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EDITORS:

JOHN MERLE COULTER AND CHARLES REID BARNES

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JANUARY-JUNE, 1910

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BRIEFER ARTICLES—

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No. 1, January 22; No. 2, February 16; No. 3, March 15; No. 4, April 19; No. 5, May 17; No. 6, June 23.

ERRATA

Volume XLVIII

P. 69, last line, for tubellarian read turbellarian.

Volume XLIX

P. 102, table IV, transfer plants from first line of legend to first word in second line.

P. 114, table I, last line, ratio should read 21♀ : 2☿ : 11♂.

P. 120, fig. 1, below five vertical lines (beginning second from left) insert respectively, left to right, 0%, 25%, 50%, 75%, 100%.

———, opposite horizontal lines insert respectively, bottom to top, 0, 5, 10, 15, 20, 25.

P. 121, fig. 2, below vertical lines insert respectively, beginning with second, left to right, 30%, 40%, 50%, 60%, 70%, 80%, 90%.

———, opposite horizontal lines insert respectively, bottom to top, 0, 5, 10, 15, 20, 25, 30.

P. 133, line 5 from bottom, for Hammamelis read Hamamelis.

P. 136, line 9 from bottom, for artemisiaefolia read artemisiifolia.

———, line 7 from bottom, for canadense read canadensis.

P. 146, line 7 from bottom, for rangifera read rangiferina.

P. 155, line 2, for aso read also.

———, line 7, for Morremia read Morrenia.

———, line 7 from bottom, for Wolff, K. read Wolff, H.

P. 156, line 7 from bottom, for Polyblastis read Polyblastia.

P. 177, line 16, for Greeman read Greenman.

P. 180, citation 17, for Wachen read Wachsen.

P. 267, fig. 7, line 2 of legend, for smaller read greater.

P. 310, line 24 from top, for Scaveola read Scaevola.

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January 1910

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CONTENTS

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VOLUME XLIX NUMBER 1

BOTANICAL GAZETTE

JANUARY 1910

CHROMOSOMES IN OSMUNDA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 132

SHIGÉO YAMANOUCHI

(WITH PLATE I)

This paper presents the results of a study of the behavior of chromosomes during both homotypic and heterotypic mitoses in *Osmunda cinnamomea* L.

The material was collected in the vicinity of Chicago, Illinois, in the late summer of 1906 and the spring of 1908. The study was made on both living and fixed material. Fixation was most satisfactory in Flemming's weak solution containing osmic acid. The chromosome conditions were studied not only in vegetative mitosis in sporophytes, and in sporogenesis, but also in germinating spores and in mature prothallia. This paper, however, will be limited to a brief account of chromosomes in the sporophyte.

Papers dealing with the cytology of Osmunda have been published by HUMPHREY (**7**), STRASBURGER (**15**), SMITH (**14**), FARMER and MOORE (**2**), and by GRÉGOIRE (**4**). These authors have all chosen *Osmunda regalis*. HUMPHREY and SMITH devoted their attention chiefly to the achromatic substance; STRASBURGER studied sporogenesis and the number of chromosomes; FARMER and MOORE claimed that the bivalent chromosomes arise by a folding of the spirem; and GRÉGOIRE studied chiefly the structure of the double spirem of synapsis, which he found to originate by the association of two independent chromatin threads. GRÉGOIRE'S account is in accord with the present study of *Osmunda cinnamomea*.

The cytological investigation was carried on in the Hull Botanical Laboratory of the University of Chicago, under the direction of

Professors JOHN M. COULTER and CHARLES J. CHAMBERLAIN, and I wish to express my sincere gratitude for their kind suggestions and criticism during the progress of the work.

Description

CHROMOSOMES IN TELOPHASE OF VEGETATIVE MITOSIS

In order to make a detailed study of the behavior of the chromatin material throughout nuclear division, it is necessary to begin with the study at the earliest possible stage of division. To begin with the resting nucleus is not early enough, and so I have started at the telophase of the previous division.

The nucleus in the vegetative tissue, whatever its location may be, presents similar features, so that the description can be applied to the process of nuclear division in any tissue, although the figures in the accompanying plate were drawn from vegetative mitosis in young fronds, previous to the formation of spore mother cells.

The chromosomes in the equatorial plate in typical mitosis generally appear homogeneous. They split longitudinally and the two sets of daughter chromosomes begin to pass toward the poles. The slender and straight daughter chromosomes always retain this form until they reach the poles, where they are drawn more closely together and become more or less parallel. They remain for a while aggregated thus, in contact with the surrounding cytoplasm. If the chromosomes in this state could be called a nuclear primordium, evidently the daughter nucleus in the telophase consists of chromatin only. Then the process of vacuolation begins as follows.

The loosely aggregated chromosomes draw near together and come into closer contact; at the same time each gradually loses its hitherto compact structure and vacuolation occurs irregularly at different places (*fig. 1*). The set of daughter chromosomes is thus a mere aggregate of vacuolate chromosomes. The limits of the individual chromosomes are not difficult to trace. The vacuolation seems to mean that there is either a secretion of fluid from the chromosomes or a dissolution of portions of them into liquid; and the contact of this fluid with the surrounding cytoplasm may precipitate a membrane which will separate the products of the vacuolate chromatin from the cytoplasm. The daughter nucleus formed in this manner has no possible chance of including achromatic substances, so that the only substances within the nuclear membrane are the chromatin and substances derived from chromatin. This is in accord with GRÉGOIRE and WYGAERTS' results (**5**).

At the beginning of the process of vacuolation the chromosomes do not lie strictly parallel, but converge toward the pole (*fig. 1*). Naturally, chromosomes thus aggregated leave unoccupied space at both their convergent and divergent ends; and during the process of vacuolation a nucleolus always appears in the young nucleus at or near the vacant space in the nuclear cavity beyond the convergent ends of the chromosomes (*fig. 2*). Such a manifestation of polarity is usual in the telophase of typical mitosis.

By careful observation the limits of each of these chromosomes are discernible for some time. When vacuolation accompanied by nuclear growth has proceeded still farther, and the chromatin networks resulting from the individual chromosomes have become connected one with another, so as to appear like a single network irregularly distributed throughout the nuclear cavity, the polarity is no longer recognizable (*fig. 3*), and this is regarded as the resting state of the nucleus.

The nucleus in the resting state is a reticulum, consisting of ragged clumps and strands of irregular shape. The clumps and strands are chromatin; the former are more deeply colored by stains than the latter, not because they are substances of a different nature, but simply because of differences in density.

The number of the chromatin clumps in the resting nucleus in Osmunda is large and variable, always far greater than the number of chromosomes. Without doubt, certain areas of these clumps and strands may represent the limits of certain chromosomes in the resting condition, but even after tracing a very close series of stages from the early telophase to the resting nucleus, the limits of individual chromosomes in the resting reticulum are difficult or impossible to discern.

FORMATION OF CHROMOSOMES IN VEGETATIVE MITOSIS

In early prophase the chromatin of the resting state, composed of fine ragged clumps and strands, becomes more and more evident at certain parts, possibly by translocation of material from other parts. This gradual translocation of material tends to produce, out of the reticulum, smoother and smoother threads of somewhat uniform thickness, extending for some distance without branching.

Such smooth strands are formed here and there from different parts of the reticulum. Of course, for some time these strands bear fine fibrils by which the various strands are connected into a single nuclear network (*fig. 4*). But finally these fine fibrils, which consist of chromatin, become disconnected; evidently the material is drawn into the strands, which naturally grow thicker on this account. The strands represent an early stage of the somatic chromosomes. When the chromosomes are just organized as a number of independent elements (*fig. 5*), they are slender and very much curved, evidently lying in the position where they had first arisen out of the network as smooth thick strands.

Owing chiefly to the curved nature of the chromosomes at their first appearance, it is difficult to prove that the place where a chromosome first appears is identical with the limit of the chromosome when last distinguishable in the telophase of the previous mitosis. This does not prove, however, that a chromosome may not appear in prophase in the same position in which it was last seen in the preceding telophase.

LONGITUDINAL SPLITTING OF SOMATIC CHROMOSOMES

The chromosomes thus formed are homogeneous and are strictly univalent during the prophase. The longitudinal splitting is first indicated very late in the prophase, just before arrangement at the equatorial plate. The process of longitudinal splitting is gradual and slow. Each chromosome, which has been compact throughout, becomes rather faintly stained in the central region, where the density of the aggregated chromosomes becomes less, although no change has taken place in the contour (*fig. 6*). Then contractions occur simultaneously along the two lateral lines on opposite sides of the strand, where the structure has already become looser (*fig. 7*). The constriction proceeds inward from the two opposite lateral lines and meets in the center, thus dividing the chromosomes longitudinally into two similar halves. The longitudinal halves of each of these chromosomes, separating at the equatorial plate, proceed to the poles and the vacuolation process follows, as already described.

FORMATION OF CHROMOSOMES IN HETEROTYPIC MITOSIS

The origin of the chromosomes in the spore mother cell is entirely different from that in vegetative mitosis. Some facts are well known and there is an immense literature based upon various material, but the extensive literature does not necessarily mean that all questions have been settled; on the contrary, opinions and interpretations are still conflicting.

Although the nucleus of a spore mother cell in the resting state does not appear very different from that of a vegetative cell, it has characteristic differences, such as its immense increase during the growth period, and the behavior of the chromatic substances outside the nucleus. The most important difference, however, is seen inside the nucleus, in connection with the origin of chromosomes.

The chromatin network in the resting state, consisting of irregular ragged clumps and strands, at first begins to be transformed into more or less regular and less ragged strands, which are uniform in thickness for some distance. These strands are developed simultaneously in various parts of the chromatin network, and at the very beginning of the transformation each chromatin thread thus formed has a thread running parallel to it; in other words, the threads come out of the network as two independent threads from the start.

The pairs of threads at their first appearance are connected by fine fibrils, by means of which all these threads are connected into the single framework of the nucleus. As the delicate connecting fibrils become less and less conspicuous, the duality of the threads is shown with more clearness. The course of the threads being irregularly curved, it is hardly possible to determine their number at this time. The number is certainly less than the reduced number of chromosomes, and there may be only a single pair of threads.

A close examination of the double threads or spirems in this stage shows that they are not uniform in density or in thickness, but the chromatin material is distributed irregularly, so that the parts where it is less densely aggregated stain lighter than the parts where it is denser (*fig. 8*). The knots in one of the double threads do not necessarily lie side by side with those in the other; in other words, there is no uniformity in the relative position of the knots in the two parallel threads.

The double threads, having such a structure and traversing the nuclear cavity in various directions, now become tangled in a mass at one side of the cavity in the condition called synapsis (*fig. 9*). Synapsis is not an artifact, but a normal stage of prophase, which may be observed in living material. The position of the nucleolus at synapsis is variable; sometimes it lies at a distance from the synaptic mass, but more often it is caught in the tangle. Its form is generally spherical.

Very frequently it occurs that in the tangled mass many parts of the threads are seen converging to that point where the mass is in contact with the nuclear membrane. A similar condition is described by GRÉGOIRE in *O. regalis* (**5**). In this case, some of these parts are continuous with the other parts, and evidently they do not yet represent chromosome primordia already disconnected and independent.

The chromatin structure of the double threads, as seen in the presynaptic stage, is kept throughout this synaptic condition; the two members of the pair may come into closer association in some places than before, but the duality is never lost, even in the culmination of synapsis (*fig. 10*). This means there is no actual fusion of the two threads.

The synaptic mass then begins to disentangle and the double threads again assume a position traversing the entire cavity, the two being always clearly in close association. Each element of the double thread then shortens. During the strepsinema stage some parts of the double threads gather somewhat at a part of the nuclear cavity, looking like a second contraction stage (*fig. 11;* in which only a part of the threads are represented, as they are seen in one focus). Soon after this stage the double threads rapidly shorten and thicken, and finally in a diakinetic stage there are formed 22 bivalent chromosomes (*fig. 12*). In some cases the two elements of each bivalent chromosome remain in close contact, but in other cases they become somewhat separated, and, as a consequence, there are produced the various familiar aspects of bivalent chromosomes.

After the formation of the bivalent chromosomes, the shortening and thickening proceeds until metaphase, when the structure, instead of being of irregular density, becomes evenly compact and homogeneous. The two chromosomes of the pair separate in metaphase (*fig. 13*) and proceed during anaphase to the poles. But before they reach the poles, there occurs a genuine longitudinal splitting of the univalent chromosomes in preparation for the second division. The splitting generally does not proceed throughout the whole length of the chromosomes, one end remaining unsplit and the parts already divided diverging so that there naturally results a V-shaped chromosome. Therefore in the heterotypic division there is no longitudinal splitting of chromosomes. The two chromosomes lying side by side simply separate at metaphase; there is, of course, a single longitudinal splitting in metaphase of the heterotypic division, but this is a provision for the second division.

The V-shaped chromosomes in late anaphase of the first division (*fig. 14*) gather into a group at the pole. Vacuolation occurs and a nuclear membrane is formed.

FORMATION OF CHROMOSOMES IN HOMOTYPIC MITOSIS

The group of vacuolate chromosomes is distinctly recognizable after the formation of the nuclear membrane. As the vacuolation proceeds farther, the chromosomes become very alveolate, but as the process is more active in the lateral parts of each chromosome, the central part remains as a rather thick strand, so that for a considerable period after the organization of the daughter nucleus the V-shaped chromosomes could be traced with perfect distinctness.

Progressive vacuolation with the accompanying nuclear growth tends to change the general aspect of the ragged chromatin network of the newly formed nucleus. The process, however, before proceeding so far as to result in a resting stage, begins to reorganize the chromosome primordia out of the ragged chromatin reticulum.

The chromosome primordium appears first in V-shape (*fig. 15*), but the location does not seem to agree exactly with the location of the daughter chromosomes as last seen in the previous telophase. In the nuclear cavity, during the period intermediate between the last telophase and the present prophase, there might have occurred some movement of parts of the chromatin network. But the uniformity in the number of chromosomes and their appearance as exactly V-shaped as when they entered into the alveolate and reticulate condition, seem to indicate strongly that the limits of the individual chromosomes are distinctly maintained during the nuclear changes.

After the disappearance of the nuclear membrane the divergent arms of the V-shaped chromosomes draw near to one another, and as they are arranged in an equatorial plate the two arms lie closely parallel. In metaphase the two arms separate. The two sets of daughter chromosomes reach the poles and vacuolation begins (*fig. 16*); their aspect in this stage is like the telophase of the vegetative mitosis, except in the number of chromosomes.

Discussion

The object of this paper is to present briefly the results obtained in the study of the chromosomes of *Osmunda cinnamomea*, and no detailed discussion of the literature of the subject is intended. Only a few remarks on the morphology of the chromatin substance will be made at this time.

SYNAPSIS

Although there are a few authors, as McClung (**9**), Schaffner (**13**), Janssen (**8**), and Haecker (**6**), who believe that synapsis is either an artifact or has no significance in the reduction division, yet the phenomenon has been demonstrated in many cases in living material, and now a majority of workers agree that the stage is of perfectly normal occurrence and that it always directly precedes the reduction division.

The details of synapsis in the plant cell have been followed by various botanists in a great number of plants, the most detailed accounts relating to flowering plants. Excepting Strasburger's *Gamosomen* theory based on his study of Galtonia (**16**), many botanical cytologists agree that there are parallel nuclear threads. As regards the structure of the nuclear threads the views differ; some (Farmer and Moore **2**, and others) believe the threads to be composed of chromatin imbedded in linin groundwork; some (Overton **11**, and others) claim that it is composed of prochromosomes connected with the linin intervals; and still others (GRÉGOIRE **3**, and others) conclude that the threads are composed exclusively of chromatin.

Regarding the origin of the parallel threads, FARMER and MOORE (2) and others believe they result from a longitudinal splitting; GRÉGOIRE (4), ALLEN (1), and others contend that the two are associated but independent; and the interpretations of synapsis naturally differ according to the views held in regard to the structure and origin of the nuclear threads.

In Osmunda, although the chromosomes during the resting period undergo changes so that their form differs from that seen during division, tracing the progressive changes makes it seem probable that the vacuolation does not destroy the individuality of the chromosomes. On the contrary, the individual chromosomes are preserved as vacuolate and alveolate masses during the resting period, and they again reappear in compact form at the next division. The interval between the heterotypic and homotypic divisions is much shorter than the period occupied by their divisions, and the V-shaped chromosomes reappear in the exact V-form in which they entered into the formation of the network.

These somatic chromosomes are of maternal and paternal origin, and they have come to be included within a common nuclear wall at the time of fertilization. After fertilization, during the succeeding mitoses, the individuality of chromosomes is thus maintained, and there is no time when these maternal and paternal chromosomes come into contact as regularly formed chromatin threads until the time of synapsis. How much difference there exists between the association of maternal and paternal chromatin material in the vacuolate and alveolate condition and in the form of regularly ordered chromatin threads cannot be suggested; but the importance of synapsis as occurring only once in the cycle of chromosome history, directly preceding the reduction division, cannot be overestimated.

ORIGIN OF HETEROTYPIC CHROMOSOMES

The heterotypic chromosomes in Osmunda arise as independent pairs at the early prophase of the reduction division. This result is in accord with the views held by GRÉGOIRE (4), ALLEN (1), ROSENBERG (12), OVERTON (11), and others. However, the method of forming heterotypic chromosomes in Fucus (YAMANOUCHI **17**) is different; the threads seemed to indicate no association at the beginning of early prophase, and even after they become tangled in a mass at synapsis parts of them seem to be single. In the postsynaptic stage a reduced number of loops is formed from the threads. Evidently the bivalent chromosomes are formed from the two associated arms of each loop. Unless there be some failure in observation, there must be two ways of forming heterotypic chromosomes. If the association of parental chromosomes occurs in the regularly formed chromatin threads in synapsis, the end-to-end hypothesis, held by FARMER and MOORE (**2**), SCHAFFNER (**13**), MOTTIER (**10**), STRASBURGER (**16**), and others, seems to be the correct interpretation.

Probably there may be more than one series of details in mitosis, and it would be too hasty to make any generalization from comparatively few observations. The present account simply deals with the observations upon *Osmunda cinnamomea*.

Summary

1. The reticulum in the young nucleus arises fron the chromosomes of the previous division by vacuolation. It consists chiefly of chromatin material.

2. The chromatin network during the resting stage shows no indication of a pairing of knots or strands.

3. Individuality of the chromosomes is retained in the vacuolate and reticulate form during the resting stage, although the limits of individual chromosomes become hard to trace.

4. The pairing of chromatin material, perhaps of maternal and paternal derivation, appears only at the early prophase of heterotypic mitosis. The pairs may come into the closest association during synapsis, but the duality is maintained. As a consequence no actual fusion occurs.

5. There is no splitting of chromosomes in the heterotypic mitosis; each bivalent chromosome is formed by the association of two independent chromosomes. The separation of the two gives an appearance of longitudinal division.

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EXPLANATION OF PLATE I

The figures are drawn with the aid of an Abbé camera lucida, with Zeiss apochromatic obj. 1.5mm N. A. 1.30, combined with compensating ocular 18, except *figs. 1, 15, 16*, drawn with compensating ocular 12, and *figs. 8, 9, 10, 11, 12*, drawn with compensating ocular 8. The plate is reduced to two-thirds the original size.

Figs. 1–7.—Vegetative mitosis in the young sporogenous tissue

FIG. 1.—Vacuolate chromosomes in late telophase.

FIG. 2.—A young daughter nucleus with the manifestation of polarity by the location of the chromatin network and a nucleolus.

FIG. 3.—A portion of the chromatin reticulum in the resting nucleus.

FIG. 4.—A part of the chromatin threads arising from a ragged chromatin reticulum.

FIG. 5.—A nucleus in which homogeneous chromosomes are just organized.

FIG. 6.—Portions of chromosomes from an equatorial plate; the chromatin material in the central region has become less compact.

FIG. 7.—Portions of chromosomes in a later stage than *fig. 6;* constriction has begun along two lateral lines.

Figs. 8–16.—Mitosis in the spore mother cell

FIG. 8.—Portions of double threads from the nucleus a little before the leptonema stage; chromatin material of different density in different parts of the threads.

FIG. 8*a*.—A spore mother cell with a nucleus whose chromatin is shown under higher magnification in *fig. 8*.

FIG. 9.—Portions of double threads from the nucleus in a climax condition of synapsis (so-called zygonema stage).

FIG. 9*a*.—A spore mother cell with a nucleus whose chromatin threads are shown under higher magnification in *fig. 9*.

FIG. 10.—Portions of chromatin double threads from the nucleus in pachynema stage.

FIG. 10*a*.—A spore mother cell with a nucleus whose chromatin threads are shown under higher magnification in *fig. 10*.

FIG. 11.—Portions of double threads in strepsinema stage; the independent two have begun to separate.

FIG. 11*a*.—A spore mother cell with a nucleus whose chromatin threads are shown under higher magnification in *fig. 11*.

FIG. 12.—Portions of chromosomes in diakinetic stage.

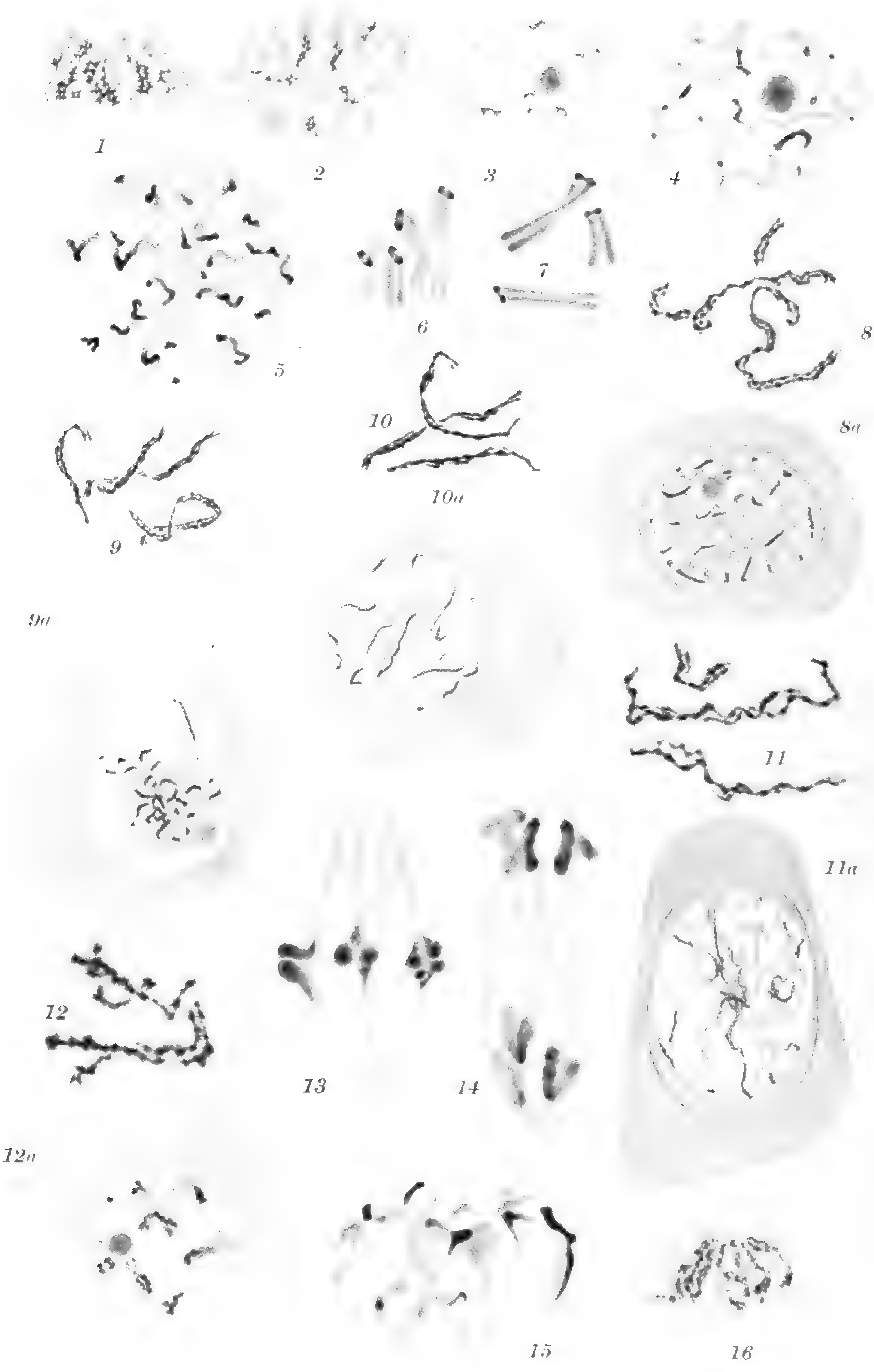
FIG. 12*a*.—A spore mother cell with a nucleus whose chromosomes are shown under higher magnification in *fig. 12*.

FIG. 13.—Portions of chromosomes with spindles in an equatorial plate.

FIG. 14.—Portions of chromosomes with spindles at the anaphase of the heterotypic division; longitudinal splitting in each chromosome.

FIG. 15.—Early prophase of the second division; the V-shaped chromosomes are distinctly recognizable.

FIG. 16.—Telophase in the second division.



YAMANOUCHI on OSMUNDA

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THE DEVELOPMENT OF THE EMBRYO OF ENCEPHALARTOS

W. T. SAXTON

(WITH PLATE II AND ONE FIGURE)

Toward the close of 1906 Dr. H. H. W. PEARSON offered to turn over to me some material collected[1] with a view to following the development of the proembryo and embryo of Encephalartos. We hoped to publish a joint paper, of which the present account, completed two years ago, was to have been my contribution. As Dr. PEARSON now finds that the publication of his share will have to be delayed still further, he has suggested that I should publish the account separately. I am glad to take this opportunity of thanking him for his help, and especially for the drawings to which his initials are appended. I also wish to thank Professor SEWARD for assisting me with the microphotograph from which *fig. 18* is reproduced.

All sections were cut with a Cambridge rocking microtome, except that from which *figs. 16* and *17* were drawn, which was cut by hand. All figures were drawn with the aid of a Zeiss camera lucida, microscope, and lenses, except *fig. 18*, which is from a microphotograph. *Figs. 1, 2, 6–8, 12–15* were drawn by Dr. PEARSON, the others by myself.

The material at my disposal afforded a fairly complete series of the development of the embryo, but the stages to illustrate the proembryo and early post-fertilization stages are almost entirely wanting and will not be referred to. The first account of embryo development in cycads seems to have been that by WARMING[2] for Ceratozamia, but only a very few stages are described and figured. Proembryo development has been described in Cycas by TREUB[3] and

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[1] With the aid of a grant from the British Association for the Advancement of Science.

[2] WARMING, E., Undersogelser of Betragtninger over Cycadeerne. 1877.

[3] TREUB, M., Recherches sur les Cycadées. 3. Embryogénie du *Cycas circinalis*. Ann. Jard. Bot. Buit. **4**:1–11. *pls. 1–3*. 1884.

IKENO,[4] and in Zamia by COULTER and CHAMBERLAIN,[5] but later stages have not been closely followed for any cycad, and the results now presented fill in some of the gaps still remaining in our knowledge of this interesting group.

Description

The intraseminal development of the embryo for descriptive purposes may be divided into four stages, each of which passes gradually into the next: (1) the differentiation of a small mass of meristematic tissue at the base of the proembryo; (2) the rapid division and elongation of a group of cells at the proximal end of this meristematic tissue, forming the suspensor; (3) the differentiation of the cotyledons and stem apex; (4) the development of plumular leaves and the fusion of the distal halves of the cotyledons.

The youngest stages figured are from the embryos of *Encephalartos villosus* (*figs. 1, 2*). *Fig. 1* represents a stage in the development of the suspensor, the embryo being shaded. *Fig. 2* is drawn from a slightly older embryo, showing the latter in detail and a small part of the suspensor. The small group of actively dividing cells, about 40–50 in number (12–16 in sections), which is forming the suspensor, can be recognized readily by the fact that the cells are arranged in regular longitudinal rows.

The remaining figures (*3–18*) are from embryo of *E. Friderici-Guilielmi.*[6] *Fig. 3* represents the only case met with in which the suspensor was branched, the branches bearing two equally developed embryos. The figure shows the two branches of the suspensor only up to the point of junction; the suspensor was injured in sectioning just above this point, and it is impossible to say whether the branching is dichotomous or monopodial.

Fig. 4 is an outline of a longitudinal section of an embryo at the close of the second stage of its development. The part inclosed by a

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[4] IKENO, S., Untersuchungen über die Entwickelung der Geschlechtsorgane und der Vorgang der Befruchtung bei *Cycas revoluta.* Jahrb. Wiss. Bot. **32**:557–602. *pls. 8–10.* 1898.

[5] COULTER, J. M., AND CHAMBERLAIN, C. J., The embryogeny of Zamia. BOT. GAZETTE **35**:184–194. *pls. 6–8.* 1903.

[6] This appears in *Index Kewensis* as a synonym of *E. cycadifolius,* but Dr. PEARSON informs me that he finds the two species to be quite distinct.

dotted line is drawn in detail in *fig. 5*. The group of suspensor-forming cells has now become the root meristem, and is not sharply differentiated from the distal part of the suspensor. At this stage cell division has recommenced in the distal half of the embryo, though as yet no further differentiation has taken place.

The first appearance of the cotyledons is shown in *fig. 6*. They clearly arise, as described for Ginkgo by Lyon,[7] by the more rapid growth of two groups of cells of the distal meristem. The cotyledons of Pinus also are initiated by the more rapid growth of groups of cells of the apical meristem,[8] and it is probable that this is normally the case in all gymnosperms. The dermatogen is distinct at this stage, and the root meristem is more clearly shown than in *fig. 5*. The latter point is shown better in *fig. 7*, where the central part of *fig. 6* is drawn in detail.

Figs. 8, 9, and *10* show later stages, in which the principal changes are the elongation of the cotyledons and the development of the canals. The first indications of the formation of canals can be seen in the stage outlined in *fig. 9*, and their position is indicated in *fig. 10*. The canal marked *x* in *fig. 10* is drawn in detail in *fig. 11*. The dense contents contain tannin, and probably mucilage also, though it is not easy to demonstrate its presence. The canals are formed lysigenously, that is, by the breaking-down of rows of cells. The boundary of the root meristem is indicated by a dotted line in *figs. 9* and *10*. In the stage represented by *fig. 10* the tissue lying between the apical meristem and the root meristem is beginning to lose its meristematic character; the cells of this region are somewhat flattened longitudinally. *Figs. 12–15* show the outline of transverse sections of an embryo of approximately the same age as that drawn in longitudinal section in *fig. 10*. *Fig. 12* shows the base of the cotyledons and their attachment to the stem; *fig. 13* is taken just below the stem apex; *fig. 14* is somewhat higher up; and *fig. 15* is near the apex of the cotyledons. The principal point shown by this series is that at this stage the cotyledons are fused only in the proximal half of their length.

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[7] Lyon, H. L., The embryogeny of Ginkgo. Minn. Bot. Studies 3:275–290. *pls. 29–43*. 1904.

[8] The writer hopes to publish later an account of the development of the embryo in Pinus.

FIG. 18.—*E. Friderici-Guilielmi:* microphotograph of part of a longitudinal section of a nearly mature embryo. ×50.

In the last stage of intraseminal development the primordia of one or two plumular leaves reach a moderate size. The cotyledons in the mature embryo are fused throughout their whole length, by both margins at the base, and by either one or both margins near the apex. *Fig. 16* represents a transverse section in which they were fused by one margin only; the part of the section marked *x* is drawn in detail in *fig. 17*. This shows the very intimate union of the epidermal cells and their collenchymatous thickenings.

Fig. 18 represents the root and stem apices, the bases of the cotyledons, and the first plumular leaf. The root meristem has now increased considerably in size, but has not otherwise changed its character in any way, so that what is physiologically the root cap is only the distal end of the suspensor as morphologically equivalent to part of the root cap of any ordinary angiospermous embryo. The embryonal tubes in certain conifers are evidently equivalent to the whole suspensor of Encephalartos.

From the preceding account it is clear that there is a very close resemblance between the embryogeny of Encephalartos and that of Ginkgo as described by LYON (*l. c.*).

Summary

1. The suspensor is developed by the division and elongation of a group of cells at the proximal end of the embryo.

2. This group of cells forms later the root meristem.

3. Branching of the suspensor has been observed once, resulting in the formation of two approximately equal embryos.

4. The cotyledons are initiated by the more rapid growth of two groups of cells of the apical meristem.

5. The canals appear before the differentiation of plumular leaves, and probably contain both tannin and mucilage, being formed lysigenously.

6. A very intimate connection is established between the epidermal cells of fusing cotyledons.

7. The suspensor is morphologically a root cap.

8. The embryogeny of Encephalartos is very similar to that of Gingko.

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CAPE TOWN

EXPLANATION OF PLATE II

Encephalartos villosus

FIG. 1.—Suspensor carrying down young embryo (shaded) into the endosperm; *aw*, archegonium wall. ×77.

FIG. 2.—Young embryo slightly older. ×310.

Encephalartos Friderici-Guilielmi

FIG. 3.—Branching of the suspensor forming two approximately equal embryos. ×77.

FIG. 4.—Outline of embryo and part of suspensor, just before differentiation of cotyledons. ×40.

FIG. 5.—Detailed drawing of part of *fig. 4* indicated by dotted line. ×300.

FIG. 6.—Cell outline of embryo just after differentiation of cotyledons. ×117.

FIG. 7.—Detailed drawing of part of *fig. 6;* junction of root and stem meristems. ×300.

FIG. 8.—Outline of slightly older embryo. ×24.

FIG. 9.—Older embryo than *fig. 8;* root meristem outlined with dotted line. ×40.

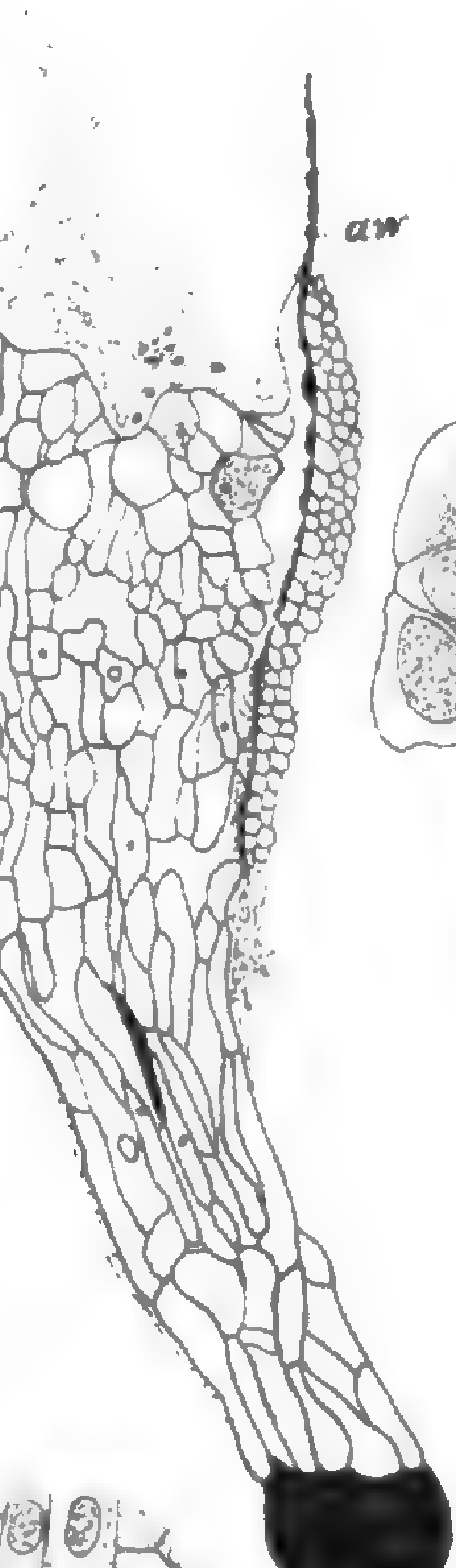
FIG. 10.—Embryo older than *fig. 9;* canals outlined, that marked *x* shown in next figure. ×40.

FIG. 11.—Canal from *fig. 10* drawn in detail. ×310.

FIGS. 12–15.—For explanation see text.

FIG. 16.—Cross-section of cotyledons of a mature embryo. ×24.

FIG. 17.—Part of *fig. 12* marked *x* drawn in detail. ×310.



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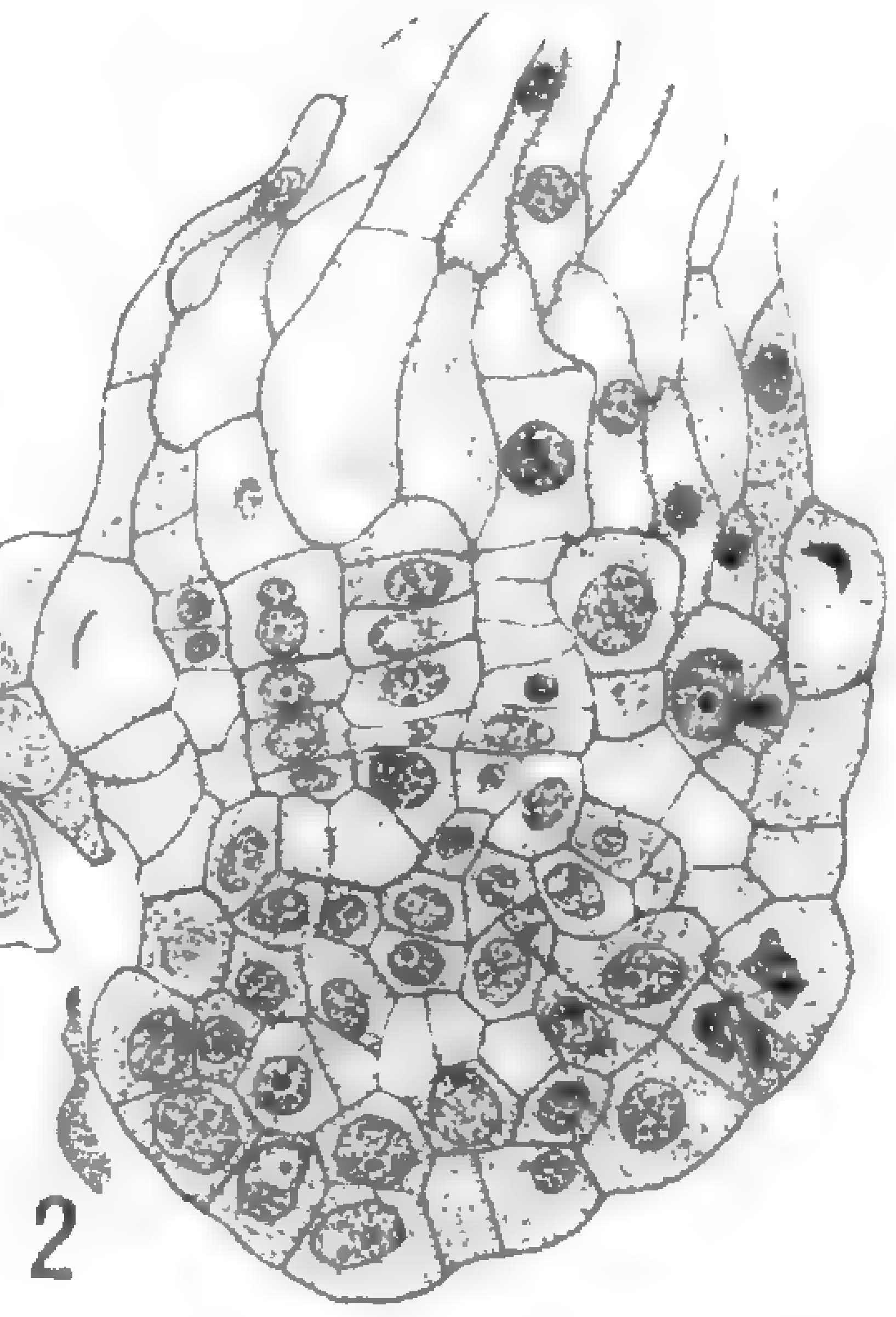

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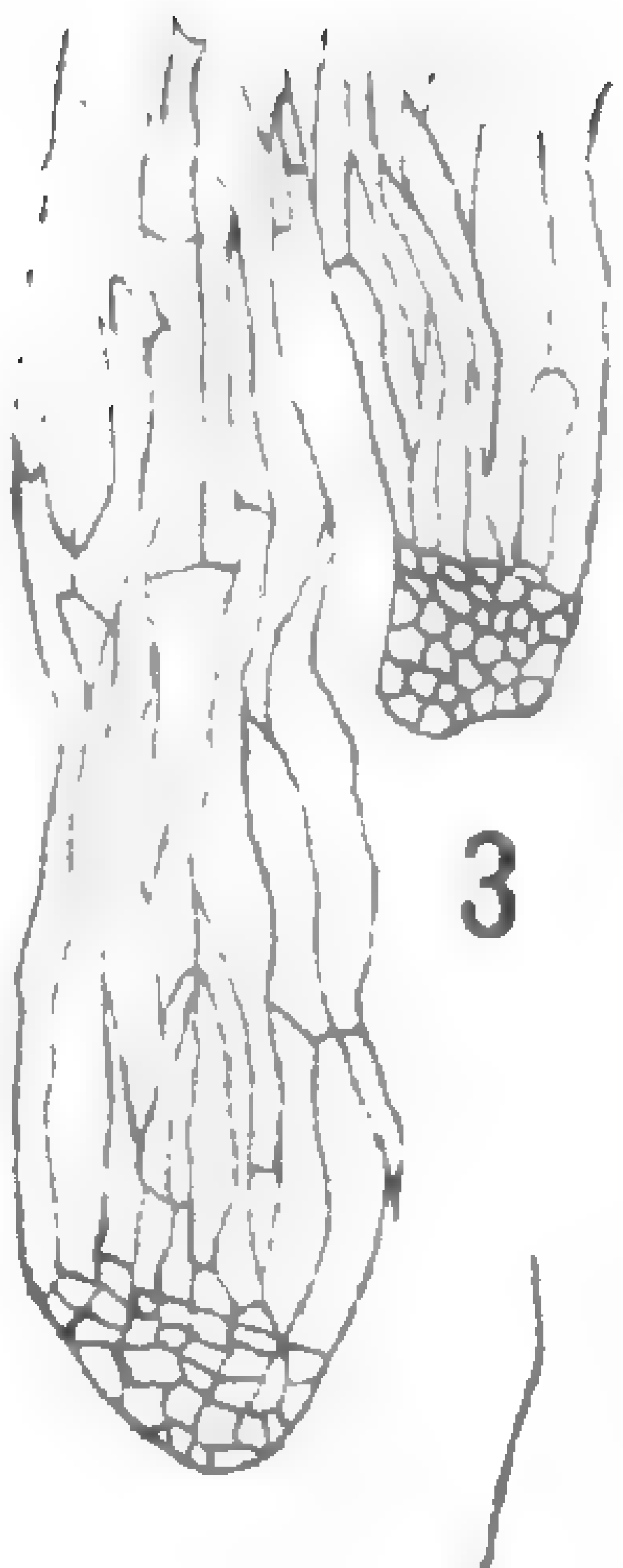

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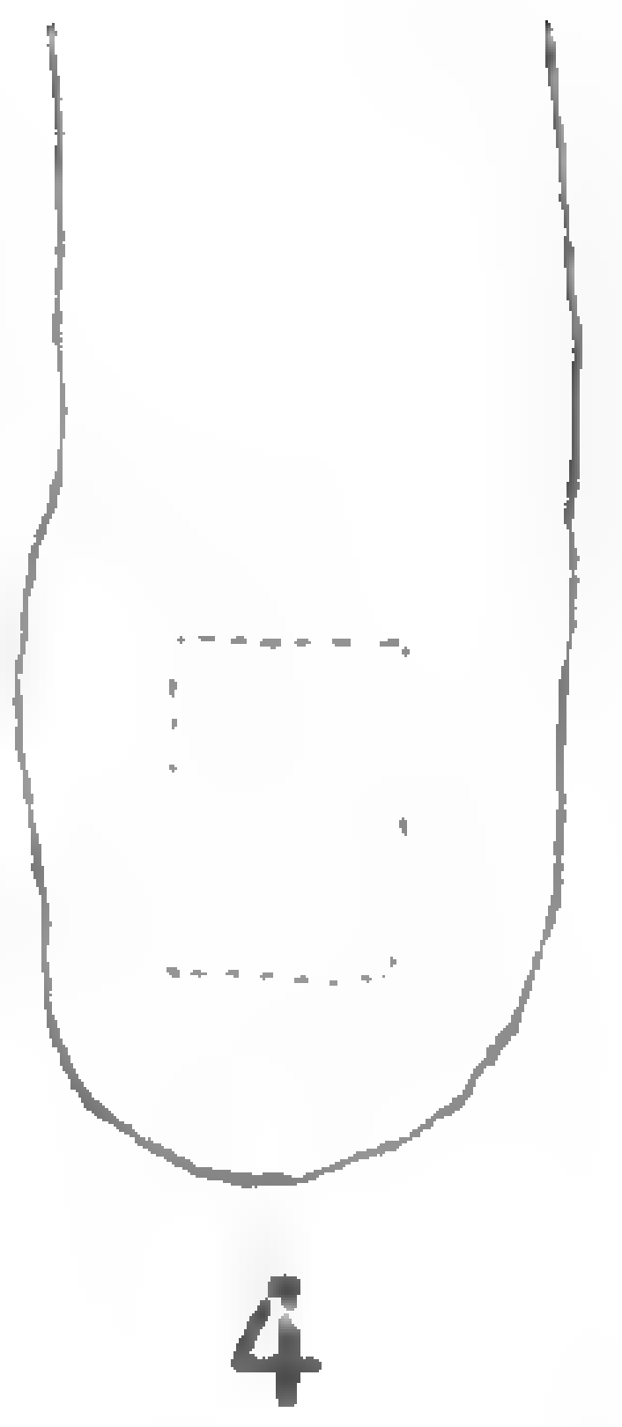

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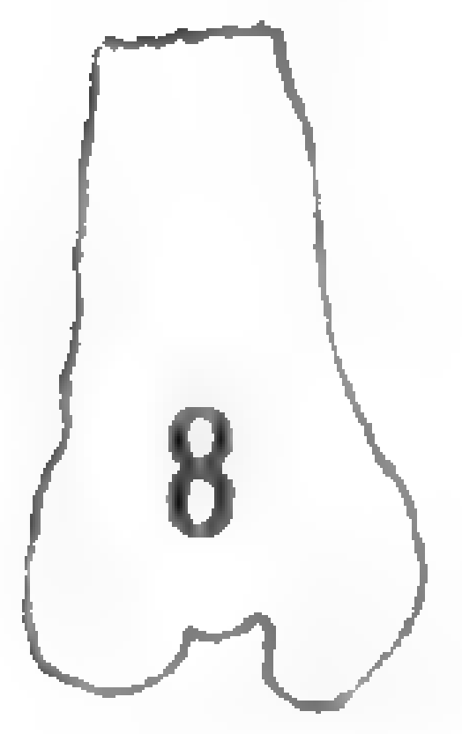

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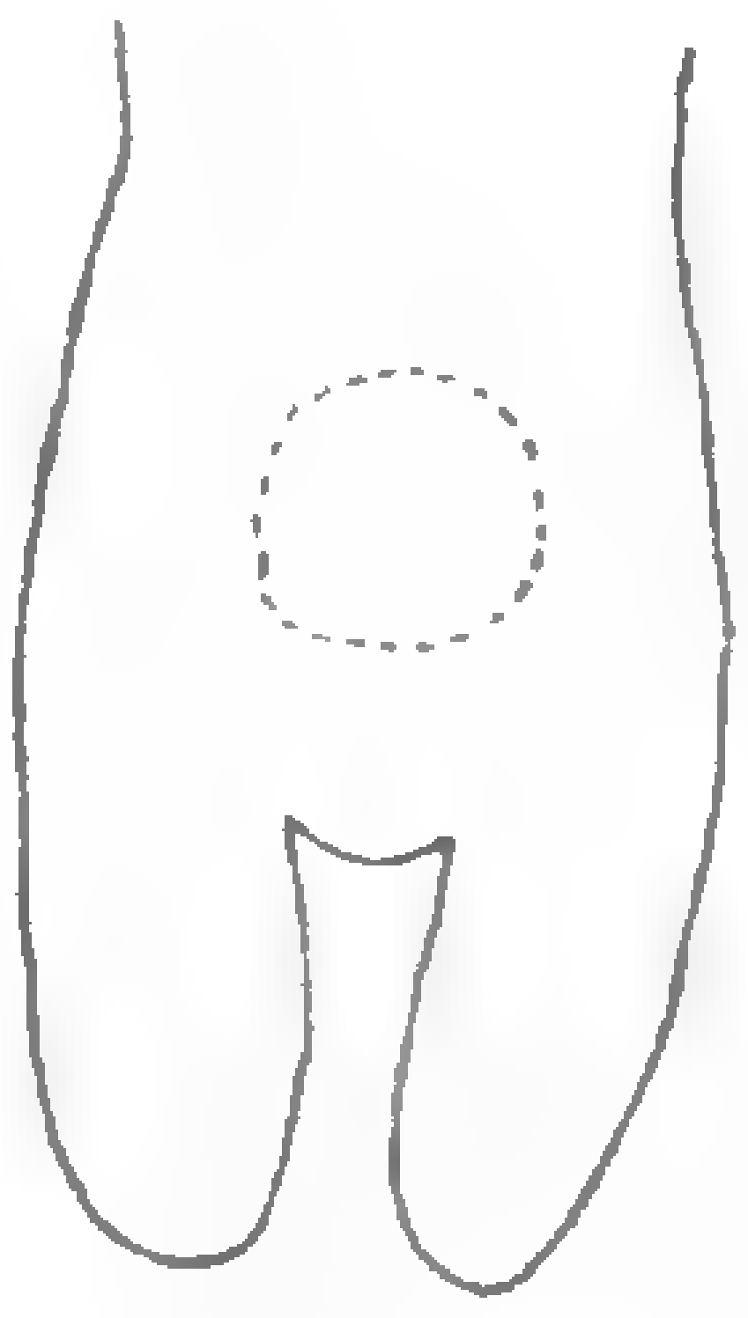

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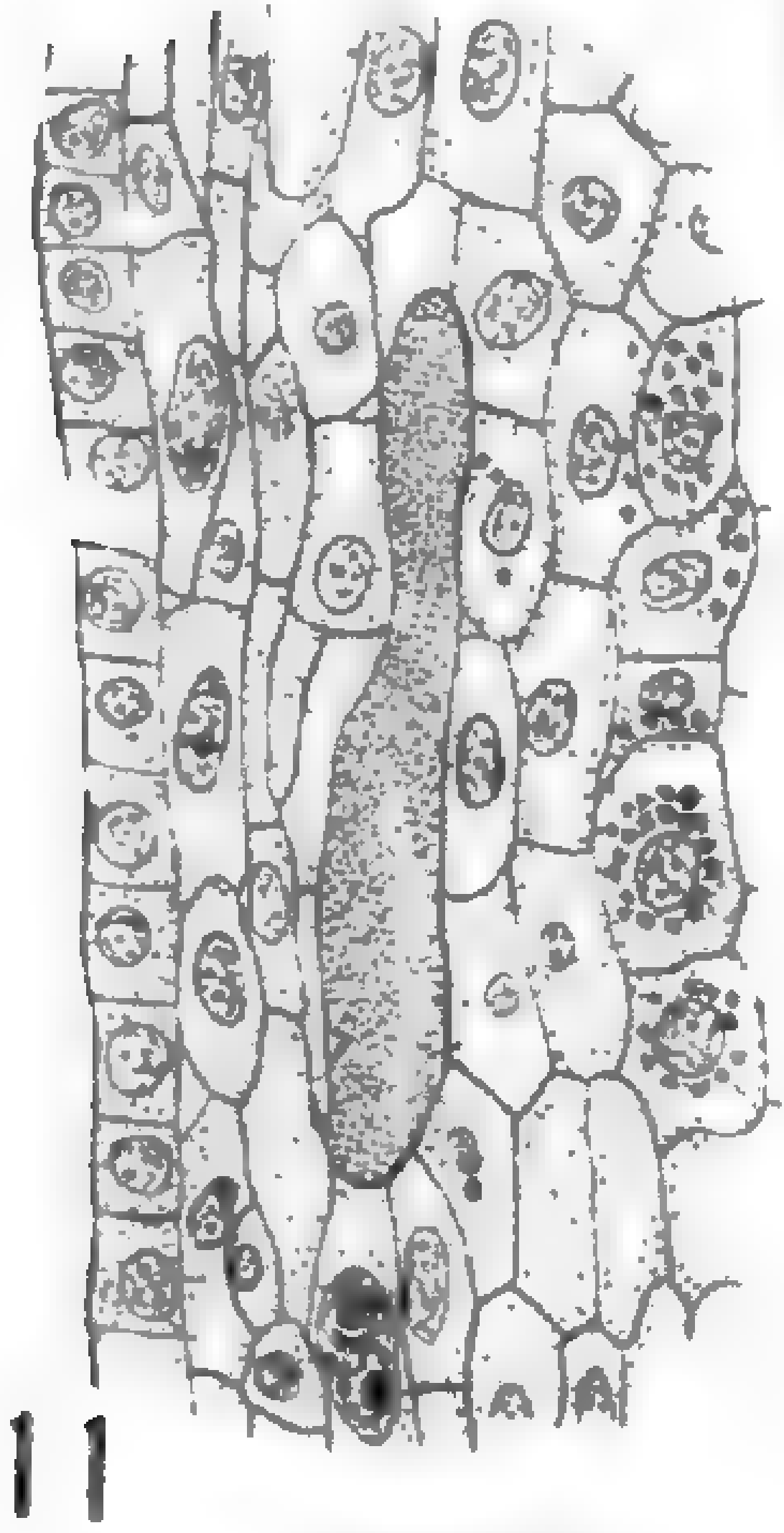

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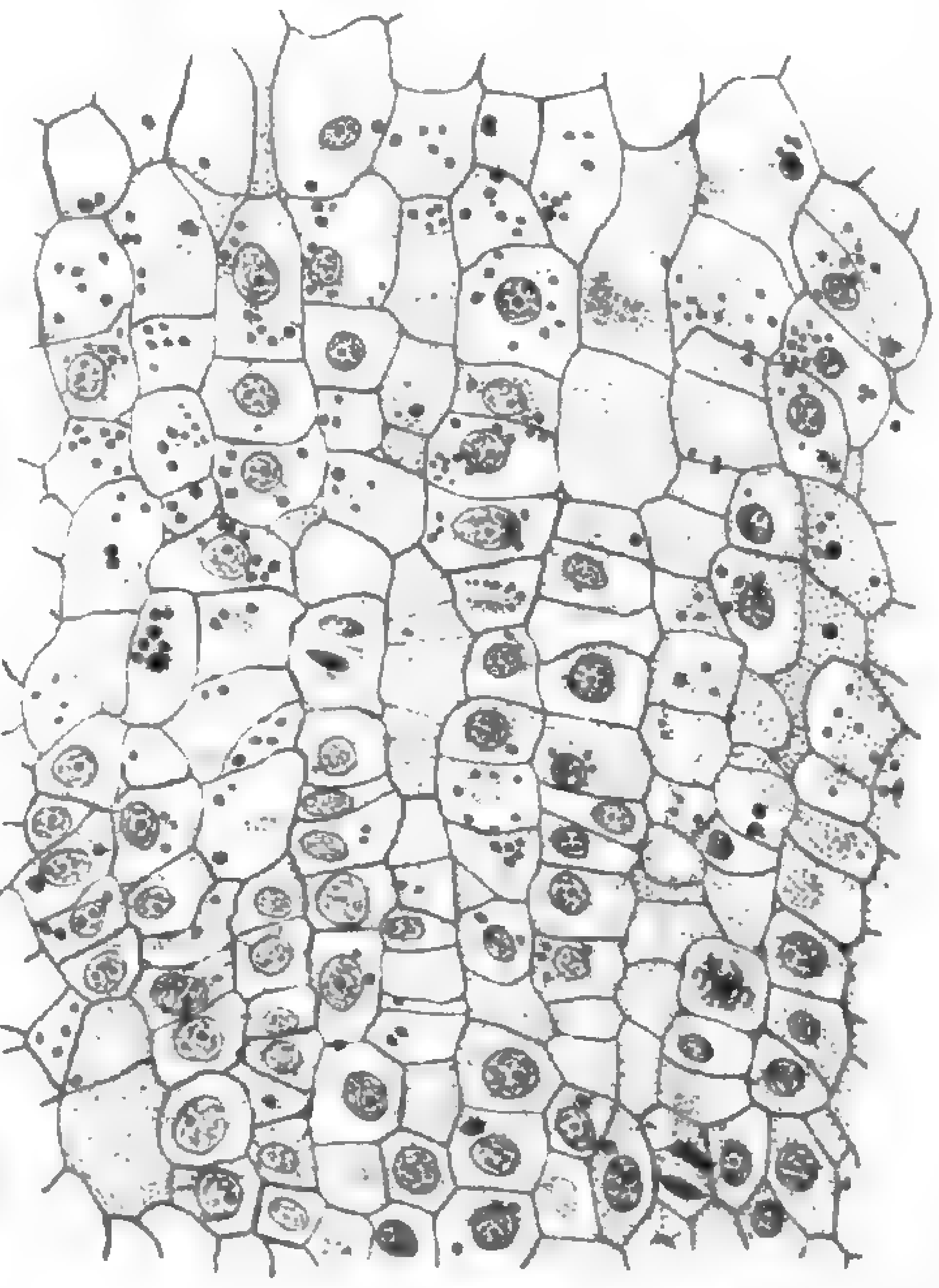

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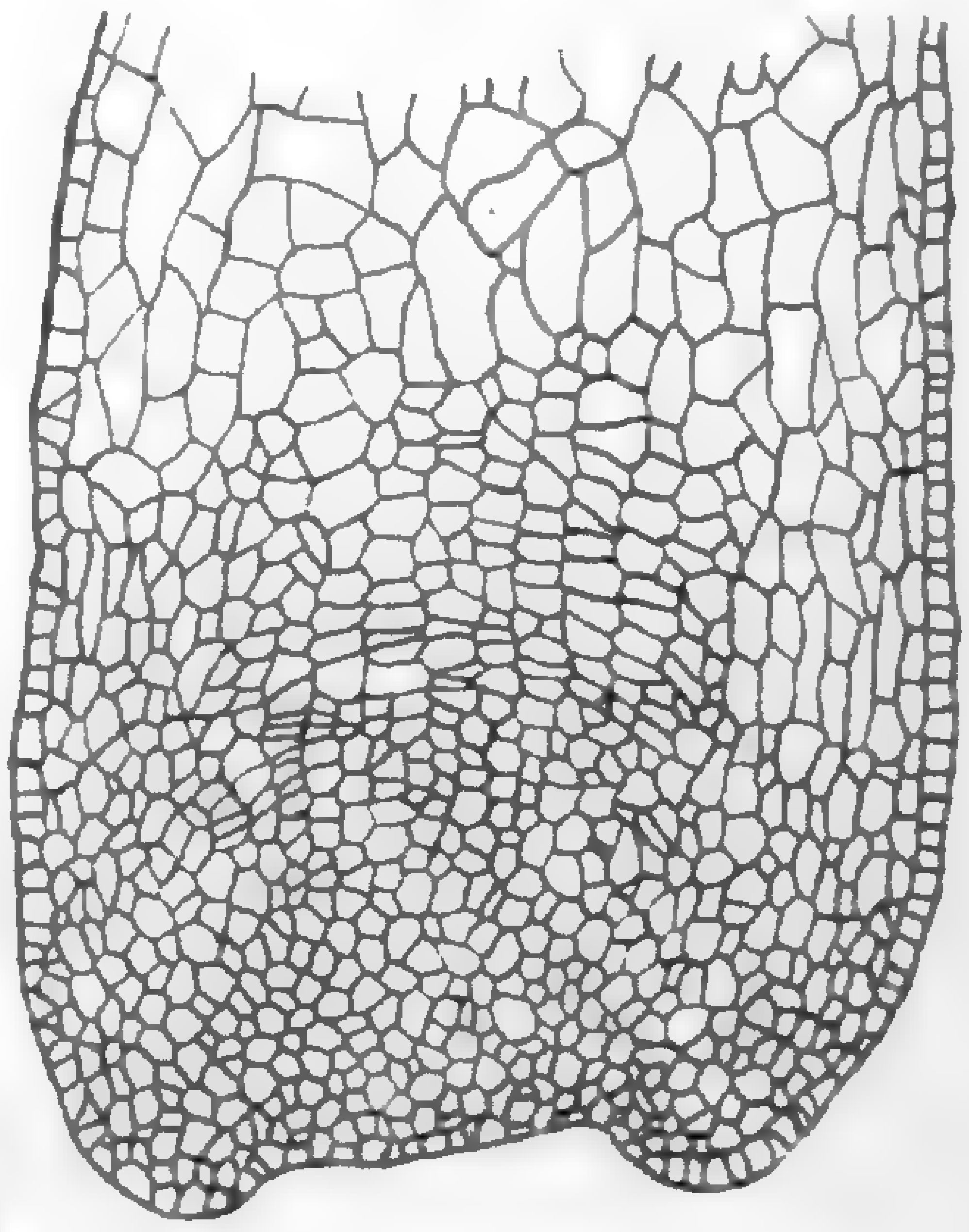

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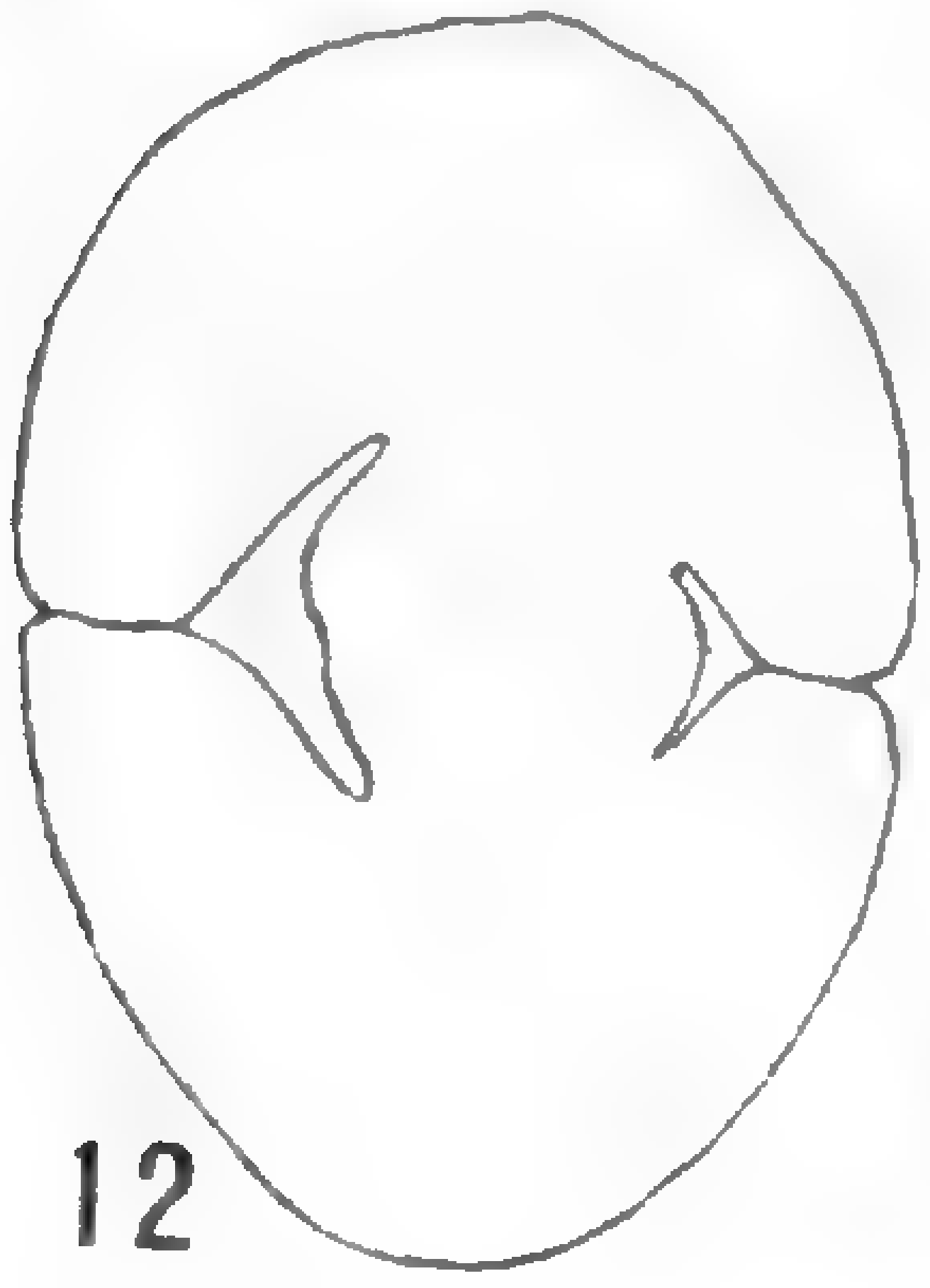

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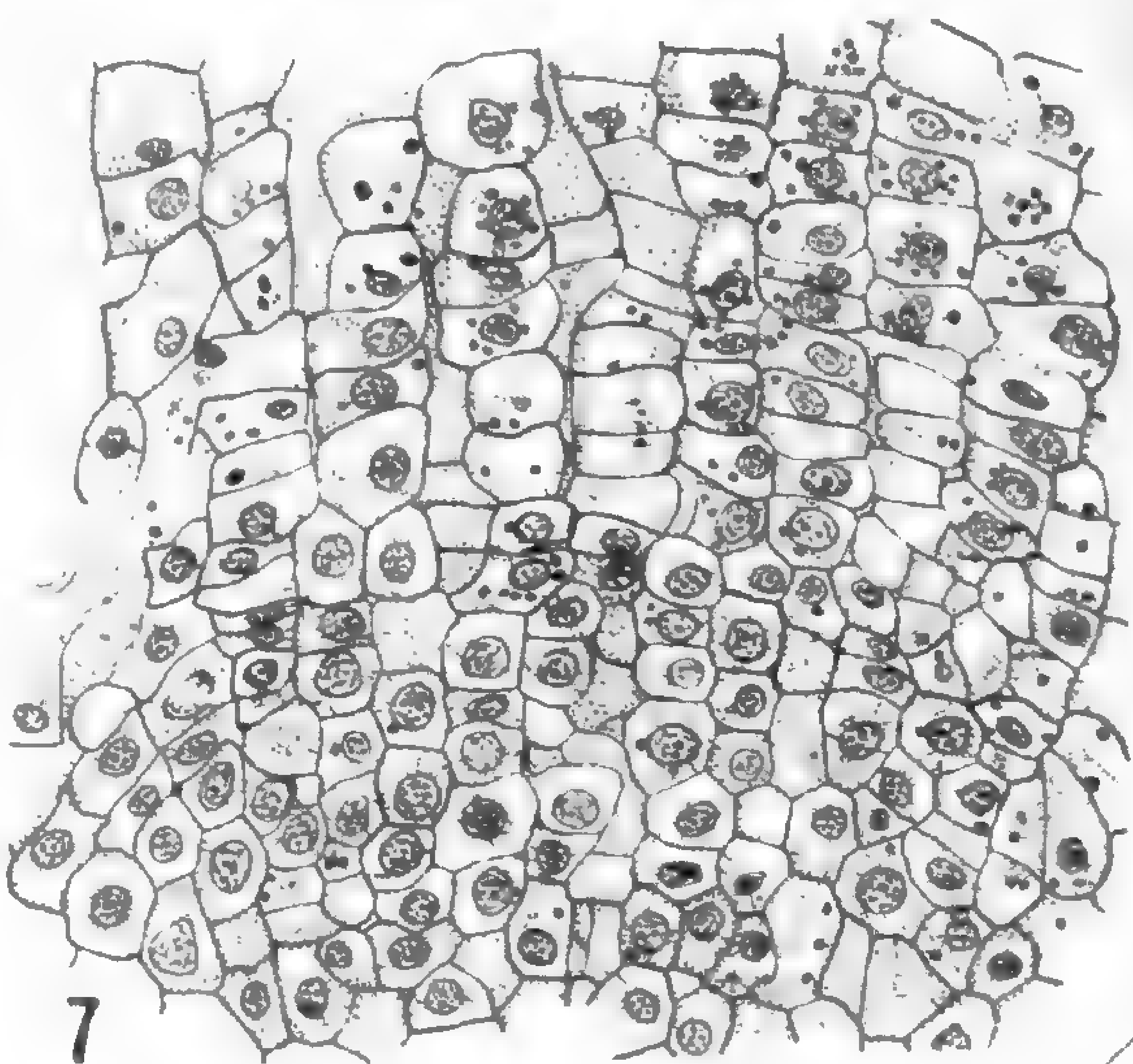

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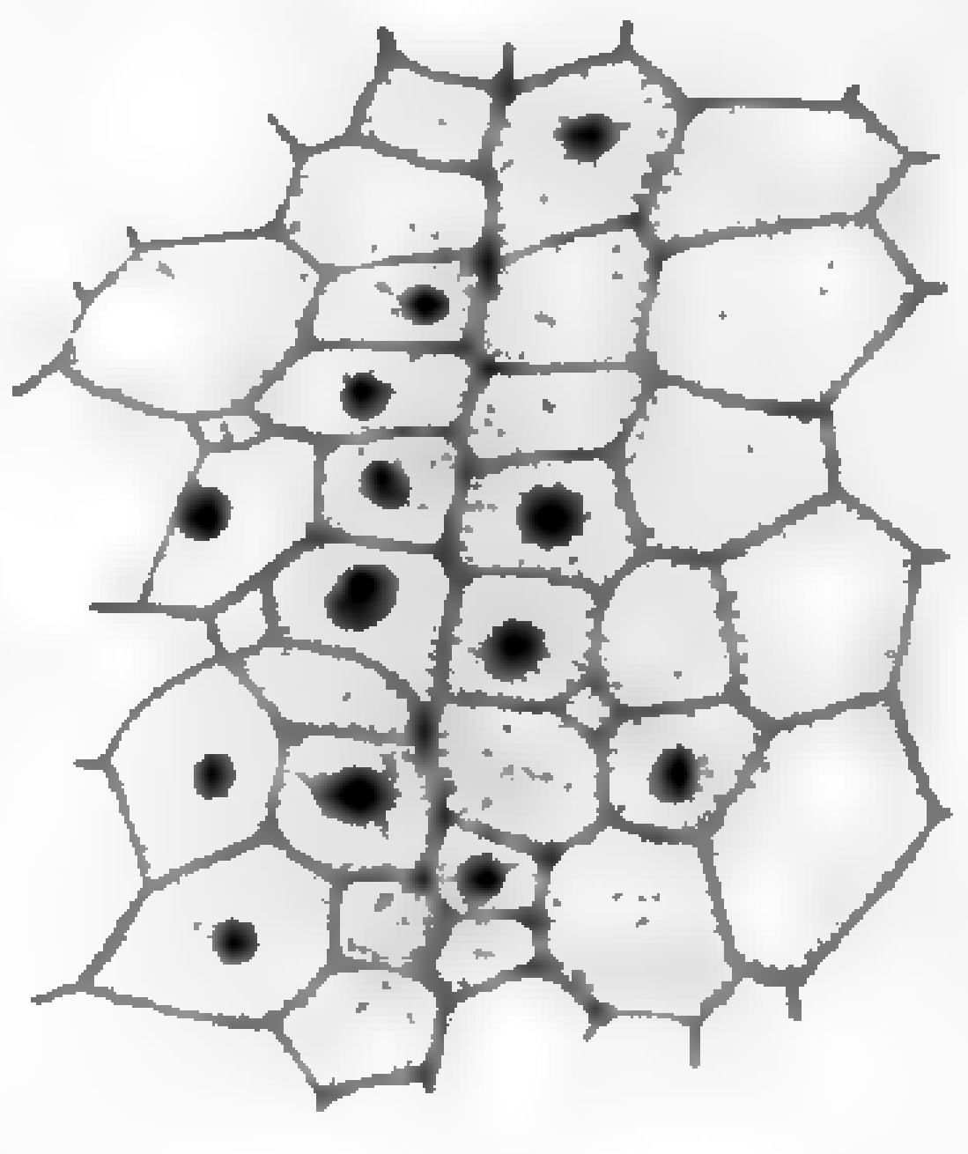

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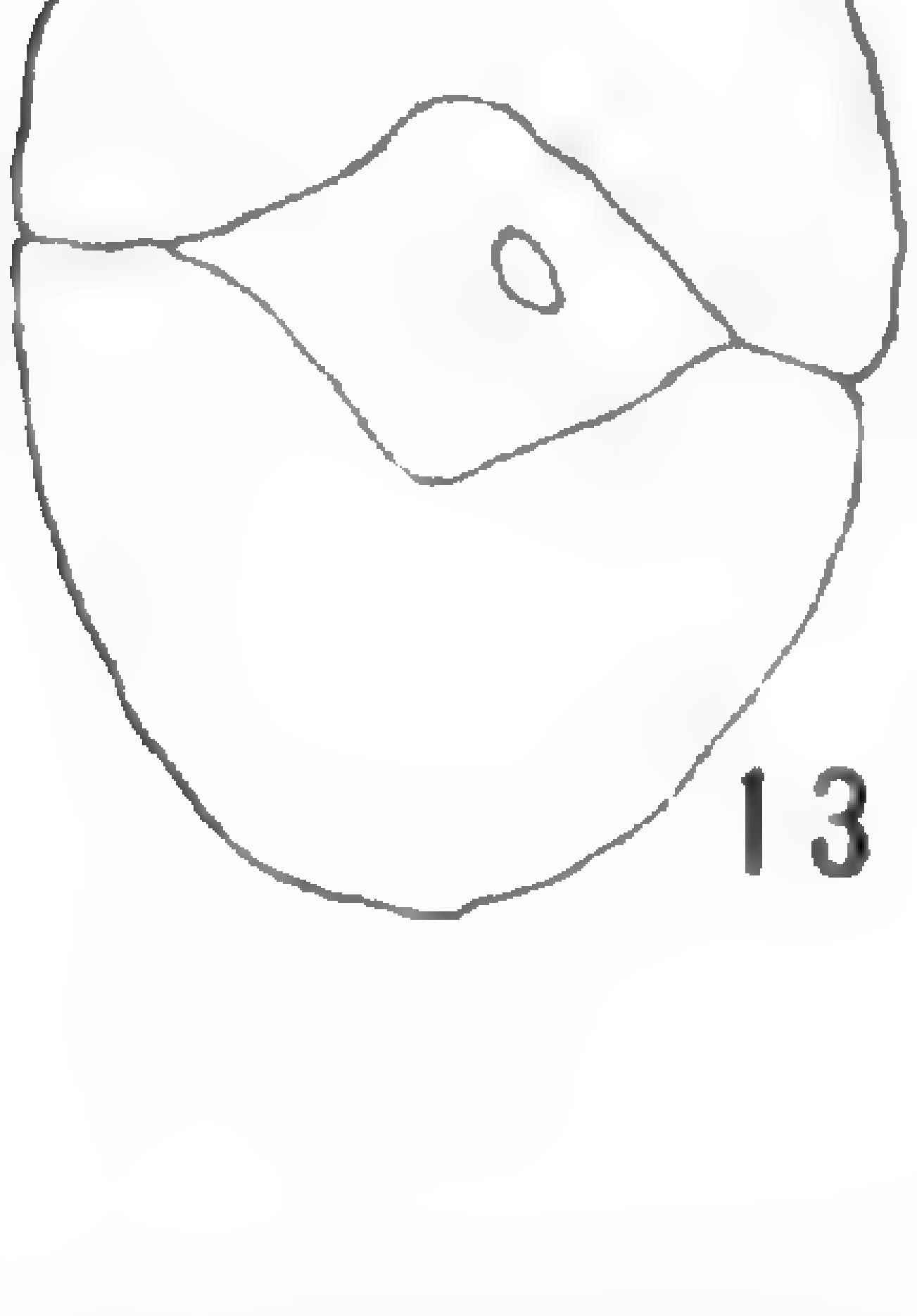

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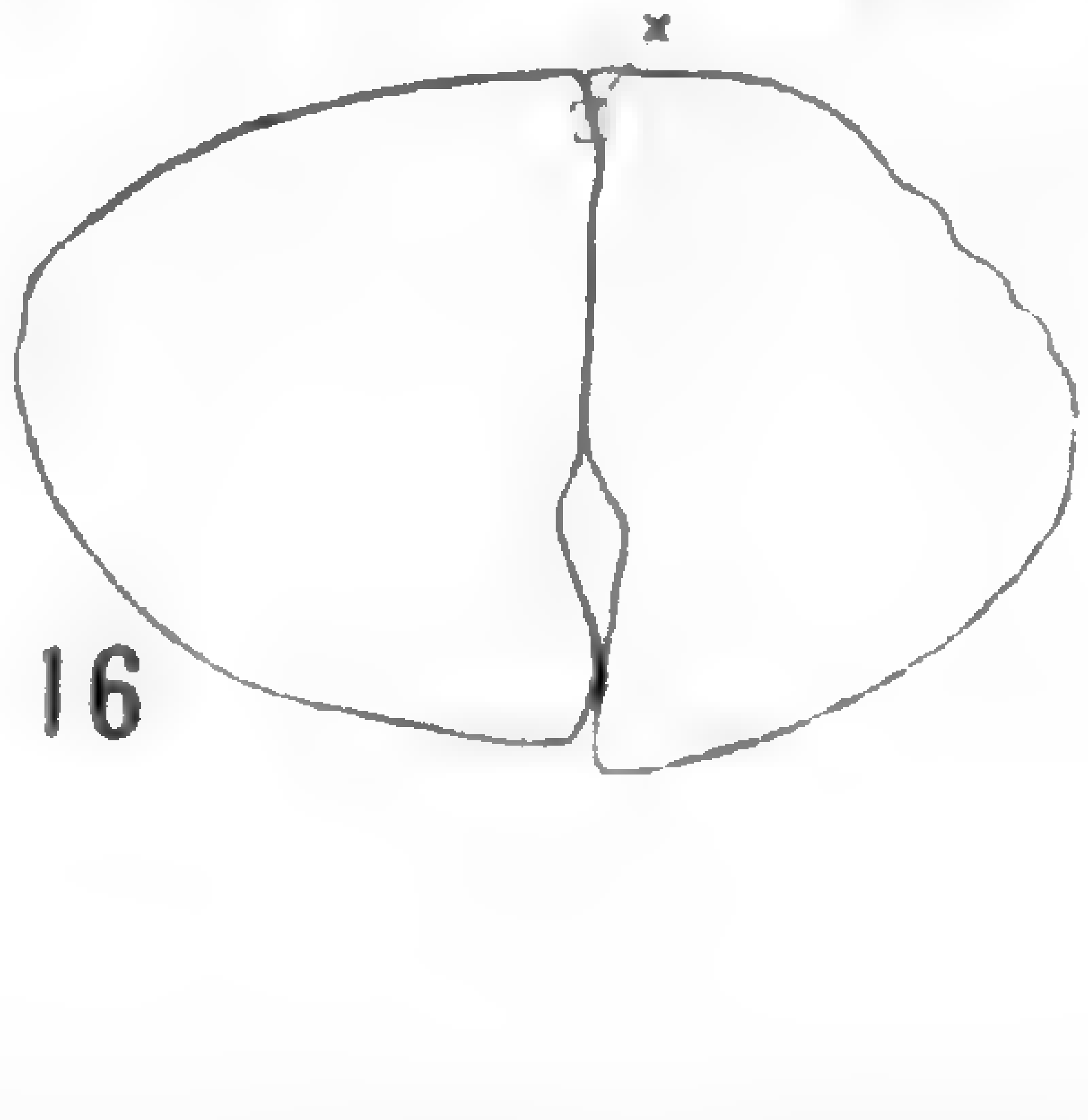

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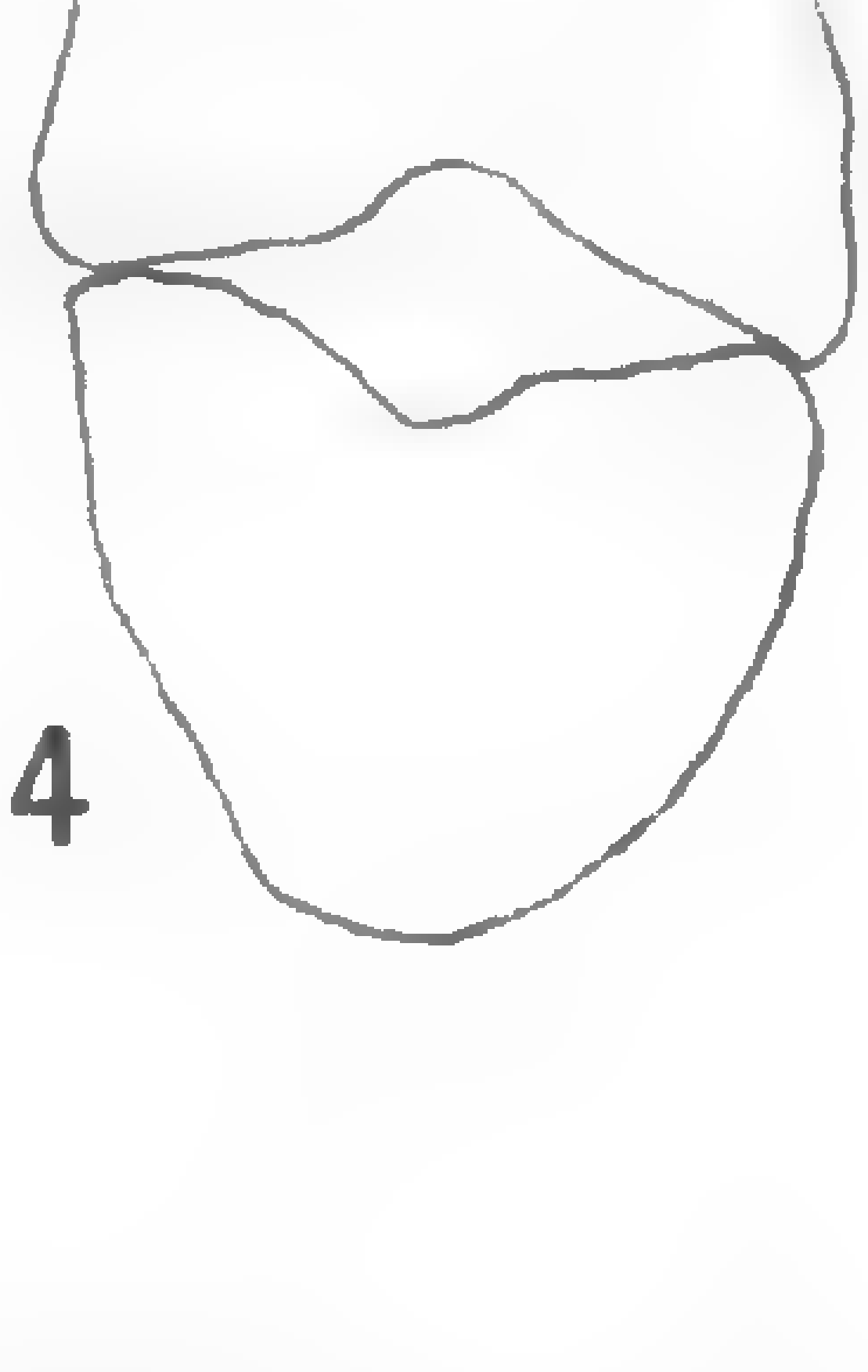

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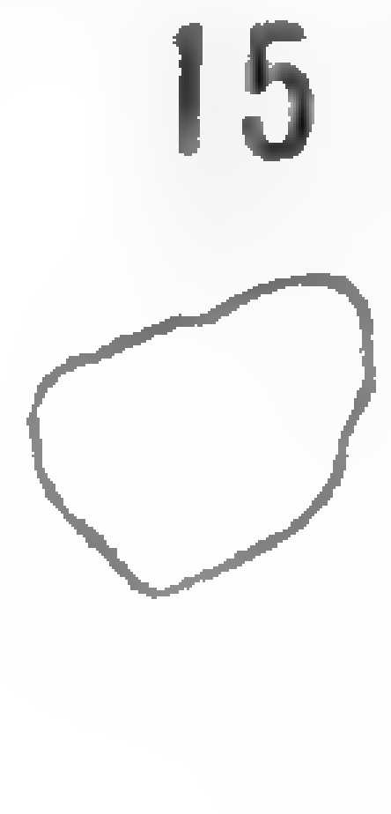

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SAXTON on ENCEPHALARTOS

THE ORIGIN OF HETEROSPORY IN MARSILIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 133

CHARLES H. SHATTUCK

(WITH PLATES III–VI AND ONE FIGURE)

Much morphological work has been done among the heterosporous pteridophytes, but they have not been subjected to experimental methods to obtain some suggestion as to the origin of heterospory. From certain phenomena that I observed in making a morphological investigation of *Marsilia quadrifolia*, it seemed possible that an experimental study might furnish some evidence as to the way in which the heterosporous habit began in this form.

Historical

The natural presumption has been that the Marsiliaceae have sprung from a homosporous ancestry, but there is little definite evidence to substantiate this view. CAMPBELL (4) has suggested that a near relationship exists between Marsiliaceae and Schizaeaceae. BOWER (2) calls attention to the striking morphological resemblance between the sporocarp of the Marsiliaceae and the spike of Ophioglossaceae.

JOHNSON (14), GOEBEL (11), and others have pointed out features suggesting that Marsiliaceae are not far removed from the homosporous ferns, but apparently no experimental work has been done which might show that the Marsiliaceae were originally homosporous and by what process they have attained their present heterosporous condition, or in fact how this condition has arisen in any other form.

In 1887 BUCHTIEN (1) called attention to the fact that in Equisetum the sex of the prothallium is controlled very largely by nutrition, and drew the conclusion that dioecious prothallia are an indication of incipient heterospory. This view will be discussed later.

The first literature bearing directly upon the origin of heterospory appeared in 1894. WILLIAMSON and SCOTT (24, 28), in their work on Calamaria, were the first investigators to offer a tenable theory. After an extensive study of two species of Calamostachys, in which they found abortion in all of the sporangia in *C. Binneyana* and in only one-fourth of the sporangia in *C. Casheana*, they suggested that the abortion of certain of the spores and the consequent increased nutrition of their surviving fellows may have been the physiological condition that ultimately rendered possible the development of megaspores.

In 1908 THODAY (**27**) added further and convincing evidence from *Sphenophyllum Dawsonii*, to that already furnished by WILLIAMSON and SCOTT (**28**). He shows that the size of the spore varies with the amount of abortion, and that while the average diameter of the spores in this form is 83 μ, the maximum diameter where abortion is extensive is as much as 120 μ, or nearly one-third larger. These are both striking examples of heterospory as it must have appeared in its incipiency, and both show a very definite relation between the size of the spore and the extent of abortion.

Statement

Many have insisted that the only clue furnished as to the possible origin of heterospory is that found in Equisetum, where the prothallia are usually dioecious. This dioecism seems to be due rather to external than to internal conditions, as shown by HOFMEISTER (**13**) as early as 1855, when he pointed out that while the prothallia were for the most part dioecious, they could be made to produce either male or female sex organs, or both, by varying the external conditions. He states that archegonia may appear on late shoots of the so-called male prothallia; while SADEBECK (**23**) shows that antheridia may appear at a later period on the lobes of the female prothallia.

GOEBEL (**12**) says that "it is probable that in this, as in other cases, the male prothallia are those which have been insufficiently fed." BOWER (**2**) calls attention to the fact that the spores of Equisetum show no differentiation in size, or apparently in sex. CAMPBELL (**3**) also states (p. 453) that "external conditions influence the production of males or females as in the ferns, and that while the prothallia are normally dioecious, this is not exclusively the case." I have examined critically several laboratory cultures of the prothallia of Equisetum in which only antheridia were produced in the crowded portions of the sowing. In fact I have grown a number of cultures in which I could not find a single plant bearing archegonia, though plants bearing antheridia were very numerous. This shows that Equisetum is only slightly more advanced in its tendency to produce dioecious prothallia than the ferns, and that this tendency is largely, if not wholly, controlled by external conditions after the spore begins to germinate, and probably not until the prothallium consists of many cells. This has also been mentioned by PRANTL (**21**) and others. Varied external conditions operating on the plant during the formation and maturation of the spore seem to make no difference in its size or tendency after germination to produce male or female prothallia. In other words, the plant makes no preparation in its spore for the production of female prothallia, the sex being determined long after germination and wholly by chance external conditions.

From a consideration of these facts it appears that the genus Equisetum, as we now know it, furnishes no clue to the origin of heterospory, because it makes no preparation which we can discover in the organization of its spores, either in size, shape, or extra storage of food material for the production of specially large gametophytes. In other words, the sex of the prothallium seems to be determined after germination and wholly by external conditions. In this particular we find it no farther advanced than the true ferns.

When we compare this form with one of the heterosporous pteridophytes, for example Marsilia, we find that the latter plant begins to prepare a few special spores as soon as the tetrad divisions have occurred, which are to produce the female prothallia. These few large spores are produced at the expense of many aborting ones whose substance is gradually absorbed by them. Moreover, these large spores are formed, under normal conditions, in the oldest and most favorably placed sporangia (*figs. 1, 2*), thus showing that here the sporophyte makes definite preparation for the production of spores which are to produce female prothallia.

In the microsporangium every one of the 16 mother cells (*fig. 3*) produces four functioning microspores, 64 in all; while in the megasporangium only one spore matures out of 64, all of which seem to be identical in every particular when the tetrads are first formed (*fig. 4*). A closer examination reveals the fact that this one megaspore does not gain the ascendency without a struggle. In fact, many instances were found in which there was sharp rivalry between two or more enlarging potential megaspores (*figs. 5–9*). Sometimes this occurs in the same tetrad, occasionally all four enlarging (*figs. 5–7*); sometimes two members of the same tetrad enlarge (*figs. 5, 8, 9*); and sometimes one each of two or more tetrads enlarges. Yet in the end, one centrally placed spore always gains the ascendency, the others becoming abortive.

This apparent plasticity of Marsilia led me to take up a further study of it grown in the greenhouse, and under such conditions that a very careful record of results could be kept. My object was to see what effect varying conditions of light, heat, moisture, etc., might have on the production of the two kinds of spores.

Even among seed plants the development of the megaspore is by no means so uniform as is that of the microspore, even the formation of the well-known tetrad being dispensed with in many forms, such as Lilium, where the mother cell forms four nuclei but fails to develop walls. These nuclei are thought by many to represent four megaspores. We find also that from a single megaspore there may come a varying number of cells within the embryo sac, as found by CAMPBELL (**5**) and JOHNSON (**15**) in Peperomia, where 16 nuclei are formed; and by the writer in *Ulmus americana* (**25**), where 8 to 16 nuclei are formed; and while 8 is the usual number for angiosperms, some plants fail to form even so many, as was shown by Miss PACE in Cypripedium (**19**), where only four are formed.

Also, where the row of four megaspores is formed, there is often a sharp struggle for the mastery; sometimes the lower one, sometimes the upper one, and even one of the middle ones finally functioning as the embryo sac. This is well shown in such forms as Diospyros, in which Miss HAGUE, in an unpublished paper, finds the above conditions. Occasionally two megaspores function, forming two embryo sacs, as shown by ERNST (**10**), and by the writer in Ulmus (**25**) and Pinus (unpublished).

The nuclei within the sac also contend as to which will function as the egg, as shown by CHAMBERLAIN (**6**) in Aster, and by Miss OPPERMAN (**18**), and by the writer (**25**). In contrast with the above varying conditions of the megaspore we find a very constant method of development for the microspore, the mother cell nearly always forming four spores (rarely 3 or 5), and a very large percentage of these developing, which are very constant in size, number, and behavior.

After reviewing these facts we must conclude that the megaspore condition is a derived condition, that is, derived from the original homosporous condition of the ferns; that it is therefore more recent, and consequently more plastic, and more likely to yield interesting variations when subjected to experimental methods.[1] With these general facts in mind the experimental work was begun.

Methods

In attacking this problem it was first necessary to determine definitely at what stage in its development the contents of the sporangium give positive evidence as to whether a megaspore or microspores are to be formed. JOHNSON (**15**) determined that the megasporangium is the first sporogenous tissue to be differentiated, but did not trace the development much farther. This has been done, and we find that all sporangia have identically the same development until the tetrads are formed (*fig. 4*), at which stage a very slight difference is observed.

In the older sporangia (*fig. 2*), which are also the most centrally located, the four young spores of each tetrad show a marked tendency to hang together by strong protoplasmic strands, as figured by STRASBURGER (**26**) and shown in *figs. 5–10*. These strands are the first recognizable morphological feature by which one can determine that a sporangium is to form a megaspore rather than microspores. They persist until the megaspore is quite mature, and in very many instances can be seen on the papilla of the germinating megaspore, which still subtends the three abortive members of the tetrad (*fig. 10, a*). This condition was figured by WILLIAMSON and SCOTT (**28**) for *C. Binneyana*, although they did not attempt an explanation. In the case of sporangia which were to form microspores it was observed that the protoplasmic strands are not so strong, and that the young spores, while held together during their early development, are in the end separated completely from each other. The fact that the megaspores are held together by stronger protoplasmic strands was first noticed by SACHS in 1866 in *Pilularia globulifera* (**22**).

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[1] After this work was well under way Miss PFEIFFER (**20**) reported cases in Azolla where two megaspores have matured instead of one, which is the normal number.

The cause for the varying behavior of the strands in the two kinds of spores was not determined, but the establishment of this fact suggested that any experiments on the plant which might affect nutrition and growth ought to have a more marked influence in determining the kind of spore formed if applied when the sporocarps contained sporangia about ready to form tetrads. The various methods herein described were all found to give the best results if applied at this time.

Various cultures were grown in ponds, in the open air, and in the greenhouse. Careful records were kept covering such points as rate of vegetative growth, color, and vigor of plants, length of petioles, length of time before the appearance of sporocarps, the nature of the sporocarp, the causes producing the largest and most abundant sporocarps, and the causes of blasting of sporocarps and of their complete suppression (details of these cultures will be published in a later paper).

The experimental work was begun in Chicago, June 20, 1905, and continued until the latter part of September; it was repeated again during the same period in 1906; and then carried on continuously from June 1907 until the present time.

On June 20, 1905, I found *Marsilia quadrifolia* growing in Hull Court pond at all depths from 30^{cm} beneath the surface to $20–25^{cm}$ above it on the banks. It was in a most luxuriant condition, some of the rhizomes being more than 2^{m} in length. There was also one tank of growing plants in the greenhouse. Sods from the pond were taken up and transferred to the greenhouse, where they were placed in four large tanks (60 by 90^{cm} and 30^{cm} deep). These were supplied with soil (a rich black loam) spread evenly over the bottom to a depth of 10^{cm}, in which the sods were transplanted at one end of the tank and covered with water to the depth of 5^{cm}. In a few days these tanks were elevated 10^{cm} at one end. This left the soil at the upper end out of water, but submerged the plants, which were at the other end, about 10^{cm}. The tanks were then numbered 2, 3, 4, and 5, and placed under as great a variation of light as was possible to obtain in the greenhouse. All other conditions were kept as nearly uniform in all the tanks as possible, but on clear days there was considerable variation in temperature, as shown by the table of temperature readings.

TABLE I

LIGHT READINGS TAKEN IN OPEN AIR AND IN WATER AT DEPTHS OF 2.5, 5, AND 10^{cm}, AND ALSO IN NORTH AND SOUTH ENDS OF GREENHOUSE

These readings were taken with a solio-paper actinometer and show approximately the varying intensities of the light where different cultures were grown.

				UNDER WATER			GREENHOUSE	
1907	Time	Weather	Open air	2.5^{cm}	5^{cm}	10^{cm}	South end	North end
September 14	3:45	clear	15 sec.	..	..	..	35	65
September 20	12:20–12:40	clear	10 sec.	14	20	..	..	...
September 25	2:00– 2:20	clear (?)	20 sec.	..	..	35	70	210 (shade)
September 26	2:30– 2:40	cloudy	45 sec.	..	..	70	120	170

The plants in the best lighted positions recovered from the effect of transplanting more rapidly and grew much more vigorously than those in more subdued light. This was shown by the rate of growth of rhizomes, which under the most favorable conditions was as much as 12.5^{cm} daily; while for those in the most subdued light 6^{cm} was the maximum daily growth. The color of the plants in good light was also a darker green and the thickness of the leaf blades, rhizomes, and petioles was also greater. Neither the length of the petioles nor the size of the leaves was so great as those of the shaded plants.

On August 6, the first sporocarps were discovered in tank 5, which had been placed in strong light; these were evidently several days old and must have been evident as early as August 3. On August 8, tank 4 showed some sporocarps that had probably been in evidence about two days; while in tank 3 the very first indication of sporocarps was noticed. Tank 2 was in diffused light except for about two hours in the middle of the day, and while the plants grew well they stubbornly refused to fruit either above or below the surface of the water. Finally on August 17 some sporocarps were found in this tank out of water. These soon turned brown, however, and on sectioning were found to be blasted. This tank continued to produce a few blasting sporocarps for 18 days, but it produced good sporocarps as soon as it was placed in a strong light.

Influence of water

It has been observed that *Marsilia quadrifolia* fruits most profusely at the surface or a few centimeters above the surface of the water.

It fruits sparingly under water, and at a depth of 10^{cm} very few sporocarps appear. I observed that most of these blast when about half grown.

In my greenhouse cultures in 1905 I found that all the first sporocarps that appeared in tank 1 blasted when about half grown, except two that happened to be about 8^{cm} higher than the others, due to the uneven surface of the soil in the tank (*fig. 12, m*). After the rhizome passed over this elevation and again sank into $8–10^{cm}$ of water, the sporocarps began to blast as before. In order to be sure that this was not accidental, on July 5 I lowered the water in this tank until it was not more than 1^{cm} in depth; and then nearly all the sporocarps matured. On July 11 I raised the water to the original level, and by July 16 many of the oldest of the newly formed sporocarps were blasting. On July 21 I again lowered the water to 1^{cm} in depth, and by July 25 the oldest of the sporocarps, formed after that date, had safely passed the period where blasting had occurred. I then put on 20^{cm} of water and found that the blasting occurred after the sporocarp had been visible only about two days, instead of four to six days as observed at the 10^{cm} level. I imbedded and sectioned many of these sporocarps in order to determine the relative vitality of megaspores and microspores. It was from a study of these that I conceived the idea of blasting the megaspores and continuing the development of the sporocarps containing only the surviving microspores. I shall speak later of the methods employed.

I was at a loss to know just what had caused the blasting. While mere depth of water seemed to be the immediate cause, several factors were involved, such as oxygen supply, intensity of light, and temperature, all of which were varied with the change in depth. On August 5 I moved this tank, which had been in subdued light, to the east side of the greenhouse into strong light, and threw a mist of tap water over the plants in order to keep them saturated, but at the same time aerated. This water was siphoned off constantly, so that most of the sporocarps were at the surface. In a few days (August 11) I noted that blasting was occurring quite as universally as before. While the plants now had more light and a better oxygen supply than before, I had lowered the temperature during the middle of the day about 8° and at night about 3°. It was plain that this variation in the temperature was a very important factor. I then grew the plants out of water for a week without applying the spray, and had no trouble with blasting. This process was repeated several times with the same

TABLE II

OPEN AIR TEMPERATURE READINGS TAKEN FROM 2:00 P. M. TO 3:00 P. M.

1907	Weather	Open air	Pond surface	15^{cm} under water	Tank	Dry soil	Wet soil
August 21.......	cloudy	....	20	23.5	....	....	....
August 22.......	clear	....	23	....	25	....	....
August 23.......	clear	21	20	20	21.5	....	....
August 24.......	clear	..	25	21.5	27	....	....
August 25.......	clear	24.5	27	20	28	35.5	31.5
August 26.......	cloudy	24	22.75	19	24	23	24
August 27.......	cloudy	22.5	23	20.5	24	24	23.5
August 28.......	clear	24	26	22	27.25	29	28
August 29.......	cloudy	20	21	19.25	21	..	22
August 31.......	cloudy	24	28	23	28.5	30.5	....
September 1.....	clear	33.5	30.75	25.5	33.5	33	....
September 14....	clear	....	26	21	27	....	....
Average readings	....	24.18	24.37	21.39	26.06	29.16	25.8

TABLE III

GREENHOUSE TEMPERATURE READINGS TAKEN FROM 2:00 P. M. TO 3:00 P. M.*

			SOUTH TANK		NORTH TANK			
1907	Weather	Air	Wet soil	Surface	Surface	Tap	Jet	Spray
August 19............	clear	34	....	35.5	30	15.5	....	....
August 20............	cloudy	28.5	....	....	20.5	16	....	....
August 21............	cloudy	25	....	....	....	....	....	....
August 22............	clear	30	....	....	....	19	30	25
August 23............	.....	26	....	24	23	....	....	....
August 24............	clear	30	32	32	23.5	24	34	24.5
August 25............	clear	27.75	29.75	29.5	....	21	25.5	21.5
August 26............	cloudy	29	27	27.25	23.5	19.5	31	25
August 27............	cloudy	25	....	24.5	22	18.75	24	23
August 28............	clear	30	30.5	28	26	19.5	31	23.5
August 29............	cloudy	22	22	21.5	....	20	22	20.5
August 31............	cloudy	33	33	30	28.5	19	35.5	28
September 1.........	clear	39.5	35.25	34.5	33	....	41	26
September 14.........	clear	32.75	....	30	27	....	34	28
Average readings		29.45	29.93	28.8	25.7	19.22	30.8	24.5

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*It will be noted that this table of readings was taken in 1907. It is more complete than the one taken in 1905, but does not vary materially from it, except in the columns marked jet and spray. These are higher in this table because the water was heated by means of the sun which shone on about 12^m of the pipe, raising the average reading for the jet 9°, and for the spray 4°. The spray was in the north end of greenhouse in 1905, close to the riser pipe; and the temperature of the jet was very little above the tap in this place. (See diagram of piping.)

results. By this time I had discovered that the megaspores were the first to succumb when the plants were chilled, and I also found an occasional sporocarp, among those which had not apparently been blasted, which showed that the megasporangia and oldest set of microsporangia had been killed, but the younger microsporangia were in a healthy state (*fig. 13, b, c*). So far as I could determine, these sporocarps were in a fair way to reach maturity, notwithstanding the fact that the megaspores were all dead. I then shortened the time of application of the spray, in order to determine the shortest period which would kill the megaspores and yet not blast the entire sporocarp. This I found to be no easy task, as it is not possible to determine exactly, from external appearance, the stage of development of the sporogenous tissue. I was able finally to be reasonably sure from their size and thickness when sporocarps had reached the mother cell stage. In such sporocarps, under the conditions of this experiment, the application of the cold spray day and night for 48–60 hours would not cause the entire sporocarp to damp off, but most of the sporocarps when sectioned showed only traces of megaspores in the sporangium. It was in these sporocarps that I got such a great variety of forms of microspores (*figs. 15–22*).

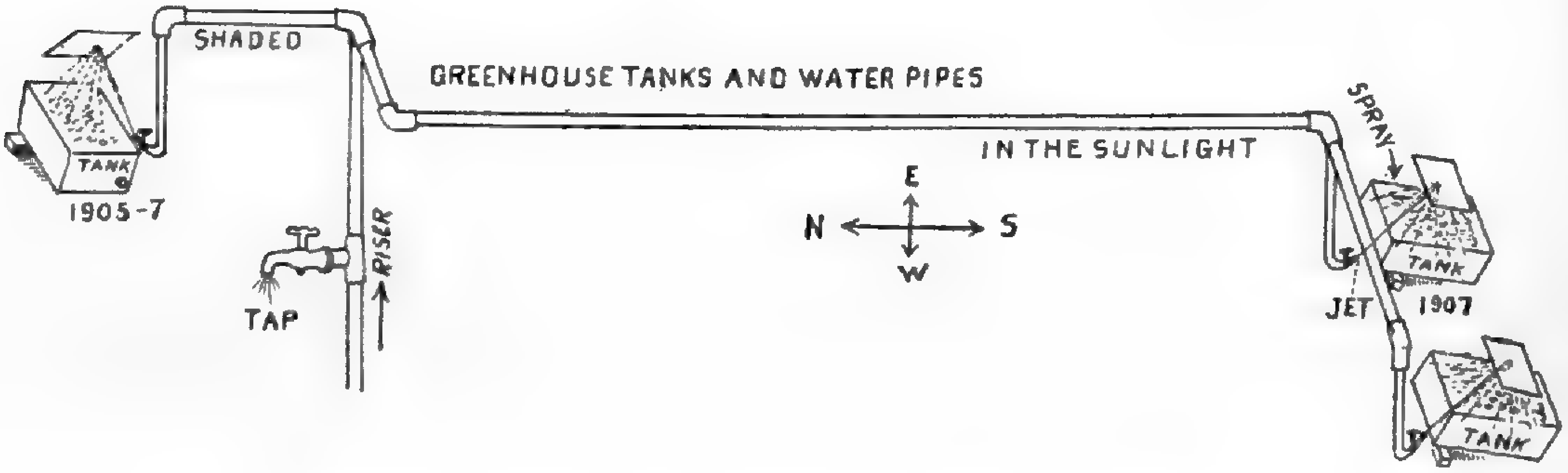

Diagram of piping and position of tanks in greenhouse

The sporocarps treated less than 48 hours generally developed normally, while those treated for a longer period than 60 hours generally damped off. I was able to treat plants in August and September 1907, in the south end of the greenhouse, in stronger light and at a higher temperature (see table) for a much longer time (76–96 hours) before blasting occurred. Also in the same year I was able to grow abundant and normal sporocarps in tanks out of doors, at temperatures shown in the table, in as much as 20^{cm} of water. At the same time, plants in the same tank, in 8 to 12^{cm} of water, at the same temperature but shielded from the direct rays of the sun, either blasted completely or showed more or less abortion among the megaspores and occasionally enlargement of some of the microspores. It is evident, therefore, that the plants are dependent on strong light and high temperature in order to mature perfect sporocarps, and that water at any depth less than 20^{cm} need not cause blasting unless it greatly lowers the temperature or reduces the light below a certain minimum.

Discussion

A close inspection of this process of blasting brought to light the important fact that under the conditions of growth to which these plants were subjected the megaspore was the first to show signs of abortion. It might be added that through a long list of experiments on the younger stages of sporocarps this was the invariable rule. Unfavorable conditions of growth, whether brought about by depth of water, lack of light, low temperature, or drought, without exception always affected the megaspores more than the microspores. Later experiments revealed the fact that in the more mature sporocarps this was not the case. Hard conditions brought on after the megaspores are well formed, but about the time the microspores are in the mother cell stage, will produce abortion among the microspores. The critical period in the life of the spore, whether microspore or megaspore, seems to be from the time when the mother cell comes into the synapsis stage until the tetrads are well on the way to becoming spores. This also agrees with Miss PFEIFFER's observations on Azolla (**20**). However, it proved to be much easier to arrest the development of the megaspores than to affect the microspores in this way, and when abortion did occur it was much more nearly universal in the case of the megaspores than in that of the microspores.

Excellent examples were secured showing sporocarps without a single megaspore, while I was never able to secure the complete blasting or abortion of the microspores alone. Many experiments were made in which both were completely blasted, but if either survived it was always the microspores, though sometimes only a small number. It was also noticeable that when the sporocarps were subjected to such treatment as to blast the megaspores in their early stages, sometimes, when the plants were afterward placed under the best of growing conditions, only part of the microspores survived the change. The surviving ones would then respond with vigor, becoming sometimes three times the usual size for the normal microspores (*figs. 26, 28*). It was noticed also that when a sporocarp, whose oldest sporangia were just forming tetrads, was subjected to a spray of cold water for several days, the megaspores would abort, and the microspores, which at this time would be just coming into the mother cell stage, would not undergo the reduction division while under the spray, but would continue to grow until they became much larger than the ordinary microspores, assuming at the same time many unsymmetrical and unusual shapes (*figs. 15–22*). When these were placed later in good growing conditions, both reduction divisions occurred without the formation of more than mere traces of walls (*fig. 14, c*), but the entire wall of the mother cell became much heavier. Repeated attempts at germination under the most favorable conditions have so far failed to demonstrate what these spores might become ultimately. The failure to germinate seems to find its explanation, not in any want of vitality of the cell, but rather in the rigidity and continuity of the surrounding wall. As is well known, the heavy walls of both megaspores and microspores are interrupted at the papilla, which has only a light membranous covering, due to the presence of radiating protoplasmic strands (figured in SACHS **22** for *Pilularia globulifera*) that hold the four spores in close proximity until the wall is well developed over the free surfaces. The tapetal layer always incloses the tetrad, but forms a perinium only where it comes in contact with the cell membrane of the functioning spore. It is prevented from touching this wall at the papilla by the other three members of the tetrad (*figs. 6–10*), yet the perinium will not form around an aborting spore. The microspores separate earlier than the megaspores, hence the papilla is less evident in them than in the megaspores where the abortive members of the tetrad may not be cast off at all, often remaining until germination has begun. When the tetrad divisions are delayed, there is not a corresponding delay in wall formation, which goes forward at such a rate that when the divisions occur the wall is too strong to disrupt, though in the second division evanescent cell plates are sometimes evident (*fig. 14, c*).

As there is nothing to interfere, the wall is laid down continuously over the entire surface of the cell, being thicker than the ordinary microspore wall, with no thin places, and absolutely unresponsive to germinative conditions. Cases of delayed or estopped germination due to resistant seed and spore coats are not uncommon, as shown by CROCKER (15) in the cocklebur and other plants.

As said before, unfavorable conditions in the early life of the sporocarp produced blasting of the megaspores, and sometimes delayed the reduction divisions in the 16 mother cells. However, unfavorable conditions at a later date permitted a very complex set of results, most of the megaspores blasting, while some of the microspore mother cells would undergo division and separate into spores (*fig. 21*). An interesting condition was obtained by blasting just as the microspore tetrads were formed, and then transferring the plants to the best condition for growth. In this case a few microspores would survive in a few of the sporangia, growing with astonishing vigor, some of them reaching a size quite beyond the ordinary microspores (*figs. 24–27*). We have in this case an intermediate sized spore, sufficiently unlike the microspore to warrant the question whether the abortion of tetrads among the megaspores did not begin in this way. The difference in size between the ordinary microspores and these unusual ones is as great as that shown between the reputed microspores and megaspores of Calamostachys and Sphenophyllum.

Probably the most interesting of all the results were obtained by growing Marsilia in subdued light during the usual time of sporocarp-formation (July and August), and then forcing the plants to develop sporocarps at a later period. I had previously determined that although the plants grew luxuriantly in subdued light, they would not produce sporocarps. On August 15, 1906, plants were moved to the south end of the greenhouse and given the maximum amount of heat and light. My intention in this experiment was to throw all the vigor of the plant into a few sporocarps and then to inhibit further sporocarp-formation by means of a spray of cold water. A few sporocarps appeared by September 10, which was more than two months later than the usual time for sporocarp-formation. These grew with great vigor until the occurrence of exceptionally cool and cloudy weather, which began September 19. After this time no more sporocarps appeared, and all the younger ones, already in evidence, began to blast, although I did not use the spray. Sections of these showed, as usual, that the megasporangia were the first to succumb to the unfavorable conditions. Sections of the older ones showed a condition which I had not seen before, namely that the blasting was much more general in the microsporangia, and that in many of the oldest sets of microsporangia megaspores were developing (*figs. 32–37*); while in a few microsporangia abortion had proceeded until only one microspore, which was 8–16 times larger than the ordinary ones, remained (*figs. 28, 31*). The few remaining sporocarps were carefully grown to maturity, and on dissection showed a number of sori containing two megaspores instead of one, as I had found in all the cases thus far noted. That these secondary forms (called secondary because of forming at a later date than the original or primary megaspores, and also because of being smaller; *figs. 32–43*) were megaspores there could be no doubt. Every distinguishing character peculiar to the megaspore was present, such as size, shape, thickness of wall, position and shape of nucleus (which is always apical and meniscoid), and manner of vacuolation. There could be no doubt that these forms, though occurring in microsporangia, were far beyond any microspore in special characters; but they still retained some undoubted microspore characters; such as an approach to the general spherical form, the long axes of the smaller (intermediate) size being proportionally shorter than those of the primary megaspores (*figs. 38–43*). So far I have failed to induce germination in any of these induced forms.

A number of the enlarged microspores from this culture were sectioned and showed certain characters belonging to megaspores. The ordinary microspore nucleus is spherical and central, while that of the megaspore is generally meniscoid and apical. It was easy to secure transition forms of nuclei among these microspores, which ranged from spherical, central ones in the case of the smaller spores, through a series of spheroidal, parietally placed nuclei in larger spores (*fig. 30*), until in the largest sizes, which were also more vacuolated, there was always found a meniscoid nucleus in the apical region of the slightly elongated spore (*fig. 31*).

The microsporangium represented in *figs. 28, 29* shows several functionless tetrads, which, while now distorted and shriveled, must have drawn heavily upon the supply of nutrition. This may explain why the largest microspores, while acquiring certain megaspore characters, were not able to attain more fully to megaspore proportions. In examining the sporangia that contained secondary megaspores, I was never able to find these large shriveled tetrads. This shows that all the tetrads must have aborted during the early stages of development, thus permitting the whole of the nutrition to be concentrated in this one spore, as is the usual case in primary megasporangia. *Fig. 36* is unusual for secondary megaspores, and shows in addition to the successful spore a single member in each of the three tetrads slightly enlarging. *Fig. 37* is more usual, and shows five tetrads which aborted much earlier. Two cultures were grown in 1907 under conditions similar to those just described, and the same results were obtained. Occasionally in all of these cultures I found megasporangia containing well-developed microspores (*figs. 2, 33, 35, 37*). In ordinary plants these were always found on the periphery of the sporogenous area and appeared to be related to the food supply. Scant nutrition may cause the sporogenous tissue in some megasporangia to revert to the probable ancient homosporous condition.

This production of secondary megaspores I believe to be as closely related to nutrition as is the formation of primary megaspores. In numerous cultures I was able to observe that the formation of megaspores is possible only when the plants are well nourished. In the cultures in which I secured secondary megaspores, I always had long and strong rhizomes and allowed only a few sporocarps to form just at the end of or after the fruiting season. Then by cutting off all later sporocarps I was able to throw all the energies of the plant into a very few. By this means I was able to secure not only the most marked abortion and enlargement of the microspores, but also the formation of secondary megaspores, which, since they occur in microsporangia, would undoubtedly have developed, under ordinary conditions, as microspores.

In a plant so plastic as Marsilia, it is not difficult for one to conceive how the heterosporous habit may have become fixed. If excessive nutrition will now cause certain microsporangia to develop megaspores, and excessively hard conditions will cause the plant to revert to the homosporous habit, it would seem reasonable to conclude that the plant had attained to heterospory gradually, a few of the better nourished sporangia each developing a few spores slightly larger than the rest. Other things being equal, these spores in germinating would naturally develop the larger prothallia, because of a larger amount of food material within the spore. We might expect that these prothallia would bear archegonia. Thus the determination of the sex of the prothallia would be at once shifted from dependence on the chance external conditions after the spore germinates, as found in the homosporous ferns, to dependence on nutritive conditions while the spore is being formed. This, it appears to me, must have been the process by which heterospory made its appearance in Marsilia.

I should also state that megaspores were noticed which were packed unusually full of starch grains (*figs. 44, 45*). These forms were larger than any megaspores that I have seen and had developed no perinium. I was not able to observe stages in their development nor to account for the phenomenon.

Theoretical discussion

If the doctrine of recapitulation be applied here, we may say that Marsilia can be so manipulated as to show in the development of its sporocarps the various stages in the production of complete heterospory, through the abortion of many spores and the special nutrition of a few.

We know that the heterospory described by WILLIAMSON and SCOTT in such forms as *Calamostachys Casheana* began in a very modest way, the diameter of the megaspores being not more than three times that of the microspores in the most extreme cases. We are also told that in the genus Calamostachys, *C. Binneyana* is homosporous and *C. Casheana* is heterosporous; but even in *C. Binneyana* abortive spores are found, and the remaining spores are larger in proportion as fewer develop in each tetrad, the diameter being fully twice as great when only one develops as when three remain.

WILLIAMSON and SCOTT point out that in *C. Casheana*, also, abortion is evident, but is confined to the megasporangia; in fact, their figures show no abortion in the microsporangia. They conclude, therefore, that heterospory was reached by the abortion of the spores in certain sporangia; then better nutrition caused the excessive development of the survivors at the expense of the aborting ones; and this process continued until specialized spores (megaspores) were formed.

Heterospory, as found in Calamostachys, is in its incipiency. We see its very beginnings in *C. Binneyana*, where all the sporangia show a tendency toward it by the promiscuous abortion of some members of all the tetrads, with the corresponding enlargement of the survivors. In *C. Casheana* we see it feebly established, abortion being confined to certain sporangia, yet fully three-fourths of them showing abortive spores quite variable in size.

In Marsilia, in ordinary plants, heterospory is much more firmly established, abortion being confined to not more than one-fifth or one-sixth of the sporangia, and at maturity the megaspores are very nearly equal in size, and many times larger than the microspores. But when by any means the fertility of these megaspores is destroyed, there is still a very large number of potential spores in the original homosporous condition and sufficiently young to respond to the stimulus given them by the added nutrition which should have gone toward maturing the megaspores. We then see the plant repeating its probable ancient habit of developing some of the spores to greater size at the expense of the others; and we have repeated in every detail the processes observed in *C. Binneyana*, which is homosporous. Again, well-nourished plants, allowed to produce only a limited number of sporocarps, carry this abortion and enlargement still farther, and a few sporangia produce still larger spores, varying as much in size as in *C. Casheana*, which is heterosporous. *Figs. 32–43* show that in many sporangia abortion and enlargement continue much farther than in *C. Casheana*, in that an intermediate sized megaspore is produced. This adds more evidence as to the plasticity of the plant and the manner in which heterospory may have originated in it.

Summary

1. It is possible by means of a spray of cold water to kill the megaspores of Marsilia, which occur only in the oldest sporangia, and then by putting the plant under good conditions to mature sporocarps without megaspores.

2. The greatest variations occur when the megaspores and the oldest microspores are blasted, and when strong plants develop a few sporocarps out of season.

3. Enlargement does not appear among the microspores when less than half the spores abort, and the surviving spores are larger the greater the amount of abortion.

4. The mother cells may be checked in their development till the tapetal nuclei completely invest them. A perinium will then form around the mother cell wall, which invests the four young spores. In such cases the sporangium invariably contains sixteen large forms each containing four nuclei. At other times, when growth is less checked, the spores are more or less completely free and show great variation in size and shape.

5. The contest for supremacy among the young megaspores of each sporangium is very evident, many of them assuming considerable proportions, but one, centrally located, invariably secures the ascendency. Sometimes the contest is very close between two or more members of the same tetrad. Very often the surviving member will carry attached to its papilla the aborted members even to germination.

6. The enlarged microspores vary in size, the largest being 8–16 times the size of the ordinary ones; the position of the nucleus changing from a central (usual) to an apical one, as in the megaspores. As vacuolation is more extensive, the shape of the nucleus also varies from the usual spherical form to the oval, and finally in the largest to the meniscus shape, as in the megaspore.

7. In extreme cases of abortion in the microsporangia only one spore survives, which is about 16 times as large as the normal microspore. The aborted tetrads remain as in the megasporangium, but are much larger and better developed, thus showing a sharper and more prolonged contest for supremacy.

8. In plants kept from sporocarp-formation until September 10, many microsporangia developed secondary megaspores, so called because they are formed after the first or primary ones. Such megaspores are intermediate in size and are also more nearly the spherical shape of the microspores.

9. A few cases were noted in which the megaspores did not

develop a perinium, but enlarged considerably and became gorged with starch.

10. In the normal plants, and in all cultures, a close examination reveals a homosporous tendency, shown by the formation of microspores in the megasporangia, especially in those most distant from the nutritive supply.

11. Marsilia may be made to repeat, under culture, all the phases in the development of heterospory reported by WILLIAMSON and SCOTT for *Calamostachys Binneyana* and *C. Casheana*, and in addition to produce a megaspore of intermediate size.

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EXPLANATION OF PLATES III–VI

All drawings were made with a Spencer camera lucida. In all drawings showing nuclear detail a Zeiss 2^{mm} apochromatic objective with compensating oculars was used. The drawings and photomicrographs were then reduced to the magnifications indicated in the explanation of figures.

PLATE III

Fig. 1.—Diagrammatic sectional view of sporocarp; *A*, *B*, *C*, *D* designate planes; *C′*, soral pad attached to vascular bundle and subtending a single sorus. ×7.

Fig. 2.—Portion of a section showing three sporangia of the oldest series (right) containing megaspores, and one (left) containing microspores. ×40.

FIG. 3—Young sporangium, showing 8 of the 16 mother cells in synapsis, just as the tapetum begins to form the plasmodium. ×292.

FIG. 4.—Older sporangium, showing tetrads with the tapetal plasmodium dispersed among them. ×292.

FIG. 5.—First stage in which one can determine that the sporangium is to contain megaspores; several spores are enlarging, but the mass of tapetal nuclei is collected about the larger one in the center. ×292.

FIGS. 6–10.—Showing the competition among the members of the tetrad and the persistence of the three aborting members through the various stages of megaspore formation; they are often evident even after germination, as shown in *fig. 10a*. *Figs. 6, 7, 8, 9*, ×300; *10b*, ×85.

PLATE IV

FIG. 11.—Photomicrograph showing the aborted members of the tetrad still attached to the papilla of mature megaspore. ×85.

FIG. 12.—Diagrammatic representation of fruiting rhizomes, showing the effect of varying the depth of water when the plants are in such subdued light as to be just able to produce sporocarps; *b*, blasting; *m*, maturing.

FIG. 13.—Condition of various sporangia of a sorus during the process of blasting; *a*, old aborted microsporangium, megasporangium in the center; *b*, *c*, young microsporangia from same sorus.

FIG. 14.—*a*, normal microsporangium; *b*, sporangium in which the 16 mother cells have not formed walls during the tetrad divisions; *c*, same in section; *d*, sporangium with extensive abortion, a few of the surviving spores enlarged.

FIG. 15.—Portion of a section of a sporocarp in which all the megaspores have aborted, as shown by the empty megasporangia, *m;* in the microsporangia no walls have been formed in the tetrad divisions, so that each sporangium contains but 16 enlarged and irregular bodies instead of the usual number of 64 spherical spores. ×55.

FIGS. 16, 17.—Single entire sporangia, showing the 16 bodies as in *figs. 14b*, and *15*. ×105.

FIG. 18.—Three sections, *a*, *b*, *c*, of various bodies from sporangia as in *figs. 16, 17*, showing nuclear structure and behavior. ×400.

PLATE V

FIGS. 19, 20.—Similar to *fig. 18*; forms more irregular. ×400.

FIG. 21.—Microspores resulting from tetrads which have had varying success in forming walls during the second division, due to unfavorable conditions of growth. ×133.

FIG. 22.—Nuclear structure and behavior in earlier stages of such microspores. ×400.

FIG. 23.—A normal microsporangium at maturity, containing 64 spores. ×95.

FIGS. 24, 25.—Microsporangia in which many of the microspores have aborted, showing at maturity a number of normal spores and a single enlarged microspore. ×95.

FIG. 26.—More complete abortion of microspores, with four enlarged. ×95.

FIG. 27.—Same more highly magnified.

PLATE VI

FIG. 28.—Microsporangium showing a few remaining but abortive tetrads, and only one (much enlarged) microspore. ×95.

FIG. 29.—Same more highly magnified.

FIGS. 30, 31.—Sectional views showing internal and external transitions from the ordinary spherical microspore, which has a central nucleus and no vacuolation, toward the megaspore form and condition; *fig. 30* shows an enlarged, spherical, but vacuolated spore, with spheroidal nucleus laterally placed; *fig. 31*, a more enlarged, spheroidal spore, more vacuolated, with meniscoid nucleus apically placed. ×180.

FIG. 32.—Section of sporocarp showing primary (*p*) and secondary (*s*) megaspores, as determined by age, position, size, and stage of wall formation. ×33.

FIG. 33.—Same showing three primary (*p*) and two secondary (*s*) megaspores, and one megasporangium, *m*, containing microspores. ×33.

FIG. 34.—Same, showing one central and one lateral section of primary megaspores, *p*, and six secondary megaspores, *s*. ×33.

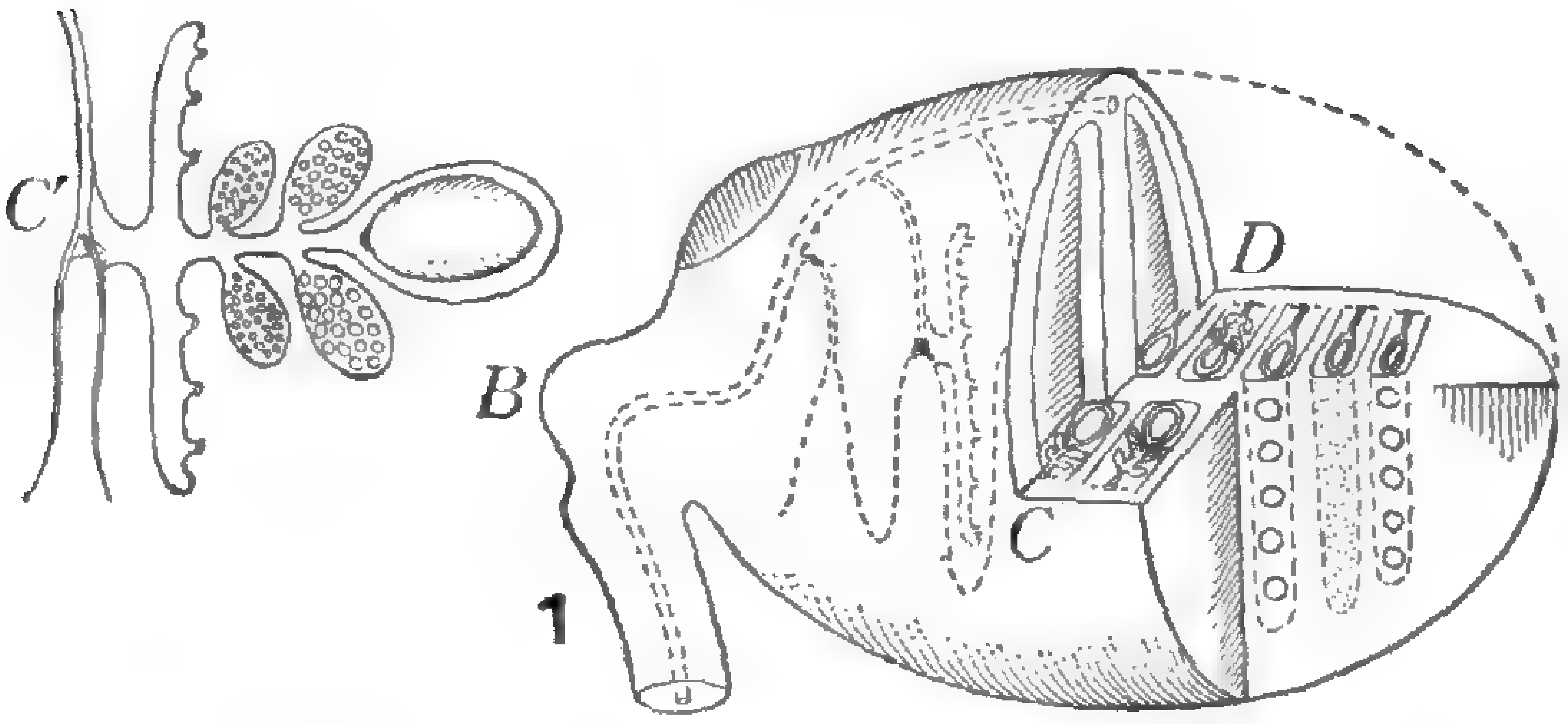
FIG. 35.—Same showing two primary (*p*) and two secondary (*s*) megaspores, and one primary megasporangium, *m*, containing normal and aborting microspores. ×33.

FIG. 36.—Primary and secondary megaspores more highly magnified; the secondary megasporangium showing three sets of tetrads in which one of the spores in each set has enlarged and become vacuolated (not marked in the figure), thus competing sharply with the functioning megaspore, *s*, for supremacy. ×87.

FIG. 37.—Primary megasporangium, *n*, containing microspores nearly mature, one of the oldest microsporangia, *o*, containing a young secondary megaspore, the same age as that shown in *fig. 36;* the microspores are the same age as the primary megaspore in *fig. 36*. ×87.

FIGS. 38–43.—Variation in size and shape between the primary (*p*) and the secondary (*s*) megaspores at maturity. ×44.

FIGS. 44, 45.—Enlarged megaspores packed full of starch grains, but having no perinium. ×44.



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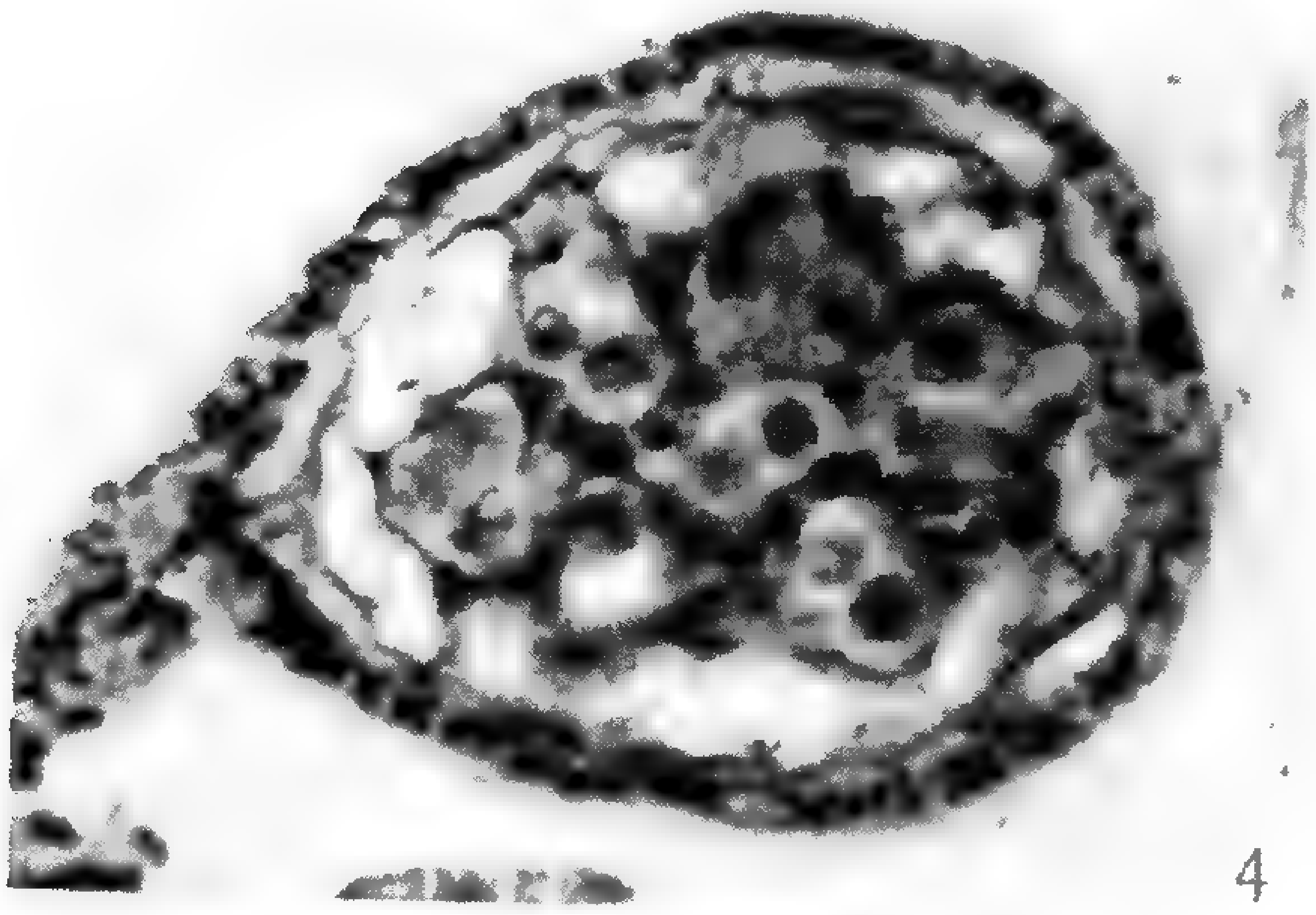

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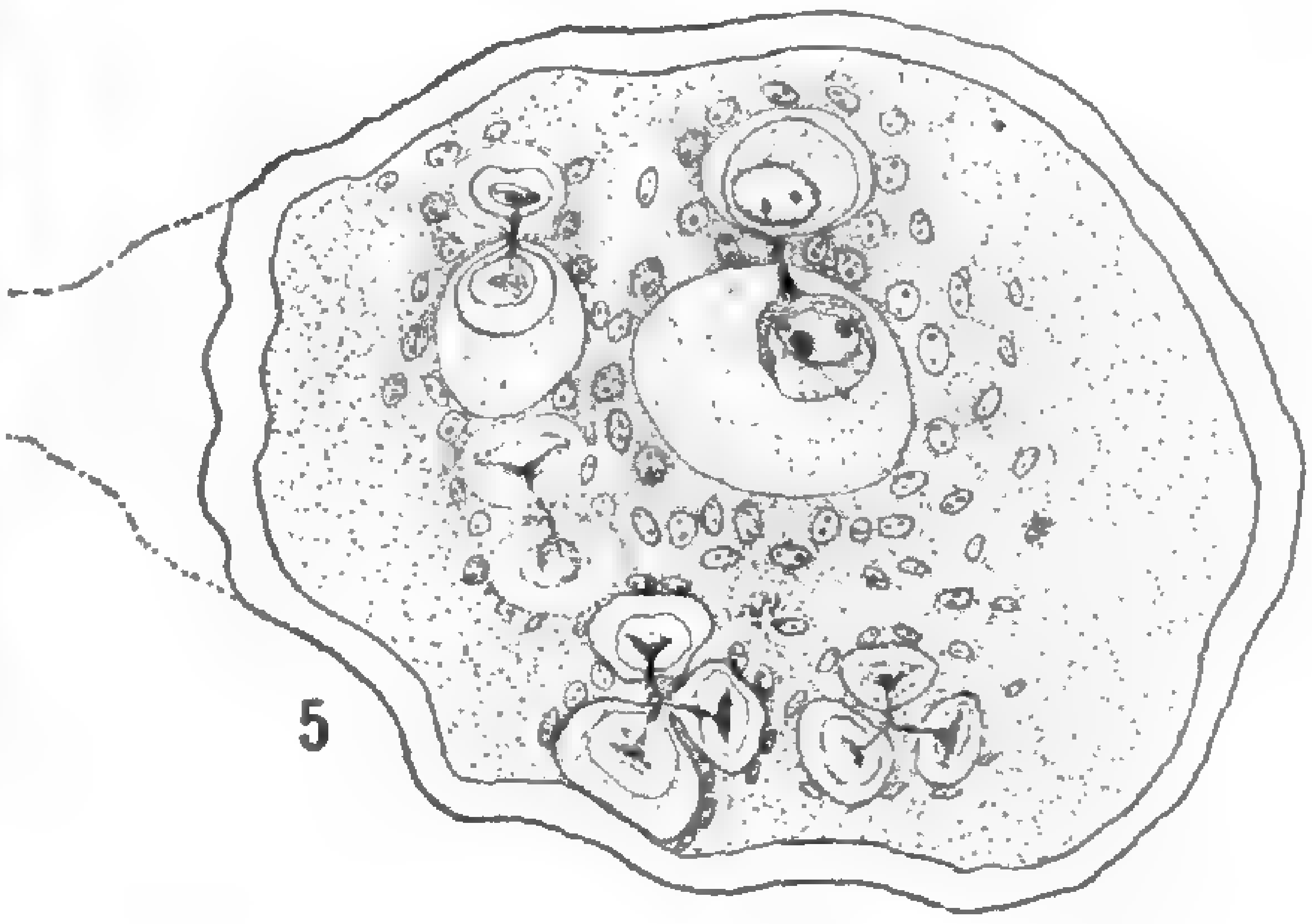

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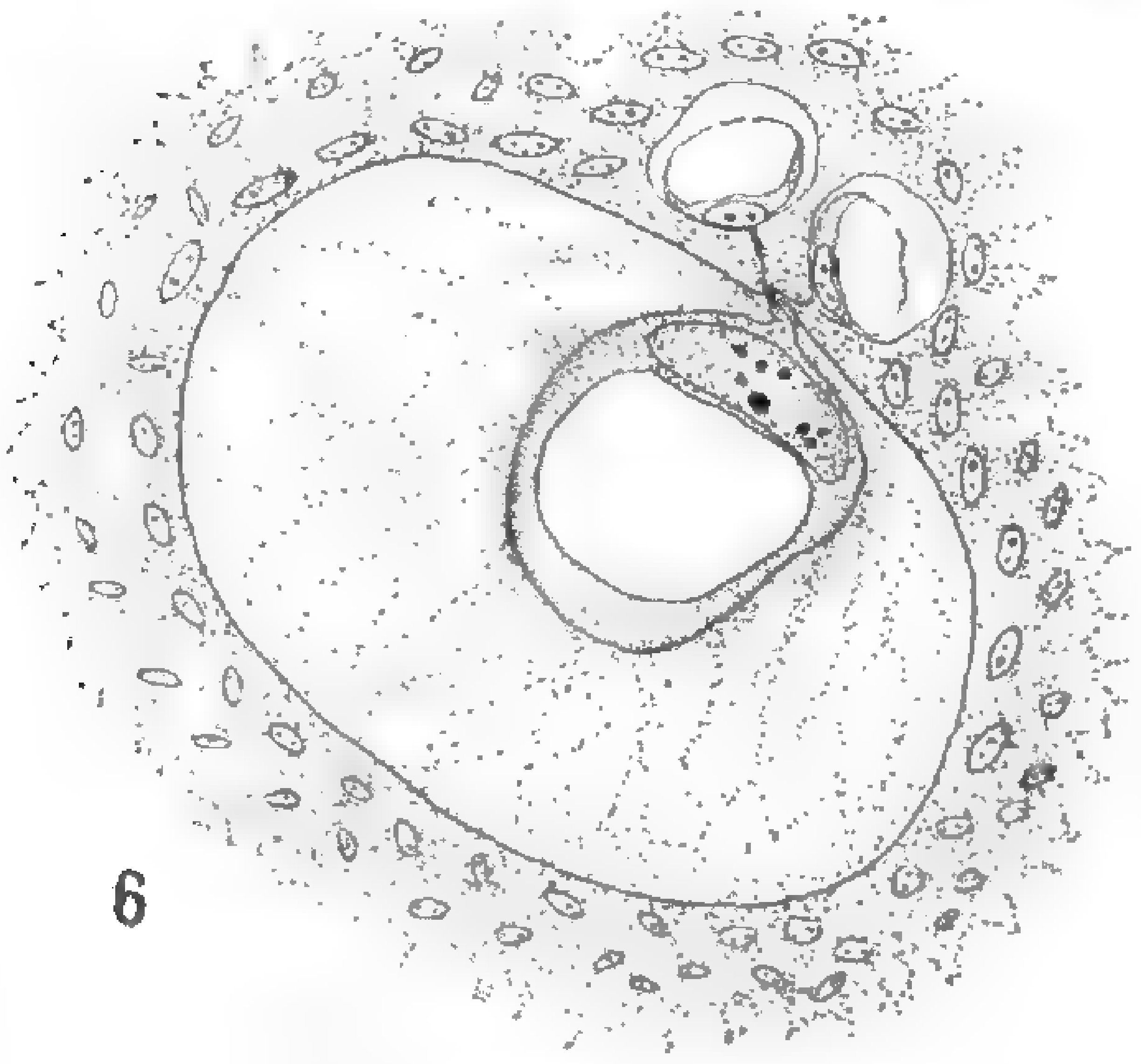

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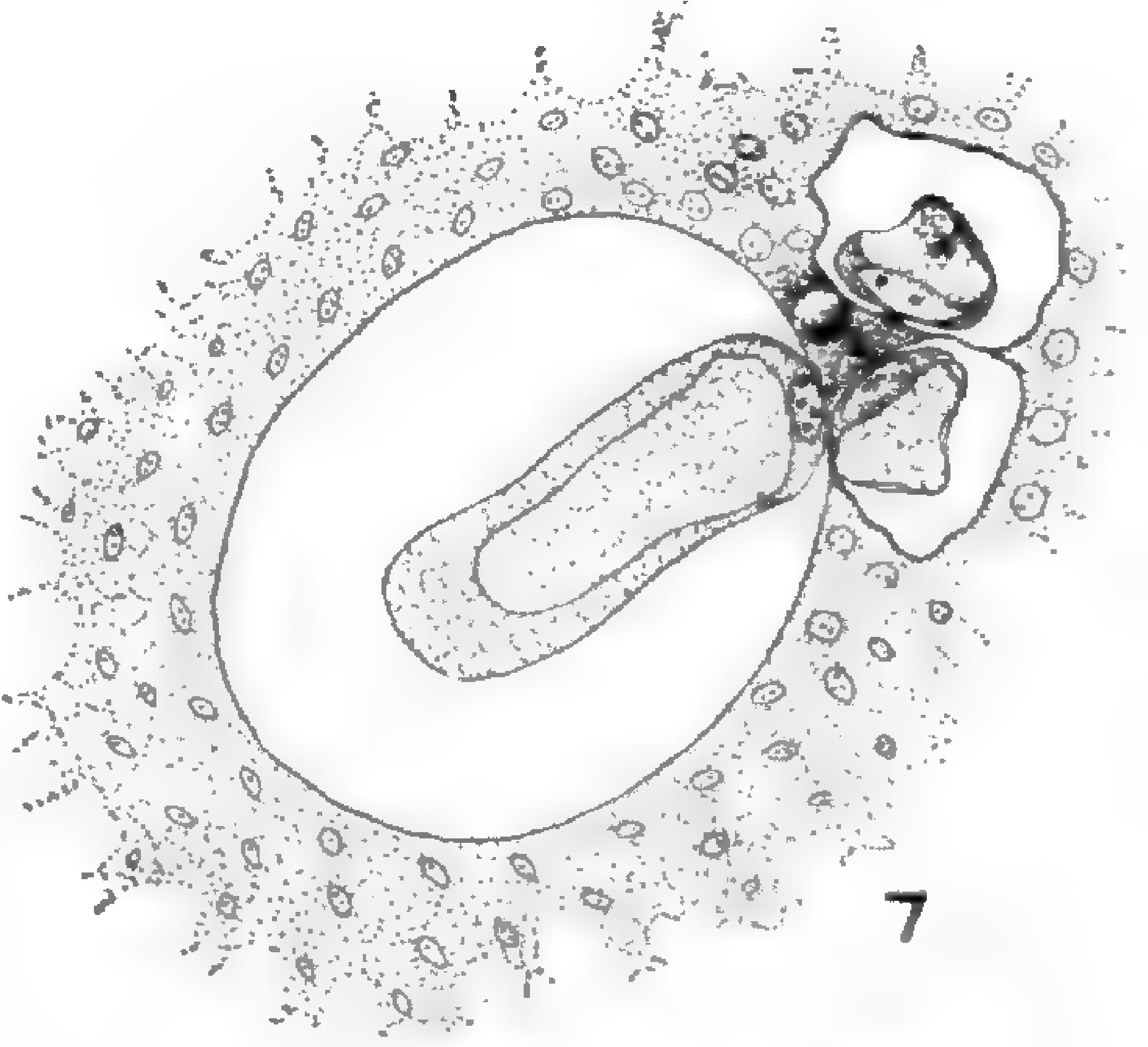

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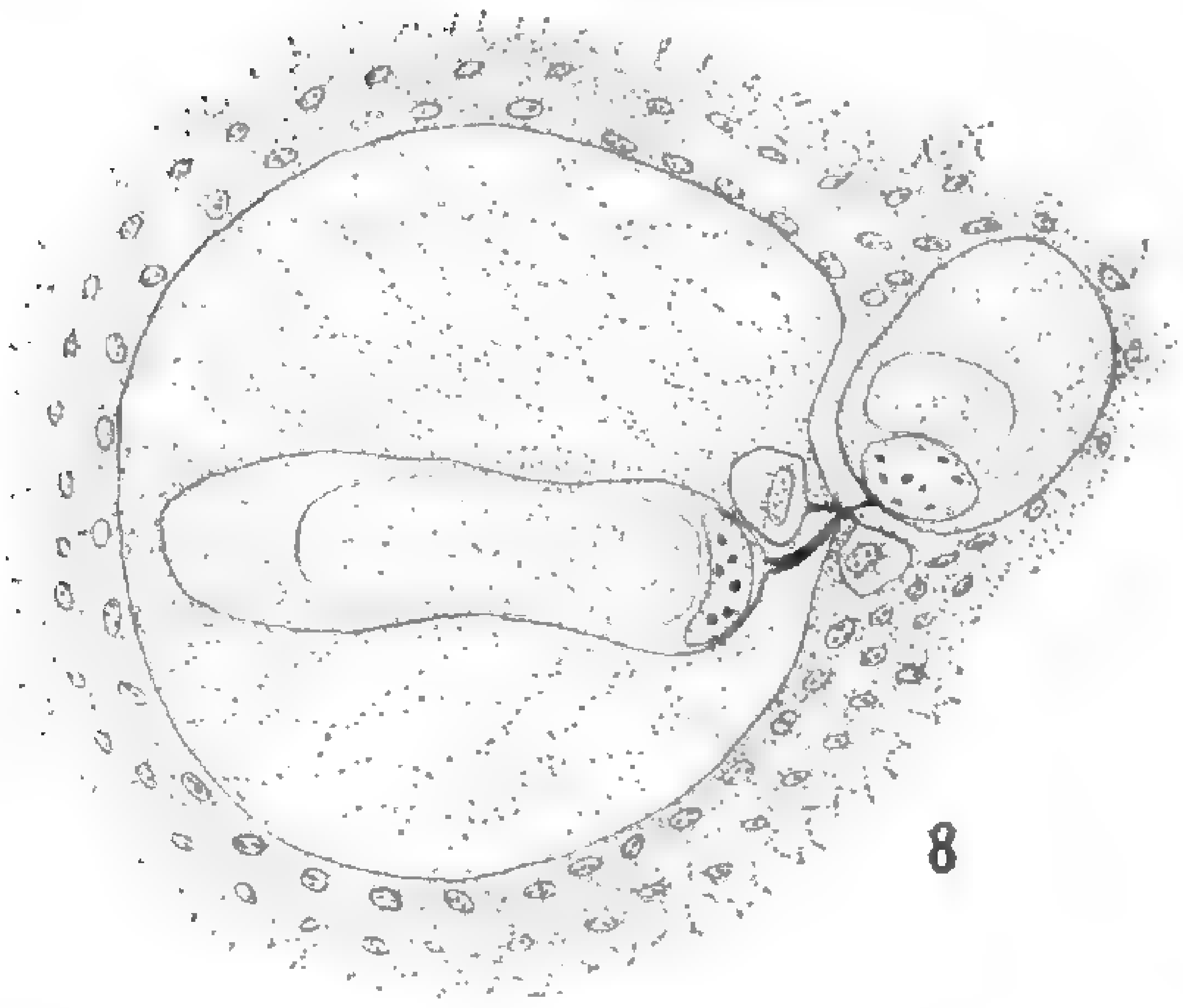

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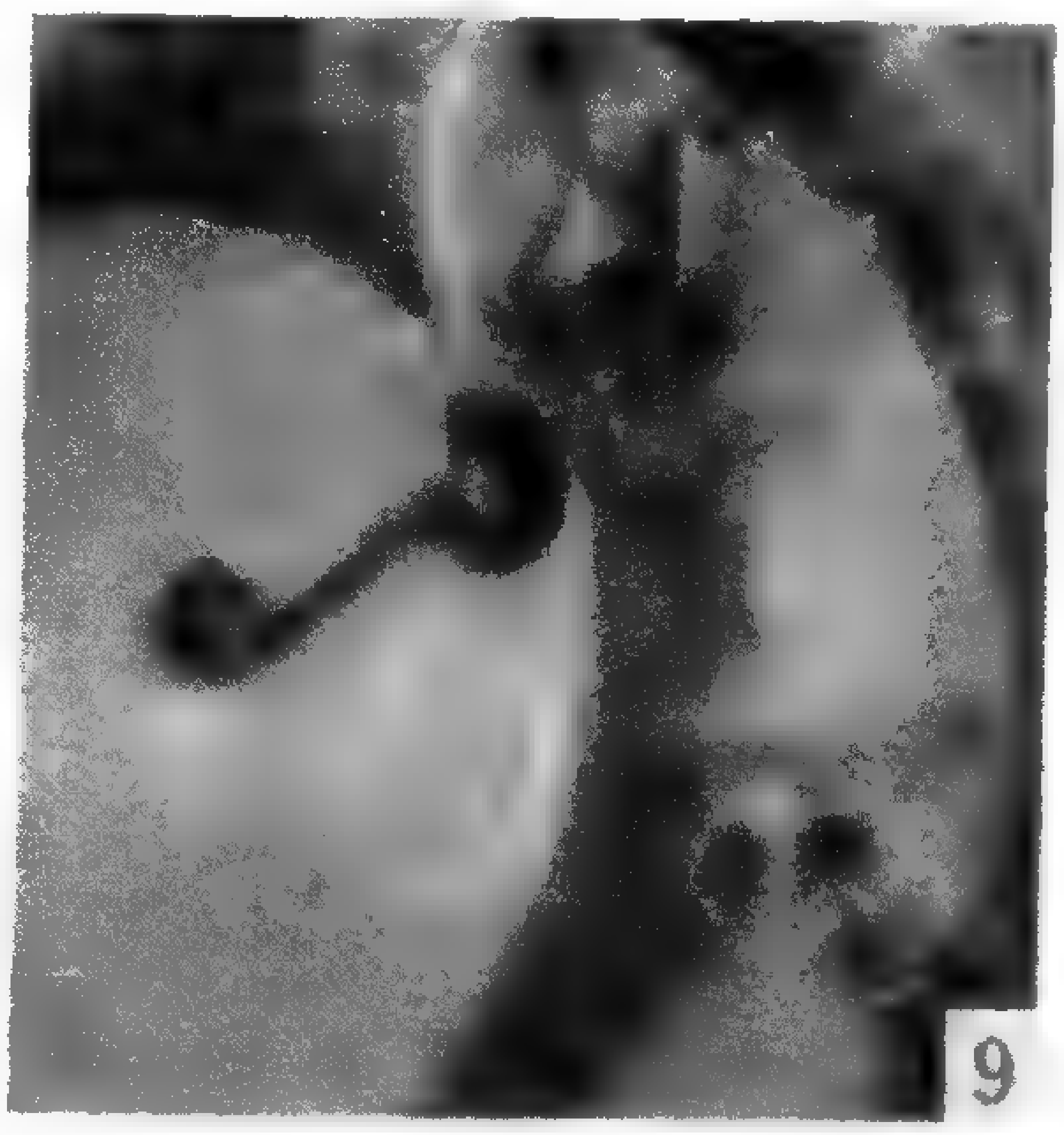

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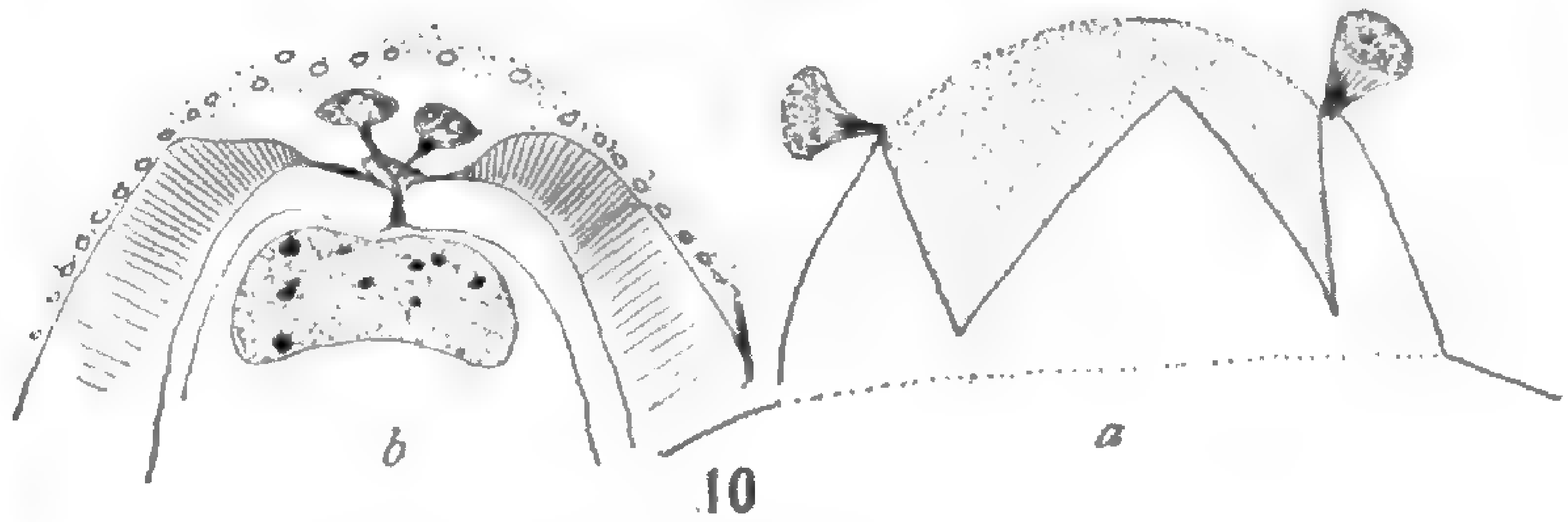

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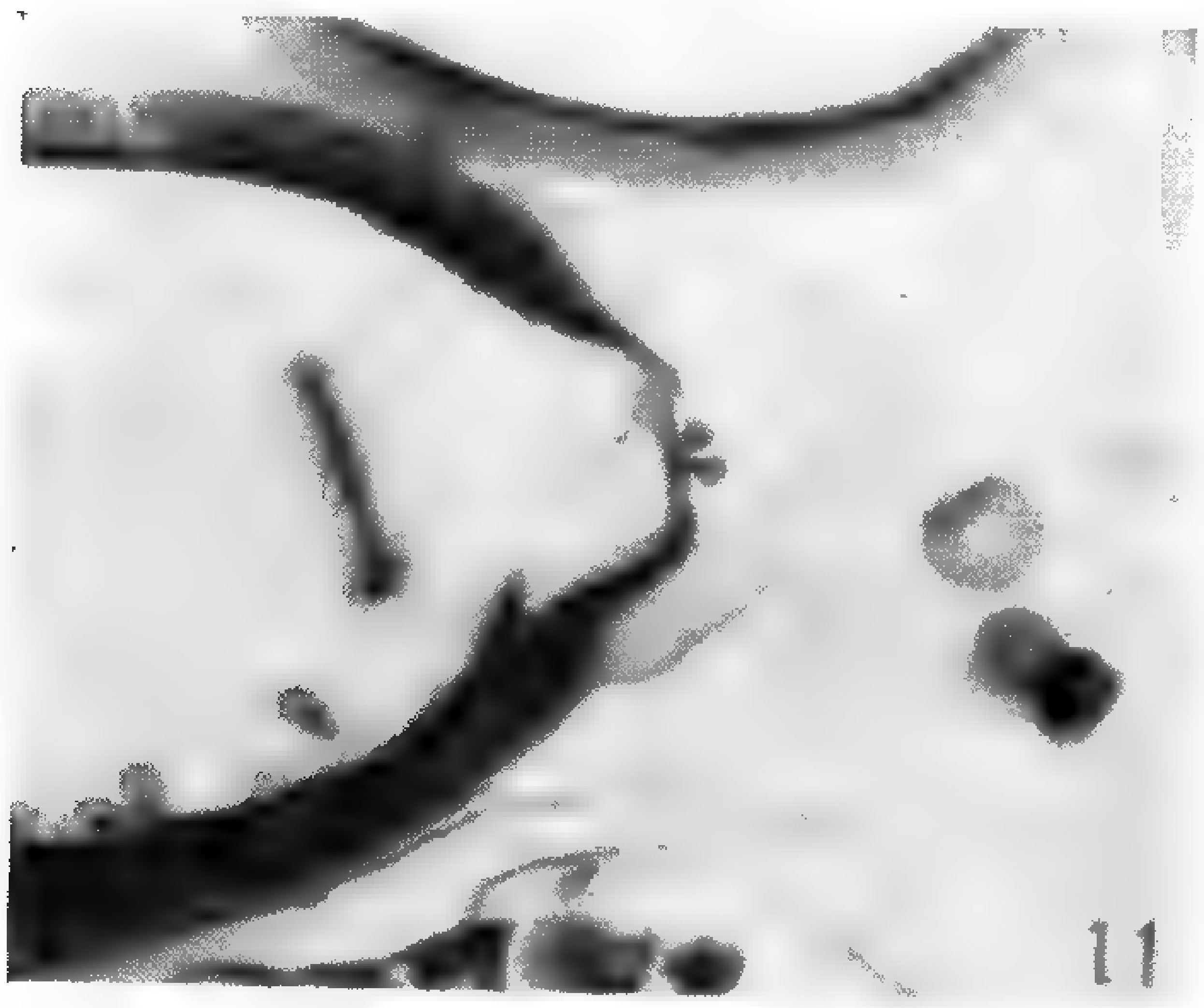
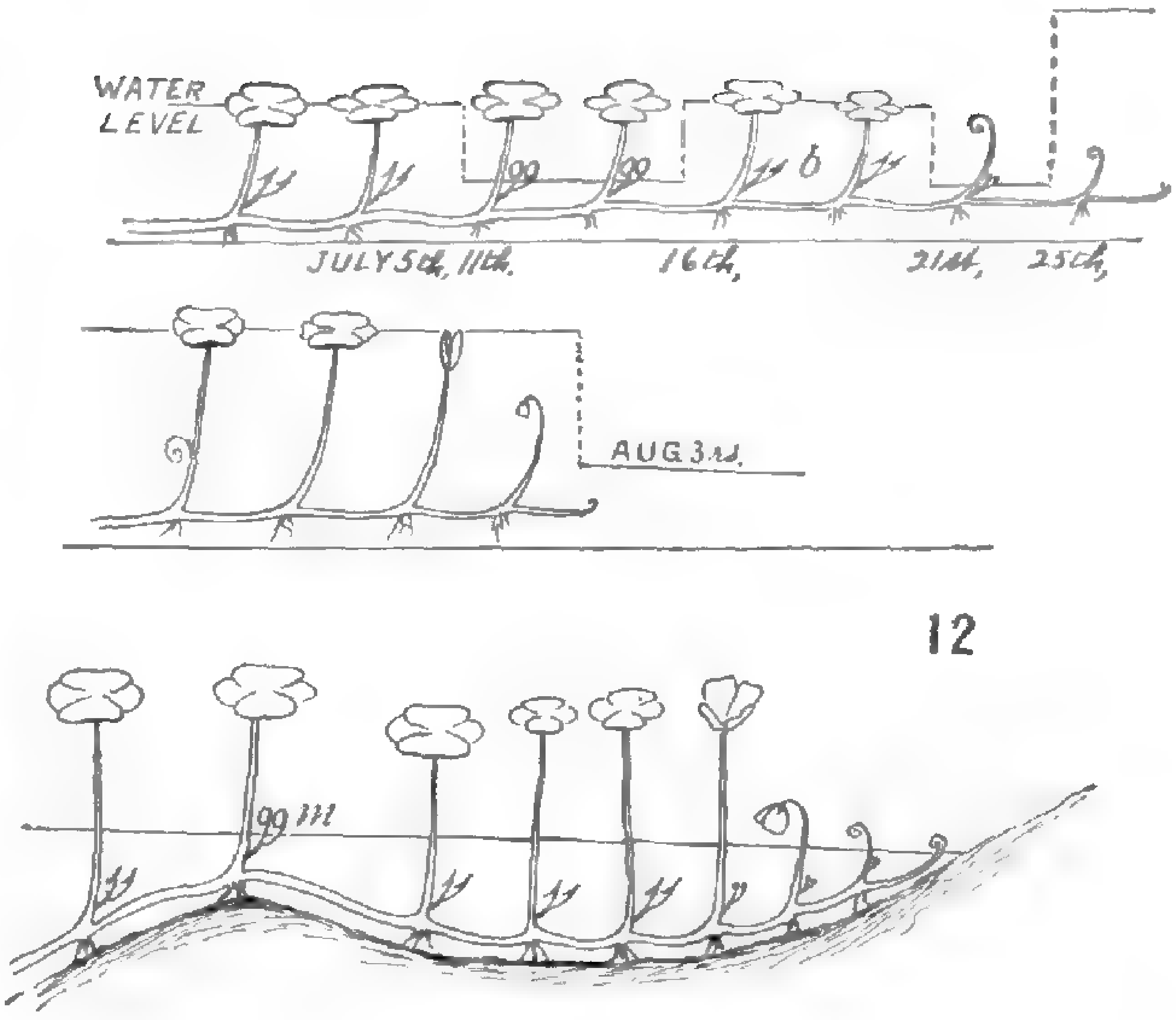
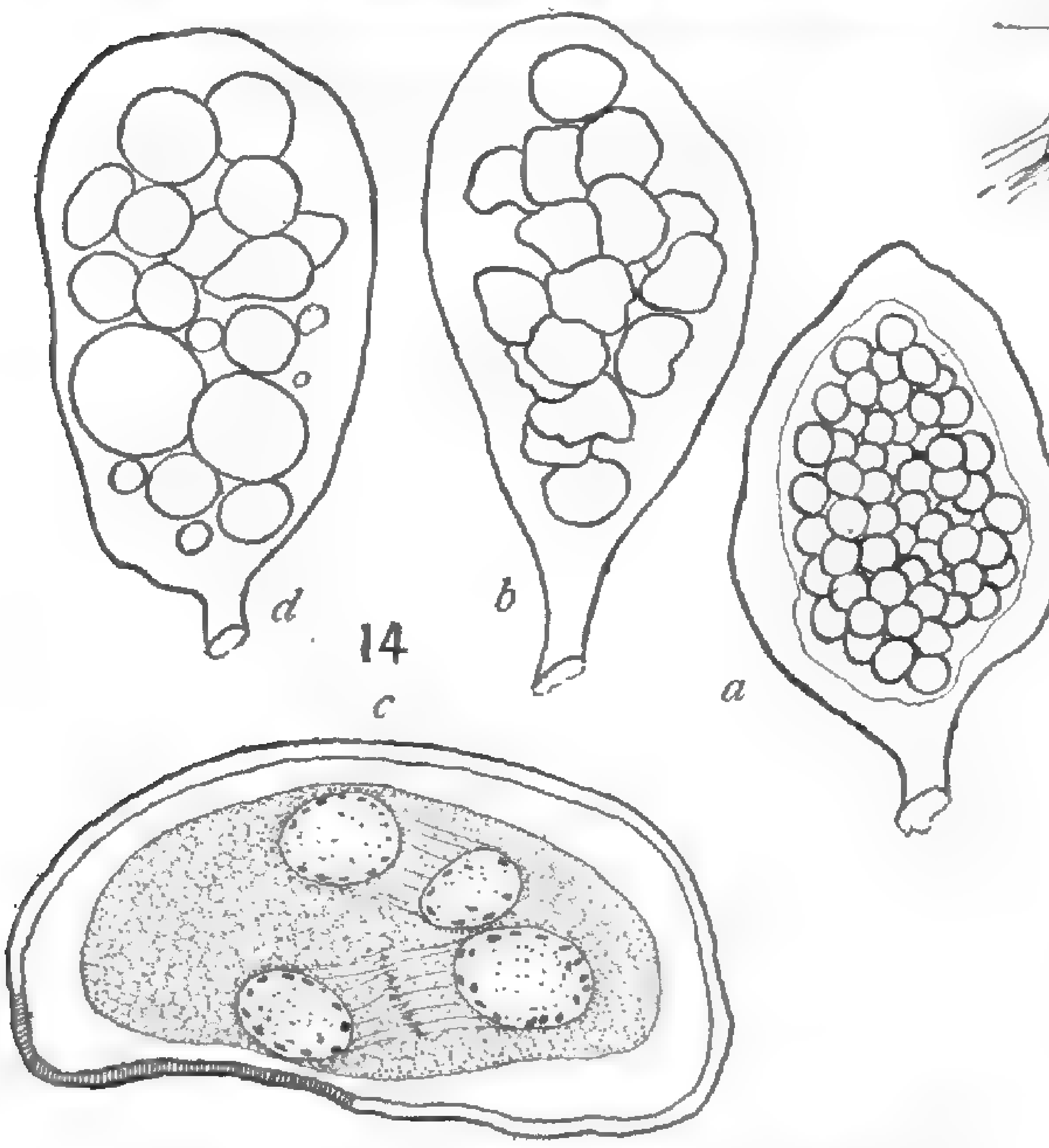
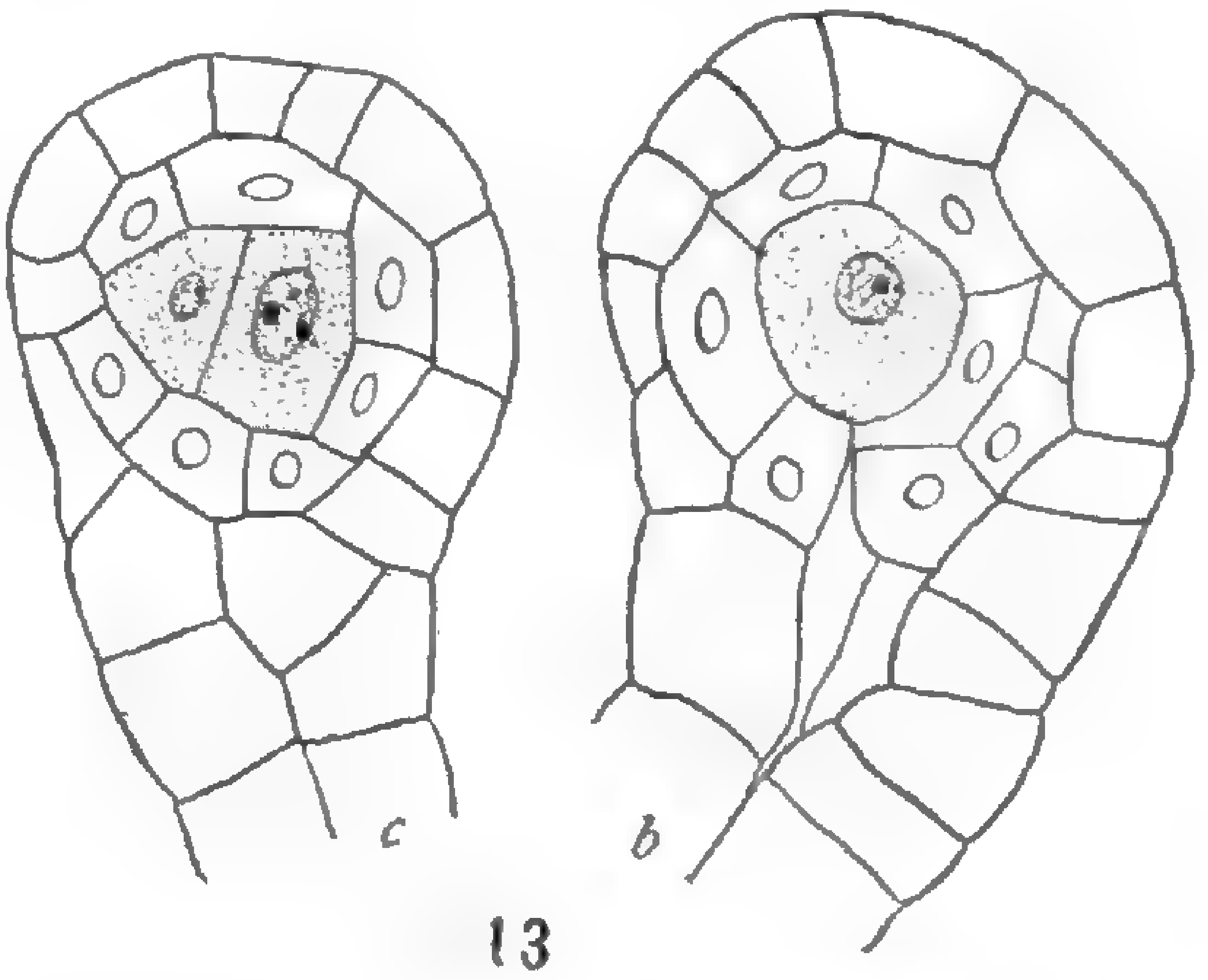
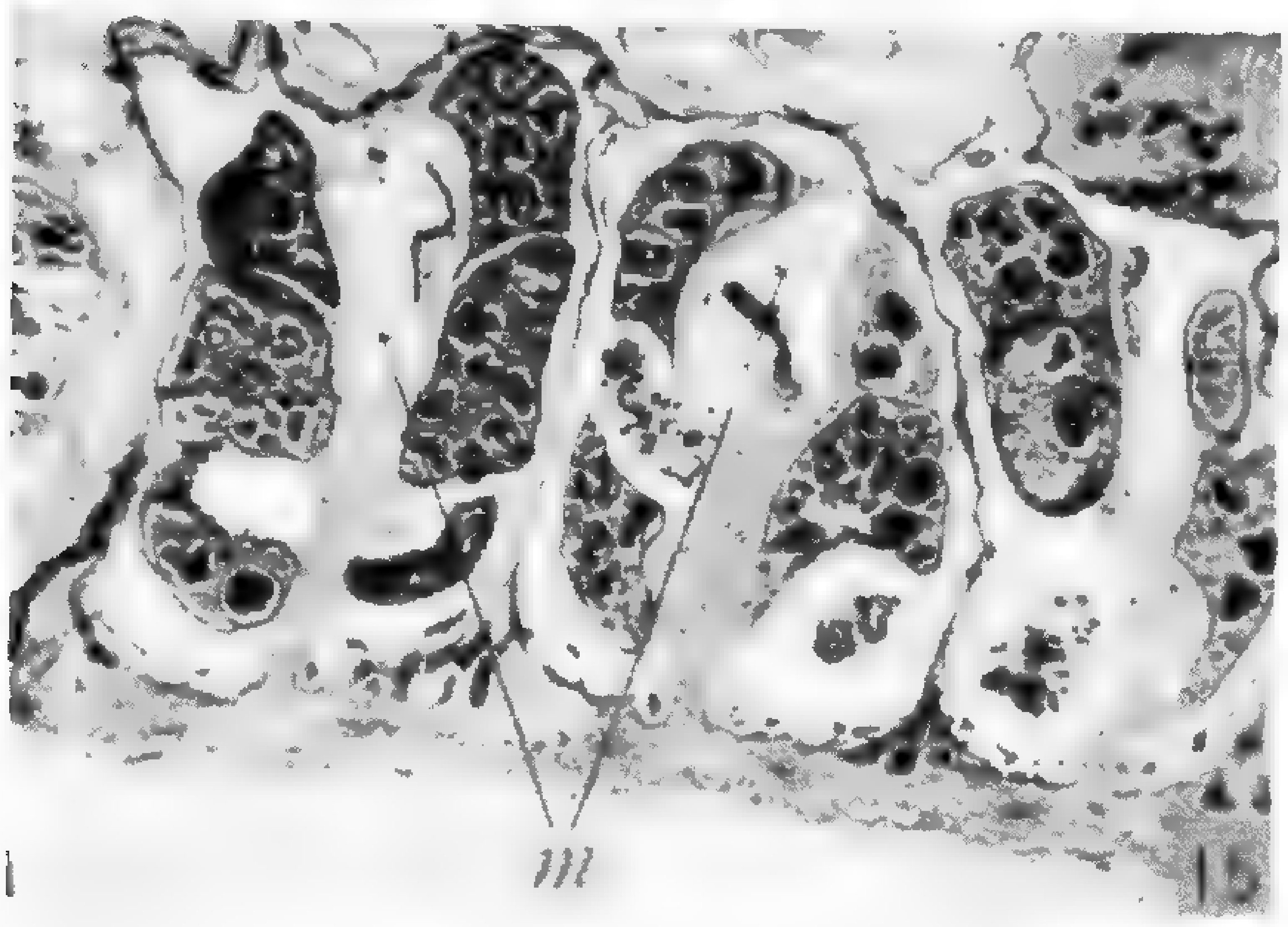
SHATTUCK on MARSILIA

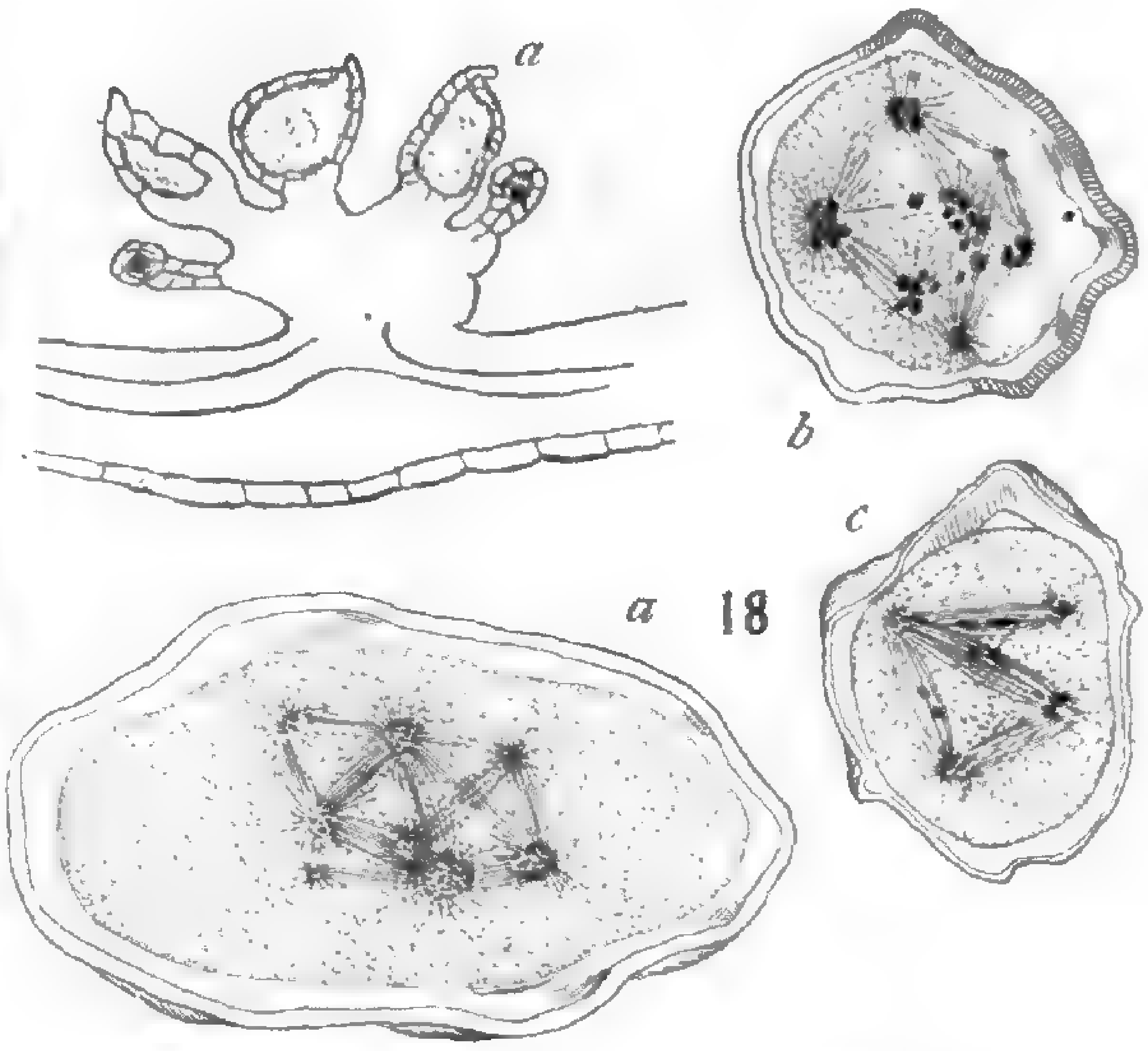


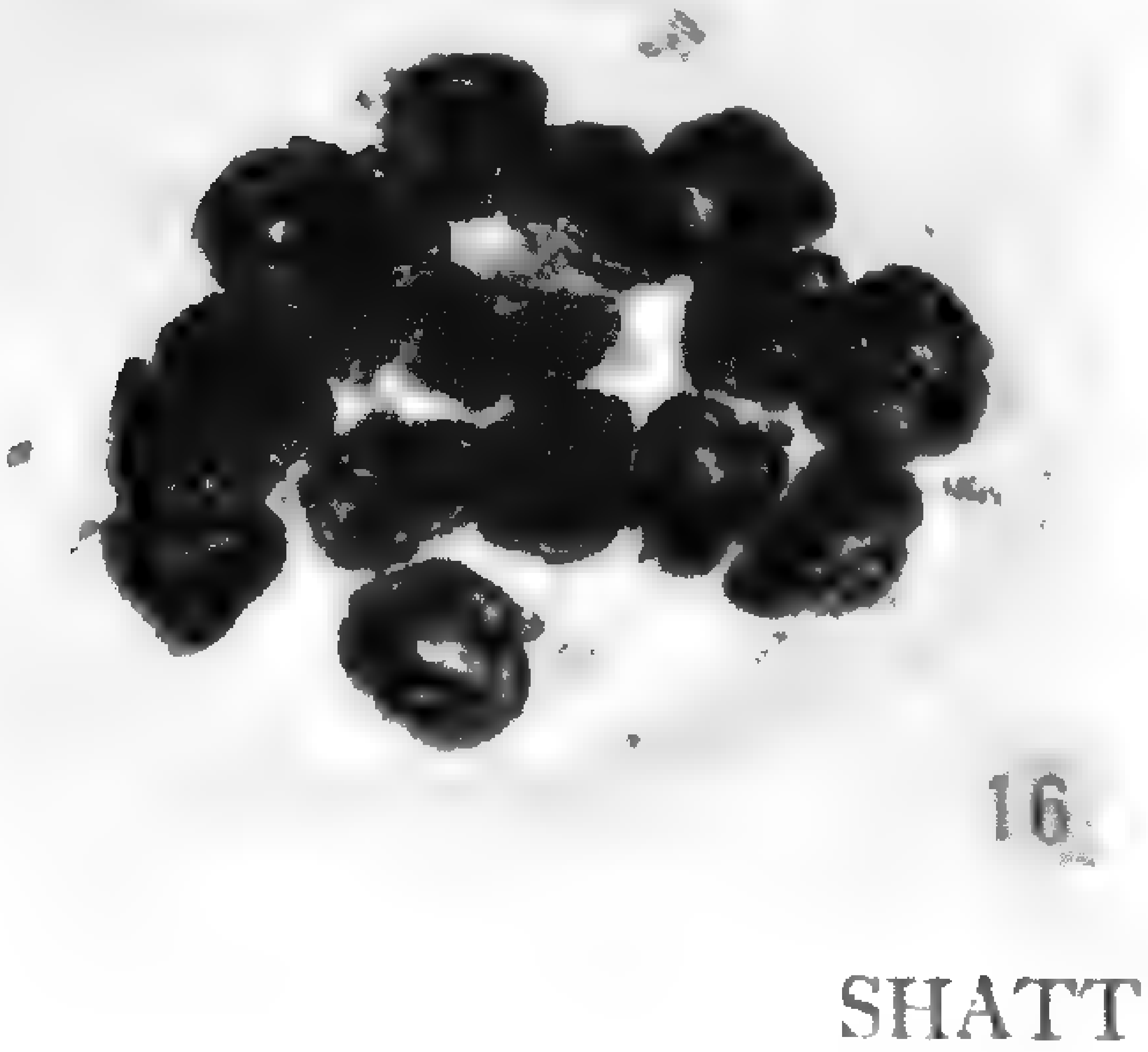


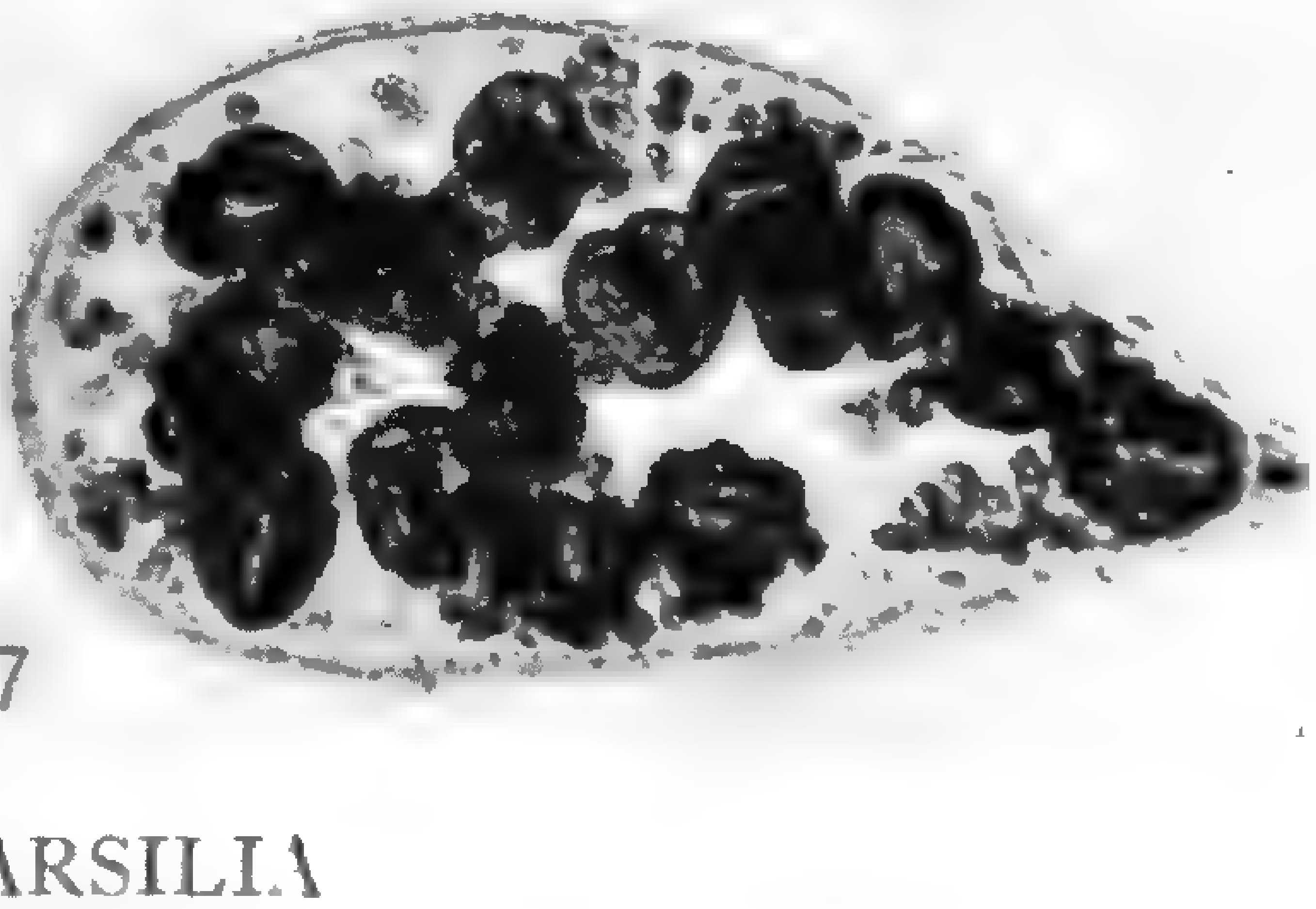












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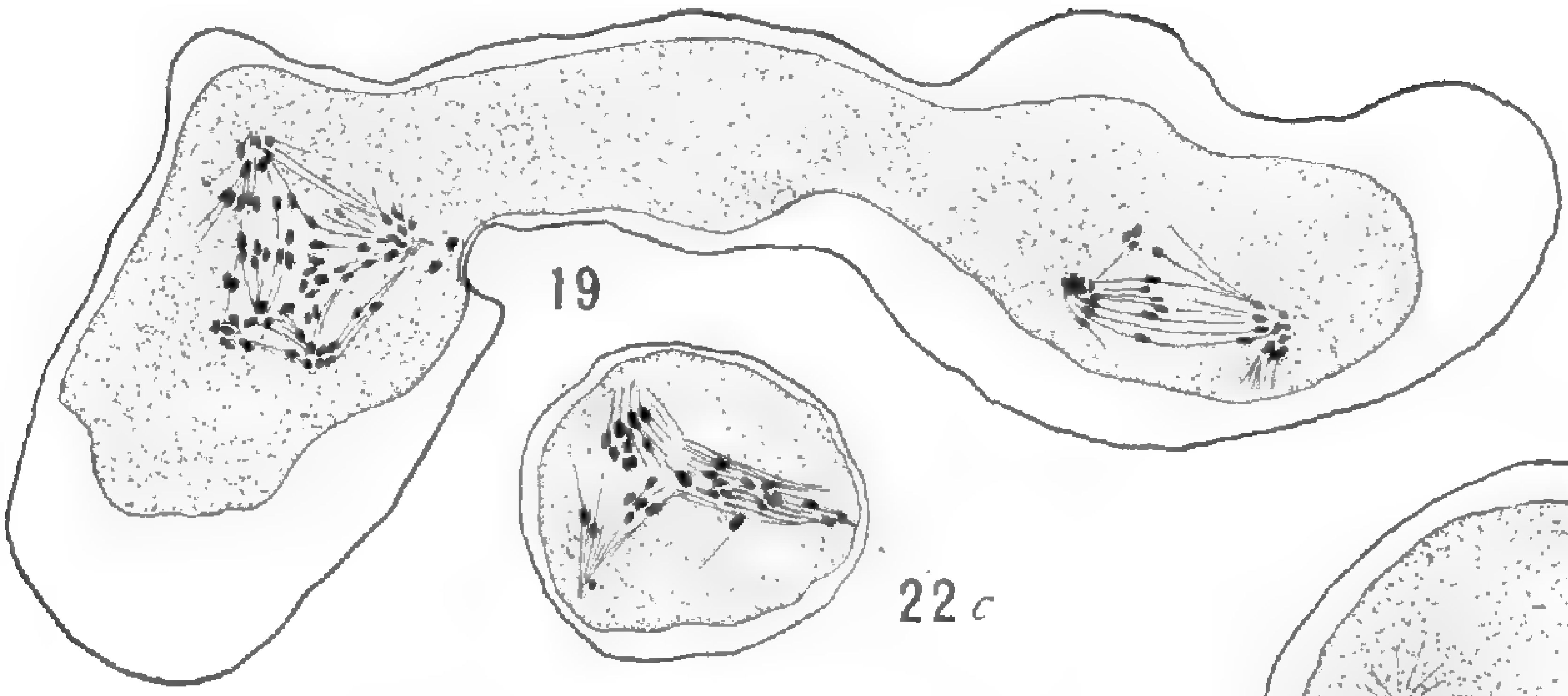

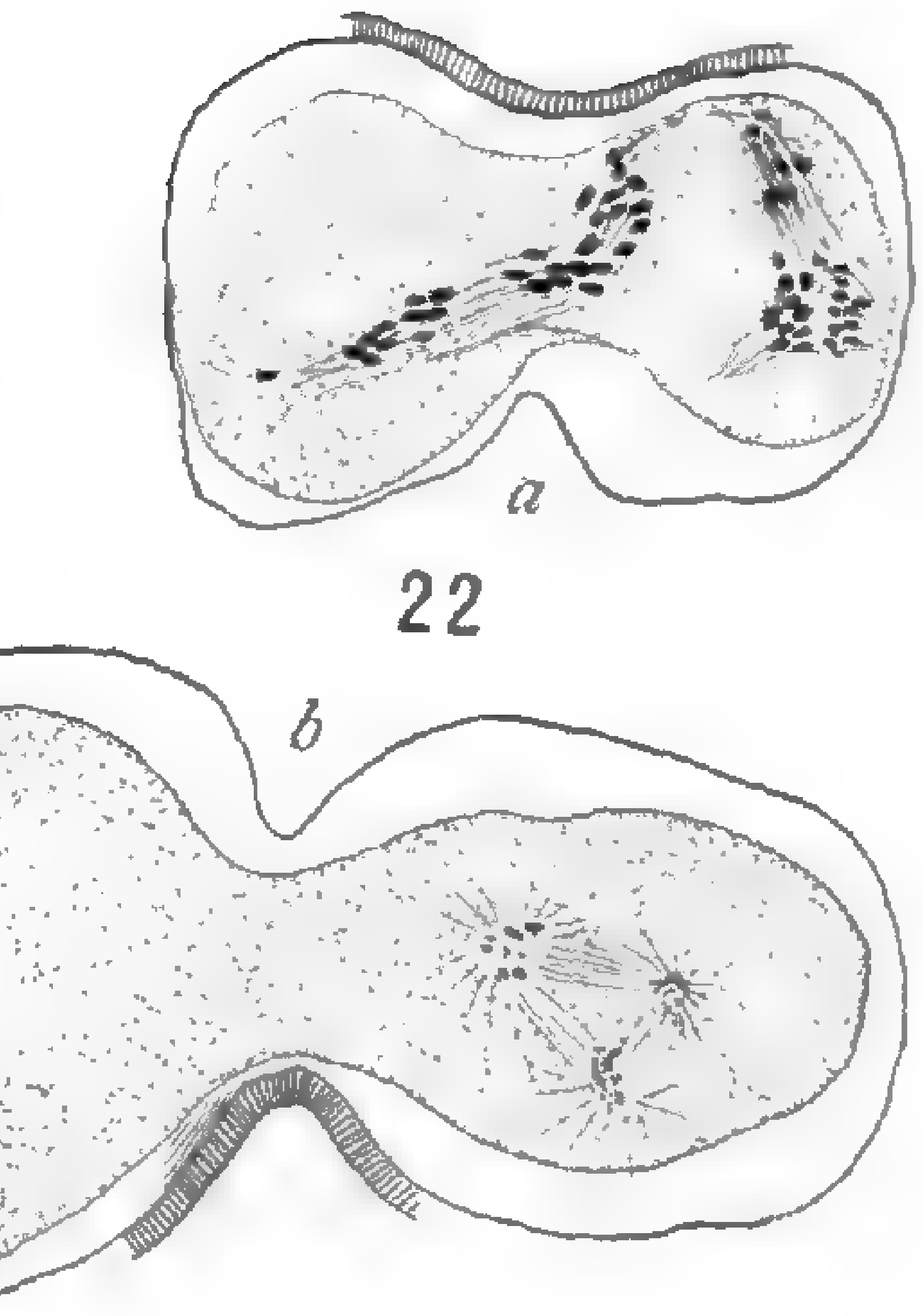

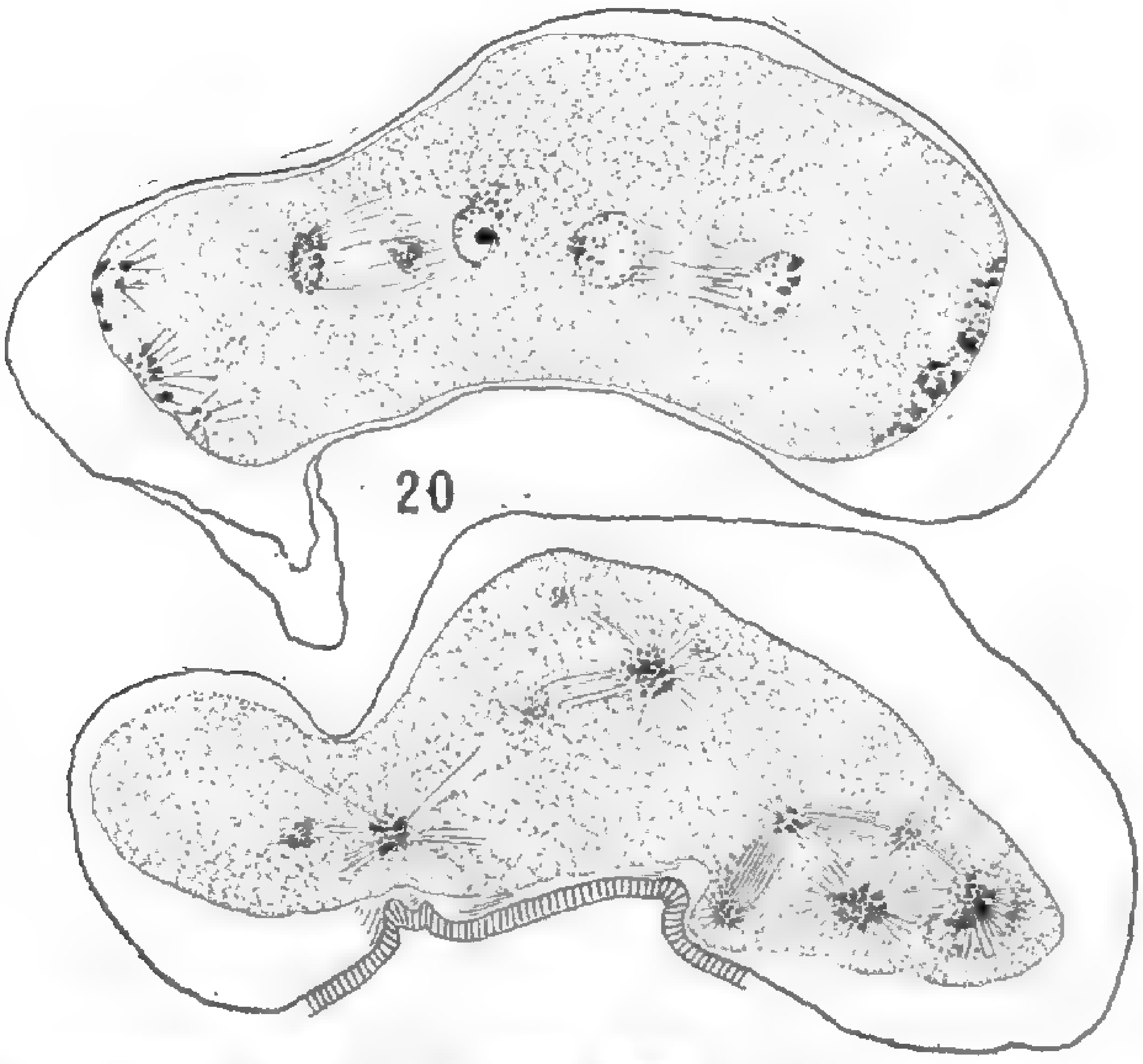

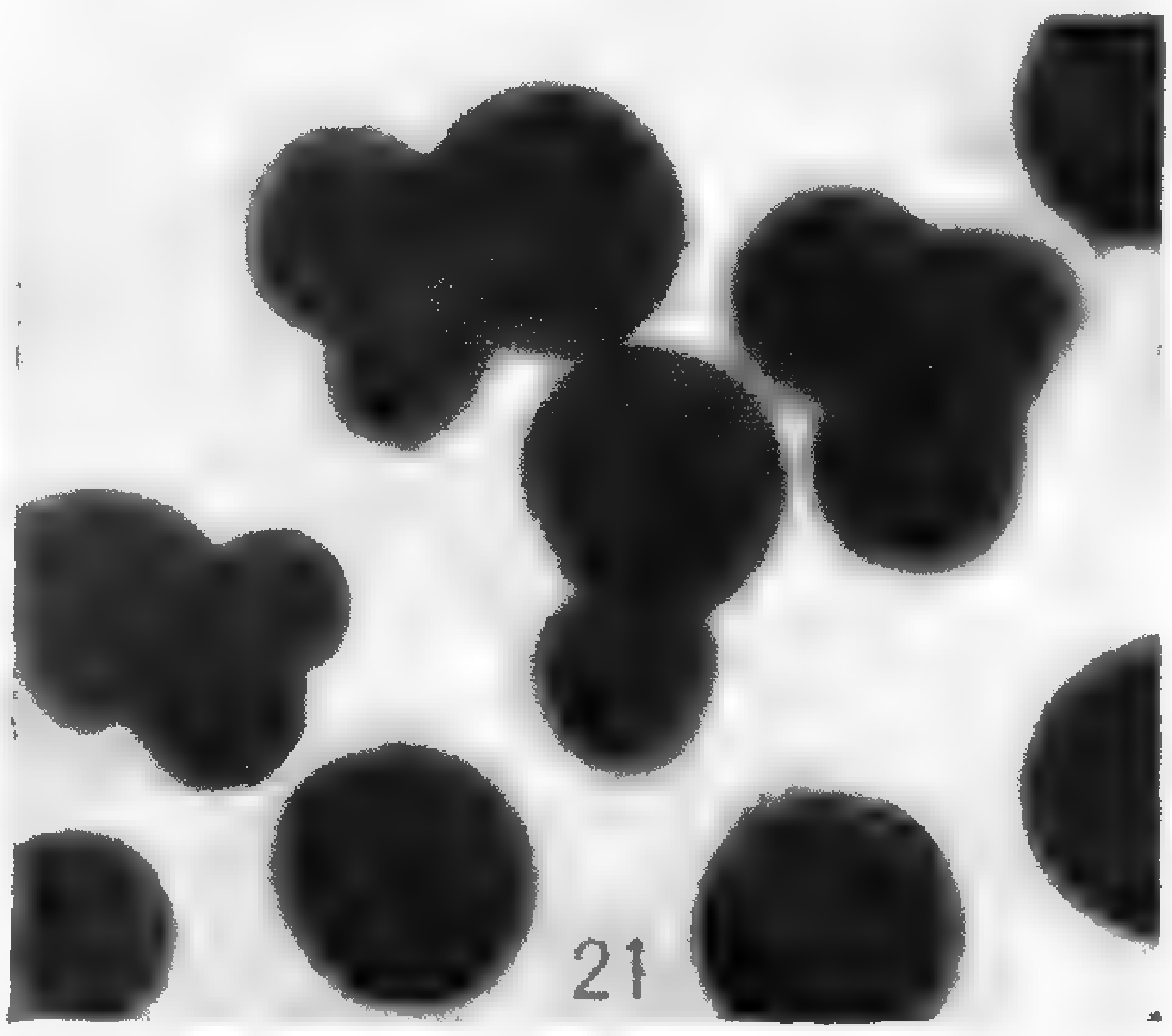


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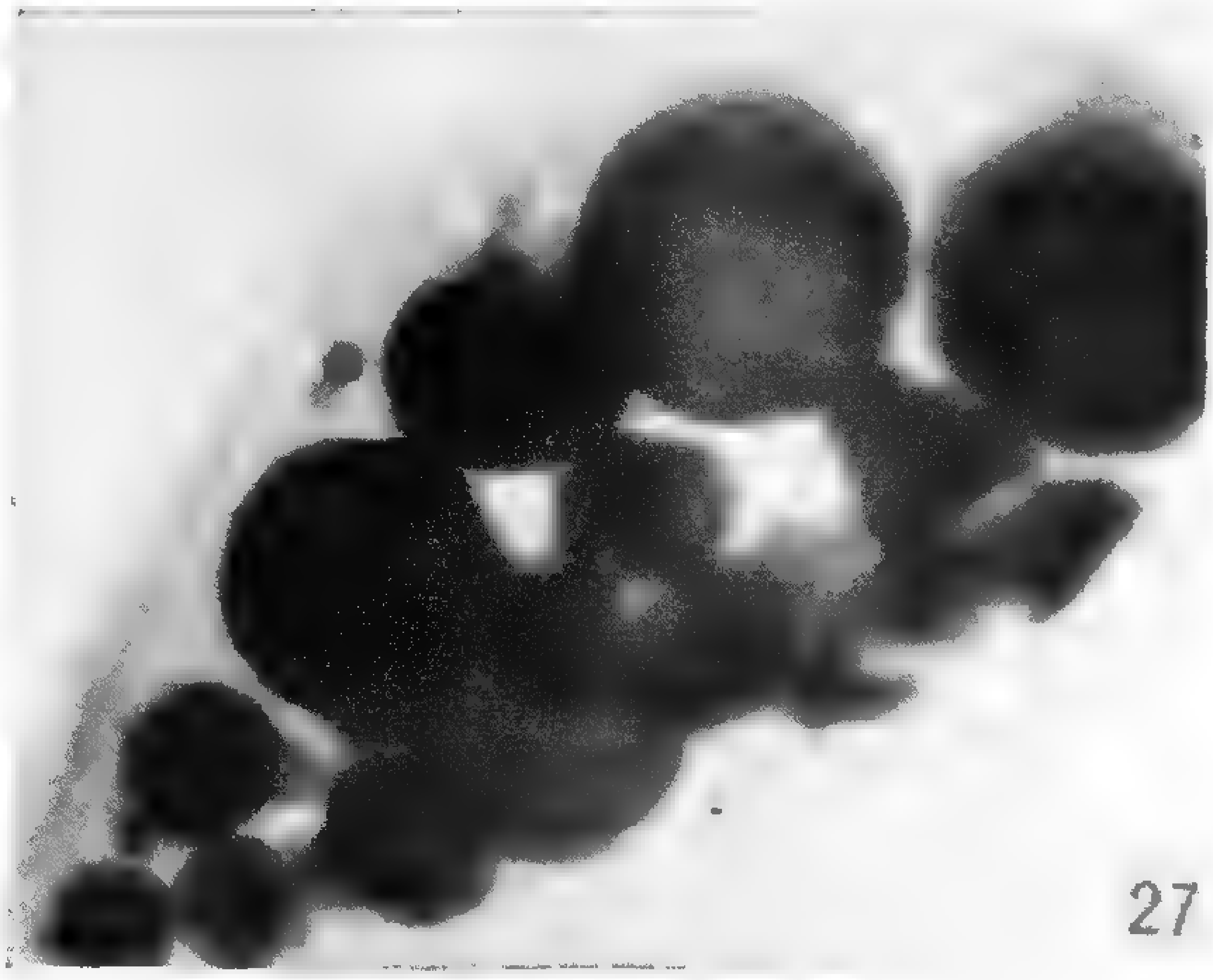

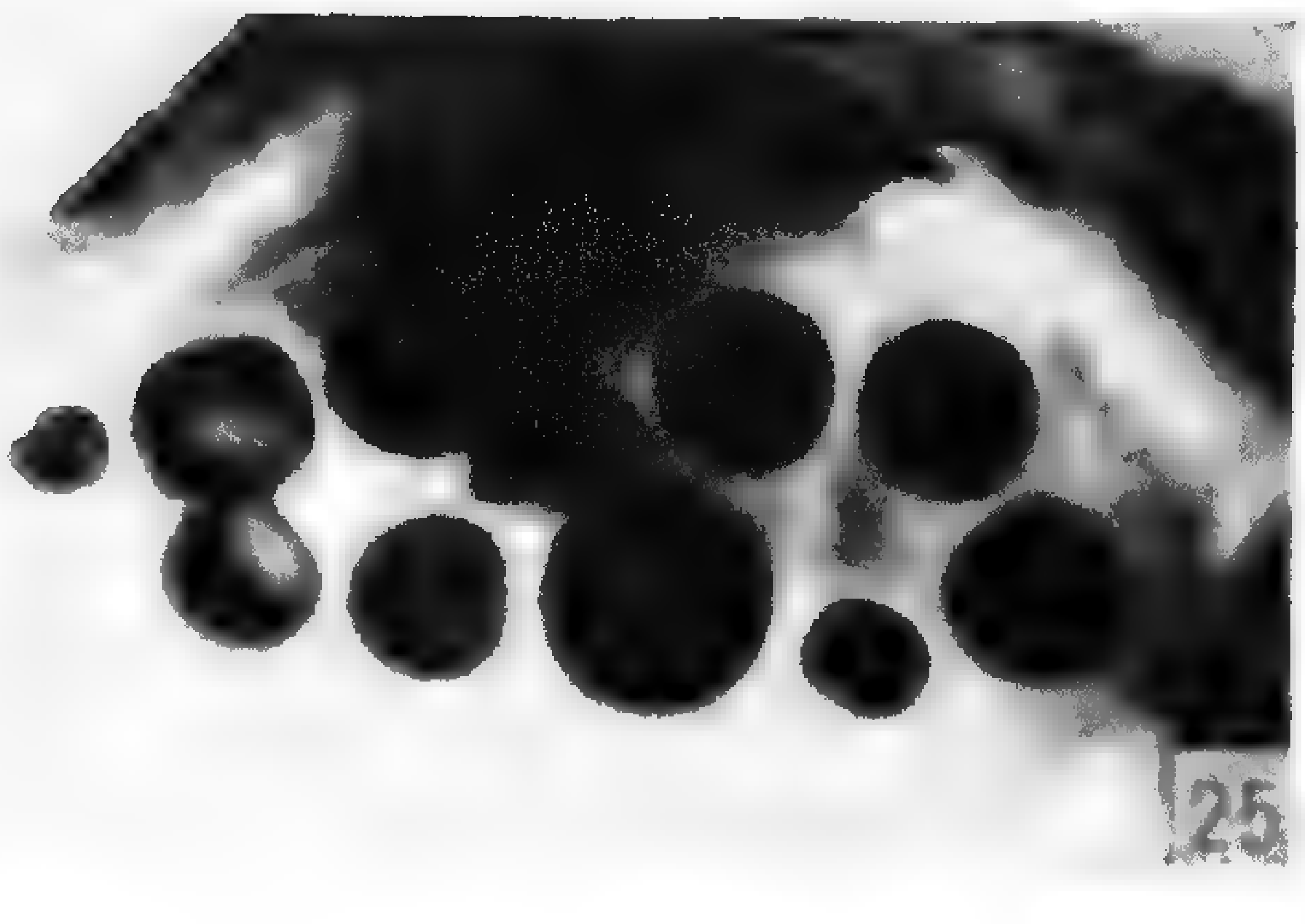

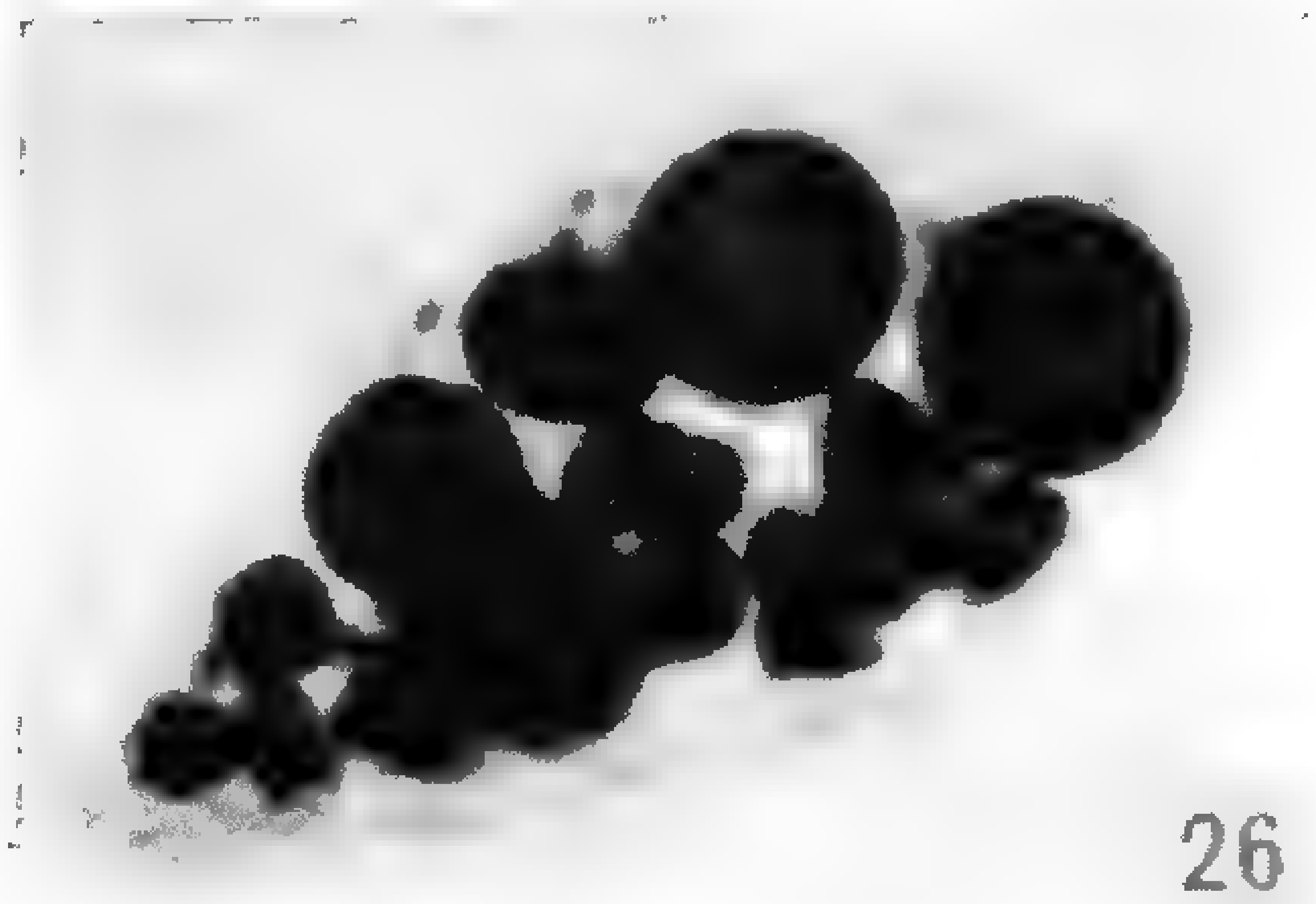
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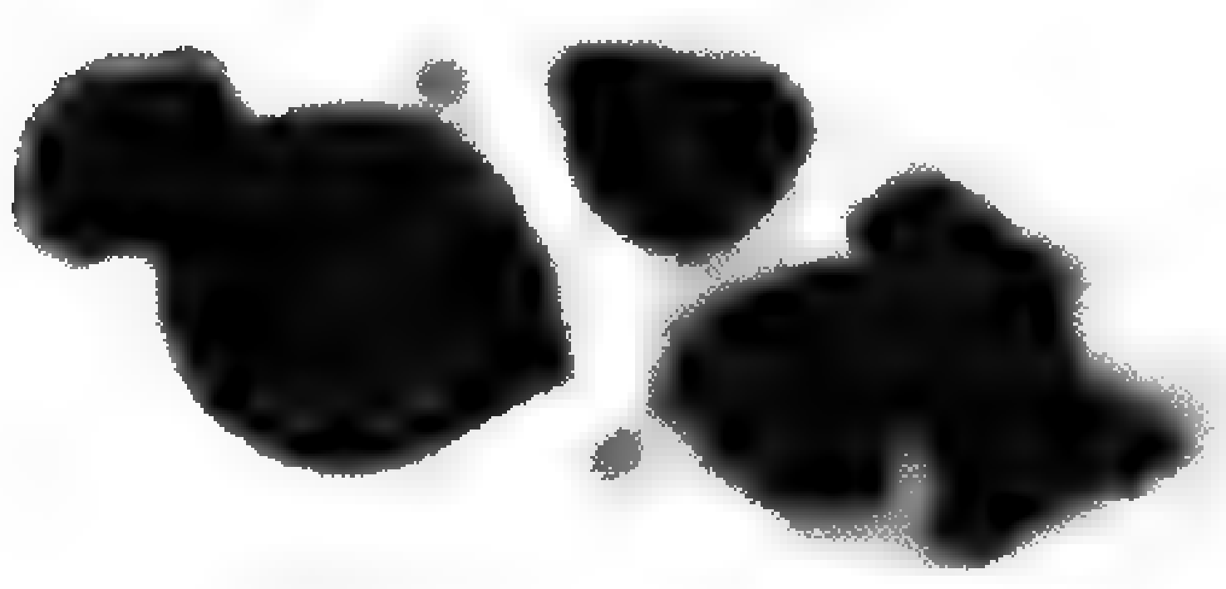

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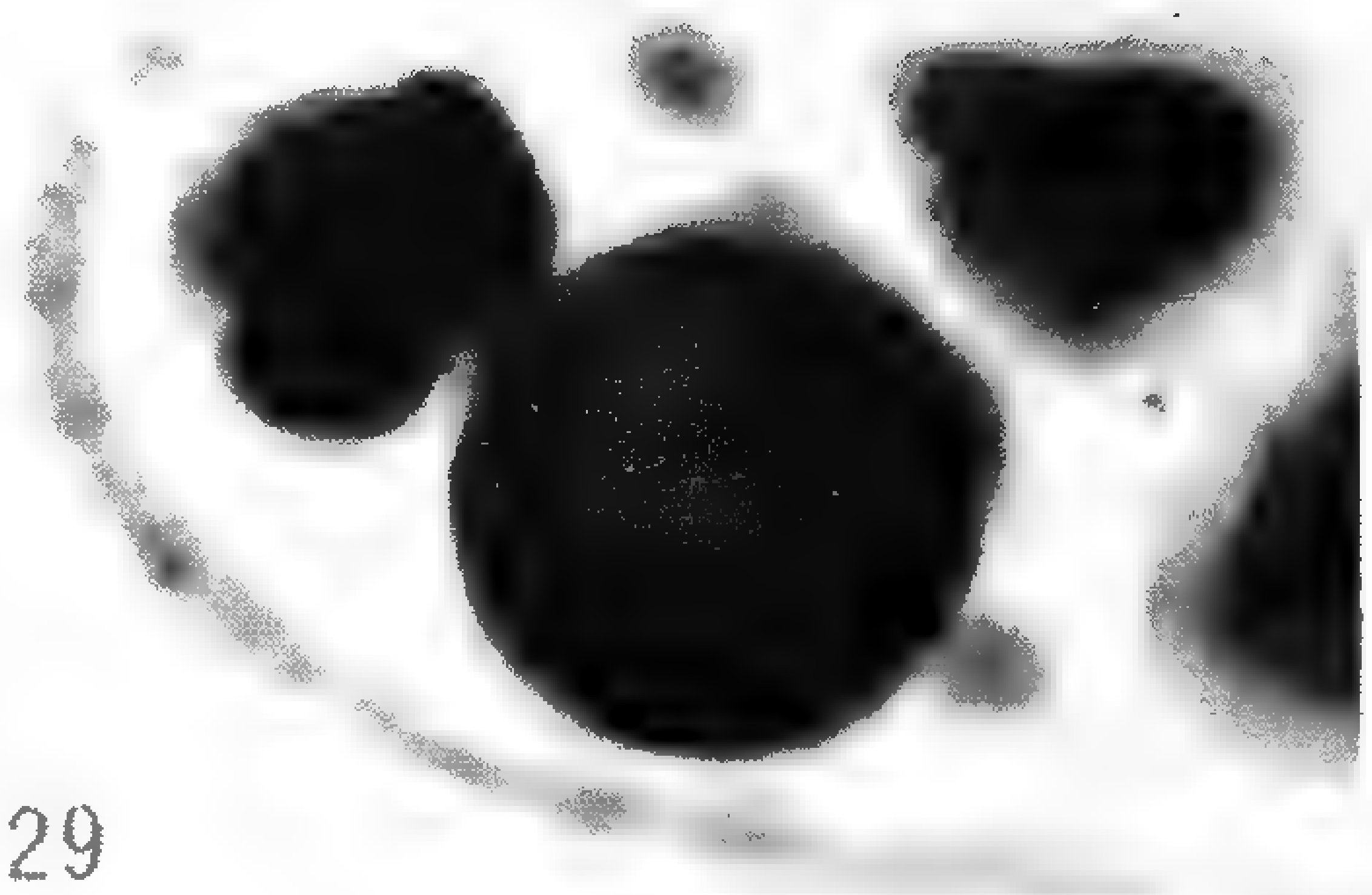

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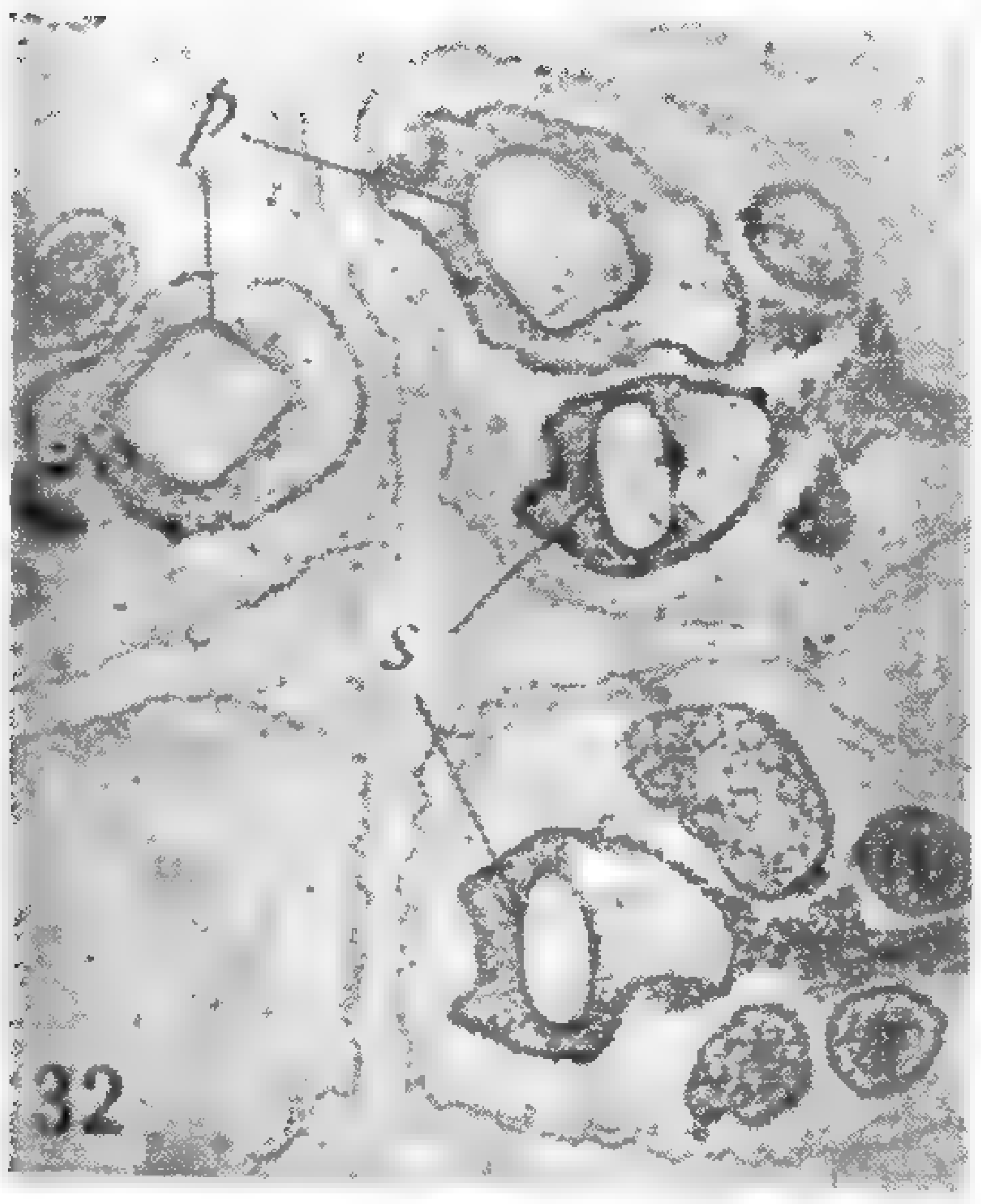

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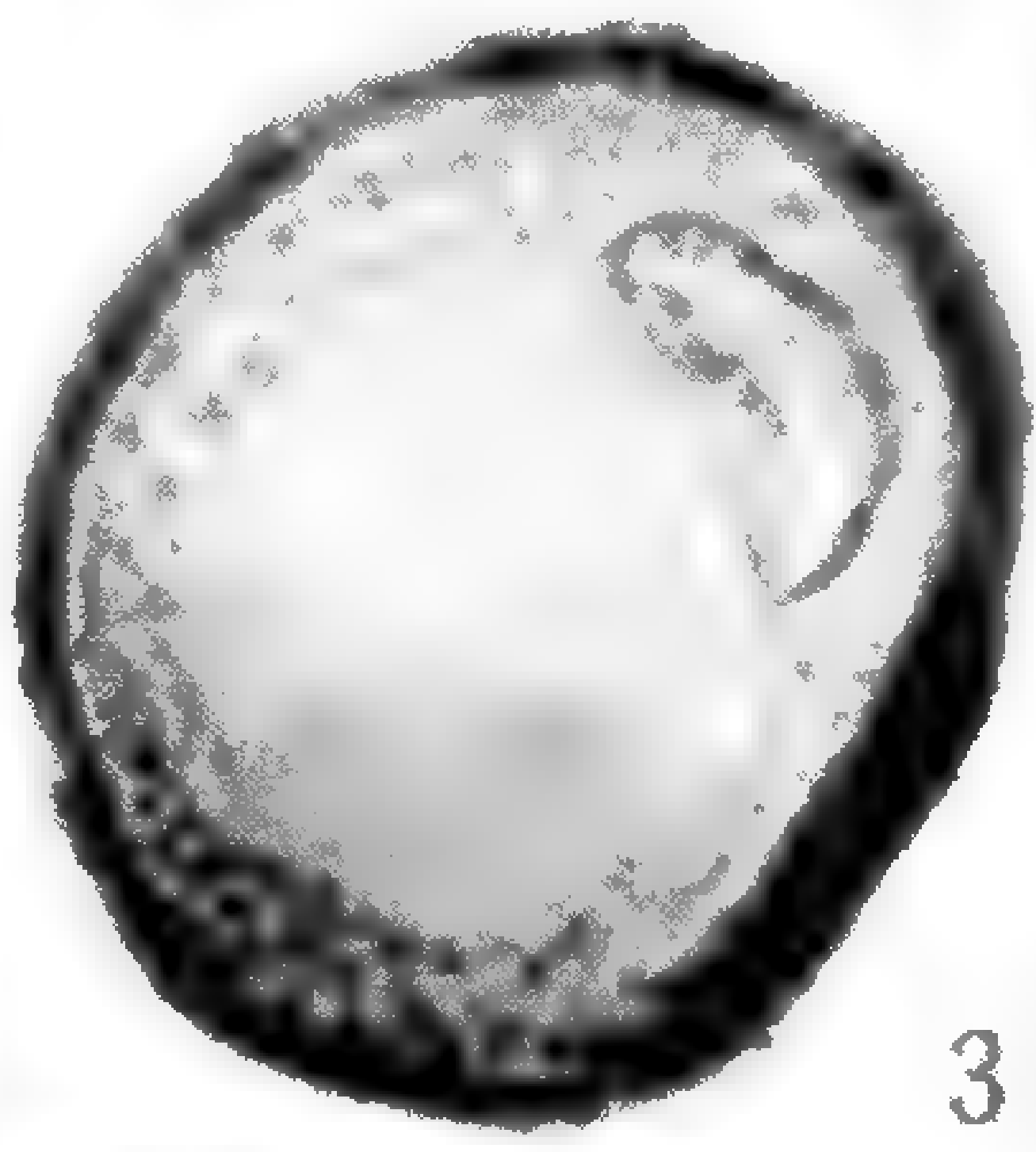

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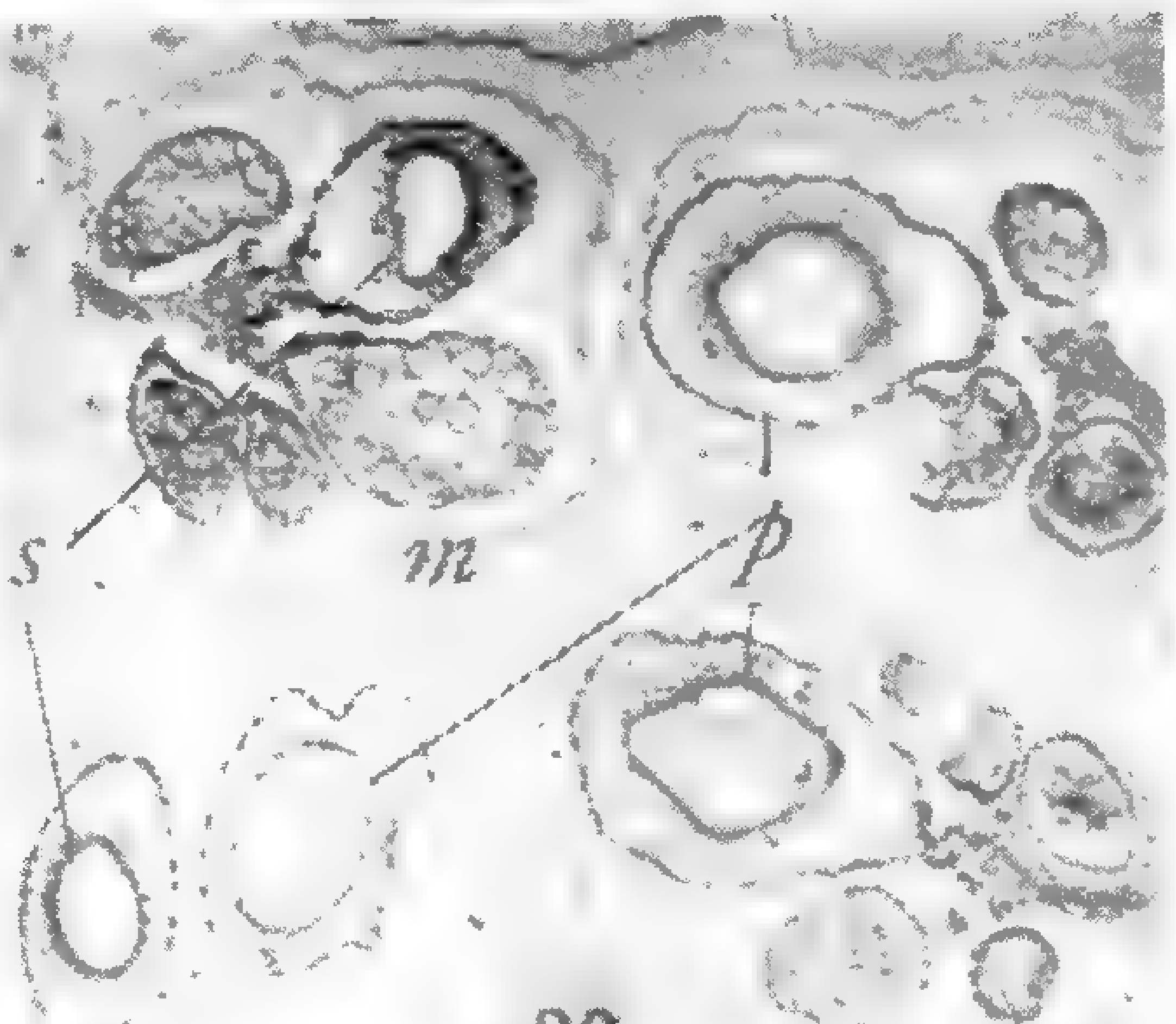

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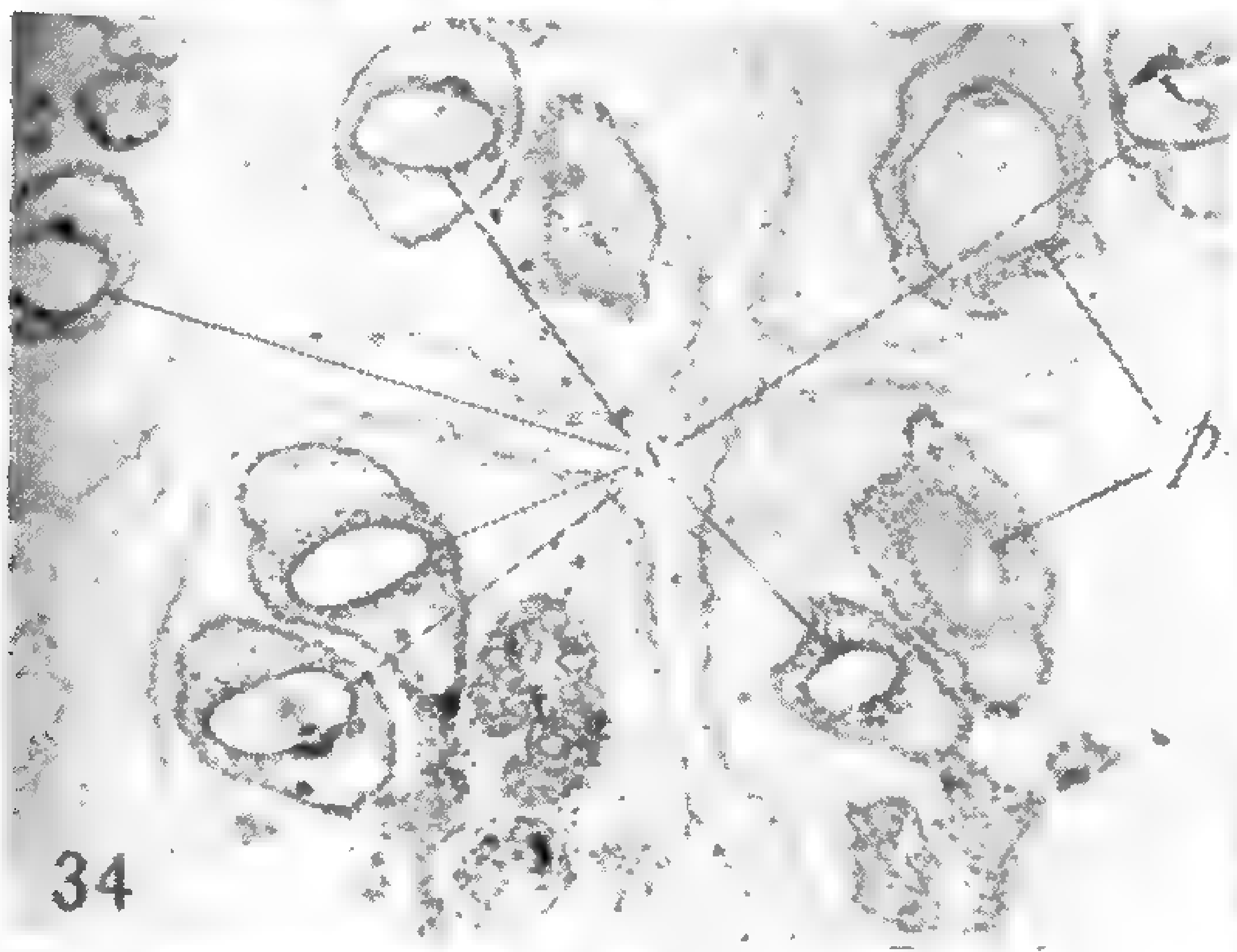

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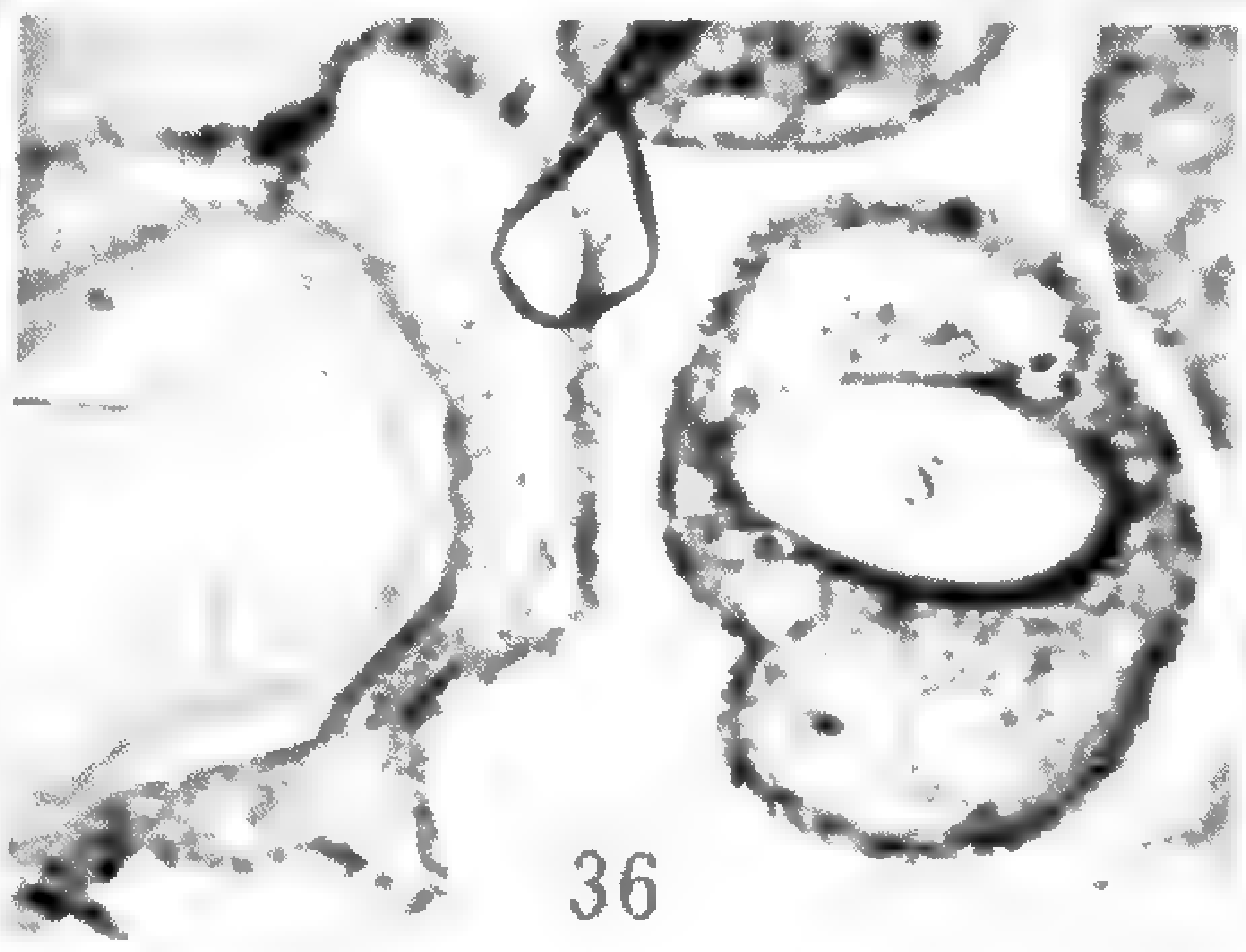

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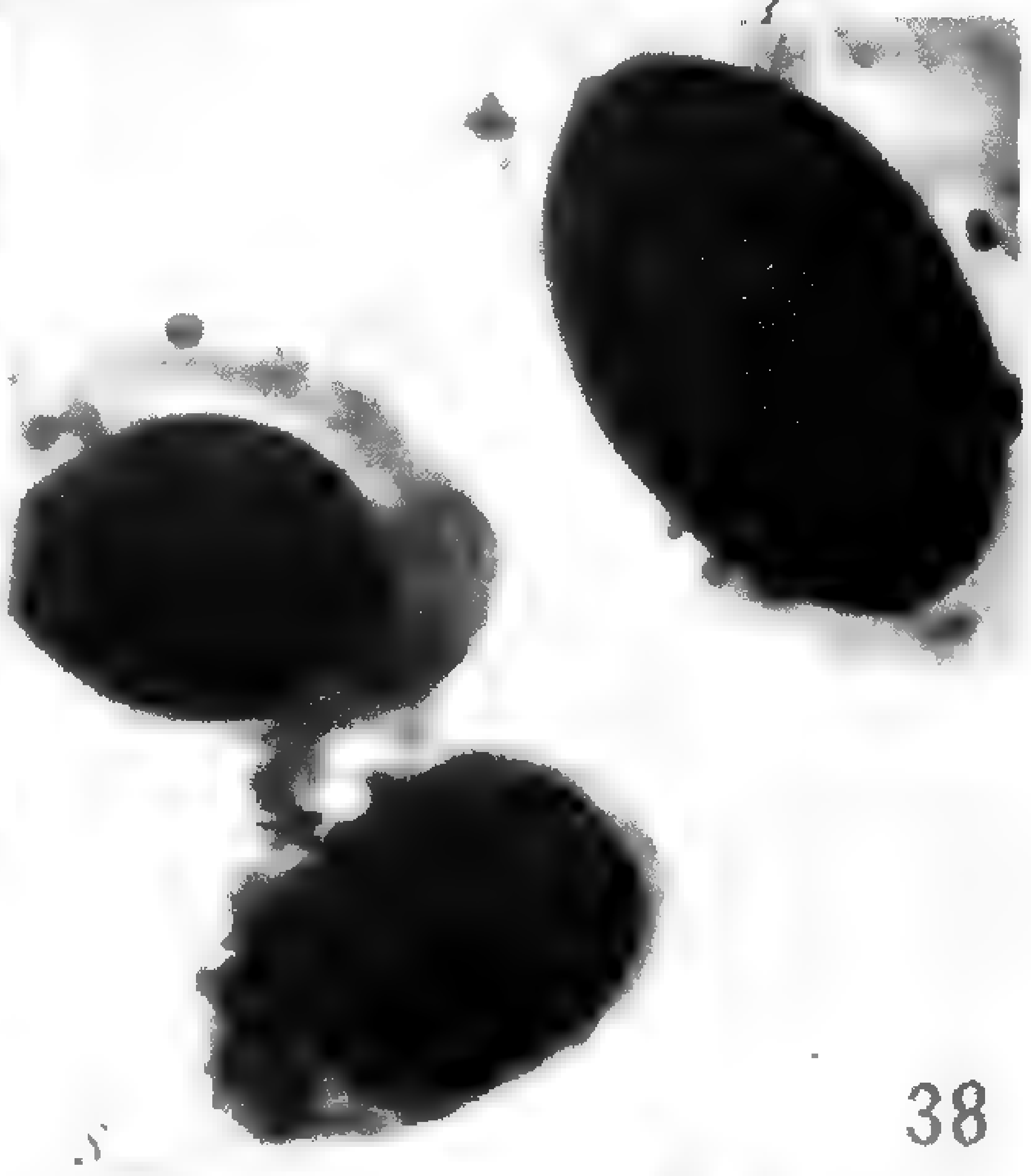

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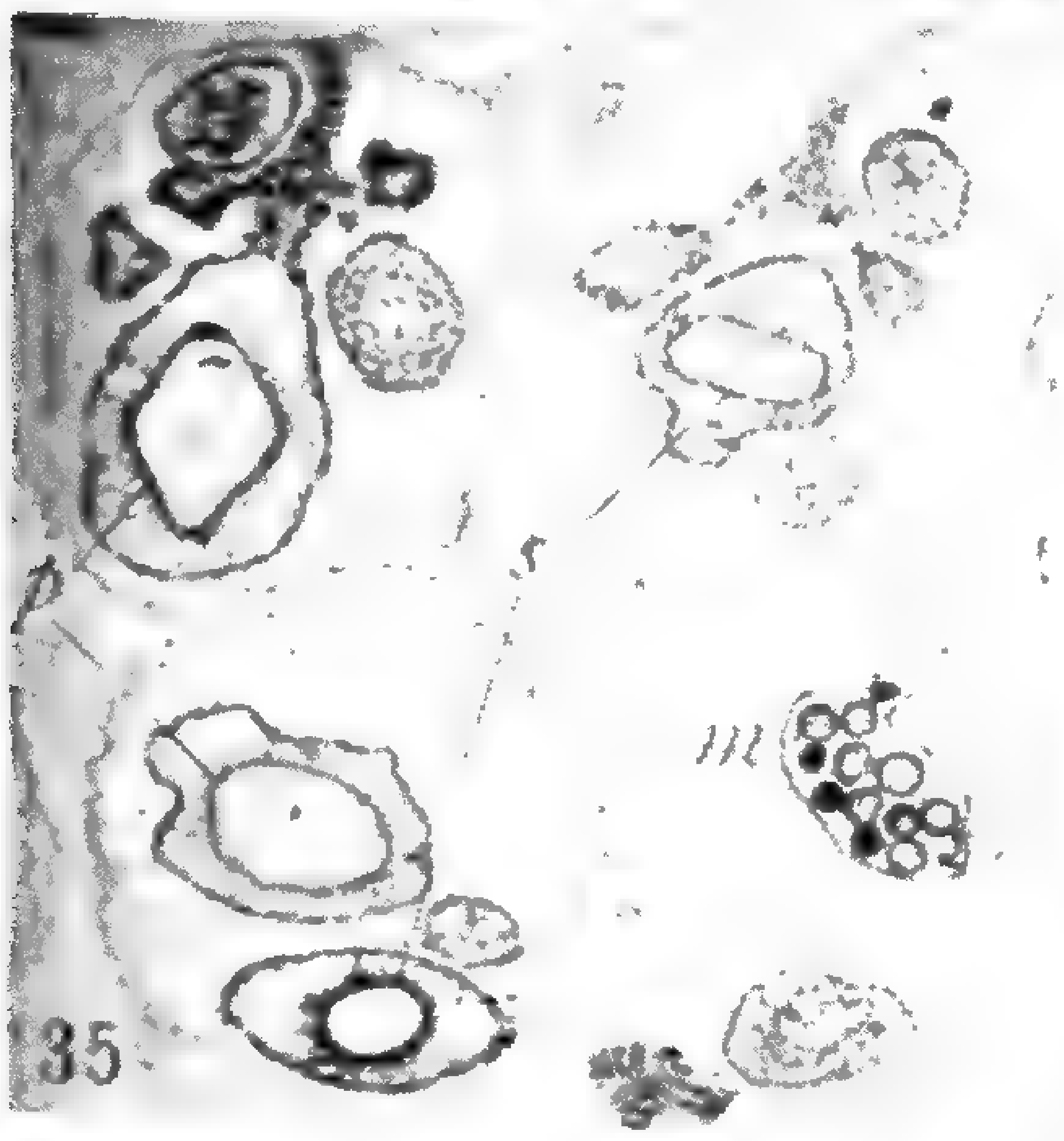

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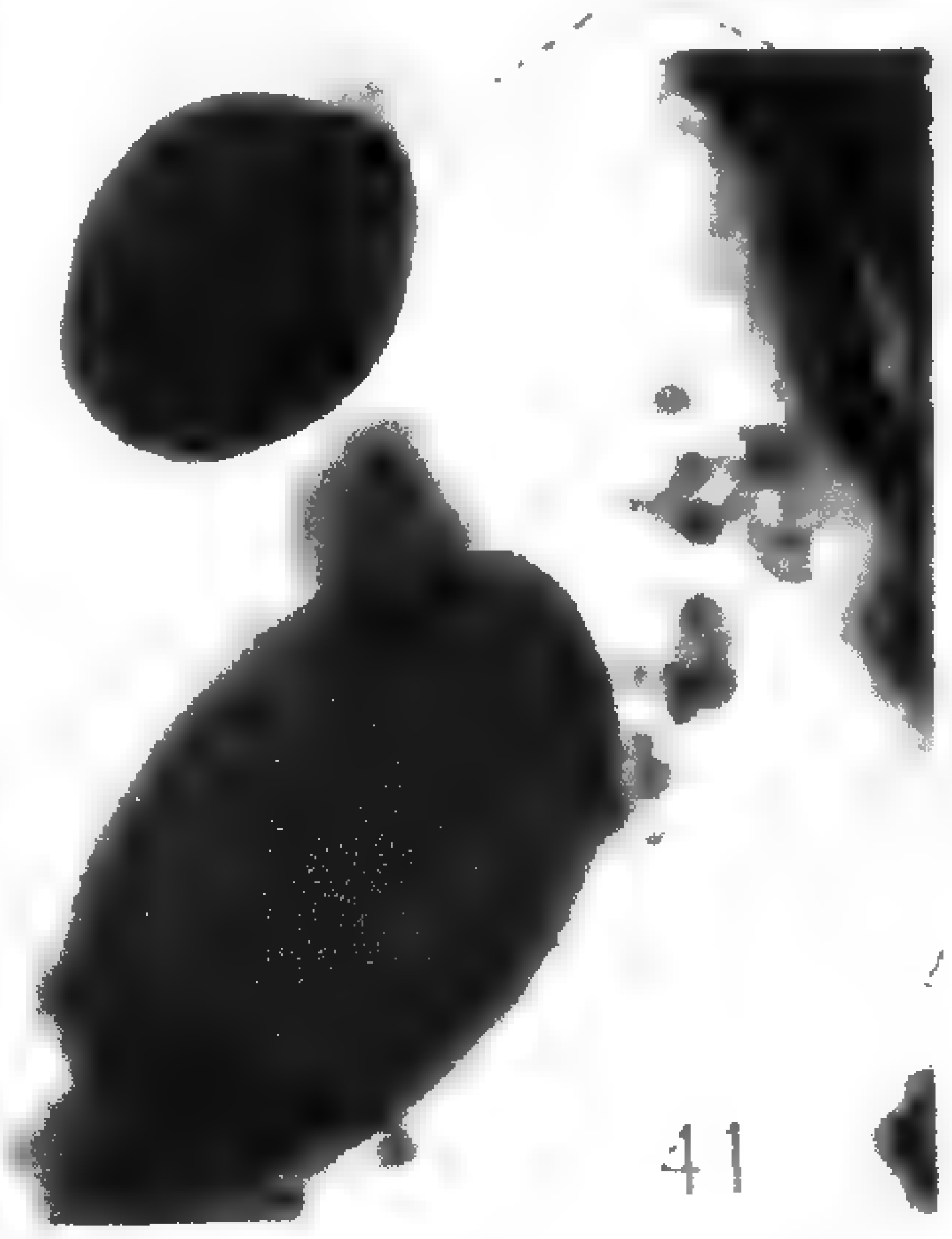

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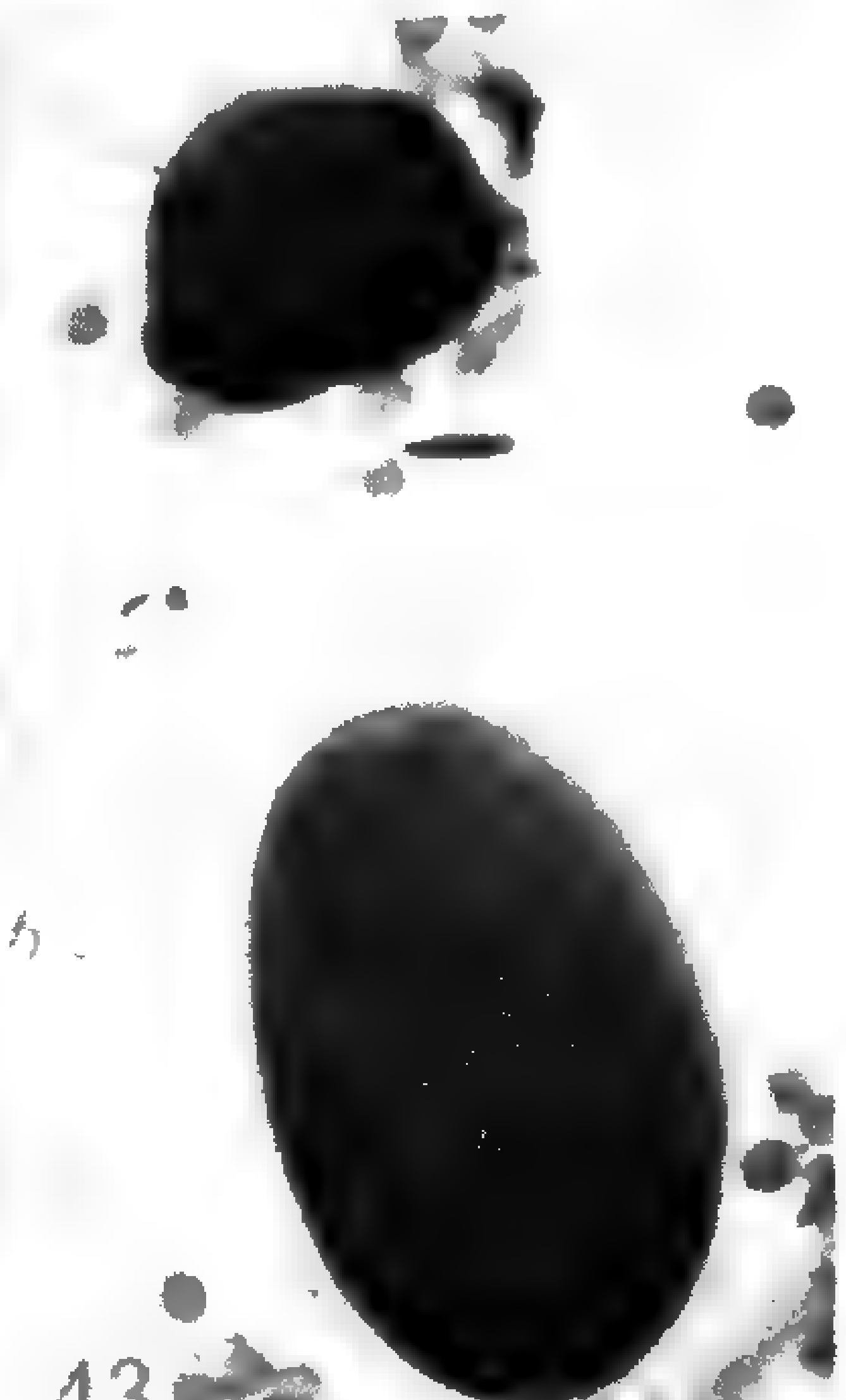

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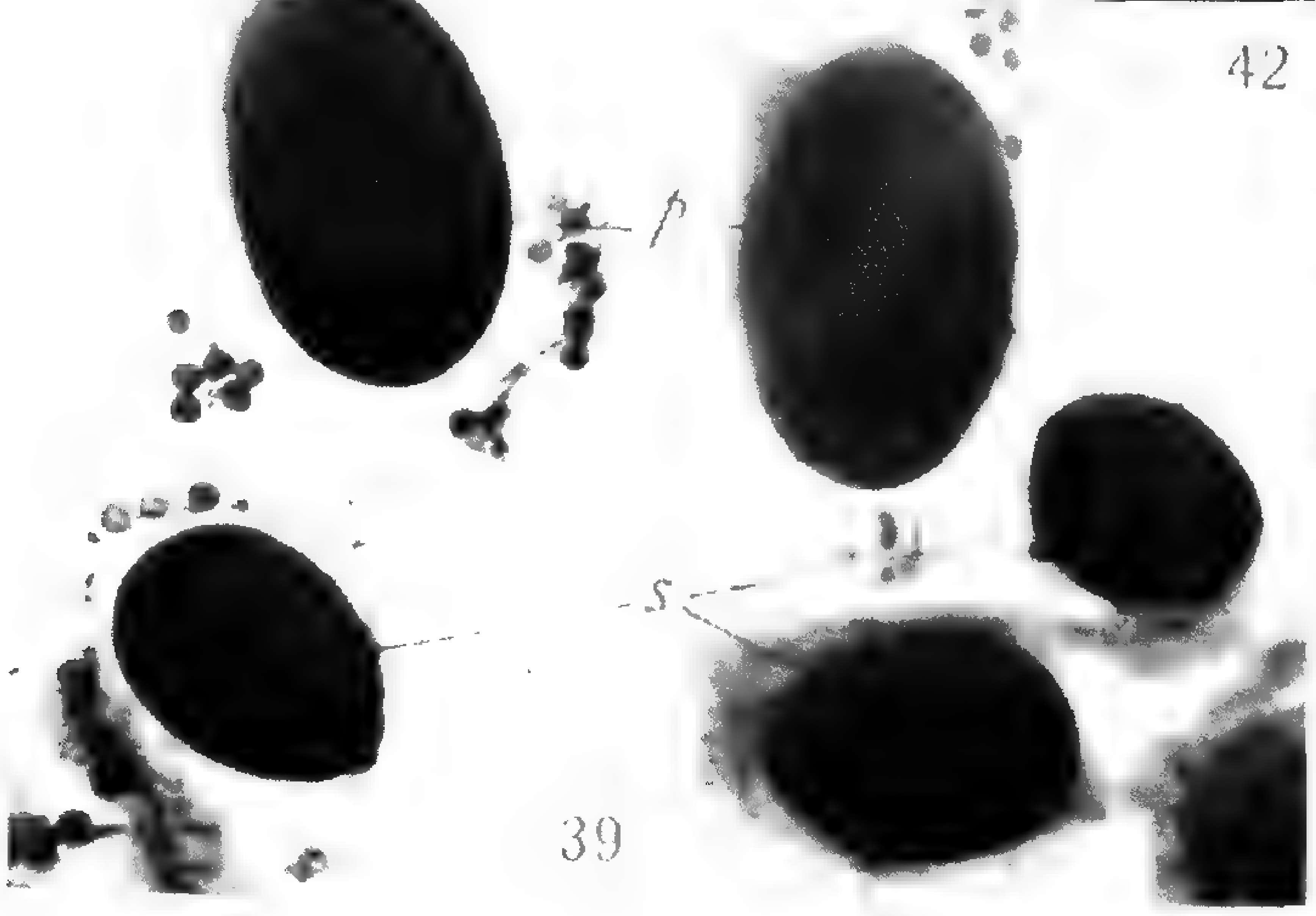

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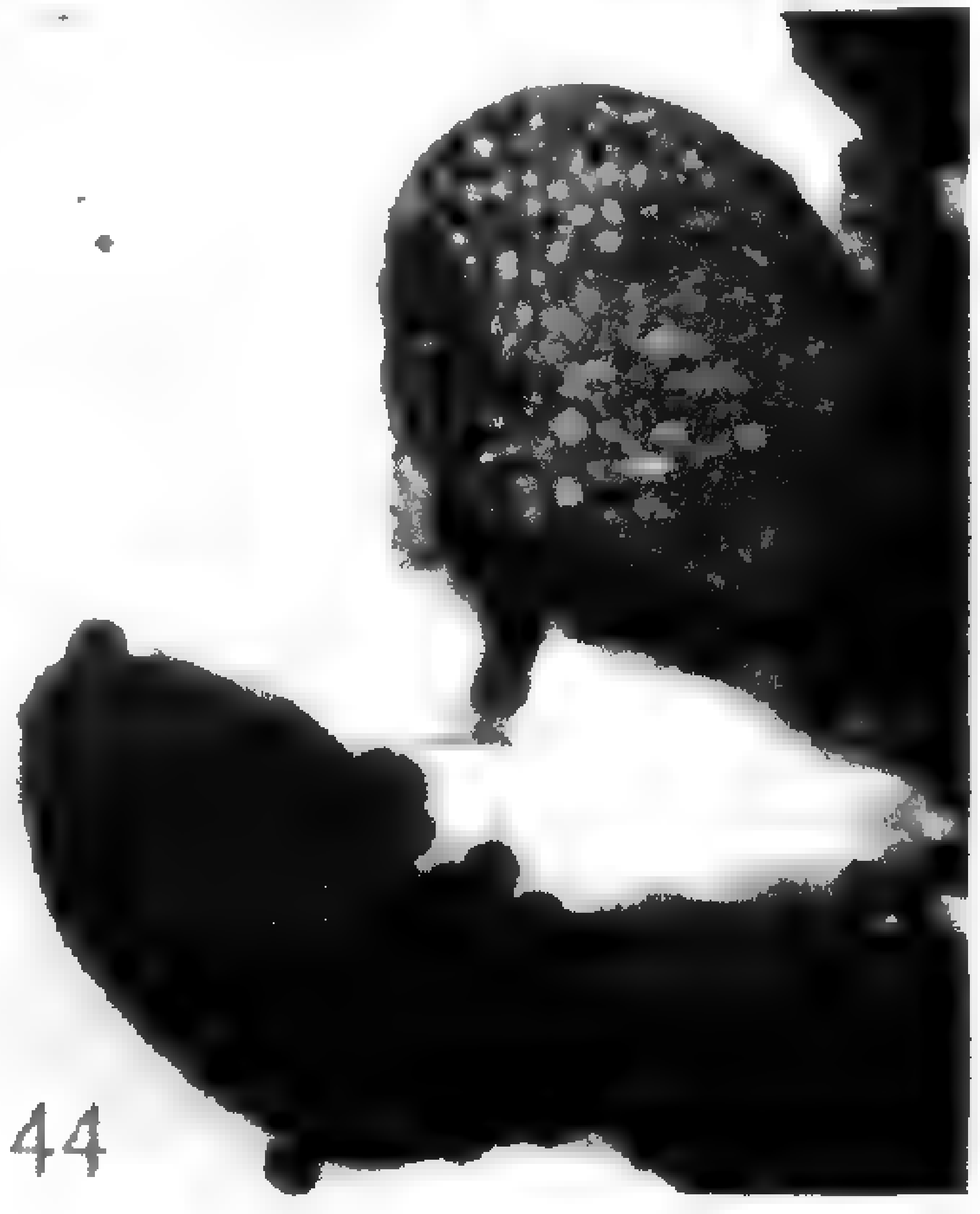

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SHATTUCK on MARSILIA

ON THE LACK OF ANTAGONISM BETWEEN CALCIUM VERSUS MAGNESIUM AND ALSO BETWEEN CALCIUM VERSUS SODIUM

CHAS. B. LIPMAN

(WITH TWO FIGURES)

In a former paper,[1] I have shown that many of the facts relating to the toxic and antitoxic effects of salt for animals and plants, as shown by the work of LOEB and OSTERHOUT in particular, hold in a general way with regard to the ammonifying power of *Bacillus subtilis*. In the same paper I also reported the results of experiments which showed that there is in respect to the ammonification by *B. subtilis* no antagonism between calcium and magnesium. As this is so striking an exception to the results obtained by LOEW[2] in his well-known experiments on green plants, it was thought advisable to emphasize the writer's results in a separate article, along with another new and strikingly exceptional case, namely a lack of antagonism between calcium and sodium. The latter case is of great interest, inasmuch as KEARNEY and CAMERON,[3] BENECKE,[4] and OSTERHOUT[5] have all found very pronounced antagonism between sodium and calcium in green plants. OSTERHOUT has also found this to be the case for a mold (Botrytis).[6]

In general, the technic employed in the two sets of experiments reported was as follows: Solutions of chemically pure salts, previously submitted to the flame test, were made up at a concentration of 0.35*m* containing 0.75 per cent. Witte's peptone. Inoculations were made from a 48-hour peptone culture into solutions made up as described in detail below. At the end of the incubation period of 2.5 days at

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[1] BOT. GAZETTE **48**:105–125. 1909.

[2] Literature in LOEW, Bull. 18, Div. Veg. Physiol. and Path., U. S. Depart. Agric. 1899; also LOEW and ASO, Bull. Coll. Agric. Tokyo **7**:395. 1907.

[3] Report 71, U. S. Depart. Agric. 1902.

[4] Ber. Deutsch. Bot. Gesells. **25**:322. 1907.

[5] BOT. GAZETTE **42**:127. 1906; **44**:259. 1907; Jahrb. Wiss. Bot. **46**:121. 1908.

[6] Univ. Calif. Publ. Botany **2**:317. 1907.

28–29° C., the culture solutions were transferred to Jena distillation flasks and distilled after adding a slight excess of magnesium oxid. The distillate (about 150^{cc} in bulk) was titrated against tenth normal acid, cochineal being used as the indicator, and the amount of ammonia nitrogen formed thus determined Sterile controls were run on all determinations to allow of an accurate estimation of the ammonia actually formed by *B. subtilis* during the period of incubation.

Series I. $CaCl_2$ versus $MgCl_2$

Solutions of calcium chlorid and magnesium chlorid of 0.35*m* each were made up in bulk to contain 0.75 per cent. peptone. The culture solutions were made and placed in 250^{cc} Erlenmeyer flasks as follows: Flask *A* contained 100^{cc} of the $MgCl_2$ solution made up as noted above; flask *B*, 100^{cc} $MgCl_2 + 5^{cc}$ $CaCl_2$; flask *C*, 100^{cc} $MgCl_2 + 10^{cc}$ $CaCl_2$; flask *D*, 100^{cc} $MgCl_2 + 25^{cc}$ $CaCl_2$; flask *E*, 100^{cc} $MgCl_2 + 50^{cc}$ $CaCl_2$; flask *F*, 100^{cc} $MgCl_2 + 100^{cc}$ $CaCl_2$. Then beginning at the other end of the series, flask *K* contained 100^{cc} of the $CaCl_2$ solution; flask *J*, 100^{cc} $CaCl_2 + 5^{cc}$ $MgCl_2$; flask *I*, 100^{cc} $CaCl_2 + 10^{cc}$ $MgCl_2$; flask *H*, 100^{cc} $CaCl_2 + 25^{cc}$ $MgCl_2$; flask *G*, 100^{cc} $CaCl_2 + 50^{cc}$ $MgCl_2$.

After the solutions were made up, the mixed solutions in each flask amounted to more than 100^{cc}, while the flasks with pure salts (plus peptone) contained only 100^{cc}. In order to make the conditions the same for all the flasks (particularly in respect to the amount of fluid surface exposed to the air), enough liquid was pipetted out of the flasks containing mixed solutions to leave just 100^{cc} in each flask. The flasks were then sterilized in the autoclave at 1.25 atmospheres of pressure for 30 minutes. A 48-hour culture of *B. subtilis* in 1 per cent. peptone was used as inoculating material. By slight shaking the membrane formed at the surface was precipitated to the bottom, and by tilting the flask to one side and carefully setting it down again, one part of the bottom of the flask remained free of membranous material and the liquid above was homogeneous in character. Of this homogeneous liquid 1^{cc} was taken for inoculation in each of the flasks prepared as above described. The table of results follows:

TABLE I

Numbers in first column refer to c.c. of 0.35*m* solutions

Culture solution	Corresponding points on curve	N as NH_3 formed in cultures, in mg
100 $MgCl_2$	A	3.08
100 $MgCl_2$ 5 $CaCl_2$	B	2.59
100 $MgCl_2$ 10 $CaCl_2$	C	1.68
100 $MgCl_2$ 25 $CaCl_2$	D	0.98
100 $MgCl_2$ 50 $CaCl_2$	E	0.21
100 $MgCl_2$ 100 $CaCl_2$	F	0.07
50 $MgCl_2$ 100 $CaCl_2$	G	0.00
25 $MgCl_2$ 100 $CaCl_2$	H	0.00
10 $MgCl_2$ 100 $CaCl_2$	I	0.00
5 $MgCl_2$ 100 $CaCl_2$	J	0.00
100 $CaCl_2$	K	0.49

By an examination of the curve drawn on the basis of table I (*fig. 1*), we are confronted by the very striking instance of no antagonism between the two salts employed. On the contrary, there is a constant increase of the toxic properties of each when the other is added to it in increasing amounts. In this exceptional behavior, so far as I can ascertain, *B. subtilis* (and probably all the ammonifiers) stand alone when their physiological efficiency in such salt mixtures is compared with that of the higher plants and animals. No instance of such behavior on the part of any member of the latter two groups of organisms has come to my notice in reviewing the results of similar researches on animals and the higher plants.

We find among plants the well-known researches of LOEW[7] and his pupils, and later the researches of KEARNEY and CAMERON,[8] which show the strong antagonism between calcium and magnesium.

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[7] Bull. 45, Bureau Pl. Ind., U. S. Depart. Agric.; also LOEW and ASO, Bull. Coll. Agric. Tokyo 7:no. 3. 1907.

[8] Report 71, U. S. Depart. Agric.

The last-named investigators found in their experiments with the white lupine (*Lupinus albus*) and with alfalfa (*Medicago sativa*) that when $CaCl_2$ was added to $MgSO_4$ in about equal proportions the plants exhibited about 160 times the tolerance for the latter salt that they did in solutions of $MgSO_4$ alone. They found further that the antagonism between $CaCl_2$ and $MgCl_2$, though not so great (increasing the tolerance about 40 times), was nevertheless very marked, and where $CaSO_4$ replaced $CaCl_2$ the antagonism was very much greater between Ca and Mg than in either of the cases above cited. BENECKE[9] likewise found antagonism between magnesium and calcium in his work with Spirogyra.

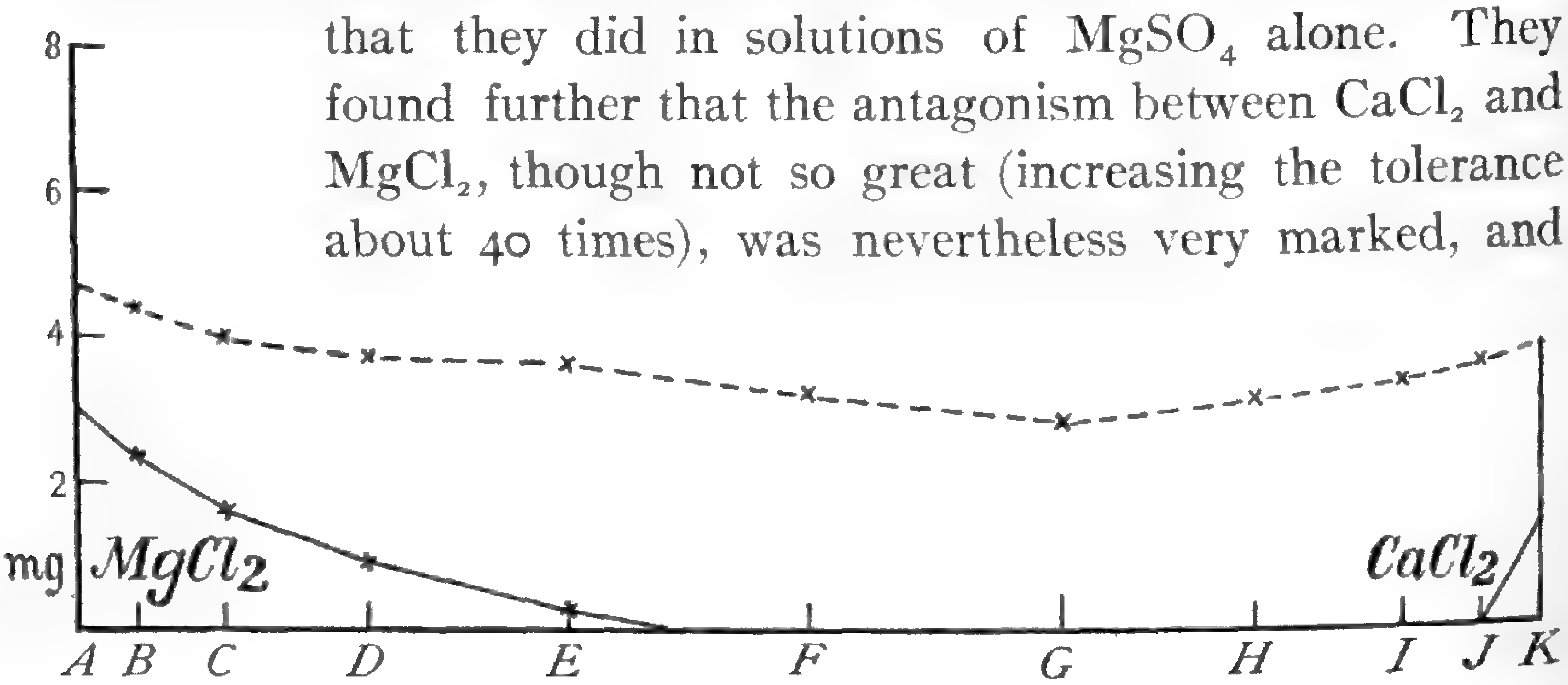

FIG. 1.—The ordinate at *A* represents the amount of ammonia nitrogen in milligrams formed in a pure 0.35*m* solution of $MgCl_2$ containing 0.75 per cent. peptone. The ordinate at *K* represents the amount of ammonia nitrogen formed in a pure $CaCl_2$ solution of the same strength and with the same peptone content. The ordinates at the intermediate points represent the amounts of ammonia nitrogen formed in various combinations of the two salts as indicated in tables I and II. The full line represents results in table I; the broken line represents results in table II.

An antagonism between $CaCl_2$ and $MgCl_2$, though slight, was found to be none the less definite by LOEB[10] in experiments which showed that sea urchin blastulae and gastrulae would swim about in a mixture of the salts above mentioned for 48 hours, while each salt by itself would immediately prove poisonous at the concentration employed in the combination. Another interesting case in point may be noted in the experiments of the same investigator on Polyorchis,[11] a jellyfish of San Francisco Bay. In a solution of 50^{cc} NaCl + 6^{cc} $MgCl_2$ + 1^{cc} $CaCl_2$, the rhythmical contractions of the margin go

[9] Ber. Deutsch. Bot. Gesells. **25**:322. 1907.

[10] Amer. Jour. Physiol. **3**:327. 1900.

[11] Jour. Biol. Chem. **1**:427. 1906.

on normally, but with a slight increase of $CaCl_2$ the contractions are inhibited, and when 5^{cc} of a $0.375m$ solution of $CaCl_2$ are added, they are completely suppressed. On the other hand, when the margin of the fish, containing the sense organs and the central nervous system, is cut off, $CaCl_2$ exercises a stimulating action on the isolated center of Polyorchis and contractions go on normally; but when $MgCl_2$ is added to the solution in the ratio of 4 parts $MgCl_2$ to 1 part $CaCl_2$, the stimulating action of the $CaCl_2$ is suppressed and contractions cease. In both cases, therefore, there is evidence of a definite antagonism between calcium and magnesium. LILLIE[12] also proved the existence of antagonism between the two salts when he found that the ciliary activity of the larvae of Arenicola would go on normally for some time in a mixture of approximately 4 parts $MgCl_2$ to 1 part $CaCl_2$, whereas it would cease immediately if either of the salts at the same concentration was present alone. The same investigator found in other work that calcium salts inhibit the spontaneous contractility of the swimming plate in ctenophores, when added to solutions made up of 90 parts by volume NaCl and 10 parts $MgCl_2$. Only 2 volumes of $CaCl_2$ of the same concentration as the other salts inhibit movements of the swimming plate in the sodium and magnesium solution above described, while 4 volumes of $CaCl_2$ allow but little spontaneous movement. The latter is entirely inhibited by the addition of 8 volumes of the $CaCl_2$ solution.

I wish to cite only one more case, which emphasizes by contrast most strongly the exceptional results obtained above in experiments with *B. subtilis*, and that is, the remarkable results obtained in a highly ingenious series of experiments recently carried out by MELTZER and AUER[13] on the antagonistic effect of calcium on the inhibitory effect of magnesium. The experiments were carried out on rabbits, and in one case on a monkey, and as a typical instance of the remarkable antagonistic effect between calcium and magnesium may be cited the first experiment of the series, in which about 13^{cc} of an $m/1$ solution of $MgCl_2$ was injected subcutaneously into a rabbit. Less than one-half hour later there was produced general anaesthesia, with all the attending symptoms, and a $0.125m$ solution of

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[12] Amer. Jour. Physiol. **5**:56. 1901.

[13] Amer. Jour. Physiol. **21**:403. 1909.

$CaCl_2$ was injected intravenously in the ear vein. When only 2^{cc} had thus been injected, the rabbit was again breathing normally, and when 8^{cc} had been given, the animal sat up and appeared entirely recovered, except for a stiffness in the hind legs.

In these experiments, some of which were even more striking than the one cited, MELTZER and AUER employed, besides the chlorids of calcium and magnesium, the acetate and nitrate of the former, and the acetate, nitrate, and sulfate of the latter, and the same strong antagonism was noted in all cases.

In addition to the confirmation of the results obtained above in my experiments with the same material, one series was also carried out with a culture of *B. subtilis* obtained from an entirely different source, and the salt solutions made up from a different grade of chemically pure salt. As can be seen from the following table, the results fully confirm those above given, and though the absolute amounts are different, the results are relatively the same (see also *fig. 1*).

TABLE II

Numbers in first column refer to c.c. of 0.35*m* solutions

Culture solutions	Corresponding points on curve	N as NH_3 formed in cultures, in mg
100 $MgCl_2$	A	4.76
100 $MgCl_2$ 5 $CaCl_2$	B	4.48
100 $MgCl_2$ 10 $CaCl_2$	C	4.20
100 $MgCl_2$ 25 $CaCl_2$	D	3.78
100 $MgCl_2$ 50 $CaCl_2$	E	3.64
100 $MgCl_2$ 100 $CaCl_2$	F	3.22
50 $MgCl_2$ 100 $CaCl_2$	G	3.08
25 $MgCl_2$ 100 $CaCl_2$	H	3.29
10 $MgCl_2$ 100 $CaCl_2$	I	3.43
5 $MgCl_2$ 100 $CaCl_2$	J	3.57
100 $CaCl_2$	K	3.78

It may be of interest to note here that *B. subtilis* from a 24-hour peptone agar slope culture was examined in hanging drops of molecular solutions of calcium chlorid and showed no perceptible ill-effects from the action of the solution. The ciliary movements appeared normal even after 24 hours in the hanging drop. It was noticed, however, that there was little or no division among the bacilli during the 24 hours, and it is likely that the calcium and magnesium salts exercise their toxic effects by inhibiting reproduction, since the ciliary movements seems to go on without interruption. These remarks, however, are based on too meager experimental evidence to partake of anything else than the nature of conjecture, but they serve to indicate a field of most interesting possibilities in research.

Though they are not analogous instances of the lack of antagonism between calcium and magnesium as shown above, it is interesting to note two cases on record, in which the addition of one salt to another made a combination more toxic than either. One case is that of OSTWALD'S[14] experiments on the fresh-water Gammarus, in which it was found that a combination of $MgCl_2$ and NaCl in solution was more toxic to that animal than NaCl in solution alone. The other case is that noted in the experiments of PAUL and KRÖNIG,[15] who found that the value of mercuric sulfate, acetate, and nitrate as disinfectants was enhanced by the addition of small amounts of the chlorids of potassium and sodium; but, on the other hand, the addition of the same chlorids to $HgCl_2$ reduced considerably the disinfecting power of the latter. The first instance is not analogous to my results, because one of the salts used by OSTWALD was different and the experiment was carried out under conditions so totally different that the value of a comparison here is doubtful. In the second instance, as PAUL and KRÖNIG themselves suggest, the increase of toxicity is not necessarily owing to a lack of antagonism between the two salts, but rather to the formation of complex double salts of mercury, characteristic of that element, and therefore this again cannot be compared with the lack of antagonism between calcium and magnesium above noted.

[14] Univ. Calif. Publ. Physiology **2**:163. 1905.

[15] Zeitschr. Hyg. und Infectionskrank. **25**:57. 1897.

Series II. $CaCl_2$ versus NaCl

In this series the solutions were made up in the same way as in the preceding one, and the same concentration of salts and peptone was employed, the only difference being that $CaCl_2$ and NaCl were tested instead of $CaCl_2$ and $MgCl_2$. The incubation was carried out for two and one-half days at 28–29° C., and the distillations and determinations were made as above described. The table of results follows:

TABLE III

Numbers in first column refer to c.c. of 0.35*m* solutions

Culture solutions	Corresponding points on curve	N as NH_3 formed in cultures, in mg
100 NaCl	A	14.48
100 NaCl 5 $CaCl_2$	B	10.94
100 NaCl 10 $CaCl_2$	C	8.46
100 NaCl 25 $CaCl_2$	D	8.18
100 NaCl 50 $CaCl_2$	E	6.64
100 NaCl 100 $CaCl_2$	F	5.99
50 NaCl 100 $CaCl_2$	G	2.54
25 NaCl 100 $CaCl_2$	H	1.53
10 NaCl 100 $CaCl_2$	I	0.07
5 NaCl 100 $CaCl_2$	J	0.00
100 $CaCl_2$	K	0.00

In the curve drawn on the basis of the foregoing table (*fig. 2*) we note again the striking instance of the lack of antagonism for *B. subtilis* of two salts which showed a strong antagonism in all experiments on animals and plants thus far carried out. OSTERHOUT[16] showed, for example, that a strong antagonism exists between NaCl and $CaCl_2$ for wheat, and that the curve obtained there was very similar

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[16] BOT. GAZETTE **48**:98–104. 1909.

to the curve obtained for the antagonism between KCl and $CaCl_2$. This latter fact is especially interesting, since for *B. subtilis* a strong antagonism is exhibited between KCl and $CaCl_2$, while in the case of NaCl and $CaCl_2$ there is a constant increase of toxicity as $CaCl_2$ is added in larger and larger amounts to the NaCl solutions.

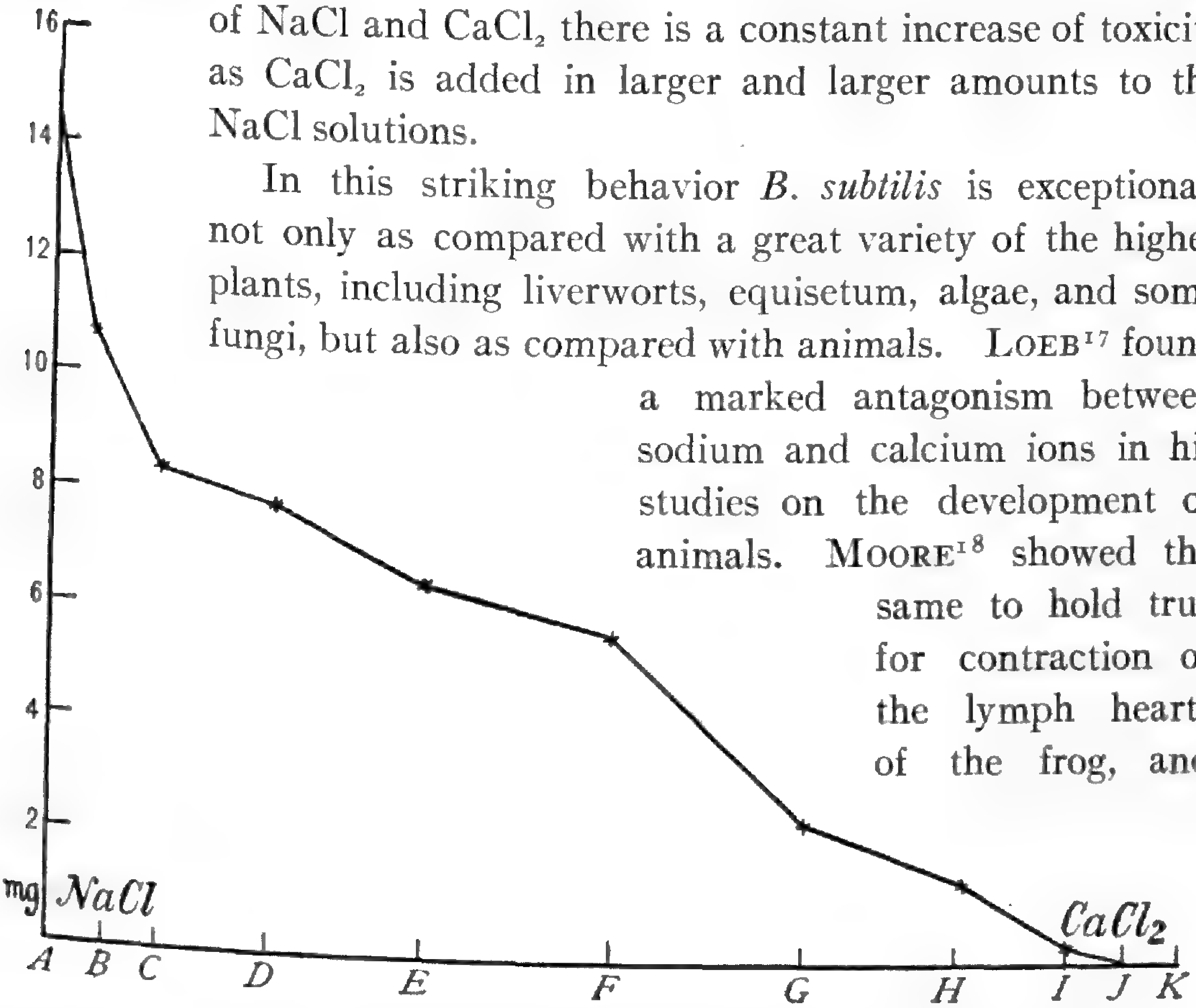

FIG. 2.—The ordinate at *A* represents the amount of ammonia nitrogen formed in a pure 0.35*m* solution of NaCl containing 0.75 per cent. peptone. The ordinate at *K* represents the amount of ammonia nitrogen formed in a pure 0.35*m* solution of $CaCl_2$ and with the same content of peptone. The ordinates at the intermediate points represent the amounts of ammonia nitrogen formed in various combinations of the two salts as indicated in table III.

In this striking behavior *B. subtilis* is exceptional, not only as compared with a great variety of the higher plants, including liverworts, equisetum, algae, and some fungi, but also as compared with animals. LOEB[17] found a marked antagonism between sodium and calcium ions in his studies on the development of animals. MOORE[18] showed the same to hold true for contraction of the lymph hearts of the frog, and LINGLE[19] also demonstrated that fact in the case of the turtle's heart. In addition to these facts, we have the work of LILLIE[20] to show also that as regards ciliary activity an antagonism between $CaCl_2$ and NaCl was found to exist, and MCCALLUM in his work on cathartics showed the same facts to hold true there.

Many more instances could be cited to show by contrast the strikingly exceptional behavior of *B. subtilis* as regards the two salts

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[17] Amer. Jour. Physiol. **3**:328, 383. 1909.

[18] *Ibid.* **5**:87. 1901.

[19] *Ibid.* **4**:265. 1900.

[20] *Ibid.* **5**:56. 1901.

in question, but only one important case comes to my notice which resembles that of *B. subtilis* just cited, and that is to be found in the work of LOEB with the marine Gammarus, in which he found that the animals die more quickly in a solution of 100^{cc} $0.375m$ NaCl to which 1^{cc} of a $0.375m$ $CaCl_2$ solution was added than in a pure $0.375m$ NaCl solution.

The results set forth in the foregoing pages, as well as those contained in a previous paper, tend to show that in their behavior toward salts bacteria differ in some respects from both plants and animals and occupy a position by themselves. It is evident that mineral fertilizers applied to the soil will not have altogether the same effect on the bacteria as on the higher plants. Further studies in this direction may lead to important practical application.

Summary

1. No antagonism exists between magnesium and calcium. Any combination of the two salts is more toxic than $MgCl_2$ alone for *B. subtilis*.

2. No antagonism exists between sodium and calcium. Any combination of the two salts renders it more poisonous than the NaCl alone for *B. subtilis*.

3. In these two respects, the behavior of *B. subtilis* finds no parallel among plants so far as studied, and scarcely any among animals.

My thanks are due Professor W. J. V. OSTERHOUT for helpful suggestions and criticisms in this work.

LABORATORY OF SOIL BACTERIOLOGY
UNIVERSITY OF CALIFORNIA

BRIEFER ARTICLES

THE MICROSPOROPHYLLS OF GINKGO

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **134**

(WITH PLATE VII)

This study was undertaken in the first place to determine the origin of the mucilage ducts in the hump of the microsporophyll. As there is a general resemblance among the microsporophylls of Taxus, Torreya, and Ginkgo, and as in Torreya, according to COULTER and LAND[1] (p. 163), the resin ducts are formed from the disorganization of three of the seven sporangia, it seemed possible that in Ginkgo the mucilage ducts might have been formed from abortive sporangia also. As my material showed the development of the strobili and microsporangia, I have included an account of them, so as to give a general history of the development of the microsporophyll. The buds were collected during July, August, and September of 1907 from a tree in Elyria, Ohio, in grounds then owned by Mr. I. W. METCALF. Thanks are due him for the material and also Professor F. O. GROVER of Oberlin College and Mr. FRED STOKEY for collecting.

Development of the strobili

The strobili which will mature pollen the following year are formed in June or early July, but are hidden in buds which cannot be distinguished from leaf buds. In the latter part of July, if the scale leaves are removed from the buds, the strobili can be seen as small papillae in the axils of the scale leaves. Examined with a microscope, strobili of the same bud often show different stages of development, some being short, with the sporophylls just evident as small rounded elevations (*fig. 1*), others being elongated cones with the lower sporophylls beginning to show differentiation into sporogenous part and hump (*fig. 2*). The development of the two sides of the strobilus is often very uneven, due to greater crowding on one side than on the other. At this stage there is no differentiation of tissue in the sporophylls at the top of the strobilus, but in those lower down mucilage ducts are beginning to form in the most external portion of the sporophylls; and in sporophylls at the base the ducts are fully formed and functioning sporogenous tissue is beginning to be evident in the part nearest the axis. Occasionally

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[1] COULTER, JOHN M., AND LAND, W. J. G., Gametophytes and embryo of *Torreya taxifolia*. BOT. GAZETTE **39**:161–178. *pls. A, 1–3.* 1905.

the sporangium that will finally function appears in advance of the mucilage ducts, or the two may start together, but generally the ducts are formed before the functioning sporogenous tissue is very evident. By August 8 the sporophylls at the base of the strobilus show the formation of the stalk and the elongation of the functioning sporangium (*fig. 3*), while the sporophylls from the base to half-way up the strobilus have well-developed mucilage ducts. The stalks are formed by an increase in the number of cells as well as by elongation of the cells. By August 20 all the sporophylls have stalks and mucilage ducts, but the functioning sporogenous tissue is conspicuous only in the lower sporophylls. Early in September (*fig. 4*) the strobili have reached a length of 3^{mm}, the sporophylls have the typical shape, the mucilage ducts are enormous, and the cells of the sporogenous mass are separating for the mother cell stage, which the oldest sporangia reach before winter, according to SPRECHER[2] (p. 156). Material that I collected in April shows some sporangia in the mother cell stage and others with tetrads formed.

Development of the functioning sporangium

The early development of the functioning sporangium is probably like that of the cycads,[3] though I have not yet been able to determine that the archesporium starts as a single cell, but stages like that in *fig. 5* probably indicate that a single cell has divided anticlinally and then periclinally. Sometimes the order seems to be reversed. The outer cells are the primary wall cells, giving rise to several layers of wall cells with scanty cytoplasm; the inner are the primary sporogenous cells, by further division producing a large mass of sporogenous cells with dense cytoplasm, larger nuclei with heavily staining chromatin, and frequently conspicuous nucleoli. In the mature sporangium the hypodermal layer of cells and the layer below it have thickening bands in the walls, and in the upper part of the sporangium near the mucilage duct the walls of deeper cells are also thickened. In this respect the microsporangium of Ginkgo differs from the microsporangium of all other gymnosperms and is like that of angiosperms.

The tapetum seems to come entirely from the sporogenous mass.

Development of the mucilage ducts

The upper, sterile part of the sporophyll is developed into a humplike projection called by ČELAKOVSKÝ[4] (p. 283) a crest (*crista*). In this are

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[2] SPRECHER, ANDREAS, Le *Ginkgo biloba* L. pp. 206. *figs. 225*. Genève. 1907.

[3] SMITH, FRANCES GRACE, Morphology of the trunk and development of the microsporangium of cycads. BOT. GAZETTE **43**:187–204. *pl. 10*. 1907.

[4] ČELAKOVSKÝ, L. J., Die Vermehrung der Sporangium von *Ginkgo biloba* L. Oesterr. Bot. Zeitschrift **50**:276–283. 1900.

large mucilage ducts, cells containing calcium oxalate, and epidermal cells containing tannin. The mucilage ducts begin development like sporangia, and for some time look like the functioning sporogenous tissue in the lower part of the sporophyll. Several hypodermal cells are differentiated from the rest by their greater size and their more vacuolate contents (*fig. 6*). Each of the cells divides into an outer and an inner cell, suggesting the primary wall cell and primary sporogenous cell of the cycads (*fig. 7*). The inner cells by further division produce a mass of deeply staining tissue beneath several layers of cells with scanty cytoplasm formed by the division of the outer cells (*fig. 8*). As soon as this stage is reached the walls of the central mass of cells begin to disintegrate, probably by becoming mucilaginous (*fig. 9*), as soon the nuclei appear to be floating in a cavity filled with mucilage. Then the nuclei also disintegrate, and some of them with the remains of their surrounding cytoplasm are flattened against the wall of the widening cavity, forming a tapetum-like layer (*fig. 10*). Finally the whole central mass is replaced by a mucilage cavity.

Discussion of the nature of the hump

The sporophylls of Ginkgo resemble those of Taxus and Torreya. Taxus has a group of sporangia, five or more in number, surrounding a central axis. Torreya has four sporangia on one side of the axis, but in the primary sporogenous cell stage seven sporangia appear; three of these disorganize, being replaced by a single large resin cavity, leaving only four to come to maturity. Ginkgo has two sporophylls on one side of the axis, surmounted by the conspicuous hump containing mucilage ducts. The development of the mucilage ducts from what appear to be abortive sporangia seems to indicate that the microsporophylls of Ginkgo may have come from a peltate type like that of Taxus. The fact that the sporophylls of living Ginkgo sometimes, and of fossil Ginkgoales as Baiera regularly, bear more than two microsporangia is additional evidence in favor of this view.

The case would be quite clear if evidence could stop with the hump, but in examining the mucilage ducts in the leaves, I find that they also at first look like sporogenous tissue (*fig. 11*). So there are three lines of development that resemble one another: the functioning sporogenous tissue, the mucilage ducts in the hump of the sporophyll, and the mucilage ducts in the leaves; all have the same early history, starting with one or more cells which divide periclinally into outer and inner cells, the inner by further division forming a deeply staining mass, the outer forming several layers of wall cells. The tissue formed in the functioning sporangium we know is sporogenous as it later produces spores; the tissue in the hump of the sporophyll that forms mucilage ducts, we think is sporogenous from analogy with Torreya and Taxus; but as to the mucilage ducts in the leaves we have no evidence that the tissue is sporogenous. Can we say that the ducts in the leaves, though they look like abortive sporangia, are not abortive sporangia, while the ducts in the hump having the same appearance are really abortive sporangia? On the other hand, does the presumption that the ducts in the leaves are not abortive sporangia forbid entirely the view that the ducts in the hump are abortive sporangia?

It seems reasonable to conclude, if the resin cavity of Torreya originates in abortive sporangia, that the mucilage ducts of Ginkgo also owe their origin to abortive sporangia.

Summary

1. The development of the strobilus proceeds from the bottom toward the top, the oldest sporophylls being at the base.
2. The development of the functioning microsporangium is probably like that of the cycads.
3. The development of the mucilage ducts in the hump of the microsporophylls is in general like that of sporogenous tissue.
4. This origin of the mucilage ducts in the hump may indicate that the microsporophylls of Ginkgo have come from a peltate type like the microsporophylls of Taxus.

I wish to acknowledge my indebtedness to Professor CHARLES J. CHAMBERLAIN, by whose suggestion and under whose direction the work was done.—ANNA M. STARR, *The University of Chicago.*

EXPLANATION OF PLATE VII

FIG. 1.—Longitudinal section of young strobilus, with sporophylls beginning to be evident; August 7. ×20.

FIG. 2.—Longitudinal section of older strobilus, with mucilage ducts (*d*) and sporogenous tissue (*s*) starting at the base; July 29. ×20.

FIG. 3.—Longitudinal section of strobilus older than *fig. 2*, showing development proceeding toward the top; August 7. ×20.

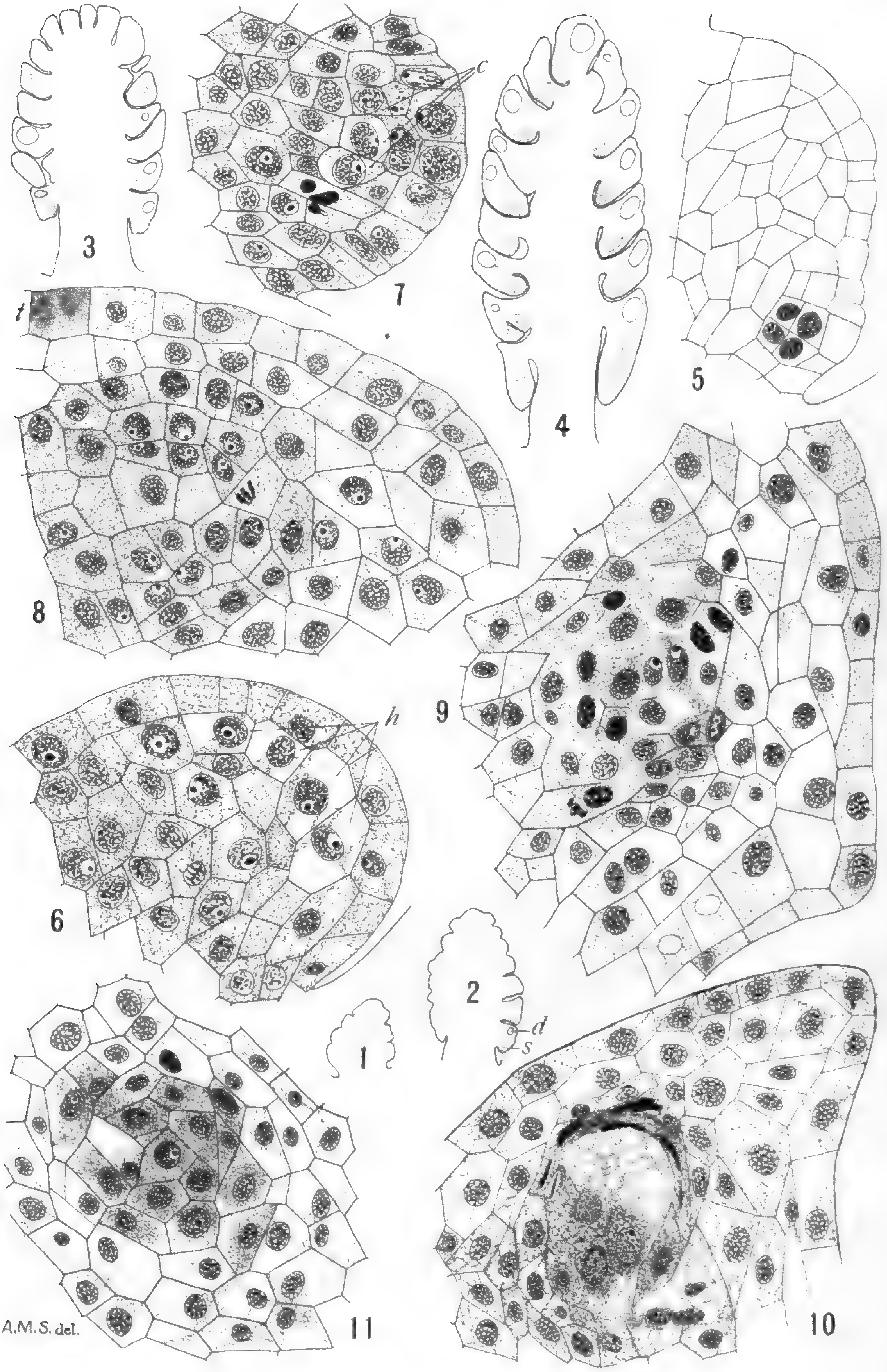
FIG. 4.—Longitudinal section of strobilus with mucilage ducts in all the sporophylls and the sporangia in the mother cell stage; September 2. ×20.

FIG. 5.—Longitudinal section of young sporophyll, showing four cells that have probably come from a single archesporial cell. ×485.

FIG. 6.—Longitudinal section of the hump of a young sporophyll showing a hypodermal plate of four cells (*h*) strongly differentiated. ×485.

FIG. 7.—Longitudinal section of the same region of another sporophyll with three hypodermal cells (*c*) that have divided periclinally. ×485.

FIG. 8.—Longitudinal section of the same region of an older sporophyll



STARR on GINKGO

showing differentiation into wall cells and a central mass of cells like sporogenous tissue. ×485.

FIG. 9.—The walls of the cells of the central mass are becoming mucilaginous and some of the nuclei are disintegrating. ×485.

FIG. 10.—The mucilage cavity is formed, some nuclei still floating in the fluid contents, others being flattened against the wall. ×485.

FIG. 11.—Section of an early stage of a mucilage duct in a leaf, showing cells resembling sporogenous tissue. ×485.

ALTERNATION OF GENERATIONS AND SEXUALITY IN *DICTYOTA DICHOTOMA*

After the failure of many attempts made during the past three summers to raise *Dictyota dichotoma* (Huds.) Lamour. from the spores and fertilized eggs to maturity, I have succeeded in raising nearly 100 plants to a fruiting condition. Since all attempts to raise plants to maturity in the laboratory have failed so far, the cultures were started in the laboratory and then transferred to the harbor. The method employed was as follows. Several days before the time for the maturing of the crop of sexual cells, when therefore no eggs were present in the water to serve as a possible source of contamination, two good fruiting tetrasporic plants were gathered late in the afternoon and placed in two jars of sea water, one in each jar. Since the spores will not attach themselves to glass, oyster shells which had lain on land for several years were placed in these jars. On the following day many tetraspores had been liberated and had attached themselves to the shells. The parent tetrasporic plants were then removed.

On the day when eggs and spermatozoids were mature, several sexual plants were gathered late in the afternoon and placed in a jar of sea water with oyster shells in the bottom, as before. Abundant liberation of eggs and spermatozoids occurred the next morning, as usual, and the parent sexual plants were then removed.

Three cultures were thus obtained, one containing fertilized eggs, and the other two containing tetraspores, each of the latter containing the spores from a single plant. These cultures were placed in front of a north window of the laboratory.

After about two weeks, when the young plants had reached a height of $1.5–2^{mm}$,[5] one shell bearing many young plants was removed from each of these jars and suspended between posts about 30^{cm} below low water in a favorable situation in the harbor, and all plants of Dictyota in the immediate vicinity were removed.

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[5] This rate of growth is probably less than normal, since plants of Dictyota grow much more slowly in cultures than they do under natural conditions.

After about two months, on the day when general liberation of the sexual cells occurred, when therefore all sexual plants could be certainly distinguished, these three shells were brought to the laboratory and examined. Each shell bore many plants of Dictyota 1.2–15^{cm} high.[6] Every plant was removed and examined under the microscope. The shell to which fertilized eggs had attached themselves bore 33 plants 2.5–15^{cm} high, all fruiting and all tetrasporic, as was shown by the presence of tetraspores or tetraspore mother cells on every plant. The two shells to which tetraspores had attached themselves bore 64 plants 2.2–13.75^{cm} high, all fruiting, and all sexual, and a few plants 1.2–2.5^{cm} high which were sterile. In handling these cultures many fragments were broken off; these were all examined with the microscope in order to be certain that no plant from any culture was overlooked. The evidence from these fragments agreed entirely with that given above for whole plants.

Since these cultures were placed in the open harbor, the possibility of contamination by spores or eggs floating in the water must be considered. In fact, a few specimens of several other species of algae and many animals (ascidians, worms, molluscs, hydroids, etc.) did attach themselves to the shells. However, the fact that all the 33 plants on the shell to which fertilized eggs had attached themselves were tetrasporic, and all the 64 fruiting plants on the shells to which tetraspores had attached themselves were sexual, seems convincing evidence that no contamination by Dictyota spores or eggs occurred. Thus the belief in the alternation of tetrasporic and sexual generations in *Dictyota dichotoma*, previously based on cytological evidence alone, seems proven by the results of these cultures.

As was noted above, each of the cultures of sexual plants was produced from the tetraspores of a single plant. One of these cultures bore 17 plants (14 females and 3 males), the other bore 47 plants (26 females and 21 males). The tetraspores of a single plant are thus seen to produce plants of both sexes. From the proportion of male and female in the latter culture and from the fact that plants gathered in the harbor at random show males and females in nearly equal numbers, the possibility is suggested that half of the tetraspores produce males and the other half produce females. Material has been preserved for a cytological study of this plant, to discover whether sex determinants occur in this species. These and other results bearing on the process of reproduction in Dictyota will be given in a subsequent article.

This work has been done at the laboratory of the Bureau of Fisheries

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[6] This rate of growth is much less than that observed in Dictyota under other conditions.

at Beaufort, N. C. I am indebted to Hon. George M. Bowers, U. S. Fish Commissioner, for the privilege of working in this laboratory, and to the director, Mr. Henry D. Aller, for many courtesies extended to me during this investigation.

Summary

Plants of *Dictyota dichotoma* raised from fertilized eggs gave 33 tetrasporic plants and no sexual ones. Plants raised from tetraspores gave 64 sexual plants and no tetrasporic ones.

The tetraspores of a single plant produced both male and female plants, in one case in about equal numbers.—W. D. Hoyt, *The Johns Hopkins University.*

MICROTECHNIQUE FOR WOODY STRUCTURES

In the preparation of thin sections (5 μ or less) of hard tissues the celloidin method has been largely used with excellent results. The method as originally described by Plowman[7] has been modified during the last few years at the laboratories of plant morphology of Harvard University, to meet the demands of work with special classes of hard tissues.

In reply to numerous inquiries as to the best method of preparing thin sections of woody tissues (trees and shrubs), and as to the advisability of using the celloidin technique, the following methods of treatment used in preparing slides for photomicrography, the study of wood structure, and instruction in wood technology are described.

1. Selection of material.—In working with old and thoroughly dried material, the blocks for treatment should be cut from the interior of the piece and as far from the finely checked outer surface as possible. Green material and sapwood are often preferable in working with the woods of gymnosperms, especially with the pines, in order to prevent shredding of the transverse sections and tearing-out of the resin canals. The blocks should be cut in such a manner that the faces represent sections which are as nearly transverse, radial, and tangential as possible. In working with soft woods, larger blocks may be used to advantage than with hard woods, and in the case of extremely hard woods the transverse face particularly must be trimmed down to small dimensions.

2. Boiling.—The blocks should be given a very thorough boiling in water to drive out the air and allow the hydrofluoric acid, used in the next step of the process, to penetrate to all parts of the wood. Repeated boilings and additions of cold water hasten the process of driving out the air.

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[7] Plowman, A. B., The celloidin method with hard tissues. Bot. Gazette **37**:456–461. 1904.

3. Demineralization.—It will be found advantagous to use much stronger solutions of hydrofluoric acid with the harder woods. The material should be allowed to remain about two weeks in a solution of one part commercial acid to one part water. In the case of very hard woods, such as live oak, ebony, eucalyptus, etc., pure acid may be used to advantage and the wood soaked two to three weeks. The percentage of solution and length of immersion depend on the hardness of the wood, and should be varied to meet the demands of each species. The acid should be thoroughly washed out, and the material left for several days in a mixture of one part 30 per cent. alcohol to one part glycerin.

4. Sectioning.—This part of the process requires considerable skill and experience, besides the use of the best microtomes and knives. The Jung sliding microtome for wood sectioning is the best, but needs much heavier and more solid carriers. The carriers should have long antifriction-metal bearings and some device similar to that provided with the celloidin microtome for adjusting the object carrier to the desired plane of section. The success of working the microtome depends upon keeping the knife absolutely free from nicks and extremely sharp, in having all the bearings free from dust and dirt and well oiled, in regulating the angle at which the knife cuts, and in orienting the surface of the block in accordance with the hardness and structure of the wood.

5. Use of celloidin.—The celloidin method is unnecessary in cutting thin sections of woody tissues except in the case of small fragments. Even the latter may often be cut successfully without imbedding by gluing to the carrier block with a few coats of 4 per cent. celloidin. In working with extremely soft woods, decayed woods, or in making careful studies of soft structures like the resin canals of the white pines, the celloidin method is useful.

6. Cutting without demineralization.—Sections of soft woods as thin as 5 μ may be cut after boiling without demineralization, but for this purpose an old knife which can be repeatedly honed and sharpened is needed.

7. Staining.—For most purposes the hematoxylin-safranin double stain is the most serviceable; but in studying special structures, such as spiral markings and the pitting of conifers, unstained sections mounted in glycerin jelly are preferable. In fact, in any given problem experiment with the various steps of the method is necessary to secure the best results. When the structures are obscured by deposits of resinous materials, tannins, etc., these must often be removed to reveal the pitting and sculpture of the cell walls.—Irving W. Bailey, *Harvard University.*

VIVIPARY IN *TILLANDSIA TENUIFOLIA* L.

(WITH ONE FIGURE)

SMALL, in his *Flora S. E. United States*, gives the range of this species of Tillandsia as in swamps and about rivers in Georgia and Florida, also in tropic America. Its normal method of reproduction is by small, light, pointed seeds, to which are attached a bunch of hairs that spread out at the top horizontally, thus acting as a parachute for wind carriage. This in connection with the epiphytic life is the most suitable method by which the seeds can find lodgment upon some limb or tree trunk and grow attached some distance above the ground.

FIG. 1

Another method of reproduction by the adoption of a viviparous habit was discovered in this plant in a specimen brought from the south on the branch of a forest tree which was hung in the greenhouses of the University of Pennsylvania. In the three or four plants examined, it was found that the seeds in all cases (*fig. 1, b*) had germinated in the capsules (*fig. 1, a*), and that the seedling plants thus produced (*fig. 1, c*) had two or three short shoots, as well as four or five awl-shaped leaves arranged in the tufted manner of the mature plant. These small plants were ready to fall out of the cells of the capsule whenever the dry valves spread far enough apart to permit this discharge to take place. Whether this viviparous habit is shown by all the species of Tillandsia, I cannot state, but it seems to be a method by which additional surety is given to the perpetuation of the species. —JOHN W. HARSHBERGER, *University of Pennsylvania*.

CURRENT LITERATURE

BOOK REVIEWS

Studies in fossil botany

SCOTT'S *Studies in fossil botany* has been the standard text in its field since 1900. It is not a text on paleobotany in the ordinary sense, but is restricted to the vascular plants, and in presenting them deals especially with their "morphological and evolutionary aspects." This means an expert culling of significant structures from the enormous mass of published paleobotanical material, and it has been of immense service to those morphologists who wish to use the historical background. During the present decade this kind of paleobotany has not only made notable advance in the precision of its methods, but it has made some very remarkable discoveries. The rapid progress in knowledge has compelled a second edition of SCOTT'S *Studies*,[1] which has grown from a book of 533 pages to one of 683 pages, the illustrations having increased from 151 to 213.

To note even all of the important changes would be impossible in a brief review, and this is not necessary for those morphologists who have followed the literature of the subject since 1900; but the assembling of the results recorded in scattered papers is very impressive. A few of the advances that should be borne in mind even by the general morphologist may be noted.

The primary divisions of pteridophytes are increased in number by the admission of NATHORST'S Pseudoborniales, discovered in the Upper Devonian of the arctic regions and described in 1902. These remarkable forms are known as yet only from impressions, but the stems are articulated, branching, probably creeping, bearing whorls of repeatedly dichotomous leaves with deeply pinnatifid leaflets and long loose strobili ("spikes") with whorled sporophylls resembling reduced foliage leaves.

The seedlike megasporangia of some of the paleozoic Lycopodiales, referred to briefly in the first edition, assume greater proportions in the second. The conclusion is becoming irresistible that no definition of a seed can be constructed which will exclude the megasporangiate structures of these ancient lycopods, and yet it is evident that they should not belong to the Spermatophyta. The definition of a great group can no longer be based upon a single character, but must be based upon a plexus of characters.

The presentation of paleozoic Filicales has been absolutely transformed. It is during the present decade that the "Pteridospermeae" have practically replaced the supposed paleozoic "ferns," and the present volume can claim only

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[1] SCOTT, DUKINFIELD HENRY, Studies in fossil botany. Second edition. 8vo. pp. xxiv+683. *figs. 213.* London: Adam and Charles Black. 1909. 10*s* 6*d*.

the Botryopterideae as sure representatives of paleozoic Filicales. It must always be remembered, however, that all the members of the great frond genera have not been proved to be seed plants, but they are all under suspicion.

Of course the "pteridosperms" are presented with a completeness that has not been possible heretofore. In traversing the evidence, SCOTT reaches the conclusion that every great frond genus is involved in the seed-bearing habit, and also in the discovery of stamens. It is of interest to note that the Crossotheca ("epaulet") type of stamens is probably the prevailing kind, and that the so-called Calymmatotheca ("cupule") type is likely to be the husk or cupule of seeds. The statement that *Gnetopsis elliptica*, which has been one of the guesses at a history for the Gnetales, is probably a seed of the Lyginodendreae relieves a very doubtful situation.

The perspective of the Cordaitales is increased by the recognition of Poroxylon and Pitys as intermediate in vascular structure between Lyginodendron and Cordaites, the gradation from the mesarch cylinder of the former to the endarch cylinder of the latter being very complete. As a consequence, the group Cordaitales is made to comprise Pityeae, Poroxlyeae, and Cordaiteae.

The mesozoic Bennettitales represent the second great vascular group that has been brought to light during the last decade, and their presentation is another new feature of the volume. WIELAND's laborious researches have developed a knowledge of this extinct and widely distributed cycadean group that almost rivals that of the living groups. SCOTT inclines to follow WIELAND's suggestion that the remarkable strobilus of Bennettitales must be taken into consideration in searching for the origin of the angiosperms, a view that is certainly not contradicted at present by the history of the two groups.

Perhaps the most significant suggestion in the volume is a proposed new classification of vascular plants. SCOTT evidently feels that the old division into pteridophytes and spermatophytes has about outlived its usefulness, a feeling doubtless shared by all morphologists who deal specially with the two groups. Whether the exact form of the suggestion will be acceptable or not remains to be seen, but the author is to be congratulated upon being bold enough to break the silence again. His suggestion is that vascular plants be grouped in three primary assemblages: *Sphenopsida* (Equisetales, Pseudoborniales, Sphenophyllales, Psilotales), *Lycopsida* (Lycopodiales), and *Pteropsida* (Filicales, Pteridospermeae, Gymnospermeae, and Angiospermeae). This crosses the old division, and the author expresses the opinion that "the traditional classification will no doubt continue to be used on grounds of convenience;" in fact, the two volumes, in which the present work also appears, bear the subtitles "Pteridophyta" and "Spermophyta." Pteropsida and Lycopsida are names proposed by JEFFREY, who made a similar proposition years ago. The former name is used as JEFFREY defined it; but the latter is limited to the Lycopodiales, as the only "typically microphyllous phylum." SCOTT does not think that the "sporangiophoric pteridophytes" (BOWER's name for SCOTT's Sphenopsida) show an affinity for the lycopods that would justify their inclusion under a common name.—J. M. C.

The mutation theory

In 1901 the first volume of DEVRIES'S *Mutationstheorie* was published, and was reviewed in this journal.[2] It put the doctrine of evolution upon an experimental basis and has been the stimulus of a large amount of important investigation. Such a contribution to biology is of the first order, whether the theory of mutation proves to be a general explanation of the origin of species or not. It has been unfortunate that many who are interested in evolution, even investigators, have not understood fully the theory of mutation, because they know of it only from condensed statements or reviews. This applies to all who do not read German or who do not read it with facility. This condition has now been remedied by the appearance of an Engish translation[3] of this great work. It is possible now for all English-reading biologists to judge of the theory from the full presentation by its author, and to substitute knowledge for superficial familiarity.

The full review of the original volume by this journal makes it necessary only to announce the appearance of the translation. And yet, eight years have elapsed since the theory was formally proposed and much could be said of its standing and influence. During the same period DEVRIES has twice visited the United States, and by conversation and lecture and personality has impressed himself and his views in a peculiar way upon American biologists. His influence upon scientific plant and animal breeding in this country has been very great, and the general result has been an increasing conviction that his views and his example have advanced biological science immensely.

The thesis of this first volume, as its author states, is the promulgation of the principle of unit characters. At the time of its announcement in 1900 this view was in opposition to the current belief; but the author is convinced that it has now gained almost universal acceptance. This conception that "the attributes of organisms consist of distinct, separate, and independent units" was derived chiefly from three sources: (1) an analysis of the processes of selection in practical plant breeding; (2) the experimental evidence afforded by Oenothera; and (3) Mendelism. This means that the origin of species by mutation is only one feature connected with the more fundamental conception of unit characters, and that a wide range of problems is opened up to experimental investigation. The only important change introduced into the translation is the incorporation of NILSSON'S results in the selection and improvement of cereals in Sweden.

The selection of translators could not have been more happy and effective; and the publishers are to be congratulated, not only for the worthy appearance of this book, but also for their real contribution to the advancement of knowledge in assuming the responsibility of publication.

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[2] BOT. GAZETTE **33**:236–239. 1902.

[3] DEVRIES, HUGO, The mutation theory; experiments and observations on the origin of species in the vegetable kingdom. Translated by J. B. FARMER and A. D. DARBISHIRE. Vol. I. The origin of species by mutation. 8vo. pp. xv+582. *colored pls. 6. figs. 119.* Chicago: The Open Court Publishing Company. 1909. $4.00.

The English translation will consist of two volumes, the second treating of the origin of varieties and also of the general problems of the origin of new forms. The second volume is announced to appear in April.—J. M. C.

MINOR NOTICES

Knuth's handbook.—The third volume of the English translation of KNUTH'S *Handbuch der Blutenbiologie* has just appeared[4] and completes the work. The original volumes and the two preceding volumes of the translation were reviewed in this journal,[5] so that the general scope and character of the work have been noted. The first volume is a general one, treating of the structure of flowers and of insects in relation to pollination. The second volume is a record of observations on flower pollination made in Europe and the arctic regions, arranged by natural orders and extending from "Ranunculaceae to Stylideae." The present volume continues the subject of the second and includes the natural orders from "Goodenovieae to Cycadeae." The encyclopedic character of the work may be judged by the fact that the second and third volumes contain observations on 1048 genera and 3112 species of plants. There is appended a systematic list of insect visitors recorded in these two volumes, arranged alphabetically and with the names of the plants visited, and the number of species reaches 2888.

Such a work cannot be reviewed, it can only be announced. The burden of translation must have been enormous, but it has introduced English-reading botanists to an immense body of facts, and may serve to stimulate work in this attractive field. The total cost of the three volumes ($24.25 in cloth, and $27.25 in half morocco) may seem somewhat prohibitive, but the work may be made available in libraries.—J. M. C.

A new laboratory guide.—The widespread interest in the teaching of botany in secondary schools is shown by the abundance of new textbooks and laboratory manuals. One of the latest of the latter is by CLUTE.[6] It is divided into two parts; the first deals with the usual topics in connection with the structure and activities of angiosperms, and the latter with the great plant groups. Its most striking features seem to be the small number of exercises, each of which is very comprehensive; the large number of suggestive questions; and the useful set of definitions accompanying each exercise. The directions to the pupil are mainly contained in the questions, and these are very numerous (99 in one of the exercises). Complete answering of these would demand careful study of the material used,

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[4] KNUTH, PAUL, Handbook of flower pollination, based upon HERMANN MÜLLER'S work "The fertilization of flowers by insects." Translated by J. R. AINSWORTH DAVIS. Vol. III. 8vo. pp. iv+644. *figs. 208*. Oxford: Clarendon Press. 1909. Cloth $8.75.

[5] BOT. GAZETTE **28**:280. 1899; **28**:432. 1899; **42**:494. 1906; **46**:63. 1908.

[6] CLUTE, WILLARD N., Laboratory botany for the high school. pp. xiv+177. Boston: Ginn & Co. 1909. 75 cents.

though possibly without sufficiently encouraging initiative. The book should be useful in classes somewhat above the grade of the first year in the high school, especially in those laboratories where very full directions are needed. At the same time, it is a question whether the author does not err, in common with many other writers of textbooks of this class, in giving structure complete predominance. In the study of living things it would appear that vital processes and relations should furnish the motive of the course. At any rate, it is scarcely fair to the pupil's perspective to relegate physiology to a few pages, in the nature of an appendix, with occasional references from the body of the text. One would prefer it to be an integral and important part of the laboratory directions.—W. L. EIKENBERRY.

North American flora.[7]—Volume XVI, part I, of this work contains an elaboration of the Ophioglossales-Filicales as follows: Ophioglossaceae by L. M. UNDERWOOD and R. C. BENEDICT; Marattiaceae by L. M. UNDERWOOD; Osmundaceae and Ceratopteridaceae by R. C. BENEDICT; Schizaeaceae, Gleicheniaceae, and Cyatheaceae (pars) by W. R. MAXON. New species are described in the following genera: Ophioglossum (1), Danaea (1), Marattia (1), Aneimia (7), Dicranopteris (1), and Cyathea (4).—J. M. GREENMAN.

NOTES FOR STUDENTS

Chromosome reduction in Oenothera.—DAVIS[8] publishes an account of chromosome reduction in *Oenothera grandiflora* which is a strong confirmation of the earlier work of GEERTS[9] on *O. Lamarckiana*, and of the reviewer on *O. Lamarckiana* and a number of its mutants and hybrids, especially *O. rubrinervis.*[10] As regards the main facts of reduction the results are the same in all three cases, and even many of the finer details of the reviewer's results are here corroborated, though there are evidently certain differences of behavior between *O. Lamarckiana*

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[7] North American Flora, Vol. XVI, part I, pp. 1–88. New York Botanical Garden. 1909.

[8] DAVIS, B. M., Cytological studies on Oenothera. I. Pollen development of *Oenothera grandiflora.* Annals of Botany **23**:551–571. *pls. 41, 42.* 1909.

[9] GEERTS, J. M., Beiträge zur Kenntnis der cytologischen Entwicklung von *Oenothera Lamarckiana.* Ber. Deutsch. Bot. Gesells. **26a**:608–614. 1908.

———, Beiträge zur Kenntnis der Cytologie und der partiellen Sterilität von *Oenothera Lamarckiana.* Rec. Travaux Bot. Néerlandais **5**:93–208. *pls. 5–22.* 1909.

[10] GATES, R. R., Pollen development in hybrids of *Oenothera lata* × *O. Lamarckiana,* and its relation to mutation. BOT. GAZETTE **43**:81–115. *pls. 2–4.* 1907.

———, Hybridization and germ cells of *Oenothera mutants.* BOT. GAZETTE **44**:1–21. *figs. 3.* 1907.

———, A study of reduction in *Oenothera rubrinervis.* BOT. GAZETTE **46**:1–34. *pls. 1–3.* 1908.

———, The behavior of chromosomes in *Oenothera lata* × *O. gigas.* BOT. GAZETTE **48**:179–199. *pls. 12–14.* 1909.

and *O. grandiflora*, as well as certain differences in interpretation, which will be pointed out.

The present account substantiates the earlier one in two fundamental points: (1) in synapsis the nuclear reticulum contracts into a ball, during which a more or less continuous thread is formed, but there is no evidence of a pairing of separate threads; (2) the thick spirem finally segments in such a way as to show that the chromosomes must have been arranged in a single series end-to-end. These are the two essentials of the method of heterotypic chromosome formation according to the account of FARMER and MOORE, MOTTIER, and others.

The author of the paper under review was formerly a strong advocate of the method of reduction by a lateral pairing of spirems previous to synapsis. This fact, together with the fact that he is the third investigator who has now given the same account as regards the essential points of chromosome reduction in Oenothera, places practically beyond question the presence of a telosynapsis (end-to-end pairing) instead of a parasynapsis (side-by-side pairing) in this genus.

In the nature of things, a lateral pairing of delicate threads previous to synapsis is more difficult to demonstrate than the cross-segmentation of a thick spirem after synapsis (see GATES **'08**, *figs. 22–26*). But ROSENBERG has reiterated his belief in a parasynapsis in Drosera, and has recently[11] brought forward some particularly clear evidence of a lateral pairing in that genus. A number of other investigators have given more or less convincing evidence of a parasynapsis in other forms. In the light of these facts it seems pretty evident that both these general methods of reduction occur in plants, a view which I have advanced in former papers. When cytologists become ready to admit that the evident differences in accounts of reduction are not all differences of interpretation, but are in many cases differences in fact, we shall have taken a forward step in the science and shall be ready to attack the problem of the meaning of the differences in chromatin behavior involved. To admit that *all* differences in accounts are due to real differences in chromatin behavior, would introduce laxity into interpretations which must necessarily always be critical, but nevertheless it must be admitted that in some of the more recent papers, clear and important differences in the method of the chromatin behavior have been established.

Several differences between DAVIS'S account of reduction in *O. grandiflora* and my account of that process in the *O. Lamarckiana* forms may now be pointed out. They are partly differences of interpretation and partly differences of fact. DAVIS states that the chromatic bodies in the resting nuclei are probably prochromosomes, but this is evidently the statement of a pious wish rather than an observation of fact, for he himself finds variation in the size and number of such bodies. He has unfortunately failed to distinguish between the true synapsis or synizesis, which is familiar to all cytologists as the stage in which the thin and delicate spirem is contracted into a ball, and the second contraction phase,

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[11] ROSENBERG, O., Cytologische und morphologische studien über *Drosera longifolia rotundifolia.* Kungl. Svenska Vetenskapsakad. Handl. **43**:1–64. *pls. 1–4.* 1909.

which comes much later in the history of reduction, after the spirem has undergone an enormous amount of shortening and thickening. In Oenothera it is a well-marked stage, immediately preceding the transverse segmentation of the spirem to form chromosomes; and separated from synizesis by a long interval, during which the spirem loosens its coils, enabling the rearrangement and thickening of the threads to go on.

The author's account of the heterotypic chromosomes in *O. grandiflora* shows an evident difference between this species and the *O. Lamarckiana* forms. In the former, rings are said always to be produced, although no adequate evidence of their method of origin is presented. While it is probable that many of the rings figured are really open at one end, or with the chromosomes merely in contact and not fused, yet a comparison of DAVIS's *figs. 27–30* with my *figs. 26–34* (*O. rubrinervis*, **'08**) shows that evidently the attraction which leads a chromosome to pair with its mate is greater in *O. grandiflora* than in *O. Lamarckiana* forms. This condition in *O. Lamarckiana* forms may have come about as a result of conditions of cultivation or hybridization, and, as I have pointed out elsewhere, may be directly connected with the mutation phenomena in *O. Lamarckiana*. Whether or not this is the case, I have shown that, as a result of this weak attraction between chromosomes, irregularities in chromosome distribution during reduction actually do occur.—R. R. GATES.

Cytology of the ascus.—BLACKMAN and Miss FRASER,[12] and more recently Miss FRASER[13] and Miss WELSFORD,[14, 15] have concluded that in *Humaria granulata*, *Ascobolus furfuraceus*, and *Lachnea stercorea* a normal sexual process does not obtain. Instead of a fusion of sexual nuclei in the oogonium, a reduced sexual process occurs in which the female nuclei fuse in pairs with a subsequent asexual fusion in the ascus.

Still more recently FRASER and BROOKS[16] have studied further the process of nuclear division, methods of chromosome reduction, and spore formation in the above-mentioned pseudo-apogamous forms. They find in each of these plants two sorts of reducing divisions occurring in the ascus. The first two divisions are heterotypic and homeotypic respectively, and thus bring about a chromosome reduction in the manner described for higher plants. They regard this type of reduction as being associated with fertilization or its equivalent. The third

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[12] BLACKMAN, V. H., AND FRASER, HELEN C. I., On the sexuality and development of the ascocarp of *Humaria granulata*. Proc. Roy. Soc. London B **77**:354–368. 1906.

[13] FRASER, HELEN C. I., On the sexuality and development of the ascocarp of *Lachnea stercorea*. Annals of Botany **21**:349–360. 1907.

[14] WELSFORD, E. J., Fertilization in *Ascobolus furfuraceus*. New Phytol. **7**:156–161. 1907.

[15] FRASER, H. C. I., AND WELSFORD, E. J., Further contributions to the cytology of the Ascomycetes. Annals of Botany **22**:465–477. 1908.

[16] FRASER, H. C. I., AND BROOKS, W. E. ST. J., Further studies on the cytology of the ascus. Annals of Botany **23**:537–549. 1909.

division of the ascus nucleus, which differs little in appearance from the normal vegetative type of division, is described as brachymeiotic, in which half the heterotype number of chromosomes is present, thus bringing about, as is believed, a second reduction in the number of chromosomes. In *Ascobolus furfuraceus* and *Humaria granulata* they find that the eight chromosomes are paired throughout the second and also in the prophases of the third division. In *Lachnea stercorea*, in which the meiotic prophases were studied more in detail, the heterotype number of chromosomes is four, two chromosomes being much longer than the other two. The first numerical reduction occurs by an end-to-end union of the chromosomes, which are subsequently separated transversely. In the third metaphase four chromosomes are present. Two entire chromosomes, one long and one short, pass to each daughter nucleus.

Brachymeiosis is believed to differ markedly from meiosis in several particulars. In meiosis it is held that the most essential feature seems to be the union of two chromosomes to form so-called gemini, while brachymeiosis may be accomplished without visible union of the chromosomes, as described for *Lachnea stercorea*, and when pairing does occur in this division, as described for *Ascobolus furfuraceus* and *Humaria granulata*, the opportunity for interchange of material is held to be much less than in meiosis. It is believed, therefore, that it is possible to distinguish between sexual and asexual fusions by a study of the subsequent reduction divisions. (The reviewer cannot agree with these authors that the distinguishing characteristic of meiosis, at least the visible distinction, rests on the close association of the chromosomes. The conspicuous fact is the formation of tetrads or so-called four-parted chromosomes. The formation of tetrads does not necessarily imply any very close association of the constituent parts of two-parted chromosomes.)

In the opinion of the authors the parental allelomorphs and also those brought together by the nuclear fusion in the ascus may show varying degrees of association, and this is brought out by a text figure, in which the forms here studied are compared with several other Ascomycetes. In *Humaria granulata* pairing of the chromosomes is present in the pre-meiotic divisions, while this pairing occurs in the meiotic prophases in *Ascobolus furfuraceus*, thus resembling *Otidea aurantia* and *Peziza vesiculosa* in this respect.

The authors also find that an important part is played by vacuoles in spore delimitation. They find in Ascobolus a differentiation into dense and vacuolated areas, but also that the center and astral rays are essential to spore delimitation. After the third division the cytoplasm becomes traversed by an irregular series of vacuoles or areas of cleavage, which separates the sporeplasms. It is held that a substance flows out from the center, capable of producing alterations in the cytoplasm, probably an enzyme. A definite membrane is put about the sporeplasm, and a similar one limits the neighboring periplasm, with a clear space between, marking the old lines of cleavage. Although these observations support FAULL's views, they also support the view that the astral rays play an important part in spore delimitation.—J. B. OVERTON.

A new color guide.—Several years ago I was appointed on a committee, with Dr. A. W. MURRILL and the late Dr. L. M. UNDERWOOD, by the American Mycological Society (now united with the Botanical Society of America) to prepare a color guide adequate to the needs of botanists and mycologists. After working on it for about two years I learned of a similar work in preparation by Dr. ROBERT RIDGWAY, the well-known ornithologist and author of a nomenclature of colors (1886) which contains 186 colors, shades, and tints. After a consultation with Dr. RIDGWAY, and later with the other members of the committee, it was decided to leave the field of color work to him. I am now glad to announce that Dr. RIDGWAY has been particularly fortunate in securing competent publishers, who state that the work will probably be ready in about six months. The chemist of the firm is an expert in colors, and has in fact been engaged at odd times for several years in preparing for a similar work. Dr. RIDGWAY has been at the revision of his old work, as his time would permit, for about twenty years, and it is safe to say that no similar work has ever been prepared with the same degree of physical and mathematical precision. This will be better understood by those familiar with MICHELSON's interferometer (an instrument by which it is possible to measure the wave-lengths of all light colors in millionths of a millimeter) when it is stated that each primary and secondary color in this work is a composite resulting from the measurement, in wave-lengths of light, of each color as represented in nine standard works upon the subject, the measurements being made by Professor P. G. NUTTING of the U. S. Bureau of Standards.

The work will contain 64 plates, each with 27 blocks of color, in three rows of nine blocks each, or a total of about 1350 blocks, the blocks being 1.25 by 2.5$^{\text{cm}}$, as in RIDGWAY's first color work. These will be named so far as possible, it being manifestly impossible to name all of them satisfactorily; and in addition the horizontal rows will be numbered and the vertical rows lettered, intermediate figures and letters between each row being used to represent intermediate shades or tints when that degree of accuracy is necessary. Instead of the degree of variation between blocks of color in various parts of the work being very unequal, as in all previous color guides of any size, the intermediate shades, tints, and hues are determined by a uniform scale of percentages by the use of MAXWELL's color wheel. There will be a probable edition of 2,500 copies, the volumes being about 14 by 20$^{\text{cm}}$, and 2.5$^{\text{cm}}$ thick. For field use it is expected about 800 of these copies will have their margins trimmed and be bound in flexible leather binding, easily fitting a coat pocket. The price with board covers will be about $5.00. The only work extant which approaches this in any respect is the *Répertoire de couleurs* of the Société Française de Chrysanthémistes, containing 1385 color shades and tints, of which only about 365 are named, and no method is provided for designating the others. It consists of two bulky volumes of loose plates in portfolios; many of the intermediate shades, tints, and hues are too near alike; and a prohibitive import duty brings the price in this country to about $10.00. The paper is too heavy, and its form entirely unsuited for field work.—P. L. RICKER, *Bureau of Plant Industry, Washington, D. C.*

Monograph of the Elaeagnaceae.—This elaborate paper by SERVETTAZ extends through 420 pages, and is a remarkable attempt by a single student to investigate every phase of a whole family. Naturally it is encyclopedic, and therefore cannot be reviewed in any real sense, but its general contents may be indicated. The first part[17] is concerned exclusively with the taxonomy of the family. The author recognizes two tribes and three well-marked genera: Hippophaë, Shepherdia, and Elaeagnus. The first genus is represented by a single species and three subspecies, the second by three species, and the third by 39 species, numerous subspecies and varieties, several of which are new to science. The genus Elaeagnus is divided into two sections, based on the time of flowering and the persistency of the leaves, and a very clear key leads to the species under which is given further a key to the subspecies and occasionally to the varieties, thus greatly facilitating the use of the monograph, particularly in the interpretation of the subordinate categories. Bibliography and synonomy, for the most part, are very fully given, but the few citations of American exsiccatae suggest a paucity of material as well as unfamiliarity with the names of American collectors. For instance, on page 21 we find under *Shepherdia canadensis* "no. 1205 Waghome," which is doubtless intended for WAGHORNE. Again, on the same page is noted "Charlotte Vermont no. 2452 Hall et Harbour;" this citation needs verification; it suggests a record made from a misleading label (HALL AND HARBOUR collected this species in Colorado and distributed it under 506). Furthermore, under *S. argentea* we find "Oregon no. 2013 Cusik," which is meant for the collection of WILLIAM C. CUSICK. These are minor details; nevertheless, they are inaccuracies in citation, and such inaccuracies often lead to confusion and are sometimes difficult of elimination. The descriptions are well drawn, the keys are clear, and the text figures are numerous. On the whole, therefore, the taxonomic part of the work represents a comprehensive and commendable study of the group.—J. M. GREENMAN.

The second part[18] deals with "anatomy and biology." The three genera above named are treated separately under each head, so that any anatomical, morphological, or "biological" fact belonging to any one of them may be looked up as readily as in a card catalogue.

The chapter titles of this second part are essentially as follows: (1) germination and the vegetation of the adult plant, (2) anatomy and development of the root, (3) anatomy and development of the stem, (4) anatomy and development of the leaf, (5) anatomy and development of the flower, fruit, and seed, (6) discussion of affinities, (7) summary and conclusions.

To the morphologist, as distinct from the anatomist, the items of interest recorded are the development of abundant sterile tissue capping the solitary

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[17] SERVETTAZ, CAMILLE, Monographie des Eléagnacées. I. Systematik. Beih. Bot. Centralbl. **25**:1–128. *figs. 15.* 1909.

[18] SERVETTAZ, Monographie des Eléagnacées. II. Anatomie et Biologie. *Ibid.* **25**:129–420. *figs. 140.* 1909.

megaspore mother cell; the appearance of an ordinary tetrad; the formation of a chalazal haustorium by the embryo sac, into which the three persistent and very active antipodal cells pass; and the development of a massive supsensor from the filamentous proembryo. The anatomical details are fully presented, and are directed chiefly toward taxonomic distinctions. The "biological" topics deal with the influence of various conditions (especially mesophytic), the crystals of calcium oxalate, starch, tannins, and elaeagnin. The taxonomist will discover that the three genera are quite justifiable, and will receive no shock upon finding that the family belongs just where it is now located in the ENGLER sequence.—J. M. C.

Cretaceous conifers.—The remarkable results obtained by HOLLICK and JEFFREY from a study of the plant remains preserved in Cretaceous clays of Staten Island have now been published.[19] Much of the material consisted of fragments of lignite, and this required the development of a special technic, which is described. Structural material of leafy twigs and cone scales was also secured. The recent and rapid organization of vascular anatomy as a scientific instrument is well exemplified in this memoir, not only in the identification of material, but still more in the interpretation of its significance.

The descriptions of specimens include three genera of Abietineae, Pinus (3 spp., 2 new), Prepinus (1 sp.), and Pityoxylon (1 sp.); but most important is the surprising display of Araucarineae, 16 genera being included, 9 of which are described as new (*Androvettia, Raritania, Eugeinitzia, Pseudogeinitzia, Anomaspis, Sphenaspis, Dactyolepis, Pityoidolepis, Brachyoxylon*), the remaining 7 genera being Widdringtonites, Thuites, Brachyphyllum, Geinitzia, Protodammara, Araucariopitys, and Araucarioxylon.

The great interest of these results lies in their bearing on the relationship of araucarians to the other conifers. The remains investigated include many that have been referred heretofore, from the appearance of their leafy branches or of their cones, to Taxodineae, Cupressineae, and Podocarpineae. The conifers referred to these tribes are now shown, by the microscopic structure of their leafy twigs and cone scales, to be araucarians, and represent a special subtribe, for which the name Brachyphylloideae is proposed. They are characterized by a special type of wood, the Brachyoxylon type, which is said to "ally them with both the Araucarineae (in the narrower sense) and the Abietineae." The authors believe that the araucarians of today have come from abietineous ancestors through Brachyphylloideae. The species of Pinus investigated are in general more archaic than any living species, and Prepinus shows structural features more primitive than in any other living or extinct conifer.—J. M. C.

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[19] HOLLICK, ARTHUR, AND JEFFREY, EDWARD CHARLES, Studies of Cretaceous coniferous remains from Kreischerville, New York. Mem. N. Y. Bot. Garden 3: viii + 138. *pls. 29.* 1909.

Enzymes of germination.—DELEANO[20] has made a somewhat disconnected study of the transformation of oil and the concomitant occurrence of various enzymes in the castor bean during the process of germination. The tables relating to the oil content of the seeds (freed from coats) on successive days of germination show that the oil content is practically constant during the first eight days of germination, after that decreasing so rapidly that by the fifteenth day it has nearly all disappeared. Samples equivalent to those used for analysis were taken each day, ground up, and subjected to autolysis in 50–100^{cc} of water, with a little toluene, for ten hours. The oil was saponified with increasing rapidity as germination advanced. Thus on the first day no autolysis took place; on the fourth day 5 per cent.; and on the sixth day 98 per cent. of the oil was hydrolyzed in ten hours. The accumulation of fatty acids did not take place. From these experiments the author concludes, in agreement as he supposes with LECLERC DU SABLON, that the oil is not saponified in the cells, but that saponification takes place only when the correlation of the cells is destroyed. This conclusion is scarcely warranted, since the products of hydrolysis of the oil are probably removed as soon as formed and still further changed. This is the almost universal course of enzymic activity in living plants, while it is also universally true that only when the correlation of the cellular processes is interrupted can the activity of the enzymes be clearly demonstrated by the accumulation of the products of enzymic activity.

The relative abundance of some of the enzymes at successive stages of germination was also determined. Catalase increases at first and then decreases with the disappearance of the oil. The oxidases increase for a time and then remain fairly constant. The author also believes that he has shown the presence of a reducing enzyme. The work on these enzymes is not of sufficient extent to allow any general conclusions regarding their functions.—H. HASSELBRING.

Ambrosia fungi.—NEGER has been giving attention to the fungi associated with certain insects, which utilize them for food. The monilia-like cells that the insects eat he proposes to call ambrosia, a generic term like nectar, bee-bread, etc., and the fungi are to be designated as ambrosia fungi. In his first paper[21] he considers the ambrosia galls (a happy substitute for zoomycocecidia) produced by gall-mites of the genus Asphondylia, in which the insect undergoes its development from egg to imago. The gall cavity is lined with a hymenium-like layer of fungus filaments producing spherical monilia-like cells, the ambrosia. Later pycnidia are formed on the external surface of the gall after the insect has

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[20] DELEANO, N. J., Recherches chimiques sur la germination. Centralbl. Bakt. Parasit. Infectionskrank. **24**^{2}**:**130–146. 1909.

[21] NEGER, F. W., Ambrosiapilze. Ber Deutsch. Bot. Gesells. **26a:**735–754. *pl. 12. figs. 2.* 1908.

escaped. The fungi peculiar to these galls belong to the genus Macrophoma, and are not referable to the species of Phoma that inhabit the same hosts.

In a second paper[22] NEGER treats the fungi associated with certain wood-boring beetles, *Xyloterus dispar*, *X. lineatus*, and *Hylecoetus dermestoides*, which form ambrosia upon the walls of their tunnels. The fungus related to Hylecoetus is probably a species of Endomyces; the other two are closely similar, but not identical, and are not identifiable. The species of Ceratostomella, which NEGER formerly mistook for ambrosia fungi in this case, are merely weeds in the fungus garden (as are also yeasts and bacteria), which have no part in producing the edible cells. The larvae of these beetles have thus, in their mouths almost, nutritious food abstracted by the vegetative mycelium from the more distant wood cells, instead of the relatively poor food, the wood itself; moreover, the borings are confined to the sap-wood, where the fungi find appropriate conditions for growth.—C. R. B.

Ovule and ovulate flower of Juglans.—BENSON and WELSFORD[23] have investigated the ovule and ovulate flower of Juglans in reference to the discordant results obtained by VAN TIEGHEM (1869) and NICOLOFF (1905). The "allied genera" examined for comparative study were Myrica, Carpinus, Morus, Urtica, and Rheum. In brief, it may be said that the account of VAN TIEGHEM was confirmed in all particulars. Interesting phases of "reduction" exhibited by the flowers of *Juglans regia* are as follows: (1) the origin of a dimerous condition from a trimerous, (2) barren placentae with a vascular supply, (3) one mode of the phylogenetic origin of the orthotropous basal ovule from an anatropous parietal type.

More extended conclusions deal with the so-called epigyny of the group considered, and with the ovule in angiosperms. The investigators find in the group "no trace of that form of epigyny which is brought about by the concavity of the axis and sinking and inclusion of the ovary within it," which description hardly applies to epigyny anywhere. It is concluded that the described epigyny of Amentiferae need not be regarded as an advanced character, and that the term had better be avoided. The conclusions as to the ovule of angiosperms are: (1) it is appendicular, (2) it is phylogenetically provided with a dual integument, and (3) the vascular supply may be compared with that of the outer integument or "cupule" of Lagenostoma.—J. M. C.

Aridity and evolution.—Of the external factors which have influenced or caused the evolution of the plant kingdom, MACDOUGAL[24] places much stress

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[22] NEGER, F. W., Ambrosiapilze II. Ber. Deutsch. Bot. Gesells. **27**:372–389. *pl. 17. figs. 2.* 1909.

[23] BENSON, M., AND WELSFORD, E. J., The morphology of the ovule and female flower of *Juglans regia* and of a few allied genera. Annals of Botany **23**:623–633. *figs. 8.* 1909.

[24] MACDOUGAL, D. T., Influence of aridity upon the evolutionary development of plants. Plant World **12**:217–231. 1909.

upon the abundance of the water supply. Assuming that free water was a very important agent in the origination of living matter, the development of the gametophytic stage of plant life is shown to be dependent upon the same factor. As aridity was encountered over extended land areas, the stress thus produced led to the development of the sporophyte with its vascular system and finally its seed habit. The earlier geological strata from arid areas contain no plant fossils, because at that period vegetation was characterized by the predominance of plants with separate gametophytes. Cycads and Bennettitales were the first plants to show xerophytic structures, and from their beginning the history of desert forms may be traced. Aridity, causing the reduction of surface area and the thickening of tissues, has evolved spinose and switchlike forms; while in the regions of most extreme aridity this evolutionary development has gone much farther, with the development of remarkable storage structures in leaf and stem organs. These succulent xerophytes represent the highest degree of differentiation in seed plants, and are found most abundantly in the very arid regions of the Karoo in South Africa, in the deserts of Brazil and Chili, in the arid regions of southern Mexico, and in the Sonoran and Chihuahuan deserts.—GEO. D. FULLER.

Algae in the laboratory.—Teachers will be interested in the practical methods which have made NIEUWLAND[25] so successful in growing algae in the laboratory. Large aquaria are not necessary, the best results often being obtained with gallon or two-gallon jars. The commonest mistake is to change the water, even the single change usually involved in bringing algae from the field to the laboratory often being disastrous. It is safer to bring the water in which the plants are growing. When necessary to renew the water, not more than one-fifth the volume should be added, and tap water should be allowed to run for a moment to avoid the introduction of undesirable salts. Bacterial decomposition is best prevented by introducing only a small amount of material, not more than one cubic inch to the gallon. As the material grows, the increasing amount can be accommodated because of the developing adaptation to the environment. A few plants of Chara are often desirable, since they prevent the water from becoming too hard, and a little Utricularia will rid the culture of undesirable animal life. When the algae disappear, the culture should not be thrown out, for the forms usually reappear after a time. Mud and sticks from spots where algae have been noticed may be brought into the laboratory in midwinter and soon yield vigorous cultures. Detailed directions are given for securing and keeping many of the most desirable laboratory types.—CHARLES J. CHAMBERLAIN.

A new maize from China.—The Department of Agriculture has been investigating a new type of corn received from near Shanghai, China, in March 1906,

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[25] NIEUWLAND, J. A., Hints on collecting and growing algae for class work. Midland Naturalist **1**:85–97. 1909.

and the results have just been published by COLLINS.[26] It is distinct from all hitherto known types in its erect and one-ranked leaf blades, in the development of its "silks" while still within the leaf sheath, and in its peculiar endosperm. The first two of these unique characters insure pollination and prevent the drying-out of the silks, the pollen being blown against the erect leaf blades and accumulating at their bases, and the silks pushing into these accumulations before they are exposed to the air. The endosperm is neither starchy nor horny, resembling the latter in location and hardness, but having the texture and optical properties of very hard wax, and hence the suggested name is "waxy endosperm." The xenia characters in hybrids showed that colored aleurone is dominant to transparent, yellow endosperm to white, and horny endosperm to waxy. This Chinese corn also raises the question as to whether maize was known in China before the discovery of America. That it is of American origin does not seem to be open to doubt, but Chinese literature of the sixteenth century refers to its introduction and widespread use, and this specialized type may have developed in China.—J. M. C.

Leaf structure of strand plants.—HARSHBERGER[27] has studied the leaves of twenty plants from the sandy shores of New Jersey and eleven from its salt marshes. All exhibit xerophytic structures and almost without exception have thickly cutinized epidermis. Four of the strand plants and six of the salt marsh species are succulents, while nine from the strand and three from the salt marsh have epidermal hairs. The drawings will form convenient plates of reference for students interested in these plants. It is to be regretted that they are not on a larger scale and that more attention has not been given to the differentiation of chlorophyll-bearing and mechanical tissues. The same criticism will apply to a previous paper by the same author[28] on the sand dune plants of Bermuda, which records observations for the leaves of seventeen plants. The author is confident that the various xerophytic leaf structures have been produced largely in response to intense illumination, exposure to strong winds, and in a few instances to the action of salt spray blown inland. He is inclined to overemphasize the influence of light, and says "chlorenchyma is converted into two kinds of tissues, palisade and spongy parenchyma, as a direct result of the unequal illumination of the leaf surfaces."—GEO. D. FULLER.

Ferments of fungi.—PRINGSHEIM and ZEMPTEN[29] have applied the Buchner method of extracting enzymes from yeast cells to the extraction of sugar-splitting

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[26] COLLINS, G. N., A new type of Indian corn from China. Bull. 161, Bureau Pl. Ind., Depart. Agric. pp. 30. *pls. 2.* 1909.

[27] HARSHBERGER, JOHN W., The comparative leaf structure of the strand plants of New Jersey. Proc. Amer. Phil. Soc. **48**: 72–89. *pls. 2–5.* 1909.

[28] ———, The comparative leaf structure of the sand dune plants of Bermuda. Proc. Amer. Phil. Soc. **47**: 97–110. *pls. 1–3.* 1908.

[29] PRINGSHEIM, H., AND ZEMPTEN, G., Studien über die Polysaccharide spaltenden Fermente in Pilzpresssäften. HOPPE-SEYLER'S Zeitschr. Physiol. Chemie **62**: 367–385. 1909.

ferments of various fungi. The results constitute a number of detached facts not readily summed up in a review; however, some of the main points may be noted. The press-extract of some of the fungi was found to be incapable of splitting any of the sugars used, while the residue was found capable of active fermentation, showing that the ferments in these cases are incapable of being separated from the rest of the cell by the Buchner process. In the case of *Aspergillus Wentii*, both the extract and the residue fermented cane sugar, milk sugar, maltose, cellobiose, and raffinose. It is of special interest to note that some of the fungi were able to utilize as food disaccharides, which neither the expressed juice nor the residue were able to ferment. These sugars were probably assimilated directly. The behavior of raffinose varied with different fungi. With *Aspergillus Wentii* this sugar was split into *d*-glucose, *d*-fructose, and *d*-galactose. In five other cases it was split into *d*-fructose and melibiose, and in three cases into *d*-galactose and cane sugar.—H. HASSELBRING.

The ring and cell wall of Oedogonium.—According to VAN WISSELINGH,[30] the cell wall of Oedogonium consists of two distinct layers; the outer containing little cellulose, but a large proportion of a characteristic membrane-forming material whose reactions are described, but whose chemical composition was not determined; while the inner wall is rich in cellulose and has a lamellate structure. The outer layer is lacking in the basal cell. The ring is a portion of the cell wall which arises by the intussusception of various membrane-forming materials, among which cellulose is prominent, especially in the centripetal portion. The rupture of the old wall and the stretching of the ring to form a new wall is about as usually described. The inner cellulose layer of the wall arises by apposition. The chemical tests and the observations are satisfactory so far as they go, but the subject is a much described and much discussed one, and it would seem that an investigator acquainted with technic, as VAN WISSELINGH is, could have advanced our knowledge much farther by adding a study of carefully stained sections.—CHARLES J. CHAMBERLAIN.

Anatomy of Saxegothaea.—TISON[31] has investigated the vascular anatomy of *Saxegothaea conspicua*, especially that of the ovulate strobilus. This genus has received much attention recently (NORÉN, STILES, THOMSON), and investigators have been impressed by its suggestion of araucarian affinities. TISON concludes, from the behavior and distribution of the two systems of bundles found in the megasporophyll (one serving the sporophyll and the other the ovule), that Saxeogothaea is more nearly related to the araucarians than to the podocarps, but that through Microcachrys it is so definitely connected with the latter that the araucarians, Saxegothaea, and the podocarps should constitute a single group,

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[30] WISSELINGH, C. VAN, Ueber den Ring und die Zellwand bei Oedogonium. Beih. Bot. Centralbl. **23**:157–190. *pls. 13–16.* 1908.

[31] TISON, A., Sur le *Saxegothaea* Lndl. Mém. Soc. Linn. Normandie **23**:139–160. *pls. 9, 10.* 1909.

with the three subdivisions indicated. This conclusion depends upon the view that the structure of the ovulate cone, especially its vascular structure, is the paramount feature in determining relationship. An interesting incidental suggestion (following BERTRAND) is that the aril of Saxegothaea is the equivalent of the ligule of Araucaria and the ovuliferous scale of other conifers.—J. M. C.

A primitive lichen.—*Botrydina vulgaris*, regarded in general as a problematical green alga, has now been investigated by Miss ACTON.[32] It occurs as dark green, globular structures, which in the material examined were covering the shoots of a moss and a liverwort. Each one of these structures proved to consist of a central group of algal cells imbedded in mucilage, which in turn was traversed by investing fungal hyphae that formed also a colorless envelope of considerable thickness. The cultures showed that both the alga and the fungus are "able to develop quite well apart, and multiplication of Botrydina is probably due to this." Since this structure consists of an alga and a fungus growing symbiotically, the conclusion is that it should be regarded as a lichen, and that it is "possibly one of the most primitive of existing lichens." The alga and the fungus were both determined, and the habitat is said to be "in damp shady situations among various bryophytes, generally on rocks, but sometimes on damp ground."—J. M. C.

Movements of Myriophyllum leaves.—WÄCHTER has recorded[33] some interesting phenomena regarding the young leaves of *Myriophyllum proserpinacoides*. The leaves of both the land and water form of this plant have already been known to execute so-called sleep movements, so long as they are capable of growth; and such movements would be very properly called photonastic.[34] In studying these movements WÄCHTER has discovered that leaves which had almost or quite ceased to respond to light would resume these curvatures if the shoot were decapitated. This seems to be a phenomenon analogous to the reactivation of growth in the nodes of grasses under a gravity stimulus, and still more like the reaction of certain conifers to decapitation, though different in details from either. It has also relations to the excitation of growth by a wound stimulus, and compensative growth such as that in Streptocarpus when the big cotyledon is removed or incased in plaster and the small one resumes its development.—C. R. B.

The mycorhiza of Cordaites.—*Amyelon radicans* is a root of the Coal Measures, which has been shown to belong to Cordaites. It bears such remarkable and irregularly arranged bunches of lateral roots, that OSBORN[35] has examined

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[32] ACTON, ELIZABETH, *Botrydina vulgaris* Brebisson, a primitive lichen. Annals of Botany **23**: 579–585. *pl. 44*. 1909.

[33] WÄCHTER, W., Beobachtungen über die Bewegungen der Blätter von *Myriophyllum proserpinacoides*. Jahrb. Wiss. Bot. **46**:418–442. *figs. 2*. 1909.

[34] Cf. BOT. GAZETTE **48**:313. 1909.

[35] OSBORN, T. G. B., The lateral roots of *Amyelon radicans* Will., and their mycorhiza. Annals of Botany **23**:603–611. *pls. 46, 47*. 1909.

them to discover if these bunches might correspond in any way with the "root tubercles" of recent plants. As only one such case has been recorded from the Coal Measures, the result is of special interest. These lateral roots are found to have a thick cortex divisible into two regions, the inner of which contains dark cells that show evident fungal hyphae. The fungus occurs in knots of non-septate hyphae that bear sometimes terminal vesicles, but there was no trace of any spore-formation. The conclusion is reached that "Cordaites was probably a tree inhabiting saline swamps, and having bunches of coralline rootlets on its roots, such as are known to occur in many recent plants growing under similar conditions."—J. M. C.

Anatomy of Equisetum.—EAMES[36] has discovered that although the xylem of Equisetum is centrifugal throughout the vegetative stem, it is also centripetal in the axial bundles of the strobilus and of the sporophylls; in the former the bundles are "weakly mesarch," in the latter "strongly so." This suggests that the most primitive representatives of Equisetales had well-developed centripetal wood, and connects them with such ancient forms as Sphenophyllales, already suggested by SCOTT's discovery of centripetal wood in a calamite. All the large groups of pteridophytes are now known to possess centripetal wood, so that "such bundles in higher plants can be of no other phylogenetic value than as indicating general cryptogamic affinities." At the same time, Equisetum confirms the value of the leaf gap as a phylogenetic character, since in no case does the passage of a leaf trace from the stele leave a gap.—J. M. C.

Protection against light.—MARLOTH describes some very remarkable ways in which a few African desert plants reduce the amount of light which the green tissues of their leaves receive.[37] He refers to three categories: (1) plants with fleshy and green leaves, having membranous stipules which extend beyond and conceal them; (2) plants with fleshy and green leaves, without stipules, but invested by the dried-up remnants of the older leaves; (3) plants with windowed leaves. This most curious arrangement is characteristic of plants with very fleshy leaves whose blunt, plane, or erose tips alone reach the surface of the soil, the body of the leaf being completely buried. This exposed tip lacks chlorophyll, and through this as through a window the light reaches the green tissue, which is restricted to the sides of the fat leaf. Several species of Mesembryanthemum have this peculiarity.—C. R. B.

"Transpiration" in aquatics.—Under a similar misleading title THODAY and SYKES[38] present a brief account of a few experiments that show movement of

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[36] EAMES, ARTHUR J., On the occurrence of centripetal xylem in Equisetum. Annals of Botany **23**:587–601. *pl. 45.* 1909.

[37] MARLOTH, R., Die Schutzmittel der Pflanzen gegen übermässige Insolation. Ber. Deutsch. Bot. Gesells. **27**:362–371. *figs. 2.* 1909.

[38] THODAY, D., AND SYKES, M. G., Preliminary observations on the transpiration current in submerged water-plants. Annals of Botany **23**:635–637. 1909.

water through the stems of submerged aquatics. To call such a stream "the transpiration current" is manifestly absurd, unless one changes the meaning of the word transpiration. It will be remembered that others have found evidence of like movements, so that these new experiments only add somewhat clearer evidence as to its existence, which the most elementary consideration of the physical conditions would lead one to expect. Yet these authors naïvely say: "Probably external conditions also affect the results; this point we hope to investigate later." This really is the fundamental point: does not the heating of the leaves create the conditions for the circulation of water as truly in this case as in a house heating system?—C. R. B.

Fixation of free nitrogen.—POLLACCI reports in a preliminary note[39] that in a large number of experiments he has demonstrated the fixation of free nitrogen in such plants as lichen, salvinia, azolla, fern prothallia, and duckweed. The increase of total N in a few cases cited amounts to 33–67 per cent. The full paper will be awaited with interest. POLLACCI has a heavy weight of adverse evidence to counterbalance. He indicates that the contradictory results of the earlier observers, e. g., BOUSSINGAULT and VILLE, were probably due to differences in the capacity of different plants for this fixation. It is to be remembered, however, that all the recent evidence under improved chemical methods is adverse to the idea that ordinary plants are able to utilize N_2.—C. R. B.

Prothallium and embryo of Danaea.—CAMPBELL[40] has made a preliminary investigation of the prothallium and embryo in several species of Danaea secured in Jamaica. The archegonia are remarkable for the imperfect development of the ventral canal cell, which in many cases could not be demonstrated at all. The fertilized egg becomes elongated in the direction of the axis of the archegonium before the first division. The hypobasal cell does not divide or there is a single division, resulting in a short suspensor, all of the regions of the embryo arising from the epibasal cell. This cell gives rise to somewhat irregular quadrants, the two lower ones forming the foot, and the two upper giving rise to stem tip and leaf, and later to the root.—J. M. C.

Chromosomes of Hyacinthus.—Miss HYDE[41] finds that in Hyacinthus in the prophase of the heterotypic mitosis the spirem twists into 8 loops which become 8 chromosomes. The loops break apart at the center so as to form 8 bivalent chromosomes. When fully formed, the chromosomes show a striking difference in size, 4 being comparatively large, 3 small, and the remaining one intermediate.

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[39] POLLACCI, G., Ricerche sull' assimilazione dell' azoto atmosferico nei vegetali. Atti Ist. Bot. Univ. Pavia II. **13**:351–354. 1909.

[40] CAMPBELL, D. H., The prothallium and embryo of Danaea. Preliminary note. Annals of Botany **23**:691. 1909.

[41] HYDE, EDITH, The reduction division in the anthers of *Hyacinthus orientalis* Ohio Naturalist **9**:539–544. *pl. 32.* 1909.

Miss HYDE believes that the two chromosomes which must have united to form a bivalent chromosome are alike in size and shape, and that they represent paternal and maternal bodies. If extended observation should show that the differentiation of chromosomes shown in the figures is constant, this form would repay a thorough investigation.—CHARLES J. CHAMBERLAIN.

Apogamy in Oenothera.—In connection with his cultures of Oenothera, GATES[42] has discovered apogamy in *O. lata*, one of the mutants of *O. Lamarckiana*. The anthers of *O. lata* from the Amsterdam cultures are persistently sterile, and this fact, associated in certain other genera with apogamy, suggested the possibility of apogamy in this form. To determine this, the anthers and styles of several flowers (on one individual) were removed and the flowers bagged as usual in making guarded crosses. All of these flowers gave negative results except one, which produced three fairly good seeds. The cytological investigation necessary to substantiate and explain this result is being made.—J. M. C.

Heath vegetation.—Some of the ecological similarities of the coastal and barren regions of New York and New Jersey and the heath of Luneneburg are pointed out by LIVINGSTON,[43] who would account for the desert-like aspect of the vegetation of the heath of Luneneburg by the too rapid drainage of the soil and the short growing season. The areas of bog or marsh found scattered through the heath are also physiologically dry, perhaps mainly because of the toxic organic matter present in the soil; hence such areas differ little in aspect from the heath. Both the heath and the moor are dominated by *Calluna vulgaris*, while *Juniperus communis* is conspicuous on the open heath.—GEO. D. FULLER.

The "knee joint" of Mougeotia.—Observations upon several species of Mougeotia indicate to NIEUWLAND[44] that the prevalent interpretation of "knee joints" as a stage in conjugation is incorrect, for the joints are present only in vegetative stages and never in typically conjugating material. Usually the cells of the filament hold together so firmly that the cells break through the middle rather than separate at the ends, but in material with the knee joints, the cells are easily dissociated, and, succeeding the appearance of the joints, the amount of material increases enormously, so that the joints seem to be related to vegetative multiplication.—CHARLES J. CHAMBERLAIN.

Absorption of water by leaves.—In a lecture before the Royal Horticultural Society of London,[45] HENSLOW presented reasons derived from the older experiments and some recent ones by himself (which, by the way, are not all well con-

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[42] GATES, R. R., Apogamy in Oenothera. Science N. S. **30**: 691–694. 1909.

[43] LIVINGSTON, B. E., The heath of Luneneburg. Plant World **12**: 231–240. 1909.

[44] NIEUWLAND, J. A., The "knee joint" of species of Mougeotia. Midland Naturalist **1**: 82–84. 1909.

[45] HENSLOW, G., On the absorption of rain and dew by the green parts of plants. Jour. Roy. Hort. Soc. London **34**: 167–178. 1908.

ceived or convincing) that the leaves of plants admit water. He therefore justifies the practice of spraying the foliage. The most positive evidence that leaves admit water, as well as an indication of the magnitudes involved, is to be found in the cuticular evaporation. This does not seem to have occurred to HENSLOW, perhaps because he does not conceive of absorption and evaporation as a physical process.—C. R. B.

Imbedded antheridia in Dryopteris and Nephrodium.—In cultures of these two ferns to obtain apogamy, Miss BLACK[46] discovered "imbedded antheridia" in prothallia of both species, that is, such antheridia as occur in the eusporangiate forms. Although apogamy was not induced, these antheridia are of sufficient interest to justify the cultures. The association of the two kinds of antheridia in the same form, dependent upon conditions, is well known in Equisetum, but it does not seem to have been recorded before for ferns.—J. M. C.

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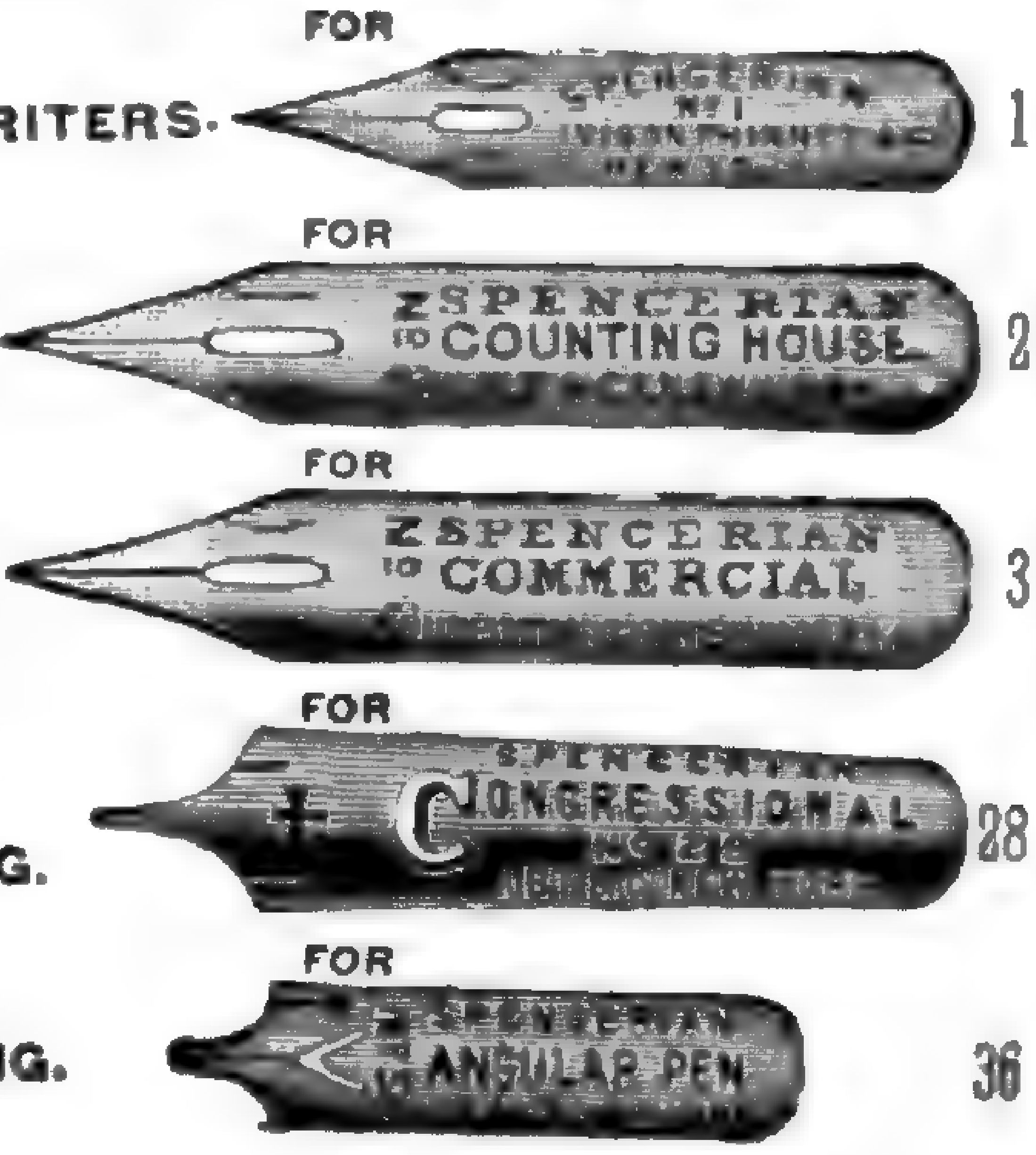
[46] BLACK, CAROLINE A., The development of the imbedded antheridium in *Dryopteris stipularis* (Willd.) Maxon and "*Nephrodium molle.*" Bull. Torr. Bot. Club **36**:557–571. *pls. 26–28.* 1909.


HORSFORD'S
Acid Phosphate
Wakefulness, Nervousness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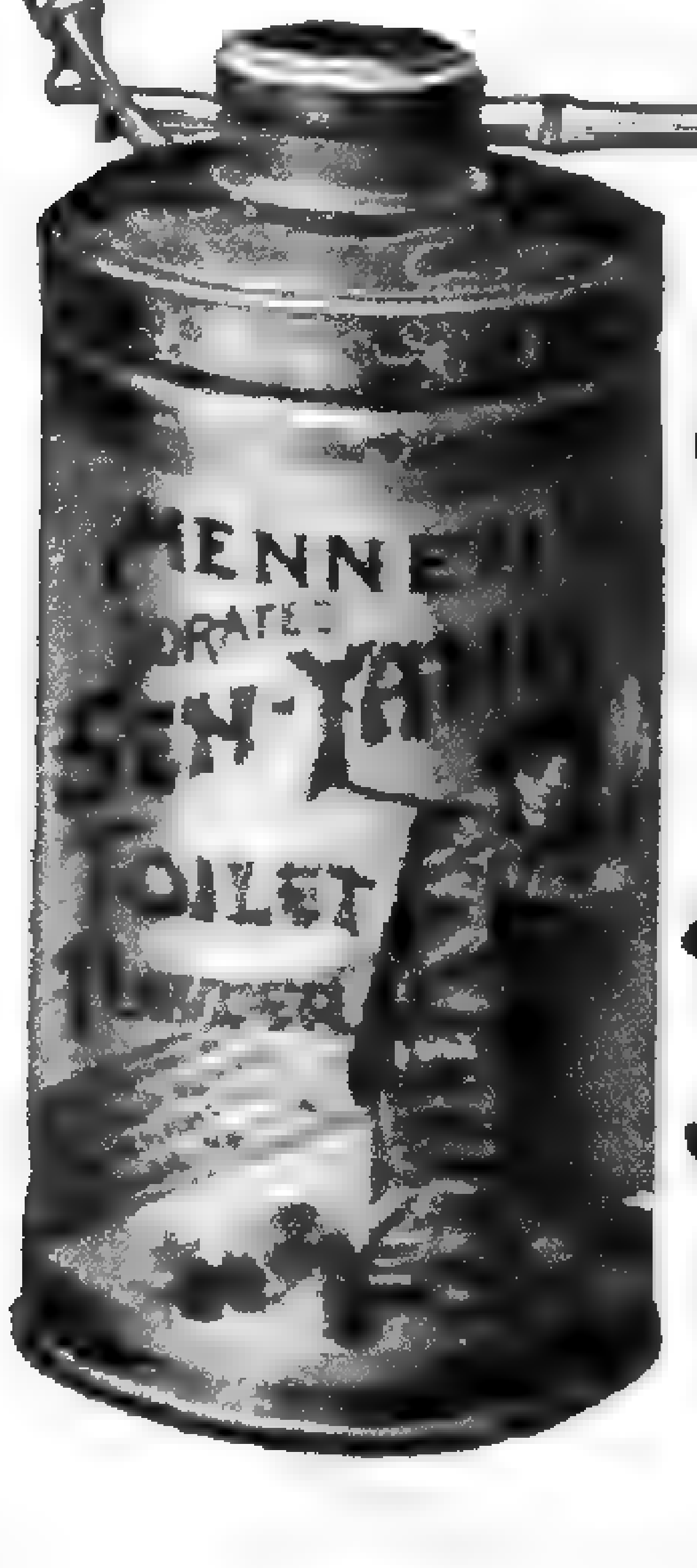
MENNEN'S
BORATED
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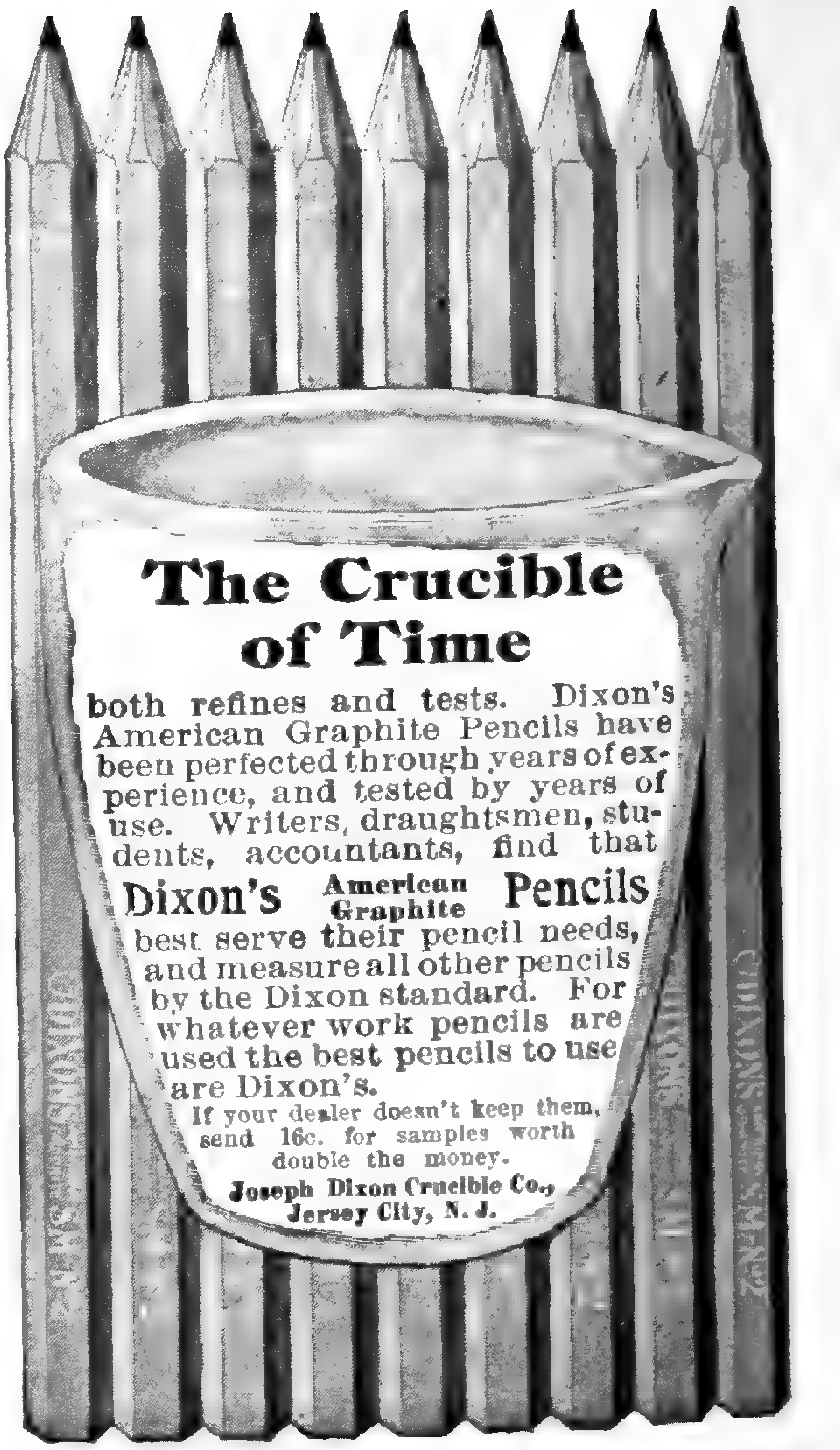

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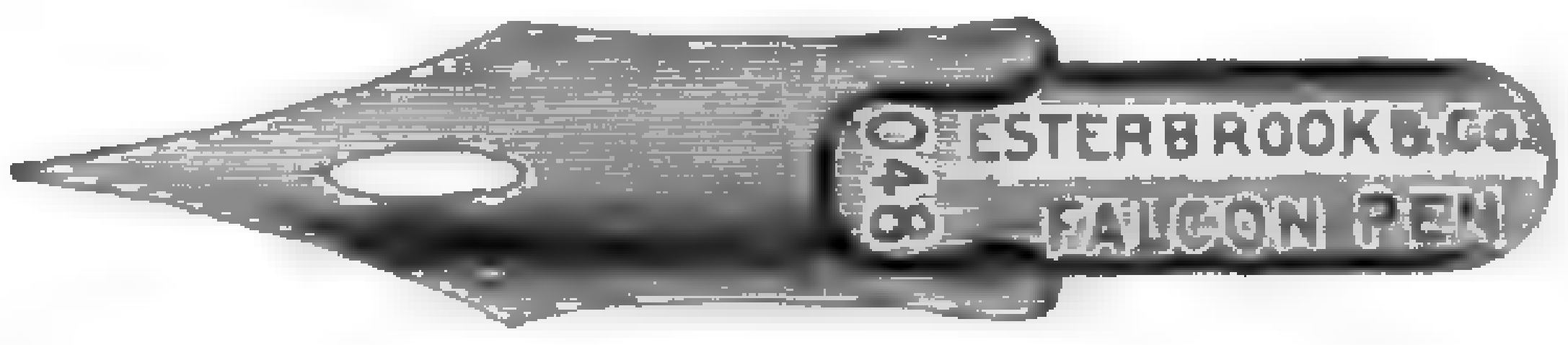
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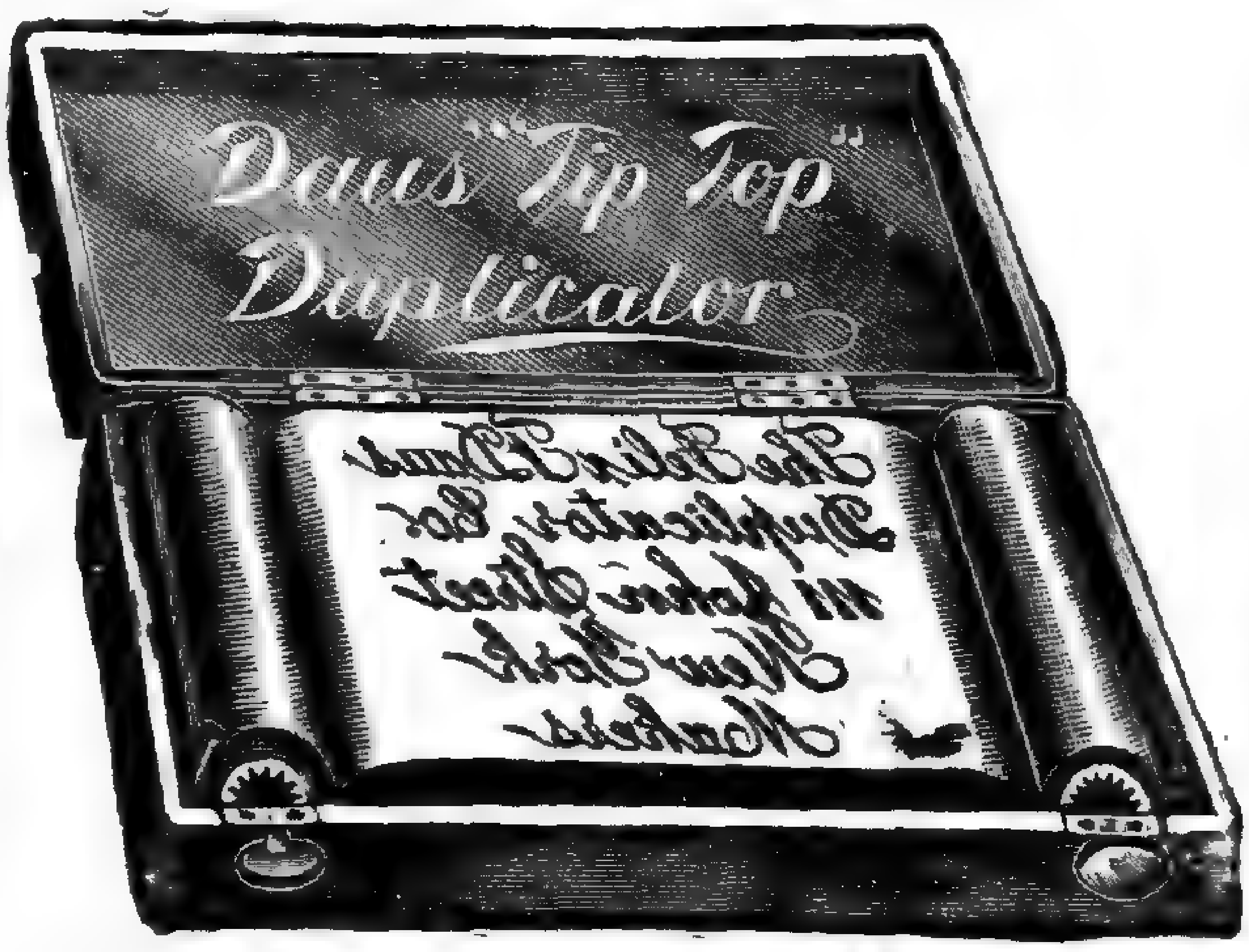
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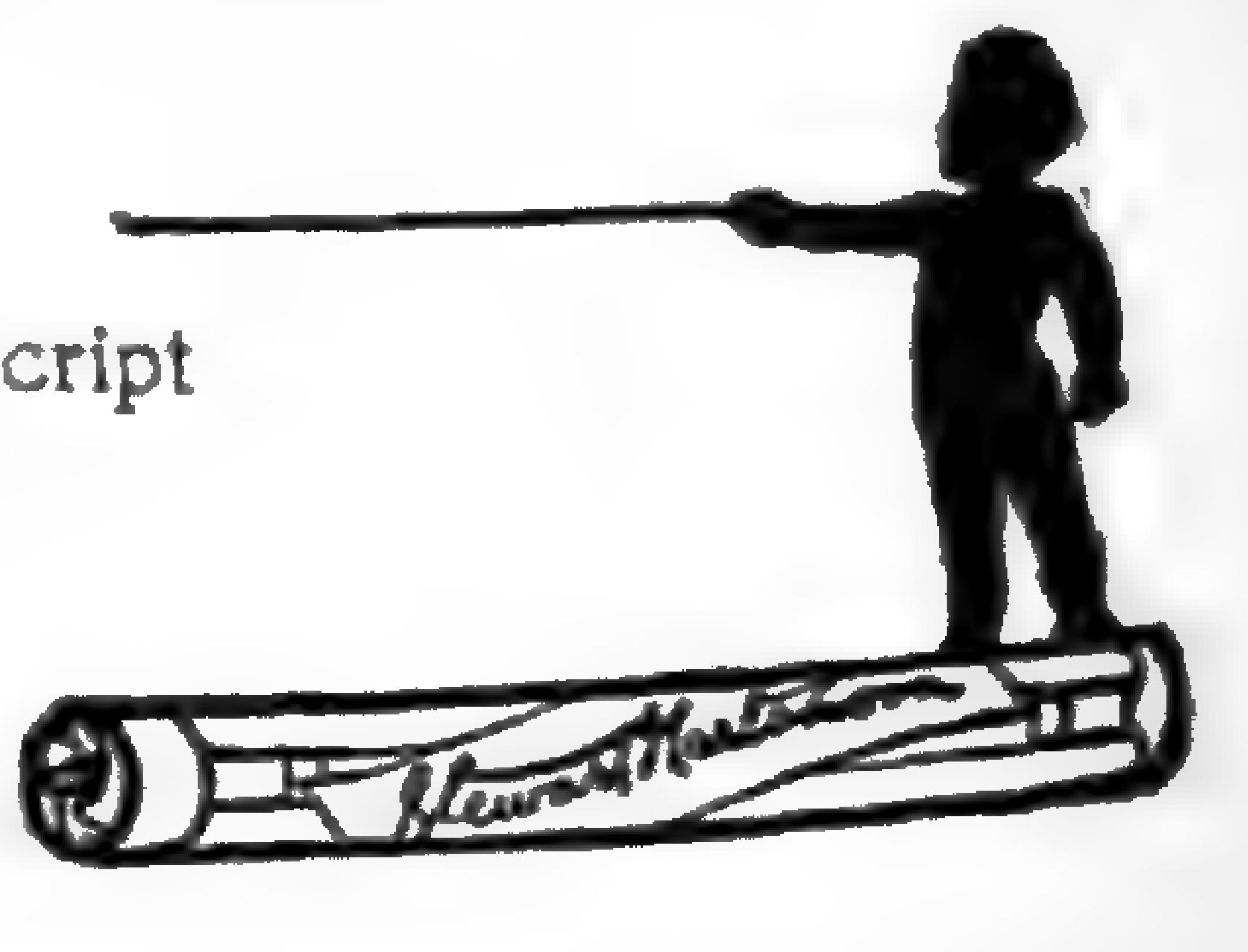
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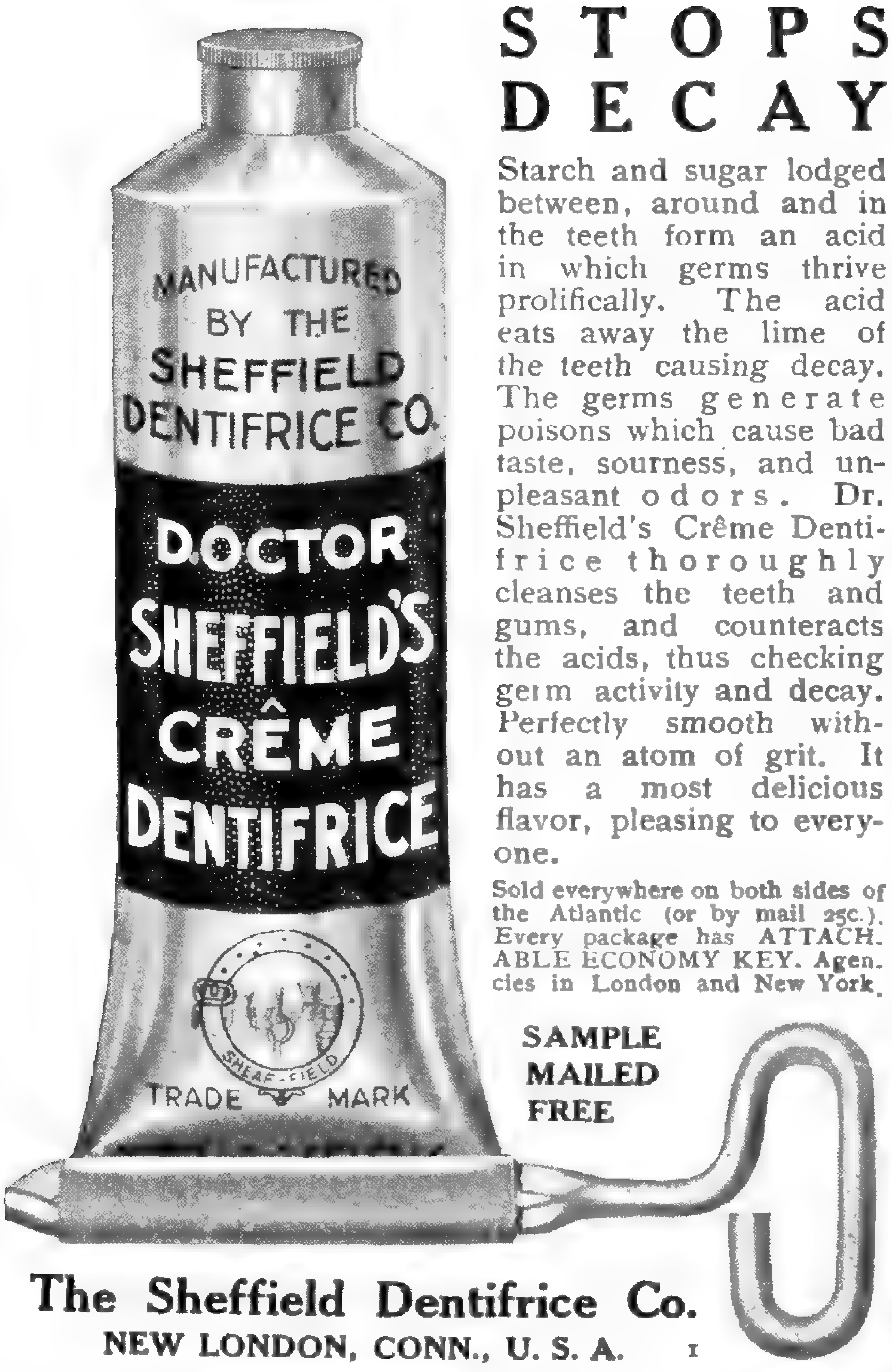
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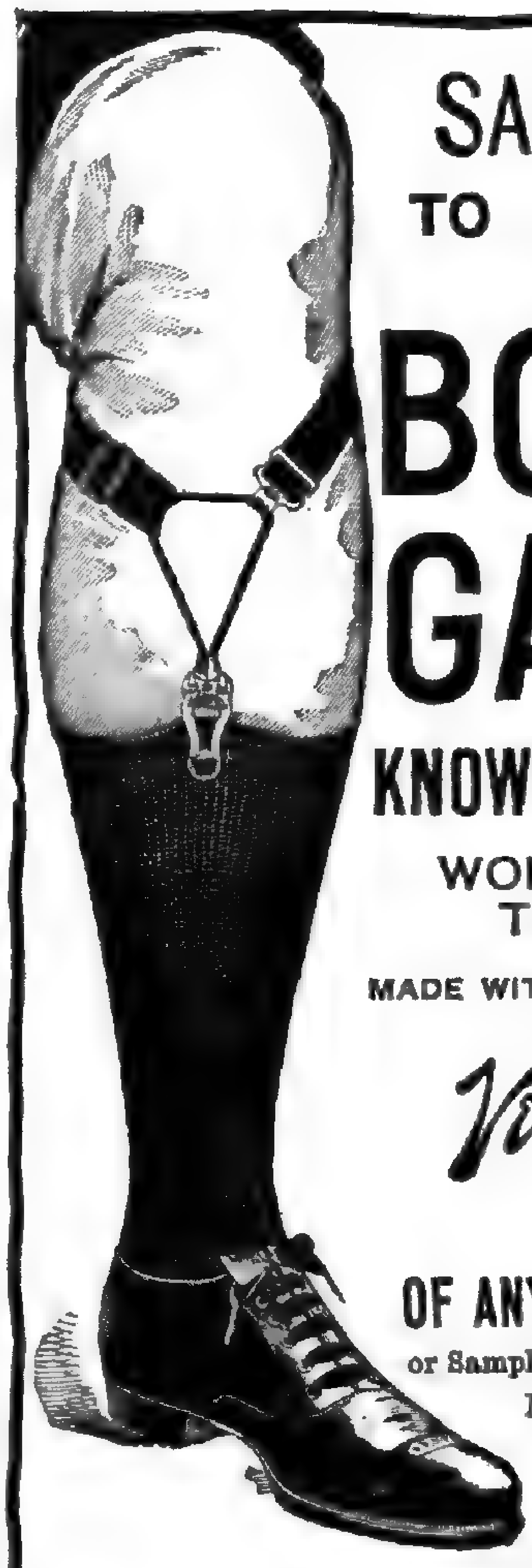

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THE BOTANICAL GAZETTE

February 1910

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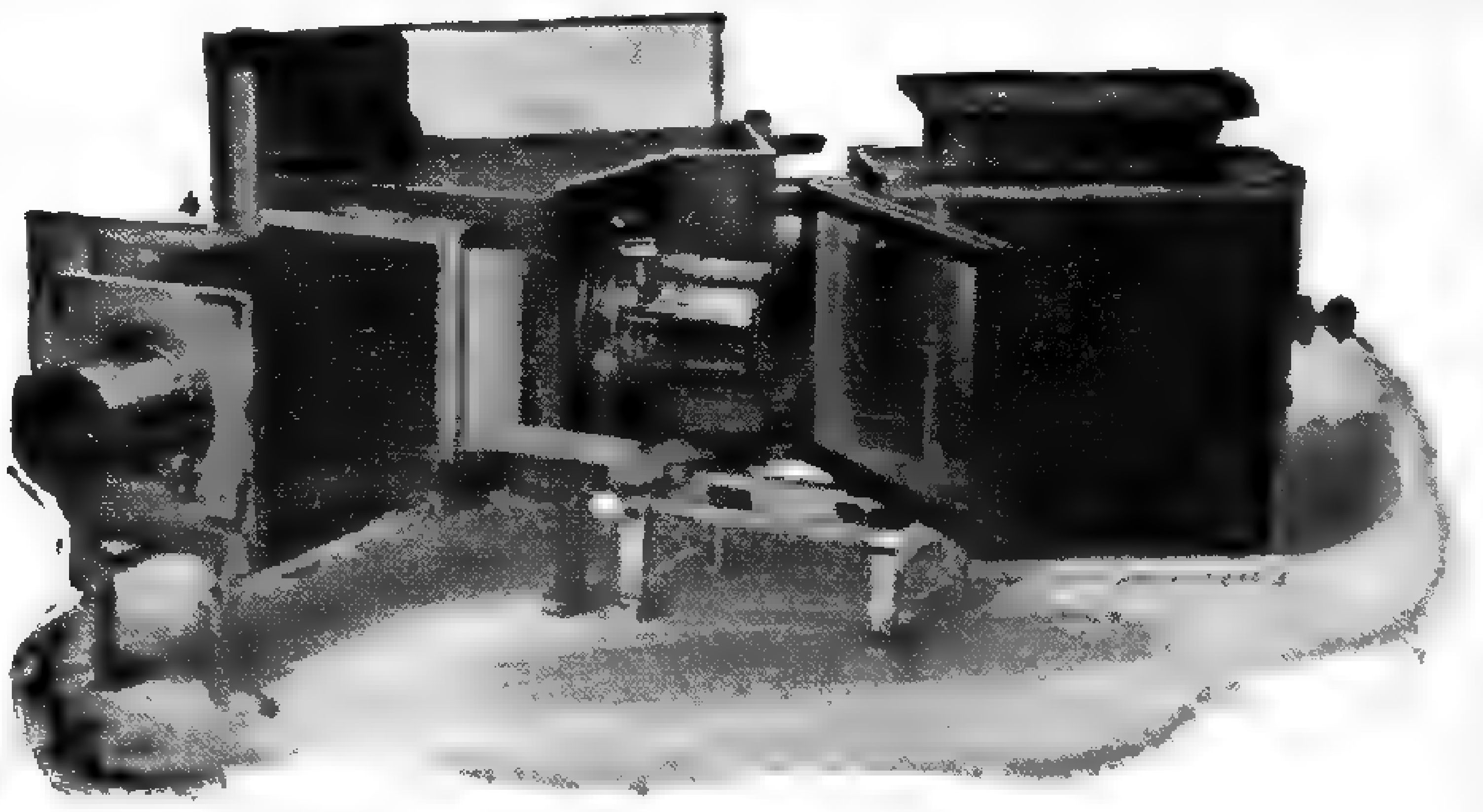

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FEBRUARY 1910

THE EFFECT OF CERTAIN CHEMICAL AGENTS UPON THE TRANSPIRATION AND GROWTH OF WHEAT SEEDLINGS

HOWARD S. REED

(WITH NINE FIGURES)

The physiological factors involved in transpiration present numerous opportunities for critical study. A vast number of researches upon these factors have been made and our knowledge has been increased thereby; nevertheless the results of some important pieces of work are contradicted by others and more data seem to be necessary to elucidate certain questions.

The present paper is intended to set forth some data upon the effect of certain chemical compounds (mostly salts) upon the transpiration of wheat plants in relation to the effect of the same compounds upon the growth of the plants. In other words, the paper is in part a study of the effect of these compounds upon the units of water transpired for unit of plant substance produced.

The general literature bearing upon the effect of chemicals upon transpiration has been so well brought together and summarized by BURGERSTEIN (2) that a general review of literature need not be given at this place. A few studies which have especial bearing upon the present work, however, will be mentioned.

LAWES (**6**) made a careful investigation of the amount of water required by several plants grown to maturity, where possible, in sealed pots of soil. He used in one series soil to which no application of fertilizing compounds was added; in the second series a mineral fertilizer consisting of potassium sulfate, magnesium sulfate, sodium chlorid, and mono-calcium phosphate was added to the soil; in the third series the mineral fertilizer used in the second series was supplemented with ammonium chlorid. In each series wheat, barley, beans, peas, and clover were grown. The third series having the ammonium chlorid failed to make satisfactory growth, but the other two yielded data of interest.

The application of the mineral fertilizer to soil in which wheat was grown diminished the amount of water required for the production of a unit of dry matter, and the mineral plus ammoniacal fertilizer diminished the amount still farther. The same relations held in the case of peas and clover. On the contrary, the amount of water transpired per unit of dry matter in beans was somewhat increased where the mineral fertilizer was present, and the same was true to a rather small extent in the case of barley, but only when the mineral fertilizer plus ammonium chlorid was present.

The experiments of SACHS (**12**), which have become classical, consisted in adding pure chemicals to sand, earth, or solution in which a plant was growing, and carefully observing the effect on the transpiration for a few days. In some experiments the supply of water in the soil was replenished after a few days, in others it was not. It was observed that the addition of KNO_3, $(NH_4)_2SO_4$, or gypsum to the soil decreased the amount of transpiration compared with that of a similar plant in control soil. Similarly, the addition of NaCl or $(NH_4)_2SO_4$ to distilled water decreased transpiration. A small amount of HNO_3 added to distilled water caused a great increase in transpiration, but a small amount of KOH caused retardation.

The investigations of BURGERSTEIN (**1**) confirmed the statements of SACHS and others in finding that acids accelerate transpiration and alkalies retard it. Solutions of calcium nitrate, potassium nitrate, potassium phosphate, potassium carbonate, ammonium nitrate, ammonium sulfate, magnesium sulfate, and sodium chlorid were tried, and all found to increase transpiration up to a certain point.

The observations of MAERCKER (**10**) upon the effects of potash fertilizers showed that the application of substances like kainit and carnallit has an effect upon the water requirement of white mustard. In his experiments the plants were grown in an artificial soil in large zinc pots. The soil, which consisted of sand containing 2.5 per cent. of peat, received the raw potash salts at the rate of 1000 and

2000^{kg} per hectare. In one set of experiments the soil received 60 per cent. of its capacity, and in another set 27 per cent. The effect of these treatments was found to be as follows:

Soil containing 60 per cent. of its water capacity. Treatment	Relative amounts of water required to produce one unit of dry weight	Soil containing 27 per cent. of its water capacity. Treatment	Relative amounts of water required to produce one unit of dry weight
No potash salts	100.0	No potash salts	100.0
1000^{kg} kainit per hectare	90.5	1000^{kg} kainit per hectare	77.1
2000^{kg} kainit per hectare	88.4	2000^{kg} carnallit per hectare	68.9
2000^{kg} carnallit per hectare	91.9		

The economizing influence of the potash salts naturally showed itself more strongly upon the soil which contained the smaller proportion of water.

The pots in MAERCKER's experiments were not sealed to prevent loss of water from the surface of the soil; his figures therefore represent the total amount of water evaporated from the soil directly and through the activity of the plants, but they show very distinctly a tendency toward economy in water absorption where the potassium salts were applied.

HARTWELL, WHEELER, and PEMBER (5) have also reported that the application of potassium chlorid to wheat seedlings in soil causes an increase in green weight relatively larger than the increase in transpiration. In nutrient solutions it was found that sodium usually had a similar effect in retarding transpiration in comparison with growth.

GARDNER (3) has reported results which also show that the general effects of fertilizers applied to soils in pots was to increase in various ratios the amount of green weight in proportion to the water transpired.

SORAUER (15) and HARTER (4) have reported the results of experiments in which a large amount of soluble salt was added to soil or solution and the effect upon transpiration noted. The large amounts of salts which they employed produced halophytic conditions with corresponding changes in the anatomy of the plants, therefore their results will not be compared with those which follow in this paper, because in them the amounts of salt added were not sufficient to alter materially the concentration of the soil solution.

The data to be presented in this paper were drawn from upward of 6000 tests employing soils, soil extracts, and salt solutions. The data showing the effects of treatments upon soils were obtained from experiments which employed 189 soils from various parts of the United States. These data were obtained in the course of fertility tests made by the Bureau of Soils of the U. S. Department of Agriculture, and were kindly furnished by Mr. F. D. GARDNER, who was in charge of the work; the other data are drawn from experiments made by the author while a member of the staff of that bureau's laboratory.[1]

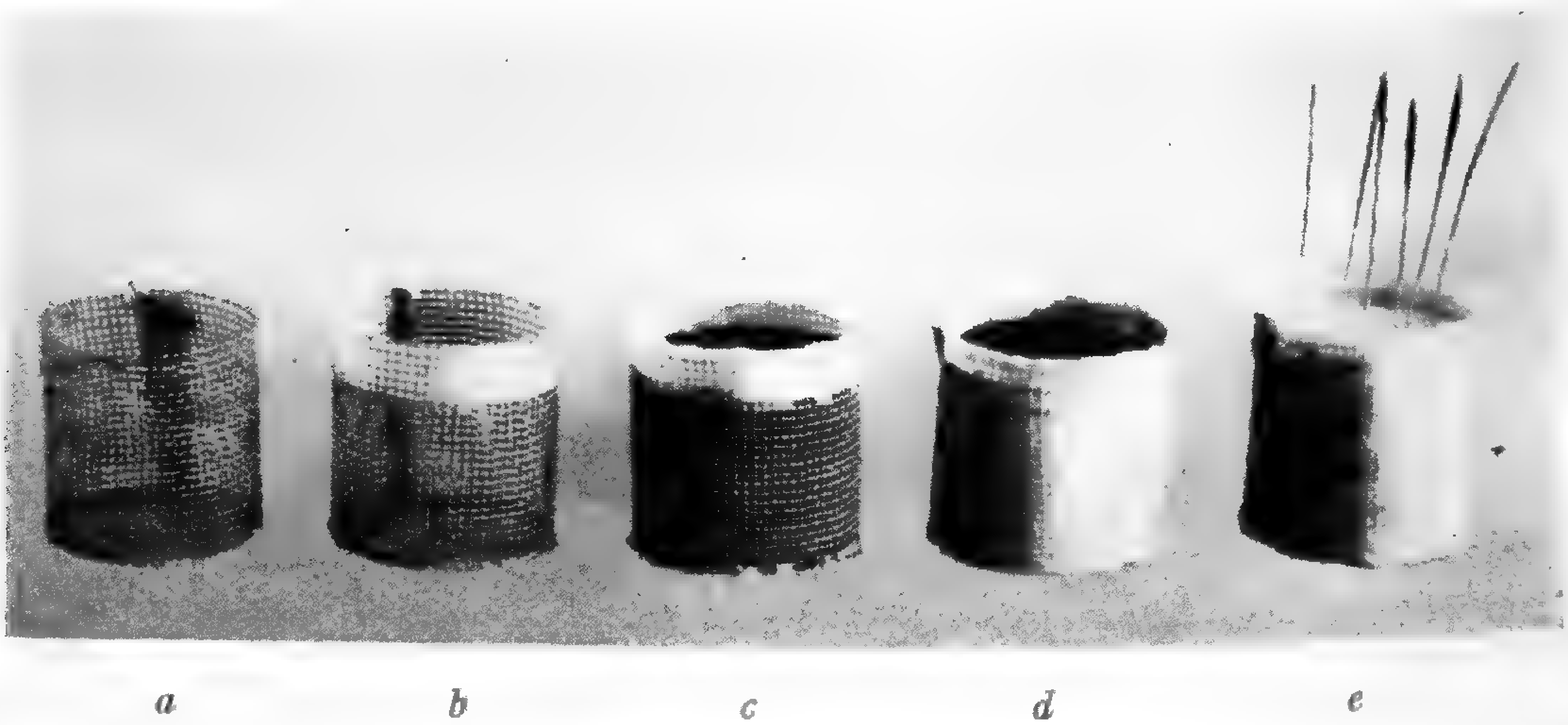

FIG. 1.—Method of making paraffined wire pots: *a*, wire frame; *b*, same with rim of paraffin; *c*, same filled with soil; *d*, completed pot, having wall formed by repeated dipping in melted paraffin; *e*, pot containing plants four days old and showing the cover of paraffined paper sealed to rim of the pot.

All tests conducted with soils were made in the standard paraffin wire pot employed extensively for experimental work in plant physiology and agronomy. As an instrument of research it commends itself especially because of its easy construction and its ability to yield accurate experimental results.[2]

The method of making these pots is illustrated by *fig. 1*. The framework of wire netting is 10^{cm} in diameter and of the same height (a). After coating the rim of the framework by dipping several

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[1] For making most of the computations upon which this paper is based, I am indebted to my wife, HANNAH D. REED.

[2] This method finds commendatory mention in GANONG'S *Plant physiology*, 2d ed., 1908, p. 173.

times in melted paraffin (*b*), the pot is filled slightly above the edge of the paraffined rim with soil which has received enough water to place it in optimum condition (*c*). The pot is then dipped in melted paraffin with intermediate cooling until a firm wall is formed (*d*). At the first dipping the paraffin penetrates a short distance into the soil and thus cements the outer surface of the mass of soil to the wall of the pot. A straight, shallow furrow is then made across the surface of the soil and the seeds planted in it. In the present work, where wheat was used, it was previously soaked in tap water until undoubted signs of germination were shown and seven seeds were planted in each pot. If seven plants appeared above the surface of the soil, one was subsequently removed, leaving six to grow in each pot. It is advisable to cover the surface of the soil in the pot with a layer of clean sand to prevent a crust from forming on the soil, as well as to aid in uniformly distributing the water which is added. The pots are carefully weighed on the day of planting, when the soil is in the optimum moisture condition, and their weight recorded. A few days after the plants appear above the surface of the soil, the pot is sealed by covering the top with a circular piece of paraffined paper provided with a narrow slit in a position which allows the row of plants to pass. The paper is sealed to the inner surface of the wall of the pot with paraffin. Such a pot is shown at *e* in *fig. 1*. The pot is weighed immediately before and after sealing, and the increase of weight due to the addition of paper and paraffin is added to the initial weight recorded as the "optimum" for each pot. The paraffined paper prevents the loss of all but a very slight amount of moisture by evaporation from the soil. Since it is transpiration relative to control cultures and not absolute transpiration which was determined, the small amount of water lost through the slit may be neglected. Thereafter distilled water is added in sufficient quantity at intervals of three or four days to keep the weight of the pots near that of the original. When water was required by the pots, it was introduced through the slit in the paraffined paper cover by means of a pipette.

One of the conspicuous points of superiority which the paraffined wire pot possesses over the ordinary pot with a non-adhesive wall is shown in *fig. 2*. In experiments of this character, where the effect of soil treatment is to be estimated by the result upon plant growth, it is essential that the roots of the test plants be living within the soil instead of being external to it. *Fig. 2* shows at the left the soil mass from a paraffined wire pot, and at the right that from a pot with a non-adhesive wall. Wheat plants had grown in each pot for three weeks at the time the photograph was made. In the paraffined pot the plant roots were entirely restricted to the soil mass, while in the other pot the absorbing region of a majority of the roots was external to the soil and hence not indicating response to the treatment given to that soil.

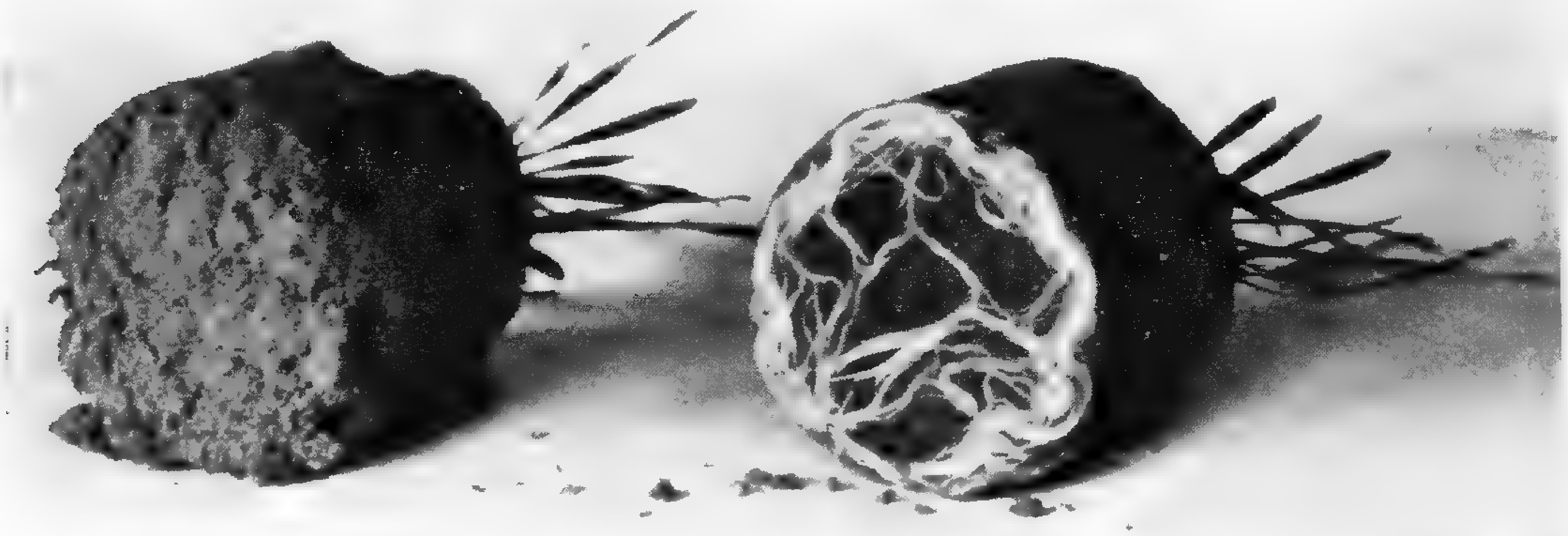

FIG. 2.—Root distribution in paraffined wire pot and in ordinary pot; on the left is shown the contents of a paraffined wire pot, and on the right those of an ordinary pot.

During the course of an experiment the pots were kept in situations where the conditions of heat and light were as nearly uniform as possible.

The exact duration of the different experiments naturally varied somewhat on account of external factors, but was usually 18 to 21 days. During very hot summer weather the period was often somewhat shortened; the best conditions for growth in Washington, D. C., being found in the months of May and September. In order to eliminate errors which might unavoidably arise, as well as inherent differences in individual plants, five pots, each containing six seedlings, were used for each test; therefore, in recording the effect of any treatment, the total transpiration and green weight of the 30 plants distributed in five pots were taken. The total transpiration was determined by summing up the total losses of water from the pots during the experiment; the green weight was found by cutting the plants at the surface of the soil in the pot and weighing them immediately, before any material loss of water occurred. If the dry weight was to be recorded, the plants from each set of pots were placed in unsealed paper envelopes and slowly dried at room temperature.

Many experiments described in this paper were carried out in water cultures, in which the aqueous extract of a soil, or a salt solution was used as the culture fluid. The water cultures were prepared and conducted according to the methods described by LIVINGSTON (**8**) and SCHREINER and REED (**14**), in which 10 wheat seedlings are installed in each culture jar. The culture jars employed in this work were saltmouth green flint glass bottles of 240^{cc} capacity. Flat corks which fitted the mouths of these bottles were notched by cutting ten vertical wedges from their lateral surface. Each wedge was about 4^{mm} broad and 5 or 6^{mm} deep, and extended from top to bottom of the stopper. The cork wedges, after being cut out, were truncated at their inner angles by the removal of enough cork to allow them to be replaced in position after a seedling had been placed in the inner apex of the space from which each wedge had been cut. The stem of the seedling was placed in its groove, with the seeds just below the lower surface of the cork, and the wedges were pressed into position. Each wedge should exert sufficient pressure on the seedling to hold it in place when the stopper is inserted in the bottle. After all were in position, a rubber band was placed around the stopper to hold the wedges in place, and the stopper was then pressed firmly into the neck of the bottle which contained the culture fluid. The cultures prepared by this method afford practically no opportunity for the direct evaporation of water from the bottles. Practically all the water lost occurs as transpiration from the plants grown in the cultures. To keep conditions equable, the solution in the bottles should be renewed or the bottles replenished with distilled water every four or five days.

Since the water loss is only through the plants, the cultures may be weighed at each change, and the sum of the losses recorded may be taken as the total transpiration of the 10 plants for the period of the experiment. This total water loss being proportional to the leaf area when wheat is used, it is consequently a practical method for comparing growth of several cultures when grown simultaneously under the same conditions.

It seems not improper to point out that, under these conditions of experiment, the water content of the medium in which the plants were grown was very nearly constant during the period of the experiment, a condition which has been lacking in many experiments upon transpiration. SACHS, for example, supplied water to the soil at the beginning of an experiment, but usually added no additional water during the course of the experiment.

Most of the studies recorded in this paper are based upon the amount of water transpired per gram of green substance produced under different conditions of experimentation, a factor which in the present study is designated "correlative transpiration."

In most of the experiments involving the use of soil, four different chemical compounds were used, viz., nitrogen as sodium nitrate, potassium as potassium sulfate, phosphorus as mono-calcium phosphate, and calcium as calcium carbonate. The first three salts were applied to the soils, where used, at the rate of 100 parts to a million of soil, but calcium carbonate was added at the rate of 1000 parts per million of soil. To facilitate accuracy and rapidity, the first three salts were applied in the form of solutions, but the calcium carbonate was added in a dry, finely ground condition.

A general survey of the data presented in the following pages shows that, in the majority of cases, the plant growth was increased by the addition of various compounds commonly used as fertilizers in agricultural practice. The paper by GARDNER (**3**) contains extensive data upon this point, all of which were obtained by the use of the paraffined wire pot. GARDNER'S data are consonant in showing an increase in plant growth. Some of the soils employed were what might be termed unproductive soils; their unproductiveness, however, was in some cases due rather to the presence in them of deleterious compounds than to actual poverty in nutrient substances. Others of the soils he employed were productive. Naturally the increases due to the addition of fertilizer compounds were greater in the former class of soils.

The studies under consideration in this paper relate to the transpiration correlated with growth as affected by the addition of definite chemical agents to the soil or solution in which the plants were grown.

Experimental results

STUDIES ON THE TRANSPIRATION OF PLANTS GROWN IN SOILS

The first data presented deal with the average effect of the four different salts upon the transpiration of plants grown in 189 soils from different localities.

The untreated pots used as controls exhibited an average transpiration of 103.3^g water for each gram of green weight produced. In the pots where the salts were added the amounts of water transpired per gram of green weight were: $NaNO_3$, 93.36^g; K_2SO_4, 97.95^g; $CaH_4(PO_4)_2$, 104.07^g; $CaCO_3$, 101.09^g. Using the transpiration of the controls as a basis and representing it as 100, the different treatments would have the following values: $NaNO_3$, 90.40 per cent.; K_2SO_4, 94.80 per cent.; $CaH_4(PO_4)_2$, 100.8 per cent.; $CaCO_3$, 97.9 per cent.

These figures show that at least two of the four salts employed were responsible for a proportionally diminished transpiration. In the case of the other two, the differences from the control were not so great, in fact in the case of mono-calcium phosphate the units of water used were almost precisely the same as in the controls. It may be said in passing that in individual cases the economy of water used was much greater than would appear from the average result. For example, one sample of Crawford clay, to which $NaNO_3$ was added, showed only 69 per cent. as many units of water required for a unit of growth as in the untreated soil, at the same time growth was increased 31 per cent. Also, in a sample of Portsmouth swamp soil, to which K_2SO_4 was added, the units of water required for a unit of growth were only 71.2 per cent. of what was required in the controls, while growth was increased 112 per cent.[3]

Since the introduction of extraordinarily low figures brought down the average figures, I next made an investigation of the amounts of

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[3] In this connection it may be said that the opposite relation was sometimes observed, namely, an increased consumption of water when growth was diminished by the addition of a salt. In a sample of Memphis silt loam, to which K_2SO_4 was added, the resulting growth was but 91 per cent. of that in untreated soil, while the water required per unit of growth was 17 per cent. more than in the controls.

water transpired in experiments where the salts had a slight influence upon growth and also in experiments where influence was large. I selected for this purpose two classes of results, in one of which the effect of the added salt upon the green weight of the plants was so small as to be doubtful, and in the other there was a distinct acceleration. In the first class of results the response as measured by green weight varied between 95 and 105, and is regarded as doubtful response, since a variation of only 5 per cent. above or below the controls may be regarded as within the limit of error. In the other class of results the response was 120 or greater, and therefore includes cases in which there was undoubted acceleration.

A summary of the results of these tests is presented in table I. Each computation is the average of 25 tests, with the exception of no. 1, which is the average of 20 tests.

TABLE I

EFFECT OF VARIOUS SALTS UPON TRANSPIRATION OF WHEAT PLANTS IN CASES WHERE THE CORRELATED EFFECT UPON THE GROWTH WAS VERY SMALL AND IN CASES WHERE IT WAS DISTINCTLY INCREASED. SALTS ADDED TO SOIL IN WHICH PLANTS GREW

No.	Salts added	Green weight of plants grown in soils receiving the salt. Controls =100 in each case	Units of water transpired per unit of green weight. Controls=100 in each case
1	$NaNO_3$	100.25	95.3
2	"	130.00	84.0
3	K_2SO_4	101.00	94.0
4	"	128.00	86.0
5	$CaH_4(PO_4)_2$	100.16	100.4
6	"	128.00	95.5
7	$CaCO_3$	100.5	99.9
8	"	142.0	99.0

These results may be regarded as giving added light to those previously presented. They show that in the case of $NaNO_3$ and K_2SO_4 there was greater economy of water used the greater the effect upon growth as indicated by the green weight. In the case of $CaH_4(PO_4)_2$ and $CaCO_3$, it has already been shown that their inhibiting effect upon transpiration is much inferior to that of $NaNO_3$

and K_2SO_4. In the case of $CaH_4(PO_4)_2$, as shown in table I, there is, however, a slight decrease in the units of water required for a unit of green weight where the growth response was greater. In the case of $CaCO_3$ the difference is too slight to warrant any statement one way or the other.

The relations between green weight and transpiration are further illustrated by the graphic representation given in *figs. 3, 4,* and *5*. To construct the curves there shown I selected from each set of experimental data an ascending series of green weights. These figures ranged, as shown, from a value slightly less than that of the controls to a value indicating a growth approximately twice as great as that of the controls. The control for each one is represented by 100, therefore the position of the points above or below 100 on the chart represents the effect of the salt which was added to the soil in that particular series of experiments.

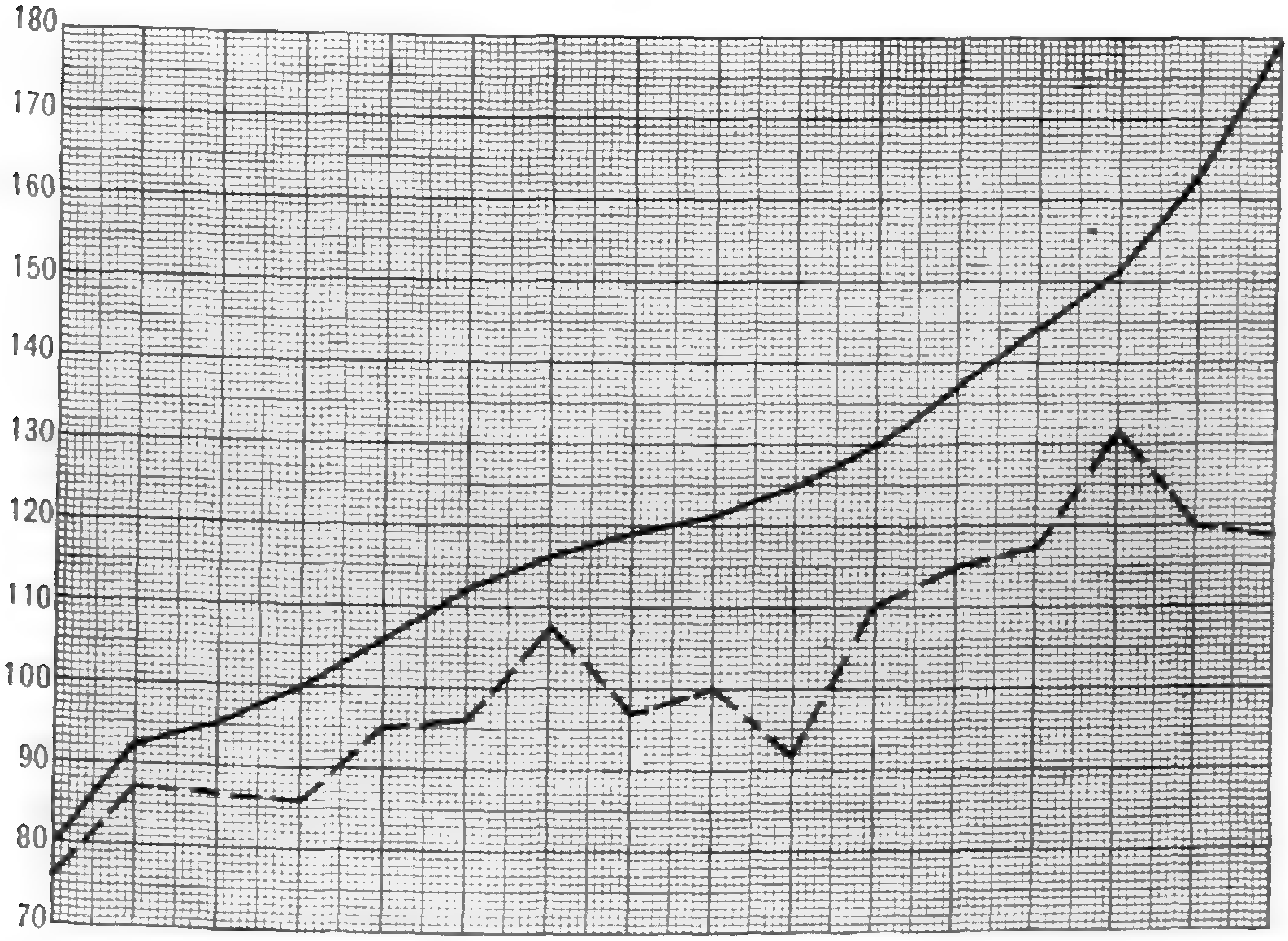

FIG. 3.—Correlative growth and transpiration in soils to which K_2SO_4 was added; in all charts the continuous line represents green weight, and the broken line transpiration.

Arranging the figures representing the green weights in an ascending order, I let the respective transpiration figures fall as they might.

The transpiration was estimated in each case by comparison with the transpiration of the control plants, the transpiration controls being also represented as 100. By joining these points, a curve was obtained representing the rise and fall of the transpiration in comparison with the somewhat steady rise of the green weight in these selected cases. In all charts green weight is represented by the continuous line and transpiration by the broken line.

In selecting these figures, care was taken to omit all in which the results might appear to be large on account of very small growth in the control. Had such been included the results would have been even more striking than they stand.

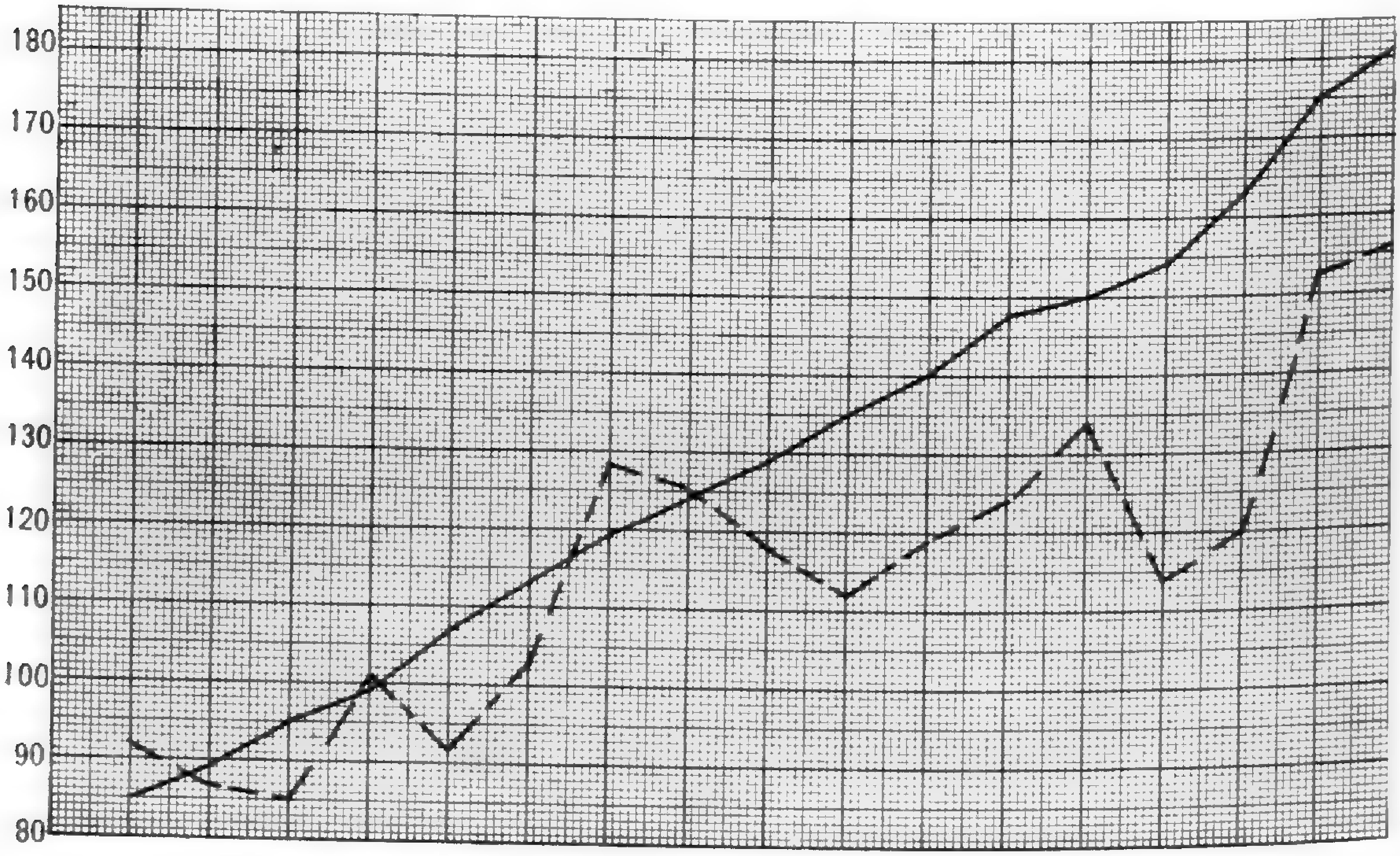

FIG. 4.—Correlative growth and transpiration in soils to which $NaNO_3$ was added.

An inspection of *fig. 3* shows that potassium sulfate in particular acts as an economizing factor (agent) in transpiration. In this case the curve representing the transpiration of the plants lies entirely beneath the green weight curve. The transpiration curve rises as the green weight curve rises but the rise is not exactly parallel. This fact harmonizes with the relation brought out in a preceding paragraph dealing with the relative quantities of water required where the corresponding increase in green weight was small and where it was large. In the lower part of the figure, where the green weight is near 100, the two curves lie closer together and more nearly parallel than in the upper part of the figure. From these relations it appears that the transpiration per unit of green weight is smallest when the acceleration of growth caused by the application of K_2SO_4 was greatest.

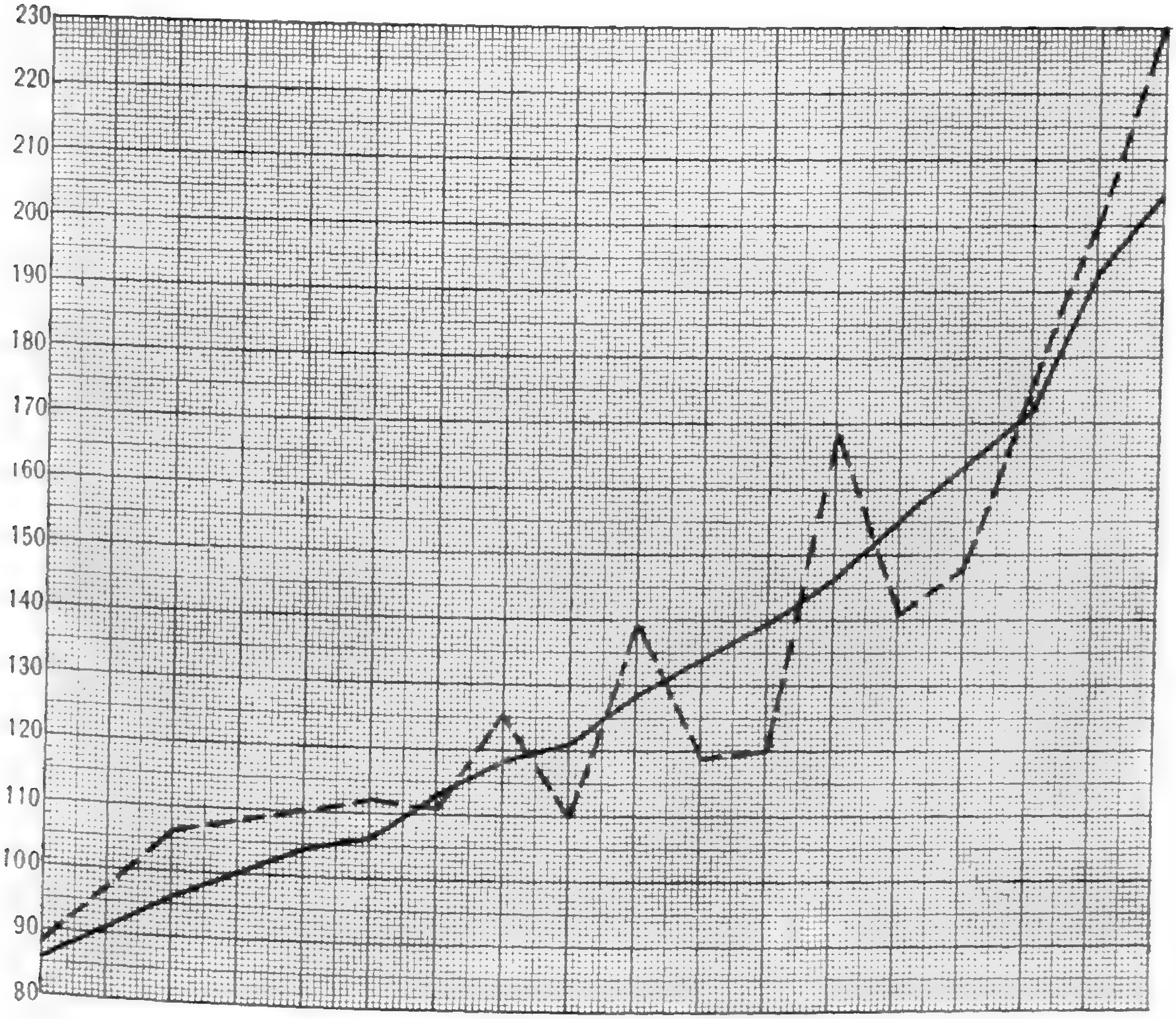

FIG. 5.—Correlative growth and transpiration in soils to which $CaCO_3$ was added.

Fig. 4 shows curves constructed in a similar way to show the action of sodium nitrate upon green weight and transpiration. As before, the numerical values representing the green weight of the various experimental plants are arranged in an ascending series. The curve representing the transpiration of the plants is somewhat more irregular than in the case of the K_2SO_4 experiments, yet its mean position lies somewhat below the green weight curve. This is interpreted to mean that the transpiration of plants grown in pots to which $NaNO_3$ was added was relatively less than the correlated green weight; in other words, that the influence of the $NaNO_3$ was to reduce the amount of water required per unit of green weight.

In the lower part of the figure the mean of the transpiration curve lies closer and more nearly parallel to the green weight curve than in the upper part. This relation is in harmony with the facts previously presented in showing that the economizing action of the $NaNO_3$ was greater where the greatest acceleration in growth was produced (compare table I).

Fig. 5 likewise represents similar relations between green weight and the transpiration in experiments where calcium carbonate was added to the soils. A brief inspection suffices to show that the mean curve of transpiration lies very close to the green weight curve. In the lower part of the figure the transpiration curve is slightly above that for green weight; however, the mean of the former curve approximates closely that of the green weight.

Contrary to the relations exhibited by the two preceding pairs of graphs, the transpiration curve does not perceptibly diverge from the green weight curve in the upper part of its course; thus showing that increased growth due to the action of this salt was not correlated with a reduction of water transpired per unit of green weight produced. This relation is corroborated by the results presented in table I, where the units of water transpired per unit of green weight were scarcely different in cases of low response and high response.

STUDIES ON THE GROWTH AND TRANSPIRATION OF PLANTS GROWN IN SOIL EXTRACTS AND SOLUTION CULTURES

A comparative set of experiments was carried out by the use of aqueous soil extracts as a medium for plant growth. The extracts were made by stirring one part soil with five parts non-toxic distilled water. The mixture was stirred five minutes, allowed to stand thirty minutes, and then filtered through a Pasteur-Chamberland filter. This method gives a good, clear soil extract and is easily employed. Salts were added to the soil extracts and their effect upon transpiration observed as in the case of the pot experiments in which soil was used. As in the case of the former series of experiments, there was, on the aggregate, increased growth, resulting from the addition of salts commonly used as fertilizers. A few cases in each series gave growth somewhat less than the controls and others were practically equal to the controls, but a goodly number in each series gave material responses in the positive direction. On account of a smaller number of experiments, not so many comparisons are possible, however, as in the case of the former series.

One feature associated with the growth of wheat plants in soil extracts or nutrient solutions is deserving of especial mention. When the compounds added to a medium caused (as many of them did) a material increase in root growth, there was usually a corresponding increase in transpiration, regardless of whether the growth of the green parts of the plants was greatly increased or not. It is held that the increase in size of the absorptive system is connected in some way with an accelerating action upon the escape of water from the subaerial portions of the plant.

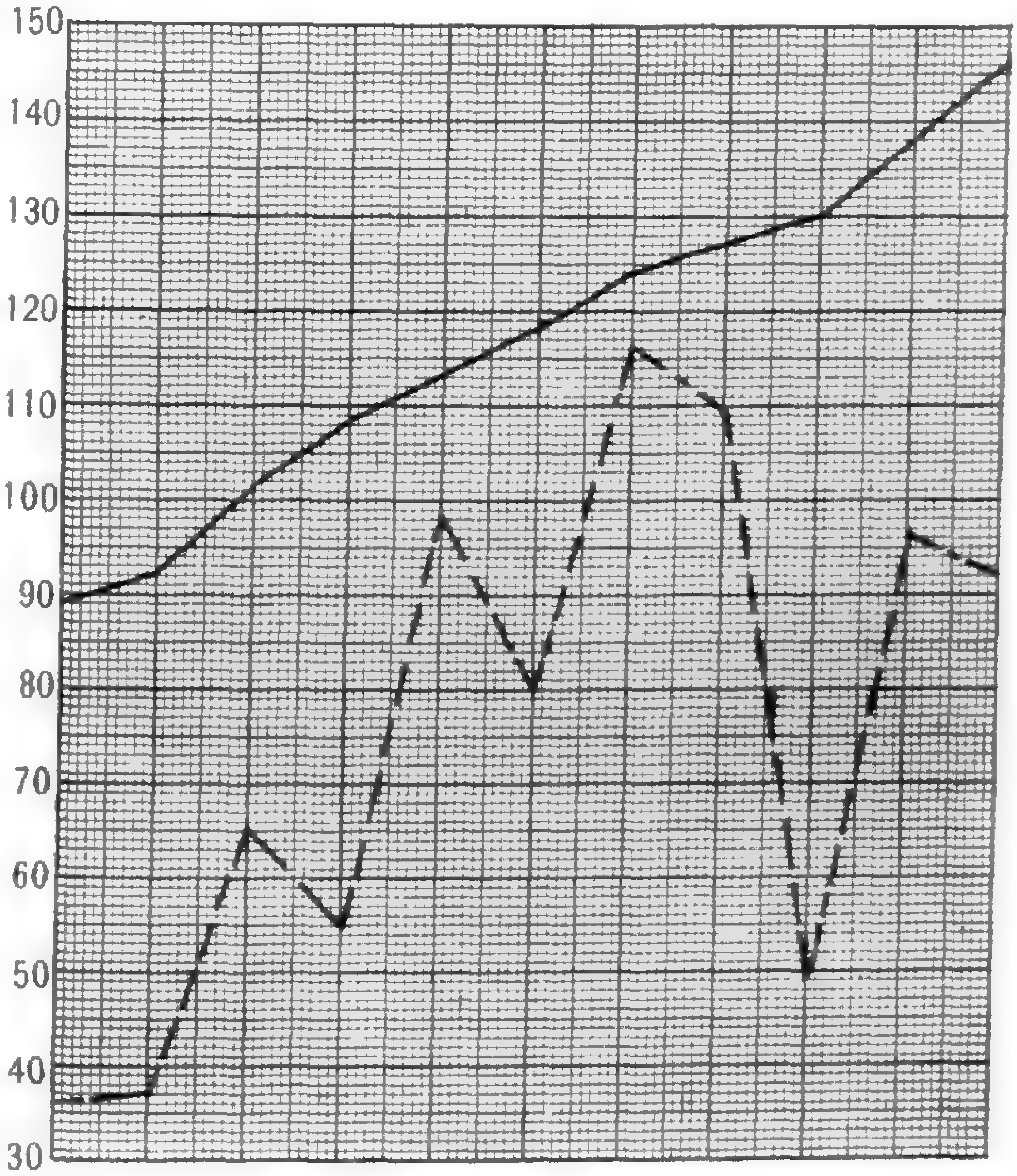

FIG. 6.—Correlative growth and transpiration in soil extracts to which K_2SO_4 was added.

The first computations are concerned with the units of water required to produce a unit of green weight, and the influence of various compounds thereupon.

The plants grown in soil extract to which sodium nitrate was added showed a transpiration per unit green growth 96.7 per cent. of transpiration in the controls. Similarly, the transpiration in soil extract plus potassium sulfate was 85.3 per cent.; in extracts plus sodium phosphate, 110 per cent.; in extracts plus calcium carbonate (saturated solution), 163 per cent. of the controls.

In the former series of experiments there was no comparison between the sodium and the potassium salts of the same acid. A few comparisons were made in this series of experiments employing K_2SO_4 and Na_2SO_4, the results of which are of some interest, since one of the salts functions as a plant nutrient and the other probably does not. In the comparison at present under consideration it was found that plants grown in soil extracts receiving sodium sulfate exhibited a transpiration per unit of green weight equal to 93.9 per cent. that of the controls, whereas an equivalent amount of potassium sulfate added to extracts of the same soils and in which plants were simultaneously grown gave 85.3 per cent.

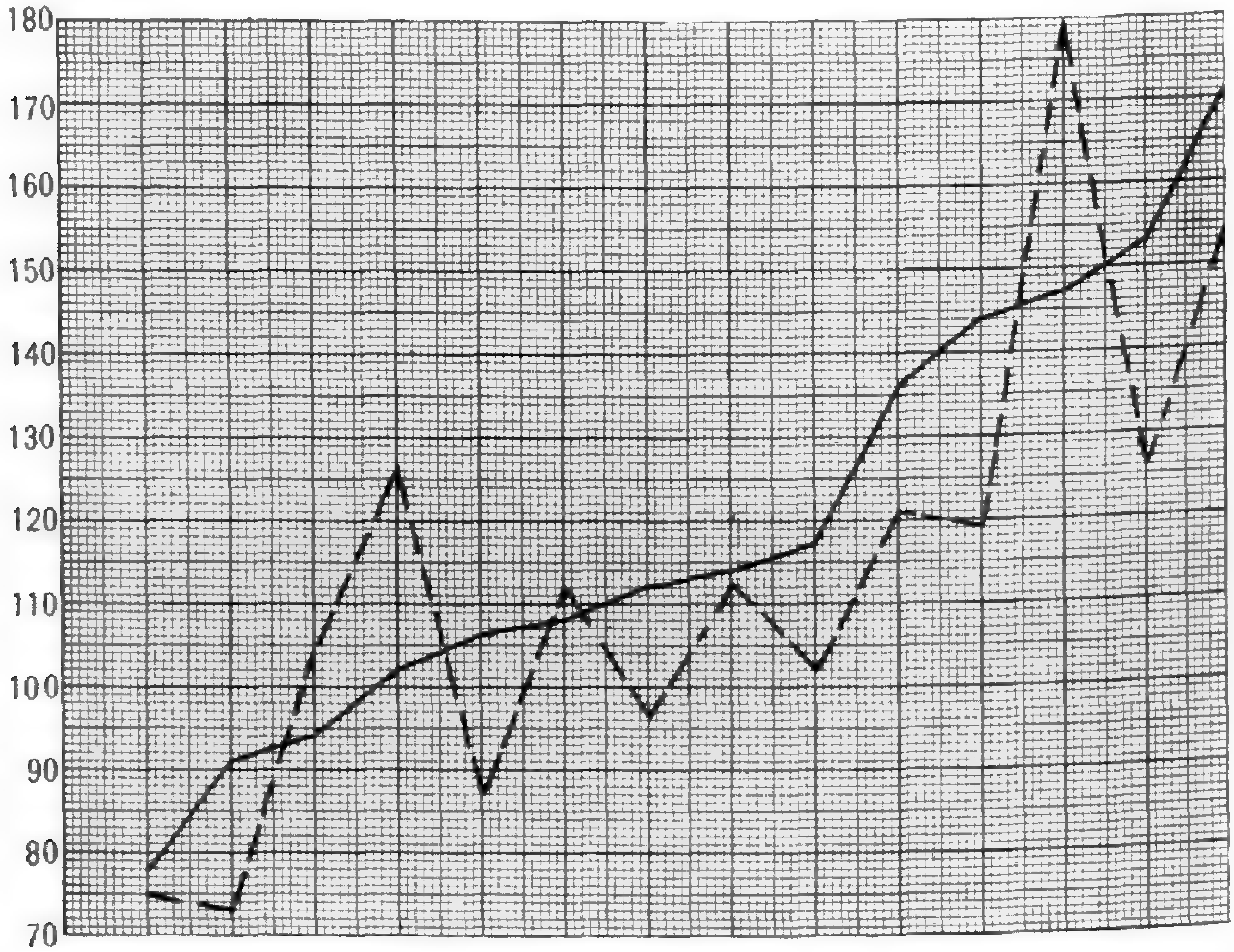

FIG. 7.—Correlative growth and transpiration in soil extracts to which $NaNO_3$ was added.

A comparison of the effects of two different salts of potassium was afforded by the results from the use of potassium chlorid and potassium sulfate in extracts of the same soil. Sixteen experiments were selected in which these two salts had been added to extracts of the same soil, and plants grown simultaneously.

The average transpiration for unit of green weight was 56.77^g in the controls, 34.81^g for KCl, and 34.05^g for K_2SO_4. Expressed in percentage of the controls, the addition of KCl caused a use of water amounting to 61.4 per cent. of the controls, and K_2SO_4 caused a use of water amounting to 60 per cent. of that used by the controls in untreated soil extract.

It appears, therefore, that potassium is more efficient than sodium in diminishing the transpiration per unit of green growth produced. Different salts of potassium did not exhibit wide variation in their inhibiting action upon transpiration. Sodium, however, is able, to some extent, to retard the transpiration per unit growth, and part of the retarding action of sodium nitrate is therefore attributable to the action of the sodium ion.

The effect of adding these salts to soil extracts is shown by curves in *figs. 6, 7, 8,* and *9,* where the method of constructing the curves was similar to that used for *figs. 3, 4,* and *5.* In *fig. 6,* which shows the effect of K_2SO_4, it is evident that the correlative transpiration is much lower than the growth, since every point in this transpiration curve is below the green weight curve. The middle portion of the transpiration curve lies nearer the green weight curve than either of the extremities, but the general trend of this curve shows that constant retarding action upon transpiration in all cases whether the green weight of the plant was increased much or little.

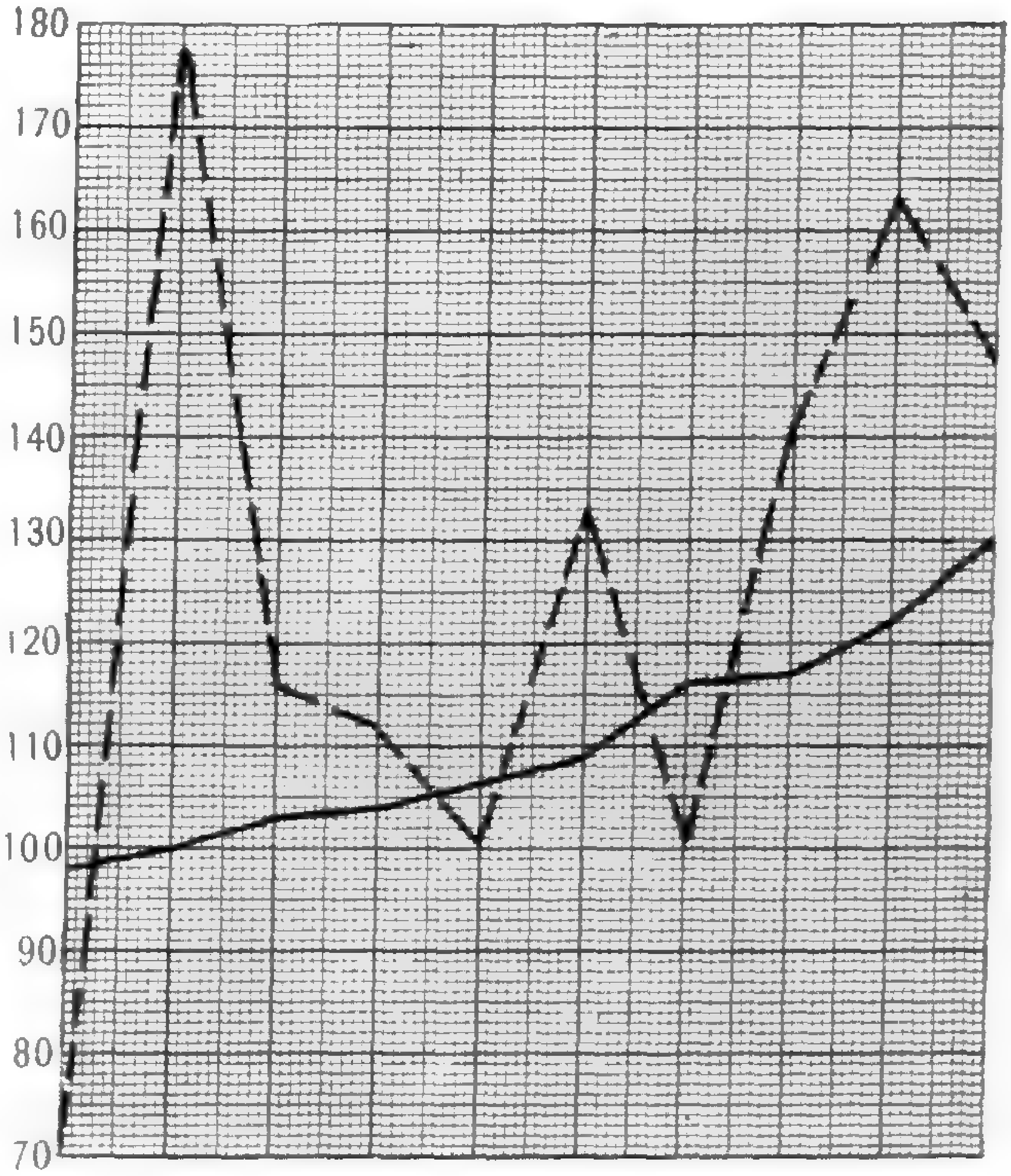

FIG. 8.—Correlative growth and transpiration in soil extracts to which Na_2HPO_4 was added.

The effect of $NaNO_3$, as shown in *fig. 7,* is not so marked in retarding transpiration. Here the mean of the transpiration curve lies very close to the green weight curve, and is generally parallel to it. The upper part of the transpiration curve, which lies somewhat below the green weight curve, may probably be regarded as showing a retardation of transpiration in those examples.

Fig. 8, showing the relationship between green weight and transpiration in cultures to which Na_2HPO_4 was added, may be regarded as a general indication of the effect of the PO_4 ion. The transpiration here appears to be generally higher than the correlative green weight and is accordingly consonant with former results.

The effects of $CaCO_3$, as shown by the curves in *fig. 9*, is very accelerating upon transpiration. Although the transpiration curve is subject to somewhat extreme fluctuation, all its points lie above the green weight curve and the mean of the transpiration curve lies far above.

It may be said that, in the main, the salts had the same effect when added to soil extracts as when added to the soil in which plants were grown, although, in the case of $CaCO_3$ the results were somewhat more emphasized in the soil extracts.

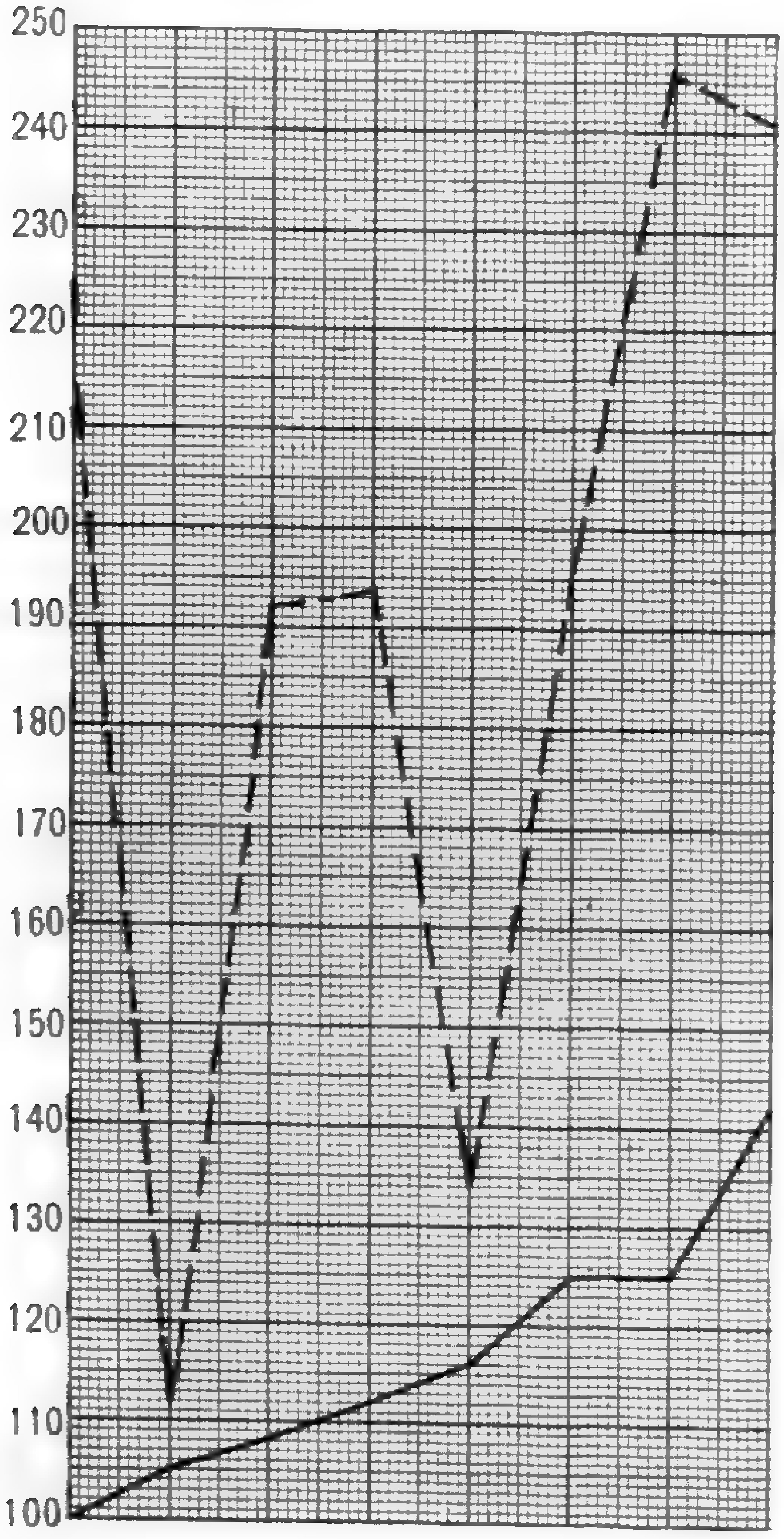

Fig. 9.—Correlative growth and transpiration in soil extracts to which $CaCO_3$ was added.

The next studies taken up were devoted to the effect of acids and alkalies upon transpiration. This question has previously been studied by numerous investigators, notably Senebier, Sachs, and Burgerstein, all of whom apparently agree in showing that the addition of a small amount of an acid increases the transpiration, while the addition of a small amount of alkali decreases transpiration.

In my experiments the acids or alkalies employed were added in smaller amounts than used by SACHS or BURGERSTEIN; and the experiments were extended for 12 to 15 days instead of 1 to 4 days, as in BURGERSTEIN'S experiments. The cultures were set up in duplicate with ten wheat plants to each culture.

In the two experiments first presented tests were made with organic and inorganic acids. The effect of these acids upon transpiration, green weight, and the correlation between the two is shown in tables II and III.

TABLE II

UNITS OF WATER TRANSPIRED PER UNIT OF GREEN WEIGHT IN WHEAT CULTURES CONTAINING VARIOUS AMOUNTS OF OXALIC AND ACETIC ACIDS

No.	Solution	Transpiration grams	Green weight grams	Units H_2O per unit green weight
1	Control in H_2O	64.5	1.47	43.8
2	$C_2H_2O_4$ $\frac{n}{2500}$	105.0	1.82	57.7
3	" $\frac{n}{5000}$	106.0	1.93	54.9
4	" $\frac{n}{10000}$	60.0	1.56	38.4
5	" $\frac{n}{20000}$	106.5	2.03	52.4
6	" $\frac{n}{40000}$	72.0	1.91	44.7
7	$CH_3 \cdot COOH$ $\frac{n}{2500}$	65.5	1.61	40.7
8	" $\frac{n}{5000}$	137.5	2.48	55.5
9	" $\frac{n}{10000}$	69.5	1.67	41.6
10	" $\frac{n}{20000}$	78.5	1.56	50.3
11	" $\frac{n}{40000}$	87.0	1.76	49.4

Several relations are indicated by the results presented in these tables. The figures indicate that the transpiration of the plants was slightly increased by the addition of small amounts of inorganic acids, and in most cases was perceptibly increased by the addition of the organic acids. The figures expressing the green weight show that the addition of acids generally increased the green weight, possibly excepting H_2SO_4 and the stronger solutions of HCl. This relation is perhaps due to the fact that these solutions proved injurious to growth as indicated by transpiration and green weight. When one examines the figures showing the units of water transpired per unit of green weight, he finds that the presence of inorganic acids in the concentrations there used did not cause an increase in the amount transpired per unit green growth, but caused instead a greater or less retardation in transpiration. In the experiments where organic acids were added the proportional transpiration, in most of the cases, was somewhat larger than that of control plants. Here then the results may be said to agree with those of the authors previously mentioned. But the results given in table III show quite general disagreement.

TABLE III

UNITS OF WATER TRANSPIRED PER UNIT OF GREEN WEIGHT IN WHEAT CULTURES CONTAINING VARIOUS AMOUNTS OF INORGANIC ACID

No.	Solution	Transpiration grams	Green weight grams	Units H_2O per unit green weight
1	Control in H_2O	53.0	1.46	36.3
2	HCl $\frac{n}{2500}$	26.0	.90	28.8
3	" $\frac{n}{5000}$	27.5	1.08	25.4
4	" $\frac{n}{10000}$	32.5	1.50	21.7
5	" $\frac{n}{20000}$	52.0	1.75	29.1
6	" $\frac{n}{40000}$	57.2	1.73	33.0
7	HNO_3 $\frac{n}{2500}$	35.5	1.40	25.3
8	" $\frac{n}{5000}$	46.5	1.61	25.1
9	" $\frac{n}{10000}$	61.5	1.84	33.4
10	" $\frac{n}{20000}$	59.5	1.75	34.0
11	" $\frac{n}{40000}$	47.5	1.67	28.4
12	H_2SO_4 $\frac{n}{2500}$	15.5	1.24	12.5
13	" $\frac{n}{5000}$	32.0	1.19	26.9
14	" $\frac{n}{10000}$	49.5	1.60	30.9
15	" $\frac{n}{20000}$	45.0	1.46	30.8
16	" $\frac{n}{40000}$	30.0	1.38	21.7

In attempting an explanation for these differences, attention may be directed first to the fact that the plants in my experiments were grown for longer periods of time in the acid solutions than those of the previous investigators, and the possibility exists that accelerated transpiration of these plants was temporary and would eventually have given place to a retardation. The plants upon which my observations were made had developed almost from germination in the solutions to be tested, since they were transferred to the solutions when the longest roots were 2–3^{cm} long.

The greatest reason for the apparent difference in results is believed to be due to the fact that the previous writers have taken no account of the correlated growth in measuring transpiration. Transpiration is probably a function of growth, and as such cannot be separated from it. It seems more correct, therefore, to estimate the effect of a treatment in terms of the transpiration per unit of green weight, or, since in my experiments the green weight was at the beginning of the experiment almost *nil*, to estimate the effect of the treatment in terms of the transpiration *per unit increase* in green weight.

THE ACTION OF ALKALIES

This problem was also studied by the earlier investigators in manner similar to that employed for studying the action of acids, which, as previously stated, is open to certain objections. The results of my experiments, which record the amount of transpiration per unit of green growth, disagree with those of the writers quoted. My experiments on this point were conducted upon wheat plants growing in water cultures, prepared by the methods previously described. The hydroxids of potassium and of sodium were present in these cultures in concentration of $n/100$; this involved the addition of 39 parts per million of K in the form of KOH, and 23 parts of Na as NaOH, amounts approximating those employed in the other experiments.

Table IV presents the average result of two experiments in which KOH and NaOH were added to extract of Hagerstown loam, a sample which was known to "respond" to potash fertilizers being used.

Unfortunately, the number of my observations is small, and it would be unsafe, therefore, to make any extended discussion of the results, although they are believed to be entirely consonant with the true state of affairs. So far as they go, they disagree with those of previous workers in showing that both the absolute and the relative amount of transpiration was increased by the addition of KOH and NaOH in small amounts. In these small amounts the effect upon growth appears to be distinctly beneficial. The transpiration per unit of green growth appears to have been increased slightly where the hydroxids were added.

TABLE IV

Plants Effect of KOH and NaOH upon growth and transpiration of in extract of Hagerstown loam. Average of two experiments

No.	Solution	Transpiration	Green weight	Units water transpired per unit green weight
1	Untreated soil ext.	100	100	26.9
2	Soil ext. plus $\frac{n}{100}$ KOH	182	160	30.5
3	Soil ext. plus $\frac{n}{100}$ NaOH	157	138	29.2

The effects of pyrogallol and tannic acid were studied on plants grown in soil extracts. The addition to the extract of a soil, especially if it be an unproductive soil, of these substances which probably possess no nutrient value usually causes increased growth and greatly increased transpiration. The effects of small amounts of these substances is shown in table V, where the figures are the average of six experiments on soil taken from six different plots at one of the state agricultural experiment stations.

TABLE V

Effect of pyrogallol and tannic acid on soil extract. Average of six experiments

No.	Solution	Transpiration	Green weight	Units water transpired per unit of green weight
1	Control	100	100	100
2	Soil ext. plus 5 parts per million pyrogallol	160	109	139
3	Soil ext. plus 5 parts per million tannic acid	139	100	133

From these results it would appear that the pyrogallol and tannic were responsible for very marked increases in transpiration, without causing correspondingly marked increase in green weight, in fact the average effect of tannic acid shows no increase in green weight. Where the action of these compounds upon soil extracts has been studied, they have been found to accelerate principally two things, transpiration and root growth. In this respect their effect resembles that of manure extract, as has been pointed out by SCHREINER and REED (13). From a rather extended study of this phenomenon under various conditions, it seems only logical to conclude that pyrogallol in a soil extract acts to improve the conditions for growth by acting upon deleterious organic compounds present in those extracts. In non-toxic distilled water, similar effects are not observed. The improvement in growth conditions which follows the action of pyrogallol and other phenol derivatives is more quickly and markedly manifested by the roots than by the green parts of the plant (cf. the illustrations reproduced in the last-named publication). This point is well illustrated by an experiment whose results are presented in table VI. In this experiment pyrogallol was added at the rate of 2, 4, and 8 parts per million to extracts of two soils taken from the experiment grounds of an experiment station. Soil "A" was taken from a rich cabbage field; soil "B" was taken from an unproduc-

TABLE VI

EFFECT OF PYROGALLOL UPON ROOT GROWTH, TOP GROWTH, AND TRANSPIRATION IN TWO SOIL EXTRACTS

No.	Solution	Transpiration	Weight of entire plant	Weight of tops	Weight of roots*	Units water transpired per unit green weight
1	Extract of soil "A"	100	100	100	100	100
2	Same plus 2 p.p.m. pyrogallol	100	94	88	100	113
3	Same plus 4 p.p.m. pyrogallol	122	114	85	146	144
4	Same plus 8 p.p.m. pyrogallol	76	117	81	156	94
5	Extract of soil "B"	100	100	100	100	100
6	Same plus 2 p.p.m. pyrogallol	119	98	95	104	125
7	Same plus 4 p.p.m. pyrogallol	138	116	99	143	140
8	Same plus 8 p.p.m. pyrogallol	152	132	106	171	143

* The roots were taken from the solution, quickly dried between sheets of filter paper, and weighed. A small amount of capillary water was present, but the error is minimized by the fact that the figures given are comparative, not absolute.

tive timothy meadow. In estimating the results the weight of the roots and tops was separately taken.

These results show (with the exception of no. 4) a good correlation between transpiration and root growth. The order of responses is the same in the respective columns. In the case of no. 2, where no increase or decrease was observed in transpiration, a like relation is observed in the root growth. There was a slight increase, however, in the transpiration per unit of green growth, due perhaps to the fact that the green weight of these plants was below normal.

The general import of the experiments presented in tables V and VI seems to be that the addition of pyrogallol or tannic acid causes a marked acceleration in transpiration, and that this acceleration is correlated more with the growth of roots than of the green parts of the plant. As a consequence of this response, the amount of water transpired per unit of green weight appears larger than the response to any other agent used.

In many respects the growth of wheat plants in a soil extract previously treated with finely divided solids resembles that in extracts to which pyrogallol has been added. Undoubtedly the action of the two is similar in alleviating some unfavorable condition which previously existed, but was removed by the treatment in question. The pyrogallol must enter into chemical combination with some deleterious compounds in the soil extract or cause some process of oxidation, while the finely divided solids such as carbon black or ferric hydrate absorb and remove from solution the same deleterious substances. It is not proposed to dwell upon the general aspect of this problem in this place, since it has been treated in other papers and by various authors. The point to be demonstrated here is the effect of this treatment upon the transpiration per unit of green weight.

A large increase in transpiration is usually caused by the treatment with absorbing agents. In most cases, the substance employed as an absorbing agent was added to the soil extract, stirred or shaken frequently during a half-hour, and then filtered out before the extract was used as a culture medium for plants; but the same or slightly greater increases were produced by leaving the absorbing agent in the solution during the time the plants were growing.

Ordinary distilled water, which contains small amounts of poisonous metals from the distilling apparatus, together with small amounts of volatile organic substances which pass over in an ordinary still, may show similar amelioration by treatment with absorbing agents. A representative instance is shown in table VII; other cases have been given by LIVINGSTON (**9**).

TABLE VII

EFFECT OF VARIOUS ABSORBING AGENTS UPON CORRELATIVE TRANSPIRATION OF WHEAT PLANTS GROWN IN DISTILLED WATER

No.	Treatment	Transpiration	Green weight	Units water transpired per unit green weight (relative)
1	Distilled water, control	100	100	100
2	Distilled water, carbon treated	208	120	173
3	Distilled water, ferric hydrate treated	225	115	196
4	Distilled water, quartz flour treated	245	135	181

These figures show among other things that the proportional transpiration was greatly increased by these treatments. It might be argued logically that the transpiration of the plants in the untreated distilled water is abnormally low, due to the probable presence of poisonous metals in the untreated distilled water, as such substances have the effect of depressing transpiration, while the transpiration of the plants in the treated solutions is normal. The removal of these substances by the absorbing solids leaves the solution in a better physiological condition for plant growth, as evidenced by the increased transpiration and green weight. The same result is also produced to a greater or less extent by redistillation in glass.

Such treatments are generally accompanied by an increased root development, especially in branching, but as a rule this relation is not brought out in the dry weight of the roots, it being often found that a set of long, well-branched roots weigh no more than a set of shorter, more poorly branched roots of the same number of plants, due to the greater thickness of the latter. The weight of the fresh roots would be, however, a more accurate indication of the effect of the treatment, as was shown in table VI. The longer and better branched roots in the culture solutions treated with absorbing solids are to be regarded as indicative of superior conditions for growth, and undoubtedly contribute largely to the increased transpiration.

The general effect of treatment by an absorbing agent in case of soil extracts also is to increase transpiration and root growth of the plants, although there are occasional cases where the increased transpiration is small or negative. Table VIII presents the results of a number of experiments upon this question in which a variety of soil extracts were used. The results of the experiments, made at different times, are presented in terms of the growth of plants grown in control cultures. These control results (not presented in the table) were always taken as 100, and the response to treatment with the absorbing agent expressed by proportional figures.

TABLE VIII

EFFECT ON TRANSPIRATION OF TREATING VARIOUS SOIL EXTRACTS WITH ABSORBING AGENTS BEFORE USING THEM AS CULTURE MEDIA*

No.	Soil extract	Transpiration	Green weight	Units water transpired per unit green weight
1	Elkton silt loam	178	107	167
2	Lyons silt loam	95	121	81
3	Alloway clay	465	147	316
4	Kingston soil	81	83	97
5	Takoma lawn soil	190	104	182
6	Arlington soil	142	110	128
7	Dunkirk sandy loam	96	87	110
8	Memphis silt loam	154	118	129
9	Arlington clay loam	108	110	97
10	Takoma lawn soil	137	109	125
11	Kingston soil	116	109	106
12	Memphis silt loam	117	99	119
13	Dunkirk sandy loam	114	114	100
14	Arlington clay loam	158	102	155
15	DeKalb silt loam	133	103	126
16	Cecil sandy loam	112	97	108
17	Hagerstown loam	229	102	225
18	Dutchess silt loam	110	89	122
19	Cecil sandy loam	193	114	171
20	Lyons silt loam	226	131	181
21	Penn clay	402	111	364
22	Miami black clay loam	142	98	144
23	Miami silt loam	172	123	139
24	Lyons silt loam	626	135	461
25	Park soil	136	97	153
	Average	185.3	108.8	164.2

* The absorbing agent used for treating the first 19 soil extracts was carbon black; for the remainder ferric hydroxid was used.

These results show, almost without exception, that the transpiration and growth were accelerated by previously treating the soil extract with an absorbing agent; also, that the units of water transpired per unit of green growth were greater as a result of the treatment employed. In respect to their effect upon the resulting morphogenesis of the plant, the absorbing agents resemble such substances as pyrogallol.

Discussion and summary

The studies presented in the foregoing pages are devoted mainly to an investigation of the relation of transpiration to the green growth of the plant under the influence of various chemical agents. Higher concentrations of the chemical agents were avoided, since it is well known that a sufficiently concentrated solution of a non-toxic salt will retard growth and produce the effect of a "physiological drought."

The small amounts of the respective chemical agents used had a definite influence upon the correlative transpiration. In the case of lime and sodium phosphate, the transpiration showed material increases, but potassium salts decreased it; while sodium nitrate was somewhat variable, usually operating however to cause a decrease in transpiration. Inorganic acids retarded transpiration, while organic acids were somewhat variable. Pyrogallol and tannic acid resembled the action of absorbing agents in causing large increases in the transpiration per unit of green growth.

These effects appear in all cases to be a specific action of the ions constituting any given agent. For example, K always showed its inhibiting action on transpiration, regardless of whether it was combined with Cl, NO_3, or SO_4; so also was the accelerating action of Ca. In this respect the rôle of these ions is doubtless comparable in specificity with their rôle in nutrition and other physiological processes.

The action of certain of these fertilizer constituents might be, as LAWES suggested, of practical advantage in agricultural operations. Under more or less critical conditions, it is conceivable that the effect of a salt like K_2SO_4, which retards transpiration, might make an appreciable difference in plant growth. An experimental study of this question would be extremely interesting.

There are rather extensive areas where the salts of potassium, but more especially those of sodium, are present in the soil in amounts appreciable to plant life, but insufficient to cause distinct xerophily. Since these areas usually receive scanty rainfall, it is altogether probable that the action of those ions and salts which are here shown to retard the correlative transpiration would play an important part in plant growth.

Concerning the action of pyrogallol and tannic acid, both of which greatly accelerated transpiration, but little remains to be said in this discussion. It may be added, however, that these, or closely related substances, are quite common in plants, and it is conceivable that their presence may influence transpiration independently of other factors. A similar view might be held of the action of oxalic and other organic acids which occur naturally as such in plants.

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INHERITANCE OF SEX IN LYCHNIS[1]

GEORGE HARRISON SHULL

(WITH TWO FIGURES)

Since CORRENS (**4**) made his brilliant investigations with Bryonia, in which he showed that crosses between the monoecious *B. alba* and the two sexes of the dioecious *B. dioica* do not give equivalent results in regard to the sex of the offspring, and since DONCASTER and RAYNOR (**6**) published their equally interesting studies with the currant moth, *Abraxas grossulariata*, and its variety *lacticolor*, in which it was found that reciprocal crosses were not equal with respect to sex, but that the Mendelian color character of the variety *lacticolor* is sex-limited, the interest of all students of genetics has been more or less strongly directed toward the problems of sex inheritance, and toward the attempt to describe or explain the heredity of sex on the basis of Mendelian inheritance.

It has been of great interest to find that these two classic cases of Bryonia and Abraxas apparently lead to opposite conclusions as to which sex determines the sex of the offspring, but both seem to favor the conception that one sex is homozygous with respect to sex, and the other heterozygous. BATESON (**1**) attempts to make the results with Bryonia agree with those in Abraxas, but his interpretation is certainly not as simple as that of CORRENS. BATESON'S explanation would require that *Bryonia alba* be gynodioecious, having larger numbers of pure females than of monoecists, instead of being wholly monoecious as described in the manuals. It does not seem likely that so striking a relation as this would have been overlooked by the taxonomists. Moreover, in the attempt to bring harmony between Bryonia and Abraxas, BATESON introduces fully as fundamental inharmony between the two species of Bryonia, when he assumes that the males of *B. dioica* are pure males with pollen bearing only the male character, while the pollen of *B. alba* is all female. Certainly we are justified in expecting a more complete

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[1] Read by invitation before the American Society of Naturalists, Boston, December 28, 1909.

harmony among the species of a single genus than between a species of plants and a species of animals. CASTLE (**3**) has also attempted to relate the Bryonia and Abraxas types of behavior by the assumption that in each case the female is the equivalent of the male plus an x element, the female in Bryonia being a *positive* homozygote and the male a heterozygote, while in Abraxas the female is a heterozygote and the male a *negative* homozygote. This explanation recognizes that Bryonia and Abraxas present fundamentally different conditions.

It is not my intention to present a general discussion of the present state of our knowledge regarding the inheritance of sex, as this has been well done recently by WILSON (**12**), CASTLE (**3**), BATESON (**1**), DONCASTER (**5**), and MORGAN (**8**). However, it may be said that the number of studies which have been made in this field are entirely too few as yet to warrant far-reaching generalizations on the question of sex inheritance, and further data bearing on the subject will be awaited with great interest. It has appeared to me that a serious criticism can be offered to the results of crosses between *Bryonia alba* and *B. dioica* as a basis for conclusions regarding the whole problem of sex inheritance. These crosses are interspecific, and, as is very often true of crosses between distinct species, the sterility of the F_1 offspring did not allow any test of the correctness of assumptions regarding the gametic composition of the hybrids. While it is true that in many species-crosses in which the hybrids are fertile, certain characteristics segregate normally, it has not been uncommon to find that many characters do not segregate, or at least that their segregation is very doubtful and obscure. The simple, typical segregation of characters is best exemplified by the most closely related forms, between which also the fertility is most perfect, and this may be expected to hold true of sex characters as well as of other alternative characters.

BATESON (**1**, p. 166) has repeated the experiments with Bryonia and has fully confirmed the results of CORRENS. BATESON is also convinced of the unsafe character of the Bryonia results as a basis for generalizations, and says that "the relation of dioecious to hermaphrodite and monoecious forms will not in all probability be satisfactorily or rapidly elucidated until some case can be found in which the two types can be crossed together with a fertile result."

I have some material now in hand which meets this requirement, but have not yet continued the experiments long enough to allow more than a preliminary report upon its behavior. For several years I have been investigating the sex ratios in *Lychnis dioica* L., and for this purpose have made carefully controlled pollinations yearly in this usually dioecious species. It was my good fortune during the summer of 1908 to find among these pure-bred cultures six hermaphrodite individuals, the first which I had seen in the several years during which I had been working with this species, in which time I had examined some 8000 pedigreed individuals. In the past season I have noted eight hermaphrodites, usually more or less imperfect, in pure-bred normal families including a total of 10,320 individuals. Only two of these eight were well developed and appeared to be fully functional both as males and females.

Although the occasional occurrence of hermaphrodite individuals in this species has been frequently noted,[2] I have never seen any of them growing wild in the vicinity of Cold Spring Harbor, where the original material for my cultures was collected. STRASBURGER (**11**) found that hermaphrodite plants in his cultures at Bonn were invariably affected by a smut, *Ustilago violacea*, which fruits in the anthers, and he ventured the suggestion that all the reported hermaphrodites in this species may have been such diseased individuals; but, fortunately for my experiments, *Ustilago violacea* has never appeared among my Lychnis cultures, and some, at least, of the hermaphrodite individuals were capable of functioning both as males and females. Five of the hermaphrodites found in 1908 were members of a single family (0739). Several of these hermaphrodite mutants did not have the ovaries and pistils fully developed, and consequently my ability to secure offspring from them was somewhat limited. However, during the past summer, I had 13 families in which one of these hermaphrodite plants entered as either the male or female parent. Two of the six original hermaphrodites died before I had opportunity to use them in crossing. Of the remaining four, two were successfully self fertilized, and one of these was also successfully used as a mother in crosses with a normal male.

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[2] See PENZIG, O., Pflanzenteratologie **1**:300; and KNUTH, P., Handbuch der Blütenbiologie 2^1:174, 175.

For convenience, I will designate the four plants successfully used in breeding by the letters *A*, *B*, *C*, and *D*. When *A* was self fertilized it produced, as a result of two different operations, 33 females and 25 hermaphrodites. When its pollen was used to fertilize four different females, the resultant progenies consisted of 236 females, 161 hermaphrodites, and 2 males. When castrated and fertilized with pollen from a normal male, *A* gave rise to a progeny of 21 females, 2 hermaphrodites, and 11 males. *B* was also self fertilized and gave a progeny of 110 females and 95 hermaphrodites. When pollen of *B* was used to fertilize three different females, it produced 162 females and 144 hermaphrodites. It is thus seen that the two plants, *A* and *B*, showed identical behavior and together produced self fertilized offspring consisting of 143 females and 120 hermaphrodites, and when crossed with females gave a total of 398 females, 305 hermaphrodites, and 2 males. In any explanation of these results the occurrence of these two males will probably have to be left aside as wholly exceptional. Only further breeding will show whether they were true males, or hermaphrodites with pistils suppressed, perhaps, by some cause external to the germ cells. Plants *C* and *D* gave quite a different result. Attempts to self fertilize them and to cross them with normal males all proved futile, though more persistent efforts perhaps might have succeeded. Both were used as pollen parents in crosses with normal females. In such a cross *C* gave a progeny of 39 females and 55 normal males, and *D* gave 26 females and 18 normal males. The details of the several crosses are given in table I, p. 114.

Considering first plants *A* and *B*, and leaving out of consideration for the present the two males occurring in crosses between females and hermaphrodites, and the two hermaphrodites which appeared in the cross between a hermaphrodite and a normal male, it is apparent that the hermaphrodite character belongs only to the males, for in the families in which these hermaphrodites were the pollen parents, the offspring always showed the same ratios of females and hermaphrodites that would have been expected of females and males, had a normal male been used as the pollen parent.

It is clear that the hermaphrodite individuals, *C* and *D*, belong to an entirely different category from *A* and *B*, for in the families produced by using them as pollen parents, the offspring are exactly the same as if normal males had been used. In *A* and *B* the hermaphrodite character is borne by the male germ cells and is fully hereditary. In *C* and *D* the hermaphrodite character may have been purely somatic, in no wise affecting the germ cells, and therefore incapable of hereditary transmission; or, in case the factor for hermaphroditism is independent of the sex-producing genes, *A* and *B* may have been homozygous and *C* and *D* heterozygous with respect to the hermaphrodite modifier.

TABLE I

Pedigree no.	Cross	Result
08115	☿×self (*A*)	24♀:19☿
08117	☿×self (*A*)	9♀:6☿
08119	☿×self (*B*)	110♀:95☿
Total	☿×self	143♀:120☿
0869	♀×☿ (*A*)	58♀:36☿ :1♂
08118	♀×☿ (*A*)	60♀:40☿ :1♂
08127	♀×☿ (*A*)	51♀:52☿
08149	♀×☿ (*A*)	67♀:33☿
08106	♀×☿ (*B*)	53♀:50☿
08128	♀×☿ (*B*)	50♀:51☿
08150	♀×☿ (*B*)	59♀:43☿
08125	♀×☿ (*C*)	39♀:0 :55♂
08132	♀×☿ (*D*)	26♀:0 :18♂
Total	♀×☿ { *A* and *B* *C* and *D*	398♀:305☿: 2♂ 65♀:0 :73♂
08116	☿ (*A*)×♂	21☿:2♀ :11♂

That males, which are assumed to be heterozygous and to contain both the male and female tendencies, should occasionally show the development of characters of both the sexes as the result of some accident or environmental influence upon an individual, without in any way changing the character of the germ cells produced by that individual, is quite conceivable. The occurrence of these two different types of hermaphrodite individuals harmonizes well with many experiences met with in other studies in heredity, which have led JOHANNSEN (7) to distinguish between genotypes and phenotypes. These four hermaphrodite individuals, *A*, *B*, *C*, and *D*, belong to a single phenotype, but to two genotypes.

If now we compare these results in Lychnis with those of CORRENS in Bryonia, still leaving out of account the two exceptional males and the two hermaphrodites which occurred in pedigree no. 08116, we find that the difference is a consistent one. This comparison may be conveniently made in the following table:

TABLE II

Cross	Bryonia	Lychnis
♀×♂	♀ and ♂	♀ and ♂
☿×♂	♀ and ♂	♀ and ♂
♀×☿	♀	♀ and ☿
☿×☿	☿	♀ and ☿

In the first place, it is seen that all crosses between normal females and normal males in Lychnis result in females and normal males, just as in *Bryonia dioica*, and the same thing is true in both cases when the hermaphrodite is fertilized by a normal male. The result of self fertilizing the hermaphrodites of Lychnis, however, is (presumably) quite different from the result of self fertilizing *Bryonia alba*, for Lychnis gives rise to a progeny of females and hermaphrodites, while Bryonia (presumably) gives rise to only monoecists or hermaphrodite individuals. A similar difference is observable between these two classes of material when normal females are fertilized by pollen of hermaphrodites, as Bryonia produces in this case only females, while Lychnis produces females and hermaphrodites.

These results suggest that the differences between Bryonia and Lychnis are rather simple ones. The fact that the hermaphrodites take the place of males in each family whose male parent was a hermaphrodite, permits no other reasonable conclusion than that the hermaphrodite Lychnis is a modified male; and the capacity of the male to be thus modified so as to allow the development of both male and female organs, strongly favors the view that the male is heterozygous, as has been assumed by CORRENS (**4**) and CASTLE (**3**) for Bryonia, and as demonstrated by WILSON and his students for many insects.

There are now several possibilities regarding the nature of the females. CASTLE (**2**) long ago suggested that the female, as well as the male, is heterozygous, but in his latest communication on sex (CASTLE **3**) he definitely abandons this view and holds that in all cases only one sex is heterozygous and the other is homozygous; and this is the conception now generally entertained by those who adopt a Mendelian explanation of sex. According to this view, if the male is heterozygous, as has just been decided to be the case in Lychnis, the female must be homozygous. As there are two kinds of homozygotes, namely, "positive" and "negative" (SHULL **9**), there remain two possibilities regarding the nature of the female; it may be either a positive homozygote or a negative homozygote. While either of these assumptions will explain about equally well the facts brought to light in Bryonia, neither will fit all those observed in Lychnis without encountering important difficulties.

Making first the supposition that the female is a positive homozygote, as suggested by CASTLE (**3**), all conditions found in Bryonia will be satisfied if it be also assumed that *B. alba* is a homozygous monoecist (a modified female condition in this case) in which the absence of the monoecious character is dominant over its presence. The sterility of the F_1 hybrids in Bryonia unfortunately makes it impossible to test the correctness of these assumptions. It is less easy to make a positive homozygous condition of the female fit the results found in Lychnis as described in this paper. This can be done, however, by assuming: (*a*) that all egg cells of both females and hermaphrodites carry the gene for the female sex, and not that for hermaphroditism; and (*b*) that all the sperms of the hermaphrodites carry a gene for the hermaphrodite modification, regardless whether they possess the gene for the female sex (the "*x* element") or not. The first of these assumptions seems necessary from the fact that the results are identical in each case, whether a female or a hermaphrodite is used as the female parent; and the second from the fact that females and hermaphrodites result from pollinating a normal female by pollen from a hermaphrodite. The second proposition might be replaced by one involving spurious allelomorphism. It is expected that a second generation will demonstrate the correctness or incorrectness of these several hypotheses.

The alternative assumption, namely, that the female is a negative homozygote, will just as simply represent the conditions of the F_1 generation. If the monoecious character in Bryonia be considered a modified male condition similar to the hermaphrodite character of

Lychnis, the difference between Bryonia and Lychnis is reduced to a question of dominance of the hermaphrodite (or modified male) condition. In order that *Bryonia alba* should breed true, the monoecious (or modified male) character must be homozygous. The fact that in Bryonia a cross between the female *B. dioica* and the monoecious *B. alba* produces only females, indicates that the monoecious character is capable of coming to full expression only when present in the homozygous state. In other words, while the monoecists are modified positive male homozygotes, absence of this modified male character is almost perfectly dominant over its presence, so that the heterozygous individuals which constitute the F$_1$ of this cross almost or quite completely lack the male character. In this connection the occurrence of occasional male flowers on a few of these females of the F$_1$ may be of interest as showing a slight influence of the unpaired gene for the modified male or monoecious sex.

In Lychnis, on the other hand, the presence of the hermaphrodite character is dominant over its absence, as demonstrated by the fact that the hermaphrodite mutants are heterozygous with respect to sex. In the following table a comparison may be made between the two methods of explaining the character of the F$_1$ hybrid generation:

TABLE III

ASSUMPTION: The female is a positive homozygote

CROSS	BRYONIA			LYCHNIS		
	Assumed character of parental gametes	Resultant composition of offspring	Somatic type of offspring	Assumed character of parental gametes	Resultant composition of offspring	Somatic type of offspring
♀×♂	♀♀×♀	♀♀ and ♀	♀ and ♂	♀♀×♀	♀♀ and ♀	♀ and ♂
☿×♂	☿☿×♀	☿♀ and ☿	♀ and ♂	♀♀×♀	♀♀ and ♀	♀ and ♂
♀×☿	♀♀×☿☿	♀☿	♀	♀♀×☿	♀☿ and ☿	♀ and ☿
☿×☿	☿☿×☿☿	☿☿	☿	♀♀×☿	♀☿ and ☿	♀ and ☿
ASSUMPTION: The female is a negative homozygote						
♀×♂	♀♀ ×♀♀♂	♀♀ and ♀♀♂	♀ and ♂	♀♀×♀♀♂	♀♀ and ♀♀♂	♀ and ♂
☿×♂	♀♀☿☿×♀♀♂	♀♀☿ and ♀♀☿♂	♀ and ♂	♀♀×♀♀♂	♀♀ and ♀♀♂	♀ and ♂
♀×☿	♀♀ ×♀♀☿☿	♀♀☿	♀	♀♀×♀♀☿	♀♀ and ♀♀☿	♀ and ☿
☿×☿	♀♀☿☿×♀♀☿☿	♀♀☿☿	☿	♀♀×♀♀☿	♀♀ and ♀♀☿	♀ and ☿

No decision can be made between the two methods of explanation contrasted in this table until the F$_2$ has shown the dependence or independence of the gene whose presence results in the hermaphrodite modification of the male. If the females may carry the hermaphrodite modification as a latent character, and if the hermaphrodites of the F_1 differ in their gametic composition from those of the P_1 generation, the hypothesis that the female is a positive homozygote may be substantiated; but if the hermaphrodites of the F_1 are identical in their behavior with those of the P_1, and if the hermaphrodite modification cannot be transmitted through the female, the results will support the hypothesis that the female is a negative homozygote.

It is not at all improbable that the hermaphrodites discussed above as *C* and *D* differed from *A* and *B* in having the gene for the hermaphrodite modification in the heterozygous state, while *A* and *B* were homozygous with respect to this gene. If this should be correct, then *C* and *D* were of the type which will appear in the F_1 of crosses between normal females and such hermaphrodites as *A* and *B*, in case the hermaphrodite modification is independent of the male germ cells. The occurrence of such hermaphrodites as *C* and *D* may be accepted as rather favorable to the view that the female is a positive homozygote.

There is one fundamental difficulty with any hypothesis which assumes that the hermaphrodites are heterozygous. The eggs of these hermaphrodites are of a single kind with respect to sex, all carrying the female character. This difficulty is inherent in the material itself, however, and is not opposed in any way to the assumption that the normal females are either positive or negative homozygotes, for the male germ cells of the hermaphrodites are clearly of two types as required by the hypothesis that these hermaphrodite plants are heterozygous. Cytological investigations of oogenesis in the hermaphrodites may perhaps give a complete solution to the exceptional situation presented by the egg cells. If the females are positive homozygotes there may be simply a failure of those eggs to develop which do not possess the gene for the female sex. If the female is a negative homozygote, there may be a failure of those eggs which possess the male gene, or there may be an exclusion of this gene during oogenesis.

While I have left out of account the two hermaphrodite individuals in the cross (08116) between a hermaphrodite and a normal male, I am not unmindful of their possible importance. The number of offspring of this combination was too small to enable one to be sure that these are not mutants which bear no necessary relation to the fact that their mother was a hermaphrodite. It was found particularly difficult to secure offspring of crosses of this type, as the flowers were very often caused to drop off as a result of the process of castration. Very often also in the flowers of hermaphrodite plants the pistils are immature at the time the anthers are ready to open, and after castration these pistils frequently develop no farther, in which case there is no possibility of effecting fertilization. The occurrence of these two hermaphrodite plants in no. 08116 offers a further suggestion that the hermaphrodite character may be capable of independent movement, and that consequently it may be carried in some manner or to some degree by the female. This suggestion especially commends itself from the fact that the occurrence of the male and female organs on the same plant, as CORRENS (**4**) has pointed out, constitutes in effect a mosaic, and it is well known that mosaic inheritance is often dependent upon the presence of a definite separate unit for the mosaic condition. If further investigation should demonstrate that the hermaphrodite character may be transmitted through the female, as is suggested by this one family, we will be forced to the conclusion that here also the existence of a unit for the mosaic condition is present. In whatever manner the male may be converted into a hermaphrodite, the results seem to demonstrate that in Lychnis, as in Bryonia, *it is the male which is heterozygous* and which carries both male- and female-producing genes as concluded by CORRENS, and not the female as assumed by BATESON.

The demonstration that the hermaphrodite of *Lychnis dioica* is a modified male indicates that STRASBURGER (**11**) was mistaken in his interpretation of the effects produced by *Ustilago violacea* upon this species. He believed that the infected plants were females in which the development of stamens was stimulated by the attack of the fungus. Instead of this it is probable that they were males in which the disease somewhat lessened or modified the dominance of the male character, thus allowing the female organs to develop; or, if the female is a positive homozygote, the disease may be assumed to have stimulated the single female gene or x element of the male to develop the female organs as well as the male organs. **Strasburger** states that the development of the stamens in the diseased plants was correlated with an elongation of the floral axis between the calyx and corolla (a character peculiar to flowers of the male plants), and that not infrequently the infected plants gave the impression that they were males. On the other hand, the fibrovascular system of the calyx in infected plants more nearly assumed the distinctive features of the normal female flowers. The appearance of this secondary female character may be as readily accounted for as the appearance of the female sex organs themselves, on the ground of modified dominance of the male or of the female character in a heterozygous male.

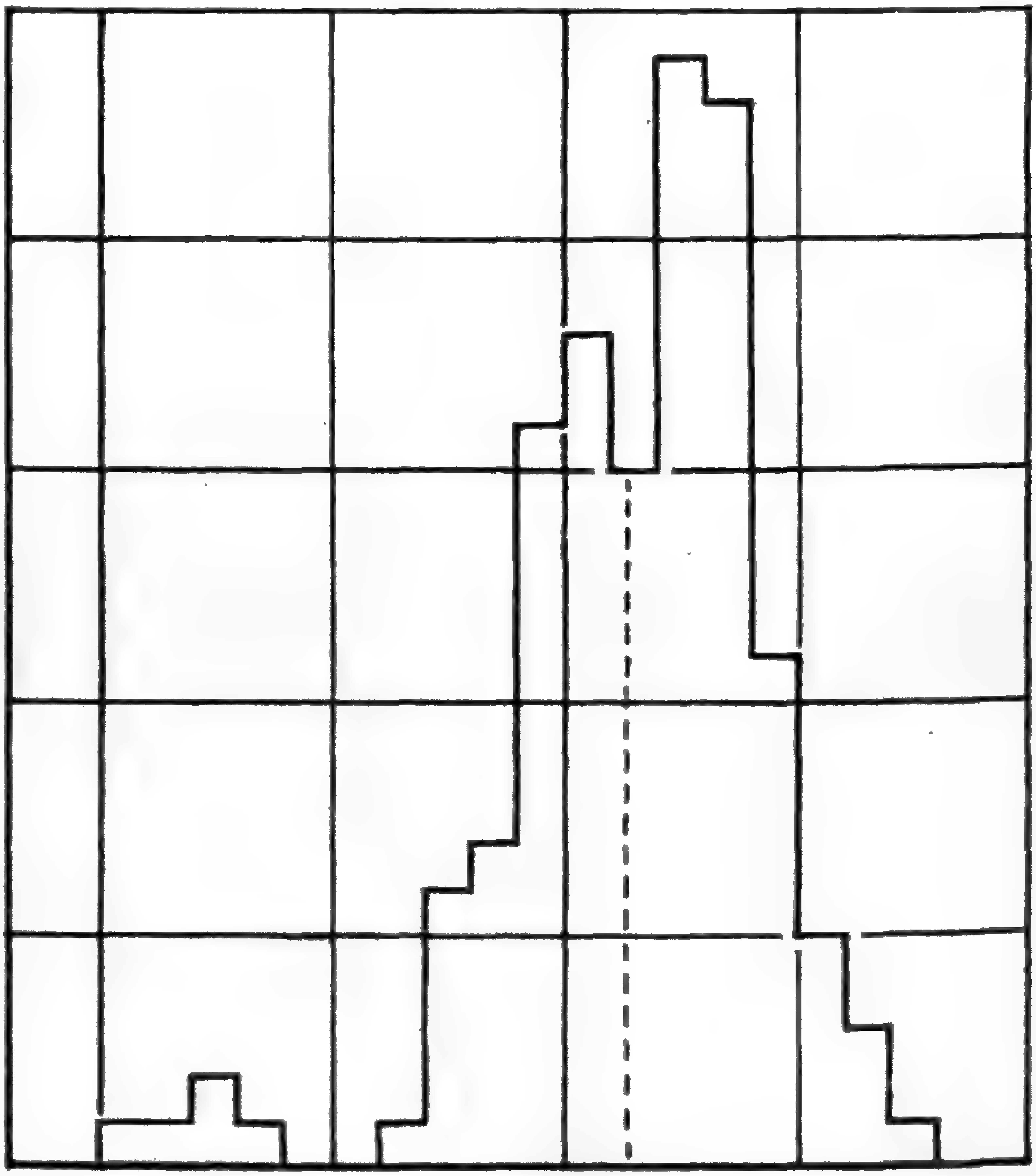

Fig. 1.—Variation in percentages of females in 135 families of *Lychnis dioica*.

Correns has pointed out that the determination of sex ratios is quite a different matter from the determination of sex, and we must maintain that this is so, provided sex is inherited as a Mendelian character. But if sex inheritance be not primarily Mendelian, but only associated with and perhaps determined by Mendelian characters in a few cases, the determination of a sex ratio might not be a process distinct from the inheritance of sex itself.

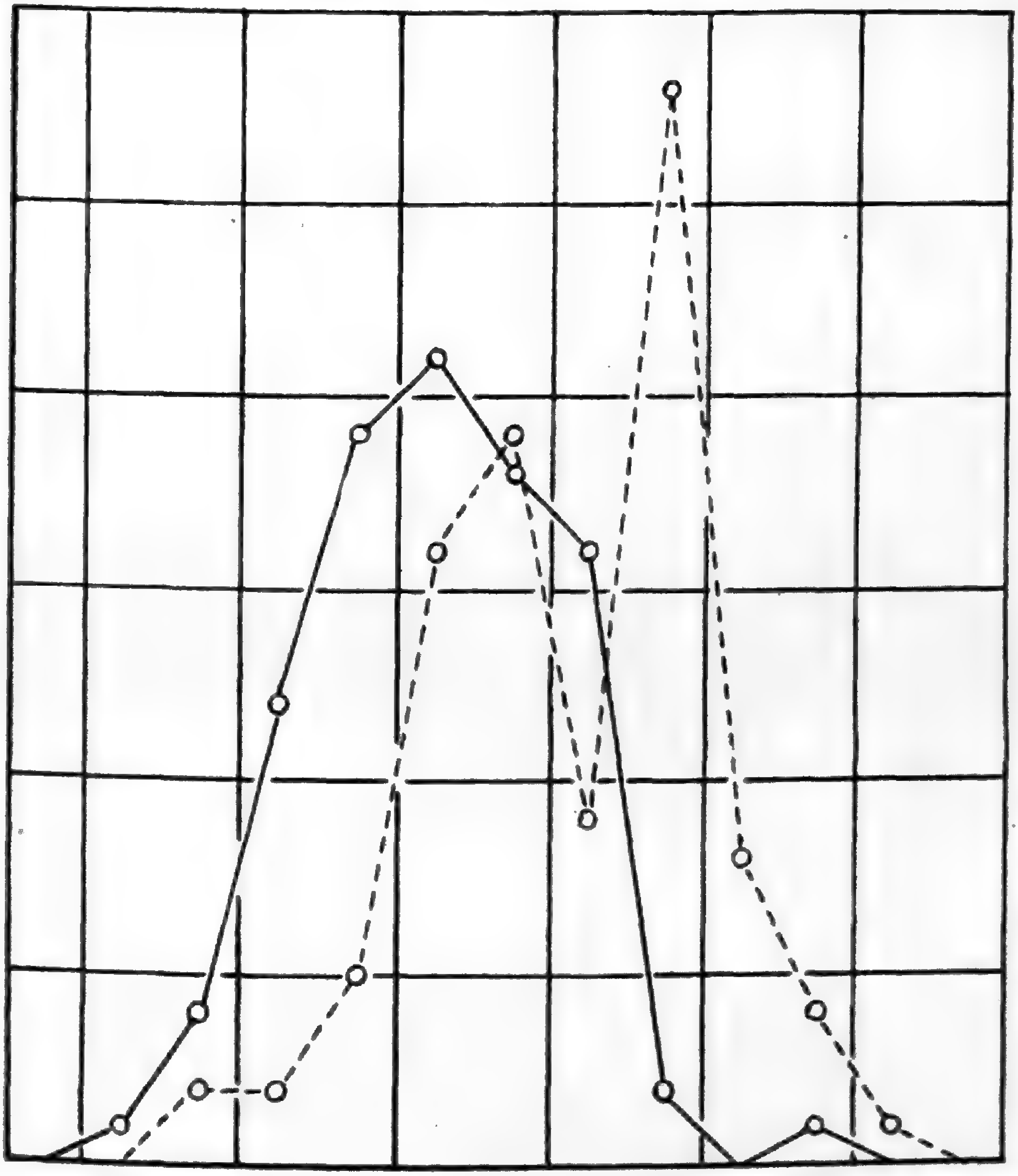

FIG. 2.—Variation in percentages of females and in percentages of purple-flowered plants in 94 families of *Lychnis dioica* produced by crossing heterozygous purple with white; broken curve represents females; both curves if monomodal belong to PEARSON'S Type I. See constants in table IV.

The assumption that the sexes differ from each other by a single unit character, and that one sex is heterozygous and the other homozygous with respect to this character, would demand equality in the average numbers of the two sexes; but each year *Lychnis dioica* has produced on the average a considerable excess of females, while the ratios in different families range all the way from less than 5 per cent. female to nearly 90 per cent. female. The percentages of females in 135 families reared during the summer of 1909 are shown in the form of a variation curve in *fig. 1*. It is difficult to believe that a family of 4 females and 100 males or of 87 females and 10 males is theoretically referable to a ratio of 1:1. In 1909 my cultures of *Lychnis dioica*, taken collectively, consisted of 6366 females and 4831 males (including hermaphrodites), or a ratio of 1.32:1, which agrees very well with ratios between 1.20:1 and 1.40:1 reported by STRASBURGER (**11**). After carrying on extensive experiments on the influence of various environmental factors, with negative results, STRASBURGER reached the conclusion that the sex ratio is determined by inherent factors. This is only another way of saying that it is hereditary in some sense. I have been attempting for several years to test the heredity of the sex ratios, but have not yet found the key to the situation. It is hoped that the numerous crosses which have been made will in the near future throw some light upon the significance of these exceedingly variable ratios and allow the causes which determine them to be understood.

In order to compare the variation in these sex ratios with that in a character known to be Mendelian, I have plotted curves representing the percentage of females and the percentage of purple-flowered individuals in all families (94 in number) raised during the years 1907, 1908, and 1909, which were produced by the union of heterozygous purple with white (see *fig. 2*). The variation constants of the two curves appear in the following table:

TABLE IV

VARIATION CONSTANTS OF CURVES CONTRASTED IN *fig. 2*

	Percentage females	Percentage purples
Mean	61.223 ±0.630	52.606 ±0.551
Standard deviation	9.051 ±0.445	7.925 ±0.490
Coefficient of variability	14.784 ±0.742	15.064 ±0.758
Theoretical mode	62.933 ±0.686	52.353 ±0.600
Coefficient of skewness	−0.0990±0.0062	+0.0282±0.0062

Aside from the remarkable difference in the value of the means, the two curves are skewed in opposite directions, the strong negative skewness and suggested bimodality of the sex curve, as contrasted with the nearly normal character of the curve for color, being particularly noteworthy. The variability represented by these two curves is properly compared by means of the standard deviations, and not by the coefficient of variability, since we are dealing here with groups of variates having similar theoretical limits of range, and similar expected mean values. On this basis the sex ratios show considerably greater variability than those of the color character. This is especially interesting in view of the fact, pointed out elsewhere (SHULL **10**), that crosses between heterozygous purple and white *Lychnis dioica* may frequently result in other ratios than 1:1, owing to the part taken by several distinct genes in the production of the purple colors in this species, and that therefore the data for the color curve may be somewhat heterogeneous, while the sex data are at present assumed to be homogeneous.

Summary

Hermaphrodite mutants occur in pure-bred families of *Lychnis dioica* L., the ratio of mutability being somewhat less than 1:1000.

None of these hermaphrodites was diseased and several were fully functional both as females and males, thus negativing the suggestion of STRASBURGER that the hermaphrodites in this species may always be due to the attacks of the smut, *Ustilago violacea*.

In their hereditary relations these hermaphrodites were of two kinds, some behaving like normal males, others having the capacity of transmitting the hermaphrodite character to their male offspring. This second class of hermaphrodites when self fertilized, or crossed with normal females, gives progenies consisting of normal females and hermaphrodites, and when fertilized by normal males gives normal females and normal males.

The hermaphrodite individuals are modified males, for in all families in which these hermaphrodites were the pollen parents the offspring showed the same ratios of females and hermaphrodites as would have been expected of females and males had a normal male been used as the pollen parent.

These results agree in a general way with those of Bryonia in that they demonstrate the homozygous character of the females and the heterozygous character of the males in Lychnis.

Whether the females are positive or negative homozygotes cannot be determined from the F_1, as both assumptions can be made to fit the facts by the aid of simple correlative hypotheses whose correctness or incorrectness can be determined only by further breeding.

A fundamental difficulty in either case is found in the fact that the egg cells of the hermaphrodites are apparently of a single type, all possessing the female-producing gene. The assumption that the hermaphrodites are heterozygous leads us to expect equal numbers of two different types of egg cells. Cytological studies may perhaps explain this difficulty. The male germ cells of the same plants are of two types, as required by theory.

The occurrence of two hermaphrodite individuals in a progeny produced by a cross between hermaphrodite and normal male suggests the possibility that the hermaphrodite character may also be transmitted through the female. This fact, together with the occurrence of two genotypes among the hermaphrodites, is held to be slightly favorable to the view that the female is a positive homozygote.

The demonstration that the hermaphrodite individuals of Lychnis are modified males indicates that STRASBURGER was mistaken in assuming that his hermaphrodites were diseased females. They were probably diseased males in which the dominance of the male character was modified by the fungus.

The sex ratios in Lychnis do not accord well with a theory of sex which requires males and females to be present in equal numbers. The ratios found in my cultures are in accord with those found by STRASBURGER, the average for the past year being 1.32 females to 1 male, with a very wide difference in the ratios of different families. The significance of these ratios is not yet understood.

When the variability in the sex ratios is compared with that in ratios produced by crossing heterozygous purple with white-flowered individuals, it is found that not only is there an undue departure in the sex ratios from the expected ratio 1 : 1, but also that there is greater variability in the sex ratios than in the color ratios, and that the curve is strongly negatively skewed and possibly not monomodal; while the color curve derived from the same families is nearly normal; with the mean departing but little from the 50 per cent. required by Mendelian theory.

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THE REFORESTATION OF SAND PLAINS IN VERMONT

A STUDY IN SUCCESSION

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 135

CLIFTON DURANT HOWE

(WITH MAP AND FIFTEEN FIGURES)

Geology

The region of this study is known as the Burlington-Colchester-Essex sand plains, which are situated at the mouth of the Winooski River, that flows into Lake Champlain from the Vermont side. The history of the plains is intimately connected with that of Lake Champlain. Previous to the Glacial period the present valley of the lake was occupied by a river[1] flowing northward. With the melting of the ice sheet a large lake was formed in the former river valley. After the Glacial period the sea invaded the region from the north, constituting what the older geologists called the Champlain epoch. At this time extensive beds of clay were laid down. The marine nature of these clays is demonstrated by the frequent occurrence of salt-water shells and by a skeleton of a whale found imbedded in them in the township of Charlotte. The Champlain epoch closed with an elevation of land which raised the marine deposits to their present location, the highest elevation being about 100^{m} above the present lake. With the withdrawal of the sea the valley was again occupied by a body of fresh water, the present Lake Champlain.

At some time during the glacial and post-glacial history of Lake Champlain outlined above, bodies of water occupied three well-marked levels. During each of these stages a delta was formed by the erosion deposits brought down by the Winooski River. From the townships in which they are located, these deltas are designated on the accompanying map, from oldest to youngest, as the Essex delta, the Colchester delta, and the Burlington delta. The broken lines on the east side of each delta represent the beach lines of the lake (or sea) during the successive elevations. The doubling of the broken lines

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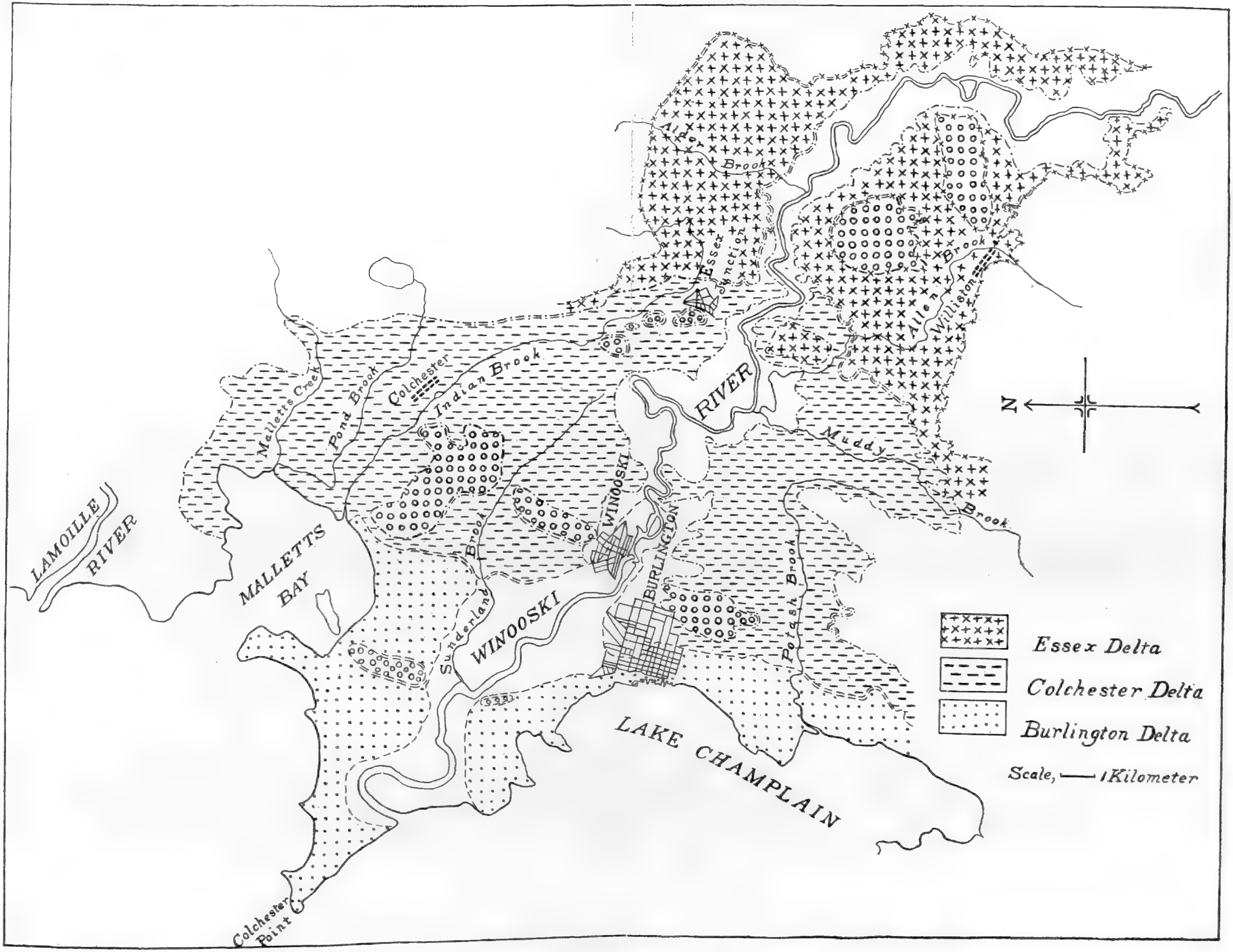
[1] BALDWIN, S. P., Am. Geol. **13**:170–184.



MAP OF THE BURLINGTON-COLCHESTER-ESSEX SAND PLAINS denotes the presence of fossil beaches, usually accompanied by low sand dunes. The areas designated by circles were islands. Those in the Essex delta are schistose rock covered with unassorted glacial till and were not submerged. Those in the Colchester and Burlington deltas, however, were submerged during the Essex stage, being limestone outcrops with the exception of the group of small islands just northwest of Essex Junction, which are schistose rock. The island south of Essex Junction, across the river, is an isolated portion of the Essex delta.

The unshaded areas on each side of the Winooski River indicate its erosion channel through the deltas. The deltas have also been much dissected by smaller streams, but their erosion channels have not been shown on the map.

The elevation of the Essex delta plain is 149^{m}, of the Colchester delta plain 98^{m}, and of the Burlington delta plain 68^{m} above the sea. Since the mean level of Lake Champlain is 30^{m}, these deltas are 119, 68, and 38^{m} respectively above the present lake level.

The surface layer of soil on each of the three delta plains is sandy, varying from pure sand to sandy loam. The texture of the sand is fine and remarkably uniform throughout, and its depth ranges from a few centimeters to 7^{m}. The subsoil of the whole area is clay. The Winooski River and its tributaries have exposed large areas of this clay, which, mixed with the sand, makes excellent farm lands. The discussion which follows, however, is confined to the vegetation of the sand plains of the three deltas, which occupy an area 36^{km} long and on the average 14^{km} wide.

Original forest conditions

While the early historians mention the dominance of pine on the area under consideration, they indicate the dominant species only by inference. For example, THOMPSON[2] says: "Along the western part of the state and bordering on Lake Champlain are extensive tracts of light sandy soil which were originally covered with white, pitch, and Norway pine." The testimony of the oldest inhabitants who took part in the clearing of the areas is that white pine was the dominant

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[2] THOMPSON, ZADOCK, History of Vermont, natural, civil, and statistical. Burlington. 1842.

tree. The prevalence of old white pine stumps beneath the present forests, as well as the numerous white pine stump fences throughout the sand plains townships, contribute corroborative evidence. The original forest evidently contained some large trees, judged from present standards. THOMPSON (*l. c.*) states that he had observed trees 52^m high, and adds that originally trees 43 to 55^m high, having a diameter of 2^m, were not uncommon. Stumps in various stages of decay which were originally at least 1.5^m in diameter may be seen frequently on the sand plains.

In the clearings for settlement the commercial use of white pine was strictly local and very limited. Later came the period of utilization on a larger scale. As early as 1800[3] great rafts of pine logs taken from the sand plains were floated down to Quebec and thence exported. In 1842 the historian THOMPSON (*l. c.*) asserted that the forests of white pine in the Champlain region had practically disappeared. In 1850 (DAVIS, *l. c.*) the importation of white pine from Canada began.

The pitch pine (*Pinus rigida*) doubtless occupied small scattered areas on the most sterile soils. Black oak and white oak (*Quercus velutina* and *Q. alba*) are now common on the sand plains, and they probably formed a minor part of both the original white pine and pitch pine forests. Norway pine (*Pinus resinosa*) is now very local in its distribution on the sand plains, and it probably always was so. No record is to be found in regard to white birch (*Betula populifolia*); for reasons to be discussed later it is doubtless much more abundant now than originally.

Succession

The succession on the Burlington, Colchester, and Essex sand plains is of two classes in respect to its place of origin, namely, upon cut-over areas and upon abandoned cultivated fields.

SUCCESSION ON CUT-OVER AREAS

As stated above, historical evidence clearly indicates that white pine was orginally the controlling tree on the Burlington, Colchester, and Essex delta plains. Only isolated trees of the original stand now

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[3] DAVIS, W. T., The New England states **3**:1524–1526.

remain. The conditions following the first cutting favored the invasion of the pitch pine upon areas which it had not previously occupied. In the first place, having no value at that time, it was not cut, so that seed trees were plentiful, a thing that cannot be said of the white pine; in the second place, pitch pine produces seed more abundantly than the white pine; and finally, being more light-demanding and being able to endure more sterile soil conditions, it is better adapted for regeneration on areas cleared by lumbering. Whatever the causes may have been, pitch pine became the controlling tree of the second generation, especially on the Colchester plain. A representative list chart in a stand 60 years old shows 2.5 pitch pine on 25^{sqm}. Beneath on one square meter are 18 *Myrica asplenifolia*, 5 *Pteris aquilina*, 7 *Kalmia angustifolia*, 30 *Vaccinium pennsylvanicum*, 11 *Vaccinium vacillans*, 4 *Carex pennsylvanica*, 4 *Diervilla Lonicera*, 3 *Solidago* sp. (rosettes), 2 *Rubus allegheniensis*.

The soil on the Burlington and Essex plains being as a whole less sandy, there is a larger proportion of mixed stands. On the average, black oak and white oak form one-third of the pitch pine stands. White pine of the second generation is more common on these two plains.

Three brickyards and a limekiln within the sand plains furnish a market for pitch pine as fuel, and the pitch pine forests have been cut for this purpose, so that by far the greater part of the area is now in its second cycle of reforestation. The stands are usually cut clean of both trees and saplings, the latter being taken down to 5^{cm} in diameter. Sometimes a few isolated pines are left for seed trees, but they almost invariably die of the exposure resulting from clean cutting. The removal of the trees stimulated the development of the undergrowth, so that in most cases Myrica and Pteris became the dominant plants, and beneath them is a carpet of blueberries (*V. pennsylvanicum* and *V. vacillans*). If fire runs through, as it usually does periodically, the association becomes so dense as to allow no reproduction of trees. Often as many as 60 Myrica plants may be found on a square meter. The fire also keeps down the coppice shoots from the oak stumps. Some areas cleared 25 years ago are still practically without tree reproduction.

When the Myrica-Pteris association is 15 to 20 years old, and when it has not been rejuvenated in the meantime by fire, it begins to die out, apparently from natural causes. The open places thus made give an opportunity for the reestablishment of pitch pine. The few lots on which this was noted show pitch pine seedlings at the rate of

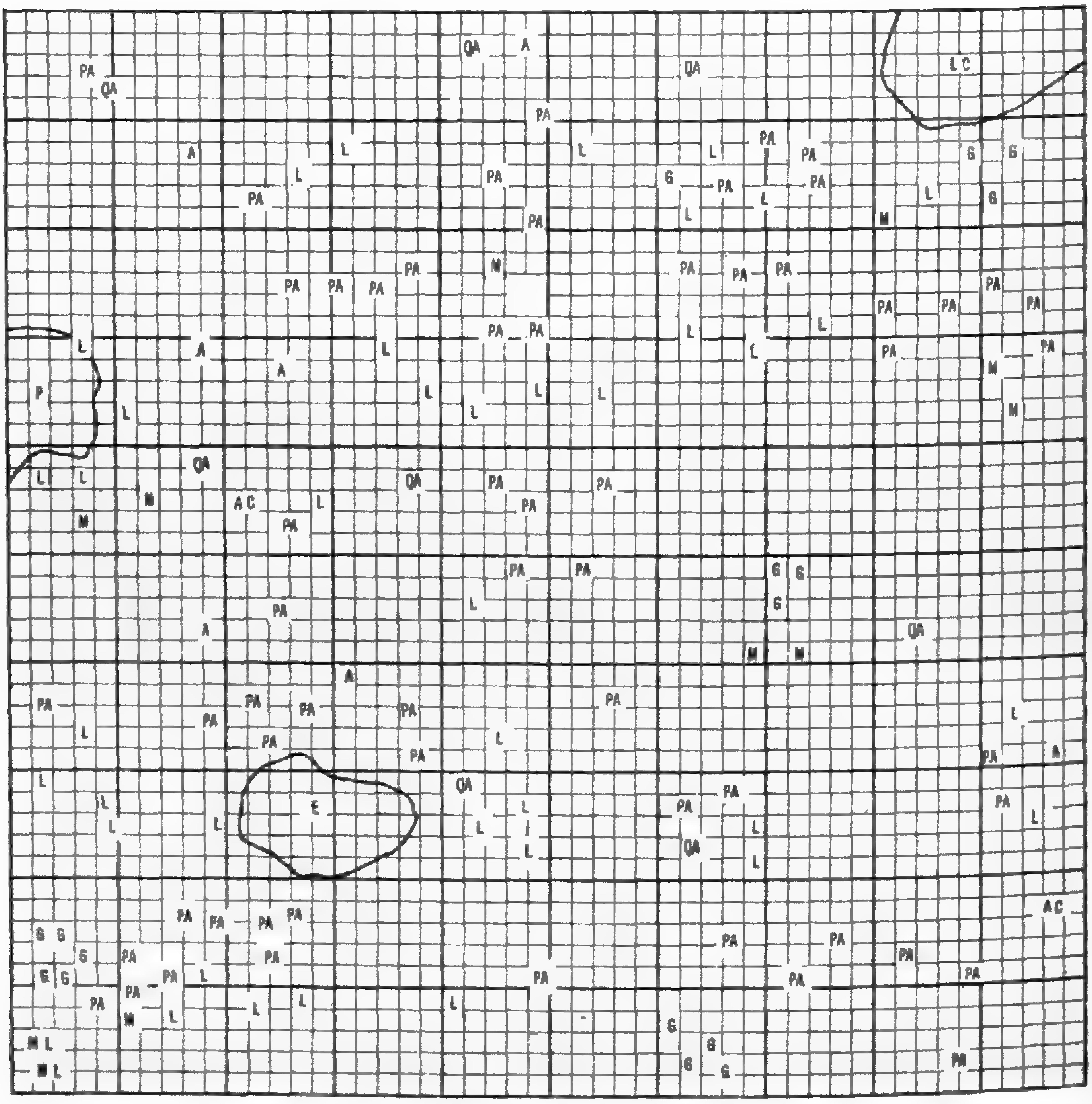

FIG. 1.—Sample plot 15. Cleared 15 years ago, Colchester plain, 5 meters square; under layer controlled by *Vaccinium pennsylvanicum* and *Kalmia angustifolia;* QA. *Q. alba* 8; A, *Acer rubrum* 5; AC, *Amelanchier canadensis* 2; PA, *Pteris aquilina* 56; L, *Lysimachia quadrifolia* 38; G, *Gaultheria procumbens* 14; M, *Myrica asplenifolia* 9; LC, *Lycopodium complanatum;* P, *Polytrichum;* E, *Epigaea repens;* ML, *Melampyrum lineare* 2.

one to $50^{\mathrm{sq\,m}}$; older stages were not found. It seems probable, however, that eventually, if unmolested by man, such areas will regain their dominance of pitch pine.

In cases where fire is kept out from the time of clearing, however, reforestation takes place more rapidly. This is brought about first by the coppice shoots of the oak and by the filling-in of the intervening spaces by white birch (*Betula populifolia*), trembling aspen, red maple, and Amelanchier. Thus, on a lot cut two years ago, black oak coppice groups averaged three on $25^{\text{sq m}}$, while on the lot as a whole, 10 per cent. of the coppice was white oak and 6 per cent. red maple. A dominant stand of pitch pine 24 years old was removed from the lot and a list chart showed on one square meter 9 Myrica, 12 Pteris, 4 *Populus tremuloides*, 22 *Kalmia angustifolia*, 34 *Vaccinium pennsylvanicum*, 1 *Rubus allegheniensis*.

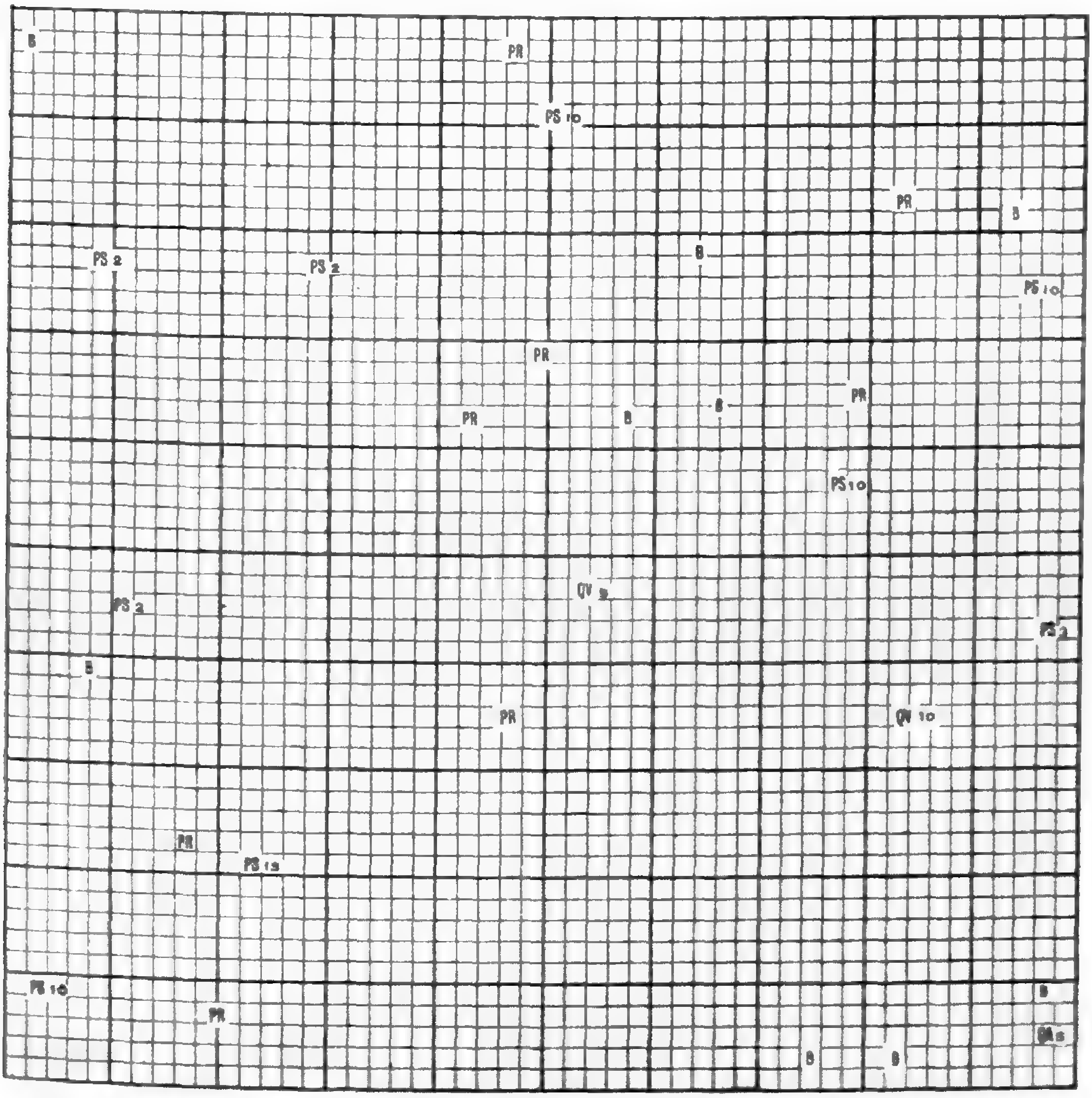

Fig. 2.—Sample plot 2. Pitch pine stand, 30 years old, Colchester plain, 5 meters square; under layer controlled by Pteris, Gaultheria, and *Vaccinium vacillans;* PR, *Pinus rigida* 8; QV, *Q. velutina* 2; QA, *Q. alba* 1; B, *Betula populifolia* 7 (dying); PS, *Pinus Strobus*.

A stand of pitch pine 45 years old with suppressed black oaks averaging one and three respectively per $25^{sq\,m}$, was cut clean eight years ago. An average square meter now supports 3 coppice groups of black oak, 3 *Corylus americana*, 1 *Amelanchier canadensis*, 1 *Salix humilis;* under layer, Myrica and Pteris; beneath this, Kalmia, *Vaccinium vacillans*, *Lysimachia quadrifolia.* The sample plot (*fig. 1*) discloses the present conditions of a lot from which pitch pine was removed 15 years ago.

When the coppice stands of oak are about 15 years old, they cover the area sufficiently to shade out much of the under vegetation. Myrica is the first to show the effects of this shading and Pteris goes next, while the species of Vaccinium persist longer than either Myrica or Pteris, *V. vacillans* enduring the competition with the trees longer than *V. pennsylvanicum.* At this stage the pines begin to reestablish themselves. Pitch pine because of its greater intolerance comes into such areas very sparsely and very slowly. Only one place was found where it had gained control, and even there the stand seems destined to be displaced by the more shade-enduring white pine, as the sample plot (*fig. 2*) shows.

For the reasons stated above, white pine is establishing itself on the clean-cut areas, formerly controlled by pitch pine, to a greater extent than the pitch pine. For example, in a lot cut 12 years ago, on $25^{sq\,m}$ one finds 8 white birch saplings, 3 black oak coppice groups, 6 pitch pine seedlings, and 3 white pine seedlings; this is 100^{m} from white pine seed trees. A distance of 50^{m} from seed trees there are on $25^{sq\,m}$ 3 black oak coppice groups, 2 *Amelanchier canadensis*, 1 white birch, 1 red maple, 2 pitch pine seedlings, and 13 white pine seedlings. A still older stand is shown in sample plot no. 14 (*fig. 3*).

The best white pine reproduction on clean-cut areas, however, is found where white birch controls. Thus in a clean cutting of 12 years ago, there are now 2 white birch coppice groups, 25 birch saplings and seedlings, 6 red maple coppice groups, 20 *Viburnum acerifolium*, 17 *Corylus americana*, 3 *Rhus typhina*, 4 Myrica, 20 *Vaccinium vacillans*, 2 white pine (8 years old); *Polytrichum commune* and *Carex pennsylvanica* dominant beneath. This plot is 100^{m} from a white pine seed tree. Another plot of the same size ($25^{sq\,m}$) cleared

15 years ago and only 5^m from a seed tree, shows 44 white pine seedlings mostly 4 and 8 years old. The seedlings are practically all on little hummocks covered with Polytrichum and Mitchella. The plot

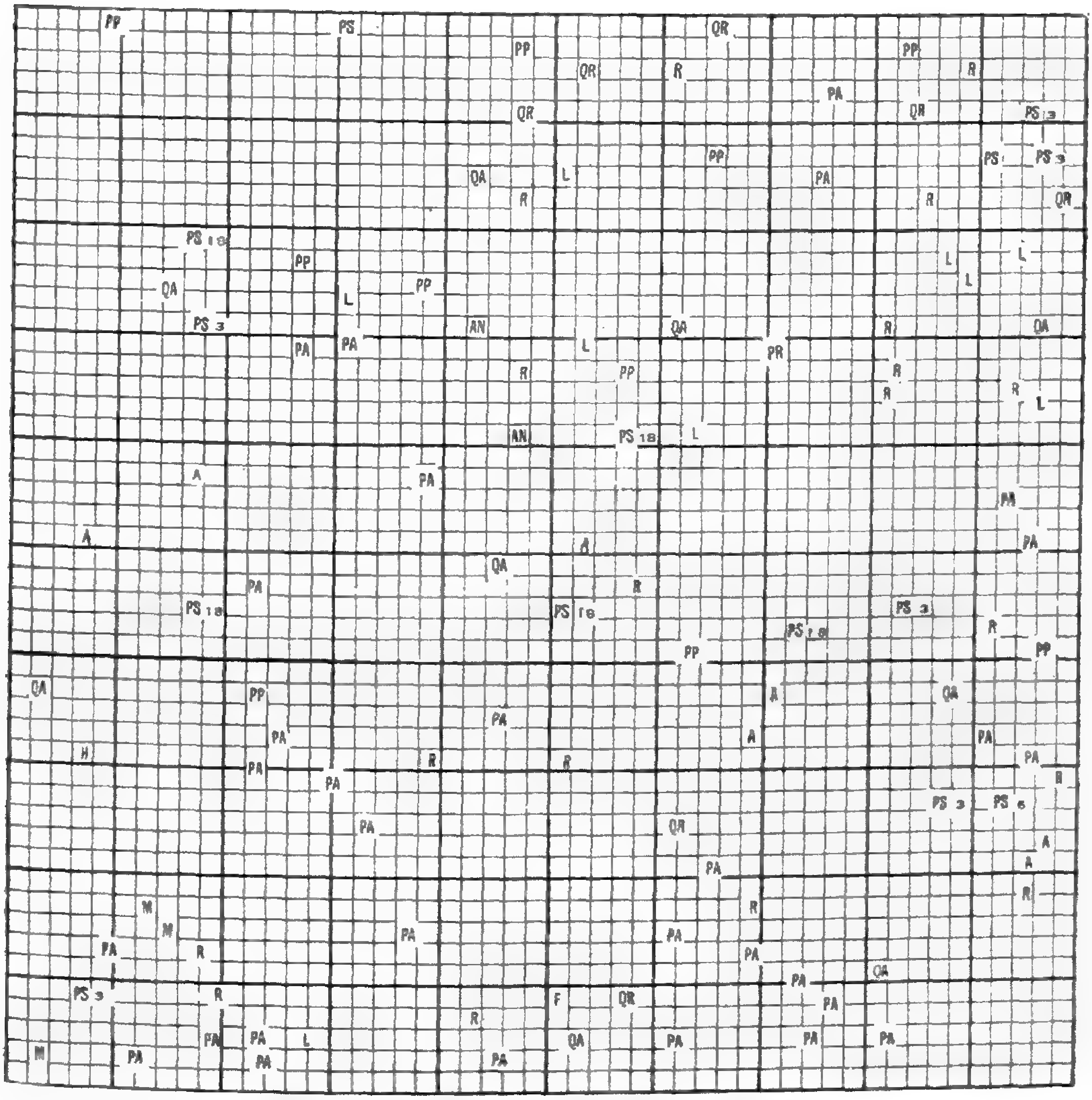

FIG. 3.—Sample plot 14. Cleared 20 years ago, Essex plain, 5 meters square; PS, *Pinus Strobus* 14; QA, *Quercus alba* 8; QR, *Q. rubra* 7; A, *Acer rubrum* 6; PP, *Prunus pennsylvanica* 10; PA, *Pteris aquilina* 29; R, *Rubus allegheniensis* 15; L, *Lysimachia quadrifolia* 9; M, *Myrica asplenifolia* 3; AN, *Aralia nudicaulis* 3; V, *Vaccinium vacillans* 2; F, *Fragaria* sp. 1; H, *Hamamelis* 1.

also contains one white pine sapling, 4 white birch and 3 black oak saplings, 3 Hammamelis, and 8 Corylus.

White birch in competition with oaks and pines persists only 20 to 30 years. Thus in a representative stand of this age one finds on $25^{\text{sq m}}$ 5 white pine (5 to 14 years old), 2 black oak, 1 white oak, 3 white birch (nearly dead). When such stands are 35 years old the white birch usually has disappeared, and they average on 25 $^{\text{sqm}}$ 2.2 white pine, 2.4 black oak, 0.6 white oak. Although the black oak appears in slightly greater numbers, the majority of them are suppressed and white pine dominates the stand.

Thus it will be seen that the clean-cut areas which pass through the white birch stage in their reforestation end in the control of the white pine, and that those areas passing through the oak coppice and Myrica-Pteris stages are more generally succeeding to white pine than to pitch pine.

SUCCESSION UPON ABANDONED CULTIVATED FIELDS

The writer had no means of determining definitely how long the various fields had been cultivated before abandonment, but the indications are that the period was relatively short, on the average probably not more than 10 years. In some cases the fields never produced any other cultivated crop than rye, while in others they were cultivated 30 or 40 years before final abandonment. Occasionally an old field partially reforested is cleaned off and a second attempt at cultivation is made.

According to the conditions in which it takes place, the succession leading to the dominance of the forest upon abandoned fields may be discussed under the following heads:

1. Succession lacking the preliminary herbaceous stages. This occurs when a plowed field near a mature stand of trees happens to be abandoned in a heavy seed year.

2. Succession lacking the sod-forming stage. The herbaceous stages are present but the complete control of grasses is absent or short-lived.

3. Succession possessing the sod-forming stage. The natural course of succession here is interrupted by man, for these areas are cropped for grass or pastured for a longer or shorter period before the trees begin to take possession.

1. SUCCESSION LACKING THE PRELIMINARY HERBACEOUS STAGES.— This occurs when the abandonment of a plowed field and an abundant seed year are in conjunction. For example, a field on the Colchester plain first bore a crop of rye, then a crop of beans, and lay fallow the third year, when it was seeded down to white birch from the trees

which surrounded the field. White birch seedlings two years old and *Spiraea tomentosa* now occupy the field at the rate of 53 and 4 respectively per square meter. A stand of pitch pine 16 years old showing 63 trees on 25^{sqm} came into existence in the same manner. A sample plot in this stand is given below (*fig. 4*). The oaks beneath are 4 years old. Other dense even-aged stands of both white birch and pitch pine probably had a similar origin, although the history of their inception is not actually known.

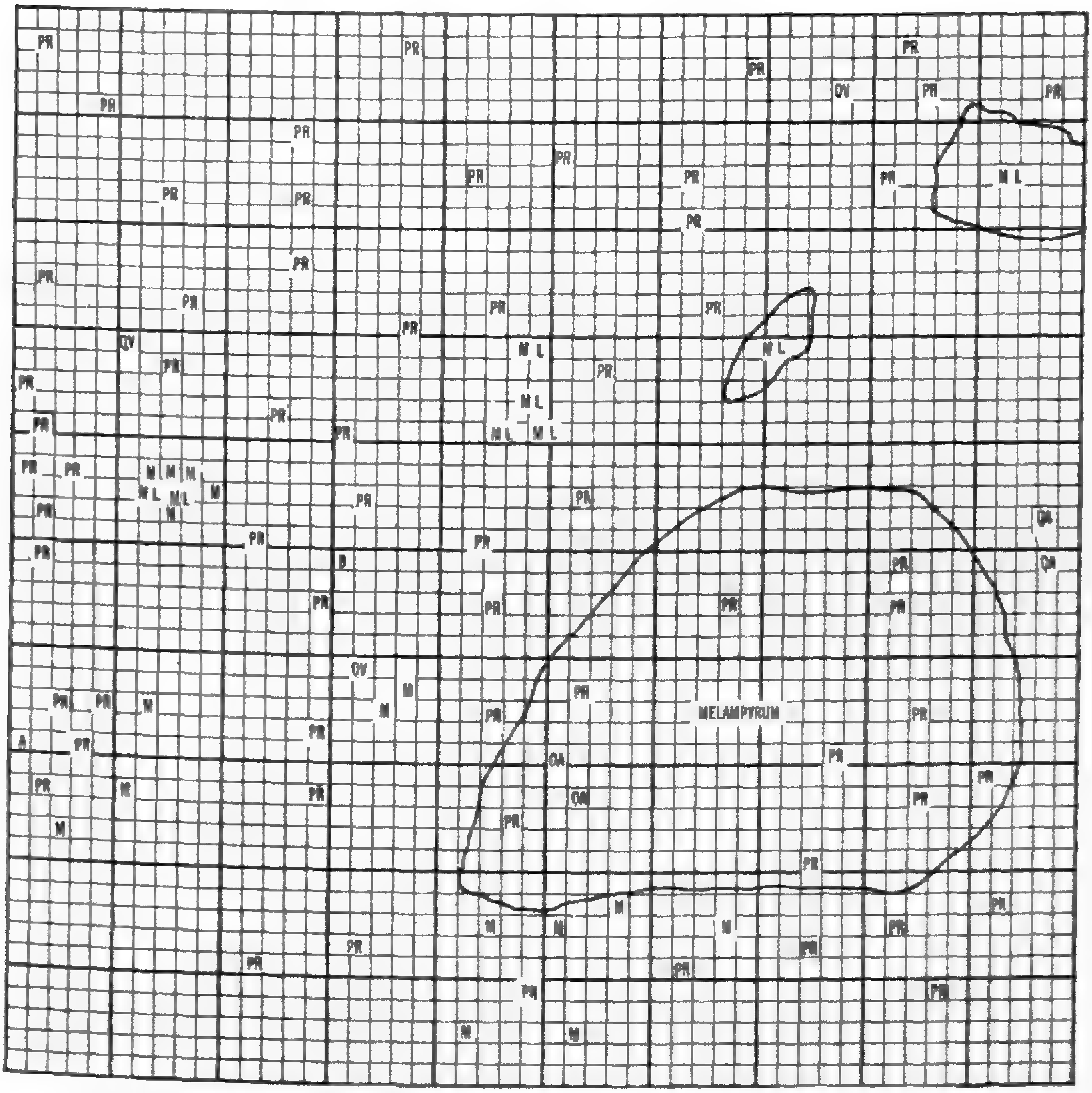

FIG. 4.—Sample plot 16. Pitch pine 16 years old, on abandoned plowed field, Colchester plain, 5 square meters; PR, *Pinus rigida* 63; QA, *Q. alba* 5; QV, *Q. velutina* 3; ML, *Melampyrum lineare;* M, *Myrica asplenifolia* 16.

2. SUCCESSION LACKING THE SOD-FORMING STAGE.—The character of the vegetation on a plowed field the first year after abandonment apparently depends upon the kind of weed seeds in the fertilizer.

The quadrant below (*fig. 5*) gives the characteristic plants of a field which supported a crop of rye in the preceding year. Some fields may be controlled by *Setaria glauca* and *Setaria viridis;* others by *Ambrosia artemisiifolia* and *Erigeron canadensis.* Fields under observation for 4 years have remained under the dominance of these annuals. Later, *Oenothera biennis*, *Rumex Acetosella*, *Gnaphalium polycephalum*, *Antennaria plantaginifolia*, *Solidago memoralis*, and *Aster linariifolius* control the old fields in patches. Between these patches occur scattered groups of *Cyperus filiculmis*, *Carex pennsylvanica*, *Andropogon scoparius*, and *Danthonia spicata*. Groups of Poly-

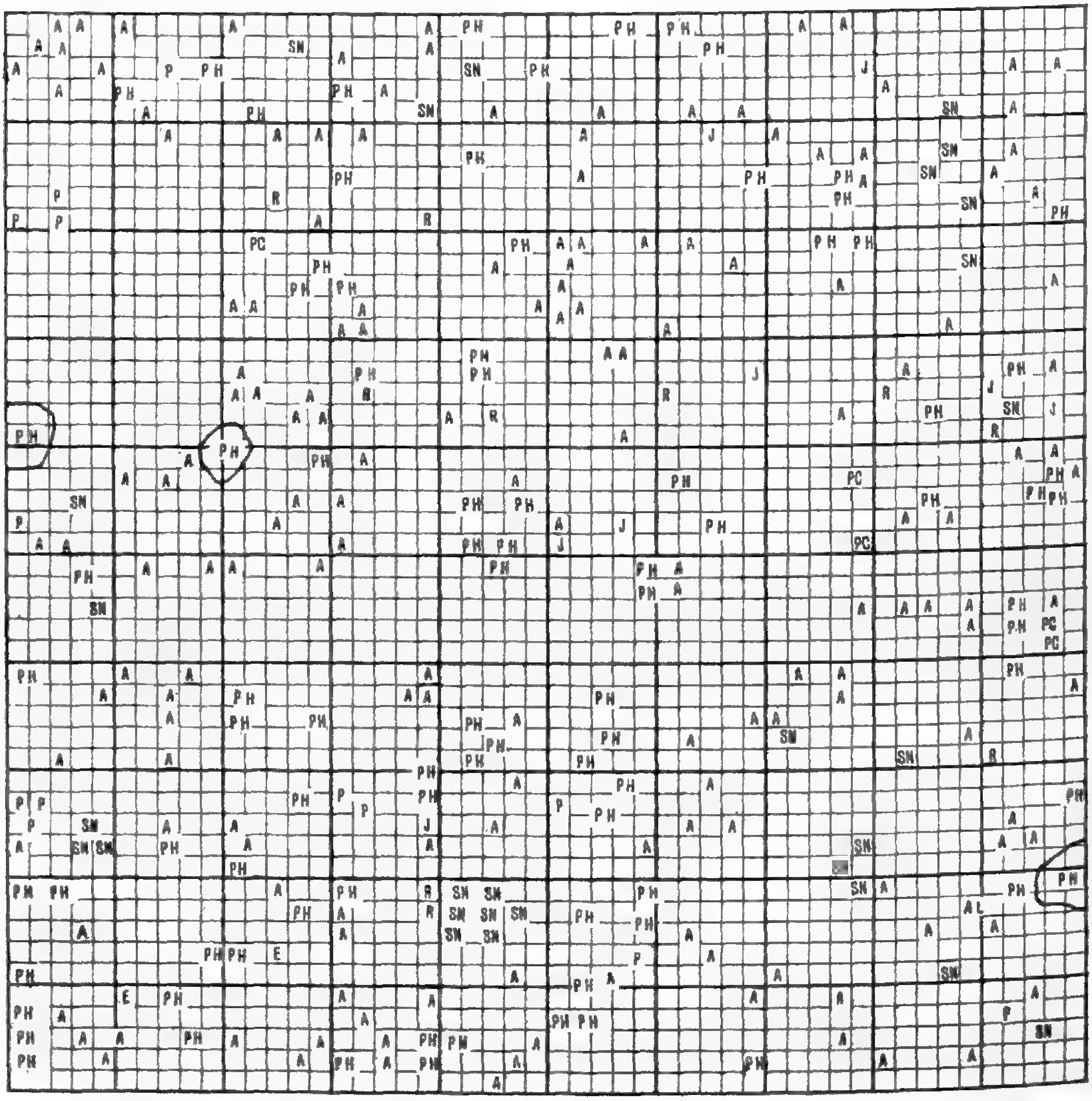

FIG. 5.—Sample plot 24. Plowed field, abandoned one year, Colchester plain, 1 square meter; A, *Ambrosia artemisiaefolia* 155; PH, *Phleum pratense* 82; SN, *Solidago nemoralis* 26; P, *Poa compressa* 14; PC, *Panicum capillare* 4; R, *Rumex Acetosella* 7; J, *Juncus* sp. 6; E, *Erigeron canadense* 2; AL, *Aster linariifolius* 1.

trichum appear in the most sterile places. Driving out the biennial and perennial weeds, the groups unite and form patches of moss a meter or more in diameter. The moss in turn may be crowded out by Cyperus and Danthonia, but it is never entirely displaced. Patches of Polytrichum often occupy one-third of the area in old fields.

Some of the plowed fields were abandoned because they began to blow away, and they have since become areas of shifting sand. This is notably the case in several places in the townships of Colchester and South Burlington. The finest sand is piled up in low dunes and the coarser grades left behind are packed hard by the wind. *Cyperus filiculmis* and *Panicum sanguinale* are the pioneers on the compact sand; the former occurs in groups, while the latter advances *en masse* upon the sand. The open spaces between the groups of Cyperus are filled up by Polytrichum.

The patches of Polytrichum in the abandoned fields described above form ideal germinating beds for the seeds of pitch pine, white pine, and white birch. This is particularly the case when the Polytrichum is young, before the dead leaves and stems have accumulated sufficiently to prevent the seeds from reaching the mineral soil. Usually, however, Myrica precedes the tree invasion. It starts in the bed of Polytrichum and itself forms patches, killing out the moss immediately beneath it. The Polytrichum, however, persists around the margins of the Myrica group and in the moss, and under the protection of the Myrica one finds the tree seedlings.

The rapidity with which trees take possession of the abandoned fields of this type chiefly depends upon the proximity of seed trees. Thus a field 370^{m} from seed trees, abandoned 20 years ago, has only 41 white birch and 6 pitch pine saplings per hectare. When the pines get old enough to produce seed, a group of young trees will be formed about each mother tree. Fields showing two generations of pitch pine formed in this manner are of common occurrence and those showing three generations are not rare. The white birch, being shorter lived and less tolerant than the pine, is gradually suppressed, and the result is a pure stand of pitch pine of uneven age. A list chart in the field mentioned above shows on one square meter 16 *Solidago memoralis*, 24 *Carex pennsylvanica*, 18 *Lysimachia quadri-*

folia, 8 *Aster linariifolius*, 6 *Danthonia spicata*, 2 *Ambrosia artemisiifolia*, 1 *Viola arenaria*, 1 group of *Andropogon scoparius*.

When the abandoned field happens to be near a mature stand of pitch pine, the reforestation is much more rapid. For example, an old field on the Colchester plain has at 270^{m} from the seed trees 1 pitch pine and 6.3 white birch saplings on $25^{\text{sq m}}$; at 170^{m} from the mother stand 3 pitch pine and 1.3 white birch; at 75^{m}, 7 pitch pine and no white birch on $25^{\text{sq m}}$. In the second case the forest cover is complete and in the third case the stand is dense. At the greatest distance from the seed trees, the area between the birch and pine is

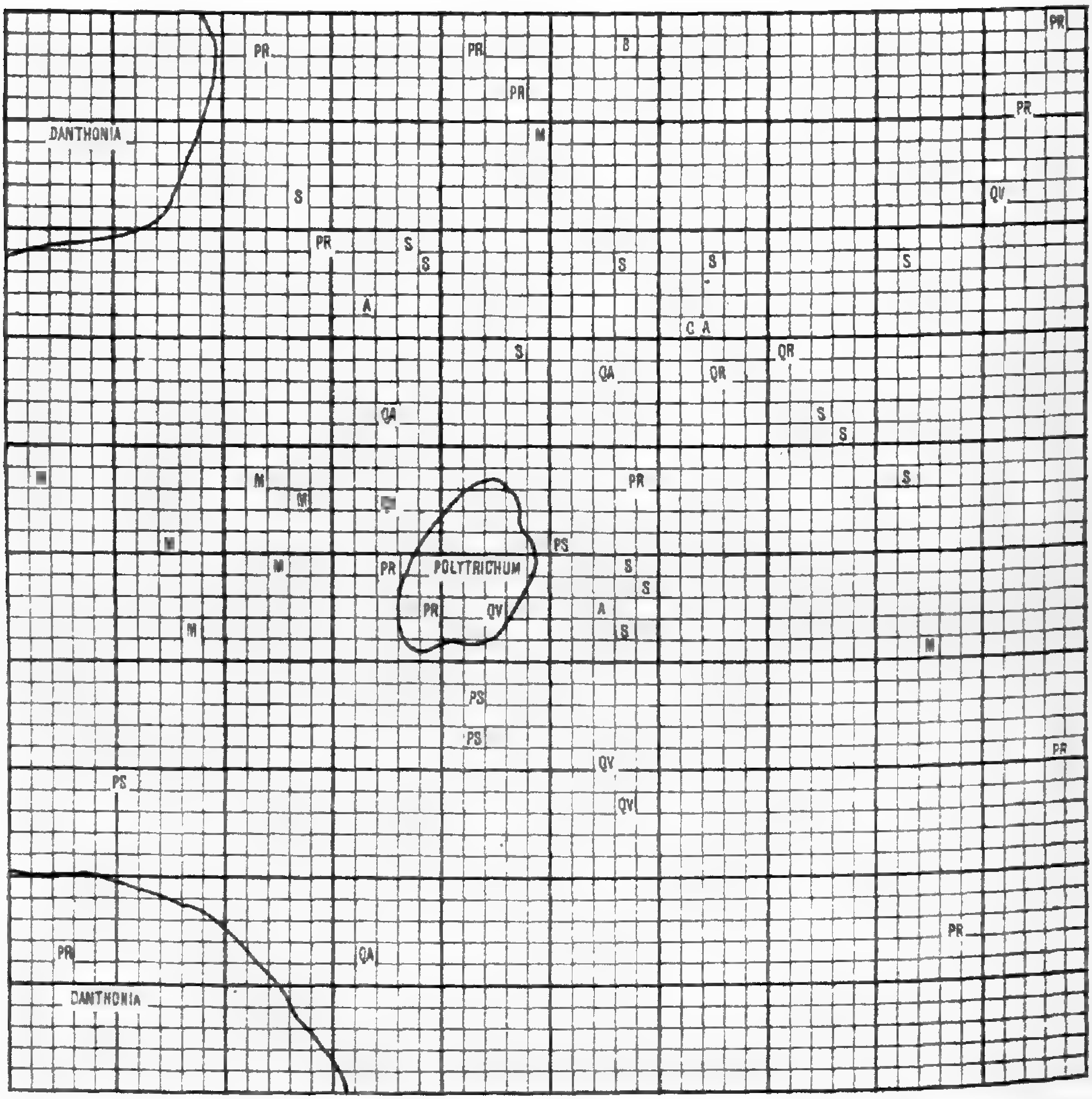

FIG. 6.—Sample plot 11. Pitch pine 25 years old in an old field, Colchester plain, 5 meters square; PR, *Pinus rigida* 12; QV, *Q. velutina* 7; QA, *Q. alba* 2; S, *Spiraea tomentosa* 12; A, *Acer rubrum* 2; B, *Betula populifolia* 1; M, *Myrica asplenifolia* 9; PS, *Pinus Strobus*.

controlled by Myrica and Pteris. As the trees become more abundant these are gradually crowded out, until beneath the dense stand they disappear. The saplings nearest the seed trees are 25 years old and those farthest from the seed trees are 8 years old.

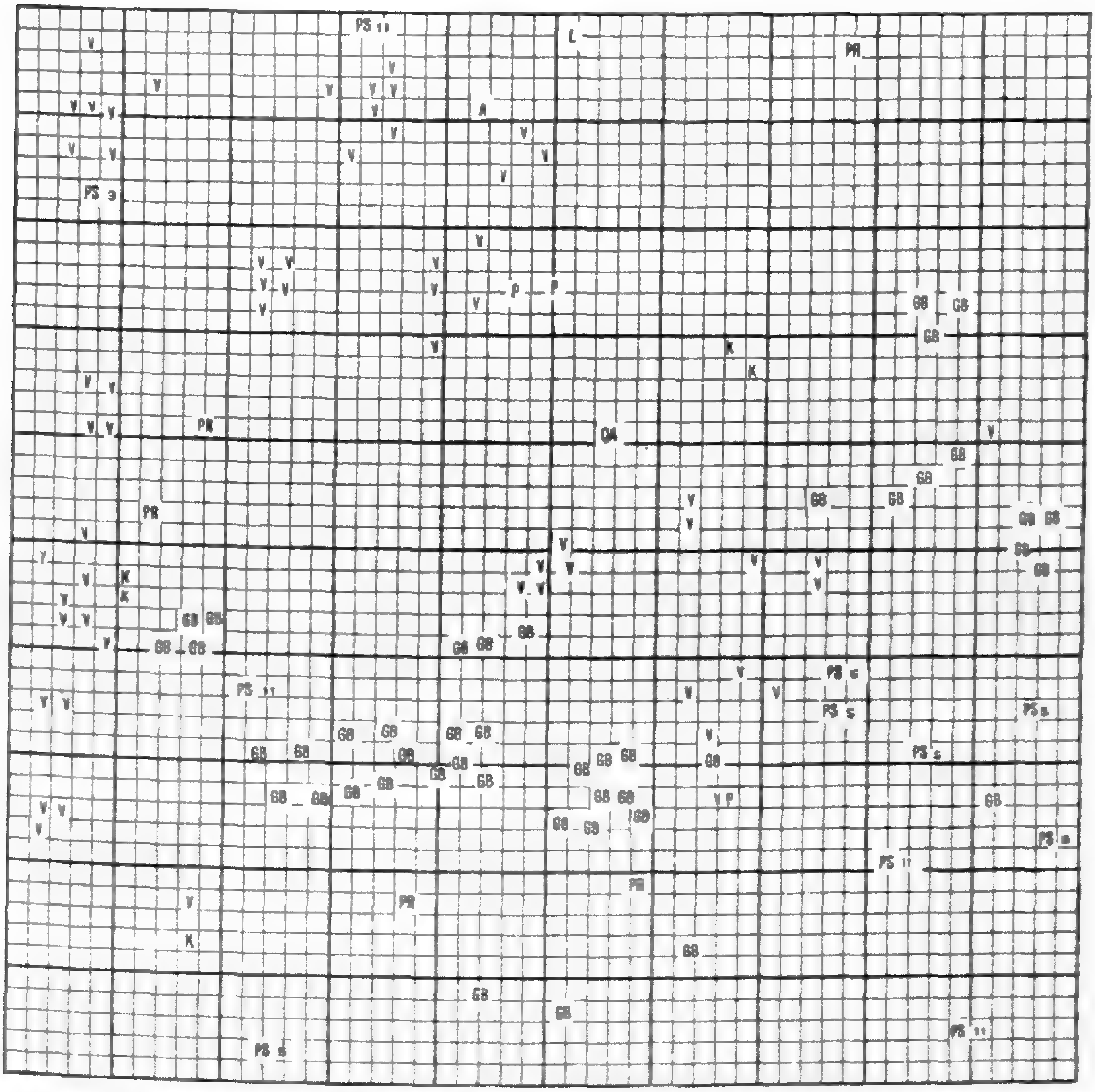

FIG. 7.—Sample plot 10. Pitch pine stand 60 years old, Colchester plain, 5 meters square; under layer, *Carex pennsylvanica*; PR, *Pinus rigida* 4; PS, *Pinus Strobus* 11; V, *Vaccinium vacillans* 59; GB, *Gaylussacia baccata* 44; K, *Kalmia angustifolia* 5; QA, *Q. alba* 1; L, *Lysimachia quadrifolia* 1; VP, *Vaccinium pennsylvanicum* 12; P, *Pteris aquilina* 26.

On p. 138 is given a sample plot (*fig. 6*) made in a stand of pitch pine 25 years old. Oaks are common in stands of this kind, but they are usually suppressed and apparently never become members of the dominant class.

An even-aged stand of pitch pine (36 years old on the stump) on the Essex plain averages 6 trees on $25^{\text{sq m}}$. *Vaccinium pennsylvanicum* forms a carpet beneath, and growing up through this, one finds on the average square meter 13 Pteris, 5 *Gaylussacia baccata*, 14 *Melampyrum lineare*, 8 *Carex pennsylvanica*, 1 *Rubus allegheniensis*, 1 *Apocynum androsaemifolium*.

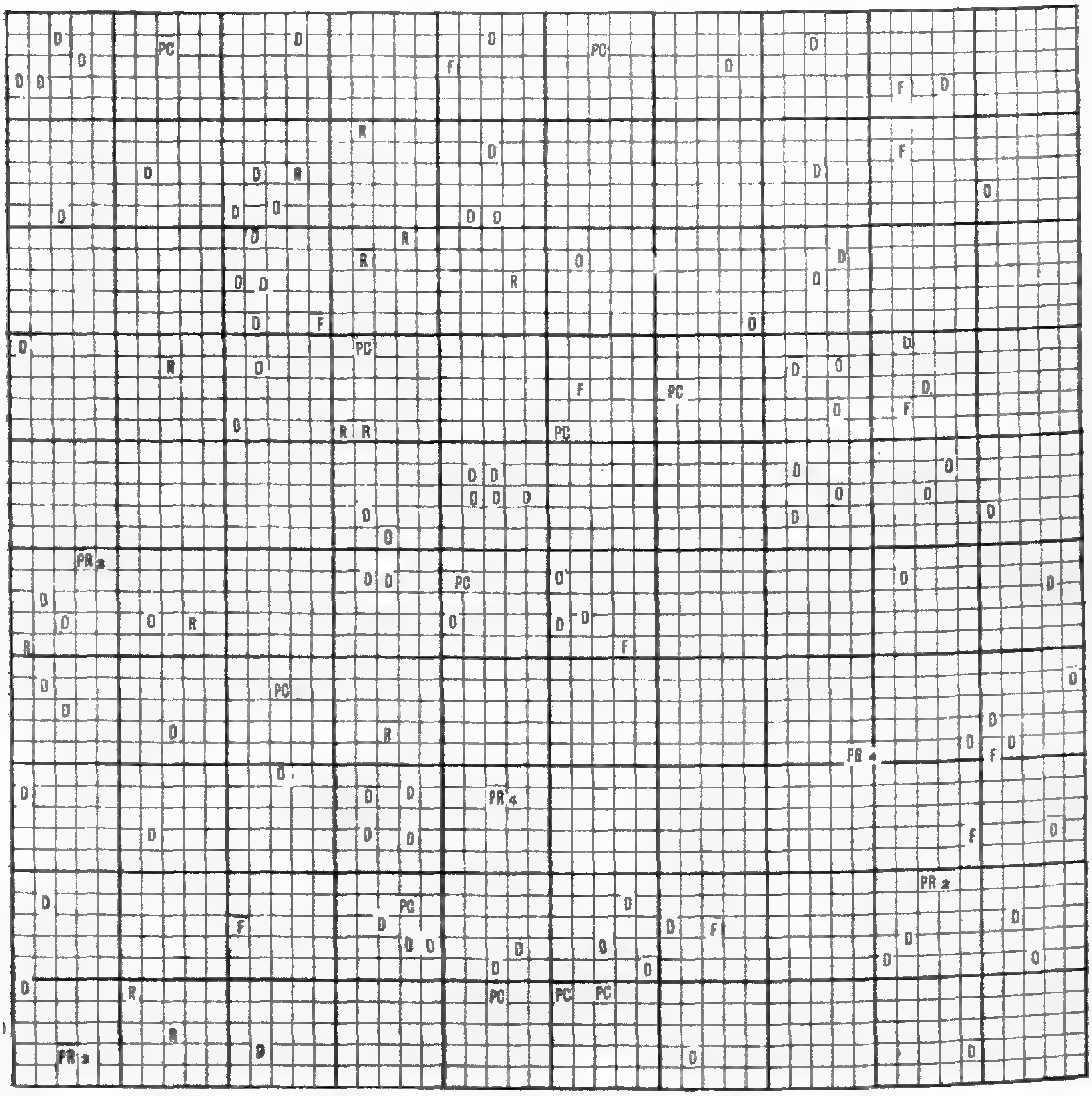

FIG. 8.—Sample plot 25. Danthonia-Polytrichum pasture being invaded by pitch pine; open patches occupied by Polytrichum; Colchester plain, 1 square meter; D, *Danthonia spicata* 89; R, *Rumex Acetosella* 13; F, *Fragaria virginiana* 10; PC, *Panicum capillare* 6; PR, *Pinus rigida* 2.

By the time pitch pine which has taken possession of the abandoned fields in the manner described above is 60 years old, the stand has become much less dense, averaging only one tree on $25^{\text{sq m}}$. The ground beneath is much less shaded and the soil is richer from the accumulation of humus. At this point white pine quite commonly reproduces itself under the protection of the pitch pine, which is shown in the sample plot given on p. 140 (*fig. 7*).

3. SUCCESSION POSSESSING THE SOD-FORMING STAGE.—Many of the cultivated fields on the sand plains were "seeded down," bore crops of hay for a few years, and then were turned over to pasturage. Other fields formed a sod naturally without artificial seeding and were used as pastures. The chief sod-formers in this case were *Poa pratensis* and *Danthonia spicata*. After pastures formed in these two ways have been grazed for several years, they begin to lose their fertility. The first manifestation of this is the dying out of *Poa pratensis*, which is replaced by Danthonia. In course of time Danthonia gives way to *Polytrichum commune*. Most of the pastures

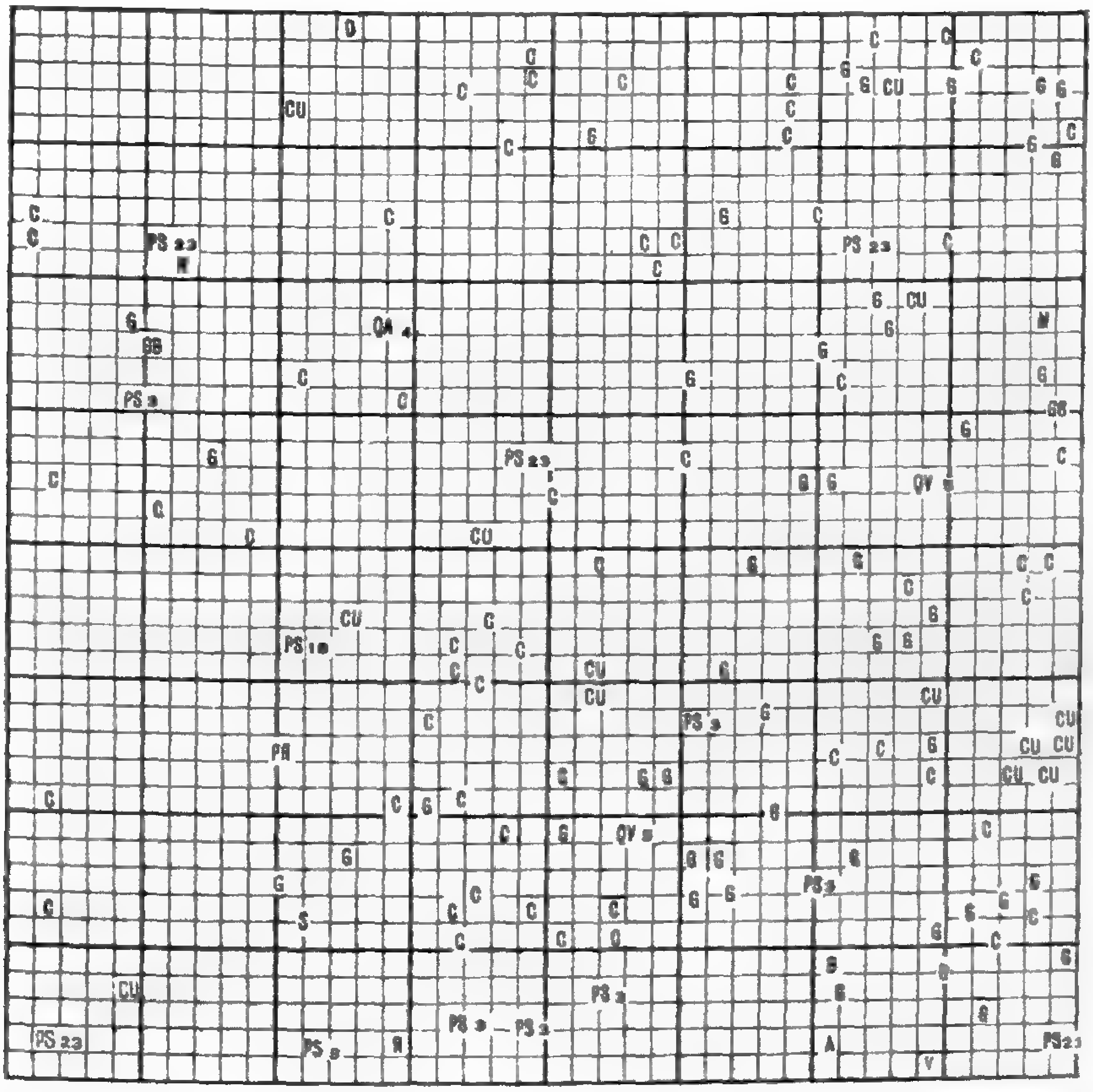

FIG. 9.—Permanent sample plot 35. Forty-year-old stand of pitch pine, Colchester plain, 4 meters square; PR, *Pinus rigida* 1; PS, *Pinus Strobus* 13; QV, *Q. velutina* 2; QA, *Q. alba*; C, *Carex pennsylvanica* 56; G, *Gaultheria procumbens* 46; CU, *Chimaphila umbellata* 11; GB, *Gaylussacia baccata* 2; D, *Diervilla Lonicera* 1; V, *Vaccinium vacillans* 1; B, *Betula populifolia* 1; A, *Acer rubrum* 1; R, *Rubus allegheniensis* 2; S, *Solidago* sp. 1.

on the area under consideration are in the Danthonia-Polytrichum stage. The principal associated species are *Cyperus filiculmis, Panicum capillare, Spiraea tomentosa, Potentilla argentea, Solidago nemoralis, Rumex Acetosella, Aster linariifolius.*

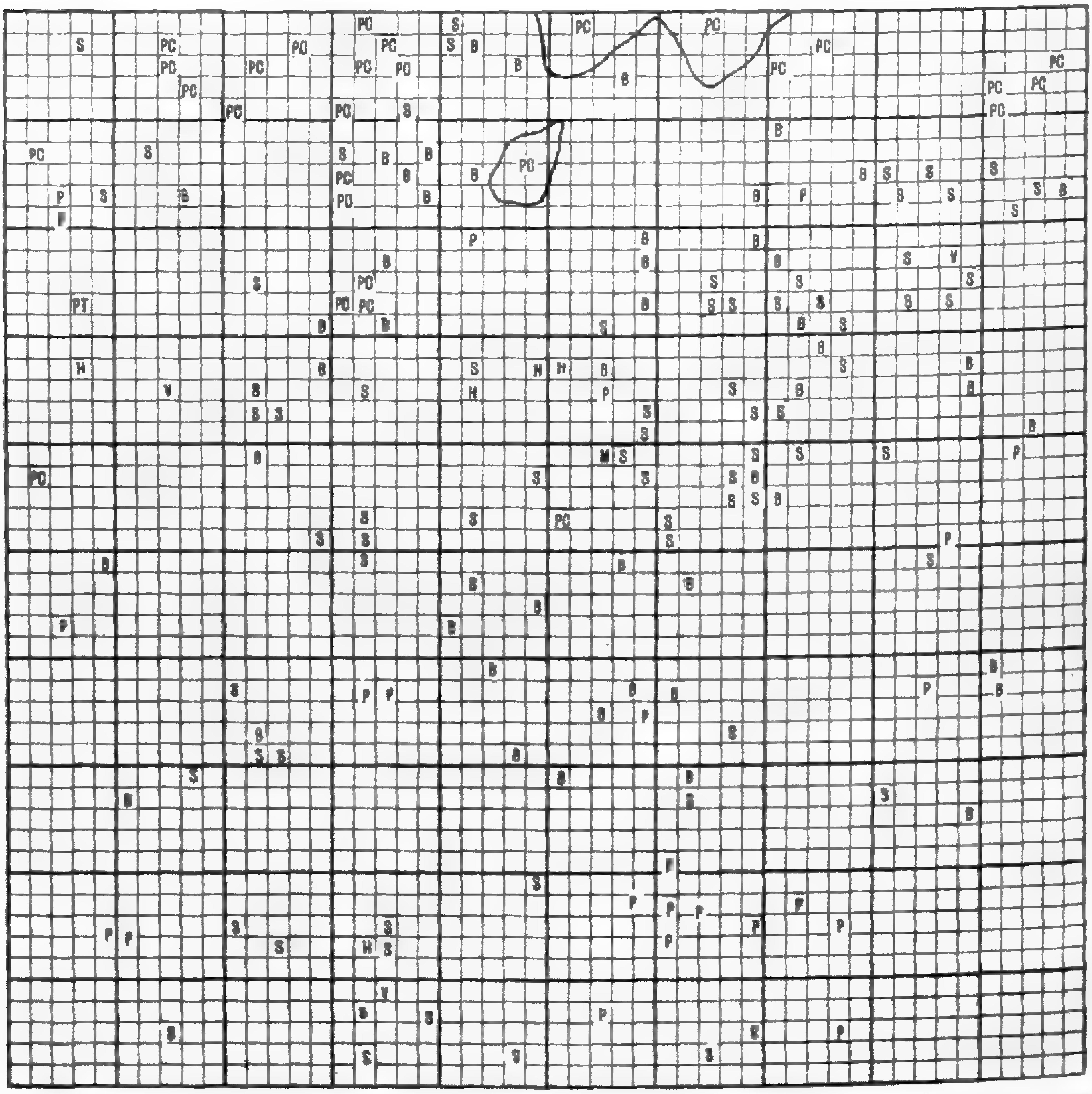

FIG. 10.—Sample plot 1. Danthonia-Polytrichum pasture, showing one-year-old white birch, Colchester plain, 1 square meter; B, *Betula populifolia* 49, at rate of 245 white birch on 25 square meters; S, *Spiraea tomentosa* 67; PC, *Poa compressa* 24; P, *Panicum capillare* 21; H, *Hypericum canadense* 5; V, *Verbena hastata* 3; PT, *Populus tremuloides* 1.

As in abandoned plowed fields, beds of Polytrichum are centers from which the tree invasion begins. As in the former case also, pitch pine and white birch are most commonly taking possession of worn-out pastures. Adjacent to mature pitch pine, pastures are transformed into pure even-aged stands of that species, while those at a distance from the seed trees are eventually covered with unevenaged stands, as described for old fields in the preceding section. Sample plot no. 25 (*fig. 8*) shows the character of a pasture in the first stages of possession by pitch pine.

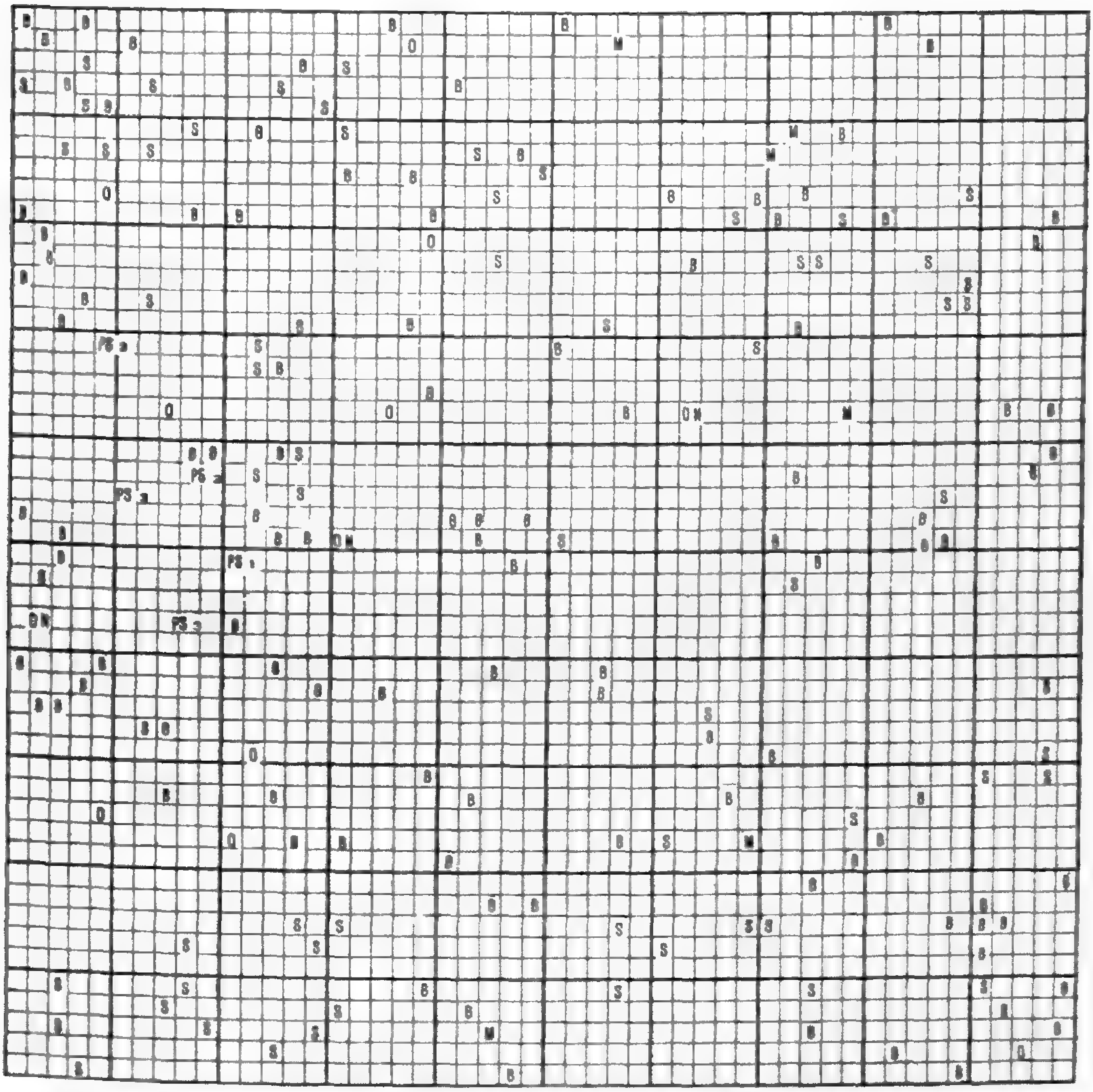

FIG. 11.—Sample plot 2. White birch 6 years old, pasture, Colchester plain, 5 meters square; a carpet of *Polytrichum commune* beneath; B, *Betula populifolia* 105; S, *Spiraea tomentosa* 64; O, *Osmunda cinnamomea* 8; M, *Myrica asplenifolia* 4; ON, *Onoclea sensibilis* 2; MU, *Monotropa uniflora* 2; R, *Rubus allegheniensis* 1; PS, *Pinus Strobus* 5.

Ten stands 5 to 15 years old averaged 34 trees on $25^{\mathrm{sq\,m}}$, while ten stands 25 to 30 years old averaged 7 trees. The older stands of pitch pine show regeneration of white pine beneath them, and plots like no. 10 (*fig. 7*) may be commonly found in the old pastures as well as in the abandoned fields. In one case white pine seedlings and saplings at the rate of 70 per $25^{\mathrm{sq\,m}}$ were found beneath a 24-year old stand. There were 7.5 pitch pine on $25^{\mathrm{sq\,m}}$. Unfortunately these stands are periodically burned and the seedlings are killed, so there is little opportunity of observing the older stages of this undergrowth of white pine. On the Macomber lot, however, where fire has been rigorously excluded for many years, one may find the older stages. Sample plot 35 (*fig. 9*) shows white pine 23 years old beneath pitch pine 40 years old. There is little doubt of the ultimate control of such pitch pine stands by white pine, were forest fires excluded.

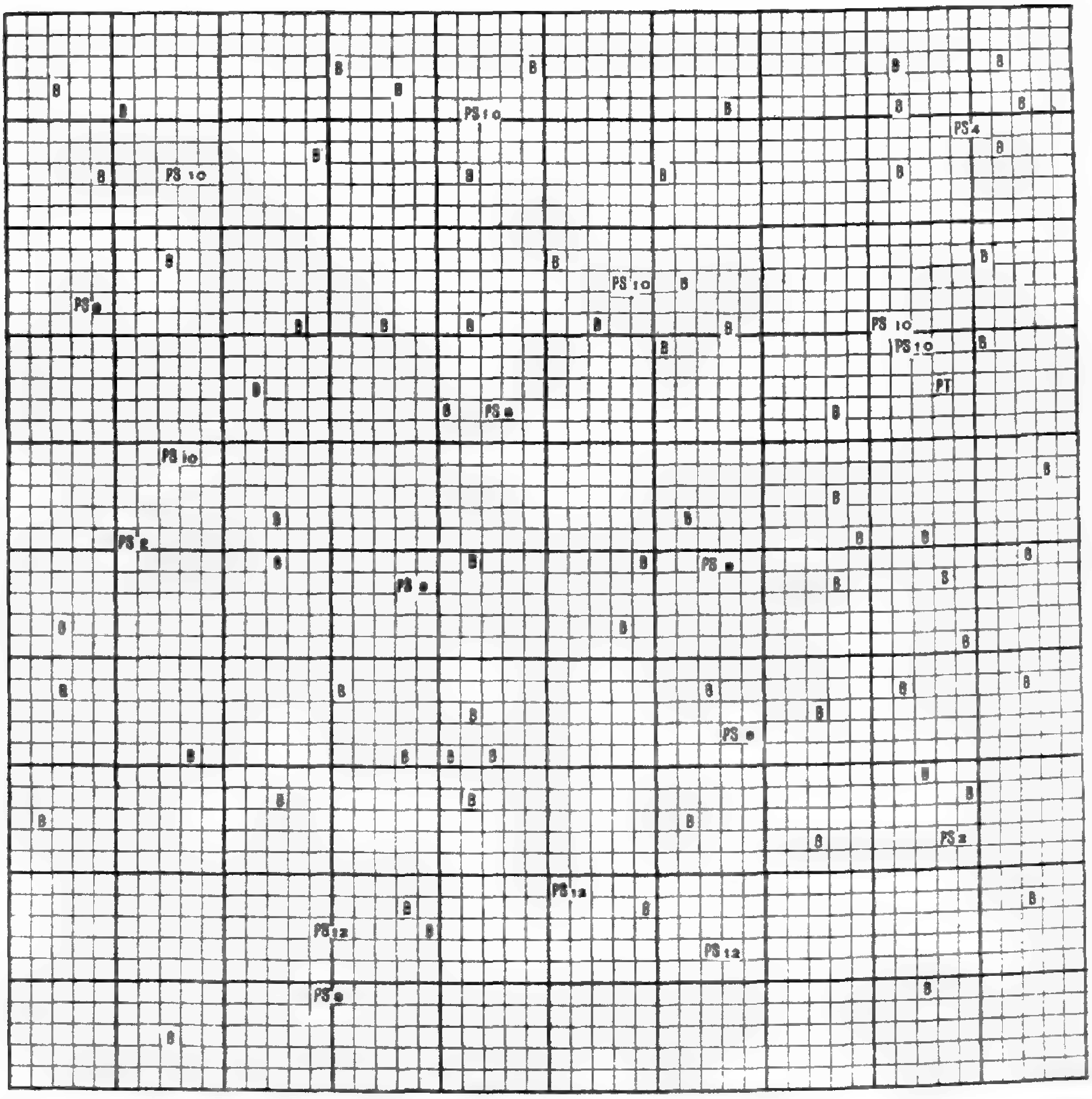

FIG. 12.—Sample plot 9. White birch 15 years old, Colchester plain, 5 meters square; under layer, Polytrichum, *Onoclea sensibilis, Rubus hispidus;* B, *Betula populifolia* 68; PS, *Pinus Strobus* 18; PT, *Populus tremuloides* 1; S, *Spiraea tomentosa* 1.

White birch in the old pastures usually forms dense pure stands. The series of stands shown in *figs. 10–13* illustrates displacement of white birch by white pine. It will be noted that the numbers of white birch on the unit area for the ages given are 245, 105, 68, and 16; and that the numbers of white pine increase as follows: 0, 5, 18, 46. This illustrates the most striking fact in the course of succession on worn-out pastures, that is, gradual replacement of white birch by white pine. If a stand of white birch is within proper distance from white pine seed trees, the birch acts as a nurse tree to the pine.

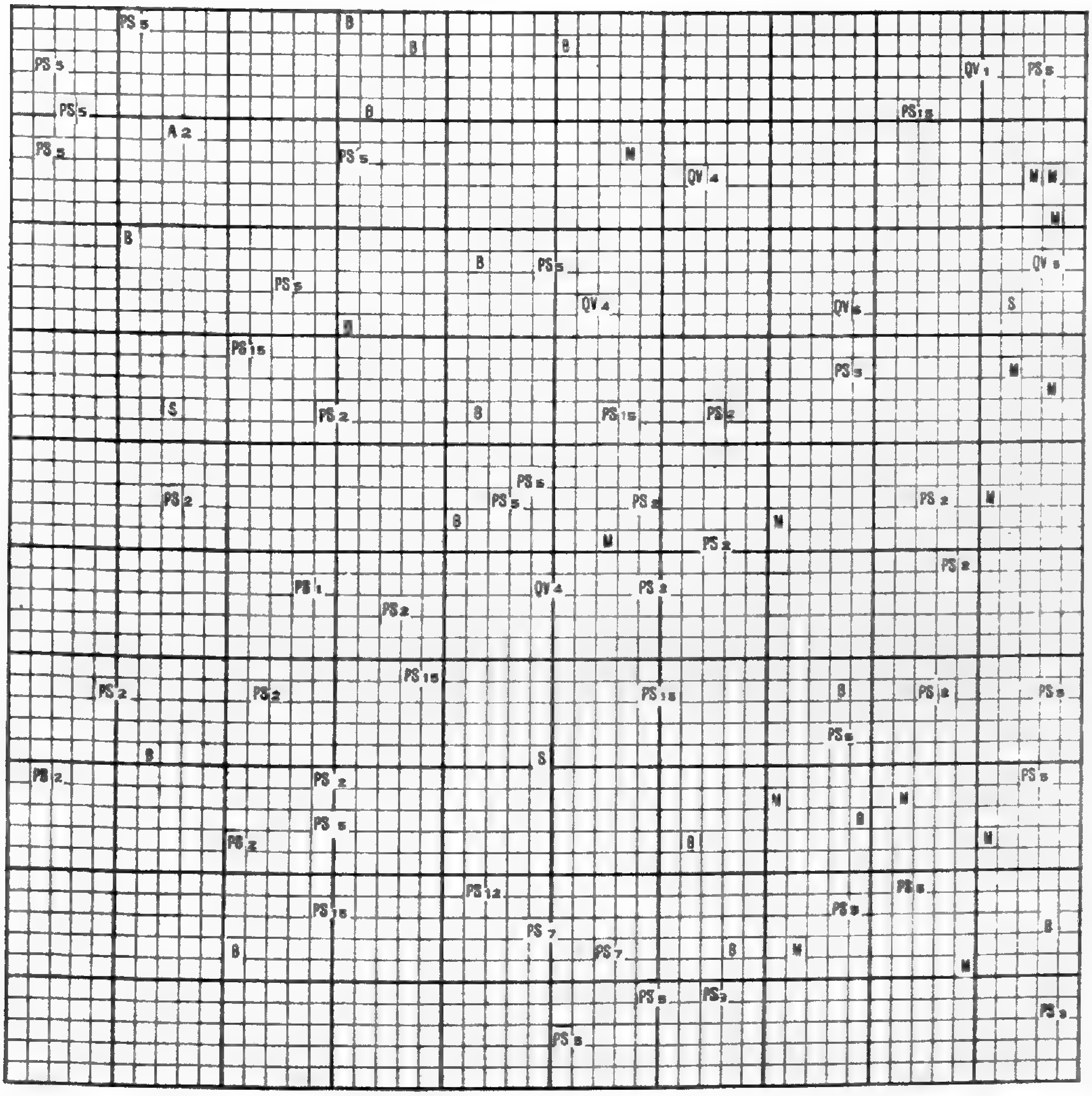

FIG. 13.—Sample plot 17. White birch 25 years old, 5 meters square, 50^{m} from white pine; under layer Polytrichum and *Rubus hispidus;* B, *Betula populifolia* 16; PS, *Pinus Strobus* 16; QV, *Quercus velutina* 6; M, *Myrica asplenifolia* 14; S, *Spiraea tomentosa* 3; A, *Acer rubrum* 1.

In the clearing of the sand plains occasional white pine trees were left along the margins of wood lots and along highways. Such trees became the originators of numerous pure stands of white pine in the old pastures. Sample plot no. 37 (*fig. 14*) gives the character of the pasture when the white pine invasion begins.

Stands of all ages occur from the seedling stage to mature trees. As in the case of pitch pine, one may find patches of white pine containing three generations of trees, each generation even-aged and in pure stand. The stands now in the process of installation offer a good opportunity to study the abundance of seedlings in relation to the distance from the mother tree. For example, the number of seedlings were counted on plots 5^m square with the following results: 30 to 25^m

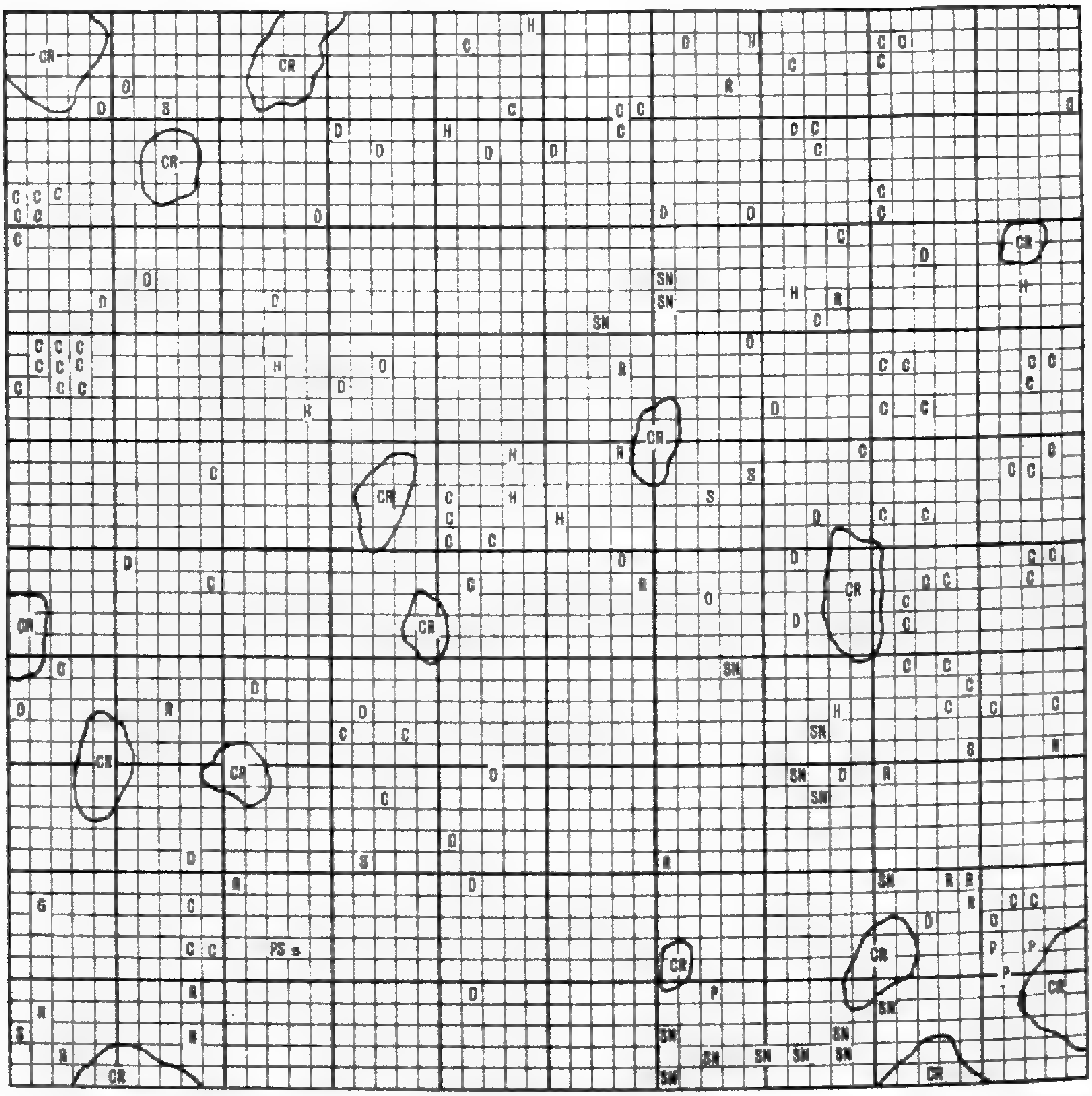

FIG. 14.—Sample plot 37. Pasture being invaded by the white pine, Colchester plain, 1 square meter; C, *Cyperus filiculmis* 72; D, *Danthonia spicata* 34; R, *Rumex Acetosella* 16; SN, *Solidago nemoralis* 14; H, *Hypericum canadense* 10; S, *Spiraea tomentosa* 6; P, *Panicum capillare* 4; CR, *Cladonia rangifera;* G, *Gnaphalium polycephalum* 1.

from the seed tree, 4 seedlings; 25 to 20m, 17 seedlings; 20 to 15m, 24 seedlings; 15 to 10m, 25 seedlings; 10 to 5m, 35 seedlings; 5–1m from a vertical line dropped from the outer margin of the crown of the seed tree, 85 seedlings. The seedlings were 3 and 8 years old.

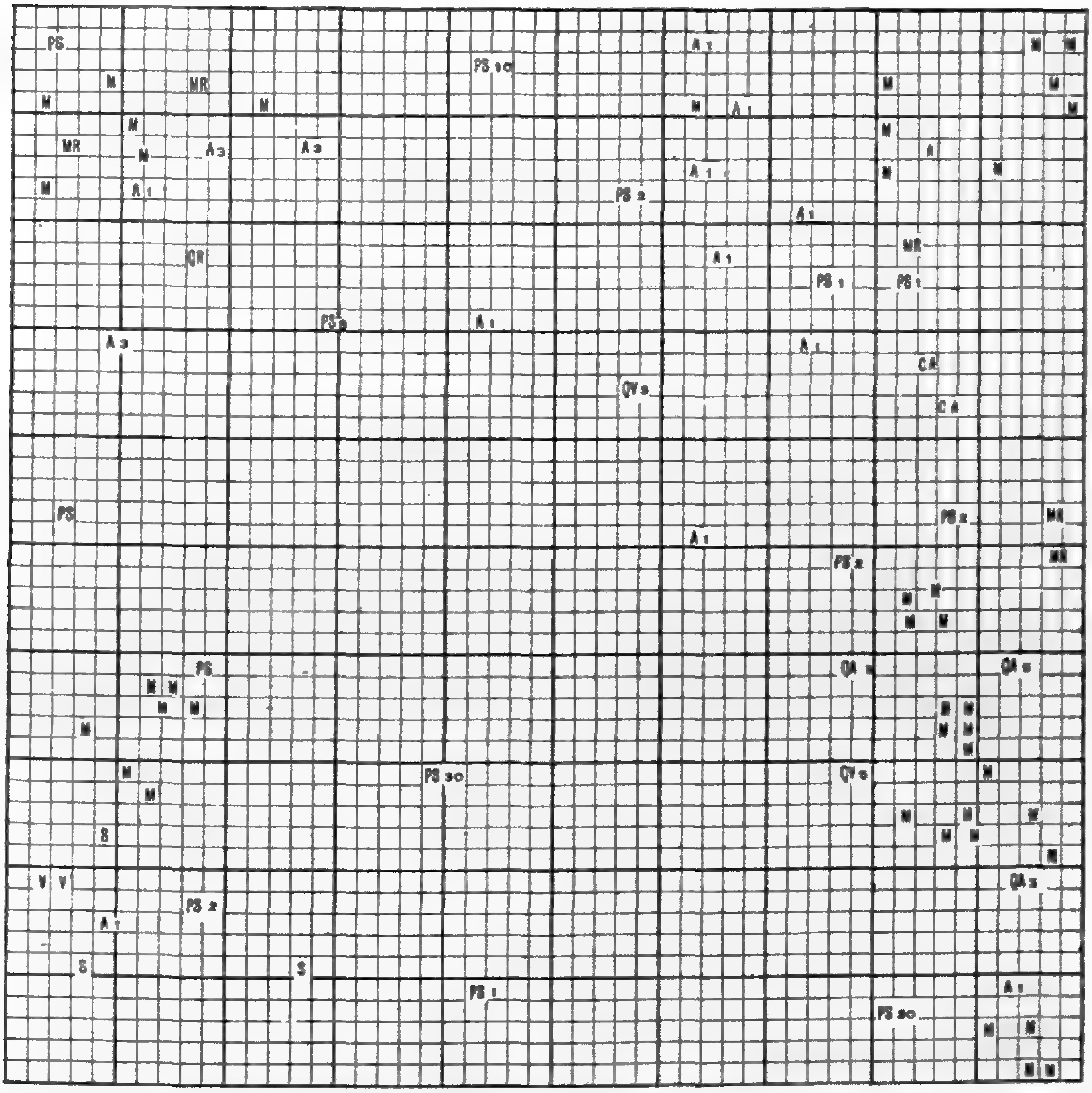

FIG. 15.—Sample plot 13. White pine stand 35 years old, an abandoned cultivated field, Essex plain, 5 meters square; PS, *Pinus Strobus* 14; QV, *Q. velutina* 2; QA, *Q. alba* 1; QR, *Q. rubra* 1; A, *Acer rubrum* 14; CA, *Corylus americana* 2; M, *Maianthemum canadense* 35; MR, *Mitchella repens* 5; V, *Vaccinium vacillans* 1; S, *Solidago* sp. (rosette) 3.

During their sapling stage the pure stands of white pine are usually so dense as to exclude secondary vegetation, but by the time they are 30 years old they have become thinned out sufficiently to allow undergrowth. This is illustrated in sample plot no. 13 (*fig. 15*), made beneath a stand 35 years old. Seedling and sapling oaks are of common occurrence beneath the older white pine in sufficient numbers to indicate an eventually mixed stand should they persist.

In the discussion of succession on abandoned fields it has been shown that white pine is gradually regaining control of the areas on which it was once dominant, by the direct reseeding leading to the establishment of pure stands, indirectly by the supplanting of white birch stands, and, were human interference withdrawn, by the replacement of pitch pine stands.

I have employed the month of vacation for the past six years in the study of the sand plain vegetation. Forty-five permanent sample plots in the stands, representing various stages of succession, have been established and mapped, and those have been given above which in my judgment best represent the conditions discussed. Most of these plots will be kept under observation in the future, so that definite records of the changes *in situ* may be recorded. Besides these, the character of the vegetation has been recorded by 100 list charts.

While investigations have been conducted in the effort to determine what changes in ecological conditions have brought about the changes in vegetation on the sand plains, I feel that they have not progressed far enough to justify their publication. Therefore it seemed best to make the present paper simply a record of succession. The nomenclature is that of GRAY's *New manual of botany*.

Summary

Pitch pine succeeded to the control of areas from which the dominant white pine had been removed.

White pine, however, is gradually regaining its control on cut-over areas, as well as on abandoned fields, by its actual replacement of white birch stands and by its probable displacement of the pitch pine stands.

The work upon this paper was begun at the suggestion of Dr. L. R. JONES of the University of Vermont and was continued under Dr. H. C. COWLES of the University of Chicago. I wish to express my appreciation of the kindly criticism and encouragement received from them.

UNIVERSITY OF TORONTO

CURRENT LITERATURE

BOOK REVIEWS

The genera of fungi

Several years ago Professor CLEMENTS began a translation of the keys to the genera of fungi in the original eight volumes of SACCARDO'S *Sylloge Fungorum*, and this has now resulted in a book.[1] With the appearance of a large number of new genera in the subsequent volumes, the keys have been arranged on an entirely different plan from that found in the *Sylloge*, although the spore sections based on the color, shape, and septation of the spores have been retained. In the case of certain groups, the arrangement differs from that found in the *Sylloge*, as well as from that generally followed; for example, the bacteria are included among the Phycomycetes, the Uredinales and Ustilaginales among the Ascomycetes. The reviewer has taken some pains to test certain portions of the key. In most of the cases tried, one would have been led astray, unless the plant were already known, and even then, were the key followed literally, the plant would often reach the wrong genus, if not the wrong group. For example, the first two paragraphs in the key are supposed to enable the student to determine whether a plant belongs in the Phycomycetes or in the second division. If the plant to be named is a Peziza, and if the student knows it is an ascomycete, he would not need the key; but if he did not know this, he would certainly place it in the Phycomycetes if he depended on the words of the key, having in mind the structures usually present in the perfect fruit body of an ascomycete. On examining a teleutospore, or other spore form of the Uredinales or Ustilaginales, who would recognize it as an ascus, or any structure in these orders as an ascomycetous structure, unless he already knew it? One must have a good knowledge of fungi before a key of this kind becomes very useful, and then the keys to the general subdivisions would not be necessary. Diagnostic characters for the general subdivisions would be more helpful. In this respect SACCARDO'S keys to the genera are useful, since they are at the same time diagnostic.

A few of the inaccuracies may be mentioned. The key to the Myxobacteriaceae (p. 8) is incorrect in the statement "cells finally forming rows of globose spores" in Myxococcus, since each rodlike cell forms a single spore (see THAXTER, BOT. GAZETTE **23**:400. 1897). The key to the Cladochytriae is incorrect, since there are species which possess both resting sporangia and zoosporangia. Not all the Syncephalidae form zygospores above conjugating progametes, as stated in the key, even in Piptocephalis. The key further says

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[1] CLEMENTS, FREDERIC EDWARD, The genera of fungi. 8vo. pp. 227. Minneapolis: The H. W. Wilson Company. 1909.

"conidia in chains." The spores are borne in sporangial filaments (see THAXTER, BOT. GAZETTE **24**:1–15. 1897). In Leptomitae there is a confusion of distinctions. "Naegeliella" should be Sapromyces (see FRITSCH, Oesterr. Bot. Zeits. **43**:420. 1893). Araiospora of THAXTER is changed to "Araeospora," whether by a typographical error or because of "faulty composition," we are not told. Gonopodya and Myrioblepharis are incorrectly placed in the Monoblepharidaceae; the former is leptomitaceous, while the latter is pythiaceous. The genus Diblepharis does not exist (see THAXTER, Rhodora **5**:103. 1903); and so on. Some of the good genera omitted from the higher Phycomycetes are Cunninghamella, Thamnocephalis, Zygorhynchus, Proabsidia, Lichtheimia, Mycocladus, Tieghemella, Sapromyces, etc. The author has revised THAXTER'S arrangement of the Laboulbeniales, and one of the first things to be noticed is that Stichomyces, with simple antheridia, is placed in the group which is characterized by compound antheridia.

"Subfamily Harpochytriae" on p. 11, and "Harpochytrium" as one of the genera is probably a slip for Hyphochytriaceae and Hyphochytrium. On p. 47 something seems to be omitted after the line "Stroma on a white subicle," unless it indicates a hypothetical group.

Although the author says that "questions of nomenclature have been left largely to one side," a large number of new names are proposed for genera, in many cases as substitute names for already existing valid ones. For example, where a generic name is longer than the author thinks it should be, he shortens it; Dimerosporopsis is changed to Dimerosporis, Trematosphaeriopsis to Trematosphaeris, Hyalethyridium to Hyalothyris, Gymnoascus to Gymnascus, Exoascus to Exascus, etc. Objection is made also to the use of generic names of "faulty composition," and many names are changed to conform to an adopted standard of word-formation; thus, Tremellopsis is changed to Tremellastrum, Coleopuccinia to Coleoma, Oscarbrefeldia to Ascodes, Podosordaria to Pedisordaria, Aureobasidium to Chrysobasidium, etc., while Tremellodon, for example, is allowed to stand. It may be admitted that authors of long generic names should have selected shorter ones, and should have used greater care in word-formation, but if we recognize CLEMENTS'S principles of nomenclature, we must accept them from anyone who chooses to change the spelling of genera or to substitute new generic names for any of the present valid ones. It requires very little imagination to foresee the result of such a policy. The object in adopting principles of botanical nomenclature is to secure as uniform methods in naming plants as possible. The name is merely a medium of exchange by which we convey to others the concept of the organism with which we are dealing, and a name employed in accordance with principles adopted by an international representative assembly of botanists is more useful than an invalid name.

Besides the large number of arbitrary changes in generic names, a large number of new generic names are proposed without any diagnosis other than the few differential words used in the key. Some have a better basis, perhaps, than others. Two which were examined at random will show on what very insufficient grounds some of them, at least, are founded. *Iotidea* is proposed as a genus for *Otidea pleurota* (Phillips) Rehm (*Peziza pleurota* Phill.) on the ground that the tips of the asci are stained blue with iodin, while in the other species of Otidea (in the sense of REHM, Rabenh. Krypt. Fl. Pilze 3:1023. 1896) the ascus usually is not stained blue with iodin. By students of the Discomycetes this character is regarded at most merely as a specific character, and some of our best students (including PHILLIPS) regard it as a variable one and do not place great stress upon it as a crucial test of specific difference.[2] *Belospora* is proposed as a genus for *Belonioscypha ciliatospora* (Fuckel) Rehm, *ibid.* 744 (*Ciboria ciliatospora* Fuckel), on the ground of the presence of a cilium at each end of the spore. Later REHM (*ibid.* 1267) says that BRESADOLA justly regards this species as only a young form of *Helotium scutula*, the cilia soon disappearing and the spores becoming divided.

Quite a number of genera have been included in others, but this is done "only for the sake of the beginner, when the descriptions reveal no differences." In some of the genera so treated the differences indicated are certainly greater than those on which some of the new genera are based. Lloydiella, for example, is included in Hymenochaete, although the differences are clearly indicated. Whether Lloydiella is a valid genus may be questioned, but it certainly does not bear so close a relationship to Hymenochaete as it does to Stereum, on certain species of which it was based because of the presence of hyaline cystidia, while Hymenochaete possesses colored setae.

There is a convenience in having the genera in all of the volumes of SACCARDO'S *Sylloge* brought together for reference. The glossary of Latin and English terms, covering 28 pages, will be of great value to students using SACCARDO'S work, who have not a good command of Latin.—GEO. F. ATKINSON.

A new laboratory manual

FRYE and RIGG have met their local needs, and perhaps more general needs as well, by the publication of a laboratory manual.[3] The outlines are the outcome of a test of two years, and they are now being used in the university with students who have not had botany in high school. Both authors have had experience in high schools, and should be able to judge what is suited to high-school pupils; both have been students of the botany of the northwest for some years, and should know what material is to be recommended for elementary classes.

The course is divided into two parts: the vegetative organs of vascular plants, and types of the larger groups of plants. The first section treats of leaves, stems, roots, seeds, and the relation of plants to their environment; while in the second the usual four groups are presented. In the first four topics of the first section the exercises are those usually found in this connection, but in the last one there

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[2] See COOKE, M. C., Observations on *Peziza calycina*. Grev. 4:169–172. 1876.

[3] FRYE, T. C., AND RIGG, GEO. B., Laboratory exercises in elementary botany based on the plants of the Pacific Northwest. pp. 75. Seattle: University Book Store. 1909.

is a distinct change in treatment. Instead of taking the typical ecological regions, a representative plant from each region is made the basis of study. The plants used are cactus (xerophyte), bladderwort (hydrophyte), Salicornia (xerophytic hydrophyte), and dodder (a parasite). Such treatment doubtless has distinct advantages, since the beginning student organizes data much more readily around an individual than around such abstractions as hydrophytes, xerophytes, etc. Some may question whether this really gives an adequate presentation of the great ecological divisions, but probably the authors would answer that it is better to have beginners get a definite idea about a few representative plants, than a somewhat hazy idea about a number of plants and definite notions about none of them. When ecology was first introduced into courses of study, it was heralded by some as a means of breaking away from the regulation type study method, and it is especially interesting in this connection to see ecology adopting the type study as the best means of presenting its data to beginners.

The exercises are fairly well written. Each begins with a definite statement of the purpose, and of the materials and apparatus needed for it. The directions for observation and study are very general, but in the hands of a good teacher such directions will stimulate good habits of laboratory study; indeed it seems quite undesirable to attempt to arrange a manual that will not require the presence of a good teacher, since the personal contact of such a teacher is the most important factor in the course.—O. W. CALDWELL.

MINOR NOTICES

A new lilac disease.—KLEBAHN[4] has described briefly the more common fungi found on lilacs used for winter forcing in Europe. The greater part of the paper is devoted to a new disease caused by *Phytophthora Syringae*. The fungus infects the twigs of the lilac plants, killing them over a distance of several internodes. Usually the upper internodes are killed, but often parts of the stems lower down are killed. The flower buds on the infected twigs do not develop, so that only leafy shoots are produced from lower uninjured buds. Since the value of a forcing lilac depends largely on the symmetry of the plants and the even distribution of the flowers, great loss is caused by the damage of a few twigs, especially since the injury is not detected until the plants are started into growth. It appears that the greater part of the infection occurs while the plants are in storage. After they are dug up in the fall, it is customary to heel them in in cold frames so that one side of the plants is in contact with the ground. Both observation and experiment showed that it is through contact with the earth that the twigs become infected.

A somewhat lengthy account is given of the characters and biological behavior of the fungus. In the lilac twigs and buds only oospores were found, which led to a former publication describing the fungus as *Ploeophthora Syringae*. In this

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[4] KLEBAHN, H., Krankheiten des Flieders. pp. 75. *figs*. 45. Berlin: Gebrüder Borntraeger. 1909.

investigation the author succeeded in growing the fungus in pure cultures, and thus obtained sporangia belonging to the genus Phytophthora. By means of zoospores, not only lilacs but also a number of other plants were infected, showing close relationship of the fungus to *Phytophthora omnivora* DeBary. The relationship is discussed at length, and although the author is somewhat doubtful in his conclusion, he is inclined to regard the fungus as a species (*P. Syringae*) differing slightly in morphological and biological characteristics from DEBARY's *P. omnivora*.—H. HASSELBRING.

The problems of life.—In 1900 GIGLIO-TOS published the first part of his work under this title.[5] The general thesis of the book is that vital phenomena are all referable to relatively simple fundamental causes, and in the first part there is an attempt to set forth a logical and consistent hypothesis of the organization of protoplasm and its fundamental functions. The second part appeared in 1903,[6] and applied the same method to the phenomena of ontogeny. In 1905 the third part was published,[7] extending the author's hypothesis to the phenomena of fertilization and heredity. Now the fourth and last part has appeared,[8] and reduces to relative simplicity the important problems of variation and the origin of species. The theory of the whole book begins with an assumption regarding the molecular structure of protoplasm and the nature of assimilation, and applies this assumption by a logical series of deductions to the most fundamental problems of biology. The logic may be good, but it cannot transform the assumption, interesting as it may be, into a fact. Even a fact is influential only in its own immediate neighborhood, and the author has traveled far beyond the region where an initial fact, much less an assumption, can be serviceable.—J. M. C.

A new flora of California.—Two parts of *A flora of California* by JEPSON[9] have been published recently. Part I contains the families Pinaceae to Taxaceae and Part II the Salicaceae to Urticaceae inclusive. The text is printed in carefully selected type which differentiates admirably the subject matter on the page. The descriptions, while full and accurate, are not overtechnical; the bibliography and synonomy are presented in sufficient detail to give a ready understanding without being cumbersome, and particular emphasis is given to the geographical distribution of species and varieties. Several well reproduced photographs and numerous original figures materially supplement the text. New species are described in Cupressus and Quercus. The publication happily combines scientific accuracy

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[5] Review in BOT. GAZETTE **31**:275. 1901.

[6] *Ibid.* **37**:151. 1904. [7] *Ibid.* **41**:450. 1909.

[8] GIGLIO-TOS, ERMANNO, Les problèmes de la vie. IV^e partie: La variation et l'origine des espèces. 8vo. pp. vii+222. Cagliari: The author, at the University. 1910. *fr.* 8.

[9] JEPSON, W. L., A flora of California. Royal 8vo. Part I, pp. 33–64. *figs. 13;* Part II, pp. 337–368. *figs. 5.* San Francisco: Cunningham, Curtiss, and Welch. 1909.

with simplicity of description, and its appearance is most gratifying to those interested in the Pacific coast flora. It is earnestly hoped that the work may continue to completion.—J. M. GREENMAN.

NOTES FOR STUDENTS

Current taxonomic literature.—J. C. ARTHUR (Mycologia **1**:225–256. 1909) under the title "Cultures in Uredineae in 1908" has published new species in Puccinia and Gymnosporangium; this article is the ninth in a series of reports on the culture of plant rusts.—O. BECCARI (Leafl. Philipp. Bot. **2**:639–650. 1909) in an article entitled "New or little known Philippine palms" describes four new species.—V. F. BROTHERUS (*ibid.* 651–658) has published 11 new species of mosses from the Philippine Islands.—C. BERNARD (Dept. Agr. Ind. Néerland. pp. 1–94. *pls. 1–6.* 1909) in a paper entitled "Sur quelques algues unicellulaires d'eau douce récoltées le Domaine Malais" has described several new species and varieties of unicellular algae and proposes a new genus (*Spinoclosterium*).—R. C. BENEDICT (Bull. Torr. Bot. Club **36**:463–476. 1909) presents a provisional revision of the genus Ceratopteris and includes one new species (*C. deltoidea*) from Jamaica.—B. T. BUTLER (*ibid.* 421–440) gives a synopsis of the west American birches in which 17 species are recognized, 7 being indicated as new; a key precedes the characterization of species.—L. CLARK (*ibid.* 299–307. *pl. 20*) under the title "Some noteworthy Hepaticae from the state of Washington" includes a new species of Jungermannia and a new variety of *Scapania paludosa* C. Müll. Frib.—W. W. EGGLESTON (*ibid.* 501–514) in an article entitled "The Crataegi of Mexico and Central America" describes 4 new species and 2 new varieties.—H. D. HOUSE (*ibid.* 595–603) in continuation of his studies in the Convolvulaceae gives a synoptical revision of the genus Quamoclit in which 8 species are recognized, one being new to science.—R. H. HOWE, Jr. (*ibid.* 309–326. *pls. 21–23*) presents an interesting article dealing with the genus Usnea as represented in New England. The text is supplemented by maps showing the distribution of species and forms occurring in that section.—E. A. MCGREGOR (*ibid.* 605–609) describes and illustrates two new spermatophytes from California. —K. K. MACKENZIE (*ibid.* 477–484) in continuation of his studies in the genus Carex has described 8 new North American species.—E. L. MORRIS (*ibid.* 515–530) in a third paper on "North American Plantaginaceae" treats in detail several technical species and proposes two new specific names.—P. A. RYDBERG (*ibid.* 531–541) under "Studies on the Rocky Mountain flora XIX" describes several new species of Gramineae.—R. E. STONE (*ibid.* 549–552) describes a new species of Puccinia which was found growing on *Rynchospora corniculata* (Lam.) Gray at Auburn, Alabama.—C. H. PECK (*ibid.* 329–339) describes 22 new species of fungi from different parts of the United States; the same author (N. Y. State Mus. Bull. 131. pp. 18–58. 1909) describes new species of American fungi, several being illustrated.—Q. BORGE (Arkiv för Botanik **8**: no. 13. pp. 29. *pl. 1.* 1909) under the title "Nordamerikanische Süsswasseralgen" describes and illustrates a new species of Closterium and a new variety of *Cosmarium cuneatum* from Florida, aso a new species of Anabaena from Lower California.—R. E. FRIES (*ibid.* no. 8. pp. 51. *pls. 1, 2*) has published 6 new species of flowering plants collected along the boundary between Bolivia and Argentina; the same author (*ibid.* no. 11. pp. 34. *pls. 1–4*) describes and illustrates several new Gasteromycetes from the same region.—G. O. MALME (*ibid.* no. 1. pp. 30. *pl. 1*) presents a synoptical revision of the South American genera Araujia and Morremia and describes a new species in the latter genus.—N. SYLVEN (*ibid.* no. 6. pp. 48. *pls. 1–7*) gives an account of the South American species of Genlisea and Utricularia, based on material in the Regnell herbarium. Four species of the former genus are recorded, of which one from Minas Geraës is new; and in Utricularia 34 species are recorded, 9 of which are new to science.—E. WAINIO (*ibid.* no. 4. pp. 175) under the title "Lichenes in viciniis hibernae expeditionis Vegae prope pagum Pitlekai in Siberia septentrionali a D:re E. Almquist collecti" has published several new species belonging to different genera and proposes a new genus (*Melanaspicilia*) to which six species are referred.—N. L. BRITTON (Torreya **9**:153–160. 1909) gives an account of the genus "Rhipsalis in the West Indies," recording three species, one of which (*R. jamaicensis*) is new.—T. D. A. COCKERELL (*ibid.* 166, 167) proposes a new generic name (*Wedeliella*) for a certain group of nyctaginaceous plants; the type of the genus is *Allionia incarnata* L.—G. V. NASH (*ibid.* 209, 210) records a new species of Danthonia from Jamaica.—H. CHRIST (Bull. Acad. Int. Geo. Bot. **18**:146–178. 1909) under the title "Fougères d'extrême Orient" has published several new speeies of ferns from Korea, Sachalin, and China.—H. LÉVEILLÉ (*ibid.* 1–138) presents a synopsis of the Chinese and Japanese species of Rubus; the author recognizes 143 species for China and 48 for Japan. The descriptions of species are preceded by a determinative key, of which the character of the leaves and the presence or absence of spines form the primary basis for division.—E. VANIOT and H. LÉVEILLÉ (*ibid.* 139–145) have published 18 new species of Compositae from Korea, 12 of which belong to the genus Aster.—C. CHRISTENSEN (Smiths. Misc. Coll. **52**:365–396. 1909) in an article entitled "The American ferns of the group of *Dryopteris opposita* contained in the U. S. National Museum" presents critical notes on several species and publishes 9 species and 3 varieties of this genus as new to science.—F. FEDDE (Rep. Nov. Sp. **7**:255–257. 1909) describes 4 new varieties of *Papaver nudicaule* L., 3 of these being from the Rocky Mountain region.—A. LINGELSHEIM, F. PAX, and H. WINKLER (*ibid.* 241–251) in continuation of their studies on the Bolivian flora have published 22 new species of dicotyledonous plants.—K. WOLFF (*ibid.* 274–279) under the title "Species novae generis Eryngii Americae centralis et australis" has published 6 species new to science.—E. L. GREENE (*ibid.* 252–255) describes 8 new species of Thalictrum, chiefly from western North America; the same author (Midland Naturalist **1**:99–104. 1909) has published 3 new species of Thalictrum from North Dakota.—A. A. HELLER (Muhlenbergia **5**:133–143. 1909) publishes the first of a series of articles on the "Nevada lupines"; the sections *Lupinellus* and *Platycarpos* are here treated, and one new species is proposed.—E. GILG and R. MUSCHLER (Bot. Jahrb. **42**:437–487. 1909) in an article entitled "Aufzählung aller zur Zeit bekannten südamerikanischen Cruciferen" have published 19 new species and have made several new combinations. The following new genera are proposed: *Sarcodraba* (1 species), based on *Draba karraikensis* Speg.; *Aschersoniodoxa* (2 species), based on *Draba Mandoniana* Wedd.; *Weberbauera* (1 species), based on *Braya densiflora* Musch.; and *Brayopsis* (9 species), based on *Eudema grandiflora* Planch.—W. HERTER (Allg. Bot. Zeits. **15**:129. 1909) has published a new species of Ibatia from Uruguay.—J. HUBER (Bull. Soc. Bot. Genève II. **1**:245–249. 1909) describes and illustrates two new species of Ericaceae from the plains of the Amazon.—L. KRAUTER (Contr. Bot. Lab. Univ. Penn. **3**:93–206. 1908) gives a synoptical revision of the genus Pentstemon, recognizing 148 species and numerous varieties.—R. E. KUNZE (Monats. Kakteenk. **19**:149, 150. 1909) describes and illustrates a new species of Echinocactus (*E. arizonicus*) from Arizona.—J. A. PURPUS (*ibid.* 133, 134) describes a new species of Opuntia from Utah; the description is accompanied by an illustration.—L. QUEHL (*ibid.* 155, 156) has published a new species of Mamillaria (*M. ceratites*) from Mexico.—W. WEINGART (*ibid.* 150–155) publishes a new species of Cereus (*C. Purpusii*) which is indigenous to western Mexico.—R. G. LEAVITT (Phil. Journ. Sci. Botany **4**:201–245. 1909) under the title "The genus Eria in the Philippine Islands" recognizes 40 species, 13 being described for the first time. A synoptical treatment with several text figures follows the Latin diagnoses of species.—E. D. MERRILL (*ibid.* 247–330) in continuation of his studies on the flora of the Philippines has pubished 83 new species of flowering plants and proposes the following new genera: *Embolanthera* of the Hamamelidaceae, *Everettiodendron* of the Euphorbiaceae, *Ahernia* of the Flacourtiaceae, and *Greeniopsis* of the Rubiaceae.—C. B. ROBINSON (*ibid.* 331–407) gives a "Preliminary revision of the Philippine Myrtaceae." Of the 10 genera recognized 7 are monotypic, 2 contain 2 species each, and one, Eugenia, is represented by 98 species, of which 62 are described as new to science.—C. F. MILLSPAUGH (Field Col. Mus. Bot. Ser. **2**:289–321. 1909) in continuation of his studies on the flora of the Bahamas has published 12 new species of dicotyledonous plants, proposes a new genus (*Euphorbiodendron*) of the Euphorbiaceae, and makes several new combinations.—A. PASCHER (Oesterr. Bot. Zeitschr. **59**:329–331. 1909) has published a new genus (*Atropanthe*) of the Solanaceae from China.—A. ZAHLBRUCKNER (*ibid.* 349–354) in pursuance of his studies on the lichen flora of Dalmatia describes several new species and characterizes a new genus (*Agonimia*), based on *Polyblastis tristicula* Th. Fr.; the same author (Ann. Mycol. **7**:472–478. 1909) under the title "Neue Flechten V" has published several new species of lichens of which 4 species and one variety are from Florida and Arizona.—R. A. ROLFE (Kew. Bull. 268–277. 1909) gives a "Revision of the genus Cycnoches," enumerating 16 species mostly native in Central and South America.—T. A. SPRAGUE (*ibid.* 264) describes a new species of Phyllanthus from Mexico.—J. M. GREENMAN.

Theory of individual development.—In a Darwin Anniversary address given at the University of Chicago and now published,[10] LILLIE analyzes organic development and the theories relating to it in an unusually clear and satisfactory way. He calls attention to the fact that ontogeny and phylogeny are not two separate and distinct series of phenomena, and that individual development is not something distinct from evolution, but is a part of the process of evolution. In fact, we have no actual experience of any other form of development than individual development, racial development being an inference from innumerable facts. The development of the individual is a series of processes, capable of resolution into simpler biological processes, and these presumably into physico-chemical events. Such attempted analyses come under the head of physiology of development, a method of attack known in Germany as developmental mechanics. Under this head the author discusses embryonic primordia and the law of genetic restriction, the principle of organization, the rôle of cell division in development, and environment.

The presentation of the last topic is especially suggestive, both extra-organic and intra-organic environment being recognized. The former needs no definition; the latter may be defined by the statement that each part of a developing embryo has an environment consisting of all the other parts, some of which constitute relatively immediate environmental factors, others relatively remote ones. Examples of experiments are given to illustrate the influence of intra-organic environment on development, which also show that an immense part of what is called inheritance is inheritance of environment only, that is, repetition of similar developmental processes under similar conditions. It is stated that we are driven to the conclusion that the apparent simplicity of the germ is real; that the germ contains no gemmules, or determinants, or other representative particles; that development is truly epigenetic, a natural series of events that succeed one another according to physico-chemical and physiological laws; and that the explanation of the sequence consists simply in the discovery of each of its steps.

The author discusses certain applications of this point of view, and shows that such biological conceptions as the inheritance of acquired characters, atavism, and unit characters are inconsistent with it, special attention being given to the last because it is essentially modern and has many adherents. The analysis of the term "character" is very effective, the term having been prescribed by taxonomists and meaning any definable feature of an anatomical kind that differentiates species. The study of the physiology of development shows that whatever else "characters" may be, they are not units; "they simply represent the sum of all physiological processes coming to expression in definable areas or ways." *Character* is essentially a static morphological term; in the study of heredity and development we are dealing with biological *processes*.

The general conclusion is that the theory of individual development must

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[10] LILLIE, FRANK R., The theory of individual development. Popular Science Monthly **75**:239–252. 1909.

more and more come to be regarded as a branch of physiology proper. The theory of representative particles must be relegated to the class of formal hypotheses whose usefulness is largely outlived; and while it may still play a part in speculations on heredity, the author believes that it will come to be generally recognized by those who use it as a mere matter of convenience of terminology, and not as an explanation of the phenomena described in its terms.—J. M. C.

The rôle of glucosides.—WEEVERS continues his researches on the glucosides of plants, with investigations of arbutin and salicin, and their allies.[11] He reports that both are to be considered as reserve foods, the combination of benzol derivatives with glucose serving to form compounds of low diffusibility, and therefore suitable for the accumulation of sugar in the cells. Arbutin in *Vaccinium Vitis-idaea* is localized in the leaves, and is used in the spring when the shoots develop, being split by an enzyme into glucose and hydrochinon. The latter remains in the leaves and is used again to combine with the glucose formed by photosynthesis, none being free in autumn. *Pirus communis* contains a glucoside which is probably identical with arbutin, and behaves in the same way. In *Salix purpurea* and *Populus monilifera* there appears to be a complex of enzymes, of which one, salicase, splits salicin into saligenol and glucose; another, saligenase, destroys saligenol and produces catechol; and a third breaks up catechol, forming a black amorphous insoluble pigment. This catecholase, however, gets at catechol only on decay of the tissues. All summer, salicin is formed daily in the leaves; nightly it is hydrolyzed and the glucose is carried away to the cortex. When in autumn the salicin content of the cortex approaches that of the leaves, this process stops. Populin is another product common to the two genera, but more variable in behavior. Populase forms catechol from it also.—C. R. B.

Hindi cotton.—COOK[12] has published a statement in reference to Hindi cotton, the interest of which extends beyond the immediate cultural problem. The name is applied in Egypt to an undesirable type of cotton that injures the high-grade varieties by infesting them with hybrids. The introduction of Egyptian cotton into the United States has introduced also the problem of Hindi cotton. There has been much speculation as to the nature and origin of this pernicious type, the name having suggested an origin from India. Experiments with Egyptian cotton in Arizona resulted in the appearance of the so-called "Hindi" variations, and comparison with other types show that Hindi cotton is of American origin. It is not identical with any of the upland varieties of the United States, but is to be associated with upland types indigenous in Mexico and Central America. Egyptian and other Sea Island types also have originated in tropical America, and the author concludes that "it becomes possible to view the Hindi variants as ex-

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[11] WEEVERS, TH., Die physiologische Bedeutung einiger Glycoside. (Fortsetzung.) Recueil Trav. Bot. Néerl. **7**:1–62. 1910.

[12] COOK, O. F., Origin of the Hindi cotton. Circ. 42, Bur. Pl. Ind., U. S. Depart. Agric. pp. 12. *figs. 2.* 1909.

amples of reversion to remote ancestral characters rather than as results of recent hybridization."—J. M. C.

Comparative leaf anatomy of Agave.—In a genus consisting of species so incompletely characterized and so hard to differentiate as those of the succulents usually are, every applicable character is valuable and its application is a real service to science. Little beyond the most general and scattered facts have heretofore been recorded for the histology of Agave, and a recently published study of its leaf anatomy, by MÜLLER,[13] therefore, stands alone on the shelves. The difficulty of such a study and the value of its outcome are as largely influenced by the accuracy of naming and the representative character of the material on which it is based as on fulness of representation. In the present case the large collections of Palermo and La Mortola, where many of the species are planted out in the open, furnished material which is as likely to have been normal and accurately named as could be hoped for in the genus Agave, and its examination seems to have been carefully and systematically made. The details of structure, which are rather fully illustrated by means of drawings and low-power photographs, are followed by an analytical key occupying five quarto pages, and yet it is doubtful whether tenable names are likely to be found for many plants by its aid.—W. TRELEASE.

Death by low temperature.—Using the molds, Aspergillus, Penicillium, and Botrytis, BARTETZKO has made a new investigation under the guidance of PFEFFER, on death by cold.[14] He finds these fungi able to bear temperatures in a sub-cooled solution (without actual freezing) which would be fatal in the same time were the solution allowed to freeze. But even in the sub-cooled solution death ensues on longer exposure. With increase in the osmotic pressure of the plant sap there is a lowering of the death point, but there is no simple relation between the two. Isotonic solutions of different sorts have nearly the same effect on the resistance of the plant to cold. Only with *Aspergillus niger* did the use of a potassium nitrate solution reduce the resistance notably. In contrast to the conclusion of MOLISCH, BARTETZKO thinks death by cold cannot be due merely to withdrawal of water, because in certain cases this will be borne, while in others death takes place above the temperature at which any considerable loss of water occurs.—C. R. B.

Root excretions.—Inasmuch as the minuteness of the quantity of root excretions has again and again prevented the determination of the kind of acid, other than H_2CO_3, whose presence the corrosion experiments have led observers to

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[13] MÜLLER, CARL, Beiträge zur vergleichenden Anatomie der Blätter der Gattung Agave und ihrer Verwertung für die Untersoheidung der Arten. Bot. Zeit. **67**^{1}:93–139. *pls. 4, 5. figs. 22.* 1909.

[14] BARTETZKO, HUGO, Untersuchungen über das Erfrieren von Schimmelpilzen. Jahrb. Wiss. Bot. **47**:57–98. 1909.

suspect, ABERSON, in reinvestigating the question,[15] sought only to determine the concentration of the H ions to which the solvent action must be due. By using the delicate electrometric method of NERNST he has found that the concentration of the H ions corresponds to that in water (8.5 to 0.5×10^{-8} in root excretions at 16–20°, as against 7.7×10^{-8} in water at 18°). He then proceeds to show that the H ions present in such a concentrated solution of H_2CO_3 as is found in the mucus investing the root hair are from 200 to 4000 times as numerous as in the other excretions, and that the results of other observers, who used indicators, are consonant with the quantities of H ions found. The carbonic acid is quite sufficient to account for all the solvent action of the roots.—C. R. B.

Sensitizing protoplasm.—A considerable number of organisms are killed by the action of light, especially by the violet and ultra-violet rays. Among them are the small crustaceans of the genus Daphnia. Acting upon a suggestion of DREYER, HANSSEN[16] has conducted experiments to determine whether it is possible to sensitize the organism by appropriate dyes so that death would be hastened. Selecting substances that apparently do not harm the daphnias in darkness, he found that erythrosin, methylene blue, eosin, Bengal rose, and neutral red were particularly effective. He ascribes the effect to a process analogous to the sensitizing of a photographic plate to additional wave lengths, so that the added energy absorbed produces the desired effect more quickly than without the sensitizer. The paper adds strength to the theory that chlorophyll acts as an optical sensitizer in photosynthesis.—C. R. B.

Vascular anatomy of ferns.—PELOURDE[17] proposes to classify the vascular structures of the petioles of recent and fossil ferns by arranging them in four groups: (1) with a pair of vascular bundles, each having the form of a "hippocampus," which may nearly or quite meet on the lower (abaxial) side, forming a horseshoe; (2) with several bundles arranged as in the first class, each of the two adaxial bundles showing a crook which corresponds to the head of the hippocampus; (3) with a single arc-shaped strand, open above; (4) similar to the last but open below and closed above. No mention is made of the extensive memoir of BERTRAND and CORNAILLE,[18] who consider that type (3), found in Osmunda, represents the primitive condition from which all the others may be derived.—M. A. CHRYSLER.

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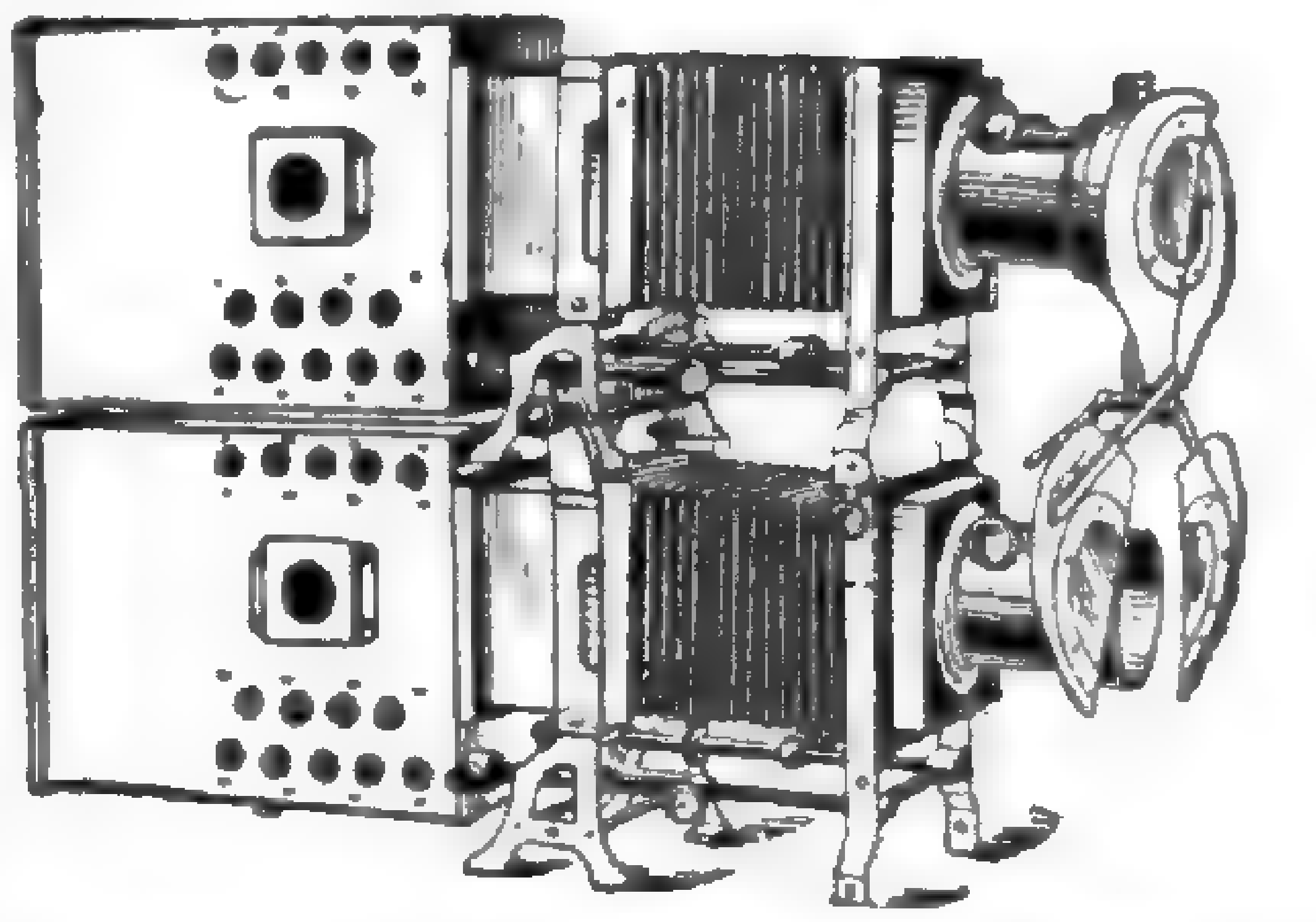
[15] ABERSON, J. H., Ein Beitrag zur Kenntnis der Wurzelausscheidungen. Jahrb. Wiss. Bot. **47**:41–56. 1909.

[16] HANSSEN, OLAV, Recherches experimentales sur la sensibilisation optique du protoplasma. Overs. Kgl. Danske Vidensk. Selsk. Forh. **1908**:113–132. *pls. 4.*

[17] PELOURDE, F., Recherches comparatives sur la structure des fougères fossiles et vivantes. Ann. Sci. Nat. Bot. IX. **10**:115–147. *figs. 32.* 1909.

[18] BERTRAND, C. EG., ET CORNAILLE, F., La masse libéroligneuse élémentaire des filicinées actuelles et ses principaux modes d'agencement dans la fronde. Trav. et Mém. Univ. Lille **10**:1–221. 1902.



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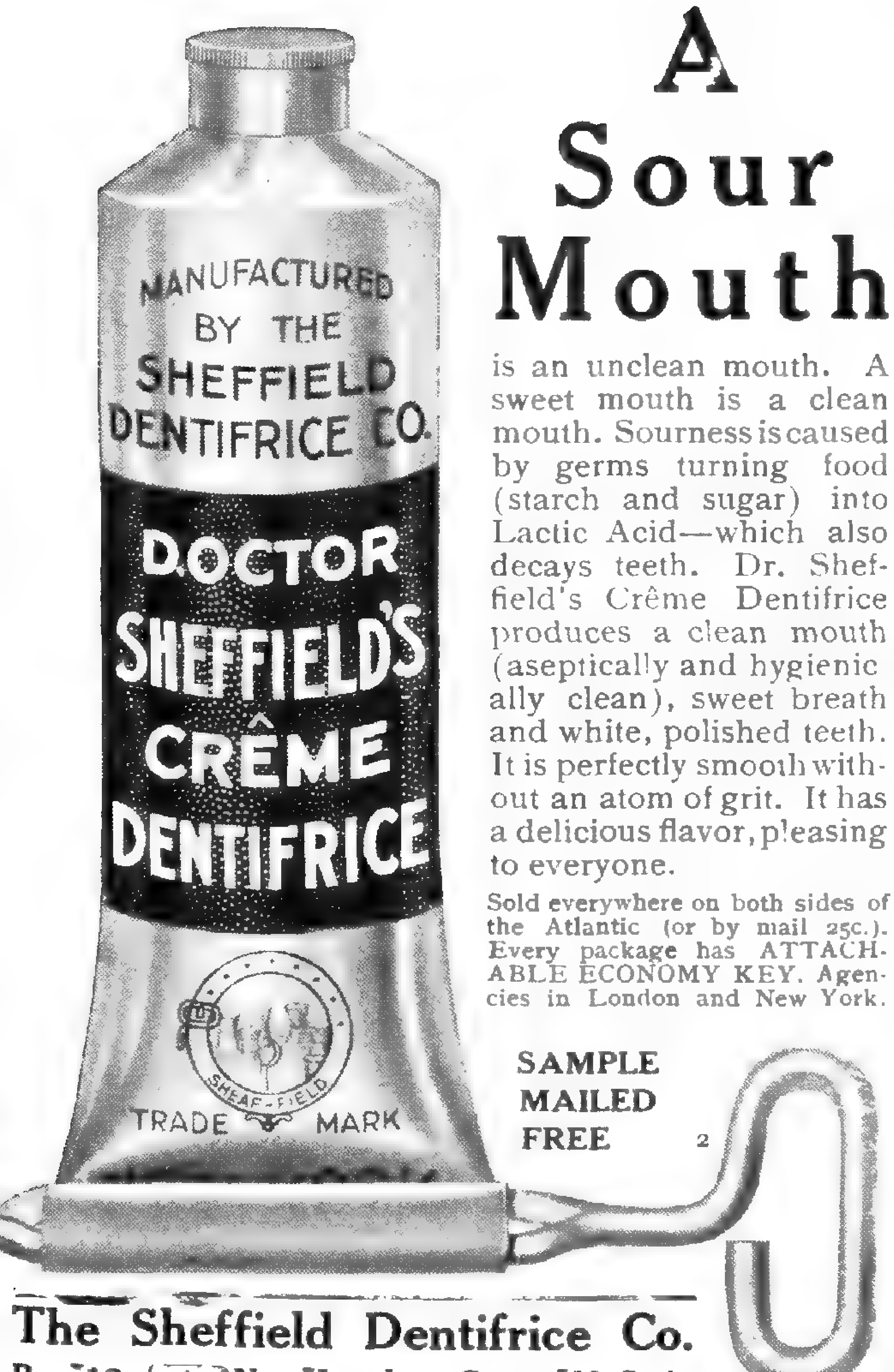
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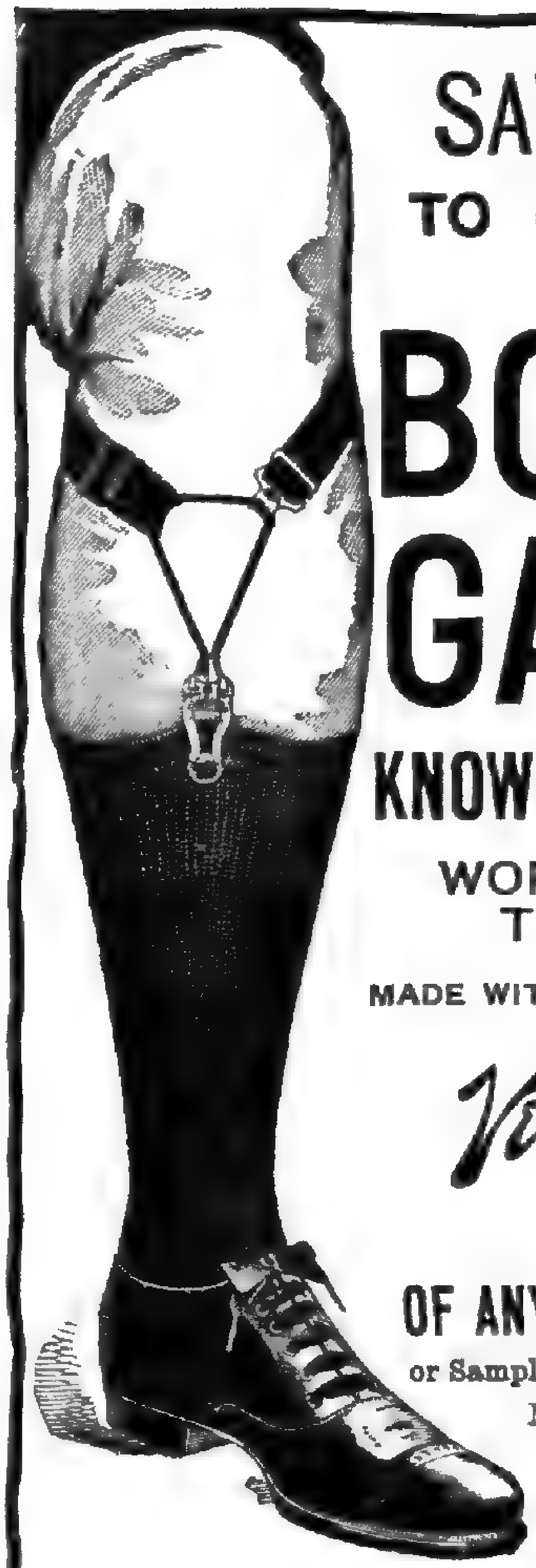

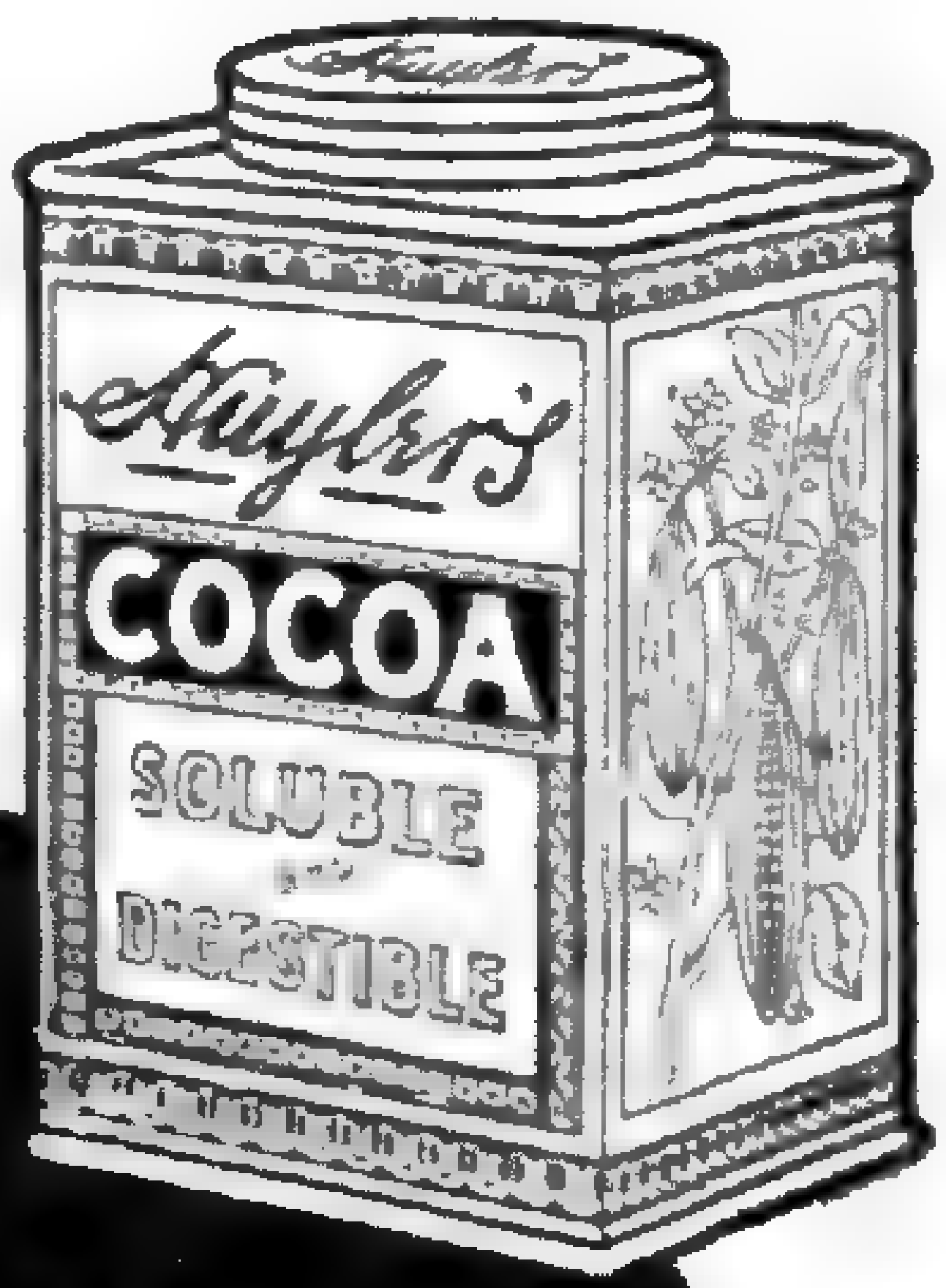
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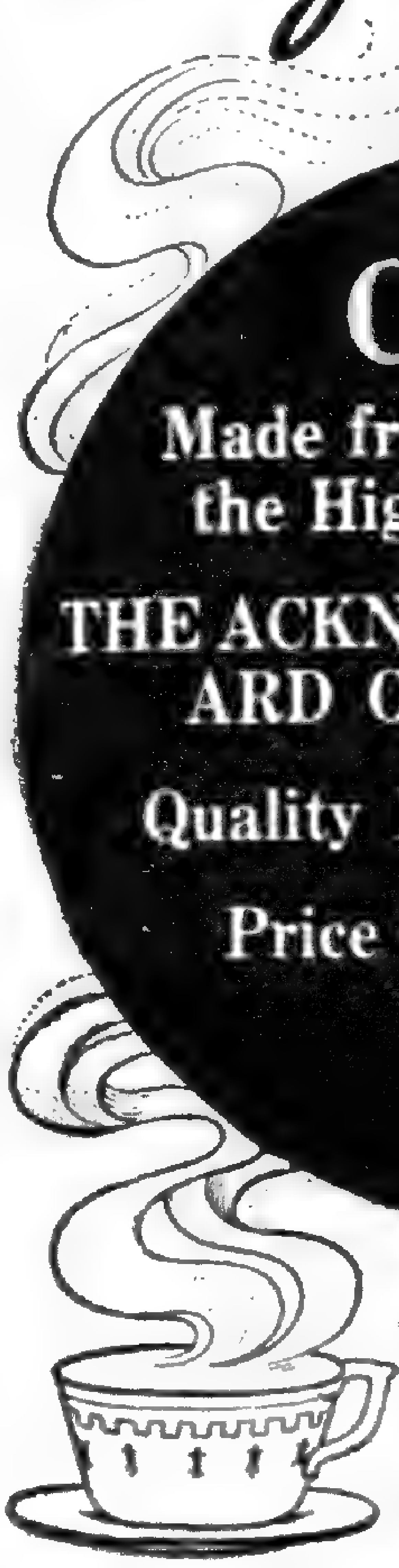

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No. 3

THE BOTANICAL GAZETTE

March 1910

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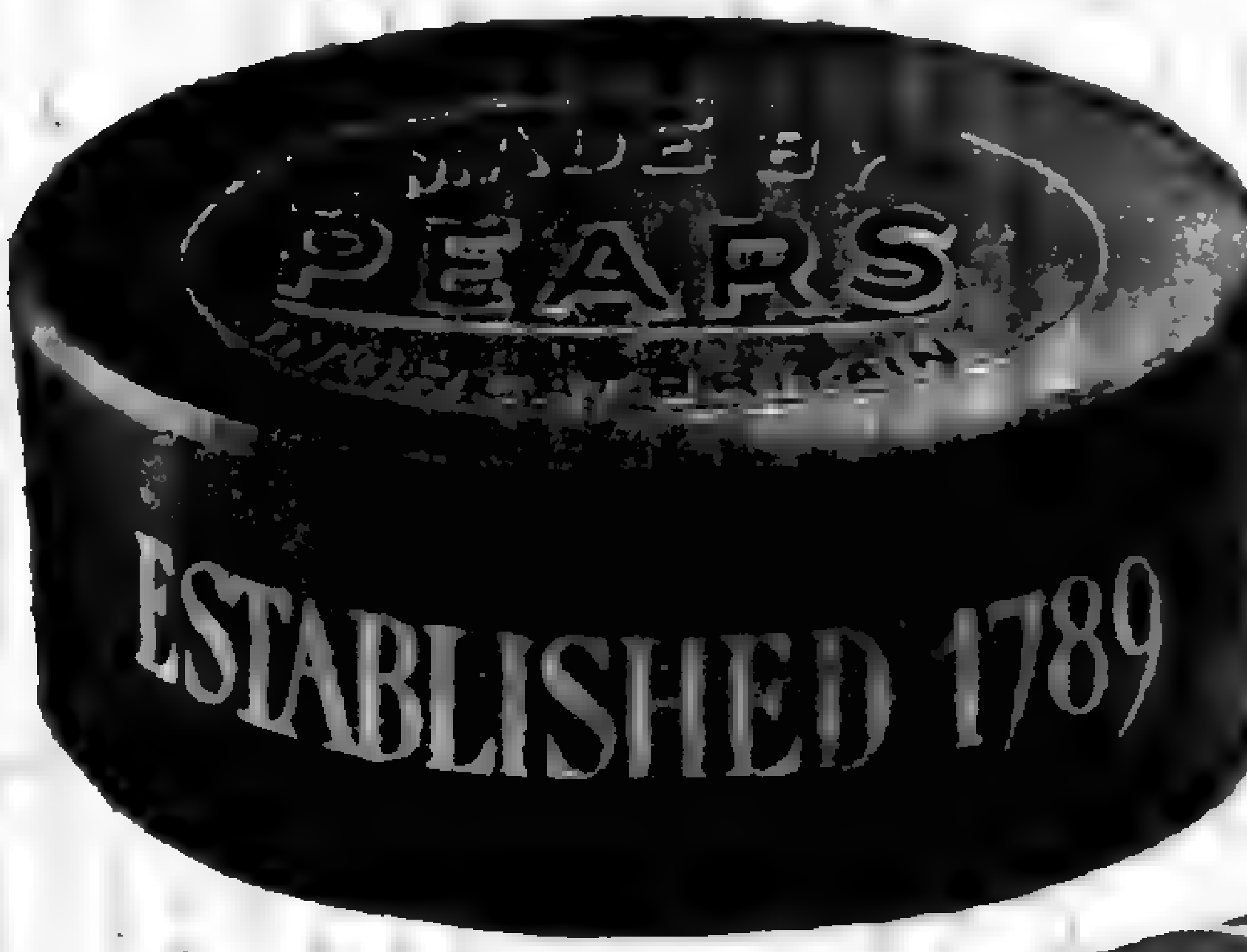
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VOLUME XLIX NUMBER 3

BOTANICAL GAZETTE

MARCH 1910

ON THE ORIGIN OF THE BROAD RAY IN QUERCUS

CONTRIBUTION FROM THE PHANEROGAMIC LABORATORY OF HARVARD UNIVERSITY NO. 17

ARTHUR J. EAMES

(WITH PLATES VIII AND IX)

As is shown in KNY'S *Botanische Wandtafeln*, nos. 75 and 76, the wood of Quercus consists of vessels, tracheids, fibers, and parenchyma. The last is disposed in two systems: the vertical, consisting of more or less scattered rows of cells, forming the xylem parenchyma; and the horizontal, made up of plates of cells extending radially, the medullary rays. The latter are of two sorts: small, numerous rays, which are thin sheets of tissue, linear, and of a single row of cells as seen in transverse and tangential sections; and occasional broad, generally fusiform masses, many cells wide, which form the most prominent feature of oak wood, its remarkable "silver grain." In our first two figures both kinds of rays are seen: *fig. 1* shows in transverse section a portion of a large ray, and of several small ones from the wood of *Quercus rubra;* and *fig. 2*, the tangential view of similar rays in the same species.

In the study of sections of a fossil oak from the gold gravels of California (Miocene), the material for which was kindly loaned the Phanerogamic Laboratories of Harvard University for investigation, an unusual ray structure was noticed. The uniseriate rays are present as in the living oaks; the large rays, however, are not homogeneous masses of parenchyma, but are represented by groups of smaller rays. *Fig. 6* shows such a group in tangential view. The smaller rays are so arranged as to form, in aggregate, the elongate fusiform mass of the normal large ray. They are separated from each other, however, by fibers, or by fibers and wood parenchyma.

A portion of the cluster more highly magnified is shown in *fig. 10*. *Fig. 5* shows the appearance of this "false" ray in transverse section.

This structure led to the suspicion that the large rays of the existent oaks might be derived from the so-called "false rays" of the lower Cupuliferae; that is, that the former have been "built up" by the aggregation and fusion of the small rays. The Miocene fossil would then represent a comparatively recent ancestral condition in ray structure. Two American species of Quercinium from Tertiary deposits in the Yellowstone National Park, *Quercinium Knowltonii* Felix[1] and *Q. lamarense* Knowlton,[2] have rays which seem, from the figures and descriptions, to be very much like those of the fossil here figured. The question then arose whether the seedlings of our living species of Quercus do not present some evidence as to the origin of the larger rays in living oaks, inasmuch as the seedling is known to be a seat of ancestral characters. The investigation of a number of North American species showed that we have in the oaks a good example of seedling recapitulation.

The oaks, from paleobotanical evidence, seem to have descended from ancestors that resembled the living chestnuts. There is much similarity in the structure of the reproductive organs, and in the type of leaf shape of the oldest oaks, and of the chestnuts. Confirmatory evidence is presented by the seedlings of some of our living oaks; especially worthy of notice is the fact that the first rays formed are all of the type which is found throughout chestnut wood.

In respect to ray structure in the seedlings, the species examined fall into two groups, corresponding with the subgenera Lepidobalanus (white oaks), and Erythrobalanus (red or black oaks).

The seedlings of the black oaks that were examined by the writer (*Q. rubra* L., *Q. velutina* Lam., *Q. coccinea* Moench., and *Q. ilicifolia* Wang.) all show a ray structure very much like that of the gold gravel oak above described. In the early annual rings, from the first or third to about the fifteenth, a progressive compounding, that is grouping and fusion, of the linear rays occurs, with the final production, after the considerable period of compounding, of a single,

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[1] FELIX, J., Untersuchung über fossile Hölzer. Zeit. Deutsch. Geol. Gesells. —:250. *pl. 6.* 1896.

[2] KNOWLTON, F. H., Geology of the Yellowstone National Park. Part II. U. S. Geol. Survey. p. 771. *pls. 118, 120, 121.* 1899.

huge, homogeneous ray. *Fig. 3* shows this process in a seedling of *Q. velutina*, the partial formation of three rays being evident. The ultimate shape and structure is brought about by the loss of the separating rows of fibers, tracheids, or wood parenchyma, or rather by the transformation of the elements included by the rays as they approach one another. This change is gradual; more and more parenchyma is formed, with corresponding decrease in fibers, until the cambial cells that lay down these radial rows cut off only ray cells. Ray formation of this sort exists in these species only as a passing phase in the seedling. In the wood of the mature plants large rays, of course, are continually formed, but their origin is nearly always abrupt. The transition from lignified elements to parenchyma occurs generally within the width of a single annual ring, or sometimes two or three. Later there is usually an increase in width which is due, however, not to the uniting of any neighboring small rays and the transformation of adjacent elements, but to simple growth in size with the increase of the stem in diameter. The seedlings of the black oaks, then, give evidence of the mode of origin of the broad rays so characteristic of the mature wood of the group. In so doing they repeat the ray structure that probably occurred throughout the wood of their rather recent ancestors.

Among the white oaks, seedlings of *Q. alba* L., *Q. bicolor* Willd., and *Q. prinoides* Willd. were examined. In all three species the wood of the stem for a distance of several inches, or even one or two feet, above the root possesses only uniseriate rays. Moreover, until the plant has attained a considerable size no large rays nor any signs of grouping of the small rays appear. Cases were seen in *Q. alba* and *Q. bicolor*, where in seedlings 15 to 20 years old only the linear rays existed. This condition would suggest that these white oaks, perhaps, are somewhat more primitive than the black oaks, for the seedlings of the former revert in structure to an ancestral type in which only uniseriate rays existed, and had not as yet begun to aggregate. *Fig. 7* shows a transverse view of this condition in *Q. alba* in about the fifteenth to twentieth annual rings. When the large rays do appear in these species, they are formed as in the black oaks, rather abruptly, the phase of compounding being confined to only one or two annual rings. Often nearly the whole ray arises at once at the beginning of a season's growth; a continuous row of cambial cells which have hitherto laid down chiefly fibers and tracheids, beginning with the first divisions of the year, form ray cells and only such thereafter. This is also the method in the stem of the mature plant.

Among the living oaks there are exceptions, however, to the possession of rays of the type shown in *figs. 1* and *2*. *Q. virginiana* Mill. (*Q. virens* Ait.), the live oak, has large rays of a type in which the compounding has become nearly complete. This species is probably somewhat more primitive than the above-mentioned species. *Fig. 8* shows a tangential section of a ray from near the pith in a large seedling of this plant. The structure of this ray very much resembles that of the fossil oak and of the black oak seedlings. In *fig. 9* a portion of this ray is shown enlarged. The Japanese oaks have somewhat similar structure of the broad medullary rays, *Q. Mirbeckii* and *Q. Sieboldii* especially. In the shape of their leaves the oaks of Japan show other probable signs of primitiveness; the general type is similar to that of the chestnuts.

Not only does the large ray in its primitive condition occur in fossil and seedling oaks, and occasionally in mature plants of the genus, but it exists also in several genera of the lower Cupuliferae, namely in Corylus, Carpinus, Ostrya, Betula, Alnus, and perhaps others. The distribution of the large rays in the dicotyledons is at present being investigated in this laboratory by Mr. I. W. BAILEY. *Figs. 11* and *12*, transverse and tangential sections, respectively, of the wood of *Alnus incana* (L.) Moench., show in one of these genera this "false ray." In this case the linear rays have become grouped together, but very little fusion has yet taken place. It would seem then that this fusion of rays, perhaps for the acquisition of greater storage capacity, which began in some primitive cupuliferous plants, and which is still maintained at an early stage in some of the living members thereof, has reached a culmination in the broad, solidly parenchymatous mass, the large ray, of many living oaks.

That the "false ray" of Alnus and of other closely allied genera represents the primitive condition of the present large ray of Quercus seems undoubted, not only from its appearance in the lower Cupuliferae, and in fossil and seedling oaks, but also from many other points of resemblance. A prominent feature of the broad ray of Quercus is the strong "dipping in" of the annual ring wherever these radial masses of parenchyma occur. This is well shown in *fig. 1*. In the cases among the lower Cupuliferae, and in fossil species of Quercus where rays of the compound type exist, the same feature is noticeable. In Alnus, as appears in *fig. 11*, this condition is prominent; in the fossil oak it can be seen, but only faintly, for the annual rings are not strongly marked, probably as a result of the milder climate of the Miocene. This peculiarity serves thus further to connect the two kinds of rays.

In view, then, of the apparent phylogenetic relation of the two sorts of medullary rays found in Quercus, the designation of the broad ray as *primary* and of the small one as *secondary*, a use that is to some extent prevalent, seems inadmissible. The terms would certainly be more applicable if interchanged, but the adjectives *small* and *broad* or *large*, or *small* and *compounded* may perhaps be more appropriately applied.

Summary

The medullary rays of the oak are of two sorts: small, linear sheets of parenchyma, only a single row of cells wide, as seen in transverse and tangential sections; and large, generally fusiform masses, many cells in width. The former have been to some extent called secondary rays, the latter primary rays.

Fossil evidence points to the probable derivation of the existent oaks from ancestors which possessed only the linear type of ray. The large ray has apparently originated by the aggregation and fusion of many of these small rays, through the loss of the separating elements, or the transformation of the latter into ray cells. A fossil oak from the Miocene gold gravels of California shows an intermediate condition, a stage where all the large rays consist merely of aggregations of small rays, with separating fibers. The seedlings of some, at least, of the black oaks form rays of this nature for a brief period, usually during the first ten to fifteen years. There is during this time a recapitulation of the history of the development of the ray; the small, uniseriate rays, which are at first formed, gradually approach each other in groups, and fusion slowly occurs as growth of the stems continues, until a good-sized, homogeneous, parenchymatous ray is formed. In the wood of the mature plant the large ray is formed more abruptly, and is not so much the result of fusion of smaller rays, as of the transformation of all tissue, within a region of the size of the ray to be formed, into ray parenchyma, such change being rather abrupt and occurring largely at the beginning of a season's growth. The seedlings of the white oaks possess in their early wood only uniseriate rays, suggesting a somewhat more primitive state. A few living oaks show the transitional stage, that is, large rays composed of ununited aggregations of small rays in the wood of mature plants. The Japanese oaks especially belong in this group.

The oaks present an excellent case of recapitulation of ancestral characters by seedlings. The phylogenetic history of ray structure in the genus is well displayed, step by step, in the wood of the seedling stem during the first few years.

The work has been carried on in the Phanerogamic Laboratories of Harvard University. The writer desires to express his thanks to Dr. F. H. Knowlton of the United States Geological Survey for the loan of material of miocene oaks, and to Mr. I. W. Bailey for opportunity to examine and use slides of several genera of cupuliferous woods. He is also very much indebted to Professor E. C. Jeffrey for suggestions and advice during the progress of the investigation.

Harvard University

EXPLANATION OF PLATES VIII AND IX

PLATE VIII

Fig. 1.—*Quercus rubra;* transverse section of wood, showing portions of large and small medullary rays. ×40.

Fig. 2.—The same; tangential section of wood, showing similar rays. ×40.

Fig. 3.—*Quercus velutina*, seedling; transverse section of portion of stem showing formation of large rays. ×40.

Fig. 4.—*Quercus rubra*, seedling; tangential section of a large ray in process of formation. ×40.

Fig. 5.—Fossil oak from gold gravels of California (Miocene); transverse section of wood showing portion of the large ray. ×40.

Fig. 6.—The same; tangential view of portion of the large ray. ×40.

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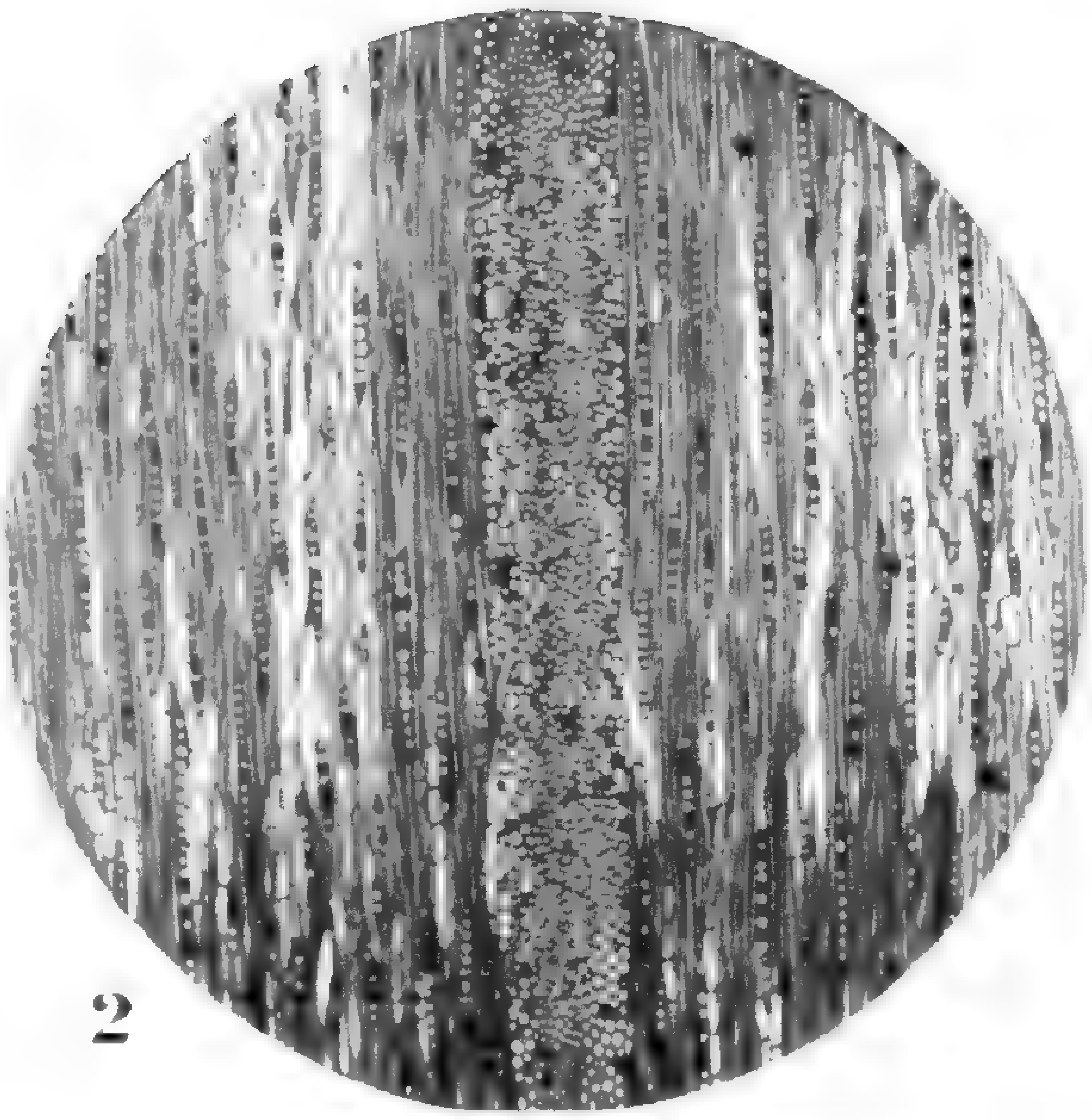

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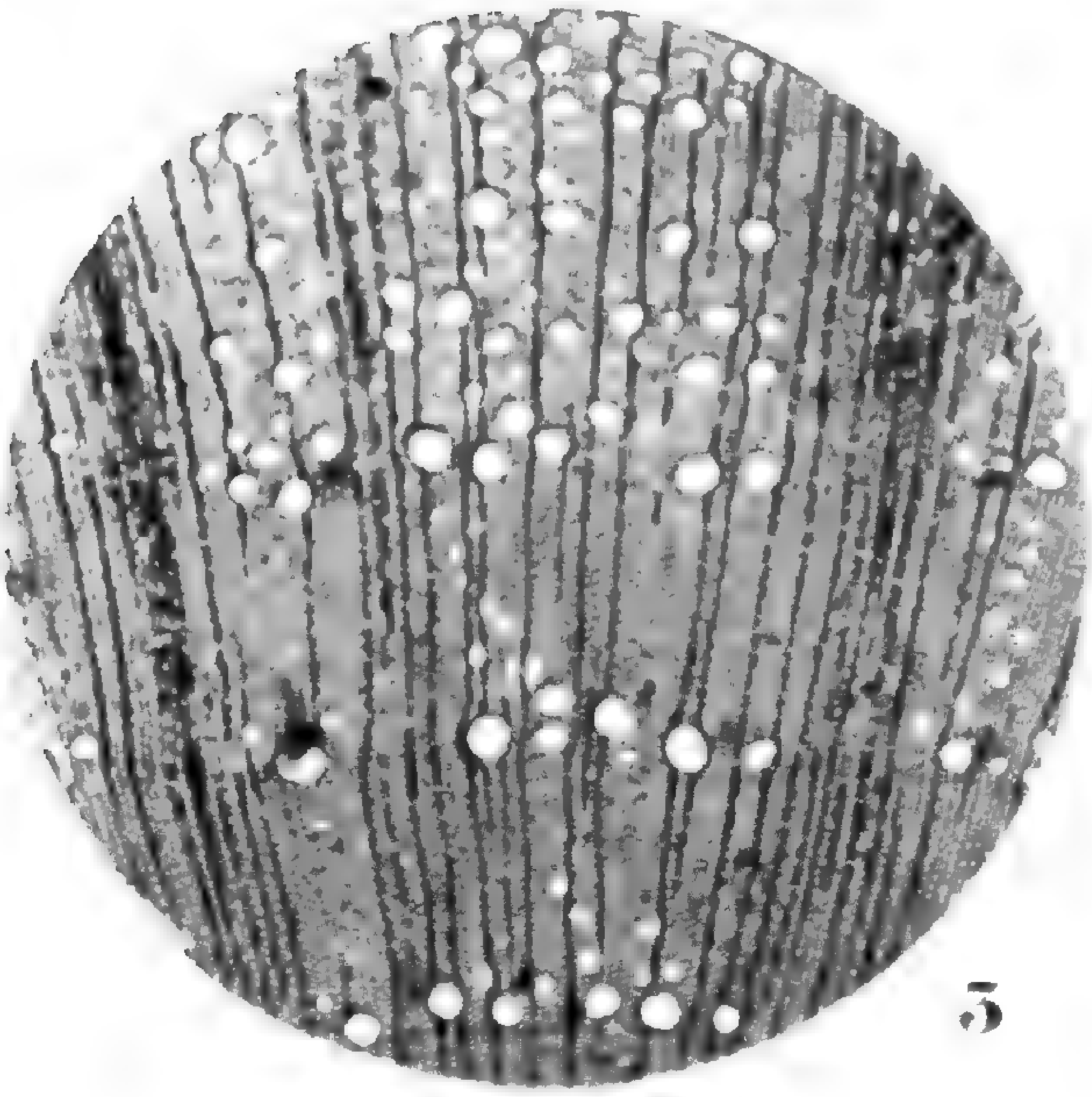

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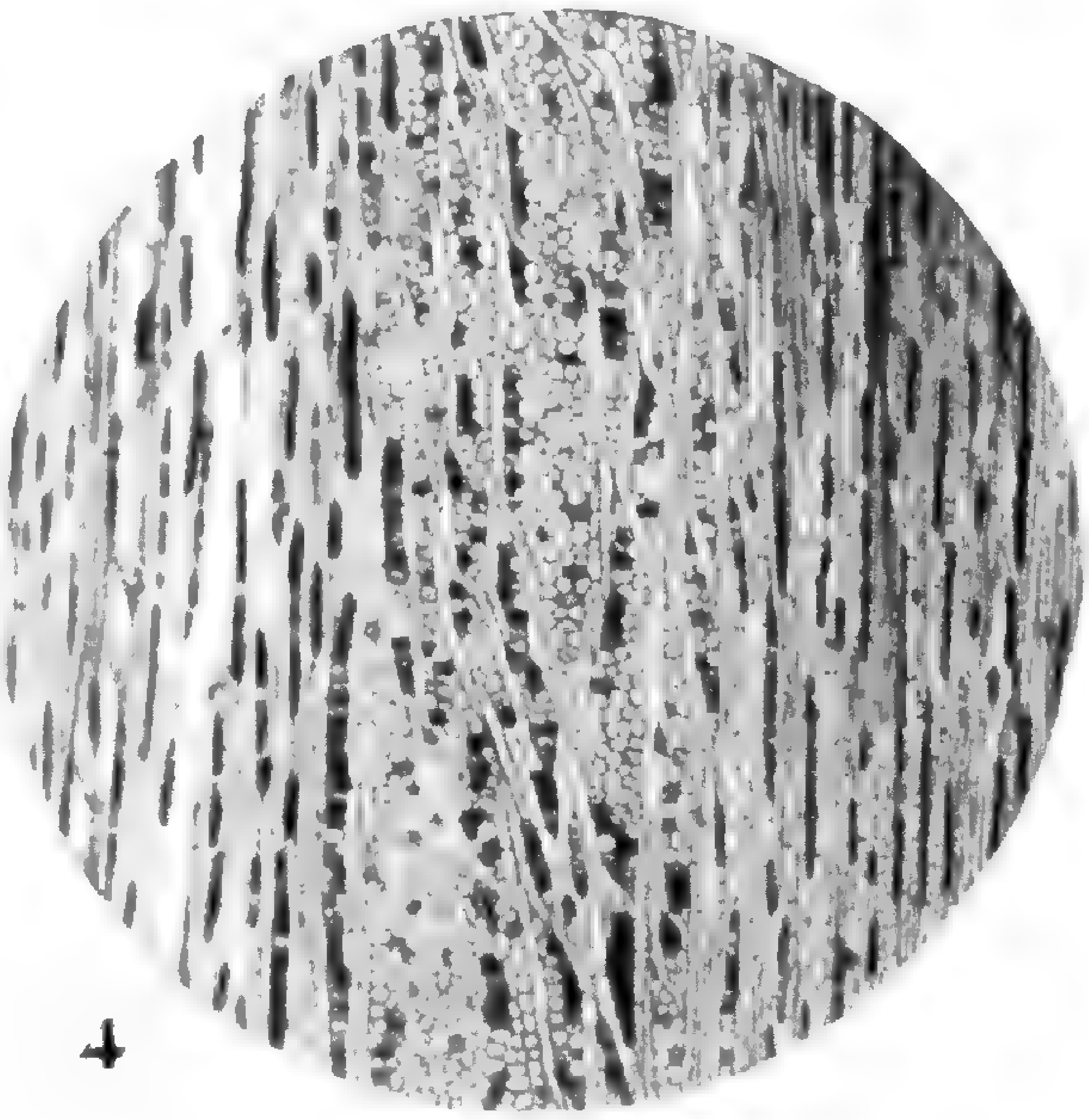

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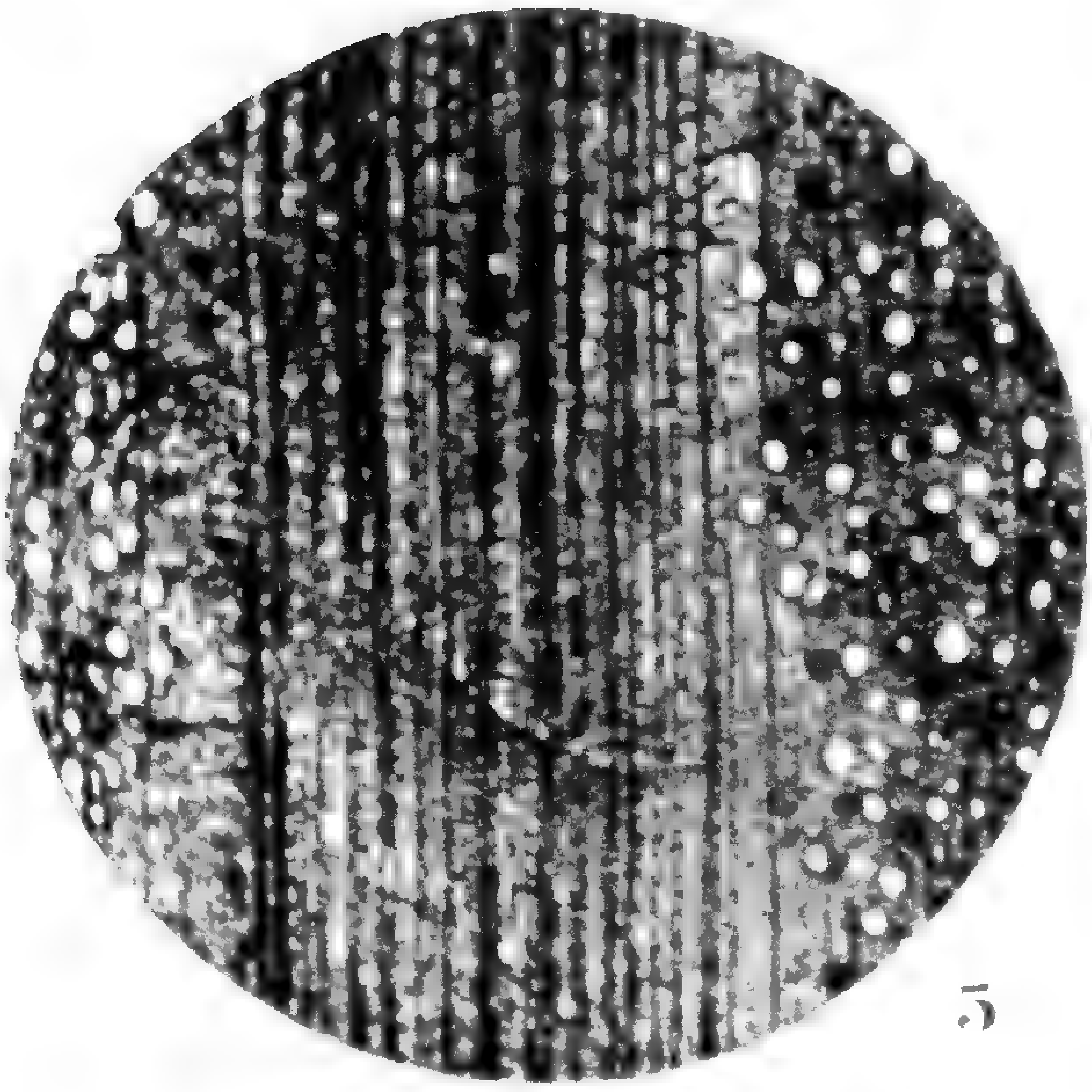

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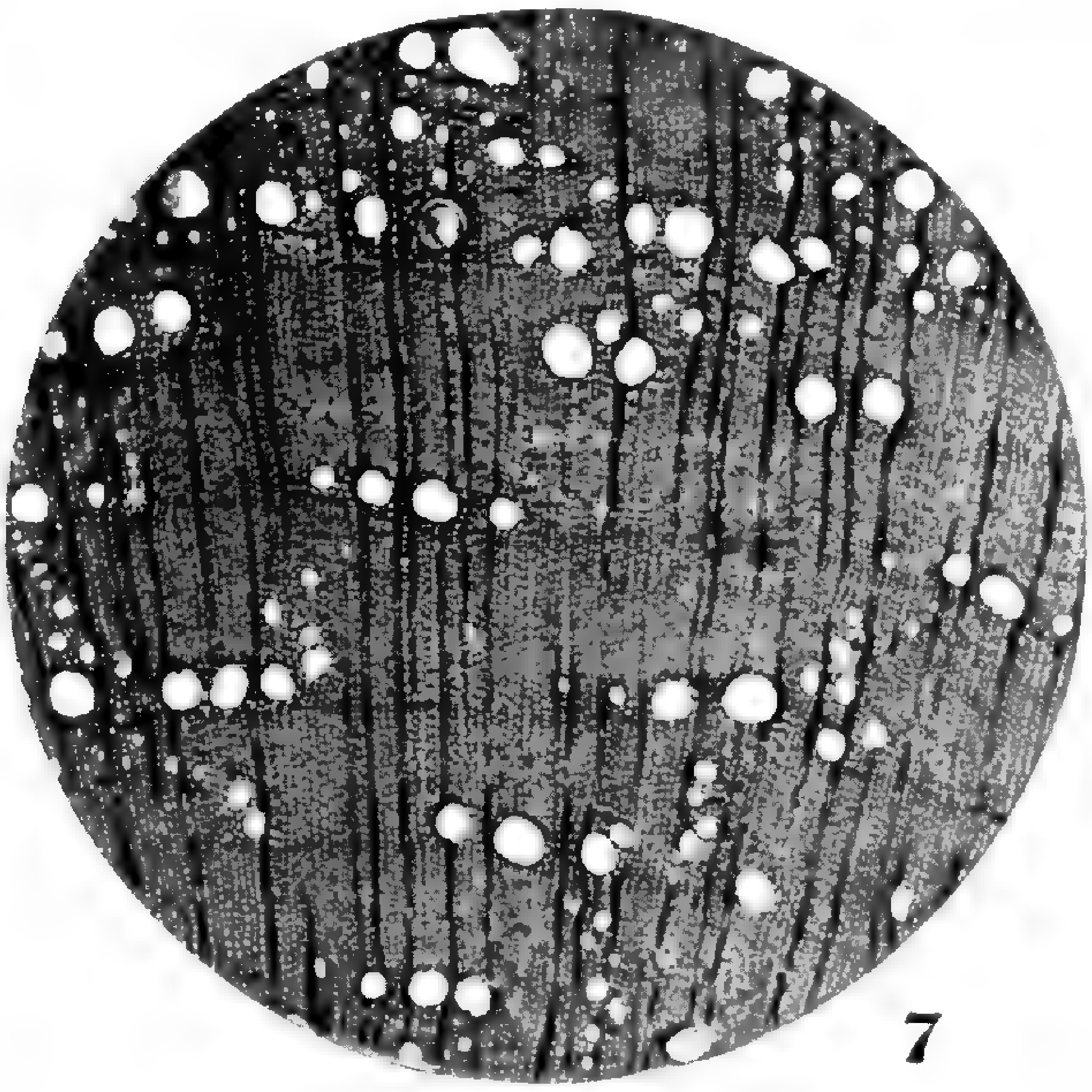
EAMES on QUERCUS



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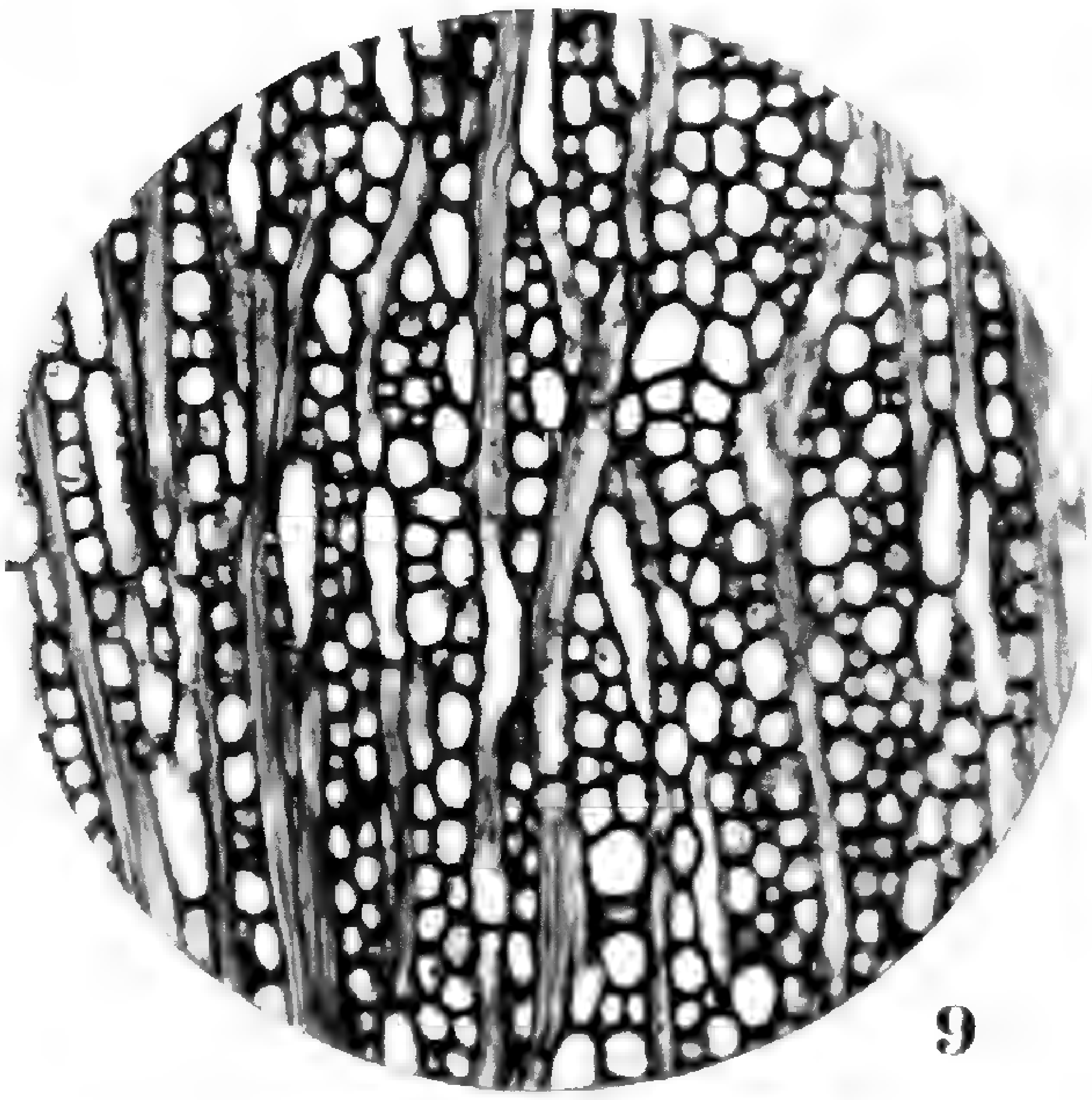

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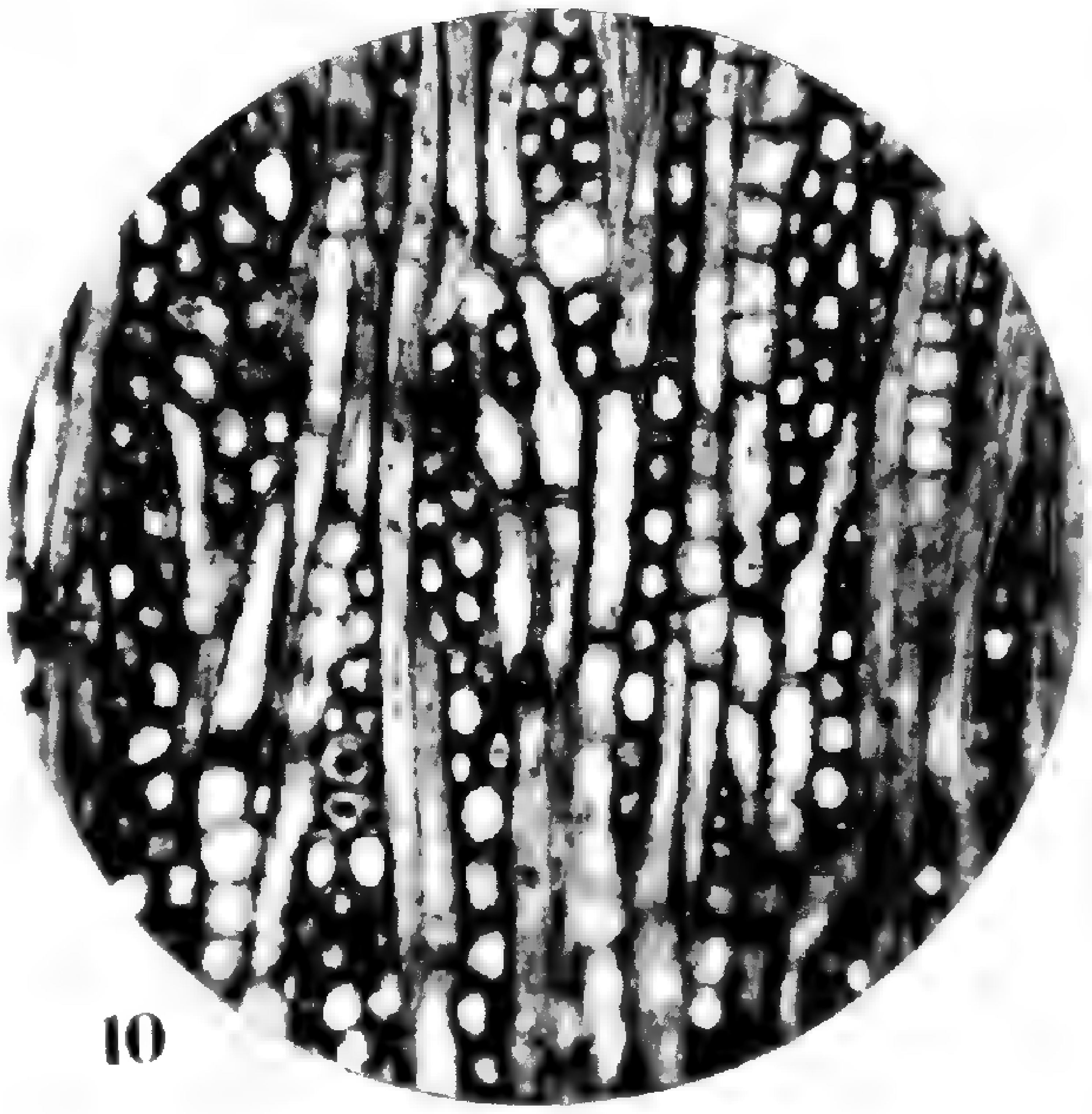

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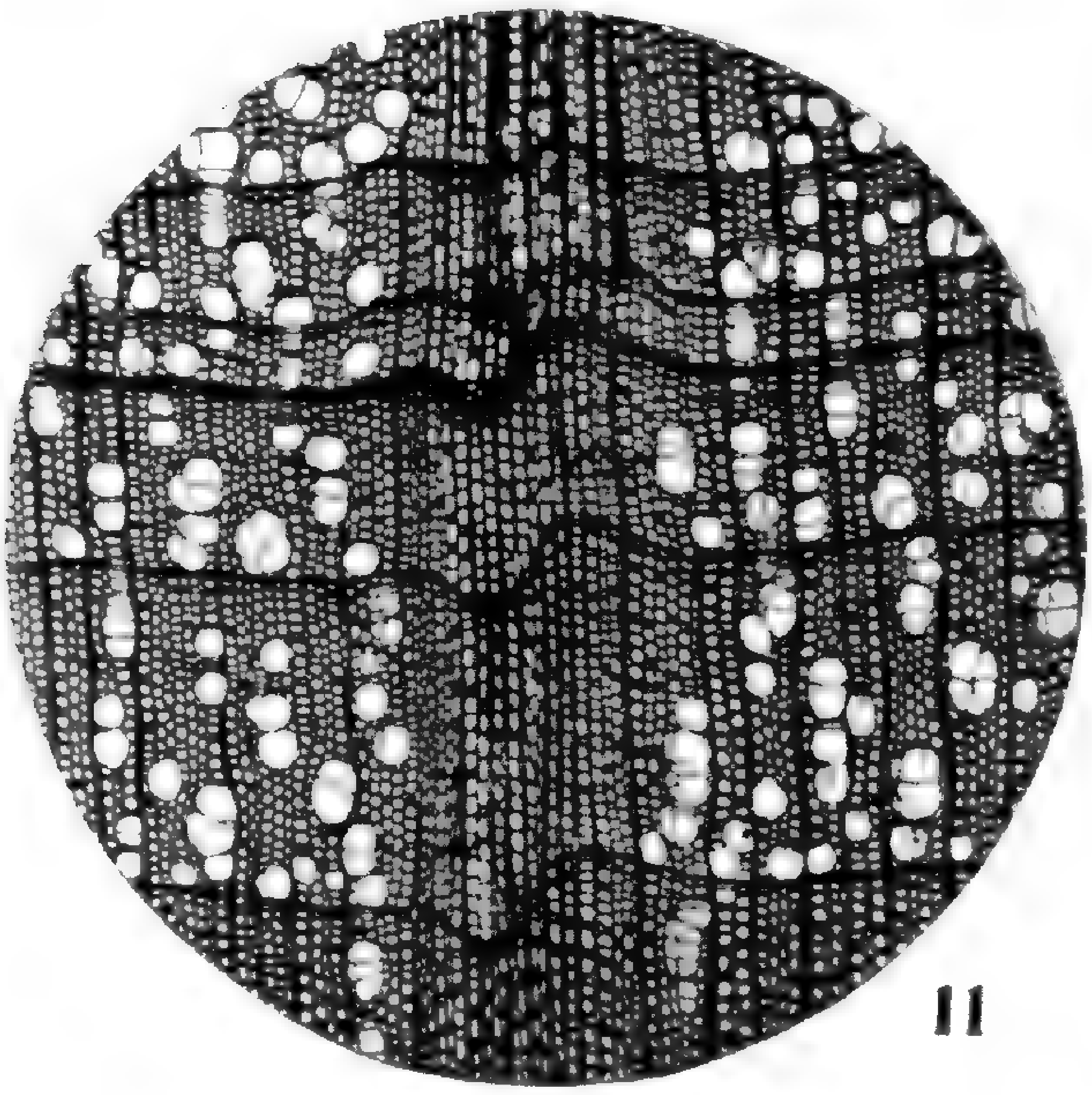

11

12

EAMES on QUERCUS

PLATE IX

Fig. 7.—*Quercus alba*, seedling; transverse section of portion of stem, showing only rays of the linear type. ×40.

Fig. 8.—*Quercus virginiana*, seedling; tangential view of portion of large ray. ×40.

Fig. 9.—The same; portion of the large ray. ×100.

Fig. 10.—Fossil oak of the gold gravels; tangential view of portion of the large ray. ×100.

Fig. 11.—*Alnus incana;* transverse section of wood. ×40.

Fig. 12.—The same; tangential section. ×40.

THE PROTHALLIA OF ANEIMIA AND LYGODIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 136

EDITH MINOT TWISS

(WITH PLATES X AND XI)

A survey of the literature on the prothallia of the Filicineae brings out plainly two points: (1) for a number of years those who have studied this side of the life history of ferns have urged that one must not consider the heart-shaped prothallium, whose development was first worked out, the norm from which all variations are comparatively rare exceptions; (2) many investigators have expressed the conviction that gametophytic characters could be used in classification.

BAUKE (**1**) was among the first to urge this latter idea when, in an effort to determine the position of the Cyatheaceae, he searched the gametophyte for decisive characters to add to those afforded by the sporophyte. The examination of the prothallium of this family convinced him that aid could be gained there, and he extended his observations to the Schizaeaceae and meant to take up other families. Before this work was completed, however, he died.

About ten years after this, GOEBEL (**9**) followed a study of the prothallia of a number of epiphytic ferns with a discussion of the light thrown by them on the possible origin of ferns from algae through bryophytes. In his later work (**11**) he adds to his account of different gametophytes and reviews his former conclusions, ending with the statement that "within the single natural groups also one may well recognize a conformity in the formation of the prothallus which is expressed in the possibility of arrranging them in series." From his investigations in 1896 HEIM (**12**) came to similar conclusions as to the value of gametophytic characters.

It certainly seems worth while to review the situation and see whether something may not be added from this side to the points already made by the study of the sporangial and vascular development of the sporophyte. Any such attempt, however, must be preceded by considerable work in two directions: (1) although the prothallia of most of the genera have been investigated, a review of the literature shows many points untouched, and much, done some years ago without the aid of modern technique, that needs reinvestigation; (2) much experimental work is yet to be done regarding the effect of different conditions upon the morphology of the thallus. As a beginning I have attempted the study of some of the Schizaeaceae.

Historical résumé

The first report on the prothallium of this group was given by KNY (**13**) at a meeting of the Gesellschaft naturforschender Freunde at Berlin in 1868, where he instanced *Aneimia hirta* as forming a cell plate immediately on emergence of the filament from the spore. BURCK (**6**) confirmed this and added that the apical cell when formed was not, as in Polypodiaceae and Cyatheaceae, at the end of the thallus but at one side.

In 1875 BURCK (**7**) made a more extended study of three species of Aneimia (*A. Phyllitidis*, *A. fraxinfolia*, and *A. longifolia*), and laid considerable stress on the fact that the whole filament, by longitudinal wall formation, takes part in the formation of the thallus, while in polypods this is formed only at the end of the filament. He also finds the formation of the further stages of the thallus from a lateral cell and a later initial group and attempts to trace the course of development here more carefully. As an additional character of considerable importance, he gives what he calls the "pousse laterale normale," a lateral wing formed by some prothallia, which often becomes thickly covered with antheridia.

BAUKE in his paper (**2**) points out that this "pousse laterale normale" is only a lobe of the often very irregular male prothallium. The first point made by BURCK he modifies by saying that in the Polypodiaceae and Cyatheaceae longitudinal division does take place in several cells of the filament, but always after the wall has appeared in the terminal cell, while in Aneimia the cells near the spore divide at the same time or even earlier than those at the distal end. The lateral position of apical cell and initials is still insisted upon, though details as given by BURCK are criticized. Neither investigator finds anything to mention as especially characteristic in the development of the archegonia, and both confirm the account of antheridial development given by KNY. He (**14**) reported that the first wall in the antheridium is always flat instead of funnel-shaped, as in the polypods, and that the discharge of sperms takes place through a star-shaped break in the cover cell.

When BAUKE (**3, 4**) continued his investigation of different prothallia, he added *Lygodium japonicum* to those of the Schizaeaceae already examined. Here he pointed out the long-continued persistence of the apical cell. He also found on well-developed prothallia archegonia alone at first and antheridia only when the prothallia were considerably older. The exit of sperms here, he reported, is provided for by the throwing off of the cover cell.

HEIM (**12**), working with the same species of Lygodium, confirmed both of these points. He studied also *Aneimia Dregeana*, *A. Phyllitidis*, *A. fraxinfolia*, and *Mohria Caffrorum*, and gives as an additional distinguishing mark of the whole genus warty (*knotige*) thickenings of the side walls of the prothallial cells.

Methods

The soil in which the prothallia used in the present investigation were grown was a mixture of loam and sand. Six-inch pots were filled to within two inches of the top with coarse stones loosely mixed with Sphagnum to facilitate watering and to prevent the dirt from sifting through. One-half an inch of well-packed soil covered this, and over the top a thin layer of soil was sifted through a fine sieve. After sterilization this fineness of the upper soil facilitated the removal of prothallia for study. Pots and soil were sterilized in steam for several hours and, after the sowing of the spores, were kept covered with glass and watered from below. The prothallia were grown in a greenhouse where the temperature was always near 100° F. and lighted with diffuse light from above.

The early stages were obtained free from dirt by sowing the spores on porous clay plates and keeping these in Petri dishes with a little distilled water. Spores were also germinated on the surface of distilled water and of 0.6 per cent. Knopf's solution. Before drawings were made the prothallia were always carefully compared with the same stages on dirt, to determine whether the form or course of cell division had not been altered by the change of medium.

Fungi were kept down by the potassium permanganate solution advised by LANG (**15**). In a letter from Dr. LANG to Dr. COULTER the directions called for a solution decidedly pink; I used with success 0.015^{gr} potassium permanganate in 3.5 liters of water.

Drawings of the early stages were made from living material. The older prothallia were killed with Flemming's weaker solution (**8**), imbedded in paraffin, and the sections stained with safranin and iron alum-hematoxylin.

Lygodium

The species studied was *Lygodium circinatum* (Burm.) Sw. (*L. dichotomum* Sw.), spores of which were obtained through the kindness of Dr. J. N. ROSE, from the botanical gardens at Washington, D. C.

SPORE COATS

The coats reported for the spores of Filicineae are an outer exceedingly delicate epispore, a heavier exine having usually peculiar markings, and a thinner intine which covers the emerging papilla when germination occurs. Paraffin sections of spores of Lygodium, however, showed the possibility of a different situation, and accordingly a study of the development of the coats was undertaken. For this study I was most fortunate in having access to slides prepared by BINFORD (**5**) in his work on the sporangia of *Lygodium circinatum*, and thanks are due him for the aid afforded by his preparations. The slides were stained with safranin and gentian violet, and this should be kept in mind when reading the account of the coloring of the different coats. The sporangia are produced in acropetal succession, so that it is easy to get a clear picture of the different stages.

When the spore mother cell rounds off, the wall is exceedingly delicate, and at the tetrad stage no remnant of it could be identified with any certainty. As *fig. 1* shows, there is a clear space about the tetrad, so that the tapetal protoplasm with its large nuclei does not touch the spores. The protoplasm at the edge of this clear space was carefully examined for traces of the old mother cell wall, but none could be found. Moreover, the same clear space was seen about the spore mother cells themselves in some of the sporangia. Whether the clear space was due to plasmolysis caused by the fixing agent could not be determined, since there was no opportunity to observe living material.

The wall first formed about the spore is the exine. Very early, before any thickening of this wall has taken place, the color changes from purple to bright red, and the spores increase in size so that the tapetal protoplasm is now close against them. As the exine thickens, a difference in staining becomes apparent, the inner part being red, the outer yellow, but with no clear line of demarkation between them (*fig. 2, ex, r,* and *y*). No chemical tests could be applied to determine the nature of the substances taking these colors, but from what THOMSON (**16**) says of the colors of megaspore membranes of gymnosperms when stained with safranin, and from what he says of the course of development in these membranes, it seems probable that the red indicated the presence of suberin, and the yellow of pectin.

By this time the intine (*fig. 2, i*) has been laid down just within the exine. In the sporangia showing the stage just preceding, the spores were so collapsed that it was impossible to determine whether or not the intine was formed before the exine had differentiated into red and yellow regions.

At a stage shown in *fig. 2* there are here and there in the cytoplasm groups of reddish granules (*fig. 2, g*). These are first recognized as very small, deeply staining bodies at the intersections of the protoplasmic network. They increase in size and the protoplasm, either by the breaking down or drawing together of some of the connecting strands, assumes the appearance of a network of coarser mesh, in which, both at the intersections and along the strands, are the now redly staining granules. The nuclei (*fig. 2, n*) show the beginning of degeneration in the irregular clumping of the chromatin, and later in the disappearance of the membrane, and it is very likely that the nuclear substance contributes largely to the formation of the granules, which take on a deeper and deeper stain as the nuclei become unrecognizable.

In the older sporangia the granules are larger and larger, of fairly regular shape, as if from the rounding up of viscid matter, but of varying size (*fig. 3*). Some of them are close together, and their position suggests that the larger ones may have come from the running together of two or more of the smaller ones. Those in proximity to the spore coat adhere to it (*fig. 4*), but for some time not very tightly, so that they are easily pulled away in the cutting. The protoplasm comes to form a delicate continuous sheet between the granules and over their surface (*fig. 5*). The mature wall shows that the protuberances thus formed are still of varying sizes and somewhat irregularly placed, and that they and the exposed position of the exine are covered by the thin layer of cytoplasm (*fig. 6*). In the spores of *Lygodium circinatum* (*figs. 7, 8*), sections in which the coats have been broken apart in the cutting show clearly the delicate intine (*i*), the heavy exine (*ex*) with its two differently staining portions, and the epispore (*e*) of heavy projections formed by the tapetal protoplasm. It is probable that in this epispore we have merely a difference in degree from the more delicate one reported for Filicineae. If the granules were not developed, we should have in the thin sheet of protoplasm covering the spores just such an epispore.

DEVELOPMENT OF THALLUS

The exine of the spores is opaque, so that it was difficult to determine just when chlorophyll was formed. The first definite signs of germination are visible in five to seven days, when the spore coats split and a colorless cell, the first rhizoid, protudes (*fig. 9, a*). The first prothallial cell may be seen as a projecting papilla soon after the rhizoid, but seems to grow more slowly, so that by the time it is well out of the spore the rhizoid is five or six times the longer (*fig. 12*). Very shortly there is seen a smaller papilla pushing from the spore at the side of the first (*fig. 10*, p^1), and as the two protrude farther it becomes clear that the smaller one is a cell cut off from the side of the larger, and that the rhizoid has its origin in turn from this smaller cell (*fig. 12*). The first division of the spore does not separate the rhizoid and first prothallial cell.

The chlorophyll grains are fewer in number and smaller than those in the larger cell, where they are crowded in a dense mass about the nucleus. Sometimes two rhizoids appear, as BURCK reports is always the case in *L. japonicum*, but this seems to happen rarely. Even more seldom the prothallial cell emerges before the rhizoid. The three layers of the spore coat may be distinguished at this stage (*figs. 9, 10*). It is not at all unusual for a spore to produce two filaments (*fig. 11*), and the prothallium then is very like a young prothallium of Hymenophyllum or Trichomanes.

Even before the relation of these three cells is clear, division of the larger prothallial cell by a transverse wall has usually taken place (*fig. 10*). Development now proceeds in one of three ways: (*a*) longitudinal and transverse wall formation may follow so as to produce two rows of nearly equal cells (*figs. 13, 14, 15*); (*b*) an oblique wall may take the place of the first longitudinal wall so that, almost from the first, growth is by an apical cell cutting off segments right and left (*figs. 16, 17*); (*c*) the longitudinal walls may not come in at all, and a filament of a single row of cells is produced (*fig. 18*). The last case seems to be comparatively rare; the others appear about equally often.

This course of development may be altered by varying the conditions in which the prothallia grow. Under a screen of potassium bichromate solution, and in both weak and strong sunlight, filaments of a single row of cells were produced, and these did not broaden to a thallus. The filaments sometimes reached a length of 4 or 5^{mm}, attaining this not through numerous divisions, but by the very unusual length of many of the cells. The small cell between the rhizoid and the first prothallial cell was present in these filaments.

In none of these cultures did antheridia appear, though some of them were kept for a time longer than that within which antheridia are produced under usual conditions. The early appearance of antheridia on filamentous prothallia has been reported as usual. WORONEW (**17**), however, says that he failed to get antheridia on filaments growing in weaker light, but was able to bring about their early production by unfavorable conditions of crowding, drying, etc. In a culture growing in dirt badly overrun by algae, I did find a few prothallia with antheridia produced from the third or fourth cell.

Under a screen of ammoniated copper sulfate, the prothallia, while germinating much later and growing more slowly, broadened in the usual way.

In the ordinary cultures, by the end of ten or twelve days an apical cell is established and a thallus is produced, first spatulate and then, by the more rapid growth of the cells on either side of the apical cell, heart-shaped (*figs. 19–22*). GOEBEL (**11**, p. 204) has called attention to the fact that for a time the wings of such a prothallium are not of the same size. This unequal lobing is commonly the case with *Lygodium circinatum*, as may be seen from *fig. 22*. The apical cell, however, has clearly a terminal position (*figs. 20–22*), and the inequality of lobing seems in this case to come from the faster growth on one side than on the other. Occasionally the two wings seem to develop equally, and in the end they are of equal size in both cases. As BAUKE reports, the apical cell persists for a relatively long time, but finally gives place to several initials.

SEX ORGANS

Antheridia appear in about three weeks, before the apical cell of the prothallium has been succeeded by the group of initials. Any cell of the prothallium may grow out into a papilla which is cut off to form an antheridium. These usually appear on the lower surface, but are found now and then on the upper surface as well. The first wall of the antheridium is often flat (*fig. 23*), as KNY (**14**) reports, but may be so concave as to touch the basal wall (*fig. 24*). There seems to be nothing here, at least in the ordinary forms, that could be called peculiar to the gametophyte of this family. Occasionally, however, more of a stalk is formed in a manner resembling the antheridia of the Osmundaceae (*fig. 25*). One such case is reported by HEIM (**12**).

The formation of a dome-shaped wall and the cutting off of a cover cell follow, and the central cell divides to form a large number of spermatogenous cells; in Lygodium 128 sperms seem to be the characteristic number.

Within six weeks archegonia have appeared. Examination of a number of prothallia at this date showed some with antheridia only, two with archegonia only, and some with both antheridia and archegonia. (All these prothallia were heart-shaped; crowded prothallia of irregular shape are not included.) Of the first, with antheridia only, there were two forms: (*a*) broadly heart-shaped, with antheridia in great numbers over much of the lower surface and crowded near the initials; and (*b*) younger prothallia, with fewer, more scattered antheridia, and none very near the notch. Of the second kind, I found but two instances. All prothallia examined at a later stage were of the third kind.

The archegonial cushion is somewhat thicker than that usually figured for polypods, and the archegonia project from it in all directions except from the dorsal surface. The development seems to correspond to that reported for polypods (*figs. 26–28*). There are two neck canal nuclei (*fig. 28*); occasionally four are found, but with no walls (*fig. 29*).

Aneimia

SPORE COATS

The sporangia studied for the development of the spore coat were those of *Aneimia hirsuta* (L.) Sw., in which the spores show parallel ridges set with spines. The material, which had been killed in 70 per cent. alcohol and formalin, was imbedded in paraffin and the sections stained, like those of Lygodium, with safranin and gentian violet.

The earlier stages in the formation of the spore coats agree with those in Lygodium except that the mother cell wall is not so delicate, and traces of it may still be seen after the walls of the spores appear in the tetrad. When the exine begins to show differentiation into red and yellow parts, ridges appear on the outer surface and the red is largely confined to these ridges, only a line of it appearing near the inner edge of the coat (*fig. 30*). Stages were found before the one represented and with barely perceptible ridges, and later ones in which they were more prominent. No trace of granules in the cytoplasm can be seen, though the nuclei have an appearance of degeneration, comparable to that in the same stage of Lygodium. A surface view of the coat at this time shows ridges but none of the spines of the mature coat.

That these spines are built up on the ridges by the activity of the tapetal protoplasm seems evident from stages like that shown in *fig. 31*. The exine shows the red and yellow, but the spines stain purple, and they are very easily pulled away from the ridges. Later these spines change their nature, beginning at the part nearest the ridge, and show the yellow stain except just at the tip.

In the case of *Aneimia hirsuta*, then, the epispore consists of these spines and a general delicate coat of protoplasm. The exine is a coat of two differently staining portions and with ridges on its outer surface. The intine is first clearly seen at the same stage as in Lygodium, when the exine differentiates into red and yellow portions.

FORMATION OF THE THALLUS

The main work was done with *Aneimia Phyllitidis* (L.) Sw., which Dr. BARNES kindly sent from Mexico at the time of his botanical expedition there in 1908. Younger stages were obtained from spores of *A. hirsuta* from material sent to Dr. CHAMBERLAIN from the Philippine Islands, and from those of *A. Phyllitidis*, which Dr. TRELEASE was kind enough to send from the Missouri Botanical Gardens. Spores were also received from Dr. BRITTON from the New York Botanical Garden, but cultures from these were not successful. For the identification of the specimens I am indebted to Dr. JESSE M. GREEMAN of the Field Museum of Natural History, Chicago.

Germination is somewhat slower than in Lygodium and does not take place till the seventeenth or nineteenth day. The rhizoid is first to protrude and the first prothallial cell follows, but the small cell between them does not emerge as it does in Lygodium. It is only when the filament and rhizoid have attained considerable length that it can be seen at all (*fig. 32*).

The filament does not broaden so early or in so regular a manner as in Lygodium. A spatulate and often irregular thallus is formed (*figs. 34, 35*), and within about ten days initials appear at the side (*fig. 36*). From the rapid division of these initials the thallus takes on the heart-shaped form, the lobes being unequal in size. In this case the larger lobe is the original thallus and the smaller lobe is the younger, as GOEBEL reports for Pteris (**11**, p. 205). In prothallia hitherto studied, this inequality is reported as persistent, but while this was true of *A. hirsuta*, it was not for *A. Phyllitidis*, the lobes of this species finally becoming of equal size, as they do in Lygodium. There is here further reason for agreeing with GOEBEL (**11**, p. 205) when he says, "I do not believe that one can construct a phyletic relationship between apical and lateral position of meristem; . . . . in different sections of the Filicineae both occur."

SEX ORGANS

Antheridia appear in about forty days and the points made in the case of Lygodium may be repeated here: The first wall is *not* always flat; instances are occasionally found of several cells in the stalk; and the sperm number (156) is large. The archegonia appear about ten days later, and have two neck canal nuclei, as do those in Lygodium.

Summary

SPORE COATS

The spores of Aneimia and of Lygodium have three distinct coats. The exine is formed first, and as it broadens its composition changes from cellulose, so that with safranin it stains red, and then red and yellow. The change may be from cellulose to suberin, which stains red, and then to suberin and pectin, as pectin stains yellow. The exine of *Aneimia hirsuta* has ridges on the outer surface.

The intine is the second coat formed, and is the one which covers the filament when it emerges from the spore. It remains a delicate cellulose wall.

The epispore is the last to form, and in both Aneimia and Lygodium is produced by the activity of the tapetal protoplasm. In Lygodium granules appear in the protoplasm, increase in size, and adhere to the exine. In *Aneimia hirsuta* spines are formed on the ridges of the exine. The protoplasm forms a thin sheet over these projections and over the intervening surface of the exine.

DEVELOPMENT OF THE THALLUS

The first wall of the spore does not separate the rhizoid and first prothallial cell, but the spore contents divide into two cells of unequal size, from the smaller of which the rhizoid is produced.

The apical cell of Lygodium is terminal, appears early, and is remarkably persistent. In Aneimia it appears later and is lateral.

The lobes of the heart-shaped thallus are at first unequal. In *Aneimia hirsuta* this inequality is permanent, but in *Aneimia Phyllitidis* and in Lygodium the lobes become later of the same size.

SEX ORGANS

The general course of development in both antheridia and archegonia does not differ from that in the Polypodiaceae.

The first wall of the antheridium is not, as reported, always flat, but may be so concave as to touch the basal wall.

The number of sperms is large.

The archegonia have two neck canal nuclei.

Conclusions

There is nothing in the formation of the antheridium or in the unequal lobing of the prothallium that can be considered characteristic of the genera.

The fact that the rhizoid is not produced as a result of the first division of the spore has not yet been reported for other Filicales, and may possibly be peculiar to the Schizaeaceae.

The large number of sperms produced, the occasional stalk of the antheridium, and the frequent occurrence of two prothallial filaments from the spore, are characters which would place the Schizaeaceae with the more primitive families of the Filicineae.

I wish to express my thanks to Dr. JOHN M. COULTER, at whose suggestion this work was undertaken, and to Dr. CHARLES J. CHAMBERLAIN for his kind direction and criticism.

THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES X AND XI

Reference letters: *a*, rhizoid; *e*, epispore; *ex*, exine; *g*, granules which form epispore; *i*, intine; *n*, nucleus; *p*, *p′*, prothallial cells; *r*, red portion of exine; *y*, yellow portion of exine.

PLATE X

Lygodium circinatum

Fig. 1.—Tetrad. ×1050.

Fig. 2.—Portion of spore wall and tapetal protoplasm with granules and nucleus. ×1050.

Fig. 3.—Later stage in the formation of granules. ×1050.

Fig. 4.—Portion of exine with granules adhering to form the epispore. ×1050.

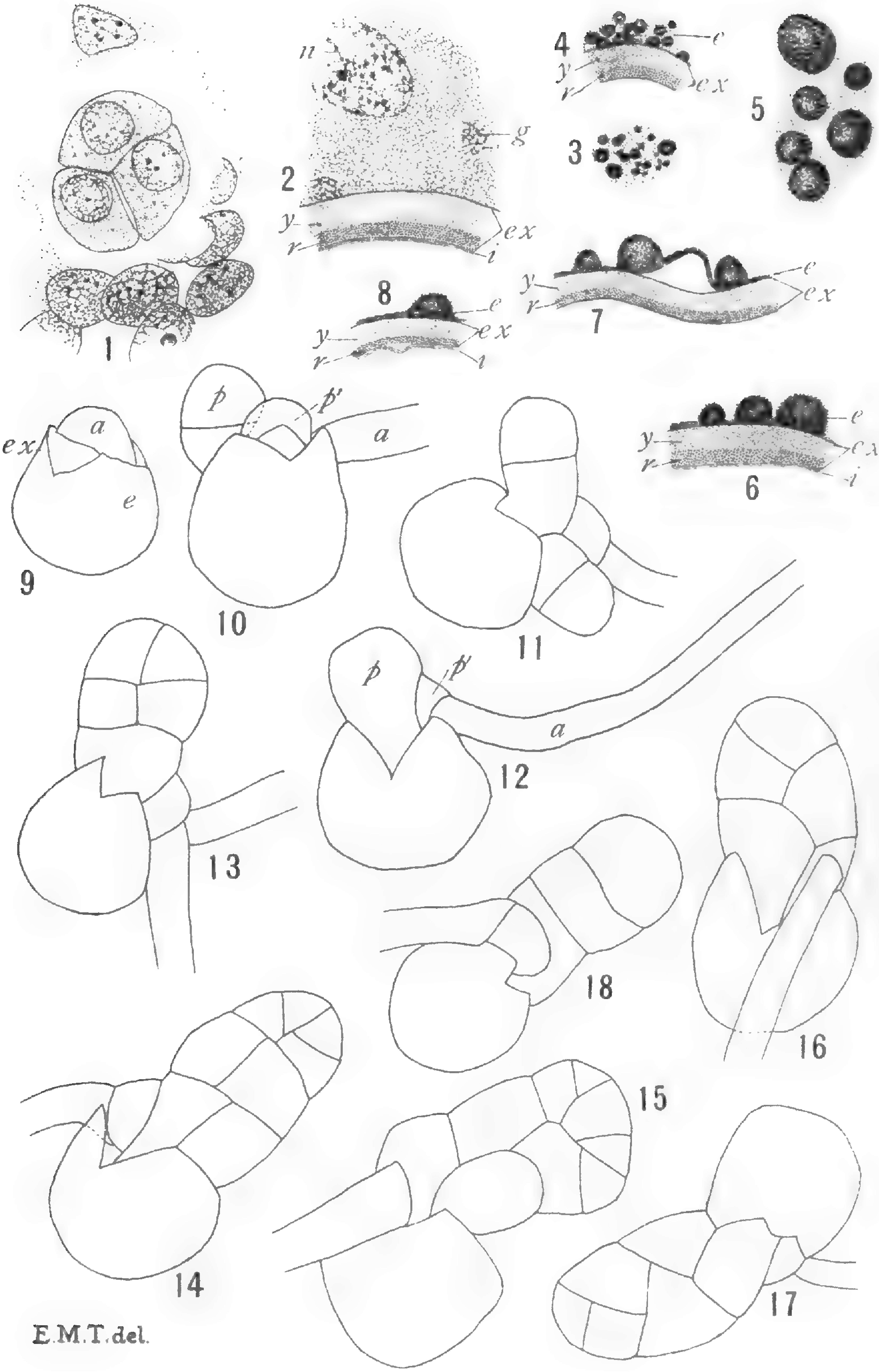
Fig. 5.—Appearance of granules and tapetal protoplasm when spores are mature, showing irregular size and distribution of granules. ×1050.

Fig. 6.—Portion of wall of mature spore, showing epispore with projections of varying size and irregular distribution. ×1050.

Fig. 7.—Portion of spore wall, showing epispore pulled away from the exine; but the view is oblique so that the epispore appears wider than it really is. ×1050.

Fig. 8.—Portion of spore wall with intine pulled away. ×1050.

Fig. 9.—Germination of spore showing rhizoid emerging. ×300.



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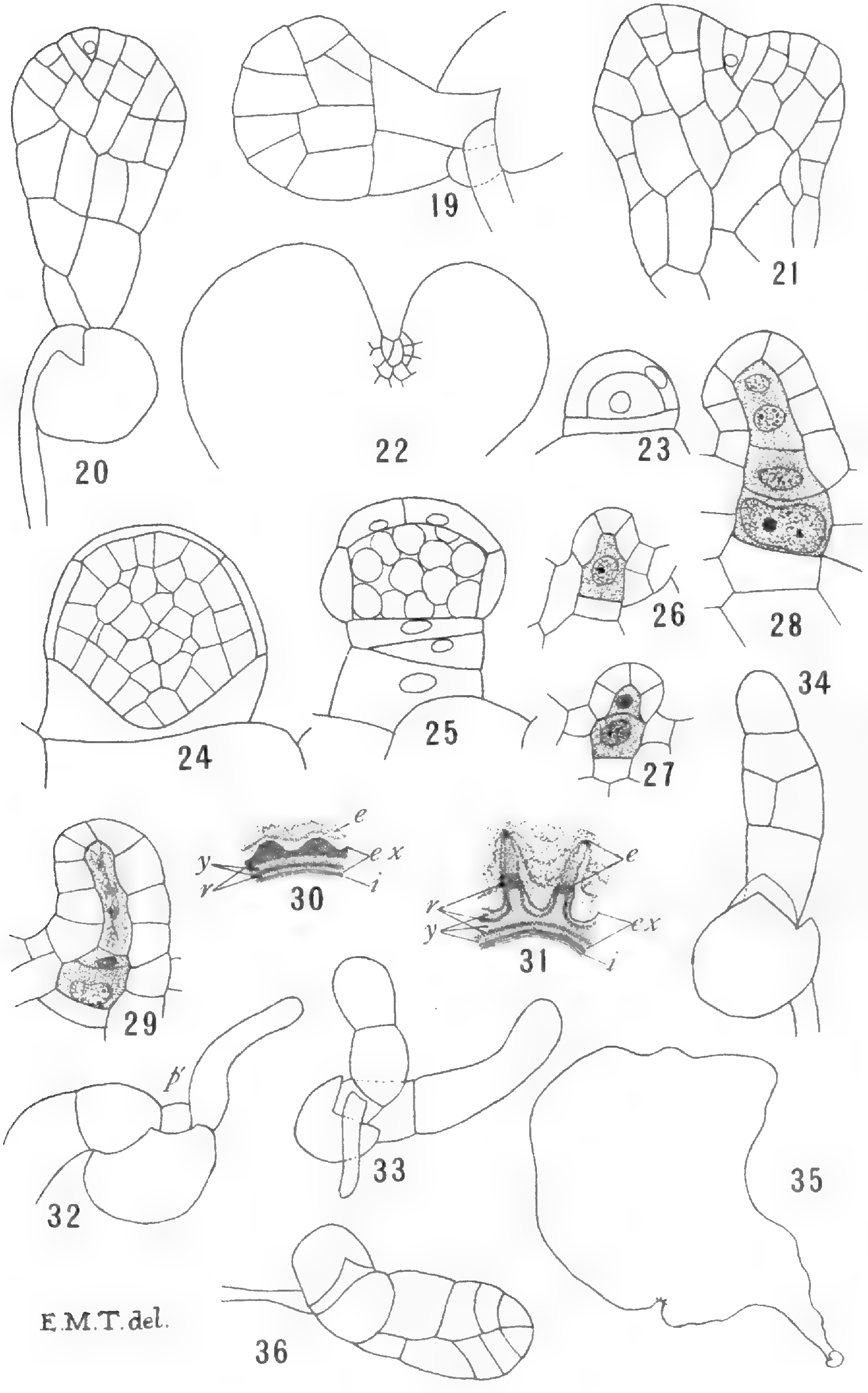
TWISS on PROTHALLIA



TWISS on PROTHALLIA

FIG. 10.—Later stage, showing two papillae (prothallial cells). ×300.

FIG. 11.—Two prothallial filaments coming from one spore. ×300.

FIG. 12.—Further stage, showing relation of prothallial cells and rhizoid. ×300.

FIGS. 13–15.—One method of development of thallus. ×300.

FIGS. 16, 17.—Same stages in thallus developed in another way. ×300.

FIG. 18.—Third way of developing the thallus. ×300.

PLATE XI

Lygodium circinatum

FIGS. 19–22.—Later stages in development of thallus, showing terminal position of apical cell, and in *fig. 22* the unequal size of the lobes. *Fig. 19*, ×300; *figs. 20, 21*, ×200; *fig. 22*, ×50.

FIG. 23.—Young antheridium with first wall flat. ×700.

FIG. 24.—Antheridium at mother cell stage, with first wall concave. ×700.

FIG. 25.—Antheridium with stalk. ×700.

FIGS. 26–28.—Development of archegonium. ×300.

FIG. 29.—Archegonium with remnants of four neck canal nuclei. ×300.

Aneimia hirsuta

FIG. 30.—Portion of spore wall. ×1050.

FIG. 31.—Later stage of same. ×1050.

FIG. 32.—Germination of spore. ×300.

FIG. 33.—Two prothallial filaments from one spore. ×200.

FIG. 34.—Development of thallus. ×300.

FIG. 36.—Still later stage showing lateral position of initials. ×200.

Aneimia Phyllitidis

FIG. 35.—Later stages of development of thallus. ×50.

THE STRUCTURE AND RELATIONSHIP OF URNULA GEASTER

F. D. HEALD AND F. A. WOLF

(WITH PLATE XII AND THREE FIGURES)

During the season of 1909 the writers found an interesting ascomycete growing abundantly in the vicinity of Austin, Texas. On attempting to identify the species it was traced to *Urnula geaster* Peck,[1] which was collected at Austin, in 1893, by Dr. L. M. UNDERWOOD and sent to Mr. C. H. PECK for identification, but the characters observed did not agree with PECK'S description in several important points. For this reason a package of fresh specimens was sent to Mr. PECK, who replied that they were the same as the original *Urnula geaster* which he had previously described, but that his description was lacking in a number of important points, since only dried specimens had been available for making the original diagnosis. This description has been corrected by Mr. PECK[2] in his recent report, in accordance with the examination of fresh specimens sent to him by the authors.

Since this fungus has recently been made the basis of a new genus, *Chorioactis*,[3] and the material used for the study consisted only of dried herbarium specimens, the careful study of its anatomy was undertaken to determine the validity of its separation from Urnula.

Habitat

The ascomata of *Urnula geaster* are found growing, either singly or in groups, from roots and portions of stumps of the small-leaved elm (*Ulmus crassifolia*) which are old and somewhat disintegrated. They may be clustered close to the base of the stump, or they may originate from the roots at some point distant from it. In all cases the stipe or stalk of the apothecium comes from a point 5–10^{cm} below the surface of the ground.

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[1] SACCARDO, P. A., Sylloge Fungorum **11**:422. 1895.

[2] PECK, C. H., Report of N. Y. State Botanist for 1908. pp. 31, 32. 1909.

[3] KUPFER, E. M., Bull. Torr. Bot. Club **29**:142. 1902.

According to the original description, the fungus was recorded as growing on the "ground"[4] (ad terram).[5] The writers have examined a large number of specimens in the field, and in every case a direct connection with subterranean roots could be established. The ease with which the stipe breaks from its point of attachment and also the depth of the roots in the soil may have been the cause of the original error in observation.

Structure

The brown septate hyphae grow over the surface of the decaying wood as a loose network, or become aggregated into strands or compact layers in intimate contact with the surface of the root.

Specimens of the apothecia have been collected in the cooler months, from October to April. Their appearance only during this portion of the year is undoubtedly due to the favorable conditions of moisture and temperature. The apothecia can generally be found in abundance following a short rainy season during the period mentioned. They begin their development, however, in May or June and grow slowly through the dry summer period, reaching maturity in the months mentioned above. This last observation was contributed by Professor W. H. Long, Amarillo, Texas, and has been confirmed by the writers.

The mature apothecium while still closed is rather thick club-shaped (*text fig. 1*), with a stalk or stipe shorter than the apothecial cavity or equaling it in length. While this is the typical form, specimens which originate from deep-lying roots may have much longer stipes; others growing from more superficial roots may be nearly sessile and rather globular in form (*text fig. 2*). The apothecia before dehiscence vary in diameter from 1.2 to 3.5^{cm} in the broadest portion, and in length from 4 to 12^{cm}. The stalk varies from 0.75 to 1.5^{cm} in diameter and is $1\text{–}5^{\mathrm{cm}}$ in length. The outer surface of the entire fructification is covered with a dense chocolate-brown tomentum. The cut surface of the stalk and wall is pure white, while the hymenial layer is yellowish white (28),[6] becoming with age light leather colored (8).[6] The fresh apothecia are of a soft leathery texture, becoming firmer with desiccation.

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[4] Peck, C. H., Report of N. Y. State Botanist **46**:39. 1893.

[5] Saccardo, P. A., *l. c.* 422.

[6] *Ibid.*, Chromotaxia. 1894.

As soon as the apothecium reaches maturity, the wall begins to show several longitudinal fissures, which ultimately separate the hymenial portion into 4–6 segments or rays (*text fig. 2*). These rays begin to curve outward as soon as they become separated at the tips, and may come to stand at right angles to the stipe (*text fig. 3*). This position of the rays gives the open apothecium a Geaster-like appearance. In the case of deep-seated apothecia, the rays do not become completely recurved, since their movement is partially prevented by contact with the surrounding soil.

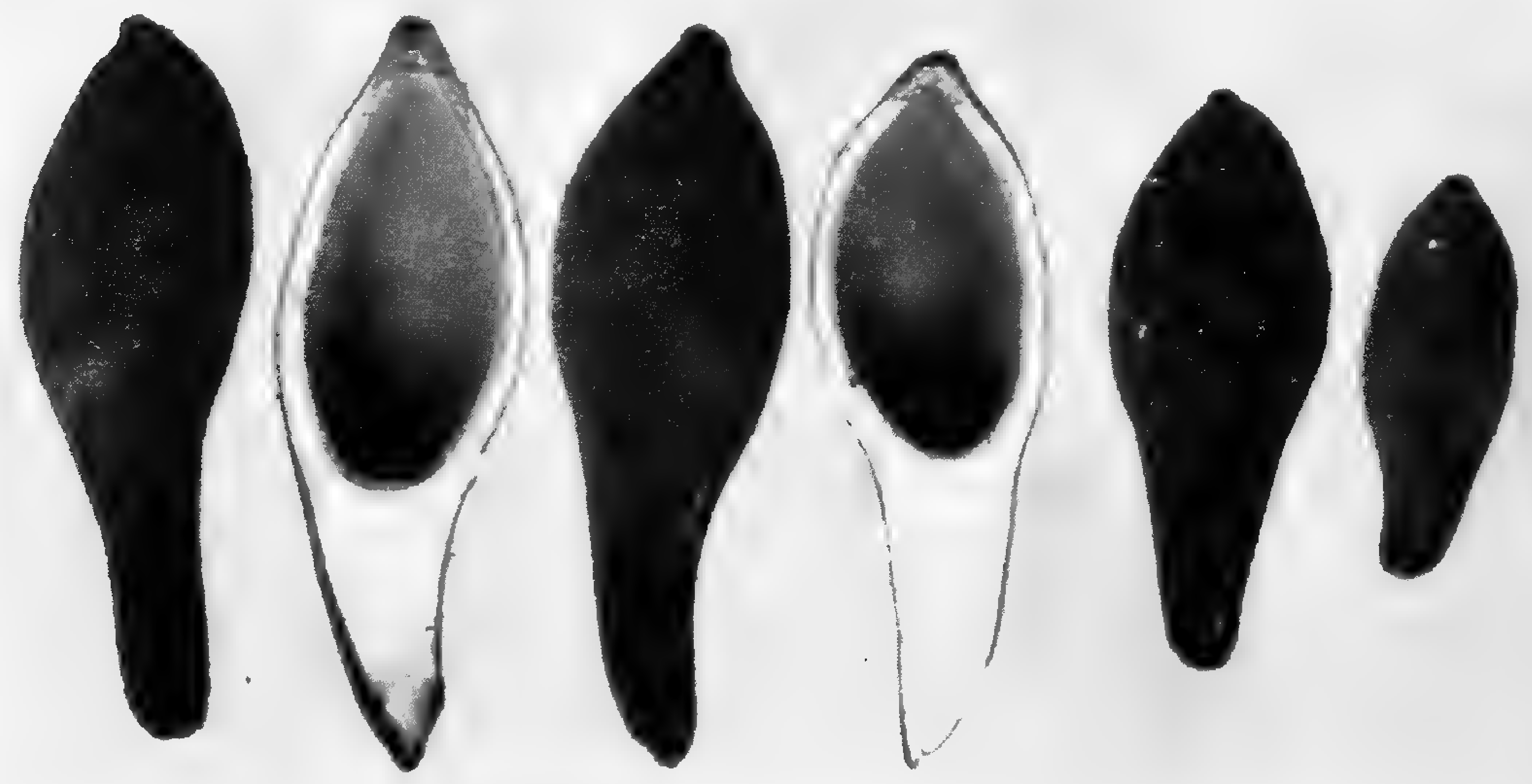

FIG. 1.—A series of ascomata of *Urnula geaster;* two of them bisected to show the extent of the apothecial cavity and the stipe.

Soon after the dehiscence of the apothecium, dustlike clouds of spores may be seen to rise in puffs from the exposed hymenial surface. This characteristic expulsion of the spores, together with the form and color of the fruiting structure, has secured for the fungus the popular name of the "devil's cigar." A somewhat similar expulsion of spores has been noted in various species of Peziza, Helvella, and Bulgaria.[7] The puffing of the spores is apparently due to loss of moisture, since mature open specimens show the characteristic puffing when removed from a damp chamber to air of the room. While this is probably

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[7] MASSEE, G., Textbook of Fungi 110. 1906.

the normal cause of the expulsion of the spores, the same phenomenon may be induced by the release of tension due to breaking the rays. After the spores have been expelled, the release of the tension in the hymenial surface causes the segments of the apothecium to be raised and curled inward (*text fig. 2*).

Fig. 2.—Apothecia of various forms, showing origin from roots and the manner of dehiscence.

The wall of the apothecium is thick, reaching 3.5^{mm} in many cases. The original description does not specify the thickness, while Kupfer[8] gives 2.5^{mm} as the extreme measurement. This difference may be explained easily by the fact that only dry material was available in all the previous studies.

The wall of the apothecium shows in section a region of brown hairs, about 0.1^{mm} in thickness, which is the cause of the brown tomentose exterior. Just below the hairy layer is a relatively narrow cortical zone made up of densely interwoven hyphae, while the remain-

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[8] Kupfer, E. M., Bull. Torr. Bot. Club **29**:143. 1902.

der of the wall consists of a loosely interwoven network of filaments which become denser and more closely aggregated in the hypothecial region. The wall, including cortical portion, medullary portion, and hypothecium, may be 2.5^{mm} in thickness, and the hymenium may be 0.75–0.85^{mm} in thickness. It should be noted in this connection that the apothecial wall is composed of distinct hyphae, and that they are never aggregated to form a pseudoparenchyma. This fact is directly opposed to the observations recorded by Kupfer,[8] stating that "the tissue is made up wholly of large parenchymatous cells." She even gives the measurements of these cells and they are also illustrated in the plate accompanying the paper. The size of these so-called parenchymatous cells agrees practically with our measurements of the intercellular spaces in the immature specimens as shown in *fig. 7*.

Fig. 3. Apothecia viewed from above, showing the Geaster-like appearance.

The erroneous observation mentioned above is without doubt due to the fact that the dry specimens, which were the only ones used, were not completely mature. Previous to the dehiscence of the apothecium the hyphae which make up the wall are very small in diameter, being about 1.5 μ. *Fig. 7*, which was drawn from fixed (chromacetic acid) and imbedded material from young specimens, might easily have been interpreted as representing a pseudoparenchyma. After the dehiscence of the apothecium, the hyphae constituting the wall enlarge rapidly to 3–6 times their diameter in young specimens, reaching a thickness of 4.5–9 μ (*fig. 8*). At this stage it would seem almost impossible for even the most careless observer to interpret the structure as a pseudoparenchyma, since the hyphae are so large that even in dried specimens they could not be mistaken for cell walls. Even in the most compact part of the subhymenium the hyphae and intercellular spaces are easily distinguished (*fig. 4*).

The asci are 700–800 μ in length and 14–17.25 μ in diameter. This is somewhat in excess of the measurements given for *Urnula craterium*,[9] the type specimen of the genus. The ascus is nearly uniform in diameter and shows a short characteristically curved basal portion. This character and the origin of the asci from the subhymenium is shown in *fig. 4*. The free end of the ascus is bluntly rounded and shows an apical pore which permits the rupture of the wall when the spores are expelled. The eight continuous hyaline spores are confined to the upper two-thirds of the ascus, and are arranged with their tips slightly overlapping, but in a single series. They are oblong-fusiform and distinctly flattened on one side, 54–68 μ long by 10–13 μ wide; each spore contains 3–5 prominent guttulae (*fig. 5*). Numerous branched septate paraphyses are present, which are uniform in diameter throughout (slightly less than 2 μ) and do not show a terminal enlargement as figured by KUPFER (*l. c. pl. 8. fig. 4*).

Systematic position and relationship

As a result of a comparative study of several species of Urnula and Geopyxis, KUPFER (*l. c.* 142) has made *Urnula geaster* Peck the type of the new genus Chorioactis. The basis for the separation is stated as follows: "That it is not an Urnula seems to me just as evident from its external appearance as from an examination of its tissues. A comparison of internal characters shows, however, that there is no possible relation with *Urnula craterium*. The tissue is

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[9] SACCARDO, P. A., Sylloge Fungorum **8**: 549. 1890.

made up wholly of large parenchymatous cells, those of the excipulum averaging 34 μ in diameter, those of the hypothecium 10–14 μ." In our study of the structure of *Urnula geaster* we have shown, by detailed examination of material fixed in chromacetic acid and stained with iron alum-hematoxylin, that the wall of the apothecium is not parenchymatous, but composed of distinct interlacing hyphae with prominent intercellular spaces. The supposed parenchymatous wall was the main character which separated *Urnula geaster* from *Urnula craterium*, the type of the genus. Since this supposed character was based entirely upon erroneous interpretation of the structure, there can be little ground for the establishment of a new genus. A comparison of some of the characters of *Urnula geaster* and *Urnula craterium* will indicate still further that there is little ground for this separation.

	Urnula craterium (Schw.) Fries	*Urnula geaster* Peck
Size................	3–7·5×7$^{\text{cm}}$	1·2–3·5×4–12$^{\text{cm}}$
Asci................	400–500×14–15 μ	700–800×14–17·25 μ
Spores..............	23·33×8–13 μ	54–68×10–13 μ
Consistency..........	Leathery	Leathery
Wall of apothecium	Interlacing hyphae	Interlacing hyphae

The agreement of our specimens with *Urnula craterium*, the type of the genus as established by FRIES, makes impossible any separation of the species under discussion from the genus Urnula. Therefore the original name of *Urnula geaster*, as given by PECK, should be retained.

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EXPLANATION OF PLATE XII

FIG. 1.—Portion of cross-section of the apothecium, showing the different layers. ×15.

FIG. 2.—A single ascus with branched paraphysis. ×83.

FIG. 3.—A single ascus, showing the position of spores. ×330.

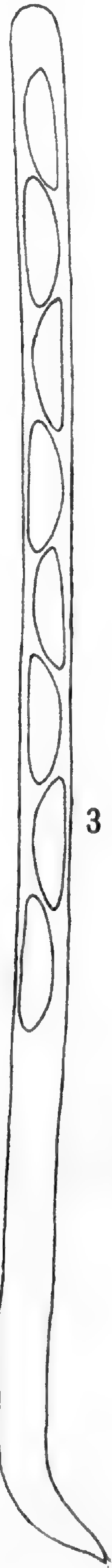
FIG. 4.—Origin of paraphyses and asci from the subhymenium. ×330.

FIG. 5.—A single spore showing empty spaces from which the reserve food in the form of oil has been dissolved. ×330.

FIG. 6.—Tip of ascus showing apical pore. ×660.

FIG. 7.—Interlacing hyphae from the wall of the apothecium preceding dehiscence. ×330.

FIG. 8.—Interlacing hyphae from the wall of a mature open apothecium. ×330.



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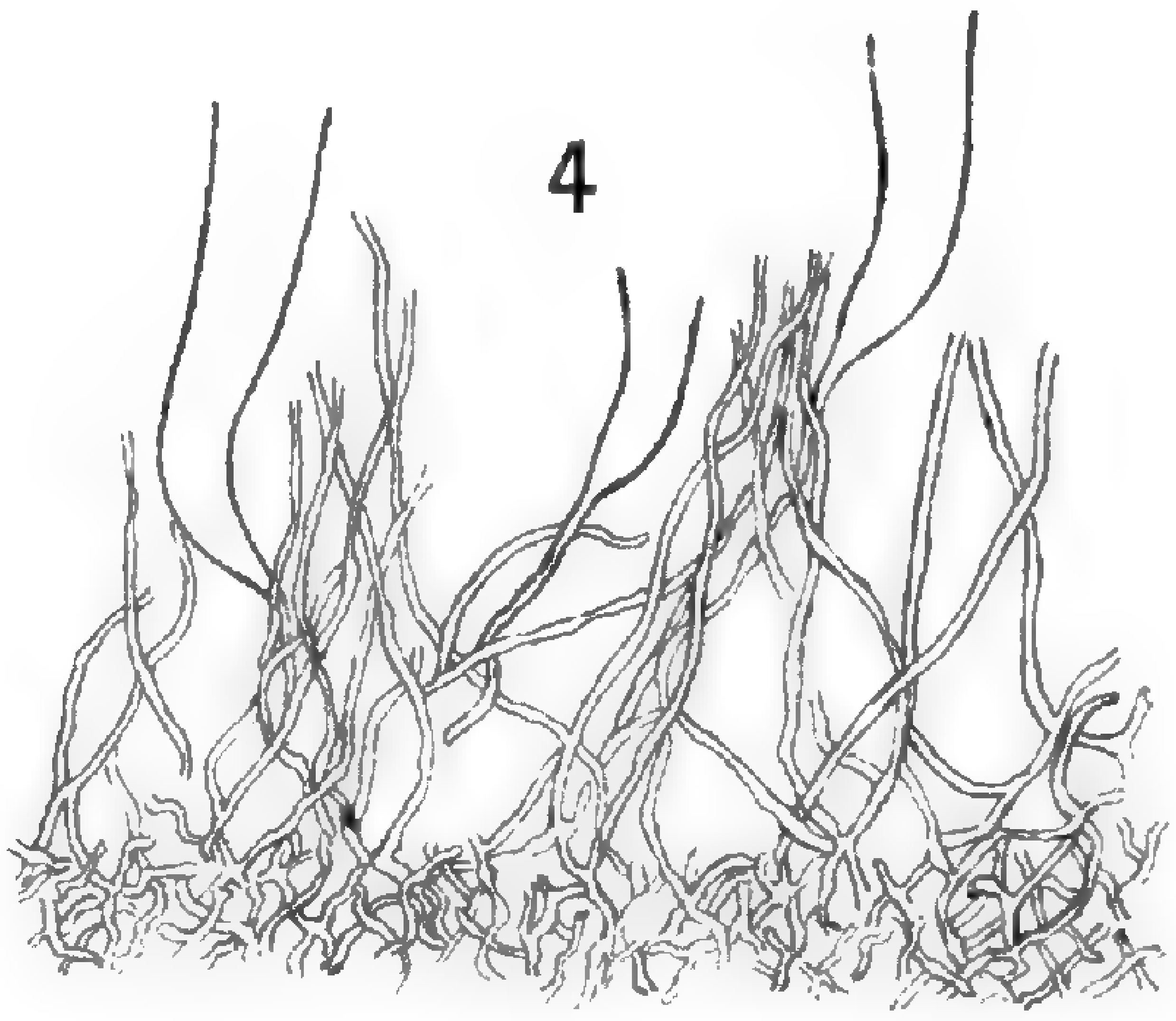

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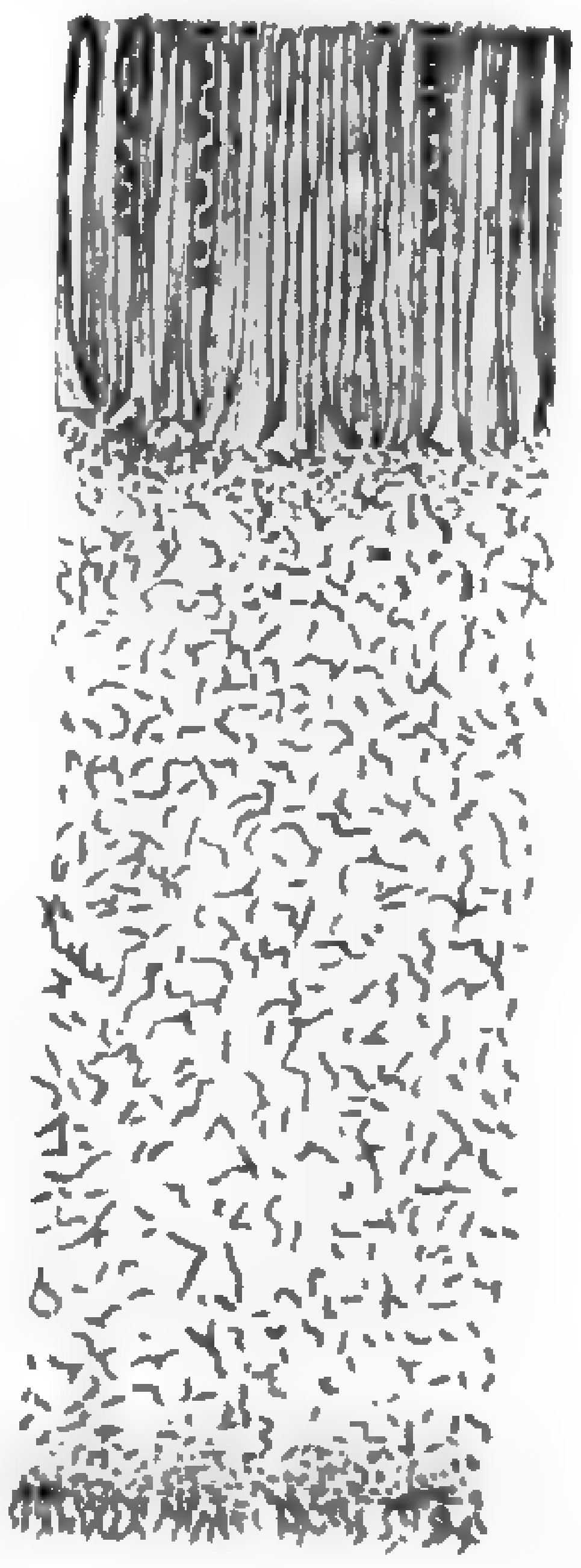

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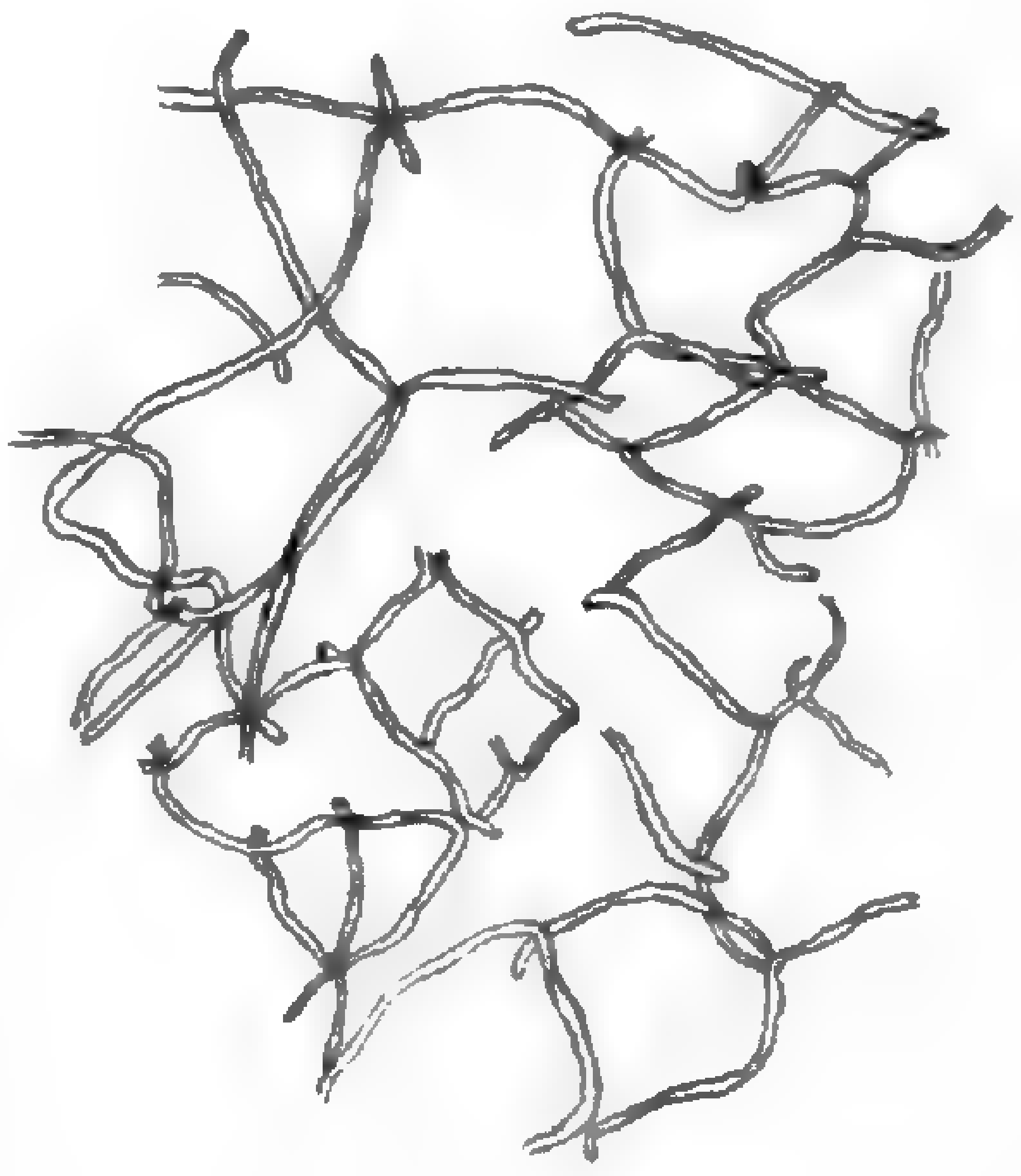

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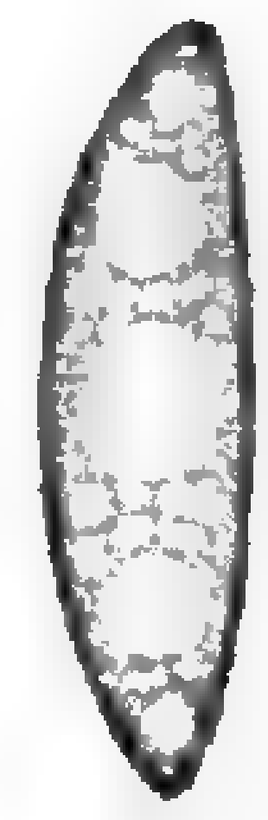

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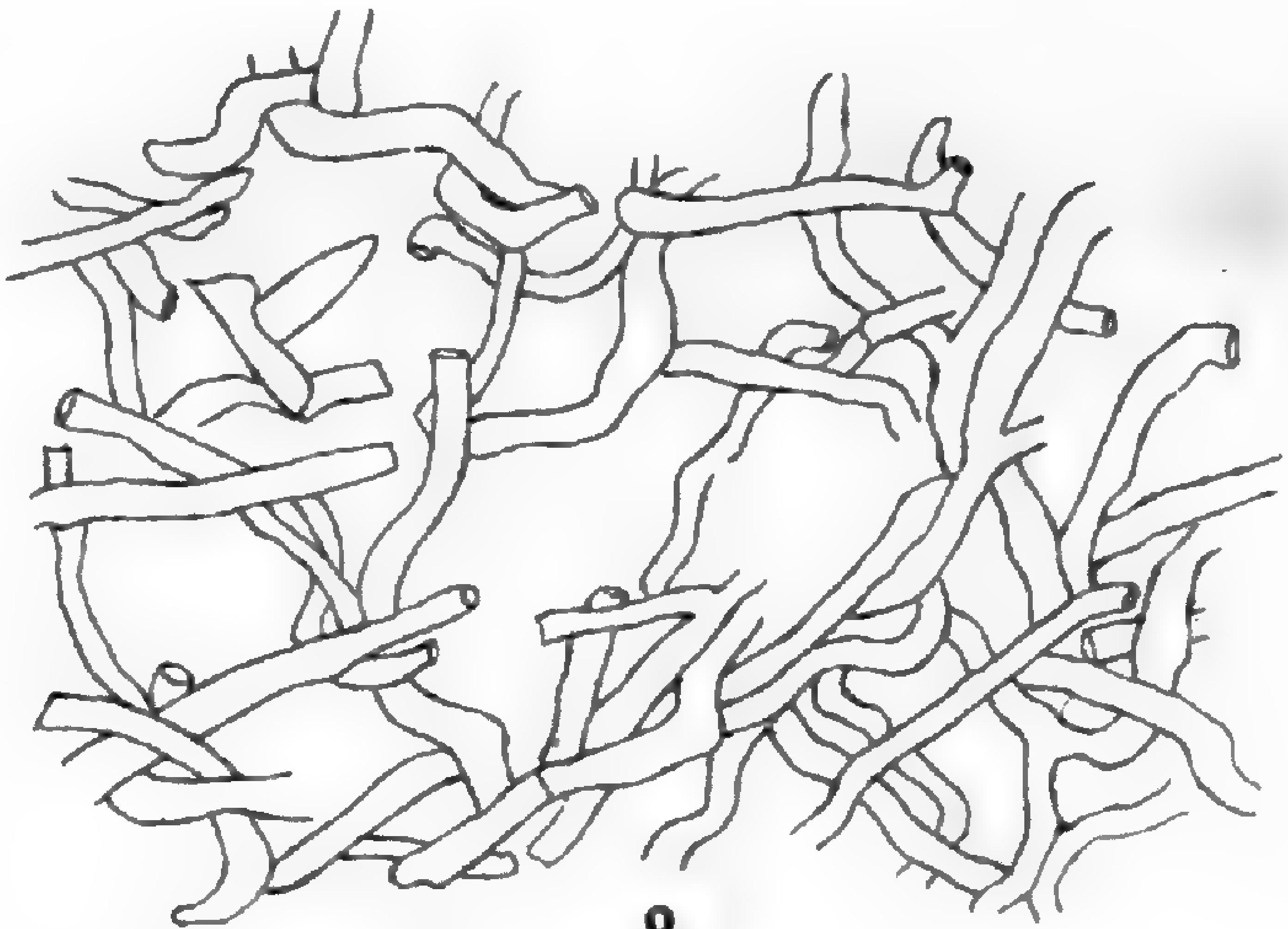

8

HEALD and WOLF on URNULA

THE EXCHANGE OF MATERIAL BETWEEN NUCLEUS AND CYTOPLASM IN PEPEROMIA SINTENISII[1]

WILLIAM H. BROWN

(WITH PLATE XIII)

In describing the development of the embryo sac of *Peperomia sintenisii*, the writer showed that at the time of the fusion of the sexual nuclei globules of cytoplasm were taken into the fusion nucleus. This phenomenon was not studied in detail at that time, but seemed to be worthy of further study, as it offered the possibility of throwing some light on the relation between cytoplasm and nucleoplasm. For the investigation of this problem material which had been fixed in chromacetic acid was cut 10 μ thick and stained with Flemming's triple or Haidenhain's iron alum-hematoxylin and eosin.

As the male nucleus of *Peperomia sintenisii* approaches the egg, just before fusion, both nuclei come to have cup-shaped depressions in the sides facing each other (*figs. 1–5*); the other parts of the nuclei, however, have a fairly regular shape. The depressions in the two nuclei may correspond closely to each other (*figs. 2, 3*), or they may not (*figs. 1, 5*). The number of depressions is also variable in different nuclei, there being one in each nucleus in *figs. 1, 2*, two in *fig. 3*, while *figs. 4* and *5*, which were taken from the same pair of nuclei, show three depressions in each nucleus. When the two nuclei come together, the nuclear membranes disappear where the nuclei touch each other, but remain intact around the depressions, the cytoplasmic contents of which appear as vesicles within the nucleus (*figs. 6–18*). *Fig. 6* shows a case in which one vesicle is caught in the nucleus while two others are probably in the process of being inclosed. *Fig. 7* shows one vesicle inclosed in the nucleus and another nearly inclosed. The number and size of the vesicles, like the depressions giving rise to them, are variable (*figs. 8–18*). When the cytoplasm is first inclosed in the vesicle, it takes the usual cytoplasmic stains (*figs. 7–9*), but it gradually stains less and less until the vesicles are distinguishable from the clear nuclear sap only by the membranes which

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[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, No. 11.

surround them. *Figs. 10–18* show various stages in the disappearance of the staining reaction in the cytoplasmic vesicles. In *figs. 10* and *11* there is a trace of stain; in *figs. 12–14* there is no stain in one of the vesicles; while *figs. 15–18* show vesicles the contents of which are indistinguishable from the surrounding clear nuclear sap. Shortly after this stage the membranes around the vesicles begin to break down and disappear (*figs. 19, 20*).

The phenomenon just described seems to be a constant characteristic of fertilization in *Peperomia sintenisii*, as no fusions were observed in which cytoplasm was not taken into the nucleus, although more than 50 nuclear fusions of this stage were studied. That the phenomenon is not due to shrinkage in fixing is shown by the regular appearance of the other nuclei in the sac, as well as of all parts of the sexual nuclei except the sides facing each other at the time of fusion. This view is confirmed by the further development, when by focusing the vesicles can be seen to be completely inclosed within the nucleus. This is shown in *figs. 12, 13*, and *15*, where one nucleolus is below and the other above the vesicle.

The growth of any nucleus must be at the expense of material obtained from the cytoplasm, and so it is evident that some material must pass from the cytoplasm to the nucleus. The phenomenon just described, where a vesicle of cytoplasm becomes nucleoplasm, seems to show that all of the essential constituents of cytoplasm may be changed into nucleoplasm.

The presence of the cytoplasmic vesicle within the nucleus gives the nucleus a greater surface for the intake of cytoplasm and this may be of advantage to it at this stage.

The membrane around the cytoplasmic vesicle did not disappear, however, before the cytoplasm seemed to be changed to nucleoplasm. This supports LAWSON's conclusion that the nuclear membrane is formed by the cytoplasm coming into contact with the nuclear sap, for the membrane here as in other fusing nuclei disappears, probably by absorption, when nucleoplasm is on both sides of it. LAWSON bases his conclusion on the fact that in the reorganization of nuclei the nuclear membrane appears at the time that the clear nuclear sap appears outside the chromosomes and in contact with the cytoplasm. The same thing appears to be true in the case of *Peperomia sintenisii*

(Brown '08). It is not necessary to assume that the process is a simple chemical precipitation, because it may be a physiological response.

The question now arises as to what happens when the nuclear membrane disappears during prophase. In *Peperomia sintenisii* the incipient spindle fibers form a dense felt over the nucleus before the membrane disappears. The appearance of spindle fibers before the disappearance of the nuclear membrane has been described in Lilium, Podophyllum, and Helleborus (Mottier '97), Equisetum (Osterhout '97), Cobea and Gladiolus (Lawson '98, '00), Pellia and Anthoceros (Davis '99, '01), Lavatera (Byxbee '09), Osmunda (Smith '00), Larix (Allen '03), and a number of other genera. In *Peperomia sintenisii*, as in a number of other forms, the appearance of the cytoplasm around the nucleus is at this stage quite different from what it was before the appearance of the fibers, and the disappearance of the membrane may be connected with this change of the cytoplasm.

When the cytoplasmic vesicle in *Peperomia sintenisii* becomes nucleoplasm, the question arises as to whether the cytoplasm has passed into the nucleus and nucleoplasm into the vesicle, or whether the cytoplasm is changed while in the vesicle. If, as seems probable, the nuclear membrane is formed by the interaction of the nuclear sap and the cytoplasm or some part of the cytoplasm, it seems evident that that part of the cytoplasm which participates in the formation of the membrane could not pass through the membrane, because, if it did, on coming into contact with the nucleoplasm it would only thicken the membrane. This does not mean, however, that no substances can pass from the nucleus to the cytoplasm or from the cytoplasm to the nucleus. It seems evident, however, that in *Peperomia sintenisii* the cytoplasmic vesicle, on account of its position, is converted into nucleoplasm through the activity of the nucleus, for there is no more reason for thinking that this part of the cytoplasm would change itself than there is for thinking that all of the cytoplasm would do the same thing. Then since the cytoplasm cannot pass unchanged into the nucleus, it is probable that some substance passes out into the cytoplasm and changes the cytoplasm in such a way that it may then be taken into the nucleus. It is not likely that this method of exchange is confined to this particular case, but since all of the essential constituents of protoplasm go into the nucleus of *Peperomia sintenisii*, it seems probable that the same thing happens in other organisms, and that this is rendered possible, as is probably the case in *P. sintenisii*, by the action of some substance or substances which continually pass out of the nucleus and cause a change in the cytoplasm.

It may be that the previously mentioned change of the cytoplasm around the nucleus, just before division, is connected with the accumulation, outside the nucleus, of the substance which has passed from the nucleus; and that the disappearance of the nuclear membrane is connected with a change of the cytoplasm causing a suspension of the reaction between the cytoplasm and nucleoplasm. The disappearance of the membrane might then be by absorption, analogous to the absorption of the nuclear membrane between two fusing nuclei. The substances which made possible this absorption, by accumulating outside the nucleus, would probably not be the same as those which, by reacting with the cytoplasm, caused the formation of the nuclear membrane. On the other hand, it seems not improbable that during division the nuclear sap loses its power of reacting with the cytoplasm, for it may become mixed with the cytoplasm or form a definite part of the cytoplasm, as in the maturation of certain animal eggs.

At the division of a cell of *Peperomia sintenisii*, as in other plants, the nuclear sap and nucleolus are lost in the cytoplasm; and so it is evident that nucleoplasm may also become a part of the cytoplasm. In many animals the clear substance which passes from the nucleus at maturation goes to form a special part of the embryo, and the passing of nucleoplasm to the cytoplasm has been considered as a method by which the chromosomes influence the development and activities of an organism. The observations on *Peperomia sintenisii* seem to show that some substance or substances are being constantly passed from the nucleus to the cytoplasm, and this may also be a means by which the nucleus controls the activities of the cell. The control of the cytoplasm by the "resting" nucleus seems to be well illustrated in the formation of the blepharoplast of Derbesia (DAVIS **'08**). Here radiations pass from the nucleus out to the cell wall, and at the ends of these radiations granules which fuse to form the blepharoplast are laid down.

Summary

At fertilization in *Peperomia sintenisii* globules of cytoplasm surrounded by a nuclear membrane are inclosed in the fusion nucleus. The cytoplasm globule gradually assumes the appearance of nuclear sap, after which the membrane around it disappears.

This phenomenon seems to show that all of the essential constituents of cytoplasm can be changed to nucleoplasm.

The appearance of a nuclear membrane when cytoplasm and nuclear sap meet, and the absorption of the membrane when nucleoplasm is on both sides of it, seem to show that the nuclear membrane is formed by the interaction of cytoplasm and nuclear sap.

If the membrane is formed in the above manner, it is probable that the contents of the cytoplasmic vesicle could not be changed to nucleoplasm by a gradual exchange of material between the nucleus and cytoplasm, for all of the constituents of the cytoplasm could not pass through the membrane, because some would react with the nucleoplasm and thicken the membrane. Since, however, the cytoplasmic contents of the vesicle are changed, this change is probably due to some substance which has come from the nucleus.

It is probable then that cytoplasm before being taken into a nucleus is changed by some substance which has passed from the nucleus, because it is not likely that *Peperomia sintenisii* differs from other organisms in such a fundamental activity of protoplasm.

The passage of substance from the nucleus is probably continual and may be a means by which the "resting" nucleus controls the cytoplasm.

The material, which made these observations possible, was collected in Jamaica by Professor D. S. Johnson, to whom the writer is greatly indebted.

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EXPLANATION OF PLATE XIII

All drawings were made with the aid of a camera lucida, using a No. 8 ocular and a 1.5^{mm} objective.

Fig. 1.—Male and female nuclei of *Peperomia sintenisii* approaching each other; each nucleus shows one depression in side facing the other.

Fig. 2.—Later stage of same.

Fig. 3.—Male and female nuclei in contact; each shows two depressions.

Figs. 4, 5.—Two sections through same pair of nuclei, each of which contains three depressions.

Fig. 6.—Early stage of fusion; nuclear membrane has disappeared where nuclei have come into contact with each other, causing the entire inclosure of one and partial inclosure of two other cytoplasmic globules.

Fig. 7.—About same stage as *fig. 6;* one globule entirely, another partially inclosed.

Fig. 8.—Fusion nucleus containing one vesicle of cytoplasm surrounded by a nuclear membrane.

Fig. 9.—Fusion nucleus containing two vesicles of cytoplasm.

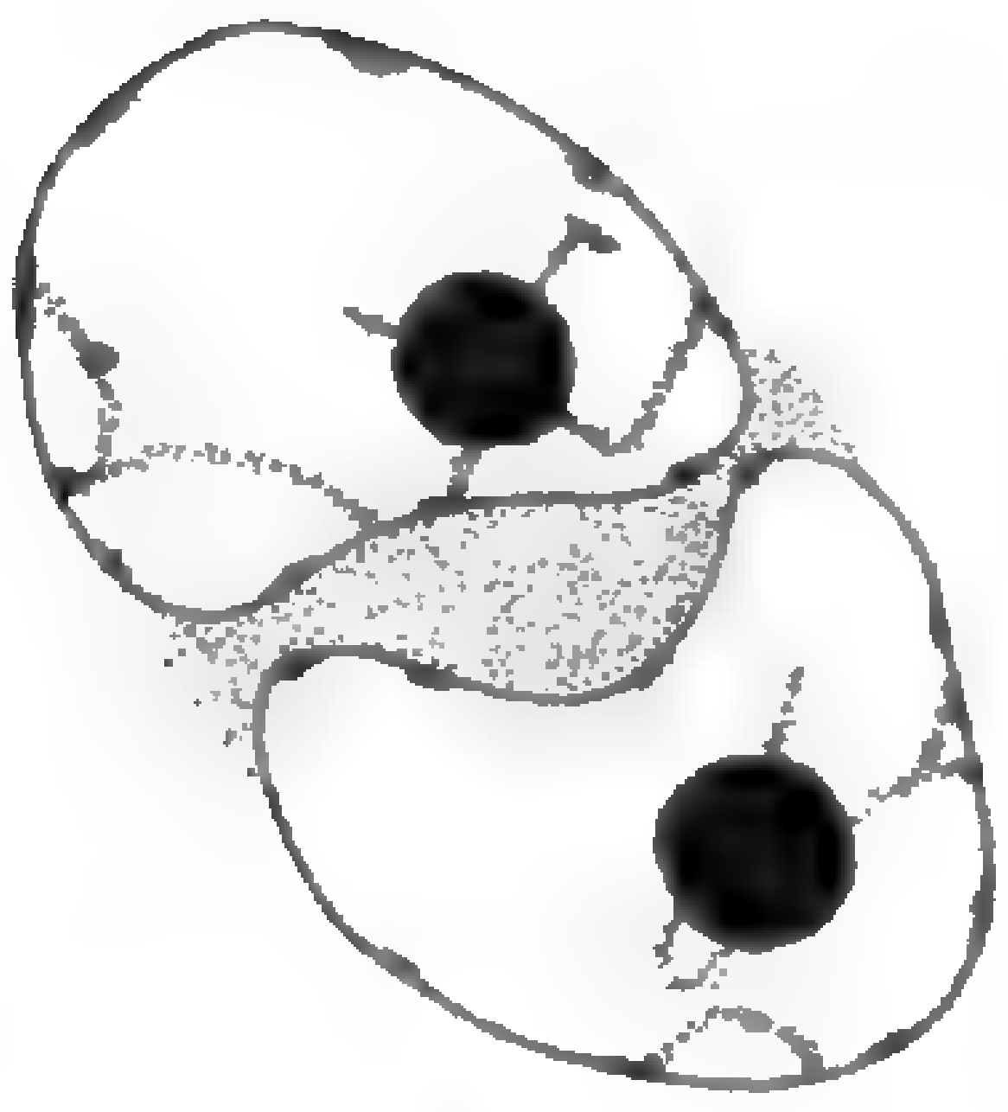
Figs. 10, 11.—Later stages; the cytoplasm stains less densely.

Figs. 12–14.—Still later stage; the staining reaction of cytoplasm has completely disappeared from one of the vesicles.

Figs. 15–18.—The contents of the vesicles are indistinguishable from the surrounding clear nuclear sap.

Fig. 19.—The membrane around the vesicle is beginning to disappear.

Fig. 20.—Later stage in the disappearance of the membrane around the vesicle.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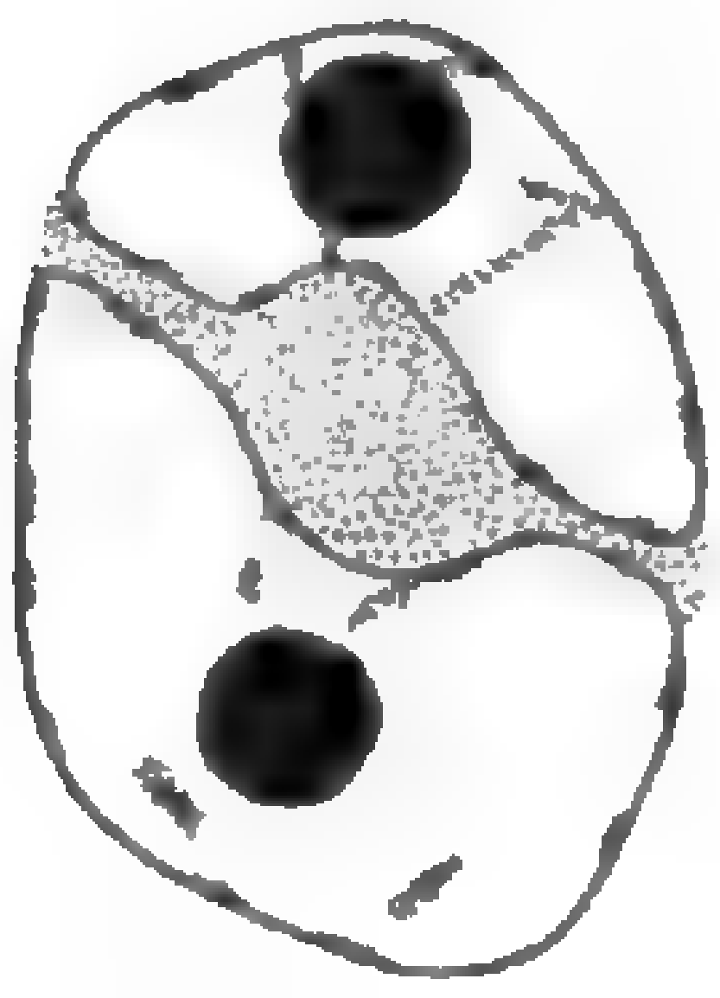
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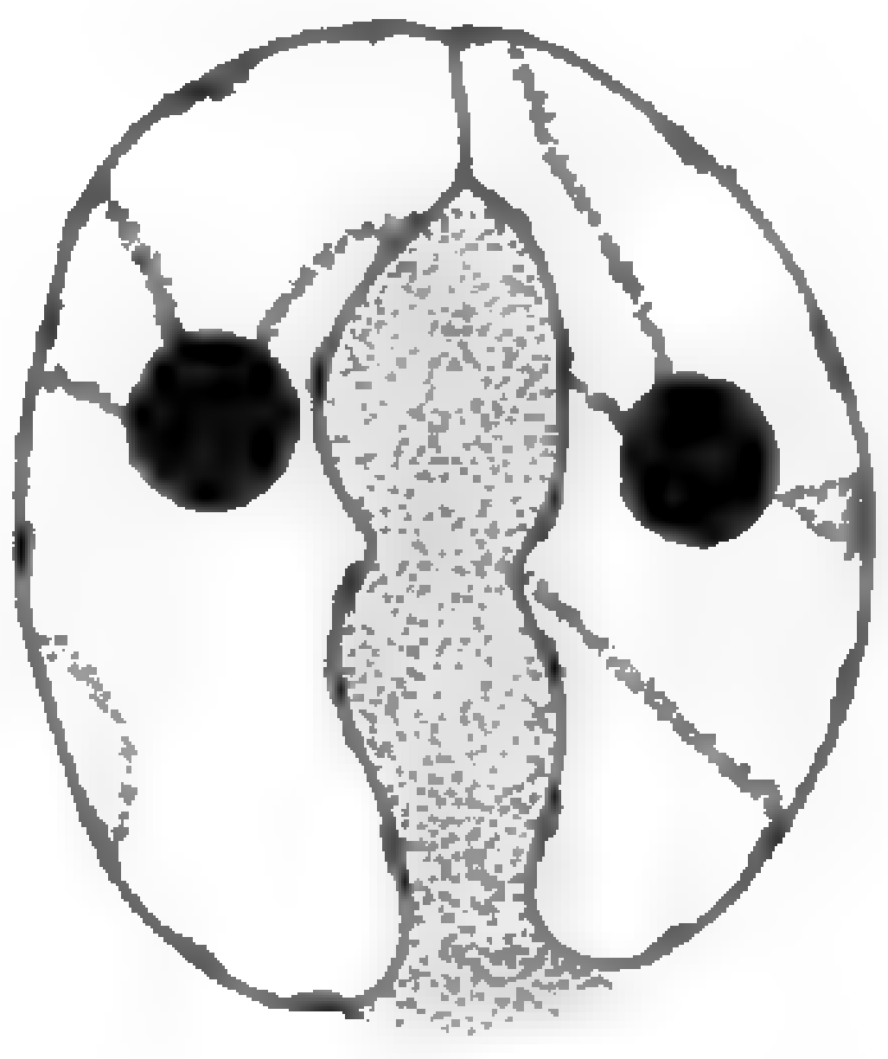
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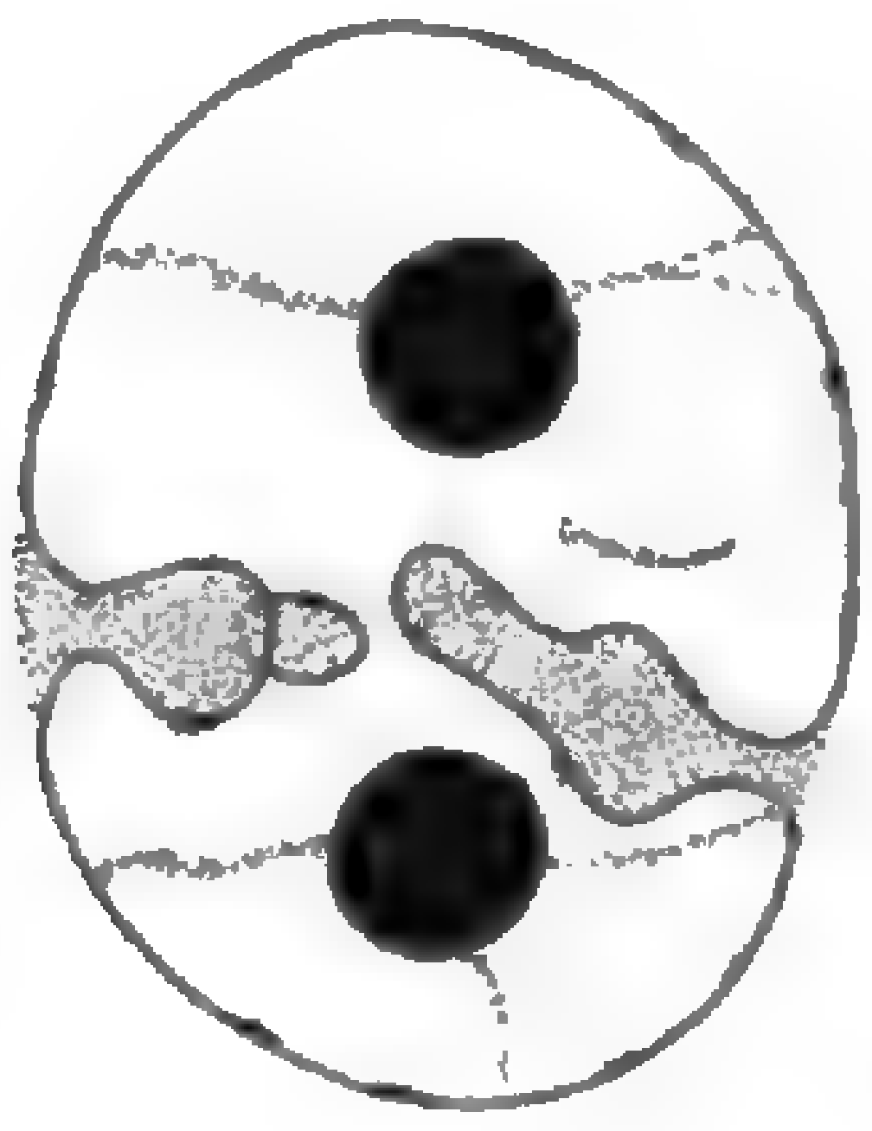
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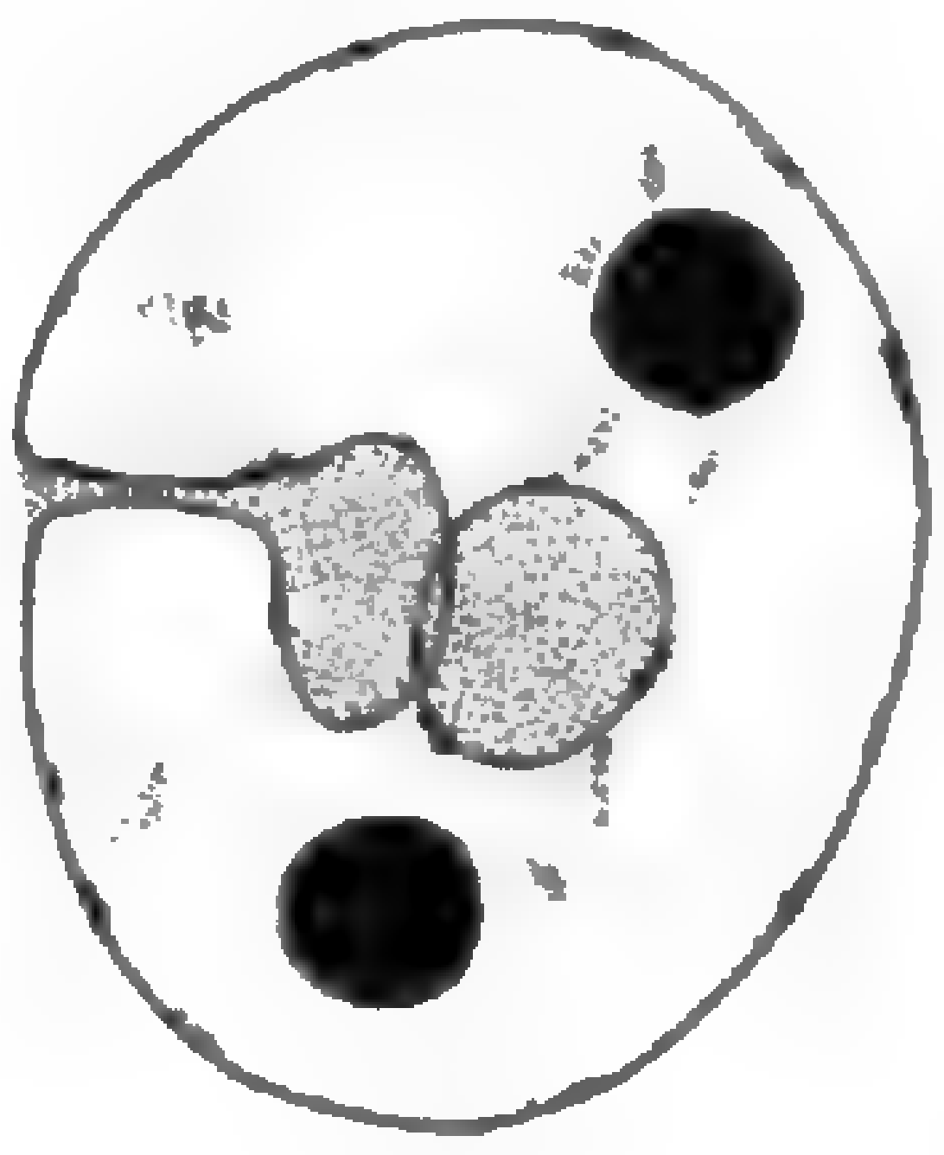
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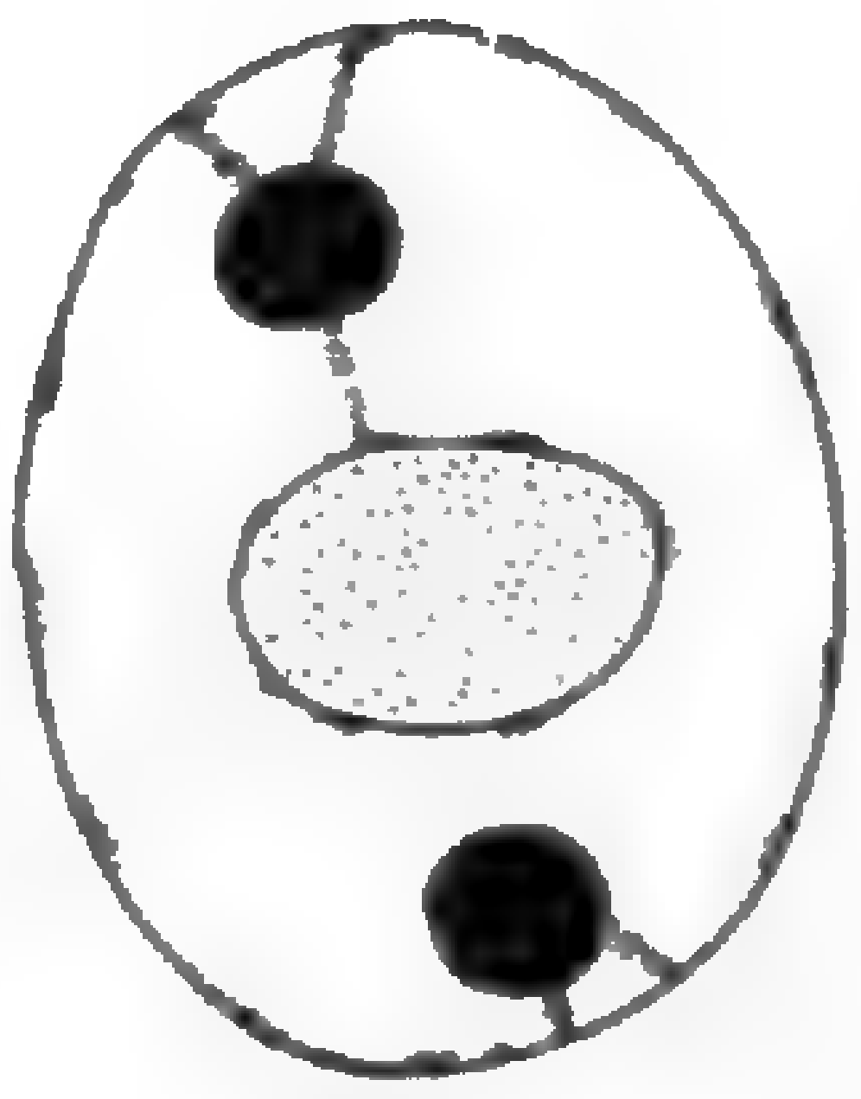
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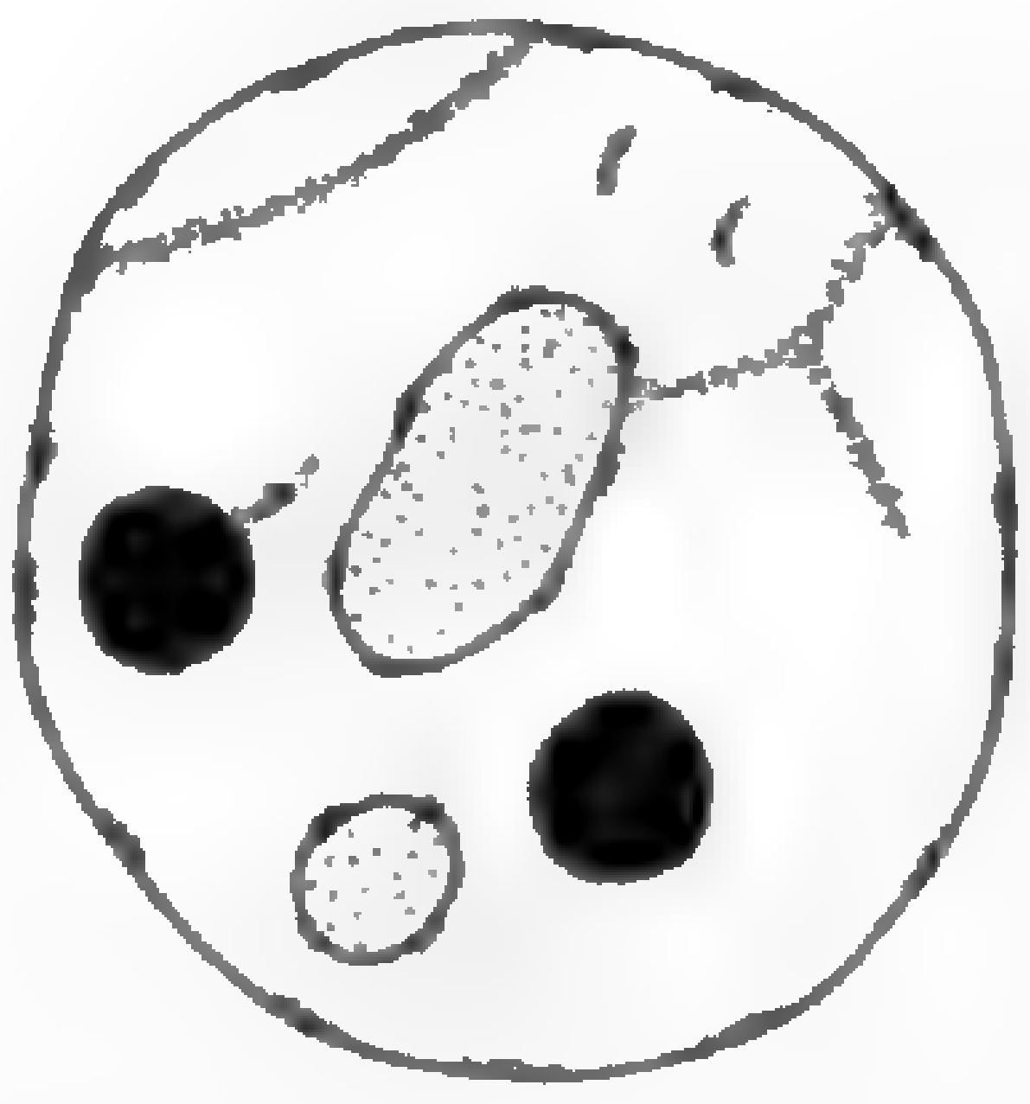
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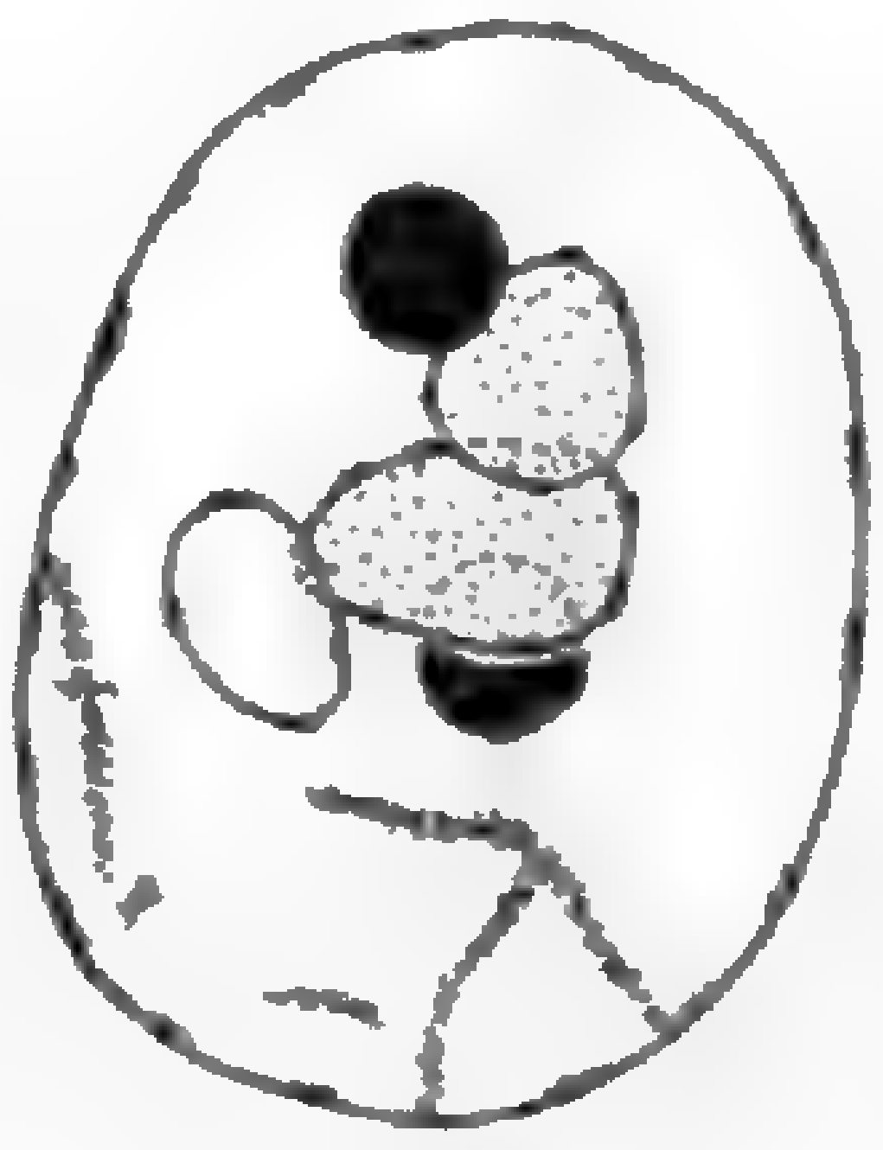
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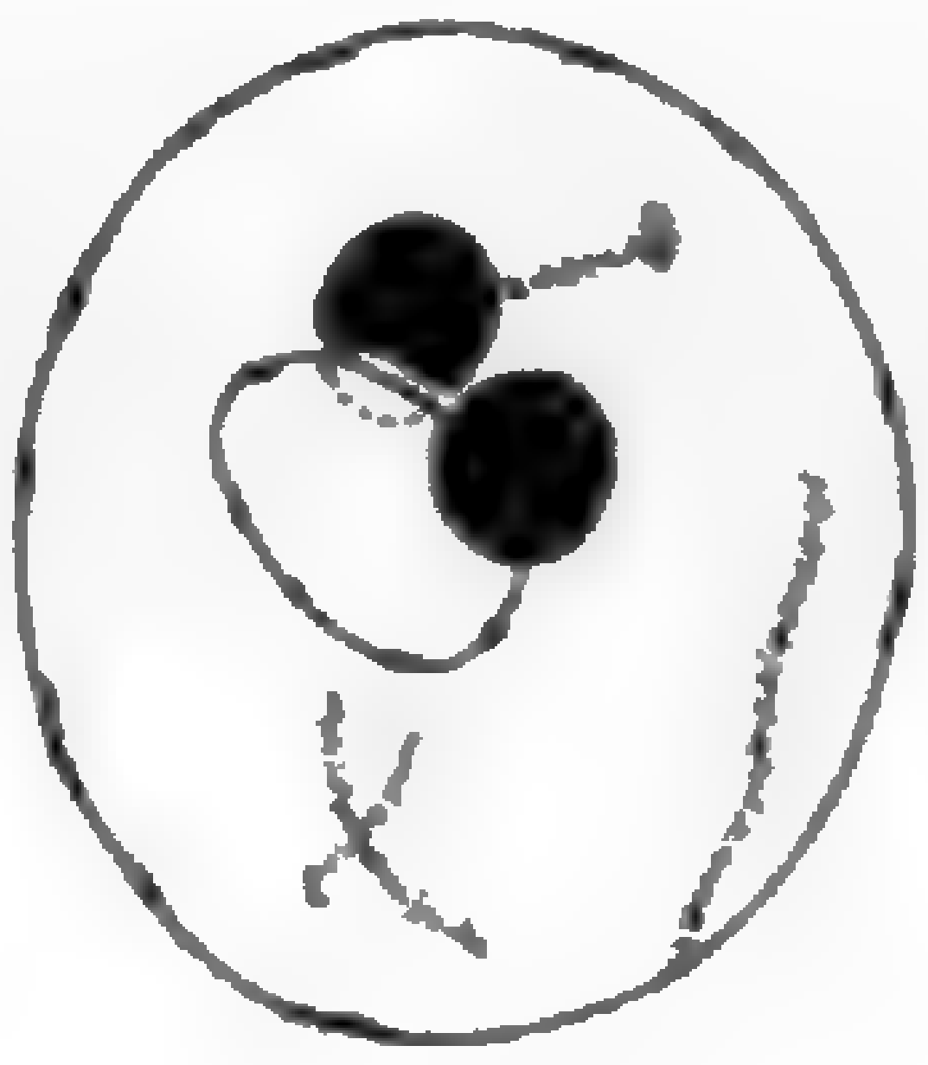
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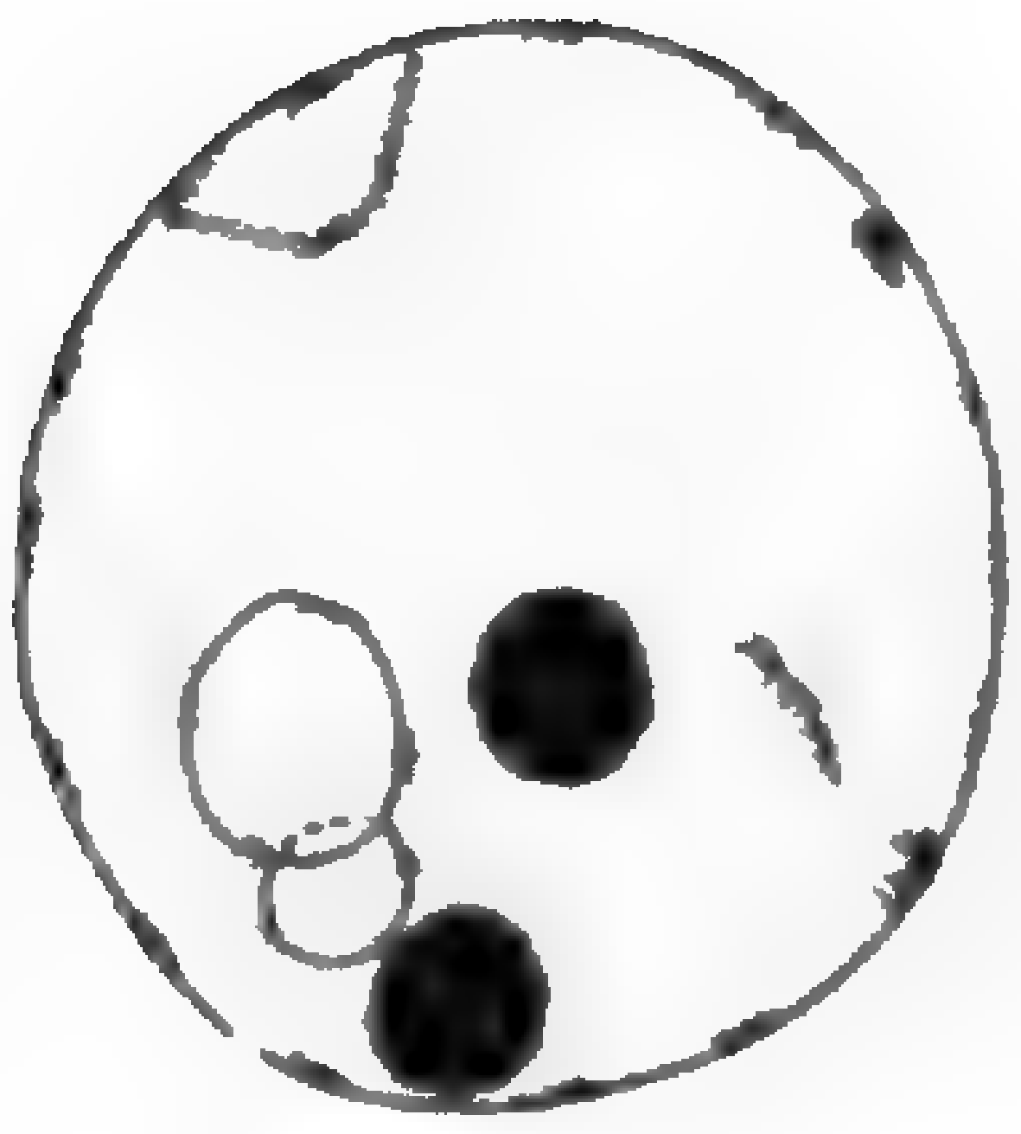
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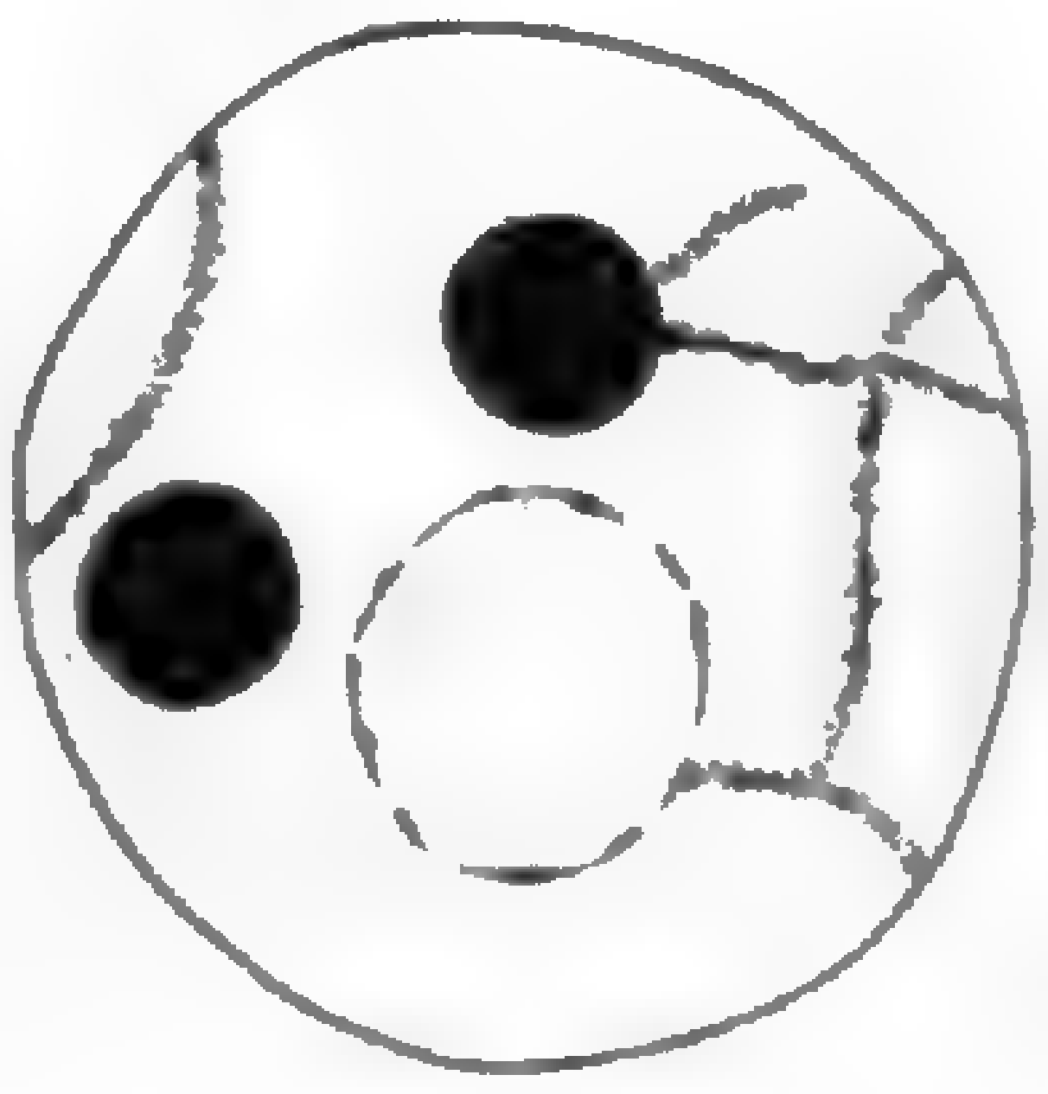
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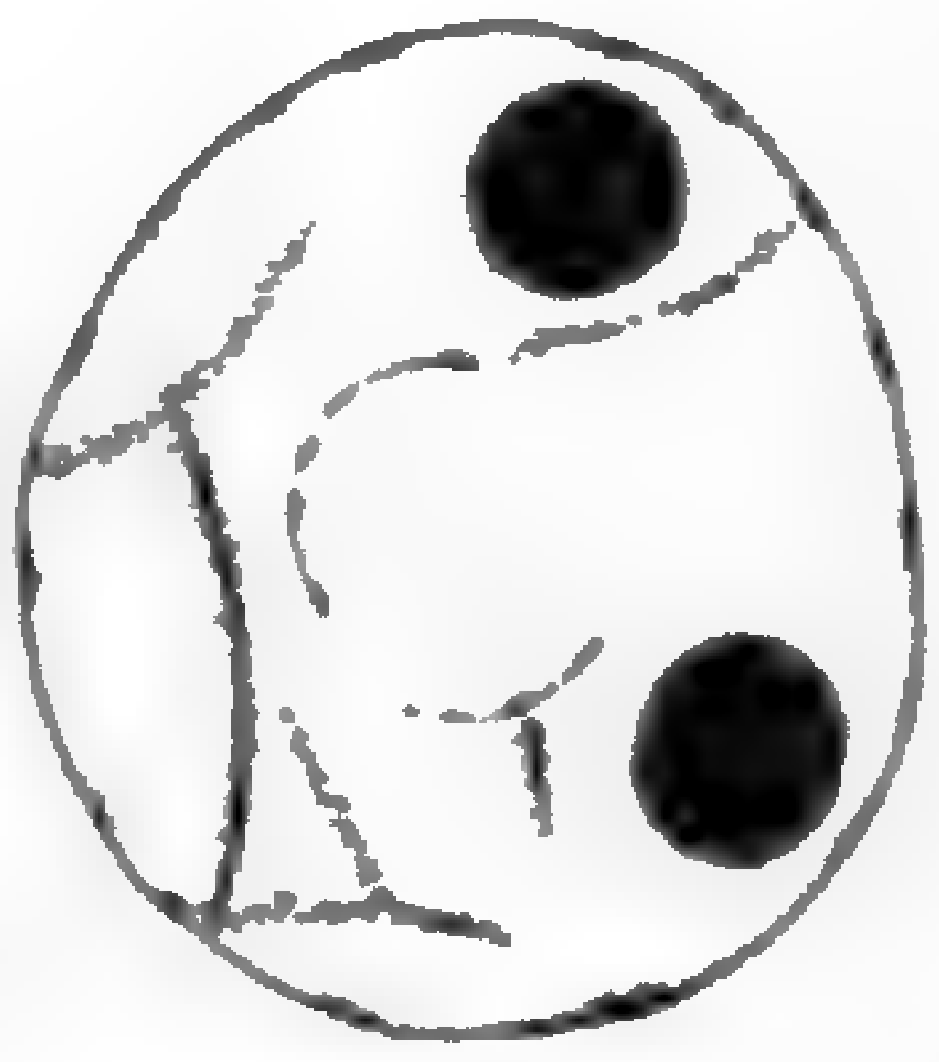
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BROWN on PEPEROMIA

DEVELOPMENT OF THE HELVELLINEAE

I. HELVELLA ELASTICA

W. A. McCubbin

(WITH PLATES XIV–XVI AND ONE FIGURE)

Our knowledge of the developmental stages of the Helvellineae has been restricted to the Geoglossaceae, and is mainly due to the researches of DITTRICH (**9**) on *Leotia gelatinosa* and *Mitrula phalloides*. Practically nothing is known of the ontogeny of the Helvellaceae and Rhizinaceae. DITTRICH's investigations on the Geoglossaceae showed, contrary to the opinion formerly held, that these forms, in their young stages at least, were unmistakably angiocarpous. He discovered that the young fruiting body of Leotia was surrounded by an envelope of hyphal filaments, which later gelatinized, and was then disrupted by the expanding ascoma beneath. In *Mitrula phalloides* the phenomena were quite similar, but among the Helvellaceae which he examined there were no stages young enough to enable him to decide as to the presence or absence of an envelope. In Mitrula the ascogenous hyphae were found to originate from hyphae which were differentiated in the central part of the fruiting body. These hyphae are long, stain readily, and are closely massed, while their nuclei are large, with a prominent nucleolus and a thin chromatin thread. From these filaments the ascogenous hyphae grow toward the hymenial layer, where a rapid branching takes place, succeeded by the formation of asci.

DURAND (**10**), in his admirable monograph on the Geoglossaceae, makes reference to DITTRICH's investigations on the envelope in Leotia and Mitrula, and remarks, "observations of my own on several different species, before I learned of DITTRICH's work, point unmistakably to the same conclusion." DURAND states that he found a veil in *Mitrula phalloides*, *Microglossum viride*, *Cudonia lutea*, and *Spathularia velutipes*, but "sections of quite young ascomata of *Geoglossum glabrum*, *Gleoglossum difforme*, and *Trichoglossum velutipes* have shown no traces of such a membrane." Finally he affirms the belief that "when the development of the Discomycetes shall be better understood, it will be found that in none of them, not even in the Helvellineae, is the hymenium exposed from the first."

An obstacle to the ready solution of this and other details of ontogeny is, as DITTRICH has already pointed out, the difficulty of obtaining young stages either by collection or culture. BREFELD (**3**) made attempts to cultivate the spores of several Helvellineae, but though a mycelium was produced in some cases, no fruiting bodies could be obtained, and often germination did not take place at all. MOLLIARD (**16**) had better success with spores of *Morchella esculenta*, from which he was able to procure a vigorous mycelial growth. This mycelium produced conidia identical with those of Costantinella, and when planted in a compost of apples gave rise to a couple of small fruiting bodies of the morel.

In regard to the taxonomy of the Helvellineae various criteria have been adopted. SCHROETER'S (**17**) classification bases the distinction between this group and the Pezizineae on the supposed gymnocarpous origin of the fruiting body in the former and the angiocarpous in the latter. BOUDIER (**2**), in endeavoring to construct a natural classification of the Discomycetes, adopts a feature other than angiocarpy or gymnocarpy as a basis. He looks upon the Helvellineae as a polyphyletic group: one part, comprising the Helvellaceae and the Rhizinaceae, being placed in that division of the Discomycetes (Operculés) whose asci open by an apical cap; and the other, consisting of the Geoglossaceae, being relegated to a second division (Inoperculés) whose asci open merely by a pore. BREFELD found on examination of several Discomycetes that when an ascogonium is present the ascogenous hyphae appear quite early, but when the fertile filaments spring from ordinary hyphae, as he stated to be the case in several of the Helvellineae and some Pezizas, the ascogenous hyphae are differentiated at a much later stage. He thought that as the ascogonium occurs in simple forms but not in the more specialized, and that as the specialized forms themselves differed, according to the species, in the time at which the ascogenous hyphae appeared, the gradually later and later differentiation of the fertile filaments would form a very good basis for the arrangement of the Discomycetes in a natural series, at the end of which the Helvellineae would probably stand.

The following investigations have been undertaken for the purpose of enlarging our knowledge of the ontogeny of the Helvellineae, and in the hope that fuller information will be of assistance in dealing with the phylogeny of the group. The complex fructifications of the Helvellineae could scarcely be expected to furnish promising material for working out some of the cytological problems that have been attracting attention in certain other divisions of the Ascomycetes, involving the sexuality of the Ascomycetes and their affinities with other Thallophyta, yet certain phenomena have come to light that prove interesting and suggestive.

Rather complete series of several genera of the Helvellineae have been accumulated and are being studied. Any theoretical considerations will be deferred to a later paper.

Helvella elastica

MATERIAL AND METHODS.—The young stages of the material examined were taken from a bank of loose damp sand in High Park, Toronto, and were collected in July 1908. They were fixed in several ways and cut in series in paraffin. Staining was tried with Erlich's hematoxylin, iron hematoxylin, safranin, eosin, rubin S, Flemming's triple stain, methylene blue, and several others. Iron hematoxylin and Flemming's triple stain gave the best results, the former making the nuclei prominent and the latter bringing out the general features. Macerations were also found to be valuable, the crushed material being stained on the slide with safranin or methylene blue.

Some tentative attempts were made to produce the mycelium of several Helvellineae from spores, with the hope of arriving at the young stages of the fruiting bodies by laboratory cultures. The results, however, are as yet insufficient to justify any statement.

I would here acknowledge my indebtedness to Professor J. H. FAULL for material and advice throughout this investigation, and to Mr. R. B. THOMSON for many courtesies.

MYCELIUM.—The mycelium of *Helvella elastica* is easily obtained by washing the earth surrounding young fruiting bodies. It consists of long, sparsely branched, interwoven filaments about 0.03–0.04^{mm} in diameter. These filaments are often connected by anastomoses (*figs. 3–5*). The cells are multinucleate, containing 2–16 or more small densely staining nuclei. These are frequently arranged in pairs (*figs. 3, 4*). Often one finds a pair separated by a septum, a condition of affairs similar to this being described by STOPPEL (**21**) for *Eremascus fertilis*. Metachromosomes such as CLAUSSEN (**7**) describes for Boudiera are also found here. Two or more are visible lying parallel to the cross walls of the thread, and appear to be more conspicuous near the end of a filament than in its older parts.

THE ASCOMA.—Here and there a specially vigorous growth of the mycelium produces knots or clumps (the fruiting bodies), the cells of which are shorter, thicker, and more branched than those of the surrounding filaments. The earliest stages of the fruiting bodies procured were about 0.5^{mm} in diameter. At this stage the young Helvella consists of a short thick stem spreading out insensibly into the mycelial growth of the substratum, and surmounted by a round bulbous cap of slightly larger diameter than the stem (*fig. 6*). There is at this period no indication of fertile filaments. A membrane and a palisade layer inclose the whole fruiting body, but the palisade hyphae are not yet well differentiated. In stage 2 (diam. 1^{mm}, *fig. 7*) storage cells appear, the palisade layer shows more regularity, while the membrane has been much broken by the rapid growth. Stage 3 (diam. 1.25^{mm}, *fig. 8*) shows the beginning of paraphyses on the site of the hymenium, an increased number of the storage organs, and the presence of a few ascogenous hyphae. The membrane is now represented merely by a few flakes. The hymenium does not grow rapidly at first, however, being outstripped in this respect by the stem and sterile part of the cap. As a result the hymenial surface may assume a flat or even concave shape, as shown in stage 4 (*figs. 9, 66*). Here the membrane has almost disappeared, only a few degenerate threads or masses of cells being distinguishable. The paraphyses are now numerous and the ascogenous hyphae are beginning to branch or even to form hooks. In *fig. 10* the fruiting body has assumed the characteristic saddle shape of the Helvellas. There has been from stage 4 a rapid enlargement of the hymenial surface, which takes place, however, as DITTRICH has pointed out, with considerable irregularity, thus accounting for the peculiar shape of the adult ascoma.

THE PALISADE LAYER.—Surrounding the entire fructification in early stages, and persisting throughout life on all but the hymenial surface, is a "palisade layer." This layer is formed from club-shaped ends of the hyphae, which arrange themselves closely and evenly at right angles to the surface. In early stages this layer is not well differentiated. Later on it becomes more regular, its threads take on a more pronounced club shape, and the cells become filled with deeply staining contents.

THE MEMBRANE.—The envelope which covers the fruiting body in its early stages arises from the palisade layer. Many of the club-shaped hyphae of the latter continue to grow out beyond the general surface, then turn at right angles, and interlacing in every direction along the surface form a matted web 2–8 threads in thickness. This membrane is very transitory, however, and undergoes degeneration at an early period. Its protoplasm takes on a granular appearance, the cell outlines become indistinct, and finally the whole disintegrates into a deeply staining mass in which the nuclei are the most prominent feature. Long before this process is complete, however, the rapid growth of the underlying tissue bursts the emvelope so that it adheres in flakes (*figs. 57, 58*). Then the paraphyses and intercalary palisade hyphae pushing out to the surface complete the separation and all traces of it are cast off.

DURAND, in speaking of this veil in *Microglossum viride*, states that "when the veil seems to break up into fragments, there are indications that the hymenium first appears through *a pore at the apex*." This phenomenon has been homologized with the opening of the apothecium in Ascobolus. But the coverings of Spathularia, Leotia, and Mitrula break up irregularly without any indication of an apical pore, and in *Helvella elastica* also it breaks irregularly. Moreover, in some forms a veil may be altogether lacking. Indeed I am able to state definitely, from observations on a very complete series of stages, that *Geoglossum hirsutum* shows no trace whatever of such a structure.

THE PARAPHYSES.—In sections of young ascomata of *Helvella elastica* the hymenial surface is not yet differentiated, being quite similar to that in other parts of the fruiting body, and covered by the common palisade layer and external veil. Very early, however, the paraphyses begin to appear, and as these force their way upward through the palisade filaments the veil is broken and thrown off. The paraphyses arise from ordinary hyphae in the interior of the fruiting body, and are in the early stages quite similar to the filaments of the palisade layer, so that the hymenium can only be distinguished at this period by the greater number and the closer and more regular arrangement of its units. Later on, however, the paraphyses elongate and become thinner, less bulbous, and more closely packed. In this older condition they are filled, especially near their ends, with dense deeply staining contents in which the nuclei seem to have degenerated. They are also septate and their more basal cells show two or more small dense nuclei. The hyphae which give rise to paraphyses may be traced for some distance into the hyphal mass of the cap, and indeed in many cases nearly to its lower surface.

STORAGE BODIES.—A conspicuous feature in sections of *Helvella elastica* is the presence of large cellular bodies filled with contents, and distributed irregularly throughout the whole of the fruiting body except the stem. These bodies are quite large, attaining sometimes 20–30 times the diameter of the surrounding hyphae, but they vary exceedingly in size and shape. Sometimes they form a chain of three or four connected cells, or they may consist of a single mass with irregular protuberances, or they may be merely filaments enlarged for a considerable portion of their length. They often occur in groups, the individuals of which are unconnected.

In most of the ascomata sectioned the protoplasm of these bodies had shrunken somewhat from the cell wall. It is coarsely granular and stains deeply. Nuclei are present in numbers varying from 1 to 20 or more. There are usually present either one or two large nuclei (*figs. 46, 48, 50, 63*), or a number of smaller ones, though both sizes may occur in the same cell (*fig. 46*). Moreover, as shown in *figs. 46–56*, which are taken from a single representative ascoma, all stages intermediate between these extremes may exist. The large nuclei are loosely reticulate in structure, while the smaller are dense and stain deeply. The latter show in many cases a tendency to occur in masses (*figs. 49, 52, 54, 56*). Another conspicuous feature among the nuclei of these large bodies is their frequent arrangement in pairs (*figs. 47, 53, 55, 61*).

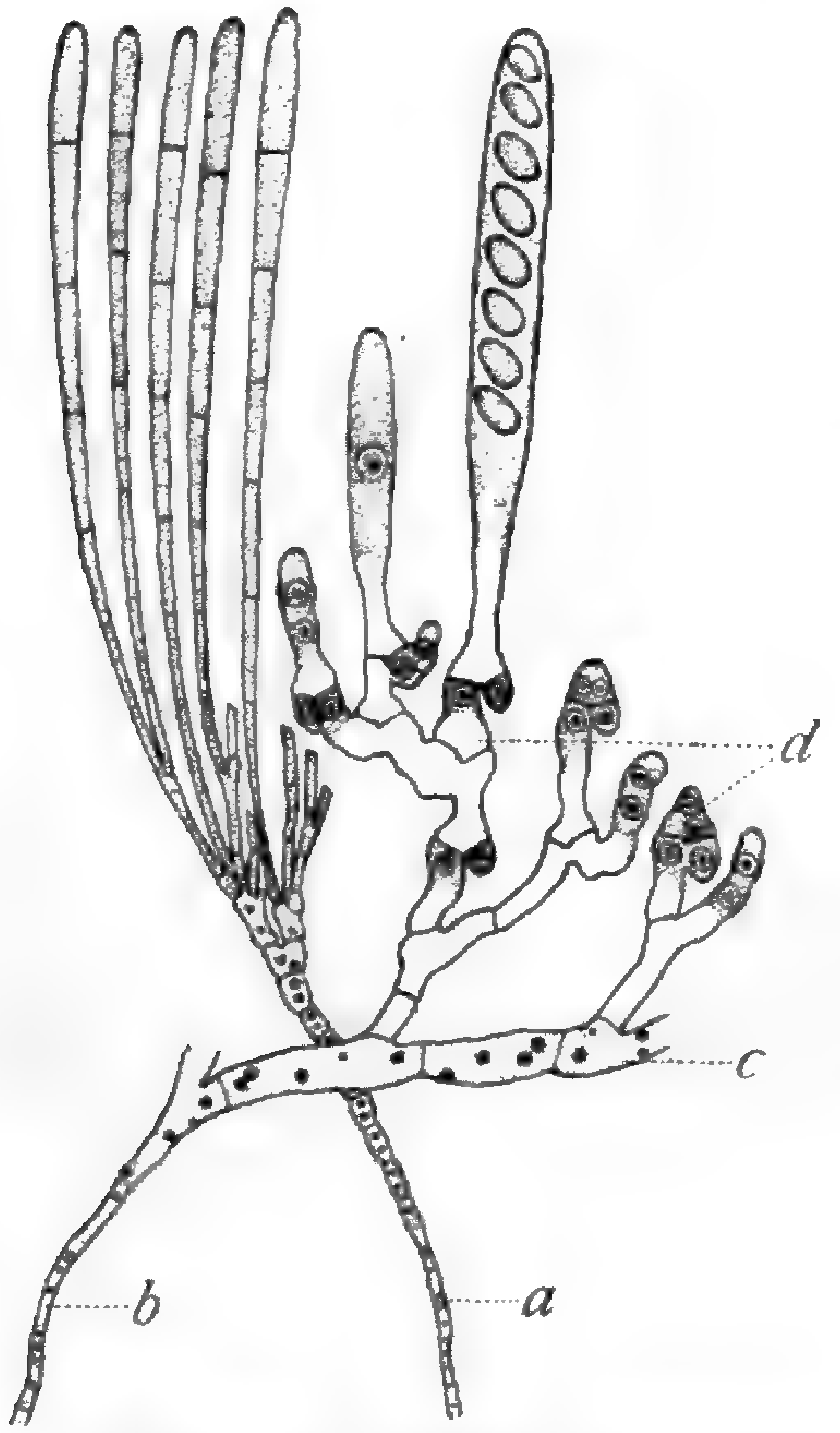
The general occurrence of these bodies throughout the cap would seem to indicate a vegetative function. They are to be found at the base of the hymenium giving off paraphyses, or within the hymenial layer, in which case they are surmounted by one or more paraphyses (*figs. 43, 64*); or they may force their way to the surface, appearing there as enlarged clublike processes plainly having the jointed structure of the paraphyses. The ends of these processes are often found ruptured and the contents, like lava from a crater, overflowing the neighboring surface. These enlargements are further found all through the subhymenial hyphal mass, and many of the palisade hyphae originate from those near the lower surface (*fig. 60*). In addition to that, these bodies are found connected with the fertile filaments either remotely in the subhymenial layer or else having the ascogenous hyphae proceeding directly from them. Often part of an ascogenous hypha, at quite as late a stage as the formation of the hooks, is greatly enlarged, the similarity of stain and nuclear structure leaving no doubt as to the close resemblance of these swellings to the bodies in other parts of the ascoma (*figs. 36, 62*). In very young stages of development these bodies are not present, but they appear quite early in the history of the ascoma, as previously mentioned. At the time when the asci are fully formed, they are usually empty, their connections have vanished, and their walls are shrunken and degenerate. Observations on a considerable number of specimens indicate that these bodies vary with the individual, being largest and most abundant in vigorous plants. They vary also in the individual, serial sections showing one-half of the fruiting body well supplied with them and the other containing scarcely one.

With the foregoing data in hand, it seems most reasonable to regard these peculiar structures as organs for the storage of food material.

ASCOGENOUS HYPHAE.—When the fruiting body is about 1.25^{mm} in diameter, the first hyphae which are undoubtedly ascogenous make their appearance. Some of the hyphal threads form a matted web a short distance below the layer of paraphyses (*fig. 59*). The threads of this web are long, straight, multinucleate, sparsely branched, and twice or thrice the thickness of the ordinary filaments. It is from these that the vertical ascus-bearing threads arise.

A comparison with what DITTRICH records for Mitrula shows that in Helvella there is a much later differentiation of the fertile filaments.

Moreover, they are not traceable to any distinct source, as were those in Mitrula, but arise merely from the ordinary hyphal threads of the fruiting body. This is an agreement with BREFELD'S observations on several species of Morchella, Helvella, and Geoglossum, as well as *Leotia lubrica* and *Peziza Sclerotiorum* (Heft IV, 130). According to him the ascogenous hyphae may arise from the common filaments of the fruiting body and even from those which had formerly produced paraphyses.



Hymenium of *Helvella elastica* (semi-diagrammatic): *a*, sterile hypha producing paraphyses; *b*, undifferentiated fertile filament; *c*, enlarged fertile filament in the sub-hymenial layer; *d*, ascogenous hyphae showing the succession of hooks, the fusion of terminal and antepenultimate cells, and the formation of the ascus (the unshaded parts are empty).

In *Helvella elastica* there is frequently a thickening of the sterile filaments before they form the profusely branched mass of paraphyses, but such enlargements have no connection with those occurring in the ascogenous hyphae. The cells of the former are short, bulbous, and usually binucleate, while in the fertile threads they are long, uniform, and multinucleate (see *text fig.*). Moreover, no connection can be traced between the two, nor can any paraphyses be seen coming from the ascogenous filaments.

From the fertile subhymenial layer lateral branches are given off in rather scanty numbers, and these grow toward the layer of paraphyses, where they branch repeatedly. The end cells of these lateral branches contain an abundance of deeply staining protoplasm and 2–5 nuclei, the usual number, however, being 2 (*figs. 11–19*). The whole energy of growth seems to be concentrated in this end cell, for usually those behind it are completely empty, and long before branching has been completed even the walls disappear. DITTRICH notes the same phenomenon in *Mitrula phalloides.* It is evident that in these cases the developing ascus must be nourished by diffusion from the surrounding cells. As growth proceeds in the vertical branch, transverse walls are formed at intervals along its course (*figs. 11–18*). When nuclei and protoplasm happen to be cut off by these walls, a lateral branch may be produced from the cells thus left behind (*figs. 12, 16*). Finally the end cell forms a hook and its two nuclei divide to form four. Then follows a septation of the hook into three cells, a daughter of each of the mother nuclei remaining in the penultimate cell and the other two being distributed to the terminal and antepenultimate respectively. From the penultimate cell a process now arises into which its two nuclei wander (*figs. 20, 27.*)

Heretofore in the Ascomycetes which have been investigated there has come into consideration only one hook (where hooks exist), the process from which becomes the ascus. Here, however, it is curious to note that the process from the first hook may proceed to form a second. Its two nuclei, instead of fusing, divide again, the resulting four being distributed in the second hook as in the first. Indeed this formation of successive hooks may go on for some time, as many as six having been observed on one ascogenous hypha. The last-formed process then becomes the ascus, its nuclei fusing to form the primary ascus nucleus, and from this spore nuclei are produced by the usual three successive divisions. One important feature is made strikingly evident by these hooks, namely the conjugate division of the nuclei in the ascogenous hyphae. It has been quite evident from my observations that the two nuclei which fuse in the young ascus are directly descended by conjugate division from the two which normally occupy the end cell of the ascogenous hypha as it first arises from the subhymenial layer.

Another phenomenon of interest is the "fusion" or "anastomosis" that quite frequently takes place between the terminal and antepenultimate cells. The nucleus of the antepenultimate cell passes into the former, and from thence the two nuclei wander into a process which invariably arises from the terminal cell (*figs. 33, 34, 36–38, 40*). It will be readily seen that this process with its two nuclei is the direct equivalent of that which originates from the penultimate cell, and indeed it conducts itself in exactly the same way, forming further series of hooks in which anastomoses may likewise take place, all the resulting processes finally ending in asci (*text fig.* and *figs. 32, 38, 40–42*).

Occasionally there has been obviously no fusion of the terminal and antepenultimate cells, yet a branch has arisen from the former. As in such cases the antepenultimate cell retains no nucleus, it is probable that pairing of the daughter nuclei has taken place before the cutting off of a binucleate penultimate cell, a case quite comparable to that observed by MAIRE (**15**) in *Galactinia succosa*.

Summary

The mycelium of *Helvella elastica* is subterranean. Its cells are multinucleate.

The fruiting body arises from clumps of thick short-celled filaments.

This fruiting body is quite early surrounded by an envelope which is transitory and breaks up irregularly. Closely associated with the veil in early stages, but persisting throughout the life of the fruiting body, is an external layer of club-shaped palisade hyphae.

Certain large irregular cells occurring in all parts of the fruiting body (except the stem) apparently have the function of storage organs.

The "ascogenous hyphae" arise as a clearly differentiated subhymenial complex of filaments. From this layer grow out vertical branches whose end cells contain usually two nuclei. Hooks are formed by these end cells, while the proximal part of the branch degenerates.

The process from the first hook, without fusion of its two nuclei, may proceed to form a second and similar hook. From this second a third may arise, and so on, up to the number of at least six, the process from the last becoming the ascus after nuclear fusion.

In any hook of such a series a "fusion" or "anastomosis" of the terminal and antepenultimate cells may take place, the nuclei of both passing into a process arising from the former. This process is equivalent to that springing from the penultimate cell, and conducts itself in the same way.

The two nuclei which fuse to form the primary ascus nucleus are directly descended by conjugate division from the two which occupied the end cell of the young ascogenous hypha.

No structure having the conventional form of an ascogonium was found.

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EXPLANATION OF PLATES XIV–XVI

Figs. 1–5.—Parts of mycelium. ×300.

Figs. 6–10.—Stages showing development; actual length indicated.

Figs. 11–19.—Young ascogenous hyphae before formation of hooks. ×360.

Figs. 20–27.—Formation of first hooks. ×360.

Fig. 28.—Young ascogenous hyphae arising from enlarged filament in the subhymenial layer. ×360.

Figs. 29–31.—Formation of successive hooks. ×360.

Figs. 32–34.—Fusion of antepenultimate and terminal cells. ×360.

Fig. 35.—Drawing from maceration showing three successive hooks ending in young ascus.

Fig. 36.—Enlarged ascogenous hypha, the enlargement involving four successive hooks. ×360.

Fig. 37.—Swollen hook from same group as *fig. 36,* showing fusion of terminal and antepenultimate cells.

Figs. 38, 40–42.—Fusion of terminal and antepenultimate cells.

Fig. 43.—Storage body in paraphyses layer.

Figs. 44, 45.—Storage bodies from palisade layer on under surface of cap. ×360.

Figs. 46–56.—Storage bodies in interior of the ascoma showing size and arrangement of the nuclei. ×360.

Fig. 57.—Young fruiting body with remnants of the envelope adhering. ×60.

Fig. 78.—Part of surface of *fig. 57,* showing palisade layer and fragments of the membrane. ×300.

Fig. 59.—Section through the cap. ×100.

Fig. 60.—Filaments of the palisade layer arising from storage bodies. ×300.

Fig. 61.—Storage bodies (outlined in ink) showing paired nuclei. ×300.

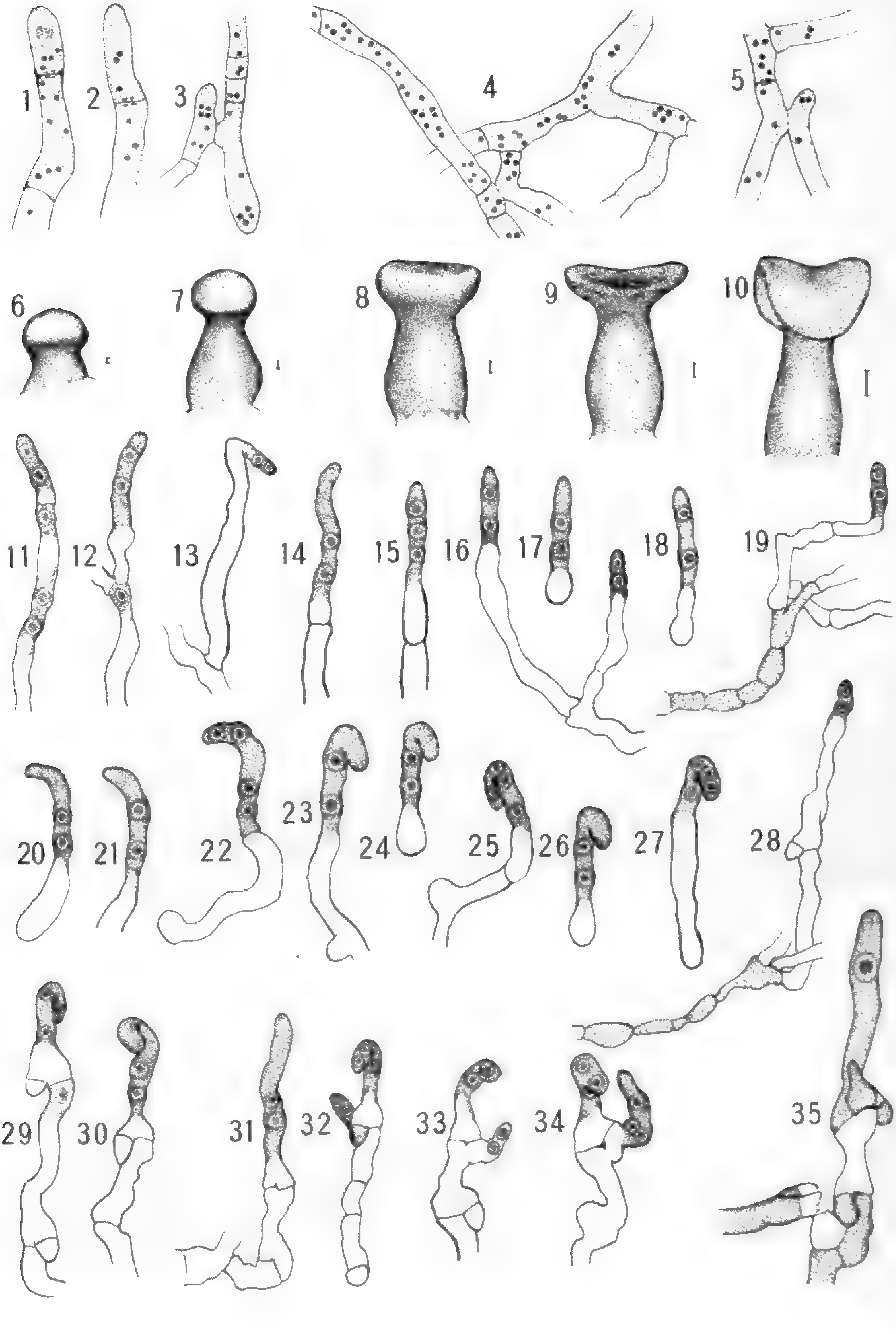
Fig. 62.—Enlargement of ascogenous hypha involving several hooks (see *fig. 36*).

Fig. 63.—Storage cell with two large and several small nuclei (*fig. 46*).

Fig. 64.—Storage bodies in the hymenial layer ending in paraphyses.

Fig. 65.—Young ascogenous hypha with two successive hooks.

Fig. 66.—Section of young fruiting body with concave hymenial surface.



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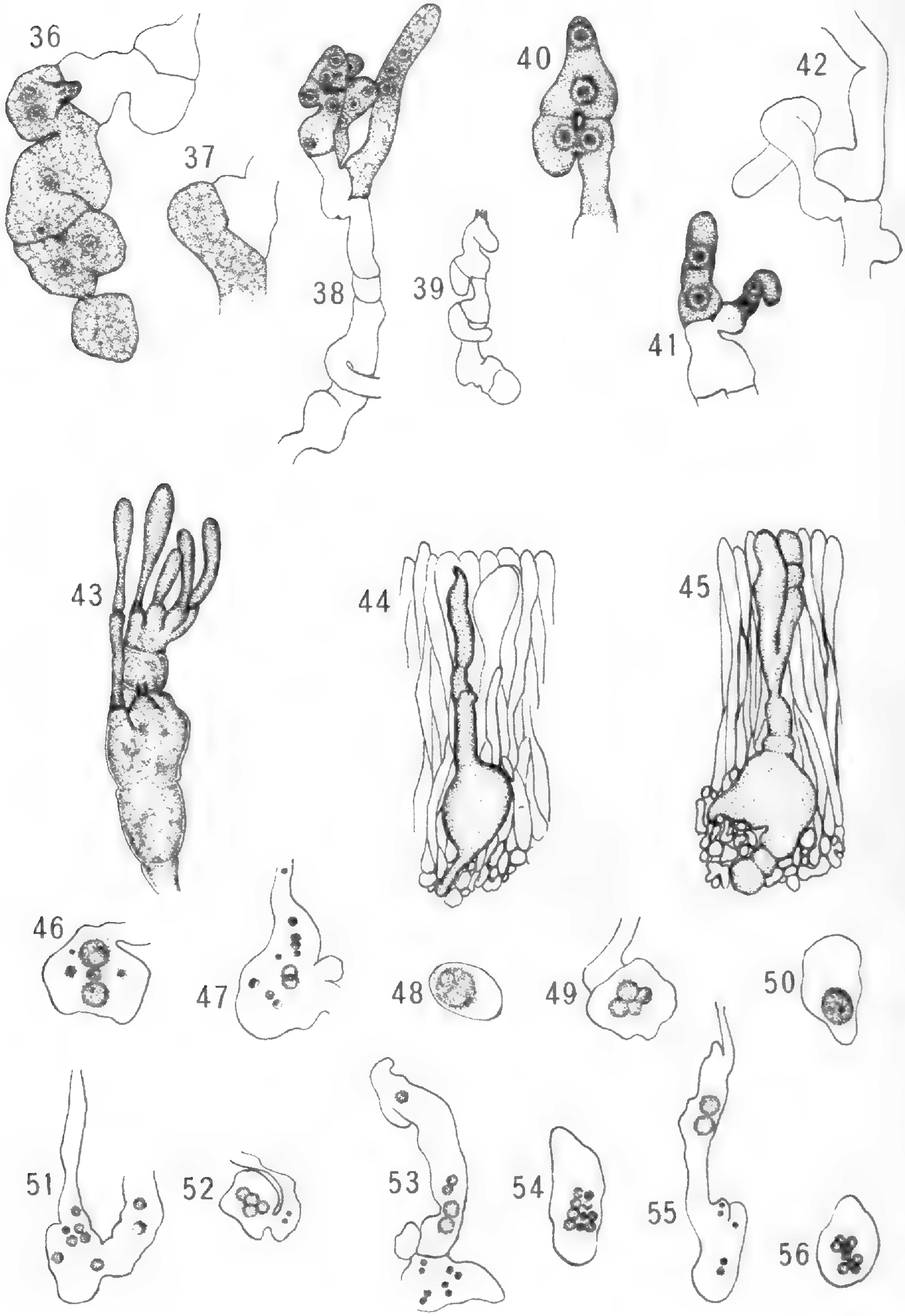

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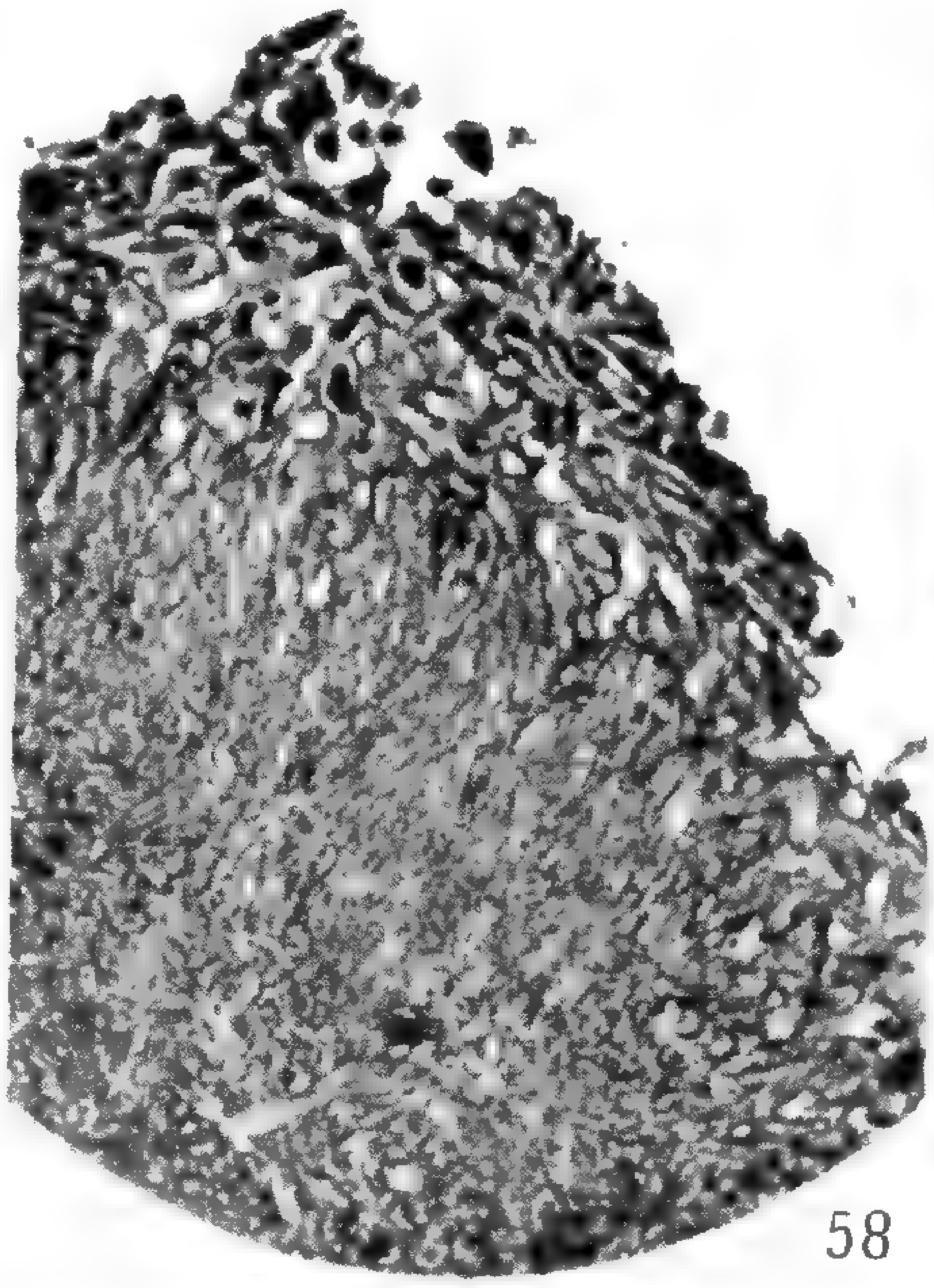

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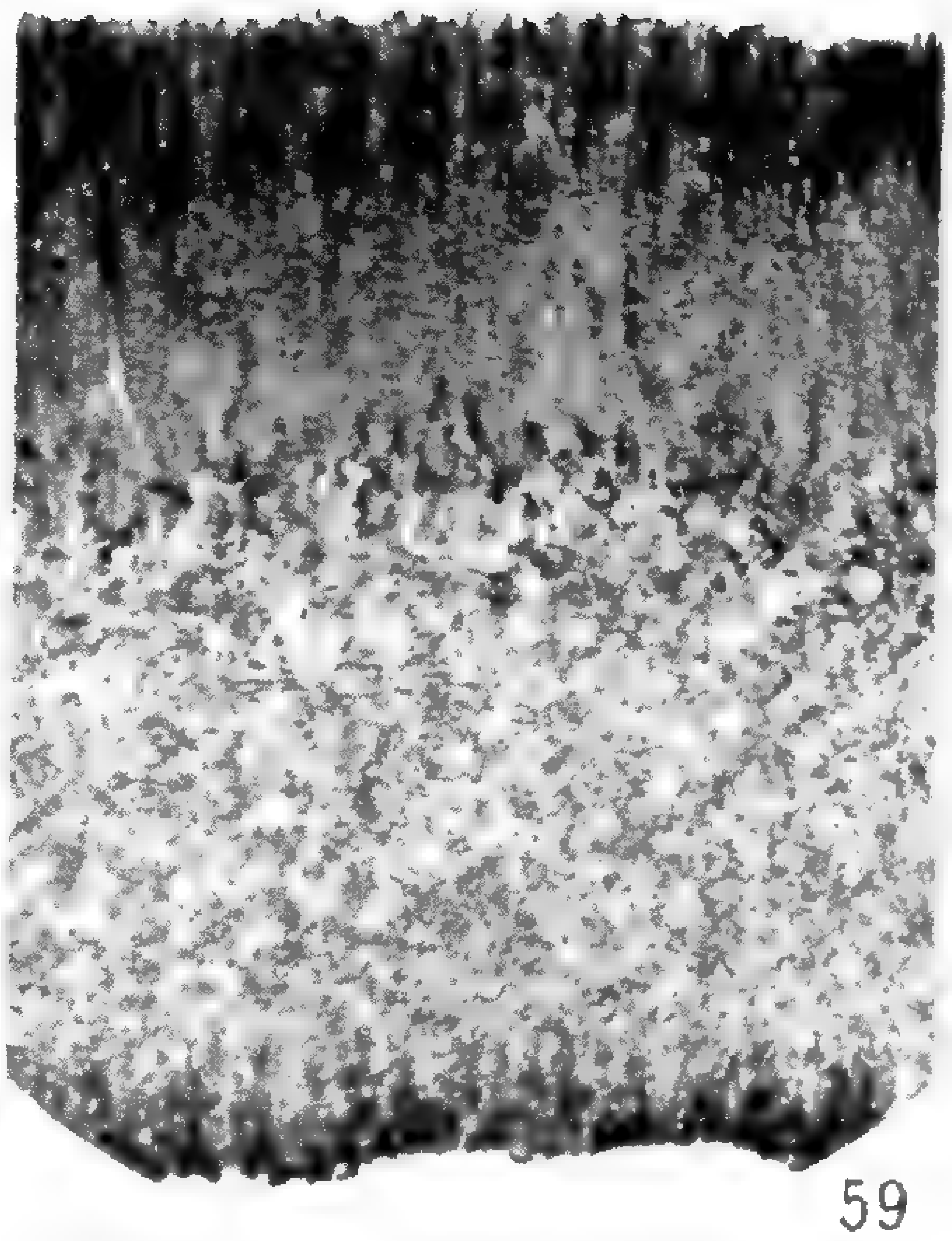

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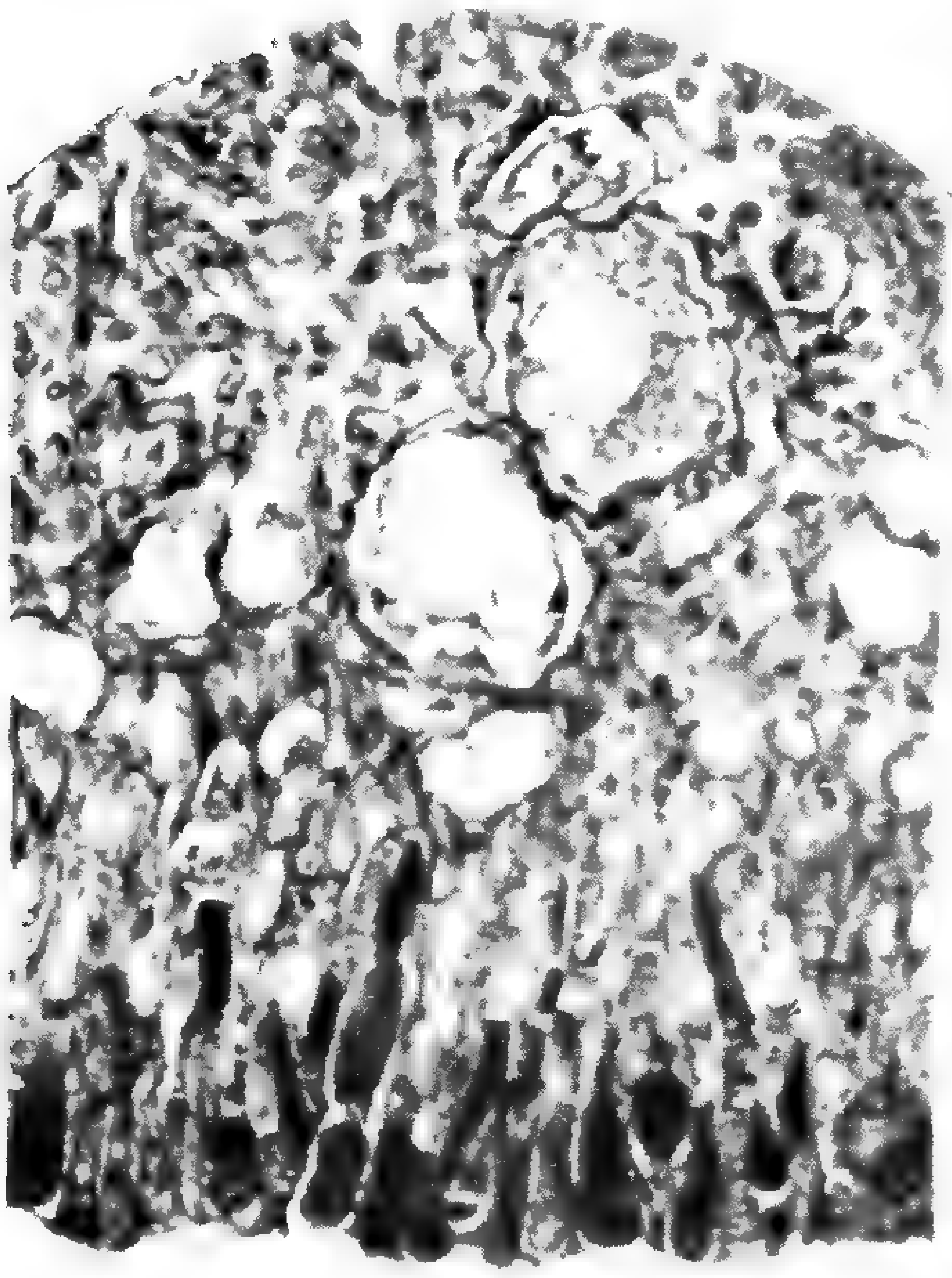

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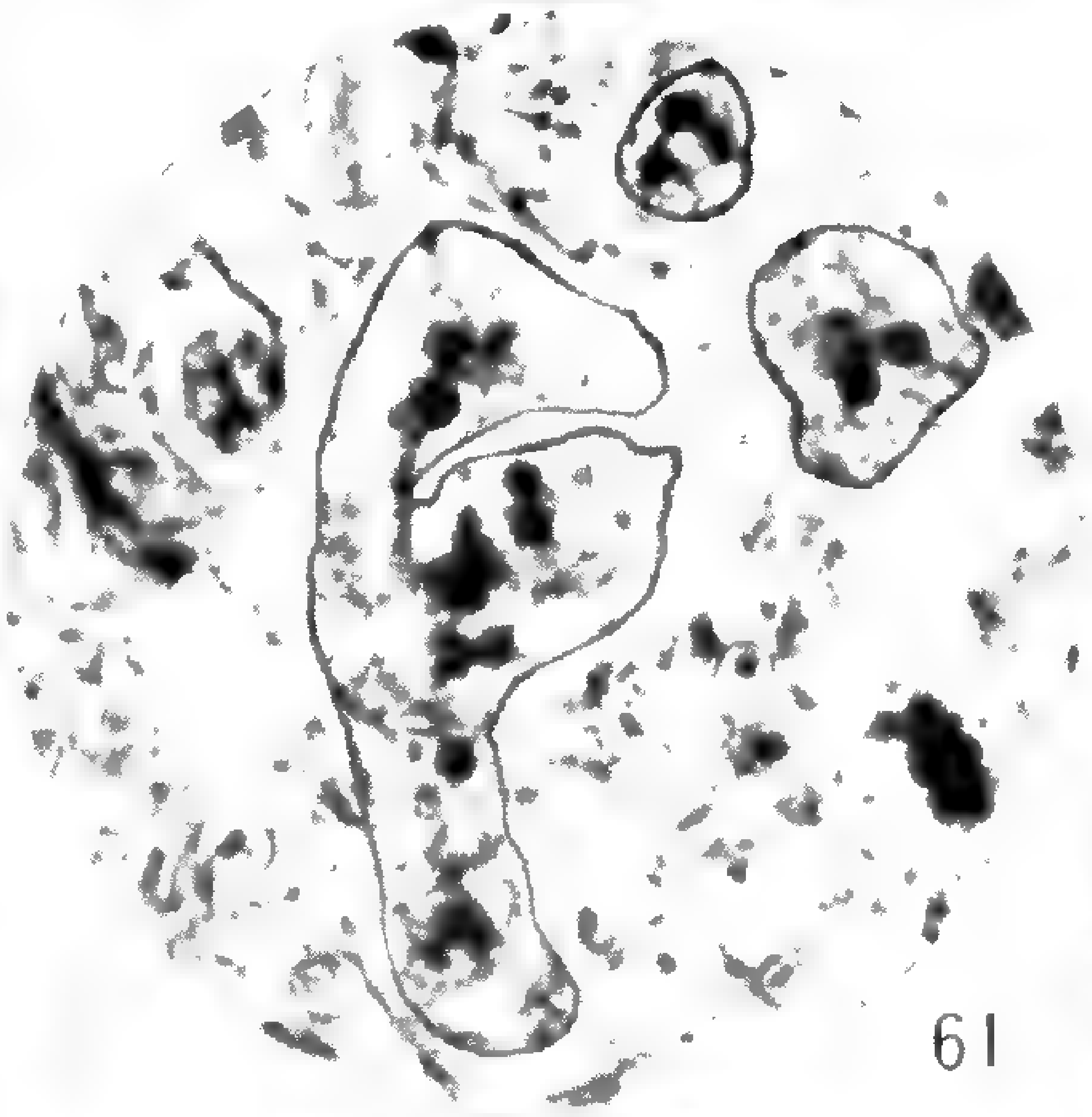

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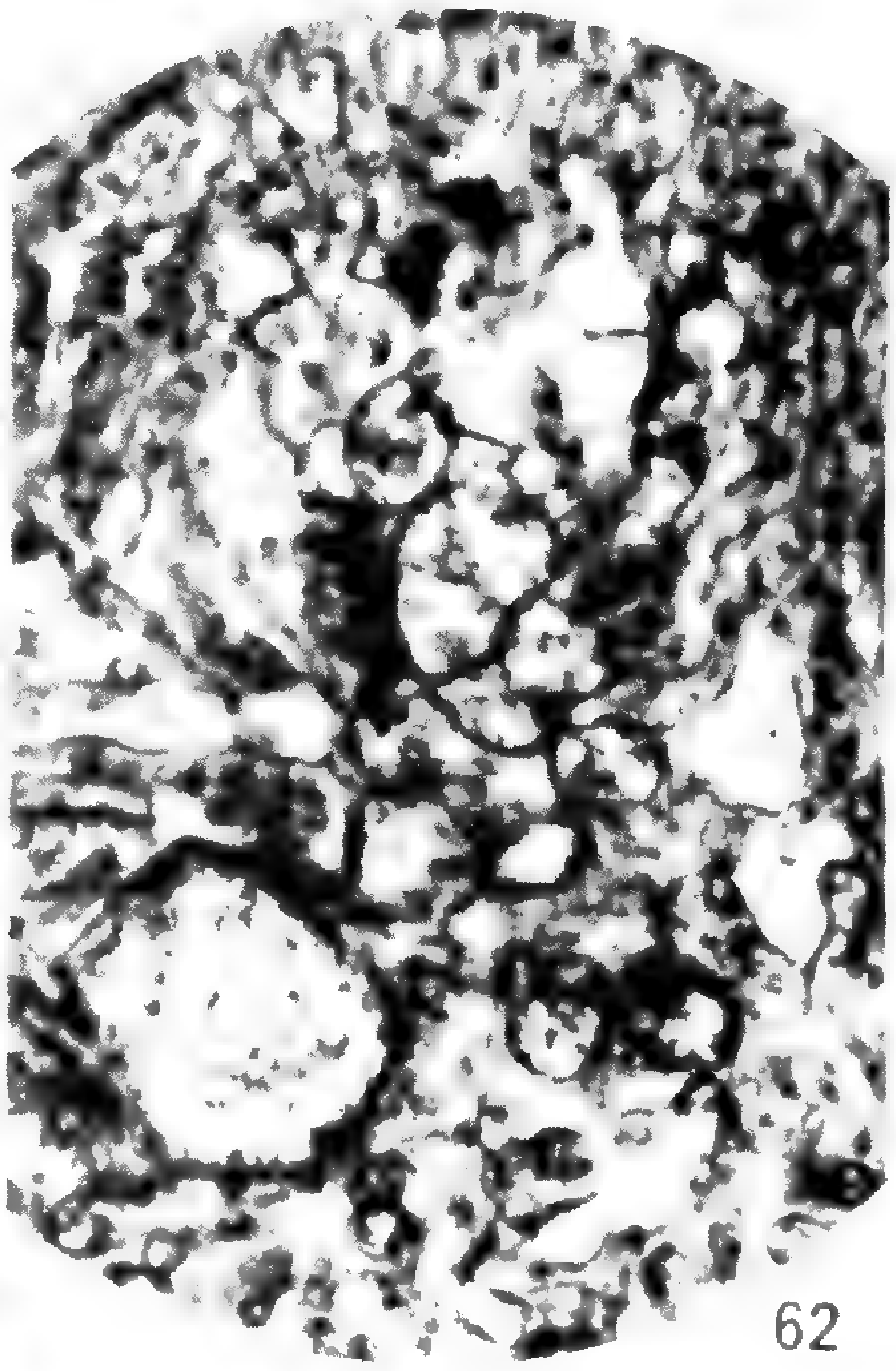

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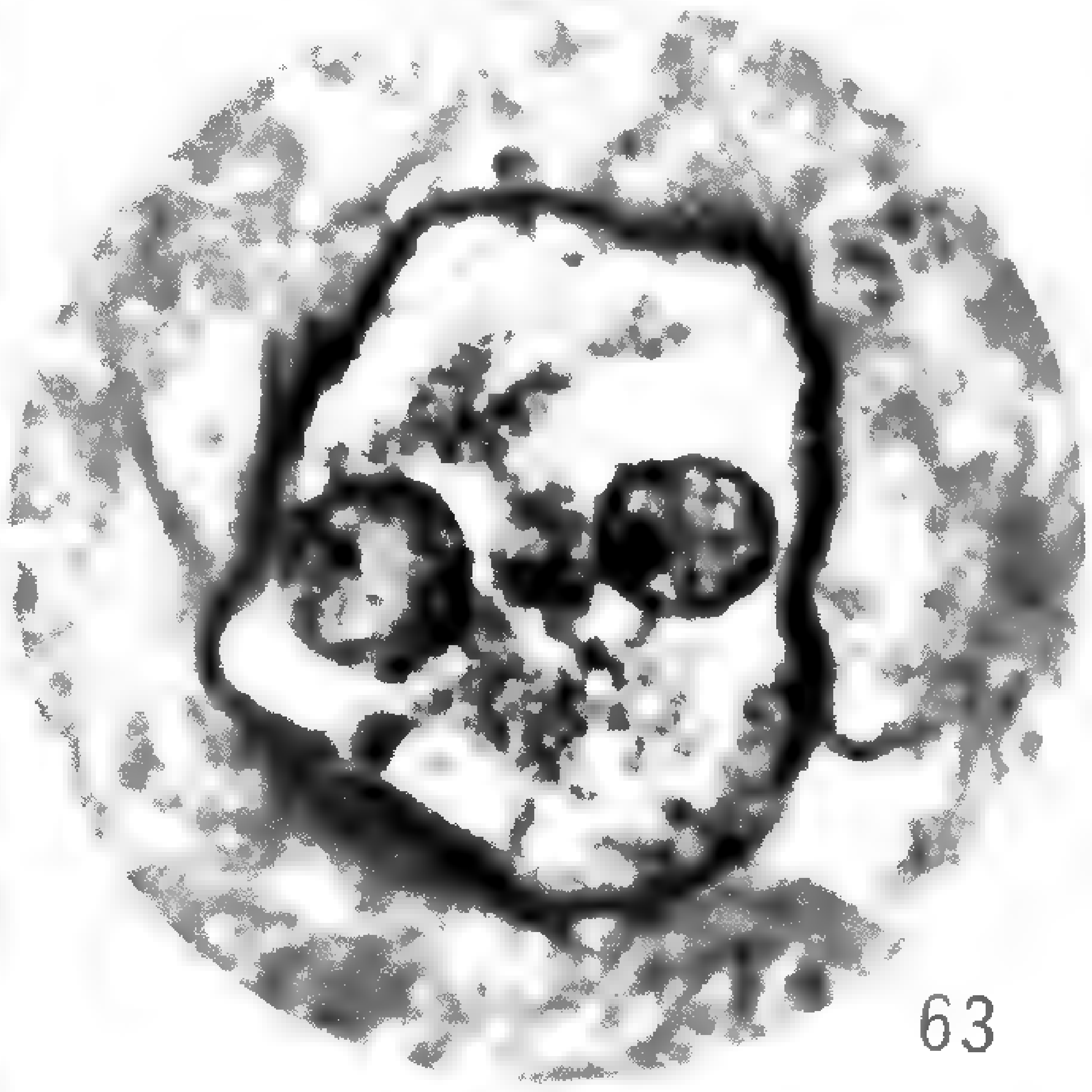

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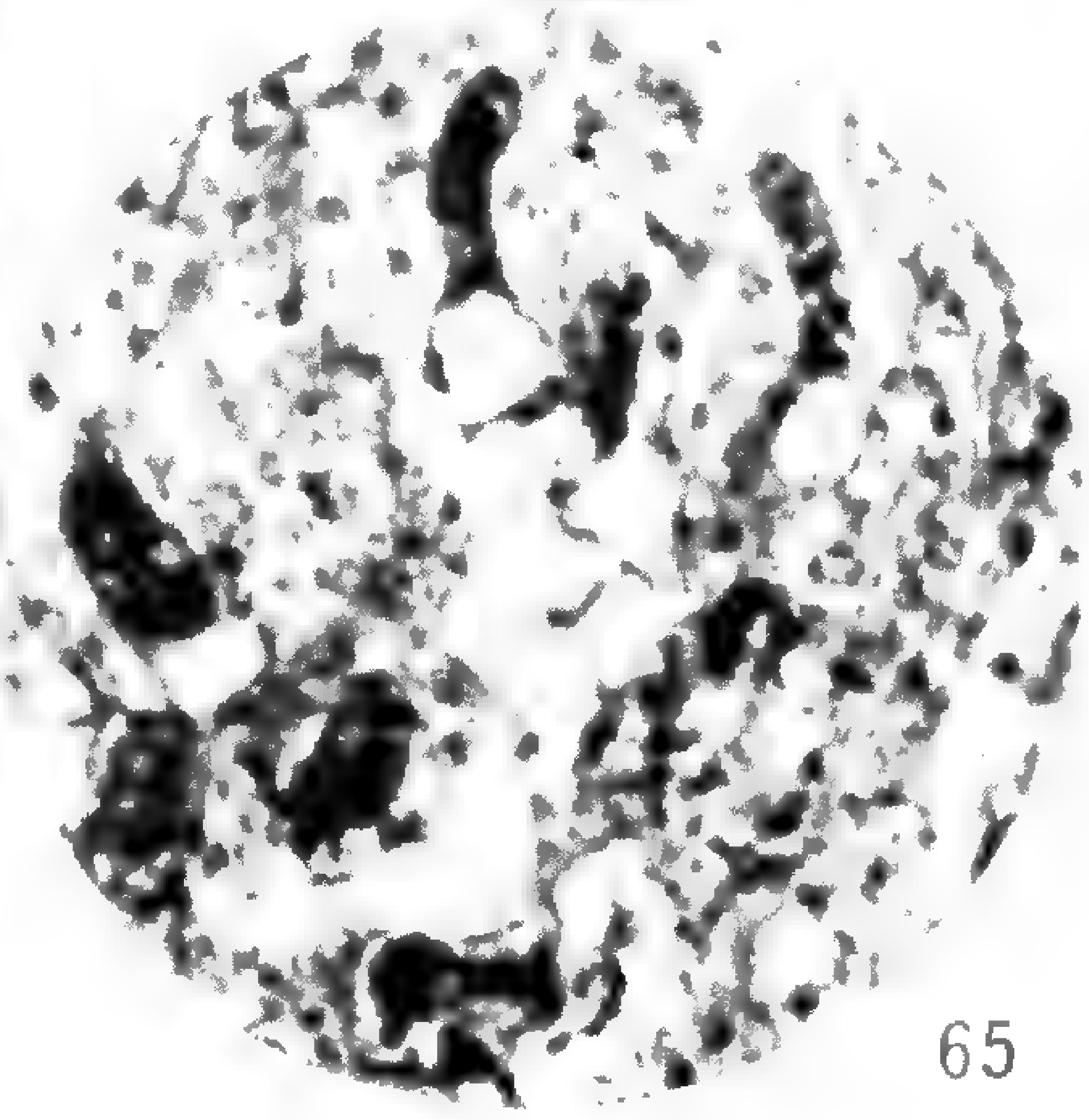

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McCUBBIN on HELVELLINEAE

ON PHYSIOLOGICALLY BALANCED SOLUTIONS FOR BACTERIA (B. SUBTILIS)

CHARLES B. LIPMAN

In a former paper[1] I have shown that the laws governing the toxic and anti-toxic effects of salts, which LOEB and OSTERHOUT have found to hold so universally for animals and plants respectively, hold also for bacteria if we may consider *B. subtilis* as representative of this group. I shall now attempt to show that as regards complete physiologically balanced solutions, the same general relation holds for bacteria as for animals and plants.

In his experiments on a marine fish (Fundulus) LOEB was able to show that the views of HERBST regarding the absolute necessity for each of the constituents of sea water for the complete development of the egg were erroneous, since Fundulus, which would not develop in a pure NaCl solution of the same osmotic pressure as sea water, would live indefinitely in distilled water, and therefore the salts contained in sea water were necessary, not for nutrient purposes, but for the purpose of overcoming toxic effects of other salts, or briefly for balancing purposes. From this and other experiments in which he was able to overcome the toxicity of NaCl solutions by the addition of small amounts of salts like $ZnSO_4$, $BaCl_2$, and Pb $(CH_3COO)_2$, which are themselves exceedingly toxic, LOEB concluded that physiologically balanced solutions, in which one constituent overcomes the toxic effect of one or more others, are essential for the proper development of animals, and further that the blood and sea water may be considered such balanced solutions in nature.

In similar experiments on plants OSTERHOUT[2] showed that LOEB's conception of "physiologically balanced solutions" holds good also for that class of organisms. In many series of tests on a great variety of marine and freshwater plants that investigator proved that the combination of NaCl, KCl, and $CaCl_2$ in the proportions in which they exist in sea water is just as uniformly beneficial for plants as for animals.

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[1] BOT. GAZETTE **48**:105–125. 1909.

[2] Univ. Calif. Publ. Bot. **2**:no. 10. 1906.

From the interesting results just cited, it was deemed important to ascertain if, contrary to the opinion of LOEW and ASO,[3] physiologically balanced solutions are necessary for bacteria as they have been found to be for plants and animals, and if the behavior of bacteria toward completely balanced solutions is in full accord with that of the other classes of organisms. Accordingly, seven series of experiments were carried out, in which were employed upward of thirty solutions of different composition. In order to have the results strictly comparable, the average of several determinations in each case is inserted in the tables. It may be said that the duplicates showed very close agreement for ammonification cultures. The technique employed in these experiments was in general the same as that described in my former experiments above cited. The cultures were incubated in Erlenmeyer flasks of 250^{cc} capacity for 2.5 days, at the end of which time the ammonia was determined. The solutions in each flask consisted of the constituents described under each in the tables, and, in order to provide uniform surfaces of aeration, were reduced to a bulk of 100^{cc} in each flask after the salts were combined in the proportions given.

SERIES I

The object here was to compare pure solutions of NaCl and KCl and combinations of them with $MgCl_2$ and $CaCl_2$ respectively (which combinations have been shown to be beneficial in the experiments with binary solutions) with a blank solution of peptone in distilled water and one of peptone in tap water. The results are given in table I.

In this series, as well as in former experiments, the salt mixtures which contained NaCl as the predominant salt always seemed to give better results, and it was decided therefore in the following series to make extensive use of the NaCl as a basis for all artificial solutions. We see from the table that the best results obtained with the salt solutions was in solution 3, as was the case in the experiments with binary solutions, but it will also be noticed that the blank peptone solutions in both tap and distilled water gave very much higher results than even solution 3. The depressing effect seen in the tap

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[3] Bull. Coll. Agric. Imp. Univ. Tokyo **7**:355. 1907.

water peptone solution when compared with the distilled water culture is possibly due to the fact that small quantities of toxic salts are dissolved from the metal pipes by the water and thus have an unfavorable effect on the growth and development of *B. subtilis*.

TABLE I

ALL QUANTITIES GIVEN REFER TO CUBIC CENTIMETERS OF 0.35 *m* SOLUTIONS
PEPTONE CONTENT 0.91 PER CENT.

Number	Culture solution	N as NH_3 formed in cultures, in mg
1	100 NaCl	20.10
2	100 KCl	15.38
3	100 NaCl 10 $MgCl_2$	23.39
4	100 KCl 5 $CaCl_2$	17.90
5	Peptone in distilled water	42.51
6	Peptone in tap water	31.90

SERIES II

The next step taken was to ascertain if salt mixtures containing three salts instead of two provide better conditions for ammonification

TABLE II

ALL QUANTITIES GIVEN REFER TO CUBIC CENTIMETERS OF 0.35 *m* SOLUTIONS
PEPTONE CONTENT 0.91 PER CENT.

Number	Culture solutions	N as NH_3 formed in cultures, in mg
1	100 NaCl 10 $MgCl_2$ 10 KCl	20.63
2	100 NaCl 10 $MgCl_2$ 10 $CaCl_2$	18.91
3	100 NaCl 10 $MgCl_2$ 5 $CaCl_2$	25.88
4	100 NaCl 10 $MgCl_2$ 25 KCl	24.90
5	100 NaCl 10 $MgCl_2$ 50 KCl	22.10
6	100 NaCl 10 $MgCl_2$	23.39

by *B. subtilis* in peptone solutions. The solutions were prepared as shown in table II, and the ammonia determined with results as given.

Comparing the first five solutions with solution 6, we find that we have not yet arrived at what might be termed a balanced solution. Some salt mixtures of three salts do not give as good results as solution 6, while solutions 3 and 4, which appear to be better than the former, are not sufficiently near the peptone water cultures (see table I) to allow them to stand without further experiments as the optimum solutions. None the less, it is plain that solution 3 is approaching the balanced solution.

SERIES III

From the results just given it was thought that the addition of another salt to the mixtures of three salts might tend to make them approach still closer than did solution 3 of the last series the optimum solution. There were prepared, therefore, solutions containing

TABLE III

ALL QUANTITIES GIVEN REFER TO CUBIC CENTIMETERS OF 0.35 *m* SOLUTIONS
PEPTONE CONTENT 0.91 PER CENT.

Number	Culture solution	N as NH_3 formed in cultures, in mg
1	100 NaCl 10 $MgCl_2$ 10 $CaCl_2$ 10 KCl	19.37
2	100 NaCl 10 $MgCl_2$ 5 $CaCl_2$ 10 KCl	18.91
3	100 NaCl 5 $CaCl_2$ 10 $MgCl_2$ 25 KCl	21.75
4	100 NaCl 10 $CaCl_2$ 10 $MgCl_2$ 25 KCl	22.87
5	100 NaCl 10 $MgCl_2$ 5 $CaCl_2$	25.88
6	100 NaCl 10 $MgCl_2$	23.39

various combinations of four salts each, and for comparison with them solution 3 of table II containing three salts and solution 6 of table II containing only two salts.

From table III it is plain that the various combinations of four salts, though allowing a fairly good production of ammonia, are not as favorable to *B. subtilis* as either 5 or 6, which contain respectively only three and two salts. It appears evident that the combinations of four salts there employed have not the favorable composition of a balanced solution, and since it could not easily be ascertained as to what was the depressing agent in these solutions, it was decided to run another series with different combinations of four salts each, to see if any other combination of four salts can more nearly be made to approach the balanced solution.

SERIES IV

Since calcium proved to be so toxic a salt to *B. subtilis*,[4] it was thought that an improvement could be made in the combinations of four salts by using smaller amounts of calcium than were employed in the last series, and solutions of four salts each (shown in table IV)

TABLE IV

All quantities given refer to cubic centimeters of 0.35 *m* solutions
Peptone content 0.91 per cent.

Number	Culture solutions	N as NH_3 formed in cultures, in mg
1...........	100 NaCl 25 KCl 10 $MgCl_2$ 2 $CaCl_2$	20.70
2...........	100 NaCl 25 KCl 10 $MgCl_2$ 1 $CaCl_2$	21.12
3...........	100 NaCl 10 KCl 10 $MgCl_2$ 2 $CaCl_2$	28.42
4...........	100 NaCl 10 $MgCl_2$ 5 $CaCl_2$	25.88
5...........	Peptone in distilled water	42.51
6...........	Peptone in tap water	31.90

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[4] Lipman, Chas. B., Bot. Gazette **48**:105–125. 1909.

were arranged and compared with solution 5 of the last series containing three salts and with a solution of peptone in distilled water and one in tap water.

The large proportion of the potassium salt interfered with the beneficial action of the calcium in solutions 1 and 2, as can be seen by comparing them with solution 3, which differed from the others only in having less potassium and in consequence seems to approach quite closely the peptone solution in tap water, and also is far better than solution 4, which until now showed up as the most favorable solution of all the artificial salt mixtures employed. Solution 5 as before shows the optimum conditions, since there is neither high osmotic pressure nor any toxicity in it to interfere with the ammonification by *B. subtilis*.

SERIES V

Since in the foregoing series we have been gradually approaching a balanced solution in some of the salt mixtures, it is appropriate to compare them now with sea water, both in its original and diluted forms, as well as with RINGER'S solution (which consists of 100 parts NaCl, plus two parts KCl, plus two parts $CaCl_2$), and with a solution made up so as to constitute an artificial sea water (VAN'T HOFF'S solution). The natural sea water was obtained from Pacific Grove, California, and by titration for chlorids was found to have a con-

TABLE V

ALL QUANTITIES GIVEN REFER TO CUBIC CENTIMETERS OF 0.35 *m* SOLUTIONS, EXCEPT AS EXPLAINED ABOVE

Number	Culture solution	N as NH_3 formed in cultures, in mg
1..........	100 NaCl 10 $MgCl_2$ 5 $CaCl_2$	25.88
2..........	100 NaCl 10 KCl 10 $MgCl_2$ 2 $CaCl_2$	28.42
3..........	RINGER'S solution	19.74
4..........	Natural sea water	10.72
5..........	Dilute sea water	31.35
6..........	Artificial sea water (VANT' HOFF'S solution)	31.41

centration of 0.53 *m with an alkaline reaction.* The dilute sea water was made by adding distilled water to the concentrated sea water until a concentration of 0.35 *m* (or that used in all the other solutions) was obtained. The artificial sea water is VAN'T HOFF'S solution and is neutral in reaction, thus according with the reaction of all other solutions employed.

The superiority of the sea water solutions whose concentration does not exceed 0.35 *m* can be easily seen from table V. It is plain that the artificial sea water and the natural sea water of the same concentration are by far the most superior of any salt mixtures tried, and though in the last table it is compared with the most favorable salt mixtures and those which appear to approach most closely to a balanced solution, it excels even those to quite a marked extent. RINGER'S solution, not having the magnesium salt which seems to act so beneficially in balancing solutions for *B. subtilis*, gives only a fair ammonification coefficient as compared with other salt mixtures.

SERIES VI

It seemed of interest to see what effect the addition of magnesium to the RINGER'S solution would have, and a series was therefore arranged to show this.

TABLE VI

ALL QUANTITIES GIVEN REFER TO CUBIC CENTIMETERS OF 0.35 *m* SOLUTIONS
PEPTONE CONTENT 0.91 PER CENT.

Number	Culture solution	N as NH_3 formed in cultures, in mg
1	RINGER'S solution	19.74
2	RINGER'S solution +10 $MgCl_2$	26.44
3	Artificial sea water	31.41
4	Peptone in brook water	39.89
5	Peptone in distilled water	42.51
6	100 NaCl 10 $MgCl_2$ 10 KCl 2 $CaCl_2$	28.42

It is quite evident that the addition of magnesium to RINGER'S solution has a very favorable effect, and by slightly changing the proportion of the constituents we could easily obtain what appears here to be the optimal solution. The brook water solution was inserted here to add another solution to the number of those which allow so vigorous an ammonification owing to the low osmotic pressure. The artificial sea water, however, still remains far superior to any other salt mixture thus far tried.

SERIES VII

In order to compare to the best advantage the various salt mixtures with the artificial sea water and distilled water solutions, it was decided to arrange in one series the best representatives of the single, binary, ternary, and quaternary salt solutions, along with the artificial sea water and the distilled water peptone solutions.

TABLE VII

ALL QUANTITIES GIVEN REFER TO CUBIC CENTIMETERS OF 0.35 *m* SOLUTIONS
PEPTONE CONTENT 0.91 PER CENT.

Number	Culture solution	N as NH_3 formed in cultures, in mg
1	100 NaCl	20.10
2	100 NaCl 10 $MgCl_2$	23.39
3	100 NaCl 10 $MgCl_2$ 5 $CaCl_2$	25.88
4	100 NaCl 10 $MgCl_2$ 10 KCl 2 $CaCl_2$	28.42
5	Artificial sea water	31.41
6	Peptone in distilled water	42.51

We see here to good advantage the beneficial effects of balancing solutions. Of the large variety of single salts and combinations of salts of various kinds, there was none that could quite approach in efficiency the artificial sea water or the natural sea water of the same concentration, and we are obliged to accept the fact that for bacteria (or at least for that group represented by *B. subtilis*) physiologically balanced solutions are necessary if optimal development of the bacteria is sought for.

DISCUSSION OF RESULTS

The number of combinations of salts that could be experimented with in a manner similar to that above given is of course unlimited, and it is impossible to make determinations of all of them, but in the foregoing series of experiments enough combinations have been tried and sufficient evidence has been adduced to make it quite clear that, for at least one class of bacteria, sea water is a physiologically balanced solution just as truly as it is for animals and the higher plants. Therefore, although some of the results exhibit some puzzling aspects, the prime object of these investigations—to discover whether sea water or other balanced solutions are superior to unbalanced solutions—is attained. The inexplicable facts which are bound to arise in such investigations must be accounted for by future research, but the universality of LOEB'S conception of "physiologically balanced solutions" is more firmly grounded than ever. To the experimental proof of it for animals in the ingenious experiments of LOEB himself are added the no less remarkable results of OSTERHOUT[5] in his work on marine as well as freshwater and terrestrial plants, and to both of these are now added the results above described on the third great class of living organisms which seem to hold the same general relation to balanced solutions as the other two.

SUMMARY

1. The ammonifying power of *B. subtilis* is stronger in artificial sea water or in natural sea water of the same concentration than in any other salt mixture.

2. Sea water may be looked upon therefore as a physiologically balanced solution for *B. subtilis* as truly as it is for animals and the higher plants.

I am indebted to Professor W. J. V. OSTERHOUT of Harvard University for helpful suggestions and critical reading of the manuscript.

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[5] BOT. GAZETTE **42**:127–134. 1906; **44**:259–272. 1907.

BRIEFER ARTICLES

THE PHYSIOLOGICAL CONDITIONS FOR THE DEVELOPMENT OF MONOECIOUS PROTHALLIA IN ONOCLEA STRUTHIOPTERIS[1]

The following investigation was undertaken with the view of ascertaining the validity of the statement made by CAMPBELL concerning the dioeciousness of *Onoclea Struthiopteris*. He says: "In the genus Onoclea, as well as some other Polypodiaceae, the prothallia are regularly dioecious, and only a part of them develop the archegonial meristem. The others remain one-layered, and are often of very irregular form, and may be reduced to a short row of a few cells. All of the 'ameristic prothallia,' as PRANTL calls them, are males. In the majority of the Polypodiaceae these occur more or less plentifully, and are often the result of insufficient nutrition; but in Onoclea it is something more than this, as not only the small prothallia are males, but the large ones are exclusively females, and not hermaphrodite, as in most ferns."[2]

The development of fern prothallia, and their reproductive organs, has been studied until recently more from the morphological than the physiological point of view. Much of the work of physiological importance demonstrates the effect of various light intensities. PRANTL (in 1881) was one of the first to investigate carefully the effect of nutrition. His observations upon cultures of *Polypodium vulgare*, *Aspidium filix-mas*, *Ceratopteris thalictroides*, and *Osmunda regalis* led him to draw the following conclusions: that the food supply determines the development of the prothallia and the separation of the sexual organs; that good cultural conditions favor the production of meristem and the development of archegonia; that poor cultural conditions retard the production of meristem and favor the development of antheridia; that as nitrogen is one of the requisites of a good cultural condition, an insufficient nitrogen supply may be the cause of thickly grouped prothallia bearing only antheridia.

The spores of *Onoclea Struthiopteris* used in the experimental work were collected from yards about Ann Arbor in September and sown soon after

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[1] Contribution No. 114 from the Botanical Department of the University of Michigan.

[2] Mosses and ferns. Edition 2. p. 314.

collected. Cultures were made upon soil in porous clay pots, and in sterilized distilled water.

Germination began in the soil cultures, four to six days after the spores were sown. Six weeks later, antheridia and archegonia appeared. As the genus Onoclea has been considered by most writers to be dioecious, it was interesting to find monoecious prothallia occurring in about 1 per cent. of the soil cultures; the other prothallia seemed regularly dioecious. The monoecious prothallia were of medium size, slightly heart-shaped, with a meristem bearing the archegonia; the antheridia, fewer in number than the archegonia, developed from the marginal cells. Some of the dioecious prothallia were large, heart-shaped, with a meristem bearing many archegonia; others were smaller, filamentous, slightly heart-shaped, or very irregularly shaped. These prothallia were one layer of cells in thickness, lacked a meristem, and the antheridia were formed both from the marginal and ventral cells.

The development of the prothallia did not seem entirely influenced by their position, as indicated by PRANTL, for many of the smaller prothallia, the "ameristic" ones, were found in the less crowded regions; while the larger prothallia, the "meristic" ones, bearing only archegonia, were often found in the more crowded regions.

An attempt was made to produce monoecious prothallia through the influence of an inorganic solution. For this purpose large, heart-shaped prothallia with archegonia in various stages of development were selected and transferred from the soil to BEYERINCK'S solution. Four to seven days later, in one-half of the cultures examined, a number of monoecious prothallia were found, antheridia having developed from the marginal cells of the prothallia, near the notch. In all cases, death of the prothallia immediately followed, which seemed to be due in some cases to too long exposure to direct sunlight, in others to injury of tissue in transferring from the soil to the solution.

Other cultures were transferred from the sterilized distilled water to solutions and kept in moderately weakened light. Two to four weeks later, in these cultures, *the majority of the prothallia became monoecious;* numerous antheridia were produced, both from marginal cells and from the ventral surface cells on the sides, and near the apex of the prothallia. Other prothallia gave rise to numerous proliferations; some were mere filaments bearing antheridia at their apices; others had the thallus form, were distinctly notched, and produced antheridia from the marginal and ventral surface cells.

After all the prothallia needed for experimental purposes had been removed, the pots were set aside and neglected for about two weeks. At the end of this time, the surface of the soil was brown, and all the prothallia appeared dead. The pots were then kept moist under bell jars in weakened light. After a period varying from six to eight weeks, many of the old prothallia had developed adventitious outgrowths. Some of these outgrowths were filaments or irregularly shaped prothallia covered with antheridia. Others developed into elongated prothallia bearing archegonia, which in turn frequently became monoecious by developing adventitious shoots bearing antheridia.

Germination began in the sterilized water cultures four days after the spores were sown. Six days later the prothallia had attained a growth of ten cells. A set of cultures was then made, by transferring 100 prothallia to each of several nutritive solutions. For each of these sets a control set was kept in sterilized distilled water. Six weeks after the prothallia had been transferred to the nutritive solutions, male prothallia bearing antheridia and female prothallia bearing archegonia were observed in about equal proportions. The prothallia were regularly dioecious, and at this time no monoecious prothallia were observed. That these antheridia and archegonia were functional is shown by the production of vigorous young sporophytes. One of these sporophytes lived five months in KNOP'S solution, and developed five fronds, one of which was 2.5^{cm} in length. Twelve weeks after the transference of the prothallia to the nutritive solutions, many monoecious ones were observed in the cultures of KNOP'S solution. These first developed the meristem with archegonia, afterward antheridia were formed from the marginal and ventral cells of the adventitious outgrowths.

CAMPBELL (*l. c.* 321) makes the statement that "as soon as an archegonium is fertilized, no new ones form, but it frequently happens that a very large number prove abortive before finally fertilization is effected." In all the cultures examined, both from the soil and the nutritive solutions, frequently prothallia have been observed producing new archegonia after fertilization had taken place. In the solution cultures young archegonia, antheridia, and sporophytes were present at the same time upon the same prothallia.

A further attempt to produce monoeciousness was made, by transferring prothallia bearing archegonia from one nutritive solution to another. Results were obtained in the following cultures: (*a*) from KNOP'S solution to BEYERINCK'S solution, lacking potassium dihydrogen phosphate; (*b*) from SACHS'S solution with 1 per cent. potassium phosphate, to KNOP'S solution. In these cultures, three to four weeks after the transfer had been made, monoecious prothallia were observed. The prothallia continued to grow for ten to eleven weeks and developed many adventitious outgrowths bearing antheridia. Young sporophytes were also developed.

In summing up, therefore, it may be said: monoecious prothallia, as well as dioecious prothallia, were observed in soil cultures; monoecious prothallia were obtained from "female" prothallia transferred at a ten-celled stage from distilled water to KNOP'S solution; monoecious prothallia were obtained by transferring "female" prothallia from the soil to a nutritive solution; they were also obtained by transferring prothallia from one nutritive solution to another.

The experimental work of this paper was done in the botanical laboratory of the University of Michigan. I wish to express my indebtedness to Dr. C. H. KAUFFMAN, who suggested the problem and under whose guidance and inspiration the work was carried on.—ELIZABETH DOROTHY WUIST, *University of Michigan.*

CECIDOLOGY IN AMERICA

Botanists are usually interested in the malformation of plants, and some of the earliest literature contains references to these abnormal structures. However, cecidology is one of the latest of the biological sciences to be developed. The literature is so involved with other branches of biology that only those who have given special attention to the subject can have a very clear conception of the dimensions of modern cecidology and the character of its problems. The entomologists have given far more attention to the subject, in both Europe and America, than any other group of scientists. For this reason many have come to consider cecidology as a branch of entomology, while as a matter of fact the entomologist has much greater interest in the insects than in the galls.

Cecidology now includes all hypertrophies caused by specific organisms, as insects, nematodes, fungi, and bacteria. It has been suggested that the term "gall," which has been in use since the sixteenth century, be discontinued and the word *cecidium* be substituted; also that the structures caused by these different organisms be designated as diptero-cecidia, phyto-cecidia, nemato-cecidia, myco-cecidia, etc. Some writers have been inclined to include that very much confused and mysterious class of diseases known as teratology under the head of cecidology, and there appears to be no conclusive argument as to why it should or should not be so considered.

The early literature is so thoroughly involved with other subjects as to be practically unavailable to the general students, many valuable references being found in papers upon other subjects, with nothing whatever in the titles to indicate their presence. For this reason many workers in both botany and entomology have frequently thrown aside interesting material.

A brief résumé of the subject may be of interest to the students of botany. Very little work was done and very few papers published before 1861, when C. R. von Osten-Sacken, of the foreign diplomatic service in Washington, began the publication of a series of papers which appeared in the Proceedings of the Entomological Society of Philadelphia, various U. S. government publications, Smithsonian Institution publications, etc. Since that time many entomologists have published valuable papers on this subject and also many important notes in connection with papers on other phases of entomology. Up to the present time there have been about 125 workers who have given some attention to this subject in North America, and they have published approximately 350 papers and notes.

In Europe the subject is very little older than in America, but has attracted the attention of far more workers. Although there have been approximately 350 workers, who have issued about 1200 publications, not more than 100 were published before 1861, which date may be considered the beginning of the subject in this country. It is also true that the greater part of the work in Europe has been done by the entomologists, but in recent years a great deal of attention has been devoted to the study of the cecidia themselves.

From the viewpoint of the botanist, cecidology presents a most interesting field for research. Both botanist and entomologist are continually confusing the cecidia caused by fungi and insects, and the confused state of the literature has led to the neglect or abandonment of many interesting problems. The fact that most of the work has been done by the entomologist has made the literature somewhat inaccessible to the botanist, and has also given the younger botanists a misconception of the character of the subject.

Not only has the confusion caused the neglect and abandonment of problems, but has caused some rather interesting and amusing statements as the result of misinterpretations. This may be illustrated by *Bucida buceras*, a tropical plant which produces two kinds of fruits, one small and the other long. Both names (*Bucida* proposed by Linnaeus in 1759 and *buceras* by P. Browne in 1756) are derived from the long fruits, which authors considered as resembling the horn of a bull. However, recent studies have shown that the long fruits were hypertrophied as the result of mite injuries.[3]

Cecidology is not only closely interwoven with entomology, but also

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[3] Britton, N. L., The generic name Bucida; and Cook, Mel. T., The hypertrophied fruit of *Bucida buceras*. Bull. Torr. Bot. Club **35**:303–306. 1908.

with mycology, bacteriology, plant pathology, and plant physiology. The connection with entomology is fully appreciated and needs no comment at this time. Many fungi produce cecidia, but the character of these cecidia have received as little or less attention from the mycologist than the insect cecidia from the entomologist. The cecidia on the roots of legumes and the recent investigations of SMITH and TOWNSEND on crown galls demonstrate the relationship to bacteriology. Since the cecidia from whatever cause are pathological conditions of the plants, cecidology becomes a well-defined part of plant pathology. Until recently, plant pathology has been more especially interested with the cause and control of diseases, in fact has been a branch of mycology. However, with the further progress of the subject we must come more and more to recognize the necessity of a study of the pathological condition of the plant. This feature of the work will involve the most careful and exact methods of the plant physiologist. However, the connection of cecidology with physiology is not only through pathology, but direct. There is that long-mooted question concerning the character of the stimuli in the formation of cecidia, which has never been answered satisfactorily.

An explanation of the character of the stimuli in the formation of myco-cecidia might give some aid in answering the question, and this latter problem is undoubtedly within the province of plant physiology. The explanation of why injuries result in hypertrophies in some cases and atrophies in others is also an interesting problem for some ambitious student of botany. The fact that "the morphological character of the gall depends upon the genus of the insect producing it rather than upon the plant on which it is produced," as demonstrated by the writer,[4] suggests an interesting field of investigation. The so-called evolution of the cecidia may be a response to physiological conditions rather than to evolutionary factors.

The distribution of cecidia as compared with the distribution of the host plant furnishes a good supply of work for the ecologist, while the injurious character and valuable properties of many cecidia will give profitable fields for the economic phases of the biological sciences.

The greatest need of cecidology in America at the present time is the cataloguing and indexing of the literature and the indexing of the cecidia with reference both to the causes and to the host plants. To this should be added up-to-date, available descriptions of the cecidia and the organisms which cause them. Some work along this line has been done by MR. WM. BEUTENMÜLLER of the American Museum of Natural History, and by the writer.

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[4] COOK, MEL. T., Galls and insects producing them. Ohio Naturalist **2**:263–278. 1901.

There is at the present time one international publication devoted entirely to cecidology, *Marcellia*, now in its eighth volume, edited by Dr. A. TROTTER, Avellino, Italy, which publishes original papers and also current bibliography.— MEL. T. COOK, *Delaware Agric. Exper. Station, Newark.*

FIXING AND STAINING TANNIN IN PLANT TISSUES WITH NITROUS ETHERS

(WITH EIGHT FIGURES)

Immature dates exposed to the vapor of amyl or ethyl nitrite to stimulate premature ripening were observed to turn dark brown very rapidly. This was found to result from the staining of the giant tannin cells which occur near the cuticle. After several hours' exposure, hard tannin grains were formed in the tannin cells of green dates and persimmons, which had the same physical characters as the grains occurring naturally in ripe fruit; they could be separated quite pure by gravity in water, and when pressed beneath the cover glass fractured like grains of gelatin.

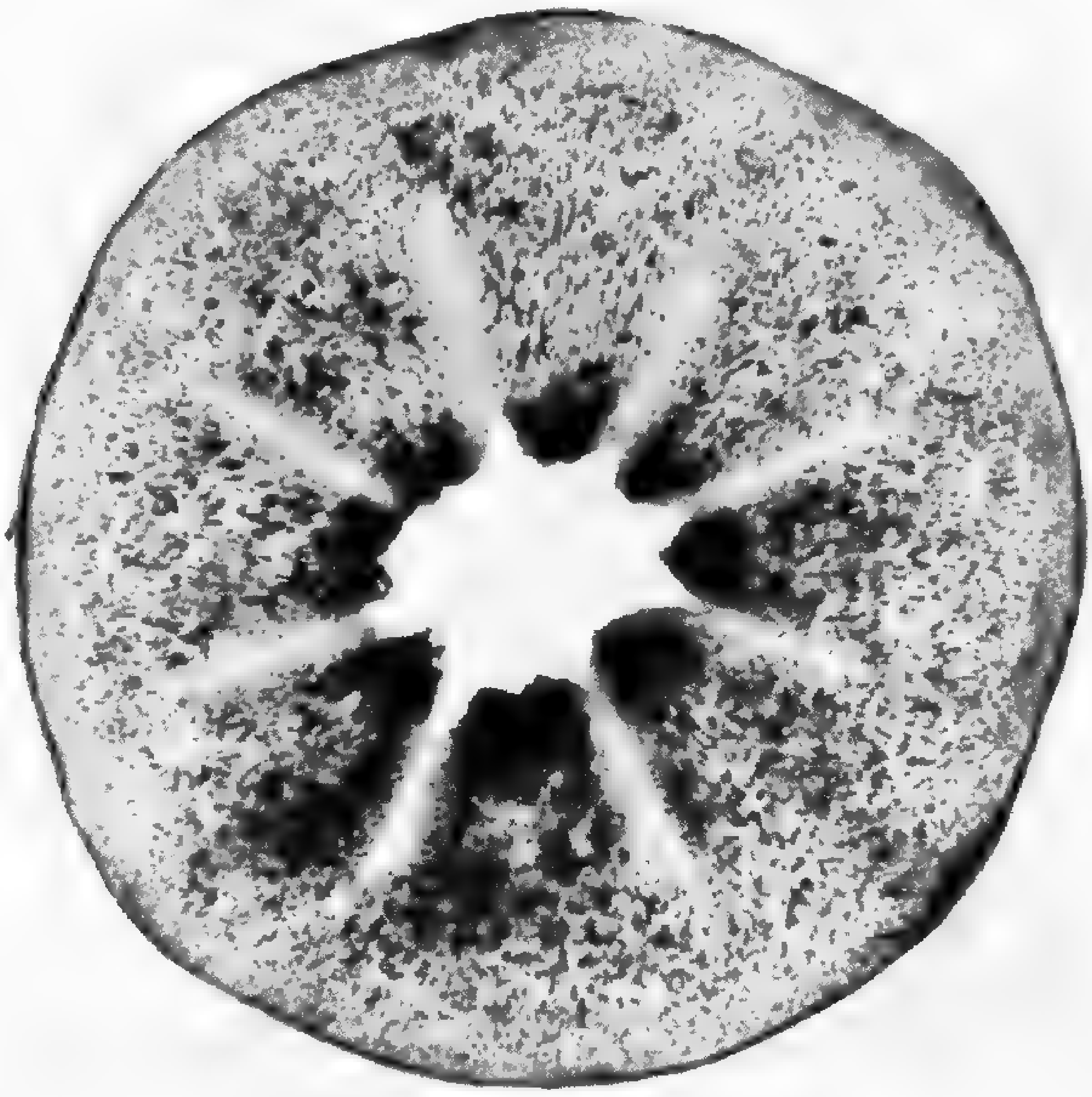
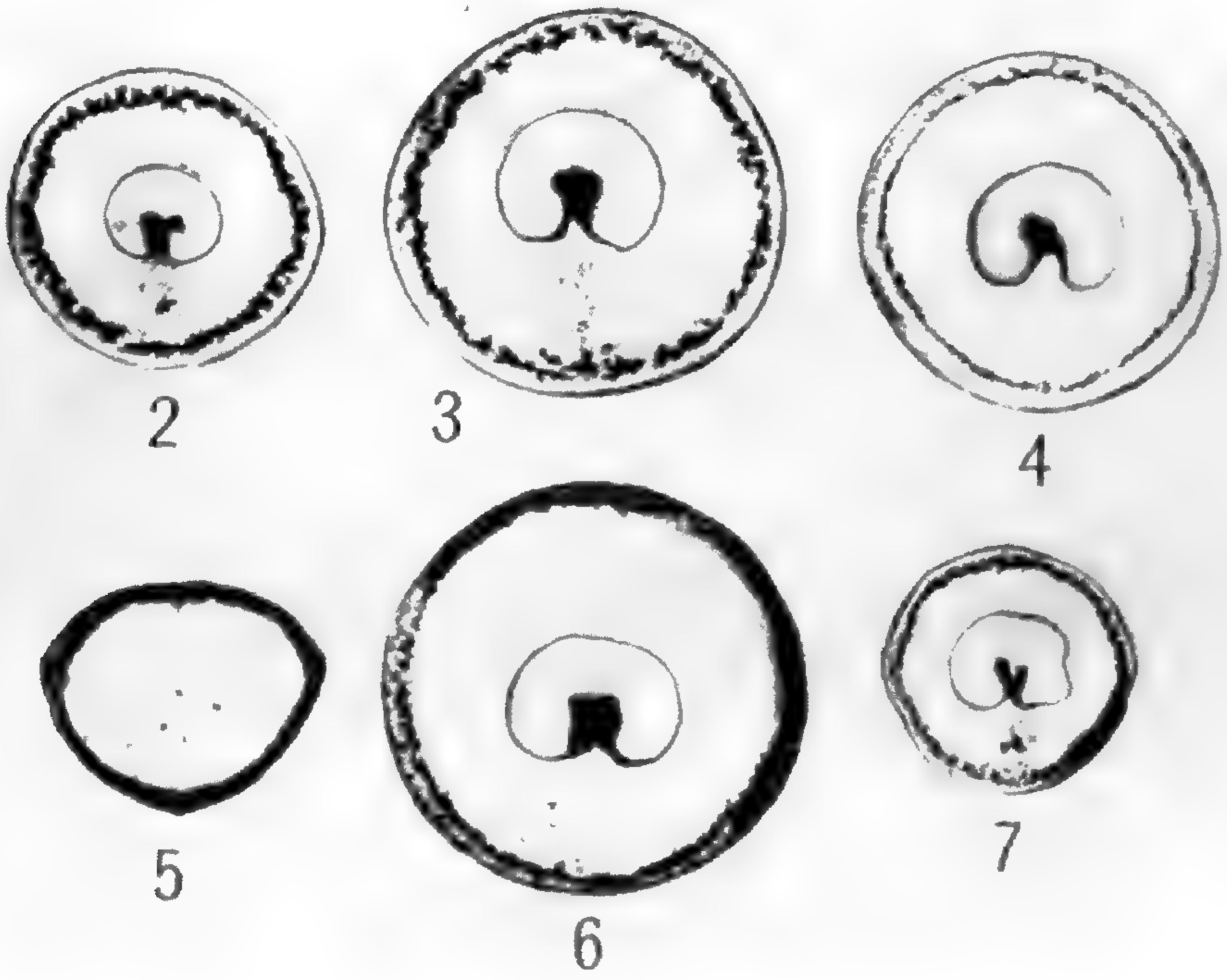


FIG. 1.—Japanese persimmon.

The juice of the unripe date gives a dense brown precipitate with ethyl or amyl nitrite or with sodium nitrite and free acid. Persimmon juice gives an intense deep wine-red color, but no precipitate. Tannic and gallic acids give yellow, while phloroglucin and some other higher phenols give a red color very similar to that given by date or persimmon juice. Phloroglucin also gives a precipitate, but it does not correspond in appearance with that given by date juice. The other higher phenols also give yellow or red color reactions with nitrous ether. The gummy matter, pectin, etc., precipitated from the juice by alcohol carries with it much of the substance that reacts with the nitrite, and the color given by this precipitate increases by repeated precipitations. Date juice obtained under low pressure continues for many weeks to give the ethyl nitrite reaction, as also the reactions with formaldehyde and ferric chlorid, but juices obtained under very high pressure, after standing, lose the property of giving these reactions, excepting that with ethyl nitrite a very much lighter colored precipitate is formed. Davy[5] found the color reaction between gallic acid and nitrous acid very delicate, and applied it to the colorimetric estimation of nitrites.



Figs. 2–7.—*Fig. 2*, Deglet Noor date; *fig. 3*, Oga de Bedreschen; *fig. 4*, Birket el Haggi; *fig. 5*, seedling unfertilized; *fig. 6*, same seedling fertilized; *fig. 7*, M'Kentichie Degla.

It is thus not easily proven whether the precipitate formed in the date juice is due to date tannin alone or whether other substances enter the reaction. Tannin or its derivatives, however, are essential to the reaction, as shown by the following evidence. Only those cells in the date are stained by ethyl nitrite which have been shown to carry tannin by the ferric chlorid, ammonium molybdate, and cupric acetate reactions. Ripe date juice no longer gives the reaction, and immature fruits lose their astringency after very moderate treatment with ethyl nitrite. Juices treated with lead subacetate, gelatin acid salt solution, and hide powder no longer

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[5] Through J. Dekker, De Looistoffen II. p. 44. Amsterdam. 1908.

give the reaction. The lead subacetate precipitate, as also the gelatin and hide powder residues, is stained very dark brown by the reagent.

The method proves very convenient in studying the distribution of tannin in fruits and other parts of plants. Tissues which can be distinguished only with difficulty in the unstained hand section become very sharply differentiated after treatment with nitrous ether vapor. For example, a piece of the woody fruit stem of the date stained in this way reveals a very narrow tannin zone near the cuticle, corresponding very closely to the more prominent one in the fruit. In thin section this zone resolves into rather widely separated, very small, dark-colored cells. A large Japanese persimmon weighing one-half pound can be completely stained in 24 to 48 hours without any abrasion of the cuticle. The process offers the further advantage that the tannin is deposited in the cells where it occurs, and thus eliminates all danger of carrying soluble tannin across the face of a section. In the date the outer tannin-bearing tissue detaches and may be separated very easily and sharply from the inner tannin-free tissue after prolonged exposure to ethyl nitrite. In some fruits, certain cells stain violet or lilac instead of brown, while others take no stain whatever until after prolonged treatment. This is notably true in the wild persimmon, which stains brown very readily just beneath the skin and again at the center of the fruit, with the exception of occasional cells interspersed through the flesh. Further exposure to the vapor of nitrous ether stains all the tannin cells uniformly brown. It is not evident whether this phenomenon depends entirely on permeability of the cell walls, or whether there is an actual difference in chemical composition of the cell contents.

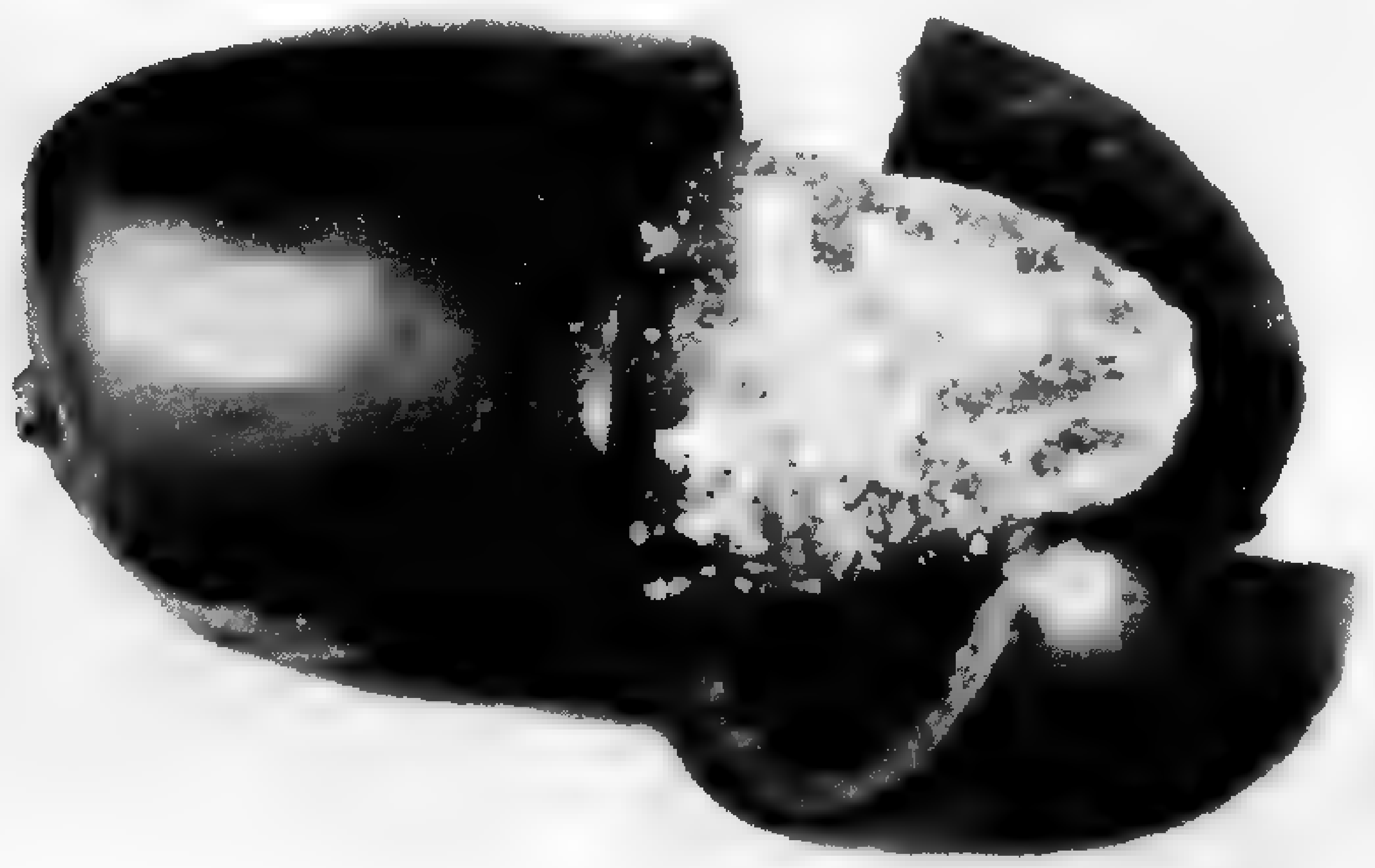

FIG. 8.—Deglet Noor date showing sharp separation of tannin layer from inner flesh after ethyl nitrite treatment.

For laboratory use a 20 per cent. alcoholic solution made by diluting the 90 per cent. commercial nitrous ether is recommended. Amyl nitrite may be used, but is disagreeable to work with. Ordinary sweet spirits of niter, which contain about 4 per cent. ethyl nitrite, may be used, but will require much longer exposure.—A. E. VINSON, *Arizona Agric. Exper. Station, Tucson, Arizona.*

CURRENT LITERATURE

BOOK REVIEWS

Phylogeny of plants

The first volume of LOTSY's huge work, dealing with the thallophytes, was published in 1907 and was noticed in this journal.[1] The second volume has now appeared[2] and includes the "archegoniates." The speed at which such large volumes have been organized for publication, and the extensive range of literature traversed in compiling the facts and the illustrations, are both impressive. But no one man can deal authoritatively with the whole plant kingdom, and the wisdom of so comprehensive a plan by one author is questionable. If it be undertaken, the usefulness of the work depends upon his appreciation of the relative values of investigations, his general perspective, and his organizing power. LOTSY has stood this test as well as could be expected, and although there are abundant grounds for criticism, the book is on the whole a fairly logical and copiously illustrated digest of the current literature. It will serve as a useful encyclopaedia of general information in reference to the present knowledge of bryophytes, pteridophytes, and gymnosperms, and the current speculations regarding them. Of course the whole thesis is the evolution of the plant kingdom.

The chief criticism must fall undoubtedly on the sometimes radical changes proposed in classification on debatable grounds, and on the author's conceptions of phylogeny, which others may be disposed to consider erratic. Thus, in the bryophytes, Anthoceros is accorded the status of the most primitive liverwort, on the ground that it is nearest the algae in having in each cell only one chloroplast and this furnished with a pyrenoid. Then, having discussed Riccia as the liverwort with the simplest sporophyte and Sphaerocarpus as "the simplest known liverwort," LOTSY predicates a "Sphaeroriccia" as the hypothetic *Urform*, from which Anthocerotales, Marchantiales, and "Metzgeriales" separately sprang, the latter spraying out into the Jungermanniales (Acrogynae).

The portion of the volume dealing with pteridophytes (318 pp.) and the "polyciliate" gymnosperms (80 pp.) gives opportunity to add to the older data an unusually large volume of recent work, and LOTSY does not hesitate to formulate here also his own theories, even in connection with groups in which he has done no investigation. The following statements may be taken as illustrations:

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[1] BOT. GAZETTE **43**:421. 1907.

[2] LOTSY, J. P., Vorträge über botanische Stammesgeschichte, gehalten an der Reichsuniversität zu Leiden. Ein Lehrbuch der Pflanzensystematik. Zweiter Band: Cormophyta Zoidogamia. Imp. 8vo. pp. 902. *figs. 553.* Jena: Gustav Fischer. 1909. *M* 20.

"We can think of Marattia as having come from Angiopteris by the fusion of sporangia"; "the fertile spike of Botrychium is not a whole leaf, but only a branch of the foliage leaf"; "Marattiales and Cycadofilices are two branches differentiated from Primofilices."

The taxonomic groupings in certain particulars seem to be more original than necessary. The Sphaerocarpaceae, including as a tribe the Rielleae, appear among the Marchantiales; the Jungermanniales Anacrogynae have become the Metzgeriales, leaving the Acrogynae only as the Jungermanniales; and many novel arrangements appear in the Bryales, which cannot be stated in detail. Of course the vascular groups presented are all "Diploidales," and the two principal divisions are the *Biciliaten* and the *Polyciliaten.* This naturally results not only in detaching Isoetes from the Lycopodiales, but also subordinates the boundary between pteridophytes and spermatophytes. There may be no objection to either of these results, but the single character used to secure them is more than questionable.

The bibliography is copious, but by the method of its presentation it is repetitious and not specific; nor is it so complete in its citations as one would expect from the editor of a bibliographical journal. The index is unfortunately double, but otherwise excellent, and puts the reader in easy command of the contents.—J. M. C. and C. R. B.

MINOR NOTICES

A flora of the Dutch West Indies.[3]—The first volume of this work deals with the flora of the islands of St. Eustatius, Saba, and St. Martin. The work is divided into three parts. The first part is concerned with taxonomy, the second presents a historical account of the flora, and the third deals with the phytogeography of the islands. The taxonomic portion is based mainly on the collections of SURINGAR, VAN GROL-MEYERS, LIONARONS, and BOLDINGH, whose collections are deposited either in the Rijks herbarium at Leiden, the herbarium at Utrecht, the Colonial Museum at Haarlem, or in the herbarium of KRUG and URBAN at Berlin. The sequence of the families and genera is essentially that of DE DALLA TORRE and HARMS'S *Genera Siphonogamarum*, and the nomenclature is in accordance with the International Rules adopted at Vienna in 1905. The taxonomy occupies the major part of the volume, covering over 200 pages, and consists of an enumeration of the species with reference to original publications, a very limited synonomy, and the citation of plants collected on the different islands. About 500 genera and approximately 800 species are recorded. The second part contains interesting and important historical matter, particularly as to itineraries of collectors and lists of their plants. The third part embraces detailed information as to the natural features of the islands, a series of tables on distribution, a bibliography, and finally an index to vernacular and scientific

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[3] BOLDINGH, I., The flora of the Dutch West Indian Islands St. Eustatius, Saba, and St. Martin. Roy. 8vo. pp. xii+321. *maps 3.* Leiden: E. J. Brill. 1909.

names. The volume is of moderate size and well printed, but the introduction of keys, especially in case of some of the larger genera, would have added somewhat to the usefulness of the work in the identification of species. Nevertheless, as a catalogue of the known species of the islands, it is a commendable contribution to taxonomic literature and will serve as an excellent basis for future studies on the flora of the region.—J. M. GREENMAN.

Natürlichen Pflanzenfamilien.[4]—Parts 236 and 237 contain a supplement to the Conjugatae and Chlorophyceae by the distinguished algologist Professor N. WILLE. Two new genera are included, namely *Pseudopringsheimia* and *Pseudulvella* of the Chaetophoraceae; the former is based on *Ulvella confluens* Rosenv., an epiphyte growing on marine algae of the north Atlantic; the latter is based on *Ulvella americana* Snow, also an epiphyte, and occurs on freshwater algae of North America. Parts 238–240, likewise of recent issue, consist of a general index to Teil I of this great work.—J. M. GREENMAN.

NOTES FOR STUDENTS

The life history of Griffithsia.—LEWIS[5] has published a paper on the life history of *Griffithsia Bornetiana*. The paper begins with the presentation of the vegetative characters of the three different individuals of this species: antheridial, procarpic, and tetrasporic. The author records comparative studies of the size of the cells in the three individuals, discusses the nature of intercellular connections, describes the division of chromatophores, and calls attention to the phenomenon of an approximate simultaneous occurrence of the nuclear divisions in multinucleate cells. There are then described the development of antheridia, cystocarps, and tetraspores; the methods of vegetative propagation; germination of spores; and tetraspore-like structures on sexual plants. The paper closes with a discussion of results, in which the author presents his views on alternation of generations in Griffithsia.

Some of the cytological results are as follows. The nuclei in Griffithsia are throughout their history very poor in linin. The chromatin of the resting nucleus, therefore, is not distributed on a linin reticulum, but is chiefly contained in a centrally placed, homogeneous nucleolus or "karyosome." As regards the mode of formation of chromosomes, the chromatin passes out of the nucleolus until the whole chromatin content is distributed through the nuclear cavity in the form of granules. These granules are much more numerous than the chromosomes, and probably by the fusion of separate granules chromosomes are formed. The number of chromosomes in the nucleus of vegetative cells in the tetrasporic plant

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[4] ENGLER UND PRANTL, Die natürlichen Pflanzenfamilien, etc. 236 and 237 Lieferung. Conjugatae und Chlorophyceae von N. WILLE. Nachträge zum I. Teil, 2 Abt., Bogen 1–6, pp. 96; 238 bis 240 Lieferung. Register zu Teil I (vollständig), pp. 242. Leipzig: Wilhelm Engelmann. 1909. *M* 3, *M* 4.50.

[5] LEWIS, I. F., The life history of *Griffithsia Bornetiana*. Annals of Botany 23:639–690. *pls. 49–53.* 1909.

seems to be with certainty fourteen, and that of the sexual plant is about seven. Spindle fibers are formed, apparently by the rearrangement of the linin thread, so that the spindle is intranuclear. Kinoplasmic caps are present only during the nuclear division. The changes in the nucleus of the tetraspore mother cells are striking. The nucleolus fragments into several rounded bodies of various sizes, which after continuous fragmentation yield 12–14 rounded masses of chromatin of about the same size. These bodies become again irregular in form, and fuse with one another, so that their number is reduced by more than half. This stage LEWIS considers to represent synapsis, but it differs from the usual type. Fourteen chromosomes then appear and are scattered in the nuclear cavity. After telophase of the first division in the tetraspore mother cell, the daughter nuclei rest before commencing the second division. In the sporelings from tetraspores about six or seven chromosomes appear; in those from carpospores the number has not been ascertained exactly, but the author believes them to be diploid. Cell division in sporelings occurs usually when about sixteen nuclei are present, so that the coenocytic condition is attained very early in Griffithsia. Tetraspore-like structures on an antheridial plant have been found in only one case out of all plants examined. In this structure the cleavage furrow either does not reach the center of the cell or no trace of it occurs. Nuclear conditions have not yet been followed thoroughly.

From the cytological evidence brought forth in this paper, LEWIS considers that there exists in *Griffithsia Bornetiana* an alternation of generations similar to that described for *Polysiphonia violacea* by the reviewer. The fusion nucleus, which contains fourteen chromosomes, produces the cystocarp in which are formed carpospores. The nuclei of tetrasporic plants contain fourteen chromosomes, and it seems reasonable therefore to assume that the tetrasporic plants arise from carpospores. In tetraspore formation the number is reduced one-half, and seven chromosomes enter the nucleus of the tetraspore. It seems probable that on germination the tetraspore gives rise to the individual whose nuclei contain seven chromosomes and which bears sexual organs.

As to whether the alternation of generations in Griffithsia is to be regarded as antithetic or homologous, the conclusions are as follows: (1) "There is in Griffithsia an antithetic alternation of generations, the gametophyte being represented by the sexual plants, the sporophyte by the sporogenous cells of the cystocarp." (2) "In addition to this there is a regular succession of tetrasporic individuals and sexual individuals. The tetrasporic individuals resemble the sporophyte in the number of chromosomes; they resemble the gametophyte in morphological differentiation. They are to be considered as a phase of an homologous alternation of generations, not the equivalent, wholly or in part, of the sporophytes of archegoniates." To draw these conclusions, LEWIS has put more weight upon the two following factors than upon the fundamental chromosome difference between sporophytic and gametophytic nuclei: (1) the outer morphological similarity of the tetrasporic plant to the sexual plant; (2) the fact that either seems capable of producing the outer morphological equivalent of the reproductive structures of the other, although the real nature of the structures has not yet been determined.—SHIGÉO YAMANOUCHI.

Development and biology of Armillaria.—FISCHER,[6] of the Indian Forest Service, has given a brief but interesting account of the development of the fruit bodies of *Armillaria mucida* Schräd., an agaric with a very slimy outer surface, which is common in parts of Europe, growing often in dense tufts on certain of the hard-wood trees. There is a thin universal veil present from the primordium stage to the time that the fruit body is rapidly expanding, which consists of interwoven threads forming a layer two or three cells deep. In an early stage of the primordium a palisade layer of cells is formed over its convex upper surface, just underneath the universal veil. This marks off the pileus, which now begins to expand laterally, also loosening the fundamental tissue between its lower margin and the future stipe, thus providing for the gill cavity, while at the same time the development of a palisade layer is continued from the margin inward over the roof of the gill cavity to form the primordium of the hymenium. The loose fundamental tissue between the margin of the pileus and the outer surface of the stem forms the partial veil. The slime which covers the plant is formed from the mucilaginization of the outer ends of the palisade tissue on the surface of the pileus.

The writer states (p. 504) that the present reviewer "seems to accept HARTIG'S account of the development in *Armillaria mellea* as substantially correct." Thus is discretion in the matter of not prejudging a case which is under investigation rewarded! A study of the development of *Armillaria mellea* was made by the reviewer several years ago, and an account[7] of it was presented before Section G of the A. A. A. S. at the New Orleans meeting, in connection with that on *Agaricus campestris*, the latter of which was published.[8] He has been holding the work on *Armillaria mellea* for some further study to clear up some details. There is nothing in this paper on *Agaricus campestris* which can be construed as either supporting or contradicting HARTIG'S account, and the writer carefully held to neutral ground.

It is to be hoped that FISCHER will continue his studies in the Agaricaceae, and that others also may be induced to undertake similar work. But it is just as much to be desired that either good photomicrographs be used to illustrate the work, or that good drawings be made, for little praise can be given to the illustrations accompanying this otherwise creditable paper.—GEO. F. ATKINSON.

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[6] FISCHER, C. C. E., On the development of the fructification of *Armillaria mucida* Schräd. Annals of Botany **23**:503–507. *pl.* 35. *figs.* 1–7. 1909.

[7] ATKINSON, GEO. F., The development of *Armillaria mellea;* the development of *Agaricus campestris*. Proc. A. A. A. S. 53rd Meeting, Dec. 1905—Jan. 1906. *Ibid.* Science N. S. **23**:203. 1906.

[8] ———, The development of *Agaricus campestris*. BOT. GAZETTE **43**:215–221. *pls.* 7–12. 1906

FISCHER has also investigated the biology of *Armillaria mucida*,[9] more especially with a view to determining whether the fungus is a parasite or a saprophyte. Most writers simply state that the fungus grows on beech trees, but MASSEE records that "at High Beech, Epping Forest, ... a healthy branch of a beech having been broken off, the wound was inoculated with the spores of *A. mucida*. At the end of the second season after the inoculation the branch was killed for a considerable distance, and the sporophores of the fungus appeared in abundance." FISCHER, unwilling to accept this observation as proof that the fungus is a parasite, has attempted to infect wounds made in living beech trees with spores or with mycelium. His experiments gave negative results, so that he was unable to obtain any proof of the alleged parasitism of the fungus. On the other hand, he found that the fungus could be grown readily as a saprophyte on various substrata, such as bread, dead beech wood and twigs, and also upon gelatin containing beerwort, meat extract, or malt extract. The time elapsing between the sowing of the spores and the ripening of the fruit bodies in pure cultures varied from 51 to 109 days. The spores germinate readily in water as well as in various culture media. FISCHER'S inoculations were carried out on thin branches. Possibly, if stouter branches containing older wood had been used, positive results might have been obtained. So far, however, there does not seem to be any clear evidence that the mycelium of *A. mucida* can kill the living parenchyma and medullary ray cells in beech wood.

FISCHER states that a spore, after arising somewhat laterally on its sterigma, "only assumes the central position later on as it approaches maturity." The figure given of the mature basidium does not support the statement that the spore is situated symmetrically over the sterigma. If FISCHER'S observation is correct, then *Armillaria mucida* is a marked exception to the general rule for the position of the mature spores in Hymenomycetes. There is one misquotation, doubtless due to a printer's error, from a paper by the writer. The number of spores that I found to have been produced from a large fruit body of *Polyporus squamosus* was 11,112,500,000, and not 11,112,500 as stated.[10] FISCHER urges that since the number of spores produced from a fruit body is so vast, wounds on trees must often become infected, and that stumps or timber infected with *Armillaria mucida*, as well as its fruit bodies, should be destroyed when possible. It may be added that eleven thousand million spores would be sufficient to provide one for each square inch in nearly three square miles of level ground.—A. H. REGINALD BULLER.

Chemotropism of pollen tubes.—In 1889 MOLISCH showed that pollen tubes grow toward pieces of the stigma (chemotropism), and grow away from the edge of a cover-glass preparation (aerotropism). Five years later MIYOSHI found that

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[9] FISCHER, C. C. E., The biology of *Armillaria mucida* Schräder. Annals of Botany **23**:515–535. *pls. 36, 37*. 1909.

[10] BULLER, A. H. R., The biology of *Polyporus squamosus* Huds., a timber-destroying fungus. Jour. Econ. Biol. **1**:114. *fig. 6*. 1906; also Researches on Fungi. Part I, chap. 5, 1909. London: Longmans, Green & Co.

various carbohydrates deflected pollen tubes, and in 1899 LIDFORSS reported that they were responsive also to certain proteins. In the last ten years, with the exception of a few papers by the same author, nothing has appeared on the responses of pollen tubes. Now LIDFORSS, who has been prosecuting his researches year after year, in the short periods available each season for any particular plant, presents the results in detail.[11] First he discusses the effect of various chemical agents upon the germination of the pollen. In the section on proteo-chemotropism, LIDFORSS lists the large number of proteins of various groups that have yielded definite results. In general it may be seen that the pollen tubes are indifferent to cleavage products of proteins, and are harmed by the albumoses and peptones tried. On the contrary, to the albumins, globulins, nucleo-albumins, coagulated proteins, and glycoproteins, nineteen in all, the tubes respond by positive curvatures. The nucleo-proteins differ much, some being attractive, some apparently indifferent, and some poisonous. Besides the tropic action of the proteins, they accelerate the growth of the tubes, which also tend to branch in some cases. The reaction time in most favorable cases for *Vallota purpurea* is less than 5 min., and for *Narcissus Tazetta* and *Tradescentia virginica* less than 2–3 min. The liminal value of the concentration was difficult to determine. In the case of diastase with *Vallota purpurea* it was about 0.1 per cent. Only one case of apochemotropism with proteins was observed (*Scilla campanulata* with diastase), and as this could not be confirmed by later experiments it was possibly due to some impurity of the diastase used. Proteo-chemotropism has been found in 13 families of monocotyls and 42 families of dicotyls, so that it may be considered as of general occurrence in angiosperms.

Saccharo-chemotropism was not investigated extensively by LIDFORSS, but his limited observations, combined with those of MIYOSHI, make it probable that responses to various carbohydrates are also general among angiosperms. Osmotropism was clearly shown by some tubes, and the author promises a later paper on this subject. In a special part, an appendix to the body of the paper, there are details regarding all the species of pollen studied, as to favorable conditions for germination and the responses obtained. These furnish useful details for laboratory directions in employing these experiments in instruction.—C. R. B.

Persistence of characters in Aspergillus.—KOMINAMI[12] has investigated the persistence of characteristics induced in *Aspergillus niger* by subjecting that mold to unusual cultural conditions, in this case strong solutions of common salt. The conidia used in the experiments were obtained from three strains: (1) from cultures on normal nutrient media; (2) from cultures grown for one generation on nutrient solution containing 6 per cent. of salt; and (3) from cultures grown for

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[11] LIDFORSS, B., Untersuchungen über die Reizbewegungen der Pollenschläuche. I. Der Chemotropismus. Zeit. Bot. **1**:443–496. *pl. 3.* 1909.

[12] KOMINAMI, K., Biologisch-physiologische Untersuchungen über Schimmelpilze. Jour. Coll. Sci. Tokyo **27**:1–33. *pls. 3.* 1909.

ten generations on media containing 5 or 6 per cent. of salt. Conidia from each of these strains were sown in solutions containing 20.4 to 22 per cent. of salt. It was found that conidia from strains which had previously been accustomed to 6 per cent. salt solution germinated more rapidly and grew more vigorously than conidia from normal solutions. Conidia from the strain accustomed for ten generations to salt showed the same effect in a more pronounced manner. When conidia from all strains were sown on normal nutrient solution, the strains adapted to salt grew more poorly and consequently fruited sooner than the strains not adapted. When all strains were sown on salt solution, the reverse effect was observed. The accommodation to salt solution did not disappear after ten generations of culture on normal media. Attempts to establish persistency of accommodation to higher osmotic pressures and to some poisons gave negative results.

The author has attacked this problem, as he states in the introduction, from the standpoint of inheritance of acquired characters. It seems doubtful if the idea of inheritance can be applied perfectly in such cases as described in the foregoing, where the whole protoplasm in the organism is modified by a factor in the environment, and a part of this modified protoplasm passes into the conidium—an asexually formed bud of the original stem. So long as no sexual process intervenes, the succeeding "generations" must be looked upon as a continuation of the original plant. Therefore, organisms with only asexual reproduction are not well suited to the study of the inheritance of acquired characters. That some of the characteristics should not be lost readily, i. e., that the organism should not readapt itself readily to the former condition, may appear unusual, but it is possible that the reactions by virtue of which the accommodation occurs are not readily reversible. If this principle were general, it would lead to the existence of numerous physiological races. Such races are common among parasitic fungi, and it may be that they are even more numerous and as highly specialized among the saprophytes.—H. HASSELBRING.

Tubercle bacteria.—DE'ROSSI working at Perugia has been investigating anew the *Bacillus radicicola* of BEIJERINCK, and has reached results so at variance with those of previous observers as to need ample confirmation.[13] His conclusions may be stated briefly as follows:

An examination of the literature convinces him that many observers have mistaken *germi banali* of the soils for the real *B. radicicola;* and others have worked with impure cultures of it. The certain isolation of the true germ is attained by spreading the contents of a tubercle on a plate of gelatin with a leguminous extract containing glucose, and rejecting the colonies which develop rapidly, in favor of those which become visible to the microscope on the fifth or sixth day and to the eye on the tenth to twelfth, the form really desired being apparently a contaminant. These show the true morphological, cultural, and biological characters of *B. radicicola*.

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[13] DE'ROSSI, G., Studi sul microorganismo produttore dei tubercoli delle leguminose. Annali di Botanica **7**:617–669. *pl. 23.* 1909.

Of the various preparations proposed for the inoculation of fields, the dried cultures of MOORE and of BOTTOMLEY are absolutely useless; it is certain that they either do not contain the tubercle organism at all, or it is in such condition as to be unable to show its action in any way. As to the efficacy of fresh cultures (like the nitragine of HILTNER) opinions are not unanimous, and one cause of the uncertainty of the results may be that the culture is eventually impure.

In soils without tubercle bacteria those properly isolated by DE'ROSSI from the same species of host have given him good results in increased crops and added proportion of nitrogenous content. The manner of infection has had no effect, and he has not been able to discover any such unfavorable influence as was attributed by HILTNER and STORMER to substances in the soil or on the seed at the time of germination. From negative results DE'ROSSI doubts the possibility (affirmed by some) of improving the crop by inoculation when the soil already contains the organism. In another paper of the same title (included in above citation) DE'ROSSI asserts that in his cultures, certainly pure and surely identified as the tubercle bacillus, no fixation of free nitrogen has taken place. As this is not observed in the tubercle until the bacteroids are formed, and as few bacteroids are formed in cultures, the result appears quite proper. Evidently the questions raised will require new examination.—C. R. B.

Evolution of fungi.—The construction of a phylogenetic system for the fungi has always been peculiarly difficult on account of the heterogeneity of the group and the lack of common characters uniting the forms into evolutionary series. Two theories have generally been suggested; one regarding the fungi as an autonomous group, and the other regarding them as offshoots from various groups of algae. Among the adherents of the algal theory of descent, a favorite method of treating the lower Phycomycetes (or Chytridiales) has been to consider them as forms derived from the higher Phycomycetes through the degenerating influence of parasitism.

ATKINSON[14] in dealing with the evolution of this group favors the view that the Phycomycetes constitute an ascending evolutionary series. In support of this view he points out that the favorite method of accounting for the lower forms is fallacious, for whatever evolution occurred among the fungi took place after they had acquired a parasitic or saprophytic mode of life. Parasitism and saprophytism, therefore, were general modes of life under which the whole group existed, and hence cannot be invoked as special factors to account for particular minor offshoots. Another argument for the unity of the group is found in the phenomenon of diplanetism, that is, the occurrence of two swarming periods of the zoospores. Although this phenomenon is most clearly developed in the Saprolegniales, the author believes it occurs in a primitive state in the Chytridiales, in some of which the protoplasm breaks up into the sporangium, where after an interval the zoo-

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[14] ATKINSON, G. F., Some problems in the evolution of the lower fungi. Annal. Mycol. **7**:441–472. *figs. 20.* 1909.

spores are differentiated and set free. The first partial differentiation and movement of the spore-origins is regarded as the counterpart of the first swarming period of the zoospores of the Saprolegniales. This view derives diplanetism from a more primitive state among the lower fungi, while there is nothing among the algae which corresponds to the phenomenon.

It is further pointed out that some other phenomenon, such as heterogamy, isogamy, and the proliferation of the sporangium, each have a primitive counterpart among the Chytridiales, and can be traced in a natural series to the Saprolegniales and Oomycetes. For some of the phenomena, like the proliferation of the sporangium, there is no counterpart whatever among the algae.—H. HASSELBRING.

Cultures of Uredineae.—In continuation of the long series of experiments in his cultural work on the Uredineae, the cultures made in 1908 have been reported by ARTHUR.[15] The most interesting result of the work of that year is the discovery that the aecidial stage of *Gymnosporangium externum* Arthur and Kern (described as new) occurs on a herbaceous perennial, *Porteranthus stipulatus* (Muhl.) Britton. This is the only case known of the occurrence of an aecidium of Gymnosporangium on a plant outside of the Pomaceae. Another unusual case is that of *G. Libocedri* (P. Henn.) Kern, whose aecidial stage is shown to be *Aecidium Blasdaleanum* D. and H., a true aecidium and not belonging to the Roestelia type as in all other Gymnosporangia. Series of cultures with 13 species of rusts gave negative results, and cultures with 23 species confirmed and supplemented work previously reported. The relations of the following species have been worked out for the first time: *Puccinia absinthii* DC. on *Artemisia dracunculoides* Pursh has no aecidia, but has pycnidia on the same host; *P. macrospora* (Peck) Arthur on *Carex comosa* Boott sown on *Smilax hispida* Muhl.; *P. patruelis* Arth. on *Carex pratensis* Dreej. sown on *Agoseris glauca* (Pursh) Green; *P. cinerea* Arth. on *Puccinellia airoides* (Nutt.) Wats. and Coult. sown on *Oxygraphis cymbalaria* (Pursh) Prantl; *P. Koeleriae* Arth. on *Koeleria cristata* (L.) Pers. sown on *Mahonia aquifolium* (Pursh) Nutt.; *P. alternans* Arth. on *Bromus Porteri* (Coult.) Nash sown on *Thalictrum dioicum* L.; *P. obliterata* Arth. on *Agropyron biflorum* R. and S. sown on *Aquilegia canadensis* L.; *P. Muhlenbergiae* Arth. and Holw. on *Muhlenbergia glomerata* Trin. sown on *Callirhoe involucrata* (T. and G.) A. Gray; *Gymnosporangium Libocedri* (P. Henn.) Kern on *Libocedrus decurrens* Torr. sown on *Crataegus Pringlei* Sarg.; and *G. externum* Arth. and Kern on *Juniperus virginiana* L. sown on *Porteranthus stipulatus* (Muhl.) Britt.—H. HASSELBRING.

Biology of Gymnosporangium.—Another interesting example showing the slight degree of differentiation existing among some species of parasitic fungi

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[15] ARTHUR, J. C., Cultures of Uredineae in 1908. Mycologia 1:225–256. 1909.

has been brought out by FISCHER[16] in the case of the gymnosporangia inhabiting Juniperus. A casual attempt to infect *Sorbus aria*, *S. aucuparia*, and some other species, with teleutospores obtained from *Juniperus communis* and supposed to be those of *Gymnosporangium tremelloides*, resulted in no infections. This experiment showed that the teleutospores were neither those of *G. tremelloides* nor those of *G. juniperinum*, whose aecidial host is *Sorbus aucuparia*. These results led to a series of cross infections, in which the teleutospores of the Gymnosporangium were used to infect a number of pomaceous plants, and aecidial spores from these plants were sown on Juniperus. The work showed that two forms of Gymnosporangium occur on *Juniperus communis* and *J. nana*. The first form occurs chiefly on the stems and branches, rarely on the leaves, and has its aecidial form on *Amelanchier ovalis*. The first aecidia appear on *A. ovalis* 55 to 60 days after the sowing of teleutospores, and the teleutospores appear on Juniperus about 20 months after the sowing of aecidiospores. For this form the specific name *Amelanchieris*, originally applied to the Roestelia on Amelanchier, is reserved. The second form occurs chiefly on the leaves of Juniperus, and has its aecidial form on *Sorbus aucuparia*, but does not infect *A. ovalis*. The aecidia appear 45 to 50 days after the sowing of teleutospores, and teleutospores are produced in the spring following the sowing of the aecidiospores in late summer. This is the form known as *G. juniperinum*.

For a discussion of the history, nomenclature, and geographical distribution of the two forms, as well as of their respective hosts, the reader is referred to the original paper.—H. HASSELBRING.

Fermentation of tobacco.—Theories relating to the fermentation of tobacco have been based either on the view that the process is due to bacterial action, or to the action of enzymes without the intervention of bacteria. One investigator alone, SCHLOESING, seems to have believed that the later part of the fermentation is due to purely chemical oxidations. In view of these conflicting theories describing the process, the experiments of BOEKHOUT and DEVRIES are especially interesting.[17] These authors attacked the problem by methods similar to those used in their recent work on the spontaneous heating of hay. Dry samples of cured tobacco were sealed up in tubes with oxygen or air, and in some cases water was added to the samples. The tubes were then heated to 100° or to 33°, according to the purpose of the experiment, and after a definite period of heating the gas in the tubes was analyzed. It was found that oxidation took place at both temperatures, but more rapidly at the higher temperature. The presence of water increased the rate of oxidation. By the process of oxidation carbon dioxid was liberated and oxygen was fixed. It was found that starch and pentosans were

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[16] FISCHER, ED., Studien zur Biologie von *Gymnosporangium juniperinum*. Zeit. Bot. **1**:683–714. *figs. 8*. 1909.

[17] BOEKHOUT, F. W., AND DEVRIES, O. J. J., Ueber Tabaksfermentation. Centralbl. Bakt. II. **24**:496–511. 1909.

the principal substances which disappeared. In seeking for a catalyzer, iron and manganese were considered. It was found that starch paste with traces of ferrosulfate was completely hydrolyzed in six days at 100°. In a similar experiment without iron salts no hydrolysis took place.

The authors conclude from their work that the fermentation of tobacco is a process of oxidation, in which iron salts may act as catalyzers. They believe that it is almost certain that the processes are of a purely chemical nature, that is, take place without the action of enzymes or bacteria.—H. HASSELBRING.

Ascent of water.—DIXON recounts[18] some experiments intended to show that the living cells of the wood do not influence the rate at which water is transmitted through a stem. Arguing that if there is any sort of action which even facilitates the passage of water upward, its effect would be noticeable experimentally by a downward filtration of water more rapid in a killed stem than in a living one, he arranged two like shoots of syringa so that he could keep the two at the same temperature and could determine the amount of water that would pass downward through them, both being alive, under a given head of pressure in a short time, say 10 minutes. One shoot was then killed, by steam or by poison, with no disturbance, and the amount of water transmitted by both again determined. No appreciable or constant difference was found; whence DIXON argues that vital action is at least unlikely.

On the basis of the strain borne by the water of a soap-bubble film, DIXON calculates that the tensile strength of water, even when saturated with air, is not less than 42.5 *A*, a figure which agrees fairly well with BERTHELOT's early determination, 50 *A*, to which he calls attention. In another paper,[19] DIXON presents some further experimental work on this point. He finds a tensile strength under certain conditions of more than 150 *A*. There is no longer doubt that the cohesion of water is sufficient to stand the strain involved in a lift; but what are the resistances to be overcome? EWART says about 50 *A*; DIXON thinks this too high, and suggests a maximum of 20 *A* for the tallest trees (100^m). In the absence of determinations of the osmotic pressure in the leaves of such trees, DIXON thinks it fair to assume that it is as much as 20 *A*. Others will deny the assumption. And, as Mr. Dooley pointedly says, "There y' are!"—C. R. B.

Life of pollen.—PFUNDT,[20] working under the guidance of PFEFFER, has determined the viability of pollen in air of various degrees of humidity. Incidentally he presents many data regarding the germination of pollen that will be useful.

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[18] DIXON, H. H., Vitality and the transmission of water through the stems of plants. Notes from the Botany School of Trinity College **2**:5–18. 1909.

[19] ———, Note on the tensile strength of water. *Ibid.* 38–43. Both "Reprinted from Proc. Roy. Dublin Soc.," without citation of volume or pages.

[20] PFUNDT, MAX, Der Einfluss der Luftfeuchtigkeit auf die Lebensdauer der Blüthenstaubes. Jahrb. Wiss. Bot. **47**:1–40. 1909.

It is found that the duration of life depends directly upon the humidity of the air, being greatest at one vapor pressure and least at another; but these points do not coincide for all kinds of pollen. There are only a few species which live longest in very moist air (90–60 per cent.), and only one that lives the same length of time in moist as in dry air; but there are many species which live longest in very dry air (30–0 per cent.). (A priori, it would seem that all pollen should remain alive longest in absolutely dry air, and one wonders whether the differences found by PFUNDT are not due to some other factors, for whose operation there is ample room in the handling of the material, and particularly in the artificial germination tests on which the conclusions are based.) In nature the duration of life is very variable because of the variations in the moisture of the air. The influence of a single change from moist to dry is not very evident, but repeated changes shorten life, and the drying of wet pollen leads quickly to death, the sooner the longer it was wet. Ecological adaptations are not clear; the pollen of early spring and late autumn flowers, however, is generally long-lived, shows little sensitiveness to moisture, and germinates at minimum temperatures, even below 4–5°. Whereas freshly gathered pollen may germinate in dilute or in concentrated solutions indifferently, that which is about to die produces tubes only in the most favorable concentration.—C. R. B.

Morphology of Salvinia.—ARNOLDI[21] has published the results of a study of *Salvinia natans*. The paper is divided into three parts: (1) the germination of the microspore and the development of the male gametophyte; (2) the germination of the megaspore and the development of the female gametophyte, fertilization, and embryo formation; (3) a series of experiments on the female gametophyte. In the first part little is added to BELAJEFF'S account except such cytological details as the size of nuclei and chromosomes, the number of chromosomes (4), and the spermatogenesis. The early stages of the female gametophyte were followed more closely than by previous authors. It is found to be composed of a coenocytic portion contained within the old spore wall, and an exposed chlorophyll-bearing tissue, one side of which bears archegonia. In the mature archegonium, the axial row consists of the egg, the ventral canal cell, and a broad wedge-shaped neck canal cell which is binucleate. In the third part of the paper the following facts are recorded: (1) an unsuccessful attempt to produce apogamous embryos: (2) the appearance of the archegonia in the upper or lighter side of the prothallium is not a response to light; (3) the development of the winglike appendages, characteristic of the female gametophyte of Salvinia, occur only when fertilization and embryo formation precede it; (4) the food material used by the developing embryos is not made by the chlorophyllose tissue of the gametophyte, but is that which was stored in the megaspore; (5) spores sown on damp clay germinated and produced good prothallia with normal archegonia and embryos.—WANDA M. PFEIFFER.

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[21] ARNOLDI, W., Beiträge zur Morphologie der Keimung von *Salvinia natans*. Flora **100**:121–139. *figs. 47*. 1909.

Geotropism.—GROTTIÄN[22] finds that by the use of proper concentrations of amyl alcohol and other anesthetics it is possible to stop geotropic response in horizontally placed roots without entirely stopping growth. He believes he has shown that anesthetics may abrogate the power of perception without entirely eliminating the power of reaction. He finds that certain concentrations of the anesthetics accelerate growth, as has been shown by several other investigators. He finds likewise much evidence, though not entirely conclusive, that concentrations which greatly stimulate growth also shorten reaction time.

The same author has repeated all of CZAPEK'S experiments on the change of metabolism due to geotropic stimulation. As is well known, CZAPEK claims that geotropically stimulated root tips show a greater percentage of homogentisic acid than unstimulated ones, and that the accumulation is due to the development of an antienzyme which stops the action of the enzyme which carries on the further metabolism of the acid. Several authors have already shown that CZAPEK'S method of detecting the acid are not at all reliable, and even that neither tyrosin from which the acid is derived nor the acid itself is present in the root (geotropically stimulated or not) in detectible quantities. GROTTIÄN finds that even CZAPEK'S inadequate methods do not give, on the average, any difference between stimulated and unstimulated roots. It seems then that CZAPEK'S methods do not indicate any change in the metabolic products due to geotropic stimulation, much less the accumulation of homogentisic acid.—WILLIAM CROCKER.

In 1908 BLAAUW determined that in stimulation by light the presentation time is inversely proportional to the intensity of the light used. The suggestion that the same would be found true with the effective force in stimulation by gravitational and centrifugal acceleration has been tested by Miss C. J. PEKELHARING, who reports[23] that she has established this relation for the same plant under identical conditions with continuous stimulation. This completes the proof that with both sorts of stimuli and with both continuous and intermittent application, the product of the presentation time and the force of the stimulus is a constant. The validity of WEBER'S law for geotropic curvatures is questioned, and FITTING'S experiments on this point are considered inconclusive. By testing the action of gravity and light together, it appeared that the mode of perception of the two is not the same. There was not the least evidence that positive or negative reaction to gravity could be obtained by increasing or decreasing the strength of the stimulus. One of the most striking results of the investigation has been emphasized by WENT (under whose direction it was conducted) in a separate

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[22] GROTTIÄN, WALTER, Beiträge zur Kenntniss des Geotropism. Beih. Bot. Centralbl. **24**:255–285. 1909.

[23] PEKELHARING, CATHARINA J., Onderzoekingen over die perceptie van den zwaartekrachtprikkel door planten. Proefschrift ter verkrijging van der graad Doctor in die plant- en dierkunde, aan de Rijks-Universiteit te Utrecht. 8vo. pp. 105. *pls. 4.* 1909.

communication to the Amsterdam Academy.[24] Miss PEKELHARING found it possible, by using potash-alum properly balanced in the culture solution, to grow some roots of *Lepidium sativum* fairly straight and free of starch grains. Nevertheless, these roots, in many cases, showed geotropic curvatures; from which it is evident that there is perception independent of statolith starch, however useful this may be when present.—C. R. B.

Chromosomes of Taraxacum and Rosa.—In 1903 RAUNKIAER found that Taraxacum developed embryos even when all the anthers had been removed, and a subsequent cytological study by MURBECK and JUEL showed that the embryos developed from the egg without fertilization. A recent study by ROSENBERG[25] shows that in the form called *Taraxacum confertum* a typical tetrad of megaspores is formed from the megaspore mother cell, and that the reduced number of chromosomes is 8, which can be counted in an early stage as prochromosomes. JUEL had reported 12 or 13 as the reduced number and 26 as the diploid number in apogamous forms of Taraxacum.

In several forms of Rosa it has been known that embryos develop even when the anthers have been removed, but ROSENBERG is not yet able to say upon cytological evidence whether these forms are apogamous or not. In the pollen mother cells of *Rosa canina* he finds, usually, about 20 univalent chromosomes and 7 bivalent ones. During the first mitosis chromosomes become disarranged, as in Hemerocallis, and more than four pollen grains are formed from a single mother cell. He thinks that the suggestion may not be entirely unfounded that the univalent chromosomes, which normally split at the second mitosis, may split at the first, and thus show a transition to the vegetative mode of division. He gives a table showing the relatively high chromosome numbers of apogamous forms.—CHARLES J. CHAMBERLAIN.

Light and germination.—HEINRICHER[26] finds, in agreement with REMER, that the seeds of *Phacelia tanacetifolia* are greatly hindered in their germination by light. Seeds just harvested and not first dried out will not germinate at all in white light, nor in the less refrangible rays, while a considerable percentage germinate in darkness and a smaller percentage in the more refrangible rays. A period of drying, whether it occurs in darkness or light, greatly increases germination in darkness and in the more refrangible rays, while it leads to a low percentage of germination in white light and in the less refrangible rays. The behavior of these seeds toward light is in most respects just opposite to that of the seeds of *Veronica peregrina*.

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[24] WENT, F. A. F. C., The inadmissibility of the statolith theory of geotropism. Proc. Koninkl. Akad. Wetens. Amsterdam **1909**:343–345.

[25] ROSENBERG, O., Ueber die Chromosomenzahlen bei Taraxacum und Rosa. Svensk. Bot. Tidskrift **3**:150–162. *figs. 7.* 1909.

[26] HEINRICHER, E., Keimung von *Phacelia tanacetifolia* Benth. und das Licht. Bot. Zeit. **67**¹:45–66. 1909.

The stored food in the seeds of *Phacelia tanacetifolia* is largely fat. HEINRICHER argues that germination is hindered by light because acid formation is greatly fostered by darkness of by the more refrangible rays, which create more favorable conditions for the formation and action of lipase. There seems to be little evidence offered for this conclusion. In fact it looks as if our knowledge of the germination processes must be greatly extended before we can announce any one process that must be stimulated to induce germination. However this may be, it is certain that such conclusions, if tenable, must have far more experimental evidence than HEINRICHER has offered.—WILLIAM CROCKER.

Suspended life.—BECQUEREL reports to the Paris Academy of Science[27] further experiments on the question of the life of seeds, whether it is slow or stopped. He perforated the seed coats of seeds of lucerne, white mustard, and wheat, dried them in a vacuum with BaOH at 40° C. for six months, sealed them in a glass tube exhausted to 0.002^{mm} mercury, and kept them for a year; they were then submitted to a temperature of liquid air (−190°) for three weeks, and without warming up to the temperature of liquid hydrogen (−250°) for 72 hours. On being kept upon moist cotton at 28° all except one grain of wheat out of five germinated in a perfectly normal fashion. BECQUEREL finds it impossible to conceive of "life" under the conditions named, and holds that life can be interrupted completely with no prejudice to its resumption.—C. R. B.

Individual variation.—An elaborate paper upon the individual differences in the development of growing plants, with special reference to the influence of external conditions, has been published by KORIBA.[28] It is too detailed for any intelligible summary, but its data should be considered by those who are conducting experiments of any kind in which a limited number of plants furnish the basis for conclusions. It emphasizes strongly the necessity of taking account of these individual peculiarities.—C. R. B.

Respiration and temperature.—KUYPER reports[29] that BLACKMAN'S theory of limiting factors holds good for respiration, which as a chemical process agrees with the VAN'T HOFF-ARRHENIUS law between 0° and 20–25°, but shows a falling-off in an almost logarithmic curve above 40°. The "optimum" is no fixed point, for the duration of respiration at any given temperature will displace it. The course of respiration, KUYPER finds, is also dependent on the nature of the reserve food.—C. R. B.

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[27] BECQUEREL, PAUL, Sur la suspension momentanée de la vie chez certaines graines. Compt. Rend. Acad. Sci. Paris **148**:1052–1054. 1909.

[28] KORIBA, K., Ueber die individuelle Verschiedenheit in der Entwicklung einiger fortwachsenden Pflanzen mit besonderer Rücksicht auf die Aussenbedingungen. Jour. Coll. Sci. Imp. Univ. Tokyo **27**: art. 3. (pp. 86.) *pls. 5.* 1909.

[29] KUYPER, J., The influence of temperature on the respiration of the higher plants. Konink. Akad. Wetens. Amsterdam **12**:219–227. 1909.


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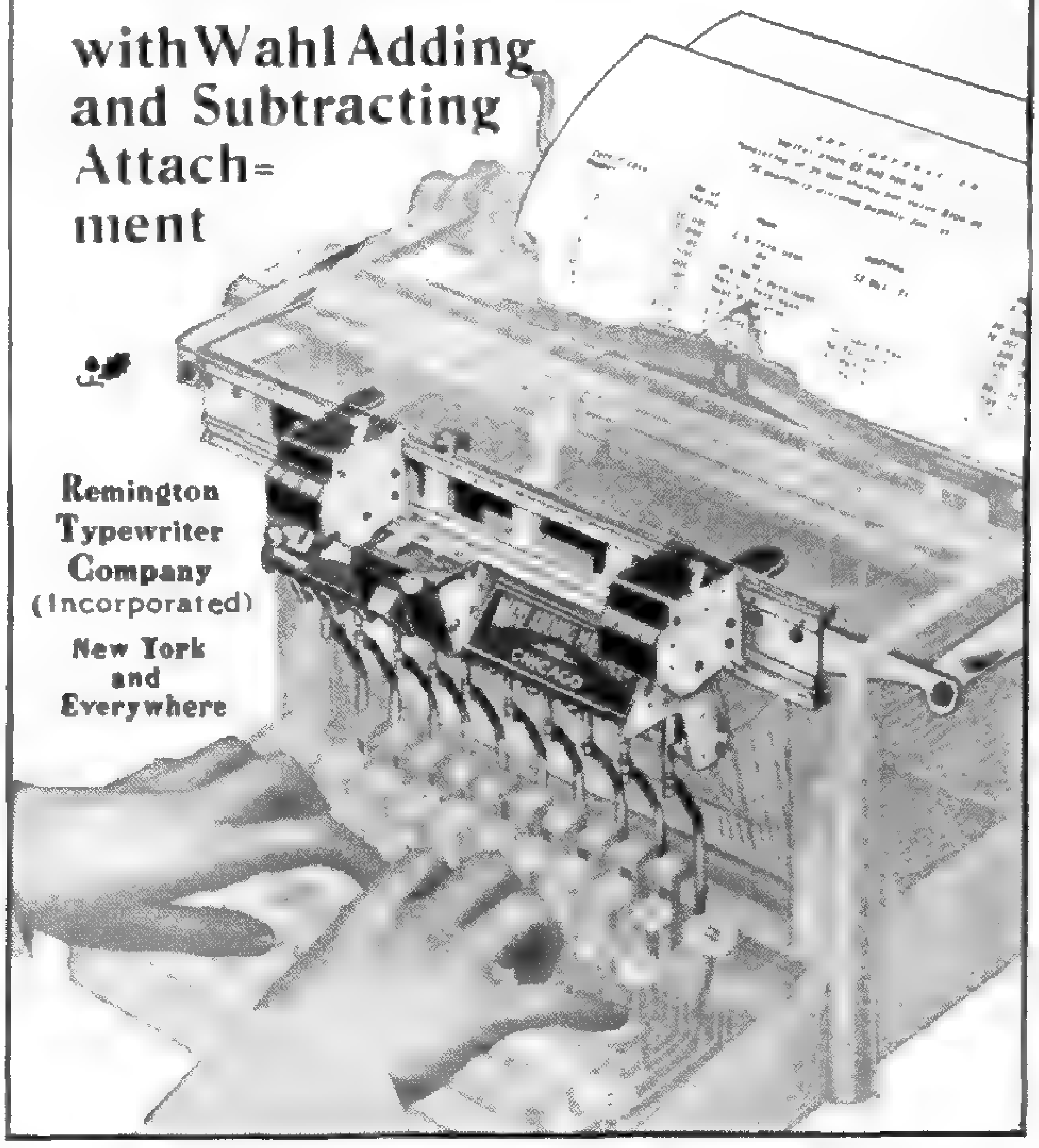

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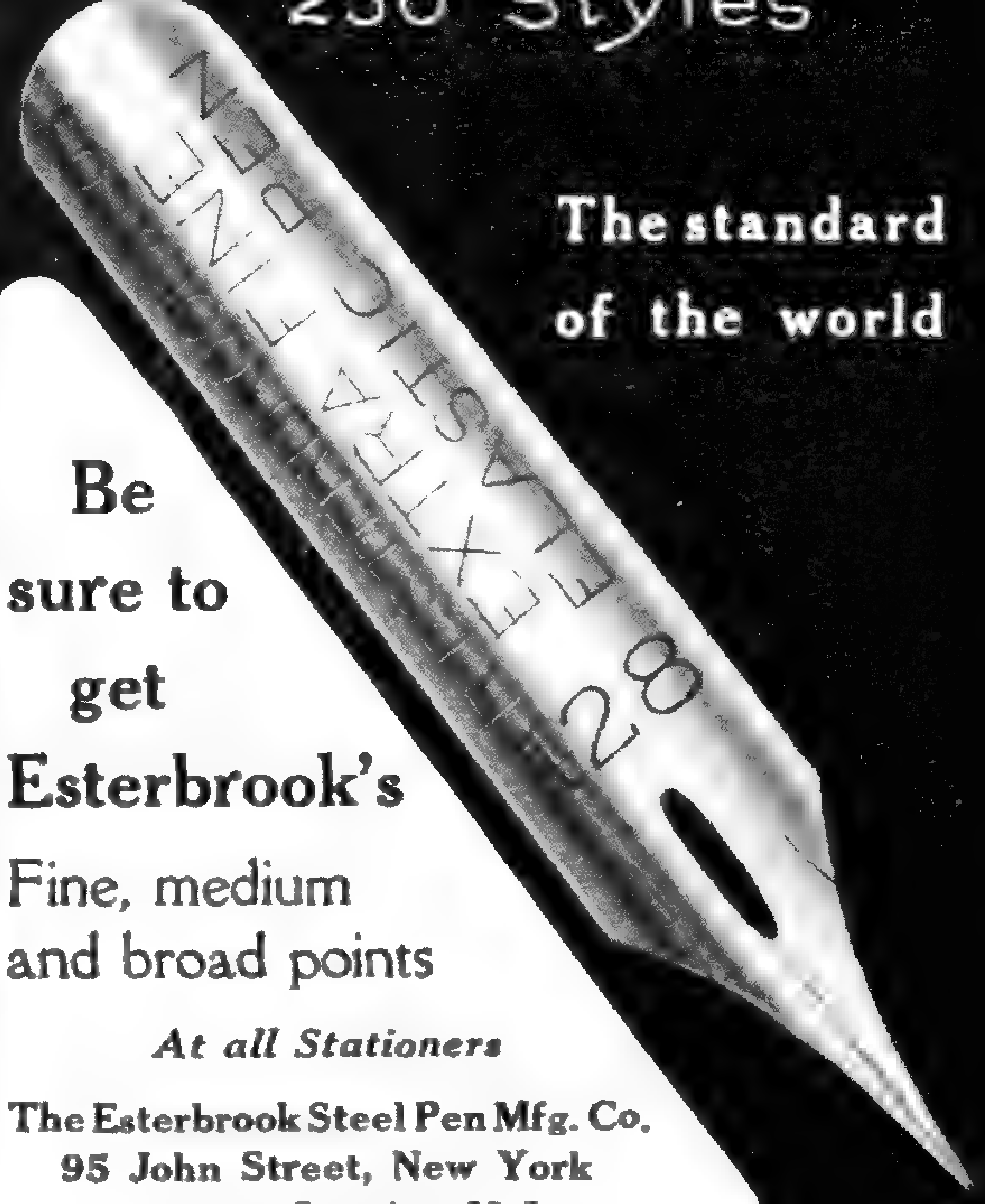
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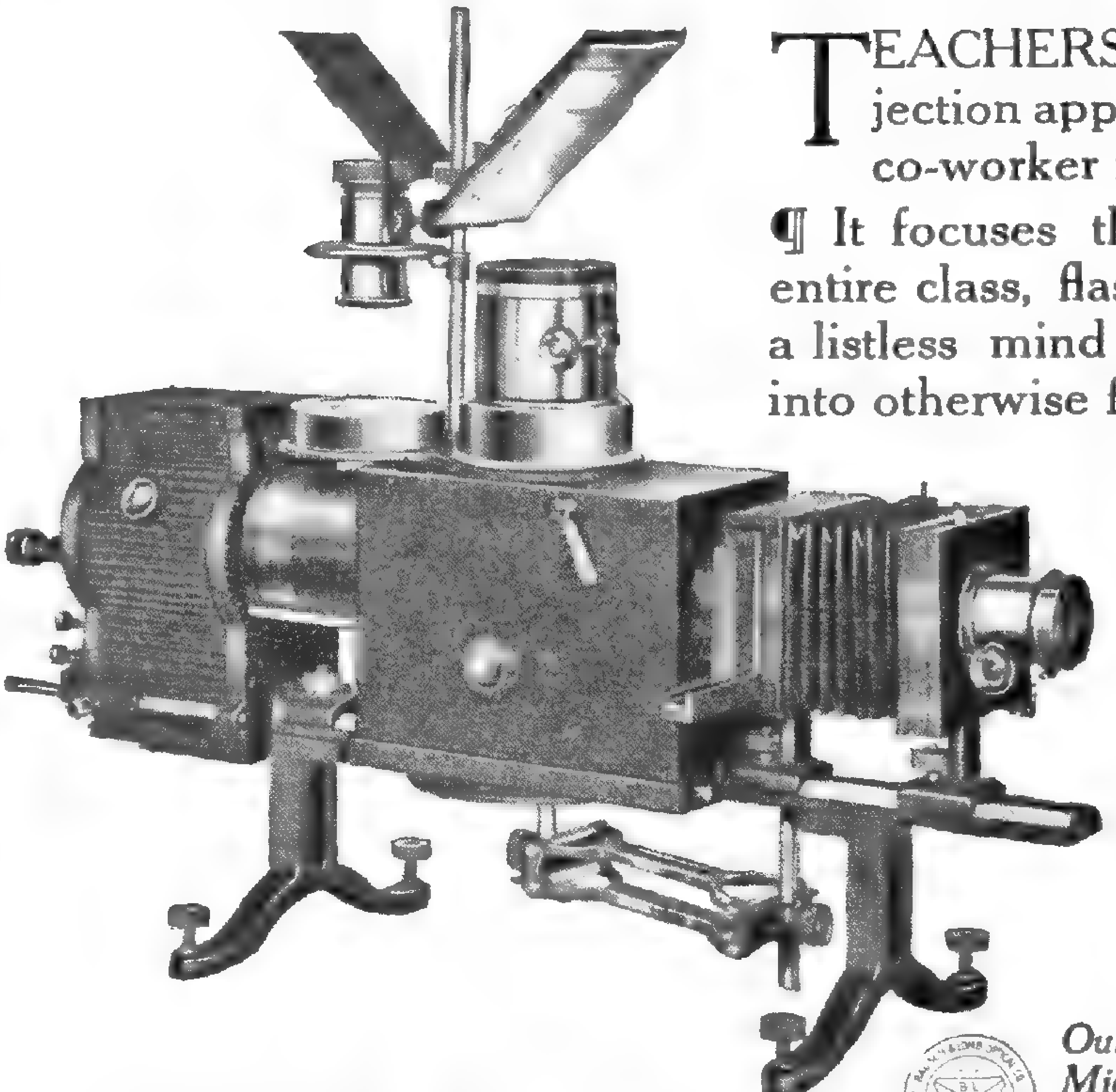

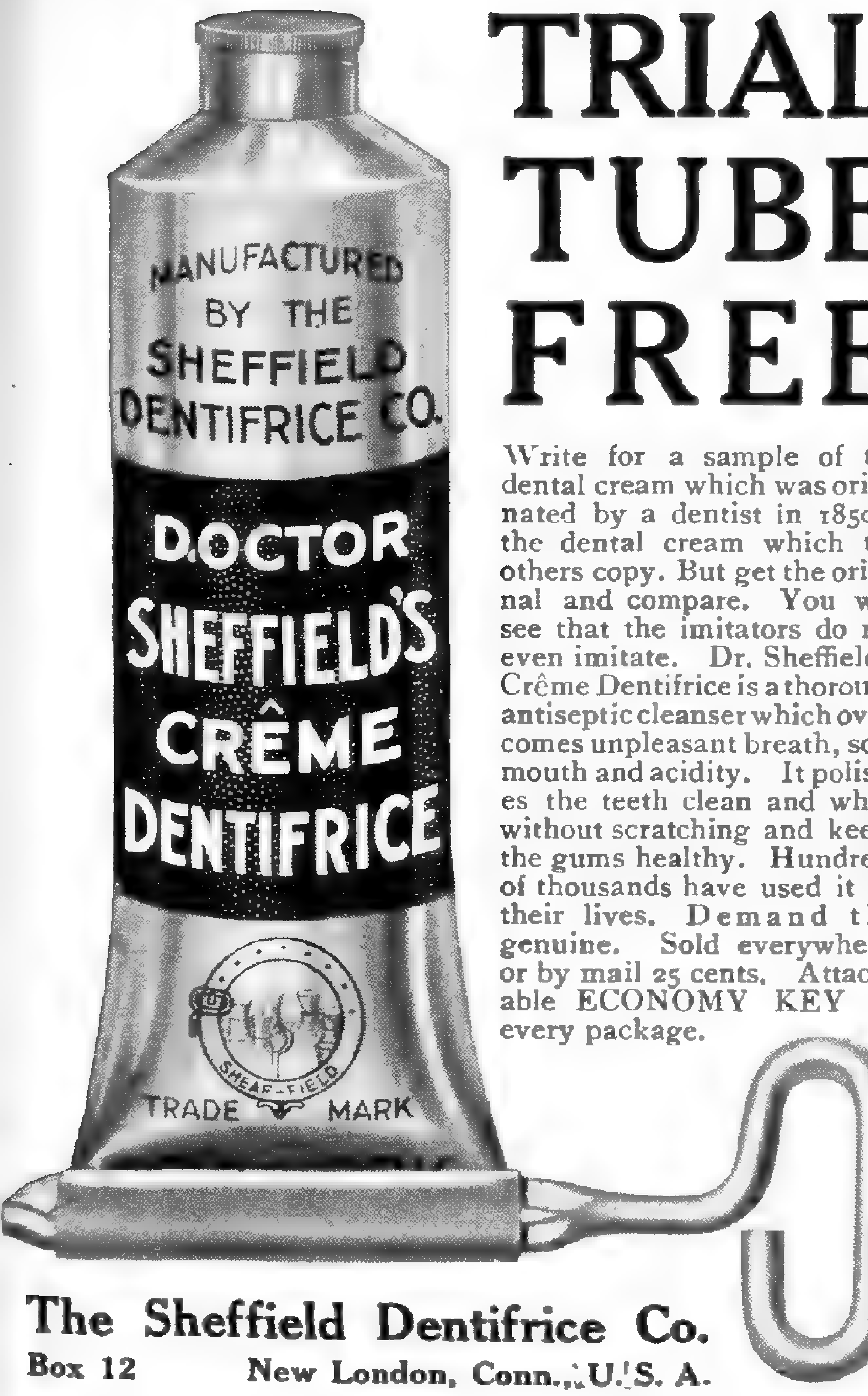
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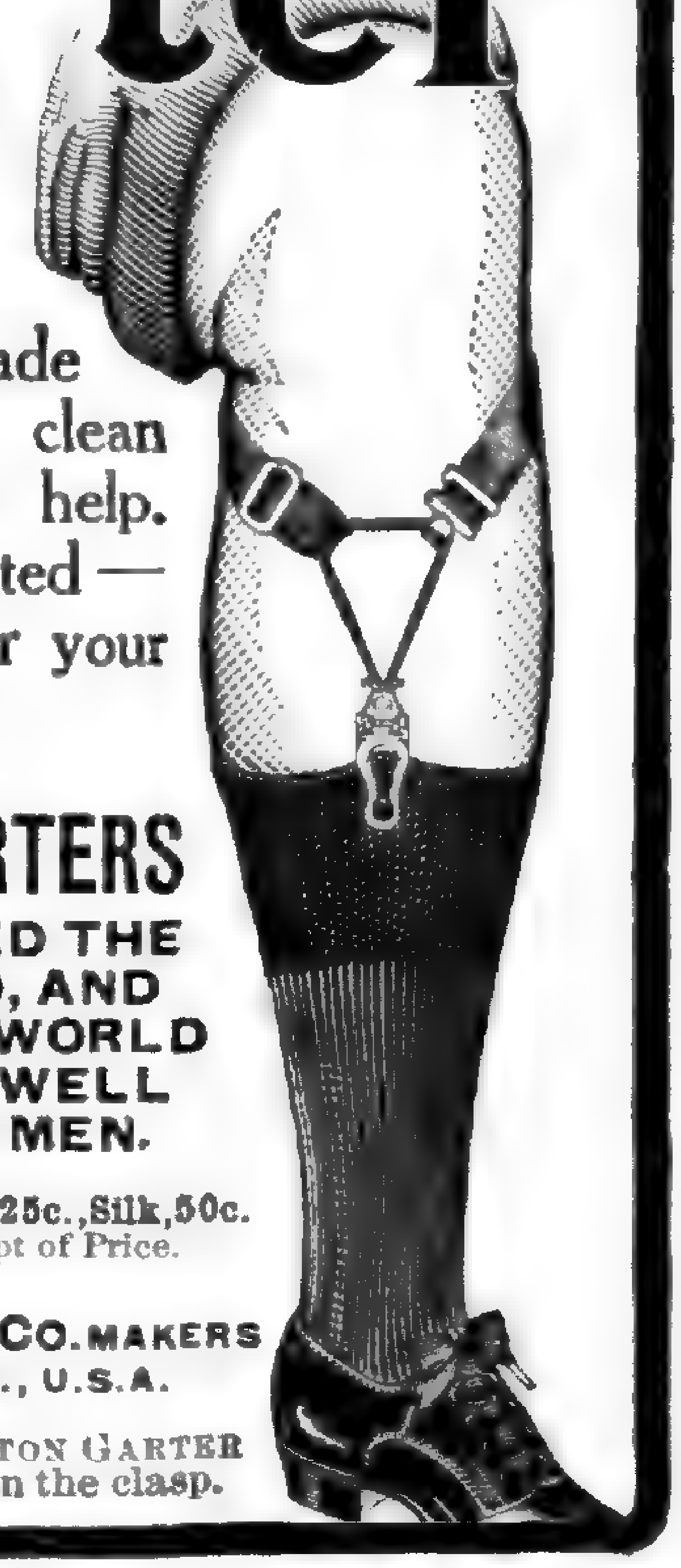

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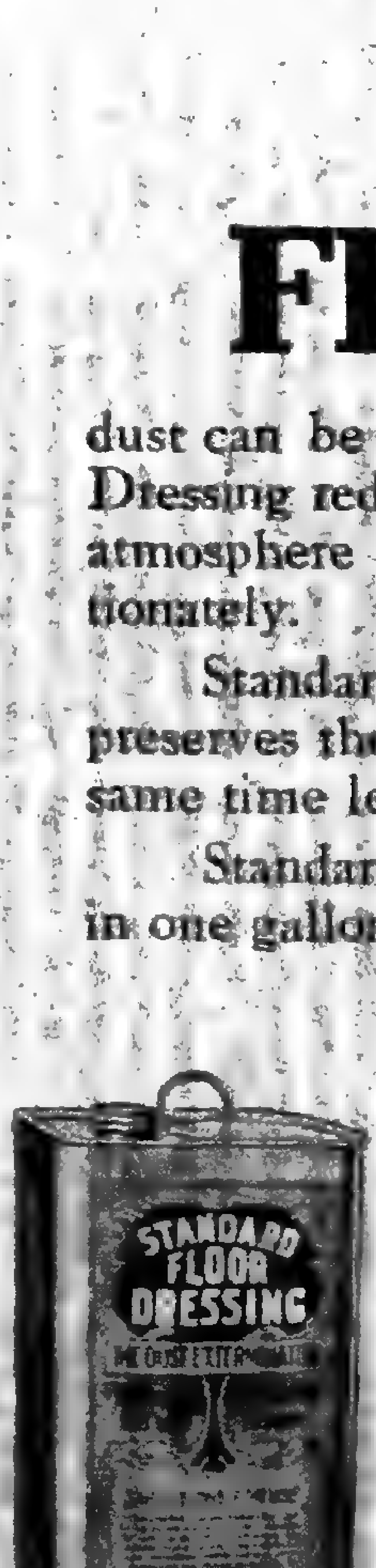
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BOTANICAL GAZETTE

April 1910

Editors: JOHN M. COULTER and CHARLES R. BARNES

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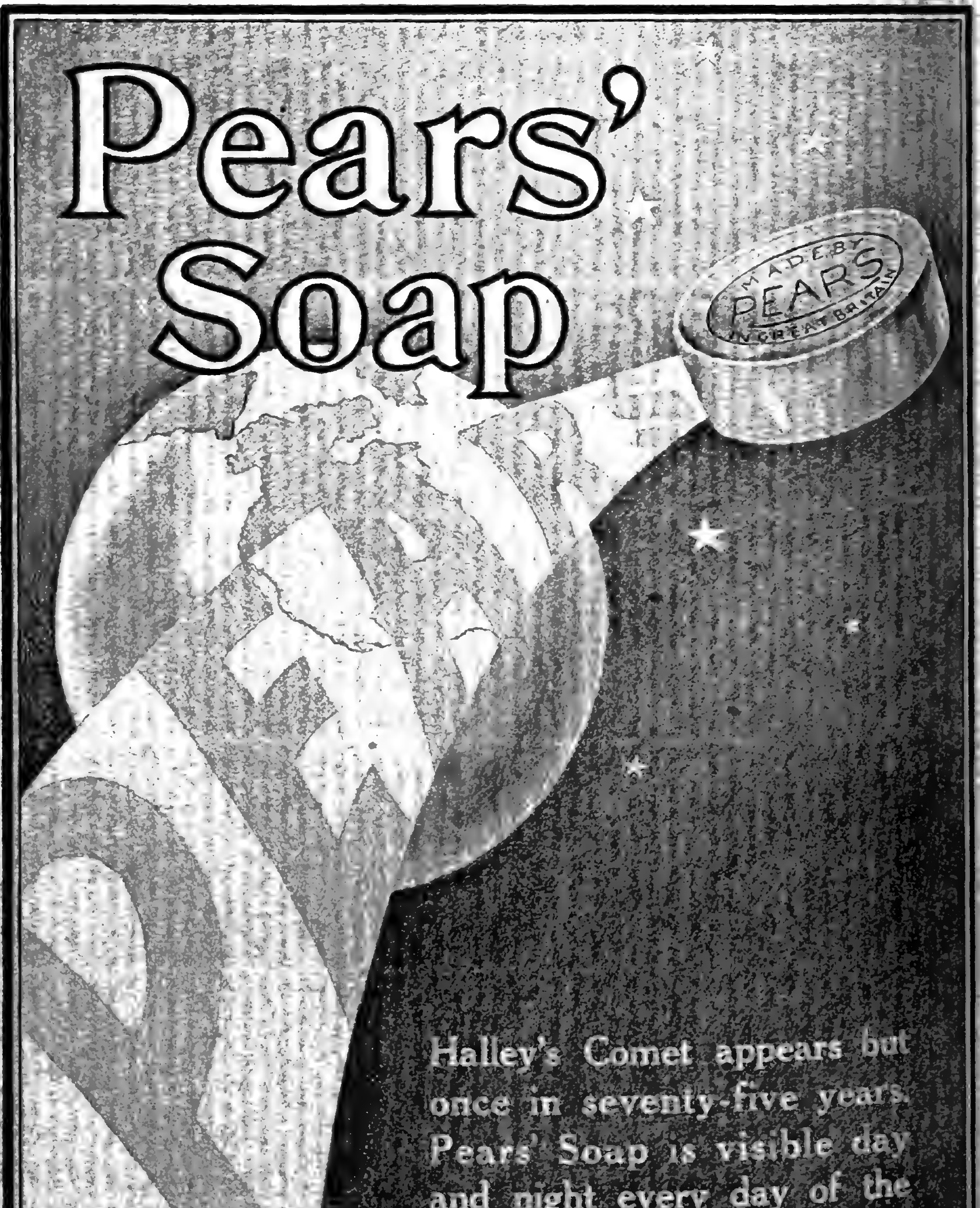

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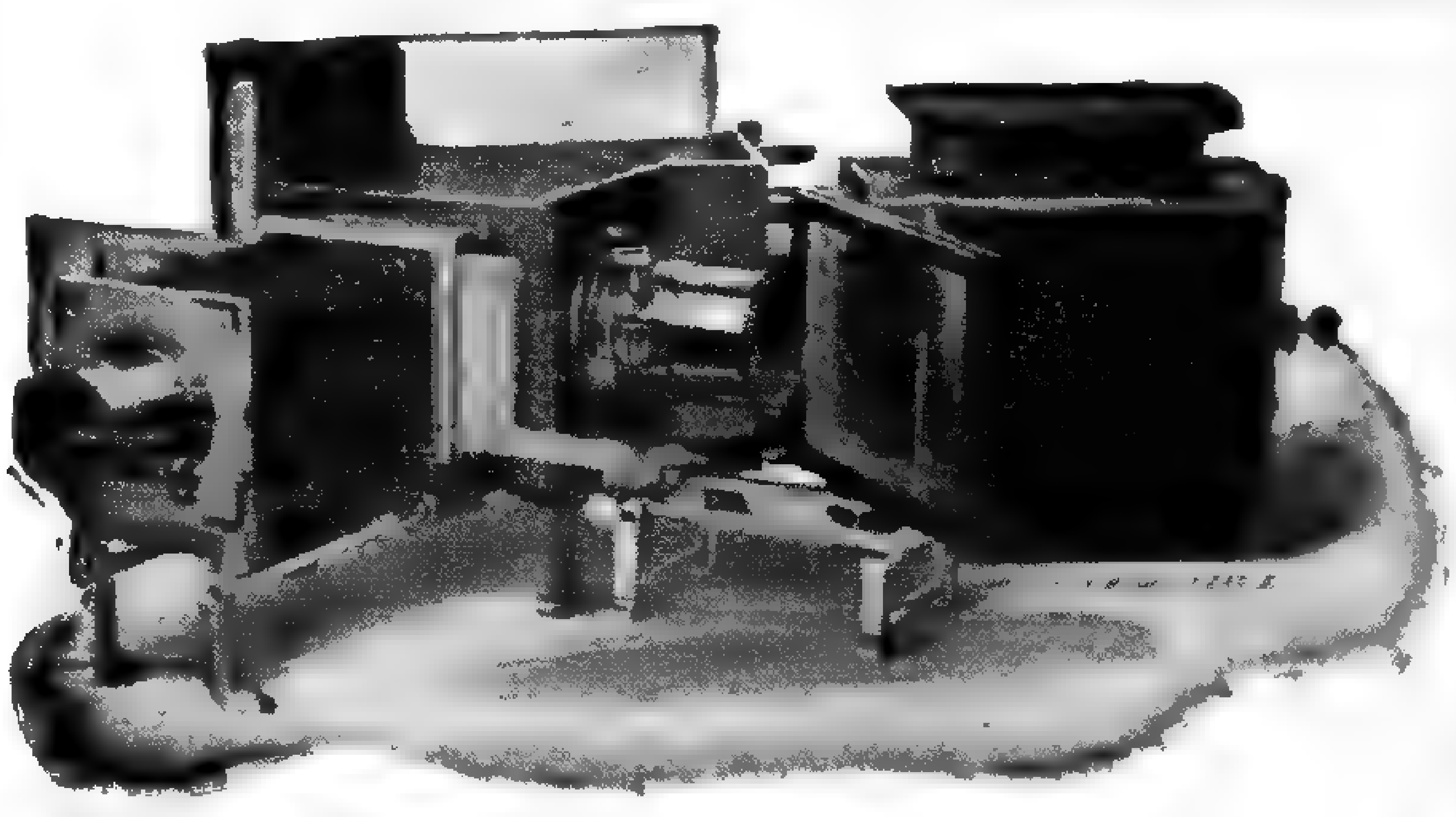

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APRIL 1910

THE CELL STRUCTURE OF CLOSTERIUM EHRENBERGII AND CLOSTERIUM MONILIFERUM

B. F. LUTMAN

(WITH PLATES XVII AND XVIII)

Little has been contributed to our knowledge of the chromatophore and pyrenoids of Closterium since the time of NÄGELI and DEBARY, though several investigators have worked on the cell division, conjugation, and peculiar mode of locomotion of these plants.

NÄGELI (**5**) described the chromatophore, nucleus, end vacuoles, pyrenoids, and cell wall of the genus. He figures only *C. moniliferum* and *C. parvulum*, but mentions eleven other species as belonging to the genus, not including, however, *C. Ehrenbergii* among them. The chromatophore as described by him consists of three or more chlorophyll plates whose inner edges rest in the axis of the cell and whose outer edges extend to the cell wall. In optical cross section, obtained by examining the plant when it was standing on end, the chromatophore appeared to be made up of 3 to 15 plates extending radially from center to periphery. The nucleus he describes as a clear sac containing a denser body. In the colorless ends of the plant body are the clear vacuoles containing little black granules showing a motion which he calls molecular; these vacuoles are usually spherical, although at times irregular in shape. The pyrenoids, "little chlorophyll sacs," are arranged in *C. moniliferum* and *C. parvulum* in a single row of 2 to 20. The cell wall is striate. NÄGELI'S figures show, besides the external views, optical cross sections of *C. moniliferum* and *C. parvulum*. These are the only figures extant and they have been copied by OLTMANNS (**17**) and LOTSY (**12**).

DEBARY (**5**) also described Closterium, but adds little to NÄGELI'S account except that he recognizes the pyrenoids (*Amylonkerne*) as depositing starch in their interior, and made out that the little granules in the end vacuoles are rhombic plates with sharp angles, composed, as he discovered by tests, of gypsum. DEBARY used the term *Amylonkerne* for the pyrenoids because of the many analogies they offer to the cell nuclei. He had discovered by means of the iodin reaction that the outer layer is starch, and by means of the red coloration with sugar and sulfuric acid that the central body is composed of protein. He described the starch which appears in the outer layer as either forming a homogeneous shell on the outside of this central body, or in the cells rich in starch as composed of grains that give to the pyrenoid an irregularly cracked appearance. DEBARY was the first to give an adequate account of the appearance and chemical constitution of this body in Closterium, and little of real importance as to its chemical nature has been added since.

FISCHER (**7**) examined the crystals in the end vacuoles both as to their origin and composition. In his opinion they originate in the plasma, in which he claims there are many of them, from which they wander into the vacuoles.

LÜTKEMÜLLER (**13**) and a number of other observers have studied the structure and the beautiful and characteristic markings on the cell walls of the different species.

Later authors, working on other forms, have found little to correct in DEBARY'S account of the appearance and chemical composition of pyrenoids, but DEBARY gave no adequate suggestion as to their relation to starch formation. TIMBERLAKE (**22**) has reviewed the literature fairly thoroughly, and as little has appeared since his time all that will be necessary is a brief account of the points called in question in this paper.

According to SCHMITZ (**18**), who was the first to observe and figure the process, the pyrenoid reproduces by the simple method of pinching in two, the starch mass being divided between the two daughter pyrenoids and being replaced by growth on their sides where the division had occurred. SCHMITZ'S work, which was done on Hyalotheca, has been confirmed by CHMIELEVSKY (**3**) on Spirogyra, KLEBAHN (**9**) on Cosmarium, KARSTEN (**8**) on Grammatophora, STRASBURGER (**20**) on Zygnema, and TIMBERLAKE (**21**) on Hydrodictyon. In addition to reproduction by division, it is frequently assumed that they may arise *de novo* in the chromatophore, or at least arise from bodies too minute to be seen with the microscope. The apparent disappearance of the pyrenoids is characteristic of the time of spore formation and has been observed by STRASBURGER (**20**) in Cladophora, KLEBS (**11**) in Chlamydomonas and in Hydrodictyon, and OVERTON (**18**) in Volvox. They reappear when the spores begin to grow again and apparently arise *de novo.*

The commonly accepted view as to the formation of starch around the pyrenoid, as given by OLTMANNS, is that of SCHMITZ. "The origin of the starch layer out of the individual grains is very difficult to follow. If algae are taken from which the starch has been removed and put under favorable conditions for observation, there will at first appear, according to SCHMITZ, little round grains that are isolated from one another but which later grow and flatten themselves through pressure on each other." In contradistinction to this view is that of TIMBERLAKE (**21**), who found segments of the pyrenoid of Hydrodictyon breaking off and becoming converted into starch grains by the deposition of starch in each segment so cut off.

TIMBERLAKE has described many of the pyrenoids of Hydrodictyon, especially where starch formation was going on rapidly, as having two or three concentric layers of starch around them. In Cladophora (**22**) he has described the pyrenoid as a double convex lens-shaped body, from which starch grains are cut off first on one side and then on the other. These grains not being removed at once may form several layers of starch on either side. All the other pyrenoids so far described, such as those of Spirogyra, Zygnema, etc., have only a single layer of starch around them.

BÜTSCHLI (**2**) has recently made a careful study of the paramylon bodies of Euglena, and has found that in preserved material they break up into a number of disks which he regards as due to their internal structure.

The staining reactions of the pyrenoids are quite interesting and have been described by TIMBERLAKE (**21**). The pyrenoid stains a brilliant red in the triple stain, while the starch around it, and in the stroma, is colored as bright a blue.

NĚMEC (**16**) has called attention recently again to the reaction of starch to gentian violet, but uses a more complicated technique to obtain the same result that may be had with the ordinary triple stain when properly used. He soaks his sections on the slide in a 2 per cent. aqueous solution of tannin for 10–60 minutes, washes for a minute in water, puts them into a 1.5 per cent. solution of tartar emetic for 5–15 minutes, and then stains them, after washing in water, for about 30 minutes in an aqueous solution of gentian violet. By this procedure he gets what he calls an inverse staining, in which the starch is stained a brilliant violet while the cytoplasm and chromatin remain unstained. In order to stain the chromatin he suggests a nuclear stain previously with paracarmin *in toto*. This lengthy and troublesome process is entirely unnecessary however, for the triple stain used after Flemming's fixing solutions gives sharply defined starch grains stained a brilliant blue, which is permanent for years, as our slides in use in the laboratory show, while the chromatin is a red or violet. This reaction of starch in the triple stain has been noted not only by TIMBERLAKE for pyrenoid starch, but also more recently by DENNISTON (**6**) of this laboratory for the starch of the higher plants.

Methods

While Closterium is one of the commonest of the fresh water algae in this region, it does not frequently occur so abundantly that a cytological study by means of sections can be made of it. For the past three years, however, the bottoms and sides of the lily banks in the university greenhouses, as well as the larger filamentous algae, such as Oedogonium, growing on the bottom of the tanks, have been covered during the summer months by an abundant and almost pure growth of *C. Ehrenbergii* Menegh., and during the last spring with a mixed growth of *C. Ehrenbergii* and *C. moniliferum* Ehrenb.

The Closterium was so abundant in these tanks that all that was necessary was to shake some of the plants to which they were attached in a vial of water. The Closterium would sink to the bottom and form there a layer of considerable thickness. The water could then be pipetted or decanted off and the fixing fluid added. Washing the plants and changing the alcohols and paraffins were all done in the same way, either by decantation or by pipetting off the liquid above them. About twelve hours after the change to 52° paraffin the vial was set in ice water to harden the paraffin. The vial was then broken, the glass carefully picked away from the paraffin, and the bottom layer sectioned. I am indebted for this method to Dr. OVERTON of this laboratory, who has used it very successfully in sectioning Paramoecium.

Material was fixed in Flemming's medium, Flemming's weaker, and Flemming's weaker half strength, and Merkel's solutions. Flemming's weaker half solution strength gave the best results both on the nuclei and on the pyrenoids, causing very little shrinkage and preserving the internal structures well. With the exception of the pyrenoids, Merkel's solution preserved the cytoplasm structures better, but in the former caused shrinkage, as did the Flemming's medium solution. The sections were stained with the triple stain, the pyrenoid itself taking on a brilliant red color, while the starch around it always took the gentian stain as has already been described.

The chromatophore

As noted above, the only figures of the cross section of a chromatophore of Closterium, so far published, are those of NÄGELI, in which it is shown as composed of a central cylinder from which radiate ridges like the spokes of a wheel. In his figures NÄGELI does not show these ridges as extending to the cell wall, but in his description he says they do. The form of the chromatophore is quite different in *C. Ehrenbergii* from that described by NÄGELI for *C. parvulum* and *C. moniliferum*. In this form the central cylinder is quite large, occupying practically the entire cell space, while the ridges are comparatively narrow and extend practically to the cell wall, only an extremely thin layer of cytoplasm separating the latter from it. The chromatophore of *C. Ehrenbergii* in cross section (*fig. 2*), instead of resembling a hub with radiating spokes, as in NÄGELI'S two forms, is more like a coarsely cogged wheel. The cytoplasm of the grooves between the ridges is sometimes very densely stained, being much darker than the chromatophore itself, but containing a great number of vacuoles of varying sizes (*figs. 1, 2*). At other times, however, these spaces between the ridges are almost free from stainable materials, showing only a few large vacuoles or having a very reticulate structure (*fig. 2*). When the green plants in the living condition are examined under the microscope, it can be noticed at once that there is great variation among them; some of them are so dark green as to be almost opaque, while others are much lighter green and are semi-transparent. It is clear that the density of the cytoplasm between the ridges determines in a large degree the external appearance of the plant. DEBARY has described the chromatophore as being homogeneous, except for the pyrenoids, in surface view, but a careful examination shows that the larger vacuoles of the cytoplasm between the ridges appear as lighter areas in the darker green of the chromatophore.

The material of the chromatophore itself is in the form of a very fine reticulum, the meshes of which run out into the ridges in such a manner that in cross section the latter appear to be almost radially striate. The meshes are quite small in the outer layer of the chromatophore, but its central region shows a much coarser reticulum. The meshes here vary much in coarseness, and their structure, in connection with the cytoplasm in the grooves, determines whether the plant has a dark or light green color.

The number of ridges on the chromatophore varies from 12 to 18; this is more than is given in the systematic descriptions of this form, but it is practically impossible to count the number of ridges accurately except in sections.

Toward the ends of the Closterium the ridges seem to withdraw from the walls, and a cross section at these points shows a chromatophore with a somewhat star-shaped form and a rather thick layer of cytoplasm between the outer edges of the ridges and the cell wall (*fig. 3*). The ridges are fewer in number also, owing to the fact that some of them do not extend to the ends, and their outer edges are acute instead of blunt and rounded as is the case nearer the center.

In *C. moniliferum* (*figs. 5–7*) the structure of the chromatophore is practically the same except that the number of the ridges in my form is always 10; NÄGELI's figures show 10 and 6. This gives an easy additional means of identifying the species in section, as the ridges of *C. Ehrenbergii* are always more numerous. The central core of the chromatophore is always larger than NÄGELI figured it. In optical cross section it gives the appearance he shows, but actual cross sections show clearly that it is essentially similar to that of *C.*

Ehrenbergii. The relative thickness of the central core as compared with the width of the ridges is shown in *fig. 4*.

The pyrenoids of *C. Ehrenbergii* are imbedded in the substance of the chromatophore close to its surface. It is very rare, except near the ends of the plant, to find a pyrenoid placed far toward the interior of the plant. In cross section it will be seen that many are either placed in the ridges of the chromatophore or lie at their bases. Although many of them lie in the ridges, none of them are found in their extreme outer edges (*fig. 2*).

Where strands of cytoplasm run across the central part of the cell body, they seem to tend to be oriented on the pyrenoids. If streaming of the cytoplasm occurs in these strands, as so frequently happens in the algae, this arrangement would put the pyrenoid in quick communication with all parts of the cell and would facilitate the movement of food products toward or away from it. It would seem to occupy a favorable position in its location so close to the surface of the chromatophore and also in its relation to other parts of the cell.

In *C. moniliferum* there is a single row of pyrenoids down the central axis. In cross section (*figs. 6, 7*) the pyrenoids occupy the center of the chromatophore. As this species is so much smaller than *C. Ehrenbergii*, there is apparently not so much necessity for the pyrenoids being at the surface.

As mentioned above, the pyrenoids in *C. Ehrenbergii* do not lie in the ridges in all cases, although many of them do. In addition to the layer of starch which incloses each pyrenoid, there are, as in Hydrodictyon, numerous starch grains lying free in the cytoplasm. These starch grains practically all lie arranged in longitudinal series in the ridges (*fig. 1*). In a longitudinal section it is rather common to see a number of pyrenoids lying in a ridge in a row, and scattered among them a number of starch grains. The grains seem to have a tendency to collect in these parts. These free grains undoubtedly had their origin around a pyrenoid, as their shape is exactly that of such grains, being angular at the edges and concave (*fig. 8*). Whether these grains became free by a second layer of starch forming around the pyrenoid and crowding out the older layer, or by the disintegration of some of the pyrenoids themselves, or in some other way, I cannot say, but as to the common origin of both plasma starch and pyrenoid starch around some pyrenoid I can entirely confirm TIMBERLAKE'S results on Hydrodictyon. In *C. moniliferum* the stroma starch is also present and is located in the same position, at the surface of the chromatophore.

The pyrenoids

The pyrenoids of Closterium, like those of all the Conjugatae and unlike those of Hydrodictyon, as described by TIMBERLAKE, have a single layer of starch grains around them. In size the pyrenoids vary all the way from bodies almost impossible to see even with the highest magnification to spheres whose diameter is a fifteenth that of the Closterium body itself. Even the small pyrenoids have usually a little starch around them; frequently this is only on one side, but at other times it may extend all the way around (*figs. 18, 21*). These forms in which the starch occurs largely on one side are rather difficult of explanation; the one-sidedness may be due to a difference in the amount of carbohydrate food supply furnished to the two sides, or it may be due to the method of origin of the pyrenoid, as will be discussed later. A more typical form and one more frequently figured is that in which the starch lies as a mass of about uniform thickness in the form of a hollow sphere about the pyrenoid body (*figs. 10–13*). This sphere is only one layer of grains in thickness, although there were a few cases where more than one layer was suggested by the appearance of other grains just outside the regular layer. The clefts between the grains usually extend out radially, but may at times be almost tangential. The grains around any one pyrenoid vary greatly in thickness, and there are usually one or two grains of relatively larger size. The number of grains in the series around a pyrenoid is correlated with their thickness; the thicker the grains the more numerous they are and the more irregular their shape. No two pyrenoids are alike as to the shape of the grains around them. No stratification is visible either in grains or pyrenoids.

It must not be inferred that there is a correlation between the size of the pyrenoid and the thickness of the grains around it. In a general way large pyrenoids have thick grains around them (*fig. 12*), but many very small pyrenoids have thick layers of starch around them, and some of the very largest may be without starch or have only a very thin layer. It is apparent that it is the physiological condition of the plant concerned and not the size of the pyrenoids that determines this difference. This is in harmony with the observed fact that in any one Closterium the starch layers around its pyrenoids will all tend to have the same thickness.

In fixed material, at least, the starch grains are not in direct contact with the pyrenoid. Between the body of the pyrenoid itself and the starch around it there is a layer of substance which either does not stain or stains the same color as the cytoplasm. It seems natural, of course, that there must continue to be some organic connection between the pyrenoid and the starch grains surrounding it; otherwise the starch would be moved away from its pyrenoid by the streaming of the cytoplasm, which undoubtedly occurs here in the chromatophore even if not so rapidly as it does in the cytoplasm next the cell wall. Whatever the connection may be, it must be maintained through this unstained layer, which seems from its staining reaction to be neither pyrenoid nor starch.

There is great variation in the appearance of the pyrenoid itself in different specimens. In one specimen the pyrenoids may all appear angular, while in the specimen lying next to it they are full and globular. This difference may be due to differences in the way in which the fixing solutions happen to affect the particular Closterium containing the pyrenoids, but I am inclined to think that it is rather due to some condition in the pyrenoid itself. The angular form was especially noticeable where the pyrenoids were very large and with little starch. The fixation of the general cell structure with the Flemming weak, half strength, was good in these cases, and many details in the structure of the pyrenoid could be made out. It is an interesting fact that a single cell presents in general the same type of pyrenoid throughout its whole extent.

Very few of the pyrenoids are homogeneous, although they are usually described as being so; practically all of them show parts that are denser. One of the more common forms which this dense region takes is that of an irregular star-shaped portion toward the center of the pyrenoid (*fig. 15*). In this case the central part may be very irregular, with rays extending out from it. The denser portion has sometimes the appearance of a zone or band of darker staining material extending throughout the pyrenoid body (*fig. 22*). The ends of this zone may be split so as to give a Y-shaped figure in cross section. In a Closterium that had been fixed at night I have observed a large vacuole in the pyrenoid (*fig. 23*).

In a great number of cases the denser portions are numerous and are scattered apparently irregularly throughout the pyrenoid. A careful examination will show, however, that each dense area is opposite a starch grain, while the lighter portions are opposite the clefts between the grains, appearing merely as continuations of the latter (*figs. 10, 11*). This concentration of pyrenoid material so near to the place where starch is being laid down in the starch grain is an interesting fact, indicating that even though the rudiment of the grain may be formed as TIMBERLAKE has suggested some kind of organic connection is still retained between the young grain and the part of the pyrenoid nearest to it. The same relation might be expected to exist also if the grain is wholly a deposition product of the pyrenoid. How long this connection is retained cannot be determined. In any case, this increased concentration of the pyrenoid material in certain definite regions would seem to indicate that the pyrenoid is not a mere mass, but that it has a structure correlated more or less wholly with its function.

In many cases the pyrenoids seem to be in the process of cutting off pieces or of breaking up into a number of pieces. These may be in the form of a segment split off from one side (*figs. 16, 17*), or the entire pyrenoid may break up into lens-shaped segments (*figs. 25, 26*). Where the body of the pyrenoid itself shows a more densely staining band in cross section, these segments are cut off from one or both sides of this region (*fig. 16*). If the pyrenoid is made up of denser bodies placed opposite starch grains, the cutting off may occur along any of the lighter, less dense lines (*fig. 10*); however, hardly ever more than two of these segments are cut off and usually only one of them at any one time. The process may be traced in all its stages, from a lightly stained zone in the pyrenoid body to a small cleft, and finally to the separation of a free segment. TIMBERLAKE was able to find in the pyrenoids of Hydrodictyon that the segments changed their staining reactions from the bright red of the pyrenoid by a series of transition stages to the violet color characteristic of the starch, but no such series of transition stages could be found in Closterium, although the segments cut off frequently appear as if stained a lighter red, owing to their smaller size. It is a question as to what becomes of these pieces of pyrenoids. Some figures seem to suggest that they round up and form smaller pyrenoids. It is very difficult to get any series of stages showing the migration of the parts away from each other, if such is the case. The hypothesis that they form other pyrenoids is supported by the fact that the starch layer is frequently of varying thickness, and may be quite thin on one side, as would happen if a segment had been cut off that side and the layer of starch had not been redeposited to any great degree (*fig. 9*).

The great variation in size of the pyrenoids is a conspicuous fact. SCHMITZ, who first observed pyrenoid division, says distinctly that they may divide equally or very unequally. It is certainly true that they are capable of splitting up into segments, whether these segments become independent pyrenoids or develop into starch grains.

In this connection the observation of BÜTSCHLI that the paramylon bodies of Euglena split up into similar shaped disks is very interesting. He regards it as due to their internal structure. The similarity of his figures to those of the pyrenoids in Closterium may indicate that paramylon bodies and pyrenoids are alike in their essential structure, even though not in chemical composition.

It should also be stated that these clefts in the body of the pyrenoid appear also in fixed and stained specimens that have not been sectioned but are examined whole.

I have observed many of the typical figures of the division of one pyrenoid to form two in material fixed at night. These figures are in all essentials like those observed by SCHMITZ in Hyalotheca and by a number of investigators since his day. It seems to consist simply in a pinching in two of the pyrenoid, and it is a curious fact that some of these same pyrenoids show the composite structure just described (*fig. 26*).

In Hydrodictyon, according to TIMBERLAKE, the pyrenoids show no such numerous clefts as are present in Closterium, and this fact makes it still more difficult to believe that the segments in Closterium are destined to form starch grains. The origin of the starch grains and the nature and fate of the pyrenoid segments are difficult questions. That the two problems are closely related, as maintained by TIMBERLAKE, is the most suggestive conception that has so far been advanced, but the whole matter is less clear in Closterium than in Hydrodictyon. Further comparative studies on the pyrenoids of the Conjugatae will doubtless make the significance of the pyrenoid segments more clear.

A culture of Closterium was kept in the dark for three days, and then when treated with iodin showed very little starch present around the pyrenoids. Specimens from this culture were imbedded and sectioned. It was found that in most cases the starch had entirely disappeared, but that in others there were still traces of it present in the form of a thin layer around the pyrenoids (*fig. 24*). Some stroma starch was also present. The stroma starch seems to persist longer than that formed more recently around the pyrenoids. Staining the pyrenoids after keeping them in the dark was rather difficult, requiring 10–20 minutes, where before it had not taken that number of seconds; the stain was not brilliant even then. It was noticeable too that the pyrenoids had diminished one-third to one-fourth in size, showing that some of the pyrenoid substance had been used up.

The nucleus

Only a brief description of the nucleus will be given here, my principal aim at this time being to correct the erroneous view as to the shape of the chromatophore of Closterium, and to give further details as to the structure of the pyrenoids. The nucleus has in longitudinal section the form of a double convex lens (*figs. 1, 29*). Its body in both species is made up of a finely reticulate network of rather lightly staining fibers, forming meshes of almost uniform size. There seem to be no differentially stained chromatin granules on the strands. There are darker masses in the fibers which may be the net knots of the older authors; the extreme fineness of the network makes this point especially difficult to determine. The most striking part of the nucleus is the great mass of granules which lie in a group in the center of this reticulum and which stain a brilliant red in the triple stain. These bodies are globular or sometimes somewhat angular granules of varying size, apparently unconnected and lying free in the reticulum. The strands from the fine-meshed reticulum surrounding them seem to come up to these granules and apparently hold them in position. These granules in *C. Ehrenbergii* are usually arranged in a fairly compact mass of varying size at the center of the nucleus (*fig. 1*), but they may be scattered out in an irregular manner across the long axis of the nucleus (*fig. 29*). In *C. moniliferum* (*fig. 28*) these bodies form a mass that is practically spherical, but shows a few irregularities on its surface. The nucleus in this species resembles that of Spirogyra very much, but it can be made out that the central spherical mass is made up of smaller pieces, while in Spirogyra the so-called nucleole appears as a homogeneous sphere.

The real significance of these granules and of the meshwork that surrounds them, and the part which each takes in cell division, can be determined only by seeing them during the time of chromosome formation. Their behavior will throw light on the nature of the so-called chromatin nucleolus of Spirogyra, in which, as described by MITZKEWITSCH (14), BERGH (1), and others, is contained all the chromatin in the nucleus. I shall discuss the phenomena of nuclear and cell division in a further paper.

My indebtedness to Professor R. A. HARPER for his advice and criticism during the progress of this work is very great, and I take this opportunity of expressing my appreciation of them.

Summary

1. The current figures and descriptions of the chromatophore of Closterium derived from NÄGELI are fundamentally incorrect. The chromatophore is not made up of a series of radiating plates about a slender central core, but is a curved cone-shaped structure with relatively narrow ridges on its surface.

2. The pyrenoids are imbedded in the periphery of this chromatophore in *C. Ehrenbergii* and exactly at its center in *C. moniliferum*.

3. Pyrenoid starch and stroma starch both have the same origin, all the starch being formed around pyrenoids.

4. The pyrenoids show considerable internal structure, frequently containing denser and lighter portions, vacuoles, etc., and often are cleft into a mass of disks or segments of varying number and form.

AGRICULTURAL EXPERIMENT STATION
BURLINGTON, VERMONT

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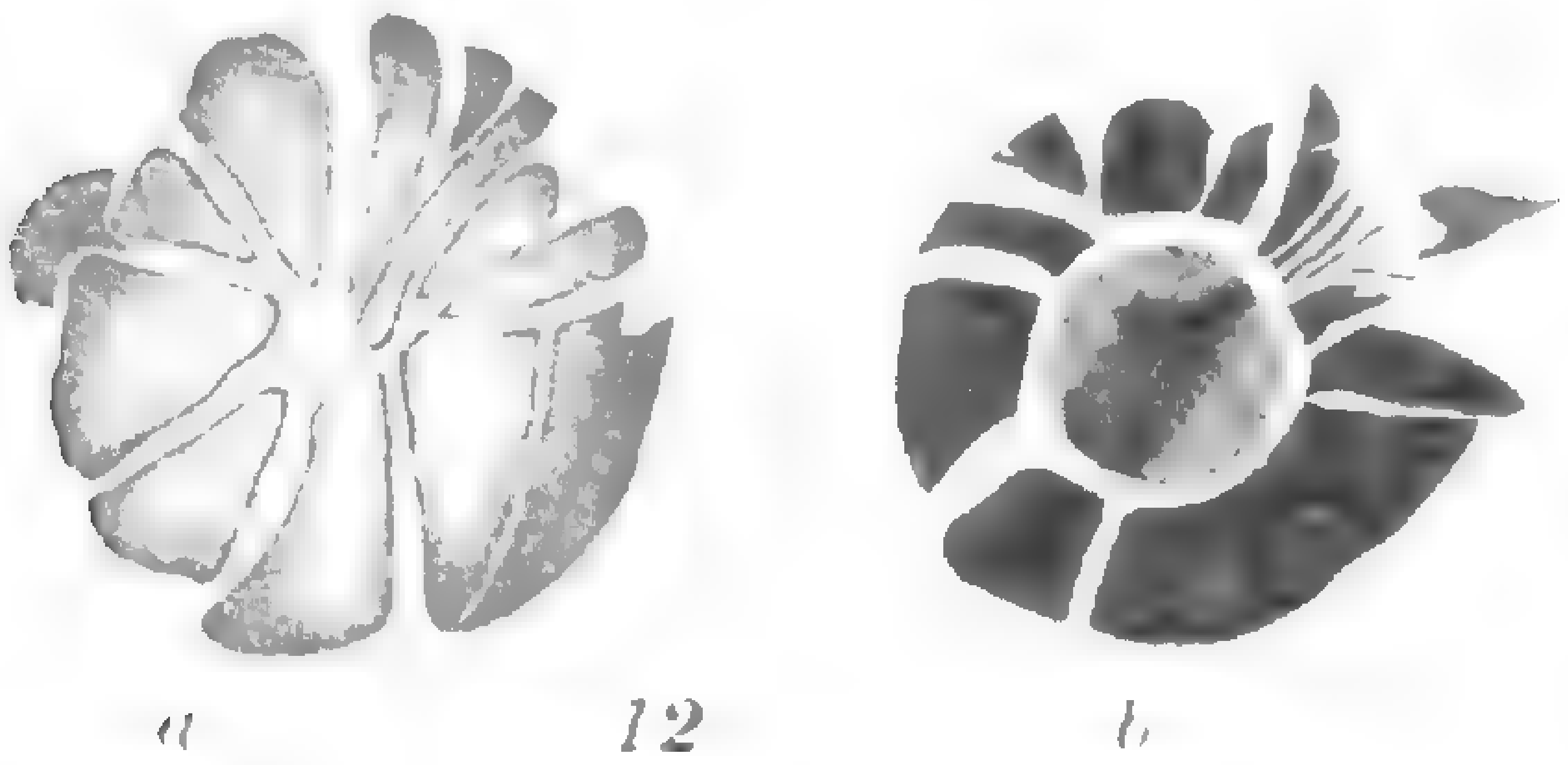
LUTMAN on CLOSTERIUM



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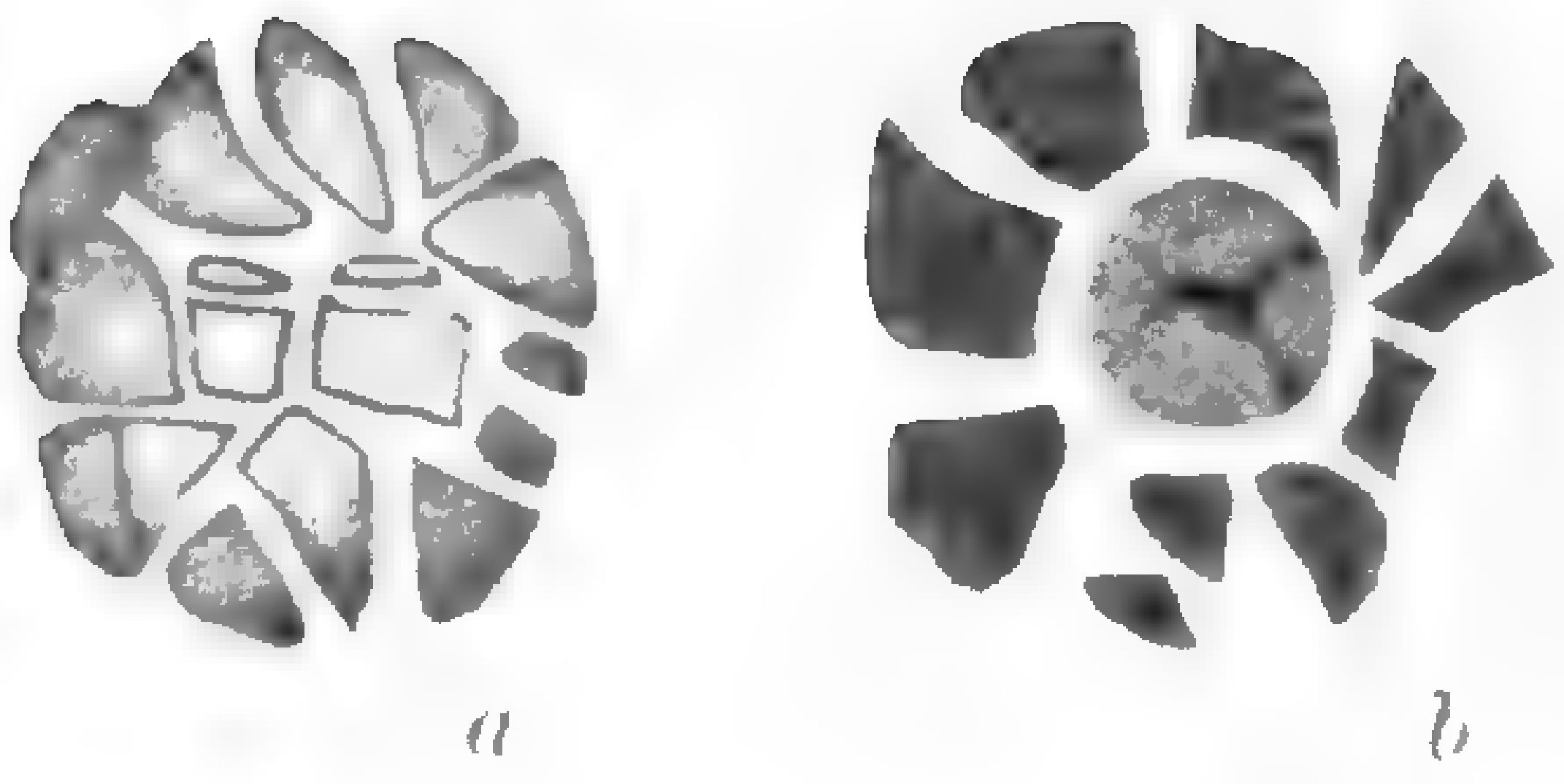

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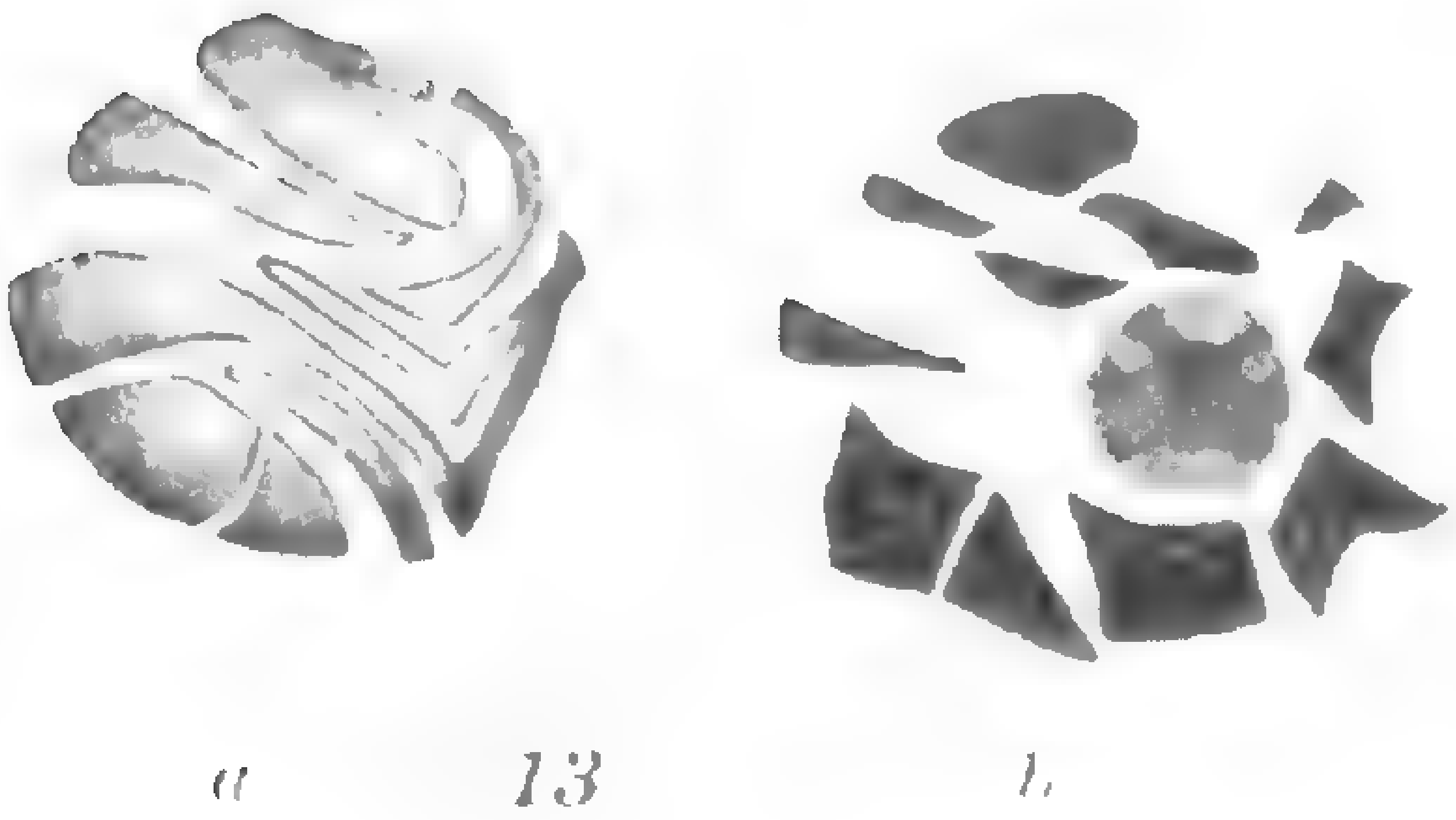

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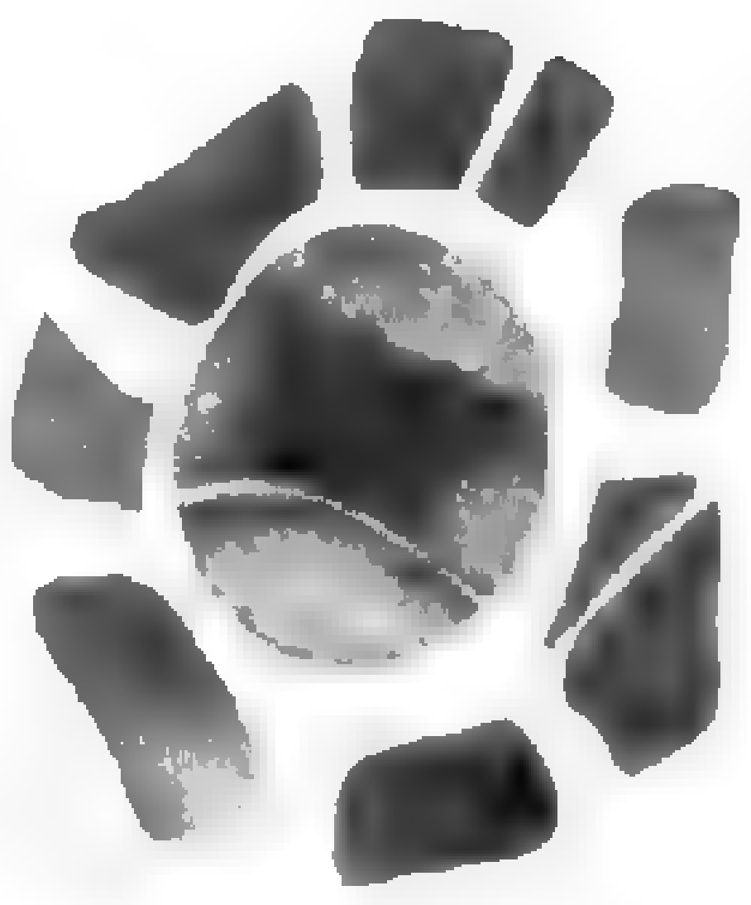

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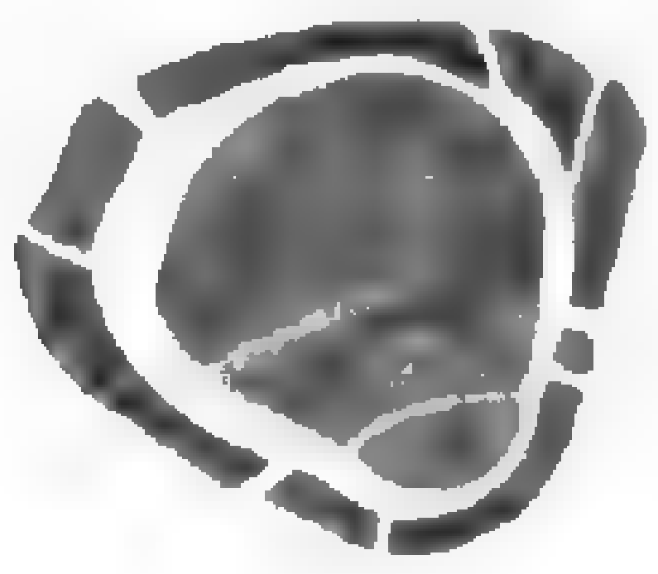

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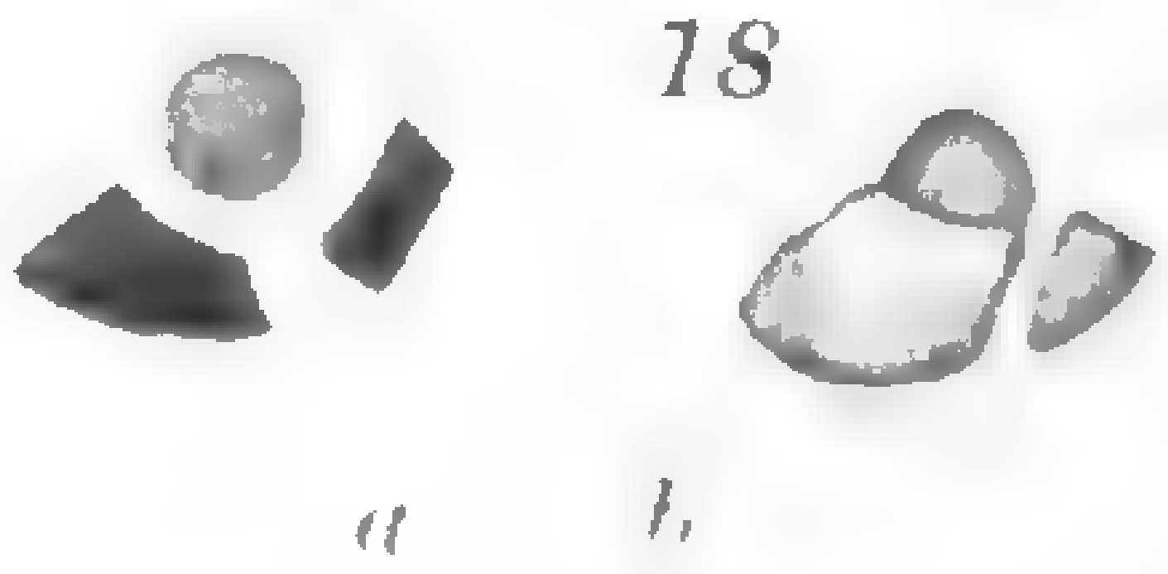

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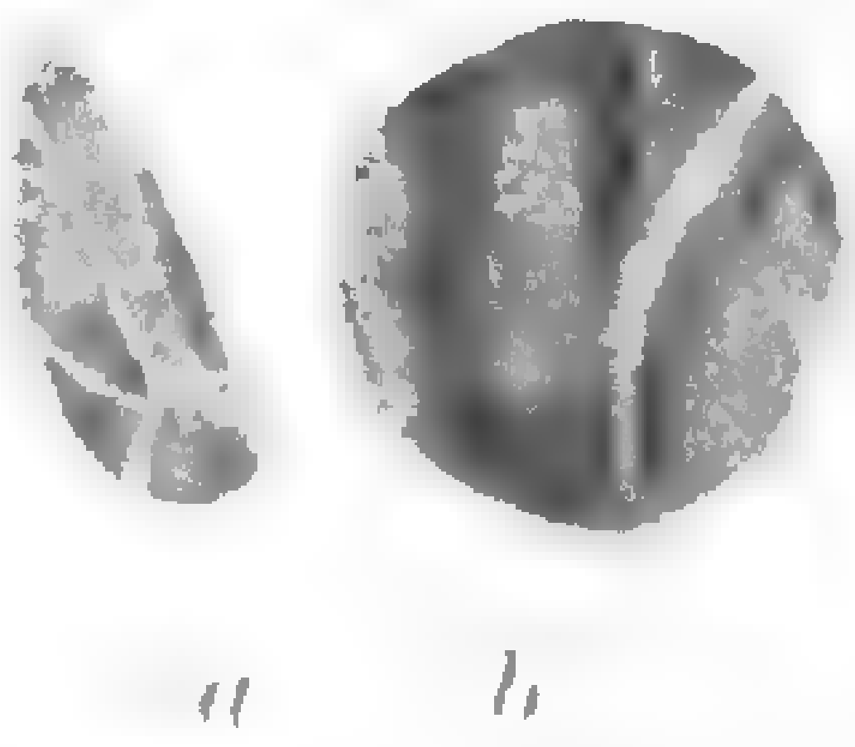

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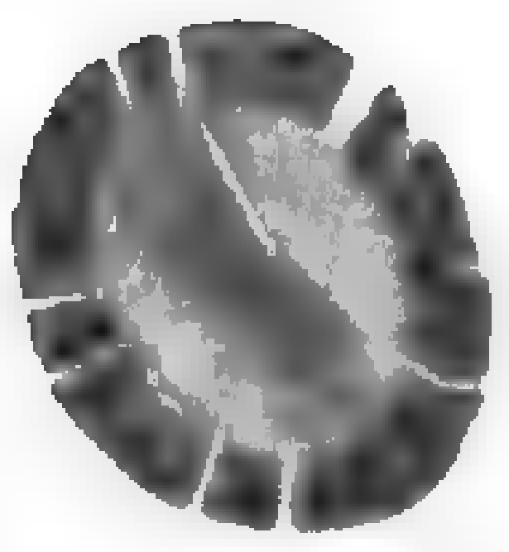

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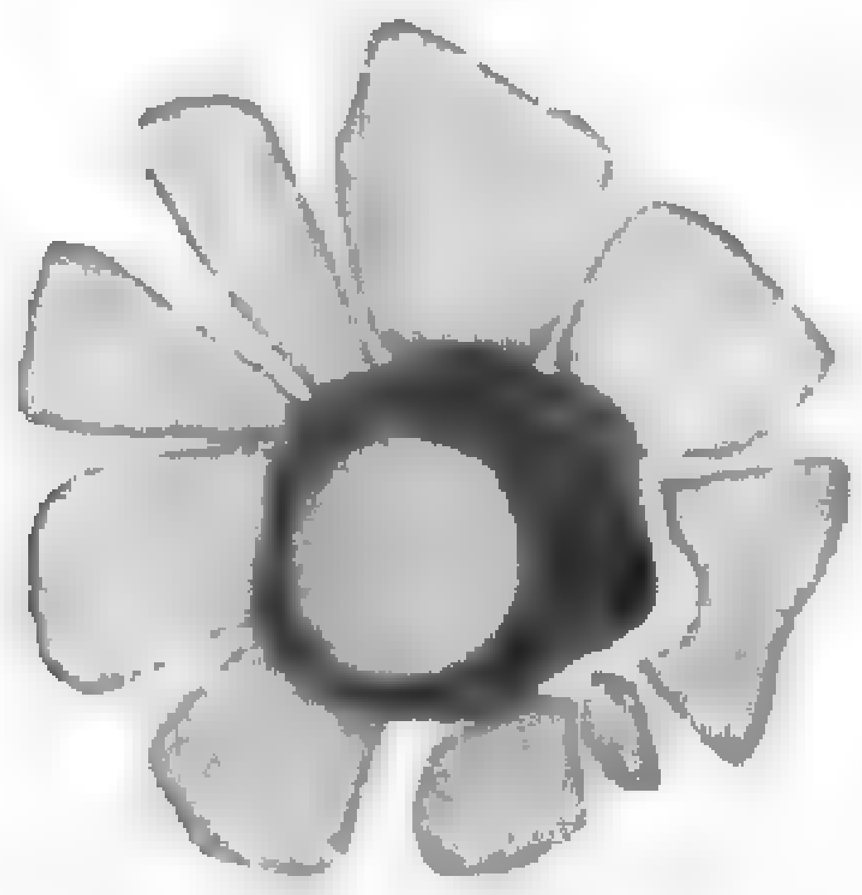

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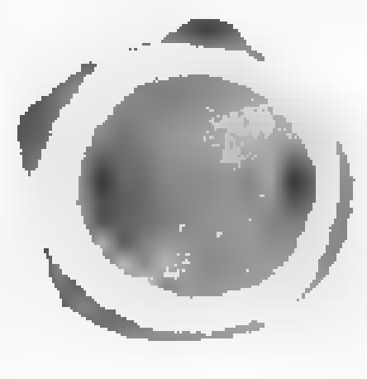

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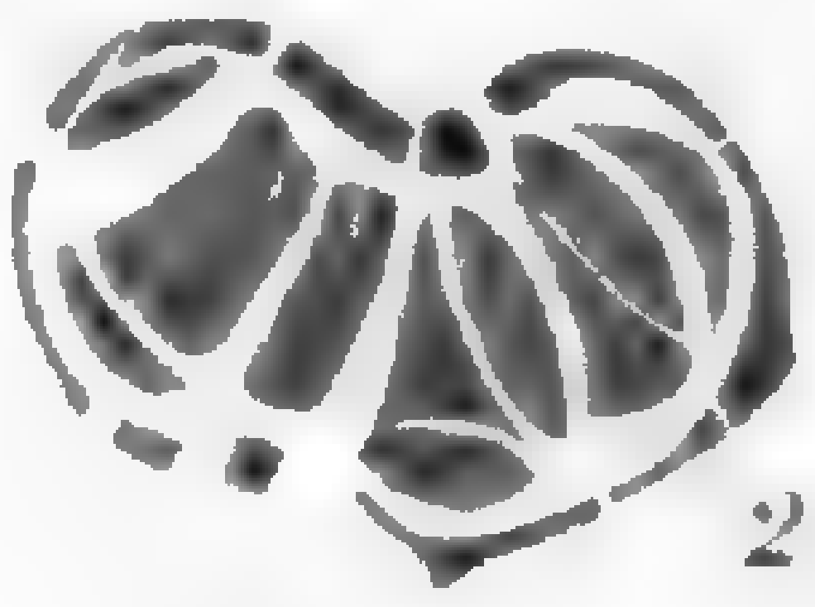

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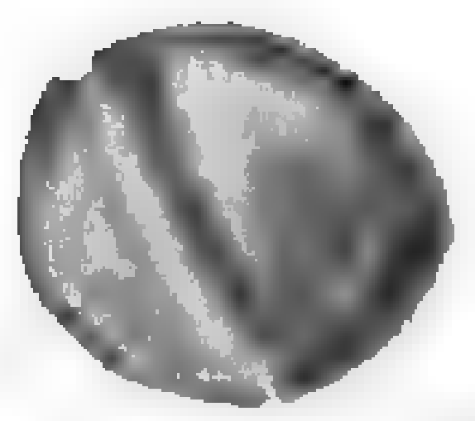

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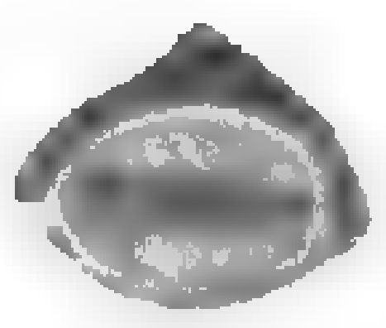

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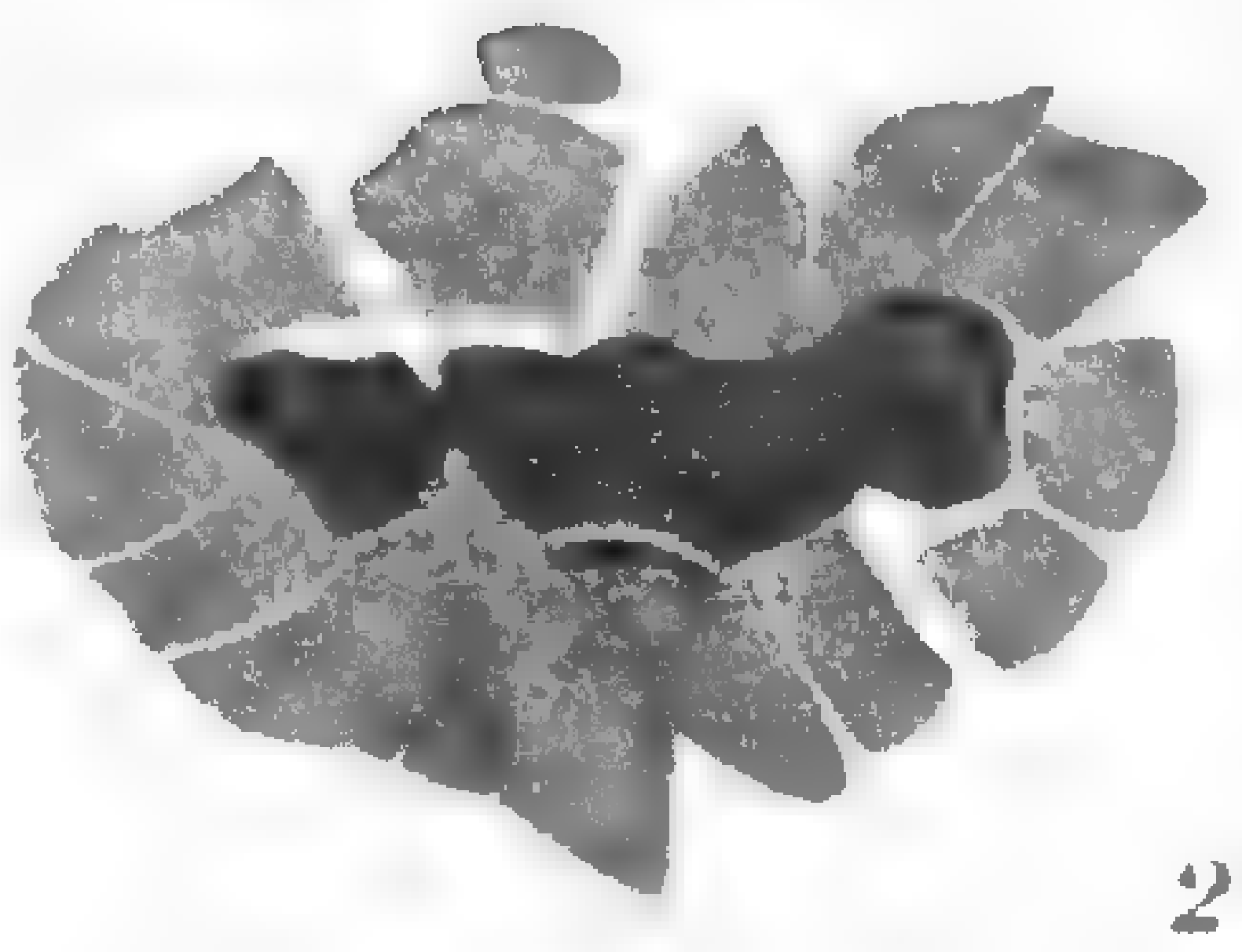

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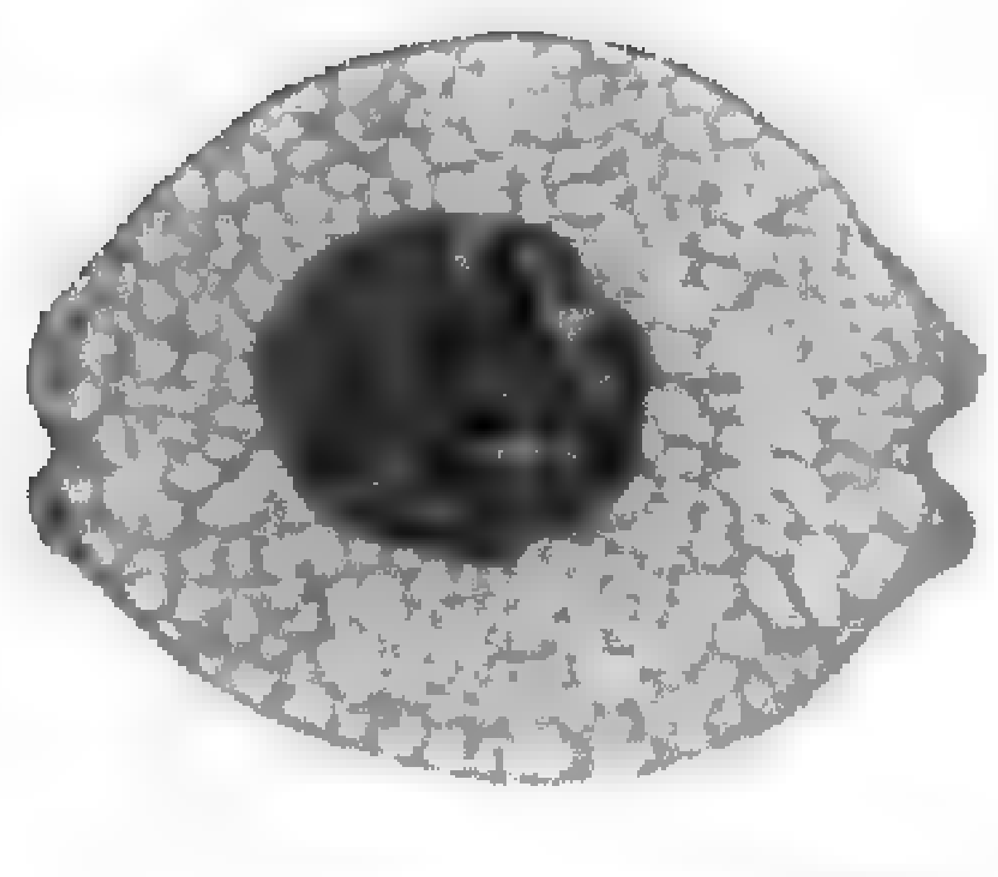

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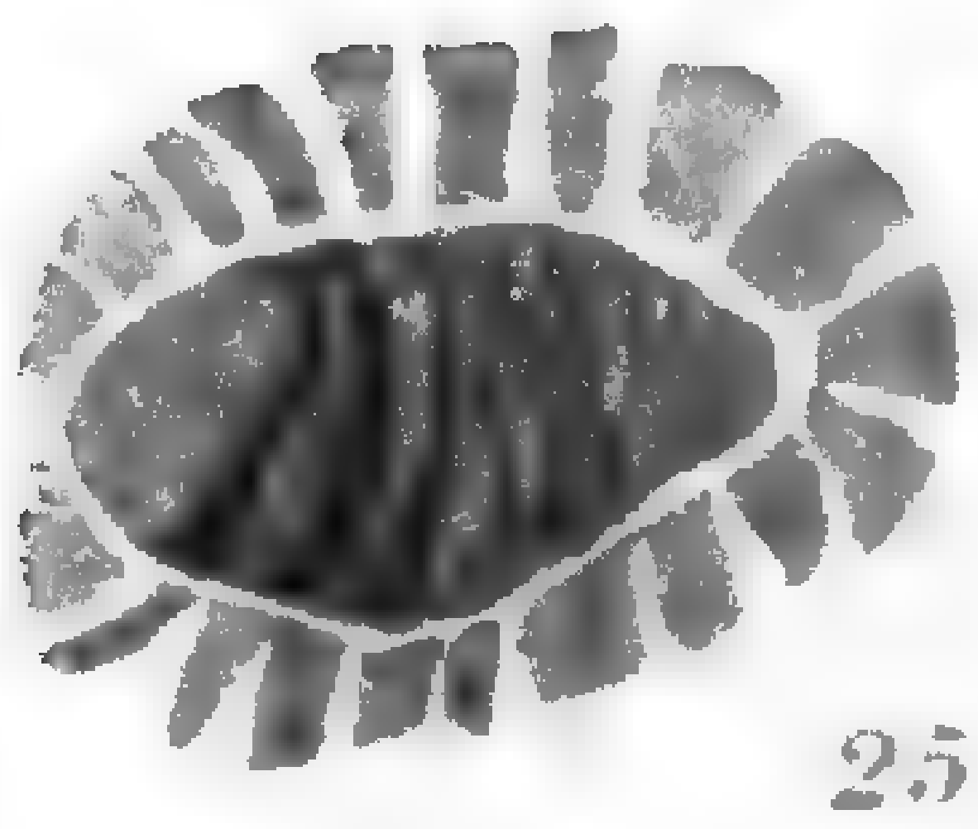

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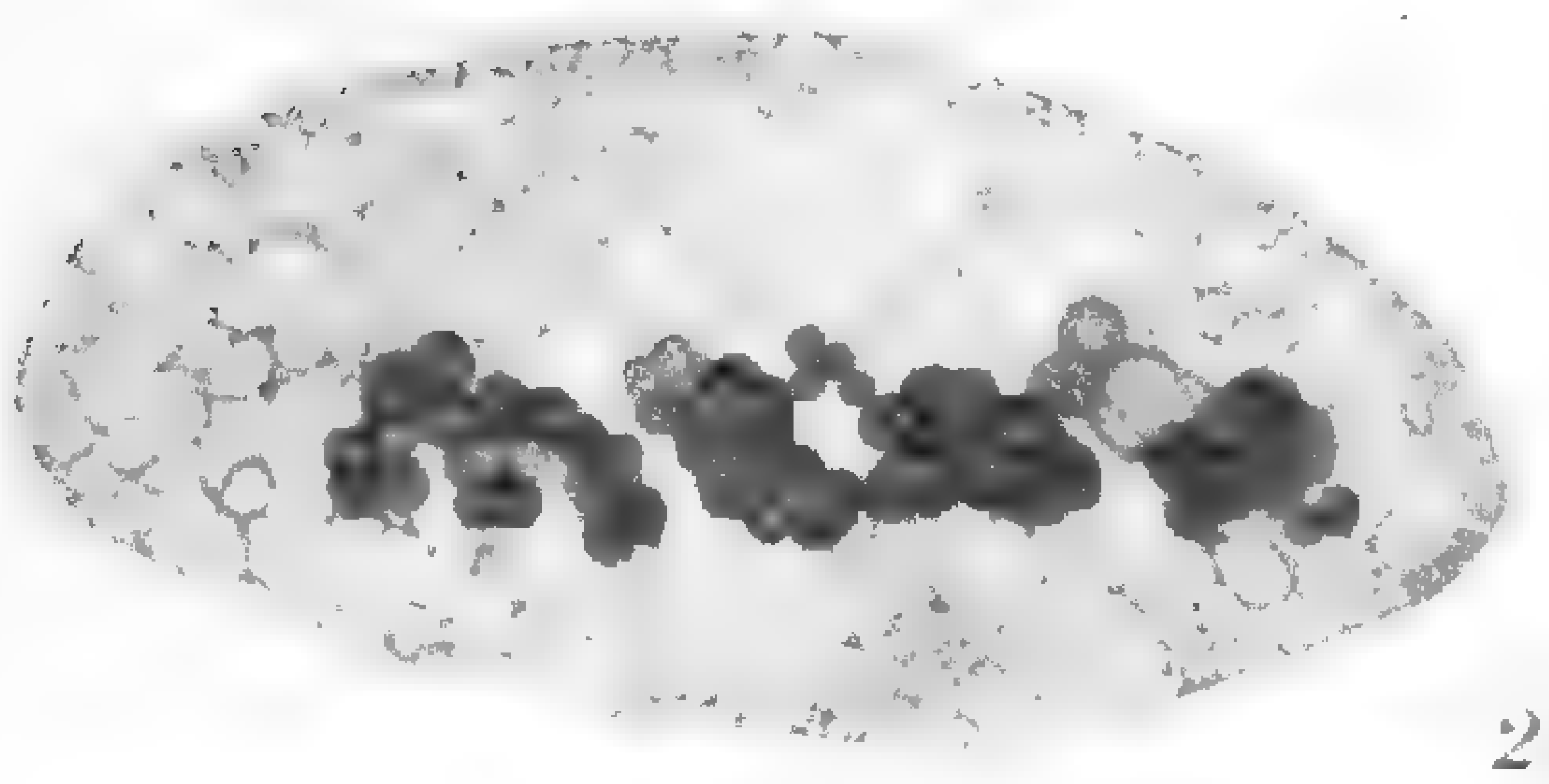

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LUTMAN on CLOSTERIUM

HELIOTYPE CO., BOSTON.

EXPLANATION OF PLATES XVII AND XVIII

MAGNIFICATION.—*Figs. 1, 2, 5, 6, 7*, about ×900; all the others, about ×1250.

FIG. 1.—*C. Ehrenbergii;* longitudinal section; on the left the section is through one of the ridges; on the right it is through one of the furrows; *n*, nucleus; *p*, pyrenoids; *s*, stroma starch.

FIG. 2.—*C. Ehrenbergii;* cross section.

FIG. 3.—*C. Ehrenbergii;* cross section near one end, showing star-shaped chromatophore.

FIG. 4.—*C. moniliferum;* shaded portion is the central part of the chromatophore.

FIG. 5.—*C. moniliferum;* schematic cross section through the nucleus (*n*); *gc*, granular cytoplasm.

FIG. 6.—*C. moniliferum;* cross section about half-way to the tip.

FIG. 7.—*C. moniliferum;* cross section nearer the tip.

FIGS. 8–26.—*C. Ehrenbergii;* details of starch and pyrenoids.

FIG. 8.—Stroma starch.

FIG. 9.—Pyrenoid showing internal markings; *a*, in section; *b*, surface view of the starch mass.

FIG. 10.—Pyrenoid showing internal markings; *a*, section of starch showing top of pyrenoid; *b*, section of starch and pyrenoid; *c*, section showing lower part of the starch.

FIG. 11.—Pyrenoid; *a*, section; *b*, top surface of starch mass; *c*, bottom of same.

FIGS. 12, 13.—Pyrenoids; *a*, surface view of starch; *b*, section of pyrenoid.

FIG. 14.—Pyrenoid; *a*, section; *b*, surface view of starch; *c*, view of the starch at deeper level.

FIG. 15.—Pyrenoid; *a*, surface of starch; *b*, section of pyrenoid.

FIGS. 16–22.—Pyrenoids showing pieces cut off.

FIG. 23.—Pyrenoid with large vacuole.

FIG. 24.—Pyrenoid after Closterium has been kept in the darkness for three days.

FIGS. 25, 26.—Pyrenoids showing peculiar disks into which the pyrenoid body has broken up.

FIG. 27.—Pyrenoid as ordinarily figured in division.

FIG. 28.—Nucleus of *C. moniliferum.*

FIG. 29.—Nucleus of *C. Ehrenbergii.*

CLIMATOLOGY AND VEGETATION IN COLORADO

W. W. ROBBINS

(WITH SEVEN FIGURES)

To the student of botany, it matters not in what part of the United States he lives or in what branch of botanical work he is engaged, the state of Colorado is an interesting and attractive area. The general inland location of the state, great differences of altitude, of latitude, and of topography, are factors which bring about varied climatic conditions, resulting in corresponding vegetative differences. It is the purpose of this paper to give a general view of the climatological conditions of Colorado in their relation to vegetation. The necessity of pointing out in ecological and phytogeographical studies the relation between the climatology of an area, extended or restricted in its range, and the vegetative covering, is being increasingly recognized. The climatologist and the field botanist must join hands. Not only is the botanist coming to realize his dependence upon a thorough knowledge of climatology as a basis for his phytogeographical studies, but in a like manner is the climatologist coming to see that the distribution of the indigenous vegetation will aid him. This fact has been recognized by the Maryland Weather Service, which has undertaken a botanical survey of that state as a part of its climatic studies.

Physiography and climatology

PHYSIOGRAPHY

TOPOGRAPHY.—The general topographic features of the state are given in *fig. 1*. The eastern half of the state is plains. This region is limited on the west by the foothills, which extend from the northern to the southern borders of the state, following closely the 6000-foot contour line. The foothills rise one over the other, extending westward to the main range. The continental divide passes irregularly in a north and south direction through the state. It is therefore a barrier to the east and west distribution of plants. In the mountainous region there are four large parks or high valleys: North, Middle, South, and San Luis parks. They are broad, level expanses of country having an elevation of 6000–10,000 feet and inclosed by high mountains; hence they are very dry and the vegetation is more xerophytic than that growing at the same altitudes in uninclosed areas. There are parts of western Colorado, however, where xerophytic conditions exist at high altitudes, the dryness in this case being due to the unequal seasonal distribution of precipitation. Western Colorado is for the most part high; high, flat tablelands and mesas, dissected by narrow steep canyons, are characteristic. Many of the minor mountain ranges have an east and west trend.

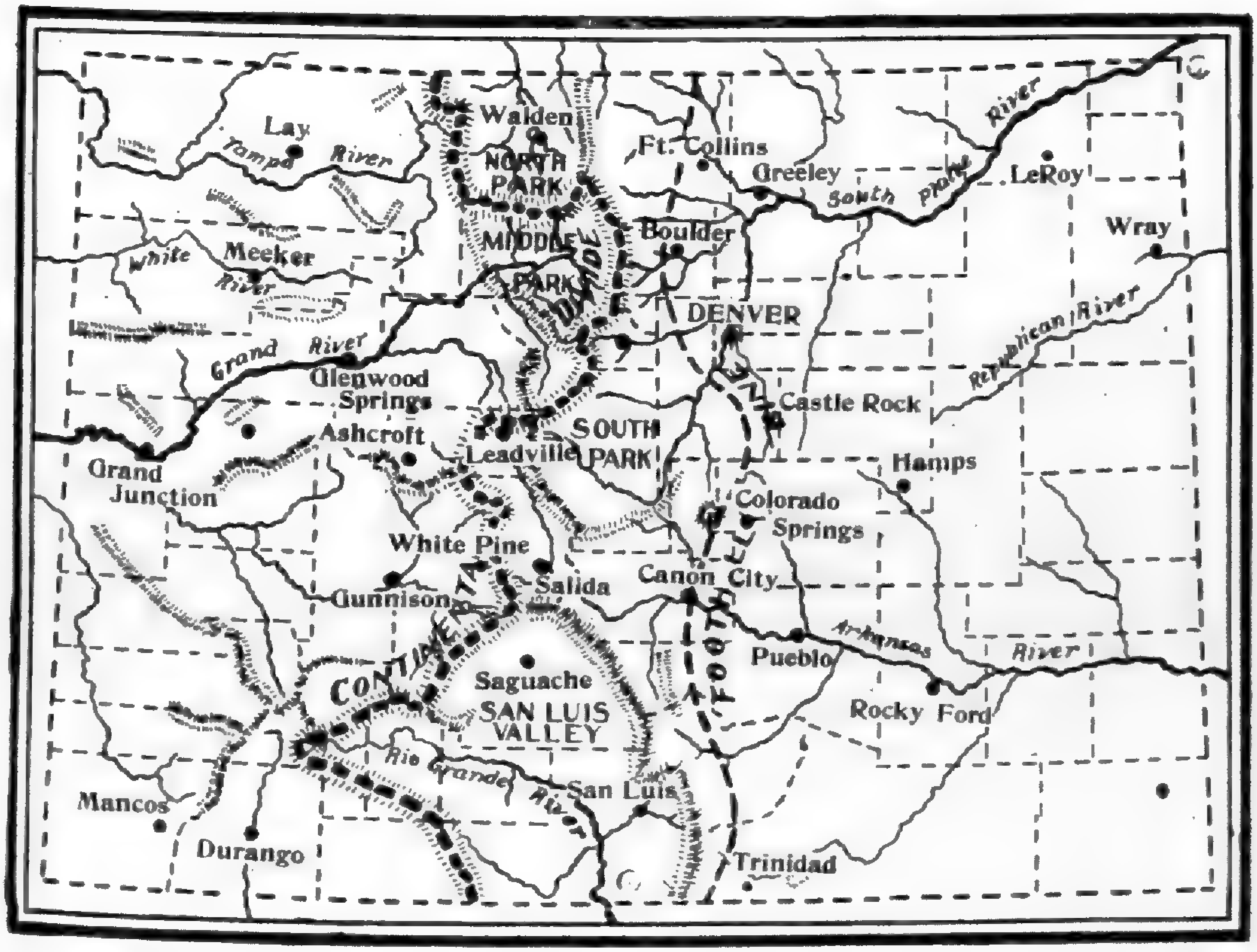

FIG. 1.—General topographic features of the state; east of the foothill line lie the great plains.

An important topographic feature of the eastern part of the state is the Arkansas-Platte Divide, extending plainward from the foothills in the middle of the state. Foothill forms of vegetation have an eastward extension on this divide. It also marks the northern and southern limit of some species, such as the pinyon pine (*Pinus edulis* Engelm.), the chandelier cactus (*Opuntia arborescens* Engelm.), and *Populus Wislizenii* (S. Wats.) Sarg., which do not occur north of the divide. The same is true to a less extent of the scrub oak; on the eastern slope this plant is not abundant north of the Arkansas-Platte Divide.

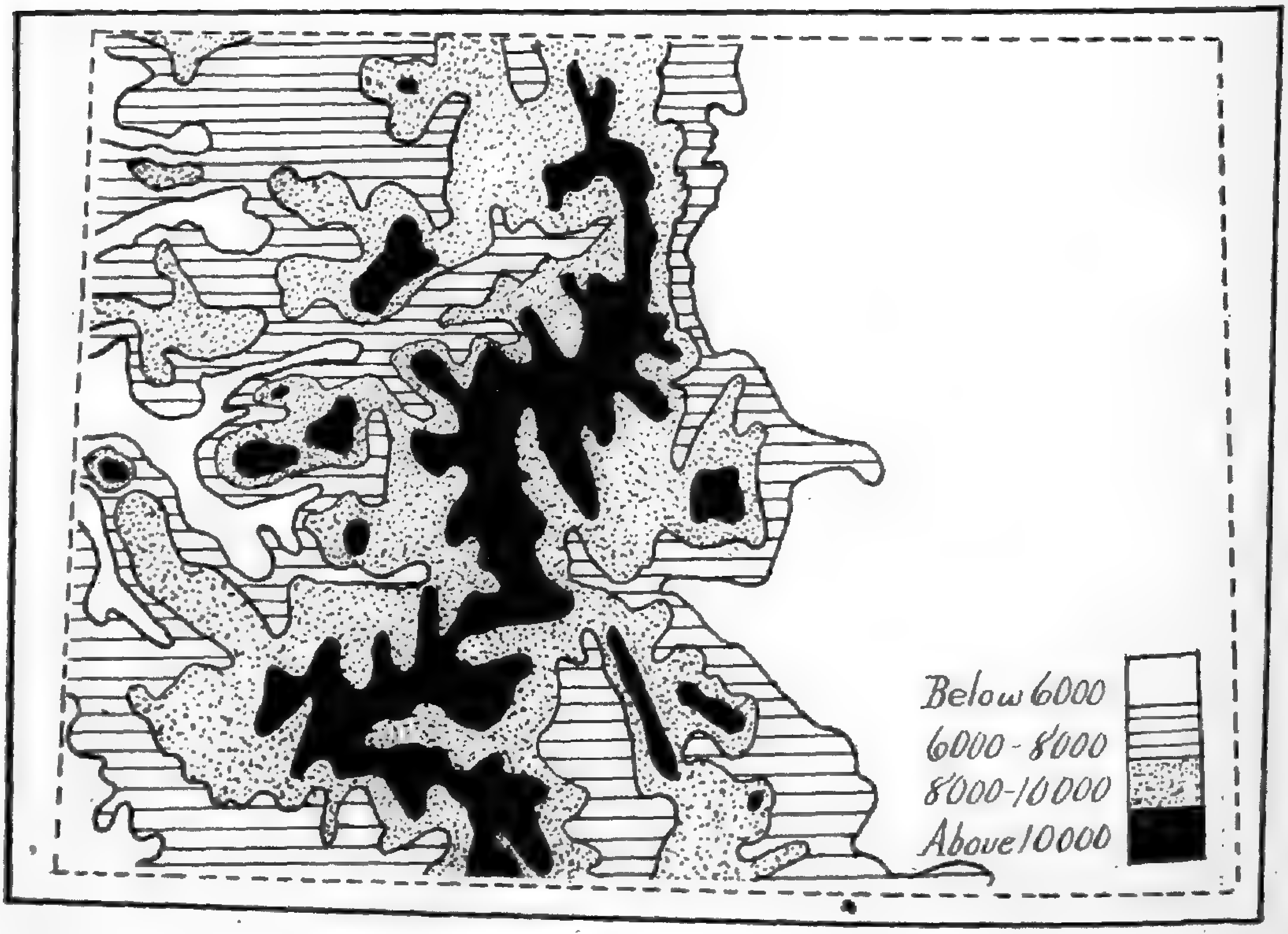

FIG. 2.—Mass elevations of Colorado.

ELEVATION.—Colorado has an area of 103,480 square miles.[1] The following table gives the mass elevations of the state in area and percentages.

TABLE I

MASS ELEVATIONS

Elevation	Area in sq. miles	Percentage of total area
6000 feet and below	45,000	43
6000–8000 feet.............	22,000	20
8000–10,000 feet	24,000	23
10,000 feet and above........	12,500	14

From the above table and the accompanying map showing mass elevations (*fig. 2*), it is seen that a great proportion of the state is highly

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[1] GANNETT, HENRY, Report U. S. Geol. and Geog. Survey of the Territories (Hayden Survey) 313. 1876.

mountainous. The lowest point in the state has an elevation of 3386 feet; there are a number of peaks over 14,000 feet high; thus there is an altitudinal range considerably over 11,500 feet.

Drainage systems.—The general north and south direction of the mountains of Colorado determines the general east and west direction of the streams. In the mountainous country small streams are very abundant, and they usually have their head in a wet mountain meadow which is fed by water from melting snow. The prevalent east and west direction of the streams is a condition affecting the migration of riparian species. Generally speaking, the streamside flora and vegetation at any point is more like that east and west than that north and south.

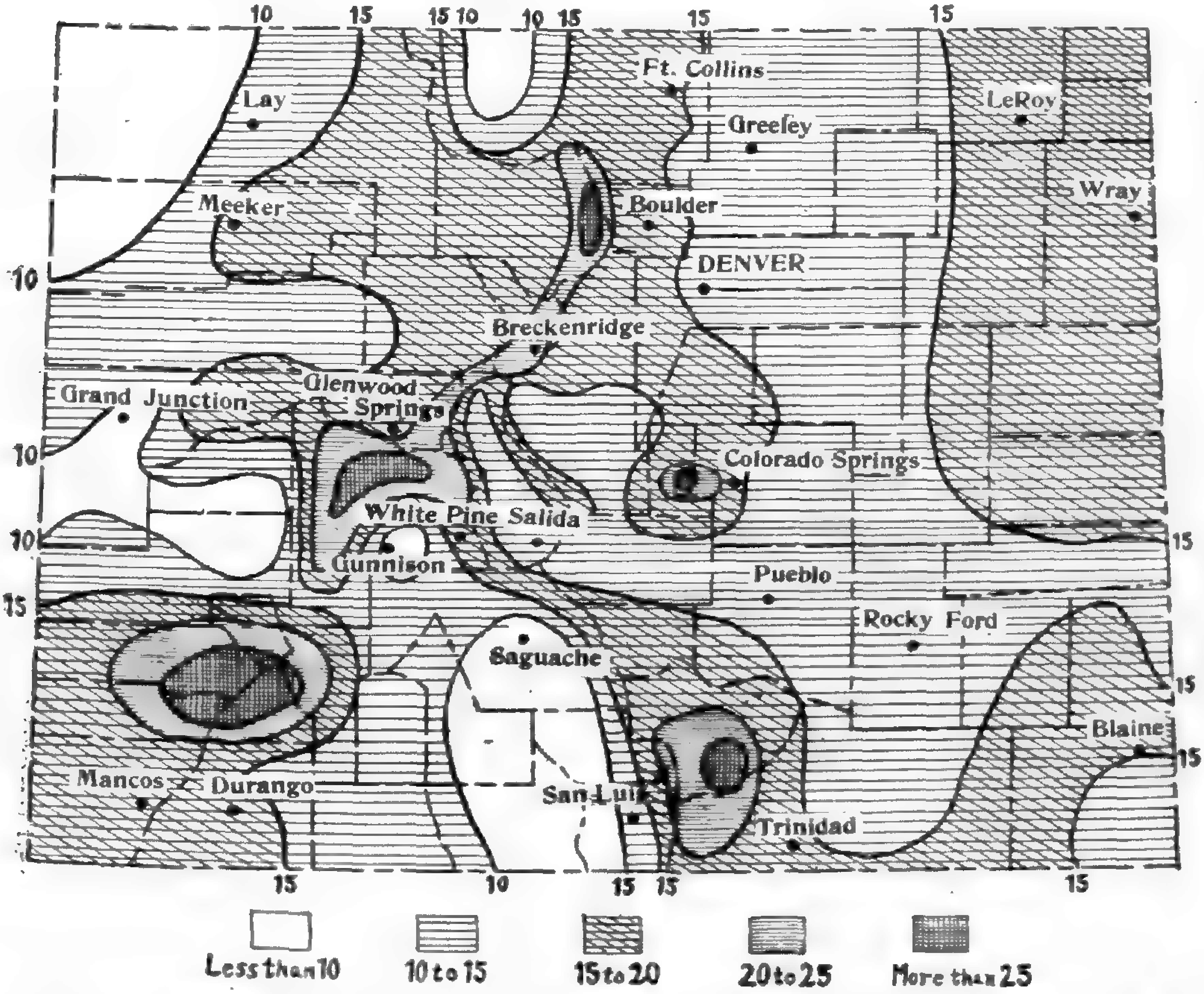

Fig. 3.—Mean annual precipitation: the area along the eastern border of the state having 15–20 inches annually is called the "rainbelt"; dry farming is more successful here than in the belt on the west of it.

PRECIPITATION

General account.—The precipitation amounts of Colorado are shown in *fig. 3*. In making a rainfall map it is found difficult to depend upon rain gauge records alone, because of the variety of conditions at intermediate points which are brought about by topographical conditions. Hence in preparing this map, as well as the ones of temperature, the influence of the larger topographic features and of altitude have been taken into consideration. Fortunately, however, the meteorological stations in Colorado are numerous enough and so happily distributed, that one is able to rely upon them as being fairly representative.

TABLE II

SEASONAL DISTRIBUTION OF PRECIPITATION EAST AND WEST OF DIVIDE

STATION	ALT. (FEET)	EAST OF CONTINENTAL DIVIDE			WEST OF CONTINENTAL DIVIDE		
		Mean for growing season	Mean for year	Perc'tage during growing season	Mean for growing season	Mean for year	Perc'tage during growing season
Ashcroft	9483	.....	.....	..	10.67	19.38	55
Blaine	3935	12.36	16.08	77			
Boulder	5347	12.83	18.46	69			
Breckenridge	9536	.....	.....	..	11.99	26.76	72
Castle Rock	6220	12.73	17.65	72			
Cheyenne	6088	9.40	12.20	77			
Collbran	6000	.....	.....	..	7.33	14.59	50
Colorado Springs	6098	13.00	14.41	90			
Denver	5272	10.03	14.02	72			
Durango	6534	.....	.....	..	8.25	16.62	50
Ft. Collins	4985	11.06	14.91	73			
Grand Junction	4608	.....	.....	..	4.27	8.50	50
Hamps	5400	11.82	14.56	81			
Holly	3386	12.71	15.32	71			
Idaho Springs	7543	10.65	15.44	68			
Lake Moraine	10625	18.44	25.59	72			
Lay	6162	.....	.....	..	6.37	12.72	50
LeRoy	4380	12.22	16.05	76			
Mancos	6960	.....	.....	..	9.29	17.29	53
Meeker	6182	.....	.....	..	8.42	15.91	53
Pike's Peak	14108	19.07	28.65	66			
Pueblo	4734	9.17	12.11	75			
Saguache	7745	5.45	7.21	75			
Salida	7035	7.62	11.47	67			
Wray	3512	14.57	18.11	80			
Mean average		11.84	15.90	**74**	8.57	16.45	**52**

The eastern part of the state has more rain (15–20 inches) than a strip closer to the mountains (10–15 inches). On the eastern slope of the mountains, localities between 6000 and 10,000 feet altitude have an annual precipitation of 15–20 inches; many localities have greater amounts. The higher mountainous parts receive over 20 inches annually. North, Middle, and San Luis parks are very dry, the annual precipitation being less than 10 inches; South Park is drier than localities at the same altitude on the eastern slope. On the western slope there is a gradual decrease westward in the annual rainfall, which becomes on the western border less than 10 inches.

SEASONAL DISTRIBUTION.—The precipitation of Colorado shows great variability, not only in amount but also in seasonal distribution.

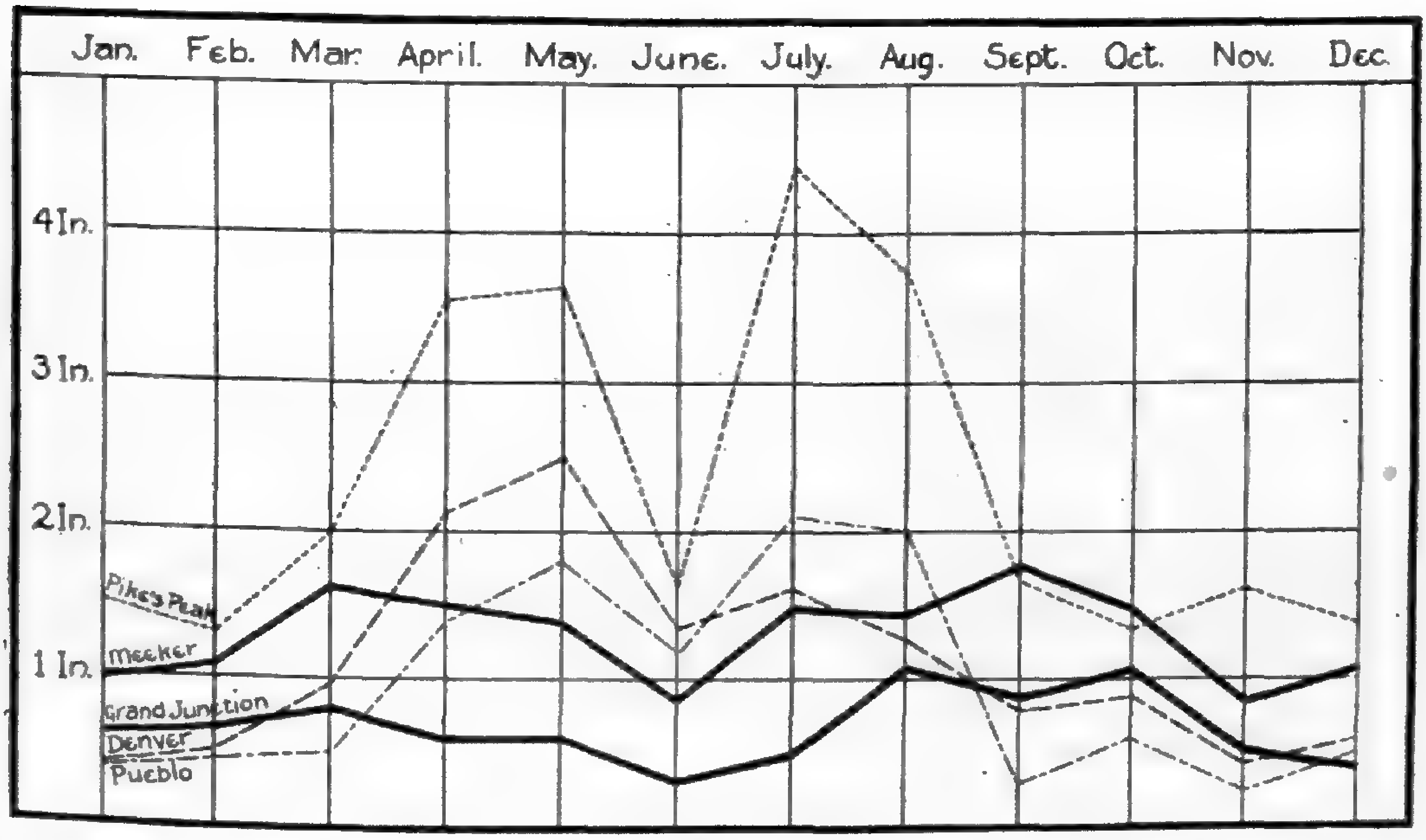

FIG. 4.—Mean annual precipitation curves: Meeker (6182 feet) and Grand Junction (4594 feet) are west of the continental divide; Pike's Peak (14,108 feet), Denver (5275 feet), and Pueblo (4672 feet) are east of the continental divide; the curves for Meeker and Grand Junction in heavy lines are very regular, showing an equal distribution of precipitation throughout the year; on the other hand, the curves for Denver, Pike's Peak, and Pueblo show for those stations a very unequal seasonal distribution; the season of maximum rainfall for each station will be noted.

From table II and *fig. 4*, it is seen that at stations east of the continental divide the greater part (average 74 per cent.) of the precipitation occurs during the growing season, when vegetation needs it, and this usually in the months of April, May, and June. On the other hand, west of the continental divide only about one-half (average 52 per cent.) occurs during the growing season, the most rainy months being July, August, and September. For this reason, so far as plant life is concerned, localities on the western slope are drier than localities at the same altitudes on the eastern slope. The precipitation of Colorado comes in showers rather than in prolonged rainy spells.

There is considerable variability as to the wettest part of the growing season. In the region north of the Arkansas-Platte Divide, the rainy months are April and May, with the exception of localities over the extreme eastern part of the state, where the maximum rainfall occurs in June. Consequently, the vernal vegetation of this region is more luxuriant than one would judge from the annual precipitation; the rest of the season is dry and is marked by the blooming of xerophytic species, mainly composites. The Arkansas-Platte Divide and the entire Arkansas Valley receive their maximum rainfall during the summer, July showing the greatest monthly amount. In the mountains July and August are the wettest months. Over the western slope the spring is wetter than the other seasons, but July or August generally shows the greatest monthly precipitation.

On account of the seasonal distribution of precipitation east of the continental divide there is very little snow. Furthermore, on account of the dry soil and air the snow soon disappears after falling. This is especially true of the plains, and as a result the vegetation does not have during the winter the protection which snow offers. The absence of snow on the plains, with the consequent low soil-moisture content, the great diurnal and annual ranges of temperature, together with the presence of a low relative humidity and dry winds, bring about conditions which account for the absence of trees.

As a result of the shortness of the rainy season, at most localities on the plains and lower foothills there is an acceleration in the growth of vegetation. Seasonal rains are usually followed by drought periods, and mesophytic plants must hasten to complete their development; hence the vegetative appearance changes rapidly.

Very wet and very dry years, or a consecutive series of these, are not uncommon in Colorado. The mean difference between the wettest and driest years is somewhat greater for localities east of the continental divide than for localities west. Plants living in a place where there are occasional very dry and very wet years must be those that have adapted themselves more or less successfully, not only to the normal precipitation, but to the variability of the same.

INCREASE OF PRECIPITATION WITH INCREASE OF ALTITUDE.[2]—It may be stated as a general rule that rainfall increases in amount and frequency with an increase in altitude. There are numerous exceptions which are due to topography. It has been pointed out by HANN (*l. c.* 305) that high mountains possess a zone of maximum precipitation above which there is a decrease. So far as the records for high altitudes in Colorado go, they indicate no such maximum zone, there being an increase to the summits.

It is well known that the increase in the amount and frequency of the precipitation in passing from lower to higher altitudes has its influence upon the vegetation. This influence finds its best expression in the arborescent vegetation. The forests on the lower slopes of the mountains are chiefly xerophytic, while those of the higher altitudes are predominantly mesophytic.

Table III gives an idea of the rate of increase of precipitation with an increase of altitude as it occurs in Colorado. Hence it indicates as well the frequency of vegetational changes, which are due in the main to precipitation amounts.

TABLE III

RATE OF INCREASE OF PRECIPITATION WITH INCREASE OF ALTITUDE

Station	Altitude (feet)	Precipitation (inches)	Number of feet increase in altitude giving increase of one inch of precipitation
Colorado Springs	6046	14.41	377
Lake Moraine	10246	25.59	1272
Pike's Peak	14108	28.65	
Denver	5272	14.02	1599
Idaho Springs	7543	15.44	
Gunnison*	7670	9.19	269
White Pine*	9500	16.00	
Glenwood Springs*	5823	13.20	592
Ashcroft*	9483	19.38	

* West of continental divide.

From the above table it will be seen that the rate of increase of precipitation is less at higher altitudes than at lower; also that on the western slope the rate of increase is more rapid than on the eastern slope.

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[2] HANN, Handbook of climatology, p. 301.

TEMPERATURE

General account.—*Fig. 5* shows the mean annual temperatures of Colorado. The general north-south direction of the isotherms readily shows the influence of the mountains. The eastern portion of the state and a small area along the Grand River in the western part have a mean annual temperature above 50° F.[3] The influence of the Arkansas-Platte Divide is seen in the eastward deflection of the isotherm 50. Isotherm 45 follows closely the eastern foothill line, 6000 feet altitude; it indicates the lower limit of the Rocky Mountain yellow pine (*Pinus scopulorum* [Engelm.] Lemmon). Isotherm 40 follows closely the 8000-foot contour line, and marks the lower limit of the lodgepole pine (*Pinus Murrayana* Oreg. Com.) and the usual upper limit of the Rocky Mountain yellow pine. On the western slope these isotherms run to higher altitudes. There is a decrease in the temperature with an increase in altitude, most localities

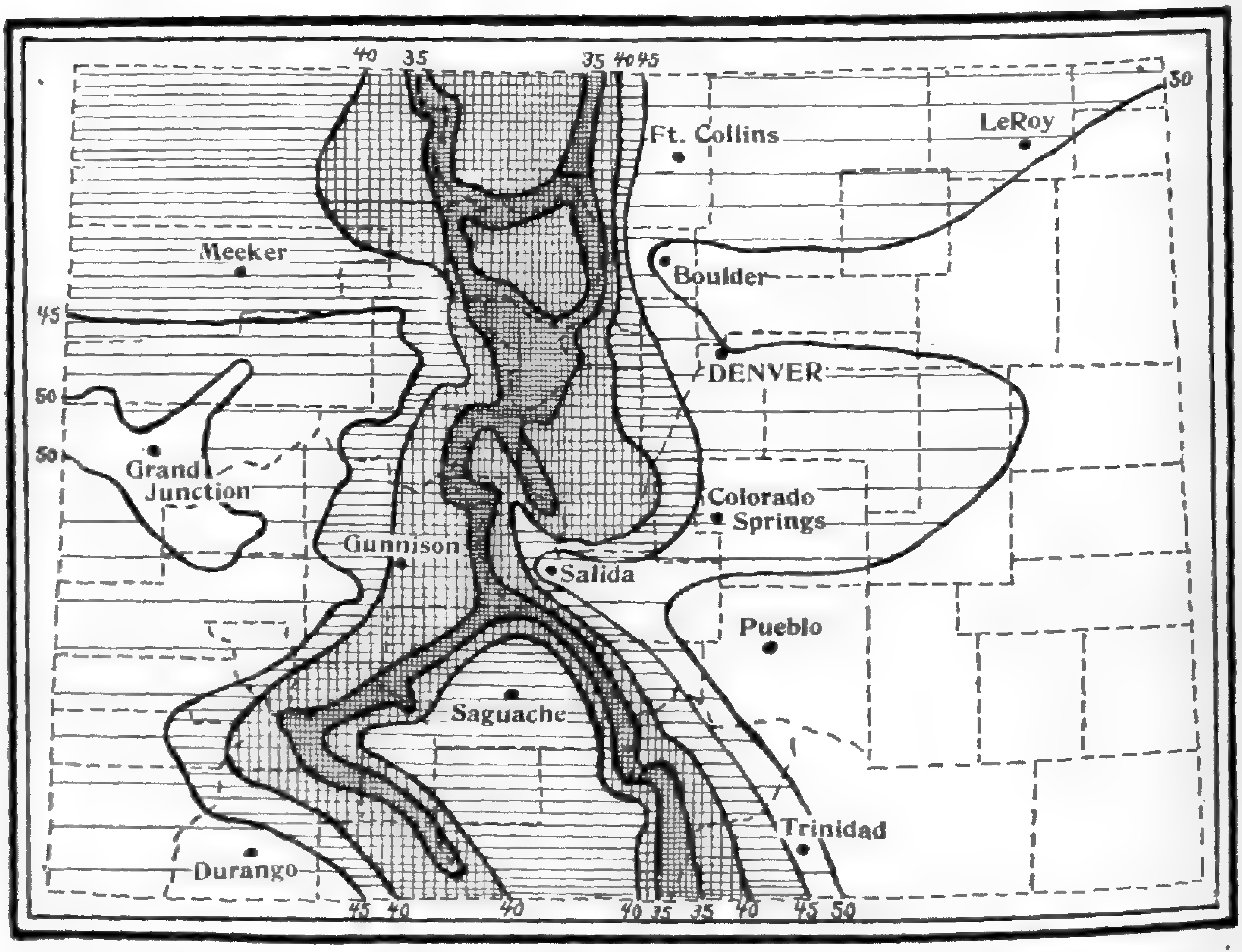

Fig. 5.—Mean annual temperatures: the general appearance of this figure is very similar to the one giving mean summer temperatures (*fig. 6*), and to the one showing mass elevations (*fig. 2*).

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[3] Throughout this paper all temperature readings are Fahrenheit.

above 10,000 feet having a mean annual temperature below 35°. Isotherm 35 follows approximately the upper limit of lodgepole pine, separating the montane from the subalpine zone. The mean autumn and spring temperatures are very nearly the same as the annual mean. As a rule, the fall mean is somewhat higher and the spring mean lower than the annual mean. *Fig. 6* gives the mean summer temperatures of Colorado. Its general appearance is similar to the mean annual temperature map. On the eastern slope isotherm 65 marks the lower limit of the foothill zone. Isotherm 60 on both slopes follows the lower limit of the montane zone and isotherm 55 the lower limit of the subalpine zone. No data are at hand to show the temperature conditions at timber line.

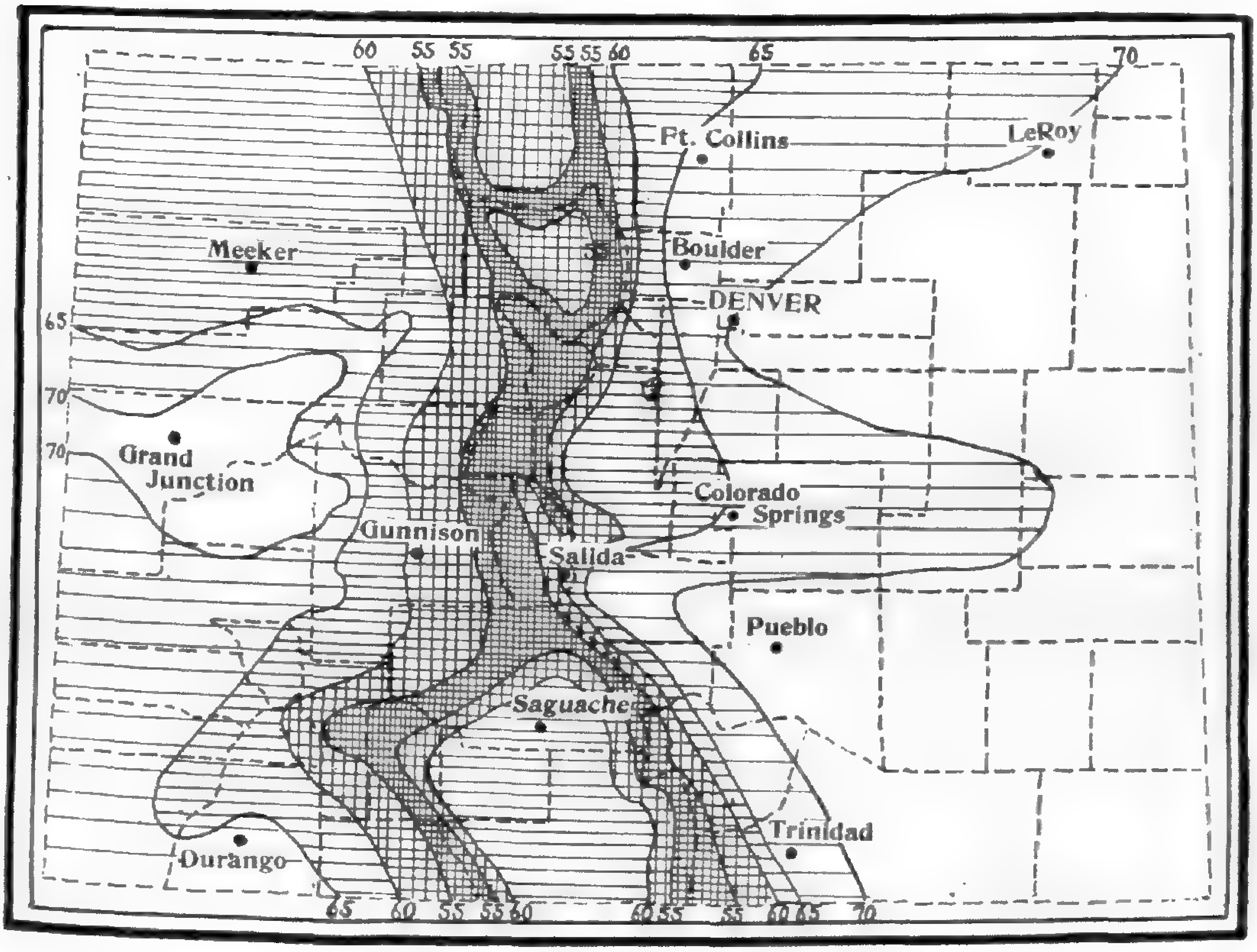

FIG. 6.—Mean summer temperatures.

RANGE OF TEMPERATURE.[4]—For the state as a whole the mean annual range (difference between the mean temperature for the warmest month and mean temperature for coldest month) is great (see table IV). In the Arkansas Valley, Platte Valley, Grand Valley,

[4] HANN, *l. c.*, p. 273.

and northwestern part of the state the mean annual range is greatest. There is a decrease in the range with an increase of altitude. The annual march of temperature for typical localities is shown in *fig. 7*. For most stations in the state January is the coldest month, July the warmest.

TABLE IV

MEAN ANNUAL RANGE OF TEMPERATURE

Locality	Coldest month	Mean temperature	Warmest month	Mean temperature	Mean annual range
Blaine	February	31.6	July	76.2	44.6
Boulder	February	30.7	August	70.7	40.0
Breckenridge	January	15.4	August	53.5	38.1
Cañon City	January	33.7	July	73.0	39.3
Castle Rock	January	26.6	July	68.3	41.7
Cheyenne	January	25.6	July	67.4	41.8
Collbran	January	22.0	July	68.8	46.8
Colorado Springs	January	27.5	July	68.0	40.5
Cope	February	27.4	August	74.9	47.5
Denver	January	29.1	July	71.8	42.7
Durango	January	24.5	July	68.7	44.2
Fort Collins	February	26.1	July	68.5	42.4
Fort Morgan	January	25.0	July	72.8	47.8
Garnett	January	14.2	July	61.1	46.9
Grand Junction	January	24.7	July	79.2	54.5
Grand Valley	January	23.9	July	72.9	49.0
Gunnison	January	7.3	July	60.9	53.6
Hamps	February	26.1	July	67.1	41.0
Hoehne	January	29.9	July	70.5	40.6
Idaho Springs	January	27.4	July	62.2	34.8
Lake Moraine	February	20.4	August	53.5	33.1
Lamar	January	31.4	July	77.5	46.1
Las Animas	January	26.4	July	76.9	50.5
Lay	January	18.1	July	67.3	49.2
LeRoy	February	25.4	August	71.5	46.1
Mancos	January	26.3	July	66.0	39.7
Meeker	January	19.6	July	65.9	46.3
Pagoda	January	19.4	July	63.9	44.5
Pueblo	January	29.1	July	74.2	45.1
Rangely	January	13.9	July	70.2	56.3
Rocky Ford	January	28.9	July	74.3	45.4
Salida	January	27.7	July	64.9	37.2
San Luis	January	19.8	July	62.8	43.0
West Cliffe	January	24.3	July	61.1	36.8
Wray	February	28.9	July	73.7	44.8

The diurnal range of temperature is great over the entire state. This is especially so on the plains, in the western part of the state, and in the parks. It is least in the higher mountain regions.

The high annual and diurnal ranges of temperature on the plains and other treeless areas of the state must receive no little consideration in explanation of the cause of the treeless condition. For example, the Rocky Mountain yellow pine will grow on the plains without irrigation if it is tided through the seedling stage. The seedling cannot tolerate great extremes of temperature.

DECREASE OF TEMPERATURE WITH INCREASE OF ALTITUDE.[5]—The rate of decrease varies with the topography, altitude, and season. It is less at high altitudes than at lower and less in winter than in summer. Table V gives the decrease in temperature for an increase in altitude for several Colorado stations.

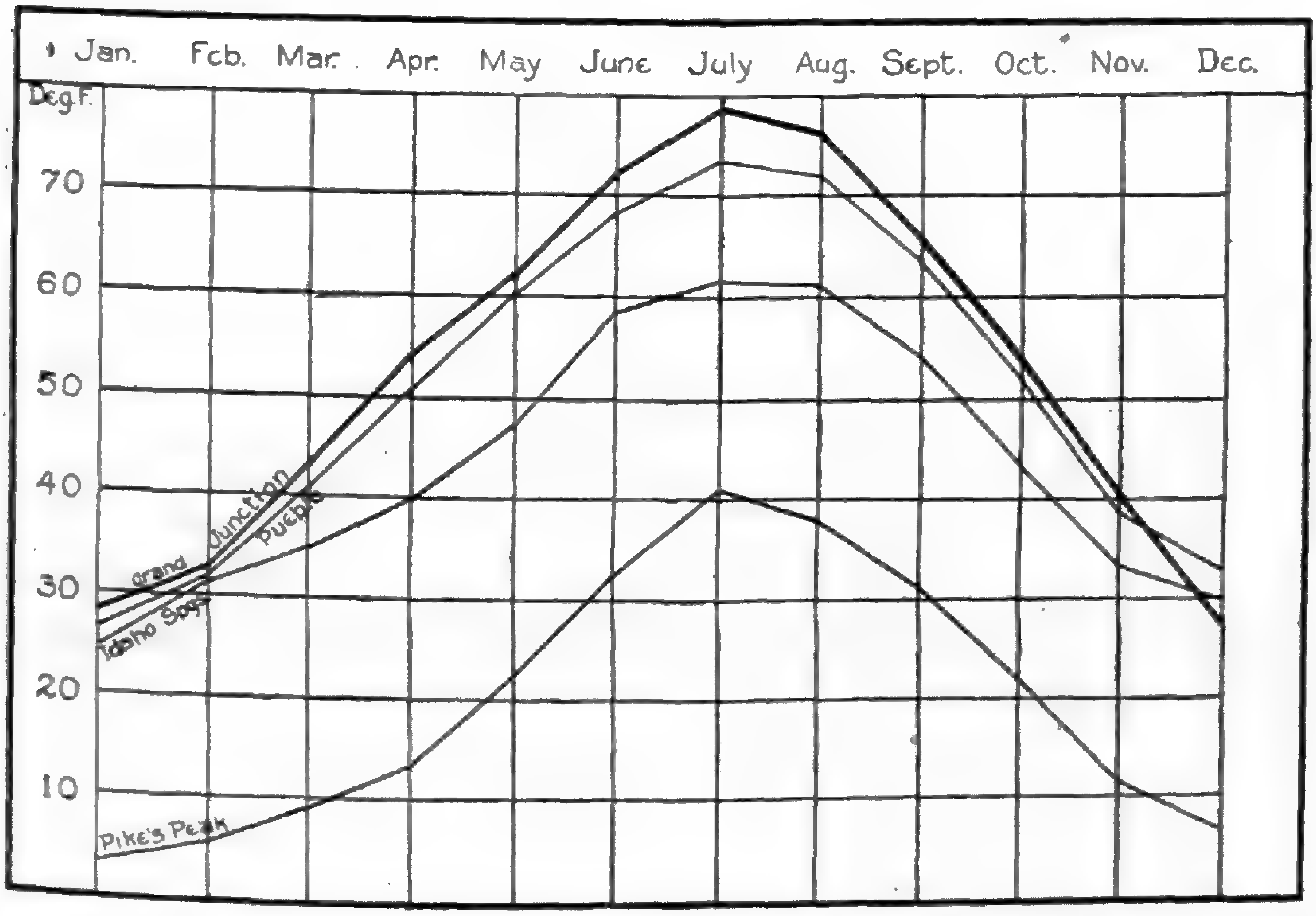

FIG. 7.—Mean annual march of temperatures: Grand Junction (4594 feet) in the western part of Colorado and Pueblo (4672 feet) on the plains have a much smaller range of temperature than do the mountain stations Idaho Springs (7453 feet) and Pike's Peak (14,108 feet).

Colorado Springs is at the base of Pike's Peak; Lake Moraine is at an elevation of 10,265 feet on its eastern slope. It will be seen from the table that the decrease of temperature between Lake Moraine and Colorado Springs is less than that between Lake Moraine and Pike's Peak. This is contrary to the general rule, and is probably due to the inversion of temperature which occurs at the base of the moun-

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[5] HANN, *l. c.*, p. 243.

tain, bringing the mean temperature of Colorado Springs lower than it would be if inversion did not take place. The data for the last three sets of localities in the table are for one season only.

TABLE V

DECREASE IN TEMPERATURE WITH INCREASE OF ALTITUDE

Stations compared	Decrease of temperature per 1000 feet (in degrees F.)
Pike's Peak–Colorado Springs*	3.4
Pike's Peak–Lake Moraine*	4.3
Lake Moraine–Colorado Springs*	2.6
Boulder–Arapahoe Peak at timber line†	3.2
Denver-Corona*	3.6
Boulder–Redrock Lake‡	3.2

* Data from Annual Summary of Colorado Division of the Climatological Service.

† Data from YOUNG, ROBERT T., Forest formations of Boulder County, Colorado. BOT. GAZETTE 46:321–352. 1907.

‡ Data from RAMALEY, FRANCIS, AND ROBBINS, W. W., Studies in lake and streamside vegetation. I. Redrock Lake near Ward, Colorado. Univ. Colo. Studies 6:133–168. 1909.

INVERSION OF TEMPERATURE.[6]—This phenomenon is common in mountainous regions, being particularly noticeable in the spring and autumn. The valleys and canyon bottoms are often cooler than the adjacent hillsides; the plains are cooler and have greater diurnal range of temperature than the overhanging foothills.[7]

A comparative study of temperatures of the University of Colorado campus[8] and the mesas near by, 415 feet higher, showed for May 1908 the mean monthly difference in temperature to be 2°6 higher on the mesas than on the campus. Furthermore, the last frost in the spring was 16 days later on the campus than on the mesa. This inversion is undoubtedly present all along the foothills. Mesas have a milder climate than adjacent plains, and the early spring vegetation is in advance of that on the plains. On account of temperature inversion in canyons and gulches, high altitude forms find their lower

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[6] HANN, *l. c.*, p. 252.

[7] In the southern Alleghenies, CHICKERING (J. W., JR., Thermal belts. *Amer. Meteor. Jour.* 1:213–218. 1884–85), quoting SILAS MCDOWELL of Franklin, Macon County, N. C., describes the presence there of a "thermal belt" or "frostless zone" upon the mountain sides, commencing at about 300 feet vertical height above the valley and having a breadth of 400 feet vertical height.

[8] RAMALEY, FRANCIS, Climatology of the mesas near Boulder, Colo., in Studies on mesa and foothill vegetation. Univ. Colo. Studies 6:11–49. 1909.

limit of distribution in gulches rather than on ridges, and low altitude forms extend farther up the ridges than up the gulches.

At certain periods, inversion of temperature of more than local influence occurs along the eastern edge of the foothills, which up to a considerable altitude experience a higher temperature than the plains. LOUD[9] points out that on the eastern slope of the Rocky Mountains in Colorado he has often noticed that elevated stations retain a mild temperature for some time after a cold wave has set in at a lower level.

There is much need of thorough investigation of the amount of temperature inversion for various localities; of determining its limits, time of occurrence, and effect upon the vegetation. There is little doubt that an investigation of such a nature would reveal information of practical importance to horticulturists and throw light on problems of plant distribution.

FROST.—The average date of the last killing frost in spring, of the first killing frost in autumn, and the average length of the growing season (period without frost) are important climatic factors. In Colorado these factors are affected to a considerable degree by temperature inversion, and have a great range on account of altitudinal differences. Grand Junction has the longest growing season of any locality in the state (6 months and 18 days), while on the highest peaks there is no day in the year without frost.

TABLE VI

EFFECT OF ALTITUDE UPON AVERAGE LENGTH OF GROWING SEASON AND AVERAGE DATE OF LAST KILLING FROST

Altitude (feet)	Average date of last killing frost	Average length of growing season (period without frost)
5000 and below	April 28	5 months, 6 days
5000–6000	May 5	4 months, 21 days
6000–7000	May 30	3 months, 21 days
7000–8000	June 6	3 months, 6 days

There are no data for higher altitudes. During the summer of 1908, the length of the growing season at Redrock Lake, altitude 10,100 feet, was about 6 weeks. Table VI shows that the retardation in the development of vegetation is about 13 days for every 1000 feet increase in altitude.

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[9] LOUD, F. H., The Colorado sky 1:1–9. 1908.

HUMIDITY

Unfortunately very little information regarding the relative humidity of different parts of Colorado is to be had. The state as a whole, however, has a low relative humidity. Along the eastern border of the state the mean annual relative humidity is about 60 per cent.; east of the foothills the mean annual amount is 48–50 per cent.; in the extreme western part of the state the annual relative humidity is 46–50 per cent. In the mountains there are rapid variations and great extremes of relative humidity.[10] The following from HANN (*l. c.* 289) gives the seasonal march of relative humidity on Pike's Peak, altitude 14,147 feet: winter, 79 per cent.; spring, 81 per cent.; summer, 75 per cent.; autumn, 77 per cent.; year, 78 per cent. Over the entire state, the relative humidity is greatest in the winter. Because of low relative humidity thin-leaved plants are almost unknown in the state, only a very few being able to maintain themselves in the densest shade of steep-walled canyons.

WIND

On the western slope the average wind velocity is 5–6 miles per hour; on the eastern slope 7–7.5 miles per hour; on the northern and eastern borders 10 miles per hour. In the higher mountains, especially on exposed ridges and peaks, the wind has a great velocity and blows almost steadily the year round. Here the winters are extremely windy. Over the whole state, the prevailing direction of the wind is from the west. Along the eastern base of the mountains there occur, during the winter and early spring, warm west winds, called "chinooks." These cause the sap to flow and the buds to swell, only to be followed by a low temperature which proves destructive to vegetation. Mountain and valley winds, which during the day blow up the valleys and at night toward the plains, bring about diurnal variations of humidity, cloudiness, and precipitation. As a result of the day direction of the winds, the mountains are often visited by afternoon showers.

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[10] I am informed by Professor FRANCIS RAMALEY that records of relative humidity made at Tolland, Colorado, altitude 8889 feet, during the summer of 1909, do not show as great fluctuations as is usually expected in mountain regions.

SUNSHINE AND CLOUDINESS

Colorado is a state of sunshine. On the average, 50 per cent. of the days are clear, 33 per cent. partly cloudy, and 17 per cent. cloudy.

Vegetation

PLAINS[11]

Precipitation: mean annual 10–20 inches; about 75 per cent. during the growing season; small amount of snow. *Temperature:* mean annual 45°–50° and above; mean summer 65°–70° and above; mean annual range 40°–50°; diurnal range great. Average date of the last spring frost varies in different localities from April 28 to May 10; average length of growing season about 5 months, 6 days. *Relative humidity:* annual amount 50–60 per cent.

The plains are generally spoken of as including that portion of the state east of the foothills. The climatic and vegetative conditions vary, however, in different parts. The "high plains"[12] north of the South Platte River, the Arkansas-Platte Divide, and the high lands east of the foothills in the southern part of the state are regions over which foothill forms have extended. It will be observed from *figs. 5* and *6* that these areas have a lower mean annual temperature (45°–50°) and a lower mean summer temperature (65°–70°), with a consequent less evaporation rate than the plains proper.

Over the entire plains area grasses are the dominant forms of vegetation; in some places not more than 25 per cent. of the ground is covered. Some of the common grasses are *Andropogon Hallii* Hack., *Calamovilfa longifolia* (Hook.) Hack., *Bouteloua oligostachya* (Nutt.) Torr., and *Bulbilis dactyloides* (Nutt.) Raf. *Eurotia lanata* (Pursh) Moq., *Sarcobatus vermiculatus* (Hook.) Torr., and *Chrysothamnus graveolens* (Nutt.) Greene are abundant in many localities. On ridges and buttes occur various shrubs, such as *Yucca glauca* Nutt., *Prunus Besseyi* Bailey, and *Ceanothus pubescens* (T. and G.) Rydb., also various mat and rosette-forming herbs. *Populus angustifolia* James, *P. Sargentii* Dode, *P. acuminata* Rydb., *P. Wislizenii* (S.

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[11] The classification of the plant zones into plains, foothill, montane, subalpine, and alpine are as outlined by RAMALEY, FRANCIS, Plant zones in the Rocky Mountains of Colorado. Science N. S. **26**:642, 643. (Nov. 8) 1907.

[12] RAMALEY, FRANCIS, Scientific expedition to northeastern Colorado; 8. Botany. Account of collections made. Univ. Colo. Studies **4**:161–164. 1907. This report gives a list of plants characteristic of the "high plains."

Wats.) Sarg., and *Salix* spp. fringe the streams. East of the continental divide, *P. Wislizenii* occurs only in the southern part of Colorado.[13] *Opuntia arborescens*, the chandelier cactus, extends over large areas in the Arkansas Valley; this plant is also restricted in its distribution on the plains to the southern part of the state.

In their *Phytogeography of Nebraska*, POUND and CLEMENTS have divided that state into four regions, two of which, the sand-hill region and the foothill region, extend into Colorado. The sand-hill region in Colorado includes a narrow strip along the eastern part of the state. Their "foothill region," so called because of the great number of mountain plants which here find their eastward distributional limit, occupies the rest of the plains area. In describing the general appearance of the sand-hill region, they say: "The most noticeable character of the sand-hill vegetation, after one has become accustomed to the great variety of species which the sparse vegetation of each hill affords, is its extreme monotony. This is due to the predominance of bunch grasses, which are the controlling element in the covering of the hills, hillsides, sandy ridges, and sandy tablelands of the water sheds. The principal formation of the sand-hills, then, is the bunch grass formation, a grass formation of exposed hills and ridges of pure sand."

EASTERN LOWER FOOTHILLS AND MESAS[14]

Precipitation: mean annual 15–20 inches; about 75 per cent. during the growing season; in the northern part of the state the early spring is the wettest season, in the southern part July and August are the wettest months; more snow than on the plains. *Temperature:* mean annual 45°–50°; mean summer 65°–70°; mean annual and diurnal ranges less than on the plains. Average date of last spring frost April 27 to June 16. As a result of temperature inver-

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[13] The writer recently found a few trees of this species at localities in the southern part of Rio Blanco County. This locality is west of the continental divide and far north.

[14] The following botanical papers discuss quite fully the ecology of the eastern lower foothills and mesas of northern Colorado: RAMALEY, FRANCIS, Botany of northeastern Larimer County, Colorado. Univ. Colo. Studies **5**:119–131. 1908. RAMALEY, FRANCIS, AND ROBBINS, W. W., Ecological notes from north-central Colorado. *Ibid.* **5**:111–117. 1908. ROBBINS, W. W., Studies of mesa and foothill vegetation; 4. Deciduous trees and shrubs of the mesas. *Ibid.* **6**:36–49. 1908. ROBBINS, W. W., AND DODDS, G. S., Studies in mesa and foothill vegetation; 3. Distribution of conifers on the mesas. *Ibid.* **6**:31–36. 1908.

sion, the mesas are not subject to as late spring frosts as are the adjacent plains. Average length of growing season (period without frost) about 4 months, 21 days. *Relative humidity:* mean annual 48–50 per cent.

The lower foothills and mesas of northeastern Colorado represent the meeting ground of grass and forest formations. The trees here are Rocky Mountain yellow pine and Douglas fir (*Pseudotsuga mucronata* [Raf.] Sudw.), the latter occurring in the moister situations. The Rocky Mountain yellow pine meets the grassland formation on the lower parts of the mesas; this formation consists chiefly of *Bouteloua oligostachya* and *Koeleria cristata* (L.) Pers. *Cercocarpus parvifolius* Nutt., the mountain mahogany, and *Yucca glauca* are common on ridges. Other common shrubs of this region are *Prunus melanocarpa* (A. Nels.) Rydb., *P. pennsylvanica* L.f., *Symphoricarpos occidentalis* Hook., *Rhus trilobata* Nutt., *R. glabra* L., *Ribes longiflorum* Nutt., *R. pumilum* Nutt., *R. vallicola* Greene, *Opulaster* spp., *Ceanothus Fendleri* A. Gray, *C. pubescens* (T. and G.) Rydb., *Crataegus* spp., *Rosa Sayi* Schwein., *Berberis repens* Lindl., and *Edwinia americana* (T. and G.) Heller.

The lower foothills and mesas of southeastern Colorado differ from the corresponding regions in northern Colorado. The mesas are grassland composed chiefly of *Bouteloua oligostachya.* Scrub oak and mountain mahogany form a chaparral between the grassland and Rocky Mountain yellow pine formations of the lower foothills. Pinyon pine (*Pinus edulis* Engelm.), the one-seeded juniper (*Sabina monosperma* [Engelm.] Rydb.), and the Rocky Mountain juniper (*Sabina scopulorum* [Sarg.] Rydb.) are common in the lower portion of the foothills. The Rocky Mountain yellow pine and other foothill forms extend far out on the Arkansas-Platte Divide.[15]

EASTERN UPPER FOOTHILLS

Precipitation: mean annual 15–20 inches; about 75 per cent. during the growing season; the early summer is the season of maximum rainfall. *Temperature:* mean annual 40°–45°; mean summer 60°–65°; mean annual range

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[15] For an extended account of the mesas and foothills of southern Colorado see the following papers: SHANTZ, H. L., A study of the vegetation of the mesa region east of Pike's Peak; the Bouteloua formation. BOT. GAZETTE **42**:16–47, 179–207. 1906. SCHNEIDER, E. C., The distribution of woody plants in the Pike's Peak region. Colorado Coll. Publ. Science Series **12**:137–170. 1909.

30°–40°; diurnal range decreases with an increase of altitude. Average date of last spring frost May 30 to June 31; average length of growing season 3 months, 21 days, to 3 months, 6 days. *Relative humidity:* annual amount greater than on plains and mesas.

This area extends the full length of the state along the eastern slope. It is between the altitudes of 6000 and 8000 feet. It is dominated by a forest of Rocky Mountain yellow pine and Douglas fir. The upper limit of the zone is coextensive with the upper limit of abundant growth of Rocky Mountain yellow pine. South Park, although mostly above 8000 feet, has a foothill vegetation and should be classed as upper foothill country. It is much drier than localities at the same altitudes on the eastern slope. It is an upland country supporting a xerophytic vegetation.[16]

MONTANE ZONE

Precipitation: mean annual 15–20 inches; many localities have greater amounts; July and August are the wettest months; snow abundant. *Temperature:* mean annual 35°–40°; mean summer 55°–60°; mean annual and diurnal ranges of temperature generally small but varying greatly with exposure. No data for average date of last spring frost and average length of growing season. *Relative humidity:* fluctuating between high and low; annual amount increases with increase of altitude.

This zone roughly includes those portions of the state with an altitude between 8000 feet and 10,000 feet. On the western slope and on the minor mountain ranges and plateaus of the western part of the state, the montane zone often extends to higher altitudes, which is due chiefly to the generally drier condition of this slope.

The vegetational composition and appearance of the montane zone varies in different sections of Colorado. In the northeastern part of the state it is dominated by lodgepole pine, being adjoined by the Rocky Mountain yellow pine forests of the foothills and the Engelmann spruce forests of the subalpine regions. Other less abundant conifers of this zone are the bristle cone pine (*Pinus aristata* Engelm.), limber pine (*Pinus flexilis* James), Colorado blue spruce (*Picea Parryana* [Andree] Sarg.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). In southern Colorado lodgepole pine does

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[16] RAMALEY, FRANCIS, Plants of the Florissant region in Colorado. Univ. Colo Studies 3:178–185. 1906.

not form so extensive forests as it does in the northern part of the state. East and west of the continental divide the white fir (*Abies concolor* Lindl.) occurs in the montane zone of southern Colorado, but not in the northern part. Aspen (*Populus tremuloides* Michx.) is common throughout the montane zone in all parts of the state, but particularly so on the western slope. There it covers extensive areas and grows to a considerable size. In northwestern Colorado it often dominates extensive areas, or may be mixed with lodgepole pine. Here oak shrubbery is often abundant in the lower parts of the zone. In southwestern Colorado the montane zone extends between the altitudes 9000 feet and 10,500 feet and is chiefly aspen-covered.

SUBALPINE ZONE

Precipitation: mean annual above 20 inches; often 35 or 40 in some localities; maximum amount in the summer; daily afternoon showers common. *Temperature:* mean annual below 35°; mean summer below 55°; mean annual and diurnal ranges low. *Relative humidity:* fluctuating between high and low but generally high.

In all parts of the state, except the extreme southern part, this zone extends from an average altitude of 10,000 feet to timber line; it is the highest timbered zone. The dominant and characteristic tree in all parts of the state is the Englemann spruce. It is nearly always accompanied by limber pine and subalpine fir. Other common trees and shrubs are *Salix chlorophylla* Anders., *S. glaucops* Anders., *S. Bebbiana* Sarg., *S. pseudolapponum* Seem., *Betula glandulosa* Michx., *Ribes parvulum* (A. Gray) Rydb., *R. lentum* (Jones) Coville & Rose, *Sambucus microbotrys* Rydb., and *Lonicera involucrata* Banks. *Vaccinium oreophilum* Rydb. and *V. caespitosum* Michx. are common shrubs growing on the forest floor. Meadows and swampy areas are abundant throughout the zone.

TIMBER LINE.—Timber line is the upper limit of tree growth. In Colorado it usually marks the limit above which trees are climatically excluded. HARVEY[17] has pointed out that timber line on Mt. Ktaadn in Maine is not climatic but physical. COOPER,[18] although

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[17] HARVEY, L. H., A study of the physiographic ecology of Mt. Ktaadn, Maine. Univ. Maine Studies. 1903.

[18] COOPER, W. S., Alpine vegetation in the vicinity of Long's Peak, Colorado. BOT. GAZETTE **45**:319–337. 1908.

recognizing timber line to be a climatic division line, has shown that in the Long's Peak region, Engelmann spruce has not reached the point where tree growth is climatically excluded, and that the present timber line as represented by Engelmann spruce is not the true climatic timber line. In this region, however, limber pine forms a true climatic timber line.

The average height of timber line in Colorado is near 11,500 feet. It is higher on the ridges than in the gulches, on south and west exposures than on north and east exposures. Engelmann spruce, subalpine fir, and limber pine are the principal timber line trees.

ALPINE ZONE

Climatic conditions for this zone in Colorado are not well known. The lower limit of the alpine zone is timber line. Although precipitation is ample and the relative humidity frequently high, tree growth is absent partly because of the thin soil, steep slope which cannot retain sufficient moisture, low air and soil temperatures, high winds, snow,[19] rapid transpiration, and liability to frosts. The lower portions of the zone are covered with grasses and low alpine mat forms. The upper parts are usually rock fields supporting little except a lichen vegetation.

Some of the most common alpine plants of Colorado are *Deschampsia caespitosa* (L.) Beauv., *Phleum alpinum* L., *Trisetum subspicatum* (L.) Beauv., *Festuca brachyphylla* Schultes, *Carex atrata* L., *Polygonum viviparum* L., *Silene acaulis* L., *Caltha leptosepala* Hook., *Dryas octopetala* L., *Clementsia rhodantha* (A. Gray) Rose, *Sieversia turbinata* (Rydb.) Greene, *Castilleja occidentalis* Torr., *Campanula petiolata* DC, *Mertensia alpina* (Torr.) Don., *Rydbergia grandiflora* (T. and G.) Greene, *Artemisia scopulorum* A. Gray, *Eritrichium argenteum* Wight, *Trifolium dasyphyllum* Torr., *T. Parryi* A. Gray, and *Tetraneuris lanata* (Nutt.) Greene.[20]

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[19] SHAW, C. H., Causes of timber line on mountains. Plant World **12**:169–181. 1909.

[20] For a list of the alpine plants of Colorado with statistics of their geographical distribution, see article by COCKERELL, T. D. A., Alpine flora of Colorado. Amer. Nat. **40**:861–873. 1906.

SAN LUIS VALLEY

Precipitation: mean annual below 10 inches; about 75 per cent. during growing season; July and August wettest months; small amount of snow. *Temperature:* mean annual 40°–45°; mean summer 60°–65°; mean annual and daily range great. Average date of last spring frost May 24 to June 12; average length of growing season (period without frost) 3 months, 15 days. *Relative humidity:* low.

This dry, level country is covered with *Artemisia tridentata,* which spreads over extensive areas, the plants often reaching a height of 8 feet. *Chrysothamnus* spp., *Sarcobatus vermiculatus,* and *Atriplex* spp. are abundant, alternating in some places with bunch grasses. On the slopes occur pinyon pines, cedars, and Rocky Mountain yellow pines. The higher plant zones are very similar to corresponding zones in other parts of southern Colorado.

The level parts of San Luis Valley have the same altitude as the eastern foothill region (7000–9000 feet). The climatic conditions are practically the same, with the exception of the precipitation and the daily and annual ranges of temperature. In the eastern foothills the precipitation is 15–20 inches; in San Luis Valley below 10 inches. In the eastern foothills the ranges of temperature are considerably less than in San Luis Valley. In comparing the monthly temperatures of Garnett, San Luis, and Saguache, all in San Luis Valley, with Idaho Springs, Georgetown, and Silver Cliff, all within the eastern foothills, it was found that, although the mean summer and mean annual temperatures were about the same, the winters of San Luis Valley are much severer than those of the foothills, the months of December, January, and February being 10°–15° colder. As a result of these differences in range of temperature and rainfall, the foothills support a forest growth, while grass and sage predominate in San Luis Valley.

MIDDLE PARK

Climatological data for this region are not sufficient to be of much use. It is very probable, however, that the lower and flatter portions of the park have nearly 10 inches of rainfall. There are great extremes of temperature. *Artemisia tridentata* produces the principal formation on the dry, level stretches. It is associated with *Chrysothamnus* spp. and *Symphoricarpos oreophilus* A. Gray. Other common shrubs growing on dry hillsides are *Kunzia tridentata* (Pursh) Spreng., *Amelanchier elliptica* A. Nels., and *Holodiscus dumosus* (Nutt.) Heller. Grassland alternates with the sage in mesophytic level places. The hills, except south exposures, are covered with lodgepole pine. Engelmann spruce occurs in the deep and narrow canyons, even in the lower parts of the park, but it is not abundant below 9000 feet. Rocky Mountain yellow pine is very uncommon in Middle Park.[21]

WESTERN SAGE PLAINS AND LOWER FOOTHILLS

Under this head will be discussed that portion of the state west of the continental divide, which extends up to the montane zone, with the exception of Middle Park.

Precipitation: below 10 inches in the western part and 10–15 inches in the eastern part; about 50 per cent. during the growing season. *Temperature:* mean annual 40°–50° and above; mean summer 60°–70° and above; mean annual range above 45; diurnal range great. *Relative humidity*: generally low.

The dominant forms of vegetation of this area are sage brush, pinyon pine, scrub oak, and Rocky Mountain yellow pine. The northwestern part of the state, however, has climatic conditions which are appreciably different from those of the middle and southwestern part (see *figs.* 5 and 6). In the former area the mean annual and mean summer temperatures are about 5° cooler than in the southwestern area, and although the precipitation is about the same in amount and distribution, the effect of the lower temperature is indicated by the lower altitudinal distribution of typical arborescent forms. In northwestern Colorado, Rocky Mountain yellow pine grows to some extent on slopes between 6000 feet and 8000 feet; scrub oak occurs between the same altitudes; aspen comes in abundantly at 7500 feet, and scattered groves are found at lower elevations. In southwestern Colorado, Rocky Mountain yellow pine is not abundant below 8000 feet; scrub oak is seldom abundant below 8000 feet, and aspens do not occur commonly below 9000 feet.

In southwestern Colorado along streams, *Populus angustifolia*, *Lonicera involucrata*, and *Lepargyraea argentea* (Nutt.) Greene are

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[21] The writer is not sufficiently familiar with conditions in North Park to discuss them.

common. Sage plains stretch from the streams to the foothills; associated with the sage is *Sarcobatus vermiculatus.* Other characteristic shrubs are *Fendlera rupicola* Engelm. & Gray, *Peraphyllum ramosissimum* Nutt., *Kunzia tridentata, Cercocarpus parvifolius, Amelanchier alnifolia* Nutt., and *Yucca baccata* Torr. The alkaline flats are covered with chenopodiaceous plants.[22] The foothills up to 7500 feet are covered with pinyon pines and cedars. Above these come Rocky Mountain yellow pine, forming a distinct zone up to 9000 feet.

As in southwestern Colorado, the greater portion of middle and northwestern Colorado, up to an altitude of 7500 feet, is covered with sage brush, *Chrysothamnus* spp., and *Sarcobatus vermiculatus.* There is very little grassland country until an altitude of 7000 feet is reached. Oak chaparral grows to some extent below 7500 feet, but in many localities forms a distinct zone between the pinyon-cedar and montane zones. Pinyon pine and cedars are common associates here as in other parts of Colorado. On the lower slopes cedar is predominant, forming nearly 90 per cent. of the tree growth; at higher altitudes pinyon becomes relatively more abundant. Sage brush reaches the height of its development, both in size and numbers, on level expanses below 7500 feet; it extends up to 10,000 feet, however, being confined to dry ridges. *Populus angustifolia, Alnus tenuifolia* Nutt., *Lepargyraea argentea,* and *Crataegus* spp. are common streamside plants up to an altitude of 7000 feet. *Cercocarpus parvifolius, Amelanchier oreophila* A. Nels., *Symphoricarpos* spp., and *Kunzia tridentata* occur on dry and stony hillsides.

It is generally held that the vegetation and flora of the eastern slope is very different from that of the western slope. This is especially true for altitudes below 8000 feet. The vegetation of the alpine, subalpine, and to a less extent of the montane zones, however, is very similar on both slopes. Below 8000 feet the climatic and zonal

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[22] For excellent discussions of the flora and vegetation of the southwestern part of Colorado see the following articles: BRANDEGEE, T. S., The flora of southwestern Colorado. Bull. U. S. Geol. and Geog. Surv. of the Territories (Hayden Survey) **11**: 227–248. EASTWOOD, ALICE, Report on a collection of plants from San Juan County in southeastern Utah. Proc. Cal. Acad. Sci. **6**:270–329. 1896. BAKER, CARL F., AND EARLE, F. S., Narrative accounts of collecting trips in southern and western Colorado in *Plantae Bakerianae.*

relations are quite different on the two slopes. On the eastern slope the foothill zone extends from an altitude of 8000 feet down to 6000 feet, and is an area timbered with Rocky Mountain yellow pine. On the western slope, localities between 6000 feet and 7500 feet are dry, having a precipitation 5 to 10 inches less than similar altitudes of the eastern slope; the vegetation is chiefly sage brush, associated with *Sarcobatus vermiculatus* and *Chrysothamnus* spp. Pinyon pine and cedars occur on the ridges. Rocky Mountain yellow pine is scattered in northwestern Colorado; it extends up to 8000 feet, but forms no distinct zone. Below 6000 feet east of the continental divide are grass-covered plains with a precipitation of 10–20 inches. At the same altitudes on the western slope one meets with semi-desert conditions. The annual precipitation is below 10 inches and the vegetation is predominantly sage brush.

In general it may be said that the state west of the continental divide is drier from the vegetation standpoint than the eastern slope. Only about 50 per cent. of the rainfall on the western slope occurs during the growing season, in contrast with the occurrence on the eastern slope of about 75 per cent. during the same period. Hence for any two localities east and west of the continental divide with equal annual precipitation amounts, the locality west will have the more xerophytic vegetation.

In connection with the preparation of this paper, the writer wishes to express his deep appreciation of helpful suggestions and criticisms given by Professor FRANCIS RAMALEY.

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THE FLORAL DEVELOPMENT AND EMBRYOGENY OF ERIOCAULON SEPTANGULARE

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(WITH PLATES XIX AND XX)

Flowers

The inflorescence of *Eriocaulon septangulare* is a compact head of staminate and pistillate flowers. The two kinds of flowers are sometimes intermingled, but the most common arrangement is in groups of 10–30, all the members of each group exhibiting nearly the same stage of development. During the season there are usually about three successive groups of each kind of flower.

Longitudinal sections of the flower show that the parts appear in acropetal succession. The two sepals, and likewise the two petals, arise from the floral axis at somewhat different levels. This is probably to be interpreted, not as the survival of a primitive spiral arrangement, but as a result of the intercalary growth which is a marked feature especially of the inner flowers (*fig. 5*). Rudimentary carpels surrounding the tips of the floral axis occupy the center of the staminate flower (*fig. 1*), but do not progress beyond the stage shown in the figure; they can still be recognized readily in the old flowers. In the pistillate flowers the stamens are represented by rudimentary outgrowths put out above the petals and having their extremities of withered and blackened cells (*fig. 2*). Each flower is subtended by a bract and bears large conspicuous nectaries upon the petals. Transverse sections are shown in *figs. 3* and *4*. *Fig. 3b* and corresponding sections of the pistillate flowers show that the stamens belong to one cycle, and hence the flowers are tetracyclic.

The manuals describe this and other species of Eriocaulon as having the parts of the flowers in twos and threes, but in and about Lake Joseph, Ontario, where this material was collected, I have been able to find only the former type of flowers. Do these constitute a local race, or will other localities furnish similar examples of the constancy of dimerous symmetry?

Stamens

The stamens bear four narrow sporangia, whose hypodermal cell walls show the usual thickening, but not prominently so, and whose cavities before dehiscence unite in pairs. The pollen mother cells of each sporangium are in a single row, surrounded completely by a tapetum, and externally by two or sometimes three cell layers (*fig. 6*). They are somewhat flattened lengthwise of the anther, and in conformity with this peculiarity of shape and arrangement they exhibit an interesting polarity, the spindles of both divisions standing at right angles to the long axis of the sporangium. Many of the stamens fail to mature their microspores. The ripe microspores contain a large vegetative nucleus and two male cells. In good sections the latter can be seen to have an elongated pointed outline, and to be distinctly delimited from the remaining cytoplasm by a plasma membrane (*fig. 7*). The exine possesses strong thickening bands studded with minute spines (*fig. 8*).

Ovule and embryo sac

The position of the ovules and their relation to the carpels are illustrated in *fig. 5*. It will be seen that they are distinctly axial. They point outward at first toward the carpels, but gradually bend downward so that finally the micropyle is directed toward the base of the flower. The archesporial cell remains undivided for a long time, lengthening with the enlarging ovule (*figs. 9, 10*). Finally, without cutting off any parietal cell it segments into four megaspores, the innermost of which becomes the embryo sac (*fig. 10*). In a large number of cases several or all of the megaspores germinate, both by increase of size and by division of their nuclei. While thus increasing in size, some of them accommodate themselves to the space in which they lie by slipping past one another so as to lie side by side. Many cases somewhat similar to *fig. 12* were observed; also in sections of the same age as *fig. 13* a group of five or six nuclei above the embryo sac, and no doubt consisting of the unabsorbed nuclei of the sterile megaspores, can frequently be seen. But while it is perhaps the rule for more than one megaspore to germinate, I have never found two fully formed embryo sacs in one ovule, nor other than the lowermost megaspore the successful competitor.

About this time or a little later the nucellar tissue lateral to the megaspores begins to be broken down and absorbed by the growing embryo sac. A few of the apical cells of the nucellus, however, persist for a long time, and enlarging assume the appearance of a "tapetum" (*figs. 12–14, n*). These too are ultimately absorbed, and then the embryo sac abuts directly upon the inner integument and micropyle.

The development of the embryo sac is quite normal, so that little explanation need be added to the figures. The central vacuole first appears at the four-nucleate stage. During the three successive divisions there is little if any increase of nuclear material; probably the eight nuclei of *fig. 16* have no greater aggregate volume than the single nucleus of the megaspore.

In the succeeding pre-fertilization organization of the embryo sac some of these nuclei become greatly enlarged (cf. *figs. 16* and *18*, which are drawn to the same magnification). A nearly mature embryo sac is shown in *fig. 17*. The antipodals are never conspicuous. After the inception of endosperm formation they become difficult of recognition, but occasionally may be seen in a small pocket below the endosperm. The upper polar nucleus moves down to meet the lower one near the antipodals. From the frequency with which they are found in contact with each other, it may be inferred that their fusion is very gradual. It is attended with considerable growth of the fusing nuclei, and there is still further growth subsequent to their fusion (cf. *figs. 17, 18, 22*). Probably this enlargement of the definitive nucleus is correlated with the rapid production of endosperm consequent on fertilization. There is much variation among plants as to the time when the polar nuclei fuse and the relation of this fusion to pollination and fertilization. Thus in Elodea WYLIE (**15**) found that the actual presence of the pollen tube in the embryo sac is necessary to bring about the fusion. In Eichhornia (SMITH **14**) the fusion occurs before pollination, and in Sagittaria (SCHAFFNER **13**) before the entrance of the pollen tube. Further examples are given in COULTER and CHAMBERLAIN'S *Morphology of angiosperms* (**6**, pp. 95, 96). There can be no doubt that in Eriocaulon the fusion is independent of the stimulus of pollination, for it was found complete in numerous heads taken from beneath the surface of the water. On the other hand, division of the endosperm nucleus does not appear to take place in the absence of fertilization.

Beneath the embryo sac there is a group of strongly thickened cells which probably function as conduction tissue. They stain deeply, and occasionally one of them proliferates into the embryo sac (*fig. 19*).

Fertilization

Fertilization was not observed in a sufficient number of cases to make possible a very definite description of the process. The observations indicate that the pollen tube entering the micropyle passes through one of the synergids or between them without destroying either. The contents of the undischarged tube shown in *fig. 20* could not be made out, but there can be no doubt that both of the male cells or their nuclei enter the embryo sac. Three or four cases similar to *fig. 22* were seen, and once I found a sperm nucleus (which had then lost its cytoplasmic sheath) about half-way between the egg and the definitive nucleus. Pollination and fertilization are apparently effected in the first flowers within the first day of their emergence from the water. The sexual nuclei in the egg fuse without delay, and their fusion is soon followed by that of the second sperm and the definitive nucleus.

Only one case of polyembryony was observed, the three embryos apparently originating from the two synergids and the egg (*fig. 34*).

Endosperm

The first division of the endosperm nucleus was not seen. The nuclei multiply rapidly, so that 16–32 of them are distributed about the periphery of the embryo sac before the first segmentation of the egg. They are elongated and flattened, and invariably take a position in the inner border of the parietal cytoplasm (*fig. 23*). When their number is about 64, tissue formation begins by the appearance of delicate walls across the cytoplasmic layer. The walls appear first in the micropylar and antipodal regions, and somewhat later about the sides of the embryo sac. At this time the inner boundary of the cytoplasmic layer has no definite wall (*fig. 24*), and the general appearance is similar to that figured and described by LAWSON (11) as occurring in the gametophyte of Cryptomeria;

but the analogy stops here. In Eriocaulon the endosperm cells are never binucleate and the first-formed walls are permanent.

The cells continue to extend centripetally by vacuolization, and then undergo periclinal division, resulting in an outer layer of flat cells which do not divide further, and an inner layer of larger cells (*fig. 25*). At this time no starch is present. The inner layer by further divisions obliterates the central cavity of the embryo sac and then rapidly fills with starch grains. In the ripe seed three regions of the endosperm are recognizable: (1) the outer layer, still more flattened and containing little starch; (2) the large thin-walled cells of the interior, with abundant starch; (3) a deeply staining group of starch-containing and elongated cells near the base.

Embryo

It is in the development of the embryo that this plant deviates more widely from ordinary angiosperms. The first division is, as usual, transverse (*fig. 27*). Each of the two resulting cells then divides in a longitudinal direction, the one toward the base of the sac dividing first as a rule (*figs. 28, 29*). The next divisions are also longitudinal, and at right angles to the preceding (*fig. 30*). Thus the embryo has no suspensor whatever, and passes through regular quadrant and octant stages. While these divisions are taking place, the embryo becomes globular in form and its cytoplasm beautifully vacuolated. The octant division is followed by the cutting off of a dermatogen. The process is not simultaneous in the two halves. Thus in *figs. 31* and *32* it will be seen that the micropylar half has divided most rapidly, while in *fig. 35* it is the basal half. The embryo of the ripe seed is shown in *fig. 36*. It is bell-shaped with flaring edges, and quite frequently the edges are upturned, owing to the pressure of the endosperm. There is no differentiation of the embryonic organs, nor any indication where these shall have their origin.

It is doubtful if a comparison of the early segmentation of the embryo is of value in determining relationship. There is too much variation within certain orders, and often the peculiarities are too manifestly adaptive. The nature of the endosperm and the embryonic organs is much more significant.

I have found no detailed study of plants nearly related to Eriocaulon. In other plants mature undifferentiated embryos have been reported within recent years in numerous instances; for example, in Aigenetia (KUSANO **10**) and Peperomia (CAMPBELL **2**); also Gunnera (MODILEWSKI **12**) has no suspensor, and Piper (JOHNSON **8**) but a slight one. But undoubtedly the nearest parallels to the embryo sac of Eriocaulon as yet described are among the Araceae and the Nymphaeaceae. Thus in Arisaema (GOW **7**) the mature embryo sac is globular and without differentiation of organs; but its first three cells are in a row, and its early divisions are less regular. From CAMPBELL'S studies of the Araceae (**1, 3, 4**) it appears that the globular form of the embryo is characteristic of that order. But the embryos figured by him show far more irregularity in their development than is the case in Eriocaulon. CAMPBELL regards the absence or slight development of the suspensor (as in Aglaonema **1** and Spathicarpa **3**) as correlated with the complete investment of the embryo by endosperm tissue. In all the Araceae examined the endosperm was found to be septate from the beginning. The same is the case in Gunnera. It will be seen, however, that this explanation will not apply to the lack of a suspensor in Eriocaulon, since divisions of the embryo up to the octant stage precede tissue formation in the endosperm, and even for some time afterward the walls of the endosperm are too weak to exert much pressure. Pistia, another aroid, was investigated by HEGELMAIER (**8**) in 1874, and its embryo as described by him is in its early history practically identical with that of Eriocaulon. It shows the same regularity of form and sequence up to the cutting off of the "dermatogen-like outer layer," and for some time thereafter, except that for a time in individual cells of this layer periclinal divisions now and then occur, a phenomenon I have not observed in Eriocaulon. In the ripening seed of Pistia the globular embryo becomes indented, and root tip and cotyledon are developed.

Somewhat similar embryos occur in *Castalia odorata* and *Nymphaea advena* (COOK **5**) and in Nelumbo (YORK **16**). These are described as passing through quadrant and octant stages, less regular than those of Eriocaulon and Pistia. The case of Nymphaea is particularly interesting. Though the extent of the dermatogen is not stated, from the figures it appears to invest the embryo completely, and there is no trace of a suspensor. Later, however, after the position of the cotyledon is indicated, a short suspensor is developed through the activity of one of the basal cells.

Experiments are now in progress to ascertain what changes the embryo of Eriocaulon undergoes in germination.

Summary

1. Eriocaulon gives evidence of derivation from a bisporangiate ancestor in that the pistillate and staminate flowers possess rudimentary stamens and pistil respectively.

2. The flower is tetracyclic.

3. The ovules are placed laterally upon the axis.

4. Four megaspores are produced, the innermost of which is fertile, but the others in a large number of ovules begin germination.

5. The embryo sac develops in the usual way.

6. "Double fertilization" occurs.

7. The embryo has no suspensor; its first division wall is transverse; quadrant, octant, and periclinal divisions follow; and no embryonic organs are recognizable in the ripe seed.

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EXPLANATION OF PLATES XIX AND XX

All the figures were drawn with the aid of an Abbé camera and a Leitz microscope, and have been reduced one-half in reproduction. The reference letters are as follows: *b*, bract; *s*, sepal; *p*, petal; *a*, stamen; *c*, carpel; *t*, tapetum; *n*, apex of nucellus.

FIG. 1.—Longitudinal section of staminate flower. ×105.

FIG. 2.—Longitudinal section of pistillate flower. ×105.

FIG. 3*a*.—Transverse section of staminate flower. ×105.

FIG. 3*b*.—Transverse section of same flower at the level of the origin of the stamens; *p*, petals and gland. ×105.

FIG. 4.—Transverse section of pistillate flower. ×105.

FIG. 5.—Superficial view of pistillate flower with bract (*b*), sepals (*s*), and petals (*p*) removed; ovules and apex of flower axis seen through the ovary wall. ×80.

FIG. 6*a*.—Transverse section of a microsporangium at the mother cell stage. ×730.

FIG. 6*b*.—Part of longitudinal section of microsporangium of same age as the preceding. ×730.

FIG. 7.—Section of mature microspore. ×730.

FIG. 8.—Surface view of mature microspore. ×730.

FIG. 9.—Longitudinal section of ovary with archesporium. ×730.

FIG. 10.—Same at older stage. ×730.

FIG. 11.—The four megaspores. ×730.

FIG. 12.—Germination of megaspores. ×730.

FIGS. 13–17.—Successive stages in development of embryo sac. ×730.

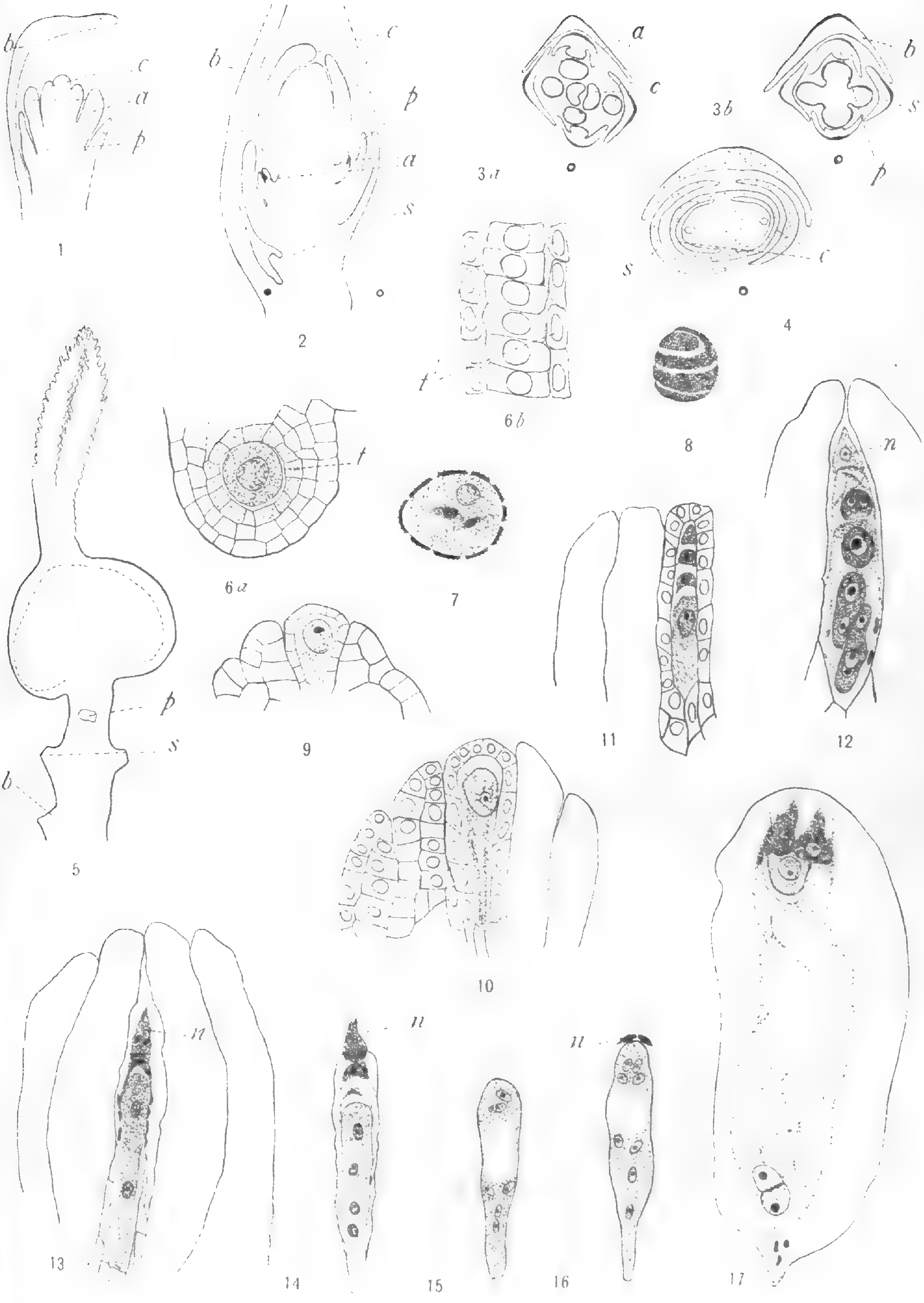
FIG. 18.—Definitive nucleus before fertilization. ×730.

FIG. 19.—Proliferation into the base of the embryo sac. ×730.

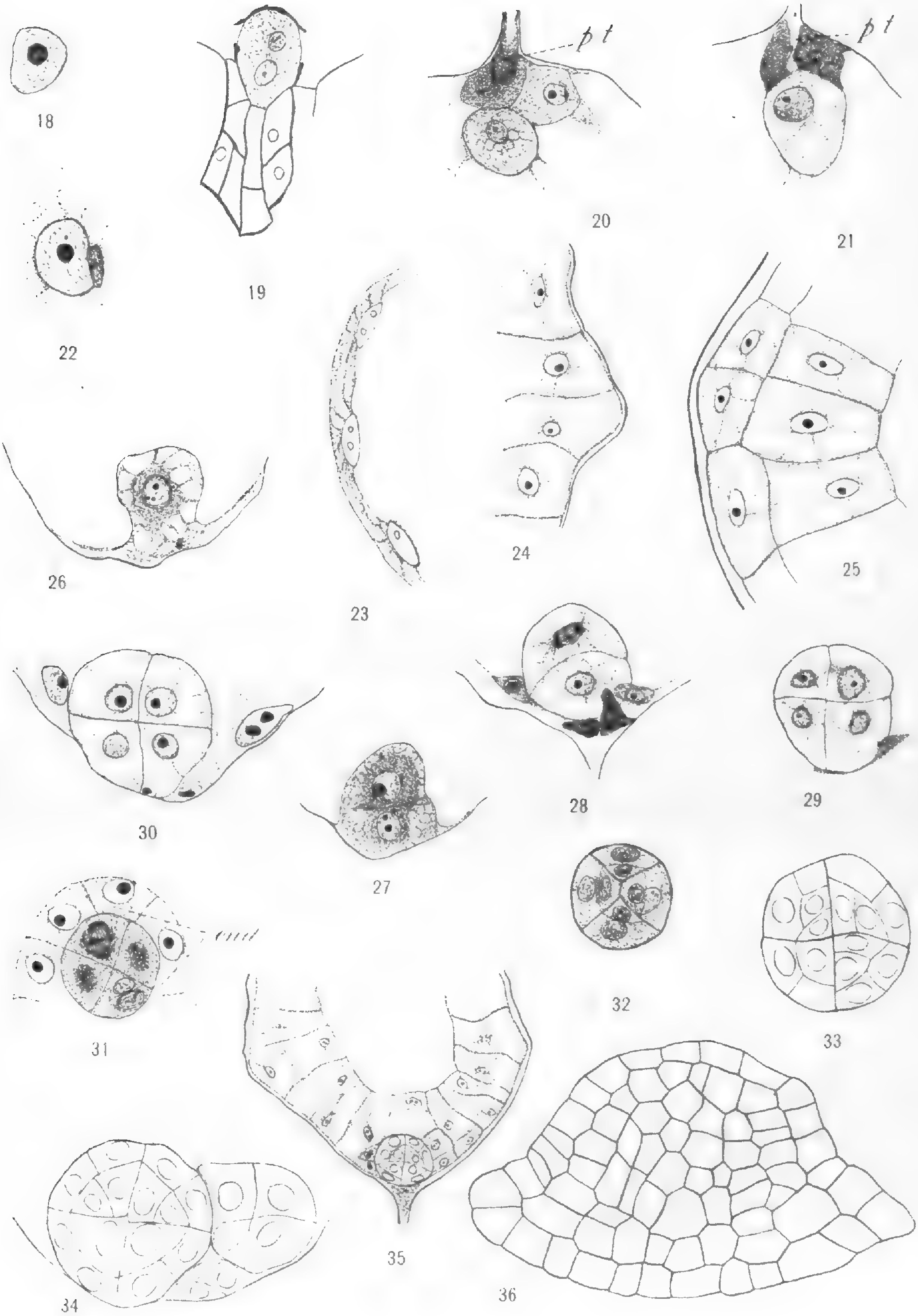
FIG. 20.—Egg apparatus and entrance of pollen tube. ×730.

FIG. 21.—Egg apparatus after fertilization. ×730.

FIG. 22.—Fusion of second male nucleus with definitive nucleus. ×730.



SMITH on ERIOCAULON



SMITH on ERIOCAULON

FIG. 23.—Endosperm before tissue formation. ×730.

FIG. 24.—Tissue formation in endosperm. ×490.

FIG. 25.—Division of parietal layer of endosperm. ×730.

FIG. 26.—One-celled embryo. ×730.

FIG. 27.—Two-celled embryo. ×730.

FIG. 28.—Second division of embryo. ×730.

FIG. 29.—Quadrant stage of embryo. ×730.

FIG. 30.—Octant stage of embryo. ×730.

FIG. 31.—Transverse section of inner half of embryo, showing origin of dermatogen. ×730.

FIG. 32.—Transverse section of micropylar half of same embryo. ×730.

FIG. 33.—Transverse section of an older embryo. ×730.

FIG. 34.—Polyembryony.

FIG. 35.—Micropylar end of embryo sac, showing embryo and endosperm. ×240.

FIG. 36. Longitudinal section of embryo of mature seed. ×730.

THE CLOSING RESPONSE IN DIONAEA[1]

WILLIAM H. BROWN AND LESTER W. SHARP

(WITH ONE FIGURE)

Despite the attention attracted during the past century by the extraordinary reactions of *Dionaea muscipula* Ellis, there remains much uncertainty with regard to many points in its behavior. This uncertainty has led the present writers to carry out the work here reported.

The structure of the leaf is so well known that its description here is unnecessary. It may be well, however, to recall the fact that the leaf blade consists of two valves, each of which bears upon its upper surface three short, rather stiff bristles. Mechanical contact with these bristles causes the two valves to close together upon each other.

Relation of intensity to number of stimuli

DARWIN (3), SACHS (9), BATALIN (1), DETMER (4), MUNK (7), and others held that one contact stimulus was sufficient to produce the closing response. DARWIN (3) and BURDON-SANDERSON (2) showed that an extremely slight stimulus might be inadequate, while MACFARLANE (6) concluded from his researches that under ordinary conditions two mechanical stimuli are always necessary. In investigating this question it is of course necessary to avoid all possibility of shaking, which might cause uncertainty as to the number of stimuli applied. In the present experiments a stiff straw was so supported that it could be adjusted to any desired position and moved mechanically by means of a rack and pinion and milled head. By this method the movement of the straw could be accurately controlled, and the number of stimuli definitely known.

Leaves of plants which had been kept at 15° C. for one to two hours were stimulated by pressure upon one of the sensitive hairs, and it was found that closure almost never resulted after one such stimulus, even though the hair was bent down so as to touch the

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[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, No. 12.

leaf. If, however, a second stimulus was applied either on the same or another hair, after an interval of 1.5 to 20 seconds the leaf responded, and in nearly every case by complete closure. The leaves of plants which had been kept about the same length of time at 35° C. frequently responded to one contact stimulus, while those kept at 40° C. closed with the first stimulus about as often as with the second. Slight individual differences were sometimes found in the leaves tested. These results seem to show that while under ordinary conditions two mechanical stimuli are usually necessary for closure, the number is not fixed, but varies with the environment and to some extent with different leaves.

The question now arises as to whether a certain amount of stimulation, rather than a certain number of stimuli, is required to effect closure. This was first investigated by the use of electrical stimuli, the intensity of which could be accurately controlled. MACFARLANE (**6**) was inclined toward the belief that two electrical shocks are necessary to cause the closing response.

Two series of experiments were carried out, in one of which the terminals of an induction coil were connected by wires with the petiole and keel, and in the other with the petiole and a sensitive hair. These connections were made by one gentle touch in such a manner as not to cause closure as a result of contact. The leaves were allowed five minutes in which to recover from any after-effect of the contact stimulus. They were then stimulated with opening shocks at intervals of 15 seconds, a single dry cell being used in the primary circuit. The result in both series was essentially the same, the number of shocks necessary to cause closure increasing as the intensity of the stimulus decreased. One strong shock was always sufficient to cause the response, but when weaker shocks were applied the number increased until in one case 26 were required. As with mechanical stimuli, the leaves showed slight individual variations. These results are shown in table I, in which the numbers indicating the position of the sliding secondary coil indicate the intensity of the induced current produced, the greatest electromotive force corresponding, of course, to the position marked 0, while the lowest corresponds to position 6. The effect of a stronger current, obtained by the use of two cells in place of one in the primary circuit, was tested at position 0, but no difference was observable between the response in this case and that in which only a single cell was used. Partial closures were obtained before the complete closures in four cases with the first arrangement of contacts, and in a single case with the second arrangement. These are indicated by footnotes below the table.

TABLE I

NUMBER OF ELECTRIC SHOCKS REQUIRED TO PRODUCE COMPLETE CLOSURE WITH VARYING INTENSITY OF CURRENT; SHOCKS AT INTERVALS OF 15 SECONDS

CONTACT ON SENSITIVE HAIR AND PETIOLE									CONTACTS ON KEEL AND PETIOLE							
Position of coil	No. of test	0	½	2	3	4	5	6	Position of coil	No. of test	0	½	2	3	4	5
Number of shocks required for complete closure	1	1	1	1	4*	6‡	7	10¶	Number of shocks required for complete closure	1	1	1	2	1	3†	4
	2		2	2	3‡	1†		26		2		1	2	2	2	5
	3		1							3		1				
Average		1.0	1.3	1.5	3.5	3.5	7.0	18.0	Average		1.0	1.0	2.0	1.5	2.5	4.5

* Partial closure with 3 shocks.

† Partial closure with 2 shocks.

‡ Partial closure with 5 shocks.

¶ Partial closure with 9 shocks.

It is apparent from these tests that closure is due to intensity of stimulation rather than to number of stimuli, and that there exists a definite after-effect with a duration of over 15 seconds, the summation of these after-effects finally producing the response in the case of the weaker electric shocks.

We have heretofore considered mechanical stimuli as though all were of the same intensity, a condition which appears to be true if the hair is markedly bent. As has been stated, leaves kept at a temperature of 15° C. usually close on the application of the second stimulus, and in this case it appears to make no difference whether the bending of the sensitive hair is comparatively slight, or great enough to bring the hair against the leaf. At higher temperatures the leaf responds to one stimulus as frequently with slight as with more marked bending of the sensitive hairs. This is shown even more conclusively by the fact that at a temperature of 15° C. the leaf fails to respond when the hair is bent down against the leaf by one movement, while less bending, if accomplished by two movements, brings about response.

If, however, the bending is so slight as to be scarcely apparent, three to five stimuli, rather than two, are usually necessary to produce response. It appears, in general, that in both mechanical and electrical stimulation closure is due to the amount of stimulation rather than to the number of stimuli, but the amount of stimulation appears not always to be proportional to the amount of bending of the sensitive hair. If this is true, the number of contact stimuli necessary to cause closure should increase with the length of the time interval between them, since the effect of stimulation would be expected to disappear to a greater extent as the length of the time interval is increased. This hypothesis was tested with the result that leaves at a temperature of 15° C., stimulated mechanically at intervals of 20 seconds, closed with the second stimulus; when the interval was increased to a minute, they responded with 2 to 5 stimuli; at intervals of 2 minutes, a response was produced with 5 to 7 stimuli; while at intervals of 3 minutes, about 6 to 9 stimuli were necessary to bring about closure. These results are shown in table II, in which — denotes no response; P, partial closure; +, complete closure.

TABLE II

RESPONSE TO CONSECUTIVE CONTACT STIMULI AT VARYING TIME INTERVALS

Time interval between stimuli	No. of experiment	Number of stimuli								
		1	2	3	4	5	6	7	8	9
20 seconds	1	—	+							
	2	—	+							
	3	—	+							
	4	—	+							
1 minute	1	—	P	+						
	2	—	P	+						
	3	—	—	P	+					
	4	—	—	—	P	+				
2 minutes	1	—	—	—	P	+				
	2	—	—	—	—	P	+			
	3	—	—	—	—	P	+			
	4	—	—	—	—	P	+			
	5	—	—	—	—	—	P	+		
	6	—	—	—	—	—	P	+		
3 minutes	1	—	—	—	—	—	P	P	+	
	2	—	—	—	—	—	—	P	P	+
	3	—	—	—	—	—	—	—	P	+

It is seen at once that with increasing length of time interval the number of stimuli required to produce a response increases also. Considering only the number of stimuli required for complete closure, these results are tabulated in table III.

TABLE III

NUMBER OF STIMULI NECESSARY TO PRODUCE COMPLETE CLOSURE, THE TIME INTERVAL VARYING FROM 20 SECONDS TO 3 MINUTES

EXPERIMENT NO.	TIME INTERVALS BETWEEN STIMULI			
	20 seconds	1 minute	2 minutes	3 minutes
1	2	3	5	8
2	2	3	6	9
3	2	4	6	9
4	2	5	6	
5			7	
6			7	
Average	2.0	3.8	6.2	8.7

The averages from this table are plotted on the graph of *fig. 1*, in which the abcissas represent the length of the time intervals between stimuli, and the ordinates the average number of stimuli required for complete closure. In this region the graph shows only a slight curvature. It is nearly a straight line, which would seem to denote that at intensities ranging from 20 seconds to 3 minutes—and of course for these particular plants—the number of stimuli necessary for complete response varies almost directly with the length of the intervals.

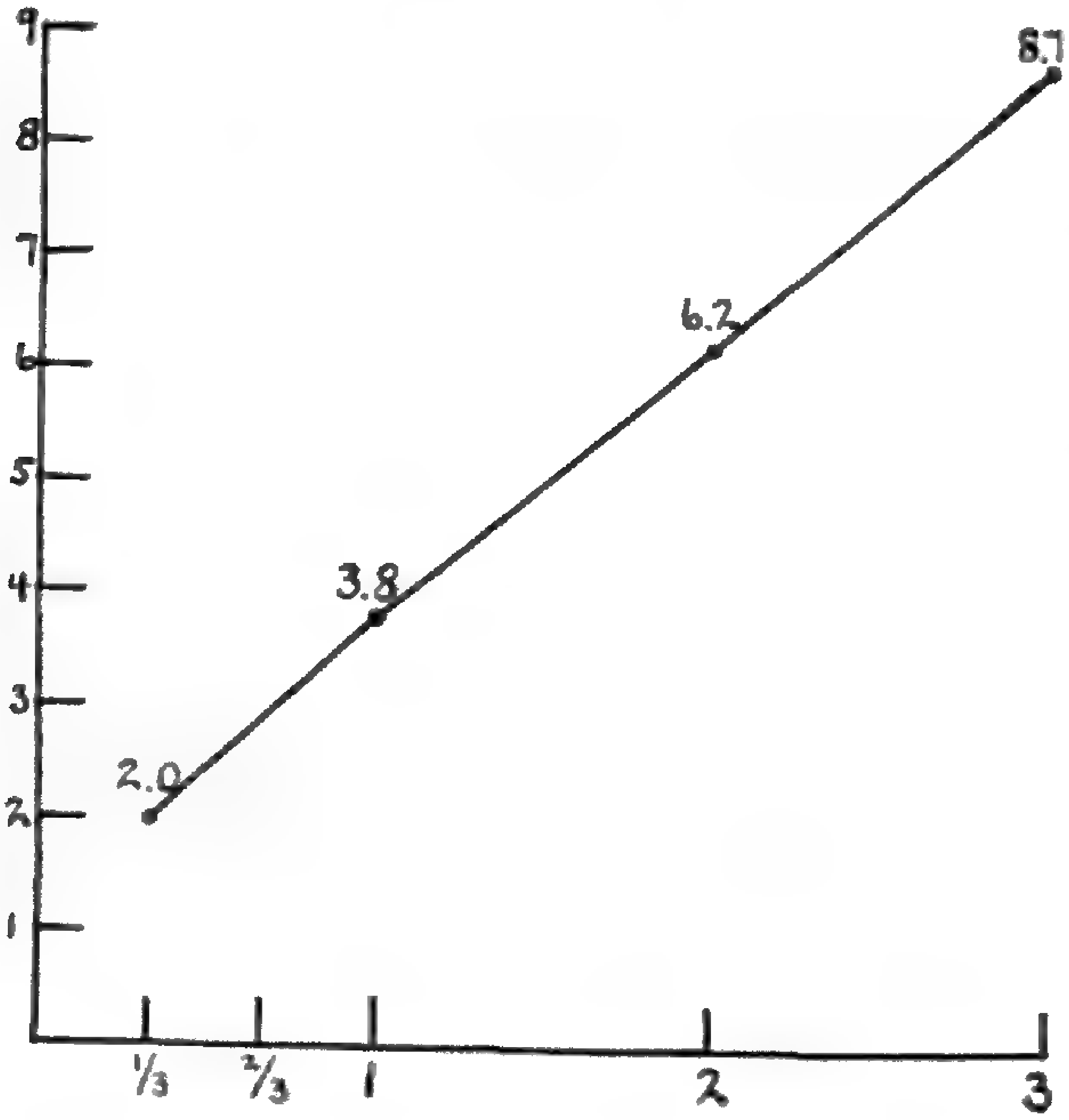

Fig. 1

It may be concluded from the foregoing that leaves seem to respond by closing to a definite amount of accumulated effect, possibly the production of some chemical substance as the result of excitation; that the amount of this effect varies with the intensity of the stimulus; and that the amount of stimulation necessary for closure varies with different leaves, probably with different conditions of the plant.

Localization of perception

DARWIN (**3**) held that the surface of the blade is very slightly, and the footstalk not at all sensitive. MACFARLANE (**6**) showed that scraping the surface or squeezing the blade with steel forceps would cause closure, and concluded that "the leaf of Dionaea, then, is truly sensitive throughout its halves to mechanical stimulation, but the capacity for receiving sensation impulses is highly concentrated in the hairs." This writer states, however, that two pinches with the forceps are required to cause closure. In our experiments, leaves responded to one, two, or even more such pinches, according to the strength of the stimulus and the condition of the leaf. It thus appears that MACFARLANE'S conclusion is supported, in that all parts of the leaf are sensitive, and the question is raised whether the protoplasm of all parts may not be equally sensitive to stimulation, and that the hair functions simply as a mechanism which compresses certain cells. OUDEMANS (**8**) and BATALIN (**1**) came to the conclusion that the base of the hair is the sensitive region, while HABERLANDT (**5**) has pointed out near the base of the hair a layer of cells which appear especially fitted for being bent, and thus having their contents compressed. The latter author considered this layer the sensitive region, and expressed surprise that the rest of the leaf should be sensitive at all.

When a hair is stimulated by contact, it is first bent laterally and downward, held in this deformed position for a short time, and then allowed to spring back to its original position. If stimulation be due to a compression of cells at the base of the hair, the downward movement alone should cause closure. To test this, a stiff straw was supported as in former experiments, so that it could be accurately adjusted and held definitely in any position. Two downward thrusts on the same sensitive hair without an intervening release caused in every case at 15° complete closure. With a temperature of 35° C. to 40° C. the leaves frequently responded to one downward thrust without a release.

When a sensitive hair was bent down and held mechanically in that position for 5 minutes, the leaf nearly always failed to respond. This experiment was repeated many times, but response followed in only a very few cases, and then only a few seconds after the contact. These exceptional closures seem to have been due to the downward thrust.

In order to determine the effect of the upward movement of the hair, the latter was bent down carefully against the leaf without causing closure, and held in that position for a period of 5 minutes in order that the effect of the compression stimulus might disappear. The hair was then allowed to spring back to its original position by two successive upward movements. This experiment was repeated many times, but the leaves never exhibited any response. The same operation was then repeated with the addition of alternate bendings and releases subsequent to the two upward movements, at intervals of 15 seconds. In no case did the leaf respond to a release, but always to a downward movement. The leaf is thus seen to respond only to a downward bending of the hair, and it seems probable that stimulation is due to a compression of the cells at its base, and that this compression is analogous to the compression of the cells of the blade when the latter is squeezed with forceps.

That the bending of the cells at the base is alone sufficient to cause response was shown in the following manner. A hair was cut off near the base and the leaf allowed ample time to recover from any possible shock produced by the cutting. The remaining portion was then pressed with a needle. In this operation it could be seen by means of a lens that bending took place only in the region where lie the cells shown by HABERLANDT to be especially suited to a compression stimulus. In such cases the leaves responded normally. That simple bending of the sensitive hair, without contact with a hard object, is sufficient to cause closure was shown by directing jets of air against it, when the leaf responded as if stimulated by contact.

We have seen that all parts of the leaf are sensitive to mechanical pressure, and that the hair probably functions as a mechanism for the compression of certain cells. It next remains to be seen whether the protoplasm of these cells is more sensitive than that of the other cells of the leaf. Inspection of table I will show that when electrical shock was conducted through the keel to the petiole, and therefore not passed through the region at the base of the hair, it was just as effective, or perhaps slightly more so, than when passed through the sensitive hair itself.

It was found that water at room temperature when carefully applied to either surface of the leaf blade does not cause it to close. Water at 65° C., however, will cause closure without harming the leaf, and this response is just as marked, so far as could be determined, when the water is applied to the back of the leaf as when applied to the inner surface or to the bases of the sensitive hairs. These experiments with heat and electricity seem to indicate that the other cells of the blade are just as sensitive as those at the bases of the hairs. Contrary to DARWIN's opinion, the petiole is also sensitive, as we have found that passage of electrical shocks through it will cause closure of the valves. In this case, however, a much stronger stimulation is required to effect closure than when the shock is applied directly to the blade. This difference may very well be due to loss in conduction of the stimulus from the petiole to the region of bending.

Stimuli of various forms

In the experiments already recorded, it has been shown that closure may result from the application of mechanical, electrical, and thermal stimuli. DARWIN (3), MACFARLANE (6), and others have shown that the leaf may also be closed as the result of chemical stimulation. For convenience, these various kinds of stimuli may be discussed separately.

MECHANICAL STIMULI.—It has been seen that all parts of the leaf are sensitive to mechanical stimulation, and that this acts through compression of cells. DARWIN (3) states that water falling on the sensitive hairs does not cause closure, while MACFARLANE (6) observed that a steady stream directed against a hair, or the gradual immersion of the leaf, does cause the response. In our experiments it was found that the leaves could be filled carefully with water, or wholly immersed, without causing the response, but that the dropping of water on the hairs, or the movement of the leaf while immersed, caused it to close if the hairs were thereby bent. The effect of water seems to be entirely due, therefore, to its mechanical action.

It is well known that a slight shaking will cause movement in the leaf of Mimosa. Experiments were undertaken to determine whether the leaf of Dionaea would also respond to shaking. These were not conclusive, but showed at least that the leaves can endure much shaking without showing response. In one case a long-petioled leaf was arranged so that it was struck near the distal end on alternate sides by the bar of a metronome beating 200 times per minute; and after 45 minutes the leaf showed no change. When the leaves of Mimosa are shaken, the large leaflets offer a considerable resistance to the air, which, together with their inertia, results in the bending of them and of the pulvini. The only parts of a Dionaea leaf which could be so affected are the cells at the bases of the sensitive hairs, as all the rest of the leaf is comparatively rigid. The hairs are so slender that they offer little resistance to the air, and on account of their small mass have a relatively slight inertia, and so when moved through the air can have little tendency to bend the cells at their bases. In experiments, however, in which the leaves were shaken under water, which offers a greater resistance to the passage of the hairs, the result was the same as in a Mimosa leaf shaken in air. It would thus seem that the nature of the response is the same in the two cases, the effect of the denser medium in the former balancing the effect of the large leaflets in the latter. This conclusion is further supported by the experiment already noted, in which the leaf closed as a result of bending produced in a sensitive hair by jets of air directed against it.

MACFARLANE (**6**) found that leaves stimulated twice mechanically at an interval of 0.25 second did not close on the second stimulus. If, however, the interval was 0.33 second or more they did close on the second stimulus.

Leaves which had been kept for an hour at 15° C. were stimulated twice mechanically at intervals of 0.25 to 2 seconds. When the interval was less than 0.75 second, response never followed; when it was 1 second, response was frequent; while at intervals of 1.5 seconds or more the leaves invariably closed. At temperatures of 35° C. to 40° C. the leaves rarely failed to respond to two mechanical stimuli separated by an interval of 0.25 second. They always responded when the interval was longer than this and failed to respond with shorter intervals. This is added evidence that the leaves respond more readily at higher temperatures than at lower. As in the case of animal muscle, there seems to be in Dionaea a short interval after one stimulus during which another has no effect.

THERMAL STIMULI.—MACFARLANE (**6**) allowed drops of water at temperatures varying from 50° C. to 75° C. to fall upon open leaves. At the higher temperature one drop caused closure, while at the lower several applications were necessary. Only four of the leaves so treated reopened, and he says, "the subsequent fate of most of the leaves points to a permanent injury." It is not stated whether or not the water was dropped on the sensitive hairs. The present writers found that water at room temperature, dropped directly upon the hairs, causes closure, while the gentle application of water at 50° C. does not cause the response. When warm water is dropped in this manner, it is of course cooled somewhat before it reaches the leaf. Since it is possible to interpret the cases reported by MACFARLANE as being due either to a heat stimulus, to a mechanical stimulation of the sensitive hairs, or to injury, it was thought advisable to reinvestigate the effects of heat. Water at 65° C. was applied in some cases to the inner, and in other cases to the outer surface of the leaves. In all cases closure resulted. These leaves exhibited no appearance of injury, and after reopening responded again quite normally. As a control for these experiments, water at room temperature was applied for several minutes to both inner and outer surfaces of the leaves without effect. This seems to indicate that heat causes the closing response. Water at 75° C. was then applied as above. Closure resulted in all cases, but two days later the parts of the leaves touched by the water were dead and black. Only small areas on some of them had been injured, and in several such cases the rest of the leaf responded normally. We can also confirm MACFARLANE'S statement that cold water will cause closure. This is true whether it be applied to the inner or to the outer surface.

ELECTRICAL STIMULI.—Experiments already described show that electrical stimuli, when applied to various parts of the leaf and petiole, cause closure, and that the effect depends upon the intensity of the stimulation rather than upon the number of stimuli. The response is brought about by either opening or closing shocks from an induction coil, but the former are much more effective than the latter. The feeble effect of closing shocks is shown by the fact that when as many as 100 of these were applied to leaves at intervals of 15 seconds, the coil being at position 0 (see table I), the leaves showed no sign of response. When the closing shocks were followed by opening shocks, the leaves responded to two of the latter as if nothing had preceded them. In another case two dry cells were used in the primary circuit, and the leaf closed on the 21st closing shock. Continuous current from a dry cell failed to cause closure.

EFFECT OF COMBINING STIMULI OF TWO FORMS.—As has been shown, leaves kept at 15° C. usually respond to two marked bendings of the sensitive hairs. A series of such plants was stimulated first by a single contact and then by an electric shock of such strength that two of these would be required to cause closure if used alone. These plants usually responded on the first electrical stimulus, while in two control series, in one of which only contact stimuli were used and in the other only electrical stimuli, they usually responded on the second stimulus. Table IV represents these three series.

TABLE IV

STIMULATION OF SENSITIVE HAIR BY MECHANICAL AND ELECTRICAL STIMULI

SERIES I HAIR STIMULATED BY ONE MECHANICAL CONTACT FOLLOWED BY OPENING SHOCKS				SERIES II HAIR STIMULATED ONLY BY OPENING SHOCKS OF THE SAME INTENSITY AS THOSE OF SERIES I		SERIES III HAIR STIMULATED ONLY BY MECHANICAL CONTACTS SIMILAR TO THOSE OF SERIES I	
Experiment number	Number of shocks required for complete closure			Experiment number	No. of shocks required for complete closure	Experiment number	No. of contacts required for complete closure
	Mechanical	Electrical	Total				
1	1	1	2	1	2	1	2
2	1	1	2	2	2	2	2
3	1	1	2	3	3	3	2
4	1	2	3	4	2	4	2
5	1	1	2	5	2	5	2

The results given in table IV seem to show that stimuli of different forms produce a similar internal effect, and that the leaves respond, as has already been pointed out, only with the accumulation of a certain amount of this effect.

Summary

The closing response in Dionaea depends upon the intensity rather than upon the number of stimuli, the number of stimuli required varying in the inverse order of their intensity.

Response is normally brought about by the compression of certain cells at the bases of the sensitive hairs, but the compression of other cells of the blade also causes closure, and it is probable that the latter cells are equally sensitive with the cells at the bases of the hairs, as is indicated by electrical and thermal stimulation.

The closing response follows the application of mechanical, electrical, and thermal stimulation. It also follows a combination of stimuli of two kinds when consecutively applied, the individual stimuli being of an intensity such that either alone would be insufficient.

The effect of mechanical stimulation is due to compression of cells, and not to contact with a hard object, continued pressure, or release of pressure. The failure of the leaf to respond to shaking is probably connected with the small inertia of the sensitive hairs, and the slight resistance offered by the air to their passage through it.

Water at room temperature causes closure only when it bends a sensitive hair.

After one mechanical stimulus there is a short period during which a second mechanical stimulus is ineffective.

The writers are indebted to Dr. W. D. Hoyt for collecting the plants used, and for help during the course of the work; to Professor D. S. Johnson for his encouraging interest; and to Professor B. E. Livingston for valuable aid in the preparation of this paper.

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BRIEFER ARTICLES

AN ABNORMAL BRACT-MODIFICATION IN COTTON

(WITH ONE FIGURE)

At Thompson's Mills, northern Georgia, during the season of 1909, the writer's attention was called to an exceedingly interesting modification in one of the involucral bracts of upland cotton. This is shown natural size in the accompanying photograph. A portion of this particular member of the involucre retains the usual features of a normal bract, while the rest has become a typical leaf in shape. A more perfect combination of bract and leaf could hardly be expected. The bractlike portion appears to replace a single lobe of the leaf.

Aberrant variations of this nature are not readily explained. The earlier morphologists were wont to regard them too seriously as reversionary variations which really brought to light particular features of ancient progenitors. In many instances it would appear that considerable skill obtained in the invention of fanciful conceptions of evolutionary developments. Modern botanists, however, do not find it quite as convenient to explain many variations in this way.

The involucral bracts of cotton may have originated from typical foliage leaves which have become reduced by evolutionary processes, but the best of our evidence is exceedingly incomplete. The modification here shown is an interesting fact of variation, but whether or not it expresses any fact of evolutionary significance can be only roughly surmised. Any study of plants or animals reveals striking variations in all characters, and many are as incomprehensible in their origin or significance as life itself. Irregular variations, however, deserve to be carefully preserved. Although, taken singly, they may not appear very significant, large numbers may be more productive of significant conclusions.—H. A. ALLARD, *Bureau of Plant Industry, Department of Agriculture, Washington, D.C.*

THE BIOLOGICAL ANTAGONISM BETWEEN CALCIUM AND MAGNESIUM

In a recent number of the BOTANICAL GAZETTE (**49**:41–50. 1910), CHAS. B. LIPMAN stated that in regard to *Bacillus subtilis* an antagonism does not exist between calcium and magnesium. This fact is quite natural, however, since the microbes (with rare exceptions, as for example Azotobacter) do not require lime for their life and multiplication, and on the other hand an antagonism does not exist between those elements themselves, but merely between their functions. Magnesium salts, in the usual biological concentrations, cannot exert any poisonous action on lower fungi and algae, hence there is no need of any antagonistic element. These points have been extensively treated in a paper entitled "The physiological rôle of mineral nutrients in plants,"[1] to which the reader may be referred.—OSCAR LOEW, *Munich, Germany*.

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[1] Bull. 45, Bur. Pl. Ind., U. S. Dept. Agric. 1903; especially on p. 44 and pp. 49–54.

CURRENT LITERATURE

BOOK REVIEWS

Vegetation in Belgium

One of the most important of ecological investigations is represented by the work of MASSART[1] along the Belgian coast and the neighboring alluvial lowlands. Perhaps no other similar work has been so detailed, and certainly no results of such a study have ever been presented in so sumptuous a form. For a decade and a half MASSART has carefully studied the restricted area here considered, and now there is presented a comprehensive monograph, though modestly entitled an essay. The first chapter deals with the past history of the region from the Miocene on. The modern (Holocene) period was initiated by the withdrawal of the sea and the formation of extensive peat deposits. Later came another invasion of the sea, Roman remains having been found beyond the present shore line. In the ninth century A.D. the Normans began a system of diking, which arrested the incursions of the sea and incited dune formation. At present there are extensive dune areas near the French border and also beyond Ostend and near the Dutch border. The alluvial deposits include chiefly the *polders*, fertile tracts within the dunes lying below sea-level and long ago reclaimed from the sea. Flat depressions among the dunes are known as *pannes* (perhaps to be translated into English as "pans"); an alluvial shore inundated at ordinary high tides is called a *slikke*, while the higher level inundated at the highest tides is called a *schorre*.

The second chapter, dealing with the conditions of plant existence, calls attention to the imperfections of ordinary meteorological data; for example, readings of ordinary air temperatures mean but little and should be replaced by readings of temperatures where the various plant organs, aerial and subterranean, are located; again it is shown how much more important are evaporation data than the more common humidity data. Various southern plants that cannot endure the winter at Brussels are uninjured on the coast. The influence of the winds on tree shape is very marked, and MASSART agrees with those who regard the influence of salt in causing deformity as insignificant when compared with desiccation; the trees most likely to be deformed are the silver poplar, linden, and elm. Very full tables

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[1] MASSART, J., Essai de géographie botanique des districts littoraux et alluviaux de la Belgique, avec annexe contenant des listes de plantes, trente-deux planches doubles en phototypie, neuf planches de diagrammes et quatorze cartes. Recueil de l'Institut Botanique LÉO ERRERA 7:167–584+pp. 121. 1908.

BOMMER ET MASSART, Les aspects de la végétation en Belgique; I. MASSART, J., Les districts littoraux et alluviaux. *pls. 86.* Ministère de l'intérieur et de l'agriculture; Jardin botanique de l'état. Brussels. 1908.

are given, comparing the littoral climate of Belgium with that on other European coasts. By reason of mild temperatures, many plants retain green leaves through the winter, notably winter annuals, biennials, and many evergreen herbs. Other topics here treated are bud protection (RAUNKIAER'S classification being followed), fixation of dunes by vegetation (mosses and lichens being of great importance in this), reactions to the deposit and denudation of sand (e.g., ascent or descent of rhizomes), rigidity of the aerial organs, "adaptations" against desiccation. Consideration is next given to the soil, many analyses being presented, and to the influence of animals and of other plants upon the vegetation. Some attention is devoted to succession, as on the dunes, where Erodium often appears on a fresh surface, giving way later to *Festuca rubra*, and this to Tortula, and this again to various herbs, the succession culminating in a stand of *Salix repens*.

The third chapter has to do with the plant associations (the term formation being discarded). An association is defined as "l'ensemble des espèces végétales qui sont adaptées aux mêmes conditions d'existence et qui vivent donc en mélange dans une station, c'est-à-dire dans l'endroit où ces conditions d'existence sont réalisées." After considering the conditions obtaining on the littoral dunes, MASSART takes up the detailed features of the mobile and fixed dunes, the dry and wet "pans," winter pools and permanent pools, cultivated lands and forest plantations. The marine and fluvial alluvia are next considered, attention being given to the tidal belts (*slikke* and *schorre*), ditches, mounds, *polders*, brackish and fresh waters, ponds, canals, dikes, and cultivated areas. Finally there are treated the plants of the Cardium sands.

A chapter is devoted to a floristic comparison between the littoral and alluvial districts and other neighboring districts, Belgium being regarded as divided into two main regions, the domain of the plains and the domain of the hills and mountains. The final chapter deals with the origin of the flora. In the region considered there is not a single endemic species. The dune flora is dominantly "calcicole," thus differing from the dune floras of Holland, Denmark, and Germany. The Cardium sands, on the other hand, are tenanted mainly by "calcifuges."

The *Annexe* is devoted in part to a detailed list of plants, with data arranged in columns showing distribution in Belgium and elsewhere in Europe, and also giving the characteristic vegetative features of the plants considered, a unique and most suggestive kind of tabulation. Most of the *Annexe*, however, is filled with photographic reproductions of the various habitats, diagrams, and maps. The work on "Aspects de la végétation" (following out a plan elaborated by BOMMER in 1903) presents the same or similar photographs in most sumptuous form, the plates having the unusual size of 30×40^{cm}. Doubtless these are the most excellent ecological photographs that have ever been taken, and they are also issued in the most perfect form of any that have yet appeared. Indeed the entire monograph, including the detailed text with its many tables of climatic and edaphic data and vegetative features, as well as the numerous illustrations, may serve as one of the best models now extant for future ecological workers. Many of our

American ecologists who issue several papers a year, giving the results of a few days or weeks of study, may well follow the example of MASSART, who has minutely studied his restricted Belgian littoral in every season for fifteen years and more.—H. C. COWLES.

A new manual of Rocky Mountain botany

To those familiar with the *Manual of the botany of the Rocky Mountain region* which has been the standard field book for that section of the country for practically a quarter of a century, the appearance of a revised edition[2] will appeal with special interest. The territory covered by the present volume remains essentially the same as in the original edition, namely the Rocky Mountain region from Montana and southern Idaho to northern New Mexico and Arizona.

The text in the new edition has been entirely recast; the arrangement of families has been brought into the sequence of ENGLER and PRANTL; the descriptions of the older species in many cases have been rewritten in the light of more complete material and printed in uniform type; the results of taxonomic researches made on the flora of the region during recent years have been incorporated with few exceptions, thus bringing the manual to date; concise and well-contrasting keys have been placed at the beginning of all the larger genera; bibliographical reference is made to the original publication of species and varieties recognized; and limited synonomy is given, particularly wherever a change of name or new combination has been made. These are the salient features which characterize the revised edition.

The circumscription of families continues unchanged; and it is a pleasure to see such natural groups as Leguminosae and Compositae remain intact. The most striking contrast, however, when compared critically with the first edition, is in the matter of generic limitations. Here the reviser has had a difficult task, because of the very great botanical activity in exploration and taxonomic publication in recent years and the tendency toward segregation. Thus the effort to bring together in perfect harmony and to bestow proper value on all genera and species that have been proposed during the past twenty years from the Rocky Mountain region alone has been no light undertaking. And to be absolutely consistent would require essentially a monographic knowledge of every group represented within the limits of the flora. The taxonomist, therefore, may find himself at variance with the treatment of certain groups as delineated in the text. For example, Batrachium, Ranunculus, Halerpestes, Onagra, Anogra, Pachylophus, Lavauxia, Gaurella, Galpinsia, Meriolix, and Taraxia receive equal generic recognition; while other recently segregated groups like Saxifraga, Astragalus, Euphorbia, and Mentzelia have been retained in their broader sense, as they are

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[2] COULTER, JOHN M., New manual of botany of the Central Rocky Mountains (vascular plants), revised by AVEN NELSON. 8vo. pp. 646. New York, Cincinnati, and Chicago: American Book Co. Actual date of publication, December 22, 1909.

usually defined. Hence in the treatment of genera a somewhat intermediate course has been followed.

In the interpretation and definition of species the work is conservative; in fact many of the recently proposed Rocky Mountain species have been reduced to synonomy. All categories subordinate to the species are treated uniformly under the trinomial, without further indication as to the supposed relationship to species; and it is only in the summary that we learn incidentally these are all regarded as varieties. The flora contains according to the summary given 116 families, 649 genera, 2733 species, and 186 varieties. This is by no means an excessive number for such a diversified region. A "list of new names and combinations" is also appended, which totals 169. Some of these combinations seem scarcely justifiable; for example, "*Krigia virginica* (L.) A. Nels." This is a name taken up for *K. amplexicaulis* Nutt. apparently on the basis of absolute priority, but which is in direct violation of section 7, article 53, of the International Rules of Botanical Nomenclature. A very complete and convenient index, including scientific and common names, arranged similar to that of the seventh edition of GRAY'S *Manual*, concludes the volume.

The press work is excellent, and there are comparatively few typographical errors. On page 529, under *Erigeron ramosus*, the date of publication for the *Preliminary catalogue*, etc., is given as "1788," a mere typographical error for 1888. On the whole the revised edition gives a concise, reasonably complete, inexpensive, and in general conservative treatise on the flora of a region which is always fascinating to the naturalist; and the clear-cut keys, and brief and lucid descriptions render the book particularly well adapted for the field identification of species. The botanical public is to be congratulated on having the revision of this well-known manual made by one whose continued activities in the field and extended knowledge of the Rocky Mountain flora have peculiarly fitted him for the work in hand.—J. M. GREENMAN.

NOTES FOR STUDENTS

Current taxonomic literature.—O. AMES (Phil. Journ. Sci. Bot. **4**:593–600. 1909) under the title "Notes on Philippine orchids with descriptions of new species I" gives critical notes on several known orchidaceous plants and describes 3 species hitherto unknown.—O. BECCARI (*ibid.* 601–639. *pls. 30, 31*) has published, as new, 20 species and 7 varieties of Philippine palms.—W. BECKER (Beih. Bot. Centralbl. **26**: 1–44. 1909) has issued the first of a series of articles on the taxonomy of European violets.—A. CHEVALIER (Journ. Bot. **22**:112–128. 1909) under the title "Diagnoses plantarum Africae" has published several new species of flowering plants, including a new genus (*Leocus*) of the Labiatae.—H. CHRIST (Journ. Linn. Soc. **39**:213–215. 1909) describes new species of ferns, 2 of which are from the Philippines.—C. CHRISTENSEN (Bot. Tidsskr. **29**:291–304. *figs. 15.* 1909) has published a new genus (*Stigmatopteris*) of ferns, based on *Polypodium flavopunctatum* Kaulf. (*Aspidium rotundatum* Willd.) and refers thereto 12 species from tropical America.—W. W. EGGLESTON (Bull. Torr. Bot.

Club **36**:639–642. 1909) describes 3 new species of North American Crataegi.—F. EICHLAM (Monats. Kakteenk. **19**:177–180. 1909) has described a new species of Cereus (*C. lepidanthus*) from Guatemala.—A. D. E. ELMER (Leafl. Philip. Bot. **2**:631, 632. 1909) proposes a new species of Grewia (*G. negrosensis*) from the Philippine Islands.—A. J. EWART, J. WHITE, and B. REES (Proc. Roy. Soc. Victoria **22**:6–23. *pls. 3–10.* 1909) under "Contributions to the flora of Australia, no. 11," have published several new species, referred to different genera, and include a new genus (*Gilruthia*) of the Compositae.—C. FERDINANDSEN and O. WINGE (Bot. Tidsskr. **29**:317–319. *figs. 6–8.* 1909) have published 3 new American species of fungi.—M. GANDOGER (Bull. Soc. Bot. Fr. IV. **9**:458–464. 1909) under the title "Les Anthurium de l'Ecuador" gives a conspectus of the known Ecuadorian species and publishes one species new to science.—R. R. GATES (Rep. Mo. Bot. Gard. **20**:123–137. 1909) presents a very useful analytical key to some of the segregates of Oenothera; the key is supplemented by a bibliography and descriptive notes.—D. GRIFFITHS (*ibid.* 81–95. *pls. 2–13*) under "Illustrated studies in the genus Opuntia II" describes 11 new species from southwestern United States.—L. S. GIBBS (Journ. Linn. Soc. **39**:130–212. *pls. 11–16.* 1909) in cooperation with several specialists contributes an important article on the montane flora of the Fiji Archipelago; the paper includes a number of species new to science.—E. L. GREENE (Muhlenbergia **6**:1–3. 1910) has described 3 new species of Eriogonum from southwestern United States.—A. E. GROBÉTY (Bull. Soc. Bot. Genève II. **1**:357, 358. 1909) proposes a new genus (*Ourococcus*) of the green algae, based on *Dactylococcus bicaudatus* A. Braun.—E. HACKEL (Rep. Nov. Sp. **7**:311–327. 1909) under the title "Gramineae novae VI" has published 17 new species of grasses, chiefly from South America; one genus (*Schizachne*) is new to science.—E. HACKEL and E. HASSLER (*ibid.* 369–383) under the title "Ex herbario Hassleriano: Novitates paraguariensis III" have described new species and varieties in the Gramineae, Rosaceae, and Malvaceae.—T. HERZOG (*ibid.* 354–359), supplementing a recent article on new siphonogamous plants from Bolivia, has published 6 additional species; the same author (Beih. Bot. Centralbl. **26**:45–102. *pls. 1–3.* 1909) has published 73 new species of mosses from Bolivia, and proposes three new genera (*Polymerodon*, *Simplicidens*, and *Wollnya*).—A. A. HELLER (Muhlenbergia **5**:145–153. *pls. 4, 5.* 1909) presents a second article on the "Nevada lupines," including a description and illustration of one new species.—A. W. HILL (Journ. Linn. Soc. **39**:216–230. 1909) gives a synopsis of the "Acaulescent species of Malvastrum," recognizing 18 species of which 5 from South America are new to science.—E. JANCHEN (Mitt. Naturwis. Ver. Univ. Wien **7**:1–124. 1909) has published a monographic treatment of the Cistaceae of Austria-Hungary, recognizing four genera, as follows: Cistus (4 species), Tuberaria (1 species), Helianthemum (11 species), and Fumana (5 species); bibliography and synonomy are given in detail.—M. E. JONES (Contr. West. Bot. no. 13. pp. 1–16. 1910) under the heading "New species and notes" characterizes 15 new species and 9 new varieties of flowering plants from western United States.—C. H. KAUFMAN (Rep. Mich. Acad. Sci. **11**:55–91. *figs. 3.* 1909) records a list of fungi new to the state and gives a mongraphic treatment of the Michigan representation of Russula, in which 56 species are recognized, 5 being described as new to science.—N. C. KINDBERG (Ottawa Nat. **23**:180–191. 1910) in continuation of his studies on Canadian bryology records several species of mosses, as either new or noteworthy, from Canada.—M. BOULY DE LESDAIN (Bull. Soc. Bot. Fr. IV. **9**:473–477. 1909) has published 8 new species of lichens from Mexico and Peru.—G. MASSEE (Kew Bull. 1–6. *figs. 21.* 1910) has published several new species of fungi, 7 being from the West Indies. A new genus (*Hartiella*) of the Hyphomycetaceae is described from Trinidad; the fungus is parasitic on shells of the cacao pod.—E. D. MERRILL (Phil. Journ. Sci. Bot. **4**:641–650. 1909) has published a "Preliminary revision of Philippine Combretaceae," in which he recognizes four genera represented by 18 species; one new species of Terminalia is described.—W. A. MURRILL (Mycologia **2**:25, 26. 1910) describes a new phalloid genus (*Protophallus*) from Jamaica.—A. PASCHER (Ber. Deutsch. Bot. Gesell. **27**:555–562. *pl. 20.* 1909) describes and illustrates a new genus (*Pyramidochrysis*) of the Chromulinaceae; two species are recorded; both are found in stagnant water near Mugrau in southern Bohemia.—L. QUEHL (Monats. Kakteenk. **19**:188–189. 1909) describes a new species of Mamillaria (*M. pseudoperbella*) from Mexico.—A. REHDER (Rhodora **12**:1–3. 1910) records several noteworthy forms of *Kalmia latifolia*.—H. REHM (Ann. Mycol. **7**:524–542. 1909) has published several new species of Ascomycetes, 13 being from North America and 20 from South America; two new Brazilian genera are proposed, namely *Dictyomollisia* and *Phaeofabraea*.—J. F. ROCK (Bull. Torr. Bot. Club **36**:645, 646. 1909) describes and illustrates a new species of Scaveola from the Hawaiian Islands.—R. ROLAND-GOSSELIN (Rev. Hort. Paris **82**:28, 29. *fig. 8.* 1910) has published a new species of Cereus (*C. tricostatus*) which has been introduced into cultivation from Mexico.—R. A. ROLFE (Kew Bull. 364–368. 1909) has published several new species of orchids, of which 4 are from South America. —J. N. ROSE and J. A. PURPUS (Contr. U. S. Nat. Herb. **13**:45, 46. *pls. 10–14.* 1910) have described 3 new species of Echeveria from Mexico.—E. ROSENSTOCK (Rep. Nov. Sp. **7**:289–310. 1909) has published 38 new species and varieties of ferns. These species are based on collections made by Mr. R. SPRUCE in the region of the Amazon, in eastern Peru, and in Ecuador.—P. A. RYDBERG (Bull. Torr. Bot. Club **36**:675–698. 1909) under "Studies on the Rocky Mountain flora XX" has described several new species of sympetalous plants.—F. GRAF VON SCHWERIN (Mitt. Deutsch. Dendr. Gesell. 1–56. 1909) presents a monograph of the genus Sambucus, in which 21 species and numerous varieties are recognized; the text is accompanied by numerous illustrations and distribution-maps. —T. A. SPRAGUE (Kew Bull. 362–364. 1909) gives a synopsis of the American species of Microtropis, recognizing 5 species from Mexico and Central America, 2 being new to science.—F. THEISEN (Broteria Bot. Ser. **8**:53–65. *pls. 1–6.* 1909) under the title "Marasmii austro-brasilienses" enumerates 38 species of Marasmium, including 2 new species and 8 new varieties.—E. A. WAINIO (Phil. Journ. Sci. Bot. **4**:651–662. 1909) under the heading "Lichenes insularum philippinarum I" records 10 species and several varieties as new to science.—F. A. WOLF (Mycologia **2**:19–22. *pl. 18.* 1901) has published a new species of Fusarium, parasitic on *Viola tricolor*.—H. WOLFF (Rep. Nov. Sp. **7**:345, 346. 1909) has published a new species of Eryngium (*E. affine*) from Costa Rica.—C. H. WRIGHT (Kew Bull. 24. 1910) describes a new species of Urceocharis from Peru.—Different authors (*ibid.* 357–362. 1909) under the heading "Decades kewensis LIV" have published a number of new species of flowering plants, including a new genus (*Micholtzia*) of the Asclepiadaceae from India; also a new genus (*Ennealophus*) of the Iridaceae from Brazil.—J. M. GREENMAN.

A new genus of chytrids.—A minute organism parasitic in the leaf blades and petioles of the ragweed (*Ambrosia artemisiaefolia*) is described by GRIGGS[3] as a new genus. The swarm spores perforate the cell wall and enter the cells (epidermal, hypodermal, or chlorenchymal), sometimes in large numbers, where they present amoeboid forms within the plasma of the host. Some of the "amoebulae" unite in pairs by the fusion of their plasma while the nuclei remain distinct. This minute amoeboid zygote grows to form a binucleate resting spore which at maturity is provided with a stout exospore wall. The germination has not been studied. Other swarm spores, in the same or other cells, grow to form zoosporangia about 70 μ in diameter, showing also amoeboid movements in the vegetative stage. The nucleus of the young "amoebula" which is to form a zoosporangium is said to "fragment" into four nuclei at an early stage. Since the figure given presents just as much evidence that the four nuclei are derived by mitotic division as by fragmentation, it would be interesting to know if this is the period of meiosis. A rather extended period then follows before further successive division of these four nuclei to form the zoospores, which are 2.5 μ. The author saw no mitotic figures, but states that in some cases at least there is evidence that the nuclei fragment. The formation and escape of the zoospores was not observed, and he does not know whether the zoospores are ciliate or amoeboid, the latter he thinks more likely. Since the escape of the zoospores was not observed, he does not know whether or not an exit tube is formed from the sporangium. The species, which he names *M. stevensianum*, is associated with *Rhodochytrium spilanthides*, and while the infected cells increase greatly in size, very little deformity of the host occurs, although large numbers of cells in a limited area are affected.

Some of the speculations appear to be based on a misinterpretation of some statements of the reviewer in regard to the behavior of the zoospores of Rhizophidium, for he says: "ATKINSON has shown that when liberated inside the sporangium the zoospores swim actively forward until they strike the wall of the sporangium, when the flagella are retracted and the zoospore puts out pseudopodia by which it gropes for the opening of the sporangium. In case it is located too far from the ostiole to reach it with its pseudopodia, it resumes its flagellate form and

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[3] GRIGGS, R. F., Monochytrium, a new genus of the Chytridiales, its life history and cytology. Ohio Nat. **10**:44–54. *pls. 3, 4.* 1910.

swims about again until it finally escapes." The reviewer did not state that the flagellum is retracted[4] when the amoeboid movements take place and does not regard it as at all likely that such is the case.

Griggs places the organism in the Olpideaceae, and states that it may be separated at once from all other genera of this family by its habitat. "All the other genera are parasites of aquatic plants or animals except Asterocystis, which infests the roots of the seed plants." He has probably overlooked certain species of Olpidium. *O. brassicae* (Wor.[5]) Dang.,[6] a typical Olpidium, is parasitic in the stems of cabbage seedlings. *O. simulans* (DeBary and Wor.[7]) Dang.[8] (see also A. Fischer[9]) is parasitic in young leaves of *Taraxacum officinale* and is associated with *Synchytrium taraxaci.* Schroeter[10] is inclined to believe this is a Pleolpidium, but it would still be a member of the Olpidiaceae. *Olpidium trifolii* (Pass.[11]) Schroeter[12] on petioles and leaf blades of *Trifolium repens* is more doubtful; A. Fischer[13] thinks it is a Synchytrium.

It is unfortunate that the author did not compare his organism with the genus *Reesia* Fisch[14] (pp. 8–17), since until we know more about the dehiscence of the zoosporangium and the form of the active zoospores, it would seem more reasonable to place it in this genus than to create a new one, largely hypothetical; for if the zoosporangia develop exit tubes and the zoospores are uniciliate, which is not unlikely, it would be a true Reesia.—Geo. F. Atkinson.

Morphology of the grass flower.—Schuster[15] has recently made extended investigations upon the structure and morphology of the flowers and spikelets of grasses. His results are based upon an examination of fresh and alcoholic

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[4] See Bot. Gazette **48**:321, 322, 324. 1909.

[5] *Chytridium brassicae* Woronin, M. (see pp. 556–558. *pl. 31. figs. 12–18*) in *Plasmodiophora brassicae,* Urheber der Kohlpflanzen-Hernie. Jahrb. Wiss. Bot. **11**:549–574. *pls. 29–34.* 1878.

[6] Dangeard, P., Ann. Sci. Nat. Bot. VII. **4**:285, 327. 1886.

[7] *Chytridium* (*Olpidium*) *simulans* DeBary and Wor. (see p. 29. *pl. 2. figs. 11–16*), Beitrag zur Kenntniss der Chytridieen. Ber. Naturf. Ges. Freiburg **3**:Heft 2 (1–40 of separate). *pl. 1.* 1863.

[8] Rabenh., Krypt. Fl. Pilze **4**:29. 1892.

[9] Engler and Prantl, Pflanzenfam. **1**^{1}:70. 1889.

[10] *Synchytrium trifolii* Pass. in Rab. Fung. Europ. 2419. 1877.

[11] Cohn's Krypt. Fl. Schles. Pilze **1**:181. 1889; and Engler und Prantl, Pflanzenf. **1**^{1}:68. 1889.

[12] Rabenh., Krypt. Fl. Pilze **4**:51. 1892.

[13] Fisch, Carl, Beitrag zur Kenntniss der Chytridiaceen. pp. 48. *pl. 1.* Erlangen. 1884.

[14] Schuster, J., Ueber die Morphologie der Grasblüte. Flora **100**:213–266. *pls. 2–5. figs. 35.* 1910.

material, with special reference to the developmental history of the parts. By means of dissections and microtome sections of spikelets in various stages of growth, he arrives at what are represented to be definite conclusions concerning certain species in twenty-five genera. Among his results the following are of special interest:

From a phylogenetic standpoint he considers the grasses to have descended from lily-like plants in which there were six perianth divisions in two circles, six stamens, and a tricarpellate pistil. Among existing grass genera he places Streptochaeta as most primitive. In this genus there are three stigmas, six stamens, three inner and two outer organs which the author interprets as representing the inner perianth and the posterior segments of the outer perianth, all in the axil of the flowering glume or lemma. In the majority of grasses the floret, borne in the axil of the lemma, consists of a two-keeled palea, three stamens, two lodicules, and a pistil with a two-parted style. HACKEL and others have considered the palea to represent the prophyllum, an organ found at the base of a branch, between that and the main stem. SCHUSTER states, however, that the palea is formed by the union of the two posterior segments of the outer perianth circle of the primitive flower. The inner perianth circle is well developed in Streptochaeta, but is usually reduced to small organs, the lodicules, which commonly function as spreaders during anthesis. The swelling of the lodicules pries open the lemma, thus exposing the stamens and stigmas. Usually there are present only two lodicules, the posterior being absent, but in bamboos and some other grasses all three are present. In the more primitive forms, such as bamboos, there are six stamens, but in most grasses three are suppressed, while more rarely only one or two are present. He accounts for the numerous stamens of certain genera, such as Pariana and Luzuola, by the splitting up of the original six stamens. The pistil consists of three carpels, but the anterior carpel usually fails to produce a style branch.

Recently the morphology of the glumes of Elymus and Hordeum were investigated by SCHENCK,[15] who considered the glumes to be developed from lateral branches at the base of the spikelet. SCHUSTER controverts this, and states that the lower or outer glume originates as a single organ, but soon divides into two portions which stand side by side below the spikelet, the upper glume being suppressed. In certain species of Elymus, such as *E. arenarius*, the glumes are in nearly normal position, for which reason the author follows HOCHSTETTER[16] in separating this group under the genus name Leymus. The author further states that in the end spikelets of the spikes in Elymus and Hordeum, the glumes develop normally, that is, both are present and entire.

Concerning viviparous grasses, it was found that the bulblet-bearing character was more or less constantly inherited, but that by culture in a dry and nitrogen-poor substratum, these forms tended to revert to the normal seed-bearing state.—A. S. HITCHCOCK.

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[15] ENGLER'S Jahrb. **40**:97–113. 1907.

[16] Flora **31**:118. 1848.

Transpiration of evergreens.—PUGLISI[17] has recently published a long and detailed paper on the comparative transpiration of evergreen dicotyledons in winter, spring, and summer. He discusses *Laurus nobilis* L., *Laurus canariensis* Willd., *Persea indica* Spreng., *Persea gratissima* Gaertn., *Oreodaphne californica* Nees., *Cinnamomum Camphora* Nees. et Eberm., *Litsea* (*Tetranthera*) *japonica* Spreng. GARREAU's method is used to determine the relative transpiration of the upper and the lower surface of the leaf, and the potometers of MOLL and of PFEFFER for observations on detached shoots, sometimes continued for a week.

The author's most important conclusions are: that the volatile oils present are highly efficient in preventing excessive transpiration; that the safeguards against an injurious amount of transpiration in the leaves studied do not prevent rapid transpiration when there is an adequate water supply from the roots; that the relative transpiration rate of the upper and lower leaf surfaces varies decidedly at different seasons; that transpiration varies with the season, having a winter minimum, a maximum at the beginning of spring, and a lowering to or nearly to the winter rate during the extreme heat and drought of summer.

The memoir is sufficiently important to merit attentive reading by everyone who is investigating similar problems. The results, however, should be scrutinized with care, since some of the values obtained by the potometer method are open to doubt. For example, in the losses per square decimeter of leaf surface obtained in the six sets of potometer measurements on transpiration of *Cinnamomum Camphora*, the values for the first day average nearly one and one-half times as large as those for the fourth day, of consecutive potometer readings for the same shoot. In the June readings for this species, the daily transpiration in grams per square decimeter with the MOLL potometer fell from 6^{gm} on the first day to 1.13^{gm} on the sixth day. Evidently some cause, perhaps the plugging of the vessels of the cut end of the shoot by bacteria, rendered the later observations valueless.

The author cites some of the best literature on the subject, but apparently has not seen VON GUTTENBERG's most important paper.[18]—JOSEPH Y. BERGEN.

Mistletoe as a pest.—BRAY[19] has investigated the so-called mistletoe pest of the southwest, especially its destructive work in central Texas. It seems that the mistletoe is most destructive in the region of transition from a humid forest climate to a dry climate less favorable for trees, for it is in such a region that the light becomes more favorable for the parasite. The destruction is due in part to mechanical injury, but more especially to the drain on the water and nutritive supplies of the host, which is effected by the "sinkers" connecting the parasite

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[17] PUGLISI, M., Contribuzione allo studio della transpirazione nelle piante sempre verdi. Annali di Botanica **7**:517–652. *pl. 22.* 1909.

[18] GUTTENBERG, H. VON, Anatomisch-physiologische Untersuchungen über das immergrüne Laubblatt der Mediterranflora. Bot. Jahrb. **38**:383–444. *pls. 7–9.* 1907.

[19] BRAY, WILLIAM L., The mistletoe pest in the southwest. Bull. 166, Bur. Pl. Ind., U. S. Depart. Agric. pp. 39. *pls. 2. figs. 7.* 1910.

with the xylem vessels, and by the "cortical roots" that traverse the "soft bark." An interesting description is given of the behavior of these digesting roots ("sinkers") in penetrating tissue, and in sending out lateral outgrowths ("cortical roots") which spread extensively through the cortex of the host and in turn give rise to other "sinkers" that connect with the xylem. The first infection of a tree is brought about by birds, and the subsequent spread of the parasite is caused by the falling or washing of berries upon other parts of the host. The seed and seedling exhibit unusual resistance to desiccation, and so survive the more or less prolonged period of establishment, a period which may extend beyond the first growing season. A tree may become affected at any point where living tissue is exposed or covered only by a thin layer of cork with lenticels, but the most vulnerable points are the young branches, and sometimes the buds. Various suggestions are made as to the treatment of trees subject to the attacks of this parasite. —J. M. C.

Latex.—Miss DIANA BRUSCHI has made a study of the latex of five species of Euphorbia and three of Ficus,[20] in an endeavor to clear up in a measure the contradictory results of various investigators, of which the two most recent studies by MOLISCH (1901) and KNIEP (1905) are characteristic. Dr. BRUSCHI finds that the quantity of latex, its pressure, and its aspect vary with the season in the figs, *Ficus Carica* and *F. pseudocarica*, but not the euphorbias. Of the components of the latex the proteins vary in quantity with the season in the two figs named, in which they are abundant; but they are scant in *F. elastica* and the euphorbias. The fats are without doubt the most important plastic components and they clearly follow the variations in photosynthesis. The starch remains an enigma. Reducing sugars increase a little in *F. Carica* and *F. pseudocarica* but change little in the others. On the whole Miss BRUSCHI upholds MOLISCH's view of the latex as a cell sap circulating in a living plasma sac, which is not entirely aplastic. Inasmuch as it contains many substances easily utilizable as foods, the utilization of these foods is correlated with the activation and activity of the related enzymes. The ready use of the fats is certain, and they are the principal if not the only plastic material; the indifference of the starch is supposed to be due to the lack of an amylase energetic enough to attack it. As the latex tubes run usually in the midst of organs well supplied with foods by photosynthesis, their content is yielded only when all other foods are exhausted.—C. R. B.

Rhizoids of liverworts.—WEINERT has investigated the growth and tropisms of the rhizoids of Marchantia and Lunularia.[21] He finds that light promotes the formation of rhizoids from gemmae, and is quite indispensable for the development of the divergent rhizoids of the thallus; further, only a few of the appressed

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[20] BRUSCHI, DIANA, Contributo allo studio fisiologico del latice. Annali di Botanica 7:671–701. 1909.

[21] WEINERT, HANS, Untersuchungen über Wachstum und tropistische Bewegungserscheinungen der Rhizoiden thallöser Lebermoose. Bot. Zeit. 67^1:201–230. *figs. 11.* 1909.

sort, and these with poor pegs, are formed in darkness. Even if a thallus raised in darkness be afterward lighted, it forms no divergent rhizoids; and if such a thallus after being cut off regenerates itself, the new part forms none; the power once lost seems finally gone. Rhizoids cut off are not regenerated, but new ones are formed, either from surface cells of the thallus or from a cell internal to the first rhizoid-producing cell, in which case the new one grows through the old, as previously reported by Kny, Dixon, and others. Weinert finds that small pegs occur even in true divergent rhizoids, which indicates to the reviewer that the possession of rhizoids of two kinds has been overvalued as a marchantiaceous character, for example in the case of Monoclea.

While the formation of rhizoids on the under side of gemmae is promoted by gravity, the hairs themselves are not geotropic, but are highly sensitive to light, being negatively phototropic even in weak red light, but strangely enough, not in blue light. The divergent rhizoids of the thallus are very slightly phototropic (negative). The appressed rhizoids show no tropisms.—C. R. B.

The origin of Oenothera gigas.—Gates[22] has investigated the relation of the number of chromosomes in *Oenothera gigas* to its size. This mutant from *O. Lamarckiana* has double the number of chromosomes (28) possessed by the parent form and by the other mutants examined. In every tissue examined, the cells of the mutant are conspicuously larger than those of the parent form, and the nuclei of the pollen mother cells during synapsis are about twice as large. The author suggests that increase in the size of nuclei and cells, consequent upon or coincident with the doubling of the chromosome number, and change in the relative dimensions of the cells in some cases, will account for all the differences between the two species. There is no evidence of the presence of new or additional unit characters in *O. gigas*. It is concluded that the facts strongly support the view of the independence and genetic continuity of the chromosomes, whatever may be their rôle in heredity. It is suggested as most probable that the double number of chromosomes in *O. gigas* originated soon after fertilization, by the failure of a nucleus to complete its division after the chromosomes had divided. This doubling of the number of chromosomes, the author thinks, "cannot be a common method of species formation, and bear no necessary relation to the general processes of evolution in the group." He speaks of it rather as an incident among evolutionary phenomena.—J. M. C.

Farm water supplies.—The Bureau of Plant Industry has been cooperating with the Minnesota State Board of Health in an investigation of the farm water supplies of that state, and a report by Kellerman and Whittaker has now been published.[23] Numerous cases and their details are presented, classified under

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[22] Gates, Reginald Ruggles, The stature and chromosomes of *Oenothera gigas* DeVries. Archiv. für Zellforschung **3**:525–552. 1909.

[23] Kellerman, Karl F., and Whittaker, H. A., Farm water supplies of Minnesota. Bull. 154, Bur. Pl. Ind., U. S. Depart. Agric. pp. 89. *figs. 73*. 1909.

the following headings: dug wells, bored wells, drilled wells, driven wells, springs, rivers, surface reservoirs, and cisterns. Some of the general conclusions are as follows: Both farm and city are suffering from the careless management of rural sanitation. Exhaustive data upon 79 carefully selected and representative rural water supplies show that 20 were good and 59 polluted, usually because of careless or ignorant management. Some of the polluted wells are so located that even extreme care would not make them safe, but a large majority of them could be made safe. The rivers, surface reservoirs, and cisterns are all polluted, and it is doubtful whether satisfactory supplies can be secured for farm use from such sources, except by disinfection. During the investigation 23 of the farms examined showed a record of typhoid fever. It is stated that "the protection of farm supplies by common-sense methods, obvious to anyone who will try to discover the dangers incident to his own water supply, would render safe the majority of the farm supplies which are now polluted."—J. M. C.

Ferments of resting seeds.—Miss WHITE[24] has shown that the enzymes present in seeds of wheat, maize, barley, oats, and rye retain their activity long after the power of germination of the seeds has disappeared. Diastatic and proteolytic enzymes were shown to be present in wheat after twenty years of storage, and in oats, rye, and barley after eight to ten years of storage, although the seeds had lost their power of germinating. The enzymes persisted apparently unaffected by the long period of storage. The resistance of the enzymes to heat was also tested. In a moist condition all the enzymes are destroyed at 100°, but in a dry state they can resist higher temperatures. Pepsin was destroyed in one hour at 124°, erepsin in one hour at 124°–128°, and diastase at 124°–131.° Both as to duration of time and effects of heat the enzymes are more persistent than the power of germination, showing that failure to germinate is not necessarily correlated with loss of enzymes. In the final part of the paper the respiratory activity of resting seeds is taken up. Many air-dried seeds give off appreciable quantities of carbon dioxid, but others show no respiration. When seeds are moderately desiccated at 45° all respiration ceases.—H. HASSELBRING.

Position of chloroplasts.—SENN'S continued investigations[25] on some details of the position of chloroplasts offer opportunity to call attention to his independently published work,[26] which was not received by the GAZETTE. In his last contribution, after alluding to certain adverse criticisms on his former results, he reports investigations on the winter position of the chloroplasts in the palisade cells of winter-green foliage. He concludes that the heaping up of the

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[24] WHITE, MISS JEAN, The ferments and latent life of resting seeds. Proc. Roy. Soc. B **81**:417–442. 1909.

[25] SENN, G., Weitere Untersuchungen über die Gestalts- und Lageveränderung der Chromatophoren. Ber. Deutsch. Bot. Gesells. **27**:(12)–(27). 1909.

[26] ———, Die Gestalts- und Lageveränderung der Pflanzen-Chromatophoren. Leipzig: Wilhelm Engelmann. 1908.

chloroplasts in the bottom of the palisades is a local effect of the frost, which induces in the chloroplasts, and perhaps in the semifluid protoplasm also, a negative thermotactic migration.

SENN has also studied the migration of one of the chloroplasts of *Synedra Ulna* after division. The division of the diatom is of course longitudinal, while the two chromatophores divide transversely. One of each new pair, therefore, must move diagonally from one end of the old valve to the face of the new, elongating at the same time, while its fellow merely elongates to fill the old valve. The movement seems to be a true migration, not simultaneous in all parts of the chloroplast, but progressive while the elongation is going on.—C. R. B.

Coloring matter of tomato.—WILLSTÄTTER and ESCHER[27] have investigated the coloring matter of the tomato and come to the conclusion that it is a compound isomeric with carotin, but not identical with it as other investigators have claimed. The coloring matter, for which they retain SCHUNCK's name lycopin, was extracted from both fresh and preserved tomatoes. The yield from 135^{kg} fresh tomatoes was 2.7^{gm}, and from 74^{kg} preserved tomatoes 11^{gm}. The tomatoes are dried by repeated washing with alcohol, which is finally pressed out. The residue is further dried on a water bath, ground to powder, and extracted with carbon bisulfid, which is driven off under reduced pressure. After being washed with alcohol and petroleum ether, the raw lycopin was most advantageously recrystallized from gasoline. The empirical formula is C_5H_7, and the molecular formula $C_{40}H_{56}$ corresponds with carotin. Lycopin differs from carotin, however, in its crystal form and other physical properties, and in its chemical behavior toward oxygen and halogens. Both substances undergo auto-oxidation, but the quantities of oxygen absorbed differ in the two cases.—H. HASSELBRING.

Plant succession in Nova Scotia.—TRANSEAU[28] has outlined the succession of plant societies found on a portion of the southwestern coast of Nova Scotia. Several lines of physiographic succession have been investigated, and all are found to lead to the Picea formation, a forest association dominated by *Picea mariana* with a small percentage of *Abies balsamea* and *Picea canadensis*. The marine line of succession leads from the Laminaria and Fucus formations through a salt marsh with typical associations passing through an Alnus-Myrica shrub association to the final forest stage. The hydrophytic series has the same fate, the Sphagnum and Larix associations being two stages which usually precede the spruce. From the dry beach with Ammophila and Atriplex the transition is through the Alnus-Myrica association to the Picea forest. The final coniferous association varies considerably in density, but the trees are seldom more than 10^{m} high; geographically it belongs to the author's northeastern conifer forest center.—GEO. D. FULLER.

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[27] WILLSTÄTTER, R., AND ESCHER, H. H., Ueber den Farbstoff der Tomate. Zeit. Physiol. Chemie **64**:47–61. *pl. 1. figs. 1.* 1910.

[28] TRANSEAU, EDGAR N., Successional relations of the vegetation about Yarmouth, Nova Scotia. Plant World **12**:271–281. *figs. 4.* 1909.

Oxidase of Medicago.—EULER and BOLIN[29] claim to have succeeded in purifying and determining the chemical constitution of the oxidase (laccase) of Medicago. The purification was greatly furthered by the discovery that the substance was not sensitive to high temperatures. By boiling the extracted juice, the protein bodies were thrown down, and by treatment with animal charcoal, the dextrin-like substances withdrawn. They concluded that this pure laccase consists of mono-, di-, and tribasic aliphatic oxy-acids. The presence of the citrate, malate, and mesoxalate of this base was certainly established, and it is almost certain that the glycolate is a fourth salt.

They have already[30] shown that various salts of this type will produce oxidations qualitatively and quantitatively, similar to those produced by the laccase of Medicago. They now extend these tests to the new salts found, and to mixtures of the salts, and find marked agreement between the oxidations produced by them and those produced by laccase.—WILLIAM CROCKER.

Origin of the cell wall.—In an extended paper on vegetative cell division in the higher plants, POSTMA[31] pays particular attention to the origin and development of the cell wall. Half of the paper consists of an excellent presentation and discussion of the literature, while the writer's own researches deal with the stomata of *Aneimia fraxinifolia*, root tips of *Allium Cepa*, and stem tips of *Psilotum triquetrum*. In case of the peculiar, isolated stomata of Aneimia, the cell wall is formed as in other vegetative cells, and consequently the problem in the three forms is much the same. While the writer finds that the cell wall arises in greater or less connection with the spindle, the material of the spindle is not believed to furnish all the material for the beginning of the wall. A mother *Hautschicht* splitting into two daughter *Hautschichts*, as sometimes described, could not be found. A single plate with rather small figures is hardly sufficient to illustrate so difficult and so important a problem.—CHARLES J. CHAMBERLAIN.

Seedlings of monocotyledons.—EVANS[32] has undertaken a somewhat extensive study of monocotyledonous seedlings and also of the mature embryos. Not only has the structure at various stages been investigated, but also the effect of deep and shallow seed-sowing. The present paper is a record of some of the results, chiefly those in reference to the "plumular meristem"; and a final paper will review all the facts and suggest the conclusions. The facts are to be used, in part, in connection with the question as to the origin of the lateral position of

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[29] EULER, H., AND BOLIN, IVAN, Ueber die Reindarstellung und die chemische Konstitution einer Oxydase. Arkiv for Kemi, Mineralogi, och Geologi **3**:000. 1909.

[30] ———, Zeit. Physiol. Chem. **51**:80. 1908.

[31] POSTMA, G., Bigdrage tot de Kennis van de vegetatieve celdeling bij de hogere plants. Dissertation. pp. 117. *pl. 1.* Groningen: M. de Waal. 1909.

[32] EVANS, W. EDGAR, On the further development during germination of monocotylous embryos; with special reference to their plumular meristem. Notes Roy. Bot. Gard. Edinburg No. 21:1–21. *pls. 53, 54. figs. 8.* 1909.

monocotyledonous leaves, which involves the nature of the cotyledon and the origin of the stem. The arrangement of the material is in a series beginning with an illustration "in which the leaves always appear lateral, and ending with as extreme a case of stem suppression as possible." The genera presented in the present paper are Asparagus, Ruscus, Danae, Semele, Polygonatum, and Smilax. —J. M. C.

Physcia villosa from North America.—In the HASSE collection of lichens, recently purchased by the New York Botanic Gardens, I found included with the genus Evernia, and labelled *E. prunastri* (L.), a specimen of *Physcia villosa* (Ach.) Duby, collected in 1892 at the Santa Barbara Islands, California, by BLANCH TRASK. The specimen is fertile; the spores normal, bilocular, 5–6 by 13–16 μ. This is the first record for this plant in North America, so far as I am aware. The type came apparently from Peru. Through the kindness of DR. N. L. BRITTON the specimen was forwarded by MR. R. S. WILLIAMS to DR. HASSE, who writes me under date of February 25, 1910: "I have collected the same [plant] near Point Loma, near San Diego, California, and farther north near Newport, Orange Co.—R. HEBER HOWE, JR., *Thoreau Museum, Concord, Mass.*

The resting nucleus.—In discussing the structure of the resting nucleus ROSENBERG[33] pays particular attention to the occurrence of distinguishable chromosomes in the resting cells of various parts of plants of several families. These chromosomes, or "prochromosomes," the existence of which has been denied by some writers, he now identifies in about forty new cases, figuring the debatable structures in Nuphar, Helianthus, Atriplex, Lupinus, Pinguicula, and Drosera. The paper is an added argument for the theory of the individuality of the chromosome.—CHARLES J. CHAMBERLAIN.

Morphology of Geissoloma.—STEPHENS[34] has studied the embryo sac and embryo of *Geissoloma marginata*, a small shrub of southwestern South Africa, and representing a family (Geissolomaceae) closely related to Penaeaceae, whose genera he had investigated previously. It proved to be "normal" in these structures, showing none of the peculiarities of Penaeaceae. In general, the results showed an embryo sac derived from one of a row of megaspores, very evanescent antipodal cells, a pear-shaped (later spherical) proembryo, and no suspensor.—J. M. C.

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[33] ROSENBERG, O., Ueber den Bau der Ruhekerns. Svensk. Bot. Tidskrift **3**:163–173. *pl. 5.* 1909.

[34] STEPHENS, E. L., The embryo sac and embryo of *Geissoloma marginata.* New Phytol. **8**:345–348. *pl. 6.* 1909.

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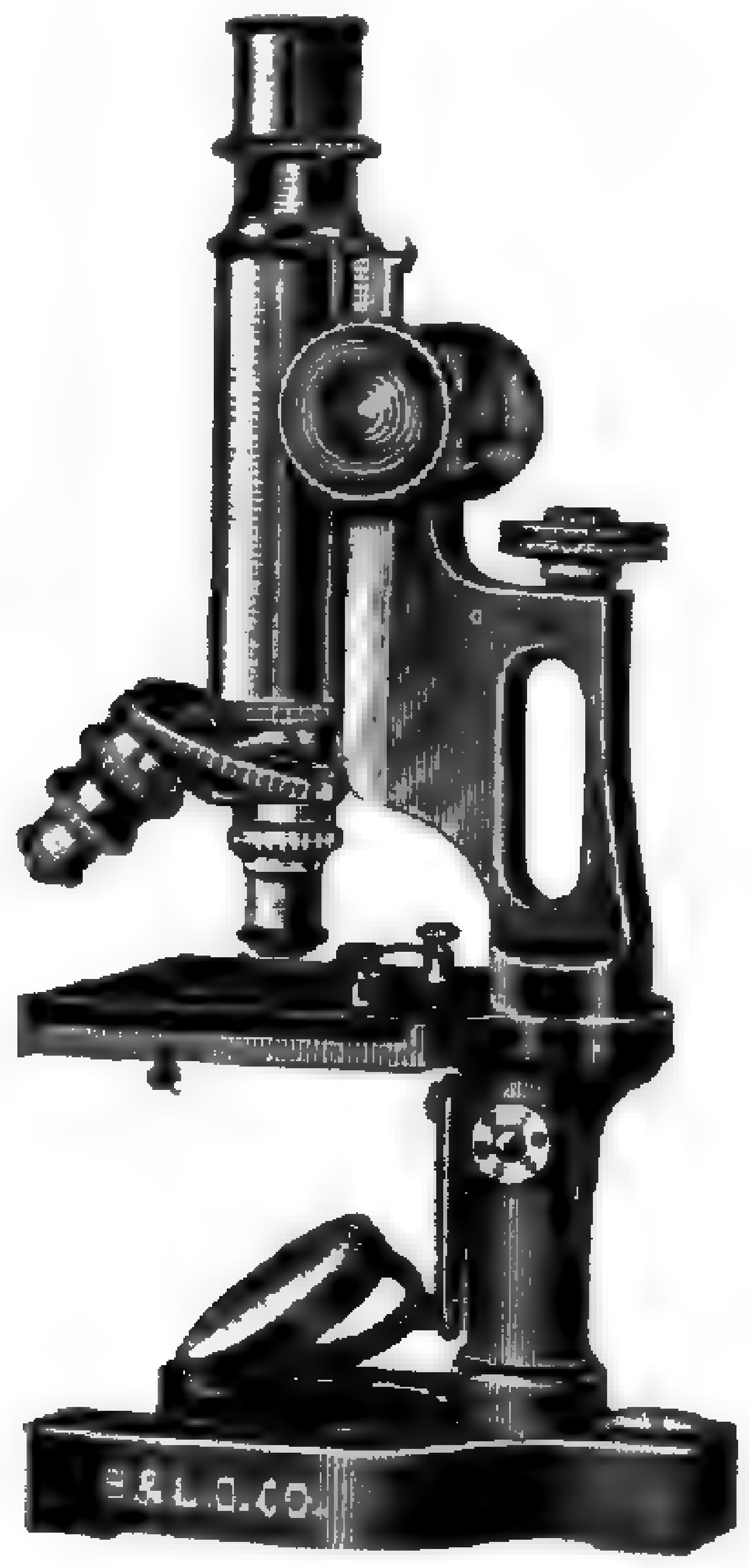

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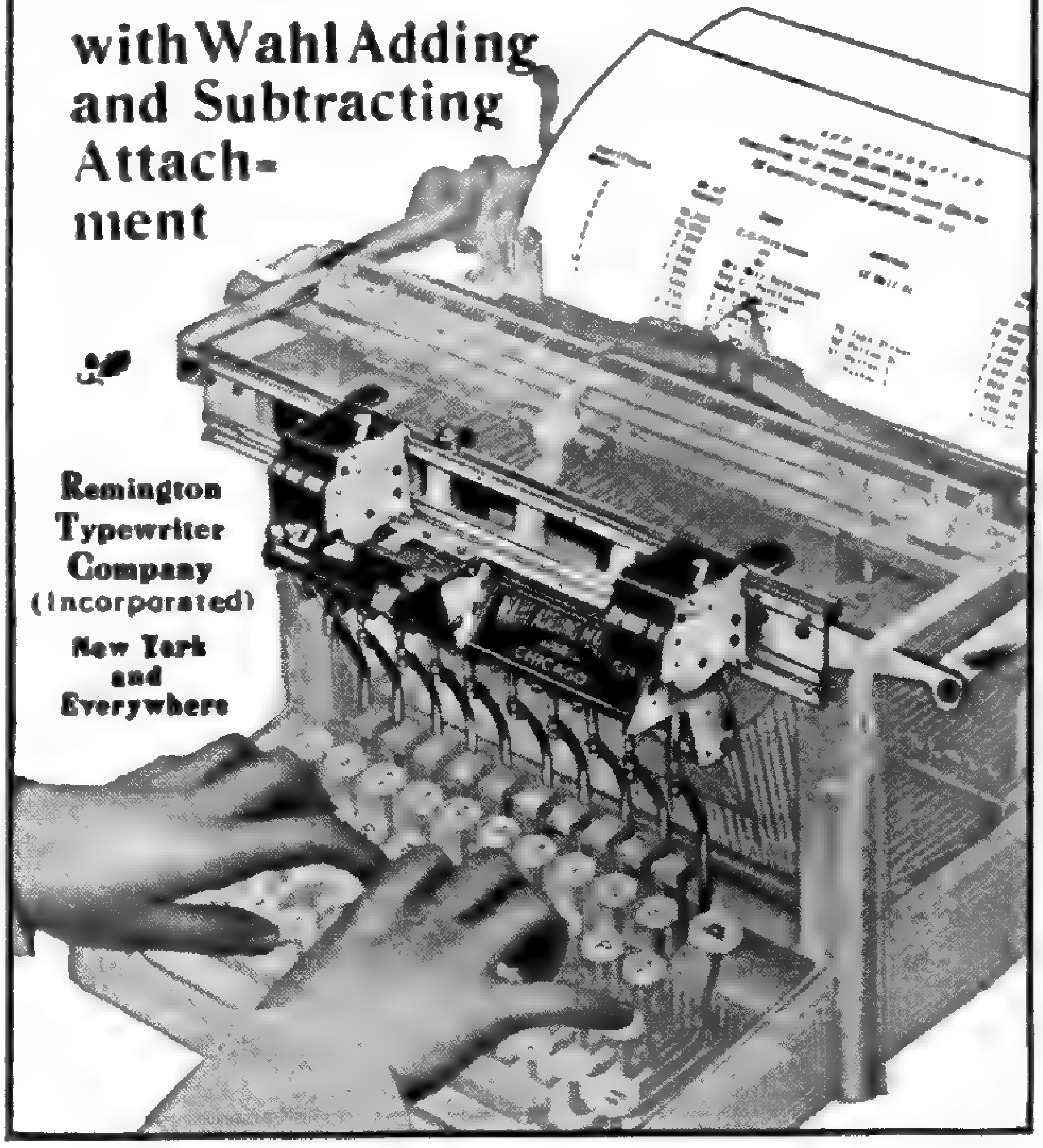

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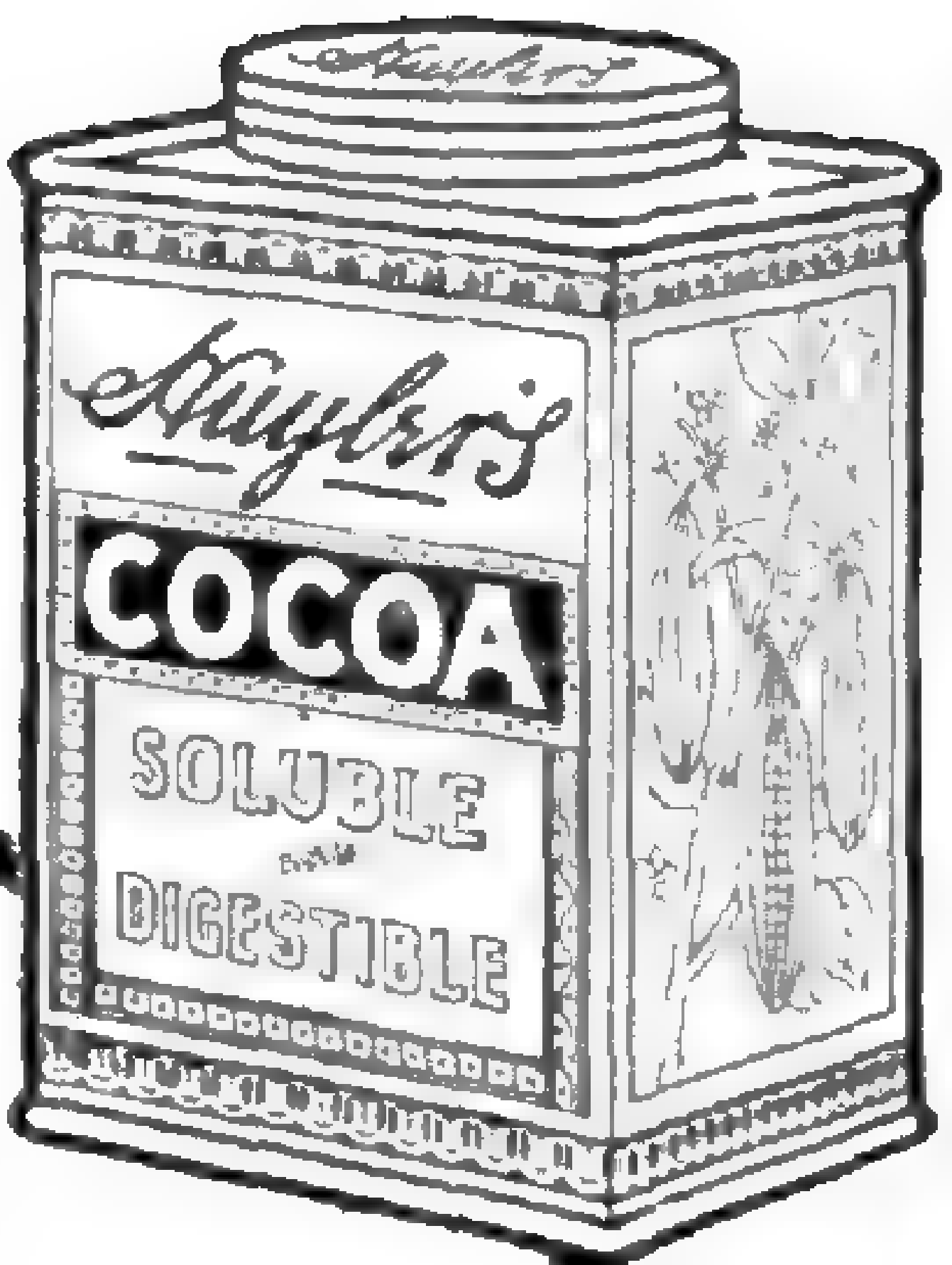

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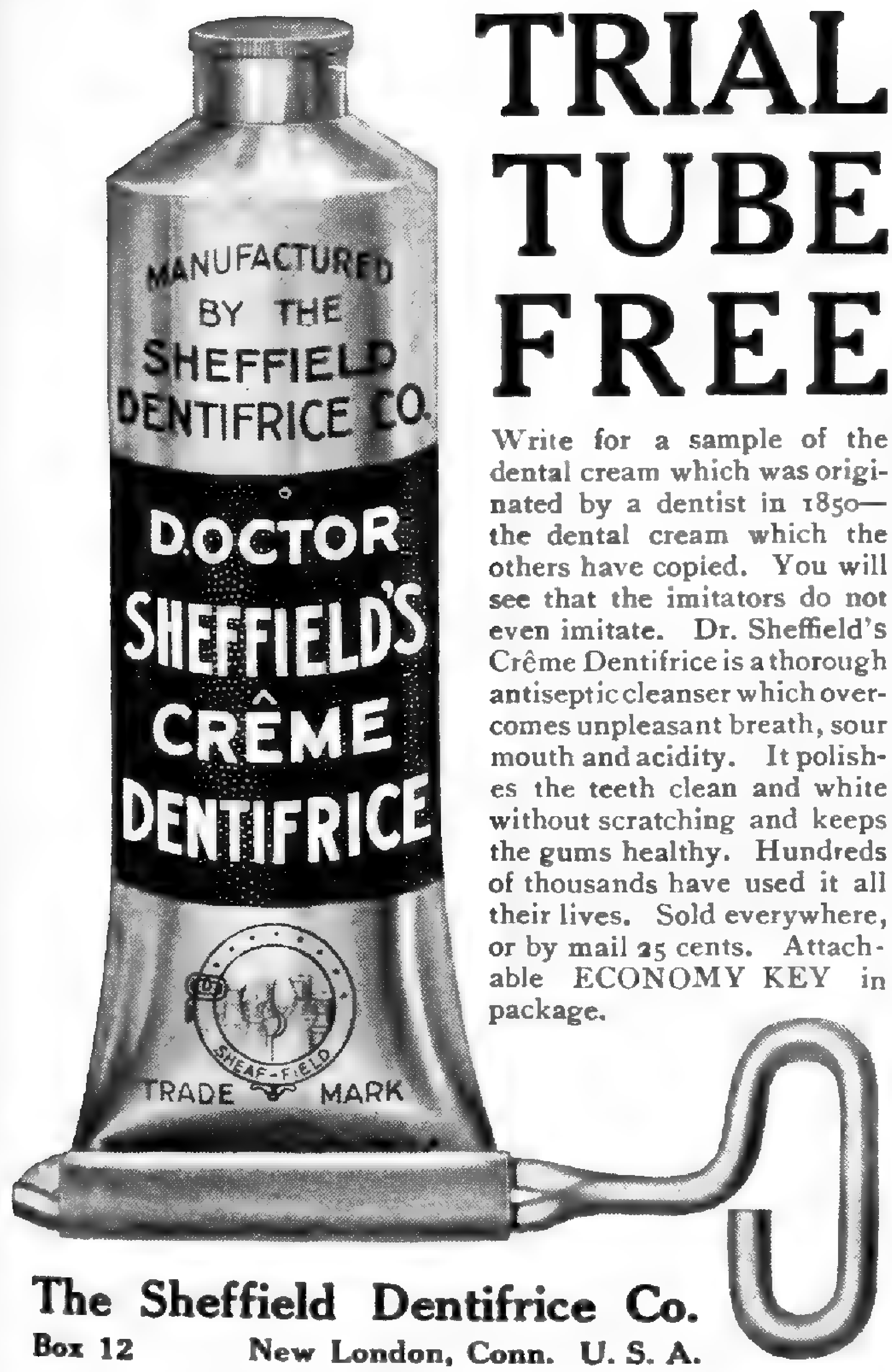
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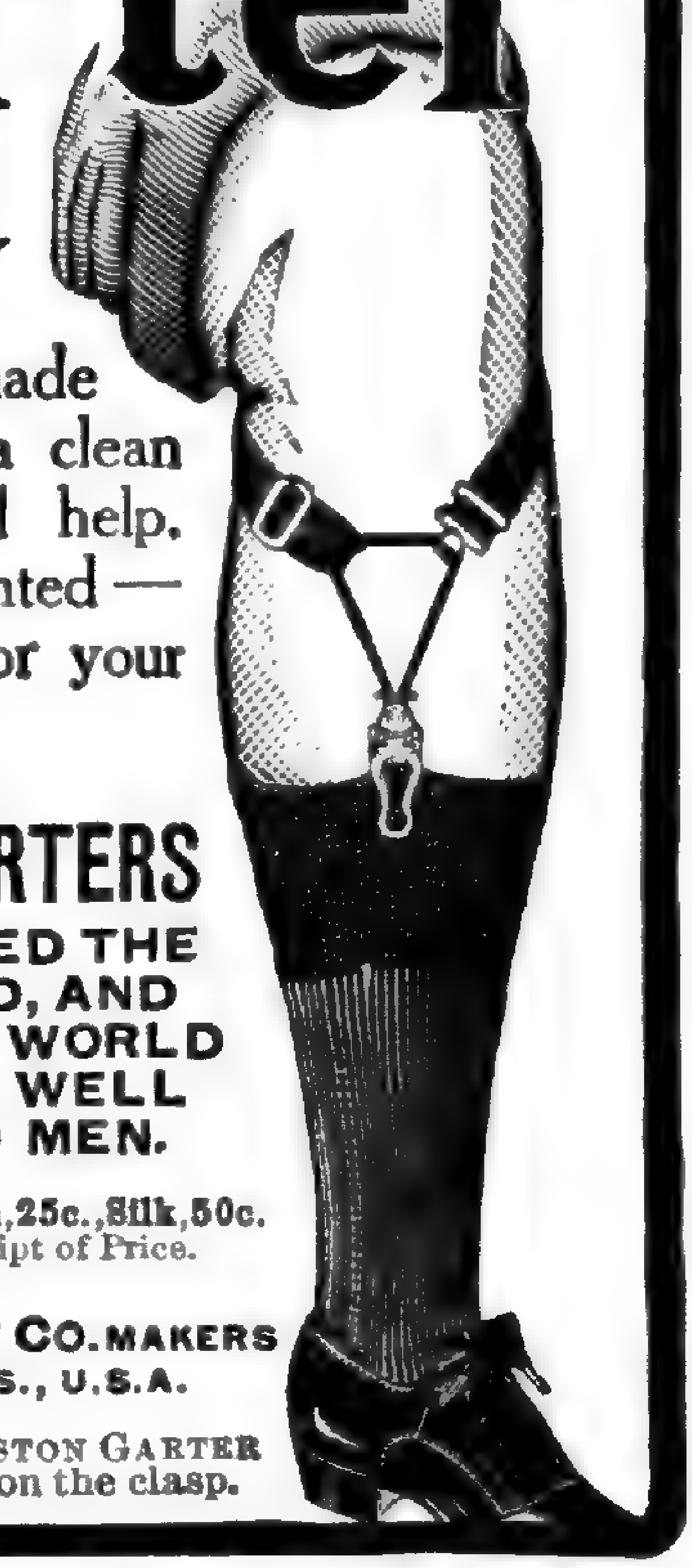

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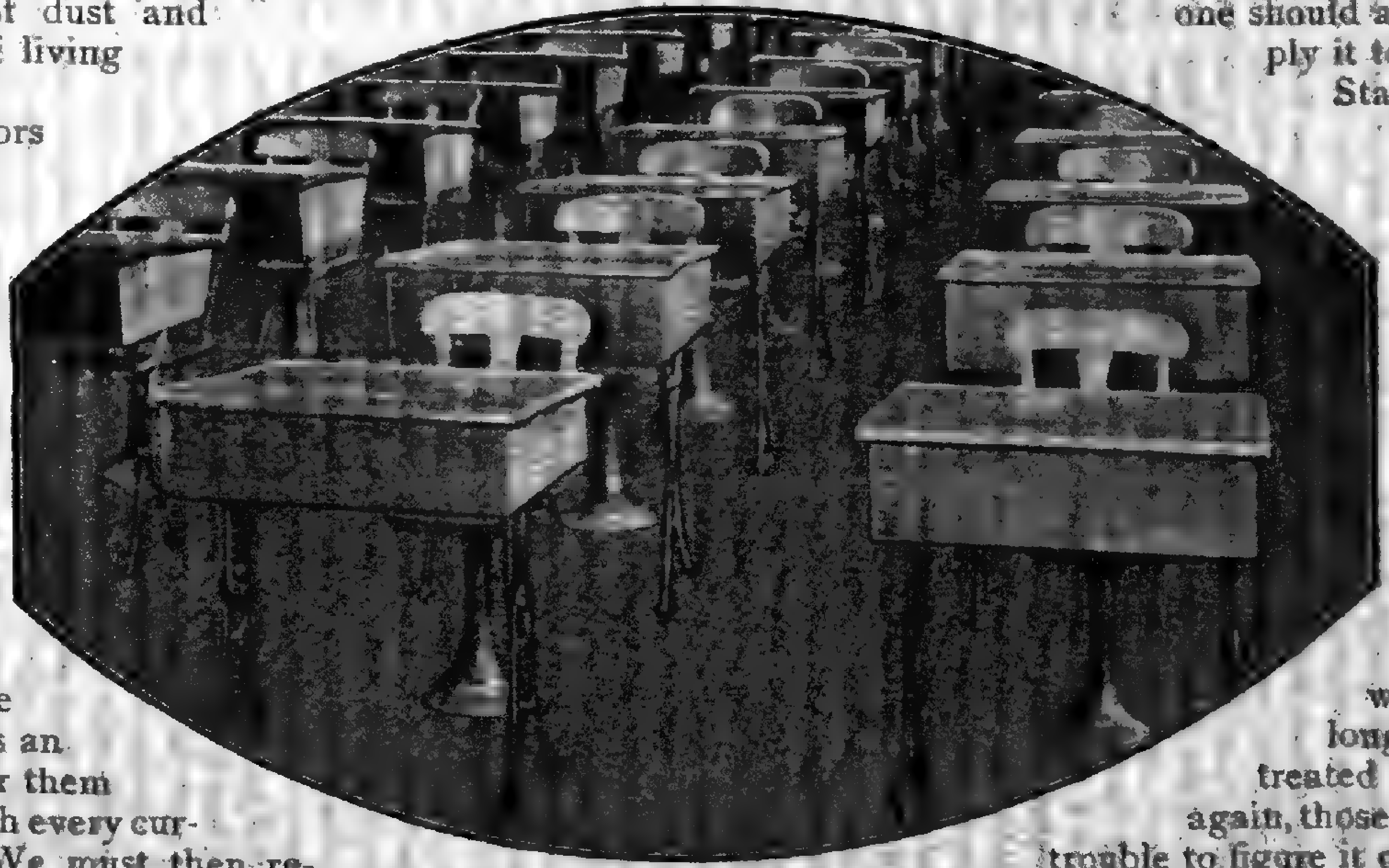

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Vol. XLIX No. 5

THE
BOTANICAL GAZETTE

May 1910

Editors: JOHN M. COULTER and CHARLES R. BARNES

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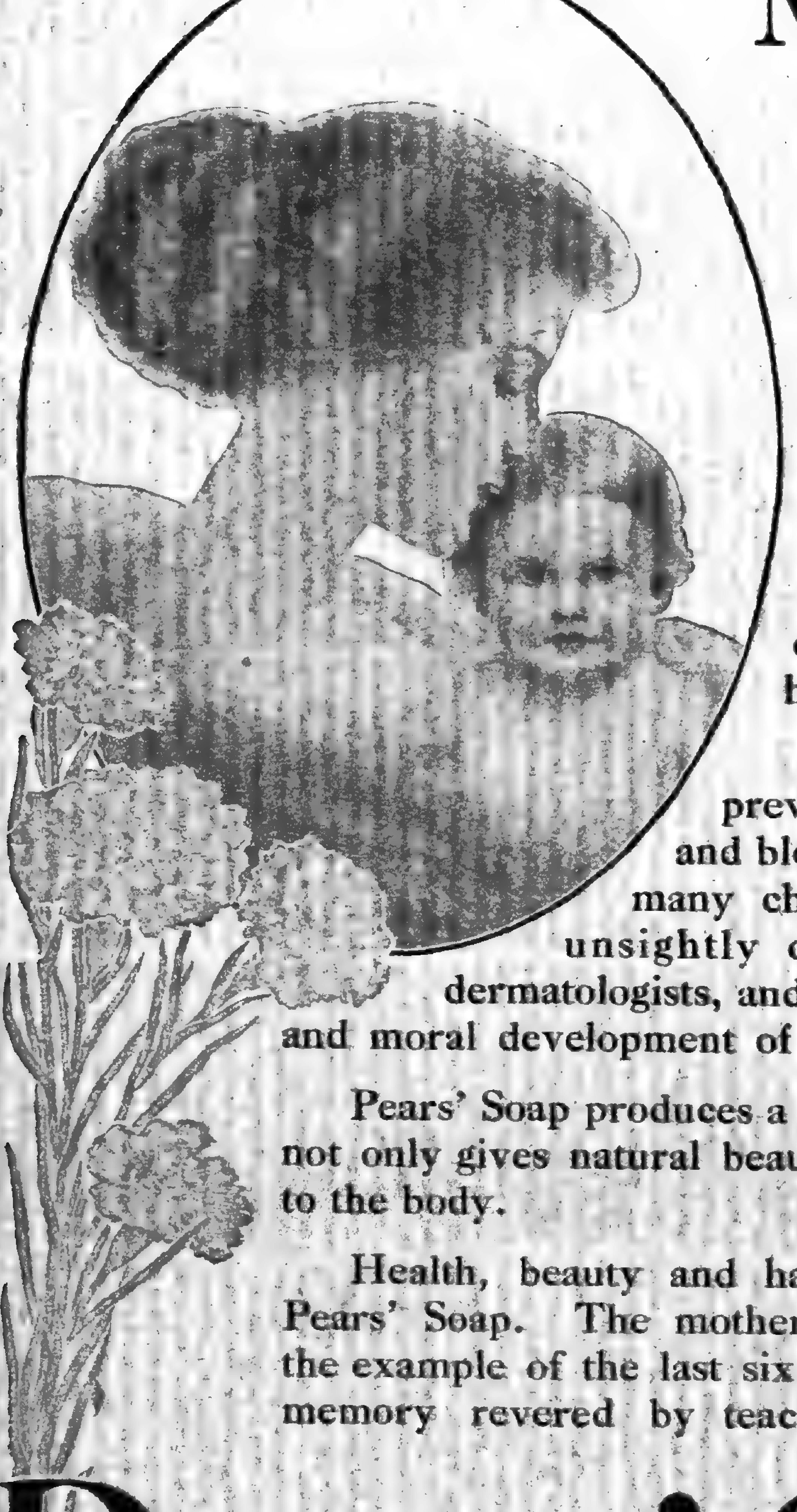

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Edited by JOHN M. COULTER and CHARLES R. BARNES, with the assistance of other members of the botanical staff of the University of Chicago.

Issued May 17, 1910

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C R Barnes

VOLUME XLIX NUMBER 5

BOTANICAL GAZETTE

MAY 1910

CHARLES REID BARNES

(WITH PORTRAIT)

CHARLES REID BARNES was born at Madison, Indiana, September 7, 1858, and died at Chicago, from an accidental fall, February 24, 1910. He graduated at Hanover College in 1877, and afterward studied at Harvard University, where he secured the friendship of Professor ASA GRAY. After teaching in the public schools for a few years, he became professor of botany at Purdue University in 1882. In 1887 he was called to the University of Wisconsin, and for eleven years developed and maintained a vigorous department of botany in that growing institution. In 1898 he became professor of plant physiology at the University of Chicago, and completed twenty-eight years as a university professor. At Hanover College he met Professor COULTER as his instructor in botany, and from that time they became intimately associated, first as joint editors of the BOTANICAL GAZETTE, and later as colleagues in the same university.

He was always active in scientific societies, and the esteem in which he was held by his colleagues is indicated by the positions he held. He became a member of the American Association for the Advancement of Science in 1884 and a fellow in 1885; was secretary of the botanical section in 1894, secretary of the council in 1895, general secretary in 1896, and vice-president (chairman) of the botanical section in 1898, giving his retiring address at Columbus in 1899 on "The progress and problems of plant physiology." He was secretary of the Botanical Society of America from its organization in 1894 to 1898, and became its president in 1903, giving his retiring address at Philadelphia in 1904 on "The theory of respiration." In 1905 he was a delegate from the botanical section of the

American Association to the International Botanical Congress at Vienna.

As a teacher Professor BARNES had few equals. There was a clearness and precision in his statements that left nothing to be desired. This power of presentation was reinforced by a personality so winning, on account of its brightness and friendliness, that students were attracted not only to the subject, but also to the man. This is teaching at its highest level, and his many students throughout the country are feeling the loss of a friend of powerful personality even more than of a teacher of unusual ability. His power of training men was conspicuous, and his critical sense was an unusually valuable asset in a department active in research. An investigation or a thesis which had run the gauntlet of his frank and keen criticism was equipped to face the public.

In 1883 Professor BARNES became coeditor of the BOTANICAL GAZETTE, and for twenty-seven years filled this position with remarkable efficiency. He had the editorial genius, which entered into every detail, from general policy to printing. He was complete master of all the details that belong to such work, and was continuously solicitous as to form, accuracy, and high standards of every kind. He was especially expert in the work of illustration, and with remarkable patience corrected the blunders of inexperienced or careless contributors. The laborious work of editing manuscripts and illustrations obtains little or no public recognition, but in his work as a reviewer Professor BARNES achieved high reputation. He grasped the significant things and presented them with a clearness and a force that is unusual. Moreover, he felt keenly his responsibility to the readers of the journal and to his science, and let no doubtful results or inferior work slip by without incisive comment.

As a writer Professor BARNES was not voluminous, but very effective. He never wrote for the sake of writing, but because he had something to say. He had a style and a grasp that are sadly lacking in most scientific writing today. He felt that clear statement comes naturally from clear understanding, and that muddy statement throws suspicion on the understanding. When the organizing instinct of the teacher deals with clear and sharp-cut statements, the result is a presentation that is a real contribution not only to knowledge, but also to good writing. Aside from his work as editor and reviewer, his botanical writings fall into four categories.

1. Textbooks.—Professor Barnes played an important part in the development of laboratory work in this country. The spirit of the *Lehrbuch* of Sachs had been introduced into this country by Professor Bessey, but many teachers at that time needed specific directions for studying the material called for. To meet this need, the then editors of the Botanical Gazette, Professors Arthur, Barnes, and Coulter, prepared the *Handbook of plant dissection*, which was published in 1886. The accident of the names of the joint authors and the sequence of their parts in the book led to its informal designation as "the A B C of botany." Through the whole period of laboratory organization and development this book played its part as a guide, and through it the teaching power and technical facility of Professor Barnes reached the teachers.

In 1898 he published his *Plant life*, a textbook for secondary schools. This was about the first text in this country that recognized physiology and ecology as subjects for study in secondary schools, and was considerably in advance of the preparation of the teachers. A briefer edition appeared in 1900, entitled *Outlines of plant life*.

His ripened experience as a teacher and an investigator had just expressed itself in a textbook on plant physiology for college use. He was permitted to read the final proofs, so that the work will appear just as he had it in mind. This will stand as a permanent record of his point of view, of his characteristic and telling way of putting things, of his critical analysis of difficult problems and doubtful situations.

2. Taxonomy.—Like almost every American botanist whose training began thirty years ago, his first contact with the subject was through the Gray texts, and his first interest was in local floras. Various small papers were published, but soon the mosses attracted his attention as a group needing investigators at that time. Perhaps his first general recognition among botanists came through his taxonomic work on this group, the most important publications being *Analytic key to the genera of mosses* (1886); *Revision of the North American species of Fissidens* (1887); *Artificial keys to the genera and species of North American mosses* (1890), revised in col-

laboration with HEALD in 1897; and a series entitled *Notes on North American mosses* in the BOTANICAL GAZETTE, leading to a revision of Dicranum in collaboration with TRUE.

3. PHYSIOLOGY.—The chief contributions of Professor BARNES in plant physiology were as a critical reviewer, a teacher and effective guide in research, and a sponsor for certain points of view. He was an early champion of the restricted use of the term plant food now generally held; advocated many years ago the use of the term photosynthesis (or photosyntax), in place of assimilation, for the first stages of food-making; and consistently advocated the restriction of sex terms to sex organs. The vice-presidential address of 1899, and even more the presidential address of 1904, gave stimulating points of view much in advance of current usage. To few is given the ability to make so clear the actual status when the subject is foggy and uncertain, as is the case in so many regions of physiology.

4. MORPHOLOGY.—After his removal to Chicago, Professor BARNES became greatly interested in the special morphological problems presented by the bryophytes, and for a number of years offered courses in the subject, in cooperation with Dr. LAND. In connection with this work, Drs. BARNES and LAND made extensive field studies and collections in Mexico in 1906 and 1908. There had already appeared two joint papers, one on *The origin of air chambers,* and the other on *The origin of the cupule of Marchantia.* Several other joint papers are in various stages of preparation, and are to be issued by the junior author. It was planned that this series of studies should lead to the preparation of a general work on the special morphology of bryophytes.

The intellectual horizon of Professor BARNES swept in a much larger circle than his professional subject. No man had wider interests, or brought to them a saner mind. There was no assurance or dogmatism on the one hand, or no wabbling uncertainty on the other. The whole mental attitude was judicial, one of perfect poise, friendly to truth from every direction; and the judgment was clean cut, but never final. His loss to his department, his university, and his science is irreparable, for although institutions and subjects outlive their men, a resource that may be replaced in amount, but never in kind, has now become a memory.

PHYSIOLOGICALLY ARID HABITATS AND DROUGHT RESISTANCE IN PLANTS[1]

ALFRED DACHNOWSKI

In the course of the investigations on the ecology of a local bog, the trend of the work has invited a closer consideration of a number of points of interest to a physiologist. The importance of these in life processes has been the occasion to offer, in the following, a statement of at least the more special cases.

In previous papers (this journal) attention has been called to the fact that the physiological effect of bog water and bog soil to a great extent plays an important primary rôle in the determination of the flora which can best succeed in bogs. It was shown that a number of cultivated plants and plants from different but neighboring habitats in the same locality fail to develop normally when grown in the bog or under laboratory conditions, and that the toxicity of the habitat appeared, therefore, to exert a marked influence in determining not only the character but also the distribution of plants within the same habitat. A difference was shown to exist between different species in their power of resistance to the toxic action of the substratum, so as to leave no doubt that some species of plants are better adapted than others to growing in soils containing relatively large amounts of these toxins. It was further shown that in the effect of a salt of calcium, and especially in the presence of a number of insoluble adsorbing bodies, these differences are much less pronounced, and that the substances tend very greatly to diminish, not only the difference between different species as to their tolerance, but also the differences in physiological aridity existing between different zones within the same habitat. With the establishment of certain definite relations between toxicity and physiological behavior of plants, it seemed desirable to study somewhat more closely the nature of the resistance in bog plants to toxicity, and consequently to physiological drought.

One of the most effective methods of dealing with the problem,

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[1] Contribution from the Botanical Laboratory of Ohio State University, 55.

and one which is particularly apropos at this time, is the study of the character and the development of drought resistance in bog plants. This should naturally be the first consideration. Too little experimental information is available in the whole field of plant responses, whether as adjustments or adaptations, and our knowledge of plant problems connected with resistance in plants to sterile soils or to unfavorable climate is particularly limited. The modifications of structure which can be attributed to the action of these and other environmental factors are well known, and may be referred to structures serving to reduce the evaporation of water from leaves. The necessity for such protection in bog plants is the greater, not on account of the fact that the vegetation is directly exposed to the drying effect of wind, to lower humidity, and to stronger light, but because roots absorb water with difficulty when it contains any considerable percentage of toxic ingredients. Unless bog plants differ from other plants in some phase of root function, the amount of transpiration must be kept low by structural modifications, that is, in order to compensate a reduced absorbing activity of the roots, the escape of water from the shoots must be correspondingly checked. It is unnecessary here to cite in detail the structural modifications in bog plants that are effective in diminishing transpiration: the general reduction in size of the leaves; the thick-walled epidermis and hypodermal tissues, reinforced by cuticle, wax, and hairs; the mucilaginous and resinous bodies found in roots and leaves; and the prevailing grasslike form are well-known characteristics. But much of the local bog vegetation exhibits little or no xerophytic structure. In some places the outermost growth which immediately borders the open water is, indeed, for the most part hygrophile. It is dominated, in part, by *Typha latifolia*, forming sometimes a nearly pure association. *Sagittaria latifolia, Pontederia cordata, Peltandra virginica, Decodon verticillatus, Polygonum hydropiperoides,* and others are ordinarily abundant with Typha. The xerophytic quality is least marked in this vegetation. Differences such as these must arise strictly from the edaphic causes, which seem to set a natural and inevitable limit to what may be accomplished through invasion. There is but one important point of difference between the environment of the bordering vegetation and that of the bog plants occurring more centrally on the island, and that is the relative absence of toxic ingredients in the water and in the upper limits of the substratum. The transpiration quantity of such hydrophytic plants is correspondingly less when grown in bog water from the central habitat. The low rate of transpiration can be increased again with the addition of adsorbents, or with the dilution of the bog water to a point no longer fatal in its effects. The peat substratum of the border zone permits, on that account, a dense luxuriant growth of hydrophytes, and neither a smaller percentage of free oxygen in the water, nor the absence of a mineral soil, nor the incoherency of the substratum affords precarious conditions for growth.

How much of the salts dissolved in the lake water is retained by absorption in the humus soils along the margin of the bog has not been determined. There is usually a slight difference between the total mineral content of bog water and that of the lake water adjoining. The figures obtained, however, are not high. The osmotic pressure and the acidity have been found to be the same for both habitats. The stress laid by various authors upon the relation of these two factors to plant societies in bogs, in so far at least as this region is concerned, will not hold. They are not the factors in the selection and distribution of species.

Water culture experiments are here considered as giving a relatively normal indication of conditions obtained in the bog, since the bog island itself is merely a water culture on a larger scale, with the mineral soil at a depth of more than 10^m from the surface vegetation. In the bog habitat of the island, however, the ratio between the amounts of water absorbed and transpired is never constant. It varies most during the growing season, and yet it must be always more than unity, if the plants are to survive the occasional periods of extreme physiological drought during the summer and autumn months. This is evident in the scattered small trees of *Acer rubrum*, *Rhus vernix*, and in *Cephalanthus occidentalis*, *Osmunda cinnamomea*, and other plants from the adjoining relatively forested maple-alder zone. The stunted growth of these plants, their numerous dead branches, and ragged crown of foliage exhibit to a marked degree the physiological action of the substratum. The resistance offered by the invading mesophytic vegetation is, indeed, but slightly effectual. The relative power in the bog plants for absorbing or rejecting the various injurious constituents of bog water and bog soil is here the controlling factor. This regulatory compensation within certain limits, therefore, is of utmost importance in these species, for we have here an instance of the fact that while the presence of structural modifications is generally regarded as a circumstance in favor of a bog vegetation, the most noteworthy characteristic is the ability to neutralize the injurious action of the substratum. In so far as the adjustments arise through resistance to toxicity and consequent drought, one is painfully aware that neither the nature of the drought resistance, its origin, its specific governing factors, nor the specific type of resistance involved in the adaptation of plants to toxic bog conditions is known.

Another matter of fundamental importance is the degree in which this drought resistance in physiologically arid habitats varies, and the extent to which it is inherited. That activities are not constant but variable in degree and in kind, and that functional characteristics in plants are transmitted as effectively as habit of growth, form, flower, and seed, is generally admitted. The conditions of life in bogs are always active in stimulating or depressing normal functions, and they are not without effect upon their degree and character as well. The disturbing effect of adverse conditions, if not too severe, may be gradually overcome through variations in the degree of activity. Often the unfavorable external conditions are conducive to the development of a new *place-function*, and the immunization may extend to the point that would be fatal at the outset. Thus plants reared in a gradually intensified toxic solution have reached a power of resistance above that of the organisms under normal conditions. It seems possible to raise forms in which the special resistant power becomes a permanent hereditary character. Phenomena such as these are remarkable for what they suggest rather than for conclusions that can be positively drawn, since the degree of resistance which plants acquire by external or other influences to poisons and drought, or to other adverse conditions of life, may be one in which the activities are modified, resulting, as has been stated, in a new place-function, or one in which the plants succeed in resisting the changed conditions through greater elasticity in functions. A knowledge of the limits of functional variation within species, therefore, is very essential. Deviations in the very functioning of the process, and in transmission as well, cannot but be fruitful in a greater efficiency of responses in plants, and without doubt these are the differences that go far toward constituting the essential difference between relative power of endurance and resistance against drought, disease, or abnormal conditions in any plant. The circumstances under which bog plants can function unaltered, either in character or degree, and the limits beyond which such functions must cease or become altered, are questions of special significance in physiological ecology. They throw no little light upon the nature of tolerance and drought resistance, a topic upon which information is sorely needed if we are to regard functions no less important in the light of development and heredity than form or structural organization.

Of still greater consequence is the study of such limiting factors of soil and climate as operate to preserve adapted forms, or eliminate species in which the responses fail to secure better adaptation to the factors provided by a local region. The presence and fitness of bog plants and of invading hydrophytes and mesophytes resistant to physiological drought seem to be due mainly to more efficient responses to edaphic conditions. In most cases, at least, drought resistance involves a specific reaction on the part of the plant to more than one factor of the physical and biotic environment, the ratio between the factors in the process being more significant than the structural modifications or the regulatory compensation which may be possible within the plants. The reaction may be in part one of structural differences, and in part one of endurance. The evidence cited in the work published, and experiments now in progress indicate that drought resistance in physiologically arid habitats is due to a specific protective functional root activity. It is fundamentally a chemical reaction, but one too complex to solve by ordinary methods of chemistry. The delicacy of the reaction may be better understood if we recall the fact that it is adjusted to meet a specific limiting condition. Whether the toxic action of bog water and bog soil is determined by the action of one constituent, or by the combined action of several, needs more detailed study. As has been noted elsewhere, the toxicity of any bog soil is but a function of the number of the conditions of its development, and of the physiological efficiency of these factors.

Recent work of an experimental nature with cultures of isolated bog bacteria has shown that the injurious products of the bacterial bog flora accumulating in definite layers of the peat substratum are the leading factor to be considered in the physiological aridity of the local study. The observation was made that a sample of bog water in a well-corked glass jar, when kept in the dark at 20–25° C., soon shows the formation of methane and other gases, and that in a few weeks a thin surface layer becomes noticeable made of up bacteria imbedded in a matrix. Exclusion of air prevents further growth of aerobs, for in flasks with narrow necks and closed with a cotton plug a surface growth is never evident. The breaking down of organic matter by bacteria seems to involve, therefore, not only the growth and multiplication of the agents of decomposition, but also an accumulation of by-products which soon decreases the rapidity of aerobic bacterial action. Facts to justify the position as to the presence of a constituent that imparts an antiseptic action to bog water and bog soil are still lacking, but there is sufficient experimental evidence to justify the statement that the bacterial flora has the greater share, not only in the formation of these toxins, but also in the slow and partial decay of bog and swamp plants, that is, in the formation and preservation of peat. An attempt has been made to study the physiological reaction of the products formed from the activity of single isolated species, as well as the effects of the residual products due to mixtures of bog bacteria. Without going into too much detail it is sufficient to point out here the following:

From a fresh sample of bog water and bog soil dilution cultures were prepared. The isolation of the various species was continued upon peat-agar plates, and later in test tubes containing a beef-broth-agar medium, until from the bacterial colonies which appeared upon them, pure cultures were obtained. About 35 different species of bacteria have thus far been isolated. The organisms belong for the most part to the aerobs. Of the bacteria thus isolated, 21 were tested for their toxin-producing power upon a sterilized solution of bog water and peat. A number of flasks of a liter capacity containing the sterilized solution were then inoculated with the respective pure cultures. Several flasks were left sterile to serve as controls, while others were inoculated with a mixture of the various species and with the bacteria found in 1^{cc} of fresh bog water. An additional test condition was arranged at the same time from the normal untreated bog water. All flasks were placed in an incubator for a period varying from two to four or six weeks, and at such times were then brought to the laboratory. All physiological tests were made in duplicate series, and the greatest caution was observed to reduce the dangers of contamination during the preparation of the cultures. Wheat seedlings germinated in sterilized quartz and carefully washed in distilled water were used as indicators. They were transplanted to half-liter "Mason" jars in a manner as described in previous papers.

From the data at hand the following have been selected to illustrate the variation in virulency of bacterial products. Using the transpiration of the controls as a basis, and representing it as 100, the different bacterial cultures have values in the order as indicated in the last two columns of the tables below.

These figures show conclusively that in all cases the bacteria are responsible for the proportionally diminished transpiration and growth of the wheat plants. In all cultures the transpiration values lie below that of the control, varying from 20 to 52 per cent. The evidence derived from the duplicate series is omitted in tables II and III, showing as it does results closely parallel.

More recent experiments with pure and mixed cultures of bog bacteria confirm the earlier experiments as to the ability of these organisms to increase the amount of toxins present in the peat substratum. These results are significant in that they demonstrate the active participation of microorganisms in bog habitats, a fact contrary to the position taken by FRÜH and SCHRÖTER, who regard the bacterial influence as very small. To what extent the tables suggest the possibility that bacterial diagnosis when correlated with physiological criteria may determine the crop-producing power of different agricultural soils need not be discussed here.

Chemically peat is made up of substances which are commonly classified among the dehydration products of the carbohydrates. The analyses which have been made agree in showing that the phosphoric acid content of peat soils is high and partially in an available condition for plant use. In potassium content they are deficient; potassium salts are generally added in an alkaline form in order to produce crops. In nitrogenous materials peat soils are unusually rich, but the nitrogen remains bound up in organic compounds unavailable for the growing cultivated plants. In order to determine the ability of the microorganisms to convert soluble proteids into amido-acids and allied products of the disintegration of proteids,

TABLE I

TRANSPIRATION DATA FOR SOLUTIONS INOCULATED WITH PURE CULTURES OF BOG BACTERIA

SERIES III	BACTERIA	TRANSPIRATION IN GRAMS				COMPARATIVE TRANSPIRATION	PERCENTAGE OF DECREASE
		5th day	10th day	15th day	Total		
	Control	9.33	42.92	66.85	119.10	100	0
	B. 20	8.85	41.30	44.06	94.21	79.10	20.90
	B. 22	8.30	38.15	42.90	89.35	75.02	24.98
	B. 7	8.55	31.80	42.80	83.15	69.81	30.19
	C. 3	7.15	30.90	43.95	82.00	68.85	31.15
	C. 4	7.60	29.70	44.40	81.70	68.59	31.41
Duplicate series....	Control	8.80	44.50	66.83	120.13	100	0
	B. 20	8.40	34.25	45.98	88.63	73.77	26.23
	B. 22	7.05	35.40	46.10	88.55	73.71	26.29
	B. 7	8.15	34.45	42.21	84.81	70.59	29.41
	C. 3	8.10	30.90	44.25	83.25	69.30	30.70
	C. 4	8.40	31.15	41.65	81.20	67.59	32.41
Atmometer..		102 gr.	136 gr.	125 gr.			

TABLE II

TRANSPIRATION DATA FOR SOLUTIONS INOCULATED WITH PURE CULTURES OF BOG BACTERIA

SERIES VII	BACTERIA	TRANSPIRATION IN GRAMS				COMPARATIVE TRANSPIRATION	PERCENTAGE OF DECREASE
		5th day	10th day	15th day	Total		
	Control	17.65	36.20	36.60	90.45	100	0
	Bog water	7.65	11.30	8.90	27.85	30.79	69.21
	B. 25	18.15	29.30	26.85	74.30	82.14	17.86
	Bg. w. 1^{cc}	18.27	30.15	25.70	74.12	81.94	18.06
	B. 13	15.72	24.65	30.85	71.22	78.74	21.26
	B. 2	17.45	29.05	24.30	70.80	78.27	21.73
	B. 1	16.60	28.95	24.85	70.40	77.83	22.17
	B. 27	12.60	24.90	22.80	60.50	66.66	33.34
	B. 6	14.00	25.40	20.80	60.20	66.55	33.45
	B. 4	14.95	23.80	20.45	59.20	65.46	34.54
	B. 29	11.60	15.55	15.85	43.00	47.54	52.46
Atmometer..		114 gr.	117 gr.	102 gr.			

enough pepton was added to sterilized solutions to make an equivalent of a 1 per cent pepton culture. After sterilization the solutions were inoculated with the bacteria indicated in table III. The cultures were tested physiologically at the end of a two-week incubation period. Since the danger of contamination in pepton cultures becomes increasingly greater, the transpiration figures for only the first five days are tabulated. The wheat plants had grown in each experiment for three days when they were photographed.

TABLE III

TRANSPIRATION DATA FOR 1 PER CENT PEPTON CULTURE SOLUTIONS, INOCULATED WITH BOG BACTERIA

Series IX	No.	Bacteria	Transp. (5th day), in grams	Comparative transpiration	Percentage of decrease
	6	Control	17.65	100	0
	7	Pepton check	7.00	39.65	60.35
	13	B. 13	4.85	27.47	72.53
	14	B. 25	2.70	15.30	84.70
	11	B. 2	2.30	13.03	86.97
	12	B. 4	2.40	13.60	86.40
	15	Bg. w. 1^{cc}	1.87	10.60	89.40

A brief inspection of the figures suffices to show that transpiration, growth, green and dry weight of plants are in this case proportionally reduced. The mixed culture solution (Bg. w. 1^{cc}) in which the percentage decrease in transpiration is as low as 90, seems to show that it is the function of some of the bacterial organisms to do the initial work of rendering soluble the protein compounds in a peat substratum. The process of denitrification is carried on up to a point where the products become further decomposed by other organisms. A whole series of bacteria, therefore, seems to be involved, to which are due the residual products, the sum of which in part constitutes the toxicity of the habitat encountered on Cranberry Island, the formation of methane gas, and the reactions which form the basis of the process of humification.

At the end of the experiment a chemical examination of these culture solutions indicated the presence of indol, ammonia, and various non-volatile products in various proportions. A marked difference was noted in the ability of the different species of bacteria to produce indol and ammonia. The highest quantity of ammonia was produced by B. 13; the least amount was recorded for Bg. w. 1^{cc}, the culture solution, it will be remembered, which consisted of a mixture of the bacteria found in 1^{cc} of fresh bog water. None of these products were found in the control (sterilized bog water and peat). It is also to be noted that in the various pure bacterial cultures neither the organic acids nor the ammonia underwent a further change; in the mixed cultures, however, the decomposition continued, the amido-acids being formed to ammonia and to compounds of the fatty acid series. The extent to which the latter substances may be still further disintegrated to carbon dioxid, hydrogen, and methane is now being determined. Thus far the isolation of bacteria involved in the decomposition of carbohydrates has not been successful. Certain microorganisms have been found to possess the ability to dissolve cellulose (filter paper) in the presence of air. To what extent these forms and the anaerobs play à rôle in the relation of deleterious products in the soils and the cultivation of crops is still uncertain. In a previous paper (BOT. GAZETTE **47**:400. 1909) the writer has reported that the poisonous matter injurious to plant growth is present in the agricultural soils used as filters for bog water. The retardation seen in the contaminated soils lacked the corresponding control average in dry weight of plants to an amount of 18 per cent, 3 per cent, and 36 per cent, for sand, clay, and humus soil respectively. It was further shown that the absorption and retention capacity of soils for toxins became generally higher the greater the content in humus.

In concluding this part of the discussion it is well to note the extent to which the results show clearly that, in the laboratory cultures at least, the retardation in growth of wheat plants is not caused by physical or chemical conditions, but through the direct activity of the bacterial flora upon the peat substratum.

It has long been suspected that a reciprocal relation exists between groups of soil bacteria and the plants growing upon the soil. Various writers have been able to point out that marked differences in the productive power of different soils followed the growth of wild plants, and that these differences persist for some time. It is generally concluded, therefore, that the injury caused to cultivated plants by weeds or previous crops is due to influences on the bacterial life in the soil, and in a direction unfavorable to succeeding agricultural crops. No doubt, the "exhaustion" of soils which is frequently met with, and which cannot always be attributed to the removal of plant nutrients is, in part, an allied phenomenon. It cannot remain a matter of indifference to physiological ecologists whether a strong, intimate, and controlling relation exists between soil bacteria and surface flora, and how the bacterial organisms affect the character, and the association and succession of plants. At best very little is known of this phase of the process, and of the reactions and effects of the bacterial products upon plant life. It would be idle, also, to expect that the bacteriological data in themselves are sufficient for a clear interpretation of toxicity and drought relations, or of sterility of soils. If attempted, the interpretation would be, indeed, one-sided; there is a coordination of factors, each and all of which exert a relatively marked influence. Temperature, water, and air conditions in the soil, as well as the physical and chemical character of it, and the surface flora play an important rôle in determining the character of the bacterial flora, and therefore also the character of the chemical products formed. The bacteriological-chemical, as well as the physiological method, deserves on that account a closer consideration. The determination of the transformation products in various media inoculated with bog bacteria should possess an exactness and a reliability that should make it suitable for the solution not only of agricultural but of ecological problems as well. It is hardly necessary to go into further detail. It is only too clear that the need for new investigations is pressing, and that especially new points of view and new lines of research are imperatively required.

From the point of view of limiting environmental factors, structural differences do not seem to play much part in enabling plants to exist in bog conditions, for the bog xerophytes, as CLEMENTS contends, are dry-land plants, which have retained the distinguishing marks of the original habitat. They are characterized by their ability to adjust themselves to changed conditions without undergoing a corresponding change of structure. Indeed, drought resistance too often results from exceptional vigor and power of endurance rather than from persistence of ancestral or new variant characters. Injury and death result only when the condition surpasses the maximal limit. The inspection of even a few experiments with these distinctions in mind is likely to convince anyone at all familiar with such observations, that the best functioning plants, rather than the general average, represent the proper test of the possibilities of the species under the given conditions. Adjustment to local conditions is in these cases a more striking phenomenon than acclimatization, and it is to be looked upon as quite apart from structural divergence. While conclusive experiments may not as yet be admissible, the data at hand make it highly probable that the resistant forms among the hydrophytes and mesophytes in the mixed bog formations arise through gradual rather than sudden development, and that functional variation is the essential criterion. One of the results of introducing agricultural varieties into bog conditions is the comparative lack of uniformity in type, variants departing in both directions from the normal, and different varieties responding in different ways to the same conditions. Planting a species in a new place is in the nature of a test of the stability of its characters under the new conditions. Some changes result in a new place-function, but many of the changes of character that occur do not serve as responses, but result in wide individual differences and deterioration from loss or from disturbance of functional adjustments to previous established conditions. To inquire, therefore, into the nature of the adjustments of disturbed characters is to gain an indication, not so much of the many forms that the plant is able to assume, as especially the possibilities of the restoration of a balanced expression of functions which thus allow the most advantageous changes again to be established. An adapted and resistant form, if segregated through continued selection, may thus prove the basis of valuable data in the study of plasticity and fixity of organs or of type. It may prove doubtful whether the substratum solution is of a nature to bring out the greatest variation in form and in resistance. Experiments will have to be performed on a larger number of plants of widely different relationship before definite conclusions can be reached. Much economic value would attach to an extension of these experiments by using a salt or a mixture of more than one salt to ascertain a physiologically balanced solution for other kinds of plants. As has been stated above, there is an indication that the toxicity of the habitat is not the same for all agricultural plants and forest trees, and that, hence, from the point of view of the economic importance of these results, it may be found that a certain species, that is, that one crop, is better adapted than another to withstand the effects of this type of soil. Certainly an opportunity exists through such studies for an increase in the utility of these soils, and for a better understanding as to the character and the nature of functional responses of plants adapted to them.

Leaving out of consideration for the present studies of plants which deal with functional variability and with selection, we may speak with much more confidence of the fact which environmental factors exert upon diversity of function. This effect can be much more readily studied and shows itself much more conspicuously. In fact, a knowledge of drought resistance in plants within a physiologically arid habitat will be gained mainly by securing data as to the relation of plants to environmental factors. It is quite generally agreed that transpiration is one of the most important criteria in physiological ecology. Transpiration data are more conveniently obtained, if not more serviceable in this respect, than data on respiration differences or on green and dry weight of plants. Aside from the physiological responses of roots and leaves, the most significant physical conditions which more than others directly affect transpiration in plants, are the supply of available water to the roots, and the evaporation power of the air. On account of this distinctive feature, the problem separates itself into two phases, each of which must be considered by itself. The one relates to the influence of the varying edaphic conditions, the other to the effects of climate. The two are quite different, and each is of relatively great importance. Taken by themselves neither should be unduly drawn upon in the interpretation of drought or other resistance. The futility of the point of view which disregards all but one or two influences is seen clearly enough in the laboratory. But the inadequacy of such proposals is still more apparent when we attempt field work.

A consideration of the physiological causes underlying the conditions stated has led to the conclusion that for the local study extensive investigations in the heat requirements of bog plants and the location of their minimum temperature below which growth ceases (MERRIAM, also SWINGLE) do not have the importance which must be ascribed to temperature as a limiting factor for regions widely separated geographically. Except for the fact that growth in local bogs begins earlier in spring and continues later in autumn than in bogs of more northern regions, the data at hand on the differences between air and soil temperatures and on the total temperature exposure of plants covering a period of three years, show that low substratum temperatures, i.e., winter temperatures below 0° C. at the one-foot level (30^{cm}) and below $+3°$ C. at the 5-foot level (1.5^{m}), do not exist here, and hence play no part in bog structure or bog development. The more detailed account of this and other phases of the study appears elsewhere. The values of both heat-conductivity and heat-diffusion are in general lower in peat than in soils or in water, and hence prevent a rapid loss of temperature in the peat strata below the surface of vegetation. A persistence of the winter cold and ice through the summer months has not been observed in this region. Contrary, therefore, to the accepted interpretation, it is found that the imperfect decomposition of bog plants is not dependent upon supposedly low temperatures. One can readily understand that if any influence does exist the process of peat formation and preservation must be due to the presence of bog toxins and their antiseptic properties.

Livingston has shown that the evaporating power of the air furnishes an extremely valuable criterion for the differentiation between great centers of plant distribution, and also for the differentiation of certain habitats and the succession of plant societies. In connection with the problem of the transpiration values of bog plants, atmometer readings were obtained from the two stations on the bog island during the past year. A third instrument was established on the campus near the University Observatory, in an open place with an exposure to wind and sunlight similar to that in the central station on the bog. The readings of the instrument on the campus were taken three times daily, in connection with the climatological observations called for by the U. S. Weather Bureau Service. The data collected on the evaporating power of the air in the bog habitat, if compared with the evaporation rate on the campus of the University, show that the evaporating power of the air in bogs is not an important limiting factor in controlling bog vegetation, or determining the character of it. It is on the University campus that the greatest rate of evaporation was constantly recorded. The differences in the rate of evaporation between the campus and the central station on the bog island varied from 16.6 per cent to 50.4 per cent—a relative rate of evaporation at times more than twice the rate observed in the bog habitat. This relation seemed wholly unexpected and very surprising at first, for the campus area on the basis of its vegetation cannot be considered xerophytic. The general indications, therefore, point to the conclusion that at Buckeye Lake the evaporation from the water surface and from the vegetation produces a vapor blanket. The action of this invisible vapor blanket influences to a great extent the rate of transpiration of bog plants, for it conserves the moisture that would otherwise be lost by evaporation. The character of the flora and the structural conditions of bog plants, therefore, cannot be ascribed to a greater evaporating power of the air, nor to alterations in temperature conditions as has been stated so frequently. The weight of evidence from this and other investigations is again decidedly in favor of the conclusion that the real determining factor in the bog habitat is the ratio of the possible rate of water absorption to the rate of transpiration, and that the toxicity of the bog habitat has a primary rôle in bringing about bog conditions.

The extent of incontrovertible facts is still scanty. Only of late has the question of the physiological aridity of a bog habitat been removed from opinion, scientific and unscientific, to the field of experiment; and further experiments will be necessary to set clear the many complicated questions still connected with this inquiry.

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PHYSIOLOGICAL ASPECTS OF FERTILIZATION AND HYBRIDIZATION IN FERNS[1]

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(WITH TWELVE FIGURES)

The present investigation was undertaken as the first part of a study of the physiology of cell fusions. The first thing to be done in such a study is to determine what cells will fuse under normal conditions; the next step is to discover, in cases where fusions do not normally occur, the point in the events occurring in normal fusions where the process has stopped, and, so far as possible, the conditions causing the cessation of this process; the third step will be to discover conditions permitting the fusion of cells which will not fuse under normal conditions.

The results obtained in the present study will be considered under three heads: (1) under the heading *Hybridization* the evidence bearing on the occurrence of hybrids in ferns will be considered, and the results of many attempts to induce experimentally hybridization between many species and several genera will be given; (2) under the heading *Fertilization* it has been possible to show, in some of the cases where fusions have not been obtained, at what point in the progress of normal fertilization the process has stopped, and to indicate some of the factors determining this cessation; (3) under the heading *Movements and reactions of sperms* will be given the observations made to determine whether the reactions of fern sperms are of the same kind as those described for protozoa or whether they are of a different kind.

A. Hybridization

1. HISTORICAL AND CRITICAL

A fern hybrid was described as early as 1837 (**29**), when the nature of the spores and the prothallus were still unknown and the ideas concerning reproduction among pteridophytes were still shadowy.

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[1] Contributions from the Botanical Laboratory of the Johns Hopkins University, No. 13.

In this case two species, *Gymnogramme chrysophylla* and *G. calomelanos*, were growing near each other; spores of the former, when planted, produced ferns which were supposed to show characters approaching those of the other species. This case is described here because it shows a tendency which has persisted among students of ferns to the present day, that of describing as hybrids plants which are supposed to show intermediate characters, without sufficient evidence as to the real origin of these plants.

All later studies of fern hybrids fall into three groups. The first includes the numerous cases where plants have been found in the field or greenhouse differing in some respects from the characters considered as typical for one species, and supposedly approaching in these respects the characters considered as typical for another species. The second group includes those cases where spores, prothalli, or portions of prothalli of two or more species have been planted together in the hope that cross-fertilization might occur, and plants arising from these cultures showing supposedly intermediate characters have been described as hybrids. The third group is composed of a single case where sperms of a known species were presented to prothalli of another species bearing only archegonia, and the attempt was made to determine whether development of the embryo occurred or not.

The first group is represented by the works of LUERSSEN (**28**), DRUERY (**10, 11**), Miss SLOSSON (**45**), HAHNE (**15**), DOWELL (**8**), BENEDICT (**1, 2**), and others. FOCKE (**14**) lists the supposed hybrids described before 1881, and concludes that, except in the genus Gymnogramme, all are doubtful. It is not evident why FOCKE excepts Gymnogramme in this conclusion.

The reasons for regarding the kind of evidence considered by these authors as sufficient to prove the hybrid nature of the supposed crosses are given by BENEDICT (**2**) in a recent paper. These reasons are (1) the intermediate character of the supposed hybrid, (2) its sterility, abnormality, and greater vigor as compared with the supposed parents, (3) its occurrence being found only occasionally and then usually with the supposed parents. BENEDICT states, however, that "irregular plants, which are to be explained as due to ecological conditions or as sports rather than as hybrids, are not unusual. The immediate presence of the parent species is not a necessity, since fern plants are often long-lived, and the greater vigor of the crosses might render them resistant to conditions sufficiently adverse to destroy the parent species." While many of the plants studied by BENEDICT and others may be hybrids, it would be extremely difficult to distinguish, in such cases, between "sports" and "hybrids," especially when the supposed parents are not present, and the conclusions founded on such evidence must always have a large element of uncertainty. Ferns, like other plants, are known to vary widely under different conditions, and certain tendencies toward variation are recognized by students of this group (**31**, p. 272).

The uncertainty of conclusions founded on a study of the sporophyte is emphasized by the work of SADEBECK (**40, 41**). This author, sowing spores of *Asplenium adulterinum* and of *A. Serpentini* on a serpentine-free substratum for successive generations, obtained respectively *Asplenium viride* and *A. Adiantum nigrum*, thus showing that forms previously described as species were but serpentine varieties. The first transformation to the non-serpentine form of the species occurred in the former case in the fourth, in the latter case in the fifth generation, the serpentine form being maintained for several generations on a serpentine-free substratum. Even cultures, therefore, unless continued for many generations under different conditions, may fail to show the real nature of a supposed species.

In discussions concerning hybridity, much weight is given to the point that in the characters in which the specimens differ from the "type of the species," they approach those of some other species. This may be due to hybridization as supposed, or it may be due to some other cause. The serpentine form of *Asplenium viride* ("*A. adulterinum*") assumes, in many respects, an intermediate form between the "typical" *A. viride* and *A. trichomanes*, showing that an ecological variety may assume a form approaching that of another species.

If species were clearly recognizable units with distinct limits, and if these units were changeable only by hybridization, we should be justified in describing intermediate forms as hybrids. But, considering the cases mentioned above and the variation that is known to occur in all groups, this kind of evidence seems entirely inadequate to prove the hybrid nature of any individual. While, if all the three lines of evidence given above concurred in indicating any single form as a hybrid, they would furnish some reason for so regarding it, but they would not furnish conclusive proof of its hybridity. This proof could be obtained only by producing experimentally the form in question from a cross between cells of known parentage.

The second class of evidence is given in the works of DRUERY (**9**), FARMER (**12**), LOWE (**27**), Miss SLOSSON (**46, 47**), HANS (**16, 17**), and others. The supposed hybrids described by these authors were obtained by planting together spores, prothalli, or parts of prothalli of different species and trusting to chance to obtain a cross. Some of the resulting offspring were adjudged hybrids because of their apparently intermediate character between their supposed parents. This evidence, while more trustworthy than that considered above, is not beyond question. LOWE obtained such various results from his sowings of mixed spores that he was led to propose the theory of "multiple parentage" to account for all the differences in the offspring. MAXON (**30**) lists the three authentic cases of hybridization between species as the *Phyllitis scolopendrium* (*Scolopendrium vulgare*)×*Ceterarch officinarum* described by DRUERY (**10, 11**), the *Polypodium vulgare elegantissimum*×*Phlebodium aureum* described by FARMER (**12**), and the *Polystichum aculeatum*×*Polystichum angulare* described by LOWE (**27**) and DRUERY (**11**).

DAVENPORT (**6**) considers the last two cases uncertain and expresses no opinion about the first case. He concludes (p. 7): "I do not see how we can ever obtain absolute proof of hybridity in nature, because it is manifestly impossible for us to observe the process through which it is brought about; nor do I see how we can obtain positive proof through mixed sowing, as it is equally impossible for us to determine from which species the germinating spores come. It seems to me that in all such cases there will always be an element of uncertainty that will compel us to rely altogether upon inductive reasoning for our conclusions, which are not always likely to be safe."

The best work in this line is that of Miss SLOSSON (**46, 47**). By planting together portions of the prothalli of the supposed parents, she obtained offspring resembling the plants previously described as hybrids, *Dryopteris cristata*×*D. marginalis* and *Asplenium platyneuron*×*Camptosorus rhizophyllus* (the well-known *Asplenium ebenoides*). These results are almost convincing, but do not place the subject beyond question. Cutting does not, in every case, separate the antheridia and archegonia; then, too, the prothalli formed branches and produced new sexual organs, so that, in the case of *Asplenium platyneuron* and *Camptosorus rhizophyllus*, many plants of each species appeared together with a few of the supposed hybrids. These experiments, therefore, are open to the objection raised by Miss SLOSSON (**46**) herself against the method of planting spores or whole prothalli together. They prove that the offspring come from one of the species planted, but do not prove whether this is by hybridization or some other method of variation. So far as the author is aware, no experiments have been made to prove that *Asplenium platyneuron* may not at times give rise to *Asplenium ebenoides*. Specimens of *Asplenium pinnatifidum* observed by COPELAND (**5**) approached, in their variable characters, *Camptosorus rhizophyllus* and bore a striking resemblance to *Asplenium ebenoides*, although no Camptosorus was found in the immediate neighborhood.

DRUERY (**9**) observed variation in plants of *Crytomium falcatum* and *Lastrea pseudo-mas cristata* produced apogamously. In another experiment he obtained from spores of a single plant of *Athyrium plumosum* offspring showing almost as many differences in the leaves as were found by LOWE in his "plants with multiple parentage."

In a recent article LEAVITT (**23**) has described the origin, through vegetative variation, of the Pierson and Whitman ferns, and has described the particular type of variation called "homoeosis" in ten species of wild ferns distributed among six genera.

It is clear that other means than hybridization may produce variations among ferns, and that some of these variations may give characters approaching those which are supposed to belong to other species. This being the case, we must regard as unproved all cases of supposed hybridization founded on structural characters of the sporophyte.

In the third class of evidence mentioned comes the work of VOEGLER (**51**). This is the one case of experimental studies on hybridization in ferns where the experimenter attempted to work with known units;

it is, therefore, the only case where the results are trustworthy. VOEGLER presented the sperms of several species to the archegonia of other species and attempted to determine, by observing the living sperms after their entrance into the archegonium, whether they fused with the egg or not. The following combinations were tried: *Dicksonia antarctica*♀×*Nephrolepis davalloides*♂; *Ceratopteris thalictroides*♀ or *Nephrolepis davalloides*♀×*Dicksonia antarctica*♂, or *Blechnum occidentale*♂, or *Gymnogramme Laucheana*♂. In more than 100 cases of entrance, no fusion of the sperm with the egg was observed. VOEGLER also presented the sperm of several species to the prothalli of other species bearing only archegonia, and, having replanted these, examined them after one or two days to determine by the appearance of the archegonia whether development of the egg had begun or not. In all cases negative results were obtained; the archegonia had turned brown.

There are obvious objections to the methods used: (1) there were not sufficient precautions to insure the absence of sperms on the archegonial prothalli; (2) observations on the surface can scarcely give certain conclusions about the fusion of sperm with the egg; (3) reliance is placed on the appearance of the archegonia after one or two days to determine whether development of the egg has occurred or not. Since in the two species where the time has been noted (SHAW **42**, CONARD **4**) the first division of the egg does not occur until after seven days, and since in this investigation the same time has been found to hold for other species, the method used does not seem beyond question.

In this work of VOEGLER'S, the most reliable study of hybridization in ferns, all the results are negative. The author concludes that while hybridization is not thereby disproved, this must seldom occur and then only between certain species.

2. METHODS

Since the value of all work of this sort depends on knowing with certainty the origin of the sexual cells brought together in the archegonium, it will be well to describe in some detail the methods used for insuring this in the present investigation.

The prothalli used were in every case raised from spores. The determination of every species used was made or verified by Mr. W. R. Maxon. Antheridial prothalli were placed in water on a slide, and prothalli bearing only archegonia of the species necessary to make the desired cross were added to these; the entrance of sperms into the archegonia was then followed under the microscope. After being left on the slide for one to four hours, the prothalli were either planted on soil in separate pots or were fixed and studied in section to see whether fusion of sperm and egg had occurred. About half of the prothalli in which experimental fertilization was attempted were planted and the other half sectioned.

In this method there are four places where an error is especially likely to occur: (1) in gathering the spores of several species in one day, these may become mixed; (2) in planting the spores, or after these are sown, spores of other species may fall into the pot and contaminate the culture; (3) fertilization may have taken place before the prothalli are removed from the pot for the experiment; (4) the female prothalli may bear antheridia.

All these dangers were especially guarded against. In collecting spores, mature fronds were chosen, and being shaken as little as possible were carefully wrapped in several thicknesses of paper. The fruiting portions of the fronds were touched as little as possible, and the hands were washed or carefully wiped with a damp cloth between each collection.

The spores were sown on soil which was sterilized by heating to 150° C. for six to twenty-four hours. All sowings were made in rooms in which no other ferns were ever kept. When more than one sowing was made on any day, these were made in widely separated parts of the rooms, and after each sowing all the surrounding furniture and walls were wiped with a wet cloth. Before and after each sowing the hands were carefully washed and all instruments used were sterilized by boiling. The pots were kept in the laboratory where no other ferns were grown, or in the greenhouse. In this room of the greenhouse there were three fruiting specimens of ferns, but these were on the opposite side of the room. The cultures were covered with glass. In spite of these precautions, a small amount of moss appeared in several of the pots, and fungi occasionally made their entrance. It is not believed that the cultures were contaminated by fern spores, however, because more than 100 young sporophytes from the different pots were obtained and raised to a distinguishable age, and all were of the species which was planted in the pot from which they came.

In order to prevent the occurrence of fertilizations in the pots, all cultures were watered very sparingly and only from below—by pouring water into the saucers. The soil and air were kept just moist enough to keep the prothalli in good condition. The soil was not allowed to become wet and no water was allowed to collect on the glass. In spite of these precautions, many fertilizations took place in some of the pots. Except in one case noted, however, no culture was used for archegonia unless it was free from sporelings for at least a week before and two weeks after the experiment.

In most cases the prothalli used for archegonia were examined under the microscope before being placed in water, and any portions of the prothalli bearing antheridia were cut off, and all adherent male prothalli were removed. In some cases the prothalli were not examined dry, but were placed directly in water. Antheridia or male prothalli, if present, were removed before escape of the sperms had occurred. All such cases were recorded, and no female prothallus was used for crossing if there was any reason to believe that sperms of its own species were present. By these means it was possible to be fairly sure that no antheridia of the species to be used as female were present; sometimes, however, antheridia were overlooked. In cases where the prothalli were fixed, therefore, the entire prothallus was sectioned and every section was examined for antheridia. Over 150 prothalli were thus sectioned and examined, and among these, antheridia were found in only two cases where they had not been detected by the previous examination. This method, therefore, seems to be a satisfactory one.

From the fact that the above methods were carrried out faithfully, the conclusion seems warranted that, in this work, we are dealing with sperms and eggs of known parentage.

3. RESULTS

Abundant entrance of sperms has occurred into archegonia of the same species and of different species. When the sperm and egg were of the same species, many fusions were obtained; but in not a single case among the combinations tried was fusion obtained between an egg and a sperm of different species, in spite of the fact that sperms were in a few cases observed in contact with the egg.

The results of this portion of the investigation are shown in the following tables. In the first table are given the results of the experiments where the prothalli were sectioned and examined for fusions; in the second table are given the results of the experiments where the prothalli were replanted on soil in the effort to obtain sporelings.

In the first table only those cases are included in which sperms were observed, in the sections, within the venters; in several other cases sperms were found in the necks of the archegonia, but not in contact with the egg. Not every entrance means the possibility of fusion, since entrance often occurs in archegonia whose eggs are bad and even in empty archegonia. It is impossible, however, to tell with certainty from sections whether an egg is good or bad. In order to eliminate the error of personal judgment, entrances have been counted in all cases where the venter contained an egg, regardless of whether this egg was good or bad. It was very evident in many

TABLE OF RESULTS OBTAINED FROM SECTIONS

♀	♂	Number of prothalli	Number of entrances	Number of fusions
Dryopteris noveboracensis..	D. noveboracensis	6	10	7
D. noveboracensis..........	D. Thelypteris	8	67	0
D. Thelypteris.............	D. noveboracensis	1	1	0
D. marginalis..............	D. marginalis	5	0	0
D. Thelypteris.............	D. Thelypteris	1	0	0
D. marginalis..............	D. Thelypteris	4	1	0
D. Thelypteris.............	D. marginalis	5	1	0
D. marginalis..............	D. noveboracensis	16	5	0
D. marginalis..............	Pteris multifida	8	9	0
Pteris multifida*..........	P. multifida	41	78	26
Athyrium Filix-foemina.....	P. multifida	14	15	0
A. Filix-foemina...........	A. Filix-foemina	6	9	4
A. Filix-foemina...........	Asplenium montanum	5	6	0
A. Filix-foemina...........	As. platyneuron	11	17	0
A. Filix-foemina...........	As. platyneuron and A. Filix-foemina	2	9	1
As. platyneuron............	A. Filix-foemina and As. platyneuron	2	1	0
As. platyneuron............	Camp. rhizophyllus	2	1	0
Camptosorus rhizophyllus ..	As. platyneuron	4	4	0
As. montanum...............	As. Bradleyi	28	2	0

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* *Pteris multifida* Poir., CHRISTENSEN in Index Filicum 602. 1906.

TABLE OF RESULTS OBTAINED FROM PROTHALLI REPLANTED ON SOIL

♀	♂	Number of prothalli	Number of entrances	Number of sporelings
D. marginalis	D. marginalis	6	0	0
D. Thelypteris	D. Thelypteris	5	0	0
D. marginalis	D. Thelypteris	23	0	0
D. marginalis	D. noveboracensis	1	3	0
D. marginalis	Pteris multifida	10	0	0
Pteris multifida	P. multifida	24	24	5
A. Filix-foemina	P. multifida	3	10	0
A. Filix-foemina	A. Filix-foemina	43	36	6
A. Filix-foemina	As. montanum	3	0	0
A. Filix-foemina	As. platyneuron	8	10	0
As. platyneuron	As. platyneuron	40	?	6
As. platyneuron	A. Filix-foemina and As. platyneuron	2	6	2*
As. platyneuron	Camp. rhizophyllus and As. platyneuron	1	1	0
Camp. rhizophyllus	As. platyneuron	12	6?	0

* As. platyneuron.

of the entrances counted that the egg was bad, but the egg is no more likely to be bad in the cases of the entrance of a foreign sperm than in the cases of the entrance of its own sperm. It is believed, therefore, that the proportion of entrances in which fusions have been obtained may be compared in the two cases.

In the second table, the number of entrances obtained can only be approximated, since on the one hand not every entrance is observed, and on the other hand an observed entrance does not necessarily mean that the sperms have reached the venter.

These results for most of the combinations tried are not conclusive, but taken all together they constitute a considerable mass of evidence against the occurrence of hybridization in these ferns. Entrance of sperms of its own species into 97 archegonia on 59 prothalli, as shown in sections, gave 37 fusions; while the entrance of sperms of other species into 129 archegonia on 111 prothalli failed to give a single fusion.

The results obtained from replanting the prothalli on soil confirm those obtained from sections; all point against the occurrence of hybrids among these ferns.

The most noteworthy cases observed in sections are the following: Sixty-seven entrances of the sperms of *Dryopteris Thelypteris* into the archegonia of *D. noveboracensis* gave no fusions; while ten entrances of its own sperms into the archegonia of *D. noveboracensis* gave seven fusions.

It should be stated that most of these 67 eggs looked bad. Some, however, seemed good and appeared to be in the stage in which fusion would have been expected to occur if sperms of its own species had been present. Young archegonia in various stages were present on the prothalli sectioned, and sporelings appeared in this culture of *Dryopteris noveboracensis* before, during, and after the time that the experiments were made, so that it seems very improbable that the eggs were bad at the time of entrance in all the 67 archegonia in which entrance was obtained. In view of the supposed hybrids described among Dryopteris species by DOWELL (**8**) and BENEDICT (**1, 2**), this result is of considerable interest.

Using *Athyrium Filix-foemina* as the female parent, the entrance of the sperms of *Pteris multifida* into fifteen archegonia, and of the sperms of *Asplenium montanum* into the six archegonia, and of the sperms of *Asplenium platyneuron* into seventeen archegonia gave no fusions, while the entrance of its own sperms into nine archegonia gave four fusions.

In one attempted cross of *Asplenium platyneuron* sperms with *Athyrium Filix-foemina* eggs, antheridia of *A. Filix-foemina* also were present. In this case nine entrances were obtained and one fusion resulted. In the attempted reciprocal cross of *Athyrium Filix-foemina* sperms with *Asplenium platyneuron* eggs, sperms of *Asplenium platyneuron* were present; six entrances and two sporelings of *Asplenium platyneuron* were obtained. Evidently when sperms of two species are present, fusion may still take place between the egg and sperm of its own species; the presence of foreign sperms does not prevent this fusion.

As these experiments were made at the same time as the attempted crosses between the eggs of *Athyrium Filix-foemina* and the sperms of *Asplenium platyneuron*, they show that the failure to obtain fusions in that case was not due to a bad condition of the eggs or sperms.

The results given above do not disprove the existence of hybrids or the possibility of obtaining them. Owing to lack of material and to various accidents during the investigation, experiments were not made on a sufficient number of closely related species, and the results in most cases are not sufficiently conclusive to settle the question. But these experiments do show that not every combination of egg and sperm will yield a hybrid. Such a result is to be expected, but in view of the supposed cross between *Camptosorus rhizophyllus* and *Asplenium platyneuron*, it cannot be assumed without proof. A priori, we should expect hybrids to occur in some cases, but the fact remains that in the two investigations on the subject where known elements have been used, only negative results have been obtained.

B. Fertilization

It is well known that fusion will occur between the sexual cells of different species in some cases and will not occur in others, but few attempts have been made to determine in the cases where fusion does not occur the point at which the processes stop and the conditions causing this cessation, or to induce fusion in cases where it does not occur under normal conditions.

In ferns the process of normal fertilization has been described by STRASBURGER (**48**), SHAW (**42**), VOEGLER (**51**), THOM (**50**), MOTTIER (**34**), CONARD (**4**), and YAMANOUCHI (**53**). PFEFFER (**36**) and VOEGLER (**51**) obtained entrance of the sperms of one species into the venters of other species in every combination tried. VOEGLER attempted to follow in more than 100 living prothalli the movements of sperms which had entered the venters of other species. In every case, although the sperms came into contact with the eggs, they were unable to enter, and finally ceased their movements, or after several attempts to enter the egg left the archegonium. Presumably the phenomena observed were the same as those described below.

In the present investigation attraction of the sperms and their entrance into the venter has been obtained in every combination used, and in several cases the living sperms have been observed and their movements followed within the venters of the same species and of different species. In most cases the sperms were seen as an actively moving mass lying against the egg on the side turned toward the archegonial neck, the so-called receptive spot. The egg looked round and turgid. The individual sperms, when distinguished, had their anterior ends apparently in contact with the egg and were lashing about vigorously and revolving on their axes. Sometimes no locomotion was observed, the entire mass of sperms appearing to remain at the receptive spot, but often some of the sperms were observed to change their places and occasionally to leave the venter. In one case five sperms of *Athyrium Filix-foemina* were observed within an archegonium of the same species. All of these swam about within the venter and were observed to leave and reenter the venter several times. This prothallus when replanted on soil gave no embryo; the egg, therefore, was probably bad. In every case when sperms were observed within the venter and fusion resulted, the mass of sperms was observed to remain in contact with the egg. Perhaps a good egg attracts the sperms, while a bad egg does not.

Since in the cases mentioned the sperms were observed to bore against the receptive spot of the egg of another species as vigorously as they bored against the egg of their own species, it seems that the failure of such sperms to penetrate the egg is not due to any failure of the sperm to perform its part in the process. The failure of such sperms to enter the egg seems to be due either to some hindrance on the part of the egg or to some interaction of egg and sperm. There is little evidence to help us to decide between these two possibilities.

VOEGLER observed that, after the entrance of one sperm, a second sperm, although boring against the egg, was unable to enter. This would appear to be due to some change occurring within the egg, perhaps comparable to the formation of a membrane in the fertilized animal egg.

FARMER (**13**) suggests that the entrance of more than one sperm into the egg is prevented by the occurrence of chemical changes in the cytoplasm of the egg immediately upon fertilization. He believes that these chemical changes produce substances which are injurious to the sperms, and presents some evidence for such an occurrence in the alga Halidrys. The entrance of a second sperm is not, however, always prevented. MOTTIER (**34**) has figured two sperms within one egg of *Onoclea Struthiopteris*, and WOODBURN (**52**) has described two remarkable cases of polyspermy in the same species; in one of these, seven sperms were observed within the egg nucleus. Whether similar phenomena may occur in other species is not known.

MORGAN (**32, 33**) has shown that in the ascidian Ciona, the sperms are practically incapable of fertilizing the eggs of the same individual and of certain other individuals, and has suggested that this is due to substances present in the egg furnishing a sort of "immunity" against these sperms.

NEWMAN (**35**) was able, by treating the eggs of Fundulus with solutions of salts that precipitate colloids and increase the surface tension, to destroy the permeability of the egg membrane to the sperm, and then, by treating such eggs with solutions of salts that dissolve precipitated colloids and decrease surface tension, to restore the permeability of the membrane. The results of MORGAN on Ciona, according to this author, are capable of being explained by the assumption that different eggs and sperms have different relative surface tensions. NEWMAN states that "these experiments and those of LOEB and MORGAN seem to indicate that the relative surface tension of the egg and of the sperm is one important factor governing fertilization."

MOENKHAUS, however, in cross-fertilizing fishes that in many cases belong to widely separated orders, often found the percentage of eggs impregnated to be as great as in the check experiments where the sperm and eggs were of the same species. When eggs of *Fundulus heteroclitus* were subjected to a mixture of equal parts of sperms of the same species and of sperms of *Menidia notata* or *M. gracilis*, there were often more fertilizations by the foreign sperms than by the sperms of Fundulus. The foreign sperms were prepotent. MOENKHAUS concluded that, among the forms used in the experiments, there is no specific adaptation such as chemical affinity, surface tension, etc., but that the prepotency of the foreign sperm is due to its being more active and hence a swifter fertilizer.

TENNENT (**49**) was unable to obtain crosses between different genera of echinoderms when the sperms were added to the eggs immediately after their removal from the ovary, but obtained fusion in every combination tried when the eggs had been allowed to stand for several hours. The time after removal from the ovary when fertilization with foreign sperms can be obtained is definite for any particular combination and is different in different combinations; it appears to depend on the species of sperm as well as on the egg employed. The eggs, after standing and becoming capable of fertilization by foreign sperms, are still able to be fertilized by their own sperms. Apparently changes take place progressively in the egg after its removal from the ovary, so that at different times it is capable of being fertilized by different species of foreign sperms, but these changes do not prevent the entrance of its own sperms. In a paper soon to be published, TENNENT considers the effect of variation in the concentration of OH ions in the sea water in which the eggs stand before and during fertilization, and suggests that the variation in alkalinity brought about by artificial means in the experiments may imitate a natural seasonal variation in the concentration of the OH ions in ordinary sea water.

In crossing the eggs of the starfish *Asterias ochracea* with the sperms of the sea urchins *Stronglyocentrotus purpuratus* and *S. franciscanus*, LOEB (**26**) found that in sea water the sperms would fuse with the eggs of their own species, but not with those of the starfish; while in sea water made slightly alkaline, the sperms would unite with the eggs of the starfish, but not with those of their own species.

The failure of fern sperms to fuse with eggs of their own species which are just past maturity seems to be due, in part, to the physical condition of these eggs. Eggs which are evidently good have clear, soft-looking surfaces; while eggs as they become bad have darker surfaces that resemble more and more the appearance of a dried colloid. While it may be safely assumed that chemical changes are taking place within the egg at the same time, these physical changes would alone probably be sufficient to prevent the entrance of sperms.

We have no evidence to help us to decide whether a similar explanation would account for the failure of a second sperm to enter an egg of its own species, since no constant difference between fertilized and unfertilized eggs was detected. An attempt to apply the same explanation to the lack of fusion of foreign sperms meets with still greater difficulties. A careful scrutiny failed to show that eggs of other species, which as mentioned were not entered by sperms, had thicker membranes than did the eggs of their own species. If such a structure were present, we should find eggs of other species with thinner membranes than those of their own species, and should be able to obtain entrance of sperms into them; but no such case has been observed.

It is well known that different degrees of fusion of egg and sperm are obtained in different combinations. In some cases apparent fusion occurs, but the offspring remain sterile; in others a partial fusion occurs, but the offspring fail to develop; while in others no fusion occurs. A good discussion of the cases where after fusion the offspring remain sterile or undeveloped is given by DEVRIES (**7**). Such cases seem to be due to some interrelation of the chromatin content of the two sexual cells. The failure of egg and sperm to fuse seems to be caused by some physical or chemical interaction between the two. It remains to be seen whether there is any sharp line between these two classes of phenomena.

The possibility of fusion seems to be determined by different factors in different species of plants and animals. In some fish there is no specific adaptation; in echinoderms changes occurring after the removal of the eggs from the ovary permit the fusion of sperms of different species at different intervals of time; in some echinoderms the alkalinity of the sea water determines the possibility of the fusion of certain sperms; in some cases the relative surface tension of egg and sperm may determine the possibility of fusion; in other cases the presence of certain substances in the egg may prevent the fusion of certain sperms; and lastly double fertilization may be prevented by the formation of certain substances or by physical changes in the egg. The possibility of fusion seems, then, to be determined in some cases chiefly by physical, in others by chemical conditions.

In ferns we have no evidence of the existence of any physical barrier in the ripe egg that might prevent the entrance of foreign sperms. In the present state of knowledge, it seems probable that the failure of egg and sperm to fuse is due to some interaction between the two. It is greatly to be hoped that we shall some day be able to obtain crosses. We may then be able to obtain some evidence concerning the nature of this interaction.

C. Movements and reactions of sperms

The accounts of the movements of motile organisms may in general be considered in two groups. In the first of these, the positive response of an organism to a stimulus is as follows: the organism, swimming about at random and coming to that portion of the medium in which the stimulant is present, has its movements directly modified by the stimulating agent, so that the direction of its axis is turned toward the region of stimulation; it then proceeds in a straight line toward the stimulus. This is the "local action theory of tropisms" discussed by JENNINGS (**18, 19**), and includes the "strophic" movements of ROTHERT (**39**) and the "topotactic" movements of PFEFFER (**38**). According to the other view, the organism, coming into the region of a stimulant to which it reacts "positively," enters this region without reacting, but upon tending to leave the region, it reacts by turning back; the "positive" response is thus obtained by a series of "negative" reactions whenever the organism tends to go in a direction leading away from the source of stimulation. This is the reaction described by JENNINGS (**18, 19**) for many protozoa and bacteria, and includes the "apobatic" movements of ROTHERT, and the "phobotactic" movements of PFEFFER. Similar explanations to those accounting for the positive reactions in the two views are given for negative reactions.

According to the former account, the source of stimulation is the unequal distribution of the stimulant on different parts of the organism; this acts locally on the organism, directly influencing the motor organs; and the essential part of the reaction is the orientation of the organism so that its axis is placed parallel to the direction of greatest stimulation. According to the latter account, the source of stimulation is the change of the conditions to which the organism is subjected; this change acts on the organism as a whole; and the essential nature of the reaction is that the organism shows no response in passing toward the optimum, but reacts by turning back upon tending to pass from the optimum.

The reaction of motile plant cells to chemical stimuli has been studied by PFEFFER (**36, 37**) in ferns, Marsilia, Selaginella, mosses, liverworts, Chara, bacteria, the swarmspores of Saprolegnia, and certain flagellates; by LIDFORSS (**24, 25**) in Marchantia and Equisetum; by SHIBATA (**43, 44**) in Salvinia and Isoetes; by VOEGLER (**51**) and BULLER (**3**) in ferns; and by ROTHERT (**39**), KNIEP (**22**), and JENNINGS and CROSBY (**20**) in bacteria.

PFEFFER (**38,** p. 757) suggests that, in rapidly reacting swarmcells, the positive, apparently "topotactic," response may be the result of a series of negative responses as is outlined above, but considers the reactions of many flagellates, the swarmspores of many algae, the sperms of ferns, and the swarmspores of Saprolegnia to be accomplished by tropistic orientation, "durch die typische tropistische Richtung der Körperachse" (**38,** p. 754).[2] The same view is held by LIDFORSS for the movements of the sperms of Marchantia and Equisetum. SHIBATA explained the positive reactions of Isoetes sperms in the same manner, but considered certain negative reactions shown by them to be phobotactic, believing that both kinds of reaction exist in the same organism. The same possibility is suggested by LIDFORSS for the sperms of Marchantia. VOEGLER and BULLER do not discuss the nature of the reaction. ROTHERT showed that certain bacteria react only in tending to pass from the optimum in the manner outlined above; they thus finally collect in the region of optimum stimulation.

JENNINGS (**18**) has shown that the reactions of many of the lower organisms consist of a series of random movements performed when the organism tends to pass from the optimum, with the continuance of such of these movements as take it toward the optimum. The movements leading toward the optimum may in Stentor and other organisms be performed more readily after repetition, and in some organisms the final response—toward the region of optimal stimulation—may be attained with practically no random movements, thus giving a directive reaction. The difference between this type of reaction and that favored by the holders of the other view mentioned is, that in this one it is held that the stimulant acts on the organism as a whole and that the organism responds as a whole, performing complex and coordinated movements; in the other it is held that the stimulant acts on certain parts of the organism, directly modifying the action of these parts. According to JENNINGS, the reaction obtained depends on the physiological condition of the organism, which is in turn partly determined by the past experiences of the organism.

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[2] The reference to the German edition is given here because of the abridgment of the English translation at this point.

The positive response of fern sperms to the archegonium and to the salts of malic acid is too well known to need description. This is believed by most authors to be due to the directive action of the stimulating substance on the motor organs, the axis being thus turned toward the stimulant. Most workers, however, while holding this view, have noted that many sperms do not react as thus described, but may wander about the field, or pass through it indifferently, or may avoid it. Such reactions have been ascribed to individual differences.

Thus JOST (**21**, p. 542) states that "whenever they (the sperms) come into the neighborhood of an archegonium, they twist sharply round, so as to direct their anterior ends toward the mouth of the archegonium; they thus rapidly approach it, enter its neck, and fuse with the ovum in the interior." In describing experiments with malic acid, JOST states (**21**, p. 542): "It may be clearly seen that the sperms curve around sharply the moment they come within the sphere of influence of the malic acid diffusing out of the tube, and place their long axes parallel with the course of the diffusion current. Without any acceleration of their movements they then steer their way toward the more concentrated solution straight for the mouth of the tube. Since the sperms distribute themselves equally in a homogeneous solution of malic acid, just as they do in water, we are bound to regard the unequal distribution of the acid as the directive stimulus."

The question before us is: Are the movements of fern sperms best explained as being due to the local action of different concentrations of a stimulant on different parts of the body, thus producing movements leading to an orientation of the axis; or are they to be regarded as the result of the action of the stimulant on the organism as a whole, the resulting movements being such as to take the organism toward the region of optimal concentration?

In the present investigation a few observations were made on the reactions of sperms to malic acid in capillary tubes, but most of the results on positive responses were obtained from the reaction of the sperms to the substance extruded from the archegonia of either the same or of different species. In such cases the prothalli bearing the antheridia and the archegonia were rinsed and placed in water on the slide under a cover glass, and the movements of the sperms followed. For other experiments the antheridial prothalli, after being rinsed, were placed in a few drops of water; and the sperms, after their escape, were transferred to the slide with a pipette. Since the sperms are too small to be studied with a binocular microscope, most of the observations were made with an ordinary microscope, using a Zeiss 8^{mm} objective. The results given are based on the observation of thousands of sperms; they will, of course, not apply to every sperm whose movements were followed, but will apply only as a kind of average, stating in general the manner of reaction observed.

Most of the observations were made on the sperms of *Pteris multifida*,[3] but these results were verified with the sperm of every species studied. The structure of the sperms is that of a flat, spirally coiled band bearing numerous cilia, especially near their anterior ends. Some of them are coiled to the left, others to the right; some of them appear to revolve clockwise, others in a counter-clockwise direction, and some of them seem at times to change their direction of rotation.

In water the sperms swim by rapid movements of their cilia, at the same time rotating on their axes and swinging their anterior ends through small circles. The result of this is that they progress in narrow spirals; their course in water approaches a straight line, but has occasional turnings. When the sperms are placed in quince seed jelly or a solution of India ink, however, their movements are strikingly different from those shown in water. They now swing their anterior ends through large circles, so that they proceed along wide spirals; they no longer pursue a course approaching a straight line, but turn here and there again and again. In thick ink they pass through spirals larger than those made in thin ink. *Fig. 1* shows the differences in the spiral courses of sperms in thick ink, in thin ink, and in water. When they change the direction of movement, they accomplish this by swinging their anterior ends through large circles, at the same time revolving on their axes, and then going forward in a

[3] The material of *Pteris multifida* used in this investigation was obtained from Jamaica, B.W.I., during a visit made by the writer to that island, aided by a grant from the Bache Fund. Acknowledgment is here made to the trustees of that fund for this assistance.

new direction. The result of this is that they experience the conditions on all sides before they continue their course in a new direction. In going in a new direction they may turn up, down, or to one side. Apparently the direction toward which they turn is that toward which the anterior end of their spiral points, but their small size made it impossible to determine this with certainty.

The movements shown in the negative and positive reactions are of the same kind as those described above. If a crystal of some salt, such as potassium nitrate, sodium chloride, etc., be placed at the edge of a drop containing sperms, a solution repellent to the sperms diffuses into the water. Sperms approaching this solution show various movements. Some of them swing their anterior ends through large circles, at the same time revolving on their axes, and then go forward as described above; such sperms often turn almost immediately from the stimulant and leave the injurious region. Most sperms, however, swing their anterior ends through smaller circles and make small turns. Such a turn may carry them into the solution, alongside of it, or away from it. If it carries them away, they usually continue this course; but if it carries them in or alongside, they turn again and again until they are headed away from the source of stimulation, and then continue forward. These sperms, therefore, usually wander here and there about the field before being headed away from the stimulant. *Fig. 2* illustrates the course pursued by such sperms.

In a study of the positive responses of the sperms to the archegonium, it is immediately seen that the reactions are varied. While some sperms seem at first sight to turn directly and enter the archegonium immediately (*figs. 3* and *4*), others enter only after wandering about the field, occasionally going past the archegonial mouth and then turning back (*figs. 5* and *6*), while others pass indifferently (*fig. 7*), or change their courses without entering (*figs. 8–10*), or turn and leave the region (*figs. 11* and *12*). The sperms swimming in water move with great speed, but upon reaching the region in front of an open archegonium, they are slowed up by the extruded slime. A close examination of those sperms which seem to enter by turning directly to the archegonium shows that some of these slow up suddenly and swing their anterior ends through large circles, at the same time revolving on their axes, as previously described; they then go forward. This movement usually results in their turning toward the archegonium, but not directly toward it; and their subsequent orientation and entrance into the archegonium is attained by a series of gradual swingings toward the archegonial mouth as they go forward. Most sperms, however, react less immediately and attain their orientation

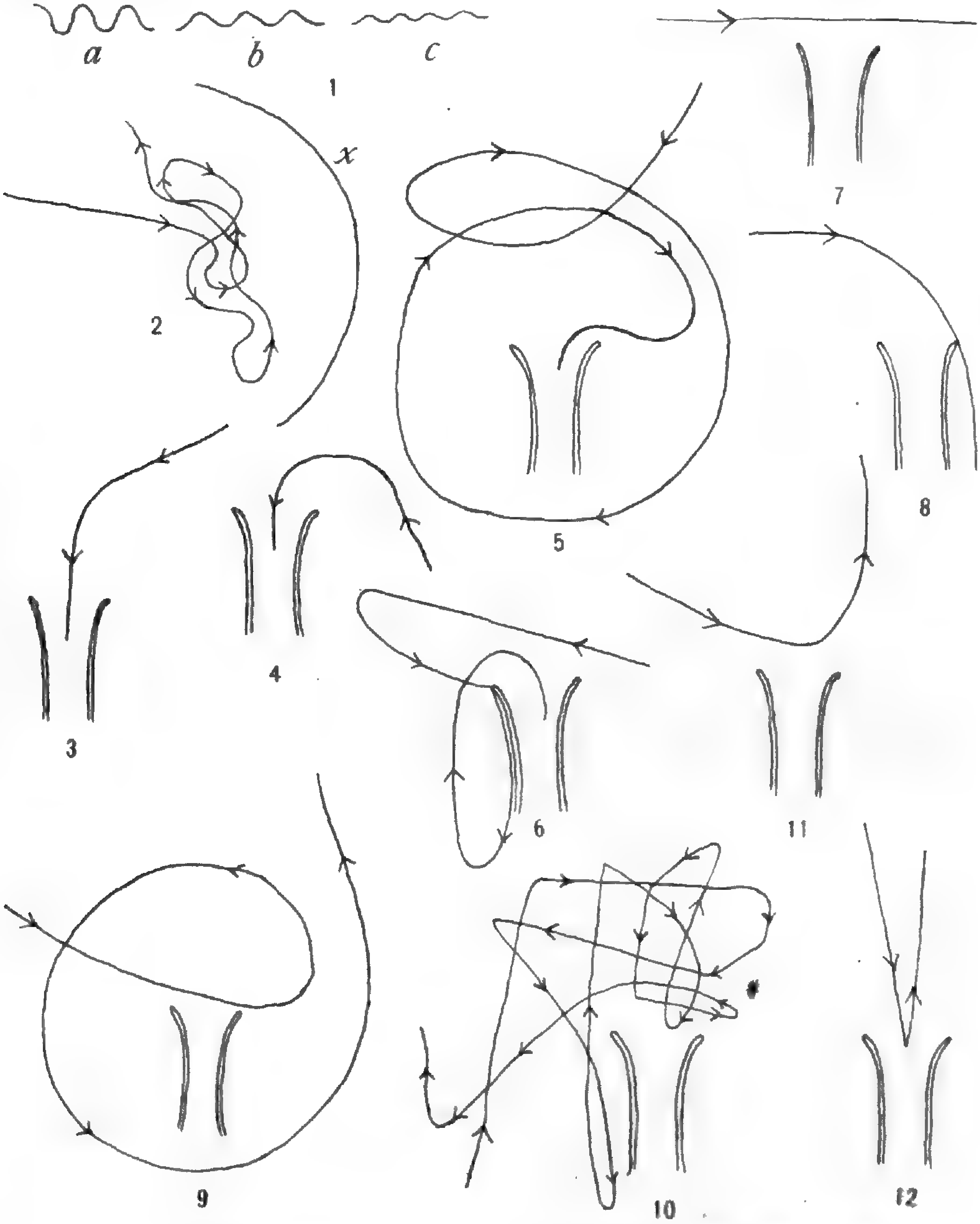

FIG. 1.—Spiral courses of sperms: *a*, thick ink; *b*, thin ink; *c*, water.
FIG. 2.—The position of the salt crystal is indicated by *x*.
FIGS. 3–12.—Various responses of sperms.

with respect to the archegonium, not by one large swing, but by a series of small swingings of their anterior ends and rotation on their axes as they go forward, thus reaching the archegonium by a number of successive changes in their spiral course. This reaction is characteristic for those sperms whose movements were sufficiently slow to be followed exactly. A few sperms were observed pursuing a markedly spiral course to the archegonium, and turning back whenever their movements tended to carry them away from it; and in all these cases where the movement was sufficiently slow to be followed, the sperms attained their orientation by a series of gradual swingings of their axes toward or away from the archegonium.

Occasionally, the sperms are observed to collect in a certain region, either in front of an archegonium or at some spot on a prothallus, and to swim about in this field. These react by turning back when they reach the boundaries of a fairly definite region, and only occasionally does one leave the group. Sperms entering this region do not react, but upon passing through and tending to leave it on the other side they react by turning back (*fig. 10*). These reactions are strictly comparable with those described by JENNINGS for Paramecium, and with the "apobatic" movements described by ROTHERT for certain bacteria.

It has been mentioned that some sperms will approach an archegonium without entering. Many of those which have been attracted and have gathered at the mouth of a full neck will suddenly leave the field of attraction; others which have entered and have passed down the neck will suddenly emerge at great speed, although others at the same time are being attracted and are entering. Since others are attracted it does not seem probable that the attractive substance has become repellent. We must believe, rather, that these sperms have become physiologically changed, so that they now react negatively to a substance to which they previously reacted positively.

Such emerging sperms are long and drawn out to almost a straight line; they shoot out violently from the archegonium, often forcing their way through the crowd of sperms collected at the mouth. They sometimes emerge backward, but usually come out with their anterior end foremost. They are sometimes seen to come from a great distance down the neck, apparently from the venter, and may begin to emerge within two minutes after the entrance has occurred. Sometimes they remain almost motionless in front of the archegonium and die after a few minutes; but often they recover and swim away. The movements of such sperms are strikingly different from normal movements. They move away quickly in almost a straight line, sometimes swerving slightly from their straight course, sometimes, upon striking an obstacle, turning slightly to one side and passing this; or they may move about irregularly, with irregular rotation on their axes. They move more in one plane than do the normal sperms, and do not show the marked swinging of their anterior ends that is characteristic of the normal movements. Often such sperms gradually regain their spiral form and their normal spiral movements, and finally swim off in a fairly normal manner. A few sperms which had left the archegonium were observed to go to the boundary of the attractive region, and then turn and reenter the archegonium.

The movements of the sperms under other conditions are exceedingly complex and varied. When sperms are placed in a very thick quince seed jelly, or when they enter far into a strong salt solution, they constantly swing their anterior ends about in large circles, at the same time rotating on their axes; they turn here and there, constantly changing their direction of movement, and frequently changing their direction of rotation. Thus one sperm in thick jelly was observed moving slowly forward in short jerks, by half-revolutions first in one direction and then in the other. Such movements are continued as long as the sperms are alive.

Sperms which have become attached to some solid body by their cilia or their vesicles perform almost every conceivable variety of movement which is possible for them under these conditions. They frequently whirl their unattached ends round and round in one direction, and then suddenly reverse this, making several or many turns in the other direction. After continuing this whirling for some time, they often swing from side to side several times and then continue whirling round and round as before. They give occasional violent jerks and swings, sometimes almost breaking themselves in two, and continue their complex movements until they die or free themselves.

Often sperms approach an open archegonium without entering, but remain at the mouth, uncoiling and coiling again and lashing about with their posterior ends. Since other sperms enter at the same time, it is difficult to explain these movements as being due to an injurious effect of the substance extruded from the archegonium.

On several occasions a peculiar reaction of the sperms was observed. This resembled the darting movements often seen in a swarm of gnats and will be described as the "darting reaction." Sperms exhibiting these movements collected in a fairly definite region, and showed almost constant motion, keeping one end still and swinging the other end about, or darting about in the field, here and there, with constant changes in their direction of movement. They move in every direction, sometimes approaching the archegonium, sometimes passing it, sometimes going away from it. Occasionally one proceeds in a fairly direct spiral to the boundary of the region, then turns directly back, approaches the archegonium, and resumes its darting movements. Such sperms usually do not enter the archegonium directly, but may wander in and out of the mouth. Some, however, remain in the archegonium, so that an accumulation of sperms finally occurs within the archegonial neck. A few of the sperms leave this field, but most of them remain in it until they die. Other sperms upon entering the field show the darting reactions immediately, and usually react by turning back whenever they approach the boundary of the region. This collection usually occurred in front of an open archegonium, but sometimes at other places, presumably where some of the cells of the prothallus were injured. The movements described were shown especially in the reactions of sperms of the same species and of other species toward the archegonia of *Athyrium Filix-foemina*, but were not shown in every case of entrance in this species, and were shown in a few cases of entrance in other species.

It now remains for us to consider which of the views stated above will best explain the movements and reactions described. We will first sum up the observed facts. It has been shown that any interference with the movements of sperms, whether by jelly, thick ink, a salt solution, or attachment to a solid particle, produces a series of complex movements; the sperms swing their anterior ends through large circles, at the same time rotating on their axes, and then go forward. If these movements free them from the hindrance, they resume their normal movements; but if the hindrance continues, they perform other complex movements, finally performing almost every conceivable variety of movement that is possible for them, and they continue these movements until they die or free themselves from the obstacle.

A few of the sperms showing the positive and negative reactions appear to turn directly toward or away from the stimulant. These swing their anterior ends through large circles, rotating on their axes, and then go forward in the new direction. Such movements often do not result, however, in the complete orientation of the sperms with respect to the stimulus; the final orientation is then attained by further successive swingings of their axes as they go forward. Most sperms attain their orientation by such small swingings of their axes toward or away from the stimulant as they go forward.

Occasionally sperms collect in a definite region by passing into this without reacting, and then turning back whenever they tend to leave it.

Finally, it has been shown that different sperms react differently to the same stimulus at the same time, and that the same sperm may react differently to the same stimulus at different times. In some cases these differences in reaction are due to different physiological conditions induced by different past experiences.

All these facts indicate that the reactions of fern sperms are due to the action of stimulants on the organism as a whole, and not to the direct action of a stimulant on local parts of the organism. The sperms possess a certain mechanism of reaction, and this mechanism is called into play by a change of conditions or by an interference with the normal movements. This mechanism is different in different sperms, and may be altered by different external conditions.

The strongest evidence for the direct orientation of the axes of the sperms by the stimulant is furnished by those cases in which the sperms respond by large swingings of their anterior ends and then go forward, turning fairly directly toward or away from the source of stimulation. Such cases do not prove, however, the "local action" theory of the reaction. These sperms may be regarded as having a mechanism of response by which they swing about until they are headed toward or away from the region of greater stimulation. They experience the conditions on all sides before continuing in their new direction, just as do those sperms which attain their orientation by many small spiral swingings in different directions. Furthermore, their new direction does not always take them directly toward or away from the source of stimulation, and their subsequent orientation is then attained by successive changes of their course as described for other sperms. Their reactions thus seem to be of the same kind as those described for other sperms. Sperms which react in this manner form a small part of those observed, and the reactions of other sperms do not accord with the "local action theory." It has been shown that some sperms collect in a region by strictly "phobotactic" responses. If we hold that the sperms described above react by "topotactic" movements, therefore, we must suppose that in both the positive and negative responses different sperms of the same species respond to the same stimulus by reactions of different natures. This is hard to believe. It seems, rather, that the sperms mentioned have their mechanisms of response called into play by the effect of the stimulant on the organism as a whole, and not by the action of the stimulant on local parts of the organism.

The reactions of fern sperms thus seem to be of the same kind as those described for protozoa.

Summary

1. Entrance of sperms into archegonia was obtained in every combination of species tried.

2. When the egg and sperm were of the same species, entrance into 97 archegonia, as shown by sections, resulted in 37 fusions; but when the egg and sperm were of different species, entrance into 129 archegonia failed to give a single fusion. A similar result was obtained by replanting prothalli on soil after entrance had occurred.

3. The results obtained, while not disproving the existence of fern hybrids, indicate that conclusions based on the structure of the sporophyte should not be accepted without additional experimental evidence, and show that not every combination of egg and sperm can result in a fusion.

4. Sperms of one species were observed within the archegonia of another species boring against the egg. The failure of such sperms

to enter the egg does not seem to be due to any failure of the sperm to perform its part in the process.

5. The failure of such sperms to enter the egg seems to be due either to some hindrance interposed by the egg, or to the interaction of egg and sperm. Since no means of hindrance on the part of the egg could be detected, it seems probable that this failure of the sperms to enter the eggs is due to an interaction of the egg and sperm. Such an interaction may be physical or chemical, or more probably both physical and chemical.

6. The movements of fern sperms are complex and varied. The reactions of the sperms depend on their physiological state, and this depends in part on the past experiences of the sperms.

7. Sperms have a mechanism of response which is called into action by a change of conditions or by an interference with the normal movements. In such cases they perform a series of complex movements and continue these until they die or free themselves from the stimulus.

8. Orientation of the sperms in both the positive and negative reactions is usually attained by a series of gradual swingings of their anterior ends accompanied by a rotation on their axes, and not by a sudden turning toward or away from the stimulant.

9. The observed movements and reactions seem due to the effect of the stimulant on the organism as a whole, and not to the action of different concentrations of the stimulant on local parts of the organism.

10. The reactions of fern sperms thus seem to be of the same kind as those described for protozoa.

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VARIATION AND CORRELATION IN RAYS AND DISK FLORETS OF ASTER FASTIGIATUS[1]

H. NAKANO

(WITH FOUR FIGURES)

Through various researches on the variation of Compositae, Umbelliferae, etc., LUDWIG (**1, 2, 3, 5, 6, 7, 10**) came to the conclusion that multimodal curves prevail in plants, and that the mode always falls on some member of the Fibonacci series, or often on some member of SCHIMPER-BRAUN'S accessory series, that is, on the so-called "Nebenzahlen." When a mode comes on a number other than that in the principal and accessory series, he considers this as a *Scheingipfel,* in which two curves with modes on two adjacent classes are combined.

On the other hand, in the variation of the rays of *Chrysanthemum Leucanthemum,* LUCAS (**8**) obtained the principal mode on 22, a result which is an exception to LUDWIG'S rule, but which seemed to find confirmation later in the researches of SHULL (**12**) and TOWER (**13**). The curves of these two authors, however, were altogether multimodal and obtained from comparatively scanty material. For example, SHULL doubled the classes on account of the sparseness of his material, so that the apparent multimodal curves changed to monomodal ones. It may not be useless, therefore, to examine the applicability of LUDWIG'S rule in the variation of the rays and disk florets of *Aster fastigiatus* Fisch. and Mey., using a tolerably large number of variates.

The true significance of two different results in LUCAS'S calculation was not clearly known until TOWER'S discussion (**13**) appeared. According to him, the number of rays of *Chrysanthemum Leucanthemum* decreases continuously during the flowering season (27.87–21.38 between July 5 and July 30), and LUCAS'S curve and his own were not influenced by the difference of the place-modes.

A little before the publication of TOWER'S work, SHULL'S admirable paper (**12**) on the variation and correlation in the bracts, rays, and

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[1] Preliminary note.

disk florets of *Aster Shortii, A. novae-angliae, A. puniceus,* and *A. prenanthoides* appeared. In this he recognized clearly the decrease of the number of the bracts, rays, and disk florets of *Aster prenanthoides* in the successive collections.[2]

The cause of the seasonal change of flowers in the multicipital Compositae is probably partly due to a change in nutrition, as HAACKE (**4**) and SHULL (**12**) have suggested; but an environmental condition seems to influence this decrease also. Recently Dr. KORIBA (**16**) of this laboratory found favorable material in the single-headed *Arnica unalaschensis,* which he collected on Mt. Hakkôda (Aomori), because the mean number of the rays changed exclusively from environmental changes. According to him, the mean increased from 14.389 to 15.741 between July 29 and August 5, for this was the season of thawing snow, and hence a favorable condition; then it decreased continuously to 15.081 on August 30.

During the summer of 1909 my attention was called to large patches of *Aster fastigiatus* on the banks of the Tone River, near Kokoku, Simosa Province, about thirty miles east of Tokyo. The number of rays and of disk florets was rather small, so that I was induced to calculate the coefficient of correlation between them. The present preliminary note seeks to verify LUDWIG's rule in the variation of these rays and disk florets, and to find the seasonal change in rays and the range of correlation between rays and disk florets.

The material was taken from three patches scattered through a grassy field (about 100 meters square) along the river bank. The environmental condition of these three patches was almost the same, and seems not to affect in any degree the variation of the flowers; therefore, only the difference of time seems to account for the differences in the three collections. The first collection was made in the eastern part of the field, the second in the western, and the third in the middle. In collecting specimens care must be taken, for random collection seems to give a little larger value than picking all flowers from every individual (LUCAS **14**); and the latter method, adopted in this investigation, may probably avoid personal error. All flowers that were injured by insects or that were extremely old or young were rejected.

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[2] From September 27 to October 8 the mean number of rays decreased from 30.769 to 26.335.

As shown later, the class range in an individual is very restricted, and falls perhaps on one part of the curve of the racial variation. For this reason a more reliable result can be obtained by taking into account the flowers from an equal number of individuals, rather than an equal number of flowers from an unequal number of individuals. Hence I have counted in all cases all the flowers in ninety plants. The calculation has been made wholly according to DAVENPORT (**15**), and the results obtained are as follows:

Variations of rays

The first collection was made August 7, 1909, when the flowers had first begun to bloom, and the following data were obtained:

Number	Range	Mode	A	σ	C
1392	10–31	17	17.921 ±0.051	2.831 ±0.032	15.799

The curve (*fig. 1*) of this variation gives the positive skewness (PEARSON **9,** p. 408) 0.325, the mean value being very near 18. On the mode 17 fall 17.10 per cent and on 18 fall 16.38 per cent of all variates.

The second collection was made August 11, with the following results:

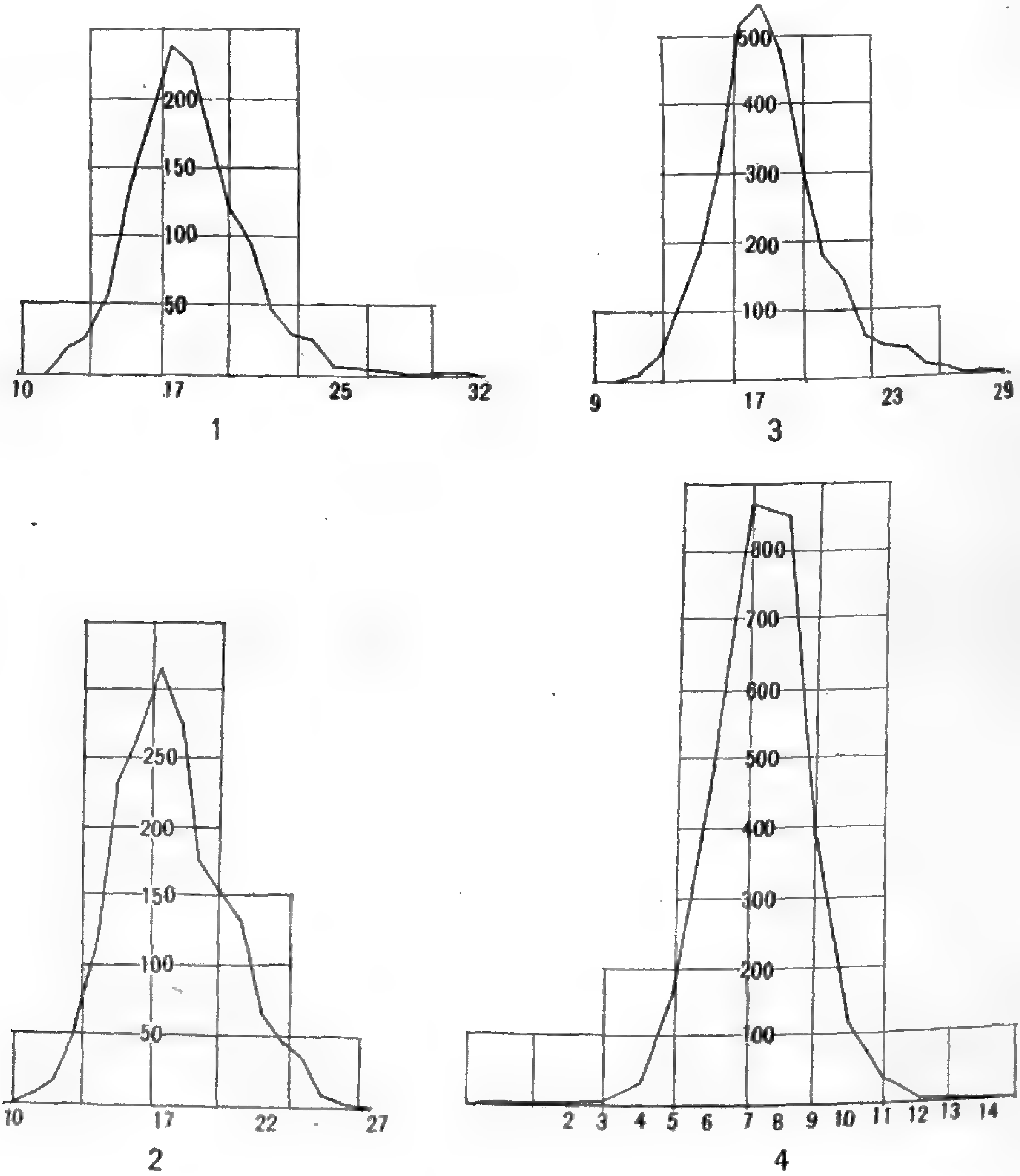
Number	Range	Mode	A	σ	C
1904	10–26	17	17.606 ±0.041	2.618 ±0.029	14.872

The percentage of variates occurring on mode 17 became a little less (16.55 per cent). This is due to the fact that the ordinates of the two classes 18 and 16 come nearly to the same height. The positive skewness became 0.231; the curve lessened the degree of asymmetry on account of the diminution in number of right-hand abscissae (*fig. 2*).

The third collection was made August 19, with the following results:

Number	Range	Mode	A	σ	C
2959	10–28	17	17.339 ±0.031	2.521 ±0.022	14.542

In this collection the range became somewhat wider than in the second, but all other elements decreased continuously. The mode came near to class 16, and the point of inflection of the curve came nearer to the origin than in the two foregoing collections. The variates falling on the mode 17 increased to 18.28 per cent, and the positive skewness became only 0.134 (*fig. 3*).



FIGS. 1–4

On comparing the above three collections, it can be seen easily that the constants of variation decrease continuously from the beginning to the end of the flowering season. The mean value of the rays decreased from 17.921 to 17.339 during twelve days, but no change of the mode was observed, the mode always holding its position on 17, which does not belong to the Fibonacci series. However, the oscillation of the mode between 18 and 16 may be observed from the first and third collections.

Variation of disk florets

This material was taken from the same flowers used in the third collection, and the constants calculated are as follows:

Number	Range	Mode	A	σ	C
2959	0–13	7–8	7.401 ±0.017	1.329 ±0.012	17.963

Lᴜᴅᴡɪɢ's rule did not hold in this case, since the mode falls on 7 rather than on 8, although 7 is a member of Sᴄʜɪᴍᴘᴇʀ-Bʀᴀᴜɴ's accessory series.

Individual correlation

I call briefly the correlation between the organs of the same individual the "individual correlation." Pᴇᴀʀsᴏɴ says (**9**, p. 392): "We have seen that the racial variation is greater than the individual variation, that capsules on the same poppy plant are more alike to each other than they are to the capsules of a second plant, or the leaves of one beech tree to each other than to those of a second beech tree. The resemblance of the like organs of the same individual is a special case of correlation, and we now want a quantitative measure of such correlation." I have tried, therefore, to find the value of the individual correlation, if such exists in my collections, and to throw some light upon this problem. For this purpose, I calculated the number (*R*) of classes and the difference (*D*) of the minimum and maximum classes in each individual variation, using the three collections mentioned above.

In the racial variation the class range was 10–31, that is, there occurred 21 different classes (one deficient in 11); while in the individual variation, as the above result (*R*) shows, only 2–10 different classes (rarely more than 6) occur, and curiously enough these classes happen to be almost continuous, as *D* clearly shows. From these facts we know that all the classes occurring in any individual, fall most probably on one part (perhaps on one side) of the curve in the racial variation, and that the classes in the individual variation are almost continuous.

1. NINETY PLANTS COLLECTED AUGUST 7

R	2	3	4	5	6	7	8	9	10	Total	*D*	2	3	4	5	6	7	8	10	11	Total
f	1	4	13	24	27	14	5	1	1	90	*f*	1	11	18	22	15	16	4	2	1	90

From this point of view, we should take into account the flowers in an equal number of individuals, if we wish to compare two collections in two different conditions, and not an equal number of flowers, because in the latter case we would probably obtain a curve that declines to one side or the other. For example, when in the second collection of rays 1431 heads from 70 plants were taken into account, the mean was 17.777; and when in the third collection 1366 heads from 49 plants were taken, the mean was 17.694; these are due undoubtedly to the smaller number of individuals that were in the first collection.

I have examined also whether the shifting of *R* and *D* occurs with the change of the flowering season.

2. NINETY PLANTS COLLECTED AUGUST 11

R	3	4	5	6	7	8	9	Total	*D*	2	3	4	5	6	7	8	9	Total
f	3	7	25	28	19	5	3	90	*f*	3	4	20	24	18	11	7	3	90

3. NINETY PLANTS COLLECTED AUGUST 19

R	3	4	5	6	7	8	9	10	Total	*D*	2	3	4	5	6	7	8	9	10	11	13	Total
f	1	2	9	23	30	14	7	4	90	*f*	1	2	5	22	29	11	12	5	1	1	1	90

In the second collection only a slight change occurred, while in the third collection the number of different classes in each individual increased to 7 (the most probable one), and accordingly the number of *D* shifted from 5 to 6. These increases result from the addition of classes of lower value, to which the seasonal change of rays is due.

Correlation between the number of rays and of disk florets

The material of the third collection was used in this calculation. A glance at the correlation surface in the accompanying table shows that correlation certainly exists in some degree. From the data of this table, I computed by PEARSON'S method the coefficient of correlation between the rays and disk florets of *Aster fastigiatus.* The result of my calculation is $r=0.3219\pm0.0111$. Since the coefficient of correlation always lies between 0 and 1, my result shows a significant correlation, though not in a high degree. Generally the correlation between the rays and disk florets appears not very large (SHULL **12**), so that SHULL found this coefficient only 0.574+–0.353 in *Aster prenanthoides;* while he obtained in the correlation of its rays and bracts 0.8559–0.7986. As to the change of the coefficient of correlation in the flowering season, which WELDON (**11**) and SHULL (**12**) discovered in another species, a future investigation of *Aster fastigiatus* is necessary.

CORRELATION SURFACE

RAYS	DISK FLORETS														TOTALS	MEAN OF DISK FLORETS
	0	1	2	3	4	5	6	7	8	9	10	11	12	13		
10	1	..	..	..	..	..	..	..	..	..	..	..	..	..	1	0
11	..	..	..	..	..	1	2	..	1	..	..	..	..	..	4	6.250
12	..	..	..	2	6	9	7	5	3	..	..	..	..	..	32	5.500
13	..	..	..	1	4	15	44	21	14	3	1	..	..	..	103	6.342
14	..	..	..	..	3	26	43	62	39	10	..	..	..	..	183	6.754
15	..	..	..	..	5	37	52	119	77	19	7	1	..	..	317	6.997
16	..	..	..	1	4	30	109	153	130	66	14	4	..	..	511	7.225
17	..	..	..	..	1	23	72	185	162	76	19	3	..	..	541	7.484
18	..	1	..	..	2	16	58	120	168	83	21	1	1	..	471	7.645
19	..	..	1	..	..	7	53	72	93	52	20	5	..	..	303	7.677
20	..	..	..	..	..	3	25	55	57	27	7	3	..	..	177	7.633
21	..	..	..	..	..	2	15	37	46	24	8	3	..	..	135	7.822
22	..	..	..	..	..	2	2	18	17	10	5	4	..	1	59	8.153
23	..	..	..	..	..	..	9	10	18	8	..	3	..	..	48	7.711
24	..	..	..	..	..	1	1	11	15	3	7	4	..	1	43	8.419
25	..	..	..	..	..	..	..	4	7	2	3	1	..	..	17	8.412
26	..	..	..	..	..	..	1	..	2	..	4	2	1	..	10	9.600
27	..	..	..	..	..	..	..	..	..	1	1	..	..	..	2	9.500
28	..	..	..	..	..	..	..	..	1	..	..	..	1	..	2	10.000
Totals	1	1	1	4	25	172	493	872	850	384	117	34	3	2	2959	

My thanks are due to Professor MIYOSHI for his valuable suggestions.

Summary

1. In the variation of the number of the rays and disk florets of *Aster fastigiatus* Fisch. and Mey., the curve is always monomodal, and its mode does not belong to the Fibonacci series.

2. The seasonal change in the number of rays is clearly observable in this species.

3. All the classes in individual variation have a tendency to fluctuate on one side or other of the curve of the racial variation, and appear to be almost continuous.

4. The number of rays and that of disk florets change correlatively to each other in a tolerably marked degree.

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CURRENT LITERATURE

BOOK REVIEWS

A history of botany

In considering a work professedly containing selections from the contributors to botany,[1] it is important to discover the reasons for the choice. Professor GREENE states that it is not his purpose to write a history of botany, or to treat in chronological succession of those who have upbuilt the science. As the introduction discusses a "philosophy of botanical history," the author's point of view may be looked for there.

There have been famous treatises on the philosophy of history, but there has been so little agreement that some are skeptical as to its reality. The author illustrates this from botanical writers, and concludes that "everyone may be permitted to have his own philosophy." He proceeds to state his own in the following words: "Upon the historian of botany it seems to devolve that he shall have some forecast of what botany in its perfection as a science shall be like; for in practice he sits in judgment on each epoch and decides whether as an epoch its tendency was more to the advancement of the science or to its retardation; from which kind of procedure it becomes certain that some ideal of perfection is in his mind." What the ideal is in this history may be inferred from the closing paragraph of the introduction: "I am unwilling to conclude this introduction without repeating it, that the essence and substance of botany proper are organography and the logical deductions that we draw from organography. They may not be said to be the whole of the science, yet duly and comprehensively considered they will be found to come near it. The line of development of organography—organography as necessarily including terminology—is that along which a truly coherent and philosophic history of botany must needs be written." It is legitimate to ask how far the subjective is involved in this, and how it may shape the ideal of the historian. The work gives evidence throughout that the taxonomic features of botany and the related subjects receive the fullest treatment. Organography comes to its own in systematic botany. No fault can be found with this in itself, for each man should do what he is best qualified to do by training and experience. But when we deal with history as such, there is danger of confusing the advocate and the historian.

Considerable pains are taken to show that classifying is a very ancient process,

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[1] GREENE, EDWARD LEE, Landmarks of botanical history. A study of certain epochs in the development of the science of botany. Part I, Prior to 1562 A.D. 8vo. pp. 329. Published by the Smithsonian Institution, Washington. 1909.

and that the roots of the science of botany are to be found before there was anything written. The author states that he has found no allusion among botanical writers to the fact of the universal existence of a crude primitive system of plant classification. The reviewer recalls that Dr. WHEEWELL, although not a "botanical writer," in his *History of the inductive sciences* develops in considerable detail the same idea, using botany and zoology as the best representatives of the classificatory sciences. The author seems to have laid emphasis on these older stages to show that due credit is not given to the older writers. This plea appears frequently in the book; one is not allowed to forget it. Such men as ADANSON, TOURNEFORT, and LINNAEUS were improvers, not creators. While granting all the truth there is in this, it seems to the reviewer that its importance has been overestimated. There has been some neglect in this respect, but the lack of definiteness and the changeableness in applying names and definitions have furnished a plausible excuse for the neglect.

Like SPRENGEL and MEYER, the author begins with the rhizotomi, or root-gatherers, who sought plants for religious, culinary, or medicinal purposes. Their experience, traditions, and written accounts were drawn upon by THEOPHRASTOS and others. The longest chapter, more than one-fourth of the volume, is given to THEOPHRASTOS, the "father of botany." It is based on a study of his *Historia plantarum*, a very full summary of its contents being given, with conclusions derived from their study. They are presented under the following heads: methods, vegetative organography, anthology, fruit and seed, anatomy, phytography, taxonomy, nomenclature, ecology, dendrology, and transmutation. I find phenology given in the case of TRAGUS, and physiology and pomology in that of VALERIUS CORDUS. These topics indicate what the author has sought or found in the works that have been studied. It is evident that he made a careful study of the *Historia plantarum*. In a recapitulation, containing seventeen items, there is a "list of facts botanical which THEOPHRASTOS saw, and in the main discovered." It is said to embrace "well-nigh all the first rudiments of what even today is universal scientific botany. It illustrates superabundantly the fact that THEOPHRASTOS, and no man of later time, is the father of the science as we now have and hold it." I find no reference, except in the biography and in two footnotes, to the other principal work of THEOPHRASTOS, the *De causis plantarum*, which in WIMMER's edition of his works, in pure Greek text without note or comment, takes only twelve pages less than the *Historia*. It would not fit so well into the author's ideal, since it deals more with matters physiologic, ecologic, and especially economic, how plants behave, how they are to be treated in cultivation, etc. MEYER complains that botanists, in their proclivity for the *Historia*, have "hitherto neglected in an unjustifiable way" this other "not less important" work.

Another chapter deals with those Greek and Roman authors whose botanical writings have survived. The Greeks are NICANDER, who wrote in verse on poisons and their antidotes; and DIOSCORIDES and GALEN, physicians, whose works are pharmaceutical and medical chiefly. Among the Romans the most important is PLINY, much like DIOSCORIDES in his treatment of plants; VERGIL, with his *Georgics* and *Bucolics;* and the writers on agriculture whose works are known under the title *De re rustica*. While all of these writers contributed something to botany, about all the phytography that has come to us from the ancients is to be found in the works of THEOPHRASTOS, DIOSCORIDES, and PLINY.

The remainder of the volume is taken up with those who have been called by the German writers "the fathers of German botany," or "the botanical reformers of the 16th century." Beginning with BRUNFELS and FUCHS, it is shown that to them is due an improved iconography, but not any reform in phytography. Their drawings from nature were substituted for the wretched and incorrect figures of the old herbals, but the accompanying descriptions were translations or compilations from the ancient authors. It was assumed that the plants of the Mediterranean region, which the old books described, grew in the fields and forests of Germany. Some changes were made by BRUNFELS in grouping plants, foreshadowing genera more akin to those now recognized, and real reform in phytography was made by BOCK, better known as TRAGUS. He studied plants in the field, and those not included in the older books were described in his clear and graphic style. Professor GREENE regards him as the "first father of phytography after THEOPHRASTOS." Although often paying close attention to the floral parts, he was still dominated by the idea that likeness in foliage, stem, and root, and sensible qualities like odor and taste, were better criteria of affinities than similarities in fruit and seed.

The two remaining chapters are devoted to EURICIUS CORDUS and his son VALERIUS CORDUS. EURICIUS published only one botanical work, the *Botanologicon*, but it so fully exposed the mistake of identifying the plants of Germany with those of the ancient writers that a decided advance was made in botany. To VALERIUS CORDUS the author assigns a high position, and from all that is known of his life and work he was an exceptional man. Dying at the age of twenty-nine, from exposure to the miasmatic climate of that part of Italy he was exploring in the heat of summer, it is felt that what was so well done in a life so short would have been greatly extended had his life been prolonged. In his *Geschichte der Botanik*, MEYER speaks of him as "a shining but fleeting phenomenon," and says "few have accomplished work of so many kinds and so great in so short a life." He was a lecturer on medicine, a botanical explorer, and a writer; and also a chemist and a mineralogist. TOURNEFORT speaks of him as "the first of all to excel in the description of plants"; and MEYER says that "his descriptions surpassed those of all his predecessors in precision and in the clearness with which they were brought home to perception" (*Anshaulichkeit*). Professor GREENE outlines the orderly plan of description adopted by CORDUS, and considers his special title to distinction to be that of "the inventor of the art of phytography," in doing away with the need of pictures of plants, and by showing that "every species could be so characterized in words as to be identifiable by description alone." His *Historia plantarum* was left in manuscript and was not published until several years after his death.

In these *Landmarks* Professor GREENE has made a very interesting and important contribution to the history of botany for a period which is comparatively inaccessible to readers of English alone. One appreciates how gradually the science has evolved. Although the epoch-makers of the modern science were to come later, the roots of many of the leading principles are here disclosed. The style is clear and animated, requiring no needless effort to grasp the author's meaning. An excellent index is an additional source of satisfaction.—E. J. HILL.

Vegetation dynamics in the desert

There is no habitat where the vegetation appears more static than in the desert, but SPALDING[2] has now clearly shown that well-defined successions are to be found there as well as elsewhere, and that the "struggle for existence" involves "competition" between plant individuals as well as strenuous relations with untoward physical surroundings. The material here presented is the result of several years of intensive study on Tumamoc Hill (the location of the Desert Laboratory) and the adjoining valley, and it is concluded that the distribution of plants in that neighborhood can be accounted for by causes now in operation. The first chapter considers the plant associations and habitats. The river and irrigating ditches are relatively poor in aquatics. The river margin is fringed with an association in which cottonwoods and willows dominate, while the mesquite (*Prosopis velutina*) is the dominating species of the floodplain; an interesting phenomenon in the latter habitat is the invasion of the more xerophytic *Bigelovia Hartwegii*. Salt spots are present with characteristic halophytes, but the most pronounced of the latter (i.e., *Suaeda Moquini*) grows more luxuriantly along irrigating ditches than in salt spots. The washes, which are dry drainage channels, are characterized by the palo verde (Cercidium) and catclaw (*Acacia Greggii*), while the more xerophytic slopes are tenanted largely by the creosote bush (Larrea) and Franseria associations. The hill is characterized by Fouquieria and Parkinsonia on any exposure, while the giant cactus (*Cereus giganteus*) and *Encelia farinosa* are essentially south-slope species; *Lippia Wrightii* equally characterizes north slopes, which are also much richer in the aggregate number of species and individuals than are other slopes. An account of the lichens is given by FINK, Acarospora being the most characteristic genus; the lichens generally are unusually xerophytic in structure.

The second chapter considers the detailed distribution (with maps) of some of the more characteristic species, and the third chapter has to do with environmental and historical factors. An account of the geology of the region is presented by TOLMAN, and of the soils by LIVINGSTON. There are extensive tables depicting the soil moisture, rainfall, temperature, and evaporation. MACDOUGAL contributes an interesting chapter on the origin of desert floras; xerophytes are regarded as of recent origin, and the view, formerly current, that the desert xerophytes have arisen through adaptation is opposed, at least as a general explanation. The final chapters give a review, discussion, and summary.

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[2] SPALDING, VOLNEY M. Distribution and movements of desert plants. pp. v + 144. *pls. 31.* Carnegie Institution of Washington, Publication 113. 1909.

Spalding concludes that even in deserts soils play a great part in distribution, and that physiographic factors play an efficient part as in the East. He finds that as the region is gradually base-leveled, the area of the mesquite association widens, that the palo verde-catclaw association advances similarly along the washes, and that the creosote bush advances along the slopes. The latter species is of wide range, appearing in areas as a pioneer and also remaining as the final possessor; and yet the xerophytic structures of this plant are simple as compared with the spectacular features of the giant cactus, whose range is much more restricted. The soil factors that appear most important are the soil water content, the percentage of alkali, and the soil texture (involving aeration). That not all distributional factors reside in the soil is shown by the fact that the giant cactus is chiefly an inhabitant of south slopes (attributed to the need for high temperatures), and especially by the fact that *Lippia Wrightii* is restricted to the north slope about the laboratory, while it is just as definitely restricted to the south slope in the mountains at an altitude of 1000^m above the laboratory. Spalding has here given us one of the most notable of recent contributions, clearly showing that the intensive study of plant associations is quite as productive in results in deserts as in mesophytic climates.—H. C. Cowles.

Evolution

It is a matter for congratulation when the subject-matter of any great field is gathered together and systematized by a master hand. The first volume of Lotsy's lectures on the theories of descent has been reviewed in these pages,[3] and the second volume should have been noticed sooner.[4] The first chapters of the second volume consider various phases of Darwinism, noting first the factors that influenced Darwin's investigations. The various prerequisites of Darwinism, such as variability, selective value, and the struggle for existence, are first considered. It is recognized that Darwin did not attempt to explain variability, assuming it as given. Nor did Darwin distinguish sharply between variations and mutations, a view that seems to the author to be borne out by Klebs's experiments. After lectures on orthogenesis, selective value, the struggle for existence, the inheritance of deviations, there follow several lectures on the facts of paleontology and plant geography that are explained by the Darwinian theory. The objections to Darwinism are considered, the matter of the isolation of deviating individuals being considered one of the more important. The closing lectures deal with post-Darwinian theories, notably those of Wallace, Nägeli, and DeVries, while one lecture is devoted to Neolamarckism. At the close is an excellent bibliography. Lotsy's volumes form an indispensable compendium of information, not alone to students of evolution, but to all biologists, and particu-

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[3] Bot. Gazette **42**:60–61. 1906.

[4] Lotsy, J. P., Vorlesungen über Descendenztheorien mit besonderer Berücksichtigung der botanischen Seite der Frage, gehalten an der Reichsuniversität zu Leiden. Zweiter Teil. 8vo. pp. vi+420. *pls. 13. figs. 101.* Jena: Gustav Fischer. 1908. *M* 12; geb. *M* 15.

larly to all botanists, since this work presents especially the botanical aspects of the evolutionary theories; most former works of similar character have had a strong zoological bias, which has resulted in a most imperfect consideration of botanical material.—H. C. Cowles.

MINOR NOTICES

Monograph of Oenothera.—Léveillé[5] has issued another fascicle of his monograph of the genus Oenothera, which includes the Onagras *O. Lamarckiana*, *O. biennis*, *O. grandiflora*, and related forms. His work on most of the species has been entirely from herbarium material, with the result that the process of "lumping" rather than "splitting" the species is carried to an extreme. Numbers of species are combined into larger groups, for which new names are proposed. For example, *O. pyramidalis* Lévl. is to include *O. rhombipetala* Engelm. and Gray, *O. heterophylla* Spach, and several others. Similarly, *O. polymorpha* Lévl. includes *O. mollissima* L., *O. longiflora* Jacq., *O. nocturna* Jacq., and a number of others. The "lumping" process reaches an extreme, however, in the treatment of *O. biennis*, *O. Lamarckiana*, and related forms. All are gathered into one comprehensive "species," *O. communis* Léveillé, having three "races": *biennis* L., *Vriesiana* Lévl., and *japonica* Guffroy. The last is a Japanese form with triangular seeds. The race *Vriesiana* includes *O. Lamarckiana* and all its mutants, and one or two other species. The race *biennis* L. includes such well-recognized species as *O. muricata* L., *O. parviflora* L., *O. Hookeri* Torr. and Gr., *O. Oakesiana* Robb. and Wats., *O. strigosa* Rydb., *O. cruciata* Nutt., and a number of others. Many of these have been shown to come true in cultures, and the types are sufficiently distinct to be easily recognizable even as very young seedlings. The present *O. biennis* L., after excluding all the segregates, is probably still considered sufficiently "polymorphic" by most American botanists.

DeVries has emphasized the necessity of differentiating between elementary species and Linnean species, the latter only being recognized in the floras and manuals, and the elementary species being enumerated in their subordinate rank. But the indiscriminate "lumping" practiced here far surpasses the necessities of even the manuals.

Having thus combined this host of forms into one "species" (*O. communis*), Léveillé proceeds to argue that mutation accounts for the origin of races, but that the origin of species is another problem. He states that he grew *O. Lamarckiana* and several of the mutants in his garden for five years, from seeds of DeVries, and reports various wonderful transformations of one form into another. DeVries's investigations have been verified abundantly by later careful workers, so that Léveillé's statements need not be taken seriously, especially since he made no attempt to prevent crossing. He naïvely states that the plants were grown in two separate gardens, and that, in one case at least, the forms were sufficiently distant to prevent crossing!—R. R. Gates.

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[5] Léveillé, H., Monographie du genre Oenothera (with the collaboration of Ch. Guffroy). pp. 339–408. Le Mans. 1909.

Vegetationsbilder.[6]—The sixth and seventh parts of the seventh series of KARSTEN and SCHENCK'S well-known work reproduces twelve photographs of typical plant formations in East Bolivia, with text by TH. HERZOG. The illustrations include studies from the rain forest, the xerophytic mountain slope, the scrub, and desert societies. The series is completed in an eighth part illustrating the plant formations of Danish West Greenland in six photographs, with descriptive text by M. RIKLI. The illustrations include type areas from birch forest, heath, bog, arctic meadow, and polster societies.

The eighth series of the same work is begun with six plates from photographs by FRANZ SEINER, who also contributes the descriptive text. The plates are of the same superior quality which characterizes the entire series, and illustrates the vegetation of the dry steppes of northern and central Kalahari. Small leguminous trees form a conspicuous part of the vegetation, and among the species illustrated are *Copaifera coleosperma*, *C. mopane*, *Acacia haematoxylon*, *A. hebeclada*, *A. detinens*, and *A. horrida*, the last overgrown with *Loranthus Dregei*.—GEO. D. FULLER.

Das Pflanzenreich.[7]—Part 40 consists of a monographic presentation of the Papaveraceae by DR. FRIEDRICH FEDDE. About 80 pages, devoted to a general account of the family, precede the taxonomy. The author divides the family into three subfamilies, namely Hypecoideae, Papaveroideae, and Fumarioideae; the first two only are elaborated in the present volume. Twenty-six genera are treated, to which are referred over 400 recognized species and numerous varieties; of these about 30 species and approximately 70 varieties are new to science. New species are described in Glaucium, Papaver, Platystemon, and Roemeria. Excellent keys precede the enumeration and description of species; bibliography and exsiccatae are very fully given; and numerous illustrations materially supplement the text. The work is an exhaustive and authoritative treatise of this interesting group of plants.—J. M. GREENMAN.

Symbolae Antillanae.[8]—The second fascicle of volume VI of this scholarly work continues the presentation of the Solanaceae by O. E. SCHULZ, in which 38 species of Solanum are recorded, 4 species and 5 varieties being new to science. The genus Cestrum is represented by 19 species. Professor URBAN contributes an article on the high mountain flora of Sto. Domingo, and A. COGNIAUX begins a detailed consideration of the Orchidaceae, treating 26 genera to which are referred 176 species; new species are described in Spiranthes, Pseudocentrum, Stelis,

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[6] KARSTEN, G., AND SCHENCK, H., Vegetationsbilder. Series vii, parts 6–8. Text and *pls. 31–48;* Series viii, part 1. Text and *pls. 1–6.* 4to. Jena: Gustav Fischer. 1910. *M* 4 per part.

[7] ENGLER, A., Das Pflanzenreich. Heft 40 (IV. 104). Papaveraceae-Hypecoideae et Papaveraceae-Papaveroideae von FRIEDRICH FEDDE. pp. 430. *figs. 43* (*532*). Leipzig: Wilhelm Englemann. 1909. *M* 21.60.

[8] URBAN, I., Symbolae Antillanae seu fundamenta florae Indiae Occidentalis. Vol. VI, fasc. 2. pp. 193–432. Leipzig: Fratres Borntraeger. 1909.

Pleurothallis, Habenaria, Pogonia, and Microstylis. The descriptions of species in each genus are preceded by determinative keys.—J. M. GREENMAN.

North American flora.[9]—Volume IX, part 3, of this work consists of an elaboration of the Agaricales as follows: Boletaceae and Chantereleae by W. A. MURRILL, and Lactarieae (pars) by G. S. BURLINGHAM. New species are described in Gyroporus (1), Ceriomyces (5), and Suillellus (1). Three new monotypic genera of the Agaricaceae are proposed, namely, *Polyozellus, Plicaturella,* and *Chlorophyllum.*—J. M. GREENMAN.

NOTES FOR STUDENTS

Graft hybrids.—The question of graft hybrids continues to grow in interest. WINKLER's previous papers on this subject have already been reviewed in this journal.[10] His latest contribution[11] deals with the second and later generations of the graft hybrids between *Solanum nigrum* and *S. lycopersicum,* and with the chromosome numbers in these forms. It is found that the different graft hybrids fall into a series resembling most one or the other parent, in the following order: *S. nigrum, S. Gaertnerianum, S. Darwinianum, S. tubingense, S. proteus, S Koelreuterianum, S. lycopersicum,* the first three graft hybrids being most like *S. nigrum* and the last two nearest *S. lycopersicum.* In the F_2 the first three revert to *S. nigrum,* while the other two produce the tomato. Large numbers of offspring were grown in some cases, e.g., 1200 individuals in the F_2 of *S. tubingense,* all of which without exception were pure *S. nigrum.* The F_3 and F_4 and later generations continued true *S. nigrum.* Regenerated adventive shoots also reverted only to the nightshade, but in the case of *S. proteus* reversions to both parents occurred, and in this and other cases various chimeras appeared from adventive shoots. *S. Gaertnerianum* is almost sterile and shows little tendency even to parthenocarpy, which is more frequent in some of the others.

Crosses of the graft hybrids with the parent they most resembled gave similar results, e.g., *S. tubingense*×*S. nigrum* gave only *S. nigrum.* Crosses with the more distant parent, as *S. tubingense*×*S. lycopersicum,* failed to produce seeds, although parthenocarpy frequently occurred.

Regarding the chromosomes, in *S. lycopersicum* the numbers were 12 (haploid) and 24 (diploid), and in *S. nigrum* 36 and approximately 72, therefore three times as many. If a fusion of nuclei took place in the production of the graft hybrid, one might expect the latter to have 72+24 (96) chromosomes unless a regulation in the number afterward occurred; but this number is not found. Instead, *S. tubingense, S. Darwinianum,* and *S. Gaertnerianum* were found to have 36 chromosomes in their pollen mother cells (after reduction), while the other two

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[9] North American flora. Vol. IX, part 3. pp. 133–200. New York Botanical Garden. 1910.

[10] BOT. GAZETTE **47**:84, 250; **48**:478. 1909.

[11] WINKLER, HANS, Ueber die Nachkommenschaft der Solanum-Pfropfbastarde und die Chromozomenzahlen ihrer Keimzellen. Zeit. Bot. **2**:1–38. 1909.

possessed 12 chromosomes. Therefore in both cases the numbers are the same as in the parents to which they revert in the F_2. This of course does not eliminate the possibility that a fusion of nuclei had occurred, and that afterward a regulation in the number took place, perhaps just previous to reduction or at the time of reduction.

STRASBURGER[12] has made a number of Solanum grafts according to WINKLER'S method, and examined the growing tissues along their line of union, to determine whether cell fusions take place. He found no indication that such is the case, but of course negative evidence in such a matter is inconclusive, for the graft hybrids are rare at best. STRASBURGER concludes that WINKLER'S cases are really complicated chimeras, in which the tissues of the two parents are intimately blended in the growing points. He proposes to call them "hyperchimeras," and cites various analogous cases of very intimate relationship, such as between parasite and host.

WINKLER, however, is still convinced that these cases are true graft hybrids, although concurring in STRASBURGER'S opinion that *Cytisus Adami*, which STRASBURGER[13] showed to have the same number of chromosomes as its parents, is a chimera. He proposes to determine the chromosome number in the somatic cells of the Solanum hybrids to see whether it is higher than in the germ cells, and contends that, even though no fusion of nuclei occurs, in its absence the effect of the cytoplasm of one type of cell upon the other will be necessary to explain the production of the characters of the graft hybrids. This view scarcely seems necessary to explain the present facts, but WINKLER'S further cytological papers to determine what actually occurs will be awaited with interest. It is hoped that full accounts, with figures, will be forthcoming.

BAUR[14] has reiterated recently his belief that these forms are explainable as periclinal chimeras, varying in the arrangement of the layers in the growing point, and thinks that the case of Crataegomespilus can be explained in the same way.

The fact that in these Solanums the number of chromosomes is so unlike adds much to the interest of the situation.—R. R. GATES.

Sexuality of the rusts.—The differences of nuclear behavior in the rusts as described by BLACKMAN and CHRISTMAN have led KURSSANOW[15] to investigate a similar form. According to BLACKMAN,[16] in the caeoma of *Phragmidium violaceum* the nucleus of a vegetative cell passes into that of a specially differentiated female

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[12] STRASBURGER, E., Meine Stellungnahme zur Frage der Pfropfbastarde. Ber. Deutsch. Bot. Gesell. **27**:511–528. 1909.

[13] ———, Ueber die Individualität der Chromosomen und die Pfropfhybriden-Frage. Jahrb. Wiss. Bot. **44**:482–555. *pls. 5–7. fig. 1.* 1907.

[14] BAUR, E., Pfropfbastarde, Periklinalchimären, und Hyperchimären. Ber. Deutsch. Bot. Gesell. **27**:603–605. 1910.

[15] KURSSANOW, L., Zur Sexualität der Rostpilze. Zeit. Bot. **2**:81–93. *pl. 1.* 1910.

[16] BLACKMAN, V. H., On the fertilization, alternation of generations, and the general cytology of the Uredineae. Annals of Botany **18**:323–373. 1904.

cell, which bears an abortive trichogyne-like organ. According to CHRISTMAN,[17] on the other hand, in the caeoma of *Phragmidium speciosum* we have the conjugation of two equally differentiated cells. BLACKMAN, therefore, believes that a heterogamous condition obtains, while CHRISTMAN describes an isogamous one. In the subsequent papers of these two authors this essential difference is still manifest (see BLACKMAN and FRASER,[18] CHRISTMAN[19]). In a more recent publication, OLIVE[20] compares these differences and takes a middle ground, believing that both BLACKMAN and CHRISTMAN are in particular cases right. In four forms of the same caeoma type as Phragmidium, OLIVE finds that the cells conjugate as described by CHRISTMAN, but that one is larger than the other, that is, a male and a female cell conjugate, the male cell lying a little below the female, which is always surmounted by a trichogyne-like abortive cell, while the male cell has no such abortive portion. During conjugation a broad opening may be present between the two cells, allowing the protoplasmic contents to mix, as described by CHRISTMAN, or only a narrow opening between the two cells may be present, so that only the nuclei of the male cells pass into the female cells, a condition which OLIVE believes to agree with BLACKMAN'S description. The two phenomena may be observed in the same plant. OLIVE thus seeks to harmonize the views of BLACKMAN and CHRISTMAN.

KURSSANOW has investigated a caeoma, which he found growing on *Rubus saxatilis* near Moscow, and which he regards as the same or a very similar form to the caeoma studied by CHRISTMAN. He regards CHRISTMAN'S studies as too brief to be conclusive, and endeavors to extend the observations. The cells of the vegetative hyphae and haustoria are uninucleate, the nuclei being comparatively large and distinct. Numerous spermatogonia are present on both surfaces of the leaves, whose origin and development are described, with the result that the cells are always uninucleate. The caeomas appear only on the under sides of the leaves. The formation of a sort of palisade arrangement of uninucleate large terminal cells as described by CHRISTMAN is also described by KURSSANOW. There is a conjugation in pairs of these cells, which he regards as equal in size. There is no condition found which could be made to agree with OLIVE'S description, but his account is in complete harmony with CHRISTMAN'S results. The differences in the methods of conjugation as described by BLACKMAN, CHRISTMAN, and OLIVE, this author believes may be due to differences in the forms investigated

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[17] CHRISTMAN, A. H., Sexual reproduction in the rusts. BOT. GAZETTE **39**:267–274. 1905.

[18] BLACKMAN, V. H., AND FRAZER, MISS H. C. I., Further studies on the sexuality of the Uredineae. Annals of Botany **20**:35–48. 1906.

[19] CHRISTMAN, A. H., The nature and development of the primary uredospore. Trans. Wis. Acad. Sci. **25**:517–526. 1907; Alternation of generations and the morphology of the spore forms in the rusts. BOT. GAZETTE **44**:81–101. 1907.

[20] OLIVE, E. W., Sexual cell fusions and vegetative nuclear divisions in the rusts. Annals of Botany **22**:331–360. 1908.

or to a pathological nuclear migration, as suggested by CHRISTMAN, which KURSSANOW has often observed accompanying the normal sexual process. He believes the sterile cells, which are equally well formed on all of the fertile ones, are not to be regarded as trichogynes. They appear to act only as buffers between the epidermis and the fertile cells. He strongly doubts any connection or direct relationship of the rusts to the red algae.—J. B. OVERTON.

Animal ecology.—It is pleasant to note greatly increased activity along ecological lines on the part of zoologists. Contributions that should have been noticed here long since are found in papers by SHELFORD, RUTHVEN, and HANKINSON. SHELFORD[21] has considered the relation of tiger beetles to plant succession, and has found that there is quite as definite a succession of forms, when the physiography changes, as has been recorded for plants. For example, certain species of Cicindela characterize the beach of the dune region near Chicago, while others take their place as the dunes develop, and still others as the dunes become established. Similar succession stages are given for depressions. No species seems to be fitted for life in the climax mesophytic forest of the region.

RUTHVEN,[22] after presenting the environmental features of certain regions of New Mexico and Arizona together with full descriptions of the animals collected, gives an exceedingly interesting summary. It is concluded "that each set of environmental conditions which is marked out by a distinct plant association has a definite reptile fauna," and that the sharpest line between the animal associations is that corresponding to the line between the pinyon-cedar association and the more arid treeless associations. It is also noted that continued denudation may be expected to result in the increased development of the arid associations. Plant ecologists, who as a class have long recognized the fundamental errors in MERRIAM'S zonal classification as applied to plants, will be interested in observing RUTHVEN'S conclusion, based on reptiles and amphibians, that "it seems advisable not to stretch any one zone over the entire continent." The paper is illustrated by a number of halftones showing characteristic animals and habitats.

HANKINSON[23] has given a detailed account of a biological survey of a small Michigan lake. Following an account by DAVIS on the physiography and geology of the region, HANKINSON gives a detailed statement concerning the various field stations and their characteristics, nine kinds of habitats being recognized between the shore and deep water. After an ecological account of the fish fauna by HANKINSON, DAVIS treats of the flora and its ecological features, giving a list of the

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[21] SHELFORD, V. E., Preliminary note on the distribution of the tiger beetles (Cicindela) and its relation to plant succession. Biol. Bull. **14**:9–14. 1907.

[22] RUTHVEN, A. G., A collection of reptiles and amphibians from southern New Mexico and Arizona. Bull. Amer. Mus. Nat. Hist. **23**:483–604. 1907.

[23] HANKINSON, T. L., A biological survey of Walnut Lake, Michigan, with chapters on the physiography, geology, and flora of the region by CHARLES A. DAVIS, and a paper on the aquatic insects of the lake by JAMES G. NEEDHAM. Rep. Mich. Geol. Surv. **1907**:157–288. 1908.

aquatic plants collected. HANKINSON then considers the lake fauna in general, concluding with a summary of the life and the life conditions of the littoral and abyssal parts of the lake. Following an appendix with diversified matter are a large number of excellent plates, most of which illustrate the characteristic lake habitats.—HENRY C. COWLES.

Various colored lights and photosynthesis.—It is fast becoming evident that the telling work in the advance of plant physiology is to be done by men who are prepared to work by the exact methods of the physicist and chemist. One feels that KNIEP and MINDER[24] have indicated the way for the final settlement of the perplexing question of the part played in photosynthesis by the various portions of the spectrum. They have given great attention to developing suitable screens and to accurate methods of determining the energy values of the light thus obtained. This is apparently done with exact knowledge and application of the physics involved. Although it is unfortunate that the rate of synthesis must be tested by the bubble method, this seems to be the least objectionable method available. In the light used all heat, as well as infra-red and ultra-violet rays, was cut out by distilled water containing traces of potassium bichromate and ammoniacal copper sulfate. The screens were specially made colored glass, the spectra of which were fully studied. The measurements were made between 11 A.M. and 12:30 P.M. by means of reflected sunlight. The present paper reports the results of measurements of the synthetic value of equal energy intensities (as shown by the blackened thermopyle) of red light (620 $\mu\mu$ toward the infra-red), blue light (523.8 $\mu\mu$ toward the ultra-violet—little transmission to the left of 509 $\mu\mu$), and green light (512–524 $\mu\mu$). Green gave no photosynthesis. Red and blue of equal energy value gave equal photosynthesis. This finding is quite in contrast with the current conception of plant physiologists who hold that the blue end of the spectrum plays little part in the process. This view is due to the fact that the blue screens commonly used reduce to a much greater degree the energy intensity than do the red. It is evident that the relative value of the two portions of the solar spectrum is approximately proportional to the relative energy amounts of the two portions. These relative amounts vary with the time of day, cloudiness, humidity, altitude, etc., the red, of course, being in general greater, but the blue far from negligible. The writers mention that this is only the first step in this important work. They hope by the use of suitable screens, or prism-resolving methods, to study the photosynthetic value of each portion of the spectrum on the basis of its energy value, and to construct a complete curve of this value.—WM. CROCKER.

Germination of the seeds of certain parasites.—The germination of the seeds of various parasites belonging to the Rhinanthaceae has been rather extensively investigated. Two of the more recent studies illustrate two of the more prominent

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[24] KNIEP, H., UND MINDER, F., Ueber den Einfluss verschiedenfarbigen Lichtes auf die Kohlensäureassimilation. Zeit. Bot. 1:619–650. 1909.

types of development. In the hemiparasite *Melampyrum pratense*, GAUTHIER[25] found that the seeds germinated without any stimulus from other organisms, and that the seedlings had a short independent existence, during which the roots branched freely. Root hairs developed in abundance, many of them consisting of two or three cells, but before the food stored in the seed became exhausted, the root hairs began to be replaced by haustoria which penetrated the roots of the host. Trees with mycorhiza upon their roots were the hosts, the beech much more frequently than other species. Failure to effect a contact with a suitable host resulted in the early death of the seedlings. The investigator stated that the seeds, in common with those of Rhinanthus, Euphrasia, and Pedicularis, would not germinate if allowed to become dry.

HEINRICHER studied the same species,[26] obtaining results essentially similar to the above, but he claims[27] that in general the seeds of Rhinanthus, Euphrasia, and Pedicularis are not so sensitive to desiccation, but retain their vitality for several months, although some of them germinate only during the spring. He has studied the group extensively, and in the recent article summarizes the life history of a highly specialized type discussed in a former paper.[28] The seeds of Tozzia germinate only with the chemical stimulus afforded by the roots of the host, its cotyledons never appear above the soil, and for two or three years it is a subterranean holoparasite. Finally it sends up an aerial shoot which becomes green, flowers, and produces seeds. As the seeds mature the plant dies, each individual flowering once only.—GEO. D. FULLER.

Vegetation of the Danish West Indies.—As a result of further study of the halophytic vegetation of the Danish West Indian Islands, BØRGESEN[29] has modified somewhat his former classification of the plant societies involved, and now distinguishes a hydrophytic vegetation composed of sea grass and algae, and a halophytic vegetation embracing the muddy soil vegetation, the sand strand vegetation, and the rocky coast vegetation. The muddy soil vegetation is made to include the mangrove, Salicornia, and Conocarpus formations. The author places emphasis upon the influence of exposure and soil consistency as the deciding factors in limiting the mangrove formation, which he defines as a formation of treelike evergreen plants growing on the sheltered shores, partly in shallow salt or

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[25] GAUTHIER, L., Sur le parasitisme du *Melampyrum pratense*. Rev. Gén. Bot. **20**:67–84. 1908.

[26] HEINRICHER, E., Die grünen Halbschmarotzer, V. Melampyrum. Jahrb. Wiss. Bot. **46**:273–376. 1909.

[27] ———, Germination des graines des plantes parasites. Rev. Gén. Bot. **21**:329–337. 1909.

[28] ———, Die grünen Halbschmarotzer. III. Bartschia und Tozzia. Jahrb. Wiss. Bot. **36**:665–752. 1901.

[29] BØRGESEN, F., Notes on the shore vegetation of the Danish West Indian Islands. Bot. Tidssk. **29**:201–259. *pls. 3–6.* 1909.

brackish water, partly on low-lying soil which is rarely, sometimes never, covered by salt or brackish water.

While visiting the islands in 1906, he noted that the extensive mangrove forest occupying one of the larger lagoons had perished. The explanation seems to be that in 1899 the island was ravaged by a serious hurricane, which so violently agitated the sea that large quantities of clay and gravel were washed into the lagoon and deposited as a layer several inches thick. This caused so sudden a change in the soil constitution as to destroy the forest, although there were clear indications that the same formation would eventually reclaim much of the area formerly occupied.

The small trees growing in drier situations seem sufficiently distinct from the mangroves to be regarded as a distinct society, which is named the "Conocarpus formation," after the most conspicuous member. This formation is regarded as very nearly the ecological equivalent of the Nipa formation of SCHIMPER in the Indo-Malayan strand flora. The vegetation of the sand strand exposed to the wind includes the well-known Pes-caprae formation, an aggregation of shrubs designated the Tournefortia formation, and the forest Coccoloba-Manchineel formation. The anatomy of several of the strand plants has been investigated, and some further studies made of the more xerophytic vegetation of the rocky coasts.—GEO. D. FULLER.

Loess and plant societies.—The intimate relation between physiographic plant ecology and geology receives emphasis in the evidence deduced by SHIMEK[30] to prove that the irregular distribution of loess deposits has been effected by the character of formerly existing plant societies. Vegetation is known to play an important part in pulverizing the soil, affording anchorage for fine wind-blown particles, and finally in returning its own substance to the soil in a finely subdivided condition. Thus well-drained areas supporting heavy mesophytic vegetation accumulated fine material now appearing as moderate deposits of loess of uniform quality. Xerophytic societies of unequal density resulted in inequality and irregularity of the deposits, while hydrophytic areas, as well as those of such elevation or aridity as to be without vegetation, collected no loess. The very diverse aspect of the plant societies on the east and west sides of large streams like the Mississippi is found to correspond exactly with the difference in quality and distribution of their loess deposits. The interstratification of sand the author believes to have resulted from periods of very scanty vegetation caused by climatic changes.

While the thesis is essentially an argument in support of the eolian hypothesis for the formation of loess, it has many points of interest for the ecologist; for should further evidence prove the soundness of the author's views, it would afford a useful key to the distribution of plant societies during recent geologic times. The author finds the present edaphic influence of loess evident in the vegetation, even

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[30] SHIMEK, B., The genesis of loess a problem in plant ecology. Proc. Iowa Acad. Sci. **15**:57–74. *pls. 3–7.* 1909.

where the surface overwash has hidden the character of the substratum. The forest on the loess is dominated by *Quercus alba* and *Q. ruba*, while the adjacent sandy areas are covered by the more xerophytic *Q. velutina* and *Q. macrocarpa*.—Geo. D. Fuller.

Air chambers of Ricciaceae.—Miss Hirsh,[31] under the direction of Dr. E. J. Durand, has examined a number of species of Riccia to determine the correctness of the statement of Barnes and Land that the air chambers of Marchantiales arise invariably by the splitting of internal walls. She finds that in the Ricciaceae the statement is true only for *Riccia natans* and *Riccia fluitans*, and that in all other species which she examined the air chambers arise according to the method described by Leitgeb, and cites as proof three figures of *Riccia Frostii*. To critical students of the group these figures do not furnish conclusive evidence one way or the other, for they are made in such a manner that the relation to each other of the rows of the cells back of the growing point cannot be made out with any certainty. In *fig. 4* of *Riccia Frostii* the first air chambers can as easily be interpreted as having split from within the thallus and having just reached the surface, as that the cells have become papillate. In fact, the contour of the section drawn seems to show that all the filaments actually originated by splitting and intercalary growth. The same is true in a more marked degree of *fig. 5*, and less so of *fig. 6*. In the latter figure the arching of the superficial cells due to turgor is interpreted by Miss Hirsh as the beginning of the papillate outgrowths of Leitgeb. Such investigations should be preceded by a careful study of the development of the thallus from the growing point, and there should be a clear conception of the arrangement of the cells which result from this growing point. While the style of the drawings is admirable, the position of cells and cell walls shows that such study must have been neglected in this case.—W. J. G. Land.

Light and germination.—Kinzel[32] has devised apparatus that answers all objections to his former methods, which indicated that light favored or was even necessary for the germination of various seeds. Both illuminated and darkened after-ripened seeds of *Veronica Anagallis* were kept in germinators at a constant temperature of 16.°7 C. Within a week 100 per cent of the illuminated cultures had germinated, while none of the darkened ones grew even after three months. He lists 63 species that germinate only in light, of which the following are examples: *Scheuchzeria palustris, Luzula albida, Thalictrum angustifolium, T. aquilegiifolium, Drosera rotundifolia, D. anglica, D. intermedia, Primula pubescens, P. spectabilis, Verbascum Thapsus, V. nigrum, Mimulus luteus, Veronica Anagallis*, and *Campanula rotundifolia*. He does not state whether high temperatures will dispose of the necessity of light, as is the case with various fern spores. It also

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[31] Hirsh, Pauline E., The development of air chambers in the Ricciaceae. Bull. Torr. Bot. Club **37**:73–77. *figs. 6.* 1910.

[32] Kinzel, W., Lichtkeimung: Erläuterungen und Ergänzungen. Ber. Deutsch. Bot. Gesell. **27**:536–545. *pl. 19.* 1909.

appears that he used the very low temperature of 16°7 C. He finds that some seeds germinate much better in darkness than in light, for example, *Leucojum vernum*, Asphodelus, *Anthericus ramosus*, *Paris Smilacina*, Polygonatum, and Veratrum. Phacelia and *Nemophila insignis* germinate very slowly and sparingly in white light, more rapidly and abundantly in darkness, and very quickly and completely in blue light. KINZEL finds the favorable action of the light is not due to the actinic rays, for in many cases the rays exerting least actinic power are most effective in bringing about germination.—WILLIAM CROCKER.

Heterotypic mitosis in Lilium.—In a paper on the prophase of the heterotypic mitosis in the embryo sac mother cell, MOTTIER[33] describes the effect of fixing fluids and traces the early development of the heterotypic spirem in the megaspore mother cell of *Lilium Martagon* and *L. candidum*. The following conclusions are reached: (1) Previous to synapsis a single nuclear thread is developed, which in many cases can be demonstrated clearly as a definite spirem with somewhat regular and uniform chromatin granules. (2) There is no union side by side of two distinct chromatin spirems before or during synapsis, which is regarded as a normal process, but the greater compactness of the balled-up mass may be due partly to the reagent. (3) The hollow spirem following synapsis is double, due to the longitudinal fission, which as a rule becomes completely obscured before the transverse segmentation. (4) The first mitosis, therefore, separates transversely the two members of the bivalent chromosome. (5) The heterotypic mitosis is thus a reduction division, and if one chromosome differs from another potentially or otherwise, it is also qualitative. (6) In the presynaptic phase, that the chromatin may appear as large clumps instead of smaller and uniform granules has been suggested as being due in part to the fixing fluids, the finer and more uniform granules being nearer the normal. The wide divergence of the halves of the chromatin thread appearing occasionally in the stage of the hollow spirem may also be due in part to the reagent.—SHIGÉO YAMANOUCHI.

Germination of zygotes of Spirogyra.—The germination of zygotes of *Spirogyra jugalis* Ktzg. has been studied by KARSTEN.[34] The germinating stage of the zygotes was obtained during November and December, and some of the cytological results are as follows: Two nuclei in the zygote are in close contact, the membranes between them staining faintly and evidently becoming dissolved. In the fusion nucleus two nucleoli derived from two gamete nuclei are seen for a time, but they finally fuse. The interior of the fusion nucleolus is vacuolized, but the outer portion remains and stains deeply. At the first division of the nucleus the synaptic stage is represented by a peculiar and irregular massing of the nucleolar membrane and a peculiar elongated condition of the nucleolus, which is now

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[33] MOTTIER, DAVID M., On the prophases of the heterotypic mitosis in the embryo sac mother cell of Lilium. Annals of Botany **23**:343–353. *pl. 23.* 1909.

[34] KARSTEN, G., Die Entwicklung der Zygoten von *Spirogyra jugalis* Ktzg. Flora **99**:1–11. *pl. 1.* 1908.

directly surrounded by the cytoplasm. The nucleolus then gradually assumes a rounded form, in which are seen 14 deeply stained tetrads that differentiate later into 28 chromosomes. The chromosomes become united in pairs and 14 bivalent chromosomes are established. The spindle is at first multipolar, but gradually becomes bipolar. The daughter chromosomes grouped at the poles, after the first division, again take the form of nucleoli in the daughter nuclei. In the second division 14 chromosomes are clearly distinguishable in the polar view of the equatorial plate. Consequently in *Spirogyra jugalis* 14 is the haploid number of chromosomes and 28 the diploid number.—SHIGÉO YAMANOUCHI.

Oxidizing enzymes.—EULER and BOLIN[35] have published a third paper on oxidizing enzymes. They have developed a method for the quantitative determination of peroxidase. They have also devised methods for the purification of the peroxidase of the horseradish, which gives a far superior product to that obtained by BACH and CHODAT. The most highly purified product showed 10.4 per cent of nitrogen and 2.5 per cent of ash. Contrary to the belief of many, the action of this substance cannot be attributed to the trivalent iron and chinons it contains, but it is a true enzyme. They believe the peroxidases of various plants are not identical.

The oxidase of *Rhus vernicifera* was purified and compared with the oxidase of Medicago, which they have already studied in great detail.[36] The latter they have shown to be a mixture of calcium salts of various oxy-acids and it is not destroyed by boiling in water. The former contains nitrogen and is very sensitive to heat. Contrary to the contention of many, they find that the action of Rhus oxydase cannot be attributed to the joint action of contained manganese and hydroxyl, for it is equally effective in slightly acid, neutral, and slightly basic solutions.

These investigators, through their excellent chemical training, are making valuable contributions in this important field of plant physiology.—WM. CROCKER.

The giant form of Primula sinensis.—GREGORY[37] has examined the giant form of *Primula sinensis*, thinking it might have the tetraploid number of chromosomes, as Miss LUTZ and the reviewer found to be the case in *Oenothera gigas*. A doubling, however, does not occur, the numbers being 12 and 24, as in the ordinary form of *Primula sinensis*. It should be said that this giant Primula differs from the ordinary form in practically no respect except the larger size of its organs, while in *O. gigas* many of the characters have been sharply modified from those of *O. Lamarckiana*. While GREGORY finds the number of the chromosomes unchanged, he believes that the chromosomes are larger in the giant form,

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[35] EULER, H., UND BOLIN, IVAN, Zur Kenntnis biologisch wichtiger Oxydationen. III. Zeit. Physiol. Chemie **61**:72–92. 1909.

[36] *Ibid.* **61**:1–15. 1909.

[37] GREGORY, R. P., Note on the histology of the giant and ordinary forms of *Primula sinensis*. Proc. Cambridge Phil. Soc. **15**^{3}:239–246. *pl. 10.* 1909.

although this is difficult to prove. The cells and nuclei are found to be distinctly larger, as shown by measurements of nuclei of the pollen mother cells and of various other tissues. Drawings from transverse sections of the stems show clearly the larger size of the cells in the giant form. He concludes that "the character of giantness manifests itself in the cells themselves and not merely in the plant as a whole."

The reviewer has shown[38] that in *Oenothera gigas* the cells and nuclei are constantly larger than in *O. Lamarckiana*, but that the ratio of increase varies in different cases, the sizes being 1.5:1, 2:1, 3:1, or even more, though apparently constant for each tissue examined.—R. R. GATES.

Secondary growth in monocotyledons.—Evidence against the significance of histogenic layers in the stem apex continues to accumulate. SCHOUTE[39] dealt a severe blow to HANSTEIN'S theory when he showed that in Hippuris the plerome gives rise not only to the central cylinder but also to part of the cortex. As to vascular cryptogams, CAMPBELL[40] found that the vascular bundles of Equisetum originate from the cortical region. A monocotyledon has recently been studied by CARANO,[41] who finds that in the young stem and leaf of *Yucca aloifolia* it is impossible to distinguish between plerome and periblem. The author concludes that in this stem the existence of two distinct regions, central cylinder and primary cortex, is absolutely unfounded. It may be objected, however, that in this case there is merely negative evidence, which will not settle the question for the monocotyledons. In the stem of this plant there is nothing corresponding to the pericycle of the dicotyledons, and the meristematic zone which gives rise to the secondary tissues is continuous with the apical meristem. Hence this zone is considered to be primary at the outset, though the cambial activity later spreads outward to mature cells, when the meristem and its products of course become secondary. The permanently active layer so established produces vascular bundles and parenchyma internally, and parenchyma externally.—M. A. CHRYSLER.

Affinities of an alpine flora.—Following the glacial relic theory postulated by GRAY and elaborated by HOOKER and others, HARVEY[42] has studied the vascular flora of Mt. Ktaadn, Maine. Four distinct elements are distinguished: (1) the arctic-relic, (2) the pre-glacial alpine, (3) the endemic, and (4) the subalpine-lowland. Of these the last is regarded as not truly alpine, while the endemic flora consists of the single initial endemic *Carex Grahamii* and the relic endemic

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[38] GATES, R. R., The stature and chromosomes of *Oenothera gigas* DeVries. Arch. f. Zellforsch. **3**:525–552. 1909.

[39] SCHOUTE, J. C., Die stelär Theorie. Jena. 1903.

[40] CAMPBELL, D. H., Affinities of the genus Equisetum. Amer. Nat. **39**:273–285. 1905.

[41] CARANO, E., Su le formazioni secondarie nel caule delle Monocotiledoni. Annali di Botanica **8**:1–42. *pls. 1–4.* 1910.

[42] HARVEY, LEROY H., The floristic composition of the vascular flora of Mount Ktaadn, Maine. Mich. Acad. Sci. Report **11**:37–47. 1909.

Euphrasia Oakesii. The remaining arctic-alpine flora consists of 118 species, all but four of which are also found upon Mt. Washington. In the various tabular presentations of the affinities of this alpine flora, attention is directed to the ecological as well as the floristic similarity of mountains, coast, bog, and arctic habitats, and various arctic and alpine floristic areas are compared with Mt. Ktaadn. From the large number of common species (56 per cent), arctic Europe is considered to have been the center of distribution of the Ktaadn alpine flora, while its glacial migration seems to have been by the Greenland-Laborador route. Over 75 per cent of this flora is of arctic affinity.—GEO. D. FULLER.

Diffusion stream in plant organs.—RYWOSCH[43] continues his work on the movement of food materials in plant organs. The movements of course obey the laws of diffusion, a given substance moving in the direction of its lowest concentration. The thing of interest in his work is the discovery of various means by which the gradient is maintained. Two illustrations will show the nature of the results. If the cuticle is removed from any side of a starch-free pine needle and the needle placed in a 9 per cent sugar solution, the first deposit of starch is not on the side of the removed cuticle, where of course the sugar is most concentrated, but in the cells on the distal side. The entrance on one side through irritability leads to the more complete condensation of the sugar on the opposite side, thus maintaining a falling gradient and a continual diffusion stream of the sugar toward the distal side. In the cotyledons of the pea, also, he finds that the sugar is more completely condensed as the vascular bundle is approached, thus maintaining a falling gradient and continuous sugar diffusion toward the bundle.—WM. CROCKER.

Chromatin bodies.—Miss DIGBY describes[44] a peculiar phenomenon of a constant extension of chromatin bodies during the presynaptic and synaptic stage of the first nuclear division of the pollen mother cells of *Galtonia candicans.* According to her observations, the chromatin bodies may originate as portions of the nuclear network, or of the synaptic knots, or as nucleolar buds. They are composed of linin in which chromatin is imbedded, or of nucleolar material. Those bodies that come from the chromatic portion of the nucleus retain their connection with the nucleus, by means of a fine thread, until their disintegration. The bodies that pass from the nucleolus into the surrounding cytoplasm penetrate the cell wall and enter the neighboring cell. The chromatic bodies which originate as buds from the nucleolus at first take an acid stain, but as they pass into the cytoplasm they become increasingly chromatic. It is not known whether the bodies as formed become secondarily attached to the nucleus. Regarding the significance of this phenomenon, no interpretation is given by the author.—SHIGÉO YAMANOUCHI.

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[43] RYWOSCH, S., Ueber Stoffwanderung und Diffusionströme in Pflanzenorganen. Zeit. Bot. **1**:571–591. *figs. 4.* 1909.

[44] DIGBY, L., Observations on chromatin bodies and their relation to the nucleolus in *Galtonia candicans* Decsne. Annals of Botany **23**:491–502. *pls. 33, 34.* 1909.

Forests and floods.—According to MOORE,[45] forests exert no controlling influence upon rainfall, and very little upon the flow of the water after it reaches the earth's surface. While regretting the paucity of the data, he decides that the run-off of our rivers is not materially affected by any other factor than precipitation, that high waters are not higher and low waters are not lower than formerly, nor do floods occur more frequently and continue longer than formerly. In support of his contention that forestation exerts little or no effect upon precipitation, he shows that the presence or absence of forest covering affects only a thin stratum of air over the surface of the areas in question, whereas the conditions that control precipitation are confined to a much greater altitude and one not affected by the local irregularities occurring in the lower stratum. Statistics given for the Ohio River basin, where deforestation has been great, show that the flow of water in that river has exhibited no material change for the thirty-seven years for which measurements are available.—GEO. D. FULLER.

Evaporation and plant societies.—Evaporation is regarded as a very mportant factor in determining the character of plant societies, and several ecologists, measuring it with the most accurate instruments now available, are collecting interesting data from various localities. SHAW[46] determined the amount of evaporation at various stations in the Selkirk Mountains, ranging from 800 to 2900^m in altitude, extending his observations over a period of 12 weeks. The maximum evaporation was at 1100^m, while above this altitude there was a gradual but somewhat irregular diminution.

DICKEY,[47] in a bog habitat, found evaporation in the open central area occupied by Sphagnum, Oxycoccus, and Eriophorum much greater than in the surrounding maple-alder zone, and that rainfall had a more marked effect upon the rate of evaporation in the latter situation. In the maple-alder zone the appearance of foliage in the spring and the fall of leaves in the autumn affected the rate materially.—GEO. D. FULLER.

Stem gall on Commelina.—The LEEUWEN-REIJNVAANS[48] give a discussion of the gross and anatomical character of a stem gall on *Commelina communis* L. It is caused by the larva of a lepidopterous insect, *Aegeria uniformis* Snellen. The larval chamber originates in the central axis of the stem, and the enlargement of the stem at this point is on one side, instead of radial as is the case with most galls which originate in the central axis of the stem. The enlargement is due mainly to the increase in the amount of the parenchyma tissue. The collenchyma is

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[45] MOORE, WILLIS L., Influence of forests on climate and on floods. Report to Committee on Agriculture, U.S. House of Representatives. pp. 38. 1910.

[46] SHAW, C. H., Present problems in plant ecology. III. Vegetation and altitude. Amer. Nat. **43**:420–431. 1909.

[47] DICKEY, MALCOLM G., Evaporation in a bog habitat. Ohio Nat. **10**:17–23. 1909.

[48] LEEUWEN-REIJNVAAN, J. UND W., DRS. VON. Kleinere cecidologische Mitteilungen. Ber. Deutsch. Bot. Gesell. **27**:572–581. *figs. 6.* 1910.

broken on the side of the greatest enlargement, so that in cross-section it appears as a crescent partly inclosing the gall. The vascular bundles are pushed apart on the side where the swelling is greatest, and in cross-section form a crescent pattern instead of a ring. Small vascular bundles penetrate the tissues of the gall. The nutritive tissue is abundant and the sclerenchyma tissue is more abundant than in most lepidopterous galls.—MEL. T. COOK.

Light and germination.—Where light was supposed to be necessary for any considerable germination, LEHMAN finds[49] that in *Ranunculus sceleratus* other stimuli can be substituted for light. One per cent KNOP's solution gives a greater percentage of germination in darkness than distilled water in light. In contrast to wet filter paper generally used as a substratum in such experiments, earth was found to stimulate germination greatly, water extracts of earth made by boiling were less effective, and extracts made with cold water showed no stimulation. If these seeds are exposed to germinative conditions in darkness for twenty or more days, light is then not effective. The author calls such seeds "dunkelharten" or "dunkelstarren," in contrast to the "lichtharte" seeds of Nigella.[50] *Stellaria media,* indifferent to light in its germination, was greatly stimulated by such substrata as KNOP's solution and earth.—WILLIAM CROCKER.

Selaginella preissiana.—The extremely small xerophytic *Selaginella preissiana*, found in West Australia, Victoria, and Tasmania, is described by BRUCHMANN.[51] The cotyledons are slightly larger than the foliage leaves. The first dichotomy gives an erect branch about 3^{cm} high; the other branch becomes the creeping rhizome, which gives off erect shoots right and left. Growth is by means of a single polyhedral apical cell. The stem is protostelic, the hypocotyl having a single exarch protoxylem point.

In the root there are three groups of initials: periblem and plerome having a common group, and dermatogen and calyptrogen each having a group. Root hairs are wanting, and epidermis and cortex are infested with an endophytic fungus. The hyphae were observed penetrating the epidermis from the soil.—W. J. G. LAND.

Cellulose-forming enzyme.—In continuing his capillary analysis of enzymes, GRÜSS[52] claims to have found, as his most important result, a cellulose-forming enzyme which he terms cytocoagulase. The material condensed was dissolved

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[49] LEHMAN, ERNST, Zur Keimungsphysiologie und Biologie von *Ranunculus sceleratus* L. und einiger anderen Samen. Ber. Deutsch. Bot. Gesell. **27**:476–494. 1909.

[50] KINZEL, WILHELM, Ueber den Einfluss des Lichtes auf die Keimung. "Lichtharte" Samen. Ber. Deutsch. Bot. Gesell. **25**:269–276. 1907.

[51] BRUCHMANN, H., Ueber *Selaginella preissiana* Spring. Flora **100**:288–295. *figs. 8.* 1910.

[52] GRÜSS, J., Kapillaranalyse einiger Enzyme. II. Ber. Deutsch. Bot. Gesell. **27**:313–319. 1909.

from cherry gum, and the crystalline precipitate stained red with phloxin. It is not difficult to see that his evidence is hardly conclusive, since the material condensed is not known, and the product of the condensation is evidenced by the uncertainty of a stain. If, as seems probable, enzymes capable of condensing the simplex carbohydrates into more complex ones exist in plants, their demonstration and study is very important to plant physiology. There is need, however, of far more conclusive methods.—WM. CROCKER.

River dunes.—A study of the vegetation of the river dunes of Illinois by GLEASON[53] proves them to be very similar to those of Lake Michigan, although differing somewhat in the sand-binding plants that assist in their formation. These are notably *Ceanothus ovatus*, *Panicum virgatum*, and *Rhus canadensis*. The first forest stage is characterized by the dominance of *Quercus velutina*, with which is associated *Q. marilandica* in the Oquawka area. The underbrush in this forest consists almost entirely of young trees of the same species. The successional stages to the maple forest are suggested, and a more exhaustive treatment of the relation of the different associations promised for the near future.—GEO. D. FULLER.

Leaf position.—BÄSSLER investigated the effect of decapitation upon the position of adjacent leaves. He reports[54] that the youngest leaves react by erecting themselves more, unless a branch has already developed in the axil, in which case the branch erects itself. The closer the leaf to the cut, the more the erection, but wounding without decapitation has no effect. Light does not influence the reaction; gravity slows it. BÄSSLER was unable to determine or analyze further the cause of the reaction.—C. R. B.

Parthenocarpy.—LONGO, in testing the effects of preventing pollination in diclinous flowers, found that a dozen flowers of *Diospyros virginiana* L., unpollinated, set fruit as well as the pollinated ones.[55] The fruits matured, but the seeds were merely coriaceous brown laminae, within whose seed coats was only the excessively developed tapetum of the embryo sac. *Diospyros Kaki* L. was already known to be parthenocarpic.—C. R. B.

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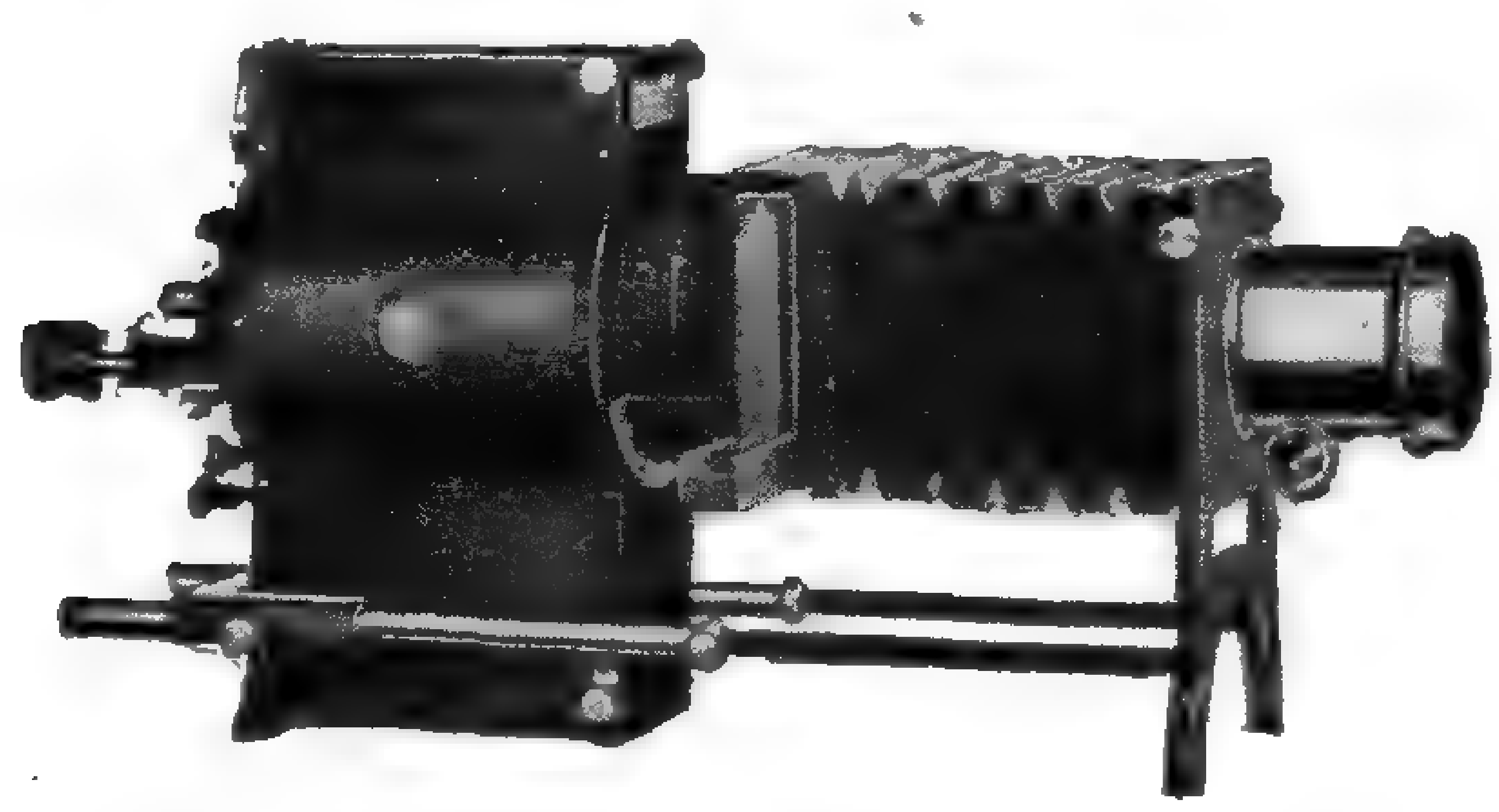
[53] GLEASON, HENRY A., The vegetational history of a river dune. Trans. Ill. State Acad. Sci. **2**:19–26. 1909.

[54] BÄSSLER, FRIEDRICH, Ueber den Einfluss des Dekapitierens auf die Richtung der Blätter an orthotropen Sprossen. Bot. Zeit. **67**^{1}:67–91. 1909.

[55] LONGO, B., La partenocarpia nel *Diospyros virginiana* L. Rendic. R. Accad. Lincei, Cl. Sci. V. **18**:632–635. *fig. 1.* 1909.



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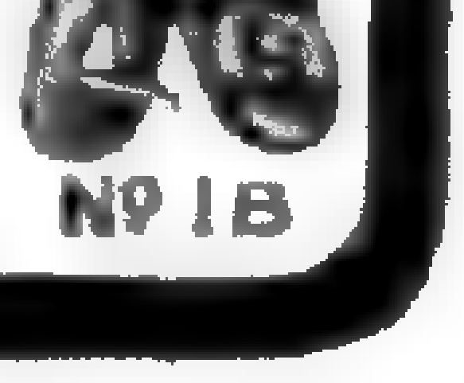
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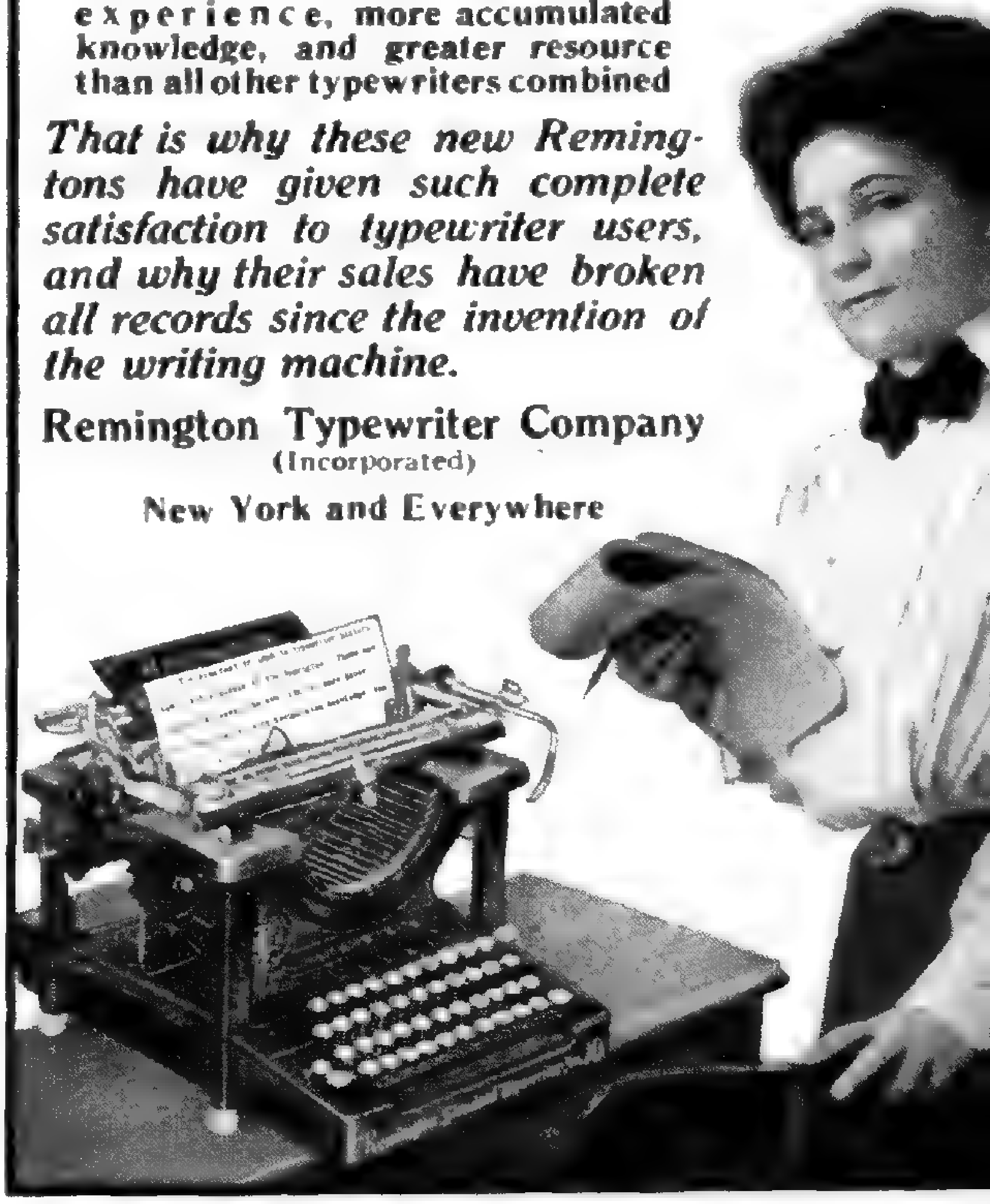


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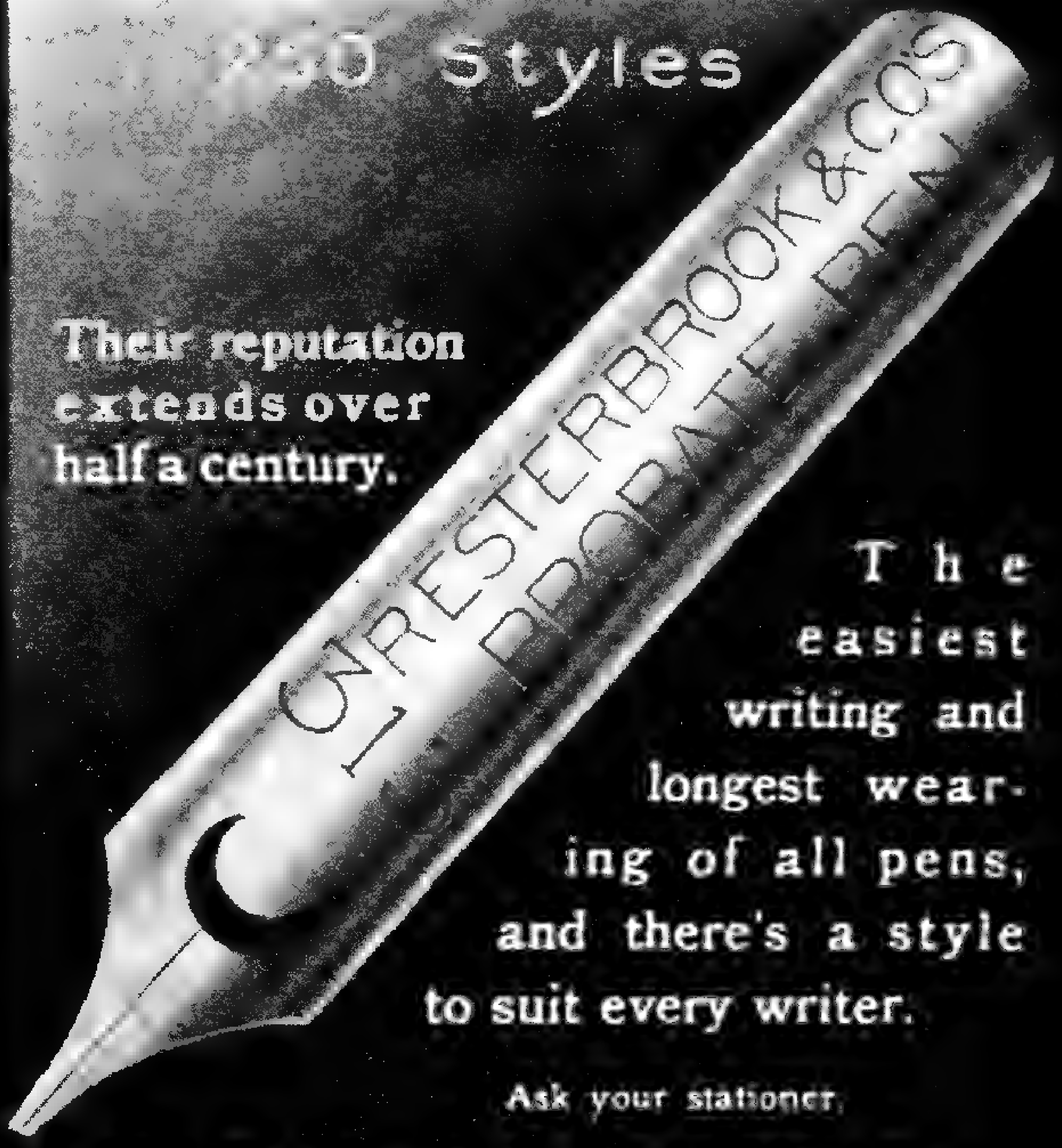
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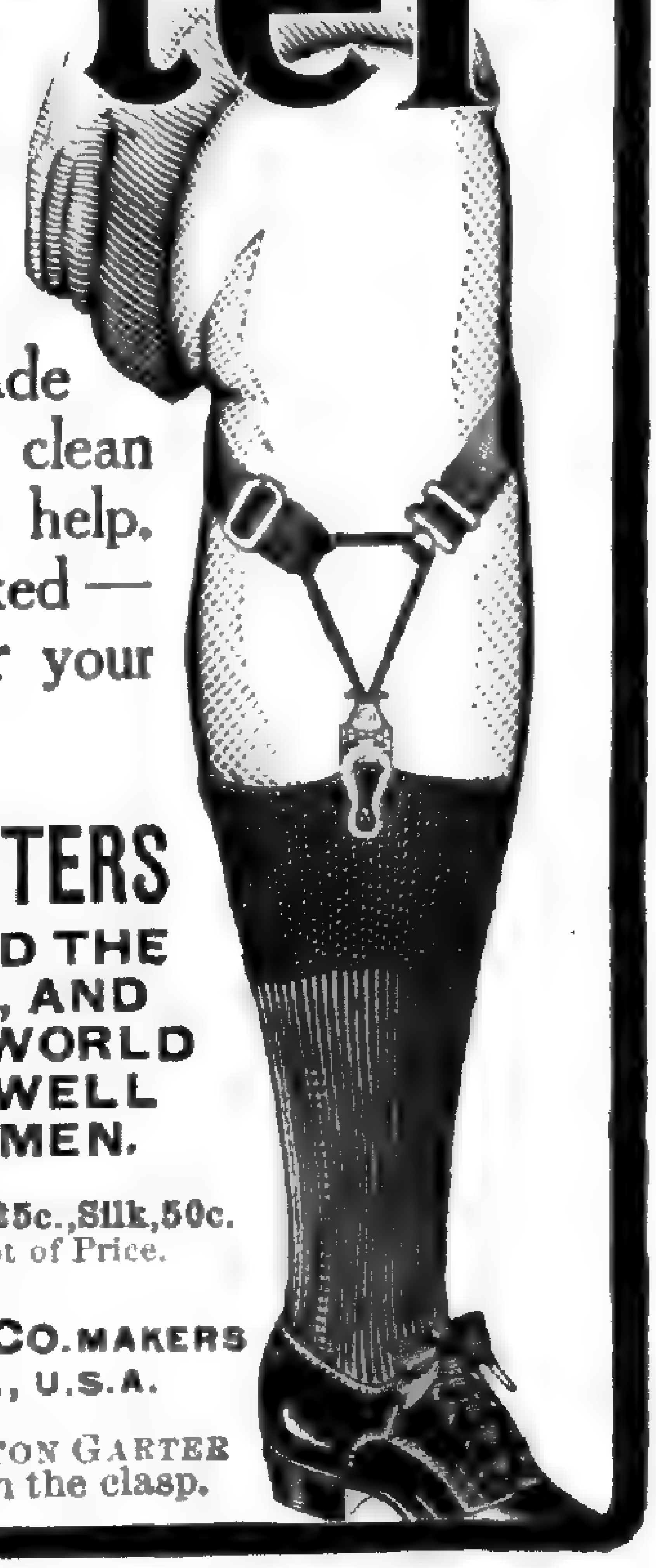

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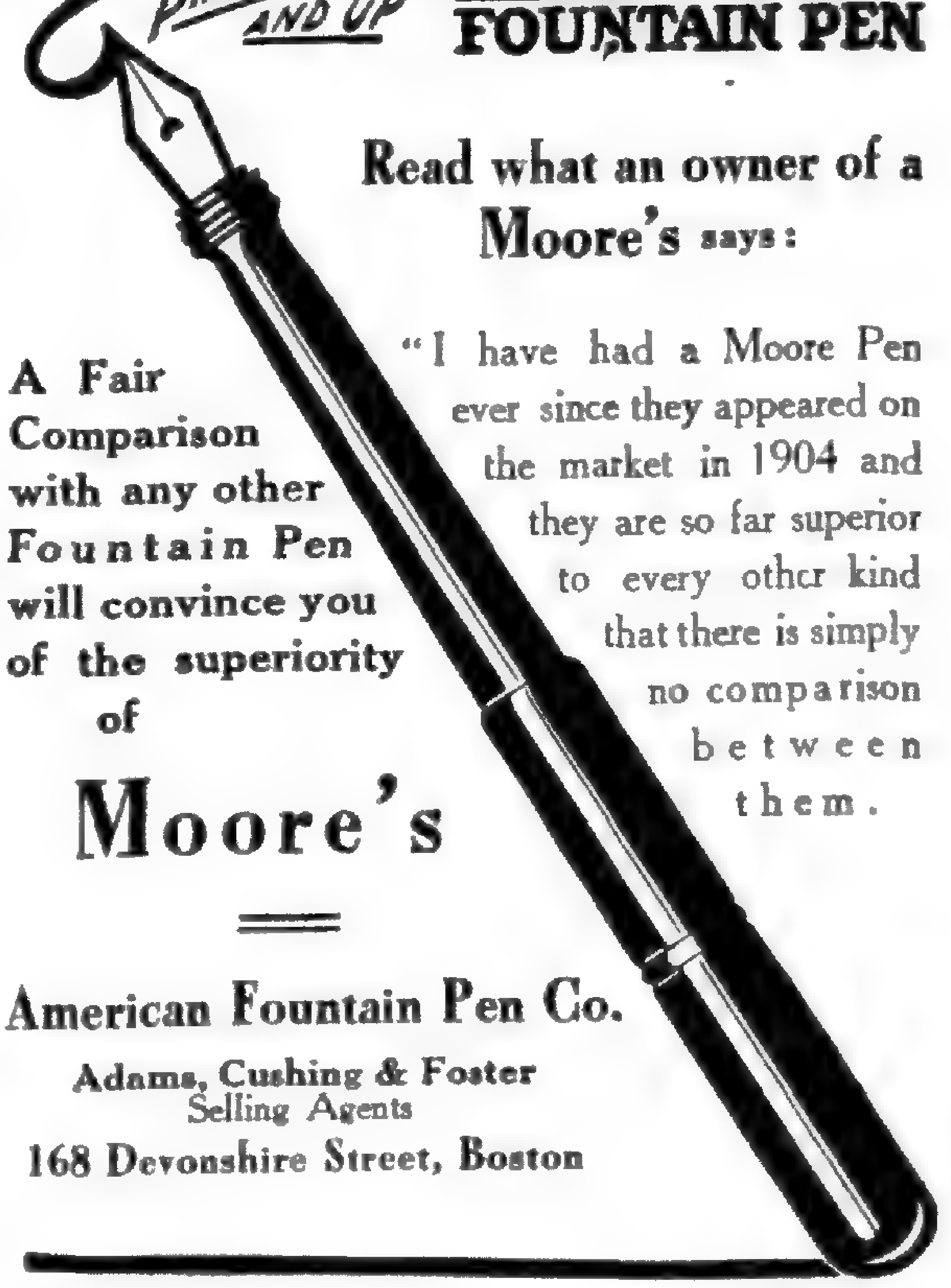

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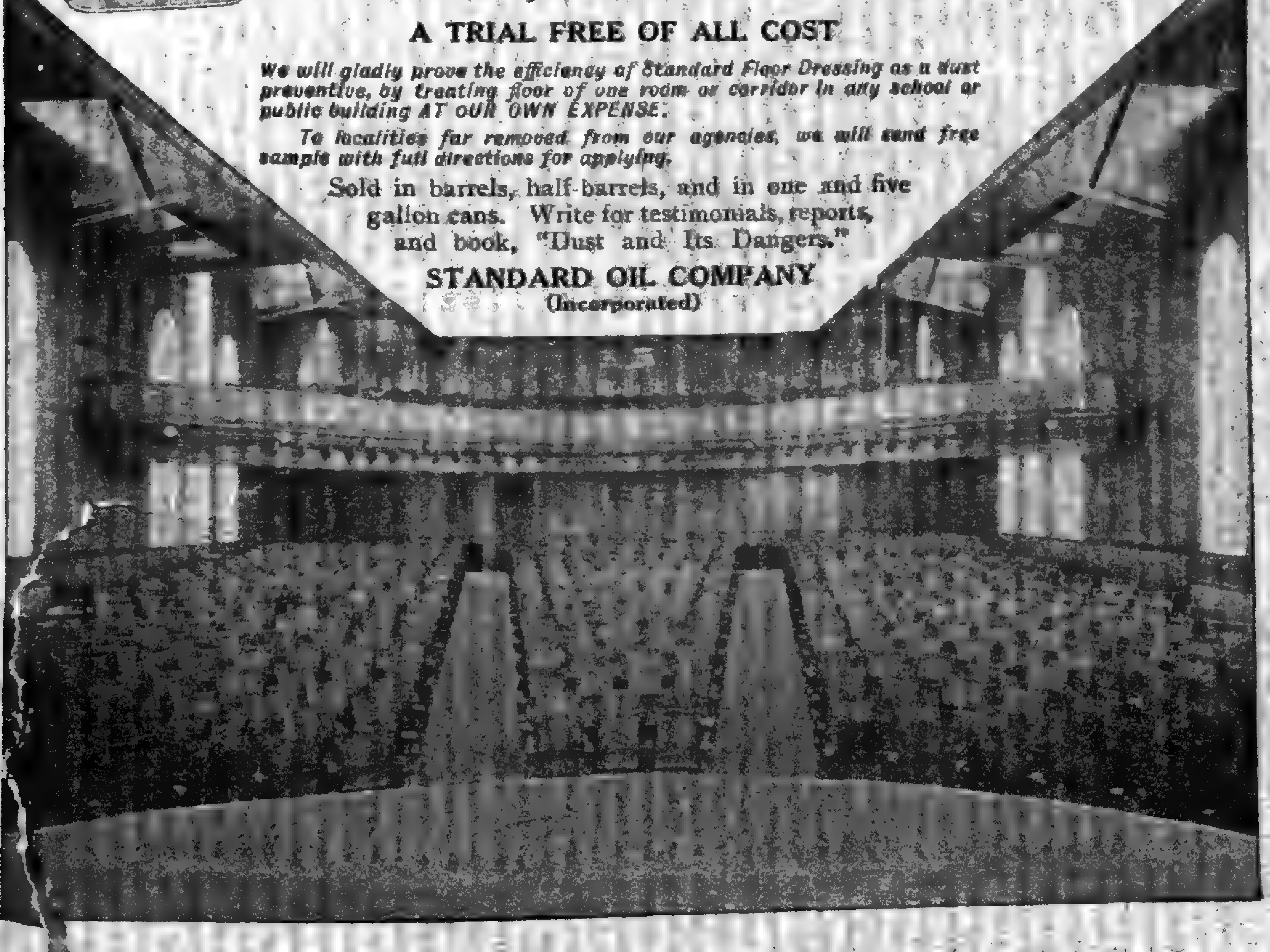


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Vol. XLIX No. 6

THE BOTANICAL GAZETTE

June 1910

Editors: JOHN M. COULTER and CHARLES R. BARNES

CONTENTS

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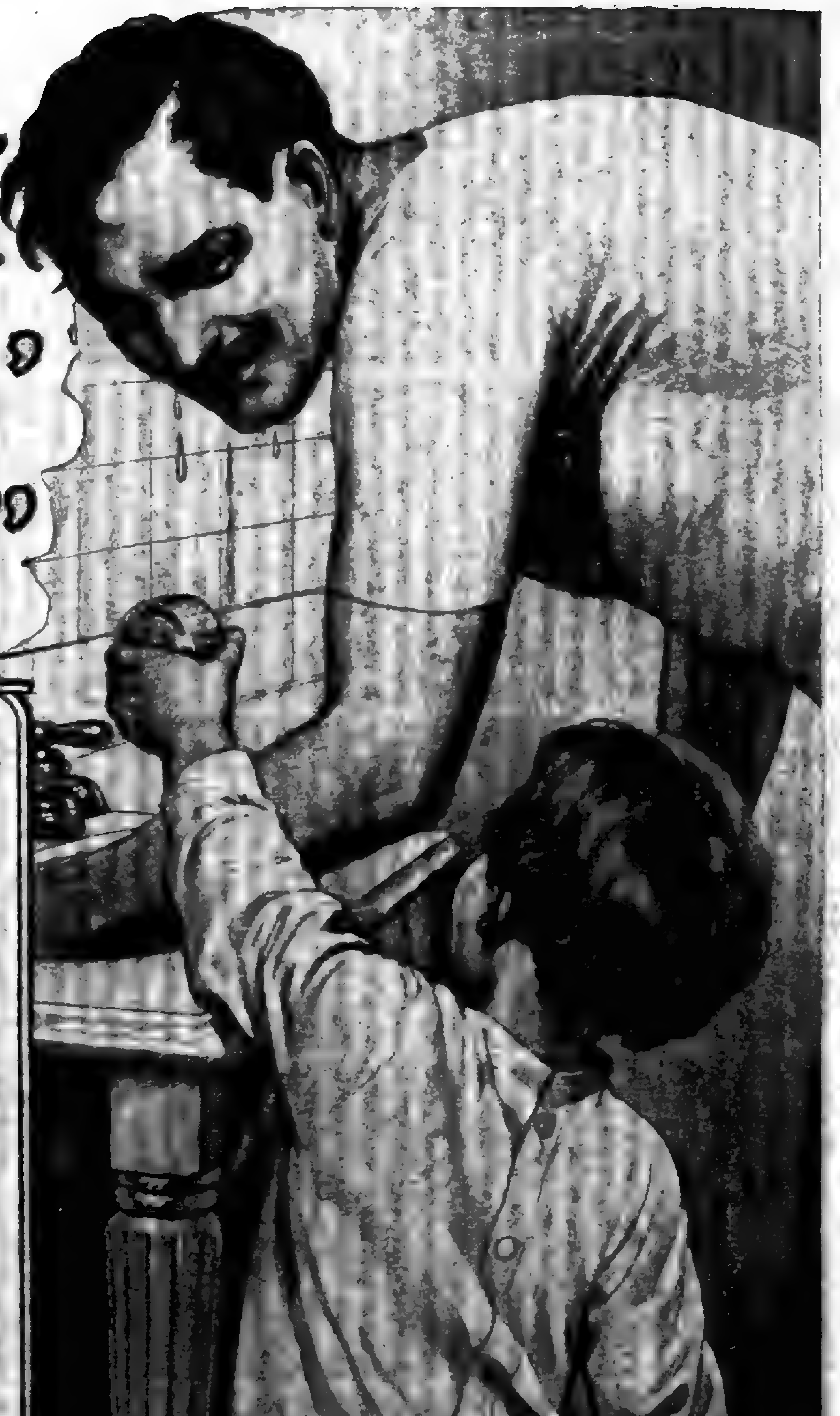

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Edited by JOHN M. COULTER and CHARLES R. BARNES, with the assistance of other members of the botanical staff of the University of Chicago.

Issued June 23, 1910

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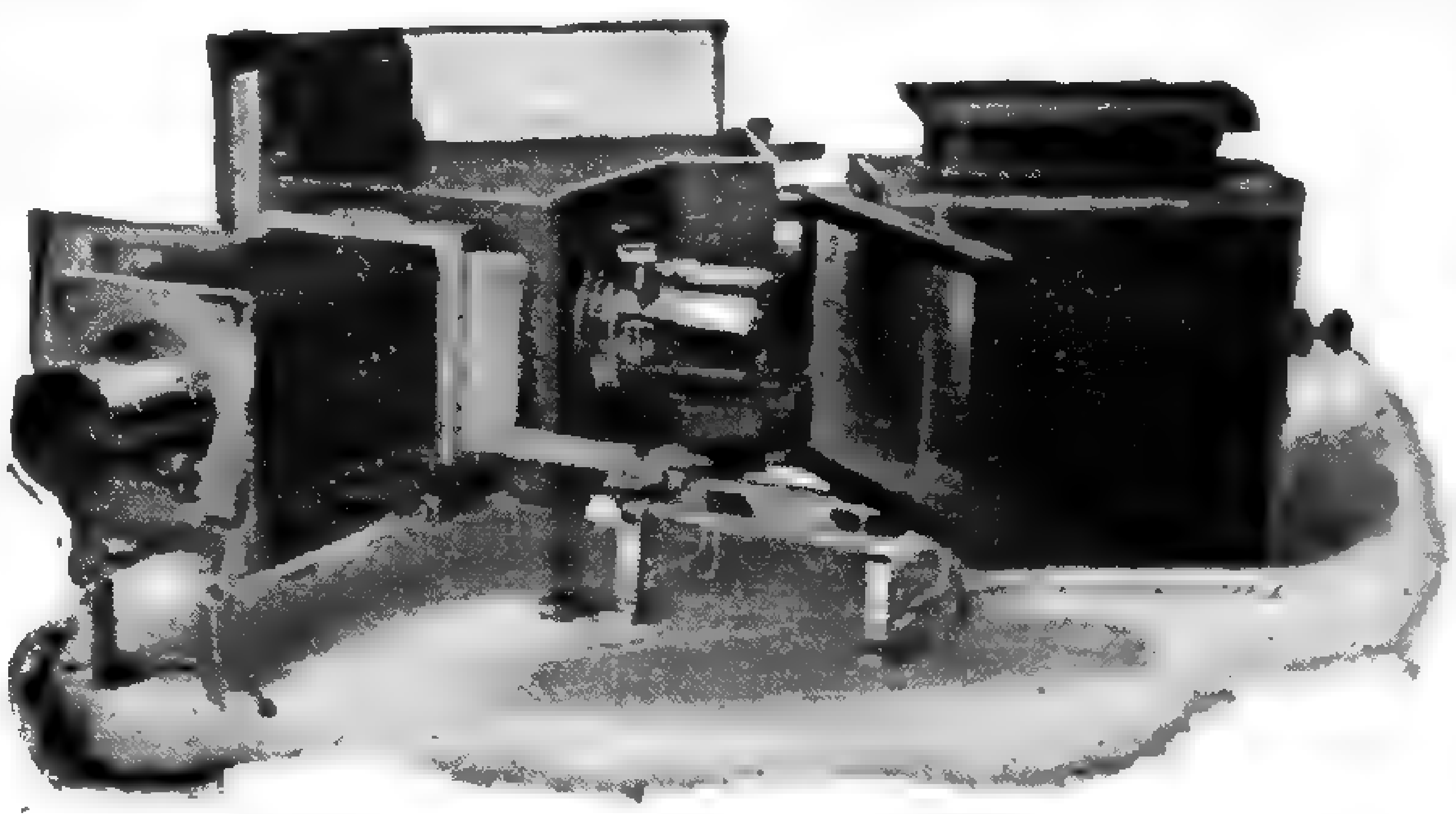

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VOLUME XLIX NUMBER 6

BOTANICAL GAZETTE

JUNE 1910

THE EFFECT OF SOME TOXIC SOLUTIONS ON MITOSIS

WARNER W. STOCKBERGER

(WITH SEVEN TEXT FIGURES)

During the two decades just past there has arisen a considerable body of literature from the researches which have been made upon the physiology of the cell under the influence of various external conditions. The effect of certain stimuli on the growth and form of the organism and the modifications in the normal processes of cell and nuclear division induced thereby have been made the basis of numerous generalizations with respect to cellular activities.

Owing to its bearing upon questions of general and practical interest, the action of toxic substances on the growth of plants has been widely investigated. Notwithstanding this fact, our knowledge of the effect of such substances on cellular development in phanerogams is far from extensive, and the nature of toxicity itself yet lacks a satisfactory explanation. What may be called the modern epoch of the toxicity studies began with the researches of **KAHLENBERG** and **TRUE** (**10**), in which the action of chemically equivalent solutions of substances experimented with were for the first time compared.

According to the accounts of a number of writers, various departures from the normal course of nuclear and cell division have been caused experimentally by the action of solutions of various chemical constitution. The technic of this type of investigation was first developed by **GERASSIMOW** in the study of the cells of thallophytes, and later adapted to the study of higher forms.

Numerous investigators have studied the action of ether, chloroform, chloral hydrate, potassium nitrate, phenol, benzol, and copper sulfate upon cell processes in certain plants, including Spirogyra, Tradescantia, Phaseolus, Lupinus, Vicia, Pisum, Allium, and Larix. The published accounts of these studies show a general agreement as to the production of certain abnormalities in cell and nuclear development. However, as to the occurrence of amitosis, binucleate cells, fusion nuclei with double the normal number of chromosomes and a heterotypic reducing division in the same, opinions are very conflicting.

GERASSIMOW (**8, 9**), NATHANSON (**16, 17**), PFEFFER (**24**), and WASIELEWSKI (**30**) found amitotic division of nuclei, but WISSELINGH (**32, 33**), NEMEC (**22**), ANDREWS (**2**), and WOYCICKI (**34**) saw no cases of amitosis.

Binucleate cells were observed by GERASSIMOW (**8, 9**), NATHANSON (**16, 17**), PFEFFER (**24**), NEMEC (**18, 20, 21, 22, 23**), BLAZEK (**3**), WASIELEWSKI (**30**), WOYCICKI (**34**), and STRASBURGER (**29**), but they were not found by WISSELINGH (**31**), ANDREWS (**2**), and KARPOFF (**11**).

Fusion nuclei were reported by GERASSIMOW (**8, 9**), NEMEC (**20, 21, 22, 23**), who found also double the normal number of chromosomes, and by STRASBURGER (**29**), but not by the other authors mentioned. The disappearance of the nuclei with the double chromosome number was explained by NEMEC (**22**) as due to a reduction division, in which he is followed by WOYCICKI (**34**). This conclusion is severely criticized by STRASBURGER (**29**) and by LAIBACH (**12**).

From this brief statement of the conflicting opinions advanced in some of the more important papers dealing with the direct effect of various chemical substances upon nuclear and cell division, it is evident that a much wider range of observation and experiment is required before conclusive generalizations can be drawn or the discordant results of the various investigators be brought into harmony. Moreover, in the higher plants the rate and the amount of growth in the seedling stages have been used almost entirely in the measure of the toxic effect, or when such was not the case some microscopic factor has been employed. Apparently there has been little detailed comparative study of the cell and nuclear activities in the higher plants during the course of treatment with an extended series of dilutions of a toxic agent.

The present investigation was carried out in order to observe the process of nuclear and cell division under certain definite conditions of physiological experiment with a series of toxic substances.

Materials and methods

In this study young seedlings of *Vicia Faba* were used, as they have furnished material for many similar investigations on the physiology of the cell and are well known as suitable material for the study of cellular activities. Uniform series of seedlings selected for the comparative tests were taken from the thoroughly washed sphagnum in which they had germinated, and suspended on glass rods in such a manner that the radicle for about 20^{mm} of its length was immersed in the solution. New nonsol glass beakers of 300^{cc} capacity were used, and a careful distinction was maintained throughout the experiments between those used for the controls and those used for the toxic solutions. This precaution was taken in order to avoid the possibility of the controls being injured by the residuum of copper which, as pointed out by NÄGELI (**15**), is taken up by the glass and may be given off later to contained solutions in quantity sufficient to affect seriously the radicles of plants grown therein.

The radicles were marked with India ink at a point 15^{mm} from the tip just before they were placed in the solution. When not under direct observation, the seedlings were kept in a dark cabinet in the laboratory at a fairly uniform temperature. The agents used were dilutions made from carefully prepared solutions of copper sulfate, strychnin sulfate, and phenol. The controls in the observations on growth rate were grown in distilled water. Either triple distilled water was used or the water was redistilled from glass just before use. Four seedlings were regularly used in each solution and their average growth was taken as the basis of comparison. Except in a few cases, when one or two tips were dead, four tips from each set of seedlings were prepared for microscopical examination.

In preparing the material for microscopical study, various modifications of Flemming's fluids were used in killing and fixing. Dehydration was followed by imbedding in 53° paraffin. The sections were cut 3–5 μ in thickness and stained on the slide with iron-alum-hematoxylin, safranin-gentian-violet, or the triple stain. A Zeiss

1.5^{mm} apochromatic objective and compensating oculars were used in studying the preparations.

This investigation was begun in 1904, at the suggestion of Dr. RODNEY H. TRUE, to whom I am indebted for constant advice and criticism. I am also under obligations to Dr. G. F. KLUGH, who was of great assistance with the seedling cultures.

Experimental

In all work with the radicles which involved measurement of growth, and in the preparation of material for killing and fixing, great precautions were taken to guard against the introduction of undesirable factors, such as loss of moisture, change in temperature, or shock in handling, which might interfere with the results sought.

THE EFFECT OF COPPER SULFATE SOLUTIONS ON GROWTH

Growth and cell activity in the root tips of *Vicia Faba* upon which copper sulfate solutions of various concentrations had acted continuously were the first subjects of study. Seedlings were placed in a series of solutions with a constant difference of dilution of $n/10,000$, in order to determine the concentrations in which the toxic effect would not be so strong as to prevent growth to some degree, after allowing time for recovery from the shock due to the change of medium and for partial acclimatization to the toxic substance. Table I shows the average growth of four seedlings in the various concentrations used, and also the growth made by the corresponding controls in distilled water. From the table it is apparent that, in the lower concentrations, the effect of a difference in dilution of $n/10,000$ is masked by the variability of the individual groups of seedlings, and in the higher dilutions this difference was increased many fold before changes in the growth rate were observed which could be reasonably ascribed to the action of the toxic solution. A comparison of the average growth per hour in the copper solution and in distilled water shows that there is a wide range of toxic effect between the concentrations $n/20,000$ and $n/500,000$, with a probable corresponding difference in cell activity, as shown by the slower rate of elongation in the stronger solutions.

TABLE I

COMPARATIVE GROWTH IN $CuSO_4$ AND DISTILLED WATER DURING THE FIRST DAY

RADICLES IN COPPER SULFATE SOLUTIONS				CONTROLS IN DISTILLED WATER	
Concentration	Time in solutions in hours	Total growth in mm	Average growth per hour in mm	Growth of corresponding control in mm	Average growth per hour in mm
n/20,000.....	16.5	0.5	....	8.7	0.52
n/30,000.....	19.5	0.5	....	5.0	0.25
n/40,000.....	19.5	1.8	0.09	12.8	0.65
	23.5	1.1	0.04	11.8	0.50
n/50,000.....	19.5	3.0	0.15	12.8	0.65
	20.0	3.7	0.18	7.8	0.39
	21.5	3.8	0.17	11.8	0.54
n/60,000.....	19.5	4.4	0.22	7.8	0.40
	21.5	1.8	0.07	10.2	0.47
n/70,000.....	19.0	8.0	0.42	12.1	0.63
	20.0	6.0	0.30	11.0	0.55
	20.0	5.7	0.28	13.0	0.65
n/80,000.....	18.5	4.5	0.24	11.3	0.61
	19.0	9.2	0.48	12.1	0.63
	20.0	5.9	0.29	13.0	0.65
n/90,000.....	18.5	5.1	0.26	11.3	0.61
	19.0	9.7	0.51	12.1	0.63
	20.0	5.4	0.27	13.0	0.65
n/100,000....	18.5	7.0	0.37	11.3	0.61
	19.0	11.2	0.58	12.1	0.63
	20.0	8.3	0.41	13.0	0.65
n/110,000....	18.5	7.0	0.37	11.3	0.61
	21.5	6.5	0.30	14.6	0.67
	24.0	8.5	0.35	14.3	0.59
n/120,000....	21.5	6.8	0.31	14.6	0.67
	24.0	9.5	0.39	14.3	0.59
n/130,000....	21.5	8.0	0.37	14.6	0.67
	24.0	12.3	0.51	14.3	0.59
n/140,000....	21.0	5.0	0.23	8.3	0.39
	24.0	11.8	0.49	16.0	0.66
n/150,000....	21.0	6.5	0.30	8.3	0.39
	22.0	13.5	0.61	16.5	0.75
n/160,000....	24.0	12.8	0.53	16.0	0.66
n/250,000....	19.0	11.5	0.60	14.2	0.74
	19.0	8.8	0.46	10.3	0.54

TABLE I—*Continued*

Radicles in copper sulfate solutions				Controls in distilled water	
Concentration	Time in solutions in hours	Total growth in mm	Average growth per hour in mm	Growth of corresponding control in mm	Average growth per hour in mm
n/275,000....	19.0	11.8	0.61	14.2	0.74
	19.0	11.0	0.57	10.3	0.54
	18.0	7.8	0.42	15.0	0.83
n/300,000....	19.0	11.2	0.58	14.2	0.74
	19.0	10.3	0.54	11.5	0.60
	19.0	14.0	0.71	10.3	0.54
	18.0	6.0	0.33	15.0	0.83
n/400,000....	19.0	10.0	0.52	11.5	0.60
	18.0	12.7	0.70	15.0	0.83
	24.0	14.8	0.61	15.8	0.65
n/500,000....	18.0	16.0	0.88	15.0	0.83
	24.0	13.7	0.57	15.8	0.65

Observations were next made on the growth rate to ascertain whether the retardation occasioned a gradually increasing lag in rate of elongation, or an abrupt termination of growth due perhaps to the sudden failure of vitality in the cell. Table II shows the average growth of several groups of four radicles, each selected from the various concentrations, and of the corresponding controls in distilled water. The several growth periods recorded for each concentration were consecutive.

With one exception, growth was in every case less in the copper sulfate solution than that made by the control in distilled water. In the higher concentrations growth was practically inhibited at the end of a twenty-four hour period. Passing down the series the growth is seen to be gradually diminished after the first twenty-four hours. A similar reduction in growth rate is apparent in the controls, though in a degree much less marked.

The observations summarized in tables I and II indicated that the series of concentrations selected would afford material showing strong toxic action resulting ultimately in death (*n*/20,000 to *n*/50,000), as well as the more prolonged and gradual though no less fatal effect of higher dilutions.

TABLE II

AVERAGE GROWTH IN COPPER SULFATE SOLUTIONS AND DISTILLED WATER*

Copper sulfate solution			Distilled water
Concentration	Time in solution in hours	Growth in mm	Growth of corresponding control in mm
n/50,000	21.5	2.3	10.2
	24.5	0.0	8.0
	49.0	0.0	11.6
n/90,000	20.0	4.5	11.0
	24.0	1.2	12.3
n/110,000	18.5	7.0	11.3
	25.0	2.0	11.7
	22.5	0.5	9.7
n/150,000	21.0	6.5	8.3
	22.0	4.0	10.2
	24.0	0.7	10.2
n/250,000	19.0	11.5	14.2
	24.0	9.2	14.0
	24.0	3.7	11.2
n/300,000	19.0	11.2	14.2
	24.0	5.7	14.0
	24.0	0.5	11.2
n/400,000	18.0	12.7	15.0
	24.0	10.5	13.0
	24.0	4.2	10.0
n/500,000	18.0	16.0	15.0
	24.0	15.2	13.0
	24.0	7.2	10.0
n/500,000	24.0	13.7	17.2
	24.0	7.5	14.7
	24.0	1.5	2.7
	24.0	0.5	3.0

* The intervals under each concentration represent consecutive periods of exposure for a single group of seedlings. The sum of these intervals will give the total time in the solution.

THE EFFECT OF DILUTE SOLUTIONS OF COPPER SULFATE ON MITOSIS

The material discussed in this section was selected from cultures in various concentrations of copper sulfate, and the root tips chosen for study, together with the corresponding control in distilled water, were fixed in the manner noted above at intervals of approximately twenty-four hours. Some preparations were made at other intervals in order to increase the range of observations.

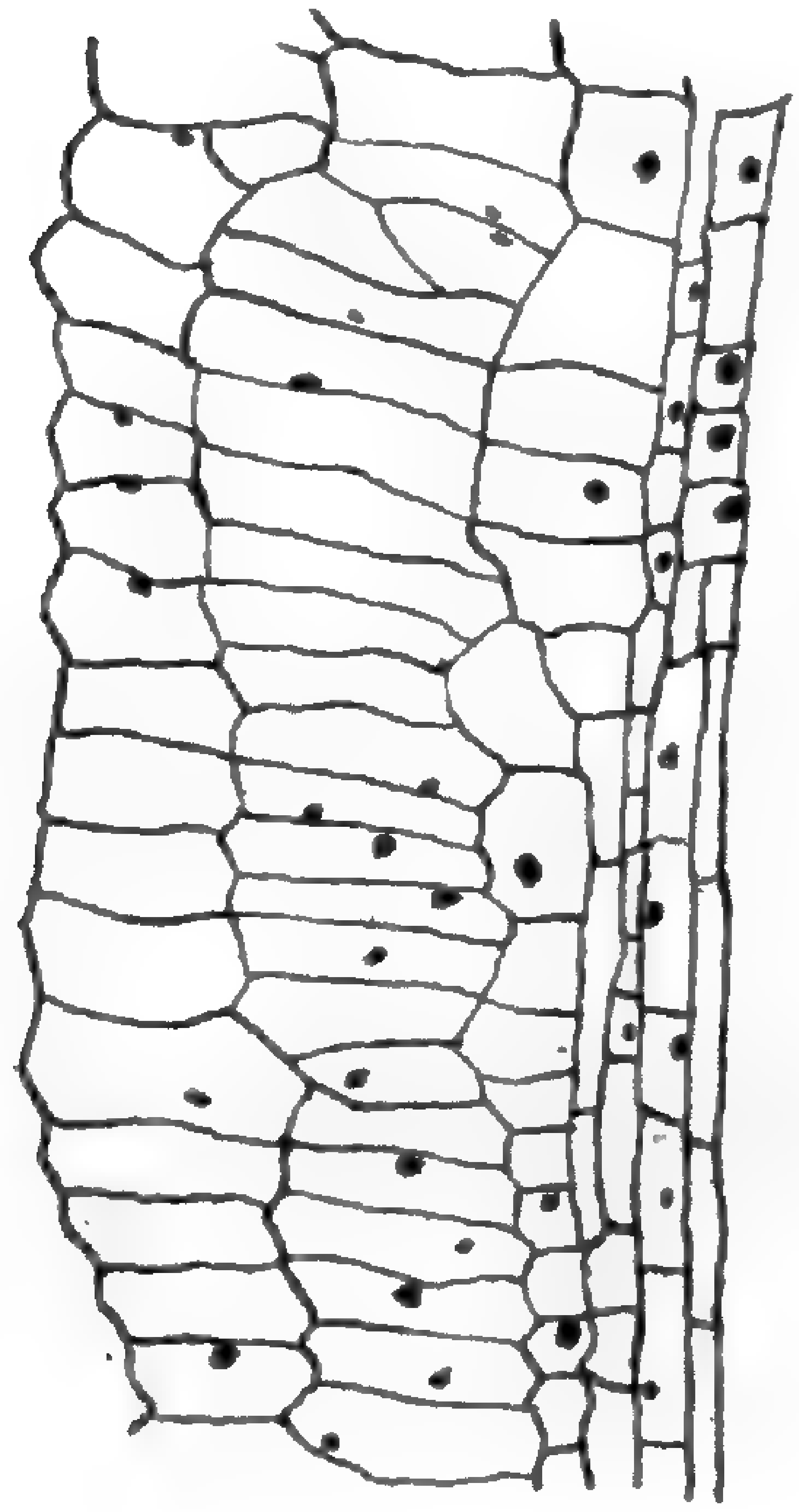
In root tips fixed after an exposure of one hour to *n*/20,000, mitosis was arrested; after 16 hours the root tips were dead. After 20 hours in *n*/30,000 there were no mitoses, and the cells of the dermatogen, outer periblem, and meristem were dead and disintegrating. The nuclei of the cells not disorganized were of normal size and occasionally contained two nucleoli.

After exposure for 40 hours to *n*/40,000 there were only rare mitoses. The outer cell layers were plasmolyzed, the mid-plerome cells were vacuolate, and the persistent nuclei shriveled. The nuclei of the larger number of the other cells of the plerome were resting and very frequently contained two nucleoli. The apex of the tip was dead, but some development in the plerome region was evidenced by the thickened walls of the cells destined to form the fibrovascular bundle. These thickened cells extended down to within 2^{mm} of the end of the radicle. At 3^{mm} from the apex of the tip there was an area of hypertrophied periblem cells (*fig. 1*) which had developed to several times the normal size, producing distortion of the radicle and giving it a swollen edematous appearance on one side. Since the nuclei in these cells were disorganized, a corresponding increase in size could not be determined.

In tips exposed for 6 hours to *n*/50,000 there were a few division figures. An exposure of 20 hours to this concentration killed all the cells in the meristem region. Many of the middle periblem cells were greatly enlarged, and in the others practically all nuclei were in the resting stage and were rich in chromatin. Cells with two nucleoli were very common in the plerome region, where also a few cells were observed containing three nucleoli. In general appearance the plerome cells resembled those shown in *fig. 2b*. After 44 hours practically all the cells were dead and disintegrating.

An exposure of 20 hours to *n*/70,000 killed the outer layers of cells, but in the inner periblem normal chromatic figures were present, and as in the preceding cases the achromatic figures were obscure. At the end of 46 hours large vacuoles appeared in the cytoplasm of many cells, and frequently so crowded upon the nucleus that it was driven to one side of the cell. Nearly all of these cells were enlarged in size and irregular in outline. In the inner periblem practically all stages of the chromatic figure occurred, although very few cells contained other than resting nuclei. After 69 hours' exposure to this concentration the older periblem cells were still more enlarged and the outer ones were disintegrating. A few of the inner periblem cells showed division stages, none of which were later than early anaphase.

The cells of the root tips treated with $n/190,000$ for 44 hours differed little from those in $n/70,000$ for the same length of time. After 72 hours there was no division, and the periblem cells were frequently enlarged.



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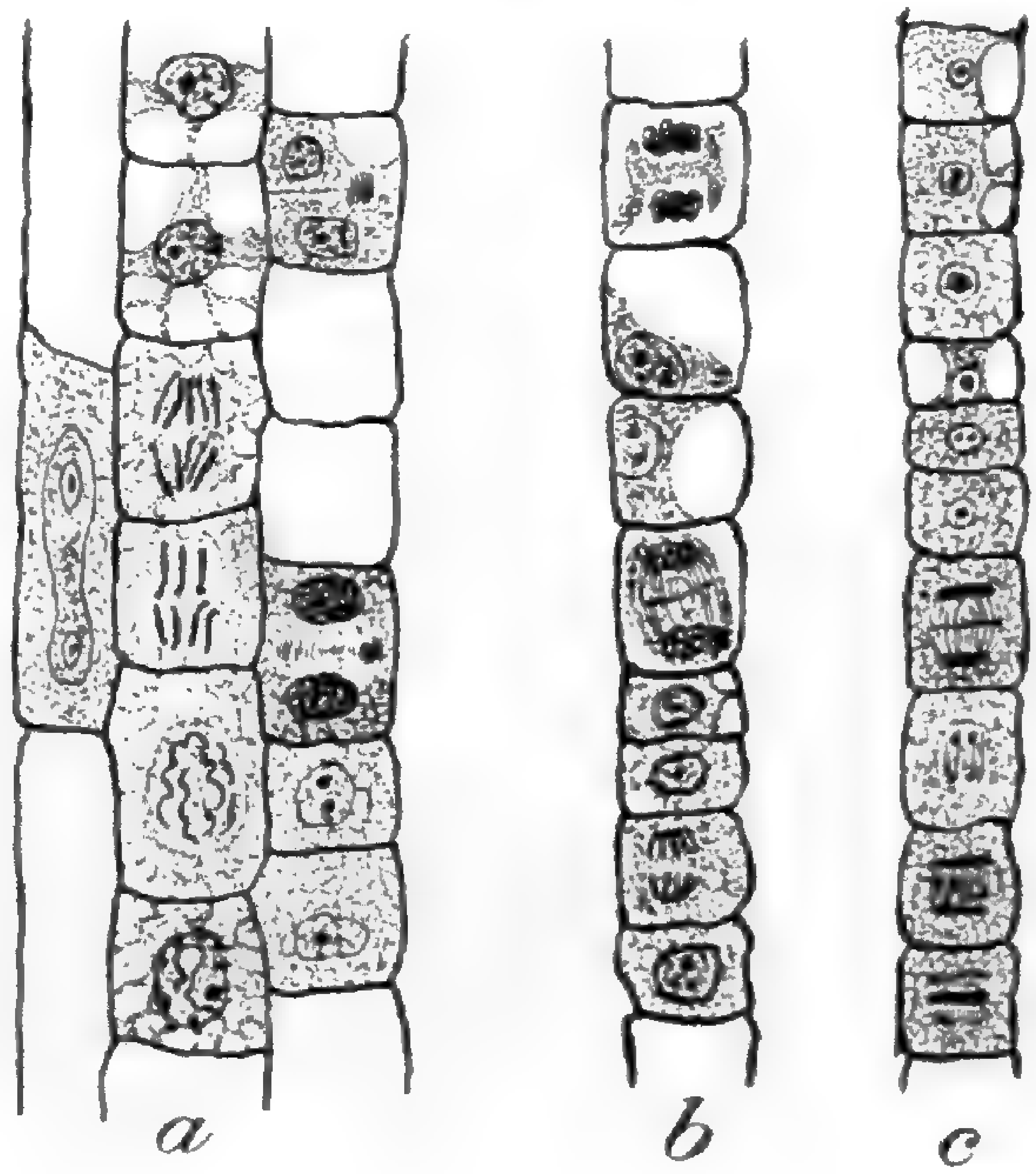

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FIG. 1. Proliferated cells of root tip grown in dilute copper sulfate solution.—FIG. 2. *a*, cells of root tip of *Vicia Faba* after 96 hours in distilled water; *b*, the same after 46 hours; *c*, *Lupinus albus* 69 hours in distilled water.

In the outer periblem of the material treated with $n/100,000$ for 43 hours, a few cells occurred containing division figures. In the inner periblem many nuclei were in the spireme stage and the meristem area was especially active. In these inner cells the achromatic figure appeared to be normally developed, but in the outer layers the cells were more or less vacuolized, and the spindle fibers were degenerating. In 93 hours this condition had spread to all the cells.

Approximately similar conditions occurred in the radicles treated in the concentrations $n/140,000$ and $n/150,000$. In 93 hours practically all cells were dead, the outer layers being also disorganized. However, in the case of the material in $n/150,000$ for 93 hours, in the periblem cells about 3^{mm} from the apex of the root tip a few mitotic figures occurred. In the corresponding controls in distilled water, chromatic figures were frequent even in the outer periblem cells, but many abnormalities occurred in the achromatic figures and cytoplasm (*fig. 2b*). Nuclear division occurred here and there in the inner periblem of tips which had been 93 hours in a $n/160,000$ solution, but the outer periblem was dead and disorganized. The division figures did not differ from those in the controls, and the nuclei in the resting stage were normal in appearance. In tips exposed for 68 hours to the action of $n/300,000$, $n/400,000$, and $n/500,000$ solutions, division was frequent in all parts of the active tissue and did not differ essentially from that in the corresponding controls. However, the outer cell layers of the tips in the copper solutions were less active, and the total number of mitoses was smaller than in the controls. The cytoplasm of many cells contained vacuoles of variable size, some being so large as to crowd heavily upon the nucleus. The same phenomenon occurred, though less frequently, in the controls.

DEMOOR (**7**), who studied the effect of chloroform on the cell protoplasm, observed therein a marked vacuolization which he regarded as the direct result of the action of this reagent. Also NEMEC (**18**) found that chloroform and potassium nitrate produced vacuoles in both chromosomes and cytoplasm of *Vicia Faba*, and BLAZEK (**3**) states that benzol vapor caused the vacuoles of the cytoplasm so to increase in size that they caused deformation of the nuclei. However, since vacuoles, similar to those observed in the course of these experiments with copper sulfate, occurred also in the controls in distilled water, it would appear to follow that this phenomenon is not necessarily due to a narcotic or poisonous action, but may result from an alteration in the concentration of the cell fluids.

Before the examination of the toxicated material had proceeded very far, it became evident that the conditions of mitosis in the controls grown in distilled water were far from normal. The entire series of controls was thereupon reexamined, and a progressive degeneration demonstrated therein closely resembling that in the cells treated with the copper solutions. After 7 hours in distilled water there was little division in the periblem, the figure in a few cells being in early prophase. Division was active in the plerome. After 22 hours division had ceased in the outer layers, but still occurred normally in the inner tissues. In 46 hours the radicles were curved, numerous cells were dead, large vacuoles occurred in the cytoplasm, and in many cells the achromatic figure was degenerating (*fig. 2b*). The general condition after 96 hours is illustrated in *fig. 2a*. Particularly striking are the large nuclei, the cytoplasmic vacuoles, and the interrupted cell plate seen in one of the upper cells of the figure. *Fig. 2c* represents a group of cells from a radicle of *Lupinus albus* after 46 hours' exposure to distilled water, and is inserted here for the purpose of comparison. In these cells also vacuoles occurred in the cytoplasm, and there was some degeneration of cytoplasmic structure.

It appears that the distilled water exerted practically the same effect on mitosis as was produced by the dilute copper sulfate solutions, but only after a more prolonged exposure.

THE EFFECT OF MORE CONCENTRATED SOLUTIONS OF COPPER SULFATE

In planning the experiments with stronger solutions of copper sulfate, some paragraphs from NEMEC's "Ueber ungeschlechtliche Kernverschmelzungen" (**21**) were held in mind. In this paper NEMEC describes the production of binucleate cells and other abnormalities by placing the radicles of *Vicia Faba* for thirty minutes in 1 per cent solution of copper sulfate and then transferring them to moist sawdust for seven hours. NEMEC's experiment seemed to indicate that *Vicia Faba* was remarkably resistant to the action of copper solutions, indeed to a far greater degree than in *Lupinus albus*, in which, as was learned through access to some unpublished notes of Dr. R. H. TRUE, some growth can occur after an exposure of eight minutes' duration to a *n*/16 solution of copper sulfate. A test quickly showed that thirty minutes' exposure to a 1 per cent copper sulfate solution (approximately *n*/12) was fatal to the material being used in these experiments. A series of preliminary experiments was carried out, therefore, to establish approximately the time limit which would just permit growth in $n/4$ and $n/12$ solutions as boundary concentrations, with results indicating that a slight amount of growth would follow exposure to a $n/4$ solution for three minutes, and that seven minutes' exposure to the $n/12$ solution, while permitting some growth, was not far from the point of killing.

For the experimental work the solution $n/12$ was chiefly relied upon as being best suited to give a sharp toxic effect, without endangering the loss of the material through death. The radicles were exposed to this solution for periods of three and seven minutes, respectively, were then rinsed quickly in distilled water, and at once transferred to the medium in which they were kept until the time for killing and fixing. Another dilution and longer interval of exposure were also employed to furnish a broader basis for observation.

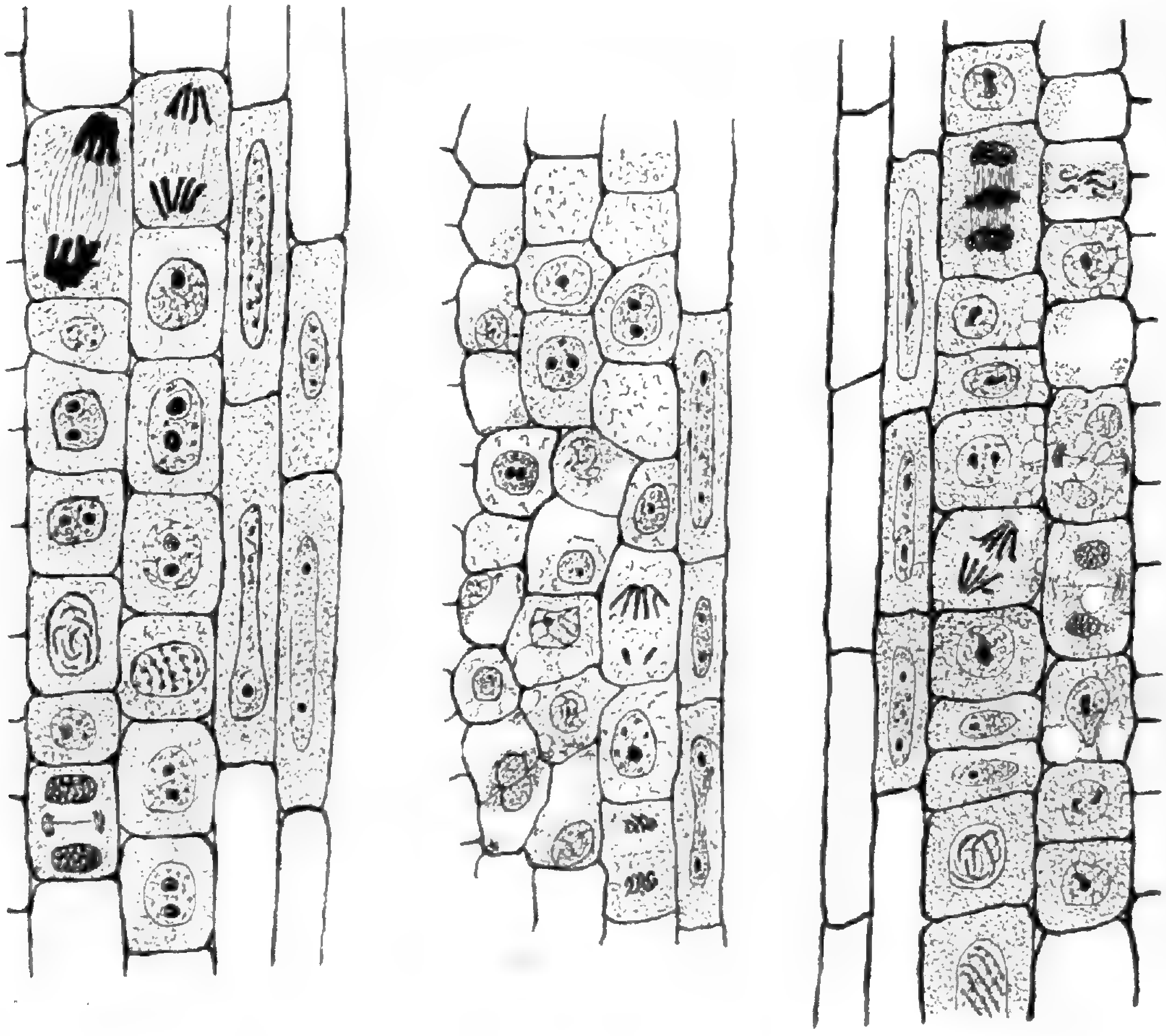
In order to have at hand for constant comparison material grown under parallel conditions with the toxicated radicles, except for the treatment with the copper sulfate solutions, a uniform lot of seedlings was taken from the germinating chamber, selected to approximately the same size, and divided into six groups which were then prepared as follows: (*a*) one group in moist sphagnum; (*b*) one in distilled water; (*c*) one in $n/12$ copper sulfate three minutes, then sphagnum; (*d*) one in $n/12$ copper sulfate three minutes, then distilled water; (*e*) one in $n/12$ copper sulfate seven minutes, then sphagnum; (*f*) one in $n/320$ copper sulfate ten minutes, then distilled water.

Four root tips were fixed from each series at intervals of 3, 7, 22, and 30 hours. Sections of the tips from the first two series, designated as the controls in the following pages, were compared at every stage with the sections studied in the remaining series.

The cell growth and nuclear division observed in the controls placed in sphagnum were considered as normal, since good preparations were secured showing abundant mitoses, all of which conformed to the type generally reported as occurring in vegetative tissues of *Vicia Faba* (*fig. 6*). Departures from the normal cell division were observed in the controls grown in distilled water similar to those observed in the controls paralleling the cultures in dilute copper sulfate solutions (*figs. 2a, 2b*). Since the radicles in the copper sulfate solutions were manipulated under conditions identical with those obtaining in the controls, except for the exposure to the toxic solution, marked discrepancies in nuclear behavior, it was believed, could safely be regarded as a result of toxic action.

Root tips which were exposed to *n*/12 copper sulfate solution for three minutes and then transferred to distilled water for three hours showed the effect of strong toxic action in the peripheral cell layers. Here the cells were dead, but in the inner periblem occasional nuclei were in division, but frequently the cell plate had failed to form (*fig. 3*). In the majority of the uninjured cells the nuclei were in the typical resting stage. In no case did nuclei which were in the spireme stage show the hyaline polar caps, frequently figured as characteristic of the development of the normal achromatic figure in *Vicia Faba*, and occurring in the controls grown in sphagnum in these experiments (*fig. 6*). The nucleoli were usually large and frequently occupied a clear area surrounded by the linin network, as seen in *fig. 3*. Many nuclei contained two large nucleoli, each lying within a distinct clear area. In the degenerating nuclei of the injured cells the persistent nucleolus was generally of very large size, and the form of the nucleus was usually outlined only by the linin network, all chromatic substances other than the nucleolus having lost their usual staining properties. In some cells the cytoplasm showed modifications apparently due to the action of the copper sulfate, although these were usually not sharply defined, but in some cases numerous large vacuoles occurred distributed through the cytoplasm, in others huge vacuoles had formed at the sides of the nucleolus, presenting much the appearance of the older cells in which large sap cavities had formed.

In root tips which had been exposed for three minutes to *n*/12 copper sulfate solution and then placed in water for seven hours, the cells presented much the same general appearance as those examined at the end of the three-hour period. The greater part of the nuclei were in the resting stage, though a few cells of the inner periblem showed spiremes forming. Occasional nuclei were farther advanced in division, but no stage later than middle anaphase was seen. In the distribution of the chromosomes, and in their manner of passing from the nuclear plate, no deviation from the typical process occurring in the controls in sphagnum was observed. After 22 hours a decided change in the appearance of the cells of the root tip was apparent. The dermatogen had exfoliated and the periblem cells, having lost their normal rectangular form, were irregularly rounded. All early stages of mitosis were present, and the development of the chromosomes had proceeded normally. All stages of mitosis up to the formation of the cell plate occurred, but with frequent degeneration of the spindle fibers (*fig. 4*). The newly formed division walls separating certain cells were very thin and indistinct, and the appearance presented on first examination suggested the binucleate cells described by NEMEC (**22**) and others. These division walls were usually asymmetric with the other cell walls. In



3 4 5

FIG. 3. *Vicia Faba* three minutes in $n/12$ copper sulfate, then three hours in distilled water.—FIG. 4. *Vicia Faba* three minutes in $n/12$ copper sulfate, then twenty hours in distilled water.—FIG. 5. *Vicia Faba* seven minutes in $n/12$ copper sulfate, then three hours in distilled water.

the root tips examined after 30 hours, division still occurred in the periblem cells. The chromatic figure was regularly found, but only in the inmost layers of cells was the spindle unaffected. The nuclear plate had formed in the central spindle region of most cells, but usually failed to reach the walls.

In the root tips placed in distilled water for three hours after seven minutes' exposure to *n*/12 copper sulfate, very few mitoses occurred in the periblem cells, but in these the chromatic figure presented a normal appearance. The cytoplasm of all the outer periblem cells exhibited large vacuoles, some of which had enlarged sufficiently to drive the nucleus to one side of the cell, and in the inner periblem frequent cells developed unusual vacuoles. In some cells in late anaphase vacuoles occurred between the cell plate and the daughter nuclei (*fig. 5*), a condition which occurred also in the distilled water controls, but division did not proceed farther in the copper solution. At one side of some cells the plate, failing to reach the lateral wall, ended in a fibrous plasma mass about half-way between the axis of the spindle and the wall of the cell. In the cells at the apex of the root tip occasional nuclei were in early prophase, anaphase was frequent, and a few nuclei were at telophase. In the latter stage the cell plate had formed in the normal manner, but in practically all the nuclei at anaphase no trace of cell plate appeared. In some cells the spindle fibers were only faintly visible, in others a perceptible thickening of the fibers had occurred in the equator of the spindle, but no figure showed the line of granules characteristic of cell plate formation. In the resting nuclei, as usual, there occurred one or two large nucleoli. These were rarely circular as viewed in optical section, but were amoeboid in form.

In radicles placed for ten minutes in *n*/320 copper sulfate, then transferred to distilled water for three hours, the dermatogen cells were dead and many of the outer periblem cells lacked nuclei. The nuclei present were in the resting stage. Numerous mitoses occurred in the cells of the plerome and inner periblem, but the larger number showed a tendency toward degeneration in the spindle fibers. After seven hours the general appearance of the cells was much the same, but there were very few mitoses. After 22 and 30 hours, respectively, no division figures occurred in the outer cell layers, but a few cells in the periblem and inner plerome still showed normal chromatic figures; some nuclei were in the spireme stage, although the majority were resting; cellular activity, as expressed in division, had practically ceased.

A comparative estimate of the proportion of cells in course of division in each of the several experiments did not show that any concentration used had stimulated division; on the contrary, the retarding influences, particularly in the more concentrated solutions, were very pronounced. The first apparent effect of the toxic solution was arrest of nuclear division through inhibition of the activities of the achromatic figure. In the early division stages this was soon followed by degeneration of the spindle fibers. In the later stages of division the failure of cell plate formation was characteristic. These phenomena were accompanied or followed by an increase in the number and size of the vacuoles in the cytoplasm. The death of the cell evidently occurred shortly after this condition was reached.

It seems probable that the toxic solution penetrates somewhat slowly to the inner cell layers, since under its influence the outer layers of cells are killed, while in the inner regions not yet visibly affected, normal development continues.

There was no satisfactory evidence of the occurrence of amitosis. Double nucleoli occurred as frequently in the cells of the controls as in those treated with the copper solutions, a result which, so far as these experiments have extended, directly controverts the statement of WASIELEWSKI (**30**) that "das erste Kennzeichen, dass ein Kern sich zur amitotischen Theilung anschickt, besteht in einer Verdoppelung des Nucleolus."

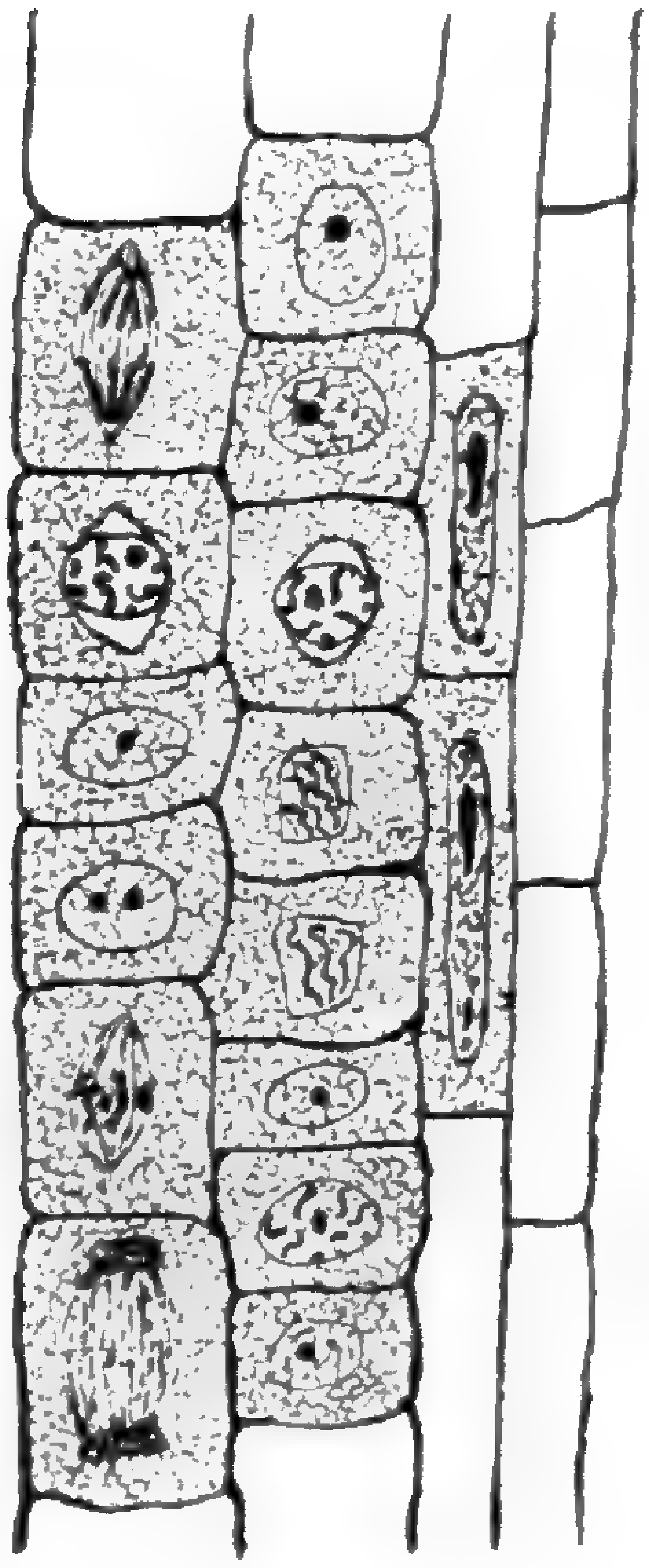
The copper solutions did not cause abnormalities in the development of the chromatic figure. There was no doubling of the normal number of chromosomes. Occasionally two daughter chromosomes remained attached by their ends for some time after the others had left the nuclear plate, apparently forming an attachment between the daughter chromosome groups. However, this irregularity was also observed in the controls. NEMEC (**21**) states that treatment with 1 per cent copper sulfate solution produced binucleate cells in root tips of *Vicia Faba.* After 17 hours' sojourn under normal conditions binucleate cells no longer appeared, and he concluded, therefore, that the nuclei in the binucleate cells had fused. The experiments here described furnish no support to this theory of nuclear fusion, since no cells were observed that contained more than one nucleus. Occasionally, through failure of the nuclear plate, cells appeared to contain two nuclei, but these daughter nuclei were never fully reconstituted, and the cells were degenerating.

The stronger copper solutions inhibited mitosis, disorganized the spindle fibers or interrupted their formation, arrested the development of the cell plate, and produced large vacuoles in the cytoplasm. The same effects were produced in the controls in distilled water, though to a less marked degree, and after a longer period of exposure. There were no abnormalities in the controls grown in sphagnum.

THE ACTION OF PHENOL

In studying the action of phenol a normal solution was prepared, and various dilutions were made therefrom in the course of the experiment. Controls were grown in moist sphagnum and in distilled water. The continuous action of phenol was observed in *n*/94 and *n*/188 solutions, respectively. Solutions of 10/94, 5/94, and 1/188 normal were allowed to act on radicles for 20 minutes, after which they were placed in distilled water and material killed and fixed therefrom at intervals of 4, 21, and 45 hours. Material from the controls received parallel preparation. In the microscopical examination of the toxicated root tips no unusual structure or condition was considered as due to the action of the phenol until careful search had shown that its equivalent did not exist in the controls.

The continuous action of a *n*/94 solution of phenol for four hours seriously injured both the cytoplasm, which showed numerous small vacuoles, and the achromatic portion of the nucleus. Numerous spireme nuclei were observed, many of which were much enlarged and irregularly distended apparently by a great increase in the amount of nuclear sap within them. Occasionally these enlarged spireme nuclei were laterally indented by the formation of a dense plasma mass at one side (*fig. 7a*). These nuclei very much resembled those described by NEMEC (**22**) as formed under the influence of chloral, of which he says: "In einiger Zellen giebt es mehr oder weniger tief eingeschnürte Kerne." At this point the resemblance ceases, and no support can be given to **Nemec's** further statement that "diese Zellen können Scheidewandanlage besitzen." Since no other unusual forms were observed in either cell or nucleus, these are regarded as nuclei in the course of disorganization. In the older as well as in the younger portions of the root tip nuclear figures occurred which usually showed the achromatic spindle or its remnants. However, no division stage later than very early anaphase was present. The chromosomes in part of these figures had split longitudinally, in others no splitting occurred. In no case had the chromosomes left the nuclear plate. Evidently the movement of the daughter chromosomes from the nuclear plate to the poles of the spindle had here been inhibited by the action of the phenol upon the mantle fibers.



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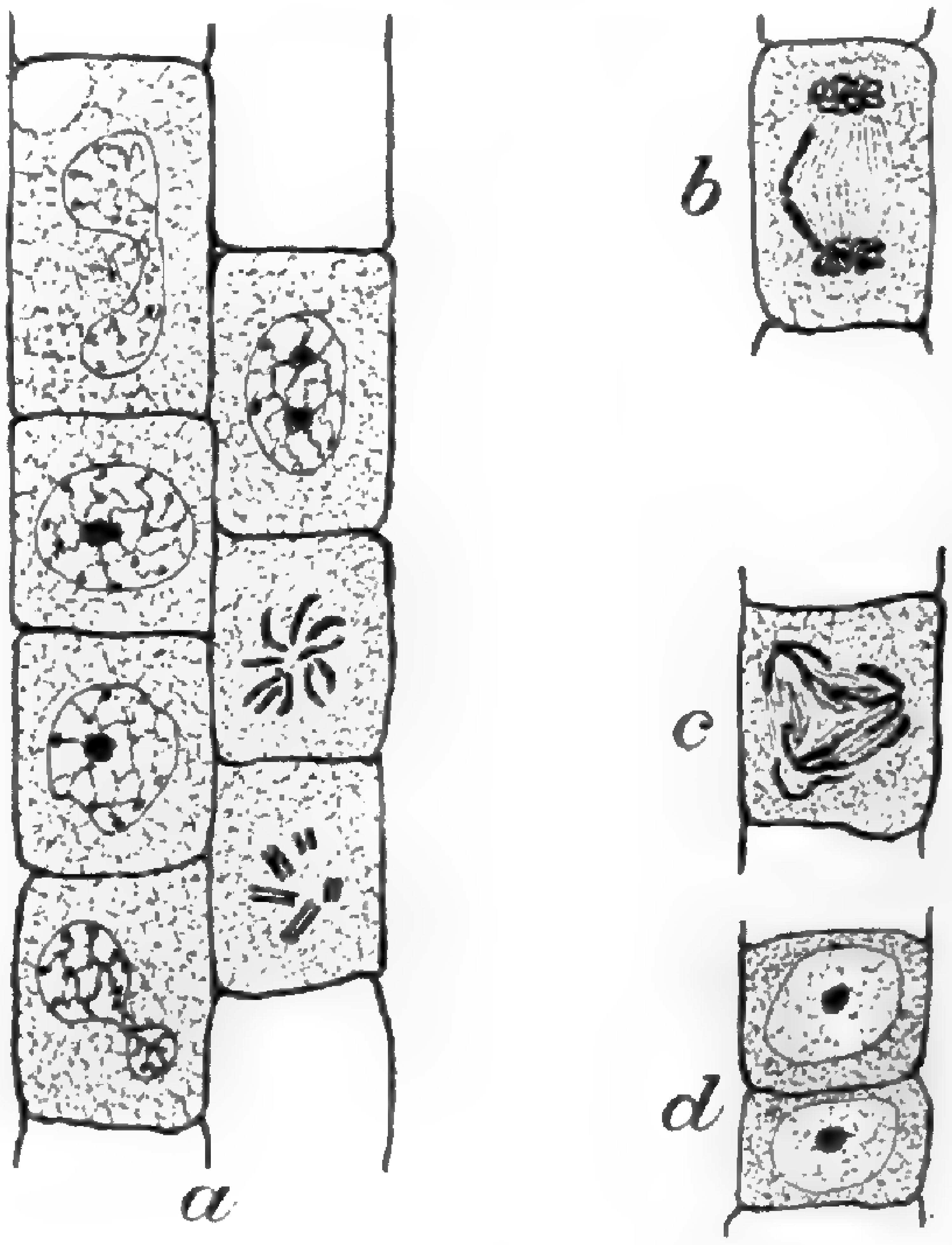

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Fig. 6. Normal cells from a root tip of *Vicia Faba* grown in moist sphagnum.—Fig. 7. *a*, *Vicia Faba* in *n*/94 phenol four hours; *b*, retarded separation to chromosomes; *c*, multipolar spindle; *d*, enlarged nuclear areas.

At the end of 21 hours the root tips had a dull white luster, and were evidently dead. Upon examination all the cells were found to be plasmolyzed.

The radicles which had been for four hours in $n/188$ phenol were next examined and all stages of mitosis found. The cytoplasm of the cells of the outer layers exhibited a coarsely netted structure due to the formation of numerous small vacuoles. Occasional spireme nuclei were unduly enlarged, and in a very few cases the nuclei were constricted in one diameter, apparently by the development of a plasma mass as previously noted. The early stages of the spindle were very obscure, but during anaphase the fibers became quite distinct. A few cases of late anaphase occurred in which occasional chromosomes had not left the nuclear plate, but remained at one side of the spindle in line with the row of granules marking the early stages of cell plate formation (*fig. 7b*). A similar occurrence was observed by BLAZEK (**3**) in the cells of root tips of Pisum treated with benzol, and in *Vicia Faba* also by SCHRAMMEN (**27**), who says: "Eine nicht seltene Erscheinung bei der plötzlichen Einwirkung von hohen Temperaturen ist das Nichterfassen von Chromosomen durch die Spindelfasern und das Zurückbleiben einzelner Chromosomen bei dem raschen Transport zu den Spindelpolen." In a few cases the chromosomes at one pole of a spindle had diverged and formed two groups, to each of which a portion of the spindle extended (*fig. 7c*). SABLINE (**26**), who produced similar phenomena by the use of sulfate of quinine, says, "Sur quelques figures multipolaires on peut voir deux et quelquefois trois fuseaux." In the material treated with phenol, however, multipolar spindles occur so rarely that there seems to be no good ground for assuming that they are produced by the action of this reagent.

After an interval of 21 hours in $n/188$ phenol there were no mitoses. The nuclei were all in the resting stage and for the most part contained but a single nucleolus. General disorganization of the cells of the root tips had begun.

Tips of radicles were treated for 20 minutes with 10/94 normal phenol and then transferred to distilled water for four hours. At the end of this time all nuclear activity had ceased. In most cases the nucleus was enlarged, and in the field of the microscope appeared as a light area against the darker background of the cytoplasm of the cell (*fig. 7d*). The chromatin had almost entirely disappeared from the nuclear network. Very prominent in the nucleus appeared one or two large and deeply staining nucleoli. After 24 hours under similar conditions there was little change in the appearance of the cells. Plasmolysis in occasional cells and the collapsed walls of the outer cell layer indicated that disorganization had begun.

Next 5/94 normal phenol was allowed to act for 20 minutes on root tips, which were then transferred to distilled water for four hours. There were no mitoses. In certain cells of the inner periblem and in some plerome cells elongating to form procambium, large vacuoles occurred, while many enlarged nuclei had partially collapsed. The general condition of the cells resembled very closely that obtaining after the exposure for four hours to the 10/94 normal solution. After 21 hours the root tips had made no further growth and were evidently dead. Disorganization of the cell structures, however, had not progressed so far as in the case of the material with 10/94 normal for the same time. Here again the nuclear area was enlarged, though very regular in form, and had a lighter hue than the surrounding cytoplasm. In the radicles treated for 20 minutes in the other dilutions employed, continuous growth occurred and development was apparently normal. After 20 minutes' treatment with $n/94$ and $n/188$ phenol, respectively, and then with distilled water for 45 hours, the root tips were fresh and crisp and had elongated at approximately the same rate as the distilled water controls. Mitoses were frequent, and the more active regions of the cytoplasm, particularly the achromatic figure, showed no injury as a result of the action of the phenol.

Phenol in common with most antiseptics is a marked protoplasmic poison. Certain results of its action were especially apparent in the cells of the root tips treated continuously with this reagent. The achromatic figure of the division nucleus in early anaphase was seriously injured and mitosis inhibited. The nuclear plate stage was apparently unusually sensitive to the action of the phenol, since the spindle fibers as a rule failed to function normally in drawing apart the daughter chromosomes. As previously noted, the development of small vacuoles in the cytoplasm appears to be a characteristic effect produced by the phenol. There was no amitotic division and no tendency toward the production of binucleate cells was observed.

In the material treated for 20 minutes with the stronger solutions and then with distilled water, the most striking modification was the enlarged nuclear area surrounded by cytoplasm of a darker hue. Here also the cytoplasm usually contained small vacuoles, but neither amitosis nor abnormal division figures occurred. The general course of events under the action of the phenol seems to be the progressive decline of the cell functions, beginning in the most active and labile regions of the cytoplasm. The visible form changes are confined almost entirely to the enlargement of the nuclear area and the formation of numerous small vacuoles in the cytoplasm. The abnormalities due to the action of phenol are clearly differentiated from those occurring in the distilled water controls as previously described. The sphagnum controls were normal as usual.

THE EFFECT OF STRYCHNIN SULFATE

The preparation of the solution of strychnin sulfate and the manipulation of the material accorded closely with the plan pursued with the phenol. Five strengths of solution were used, which for convenience in comparison are expressed approximately in terms of percentage solutions, viz., 1, 0.5, 0.25, 0.1, and 0.01 per cent. In the first group of experiments the radicles were exposed to the constant action of the several solutions for intervals of 3, 6, and 24 hours. In the second group the root tips were treated with the various dilutions for ten minutes, and were then transferred to distilled water for the time intervals mentioned above. The usual controls were carried in sphagnum and in distilled water.

The 1 per cent solution was allowed to act on radicles for three hours. The tips were then a dull white color and had become flaccid. The cells were all plasmolyzed, and in the outer layers they were disintegrating.

From the external appearance after three hours' immersion in the 0.5 per cent solution death was inferred. However, in plerome and inner periblem a few nuclei were dividing. The outer cells were plasmolyzed and the cell walls were breaking down. In the inner cells the few scattered spireme nuclei and chromatic figures retained their normal shape and orientation in the presence of large vacuoles, one or more of which frequently occurred in the cytoplasm of these cells.

After three hours in the 0.25 per cent solution there were no mitoses.

The cytoplasm of many cells was plasmolyzed, while that of others exhibited a coarse web or net structure, but the cells themselves retained their shape and the outer layers were not disintegrated.

In the tips of radicles acted on by a 0.1 per cent solution for three hours all stages of division were observed. The achromatic figures were very distinct, and nuclei with two nucleoli occurred frequently. After six hours in this concentration the cells of the outer layers were dead and the cell walls had collapsed. There were some spireme nuclei in the inner periblem and a few nuclei were at anaphase. The large deeply staining nucleoli were prominent features of all nuclei not disorganized.

The cells of the outer layers of root tips in 0.01 per cent strychnin for three hours were mostly dead and collapsed. Division figures occurred occasionally in the plerome and were frequent in the inner periblem cells. The spindle fibers of anaphase were clear and distinct, but no polar caps were observed in spireme nuclei. The cell plate was regularly laid down in late anaphase and two nucleoli were frequent in resting nuclei. After five hours in the 0.01 per cent solution some division figures were present. The number of spireme nuclei in proportion to those in the later division stages was greater than at the end of three hours. Very few nuclei were in late anaphase. After 20 hours the area of dead cells included all but those of the inner periblem at some distance from the apex of the tip. No deformation of the nuclei occurred. Even in cells in which the cytoplasm was disorganized, the nuclei frequently retained their normal shape and general appearance. Growth and nuclear activity seemed to have been arrested by the gradual failure of cytoplasmic activity.

The radicles exposed for ten minutes to the strychnin solutions, then transferred to distilled water, were next considered. After ten minutes in 1 per cent solution and three hours in water the cells of the outer layer were dead. In many of the plerome and inner periblem cells containing division figures the cytoplasm was vacuolate, but the figures were not disturbed. All stages of division were observed, but there were no aberrant mitoses.

After six hours in this concentration further disintegration of the outer cells had taken place. Normal division figures persisted in the plerome and inner periblem cells, and a few rare spireme nuclei showed clearly the polar caps. There were no abnormal structures. At the end of 24 hours there were no mitoses, all the cells were evidently dead.

In the tips exposed for ten minutes to the 0.5 per cent solution, and then placed in distilled water for three hours, mitotic figures occurred even in the outer cells of the periblem. The cytoplasm of these cells usually contained several large vacuoles and the nuclei were all normal in appearance. All stages of normal mitosis were abundant. After 6 hours little change in appearance was visible, but after 24 hours the cells of the outer layers were dead. However, all stages of normal division were abundant in the plerome and inner periblem.

Normal mitoses were abundant in the tips of radicles placed in the 0.25, 0.1, and 0.01 per cent strychnin solution for ten minutes, then in distilled water for 3, 6, and 24 hours. There was no evidence that the strychnin solution had exerted any harmful action in the last three concentrations, during ten minutes' exposure.

The data on the effects of strychnin on higher plants are not very extensive. According to PFEFFER (**25**), it has not been satisfactorily determined that alkaloids affect the protoplasm of plants. In his discussion of the effects of alkaloids in general, CZAPEK (**5**) says: "Für höhere Pflanzen stellte schon Knop an Mais fest, dass Chinin, Cinchonin, Morphin schädlich wirken, und auch hier gehören Chinin, Strychnin, Cocain zu den giftigsten Substanzen, während Morphin relativ schwach einwirkt (Marcacci)." MOSSO (**14**) found that 0.05 per cent solutions of strychnin stimulated germination in *Phaseolus multiflorus*, but that more concentrated solutions retarded it. DAVENPORT (**6**) states that the protoplasm in the tentacles of Drosera is killed by the action of strychnin. He mentions also its retarding action on the germination of peas, corn, and lupines, but unfortunately the concentrations which exerted a harmful action were not given.

The action of alkaloids on Protozoa has been investigated by SCHÜRMAYER (**28**) and others, with results that apparently confirm the theory advanced by LOEW (**13**) that the action of alkaloids is mainly confined to the plasma of the ganglion cells. CLARK (**4**) found that species of fungi, notably Sterigmatocystis, as well as Aspergillus and Oedocephalum, grew and fruited in a saturated solution of strychnin sulfate. CLARK finds that his studies on the molds harmonize with the theory of LOEW, and concludes that the fungi and bacteria are practically unharmed by this alkaloid, since they have no differentiation of nerve protoplasm. This line of reasoning carried logically forward would argue for the presence of protoplasmic structure in the higher plants which should be comparable with the nerve fibers of animals. Such structures have indeed been described by NEMEC (**19**) from root tips of Allium and *Vicia Faba*. In the latter plant the longitudinal protoplasmic strands of the large plerome cells of the root are regarded by NEMEC as bundles of fibrillae surrounded by a definite sheath and lying imbedded in a special plasma. NEMEC concludes that these fibrils are strands of protoplasm specialized for the conduction of traumatropic, geotropic, and other stimuli, and compares them, although with little apparent warrant, to the nerve fibers of animals. Since the protoplasm often develops a fibrillar structure in connection with other functions, it is not certain that the systems of fibrillae observed by NEMEC are specially adapted for the transmission of these stimuli, and therefore the portion of the protoplasm peculiarly sensitive to the action of alkaloids. ANDREWS (**1**) found that many marine plants, including Cladophora, Ectocarpus, and Polysiphonia, were uninjured by a solution of strychnin sulfate having one part in 1000 of water, but that a solution of the same having one part in 250 killed all the plants in 24 hours.

Although the experiments carried out with strychnin sulfate on *Vicia Faba* were far from satisfactory, they indicate clearly that this reagent is an active poison to the plant used. The cytoplasm first becomes vacuolate, and then degenerates in the outer cell layers, and this condition progresses toward the center of the root tip as the time of exposure to the strychnin solution is extended. It is planned to pursue this line of experimentation farther, in order to determine whether this reagent produces definite and characteristic form changes in the protoplasm.

Summary and conclusions

The cell studies here described were made in the hope of obtaining some further data on the physiology of toxic action. The work which has been done in this direction seems to be concerned more with the production and study of abnormal cell phenomena than with the comparison of cell activities under a series of abnormal conditions varying in intensity. It is well known that in a series of dilutions of a toxic substance growth diminishes usually as the concentration increases, and the end sought in these studies was to contrast cell activities under such abnormal conditions of development. No deliberate attempt was made to induce abnormal cell behavior.

The toxic solutions experimented with were (1) copper sulfate, a metallic base which readily ionizes; (2) phenol, a non-electrolyte; and (3) strychnin, an alkaloid presumably poisonous to protoplasm. First the rate of growth of radicles of *Vicia Faba* was determined in a series of concentrations of copper sulfate ranging from *n*/20,000 to *n*/500,000, then the number of hours required for growth to be reduced to the minimum was next observed in order to determine the range within which to choose material for study. Root tips grown in the above and intervening concentrations were examined at intervals ranging from 1 to 93 hours. Radicles were also subjected to the action of stronger solutions, *n*/12, *n*/320, for intervals of 3 to 10 minutes, and the cells were examined after a lapse of 3 to 30 hours. The results indicate that the toxic effect was first felt in the kinoplasm of dividing cells, as shown by the loss of function and subsequent degeneration of the achromatic figure. Large vacuoles arose in the cytoplasm, frequently deforming achromatic figure and nucleus. Later the entire cytoplasm was disorganized. Development of the chromatic figure was consequently inhibited, but neither amitosis nor abnormal mitosis was observed. In the controls in distilled water, also, the cytoplasm became vacuolate; some of the nuclei were enlarged, and occasionally the formation of the cell plate was interrupted. In both copper sulfate solutions and distilled water the course of events was arrest of mitosis by loss of functions in the achromatic figure, followed by the death and disorganization of the cell contents.

The treatment of root tips with solutions of phenol ranging from *n*/188 to 10/94 normal produced enlarged achromatic figures and caused the cytoplasm to become very coarsely netted or vacuolate. The chromatic figure was regularly formed and presented no special abnormalities. Neither amitosis nor binucleate cells occurred. The chromosomes were normal in number and structure. Spindle formation was frequently inhibited, in consequence of which the chromosomes failed to separate normally. With the arrest of mitosis further development apparently ceased.

The experiments with strychnin were unsatisfactory. Solutions ranging from 0.01 to 1 per cent inhibited mitosis and disorganized the cytoplasm, causing the death of the cells. The nuclei were not deformed and the chromatic figures were normal. Strychnin seems to arrest cytoplasmic activity swiftly, without producing visible changes in the mitotic figure.

As a result of their investigations, certain authors state that nuclei can be made to divide amitotically through the influence of toxic solutions. Others, who used the same technic and methods, deny that such solutions produce amitosis, and find that in every case when division occurred the resulting nuclei were formed only by mitosis. BLAZEK (**3**) found that benzol caused the vacuoles in the cytoplasm to increase greatly in size; NEMEC (**18**) observed that chloroform and potassium nitrate produced granulation of the spindle fibers; WASIELEWSKI (**30**) ascribed doubling of the nucleoli to the action of chloral hydrate; WOYCICKI (**34**) states that ether prevented the formation of division walls in dividing cells; and WISSELINGH (**31**) found that under the influence of phenol the cell structures were poorly differentiated.

The authors just cited attributed the above-mentioned abnormalities solely to the action of the toxic substances used. In the experiments described in this paper all these abnormalities were observed in the toxicated material, and also in the controls grown in distilled water. These results appear to indicate that the action of distilled water is a factor which has been overlooked in interpreting the effect of toxic solutions on mitosis, and that numerous abnormalities ascribed to the action of toxic substances are not necessarily so produced.

CONCLUSIONS

1. The practice of growing controls in distilled water, common in certain physiological experiments, is open to serious objections, since these controls are themselves under abnormal conditions, and are subject to the same progressive decline of cell function as occurs in dilute toxic solutions, though at a slower rate.

2. Judged by its effect on mitosis, as compared with the effect of dilute solutions of copper sulfate, *distilled water is itself a toxic solution.* Apparently many abnormalities of cell behavior which have been attributed to the effect of toxic salts may be due instead to the osmotic action of the solution.

3. The achromatic structures organized from the kinoplasm are most sensitive to toxic action. Since the spindle fibers are reduced to a granular mass or otherwise disorganized, the further progress of division is inhibited.

4. Copper sulfate, phenol, and strychnin, under the conditions of these experiments, produce neither amitosis nor truly binucleate cells.

5. No structures occurred in the material studied which the most charitable interpretation could homologize with the large fusion nuclei containing double the normal number of chromosomes, produced, as stated by NEMEC, by a copper sulfate solution acting on radicles of *Vicia Faba.*

6. Doubling of the nucleolus is not a preparatory stage of amitosis, as stated by WASIELEWSKI.

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21. ———, *Ibid.* 1903:Mitt. 27.

22. ———, Ueber die Einwirkung des Chloralhydrats auf die Kern- und Zellteilung. Jahrb. Wiss. Bot. **39**:645–730. 1904.

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THE RELATION OF HAIRY AND CUTINIZED COVERINGS TO TRANSPIRATION

KARL M. WIEGAND

(WITH ONE FIGURE)

Numerous experiments have shown that cutin is a very efficient means of retarding the loss of water from plant tissue. We may cite only such cases as the paring of the apple and its consequent much increased loss of water as shown by weighing, and of various other plant tissues similarly treated. In regard to the function of hairy coverings, however, the lack of experimentation has left us very much in doubt. We find two theories advanced: one holding that such coverings are to retard transpiration, the other that they are to protect the tissue from too intense light. Some have held also that they may, and probably do, serve both purposes, either at the same time or in different cases.

It has long been recognized that hairy coverings must be divided into two classes when function is considered, namely the living and the non-living.[1] The cells of the former contain protoplasm, and therefore are themselves in danger of drying out. Such hairs naturally cannot be used by the plant for restricting loss of water. The non-living hairs, however, are soon free of protoplasmic contents and are filled with air. In such a form, spread out over the plant surface, they may well be conceived of as constituting a restricting screen to the passage of water vapor. By the refraction of light from the contained air this type of hair may also act as a light screen. We shall have to do, therefore, only with this latter group in the following pages.

Experimental evidence for or against either of these theories of the function of air-containing plant hairs is very meager, however, and this is the more remarkable when the very common occurrence

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[1] FLEISCHER, E., Die Schutzeinrichtungen der Pflanzenblätter gegen Vertrocknung. 16. Bericht. über das K. Realgymnas. zu Döbeln. 1885.

VOLKENS, G., Die Flora der ägyptisch-arabischen Wüste auf Grundlage anatomisch-physiologischer Forschungen. Berlin. 1887.

of such coverings is considered. In the absence of such evidence the following questions have frequently occurred to the writer: 1. Do such coverings actually retard the loss of water sufficiently to justify their maintenance on this basis through natural selection? 2. Is it not highly improbable that coverings so thin as are "strigose" coverings should affect the loss of water in any way, and does not this count as an objection to the water-retarding theory? 3. If the function of hairs is to retard the loss of water, why should some plants employ thick cutin and others a resinous coating instead of plant hairs to attain the same end? 4. Has the relation to light or the relation to loss of water been the principal factor in the evolution of hairy coverings? Since the answering of these questions has seemed to be of rather fundamental importance in the teaching of ecology, an attempt has been made to obtain evidence, either circumstantial or direct, and the results obtained form the basis of this paper.

The few actual experiments with hairy coverings, so far as I have been able to find, may be summarized as follows. KERNER[2] bound two raspberry leaves around two thermometer bulbs in such a way that in one case the green upper leaf surface and in the other case the white tomentose under surface was outermost. When placed in the sun, the mercury in the green bulb rose to a point 2–5° above that in the white bulb. Two more raspberry leaves were entirely removed from the plant and laid side by side in the sun. The one with the green surface uppermost dried and shriveled much sooner than the one with the white surface uppermost. GOEBELER[3] investigated the effect of trichome structures on the stems of ferns. He found by weighing that the living trichomes markedly increased the transpiration. VESQUE[4] found by means of cultural experiments with certain plants that when the dryness increased, the hairy covering increased in density also. BRENNER[5] found that the hairy

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[2] KERNER, A., AND OLIVER, F. W., The natural history of plants **1**:314.

[3] GOEBELER, E., Die Schutzvorrichtungen am Stammscheitel der Farne. Flora **69**:487. 1886.

[4] VESQUE, M. J., ET VIET, M. C., De l'influence du milieu sur la structure anatomique des végétaux. Ann. Sci. Nat. Bot. VI. **12**:176. 1881.

[5] BRENNER, M., see BURGERSTEIN, Die Transpiration der Pflanzen 210. 1904.

covering of certain species of Quercus became thicker when exposed to greater intensity of sunlight.

Haberlandt[6] selected two nearly equal leaves of the same opposite pair from a plant of *Stachys lanata*. The under side of each was coated with cocoa butter, and from the upper side of one the hair was carefully removed with curved scissors. The two petioles were placed in dishes containing water, and the leaves were left to transpire 24 hours at 20 to 25° C. in the shade. The hairy leaf lost 0.646^{gm} of water and the hairless one 0.915^{gm}, which was therefore in the ratio of 1:1.42. The leaves were then exposed to intermittent sunshine for one hour; the hairy leaf now lost 0.08^{gm} and the hairless one 0.167^{gm}, or in the ratio 1:2.09. He concludes therefore that the hairy covering is especially important in restricting the transpiration in sunlight, but that it also operates in a less degree in diffuse light. In the sunshine it probably prevents the extreme heating of the leaf, in diffuse light it retards the diffusion of the air. The error that might be expected from the exposure of uncutinized surfaces, when the hairs are cross-sectioned, Haberlandt found by mathematical calculation to be insignificant.

Baumert[7] tested the heat screening power of hairy coverings and found that in one case a leaf deprived of hair became 37.5 per cent warmer than a normal one.

It was soon found that to obtain experimental data regarding the effectiveness of various coverings was not easy. In fact, it seems almost impossible to obtain accurate and detailed results because of the many factors that enter. No two leaves are exactly alike in size, or in thickness of cutin, or in water content; and it is very difficult to remove the hairy covering for comparative experiments without injuring the tissue of the leaf. Moreover, the stomates may be open at times and closed at others, and the two leaves used may not be alike in this respect.

Fortunately there seemed to be a method of approaching the problem in an indirect way. It is quite generally recognized that by far

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[6] Haberlandt, G., Physiologische Pflanzenanatomie. 3. Aufl. 116. 1904, and possibly in earlier editions.

[7] Baumert, K., Experimentelle Untersuchungen über Lichtschutzeinrichtungen an grünen Blättern. Beitr. Biol. Pflanz. **9**:83–162. 1907; and Inaug. Diss. Erlangen. 1907.

the most important factor in transpiration is evaporation; indeed we may say that transpiration is really evaporation modified and regulated by the plant. Therefore, it seemed that a detailed study of the relation of cutin and hairy coverings to evaporation would throw much light on the relation of these same coverings to transpiration.

The first desideratum for such experimental work was a suitable evaporating surface. Several substances were tried, but the choice finally fell on good quality blotting paper. This possessed the desired property of wetting quickly and evenly, and of having a very homogeneous evaporating surface. The pieces used were all cut, for convenience, exactly 7^{cm} square. The plan followed was to expose saturated squares of this paper to the air, each having been previously weighed and then covered with the material to be experimented with. After a given time each was again weighed, and the difference in weight of course represented the quantity of water lost by evaporation. One set of readings in each case was taken in very quiet stagnant air, and another set in air actively in motion. The former condition was obtained by completely inclosing a portion of table top with botanical drying felts placed on edge and covered with the same. For the wind, a small electric fan was stationed at one end of a table on which the evaporating blotters were placed. After a large number of erratic readings were obtained, it was recognized that the following precautions must be taken to eliminate errors. The blotters should be rolled with a round pencil to remove surface water. They should be placed on slightly larger squares of glass and gently rolled again, while with the finger the edges are carefully pressed in contact with the glass. The glass plate and coverings should be weighed with the blotter both before and after. The substance in contact with the blotter should have been previously rendered waterproof in a dilute solution of paraffin in gasoline, otherwise water will be absorbed. The cotton coverings used were always separated from the blotter by a very thin linen cloth so treated. Various materials, in most cases composed of cotton, were used to simulate a hairy covering, but in place of cutin beeswax alone was finally employed. This, while melted, was evenly and thinly spread over the damp blotter with a brush. In order to avoid reducing the supply of water in one case far below that in the other, and thus possibly introducing error, it was found desirable to conduct the experiments in the wind for only a fraction of the time that they were conducted in still air; but afterward, for comparison, all readings were computed on the basis of quantity lost per hour, and finally on the basis of 1^{gm} lost by the naked blotter per hour. When all the above requirements had been discovered and complied with, a great many readings were obtained in each series, all agreeing within the limits of experimental fluctuation. All the experiments were conducted in the laboratory in February, March, and early April, and therefore in an artificially heated very dry room. The fan was run very rapidly in all cases.

In the following tables the first and fourth columns represent the average quantity in grams lost by each blotter per hour in all the later readings taken. The second and fifth columns show the same quantities reduced to the basis of 1^{gm} for the naked blotter. The retarding effect in the third and sixth columns was obtained by subtracting the loss under cloth, hair, cotton, or wax from the quantity (1^{gm}) lost by the naked blotter. By "increase in efficiency" in the seventh column is meant the number of times greater the retarded effect in wind was compared with the same in still air. The last column represents the number of times this increase in efficiency in wind was greater than the increase in efficiency of wax.

SERIES I.—Coverings used: (*a*) one layer of very thin linen cloth, (*b*) two layers of the same cloth, (*c*) wax coating.

	STILL AIR			WIND				
	Gm per hour	Ratio to 1 gm naked	Retarding, gm	Gm per hour	Ratio to 1 gm naked	Retarding, gm	Increase eff.	Times wax
Naked blotter...	0.398	1.000	.....	4.210	1.000	.....	.....	.....
1 layer cloth....	0.358	0.899	0.101	2.670	0.634	0.365	3.6	2.4
2 layers cloth...	0.338	0.849	0.151	2.110	0.501	0.497	3.3+	2.2
Wax..........	0.181	0.455	0.545	0.780	0.185	0.815	1.5	...

SERIES II.—Coverings: (*a*) one layer thin linen cloth covered with very thin layer of cotton, texture of linen easily seen through the cotton, (*b*) one layer of linen and one layer of thick cotton batting about 2^{cm} thick, (*c*) wax.

Naked blotter...	0.303	1.000	.....	3.310	1.000	.....	....	...
Thin cotton.....	0.262	0.864	0.136	1.430	0.432	0.568	4.17	2.7
Thick cotton....	0.219	0.722	0.278	0.870	0.263	0.737	2.65	1.7
Wax..........	0.153	0.505	0.495	0.740	0.223	0.777	1.55	...

SERIES IIA.—Same coverings as in the last; experiment conducted in sunlight, on a black table top.

Naked blotter...	3.700	1.000	.....	6.820	1.000	.....	....	...
Thin cotton.....	2.590	0.700	0.300	3.320	0.486	0.514	1.71	1.4
Thick cotton....	1.410	0.381	0.619	2.110	0.309	0.691	1.11	0.9
Wax...........	1.220	0.329	0.671	1.350	0.198	0.802	1.19	...

SERIES III.—Coverings: (*a*) one layer of outing flannel (cotton), (*b*) one layer thin ordinary flannel, (*c*) wax.

Naked blotter...	0.343	1.000	.....	3.870	1.000	.....	....	...
Outing flannel ..	0.301	0.877	0.123	1.540	0.398	0.602	4.88	3.37
Ordinary flannel	0.300	0.874	0.126	1.880	0.486	0.514	4.08	2.80
Wax...........	0.157	0.457	0.543	0.810	0.209	0.791	1.45	....

SERIES IV.—Coverings: (*a*) one layer mosquito netting, (*b*) wax.

Naked blotter...	0.340	1.000	.....	3.44	1.000	.....	.....	....
Mosquito netting	0.337	0.991	0.009	2.85	0.828	0.172	19.11	12.7
Wax...........	0.160	0.470	0.530	0.69	0.200	0.800	1.51	....

SERIES V.—Coverings: (*a*) human hair soaked in gasoline and paraffin, cut up into 1–3^{mm} lengths, and sprinkled sparingly over a blotter, to simulate a strigose covering, (*b*) wax.

Naked blotter...	0.3444	1.000	.....	3.58	1.000	.....	....	...
Strigose hair	0.3399	0.987	0.013	3.38	0.944	0.056	4.30	2.9
Wax...........	0.1580	0.459	0.541	0.73	0.204	0.796	1.47	...

From the above five series of readings the following may be deduced:

1. Evaporation from an uncovered surface was about 10.6 or 10.8 times as great in the wind of the fan as in still air (series I and II, columns 1 and 4).

2. In sunshine, under the conditions of the experiment, it was only 1.8 times as great in wind as in still air (series IIA, columns 1 and 4).

3. In still air it was 9.3 to 12.2 times as great in the sunshine as in the shade (series I, II, and IIA, column 1).

4. In the wind it was only 1.6 to 2 times as great in sunshine as in shade (series I, II, and IIA, column 4).

5. Hairy coverings of all kinds and thicknesses used were less efficient in retarding evaporation than the layer of wax employed (columns 3 and 6 in all series).

6. All coverings became more efficient in the wind (column 7 in all series).

7. The efficiency of hairy coverings, in thicknesses at all approaching those actually found on leaves, was very slight in still air (series I, II, and III, column 3, line 2, etc.).

8. Such coverings became very efficient in wind (same series, columns 6 and 7).

9. Their efficiency increased in wind much more rapidly than did that of wax (same series, column 8).

10. Even the layer of cotton 2^{cm} thick did not equal the layer of wax as a protective device. In still air the difference between the two was marked, but in wind became less evident.

11. The thinner coverings showed a greater increase in efficiency over wax than did the thicker (cf. column 8 in series I, II, III, IV, and V).

12. Such thin coverings as strigose hairs and mosquito netting produced scarcely any effect in still air, but showed a marked efficiency in the wind, the increase being 4–20 times, which was 2.9–12.8 times that of wax respectively (series IV and V, columns 7 and 8). Both of these materials may retard in wind as much as 5.6 to 17.4 per cent (series IV and V, column 6).

13. The effect of sunshine was marked. In still air the thin and thick hairy covering became 1.5–1.6 times more efficient when compared with wax. In the wind in sunshine the increase in efficiency was not the sum of the increase due to wind in shade and to sunlight in still air, as one might at first expect, but represented an increase in efficiency over still air in shade that was even somewhat less than the increase in wind shade over still air shade (series II, column 3, series IIA, column 6, and series II, column 7).

14. If hairy coverings on leaves behave in the same way as our artificial hairy coverings, we may say that they produce comparatively little effect in retarding transpiration in still air, but have a marked protective action in wind. Thin strigose coverings produce no appreciable effect in still air, but become important factors in wind. A waxy (i.e., cutinized) covering is more efficient, and has a more constant retarding effect at all times. In sunshine hairy coverings are increasingly protective, their increase in efficiency being

also greater than that of cutin in this respect. Their relative efficiency in wind is not markedly different, whether the sun shines or not (series II and IIA, column 6), being somewhat less perhaps in the former case. Their actual protection, of course, is greater the larger the quantity of water lost, i.e., in wind and in sunlight.

Some experiments were conducted with shellac in the place of the waxy coating on the blotter. The shellac was considered to represent more nearly the resinous coatings so frequently spread over leaves and twigs in dry regions. The readings showed the behavior of waxy and resinous coatings to be very similar.

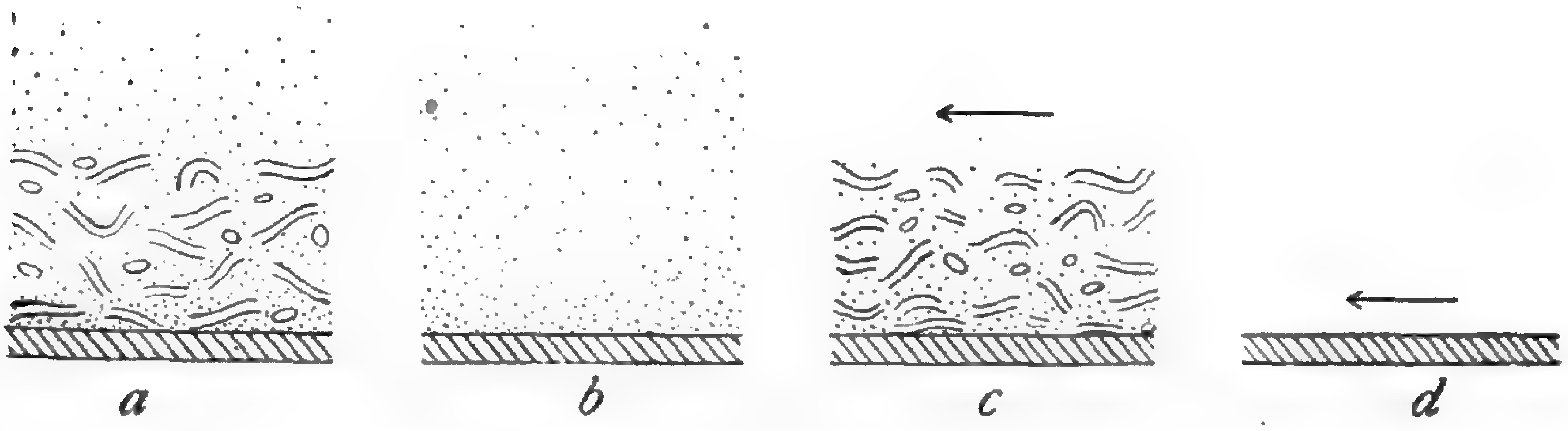

FIG. 1.—Diagrams illustrating the relation of evaporation from naked and hair-covered surfaces in wind and in still air: *a*, hair-covered in still air; *b*, naked in still air; *c*, hair-covered in wind; *d*, naked in wind.

Many readings were taken with actual leaves substituted for the blotters, but in the main they were very erratic. It was found, however, that leaves of Hydrangea and of Nicotiana especially, when covered with layers of cloth and cotton, behaved essentially the same as did the blotting papers. Probably all would have done so if the other factors could have been eliminated.

The reason for the slight efficiency of hairy coverings in still air and their greatly increased efficiency in wind is not at first apparent. The following is the only plausible theory occurring to me. As indicated in the accompanying diagrammatic drawings, in still air a layer of nearly saturated air is soon formed and maintained above the naked as well as above the hair-covered blotter (*fig. 1*, *a* and *b*). If the hair is thin, it is imbedded in this layer, and the latter is modified little if at all by the hair. Evaporation, therefore, with or without the hair, is into an atmosphere of about equal saturation, and therefore should be about the same. If the hair is very thick, then the saturated layer of air will be somewhat increased and evaporation will be correspondingly retarded.

In wind, however, molecules are immediately blown away from the naked or wax-covered surface (*d*), while in the hairy covering (*c*) there is retained a partially saturated atmosphere. Air currents do not easily penetrate the interstices between the hairs, and the vapor molecules probably find more difficulty in rapidly passing through the hairs. Since evaporation from a surface is in proportion to the saturation of the adjacent atmosphere, it follows that evaporation in diagrams *a* and *b* will differ but slightly, while between *c* and *d* there will be a much greater difference.

Evaporation is also proportional to temperature. It is reasonable, therefore, to expect an increase when the blotter is exposed to the heat of the sun's rays. Hairy coverings act as a screen to the heat rays, and therefore the cooler blotters beneath them evaporate less. It is probable, however, that the effect of sunshine in nature is rarely if ever as great as in our experiments, except possibly in the case of leaves lying flat on the ground, because of the absorbing effect of the black background of the laboratory tables used.

Significance of the results

We are now able to answer at once the first two questions propounded in the introduction to this paper. A protective action of 35–40 per cent in wind with coverings of the thickness of outing flannel certainly warrants us in saying that hairy coverings are sufficiently efficient in retarding loss of water to justify their maintenance on the basis of natural selection. A protection of 5.6 per cent in wind shows also that strigose coverings may materially affect the loss of water. In the case of strigose plants the hairs are usually developed very early, and therefore while the leaves and shoots are small. The hairy covering is therefore more concentrated and denser at this time, but becomes more scattered as the surface increases. As COVILLE[8] has suggested, such strigose hairs probably function mainly while the organs are young. Hairs which on the mature leaves are scattered far apart may have been of considerable service

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[8] COVILLE, F. V., Botany of the Death Valley Expedition. Contr. U.S. Nat. Herb. **4**:53. 1893.

to the young leaf. It now remains to determine what relation the experiments bear to the solution of the last two questions.

From a consideration of the thin unprotected epidermis of hygrophytic plants, guttation through water pores, root pressure, and possibly other methods of increasing the transpiration stream, we may reasonably infer that most if not all plants find it advantageous to maintain as great a transpiration stream at all times as is consistent with their water supply. From this point of view, plants living in a highly desiccating atmosphere may be divided into two groups. In one group the water supply is very limited; in the other, through the presence of water in the soil, the supply is much greater. It would seem highly advantageous, therefore, for plants of the latter group to possess some mechanism by which the transpiration could be retarded when tending to be so excessive as to exceed the water supply, as for instance in strong dry winds or bright sunshine; but which would allow almost uninterrupted transpiration when the transpiration tends to be less, as at night. Plants of the former group would find continued protection desirable. This they would find in the waxy and resinous coatings, while those of the second group would find hairy coverings better adapted to their needs. If our interpretation is correct, we should expect desert plants with very scanty water supply to be highly cutinized, instead of hairy, while the hairy desert plants would be found in some way connected with a greater supply of subterranean water. Such a hairy plant in the desert might be supposed to act as follows. During the day the hot dry winds blow and the sun shining upon the leaflets tends still further to increase the transpiration. The requisite protection is now afforded by the hairy covering; but at night the winds die down, the atmosphere becomes humid, dew falls, and transpiration becomes more difficult. At such times the hairy covering does not materially impede the transpiration.

Known facts do not seem opposed to this interpretation, but rather in its favor. The writer has had no opportunity to determine the available water supply of desert plants, but an inspection of COVILLE's Death Valley report shows that the habitat of a great majority of the characteristically hairy shrubs cited (p. 52) is given as either dry river bottoms, lake shores, or high on the mountains.

Two densely canescent plants are cited particularly as occurring near timber line on Mt. Whitney (p. 55). Since the mountains according to this report (pp. 22 and 42) are not so arid as are the lowlands, and the soil is generally more moist, all three habitats, therefore, are likely to possess considerable soil moisture. However, to draw generalizations from a report is unsatisfactory, since so much depends on depth of root system, persistence of foliage, etc. Special study of individual conditions in the Death Valley is really necessary.

In the eastern United States, where conditions are mesophytic, hairy plants are found mainly on dry exposed gravelly or sandy knolls and hills, as for example *Verbascum Thapsus,* various species of Antennaria, Gnaphalium, Anaphalis, *Solidago bicolor,* and *S. nemoralis.* Here drying winds and hot sunshine prevail during the day, but at night the air is still and damp. The soil is not excessively dry, but the Verbascum, to still further guard against danger, possesses a long tap root which descends to a considerable depth, where a sufficient supply of water is assured. A hairy covering, therefore, would best meet the needs of such plants.

The most complete account of the occurrence and function of hairy coverings seems to be that given by KERNER.[9] He seems to have believed that the hairy covering so frequently on the under side of the leaf alone could be of functional importance only when bathed with sunlight. To explain this difficulty he showed how when the dry winds blow violently the leaves of the side facing the wind all become inverted, so that the silvery under surface faces the sun. The present experiments show, on the other hand, that the protective action of the hair covering the stomate-bearing surface would be great in wind without sunshine. The inversion of the leaves is not necessary to explain the functioning; indeed, it is doubtful if such inversion continues long enough to be of any great importance. The more important fact is that the hairs cover the stomate-bearing surface rather than the upper surface.

KERNER says that hairy coverings are especially pronounced in the Alps and in the Mediterranean region, but are almost absent from the arctic region. He says that the relation between hairy coverings and transpiration stands out strikingly in those districts

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[9] KERNER, A., AND OLIVER, F. W., The natural history of plants 1:313.

where plants during their vegetative period are as a rule exposed to dry air for only a few hours each day, and where their activity is not interrupted by a warm dry period but by frost and cold. On the Alps the complete drying-up of plants by the sun is rare, but the dry winds and hot sun at times make a lessening of the transpiration very desirable. On other mountains of the same latitude in Europe and Asia many hairy plants occur. Indeed, the account given by **Kerner** is almost an exact picture of what we should expect from the point of view of the present experiments. On the slopes and in the pockets on the Alps, where vegetation exists, the soil is warmed in summer and there is probably an available supply of water throughout the vegetative period.

Quite different is the condition in the arctic regions. Thick evergreen leaves replace the hairy ones. **Kerner** says: "When hairy coverings are present they are restricted to the under surface, especially to that of rolled leaves. They are never found on plants of rocky slopes, but only on those of damp marshy ground, or by the side of water which is for a short time free from ice." He believes that such coverings are not concerned with transpiration at all, and that the absence of hairy coverings in the arctic regions is due to the moisture in the soil and the consequent absence of danger of drying out. This explanation, however, seems insufficient. If it were true, why should we find thick, highly cutinized, xerophytic leaves on such plants as Diapensia, Empetrum, Vaccinium, etc.? Our explanation now would be that the soil in the arctic regions is too cold for root absorption even in summer, since it remains frozen only a few inches below the surface. The water even if present is therefore not readily available, and there is constant physiological dryness. These are exactly the conditions necessary to demand a cutinized rather than a hairy flora.

Our evergreen leaves, such as those of Rhododendron and Kalmia, are heavily cutinized, not tomentose. According to our theory this would be owing to limited water supply in winter, which is true. Owing to the coldness of the soil and the inactivity of all the living cells of the plant, there is constant physiological dryness.

Plants of the great plains, where the wind is excessive but the ground not extremely dry, are commonly silky, strigose, or tomentose.

Plants of the eastern peat bogs find difficulty in absorbing water, possibly because of toxic substances in the soil, and these are cutinized, not hairy (except Ledum).

KERNER emphasizes the prominence of hairy plants in the Mediterranean region and notes that they are not so numerous in the adjacent steppe region, because "in the steppes and deserts the dryness of the summer is greater, and even thick hairy coverings are not always a sufficient protection against this dryness; and also because in some districts the dry period passes directly into a severe winter." In the Mediterranean region, as the dry summer follows the rains of winter and spring, "their transpiration is very active in consequence of the rapidly increasing temperature of the air, but the saturated soil provides a sufficient substitute for the evaporated water." Toward midsummer, as the drought increases, "if such a plant is to be protected from drying up, its transpiration must be lessened. This is effected by various protective arrangements, but best of all by a thick coating of hair." Very interesting are the biennial plants cited by KERNER. The leaves of these plants formed the first year must pass through the summer and so are abundantly hairy, while those of the leafy flowering shoot the second spring are green instead, because this shoot dies before the summer begins. The whole of KERNER's account of Mediterranean plants is just what we should expect from the standpoint of the present experiments. There is sufficient water in the soil at all times to make moderate transpiration possible even in summer. At times when this supply is at its minimum and when the sun and wind are exceptionally drying, the leaves are protected from too excessive transpiration by the hairy covering.

GOEBEL,[10] in describing the flora on the Venezuelan Andes between tree line and snow line, remarks on the great number of hairy plants. The white-woolly rosettes of certain species are characteristic of the landscape. The climate here is subject to great and frequent changes from rain, snow, or fog, to sunshine and an exceedingly drying wind. The temperature varies also from 0° to 18°. The soil contains plenty of water, with frequent puddles standing on the surface. The soil is cold and absorption is slow, but the transpiration at times

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[10] GOEBEL, K., Die Vegetation der venezolanischen Paramos. Pflanzenbiolog. Schilderungen **2**:1. 1893.

is great. This is a fine picture of just such conditions as we should expect would demand hairy plants; absorption somewhat below normal, transpiration at times excessive, and at other times, as in foggy weather, very slight.

The use by epiphytic plants of cutin rather than hair for retarding transpiration is well known. Even though the air is humid, the scantiness and uncertainty of the water supply actually obtainable by the plant warrants the employment of cutin. The most notable exception is the Florida moss (*Tillandsia usneoides*), the ecological relations of which I have not been able yet to fully make out. It seems probable, however, that the excessive development of the scaly absorbing glands of the leaves is for still further increasing the efficiency of absorption, rather than primarily to retard transpiration.

Hairs are provided on growing shoots and unfolding leaves to retard the transpiration during windy and sunny times in spring, before the cutin has become fully developed. Some plants make use of resin for this purpose instead (e.g., Larrea in the desert, and Gaylussacia in New England). It is probable that in these cases a more efficient covering is here desired. Such resinous coverings may be superior to cutin in that they may be easily shed or be much interrupted when their early protective action is no longer desired. This actually takes place in both of the above-named examples.

In regard to the last question propounded in the introduction, whether the relation to light or to loss of water has been the principal factor in the evolution of hairy coverings, the following facts may be cited. In practically all cases where one leaf surface is devoid of hairy covering it is the upper. Such cases are very common, e.g., Ledum, Antennaria, Quercus, etc. This would not be true if the primary function was as a light screen. Instead, the covering is maintained over the stomate-bearing surface. The multitude of such cases makes it seem almost obvious that the main function of hairy coverings lies in their relation to transpiration, not to the intensity of the light.

From the foregoing statements it is not to be understood that wherever conditions are as described only hairy plants are to be expected, and that in a given locality plants should be either all hairy or all cutinized, or even that hairy and smooth individuals of the same species should not be found occasionally side by side. If we go more into the details of distribution than into the consideration of the general trends of vegetation and the general examples already given, we must then consider the individual plants; for it often happens that species growing side by side may in one case have a deep root system reaching ground water, in the other have a root system confined to the driest superficial layers of the soil. It is also conceivable that there may be inherent physiological differences between species, and even between individuals of the same species, calling for variations in the amount and kind of protection. The life economy must be studied out in each individual case. We must not fail to remember, also, that the whole seasonal cycle, as well as the life cycle of the individual, must be considered before a full conclusion may be drawn; for a hairy covering which seems not to fit into the general scheme may have done so at an earlier period of development or in an earlier season.

General conclusions

The evaporation experiments outlined in this paper tend to show that porous coverings like cotton, wool, or hair must be very thick to produce any appreciable effect in retarding evaporation if the surrounding atmosphere is quiet, but become very efficient even in thin layers when the air is in motion. On the other hand, a waxy covering is effective at all times, though of course somewhat more so in wind. In sunshine, also, the hairy covering shows a greater increase in efficiency than does wax.

It seems probable that those plants employ a hairy covering to retard transpiration that live in situations where a moderate water supply is available, but where transpiration must be reduced in excessively dry times, but not interfered with when the surrounding air is damp and transpiration therefore difficult. Cutin, on the other hand, is probably employed when there is considerable danger of too great desiccation at all times.

A contemplation of the general occurrence of excessively hairy plants lends probability to this view.

WELLESLEY COLLEGE

THE MORPHOLOGY OF THE PERIDIAL CELLS IN THE ROESTELIAE[1]

FRANK DUNN KERN

(WITH PLATES XXI AND XXII AND TWO FIGURES)

While making a study of the morphological characters of various species of Roestelia, attention has been especially attracted to the peridial cells. They are much more characteristic than are the roestelial spores, and so strikingly different, except in two known cases, from the peridial cells of the aecia of pucciniaceous species that they are at once conspicuous upon the most cursory examination. The two exceptions just cited are *Aecidium Blasdaleanum* D. & H. and *Aecidium Sorbi* Arth., which are classed with the Roesteliae on account of their life histories, but which have the morphological characters of the pucciniaceous aecia and are therefore not included in the discussions in this paper. The taxonomic importance of the peridial cells in defining the species of Roestelia has been ably pointed out by Dr. ED. FISCHER,[2] and a number of American species have been figured and described[3] in considerable detail by him. FISCHER took into account only the surface sculpturing on the cells, but aside from this there are a number of other features of the morphology which seem worthy of consideration. The microscopical structure is described with some detail in this paper, with the hope that it may be of interest.

The manner in which the individual cells are joined together to make up the peridium is one of the first characteristics worthy of mention. If a bit of the mature peridium of almost any of the species is mounted in water for a microscopical examination, the cells are usually seen separated from one another, or perhaps a few short chains made up of cells attached together at the ends remain. In case the cells do not separate while the mount is being prepared, a

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[1] Read before the Botanical Section of the American Association for the Advancement of Science at the Baltimore meeting, December 29, 1908.

[2] Zeit. f. Pflanzenkr. **1**:271. 1891.

[3] Hedwigia **34**:3, 4. *figs. 1–10.* 1895.

slight movement of the cover glass will usually serve to dislodge them. This loose union along the sides of the cells as they are joined to make up the peridial tissue, tends to make the peridium rupture at its maturity by longitudinal slits along the sides rather than at the apex, and gives the lacerated and fimbriated appearance so characteristic of most of the species. Only two species of the true Roestelia type have been observed which have peridia that do not become more or less split up; these are *R. Harknessiana* E. & E., an unattached species from California, and *G. inconspicuum* Kern (*R. Harknessianoides* Kern), from the western mountain region. In these the peridia are firm and remain tubular even after months of weathering.

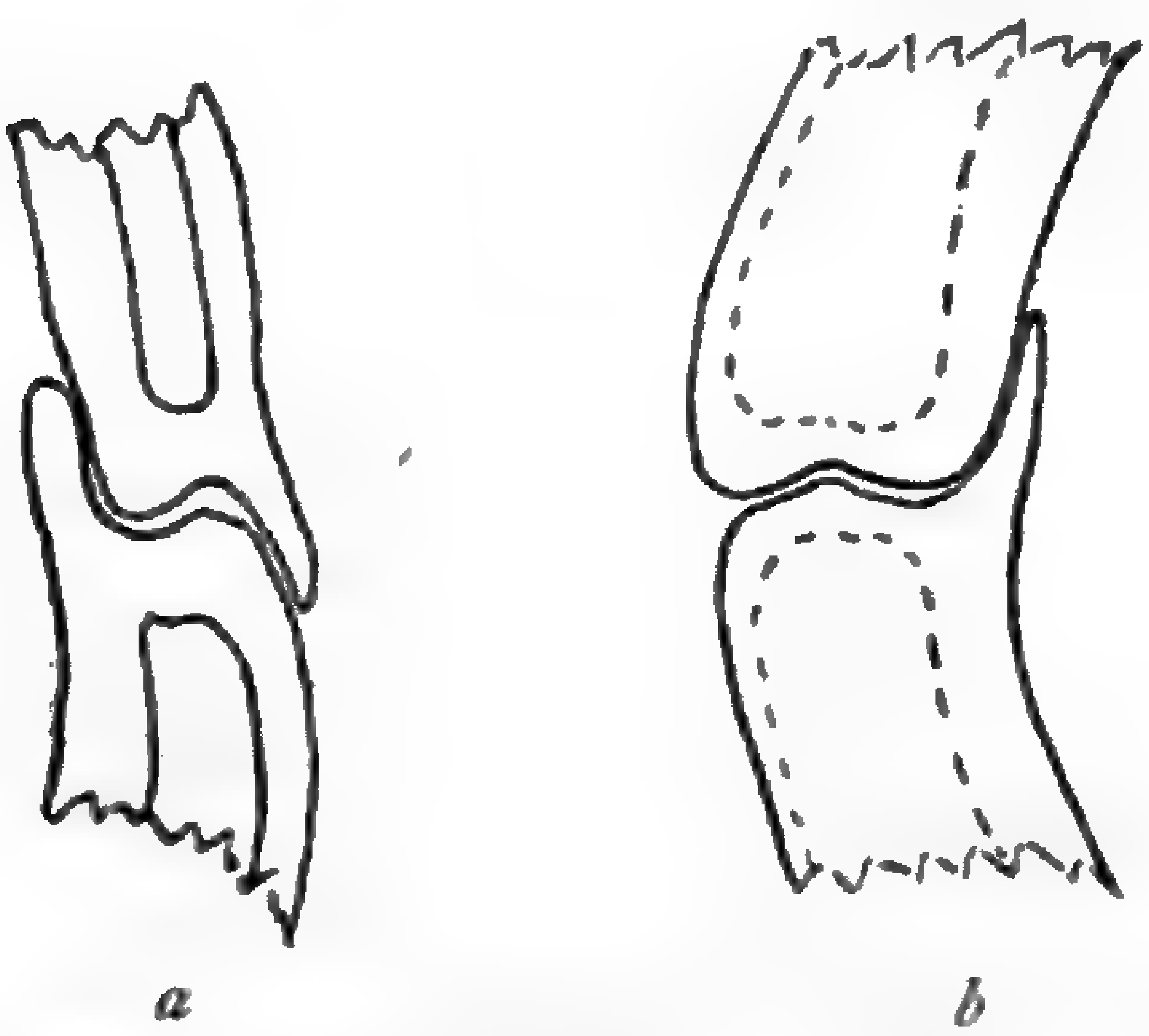

Fig. 1.—Showing how the cells of some species are joined end to end; the portions uppermost are toward the apex of the peridium; in *a* the outer wall of the upper cell overlaps considerably; in *b* this is much less pronounced.

The way in which the cells are joined end to end is another distinctive feature of this group. In addition to being imbricate, a character common to many aecial forms, the ends of the cells are, with a few possible exceptions, articulated in such a manner as to make movable joints (*text fig. 1*). This power of yielding at these joints permits the ruptured peridium to curl and twist in a manner particularly prominent in some of the species.

In shape one finds a considerable variety. In some species the cells are long and thin (*figs. 7, 12*), in others short and very stout (*figs. 8, 15, 16*). With respect to shape, it is necessary to consider the cells from two points of view, viz., side view and face view. The side view, which is the longitudinal radial view, shows the dimensions of length and thickness. In this view the outer and inner walls are practically parallel. In some of the species which have short and rather thick cells, the imbrication at the ends gives an oblique effect which makes a rhomboidal shape (*figs. 15, 16*). Where they are longer and thinner, the length becomes more pronounced, and linear-rhomboidal (*figs. 3, 4, 10*) is a more accurate description; or where the length is very great comparatively, the obliqueness at the ends is inconspicuous and they may best be described as linear (*fig. 7*). In face view, which is the longitudinal tangential view, length and breadth are the dimensions in the plane of vision. The cell may be regarded as having two faces, the one which is to the outside, and the one which is to the inside as it is in place in the peridial wall. The distance from the outer face to the inner face constitutes the thickness of the cell. In considering shape in face view it makes no difference which face is turned toward us. The cells of some of the species are not easily seen in face view, but of those that will lie so as to be readily examined the majority do not have the side walls parallel, but vary from lanceolate or broadly lanceolate (*fig. 16*) to polygonal-ovate or polygonal-oblong (*fig. 9b*). Most of the cells are more or less narrowed both above and below (*fig. 17b*). There is one species, *G. Botryapites* (Schw.) Kern (*R. Ellisii* Peck), which does not conform to any of the shapes mentioned. It has cylindrical hypha-like cells which are sometimes irregularly bent (*fig. 12*).

The accompanying table will serve to show the variation in size of the cells and in thickness of the walls. In the measurements given an attempt is made to make some allowance for the variation within any particular species, it being the case in most instances that the cells near the apex are proportionately shorter. *G. Bermudianum* (Farl.) Earle, the only autoecious species known to exist, has the shortest cells of any examined (*fig. 1*). The maximum length is three to four times greater than the minimum, and is found in the cells of *R. transformans* Ellis (*fig. 7*), a species developing in the leaves and fruit of *Aronia arbutifolia* (*Pyrus arbutifolia*). In most of the species the breadth is greater than the thickness, but in three or four (nos. 9, 14, 15, 16 in the table) having especially firm peridia, which do not become much split or lacerated, the reverse is the case.

With respect to thickness of walls, the general type of peridial cell has inner and side walls rather thick with outer wall rather thin. The side walls appear to be about equal in thickness with the inner wall in the species where the inner wall is only moderately thickened (*text fig. 2, a, b*). In some very thick and proportionally narrow cells, where the inner wall is excessively thickened, the side walls are much less and become gradually thinner toward the outer side of the cell (*text fig. 2c*). The outer wall is usually never more than half as thick as the inner and is commonly considerably less. There are two exceptions to the above statements which should be noted here, *G. Botryapites* (Schw.) Kern (no. 12), which has the conditions of the general type reversed, a very thick outer wall and rather thin inner wall (*fig. 11a*). The table indicates the variations to be found in a number of species. Not taking into account the exceptions noted above, the thinnest outer wall found was 1 μ, while the thickest was 8 μ. The inner and side walls vary from 3 or 4 μ (*figs. 1, 4*) to 35 μ (*fig. 16*).

TABLE SHOWING SIZE AND THICKNESS OF WALLS OF PERIDIAL CELLS IN SIXTEEN SPECIES OF ROESTELIA*

SPECIES †	LENGTH (FROM END TO END)	BREADTH (FROM SIDE TO SIDE)	THICKNESS (FROM FACE TO FACE)	THICKNESS OF WALLS	
				Outer wall	Inner and side walls
1. G. Bermudianum	50–75 μ	18–25 μ	15–18 μ	1.5 μ	3–5 μ
2. G. Juniperi-virginianae (*R. pyrata*)	65–100	(16–22)	10–16	2.5–3	4–6
3. G. floriforme	65–85	(14–18)	10–14	1.5–2	4–5
4. G. globosum	60–90	15–23	13.19	1.5	3–5
5. G. Betheli	60–90	20–25	13–20	1–1.5	4–6
6. G. clavariaeforme (*R. lacerata*)	80–130	18–30	15–25	1–2	5–7
7. R. transformans	150–300	(20–30)	12–18	2–3	4–6
8. G. juniperinum (*R. penicillata*)	60–90	(45–55)	30–35	2–3	7–10
9. G. germinale (*R. aurantiaca*)	45–95	19–39	25–40	3–5	13–23
10. G. Nidus-avis (*R. Nidus-avis*)	55–88	15–23	14–18	1–1.5	5–7
11. R. hyalina	87–105	19–29	(20–26)	(12–16)	3–4
12. G. Botryapites (*R. Ellisii*)	145–190	9–14	9–14	1.5–2	1.5–2
13. G. Nelsoni (*R. Nelsoni*)	65–110	18–32	17–27	1–1.5	5.7
14. R. cornuta	60–110	19–29	30–35	2	8–12
15. G. inconspicuum (*R. Harknessianoides*)	65–100	25–35	45–55	5–8	20–35
16. R. Harknessiana	90–112	40–65	58–74	4–6	15–20

* Where the measurements are included within parentheses, it indicates that the cell, owing to some peculiarity in shape or to its hygroscopic properties, does not ordinarily lie in a loose water mount so that this measurement can readily be taken.

† Where the telial connection is known, the species are referred to Gymnosporangium in this table, with the roestelial name, if one exists, included as a synonym.

The cells of some of the species when examined in loose mounts may be seen easily in either face or side views. When this is the case the cells lie straight, and there is usually not much disparity between the breadth and thickness (*figs. 1, 10, 13, 14*). There are a number of species, however, in which the cells tend to lie only on their sides when mounted in water, and it is only with difficulty that a face view can be observed. The cause for the cells taking this position is that they become much curved in water (*figs. 2, 5, 6, 7*), and their equilibrium, therefore, is much more stable when they lie on their sides. Such cells are hygroscopic and will straighten out when they become dry. It has been found that the curvature is always inward, the outer wall being on the outer side of the curve. It is interesting to note the effect which this incurving of the individual cells has upon the peridium as a whole. *R. pyrata* (Schw.) Thaxt., the aecial stage of *G. Juniperi-virginianae* Schw., is one of the species which has very marked hygroscopic cells. In the ordinary dried condition of herbarium specimens, the peridium of this species is finely fimbriate and strongly recurved, giving the appearance of having been combed outward. In a saturated atmosphere or in any way under the influence of moisture, the revolute chains of cells may be seen to unroll themselves and take a more or less erect position, or even become somewhat bent inward. They assume their recurved position again upon drying.

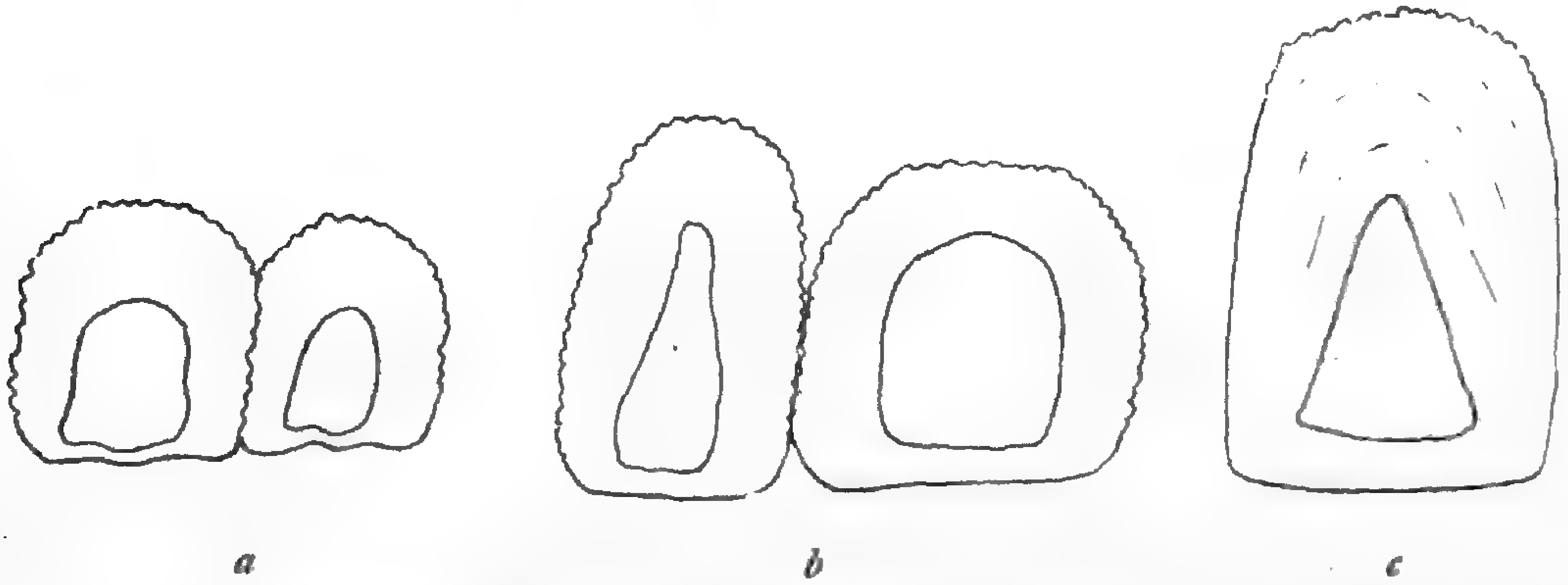

FIG. 2.—Cross-sections of peridial cells of several species: inner walls are above in the drawings; *a*, *G. clavariaeforme* (redrawn from FISCHER), inner and side walls of almost equal thickness; *b*, *R. cornutum*, inner and side walls of about same thickness; *c*, *G. inconspicuum*, inner wall excessively thickened, side walls not so thick, becoming thinner toward outside.

With regard to the surfaces of the peridial cells, it has been found that the species so far recognized divide at first into two classes, one having entirely smooth cells, the other having at least a portion of the surface roughened. I have subdivided the latter class upon the nature of the roughness, and have used the terms rugose, verrucose, verruculose, and spinulose to designate the four subdivisions.

Very little comment is needed for the class having smooth cells. It is the exception to the general rule, only two species being known which belong here. One is *R. hyalina* (*fig. 11*) and the other is *G. Botryapites* (*fig. 12*). These are unusual forms in other ways, as seen by the fact that both have been mentioned previously as being the only forms not conforming to the general type with respect to thickness of walls. Thus it will be seen that nearly all of the species have peridial cells which are sculptured in some way. No single word or even a single phrase will suffice for a description of the markings. It is necessary in most instances to resort to rather long and complicated sentences to convey details enough to be fairly accurate. The terms employed to designate the various classes are intended only to be descriptive in a general way. The rugosely sculptured cells are furnished chiefly with ridges or with elongated ridgelike papillae in such a way that the effect is that of a surface covered with rugae or folds; the verrucosely marked cells are studded with warty or tubercle-like elevations; the verruculose surfaces are covered with low wartlike protuberances; the spinulose cells have diminutive spines or spicules.

The markings always cover the entire inner wall (*figs. 1b, 9b, 17b*), extending to the side walls, in some forms reaching clear across (*figs. 1a, 3, 4, 8, 10, 13, 14, 16*), in others only a part of the distance (*figs. 2, 6, 7, 9a, 15*), leaving the remaining outer part of the side wall and the entire outer wall, with one exception, smooth. Only one species has been found which is an exception to this general type; it differs in having the outer wall also sculptured. This is an undescribed and unattached species (not included in the table), and is further notable in being the only one having cells with spinulose warts (*fig. 17*).

Of the sixteen species enumerated in the table, one-half have rugosely sculptured cells, nos. 1, 2, 3, 4, 5, 8, 10, 14.[4] In all these the ridges or ridgelike markings begin on the inner wall (as in *fig. 1b*),

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[4] These numbers also correspond to the figure numbers on the plates.

and are directed downward and outward and extend obliquely on to the side walls. In some species the ridges are of uniform width (*figs. 5, 10, 14*), in others they become somewhat broader toward the outer side (*fig. 2*). In some species the long ridgelike markings are closely and rather evenly arranged (*figs. 3, 10*), while in some they are rather sparsely set with separate and shorter, sometimes roundish papillae in the intervening spaces (*figs. 2, 5, 8*). Nos. 6, 7, 9, 15, and 16[5] have verrucosely roughened cells. The warts vary from roundish or slightly irregular (*figs. 6, 7, 15, 16*) to very irregularly branched forms (*fig. 9*), and are arranged without apparent order. They are usually more sparse toward the outer portion of the side walls. The verrucose character is pronounced in only one form, *G. Nelsoni* Arth., which consequently occupies this class by itself (*fig. 13*).

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EXPLANATION OF PLATES XXI AND XXII

The drawings were outlined with the aid of a camera lucida at a uniform magnification of 625 diameters, and were reduced about one-fifth in reproduction. In every case the end which is uppermost on the plate is the upper end of the cell, or, in other words, the end which is toward the apex of the peridium. In all figures except *11* and *12* the inner wall can readily be distinguished by its relatively greater thickness.

PLATE XXI

FIG. 1.—*G. Bermudianum* Farl.: *a*, side view; *b*, face view.
FIG. 2.—*G. Juniperi-virginianae* Schw. (*R. pyrata* [Schw.] Thaxt.).
FIG. 3.—*G. floriforme* Thaxt.
FIG. 4.—*G. globosum* Farl.
FIG. 5.—*G. Betheli* Kern.
FIG. 6.—*G. clavariaeforme* (Jacq.) DC.
FIG. 7.—*R. transformans* Ellis.
FIG. 8.—*G. juniperinum* L. (*R. pennicillata* [Pers.] Fries.).
FIG. 9.—*G. germinale* (Schw.) Kern (*R. aurantiaca* Peck).

PLATE XXII

FIG. 10.—*G. nidus-avis* Thaxt.

FIG. 11.—*R. hyalina* Cooke: *a*, side view, the thick wall is the outer wall here; *b*, face view.

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[5] These numbers also correspond to the figure numbers on the plates.

FIG. 12.—*G. Botryapites* (Schw.) Kern (*R. Ellisii* Peck): the inner wall is the one to the right.

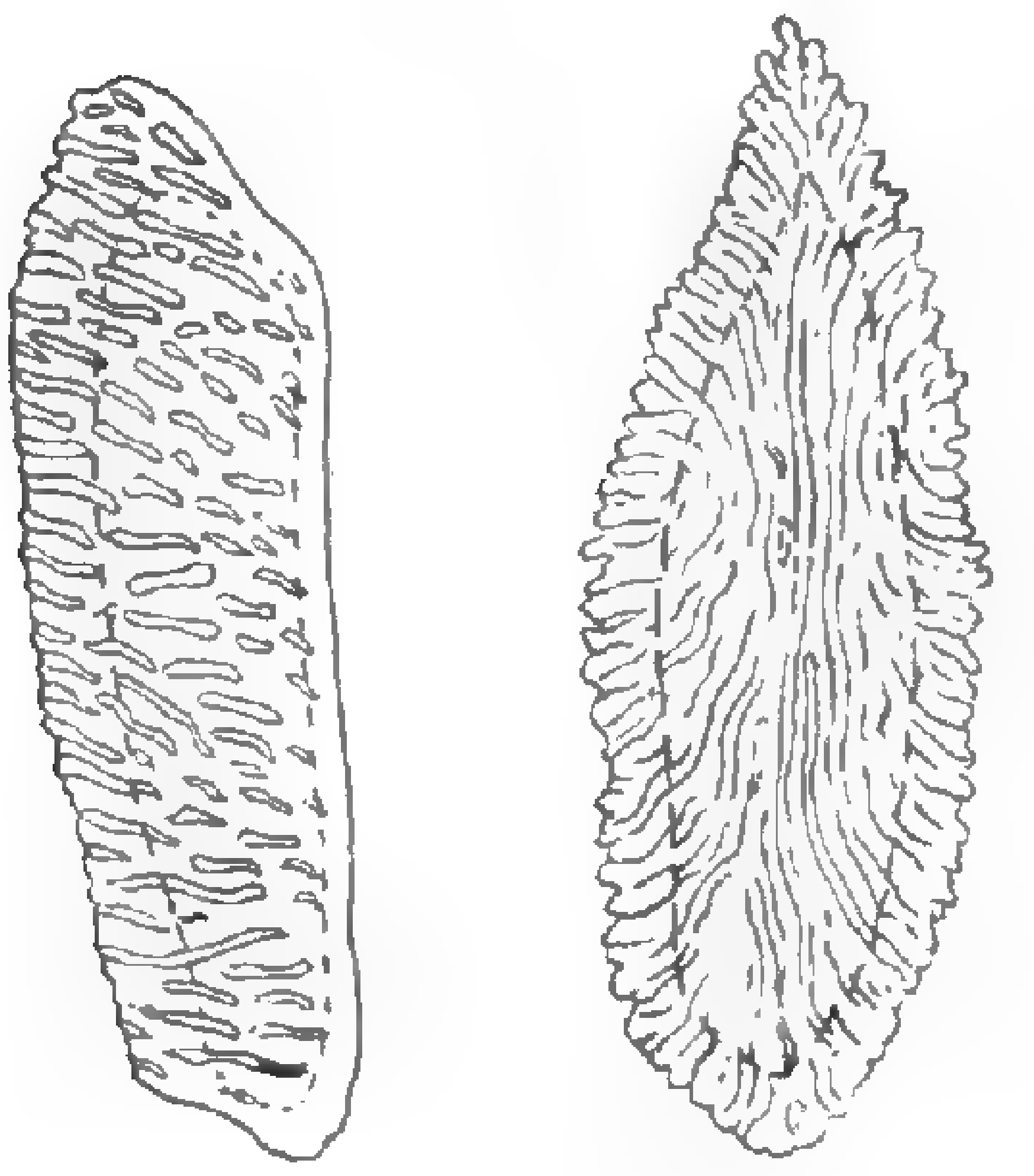
FIG. 13.—*G. Nelsoni* Arth.

FIG. 14.—*R. cornuta* (Pers.) Fries.

FIG. 15.—*G. inconspicuum* Kern (*R. Harknessianoides* Kern).

FIG. 16.—*R. Harknessiana* Ellis & Ev.

FIG. 17.—*Roestelia* sp., an unnamed species, the only one having spinulose markings: *a*, side view; *b*, face view.



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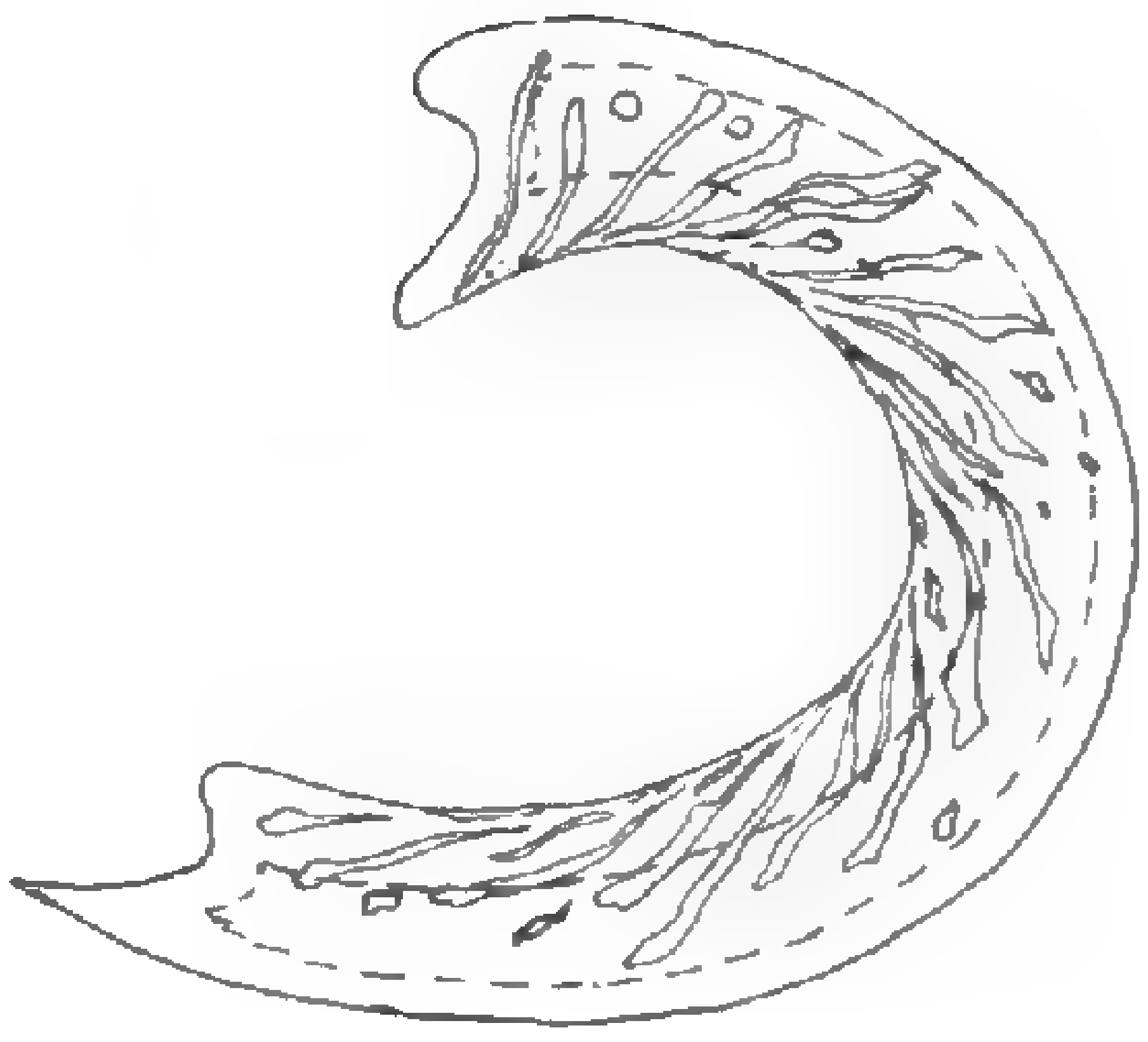

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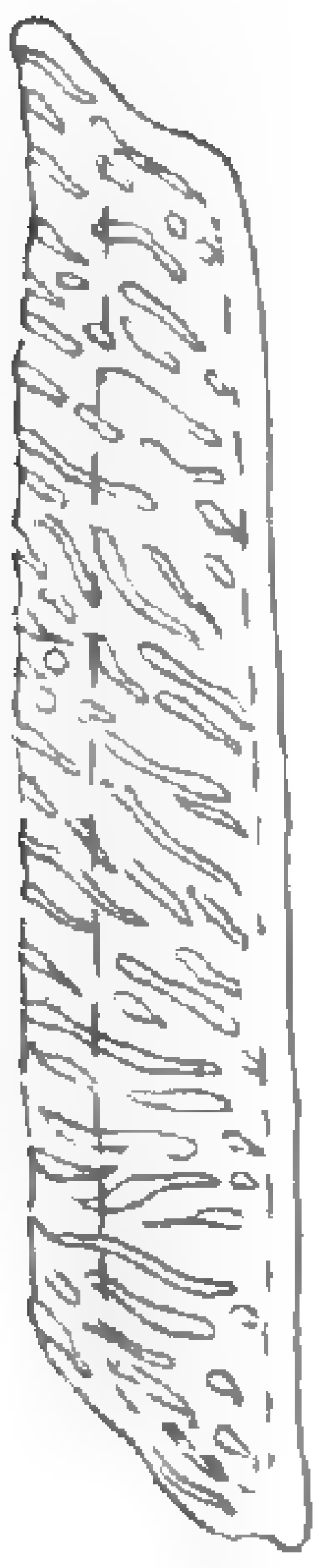

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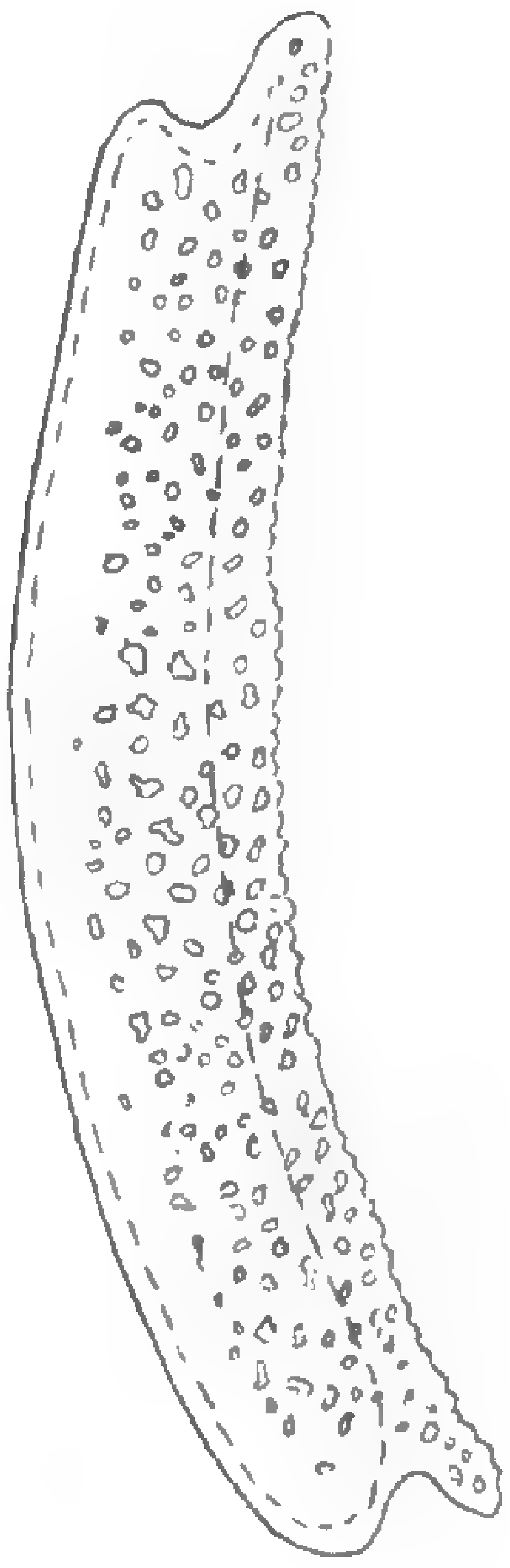

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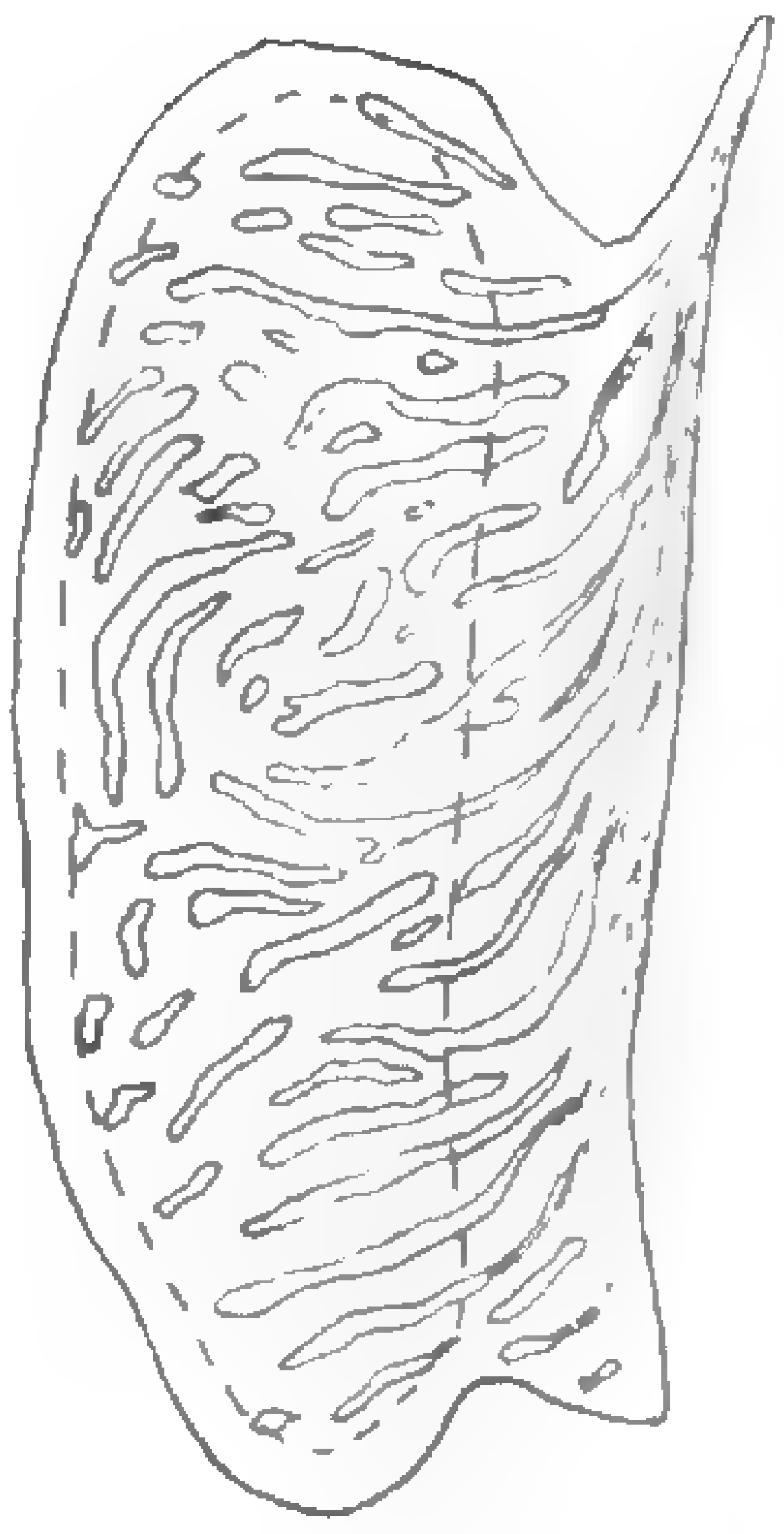

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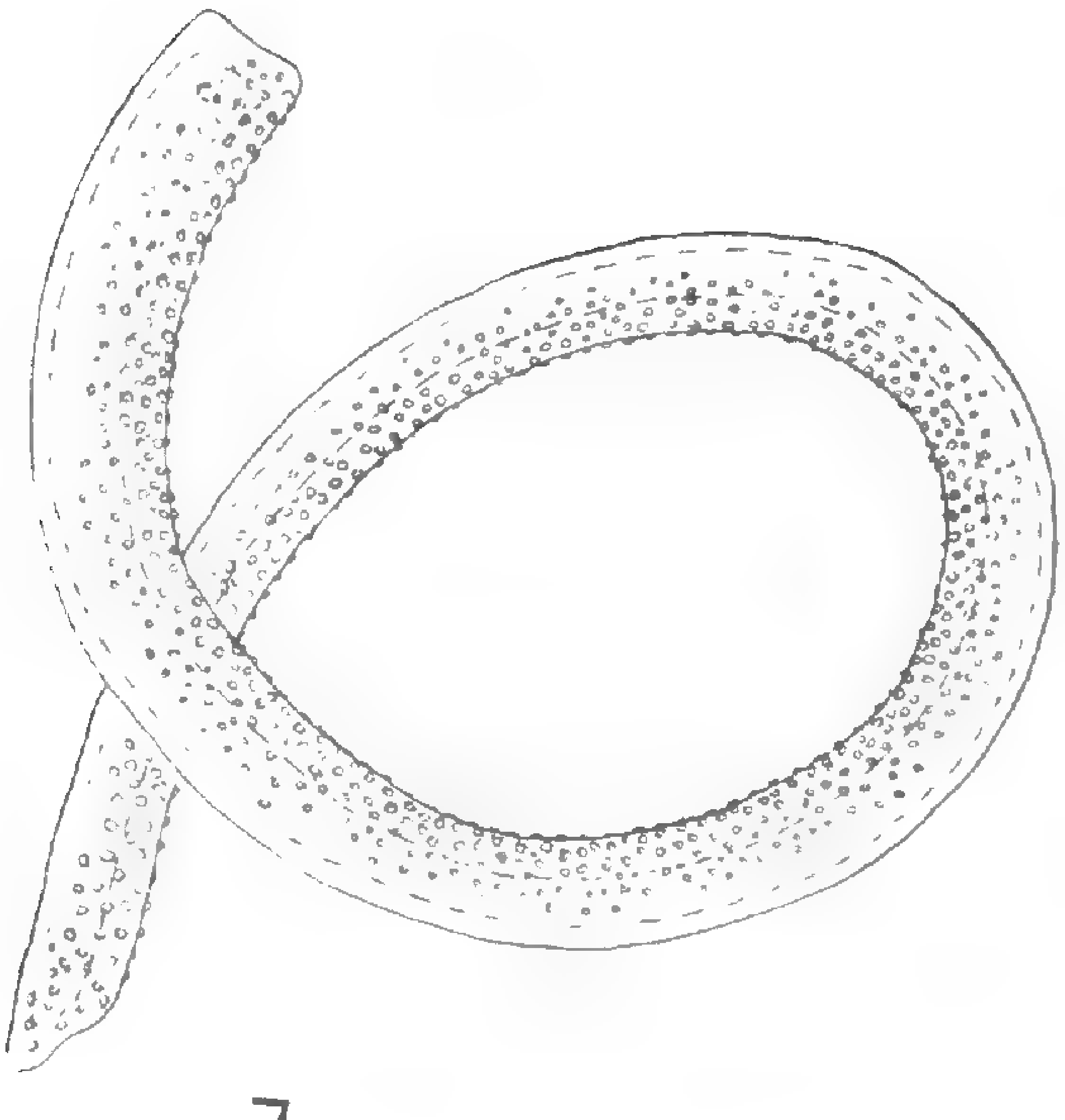

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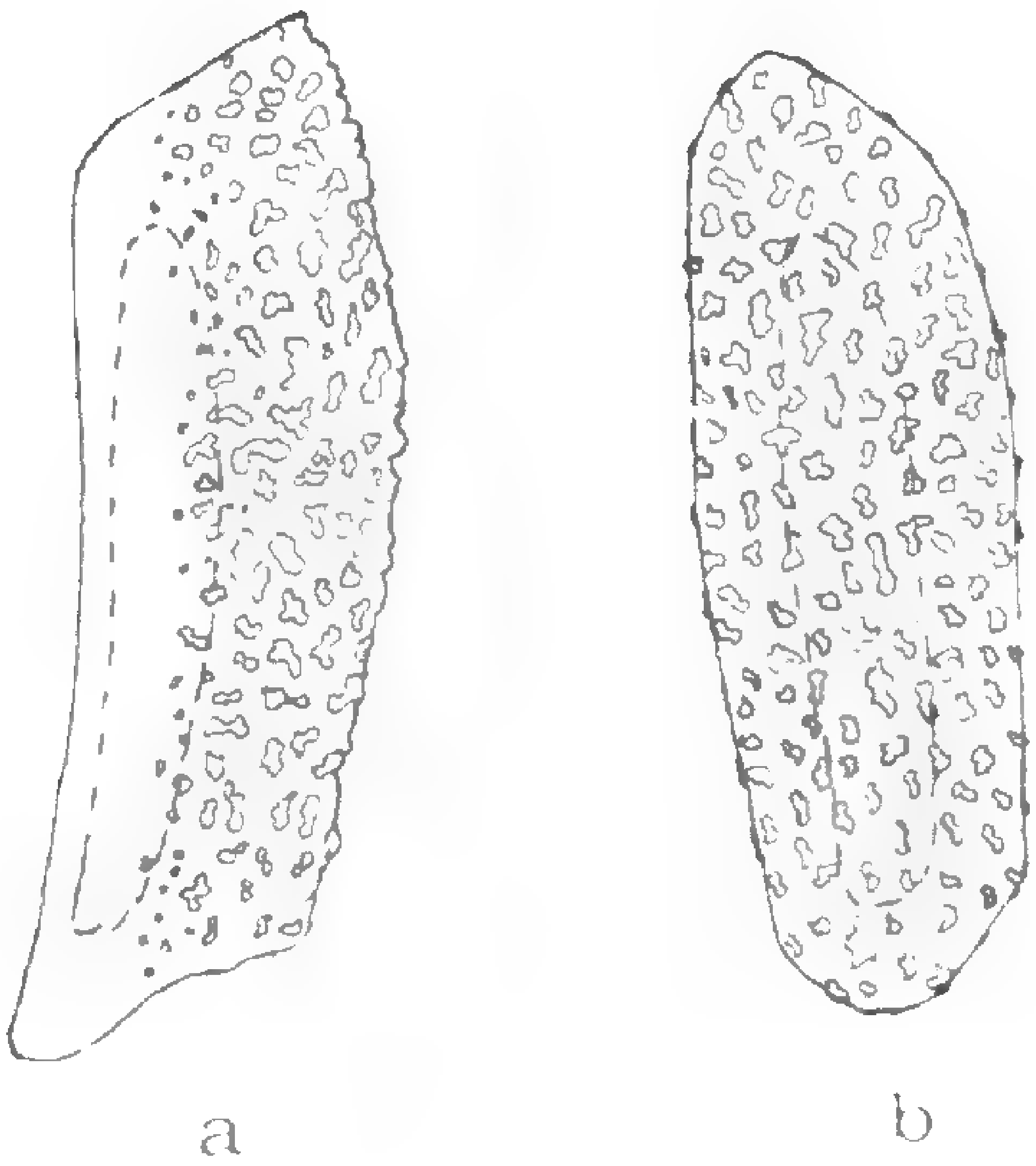

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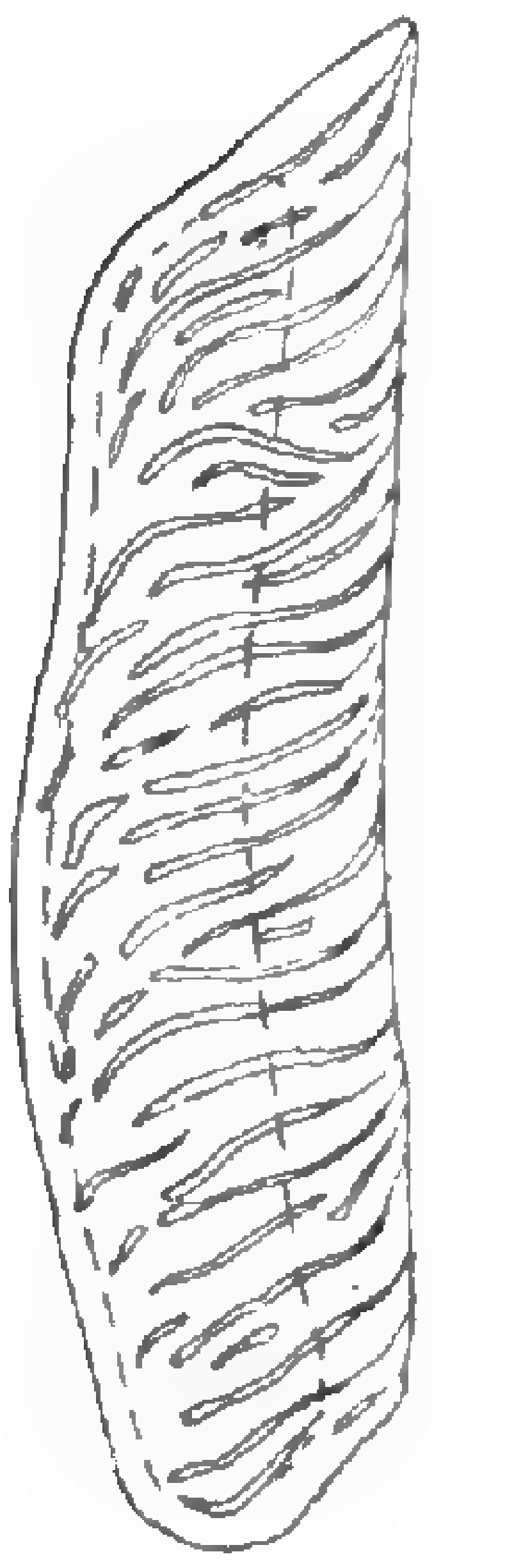
KERN on ROESTELIAE



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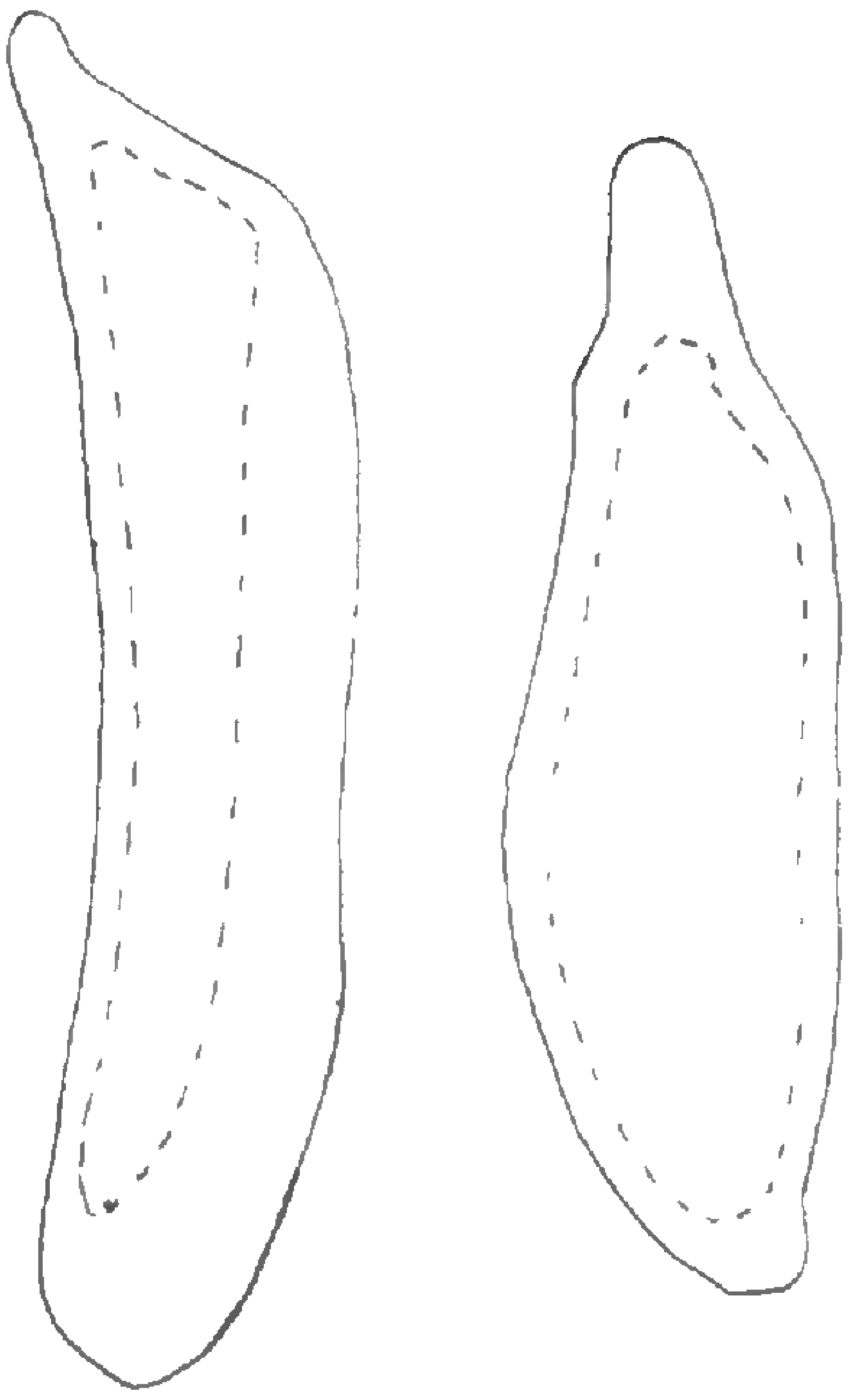

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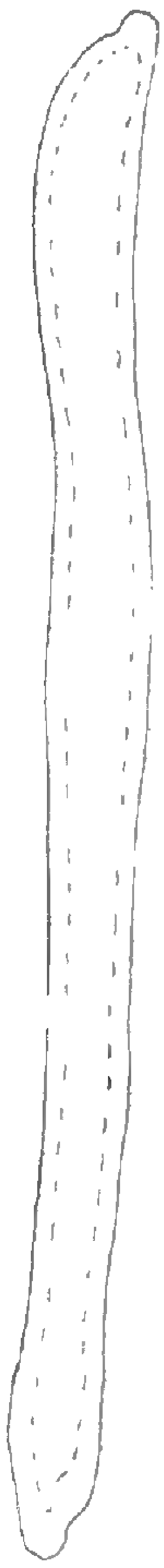

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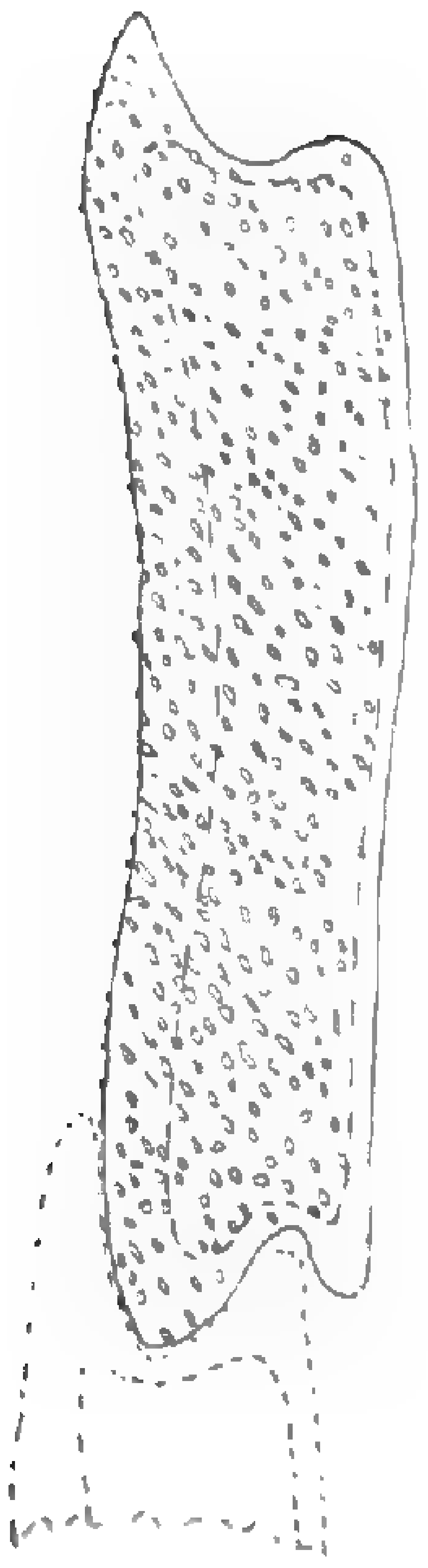

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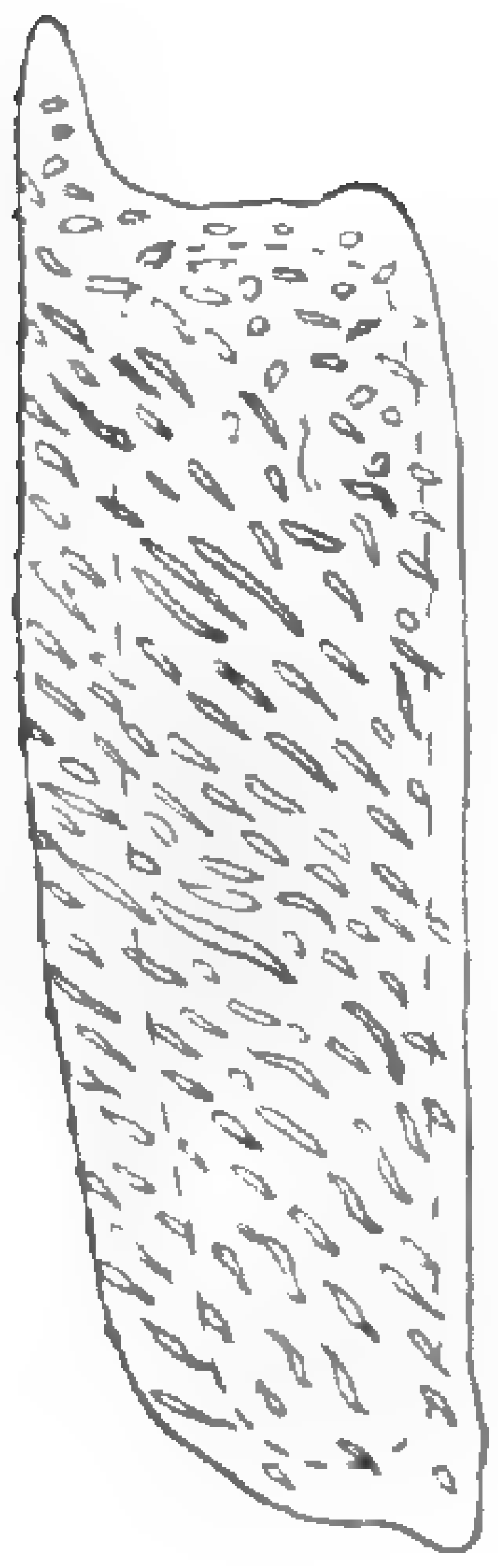

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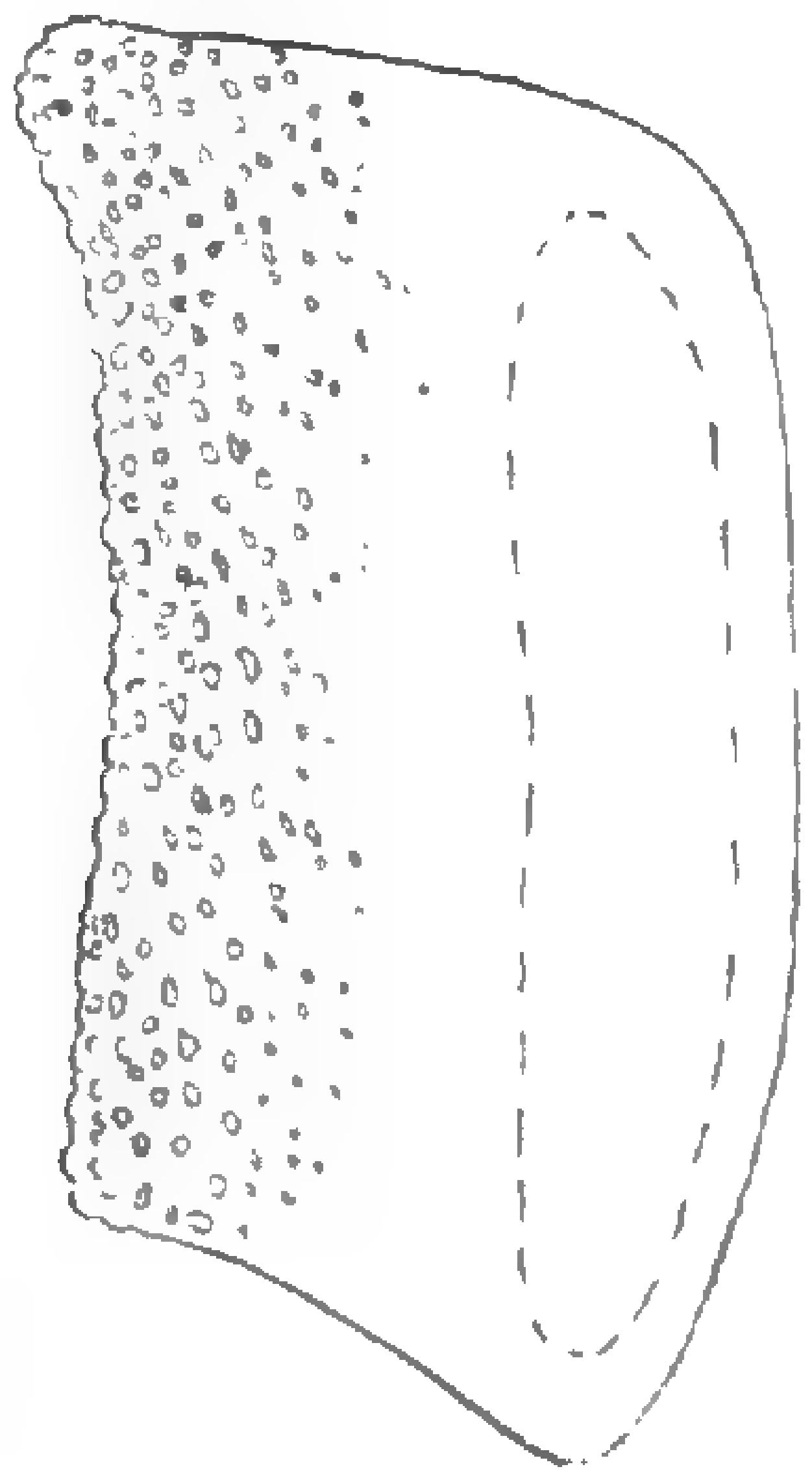

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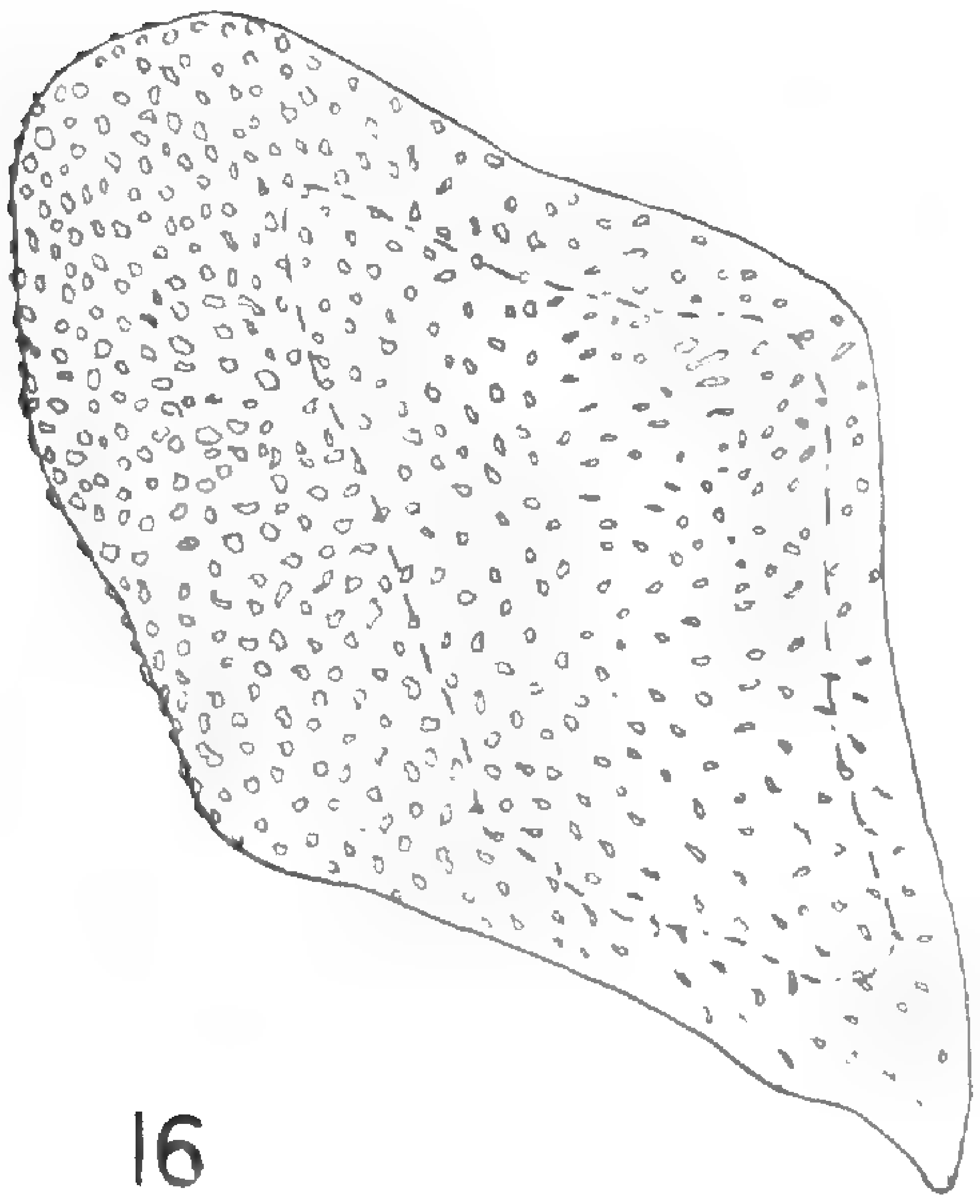

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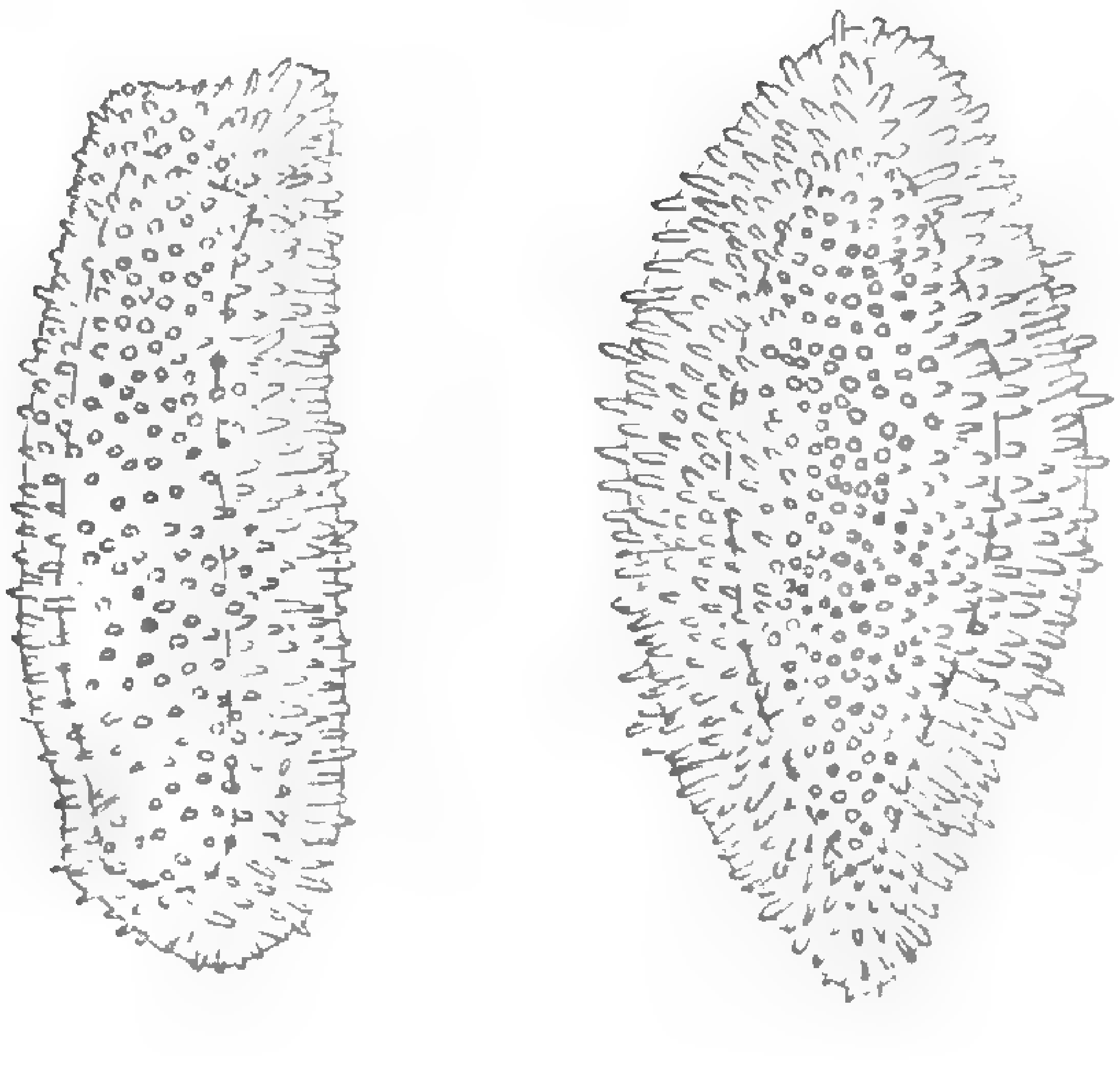

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KERN on ROESTELIAE

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

JOHN DONNELL SMITH

Anona (§ATTAE Mart.) **macroprophyllata** Donn. Sm.—Folia subsessilia parva elliptico- vel obovato-oblonga apice rotundata vel saltem obtusa basi rotundata vel retusa. Pedunculi laterales ad basin bracteis binis foliaceis cordato-orbicularibus fulti. Petala exteriora oblonga obtusa, interiora deficientia.

Frutex 3–4-metralis. Folia pergamentacea glabra 4–5.5^{cm} longa 2–3^{cm} lata 7–9-penninervia minutissime reticulata pellucido-punctulata, petiolis 2–3^{mm} longis. Pedunculi glabri 23–27^{mm} longi, bracteis suboppositis primum ferrugineo-sericeis denique praeter basin marginemque ciliatas glabrescentibus, inferiore 20–24^{mm}-diametrali quam altera subdimidio majore, bracteola ad medium pedunculi minuta lanceolata sericea. Sepala ovata 3–4^{mm} longa extus ferrugineo-villosa. Petala extus glabrescentia intus cinereo-velutina 21^{mm} longa 8^{mm} lata basi concava. Stamina 2.5^{mm} longa puberula, filamentis antheras subaequantibus, connectivo ultra loculos pulvinato. Torus staminiferus pilosus. Pistilla 2^{mm} longa. Fructus desideratur.

In praecipite prope Fiscal, Guatemala, alt. 1110^{m}, Jun. 1909, *Charles C. Deam* n. 6191.—Typus in herbario Musei Nationalis servatur.

Krameria (§TETRANDRAE Chod.) **dichrosepala** Donn. Sm.—Cano-sericea. Folia lanceolato-linearia. Pedunculi axillares folia subaequantes supra medium bibracteolati. Sepala 4, duobus intermediis et petalis flavicantibus. Petala superiora sepalis paulo breviora unguibus totis coalita, laminis flabelliformibus. Stamina infra medium unguibus petalorum adnata.

Fruticulus prostratus, ramis virgatis 3–5-decimetralibus cum foliis et pedunculis cano-sericeis hinc illinc rufescentibus. Folia sessilia 7–9^{mm} longa 1–2^{mm} lata in mucronem nigrum 0.5^{mm} longum attenuata basi rotundata margine revoluta. Pedunculi 5–8^{mm} longi, bracteis foliaceis 5–6^{mm} longis. Sepala parum inaequalia 7–8^{mm} longa oblongo-ovata obsolete mucronata extus sericea, extimo valde gibboso et intimo sanguineis, intermediis inaequilateralibus. Petala superiora 6^{mm} longa, laminis 1.5^{mm} longis 2^{mm} latis subcrenulatis, intermedio paulo minore, petalis inferioribus suborbicularibus 2^{mm}-diametralibus subdenticulatis glabris. Stamina 4.5^{mm} longa. Ovarium gibbosum ovale cano-villosum addito

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[1] Continued from BOT. GAZETTE **48**:300. 1909.

stylo aequilongo stamina paulo superans. Fructus ignotus.—Ad *K. canescentem* A. Gray et *K. bicolorem* S. Wats. indumento foliis inflorescentia accedens ab utraque inter alia petalis staminibusque connatis recedit.

Ad viam montanam flumen Montagua ultra hand procul a Gualán, Depart. Zacapa, Guatemala, Jun. 1909, *Charles C. Deam* n. 6273.—Typus in herb. Musei Nationalis servatur.

Calliandra (§Macrophyllae Benth.) **rhodocephala** Donn. Sm.—Glabra. Folia breviter petiolata, pinnis unijugis, foliolis trijugis, addito saepius foliolo infimo solitario, inaequilateralibus oblongo- vel ovato-lanceolatis acute acuminatis basi exteriore rotundatis interiore acutis binerviis. Pedunculi axillares et terminales fasciculati breves. Calyx striatus et corolla erubescens.

Frutex 2.5-metralis. Stipulae ramentaceae oblongo-ovatae 8^{mm} longae persistentes. Petiolus communis $1–1.5^{cm}$ longus, pinnarum rhachi $7–1.05^{cm}$ longa, foliolis supra praeter nervos puberulos vernicosis in jugo inaequalibus per paria deorsum decrescentibus, terminalibus $10–12^{cm}$ longis $3.5–4.2^{cm}$ latis, in pare infimo $3.5–5.5^{cm}$ longis, foliolo septimo $2–2.5^{cm}$ longo. Pedunculi circiter 1.5^{cm} longi basi bracteis striatis ovato-lanceolatis 8^{mm} longis medio bracteola minuta muniti, capitulo glabro, juvenili etiam in sicco laete rosaceo, bracteolis floralibus ovalibus 1.5^{mm} longis striatis nigro-apiculatis. Calyx obconicus 3^{mm} longus, lobis rotun- datis 0.5^{mm} longis apice nigris. Corolla 8^{mm} longa supra dimidiam tubulosam infundibuliformis, lobis triangularibus 2^{mm} longis trigono-incrassatis. Stamina rosacea 2.5^{cm} longa, tubo breviter exserto, antheris glanduloso-puberulis. Legumen ignotum.—*C. bolivianae* Britton proxima.

Prope viae ferreae pontem ad Puerto Barrios, Depart. Yzabal, Guatemala, Maj. 1909, *Charles C. Deam* n. 6015.—Typum in herb. Musei Nationalis vidi.

Casearia (§Pitumba Benth.; Warburg) **nicoyensis** Donn. Sm.—Folia lanceolato-elliptica obtuse acuminata basi acuta serrulata supra glabra subtus glabrescentia, punctis atque lineis obsoletis. Pedicelli fasciculati petiolum subaequantes bracteis majusculis bis longiores flore subbreviores. Calycis segmenta linearia. Stamina 8 glabra breviter connata, filamentis staminodia pilosa paulo superantibus.

Inermis, ramulis novellis stipulis foliorum nascentium tergo pedicellis calyce sordide pubescentibus. Folia coriacea $5.5–8.5^{cm}$ longa medio $2.5–3^{cm}$ lata minute appresseque calloso-serrulata erga lucem inspecta pellucido-reticulata, petiolis $3–5^{mm}$ longis, stipulis lanceolato-ovatis 2^{mm} longis. Bracteae ad nodos foliatos numerosae imbricatae ovatae 2^{mm} longae rufidulo-membranaceae glabrescentes, pedicellis $3.5–4^{mm}$ longis. Calycis 5^{mm} longi segmenta paene sejuncta 1^{mm} lata obtusa intus glabra. Discus staminiferus 1^{mm} altus, filamentis 2^{mm}

longis, antheris oblongo-ellipsoideis 0.5^{mm} longis nudis, staminodiis 1.5^{mm} longis totis patenter cano-pilosis. Ovarium pubescens ellipsoideum 1.5^{mm} longum in stylum aequilongum indivisum attenuatum, placentis tribus. Capsula deficit.

In fruticetis et secus vias, Peninsula Nicoya, Costa Rica, Apr. 1900, *Adrian Tonduz* n. 13901.

Reynoldsia americana Donn. Sm. Folia ter pinnata, foliolis bijugis cum impare lanceolato-ovatis glandulari-serratis. Umbellae subcapituliformes multiflorae racemosae, racemis fasciculatis pedunculatis, floribus 9–10-meris. Corolla clausa ovato-globosa, petalis oblongis.

Arbor mediocris. Ramuli fistulosi foliorum cicatricibus approximatis notati. Folia juvenilia solum visa petiolo 8–11^{cm} longo computato 27–30^{cm} longa, pinnis primariis 4-jugis, secundariis 3-jugis, foliolis 3.5^{cm} longis 2^{cm} latis, petiolo dilatato-amplexicauli, stipulis obsoletis. Pedunculi circiter 6-fasciculati 2.5–3.5^{cm} longi cum racemi rhachi 1.5–2^{cm} longa crassi, ramis 3–4^{cm} longis plerumque ad apicem rhacheos 5–8-fasciculatis, umbellis subglobosis 22–36-floris, pedicellis teretibus 5–6^{mm} longis inarticulatis, bracteis bracteolisque ovatis parvis, floribus praecocibus ecalyculatis 4^{mm} longis. Calyx hemisphaericus 3^{mm} latus, limbo integro glandulis circiter 6 apiculato. Petala 9–10 calyptratim cohaerentia et sub anthesi dejecta 3.5^{mm} longa 1^{mm} lata apice angustata. Stamina 9–10, filamentis superne inflexis, antheris oblongis 2^{mm} longis. Stigma 9–10-radiatum stylopodio conico impositum. Drupa ignota.—Species hactenus cognitae insularum Oceani Pacifici incolae sunt.

In silvis, Peninsula Nicoya, Costa Rica, Jan. 1900, *Adolfo Tonduz* n. 13823.—Nomen vernaculare *Chile*.—Typus in herb. Musei Nationalis servatur.

Bouvardia Deamii Donn. Sm.—Folia opposita rotundo- vel lanceolato-ovata obtuse acuminata basi rotundata vel acutiuscula. Stipulae integrae deltoideae mucronatae. Pedunculus terminalis 3–5-florus interdum in axilla utraque paenultima uniflorus. Corollae limbus intus cano-velutinus, lobi suborbiculares.

Frutex orgyalis, ramulis divaricatis, novellis sicut stipulae petioli folia nascentia inflorescentia puberulis. Folia supra glabrescentia subtus nervis puberula concoloria 33–38^{mm} longa 15–25^{mm} lata, nervis lateralibus utrinque 3–4, petiolis 1^{mm} longis, stipulis 1.5^{mm} longis. Pedunculus saepius triflorus 2.3^{mm} longus, pedicellis bracteolisque 1.5–2^{mm} longis. Calycis tubus velutinus globosus 1.5–2^{mm}-diametralis lobos subulatos 2–3-plo superans. Corollae tubus cylindricus 9–10^{mm} longus rufescens extus sparsim puberulus intus glaber faucibus staminiferis ampliatus ore constrictus, lobi late patentes 3–3.5^{mm} longi carnulosi intensius coccinei extus glabri. Filamenta tubo ad 2^{mm} infra os breviter adnata, antheris subsessilibus basifixis 2^{mm} longis. Discus glaber. Stylus glaber 4^{mm} longus, stigmatis bipartiti ramis 1.5^{mm} longis. Placentae ovula involventes. Capsula non adest.

Ad fundum praecipitii prope Fiscal, Guatemala, alt. 1110^{m}, Jun. 1909, *Charles C. Deam* n. 6190.—Typus in herb. Musei Nationalis servatur.

Tonduzia Pittieri Donn. Sm.—Folia 3–4-natim verticillata membranacea lanceolato-elliptica 3–4-plo longiora quam latiora. Calycis segmenta acuta membranacea margine hyalina. Corolla ore canopilosa ceteroquin glabra tubo medio staminifero dilatata. Discus obsoletus. Folliculi divaricati.

Arbuscula 3.5–4.5-metralis omnibus in partibus excepto corollae ore glaberrima. Folia cujusque paris inaequalia $8\text{–}12^{\mathrm{cm}}$ longa $3\text{–}3.5^{\mathrm{cm}}$ lata utrinque praesertim superne acuminata nitida subtus pallidiora pellucido-nervata et punctulata, superiora ternata, nervis lateralibus sub margine arcuatis, interjecto interdum altero breviore, venis obsoletis, petiolis $6\text{–}9^{\mathrm{mm}}$ longis. Cyma pseudoterminalis corymbiformis laxe ramosa resinoso-glandulosa $5\text{–}7^{\mathrm{cm}}$ alta $9\text{–}10^{\mathrm{cm}}$ lata, bracteolis membranaceis lanceolato-ovatis acutis, pedicellis $3\text{–}5^{\mathrm{mm}}$ longis. Calyx 1.5^{mm} longus, segmentis ovatis aegre 1^{mm} longis. Corollae totae 1^{cm} longae segmenta tubum aequantia oblongo-ovalia bis longiora quam latiora apice rotundata tenuiter membrancea venosa. Stamina glabra, antheris subsessilibus. Ovarii carpella semiconnata, stylo basi vix fisso 1^{mm} longo uti stigma 0.5^{mm} longum glabro, ovulis in utraque serie circiter 6. Folliculi $6.5\text{–}7^{\mathrm{cm}}$ longi 5^{mm} crassi. Semina ignota.—Hanc ab utraque specie hucusque cognita foliis pro rata latioribus facile dignoscendam claro *H. Pittier*, TONDUZIAE auctori, dicavi.

In praecipite ad Fiscal, Guatemala, alt. 1110^{m}, Jun. 1909, *Charles C. Deam* n. 6098.—In silvis prope Gualán, Depart. Zacapa, Guatemala, alt. 186^{m}, Jun. 1909, *Charles C. Deam* n. 6307.—Typos in herb. Musei Nationalis servatos vidi.

Marsdenia gualanensis Donn. Sm.—Folia utrinque puberula punctata orbiculari-cordata cuspidata 5-nervia. Paniculae axillares sessiles vel breviter pedunculatae petiolum subaequantes inferne bis terve furcatae, ramis suberectis incrassatis, pedicellis gracilibus. Corolla extrorsum glabra, faucibus biseriatim cano-barbatis.

Frutex volubilis 3-metralis, ramis petiolisque glabrescentibus. Folia membranacea in cuspidem $1\text{–}1.5^{\mathrm{cm}}$ longam acutam mucrunculatam subabrupte acuminata absque cuspide $6\text{–}8^{\mathrm{cm}}$ longa atque lata, sinu rotundato, ima basi cuneata supra glanduloso-maculata, nervis lateralibus praeter basales utrinsecus tribus, venis subtransversalibus, venulis reticulatis pellucidis, petiolis $2.5\text{–}3^{\mathrm{cm}}$ longis. Paniculae pubescentes $3\text{–}3.5^{\mathrm{cm}}$ longae, ramis bracteosis $12\text{–}18^{\mathrm{mm}}$ longis, pedicellis $4\text{–}7^{\mathrm{mm}}$ longis. Calyx pubescens 2^{mm} longus, segmentis oblongo-ovatis obtusis, sinubus eglandulosis. Corollae tubus campanulatus lobos obtuse ovatos atque calycem aequans. Coronae squamae oblongo-ellipticae 0.5^{mm} longae gynostegio dimidio breviores obtusae superne hyalinae. Discus stylinus 0.5^{mm}-diametralis breviter rostellatus. Carpidia glabra ovoidea 0.5^{mm} longa. Folliculi desunt.

✓In fruticetis ad viam prope Gualán, Depart. Zacapa, Guatemala, alt. 186^{m}, Jun. 1909, *Charles C. Deam* n. 6333.—Specimen typicum in herb. Musei Nationalis servatur.

Heliotropium (§ORTHOSTACHYS A.DC.) **physocalycium** Donn. Sm.—Omnibus fere in partibus glanduliferum. Folia supra scabridiuscula sparsim strigillosa subtus molliter pilosa lanceolato-oblonga transversim venosa. Pedunculi laterales et terminales dichotomi. Calyx fructiferus auctus inflatus. Stylus brevissimus. Fructus oblato-globosus, nucibus dorso exsculpato-reticulatis.

Frutex 3-metralis. Rami petioli pedunculi spicae necnon calyces simul pubescentes et pilis longis patentibus glandularibus conspersi. Folia 8–11.5^{cm} longa 2.5–4^{cm} lata utrinque attenuata, petiolis 8–15^{mm} longis. Pedunculi bis terve dichotomi 5–8^{cm} longi, spicis 7–14^{cm} longis, junioribus scorpioidibus, bracteis bracteolisque obsoletis. Calycis floriferi 3^{mm} longi segmenta lanceolato-ovata herbacea nervosa, fructiferi pentagono-globosi segmenta sibi invicem marginibus applicata late ovata cuspidato-acuminata 4^{mm} longa. Corollae tubus 4–4.5^{mm} longus extus glandulari-puberulus intus glaber ad 1.5^{mm} supra basin staminiferus, lobi semiorbiculares 1^{mm} longi, sinubus nudis. Antherae vix cohaerentes lineari-oblongae 1.5^{mm} longae apice papillosae. Stigma 1^{mm} longum stylo paulo longius, apice truncato-conico glabro. Fructus glandulari-puberulus 1.5^{mm} altus 2^{mm} latus profunde 4-sulcatus, nucibus leviter cohaerentibus, seminibus rectis.

Capetillo, Depart. Zacatepéquez, Guatemala, alt. 1400^{m}, Mart. 1892, *John Donnell Smith* n. 2472 ex Pl. Guat. etc. quas ed. Donn. Sm.—Laguna de Ayarza, Depart. Jalapa, Guatemala, alt. 2400^{m}, Sept. 1892, *Heyde et Lux*, no. 3990 ex Pl. Guat. etc. quas ed. Donn. Sm.—Guatemala, Depart. Guatemala, alt. 1465^{m}, Feb. 1905, *W. A. Kellerman* n. 4559.—El Salvador, 1905, *Cárlos Rénson* n. 258.—(Exemplum utrumque nempe Kellermanianum et Rensonianum in herb. Musei Nationalis vidi.)

Eandem plantam in Ecuador collegit et sub numeris 1443^{a} et 14850 distribuit cl. *Eggers.*

Blechum (§EUBLECHUM Oerst.) **pedunculatum** Donn. Sm.—Folia ovata in petiolum decurrentia. Pedunculi axillares spicam ovoideam subaequantes vel superantes, bracteis obovatis 3–5-nerviis unifloris. Corollae lobi obovati tubo longiores. Capsula tetrasperma, seminibus barbatis.

Fruticulus ascendens 24–30-centimetralis, ramis bifariam pubescentibus. Folia utrinque sparsim bulboso-strigillosa subtus nervis patenter pubescentia 3.5–5^{cm}

longa 2–3$^{\mathrm{cm}}$ lata obtuse acuminata ima basi in petiolum totum alatum 1–1.5$^{\mathrm{cm}}$ longum abrupte contracta. Pedunculi pubescentes 1–2$^{\mathrm{cm}}$ longi, spica 11–17$^{\mathrm{mm}}$ longa, axe 6–9$^{\mathrm{mm}}$ longo, bracteis circiter 10–16 apice rotundatis basi attenuatis ciliatis 7–11$^{\mathrm{mm}}$ longis 4–8$^{\mathrm{mm}}$ latis, bracteolis linearibus 1$^{\mathrm{mm}}$ longis hyalinis. Calycis segmenta lineari-lanceolata 3$^{\mathrm{mm}}$ longa scariosa nervata. Corollae tubus rectus superne angustatus 5$^{\mathrm{mm}}$ longus, lobi inaequales, extimus maximus 8$^{\mathrm{mm}}$ longus atque latus extus pubescens basi intus aurantiaceus. Stamina summo tubo inserta, antheris subsessilibus. Stylus 3$^{\mathrm{mm}}$ longus. Capsula elliptico-oblonga 7$^{\mathrm{mm}}$ longa supra medium vacua. Semina pilis rectis glandularibus scabridiusculis munita, retinaculis lanceolato-dilatatis.

Ad viam montanam prope Gualán, Depart. Zacapa, Guatemala, alt. 186$^{\mathrm{m}}$, Jun. 1909, *Charles C. Deam* n. 6277.—Typus in herb. Musei Nationalis servatur.

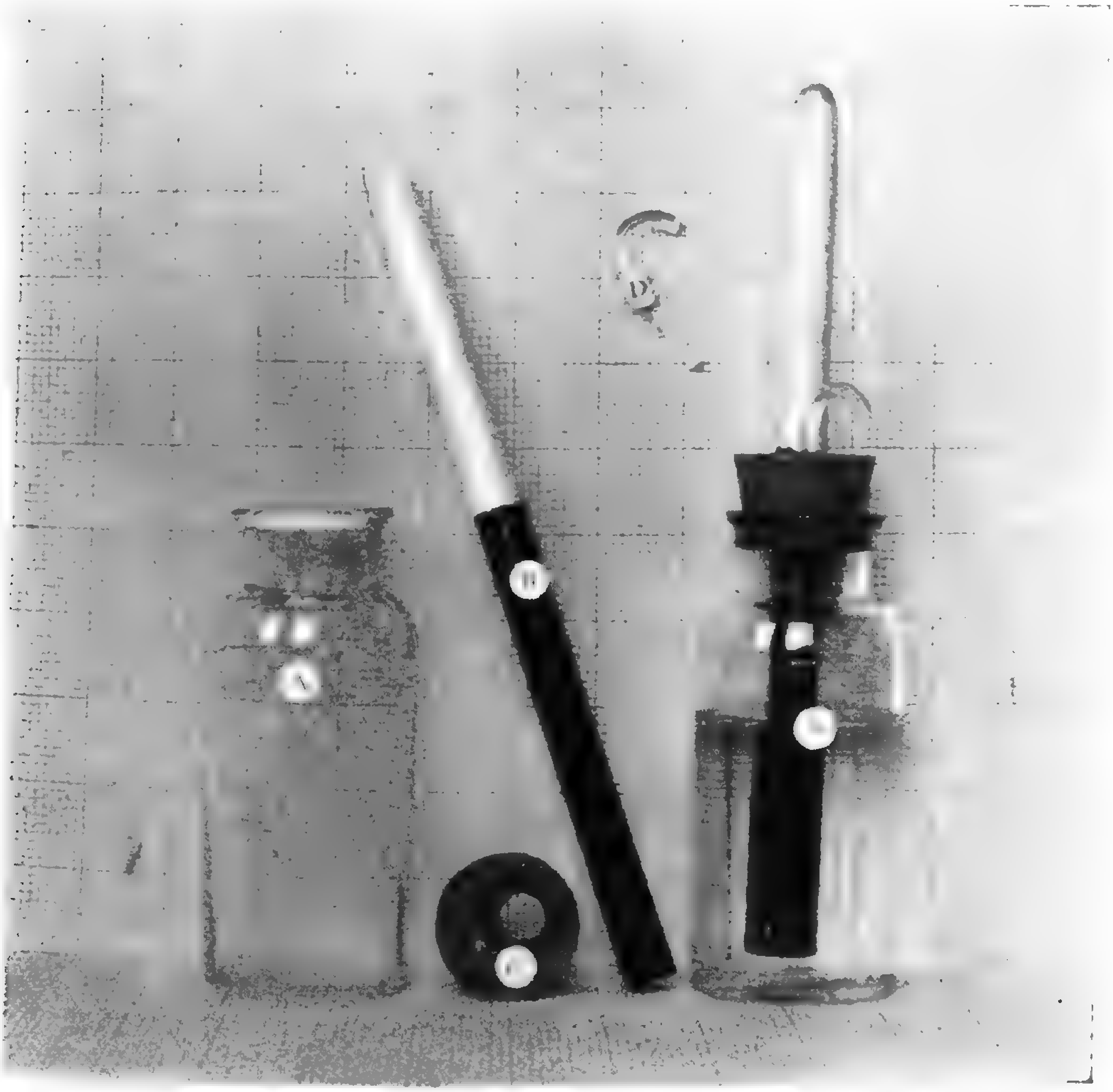
BALTIMORE, MARYLAND

BRIEFER ARTICLES

A SIMPLE VAPORIMETER

(WITH ONE FIGURE)

The accompanying figure shows a simple form of vaporimeter which two years' use has shown to possess some advantages over previously described forms. *A* is a 250^{cc} bottle closed with a rubber stopper (*C*), through which pass tightly a 25^{cm} hollow porous tube (*B*) and a capillary tube (*D*). The capillary tube permits equalization of pressure without allowing an appreciable evaporation from the bottle except through the porous tube. The use of uniform capillary tubes insures the same sized opening in all of the bottles of a series, prevents the entrance of rainwater,



and has other obvious advantages over the use of loose corks. The lower portion of the porous tube is glazed with DeKotinsky cement to insure a constant evaporating surface. (This cement, by the way, when properly heated is far superior to sealing-wax for most laboratory purposes.) In refilling the bottle or determining the water loss it is only necessary to remove the capillary tube and insert the burette tip. If air bubbles collect in the porous tube when first set up, they may be removed by inverting the instrument and allowing the water to force them out. The collection of air bubbles may be avoided, however, by first placing the tubes in alcohol and then in distilled water, or by boiling in water before setting up. For determining the water loss I found it in some instances advantageous to weigh the entire instrument from time to time. Because of the small size of the porous tube, 250^{cc} of water is sufficient for two weeks of exposure under ordinary Illinois conditions. Under certain circumstances the smaller size is an advantage, because the instrument is less conspicuous.—EDGAR N. TRANSEAU, *Charleston, Illinois.*

PHYLOGENY OF PLANTS

The following statement has been received from Dr. LOTSY in reference to the recent review of the second volume of his *Vorträge über botanische Stammesgeschichte* in this journal:[1]

May I call your attention to an error in your review in saying that "Anthoceros is accorded the status of the most primitive liverwort on the ground that it is nearest the algae in having in each cell only one chloroplast and this furnished with a pyrenoid." Now I certainly do *not* consider Anthoceros as the most primitive liverwort, as I can prove by the following passage on page 74 of my book: "Das primitivste Lebermoos in Bezug auf die Struktur seiner Chromatophoren ist Anthoceros, zu gleicher Zeit das höchste in Bezug auf seine 2*x*-Generation. . . . . Ihm und seinen Verwandten ist also eine isolierte Stellung anzuweisen. . . . . Jedenfalls hat Anthoceros eine sehr hoch entwickelte 2*x*-Generation und kann uns also bei der Suche nach einer sehr niedrigen Archegoniate nicht behilflich sein. Sehen wir also einmal, ob wir irgendwo anders glücklicher sind." Your deduction that I consider Anthoceros the most primitive liverwort is probably derived from a passage on page 61, which you either understood imperfectly or in which I expressed myself imperfectly. In either case we can both be excused, I think, as you read and I write a foreign language.

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[1] BOT. GAZETTE **49**:225. 1910.

I may perhaps be allowed, therefore, to explain in a few words how I tried to get at the "Urform" of the liverworts. I began by saying to myself: liverworts must be derived from an alga-like ancestor, so let us see which liverwort has in its cells the greatest similarity to algae. As such I took Anthoceros, and started to examine it as a possible candidate for the position of the most primitive liverwort, but *rejected* it as such on account of its highly developed $2x$ generation. Having thus failed with Anthoceros, which I had chosen as a possible candidate on account of the cell structure of the x generation, I tried whether I would have better luck in examining Riccia as a candidate, which, on account of its having the most primitive $2x$ generation, seemed to have some qualifications to fill the post of the most primitive liverwort. Unfortunately, I had to reject this candidate also, on account of the high development of its x generation. Having thus found that neither Anthoceros nor Riccia would fill the post, I applied to Sphaerocarpus as the all-round "simplest known" liverwort. In this expression I plead guilty; it would have been better to say "the simplest liverwort now living." This candidate I had to reject also, as its $2x$ generation was already too highly developed, higher in fact than that of Riccia. The "Urform" was therefore evidently extinct, and I concluded that it must have had a very simple thallus, somewhat like that of Sphaerocarpus, and a sporophyte somewhat like that of Riccia; for this reason, I designated this hypothetical form as "Sphaeroriccia." It seems to me that this way of getting at the problem is not so very erratic, but fairly logical; but I regret if I failed to express myself with sufficient clearness; and I am grateful for the opportunity the review gives me to explain my views in this respect in a more satisfactory way.—J. P. LOTSY, *Leiden.*

CURRENT LITERATURE

BOOK REVIEWS

The trees of California

Recent years have witnessed a national awakening to the great importance of forestry, and this in turn has excited a new interest in the trees themselves. People wish to learn something about them, their characteristics, how to distinguish one from another, and their proper names, so that there is an evident demand for books which shall impart this knowledge, not only in a form suited to botanists and technical students, but to any intelligent reader. Too often, however, in the effort to treat a scientific subject in a popular way, the science is so attenuated as to be practically valueless. Fortunately, DR. JEPSON, in supplying California with what is really a popular Sylva of the state,[1] has not fallen into this error. On the contrary, in his keys and descriptions he has adhered strictly to the methods of systematic botany, but so far as possible he has simplified them, and has made no unnecessary use of technical terms.

The first fifty pages are devoted to a number of somewhat detached papers, relating to the characteristics of various tree groups, a consideration of the forest distribution in different parts of the state, and other pertinent topics. A section on "second-growth circles" is of much interest. These circles result, as is well known, from stump sprouts, and the author here considers the extent to which various species of Californian trees possess this valuable regenerative power. The redwood possesses it to a preeminent degree, and the author holds that 80 per cent of the adult trees in a redwood forest originated from stump sprouts, and not from seeds; while some of the circles must have begun their existence more than 1000 years ago.

Of equal interest is the discussion of the relation of periodic fires to the native trees. Such fires are held to have exerted a selective effect on the forest growth, due to the degree of resistance to fire possessed by different trees. In this ability, again, the redwood surpasses all others. For unnumbered centuries it was the custom of the Californian Indians periodically to burn over the country, a habit which appears to have been universal among the aborigines, from the Atlantic to the Pacific. References to it are frequent in the accounts of early settlers and explorers. Perhaps the earliest is that of THOMAS MORTON, in "New English Canaan," published in 1637, where he describes such a custom among the Indians of Massachusetts, and the passage is worth quoting. "The salvages," he writes, "are accustomed to set fire to the country in all places where they come, and to

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[1] JEPSON, WILLIS LINN, The trees of California. pp. 228. *photogravures 34. text figs. 91.* San Francisco: Cunningham, Curtis, and Welch. 1910.

burn it twize a year, viz., at the spring, and the fall of the leafe. The reason that mooves them to doe so is because it would otherwise be so overgrowne with underweedes that it would be all a coppice-wood, and the people would not be able in any wise to passe through the country out of a beaten path. This custom hath bin continual from the beginning." Too little account has been taken of the selective effect of such burning, "from the beginning," on the vegetation of our country, and DR. JEPSON has done well in devoting some pages to a consideration of its influence on the trees of California.

The second and larger part of DR. JEPSON's volume is given to systematic descriptions of the different trees, with the necessary keys for the guidance of the reader to their identification. Both keys and descriptions are satisfactory to the botanist, while not presenting difficulties too great for anyone of fair education and mental ability. The full notes on distribution, economic uses, and cognate topics add much to the interest of the book, whose value is further enhanced by the numerous and excellent figures in the text.—S. B. PARISH.

The trees of Kentucky

There is no more expeditious way to interest people generally in trees and thus promote the conservation of forests than by issuing well-illustrated, non-technical handbooks on the trees of the various states. Thus there is stimulated local pride in the particular trees and forests of any section. One of the neatest and most satisfactory of such handbooks, dealing with the trees of Kentucky, has just appeared.[2] Few states have a more diversified tree flora than Kentucky, which in its eastern portion has a representative development of the Alleghany forests, while in the west there is found a northern extension of the characteristic trees of the Lower Mississippi. The trees are arranged in modern fashion, and there are many excellent photographic reproductions showing leaf, bark, or fruit characters, with a smaller number of full-page plates showing field habits and habitats. The descriptions are particularly good, since the chief distinguishing characters are tersely presented in simple terms, the usual mass of technical description being properly avoided. To the uninitiated it may seem surprising that there are 108 species of trees known to be native to the state (exclusive of Crataegus), while the presence of eight others is suspected; in addition there are ten species of large shrubs that may at times be regarded as trees. The Kentucky Federation of Women's Clubs is to be congratulated on its unusual foresight and good sense in issuing a book of this character and providing for its free distribution within the state; the federation is also to be congratulated for having been able to enlist so capable a person as MRS. MAURY in the preparation of the volume.—H. C. COWLES.

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[2] MAURY, SARAH WEBB, Native trees of Kentucky, a handbook. pp. 140. *figs. 47.* Louisville: published by the Kentucky Federation of Women's Clubs. 1910. $1.00. (Copies may be obtained from Mrs. H. C. Muir, Nicholasville, Ky.)

MINOR NOTICES

Scientific expedition to New Guinea.—The botanical results, so far as published, of the Dutch scientific expedition to New Guinea in 1907 under the auspices of Dr. H. A. LORENTZ are embodied in the present volume.[3] The groups of plants treated and the specialists who have collaborated in the work are as follows: Filices by H. CHRIST; Palmae by O. BECCARI; Ebenaceae and Loganiaceae by W. P. HIERN; Taxaceae, Sapindaceae, Elaeocarpaceae, Ericaceae, and Gentianaceae by S. H. KOORDERS; Stemonaceae, Burmanniaceae, Corsiaceae, and Orchidaceae by J. J. SMITH; and the Triuridaceae and Polygalaceae by F. A. F. C. WENT. The work is based primarily on the collections made by Dr. G. M. VERSTEEG, collector of the expedition, although plants obtained from other recent expeditions have been included. The treatment of the Orchidaceae occupies by far the greater part of the volume, this family alone being represented by about 60 genera and approximately 240 species. Of these, five species and eleven varieties are described here for the first time, and several are of recent publication. The descriptions of the orchids are supplemented by 46 lithographic plates which beautifully portray the floral characters of more than 150 different species. Of the 73 species of ferns listed, 17 are new to science. The other groups contained in the volume are represented by fewer species, not over 50 in all, but about one-half of these are new. One new genus (*Neojunghuhnia*) of the Ericaceae is described and illustrated. The publication is an important contribution to taxonomic literature.—J. M. GREENMAN.

A memorial volume for Junghuhn.—FRANZ JUNGHUHN was one of the pioneer scientific explorers of Java, and it is very fitting that the centenary of his birth should be celebrated by the publication of a memorial volume,[4] which recalls his many-sided activities and large contributions. JUNGHUHN was born the same year as DARWIN, and after a somewhat stormy youth in his German fatherland, he journeyed to Java, where he remained for many years. Upon his return he became a citizen of the Netherlands, but again returned to Java, occupying a government position there until his death in 1864. The volume contains an account of his life by M. SCHMIDT, and sketches of JUNGHUHN'S contributions to geology, geography, botany, climatology, ethnography, etc., by those best fitted to speak. The botanical sketches are by KOORDERS, who contributes *Plantae Junghuhnianae ineditae, Kritische opmerkingen over de etiketteering van Junghuhn's botanische collecties in 's Rijks Herbarium*, and *Over Junghuhn's verdiensten voor de plantengeographie van Java*. JUNGHUHN is probably best

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[3] Nova Guinea. Résultats de l'expédition scientifique Néerlandaise à la Nouvelle-Guinée en 1907 sous les auspices du Dr. H. A. LORENTZ. Vol. VIII, Botanique. Livraison 1. 4to. pp. 220. *pls. 51.* Leide: E. J. Brill. 1909.

[4] Gedenkboek FRANZ JUNGHUHN 1809–1909. pp. x+361, with portraits of FRANZ and MEVROUW JUNGHUHN, 5 plates, and 48 reproductions of photographs taken by JUNGHUHN. Published by De Junghuhn Commissie. The Hague: Martinus Nijhoff. 1910. *Fl.* 8; geb. *Fl.* 10.

known by his book entitled *Java, seine Gestalt, Pflanzendecke und innere Bauart*, published in 1852, though the first Dutch edition appeared in 1849. The sketches of the Javan vegetation here presented are among the best descriptions of tropical plant life.—HENRY C. COWLES.

Carbohydrates and glucosides.—Another of the monographs on biochemistry, under preparation by English workers, has just appeared.[5] It deals with the monosaccharides, disaccharides, and the more common natural and synthesized glucosides, and forms an invaluable critical consideration of our present knowledge of these physiologically important substances. The seven chapter headings give a good idea of the scope of the work: glucose; the chemical properties of glucose; the hexoses and pentoses; the disaccharides; the relation between configuration and properties; hydrolysis and synthesis; natural and synthetic glucosides. A bibliography of 18 pages adds much to the value of the book.—WILLIAM CROCKER.

Vegetationsbilder.—The island of Juan Fernandez has a vegetation remarkable for the large number of endemic species, which give a peculiar interest to the six plates of KARSTEN AND SCHENCK's well-known work[6] recently issued as a part of the eighth series. Among the species illustrated are *Boehmeria excelsa*, *Arthopteris altescandens*, *Gunnera peltata*, *Dendroseris pinnata*, and *Robinsonia gayana*. The photographs and brief descriptive text are by CARL SKOTTSBERG. The vegetation of the Swabian Mountains is also shown in six excellent plates after photographs by OTTO FENCHT, who also contributes the descriptive text.—GEO. D. FULLER.

NOTES FOR STUDENTS

Cytology and taxonomy of Endomycetes.—GUILLIERMOND[7] has given an account of his further studies on *Eremascus fertilis*, discovered by Mlle STOPPEL;[8] *Endomyces fibuliger*, discovered by LINDNER;[9] *Saccharomycopsis capsularis*,

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[5] ARMSTRONG, FRANKLAND E., The simple carbohydrates and the glucosides. pp. vii+112. London: Longmans, Green & Co. 1910.

[6] KARSTEN, G., AND SCHENCK, H., Vegetationsbilder. Series VIII. parts 2, 3. Text and *pls. 7–18*. 4to. Jena: Gustav Fischer. 1910. *M* 4 per part.

[7] GUILLIERMOND, M. A., Recherches cytologiques et taxonomiques sur les Endomycétées. Rev. Gén. Bot. **21**:353–391, 401–419. *pls. 12–19*. 1909.

———, Sur la reproduction sexuelle de l'*Endomyces magnusii* Ludwig. Compt. Rend. Acad. Sci. **148**:941. 1909.

———, Quelques remarques sur l'*Eremascus fertilis* Stoppel et sur ses rapports avec l'*Endomyces fibuliger* Lindner. Compt. Rend. Soc. Biol. **66**:925–926. 1909.

[8] STOPPEL, ROSE, *Eremascus fertilis*, nov. spec. Flora **97**:332–346. 1907.

[9] LINDNER, P., *Endomyces fibuliger*, n. sp., ein neuer Gärungspilz und Erzeuger des fol. Kreidekrankheit des Brotes. Wochenschr. f. Brauerei **24**:no. 36.

discovered by SCHIONNING;[10] and *Endomyces magnusii*, discovered by LUDWIG.[11]

Eremascus fertilis is described as having a branched, septate mycelium, the cells of which are two to four-nucleate. The cells which are about to produce the gametes become uninucleate by putting in septa. Isogamous conjugation results from the fusion of the contents of lateral diverticula from adjoining cells. At the point of fusion an eight-spored ascus is formed, in which spore formation is like that in the yeasts. Later parthenogenetic asci are formed, which after the usual nuclear divisions contain four or more spores, some of which may abort. The nuclei of the vegetative cells are so small that their divisions could not be observed. *Endomyces fibuliger* differs from *Eremascus fertilis* in having uninucleate cells, yeastlike conidia which bud off from the cells of the mycelium, and no fusion of the contents of the diverticula. The asci are always parthenogenetically formed in the faster growing protuberance. The author thinks that we have here the remains of an ancestral conjugation absolutely identical with that in *Eremascus fertilis*. *Saccharomycopsis capsularis* differs from *Endomyces fibuliger* in that the cells of the mycelium may become asci or these may bud off from the mycelial cells. *Endomyces magnusii* differs from the preceding forms in having no yeastlike conidia, but the cells of the mycelium readily separate to form oidia. Asci result from the fusion of the contents of uninucleate oogones and antheridia, which are formed at the ends of closely or distantly related hyphae. About one-fourth of the asci arise parthenogenetically. The author holds that this form is related to the Schizosaccharomycetes through its oidia.

According to VAN TIEGHEM'S[12] classification, the family Eremascaceae includes Eremascus, Endomyces, Saccharomyces, Podocapsa, Olinea, Protomyces, Ascoidea, and Dipodascus. GUILLIERMOND would place the last of these genera in a separate group because in these the asci arise as plurinucleate structures and form many (a variable number) spores. He would group the yeasts, Eremascus, and Endomyces together.

DANGEARD[13] thought that the gametes of Eremascus were multinucleate and has placed this genus with Dipodascus, but the author holds that STOPPEL'S work and his own show that Eremascus and Endomyces should be in the same group. The author criticizes ENGLER and PRANTL'S description of Eremascus, and says that it is no longer valid because isogamous conjugation with twisting of gametes is not present in all species. He would retain the genus Eremascus, including *E. fertilis* and *E. albus*, and characterize it by the absence of conidia

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[10] SCHIONNING, H., Nouveau genre de la famille des Saccharomycetes. C. R. des traveaux du lab. Carlsberg **6**:93–113. 1903.

[11] LUDWIG, F., Ueber Alkoholgärung und Schleimfluss lebender Bäume. Ber. Deutsch. Bot. Gesell. **4**: Gen. Versammlungs-Heft. XVII–XXVII. 1886.

[12] VAN TIEGHEM, PH., Eléments de botanique. 1908.

[13] DANGEARD, P. A., L'origine du périthèce chez les ascomycètes. Le Botaniste **9** and **10**:1906.

and by the presence of eight-spored asci derived from an isogamous conjugation. According to ENGLER and PRANTL, Olinea also differs from Endomyces in the number of its spores, but this is not an essential character, because in two species of Endomyces there are four to eight spores.

On account of the great resemblance between *Endomyces fibuliger* and *Saccharomyces capsularis*, the latter is placed by the author in the genus Endomyces, which differs from the yeasts in the great differentiation of its mycelium and by having its asci arise almost always from the ends of mycelial branches and not from conidia. The genus Endomyces is characterized by a tendency of the mycelium to form conidia or oidia and by the asci arising from the ends of mycelial branches.

The yeasts are thought to be descended from a form similar to *Eremascus fertilis*. From it there are two main lines, one of which again branches to give rise to Saccharomyces, Zygosaccharomyces, and *Endomyces fibuliger* and *E. capsularis;* while the other main branch gives rise to Schizosaccharomyces, *Endomyces magnusii*, and *E. dicipiens*.—FREDA M. BACHMAN.

Vegetation of the Faeröes.—Several years ago Professor WARMING and his colleagues projected a systematic study of the flora of the Faeröes from various points of view, and there have been published in a special serial devoted to the purpose papers dealing with plant lists of various groups, floristic treatises, and the like. For ecologists the most important paper of the series thus far is one by OSTENFELD[14] on the plant associations and their life conditions, representing a translation of an earlier Danish paper, published in 1906. After reviewing the literature and noting that the best previous account of the vegetation is in ROSTRUP'S work published in 1870, OSTENFELD considers the climatic and edaphic factors in some detail. The climate is decidedly insular, the rainfall and humidity being high and the winter temperature so frequently above 0° that the snow cover is not permanent; the average number of rainless days is 85, while only 18 days per annum are clear. The abundance of sheep is responsible for a high degree of modification in the vegetation covering. In a chapter on the biological features the plants are classified according to their biological type (in the sense of RAUNKIAER), duration of life, type of vegetative propagation, and altitudinal distribution. There are no trees on the islands and there is a striking dominance of perennial herbs; only one autophytic species of the natural land vegetation (*Koenigia islandica*) is an annual. Thirty-six species have never been known to produce viable seeds; this is partly due to climate and partly to the absence of such important pollinating insects as bees and butterflies.

The body of the work deals with the plant formations, which are closely related to one another and separable with difficulty; the author regards this as a feature of an insular climate, which seems reasonable to the reviewer, who has

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[14] OSTENFELD, C. H., The land vegetation of the Faeröes, with special reference to the higher plants. Botany of the Faeröes **3**:867–1026. *figs. 31.* 1908.

found similar situations in humid climates generally. The chief categories of natural formations are halophile, subalpine, alpine, and the sea-fowl cliffs, and all but the latter are further subdivided. The halophytic formations are much as elsewhere, and the subalpine formations are mainly those of ponds, swamps, moors, heaths, and cliffs. The cliffs are of much interest, since there is a luxuriant vegetation on sunny southern slopes, while there is a poorer vegetation, mainly of shade mosses, on north slopes. Of rather more interest than usual are the culture formations, the most important of which is the grass meadow. One of the most striking features of the islands is the roof vegetation, which has always been mentioned by travelers; the inhabitants thatch the roofs with grass turf, and very characteristic roof associations develop. The custom of the people is to sow potatoes in cleared ground for two years, after which barley is grown, whereupon the field is left fallow; under the heading "Metamorphic formations," OSTENFELD traces the history of such areas into the grass meadow.—H. C. COWLES.

Some plant diseases.—LANG[15] has given a detailed account of the biology of *Ustilago Tritici* Jens., which, as BREFELD has shown, is peculiar and almost unique among the fungi on account of its habit of infecting the ovule and remaining dormant in the seed until the latter germinates. LANG finds that the spores of this fungus placed upon the stigmas of wheat flowers just opened germinate readily, but the germ tubes show no tendency to penetrate the stylar tissue. Only when the papillae of the stigma have begun to wither and collapse can the germ tubes penetrate between the cells. The fungus apparently has no power of penetrating the sound turgid tissue, a fact which has an interesting bearing in view of the usually strict parasitism of the vegetative phase in this group. The germ tube, without branching, makes its way down the intercellular spaces of the style, or sometimes down the canal formed by the pollen tube, and penetrates the inner integument near the micropylar end, the outer integument having mostly disappeared by that time. When the hyphae reach the chalazal region, they become branched and nodular, apparently showing greater vigor of growth in the region of more abundant nourishment. About three weeks after infection the fungus has reached the embryo. At first it spreads through the scutellum, but later the mycelium pervades every part of the embryo except the radicle. This stage is attained simultaneously with the ripening of the grain. The mycelium remains dormant in the ripe seed, and, when the latter germinates, progressively infects the growing points of the plant, but causes no apparent injury until spores are formed in the ovaries.

GÜSSOW[16] reports the appearance in Newfoundland of a potato disease known as "cauliflower disease" or "potato-canker." The disease is caused by a chytri-

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[15] LANG, WILHELM, Die Blüteninfection beim Weizenflugbrand. Centralbl. Bakt. II. **25**:86–101. *pl. 1* (double). *figs. 2.* 1909.

[16] GÜSSOW, H. T., A serious potato disease occurring in Newfoundland. Cent. Exp. Farm, Depart. Agric., Ottawa, Canada. Bull. 63. pp. 8. *pls. 2. fig. 1.* 1909.

diaceous fungus, *Chrysophlyctis endobiotica* Schilberszky. It has been known in Europe for a long time, but has not hitherto been reported as occurring in America. The present article gives a general description of the disease, with figures showing its character. The purpose of the paper is one of warning, to enable farmers in the Dominion to recognize the trouble and prevent its introduction and spread into Canada.

Three fungous diseases of plants, not before reported, are briefly described by OSTERWALDER.[17] He finds that a disease of *Levisticum officinale* Koch., affecting the leaves and stems on which it appears in the form of spots, is caused by a bacterium which is described as *Pseudomonas Levistici*. He was able to produce infections from pure cultures, but only in wounds. A disease of *Calceolaria rugosa* Hort., characterized by rotting of the stems at the ground, is ascribed to *Phytophthora omnivora* DeBary. *Sclerotinia Libertiana* Fuckel is described as attacking *Omphalodes verna* during wet weather.—H. HASSELBRING.

Chemotaxy.—ÅKERMAN[18] studied the chemotactic responses of the sperms of Marchantia by the usual capillary tube method. They react strongly positively to the ions of potassium, rubidium, and caesium (agreeing with the behavior towards proteins as found by LIDFORSS[19]), and weakly to magnesium and ammonium. They are indifferent to sodium and calcium, and react negatively to the ions of hydrogen and zinc and to the bivalent ions of mercury, iron, and copper. In a potassium-free medium the tubes must contain at least 1/1000 mol. KNO_3 in order to attract, while in a potassium-containing medium the tube must have 40 times the concentration of the potassium shown by the medium. The corresponding gradient for proteins is 20. No evidence of osmotaxy was found in the organism. The tactic responses were greatly disturbed by gaseous impurities of the laboratory and by lack of oxygen.

KUSANO[20] has published a full statement of his work in the chemotactic and related reactions of the swarmspores of Myxomycetes. It is characterized by excellence of experimentation, critical consideration, and clear statement of results. *Aethalium septicum*, *Stemonitis fusca*, and *Comantricha longa* were the forms used. It was found that the activity and responses of the spores are not at all affected by a great decrease in oxygen, so the capillary method was used with a cover glass. All acids attract and bases repel; while neutral substances, if of moderate concentration and not highly toxic, act indifferently. Sodium hydrate

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[17] OSTERWALDER, A., Unbekannte Krankheiten an Kulturpflanzen und deren Ursachen. Centralbl. Bakt. II. **25**:260–270. *pls. 2.* 1909.

[18] ÅKERMAN, ÅKE, Ueber die Chemotaxis der Marchantia Spermatozoiden. Zeit. für Bot. **2**:94–103. 1910.

[19] LIDFORSS, B., Ueber die Reizbewegungen der Marchantia Spermatozoiden. Jahrb. Wiss. Bot. **41**:65–87. 1905.

[20] KUSANO, S., Studies on the chemotactic and other related reactions of the swarmspores of Myxomycetes. Jour. Coll. Agr. Imp. Univ. Tokyo **2**:1–83. 1909.

1/1,000,000 mol. repels, while it requires a somewhat stronger solution of hydrochloric acid to attract, and 1/600 mol. of the latter is the optimum for attraction. In acids the attraction is parallel to the dissociability. In high concentrations acids repel, due in strong mineral acids to the excess of hydrogen ions, and in weak organic acids to the undissociated molecules. In many of the latter acids the strong attraction of the hydrogen ion and weak repulsion of the molecule leads to injury and death of the spores because of the toxicity of the latter. The reaction, both negative and positive, is "apobatic" (PFEFFER'S terminology) or involves "motor reflex" (JENNINGS). JENNINGS maintains that all tactic responses in animals are of this type, and that PFEFFER'S so-called "strophic" reactions do not appear. He thinks it likely also that the same is the case in plants, and KUSANO'S work brings more evidence for the support of this probable contention.—WILLIAM CROCKER.

Germination of spores of rusts.—In a paper by SCHAFFNIT[21] some observations and experiments are given which seem to throw some light on the questions relating to the germination of uredospores and aecidiospores of the rusts. The irregularity of germination of these spores is well known to all experimenters, but no satisfactory explanation for their behavior has been given. SCHAFFNIT finds that the capacity for germination depends largely upon the degree of maturity of the spores. By mature spores he understands only those which have fallen from their stalks without being shaken by air currents or rain. Ordinarily large numbers of spores fall from the sori on account of the motion of the infected leaves, caused by the wind. The majority of these spores do not germinate, but if spores are gathered on a hot quiet day, when there is no wind, 80–100 per cent germinate within two hours. The thoroughly ripened spores have a darker color than the immature ones. Spores which have been separated prematurely from their pedicels are incapable of being ripened afterward. It seems, also, that spores cannot be ripened on leaves that have been cut from the plants. These observations suggest an interesting field for further investigation in the ecology of fungi. It must be confessed that our knowledge of the actual behavior, means of distribution, and germination of fungus spores in nature is very meager, even as to fungi of economic importance. Any contribution to this subject is important. The wide application of these results, which the author makes, would hardly seem justifiable until more extended and more accurate experiments have been conducted.—H. HASSELBRING.

Color production in Penicillium.—The effect of external factors on the color production of a certain species of Penicillium has been investigated by DOEBELT.[22] It seems that in agar cultures the pigment, which is red, appears first near the

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[21] SCHAFFNIT, ERNST, Biologische Beobachtungen über die Keimfähigkeit und Keimung der Uredo- und Aecidiensporen der Getreideroste. Ann. Myc. **7**:509–523. 1909.

[22] DOEBELT, H., Beiträge zur Kenntnis eines pigmentbildenden Penicilliums. Ann. Myc. **7**:315–338. 1909.

center of the colony. It would seem, therefore, that the pigment formation is the result of catabolic processes in the older parts of the mycelium. A general survey of the paper shows that substances which are favorable to growth, as carbohydrates, also favor the production of pigment; while substances like polyatomic alcohols, which are poor nutrients, result in little color production. It does not seem that the absence or presence of color in these cases can be attributed to any specific action of the compounds, but is rather associated with the general growth of the fungus. The same may be said of the experiments in which pigment production was depressed by withholding necessary mineral nutrients or by high osmotic pressure. A more interesting relation is shown when nitrogen is offered in the form of inorganic salts or as asparagin and peptone. All these substances in the presence of sugar and mineral nutrients favored the production of pigment, but if magnesium sulfate and monopotassium phosphate were withdrawn, color was produced only in the presence of the organic nitrogen compounds. Moreover, in this case abundant pigments were produced in asparagin cultures which gave poor growth. A striking effect on the permeability of the protoplasm was noted when phosphates were absent from the nutrient solutions. In all such cultures the pigment diffused into the culture medium, while in all other cases it remained in the cells.—H. HASSELBRING.

Agricultural experiment station in Palestine.—What is called an American institute of research has been established in Palestine, supported by American capital furnished by several philanthropic Jews. Details of the organization and purpose of this experiment station have been published by FAIRCHILD.[23] It is to be located at the foot of Mt. Carmel, seven miles from Haifa, and will be under the directorship of Mr. AARON AARONSOHN. The director is well known among botanists through his discovery of the long-sought wild prototype of wheat, his personal acquaintanceship having been extended by a recent visit to this country, when he was impressed by the remarkably close agricultural resemblance between California and Palestine. His discoveries of drought-resistant plants, and especially the possibility of using his wild wheat in the more arid regions of the United States, have led to an invitation to prepare a bulletin for the U.S. Bureau of Plant Industry.

The special purpose of the station is to develop rational agriculture in Palestine, but the director has in mind also a wider application of his results, and will issue annual reports in English of the work of the station. It seems that the study of plant pathology is unknown in Palestine, and as a nucleus for such work the collection of the late PROFESSOR W. A. KELLERMAN has been purchased, which the Department of Agriculture has materially supplemented.

The whole movement is one of great interest and promise, not only to Palestine, but to our own country as well.—J. M. C.

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[23] FAIRCHILD, DAVID, An American research institution in Palestine; the Jewish agricultural experiment station at Haifa. Science N.S. **31**:376, 377. 1910.

Effects of carbon monoxid on plants.—SEELÄNDER[24] concludes from numerous experiments that carbon monoxid is to be regarded in general as a plant poison and should be classed as an anaesthetic weaker than chloroform. It exerts injurious effects upon seedlings of *Lupinus albus* and upon germinating spores of *Mucor stolonifer*, *M. Mucedo*, *Penicillium glaucum*, *Aspergillus niger*, and *Botrytis cinerea*. The injurious effect upon seedlings of *Lupinus albus* is shown by an inhibition in rate of growth of the rootlets, which effect is observable with concentrations varying from 75 per cent to 0.5 per cent. Injurious after-effects are to be observed only when the higher concentrations and long exposures are used. Seedlings exposed to the gas show an increased resistance to drying. The spores of the fungi named, germinated on nutrient gelatin in the presence of carbon monoxid, showed delay in germination, and an inhibition in rate of growth of the hyphae, which, especially in the higher concentrations, were irregularly bent and swollen. The minimum concentration necessary to produce the observed results was 1 per cent. The amount of respiration in tubers of *Solanum tuberosum*, bulbs of *Allium Cepa*, petals of roses and dahlias, and swollen seeds of *Pisum sativum* and *Brassica Napus* was little affected by a mixture of 79 per cent carbon monoxid and 21 per cent oxygen. The streaming of the protoplasm in Nitella and in the hairs of various plants, and the ciliary movements of Chlamydomonas and Haematococcus are not affected by several hours' exposure to the gas.—R. C. ROSE.

Permeability.—RUHLAND has already published a paper[25] showing that many dyes highly soluble in lipoids do not enter the protoplasm, while many not soluble in lipoids do. He now offers still more evidence[26] against OVERTON'S lipoid theory of permeability, especially directing attention to the nature of the water solutions formed by the various dyes as shown by the ultramicroscope. He finds that many of the dyes, the water solutions of which are of a colloidal nature, readily enter the protoplasm; methylorange is an example. Others (wollvioletts and erioglaucin), highly soluble in lipoids and forming true solutions in water, do not enter protoplasm.

RUHLAND also offers evidence[27] against the NATHANSOHN and MEURER'S ion permeability hypothesis, which holds that in the exchange of electrolytes between cells and a bathing solution, an electro-chemical balance is maintained. He points out that OSTWALD'S hypothesis, with which this agrees, has long since become untenable from the physical standpoint. He also believes that the large amount of Ca^{++} and Mg^{++} given off in NATHANSOHN'S experiments in

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[24] SEELÄNDER, KARL, Untersuchungen über die Wirkung des Kohlenoxyds auf Pflanzen. Beih. Bot. Centralbl. **24**^{1}:357–393. 1909.

[25] Rev. BOT. GAZETTE **47**:342. 1909.

[26] RUHLAND, W., Die Bedeutung der Kolloidalnatur wasseriger Farnstofflosung für ihr Eindringen in lebende Zellen. Ber. Deutsch. Bot. Gesell. **26**:772–782. 1909.

[27] ———, Zur Frage der Ionenpermeabilität. Zeit. für Bot. **1**:747–762. 1909.

balance with the Na^+ and K^+ taken up was due to the toxic conditions of the experiments. He ends by saying that NATHANSOHN'S methods are not at all reliable for permeability measurements, and that they cannot be taken as the basis of any explanation of the regulatory permeability of the *Plasmahaut*.—WILLIAM CROCKER.

Fossil woods of Germany.—GOTHAN[28] has described two fossil woods occurring in the brown coals at Senftenberg, from the Lower Miocene. One is a Cupressinoxylon type, *Taxodioxylon sequoianum* Gothan, the structure corresponding to that of *Sequoia sempervirens*. The Cupressinoxylon type of wood in this locality, as in general, is the form most abundantly represented in the brown coals of the Miocene as well as in the Oligocene. The reference of this wood to *Sequoia sempervirens*, or to a closely related species, is in accordance with reports by WEBER, according to whom leaf impressions in beds of similar age at Bonn all belong to *Sequoia Langsdorfii*. The second wood described is that of a new species of pine, *Pinus parryoides*. Although woods of the Abietineae are not nearly so abundant in the brown coals of this horizon as are those of Taxodioxylon structure, they are not rare, and always belong to the group with resin ducts. The epithelium cell walls of the resin ducts of the new pine are provided with pores like those of Picea and Larix, a character not found in any of the recent pines. The question as to its true position is considered at some length, the author arriving at the conclusion that it is the wood of a true Pinus, the character at variance having been lost in recent forms, and that it should be placed in either §PARRYA or §BALFOURIA. Representatives of either of these sections are found only in western North America and eastern Asia.—REINHARDT THIESSEN.

Morphology of Juniperus.—NICHOLS[29] has made a detailed study of the morphology of the American variety (*depressa*) of *Juniperus communis*, obtaining his material from three seasons of collecting near New Haven, Conn. Naturally it is largely confirmatory of the work of NORÉN, SLUDSKY, and Miss OTTLEY, but is especially interesting in its establishment of the time intervals. The staminate strobilus begins to develop during the summer of the year preceding pollination, the mother cells enter into the synapsis stage about May 1, and there is a period of about twelve and one-half months between pollination (May 25) and fertilization. The ovulate strobili begin to appear a few weeks before pollination, the megaspore tetrad is formed late in April, and the female gametophyte develops in about six weeks. The body cell and the central cell divide about three days before fertilization, so that at fusion the egg and sperm are not more than three days old. Some of the more interesting details are as follows: the wall of the microsporangium

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[28] GOTHAN, W., Ueber Braunkohlenhölzer des rheinischen Tertaers. Jahrb. König. Preuss. Geol. Landesanstalt **30**:516–532. 1909.

[29] NICHOLS, GEORGE E., A morphological study of *Juniperus communis* var. *depressa*. Beih. Bot. Centralbl. **25**:201–241. *pls. 8–17. figs. 4.* 1910.

is two-layered (overlaid by the epidermis), the inner layer differentiating as the tapetum; the stalk cell is represented only by a nucleus; the two male cells are equal, and occasionally three or four male cells derived from a single body cell were observed; four to ten archegonia are included in the single complex; the fusion nucleus becomes invested by the starch-filled cytoplasm of the male cell; at the first segmentation the male and female chromatin groups are still distinct.—J. M. C.

Respiration.—CZAPEK[30] gives an excellent summary of all work done on respiration of plants up to the present time. It is marked by conciseness and by emphasis on important points. One is surprised that the subject can be treated so thoroughly within the limits of twenty-five pages. The following topics are considered: definition and history, the amount and distribution of aerobic respiration in plants, physical and chemical factors capable of influencing respiration, postmortem carbon dioxid production and oxygen absorption, chemical materials of aerobic respiration, and the mechanism of vital oxidation (statement of our knowledge of respiratory enzymes). The literature considered involves 126 citations.

In discussing the materials used (oxidized) in aerobic respiration, CZAPEK mentions sugars and fats as the principal ones; but emphasizes the fact that in many bacteria (hydrogen, sulfur, nitrifying, etc.) the simplest inorganic substances are oxidized as a source of energy for carrying on life processes, while in many other cases the most complex proteins are split and finally oxidized for the same purpose. It is evident that this gives aerobic respiration a broad meaning. CZAPEK seems very much inclined to distinguish vital oxidations (*vitalen Verbrennungsprozess*) from other oxidations. Vital seems to mean more to him than merely a term to express the unknown.—WILLIAM CROCKER.

The fertile spike of Ophioglossaceae.—The nature of the so-called fertile spike of the Ophioglossaceae has been a prolific cause of discussion, culminating in the divergent views of BOWER and CAMPBELL. CHRYSLER[31] has now attacked the problem from the standpoint of vascular anatomy, examining all the genera, and has reached some important and apparently convincing conclusions.

The fertile spike is regarded as representing two fused leaflets or pinnae (basal pair) of a fern leaf. The proof is most obvious in *Botrychium virginianum*, in which each one of the pair of vascular bundles that supply the fertile spike leaves a gap in the trough-shaped leaf trace. This is sometimes less distinct in *B. ternatum* and *B. obliquum*, and certain other species show no trace of the gap; all of which are taken as indications of reduction. Abnormal specimens also confirm the view. The condition in Ophioglossum is considered to be derived

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[30] CZAPEK, FR., Die Atmung der Pflanzen. Ergebnisse der Physiologie **9**:587–613. 1910.

[31] CHRYSLER, M. A., The nature of the fertile spike in the Ophioglossaceae. Annals of Botany **24**:1–18. *pls. 1, 2. figs. 16.* 1910.

from that found in Botrychium; while in Helminthostachys the fertile spike is interpreted as representing a single pinna. This would dispose of the sporangiophore nature of the spike, and revert to ROEPER'S view (in 1826) that it represents two fused basal pinnae.

The general conclusion is that the Ophioglossaceae are related to the ferns, and "have sprung from near the level of the Osmundaceae."—J. M. C.

The strobilus of Selaginella.—Miss GERTRUDE MITCHELL[32] has recorded some general studies of the strobilus of Selaginella, which fill up certain gaps in our knowledge, and "confirm or controvert statements" of other investigators.

In some species the axis was observed to renew its ordinary vegetative character beyond the strobilus: in one case abortive sporangia were produced in the axils of the foliage leaves just beyond the tip of the strobilus; in another species a second strobilus was produced upon such an axis, the two strobili being separated by a sterile region; and in still another case a branched strobilus was noted. The distribution of sporangia is variable, and species are enumerated under the following heads; one large basal megasporangium, several basal megasporangia succeeded by microsporangia, strobili wholly megasporangiate or microsporangiate, and an indiscriminate arrangement. The species are also enumerated that mature one, two, or three megaspores, instead of the more usual four, and also two rare cases in which there are twelve (*S. Vogelii*) and eight (*S. involvens*) megaspores. Considerable attention is given to the sporangium wall and its mechanism for dehiscence, involving what are spoken of as "its wonderful adaptations for cross-fertilization." The paper closes with a brief consideration of the vascular anatomy of the strobilus and the ligule.—J. M. C.

The stele of Osmunda.—The vascular anatomy of this genus has given rise to much discussion and to divergent opinions as to its phylogenetic significance. FAULL[33] has now investigated abundant material of the sporelings of *O. cinnamomea* in all stages, and has reached the following results and conclusions: The cortical cells at the base of the sporeling are inhabited by a fungus. While there is considerable variation in the development of different individuals, in no case is the transition from protostele to siphonostele effected by a simple expansion, as has been claimed for Osmundaceae. There are bays or gaps in the xylem near the nodes, which may result in inclosing a "stelar" pith. Rarely and only in adult stems does the internal endodermis and "extrastelar" pith connect with the external endodermis and cortex through leaf gaps. Internal phloem has been found in unbranched adult plants, and this fact, together with the absence of branching in the sporeling, is thought to indicate that internal phloem and

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[32] MITCHELL, GERTRUDE, Contributions towards a knowledge of the anatomy of the genus *Selaginella* Spr. Part V. The strobilus. Annals of Botany **24**:19–34. *pls. 3, 4.* 1910.

[33] FAULL, J. H., The stele of *Osmunda cinnamomea.* Trans. Canadian Inst. **8**:515–534. *pls. 4–6.* 1909.

internal endodermis in this family have not "intruded" through branch gaps. The general conclusion is that the stele of the existing Osmundaceae is a "reduced amphiphloic siphonostele," and that it is consistent with JEFFREY's theory of the origin of the siphonostele and the homology of the pith.—J. M. C.

Morphology of Laminaria.—A knowledge of the reproduction of Laminaria has long been a desideratum, and this has now been supplied to some extent by DREW,[34] who has succeeded in making cultures according to methods he describes. He has concluded that the "sporangia" described as imbedded in the reproductive areas are in reality gametangia. These gametangia produce gametes (heretofore thought to be zoospores) which conjugate and produce zygospores. The zygospores give rise to a chain or mass of cells which may represent the $2x$ generation; and this in turn gives rise to the Laminaria plant, which represents the x generation. The x and $2x$ conditions are inferences, as no cytological work was done; and the direct outgrowth of the young Laminaria plants from the "chain or mass of cells" would hardly suggest an intervening reduction division. However, the discovery that the reproductive areas consist of gametangia and paraphyses is of sufficient interest. The gametes when liberated seem to have no cilia, but soon develop them. The cells of the structure (chain or mass) produced by the zygospore "rupture, and their contents grow out to form the gametophyte." Details are given of the development of the various regions and tissues of the young plant.—J. M. C.

The ecology of Zostera.—OSTENFELD has given an interesting ecological account of *Zostera marina*, as seen in Denmark.[35] The structure and growth of the plant is first treated in detail, following which is an account of the necessary life conditions of the plant and the variations in diverse habitats. While Zostera requires salinity, it thrives where the percentage of salt is high (3.3 per cent), and also where it is very low (0.6 per cent). It occurs only in relatively quiet waters, and grows at greater depths in clear than in muddy waters, sometimes living at as great a depth as 11^m where the water is very transparent. The most important factor in determining its luxuriance appears to be the character of the bottom, plants on firm sand having short narrow leaves, whereas plants in mud have long broad leaves (sometimes more than 2^m in length). A detailed account of the distribution of Zostera in Danish waters is followed by a discussion of the Zostera vegetation as a habitat; many plants and animals live where a Zostera vegetation has become established, the plants themselves often being covered with many forms. Other flowering plants that grow with Zostera are briefly described.—H. C. COWLES.

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[34] DREW, G. HAROLD, The reproduction and early development of *Laminaria digitata* and *Laminaria saccharina*. Annals of Botany **24**:177–190. *pls. 14, 15.* 1910.

[35] OSTENFELD, C. H., On the ecology and distribution of the grass-wrack (*Zostera marina*) in Danish waters. From Report Danish Biological Station. pp. 62. *figs. 9.* Copenhagen. 1908.

Seedlings of Cactaceae.—Among the Cactaceae certain members, including the genus Pereskia, have a seedling with two fairly thin cotyledons and a slender hypocotyl; while others, as Mamillaria, have minute cotyledons and a globular hypocotyl. Miss DeFraine[36] finds that the mode of transition from stem structure to root structure in these two groups is different; in other words, the adaptations to environment shown by the adult plants has spread to the seedlings, and has also had an effect on the internal structure. Since some species show a pair of bundles in the hypocotyl, a comparison is instituted with the liliaceous genus Anemarrhena, in which the same condition appears. The presence of the double bundle in the cotyledon of this genus has been used by Miss Sargant as the basis of her argument for the derivation of monocotyledons from dicotyledons by fusion of the two cotyledons, but Miss DeFraine finds the origin of the double strand in the Cactaceae so various that she considers the validity of the argument to be seriously weakened. A number of interesting points of detail are recorded in the paper, supplementing the work of Ganong[37] on the cactus family. —M. A. Chrysler.

Foliar gaps of Osmundaceae.—Jeffrey's Pteropsida are characterized by the presence of leaf gaps, but it has been urged by some recent investigators (notably Kidston and Gwynne-Vaughan) that they are absent frequently in the Osmundaceae. Sinnott[38] has undertaken to investigate this group, and concludes that leaf gaps are always present. In the six living species studied a number of cases of mature stems were observed in which the gap did not become complete for some time after the departure of the leaf trace, "which thus at first seemed to go off in a gapless manner." All of the known fossil Osmundaceae with true parenchymatous pith show leaf gaps, with one exception, and this is explained as "a form with very short and narrow gaps, which have been largely obliterated in the process of fossilization." In all the young plants investigated, leaf gaps were evident from the earliest stages. Putting together the testimony from fossil and living forms, and also the juvenile and mature stages of the latter, the conclusion is reached that the presence of leaf gaps is a primitive feature of the Osmundaceae, and that they are placed properly among the Pteropsida.—J. M. C.

Embryo of Pinus Pinaster.—Saxton[39] has studied the development of the embryo of this species as it grows in Cape Colony. The general results are as

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[36] DeFraine, E., The seedling structure of certain Cactaceae. Annals of Botany **24**:125–175. 1910.

[37] Ganong, W. F., Contributions to a knowledge of the morphology and ecology of the Cactaceae. Annals of Botany **12**:423–472. *pl. 26.* 1898.

[38] Sinnott, Edmund W., Foliar gaps in the Osmundaceae. Annals of Botany **24**:107–118. *pls. 11, 12.* 1910.

[39] Saxton, W. T., The development of the embryo in *Pinus Pinaster* Soland., with some notes on the life history of the species in Cape Colony. S. African Jour. Sci. **6**:52–59. *pl. 2.* 1909.

follows: the embryo does not penetrate the endosperm mechanically, by means of the elongating suspensor, but probably by the secretion of an enzyme; it grows for a time by means of a true apical cell, which later is replaced by a group of initials; after this, the most active growth is at the proximal end of the embryo, the first differentiation being the root periblem, the cotyledons and stem tip appearing later. It is an interesting fact that the species produces only two archegonia.

The seasonal differences between Cape Colony and the northern hemisphere in reference to the development of structures are very interesting. Pollination occurs during the winter; the ovule is in the resting stage during the late summer and autumn; pollination and fertilization are separated by 14–15 months (12–13 in England, etc.); the archegonia mature more slowly, the central cell persisting for at least three weeks (as compared with one or two weeks).—J. M. C.

Capsella Bursa-pastoris and C. Heegeri.—The relation of *Capsella Heegeri*, discovered growing wild in Germany ten years ago, to the cosmopolitan *C. Bursa-pastoris* has been in question. Its appearance in a region whose plants are so well known suggested its recent origin by mutation, and in that case the parent plant should be *C. Bursa-pastoris*. SHULL[40] conducted a series of cultures and reported the results at the Boston Meeting of the International Zoological Congress in 1907, and the report has just now appeared as an advance print from the Proceedings! The matter is old, but this publication of it may be noted. The results showed that *C. Heegeri* has the same Mendelian units in its leaves as occur in *C. Bursa-pastoris;* that the crossing of the two species gives rise to corresponding series of elementary species; that leaf characters are inherited in strict Mendelian ratios, but the capsule shows a very great departure; and that the capacity of *C. Heegeri* for self-maintenance in competition with *C. Bursa-pastoris* rests upon the comparative infrequency of cross-fertilization.—J. M. C.

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[40] SHULL, GEORGE H., Results of crossing of *Bursa bursa-pastoris* and *Bursa Heegeri*. Advance print from Proc. 7th Internat. Zool. Congress. pp. 6. 1910.

GENERAL INDEX

Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.


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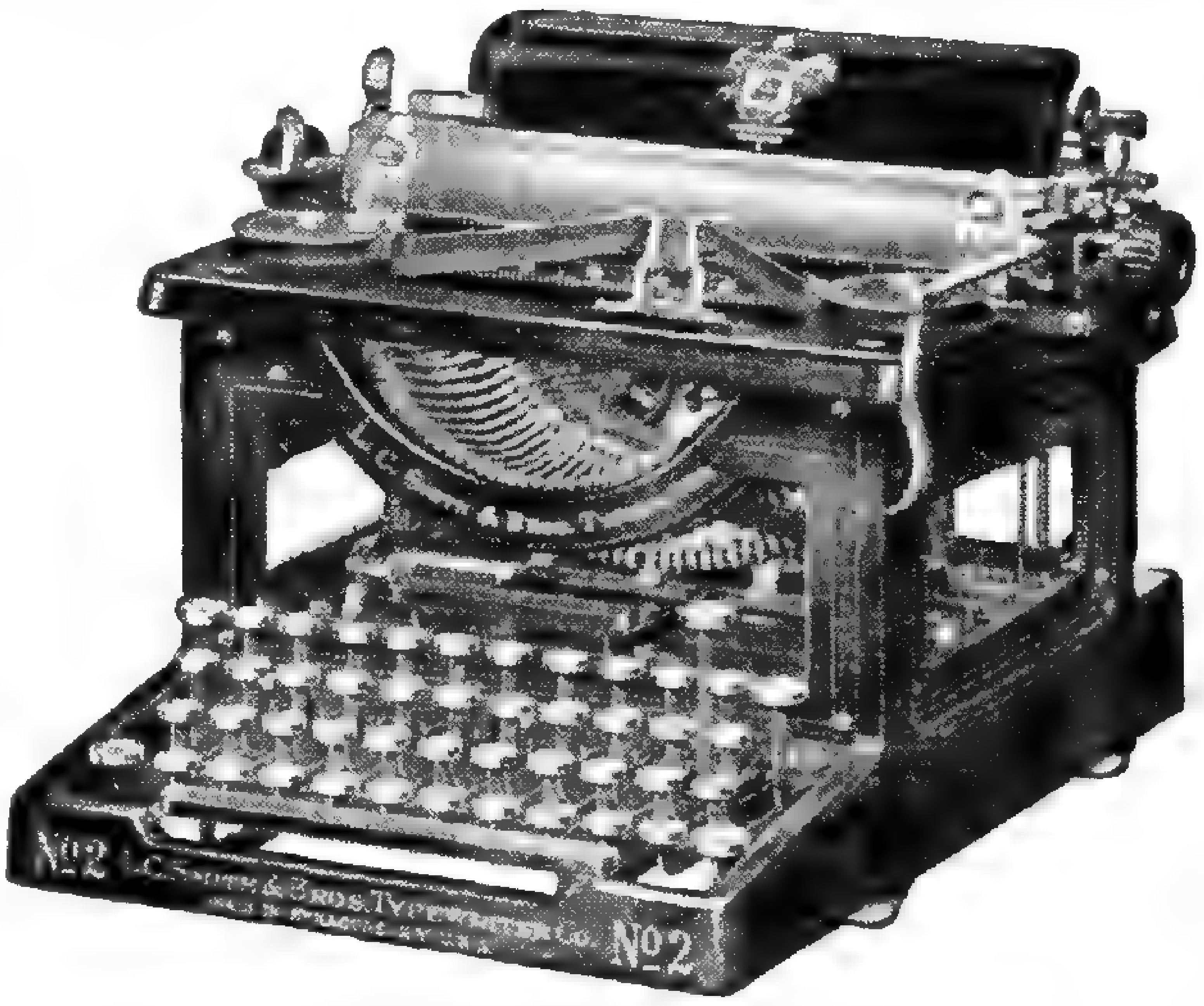
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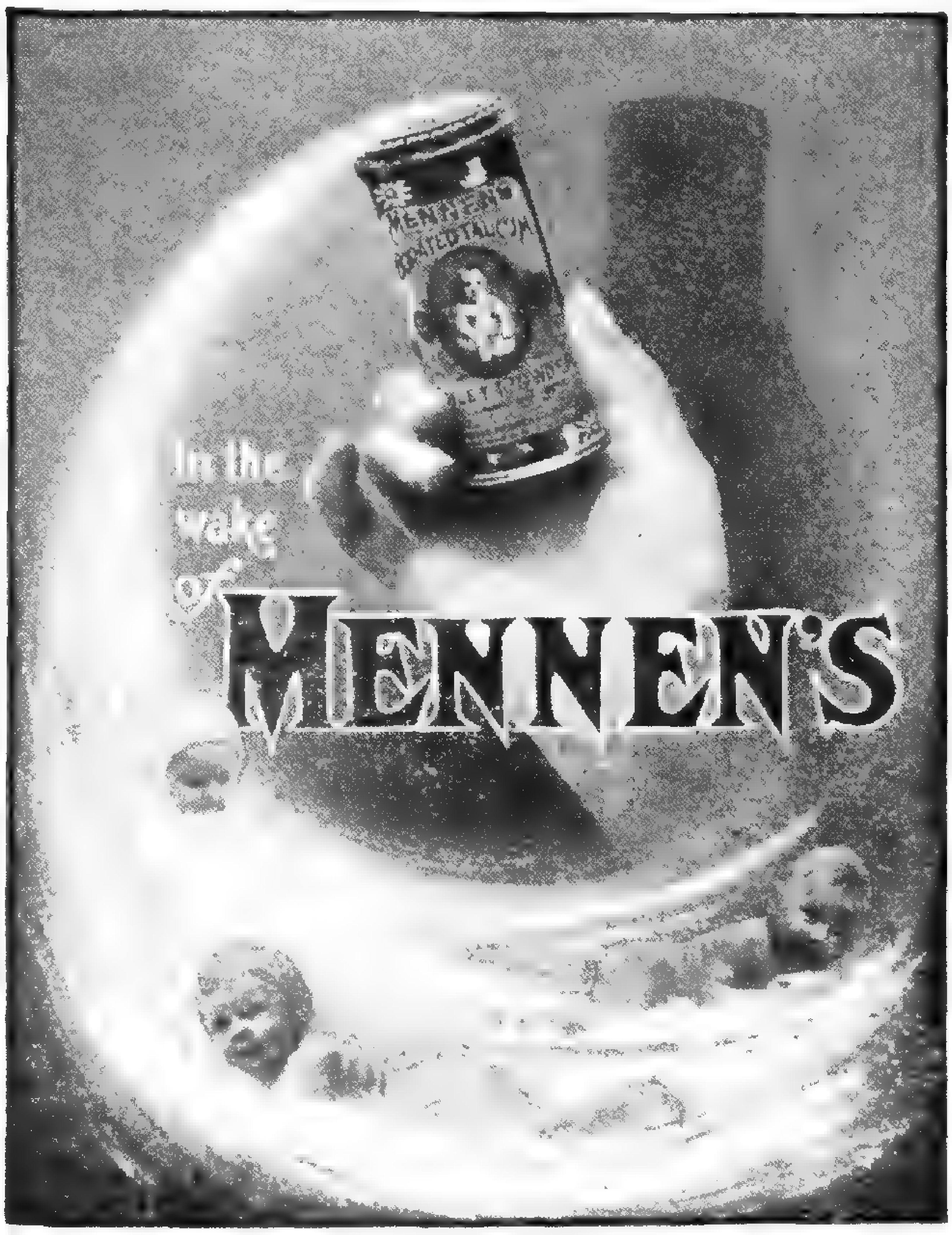
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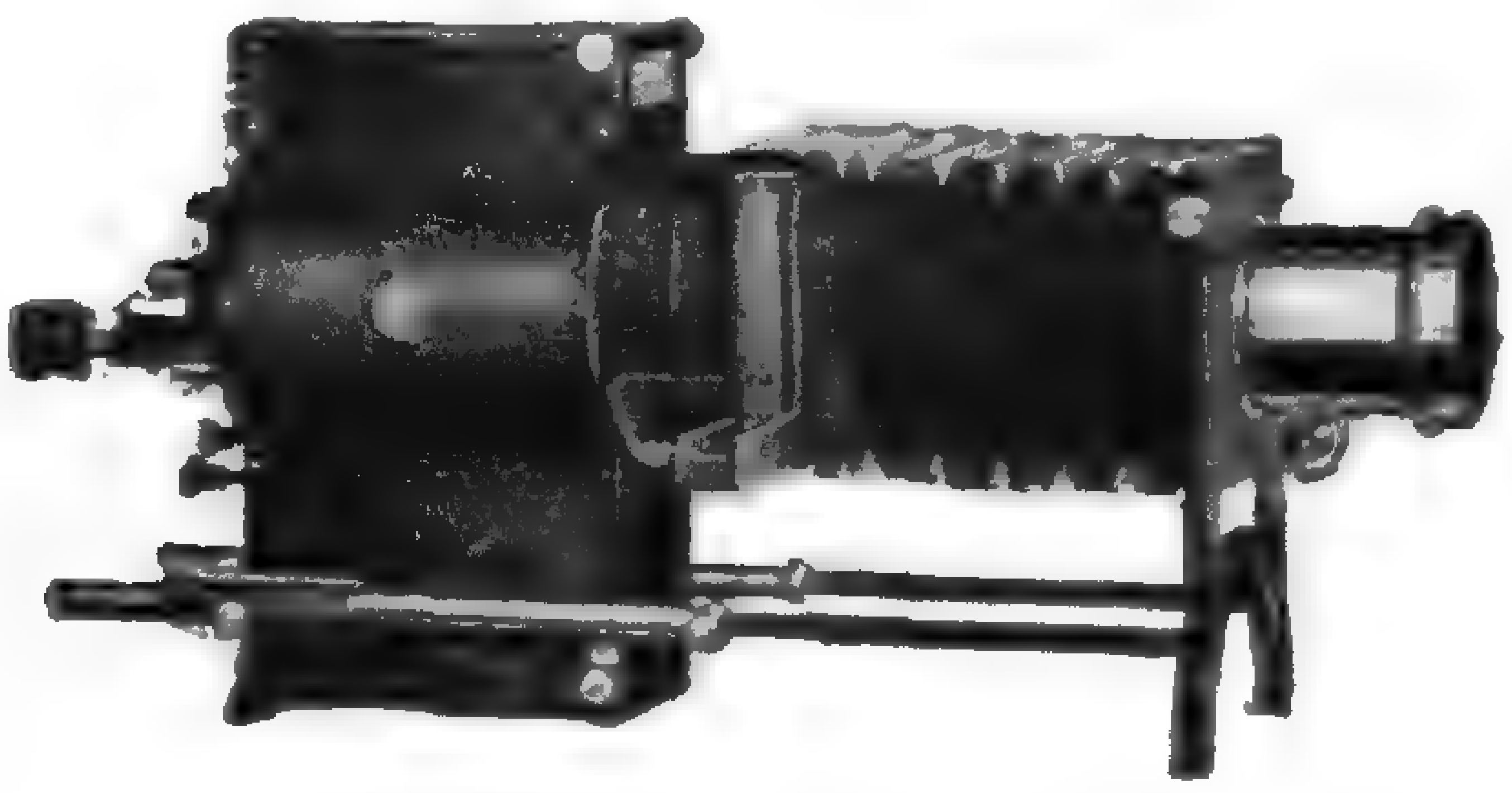

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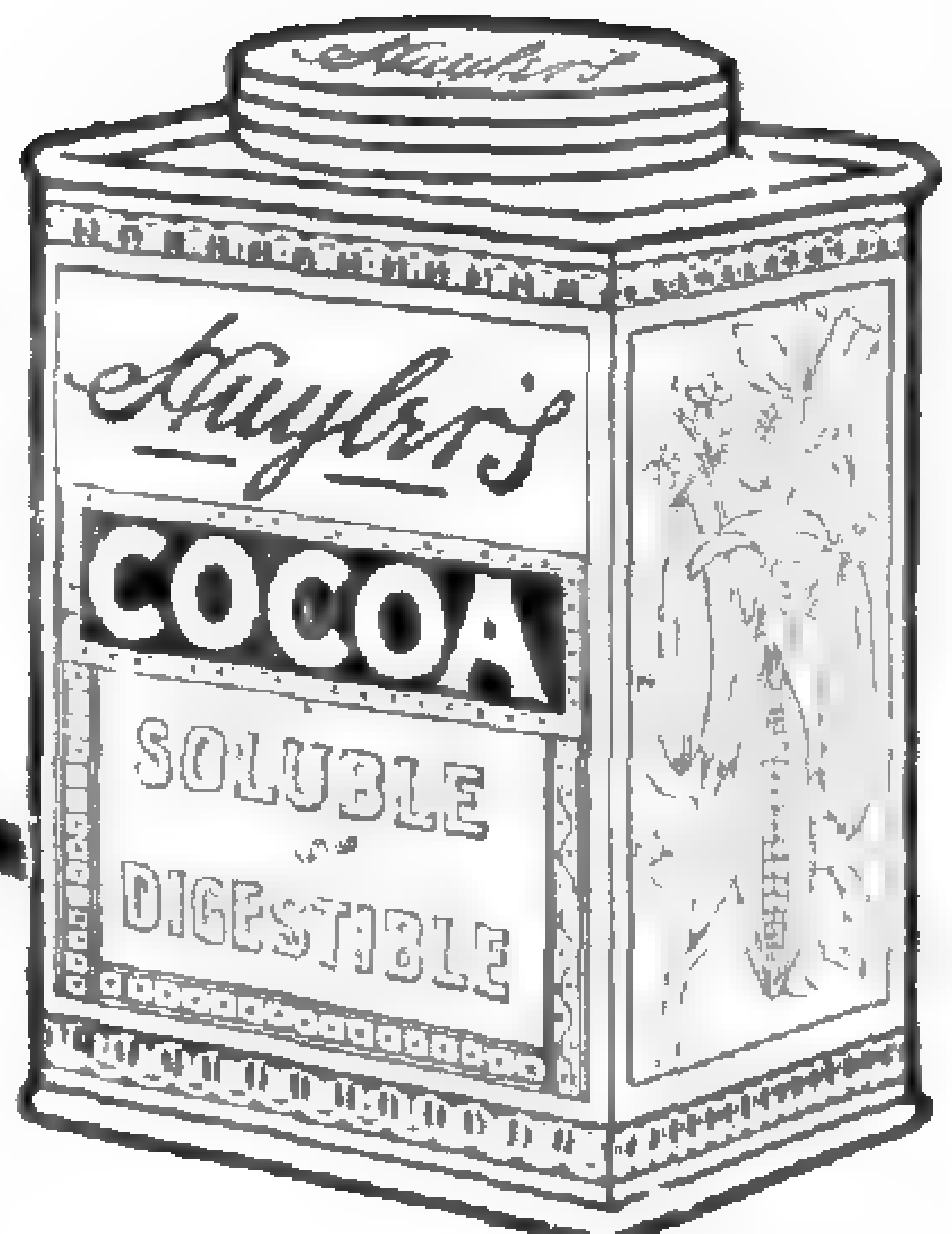

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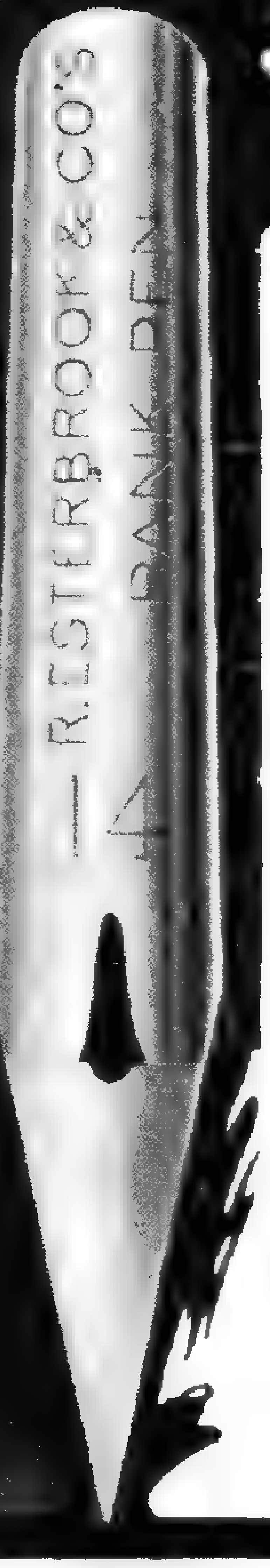

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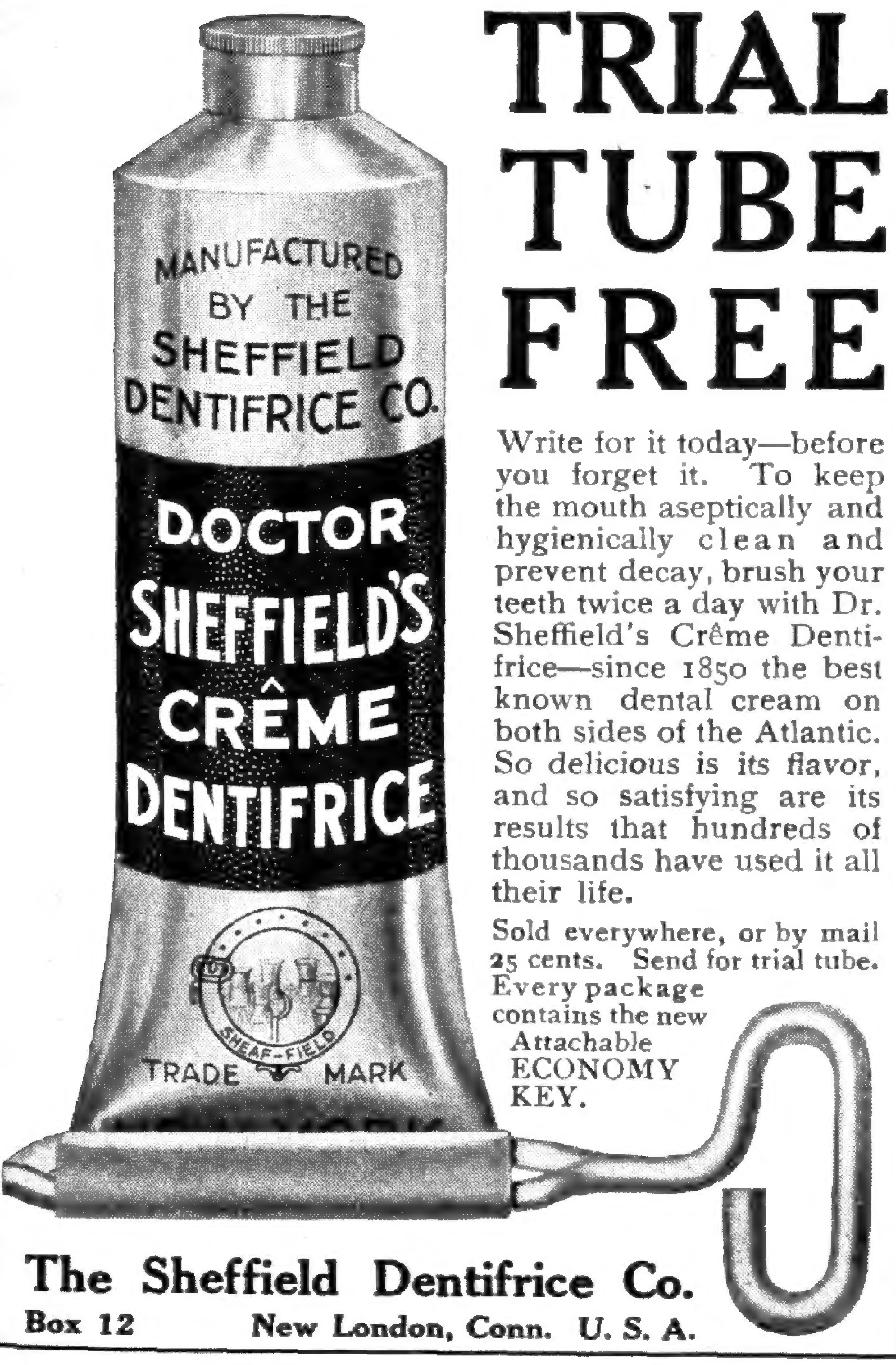
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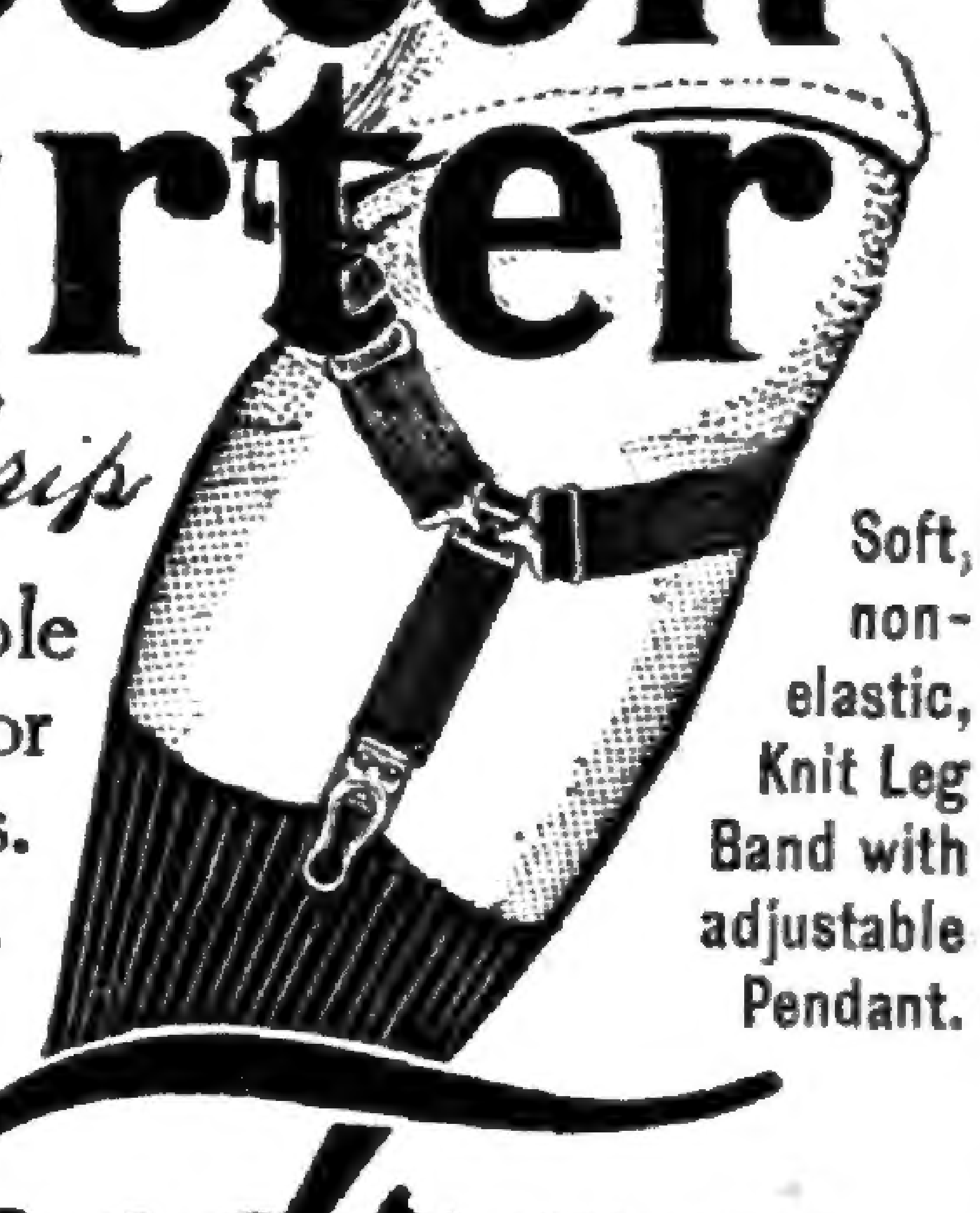
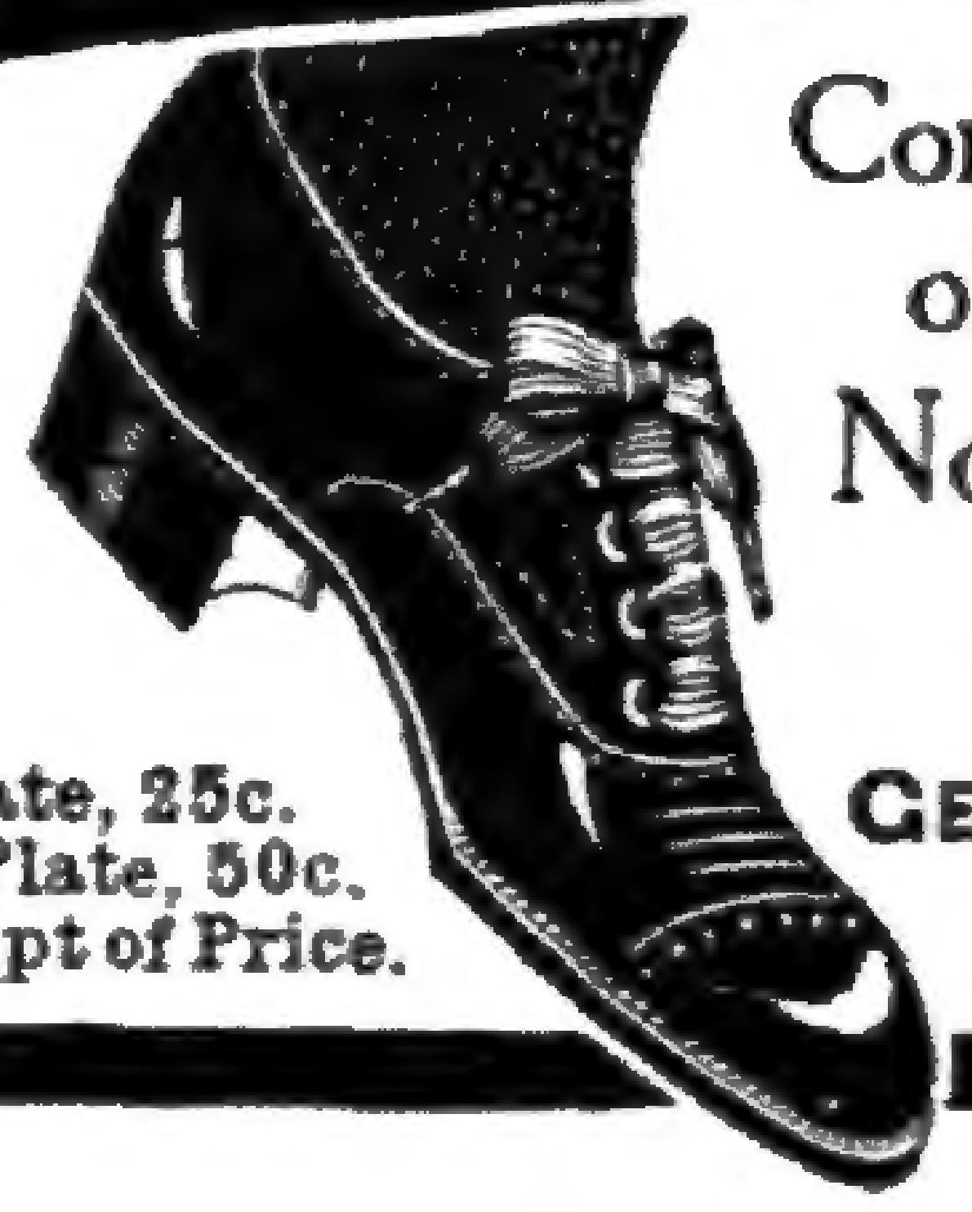

Velvet Grip

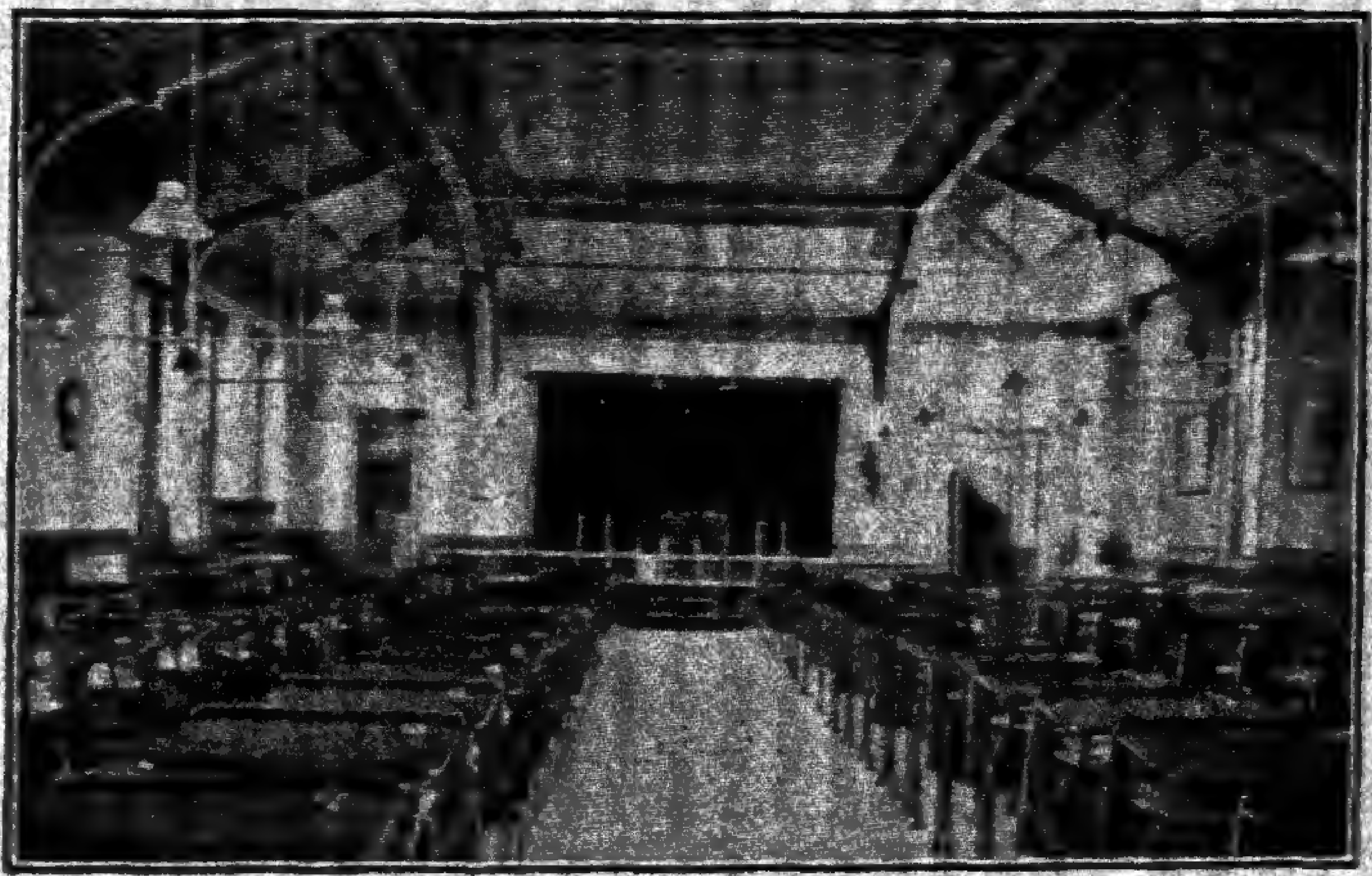


Why Contagious Diseases Are So Quickly Transmitted in Schoolrooms.

A SURE METHOD OF PREVENTION

THE time is not far distant when action will be taken by the Boards of Health in every city, town and village of this country, to *compel* the elimination of the dust in schoolrooms by proper care of the floors.

Educators are rapidly coming to a realization of the fact that "dust" is the principal cause of disease transmission among school children. The floors in schoolrooms are bare, and when large numbers of pupils are assembled the constant motion of feet produces a continuous circulation of dust. These dust particles are composed of vegetable, animal, and mineral material finely pulverized. From tests made with dust collected from schoolrooms and other places of public assembly, it has been found that with the dust were uncountable myriads of disease germs—bacilli of Tuberculosis, Typhoid Fever, Diptheria, Pneumonia and other dangerous diseases. These experiments afford irrefutable proof of the dangers arising from dust and explain why contagious diseases are so quickly transmitted in schoolrooms.



To do away with this menace—to avoid the dangers of dust poisoning, it is not only necessary to provide a system of ample ventilation, but also to *treat the wood floors* in such a way that dust and germs cannot pollute the atmosphere.

Standard Floor Dressing has proved itself a perfectly satisfactory dust-preventive. By keeping the floors at a proper degree of moisture the dressing catches and *holds* every particle of dust and every germ coming in contact with it. Tests have been conducted to determine the quantity of dust and number of organisms which would settle on a given surface. Results prove that the dust from floors treated with Standard Floor Dressing is twelve times greater in weight than that collected from *untreated* floors. The inference is obvious—the balance of disease-laden dust in the rooms with *untreated* floors *was circulating through the air*, because even after settling on the floor every current of air would disturb it and start it afloat again. Another test proved that dust once settled upon a floor treated with Standard Floor Dressing remained there, and a bacteriological examination demonstrated that 97½% of all the disease germs caught with the dust were destroyed outright.

Such tangible proofs should convince anyone that Standard Floor Dressing is invaluable for use in schools as a *preventive* of disease.

In addition to its germicidal properties, Standard Floor Dressing does splendid work in keeping the floors themselves in a state of excellent preservation. It prevents the wood from splintering and cracking and renders sweeping and caretaking a comparatively easy task.

While Standard Floor Dressing is not intended for use *in the home*, it *is* intended for use in schools, hospitals, sanitariums, stores, and public buildings of every description.

It is sold in convenient form by dealers in every locality, and may be had in full barrels, half-barrels, one gallon, and five gallon cans.

Three or four treatments a year give best results, and when spread with the patent *Standard Oiler* may be used very economically. The Oiler distributes just the right amount to every part of the floor, and as the dressing does not evaporate, one application will last for several months.

Standard Floor Dressing is now being used with remarkable success in thousands of schools, colleges, stores, and public buildings, and we have yet to hear of an instance where the dressing has failed to reduce the circulating dust and kill the floating disease germs. All we ask is an opportunity to *prove* the merits of Standard Floor Dressing.

In order to convince those who may be skeptical, and those who are really interested, we are making an extraordinary offer. Select one room or corridor in any public building under your supervision and we will dress the floor with Standard Floor Dressing AT OUR OWN EXPENSE—the test will not cost you one cent.

To localities far removed from our agencies, we will send free sample with full directions for applying.

Correspondence is desired with those responsible for the care of schools and public buildings. Our book, "Dust and Its Dangers," with testimonials and reports is sent free on request.

STANDARD OIL COMPANY
(Incorporated)

Platt's