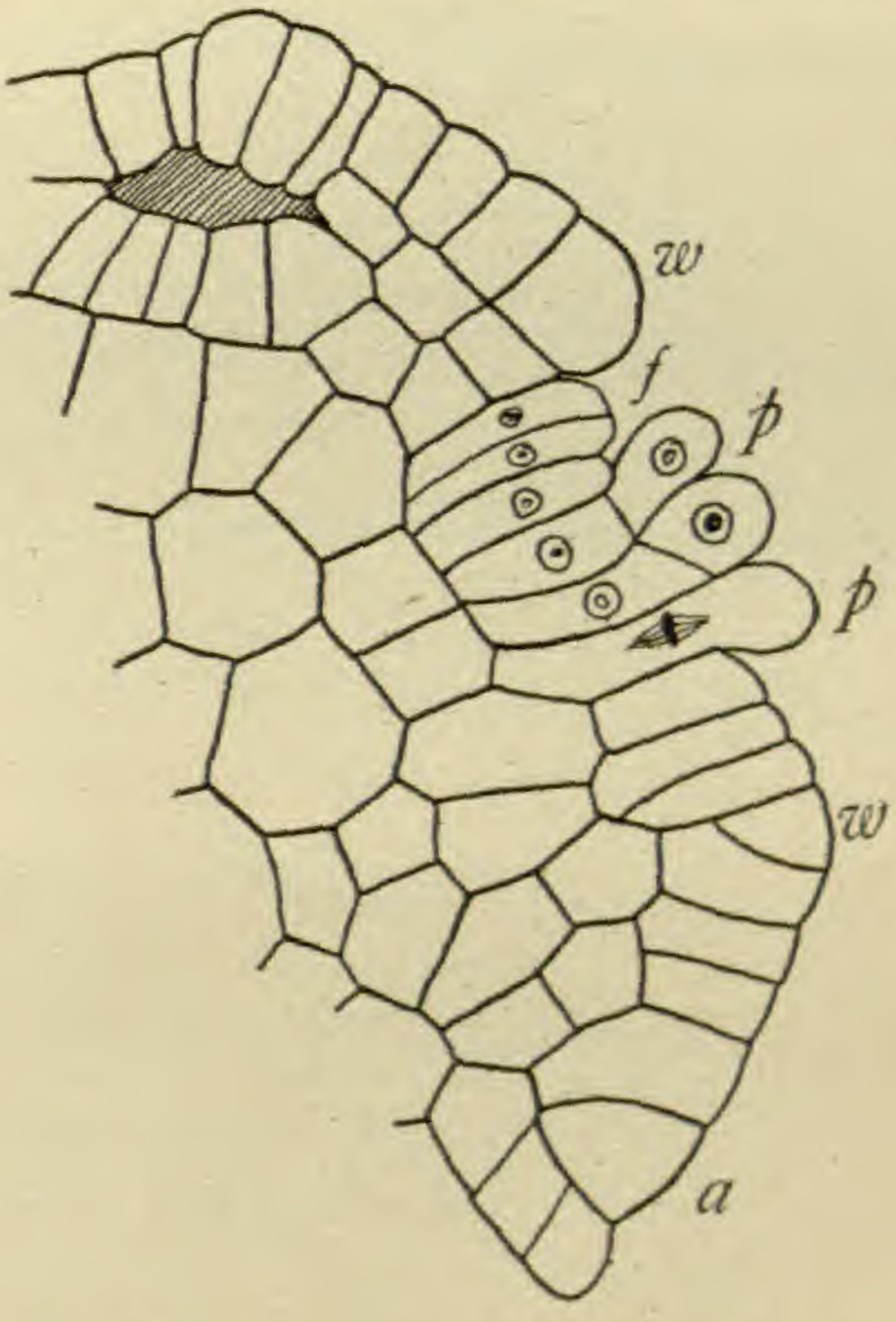

FIG. 8.—Further elongation and first division of gemmiparous cells (*p*, *p*); in *f* longitudinal division; *w*, rim cells.

After some further extension and enlargement, the gemmiparous cells divide transversely (*p*, *p*, *fig. 8*), and soon another division occurs (*p*, *fig. 9*), by which three cells are formed, a basal cell (*b*), a stalk cell (*s*), and a gemma cell (*g*). The latter continues to divide in the fashion frequently described and figured (cf. also *figs. 11, 12, 13*), and finally produces the gemma. The stalk cell undergoes no further division, but the basal cell divides longitudinally at least once (*p*, *fig. 11*). Later it may undergo repeated division, producing new

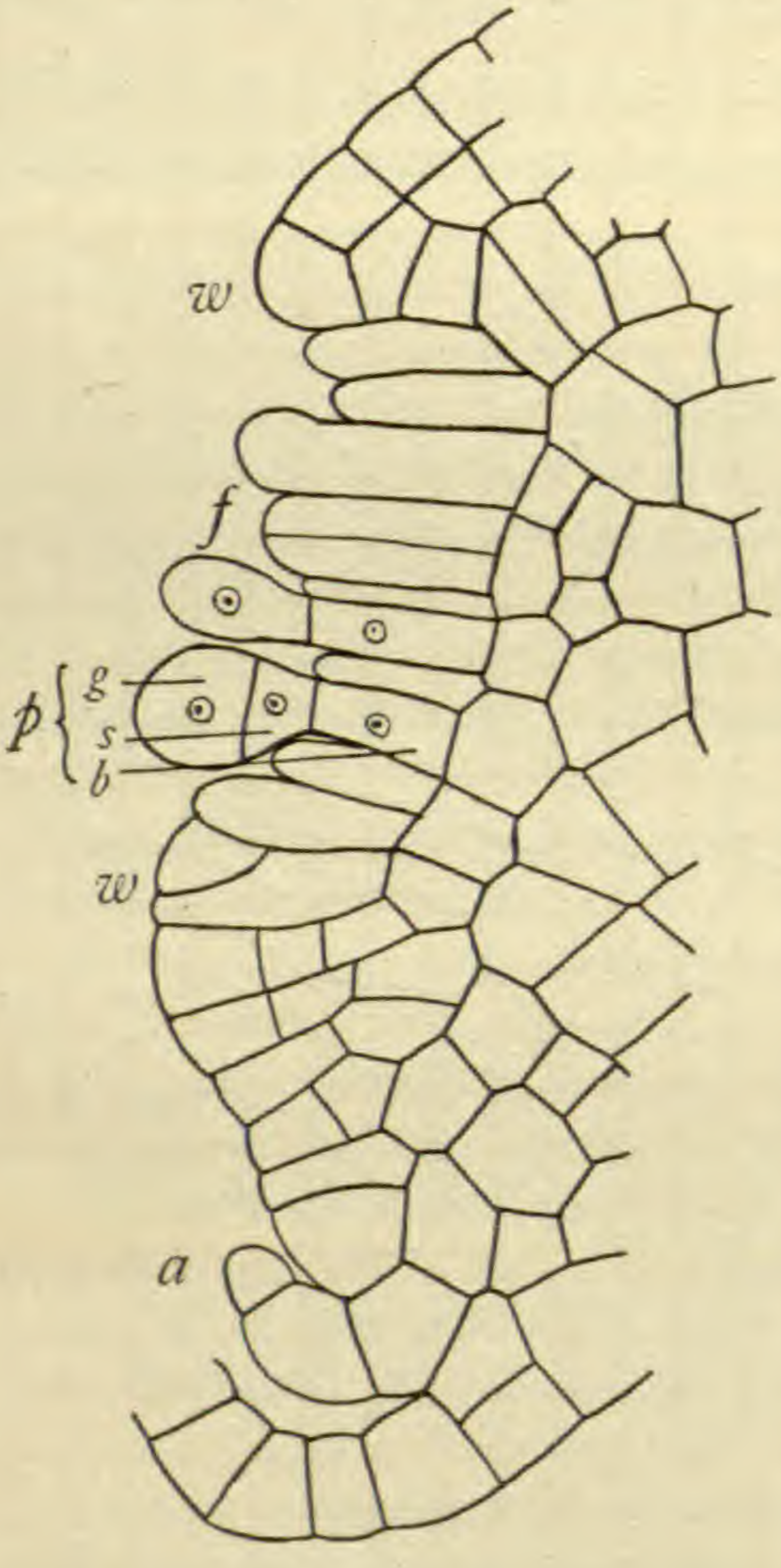

FIG. 9.—Progressing transverse (*p*) and longitudinal (*f*) division of gemmiparous cells; the former producing a basal cell (*b*), a stalk cell (*s*), and a gemma cell (*g*).

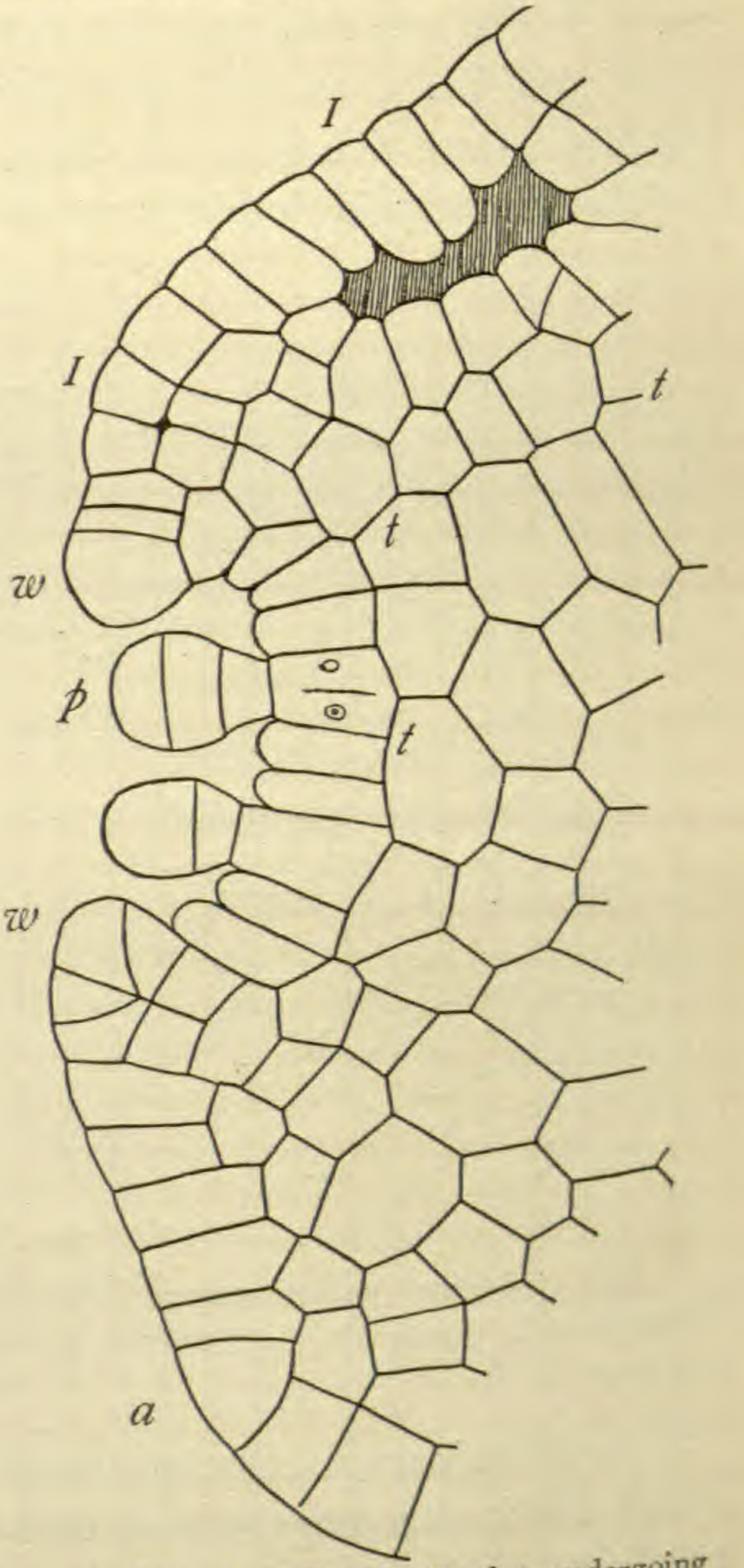

FIG. 10.—Basal cell of *p* undergoing longitudinal division; *w*, much further developed and depression deepened; *I*, young air chamber; *t*, *t*, *t*, shows relation of cupule and air chamber.

gemmiparous cells, so that each basal cell ultimately becomes the center of a group.

As the primordium of a cupule grows older, the number of gemmiparous cells forming its floor is increased by longitudinal (anticlinal) divisions (*f*, *figs. 8, 9*). The new floor cells so produced grow into papillae and soon produce gemma cells. Thus the gemmiparous area is increased in two ways: by the anticlinal division of the primordial cells, and by a similar division of basal cells that have borne or are bearing gemmae. The tissues adjacent grow rapidly, leaving the floor of the cupule soon far below the general surface (*fig. 12*), and the rim continues to outgrow the developing gemmae, which are embedded in mucus. The antero-posterior diameter of the young

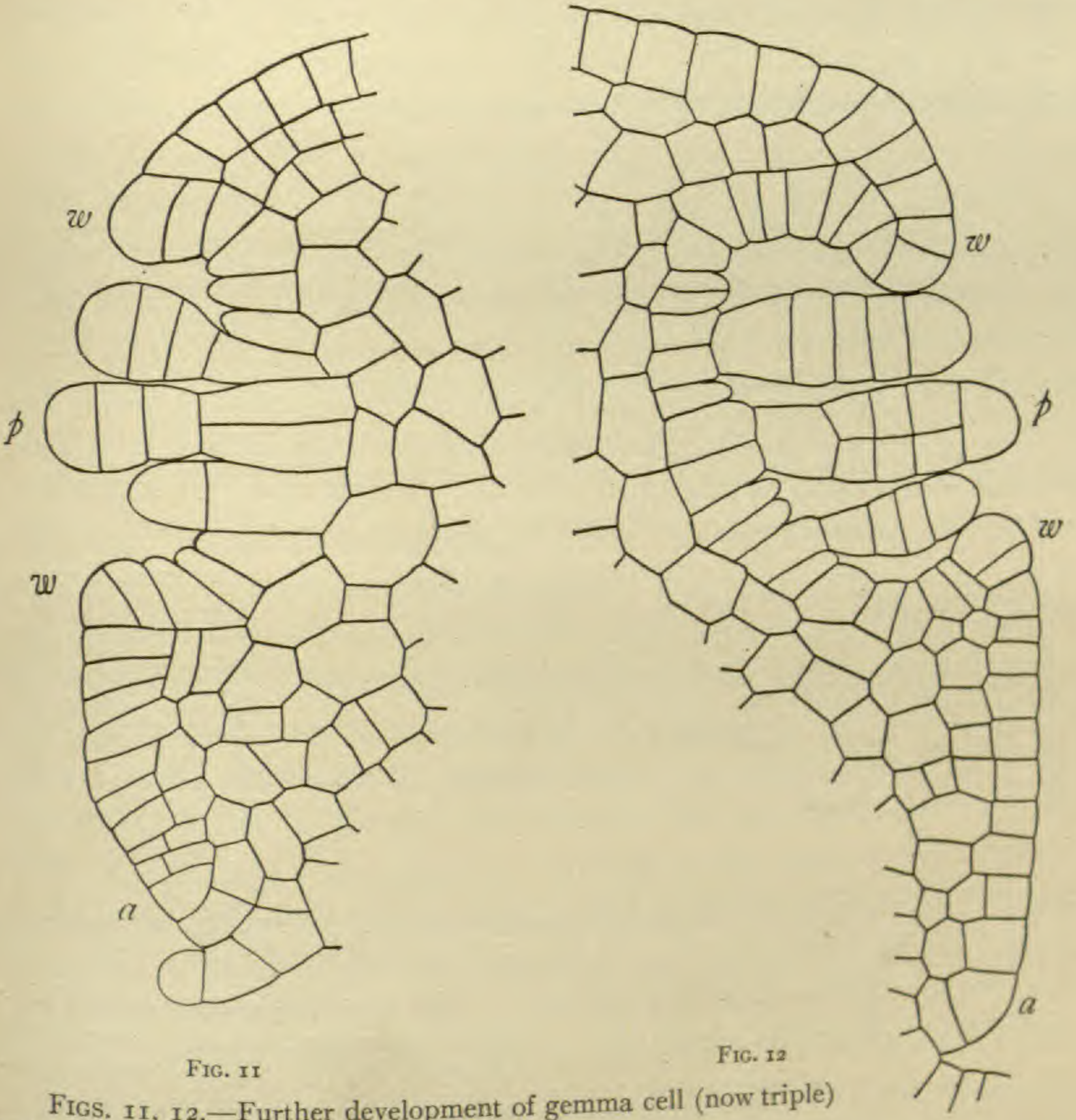

FIG. 11

FIG. 12

FIGS. 11, 12.—Further development of gemma cell (now triple) and rim (*w*).

cupule is less than the transverse diameter, as shown by *figs. 12* and *13*, which represent respectively longitudinal and transverse sections through cupules of about the same age.

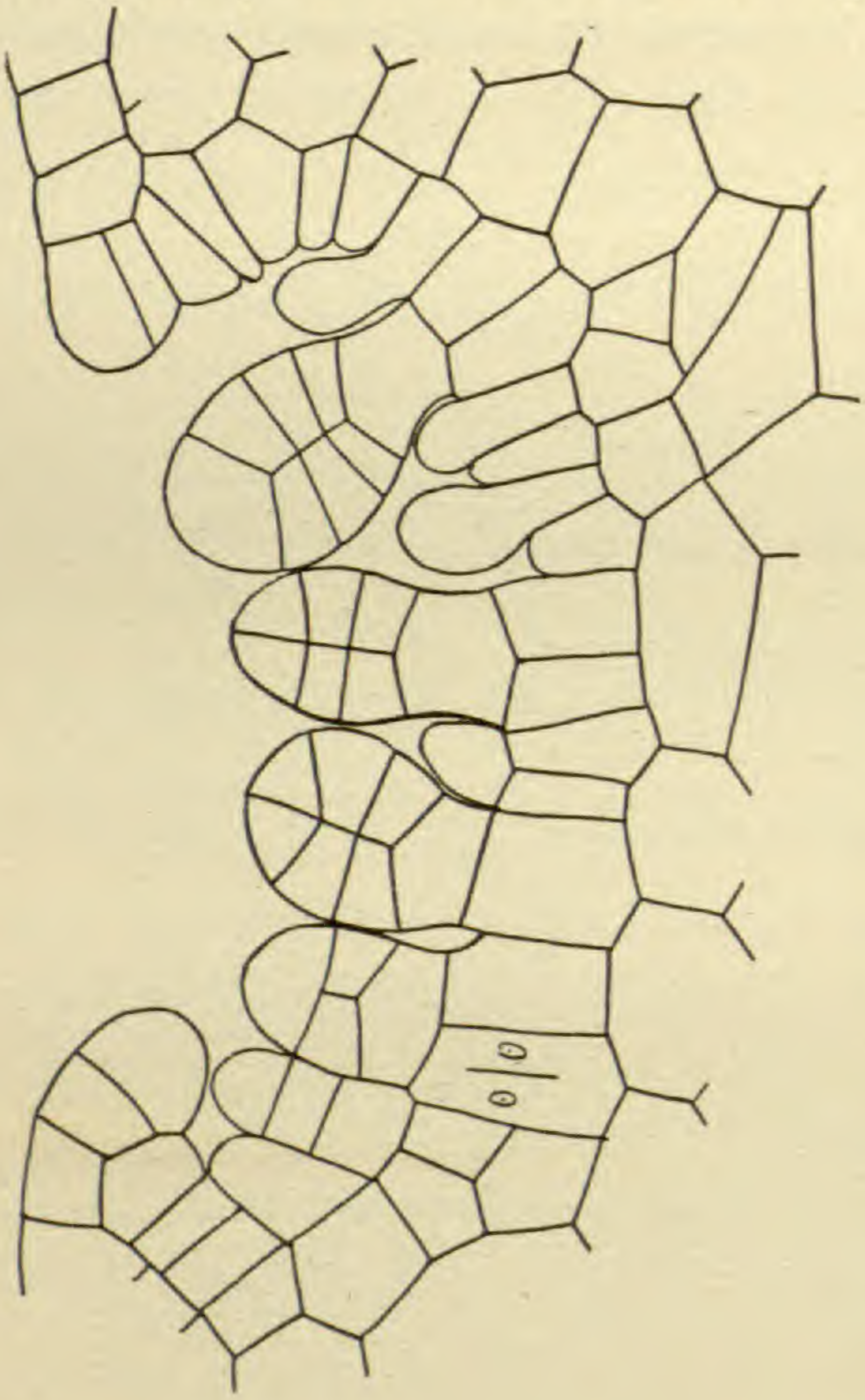

FIG. 13.—Transverse section of a cupule about the same age as *fig. 12*.

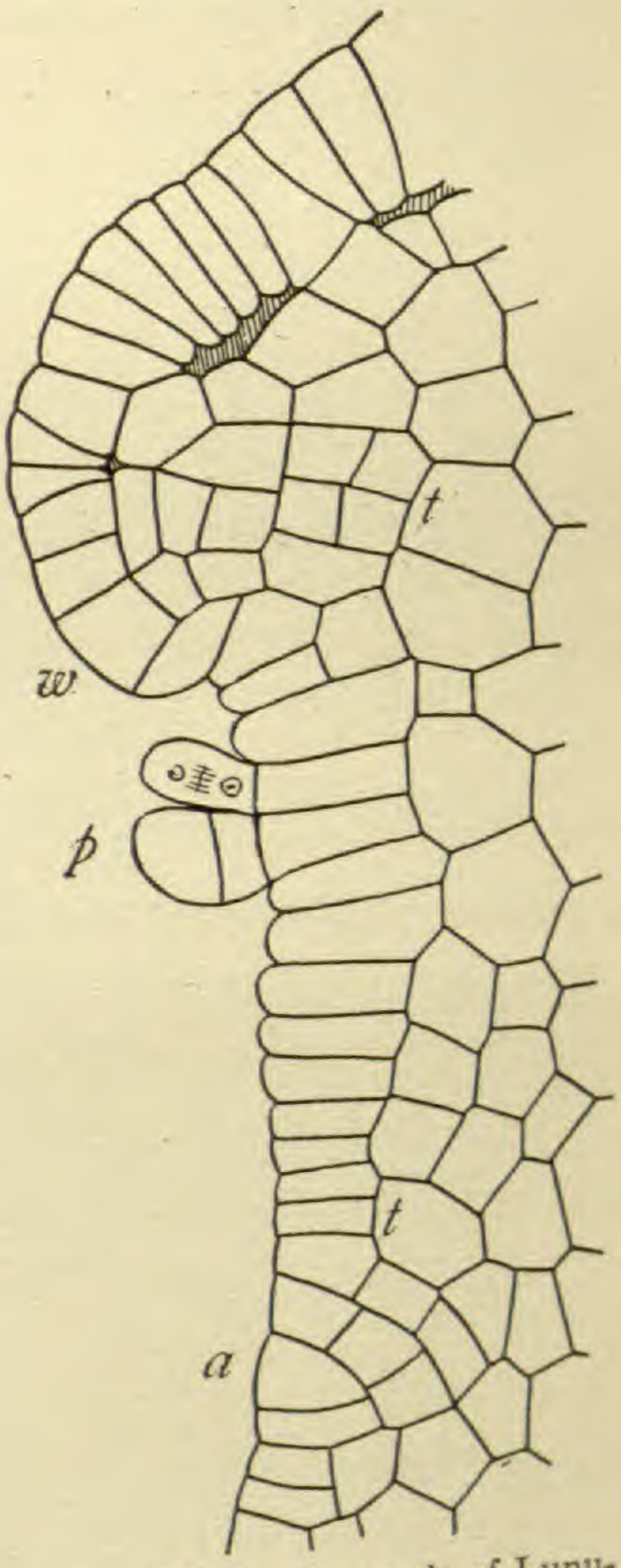

FIG. 14.—Origin of cupule of Lunularia; *p*, gemmiparous cells elongated and dividing; rim (*w*) developed only on posterior margin; *I*, young air chamber.

It is not necessary to follow the history of the cupule further, for it is a familiar object in all laboratories of instruction and has been well described.

The cupule of Lunularia has also been investigated sufficiently to show that its origin is essentially the same as that of Marchantia (*fig. 14*), except that the development of the rim takes place only on the posterior side of the gemmiparous region, which is also far more extensive. In some cases, late in development, a slight anterior elevation continues the line of the posterior rim and so suggests the circular cup of Marchantia.

The superficial origin of the gemmae is thus perfectly clear. They cannot be considered as in any sense homologous with the chlorophyllose filaments of an opened air chamber, nor has the cup any relation to the epidermal roof. The thicker part of it *contains* air chambers, and the thin part is simply a scalelike outgrowth of the epidermis. The difference between an air chamber and a cupule becomes especially striking when a cupule originates near an air chamber, as shown in *figs. 2, 7, 10, 14*, at *I*. Then, although the gemmiparous cells are seen to be superficial, they evidently represent cells that otherwise might produce not only the roof, filaments, and floor of an air chamber, but also a considerable portion of the thallus beneath the air chamber. In *figs. 2, 7, 10*, the line, *t*, *t*, can be followed clearly, showing how deeply the gemmiparous cells involve the tissues of the thallus. It is not surprising, therefore, that the gemma cup, though of superficial origin, is a depression in the thallus, and that air chambers clothe its sides.

Incidentally we may add that the origin of the gemmiparous cells, as herein shown, precludes our acceptance of GOEBEL's conception that in Marchantia the gemmae are homologous with "slime papillae."[5] The formation of mucus cannot be considered as a special function of any particular cells, though the so-called slime papillae have the name of "secreting" it. In fact young cells of very different origin and fate form mucus, and it is doubtful if any of the younger ones fail to form it. These "papillae" are purely superficial organs, and scarcely agree with the gemmiparous cells in anything except that at one time both project above the surface. How can the latter, which involve so considerable a part of the thallus, corresponding, as above shown, to the whole air chamber region and two or more layers of cells below it, be properly likened to such transient and superficial outgrowths as the "slime papillae"? To pronounce the two homologous throws no real light upon the nature of the gemmae, for the production of which there is such early and striking preparation.

THE UNIVERSITY OF CHICAGO

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[5] GOEBEL, K., "Die Brutknospe von Marchantia und Lunularia kann auch als einer Schleimpapille homolog betrachten werden." Archegoniatenstudien XII. Flora 98:314. 1908.

EMERGENCE OF LATERAL ROOTS[1]

RAYMOND H. POND

(WITH THREE FIGURES)

Our present conception of the method of emergence of lateral roots is based upon the elaborate exposition of the process made by VAN TIEGHEM in 1891. Since that time I am unable to find any record of emphatic disagreement with VAN TIEGHEM, though the results incidentally mentioned by later investigators of more or less related problems suggest the desirability of an examination of the evidence for his conclusion. Such an examination convinced me that we do not know whether the passage of the lateral root through the cortex is accomplished merely by mechanical pressure, or by a digestion of the cortical tissue, or by a combination of such methods.

It was my good fortune to be able to investigate this problem during the winter of 1907–1908 under the direction of Professor LUDWIG JOST at Bonn and at Strassburg. I am also indebted to the New York Botanical Garden for courtesies extended during the preparation of the manuscript.

Literature

After an extended anatomical study of the origin and emergence of lateral roots, VAN TIEGHEM[2] concluded that the young lateral root emerges by the dissolution of intervening tissue, and that this dissolution is accomplished by enzymes. In the case of the vascular cryptogams the meristematic pericycle is the secreting tissue, and in the case of the phanerogams this function is performed by the meristematic endodermis. His conception is that the young lateral root digests its way through the cortex just as an embryo digests its endosperm. Why VAN TIEGHEM was led to this conclusion is not clear, as he does not offer any substantial evidence, and I have been unable

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[1] From the botanical laboratory of the Kaiser Wilhelm University, Strassburg.

[2] VAN TIEGHEM, PH., Traité de botanique. Deuxième édition. pp. 709–711. Paris. 1891.

to find in the numerous figures of VAN TIEGHEM and DOULIOT[3] any trace of corrosion of cell walls or actual evidence of digestion. The figures do not show the stratum of compressed and collapsed cells which surrounds the young lateral root, at least in the cases of *Lupinus albus* and *Vicia Faba*.

Before VAN TIEGHEM, the same general conclusion as to the digestive action of the lateral root was expressed by REINKE.[4] The figures of REINKE are more accurate than VAN TIEGHEM'S, as in *pl. 2, figs. 5, 9*, the layer of distorted and collapsed cells which surrounds the young lateral root is shown. Still the figures do not show actual evidence of digestion.

Earlier than VAN TIEGHEM but later than REINKE, VONHÖNE[5] undertook to ascertain the relative importance of mechanical pressure and enzyme activity in the emergence of endogenous organs. His conclusion is (p. 230) that the young lateral root secretes a substance which acts upon the cortical tissue and digests it, just as does the enzyme secreted by the embryo of a seed digest its endosperm.

PFEFFER[6] (p. 367) notes that the passage of lateral roots through the cortex may be purely mechanical, though aided perhaps by some correlative activity on the part of the cortical tissue.

PEIRCE,[7] in his study of the penetration of living tissue by the roots of Vicia and Pisum, found that the root mechanically pushes its way through the various tissues tested. The results of CZAPEK[8] also support PEIRCE, since the former was unable to find any evidence of diastatic or of inverting ferments in the excretion of the

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[3] VAN TIEGHEM, PH., ET DOULIOT, H., Recherches comparatives sur l'origine des membres endogènes dans les plantes vasculaires. Ann. Sci. Nat. Bot. VII. **8**: 1–660. *pls. 1–40*. 1888.

[4] REINKE, JOHANNES, Untersuchungen über Wachsthumsgeschichte und Morphologie der Phanerogamen-Wurzel. HANSTEIN'S Bot. Abhand. Gebiet Morphol. und Physiol. **1**3:1–38. 1871.

[5] VONHÖNE, H. VON, Ueber das Hervorbrechen endogener Organe aus dem Mutterorgane. Flora **63**:227–234, 243–257, 268–274. 1880.

[6] PFEFFER, W., Druck- und Arbeitleistung durch wachsende Pflanzen. Abhand. Königl. Sächs. Gesells. Wiss. **20**3:235–474. 1893.

[7] PEIRCE, GEO. J., Das Eindringen von Wurzeln in lebendige Gewebe. Bot. Zeit. **52**:169–176. 1894.

[8] CZAPEK, FRIEDRICH, Zur Lehre der Wurzelausscheidungen. Jahrb. Wiss. Bot. **29**:321–390. 1896.

roots of higher plants. PEIRCE's conclusion is also supported by the results of OLUFSEN.[9]

Macroscopic study of the seedling

By examination of the seedlings of *Vicia Faba* one may find instances in which the cortex in the region of juncture of radicle and hypocotyl is strongly ruptured. In such cases one usually finds that two or more lateral roots have originated side by side, and their combined mechanical pressure has caused a rupture of the cortical tissue. The mere observation was made by VONHÖNE, but its significance apparently did not impress him. Evidently any digestion of the cortex that may occur is too slow to provide space for the advancing lateral root. Of course one cannot say positively that the fissure of the cortex is directly caused by the emerging lateral root. However, I have not found a rupture of the cortex except in association with lateral roots. Further, one may find swollen places on the radicle which are beyond doubt caused by the pressure of the advancing lateral root (*fig. 1*).

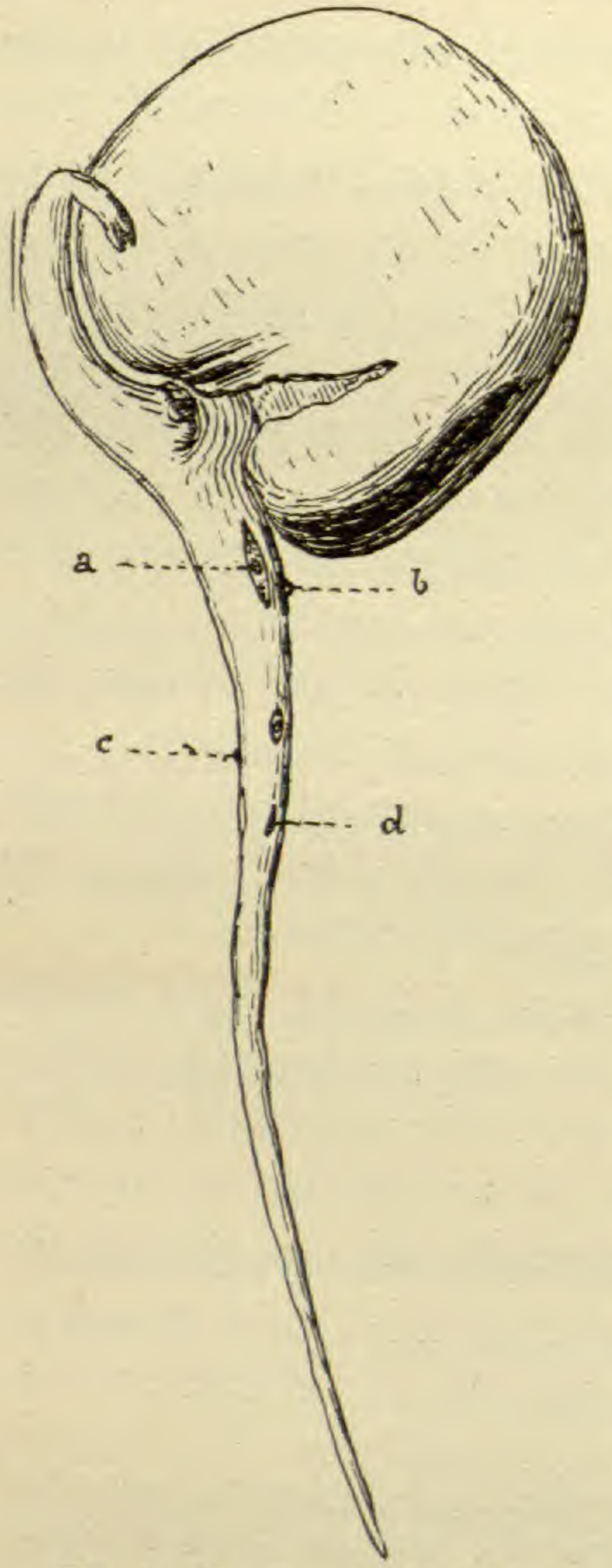

FIG. 1.—Seedling of *Vicia Faba:* *a*, rupture of cortex through which lateral root is emerging; *b*, c, cortex bulging because of pressure exerted by the lateral roots, which have not yet emerged; *d*, early rupture of cortex at point of emergence of lateral root.

Microscopic study of unemerged lateral root

All attempts to get microtome sections were unsuccessful, as the collapsed cells surrounding the young lateral root are lost in the preparation of the sections. All of my observations were

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[9] OLUFSEN, LAURITS, Untersuchungen über Wundperidermbildung an Kartoffelknollen. Bot. Centralbl. Beih. 15:267–308. 1903.

made, therefore, from freehand sections mounted in pure lactic acid mixed with iodin. In order to have the sections clear and free from air, they were exhausted under the air pump. Only *Vicia Faba* and *Lupinus albus* were studied. Radial sections of the radicle showing the lateral root in median view are the best.

The cells of the cortex are not compressed to the stage of collapse until the lateral root has advanced about one-half the distance toward the epidermis. In earlier stages, when the lateral root has advanced only two-fifths the distance toward the cuticle, one may still find all the cells of the cortex uncollapsed and in natural cell connection, though of course displaced and compressed. The lateral root, therefore, has made a very difficult part of its journey without the slightest possibility of any digestion of the cortical cells. In the lupin the cells of the cortex have too little starch to note any possible autolysis, but in Vicia there is plenty of starch, and one can easily see that there is no difference in the starch content of the cells immediately surrounding the lateral root in comparison with those of other regions of the cortex. The same is true when the lateral root has advanced to the epidermis. Even in the cells which have been compressed to collapse, and in which the protoplasm looks wasted, the starch seems to be present in undiminished quantity. When the lateral root has advanced about one-half the distance toward the cuticle, the cell connection of the cells just outside the apex of the lateral root is broken in that region, and the cortical cells are thus pushed aside by the lateral root as is water by a boat. Those cells though now collapsed may remain undigested and be carried by the lateral root outside the epidermis. I have found, though very rarely, cases in which the cell connection of the displaced cortical cells was complete along the side of the lateral root, even at the time of the arrival of the latter at the epidermis. Any digestion of such cells is therefore excluded. Usually the cortical cells are so dislocated and so disarranged that the cell connection cannot be established. However, a few cases only are necessary to show that there can be no digestive action on the part of the lateral root either upon the cells of the cortex or of their contents.

Of course there must be some resorption of substance, and whether this is done by the cortex or by the lateral root I cannot say. As the cortical cells collapse, the protoplasm of course loses its turgor and further compression drives the cell sap from the cell. Since the osmotic pressure of the lateral root is much higher than that of the cortical cells, there is probably some adjustment in the matter of resorption. Some of the solutes may go into the cortex and others into the lateral root. The apical cells of the lateral root are abundantly filled with starch, much more so than those of the cortex.

Turgor estimations

If the young lateral root mechanically pushes its way through the cortex, one would expect to find that the turgor of the cortical cells is less than that of the cells of the advancing lateral root. Longitudinal sections of the main root showing the lateral root in median view were immersed in various concentrations of potassium nitrate and of ammonium chlorid. After being exhausted under the air pump for thirty minutes, the degree of plasmolysis was determined. Essentially the same figures were obtained for *Vicia Faba* and for *Lupinus albus*. The figures given hold for sections in which the lateral root has nearly emerged. In 2 per cent. KNO_3 no plasmolysis could be observed in any of the tissues; in 3 per cent. KNO_3 there was initial plasmolysis of the cortical cells only. The turgor of the cells of the central cylinder and of those of the endodermis undisturbed by a lateral root seems to be a little higher than that of the cortical cells. In 4 per cent. KNO_3 the cortical cells are strongly plasmolysed, the endodermal cells covering the apex of the lateral root are not at all plasmolysed, the cells of the central cylinder and those of the undisturbed endodermis are somewhat though not strongly plasmolysed. In 5 per cent. KNO_3 there is total plasmolysis of all the cells except those of the lateral root itself and of the endodermal cells covering the apex of the lateral root. Some cells at the base of the lateral root show plasmolysis in 5 per cent. KNO_3. In 6 per cent. KNO_3 the endodermal cells covering the apex of the lateral root show initial plasmolysis. The maximum turgor for the endodermis is found in those cells which cover the apex of the young lateral root. From the apical cells toward the base of the lateral root the turgor of the endodermal cells seems to gradually decline, until only a short distance in longitudinal direction of the main root from the base of the lateral root the turgor is the same as that of the undisturbed endodermis. The turgor of the cells of the central cylinder was also found to be 0.5 to 1 per cent. KNO_3 higher than that of the cells of the cortex. Similar estimates were made with ammonium chlorid, whose osmotic pressure is practically twice that of KNO_3, and it was found that one-half the concentration produced corresponding degrees of plasmolysis. In other sections in which the young lateral root is just beginning to dislocate the endodermis, the turgor of the endodermal cells is not so high, only about 4 per cent. KNO_3. It is thus apparent that as the very young lateral root commences to make new cells, the difference between the turgor of the cortical cells and that of the endodermal cells covering the apex of the lateral root increases until it amounts to about ten atmospheres before the lateral root ruptures the epidermis. *There can be no doubt that the tissue of the lateral root is capable of sustaining a growth push far greater than the cortex is capable of resisting.*

I was not able to observe plasmolysis in the meristematic cells at the apex of the lateral root inside the endodermis. It is quite likely that volume determinations would have revealed some shrinkage, but in saturated KNO_3 no separation of protoplasm from the cell wall was seen. It is possible that the protoplasm was suddenly killed. RHEINHARDT[10] found that the lateral roots of *Vicia Faba* will develop and grow in solutions of sufficient concentration to mortally plasmolyse the surrounding tissue.

The penetration of one living root by another

For the purpose of auxiliary evidence, several tests were made to ascertain whether one main or lateral root can penetrate another radicle. A seedling with radicle 6 or 7^{cm} in length was pinned to a sheet of cork through the cotyledons, and under the hypocotyl, 1 or 2^{cm} from the cotyledons, a small block of cork was placed to raise the hypocotyl. A root model of glass tubing was drawn out and vertically held upon the hypocotyl while gypsum was placed around the tube and the seedling. As soon as the gypsum was hard

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[10] RHEINHARDT, M. O., Plasmolytische Studien zur Kenntniss des Wachstums der Zellmembranen. Sonderabdruck aus der Festschrift für Schwendener. pp. 41. *pl. 14.* Berlin. 1899.

the model was withdrawn, and into the canal was inserted the radicle of another seedling, so that the tip of the latter almost touched the horizontal hypocotyl (*fig. 2*). The inserted seedling was then almost entirely covered with gypsum, and when hard the preparation was placed in sawdust. The block of cork under the hypocotyl was of course withdrawn, and thus the side of the hypocotyl opposite the entering root was not covered with gypsum, and if the entering root penetrated the hypocotyl it could find exit unobstructed by gypsum. Many such tests were made in which the main and lateral roots of *Vicia Faba*, *Lupinus albus*, and *Phaseolus multiflorus* were used in the various combinations, but the results were always negative. The preparations were allowed to stand undisturbed for various periods up to seven days, but the result was always negative. The radicle of the inserted seedling turned its tip as far as the canal would allow (less than the diameter of the radicle a mm. above the tip) and became imbedded in the callus subsequently formed. A strong imprint of the blunted radicle was always found on the hypocotyl, but microscopic examination showed the cuticle to be uncorroded and entirely intact. It is evident that if the radicle or the lateral root secretes an enzyme, such enzyme has no digestive action upon the cuticle. Apparently the mechanical push of the advancing root was not strong enough to break through the cuticle. However, no conclusion on this point is drawn here. It is significant, however, that in case the epidermis is ever so slightly wounded, as by piercing with a small glass point, either a main root or a lateral root will enter and pass entirely through the hypocotyl without formation of callus or other visible evidence of obstructed passage. Of course it is much easier to make an exit than an entrance through intact

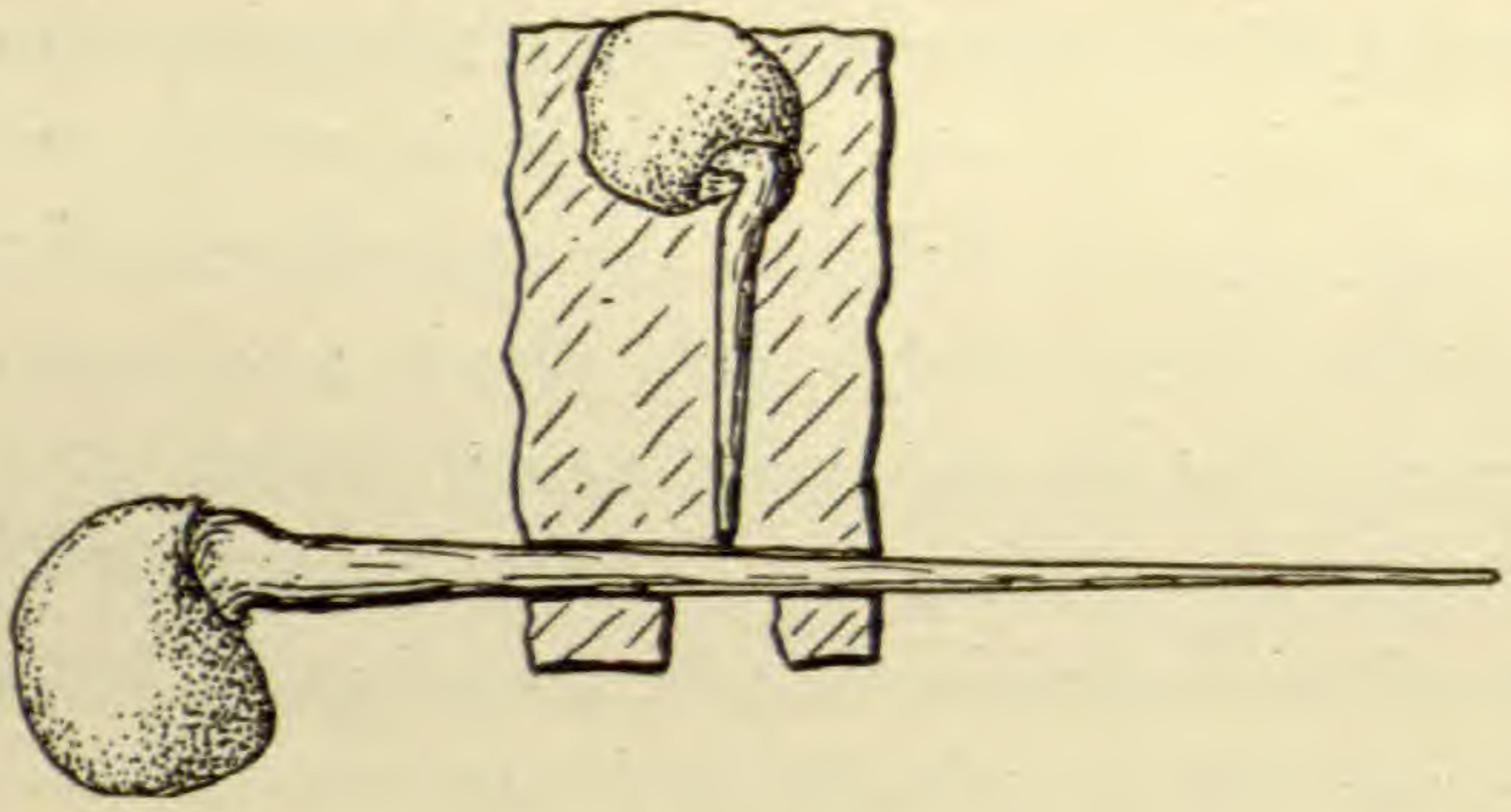

FIG. 2.—Arrangement of seedlings for penetration at right angles, the line-shaded portion representing solid gypsum.

cuticle if the latter is unwounded. When a root does enter, the passage is always around and not through the central cylinder, showing that the latter offers greater resistance than the cortex. Microscopic examination failed to reveal the slightest evidence of digestion of tissue. Many of the displaced cells of the cortex were found, but cells with broken walls were very scarce. The entering root apparently presses the cortical cells until they collapse, and then laterally displaces them without breaking the walls. No trace of corrosion of cell walls could be found. It seems probable that the mechanical push of the root is not sufficient to break through the cuticle when the latter is supported by underlying tissue. A demonstration for this, however, is not claimed.

Several tests were made to ascertain whether the central cylinder can be penetrated by another root at right angles. For this purpose enough cortex was removed to expose the stele, and the glass root model held so that when withdrawn from the gypsum the canal led directly to the central cylinder. In this way the entering root was compelled to enter the central cylinder at right angles or not at all. The result was negative in every case, and the entering root formed callus the same as in cases where the attempt was to enter the unwounded cuticle. The central cylinder was found to be strongly impressed, but no sign of corrosion or digestion of tissue could be observed. In some instances the entering root was able to shy from the stele and make passage through the cortex. Microscopic examination showed the cortex to contain compressed and collapsed cells. The appearance was the same as seen when the cortex is penetrated naturally by the lateral root. There was no evidence of corrosion, the walls of the collapsed cells being just as thick and regular in outline as those of the cortex in regions not affected by pressure.

Longitudinal passage through the stele by main and lateral roots

When the hypocotyl is traversed at right angles by another root, the tissue surrounding the path of the penetrating root cannot be examined microscopically with such advantage as is possible when the penetrating root traverses the hypocotyl longitudinally for a considerable distance.

The radicles of lupin seedlings having hypocotyls several centimeters long were amputated at the junction of stem and root. In the stele of the hypocotyl a vertical canal was made by inserting a small glass tube a few mm. and then withdrawing the tube. Into the canal was then inserted the root tip of a very young lupin seedling, and the whole preparation was then incased with gypsum and later placed in moist sawdust in vertical position (*fig. 3*). The parenchyma of the central cylinder offers the entering root the path of least resistance, so that the stele is often thus traversed its whole length. One may then make cross and longitudinal sections and very clearly study any changes in the tissues. As in the tests already described, no essential difference can be noted between the action of a main root and a lateral root on the tissues traversed by them.

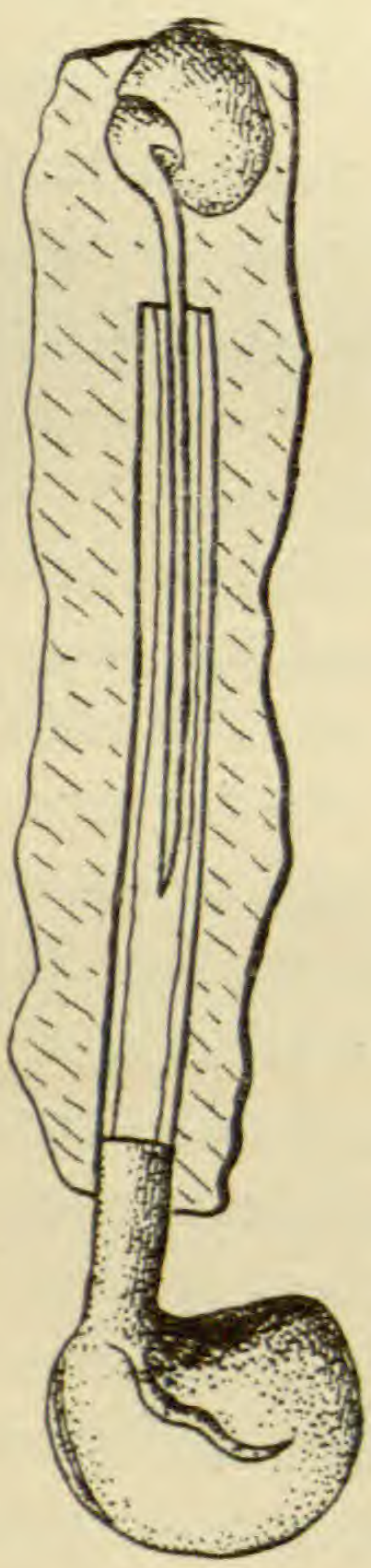

FIG. 3.—The radicle of the smaller seedling is growing downward through the central cylinder of the larger seedling's hypocotyl; the line-shaded portion represents solid gypsum.

The stele of the lupin is surrounded by a sheath which is only one cell in width, and the cells of this sheath only contain starch in any abundance. The cross-section thus stained with iodin shows the cylinder inclosed by a circle of starch-bearing cells. In cases in which the traversing root has pressed against this sheath, one may easily observe that even in cells of the sheath collapsed by the pressure the starch is present in undiminished quantity. There is no evidence of digestion of the starch either on the part of the entered root or by autolysis in the cells themselves. As one sections farther and farther along the hypocotyl, until only about 6 or 7^{mm} of the radicle remain within the hypocotyl, it may be observed, if the hypocotyl is allowed to remain undisturbed for a moment, that the radicle is gradually pressed out of the central cylinder, showing that it has encountered resistance from the tissues and that the latter recover from the pressure of the root. That the cells of the central cylinder are under compression there can be no doubt, and that this compression provides some of the space occupied by the advancing root is also very clear. The collapse of some of the cells also provides space, and I am inclined to believe that in those two ways alone is the space occupied by the ingrowing root to be accounted for. Immediately surrounding the radicle, as seen in cross-section of the hypocotyl containing it, is to be found a stratum of collapsed cells which are so tightly compressed that one cannot count the individual cells. The walls are not corroded, however, and there is no evidence of wasting away of the tissue or of resorption of the cell walls. In some cells the protoplasm shows a little indication of wasting away, but it is too slight to count as a factor so far as the progress of the in-growing root is concerned. Beyond the cells which cannot be distinguished as separate units are those which can be so distinguished but which show compression without collapse. I have not in any case been able to account for each cell, but more than one-half the number can be found, which, together with those too much compressed to be distinguished, plus the space provided by compression, practically accounts for all the space occupied by the in-grown root. The compression is quite strong, as one may find cases in which the central cylinder is widely ruptured with the fissure extending for some distance into the cortex. Examination of the cells in immediate contact with the apex of the in-grown root shows them to be intact, so far as any corrosion or wasting-away of the walls is concerned.

Substitution of glass rod for the entering root

For the sake of greater certainty, preparations like the above were made except that a glass rod was vertically pushed into the central cylinder by a weight of from 300 to 400^{gm}. The rod was drawn out to resemble a root in form. After 48 hours under the weight the rod was removed and the tissues examined. The progress of the rod into the cylinder was somewhat slower than that of the growing root. The examination showed, however, no essential difference in the effect upon the tissues of the hypocotyl. One could not say from the microscopical examination whether the cylinder had been traversed by a root or by a glass rod. The compressed and collapsed cells had the same appearance as seen in other tests with root.

The passage of radicles and lateral roots through potato

Since PEIRCE found the penetration of living tissue by roots to be purely mechanical, I was not surprised at my failure to find sign of chemical activity on the part of penetrating roots in the tests above described. PEIRCE, however, found the radicle of Pisum able to enter the unwounded potato, a result which was difficult to understand, as I was inclined to assume the hypocotyl of Vicia and Lupinus to be more delicate than the epidermis or periderm of potato. A repetition of PEIRCE's experiment gave negative results. I tried both old and new potatoes, and also fitted glass tube tips to the advancing root to reduce deviation of the tip, but in each test the result was negative. Since PEIRCE used Pisum in his test, I tried that also, in addition to Lupinus and Vicia. If the periderm or epidermis is wounded, an easy entrance is effected by those radicles, and the root advances into the flesh of the potato. In tests with unwounded periderm there was always a deep impression of the potato. Microscopic examination showed that the periderm cells were compressed and to some extent the hypodermal tissue also, but there was no sign of corrosion. The advancing root formed callus, but when the periderm is wounded the callus does not form, and no evidence of obstructed passage is visible.

For the sake of another method a potato was cut into halves and the two halves tightly bound together with cord, so that the outside of one half was in contact with the outside of the other half. Perforations extending to within a few mm. of the periderm were made in one half, and into each perforation a seedling was inserted. The whole preparation was then incased with gypsum. Thus each radicle after penetrating a few mm. of the potato hypoderm found itself in contact with the inner side of the periderm. Further advance brought the tip of the radicle against the periderm of the other half of the potato from the outside. Strong impressions were made upon the periderm from outside. Microscopical examination showed no sign of any chemical activity. Since those same radicles readily traverse the flesh of the potato but do not enter the periderm from the outside, one is almost forced to the conclusion that the mechanical push is too weak. The advancing root simply follows the path of least resistance as long as an advance or deviation is possible. When further advance is impossible, callus forms. Microscopical examination of the flesh of a potato through which a radicle has passed showed no evidence of any digestive action. The collapsed cells with uncorroded walls could be easily found, though the full number of cells required to occupy the volume of the tissue displaced by the radicle was not found in any given section. Compressed tissue too strongly compressed to allow a cell count was however present. No remnants of cells with frayed walls could be found. I did not see evidence of starch digestion in the immediate region through which the radicle passed. In many of the collapsed cells whose protoplasm appeared partially disintegrated, apparently intact starch grains were easily visible. There was no evidence of an active autolysis of starch grains in the cells.

Conclusion

The lateral roots of *Vicia Faba* and of *Lupinus albus* push out from the central cylinder through the cortex *mechanically* and do not have a digestive action upon the surrounding tissue.

NEW YORK CITY

STUDIES IN THE GRAMINEAE

IX. THE GRAMINEAE OF THE ALPINE REGION OF THE ROCKY MOUNTAINS IN COLORADO

THEO. HOLM

(WITH FIVE FIGURES AND PLATE XXX)

The object of the present paper is to offer a small contribution to the knowledge of the alpine vegetation of the Rocky Mountains, which I explored during the summers of 1896 and 1899. It is the intention especially to present some data in regard to the geographical distribution and to make a comparison between the grass vegetation of these mountains and that of mountains in the Old World; also that of the polar regions, which I had the opportunity to visit as a member of three Danish expeditions. Furthermore, I thought that a comparison of the alpine species with those from the wooded belts and the plains of Colorado might be of some interest; and finally a brief anatomical description of the alpine types has been inserted, since thus far the Gramineae have been much neglected in works dealing with structures of alpine plants. It will be seen that the geographical distribution of these species shows several points of interest, more so than their structure; nevertheless, to do full justice to the study of the anatomical characteristics of alpine plants, a consideration of all the families that are represented in these regions is necessary, even if the monocotyledons are of less importance on account of the frequent uniformity in their internal structure.

The exact number of alpine species in Colorado is of course not known; the wild country is very far from being well explored, and the literature is scanty. A very instructive paper was published by Parry,[1] however, who gives a long list of species from these regions, among which 56 species are said to be confined to the bald exposures above the timber line, while 86 others are also to be found at lower

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[1] PARRY, C. C., The Rocky Mountain alpine region. Am. Ass. Adv. Sci. **18**:248; see also PORTER and COULTER, Synopsis of the flora of Colorado. Washington. 1874; GRAY and HOOKER, The vegetation of the Rocky Mountain region. Bull. U. S. Geol. Survey **6**: No. 1. 1880.

elevations. According to this author 58 of these species occur also in the European and Asiatic mountains, or in high northern latitudes of both hemispheres. He enumerates 9 Gramineae. Among the 168 species of flowering plants I collected in this region only 17 belong to the Gramineae. The largest family is the Compositae with 25 species; then follow the Cyperaceae with 20, and then the Gramineae. Just above timberline the vegetation is luxuriant to the full extent of the word, and a number of very different plants abound in the willow-thickets along the mountain brooks; at higher elevations we may observe a rich vegetation on the slopes, especially near the snowbanks; but when we cross the bowlder fields we meet only with a very scant, often extremely poor, vegetation. Among the plants which were observed on the very summit of these mountains may be mentioned *Poa Lettermanni*, *Festuca ovina supina*, *Claytonia megarrhiza*, *Stellaria umbellata*, etc., but none of the Cyperaceae. It seems as if the Gramineae are able to thrive at very high elevations, judging from the various records of alpine plants in Europe and Asia, as will be shown later. It might be stated at the same time that some of these are among those that occur in the most northerly points; for instance, *Alopecurus alpinus* at 83° 4′, *Poa flexuosa* at 82° 50′, and *Festuca brevifolia* at 82° 27′.

In the accompanying Table (I) I have enumerated the alpine species of Gramineae, which I collected on the following mountains: Long's Peak, James' Peak, Pike's Peak, Mt. Elbert, Mt. Massive, Mt. Kelso, Gray's Peak, and along the headwaters of Clear Creek. To these may be added *Deschampsia calycina* Presl. from the summit of Gray's Peak, collected by B. H. SMITH; and *Poa Pattersoni* Vas. from mountains near Gray's Peak, collected by H. N. PATTERSON. The altitude where these alpine species occur lies between 3350 and 4300^{m}. *Agrostis canina* var., *A. varians*, *Avena Mortoniana*, *Poa flexuosa*, *P. gracillima*, *P. Fendleriana*, *P. Lettermanni*, *P. Pattersoni*, *P. alpina*, *Festuca ovina supina*, *Deschampsia calycina*, *Agropyrum Scribneri*, and *A. violaceum* are in Colorado confined to the alpine region. The remaining species, on the other hand, were also observed at lower elevations, from the aspen zone (about 2500^{m}) to the spruce zone (about 3100^{m}). *Phleum alpinum*, for instance, descends to the aspen zone on Long's Peak, where it is very frequent in swamps; *Calamagrostis purpurascens* follows the creeks throughout the spruce zone on Long's Peak and the region of Clear Creek Canyon; *C. canadensis acuminata* is only exceptionally alpine, and thrives best in the swamps of the aspen zone; *Deschampsia caespitosa* is most frequent and typically developed in the swamps of the aspen zone, but it is also very common near the snowbanks at high elevations; *Trisetum subspicatum* does not descend much farther than just to the timberline; *Poa rupicola* descends to the aspen zone on James' Peak and near Central City, but only seldom; *Festuca ovina* was collected in the aspen zone near Central City, and in the spruce zone on Mt. Massive and Long's Peak.

TABLE I

Alpine Gramineae from Colorado	Long's Peak	James' Peak	Pike's Peak	Mt. Elbert	Mt. Massive	Mt. Kelso	Gray's Peak	Headwaters of Clear Creek
Phleum alpinum L.*	..	..	..	+	+	..	..	..
Agrostis varians Trin	+	+	..	..	..	..	..	..
A. canina L. var	..	..	..	..	+	..	..	..
Calamagrostis purpurascens R. Br	+	..	..	..	+	..	+	..
C. canadensis acuminata Vas	..	..	..	..	..	+	..	..
Deschampsia caespitosa Beauv	..	+	..	..	+	+	+	+
Trisetum subspicatum Beauv	..	+	..	+	+	+	..	..
Avena Mortoniana Scribn	..	+	..	..	..	..	..	..
Poa rupicola (Vas.) Nash	..	..	..	+	+	..	+	..
P. flexuosa Wahl	+	..	..	+	..	+	+	..
P. gracillima Vas	..	..	..	..	..	+	..	..
P. Fendleriana (Steud.)	..	+	..	+	..	..	+	..
P. alpina L	+	..	..	+	+	+	..	..
P. Lettermanni Vas	..	..	+	..	..	..	..	..
Festuca ovina L	+	+	..	+	+	+	..	..
F. ovina supina Hack	+	..	+	+	..	..	+	..
Agropyrum violaceum Lge	..	..	..	..	..	+	..	..
A. Scribneri Vas	+	+	..	+	..	..	+	..

* A + indicates the presence of the species, dots its absence.

The distribution of these alpine species on the Pacific and Atlantic coasts is shown in Table II.

It will be seen from this list that of the 20 alpine species from Colorado 13 occur also on the Pacific coast, and 7 on the Atlantic, where they are either alpine or arctic, with the exception of *Deschampsia calycina*. Only 9 of these occur also in the Old World. Table III shows their distribution in the polar regions, in the northern parts of Europe and Asia, but south of the arctic, and in the mountains farther south.

TABLE II

	Pacific	Atlantic
Phleum alpinum	+	+
Agrostis varians	+	..
Calamagrostis purpurascens	+	..
C. canadensis acuminata	+	+
Deschampsia caespitosa	+	+
D. calycina	+	..
Trisetum subspicatum	+	+
Poa flexuosa	+	+
P. gracillima	+	..
P. Fendleriana	+	..
P. alpina	+	+
P. Lettermanni	+	..
Festuca ovina supina	+	+

TABLE III

	Polar regions														
	Arctic America	Greenland	Spitzbergen	Finmark	Russia	Novaja Zemlja	Siberia	Iceland	Faeroe Islands	Great Britain	Alps and Pyrenees	Caucasus	Bajkal' and Altai Mts.	Himalaya	Asiatic coast of Bering Strait
Phleum alpinum	+	+	..	+	+	..	..	+	..	+	+	+	+	+	+
Calamagrostis purpurascens	+	+	..	..	..	..	..	..	..	..	..	..	..	..	..
Deschampsia caespitosa	..	..	..	..	+	..	+	+	+	+	+	+	+	+	..
Trisetum subspicatum	+	+	+	+	+	+	+	+	..	..	+	+	+	+	+
Poa flexuosa	+	+	+	+	+	+	+	..	..	..	..	..	+	+	+
P. alpina	+	+	+	+	+	+	+	+	+	+	+	+	+	+	..
Festuca ovina	+	+	+	+	+	+	+	+	+	+	+	+	+	..	+
F. ovina supina	+	+	+	+	+	+	+	..	..	..	..	..	..	..	+
Agropyrum violaceum	+	+	..	+	..	..	+	..	..	..	..	..	..	..	..

Four of these are circumpolar: *Trisetum subspicatum*, *Poa flexuosa*, *P. alpina*, and *Festuca ovina*, also the var. *supina*. *Calamagrostis purpurascens* is the only one that is confined to this continent and Greenland; *Agropyrum violaceum* occurs in the arctic regions of both hemispheres, and var. *supina* of *Festuca ovina* is also an inhabitant of these high northern regions outside America. All the others extend to the mountains farther south, and five of these have even reached the Himalayas. According to CHEESEMAN,[2] *Deschampsia caespitosa macrantha* Hack. and *Trisetum subspicatum* occur in New Zealand, and the latter has also been recorded from the antarctic regions. *Deschampsia caespitosa* is in Arctic America, Greenland, Novaja Zemlja, and Arctic Siberia, mostly represented by vars. *brevifolia* Trautv. and *borealis* Trautv. *Agrostis canina* occurs in Greenland and in several forms, but the variety which I collected in Colorado is not among these. Professor HACKEL, who has kindly examined my specimens of Agrostis, thinks that my alpine *A. canina* is nearest to var. *pusilla* Aschers. et Graebn.

Tables II and III thus demonstrate the fact that the alpine Gramineae in Colorado represent an assemblage of several very distinct geographical types: some that are endemic to this particular region; some that occur also on the Pacific and Atlantic coasts; some that have reached the polar regions in certain parts of both hemispheres; some that are circumpolar; and finally some that have become dispersed throughout the mountainous districts farther south in Europe and Asia. Of the 20 species enumerated from the mountains of Colorado, 7 are arctic-alpine types. *Deschampsia caespitosa* and *Festuca ovina* are quite frequent in these alpine and arctic regions, but their widest distribution is within the lowlands of the temperate zones of both hemispheres; hence they are not "arctic-alpine" in the strict sense of the word.

The tribes that are thus represented in this alpine region are AGROSTIDEAE (5 spp.), AVENEAE (4 spp.), FESTUCEAE (8 spp.), and HORDEAE (2 spp.). They are represented by genera that are really cosmopolitan, and from Table III we have seen that some of the species are widely distributed in both hemispheres. These data alone might suffice to illustrate the principal points in regard to composition and geographical distribution; but in order to make the illustration more complete, it seems necessary to extend our comparison to the grass vegetation in the timbered belts and on the plains below; also to the vegetation of alpine regions of other mountains.

Beginning with the species of the spruce zone, it has been stated that some of the alpine species are found among them, where they become associated with a few types characteristic of the zone; and

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[2] CHEESEMAN, T. F., Manual of the New Zealand flora. 1906.

with some others which are common also to the aspen zone below. The following were observed only in the spruce zone: *Sporobolus brevicalyx* Scribn., *Calamagrostis Langsdorffii* (Link) Trin., *C. Scribneri* Beal, *Agrostis humilis* Vas., *Poa reflexa* Vas. and Scribn., and *Festuca ovina pseudo-ovina;* while *Poa pratensis* L. was also collected in the aspen zone.

If we continue the comparison, and examine the species that occur in the aspen zone, we meet with a larger number of species of the same tribes that were observed at higher elevations, and with them there also occur some of the Chlorideae. Peculiar to this zone are: *Stipa minor* Scribn., *Muehlenbergia comata* Benth., *M. gracilis* Trin. and the var. *breviaristata* Vas., *Alopecurus aristulatus* Michx., *Sporobolus depauperatus* (Torr.) Scribn., *Agrostis exarata* Trin., *Trisetum montanum* Vas., *Koeleria cristata* Pers., *Glyceria americana* (Torr.), *G. Holmii* Beal, *Poa annua* L., *P. nemoralis* L., *Festuca Thurberi* Vas., *Bromus breviaristatus* Thurb., *B. Richardsonis* Link, *Hordeum nodosum* L., *Elymus Sitanion* Schult., and *E. brevifolius* (Sm.). Besides these there are a few species which occur here, but which more properly belong to the plains, where they are more abundant and more typically developed. These are *Agrostis scabra* Willd., *Schedonnardus texanus* Steud., *Bouteloua oligostachya* Torr., and *Atropis airoides* (Nutt.). The number of species of Gramineae observed in the mountainous regions, from the aspen zone to the summits, averages about 50, among which the Chlorideae are rather scantily represented.

Descending to the plains, at an elevation of 1500$^{\text{m}}$ about 40 species belonging to the same tribes are found; the Andropogoneae and Paniceae are added; and the Chlorideae abound. The following species are very frequent: *Panicum virgatum* L., *P. capillare* L., *Aristida fasciculata* Torr., *Stipa comata* Trin. and Rupr., *S. viridula* Trin., *Eriocoma cuspidata* Nutt., *Cenchrus tribuloides* L., *Sporobolus cryptandrus* Muehl., *S. asperifolius* Thurb., *S. airoides* Torr., *Calamovilfa longifolia* (Hook.) Hack., *Agrostis scabra* Willd., *A. intermedia* Scribn., *A. alba* L., *Schedonnardus texanus* Steud., *Bouteloua oligostachya* Torr., *B. racemosa* Lag., *Buchloë dactyloides* Engelm., *Munroa squarrosa* (Nutt.) Torr., *Distichlis spicata* (L.) Grne., *Atropis airoides* (Nutt.), *Poa Buckleyana* Nash, *Festuca tenella* Willd., *Agro-*

pyrum occidentale Scribn. vars. *mollis* and *vivipara*, *A. tenerum* Vas., *A. spicatum* Pursh, *Hordeum jubatum* L., and *Elymus canadensis* L. Some others are more scattered, for instance: *Andropogon furcatus* Muehl., *Echinochloa crus-galli* (L.) Beauv., *Muehlenbergia glomerata* Trin., *Lycurus phleoides* H. B. K., *Setaria glauca* L., *Bouteloua prostrata* Lag., *Diplachne fascicularis* (Lam.) Beauv., *Eragrostis major* Host., etc.

This grass vegetation in the wooded belts and on the plains consists mostly of American types, and the very few species that are also represented in the Old World are mostly introduced, for instance: *Echinochloa crus-galli*, *Digitaria glabra*, *Setaria glauca*, *Eragrostis major*, and *Agrostis alba*. *Calamagrostis Langsdorffii*, which I found in the spruce zone on Mt. Massive, occurs also in the mountains of New England, Canada, Alaska, south to California, and is also an inhabitant of Europe and Asia. *Poa annua*, *P. nemoralis*, *P. pratensis*, and *Koeleria cristata*, widely distributed species in the Old World, especially in the lowlands of the cold temperate zone, are also represented in the aspen zone. *P. nemoralis* is very common and varies according to the substratum, whether dry rocks or rich soil, in thickets, along streams, etc.

In comparing the geographical distribution of these various species of Gramineae which occur in the alpine region, in the wooded belts of the mountains, and on the plains, it is noticeable that the genera of the alpine flora are more cosmopolitan than those of the lower levels. None of the genera of the alpine Gramineae are endemic, and about one-half of the species occur also in the Old World (cf. Table III). On the other hand, the presence of arctic and circumpolar species is characteristic of the alpine flora, species which may be regarded as remnants of an old glacial vegetation that migrated from the far north; but those endemic in Colorado may have developed in the alpine regions of these very mountains.

Let us now examine the grass vegetation of the alpine region of the Alps of Switzerland, the Pyrenees, the mountains of Norway, the Caucasus, and the Himalayas. In these mountains the tribes that occur in Colorado are found, besides the Phalarideae, of which *Hierochloa laxa* Br. has been reported from the Himalayas (5000^m), and *Anthoxanthum odoratum* L. from Switzerland and the Caucasus.

In the Alps of Switzerland the tribe Festuceae is the best represented, according to HEER.[3] There are four species of Festuca (*F. ovina* L., *F. pumila* All., *F. pilosa* Hall. fil., and *F. Halleri* Vill.) and five of Poa (*P. alpina* L., *P. caesia* Sm., *P. laxa* Hnke., *P. minor* Gaud., and *P. annua* L.). *Koeleria hirsuta* Gaud., *Sesleria coerulea* L., and *S. disticha* Pers. also are present. Four Aveneae occur here (*Avena distichophylla* Vill., *A. versicolor* Vill., *Deschampsia caespitosa* Beauv., and *Trisetum subspicatum* Beauv.); two small species of Agrostis (*A. rupestris* All. and *A. alpina* Scop.) represent, with *Phleum alpinum* L., the Agrostideae; while *Nardus stricta* L. is the only member of Hordeae, observed so far, in these regions. Of these species *Sesleria disticha* and *Poa laxa* have been recorded from the highest elevation (3000^{m}).

In the Pyrenees[4] the genera are about the same, with the addition of *Holcus caespitosus* Boiss. (Aveneae), *Molinia coerulea* Moench., and *Nardurus Lachenalii* Godr. (Festuceae). The Festuceae are here also best represented, numbering 17 species, among which the following are known also from Switzerland: *Sesleria disticha*, *Festuca Halleri*, *F. pumila*, *Poa laxa*, *P. caesia*, *P. minor*, and *P. alpina*. Among the Agrostideae, *Agrostis rupestris* and *A. alpina* are here accompanied by three other species: *A. setacea* Curt., *A. nevadensis* Boiss., and *A. capillaris* L., while *Phleum alpinum* is only known from the subalpine region of these mountains. The Aveneae are represented by *Deschampsia flexuosa*, while *D. caespitosa* occurs only at lower elevations; also by *Avena albinervis* Boiss., *A. Scheuchzerii* All., *Holcus caespitosus* Boiss., *Trisetum flavescens* Beauv., *T. velutinum* Boiss., *T. glaciale* Boiss., and *T. Gaudinianum* Boiss., while *T. subspicatum* does not reach the alpine region in these mountains. The Hordeae are also here only represented by *Nardus stricta*.

In the mountains of Norway[5] the alpine Gramineae number only 8 species: *Phleum alpinum*, *Aira alpina* L., *Trisetum subspicatum*, *Catabrosa algida* Fr., *Poa laxa*, *P. stricta* Lindeb., *P. flexuosa* Wahl., and *P. alpina*, all of which extend to the arctic region.

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[3] HEER, O., Ueber die nivale Flora der Schweitz. 1883.

[4] D. MARIANO DEL AMO Y MORA, Flora Fanerogámica de la Peninsula Iberica. Granada 1:2. 1871.

[5] BLYTT, M. N., Norges Flora. Christiania. 1861.

According to MEYER[6] 22 Gramineae are alpine in the Caucasus. Of special interest are *Phleum alpinum, Avena versicolor, Deschampsia flexuosa, Trisetum flavescens, Poa alpina, Koeleria cristata,* and *Festuca ovina.* Besides these it is interesting to notice the occurrence of *Calamagrostis caucasica* Trin., *Briza media* L., *Poa altaica* Trin., *Colpodium Steveni* Trin., and *Hordeum pratense* Huds.

If we extend the comparison to the Himalayas,[7] we notice the presence of 5 alpine species which occur also in Colorado (cf. Table III); also the occurrence of genera that are not represented in the other mountains, namely Hierochloa, Stipa, Deyeuxia, Danthonia, and Elymus (*E. sibiricus* L.). The very considerable elevation of 5500^{m} is in these mountains reached by *Trisetum subspicatum, Poa hirtiglumis* Hook. f., and *Elymus sibiricus* L.; from between 4500 and 5100^{m} the following are recorded: *Hierchloa laxa* Br., *Agrostis inaequiglumis* Griseb., *Deyeuxia compacta* Munro, *D. nivicola* Hook. f., *D. pulchella* Hook. f., *Deschampsia caespitosa, Catabrosa sikkimensis* Stapf, *Poa alpina* L., *P. attenuata* Trin., *P. nemoralis* L., *P. flexuosa* Wahl., *P. tremula* Stapf, and *Festuca valesiaca* Schleich. Two species of Stipa (*S. concinna* Hook. and *S. mongolica* Turcz.) ascend to an elevation of 4000^{m}.

The Himalayas are thus much richer in alpine types than any of the other mountains, a fact that becomes still more manifest when we compare the representatives of the other families. Nevertheless, the alpine Gramineae of the Himalayas do not possess any type which from a biologic point of view deviates to any great extent from those of Colorado. For instance, Stipa and Elymus are really the only alpine genera in which the structure of spikelets is quite distinct from that of most of the others. It seems altogether as if the alpine Gramineae are remarkably uniform in habit, and in floral structure.

In speaking of Colorado especially, we have not in the alpine region a single type that may be compared with Buchloë, Munroa, Sporobolus, or Distichlis from the lowlands. The alpine representatives are perennial, except *Deschampsia calycina;* they are mostly

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[6] MEYER, Verzeichniss der Pflanzen, welche im Caucasus etc., gefunden sind. St. Petersburg. 1831.

[7] HOOKER, J. D., Flora of British India. London. 1894. Vol. 6.

caespitose or sometimes stoloniferous, but with simple culms, and with an inflorescence (spicate or paniculate) of the usual composition. The empty glumes show no peculiar structure, and the flowering glume is either awned or awnless, and not in any way different from the usual structure among grasses in general. The average height of these alpine Gramineae is in some cases much less, in other cases about the same as that of lowland species of the same genera. *Poa Lettermanii*, the species of Agrostis, and *Festuca ovina* are mere dwarfs, but *Agropyrum Scribneri* reaches a height of 50^{cm}, even at an elevation of 4000^{m}. *Agropyrum violaceum* at the same altitude has culms about 40^{cm} high; and the culms of *Deschampsia caespitosa*, *Calamagrostis purpurascens*, and *Poa gracillima* reach about the same height. In habit the alpine Gramineae do not exhibit any characteristics which might indicate the extreme conditions under which they live. The same is the case with those grasses that occur in the arctic region, where we meet with several species that do not occur farther south, but the habit of these is of the same general kind. It is very different with the representatives of most of the dicotyledonous families from the alpine and arctic regions; in these the habit is frequently so peculiar and characteristic that they are readily recognized as being either alpine or arctic. In other words, the monocotyledons, at least the Glumiflorae, do not appear to be influenced to any great extent by climate and soil, as are most of the dicotyledons, at least not in regard to their general habit in alpine or arctic regions.

An examination of the internal structure of these alpine species from Colorado will demonstrate probable characteristics in structure; "probable," because I am not in a position to make any comparison with species from other alpine regions. It is my intention merely to present these anatomical data for future comparison, when someone may feel induced to investigate the grass vegetation of other mountains, and especially from high altitudes. I have examined roots, culms, and leaves. The leaf structure might have been sufficient, and, as already stated, most authors have so far confined their work to the leaves alone. However, it does not appear to me that the structure of culms and roots should be neglected altogether, and especially not when dealing with plants that are able to persist under such extreme conditions.

The roots

In considering the internal structure of roots that are simply nutritive and of no long duration (perhaps only one season), we must not expect to find great modifications. In regard to the Gramineae we have learned from KLINGE'S[8] interesting paper that certain modifications may be observed in the structure of the cortex, whether persisting or collapsing, whether homogeneous or differentiated as distinct zones of parenchymatic or stereomatic strata; also in the thickening of the endodermis, and in the structure of the pericambium, whether it is continuous or interrupted by the proto-hadrome. The presence or absence of an exodermis also seems to be worth mention, and the structure of the parenchyma in the stele, which sometimes represents a central pith. Much attention has been given to the position of the proto-hadrome vessels, whether they are inside the pericambium or border directly on the endodermis. In some instances all these vessels have been observed to occupy the same position in reference to the pericambium; but in other instances a variation has been noticed, where only some of the proto-hadrome vessels had broken through the pericambium. In studying root structures of different plants, especially of monocotyledons, one gets the impression that the continuity or interruption of the pericambium is of some importance and constitutes a good anatomical character. In very many roots I have found a constantly continuous pericambium or a constantly interrupted one; but on the other hand, as shown in Eriocaulon and Carex,[9] there are also cases where this structure is not constant, but varies from the base to the apex of the same root. This peculiarity I noticed by making consecutive sections of a number of roots, and it appears therefore as if the structure of the pericambium, so far as concerns its continuity or interruption, is not a character to be depended upon. In *Deschampsia caespitosa* and *Festuca ovina* from Europe, KLINGE (*l. c.*, p. 56) observed the proto-hadrome vessels bordering on the endodermis; while in these same species from Colorado all the vessels were found to be inside the pericam-

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[8] KLINGE, Vergleichend histiologische Untersuchung der Gramineen- und Cyperaceen-Wurzeln insbesondere der Wurzel-Leitbündel. Mém. Acad. Imp. St. Petersbourg VII. **26**: No. 12. 1879.

[9] BOT. GAZETTE **31**: 17. 1901; and Am. Journ. Sci. **10**:278. 1900.

bium. Such discrepancies often occur, but they are hardly of any importance.

In the alpine Gramineae from Colorado the root structure is very uniform. The epidermis is hairy in all the species; a thin-walled exodermis was observed only in *Agropyrum violaceum.* The cortical parenchyma is mostly thin-walled and solid, but a radial collapsing was noticed in the species of Poa, with the exception of *P. alpina*, in Trisetum, and in Deschampsia. In the species of Agropyrum the peripheral strata of the cortex are stereomatic, and persistent in comparison with the inner, which are thin-walled and collapsed. The endodermis is generally thick-walled (*figs. 1–5, End*), representing a typical U-endodermis, or an O-endodermis, as was observed in specimens of *Poa alpina* from bowlder fields. The pericambium was found to be continuous in all the species, and it is generally thin-walled; but in the species of Agrostis (*fig. 2*), Calamagrostis, Trisetum, and in *Poa gracillima* it is more or less thick-walled. It consists mostly of a single layer, but in the species of Agropyrum (*fig. 5*) and Avena two or three layers are developed outside the proto-hadrome vessels. The number of hadromatic rays is of course very variable; in the thick roots of Trisetum, Deschampsia, Calamagrostis, Avena, and Agropyrum there may be as many as fifteen rays, but with mostly a single proto-hadrome vessel in each ray. In the species of Agrostis and Festuca the hadrome extends to the center of the stele, while in the others a central pith is developed. This pith is quite broad, and often conspicuously thick-walled, as in Trisetum, Agropyrum, Avena, and Calamagrostis.

It is interesting to note that in some cases the root structure corresponds with the nature of the substratum. For instance, in *Poa Lettermanni*, which I found growing in wet moss near the snowbanks, the root structure resembles that of a hydrophilous plant, with open cortex, thick-walled endodermis, and thin-walled pericambium. In the species of Agropyrum from very dry, stony soil, the peripheral strata of the cortex are stereomatic. In *Calamagrostis purpurascens* from similar stations there is a very compact cortex, a heavily thickened endodermis, a thick-walled pericambium, and a broad central, very thick-walled pith. A similar, very solid structure is also characteristic of the species of Festuca and

Agrostis, inhabitants of dry soil among bowlders. The roots of these species thus show in general the structure of xerophytes. But in *Poa alpina* no such distinction seems feasible, since the structure is identical whether the specimens are from wet soil in thickets of willows along mountain brooks, or from dry soil among bowlders.

The culm

In describing the structure of the culm, attention must be given to the distribution of the mechanical tissue (stereome), to the minor structure and disposition of the mestome strands, and finally to the structure of the cortical parenchyma. In the character of the stereome our alpine Gramineae represent the type in which a circular band of this tissue (in cross-sections) is in contact with all the mestome bundles; it is the eleventh type of SCHWENDENER[10] and is the one most frequently observed in the Gramineae. While the principal feature of this type is that all the mestome strands are in contact with the mechanical tissue, some modifications are to be observed in regard to the relative development or strength of the stereome, especially in cases where the mestome bundles occur in different sizes, and in more than one circular band. Five very distinct modifications were observed in our alpine species, which may be readily distinguished by the accompanying figures, which I have drawn in a schematic way. The black represents the stereome; the peripheral white zone the cortex; the central white zone the pith; the orbicular and oval rings the mestome strands.

In these figures, *A* represents the most simple structure, where there are only five mestome strands, all the same size and outline (oval), and all imbedded in the stereome, which extends to epidermis, thus forming a strong, hypodermal support outside the leptome (*Agrostis canina*, var.). In *B* there are four large, oval mestome strands, alternating with four much smaller ones, which are orbicular in transverse section, and they are all surrounded by stereome, which only extends to the epidermis outside the larger ones (*Poa Lettermanni*, *P. alpina* from Long's Peak, and *Agrostis varians*). In *C* (*Poa rupicola*) there is also one band of mestome bundles, composed of

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[10] SCHWENDENER, Das mechanische Princip im anatomischen Bau der Monocotylen 60. Leipzig. 1874.

larger (oval) and smaller (orbicular) ones; and hypodermal stereome occurs outside each of the mestome strands, but is only in contact with the leptome side of the larger ones; the smaller strands only touch the inner stereome with their hadrome side. When two concentric bands of mestome bundles occur, the peripheral ones are the smallest and are orbicular in cross-section; the inner ones are either orbicular (*D*) or oval, often representing two sizes, as shown in *E.* In these culms (*D* and *E*) the stereome shows two well-marked modifications. It constitutes a mechanical support on the leptome side of all the mestome strands in *D;* while in *E* this hypodermal support is confined to the peripheral strands alone—those of the inner band (*E*) are imbedded in a zone of stereome, which does not extend to epidermis. The structure illustrated by *E* was observed in *Calamagrostis purpurascens*, *Agropyrum violaceum*, and *Deschampsia caespitosa* from Graymont; while *D* is the most frequent

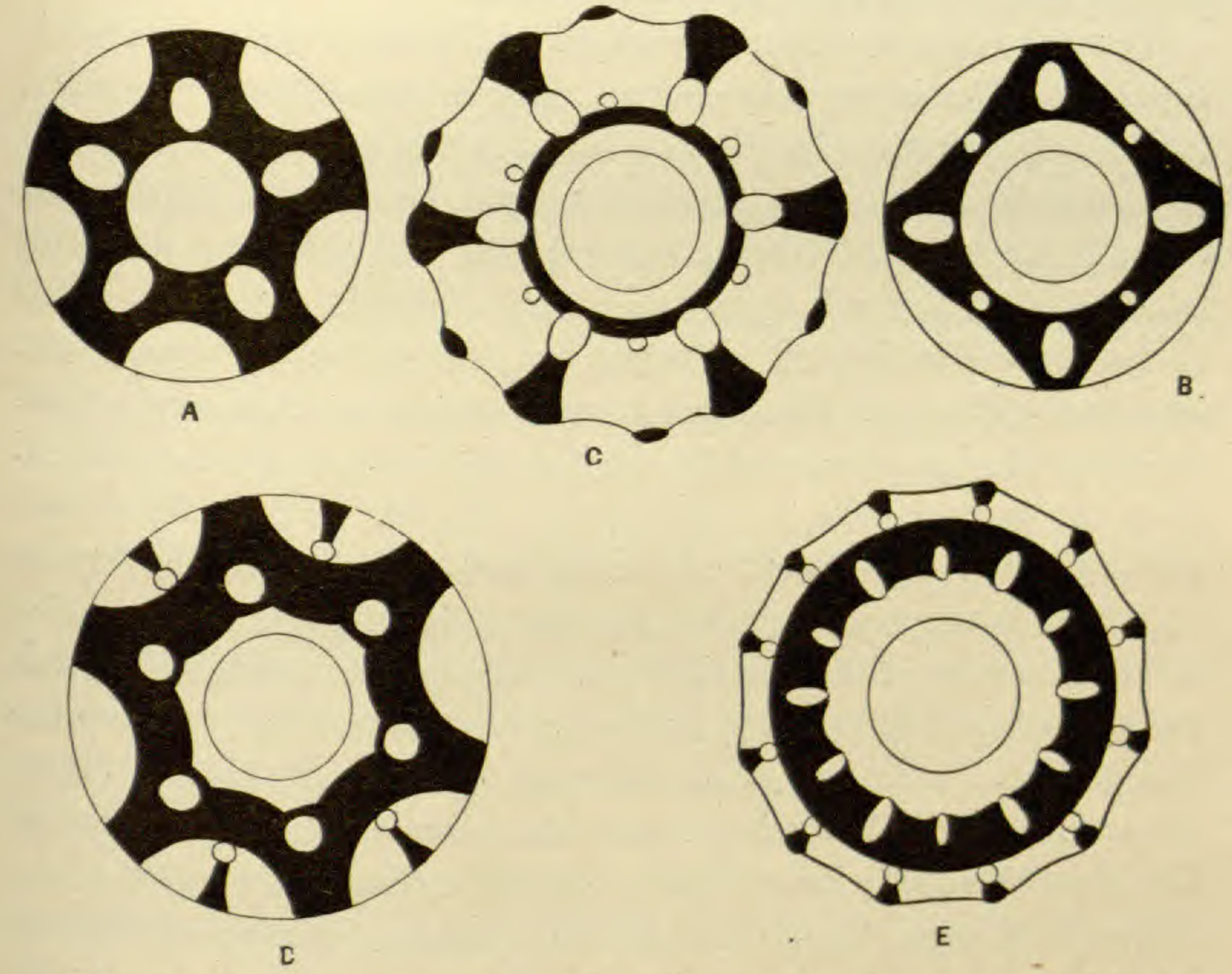

Diagram showing the structure of the culms of *Agrostis canina* var. (*A*), *Poa Lettermanni* (*B*), *P. rupicola* (*C*), *P. alpina* (*D*), and *Agropyrum violaceum* (*E*).

structure exhibited by the remaining species, including *Poa alpina* from Mt. Kelso and *Deschampsia caespitosa from* Gray's Peak. These culms thus represent five types as to the occurrence of one or two bands of mestome bundles, and as to the distribution of the stereome as a circular band extending to the epidermis as hypodermal groups in contact with or separated from some of the mestome bundles (the latter case is illustrated in *C*).

The fact that two of these types (*D* and *E*) have been observed in one species (*Deschampsia caespitosa*), though from different elevations, seems to indicate that the structure may not be constant. The type *D* appears to be the most frequent in the alpine species of Colorado, and the most important difference between this and the three preceding (*A*, *B*, and *C*) depends upon the presence of two concentric bands of mestome bundles, all of which are supported by hypodermal stereome. The type *E* is more complicated on account of the inner mestome strands being of different size and lacking the hypodermal stereome, and this type, as stated above, was observed in *Agropyrum violaceum*. If this structure be compared with that of the French species of Agropyrum described by DUVAL-JOUVE, it is observed that it does not agree with any of them. The species examined by this author were lowland species, and several were maritime. Characteristic of these species is the occurrence of hypodermal stereome outside the smaller as well as the larger mestome strands; also in some species the inner band may be located nearer the center of the culm, a considerable distance from the stereomatic zone. In other words, the lowland species of Agropyrum in France represent actually an entirely distinct type of structure, which corresponds with the twelfth type of SCHWENDENER (*l. c.*), in which the inner mestome strands are in the pith, some distance from the stereomatic cylinder.

The minor structure of the mestome strands in our alpine species agrees in most respects with that of other Gramineae. It has been shown that some variation occurs in the outline of cross-sections, some being orbicular (especially the smaller ones), and the larger ones usually oval. The leptome and hadrome differ in no way from that of other species from lower elevations. A more or less thick-

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[11] DUVAL-JOUVE, Etude anatomique de quelques Graminées et en particulier des Agropyrum de l'Hérault. Mém. Acad. Sci. Montpellier. Paris. 1870.

walled mestome sheath was observed in all the alpine Gramineae, and these species may thus be added to the list given by SCHWENDENER[12] in his paper on mestome sheaths. However, the presence or absence of the mestome sheath, as already pointed out by SCHWENDENER (*l. c.*, p. 415), is merely of taxonomic importance. This may be readily seen from his list, according to which this sheath is not developed in any of the species of Andropogoneae and Maydeae, or in certain genera of the Paniceae (Paspalum, Pennisetum, and Setaria). The fact that it occurs in some species of Panicum (*P. miliaceum, P. capillare, P. proliferum*), but not in others (*P. sanguinale, P. plicatum, P. colonum*, etc.), seems to indicate that these species represent very distinct types within the genus, as shown also by the external structure of their spikelets. The same conclusion may be drawn from the fact that the species of Aristida in which I observed a double parenchyma sheath,[13] but no mestome sheath, differ in a marked degree from those which possess this sheath, and in which only a single parenchyma sheath is developed; we have here to deal with a taxonomic, and not with an epharmonic character. By studying the anatomy of a number of Gramineae allied to or associated with Aristida, I found a mestome sheath constantly developed, whether the material was collected on the plains, the prairies, in woodlands, or in marshes. If on the other hand the structure of the mestome sheath is examined, some kind of modification in the thickening of the cell walls is noticed, which evidently constitutes an epharmonic character; in the alpine species this sheath was generally observed to be quite thick-walled. The presence or absence of thick-walled mestome parenchyma as a stratum between the leptome and the hadrome is to be considered only of taxonomic importance; such parenchyma was not observed in *Poa Lettermanni, P. gracillima, P. rupicola*, or in the species of Festuca and Avena, but in all the others.

Of much greater interest, however, is the structure of the cortical parenchyma. This tissue is very compact in these Gramineae with the exception only of *Poa Fendleriana, P. gracillima*, and *Phleum alpinum*. It is either developed as a palisade tissue of several layers

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[12] SCHWENDENER, Die Mestomscheiden der Gramineenblätter. Sitgungsber. Berliner Akad. Wiss. 413. 1890.

[13] HOLM, THEO. Some new anatomical characters for certain Gramineae. Beih. Bot. Centralbl. 11:—. 1901.

(*fig. 6, C*) or as a homogeneous tissue of roundish cells (in cross-section). The former structure is the most frequent, and especially well represented in *Poa rupicola*, *P. Lettermanni* (*fig. 6*), and *Agrostis canina;* the latter structure was observed in *Agrostis varians*, *Poa flexuosa*, Agropyrum, Calamagrostis, Deschampsia, and Festuca.

We will finally consider the structure of the cuticle and epidermis. The cuticle was observed to be smooth and quite thick in all the species, even in the densely hairy Trisetum. The epidermis is scabrous in Calamagrostis, hairy in Trisetum, but glabrous in the others. Some slight variation in the structure of the cell walls was noticed; the outer wall, for instance, is quite thick as compared with the inner and the radial, and this structure seems to be the most frequent. But in *Agrostis canina*, *Poa rupicola*, *Phleum alpinum*, and *Agropyrum violaceum* all the cell walls of epidermis were equally and quite heavily thickened.

A very firm structure is thus exhibited by the culms of our alpine Gramineae, so far as concerns the mechanical tissue and the dense cortical parenchyma covered by a thick-walled epidermis. It is also interesting to notice that the cortex generally contains much chlorophyll, and that the cells are developed as typical palisades, thus being able to perform the function of the chlorenchyma in the leaves. The modifications in structure in the culms depend mostly upon the distribution of the stereome, and upon the mestome strands (their relative size, their mechanical support, and their disposition in one or two concentric bands). The pith, on the other hand, shows no deviation from the most common structure known in this family; it was constantly found to be thin-walled and broken in the center, and with no deposits of starch.

The leaves

In the leaves the epidermis and chlorenchyma offer some distinctions of importance, and much more so than the stereome, at least in the alpine species. However, the structure is very uniform, and does not exhibit any such prominent epharmonic characters as are so well known from species of the lowlands, the plains, and the prairies. In the alpine species the leaf structure is very firm throughout; there are no wide intercellular spaces in the chlorenchyma, and no water-storage tissue surrounding the veins. The distribution of the stereome is mainly the same in all the species and rather scantily represented as compared with the culm. The mestome strands are constantly arranged in a single plane and are very uniform in structure.

In the epidermis the outer cell wall is generally quite thick on the dorsal face, but less so on the ventral; the cuticle is smooth, and very distinct in all the species. The characteristic bulliform cells between the mestome strands on the upper face of the blade were observed in all the species, but they are not very large, and are sometimes confined to a single group, one on each side of the midrib, as in *Poa Lettermanni*, *P. flexuosa*, *P. gracillima*, and *P. rupicola*; in the other species there may be four to six or even a larger number of groups in the lateral parts of the leaf blade. In *Poa Lettermanni* (*figs. 7, 8*) the leaves are glabrous on both faces, but in the other species they are generally a little scabrous from small, obtuse papillae. Pointed, prickle-like projections occur in Festuca, Agrostis, *Poa rupicola*, *P. Fendleriana*, and *P. alpina* from Long's Peak. Hairs are not frequent, but were observed on the ventral face of the blade in *Poa gracillima*, Calamagrostis, and Avena, and on both faces in Trisetum and *Agropyrum Scribneri*. With the exception of *Trisetum subspicatum*, which may be called densely hairy, the hairs in the other Gramineae are so scattered that they are often hardly visible to the naked eye.

The stomata (*fig. 7*) occur mostly on both faces of the blade, but as a rule are most frequent on the ventral face; in some species of Poa, *Agropyrum Scribneri*, Calamagrostis, and Trisetum they are confined to the ventral face. They are usually sunk, and sometimes covered by papillae or hairs, and they occur especially on the sides of the furrows between the mestome bundles. Their position in reference to the surface may sometimes vary on the same leaf; for instance, in *Agropyrum violaceum* they are free on the ventral face, but sunk on the dorsal, while the opposite is true of Avena; in *Deschampsia caespitosa* they are level with the epidermis, and not covered by the papillae. Otherwise the structure of the epidermis offers no points of particular interest.

The stereome is poorly represented in most of these species, and occurs often only as a very small hypodermal strand outside the larger mestome bundles (*fig. 8*) and not in contact with them; it is better developed in the margins of the leaves. The mestome strands show the same structure in regard to the leptome and hadrome as observed in the culm; there is also the same variation from oval to orbicular (in cross-section), and the mestome sheath is typically developed with the inner cell wall heavily thickened. Outside the mestome sheath the ordinary thin-walled parenchyma sheath is found mostly containing some chlorophyll. I have not observed a single instance in these alpine species where mestome strands occurred beneath the bulliform cells; but in *Deschampsia caespitosa* from Graymont, at a much lower elevation, some few very fine veins were observed between the larger ones, thus being located directly underneath the bulliform cells. It might be mentioned at the same time that DUVAL-JOUVE (*l. c., pl. 16, fig. 5*) figures a leaf of a French specimen in which a very small mestome strand occurs between each of the two larger veins, just beneath the bulliform cells.

The chlorenchyma is very compact in these alpine species, and is mostly developed as a palisade tissue. In *Poa Lettermanni*, however, it is developed as palisades only around the mestome strands, radiating toward their center, while in the other portions of the leaf this tissue consists of much shorter and roundish cells (*figs. 7, 8*). In *Poa flexuosa* there are no palisades at all; in Phleum the cells are hardly high enough to be called palisades, even if some distinction may be noticed between the ventral and dorsal portion of the chlorenchyma. In all the other species the chlorenchyma constitutes a homogeneous palisade tissue, vertical to the surface or radiating toward the center of the mestome bundles. It is a very compact tissue throughout the leaf blade, and rich in chlorophyll.

The leaves of the alpine Gramineae are mostly erect, though not exactly vertical, and are frequently conduplicate or with the margins involute; they are seldom spreading or perfectly flat. In this way they agree to some extent with the species from the plains, although the internal structure is very different, at least in certain genera. In the alpine species the leaves are often furrowed on the ventral face, but not to the extent so commonly observed in the lowland species, in those that inhabit the plains for instance. This may perhaps be the reason why the stomata in the alpine species are so much deeper than in those from the lowlands, where they are level with the epidermis, but protected by the more ample covering of papillae or hairs, and also by the greater depth of the furrows. In the leaves of the lowland species the stereome is better represented, the bulliform cells generally larger, and frequently accompanied by several strata of a colorless tissue, the so-called water-storage tissue, which is not developed in the alpine species. But in the chlorenchyma of the Gramineae from the plains and prairies we find a more or less homogeneous tissue of palisades occupying the position described above. Finally the fact must be mentioned that the stomata being most frequent on the ventral face of the leaf is a feature the alpine Gramineae have in common with nearly all those which I have examined from the lowlands, and especially those from the plains and prairies, with the exception of Sporobolus, Munroa, and Calamovilfa. In the woodland types of Muehlenbergia the stomata are almost equally distributed on both faces of the leaf blade; while in the species of the same genus from dry, rocky mountain slopes, the stomata are confined to the ventral face and protected by the folding of the blade. In species from wet soil, meadows, or swamps, the stomata are most frequent on the dorsal face in Leersia; while in Amphicarpum from moist pine barrens they are distributed over both faces, though most numerous on the ventral; in *Uniola latifolia* from shaded slopes the stomata occur only on the ventral face, and this same disposition is to be found also in *Pleuropogon Sabinei* from arctic swamps. DUVAL-JOUVE, who has examined a large number of Gramineae,[14] speaks of the difficulty of giving any precise information about the distribution of stomata in this family. He observed also that the ventral face of the blade is sometimes the only one where the stomata occur, but at the same time he noticed that a torsion of the leaf took place, thus exposing the dorsal face to the sun instead of the ventral. In this way the stomata become well protected, but in our alpine types the only protection seems to depend upon the folding of the blade, conduplicate or with the margins involute.

The leaf structure of alpine plants has been described and explained by several authors, but the Gramineae have been neglected, and evidently because the narrow leaves appear to be more uniform in

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[14] DUVAL-JOUVE, Histotaxie des feuilles de Graminées. Ann. Sci. Nat. Bot. VI. 1:314.

structure and apparently of less interest. I am not in the position to draw any anatomical comparison, therefore, between the species from the Rocky Mountains and those from other alpine regions. The alpine types which have been treated and studied in Europe are nearly all dicotyledons, and the results are not quite comparable to those derived from the study of our Gramineae. According to BONNIER[15] and WAGNER,[16] the palisade tissue should be far better developed in the alpine forms (dicotyledons) than in those from the lowlands; the leaves should be thicker, and the structure more open on account of the wider intercellular spaces; also the alpine leaves should be more thoroughly dorsiventral, with stomata sometimes more abundant on the ventral than on the dorsal face; the guard cells should be level with the epidermis except in species with evergreen leaves (Ericaceae, etc.).

These distinctions are not to be observed in the Gramineae. We have seen that in the alpine representatives of this family the leaves are not dorsiventral; the palisade tissue is not developed to any greater extent than in the lowland species; the chlorenchyma is not open, on the contrary it is very compact; also the stomata are not level with the epidermis but mostly sunken. It seems almost safe to conclude that the epharmonic characters are much less pronounced in the alpine Gramineae than in the dicotyledons from similar high situations, when compared with the corresponding lowland types. Much would be learned, however, by examining alpine Gramineae from other parts of the world, and especially other genera and species than those described in the preceding pages. Also the study of alpine types ought not to be restricted to a mere consideration of the foliar organs, even if these unquestionably are the most important; the structure of stem and root ought not to be excluded altogether, as is frequently or nearly always the case.

Conclusions

We have seen that the alpine Gramineae of Colorado constitute an assemblage of very distinct geographical types; some that are only

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[15] BONNIER, GASTON, Cultures expérimentales dans les hautes altitudes. Compt. Rend. Acad. Sci. 1890; Etude expérimentale sur l'influence du climat alpin sur la végétation et les fonctions des plantes. Bull. Soc. Bot. France **1888**:436.

[16] WAGNER, Zur Kenntniss des Blattbaues der Alpenpflanzen und dessen biologischer Bedeutung. Sitgungsber. K. Akad. Wiss. Wien **101**:59. 1892.

known from the alpine regions of this country; others that are known also from the higher mountains of Eurasia; some that have reached the polar regions, among which several are circumpolar; and finally some that occur also at lower altitudes in these same mountains. The alpine genera seem to be more cosmopolitan than those observed at lower levels; as a matter of fact none of these genera of Gramineae are endemic to this country, and none of the alpine genera of Europe and Asia are endemic to those countries.

The habit and floral structures of the alpine Gramineae of Colorado are remarkably uniform and simple, when compared with some of the other species and genera from the lowlands. Corresponding with this uniformity in habit, we meet with no extraordinary development of any of the tissues. The anatomical structure is rather simple, and neither the stereome, nor the chlorenchyma, nor the stomata exhibit any feature that might be looked upon as characteristic of an alpine type. In this respect the alpine Gramineae differ from most of the other families, not so much, however, from the Cyperaceae as from the Juncaceae (Luzula and Juncus), and especially from the dicotyledons. The habit and internal structure of the alpine dicotyledons of Colorado are very distinct from those of their representatives which thrive at lower elevations in mountains or on the plains and prairies; very prominent distinctions of this kind I have observed in a number of alpine genera, as Ranunculus, Trifolium, Claytonia, Stellaria, Synthyris, Mertensia, Primula, etc. Whatever conclusions may be drawn from the various treatments of alpine plants in general, and especially in regard to "adaptations," it must be borne in mind that the monocotyledons have so far been almost entirely ignored, although they are certainly of no small interest on account of their frequent occurrence and very wide distribution in the high alpine regions. It seems thus very unsafe to describe the alpine leaf "in general" without including the Gramineae, and for this purpose the present paper may be of some interest to future students of "alpine structures."

BROOKLAND, D. C.

EXPLANATION OF PLATE XXX

FIG. 1.—Cross-section of root stele of *Poa Lettermanni*: *End*, endodermis; *P*, pericambium; *PL*, proto-leptome; *PH*, proto-hadrome. ×560.

FIG. 2.—Root stele of *Agrostis canina* var.; letters as above. ×560.

FIG. 3.—Root stele of *Festuca ovina;* letters as above. ×560.

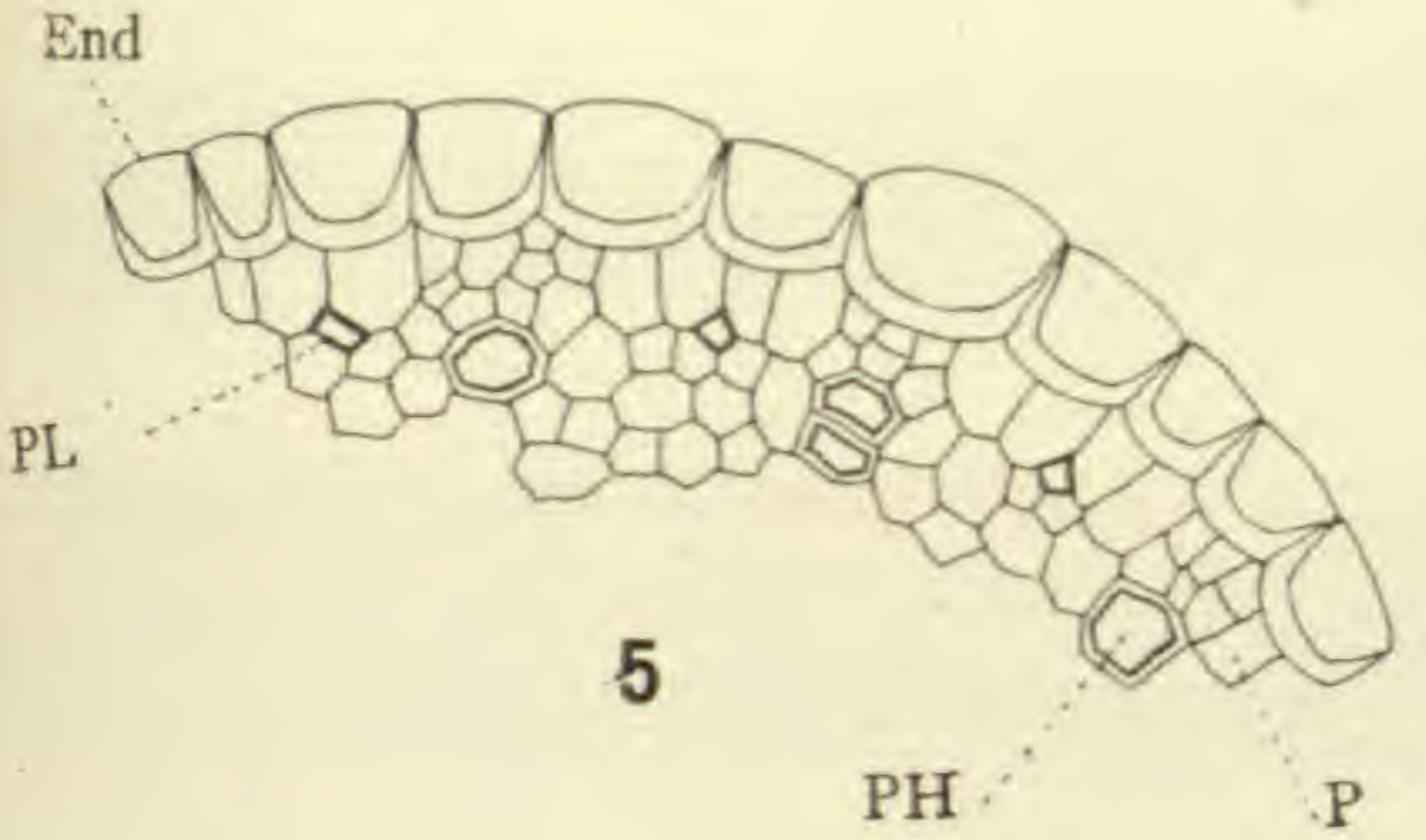
FIG. 4.—Root stele of *Poa flexuosa;* letters as above. ×560.

FIG. 5.—Part of root stele of *Agropyrum Scribneri;* letters as above. ×560.

FIG. 6.—Cross-section of part of culm of *Poa Lettermanni*, showing epidermis (*Ep*), cortex (*C*), stereome (*St*), and two mestome strands with their mestome sheaths (*MS*). ×400.

FIG. 7.—Same species; cross-section of leaf, showing ventral epidermis (*Ep*) with a stoma, and two strata of chlorenchyma (*C*). ×400.

FIG. 8.—Same species; cross-section of leaf, showing dorsal epidermis (*Ep*), hypodermal stereome (*St*), and chlorenchyma (*Ca*). ×400.



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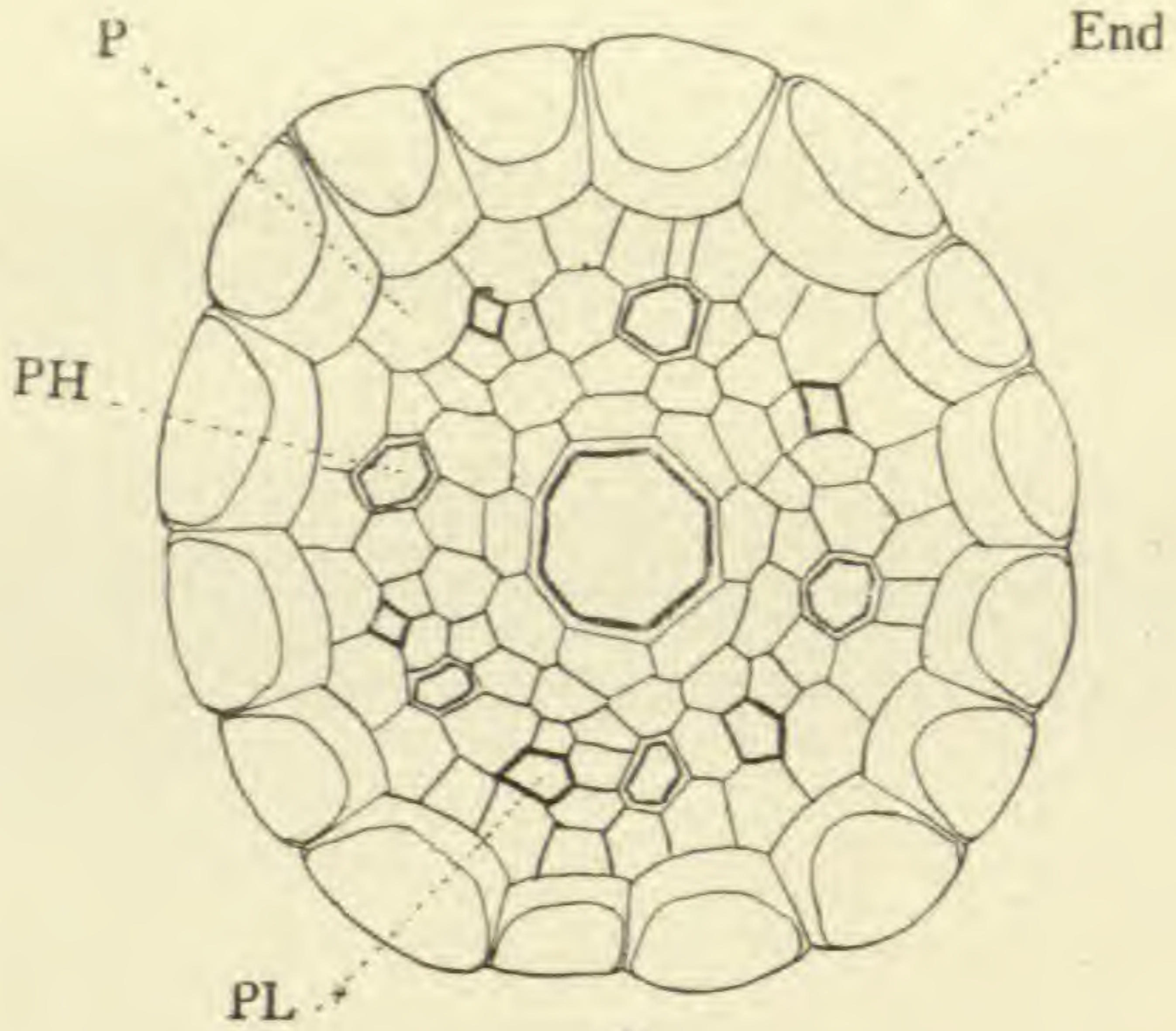

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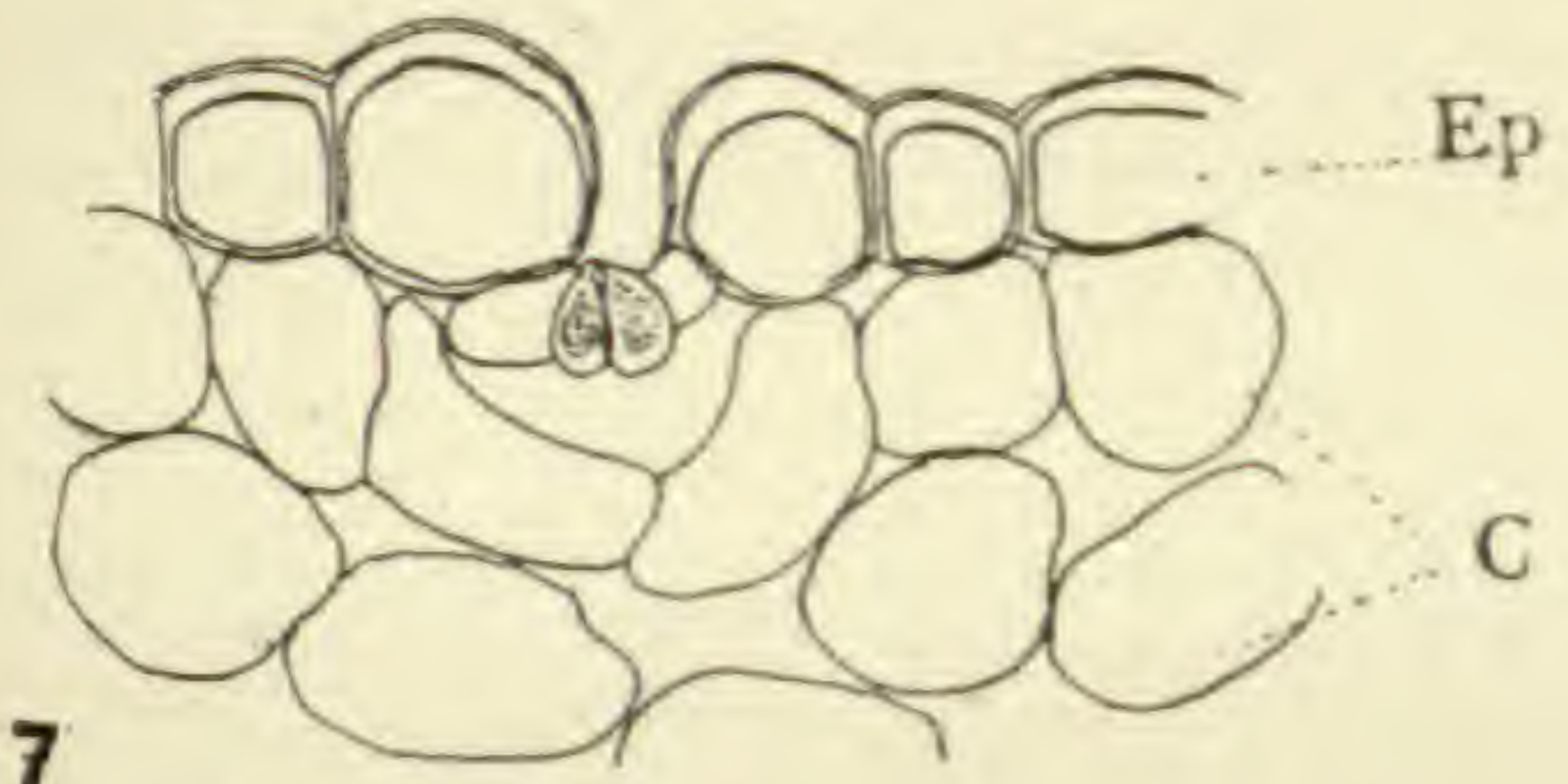

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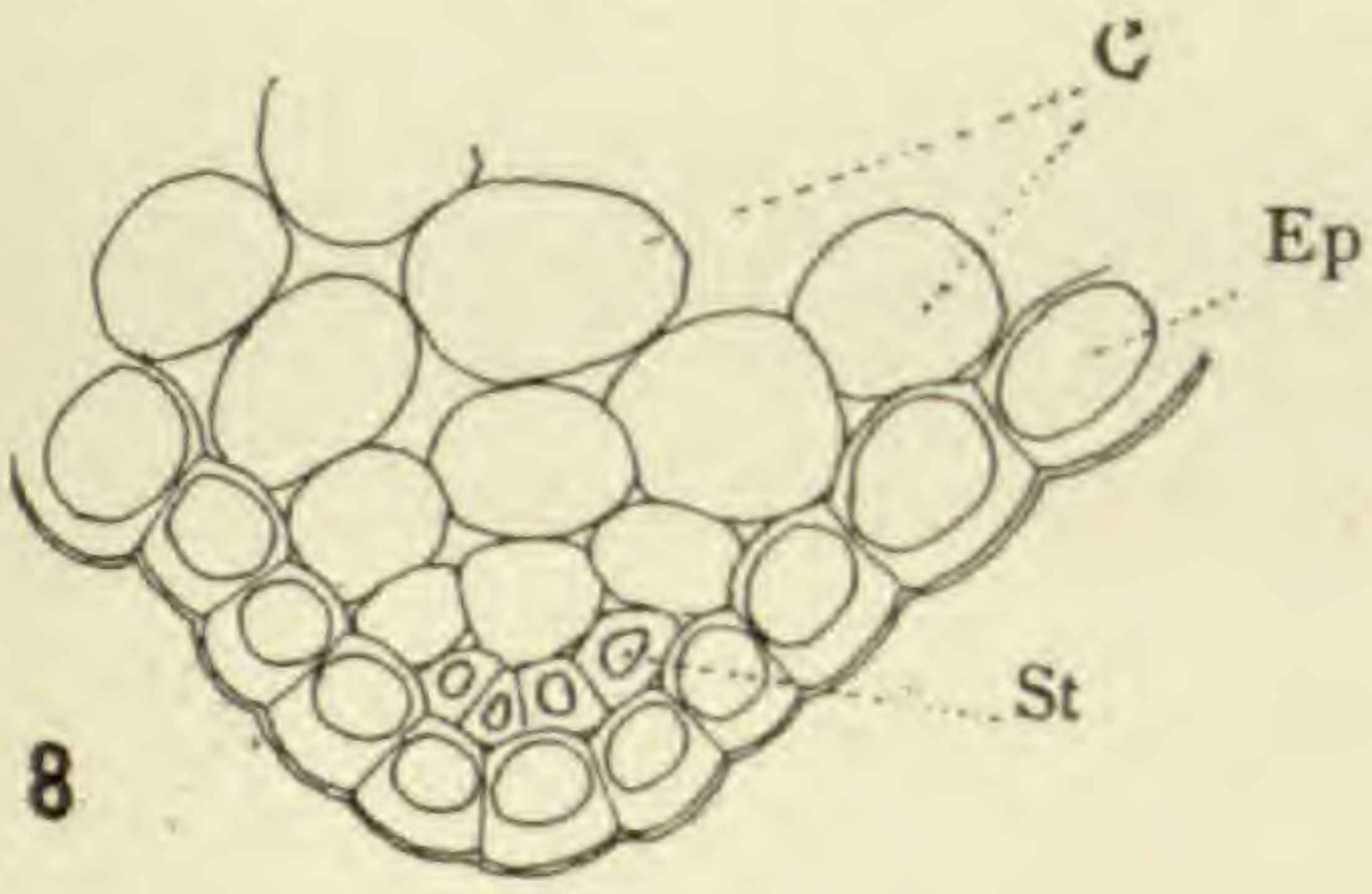

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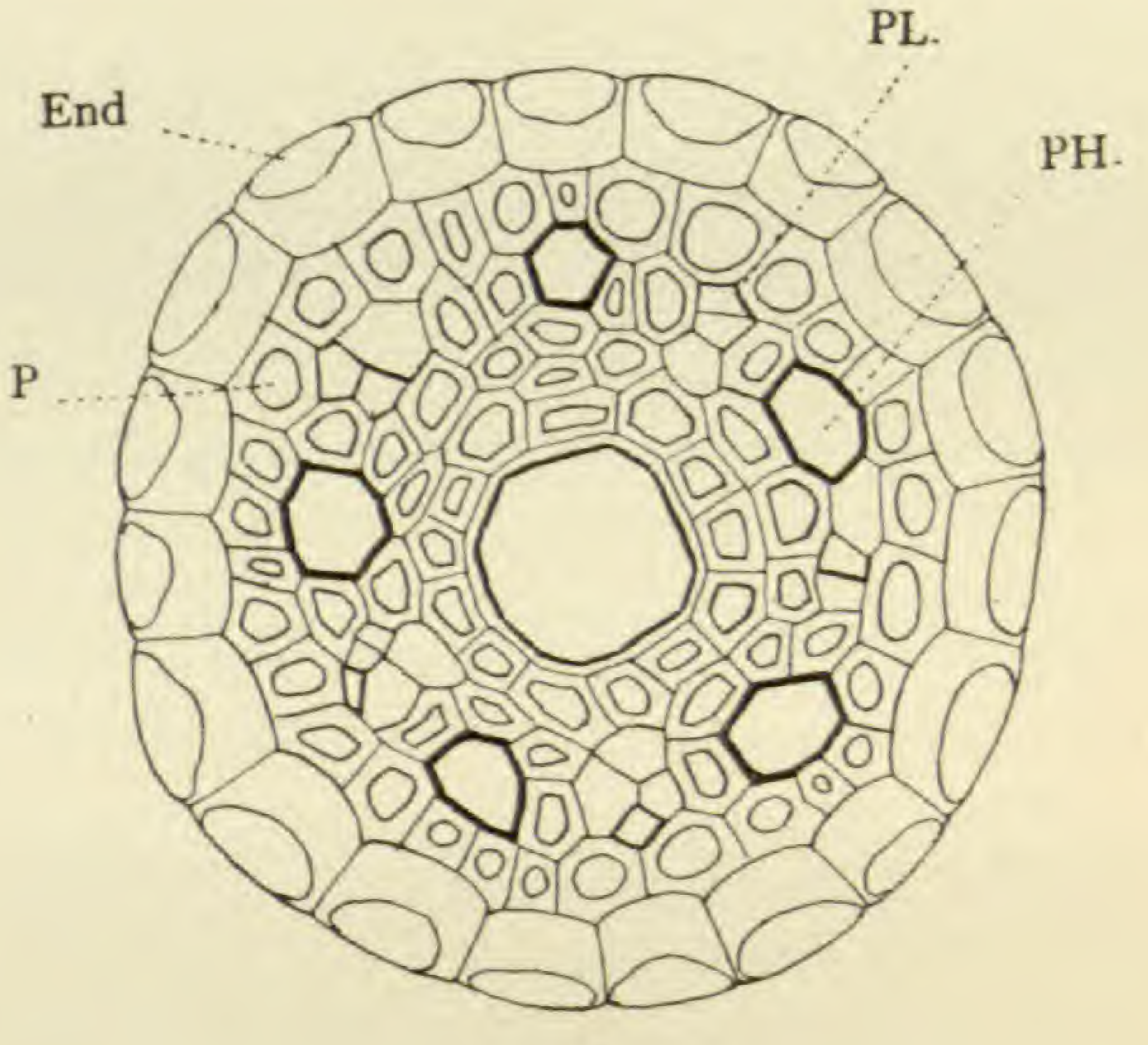

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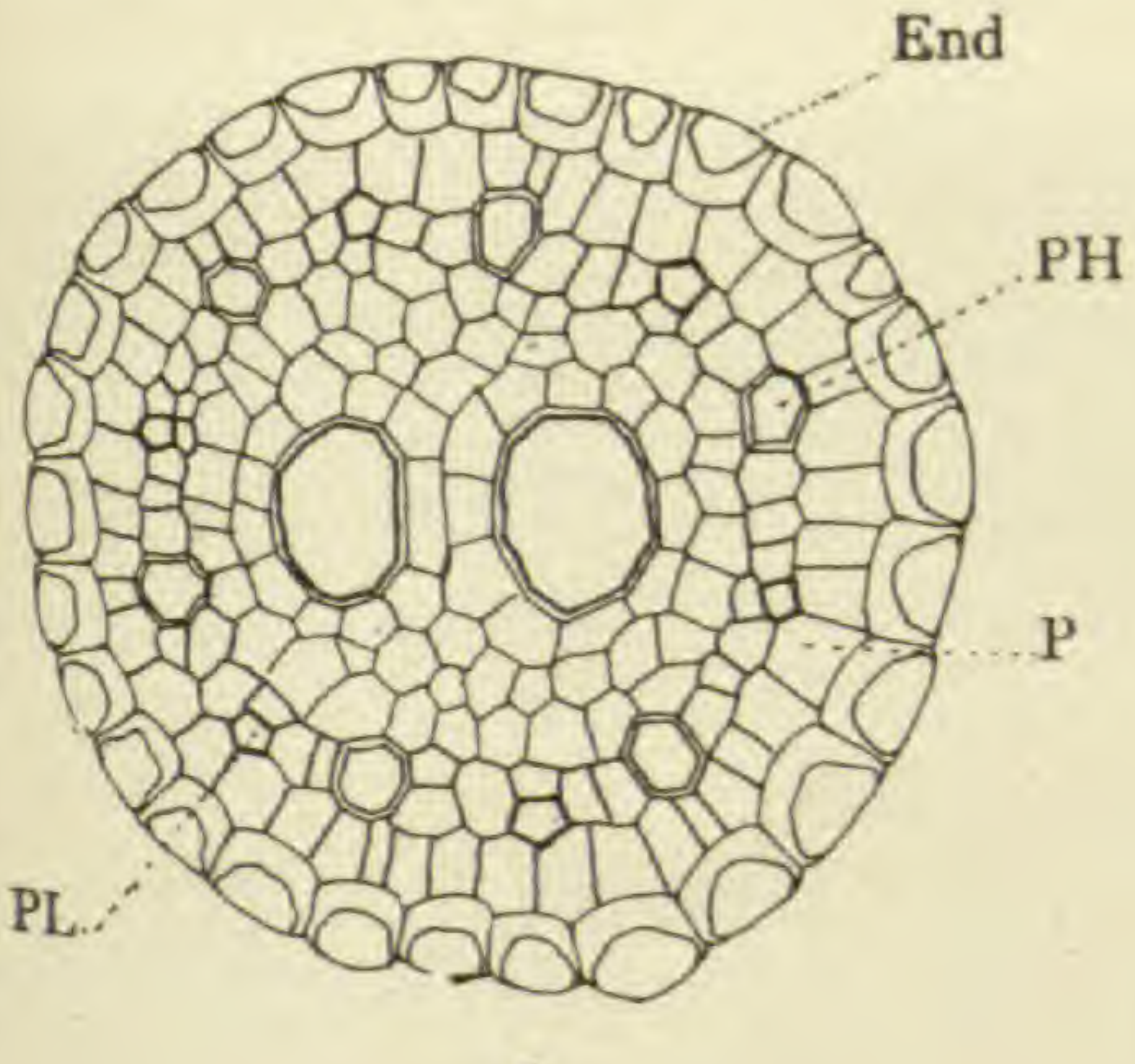

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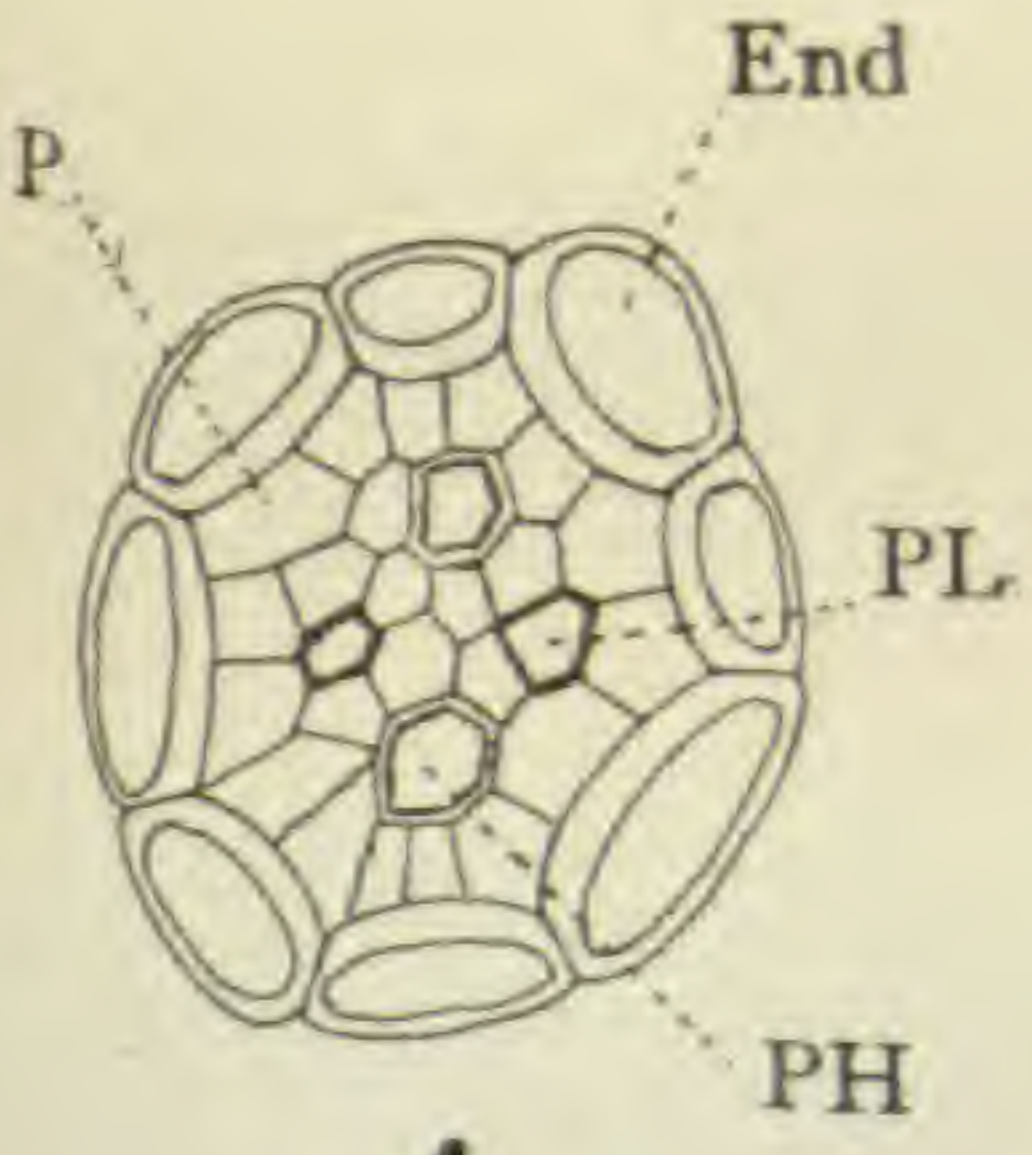

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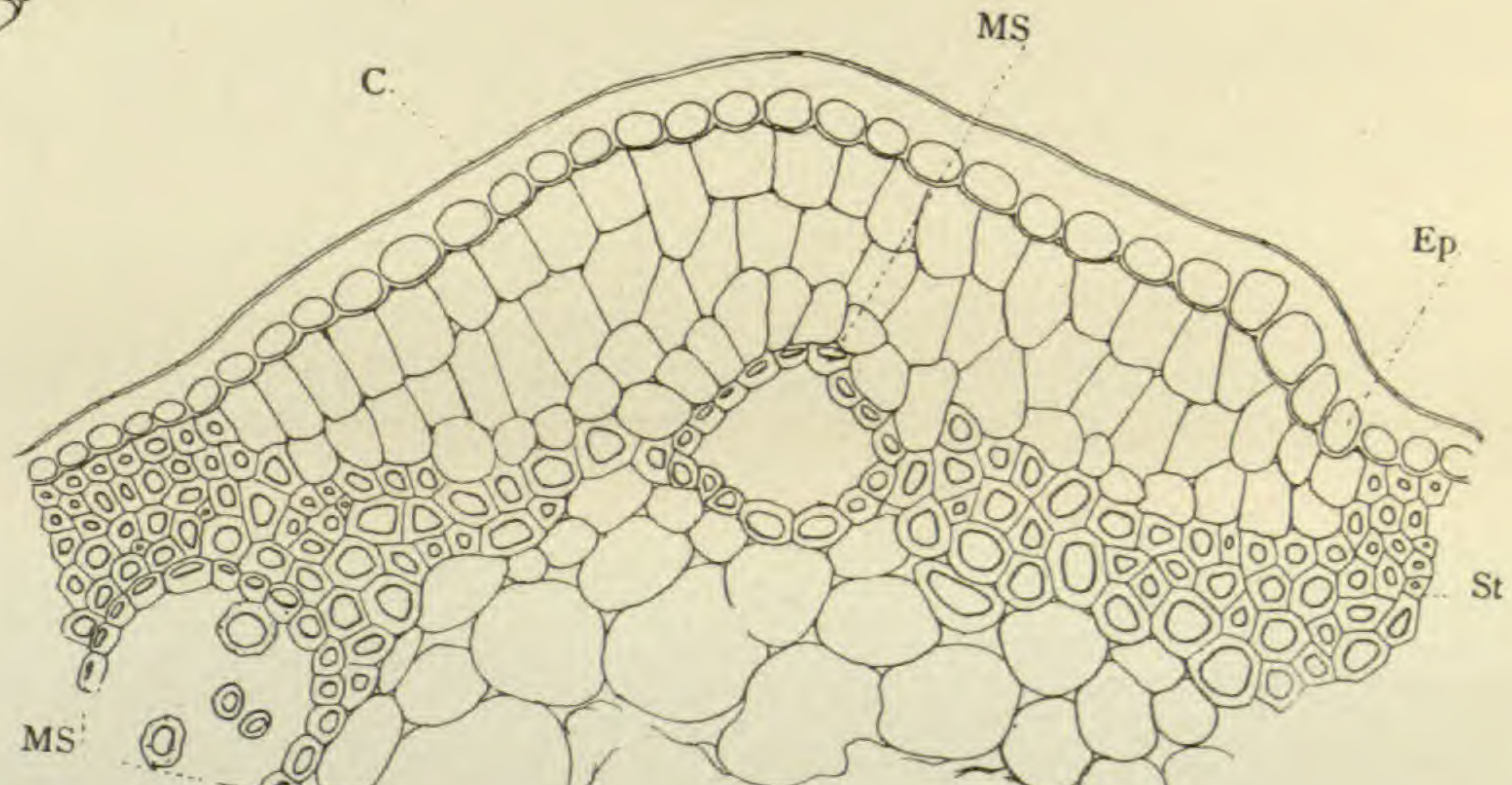

6

Auctor delin.

HOLM on ALPINE GRAMINEAE

THE NATURE OF THE EMBRYO SAC OF PEPEROMIA[1]

WILLIAM H. BROWN

(WITH PLATES XXXI–XXXIII)

At the suggestion of Professor DUNCAN S. JOHNSON, I undertook the cytological study of the development of the embryo sac of several species of Peperomia, with the purpose of finding out whether the development of this genus offered any support to the idea, recently advanced by several investigators, that when a row of megaspores is not formed, each of the first four nuclei of the embryo sac is to be regarded as a megaspore nucleus. The results found were exceptional and may be of interest, as they seem to throw some light on this question and also on the nature of the embryo sac of Peperomia.

For the investigation, Professor JOHNSON turned over to me material of three species which he had collected for this purpose. Material of *P. arifolia* was collected in the greenhouses in Baltimore. The material was fixed in chrom-acetic or Fleming's solutions. The sections were cut 10 μ thick and stained with Fleming's triple or Haidenhain's iron-alum hematoxylin. The latter stain was used alone or counterstained with gentian-violet or eosin.

This paper does not pretend to be a study of the whole life-history of Peperomia, but deals in detail only with the development of the embryo sac. It is hoped, however, that this will throw some light on the origin of the peculiarities which have been described in its later development.

The sixteen-nucleate embryo sac of Peperomia was discovered in *Peperomia pellucida* by CAMPBELL ('99), who, however, misinterpreted some of its features. JOHNSON ('00) describes the mature sac of *P. pellucida* as containing one egg, one cell with the position of a synergid, six nuclei which are cut off singly against the wall of the sac and finally degenerate, and eight which fuse to form the endosperm nucleus. The archesporium consists of a single hypodermal cell which cuts off a single parietal cell and then forms the embryo sac. In a later

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[1] Contribution from the Botanical Laboratory of The Johns Hopkins University, No. 8.

paper CAMPBELL ('01) agrees with this description, except that he does not think that there is always in the mature sac a single cell which has the position of a synergid.

That chromosome reduction takes place in the first division of the embryo sac nucleus was indicated by the presence of synapsis before this division in *P. hispidula*, as reported by JOHNSON before the Botanical Society of America at New Orleans in 1905.

CAMPBELL ('01) thinks that the embryo sac of Peperomia is a primitive one, while JOHNSON ('00) considers its peculiar structure as derived. In this paper it will be shown that the embryo sac is made up of the descendants of four nuclei which are apparently the nuclei of four megaspores, and that these nuclei have, by the loss of dividing walls, come to lie in the same cell. Some of the peculiar features of the mature sac are probably connected with this fact.

For the sake of convenience, each of the four species will be described separately, after which the general considerations will be discussed.

Peperomia Sintensii

The material of this species was collected in Jamaica by Mr. W. R. MAXON and identified by M. CASIMIR DE CANDOLLE.

The development of the flower and of the mother cell in the nucellus agrees with that described for *P. pellucida* by JOHNSON ('00). The flower consists of two stamens and a carpel in the axil of the bract. The ovule (*fig. 28*) is single and orthotropus, with a single integument (*fig. 28, i*), which makes its appearance about the time that the tapetum is cut off from the archesporium (*fig. 2*).

The archesporium arises in the apex of the nucellus as a single hypodermal cell (*fig. 1*), which is clearly distinguished from the surrounding cells by its larger size and more densely staining contents. At the micropylar end this cuts off a single parietal cell (*fig. 2*), and then, without giving rise to any other cells, forms the embryo sac. The parietal cell divides first by an anticlinal wall and then by repeated divisions gives rise to a mass of tissue between the embryo sac and micropyle (*figs. 4, 28, t*).

Owing to the scarcity of young material, I was unable to count the chromosomes in the division cutting off the tapetum, but in the tapetum and in the nucellus there were regularly about sixteen chromosomes. This is double the number found in the embryo sac, as will be described later. The chromosomes are small and short, and are therefore readily counted in a cross-section of a spindle at metaphase. *Fig. 2* shows such a section in the tapetum, while *fig. 3* represents a longitudinal view of a vegetative nucleus at a slightly older stage. Up to this time there certainly seems to have been no chromosome reduction, and nothing resembling megaspore formation.

The single sporogenous cell (*fig. 2*) which is left after the cutting-off of the tapetum and which is to form the embryo sac is apparently a megaspore mother cell, as will be shown below. Its nucleus divides to two, four, eight, and finally in the mature sac to sixteen nuclei.

The first division is heterotypic and takes place as follows. The resting nucleus (*fig. 4*) shows a meshwork of linin along which chromatin granules are scattered. In the center of this meshwork is a large clear space containing a large nucleolus. After considerable growth the nucleus goes into synapsis. The meshwork contracts rapidly around, or to one side of, or even at some distance from, the nucleolus, into a mass in which very little detail can be made out. *Fig. 5* represents an early stage of synapsis, while *fig. 6* is probably older. No evidence of a fusion of spirems was seen either before or during the early stages of synapsis.

At the end of synapsis the mass loosens up, and later appears in the form of a spirem, along which single granules are scattered at rather regular intervals (*fig. 7*). The spirem is apparently continuous and becomes loosely coiled, and the granules divide along the longitudinal axis of the spirem. A small portion of such a stage is shown in *fig. 8*. After this the spirem divides longitudinally and the two halves may diverge considerably in places (*fig. 9*), but later they come together again and all apparent traces of the division are lost. While this is taking place, the spirem is beginning to be arranged in loops (*fig. 10*), and is still apparently continuous, the loops being rounded at the ends. It does not seem possible that this appearance can have anything to do with the splitting just described. The looping becomes more pronounced and the spirem segments transversely in such a way that the loops give rise to chromosomes. There are eight of these, the haploid number, and they are apparently formed by the coming together side by side of parts of the spirem that before were arranged end to end. The chromosomes then contract and show the twisted appearance characteristic of the heterotypic division (*fig. 11*).

After considerable contraction they have the appearance of two irregular rounded masses lying together. Sometimes these are seen to be connected by strands (*fig. 13*), and just before this, when the constituent halves are about twice as long as wide, they are sometimes placed end to end with a constriction between them (*fig. 12*).

It would seem from this that the two halves originally placed end to end in the spirem, then side by side in the loops, again come to lie end to end, and that each half probably represents a chromosome (cf. *fig. 16*). The strands connecting the two halves are often seen to be double (*figs. 12, 13*), and they might always be so if seen in the right plane. Besides this, the halves sometimes show evidence of being double. This may be due, as is often supposed, to the split previously described. Before the spindle is formed the two halves come together, producing somewhat elongated chromosomes (*fig. 14*). About this time the nucleolus begins to fragment and to be thrown out into the cytoplasm. After the spindle is formed (*fig. 15*) the chromosomes divide transversely to their long axes (*fig. 16*). From what has been said it seems evident that this division separates parts of the spirem which were originally placed end to end and that it is therefore a transverse division. This is then the heterotypic and reducing division.

As the chromosomes approach the poles they become crowded together (*fig. 17*) and surrounded by a clear space. While this is going on, the chromosomes lose their distinct outlines and a nucleolus makes its appearance in their midst. While the chromosomes lose their distinct outline and probably also some of their substance, they seem nevertheless to be represented by irregular masses during most if not all of the period between the first and second divisions (*figs. 18–20*). Between the succeeding divisions they seem to go to pieces to a much greater extent (cf. *figs. 22–25*). Before the formation of the spindle, the chromosomes appear as double structures, consisting of two rods lying side by side. It may be that these represent the two halves of the spirem seen in the prophases of the first division.

and that the second division completes the longitudinal separation begun in the first.

The first two divisions differ from those in *P. pellucida* in that there are formed evanescent walls separating the daughter nuclei. When the daughter nuclei of the first division have begun to be organized, an equatorial plate is formed on the spindle (*fig. 17*). This grows until it becomes a wall stretching across the embryo sac (*fig. 18*). The plane of this wall is not constant, but it may extend longitudinally or transversely across the sac, or take any intermediate position, and may also separate the sac into equal or unequal parts (*figs. 18–20*). It persists only for a short time, disappearing before the next division or remaining as a remnant after it (*fig. 21*). There is no trace of it later in the four-nucleate stage. When the two nuclei divide to four, plates are formed on both spindles. One of these never becomes very prominent, but the other forms a wall separating one nucleus from the other three (*fig. 22*). The position of this wall is variable, as was the one in the two-nucleate stage. It may cut off a nucleus at either end or any side of the sac, but generally it appears at the lower end. This wall, like the first, persists for only a short time. It generally disappears before the next division (*fig. 23*), but may persist as a remnant after it. As in *P. pellucida,* the four nuclei assume the position of the nuclei of a tetrad of microspores. The walls just described are apparently megaspore walls. This, however, will be discussed later.

In the next two divisions all of the nuclei divide simultaneously, giving eight, and then in the mature sac sixteen nuclei. The nuclei of the eight-nucleate stage and of the mature sac are arranged about the periphery of the sac (*figs. 24–28*). As in *P. pellucida* (JOHNSON **'00**), one of the sixteen nuclei becomes an egg, another has the position of a synergid, six are cut off singly against the wall and finally degenerate, while eight fuse to form the endosperm nucleus. *Fig. 29* shows a sac in which fertilization is taking place. Four of the peripheral nuclei are shown, while five others are fusing to form the endosperm nucleus. One of these latter was probably formed by the fusion of two. The other two fusing nuclei, as well as two peripherals, are in another section.

In the division of the four nuclei to eight no cell plates are formed.

Fig. 24 represents a stage in which they should be apparent if present. In the last division (*fig. 26*), cell plates are formed on all the spindles. These give rise to walls cutting off all of the nuclei except those which are to fuse to form the endosperm nucleus, but leaving these eight free in the cytoplasm (*figs. 27, 28*). These walls are thin at first and might be easily overlooked, but later they become much more prominent. In the eight-nucleate stage two nuclei are always found together at the micropylar end (*fig. 25*). The presence of spindles show these to be sisters (*fig. 24*). In the last division one of these gives rise to the egg, the other to the nucleus with the position of a synergid (*figs. 26–29*). The sisters of the egg and synergid fuse with the sisters of the six peripherals to form the endosperm nucleus. As in *P. pellucida* (JOHNSON **'00**) the peripherals are arranged singly against the embryo sac wall (*fig. 29*) and finally degenerate. About the time of fertilization the eight nuclei which form the endosperm nucleus migrate toward the base of the sac and fuse into one large nucleus.

STRASBURGER (**'05**) assumes that owing to their position the polar nuclei in the ordinary angiosperm are not surrounded by cell walls and that their fusion is due to the fact that their development has stopped and that they are in a single cell. This explanation may apply to the eight fusing nuclei in *P. Sintensii.*

A peculiar phenomenon was noted in fertilization. The male and female nuclei at this time are in the resting stage and have one or more cavities with their concave sides facing each other (*fig. 29*). The edges fuse so that a mass of cytoplasm is apparently held in the fusion nucleus (*fig. 30*). The wall around this mass of cytoplasm grows faint and finally disappears.

The mature seed resembles that of *P. pellucida* (JOHNSON **'00**). There is a small oval embryo, while the rest of the sac is filled with a much larger endosperm, which is cellular from the first division. The sac is about the same size as at fertilization, but the cells of the nucellus have become filled with starch to form perisperm.

Peperomia arifolia

The development of *P. arifolia* was followed only as far as the sixteen-nucleate sac.

The development of the flower and of the embryo sac agrees very closely with that just described for *P. Sintensii.* There is a single archesporial cell which cuts off a tapetal cell and then forms the embryo sac. The tapetum divides as in *P. Sintensii.* The embryo sac nucleus divides to two, four, eight, and finally sixteen nuclei.

The first division is heterotypic and shows the usual synapsis. At this division a cell wall is formed across the sac. This wall is variable in position and generally disappears before the next division, but may persist as a remnant after it. At the second division plates are formed on both spindles. One soon disappears, while the other forms a wall separating one nucleus from the other three. This wall is variable in position, and all signs of it are usually lost before the next division. The next two divisions leave the mature sac with sixteen nuclei.

Peperomia ottoniana

The material of this species was collected in Mexico by Dr. C. J. CHAMBERLAIN. It is very much like *P. Sintensii,* but shows some constant differences. It was identified by M. CASIMIR DE CANDOLLE.

Owing to lack of young material the investigation of this species had to be begun with the four-nucleate stage. There were only three ovules showing a four-nucleate sac, but they are worth recording, as they appear perfectly normal, and seem to throw some light on the problem under discussion.

The youngest sac (*fig. 31*) shows the micropylar nucleus completely cut off from the other three by a very distinct and well-developed wall. This nucleus is much larger than the other three, which are all about the same size. The cell occupied by this large nucleus contains much denser protoplasm than the one containing the other three. The stage just described resembles rather closely the four megaspores of the ordinary angiosperm, where one megaspore is to form the sac while the other three degenerate. The further development, however, seems to be different, and agrees with the two species of Peperomia just described.

The two other four-nucleate sacs which were seen are larger and apparently older than the one just described, and show no sign of a wall separating the nuclei, which are all about the same size (*fig. 32*). The eight nuclei formed from these four show no appreciable difference in size.

The further development resembles very closely that of *P. Sintensii.* The mature sac contains sixteen nuclei. There is one egg and one nucleus with the position of a synergid. Six peripheral nuclei are cut off against the wall of the sac. The remaining eight fuse to form the endosperm nucleus about the time that fertilization takes place. In the fusion of male and female nuclei there was seen no sign of protoplasm being taken into the nucleus, as described for *P. Sintensii.* Many of the stages of this species resemble *P. Sintensii* so closely that one might readily be mistaken for the other.

Peperomia pellucida

The development of the embryo sac nucleus and the structure of the mature sac, as described by JOHNSON, agree with the description just given for *P. Sintensii.* Therefore only the first two divisions of the embryo sac nucleus need be considered here.

The first division is heterotypic and shows about ten or twelve chromosomes. A meshwork contracts and goes into synapsis. This stage is followed by an apparently continuous spirem, which divides into twisted heterotypic chromosomes.

In both divisions plates are formed on the spindles. These plates probably do not develop further, as no larger plates or walls were seen, although a great number of nuclei were examined at stages which should show them if present. These plates probably are the remnants of walls such as have been described for the other three species.

Discussion

As has been said, CAMPBELL (**'01**) considers the unusual structure of the embryo sac of Peperomia as primitive, and expresses the belief "that the contents of the embryo sac with the sixteen nuclei represent a prothallial tissue and the nuclei are at first entirely similar." JOHNSON (**'02**), after a study of Peperomia and allied genera, comes to the conclusion that the peculiarities of the embryo sac have been secondarily acquired from the ordinary angiosperm embryo sac.

The present investigation seems to support the latter view. The nuclei of the mature sac of *P. Sintensii,* instead of being similar at first, bear a definite relation to each other. The presence of the reducing division in the primary embryo sac nucleus and the formation of evanescent walls in the first and second divisions seem to indicate that the sac is composed of the descendants of the nuclei of four megaspores and that the primary embryo sac nucleus is a mother cell and not a megaspore nucleus.

If the walls corresponded to those of prothallial cells, we should expect to find them in the third division, but here not even a cell plate was seen. Besides this, the nearest phylogenetic relatives in which the first divisions of a megaspore result in a cellular structure are found among the leptosporangiate Filicales, where the heterospory is supposed to be of rather late origin, and it does not seem probable that Peperomia has reverted to the characters of an ancestor as remote as one in which we would find the first divisions of the megaspore giving rise to a cellular structure.

This position is strengthened when we consider the four-nucleate stage of the Mexican species. Here the nucleus which is cut off is considerably larger and surrounded by much denser protoplasm than the other three. The resemblance to the four megaspores of the ordinary angiosperm is quite striking.

The presence of the extra nuclei in the mature sac is in harmony with the view that these nuclei are the descendants of four megaspore nuclei.

The nuclei of the four-nucleate sac of Peperomia have the same position with reference to each other as the nuclei of a tetrad of fern spores or of a tetrad of microspores of a spermatophyte. This position is not always apparent when the nuclei are dividing, and as the sac is somewhat rounded it may be that this arrangement is a mechanical response to the physiological conditions.

That four potential megaspore nuclei may be included in a single cell has been shown by CANNON (**'00**) for *Avena fatua*. Here the four megaspore nuclei may or may not be separated by cell walls, but in either case three degenerate and the other forms the embryo sac. A similar phenomenon is reported by SMITH (**'98**) for Eichhornia.

The case of Crucianella (LLOYD **'02**) is interesting in this connection. Here the four megaspores are not separated by walls, but indications of plates are found on the spindles in the divisions of the megaspore mother cell nucleus. According to LLOYD, the four megaspores are physiologically and morphologically similar. Each nucleus divides to two, but afterward the nuclei derived from the three megaspores nearest the chalazal end degenerate, while those from the one nearest the micropyle form the sac. The condition in Crucianella approaches that in Peperomia, and it may be that the shape of the sac, which is much less elongated in Peperomia than in Crucianella, gives the megaspores a better chance to develop together in Peperomia.

That physiological conditions do play a part in the structure of the embryo sac of Peperomia may be indicated by the fact that while the megaspore nucleus which is cut off by a cell wall is generally at the chalazal end, it is always the one nearest the micropyle which forms the functional egg apparatus.

WIEGAND ('00) reports an evanescent wall in the first division of the embryo sac of Convallaria. Here the mother cell forms the embryo sac directly and this wall may represent a megaspore wall.

That more than one megaspore may possess the potentialities for development is indicated by the number of plants in which more than one has been reported as dividing (COULTER and CHAMBERLAIN '03).

The similarity in the fate of the four megaspores of *P. Sintensii* is striking. Each gives rise to two nuclei of the endosperm and two cut off against the embryo sac wall.

If we were to accept the view of PORSCH ('07) that an egg apparatus represents an archegonium, we might conceive of the embryo sac of Peperomia as really composed of four sacs, each of which gives rise to a single archegonium. The relationship of the nuclei of each egg apparatus, as previously described, is the same as that found in the egg apparatus of an ordinary angiosperm, if we assume that one synergid fuses with the nucleus which usually fuses to form the endosperm, that is, with the sister of the egg, as is the case in the four-nucleate sac of Cypripedium (PACE '08). That there may be in Peperomia four potential egg apparatuses is indicated by the fact that the nucleus of the four-nucleate stage, which is cut off and therefore resembles the functional megaspore of the ordinary angiosperm, does not usually form the functional egg apparatus. It must be remembered, however, that no such similarity in the fate of the megaspore nuclei as has been described for *P. Sintensii* exists in *P. his-*

pidula (JOHNSON '07), where fourteen out of sixteen nuclei fuse to form the endosperm nucleus.

Before applying the theory of PORSCH it may be well to consider the theory itself in its relation to the ordinary gymnosperms and angiosperms. In Selaginella, Isoetes, and the gymnosperms, all of the first divisions of the megaspore are non-cellular, after which there is a number of cellular divisions in all species that form archegonia. It is in the cellular tissue that the archegonia are formed by cell divisions. The first two divisions of the ordinary angiosperm embryo sac are generally homologized with the free nuclear divisions of the gymnosperm prothallus, and the fact that in the derived sac of *P. Sintensii*, where cell walls are formed at the first two or megaspore-forming divisions, there is no sign of even a cell plate at the third or prothallial division, indicates that the character of the free cell divisions in the angiosperms is quite constant. It does not seem probable that nuclei formed in the angiosperm embryo sac by free nuclear division can be homologous with the nuclei in the cellular archegonia of the gymnosperms, for we would have to explain how the archegonia became shifted back from the cellular to the non-cellular phase of the prothallus.

If the above idea is correct, the polar groups in the angiosperm embryo sac can have no such phylogenetic significance as is ascribed to them by PORSCH, but all of the nuclei in the mature sac must be homologous or at least differentiated only in the last division.

From what has been said, it seems possible that in some angiosperms besides Peperomia, in which the embryo sac is not developed from one of a row of megaspores, the first four nuclei of the sac are megaspore nuclei. It must be remembered, however, that in most cases we have no evidence for this, other than the presence of the reducing division in the embryo sac mother cell, and it is a mistake to suppose that the same structure may not come about in plants in more than one way. Besides this, it is hard to see how four embryo sacs can have become merged into one in the large number of cases in which a row of megaspores is not formed (COULTER and CHAMBERLAIN '03) without disturbing the normal number and position of the nuclei, as has been done in Peperomia.

Some workers have been inclined to regard the presence of the heterotypic division in a cell of the nucellus as the sole criterion for determining that this cell is a megaspore mother cell, and that the first four resulting nuclei are the nuclei of megaspores. This view seems to leave out of consideration the great number of points in the life-history of plants at which reduction may take place, and the evident tendency among vascular plants toward the reduction of sporogenous tissue in the megasporangium and nucellus.

In the Archegoniatae the archesporial cell may give rise to a large mass of tapetum and a considerable number of functional spore mother cells. Since we can trace the reduction of these divisions until among angiosperms the archesporial cell may without dividing form one megaspore mother cell, it does not seem reasonable to suppose that the divisions of the mother cell to four megaspores may not also be left out and the mother cell function directly as a megaspore. In this case the heterotypic division might be pushed forward and take place in the embryo sac.

Among the lower plants this reducing division may take place at almost any point in the life-history and there seems to be no sufficient reason for thinking that it must occur at the same place in all angiosperms.

If the two divisions which form the spores from the mother cell, or one of them, have been left out, we could of course expect to find no evidence of it other than the entire absence of any signs of the division.

In a recent paper on Cypripedium, Miss PACE (**'08**) shows that the sporogenous cell divides once and one of the resulting cells forms the embryo sac, while the other may occasionally divide once. There is not even a sign of a cell plate in the first division of the nucleus which forms the embryo sac. Miss PACE calls the first two nuclei of the embryo sac megaspores, but does not state her reasons for doing so. The question might arise as to whether they are megaspores or whether one division in spore formation has been left out. That the nucleus of the degenerating cell should occasionally divide does not seem surprising when we remember the large number of plants in which the nucleus of a degenerating megaspore may do so.

The writer does not wish to be understood as denying that there are two megaspores in the embryo sac of Cypripedium, or that the first four nuclei in the embryo sac of any plant in which a row of megaspores is not formed are megaspore nuclei, but simply as suggesting that in most cases we have no adequate proof of this, and that in the present state of our knowledge there is at least one other way in which some of them may be regarded.

The homologies in all these cases may be cleared up by further work. We have, however, no right to push them further than the present evidence justifies, or to suppose that all plants must behave alike in this respect, when we consider the large number of different analogous organs which have been arrived at by very diverse methods.

Summary

The archesporium of the species of Peperomia studied arises as a single hypodermal cell, which cuts off a single parietal cell and then forms the embryo sac directly.

The first division of the embryo sac nucleus is heterotypic. The nucleus goes into synapsis. This stage is followed by an apparently continuous spirem. This splits longitudinally but later the two halves come together again. The chromosomes are formed from loops in the spirem. When these divide, they seem to separate two parts of the spirem which were originally placed end to end.

The second division may divide the chromosomes along the longitudinal split seen in the prophase of the first division.

In the third division of the embryo sac nucleus of *P. Sintensii*, no cell plates were seen on the spindles, but in the last division cell walls are formed on all the spindles. These walls cut off, against the embryo sac walls, one of each of the eight pairs of nuclei, and leave the other eight free in the cytoplasm. These free nuclei fuse to form the endosperm nucleus. The egg and a nucleus with the position of a synergid are cousins. The other six nuclei which are cut off against the embryo sac wall finally degenerate.

The mature sac contains sixteen-nuclei, which are apparently derived from four megaspores. That the first four nuclei of the embryo sac are megaspore nuclei is indicated by the fact that the first division of the embryo sac mother cell nucleus is heterotypic and reducing, and that in *P. pellucida* cell plates are formed on the spindles of the first two divisions, while in *P. Sintensii* and *P.*

arifolia these plates grow into evanescent walls which extend across the embryo sac and separate the nuclei.

We are not justified, however, in extending the conception of four megaspores in an embryo sac to all angiosperms in which a row of megaspores is not formed, because we do not know that the division of the mother cell to megaspores may not be omitted and the place of the heterotypic division be changed.

In the fertilization of *P. Sintensii* some cytoplasm appears to be taken into the nucleus.

NOTE.—Since the above was written, there have appeared two papers dealing with sixteen-nucleate embryo sacs. One is by COULTER,[1] in which he expands a suggestion offered by LLOYD in 1902, that when four megaspores are not formed the first four nuclei of the sac are spore nuclei so far as development is concerned, and says that the formation of megaspore nuclei cannot be omitted.

In a paper on the phylogeny of the angiosperm embryo sac, ERNST[2] describes a sixteen-nucleate embryo sac in Gunnera. Here he finds an egg, two synergids, six antipodals often in two groups of three, and seven nuclei which fuse to form the endosperm nucleus. He then attempts to fit the archegonial theory of PORSCH to Gunnera, and concludes that the egg group represents an archegonium, while two more are represented by the six antipodals together with two of the nuclei which fuse to form the endosperm. He thinks that the other four nuclei fail to form an archegonium, and that the explanation which he gives of the embryo sac of Gunnera may apply to *Peperomia pellucida*. In the case of the embryo sac of *P. Sintensii*, which resembles very closely that of *P. pellucida*, it has already been shown that if we should apply the theory of PORSCH there would be four and not three archegonia. ERNST has not worked out the relation between the nuclei in the embryo sac of Gunnera, and therefore it would seem premature to speculate as to the conditions there, but there seems to me to be no sufficient reason for thinking that the nuclei would represent three rather than four of the archegonia of PORSCH.

JOHNS HOPKINS UNIVERSITY
BALTIMORE

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[2] ERNST, A., Zur Phylogenie des Embryosackes der Angiospermen. Ber. Deutsch. Bot. Gesells. 26:419–437. *pl.* 7. 1908.

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EXPLANATION OF PLATES XXXI–XXXIII

All drawings were drawn with the aid of a camera lucida and reduced one-half. *Figs. 1, 2, 4, 18–23, 31, 32* were made with a no. 8 ocular and a 1.5^{mm} objective; *figs. 3, 5–17* with a no. 12 ocular and a 1.5^{mm} objective; *figs. 24–27, 29, 30* with a no. 8 ocular and a $\frac{1}{12}$ objective; *fig. 28* with a no. 2 ocular and a ½ objective.

Peperomia Sintensii

FIG. 1.—Primary archesporial cell in apex of nucellus.

FIG. 2.—Archesporial cell has divided to sporogenous and parietal cell; the latter dividing and showing sixteen chromosomes; integument beginning to grow up around nucellus.

FIG. 3.—Longitudinal view of an anaphase in a vegetative cell.

FIG. 4.—Nucellus containing embryo sac mother cell, which shows a stage shortly before synapsis; part of integument which now surrounds nucellus shown at base of nucellus.

FIG. 5.—Early stage of synapsis in embryo sac mother cell.

FIG. 6.—Later stage of same.

FIG. 7.—Part of an apparently continuous spirem, just after synapsis.

FIG. 8.—Later stage of same, showing divided granules.

FIG. 9.—Still later stage, showing split spirem.

FIG. 10.—Still later stage; the two halves have come together and the spirem has become looped.

FIG. 11.—Chromosomes derived from loops shown in *fig. 10.*

FIG. 12.—Later stage of same.

FIG. 13.—Still later stage.

FIG. 14.—Still later stage; the two halves have come together.

FIG. 15.—Longitudinal section of a metaphase of the first division of embryo sac mother cell.

FIG. 16.—Anaphase of same.

FIG. 17.—Early stage in formation of daughter nuclei.

FIG. 18.—Two-nucleate embryo sac, showing cross-wall separating the two nuclei.

FIG. 19.—Slightly older embryo sac.

FIG. 20.—Embryo sac showing same stage as last.

FIG. 21.—Nuclei of a two-nucleate sac dividing; remnant of dividing wall still present.

FIG. 22.—Four-nucleate sac; one nucleus separated from the other three by a wall.

FIG. 23.—Later stage; wall was disappeared.

FIG. 24.—Four nuclei have divided to eight; no cell plates on the spindles; the sister nuclei in micropylar end.

FIG. 25.—Later stage; the two sister nuclei still in micropylar end.

FIG. 26.—The eight nuclei have just divided to sixteen; cell plates seen on the spindles.

FIG. 27.—Later stage; cell plates shown in last figure have grown into walls cutting off eight nuclei against the embryo sac wall and leaving eight free in the cytoplasm.

FIG. 28.—A mature ovule; the embryo sac contains sixteen nuclei; *p*, pollen tube with nuclei; *t*, tapetum; *i*, integument.

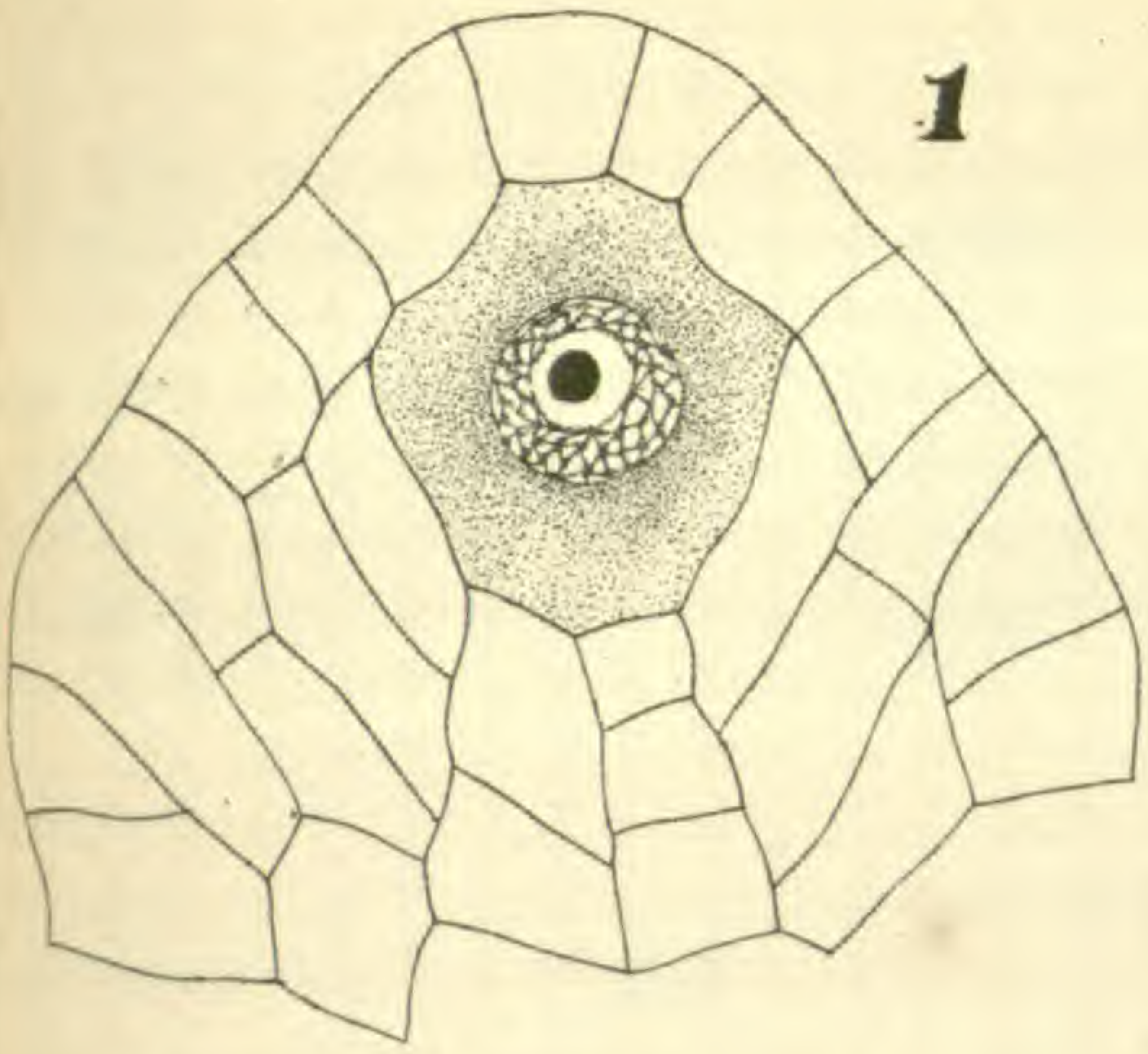
FIG. 29.—Embryo sac with fertilized egg and nuclei fusing to form the endosperm nucleus; *e*, egg with fusing nuclei; *p*, pollen tube; *s*, nucleus with the position of a synergid; *d*, peripheral nuclei which will degenerate; *f*, nuclei fusing to form endosperm nucleus.

FIG. 30.—Later stage of fusion in male and female nuclei.

Peperomia ottoniana

FIG. 31.—Four-nucleate sac; one nucleus cut off and surrounded by dense protoplasm.

FIG. 32.—Later stage; the wall dividing off one nucleus has disappeared.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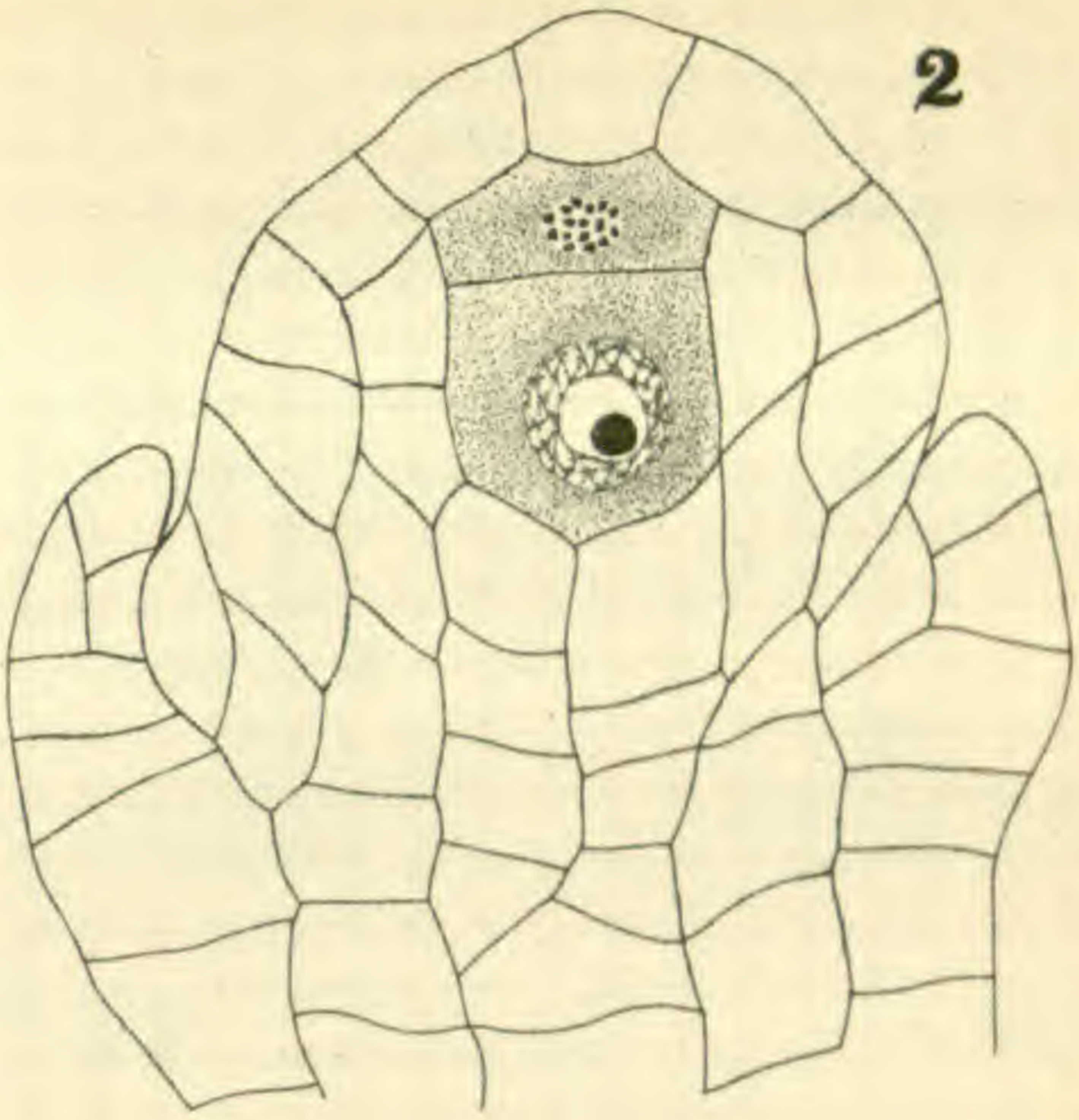
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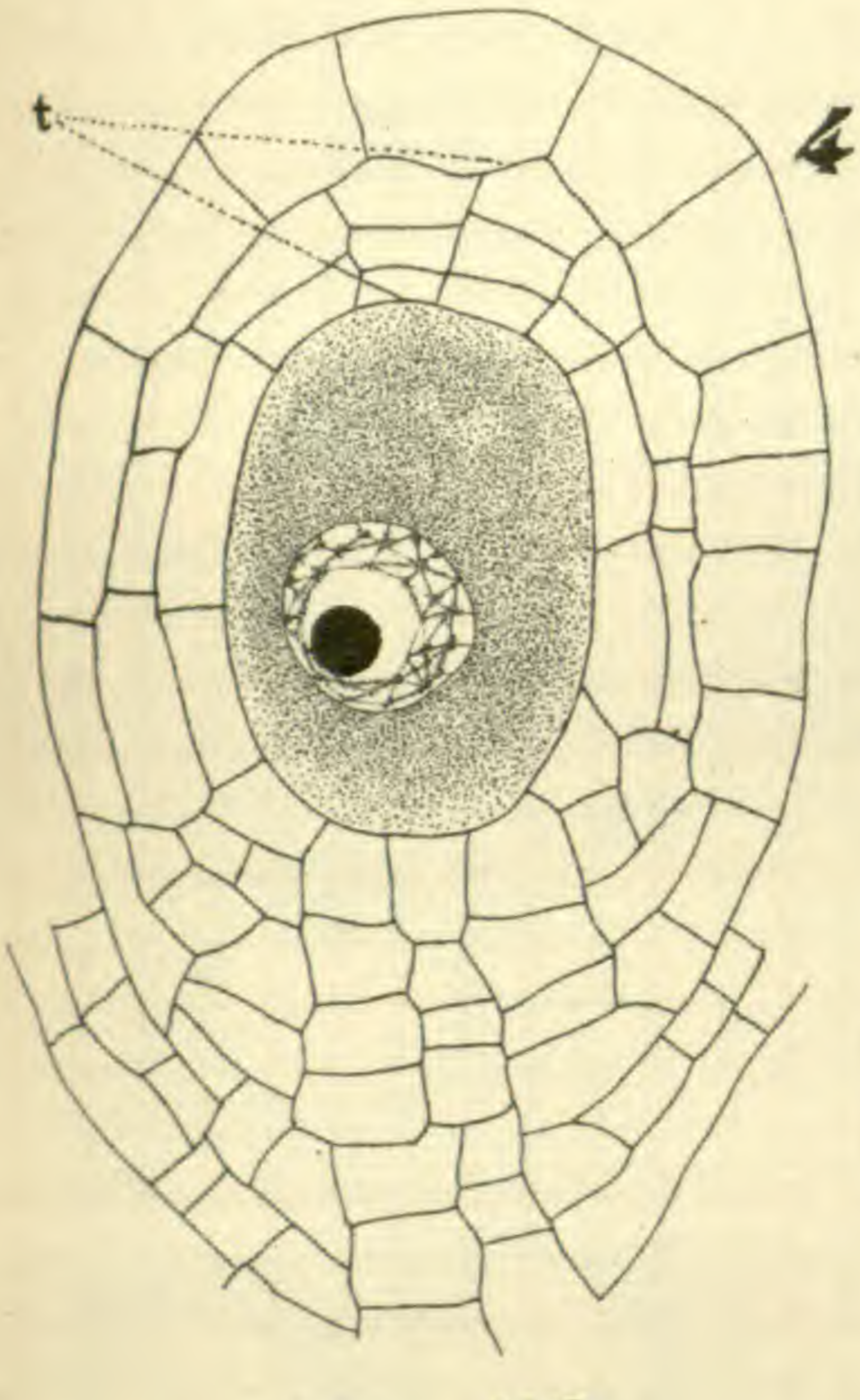

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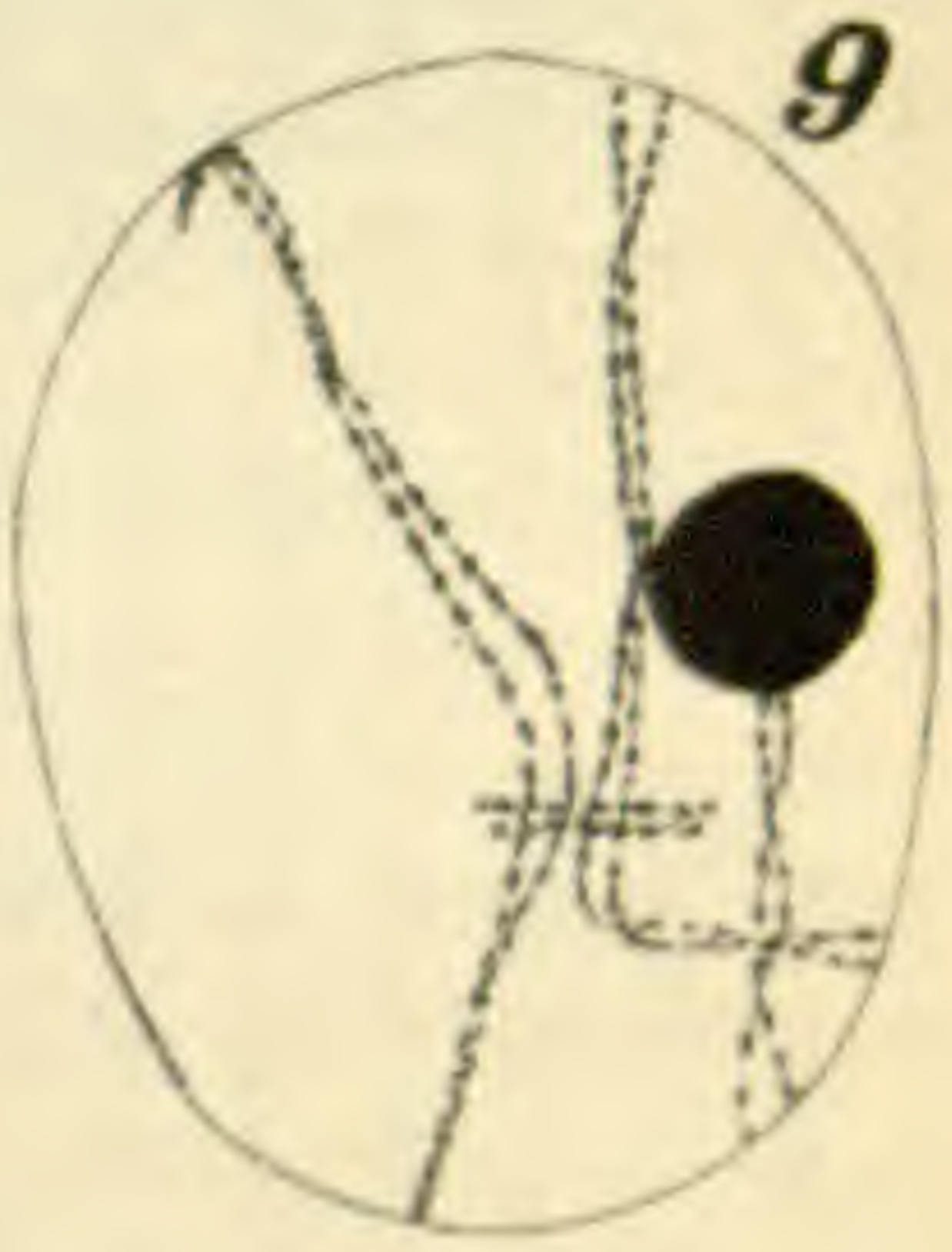
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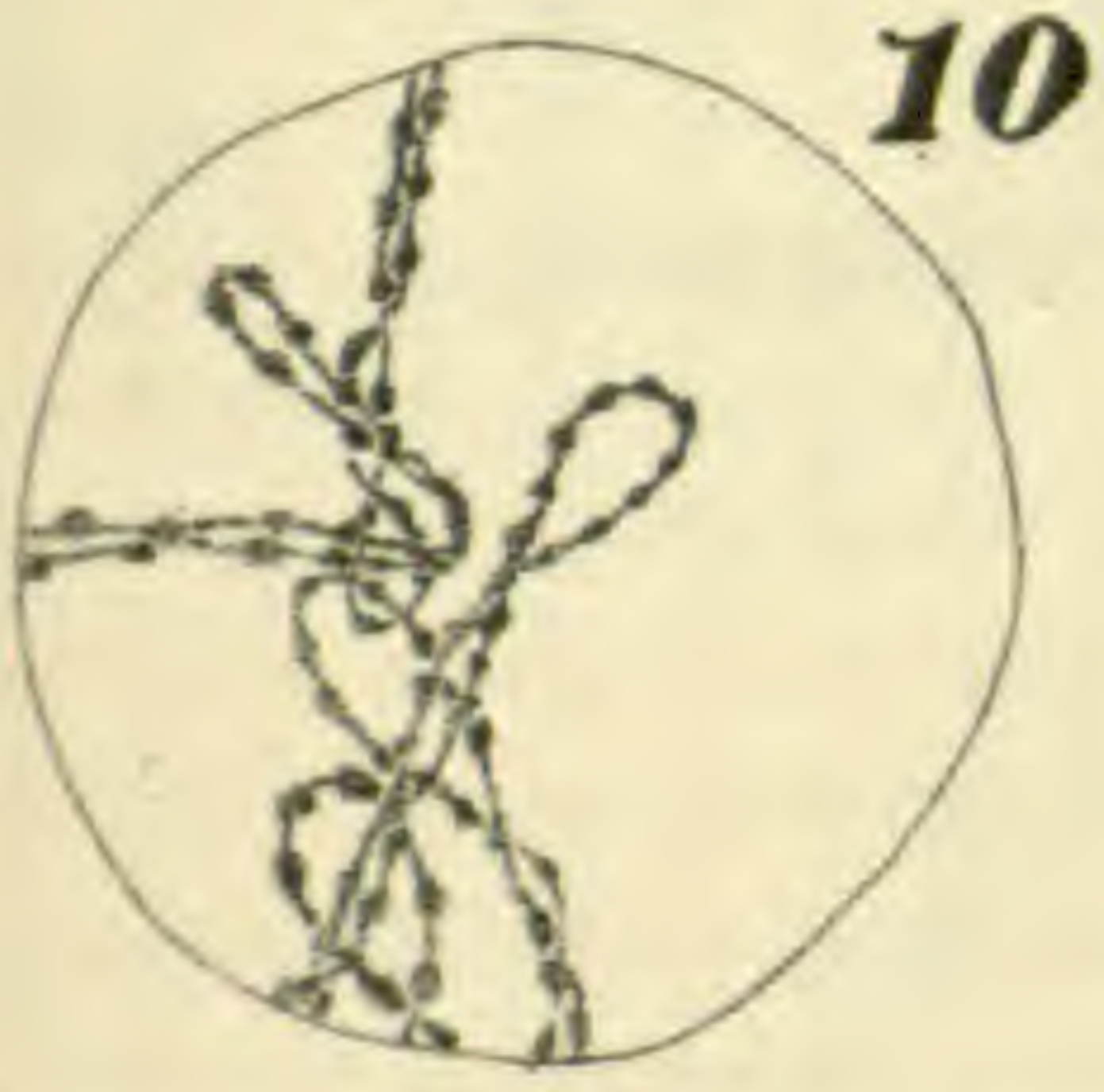
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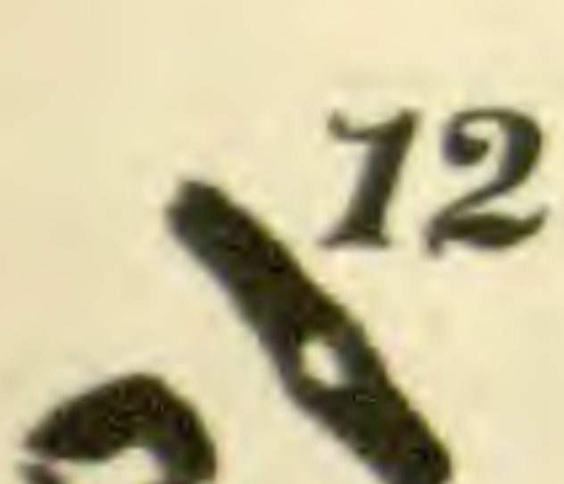
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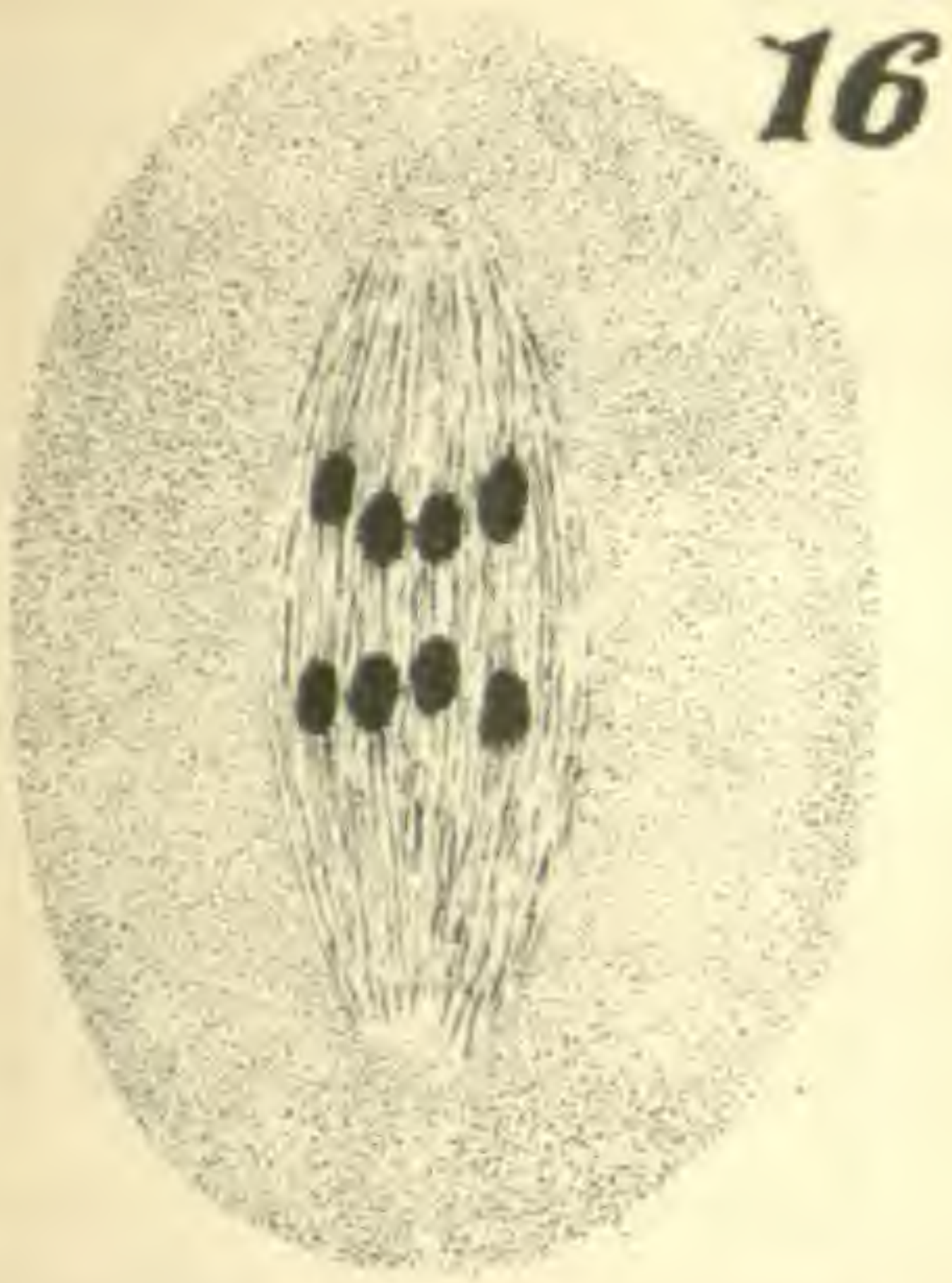
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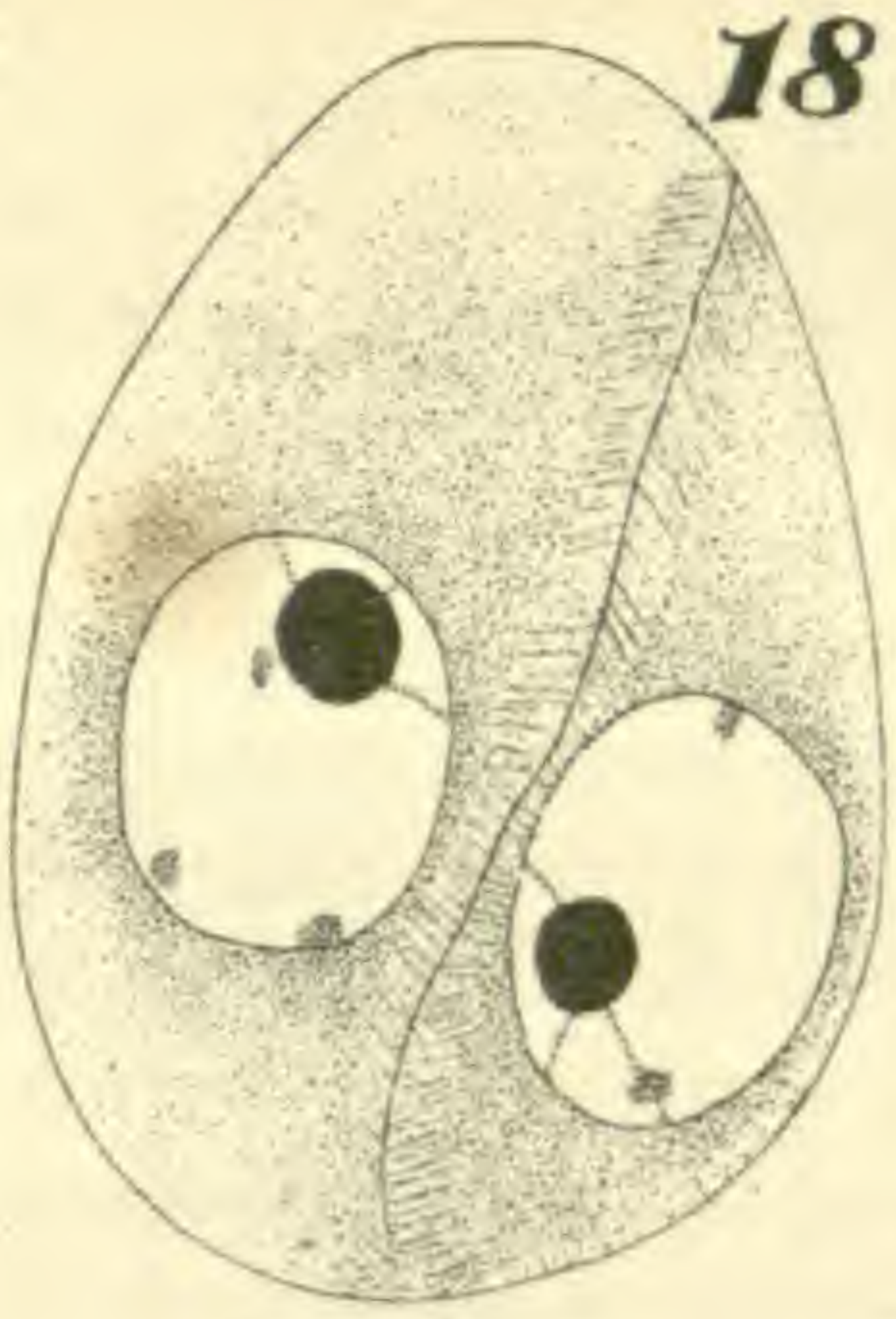
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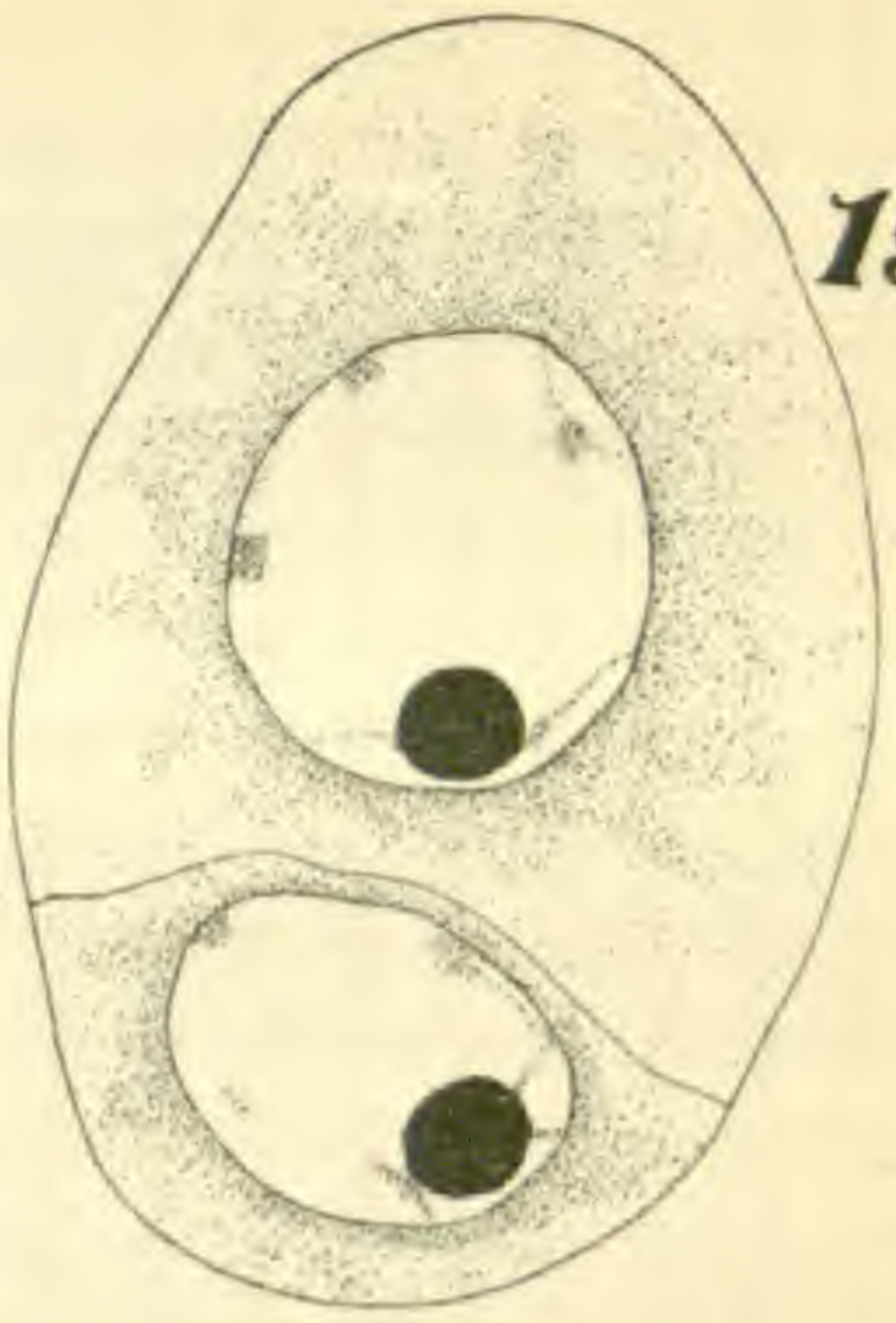
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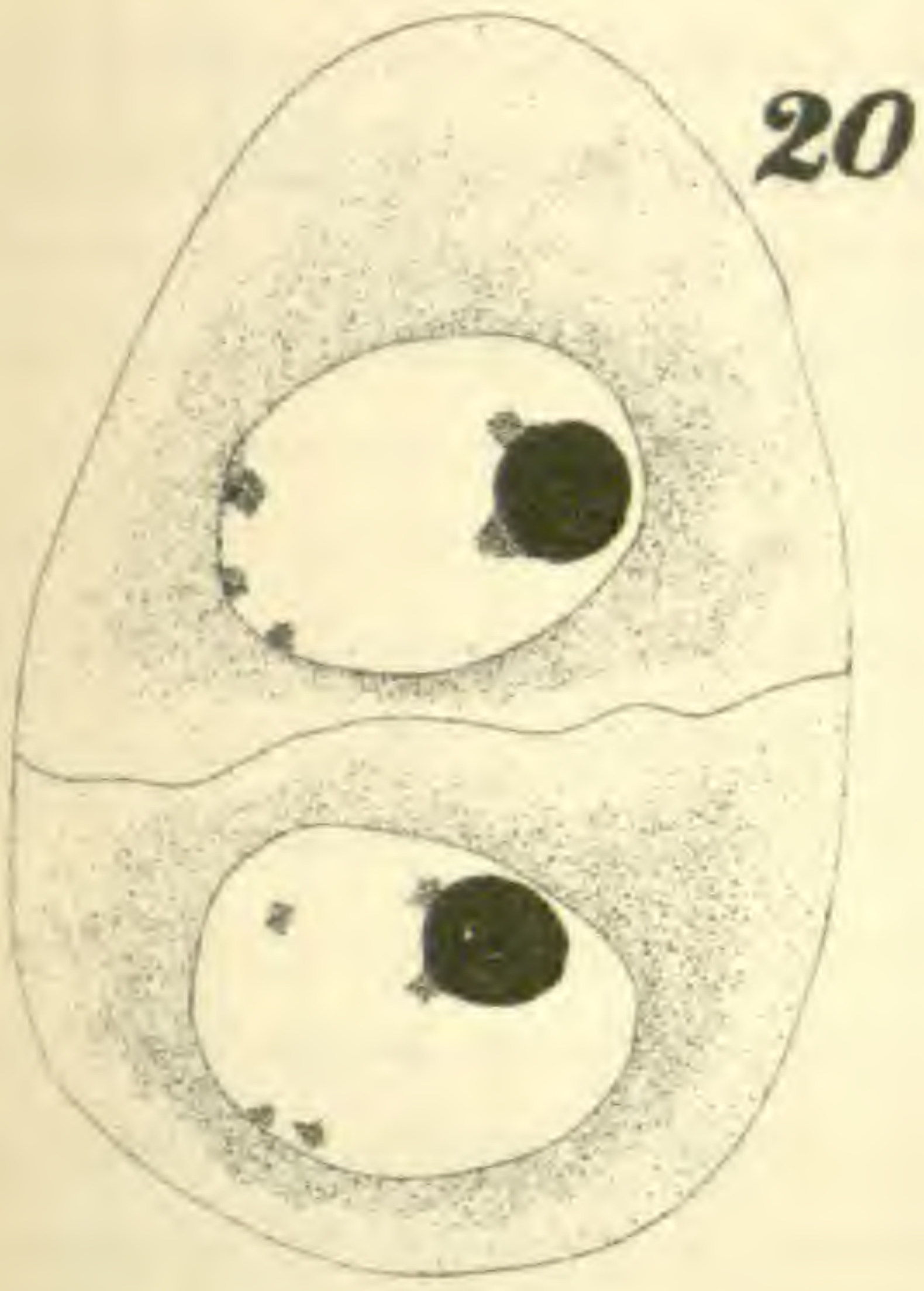
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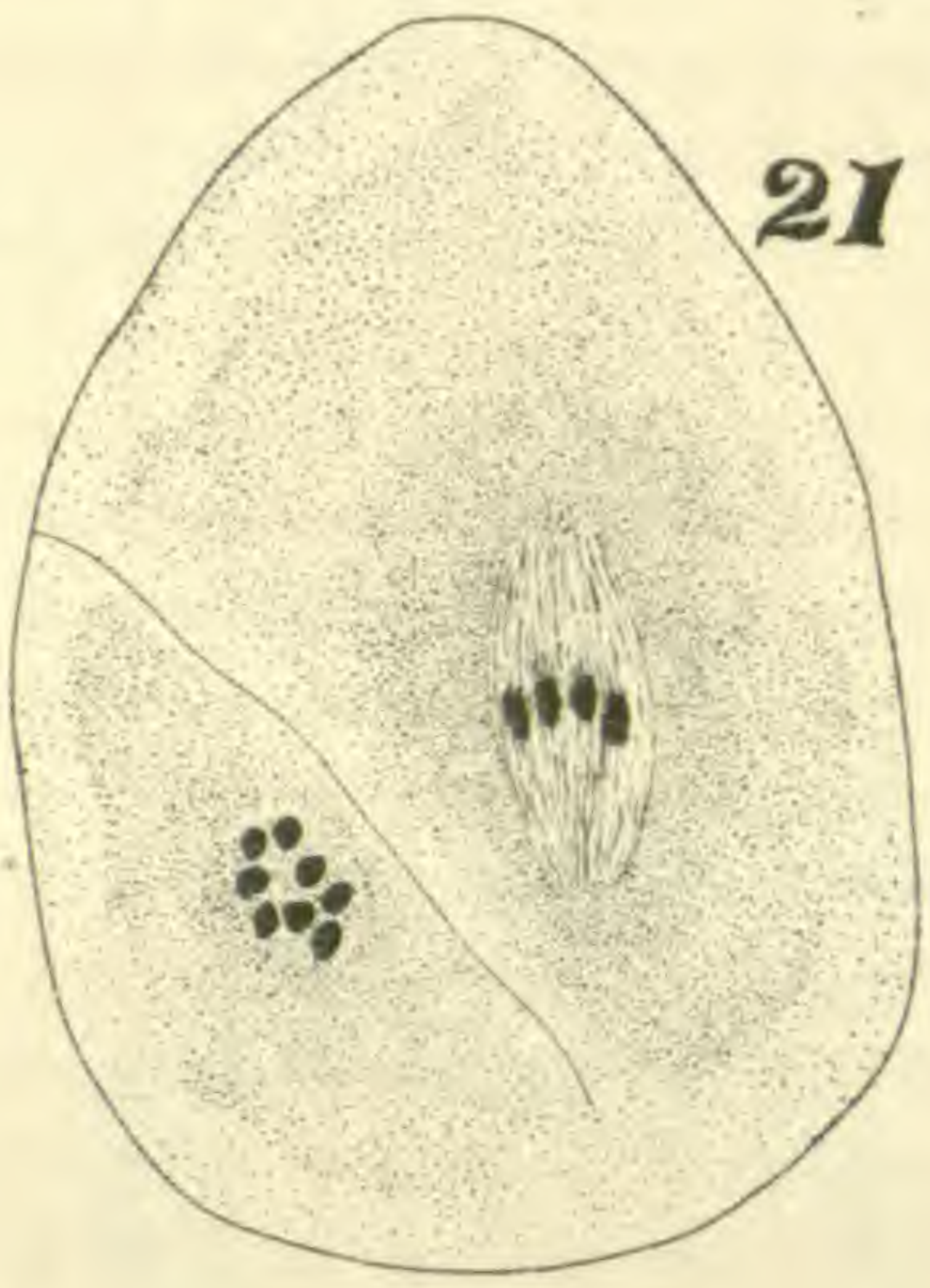
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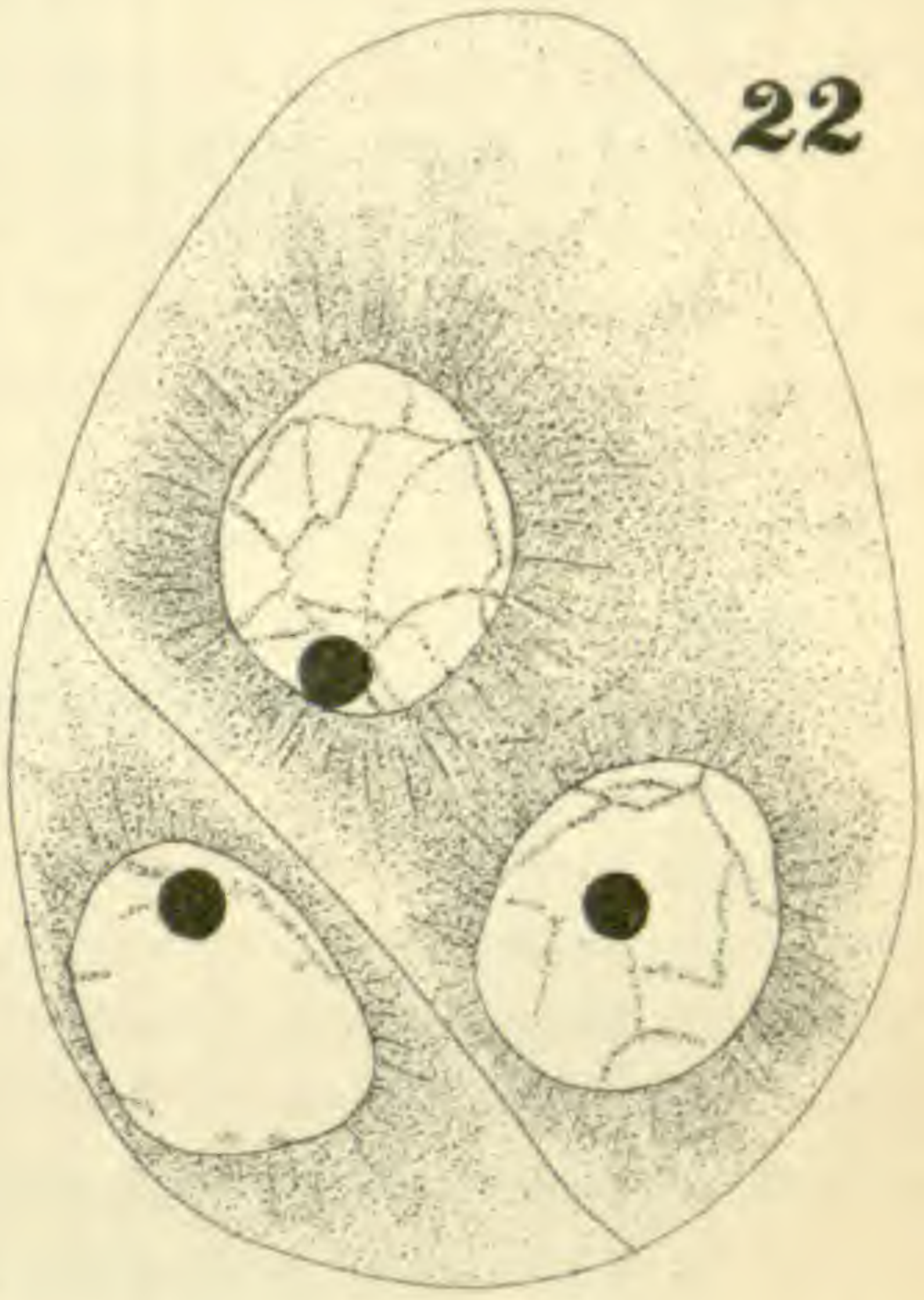
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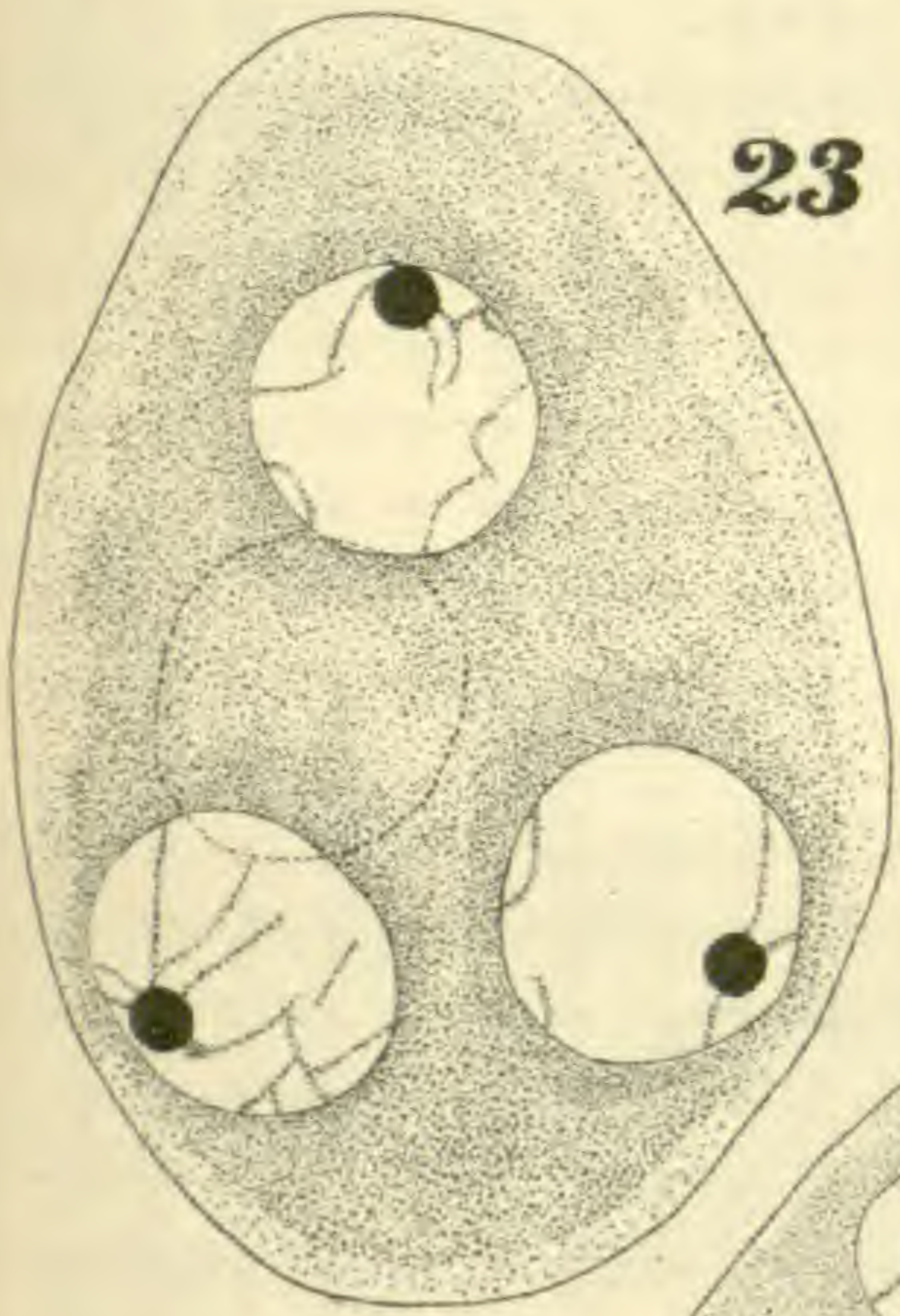
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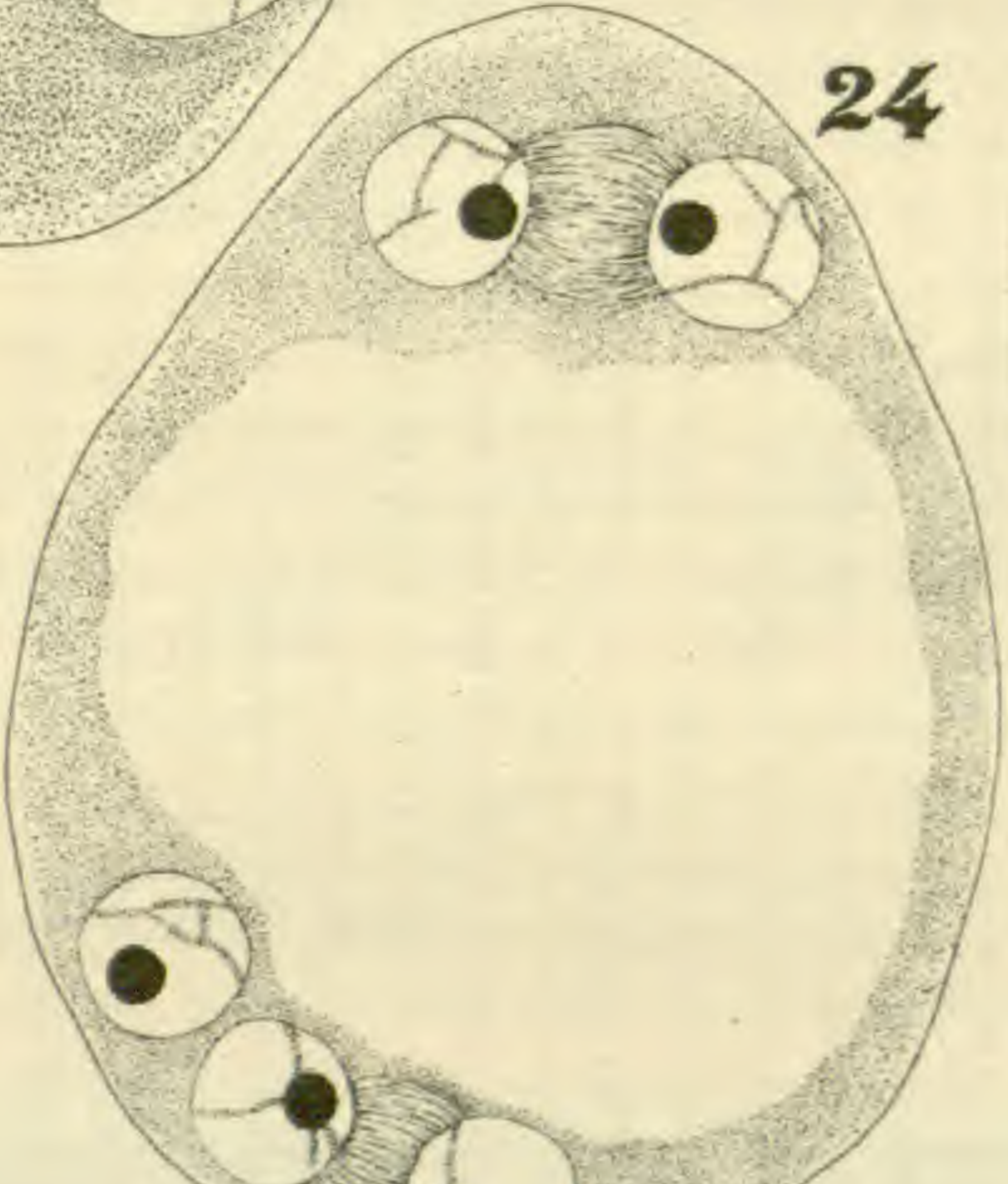
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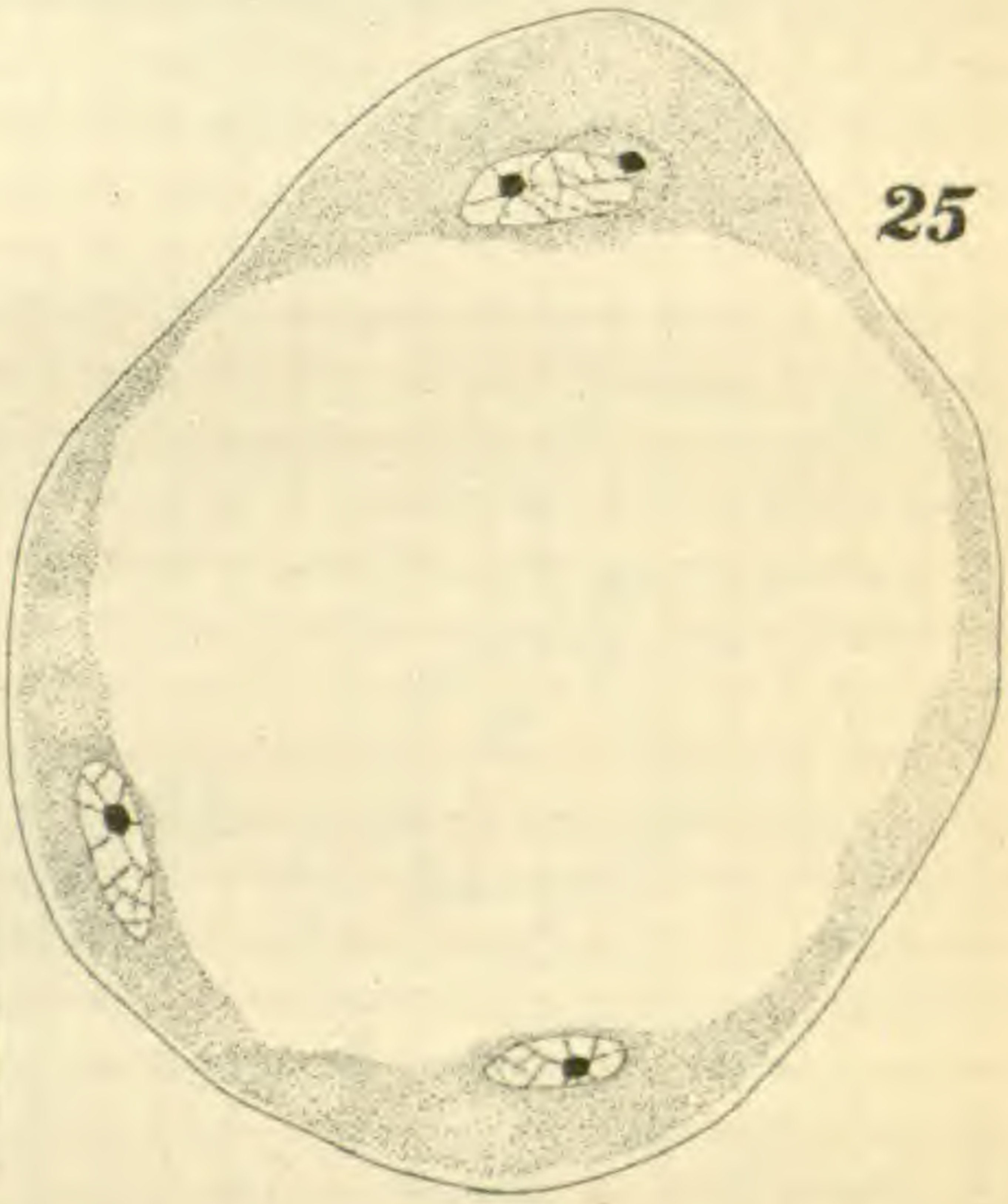
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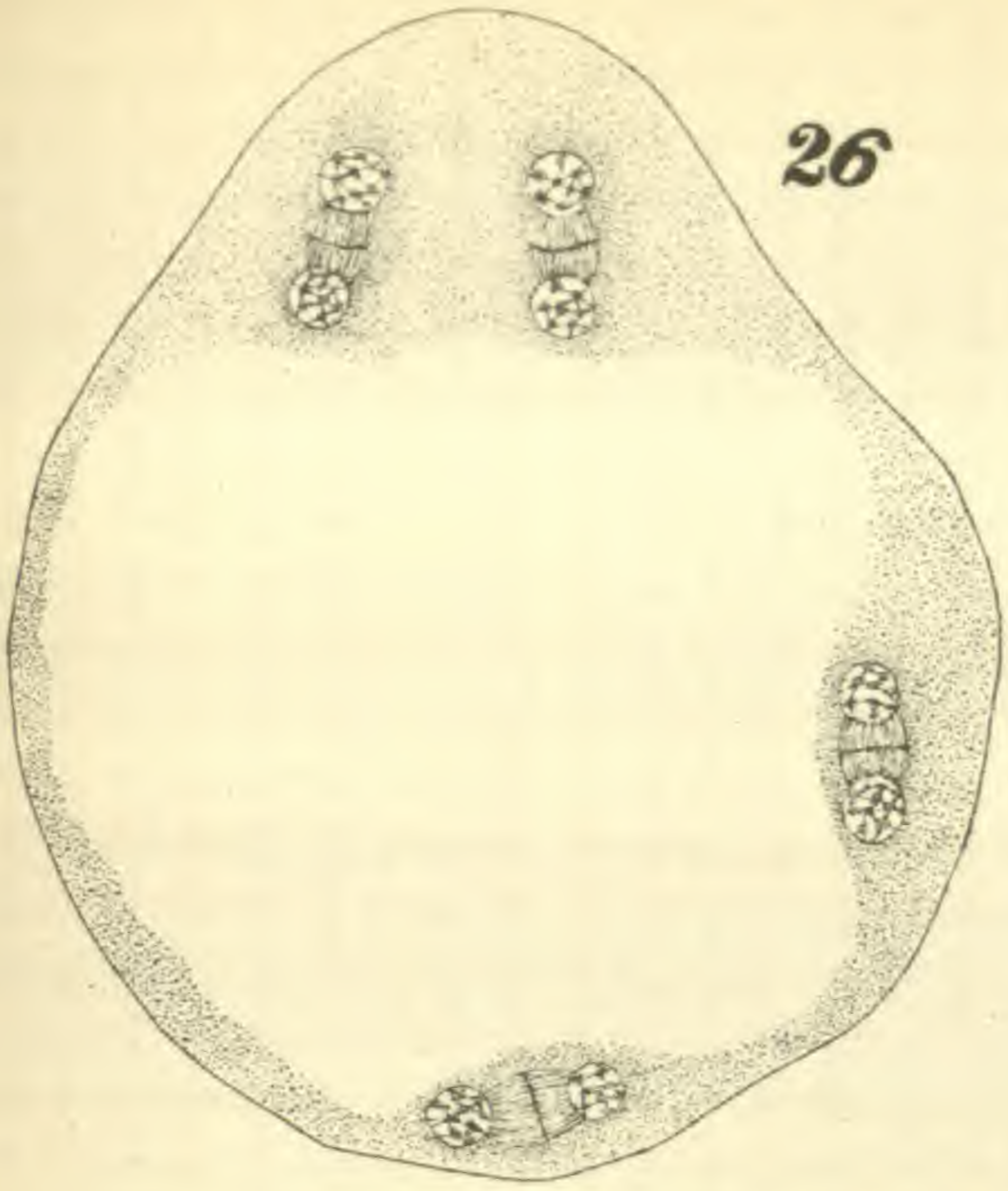
BROWN on PEPEROMIA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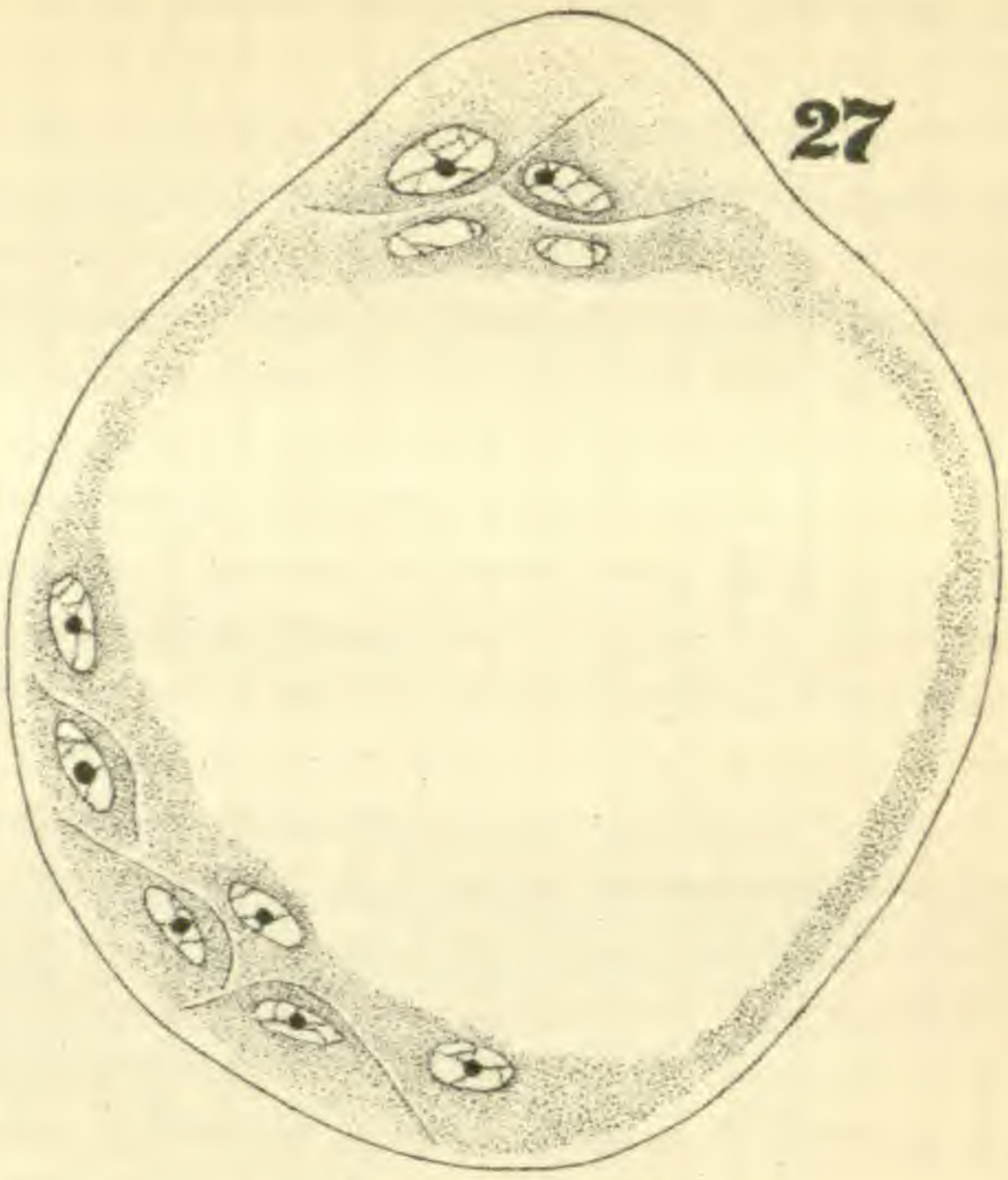
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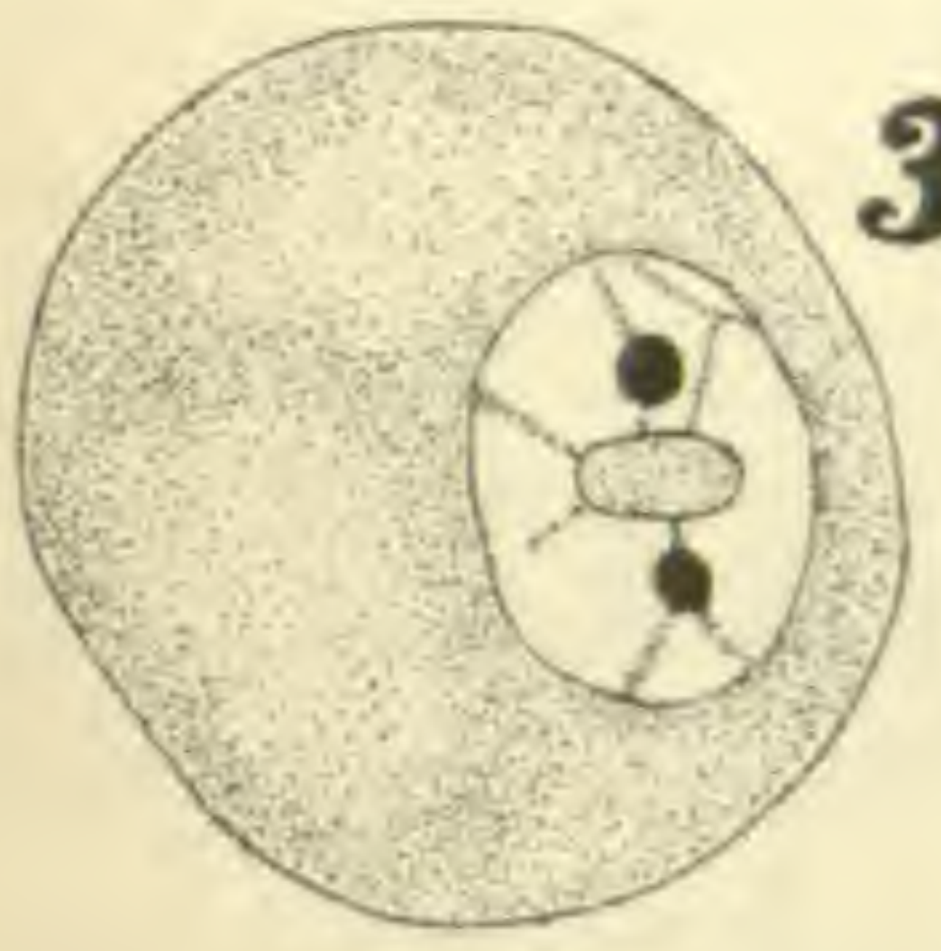
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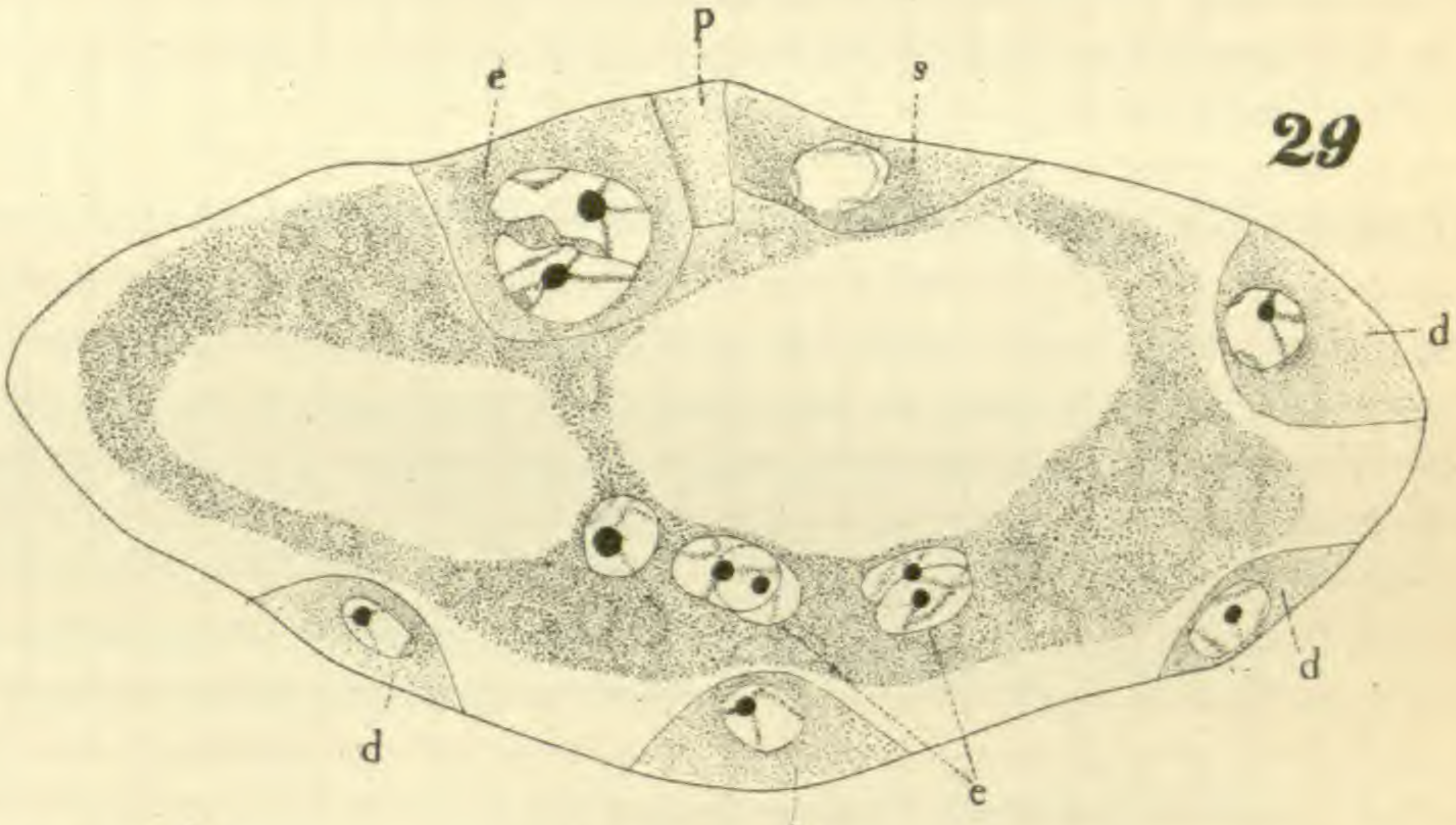
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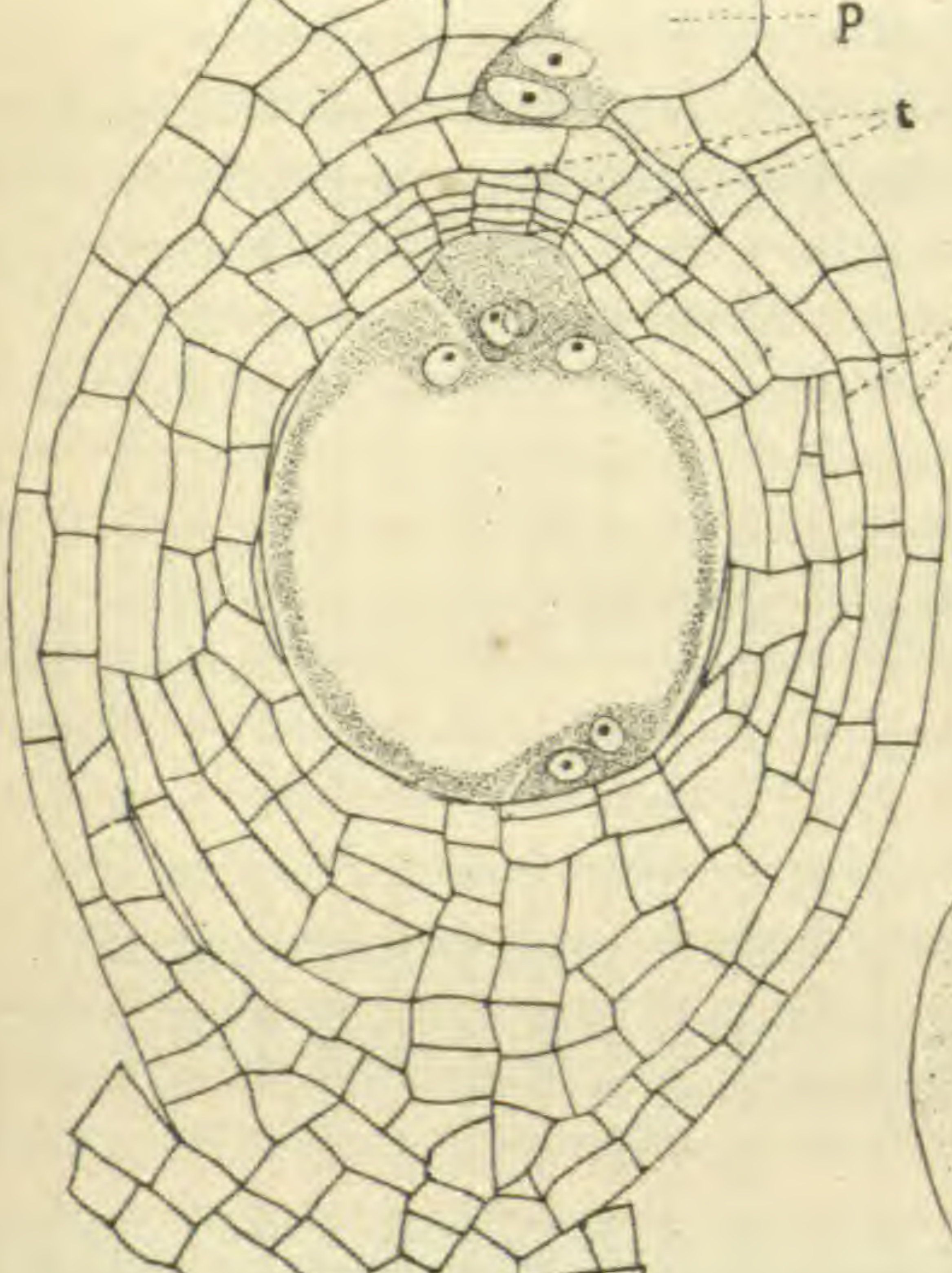
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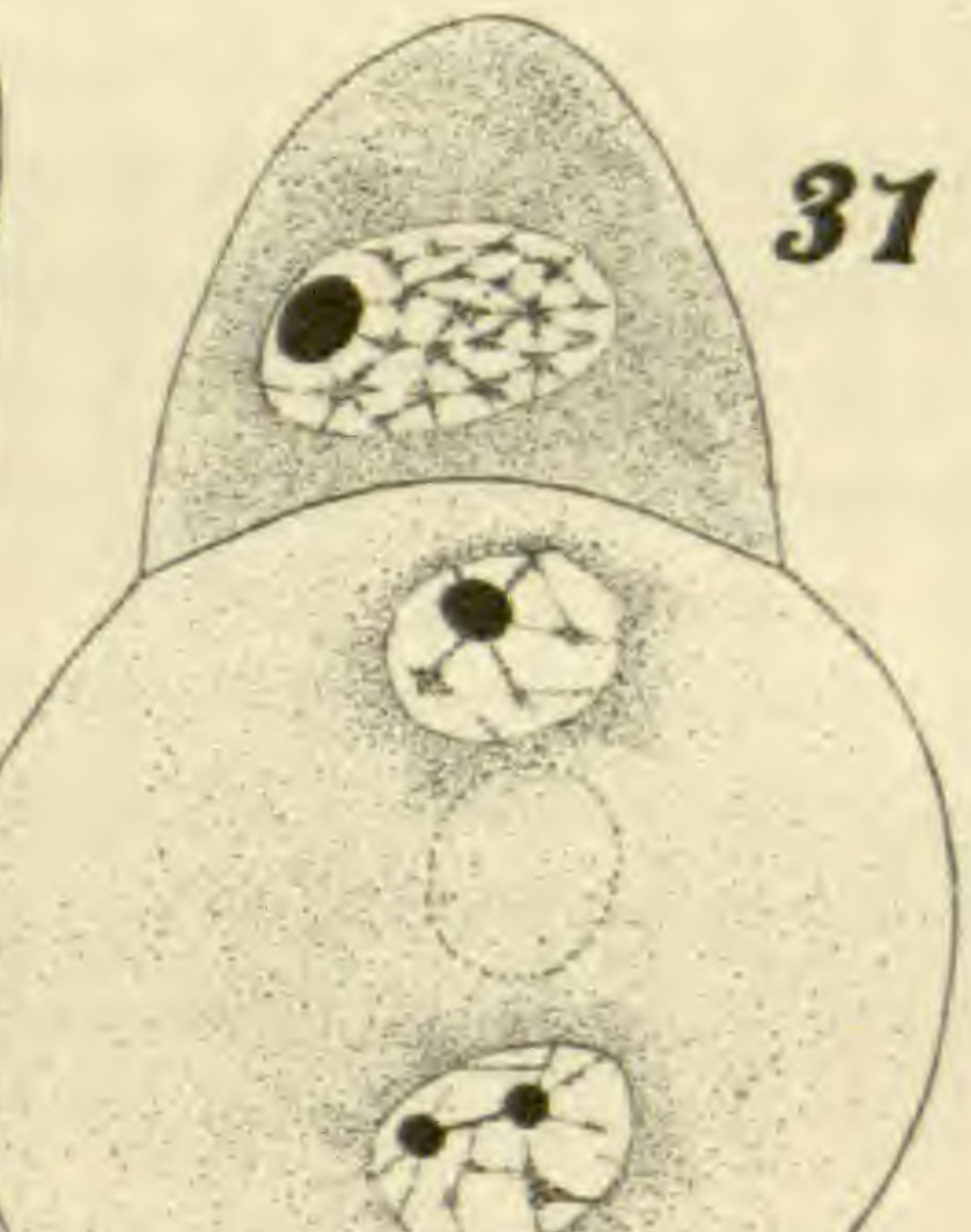
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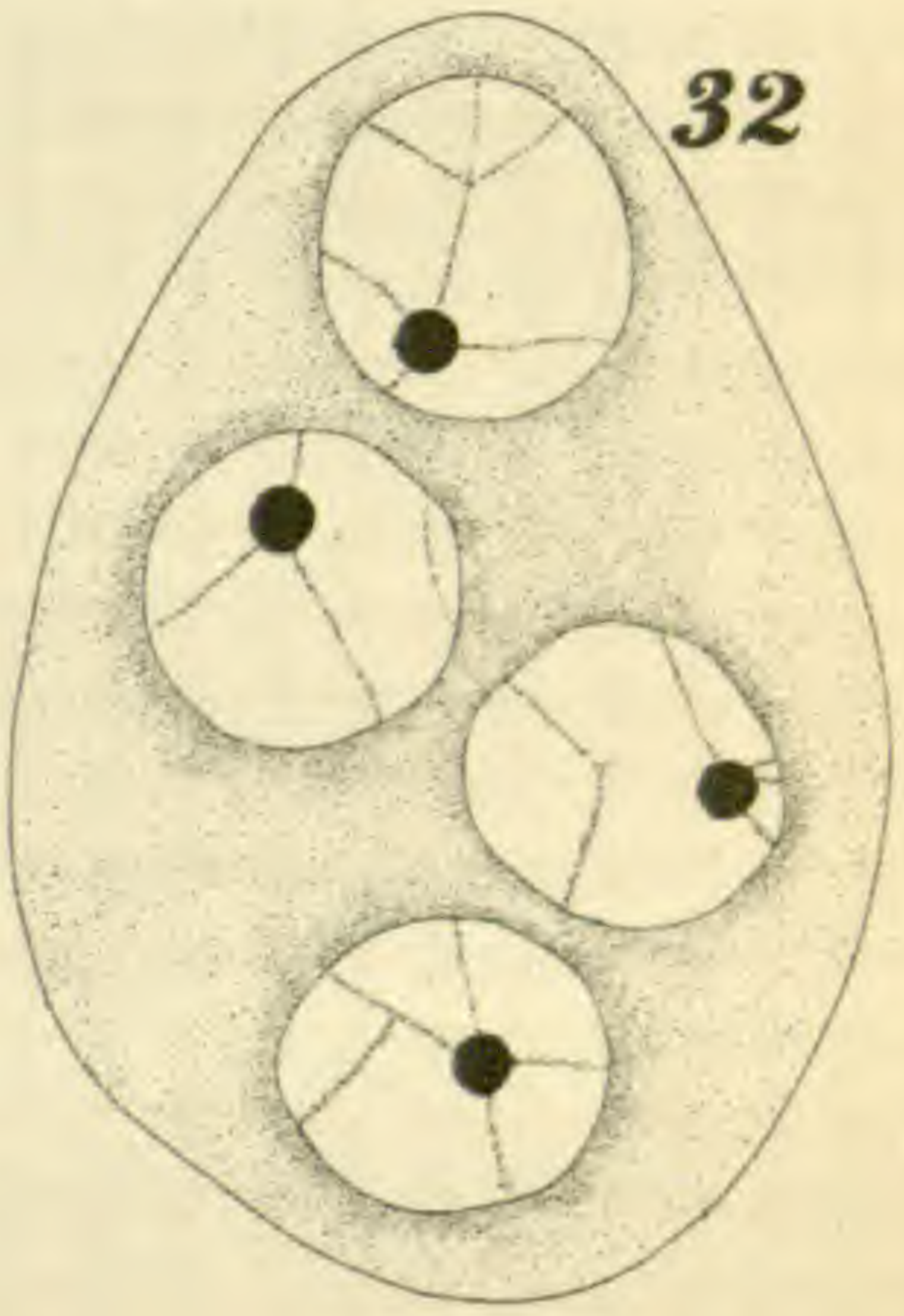
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BRIEFER ARTICLES

A NEW POISONOUS MUSHROOM

(WITH TWO FIGURES)

During last August I received from Dr. O. E. FISCHER, Detroit, Michigan, a few living plants of a species of Tricholoma, which he reports as causing several severe cases of poisoning. The specimens were sufficiently well-preserved for study and diagnosis, also for a photograph, and for casting spores for a photomicrograph. The plants are medium size, white in color with dull clay-colored tinge and stains in places. The plants are moist but not viscid, with the pileus minutely scaly but subtomentose over the center. The scales possess the darker color and under the hand lens some of them appear nearly black, but because of their minute size the dark color is not evident to the eye. The stems are subbulbous, the shape of the bulb being peculiar and resembling that of *Lepiota lenticularis*, which in side view is supposed to suggest the shape of a biconvex lens. The taste of the plants is mild, and no particular odor was observed in those received. The plants appear to be near to *Tricholoma pallidum* Pk. from Worcester, Mass., but differ in a number of particulars, as will be seen by a comparison of the diagnoses.

Before giving the technical diagnosis I quote the following from Dr. FISCHER's letter:

> I am sending you a set of agarics of unusual interest and importance, for they are the ones that made seven people very ill in Rochester, Mich., on August 21. Violent and hemorrhagic vomiting, diarrhoea, sweating, and some cardiac disturbance were the symptoms, lasting several hours and coming on one hour after eating even of minute quantities. Some of the women are still suffering from intestinal disturbance. None that ate escaped; none died. I have spent considerable time and energy in taking two of the victims to the exact spot where they picked the offenders and got the cause of the trouble. It is a white-spored agaric, growing in open grassy woods on a leafy base, in clusters and groups. I should greatly appreciate a certain identification of this agaric, the more so since it looks, tastes, and smells inviting, and was "O.K.'d" by a member of our club.

Tricholoma venenatum Atkinson, n. sp.—*Plants* 4–8^{cm} high, pileus 4–7^{cm} broad, stem 1–1.5^{cm} thick, plants white with dull clay-colored tinge and stains; *pileus* moist not viscid, convex-expanded, subumbonate, center fleshy, thin toward the margin, plane or subrepand, minutely scaly with fibrous scales, subtomentose area over center, surface pale buff to pale clay color, the scales possessing the darker color, under the lens some of them appear nearly black; *gills* adnexed, broadly sinuate, sub-

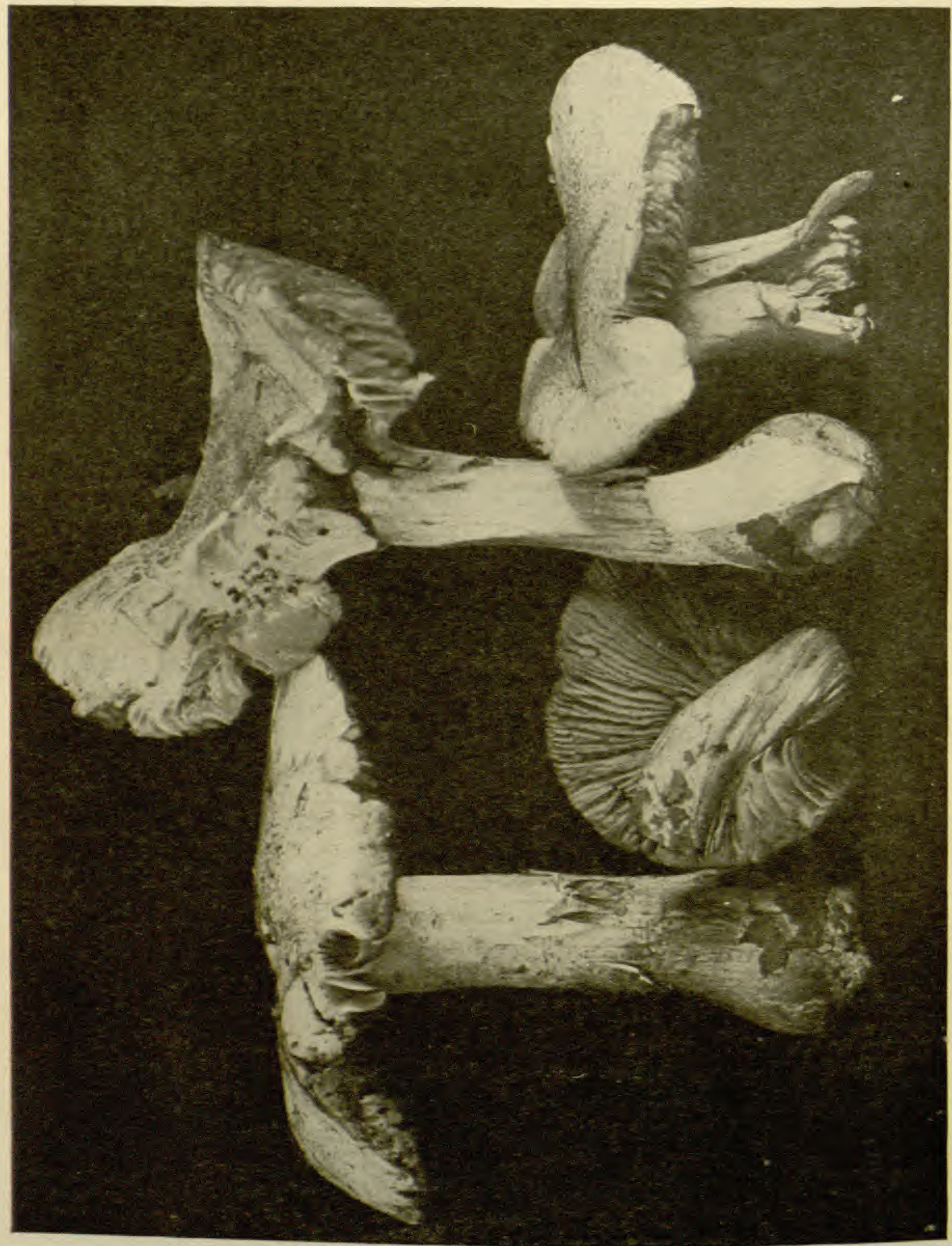

FIG. 1.—*Tricholoma venenatum* Atkinson.

distant, whitish, thin, dull clay color especially where bruised; *spores* white, smooth, oval to broadly subelliptical, 5–7×3.5–5 μ; *cystidia* none; stems subbulbous with a bulb like that of *Lepiota lenticularis*, fibrous striate, solid, sordid white, becoming in age where handled dull clay color; *odor* and *taste* mild.—No. 22573 C. U. Herb., from Dr. O. E. FISCHER, Detroit, Mich., received August 29, 1908.

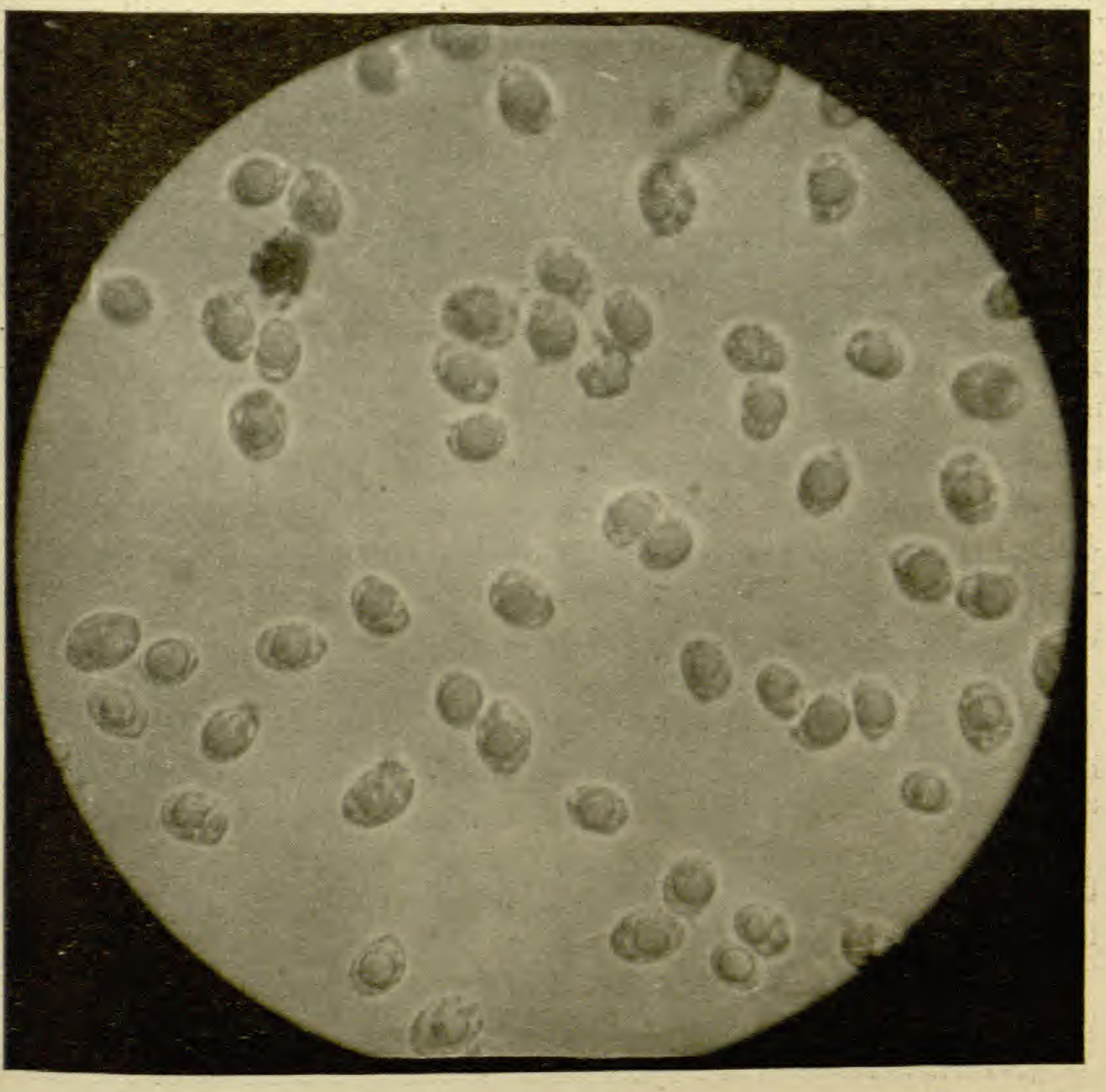

FIG. 2.—Photomicrograph of spores of *Tricholoma venenatum;* Zeiss ocular No. 18, objective 3^{mm}; object 370^{mm} from sensitive plate.

(Sporophoro albo, leniter sordide luteo, 4–8^{cm} longo, pileo 4–7^{cm} lato, stipite 1–1.5^{cm} crasso; pileo convexo-expanso, subumbonato, squamulis minutis obducto; lamellis adnexis, late sinuatis, tactu sordide luteis; sporis hyalinis, glabris, ovatis vel subellipsoideis, 5–7×3.5–5 μ; stipite subbulbo, fibroso-striato, tactu sordide luteo.)

GEO. F. ATKINSON, *Department of Botany, Cornell University.*

AFFINITIES OF PHYLLOCLADUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 121

In connection with the work on *Phyllocladus alpinus* published in this journal (BOT. GAZETTE **46**:339–348. *pls. 20–22.* 1908), it was the intention not to venture upon a discussion of the relationships until a more complete knowledge of the life-history had been obtained from further material. On account of the probable delay connected with securing and investigating the new material, it seems better to present at this time such conclusions as the results already obtained seem to justify.

In 1872 Phyllocladus was placed among the Podocarpineae by STRASBURGER,[1] the relationship being based upon external resemblances. In ENGLER and PRANTL'S *Pflanzenfamilien* it is put among the Taxineae. In 1903 PILGER[2] placed it in a separate group (Phyllocladoideae) intermediate between Taxineae and Podocarpineae; this disposition of the genus being based upon features in which Phyllocladus differs from the Taxineae, namely the two-sporangiate microsporophyll, the uniovulate scale, the arillus, and the anatomy of the vegetative structures. Miss ROBERTSON[3] follows PILGER in assigning to Phyllocladus this intermediate position, with a greater affinity for the Podocarpineae.

In comparing Phyllocladus with the Podocarpineae and with the Taxineae, its relationship to the former tribe becomes very evident. The principal features of resemblance to Podocarpineae, in contrast with the corresponding features of Taxineae, may be enumerated as follows:

1. The microsporophyll of Phyllocladus bears two abaxial sporangia; the microsporophylls of the Taxineae are all of the peltate type, bearing three to eight sporangia.

2. Each scale of Phyllocladus bears one centrally placed ovule; among the Taxineae each scale bears two lateral ovules.

3. The microspores of Phyllocladus have wings, and four or five nuclei at the time of shedding; those of the Taxineae have no wings, and only one or two nuclei at the time of shedding.

4. Male prothallial cells are formed in Phyllocladus and in all the Podocarpineae; none occur in the Taxineae.

5. The evanescent prothallial tissue of Phyllocladus is similar to that found in the Podocarpineae.

6. The megaspore membrane is well developed; this membrane is

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[1] STRASBURGER, E., Die Coniferen und die Gnetaceen. 1872.

[2] PILGER, R., Taxaceae. Pflanzenreich, nos. 4, 5. 1903.

[3] ROBERTSON, AGNES, Some points in the morphology of *Phyllocladus alpinus.* Annals of Botany **20**:259–265. *pls. 17, 18.* 1906.

present in all the gymnosperms except the Taxineae, among which it is almost entirely eliminated.[4]

The features in which Phyllocladus resembles the Taxineae and differs from the Podocarpineae are as follows:

1. The ovule is erect; in the Podocarpineae it is more or less inverted, except in *Dacrydium latifolium*.

2. The cladodes contain centripetal wood, according to Miss ROBERTSON (*l. c.*). WORSDELL[5] states that centripetal wood is more common among the Taxineae than in any other group of Coniferales; it has been found in the leaf and cotyledon of Taxus and Cephalotaxus, in the cotyledon of Torreya,[6] and in the stem of *Cephalotaxus koraiana*.[7]

3. The arillus of Phyllocladus originates at the base of the ovule, just as does that of Taxus; the so-called epimatium (PILGER, *l. c.*) of Podocarpus arises from the scale. If this epimatium represents the arillus of Phyllocladus and Taxus, it differs in origin and form; if it does not represent the arillus, it is a structure not found in those genera.

These comparisons indicate that in number and in importance the features of Phyllocladus in common with those of Podocarpineae are much greater than those in common with Taxineae. The winged microspores and the multicellular and evanescent prothallial tissue alone would seem to be of sufficient importance to associate Phyllocladus with the Podocarpineae. We are inclined, therefore, to assign Phyllocladus to the Podocarpineae, thus confirming STRASBURGER'S conclusion of 1872; and not to regard it as referable to Taxineae, or as worthy of constituting a distinct group.—N. JOHANNA KILDAHL, *The University of Chicago.*

NOTE ON THE POLLEN OF MICROCACHRYS

NORÉN[8] has recently described certain of the reproductive features of Saxegothaea. He found that the microspore, like that of the other podocarps recently described, has supernumerary prothallial cells. Unlike the other forms, however, the grains are not winged. In connection with the

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[4] THOMSON, R. B., The megaspore membrane of the gymnosperms. Univ. Toronto Biol. Series, no. 4. 1905.

[5] WORSDELL, W. C., On transfusion tissue; its origin and function in the leaves of gymnospermous plants. Trans. Linn. Soc. Bot. London II. **5**:301–319. *pls. 23–26.*

[6] CHICK, EDITH, The seedling of *Torreya myristica*. New Phytol. **2**:83. 1903.

[7] ROTHERT, W., Ueber parenchymatische Tracheiden und Harzgänge im Mark von Cephalotaxus-Arten. Ber. Deutsch. Bot. Gesells. **17**:275. 1899.

[8] NORÉN, C. O., Zur Kenntnis der Entwicklung von *Saxegothaea conspicua* Lindl. Svensk. Bot. Tidskr. **2**:101–122. *pls. 7–9.* 1908.

deposition of the pollen there is a very interesting condition. Sometimes the pollen falls in the micropyle, and sometimes in the cavity around the ovule, whence it grows over the tissues into the micropyle. This recalls the condition of affairs in the Araucarieae, and is essentially similar in this respect to Agathis, as I have found it.

In the pollen of Microcachrys there is a similar excess of prothallial tissue. The grain has wings, however, but not of so definite a character as those of Dacrydium and Podocarpus, which, as is commonly known, bear two well-developed floating appendages. In Microcachrys a large percentage of the grains have three rather poorly developed wings, though the greater number are of the type which is characteristic of the higher members of the group. The winging of the grain is, as it were, in its experimental condition in Microcachrys, and the form is to be considered in this respect as a transitional one between Saxegothaea on the one hand and Dacrydium and Podocarpus on the other.

Attention has often been directed to the biwinged condition of the pollen of the pines and podocarps as an indication of the probable affinity of the two groups. This view is no longer tenable, since the wings of the pollen in the latter are a development within the group itself, analogous but not homologous with those of the pine series. On the contrary, the relationship of the microgametophytic condition in the Podocarpeae to that in the Araucarieae is increasingly apparent.—ROBERT BOYD THOMPSON, *University of Toronto.*

CURRENT LITERATURE

BOOK REVIEWS

North American Uredineae

PROFESSOR J. C. ARTHUR has begun his presentation of the Uredineae in the *North American flora.*[1] No one who has kept informed of our mycological literature, even in the most general way, needs to be told that the author is the leading American specialist on this group of fungi, and that this is the first attempt to monograph the rusts for the whole continent. Heretofore one has had to depend on the restricted paper of BURRILL dealing with the rusts of Illinois, and FARLOW'S *Host index of North American fungi*, on the special papers by ARTHUR, HOLWAY, and others, and on the check lists and *exsiccati* that have been issued from time to time. The need of the work, therefore, cannot be questioned, and no one who has been engaged in a similar task can fail to appreciate the immense amount of effort it has required to bring it thus far toward completion. The part already issued, which includes descriptions of about 150 species and 34 genera, the writer understands to be but the advance guard of two or more parts to be issued later, as the material is worked up.

The monograph is thoroughly well done. It presents a uniform treatment of description and terminology. The bringing together and describing anew all stages, especially the pycnia which have largely been neglected before, make it especially valuable. It also reflects our latest knowledge of the life-history of the various species, to which the author has so long contributed with telling results. As to the real usefulness of the specific keys given under the genera, perhaps there may be some question, but the author no doubt has made them as valuable as they can be made. Mycologists have gone so far in describing new species of rusts (and other fungi as well) chiefly because they occur on new hosts, that one in self-defense acquires the habit of disregarding keys, so far as possible, and uses the host and specific description as the shortest route to identification. Then, too, it is very difficult to discover sufficient morphological characters for use in keys to distinguish the species of a large genus, so that frequently the host genera and families are necessary as characters to fill deficiencies. In his keys ARTHUR has made use of both hosts and morphological characters, using the latter apparently whenever possible.

Aside from the unquestioned merit of the work, the reviewer would dissent strongly from the point of view that compelled the author to split up old genera and to coin many new specific names. These changes did not all appear for the first

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[1] ARTHUR, JOSEPH CHARLES, North American Flora.—Uredinales (Coleosporiaceae, Uredinaceae, Aecidiaceae pars) 7:83–160. 1907.

time in the work under review, but they are all brought together here, and so focus our attention on the ninety (about) specific names (considerably over one-half) that bear ARTHUR's name as their authority; and he is also responsible for sixteen (about one-half) of the genera. However, he is not quite so extreme in this respect as MURRILL has been in his monograph of the Polyporaceae. ARTHUR has obtained part of his genera from new material and part by splitting up old genera, basing the new genera largely upon their possession of one or more of the O, I, II, III stages characteristic of the rusts. His familiarity with the rusts is such that he is able apparently, if given only the II stage, to tell what other stages it possesses, and so can place it in a genus.

Judging from this past tendency to publish new species under the old recognized genera, a tendency he has not yet entirely lost, I expressed doubt to the late Professor UNDERWOOD, editor of the *Flora*, that ARTHUR would follow his Vienna paper in his treatment of the North American Uredinales. As he did follow it, however, I promptly received from UNDERWOOD the following: "Some time ago you charged that ARTHUR was not possessed of the courage of his convictions in regard to his publication of genera in the Uredinales. I commend to your prayerful attention the second part of Vol. VII of *North American flora*, issued March 6, and move that it is time to have a retraction of that charge." I herewith publicly make that retraction; but what will become of this nomenclature when some ambitious name-juggler revises our rusts fifty years hence, or possibly even after the next botanical congress!—G. P. CLINTON.

NOTES FOR STUDENTS

Turgor and osmotic pressure.—The relation between these stands in great need of accurate study. LEPESCHKIN, a few months ago, discussed the matter before the German Botanical Society.[2] After reviewing the terminology, he designates as turgor and turgescence the condition of tenseness of the tissues due to internal pressure in the cells. For quantitative purposes he defines as a turgor pressure (*Turgordruck*) the total pressure exercised by "cell contents" upon the "cell walls;" but he evidently means by *Zellinhalt* the cell sap, for he explains that the *Zellwände* must be of plasmatic nature. By turgor tension (*Turgordehnung*) he designates the elastic elongation of the walls in any dimension, wrought by turgor pressure. This only partly accords with the best usage in this country, where turgidity rather than turgescence names the condition, and turgor the internal pressure which produces turgidity, while turgor tension has seldom been considered quantitatively. LEPESCHKIN then analyses turgor pressure into four components: (*a*) surface tension (*Zentraldruck*), varying between 0.016 and 1.6 atmospheres, with a variation of 10–12 per cent.; (*b*) swelling of the plasma (*Quellungsdruck*); (*c*) the osmotic pressure of substances dissolved in the plasma; and (*d*) the osmotic pressure of the cell sap and the wall

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[2] LEPESCHKIN, W. W., Ueber den Turgordruck der vacuolisierten Zellen. Ber. Deutsch. Bot. Gesells. **26a:** 198. 1908.

liquids. But since neither *b* nor *c*, as the author himself points out, can exercise any effect on turgor pressure, it is difficult to see why they should be reckoned as components. The study of the osmotic pressure of the solutes in cell sap and wall is carried out with a show of mathematical formulae that look formidable, but the data are really not yet adequate for exactness. The experimental results show that the observed osmotic pressure is always less than the calculated, which is due to the greater or less but general permeability of the protoplasts, a feature too much overlooked hitherto, though clearly pointed out by various investigators and *a priori* obvious. The effects of temperature changes, especially between 0° and 20° C., were also examined. A warning against conclusions based on the exclusive use of KNO_3 as a plasmolytic agent without correction for permeability is given.

In a later paper,[3] LEPESCHKIN reports the results of a study of the permeability of the pulvinus cells of Phaseolus and Mimosa, in which this proves to be surprisingly high. The solutes (except sugar) escape so rapidly when the tissues are brought into water, and especially into running water, as to reduce the apparent osmotic pressure (determined by the isotonic coefficient method) by 25 to 50 per cent. A change in the permeability of the plasma membranes may alter the turgor pressure by several atmospheres. LEPESCHKIN proposes to show in another article that such changes really occur (as has been hitherto assumed) under the action of various agents.—C. R. B.

The blood of plants.—PALLADIN'S preliminary paper[4] bears a rather striking title, which will be just enough if the theory proposed is fully established. Certain colorless chromogens, probably products of protein decomposition, have been found in plants, and these become pigments (already familiar to common observation in various discolorations produced on cutting or crushing) under the action of oxygen in the presence of oxidases. These respiratory enzymes are therefore to be considered as pigment producers, and the respiratory pigments doubtless include a number of pigments already known, such as those of the indigo plants. PALLADIN proposes to call all of them, irrespective of their chemical composition, phytohematins, in recognition of the identity of their physiological significance with that of the hematin of the blood. To show this it was necessary to find reductases in plant as in animal tissues, and PALLADIN announces their discovery. These enzymes reduce the respiratory pigments, which then go on down to CO_2, and H_2O, etc. The following scheme shows the relation of the various respiratory processes:

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[3] LEPESCHKIN, W. W., Ueber die osmotischen Eigenschaften und den Turgordruck der Blattgelenkzellen der Leguminosen. Ber. Deutsch. Bot. Gesells. **26a**:231–238. 1908.

[4] PALLADIN, W., Das Blut der Pflanzen. Ber. Deutsch. Bot. Gesells. **26a**:125–132. 1908.

PRIMARY PROCESSES	SECONDARY PROCESSES
Anaerobic enzymes (zymase, etc.)	Oxygen of the air
↓	↓
Catalase, reductase	Respiratory oxidases
↓	↓
Products of fermentation (alcohol and other substances)	Phytohematins
	↓
	Products of respiration (CO_2, H_2O)

To unify the respiration of animals and plants still further, it will be necessary to show that the oxygen from the air is not combined directly with the hemochromogen, but by the aid of oxidases; and this the recent discovery of these enzymes in the blood renders probable. The behavior of the colorless blood of the lower animals and the sap of plants is quite similar, according to this view.

It is not to be supposed, however, that oxygen does not have other relations than to the chromogens; but these are neglected in the above scheme, which may be taken as only a partial representation of respiratory processes. In fact the more the matter is studied, the more complex and diversified appear the chemical changes subsumed by the word respiration.—C. R. B.

Fungi and hemicelluloses.—In the hope of obtaining some insight into the action of fungi on their hosts, Schellenberg[5] has investigated the behavior of a number of species, which can be cultivated on media of known composition, in respect to their decomposition of hemicelluloses. Those used were several, the products of whose hydrolysis was known. *Molinia coerulea* among the grasses, *Lupinus hirsutus* among the Leguminosae, *Phoenix dactylifera* among palms, *Impatiens Balsamina* and *Cyclamen europaeum* with an amyloid reserve, and *Ruscus aculeatus* among the lilies furnished the hemicelluloses. On hydrolysis they yield respectively dextrose and xylose, galactose and arabinose, galactose and mannose, galactose and xylose, mannose and a little arabinose. A large number of fungi were tested. To explain their action, which he finds strictly specialized and very different from that on true celluloses, Schellenberg has to assume the existence of at least four different enzymes, which he calls the Molinia, the Lupinus, the date, and the amyloid enzymes. Study of their behavior on dead and living plant parts permits similar conclusions. Thus fungi may be used to eliminate hemicelluloses from celluloses in unlignified tissues. The effect of fungi in the destruction of the plant constituents in the soil is probably much more important than has been believed hitherto.—C. R. B.

Jurassic plants.—Seward[6] has published the results of his study of collections of Jurassic plants from Caucasia and Turkestan, sent by the Comité Géologique de Russie. The Caucasian collection contains representatives of the

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[5] Schellenberg, H. C., Untersuchungen über das Verhalten einiger Pilze gegen Hemizellulosen. Flora **98**:257–308. 1908.

[6] Seward, A. C., Jurassic plants from Caucasia and Turkestan. Mém. Comité Géol. Russie N. S. **38**:1–48. *pls. 1–8.* 1907.

following groups; Equisetales (an Equisetites), Filicales (a species each in Marattiaceae, Osmundaceae?, Schizaeaceae, and Cyatheaceae?), Bennettitales (a Williamsonia), Ginkgoales (a Baiera), and Coniferales (a Pagiophyllum); in addition to these, there are four unassigned cycadophytes and two species of Podozamites. The collection from Turkestan includes approximately the same range of forms, adding a species of Dipteridinae and eight species of unassigned Filicales, but showing no Marattiaceae or Schizaeaceae; representing Gink, goales by two species of Ginkgo; and adding three Coniferales. In conclusion, the relations of these floras to those of other regions are shown by a table; and also the wide distribution of some of the species. Among the striking facts are the existence of so many species for a considerable time during the Mesozoic; the general uniformity in the composition of both the Rhaetic and Jurassic floras in different parts of the world; and the remarkable paucity of cycadean remains in the Turkestan beds.—J. M. C.

Light perception.—ALBRECHT has examined a large number of the endemic plants of northern Germany for the organs of light perception (lenticular epidermis, ocelli, etc.) to which HABERLANDT attributes the capacity of distinguishing differences of light intensity. He finds[7] the organs very rare, and when they are present, nearly as common on the under as on the upper surface of the leaf, though it is clear that to the illumination of the upper surface alone is due the exact placing of the leaf in the fixed light position. No difference appeared in the adaptation of sun and shade leaves to the perception of light. He adduces again the experiments made by coating leaves with water, gelatin, and oil, as evidence against HABERLANDT's theory. After the reading of the paper, HABERLANDT spoke of the faulty methods in all the latter experiments, describing a mode of coating a part of the leaf with water and leaving the other part dry. On stimulating the two parts with light from different directions, the dry part was always the controlling one, even though the light was much weaker. HABERLANDT considers these experiments (to be detailed later) quite decisive. It may be pointed out, however, that other factors than light are here operative- and that the weight of evidence is clearly against HABERLANDT.—C. R. B.

Invertase of the date.—VINSON has studied further[8] the invertase of greenr and ripe dates, in an endeavor to discover the reason for its inextractability from the green fruit. He finds that the tannin present does not make it insoluble, nor can it be extracted from ground pulp, so that impermeability of the cell membranes is excluded. He proposes the theory "that green date invertase and possibly other endoenzymes are held in an insoluble combination by some constituent of the protoplasm. In some cases this combination may be broken

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[7] ALBRECHT, G., Ueber die Perception der Lichtrichtung in den Laubblättern. Ber. Deutsch. Bot. Gesells. **26a**:182–191. 1908.

[8] VINSON, A. E., The endo- and ektoinvertase of the date. Jour. Am. Chem. Soc. **30**:1005–1020. 1908. Cf. earlier paper, BOT. GAZETTE **43**:393. 1907.

down and the enzyme pass into solution while the protoplasm is living, but in others the combination may persist, even after the death of the protoplasm. The enzyme may be rendered soluble also by external chemical or physical influences. These probably act by destroying the integrity of the cell and allowing the contact of substances which have been localized in the living protoplasm. On maturity of the tissues the enzyme is generally liberated, possibly by autodigestion or other profound change in the protoplasm."—C. R. B.

Fixation of free N.—HANNIG, holding that HILTNER's statement as to fixation of free nitrogen by *Lolium temulentum* rested upon objectionable methods of experimentation, has reinvestigated the matter and confirms the latter's results.[9] About 100 per cent. increase in N of the crop over that in the seed is reported with the fungus-infested plants when N was excluded from the culture; whereas there was practically no increase in fungus-free plants. This is claimed to be the first demonstration of the fixation of free N by ectotrophic mycorhiza.—C. R. B.

Zeitschrift für Botanik.—On account of repeated and continued misunderstandings between the publisher of the *Botanische Zeitung* and its editors, FRIEDRICH OLTMANNS and GRAF ZU SOLMS-LAUBACH, the editors will sever their connection with that journal December 31, 1908, and, assisted by L. JOST, will found a new journal, *Zeitschrift für Botanik*, which will be published by Gustav Fischer of Jena. The journal will be a monthly, in the form of the BOTANICAL GAZETTE, and will contain both original investigations and critical reviews. The subscription price is 24 marks.

CO_2 from dead tissues.—NABOKICH reports in a preliminary paper[10] that CO_2 is given off by dead seeds and seedlings of various plants, no matter how killed. He is apparently oblivious of the fact that COPELAND has already described the same phenomenon in dead water plants,[11] and BECQUEREL in seed coats.[12]—C. R. B.

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[9] HANNIG, E., Die Bindung freien atmosphärischen Stickstoffes durch pilzhaltiges *Lolium temulentum*. Ber. Deutsch. Bot. Gesells. **26a**:238–246. 1908.

[10] NABOKICK, A. J., Ueber die Ausscheidung von Kohlensäure aus toten Pflanzenteilen. Ber. Deutsch. Bot. Gesells. **26a**:324–332. 1908.

[11] COPELAND, E. B., Chemical stimulation and the evolution of carbon dioxid. BOT. GAZETTE **35**:81–98, 160–183. 1903.

[12] BECQUEREL, PAUL, Recherches sur la vie latente de graines. Ann. Sci. Nat. Bot. IX. **5**:193–320. 1907.

GENERAL INDEX

The most important 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*.