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# ANNALS OF BOTANY

VOL. XVII

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# ANNALS OF BOTANY

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*ASSISTED BY OTHER BOTANISTS*

VOLUME XVII

With Forty Plates and thirty-two Figures in the Text

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# A Theory of the Origin of Monocotyledons, founded on the Structure of their Seedlings.

BY

ETHEL SARGANT.



With Plates I-VII and ten Figures in the Text.



WHEN some years ago I was working out the anatomical structure of the seedlings of *Arum maculatum* in collaboration with Mrs. Scott (36), we examined the seedlings of some other Aroids, and compared them with two species of *Lilium* seedlings. The anatomy of seedling Monocotyledons has received but little attention from botanists, and Dr. D. H. Scott suggested that I should pursue the subject by making a comparative study of those already collected by him from the material at Kew, and preserved for future investigation. I have to thank him not only for the start then made, but for his unflinching interest in the work as it developed, and for constant help in obtaining fresh supplies of material. The object proposed from the first was to throw light, if possible, on the relationship between Monocotyledons and Dicotyledons.

After some months of work in my own laboratory on the Kew material, I found it desirable to modify and extend the original scheme. The vascular system of the cotyledon, hypocotyl, and primary root appeared in the specimens I examined to be characteristic of the species. One of my

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early observations—the comparison of a seedling *Anthurium* with seedlings of *Arum* and *Lilium*—had suggested that this symmetry might furnish a new systematic character of some importance. The systematic value of any unproven character can be determined only by the careful comparative study of allied forms, and I therefore determined to confine my observations to a single family, and to work that out as fully as possible. With this object I began a careful study of seedlings belonging to the order Liliaceae.

The collection of material with all the help which Kew could give, and aided by the kindness of botanists in many countries, has been a laborious task. Seedlings have been raised from seed collected in my own garden, where I have cultivated a large collection of Liliaceous plants. I have also received seed from many sources, and I wish here to thank the Director of Kew Gardens and his Staff for their kindness in furnishing me with seedlings and seeds, and in naming the specimens which I have myself cultivated. My thanks are also due to those botanists who have sent me seeds, and in particular to Mr. Thomas Hanbury, of La Mortola, Professor S. Ikeno, of Tokyo, Mr. W. R. Guilfoyle, of Melbourne, Dr. J. H. Wilson, of St. Andrews, Mr. J. H. Maiden, of Sydney, Dr. K. Reiche, in Chili, Professor D. H. Campbell, and my neighbour, Mr. A. J. Crosfield. I have succeeded in preserving seedlings belonging to 125 species from sixty genera within the Liliaceae, and over sixty species of other Monocotyledons. The collection of Liliaceous seedlings is fairly representative of northern genera: it is weak in species from the southern hemisphere, and I am particularly in want of more forms endemic to Australia and Chili.

The examination of this material is very far from complete. I have thoroughly worked out and made notes on some sixty species from the Liliaceae, and I have sections from about twenty-five species belonging to other monocotyledonous families. During a great part of the time employed in preparing sections and indexing them, as well as in drawing and registering the material, I have been admirably assisted



by Miss E. N. Thomas. Most of the figures illustrating this paper have been drawn by Miss Agnes Robertson, who has also assisted me in many ways during the preparation of it.

#### NATURE OF THE EVIDENCE.

The examination of forms within the Liliaceae has convinced me that some vascular characters of the young seedling have real systematic value. At an age when the plant consists of cotyledon, hypocotyl, and primary root, with an embryonic plumule sheltered by the base of the cotyledon, the vascular system—in species which at that age have differentiated one—does often indicate the relationship of allied genera to each other.

The genera *Anemarrhena*, *Asphodelus*, and *Asphodeline*, for example, are placed together by all systematists, and the vascular structure of their seedlings shows an identical ground-plan, though there are considerable modifications of the type in the two latter genera. So far the embryological evidence simply confirms the conclusions already drawn from the study of the mature characters. But when the unmistakable *Anemarrhena* type of symmetry is discovered in the seedlings of *Galtonia* and *Albuca*, we have an unexpected link between two groups of genera widely separated by systematists.

The instance just quoted is of exceptional interest for reasons already suggested in a preliminary notice, which appeared in the May number of the 'New Phytologist' (35). But it is only a fragment from a considerable body of evidence, which leads to the conclusion that embryological characters of the kind described can be shown to throw light on the inter-relationship of genera within the Liliaceae and allied orders.

Until the monograph I am preparing on the comparative anatomy of seedlings within the Liliaceae is completed, this evidence will not be published in detail. But I hope to give a sufficiently full sketch of it here to justify the publication

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of a theory on the origin of Monocotyledons, founded primarily on the structure of their seedlings, and supported by the comparison of this structure with that of some Ranunculaceous genera in which the cotyledons are more or less completely united.

The argument requires that some weight should be given to the vascular system of the seedling as affording indications of its race-history. This postulate stated, I will briefly sketch the theory I have formed, and indicate the nature of the evidence on which it rests, before proceeding to give the evidence itself in greater detail than was possible in a preliminary notice.

The study of Liliaceous seedlings has led me to the conclusion that the various types of vascular symmetry found within the order can be linked with the type found in *Anemarrhena*, *Albuca*, and *Galtonia*, through more than one series of intermediate forms. I regard the *Anemarrhena* type as primitive, and as the starting-point from which most, if not all, the vascular types characteristic of Liliaceous seedlings have been historically derived.

The cotyledon of *Anemarrhena* contains two massive bundles which together form a tetrarch stele in the primary root. This structure originally suggested to me the possibility of a fusion of two seed-leaves in some remote ancestor to form the single cotyledon of *Anemarrhena*. According to this view each bundle in the hypocotyl represents the trace of one seed-leaf.

The seedlings of certain Dicotyledons possess seed-leaves which are partially united, sometimes by one margin only, but more often by both. In the latter case the united petioles form a tube, which is sometimes of considerable length. Petiolar tubes of this kind are found in several species of *Anemone* and *Delphinium*; in two species at least of *Ranunculus* and one of *Trollius*; in *Aconitum Anthora* and *Eranthis hiemalis*. The authorities for these statements will be found in Part II. Many other genera among the Ranunculaceae have cotyledons which are concrescent at the base. The petiolar tube

of *Podophyllum* from the allied order Berberidaceae is very well developed.

Petiolar tubes are not confined to the Ranunculaceae and their near allies: they are found among the Oxalideae, Cucurbitaceae, Umbelliferae, Primulaceae, Polygonaceae, and probably careful search would discover them among seedlings of other families.

In every case investigated they are accompanied by a thickened or at least much shortened hypocotyl.

The anatomical structure of the petiolar tube and thickened hypocotyl of *Eranthis*, as described by M. Sterckx (38, p. 57), early attracted my attention because it recalled that of *Anemarrhena*. I have therefore studied it in detail.

The long petioles of *Eranthis* cotyledons are united into a narrow cylinder, which is hollow for the greater part of its length. The blades are distinct (Pl. VI, Fig. 1). Throughout the length of this tube the blade of each cotyledon is represented by a single massive trace. These traces are continued downwards through the tuberous hypocotyl into the primary root. The behaviour of the cotyledonary traces in the upper part of the tuber is precisely that of the cotyledonary traces in *Anemarrhena* where they enter the transitional region. This resemblance is maintained throughout the transition, until—near the base of the tuber—the four phloëm groups of *Eranthis* unite in pairs to form two groups, instead of remaining distinct. The four protoxylem groups, however, can be observed for some time after the xylem plate is formed (Pl. VII, Figs. 1 and 3): in the end the two which are opposite the phloëm groups disappear, leaving a diarch root-stele (Pl. VII, Fig. 2).

The anatomical resemblance between the seedlings of *Eranthis* and those of *Anemarrhena* cannot be mistaken when the features just described are represented in diagrams. Its theoretical importance, however, has been denied by Mr. Tansley (40).

Three views are possible. The resemblance may be considered as accidental: as the result of inheritance from a



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common ancestor: or as the response of two unrelated forms to similar conditions.

The formation of a tetrarch root-stele from two cotyledonary traces is not common among Monocotyledons. It is, I believe, unknown among Dicotyledons. The indications of such a tetrarch formation in *Eranthis* are to my mind very clear—I cannot dismiss them as accidental. This consideration leads me to believe in a real genetic connexion between *Eranthis* and *Anemarrhena*: that they are descended from a common ancestor with two distinct seed-leaves, each represented by a single trace in the hypocotyl. If we suppose that this is in its turn descended from a form in which two traces enter the hypocotyl from each cotyledon, the tetrarch root will no longer present any difficulty.

But even if there be no historical connexion between these genera, the structure of *Eranthis* may nevertheless illustrate the double origin of the *Anemarrhena* cotyledon. For without the analogy of *Eranthis* the assumption that each trace in the cotyledon of *Anemarrhena* represented a distinct seed-leaf was groundless. Not only was direct evidence of such a double origin absent, but there was nothing to show that the union of two cotyledons, if it did take place, would actually give rise to such a type of vascular symmetry. To settle the matter by experiment was out of the question. But in *Eranthis* the cotyledons are partially united, and the vascular symmetry bears a very close resemblance to that of *Anemarrhena*. If there is no common stock from which both forms are derived, *Eranthis* may be considered as a genus in which Nature has partly repeated the experiment which she concluded in *Anemarrhena*, and with a similar result as regards the vascular system.

This is the line of argument on which my theory is based, and it remains now to give a fairly full abstract of the evidence which supports it. I propose to do so under two heads.

In the first place I shall describe the chief types of vascular symmetry which have so far been found within the Liliaceae,

and the intermediate forms which have led me to derive them from the *Anemarrhena* type. These facts will, I hope, go far to justify the preliminary assumption that the vascular symmetry of the seedling affords a new systematic character, which—at least among the Liliaceae—is often of value in indicating the historical connexion between genera. While on this subject I shall also describe more briefly some monocotyledonous seedlings outside the Liliaceae, and in particular those whose structure connects the group to which they belong with that family.

In the second place, I intend to describe in detail the first-year seedling of *Eranthis hiemalis*, comparing its vascular structure with that of *Nigella damascena*, already well known through the descriptions of MM. Gérard, Dangeard, and Sterckx. From the other Ranunculaceous species which possess cotyledonary tubes, I have examined and shall shortly describe *Anemone coronaria* and a species of *Delphinium*, and for comparison with these exceptional forms I have chosen four species with distinct cotyledons from the same family. In conclusion, the seedling of *Ranunculus Ficaria* will be fully described as a type in which the cotyledons are partly united by one margin only.

These two chapters will complete the account of the evidence on which my theory is based. This evidence is obviously incomplete. The theory itself cannot be considered as proved in any sense. It is brought forward as a working hypothesis which I have found in practice to be suggestive and illuminating. But a theory of the origin of the monocotyledonous cotyledon is in fact a theory of the origin of Monocotyledons themselves, and therefore to the two chapters which contain my own observations on the comparative anatomy of seedlings I shall add a third dealing with the theoretical aspect of the subject. In this I shall try to show that the same habit of life which leads to the partial union of some dicotyledonous seed-leaves may in the past have produced one or more distinct races with seed-leaves so completely united that they appear to form a single member.



Whether the Monocotyledons as we know them now are descended from one such race, or have branched off in this way at several distinct periods and from different dicotyledonous stocks, must remain an open question for the present.

## OBSERVATIONS ON THE ANATOMY OF SEEDLINGS.

### PART I. MONOCOTYLEDONS.

#### A. Liliaceae.

The species cut and completely examined from this family amount to sixty, representing thirty-five genera. Of these, forty-five species, representing twenty-six genera, belong to the four central tribes: Asphodeleae, Allieae, Scilleae, Tulipeae.

Three complete series of sections from the transitional regions of three seedlings, differing somewhat in age, have been examined and kept for reference before the final notes on any species were compiled. Where the first seedlings cut have shown considerable diversity of structure, more specimens have been examined: in some cases details of seven, eight, or nine seedlings are included in the notes.

The series of sections have always been followed from the cotyledon downwards through the hypocotyl into the primary root. This I have found in practice more convenient than working upwards from root to stem. But the lignification of the traces is usually at its maximum about the middle of the transitional region, and in general proceeds upwards and downwards from that level.

Many observers have remarked that the limits of the hypocotyl differ according as they are defined by external or internal characters. In this paper I am concerned chiefly with the internal anatomy of the seedling, and I therefore define the upper limit of the hypocotyl by the insertion of the plumular traces on those of the cotyledon, and its lower limit by the formation of a stele with complete root-characters.

This region is commonly very short in Monocotyledons. In bulbous or tuberous species it rarely exceeds .5 mm., and in many cases can hardly be said to exist except by a sort of legal fiction. Even in herbaceous and arborescent species the hypocotyl as defined above rarely attains a length of 3 mm.

The symmetry of the root-stele is sometimes determined by the cotyledonary traces only: sometimes by cotyledonary and plumular traces together: and in a few exceptional cases it appears to depend on the plumular traces only (*Aloineae*, *Bulbine*, *Tamus*). The systematic indications are most constant in the first case: that is, when the cotyledonary traces only are continued into the primary root, and its symmetry is unaffected by the insertion of the plumular traces. I have learnt to look on this as the primitive arrangement. It is found in species which are somewhat tardy in developing the plumular leaves. The root-stele in such species is fully differentiated, while the plumular traces are still embryonic.

The early or late development of the plumule is of course a question chiefly of the habit of the species, and this is determined by the external conditions to which it is exposed. The seedlings of climbers and arborescent species, for example, commonly develop the plumule early, and the primary root of such species is comparatively long-lived. It must therefore be polyarch in order to attain sufficient girth, and as a rule in plants of this habit many plumular traces are continued downwards into the root-stele, side by side with the cotyledonary traces.

In such cases I have found the features of the transition to vary considerably, even among individuals of the same species. The primitive characters are swamped among those which are more or less dependent on external conditions, and these are necessarily variable.

### 1. Tribe Scilleae.

Seventeen species, representing ten genera, have been examined from this tribe.

*Albuca Nelsoni*. The seedling is slender, and attains some

size before the position of the plumule is defined externally as a swelling near the base of the cotyledon ( $A_5$  in Pl. I, Fig. 1). The cylindrical cotyledon is green, and acts as the first assimilating organ. Its apex carries the seed out of the ground, and remains within it until the supply of food in the endosperm is exhausted. The primary root is still unbranched in  $A_5$ , and no other has appeared. The upper limit of the root is defined externally by a sudden increase in diameter. Later on, when the base of the cotyledon has expanded into a sheath which envelops the growing plumule ( $B_1$  in Fig. 1, Pl. I), this abrupt increase in girth is not so clear, but there is a distinct constriction separating the base of the bulb from the top of the root.

The two seedlings figured ( $A_5$  and  $B_1$ ) have been dissected. In each there are two massive bundles running the whole length of the cotyledon. Their phloëm groups are very well developed, as is generally the case when the cotyledon serves as a sucking organ for some time after germination. The cotyledonary sheath of  $A_5$  possesses in addition five lateral bundles, which are formed near the top of the sheath by the branching of the two main bundles. Near the base of the sheath they join the plumular traces above the level at which these are inserted on the main cotyledonary traces. The far larger sheath of the older seedling  $B_1$  possesses no less than twelve of these minor bundles: all given off by branching from the main bundles, and all ultimately merged in the plumular stele, or ending blindly before the transition from root to stem begins.

The presence of lateral bundles in the cotyledonary sheath, though not confined to the Scilleae, is very characteristic of the tribe. They do not always arise by the branching of others, but are sometimes formed independently, and disappear without joining other traces. When this is the case they probably serve merely to stiffen the sheath.

The seedling  $A_3$ , from which the sections drawn in Figs. 2-4 were cut, is younger than  $A_5$ , and there are only two slender lateral strands in the cotyledonary sheath in addition to the



two massive bundles on which the transition depends (Fig. 2). These behave precisely as the corresponding bundles of *Anemarrhena* (Diagram VI). The phloëm group of each divides into two parts, and the protoxylem group branches in three directions ( $px_1, px_2, px_3$  on one side, and  $px_4, px'_2, px'_3$  on the other in Fig. 3, Pl. I). The four phloëm groups thus formed continue downwards into the primary root, but the six protoxylem groups of Fig. 3 are reduced to four by the fusion of  $px_2$  with  $px'_2$  and  $px_3$  with  $px'_3$ .

So far the transition follows the *Anemarrhena* type exactly. But in *Albuca* the permanent stele of the primary root is not always tetrarch. The protoxylem group  $px_3 + px'_3$  in Fig. 4 is less prominent than the other three. A little lower down it has disappeared altogether; the phloëm groups on either side of it have united, and the root-stele is triarch. In the seedling  $A_5$  a similar suppression occurs. The primitive tetrarch structure is barely indicated before two of the protoxylem groups—those corresponding to  $px_2 + px'_2$  and  $px_3 + px'_3$  in Fig. 3—become less prominent, and for a considerable distance it appears as if the root would ultimately become diarch. In the end, however, one of the menaced protoxylem groups recovers itself, and the root is triarch as in  $A_3$ . In both seedlings the lateral protoxylem group which persists is that on the side from which the plumular traces have entered the stele.

If the irregularity just described could be thought to cast any doubt on the homology of the transition in *Albuca* with that of *Anemarrhena*, that doubt would be removed by the series from  $B_1$ , the oldest seedling cut. In this transition the two cotyledonary traces give rise to a tetrarch root. The process is the same as in *Anemarrhena*, step for step, and when once formed the root continues tetrarch to the end of the series, a distance of .75 mm. from its first formation.

The vascular structure of the seedling in *Albuca Nelsoni* is doubly interesting. In the first place it follows the *Anemarrhena* type of transition so closely as to demonstrate the existence of this type within the Scilleae. In the second,

its variations from the *Anemarrhena* structure are hardly less important.

The existence of lateral bundles in the cotyledonary sheath is, as I have said, characteristic of this tribe. In *Albuca* we see a number of such lateral bundles present side by side with the main bundles, but obviously derived from them, and exercising no influence on the symmetry of the hypocotyledonary stele. In other genera such lateral bundles assume a greater importance, and to some extent replace the main bundles, but these variants on the typical structure are linked to *Albuca* by a series of intermediate forms, some of which I shall describe in detail (*Hyacinthus romanus*, *Muscari atlanticum*, *M. armenaicum*). The comparative study of these species and others, joined with that of a series among the Asphodeleae, leaves no doubt that the lateral bundles of the cotyledon are structures of more recent date than the main bundles.

Again, the formation of a triarch root in some individuals of this species by the suppression of the median protoxylem group in one of the main bundles ( $A_3$ ,  $A_5$ ), and the temporary suppression of the corresponding group in  $A_5$ , indicates a tendency in these median protoxylem groups to disappear. Moreover, the fact that the median group which survives is that next to the plumular traces shows the influence that these—when developed early—may exercise on the symmetry of the stele.

*Galtonia candicans* and *Dipcadi serotinum* are alike in possessing several lateral bundles in the cotyledonary sheath besides the two main bundles which run the whole length of the cotyledon. In both genera two or more of these lateral bundles, together with the plumular traces inserted on them, enter the hypocotyledonary stele, and exercise a capricious influence on the symmetry of the root-stele. Individuals within the same species differ profoundly from each other in the details of transition: triarch, tetrarch, or pentarch steles are found in the primary root of *Galtonia candicans*; triarch or tetrarch steles in that of *Dipcadi serotinum*. The behaviour

of the two main bundles themselves is affected by these irregularities, but in some specimens of both species they follow the *Anemarrhena* type exactly, and in almost all they clearly begin on that plan, though it is not pursued throughout the transition.

Species in which the transition presents such irregularities cannot be fully described here: they are mentioned because in individuals of both species a modification of the *Anemarrhena* transition is found which reappears elsewhere.

In this variant the phloëm of each main bundle divides into three groups, of which the median one remains *in situ*

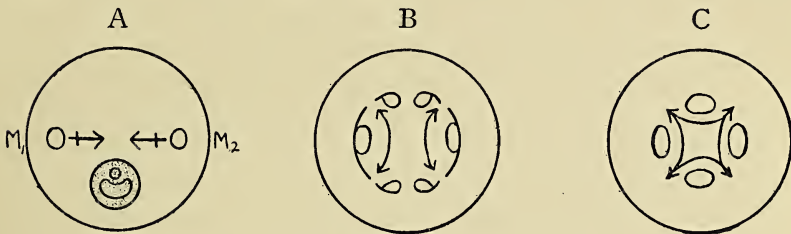


DIAGRAM I.

and is continued downwards unchanged. The right-hand branch unites with the adjacent branch from the other bundle, and a similar fusion occurs on the opposite side of the stele. The protoxylem of each main bundle divides into two groups, each of which becomes external as it takes up its position on one side or other of the median phloëm group. The root is of course tetrarch (Diagram I).

The examination of the transitional region in six seedlings of *Galtonia candicans* has convinced me that the type of transition just described is derived from type 4 (*Anemarrhena*). It stands in precisely the same relation to that type as Van Tieghem's type 3 to his type 1<sup>1</sup>, and for convenience I shall refer to it as type 5.

The genera *Hyacinthus* and *Muscari* include a number

<sup>1</sup> *Traité de Botanique*, ed. ii, 1891, vol. i, p. 782.



of forms in which the lateral bundles of the cotyledon take a perfectly regular share in the formation of the root-stele.

The species *Hyacinthus romanus*, *Muscari atlanticum*, *M. armenaicum* and *M. neglectum*, for example, form a series in which the lateral traces become more and more important until they supply a full half of the root-stele.

*Hyacinthus romanus*. In the seedling figured ( $A_5$ , Pl. I, Fig. 5) there are four slender lateral strands in the cotyledonary sheath at an age when even the midrib is not indicated in the first leaf (Pl. I, Fig. 6). These four strands unite in pairs: the two traces thus formed enter the stele just above the transitional region, and take some slight share in the process of transition from stem to root.

The two main bundles divide exactly as in *Albuca*. The bifurcation of the phloëm groups is somewhat masked by the early formation of a phloëm girdle, but in very young seedlings this is still incomplete, and there is no difficulty—when the series of sections from seedling  $A_5$  is followed with care—in identifying the phloëm group to the top or north of the section figured in Pl. I, Fig. 7 with half the phloëm of  $M_2$ . The rest has united with the adjacent phloëm group of the lateral bundle  $l_2$  to form the right-hand or eastern group. The whole of the phloëm belonging to  $M_1$  has joined that of  $l_1$ , and the united groups are now represented by the phloëm crescent on the left hand or south-western side of the stele (Pl. I, Fig. 7). The xylem is in two masses, between which extends a slender crescent of protoxylem elements. This is formed by the xylem of the two lateral bundles  $l_1$  and  $l_2$ , together with protoxylem elements from the two main bundles  $M_1$  and  $M_2$ . These will together form the protoxylem group  $px_3 + px'_3$  of figures 8 and 9 on the same plate. The corresponding group to the north of the stele in Fig. 8 is formed by the union of protoxylem branches from the two xylem masses shown in Fig. 7 (Pl. I, Fig. 8,  $px_2 + px'_2$ ). The median protoxylem group of  $M_2$  ( $px_4$  in Fig. 8) is also well developed, but that of  $M_1$  can hardly be made out. Its

position is indicated by a break in the centre of the phloëm crescent (cf. Figs. 7 and 8). Later on the development of the protoxylem ray  $px_1$  (Pl. I, Fig. 9) completes the formation of a tetrarch root.

Every step in this process can be followed in the series of sections from which Figs. 6-9 were drawn, and it is clear that the whole symmetry of the root-stele depends on the two main bundles  $M_1$ ,  $M_2$ , and is derived from them as in *Albucca*. The two lateral bundles  $l_1$ ,  $l_2$  simply contribute a few xylem elements to the group  $px_3 + px_3'$ , and some phloëm elements to the two lower phloëm groups. In these points the two other seedlings examined agree with  $A_5$ .

*Muscari atlanticum*. The apex of the cylindrical cotyledon (Pl. II, Fig. 1) contains two bundles. A little lower down each of these gives off a branch. The four bundles thus formed run downwards through the whole length of the cotyledon into the sheath. No additional bundles have been seen in the sheath of the oldest seedling examined. Throughout their course the two original bundles ( $M_1$ ,  $M_2$ , in Fig. 2, Pl. II) are larger than those derived from them.

In seedling  $A_4$ , from which Figs. 1-3 were drawn, the transition takes place very suddenly, but with diagrammatic clearness. In Fig. 2, Pl. II, the four traces are seen to approach each other. As they do so the phloëm group of each branches to right and left, and from the eight branches five definitive phloëm groups are formed by the fusion of three adjacent pairs. This is very clearly seen in the single section which separates those drawn in Figs. 2 and 3 on Plate II. The lowest phloëm group in Fig. 3 is formed by the fusion of branches from  $l_1$  and  $l_2$ . That on the left hand of the lowest group is derived from the lower branch of  $M_1$  fusing with the upper one of  $l_1$ . The phloëm group on the right of the lowest is formed from the lower branch of  $M_2$  and the upper one of  $l_2$ . The two upper phloëm groups represent the upper branches of  $M_1$  and  $M_2$  respectively.

The xylem groups of  $M_1$  and  $M_2$  each branch in three



directions. The two upper branches ( $px_2$  and  $px'_2$  in Fig. 3) unite, while the median branches ( $px_1$  and  $px_4$ ) maintain their identity. The lower branches ( $px_3$  and  $px'_3$ ) are separated by the lowest phloëm group, which is that derived from the two lateral branches. The xylem of  $l_1$  fuses with the branch  $px_3$ , and the xylem of  $l_2$  with  $px'_3$ . These changes when accomplished produce a pentarch root-stele.

Of the two other seedlings cut, one agrees in every point with  $A_4$ . The other begins in the same way, but one of the median branches of protoxylem is suppressed after it has been formed, which leads to the asymmetrical formation of a tetrarch root. This is clearly anomalous.

The lateral bundles of *Muscari atlanticum* play a more important part in the process of transition than they do in *Hyacinthus romanus*. They add a phloëm group to the stele, besides contributing elements to two others and to two protoxylem groups. The division of the two main bundles takes place exactly as in *Albuca*.

*Muscari armenaicum*. The cotyledon contains four bundles almost throughout its length. Two of these are more massive than the others. Each of the two slighter bundles gives off a branch in the upper part of the sheath. Below this level we find two main bundles and four lateral ones in the sheath. But the two supplementary bundles reunite at the first node with the bundles from which they arose, and the transition from stem to root takes place with four traces only in the stele.

Sections from the transitional region of two of the three seedlings cut are drawn in Figs. 5, 6, 7, and 8. The third seedling,  $A_4$ , is younger than the others, and the lateral traces are poorly developed. The process of transition, however, is clear, and it is precisely that just described for *M. atlanticum*. The transition in seedling  $A_3$  differs from this, and that of seedling  $A_5$  is unlike either.

In seedling  $A_3$  one of the two main bundles ( $M_1$ ) behaves in the characteristic way. Its xylem branches in three directions: its phloëm bifurcates. But in the second main bundle ( $M_2$ )

the median protoxylem branch, if formed at all, is early suppressed, and the phloëm group remains single. In the anomalous seedling of *M. atlanticum* a similar suppression led to the formation of a tetrarch root. The seedling with which we are dealing, however ( $A_3$  of *M. armenaicum*), forms a pentarch root owing to the increased activity of the lateral bundles. Their phloëm groups remain undivided, and are continued directly downwards as the two lower groups of the root-stele (Pl. II, Fig. 6). Each xylem group, on the other hand, branches to right and left; the two adjacent branches unite to form the lowest protoxylem group of the root, and

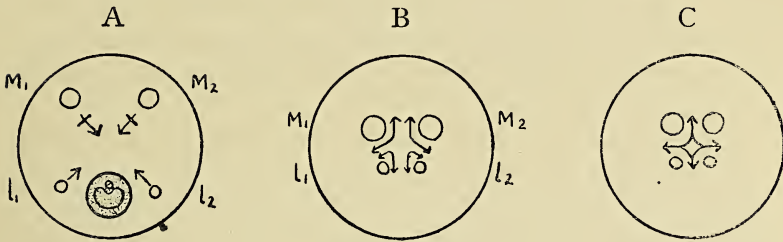


DIAGRAM II.

the upper xylem branches unite with the adjacent branches from the main bundles.

Thus the lateral traces provide two phloëm groups, one protoxylem group, and contribute elements to two other protoxylem groups of the pentarch root-stele.

Finally, in seedling  $A_5$  we find the lateral bundles contributing a full half of the tetrarch root-stele (Diagram II). The median protoxylem branches of both main bundles are suppressed. In  $M_1$  this median ray is indicated during the earlier stages of the transition: in  $M_2$  it never appears. Thus both main phloëm groups are continued downwards into the root-stele unchanged. So are the two phloëm groups of the lateral bundles, which are, however, smaller than the main groups (Pl. II, Fig. 9). The xylem of main and lateral traces alike branches to right and left, adjacent branches fusing in

pairs. Thus the tetrarch root is formed according to Van Tieghem's type 1, and the distinction between main and lateral bundles is indicated only by the slight want of symmetry due to the smaller size of the lateral traces (Pl. II, Fig. 9).

*Muscari neglectum.* The sheath of the cotyledon contains four or more lateral bundles in addition to the two main bundles. In two of the seedlings cut ( $A_5$  and  $A_7$ ) all the lateral bundles except two disappear before the transition begins: inserting themselves for the most part on the two which remain. The transition to a tetrarch root then proceeds regularly as in Diagram II.

In seedling  $A_2$ , however, two of the supernumerary bundles fuse with each other and enter the stele as a fifth trace. This behaves like the others, and a pentarch stele is formed according to Van Tieghem's type 1.

The forms just described form an unbroken series which connect the *Albica* structure, or type 4, with the simple and no less definite symmetry shown in Diagram II and Pl. II, Figs. 8 and 9. In this transition two lateral traces of the cotyledon take an equal share in forming the root-stele with the two main traces. All four traces behave alike, following Van Tieghem's type 1.

The same symmetry in essentials is characteristic of the transition in *Eucomis nana*, Jacq., but with one interesting variation.

In Fig. 5 on Pl. II the two main bundles  $M_1$  and  $M_2$  are seen to be united by a common protoxylem group, which has already begun to turn outwards. The lateral bundles are still quite distinct from the main bundles and from each other. In this case the fusion of the two main bundles has only just occurred: they were distinct .02 mm. above the section drawn in the figure. But in *Eucomis nana* the main bundles are united throughout the cotyledonary sheath. In its upper part they resemble a single massive bundle; lower down this opens out into a double bundle with distinct phloëm and xylem but a common protoxylem group. Just above the



transition the two bundles resemble those in the cotyledon of *Fritillaria imperialis* (Pl. III, Fig. 2), but are rather nearer together, the protoxylem groups fused. As in *Muscari armenaicum* A<sub>3</sub>, and in *Fritillaria* also, the protoxylem is already on the way to become external, though the transition proper has not begun.

During the transition in *Eucomis nana* the double bundle contributes an exact half to the tetrarch root-stele. Its two phloëm groups are continued directly downwards, and the protoxylem, besides forming the ray separating these phloëm groups, sends out branches to right and left, which unite with branches from the two lateral traces entering the stele.

This is in effect the transition shown in Diagram II. In that case, however, the lateral traces were throughout smaller than the main traces, and the tetrarch root-stele was, when first formed, one-sided from this cause (Fig. 9, Pl. II). In *Eucomis nana* the converse is the case. The lateral traces—on which are inserted not only the supernumerary traces of the sheath but also the plumular traces—are more massive than the reduced main bundles, and the tetrarch stele is at first less well-developed on the side from which the main traces enter it.

Throughout this description of the transition in *Eucomis nana* I have assumed that the double bundle of the cotyledon represents the two main bundles of *Muscari*. This assumption is justified, I think, not only by the behaviour of the traces in the hypocotyl, but also by their orientation within the cotyledonary sheath. The double bundle is placed in the thickest part of the sheath, exactly opposite the first leaf, and this is also the position of the two main bundles in the sheath of *Muscari*. Compare the position of M<sub>1</sub> and M<sub>2</sub> in Pl. I, Fig. 6, *Hyacinthus romanus*. It is by no means uncommon to find two separate bundles replaced by a double bundle in allied genera. For example, in *Fritillaria* (Pl. III, Fig. 2) the bundles of the cotyledonary sheath are separate: in *Lilium* they are joined as in *Eucomis*. In *Bloomeria* they are separate: in *Allium* joined.

Before describing hypocotyls, in which the main cotyledonary traces play a subordinate part, I must mention an interesting variant on the form of transition just described (*Muscari armenaicum* A<sub>5</sub>, and others), which is found in *Scilla sibirica*.

Two main traces and two lateral ones enter the hypocotyl from the cotyledon. The four xylem strands are continued straight downwards into the root, and the protoxylem of each becomes external during the passage. Each of the four phloëm groups divides into two, and the half of each bundle unites with the half of the bundle lying next to it

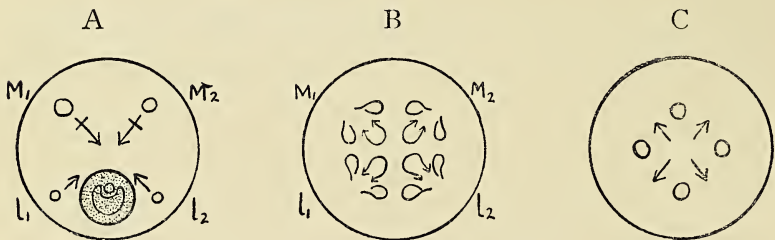


DIAGRAM III.

(B, Diagram III). In short, the four cotyledonary traces become a tetrarch root-stele according to Van Tieghem's type 3. I have examined no intermediate forms which would suggest whether this symmetry is derived from that of an ancestor resembling *Muscari armenaicum*, or more remotely from one with the vascular structure which I have called type 5 (*Galtonia, Dipcadi*).

In *Muscari comosum*, *Hyacinthus orientalis*, *Scilla festalis*, Salisb., and *Ornithogalum sulphureum*, more than two lateral traces from the cotyledon enter the hypocotyledonary stele, and the two main traces form less than half the root-stele. Such a possibility was suggested by the structure of seedling A<sub>2</sub> in *Muscari neglectum*. It is worth notice that the main traces of *Muscari comosum* and *Hyacinthus orientalis* are distinguished not merely by their orientation in the sheath, but

very commonly during the transition by the characteristic branching of their xylem in three directions. The median protoxylem ray when formed is as a rule suppressed in the course of the transition: now and then it persists and affects the symmetry of the root-stele.

Finally, in the three species *Lachenalia Nelsoni*, *Scilla peruviana*, and *Ornithogalum exscapum*, lateral bundles are either absent from the cotyledonary sheath, or, if present, they take but little share in the transition. The diarch root is formed from the much reduced main bundles, with more or less assistance from the plumular traces. The transition in these species approaches that characteristic of such bulbous genera as *Allium* and *Lilium*.

*Lachenalia Nelsoni*. The cotyledonary sheath contains three slender lateral bundles, as well as the two main bundles which lie side by side and have a common protoxylem group (cf. *Eucomis nana*). The lateral bundles of the cotyledon together with those of the plumule are all inserted on the midrib trace of the first leaf. The trace of the double bundle from the cotyledon and the single plumular trace take an equal share in the formation of the diarch root-stele. The plumular phloëm divides itself between the two phloëm groups of the cotyledon. The plumular protoxylem turns outwards. The group of protoxylem common to the two cotyledonary traces also turns outwards, and the diarch root is then complete.

*Scilla peruviana*. There are no lateral bundles in the cotyledon. The two main bundles form a double structure as in *Eucomis*. The double trace from this enters the hypocotyledonary stele together with a single plumular trace. Together they form a diarch root as in *Lachenalia*.

*Ornithogalum exscapum*. Two massive bundles run the whole length of the cotyledon. In the sheath they are placed very much as the bundles of *Albuca* (Pl. I, Fig. 2). A single plumular trace takes part in the transition, but seems to exercise no influence on the symmetry of the stele.



Very great individual differences occur within the limits of this species. The transition follows type 5—that is, the phloëm of each cotyledonary trace branches in three directions, the xylem in two. This would normally lead to a tetrarch root, and does so in one seedling ( $A_2$ ). In another ( $A_3$ ) a very interesting variation is found (Diagram IV).

The phloëm groups at first behave in the usual way (Diagram IV, B), but before the branching is accomplished and four definite groups are formed, the original groups re-assert themselves, and the phloëm elements collect once more in two large masses. The four protoxylem groups are still distinct,

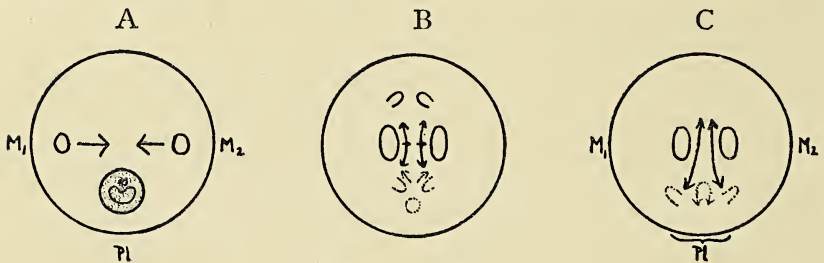


DIAGRAM IV.

but the right-hand branch of one group is not separated from the left-hand branch of the other by phloëm elements, and the four groups naturally fuse in pairs (Diagram IV, C). The diarch root-stele is then complete.

If we neglect the very small plumular trace which inserts itself on the stele during the transition without affecting its symmetry, this is precisely the structure characteristic of the Tulipeae, in which, however, the two cotyledonary traces are commonly reduced to a slender double bundle. But in *Ornithogalum exscapum* the size of the cotyledonary traces, their independence, and their behaviour during the transition in seedling  $A_2$ , leaves no doubt as to their identity with the main bundles of *Galtonia* and *Albuca*.

Before leaving the Scilleae, I must mention an anatomical peculiarity of the root-cortex which is found in a number of species belonging to it.

In most Monocotyledons the piliferous layer of the root is a direct continuation of the cell-layer lying immediately under the epidermis of the cotyledon. The absence of the epidermal layer causes an abrupt decrease in diameter at the junction of the root with the hypocotyl, and the 'collet' is defined by Van Tieghem as a plane passing through the axis immediately below the last row of epidermal cells.

The root of *Albuca*, however, has a greater diameter than the hypocotyl in the region where they join, and the same is true of many other species belonging to this tribe. The increase in girth is due to repeated tangential division in the cells of the outer cortical layer. The external layer of cells in the tissue thus formed is of course the piliferous layer.

Hitherto *Erythronium* is the only genus outside the Scilleae in which I have found this development of the cortex. I do not propose to do more than mention its existence here, but hope shortly to describe it in greater detail elsewhere.

## 2. Tribe Tulipeae.

The variety of vascular structure characteristic of seedlings belonging to the Scilleae is in strong contrast with the uniformity of type found in the Tulipeae. I have fully examined eight species belonging to four genera of this tribe, and with the exception of *Erythronium* the vascular symmetry of the cotyledon and the process of transition from stem to root are the same in all.

*Fritillaria imperialis*. The seedling of this species (Pl. III, Fig. 1) consists of cotyledon, hypocotyl, and primary root throughout the first season. The petiole of the cotyledon becomes flattened and acts as an assimilating organ. Neither foliage leaf nor cauline root is developed until the second season of growth. The primary root is very well developed.

The massive bundles run the whole length of the cotyledon. They lie close together in the sheath, but are quite distinct (Pl. III, Fig. 2). The plumule is still embryonic: its bundles become lignified lower down, where they unite to form



two traces. These traces are inserted on those of the cotyledon at the first node (Pl. III, Fig. 3).

At this point the transition to a root-like structure has already begun in the stele. The protoxylem of each main bundle is branching in two directions. The branches towards the top of the section have united with each other: those which have turned in the opposite direction are distinct, and have each joined a group of plumular xylem (Pl. III, Fig. 3).

Below the node there are two crescent-shaped xylem masses, each crescent partly encloses a very well-defined circular group of phloëm (Pl. III, Fig. 4). The extended protoxylem covers the convex surface of either crescent, but though the crescents lie close together and present their convex outline to each other, the protoxylem elements of the two bundles are united only at one point near the top of the stele.

Very little below this, the two massive xylem crescents meet in the centre of their convex surfaces, and the protoxylem sheath on both sides is broken in the centre. There are now four protoxylem rays stretching out towards the horns of the crescent. They are united in pairs to form the groups  $px_2$  and  $px_3$  in Fig. 5, Pl. III. The whole structure is that of a diarch root with the protoxylem rays extended tangentially.

So far the transition is essentially that characteristic of the Tulipeae (Diagram V). Two cotyledonary traces have formed a diarch root-stele according to Van Tieghem's type 1, that is, by branching of the xylem and fusion of adjacent branches. But in *F. imperialis* the process does not stop there. The protoxylem elements creep round the horns of the crescents until they meet on either side and form two groups external to the two phloëm-masses. Each phloëm-mass breaks into two (Pl. III, Fig. 6), and the root is then tetrarch. In a similar way it becomes first hexarch and then heptarch a little lower down.

This variation on the type is doubtless due to the persist-

ence of the primary root and its physiological activity which renders a considerable girth necessary.

The two cotyledonary traces of the slighter seedling of *Fritillaria alpina* form a diarch root-stele in much the same way. It afterwards becomes tetrarch by branching of the phloëm and division of the protoxylem, and the whole transition recalls that of *Ornithogalum exscapum*. This resemblance is probably accidental.

*Tulipa praecox* and *Tulipa* sp. (from Calcutta).

Two bundles run the whole length of the cotyledon and possess a common protoxylem group. They are orientated in the way characteristic of double bundles (A, Diagram V).

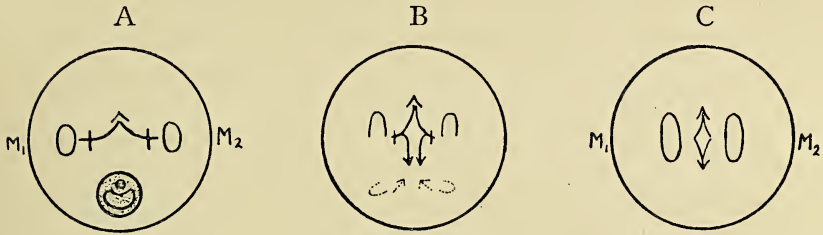


DIAGRAM V.

Two plumular traces are inserted on the cotyledonary traces, as in *Fritillaria* (B, Diagram V). A diarch root-stele is formed from the cotyledonary traces: the phloëm groups are continued straight down into the root, while the single protoxylem group branches to form a second on the opposite side of the xylem plate (Diagram V). In both species the protoxylem groups of the root are somewhat extended tangentially, and the whole xylem plate is shaped like a dumb-bell. The root-stele, however, remains diarch.

In the three species of *Lilium* which I have examined (*Lilium* sp., *L. Henryi*, *L. croceum*), the double trace of the cotyledon is even more reduced than in *Tulipa*, but the transition takes place in precisely the same way.

*Erythronium Hartwegi* is the only species I have examined from this tribe which does not follow in essentials the method

of transition indicated in Diagram V. The cotyledon possesses three bundles throughout, and they are continued downwards into a triarch root formed according to Van Tieghem's type 1. I have not so far hit on any intermediate form which would connect this structure with that of *Tulipa* and *Lilium*. The anatomy of the seedling, however, may possibly be modified by the very early transformation of the first leaf into a dropper (Irmisch). This occurs also in both species of *Tulipa*.

### 3. Tribe Asphodeleae.

In this tribe I have examined eleven species belonging to eight genera. There is no definite symmetry characteristic

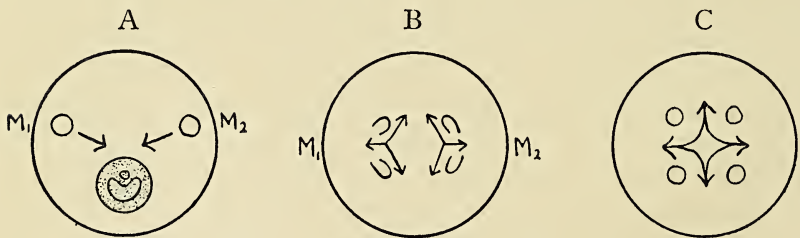


DIAGRAM VI.

of the tribe as in Tulipeae, but, with the exception of *Bulbine annua*, the vascular structure of all the species examined can be linked with great probability to that of *Anemarrhena* (Diagram VI).

The seedling of *Anemarrhena asphodeloides* has been described elsewhere in detail (Sargent, 34). It resembles that of *Albuca*, except in possessing no lateral bundles in the cotyledon, and in the regular formation of a tetrarch root.

*Asphodeline liburnica*. The cotyledon contains two massive bundles throughout, which are quite distinct but orientated in the characteristic way—that is, with their protoxylem groups directed towards each other. The symmetry of the root-stele is sometimes derived from the cotyledonary traces only,



and when this is the case the root is tetrarch or pentarch, and the transition follows the *Anemarrhena* type more or less closely.

When, as is more commonly the case, plumular traces enter the stele and take part in the transition, the process is always irregular, and the root becomes 5-7 arch.

Similar irregularities are found in the allied genus *Asphodelus*. In *A. albus* and *A. cerasifer* there are two cotyledonary bundles as in *Asphodeline*, but plumular traces play a greater part in the transition, and the likeness to *Anemarrhena* is more obscure.

The relationship to *Anemarrhena* is particularly clear in *Asphodelus fistulosus*. It possesses three massive bundles in the cotyledon, and it is clear from their position in the cotyledonary sheath, and their behaviour during the transition, that two of these correspond to the two bundles in the cotyledon of *Anemarrhena*. The third is placed between them, opposite the plumule, and I have therefore called it the median bundle.

The plumular traces do not affect the symmetry of the root-stele, though they are inserted on the cotyledonary traces during the process of transition.

Each of the two main cotyledonary traces divides as in *Anemarrhena* (Diagram VI). The xylem branches in three directions, and the median branch of the three bisects the phloëm group behind it. Of the four lateral xylem branches formed from the two main traces, the two directed towards the plumule unite, and the opposite pair would do so too—forming a tetrarch root as in *Anemarrhena*—but for the presence of the median trace on that side. The xylem of this trace branches to right and left, each branch fusing with the adjacent lateral branch from a main trace. The phloëm group does not divide, but is continued downwards *in situ*. Thus a pentarch root is formed.

*Eremurus turkestanicus* and *E. spectabilis* also possess a median bundle in the cotyledon, placed as in *Asphodelus fistulosus*. The two main bundles behave during the tran-

sition exactly as those of *Anemarrhena* (Diagram VI), and the median bundle plays the same part that it does in *Asphodelus fistulosus*. The root sometimes becomes pentarch in the same way.

More commonly, however, a plumular trace—the midrib of the first leaf—enters the hypocotyledonary stele directly opposite the median trace of the cotyledon, and divides its xylem between the adjacent branches from the main cotyledonary traces. The phloëm of this plumular trace is continued downwards into the root-stele without division. When this occurs the root is hexarch.

In all the species hitherto described from this tribe, two main bundles are present in the cotyledon. Their identity with the bundles of *Anemarrhena* cannot be mistaken, in spite of the irregularities introduced by the entrance of plumular traces, or a minor cotyledonary trace, into the hypocotyl. Of the four species examined, but not yet described, *Bulbine annua* may be dismissed at once. The symmetry of the triarch root is determined by the three traces of the first leaf. The two distinct cotyledonary traces are inserted on two of them, and the transition follows Van Tieghem's type 3.

Three species remain, *Chlorogalum pomeridianum*, *Anthericum Liliago*, and *Arthropodium cirrhatum*. The two main bundles of the cotyledon appear in all of them, but they are much reduced, and are associated in the hypocotyl with plumular traces which take a well-defined part in the transition. I have examined no forms which are clearly intermediate between *Anemarrhena* and *Chlorogalum*. Such a series as that which leads step by step from *Albuca* to *Muscari armenaicum* (Plates I and II) would, however, account completely for the structure of *Chlorogalum*, and probably such a series of links either exists now or has once existed. *Arthropodium* is quite clearly linked to the less reduced *Chlorogalum* through *Anthericum*.

*Chlorogalum pomeridianum*. The cotyledon, which remains underground and within the seed to the end (Pl. IV, Fig. 1),

contains two bundles which are quite distinct from each other though close together. Near the base of the sheath the bundles so far unite that they have a common protoxylem group, and they then form a typical double bundle such as we find in *Allium* (cf. Pl. V, Figs. 2 and 3).

The plumular bundles unite to form a single trace which then divides into two branches,  $Pl_1, Pl_2$ , and these advance to meet the double cotyledonary trace  $M_1 + M_2$  at the first node (Pl. IV, Fig. 2). The protoxylem of the double trace has formed three groups already ( $px_1, px_2, px_3$  in Fig. 2). They represent two branches from the xylem of  $M_1$  and two from that of  $M_2$ . The single group  $px_1$  is formed by the early fusion of two adjacent branches:  $px_2$  belongs to  $M_1$  and  $px_3$ , to  $M_2$ .

A little lower down, the stele threatens to become diarch (Pl. IV, Fig. 3). The phloëm from  $M_1$  has met half the plumular phloëm on one side of the stele, and that from  $M_2$  has met the other half on the opposite side. The protoxylem groups within the phloëm ( $px_2, px_3$ , in Fig. 3) seem about to be obliterated. But they recover themselves later, and the root becomes typically tetrarch (Pl. IV, Fig. 4).

Two phloëm groups in the tetrarch root are derived from the plumule and two from the cotyledon. One protoxylem group ( $px_1$ , Fig. 4) is purely cotyledonary and one purely plumular ( $px'_1$ ). With regard to the two remaining groups of protoxylem, they appear in the young seedlings I have examined to be derived from the cotyledon, but it is very possible that in older seedlings they would be found to receive elements from the plumular traces. If so, the transition would be precisely comparable with that of *Muscari armenaicum*, seedling A<sub>5</sub> (Diagram II).

*Anthericum Liliago*. The two bundles of the cotyledon are more reduced than those of *Chlorogalum*. They are united by a common protoxylem group throughout their course, and in fact appear as a typical double bundle in the upper as well as the lower part of the cotyledon.



The insertion of the plumular traces takes place as in *Chlorogalum* (Pl. IV, Fig. 6): the three traces of the first leaf (A, B, and C, in Fig. 6) unite with each other and then divide into two branches ( $Pl_1, Pl_2$ ) which join the two cotyledonary traces ( $M_1, M_2$ ).

The root-stele when first formed suggests a diarch structure, and this appearance persists for some time. In Fig. 7 (Pl. IV) there are only two phloëm groups, but the protoxylem elements internal to them are quite distinct ( $px_2, px_3$ ). They finally disappear a little further down, and the root appears truly diarch.

Finally, in the seedling  $B_1$  figured in Fig. 5, the group  $px_2$  recovers itself and divides the phloëm group lying outside it into two. The opposite phloëm group remains single, and the corresponding group of protoxylem,  $px_3$ , is suppressed permanently. The root of course is triarch.

In the two other seedlings examined both lateral protoxylem groups reappear after a temporary eclipse, and the stele of the root is tetrarch.

*Arthropodium cirrhatum*. The two bundles of the cotyledon, though slender and lying close together, are distinct from each other until they reach the base of the cotyledon. Here their protoxylem groups unite, and they assume the typical double structure.

The plumular traces unite with those of the cotyledon just as in *Chlorogalum* and *Anthericum* (Pl. IV, Fig. 9). A diarch root-stele is formed (Pl. IV, Fig. 10). During the process two lateral protoxylem groups appear, and they have not quite vanished in Fig. 10(+,+). The two massive phloëm groups, however, formed by the union of a cotyledonary with a plumular mass of phloëm on either side of the stele, are never broken up. The root remains diarch to the end.

The vascular symmetry of *Arthropodium* is so far reduced from that characteristic of *Chlorogalum*, that it precisely resembles the *Allium* symmetry (Diagram VII).

4. Tribe Allieae.

Nine species representing four genera have been examined from this tribe. The vascular structure of the hypocotyl is much reduced, and is identical in all the species examined, except *Milla biflora*.

*Allium neapolitanum*. The seedling  $A_4$  from which the sections drawn in Figs. 1-5 on Pl. V were cut was very young, and the traces but slightly lignified. The two bundles of the cotyledon are united by their common protoxylem group throughout their course. This protoxylem group

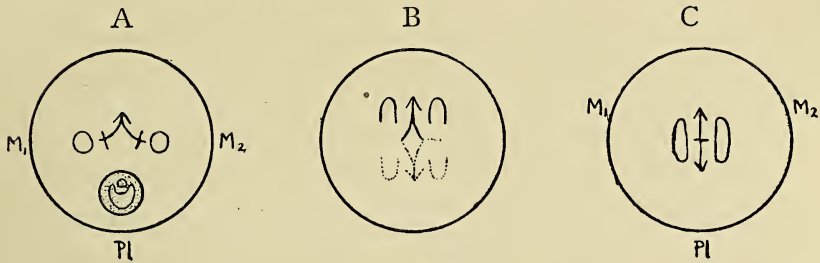


DIAGRAM VII.

begins to turn outwards early (Pl. V, Figs. 1 and 2). The plumular traces in seedling  $A_4$  are so embryonic that only one protoxylem element is lignified at the first node (Pl. V, Fig. 3): in the older seedling B it is clear that two traces from the plumule join the stele. Their phloëm groups run into those of the cotyledonary traces: their xylem will form one-half of the xylem plate (Pl. V, Figs. 4 and 5). When the series of sections cut from seedling  $A_4$  is examined with attention, it is clear that one protoxylem group of the diarch root is derived from the cotyledonary, the other from the plumular, traces. Each of the two phloëm groups is derived from both.

The method of transition represented in Diagram VII is common to all the six species of *Allium* examined (*A. neapolitanum*, *A. Cepa*, *A. Porrum*, *A. serufschanicum*, *A. asca-*

*lonicum*, *A. angulosum*) as well as to *Bloomeria aurea* and *Brodiaea lactea*. In the two species last named the bundles of the cotyledon are distinct throughout. Indeed, the cotyledonary sheath of *Bloomeria*, with its two distinct and rather massive bundles, recalls the symmetry of the Asphodeleae.

*Milla biflora* also possesses two distinct bundles in the cotyledon, which are less reduced during the transition than those of *Allium*. A small plumular trace also enters the hypocotyledonary stele, and each of the three xylem groups branches to right and left. The phloëm remains *in situ*. A triarch root is formed according to Van Tieghem's type 1.

#### 5. Tribes : Veratreae, Uvularieae, Medeoleae.

Two species from the Veratreae have been examined, *Zygadenus elegans* and *Veratrum nigrum*; one species from the Uvularieae, *Tricyrtis hirta*; and one from the Medeoleae, *Trillium grandiflorum*.

In one feature these four species resemble each other. The cotyledon contains a single and rather massive bundle, placed in the position of a midrib, and sometimes accompanied by lateral bundles. This central bundle opens out in the neighbourhood of the first node into a double trace resembling that of *Allium*.

*Zygadenus elegans*. The cylindrical cotyledon contains but one bundle throughout: a section near the top hardly suggests a double structure in the phloëm (Pl. V, Figs. 7 and 8), but it is clear lower down (Figs. 9 and 10) and also throughout the transition. The plumular bundles which take part in it separate into two branches: in Pl. V, Fig. 11 these are seen advancing to meet the cotyledonary trace exactly as in *Allium* (cf. Fig. 3).

The phloëm groups of the cotyledonary trace are now quite distinct, and separated from each other by the whole xylem. The xylem itself is in two masses, between which



are inserted the protoxylem elements. They are not yet external. In the diarch root (Pl. V, Fig. 12) one protoxylem group is derived from the double cotyledonary trace and the other from the plumular traces. The two phloëm groups are of mixed origin.

The transition in *Zygadenus elegans* resembles that of *Allium* precisely, except for the more intimate union of the two bundles in the cotyledon.

*Veratrum nigrum.* The cotyledon contains a single massive bundle throughout its length, but in the sheath two or more slender lateral bundles appear. These are ultimately inserted on the plumular traces.

During the transition two crescents of xylem appear, each with a protoxylem group at either horn. One crescent is derived from the xylem of the cotyledonary double trace: the other from the xylem of the lateral and plumular traces. The four protoxylem groups are separated by four phloëm groups: two of these are derived from the double trace and the other two from lateral and plumular traces.

In the absence of sections from allied species the homology of this transition must remain uncertain. It would be very readily derived from such a form as *Scilla sibirica* (Diagram III).

*Tricyrtis hirta.* The vascular symmetry of this seedling presents many interesting features, but it cannot be described in detail here. The mature plant is a herbaceous perennial with a short creeping rhizome. The hypocotyl of the seedling is unthickened and of some length.

The cotyledon is leaf-like, and contains but one bundle. This opens out into a very well-marked double bundle a little above the first node. Two plumular traces are inserted on the double trace at the first node (A, Diagram VIII). When the insertion is complete no sign of transition to root-structure is observed: the double trace—now surrounded by an endodermis—is continued downwards in the elongated hypocotyl (B, Diagram VIII). Cauline roots are given off from it.



The transition from stem- to root-structure takes place rather suddenly at the base of the hypocotyl (C, Diagram VIII). It resembles that of *Fritillaria* and *Lilium*.

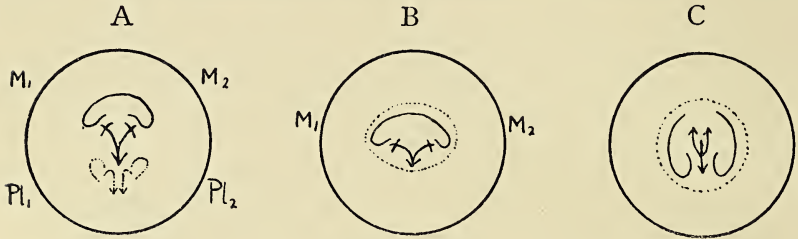


DIAGRAM VIII.

*Trillium grandiflorum*. The cotyledon contains a main bundle and two lateral ones. The main bundle opens out above the first node, and is clearly a double structure. One phloem group and two protoxylem rays of the triarch root are derived from it: the rest from the lateral and plumular traces.

There are points in this transition which suggest that of *Veratrum*, but I have not examined any allied species, and do not venture to draw a definite conclusion.

## 6. Tribes: Dracaeneae, Asparageae, Aloineae.

The species examined from these tribes are all of woody habit, or climbers. The structure of the seedling has been in most cases adapted to the conditions of life by changes in its vascular structure so profound that they disguise the primitive symmetry more or less completely. In nearly all cases the plumular traces enter the hypocotyledonary stele, and they commonly take the larger share in determining its symmetry.

Five species representing three genera have been thoroughly examined among the Dracaeneae.

*Cordyline australis*. The seedling resembles that of *Muscari* externally, but is larger. The first leaf shows early. There are two bundles in the cotyledon which are quite distinct until

they get near the base of the sheath. In that region they approach each other until the protoxylem elements unite to form a single group.

The plumular traces are inserted either on the double trace of the cotyledon or on each other. One finally enters the hypocotyledonary stele. The root is triarch, and is derived from the two cotyledonary traces and the single plumular trace according to Van Tieghem's type 1.

Three species of *Yucca* have been examined. They agree in possessing large stout seedlings with very well-developed and persistent primary roots. The first leaf appears earlier in *Y. gloriosa* and *Y. aloifolia* than in *Y. arborescens*.

*Yucca arborescens.* The cotyledon contains a number of massive bundles. These are reduced to six or seven in the neck of the cotyledon, just outside the seed, and they are continued downwards into the sheath, and form a semi-circle in the thickest part of it. Four smaller bundles are commonly found in the wings of the cotyledonary sheath.

The plumular traces are in the end all inserted on the traces of the cotyledon before the transition to a root-structure begins. The stele of the hypocotyl contains cotyledonary traces only. The six or seven main traces, which are all alike, are continued directly into it, and a seventh or eighth trace is added by the fusion with each other of the four wing-traces.

The root when first formed is heptarch or octarch. The protoxylem has become external by the branching of the xylem groups and the fusion of adjacent branches in pairs.

*Yucca aloifolia.* Three bundles are found in the cotyledon : when they reach the sheath the central one opens out into a typical double bundle. No wing-bundles appear.

The four cotyledonary bundles are continued downwards into the hypocotyl, and three traces—ultimately reduced to two—enter it from the plumule. The root is hexarch, and the transition to a root-structure takes place as in *Y. arborescens*.

*Yucca gloriosa*. There are four bundles throughout the length of the cotyledon: within the seed, and again in the lower part of the sheath, the two median bundles approach each other and their protoxylem groups unite. The structure of the cotyledon is then precisely that found in *Y. aloifolia*.

The four cotyledonary traces are continued into the hypocotyl, where they are joined by two or three from the plumule. All the traces behave alike during the transition: the xylem groups branch to right and left, and adjacent branches unite with each other. The root is either hexarch or heptarch.

*Dracaena Draco* is the only species I have examined from this genus.

The seedling is very robust: the plumular bud is developed early, and the primary root is particularly long, thick, and persistent. The cotyledon is merely a sucking organ, and it remains for a long time within the large seed, never appearing above ground.

There are seven bundles in the neck of the cotyledon where it emerges from the seed. Six are arranged in pairs to form three double bundles—each with a common protoxylem group. The seventh is single. This structure is continued into the sheath. As they descend, the three common protoxylem groups become more and more external. In this way the transition to a root-structure begins before the cotyledonary traces enter the hypocotyl.

The plumule contributes many traces to the hypocotyl—six to eleven in the seedlings I have examined—and the transition to a root-structure is very far advanced before they enter it. Both in cotyledon and plumule it proceeds—as in *Yucca*—according to Van Tieghem's type 1. The resulting root is polyarch. I have found as many as eighteen phloëm and xylem rays in it.

The four last species have been described at some length, because they display characters common to most of the arborescent forms which belong to this and allied orders. The primary root is persistent, and the insertion of the plumule



on it becomes a question of importance, particularly as the first foliage leaves are in general the earliest assimilating organs—the cotyledon commonly remaining within the seed. An early development of the plumule is usual, and when this occurs some plumular traces are commonly found in the hypocotyl. (Cf. *Yucca gloriosa* and *Y. aloifolia* with *Y. arborescens*.) This arrangement is useful in two ways: it secures uninterrupted communication between the plumule and the primary root, and it increases the girth of the latter. Among Monocotyledons a root which is to attain to any considerable diameter must be planned on a generous scale from the beginning, for there is no secondary thickening to provide fresh vascular tissue as it is needed.

Similar co-operation between plumule and cotyledon is found in the two species of *Asparagus* which I have cut, *A. officinalis* and *A. decumbens*. In both the hypocotyl contains both plumular and cotyledonary traces, which are all alike and behave in the same way during the transition.

The central double bundle found in the cotyledons of *Yucca gloriosa* and *Y. aloifolia* probably represents the two cotyledonary bundles of *Cordylina*, but it is possible that there may be no morphological connexion here. In *Dracaena* the three double bundles are no doubt formed for physiological reasons, and the double bundles of *Yucca* may arise in a similar way.

Among the Aloineae I have examined six species of *Aloë* and two of *Gasteria*. Their seedlings resemble each other very closely both in external form and internal structure.

The adaptation of these seedlings to life in a dry hot climate is very clear, and has profoundly affected their vascular structure. The cotyledon is modified to serve as a sucking organ in the upper part and as a water-jacket lower down. It contains two distinct bundles with massive phloëm groups.

The vascular symmetry of the very short transitional region is most simply explained by supposing that of the root-stele to depend solely on the three or four plumular traces which



enter it. The cotyledonary traces are inserted on them, sometimes before the transition to a root-structure begins, but more often while it is still in progress. The root is either triarch or tetrarch. In *Aloë Buchanii* the cotyledonary traces seem occasionally to exercise some influence on the symmetry of the root-stele. Four seedlings were examined from that species, and in two of them the root is diarch.

The method of transition is commonly but not invariably Van Tieghem's type 3. That is, the xylem groups rotate *in situ*, while the phloëm groups branch to right and left of them, and the branches from adjacent groups unite with each other in pairs.

## B. Monocotyledons not included in the order Liliaceae.

In working out the seedling structure of the Liliaceae I have paid most attention to the four great tribes, Asphodelae, Allieae, Scilleae, and Tulipeae, which may be considered as including the typical representatives of the order. The observations made on species from outlying groups are scattered, and serve for the most part merely to show that the vascular structure of their seedlings is not dissimilar from one or other of the central types.

The seedlings of *Allium* and *Zygadenus*, for example, are figured on the same plate and can readily be compared (Pl. V). The structure of the cotyledon is the same in both, except that the cotyledon of *Allium* contains two bundles united by a common protoxylem group (Pl. V, Figs. 1 and 2), while that of *Zygadenus* has a single bundle (Figs. 7 and 8).

Now the most salient feature distinguishing the vascular symmetry of the cotyledon in most Liliaceous seedlings is the absence of a midrib. In the first foliage leaf there are commonly three bundles, of which the central one or midrib is by far the best developed. There may be five, seven, nine, or even more bundles in each foliage leaf, but the number is

always odd, and the lateral bundles are always arranged symmetrically on either side of the midrib.

The cotyledon of the same species, however, commonly possesses two equivalent bundles, and if others are present they are arranged symmetrically with regard to both. These main bundles are often distinct and widely separate, as in *Albuca*, *Galtonia*, *Anemarrhena*, *Bloomeria*, *Aloë*, and other genera. When they approach each other more closely, as in *Muscari armenaicum* (Pl. II, Fig. 5) and *Fritillaria imperialis* (Pl. III, Fig. 2), they occupy the position of a midrib. This is still clearer in *Allium*, *Lilium* and many other genera, in which the two main bundles are much reduced in size, and are united by a common protoxylem group either in the sheath of the cotyledon only or throughout its length (Pl. V, Figs. 1 and 2).

The cotyledon of *Zygadenus* with its solitary bundle seems at first sight to be an exception to this rule. During the transition, however, this bundle opens out into a double structure perfectly comparable with that of *Allium*. In the allied genus *Veratrum* the central bundle of the cotyledon does not open out in this way during the transition, and but for the relationship with *Zygadenus* we might take it for a true midrib.

Another very striking example of the same kind is found in the two species *Yucca aloifolia* and *Y. gloriosa*. The cotyledon of *Y. aloifolia* contains three bundles, and the central one occupies the position of a midrib. During the transition this bundle opens out into the characteristic double structure (*ante*, p. 35). In the cotyledon of *Y. gloriosa* there are four bundles, but just before the transition begins the two central bundles approach each other so closely that their protoxylem groups unite. There can be no doubt as to the double origin of the 'midrib' thus formed, and it strengthens the presumption that the central bundle of *Y. aloifolia* is also double.

From these examples it is quite clear that the whole case for the absence of a true midrib in the cotyledon of Liliaceous

seedlings depends at present on the comparative study of the four central tribes within that family. The passage from two massive bundles to a reduced double bundle in the position of a midrib has been traced step by step within those tribes. From the double bundle of *Allium* to the single one of *Zygadenus* is an easy step, and if the 'midrib' of *Zygadenus* be of double origin, we can hardly, in the absence of further evidence, venture to assert that the midrib of *Veratrum* is single.

Similar reasoning applies to other characters of the vascular symmetry.

The observations which follow on the vascular system of seedlings belonging to other monocotyledonous families were made, as explained before (p. 1), on material already collected, and were purposely extended over a wide field. They led in the end to the selection of the Liliaceae for more detailed study, and in the light of the results obtained from it these preliminary observations have acquired a new value.

Many of the seedlings examined show a marked likeness in the form of their vascular skeleton to the seedlings of Liliaceous species. Such are the forms commonly found within the Amaryllidaceae and Iridaceae. *Anthurium* is a striking instance from the Aroideae.

The Palmae and Scitamineae, on the other hand, present types of their own. There is no embryological evidence to show that these are genetically connected with any Liliaceous form. But we may fairly ask whether their vascular structure is consistent with the theory of a single member formed by the union of two similar cotyledons.

#### Amaryllidaceae.

Six species belonging to four genera have been examined from this family.

Four species—*Alstroemeria* sp., *Bravoa geminiflora*, *Agave spicata*, and *A. Rovelliana*—follow Liliaceous types in the vascular structure of their seedlings.

The seedlings of *Doryanthes Palmeri* and *D. excelsa* are



remarkable both in external form and in their vascular symmetry. I shall describe the latter at some length, as it offers points of interest, though I believe it to be in all probability derived from some form resembling *Agave* rather than of more primitive character.

*Alstroemeria* (garden variety). The cotyledon remains in the seed as a sucking organ. It contains two bundles which, though distinct from each other down to the middle of the sheath, are close together, and occupy the position of a midrib. Just above the entrance of the plumular traces into the stele, the two cotyledonary traces approach each other, and their protoxylem groups unite. They now form a double bundle resembling that of *Allium* (Pl. V, Figs. 1 and 2). The plumular bundles unite to form two massive traces, and these enter the hypocotyl at the same time with the double trace from the cotyledon. The transition to a diarch root-stele takes place exactly as in *Arthropodium* (p. 30), but the stele subsequently becomes tetrarch. This takes place by the formation of new protoxylem groups (cf. *Fritillaria alpina*, p. 25); not as in *Chlorogalum* by the survival of two which were at first suppressed.

*Bravoia geminiflora*. The cotyledon remains within the seed as a sucking organ. It contains four bundles in the sheath, all quite distinct from each other. Two, distinguished from the others by their size and position, represent the main bundles. These two approach each other in the transitional region without uniting. The plumular traces insert themselves on those from the cotyledon, and the root-stele is triarch. Its formation seems to be governed by cotyledonary traces only.

*Agave spicata*. The whole seedling is succulent. The cotyledon, after sucking out the food from the endosperm, emerges from the ground as a green fleshy spike of triangular section, carrying the seed-coats on its apex. It contains four bundles, of which two, from their size and position, can be identified as the main bundles. There is a comparatively long hypocotyl in these seedlings, with a stele



containing three or four traces from the cotyledon, and these retain their stem-structure for some distance downwards. In one seedling I found six traces, for two entered it from the plumule, but this is exceptional. As a rule, a portion of each plumular trace is inserted on the ring of cotyledonary traces at the first node, without altering the symmetry of the transition, but the rest of the plumular stele is continued directly downwards, and becomes the stele of the first cauline root.

The structure of cotyledon and hypocotyl in *A. Rovelliana* seems essentially the same as that of *A. spicata*.

*Doryanthes Palmeri* The seedling is very stout and fleshy. The first leaf is rolled upon itself, and forms a trumpet-shaped cylinder which is in a straight line with the hypocotyl and primary root. The cotyledon projects horizontally from the axis. Its blade is a flat, thick disc, covered for some time by the brown seed-coats. It is attached to a very short petiole which clasps the axis with its massive sheath.

There are four main veins in the cotyledon, and they all enter the axis through the petiole. The plumular bundles form a ring of eight traces, which are joined at the node by the four traces from the cotyledon. These enter the stele in pairs, each pair displacing one of the plumular traces.

The stele of the hypocotyl now contains ten distinct bundles. Within this circle are the two plumular traces displaced by the entrance of the cotyledonary traces. The displaced traces are not adjacent to each other, but separated by two others in the original circle of eight, and with these two they now unite.

The hypocotyl in this species is comparatively long, 3 mm., even in quite young seedlings. The transition from a ring of ten stem-bundles to a 10-arch root-stele takes place gradually by branching and rotation of the xylem groups only—Van Tieghem's type 1.

The seedling of *D. excelsa* resembles that of *D. Palmeri* both in its external characters and its vascular symmetry.

For some time I was tempted to look on *Doryanthes* as a genus in which the seedling possessed characters more primitive in some respects than those of *Anemarrhena*. The two pairs of bundles, though distinct throughout, might be identified with the two massive bundles in the cotyledon of *Anemarrhena*, each of which behaves like a double bundle during the process of transition. The fact that the two pairs of cotyledonary traces enter the plumular stele at two distinct points suggested at first their origin from distinct members, but the arrangement may be merely adaptive to secure greater mechanical stability at the insertion of the cotyledon.

Until the seedlings of allied forms have been examined there can be no further comparative evidence concerning the origin of the peculiar vascular structure of *Doryanthes*. The seedlings of *Agave* and *Bravoa*—two genera nearly related to *Doryanthes* by their mature characters—are, as we have seen, designed on a Liliaceous model. I am inclined to believe the vascular symmetry of the *Doryanthes* seedling to be derived from that of some form resembling *Agave*. There are two reasons against supposing it primitive.

In the first place the seedling of *Doryanthes* is, both anatomically and in external form, of the shrubby or arborescent type, which is, as a rule, much modified in response to its environment. In the second, the floral structure of Amaryllids is clearly derived from the Liliaceous type, and we are therefore less likely to find a primitive form among them than within the Liliaceae.

### Iridaceae.

Four species representing two genera have been examined from this family.

The three species of *Iris*, *I. sibirica*, *I. Boissieri*, and an unnamed species from China, agree in possessing a single massive bundle which runs the whole length of the cotyledon, and opens out into a double bundle of characteristic form near the base of the sheath. Plumular traces take part in the transition to a root-structure, and the root is tetrarch (*Iris* sp.

and *I. sibirica*) or triarch (*I. Boissieri*). The root of *Iris sp.* appears diarch when first formed, but very soon becomes tetrarch, and the whole process of transition, so far as it could be followed in the rather old seedlings, recalled that of *Chlorogalum* (p. 29).

*Freesia sp.* (garden variety). The cotyledon contains three bundles in its lower part or sheath, and the central one appears double just above the first node. One plumular trace at least takes part in the transition. The root is tetrarch.

### Aroideae.

Three species representing three genera have been examined from this family; *Arum maculatum* very thoroughly, the others in less detail.

The structure—internal and external—of the *Arum maculatum* seedling has been described elsewhere (36). The seed ripened in the summer may germinate before winter, or remain dormant until the spring. In either case no part of it appears above ground until the second spring after the seed has been sown.

The apex of the cotyledon remains within the seed as a sucking organ, while the lower part is transformed into a cylinder which sheathes the young stem-bud and is terminated by the hypocotyl. This begins to be thickened in the early stages of germination, and it swells into a tuber as the stores of food are transferred to it from the endosperm through the bundles which run down the cotyledonary tube. By the end of the summer following the sowing of the seed, the whole cotyledon, having emptied the seed of its food-supplies, is detached from the tuber. The stem-bud is exposed by the removal of the tube which has hitherto surrounded it, and in the following spring the first green leaf pushes through the soil.

The vascular system of the cotyledon has been profoundly modified by its peculiar habit. Of its five bundles the central one is larger than the others, but it never appears double. The plumular traces are inserted at the first node on those



from the cotyledon. They rarely affect the symmetry of the root-stele, which is commonly triarch. It depends on the central trace from the cotyledon, and a lateral trace on either side of it. Each of these lateral traces is formed by the fusion of a pair of lateral bundles. The transition takes place according to Van Tieghem's type 3. The xylem groups are continued straight downwards, the protoxylem becoming external on the way, and each phloem group divides, the right-hand segment of one uniting with the left-hand segment of the next.

Nothing in the vascular symmetry of *Arum* suggests a relationship with any Liliaceous type. All that can be said is that the possibility of such relationship is not excluded. The seedling of *Arum maculatum* is hardly more unlike that of *Anemarrhena* in its vascular structure than is that of *Veratrum*, for instance.

The seedling of *Arisaema speciosum* resembles that of *Arum* in many points. The tuber is already formed very shortly after germination, and the first green leaf makes its way out of the cotyledonary sheath early in the first season of growth. The cotyledon contains seven or nine bundles, and the primary root is either triarch or tetrarch.

*Anthurium Bakerianum* differs completely from the genera just described both in the external form and in the internal structure of its seedling. The cotyledon remains underground—its apex enclosed within the endosperm of the seed. The petiole of the cotyledon is short, and its base is expanded into an open sheath which shelters the plumule without enclosing it. The first leaf develops early. It breaks through the soil and becomes green, while its base sheathes the younger leaves and the growing point. They are thus safely packed between the cotyledon and the first leaf.

Sections through the apex of the cotyledon as it lies within the endosperm show two bundles within it. They unite before passing into the petiole, and the bundle which enters the sheath of the cotyledon is apparently single. During the transition, however, it opens out into a double bundle.



A single trace from the plumule approaches the double cotyledonary trace, and with it forms a diarch root-stele. The transition from stem to root takes place precisely as in *Zygadenus* (Pl. V, Figs. 9-12).

These facts certainly suggest that *Anthurium* is a form intermediate between the typical Liliaceous type and that of *Arum* and *Arisaema*, and this is the position assigned to it by systematic botanists on the evidence of its floral structure.

If the relationship between *Arum* and the primitive Lily-type be admitted, we have still to decide which of the two is the older. Does the line of descent start from the mother-form of the Lily family and end in such genera as *Arum* and *Arisaema*, or do these represent a type earlier than that of the Lilies?

The succession suggested by the structure of their seedlings is from *Anemarrhena*, through forms perhaps resembling *Chlorogalum* and *Arthropodium*, to others like *Allium* and *Zygadenus*; thence to *Anthurium*. We may hope that future research will fill up the gap between *Anthurium* and *Arum*. Should it do so, would it be possible to read the chain backwards with equal probability?

If we make the attempt, we must suppose the point at which *Anthurium* approaches the Liliaceae to be that of greatest antiquity. A form resembling *Zygadenus* in the structure of its seedling must be accepted as the primitive type of that family. But the comparative study of seedling forms within the Liliaceae has shown that types of vascular symmetry differing so widely from each other as those of *Eremurus*, *Zygadenus*, and *Eucomis* can all be referred to a single scheme—that which I have called type 4 (Diagram VI, p. 26). It is incredible that these genera should possess three distinct types of vascular structure in their seedlings, each of which should be modified through three distinct lines of descent until they all reached the same well-marked form—a form, moreover, which then appears in two genera such as *Anemarrhena* and *Albuca*, which have been always placed in separate tribes owing to the difference in their mature characters.

These considerations lead to the conclusion that *Anthurium* must be held a more primitive type than *Arum* or *Arisaema*.

### Palmae.

A number of young Palm seedlings were included in the Kew collection, and of these I have examined nine species. In three of them my observations are very incomplete, owing partly to a want of material at the proper age, and partly to difficulties of manipulation. The vascular structure of young Palms has often to be worked out by hand sections only, as the woody tissues of the axis do not embed well in paraffin.

Good microtome series have, however, been cut through the hypocotyls of *Desmoncus minor*, *Thrinax excelsa*, *Areca sapida*, and *Phoenix dactylifera*, and hand sections have given good results in two other species, *Desmoncus sp.* and *Acantho-phoenix crinita*. I can give a fairly complete account of the vascular system in the seedlings of these six species, though even here the details are commonly obscured by the massive development of the plumular traces due to the comparatively advanced age of the seedlings.

The external characters of all the Palm seedlings I have seen are much modified from the ordinary monocotyledonous type by the arborescent habit of the family, and their internal structure is not less profoundly affected. The first leaves are developed early. Their tissues are hard and woody from the first, owing to the number of vascular bundles developed within them and the stiffening of those bundles by massive sclerenchymatous sheaths. The primary root is always pretty well developed, and is sometimes the main root for a long time (*Thrinax excelsa*, *Chamaerops humilis*). In other species it is soon surpassed in length and thickness by the first cauline root. The vascular system of the latter is commonly the direct prolongation of plumular traces, as that of the primary root is of cotyledonary traces.

The tip of the cotyledon is merely a sucking organ, which for many months after germination continues to supply the seedling with nourishment from the stores laid up in the

endosperm. The lower part of the cotyledon plays many parts, and is modified in shape and texture to suit the habit of the seedling.

In *Thrinax excelsa* the plumular axis is connected with the seed by the long and rather slender petiole of the cotyledon. This expands at the base into a tough membranous sheath which completely surrounds the axis at its insertion. The four cotyledonary bundles run downwards through the sheath, in the same direction as the plumular traces, but outside them. Just above the node these four bundles form the outermost of a series of concentric circles in which all the traces of the axis are arranged, and they are equidistant from each other. At the first node the traces from the cotyledon run inwards—from the four points of the compass, as it were. Four plumular traces alternate with them in the stele of the hypocotyl, and the remainder are inserted on one or other of the circle of eight traces. An octarch root-stele follows quite regularly, apparently according to Van Tieghem's type 1, by branching of the xylem groups.

In *Desmoncus* sp., *D. minor*, *Areca sapida*, and *Acantho-phoenix crinita*, the cotyledon has a short petiole and a thick fleshy sheath which is continuous with the primary root. The plumule is inclined to the cotyledon—sometimes almost at a right angle—and its traces are commonly continued downwards into one or more cauline roots, which penetrate the fleshy tissue of the cotyledonary sheath.

The apex of the cotyledon in the four species we are considering contains from ten to twelve bundles, irregularly disposed in a circle and without any trace of a midrib. Near the base of the petiole these become reduced to four by fusion with each other. In the sheath they approach each other in pairs, and when the plumular traces appear in the section the cotyledonary traces have united to form two massive bundles facing each other.

Sections which cut the cotyledonary traces transversely must of course pass through the plumular traces obliquely, and this distinction enables us to follow the course of the



cotyledonary traces into the root-stele. They are always accompanied by two or three plumular traces, and they enter the stele from opposite sides. Thus the two groups of cotyledonary elements in the xylem of the root-stele are separated from each other by two or more groups of plumular elements. The root is often tetrarch or pentarch: sometimes hexarch or heptarch. The details of transition are never quite clear, but the process follows Van Tieghem's type 1. In *Desmoncus* sp. the root, which is tetrarch when first formed, becomes octarch lower down.

The habit of the seedling of *Phoenix dactylifera* is very distinct from that of any of the Palm seedlings just described. The bundles of the inflated cotyledonary sheath form a circle of about ten, which are all continued into the primary root. The plumular traces are of course internal to this circle from the beginning. They are inserted on the cotyledonary traces without affecting the symmetry of the primary root-stele. The transition to a root-structure takes place by the branching of the xylem (Van Tieghem's type 1), and the root is commonly 10-arch.

The absence of a midrib in the cotyledon of the Palms is conspicuous not only in all the seedlings described, but also in two others which I have partly examined, *Geonoma oxycarpa* and *Chamaerops humilis*. But it should be added that the foliage leaves do not always possess a midrib, and that when present it is little distinguished from the others.

The adaptations to an arborescent habit are so well marked in all the species that the presumption is certainly against the primitive character of any particular feature. I may, however, mention that the well-grown cotyledon of *Chamaerops humilis* when extracted from the seed is seen to have a bifid apex. I remarked on this in my notes before the theory of a compound cotyledon had occurred to me, and compared it to the two lobes of a brain. The cotyledon of *Ch. Fortunei* is still more completely bilobed. This may very possibly be an adaptive character, but I should be glad to know whether it occurs generally among large-seeded Palms.



On the whole the point to which I attach most importance is the gathering-up of the cotyledonary bundles into two groups which occurs in four out of the six species I have examined with care. Of the three species partially examined *Euterpe edulis* appears to resemble *Thrinax*, but the whole process is obscure. The cotyledonary traces have not been followed into the hypocotyl in *Geonoma* and *Chamaerops*.

Thus in four species out of seven there is a twofold symmetry in the traces of the cotyledon within the transitional region. In two more the symmetry is fourfold. The seventh, *Phoenix dactylifera*, shows an exceptional vascular symmetry corresponding with the exceptional habit of the whole seedling.

### Scitamineae.

Five species from five different genera of this family have been worked out by Miss Thomas with success. They fall naturally into two groups.

The species of *Musa* and *Canna* are large and generally fleshy plants. Their seedlings resemble those of arborescent or shrubby genera, and their vascular symmetry corresponds to this habit. A number of massive bundles are found in the cotyledon. They are continued downwards into the hypocotyl, and with the assistance of plumular traces they form a poly-arch root-stele.

The seedlings of *Amomum*, *Elettaria*, and *Renealmia* are of a different character, less fleshy, and rather of the herbaceous than the shrubby type. The three species examined in detail are *Amomum angustifolium*, *Elettaria cardamomum*, and *Renealmia racemosa*. Their vascular symmetry is strikingly similar.

The apex of the cotyledon remains permanently in the seed. It contains two bundles which there appear equivalent. They run the whole length of the petiole and sheath. But in the upper part of the sheath they are not symmetrically placed with regard to its outline. One occupies the position of a midrib, while the other might be taken for a lateral bundle without a pendant on the other side. This want of

symmetry is probably due to mechanical causes. The seed is connected with the main axis by the long slender petiole of the cotyledon, and this enters the rather complicated cotyledonary sheath at an acute angle. The two bundles are so placed as to give strength and elasticity to the junction.

In all three species there is a fairly long hypocotyl; that is, the plumular traces join those from the cotyledon some distance above the level at which the stele becomes completely root-like. The cotyledonary traces are placed opposite each other in the sheath just above the first node, and in this region they seem perfectly equivalent.

The traces of the cotyledon enter the hypocotyledonary stele from opposite sides, and are separated by two plumular traces. The other bundles of the plumule are inserted on one or other of these four traces at the first node.

The fourfold stele below the first node has a very characteristic appearance. Each of the four xylem-masses is crescent-shaped, and each group of phloëm is placed in the concavity of a crescent. As the eight horns of the xylem crescents reach the pericycle and form four pairs of xylem rays alternating with four phloëm groups, we seem at first to be looking at a tetrarch root. Closer inspection shows that the centre of the stele is occupied by a single group of protoxylem formed by the union of four internal groups. From this centre radiate four narrow rays of parenchymatous tissue dividing the four xylem crescents from each other.

Before the protoxylem becomes external a number of cauline roots are given off from the stele almost simultaneously. There are commonly four of these, and each is placed opposite one of the parenchymatous rays.

The primary root is tetrarch in *Renalmia racemosa* and *Elettaria cardamomum*. In the only complete series cut from *Amomum angustifolium* the central stele vanishes after giving off four cauline roots simultaneously. There would seem to be no primary root at all. This may be an individual peculiarity, or the primary root may be present but inclined at such an angle as to be mistaken for a cauline root.

There are points in this structure which recall that of *Thrinax*. The most important feature is, I think, the presence of two equivalent bundles in the cotyledon.

The twenty-five species of Monocotyledons—exclusive of the Liliaceae—which have just been described, fall naturally into two groups. The anatomy of seedlings belonging to the Amaryllidaceae, Iridaceae, and Aroideae seems to be derived from a Liliaceous type. That of the Palmae and Scitamineae is distinct in character, but the dual symmetry of the cotyledon is not less marked. The evidence from these two families, so far as it goes, is perfectly consistent with the hypothesis of a double cotyledonary member, and even gives it some support.

#### PART II. RANUNCULACEAE.

No detailed comparative study of this family has been attempted. The seedling which first attracted my attention was that of *Eranthis hiemalis* as described by M. Sterckx (38), to whose excellent monograph I have referred elsewhere. Since repeating his observations on the vascular system of *Eranthis* with particular reference to the tuberous hypocotyl, I have examined the seedlings of two other species possessing cotyledonary tubes: *Delphinium* sp. (possibly *D. nudicaule*) and *Anemone coronaria*, and also two species with distinct epigaeic cotyledons, *Delphinium Requierii* and *Nigella damascena*.

M. Sterckx has shown that the single cotyledonary member of *Ranunculus Ficaria* is in all probability formed by the union of two cotyledons by one margin only. I have repeated his observations on the external features of this seedling, and have made a careful study of the course of the vascular bundles in the cotyledon, hypocotyl, and primary root. For comparison two other species which show apparent lateral insertion of the cotyledons were chosen, *Ranunculus Chius* with epigaeic, and *Anemone nemorosa* with hypogaeic cotyledons.



Eight species in all, representing five genera, have been examined, and will now be described in more or less detail.

The seedling of *Nigella damascena* has been chosen as the type of vascular structure in this family by MM. Gérard (13), Dangeard (9), and Sterckx (38). There is nothing to add to their account of the anatomy of the hypocotyl in this species. An outline of it will be sufficient here. The vascular symmetry agrees in all essentials with that of *Delphinium Requierii*, and Diagram IX represents the transition from a stem to a root structure within the hypocotyl of both species.

The three main bundles of the blade enter the petiole of each cotyledon, but soon unite to form a single massive bundle. This is particularly clear in *Delphinium Requierii* because, owing to the greater length of the petioles in this species, the union of the lateral bundles with the midrib takes place at some distance above the insertion of the cotyledons on the axis. At the level where it is joined by the lateral bundles the midrib is still to all appearance single.

Near the base of the petiole, the single massive bundle of each cotyledon opens out into a double structure precisely similar to that formed by each cotyledonary trace in *Anemarrhena* (Diagram VI). Both in *Nigella* and *Delphinium* however the double character of each bundle is very clear a short distance above the insertion of the cotyledonary traces on the plumular stele. M. Dangeard is so much struck by this feature in the cotyledon of *Nigella* that he does not hesitate to describe its petiole as containing two bundles (9, p. 85). In this interpretation of the structure I entirely agree: the vascular symmetry of this genus and those which resemble it is much simplified by supposing four cotyledonary traces to enter the root-stele. A similar assumption has already been made with regard to the two traces of the cotyledon in *Anemarrhena* (p. 6).

The resemblance between the vascular symmetry of *Delphinium* or *Nigella* and that of *Anemarrhena* is obscured at the first node from a very simple cause. The traces of the

plumular stele are much more numerous and better differentiated in the Ranunculaceous seedlings examined than in seedlings of *Anemarrhena* which have reached the same stage of development. In *Anemarrhena* the plumule lags far behind the cotyledon. Moreover, among Dicotyledons a cambium is very well developed in the traces of both. Its position is indicated by the waved line in Diagram IX.

The stele of the hypocotyl is elliptical in *Delphinium* and *Nigella*. The two groups of cotyledonary xylem are placed at the extremities of the major axis, while two of the four phloëm masses fuse with each cluster of plumular phloëm

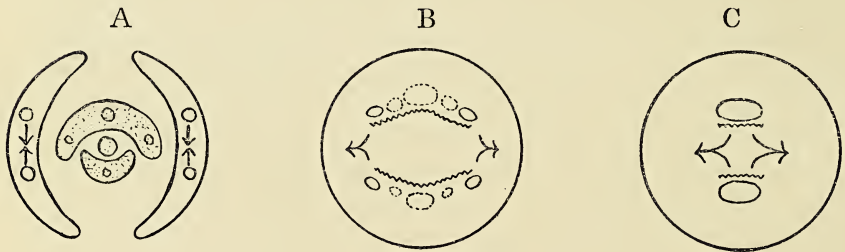


DIAGRAM IX.

groups (B, Diagram IX). The root-stele becomes diarch at once. A considerable part of the metaxylem, as well as much of both phloëm groups, is derived from plumular traces.

These changes take place in the upper part of the elongated hypocotyl, and are commonly complete a few millimetres below the first node.

Several species of *Delphinium* have the petioles of their cotyledons united into a tube, and I have made a complete examination of one such species, probably *D. nudicaule*. The first leaves of this species are developed in the summer after germination, and they soon burst out of the sheath formed by the base of the united cotyledons (Lubbock, 30, vol. i. p. 97).

The cylinder formed by the united cotyledons is solid

for about two-thirds of its length downwards from the insertion of the blades. In the lower part there is a small central cavity, not very clearly defined in transverse section, which gradually opens out as it descends, and so forms the conical chamber enclosing the stem-bud.

Two opposite bundles, one from each cotyledon, run the whole length of the cylinder, and each remains single until it reaches the level of the plumular growing-point. Here both begin to open out into a double structure. The activity of the cambium within them is already marked: at this level in a seedling so young that the first leaf is a mere rudiment in which the midrib is just indicated, two rows of radial unlignified xylem elements are found in each trace inside the cambial zone.

As in following the series of sections from this seedling we approach the first node, two unlignified plumular traces appear opposite each other between the two traces from the cotyledon. The stele is elliptical as in B, Diagram IX. A well-marked cambium is present in all the traces, and also between them. It forms a complete ellipse enclosing all the xylem. The formation of secondary tissue has already begun within the traces, where we find two or more rows of unlignified xylem elements outside the primary xylem which is also as yet unlignified.

The formation of secondary tissue reaches its maximum a little lower down, where in this young seedling the primary elements belonging to the plumular traces have almost disappeared. The four cotyledonary phloëm groups are approaching each other in pairs. They are separated from the well-lignified primary xylem of the cotyledon by a considerable bulk of secondary tissue. The secondary formations are best developed in those segments of the ellipse which were occupied by plumular traces: they are thinnest outside the two groups of cotyledonary xylem, in which the protoxylem is already external.

The diarch root-stele is formed as in Diagram IX. The activity of the cambium decreases in the lower region of



the hypocotyl, but a true cambial zone is still found in the upper part of the root.

The vascular symmetry of this species is practically identical with that figured in Diagram IX as the normal Ranunculaceous type. The only peculiarity which deserves notice is the precocious development of a cambium, and its extraordinary activity. This suggests that the growth of the hypocotyl into a spindle-shaped tuber, which is well marked at the end of the season, may be due to tissues added by the action of a normal cambium-ring. If so, the mature tuber may resemble that of *Corydalis solida* (Jost, 28).

The seedlings examined of *Anemone coronaria* are all much older than those of *Delphinium sp.*, whose structure has just been described. The vascular symmetry of their cotyledon, hypocotyl, and primary root is however identical with that of *Delphinium sp.* Much more secondary tissue is present, and the stele has become circular owing to the greater activity of the cambium opposite the plumular traces. The secondary tissues are continued downwards far below the level at which the stele has become root-like. At no level have I found lignified secondary tissue outside the two protoxylem groups of the central plate of primary xylem, but radial rows of five or six well-lignified elements are found on the outer side of the plumular metaxylem, forming buttresses as it were to the central xylem plate. The two phloëm groups of the original diarch root-stele can still be identified, but they are isolated between the secondary tissues and the pericycle at a considerable distance from the centre of the section.

The growth of *Eranthis hiemalis* from the seed has been followed by Irmisch with his usual care (24). Nothing can be added to his account of the external characters, but for convenience I will briefly describe a first-year seedling (Pl. VI, Fig. 1). The cotyledonary tube is very long, and the lower part is buried in the soil. Its base is inserted on a small tuber, which is spindle-shaped when first formed but later becomes globular. The plumule is quite rudimentary at this age: it is seated on the tuber and enclosed within the

conical sheath formed by the base of the cotyledonary tube. The lower part of the tuber tapers off into the primary root.

Irmisch describes the cotyledonary tube as hollow throughout, and speaks of the cavity enclosing the plumule as in communication with the outer air through the narrow tunnel which opens between the blades of the cotyledons (24, p. 221). In the series of sections cut by the microtome through the tuber and adjacent parts of three young seedlings, however, I find a diaphragm of thin-walled tissue above the extinguisher-shaped sheath which encloses the plumule. The narrow bore of the tube itself is far less well outlined in transverse section than the plumular cavity, and is separated from it by the diaphragm just described. So far as can be determined from a number of hand-sections at different levels through the cotyledonary tube, it is hollow throughout, but one or more diaphragms may quite possibly exist above that which seals the plumular cavity. As the tuber increases in girth and the plumule in size, the base of the cotyledonary sheath is distended, and cracks appear in the diaphragm. These fissures may connect the cavities separated by the diaphragm, but only towards the end of the season when the cotyledons are withering.

No part of the plumule appears above ground until the second season after germination, but at the end of the first summer it is no longer embryonic. The first foliage leaf is then completely formed and ready to push upwards on the approach of spring (Irmisch, 24, Fig. 15).

The massive bundles run the whole length of the cotyledonary tube and are continued into the tuber (Irmisch).

Any one of my three series of transverse sections through the tuber shows that it is simply the hypocotyl, swollen by the development of the cortex and conjunctive tissue into a storehouse for starch and other food-material. The vascular system of the first-year tuber is derived exclusively from the cotyledonary traces, for during the time that this system is developed the plumule is still so embryonic that the position of its procambial strands is not even indicated. The process

of tuber-formation in this species is thus quite distinct from that described in *Delphinium sp.* and *Anemone coronaria*. The increase of girth was there due to the formation of secondary tissue by a normal cambium, and the plumular traces took a large share in the formation of its vascular system.

The behaviour of the cotyledonary traces when they enter the axis is indicated in Diagram X and very fully illustrated on Plates VI and VII.

The sections drawn in Figs. 2-6 of Pl. VI and Figs. 1 and 2 of Pl. VII are from a single series cut through the tuber of

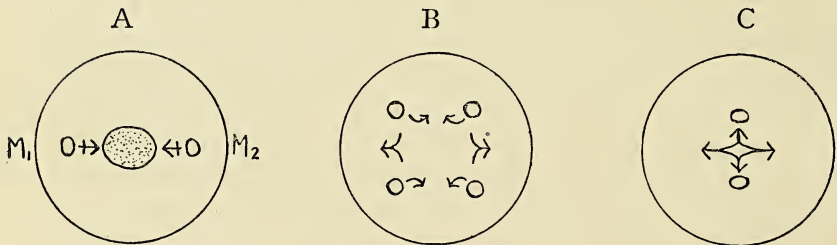


DIAGRAM X.

a seedling younger than that outlined in Fig. 1, Pl. VI. The bundles of the cotyledon show traces of double structure even before they leave the cotyledonary tube. There are traces of cambium between the phloëm and xylem of each (Pl. VI, Fig. 3). The compound nature of the traces becomes more clearly evident as they enter the tuber. A little lower down the phloëm groups of each pair have drawn further apart, and the xylem elements are in three clusters: one internal to either group of phloëm and one solitary between the other two (Fig. 4). This intermediate cluster then breaks up into two parts, and we have eight xylem and four phloëm groups arranged symmetrically in two parallel straight lines, each of which is equidistant from the periphery of the section and its centre (Fig. 5).

Down to this level the three complete series of sections



which I have compared with each other agree in every detail. They are cut from three seedlings, of which  $A_6$ , that outlined in Fig. 1 (Pl. VI), is the oldest, and  $A_2$ , from which Figs. 2-6 are drawn, is the youngest. The intermediate seedling  $A_5$  is nearly as old as  $A_6$ . The course of the bundles in the region intermediate between Fig. 5, Pl. VI and Fig. 1 on Pl. VII is indicated in B, Diagram X. The details of the process differ slightly in the three seedlings cut.

In all three the traces keep to a zone which lies about half-way between the periphery and the centre of the tuber, and their course downwards follows its outline, first curving outwards and then closing in again. The formation of a phloëm girdle is suggested even in  $A_2$ , and is indicated much more completely in the older seedlings  $A_5$  and  $A_6$ . The four groups of xylem internal to the phloëm groups (Fig. 5) show a tendency to split into two or even three strands. In seedling  $A_2$  one only of the four xylem bundles splits in this way—the lowest in Fig. 5. When the four protoxylem groups of the early root-stele are in course of construction, which is always much lower down in the tuber, we find in  $A_2$  that the xylem group in the lower left-hand corner of the section is being built up of three strands instead of two (Fig. 6). Moreover, an offshoot from the aberrant group of xylem has already ended blindly.

The four corresponding xylem groups of seedlings  $A_5$  and  $A_6$  commonly split into two or more strands. To follow each minute cluster of xylem elements through a series of sections cut from a comparatively massive tuber is a task requiring some patience. I have done so in these three seedlings, and have convinced myself that the result may be fairly represented by the generalized Figure B in Diagram X. The strands from each original group commonly unite again lower down: anastomoses with adjacent groups do occur, but are exceptional. The whole process is clearly an adaptation to the needs of the tuber. I suspected at first that a complete xylem network was indicated with which the first cauline roots would later be connected, but a series of sections

cut through a second-year tuber by Miss Thomas shows that no regular network exists there. The xylem strands are better developed than in the first-year tuber, but travel downwards in the same isolated way. Where a cauline root is given off, the xylem strands in the immediate neighbourhood collect together and anastomose.

The irregularities in the vascular system of first-year tubers affect the four xylem strands only which are in the neighbourhood of phloëm groups, and do not extend to the two pairs of slender xylem strands between them ( $x_m, x_m$ , in Fig. 5, Pl. VI). Their behaviour is remarkably uniform in all three seedlings. Each pair is derived, as has been shown, from a single xylem strand, and the two halves reunite about halfway down the tuber, or even earlier. The two xylem groups thus formed on opposite sides of the tuber preserve their identity, and are continued downwards into the root, where they form the two permanent protoxylem groups of the root-stele. It is exceedingly rare to find any connexion between these xylem groups and the other strands scattered round the tuber.

These scattered strands draw together in two groups, phloëm and xylem alike, and form two bundles facing each other. Fig. 6 on Pl. VI shows the orientation of such a stele in process of formation. To right and left are clusters of xylem elements unaccompanied by phloëm, and with the protoxylem elements already external. To the north-east of the stele, as it were, is a slender bundle having an external phloëm group, three lignified elements within it representing the primary xylem, and two radial rows of two unlignified elements each to represent the secondary formation. A similar group is in course of formation on the opposite side.

At the base of the tuber the stele closes round the centre of the section, and a tetrarch xylem plate is formed. Two phloëm groups only are present, and these are placed outside the two lateral protoxylem rays ( $px', px'$ , in Figs. 1 and 3 on Pl. VII). The outermost elements of these rays can be traced backwards and identified as part of the primary forma-

tion in the bundles of the tuber. There are often two or three unligified secondary elements in rows outside them (Pl. VII, Fig. 3).

The two protoxylem groups which are flanked by phloëm shortly die out, and the root is left with a diarch stele (Pl. VII, Fig. 2).

The vascular symmetry of *Eranthis hiemalis* has already been compared with that of *Anemarrhena* (pp. 4 and 5, and Sargent, 35, Pl. 2). The resemblance is clear from Diagrams VI and X. I will not go over the ground again. But some remarks may be offered on the difference between these types.

The formation of a diarch root-stele in the typical Ranunculaceous seedling is clearly connected with the insertion of a vigorous plumular stele on the comparatively insignificant cotyledonary traces, and the continuation of both into the persistent primary root (cf. Diagram IX). In plumule and root alike, secondary thickening is early developed and plays an important part. They are connected largely by means of secondary xylem, while the primary xylem of the cotyledon is continued downwards into that of the primary root. We may conceive a remote ancestor of the Ranunculaceae to have possessed four cotyledonary traces which regularly formed a tetrarch primary root by branching of the xylem according to Van Tieghem's type I, and that its comparatively slender plumular traces were inserted on two opposite traces of the hypocotyledonary stele. Then if the plumule began to increase in importance and develop earlier, its traces would exercise an increasing influence on the stele of the hypocotyl. The plumular phloëm would by degrees unite with the adjacent cotyledonary groups, and thus form a single huge mass on either side of the stele. The secondary formations produced by the action of plumular cambium between each mass of phloëm and the cotyledonary xylem within it would in time arrest the development of the latter, and perhaps suppress it altogether. Finally, the root-stele would become completely diarch. The vascular systems of *Albuca* (p. 9), *Chlorogalum*, *Anthericum*, and *Anthropodium* (p. 30)



show how readily a tetrarch root-stele may become diarch by suppression of opposite protoxylem rays.

The hypothetical vascular system at which we have now arrived corresponds very closely to the Ranunculaceous type (Diagram IX). In this two cotyledonary traces only enter the hypocotyl, but they give very clear evidence of their double origin, as M. Dangeard has already remarked (9). In every other respect the schemes are identical.

Returning to the hypothetical Dicotyledon, whose seedling has a fourfold symmetry throughout its vascular system, let us suppose the development of the plumule to be arrested rather than accelerated, and secondary thickening to disappear altogether from the axis. This development of the vascular scheme leads to a symmetry closely resembling that of *Anemarrhena*. The latter indeed possesses but two cotyledonary traces, but each gives very clear indications of its double origin when it enters the hypocotyl.

To derive the vascular system of *Eranthis hiemalis* from our four-partite ancestor, we must suppose the plumule to have increased in importance up to a point at which the tetrarch symmetry of the root has almost disappeared. The whole vascular system was developing on Ranunculaceous lines. But at this point the ancestor of *Eranthis* parted company with its fellows. The plant perhaps had to adapt itself to different climatic conditions. These postponed the development of the plumule, and led to the formation of a tuber from the hypocotyl by the increase in mass of cortex and conjunctive tissue. This process gradually put a stop to secondary thickening by isolation of the bundles within the tuber, and the vascular system became what we see it in *Eranthis*.

Little weight can be attached to hypothetical genealogies of this kind. They are valuable only as suggesting lines of research. In this case the investigation of forms allied to *Anemarrhena* on the one hand and to *Eranthis* on the other may yield valuable results. The seedlings of other species of *Eranthis* are, I believe, still undescribed even in their external characters. Their vascular structure is entirely unknown.

The homology of the single seed-leaf of *Ranunculus Ficaria* (Pl. VII, Fig. 4) has been much discussed. The reasons given by M. Sterckx (38, p. 43) for considering it a fusion of two cotyledons seem very strong.

He points out that the venation of the bifid blade suggests its double origin. I have repeated his observations (Fig. 5) and agree in this conclusion. The blade is folded in the seed, and retains a well-marked median crease which is easily mistaken for the midrib in fresh material. But when the blade is blanched by immersion in methylated spirit, and has then been made transparent by treatment with phenol, the course of the veins can be accurately followed. Two main veins traverse the two segments of the blade respectively. Branches from both of these run upwards near the median crease, and when such branches unite with each other they sometimes appear to form a true midrib (B<sub>1</sub>, Fig. 5). In other specimens its absence is clear (A<sub>3</sub> and A<sub>4</sub>, Fig. 5).

The formation and maturation of the embryo within the seed has been followed and described with great care by M. Sterckx (38, p. 42, and Figs. 151-9). The embryo in the ripe seed is very small. It is spherical, quite undifferentiated, and attached to a short suspensor. The cotyledonary member is lateral throughout its development. It is distinctly bilobed by the end of the summer in which the seed is sown. Throughout the following summer the development of the embryo continues within the seed. It germinates in the second spring, nearly two years after the seed was ripened.

The 'cotyledon' comes above ground at once on germination, and acts as the first assimilating organ. Its petiole is in a straight line with the hypocotyl and primary root. The lower limit of the hypocotyl is rather sharply defined externally by the sudden decrease in diameter of the axis where the primary root begins, but the upper limit cannot be determined until the position of the plumule is ascertained. It first appears as a slight swelling at the base of the cotyledon. Sometimes the first cauline root, always formed immediately below the plumule, shows first as a little tooth pointing

downwards (Fig. 4, Pl. VII). The length of the hypocotyl defined by its external characters varies from 5 mm. to 1 mm., or even less in the seedlings I have examined.

The external features of this seedling have been so fully described by Irmisch (21, p. 1) and Sterckx (l. c.) that I may go on at once to its vascular structure. The three seedlings  $A_3$ ,  $A_4$ , and  $B_1$ , from which I have cut complete series of sections, agree with each other in every detail. That figured on Pl. VII is the youngest of the three.

A single massive bundle runs down the whole length of the cotyledonary petiole. It is enclosed in a well-defined endodermis and contains a normal cambium layer. The phloëm is a compact rounded strand, and there is a single protoxylem group, but the elements of the metaxylem form two distinct clusters separated by a few thin-walled cells. At the base of the cotyledon the petiole is bordered by two membranous wings which are united round the embryonic bud of the plumule into a closed sheath. At this level the cotyledonary trace has opened out slightly: the phloëm mass is divided as well as the metaxylem. A single plumular trace joins it at the first node (Figs. 6 and 7). As they meet, the plumular trace becomes double and opens out in the same way as that from the cotyledon (Fig. 7). Very little below this both groups of protoxylem have become external, and a diarch root is constituted (Fig. 8). The process of transition recalls that found in *Zygadenus*.

The length of the hypocotyl defined by its vascular characters does not exceed .5 mm. in any of the seedlings cut.

The lateral position of the cotyledonary member is clearly an advantage to the plant. It allows the foliage leaves to develop unchecked by the necessity of bursting through a tubular sheath, as they must do in *Delphinium nudicaule* and *Anemone coronaria*. The 'cotyledon' of *Ranunculus Ficaria* may possibly have been derived from a tubular fusion such as that found in these plants. *R. parnassifolius* possesses a long cotyledonary tube (Winkler, 44), and *R. millefoliatus* a shorter one (Irmisch, 26, p. 29). But it seems more likely that the



two cotyledons from which the seed-leaf of *R. Ficaria* has been formed became united by one margin only from the first. M. Sterckx describes such a formation in *Anemone apennina* (38, Figs. 76, 77). An abnormal seedling of *Ranunculus repens* in which the cotyledons are partly united by one margin is figured by Lord Avebury (Lubbock, 30, vol. i. p. 90). I have found the cotyledons of *R. Chius* to be so united in the only three seedlings I have seen, but in no case more than halfway up the petioles.

Sections through one such seedling of *R. Chius* show that the vascular structure is by no means unilateral at the base of the cotyledons. They are united into a shallow cup round the plumular bud, and a trace from each enters the short hypocotyl at opposite extremities of a diameter. The transition to a root-structure follows the usual Ranunculaceous type (Diagram IX).

The same is true of *Anemone nemorosa*, in which the hypogaic cotyledons have a false appearance of being inserted laterally so long as they are held together by the seed-coats. The few diagrams given by M. Sterckx of the vascular structure in *A. apennina* suggest that it may possess characters really intermediate between the usual type and that of *Ranunculus Ficaria*.

### PART III. GENERAL CONSIDERATIONS ON THE ORIGIN OF MONOCOTYLEDONS.

In the first Part of this paper I have given a full abstract of my observations on the vascular symmetry of Monocotyledonous seedlings, and have attempted to show that the facts justify the following conclusions:—

The vascular symmetry characteristic of the seedling in the monotypic genus *Anemarrhena* represents a type which is comparatively primitive among the Liliaceae. For many types of seedling structure found within that family can be shown with great probability to be derived from it, and the other types described are either clearly much modified by their environment, or so isolated systematically from the rest

of the seedlings examined that the absence of intermediate links is of little weight.

The *Anemarrhena* type of vascular structure is bisymmetrical throughout, and suggests a double origin for the cotyledonary members.

The vascular symmetry of the seedlings examined from other Monocotyledonous families can be either derived from a Liliaceous type, or shown to be equally bisymmetrical.

In the second Part I have described the vascular structure of a number of seedlings belonging to the Ranunculaceae which possess cotyledons more or less completely united to each other. When the united cotyledons are symmetrical with regard to the plumular axis—as in *Eranthis hiemalis*, *Delphinium sp.*, and *Anemone coronaria*—their vascular structure is bisymmetrical, and that of *Eranthis* bears a close resemblance to the structure of *Anemarrhena*. When the cotyledonary member is unilateral, as in *Ranunculus Ficaria*, its vascular structure is asymmetrical with regard to the axis.

The strength of this comparison does not depend wholly on the suggestion of a real genetic relationship between *Anemarrhena* and *Eranthis* for example, though I am inclined to think such a relationship probable, but rather lies in the fact that a partial union between two cotyledons does actually give rise to a reduced vascular system which bears a strong likeness to that existing in *Anemarrhena* and *Albuca*, a system already shown on comparative grounds to be in all probability the original of other Monocotyledonous types.

The derivation of a seedling with unilateral vascular symmetry, such as that of *Zygadenus elegans*, from a symmetrical form like *Anemarrhena*, has been justified by the examination of vascular systems intermediate between these extremes. The actual genealogy of *Zygadenus* is still of course conjectural, but the *a priori* probability of such a descent is certainly increased by the analogy with *Ranunculus Ficaria*. The origin of the cotyledonary member in this species has already been fully discussed (p. 63). The conclusion there drawn from its external characters is that it has been formed

by the union of two seed-leaves, which were distinct in a remote ancestor, and perhaps partially united in a more recent one. If this conclusion is justified, the vascular system of such ancestors would certainly be bilaterally symmetrical, and might probably resemble that of *Eranthis*. But in the seedling of *R. Ficaria* the vascular system of the cotyledon is unilateral in a very marked degree; quite as one-sided as that of *Zygadenus*, which indeed it closely resembles. We need not be startled then by the presence of a midrib in the cotyledon of *Zygadenus*, nor by its lateral position with regard to the axis, since both characters are found in the seedling of *Ranunculus Ficaria*, together with independent evidence of the double origin of its cotyledon.

The observations condensed in the first two Parts of this paper have led me to the conclusion that the single seed-leaf of the Liliaceae and allied orders is a compound member formed from the two seed-leaves of a remote ancestor. If this be admitted, the probability is that the seed-leaf of all Monocotyledons has a similar origin, and my observations on the Palms and Scitamineae confirm this view so far as they go.

In the third and last Part of this paper I propose to discuss the whole theory of the origin of Monocotyledons which naturally arises from the view I have just expressed concerning the origin of their seed-leaf.

This discussion will raise three questions, which can be treated separately:—

1. The comparative antiquity of the Monocotyledons and Dicotyledons.

2. Assuming the superior antiquity of Dicotyledons, can the single seed-leaf of Monocotyledons have arisen otherwise than by the fusion of two cotyledons into one member?

3. Assuming the double origin of the seed-leaf in Monocotyledons, can we form any hypothesis as to the way in which the fusion first began, and concerning the correlation of this character with the others which distinguish Monocotyledons?



### 1. Comparative Antiquity of Monocotyledons and Dicotyledons.

The Angiosperms form a very well-defined group, and modern research has tended to show that the gulf between them and the Gymnosperms is even wider than was formerly supposed. To borrow an expressive phrase, we have begun to realize the isolation of the Angiosperms.

Within this group the Monocotyledons are divided from the Dicotyledons by a number of natural characters, but these two classes are undoubtedly far more closely related to each other than is either of them to any other group of plants. The presumption is strong that they come from a common stock.

A generation ago the Monocotyledons were regarded as probably the older group, but botanists have never been unanimous in this opinion, and of late the evidence of fossil botany has on the whole inclined the scale in the opposite direction. The case is so admirably summed up by Professor Bayley Balfour (in the article on Angiosperms, Supplement to *Encyclopedia Britannica*, vol. xxv, 1902), that I am tempted to quote his judgement in full :—

‘The position of Angiosperms as the highest plant-group is unassailable. . . . We readily recognize in them now-a-days the natural classes of Dicotyledones and Monocotyledones, distinguished alike in vegetative and in reproductive construction, yet showing remarkable parallel sequences in development ; and we see that the Dicotyledones are the more advanced and show the greater capacity for further progressive evolution. But there is no sound basis for the assumption that the Dicotyledones are derived from Monocotyledones ; indeed the palaeontological evidence seems to point to the Dicotyledones being the older. This however does not entitle us to assume the origin of Monocotyledones from Dicotyledones, although there is manifestly a temptation to connect helobic forms of the former with ranal ones of the

latter. There is no doubt that the phylum of Angiosperms has not sprung from that of Gymnosperms.'

The question so far then is open, and there is nothing in the present state of botanical knowledge to discredit the conclusions which I have drawn from embryological evidence because they infer the superior antiquity of the seedling with two cotyledons.

The development of the embryo within the seed has sometimes been thought to show that the seed-leaf of Monocotyledons is a terminal member, and its plumule lateral. If this conclusion were well founded, it would be difficult to derive the Monocotyledonous embryo from a Dicotyledonous form. We should be almost forced to consider the one-leaved form as the more ancient. The two seed-leaves of a Dicotyledonous embryo must then be derived from the splitting of the original terminal member.

But the comparative work of Hegelmaier (14) and others has shown how little phylogenetic importance can be attached to details of structure in the embryo at this early age. In *Corydalis ochroleuca*, for example, there is a slight but undoubted cleft in the embryo of the ripe seed which separates the cotyledons from each other, while in *C. cava* no such division exists. The embryo is Monocotyledonous from the first.

The change from a Dicotyledonous to a Monocotyledonous habit must have taken place at a comparatively recent period in this case: more recent, that is, than the origin of *Corydalis* as a genus. Yet we know from the researches of Dr. Schmid<sup>1</sup> that no traces of the original bicotyledonary structure are to be found in the early history of the embryo of *Corydalis cava*.

The very careful observations of M. Sterckx (38, p. 42) on the embryo of *Ranunculus Ficaria* up to the period of germination illustrate the same point. I have already referred to them (p. 63), and will only say here that the history of the embryo within the seed throws little light on the homology of the single cotyledonary member. Nothing in its develop-

<sup>1</sup> Schmid, Beiträge zur Embryo-Entwicklung einiger Dicotylen. Bot. Zeit. 1902. Abth. I. p. 207.

ment contradicts the theory of its double origin, but I doubt whether that origin would have been suggested by the structure of the embryo at any period had the union of the cotyledons in the mature organ been more perfect.

Finally, Count Solms-Laubach (37) has shown that the cotyledon is not always apparently terminal in the embryo of Monocotyledons. In several genera belonging to the Comelinaceae, and in *Tamus communis*, the plumule is terminal from the moment of its appearance, and the single seed-leaf lateral. Its development in these species resembles that of the cotyledonary member in *Ranunculus Ficaria*.

These considerations are sufficient to throw doubt on the theoretical conclusions drawn by Mr. H. L. Lyon (31) from his interesting observations on the development of the embryo in a single species of *Nelumbium*. Professor Strasburger (39, p. 510) has pointed out that the apparently lateral position of the growing-point described by Mr. Lyon in this species is probably due to the position of the embryo within the embryo-sac, and that the same cause might bring about the early fusion of both cotyledons into a single rudiment, though they are later quite distinct.

## 2. Homology of the Seed-leaf in Monocotyledons.

Assuming that the seedling with one seed-leaf is derived from an ancestor with two, the change may have come about in one of two ways. One cotyledon of the pair may have been suppressed by degrees, or both have united to form a single member.

The first alternative is that adopted by Mr. Henslow in 1892 (15). It has commonly been regarded as the only working hypothesis by the botanists who have seriously considered the possibility of deriving Monocotyledons from a Dicotyledonous stock.

When in 1902 I published a short paper in the *New Phytologist* (35) giving an abstract of the reasons which led me to the conclusion that the single 'cotyledon' of Monocotyledons was derived from both the cotyledons of a remote



ancestor, I was not aware that this possibility had been suggested before. But a reference in Bernardi's paper of 1832 (4, p. 584) has recently led me to consult Agardh's text-book (1, p. 197).

Agardh proposes to class the embryos of all flowering plants in four main groups, thus:—

*Dicotyledones* { *Dicotyledones verae* (all *Dicotyledones* except  
Nymphaeaceae).  
*Polycotyledones* (*Coniferae*).

*Kryptocotyledones* { *Syncotyledones*.  
*Monocotyledones* (*Gramineae*).

Under *Syncotyledones* he includes *Lilieae*, *Aroideae*, *Naiadeae*, *Palmae*, *Scitamineae* (p. 197), and afterwards mentions as belonging to the same class, *Cycades* and *Nymphaeaceae*.

This classification was probably influenced by the fact that Agardh did not distinguish clearly between the endosperm and the cotyledon in the *Monocotyledonous* embryo, and still less in that of the *Nymphaeaceae*. He treats the embryo with two seed-leaves as the type, and considers that of the *Syncotyledones* to be derived from it by the fusion of the two original seed-leaves into a thick fleshy mass.

The Grasses are considered as the only true *Monocotyledons* because their seed-leaf has become single by the suppression of the second seed-leaf opposite to it. Thus Agardh derives the structure of the Grass-embryo also from a *Dicotyledonous* type.

It is remarkable that the *Monocotyledonous* families mentioned by Agardh as typical *Syncotyledones* (*Lilieae*, *Naiadeae*, *Aroideae*, *Palmae*, *Scitamineae*) are precisely those on which I have worked. His *Lilieae* probably include *Irids* and *Amaryllids* as well as the true *Liliaceae*. So far I have not examined any seedling from the *Naiadeae*, but with this exception we have the same horizon. I cannot therefore express any opinion as to the possibility of a distinct origin for the embryo of the *Gramineae*. It has been proposed

in our own day to separate them from other Monocotyledons on embryological grounds (Van Tieghem, 44).

The structure of some Ranunculaceous seedlings in which the cotyledons are partially united has already been described at length. The similarity between their vascular symmetry and that of a type of seedling primitive among the Liliaceae has led me to a conception of the Monocotyledonous embryo nearly identical with that of Agardh. This comparison has already been emphasized, but it must not be supposed that such partial union of the seed-leaves is confined to the Ranunculaceae and their near allies. On the contrary, examples of such structure are recorded from many families, some widely separated systematically from the Ranunculaceae.

The seedlings in which partial fusion of two cotyledons occurs may be divided into two classes of very unequal size.

In the first, the cotyledons are united by both the margins of their petioles. These form a slender cylinder, which is not always hollow throughout its length. There is always a conical chamber at the base however, within which the plumular bud is developed.

In the second class, the petioles are united by one margin only. The double member thus formed is always lateral with respect to the plumular axis.

The formation of a cotyledonary tube in the first way has been recorded in a large number of species, but the literature of the subject is scattered. The following list makes no pretence to be exhaustive. I have included in it only those species of which I have seen figures, or descriptions sufficiently full to make the facts certain. The references are to such descriptions: in the choice of authorities I have preferred the more recent and more easily accessible, and have taken no account of priority in discovery.

TABLE I.

Dicotyledonous seedlings with a well-marked cotyledonary tube.

*Ranunculaceae.*

Anemone coronaria . . .	Irmisch, 23, p. 1 (Fig.).
A. alpina . . . . .	Irmisch, 23, p. 6 (Fig.).
A. blanda . . . . .	Hildebrandt, 17, p. 10 (Fig.).
A. narcissiflora . . . . .	Hildebrandt, 17, p. 18.
A. rupicola . . . . .	Lubbock, 30, I, p. 85.
Ranunculus parnassifolius	Winkler, 44, p. 127.
Trollius Ledebouri . . .	Lubbock, 30, I, p. 91 (Fig.).
Eranthis hiemalis . . . .	Irmisch, 24, p. 221 (Fig.). Sterckx, 38, p. 51 (Fig.).
Delphinium nudicaule . .	Lubbock, 30, I, p. 97 (Fig.). Darwin, 10, p. 80. Sterckx, 38, p. 59 (Fig.).
D. hybridum (vars. puni- ceum, fissum, ochroleu- cum)	Bernhardi, 4, p. 574.
Aconitum Anthora . . .	Irmisch, 27, p. 365 (Fig.).

*Berberidaceae.*

Leontice vesicaria (= L. Leontopetalon)	Bernhardi, 4, p. 577 (Fig.).
L. altaica (= Bongardia Rauwolfii)	Bernhardi, 4, p. 577.
Podophyllum peltatum .	Holm, 19, p. 419 (Fig.).
P. Emodi . . . . .	Lubbock, 30, I, p. 114 (Fig.). Dickson, 12 (Fig.).

*Cruciferae.*

Cardamine (species from section Dentaria)	Bernhardi, 4, p. 601. Hildebrandt, 17, pp. 22 and 33 (Fig.).
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*Geraniaceae.*

Oxalis (tuberous species, as <i>O. rubella</i> and others)	Hildebrandt, 16, Pl. V.
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*Rhizophoreae.*

- Rhizophora Mangle . . . Klebs, 29, p. 562.  
 Rh. conjugata . . . . Kerner and Oliver, I, p. 602  
 (Fig.).

*Cucurbitaceae.*

- Megarrhiza Californica, Darwin, 10, p. 81 (Fig. 58).  
 Torr. (= Echinocystis Lubbock, 30, I, p. 597.  
 fabacea)

*Umbelliferae.*

- Smyrniun perfoliatum . . . Lubbock, 30, II, p. 29 (Fig.).  
 S. rotundifolium . . . . Lubbock, 30, II, p. 24.  
 S. Olusatrum . . . . Lubbock, 30, II, p. 24.  
 Holm, 20, p. 66.  
 Bunium luteum (= Mu- Bernhardi, 4, p. 607 (Fig.).  
 retia tanaicensis)  
 Chaerophyllum bulbo- Irmisch, 21, p. 22 (Fig.).  
 sum  
 Prangos ferulacea . . . Bernhardi, 4, p. 575 (Fig.).

*Compositae.*

- Serratula radiata . . . Winkler, 43, p. 137 (Fig.).

*Primulaceae.*

- Dodecatheon Meadia . . Bernhardi, 4, pp. 573, 578 (Fig.).

*Polygonaceae.*

- Polygonum bistorta . . Winkler, 43 (Fig.).  
 P. sphaerostachyum . . Lubbock, 30, II, p. 439.  
 Rheum Moorcroftianum Holm, 18.

This list, though doubtless incomplete, contains no case which is not well authenticated<sup>1</sup>, and I have purposely omitted from it those species which possess a cotyledonary tube wide in proportion to its length, even when the length is considerable. In such seedlings the plumule develops without diffi-

<sup>1</sup> The petioles of the cotyledons in *Megarrhiza Californica* are said to be apparently connate but really separable (Lubbock, 30, I, p. 597). This does not agree with the description of Asa Gray, quoted by Darwin (10, pp. 81-3).

culty within the cotyledonary tube, and their habit is not dissimilar from that of seedlings with distinct cotyledons.

Short petiolar tubes are not uncommon among the seedlings of species allied to those included in Table I. For example: *Ranunculus millefoliatus* (Irmisch, 26, p. 29, Fig. 1), *Ferula foetida* (Lubbock, 30, II, p. 37), *Serratula tinctoria* (Winkler, 41) *Cotula coronopifolia* (Lubbock, 30, II, p. 134), and *Rheum officinale* (Lubbock, 30, II, p. 442, Fig. 622). They link the numerous species in which the cotyledons are merely connate at the base with those in which the cotyledonary tube is fully developed, and their existence is a strong argument for the derivation of such tubes from the fusion of two cotyledons, and not, as Professor D. H. Campbell has suggested (7, p. 11), from the division of one.

From the first class of seedlings with united cotyledons we may now pass to the second. *Ranunculus Ficaria* and *Anemone apennina* (Sterckx, 38, pp. 34 and 80, Figs. 76, 77) are the only species with which I am acquainted in which the cotyledons are normally united by one margin only. Such unions are, however, not unfrequently found in abnormal specimens of species with distinct cotyledons. *Ranunculus repens* (Lubbock, 30, I, p. 90, Fig. 129) and *R. Chius* have been mentioned already. Irmisch found this abnormality in several seedlings of *Phlomis tuberosa* (22, p. 25, Fig. 105). Mrs. Stebbing has shown me a drawing of an abnormal seedling of *Urtica dioica* in which the blades as well as the short petioles of the two cotyledons are united by one margin.

No doubt such instances could be multiplied. Their interest lies in the possibility they suggest that the single seed-leaf of some species among those Dicotyledons which possess but one may be formed in a similar way.

The seed-leaf of *Pinguicula vulgaris*, for example, looks in Buchenau's figures (6, Figs. 1 and 2) as if it might be derived from the union of two cotyledons by one margin only. Dickson (11) states that *P. grandiflora* also germinates with a single seed-leaf, the blade of which is bifid. *P. caudata* and *P. lusitanica* have separate cotyledons.

The following list of the best-known pseudo-monocotyledons is no doubt very imperfect. The only species in it which I have examined is *Cyclamen persicum*. Its vascular structure suggests very strongly that the cotyledonary member consists of two seed-leaves united into a solid tube, but until the structure of allied genera has been worked out no great weight can be attached to this observation. Bernhardt (4, p. 578) suggests this origin of the single seed-leaf on the ground that the cotyledons of *Dodecatheon Meadia* are united into a tube. Lord Avebury remarks that when *Cyclamen* is raised from seed abnormal specimens are not uncommon in which the cotyledons have divided blades (Lubbock, 30, II, p. 184).

## TABLE II.

## Pseudo-monocotyledons.

*Fumariaceae.*

- Corydalis tuberosa*, D.C. (= Irmisch, 25 (Fig.).  
*C. solida* and *C. cava*) . . Bischoff, 5 (Fig).  
*C. fabacea* . . . . . Irmisch, 25 (Fig).  
*Dicentra Cucullaria*, Bernh. Irmisch, 25.  
 (= *Capnorchis Cucullaria*)

*Umbelliferae.*

- Carum Bulbocastanum* . . Irmisch, 21, p. 17 (Fig).  
*C. alpinum*, Benth. and Hook. Bernhardt, 4, p. 575.  
 (= *Bunium petraeum*, Ten.)  
*Erigenia bulbosa*, Nutt . . Holm, 20, p. 63.

*Primulaceae.*

- Cyclamen persicum* . . . . Darwin, 10, p. 78 (Fig. 57).  
 Lubbock, 30, II, p. 184.  
 Bernhardt, 4, p. 583.

*Lentibulariaceae.*

- Pinguicula vulgaris* . . . . Buchenau, 6, p. 64 (Figs.  
 1 and 2).  
 Dickson, 11.  
*P. grandiflora* . . . . . Dickson, 11.



*Nyctagineae.*

- Abronia umbellata* . . . . Darwin, 10, p. 95 (Fig. 61).  
Klebs, 29, p. 561 (Fig. 10).  
*A. arenaria* . . . . . Klebs, 29, p. 560.  
*A. grandiflora* . . . . . Klebs, 29, p. 560.

The existence of some Dicotyledons with only one seed-leaf is commonly explained by the supposition that one seed-leaf of the pair is abortive. This may be so in some of the species in the foregoing list, as *Abronia umbellata* (see Darwin, 10, p. 95): other cases may arise through the fusion of cotyledons by one or both margins.

3. Origin of the Monocotyledonous Habit.

If the homology of the single seed-leaf in Monocotyledons with both the seed-leaves of Dicotyledons be accepted as a working hypothesis, we are at once confronted with another question. How did that fusion begin, and of what advantage was it to the ancestral Monocotyledons in which it became stereotyped? That the union of seed-leaves does offer advantages to seedlings under certain conditions is clearly shown by the existence of a number of Dicotyledonous species in which they are normally united for a great part of their length.

Comparison of the species mentioned in Table I with each other shows that they have another character in common besides the possession of a cotyledonary tube. With one exception their hypocotyl is always much reduced in length, and is commonly thickened. As a rule the first internodes of the plumular axis are likewise more or less completely suppressed. *Rhizophora* is said to have an elongated hypocotyl, but the conditions under which it grows in tropical swamps are unique, and we cannot be surprised by exceptional adaptations to them.

The great majority of the species mentioned are tuberous: the others (*Podophyllum*, *Serratula*, *Polygonum*, *Rheum*) form

an upright much shortened subterranean axis in which the first internodes of the stem, as well as the hypocotyl, are suppressed. The species of *Anemone* and *Oxalis* with united cotyledons are distinguished from their neighbours within those genera by their tuberous habit.

M. Sterckx remarks that among the Ranunculaceae the species with concrescent cotyledons have short subterranean hypocotyls which are generally tuberous (38, pp. 80, 81). The explanation he gives is that the united petioles of the cotyledons carry their blades upwards, and thus replace the elongated aërial hypocotyls of allied species. Lord Avebury gives a similar reason for the correlation of a tuberous hypocotyl with concrescent cotyledons among the Umbelliferae (Lubbock, 30, II, pp. 23, 24). Darwin speaking of several pseudo-monocotyledons, together with some other species in which both cotyledons are very much reduced in size or even absent altogether, says: 'From the several cases now given, which refer to widely different plants, we may infer that there is some close connexion between the reduced size of one or both cotyledons and the formation by the enlargement of the hypocotyl or of the radicle of a so-called bulb.' He attributes this to correlation of growth: the expenditure of material in the formation of a bulb or tuber is balanced by the economy effected in the reduction of cotyledonary tissue (10, p. 97).

The pseudo-monocotyledons of Table II are in fact also characterized by the early formation of tubers, or at least by the development of a much shortened squat axis.

The formation of underground root-stocks, of tubers, corms, and bulbs, is characteristic of the plants called 'geophilous' by Professor Areschoug (3). The general definition of the term which he gives on page 1 is very wide: 'We include under that head such plants as form the buds by which they reproduce the shoot underground: those plants in fact which develop their aërial organs more or less completely beneath the surface of the soil.' Defined in this way the term would include all biennials and herbaceous perennials of the temperate and arctic zones, for the aërial shoots of all such plants dis-

appear during the winter, and are replaced in the following spring by the development of buds formed underground.

Geophilous characters are shown most clearly by plants which put forth aërial shoots during a short annual season only. Such are the two classes of plants termed 'alpines' and 'bulbs' by gardeners. The underground organs of such plants attain to some size, not unfrequently exceeding that of the aërial shoot. They are native to situations which have a short annual period in which the conditions are favourable to vegetation, and a longer dead season. The short hot summer of the arctic regions and of alpine summits, which does not begin until the snow melts, and is followed by a long frost-bound winter; the summer in the interior of South Africa, ushered in by rains, and followed by a season of dry cold; the damp warm spring of the Mediterranean region succeeded by a hot dry summer; these are examples of climatic conditions favourable to highly specialized geophytes, and within such regions the habit was no doubt developed.

In order to use the short season of vegetation to the best advantage the geophilous plant or geophyte must be furnished with a store of nourishment, and this is placed at some distance below the surface of the soil for protection against the cold or heat of the dead season. A plant so provided can throw up leaves and flowers at a few days' notice from the bud attached to its swollen axis or tuberous root.

The leaves when once above the ground make the most of their short life. They restock the underground organs with food for the following season, and they support the flowers, and later the maturing fruit, until the seed is ripe. When this occurs before the advent of the cold or drought withers the aërial shoots, the cycle of development is complete, but in such localities it must often happen that an early frost or a dry season kills all the seed formed by a plant before it is ripe.

The fact that all the species mentioned in Table I, with the exception of *Rhizophora*, are highly specialized geophytes suggests very strongly that union of the cotyledons is an



adaptation to this habit. When we consider the conditions under which a typical geophyte lives, it is very clear that its seedlings must be even more perfectly adapted to the environment than the mature plant in order to have a chance of surviving.

The seed formed at the end of the growing period is commonly capable of resisting a considerable degree of cold or drought in the long dead season. When the genial weather returns and it germinates, the seed is confronted with a difficult problem. During the short period of vegetation the growth of the seedling must proceed in such a way that the structure completed by the end of the season is capable of living through the severe weather which follows.

Accordingly we find that the seedling begins at once to form its underground organs. Not unfrequently the whole structure remains underground during the first season of growth (*Megarrhiza Californica*, Darwin, 10, p. 82; *Arum maculatum*, Rimbach, 33). More commonly the cotyledons only appear above ground in the first season (*Eranthis hiemalis*, *Fritillaria imperialis*), or the cotyledons may remain underground in the seed and the first leaf break through the soil (*Anemone nemorosa*, Irmisch, 23, p. 17, Figs. 26-28; *Eucomis nana*, Jacq.). In other species both cotyledons and foliage leaves come up above ground in the first season and act as assimilating organs (*Delphinium nudicaule*, *Iris sp.*).

In all these cases, however, the production of assimilating surfaces seems to be an object of secondary importance to the seedling of a geophilous plant in its first season. The formation of adequate subterranean organs at a safe distance below the surface of the soil is the condition on which the life of such a seedling ultimately depends, and its powers are devoted in the first place to this task.

Concrescent cotyledons seem to be an adaptation for producing effective assimilating surfaces with the least possible expenditure of material (Lubbock, Sterckx, l. c.). The production of a single cotyledon, whether by the more complete fusion of two or in any other way, is also an economy as

compared with the formation of two cotyledons (Darwin, l. c.). It is true that in time the extra assimilating surfaces will more than repay the cost of their production, but time may fail the geophyte which dares not risk being caught by the bad weather unprepared.

These considerations have led me to look upon the Monocotyledon as an organism adapted primarily to a geophilous habit. The single cotyledon has been shown to be connected with this way of life in some Dicotyledons, and many of the features which distinguish Monocotyledons from Dicotyledons may be explained as having been formed under the conditions I have just described. Since I have adopted this view as a working hypothesis, the purpose of many details in the structure of Monocotyledons which had puzzled me before has become comprehensible.

*Distribution of the Bundles in the Stem.*

An erect subterranean axis with much shortened internodes and crowded with the sheathing bases of leaves must inevitably receive a number of traces from each leaf, and these traces—entering the axis in segments of its circumference corresponding to the breadth of the leaf-base—would naturally arrange themselves in more or less complete concentric circles. Mr. Henslow has well described the process by which this might occur (15, p. 512), but his suggestions are much more applicable to a short vertical subterranean axis such as that found in the four-year-old seedling of *Podophyllum* (Holm, 19) than to the rhizome of *Nymphaea*. In a squat underground root-stock secondary growth of the xylem in thickness would be useless: the bundles are essentially channels of communication between the leaves and the roots, and they are not required to support a great mechanical strain. Thus the extra-fascicular cambium would first disappear—as it has done in *Podophyllum*—and later the cambial zone from each bundle. The bundles of *Podophyllum* possess distinct fascicular cambium, but they are isolated from each other by the well-marked bundle-sheaths.

Miss Andersson (2) and M. Quéva (33) have found a well-defined cambial zone within the bundles of some Monocotyledons, and traces of such formation in many others.

The tuber of *Corydalis solida* (Jost, 28) appears to retain normal secondary growth in thickness. The cambium forms a new tuber every year within the old one, adding to the wood a great mass of parenchymatous elements which become filled with reserve food-material. The anatomy of Dicotyledonous tubers has been somewhat neglected, but I believe this structure to be exceptional. The seedling anatomy of *Delphinium* sp. and *Anemone coronaria* suggests that it may be found in the mature tubers of these species also (pp. 54-56). The food supply, however, is more commonly stored in the conjunctive tissue and cortex (*Eranthis*, *Podophyllum*, *Cyclamen*, and the roots of *Ranunculus Ficaria*). The development of the cortex and conjunctive tissue inevitably isolates the bundles traversing the tuber.

#### *Early disappearance of the Primary Root.*

This character is by no means universal among Monocotyledons. In many arborescent species the primary root persists for a considerable time, becoming stout and well developed (*Yucca*, Palms). But the rule among bulbous and herbaceous species certainly is that the primary root disappears at the same time with the cotyledon. Bulbous plants as a rule lose their roots at the end of each growing season, and put out new ones at the beginning of the next. This habit is no doubt correlated with the direct connexion of each leaf with a particular root so characteristic of bulbous plants (cf. a quotation from Mirbel given by Mr. Henslow, 15, p. 506). The annual crop of roots is clearly bound up with the annual recurrence of a period of vegetative activity.

*Eranthis* agrees in this respect with Monocotyledons. The primary root is replaced in the second spring by a circle of roots developed in a girdle surrounding the tuber (Irmisch, 24, Fig. 15).



*Absence of a true Epidermis in the Root above the Root-sheath.*

This character of the root is so far as we know universal among Monocotyledons, but not confined to them. It is found in the Nymphaeaceae among Dicotyledons. I can form no guess as to its origin.

*Parallel Venation of the Leaves.*

Parallel venation is general among the leaves of Monocotyledons, but by no means universal. Professor Areschoug has remarked that the linear leaves characteristic of most bulbous Monocotyledons are better adapted to push upwards through the soil than any Dicotyledonous type of leaf (3, p. 55). The bulb seems in many respects to be the most highly specialized form of geophyte: its squat axis and pointed leaves with their broad sheathing base are clearly adaptations to a geophilous life. The anatomy of the stem and the short life of the roots are characters correlated with those just mentioned.

*The Ternary Symmetry of the Flower.*

The three-whorled flower is very generally found among Monocotyledons, but is not universal. Many of the exceptions may be derived from it by reduction (Aroideae). No connexion between this symmetry and a geophilous habit occurs to me, except that the parts of the flower may perhaps pack easily into a bud when arranged in this way.

*The presence of an Endosperm in the Seed.*

This character is neither universal among Monocotyledons nor confined to them, but it is much more common in this class of plants than among Dicotyledons. I believe it to be a character common to the majority of highly specialized geophytes. This is illustrated by the fact that among the twenty-seven Dicotyledonous genera mentioned in Tables I and II, three only (*Cardamine*, *Serratula*, and *Pinguicula*)

possess exalbuminous seeds. The connexion is not difficult to understand. The seed of geophilous plants must become ripe within a short period, and the embryo therefore remains small, and commonly but little differentiated, while the endosperm is packed with food-stuff.

With this is connected the slow germination of many species with concrescent cotyledons. The prolonged maturation of the embryo within the seed of *Ranunculus Ficaria*—a process extending over nearly two years after the seed is ripe—has been mentioned already. It is fully described by M. Sterckx (38, p. 42, Figs. 151–160). A similar maturation of the embryo takes place in the seeds of *Eranthis hiemalis*, *Corydalis cava* (Schmid, l. c.), and of several species of *Anemone* after they are shed, but here the process is complete at the end of the first season and the seeds germinate in the following spring (Sterckx, 38, p. 79). M. Sterckx' observations, however, were made on plants growing in a temperate climate with a long summer. It is very probable that the seeds of these species if shed at the end of a short alpine or arctic summer might defer the maturation of their embryos to the next year, and germinate only in the second summer after dispersal. The slow germination of many Monocotyledonous seeds, particularly those belonging to bulbous species, is a fact familiar to all gardeners.

The suggestions here made as to the origin of Monocotyledons from a Dicotyledonous stock will perhaps be thought worthy of consideration by botanists. It is certain that if the theory be adopted as a working hypothesis it will suggest new lines of research, for example a more complete investigation of the embryology of Monocotyledons and the anatomical investigation of geophilous Dicotyledons. Not less important is the study of seedlings and immature plants in the field, in continuation of the work of Irmisch, Holm, and others.

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*Iris sibirica*, 43.  
*Iris* sp., 43, 80.  
  
*Lachenalia Nelsoni*, 21.  
*Leontice altaica*, 73.  
*Leontice Leontopetalon*, 73.  
*Leontice vesicaria*, 73.  
*Lilium croceum*, 25.  
*Lilium Henryi*, 25.  
*Lilium* sp., 25.  
  
*Megarrhiza californica*, 74, 80.  
*Milla biflora*, 32.  
*Muretia tanaicensis*, 74.  
*Musa Livingstonia*, 50.  
*Muscari armenaicum*, 16.  
*Muscari atlanticum*, 15.  
*Muscari comosum*, 20.  
*Muscari neglectum*, 18.  
  
*Nelumbium*, 70.  
*Nigella damascena*, 53.  
  
*Ornithogalum exscapum*, 21.  
*Ornithogalum sulphureum*, 20.  
*Oxalis*, 73.  
  
*Phlomis tuberosa*, 75.  
*Phoenix dactylifera*, 49.  
*Pinguicula caudata*, 75, 83.  
  
*Pinguicula grandiflora*, 75, 76, 83.  
*Pinguicula lusitanica*, 75, 83.  
*Pinguicula vulgaris*, 75, 76, 83.  
*Podophyllum Emodi*, 73, 77.  
*Podophyllum peltatum*, 73, 77, 81.  
*Polygonum bistorta*, 74, 77.  
*Polygonum sphaerostachyum*, 74, 77.  
*Prangos ferulacea*, 74.  
  
*Ranunculus Chius*, 65.  
*Ranunculus Ficaria*, 63, 75.  
*Ranunculus millefoliatus*, 64, 75.  
*Ranunculus parnassifolius*, 64, 73.  
*Ranunculus repens*, 65.  
*Renealmia racemosa*, 50.  
*Rheum Moorcroftianum*, 74, 77.  
*Rheum officinale*, 75, 77.  
*Rhizophora conjugata*, 74, 77.  
*Rhizophora Mangle*, 74, 77.  
  
*Scilla festalis*, 20.  
*Scilla peruviana*, 21.  
*Scilla sibirica*, 20.  
*Serratula radiata*, 74, 77, 83.  
*Serratula tinctoria*, 75, 77, 83.  
*Smyrniium Olusatrum*, 74.  
*Smyrniium perfoliatum*, 74.  
*Smyrniium rotundifolium*, 74.  
  
*Tamus communis*, 9, 70.  
*Thrinax excelsa*, 48.  
*Tricyrtis hirta*, 33.  
*Trillium grandiflorum*, 34.  
*Trollius Ledebouri*, 73.  
*Tulipa praecox*, 25.  
*Tulipa* sp., 25.  
  
*Urtica dioica*, 75.  
  
*Veratrum nigrum*, 33.  
  
*Yucca aloifolia*, 35, 39.  
*Yucca arborescens*, 35.  
*Yucca gloriosa*, 36, 39.  
  
*Zygadenus elegans*, 32.

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## EXPLANATION OF FIGURES IN PLATES I-VII.

Illustrating Miss Sargent's paper on the Origin of Monocotyledons.

The figures on Plates I and II are drawn by Miss E. Sargent, with the exception of Fig. 5 on Plate I (Miss E. N. Thomas).

The figures on Plates III-VII are drawn by Miss Agnes Robertson, with the exception of those marked (E. S.) or (E. N. T.).

### PLATE I.

#### *Albica Nelsoni.*

Fig. 1. Outline of whole seedling  $A_5$ , drawn from life.  $\times \frac{1}{1}$ . Outline of young bulb and adjacent parts from seedling  $B_1$ , preserved in spirit.  $\times \frac{1}{1}$ .

Fig. 2. From microtome series through seedling  $A_5$ . Transverse section of embryonic stem-bud enclosed in expanded base of cotyledon.  $\times 75$ .

Fig. 3. From same series, .16 mm. below Fig. 2. Transverse section through transitional region. Each main cotyledonary trace has formed three protoxylem groups:  $px_1$ ,  $px_2$ ,  $px_3$ , and  $px_4$ ,  $px_2'$ ,  $px_3'$ .  $\times 210$ .

Fig. 4. From same series, .12 mm. below Fig. 3. Triarch root forming, but original tetrarch structure indicated by presence of protoxylem group  $px_3 + px_3'$ .  $\times 210$ .

#### *Hyacinthus romanus.*

Fig. 5. Outline of seedling  $A_5$ , from life.  $\times \frac{1}{1}$ . (E. N. T.)

Fig. 6. From microtome series through seedling  $A_5$ . Transverse section through embryonic stem-bud enclosed in expanded base of cotyledon. Two main bundles,  $M_1$ ,  $M_2$ , and four lateral strands in cotyledon.  $\times 75$ .

Fig. 7. From same series, .27 mm. below Fig. 6. Formation of phloëm girdle indicated. Two lateral bundles,  $l_1$ ,  $l_2$ , unite with main bundles,  $M_1$ ,  $M_2$ , to form stele.  $\times 225$ .

Fig. 8. From same series, .04 mm. below Fig. 7. The whole xylem of bundles  $l_1$ ,  $l_2$ , has joined the lowest group derived from the main bundles,  $px_3 + px_3'$ .  $\times 225$ .

Fig. 9. From same series, .13 mm. below Fig. 8. Tetrarch root-stele. The last-formed group of protoxylem,  $px_1$ , is smaller than the others.  $\times 225$ .

### PLATE II.

#### *Muscari atlanticum.*

Fig. 1. Outline of seedling  $A_4$ , preserved in spirit.  $\times \frac{1}{1}$ .

Fig. 2. From microtome series through seedling  $A_4$ , just below first node. Two main cotyledonary traces,  $M_1$ ,  $M_2$ , and two lateral ones,  $l_1$ ,  $l_2$ , in stele.  $\times 200$ .

Fig. 3. From same series, .03 mm. below Fig. 2. Pentarch root-stele indicated. The two lateral traces ( $l_1$ ,  $l_2$  in Fig. 2) have supplied the lowest phloëm group.  $\times 300$ .

*Muscari armenaicum.*

Fig. 4. Outline of seedling  $A_3$ , drawn from life.  $\times \frac{1}{1}$ .

Fig. 5. From microtome series through seedling  $A_3$ , at base of first node. The lateral trace  $l_3$  is inserting itself on  $l_1$ . The two main traces,  $M_1$ ,  $M_2$ , are united by the common protoxylem group,  $px_2 + px_2'$ .  $\times 200$ .

Fig. 6. From same series, .07 mm. below Fig. 5. Pentarch root-stele indicated. The lateral traces supply the two lower phloëm groups and the protoxylem group between them,  $px_5$ , with part of two others.  $\times 300$ .

Fig. 7. Outline of seedling  $A_3$ , drawn from life.  $\times \frac{1}{1}$ .

Fig. 8. From microtome series through seedling  $A_3$ , just below first node. Two main cotyledonary traces,  $M_1$  and  $M_2$ , and two lateral ones,  $l_1$ ,  $l_2$ .  $\times 200$ .

Fig. 9. From same series, .07 mm. below Fig. 8. Tetrarch root-stele indicated. The lateral traces ( $l_1$ ,  $l_2$ , in Fig. 8) form half the stele, supplying the two lower phloëm groups—which are sensibly smaller than the upper ones—the whole of the protoxylem group  $px_5$ , and part of groups  $px_3$  and  $px_3'$ .  $\times 300$ .

## PLATE III.

*Fritillaria imperialis.*

Fig. 1. Outline of seedling  $A_1$ , drawn from life.  $\times \frac{1}{1}$ .

Fig. 2. From microtome series through seedling  $A_1$ . Transverse section through enlarged base of cotyledon, enclosing young stem-bud. Two massive bundles,  $M_1$ ,  $M_2$ , in cotyledon: three strands in first leaf.  $\times 66$ .

Fig. 3. From same series, .32 mm. below Fig. 2. First node. Two plumular traces are inserted on  $M_1$ ,  $M_2$ . One branch from the protoxylem of  $M_1$  goes to meet the nearest plumular trace; the other forms part of the group  $px_2$  at the top of the section. The protoxylem of  $M_2$  divides in the same way.  $\times 200$ .

Fig. 4. From same series, .18 mm. below Fig. 3. Insertion of plumular traces is completed. The xylem group of  $M_1$  and  $M_2$  are each crescent-shaped. The protoxylem of each crescent covers its convex outline: the concavity is occupied by a compact phloëm group.  $\times 133$ .

Fig. 5. From same series, .03 mm. below Fig. 4. Protoxylem crescents broken into two groups,  $px_2$ ,  $px_3$ . The structure is that of a diarch root with two thin plates of protoxylem extended tangentially.  $\times 133$ .

Fig. 6. From same series, .15 mm. below Fig. 5. Phloëm in four groups: protoxylem breaking up into four too. Tetrarch root-stele indicated.  $\times 133$ .

## PLATE IV.

*Chlorogalum pomeridianum.*

Fig. 1. Outline of seedling  $A_3'$ , preserved in spirit.  $\times \frac{1}{1}$ . (E. N. T.)

Fig. 2. From microtome series through seedling  $A_3'$ , just above first node. Double cotyledonary trace  $M_1 + M_2$  with three protoxylem groups,  $px_1$ ,  $px_2$ ,  $px_3$ . Single plumular trace, which divides as it approaches cotyledonary trace into two branches,  $Pl_1$ ,  $Pl_2$ .  $\times 250$ . (E. S.)

Fig. 3. From same series, .02 mm. below Fig. 2. Phloëm masses above and below xylem. Four protoxylem groups, of which  $px_1'$  is plumular. Diarch root-stele is suggested.  $\times 250$ .

Fig. 4. From same series, .10 mm. below Fig. 3. Tetrarch root-stele.  $\times 250$ .

*Anthericum Liliago.*

Fig. 5. Outline of seedling  $B_1$ , preserved in spirit.  $\times \frac{1}{1}$ . (E. S.)

Fig. 6. From microtome series through seedling  $B_1$ , just above first node. The section cuts each plumular trace twice: *in situ* within the first leaf ( $A, B, C$ ), and also as they approach the double trace of the cotyledon in two groups ( $Pl_1, Pl_2$ ).  $\times 190$ .

Fig. 7. From same series, .14 mm. below Fig. 6. The phloëm is in two masses, but there are four distinct groups of protoxylem,  $px_1, px_2, px_3, px_1'$ .  $\times 190$ .

*Arthropodium cirrhatum.*

Fig. 8. Outline of seedling  $B_1$ , preserved in spirit.  $\times \frac{1}{1}$ . (E. S.)

Fig. 9. From microtome series through seedling  $B_1$ , above first node. The double trace from the cotyledon is moving towards the plumular traces  $Pl$ .  $\times 250$ .

Fig. 10. From same series, .18 mm. below Fig. 9. The whole stele has been somewhat twisted in its descent. But it is clear from intermediate sections that  $px_1$  represents the cotyledonary and  $px_1'$  the plumular protoxylem. The stele is root-like and diarch, but at +, +, are two small protoxylem groups in course of extinction.  $\times 250$ .

PLATE V.

*Allium neapolitanum.*

Fig. 1. From microtome series through seedling  $A_4$ . Transverse section of embryonic stem-bud enclosed within enlarged base of cotyledon. Double bundle in cotyledon: three strands in first leaf.  $\times 75$ .

Fig. 2. From same section as Fig. 1. Double bundle of cotyledon enlarged.  $\times 200$ .

Fig. 3. From same series, .27 mm. below Fig. 1, through first node. The phloëm of the slender plumular trace has divided, and one branch fuses with each of the two cotyledonary phloëm groups.  $\times 200$ .

Fig. 4. From same series, .04 mm. below Fig. 3. Diarch root-stele.  $\times 75$ .

Fig. 5. From same section as Fig. 4. Stele enlarged.  $\times 200$ .

*Zygadenus elegans.*

Fig. 6. Outline of seedling  $A_3$ , drawn from life.  $\times \frac{1}{1}$ . (E. S.)

Fig. 7. Transverse hand-section through petiole of cotyledon, showing single bundle.  $\times 75$ .

Fig. 8. From same section as Fig. 7. Bundle enlarged.  $\times 200$ .

Fig. 9. From microtome series through seedling  $A_3$ . Transverse section of young stem-bud enclosed within enlarged base of cotyledon. Single bundle in cotyledon: three strands in first leaf.  $\times 75$ .

Fig. 10. From same section as Fig. 9. Bundle enlarged.

Fig. 11. From same series, .18 mm. below Fig. 9, through first node. A single plumular trace meets that from the cotyledon: both open out as they approach each other, and the phloëm groups unite in pairs.  $\times 200$ .

Fig. 12. From same series, .07 mm. below Fig. 11. Diarch root-stele indicated, but not yet formed. The upper protoxylem group is derived from the cotyledon; the lower from the plumular trace.  $\times 200$ .



PLATE VI.

*Eranthis hiemalis.*

- Fig. 1. Outline of seedling  $A_6$ , drawn from life.  $\times \frac{1}{1}$ . (E. S.)  
 Fig. 2. From microtome series through seedling  $A_2$ . Transverse section of embryonic stem-bud enclosed within base of cotyledonary tube.  $\times 113$ .  
 Fig. 3. From same series, .09 mm. below Fig. 2, passing through top of tuber. Each trace from the cotyledon,  $C_1$ ,  $C_2$ , shows double structure.  $\times 113$ .  
 Fig. 4. From same series, .10 mm. below Fig. 3. The two pairs of bundles are drawn side by side; the xylem of each is in three groups.  $\times 113$ .  
 Fig. 5. From same series, .07 mm. below Fig. 4. Four phloëm and eight xylem groups.  $\times 113$ .  
 Fig. 6. From same series, .73 mm. below Fig. 5, approaching the base of the tuber. The scattered traces have gathered together, and now form two phloëm and four xylem groups. Three of the latter are complete: the fourth is forming to the SW. of the section.  $\times 113$ .

PLATE VII.

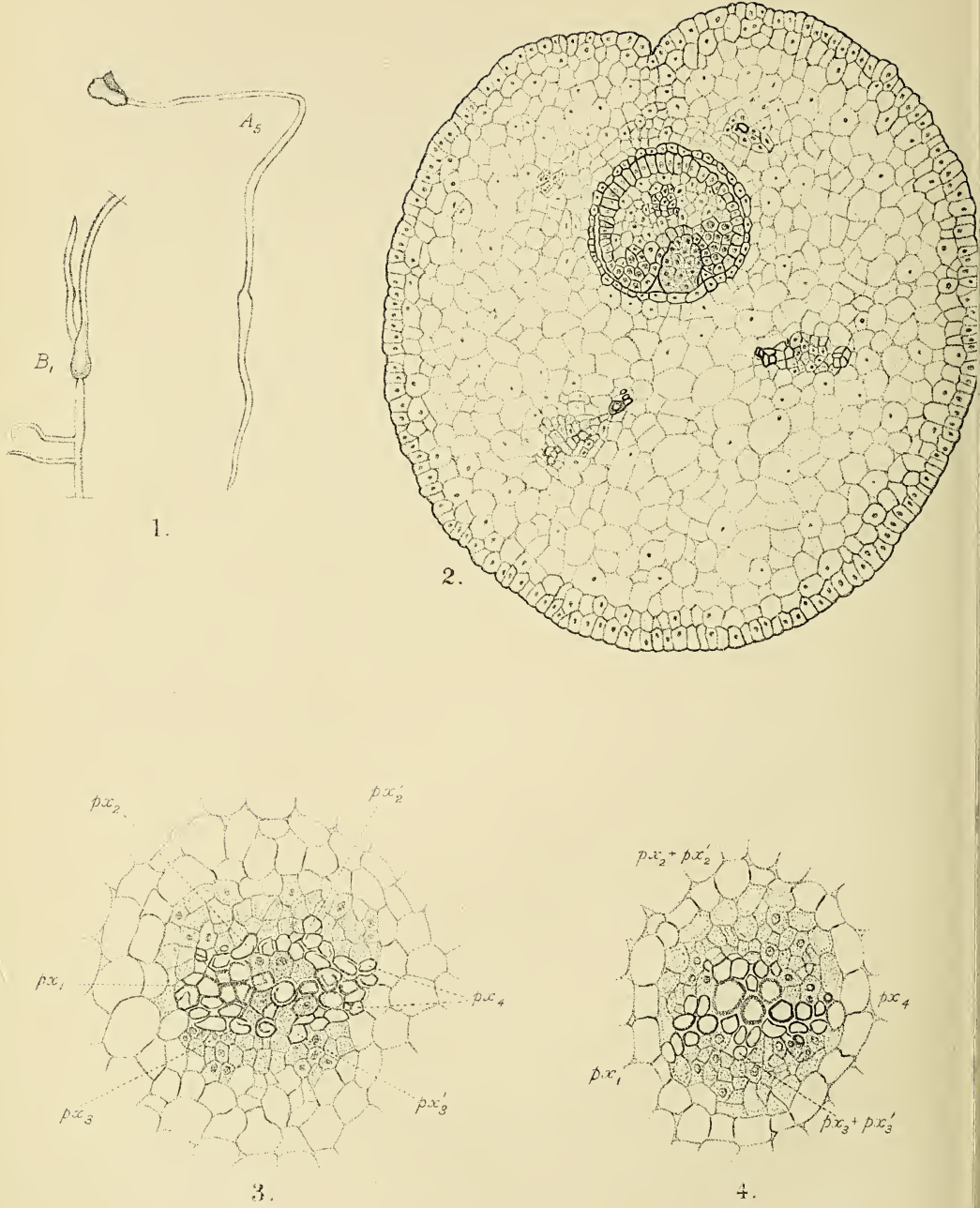
*Eranthis hiemalis.*

- Fig. 1. From same series as Fig. 6 on Plate VI, and .27 mm. below it. Between each of the two phloëm groups and the xylem internal to it, there are a few unligified secondary elements in a radial row.  $px'$ ,  $px'$ , are the two groups of protoxylem within the phloëm groups, which will disappear lower down.  $\times 200$ .  
 Fig. 2. From same series, .15 mm. below Fig. 1, through top of primary root. Diarch root-stele; the groups  $px'$ ,  $px'$ , have disappeared.  $\times 200$ .  
 Fig. 3. From microtome series through older seedling  $A_5$ . The section passes through the base of the tuber. Tetrarch xylem-plate. The elements  $px'$ ,  $px'$  are primary.  $\times 200$ .

*Ranunculus Ficaria.*

- Fig. 4. Outline of seedling  $A_3$ , drawn from life.  $\times \frac{1}{1}$ . (E. S.)  
 Fig. 5. Outlines of the cotyledons from three seedlings,  $A_3$ ,  $A_4$ ,  $B_1$ , showing the venation of the blade.  $\times 2$ . (E. S.)  
 Fig. 6. From microtome series through seedling  $A_3$ , cutting axis near insertion of first cauline root. The slender plumular trace in the upper part of the section is approaching the larger trace from the cotyledon in the lower part.  $\times 100$ .  
 Fig. 7. From same series, .09 mm. below Fig. 6, cutting axis at first node. The trace from the cotyledon is cut longitudinally as it approaches the plumular trace. Its double structure is clear, and the plumular trace is branching in two directions to meet it.  $\times 250$ .  
 Fig. 8. From same series, only .03 mm. below Fig. 7. The diarch root-stele is almost complete. The lower protoxylem group is from the cotyledon; the upper one from the plumule.  $\times 250$ .





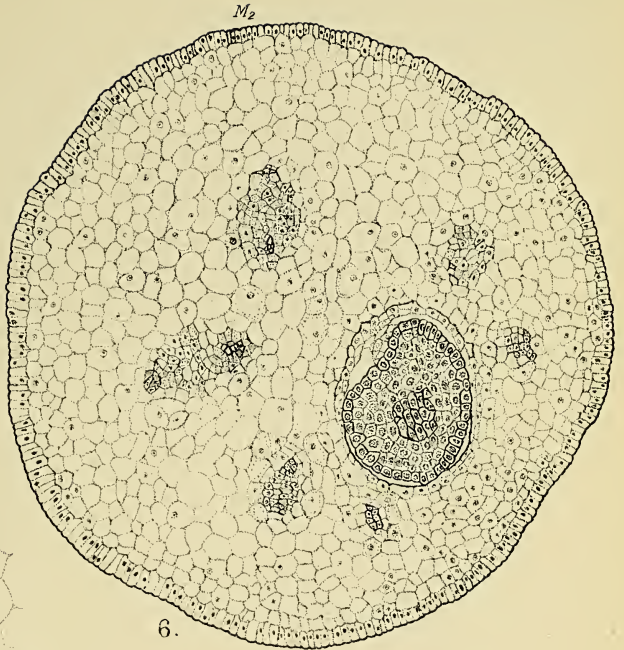
Albuca Nelsoni, Figs. 1-4.





5.

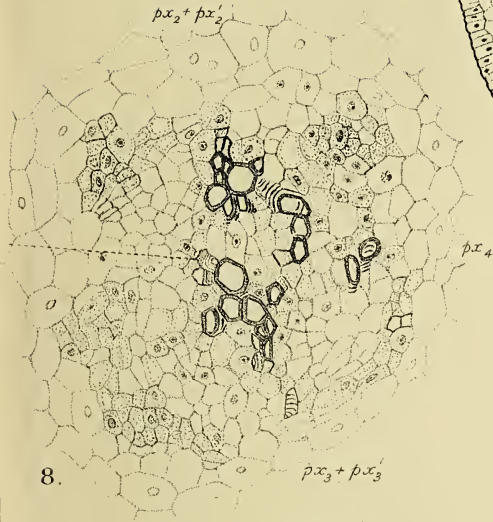
$px_2 + px'_2$



6.

$M_1$

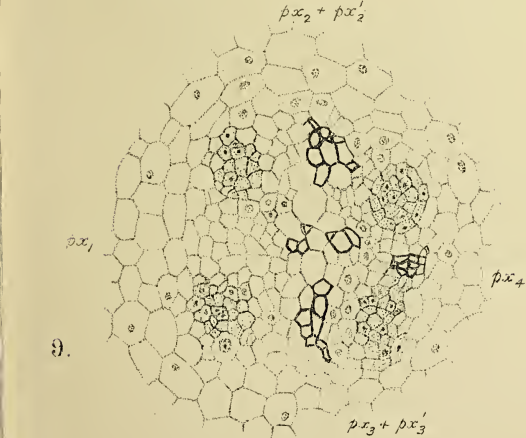
$M_2$



8.

$px_4$

$px_3 + px'_3$



9.

$px_2 + px'_2$

$px_1$

$px_4$

$px_3 + px'_3$



7.

$M_2$

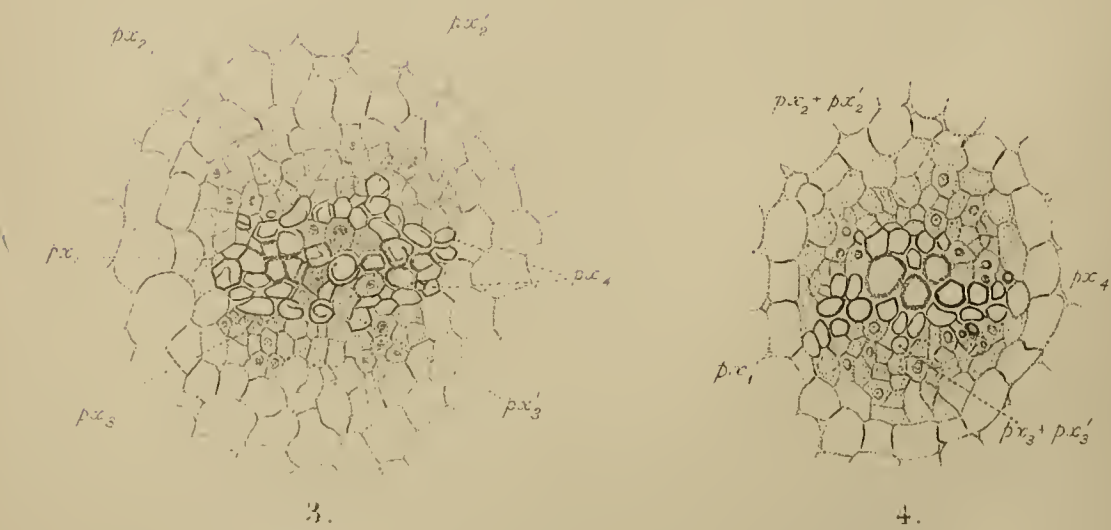
$M_1$

$l_2$

$l_1$

Hyacinthus romanus, Figs. 5-9.





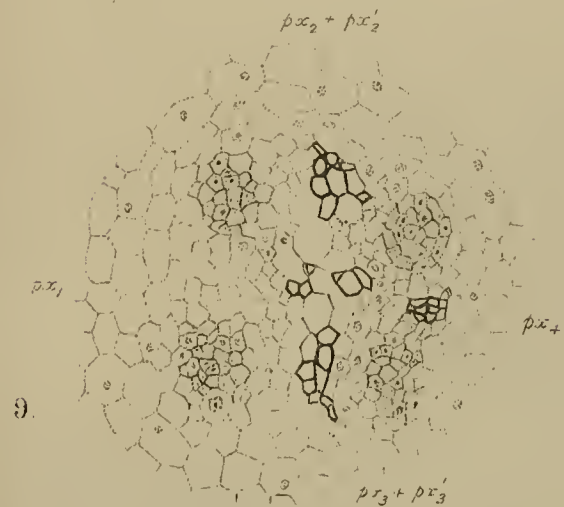
*Albuca Nelsoni*, Figs 1-4.



5.  
 $px_2 + px'_2$



8.

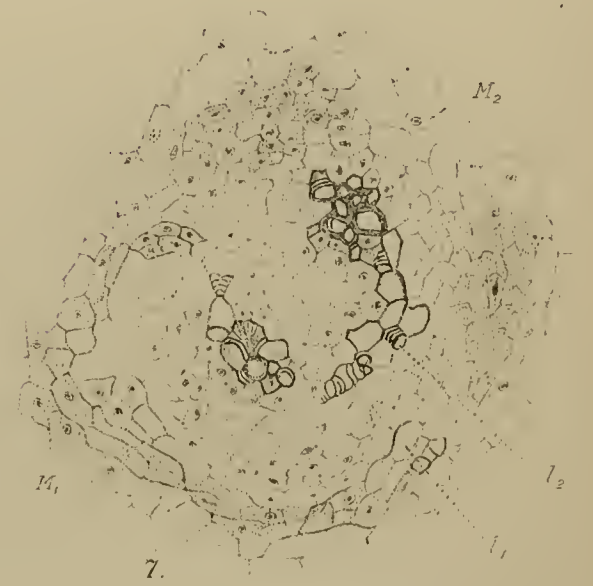


9.

*Hyacinthus romanus*, Figs 5-9.



6.

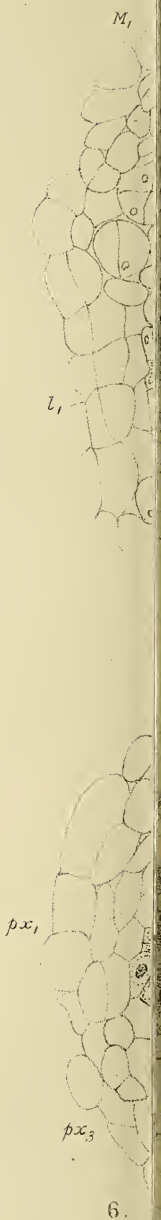
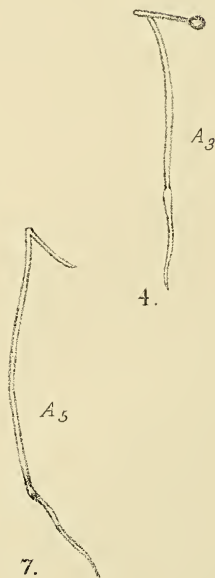
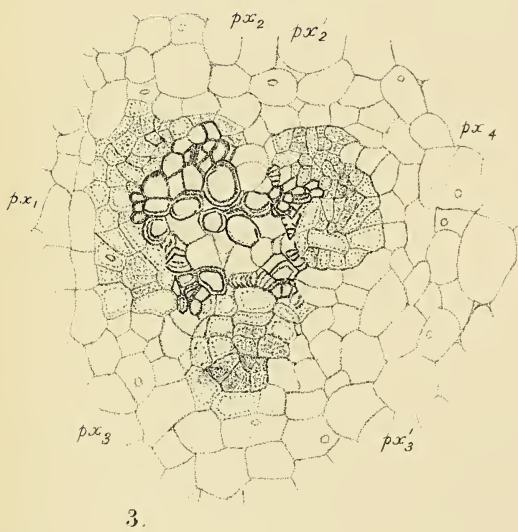
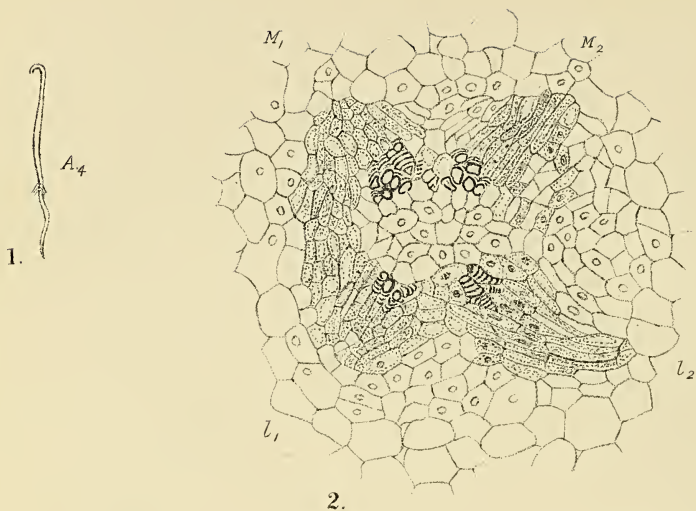


7.









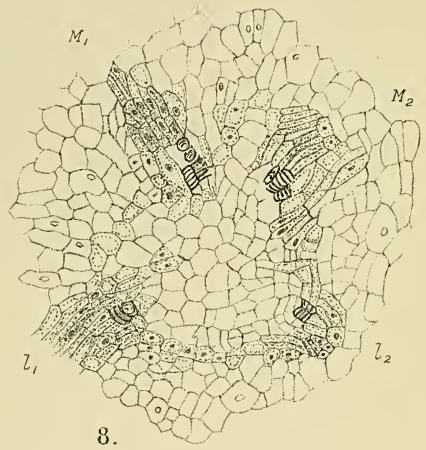
Muscari atlanticum, Figs. 1-3.

Muscari armenaicum, Figs. 4-9.





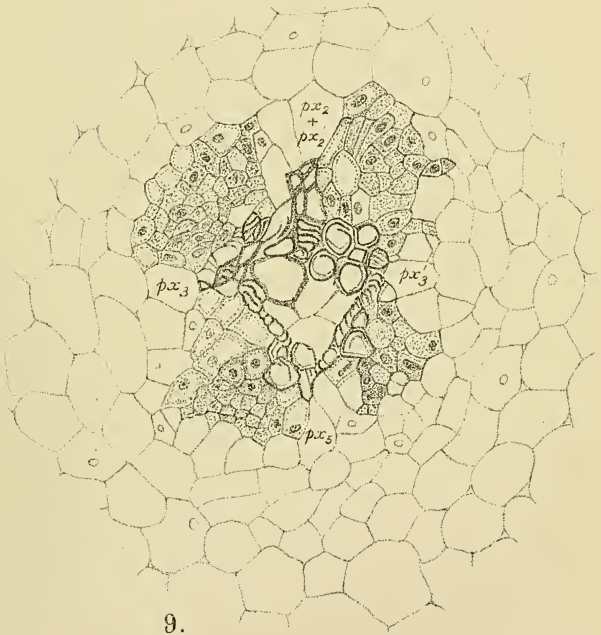
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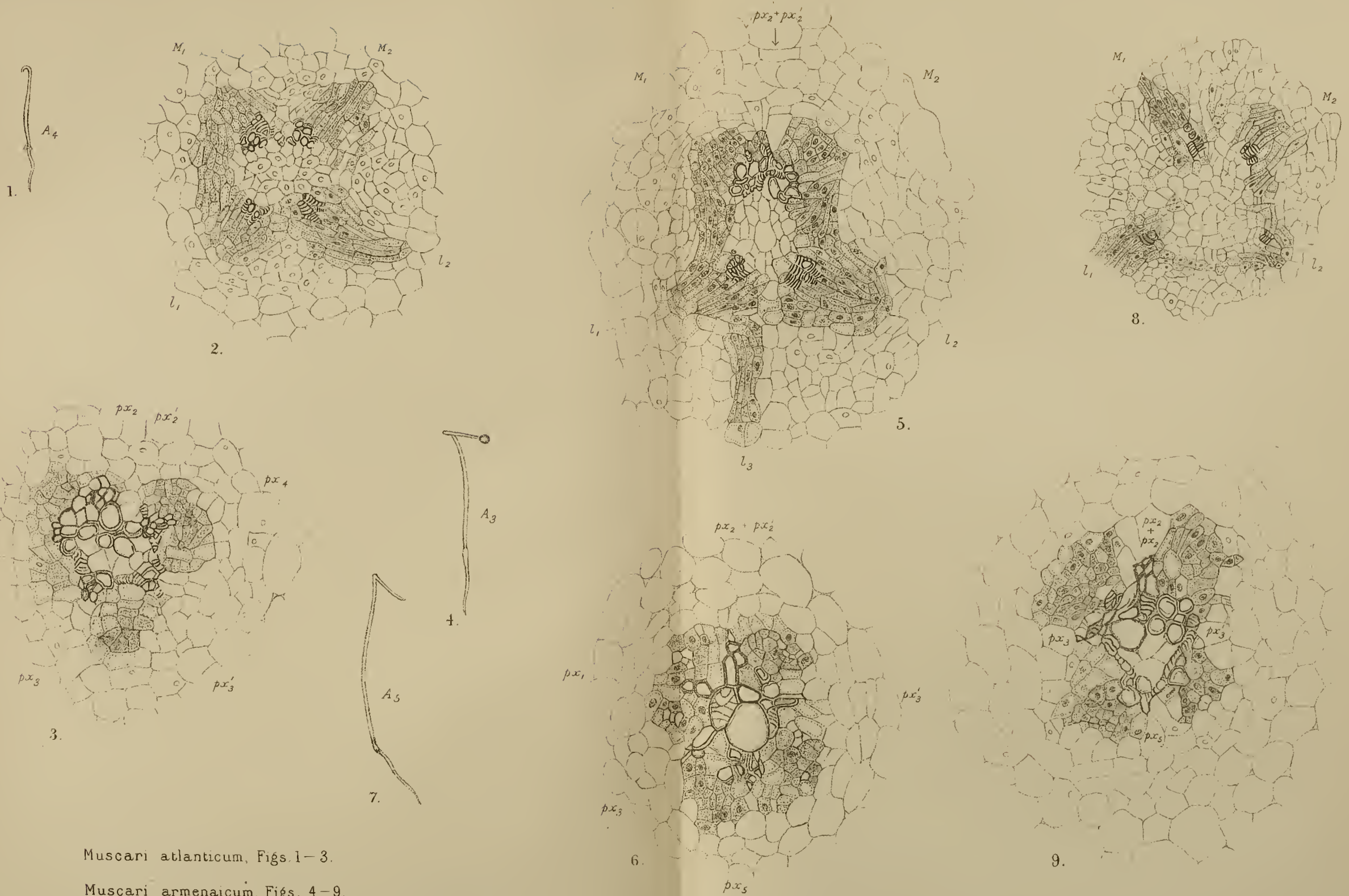


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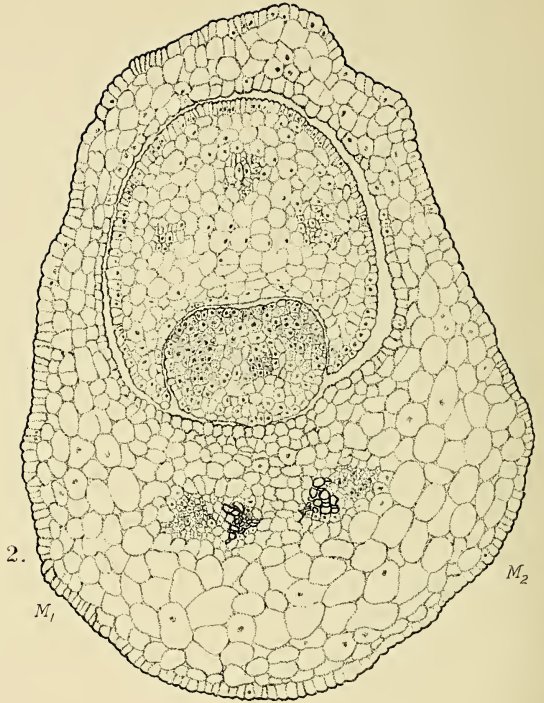
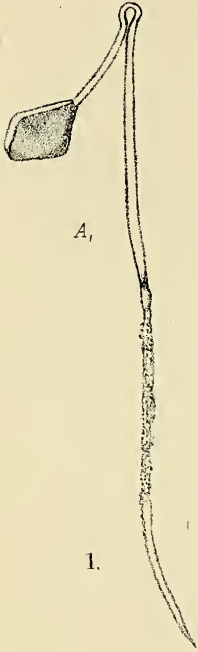
Muscari atlanticum, Figs. 1-3.

Muscari armenaicum, Figs. 4-9.









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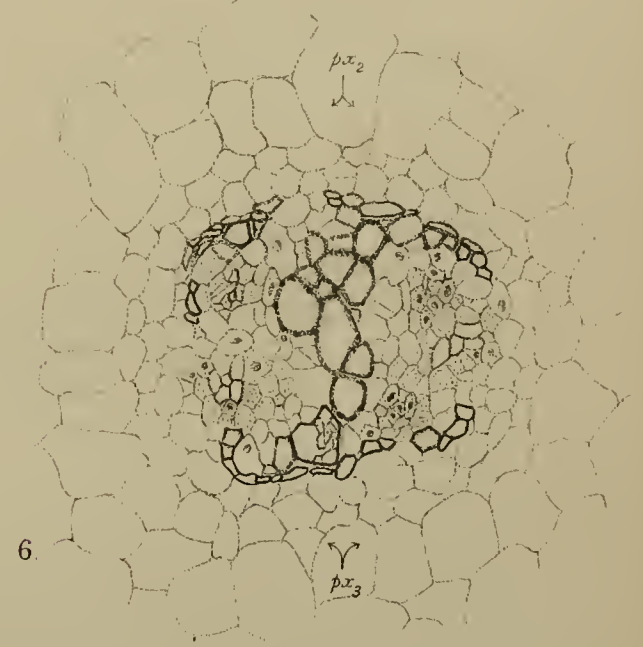
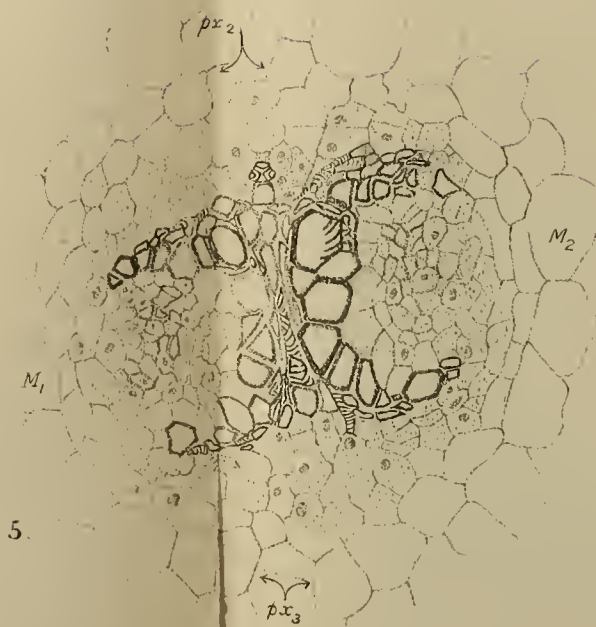
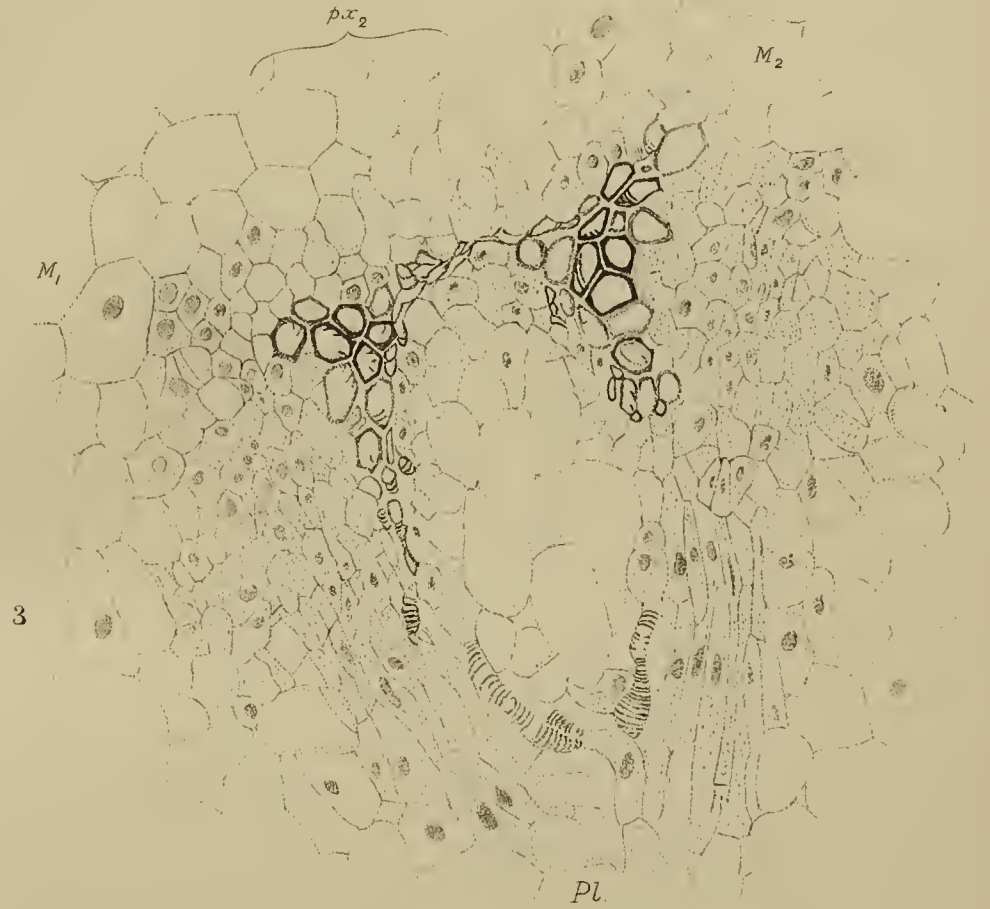
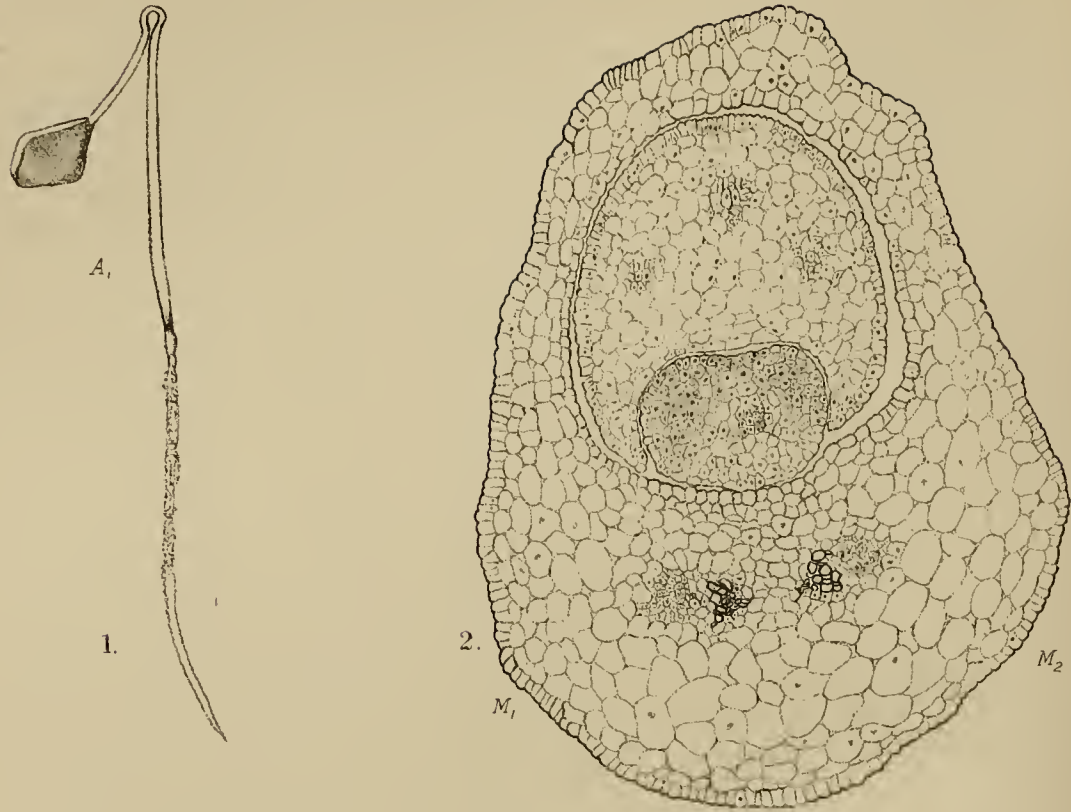
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*Fritillaria imperialis*.  
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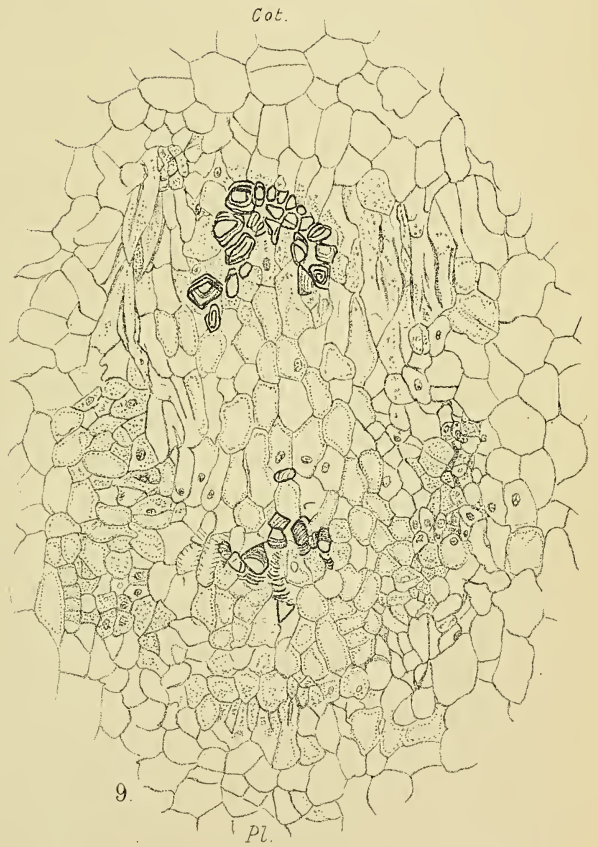
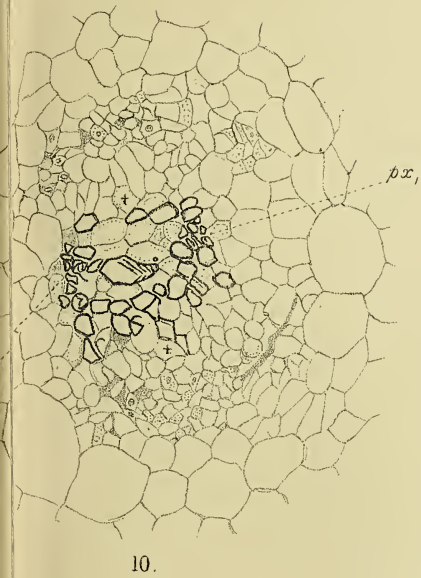
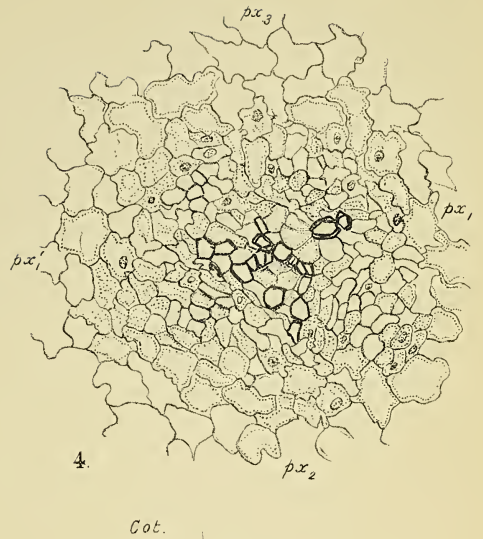
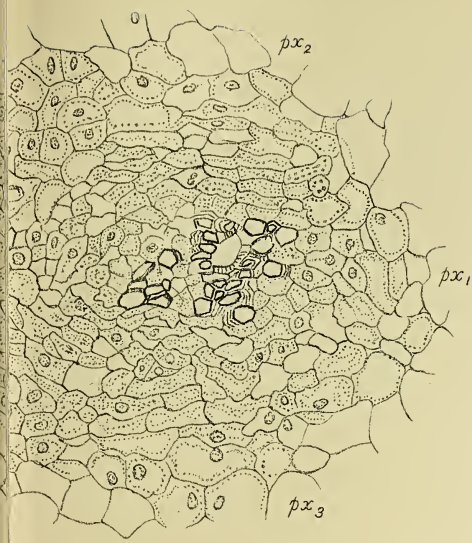




*Chlorogalum pomeridianum*, Figs 1-4.

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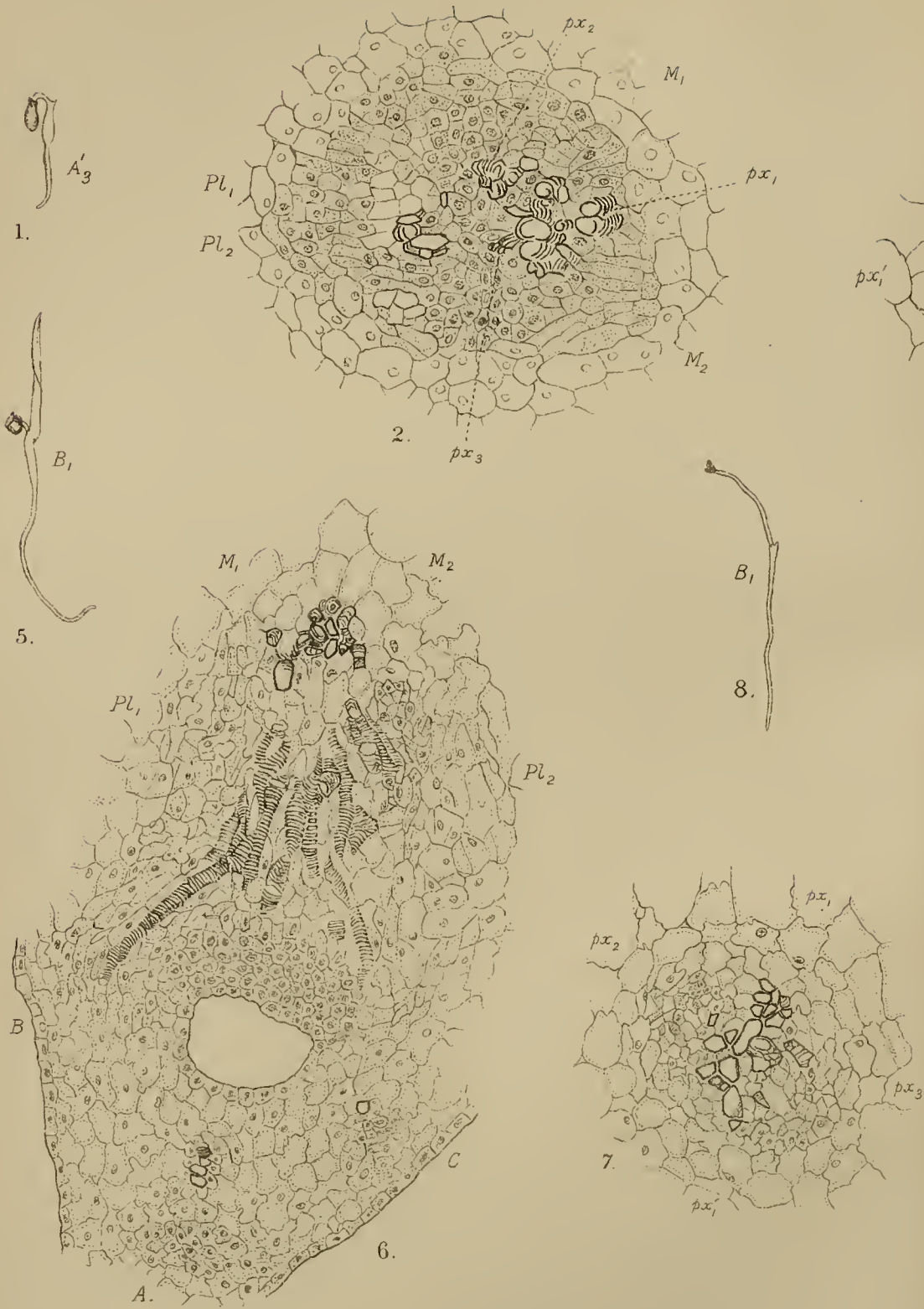


*Anthericum Liliago*, Figs. 5-7.

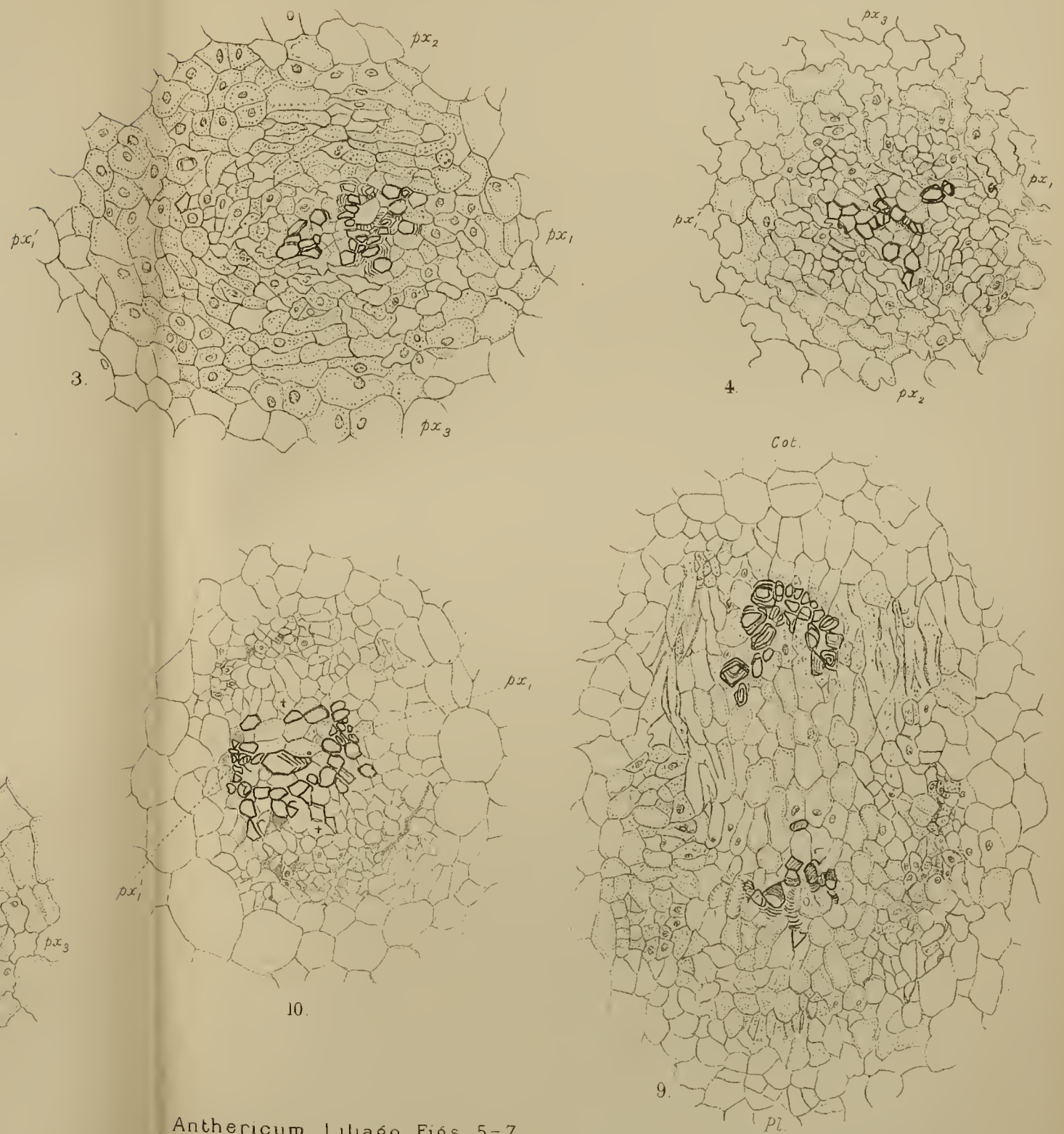
*Arthropodium cirrhatum*, Figs. 8-10.







*Chlorogalum pomeridianum*, Figs. 1-4.



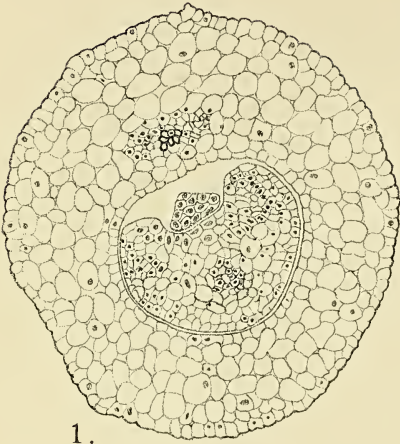
*Anthropodium cirrhatum*, Figs. 5-7.

*Anthropodium cirrhatum*, Figs. 8-10.

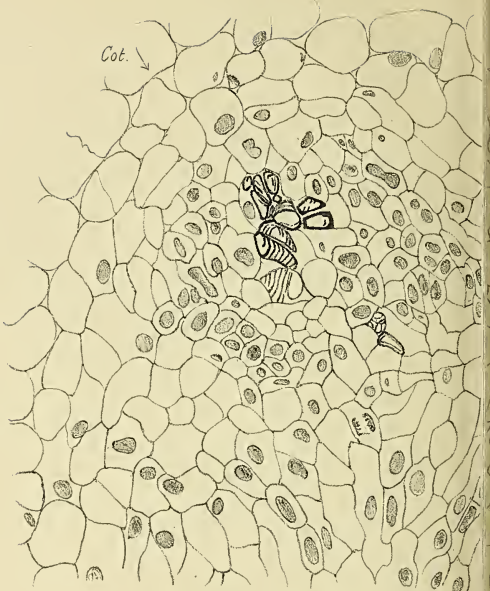








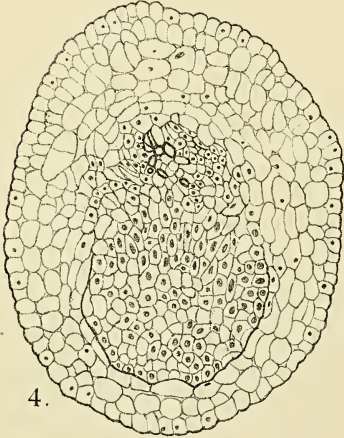
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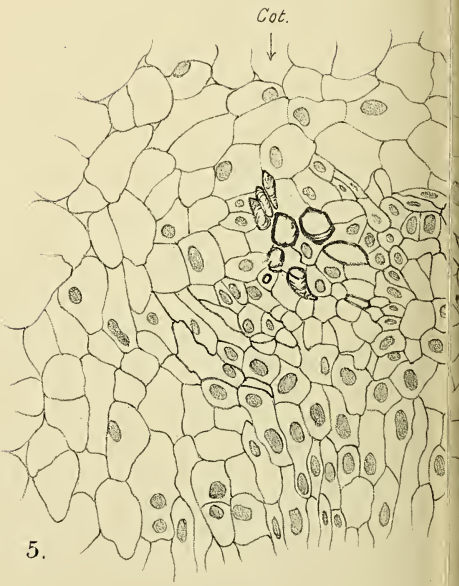
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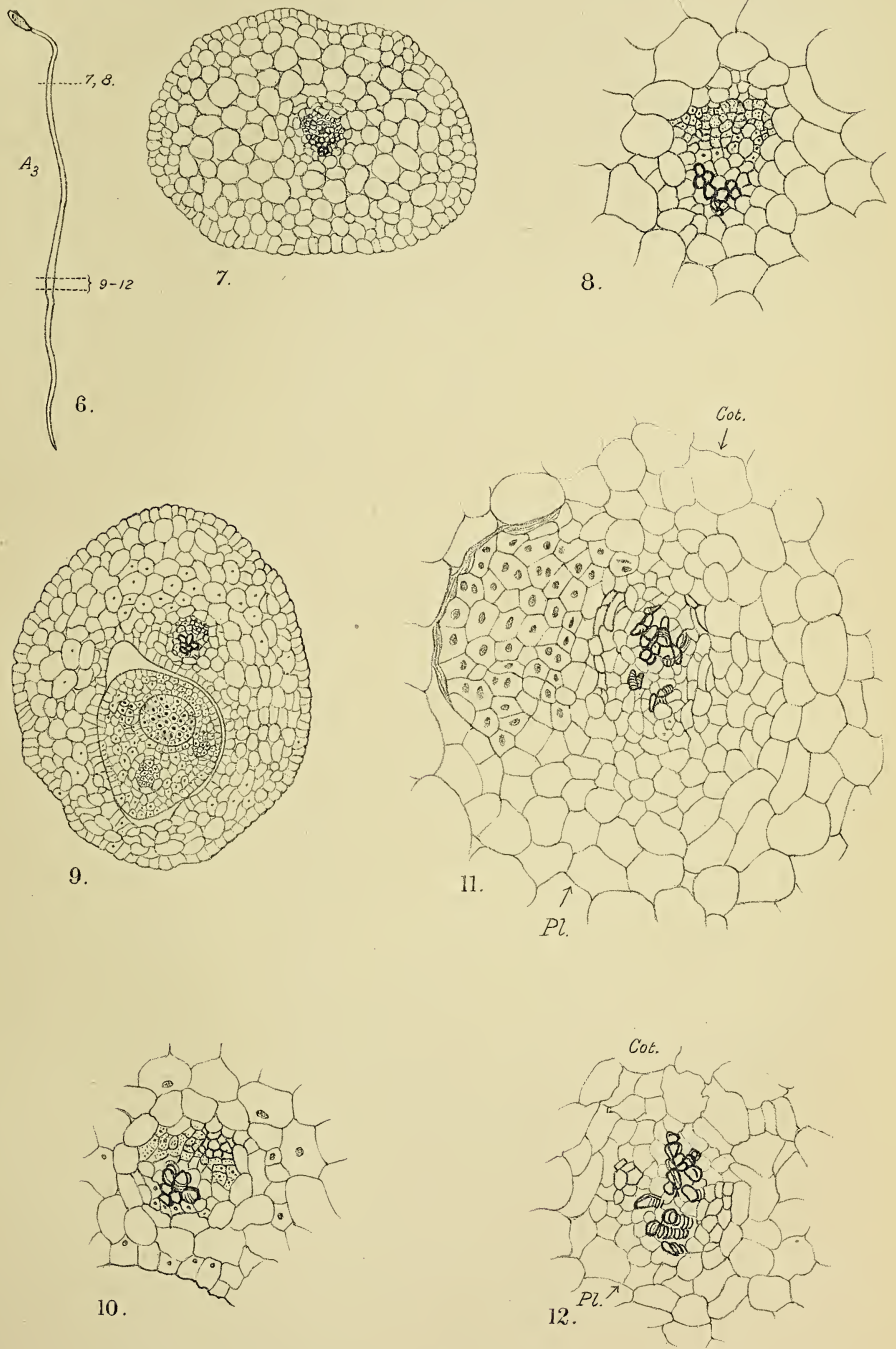


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Allium neapotitanum, Figs. 1-5.

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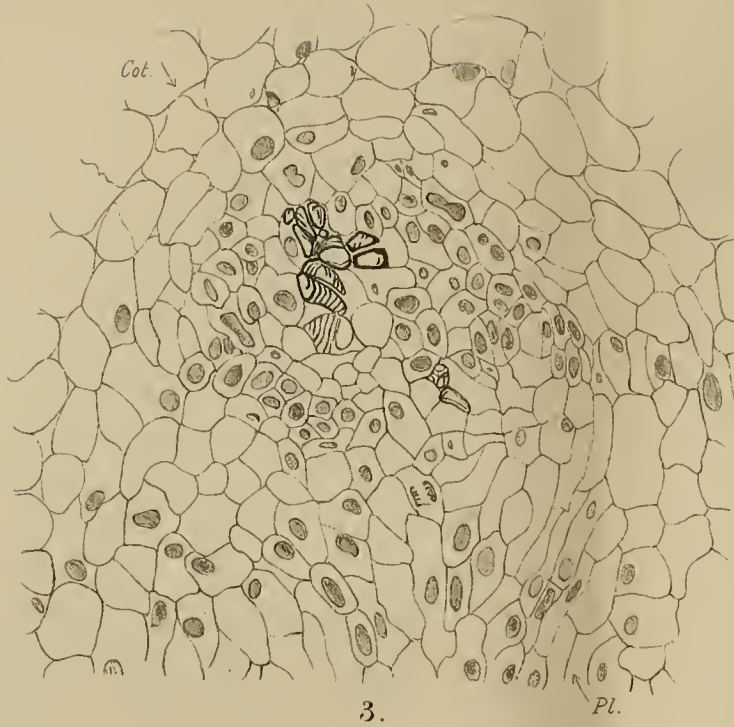


*Zygodenus elegans*, Figs. 6-12.

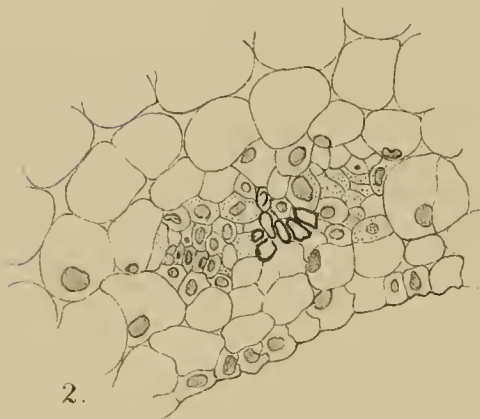




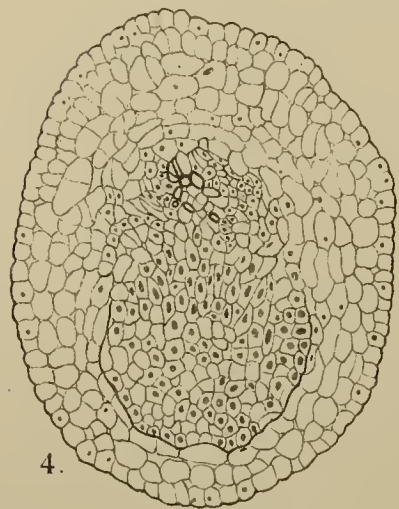
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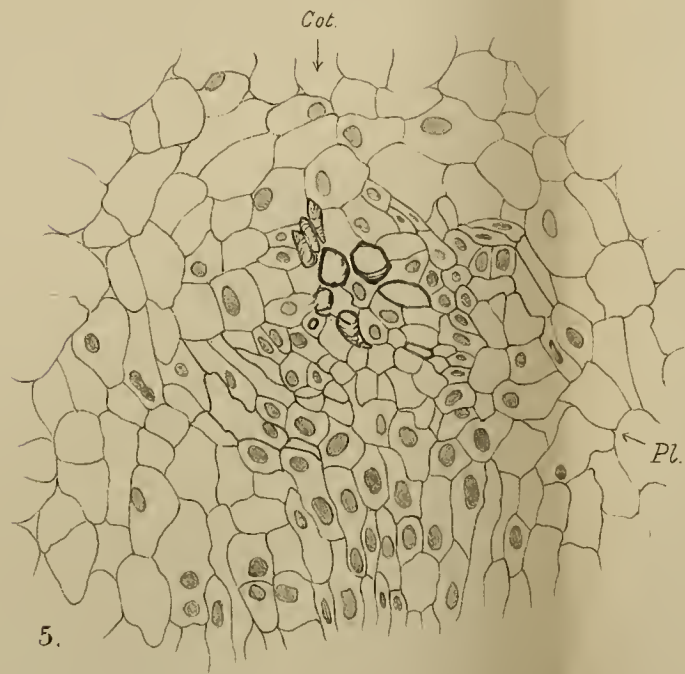
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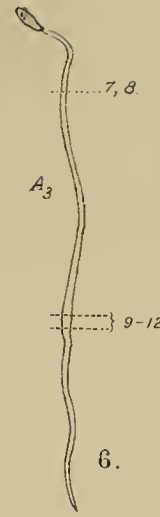
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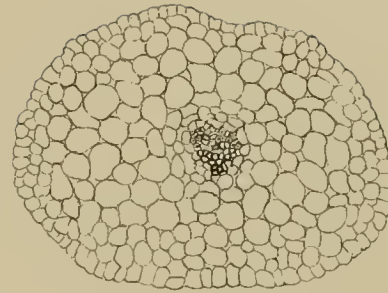
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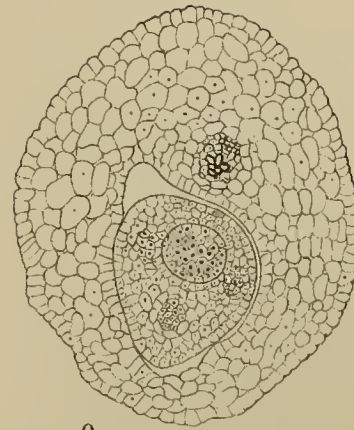
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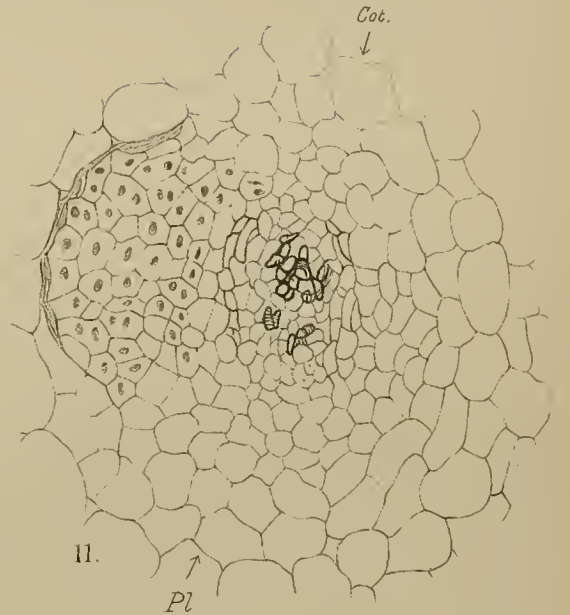
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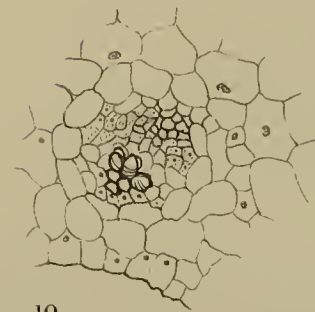
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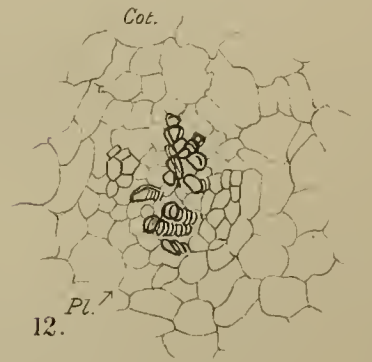
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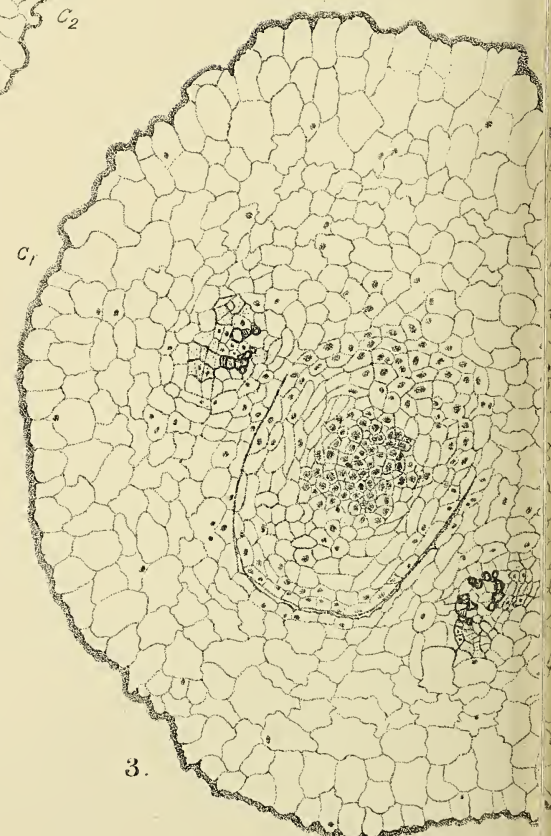
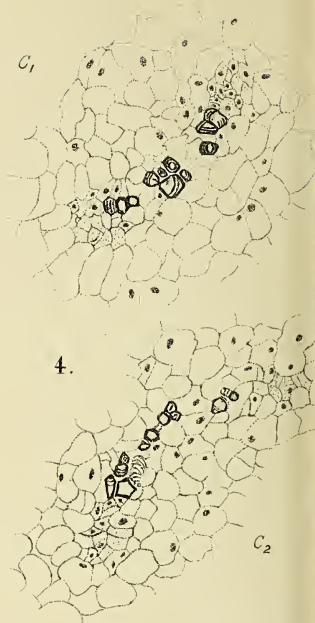
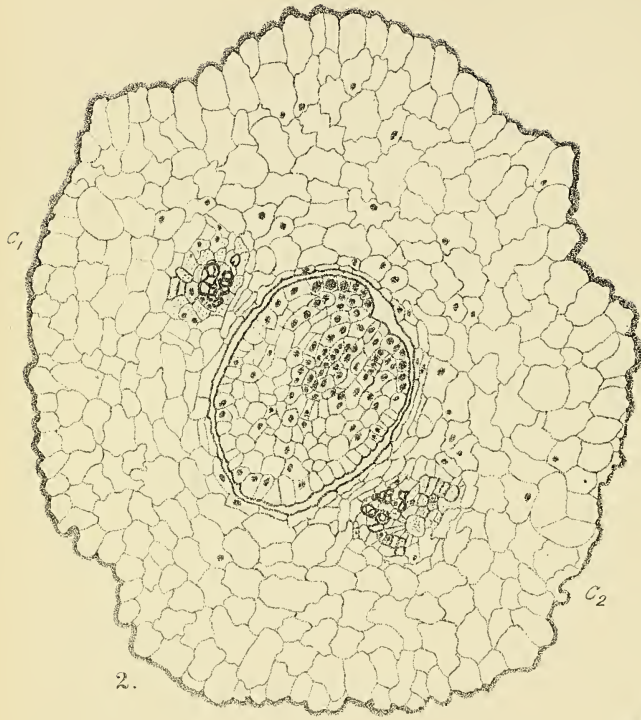
*Allium neapolitanum*, Figs. 1-5.

*Zygadenus elegans*, Figs. 6-12.





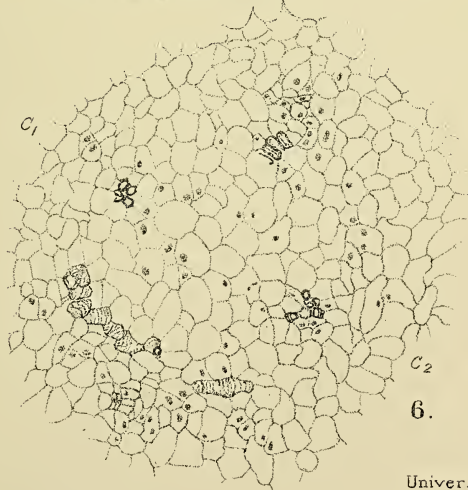
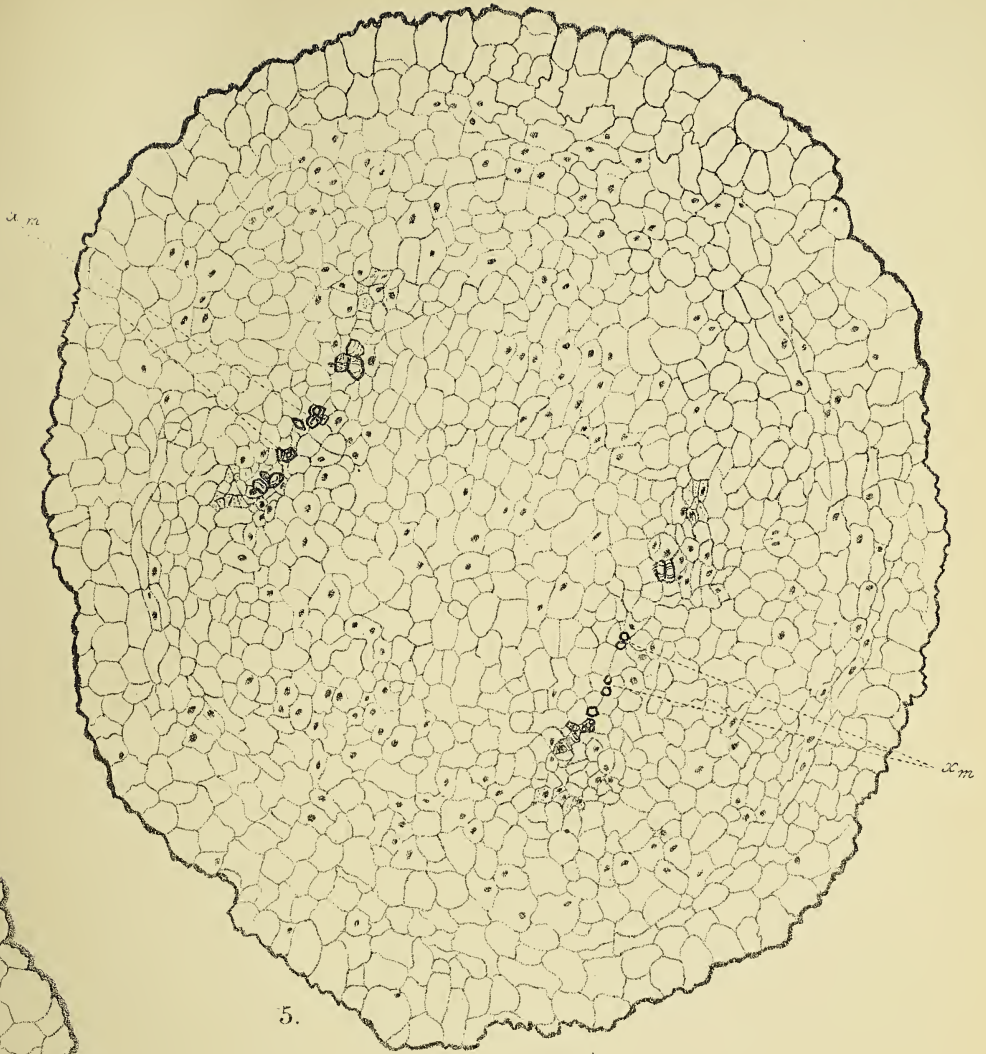




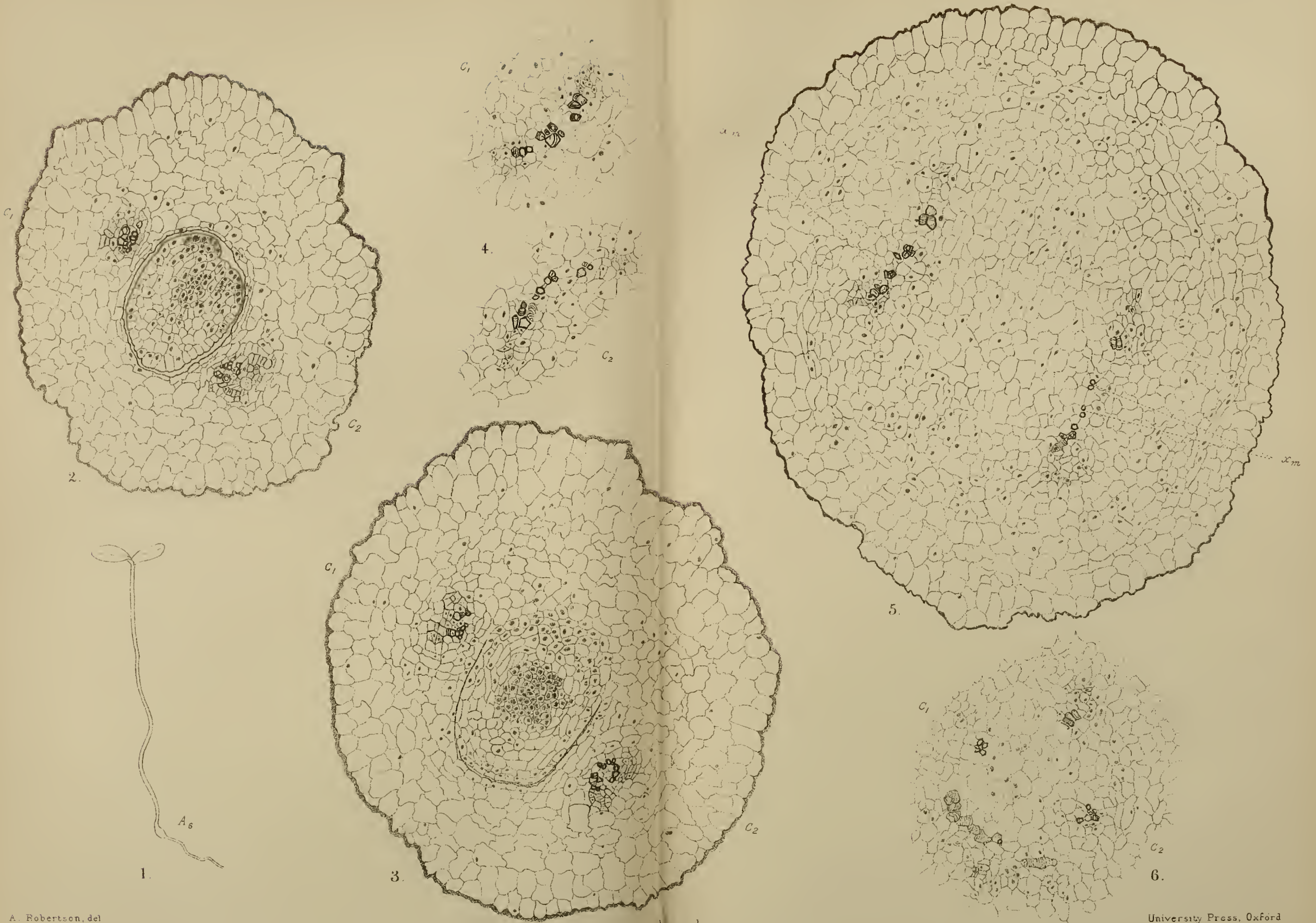
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*Eranthis hemalis*

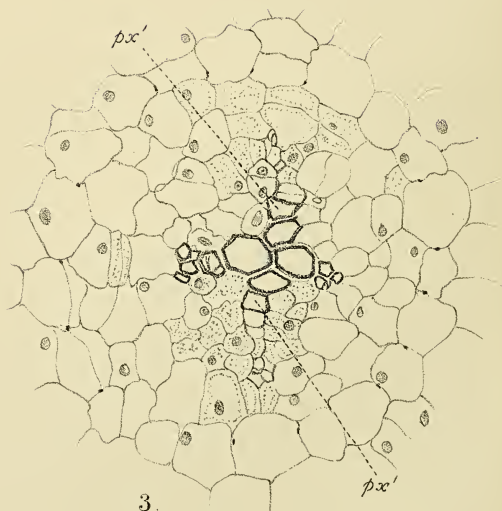
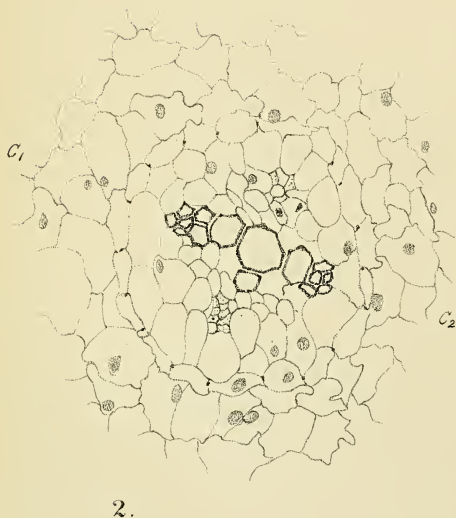
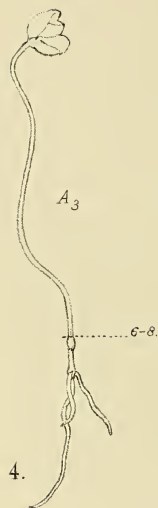
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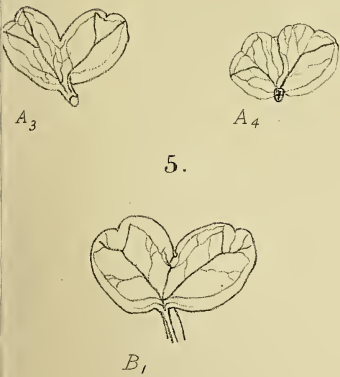
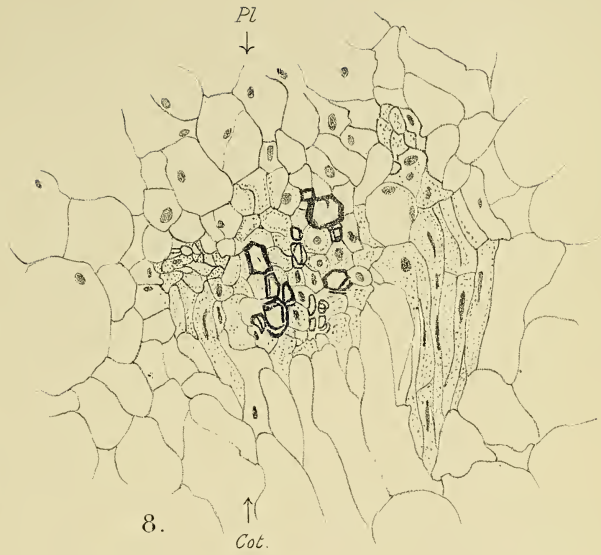
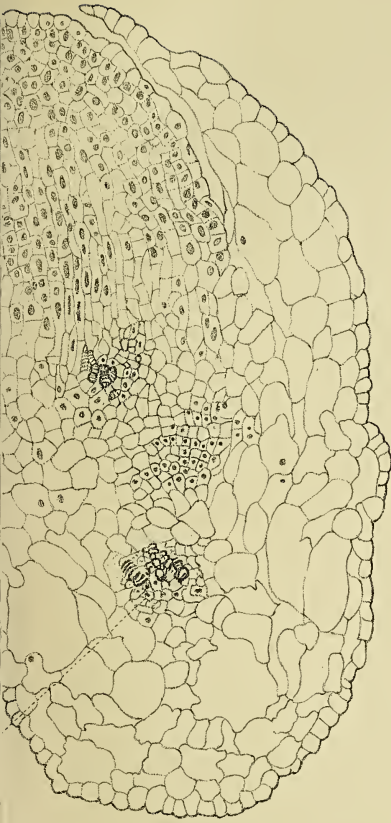




*Eranthis hiemalis*, Figs. 1-3.

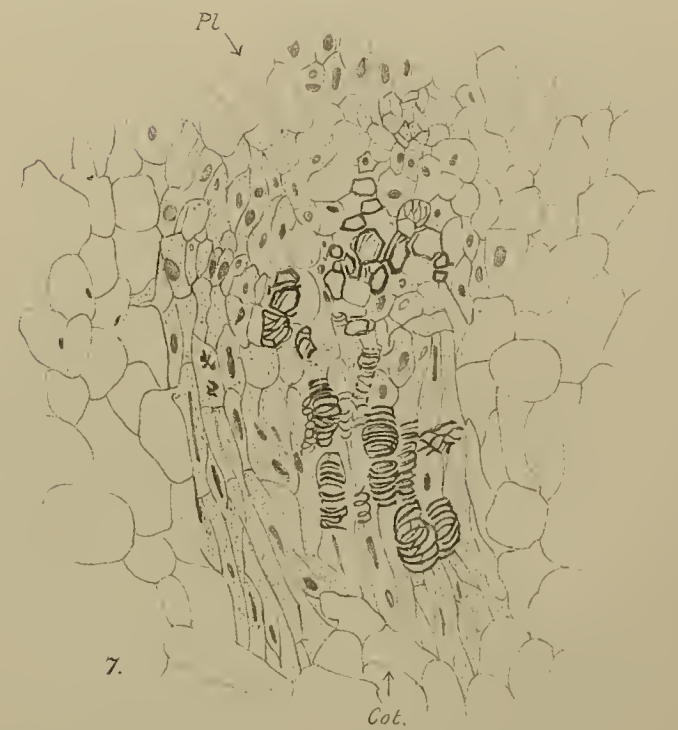
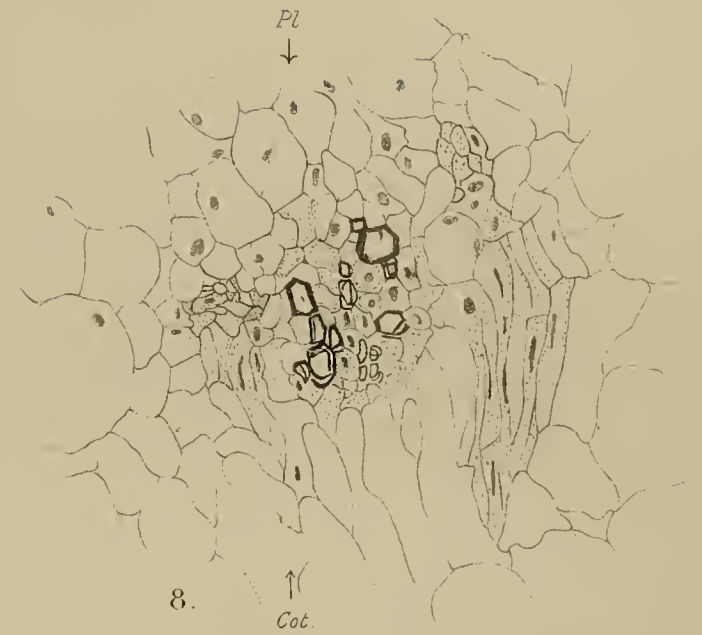
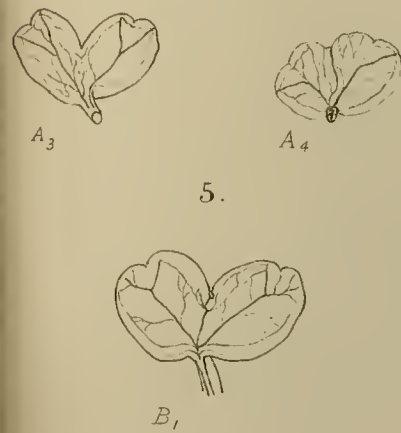
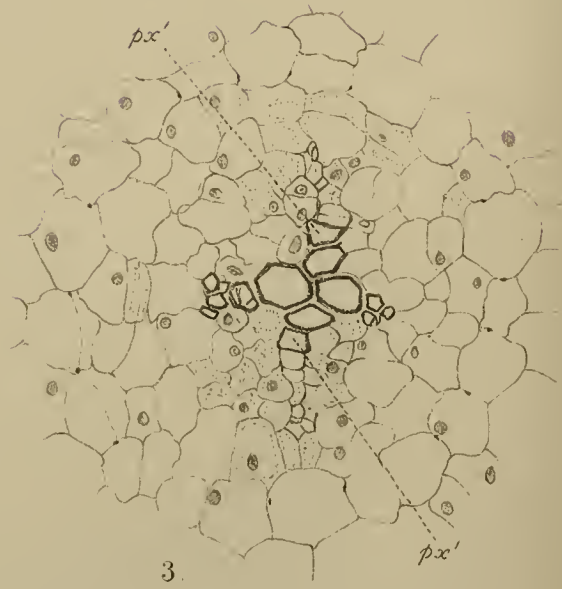
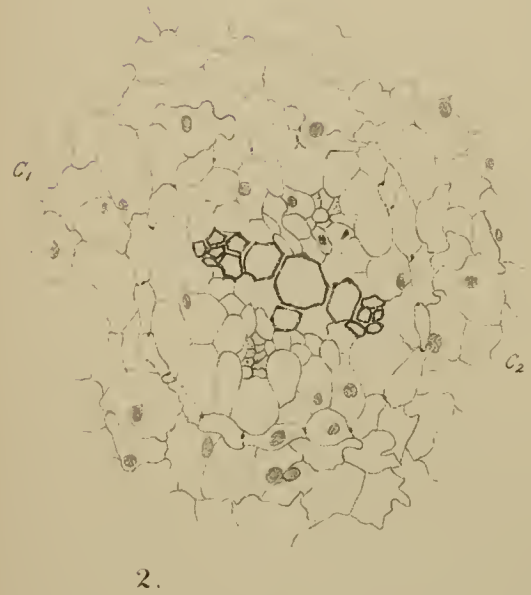
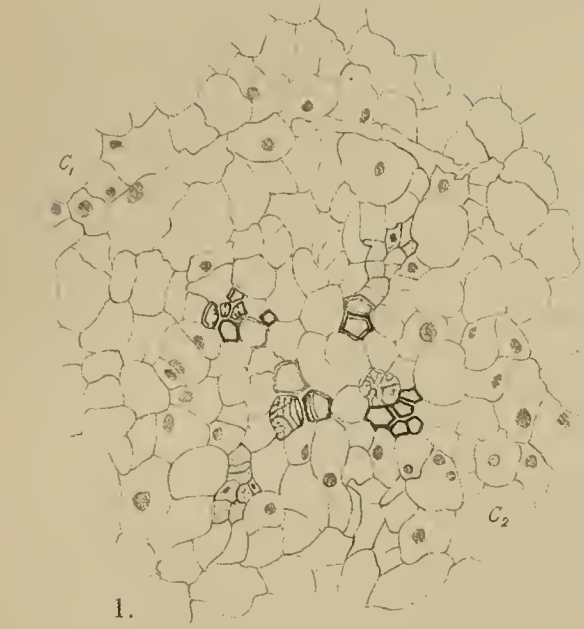
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Ranunculus Ficaria. Figs 4-8.





*Eranthis hiemalis*, Figs. 1-3.

*Ranunculus ficaria*, Figs. 4-8.





# On the artificial Production of Rhythm in Plants.

With a note on the position of maximum  
heliotropic stimulation.

BY

FRANCIS DARWIN AND DOROTHEA F. M. PERTZ<sup>1</sup>.



With four Figures in the Text.



IN the *Annals of Botany*, October, 1892 (Vol. VI, p. 245), we described a series of experiments on this subject. We remarked (p. 259) that 'Those who repeat our experiments must not expect uniform success, as there is undoubtedly a certain capriciousness in the results, which probably depends on varying degrees of vigour in the plants used.' The present research was begun in the hope of discovering a cause for this capriciousness; in this we have been disappointed, nevertheless some of our results seem worth printing.

The fundamental experiment consists in subjecting seedlings or growing shoots to a series of opposite stimuli following each other at equal intervals of time. The stimuli may be either due to gravitation or to light; in either case they tend to produce curvatures in two opposite directions. It might

<sup>1</sup> A note on our results was read before the Cambridge Phil. Soc. on January 22, 1900.

be supposed that the result would be an absence of all curvature. But this is not so: what happens is that the plant curves first in one, then in the opposite direction. These to and fro movements occur with surprising but not exact regularity in a rhythm corresponding to that of the application of the stimuli. In our former experiments the reversal of the stimulus occurred at intervals of half an hour; we have now succeeded in building up a periodic movement in a 15-minute rhythm<sup>1</sup>.

That during the continuance of the alternate stimuli a plant should nutate in a given rhythm is sufficiently remarkable, but it is far more interesting that the rhythm should continue after all stimulation has ceased, and this we again find to be the case.

#### METHOD.

We have again used the intermittent klinostat, employing of course a horizontal axis for geotropic experiments, and a vertical axis in the case of heliotropism.

A cord is wound round the rotating axle and supports a weight over a pulley; the axle also bears a pair of arms projecting from it at right angles and separated from each other by 180°. As long as one of these arms is fixed the weight cannot turn the axle, and the plant is geo- or heliotropically stimulated. At regular intervals a clock escapement frees the arm, and the axis rotates through 180°, when the plant is at once subjected to the opposite stimulus for another equal period of time. The act of rotation is rendered gentle by a fan-governor, so that the plant is not unduly jarred.

#### EXPERIMENTS.

We find that heliotropic experiments succeed with much greater regularity than those in which the stimulus is gravitational. This was to some extent evident in our 1892 results, but we can now state the case more definitely. We have made twelve heliotropic experiments<sup>2</sup> on *Phalaris canariensis*;

<sup>1</sup> We also tried an hourly period, but without success.

<sup>2</sup> Including one with an hourly period.

in eight of these the *stimulated rhythm* was apparent, i. e. the periodic movement continued as long as the alternate stimulation was kept going<sup>1</sup>. In six of the eight, the *unstimulated rhythm* was observed, i. e. the periodic movement continued after the stimulus had ceased. This is the really important result, namely, that when a *stimulated rhythm* has been formed it passes on to *unstimulated rhythm* in at least three-quarters of the cases.

In the following short series we begin with the full notes of an experiment, because in our former paper such details were omitted. No. I happens to be a geotropic experiment, and we have not thought it necessary to add full details of a heliotropic example, since the principle is identical in the two classes.

#### HALF-HOURLY PERIOD. (GEOTROPISM.)

Exp. I (Fig. 11). Mustard Seedling. March 15, 1899.

The seedling was arranged with its hypocotyl parallel to the horizontal axis of rotation, which was perpendicular to the plane of the window to avoid alternating heliotropic effects. The geotropic curvature of the seedling was observed by means of a horizontal microscope; the readings are given in column 3 of Table I. The experiment was begun on March 14, 1899; the readings here given were made on March 15 during the 97th and following periods of revolution of the klinostat, as indicated in column 1, which is headed 'Period.'

Beginning at 10.12 a.m. it will be seen that the readings (column 3) sink in value, indicating a steady upward curvature of the hypocotyl, until 10.22; at this point the curvature is reversed, as shown by the readings suddenly increasing in value. This increase continues steadily until 10.37, and at 10.38 the klinostat rotates through 180°. At this point the horizontal microscope has to be readjusted, and the readings beginning at 10.39 (Period 98) will be seen to be falling in value instead of rising. This is the obvious result of the rotation of the horizontal axis of the klinostat; the act of

<sup>1</sup> Three out of the four failures were on badly grown plants.

<i>Period.</i>	<i>Time.</i>	<i>Reading.</i>	<i>Period.</i>	<i>Time.</i>	<i>Reading.</i>
97	10.12 a.m.	40	99	11.21.5 a.m.	18
	14	37		22	19
	14.5	35		23	22
	16	28		25	28
	17	23		27	40
	18	20		28	46
	20	17		29.5	52
	<b>22</b>	<b>14</b>		30	57
	23.5	24		31	62
	24	26		32	67
	25	32		32.5	73
	27	42		34	80
	28	50		37.5	83
	30	62		38.5	86
	32	72		40	93
	34	84		42	97
	35	93		44	104
36	100	45	106		
37	103	46	107		
		<b>47.5</b>	<b>107.5</b>		
98	10.39	44	48.5	106	
	39.5	42	50	105	
	40	31	51	101	
	42	31	53	90	
	44	24	55	77	
	45	20	56	69	
	46	12	58	62	
	48	8	59	55	
	49	6	12. 1	43	
	49.5	5	2.5	35	
	50	4	3	30	
	<b>51</b>	<b>4</b>	4	26	
	52	5	5	20	
	54	11	6.5	12	
	56	15	8	4	
	58	19	10	-4	
	59	25	12	-10	
	11. 2	38	13	-15	
	3	43	14	-24	
5	52	15	-29		
6	56	16	-34		
7	60	16.5	-38		
99	11. 9	47	17.5	-43	
	10.5	44	18	-49	
	13	38	19	-52	
	14	32	19.5	-56	
	16	26	20	-59	
	17	23	21	-62	
	18	21	22	-67	
	19	18	23	-73	
	20	17	24	-75	
	<b>21</b>	<b>17</b>	24.5	-79	
			26	-87	
		30	-101		

Observations ceased.



curvature remains unchanged between 10.37 and 10.39, but owing to the rotation of the axis what was a downward becomes an upward curvature.

This is clearly shown in the diagram (Fig. 11), which gives

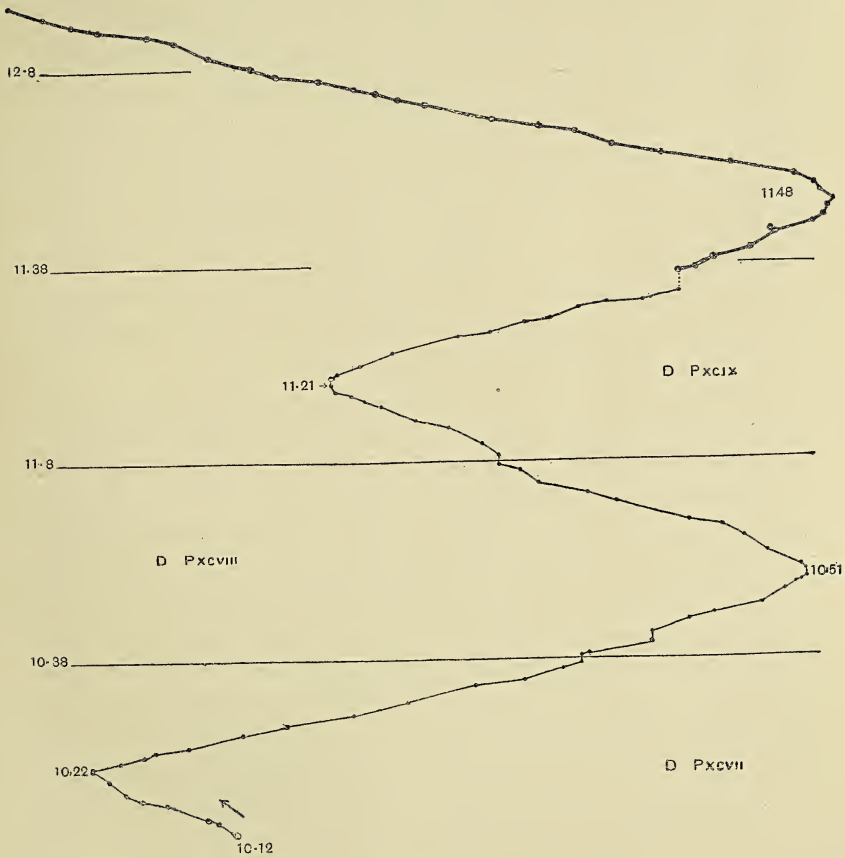


FIG. 11.

a graphic representation of Exp. I. Fig. 11 and all similar diagrams are to be read from below. The diagram is divided by a series of horizontal lines which indicate the moments at which the klinostat axis rotates; the spaces between the lines are the *periods*, beginning below with Period 97. Time

is represented along vertical lines (ordinates), and it will be seen that the times of rotation are at 10.38, 11.8, 11.38. The upward or downward curvature of the plant is represented by the line in the diagram travelling to the left or to the right. The letter *D* (for downward) being on the right in Period 97, it follows that until 10.38 movement to the *left* means an upward curvature, movement to the *right* a downward curvature. Thus from 10.12 a.m. to 10.22 the curvature was upwards; at 10.22 (as shown in Table I) the curvature is suddenly reversed, and the plant curves downwards. In Period 98, owing to the rotation of the axis at 10.38, *D* must be placed on the left; in this way it is indicated that after 10.38 the hypocotyl was bending upwards, but the continuity of the curve-line from 10.22 to 10.51 shows that, considered as a growth-curvature, it is a single act; it is in fact a single unit in what is practically half-hourly rhythm.

In Period 99 the turning-point of the curve comes at 11.21, almost exactly half an hour after 10.51, as shown in the table and in the diagram. At 11.38 the klinostat was not allowed to turn: this is indicated by a *thick* curve-line, also by the absence of a numbered period and the absence of the symbol *D* in the space 11.38–12.8. At 11.38 the plant was placed with the original plane of curvature vertical, to avoid as far as possible geotropic stimulus in that plane. In spite of the freedom from alternate stimuli, the reversal of curvature took place at 11.47½, that is, 3½ minutes before the proper moment. By referring to Table I it will be seen that after the sharp turn at 11.47½ the movement continued unchanged in direction until 12.30, when the observations were discontinued. In the diagram there is only room for the curve up to 12.10.

#### QUARTER-HOURLY PERIOD. (GEOTROPISM.)

Six experiments were made, on cut stalks of a Valerian, with a klinostat rotation through 180° at intervals of 15 minutes. In one experiment no curvature of any sort occurred, but in the other five cases a regular rhythm was

observed, which continued after the klinostat was stopped. In two experiments this (the 'unstimulated rhythm') showed two reversals of direction. We give a single example:—

Exp. II, Fig. 12. Valerian,  $\frac{1}{4}$ -hr. period. (Geotropism.) Fig. 12 will sufficiently explain the results without giving the full notes.

There are several curious points about this experiment. The change in direction of curvature takes place not in the middle of the periods (as in Fig. 11) but at the horizontal lines, that is, the beginning of each fresh period. Thus during each period the shoot was curving downwards<sup>1</sup>. It is impossible to say whether this is due to 'sagging,' i. e. to the weight of the shoot causing it to bend downwards as any flexible body would bend, or whether it is a true geotropic curvature which happens to coincide with the turning-point of the klinostat. The fact that it occurs in Period I makes it probable that it is a case of sagging. But the sequel of the experiment makes it clear that the alternation of stimulus was producing an effect. It is therefore probable that the physical drooping of the shoot concealed any geotropic curves as long as the klinostat was in action. The klinostat was stopped in the middle of Period IX; nevertheless, as the thick line shows,

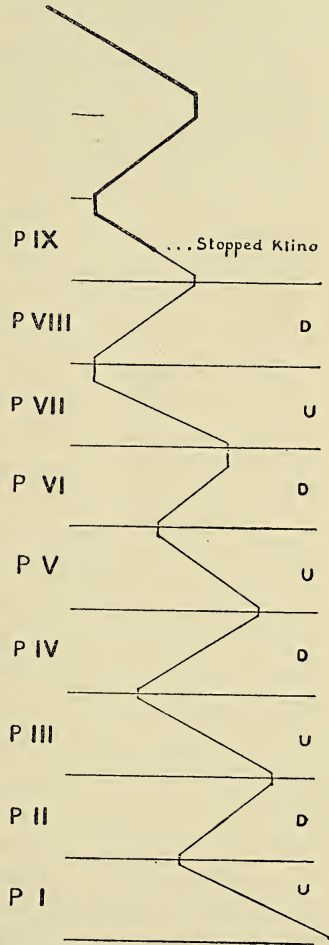


FIG. 12.

<sup>1</sup> It must be understood that Fig. 12 is an abstract of the observations, only the critical points of the curve being given. The same is true of Figs. 13 and 14.

the curvature of the plant was reversed at the end of the  $\frac{1}{4}$  hr., and again of the next  $\frac{1}{4}$  hr. These movements could not be due to physical drooping.

QUARTER-HOURLY PERIOD. (HELIOTROPISM.)

Six<sup>1</sup> experiments were made on the heliotropic curvature of *Phalaris canariensis* with the quarter-hourly rhythm. Four of these showed the 'stimulated rhythm,' and two showed also 'unstimulated rhythm,' i.e. a rhythm continued after the klinostat stopped. One of these made a single turn, and the other made two such reversals of curvature.

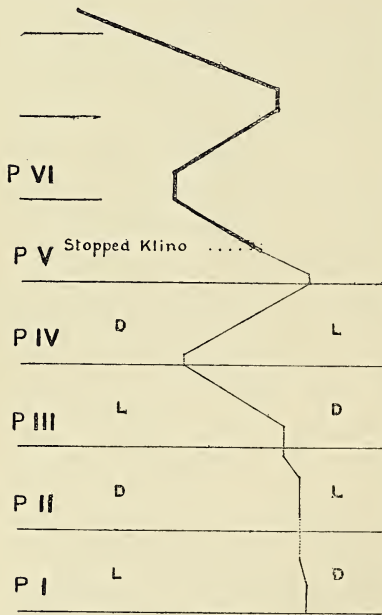


FIG. 13.

Exp. III, Fig. 13, May 10, 1900. *Phalaris*. Quarter-hourly period. (Heliotropism.)

The experiment is remarkable as showing that the plant may acquire a rhythm in a very short time, e.g. after four periods of  $\frac{1}{4}$  hr. each. It should be noted that in heliotropic diagrams the letters *D* and *L* mean *Dark* and *Light*, and that they change sides in each period precisely as the letters

*D*, *U* (for *Down* and *Up*) alternate in the geotropic diagram, Fig. 12. Here again the curve changes direction synchronously with the rotation of the klinostat, but in this case there can be no question of a purely physical droop (as in Exp. II), since the axis of rotation is vertical. Neither in heliotropic nor geotropic experiments is this synchrony

<sup>1</sup> Several experiments were vitiated by the slow or oblique growth of the seedlings, and are therefore omitted.



universal; see for instance, *Annals of Botany*, VI, pp. 257-9, where in Exps. X and XI the reversal of the curve, in light experiments on *Phalaris*, occurs in the middle of the periods. To return to Fig. 13, the klinostat was stopped in Period 5 and the plant arranged so that no fresh heliotropic stimulation could occur in the original plane. The thick line shows two reversals of curvature occurring at approximately the right times.

Exp. IV, Fig. 14, December 1, 1899. Oat seedling. Half-hourly period. (Heliotropism.)

We give this experiment in order to make it clear that there is no necessary connexion between heliotropism and the quarter-hourly period, and that a plant can equally well acquire a half-hourly rhythm by alternate light-stimuli.

It should be noted that in Fig. 14 the curvature of the seedling, as soon as it becomes regular in Period 5, is away from the light, not towards the light as in Fig. 13; we are unable to explain the difference between the two cases. The klinostat was stopped in Period 9, and the thick line shows two reversals at approximately half an hour's interval, the first turn being somewhat belated. This is another good instance of 'unstimulated rhythm.'

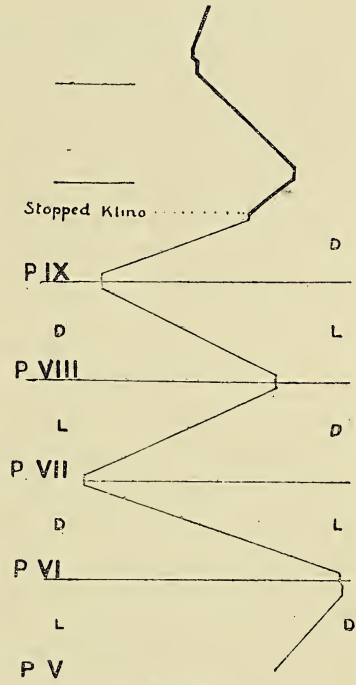


FIG. 14.

ALTERNATE UNEQUAL STIMULI.

We made a good many heliotropic experiments with alternating but *unequal* periods of illumination, in the hopes of building up an unequal rhythm. The intermittent

klinostat was so arranged that the plants were illuminated on one side for 28 minutes and then on the opposite side for 32 minutes. Twelve experiments were made, eleven with *Phalaris*, and one with an oat seedling; out of these only two failed to show stimulated rhythm, and out of these ten successful cases, three showed 'unstimulated rhythm' after the klinostat had been stopped. We hoped to find that the plants would show an inequality in the period of their rhythm corresponding to the inequality of the alternate stimuli, but the results are disappointing. If we call the number of minutes that elapse between two successive reversals of curvature, the length of the period, we can indicate the amount of regularity of the rhythm by writing in a row the lengths of successive periods. In an ideally regular half-hourly rhythm we should have—30, 30, 30, 30, 30. When we compare with this the result of an experiment made with alternate stimuli of 28 and 32 minutes, we seem to get the desired result. Thus in Exp. XXIX, the figures were—28, 30, 27, 32, 27.5. In Exp. L we got—23, 37, 22, 28, 30, 30. In Exp. LI—25, 37, 17, 40, 19. In all these there is a clear indication of the double or unequal rhythm. But unfortunately it is possible to find similar results produced by the ordinary half-hourly stimulation. Thus in Exp. II (*Annals of Botany*, VI, p. 250) with a regular half-hourly geotropic stimulus we got—18, 35, 14, 29. This is an unusually irregular rhythm for an experiment of this class, but it clearly renders it impossible to come to any conclusion as to the special character of the rhythm produced by unequal stimulation.

The experiments are nevertheless interesting in another way, for there was an undoubted difference in the *degree* of curvature in the two directions. That is to say that after some hours of alternate illuminations of 28 and 32 minutes the plants became perceptibly concave on the side which received the longer light-stimulus<sup>1</sup>.

<sup>1</sup> The same effect was seen with the radicles of *Sinapis*, which gradually bent away from the more illuminated side.

In 'The Power of Movement in Plants' it was shown that heliotropic curvature may be brought about by modified circumnutation, i. e. by a revolving movement in which the curvature towards the light is greater than that in the opposite direction. Just in the same way, in our experiments, heliotropic curvature was produced by asymmetrical nutation.

#### GENERAL REMARKS.

It is often said that periodic phenomena are due to after-effect. But this, though true in a certain sense, is too vague a statement to be called an explanation. It is known that geotropic and heliotropic curvatures continue long after the stimulus has ceased to act. So that it might at first appear as if the curvatures in one direction were the after-effect of a given half-hour's stimulus, and the opposite curvatures were the effect of the next ensuing half-hour. But we are unable to construct a scheme of this sort which fits the facts. The after-effect in a curving shoot which has been stimulated for half an hour lasts a long time, and we cannot see how the series of opposite curvatures, *each lasting half an hour*, could be caused by the combination of such after-effects. After-effect in the ordinary sense is the result of the last stimulus received, and we know of nothing to make us believe that the latent after-effect of an antecedent and opposite stimulus can be held to account for the sharp reversal of curvature which we find to occur.

We believe, moreover, that an artificial rhythm may be imagined to be produced without what is ordinarily described as after-effect. Suppose an apogeotropic shoot to be placed horizontally; after some 15 minutes of stimulation it will begin to curve upwards, and will continue so to do for another 15 minutes. At this point the klinostat rotates through  $180^\circ$ , and the stimulus is replaced by an equal and opposite one. According to our assumption (that after-



effect is non-existent) the curvature will cease at the turn of the klinostat, and the plant will be able to receive the new stimulus, and will therefore after a period of quiescence curve in the opposite direction. We can see no reason why this imaginary state of things should not build up a rhythmic condition, so that the plant would tend to nutate at half-hourly intervals after the klinostat had been stopped. We can conceive the natural circumnutation of the plant being moulded to a half-hourly rhythm under these conditions—that is to say, without the existence of after-effect.

All we can do is to compare our results with other periodic phenomena. For instance, when the stimulus is given by the alternation of day and night, we get the diurnal periodicity of sleeping plants, which, as in our experiments, continues after the stimulus has ceased. It seems to us that such natural rhythms, as well as our artificial phenomena, are intelligible only as modifications of a fundamental rhythmic faculty in plants. Such a faculty exists as circumnutation, and we may point out that the possibility of regulating artificially the rhythmic growth of a plant is in entire agreement with the fundamental idea of 'The Power of Movement in Plants,' namely that growth-curvatures are modifications of circumnutation.

It is unfortunate that the word *after-effect* has been used in two senses:—(1) To designate the continuance of curvature after the cessation of the stimulus, which may be most conveniently classed with the phenomena of the motor mechanism, although it is also a character of the percipient element. (2) To designate such a case as the continuance of periodic movements in a sleeping-plant in continuous darkness. This should be classed with habit or memory, and is a phenomenon of the percipient or quasi-nervous element in plants. Precisely the same may be said of the artificial rhythm above described.



NOTE ON THE POSITION OF MAXIMUM  
HELIOTROPIC STIMULATION.

Czapek has shown that if an apogeotropic shoot is placed at an angle of  $45^\circ$ , the tip being directed obliquely downwards, it receives a stronger geotropic stimulus than if it points  $45^\circ$  above the horizon. This may be proved to be true by the use of our intermittent klinostat. An apogeotropic organ being fixed at  $45^\circ$  with the horizontal axis of rotation, is subjected (by the periodic rotation of the axis through  $180^\circ$ ) to opposite and alternate stimuli<sup>1</sup>. If the stimulus is greater when the organ points obliquely downwards, the sum of the unequal stimuli must tend to bring the organ into line with the horizontal axis of rotation. And this was found to be the case by one of us<sup>2</sup>, who made the experiment with apogeotropic grass-haulms. We have now been able to show that the same rule applies to heliotropism.

Our experiments on heliotropism were made with *Phalaris* on a klinostat rotating on a horizontal axis through  $180^\circ$  at intervals of half an hour. The plants were fixed<sup>3</sup> so as to make an angle of  $45^\circ$  with the axis of rotation, and also, therefore,  $45^\circ$  with the horizontal light. It follows that the plants were alternately pointing obliquely from, and obliquely towards the light.

The following were the results:—

June 7, 1900 ( $\frac{1}{2}$ -hr. klinostat). Seven *Phalaris* seedlings: after 2 hours all had become slightly more parallel to the axis of rotation.

June 11, 1900. Six seedlings: after 2 hours four were more parallel, two unchanged.

June 12, 1900. Five seedlings: after  $2\frac{1}{4}$  hours all more parallel.

<sup>1</sup> This is the method used by Czapek; see Sitzber. K. Akad. Wien, civ, 1, p. 1216.

<sup>2</sup> D. F. M. Pertz, in the *Annals of Botany*, xiii. p. 620.

<sup>3</sup> The plants retained a roughly horizontal position under the influence of the alternating geotropic stimuli.

June 13, 1900 ( $\frac{1}{4}$ -hour klinostat). Five seedlings: after  $2\frac{1}{2}$  hours all more parallel.

Thus twenty-one out of twenty-three *Phalaris* seedlings, after from 2 to  $2\frac{1}{2}$  hours, approached the axis of rotation. This can only mean that they were more strongly stimulated when pointing obliquely away from the light than when pointing obliquely towards it.

BOTANICAL LABORATORY, CAMBRIDGE,  
*August 2, 1902.*

## A Monograph of the Genus *Streptopogon*, Wils.

BY

ERNEST S. SALMON, F.L.S.



With Plates VIII, IX and X.



THE genus *Streptopogon* was founded in 1851 by Wilson (33) on the South American moss described by Taylor (31) in 1846 as *Barbula erythrodonta*. The genus was then defined as follows: 'Calyptra mitriformis, superne scabra; peristomium simplex, ciliiforme; cilia 32 aequidistantia, in ciliola duo postice fissa, laevia, in spiram unam dextrorsum contorta, basi in membranam angustam coadunata; cellulae operculi contortae.—In its mitriform, scabrous calyptra this curious moss resembles some species of *Tayloria*, but the peristome is that of *Barbula*, to which genus it is closely allied.'

A few years later Mitten (12 and 12\*) referred to the present genus the moss, from Chile, described in 1842 (28) by Schwaegrichen as *Barbula mnioides*, and also the moss from Kerguelen Island published by Hooker and Wilson (8) in 1844 as *Schistidium marginatum*. In 1865 Hampe (5) described *Streptopogon Lindigii* from Colombia (New Granada). Spruce, in 1867, in his catalogue of the mosses collected by him on the Amazon and in the Andes (29), mentioned by name only *S. rigidus*, Mitt., *S. cavifolius*, Mitt., and *S. erythrodontus* var. *clavipes*, Spruce; these three plants were distributed by him in the 'Musci Amazonici et Andini.' *S. cavifolius* and *S. clavipes* (but not *S. rigidus*) were described by Mitten in his 'Musci

austro-americi' (14) in 1869, where two new species were also published, viz. *S. latifolius*, Mitt., and *S. setiferus*, Mitt. In 1873 Jaeger (10) added as a var. *prostrata* to *S. mnioides* the plant from Chili published by Montagne in 1845 as *Tortula prostrata*. In 1876 Mitten (15) added to the genus *S. australis* from Kerguelen Island. In 1879 Jaeger in the second volume of the 'Adumbratio' (10) transferred to *Streptopogon* the *Barbula crispata* of Hampe (1876) (6), from Australia. In the same year Mitten (16) gave the name *Streptopogon gemmascens* to the moss previously described in Schimper's 'Synopsis' as *Didymodon flexifolius* (Dicks.), Hook. and Tayl., var. *gemmiferus*. Müller (19), in 1882, published two new species, *S. Rutenbergii* and *S. Calymperes*, from Madagascar, and mentioned by name a third species, *S. calymperoides*, from Costa Rica. About the same time, also, Müller gave the ms. name *S. Hildebrandtii* to a moss sent out under the number 2,098 in Hildebrandt's 'Flora von Central Madagascar.' In 1885 Bescherelle (1) referred doubtfully to the genus as *S. ? mayottensis*, a male and barren moss from the island of Mayotte. In 1888 the name *S. Parkeri*, Mitt. mss., appeared in Wright's 'Mosses of Madagascar' (34). In 1894 Müller described *S. Schenckii*, from Brasil, in Brotherus's 'Musci Schenckiani' (21). In 1895 Bescherelle in his 'Essai sur le genre *Calymperes*' (2) pointed out that *Calymperes Lindigii*, Hampe, was really a *Streptopogon*, and as the specific name was already in use in the present genus, gave the name *S. Hampeanus* to Hampe's plant. In 1897 Müller (23) published as a new species *S. bolivianus* from Bolivia; and Paris in the 'Index bryologicus' (25) transferred to *Streptopogon* the two species *Barbula crispatula*, C. Müll., from Patagonia (1897), and *B. Wilhelmii*, C. Müll. (nomen) (1897), from Australia. Paris also mentioned a moss under the name '*S. maveganensis*, Besch. in Marie M. Mad. nr. 269.' In 1897 also, Brown (4) published *S. Hookeri* from New Zealand. Finally, in 1900, Müller in his 'Genera Muscorum Frondosorum' (24) mentioned by name *S. Calymperopsis* from Bolivia.



Up to the present time, therefore, there have been twenty-six species with one variety referred by different authors to the present genus. A critical comparison of many of these, however, leads us at once to exclude them from the genus. The species which are certainly not congeneric with *S. erythrodontus*, the type of the genus, are the following:—

(1) *S. mnioides* (Schwaegr.), Mitt.—Mitten himself has later (16) removed this plant from the genus *Streptopogon*, and made it the type of a new genus *Calyptopogon*. Paris (26) has since reduced *Calyptopogon* to a section of *Streptopogon*, but Brotherus (3) maintains it as a genus. *Barbula mnioides*, Schwaegr., is certainly generically distinct from *Streptopogon* in areolation.

(2) *S. marginatum* (Hook. f. and Wils.), Mitt.—When placing the species in the genus Mitten (12) remarked merely ‘another species of the genus is *S. marginatus*’; afterwards, however, we find Mitten (16 and 17) calling it ‘*S. ? marginatus*,’ and remarking, ‘This, which appears destitute of peristome, is in other respects more nearly related to *Streptopogon* than to any other genus.’ Müller (24, p. 424) has referred the species to his genus *Willia*, creating a section *Schistidiella* for its reception.

(3) *S. australis*, Mitten.—Müller (20) has stated that from the description of the plant, this species belongs to his genus *Willia*. An examination of the type specimens of *S. australis* in Mitten’s herbarium shows however that the moss clearly belongs to the genus *Didymodon*.

(4) *S. crispatus* (Hampe), Jaeger.—This species, which has been removed to the genus *Calyptopogon* by Brotherus (3), possesses an areolation quite different to anything found in the species of *Streptopogon*.

(5) and (6) *S. ? mayottensis*, Besch., and *S. maveganensis*, Besch.—Brotherus (3) has remarked under *Streptopogon*, ‘*S. mayottensis*, Besch., aus der ostafrikan. Insel Mayotte, gehört nicht zu dieser Gattung, sondern ist eine Funariacee, welche als steril nicht näher bestimmbar ist.’ I have examined the type of *S. mayottensis* in Bescherelle’s herbarium at the British Museum. The plant is certainly to be excluded from *Streptopogon*, and belongs, as Brotherus has pointed out, to the *Funariaceae*, showing the habit and areolation, and the peculiar shaped paraphyses of the male inflorescence charac-

teristic of that family. M. Bescherelle informs me that the moss sent out in Marie's Mosses of Madagascar, nr. 269, as *S. maveganensis*, Besch., is in all probability the same plant as that published under the name *S. ? mayottensis*, Besch.

(7) and (8) *S. crispatula* (C. Müll.), Paris, and *S. Wilhelmii* (C. Müll.), Paris.—Both these species differ completely in areolation from *Streptopogon*; they are referred to *Calyptopogon* by Brotherus (3).

(9) *S. mnioides*, var. *prostrata* (Mont.), Jaeger.—I have already (27) shown that this plant, the *Tortula prostrata* of Montagne, is a true *Tortula*, and that it is perfectly distinct specifically from Schwaegrichen's *Barbula mnioides*. It has no affinity whatever with the genus *Streptopogon*.

(10) *S. Hookeri*, R. Brown.—This agrees in areolation with *Barbula mnioides*, Schwaegr., and must be excluded from *Streptopogon*. Brotherus (3) has placed it in *Calyptopogon*.

I hope to treat fully in another place of most of the plants mentioned above, and need therefore only remark here that they are all certainly to be excluded from the genus *Streptopogon*.

Removing these ten plants from the genus, we are left with seventeen 'species' to deal with. A critical examination of these, however, reveals the fact that a very great multiplication of species has taken place. This has been due to imperfect or faulty descriptions of the plants; to the neglect by authors of the work of other systematists; and to the publication of a number of species without descriptions. In the following treatment of the genus these seventeen names will be found distributed among only five species and one variety. The reduction has taken place as follows:—

(1) *S. latifolius*, Mitt., and *S. setiferus*, Mitt., are indistinguishable from *S. Lindigii*, Hampe. (2) *S. Hildebrandtii*, C. Müll., and *S. Parkeri*, Mitt. mss., are indistinguishable from *S. Rutenbergii*, C. Müll., and this seems worthy of only varietal rank under *S. erythrodonthus* (Tayl.), Wils. (3) *S. rigidus*, Mitt., *S. Schenckii*, C. Müll., *S. Calymperes*, C. Müll., *S. Calymperopsis*, C. Müll., and *S. Calymperoides*, C. Müll., are specifically indistinguishable from *Calymperes Lindigii*, Hampe (*S. Hampeanus*, Besch.). (4) *S. bolivianus*, C. Müll., is identical with *S. erythrodonthus* (Tayl.), Wils.

A new variety, *S. erythrodontus* var. *intermedius*, founded on part of Spruce's 'Musci Amazon. et And. nr. 141 b,' is to be added to the genus, which thus consists of five species, with two varieties, viz.

*S. erythrodontus* (Tayl.), Wils., with its vars. *Rutenbergii* (C. Müll.) and *intermedius* var. nov., *S. rigidus*, Mitt., *S. Lindigii*, Hampe, *S. clavipes*, Spruce, and *S. cavifolius*, Mitt. The distribution of these species is as follows:—

(1) *S. erythrodontus*, South America; Colombia, Ecuador, Peru, and Bolivia; var. *intermedius*, Ecuador; var. *Rutenbergii*, Madagascar.

(2) *S. rigidus*, South America; Ecuador, Colombia, Brazil, Bolivia; Central America, Costa Rica; Madagascar.

(3) *S. Lindigii*, Hampe, South America; Colombia.

(4) *S. clavipes*, South America; Ecuador.

(5) *S. cavifolius*, South America; Ecuador, Colombia; North America, Mexico.

We see therefore that the Andes of Ecuador and Colombia are to be considered as the head quarters of the genus, whence the species spread north to Mexico and south to Brazil (Rio de Janeiro); the remarkable fact of the occurrence of two species in Madagascar is referred to more fully below (p. 129).

As regards the systematic position of *Streptopogon*, it is clear that the genus must be placed close to *Tortula* (*Syntrichia*). Mitten (14) places the genus in the tribe *Tortuleae*, where it is arranged in the key next to *Encalypta*. Müller (18) places it in his group *Pottiaceae*, which includes *Barbula*, *Trichostomum*, &c. Brotherus (3) also refers the genus to *Pottiaceae*, placing it (with *Tortula*) in the sub-family *Pottiaeae*, of which the following characters are given: 'Bl. meist breit, ei- bis spatelförmig; Rippe mit 2 medianen Deutern, mit Begleitern und nur 1 Stereidenband; Zellen oben meist locker, unten verlängert bis wasserhell; Haube meist kappenförmig.' It may be noted here, however, that in all the species of *Streptopogon* the leaf-nerve shows a complete absence of 'companion-cells'<sup>1</sup>, and that a mitraeform calyptra

<sup>1</sup> I have used the word 'pointer-cells' as a translation of the German word 'Deuter,' for the wide-lumened cells with little-thickened walls of the leaf-nerve;



is characteristic of the genus. A 'central-strand' is not differentiated in the tissues of the stem.

Although *Streptopogon* shows so close an affinity with *Tortula* (*Syntrichia*) in the structure of the peristome that there can be no doubt that the two genera belong to the same family, it is certainly distinct generically in the lax areolation of the leaves, in the cells of which the primordial utricle is conspicuous, and in the mitraeform calyptra. Müller observes (18) with reference to the species of *Streptopogon*: 'Die Aehnlichkeit aller dieser Arten mit *Syntrichia* ist zwar eine sehr grosse der Tracht nach, . . . doch ist das Blattnetz beider Typen so abweichend, dass man einen *Streptopogon* selbst steril zu unterscheiden im Stande ist. Auch will mir scheinen, als ob es bei *Streptopogon* am Grunde des Blattes keine Zellen gäbe, die wie bei *Syntrichia* porös-durchbrochene Wände besitzen.' It may be pointed out that the difference here alleged does not exist, since we find that in the lower cells of *S. erythrodontus* the walls become in age strongly porose (see Fig. 7); the same appearance, though less marked, is also found in the leaf-cells of *S. rigidus*, *S. Lindigii*, and *S. cavifolius*.

It must be noted also that two of the generic characters given by Wilson (see above), viz. 'calyptra mitriformis, superne scabra' and 'cellulae operculi contortae,' require emendation, since in one species, *S. cavifolius*, the calyptra proves to be glabrous, and in three species, *S. Lindigii*, *S. cavifolius* and *S. clavipes*, the cells of the operculum are not spirally contorted but arranged in straight rows.

Before giving a systematic account of the species of the present genus, I wish to express my obligations to the authorities at the Berlin Museum for sending me on loan the types, or portions of the types, of several mosses in Müller's herbarium; to Mr. William Mitten, A.L.S., for very kindly

and also 'companion-cells' for the German word 'Begleiter' (cf. Lorentz, Stud. zur vergleich. Anat. der Laubmoose (Flora, xxv, 247, 257: 1867); also Idem, Grundl. zu einer vergleich. Anat. der Laubmoose (Pringsheim's Jahrb. für wissenschaftl. Bot. vi, 374, 378: 1867-8)).



allowing me to examine the whole of the material belonging to *Streptopogon* contained in his herbarium; and to Mr. A. Gepp, F.L.S., for assistance rendered when examining the specimens in the Herbarium of the British Museum (Natural History).

**Streptopogon**, Wils. ex Mitt. in Hooker's Journ. of Bot. iii, 51 (1851).

Musci caespitiosi vel pulvinatim caespitiosi, saepe habitu orthotrichaceo, e olivaceo-viridi vel olivaceo-lutescente rufescentes. Caulis erectus vel adscendens, dense vel laxius foliosus, inferne radiculosus, dichotome vel fastigiatis ramosus, raro simplex. Folia humida mollia erecto-patentia vel patentia-patula sicca adpressa apice incurva vel spiraliter torquescentia, concava vel carinato-concava, ovato-oblonga vel oblongo-spathulata vel elongato-lanceolata, apice acuminata vel raro obtusiuscula cucullatae, elimbata vel limbata, limbo flavido e cellulis unistratis elongatis parietibus incrassatis composito, nervo plus minus valido aut in arista longa excedente aut in folii summo apice dilatato ibique globulum gemmarum gerente, rarissime in folii apice cucullato desinente, margine integro vel superne denticulato vel spinoso-denticulato inferne recurvo vel revoluto, cellulis superioribus plus minusve laxis hexagonis et hexagono-rectangularibus interdum marginem versus minoribus et subquadratis, utriculo primordiali contracto repletis, inferioribus longioribus subrectangularibus, omnibus (cellulis gemmiferis exceptis) laevissimis pellucidis. Folia perichaetia caulinis conformibus. Capsula immersa vel emergens vel exserta in pedunculo erecto brevi, erecta, maiuscula, oblonga vel oblongo-cylindrica, vel subcylindrica, laevis, exannulata, vel raro annulata, basi stomatibus superficialibus instructa. Peristomium rubrum, basi tubo brevi vel longo saepe pallido interdum rectangulari-tessellato instructus, exinde in crura filiformia circa axem idealem sinistrorsum plus minusve contorta divisum, cruribus aut 32 aequidistantibus aut 16 in parte inferiore tertia in fila duo seiunctis. Columella exserta, parte excedente fugace. Operculum conico-subulatum, cellulis spiraliter contortis vel rectis. Calyptra mitraeformis raro subcucullato-mitraeformis setulosa vel scabra vel raro perfecte glabra. Sporae parvulae laeves. Autoici vel dioici. Habitatio ad arborum fruticumque corticem.

**Streptopogonis Specierum Conspectus.**

Sect. I. *Eustreptopogon*, C. Müll. Gen. Musc. Frond. 423 (1900).—Folia flaccida siccitate contracta plus minusve torquescentia, superne denticulata nervo excedente longe aristata, haud gemmifera.

Folia limbata limbo distincto flavo e cellulis angustis parietibus incrassatis composito, peristomium basi breviter tubulosum exinde in crura 32 divisum.

Dioicus, capsula immersa vel emergens, peristomii tubus haud rectangulari-tessellatus, exothecii cellulae collenchymaticae, operculi cellulae haud spiraliter contortae, calyptra usque ad basin setulosa . . . **S. clavipes**, Spruce. Autoicus, capsula in pedunculo 3-4 mill. longo exserta, peristomii tubus rectangulari-tessellatus, exothecii cellulae haud collenchymaticae, operculi cellulae spiraliter contortae, calyptra basi nuda. . . **S. erythrodontus** (Tayl.), Wils.

Folia elimbata, peristomium fere ad medium tubulosum exinde in crura 16 divisum, cruribus omnibus in parte inferiore tertia in fila duo seiunctis.

Dioicus, capsula emergens, operculi cellulae haud spiraliter contortae, calyptra superne aspera haud setulosa. . . **S. Lindigii**, Hampe.

Sect. II. *Calymperella*, C. Müll. in Hedwigia, xxxiii, 128 (1894) et Gen. Musc. Frond. 422 (1900) (emend.).—Folia rigidiora haud contracta margine integro aut nervo in summo apice dilatato ibique gemmarum globulum gerente aut nervo in apice cucullato desinente et tunc gemmas e cellulis superioribus papilliferis orientes gerentia.

Folia apice perfecte cucullata, **S. cavifolius**, Mitt.

Folia haud cucullata, apice plus minus acuminata. . . **S. rigidus**, Mitt.

**S. erythrodontus** (Tayl.), Wils. (Pl. VIII, Figs. 1-27.)

*Barbula erythrodonta*, Tayl. in Hooker's Lond. Journ. of Bot. v, 50 (1846); Wilson, l. c. 450, tab. xv F (1846); C. Müll. Syn. i, 606 (1849), and ii, 630 (1851).

*Streptopogon erythrodontus* (Tayl.), Wils. ex Mitt., in Hook. Journ. of Bot. iii, 51 (1851); Hampe in Ann. sci. nat., 5<sup>e</sup> sér., iii, 350 (1865); Mitt. Musc. austr.-amer. 178 (1869); Jaeger, Adumbr. i, 254 (1873); Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 276 (1897); C. Müll., Gen. Musc. Frond., 421, 423 (sect. *Eustreptopogon*) ('1901,' i.e.

1900); Broth. in Engler and Prantl's *Natürl. Pflanzenfam.*, 214. Lief., p. 418, Fig. 272, D, E (sect. *Eustreptopogon*) (1902).

*S. bolivianus*, C. Müll. in *Nuov. Giorn. Bot. Ital.*, n.s., iv, 49 (1897); Paris, *Index bryolog. in Actes Soc. Linn. Bordeaux*, li, 275 (1897); Broth. in Engler and Prantl's *Natürl. Pflanzenfam.*, 214. Lief., p. 418 (sect. *Eustreptopogon*) (1902).

Autoicus, fasciculato-caespitans vel laxe pulvinatus, olivaceo-lutescens vel olivaceo-rufescens, caule erecto ad 3.5 cent. alto innovando dichotome et fastigiatim ramoso ad basin folioso inferne radiculoso, foliis caulinis flaccidis confertis siccitate spiraliter torquescentibus limbatis e basi ovali suberecta amplexante ad angulos haud vel vix decurrente in laminam elongato-lanceolatam acuminatam flexuosam interdum semitorquatam patentem nervo excurrente plus minus longe aristatam productis, margine utroque ad folii medium vel paullulo ultra recurvo superne erecto denticulato vel raro spinoso-denticulato, cellulis superioribus laxis irregulariter polygono-rectangularibus et subhexagonis circ.  $35-75 \times 20-25 \mu$  pellucidis utriculo primordiali contracto repletis parietibus aetate saepe subporosis, inferioribus elongatis angustioribus subrectangularibus latitudine 4-7-plo longioribus parietibus aetate interdum distincte porosis, cellulis marginalibus 1-5-seriatis elongatis angustis parietibus incrassatis limbum flavum unistratosum ad laminae summum apicem productum vel paullulo infra desinentem efformantibus, nervo mediocri luteo-rufescente in aristam longissimam laevem plus minus flexuosam concolorem vel apice subhyalinam producto, foliis perichaetialibus caulinis conformibus, capsula in pedunculo erecto 3-4 mill. longo tenui stramineo siccitate valde dextrorsum tortili oblonga vel oblongo-cylindrica aequali erecta 2-3 mill. longa 0.75-1 mill. lata interdum subcylindrica longiore angustiore subinaequali primum olivaceo-viridi deinde flavo-fusca vacua straminea exannulata ore rubro crenulato exothecii cellulis polygono-rectangularibus parietibus haud incrassatis ad capsulae os subito minoribus polygono-quadratis parietibus cellularum marginalium longitudinalibus valde incrassatis, basi ima stomatibus superficialibus sparsis instructa, peristomio rubro circ. 1.5 mill. longo basi tubuloso tubo brevi spiraliter rectangulari-tessellato interdum pallidiore exinde cruribus 32 filiformibus liberis sinistrorsum contortis dense et minute papillois, columella exserta, operculo subulato-rostrato circ. 1.25 mill. longo apice obtuse apiculato cellulis spiraliter contortis basi margine rubro crenulato, calyptra ad capsulae os vel paullulum infra



descendente conico-mitraeformi vel subcucullato-mitraeformi superne fusca setuloso-hispida basi glabra, sporis globosis laevibus 15–25  $\mu$  diam. ; flore masculo ad pedem feminei oriundo parvulo inconspicuo, foliis perigonalibus 1–2 oblongis vel obovato-oblongis margine apicem versus leniter denticulato vel subintegro, limbo nullo, nervo in aristam laevem excurrente interdum in folio medio obsoleto, cellulis laxis.

*Hab.*—*America australis* : *Ecuador* ; Pichincha, Andes of Quito, c. fr. (W. Jameson, 1846, 1847, 1848) ! ; valde frequens in montibus Pichincha, Llalla, et Chimborazo, 6,000–10,000 ped. c. fr. (R. Spruce, Musc. Amazon. et And. nrs. 141, 141 b, 141 c) ! ; Guayrapate, c. fr. (in Herb. Mitt.) ! Tunguragua, inter *S. rigidum*, Mitt., c. fr. (in Herb. Mitt.) !

*Colombia* ; Paramo Choachi, ad ramos, alt. 3,000 mtr. Aug. 1859 (A. Lindig, nr. 2,022) c. fr. ! ; Rio Arzobispo, alt. 3,700 mtr., Nov. 1859 (A. Lindig) c. fr. ! ; Bogota, Pacho, 2,200 mtr., in sylvis, c. fr. (A. Lindig, 1863) ! ; Andes Bogotenses, ad viam inter Tipaquira et Pacho, ad arborum humiliorum ramos (8,000 ped.) (Weir, nrs. 169, 188), c. fr. !

*Peru* ; Carabaya (Weddell, July 1847, nr. 17), c. fr. !

*Bolivia* ; Prov. Cochabamba, prope Choquecamata (Germain, Junio 1889), c. fr. ! ; Yungas (Pierre Jay, July 1893), c. fr. !—  
sub *S. boliviano*, C. Müll.

var. **intermedius** var. nov.

Foliis distantioribus brevioribus latioribus patulis vel patentibus limbo folii apicem versus obsoleto vel nullo.

*Hab.*—*America australis* : *Ecuador* ; Andes Quitenses, c. fr. (Spruce, Musc. Amazon. et And. nr. 141 b (pro parte)) !

var. **Rutenbergii** (C. Müll.).

*S. Rutenbergii*, C. Müll. in Abhandl. d. naturwiss. Vereins, Bremen, vii, 207, Taf. xiii, B (1882) ; Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 276 (1897) ; C. Müll., Gen. Musc. Frond., 422 ('1901,' i. e. 1900) ; Broth. in Engler and Prantl's Natürl. Pflanzenfam., 214. Lief., p. 418, Fig. 271 (sect. *Eustreptopogon*) (1902).

*S. Hildebrandtii*, C. Müll. in Hildebrandt's 'Flora von Central-Madagascar,' nr. 2,098 (nomen) ; Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 276 (1897) ; C. Müll., Gen. Musc. Frond., 422 ('1901,' i. e. 1900) ; Broth. in Engler and Prantl's Natürl. Pflanzenfam., 214. Lief., p. 418 (sect. *Eustreptopogon*) (1902).



*S. Parkeri*, Mitt. mss. ex Wright, in Journ. of Bot. xxvi, 264 (1888) (nomen); Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 276 (1897).

Foliis plerumque distantioribus et patulis vel patentibus, interdum confertioribus et erecto-patentibus, limbo angusto ad folii summum apicem producto vel longe infra apicem desinente, *cellulis laxioribus*.

*Hab.*—Africa: Madagascar; in sylva Ambatondrazaka (Rutenberg, Dec. 6, 1877), c. fr. (operculum calyptraque desunt)!—sub *S. Rutenbergii*, C. Müll.; Imerina, Andrangobaka (J. M. Hildebrandt, Nov. 1880), nr. 2,098, c. fr.!—sub *S. Hildebrandtii*, C. Müll.; Central Madagascar (G. W. Parker), c. fr.!—sub *S. Parkeri*, Mitt.

*S. erythrodontus* was discovered by Professor W. Jameson 'on Pichincha, near Quito,' and there are fine fruiting specimens in the Kew Herbarium labelled 'west side of Pichincha, 1846,' 'Andes of Quito, 1847,' and 'Pichincha, 1848,' all collected by Jameson. It was from specimens of Jameson's collecting, preserved in Greville's herbarium, that Taylor (31) in 1846 described the present species under the name of *Barbula erythrodonta*, and on which Wilson (33) in 1851 founded the genus *Streptopogon*. Later the species was collected by Spruce on Pichincha and other mountains of the Andes of Quito, where it is reported to occur abundantly; examples from here were distributed by Spruce in 'Musc. Amazon. et And., nrs. 141, 141 b, 141 c.' Lindig in 1859 and 1863, and also Weir, gathered it in Colombia (New Granada), in the Andes near Bogota, &c. These stations in the Andes of Ecuador and Colombia have been up to the present the only ones known for *S. erythrodontus*. In 1897 Müller (23) published as a new species of *Streptopogon* a moss from Bolivia under the name of *S. bolivianus*, with the following description:

'Caulis pollicaris superne in ramos perbreves fertiles fasciculatim divisus fusco-luteus horride foliosus; folia caulina siccitate et humore, huc magis, patula longiuscula setacea, e basi elongata complicato-ovata in laminam elongatam acuminatam attenuata, nervo angusto ferrugineo in aristam longissimam flexuosam ferrugineam summitate saepius hyalinam protracto carinato-exarata, limbo latiusculo flavido ubique circumducta integerrima, e cellulis basi longioribus angustioribus

superne maiusculæ hexagonis fuscatis laxiusculis eleganter reticulata; perichaetia maiora superne remote denticulata; theca in pedicello perbrevis exserta cylindrica angusta late annulata, operculo breviter conico obtuso spiraliter reticulato, calyptra conica scabra, peristomio brevi purpureo.—Ex habitu *Streptopogoni erythrodonti* Columbico simillimus et proximus, sed hæc species iam differt: foliis caulinis serratis. An varietas eiusdem?’

Through the courtesy of the authorities at the Berlin Museum I have been able to see the type specimen of this moss from Müller's herbarium. This is labelled ‘Prov. Cochabamba, prope Choquecamata (Germain, Junio 1899).’ An examination of the moss showed that undoubtedly the stem-leaves have been wrongly described. The margin in the upper part of the leaf is not entire, but distinctly denticulate as in typical *S. erythrodontus*. Sometimes, through erosion, the teeth tend to become obsolete, but all the younger leaves, and most of the old ones, show the characteristic denticulate limb of *S. erythrodontus*. In all other characters, too, as might be expected from Müller's diagnosis, the Bolivian plant agrees perfectly with *S. erythrodontus*, so that the name *S. bolivianus* may be safely referred as a synonym to the present species.

Through the kindness of Mrs. Britton I have received a specimen (now in the Kew Herbarium) of a moss labelled ‘*S. bolivianus*, C. Müll. Yungas (coll. Pierre Jay, July 1893).’ This also shows all the characters of *S. erythrodontus*, the stem-leaves being distinctly denticulate. The specimens have, however, rather an abnormal appearance; the leaves are very much twisted, and remain so in the wet state; in fact, the leaves show scarcely any signs of reviving after prolonged soaking in water. The leaves are also very caducous, separating from the stem and falling off entire on the plants being handled. All the specimens in fact have the look of plants which have grown under unfavourable conditions, and their appearance suggests the idea that they have been scorched by excessive heat.

From the two examples quoted above we can now extend

the range of *S. erythrodontus* in South America southwards to the mountains of Bolivia.

I have found, further, in Schimper's herbarium at Kew a specimen labelled '*Barbula mnioides*, Mtge. Peruvia, Carabaya, Weddell, July 1847, No. 17.' The moss, which is in fruit, is *S. erythrodontus*. This Peruvian record is interesting as tending to connect the Bolivian station with the headquarters of the species in the Andes of Quito.

It may be noted here that there is no true annulus in the present species. The exothecial cells are polygonal-rectangular, with scarcely thickened walls; at the mouth of the capsule, however, a few rows of cells become suddenly shorter and more or less quadrate in shape, with the cell-walls much thickened, so that a kind of 'false annulus' is formed (see Fig. 11). It is probably to this that Müller refers in his description of the capsule of *S. bolivianus* as 'late annulata.'

In 1882 Müller (19) described a *Streptopogon* from Madagascar as follows:

'*S. Rutenbergii*, C. Müll. n. sp. Monoicus; caulis dichotomus, mm. 10-12 altus; folia laxa, siccitate subpatentia, torquescentia, e basi angustiore elongate oblongo-lanceolata nervo excurrente piliformi-cuspidata, margine flavo-limbata, apice spinoso-dentata, laxe reticulata; theca erecta oblongo-cylindrica mm. 3 longa, in pedunculo aequilongo, peristomii dentibus rubris valde contortis papillois linea media notatis; operculum calyptraque desunt.—Wald von Ambatondrazaka, 6. Dec. 1877, in wenigen Individuen.—Species distinctissima, *Streptopog. erythrodonto*, Tayl. austro-americano valde affinis.'

About the same time Müller gave the ms. name '*Streptopogon Hildebrandtii* sp. nov.' to a moss sent out under the number 2098 in Hildebrandt's 'Flora von Central-Madagascar,' from Imerina, Andrangolòaka (Nov. 1880). This moss has been mentioned by name by several authors, but no description of it has appeared.

I have seen two specimens of *S. Rutenbergii*, one sent to me by Dr. Geheeb, the other from Müller's herbarium. On comparing these with the examples of *S. Hildebrandtii* from



Dr. Geheeb's and Müller's herbaria, and with the examples at Kew and the British Museum, I have found that the two are certainly identical.

At first sight the Madagascan plant appears to be specifically distinct from *S. erythrodontus* in the following characters: the leaves are more distant and are patent or patulous when moist, not erecto-patent; they are wider, and as regards the upper leaves shorter; the excurrent nerve is frequently shorter and the limb also frequently ceases at some distance below the apex of the leaf; finally, the areolation of the leaf is distinctly laxer. I can find no difference in the fruiting characters—the calyptra, operculum, capsule, and peristome of the Madagascan plant agreeing exactly with those of South American examples of *S. erythrodontus*. The male inflorescence is also the same in both plants. The vegetative characters noted above, however, viz. the more distant, broader, patent or patulous leaves with the limb very narrow or absent above, and the larger leaf-cells are quite constant, and might be considered of sufficient importance to give specific rank to *S. Rutenbergii* if there were no other forms showing intermediate characters to be considered. There exist, however, two other plants which give important evidence on the question of the affinity of the Madagascan plant. These are the South American plant which I have described above as *S. erythrodontus* var. *intermedius*, and a plant from Central Madagascar which has borne for some time the ms. name of *S. Parkeri*, Mitt.

The var. *intermedius* occurs in the Kew Herbarium mixed with typical *S. erythrodontus* in Spruce's 'Musc. Amazon. et And., nr. 141 b.' This plant differs from the type in possessing exactly the habit of the Madagascan plant, i. e. the leaves are more distant and wider; the upper and perichaetial ones are not long and narrow; and all the leaves are patent or patulous when moist; the leaf-cells, however, are distinctly smaller than those found in *S. Rutenbergii*, although occasionally a close approach is made. The limb of the leaf in the var. *intermedius* is frequently lost some way below the apex, and



the marginal teeth are small and formed just as in the Madagascan plant (see Fig. 6).

In '*S. Parkeri*, Mitt. mss.' the leaves have the cells of exactly the same size as in *S. Rutenbergii*, i. e. they are distinctly larger than in typical *S. erythrodontus*; the leaves, however, differ from those of the usual form of *S. Rutenbergii* in being narrower, and are erecto-patent and more or less crowded, not laxly arranged and patent or patulous. The limb of the leaf also is continued right up to the extreme apex. The inflorescence of '*S. Parkeri*' is autoicous, the male flower, as in *S. erythrodontus*, being borne on the stem, in the axil of a leaf, either immediately below the perichaetium, or a little way below it. In all characters, therefore, except in the laxer areolation, '*S. Parkeri*' agrees with *S. erythrodontus*.

The characters shown by these two plants—*S. erythrodontus* var. *intermedius* and *S. Rutenbergii*—seem to me to afford evidence that the Madagascan plant is too closely allied to *S. erythrodontus* to be allowed specific rank. I have seen specimens of '*S. Hildebrandtii*' in which a leaf here and there showed an areolation scarcely if at all laxer than that of *S. erythrodontus* var. *intermedius*, and it is quite possible that further search in other districts of the Andes will bring to light South American forms of *erythrodontus* identical with the Madagascan plant. As a rule, however, the cells of the Madagascan plant are distinctly larger than those of the South American *S. erythrodontus* var. *intermedius*, and for this reason I have kept the two plants distinct. The cells of the Madagascan plant have the walls thicker than is usually the case in *S. erythrodontus* type, so that the areolation is firmer. This character, however, is not absolutely distinctive. I have seen specimens of *S. Rutenbergii* in which the leaf-cells have the thin delicate walls characteristic of *S. erythrodontus* type; on the other hand I have found in several specimens of *S. erythrodontus* leaves, from the lower part of the stem, showing cells with the firmer and thicker walls of the Madagascan plant. This is the case, for instance, with the specimens collected by Weir, nr. 169, in Colombia (in the

Kew Herbarium), in which the lower leaves are broader and less finely acuminate than usual, and show the rather firm areolation with thickened cell-walls of the Madagascan plant.

As regards the limb of the leaf it may be noted that although this is sometimes continued to the extreme apex of the leaf in the Madagascan plant, it is in such cases always narrow, and I have not seen in the Madagascan plant the broad limb at the apex of the leaf that is found in some examples of *S. erythrodontus* from South America. This character is, however, clearly one of little importance systematically, since on the same stem of some plants of *S. erythrodontus* leaves may be found in which the limb vanishes below the apex, whilst other leaves are bordered to the apex. On one stem of '*S. Hildebrandtii*' from Müller's herbarium two upper leaves occurred in which, presumably from exposure to unusual conditions, the cells at the apex of the leaf became suddenly, for several rows, on one side of the nerve only, prosenchymatous and thick-walled, so that the apex of the leaf in that region was composed wholly of prosenchymatous cells like those of the 'limb.' This was all the more remarkable since in this form of the Madagascan plant the limb as a rule ceases at some distance below the leaf-apex. The suggestion may perhaps be made that a correlation exists between certain conditions of growth and the shape of the leaf-cells; if so, we might find an explanation in climatic or other ecological conditions of the fact that in some plants of *S. erythrodontus* the limb is composed of prosenchymatous cells continued to the apex of the leaf, whilst in others the limb ceases, and all the cells become parenchymatous.

It is perhaps worthy of note that *S. erythrodontus* type is slightly variable in the size of the leaf-cells; and although the areolation is never, so far as I have seen, quite so lax as in the Madagascan plant, on the other hand South American examples occur in which the cells are much narrower than usual.

The occurrence of the South American *S. erythrodontus* in Madagascar under the form of the variety *Rutenbergii* affords an extremely interesting case of geographical distribu-

tion. In another species of the genus, *S. rigidus*, Mitt., the same distribution is found, and in this case the Madagascan plant, although described as a distinct species by Müller, appears to be identical with the South American plant (see p. 129).

The shape of the capsule of *S. erythrodontus* is subject to considerable variation. It is most commonly, before the fall of the operculum, cylindrical-oblong in shape, measuring 2-3 mill. long and  $\cdot 75$ -1 mill. wide. After the fall of the operculum the capsule becomes shorter and wider, and broadly oblong in shape, the usual dimensions being about  $2\frac{1}{2}$  mill.  $\times$   $\frac{7}{8}$  mill., or sometimes it is larger, measuring  $3-3\frac{1}{2} \times 1$  mill. In some of Jameson's specimens in the Kew Herbarium from 'west side of Pichincha, 1846' the deoperculate capsules are cylindrical or subcylindrical, and measure about  $3 \times \frac{3}{4}$  mill. On the other hand some of the capsules on specimens collected by Lindig in Colombia (Bogota, Pacho, alt. 2,200, Sept. 1863), are only  $1\frac{3}{4}$  mill. long and  $\frac{1}{3}$  mill. wide. When deoperculate and emptied of spores, the capsules become gradually paler, until finally they are often pale straw-coloured. The above remarks on the shape of the capsule apply not only to examples of the species from South America, but also to those from Madagascar to which the names '*S. Hildebrandtii*,' '*S. Rutenbergii*,' and '*S. Parkeri*,' have been given. The shape of the capsule in the Madagascan plant inclines frequently to the subcylindric, and the capsule measures usually about  $3 \times \frac{3}{4}-\frac{7}{8}$  mill. In some specimens, however, e.g. those of '*S. Rutenbergii*' in Müller's herbarium, the deoperculate capsules are of a broadly oblong shape, and measure about  $2\frac{1}{2} \times 1$  mill. In the Kew Herbarium, in the specimens of *S. erythrodontus* in Spruce's 'Musc. Amazon. et And., nr. 141 c,' there occurs an old capsule of a remarkable shape. This capsule is long and narrowly cylindrical, slightly curved and slightly asymmetric towards the base (Fig. 1 a), and measures  $4 \times \frac{1}{2}$  mill. The same tuft bears capsules of quite normal shape and size, these being oblong and measuring  $2\frac{1}{2} \times \frac{7}{8}$  mill. (Fig. 1 a). This appears to be the extreme



limit of the cylindrical form of capsule, and is approached by other Andian specimens, in which the cylindrical capsule becomes frequently slightly inaequilateral towards the base. It is most interesting to find that the same peculiarity occurs among the Madagascan plants, where it is well seen in some of the specimens of '*S. Hildebrandtii*' (Flora von Central Madagascar, nr. 2,098), which bear long cylindrical inaequilateral and slightly curved capsules.

Sullivant (30) has recorded '*S. erythrodontus*' from the Sandwich Islands, 'East Maui, north bank of the crater Haleakala.' Müller in his 'Bryologia Hawaiica' (22) has remarked with reference to this record, 'Muscus suspectissimus a nobis nunquam visus, probabiliter generi *Streptopogon* alienus.' I have unfortunately not been able to examine the specimen in question, now in the Herbarium of Harvard University.

It must be noted that the size of the areolae of the 'tessellated' tubular base of the peristome is variable. The areolae are sometimes comparatively large and sharply defined, as e.g. in the specimens from the Andes of Quito (Spruce, Musc. Amazon. et And., nr. 141, in Herb. Kew) (see Fig. 10), also in the specimens of '*S. bolivianus*' in Müller's herbarium. In other examples the areolae are distinctly smaller and much less distinct. It may be mentioned that in taking off the operculum from the capsule the exerted part of the columella frequently comes away with it.

The stem as seen in transverse section is composed of one or two peripheral rows of thick-walled brownish cells; the walls of the external cells project somewhat, and give a crenulate outline to the stem-section. The rest of the tissue is formed of large polygonal cells with very thin flexuose walls, which are very slightly thickened at the angles; there is no 'central-strand' (see Fig. 20). The leaf-nerve is composed of 'pointer-cells' (see footnote, p. 111) and a single dorsal stereid-band; 'companion-cells' are absent. The nerve is frequently not median in the upper part of the leaf (see Fig. 24). The cells of the lamina near the nerve some-

times project on the ventral (upper) surface in a mammillate manner; in two instances a bistratose row of cells was observed near the nerve (Fig. 25).

The calyptra is conical in general shape, and is usually truly mitraeform (Fig. 13). Sometimes, however, it is deeply split on one side, and so becomes subcucullate (Fig. 14). The latter shape was perhaps observed by Müller, and caused the remark in the 'Synopsis' (18, p. 630), where, after giving Wilson's character 'calyptra mitraeformis' for the genus, Müller says, 'Calyptra revera campanulata latere nunquam fissa?' The 'setulae' on the upper part of the calyptra are formed usually of one cell; rarely, however, two cells are found (Figs. 15, 16). It may be pointed out that in the present species the setulae are not found at the base of the calyptra, whilst in the closely allied *S. clavipes*, Spruce, they are specially numerous and well developed at the base of the calyptra.

As has been remarked above (p. 112) the walls of the lower cells of the leaf become strongly porous in age (Fig. 7).

**S. rigidus**, Mitt. (Figs. 38-40, 74-96).

*Calymperes Lindigii*, Hampe, in Ann. Sci. Nat., 5<sup>o</sup> sér., iii, 342 (1865); Mitten, Musc. austr.-amer. 127 (1869); Jaeger, Adumbr. i, 327 (1873); Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 276 (1897).

*Streptopogon rigidus*, Mitt., in Spruce, Cat. Musc. Amazon. et And., 3, nr. 139 (1867) (nomen); Spruce, Musc. Amazon. et And., nr. 139.

*S. Calymperes*, C. Müll., in Abhandl. d. naturwiss. Ver., Bremen, vii, 207, Taf. xiii, A (1882); Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 275 (1897) (*sphalm. calymperifolius*); Müll., Gen. Musc. Frond., 422 (sect. *Calymperella*) ('1901,' i.e. 1900); Broth. in Engler and Prantl's Natürl. Pflanzenfam., 214, Lief., p. 419 (sect. *Calymperella*) (1902) (nomen).

*S. calymperoides*, C. Müll. in Abhandl. d. naturwiss. Ver., Bremen, vii, 207 (1882) (nomen); C. Müll., Gen. Musc. Frond., 421, 422 (sect. *Calymperella*) ('1901,' i.e. 1900) (nomen); Broth. in Engler and Prantl's Natürl. Pflanzenfam., 214, Lief., p. 419 (sect. *Calymperella*) (1902) (nomen).

*S. (Calymperella) Schenckii*, C. Müll. ex Broth. in Hedwigia, xxxiii,

128 (1894); Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 276 (1897); C. Müll., Gen. Musc. Frond., 423 (sect. *Calymperella*) ('1901,' i. e. 1900); Broth. in Engler and Prantl's Natürl., Pflanzenfam., 214. Lief., p. 419, Fig. 272 A-C (sect. *Calymperella*) (1902).

*S. Hampeanus*, Besch. in Ann. Sci. Nat., 8<sup>e</sup> sér., i, 290 (1895); Broth. in Engler and Prantl's Natürl. Pflanzenfam., 214. Lief., p. 419 (sect. *Calymperella*) (1902).

*S. Calymperopsis*, C. Müll., Gen. Musc. Frond., 421, 422 (sect. *Calymperella*) ('1901,' i. e. 1900) (nomen).

Caespitosus, rigidus, humilis vel procerior, caespitibus satis densis e viridi vel flavo-viridi ferrugineis interdum nitidiusculis, caule ad 3 cent. alto adscendente plus minus flexuoso e basi usque dense folioso inferne fusco-radiculoso simplice vel fastigiato-ramoso, foliis erecto-patentibus (iunioribus patentibus) siccitate adpressis imbricatis vel laxe incumbentibus apice incurvis mollibus 3-3.5 raro 4 mill. longis 1.25-1.75 mill. latis carinato-concavis inferioribus spathulatis vel oblongo-obovatis subito breviter cuspidato-acuminatis superioribus oblongis vel spathulato-oblongis rare oblongo-lanceolatis longioribus (ad 5 mill.) longius et magis gradatim acuminatis siccitate magis flexuoso-incurvis haud adpressis marginibus superne undulatis folii apicem versus plus minus inflexis, foliis omnibus margine utroque fere e basi ad folii medium revoluta superne erecto integerrimo vel ob parietes cellularum marginalium transversos prominentes subcrenulato, nervo rufescente in parte folii superiore valido dorso prominente in folii apice dilatato ibique globulum primum flavidum demum ferrugineum e filis numerosis subcylindricis ad 200  $\mu$  longis transverse et longitudinaliter septatis compositum gerente, foliis iunioribus interdum haud gemmiferis obovatis vel subspathulatis nervo infra summum apicem desinente, folii cellulis superioribus hexagonis et hexagono-rectangularibus 25-40  $\mu$  longis 18-25  $\mu$  latis nervum versus laxioribus subrectangularibus marginem versus gradatim minoribus subquadratis, marginalibus quadratis vel subquadratis interdum parietibus magis incrassatis et dilute flavidis, cellulis inferioribus oblongo-hexagonis vel subrectangularibus latitudine 3-4-plo longioribus marginem versus subquadratis, cellulis basilaribus proxime nervum inanibus caeteris utriculo primordiali collapso repletis omnibus pellucidis laevibus parietibus aetate saepe subporosis, capsula in pedunculo erecto fusco 5 mill. longo dextrorsum tortili subcylindrica 2.25 mill. longa 0.70 mill. lata fusca annulata . . . Caetera desunt.



*Hab.*—**America australis**:—*Colombia* (Nova Granata); Bogota, Pacho, 2,200 mtr., ad rad. arb., inter *Fabroniam polycarpam* (A. Lindig)!—(*Calymperes Lindigii*, Hampe); Boqueron, Bogota (J. Weir, Musci Novae-Granatenses, nr. 369)!—(*S. rigidus*, Mitt.). *Ecuador*; Quito, cum *Hypno scarioso*, Tayl. et *S. erythrodonto* (Tayl.), Wils. (Jameson, in Herb. Mitt.)!; Andes Quitenses (Spruce, Musc. Amazon et And., nr. 139)!; Tunguragua, cum *S. erythrodonto* (Spruce, in Herb. Mitt.)!—(*S. rigidus*, Mitt.). *Brasilia*; Rio de Janeiro, Serra do Picú. (S. Schenck, Dec. 1885, and Nov. 1886)!—(*S. Schenckii*, C. Müll.). *Bolivia*; Tipoami à Apaloberuba (Weddell, 1878)!—(*S. Calymperopsis*, C. Müll.).

**America centralis**: Costa Rica; Prov. Alajuela, on old trees in damp places in woods (Dr. H. Polakowsky, June 1875, c. fr. vetustis)!—(*S. calymperoides*, C. Müll.).

**Africa**: Madagascar; in sylva pr. Ambatondrazaka (Dr. Rutenberg, Dec. 6, 1877)!—(*S. Calymperes*, C. Müll.).

The present species was originally described by Hampe (5) under the name *Calymperes Lindigii*, from specimens collected by Lindig in Colombia. Hampe remarked of his plant 'Statura *C. Richardi* sed *C. disciformi* C. M. proximum differt: foliis immarginatis et cellulis laevibus.' Examination of the type in Hampe's herbarium at the British Museum shows, however, that the moss does not belong to the genus *Calymperes*, but to *Streptopogon*. Bescherelle has already pointed this out in his 'Essai sur le genre *Calymperes*' (2), where we find the statement '*C. Lindigii*, Hpe. in Musc. Nov. Gran., p. 6 . . . = *Streptopogon Hampeana*, Nob.' Bescherelle renamed the species as above in consequence of the specific name *Lindigii* being already in use in the genus *Streptopogon*. In the present species there is frequently a group of basal cells (adjoining the nerve) more or less sharply marked off by their slightly larger size and absence of contents (see Fig. 93) somewhat recalling the cell-structure of the base of the leaf in *Calymperes* and *Syrrhopodon*. It was doubtless this feature, together with the presence of gemmae, that led Hampe to place his species in the genus *Calymperes*.

Two years later than Hampe's publication of '*Calymperes*

*Lindigii*' a moss from the Andes of Quito was published (without a description) in Spruce's 'Catalogus Muscorum, &c.' (29) under the name *Streptopogon rigidus*, Mitt., and was distributed under the number 139 in Spruce's 'Musci Amazonici et Andini.' Curiously enough we find no mention of this plant in Mitten's 'Musci austro-americi' (1869), although there are examples of the moss so named in the set of Spruce's Exsiccati at Kew and at the British Museum (South Kensington). Comparison of these examples with '*Calymperes Lindigii*' shows that the two plants are identical, and we must adopt therefore the name *S. rigidus*, Mitt., for the present species.

In 1882 Müller (19) described and figured a plant from Madagascar as a new species of *Streptopogon*. The following description was given:—

'*S. Calymperes*, C. Müll. n. sp. Pusillum, flavo-virens; folia patentia lanceolata acuminata vel oblongo-lanceolata; integerrima, immarginata, parte inferiore leniter revoluta, costa flava valida infra apicem dilatata ibique filamentis confervoideis fasciculatim obsessa—Caetera desunt. Spärlich mit voriger Art [*S. Rutenbergii*, C. Müll.]. Ein merkwürdiges, an gewisse *Calymperes*-Arten erinnerndes Moos, das in *S. calymperoides*, C. Müll. von Costa-Rica seinen nächsten Verwandten besitzt.'

Müller comments further on the occurrence in Madagascar of '*S. Rutenbergii*' and '*S. Calymperes*' as follows:—

'Diese beiden *Streptopogon*-Arten sind das Schönste dieser ganzen Sammlung und zugleich die werthvollste geographische Bereicherung der neuesten Bryologie und lassen sonderbare Blicke in die Flora von Madagascar thun.—Wie im Andesgebirge, treten sie in einer *Bryum*-artigen grannenblättrigen und in einer *Calymperes*-Form auf. Diese Correspondenz zweier madagassischer Arten mit zwei tropisch-amerikanischen in gleicher doppelter Form ist so merkwürdig, wie ich selten etwas Aehnliches erlebt habe.—Es entspricht der wunderbaren Erscheinung, dass auch an der westafrikanischen Küste so Manches an die tropisch-amerikanische Flora erinnert.'

I have seen the type specimen of '*S. Calymperes*' from Müller's herbarium. This is labelled 'Madagascar, in sylva pr. Ambatondrazaka. Dr. Rutenberg leg. Dec. 6, 1877,' and

consists of two stems about a centimetre high. After closely comparing in every character these plants with specimens of *S. rigidus* from South America I have failed to find any points of difference. The upper leaves have the characteristic oblong or oblong-spathulate shape, and exactly the same areolation, with the marginal cells small and subquadrate. The gemmae (Fig. 39) also are of the same shape and size, and are borne at the apex of the leaf in exactly the same manner. Some of the lower leaves of '*S. Calymperes*' are not gemmiferous, and in these the nerve vanishes below the leaf-apex (Fig. 97), so that the leaf has a very different appearance. I at first thought that this might be a distinctive character of the Madagascan plant, but an investigation of young plants of *S. rigidus* from South America showed that this was not the case. The Madagascan material is very scanty, consisting (in the specimen sent to me) of only two apparently very young stems. On comparing young plants of '*S. Calymperopsis*'—which as noted below is to be referred to *S. rigidus*—from Bolivia (in Bescherelle's herbarium at the British Museum, South Kensington) exactly the same shaped leaves with a vanishing nerve were found. Further, in the specimen 'Musc. Amazon. et And., nr. 139' of *S. rigidus* in the British Museum Herbarium, the same shaped leaves occur on innovation branches, in one case with the nerve ceasing at some distance below the leaf-apex. There seems therefore no reason whatever for separating the Madagascan plant from the American *S. rigidus*. Although this distribution of the present species affords an extremely interesting and remarkable case, it is by no means unparalleled. We have seen above (p. 122) that the Madagascan plant variously known as '*Streptopogon Rutenbergii*, C. Müll.,' '*S. Hildebrandtii*, C. Müll.,' and '*S. Parkeri*, Mitt. mss.,' is so close to the South American *S. erythrodonatus* (Tayl.), Wils., that it cannot be separated specifically. It is worthy of note also that Mitten (13) in his account of the mosses of the Cameroons Mountain and the River Niger remarks, 'The species here enumerated appear to represent a Moss vegetation similar to that of



tropical America; in a few instances they are apparently identical, but for the most part they are rather cognate forms.' Baron, also, in his 'Flora of Madagascar' (Journ. Linn. Soc., xxv, 289: 1889) has pointed out the close affinity of certain plants in the phanerogamic Flora of Madagascar with those of tropical America. The same distribution is found in certain ferns (see Baker in Journ. Linn. Soc., xvi, 199: 1877), and there is a species of *Lycopodium*, *L. dichotomum*, Jacq., which is peculiar to Madagascar and tropical America.

Three other species of *Streptopogon*—*S. calymperoides*, C. Müll., from Costa Rica, *S. Schenckii*, C. Müll., from Brasil, and *S. Calymperopsis*, C. Müll., from Bolivia—have also been published. Of these '*S. Schenckii*' alone has been published with a description. In the diagnosis the characters given are those found in *S. rigidus*, and an examination of examples of '*S. Schenckii*' from Müller's herbarium and in the Kew Herbarium has convinced me that the plant is not distinct from *S. rigidus*. It is a somewhat luxuriant form of the species, with the upper leaves long and laxly incurved in the dry state, and bearing at their apex globose heads of gemmae. A still more luxuriant form, but obviously the same species, occurs in the Kew and British Museum herbaria, and in Mitten's herbarium, labelled '*S. rigidus*, Andes Bogotenses, J. Weir, Musci Novae-Granatenses, nr. 369,' and also in Mitten's herbarium from 'Tunguragua (Spruce).' In this the upper and terminal leaves are strongly flexuoso-incurved when dry, and about 5 mill. long. It may be noted that in the diagnosis of *S. Schenckii* the leaves are described as 'limbata, limbo indistincto, ab unica serie cellularum subquadratarum vel breviter rectangularium minorum formato.' It is certainly the fact that the cells towards the margin of the leaf of *S. rigidus* are different in shape from those elsewhere, but it seems to me that the change in shape takes place too gradually to allow us to speak of the leaf as being 'limbate.' The cells in the upper half of the leaf vary in shape from more or less regularly hexagonal to hexagono-rectangular or even

subrectangular. Their size is somewhat variable; in three leaves taken from the upper part of the same stem of an authentic specimen of '*S. Schenckii*' the cells measured (1)  $50 \times 25 \mu$ ; (2) 30 to (rarely)  $40 \times 20-25 \mu$ ; (3)  $30-50 \times 20-25 \mu$ . The cell-walls are usually minutely thickened at the angles; sometimes in old leaves they are distinctly porous throughout. As the margin is approached the cells become smaller and gradually assume a shortly rectangular shape. At the margin we find one or more rows of quadrate or shortly rectangular cells; the cell-walls of these rows are sometimes slightly thickened and yellowish in colour. Towards the nerve the cells become much laxer and are hexagono-rectangular in shape.

The specimen of '*S. Calymperopsis*' I have seen is from Müller's herbarium, and is labelled 'Bolivia; Tipoami à Apaloberuba (Weddel, 1878).' It consists of a few stems, the apical leaves of which bear globose heads of gemmae as shown at Fig. 89. A close comparison of the plant has convinced me that it is identical with '*S. Schenckii*' (*S. rigidus*).

With regard to '*S. calymperoides*' also I can find no characters separating it from *S. rigidus*. The specimen I have seen is from Müller's herbarium, and is labelled 'Costa Rica, Prov. de Alajuela (Dr. H. Polakowsky, June 1875).' It consists of four barren stems and one branched stem bearing a single old capsule. The upper leaves on the barren stems are rather long and flexuoso-incurved in the dry state, and in every respect agree with those of '*S. Schenckii*' (*S. rigidus*). I was not able to observe the shape of the perichaetial leaves, as these are almost completely destroyed by some parasitic growth; the other leaves of the fertile plant are gemmiferous, and of the characteristic shape for the present species. The erect subcylindric capsule measures  $2.25 \times 0.70$  mill., and is borne on a seta, twisted to the right when dry, 5 mill. long. The capsule is evidently old, and is without an operculum; a true annulus is present, separating on pressure from the mouth of the capsule. Dr. Hennings

informs me that there are four more capsules on the specimens in Müller's herbarium. These are all without an operculum, and 'show no trace of a peristome.' As the capsules are all old it is impossible to say at present whether they are gymnostomous or not. The present plant differs from other species of *Streptopogon* in the presence of a true annulus.

The stem of *S. rigidus*, as seen in transverse section, consists of large polygonal cells with thin walls, surrounded by two or three peripheral rows of thick-walled cells; there is no 'central-strand.'

The gemmae are densely crowded into a globose head at the apex of the leaf. Each gemma when mature is divided both transversely and longitudinally (see Figs. 39, 40, 80, 89, 92); the cells are brownish in colour, except frequently those at either end, which are paler or nearly colourless. The gemmae are usually to be found germinating amongst the leaves of the lower part of the stem, giving rise to long threadlike branches which frequently show the oblique septa characteristic of rhizoids (Figs. 95, 96).

The leaf-nerve is seen in transverse section to be composed of 'pointer-cells' and a single strongly developed dorsal stereid-band (Fig. 94).

**S. Lindigii**, Hampe (Figs. 41-61).

*S. Lindigii*, Hampe, in Ann. Sci. Nat., 5<sup>e</sup> sér., iii, 351 (1865); Mitt., Musc. austr.-amer., 178 (1869); Jaeger, Adumbr. i, 255 (1873); C. Müll., Gen. Musc. Frond., 421, 423 (sect. *Eustreptopogon*) ('1901,' i. e. 1900); Broth. in Engler and Prantl's Natürl. Pflanzenfam., 214. Lief., p. 418 (sect. *Eustreptopogon*) (1902).

*S. latifolius*, Mitt., Musc. austr.-amer., 179 (1869); Jaeger, Adumbr. i, 255 (1873); Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 276 (1897); C. Müll., Gen. Musc. Frond., 421, 423 (sect. *Eustreptopogon*) ('1901,' i. e. 1900); Broth. in Engler and Prantl's Natürl. Pflanzenfam., 214. Lief., p. 418 (sect. *Eustreptopogon*) (1902).

*S. setiferus*, Mitt., Musc. austr.-amer., 180 (1869); Jaeger, Adumbr. i, 255 (1873); Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 276 (1897); C. Müll., Gen. Musc. Frond., 421, 423



(sect. *Eustreptopogon*) ('1901,' i. e. 1900); Broth. in Engler and Prantl's Natürl. Pflanzenfam., 214. Lief., p. 418 (sect. *Eustreptopogon*) (1902).

Dioicus, laxe caespitosus, olivaceo-lutescens; caule erecto radiculo nunc rigidiusculo humiliore 1-2 cent. alto parce ramoso nunc procero flaccidiore subflexuoso ad 4 cent. alto ob innovationes fertiles pluries fastigiato-ramoso, foliis caulinis erecto-patentibus siccitate arcte vel laxe adpressis apicalibus subtorquescentibus superioribus maiusculis late oblongis et subobovatis concavis  $2\frac{1}{4}$ - $3\frac{3}{4}$  mill. latis circ. 5 mill. longis (nervo excurrente excluso) apice obtusiusculis vel subacutis in aristam olivaceo-rufescentem usque ad 4 mill. longam sublaevem nervi excurrentis eformatam productis inferioribus minoribus pilo brevioribus, nervo in folii lamina valido olivaceo-rufescente, margine utroque subflexuoso fere ad folii apicem revoluta apice irregulariter denticulata, limbo nullo, cellulis laxis inferioribus subrectangularibus latitudine  $2\frac{1}{2}$ - $3\frac{1}{2}$ -plo longioribus pellucidis superioribus mollibus hexagonis  $30-40 \times 18 \mu$  aetate parietibus incrassatis porosis utriculo primordiali collapso repletis foliis perichaetialibus exterioribus caulinis conformibus sed longioribus ad 6 mill. longis angustioribus concavioribus intimo minore margine haud revoluta, capsula in pedunculo quam ipsa brevioribus crasso tumido superne latiore siccitate collapsa emergente erecta ampla operculata cylindrica deoperculata oblonga et late oblonga 3-4 (raro  $2\frac{1}{2}$ ) mill. longa 1- $1\frac{1}{2}$  mill. lata plerumque  $3 \times 1\frac{1}{2}$  mill. maturitate olivaceo-rufescente ore rubro exothecii cellulis late polygono-rectangularibus ad capsulae os subito minoribus basi ima stomatibus paucis superficialibus instructa, operculo maiusculo conico-subulato cellulis haud spiraliter contortis basi rubro crenulato, peristomio fere ad medium tubuloso tubo basi albido superne intense rubro haud vel indistincte rectangulari-tessellato, exinde cruribus filiformibus 16 intense rubris minute papillosis fere rectis omnibus in parte inferiore tertia in fila duo seiunctis, columella exserta, calyptra mitraeformi  $2-2\frac{1}{2}$  mill. longa superne fusca aspera\* paullulum infra os capsulae descendente, sporis globosis laevibus  $14-17 \mu$  diam.

Planta mascula eisdem femineis minor, densius compactius fasciculato-ramosa, ramulis brevibus iterum iterumque infra florem gemmiformem crassiusculum divisa, foliis caulinis illis plantae femineae conformibus sed minoribus erectioribus nervo minus excedente, foliis perigonalibus late obovatis concavo-convolutis nervo plus

minus excedente interioribus margine erecto antheridiis numerosis paraphysibus filiformibus.

*Hab.*—America australis: Colombia (*Nova Granata*); Bogota, Pacho, altit. 2,200 metr., c. fr., in sylvis cum *S. erythro-donto* (leg. A. Lindig, July 1863)!; Los Laches, sterile (leg. A. Lindig, July 1863)!—sub *S. Lindigii*, Hampe. Andes Bogotenses, ad viam inter Tipaquira et Pacho, ad arborum humiliorum ramos, inter caespites *Acidodontii megalocarpi* (8,000 ped.), c. fr. et planta mascula (leg. Weir)!—sub *S. latifolio*, Mitt. Andes Bogotenses, ad caudices filicum sylvarum prope Pacho (6,000 ped.), c. fr. (leg. Weir, nr. 264)!—sub *S. setifero*, Mitt.

The present species was first described by Hampe in his 'Prodromus Florae Novo-Granatensis' (5) in 1865. In the diagnosis here given the leaves are described as 'marginata.' In 1869 Mitten in his 'Musci austro-americi' (14), in treating of the genus *Streptopogon*, kept up Hampe's species, of which specimens were not seen, and described as new species *S. latifolius* and *S. setiferus*. In Mitten's key to the species of the genus the three plants are thus distinguished:

Folia limbo marginata.

Folia latiora minus acuminata, *S. Lindigii*.

Folio oblongo-ovalia, *S. latifolius*.

Folia immarginata.

Folia elliptico-spathulata, *S. setiferus*.

First, as regards *S. setiferus*, Mitt. This is in all respects identical with *S. Lindigii*, Hampe, as a comparison of the types in Mitten's and Hampe's herbaria shows. If Hampe's and Mitten's diagnoses are compared it will be found that, except for the fact that Hampe describes the leaves as 'marginata,' while Mitten says 'limbo nullo,' no distinguishing characters are given. Now, as mentioned below more fully, the marginal cells of *S. Lindigii* are scarcely or not at all different from those of the rest of the leaf, and never form a true 'limb,' as e.g. is found in the leaves of *S. erythro-dontus*, which, it may be noted, Hampe (l. c.) describes also as simply 'marginata.'

*S. latifolius*, Mitt., was stated to differ as follows: 'Statura

habitu coloreque *S. setifero* simillimus, foliisque siccitate laxe adpressis, species autem diversa videtur foliis pilo brevior, perichaetialibus vix caulinis diversiformibus, haud superne angustatis, limbo angusto obscuro marginatis et floresentia.' In the diagnosis of *S. latifolius* the inflorescence is stated to be dioicous, and the leaves are described as 'e cellularum serie unica minorum obscuriorum anguste limbata'; while *S. setiferus* is stated to be monoicous. First, with respect to this alleged difference of inflorescence, it must be noted that Hampe does not describe the inflorescence of *S. Lindigii*; and on dissecting fruiting plants of authentic specimens of *S. Lindigii* in the Kew Herbarium, and of the type at the British Museum, I have not been able to find any male flowers. I have also failed to find any male flowers on the numerous fruiting stems of *S. setiferus*, Mitt., that I have examined. Mitten says of *S. setiferus*, 'flores masculi *S. erythrodonti*.' In *S. erythrodontus* the male flower is seated on the stem close below the perichaetium (see Fig. 17). Now, in *S. setiferus* there constantly occurs on the stem, just below the perichaetium, an innovation bud (see Fig. 42), and I think it is just possible that this bud, when very young, may have been mistaken for a male flower. If, as I feel convinced we must do, we regard *S. Lindigii* (*S. setiferus*, Mitt.) as really dioicous, then the only important difference alleged between this species and *S. latifolius* is the presence of a 'limbus angustus' in the leaves of the latter plant. An examination of the type specimens of *S. latifolius* in Mitten's herbarium shows that the marginal cells in the lower half of the leaf are sometimes slightly different from those of the rest of the leaf. These marginal cells have their walls unthickened, and differ only from the adjacent leaf-cells in being slightly longer (Fig. 53); at about the middle of the leaf they cease. Whether or not it is considered that these marginal cells are sufficiently distinctly marked off to constitute a 'limb'—and in my opinion they are not—they are certainly to be found also in the leaves of *S. Lindigii* (*S. setiferus*, Mitt.). Fig. 54 is drawn from the type specimen of *S. setiferus* in Mitten's



herbarium. As regards the length of the excurrent nerve and the shape of the perichaetial leaves, I can find no difference between *S. Lindigii* and *S. latifolius*. It may be noted that *S. Lindigii* varies in size and also somewhat in habit; the stems are sometimes only a centimetre high, almost or quite simple, and of a rigid habit; at other times, as is well seen in '*S. setiferus*,' the stems are more flaccid, much branched, and up to 4 cent. high. The most important characters, however, viz. the shape of the leaf, the strongly revolute margins, the characteristic areolation of hexagonal cells with pitted walls, the peristome with its long tube whitish at the base and divided above into sixteen nearly straight teeth each of which is split in its lower third into two filiform divisions, are found invariably in all the specimens, and I feel convinced that *S. Lindigii*, *S. latifolius*, and *S. setiferus* are names that have been given to one and the same well-marked species. The male plant does not seem to have been collected except in the case of the plant named *S. latifolius* in Mitten's herbarium.

The long arista, formed of the excurrent nerve, of the upper stem-leaves and perichaetial leaves is seen under a high magnification to be very minutely denticulate at intervals with subhyaline projections. The calyptra is truly mitraeform, and is minutely asperous only towards the apex, and not anywhere setulose-hispid as is the calyptra of *S. erythrodonatus* and *S. clavipes*. The stem in transverse section shows one or two peripheral rows of thick-walled cells, and is elsewhere composed uniformly of rather large polygonal cells with very thin and delicate walls, usually slightly and minutely thickened at the angles; there is no 'central-strand.' The nerve shows in transverse section two 'pointer-cells' on the ventral surface, and on the strongly convex and projecting dorsal surface a well-developed band of stereid-cells; there is a complete absence of 'companion-cells.' The superficial stomata at the extreme base of the capsule are few and scattered, with the long axis of the guard-cells sometimes parallel to that of the capsule, at others at right angles to it.

The peristome of *S. Lindigii* has a very interesting and characteristic structure, not found elsewhere in the genus. It may be noted here that Müller and many authors describe the peristome-teeth of *Barbula* (including *Syntrichia*) as thirty-two in number, while Schimper, although giving this number in the 'Bryologia Europaea,' describes them in the 'Synopsis' as being sixteen in number, 'in crura 32 divisi.' Brotherus also, in giving the characters of the family *Pottiaceae*, in which the genus *Streptopogon* is placed, says :

'Zähne 16, einer niedrigen oder höheren, zuweilen röhrenförmigen, schräg gewürfelten Basilmembran aufsitzend, entweder flach, ungeteilt, durch enge Spalten durchbrochen, oft bis zur Basis in 2 (3) lineare und paarweise genäherte, meist ungleiche Schenkel geteilt, oder die Basilmembran in 32 gleichweit gestellte, fast stielrunde, fadenförmige, aufrechte oder schräge, allermeist spiralig links gedrehte Peristomäste gespalten, die sich nach der Anlage auf 16 P.-zähne zurückführen lassen.'

The peristome of *S. Lindigii* is certainly, I think, to be regarded as being composed of sixteen filiform teeth, each of which is regularly split into two filiform divisions in its lower third, rather than of thirty-two teeth uniting above into sixteen. It affords a very interesting example of a transitional stage.

As in *S. erythrodontus*, there is at the mouth of the capsule a 'false annulus,' formed of a few rows of exothecial cells which suddenly become smaller and thicker-walled.

It is worthy of note that the operculum on being removed from a nearly mature capsule frequently carries away with it, attached to its apex, the exerted part of the columella; so that an approach is made towards those species, e. g. *Pottia Heimii* (Hedw.), Bry. eur., *Desmatodon systylius*, Bry. eur., in which the columella is permanently and regularly attached to the operculum.

***S. cavifolius*, Mitt. (Figs. 67-71).**

*S. cavifolius*, Mitt., in Spruce, Cat. Musc. Amazon. et And., 3 (1867) (nomen); Spruce, Musc. Amazon. et And., nr. 140; Mitt., Musc. austr.-amer., 180 (1869); Jaeger, Adumbr., i, 255 (1873); Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 275 (1897); C. Müll., Gen.

Musc. Frond., 421, 422, 423 (sect. *Eustreptopogon*) ('1901,' i. e. 1900); Broth. in Engler and Prantl's Natürl. Pflanzenfam., 214. Lief., p. 418 (sect. *Calymperella*) (1902).

Dioicus?, laxe caespitosus, olivaceo-fuscescens, caule ad 2.5 cent. alto dichotome vel fastigiatis ramoso inferne radiculis fuscis ramosis dense vestito, foliis caulinis confertis patentibus vel raro erectis siccitate incurvis late ovato-oblongis concavis vel cymbiformi-concavis apice perfecte cucullatis 2-3 mill. longis margine utroque ad folii medium recurvo superne erecto undique integerrimo, nervo medio-cri flavo infra folii summum apicem desinente, cellulis mediis hexagonis et hexagono-rectangularibus marginem versus gradatim minoribus hexagono-quadratis superioribus regulariter hexagonis ad marginem quadratis inferioribus longioribus rectangularibus marginem versus subquadratis cellulis omnibus pellucidis utriculo primordiali collapse repletis aetate parietibus plus minus porosis, cellulis summis subtus (rarissime etiam supra) grosse papillatis, papillis apice truncatis gemmas anguste cylindricas transverse septatas e cellulis 4-8 compositas ad 200  $\mu$  longas circ. 20  $\mu$  latas ferentibus, caeteris laevibus, interdum cellulis marginalibus 1-2-seriatis infra folii medium elongatis et limbum plus minus distinctum efformantibus, foliis perichaetialibus caulinis conformibus, sed parum maioribus e basi ampliori magis vaginante, apice cucullatis interdum gemmiferis, capsula in pedunculo perbrevis erecto crasso superne tumido-incrassato 1.5 mill. longo emergente erecta subcylindrica circa 2.5 mill. longa, peristomii immaturi dentibus filiformibus rubris fere ad operculi apicem productis basi in tubum pallidum coalitis, operculo conico-subulato 1.25 mill. longo cellulis haud spiraliter contortis, calyptra mitraeformi glabra basi subinflata 1.75 mill. longa apice fusca cellulis basin versus laxis brevibus.

*Hab.*—*America australis*: *Ecuador*, Andes Quitenses, Baños ad pedem montis Tunguragua, in ramulis praecipue malvacearum suffruticosarum, etiam in monte Guayrapata (6,000-10,000 ped.) (Spruce, Musci Amazon. et And., nr. 140), sterilis! *Colombia*; Bogota, Pacho, 2,000 mtr. inter *Fabroniam polycarpam* et *S. rigidum* (leg. A. Lindig) in Herb. Hampe, sterilis!

*America septentrionalis*: *Mexico*; inter *Hypna*, ad arbor. (in Herb. Ph. Bruch), c. fr.!

In Mitten's description of the present plant no mention



is made of the papillate gemmiferous cells at the apex of the leaves; these, however, are found constantly in all the leaves, and are very characteristic of the species. The papillate cells at the back of the leaf are confined to the apical region, where they occur at the back of the hooded (cucullate) apex, not reaching quite to the incurved apical margin of the leaf and running down the leaf for a short way in two bands at a little distance from the nerve. The papillae are large, and very truncate at the apex. The gemmae are brownish, more or less cylindrical in shape, and consist of about 3-8 cells, the walls being apparently always transverse only and not longitudinal as well as in *S. rigidus*. Very rarely a few cells on the upper (ventral) surface of the leaf, situated immediately below the incurved apex, bear the same shaped papillae, as well as those on the dorsal surface. I have observed this in the case of two leaves only amongst a considerable number of stems examined in Mitten's herbarium and at Kew; also in a single leaf on one of the stems in Hampe's herbarium, and here it was seen that the papillae bear gemmae of the same shape as those arising from the dorsal papilliferous cells. There occur also at times on the upper surface of the leaf long narrowly cylindrical gemmae, brownish in colour in the upper part and often pale below, 20 cells or more long, and sometimes slightly branched. These are somewhat similar to the gemmae which occur on the leaves of *Orthotrichum Lyellii*, Hook. and Tayl.

Up to the present, *S. cavifolius* has been known only, in the barren state, from the Andes of Quito (Spruce, Musc. Amazon. et And., nr. 140). There is, however, in Bruch's herbarium at Kew a plant labelled '*Acrocarpum* (nov. gen.) *Capsula breviseta* (*gymnostoma*?) *Calyptra mitraeformis laciniata*; fol. late-lanceolata concavo-cucullata.—Mexico, inter *Hypna*, ad arbor.' On the label has been written later '*Streptopogon*'; and the plant proves on examination to be a fruiting example of *S. cavifolius*. This specimen bears a few very old and decayed capsules, also one young capsule with an apparently mature calyptra and a riper, nearly mature,

operculate capsule (Fig. 70). The calyptra is glabrous, and if, as appears to be the case, it is really mature forms in this character a notable exception in the genus, as in all the other species the calyptra is rough. In the nearly mature operculate capsule the peristome can be seen quite clearly through the cells of the operculum; the teeth are red, almost straight, and spring from a palish basal membrane. The capsule is emergent, and is borne on a very short seta which is thickened upwards like that of *S. Lindigii*; the perichaetial leaves resemble the cauline, except that they are slightly longer, and have the lower part more sheathing. In the single fertile stem that I have dissected, I was unable to find any male inflorescence; as, however, the capsule was very old and the stem-leaves decayed, and as in the present genus the male flower in the autoicous species is very small and easily passed over, too much value must not be attached to this negative evidence, since it is possible that the antheridia may have decayed away.

I have also detected four barren stems of *S. cavifolius* growing intermixed with the type-specimens of '*Calymperes Lindigii*' (*S. rigidus*) in Hampe's herbarium at the British Museum, so that a third locality, viz. Colombia, Bogota, Pacho, 2,200 mtr., can be now added for the species.

The Mexican record noted above is of great interest, not only as adding the species to the Flora of North America, but especially by the discovery of the fruit, as establishing the position of the species in the present genus; previously, on account of its barren condition and anomalous shaped leaves, its affinity was somewhat doubtful.

In its usual form *S. cavifolius* has rather broad patent leaves, about  $\frac{1}{2}$  mill. wide, slightly concave throughout up to the hood-shaped (cucullate) apex. Sometimes, however, as is well seen in stems in Mitten's herbarium, the leaves are narrower, erect, not patent, and cymbiform-concave up to the cucullate apex (Fig. 63). The apex of the leaf in the latter case is often slightly wider than the lower part of the leaf, owing to the margins there being strongly incurved, so that

the leaf, especially in the dry state, has a distinctly spatulate outline. That this form is not separable systematically, is clearly shown by the fact that on the stems in question leaves of the more usual form, i. e. wider and less concave, occur lower down the stem, especially at the places where branching takes place. I have also seen on other stems, e. g. in the specimens in Spruce, 'Musc. Amazon. et And., nr. 140' (in Herb. Kew), leaves clearly intermediate in shape between these two extremes.

The stem seen in transverse section is composed of one or two peripheral rows of thick-walled cells enclosing a tissue formed of rather large cells with very thin and often flexuose walls; there is no 'central-strand' differentiated. The leaf-nerve is composed of two 'pointer-cells' and a strongly convex dorsal band of stereid-cells; 'companion-cells' are absent (see Fig. 68).

I have followed Brotherus (3) in placing the present species in the section *Calymperella* of the genus. In order to do this a slight emendation of the characters of that section becomes necessary (see above, p. 114). Müller (21 and 24) defined his sections as follows: '*Calymperella*, C. Müll. Blätter mit anomaler, aus der vorgeschobenen, halsartig verlängerten Rippe gebildeten Blattspitze, welche sich in *Puccinia*-artige Körper auflöst'; and '*Eustreptopogon*, C. Müll. Blätter mit normaler Spitze; Rippe auslaufend, oder in eine mehr oder weniger lange Granne austretend.' Müller, probably without seeing specimens, placed the present species in the sect. *Eustreptopogon*, but it seems clear that its proper position is in *Calymperella* with *S. rigidus*, to which species it shows affinity in leaf-areolation and in the production of gemmae.

**S. clavipes**, Spruce (Figs. 28-37, 72, 73).

*S. erythrodontus* (Tayl.), Wils., var. *clavipes*, Spruce, Cat. Musc. Amazon. et And. 3 (nomen) (1867).

*S. clavipes*, Spruce ex Mitt., Musc. austr.-amer., 178 (1869); Jaeger, Adumbr. i, 255 (1873); Paris, Index bryolog. in Actes Soc. Linn. Bordeaux, li, 275 (1897); C. Müll., Gen. Musc. Frond., 421, 423



(sect. *Eustreptopogon*) ('1901,' i.e. 1900); Broth. in Engler and Prantl's Natürl. Pflanzenfam., 214. Lief., p. 418 (sect. *Eustreptopogon*) (1902).

*S. Massei*, Mitt. mss. in Herb.

Dioicus, fasciculato-caespitans, olivaceo-fuscescens, habitu orthotrichoideo; caule circ. 3 cent. alto ob innovationes fertiles plus minus dichotome ramoso, foliis caulinis flaccidis laxe confertis interdum subbiserialis siccitate torquescentibus e basi ovali suberecta amplexante ad angulos decurrente in laminam elongato-lanceolatam flexuosam interdum semitorquatam patulo-patentem nervo excurrente plus minus longe aristatam productis, ad apicem limbatis, margine utroque ad folii medium vel paullulo ultra revoluta superne erecto denticulato vel spinoso-denticulato, cellulis superioribus plus minus regulariter hexagonis circ.  $60 \times 16-18 \mu$  utriculo primordiali contracto repletis inferioribus longioribus oblongis vel subrectangularibus pellucidis marginalibus 1-4 seriatis elongatis angustis parietibus incrassatis limbum flavum unistratosum efformantibus, nervo mediocri luteo-rufescente in aristam validam flexuosam laevem producta, foliis superioribus perichaetialibusque maioribus ad 7 mill. longis 1.50 mill. latis interdum erecto-patentibus et apice plus minus recurvis, foliis perichaetialibus caulinis superioribus conformibus apicibus capsulam superantibus, fructu ex eodem perichaetio interdum binato saepe innovatione continua ad latus deiecta, capsula in pedunculo ea tertia parte breviora superne incrassata tumida immersa vel emergente erecta oblongo-cylindrica circ. 3 mill. longa 1 mill. lata olivacea exannulata ore rubro crenulato exothecii cellulis rotundato-quadratis vel breviter rectangularibus collenchymaticis ad capsulae os subito minoribus parietibus longitudinalibus valde incrassatis, basi ima stomatibus numerosis superficialibus instructa, peristomio rubro circ. 1.5 mill. longo brevissime tubuloso tubo haud rectangulari-tessellato, exinde cruribus 32 filiformibus liberis minute papillosis inaequilongis siccitate sinistrorsum contortis humiditate rectis vel apice divergentibus, columella exserta, operculo conico-subulato 1.75 mill. longo apicem versus tenui interdum subflexuoso cellulis haud spiraliter contortis basi margine rubro crenulato, calyptra paullulum infra os capsulae descendente mitraeformi superne fuscata glabra inferne usque ad basin valde setuloso-hispido, sporis globosis laevibus  $23-30 \mu$  diam. Planta mascula feminea minore circ. 1 cent. alta ramulis brevibus infra florem gemmiformem crassiusculum oriundis repetitive dichotomo-ramosa, caule radiculoso, foliis perigonalibus late ovatis concavis elimbatis nervo excedente breviter

cuspidato-aristatis, paraphysibus filiformibus articulis superioribus subinflatis antheridia superantibus.

*Hab.*—America australis. Ecuador—Andes Quitenses: Pallatanga, 6,000 ped., c. fr. (Spruce, nr. 141 d)!; Loxa (Loja), on branches, c. fr. et pl. masc. (G. Masee, 1870), nr. 14 (sub *S. Maseei*, Mitt. mss. in Herb. Mitt.)!

The present species was first published by Spruce (29) in 1867 as a variety of *S. erythrodontus* (Wils.), but was afterwards given specific rank in Mitten's 'Musci austro-americi' in 1869. The only locality hitherto recorded for the plant has been Pallatanga in the Andes of Quito, where it was originally discovered by Spruce, and distributed by him under the number 141 d (not 1418 as is given in 'Musc. austr.-amer.') in his 'Musci Amazonici et Andini.' Although *S. clavipes* is very similar in habit and vegetative characters to *S. erythrodontus*, a close comparison of the two species shows the existence of several important differences. In the first place the capsule of *S. clavipes* is immersed or emergent, never exserted as in *S. erythrodontus*; the membrane of the tubular base of the peristome is not 'tessellated,' and the free teeth of the peristome are not at all twisted in the moist state, and in the dry state less so than those of *S. erythrodontus*; the exothecial cells are collenchymatous; the cells of the operculum are not spirally arranged, but form straight rows; and the calyptra is setulose from about the middle to the extreme base, the hairs being longer than those of *S. erythrodontus*. In vegetative characters there is much less difference between the two species; the shape of the leaf is the same, but the upper areolation of *S. clavipes* as a rule differs in the cells being narrower and more regularly hexagonal,—the cells often being arranged in a seriate manner (Fig. 36). It is to be noted, however, that occasionally the cells are quite irregularly arranged, and of the same shape as those of *S. erythrodontus* (Fig. 73). The limb is 3-4 cells wide in the lower part of the leaf, and, in all the specimens I have examined, is continued to the extreme apex, although becoming in the upper part of the leaf very narrow and reduced to one or two

cells wide. The leaves in drying shrink very much, and become slightly twisted, keeping erecto-patent and not becoming appressed.

The present species is described as 'monoicous' in 'Musc. austr.-amer.,' but no description of the male inflorescence is given. On dissecting several fertile stems of the examples in 'Musc. Amazon. et And., nr. 141 d,' no trace of any male inflorescence could be found. Further, a specimen in Mitten's herbarium shows that *S. clavipes* is really dioicous. This specimen bears the name of '*S. Massei*,' and is thus described in manuscript :

'Folia oblongo-ovalia patentia apice recurva acuminata nervo in acumen piliferum apice laeve exeunte margine recurva inferne reflexa apicem versus denticulis aculeiformibus e limbo cellularum angustissimarum seriebus 2-3 oriundis serrulata, cellulis in folii medio oblongis versus marginem abbreviatis subquadratis utriculo collapse [repletis] perichaetia parum longiora ad thecae cylindraceae apicem vel paulo infra attingentia, pedunculus brevissimus in collem thecae sensim dilatatus operculum elongato-conicum, peristomium basi coalitum.—Loxa, on branches; Massee to Spruce. Very like *S. setiferus*, but with a distinct limb; the capsule with scarcely any distinct seta which is not twisted.'

This moss is certainly *S. clavipes*, agreeing exactly with the examples in Spruce's 'Musc. Amazon. et And., nr. 141 d.' The specimen is of special interest from the fact that it bears male flowers. These are borne on what appears to be a distinct plant, the stem of which arises out of the tomentum by the side of a fertile plant. The stem of the male plant is 1 centimetre high, and is branched dichotomously at half its height beneath a male inflorescence; each branch bears a male inflorescence at its apex, beneath which the dichotomous branching is repeated. The stem at the places where the branches originate produces numerous brown radicles. In general habit, and in the rather thick gemmiform flowers, the male plant of *S. clavipes* much resembles that of *S. latifolius*, Mitt. (*S. Lindigii*, Hpe). In the single stem that



occurs in Mitten's herbarium the leaves are much damaged, especially at the apex and margins, by parasitic algae, &c., or are very old and decayed, so that only traces of the limb are here and there to be seen, while the marginal teeth have apparently been destroyed by erosion. The perigonial bracts are quite elimbate.

The structure of the stem and of the leaf-nerve of *S. clavipes* is the same as that found in *S. erythrodontus*. The stomata at the base of the capsule are rather numerous; the long axis of the guard-cells is sometimes parallel to that of the capsule, at others at right angles to it.

On the whole, *S. clavipes* must be considered to differ specifically from *S. erythrodontus* in its immersed or emergent capsule, with collenchymatous exothecial cells, in the less twisted peristome, in the cells of the operculum not being spirally arranged, the setulose base of the calyptra with longer hairs, the (usually) narrower and more regularly hexagonal cells in the upper part of the leaf, and in the inflorescence.

The difference shown in the cellular structure of the operculum by two such closely allied species as *S. erythrodontus* and *S. clavipes* is interesting as affording evidence that no generic importance can be attached to the spiral or straight arrangement of the cells of the operculum (cf. Müller (24), pp. 30, 406).

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EXPLANATION OF FIGURES IN PLATES VIII,  
IX and X.Illustrating Mr. Salmon's Monograph of *Streptopogon*.

## PLATE VIII.

Figs. 1-27. *Streptopogon erythrodontus* (Tayl.), Wils.—Fig. 1, portion of plant, natural size; 1a, two capsules (showing variation in shape), from two stems in the same tuft (Spruce, Musc. Amazon. et And., nr. 141 c, in Kew Herbarium)  $\times 2$ ; Fig. 2, stem-leaf,  $\times 14$ ; Fig. 3, apex of same, showing limb continued to apex, and non-median nerve,  $\times 52$ ; Fig. 4, areolation in upper half of same, midway between the nerve and the margin, at three-quarters the length of the leaf,  $\times 255$ ; Fig. 5, margin of another stem-leaf, at a little distance from apex of lamina, showing the spinose-denticulate marginal cells, and the limb gradually ceasing,  $\times 255$ ; Fig. 6, margin of stem-leaf in the var. *intermedius*, var. nov., at a little distance below the apex of the lamina, showing the weak denticulation and complete absence of limb,  $\times 255$  (Spruce, Musc. Amazon. et And., nr. 141 b (in part), in Kew Herbarium); Fig. 7, basal cells of stem-leaf of *S. erythrodontus*, showing pitted walls,  $\times 400$ ; Fig. 8, mouth of capsule, showing peristome with its tubular base and the exerted columella (Spruce, Musc. Amazon. et And., nr. 141, in Kew Herbarium),  $\times 52$ ; Fig. 9, four teeth of the peristome, and part of the 'tessellated' membrane of the basal tube,  $\times 68$ ; Fig. 10, areolae of the 'tessellated' membrane, from the example in Spruce, Musc. Amazon. et And., nr. 141, in Kew Herbarium,  $\times 150$ ; Fig. 11, exothelial cells at mouth of capsule, forming a 'false annulus,'  $\times 255$ ; Fig. 12, stoma at base of capsule,  $\times 255$ ; Fig. 13, mitraeform calyptra,  $\times 25$ ; Fig. 14, cucullate-mitraeform calyptra,  $\times 12$ ; Figs. 15, 16, hairs from the calyptra,  $\times 255$ ; Fig. 17, male inflorescence, seated on the stem below the perichaetium,  $\times 25$ ; Figs. 18, 19, perigonal leaves,  $\times 25$ ; Fig. 20, transverse section of stem,  $\times 150$ ; Fig. 21, transverse section in lower half of stem-leaf,  $\times 52$ ; Figs. 22, 23, transverse sections of nerve and margin of leaf, in lower half of leaf,  $\times 255$ ; Fig. 24, transverse section in upper half of stem-leaf,  $\times 52$ ; Fig. 25, transverse section of nerve and part of lamina of leaf, showing a bistratose row of cells in the lamina,  $\times 255$ ; Fig. 26, transverse section of nerve and part of lamina of another stem-leaf, showing the occurrence of mammillate cells,  $\times 255$ ; Fig. 27, transverse section of the margin in the upper half of leaf,  $\times 255$ . (Unless otherwise stated, all figures are drawn from authentic specimens (coll. Jameson), in the Kew Herbarium.)

Figs. 28-37. *S. clavipes*, Spruce; Fig. 28, capsule and perichaetial leaves,  $\times 12$ ; Fig. 29, mouth of capsule, showing peristome (in the wet state) with short tubular base (the membrane of which is not tessellated) and the exerted columella,  $\times 52$ ; Fig. 30, part of peristome, showing teeth and membrane of tubular base,  $\times 68$ ; Fig. 31, collenchymatous exothelial cells,  $\times 400$ ; Fig. 32, mitraeform calyptra,  $\times 25$ , and hair from base of same,  $\times 255$ ; Fig. 33, operculum,  $\times 14$ ; Fig. 34, stem-leaf (somewhat flattened),  $\times 12$ ; Fig. 35, margin of same, at about one-fifth from the apex,  $\times 255$ ; Fig. 36, areolation in upper half

of leaf, midway between the nerve and the margin,  $\times 255$ ; Fig. 37, two stomata at the base of the capsule,  $\times 255$ . (All figures drawn from the specimens in Spruce, *Musc. Amazon. et And.*, nr. 141 *d*, in the Kew Herbarium.)

Fig. 38. Transverse section of stem-leaf of *S. rigidus*, Mitt., from the specimen in Spruce, *Musc. Amazon. et And.*, nr. 139, in the Kew Herbarium,  $\times 255$ .

Fig. 39. Gemmae from apex of leaf of '*S. Calymperes*, C. Müll.,' from the type in Müller's herbarium,  $\times 150$ .

Fig. 40. Gemmae from apex of leaf of *S. rigidus*, Mitt., from the specimen in Spruce, *Musc. Amazon. et And.*, nr. 139, in the Kew Herbarium,  $\times 150$ .

## PLATE IX.

Figs. 41-61. *S. Lindigii*, Hampe; Fig. 41, plant, nat. size; Fig. 42, capsule and perichaetial leaves, showing an innovation bud below the perichaetium,  $\times 13$ ; also part of an arista, near its base, showing the minute denticulations,  $\times 255$ ; Figs. 43, 44, two capsules,  $\times 13$ ; Fig. 45, part of peristome, showing the basal membrane, and each tooth divided into two in its lower third,  $\times 68$ ; Fig. 46, mitraform calyptra, with its scabrous apex,  $\times 68$ ; Fig. 47, papillae towards the apex of the calyptra,  $\times 255$ ; Figs. 48, 49, two stem-leaves, showing variation in shape,  $\times 12$ ; Fig. 50, apex of a stem-leaf,  $\times 52$ ; Fig. 51, margin of same, just below apex of lamina,  $\times 255$ ; Fig. 52, areolation in upper half of stem-leaf,  $\times 255$ ; Fig. 53, marginal cells in lower half of stem-leaf, from the type of '*S. latifolius*, Mitt.' in Mitten's herbarium,  $\times 255$ ; Fig. 54, marginal cells towards the base of a stem-leaf, from the type of '*S. setiferus*, Mitt.,' in Mitten's herbarium,  $\times 255$ ; Fig. 55, transverse section of nerve in lower half of stem-leaf,  $\times 255$ ; Fig. 56, transverse section of margin in lower half of stem-leaf,  $\times 255$ ; Fig. 57, portion of male plant, nat. size; Fig. 58, male flower,  $\times 12$ ; Fig. 59, perigonal leaf and antheridium,  $\times 25$ ; Fig. 60, exothelial cells and two stomata at base of capsule,  $\times 255$ ; Fig. 61, exothelial cells at mouth of capsule, forming a 'false annulus,'  $\times 255$ . (All figures are drawn, unless otherwise stated, from the type in Hampe's herbarium.)

Figs. 62-71. *S. cavifolius*, Mitt.; Fig. 62, stem-leaf,  $\times 25$ ; Fig. 63, another stem-leaf, with incurved margins and subspathulate outline,  $\times 15$ ; Fig. 64, papillate gemmiferous cells borne by the leaf on the dorsal surface towards the apex,  $\times 400$ ; Fig. 65, side view of a papilla, showing the truncate apex,  $\times 400$ ; Fig. 66, a gemma, borne by the papillate cells,  $\times 255$ ; Fig. 67, margin and areolation in the upper half of a stem-leaf,  $\times 255$ ; Fig. 68, transverse section of nerve towards base of stem-leaf,  $\times 400$ ; Fig. 69, transverse section of margin in lower half of stem-leaf,  $\times 400$ ; Fig. 70, capsule and perichaetial leaf (from the Mexican example in Bruch's herbarium at Kew),  $\times 12$ ; Fig. 71, calyptra, slightly inflated at base,  $\times 15$ . (Unless otherwise stated, all figures are drawn from the type in Mitten's herbarium.)

Figs. 72, 73. *S. clavipes*, Spruce; Fig. 72, mouth of capsule, showing peristome in the dry state,  $\times 52$ ; Fig. 73, areolation of a stem-leaf, at about one-third from the apex, showing the irregularly shaped polygonal cells,  $\times 255$  (from the specimen in Spruce's *Musc. Amazon. et And.*, nr. 141 *d* in the Kew Herbarium).

Figs. 74-77. '*Calymperes Lindigii*, Hampe,' from the type in Hampe's herbarium; Figs. 74-76, stem-leaves; Fig. 74, a lower leaf; Figs. 75, 76, two upper leaves,  $\times 12$ ; Fig. 77, part of a gemma, showing germination,  $\times 255$ .

150 *Salmon*.—*A Monograph of the Genus Streptopogon*.

Figs. 78, 79. *S. rigidus*, Mitt., areolation of upper part of two leaves from the same stem, showing (78) subhexagonal or (79) subrectangular cells,  $\times 255$  (from specimens collected by Weir at Boqueron, Bogota, in Mitten's herbarium).

Figs. 80, 81. Two gemmae, one germinating, from an authentic specimen (ex herb. Brotherus) of '*S. Schenckii*, C. Müll.,' in the Kew Herbarium,  $\times 150$ .

PLATE X.

Figs. 82-88. '*S. Schenckii*, C. Müll.,' Fig. 82, plant in the wet state, nat. size; Fig. 83, plant, in the dry state,  $\times 9$ ; Fig. 84, one of the upper gemmiferous leaves,  $\times 13$ ; Fig. 85, apex of same, with all but five of the gemmae removed,  $\times 52$ ; Fig. 86, one of the lower stem-leaves,  $\times 13$ ; Fig. 87, areolation in the upper half of a stem-leaf,  $\times 255$ . Fig. 88, areolation at margin of stem-leaf, at about one-third from the apex,  $\times 255$ . (Figs. 82, 83, from an authentic specimen (ex herb. Brotherus) in the Kew Herbarium; Figs. 84-88, from the type in Müller's herbarium.)

Fig. 89. Gemma from leaf of '*S. Calymperopsis*, C. Müll.,' showing point of attachment at apex of leaf,  $\times 150$  (from the type in Müller's herbarium).

Figs. 90-92. '*Calymperes Lindigii*, Hampe,' from the type in Hampe's herbarium; Fig. 90, one of the lower stem-leaves,  $\times 17$ ; Fig. 91, apex of one of the upper leaves,  $\times 52$ ; Fig. 92, a gemma,  $\times 150$ .

Fig. 93. Basal areolation of stem-leaf of *S. rigidus*, Mitt., showing group of hyaline cells next the nerve,  $\times 68$  (from the specimen in Spruce, Musc. Amazon. et And., nr. 139, in the Kew Herbarium).

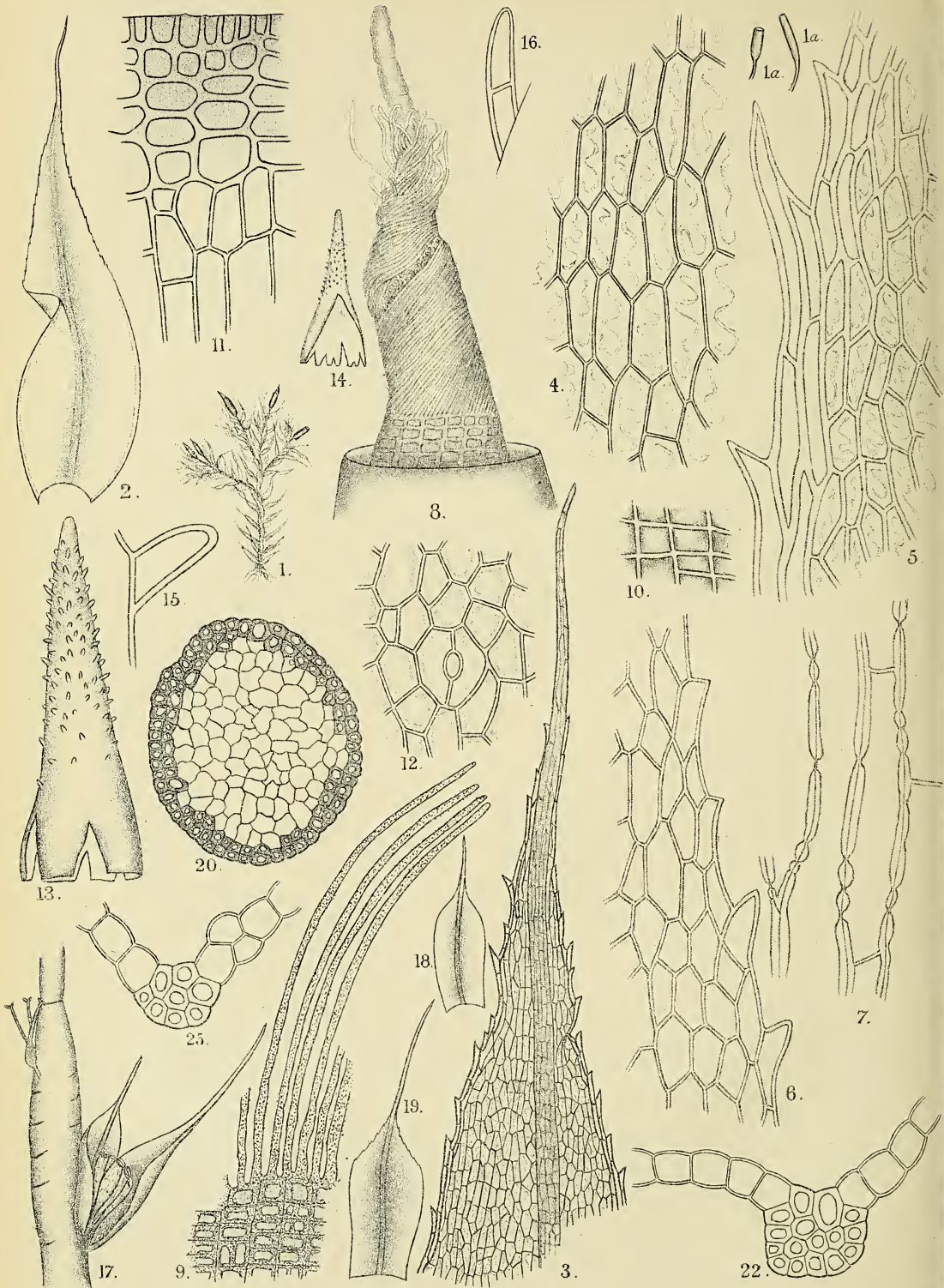
Fig. 94. Transverse section of the nerve in lower half of leaf of '*Calymperes Lindigii*, Hampe,' from the type in Hampe's herbarium,  $\times 255$ .

Figs. 95, 96. Germinating gemmae of *S. rigidus*, Mitt., occurring among the lower leaves of an example collected by Weir at Boqueron, Bogota, in Mitten's herbarium. Fig. 95,  $\times 68$ ; Fig. 96,  $\times 150$ .

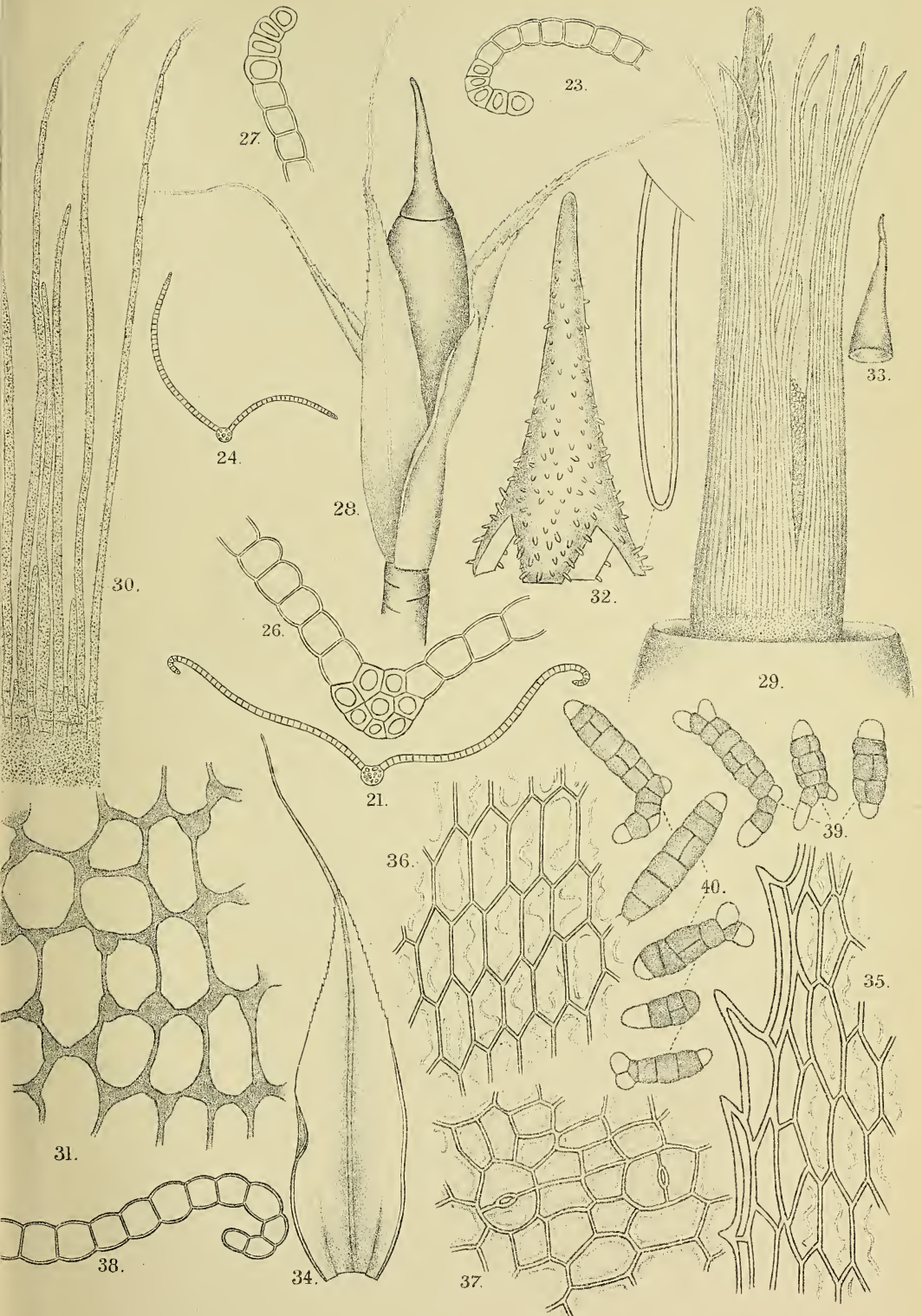
Fig. 97. Apex of a stem-leaf from '*S. Calymperes*, C. Müll.,' from the type in Müller's herbarium,  $\times 150$ .





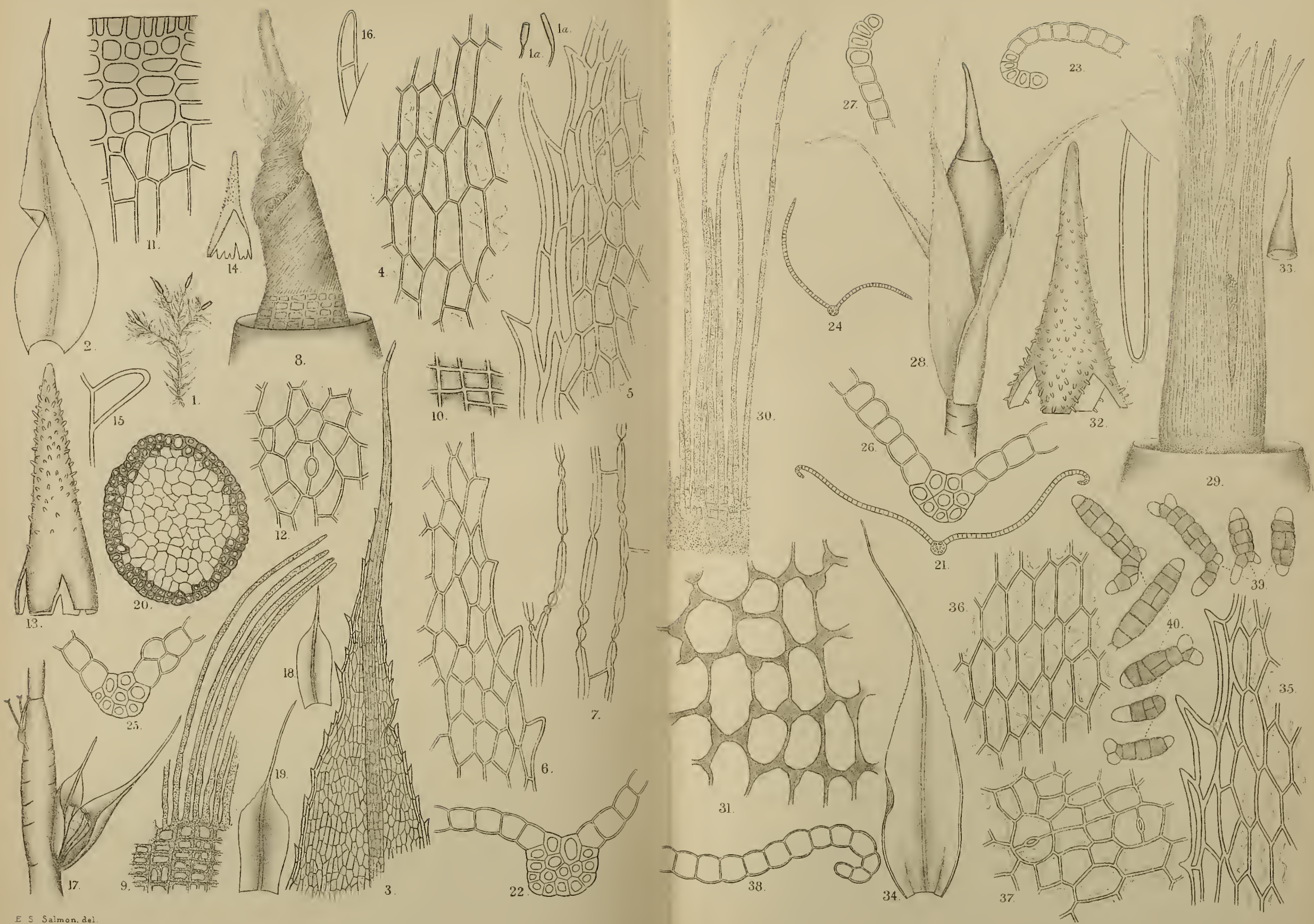


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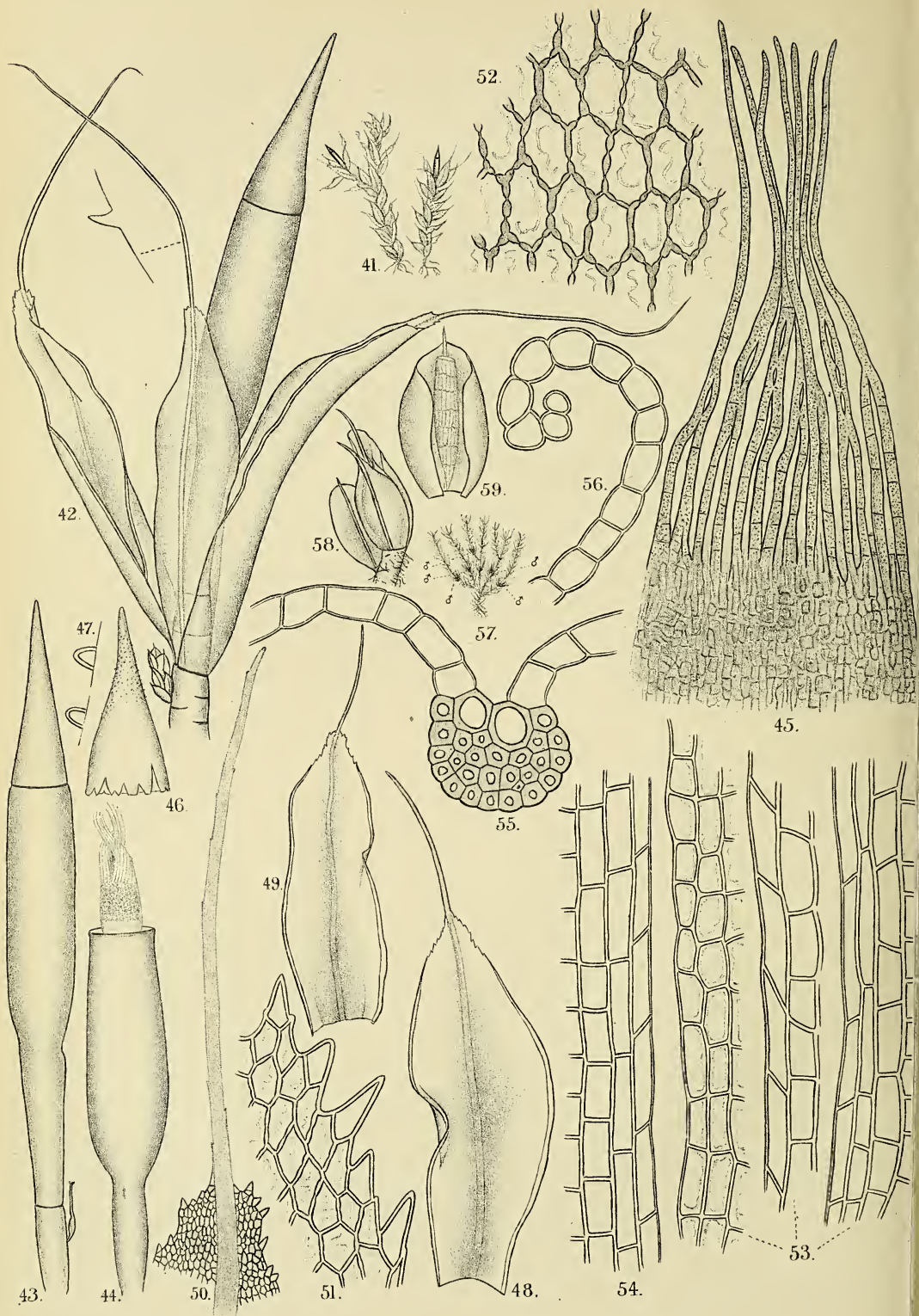
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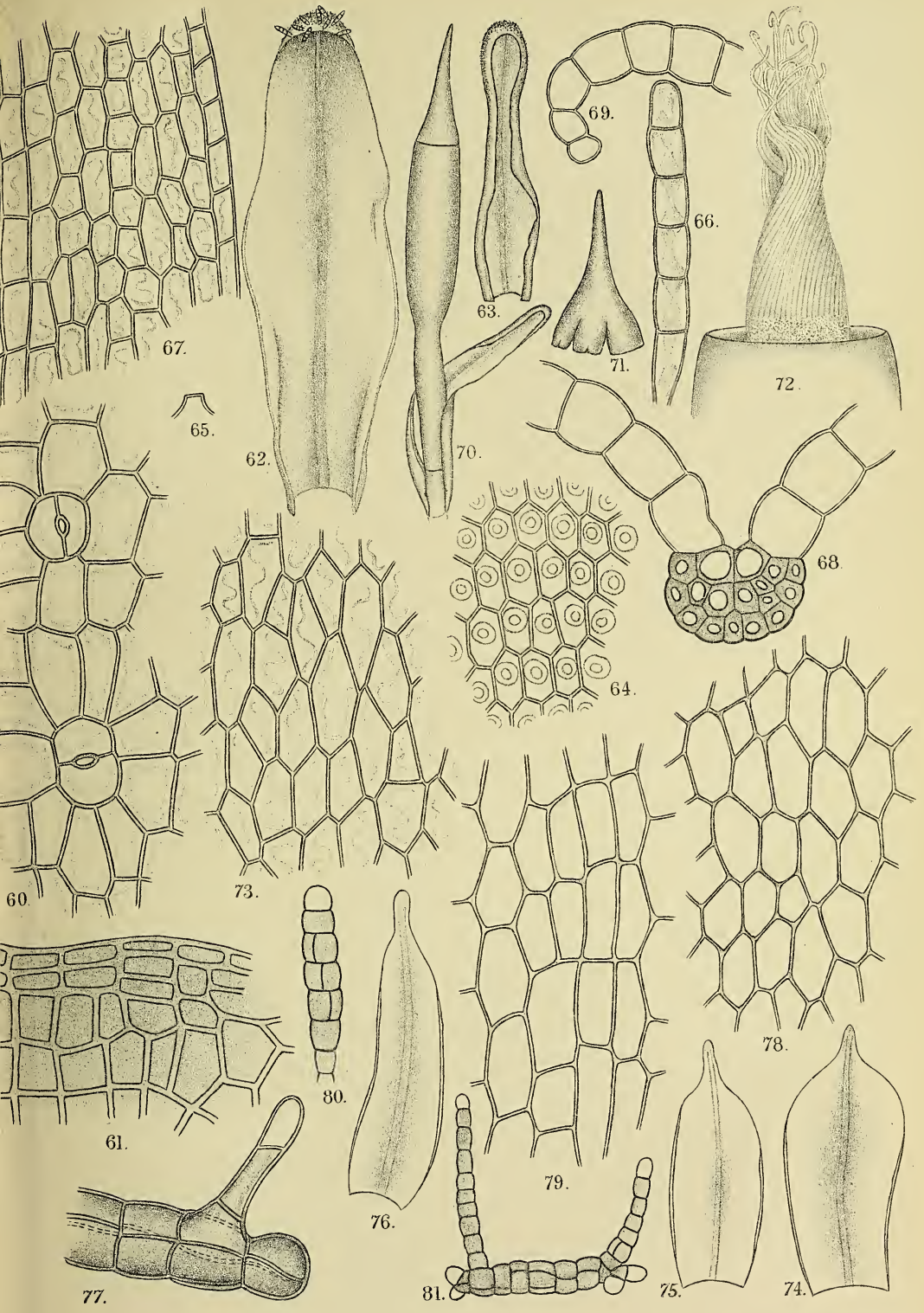






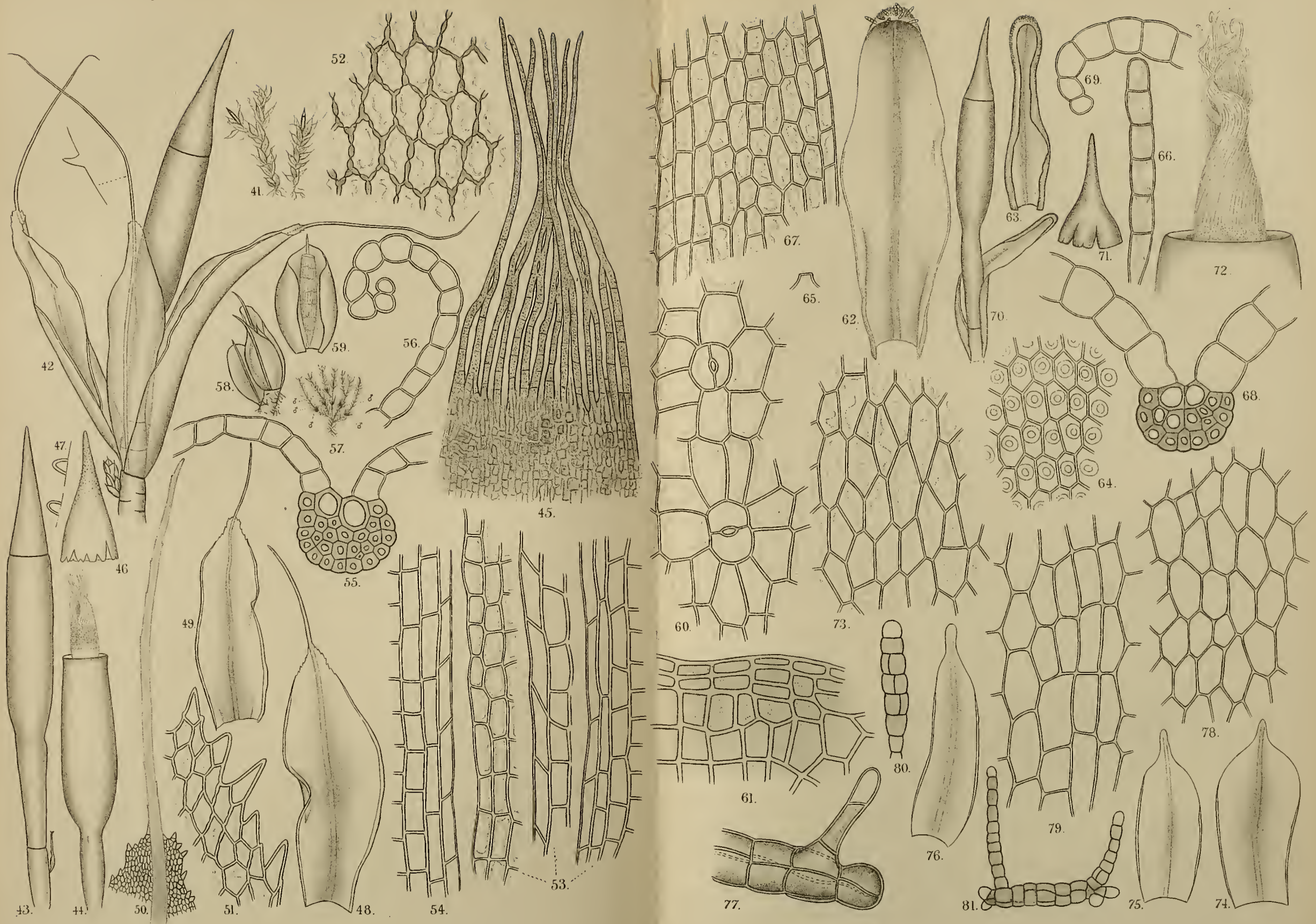


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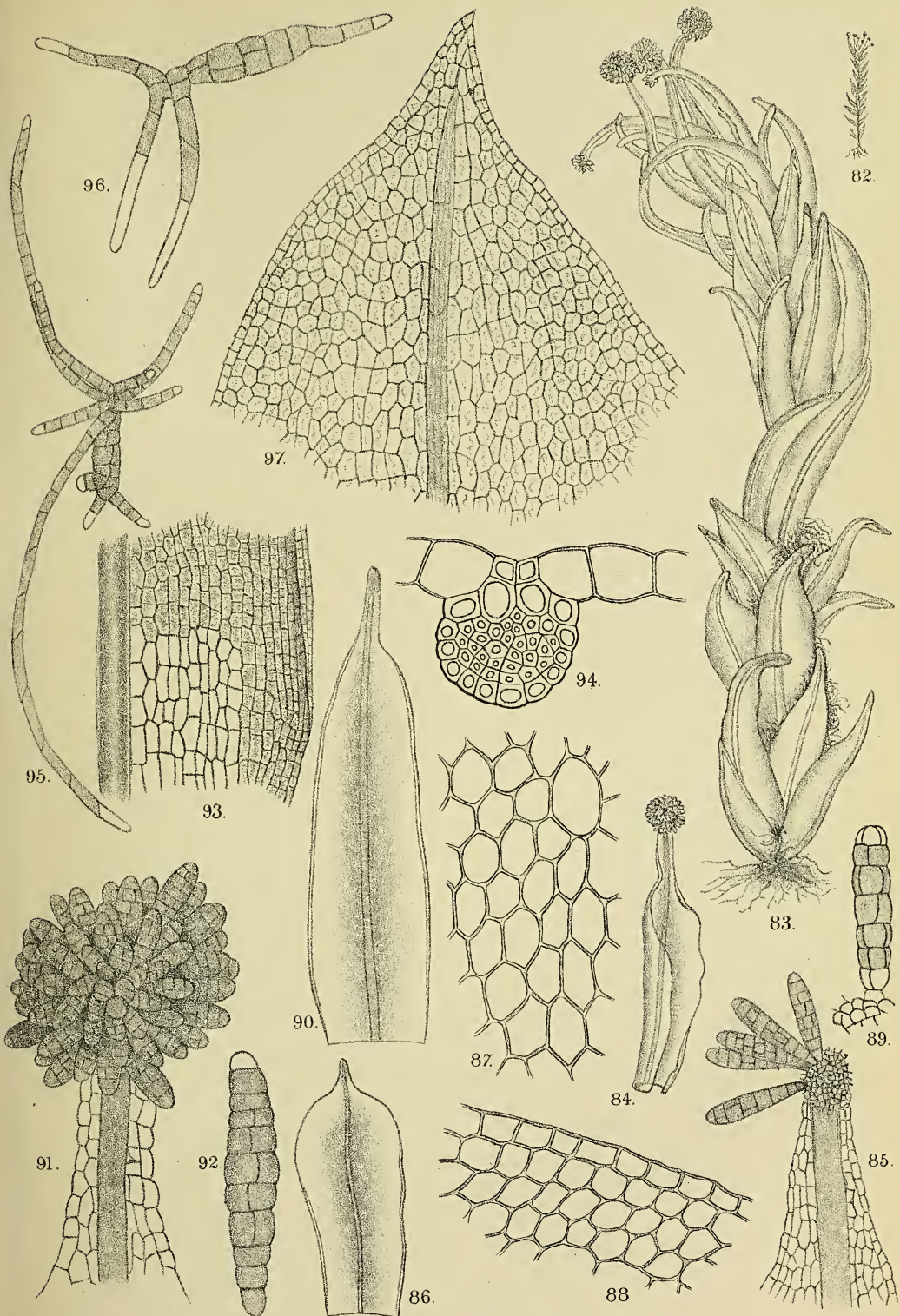
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## Some recent Observations on the Biology of *Roridula*.

BY

R. MARLOTH, Ph.D., M.A.

—+—  
With a Figure in the Text.  
—+—

AMONG the various plants which possess a special interest to the biologist there are hardly any of greater importance than the insectivorous plants. Belonging to several widely different natural orders, they are spread over all five continents, occurring in the forests of the tropics as well as in the tundra of the arctic regions, in the marshes near the shore of the sea as well as on the cloud-capped summits of the mountains.

South Africa possesses two genera of insectivorous plants, both belonging to the natural order Droseraceae, viz. *Drosera* and *Roridula*. While the European species of sundews are tiny plants with radical leaves and inconspicuous little white flowers, some of the South African species develop stalks nearly a foot high and bear large handsomely coloured flowers.

Unique in its structure, however, is the other genus, viz. *Roridula*, for while all other Droseraceae are small herbs only, *Roridula* forms shrubs. There are two species only in existence, no other shrubby Droseraceous plant being known. These two species are *R. dentata*, L. and *R. Gorgonias* Pl., which differ in their leaves as well as in the size of the plants,



for while the latter is a shrublet from 12 to 15 inches high, which possesses entire leaves, the former grows to a height of 4 feet and bears dentate leaves. The leaves of both species are closely covered with glandular hairs, similar in structure to those of *Drosera* (Fig. 15, 1 and 5). That the secretion

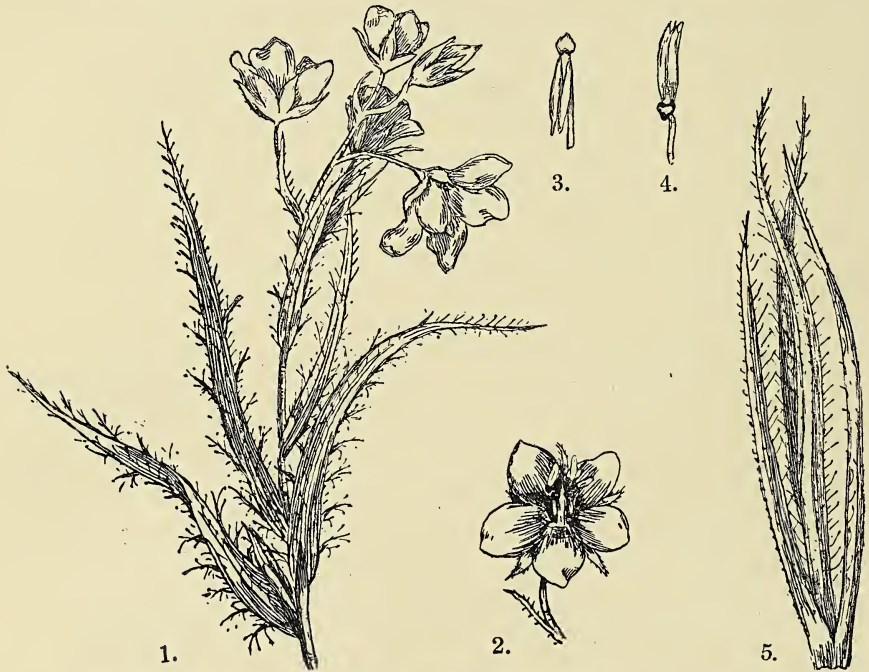


FIG. 15. 1. Flowering branch of *Roridula dentata*, L. 2. Flower. 3. Stamen in its first stage. 4. Stamen in its second stage. 5. End of a twig of *R. Gorgonias*, Pl. All natural size.

of these hairs is most effective is proved by the large number of insects which are found on every shrub of the plant. This property of the plant is well known among the people of the districts where it grows, for sometimes they suspend branches of the shrub in their houses for the purpose of catching flies. In fact it is known to the country people as the fly-bush.

When recently visiting one of the localities where *R. dentata* is known to grow, viz. the valley above the Tulbagh water-

fall, I noticed a spider walking about on the bushes, and on examining the bushes more closely I found that the spiders were quite numerous. They were all of one kind, belonging to the genus *Synaema*<sup>1</sup> (Crab-spiders). Dr. Purcell, who kindly examined the specimens, is of the opinion that it is an undescribed species. The crab-spiders spin no web, but wait for their prey and pounce upon it whenever it comes near enough. This species had selected the *Roridula* for its residence, and was evidently quite at home there, for numerous little nests were hidden among the leaves, some of which were empty and serving only as hiding-places for the spiders, while others contained a large number of young spiders.

The surprising feature of the matter was, that the spiders were able to walk or run over the leaves without the slightest hindrance from the sticky secretion of the tentacles. Whenever an insect was caught by a leaf and began to hum or to struggle, a spider in its neighbourhood would dart from its nest and secure the prey. Hence it is evident that the spider must be protected by some kind of varnish or grease against the sticky fluid, for neither their legs nor their bodies adhere to it in the slightest degree. Whether the same species of spider lives on any other plant is not known, but it has evidently adapted itself to the *Roridula*, and lives on the insects caught by the bush.

As the *R. dentata* grows also in the Cedarbergen and the Cold Bokkeveld I have endeavoured to obtain some fresh material from those regions, in order to ascertain whether the spider occurs there as well, but owing to the disturbed state of the country I have not been successful as yet.

The other species of *Roridula*, viz. *R. Gorgonias*, was for a long time only known to occur on the mountains of the river Zonder Ende, but recently Dr. Stoneman had found it in the valley of the Steenbrass river. When I visited this locality last February, I found the greater part of the valley burnt out, but finally succeeded in discovering a small patch of the plant. There were no spiders or spiders' nests on them,

<sup>1</sup> Nature, vol. lviii, 1898, p. 275.

and whether such may occur at the other locality of the plant I am unable to say.

While studying the structure of the flowers of the shrub (Fig. 15, 2), I noticed that the position of the anthers varied, for some anthers were appressed to the filament, i. e. they pointed downwards, while others formed the continuation of the filament, standing upright. I soon detected the cause of this difference of position, for, on irritating the connective of a stamen, I saw the anther swinging round with a jerk ejecting a little cloud of pollen. This showed that the stamens of *Roridula* are irritable (Fig. 15, 3 and 4).

This special contrivance showed that the fertilization of these flowers must be effected by insects; but in spite of my watching the shrubs for about an hour, I did not observe any visitor. The difficulty of the case was to understand how an insect could be adapted to visiting these flowers, for how could it escape being caught by the leaves or calyx-lobes, unless it had learnt to avoid the danger in some special way.

At last I found the solution of the problem, for I noticed a small hemipterous insect walking about between the leaves. I succeeded in securing a few of these insects, which were evidently as proof against the sticky fluid as the spiders. They were kindly identified by Dr. Purcell and Mr. Mally as a species of Capsids, apparently undescribed. The microscope showed me that these insects possess a proboscis somewhat similar to that of a mosquito, and that they consequently obtain their food by perforating the tissues of plants and sucking their juices. As I found young specimens of this hemipter two months afterwards on plants of *Roridula* which I had brought with me to Capetown, and which I was cultivating in my garden, it is evident that the eggs had been deposited on the plants and that this insect lived on the juice of the young tissues of the *Roridula*. The question suggested itself, whether the flowers possessed any special attraction for this insect. On investigating the contents of the gland-like connectives of the stamens, I ascertained by micro-chemical reactions that the internal tissue of the connective contained



sugar in its cells, while the cells of its epidermis were free from it. The connective is consequently not a nectary in the ordinary sense of the word; that means to say, it does not secrete honey on its surface, but it offers it only to insects which obtain their food by piercing the tissues. As our Capsid is not only able to do that but also to walk about freely on the plant, as if there were no tentacles with sticky glands, it is obvious that this insect is specially adapted to the fertilization of the flowers of *Roridula*.

In order to obtain, if possible, some evidence in favour of this view, I examined the few specimens of the insect which I possessed for pollen-grains. Two specimens which I examined did not contain any, but the third one carried quite a number of grains of *Roridula* pollen between the hairs of its body.

Taking all these facts into consideration, there can be no doubt with regard to the relation between this insect and the plant.

As stated above, there were no spiders on the specimens of the other species which I found in the Steenbrass river valley, but I noticed at once that *R. Gorgonias* was also inhabited by a Capsid, which was evidently quite different from that on *R. dentata*. As on that occasion I had provided myself with a muslin bag I was able to secure a larger number of the insects. On examining the spirits of wine in which I had preserved them, I found numerous pollen grains of *Roridula*, and as the structure of the stamens of this plant, especially that of its connectives, is quite similar to that of *R. dentata*, it is evident that this insect lives on *R. Gorgonias* in the same way as the other one on *R. dentata*.

Summing up these observations, we find that the *Roridula* catches insects in order to obtain an additional food-supply, but that a spider robs the plant of a share of its prey in spite of the sticky tentacles.

At the same time the Capsid takes some of the juice of the plant, having likewise acquired immunity from the dangers of the glandular hairs, but the plant utilizes this otherwise

unwelcome lodger by offering him some special tit-bits in its flowers, securing in this way, with the aid of some specially developed contrivances, the cross-fertilization of its flowers. It is hardly possible to imagine a more complicated relationship of plants and animals.

There is another peculiarity of *R. dentata* which deserves special attention. All other Droseraceous plants occur in swampy or wet places, and the annuals are found in localities which are moist during certain seasons of the year. The locality, however, where I found *R. dentata* was the dry slope of a hill, which consisted of hard iron gravel and clay. No other hydrophilous plants were to be seen. The unusual nature of the locality induced me to dig up several plants and to take a sample of the soil from the lowest layer into which its roots had penetrated. I put the sample at once into a well-corked tube and analysed it later on. It contained only 1.74 per cent. of moisture (expelled at 120° C.), and the loss by ignition, which represents the combustible matter and the chemically bound water, amounted only to 3.11 per cent. As the young plants as well as the larger shrubs possess a comparatively small root-system, and as the amount of moisture in the soil is hardly sufficient for strictly xerophilous plants, it is surprising that a shrub which belongs to a typically hygrophilous order should be able to exist in such a locality.

The locality in which I found *R. Gorgonias*, however, was of the usual nature, consisting of moist sandy soil, on which, among other plants, a species of *Drosera*, viz. *D. cuneifolia*, grew.

Dr. Purcell has drawn my attention to an article by R. I. Pocock, published in 1898 in *Nature*<sup>1</sup>, from notes supplied by Mr. A. Everett.

This gentleman has observed that a species of *Nepenthes* in North Borneo is often inhabited by another crab-spider, viz. *Misumena nepenthicola*. This spider plunges boldly into the fluid of the pitchers whenever threatened by danger, and it is

<sup>1</sup> *Nature*, vol. lviii, 1898, p. 275.

assumed that it preys upon the insects which enter the pitcher or which are caught in its fluid.

Mr. Mally, of the Cape Entomological Department, has kindly made a general list of the insects found on a handful of branches of *Roridula dentata*, gathered by me on the occasion of my visit to the Tulbagh mountains. This list shows:—

Hymenoptera : twenty-five specimens belonging to the sub-families Sphecina and Apina.

Diptera : twenty specimens of Muscidae.

Coleoptera: Of Coccinellidae were present *Chilomenes lunatus*, Fab., *Exochomus nigromaculatus*, Goeze, *Pharus sexguttatus*, Gyllh. and two other species.

Of Scarabaeidae two species were present, viz. *Lepitrix stigma*, de Geer, and *Pritrichia capicola*, Fab.

Hemiptera : One specimen each of Lygaeidae, Reduviidae and Membracidae.

CAPETOWN.

May, 1902.





# On the *Heteranthus* Section of *Cuphea* (Lythraceae).

BY

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With Plate XI.



HISTORY AND TAXONOMY.

THE section *Heteranthus* was established in 1877 by Koehne (3), who created it to receive his three new species, *Cuphea setosa*, *C. epilobiifolia*, and *C. tetrapetala*, which had this character in common that in each pair of opposite flowers one flower was older. He also placed *C. rigidula*, Benth., doubtfully in the section. In 1881 (5), while giving more detailed descriptions of his three species, he placed *C. rigidula* next to *C. setosa*, omitting all mention of the repeated dichasial branching of *C. rigidula*, which he evidently did not credit. In succeeding years Koehne added four other species, all from Colombia, one of which, *C. Lehmanni*, does not possess the character from which the section takes its name, namely the unequal age of the flowers of each pair. The two new species described in the present paper also alter the character of the section in important details, namely the presence of two petals only, and the occurrence of an erect instead of a deflexed disc. It may, therefore, be

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useful to give shortly the principal characters of the section *Heteranthus* as now constituted.

*Principal characters.* Prophylla 2. (Sub-genus *Eucuphea*.) Flores oppositi, in quovis pari inaequales (exc. *C. Lehmanni*). Bractee magnae hypsophylloideae, ciliatae. Caulis saepius pilis fuscis, crassis biserialim obtectus. Folia opposita. Petala 6, 4, vel 2. Stamina 11 alterne inaequalia. Discus saepius deflexus (in *C. tarapotensi* erectus). Ovula 3-10.

*Key to the species* (mainly from Koehne).

Filamenta inclusa vel parum exserta.

*C. setosa*, *C. rigidula*, *C. sordida*.

Filamenta valde exserta.

I. Petala 6.

*C. hispidiflora*, *C. epilobiifolia*, *C. Buravii*, *C. Lehmanni*.

II. Petala 4.

*C. tetrapetala*.

III. Petala 2.

1. Discus erectus.

*C. tarapotensis*.

2. Discus deflexus.

*C. Bombonasae*, *C. epilobiifolia* var. *Caquetae*, *C. tetrapetala* var. *Cosangae*.

*Cuphea tarapotensis*, Sprague, sp. nov.

Suffrutex. Caulis (25 cm. circ.) foliaque ut in *C. epilobiifolia*. Pedicelli 3 mm. longi, ad vel infra medium prophylla ovata acuta ciliata gerentes; bractee late ovatae, longe ciliatae. Calyx (5-5.5 mm.) calcare breviusculo recto munitus, fauce ampliata adscendens, dense breviterque hirsutus, intus infra stamina pilosa; append. lobis breviores, breviter setosae. Petala 2 (dorsalia), quam calyx paullo breviora, ovata



acuminata, ungue longo. Stamina episejala supra lobos  $\frac{1}{2}$  exserta, epipetalorum breviorum duo dorsalia calycis sinus fere aequantia. Ovarium ovato-oblongum, villosum. Discus erectus, cylindricus, 1.25 mm. longus, basi pilosus. Ovula 7-8.

*R. Spruce*, Tarapoto (Peru).

*Cuphea Bombonasae*, Sprague, sp. nov.

Suffrutex. Caulis (18-35 cm.) foliaque ut in *C. epilobiiifolia*. Pedicelli 2-3 mm. longi, ad vel supra medium prophylla ovata acuta ciliata gerentes; bracteae late ovatae, acutae, longe ciliatae. Calyx (5-6 mm.) calcare longiusculo, leviter curvato munitus, fauce ampliata ascendens, dense hirsutus, intus infra stamina pilosa; append. lobis breviores, brevissime setosae. Petala 2 (dorsalia), calycis  $\frac{2}{3}$ - $\frac{4}{5}$  aequantia, oblongo-ovata, apice rotundata, ungue lato. Stamina episejala supra lobos  $\frac{1}{2}$  exserta, epipetalorum breviorum duo dorsalia calycis sinus fere aequantia. Ovarium ovatum, pilosum. Discus deflexus, oblique ovoideus, .75 mm. longus. Ovula 6-7.

*R. Spruce*, in fl. *Bombonasae* ripis inundatis, May, 1857.

*Cuphea epilobiifolia*, Koehne.

Var. *Caquetae*, Sprague, var. nov.

Prophylla ovato-oblonga. Calyx 6-8 mm. longus, calcare quam in *C. epilobiifolia* typica tenuiore. Petala 2 (dorsalia), late ovata vel suborbicularia, salmonea, ungue .75 mm., lamina 3-3.5 mm. longis. Staminum epipetalorum duo dorsalia calycis sinu breviora. Ovula 6-7.

*Sprague*, rocky banks of a tributary of the Caquetá (Colombia), April, 1899.

*Cuphea tetrapetala*, Koehne.

Var. *Cosangae*, Sprague, var. nov.

Pedicelli prophylla ad vel supra  $\frac{1}{2}$  gerentes. Petala pro rata 2 (dorsalia), sed etiam 3-4 inveni, ovata. Staminum epipetalorum postica 2 calycis sinus haud aequantia. Ovula 9.

*W. Fameson*, 775, ad ripas fl. *Cosangae* (Ecuador), 6,000 ped., Jan.

On comparing the descriptions of the species of *Heteranthus*, the first point noticed is the remarkable uniformity in vegeta-

tive characters, and the very numerous differences in floral structure displayed by the different species. The first is obviously correlated with the similarity of habitat which obtains throughout the group, all the members of which grow in gravelly soil among rocks on the upper courses of rivers. As regards the internal classification of the section, the relationships between the several species are too intricate to admit of any satisfactory natural grouping. *C. rigidula* is separated sharply from all the rest by the dichasial branching of its inflorescence, and has perhaps its nearest ally in *C. setosa*.

#### GEOGRAPHY.

The following table shows at once that the section is characteristic of the Andes (including in this term the Coast Andes of Venezuela), and in fact inhabits the upper parts of Engler's subandine (4) region. The only species occurring outside this limit are *C. rigidula* and *C. setosa*. We have unfortunately no locality for *C. rigidula* more precise than Guiana, but it may fairly be assumed from what we know of the habitats of the other species that *C. rigidula* comes from the mountains of the interior of Guiana, and possibly from the Roraima region. The early isolation of the Guiana mountains would explain the separateness of *C. rigidula*. Taking *C. setosa* (distribn. Andes and Tobago) next into consideration, we find that it is really only an apparent exception to the andine distribution of the section, for it is a well-known fact that both Trinidad and Tobago are geologically related rather to the South American mainland than to the other West Indian islands, and form the continuation eastwards of the Coast Andes of Venezuela. The occurrence of *C. setosa* in Tobago is an excellent illustration of the South American affinity of the flora of that island first remarked by Eggers (6).

The distribution of *C. epilobiifolia* (Andes proper and Venezuelan Coast range) illustrates the truly andine character of the Venezuelan Coast range recently pointed out by

Burkill (7). *C. tetrapetala* is also of wide distribution, occurring in the Andes from Mexico to Ecuador. The area of the remaining species is much more limited. Finally, we may observe that the centre of development of the section is in Colombia, which possesses no fewer than seven out of the ten species, four of them being endemic.

	Mexico.	Central America.	Colombia.	Ecuador.	Peru.	Bolivia.	Venezuela.	Guiana.	West Indies.
<i>C. setosa</i> . . .	*	..	*	..	*	*	..	..	*
„ <i>rigidula</i> . . .	..	..	..	..	..	..	..	*	..
„ <i>sordida</i> . . .	..	..	**	..	..	..	..	..	..
„ <i>hispidiflora</i> . . .	..	..	**	..	..	..	..	..	..
„ <i>epilobifolia</i> . . .	..	*	**	..	..	..	*	..	..
„ <i>Buravii</i> . . .	..	..	**	..	..	..	..	..	..
„ <i>Lehmanni</i> . . .	..	..	**	..	..	..	..	..	..
„ <i>tetrapetala</i> . . .	*	..	*	*	..	..	..	..	..
„ <i>Bombonasae</i> . . .	..	..	..	*	..	..	..	..	..
„ <i>tarapotensis</i> . . .	..	..	..	..	*	..	..	..	..
Total . . .	2	1	7	2	2	1	1	1	1

BIOLOGY.

All the species of *Heteranthus* grow among rocks by the side of rivers, and are subjected to periodical inundation ; we find accordingly that they are all perennial and somewhat fruticose, as in such situations annuals would speedily die out unless provided with very special means of propagation. In connexion with the habitat should also be noticed the narrow linear or linear-lanceolate leaves so characteristic of the section.

No observations have been recorded as to the pollination of any of the species, but it is abundantly evident from the structure of the flowers that they are entomophilous ; moreover, their position growing gregariously by riversides is a peculiarly favourable one as regards frequency of insect visitors, which in the dense forest crowd at the top of such



trees as are in flower, and only descend in numbers to the ground in open spaces. The reduction of the petals to two in certain species must be regarded as an adaptation to insect pollination rather than as a step towards total loss of petals, for it is significant that the two remaining petals are always the posterior ones, which are situated one on each side of the entrance to the nectariferous calyx spur; the path to the honey is thus better marked after the loss of the four other petals. The same object is sometimes attained in the six-petalled species of *Cuphea* by having the two posterior petals much larger or differently coloured; in *C. rigidula* they can be distinguished at once by the intense violet colouration of their claws. It is interesting to note that the reduction of petals does not always proceed regularly; it might have been supposed *a priori* that the corresponding petals on each side of the flower would have disappeared simultaneously, but this is not the case, e.g. in *C. tetrapetala*, var. *Cosangae*, several of the flowers had three petals, the two dorsal and one lateral. It may be as well to state here that *buds* were examined in every case, to eliminate risk of error from the fugacious nature of the petals.

The function of the disc needs investigation; formerly it was thought to be the honey-producing part of the flower, and was called the gland, but Kerner (2) showed that this idea was erroneous and that the honey is really secreted by the base of the spur. The only explanation since given is that the disc helps to narrow the entrance to the spur, and thus aids in the exclusion of unbidden guests; while this may be true in some instances, it hardly seems to hold good for all the species of *Cuphea*.

The exclusion of small creeping insects is thoroughly effected in certain species of *Cuphea*, e.g. *C. micrantha*, which has the intersepaline teeth provided with glandular hairs. In the section *Heteranthus* no such efficient protection exists, but the axis of the raceme and the exterior of the calyx of all the species are more or less densely clothed with hairs, *C. hispidiflora* being especially well provided in this respect.

The tufts of hairs on the base of the filaments of *C. rigidula* are doubtless of use in restricting access to the honey.

In the whole genus *Cuphea* a peculiar mechanism exists to aid in the distribution of the seeds. After fertilization a mass of tissue just below the ovary grows rapidly and forces the placenta backwards, so that it splits the ovary wall and calyx tube, and finally projects from the posterior side of the flower bearing the ripening seeds.

The pollination and insect visitors of *C. setosa*, and the question of the occurrence or absence of the section in Trinidad, are points well worth the attention of West Indian botanists.

In conclusion, I must acknowledge a grant made by the Royal Society towards the expenses of the expedition on which the type of *C. epilobiifolia*, var. *Caquetae* was collected.

I am indebted to Professor Koehne for a list of the specimens referred by him to the various species and varieties of the section *Heteranthus*.

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EXPLANATION OF THE FIGURES IN  
PLATE XI.

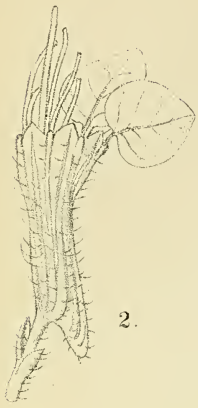
Illustrating Mr. Sprague's paper on *Cuphea*.

- Fig. 1. *C. epilobiifolia*, var. *Caquetae*. Part of plant. mag. nat.  
 Fig. 2. " Flower from side.  $\times 3.5$ .  
 Fig. 3. " Flower opened at back.  $\times 4.5$ .  
 Figs. 4 and 5. " Ovary and disc from side and back.  $\times 6$ .  
 Fig. 6. " Ovary opened, showing placenta and ovules.  $\times 6$ .  
 Fig. 7. *C. tetrapetala*, var. *Cosangae*. Flower from side.  $\times 3.75$ .  
 Fig. 8. " Flower opened at back (ovary removed).  $\times 4.5$ .  
 Figs. 9 and 10. " Ovary and disc from side and back.  $\times 5.25$ .  
 Fig. 11. " Ovary opened, showing placenta and ovules.  $\times 5.25$ .  
 Fig. 12. *C. tarapotensis*. Flower from side.  $\times 5$ .  
 Fig. 13. " Flower opened at back.  $\times 6.25$ .  
 Figs. 14 and 15. " Ovary and disc from side and back.  $\times 6.5$ .  
 Fig. 16. " Ovary opened, showing placenta and ovules.  $\times 6.5$ .  
 Fig. 17. *C. Bombonasae*. Flower from side.  $\times 5$ .  
 Fig. 18. " Flower opened at back (ovary removed).  $\times 6.25$ .  
 Figs. 19 and 20. " Ovary and disc from side and back.  $\times 6.5$ .  
 Fig. 21. " Ovary opened, showing placenta and ovules.  $\times 6.5$ .

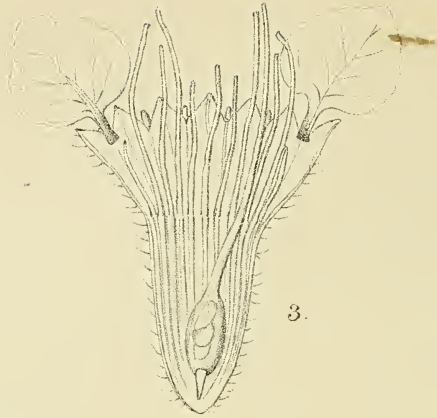
NOTE.—The artist has represented the flowers in Fig. 1 as they were in the dried specimen; in the living plant the spurs are of course uppermost (posterior)  
—T. A. S.



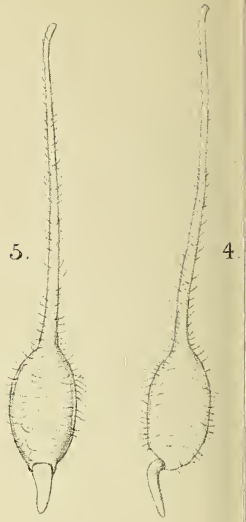




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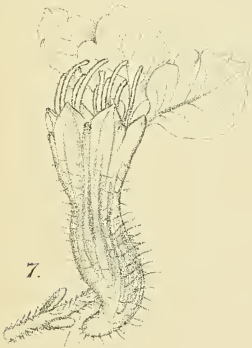


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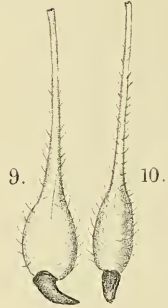
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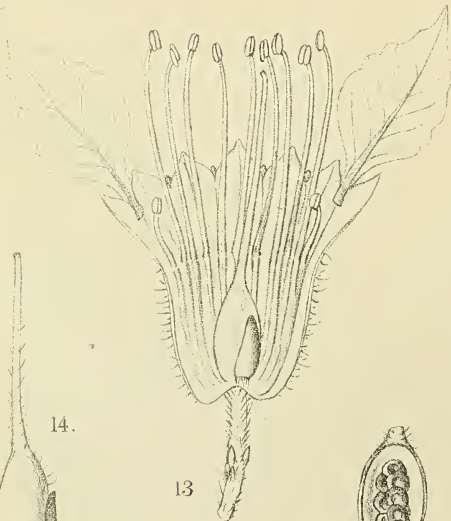
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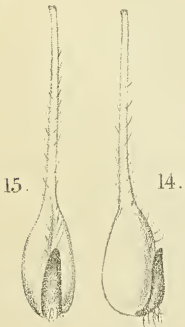
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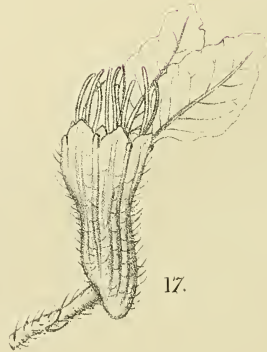


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14.



16.



17.









5. *cuphea*  
at *cuphea*

SPRAGUE.—CUPHEA.





# The Morphology and Development of the Ascocarp in *Monascus*.

BY

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—♦—

With Plates XII and XIII.

—♦—

## SOURCE.

THE fungus which forms the subject of this paper was obtained from a small cake of material which is used in the preparation of an Eastern Asiatic spirit, 'Samsu.' The cake was supplied to me by the kindness of Mr. D. T. Gwynne-Vaughan and Mr. R. H. Yapp, the former of whom collected it during the Skeat Expedition to the Malay Peninsula.

A small portion of the cake was added to a flask of sterilized rice, kept at 25° C., and an abundant mycelial growth was quickly formed. This consisted of a mixture of several Fungi, which were separated by the method of fractional plate cultures. Among them was the species here described.

It is easily grown in pure cultures on various nutrient media, especially at a temperature of 25–30° C. Growth below 20° C. is very slow. In these cultures a vigorous mycelium is quickly produced, which soon bears numerous conidia in chains. Later the mycelium becomes vividly pigmented with a pigment, from a reddish orange to a purple tinge. Ascocarps are then formed abundantly, and all stages in their development can easily be obtained.

[*Annals of Botany*, Vol. XVII. No. LXV. January, 1903.]

## METHODS.

The methods used for determining the development and structure of the ascocarp in this fungus were twofold, viz. (a) The direct observation of the developing fructification under a Zeiss  $\frac{1}{1\frac{1}{2}}$  oil immersion lens (eye pieces 4 and 8) in hanging drop cultures. The hanging drops were made of beer-wort agar (beer-wort 98 per cent., agar 2 per cent.), and were infected with conidia from pure cultures of the fungus. The temperature was kept constant at 27° C., this degree being much more suitable for the rapid development of the ascocarps than the ordinary room temperature, growth practically ceasing under 18° C.

The results of these observations were checked by the examination of living material, containing developing ascocarps in all stages, under similar powers of magnification. In this manner the results of observations of comparatively few ascocarps, the growth of which had been watched from the start to the formation of the ripe spores, were generalized.

(b) The examination of material after killing and staining. The fixing fluid used was the weak Flemming mixture. Ascocarps of various ages were not only examined whole, but also in series of sections, cut by the microtome. The material for these two methods was obtained by different means.

For the examination of the entire ascocarps cultures of the fungus in a pure condition were made by infecting a tube of beer-wort with conidia, pouring the infected wort into a sterile Petri dish until the liquid covered the bottom of the dish to a depth of one-eighth to one-quarter of an inch, and then allowing growth to take place at a temperature of 25–27° C. The first stages of the ascocarps made their appearance after forty-eight hours; and at the end of three and four days material was picked out with a sterile platinum needle and fixed. Such material contained ascocarps in all stages. After fixation, it was washed for twenty-four hours in running water and then hardened in a series of alcohols; the blackening produced by the osmic acid of the fixing fluid was

removed by treatment with hydrogen peroxide; and it was then stained with safranin for twenty-four hours. After dehydration with absolute alcohol, the stained material was placed in xylol for a few minutes until perfectly transparent, then teased out carefully and mounted in xylol-balsam.

The reason for cultivating the fungus in a thin layer of liquid in a Petri dish was that, when it was grown in any considerable depth of liquid, growth took place more slowly and ascocarps were produced more irregularly and less generally.

The material used for section cutting was obtained from plate-cultures on beer-wort agar. Such cultures showed the preliminary stages of fructifications after forty-eight to seventy-two hours from infection with conidia at 25-27°C. At intervals of twelve hours portions of the agar, containing the fungus were fixed, washed, and hardened as above. After passing successively through half-alcohol and half-xylol, pure xylol, and xylol-paraffin into paraffin, series of sections were cut by microtome. These were treated in the usual manner, decolorized by hydrogen peroxide and stained by the Fleming triple stain. In a few cases the iron-alum haematoxylin stain was used, but apart from bringing out the conspicuous nucleoli it was unsatisfactory. The cultures on beer-wort agar have a considerable advantage over those in liquid media, in that the formation of ascocarps is general and plentiful throughout, and at the same time at any given moment the majority of them are at approximately the same stage of development. Control is therefore easy. They are, however, unsuited to the previous method of examination, since satisfactory teasing of the agar material is impossible, the agar itself at the same time partially obscuring the fungus.

#### THE DEVELOPMENT OF THE ASCOCARP.

The results obtained from the examination of living material will first be considered.

In a hanging drop-culture of beer-wort agar, infected with



conidia and kept at 27° C., germination soon takes place by the putting out of one or more germ-tubes by a conidium, which at the same time increases slightly in size. The germ-tubes grow rapidly, transverse septa soon appear, and numerous branches are produced (see Fig. 1). In this way a vigorous and abundant mycelium is quickly formed. While the system of branching apparently does not follow any definite rule, it nevertheless often happens that the formation of a branch from one side of a hypha is responded to by the formation of another on the opposite side of the hypha, so that an arrangement of the branches in pairs is met with (see Fig. 1, *e*). Another point to be noticed is that there is a considerable tendency on the part of the hyphae to swell at various points (see Fig. 1, *e*). In a few cases the hanging drop almost dried up at the time of germination. In such instances the germinating conidia and hyphae swelled enormously, the subsequent branches only regaining the normal size when the drop again became more moist.

After about twenty-four hours, the time, however, depending apparently principally upon the amount of mycelium present in proportion to the size of the drop, conidia begin to be formed. These are produced by the swelling of the tips of hyphae into spherical or ovoid bodies, which are then cut off by transverse septa. Chains of these conidia are usually produced by the swelling of the hypha immediately under the terminal conidium, the swollen part being then cut off by a transverse septum to form a second conidium, and the same process being then repeated time after time immediately below the conidium last formed. Such chains may be found, composed of as many as eight to ten conidia, although usually the number is considerably less.

The conidia are developed very rapidly at first, but the rate of formation gradually becomes slower until very few fresh ones are formed. It is at about this time that the development of the ascocarps begins, being about twenty-four hours after the formation of the first conidia.

The older hyphae are then filled with large vacuoles, and

contain many large fatty-looking globules and granules. The side branches, however, are in many cases filled with dense, semi-transparent protoplasm. In certain of these a small terminal cell is cut off by the formation of a transverse septum a little distance below the tip (Fig. 2, *a*). Immediately below the septum a small lateral protuberance makes its appearance (see Fig. 2, *b*), the development of which causes the terminal cell to become bent at a slight angle from the direction of growth of the rest of the hypha. This protuberance then becomes the main growing point of the hypha, and no further growth takes place in the direction of the previous growth, but the developing hypha instead becomes closely applied to the stationary terminal cell and following its course, at the same time pushing it more and more from its original position, until eventually it assumes a direction more or less at right angles to the parent hypha (see Fig. 2, *c, d, e*). The terminal cell usually grows but little after its formation, but in some cases a more considerable increase in length, and even branching and conidial formation, occur (see Fig. 3, *a* and *b*).

Occasionally a similar process occurs at a considerable distance from the tip of a hypha, the new growing point developing immediately beneath a transverse septum and proceeding, as in the previous case, to bend the apical portion of the hypha from its original course (see Fig. 4); on some occasions also immediately beneath a conidium (see Fig. 6), or beneath the lowest member of a chain of conidia (see Fig. 7).

In both instances the subsequent development of the new growing point is similar. As already stated, it grows into a small hypha closely applied to the apical portion of the original hypha. Its course along this is usually almost strictly parallel with it but slightly curling round it, but in some cases a very pronounced spiral winding occurs, to the extent at times of more than one complete revolution (see Fig. 5). The growth in length of this hypha is limited, rarely exceeding  $40\mu$ . By the time that the limit of its growth in length has been reached, a septum has been formed in the neighbourhood of its point of origin (see

Fig. 2, *e*). The formation of the septum at this point marks off a single cell, composed of the whole of the small hypha developed as the result of the growth of the small protuberance or new growing point mentioned above. This cell, for reasons given later, will be henceforward termed the *ascogonium*, while the original terminal cell of the parent hypha, clasped by the ascogonium, will be described as the *antheridial branch*. In those instances in which the ascogonium has been produced at some distance from the apex of the parent hypha, that portion, the direction of which has been deflected by the growth of the ascogonium, will be regarded as the antheridial branch.

There have now been formed two organs, the ascogonium and the antheridial branch, the subsequent behaviour of which leads to the production of the ascocarp. They must therefore be regarded as the *archicarp*. Both of them at this period are filled with dense semi-transparent protoplasm, devoid of vacuoles but containing a few bright granules.

The next step in the development of the ascocarp consists in a fusion between the two organs. The fusion takes place in most cases at the tip of the ascogonium, between that portion of it and the part of the antheridial branch in its immediate neighbourhood (see Fig. 2, *f*). Occasionally, however, fusion takes place a little distance below the tip of the ascogonium (see Fig. 8). The fusion appears to take place in the following manner. A small papillar outgrowth is developed on the antheridial branch at the point, where fusion eventually takes place, between that organ and the closely applied ascogonium. Solution of the walls then occurs at the point of contact between the papilla and the ascogonium, the protoplasm of the two organs becoming continuous. There are two reasons for supposing the fusion to take place in this manner. Firstly, when the fused portion has become more conspicuous, the antheridial branch at the place of fusion is slightly swollen on the side in contact with the ascogonium and apparently projects into it. That is to say, it is the wall of the antheridium that constitutes the wall of the communi-



cating canal between the two hyphae (see Fig. 9). Secondly, in certain cases no fusion takes place and no ascocarp is developed; but, nevertheless, a small papilla is developed on the antheridial branch between it and the closely applied ascogonium, or, in some cases, where the ascogonium only partially develops, at the place where the tip of the ascogonium would normally be (see Fig. 10).

The exact moment of fusion is very difficult to determine in most cases, since the close contact between the two organs and their optical properties are such as to obscure almost completely the details of the process. I have never observed, either in the living state or in the fixed and stained material, a case of which it could be stated positively that fusion had occurred before the formation of the septum cutting off the ascogonium. I have, however, seen instances of undoubted fusion after the formation of the septum but before the occurrence of the next stage about to be described. It seems probable, therefore, that fusion succeeds the cutting off of the ascogonium, and is preliminary to and *also necessary* for the development of the subsequent stages. With regard to the necessity for fusion, I have never seen a developing ascocarp, in which the archicarp was still visible, that did not show perfectly clearly the existence of a fusion between the antheridial branch and the ascogonium.

It should be mentioned here also that, while the fusion is practically invisible under a one-sixth inch objective and often under a one-twelfth inch oil immersion objective in the early stages of the developing ascocarp, it becomes easily visible later, when swelling and the degeneration of the contents of the antheridial branch and of the tip of the ascogonium occur.

Positive proof of the existence of a fusion at quite an early stage is forthcoming, however, since I have seen granules pass from the ascogonium into the antheridial branch, and vice versa, in specimens in the stage now about to be described.

This stage consists in the cutting off of a cell in the ascogonium by the formation of a septum across that organ between the place of fusion and the septum at its base

(see Fig. 2, *g*). The penultimate cell thus cut off varies considerably in size at the time of formation (see Figs. 2, *g*; 3, *b*; and 5), but in all cases it has dense semi-transparent slightly granular protoplasmic contents and practically no vacuoles.

It is from this penultimate cell that the 'sporangium' of previous authors is developed.

On account of its importance and position I propose to term it the 'central cell,' the older terms 'sporangium' and 'ascus' being, as will be seen later, erroneous.

It soon begins to swell up, and vacuoles make their appearance, its shape during the earlier period of swelling being more or less reniform or bean-shaped (see Fig. 2, *h*). Later it becomes spheroid or ovoid.

The ascogonium consists during this period of two cells, viz. the central cell and a cell at its apex, which is made up of that portion of the organ which has taken part in the fusion with the antheridial branch, and is more or less comparable to a 'trichogyne' (see Fig. 2, *g*, &c.). Shortly after the formation of the central cell, investing hyphae begin to be formed around it. These are developed from the hypha which has produced the archicarp, and arise from that part of it immediately below the limiting septum of the ascogonium, i.e. just below the central cell.

In most cases a single hypha is produced in that region; and this proceeds to grow up around the central cell, closely applied to it (see Fig. 11, *a*). It begins very quickly to put out lateral branches, which also clasp the central cell. The lateral branches, especially the earlier ones, are usually produced in pairs, and grow in opposite directions. These, in their turn, produce other branches, also clasping the central cell; and development in this manner continues until the central cell is covered on every side, except those in contact with the antheridial branch and 'trichogyne cell,' by investing hyphae. The growth of these hyphae then ceases (see Fig. 11, *b-d*).

In speaking of the central cell as being invested on every side by these hyphae, it must not be understood that the whole surface is completely covered by them. What is

meant is that there is no large continuous surface left uncovered and unclasped, on every side by investing hyphae. But here and there the clasping hyphae leave exposed small portions of the surface of the central cell, and in this sense the investment is incomplete. Nevertheless, the whole of the central cell is clasped by the hyphae (see Figs. 11, *d*; and 12).

In some cases the main investing hypha does not itself become closely applied to the central cell, this function being left to some of its branches and their succeeding branches (see Fig. 12). In other cases, after growing closely applied to the cell for part of its course, it continues to grow for some distance beyond it (see Fig. 11, *a*). Occasionally also some of its branches do not become closely applied to the central cell (see Fig. 12).

In those cases which have been described up to the present, all the investing hyphae have originated from a single outgrowth from the main hypha, just beneath the ascogonium. Occasionally, however, the investment of the central cell is completed by the growth of one or more other hyphae from the same region (see Fig. 12). The development of investing hyphae is often followed by the development of small branched hyphae on other parts of the hypha bearing the ascocarp. They are sometimes irregularly branched, but often the branches are produced in pairs and grow in a curved manner, as if clasping a spherical body. Fig. 14 shows examples of both kinds. The details of the development of the investing hyphae are seen fairly easily in the earlier stages under an immersion lens, but with lower powers of magnification they can be but imperfectly traced. In the later stages, even with the use of high powers of magnification, it becomes very difficult to observe with certainty what is happening.

The hyphae are at first very small, compared with the ordinary hyphae of the fungus and with the archicarp. Their protoplasm is very dense and less transparent than that of the central cell. Consequently the course of development



of the earlier branches is easily traced. Later, however, the hyphae begin to swell, and become more transparent, and, after further growth in length and branching have ceased, the individual hyphae are very indistinctly seen, and the system could not be correctly figured if the development from a very early stage were not followed. Further swelling and, at the same time, flattening out render them, except in a few cases here and there, almost invisible. A large number of oil drops also appear, gradually increasing in size. Later still, after the protoplasmic contents seem to have entirely degenerated and to have disappeared, they appear as nothing more than flattened walls (see Fig. 13, *a-c*).

At this stage the fructification has acquired a brownish colour, due no doubt to these degenerated hyphae.

While all these changes have been taking place, important developments of the central cell have occurred. These can be seen but indistinctly owing to the obscuring effect of the investing hyphae, particularly about the period of swelling up and flattening of those structures. At the time of the formation of the first investing hypha, the central cell is comparatively small, although as has been stated above, swelling has already begun to occur. The swelling continues during the formation of the hyphae, to such an extent that the whole fructification becomes a conspicuous and comparatively large body. By this time the contents of the antheridial branch and the 'trichogyne cell' have become disorganized and eventually disappear. At the same time those two structures have swollen considerably, and the fusion between them is then very easily seen. Later, their walls collapse, and in most cases all traces of their existence are lost (see Fig. 13, *a, b, c*).

When the growth of the investing hyphae has ceased the central cell can still be seen, although with difficulty. Its outlines are no longer sharply marked; but here and there portions of its surface can be sharply focussed, where the absence of investing hyphae has left it exposed. Later, when the hyphae begin to swell and become flattened out, such

parts of the surface are seen to bulge slightly, as though there were considerable pressure being exerted inside, which forced an expansion at the unclasped points. In a few cases I have seen a comparatively conspicuous bulging at one point of the ascocarp. This may be an important fact, and will be referred to later as possibly representing the formation of the first ascogenous hypha (see Fig. 11, *a*).

After this stage the optical effects produced by the swollen central cell and the swelling and flattening investing hyphae, together with the innumerable oil drops, render further details invisible for some considerable period in the development of the ascocarp.

The general impressions produced up to the stage when the contents of the interior of the fructification again become visible are as follows:—

At some part of the interior a small spherical space becomes visible. This is clearly defined on account of its optical properties differing from those of the rest of the ascocarp. The position of this space is not necessarily the same in all cases. Sometimes it appears towards one side of the ascocarp and sometimes apparently in the centre (see Fig. 13, *a*). It increases in size until it fills almost the whole of the interior of the fructification. As it increases in size it loses its apparent homogenous appearance; and soon, when comparatively large, presents the appearance of being filled with numerous large vacuoles. This apparent structure remains until the contents of the ascocarp become more clearly visible (see Fig. 13, *b*).

As the contents gradually become more clearly visible, the misty appearance which has hitherto obscured the development is slowly lost, and it becomes possible to distinguish by degrees a mass of branching hyphae in the centre of the ascocarp, occupying the previous vacuolated space. It is undoubtedly to these hyphae that the appearance of 'vacuolation' was due.

The courses of the hyphae cannot be traced, since the

interior is filled with such a tangled mass of hyphae and structureless material that the lower ones are obscured.

Some of the hyphae are much larger than others, and are much vacuolated. Others are of varying sizes, but filled with dense protoplasm. Soon it can be seen that some of the latter have become spherical in shape, and in these, after a short time, spores are formed, eight spores in each (see Fig. 13, *c*).

There can be no doubt that these spore-containing hyphal branches are in reality asci.

The other hyphae and also the walls of the asci soon disintegrate and the spores are set free in the interior of the fructification, mixed with a mass of débris.

In this way the mature ascocarp is formed. It appears to be nothing more than a spherical body, consisting of a structureless brown wall enclosing a mass of spores mixed with mucilaginous substance. It might certainly be mistaken for a sporangium.

The spores are liberated from this structure by the breaking down of the wall.

The ripe spores are very characteristic in appearance. They have a reddish-brown colour, a bright yet almost opaque look, and in shape are ovoid with pointed ends. Their size is about  $8\ \mu$  by  $4\ \mu$ .

This account of the development of the ascocarp derived from the study of living material is supplemented by observation of fixed and stained material, an account of which will now be given.

Owing to the comparatively small size of the mature ascocarps and the transparency of all stages after mounting whole in canada balsam, very few additional details have been gained by the study of series of sections beyond those obtained by the observation of uncut, stained, and teased material; so that the results of the two methods may well be considered together. The series of sections of the various stages have an advantage over the teased material in that the nuclei are much more conspicuous, and the branching of the



hyphae from which the asci are eventually developed may be to some extent traced; but they have considerable disadvantages. Not only is there some difficulty in finding all the members of a series of sections of an ascocarp and of piecing them together accurately, but also in the cutting of the series the sections of the ascocarp become crushed or partially folded up, and in the subsequent floating out of the sections in hot water complete unfolding often does not take place; in particular great difficulty is experienced in distinguishing between certain portions of the central cell and the investing hyphae.

Starting with the formation of the ascocarp, the chief interest in the stained material is fixed on the behaviour of the nuclei. On the whole the iron-alum haematoxylin method of staining is the most satisfactory for the nuclear work.

The cells of the mycelium are multinucleate, and the same appears to be the case with the conidia from the time of their formation. The growing points of the hyphae, particularly those of the archicarp-bearing hyphae, are crowded with nuclei. The nuclei appear to stain in two ways. In the young hyphae and the archicarps the nuclei are distinguishable separately only by their nucleoli, which stain very deeply and are relatively large, the bodies of such nuclei being apparently almost unstained, each thus appearing as a light spherical space containing a deeply stained granule. The protoplasm stains rather deeply in these portions of the mycelium, not so deeply as the nucleoli, but darker than the bodies of the nuclei, this doubtless being due to the presence of some substance peculiar to the protoplasm of young hyphae which has a strong affinity for stains. On this account, and owing also to the large number of nuclei present in these parts, it is almost impossible to define the limits of any particular nucleus. Their numbers are indicated by the number of nucleoli. In the older hyphae the bodies of the nuclei stain rather deeply and almost uniformly, but no nucleolus is conspicuous, and the protoplasm with haematoxylin is almost unstained.

They are thus clearly defined. In certain parts, particularly in the antheridial branches after fusion with the ascogonia, an intermediate method of staining is found. The bodies of the nuclei stain uniformly but not deeply, while a distinct network of more deeply stained material is visible and an inconspicuous nucleolus is usually seen.

In both the antheridial branch and the young ascogonium there are numerous nuclei. At the time of fusion several may be found in both organs close to the place where fusion occurs, especially in the antheridial branch (Fig. 15, *a*). After fusion no doubt a migration of nuclei occurs from the latter into the ascogonium. At this time the canal between the two organs is practically indistinguishable, and it is impossible to determine clearly if nuclei are situated in it.

The occurrence of several nuclei in its neighbourhood is, however, significant; and in many cases nuclei appear to occupy the passage (Fig. 15, *a*). At a slightly later stage, when the canal is more easily seen and the central cell has been cut off by the formation of a wall, a nucleus can occasionally be found in the passage (see Fig. 15, *b*).

The ascogonium, after fusion with the antheridial branch, contains a large number of nuclei; and the central cell, when it is first cut off, seems to be almost entirely filled with them. They are not clearly defined on account of the affinity of the protoplasm for the stain and the slight staining capacity of their bodies. Their nucleoli alone are conspicuous (Fig. 15, *b*). Later, as the central cell grows larger, they are found grouped together at its centre in a dense mass (see Fig. 15, *c*).

The surrounding protoplasm is almost unstained, the nuclear bodies are now more darkly stained, and the nucleoli are not quite so conspicuous. Finally, when the central cell has attained a considerable size and is completely invested, the nuclei are scattered irregularly in it and are stained rather deeply and more uniformly. In the ascogenous hyphae the nuclei are not clearly defined, the staining of the younger branches being in particular very diffuse. Occasionally a few are found which show a structure similar to those of the

young ascogonium, but usually they are only to be distinguished from the surrounding protoplasm by being stained rather more deeply. At the time when it is first possible to distinguish with certainty the young asci as such, four or eight nuclei are usually found in each. Eventually eight nuclei are formed in each ascus, and the spores are produced by the accumulation of protoplasm around each nucleus.

The small size of the archicarp renders it impossible to speak with more certainty of the nuclear behaviour during the earlier periods of the formation of the ascocarp. The nuclei are relatively numerous, and consequently in whatever position the young ascogonium is viewed, even in sections, some are always superposed above the others. This fact gives rise in most instances to appearances of nuclear fusions, the majority of which by very careful observation can be made out to be due simply to superposition. Some cases cannot be clearly determined. The nuclei are so small and the amount of stainable substance in them is so inconsiderable, being especially marked owing to the stained protoplasm, rendering them comparatively transparent and therefore almost indeterminate in regard to their boundaries, that a positive statement as to fusion in such cases cannot be given. Nevertheless it is highly probable that fusions occur. There is an undoubted fusion between the antheridial branch and the young ascogonium, the extent of the fusion never being much greater than will permit of the passage of nuclei. That nuclei do pass from one organ to the other at some period is certain, since they have been found in the communicating canal. The fusion always takes place prior to the formation of the wall across the archegonium, which cuts off the central cell, so that the inference is that a nucleus or nuclei passed from the antheridial branch into that region of the ascogonium before the formation of the wall.

Probably many nuclei pass, since, after the central cell is cut off, it is found to be crowded with nuclei, while the number of nuclei in the antheridial branch seems to be less than in rather younger branches. Having admitted the



extreme likelihood of the course of events up to this point, supported as they are by direct observation, by every analogy it follows that the male nucleus or nuclei fuse with female nuclei in pairs in the central cell. The absence of one or two specially large or conspicuous nuclei supports the view that numerous fusions occur. The time of the occurrence of the fusions is probably during the state of aggregation of nuclei, at the centre of the central cell, when it is beginning to swell.

Confirmation of this interpretation of the nuclear behaviour is forthcoming by the analogy of *Pyronema*. As Harper has shown (10), a 'pore' fusion occurs in this fungus between the trichogyne and the antheridium. Numerous nuclei pass from the latter through the trichogyne into the ascogonium, which then forms a wall at the base of the trichogyne, a cell analogous to the central cell of *Monascus* thus being produced. Its nuclei aggregate at its centre, the male nuclei also travelling to that position, and numerous fusions in pairs then occur between the male and female nuclei. Similar multiple fusions have been shown by Stevens to occur in the oospheres of *Albugo Bliti* (20) and *Albugo Portulacae* (21), the details of the processes being essentially the same as in *Pyronema*. There is therefore considerable ground for believing that the nuclear behaviour in the archicarp of *Monascus* consists in numerous fusions in pairs of male and female nuclei in the central cell.

It has not been possible to distinguish nuclei in the act of division. It is probable, however, that some of the nuclei, which have been described above as having a structure consisting of a deeply stained nucleolus and an unstained nuclear body, are actually nuclei in course of division. If this is so, the structure which has been described above as the nucleolus consists probably of the individual chromosomes grouped closely together in one of the stages of karyokinesis, and appearing on account of the small size of the nucleus and nuclear figures as a single homogeneous structure. The somewhat irregular shape of the 'nucleolus' in some instances lends colour to this view, which is also supported by the facts

that such nuclei are only found in young, actively growing hyphae, where dividing nuclei must certainly occur, and that the limits of the nuclei in these regions are very difficult to determine. It is noteworthy, also, that when the conspicuous 'nucleolus' disappears from a nucleus, the latter becomes more definite, and can be distinguished as a sharply marked spherical body with a reticulate network. If this view is correct, we have in *Monascus* another instance of active nuclear division preceding the formation of male and female gametes, so characteristic of the Oomycetes and *Pyronema*.

During the formation of the first few investing hyphae, nothing of peculiar interest is seen, except that the central cell increases considerably in size (see Fig. 16). During this time it stains conspicuously, and can easily be seen. As the development of the investing hyphae proceeds, the central cell still goes on increasing in size, but stains less and less conspicuously, until at last, in many cases, all sight of it is lost. Both sections and teased material at this stage represent apparently the ascocarp as possessing only numerous small hyphae (see Figs. 17 and 18). This appearance, however, is misleading. For in the teased material careful focussing reveals the fact that the hyphae apparently within the ascocarp are in reality some of the investing hyphae, which, staining deeply, appear to be within the ascocarp, though they are actually merely in view through the unseen central cell. This illusion is heightened by the fact that the latter is ovoid or spherical, so that at every plane some of the investing hyphae are sharply in focus. In the sections it is impossible to get the ascocarps cut sufficiently thin to show a section of the central cell only with a ring of investing hyphae around it. Owing to their small size at this stage some of the investing hyphae either above or below it are sure to be included in the section, and these produce the illusion.

Such appearances cease when the investing hyphae reach the swelling and flattening stage, the continued growth of the central cell also aiding the alteration. The investing hyphae above and below the central cell now become much more

indistinct, and their course can hardly be traced. The only positions where they are clearly visible are at the sides of the central cell. The latter in consequence becomes clear in outline again, and its further development can be followed.

Its structure at this stage seems to be very variable.

On rare occasions it is a large, more or less spherical cell, filled with much vacuolated protoplasm and containing numerous nuclei (see Fig. 19).

Sometimes it appears as a large spherical cell—as in the preceding case, but with a prominent protuberance at some point of its surface (see Fig. 20).

More usually, however, it is a spherical body with a round cavity developed at some point within it. In this cavity is a greater or less number of hyphae, deeply stained for the most part and very conspicuous. The size and position of this cavity are very variable in ascocarps of the same size. In some the cavity is very small, is situated close to the surface of the cell, apparently coming to the surface at some point, and contains very few hyphae. Fig. 21 shows a case in which only a single hypha is present. Figs. 22, 23, 24 show instances in which only a few branching hyphae are developed. At the same time these figures show the varying positions of the cavity with reference to that of the stalk of the ascocarp, i.e. the main hypha from which the archicarp was developed.

In other instances the cavity is much larger and contains many hyphae, some small and conspicuously stained and others larger and much vacuolated. The cavity then occupies a large part of the interior of the central cell, sometimes occupying it so fully that the latter is nothing more than a thin double envelope of varying thickness, and often very difficult to distinguish from some of the investing hyphae. Figs. 25–28 represent this stage in various degrees.

The teased preparations show these examples much more clearly than the sections, since there is considerable confusion in the latter between the sections of the thinner parts of the central cell and the sections of the investing hyphae. The sections, however, show that in most cases in the cavity there



is a large deeply-stained central hypha with many prominent nuclei, and around this, in a circle, are other smaller hyphae which seem to arise as lateral branches of the central hypha (see Figs. 23-27). In young stages there appear to be three main hyphae in the cavity, one the prominent central hypha, and the other two springing as opposite branches from this. The main central hypha thus seems to branch in a manner similar to that of the main investing hypha. Each of these hyphae branches freely later, and produces within the cavity a densely-woven mass of hyphae of various sizes. Only the small, young hyphae then stain deeply, the older ones becoming quickly filled with large vacuoles and staining but little. In later stages these swell so much and are almost unstained, so that it becomes impossible to trace their course.

As the ascocarps increase in size, the size of the cavity in the central cell becomes much greater and the mass of hyphae within it very considerable. The central cell, in a sense, seems to develop accordingly, so that the whole ascocarp is composed practically of a solid tissue. A section across such an one shows an external ring of investing hyphae, very much flattened out and consisting of very little more than cell-walls; these are not contiguous, so that the ring is incomplete: then comes a complete ring of tissue, consisting of a section across the central cell; it has both an outer and an inner wall, and is of varying thickness. In most sections, completely enclosed by this ring, is the central cavity, filled with branching hyphae of various sizes (see Figs. 25-32).

After this stage degeneration seems to take place in the ascocarp. The internal hyphae become mixed up with a structureless substance, probably mucilaginous in nature and produced by the breaking down of some of the older ones. Some of the branches swell up into spherical bodies, the young asci, in which eight small darkly-stained round masses appear. These are the early stages of the spores. They increase in size and eventually become developed into ripe spores, ovoid in shape, with pointed ends and thick walls. The wall of the ascocarp consists now of a complete brownish

structureless thin layer of cellulose-like material, which doubtless is made up of the empty walls of both the investing hyphae and the degenerated central cell. Fig. 32 shows ascocarps at this stage, containing some asci with rudimentary spores and others with ripe spores. Further degeneration takes place within the ascocarp, the ripe spores being liberated from the asci and the remainder of the internal hyphae breaking down completely, a pseudo-sporangium being thus produced (Fig. 33).

It has been mentioned above that the central cell in some cases shows a conspicuous protuberance. This is not only seen in cases in which no cavity exists in the central cell, but also in instances where the cavity is of considerable size. In the teased preparations I have endeavoured to trace the course of such protuberances in the latter instances. As far as I can make out, the protuberance seems to be an actual outgrowth of the central cell which grows over the surface of the latter, closely applied to it, until it reaches the neighbourhood of the central cavity; then, at the point where the cavity comes nearest to the surface, it appears to penetrate into it and become continuous with the main hypha within it. I do not state positively that this is actually the case, seeing that the protuberance is not differentiated in the least from the central cell by staining, and bearing in mind that the shadow of an investing hypha may give rise to the appearance of the continuation of the protuberance above or below the central cell. But, at any rate, at certain planes the existence of such a protuberance directly from the central cell, and entirely independent of investing hyphae, is most plainly seen, and it is only about its length and course that any doubt is felt. Fig. 34 shows an example of these appearances.

In sections I have not been able to trace the course of such protuberances owing to the confusing effect of the investing hyphae.

We are now, more or less, in a position to discuss the morphological nature and mode of formation of the ascocarp from the evidence furnished by these results.

The ascocarp evidently arises from an archicarp, as is the case with many other Ascomycetes, e. g. *Sphaerotheca* and *Pyronema*. The archicarp here consists of two organs; one a male organ, the antheridial branch, and the other, the ascogonium, or female organ. A sexual process, represented by an undoubted fusion between the two, and probably also by multiple fusion between male and female nuclei, undoubtedly occurs, the antheridial branch appearing to take the most active part in the process of fusion as indicated by the formation of the small papilla. As a result of this process, a fertilized cell, the central cell, is formed. From this, with the aid of the investing hyphae, the development of which seems to be called forth by the act of fertilization, the ascocarp is produced. The central cell swells enormously, the investing hyphae keeping pace with it at first by active growth, and later, when this ceases, by swelling and flattening. The latter effect is doubtless produced by continued growth of the central cell, which is also illustrated by the slight bulging that takes place at those portions of its surface which are uncovered by investing hyphae. The next step in the development consists in the formation of ascogenous hyphae from the central cell. It has not been possible to observe the earliest formation of these hyphae, owing among other things to difficulties in distinguishing them from investing hyphae. Nevertheless at a very young stage they have been observed as short-coiled comparatively stout hyphae situated in a kind of little nest or depression in the side of the central cell. The first appearance of this nest always coincides in point of time with the first appearance of the ascogenous hyphae as such, and it has been seen at a stage so early that it has been completely occupied by a single short-coiled hypha. It is then very small compared with the size of the central cell, and is always situated at some point of the surface of the latter, its exact position varying in different instances. It soon begins to increase in size, being all the while completely filled with closely entwined hyphae. Its growth continues, until it occupies almost the whole of the interior of the ascocarp. The ascogenous hyphae



eventually produce small spherical eight-spored asci. The asci are very thin-walled, and soon break down, liberating the spores into the cavity of the nest, and at the same time the ascogenous hyphae also degenerate, so that the ripe ascocarp is filled with a large number of spores lying free in its interior amid a mass of mucilaginous substance produced by the degeneration of the other structures. During this time the central cell has undergone many changes. The nest of ascogenous hyphae in its growth displaces it and causes a considerable alteration in its shape. As the nest increases in size, it penetrates towards the centre of the central cell, which, in its growth, closes over it, so as to make it appear as if it were an internal development. Eventually the central cell ceases to grow, but the ascogenous hyphae continue to enlarge the size of the nest until asci are formed, thus causing the surrounding wall, which consists of the hollowed-out central cell, to become stretched and therefore thinner. The contents gradually disappear and the walls become cutinized, so that finally nothing remains of the central cell but its walls, which form a complete envelope around the asci and ascogenous hyphae. At first spherical, it thus gradually becomes changed in shape to a hollow sphere by the formation of a depression at one point, which extends by degrees to its centre, the mouth of the depression being roofed over by its growth. The depression itself is caused by the formation of ascogenous hyphae and its enlargement is due to the growth of these structures. The ripe ascocarp is thus a simple sporangium-like structure—a pseudo-sporangium. The complicated intermediate stages of its formation are due entirely to the curious behaviour of the central cell in growing around and thus enclosing the earliest formed ascogenous hyphae. It is thus in reality very simple in origin.

No other satisfactory interpretation of the structures observed during the development of the ascocarp seems possible. The ascogenous hyphae must arise from the central cell, since no trace of a possible origin from the investing hyphae has been seen. In specimens of fixed material mounted in

balsam the central cell and its contained structures shrink away from the investing hyphae, so that it can be seen that no outgrowth from these into the central cell has given rise to the ascogenous hyphae. Moreover, it would be contrary to every analogy if they had such an origin. Another possible cause of the curious behaviour of the central cell might be that ascogenous hyphae are produced at one point of its surface, and these, during growth, press against the investing hyphae so as to force their bases into the central cell and thus displace it, so that it surrounds them. But evidence is against this view. Nowhere can the ascogenous hyphae be seen to touch the investing hyphae, and their tips are as a matter of fact directed towards the centre of the central cell, so that during growth they tend to push themselves in or their bases outwards. An actual internal development is also quite out of the question. An investigation of young ascocarps shows that the nest invariably arises at some point on the surface of the central cell.

It is highly probable that the ascogenous hyphae have their origin from a single outgrowth of the central cell. I have never seen a case in which two nests of hyphae have been formed in the same central cell, and, as far as can be ascertained by careful examination of the youngest nests, they appear to be composed of a single coiled unbranched or slightly branched hypha. Later this branches very freely.

It is difficult to see why the first ascogenous hypha should remain in close contact with the central cell and eventually become enclosed by it. One would naturally expect to find it growing out through one of the interstices of the investing hyphae, as in the case of *Pyronema*. Perhaps the same attraction which causes the investing hyphae to grow closely applied to the central cell holds good for it also. Undoubtedly its behaviour results in the functions of protection and nutrition being very efficiently performed for the ascogenous hyphae by the central cell and the investing hyphae.

## HISTORICAL.

Van Tieghem (24) in 1884 published an account of two hitherto undescribed Fungi, which he classed with the Ascomycetes and placed among the Perisporiaceae with such little known forms as *Apiosporium* and *Cystotheca*. He considered them as constituting a new genus, which he named *Monascus*, having as its distinctive feature a novel form of perithecium. As its name implies, the perithecium consisted of a single ascus, invested by a covering of sterile hyphae, the small spherical body thus produced being regarded as the perithecium. The ascus itself was peculiar, in that it was for such a structure comparatively large and many-spored. Indeed, except for its cutinized wall and the absence of any columella, it resembled a sporangium much more than a typical ascus.

To describe the species somewhat in detail, one form, *Monascus ruber*, consisted of a much-branched regularly-septate mycelium which produced under culture two forms of reproductive organs. In the earlier stages of the cultures conidia were formed abundantly. These were produced at the end of branches in rows of varying numbers, being formed basipetally. They were colourless and somewhat spherical bodies, in size usually 10–12  $\mu$ . Later the second type of reproduction was developed. From one of the hyphae of the mycelium a short erect branch arose, which soon ceased to grow and began to swell at its apex. Immediately beneath the swollen tip a wall was formed, cutting off a terminal hemispherical cell. The other part of the branch was divided by two or three transverse walls. Beneath the terminal cell a whorl of branches was produced. These ramified and grew around it, until it was completely covered by them, without however being absolutely in contact with them until later. Contact was established eventually by the continued swelling of the terminal cell, which in the end attained a size of 40–54  $\mu$ . At this period it was brick-red in colour. During its swelling the contents of the investing hyphae gradually



disappeared, their walls finally collapsing so that their presence was only indicated by apparent reticulated thickenings of its walls. Its coloured protoplasm at length became colourless, and divided into a very large number of small oval masses, each of which became a spore. The ripe spores were oval, colourless, and refringent with homogeneous protoplasm. They measured 7-8  $\mu$  and 4-5  $\mu$ . They were liberated by the breaking down of the wall. The perithecium sometimes remained very much smaller and contained but few spores, e.g. 16  $\mu$  in diameter with 8-10 spores, and 11  $\mu$  with only 4 spores. The other species, *Monascus mucoroides*, differed from the preceding but little except in size. The conidia were larger, being usually 15-18  $\mu$  in diameter. The perithecia were also larger, having a diameter of 60-70  $\mu$ , and were produced at the end of a long branch or pedicel, in this respect resembling a *Mucor* sporangium even more than the preceding. Hence its name. The ascospores were spherical, with a mean diameter of 8  $\mu$ . The investing hyphae were similar; but in the early stages, while grouping themselves around the ascus as in the preceding species, they were not so closely applied to it, a considerable space being left between them and it, contact not being established until the latter had almost reached its full size. On this account Van Tieghem considered that there was no sexual relation between the ascogenous cell and any of the investing hyphae.

The next account of a member of this genus was that given by Harz in 1890 (12). Under the name *Physomyces heterosporus* he has described a fungus which undoubtedly is a member of Van Tieghem's genus, *Monascus*. It was met with in solutions of glycerine in a soap-factory in Bavaria, and attracted attention by its vivid carmine-red pigment. Its methods of reproduction were very similar to those of the preceding species. On nutrient gelatine substrata two kinds of conidia were formed, viz. torula-like conidia, borne either singly or in chains, 2.5-3.5  $\mu$  in diameter, corresponding to the conidia described by Van Tieghem, and macro-conidia, borne singly, more or less egg-shaped, and larger than the

preceding. The characteristic perithecia were not produced on gelatine substrata, but were soon developed in liquid media. The earliest stages of their development, which this author found, showed two or three small cells 3–4  $\mu$  in width and 2–4 times that length, situated at the apex of a branch. One of these was apparently the terminal cell of the branch, while the other one or two were placed somewhat at its side. From the central cell the ‘sporangium’ was eventually produced, and he hence considered it as an oogonium. Whether either of the other cells represented an antheridium he left undecided. Further observation of these structures was soon rendered impossible by the growth of investing hyphae from beneath the oogonium. By the time that the young fructification had reached the size 15–18  $\mu$  the oogonium was completely covered by these hyphae. The ripe fruits were spherical, 40–53  $\mu$  in diameter, and containing numerous spherical, or slightly oval, hyaline, thick-walled, colourless, refringent spores of 4.5–5.1  $\mu$  diameter. Sections of unripe fructifications, fixed in alcohol, showed the central oogonium filled with dense protoplasm and fat-drops of various sizes, surrounded by a layer of investing hyphae. Later stages showed the protoplasm regularly granular; and finally the oogonium was found filled with numerous spores, in the early stages of formation polygonal, and later more or less rounded and thick-walled. The optimum temperature of growth of this species was 30–31 C. The mycelium was freely divided by septa.

Harz seems to have been ignorant of Van Tieghem’s paper, a knowledge of which, in spite of the absence of figures accompanying it, would at once have shown him that he had to deal with a form of *Monascus*. As it was, while considering that it showed affinities with the Oomycetes, he constructed a new order, the Leptoomycetes, in which he included it with a few other little known Fungi, e.g. *Helicosporangium parasiticum*, Karsten, and *Papulaspora sepedonioides*, Preuss. To it he gave the name *Physomyces heterosporus*.

In the following year Brefeld (2) published his researches on *Ascoidea*, *Protomyces*, and *Thelebolus*, the results of which led him to consider these forms as intermediate between the Phycomycetes and the Ascomycetes, placing them accordingly in a new group, the Hemiasci. He suggested in a footnote the possibility of *Monascus* belonging to it. Into this group the genus *Monascus* seemed to fit naturally, judging from Van Tieghem's account. It was first definitely placed there by Schröter (19), who at the same time recognized that Harz's genus *Physomyces* was identical with *Monascus*. The order Leptoomycetes was therefore re-named by him Monascaceae, and in it were included the two species, described by Van Tieghem, together with *Physomyces heterosporus*, re-named *Monascus heterosporus*, *Helicosporangium*, Kars. and *Papulaspora*, Preuss., the two latter genera being included on the authority of Harz.

No new facts with regard to the genus were brought to light until 1895, when Went published a paper on 'Le Champignon de l'Ang-quac' (27). Ang-quac is a deep purple colouring matter prepared in China, and used in Eastern Asia for cooking purposes as a pigment. It consists of coloured powdered rice, the colour being produced by a fungus growing on the rice. Went isolated this organism and found it to be a new species of *Monascus*, naming it *M. purpureus* because of its characteristic colour. In studying its life-history he found several new and important facts in connexion with the development of the 'sporangium,' which the previous authors had not mentioned. The first stage consisted in the formation at the end of a hypha of two branches or cells, the one straight and apparently the terminal cell of the hypha, and the other formed just below it and slightly curving around it. The latter in course of growth continued to curve more and more, until the two were bent almost at right angles to the parent hypha. Went called the curved cell the ascogenous hypha, and regarded the straight branch as the first investing hypha. The ascogenous hypha then became divided into three cells by the



formation of transverse septa. The cell at the apex of the ascogenous hypha he called the terminal cell, the middle cell the sporangium, and the lower cell the pedicel. The latter proceeded to put out branches, which grew around the sporangium, completely enveloping it. At the same time, the sporangium itself was continually swelling up, reaching in some cases a diameter of  $75 \mu$ . The terminal cell and the first investing hypha were soon lost sight of, owing to the development of the other investing hyphae. During the enlargement of the sporangium its wall thickened and its protoplasmic contents passed through several striking changes. In the young sporangium the protoplasm contained several large vacuoles. These divided again and again until the protoplasm possessed a foam-like structure. Later it became very opaque, the vacuoles at the same time becoming exceedingly small, so that the interior of the sporangium could not be clearly seen. In the end the contents divided up into a number of spores. The exact moment of the division could not be discovered. While usually the whole of the sporangium was filled with spores, instances were occasionally met with where spores were only to be found in one portion of the sporangium, the remainder being filled with vacuolated protoplasm. When the surface of the mass of spores was carefully examined, no interstitial material was found between the spores, the latter presenting an angular appearance. The number of spores was variable, some sporangia containing only 6–10, while others contained from 150 to 500. When the spores were first liberated they retained their angular appearance, but soon assumed an oval shape. In size they were about  $5-6.5 \mu$ . Conidia were also produced soon after the formation of the perithecia. They resembled those described by the earlier authors. With regard to the systematic position of the fungus, Went, on Van Tieghem's authority, in the absence of the necessary literature placed it in the genus *Monascus*. He considered also that this genus ought to be placed among the Hemiasci, showing in particular much resemblance to *Thelebolus*. He also discussed

the significance of the first investing hypha mentioned above. From its position and period of development he considered that it showed certain correspondence with the antheridial branch of certain Ascomycetes, but, in view of the facts that it had not the constant structure of such organs and that its function, as far as he had observed it, was merely that of an investing hypha, he concluded that the relationship was not clear. He observed, however, that in certain cases a second perithecium was developed from it, thus resembling the sporangial formation in *Rhizopus*, and therefore suggested that it might be a rudimentary organ, the vestige of another sporangium, recalling the group of sporangia that is found in *Rhizopus*. The value of the ascogenous hypha seemed to him clear. The sporangium corresponded to the sporangium of the Mucorini in most instances, and the pedicel to the sporangial pedicel of the latter group. In those cases, however, where the sporangium contained but 8 spores, he considered that it approached the asci of the Erysipheae, and in particular the ascus of *Sphaerotheca*. In such cases the resemblance to the Erysipheae was so great that it might easily be mistaken for the perithecium of one of that group.

Recently Uyeda (23) published a paper dealing with the fungus of 'Beni-koji.' This substance is used in the preparation 'Anchū,' a fermented drink of Formosa. It consists of rice-grains infected with a pigment-producing fungus. The latter he found to be a species of *Monascus*. His results on the development and morphology of the 'sporangium' corresponded in essentials with those of Went. The size of the 'sporangium' was usually about 28-38.5  $\mu$  in diameter, and the number of spores 20-40, the latter being oval in shape and 5-6  $\mu$  in length by 4-5  $\mu$  in width. A dark-red pigment was produced by the fungus. Micro- and macro-conidia and intercalary gemmae were also formed. Uyeda believed the species to be identical with Went's *Monascus purpureus*.

## THE SYSTEMATIC POSITION OF MONASCUS.

Before attempting to discuss this point, in view of the results described in this paper, it seems advisable to examine the possibility that the fungus examined by me may merely bear superficial resemblances to the species of *Monascus* described by other authors, belonging in reality to an altogether different type.

Comparing it for the moment with *M. purpureus*, as described by Went, choosing this species on account of its more detailed description and illustration, the superficial resemblances between the two are extraordinarily pronounced, and, were not one in possession of the complete series of figures accompanying this paper, having instead in view merely such figures as Figs. 11, *a-d*; 13, *a*; 19, 33; representing intermediate and isolated stages, no hesitation would be felt in classing them together as members of the same genus or possibly even as identical Fungi. In each case the earliest stages of perithecial formation are represented by the formation of two branches at the apex of a hypha, the one straight and obviously the terminal cell of the parent hypha, and the other arising immediately beneath and curving around it. Then follows the division of the curved branch, the 'ascogonium' as it has been termed above, by transverse septa into two (or, as Went has it, into three) cells, leaving out of account for the time being the fusion which Went did not observe. The difference in the number of cells into which the ascogonium is thus divided is not of importance at this point, seeing that occasionally I found that a septum is formed across the parent hypha a little below the ascogonium, thus cutting off a cell which acts in every way similarly to the 'pedicel' cell of Went. After the division of the ascogonium by transverse septa the subsequent behaviour in both cases is for a time identical, this consisting in the swelling of the central or penultimate cell and the formation of investing hyphae from the 'pedicel' cell or the region of the parent hypha corresponding to it. After the full development of the investing



hyphae it is still possible in a few cases (see Fig. 19) to find a structure corresponding to that next described by Went, viz. a large sporangium-like cell invested by a wall of small hyphae. The resemblance then apparently would cease for a time were the two forms studied by series of microtome sections, owing to the formation of the internal hyphae as described above, although when viewed in the whole condition no difference would be seen. Finally, at the time of spore-formation the similarity of structure is again noticeable. The apparent angularity of the spores within the perithecium described by Went is very clearly to be seen in many cases, but I am convinced that the angularity is due to the optical effect of the arrangement of the spores under very high magnification. This can easily be verified by transverse sections in which the spores are then seen to be of the normal oval shape. The liberation of the spores is accomplished in each case by the breaking down of the perithecial walls.

After this analysis of the similarity of the two forms at different phases of the development, it will be admitted that there are strong reasons for supposing that the fungus which I have described here is closely related to *M. purpureus*. It yet remains to be shown, however, how the account of the sporangial method of spore-formation can be reconciled with the account given above of the formation of the spores in asci. That the latter method is undoubtedly the one made use of by the 'Samsu' fungus is obvious, as the accompanying figures show. Is there any possibility that it may also occur in *M. purpureus*, and that the earlier authors have overlooked it?

It has been shown earlier that the ripe perithecium bears an exceedingly strong resemblance to an invested sporangium. It has further been mentioned that the swelling of the central cell, the 'sporangium' of previous authors, can be traced for some considerable period during the development of the investing hyphae, and also that its further behaviour, when watched in the living condition, is then lost sight of owing to difficulties of observation. This is also admitted by the

previous writers. It has also been stated that the subsequent stages, visible in the living condition, consist of an apparent conspicuous vacuolization of the protoplasm of the central cell, and eventually the formation of spores within it. We have seen that the apparent vacuolization is due to the formation of much entwined hyphae, produced and practically surrounded by the much enlarged and curiously-shaped central cell; and that the spores are formed in small spherical asci arising from these internal hyphae. It has also been shown that these structures can only be seen at all clearly when the material has been suitably fixed and stained at all the different periods in the development of the perithecia.

It would not be surprising, therefore, if the earlier observers had overlooked these facts. From what has been brought forward it seems probable that they did overlook them, and this is rendered fairly certain from their papers and figures.

Considering Went's paper first, it has already been noted that, when the investing hyphae had formed a more or less complete covering to the central cell or 'sporangium,' the behaviour of the latter was obscured. In a few cases it was possible to observe changes in the protoplasmic contents of the 'sporangium,' which first presented the appearance of containing large vacuoles, this stage being followed by a somewhat similar phase in which the vacuoles were smaller and the structure more foam-like, these features in the end becoming so pronounced as to render the internal structure indistinguishable, which continued until spores appeared. Although the author searched carefully he was not able to discover the exact period or method of spore-formation. His figures, which accompany the paper, include examples of all these stages. Bearing in mind the fact that he was dealing with living material, we notice that the apparent structures of the 'sporangium,' which he has described, are in essentials identical with the stages observed above under similar conditions. But we have seen that the apparent vacuolization is really due to the formation of hyphal branches from the 'sporangium,' which organ has more or less surrounded them

owing to the exigences of the structure of the perithecium. The early large vacuoles are the first-formed hyphae, and the later small vacuoles are the numerous branches of various sizes arising from these hyphae. The confusing optical features of the mass of entwined hyphae are responsible for the opaque appearance noticeable later, while Went's failure to discern the moment and method of spore-formation is naturally due to the nature of the development of the spores in asci, they being under the surrounding conditions only clearly visible when fully formed. The apparent angularity of the spores, mentioned earlier, which gave rise to the idea that they were formed by cleavage of the protoplasm in the typical sporangial method of spore-formation—see Harper (11)—is, as already pointed out, merely an optical effect. But apart from Went's description his figures are sufficient to confirm the statements just made. His Figures 17 and 18 are practically identical with Figures 13, *a*, *b*, of this paper.

Perhaps, however, the most convincing proof is that which may be deduced from his statement that in some of the 'sporangia' he found spores in only one region, the remainder consisting of bands of protoplasm and vacuoles. Here it is clear that he had to deal with perithecia, in which the asci were not distributed throughout, but were grouped in one portion. The nature of the protoplasmic bands and vacuoles is obvious from the preceding.

Thus we find that Went's account is based on a misinterpretation of the observed facts, and that *M. purpureus* in all probability is a true Ascomycete with a perithecial formation similar to that of the 'Samsu' fungus.

Owing to the suggested identity between *M. purpureus* and the 'Beni-koji' fungus it is necessary to examine Uyeda's results to see if any fresh evidence is forthcoming in favour of the 'sporangium' view. It has been seen that this observer's results agreed entirely with those of Went. He gives, however, two figures (Figs. 9 and 10) which may be taken as representing stages not figured by Went, his insufficient description rendering it uncertain if they merely reproduce



the stages figured by Went in the latter's Figs. 20 and 22. Uyeda's Fig. 9 represents a section through a developing perithecium, showing a large 'sporangium' surrounded by a wall of hyphae. The 'sporangium' is undivided and filled with granular protoplasm. Apart from any question as to whether any 'internal hyphae' have been overlooked in this preparation, it may represent the stage shown in Fig. 19 of this paper, or it may represent a section through an older perithecium, in which none of the 'internal hyphae' have been included, a portion of the swollen central cell with its investment of hyphae being merely shown. Fig. 10 of this observer represents a section through a perithecium, similar in size to the preceding, but having the 'sporangium' completely divided into more or less angular areas. This, I suppose, represents the division of the protoplasm of the sporangium into spores, and may correspond to the stage which I have described above, where the ripe spores freed from the degenerated asci are lying within the perithecium and appear to be arranged in angular areas: but, judging from the figure, it probably represents the stage where the perithecium is entirely filled with dense entwined hyphae, shortly before the formation of the asci. There is then nothing in Uyeda's paper to lead one to suppose that the 'Beni-koji' fungus differs in any way from *M. purpureus*, and thus from the 'Samsu' fungus, in the nature and method of development of its perithecia.

Considering now Harz's paper on *Physomyces heterosporus*, seeing how closely his account of the structure and development of the 'sporangia' corresponds with the accounts given by Went and Uyeda for *M. purpureus*, it seems hardly necessary here to recount in detail the reasons for supposing that he was really dealing with a form of *Monascus*. It is true that he did not describe the earliest stages of perithecial formation in much detail, and that consequently no comparisons can be made as to the method of division of the ascogonial filament. But he stated that the earliest stages were represented by the formation of two or three small hyphae at the apex of a branch of the mycelium, and that

around these other hyphae springing from their bases were developed, so as to invest them. In the latter stages he gave a figure (Fig. 7) corresponding to Uyeda's Fig. 10, to which the same arguments can be applied as have been already given for the latter. It may then fairly be concluded that Harz's *Physomyces heterosporus*, or, as Schröter named it, *Monascus heterosporus*, forms its perithecia in the same manner as *M. purpureus*.

With regard to the two species described by Van Tieghem, *M. ruber* and *M. mucoroides*, there is not a great deal to be said. We have this observer's authority for considering *M. purpureus* as a member of the same genus, and from this fact it might be deduced that he had fallen into the same error as the subsequent authors. There is not the same amount of evidence at hand, however, since no figures accompany his paper. It is of course quite possible that the Fungi described by him possess the structure which he attributed to them, but, in view of the subsequent errors in connexion with apparently similar forms, one has considerable reason for concluding that these two species are allied to the 'Samsu' fungus.

Having now examined the relationships of these various forms to one another, and having seen that there are the strongest grounds for regarding them as members of a single genus, there remains yet another point to be discussed before the characters of this genus are set forth. It concerns the behaviour and function of the structure which has been termed above the 'antheridial branch.'

It has been shown that a fusion occurs between this organ and the ascogonium, preceding the development of the latter with its subsidiary structures into the perithecium, and that this fusion is probably accompanied by a passage of nuclei from the former into the latter, and subsequent nuclear fusion in the latter: in other words, that a sexual act takes place between the antheridium and the ascogonium. Harz and Van Tieghem have not described any definite organ corresponding to the antheridial branch, doubtless having observed it and regarded it as one of the first-formed investing hyphae.

Went and Uyeda, however, have seen and described it; and, although the former pointed out its similarity to the antheridium of certain Ascomycetes, he failed to discover the fusion between it and the ascogonium, and suggested instead that it might be a rudimentary organ, the vestige of another sporangium. Both considered that in the present case it served as nothing more than the primary investing hypha.

It seems likely that these observers have overlooked the fusion. It has been seen that the fusion is almost invisible at the time of its occurrence even under the highest powers of magnification, except in rare instances. At the time when it becomes visible, i. e. when the central cell has become much enlarged and the investing hyphae formed, they seem to have lost sight of the structure. In fact, Went stated that it was hidden by the other hyphae. These reasons, together with the significance of its constant occurrence, its time of formation, and its position, warrant us in regarding it as a true antheridial branch, and in believing that, apart from a few possible exceptional cases, in which the ascogonium may develop further parthengentially, fusion takes place between it and the latter organ. There can be no doubt in view of Went's discussion of its significance that this author would have regarded it as an antheridium, had he observed the fusion.

A minor point of interest is that which concerns the division of the ascogonium after fertilization. Both Went and Uyeda found that it became divided into three cells—the terminal cell, the 'sporangium,' and the pedicel. From the latter the investing hyphae arose. In the 'Samsu' fungus, on the other hand, only two cells are formed—the terminal cell, which includes the place of fusion, and the central cell, corresponding to the 'sporangium.' The investing hyphae arise from the region of the present hypha immediately below the latter.

From the figures of these authors I have no reason to suppose that their account of the origin of the pedicel is not generally correct. Its size and position certainly appear to



bear out their statement that it is cut off from the ascogonium. As stated above, I have found occasionally a cell cut off below the ascogonium which behaves in the same way as their pedicel, but it is merely a cell cut off immediately below the ascogonium, and has not constituted a portion of that organ. It is also not so conspicuous as their pedicel. In one or two instances figured by Went, however, his 'pedicel' cannot have the origin ascribed to it, and is in those cases nothing more than the cell of the parent hypha immediately below the ascogonium.

If their accounts be taken as correct for the majority of cases at least, we have in *M. purpureus* to deal with a more specialized form of perithecium than in the 'Samsu' fungus, a point which at once separates the two forms into different species; whereas if their 'pedicel' has really an origin similar to that in the somewhat rare instances just quoted, it is highly probable that the two Fungi are members of the same species. Since they have not given figures of the successive stages in the development of a single perithecium, such as could be obtained by observations of hanging-drop cultures, it is impossible to make a more definite statement as to the identity of the forms.

We are now in a position to state in detail the characters of the genus *Monascus*.

The mycelium consists of much-branched, septate hyphae, which produce at certain periods two kinds, at least, of reproductive organs. The asexual organs are usually spherical or ovoid bodies, formed as a rule basipetally at the ends of branch hyphae in chains of varying lengths. They are usually colourless, but, after the formation of pigment has begun in the mycelium, they may be slightly tinged with the corresponding colour. Sexual reproduction results in the formation of ascogenous hyphae. An archicarp, consisting of an ascogonial branch and an antheridial branch, is formed usually at the end of a hypha, the former arising immediately below the latter and proceeding to grow above and around it. Both are cut off into distinct organs from the parent hypha by the

formation of septa, the antheridial branch being usually the former apex of the parent hypha. Fusion then takes place between the two organs, followed probably by migration of nuclei from the antheridium into the ascogonium and subsequent fusion of these with the nuclei of the latter. The fertilized ascogonium then divides into a terminal cell and a central cell by the formation of a transverse septum, and possibly in some instances a third cell, the pedicel, is also cut off. The central cell begins to swell considerably, and becomes invested by hyphae, arising immediately beneath it, either from the parent branch or from the pedicel, when the latter is present. After swelling, the invested central cell produces one or more hyphae which develop vigorously and produce a mass of entangled ascogenous hyphae, which displace it to a certain extent, causing it to completely envelop them and to become closely adpressed to the enclosing investing hyphae. The latter soon become much flattened out and lose their contents, being represented in the later stages by a mere reticulum of brown cell-walls around the enlarged central cell. Asci are eventually produced from the ascogenous hyphae, and in each of them eight ascospores are usually formed. When the spores are ripe, the asci and ascogenous branches degenerate, the surrounding central cell having by this time lost its contents, remaining as a brown cuticularized enclosing wall. The spores are thus liberated into the cavity enclosed by this wall, and the ripe perithecium appears to be nothing more than a brown cuticularized sporangium-like structure. From it the spores escape by the degeneration of its walls. The number of spores is very variable. They are spherical or ovoid in shape, and possess thick walls. They are more or less red, brown, or orange in colour, and possess a very characteristic refringent appearance.

From this description it follows that the genus must be placed among the Ascomycetes. At the same time it does not very clearly fall into any well-defined group on account of the curious behaviour of the central cell and the incomplete character of its investment. At various stages of its develop-

ment it presents interesting resemblances to several types. Unfortunately there are but few instances in which the development of the ascocarp has been followed step by step from the earliest stages, so that the range of comparison is very limited.

The archicarp is strikingly similar to the archicarp of certain species of *Peziza*, e.g. *Peziza scutellata* as described by Woronin (29): and in those instances in which the ascogonium curves spirally around the straight antheridial branch it recalls the archicarp of *Penicillium*—see Brefeld (3)—and many Gymnoascaceae. The young perithecia resemble the young perithecia of *Sphaeria Lemanea* and *Sordaria coprophila* (30), and the similarity between the enlarged ascogonium of these forms and the developing central cell may also be pointed out. If the development of asci were to occur in the young perithecia of these forms, an ascocarp almost identical in structure with that of *Monascus* would result.

The mature perithecium with spore-containing asci is somewhat similar in structure to those of the Aspergillaceae and the multi-ascal Erysipheae.

None of the Fungi just mentioned can be classed with it throughout the complete course of the development of the perithecium, the Pezizineae and the Sphaeriales separating themselves by the structure of the mature perithecium, and the Erysipheae and Plectascineae by the method of development of the ascogonium after fertilization.

Its points of resemblance to so many widely separated groups of Ascomycetes are of particular interest when viewed in conjunction with the fact of the undoubted simplicity of the ascocarp in structure and development.

There are several features which indicate the simplicity of the genus. One of the most noticeable is the want of differentiation and of specialization of the antheridial branch and the ascogonium, shown in so many anomalous cases. Under certain conditions any living cell of any hypha of the mycelium seems to be able to take on the functions of an antheridium, and the cell immediately beneath it to produce



the ascogonium in the normal manner, further development taking place quite normally. Often, too, a normally produced antheridium, after functioning as such, proceeds to develop ordinary vegetative hyphae or conidia; while, less often, even the ascogonium or, more accurately, the terminal cell of the ascogonium behaves similarly. There is thus shown a want of constancy in the position of development and in the specialization of the sexual organs which seems to point to their primitive nature, as compared with the more strongly defined archicarp of other Ascomycetes.

The mature ascocarp is also in reality of very simple structure. While apparently a cleistocarp, as in the Erysipheae, it is actually only of that nature because of the curious development of the central cell. The exterior investment of hyphae is very incomplete and scanty, and the whole of the hyphae within the ascocarp are ascogenous and arise from the fertilized ascogonium. The extent of the development of the ascogenous hyphae themselves is also very small, speaking comparatively, and variable, and the same holds good for the number of asci.

The sexuality of the archicarp is also little developed. The male and female organs arise not only from the same hypha, but also from the same cell of it, and therefore probably the male and female nuclei have their origin from the same nucleus or nuclei with the intervention of but few generations. The method of reproduction by conidia is also very simple. No specialized conidiophores are developed, any hypha being capable of producing conidia, these being formed simply by the formation of a wall just behind the apex of the hypha and the swelling of the terminal cell thus cut off.

The primitive nature of the ascocarp has just been mentioned. Leaving out of account the complexity introduced by the behaviour of the enlarged central cell, it is clear that the asci must be regarded as being devoid of a complete investment of sterile hyphae. The comparatively feeble development of investing hyphae would be quite insufficient

to enclose the asci without the aid of the central cell. Viewed from this point of view, the ascocarp seems to be of the same nature as those of the Gymnoascaceae. A relationship to this group is also indicated by the shape, size, and method of development of the asci, and by the number and size of the ascospores. The archicarp is also very similar to that of *Gymnoascus Reessii*. In both forms the antheridium is typically a short straight hypha around which is coiled more or less the ascogonium. Fusion takes place between these organs, and the ascogonium subsequently develops further by producing a short branch, which gives rise to the ascogenous hyphae<sup>1</sup>.

While these facts point to a relationship to the Gymnoascaceae, there are certain features which are opposed to the idea of a very close connexion with this group. In the first place the investing hyphae of *Monascus* are only partially comparable to those of the Gymnoascaceae. In the former they arise from a definite point, i. e. immediately below the central cell; in the latter this is not so markedly the case. In the former also they grow closely applied to the ascogonium, resembling rather the earliest sterile hyphae of the ascocarps of the Aspergillaceae, Erysipheae, Sphaeriales, and Pezizineae; while in the latter the investment as a whole is of a comparatively loose character. Attention may here, however, be called to the curious development of small branched clasp-like hyphae from the hyphae bearing the archicarp, at some distance below this structure (see Fig. 14), and even in some cases from neighbouring hyphae. They may serve to show a possible connexion between the investments in the cases under consideration. A second difficulty is the nature of the ascogonium. In *Monascus*, although filamentous when first formed, after fertilization it swells considerably, becoming more or less spherical before the production of ascogenous hyphae. In the Gymnoascaceae it remains unchanged throughout; in some cases, e.g. in *Ctenomyces serratus* and *Gymnoascus*

<sup>1</sup> I have obtained the facts concerning *Gymnoascus* from Miss Dale, whose paper on the subject has not yet been published.

*candidus*, dividing into several cells, from which the ascogenous hyphae spring, and in other cases, e. g. in *Gymnoascus Reessii*, growing directly out into a branch, from which the ascogenous hyphae arise. The ascogonium of *Monascus* therefore resembles the enlarged more or less spherical ascogonia of the Sphaeriales and Pezizineae much more than those of the Gymnoascaceae.

While these considerations tend to place it outside the Gymnoascaceae, there is nevertheless no other group of Ascomycetes in which it could be placed.

From the lower genera, such as *Endomyces*, *Eremascus*, *Exoascus*, and *Ascocorticium*, it is at once distinguished by the formation of an ascocarp.

From the Pyrenomycetes, Discomycetes and the higher Plectascineae it is distinguished by the relatively simple ascocarp.

Of the Fungi just mentioned the ripe ascocarps of the Aspergillaceae and the Erysipheae appear from a surface view to resemble strongly those of *Monascus*. Their internal structure is also very similar, if compared with the latter at the stage when the central cell is indistinguishable from the cutinized investing hyphae and the interior is filled with a mass of tangled hyphae and asci.

The study of the method of development in each case shows, however, that this similarity in structure is of no value as indicating a close relationship between these forms. The whole of the structures within the ascocarp of *Monascus* have their origin from the ascogonium, and are of the nature of ascogenous hyphae and asci. In the other forms sterile hyphae not of ascogonial origin are mingled with the ascogenous hyphae and asci.

There is a certain amount of similarity also between the archicarps of these forms. Very little is known about these structures in the Aspergillaceae, but the resemblance shown by that of *Penicillium* has already been mentioned. In this case, however, it has not yet been shown that fusion takes place between the sexual organs. The ascogonium moreover



divides into several cells, from each of which ascogenous hyphae arise.

In the Erysipheae the ascogonium and antheridium arise from different hyphae. Otherwise they are very much like those of *Monascus*. The ascogonium, however, divides into several cells after fertilization, some or all of which produce asci.

The points of resemblance shown by the other Ascomycetes are confined to the archicarp and the earliest stages in the development of the ascocarp. The mature ascocarp of these forms, whether of the Discomycetous or Pyrenomycetous type, is a much more complicated and highly developed structure.

The archicarp of *Peziza scutellata* has already been referred to. Woronin (29), who has described it, found that the terminal cell of a short hyphal branch became somewhat enlarged, while from the cell immediately beneath it a small hypha was developed which grew around the former, becoming closely applied to it. He surmised that the former was the 'egg-cell' or ascogonium, and the latter the antheridium. The behaviour of the two structures was soon obscured by the development of investing hyphae, a perithecium eventually resulting. There is thus very little direct evidence to warrant the assumption that they represent sexual organs or that they retain their sexual functions: but in view, in particular, of Harper's work on *Pyronema* (10) and the Erysipheae (9), and also of the results of other observers, all of which tend to show that the archicarp is an organ of a sexual nature, although perhaps not necessarily always functional, to which the ascocarp owes its origin, these structures described by Woronin become invested with considerable significance and can fairly be looked upon as constituting an archicarp.

If the enlarged cell be regarded then as an ascogonium and the smaller hypha arising immediately beneath it be taken as an antheridial branch, the similarity to the corresponding structures of *Monascus* is very pronounced, since in both cases they are developed in close contact at the apex of a short branch. It is true that in the former case the antheri-

dial branch arises below the ascogonium, whereas in *Monascus* it forms the apex of the branch, the ascogonium being developed beneath by the formation of a new growing-point at that spot. This difference, however, is probably of no great importance, since it is merely a matter of the time of development. Where two or more structures are formed at the end of a hypha, it is the first-formed which appears to constitute the apex of the branch, and the others appear to arise below it. In reality, however, they are all terminal. It is thus with the cases in point, and in both instances eventually the ascogonium by its superior development assumes the apical position, the antheridial branch appearing to arise below it, although in *Monascus* the latter was really first formed.

Of the subsequent development of the ascocarp from the archicarp in *Peziza scutellata* we have insufficient details for further comparison. Fortunately, however, the complete series of changes in the case of *Pyronema confluens*, a member of the same group, is available for comparison owing to the successful and complete work of Harper (10).

This fungus differs from the former in having the antheridia and ascogonia developed on different hyphae. A slender filamentous hypha, the trichogyne, is formed as an outgrowth from the ascogonium, and fusion takes place at its tip between this and an antheridium. Nuclei then pass from the latter through the trichogyne into the ascogonium and there fuse with the nuclei of that organ. A wall is then formed cutting off the ascogonium from the trichogyne. The nuclear fusions take place during a period in which the nuclei are aggregated closely together towards the centre of the ascogonium, the outer portion of which is for the time being almost devoid of nuclei. While these processes are occurring, the neighbouring hyphae branch freely and form a close investment around the ascogonium, or rather, since these organs are usually produced in rosettes or groups, around the whole group. The ascogonium then produces numerous outgrowths, which grow out between the investing hyphae and form the ascogenous hyphae. These eventually arrange themselves in a more or

less definite layer, intermingled with and surrounded by the sterile hyphae, and eventually produce at their tips the elongated asci, the whole fructification having by this time assumed the characteristic cup-like form.

Comparing it with *Monascus*, the main point of difference from the latter is the occurrence of the sexual organs on distinct hyphae, which necessitates the formation of a trichogyne. The fusion between this and the antheridium corresponds with the fusion between the tip of the ascogonium and the antheridial branch in *Monascus*. The passage of male nuclei then takes place in both cases, followed also by the aggregation of the mixed sexual nuclei in the ascogonium.

In both cases also the ascogonium is cut off from the antheridium by the formation of a wall; in the case of *Pyronema* at the base of the trichogyne, and in the case of *Monascus* across the ascogonium just behind the place of fusion. The apical portion, i. e. the terminal cell, of the ascogonium in *Monascus* may be therefore considered as equivalent to the trichogyne of *Pyronema*. The nature of the fusion in both cases is very similar. The fusion is in no way complete as is the case, for example, where two hyphae fuse to form a zygospore. The two fusing structures maintain their individuality, and the opening between them is no more than a small pore, just sufficiently large enough to allow of the passage of nuclei.

During the period of nuclear aggregation in *Pyronema* the fusions between the sexual nuclei occur. The occurrence of a similar period in *Monascus* makes it seem likely that the sexual nuclear fusions, which almost undoubtedly occur, take place during that time. At the end of this stage the ascogonium in each instance puts out one or more branches, the ascogenous hyphae, which ramify to a greater or less extent and eventually produce asci. The investing hyphae in *Pyronema* are much more strongly developed than in *Monascus*, but in both cases the ascogonium itself is closely invested, differing in this point from the Gymnoascaceae.

Thus, although *Pyronema confluens* differs from *Monascus*



so considerably in the structure of the archicarp and of the mature ascocarp, the processes leading to the formation of the latter correspond very closely in the two forms and suggest a common origin: and if the cytological behaviour of the former is characteristic of the other Pezizineae, *Peziza scutellata* is still more closely allied on account of its simpler archicarp.

The Sphaeriales also seem to be allied in a somewhat similar manner. Woronin (30) has described structures in *Sphaeria Lemanea* and *Sordaria fimiseda* which must be regarded as the archicarps of these forms. The ascogonium is an enlarged spherical cell, to which is closely applied a smaller hypha, arising in the former from another and in the latter from the same branch of the mycelium, which seems to be the antheridial branch. Around these numerous coiled hyphae arising from the neighbouring portions of the mycelium grow closely applied, and a small spherical mass is thus formed. By the further development of this the characteristic perithecia are produced. The behaviour of the archicarp during this development is unknown, but it is surmised by analogy with *Pyronema* and other forms that it corresponds to a certain degree with these. If this be the case, the relationship suggested between the latter and *Monascus* would also hold good for them and other Sphaeriales.

These considerations point to the view that *Monascus* represents a low and comparatively simple type of Ascomycete and is not far removed from a common ancestral type, from which all the higher Ascomycetes may be supposed to have sprung. The latter are separated into distinct families by the structure of the mature ascocarp only, and there seems to be no essential difference in the nature of the reproductive organs themselves. The discovery of the archicarp or of vestiges of this structure in members of the different groups seems to indicate that the ancestral Ascomycetes possessed functional sexual organs, the ascogonium and the antheridium, the fertilization of the former by the latter resulting in the development of asci by the formation of a more or less complicated system of asco-

genous branches from the former. The sterile hyphae, which form the investing hyphae and contribute so largely to the actual vegetative portion of the ascocarp in the higher Ascomycetes, may be regarded as a secondary development, affording the ascogenous hyphae a better opportunity of producing asci successfully: and it is the form taken by their development which determines the form of the mature ascocarp, and therefore serves to create the distinctions which characterize the various families. In *Monascus* we have a form that approaches very nearly this supposed ancestral type. It possesses antheridia and ascogonia which are fully functional, though simple in type and not highly differentiated, being in fact typical of a primitive form. The investing hyphae, moreover, are very subordinate, the investment being rudimentary as compared with those of the higher Ascomycetes, while the formation of subsidiary clasping hyphae (see Fig. 14) on the lower part of the hypha bearing the archicarp and on the neighbouring hyphae may be considered as a primitive form of the much more highly developed investment of the other types. It may be urged that these structures are vestiges, and that the fungus is a much reduced form, but the complete retention of sexuality together with the feebly differentiated nature of the sexual organs seems to be entirely opposed to this idea.

The gap which separates *Monascus* from the supposed ancestral type is small. The distinguishing features are the occurrence of investing hyphae and the envelopment of the ascogenous hyphae and asci by the enlarged central cell. An explanation of the development of these features may perhaps be arrived at by a consideration of their probable functions. The investing hyphae in the higher Ascomycetes undoubtedly serve to protect the ascogenous hyphae and also the ascogonium, while producing them. This function also seems to be exercised by them in the case of *Monascus*, although by the nature of the structure only the ascogonium is directly protected, and that incompletely. The cutinization of their walls in the later stages of the development of the

ascocarp, and the manner of their arrangement around the central cell, certainly serve however to maintain the developing asci in a position of security within the cavity of the perithecium. Another possible function is suggested by the analogy of the investing hyphae to the auxiliary cells of the Florideae, a relationship of the Ascomycetes to this group having been considered likely by many authors. The function of the auxiliary cells seems to be that of supplying nourishment to the growing sporogenous ooblastema filaments. The investing hyphae may therefore serve to supply nutrient material to the developing central cell, and thus indirectly to the ascogenous hyphae, although no fusion takes place between them and the central cell as is the case between the ooblastema filaments and the auxiliary cells. The close application of the investing hyphae to the central cell doubtless renders fusion unnecessary.

If these are the functions of the investing hyphae generally among the higher Ascomycetes, and in a correspondingly less degree among the lower forms in which these structures are not so well developed, one would expect to find them performed in the latter instances to some extent by the ascogonium itself. The peculiar shape taken by the developing central cell in *Monascus* has already been mentioned above on several occasions. A little consideration shows that this shape is the one most suited to carry out the combined functions of protection and nutrition for the growing ascogenous hyphae. The protective function is undoubtedly utilized, for after it has shrunk and its walls have become cutinized the young asci are completely enclosed in the resistant envelope thus produced by it. It exercises naturally a nutritive function, since the ascogenous hyphae arise directly from it. But this is exerted in an increased degree by the method of arrangement of these hyphae in relation to it. They are so arranged that they are in close contact with it from the moment of development, and the young vigorously growing tips appear to actually press into it, the cavity eventually becoming enlarged by this means. With such



close contact the transference of nourishment from the central cell can be carried out with much greater ease than by its passage from that organ through the whole length of the ascogenous hyphae to the growing-points. Of course in the older perithecia such close contact no longer obtains, the hyphae themselves forming a somewhat considerable mass, but it is noticeable that at comparatively late stages the central cavity seems still to owe its enlargement to the burrowing of the youngest hyphae into the central cell.

An adequate explanation is thus furnished of a unique and mysterious perithecial structure. This view explains why the first formed ascogenous hyphae do not grow out through the gaps in the reticulum of investing hyphae, but remain closely attached to and hollowing out the central cell. This most important point is apparently inexplicable except by the hypothesis just suggested; and thus fresh emphasis is laid upon the already well recognized idea that asci can only be formed by young and vigorous hyphae, which moreover can only be raised to and maintained in that condition by an abundant supply of nutriment. Perhaps some light is thrown on the nature of the required nutriment in this instance. The ascocarps are by no means always formed on aerial branches: indeed they are often completely submerged in the culture medium. When the food supply in this begins to get low, the formation of ascocarps begins. If it be the ordinary form of food that is required to keep the ascogenous hyphae in a sufficiently vigorous condition, why do they not grow out into the surrounding medium and obtain the available food, instead of trusting to the more difficult mode of supply from the central cell? It seems as if the required nutriment is a substance or substances, manufactured by the fungus from the raw food material supplied by the substratum.

The view put forward here, then, is that *Monascus* is a simple sexual Ascomycete, showing the relationships to the higher forms that may be expected to exist between lowly and highly organized genera of common origin, and at the

same time presenting but few features to distinguish it from the supposed ancestral types, these being, moreover, such as serve for a more successful production of ascospores.

#### GENERAL CONSIDERATIONS.

There arise in connexion with this view two questions which must be considered.

Firstly, in what relation does *Monascus*, as representing a type not far removed from the ancestral type, stand to the lower Ascomycetes? And secondly, does *Monascus* for the same reason afford any indication of the origin of the Ascomycetes from the lower Fungi or from the Algae?

These questions can perhaps best be dealt with in conjunction.

The nature of the sexual organs suggests at once a connexion with the Oomycetes, an idea already familiar through the theory of De Bary (5) as to the relationship of the various groups of Fungi. The antheridia and oogonia of this group correspond very well with the antheridial branch and ascogonium of the archicarp of *Monascus*. Although in most forms the sexual organs are produced on different branches, yet in some cases, e.g. most Saprolegniaceae, they are borne on the same branch, the antheridia arising immediately below the oogonia. Fertilization takes place in most cases, the antheridium becoming closely applied to the oogonium and sending into it a tube which penetrates through the periplasm and then empties the contents, in whole or in part, of the antheridium in the neighbourhood of the oosphere. After fusion of the sexual gametes, the fertilized oospore becomes invested with a thick resistant wall, to the formation of which the periplasm contributes largely. After a period of rest the oospore germinates; in some cases, e.g. *Albugo candida*, producing zoospores directly, i.e. becoming converted directly into a zoosporangium; in other cases, e.g. *Phytophthora omnivora*, De Bary (6), forming a short promycelium, which produces a few conidia, the contents of each of which divide into eight zoospores; and in many other cases forming the ordinary

mycelium of the fungus, on which conidia, or zoosporangia, and sexual organs are formed. An alternation of generations is thus presented by the life-history of some of these Fungi. In every instance the ordinary mycelium of the plant represents the gametophyte, while the sporophyte is represented in such forms as *Phytophthora omnivora*, De Bary, by the promycelium, and in such forms as *Albugo candida* by the oospore itself, being unrepresented in the third case quoted above. Owing to the great diversity in behaviour shown by the members of the group from the period of fertilization onwards, it is difficult to select one particular form as a type for comparison with *Monascus*; but there can be no doubt of the relationship of the various members of the group to one another, and therefore a general comparison will serve.

Starting with the formation of the sexual organs, the first point of difference is the formation of a special egg-cell or cells in the Oomycetes, no differentiation of such a structure being apparent in *Monascus*. Some or all of the nuclei of the ascogonium of the latter are, however, in all probability fertilized by the male nuclei, and these may hence be regarded as functionally similar, although apparently undifferentiated. The papilla of the antheridium of the former group, which penetrates through the periplasm of the oogonium to fertilize the oospheres, has perhaps its analogue in the small papilla produced by the antheridium of *Monascus* at the time of fusion between this organ and the ascogonium. The different degree of development in the two cases may be due to the fact that in the former the oospheres are specially rounded distinct bodies lying within the periplasm, and therefore not so easily reached by the male elements as the female nuclei of the latter, distributed evenly in the undifferentiated protoplasm of the ascogonium. After fusion in *Monascus* a special fertilized cell, the central cell, is cut out of the ascogonium, the term 'fertilized cell' being here used in the sense described by Harper (10) for the corresponding structure in *Pyronema*, and it is then equivalent to the oospores of the former. Instead, however, of becoming clothed with a specially



thickened wall and passing through a long period of rest, as is the case with them, it proceeds at once to swell up considerably and produce ascogenous hyphae. This process must be regarded as the germination of the fertilized 'cell' and the beginning of the sporophyte generation: and therefore corresponds with the germination of the oospore and the production of the promycelium of such a form as *Phytophthora omnivora* De Bary. The generation of the sporophyte is terminated in the one case by the formation of ascospores in asci, and in the other case by the formation of zoospores in sporangia. The germination of these spores in the respective instances gives rise to the gametophyte. A difference is shown in the time of germination; the zoospores, which are naked masses of protoplasm, germinating immediately after coming to rest and clothing themselves with a cell-wall, while the ascospores, which are thick-walled resistant bodies, are specially prepared to pass through a period of rest during unfavourable external conditions before germination at a suitable time. Thus the functions of the oospores are not assumed by the fertilized 'central cell,' but are passed on to the ascospores. The shifting of the period of the resting stage of the organism here indicated suffices to explain the differences of organization of the female 'cells' in the respective cases, and renders the parallel behaviour of the respective Fungi as regards the course of their life histories much closer than appears structurally. Leaving out of the question the differences which may be taken as arising naturally from the delegation of the function of hibernating to different structures in the two cases, there is a remarkable degree of resemblance in the manner and the course of the reproductive processes of these Fungi, so widely different in habit and in the structure of the mycelium. It is certainly sufficiently marked to make the idea of relationship likely.

A further point of resemblance between *Monascus* and the Oomycetes is the nuclear behaviour during the reproductive processes. It has been shown that in *Monascus* several nuclei from the antheridium probably pass into the ascogonium and

there fuse in pairs with female nuclei as in *Pyronema*. Probably also there is an excess of female nuclei in the ascogonium, which remain unfertilized and eventually degenerate. The nuclei which remain in the terminal cell after the cutting off of the central cell can certainly be regarded in this light, and perhaps, too, some of the nuclei enclosed in the central cell come under this heading. Stevens has shown that in *Albugo Bliti* (20) and *Albugo Portulacae* (21) numerous male nuclei pass into the oogonium and fuse in pairs with female nuclei, while other nuclei of the oogonium remain unfertilized in the periplasm.

It is therefore necessary to examine more closely the details of these various features to determine, if possible, whether it is merely a case of parallel behaviour or whether a definite relationship is indicated.

The members of the Oomycetes which show a marked alternation of generations by the formation of a promycelium, e. g. *Phytophthora omnivora*, De Bary, and *Pythium proliferum* (6), are those which approach most nearly the simple sexual Ascomycetous type, of which *Monascus* is an example. In the above parallel the ascus of the latter is equivalent to the zoosporangium of the sporophyte generations of *Phytophthora* and *Pythium*. From a type similar to these forms the Ascomycetous type represented by *Monascus* could be derived by the suppression of the differentiated oospore stages and the transference of its hibernating function to the zoosporangia of the sporophyte, these structures becoming much more definite, owing to the acquirement of that function, and producing only a small limited number of resistant spores. Among the difficulties standing in the way of the acceptance of this hypothesis are the difference of the mycelium in the two instances, the lack of differentiation of the zoosporangia of the sporophyte from those of the gametophyte, the different methods of spore-formation in sporangia and asci, and the lack of intermediate forms.

Considering these in turn, the difference of the mycelia consists in the absence of septa, except in the reproductive

organs, in the Oomycetes and their presence in *Monascus*. The cells of the latter are, however, multinucleate; consequently the mycelium cannot be looked upon as very highly differentiated. Other Ascomycetes, e. g. *Erysiphe*, moreover, possess mycelia consisting chiefly of uninucleate cells. Others, e. g. *Exoascus*, have very much reduced mycelia. There is thus shown in the group of Ascomycetes itself a difference in the character of the mycelium at least as great as that between the two cases that are being considered.

The apparent similarity of the zoosporangia of the sporophyte and gametophyte of *Phytophthora omnivora* seems to make the ascus, which belongs clearly to the sporophyte, equivalent to a typically gametophytic structure. If, however, in this species the promycelium is regarded as an elementary form of sporophyte—and it has been viewed thus in the present discussion—there is a theoretical difference between the zoosporangia produced by it and those produced by the gametophyte. The delegation of the special functions of the ascus to the former would cause also a morphological distinction, so that the ascus is strictly comparable only to them. The others have their analogues in the conidia of the Ascomycetes, for both are products of the gametophyte, and among the Oomycetes conidia and zoosporangia are homologous. Harper (11) has pointed out the difference in the methods of spore-formation by cell-division in sporangia and asci. In the former the protoplasm divides directly by simple fission; in the latter a gradual aggregation of the protoplasm around each nucleus occurs. In the sporangium there is thus no epiplasm, while in the ascus it is always produced. He regards these facts as showing that there is no genetic relationship between sporangia and asci. Since the zoospores of a zoosporangium are formed by the fission method, the same objection may be raised against the homology of this type of sporangium also with the ascus. Juel (15), however, believes that the gap between the Phycomycetes and the Ascomycetes is not so wide as indicated by Harper's results, owing to the presence of periplasm in the oogonia of the Peronosporaceae, the process of the formation



of the oospheres affording a link between the processes typical of spore-formation in sporangia and asci. It is true that it may be urged against this view that the oogonium is not homologous with the ascus or with the sporangium, and that if the two latter structures be regarded as truly homologous the gap between them remains therefore as wide as before; but it is certainly shown that in some Oomycetes there exists a method of spore-formation, although not occurring in homologous structures, which is to some extent intermediate.

Stevens (21) has shown that in *Albugo Bliti*, *A. Portulacae* and *A. Tragopogonis* the method of formation of the oosphere in the oogonium is as follows:—

The protoplasm of this organ becomes much vacuolated, clumps of denser protoplasm being distributed irregularly among the more vacuolated substance. These clumps increase in size by fusion, and eventually a single dense mass, the gonoplasm of De Bary, is formed in the centre of the oogonium surrounded by the vacuolated periplasm. The nuclei are at this stage arranged in a ring around the gonoplasm in the inner portion of the periplasm. They divide, and one or more of their daughter-nuclei enter into the gonoplasm and there fuse with the male nucleus or nuclei. It is remarkable that the sharp differentiation between the gonoplasm and the periplasm seems to be associated with the zonation stage of nuclear arrangement. Karyokinetic division of the nuclei occurs at this time simultaneously, and it seems as if this division has some connexion with the final cutting out of the oosphere. Perhaps the kinoplasm of the spindles acts in combination throughout the whole region of zonation and cuts out the compound oosphere in a manner somewhat similar to that by which the ascospores are cut out by the radiating kinoplasmic threads of the asters, which has been shown by Harper (11) to be typical of the formation of spores in asci. At any rate the processes are similar up to a certain point; for in each instance the oosphere or the ascospores are formed from a dense protoplasmic mass which gradually collects at one point in the mother-cell and is distinguished from a differentiated,

less dense and more vacuolated protoplasm, and with which eventually become associated the nucleus or nuclei which produce the nuclei of the spores. The occurrence of nuclear divisions during the period of protoplasmic differentiation is also typical of both groups. The results of Wager (25 and 26), Trow (22), Berlese (1), and Miyake (28) on various other Oomycetes also agree in most details; but the zonation stage of the nuclei is not so marked, nor is the protoplasmic aggregation so pronounced in the early stages. As Stevens remarks in connexion with *Albugo candida* (21), it is the absence of this preliminary aggregation which precludes the early marshalling of the nuclei into the form of a hollow sphere.

There are then many points in common between the methods of formation of oospheres in the Oomycetes and of ascospores in the Ascomycetes, and further investigation may reveal even closer resemblances in the behaviour of the karyoplasmic threads during the final mitosis during oogenesis in the former. The hypothesis that the oogonium has been evolved from a gametangium, which has been considered by Stevens (21), makes those somewhat allied methods of spore-formation of great interest in conjunction with the hypothesis of the homology of the ascus with the zoosporangium. If it be assumed that antheridia and oogonia are homologous with gametangia, it is no great step further to admit the evolution of asci from zoosporangia, seeing that among the lower Algae gametangia and zoosporangia are in many cases identical. The view of Harper may therefore not be of such importance as at first appeared, especially when it is considered that the structures which show similarity in method of spore-formation also produce spores of a similar physiological character, the presence and survival of the periplasm being thus explained.

The lack of forms intermediate in character between Oomycetes of the type of *Peronospora omnivora* and Ascomycetes of the type of *Monascus* is a point of some importance because of the width of the gap separating these forms. The lower Ascomycetes, apart from the Gymnoascaceae, are distinguished by a complete loss of sexuality or by its isogamous character,

and the Hemiasci with one exception, viz. *Dipodascus*, appear to be asexual organisms. The likely forms are thus limited to *Dipodascus*, the heterogamous Gymnoascaceae, and perhaps the Erysipheae. The features which ought to be specially noticed are the extent of the development of the sporophyte and the nature of the asci. The sporophyte in *Dipodascus* is very little developed. According to Juel (15) and Lagerheim (16) the 'sporangium' is formed by the fusion of two very similar hyphae. One of these, which is regarded as the female branch, then continues to grow considerably in length, and a large number of spores are eventually formed in this outgrowth. The nuclear behaviour, described by Juel, consists in the passage of a nucleus from the male branch into the female hypha, where it fuses with one of the nuclei of the latter, both branches being multinucleate. The fertilized nucleus then divides repeatedly, and eventually, around each of these daughter-nuclei, protoplasm collects and spores are formed as in a typical ascus, the only difference being in the total number of spores produced. The sterile nuclei of the female branch seem to persist until spore formation, but take no part in it. Juel regards the 'sporangium' as equivalent to the whole system of ascogenous hyphae and asci. The 'sporangium' is accordingly to be looked upon as the sporophyte. *Dipodascus* therefore presents to those Oomycetes, in which the oospore itself on germination becomes a zoosporangium, exactly the same resemblances as *Monascus* does to the Oomycetes, which form promycelia. The resemblance is even closer, because in the other case the development of a simple form of ascocarp adds another complication. *Dipodascus* and *Monascus* seem thus to stand in much the same relation to one another as do *Albugo candida* and *Peronospora omnivora*, the distinction being rather greater, however, owing to the more highly evolved sporophyte in *Monascus*. The homology of the 'sporangium' of *Dipodascus* to the zoosporangium of the Oomycetes thus appears at first to correspond with the homology of the ascus of *Monascus* to the latter; but this would make the ascus and the



'sporangium' homologous, whereas it has been shown that the kind of homology between these structures is one between the whole group of asci, regarded as a unit, and the single 'sporangium.' Ought not, accordingly, the zoosporangia of the Oomycetes to be classed in a similar manner into two groups, which might be called respectively the mega- and the micro-groups? The mega-zoosporangium would, in this way, be looked upon as being formed from the whole or a portion of the thallus by the direct conversion of this into a sporangium; while the micro-zoosporangium would be formed by a differentiation of the former into sporogenous and vegetative parts, the sporogenous portions constituting the zoosporangia and being formed as specialized branches of the latter. Two kinds of zoosporangia are found among the Oomycetes, viz. the large sporangia of the Saprolegniaceae and the small conidium-like sporangia of the Pythiaceae and the Peronosporaceae. They may be taken as furnishing respectively examples of mega- and micro-sporangia, and the homologies as being between the sporangium of the former and the combined conidiophore (or sporangiophore) and conidia (or sporangia) of the latter; thus furnishing an example completely parallel with that of the 'hemi-ascus' or 'sporangium' and the ascus. The existence of such a form as *Dipodascus* must hence supply a strong argument in favour of the hypothesis of a relationship between the Oomycetes and the Ascomycetes. The organism itself can hardly be regarded as an intermediate form between *Monascus* and the nearest Oomycete, on account of the distinctions drawn above between asci, hemi-asci, mega- and micro-sporangia: it is, rather, a parallel form, but closer to its *Albugo* type than *Monascus* is to the *Phytophthora* type for reasons given above. It is, in addition, of importance as forming a link between the other Hemiasci, which are all asexual forms, and the sexual Ascomycetes. The relationship of these two groups follows from the above.

The Gymnoascaceae, although simple in structure, do not appear to stand in a position intermediate between *Monascus*

and the Oomycetes. A comparison with the former has already been made, in which the most striking difference is the behaviour of the ascogonium, which becomes divided up into several cells, ascogenous branches being formed from each. This behaviour corresponds to that of the ascogonium of the Erysipheae, the members of which group show various degrees of complexity of the process. The simplest, or most reduced, method occurs in *Sphaerotheca*, in which form Harper (31) has shown that fusion takes place between the antheridium and ascogonium, followed by the fusion of a male and female nucleus and the division of the ascogonium into a few cells, one of which becomes converted directly into the single ascus. The nature of this ascus is therefore not quite the same as that of the ascus of *Monascus*, nor yet of the 'sporangium' of *Dipodascus*, but stands between the two. There is a differentiation of the ascogonium into two portions, one sterile and the other sporogenous, the two parts being separated by walls. In *Dipodascus* the two portions are either undifferentiated or else the sterile portion is absent. In *Monascus* the ascogonium itself may be considered sterile, but a portion of its branches sporogenous. There does not seem to be a form corresponding to *Sphaerotheca* among the Oomycetes. Perhaps the Erysipheae, the Gymnoascaceae and other Plectascineae are derived from a *Dipodascus*-like fungus, and are through that related to those Oomycetes, the sporophyte generation in which is represented simply by a zoosporangium. Their relation to *Monascus* would then be close but indirect. The Erysipheae, however, may be regarded as derived from the *Monascus* type, if the view that *Sphaerotheca* is a reduced form be accepted. The genus *Erysiphe* is most like the *Monascus* type. The ascogonium, after fertilization by a single nuclear fusion, divides into a row of several cells from the penultimate one of which the whole of the ascogenous hyphae probably arise, according to Harper (9). The ascogenous hyphae are but feebly developed and soon become in part converted into asci. The penultimate cell of the ascogonium corresponds thus to the central cell of *Monascus*,

and if Went's statement as to the division of the ascogonium into three cells in *Monascus purpureus* is correct, the resemblance of the ascogonium in this species to that of *Erysiphe* is still greater than that of the 'Samsu' species. The *Sphaerotheca* form would thus be attained by the gradual loss of the ascogenous hyphae.

Of the other lower Ascomycetes, *Eremascus*, which retains a sexual process but is isogamous, is nearer to the *Dipodascus* type, and so probably are also the Saccharomycetes through the sexual form, *Zygosaccharomyces* (32). It is difficult indeed to separate either group from the Hemiasci. *Endomyces* shows occasionally a small hypha attached to the developing ascus. According to Brefeld (2) no sexual process takes place between the two structures, but the small hypha may be regarded as a rudimentary male branch. Thus this genus also approaches very nearly the *Dipodascus* type, and can only be separated from the Hemiasci by the limited number of spores in the ascus, as is the case with the other two groups just mentioned. The limited number of spores is doubtless necessitated by the small size of the ascus, the Saccharomycetes showing a variation in number corresponding with the size of the cell. The close relationship therefore indicated between these groups renders very interesting the positions of the three forms, *Ascoidea rubescens*, *Endomyces decipiens*, and *Saccharomyces anomalus*, all of which produce characteristic hat-shaped spores, such as are formed by no other Fungi (33).

The Exoascaceae and Ascocorticaceae seem to belong to the *Dipodascus* type rather than the *Monascus* type through such forms as *Taphrina*.

While *Dipodascus* appears to be the only sexual genus among the Hemiasci at present known, several of the asexual genera of that group merit further consideration. Of these *Protomyces* has been placed at different times by De Bary among the Ascomycetes (7) and later among the Ustilagineae (8); by Schröter in a special group, the Protomycetes (18), and later among the Hemiasci (19); and by Brefeld among the



Hemiasci (2). It is now generally accepted as belonging to the latter group. It is characterized by a septate mycelium, intercalary cells of which swell up and clothe themselves with a thick wall, forming chlamydospores. They germinate by the bursting of the outer wall and the escape of the protoplasmic contents, surrounded by a wall. The contents of the cell thus extruded are multinucleate, and arrange themselves in a wall layer dividing up into spores, which eventually collect at the tip of the elongated cell thus converted into a sporangium by their division. Popta (17) has recently shown that no periplasm is produced during the division into spores, and accordingly regards the genus as being nearer to the Phycomyces than *Ascoidea*, in which he finds periplasm produced, and therefore regards it as approaching the Ascomycetes. The chlamydospores of *Protomyces* resemble in appearance the intercalary ripened oogonia of *Pythium* and many Peronosporaceae. As De Bary (5) has shown, the latter are often fertilized by an antheridium formed from the cell immediately beneath or above, the fertilization taking place through the wall separating the two cells. The figures of the early stages of chlamydospore formation in *Protomyces* given by De Bary (7) and Brefeld (2) show that the cells on either side of the young chlamydospore are filled with dense protoplasm, so that these structures may be looked upon as representing the intercalary oogonia and antheridia of the above-mentioned Oomycetes. There is certainly no evidence of any fusion between these structures through the separating wall, but it may easily have been overlooked, as has happened in the cases of many Ascomycetes, where the fusion is only of sufficient size to allow the passage of a nucleus. The nuclear behaviour during the chlamydospore formation is entirely unknown at present, so that it is impossible to do more here than point out the resemblance to the intercalary sexual organs of the Oomycetes. But if it prove to be the case that the chlamydospore is sexually produced, it must then be regarded as an oospore, and we should have a member of the Hemiasci which retains its oospore stage. It would then have to be regarded as an

important connecting link between the Oomycetes and Ascomycetes.

Holtermann (13) has described a form, *Conidiascus*, which he places among the Hemiasci, in which reproductive bodies are produced as conidia like those of *Peronospora*, which later produce a few spores by the division of their contents, epiplasm being formed during the division. This form of reproduction is regarded as intermediate between conidia and asci, and thus serves to connect zoosporangia, which are homologous in the Peronosporaceae with conidia, and asci. The processes leading up to the formation of these structures do not seem to be thoroughly known at present, so that the comparison cannot be extended here.

Popta (17) has shown that the method of spore-formation in *Ascoidea* is more nearly allied to the Ascomycetous type than to that of the Phycomycetes, owing to the occurrence of periplasm. The sporangia are apparently produced asexually. Harper (11) believes that Popta's results either indicate a method of division similar to that which he has described for *Pilobolus*, or that the process is unique and differs from that occurring in the sporangia or asci studied up to that time.

Having reviewed briefly some of the features which seem to be of most importance in the question of relationship, there remain a few points which may be further considered. It has been seen that the antheridia and oogonia of the Oomycetes have probably been evolved from gametangia, the separate motile gametes of which have lost their individuality, and in the simplest forms such as *Albugo Bliti*, while several remain functional, others have lost their sexuality, or rather remain unfertilized, and constitute the periplasm, which may be supposed to have thus originated. Other forms, such as *Peronospora parasitica*, show a higher degree of differentiation, only one male and one female gamete remaining functional. Similarly, among the Ascomycetes, which still possess an archicarp of functional male and female organs, *Monascus* and *Pyronema* behave like *Albugo Bliti*, and *Sphaerotheca*—and *Dipodascus* among the Hemiasci—like *Peronospora parasitica*.

In the cases of *Monascus*, *Pyronema*, and *Dipodascus* supernumerary gametes occur in the female organ, corresponding to the periplasm of the Peronosporaceae. In *Sphaerotheca* only one gamete seems to be produced in each organ; but in this case the supernumerary gametes may be considered to have disappeared during the course of evolution, since periplasm is not needed to produce a wall for an oospore, which function it assumes in the Peronosporaceae, affording perhaps a reason for its presence in that group when only one gamete of the female organ is functional.

In *Pyronema* and probably also *Monascus*, the development and behaviour of the gametes is like those in *Albugo Bliti*. The gametes in both organs are produced by nuclear division occurring shortly before fertilization. The female gametes aggregate into a ring or dense mass, from which the functional gametes separate.

The behaviour after fertilization is the first important point of difference. Leaving out of the question the definite oospore stage of the Oomycetes, we find that the fertilized gamete or gametes in *Albugo* produce directly by division numerous spores. *Dipodascus* and *Eremascus* behave similarly. In *Phytophthora omnivora* and most Ascomycetes, hyphae are produced from the fertilized cell which bear zoosporangia or asci. In many Oomycetes a mycelium is produced which bears fresh sexual organs. Thus in the Ascomycetes there is intercalated a definite phase in the life-history, which may be regarded as a sporophyte generation between the gametophyte generations. In the Oomycetes certain members show signs of such a phase, but it is by no means general. Seeing that *Albugo Bliti* still possesses the most primitive form of fertilization, and, in addition, presents an example of an intercalated sporophyte generation, the possession of two generations by the ancestral Oomycetes ought perhaps to be assumed; and those members of that group which do not possess both ought accordingly to be regarded as having lost the sporophyte phase. The question of relationship thus turns on the homology of the ascus with the zoosporangium. At present very



little is known of the cytological behaviour in the latter leading up to spore-formation. Wager (25) has shown that five to eight nuclei are present in the zoosporangia of *Albugo candida*, when those bodies are cut off by a wall from the sporangiophore. Each nucleus remains undivided and becomes the nucleus of a zoospore, which bodies are formed according to Büsgen (4) by the simultaneous division of the protoplasm into several distinct portions. This process is thus far removed from that occurring in typical asci. But the ascus must be regarded either as a specialized sporangium or as an entirely new structure without any homologues: and it has been seen that a method of spore-formation, which may be looked upon as approaching that found in asci, occurs in the oogonium of *Albugo*, and that the latter organ is probably a derivative of a gametangium. The balance of probability thus seems to rest with the view that the ascus and the zoosporangium are homologous. Moreover, Harper's results have been obtained from typical highly evolved asci and sporangia, and it is hardly to be expected that such diverse and characteristic structures would exhibit signs of a common origin, as might be obtained from more primitive forms. Ikeno's studies on *Taphrina* (14) show that the method of spore-formation in the asci of that genus is very different from Harper's typical method.

Apart, however, from the difficulty of the manner of cell-division there is another obstacle against the acceptance of these homologies. It arises from the behaviour of the nuclei in connexion with the formation of a typical ascus. The typical ascus is formed by the cutting off of a penultimate cell from an ascogenous hypha containing two nuclei which fuse together, leaving the young ascus uninucleate. The ascus speedily becomes multinucleate by repeated divisions of the fusion-nucleus, and each of the last formed daughter-nuclei becomes the nucleus of an ascospore. In the Oomycetes the antheridia, oogonia and zoosporangia are multinucleate from the moment of formation, and the nuclei in the latter structures become without any division the nuclei of the zoospores.

As far as the difference between the young multinucleate sporangium and the young binucleate ascus is concerned the difficulty is perhaps not serious. In discussing earlier the nature of the ascus in various genera, it was seen that in some cases it was simply the fertilized ascogonium; in others that it was limited to a portion of that organ, the remainder being cut off into separate cells; and in others that it was a branch of the system of hyphae which was produced from the ascogonium. In other words, the result of the sexual process in the Ascomycetes varies, a greater or less distinction into fertile and sterile units being met with. The same kind of distinction is found in the Peronosporaceae in the germination of the oospore. The difference then comes simply in the extreme case to this: in the zoosporangium of the promycelium of *Phytophthora omnivora* (assuming that the nuclear behaviour is similar to that of *Albugo*) the nuclei of the spores are differentiated before enclosure of the mother-nuclei in the sporangium; and in the ascus of *Pyronema*, for example, the spore-nuclei are not formed until after enclosure within the ascus. That this difference is not seriously opposed to the idea of relationship is clear from the fact that the gameto-nuclei of the Oomycetes are not differentiated until after enclosure in the gametangia.

The fusion of the two nuclei of the young ascus has apparently no parallel among the Oomycetes. It may be mentioned that Trow (22) found curious 'double' nuclei in germinating oospores and conidia of *Pythium ultimum*, which may represent pairs of nuclei in the act of fusing, but whose significance is entirely obscure. The only other fusions which have been observed in that group are the sexual fusions in the oogonia. However, since the meaning of the fusions in asci does not seem to have been satisfactorily determined, the exact bearing of the phenomena on the question of relationship cannot be estimated at present.

In the foregoing discussion stress has been laid upon the analogy of spore-formation in oogonia and asci. The periplasm of both organs ought, therefore, to be regarded as having

originated by similar means. It has been already mentioned that the periplasm of oogonia probably represents the sexually functionless elements of a gametangium that was originally completely fertile. Assuming the origin of the ascus from the zoosporangium, the sterile nuclei have either disappeared or are represented by the two nuclei which are formed at the same time as those which fuse in the young ascus, one of which is cut off into the terminal cell of the ascogenous hypha and the other into a cell immediately beneath the penultimate ascus. The latter appears to be the most likely alternative, in which case the periplasm of the ascus represents a portion of the non-sporogenous protoplasm which has escaped being cut off into the sterile cells with the sterile nuclei.

The other reproductive organs of the Oomycetes and the Ascomycetes are in many cases clearly homologous. The conidia of the latter undoubtedly correspond to those of the Peronosporaceae, in which order many examples are presented of the transition from the zoosporangial to the conidial condition.

In the above comparisons only those Ascomycetes which possess a functional archicarp have been considered. It is, however, generally admitted by most botanists, with the exception of Dangeard, that the other members of that group are to be looked upon as sexually degenerate, and are therefore considered as having originated from sexual ancestors. Summarizing, *Albugo*, *Pyronema*, and *Monascus* possess a very characteristic and probably primitive method of multiple fertilization. The germination of the fertilized egg in both groups shows gradations between a direct division into spores, e. g. *Albugo* and *Dipodascus*, and a comparatively highly evolved differentiation into sterile and sporogenous structures, e. g. *Phytophthora omnivora* and *Pyronema*.

Combining these characters, the ancestral form of the Oomycetes was probably an organism possessing the method of multiple fertilization, the compound egg of which gave rise to numerous spores only by division, i. e. the species *Albugo Bliti* and *A. Portulacae* represent in those characters the



primitive form. For similar reasons the ancestor of the Ascomycetes possessed probably the same characters, but no known member of the group now possesses these characters in an unaltered form, *Monascus* being the simplest as far as fertilization is concerned, and *Dipodascus* and *Eremascus* as far as the behaviour of the egg. The dividing line between the two groups seems to have originated by the development of the oospore stage on the one hand and the development of the ascospore stage on the other.

The probable origin of the coenogamete from gametangia, and the retention of zoosporangia in many Oomycetes, afford a link with the lower Algae.

The resemblances which have been pointed out between the Florideae and certain Ascomycetes by various authors may be explained by supposing the origin of the former from the same Algal ancestor, a somewhat parallel method of evolution having occurred from that form.

Certainly for most Ascomycetes there seems to be no reason for looking back for their origin to a simpler form than that represented by *Albugo Bliti* in those characters which have just been pointed out.

In conclusion, I wish to acknowledge my indebtedness to Professor Marshall Ward for much valuable help and advice, and also for permission to carry on the work in the Cambridge University Botanical Laboratory; to Miss Dale for information on the genus *Gymnoascus*, as yet unpublished; and to Messrs. D. T. Gwynne-Vaughan and R. H. Yapp for the material and for information concerning its economical use.

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EXPLANATION OF FIGURES IN PLATES

XII AND XIII.

Illustrating Mr. Barker's paper on *Monascus*.

- Fig. 1, *a-e*. Successive stages in the germination of a conidium. × 400.  
 Fig. 2, *a-h*. Successive stages in the formation of an archicarp. × 800.  
 Fig. 3, *a, b*. Two periods in the development of an archicarp, showing the branching of the antheridial branch and the formation of a conidium by it. × 650.  
 Fig. 4. Intercalary formation of an archicarp. × 650.  
 Fig. 5. An ascogonium spirally curved around an antheridium. × 800.  
 Fig. 6. A conidium functioning as an antheridial branch. × 650.  
 Fig. 7. Archicarp formation at the base of a chain of conidia, the lowest of which behaves as an antheridial cell. × 650.  
 Fig. 8. Showing point of fusion between the ascogonium and the antheridial branch at some distance behind the apex of the former. × 800.  
 Fig. 9. Showing fusion between the ascogonium and the antheridial branch, in which the papilla developed from the latter is conspicuous. × 3000.  
 Fig. 10. Formation of papilla on the antheridial branch beyond the apex of the ascogonium, the latter having ceased to grow. × 650.  
 Fig. 11, *a-d*. Development of investing hyphae. Successive stages. × 1000.  
 Fig. 12. Formation of auxiliary investing hyphae. × 1500.  
 Fig. 13, *a-c*. Successive stages in the development of an ascocarp, showing the origin and development of the 'internal' hyphae and asci. × 1000.  
 Fig. 14. A branch bearing an ascocarp and clasping hyphae. × 800.  
 Fig. 15, *a-c*. Nuclear structures in archicarps. (*a*) Fusion between the ascogonium and antheridium doubtful: both organs crowded with nuclei, especially at the place where fusion occurs. (*b*) A nucleus occupying the canal between the ascogonium and antheridium. Central cell cut off and filled with nuclei. Nuclei in male branch comparatively few with sharp outlines. (*c*) Aggregation of nuclei in the centre of the swelling central cell. × 1200.  
 Fig. 16. Section through young ascocarp showing comparatively large central cell surrounded completely by investing hyphae. × 1000.



Fig. 17. Section through an ascocarp of the same age with the central cell not completely in view.  $\times 1000$ .

Fig. 18. Section through a slightly older ascocarp, a small part only of the central cell being included.  $\times 1000$ .

Fig. 19. Section through an ascocarp of the same age, showing a large undivided central cell.  $\times 1000$ .

Fig. 20. Similar section through a rather older ascocarp, showing a beak-like protuberance of the central cell.  $\times 1000$ .

Fig. 21. Section through an ascocarp showing a large central cell with a small nest of ascogenous hyphae at one point of its surface.  $\times 1000$ .

Figs. 22-24. Similar sections, showing varying position of the nest of ascogenous hyphae.  $\times 1000$ .

Fig. 25. Section through an ascocarp, showing the central cell as a complete ring around the ascogenous hyphae.  $\times 1000$ .

Figs. 26-31. Various stages in the further development of the ascocarp, showing the increasing complexity of the internal ascogenous hyphae and variations in the extent of the development of the central cell.  $\times 1000$ .

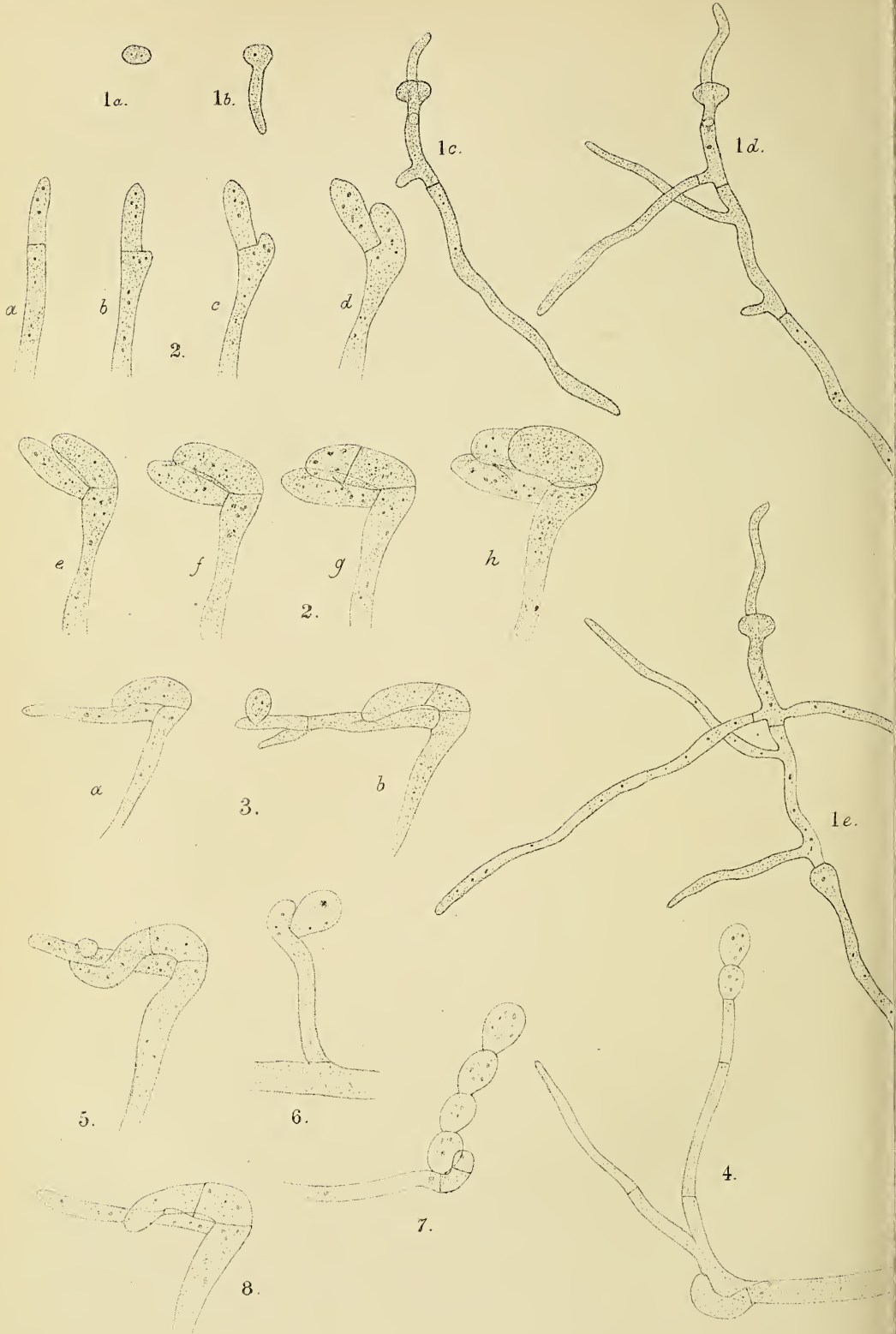
Fig. 32. Section through an ascocarp containing ripe asci. No trace of the central cell, which has degenerated.  $\times 1000$ .

Fig. 33. Section through a ripe ascocarp, showing spores lying free within the sporangium-like fructification.  $\times 500$ .

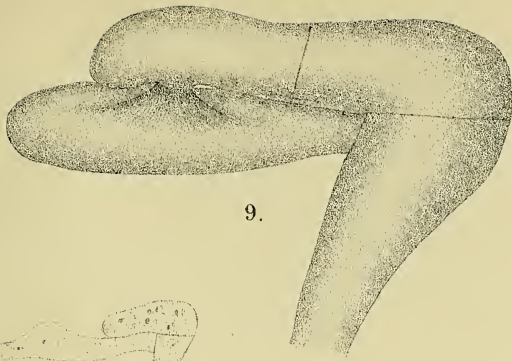
Fig. 34. Surface view of a young ascocarp, showing a conspicuous hyphal-like protuberance of the central cell. The investing hyphae are omitted with the exception of the cross sections around the central cell.  $\times 1000$ .

Figs. 1-14 were drawn from living material observed in hanging-drop cultures of beer-wort agar; Figs. 15-34 from fixed and stained material. Fig. 15, *a, b, c*, stained by the haematoxylin-iron-alum method, and Figs. 16-34 with safranin.

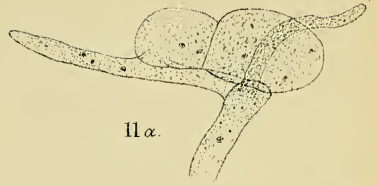








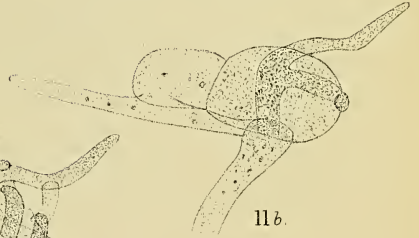
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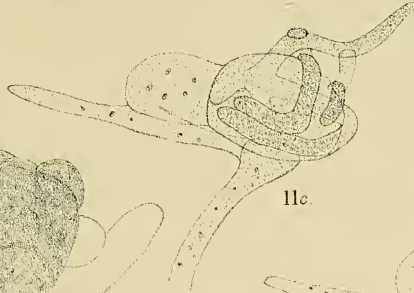
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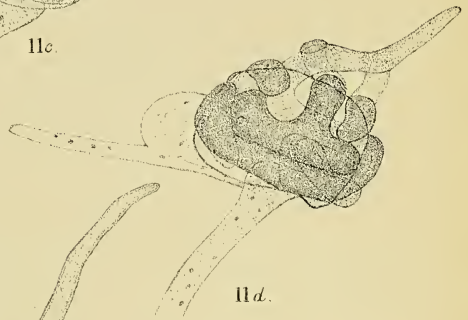
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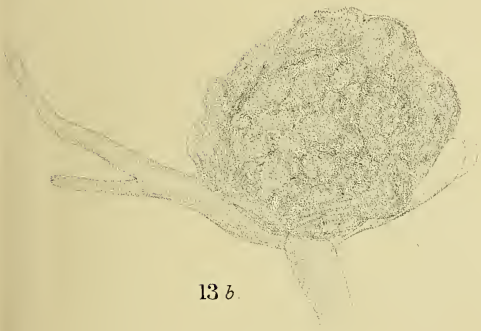
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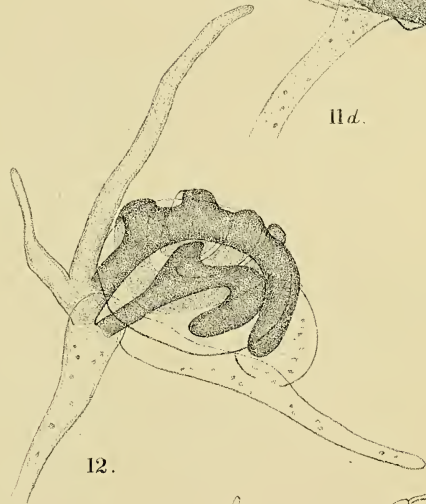
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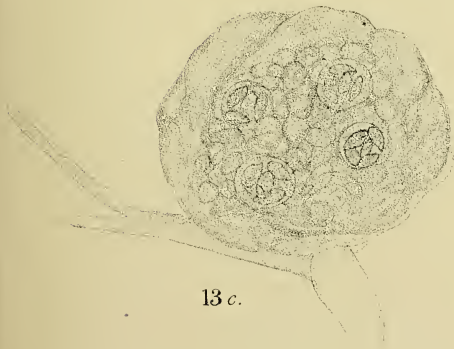
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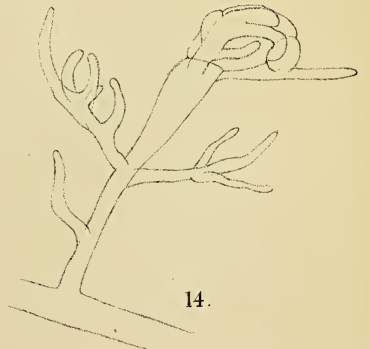
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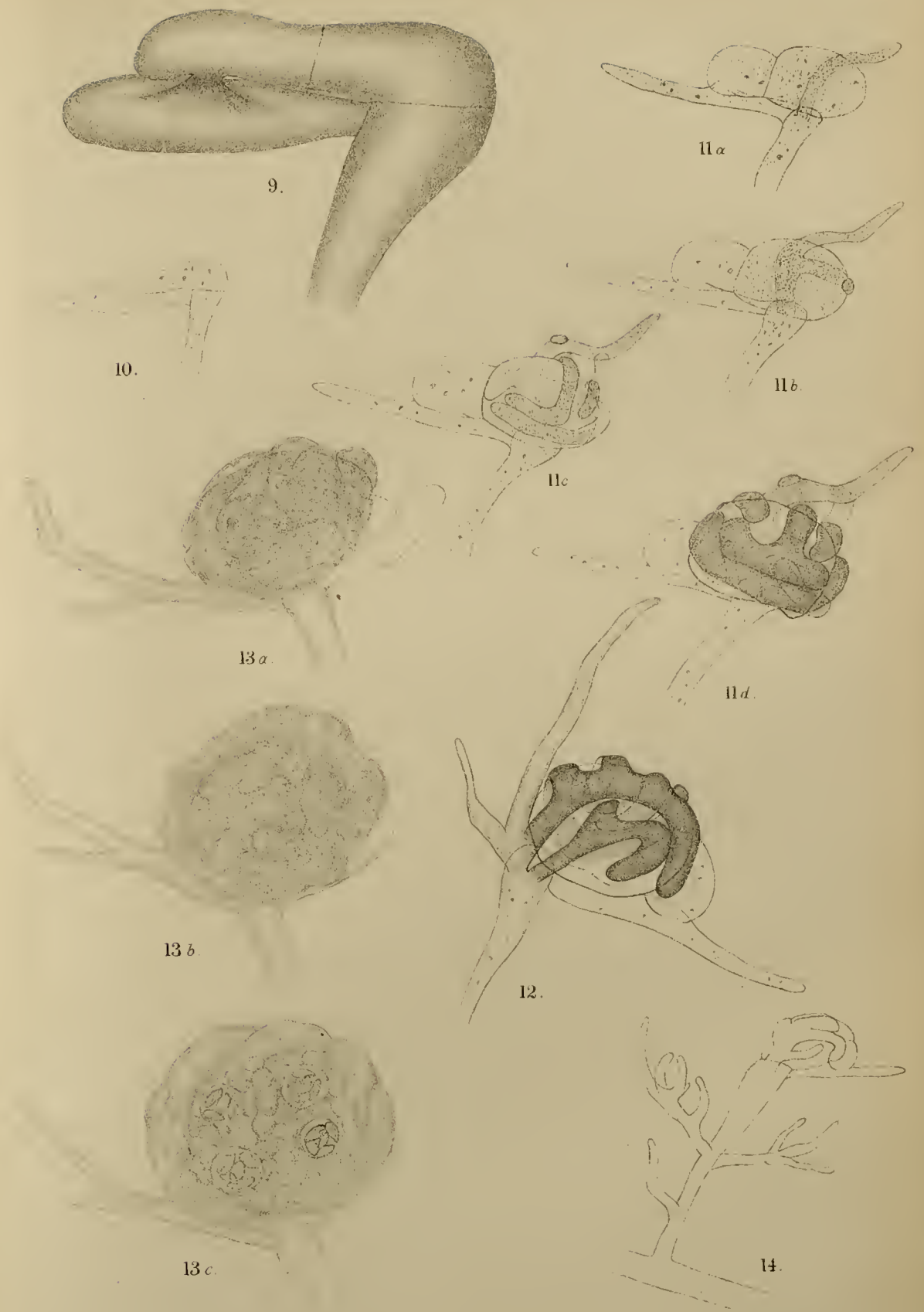


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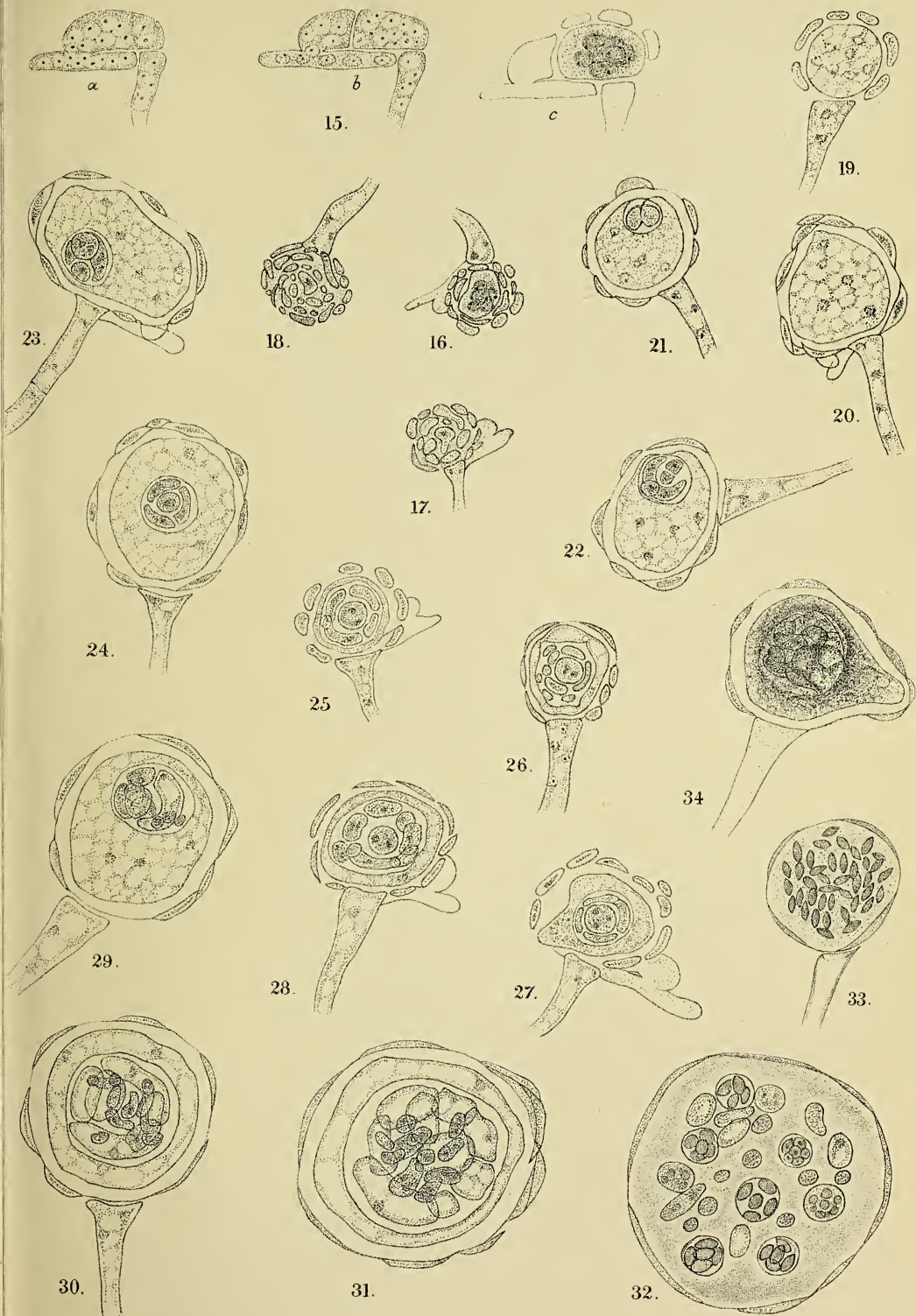
14.















## Proteolytic Enzymes in Plants<sup>1</sup>.

BY

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SINCE the publication of my paper on tryptophane (1) in the March number of the *Annals* for 1902, I have accumulated a number of new facts relating to the distribution of proteolytic enzymes, and of tryptophane, in plants, which I now place on record.

There is at present evidence that enzymes which digest proteids (proteases) occur in a number of isolated cases; in certain lowly Algae, in some Fungi, in various Phanerogams. The evidence is not, however, of the same kind in all cases: in some it is direct, in others only indirect.

The indirect evidence amounts merely to this, that the plants in question can be nourished by peptone or other proteid, no demonstration of the digestive process having been given. This applies to the Algae, *Scenedesmus acutus*, *Chlorella vulgaris*, *Chlorospora limicola*, investigated by Beyerinck (2); to certain Moulds (*Aspergillus niger*, *Penicillium glaucum*); and to the insectivorous *Drosera*, *Dionaea*, and *Pinguicula*.

The direct evidence consists of the demonstration of the digestive process by means of chemical tests. This is forthcoming in the case of certain Bacteria, of Yeast (*Saccharomyces Cerevisiae*); and, among Phanerogams, of the insectivorous *Nepenthes*, of many seeds, of some fruits such as the Pine-

<sup>1</sup> A preliminary account of these observations was given at a meeting of the Linnean Society of London, on Nov. 20, 1902.

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Apple (*Ananas sativus*), and of certain laticiferous plants such as the Papaw (*Carica Papaya*) and the Fig (*Ficus Carica*). In all these cases the process includes both the peptonization of the more complex proteids and the proteolysis of the simpler proteids.

I would recall the suggestion made years ago by Claude Bernard and by Sachs, that a digestive enzyme may be presumed to be formed in all organs, such as seeds, fruits, bulbs, tubers, &c., in which proteids are stored. This suggestion has already been fully verified in the case of seeds: indeed the ascertained facts warrant the inference that a digestive enzyme is produced in all germinating seeds. The object that I had in view, on commencing these investigations, was to supply similar verification in the other cases, and so to add to the number of known instances of the occurrence of these enzymes in plants. I have, however, carried them far beyond these prescribed limits and in an unexpected direction, as the following pages will show.

It has been customary, in investigations of this sort, to employ relatively intractable proteids (using the word in a quite general sense), either blood-fibrin or coagulated egg-albumin, as the digestible material; and the tests subsequently applied have been the biuret-test and others which indicate the presence of the lower proteids, viz. albumoses and peptones. That is to say, the investigation has been directed to the question as to whether or not a *peptonizing* enzyme was present. The methods that I have adopted are quite different to these. In the first place, it has to be borne in mind that the enzymes in the tissues of plants are not called upon to digest fibrin and egg-albumin. It is true that in several cases (e.g. Pine-Apple, Papaw, Fig, Yeast) enzymes have been found which are capable of digesting these substances: but it does not follow, as seems to have been generally assumed, that because a vegetable juice or extract cannot digest them, it therefore contains no enzyme at all. As I long ago pointed out (3), the proteids of plants are chiefly globulins and albumoses: it is therefore obvious that

these are the proteids to be employed in the search for enzymes in plants. Consequently I have employed as digestible material in these experiments either the proteids naturally present in the juice or in the tissue of the plant; or, when proteid material had to be supplied, the substance sold as 'Witte-peptone,' a dry powder consisting of a mixture of albumoses and some peptone. Moreover, the immediate object of my search was not a *peptonizing*, but a *proteolytic* enzyme; not an enzyme, that is, which hydrolyzes the higher proteids into the lower, but one that decomposes the proteid molecule altogether. The test of digestive activity has accordingly been the tryptophane-reaction: that is, the treatment of the acid digested liquid with chlorine-water which produces a characteristic, more or less marked, pink or violet colouration if tryptophane be present; and if tryptophane be present, it is presumptive evidence that proteolysis has taken place.

Incidentally, however, I found it necessary to make some experiments with the more complex proteids. Whilst they were nearly always successful when Witte-peptone was the material supplied, the results with fibrin, raw egg-albumin, and commercial casein, were often negative: but experiments with milk showed that the enzymes detected could act upon caseinogen, in several instances.

The plant-material used was, in many cases, the juice, when the parts to be investigated were sufficiently succulent, such as fruits, &c. When the parts did not yield enough juice, I had recourse, in the first instance, to watery extracts. But I sometimes found juices, and especially watery extracts, to be unsatisfactory: when unfiltered they were too thick or too highly coloured, when filtered they were almost or altogether inert. After many trials I found that the best method of preparing such material as leaves, stems, roots, &c., was to slightly bruise pieces of them in a mortar; when so prepared, they were placed in the experimental bottles with distilled water, or other liquid, and the digestible substance (Witte-peptone, fibrin, &c.) then added.



The chief source of error to be avoided was the putrefaction of the digesting mixtures. When the period of digestion was brief, extending over three or four hours or even more, this source of error did not arise: in prolonged digestions it was eliminated by the use of antiseptics, such as hydrocyanic acid (HCN), hydrochloric acid (HCl), or chloroform-water. The mixtures without antiseptics generally showed no sign of putrefaction in the course of the experiment, but occasionally they developed an offensive odour: it is, however, not necessary to attach importance to those results, as the evidence afforded by the antiseptic experiments is conclusive in itself. In many instances the results were controlled by parallel experiments in which the vegetable matter under investigation had previously been boiled.

The tryptophane-test was usually applied directly to the digested liquid acidified, when necessary, with acetic acid: in only a few cases (e.g. leaf and root of Dandelion) did the liquid become too highly coloured, in the course of digestion, to admit of accurate observation of the tryptophane-reaction. In a good many cases (e.g. Apple, leaf of *Scolopendrium*, tuber of *Helianthus tuberosus*) a marked yellow colour was produced on the addition of the chlorine-water; but this did not prevent the detection of the tryptophane-reaction. The various intensities of the tryptophane-reaction are described by the series of terms—faint, distinct, marked, strong. The fact that when the vegetable substance had previously been boiled the digested liquid gave no tryptophane-reaction, or only a faint one, due to the presence of tryptophane in the substance itself, proves that the Witte-peptone and other proteids used contained no tryptophane to begin with.

It should be mentioned that the temperature of the incubator or thermostat, in which the liquids were set to digest, was about 40° C. in all cases.

In some cases acid (either HCl or citric acid) was added to the liquids to be digested: but this is not necessary, since all the liquids used were either acid to begin with, or they naturally became so in the course of digestion. When acid

was added it was generally found to promote proteolysis. In other cases, the liquid was made alkaline with  $\text{Na}_2\text{CO}_3$ , with the effect of sometimes promoting, sometimes retarding digestion, but never inhibiting it.

#### EXPERIMENTS WITH WITTE-PEPTONE.

Most of these experiments were made with various parts of Phanerogams, such as fruits, bulbs, tubers, stems, leaves, roots: only a few were made with seeds, as these have been already so fully investigated. I have included in the experiments the leaves of a Fern (*Scolopendrium vulgare*); and a single Fungus, the Mushroom (*Agaricus campestris*). I give this last experiment first.

It must be borne in mind that in all cases more or less proteid matter, belonging to the juices or tissues under experiment, was present in addition to the Witte-peptone added.

##### *Agaricus campestris.*

5 grms. of bruised Mushroom (gills excluded) were placed in each of the bottles Nos. 1, 2, 3, of about 40 cc. capacity: in the case of No. 2, the portion of Mushroom was first of all boiled: to each bottle was added 0.3 gm. of Witte-peptone, and to No. 3, 1.5 cc. of 4 % HCN, the bottles having all been filled up with distilled water.

After 5 hours' digestion in the incubator, No. 1 gave a strong tryptophane-reaction, No. 2 a distinct reaction, and No. 3 a marked reaction: clearly proteolysis had taken place in Nos. 1 and 3: the reaction in No. 2 is to be attributed to the presence of tryptophane in the tissue to begin with.

There can be little doubt that further investigation will show that the capacity for active proteolysis is generally possessed by the Fungi.

##### Seeds.

The observations that I have made on Green Peas (*Pisum sativum*) are of some interest. The watery extract of Green Peas gives no tryptophane-reaction, but acts strongly on Witte-peptone.

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The extract is turbid, greenish, neutral : 30 cc. were placed in each of four bottles ; 6 drops of 4 % HCN solution were added to each. Further additions were made as follows :

1. Extract and HCN only ; nothing added.
2. „ „ with 2 drops of strong HCl.
3. „ „ with 2 drops of strong HCl and .3 gm. of Witte-peptone.
4. the same mixture as 3, but boiled (control).

After 3½ hours in the incubator, Nos. 1 and 2 gave distinct, and No. 3 marked, tryptophane-reaction : No. 1 had become slightly acid : no tryptophane-reaction in No. 4. After 22 hours in the incubator, No. 4 still gave no tryptophane-reaction, whilst all the others gave a strong reaction : No. 1 was strongly acid.

It is clear, therefore, that Green Peas contain a proteolytic enzyme acting in the presence of HCl.

I have also made some observations on the 'germ' of Wheat (*Triticum vulgare*) ; that is, the embryos removed from the grain in the process of milling : the presence of a proteolytic enzyme is clearly demonstrated.

50 grms. of 'germ,' ground to a fine powder, were extracted with 250 cc. of distilled water : the liquid, after straining through muslin, is turbid, slightly acid, and gives no tryptophane-reaction : 50 cc. of the liquid were placed in each of three bottles, and treated as follows :

1. added 0.5 gm. Witte-peptone and 10 drops of 4 % HCN.
2. „ 10 drops of 4 % HCN.
3. „ 0.5 gm. Witte-peptone, then boiled, and added 10 drops of 4 % HCN (control).

After 4½ hours in the incubator, No. 1 gave a strong tryptophane-reaction, No. 2 a faint reaction, No. 3 no reaction.

### Fruits.

In view of Green's discovery (4) of a protease in the Kachree Gourd (*Cucumis utilisimus*, a variety of *C. Melo*), I have given special attention to the Cucurbitaceae, and have found such a body in all the species examined, viz. a yellow, smooth-skinned, variety of Melon (*Cucumis Melo*) largely



imported from Spain; the Cucumber (*Cucumis sativus*); the Vegetable Marrow (*Cucurbita Pepo* var. *ovifera*); the Squirt-ing Cucumber (*Ecballium Elaterium*). The seeds and the rind were previously removed in most cases.

*Cucumis Melo.*

The expressed juice is a turbid, acid liquid, giving distinct tryptophane-reaction: 30 cc. of it were placed in each of three bottles, and treated as follows:—1, nothing added: 2, added 0.3 gm. Witte-peptone: 3, added 0.3 gm. of Witte-peptone, and acidified with HCl to 0.18 %.

After 4 hours in the incubator, the tryptophane-reaction had become rather stronger in Nos. 1 and 3, and was marked in 2: 19 hours later, it was rather stronger in 1, about the same in 2, and strong in 3.

*Cucumis sativus.*

The material used in the first experiment consisted of field or ridge Cucumbers which had begun to turn yellow, and were therefore nearly ripe.

The expressed juice was turbid, greenish, acid, giving distinct tryptophane-reaction: 30 cc. of it were placed in each of three bottles, treated as follows:—1, nothing added: 2, added 0.3 gm. Witte-peptone: 3, added 0.3 gm. Witte-peptone, and acidified with HCl to 0.18 %.

After 3 hours in the incubator, the tryptophane-reaction in No. 1 was as at first, whilst it had become marked in 2 and 3: 2½ hours later it was more distinct in 1, and strong in 2 and 3.

A second experiment was made with green Cucumbers grown in a house; the juice of this unripe fruit gave no tryptophane-reaction to begin with. 50 cc. of the juice were placed in each of two bottles; to No. 1 nothing was added; to No. 2, 0.25 gm. Witte-peptone. After 2 hours in the incubator, No. 1 gave a distinct, and No. 2 a marked, tryptophane-reaction: after 24 hours' digestion the reaction of No. 1 was about the same, whilst that of No. 2 had become strong.

*Cucurbita Pepo* var. *ovifera.*

The expressed juice of the Vegetable Marrow is a turbid, yellowish, almost neutral liquid, giving a marked tryptophane-reaction.

The following experiment was made with small pieces of the fruit that had been bruised in a mortar: 10 grms. of the bruised fruit were placed in each of four bottles, of about 40 cc. capacity, with 0.3 gm. of Witte-peptone:

No. 1 was filled up with distilled water.

No. 2     "     "     chloroform-water (0.5 %).

No. 3, the material was boiled with the water before adding the Witte-peptone.

No. 4 was filled up with distilled water, and 1 cc. of 4 % HCN added.

After 5 hours in the incubator, the results were:

No. 1 gave a marked tryptophane-reaction.

No. 2     "     distinct     "     "

No. 3     "     faint     "     "

No. 4     "     distinct     "     "

18 hours later, the reaction was marked in Nos. 2 and 4, and still faint in No. 3.

#### *Ecballium Elaterium.*

The expressed juice of the fruits of the Squirting Cucumber is mucilaginous and acid, giving a faint tryptophane-reaction. 20 cc. of the juice were placed in each of two bottles, to one of which nothing was added, to the second 0.2 gm. of Witte-peptone.

After 6 hours in the incubator, the contents of the first bottle gave a faint, those of the second a marked, tryptophane-reaction.

The following experiments were made with fruits belonging to various orders other than the Cucurbitaceae.

#### *Musa sapientum.*

The watery extract of the ripe Banana is a mucilaginous, acid liquid, giving distinct tryptophane-reaction; on account of its viscosity, it could not be satisfactorily used: small pieces of the fruit were used instead.

10 grms. were placed in each of two bottles with 40 cc. of distilled water: to No. 1 nothing further was added: to No. 2, HCN to 0.1 %.

After  $5\frac{1}{2}$  hours' digestion, No. 1 gave a marked, and No. 2 a distinct, tryptophane-reaction: 18 hours later, the reaction was stronger in both. Auto-digestion had taken place.

In another experiment, the action of the fruit-tissue on Witte-peptone was observed. 5 grms. were placed in a bottle to which 20 cc. of distilled water, and the same quantity of chloroform-water, with 0.3 gm. Witte-peptone, were added. After 19 hours' digestion the liquid gave a distinct tryptophane-reaction. The liquid of a control-experiment, containing no Witte-peptone, gave no reaction.

*Lycopersicum esculentum.*

The expressed juice of the Tomato is turbid, reddish in colour, acid, and seems to give a tryptophane-reaction, but this is difficult to decide on account of the colour of the liquid.

30 cc. of the juice were placed in each of three bottles: to No. 1 nothing was added; to No. 2, 0.3 gm. of Witte-peptone and 0.3 cc. of 4 % HCN; to No. 3, 0.3 gm. of Witte-peptone and 1.5 cc. of 4 % HCl (= 0.18 %).

After 2 hours' digestion, No. 1 gave a distinct tryptophane-reaction; Nos. 2 and 3 a marked reaction, rather stronger in 3 than in 2: after 22 hours' digestion, No. 1 gave a marked reaction, No. 2 a very strong, and No. 3 a strong reaction.

*Pyrus Malus.*

The not quite ripe apple used was a variety of Codlin. The expressed juice is a greenish, acid liquid, which turns bright yellow on the addition of chlorine-water, the colour gradually deepening to orange.

After 23 hours' digestion with some Witte-peptone, there was no definite tryptophane-reaction. I then tried an experiment with bruised pieces of the parenchyma of the fruit, but with the same negative result. I was, however, more successful with the peel or rind.

3 grms. of rind were placed in each of two bottles with about 40 cc. distilled water: to the one nothing was added, to the other 0.3 gm. of Witte-peptone. After 19 hours' digestion, the liquid in the bottle containing no Witte-peptone gave a bright yellow colour on the addition of chlorine-water, but no tryptophane-reaction: that in the bottle to which Witte-peptone had been added gave a distinct reaction.



*Pyrus communis.*

The variety of Pear used was the Beurré Hardi.

20 grms. of crushed, ripe, pear were placed in each of two bottles (40 cc.), filled up with chloroform-water: to No. 1 nothing was added: to No. 2, 0.5 gm. Witte-peptone.

After 4 hours' digestion, No. 2 gave a faint tryptophane-reaction; No. 1, no reaction: after 24 hours' digestion, No. 2 gave a distinct reaction; and after 48 hours, a marked reaction: No. 1 gave no reaction.

*Citrus Aurantium.*

I found that whereas the rind acts on Witte-peptone, the juice of the Orange is without effect.

In each of two bottles (45 cc.) were placed 5 grms. of orange-peel: both were filled with 50 % chloroform-water, and to the one (No. 2) 0.3 gm. of Witte-peptone was added. In each of two other similar bottles (3, 4) were placed 20 cc. of juice, and they were filled up with chloroform-water: to No. 4, 0.3 gm. of Witte-peptone was added.

After 24 hours' digestion, No. 1 gave a faint tryptophane-reaction; No. 2, a strong reaction; No. 3, no reaction; No. 4, a scarcely perceptible reaction.

*Vitis vinifera.*

55 cc. of juice and pulp of some ripe White Grapes (hothouse) were placed in each of two bottles, Nos. 1 and 2; the material in No. 2 had been previously boiled: to each, 35 cc. of chloroform-water were added, and 0.5 gm. of Witte-peptone.

After 22 hours' digestion, No. 1 gave a marked tryptophane-reaction; No. 2, no reaction.

Similar, but less striking results, were given with quite ripe Black Grapes.

**Laticiferous Plants.**

In view of the fact that the latex of the Papaw (*Carica Papaya*) and that of the Fig (*Ficus Carica*) are known to contain proteases, I tried a few experiments with other laticiferous plants.

*Euphorbia Characias.*

The latex from green herbaceous shoots is slightly acid, and gives no tryptophane-reaction.

An extract was made by grinding up some shoots (without leaves) with distilled water. About 25 cc. of the extract were placed in each of three bottles: to No. 1 nothing was added; to No. 2, a few drops of 4 % HCN; to No. 3, a few drops of HCN and 0.25 gm. of Witte-peptone.

After 5 hours' digestion, No. 3 gave marked tryptophane-reaction; Nos. 1 and 2 gave none: 17 hours later, the reaction was strong in No. 3, doubtful in No. 1, absent in No. 2.

*Lactuca sativa.*

The bruised leaves of the Lettuce were used: 10 grms. of bruised leaf were placed in each of four bottles filled with distilled water (40 cc.); to No. 1 nothing was added; to No. 2, 1 cc. of 4 % HCN; to No. 3, 0.3 gm. of Witte-peptone; to No. 4, 0.3 gm. of Witte-peptone and 1 cc. of 4 % HCN.

After 3 hours in the incubator, no tryptophane-reaction was given in any case: 18 hours later, a faint reaction was given by Nos. 1 and 2, a strong reaction by No. 3, and a marked reaction by No. 4.

Some experiments were made with the root and leaf of the Dandelion: but the liquids became so deeply coloured that the tryptophane-reaction was uncertain.

The measure of success that had been met with in the experiments with fruits and with laticiferous plants suggested to me the possibility of obtaining similar results with the stems, leaves, and roots of ordinary plants, which I accordingly proceeded to investigate.

**Stems.**

The material employed was either pieces of stem bruised in a mortar, to which about 40 cc. of distilled water were added, or the expressed juice of the stem in the same quantity.

*Dahlia variabilis.*

5 grms. of bruised stem were placed in each of five bottles: to No. 1, nothing was added but 35 cc. of distilled water; to No. 2, was

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further added 1 cc. of 4 % HCN; to No. 3, 0.3 gm. of Witte-peptone; to No. 4, 0.3 gm. of Witte-peptone and 1 cc. of HCN; in No. 5 the stem was boiled in the water before the addition of 0.3 gm. of Witte-peptone.

After 24 hours' digestion, No. 4 gave a distinct tryptophane-reaction: the liquid in No. 3 had become so darkly coloured that it could not be satisfactorily tested: none of the others gave any reaction.

*Cucurbita Pepo* var. *ovifera*.

The shoots of the Vegetable Marrow yielded, on pressure, a considerable quantity of turbid, slightly acid, juice. Some of this was placed in each of four bottles: to No. 1, nothing was added; to No. 2, 0.5 gm. of Witte-peptone; to No. 3, 0.5 gm. of Witte-peptone and 0.2 gm. of citric acid; to No. 4, 0.5 gm. of Witte-peptone and HCl to 0.2 %. After 22 hours' digestion, Nos. 1 and 2 gave a faint tryptophane-reaction, No. 3 a marked, and No. 4 a distinct reaction.

*Mirabilis Jalapa*.

Three bottles containing expressed juice were treated as follows: to No. 1, nothing was added; to No. 2, 0.3 gm. Witte-peptone; to No. 3, 0.3 gm. Witte-peptone and 1 cc. of HCN. After 20 hours' digestion, No. 1 gave a faint, and Nos. 2 and 3 a distinct tryptophane-reaction.

Similar results were obtained with *Helianthus tuberosus*.

*Cuscuta*, sp.

The special interest of this experiment lies in the fact that the plant is a parasite, and that its leafless shoots contain no chlorophyll.

A quantity of the shoots of a species, in flower, growing on some plants of *Artemisia*, was ground up fine: 40 grms. of this material were extracted with 40 cc. of distilled water. On pressure, a dark-brown acid liquid was obtained, which gave no tryptophane-reaction.

20 cc. of the unfiltered liquid were placed in each of two bottles: to each a few drops of 4 % HCN were added, and to one of them (2), 0.5 gm. of Witte-peptone.

After 20 hours' digestion, bottle No. 1 gave no tryptophane-reaction: bottle No. 2 gave a distinct reaction.



### Leaves.

The material used consisted usually of the tissue of the blade bruised in a mortar; the petioles and mid-ribs were excluded as far as possible.

#### *Spinacia oleracea.*

In each of four bottles were placed 10 grms. of bruised Spinach leaves, and they were then filled with distilled water: to No. 1, nothing was added; to No. 2, 1 cc. of HCN, 4%; to No. 3, 0.4 gm. of Witte-peptone; to No. 4, 0.4 gm. of Witte-peptone and 1 cc. of HCN. After 18 hours' digestion, No. 1 gave a distinct and No. 2 a faint tryptophane-reaction; No. 3 gave a strong reaction, but as it had an offensive smell, the reaction may be attributed to putrefaction; No. 4 gave a marked reaction.

Similar results were obtained with the leaves of the Dahlia, of *Mirabilis*, of *Tropaeolum majus*, of the Cherry-Laurel (*Prunus Lauro-cerasus*), of *Ricinus communis*, of *Helianthus tuberosus*, and of *Pelargonium zonale*.

#### *Brassica oleracea.*

The results obtained with the leaves of the Cabbage were sufficiently striking to justify special mention.

About 40 cc. of a watery extract of the leaves were placed in each of four bottles: to No. 1, nothing was added; to No. 2, 1 cc. of 4% HCN; to No. 3, 0.4 gm. of Witte-peptone; to No. 4, 0.4 gm. of Witte-peptone, and 1 cc. of HCN.

After 4 hours' digestion, No. 1 gave a distinct tryptophane-reaction; in No. 2 the reaction was rather stronger; in No. 3 it was marked, and strong in No. 4.

#### *Holcus mollis.*

In this case some stem was mixed with the leaves. 5 grms. of the bruised material were placed with 0.3 gm. of Witte-peptone in each of three bottles: to No. 1 distilled water only was added (40 cc.); the material and the water were boiled before being placed in No. 2; to the water in No. 3, HCN was added to 0.18%. After 18 hours in the incubator, No. 1 gave a strong tryptophane-reaction, but smelt rather offensively; No. 2 gave no reaction; No. 3 a marked reaction.

The only other Grass that I have investigated so far is *Phalaris canariensis*, and it gave even more definite results than *Holcus*.

*Apium graveolens.*

I experimented with the Celery with the special object of ascertaining whether or not the green leaf-blades and the etiolated petioles would give concordant results: I found this to be the case.

Experiment 1.—10 grms. of bruised green leaf-blades were placed in each of three bottles (40 cc.), together with 0.3 gm. of Witte-peptone: No. 1 was filled up with chloroform-water (0.5 %); No. 2 was filled with distilled water that had been boiled with the leaf-material before the Witte-peptone was added; No. 3 was filled with 0.1 % HCN.

After 22 hours' digestion, No. 1 gave a marked tryptophane-reaction, and No. 3 a strong one; No. 2 gave no reaction.

Experiment 2.—10 grms. of bruised etiolated petioles were placed in each of three bottles, the other contents of which were precisely the same as in the preceding experiment.

After 5 hours' digestion, No. 1 gave a distinct, and No. 3 a faint, tryptophane-reaction; after 23 hours' digestion the reaction in No. 1 was strong, marked in No. 3, and faint in No. 2.

*Scolopendrium vulgare.*

An experiment with the leaves of the Hart's Tongue Fern, as representing the Pteridophyta, is of peculiar interest.

5 grms. of bruised leaf were placed in each of three bottles (40 cc.); to each 0.3 gm. of Witte-peptone was added, and the bottles were filled up with distilled water; the leaf in No. 2 had been boiled before being placed in it; to No. 3, 1.5 cc. of 4 % HCN were added.

After 24 hours' digestion, slight indications of the tryptophane-reaction were given by Nos. 1 and 3; after 42 hours' digestion, No. 1 gave a strong reaction, and had an offensive smell; No. 2 gave no reaction; No. 3 a marked reaction.

**Bulbs.**

Experiments were made with the Tulip, the Hyacinth, and the Onion, the material used being pieces of the bulbs.

*Tulipa, sp.*

5 grms. of bulb in each of three bottles (45 cc.): all three were filled up with chloroform-water; the bulb-material in No. 2 had

previously been boiled; to No. 3, 0.3 grm. of Witte-peptone was added.

After 22 hours' digestion, No. 1 gave a distinct tryptophane-reaction; No. 2 no reaction; No. 3 a marked reaction.

Precisely similar results were obtained with the Hyacinth (*Hyacinthus orientalis*), and with the Onion (*Allium Cepa*): the expressed juice of the onion gives a marked tryptophane-reaction.

### Tubers.

#### *Solanum tuberosum.*

5 grms. of the cortical tissue of a potato were placed in each of two bottles, 1 and 2, that in 2 having been previously boiled: to each 0.3 grm. of Witte-peptone was added, and both were filled up with chloroform-water (about 50 cc.). After 24 hours' digestion, No. 1 gave distinct tryptophane-reaction, No. 2 no reaction.

Similar results were obtained with the tuber of the Jerusalem Artichoke (*Helianthus tuberosus*).

### Roots.

Experiments were made with the roots of the Tomato, the Vegetable Marrow, and the Scarlet Runner: as also with the tuberous roots of the Turnip, the Carrot, the Beet, and *Mirabilis Jalapa*.

#### *Brassica Rapa.*

The expressed juice of the turnip gives distinct tryptophane-reaction.

30 cc. of the juice were placed in each of two bottles: to No. 1, nothing was added; to No. 2, 0.3 grm. of Witte-peptone and 1.5 cc. of 4 % HCN (= 0.18 %).

After 7 hours' digestion, No. 1 gave the same tryptophane-reaction as at first, No. 2 gave a strong reaction.

Similar results were obtained with the other roots, either the bruised root or a watery extract being used.

I have so far obtained evidence of the proteolysis of Witte-peptone by all the vegetable substances employed, with the exception of the pulp and juice of the Apple and of the Orange. Proteolysis seems to be effected almost equally well when the reaction of the liquids is alkaline (0.5 %).



$\text{Na}_2\text{CO}_3$ ) as when it is acid. Experiments in alkaline medium were performed with leaves of Lettuce, Spinach, and Celery; the tuber of the Potato; the bulbs of the Tulip and the Hyacinth; the fruit of the Banana and of the Orange (peel).

#### EXPERIMENTS WITH PROTEIDS OTHER THAN WITTE-PEPTONE.

Inasmuch as nearly all the proteases known at the time when I commenced my experiments had been found to be peptonizing as well as proteolytic, it was incumbent upon me to ascertain whether or not the newly discovered proteolytic enzymes were also capable of peptonizing the higher proteids. I therefore proceeded to test some of them with such proteids as fibrin, raw egg-albumin, caseinogen (as contained in milk), and commercial casein.

##### Fibrin.

Experiments were made with the following: the juice of the Melon, the Vegetable Marrow, the Cucumber, the Tomato, the Onion; extract of *Euphorbia Characias*, and of Wheat-Germ; bruised leaves of Spinach and of Celery (etiolated); the bruised tissue of the Mushroom. The well-washed fibrin used had been preserved in dilute glycerin. The possible tests for digestion were (1) the biuret-reaction; (2) the tryptophane-reaction; (3) the disappearance of the fibrin supplied. In many cases (especially leaves) the biuret-test could not be applied on account of the presence of a substance that gave a strong yellow colour on the addition of the concentrated  $\text{NaHO}$  solution. Nor was the tryptophane-test alone altogether reliable, since the reaction might be the result of the digestion of proteids in the juice or tissue under examination, but together with the disappearance of the fibrin it could be depended on. The following instances illustrate the general methods of experiment.

##### *Cucumis sativus.*

50 cc. of the expressed juice of a nearly ripe, somewhat yellow Cucumber were placed in each of two bottles; to each was added

0.5 grm. of moist fibrin, and to (1) HCl to 0.2 %, to (2) citric acid to 1 %. After 24 hours' digestion, the fibrin had disappeared in (1), and there was but little left in (2). The juice gave marked tryptophane-reaction to begin with.

In a second experiment, a green, quite unripe Cucumber was used: the juice gave no tryptophane-reaction.

50 cc. of juice were placed in each of two bottles with 1 grm. of moist fibrin: (1) was acidified with HCl to 0.2 %; (2) with citric acid to 0.5 %. A third bottle (3) contained only juice.

After 2 hours' digestion, the contents of (1) and (3) gave a marked tryptophane-reaction; those of (2) a distinct reaction: this is clearly due to the digestion of the proteids of the juice.

After 24 hours' digestion, the fibrin in (1) and (2) had perceptibly diminished; after 48 hours it had disappeared in (1), and there was very little left in (2).

#### *Euphorbia Characias.*

A watery extract was made of the soft parts of some stems, without leaves: the extract gave no tryptophane-reaction. 30 cc. of the extract were placed in each of four bottles: to (1) nothing was added, to the other three 0.5 grm. of moist fibrin; (3) was acidified with HCl to 0.2 %; (4) with citric acid to 1 %.

After 18 hours' digestion, (1) and (2) gave a distinct, (3) a marked, and (4) a strong tryptophane-reaction; in (2), (3), and (4) the fibrin had diminished. After 45 hours' digestion, there was still a little fibrin left in (3), and rather more in (2) and (4); all three gave a strong tryptophane-reaction, whilst that of (1) had remained distinct.

#### *Wheat-Germ.*

5 grms. of finely ground 'germ' were extracted with 100 cc. distilled water: the extract gave no tryptophane-reaction. 50 cc. of extract were placed in a bottle (1) with 0.25 grm. moist fibrin, and acidified with HCl to 0.1 %; 20 cc. of extract were placed in another bottle (2), nothing being added.

After 23 hours' digestion, the fibrin in (1) was found to have diminished, and the liquid gave distinct tryptophane-reaction; the liquid in (2) gave a faint reaction. After 28 hours' digestion, the fibrin had disappeared in (1), which now gave a marked tryptophane-reaction; (2) gave a distinct reaction.

*Cucumis Melo.*

25 cc. of Melon juice and 20 cc. of chloroform-water were placed in each of two bottles: to No. 1, nothing was added; to No. 2, 0.2 gm. of moist fibrin; a third bottle contained 45 cc. of pure juice and 0.2 gm. of fibrin.

After 22 hours' digestion, No. 1 gave a distinct tryptophane-reaction; No. 2, a marked reaction, the fibrin being much broken up; No. 3, a marked reaction, and the fibrin had altogether disappeared.

*Agaricus campestris.*

5 grms. of bruised Mushroom were placed in each of two bottles, with 20 cc. chloroform-water and 20 cc. distilled water: to No. 2, 0.3 gm. moist fibrin was added.

After 22 hours' digestion, No. 1 gave a distinct tryptophane-reaction; No. 2 a marked reaction; most of the fibrin had been dissolved.

I failed to obtain similar evidence of the digestion of fibrin in experiments with the fruits of the Vegetable Marrow, the Tomato and the Orange (rind and juice); the bulbs of the Onion, the Tulip, and the Hyacinth; the leaves of Spinach and of Celery; when the liquid was naturally or artificially acid. But when the liquid was rendered alkaline by  $\text{Na}_2\text{CO}_3$ , digestion was effected by the bulbs of the Tulip and the Hyacinth.

5 grms. of bruised Tulip bulb were placed in each of two bottles, both of which were filled up with 40 cc. of chloroform-water: to No. 1, nothing was added; to No. 2, 0.2 gm. of both moist fibrin and  $\text{Na}_2\text{CO}_3$ . After 24 hours' digestion, No. 1 gave a distinct tryptophane-reaction; No. 2 gave a marked reaction, as also good biuret-reaction, and the fibrin had disappeared.

Similar experiments with Orange-peel, leaves of Spinach and Celery, and fruit of Banana, extending to 48 hours, gave no evidence of digestion. On the other hand, in that time digestion was effected by Hyacinth-bulb.

**Albumin and Casein.**

Only a few experiments were made with albumin. The form in which it was used was a 50 % watery solution



of raw white-of-egg. The vegetable material was Cucumber (green), Mushroom, leaves of *Tropaeolum* and Lettuce, and the root of the Carrot. In only one instance, that of the Mushroom, was there distinct evidence of digestion.

5 grms. of bruised Mushroom were placed in each of two bottles with 40 cc. of dilute (50 %) chloroform-water: to No. 1, nothing further was added; to No. 2, 5 cc. of the albumin-solution. After 24 hours' digestion, No. 2 gave marked biuret and tryptophane-reactions; No. 1 gave no biuret, but distinct tryptophane.

Two samples of casein were used: 'commercial' and 'pure' casein. In two instances, the Melon and the Mushroom, the casein was undoubtedly digested, whilst in others the result was negative.

25 cc. of Melon-juice, with 25 cc. of chloroform-water, were placed in each of two bottles: to No. 1, nothing was added; to No. 2, 0.3 grm. of pure casein. After 22 hours' digestion, No. 2 gave a strong tryptophane-reaction; No. 1 gave a distinct reaction, as it did at the commencement of the experiment.

A similar experiment with the Mushroom gave essentially the same result.

I failed to obtain evidence of digestion of casein by the Cucumber, the leaves of *Phalaris* and *Tropaeolum*, or by Orange-peel.

It occurred to me that although casein had proved to be relatively indigestible, yet the caseinogen of milk might prove to be more tractable, and this I found to be the case in several instances.

Since the Mushroom and the juice of the Melon had been found to digest casein, it was a foregone conclusion that they would also digest the caseinogen of milk.

15 cc. of Melon-juice, with 20 cc. of chloroform-water, were placed in each of three bottles, Nos. 1, 2, 3; the juice in No. 2 had previously been boiled; to No. 1 and 2, 15 cc. of skim-milk were added, to No. 3, 15 cc. of distilled water. After 24 hours' digestion, No. 1 gave a very strong tryptophane-reaction; No. 2, no reaction; No. 3, a faint reaction.

Similar results were obtained with the Mushroom, 5 grms. of the solid substance being used.

Less marked evidence of digestion of milk was obtained with Orange-peel, and with the bulbs of the Tulip and the Hyacinth, as also with the Banana. No digestion was observed with the Turnip, the Vegetable Marrow, the Pear, the Apple, with the leaves of the Cabbage, the Lettuce, and the Spinach, or with the 'milk' of the Coco-nut, in 19 hours.

These experiments generally included a control-bottle containing the mixture of chloroform-water and milk, without any vegetable substance at all: in no case did the contents of the control give any trace of tryptophane-reaction.

#### TRYPTOPHANE IN PLANTS.

It will have been observed that, in the foregoing account of the experiments, mention is incidentally made of the presence of tryptophane in the expressed juices or in the watery extracts of plants: for instance, in the case of the Banana, the Melon, the yellow (but not the green) Cucumber, the Vegetable Marrow, the Tomato, among fruits; of the bulb of the Onion (strong), and of the root of the Turnip. I have not found it in the juice of the Orange, the Apple, or the Grape, nor in extracts of the tubers of the Potato and the Jerusalem Artichoke, of Green Peas, of Wheat-Germ, or of any of the shoots or leaves mentioned.

I have made a few further observations upon the occurrence of this substance, and have found it in the 'milk' of the Coco-nut; in extracts of seedlings of the Bean (*Vicia Faba*) 2-3 inches in height, of the Scarlet Runner (*Phaseolus multiflorus*) 6-8 inches in height, and of the Pea (*Pisum sativum*) a foot high, excluding the cotyledons in all cases. I have not found it in seedlings of the Maize, apart from the seed: nor in the shoots of the Asparagus, nor in etiolated shoots produced by germinated tubers of the Potato and of the Jerusalem Artichoke, though it was present in the potato-shoots after they had turned green in consequence of exposure to light.

These facts are insufficient to suggest any general explanation of the conditions of the formation of tryptophane in the plant-body. In the case of fruits, its presence is certainly associated with the process of ripening; in the case of seedlings, with the presence of a supply of reserve proteid. Inasmuch as tryptophane is a product of catabolism, the detection of it in the tissues may serve as a means of determining the exact seat of these processes and the conditions under which they take place.

#### OXIDASE AND ENZYME.

If tincture of guaiacum be treated with an oxidizing agent, such as chlorine-water or potassium permanganate ( $\text{KMnO}_4$ ), it is oxidized and assumes a deep blue colour. It was ascertained by Schönbein (5) and others that various vegetable substances, for instance, roots, stems, leaves, and flowers of the Dandelion (*Leontodon Taraxacum*), the rind of the potato, &c. similarly effect the oxidation of guaiacum at the expense of the oxygen of the air. More recently, Bertrand (6) has found that the reaction is induced by many parts of plants—the roots of the Beet, the Carrot, the Turnip, and the Dahlia; the shoots of the Asparagus; the rhizome of *Canna*; the stems and leaves of Lucerne, Clover, and Rye-Grass; the leaves of the Jerusalem Artichoke (*Helianthus tuberosus*), and of the Beet; the fruits of the Apple, the Pear, and the Quince; the petals of *Gardenia*; the latex of species of *Rhus*; and he has also ascertained that the reaction is due to the presence of an extractable organic substance that may be generally termed *oxidase*.

Schönbein further observed that portions of plants that cannot induce the direct oxidation of guaiacum can do so indirectly, if a small quantity of hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) be present, the oxidation being effected by the oxygen set free on the decomposition of the  $\text{H}_2\text{O}_2$ . This property, indicative of a lower degree of oxidative activity, is very commonly possessed by plants, and attaches to a substance distinguished as *peroxidase*.



It is probable that peroxidase is a modification of oxidase. Schönbein observed that if the watery extract of a part of a plant giving the oxidase-reaction with guaiacum be allowed to stand for some hours, it loses this property, but is still capable of oxidizing guaiacum in the presence of  $H_2O_2$ . The converse change has not yet been effected. Moreover, a substance or liquid giving the oxidase-reaction also gives the peroxidase-reaction.

With these facts in mind, I took the opportunity of applying the guaiacum-test, in one form or other, to all the various parts and juices of plants that I employed in the digestion-experiments. I found that, with a few exceptions, they all gave either the oxidase- or the peroxidase-reaction. My results are as follows.

*Oxidase-reaction*: given by tissue and watery extract of the Mushroom; extract of *Cuscuta* shoots; tissue of the Pear; rind of the Apple, the pulp only when quite ripe; cortex of tuber of Potato; tuber of *Helianthus tuberosus*; root of Dandelion; feebly by the root of the Carrot; ripe Grapes (especially black); watery extract of leaves and stems of the Lettuce.

*Peroxidase-reaction*: given by the juice of the Melon, Cucumber, and Vegetable Marrow; the tissue, but not the juice, of the Tomato; the latex of *Euphorbia Characias*; the milk of the Coco-nut; extract of Green Peas; extract and root of the Turnip; the tissue of the bulb of the Onion, the Tulip, and the Hyacinth; the rind (but not the pulp or the juice) of the Orange; Wheat-germ; the pith of the Potato-tuber; the tissue of the ripe Banana and of the Beet-root; all the non-laticiferous leaves investigated. None of these gave the oxidase-reaction.

It will be seen that my results do not exactly agree with those of Bertrand. The divergence is, I believe, due probably to seasonal differences in the condition of the parts examined. It is at any rate clear that the nature of the reaction given by fruits depends upon the degree of ripeness.

So far as I am aware, there is at present no satisfactory explanation of the physiological significance of the presence

of oxidases and peroxidases in plants. I cannot presume to offer one now, as I have merely glanced at the subject. But I have observed a fact that seems to be worth recording and bears directly upon it:—it is that when I have found a liquid or a tissue to give a good reaction with guaiacum, whether with or without  $H_2O_2$ , I have also found it to be proteolytic; whereas, when its guaiacum-reaction is wanting, it is deficient in proteolytic activity. For instance, having observed that neither the juice nor the pulp of the Orange gave any guaiacum-reaction, whilst the peel gave a strong peroxidase-reaction, I found the peel to be actively proteolytic but not the juice or the pulp (see p. 246). Exactly the same occurred in the case of the Apple (see p. 245). Again, the pulp of some white Spanish grapes slowly gave a faint peroxidase-reaction, and was found to have little proteolytic action on Witte-peptone: some fully-ripe English hot-house grapes, on the contrary, both white and black, gave the oxidase-reaction and digested Witte-peptone.

The association of these oxidizing substances with enzymes may be only a coincidence, or it may indicate a relation between oxidative and enzymotic activity. It is one that has already attracted attention, for it was thought at one time that the enzymes themselves reacted with guaiacum. But this is not the case: papaïn, for instance, gives no reaction. Assuming, as seems more probable, that co-existence means correlation, it is not an impossible suggestion that oxidase or peroxidase may be concerned with the formation of the enzyme, whether protease, glucase, lipase, &c.: that, for instance, their oxidative action may determine the liberation of the enzyme from its zymogen.

This suggestion may perhaps supply the true physiological interpretation of Raciborski's (7) important observation that the sieve-tissue of plants gives the peroxidase-reaction, as also of the fact that the reaction is likewise given by latex. The latex of the Papaw and of the Fig is known to actively digest proteids; and my observations on *Euphorbia Characias* and on the Lettuce (p. 247) indicate that this is true of

these plants also. The marked proteolytic activity of the Cucurbitaceae, of which I have given several instances, taken in connexion with the great development of the sieve-tissue in plants of this Order, suggests that the proteases are specially located in this tissue. This being so, there would seem to be a definite relation between the oxidative and the digestive properties of the contents of the laticiferous and sieve tissues.

#### CONCLUDING REMARKS.

The experiments previously described suffice to prove that the juices or the tissues of various parts of the most widely different plants so act on certain proteids, whether contained in them or added to them, as to give rise to a substance giving a reaction similar to that of tryptophane with chlorine-water.

It has been tacitly assumed throughout that the substance in question is actually tryptophane: but inasmuch as the conclusions to be drawn entirely depend upon it, it is necessary that the assumption should be justified. I have not, I admit, isolated the substance, and so placed the matter beyond doubt; that is a task that could only be successfully undertaken by a professed physiological chemist; but I am able to adduce other convincing evidence. It is known that if a liquid, which has given the tryptophane-reaction, be shaken up with some amyl alcohol, the pink chlorine-compound dissolves in the alcohol which separates out as a supernatant layer coloured pink. If this coloured solution be examined spectroscopically, the spectrum is found to present a well-marked absorption-band in the green, on the yellow side of the Thallium-line ( $571-540 \mu\mu$ ). I have applied this test with success to several of the digestion-liquids, and have in all cases found that the chlorine-compound dissolves in amyl alcohol, and that the pink solution gives the absorption-band characteristic of the chlorine-compound of undoubted tryptophane. I conclude, therefore, that the substance which gave



the tryptophane-reaction in my experiments is actually the chemical substance known as tryptophane.

The formation of tryptophane in the experiments leads to the further conclusion that proteolysis must have taken place, for the presence of this substance is evidence of proteolysis. Hopkins and Cole (8) have shown that tryptophane is either an indol-amido-propionic acid, or a skatol-amido-acetic acid : in either case it cannot be regarded as other than a product of the disruption of the proteid molecule.

The experiments therefore prove that the various vegetable substances employed effected proteolysis. Inasmuch as it took place in the presence of antiseptics, such as HCN and chloroform-water, the chemical action cannot be attributed to micro-organisms. On the contrary, it is to be ascribed to a proteolytic enzyme contained in the juices or the tissues themselves.

If this be so, then I have succeeded in demonstrating that a proteolytic enzyme is widely distributed in plants ; and it may be inferred that it is much more generally present than I have shown it to be. If it is present in plants belonging to the Chenopodiaceae, the Nyctaginaceae, the Euphorbiaceae, the Cruciferae, the Geraniaceae, the Ampelidaceae, the Rosaceae, the Leguminosae, the Umbelliferae, the Cucurbitaceae, the Compositae, the Liliaceae, the Graminaceae, and the Musaceae, there is no reason why it should not equally be found in plants of other Natural Orders. Nor is it by any means confined to Phanerogams. I have demonstrated its presence in the Mushroom, among the Fungi ; and in the Hart's Tongue Fern, among Pteridophyta. I confidently anticipate that it will be duly discovered in the remaining groups of Cryptogams, the Bryophyta and the Algae.

The next point to be considered is the probable nature of the enzyme. In the previously known cases, the Pine-Apple, the Papaw, the Fig, *Nepenthes*, Yeast, Bacteria, and seeds, the evidence goes to prove, as I have explained in the paper (1) already mentioned, that the enzymes are allied to the trypsin of animals, since they both peptonize and proteolyse actively.

Amongst the plants that I have examined, there are only two, the Melon and the Mushroom, that contain enzymes which approach those just mentioned in their power of peptonization and proteolysis. Whilst all the others readily proteolysed Witte-peptone, their action on the higher proteids, so far as it was tested, was relatively feeble and in some cases altogether wanting. It may be that the precise conditions favourable for peptonization were not afforded in the experiments: that is a point for future investigation. But taking the facts as they stand, it is an inevitable conclusion that if in some cases, such as the Melon and the Mushroom, the enzyme may be regarded as a vegetable trypsin, this view cannot be extended to the others. It seemed to me, at first, that I had come upon an altogether new type of enzyme, an idea that occasioned a certain amount of temporary misgiving as to the accuracy of my observations. But it was pointed out to me by my colleague Professor Gotch, that within the last year Cohnheim (9) has described an enzyme, formed in the mucous membrane of the small intestine, which actively proteolyses peptone and casein but does not act upon the higher proteids. It is to this enzyme, termed 'erepsin' by Cohnheim, that the apparently new proteolytic enzyme of plants would correspond. It would appear, therefore, that plants form two distinct kinds of proteases, the one a trypsin, the other an erepsin; and so far as the facts go, they indicate that the former is generally associated with depositories of proteid nutriment, such as seeds, fruits, bulbs, laticiferous tissue, &c., the latter with ordinary foliage-leaves, stems, and roots. But further research is required in order to definitely establish this distinction.

I cannot too strongly emphasize the point that the results detailed in this paper must be taken as applying only to the particular season of the year during which the experiments were made; that is from August to November. I have noticed that even within this period certain variations presented themselves. The investigation of the various parts of plants, especially of leaves, at different times of the year, will

certainly yield a great deal of additional information. My observations on fruits indicate that the digestive activity, both peptonizing and proteolysing, is greatest when they are fully ripe, a condition that may be regarded as the first stage of decay.

It would be premature at present to attempt any minute discussion of the physiological significance of the wide distribution of a proteolytic enzyme in the body of the plant: it is obvious that what has hitherto been regarded as exceptional, must now be recognized as the rule, and this must profoundly affect many physiological conceptions. The most interesting point is that, in respect of their distribution, the proteases are now brought into line with the enzymes which are concerned with the carbohydrate metabolism of the plant. Just as diastase was, step by step, discovered to be everywhere present in the body of the plant, so now the same has been done for the proteolytic enzyme. No doubt the analogy also holds good with regard to their respective functions. Just as diastase facilitates the transference of temporarily deposited starch, so the proteolytic enzyme renders possible the distribution of the elaborated proteids. It is remarkable that this obvious analogy should not already have led to a search for a generally distributed proteolytic enzyme: but the difficulties in detecting and following the proteids in the tissues, difficulties which do not exist in the case of starch and sugar, are no doubt the sufficient reason.

In conclusion, I may further point out that the case of 'insectivorous' plants no longer stands alone. If leaves generally, or at any rate commonly, produce a proteolytic enzyme, it ceases to be remarkable that a similar enzyme should be formed by the leaves of certain of the 'insectivorous' plants. The peculiarity of these plants is now limited to this—that their enzyme should be poured out at the surface, so that it digests proteids supplied from without by the captured insects; whereas in ordinary plants the enzyme is retained within the tissue to digest, and so to render mobile, the proteids that are formed there.



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## NOTES.

**NOTES ON THE HISTOLOGY OF THE SIEVE-TUBES OF CERTAIN ANGIOSPERMS.**—In continuation of the researches on the sieve-tubes of Gymnosperms, which were published in the *Annals of Botany*, vol. xv, No. lx, December, 1901, the sieve-tubes of certain Angiosperms have been examined in detail by methods similar to those previously employed.

The sieve-tubes of *Vitis vinifera*, *Wistaria chinensis*, *Cucurbita maxmia*, *Tilia europaea*, and *Viscum album* have been studied with special reference to their 'connecting threads' and means of inter-communication, and they have been found to agree in their general characteristics and essential structure with the sieve-tubes of the several species of *Pinus* already described.

In the mature sieve-tubes of these five plants, the end walls or sieve-plates are traversed by relatively large slime-strings, and each slime-string is enclosed in a callus-rod. In the radial and tangential walls slime-strings occur in groups in large or small shallow pits, and, except in the case of *Viscum album*, each of these groups, composed of some three to six fine slime-strings, is contained in a callus-rod. Such a group seen in surface view constitutes a 'sieve-field.' The structure of these lateral sieves and sieve-fields is similar to that of the sieve-plates of *Pinus sylvestris*, &c. A median dot is usually visible on each thread.

In *Viscum album* the lateral walls between two sieve-tubes are crowded with groups of fine threads in small shallow pits, but no callus-reaction is given by the cell-wall in their neighbourhood. Callus, however, does occur in the end-wall sieve-plates in connexion with the slime-strings. With the approach of winter, the callus-rods increase in size at their free ends, which unite to form callus-pads on both the end and side walls. The slime-strings perforate these callus-masses so as to unite the contents of adjacent sieve-tubes.

With the increase in thickness of the callus-masses the slime-strings become progressively attenuated, and in the case of those sieve-tubes which function for a year only the callus finally blocks up the pores leading from one sieve-tube to another.

Connecting threads also occur in some abundance between sieve-tubes and other elements of the phloem. Between the sieve-tubes and their companion cells (as Gardiner and Hill had already observed) threads are very numerous and very short, for the cell-walls are furnished with a great number of deep pits elongated in the horizontal direction.

Sieve-tubes are placed in communication with adjacent bast-parenchyma cells by threads, which are in some cases fairly numerous and are usually short and occur in small and deep pits.

Cells comparable in the structure of their threads to the albuminous cells of *Pinus sylvestris*, &c., apparently occur in the phloem of *Vitis vinifera*.

In the cases just cited the groups of threads are covered in winter by callus-pads, which however are formed only on the sieve-tube side of the groups, and the connecting threads can usually be seen to traverse the callus-masses.

It is interesting in this connexion to notice that sieve-tubes appear to be the only elements of the bast in which callus is formed.

The development of the terminal sieve-plates is very difficult to investigate, owing to the thinness and delicacy of the pit-closing membrane, but the history of the lateral sieves can be more easily followed. The development of the sieves in the radial and tangential walls appears to be analogous to the development of the sieves in the radial walls of the sieve-tubes of species of *Pinus*, and the sieves in the radial and tangential walls of most Angiospermous sieve-tubes appear to pass through similar developmental stages to those which have been described for such Gymnosperms as *Pinus*. Groups of fine threads can be seen in the lateral walls of the youngest sieve-tubes, which by the action of ferments (as it would appear) are bored out and converted into slime-strings, the cellulose membrane in the immediate vicinity being at the same time altered into callus.

In this way the callus-rod enclosing a small group of slime-strings is produced.

All stages in the process have been seen. The precise mode of development of the end-wall sieve-plates has not yet been seen very



clearly. In the youngest stages there appear first to be small groups of threads in little secondary pits; very soon little rounded and bason-shaped masses of callus arise in the little depressions on either side of the thin membrane, and these finally unite to form a short callus-rod. In *Wistaria chinensis* and in *Vitis vinifera* three to five threads apparently of the nature of slime-strings have been seen in each callus-rod in sieve-plates of this age, but more detailed and careful examination is demanded before any conclusive statement can be made.

In the next older tube the boring out of these strings has proceeded further, and given rise to the single slime-string in each callus-rod so characteristic of the mature terminal sieve-plates of Angiosperms.

The views put forward to explain the origin of the callus in species of *Pinus* seem to apply with equal force in the present case: for the callus-rods appear to be formed by local alteration of the cell-wall, and to arise at first as cylindrical rods, which subsequently become hexagonal owing to growth and mutual pressure in the confined area of a pit.

As to the further production of callus towards the end of the season, it would appear that the protoplasm of the sieve-tube commences to form callus, which not only builds up the callus-pads on the callus-rods of the terminal and lateral sieve-plates, but also deposits callus-substance around all the groups of threads which connect the sieve-tubes with other elements of the phloem.

It has become clear during the progress of these researches that it is the slime-strings which are of primary importance to the sieve-tubes, and that the callus, though no doubt also playing an important rôle in the life-history of the sieve-tube, must be regarded as of altogether secondary importance, being for the most part subservient to the slime-strings and active or living sieve-tube contents, of which the slime-string itself is merely a continuation.

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Nov. 11, 1902.

**NOTE ON THE DISPERSAL OF MANGROVE SEEDLINGS.—**

During the year 1901 and for three months of the present year I was engaged in marine biological work for Sir Charles Eliot, K.C.M.G., H.B.M. Consul-General at Zanzibar and Commissioner for British East Africa. During all this time I was interested in, and at first much

puzzled, by the conditions under which I found mangroves growing in these regions.

The coasts of the whole of British and German East Africa are composed of a hard coral limestone of peculiar properties. (For a full account of this see my papers in the Proc. Phil. Soc. of Cambridge, vol. ix, pt. vi, Part i, 'On the Coral Reefs of Zanzibar.')

The erosion of the waves has cut down this rock so that at low-tide there is an almost perfectly plane surface of rock, sloping gradually from the base of the cliffs to low-water level. In creeks and sheltered places generally, near high-water mark, this rock plane is full of irregular small holes and crannies, but no loose stones or deposits, other than a very thin coating of fine mud, interrupt its uniformity.

On this hard surface, sending their roots into the crannies, the greater number of the mangroves of Zanzibar flourish so well that a considerable trade is carried on from Chuaka Bay<sup>1</sup> in their stems. (These are used in the building of all the Arab and native houses of Zanzibar, being too hard for the jaws of the termites.) Only occasionally do we find mangroves growing in mud and see the demonstration of the well-known method of planting, viz. by the impact of its fall forcing the root of the embryo into the mud. In the majority of cases one finds the embryo placed in one of the holes of the rock, which is usually of but slightly larger diameter than itself. Obviously it did not fall by chance into this position; suitable holes are not so numerous, and the insertion of the radicle into them not so easy as this would imply. Moreover, I have often observed embryos neatly planted in these holes at a distance of more than a hundred yards from the shade of the nearest possible parent tree, and in a few cases at a distance of miles.

How this planting could be done, except by human hands, remained for a long time a mystery to me. The solution came when I noticed the frequency with which I met embryos floating in the sea, being carried out of the bay by the strong tidal currents. Often I passed through fleets of them, as it were, all floating in the same peculiar way, viz. vertically, with the leaf-bud just projecting from the water. (See the figure.) A consideration of the shape of the radicle shows that not only is there a perfect adjustment of the specific gravity of the whole to that of the sea water, but a peculiar distribution of it in

<sup>1</sup> A large and very shallow bay on the east coast of Zanzibar island, where most of my time was spent.

order that the *thick* end may sink, instead of floating uppermost, as it would if the specific gravity were the same throughout. Both kinds of embryo, the thick and the slender, float in the same way.

On reaching shore the embryos are planted by the insinuation of the root-tip into any softness or crevice of the bottom by the falling

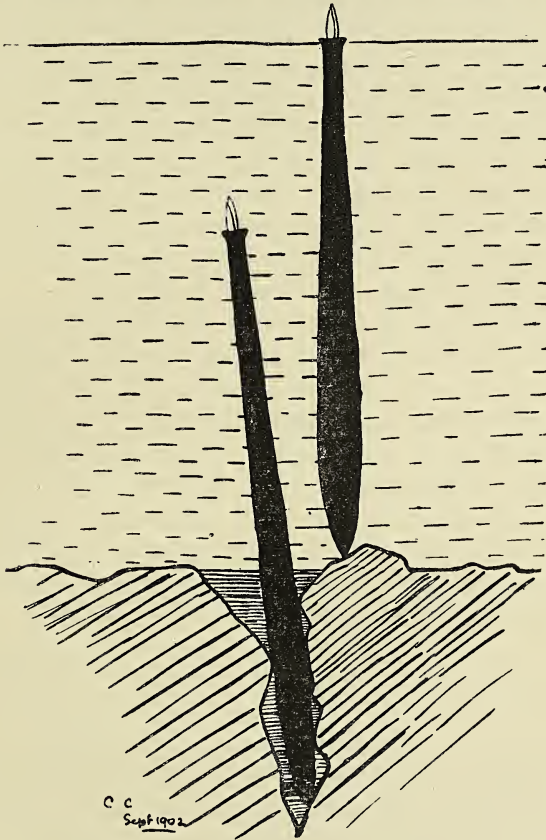


FIG. 16.

tide. The figure represents a section of the rock of the shore across a crevice, which is full of mud, as shown by the dark shading. The vertical embryo is in the position in which it floats freely. The tide has fallen until its root-tip engages a projection on the bottom. The ripples will now cause its oscillation about the tip, which will thus be kept slowly boring down into any mud or crevice present as the



falling tide brings the weight of the embryo on to its point, until it has reached the position of the lower specimen in the figure.

The success of this method depends upon the action of ripples of the water, but on an exposed shore the waves will merely throw the embryo about as any other floating stick. Suitably shaped and fairly numerous crevices in the rock are usually met with near high-tide mark, the surface of the flats lower down being smoother and its crevices too shallow, or filled in with hard sand. In short, the conditions requisite to planting are generally those suitable for the life of the adult trees, but, as in the case of other trees, those conditions are sometimes found where the embryo can never develop into the adult. Embryos are often planted too low down the shore (I have even met with one, bearing two unfolded leaves, at low tide in the sand of the boat channel of the reef on the open coast), but in this case they will be usually floated off again by succeeding tides.

There are thus *two* adaptations of the mangrove, ensuring that, in the case of those trees which are growing in mud, too many embryos shall not be swept out to sea, and also that those which are so removed shall have a good chance of taking root in fresh localities. The mangrove has thus an effective means of dispersal, and it is probable that the juxtaposition of trees from different sources, whereby continued in-and-in fertilization is avoided, is just as important for them as for the great majority of living things. Furthermore, this adaptation for dispersal enables the embryos to be planted on surfaces to which the formerly known method is inapplicable.

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**EXPLOSIVE DISCHARGE OF ANTHEROZOIDS IN FEGATELLA CONICA.**—*Fegatella* (*Conocephalus*) *conica* is one of the commonest liverworts in the neighbourhood of Leeds. It grows in great abundance in moist and shaded places, especially on stones beside streams. In the beginning of July a large supply of male plants was collected, bearing young antheridial receptacles, which, as is well known, are sessile in this genus, and have the form of oval cushions, each situated at the anterior end of one of the branches of the thallus. Most of these plants were put into shallow vessels, covered with sheets of glass, and set in a shaded place. After a few

days the plants were examined for the purpose of selecting material to show the development of the receptacles, and whilst looking over them in bright sunlight the writer observed a number of jets of fine spray arising from the upper surface of the plants. On closer examination it was found that in every case these jets, which issued in an explosive manner and sometimes reached a height of above two inches, proceeded from the little conical prominences with which the upper surface of the male receptacle is studded. On holding a glass slide a little above the surface of a receptacle and catching the spray as it escaped, it was found that it consisted of water containing antherozoids, some of which were still enclosed within the wall of the mother-cell, whilst others were free. The antherozoids of *Fegatella* are much larger than in the remaining Marchantiales which have been examined, and approach in this respect those of *Pellia*; the spirally coiled body consists usually of two complete turns, the anterior end bearing two long cilia, whilst in most cases the thicker posterior end carries a small vesicle, doubtless representing the remains of the mother-cell.

The writer has found that the discharges only take place on warm, sunny days, and are especially frequent when the plants are exposed to direct sunlight; they were not observed on dull days, nor when the plants were shaded. On bringing plants out of shade into sunlight the discharges began almost immediately, continued in rapid succession for several minutes, then became less frequent, and finally ceased. This phenomenon occurs in *Fegatella* plants growing in their natural surroundings, the writer having, after careful watching, several times observed it on the spot. It does not appear to have been hitherto described by writers on the Bryophyta. In some Fungi, e.g. *Pilobolus*<sup>1</sup>, *Ascobolus*, the spores are violently ejected by means of water-pressure giving rise to jets of spray.

*Fegatella* is strictly dioecious, and very often the male and female plants are widely separated from each other, since they do not usually occur mingled together, but form large patches, each consisting of either male or female plants. It is not at all uncommon to find a patch of female plants in fruit, although removed several feet from the nearest male plants, and it is reasonable to suppose that the fertilization of the archegonia may possibly have been effected in consequence of the antherozoids being ejected explosively from the

<sup>1</sup> Cf. Scott, Structural Botany, pt. ii, p. 230.

male plants and carried to the female plants by air-currents, each antherozoid being surrounded by a thin film of water.

Goebel<sup>1</sup> has suggested that the fertilization of the archegonia in the dioecious Marchantiales, which so often form isolated patches, might be effected by means of rain-drops falling upon the male receptacles and then splashing over the female plants. In the case of Mosses, in which similar conditions prevail, it was suggested by Kienitz-Gerloff<sup>2</sup>, and later confirmed by the observations of Gayet<sup>3</sup>, that small animals, especially insects, creeping over the patches of male and female plants may, especially in dry seasons, be instrumental in bringing antherozoids into contact with the archegonia.

The examination of sections through antheridial receptacles of different ages shows that the development of the antheridia is accompanied by that of air-spaces, which arise in the same manner as the chambers of the thallus, and whose sides are formed of cells containing abundant chloroplasts. Each antheridium becomes during its development sunk in a deep cavity, formed in essentially the same way as the air-spaces. As the antheridium grows in size, its cavity becomes flask-shaped, having a long neck opening above on the surface of the receptacle by a small pore which occupies the summit of one of the conical prominences already mentioned. Owing to the lateral pressure exerted by the growing antheridia, the air-spaces between the antheridial cavities become compressed and finally obliterated below, but in the upper portion of the receptacle they remain as wide chambers, each opening above by a pore of the 'compound' or 'barrel-shaped' type, the cells surrounding it being arranged in four or five superposed rings. The cells lining the chamber project inwards, and are often long, pointed, and colourless: exactly similar pointed cells are found in the air-chambers of the thallus, but they do not appear to have been previously described in the case of the male receptacle. As shown by the experiments of Kamerling<sup>4</sup>, it is from these colourless cells that water-vapour is given off into the air-chambers of the thallus, and very probably they have the same function here. In vertical sections the mature receptacle is seen to be divided into three well-marked zones:—(1)

<sup>1</sup> Organographie der Pflanzen, p. 310.

<sup>2</sup> Botanische Zeitung, 44. Jahrg. (1886), p. 250.

<sup>3</sup> Ann. des Sci. Nat., sér. 8, t. 3 (1897), p. 241.

<sup>4</sup> Zur Biologie u. Physiologie d. Marchantiaceen, Flora, 1897, p. 50 of reprint.



an upper zone of chlorophyll-bearing tissue, containing numerous air-spaces and traversed by the passages leading down to the antheridial cavities; (2) a middle zone of compact tissue, in which are embedded the antheridia, and which consists of large colourless cells, including scattered mucilage-sacs; (3) a lower zone continuous with

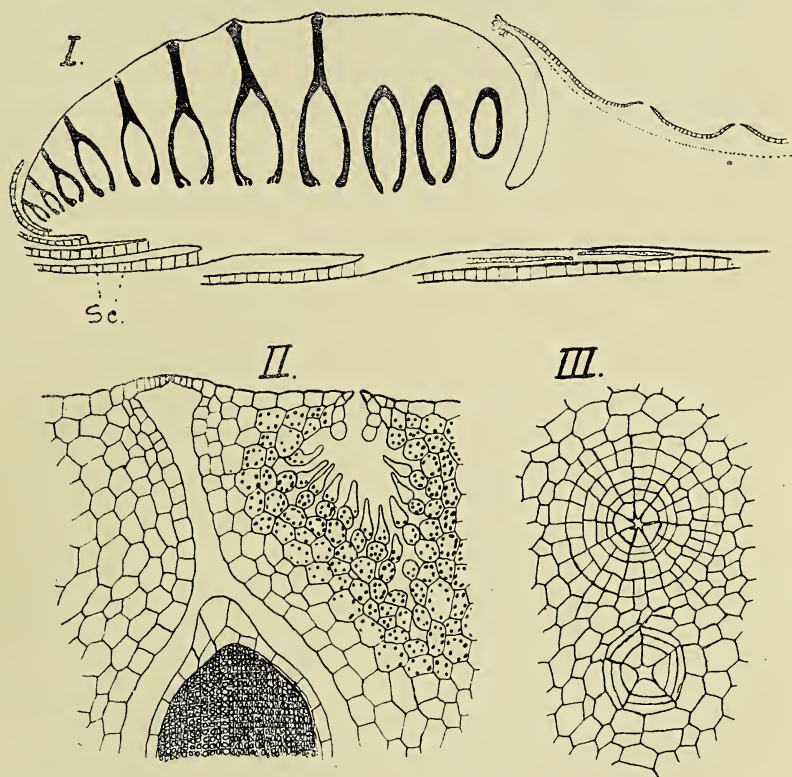


FIG. 17.—I. Longitudinal section through anterior end of thallus, with a male receptacle;  $\times 20$ . The antheridial cavities are deeply shaded; *Sc.*, ventral scales. II. Part of the same section,  $\times 200$ , showing on the left the upper portion of an antheridium and its cavity, on the right an air-chamber, opening by a 'barrel-shaped' pore. III. Surface-view of part of receptacle, showing two pores; the upper opens into an antheridial cavity, the lower into an air-chamber.

the midrib of the thallus and consisting of compact tissue, traversed by strings of mucilage-cells, and bearing the rhizoids and ventral scales beneath.

From these structural features it is clear that the male receptacle

has a well-developed assimilating tissue system, together with abundant mucilage-containing cells. Now, under circumstances which favour assimilation, e.g. strong light, sufficient warmth, and a dry atmosphere, an active transpiration-current will be set up, water-vapour being given off in the air-spaces through the pointed inward-projecting cells. To make good this loss, water will pass to the receptacle through the rhizoids. A large part of the water is absorbed by the mucilage-cells, and if any of the antheridia are ripe, the walls of the antheridium itself, as well as those of the antherozoid mother-cells, being at this time largely mucilaginous, also take up water and become swollen. The antheridia being closely packed together considerable pressure is thus set up, resulting in the expulsion of the antherozoids.

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#### ALGOLOGICAL NOTES.—

#### IV. REMARKS ON THE PERIODICAL DEVELOPMENT OF THE ALGAE IN THE ARTIFICIAL WATERS AT KEW.—

Whilst working out the algal flora of the Royal Botanic Gardens at Kew for publication by the authorities, I have made several observations on the periodicity of the flora, which I wish to remark upon more fully here. The flora <sup>1</sup> was found to be built up of a hot-house element, consisting for the greater part of Cyanophyceae; of the Thames element, due to the universal use of river-water throughout the gardens; and, lastly of the open-air terrestrial element.

The blue-green Algae, which abound in every moist hot-house, have received much attention from continental algologists, with the result that they are fairly well known. How far some of the forms may be looked upon as truly exotic and as introduced together with the higher plants, cultivated in the houses, it is difficult to say <sup>2</sup>. It should be observed that some of these blue-green forms (e. g. *Symphyosiphon*

<sup>1</sup> The constitution of the flora will be more fully discussed in the introduction to the algal flora of Kew Gardens. (See The Fauna and Flora of the Royal Botanic Gardens, Kew, which is to be published in the course of this year.)

<sup>2</sup> A large number of the blue-green Algae, which occur in the moist heat of greenhouses, have also been observed in hot springs of different parts of Europe, notably those of Carlsbad; this seems to show that they are now truly indigenous in Europe, but can only exist under the peculiar conditions (i. e. high temperature and moisture) found at these particular spots.

*Hofmanni*, Kütz., *Symploca thermalis*, Kütz., *Gloeocapsa caldariorum*, Rabh., &c.) may have been originally introduced into our parts with greenhouse plants; since reliable observations on the Algae occurring in any given district do not date back very far, whereas the cultivation of exotic plants in hot-houses is an old practice. Many of the blue-green Algae (e. g. *Scytonema cinereum*, Menegh., *Symphysiphon Hofmanni*, Kütz., &c.) are so absolutely characteristic for every moist hot-house, that it seems plausible that in our parts they first originated here, and only later on escaped to other (more natural) localities. I have also observed these characteristic species in many of the hot-houses of the gardens at Glasnevin, near Dublin.

The hot-house flora is practically equally developed during the whole year, the conditions under which it exists remaining uniform. The flora outside, however, shows quite a different character in the winter and in the summer, and attains its maximum development in August and September; in the winter only the hardy genera of Algae (*Vaucheria*, *Oedogonium*, *Cladophora*, *Rhizoclonium*) are present, whilst the smaller forms (Protococcoideae, &c.) are absent. Desmids, not very common even in the summer<sup>1</sup>, are quite absent, as also most of the other Conjugates, *Spirogyra crassa*, Kütz., being the only species that can be met with all the year round. This species usually has a very well-developed sheath, often as much as one-fifth of the diameter of the cell in thickness<sup>2</sup>, and the hardness of the species is probably due to its presence. Desmidiaceae first appear in March, and species of *Scenedesmus* and *Pediastrum* at the beginning of April or a little before<sup>3</sup>. Even in the tanks in the warmer houses (e. g.

<sup>1</sup> Very few Desmids were also observed in the Plankton of the Thames; analysis of the river-water shows that a considerable percentage of calcium carbonate is present (cp. Algological Notes, III: Preliminary Report on the Phytoplankton of the Thames; Annals of Botany, vol. xvi, 1902, p. 581). I should like at this spot to mention that since the publication of my note I have received from Professor G. S. West a paper by his father and himself (A Contribution to the Fresh-water Algae of the North of Ireland, Trans. Royal Irish Acad., vol. xxxii, sect. B, pt. i, August, 1902) which contains an account of the Plankton Algae of Lough Neagh during the months May, 1900, and August, 1901. In the same paper reference is made to a publication of Borge's: 'Süßwasser-Plankton aus der Insel Mull,' in Algologiska Notiser, 4; Botaniska Notiser, 1897.

<sup>2</sup> A somewhat similar sheath is described for *Sp. lubrica* by Braun; cp. Verjüngung, 1851, p. 261.

<sup>3</sup> Most of these unicellular or few-celled forms probably only occur when the conditions of temperatures, and especially of illumination, begin to be favourable (cp. Zacharias, Über die Ursache der Verschiedenheit des Winterplanktons in



Water-lily House, *Victoria Regia* House) this periodicity is observable. Desmids and other Conjugates are very rare before April, although some of the unicellular Protococcoideae are here to be found all the year round.

Much has already been written about the periodicity in the development of certain Plankton organisms, but little attention in this respect has been paid to those inhabiting the deeper strata of the water. In all the artificial waters at Kew a regular sequence of forms was observed; it was most pronounced in the aquatics' tank near the Jodrell Laboratory, in which, by the removal every now and then of the mass of Algae that collects there, room is constantly being furnished for the development of other forms. Table I (see next page) illustrates this periodicity in the algal flora very well.

A careful perusal of this Table will show that the flora in any one month differs more or less considerably in character from that of the preceding or succeeding month. Undoubtedly the removal of the large masses of Algae, which collect in the space of every fortnight during the summer, considerably furthers this periodical development. Thus a little time after the tank had been thoroughly cleaned out, I met with the curious red oospores of *Sphaeroplea annulina*, a species which had been found in abundance in this tank in a former year, but had since not been observed. These oospores had probably been liberated during the cleaning-out of the tank, and in a few weeks gave rise to a large number of vegetative filaments of the *Sphaeroplea*.

However, even in the lake, where no such artificial agency comes into consideration, the periodicity of the flora is well marked, as will be seen by Table II (see next page).

*Enteromorpha intestinalis*, *Tetraspora gelatinosa*, and *Oscillaria nigra*, all very abundant in the summer months, especially the first and last species, are entirely absent in the early part of the year; they thus give the algal flora of the summer an entirely different stamp to that of the winter. In addition to this we may note the development of the Desmidiaceae, which is, however, relatively poor in the calcareous waters of Kew, as already mentioned.

*Oscillaria nigra* also played an important part in the water-lily pond. In the earlier part of the year a *Cladophora* was the most abundant form here, and no trace of the *Oscillaria*

grossen u. kleinen Seen, Zoolog. Anzeiger, Bd. xxii, Nos. 577 and 578, 1899, p. 19, &c.).

I. Table illustrating the periodical development of Algae in the tank near the Fodrell Laboratory<sup>1</sup>.

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.
<i>Characium Sieboldi</i> , Braun . . . . .	—	—	—	—	—	—	—	+	+
<i>Chlamydomonas pulvisculus</i> , Ehrb. . . . .	—	—	—	+	+	+	+	+	+
<i>Chaetophora endiviaefolia</i> , Ag. . . . .	—	+	+?	—	—	—	—	—	—
<i>Draparnaldia plumosa</i> (Vauch.), Ag. . . . .	—	—	—	—	+	+	+	+	—
<i>Mesocarpus pleurocarpus</i> , De Bary . . . . .	—	—	+	+	—	—	—	—	—
<i>Spirogyra crassa</i> , Kütz. . . . .	+	+	+	+	+	+	+	+	+
„ <i>condensata</i> , Kütz. . . . .	—	—	—	—	—	+	+	—	—
„ <i>longata</i> , Kütz. . . . .	—	—	—	—	—	+	+	+	—
<i>Closterium acerosum</i> (Schrank), Ehrb. . . . .	—	—	—	—	+	+	+	+	+
<i>Sphaeroplea annulina</i> , Ag. . . . .	—	—	—	—	+	+	—	—	—
<i>Cladophora fracta</i> , Kütz. . . . .	—	—	—	—	—	+	+	+	+
<i>Ulothrix radicans</i> , Kütz. . . . .	—	—	—	—	+	—	—	—	—
<i>Scidium arbuscula</i> , Braun . . . . .	—	—	—	—	—	—	—	—	+
<i>Tetraspora lubrica</i> , Ag. . . . .	—	—	—	—	—	—	+	+	—

II. Table illustrating the periodical development of Algae in the Lake at Kew<sup>1</sup>.

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.
<i>Vaucheria geminata</i> (Vauch.), D.C., var. <i>b. racemosa</i> , Walz . . . . .	—	—	—	+	—	—	—	—	—
<i>Mesocarpus pleurocarpus</i> , De Bary . . . . .	—	—	—	+	+	+	+	+	+
<i>Sirogonium sticticum</i> , Kütz. . . . .	+	+	+	+	—	—	—	—	—
<i>Spirogyra porticalis</i> , Cleve, var. <i>a. quinina</i> , Corda . . . . .	—	—	—	—	—	+	+	+	—
<i>Gonatozygon Brebissonii</i> , De Bary . . . . .	—	—	—	—	—	—	+	—	—
<i>Closterium Jenneri</i> , Ralfs. . . . .	—	—	—	—	—	+	+	+	—
„ <i>Dianae</i> , Ehrb. . . . .	—	—	—	—	+	+	+	+	+
<i>Euastrum venustum</i> , Bréb. . . . .	—	—	—	—	+	+	+	+	+
<i>Cosmarium crenatum</i> , Ralfs. . . . .	—	—	—	+	+	+	+	+	+
„ <i>quinarium</i> , Lund. . . . .	—	—	—	—	—	—	+	+	—
„ <i>isthmochondrium</i> , Nords . . . . .	—	—	—	—	+	+	+	+	—
<i>Staurastrum striolatum</i> , Pritch. . . . .	—	—	—	—	—	—	—	+	+
„ <i>polymorphum</i> , Bréb. . . . .	—	—	—	—	—	—	+	+	+
<i>Cladophora crispata</i> . . . . .	—	—	+	+	+	+	+	+	+
<i>Aphanochaete repens</i> , Braun . . . . .	+	+	+	+	+	+	+	+	+
<i>Enteromorpha intestinalis</i> , Link. . . . .	—	—	—	—	—	+	+	+	+
<i>Eudorina elegans</i> , Ehrb. . . . .	—	—	—	+	+	+	+	+	+
<i>Pandorina morum</i> , Ehrb. . . . .	—	—	—	+	+	+	+	+	+
<i>Gonium pectorale</i> , Müll. . . . .	—	—	—	+	+	+	+	+	+
<i>Pediastrum Boryanum</i> , Turp. . . . .	—	—	—	+	+	+	+	+	+
„ <i>pertusum</i> , Kütz. . . . .	—	—	—	+	+	+	+	+	+
<i>Tetraspora gelatinosa</i> , Desv. . . . .	—	—	—	—	+	+	+	—	—
<i>Coelastrum microporum</i> (Naeg.), Braun . . . . .	—	—	—	—	—	+	+	+	+
<i>Tetrapedia setigera</i> , Archer . . . . .	—	—	—	—	—	—	—	—	+
<i>Oscillaria nigra</i> , Vauch. . . . .	—	—	—	—	—	+	+	+	+

<sup>1</sup> + indicates the presence; — the absence of any form.

was to be found. During the summer months the latter genus, however, attained an enormous development, the whole bottom of the pond being covered with a thin blue-green film from which dense, almost black masses of various shapes stood up vertically in the water.

In the introductory remarks to the many algal lists that have been published I have as yet found little discussion on the periodicity of Algae. Hilse<sup>1</sup> in 1863 remarks of the Algae in the numerous small pools in the granite quarries of the Galgenberg near Strehlen: 'Sehr bequem ist auch hier der Wechsel der einzelnen Arten zu beobachten. So findet man in den Jahreszeiten Frühling, Sommer und Herbst in ein und derselben Wassersammlung sehr oft auch verschiedene Algen, ja manche dieser Species hat kaum eine Dauer von einigen Wochen (!)'. Bohlin<sup>2</sup> quite recently, in a very comprehensive account of the algal flora of the Azores, remarks: 'Il est sûr qu'une certaine quantité de ces plantes sont, plus qu'on ne le pense en général, liées à certaines saisons.' This remark applies to a tropical flora, but might equally well be applied to the development of an algal flora in our parts. The few remarks made by Schimper<sup>3</sup> on the periodicity of the water-plants all refer to the Phanerogams or to the Plankton. The writer is at present occupied with the collection of data concerning the periodical development of Algae in different parts of the South of England, and hopes at a future date to enter much more fully into this interesting subject.

F. E. FRITSCH.

JODRELL LABORATORY, KEW,  
October 30, 1902.

**NOTE ON ABNORMAL PLURALITY OF SPORANGIA IN LYCOPODIUM RIGIDUM, Gmel.**—Though few, if any, morphological generalizations are without any exceptions, one which has hitherto stood, I believe, without any recorded instances to the contrary is that in the Lycopodinae (excl. Psilotacea) the sporophyll

<sup>1</sup> Hilse, Neue Beiträge zur Algen- u. Diatomeen-Kunde Schlesiens, insbesondere Strehlens, Abhandl. d. Schles. Ges. f. vaterl. Cultur, naturw.-medicin. Abtheilung, 1863, Heft II, p. 57.

<sup>2</sup> Bohlin, Étude sur la flore algologique d'eau douce des Açores. Bihang till K. Svenska Vet.-Akad. Handlingar, Bd. 27, Afd. III, No. 4, 1901, p. 5.

<sup>3</sup> Schimper, Pflanzengeographie, p. 857.



subtends only a single sporangium. An exception has come at last, on a specimen of *Lycopodium rigidum*, Gmel., in the Glasgow University Herbarium; the sheet is labelled, Columbia, Hartweg, No. 1463.

The specimen shows no special peculiarities beyond that to be described; the other sporophylls and sporangia are of the normal type, even those in the immediate neighbourhood of the abnormality.

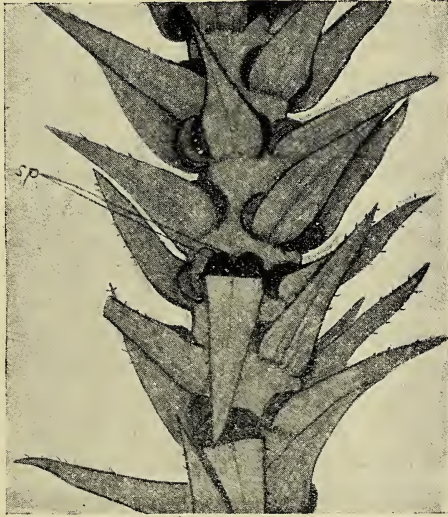


FIG. 18.

A single sporophyll, however, of slightly greater width than the average, subtends not one but two sporangia of slightly unequal size placed side by side (Fig. 18): they are individually smaller than the average sporangia in the near neighbourhood on the same axis.

The interest of this fact lies in its rarity: there is perhaps no character which marks off the plants of Lycopodinous affinity from others so clearly as the constancy of the solitary sporangium. Interpolation of accessory sporangia, which is in some groups, such as the Ferns, so frequent a source of increase in their number, is entirely absent in the Lycopods. In the Psilotaceae it is true that numerical constancy is not observed, and irregularity of number of sporangia is not infrequent both in *Psilotum* and *Tmesipteris*. But in these

genera a plurality of sporangia is the normal condition, and the closeness of relation of these organisms to the true Lycopods is open to question. The importance of a morphological character for comparative purposes depends on its constancy; and on this ground the solitary, leaf-subtended sporangium of *Lycopodium* may be held as a character of high morphological value; it stamps this series of Pteridophytes as peculiar from all others.

But it is not necessary that the simple type should always be strictly maintained; few characters in the whole series of plants are more stereotyped than the structure of the Bryophyte sporogonium; yet branched, two-headed sporogonia are occasionally found. The causes of this are obscure; probably nutritive conditions have close connexion with it. It is with such cases of plural development of parts normally single that I should rank this plurality of sporangia in *Lycopodium rigidum*.

On the other hand, it has lately been shown by Solms-Laubach (Bot. Zeit., 1902) that *Isoetes*, which has usually a simple axis, is occasionally branched; in this we may see a fresh indication of its Lycopodinous affinity, where dichotomy is common. The case is somewhat the same in *Phylloglossum*, where also, though the plant is normally unbranched, occasional dichotomies occur. These branchings seem rather reminiscent of a feature common in the main groups to which these plants belong, than to be actually new developments.

But the case of the plural sporangia in *Lycopodium rigidum* I should regard as a new development; it probably arose by a separation of the sporogenous group of a normal sporangium into two: on this point, however, it is impossible to go beyond mere conjecture, since the case is isolated and observed only in the mature condition.

I do not think it will be wise to attach high importance to this abnormality for purposes of comparative argument, beyond recognizing that it shows how even the most rigid facts of morphological experience are liable to exception, and that this applies equally to spore-bearing members, in cases where their forms seem most stereotyped.

F. O. BOWER.

GLASGOW,  
October, 1902.

OWING to the amount of material in hand, the Editors have found it desirable to hasten the publication of the present number of the *Annals of Botany*, which therefore appears in March, instead of in April, as announced. It is proposed to issue the next number as soon as it is ready.





# The Early Stages of Spindle-Formation in the Pollen-Mother-Cells of *Larix*.

BY

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With Plates XIV and XV.

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## INTRODUCTION.

NUCLEAR division in the pollen-mother-cell of *Larix davurica*, Trautv., was described and figured by Belajeff ('94). He finds, in the early prophase of the first mitosis, a system of radial fibres extending from the nuclear membrane to the cell periphery. Later, a close felt-like layer of fibres, or meshes, appears just without the nucleus; some fibres are still left in the peripheral cytoplasm. This arrangement, he suggests, may have resulted from a drawing together of the radial fibres about the nucleus; but he finds none of the intervening stages. The fibrous material already present within the nucleus increases in amount, forming a dense network; the nuclear membrane disappears, and with it the distinction between intra- and extra-nuclear fibres. The peripheral fibres group themselves so as to converge toward points (one to four in a section) near the cell-wall, and the fibres of the central mass become so arranged with reference to these points as to form a multipolar spindle. Bundles of fibres connect the chromosomes, lying in the central region of

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the spindle, with the poles. The number of poles is reduced to two, possibly by fusion, resulting in a typical bipolar spindle. Belajeff's observations of *Lilium* and *Fritillaria* pollen-mother-cells agree, so far as they go, with those of *Larix*. A dense intra-nuclear network is formed; then knots, possibly, he thinks, centrospheres, appear at various places in the cytoplasm, from which fibre-bundles penetrate the nuclear membrane and attach themselves to the chromosomes. The membrane disappears and a multipolar figure is formed, which passes into a bipolar spindle.

Strasburger's ('95) description of some stages of the same division in the pollen-mother-cell of *Larix europaea* corroborates that of Belajeff as to the felted stage, the disappearance of the nuclear membrane, the formation of a central fibrous system, a multipolar and finally a bipolar spindle. Němec ('98 *b*) describes quite differently spindle-formation in *L. decidua* (*L. europaea*, DC.). He finds an early stage of cytoplasmic radiation, succeeded by an aggregation, just without the nucleus, of granular material, sharply separated from the much-vacuolated outer cytoplasm. Next to the membrane appears a hyaline region, which grows at the expense of the granular zone. In the hyaline layer appears a reticulum; this develops into a system of fibres, which orient themselves into a multipolar figure. Fibres also appear within the nucleus, the membrane disappears, and from the whole fibre-complex a bipolar spindle is developed.

Belajeff was the first to interpret a multipolar as a stage in the development of a bipolar spindle; but Strasburger ('80) had, some years earlier, figured a tripolar spindle in the endosperm of *Reseda*, and had described similar figures in *Ornithogalum* and *Leucojum*. Later, he ('88) figured the spindle in *Leucojum*; also a multipolar spindle in the equatorial plate stage from the endosperm of *Allium*, whose great number of chromosomes led him to explain it as due to a fusion of several nuclei. A felted stage, similar to that described by Belajeff, had been found by Strasburger ('88) in *Leucojum*.



In recent years, a multipolar origin of the spindle has been found in many Spermatophytes. Such a stage is described in the pollen-mother-cell of *Lilium* by Farmer ('93, '95 *d*), by Strasburger ('95), Miss Sargent ('97), and Mottier ('97). Farmer's preliminary note ('93), indeed, preceded the publication of Belajeff's paper, just cited, but the substance of the latter's discoveries had been stated in two earlier Russian notes. Mottier finds, succeeding a radial stage, a felted layer just without the nucleus, from which fibres extend toward the cell-wall so as to form a number of poles. But as the nuclear membrane disappears and the fibres penetrate the nuclear cavity, the multipolar condition often disappears, to recur when the cavity is completely filled by the fibrous mass. In the pollen-mother-cells of *Podophyllum* and *Helleborus* the process is similar, except that there is no multipolar arrangement until after the membrane disappears. A multipolar stage occurs, too, according to Mottier, in the second mitosis in the pollen-mother-cell of *Lilium*; also ('98) in the divisions in the embryo-sac of *Lilium* and *Helleborus*. Multipolar figures which develop into bipolar spindles are described in the pollen-mother-cells of *Hemerocallis*, by Juel ('97); in those of *Nymphaea*, *Nuphar*, *Limodorum* and *Magnolia*, by Guignard ('97*a*, '97*b*, '98); of *Cobaea* and *Gladiolus*, by Lawson ('98, '00); of *Bignonia*, *Symplocarpus* and *Peltandra*, by Duggar ('99, '00); of *Convallaria* and *Potamogeton*, by Wiegand ('99); of *Arisaema*, by Atkinson ('99); of *Passiflora*, by Miss Williams ('99); of *Lavatera*, by Miss Byxbee ('00); of *Magnolia* and *Liriodendron*, by Andrews ('01); and in those of *Galtonia* and *Convallaria*, by Schniewind-Thies ('01). Schniewind-Thies finds similar figures in the embryo-sacs of *Galtonia*, *Convallaria*, *Scilla* and *Tulipa*; and Duggar ('99) describes them in the embryo-sac of *Bignonia*. Of the cases above mentioned, a felted stage preceding the multipolar is described in *Hemerocallis*, *Nymphaea*, *Nuphar*, *Limodorum*, *Magnolia* (Guignard and Andrews), *Gladiolus*, *Peltandra*, *Convallaria* (Wiegand), *Potamogeton*, *Lavatera* and *Liriodendron*; and an earlier radial stage is found in *Cobaea*, *Peltandra*,

*Passiflora* and *Lavatera*, and in the second division in *Magnolia* and *Liriodendron* (Andrews).

In a type of spindle-formation first described by Rosen ('95) in the root-tip of *Hyacinthus*, a thin hyaline extra-nuclear zone is seen, whose material becomes aggregated on two opposite sides of the nucleus. Within each cap so formed, fibres appear and grow in length, attaching themselves at one end to the nuclear membrane and finally converging at the other end to a common point. Then the membrane disappears and the spindle is completed. Němec ('97, '98*a*, '98*b*, '99*a*, '99*b*, '99*c*) describes spindle-formation from similar extra-nuclear caps in root-tips and other vegetative tissues of *Allium*, *Hemerocallis*, *Solanum*, and a long list of plants. He finds that in general the spindles in vegetative cells are from the start bipolar, while those in reproductive cells are originally multipolar. Hof ('98) finds similar polar caps in the root-tips of *Ephedra* and *Vicia*. In the former case, the spindle is originally bipolar, in the latter monaxially multipolar, becoming bipolar. Schaffner ('98, '01) describes spindles arising from similar extra-nuclear caps in the root-tips of *Allium* and *Erythronium*; and Fullmer ('98, '99) finds the same thing in pine seedlings, and also in pollen-mother-cells of *Hemerocallis*, where, however, he describes also an early radial stage. Miss McComb ('00) relates a similar history in the root-tips of *Allium*, *Vicia* and *Erythronium*, except that instead of the early hyaline layer she finds a kinoplasmic web or felt surrounding the nucleus; and it is this felt that becomes aggregated into the polar caps.

Strasburger ('00, p. 118) has pointed out that in the vegetative divisions described by Němec the spindle primordium ('Anlage') at each end of the nucleus is at first composed of separate spindle-bundles, not converging to a common point. He proposes for this condition the term 'multipolar diarch,' as distinguished from the 'multipolar polyarch' form common to reproductive cells, in which poles arise on all sides of the nucleus. He finds, in the root-tips of *Ephedra* and *Vicia*, a finely fibrous extra-nuclear layer which becomes aggregated

into polar caps, and from these caps fibres grow out into a liquid which appears between the fibrous cap and the nuclear membrane. But there is no sharp line of distinction between the two methods of spindle-formation; for in the pollen-mother-cell of *Iris* the origin of the first spindle is multipolar polyarch, that of the second multipolar diarch; while in the pollen-mother-cell of *Nymphaea* the origin of the first spindle is similar to that of the second in *Iris*. Duggar ('00) finds, too, that in the division of the microspore nucleus of *Symplocarpus* and *Peltandra* the spindle is originally multipolar diarch, the fibres being arranged perpendicularly to the wall near which the nucleus lies. Mottier ('98) describes, in the vegetative cells of *Lilium*, a multipolar stage preceded by an extra-nuclear felt, just as in pollen-mother-cells; and a multipolar spindle is figured by Ikeno ('98) in the embryo of *Cycas*.

Multipolar spindle-figures have an important bearing on the question as to the presence or absence of central bodies (attraction-spheres, centrospheres, centrosomes, &c.). We have seen that the evidence is conclusive for the general existence of a multipolar stage in the history of the spindle in the cells of the flowering plants; and such a stage seems to negative the possibility of the formation of the spindle in these plants through the agency of centrosomes which station themselves at opposite points in the cell, so initiating mitosis and determining the position of the spindle-poles. But Guignard, who ('91 *a*, '91 *b*, '91 *c*) first described attraction-spheres in Phanerogams, has more recently ('97 *a*, '97 *b*, '98) maintained that the poles of the multipolar figure are often occupied by centrosome-like granules, which are, he holds, true kinetic centres, and that the bipolar stage results from their fusion into two typical centrospheres. A very similar process has been described by Moore ('94) in certain animal cells. But even Guignard admits that the spheres may disappear in the resting stage and be formed *de novo* during mitosis, sometimes not until after the appearance of the multipolar spindle; in the latter case, the cones arise by the



activity of the kinoplasm in the absence of undifferentiated dynamic centres. In spite of numerous accounts of central bodies, the great weight of evidence now seems to be against their existence in the Seed Plants, if we except the still disputed case of the 'blepharoplast.' A full *résumé* of the centrosome discussion has lately been published by Strasburger ('00), who has still more recently ('01) applied to the pollen-mother-cells of *Asclepias* and *Cynanchum*, with negative results, all the methods used for the demonstration of the central bodies in animal tissues. The observations and experiments of Hottes (reported by Strasburger, '00) and of Němec ('99 *d*, '01) indicate that kinoplasmic or nucleolar granules or masses may often appear at or near the spindle-poles, and that their occurrence is favoured by certain stimuli, as, for instance, subjection to low temperatures. Demoor ('95) also finds that 'centrosomes' are made visible by cooling.

The only history of a multipolar spindle so far completely worked out among the Pteridophytes is that of the spore-mother-cell of *Equisetum*, described by Osterhout ('97). He finds, just without the nucleus, a blue-staining cytoplasmic layer, which becomes fibrous; the fibres are at first parallel to the nuclear membrane, but later take on a radial arrangement, many of them extending to the plasma-membrane; then they group themselves into a multipolar figure. The nuclear membrane disappears, and the extra- and intra-nuclear fibres form a continuous system, whose poles fuse in two groups, forming a sharply bipolar spindle. No centrosomes are present at any stage. The multipolar origin of this spindle is corroborated by Němec ('98 *a*); but Campbell ('95, p. 427) finds directive spheres present in the divisions of the spore-mother-cell, and describes no multipolar stage. Smith ('00 *a*) notes that the spindle in the microspore-mother-cell of *Isoëtes* appears to have a polycentric origin. In the spore-mother-cells of *Osmunda*, he ('00 *b*) describes the formation of a spindle from two extra-nuclear polar caps—a 'multipolar diarch' origin. Occasional tripolar figures he

considers abnormal. Spindle-formation from polar caps is found in the meristem of *Psilotum* by Rosen ('95), in vegetative tissues of *Equisetum*, *Aspidium* and *Alsophila* by Němec ('98 a, '98 b, '99 a), and in vegetative cells of *Aspidium* by Hof ('98). Central bodies have been described in the Pteridophytes by numerous observers; but the evidence for and against their existence here is practically the same as in the case of the Seed Plants, and here as in the higher group the preponderance seems to be on the negative side of the argument.

A peculiar form of quadripolar spindle, suggestive of the multipolar figures already described, is found by Farmer ('94, '95 a, '95 b, '95 c), in certain Hepaticae whose spores are formed by the division of the mother-cell into four lobes. In *Pallavicinia* he finds that four daughter-nuclei are formed simultaneously, one at each of the poles; but in other cases the original poles approximate in pairs to form either a sharply bipolar spindle or one with forked ends, and the division results in two daughter-nuclei, each of which again divides. Davis ('01) finds a quadripolar figure in *Pellia*, but he interprets it as a stage in spindle development in which a fibrous extra-nuclear web takes this peculiar shape in consequence of the lobing of the cell. He ('99) also finds a felted stage in the developing spindle in the spore-mother-cell of *Anthoceros*, followed apparently by a multipolar, then by a bipolar stage. Centrospheres and centrosomes have been described in a number of liverworts.

The only case of spindle-formation reported among the Thallophytes which seems to conform to the multipolar type is in the vegetative cells of *Chara*, described by Debski ('98). The bipolar spindle develops, through stages which he did not follow, from a central fibrous system; the latter is partly of nuclear and partly of cytoplasmic origin. This isolated case emphasizes the width of the gulf that seems to separate the Characeae from other Thallophytes. Central bodies which take part in spindle-formation, which divide, and, in some cases at least, persist through the resting stage, have

been found in species representing diverse groups, and it is generally recognized that a method of spindle-formation accompanied by the activity of a centrosome is at least of widespread occurrence among the lower plants.

As we have seen, there is much uncertainty and variance in the accounts of different authors as to what takes place in the early history of the spindle in the higher plants, previous to the appearance of the extra-nuclear felt. Besides, the presence of centrosomes, though rendered extremely improbable, is not admitted by all writers, at least, to be entirely excluded by known facts as to the multipolar origin of the spindles. For these reasons, special attention has been paid in the present investigation to the early prophases of mitosis, and an attempt has been made to follow closely the history of the cytoplasmic structures in these stages. The problem here involved is a purely physiological one, and the description of structures occurring in isolated stages of karyokinesis is by no means sufficient for its solution. A complete series of stages, showing the changes actually going on within the cell, must be studied, and their connexion shown. From this point of view, much of the discussion regarding the presence or absence of 'centrosome-like granules' at the spindle-poles is seen to be useless. There can be no doubt, from the citations already given, that granules or larger masses are often to be found at the poles; but nothing can be determined as to the significance of these bodies until the complete history of the spindle has been traced.

#### ORIGINAL OBSERVATIONS.

The following description applies to the first nuclear division in the pollen-mother-cells of *Larix europaea*, DC. Male cones were fixed at various times during the fall, winter and spring, both from material just taken from the trees and from that whose development was hastened by keeping it for from one to four days in a warm room. Strasburger ('00, p. 68) finds that material forced in this way yields the same karyokinetic figures as that which has developed more slowly



out-of-doors. Of several fixations tried, the best results were obtained with Flemming's stronger solution. The sections, five microns in thickness, were stained with the triple stain. I have also had the privilege of examining some similarly fixed and stained preparations made by Professor R. A. Harper and by Mr. H. G. Timberlake. Several of my drawings are from Professor Harper's preparations, and one is from one of Mr. Timberlake's. Living pollen-mother-cells have also been examined and compared with killed material.

The process of spindle-formation may be considered as divided into five periods or stages; the division is somewhat arbitrary, and consecutive stages are in no case sharply separated from one another.

### **I. The Pre-Radial Stages.**

The earliest material that I have studied was gathered and fixed October 24. The pollen-mother-cells are still packed closely together, but are beginning to round up and separate from each other. Each cell seems to be bounded only by a distinct blue-staining plasma-membrane; at least, I have been unable to distinguish, by the use of the orange stain, any layer of cell-wall material. Between the separating cells is a blue-staining material, possibly the old disorganizing cell-wall, sometimes appearing as a distinct layer of some thickness, sometimes as a cloudy mass. Fig. 1, Pl. XIV, shows a pollen-mother-cell in this stage. Groups of red-staining bodies, the chromatin tetrads, are seen in the nucleus, just within, or often in contact with, the nuclear membrane; segmentation of the spirem thread, therefore, has already occurred. There is usually a single nucleole (sometimes two), in general of a rounded and somewhat irregular shape. Much of the irregularity of outline, however, is due to adhering clumps of a usually less dense and blue-staining substance—the linin. Linin is also found in contact with the chromosomes, and, in the form of ragged, wavy, granular fibres, connecting the chromatin groups with each other, with the nucleole, or running from nucleole or chromosomes to the nuclear membrane.

Often the nucleole becomes by this means the centre of a system of radiating fibres, as is shown at a later stage in Fig. 2. The only visible structure in the cytoplasm in the earliest stage is a fibrous network. The apparently empty meshes are of varying shapes and sizes; in general they are smallest near the nucleus and increase in size toward the periphery of the cell. Scattered about upon the fibres and between them are granules, staining blue like the fibres. These granules are probably, in large part at least, cross-sections of fibres, and they are no more numerous than such sections would be likely to be in such a network. Often they are shown by focusing to extend through the thickness of the section.

Fig. 2 is from material gathered and fixed March 15; the fixation is according to Vom Rath's picric-acetic-osmic acid and platinum chloride formula. There has evidently been no great change during the winter. The Vom Rath fixation, however, does not permit of so good a differential stain as the Flemming, and the preparations are in general not as satisfactory. The fibrous network is still present, though not well brought out; between the meshes, especially near the nucleus, is a granular or cloudy substance, but the large peripheral meshes are still empty, giving the outer part of the cell a vacuolated appearance. In the cytoplasm are seen occasional small rounded bodies of distinct outline, staining homogeneously and a little more deeply than the rest of the cytoplasm.

Fig. 3 shows a somewhat later condition (in Flemming fixation, as are all the remaining figures). The cells have now rounded up and are provided with a relatively thick cell-wall. The blue intercellular substance has disappeared, and the cells float in a colourless liquid. The cytoplasm now plainly contains two constituents, the fibrous meshwork first observed, which stains blue, and a cloudy or very finely granular, orange-staining material. The latter substance does not occupy all of the inter-fibrous spaces, but clear areas of varying size are also scattered through the cytoplasm. Some-

times the clear spaces are larger and more numerous in the peripheral region, but often, as in the cell shown in Fig. 3, the cytoplasm presents in this respect a very uniform appearance. The granules, or sections of fibres, are present as before, and also the larger rounded cytoplasmic bodies, which stain less densely blue than the fibres. Often a cytoplasmic fibre can be clearly traced as it passes through the nuclear membrane and is attached to one of the chromatin groups. For this purpose sections are specially favourable which cut the nucleus tangentially; in such a section a fibre running diagonally to the cutting-plane can be followed, by a change of focus, through the membrane, which is transparent and is here visible only as a bluish cloud. A portion of such a section is shown in Fig. 4.

Comparison of living cells at this period is helpful. The outlines of the large round or elliptical nucleus, one or two nucleoles, usually near the centre of the nucleus, and the chromosomes just within the nuclear boundary, are all plainly visible; and some of the longer linin fibres can be made out. Little can be determined in living material regarding cytoplasmic structures; occasionally one of the coarser fibres can be traced for some distance.

## 2. The Radial Stages.

Very soon the cytoplasmic fibres begin to show a definite arrangement. In a section through a single cone may often be found a series of stages from the one just described to a distinctly radial arrangement (Fig. 5). The fibres arrange themselves so that many of them extend perpendicularly from the nuclear membrane out into the cytoplasm or even to the periphery of the cell. At first, however, most of the radial fibres are relatively short and end in the cytoplasm. They are also in general not straight, but rather irregularly wavy. A vacuolated region may still be present in the peripheral cytoplasm, as appears in Fig. 5.

The fibres soon increase in length, and a complete system of fairly straight radial fibres is formed, extending from the



nuclear membrane to the plasma-membrane. In the cell represented by Fig. 6, there is a very slight plasmolysis around much of the cell periphery; the plasma-membrane, stained deep blue like the fibres, is separated from the orange cell-wall, and it is plain that the fibres terminate in this membrane. The cytoplasm has also shrunk away slightly from one side of the nuclear membrane, and one fibre can be traced across the gap to the membrane and into apparent continuity with an intra-nuclear fibre. The number of blue cytoplasmic granules shown in median section is now much less than in the earlier stages, as would be expected if they are sections of fibres. Often the fibres are connected with each other by branches; this may be taken to indicate that the radial figure has resulted from a pulling out and rearrangement of the meshes of the earlier network. A study of the succession of stages tends to strengthen this view of the origin of the radial fibres. However, it seems plain that there is also an actual growth in length of the fibres after they have assumed the radial position. The possibility of a combination of the two processes—a pulling out of the meshes and a growth of the fibres—will be discussed later.

### 3. The Formation of the Felt.

A folding-over of the fibres (Figs. 7-11) now occurs, so that they come to assume a position parallel to the nuclear membrane. They are also gradually drawn in toward the nucleus, until they form a dense fibrous felt about the membrane. Not all the fibres, however, take part in the formation of this felt; many of them remain scattered about, lying in various directions in the cytoplasm. During the folding-over process, a tendency is noted for fibres to approach each other in the neighbourhood of the cell-wall (Fig. 8), so as to form figures suggestive of those shown by Osterhout ('97, Figs. 4, 5), in *Equisetum*, immediately following the radial stage. Such figures, however, do not in the Larch represent the beginnings of a multipolar spindle, as Osterhout finds to be the case in *Equisetum*. In these stages there is sometimes a zone con-

centric to the nuclear membrane, and about midway between that and the cell-wall, in which the fibres are bunched. This zone appears frequently in the preparations from this stage down to that of the equatorial plate, and is suggestive of the kinoplasmic zone figured by Mottier ('97, Figs. 5, 6) in the Lily. But every cell containing such a zone, so far as I have observed, shows a marked shrinking and distortion, and it seems extremely probable that the bunching of the fibres is here an effect of the fixation. Fig. 16, Pl. XV, shows a cell at a much later stage, which, in connexion with considerable shrinking and some plasmolysis, shows this outer fibrous zone; the fibres here are so arranged in several places as to form 'cyto-asters,' suggesting those seen by Mottier ('97, Fig. 28) in *Podophyllum*, as well as the asters found by Morgan ('96) to be produced in the unfertilized or fertilized eggs of sea-urchins and ascidians by treatment with salt solutions of a certain strength, and similar asters found by Mead ('98 *b*) in the cytoplasm of unfertilized eggs of *Chaetopterus* when placed in sea-water. In the two latter cases, the cyto-asters seem to occur as a result of the action of a solution in which the eggs are immersed, the effect being similar, perhaps, to that of a poor fixing-fluid.

During and after the formation of the extra-nuclear felt, there is often a concentration of the granular orange-staining element of the cytoplasm about the nucleus, giving again a vacuolated (not a spongy) appearance to the peripheral cytoplasm. The linin gradually becomes more regularly fibrous, but the fibres are still ragged and granular. The nuclear membrane is still intact, staining deep blue like the fibres. The cell shown in Fig. 9 is considerably shrunken in fixation; plasmolysis has pulled the nuclear membrane away from the cytoplasm on one side and into the nuclear cavity, where it can be followed, by focusing, through the thickness of the section. There can be no doubt in a case like this that the nuclear membrane is something more than a film due to surface tension between the nuclear sap and the cytoplasm. It is a distinct cell-organ, which retains its

continuity in spite of a very considerable displacement and distortion. In favourably stained sections, as that represented in Fig. 8, the cell-wall is orange, and the plasma-membrane blue like the fibres and the nuclear membrane. In optical section, the two membranes and the larger fibres closely resemble each other in colour, density, and thickness. The dark rounded bodies seen in the cytoplasm in Fig. 8 are stained red, like the nucleole. They are doubtless the bodies which have been so frequently described as extra-nuclear nucleoles, and are to be found in many preparations from this stage onwards. They are often, though seemingly not always, in contact with the fibres; there is also a tendency for them to appear more numerous near the periphery of the cell than toward the interior, especially if the peripheral region is much vacuolated. Their number is much greater than that of the blue bodies noticed in earlier stages, so they can hardly be derived from those. Besides, the blue bodies are still occasionally to be seen. On the other hand, the nucleole shows no perceptible diminution in size or density. Its apparent irregularity of shape in the figures is largely due to cohering chromatin masses and linin fibres. There are often to be seen in the liquid surrounding the pollen-mother-cells, and usually clustered about the latter, red-staining bodies of very varying size, exactly resembling those noted in the cytoplasm. This suggests the possibility that both classes of red bodies are drops of unassimilated food substances, perhaps of soluble proteids, which have been precipitated by the fixing-solution. The absence of the membrane on one side of the nucleus in Fig. 10 is due to the fact that the section is cut close to the surface of the nucleus, and is partly tangential to it.

When the extra-nuclear felt is fully formed (Fig. 12, Pl. XV), there is a tendency toward a zonal arrangement of the cytoplasm; outside the felt is a granular region, and between this and the plasma-membrane a zone containing many fibres and little granular material. But fibres can sometimes be seen running out from the inner felt toward the periphery, as



figured by Belajeff and Strasburger. The nuclear membrane now has a folded or wavy outline and often a granular appearance. The nucleole also shows signs of dissolution ; it displays a greater affinity for the orange stain, is vacuolated (Fig. 12) and often collapsed. There is about this time a marked increase in the amount of intra-nuclear fibres, which, however, are still ragged, granular, and wavy.

#### 4. The Multipolar Spindle.

After the nuclear membrane disappears (Fig. 13), a distinction may be made for a time between the fibres derived from the cytoplasmic felt and those filling the nuclear cavity, which seem to be wholly or chiefly of nuclear origin. The latter, though now forming a continuous system with the cytoplasmic fibres, are relatively loosely arranged, with large spaces between them, and are still granular, while the cytoplasmic fibres still form a rather compact layer and are much more uniform in thickness. Already a tendency can be noted to a pulling out of the fibres in certain places to form poles. This seems to come about, not under the influence of peripheral fibres, as described by Belajeff, but by an actual outward movement of the ends of some of the fibres of the central mass. At least, the study of a large number of preparations shows no regularity as to the presence of fibres running tangentially from the central mass toward the cell periphery; such fibres are sometimes present, sometimes short or slender, and often wholly absent. I have seen no evidence that these or other peripheral fibres determine the position of the cones of the multipolar figure. The nucleole has disappeared, nearly or quite simultaneously with the disappearance of the membrane. The central fibres soon lose their granular appearance and cannot be distinguished from the outer ones ; the whole mass of fibres assumes more and more the appearance of a multipolar spindle. Commonly three or four poles, sometimes indications of one or two more, appear in a section. The fibres begin to gather into bundles which run from the chromosomes to the poles. The cell

drawn at this stage (Fig. 14) is unusually rich in fibrous material, also in 'extra-nuclear nucleoles.' It is very common to find a relatively clear zone surrounding the developing spindle (Figs. 13, 15, 16); apparently on the dissolution of the nuclear membrane the kinoplasmic web presses into the cavity, leaving a clear zone between itself and the still present layer of granular cytoplasm.

### 5. The Completion of the Spindle.

The further history of the spindle is essentially what has been described by many of the writers already cited. The arrangement of the fibres into bundles becomes more regular; the fibres forming the bundles are straightened out; the number of poles decreases, apparently as a result of this straightening (Figs. 15-18), until the fibres all lie approximately parallel, forming a 'multipolar diarch' figure.

By the time the chromosomes are arranged on the equatorial plate (Fig. 19), the spindle is fully formed. Its fibres converge, not to definite points, but into two polar regions. At first view they seem to end in these regions; but by careful examination and focusing, the fibres, here very lightly stained, may be traced through the polar area into the cytoplasm beyond, where they spread out, still less deeply stained than in the body of the spindle, to form a system of polar radiations. The effect is very much as though the whole bundle of fibres seen in Fig. 18 had been constricted at two points, one not far from each end, and still allowed to spread out, fan-like, at the ends and in the equatorial region. The fibres can be followed from the polar region out into the peripheral region of the cytoplasm, but only occasionally as far as the plasma-membrane. No indication of any kind of central body has ever been seen in the polar region. Some polar radiations are seen which cannot be traced as continuations of the spindle-fibres; such radiations are more numerous in the diaster stage (Fig. 20), and here also they diverge from a general region rather than from a distinct point, and no central body is to be found.

CONCLUSIONS.

The facts observed in the pollen-mother-cell of *Larix* seem conclusive as to the continuous presence in the cytoplasm, from the very early prophases, of a distinct fibrous system, which, after a series of rearrangements and changes of position, becomes, in conjunction with another set of fibres of nuclear origin, the karyokinetic spindle. A careful study of the preparations leaves no doubt, I think, that the fibres of the reticulum first seen actually become rearranged into a radial system, that this in large part passes into a close extra-nuclear felt, and that the fibres of this felt become eventually the contribution of the cytoplasm to the completed spindle. It is impossible to determine in the mature spindle that any special portion is derived from the cytoplasm or from the nucleus; but each source clearly furnishes an important part. It follows that the active spindle-forming substance, kinoplasm, may first appear, in fibrous form, either in the nucleus or in the cytoplasm; and we may infer that the place of origin of the spindle-fibres, whether nuclear or cytoplasmic, or, as in the present case, partly nuclear and partly cytoplasmic, depends upon the conditions obtaining in, and the relations between, the nucleus and cytoplasm of the cell concerned. The facts accord with this inference; spindles of intra-nuclear origin sometimes occur in connexion with an unusual size of the nucleus, as in the generative cell of *Zamia* (Webber, '01), or where there is a paucity of cytoplasmic kinoplasm, as in instances cited by Strasburger ('00) in young anthers and nucelli of *Lilium* and in the growing point of *Viscum*; and a greater proportional supply of extra-nuclear kinoplasm may result in spindle-formation such as Nĕmec finds in many vegetative cells, where an extra-nuclear bipolar spindle is completely formed, save for a short equatorial portion, while the nuclear membrane is still intact.

But in spite of the range of variation which has been found in this and in other respects, I think that we may venture to present tentatively, in a general outline, the essential steps in



the formation of the spindle in the Spermatophytes, and perhaps in the Pteridophytes as well. Such an outline might be somewhat as follows:—

1. A considerable amount of kinoplasm is present in the cytoplasm, at least by the time of the early prophases, as a more or less uniformly distributed, fibrous reticulum. It will be important to trace still further back the history of the kinoplasm; but no observations yet made seem to throw any light upon this problem. Indeed, very few observers have followed spindle-formation back even to as early a point as this; but Miss Williams ('99) and Miss Byxbee ('00) find that the spindle primordium ('Anlage') develops from an early cytoplasmic meshwork.

2. The fibres of the reticulum become so arranged as to extend radially from the nuclear membrane out into the cytoplasm. It seems quite likely that this results partly from a radial pulling out of the meshes; but very probably there is also an actual growth in length of the fibres composing the reticulum, so that many of them finally reach to the plasma-membrane. Several authors have been cited who find a radial arrangement of fibres at this period.

3. As a result of a folding-over of the radial fibres, a felt is formed just without the nuclear membrane.

4. The nuclear membrane and the nucleole disappear, and the nuclear cavity also becomes occupied by a set of fibres.

5. The peripheral fibres of the central mass become pulled out to form several or many cones.

6. The fibres, nuclear and cytoplasmic, are gathered into bundles, forming a multipolar figure.

7. The number of poles is reduced, by fusion, to two.

The felted stage and the succeeding steps in the process have been so often noted that there can be no doubt in these later stages as to the regular course of events. Osterhout's description of the formation of the cones in *Equisetum* by a grouping of radial fibres, which in turn proceed from a felted layer, suggests the interesting possibility of a constant difference in the succession of events as between Seed Plants

and Pteridophytes; the testing of this possibility must be left to future research.

So far as I know, no study has been made in vegetative cells of the stages previous to the appearance of the felt. The difference between 'multipolar polyarch' and 'multipolar diarch' spindles seems, from the descriptions of Strasburger ('00) and Miss McComb ('00), to result from the fact that in the latter form the felted layer, instead of giving rise to spindle-cones on all sides of the nucleus, first becomes aggregated into polar caps, and so the cones arise in two groups. Strasburger shows that the extreme cases are connected by transitional forms; and Němec ('99 *a*, '99 *c*, '99 *d*) thinks that by artificial changes in the physical conditions of the cell a polyarch instead of a diarch 'Anlage' may be produced. He also finds that in normal mitoses in many vegetative cells the nuclear membrane persists until after the spindle 'Anlage' has become sharply bipolar; and, as I have suggested, this is what we might expect if the cytoplasm furnishes a larger proportion of the spindle-forming fibres than is commonly the case in spore-mother-cells. The differences between vegetative and reproductive cells therefore appear to be in matters of detail; and spindle-formation in both, so far as investigated, agrees with the general scheme just outlined.

Few of the details are known as yet in any case of intra-nuclear spindle-formation; but the above outline would certainly require modification in order to fit these cases, at least in so far as concerns the place of initial appearance and activity of the kinoplasm. That a certain parallelism, however, holds between the two methods is shown by Murrill's observation that in the first segmentation of the egg of *Tsuga*, an intra-nuclear multipolar spindle occurs, which becomes bluntly bipolar; and by Strasburger's ('00) description, in vegetative cells of *Lilium* and *Viscum*, of an intra-nuclear multipolar diarch 'Spindel-Anlage.'

Several cases have been noticed which seem to diverge still more greatly from the usual history of the building of the spindle. Such are its formation entirely out of the nucleole,

according to Stevens ('98), in the pollen-mother-cell of *Asclepias*; the origin of the fibres, as described by Murrill ('00), in the central cell of the archegonium of *Tsuga*, from two unequal polar kinoplasmic masses; and the instance described by Miss Ferguson ('01) in the division of the generative nucleus of *Pinus*, where the spindle arises as a cone of fibres from a single cytoplasmic condensation below the nucleus, the latter lying close to the upper boundary of the cell. But such cases seem to be quite unusual, and it may be that further investigation will harmonize these with what are apparently more typical instances of spindle-formation.

I have spoken of the cytoplasm in the early stages as composed apparently of a kinoplasmic network with empty meshes. The spaces between the fibres are of course filled, as the turgor of the cell shows, and it seems improbable that they are occupied only by a lifeless cell-sap. In later stages there is plainly an orange-staining inter-fibrous substance, granular rather than alveolar in structure, but in the earliest preparations I have not succeeded, by any variation of the staining process, in finding a trace of colour in the cytoplasm outside of the fibres. I have also been convinced from a careful study of Flemming and Vom Rath preparations that the fibrous appearance is not a precipitation result. Still earlier preparations of the developing male cones will be necessary to throw further light upon the cytoplasmic structures.

As has been said, the great preponderance of evidence is opposed to the existence of centrosomes in the higher plants; and conditions in the Larch seem to justify us in saying that here the possibility of a centrosome, in the sense of a directive organ, is excluded. Not only is no such body to be seen at any stage, but, if my observations are at all correct, there is no room to assume its operation. The fibres change their position without reference to any centre or to any definite number of centres. If centrosomes determine the radial arrangement, for example, we must imagine either as many centrosomes as there are radial fibres, or else a single centrosome somewhere within the nucleus; and when the multipolar



figure appears, we must assume either that the many centrosomes have now fused into relatively few, or that the one has passed from the nucleus out into the cytoplasm and there has divided into ten, twelve, fifteen, or twenty. It seems evident from such considerations that the assumption of the possible presence of organs like the animal centrosome in the cells in question involves an ignoring of the best-established facts.

The impression is given by a study of the arrangements and rearrangements of the kinoplasm that the activities concerned in the formation of the spindle centre in, or have reference to, the nucleus. Such an impression led Nĕmec ('98 *b*) to the hypothesis that the nucleus, in cells without a centrosome, is 'homo-dynamic' with the centrosome where it occurs. It is true that the ultimate function of the fibres, in the completed spindle, has reference to certain nuclear constituents—the chromosomes. From the generally accepted notion of the nucleus as the bearer of hereditary qualities, it follows, too, that that organ is the ultimate source of the stimuli which determine the synthetic processes of the cell; and this hypothesis is borne out by a considerable mass of experimental evidence (Wilson, '00; Gerassimow, '01; &c.). It is quite possible, therefore, to suppose that the ultimate directive agencies for the growth and even for the arrangement of the kinoplasm, as of other cell-constituents, may finally be traced to the nucleus. But this is very different from saying that the present seat of the energy which is manifested in the movement of a particular fibre is within the nucleus; and it seems to me that the facts which we have been considering are inexplicable on the basis of the latter assumption. It might be imagined that the nucleus, acting like an immense centrosphere, should produce some such system of rays as appears in Fig. 6; but that it should, by exerting an influence at all comparable to the supposed action of a central body, be directly concerned in the metamorphosis of the early reticulum into a radial system, or in developing from the latter a felt, a multipolar or a bipolar spindle, seems quite inconceivable.

All of my observations are opposed to the notion that the kinoplasmic fibres are only 'lines of force,' or that they are, as Farmer ('95 *b*) expresses it, simply hyaline protoplasm which has become strained along such lines of force. The appearance of the fibres throughout their history, their staining properties, their powers of movement and contraction, all set them off as distinct from the surrounding cytoplasm, and argue in favour of their chemical and physical differentiation. The well-known formation of asters about the blepharoplasts points in the same direction; for the same organs later form cilia which certainly closely resemble, if they are not essentially identical with, the intracellular fibres. Farmer ('95 *b*, p. 475) found that the fibres of the polar aster in *Fossombronia* extended as stiff projections beyond the broken edge of a cell which had been injured in cutting. In some preparations of my own of the dividing pollen-mother-cells of *Lilium*, there are numerous cases in which, after the first nuclear division and the formation and splitting of the cell-plate, some of the fibres of the central spindle may still be seen stretching, as densely stained strands, across the gap between the daughter-cells. Such facts appear consistent only with the actual existence of the fibres as differentiated structures.

This specialized fibrous constituent of the cytoplasm seems to be, as has often been pointed out, the more active element of the cell; the fibres in many ways display energy; they change their position in the cell; they bend and straighten themselves; they extend into the nuclear cavity, are attached to the chromosomes, and appear to pull these bodies out into close proximity to the nuclear membrane; when the latter disappears, the fibres arrange themselves into a figure of definite form, the bipolar spindle; they apparently pull the chromosomes into the equatorial plate, and from this situation draw the daughter-chromosomes toward the poles. These activities suggest an analogy, if not a close relationship, between the fibres in question and the cilia of motile cells, and perhaps even a relationship with the contractile elements of muscle-fibres. Since, as has been noted, there is no

evidence that the activity of the fibres is under the influence of a central body, or, directly at least, under that of the nucleus, it follows as the most plausible explanation that the fibres are self-motile—that is, that they are themselves the seat of the energy which they manifest. If, then, the central body, where it exists, really has the function of directing the processes of spindle-building, this particular function seems, in the higher plants, to have been transferred to the fibres themselves.

Other functions which have been ascribed to the central body—either the attraction-sphere with its included centrosome, or one of these parts, the sphere or centrosome, occurring without the other—must also be served, in the Seed Plants, by other organs of the cell. Such functions may be included under three heads: the central body has been conceived as furnishing a reserve supply of kinoplasm; as serving as a centre for the building of kinoplasmic fibres; and as providing for the fibres a point of insertion—the spindle-pole.

As to the first function, Boveri ('88) found that the attraction-sphere, exclusive of its central granule, is a mass of kinoplasm which is used, wholly or partly, in the building of the aster. Other bodies than the attraction-sphere, however, have been found to serve, in various cells, the same purpose—'archoplasm-spheres,' the 'Nebenkern' of animal spermatozoa, and, as Strasburger has long contended ('00, pp. 124 ff., for *résumé*), the nucleole. Watasé ('93) has sought to show that centrosomes, microsomes, the 'Zwischenkörper' of animal cells and the cell-plates of plants are all aggregations of a similar cytoplasmic material. The experiments of Hottes and Němec show that, under the influence of stimuli which retard the activity of the kinoplasmic fibres, the fibrous substance tends to round up into bodies of various size, from that of granules or 'cyto-microsomes' to that of 'extra-nuclear nucleoles'; and Hottes shows that at higher temperatures the extra-nuclear nucleoles seem to be transformed into fibres, while cooling checks kinoplasmic activity and induces the re-formation of nucleolar bodies. Němec ('01) has shown,



too, that in the higher plants other extra-nuclear masses, probably of kinoplasmic nature, sometimes occur. These facts, as well as the frequent appearance under normal conditions, at certain stages of mitosis, of extra-nuclear nucleoles, suggest that in plant-cells this function of the attraction-sphere is served by other organs, very probably in part at least by the nucleole, in part too, perhaps, by other and less permanent bodies.

The second function of the central body, that of furnishing a centre for the formation of kinoplasmic fibres, seems to be rendered unnecessary in the cells of the higher plants; at least the evidence shows that spindle-formation in these plants may go on in the absence of a specialized organ which acts as a centre. It is true, we may think of a great number of centres of growth scattered throughout the cytoplasm; but this conception is radically different from that of the centrosome, and is perhaps, in the present state of knowledge, one of little real value. On the basis of observed facts, it seems safe only to say that the forces involved in fibre-formation, instead of being centred about one or two points, are diffused throughout the cell. This is in harmony with the fact already noticed, that, after the formation of the fibres, their activities have no reference to any centre or to any limited number of centres.

The other office of the central body, that of serving as a point of insertion for the spindle-fibres, seems also to be dispensed with in many instances. Many figures found in plant-cells recall the barrel-shaped polar spindles of *Ascaris* (Boveri, '87; Häcker, '97). Very similar spindles are found by Fairchild ('97) in *Basidiobolus*, in which case, as in *Ascaris*, the fibre-bundles end in granules; a barrel-shaped spindle is described in *Spirogyra* by many writers (see Strasburger, '88, and Mitzkewitsch, '98); and among the Seed Plants, spindles which remain throughout their history blunt or barrel-shaped are described by Strasburger ('88) in the endosperm of *Dictamnus*; by Mottier ('97) in the pollen-mother-cell of *Podophyllum*; in that of *Convallaria* by Wiegand ('99);

in the division of the central archegonial cell of *Cycas* by Ikeno ('96, '98), of *Pinus* by Blackman ('98), and of *Zamia* by Webber ('01); in the segmentation of the eggs of *Cycas* and *Ginkgo* by Ikeno ('98, '01), and of those of *Cephalotaxus* by Arnoldi ('00); and in the cells of wounded potato tubers by Němec ('99 *c*). In the division of the generative nucleus of *Potamogeton*, Wiegand ('99) finds that one pole, attached to the cell-wall, is very broad, the other sharp. In the Larch we have seen that the fibres converge to a limited polar region, but not to a definite point.

Evidently, if, by their contraction, the spindle-fibres are to pull apart the daughter-chromosomes, they must have some attachment or anchorage for their polar ends. This purpose we may imagine to be well served by a special body to which they all converge, provided that body have itself some means of attachment; but the instances just cited show that the cells of many organisms, including those of higher plants, have secured means of insertion for their spindle-fibres in the absence of such a definite body, and often without even a marked convergence toward a polar region. Strasburger ('00) shows that in some cases a point of attachment is found in the plasma-membrane; but in many others, the fibres seem to end in the cytoplasm, whose substance in this region we must suppose is adapted to furnish an anchorage for the contracting fibres.

It would seem, then, that the cells of the higher plants have either found other organs to replace the centrosome, or that they have found means to dispense with its functions entirely and to arrive at substantially the same results by quite different methods. I shall not attempt to criticize the centrosome theory except as applied to the higher plants; but it is evident that the whole centrosome question for the animal cell is at present an open one; and such problems as the persistence of this organ through succeeding cell generations and its significance in nuclear division are still far from settled (Conklin, '98; Gardiner, '98; Mead, '98 *a*).

As to the energy manifested by the kinoplasmic fibres, it

seems highly probable that it is located within the fibres themselves, and that its source is to be sought in chemical transformations—destructive metabolism—occurring in the substance of the fibre concerned. Since the volume of the kinoplasm remains relatively constant during considerable periods, constructive metabolism must go on side by side with the destructive process; the kinoplasm, then, in a period of activity, is to be thought of as in a condition of more or less rapid change; it is being built up at the expense of some of the surrounding non-fibrous substance, perhaps of already living cell-constituents, perhaps of non-living but complex foods. The energy displayed by a particular fibre represents the difference between the energy of formation of the food which it receives, and that of the waste products which result from the destruction of its substance. It then becomes possible to define an active kinoplasmic fibre as the area within which certain energy-changes are occurring; and the mass of the fibre is the sum of the masses of the substances within that area at the present moment, some of which are being built up, some being torn down, while still others may remain for a greater or less period unchanged.

This notion of the nature of kinoplasm seems to be, as far as it goes, identical with the suggestion of Wilson ('95), when he defines a cell-organ as 'a differentiated area of the cell-substance in which a specific form of chemical change occurs.' From this point of view, too, it is correct to say that the spindle-fibres are expressions of forces at work within the cell; but while admitting the possibility of defining certain organs from the point of view of the energy-changes occurring in them, I think it is important to insist upon the mass of evidence already referred to which points to the existence of a distinct fibre-substance. The fibres, that is, are something more than paths or lines of force, or mere expressions of strains and stresses; they are organs built up of a substance or of substances with distinctive chemical and physical properties, which properties determine the power of the organ to do particular kinds of work. The organ owes its existence



to certain chemical processes, and it does its work by means of the energy set free by these or by other chemical processes; but it is also a machine, adapted by its structure to utilize in a definite way the energy so liberated.

The investigations here described were begun at the suggestion of Professor R. A. Harper, and have been carried on with the continued assistance of his direction and criticism.

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*June 17, 1902.*

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EXPLANATION OF FIGURES IN PLATES  
XIV and XV.

Illustrating Mr. Allen's paper on the Pollen-Mother-Cells of *Larix*.

All the figures were drawn with the aid of the *camera lucida*, and with a Zeiss apochromatic 2 mm. objective, 1.30 apert.; all except Fig. 4, Pl. XIV, with compens. oc. 8; Fig. 4, with compens. oc. 12.

PLATE XIV.

Fig. 1. Cross-section of pollen-mother-cell of *Larix europaea*, DC., material gathered and fixed October 24; very early prophase, showing fibrous network in the cytoplasm.

Fig. 2. Cell fixed March 15 following; an inter-fibrous material is now present.

Fig. 3. Somewhat later stage, with rather thick cell-wall.

Fig. 4. Small part of section of cell at same stage, cut tangentially to the nucleus; membrane not visible; the dark rounded bodies are chromatin, the lighter shaded masses linin; fibres can be traced from the chromatin bodies into continuity with the cytoplasmic network.

Fig. 5. A cell from the same section as Figs. 3 and 4; the cytoplasmic fibres have taken on a radial arrangement.

Fig. 6. Radial stage, fibres running from nuclear membrane to plasma membrane.

Fig. 7. Beginning of folding-over of fibres.

Fig. 8. Fibres are gathering into felt just outside nucleus; many extra-nuclear nucleoles present.

Fig. 9. A cell somewhat shrunken, with the nuclear membrane plasmolysed and pushed inward.

Figs. 10 and 11. Later stages in the formation of the felt.

PLATE XV.

Fig. 12. The completed felt; nuclear membrane much folded, probably on the point of dissolution; nucleole vacuolated.

Fig. 13. The nuclear membrane has disappeared; nuclear cavity contains granular fibres of nuclear origin; the outer fibres are being oriented to form the cones of the multipolar spindle.

Figs. 14 and 15. Later stages in the formation of the multipolar spindle. In Fig. 15 the fibres are gathered into bundles which run from the poles to the chromosomes.

Fig. 16. A multipolar figure; the cell somewhat shrunken and plasmolysed; a peripheral zone containing fibres and irregular 'cyto-asters.'

Fig. 17. The fibres becoming straightened out and parallel; a transition to the bipolar spindle.

Fig. 18. A 'multipolar diarch' stage.

Fig. 19. A completed spindle in the equatorial plate stage, showing polar radiations.

Fig. 20. The diaster stage; a few especially dense fibres or strands in the central spindle; the polar radiations very numerous.





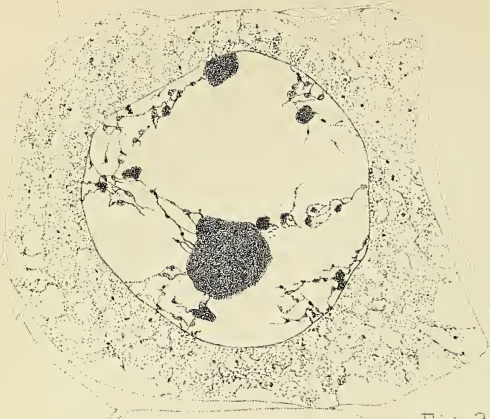


Fig 2.

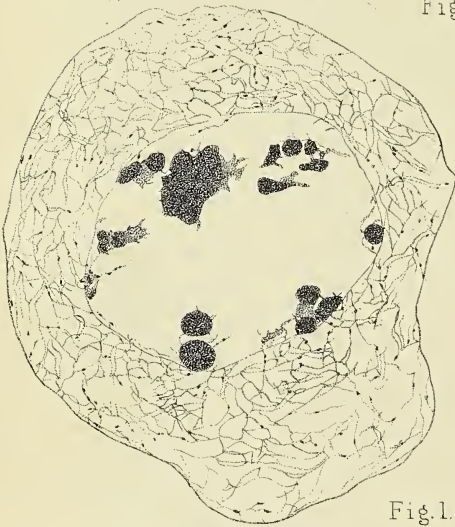


Fig. 1.

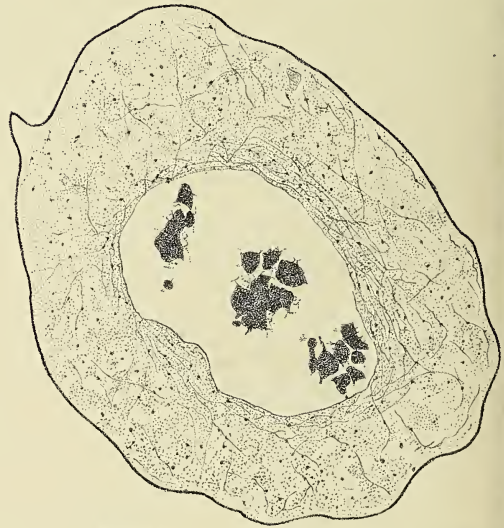


Fig. 10.



Fig. 11.



C.E.A. del.



Fig. 3.



Fig. 4.

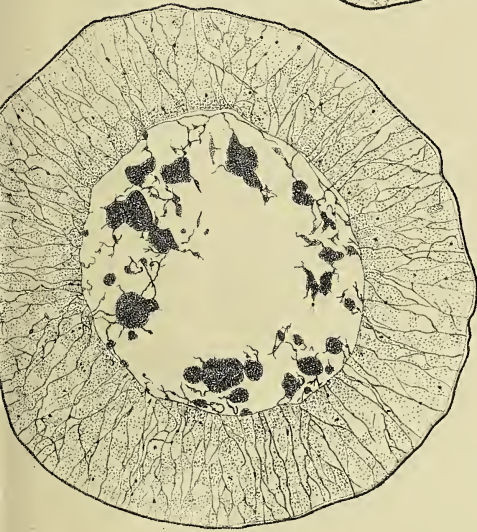


Fig. 6.



Fig. 7.



Fig. 9.



Fig. 8.





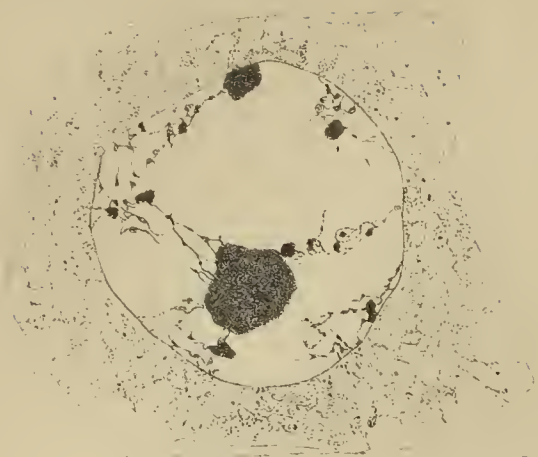


Fig. 2.

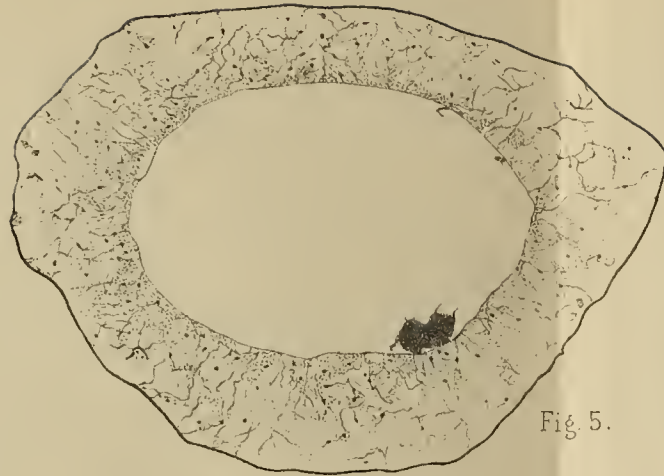


Fig. 5.



Fig. 3.

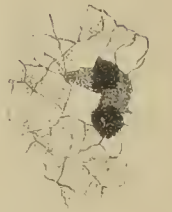


Fig. 4.



Fig. 1.

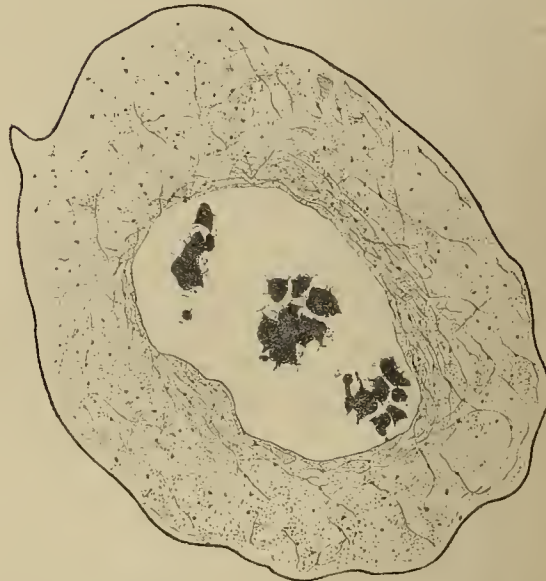


Fig. 10.

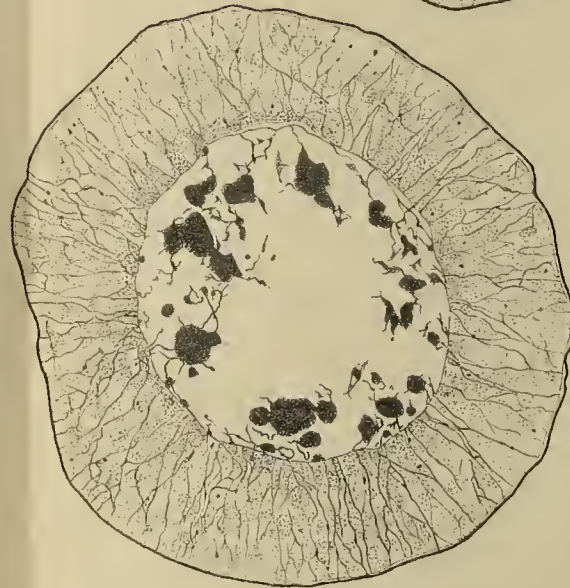


Fig. 6.



Fig. 7.



Fig. 11.



Fig. 9.



Fig. 8.

C. E. A. del.







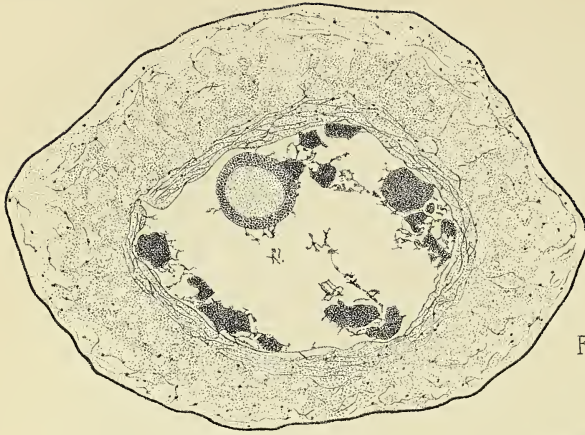


Fig. 12.



Fig. 15.



Fig. 18.

Fig. 20.

C.E.A. del.

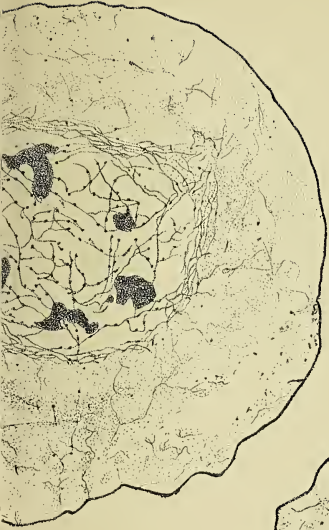


Fig. 13.

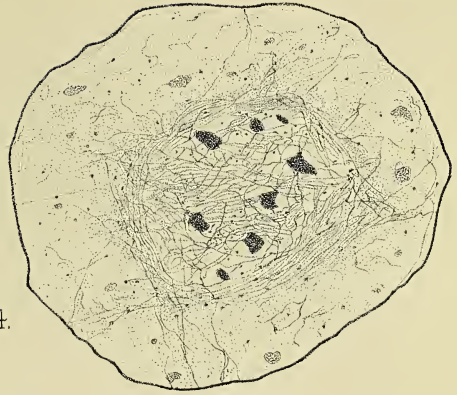


Fig. 14.



Fig. 17.

16.



Fig. 19.







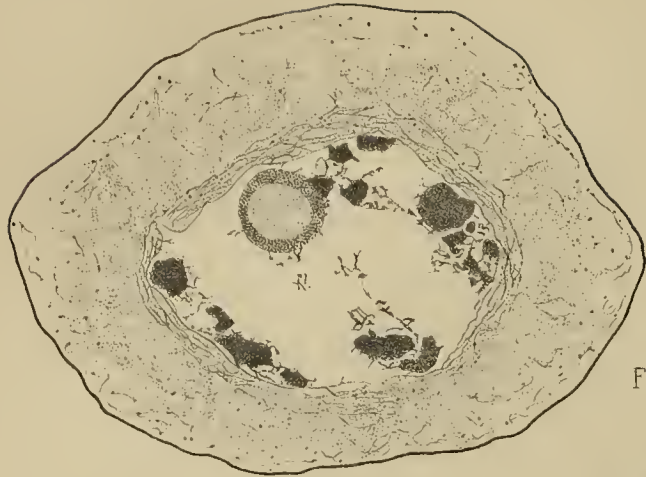


Fig. 12.

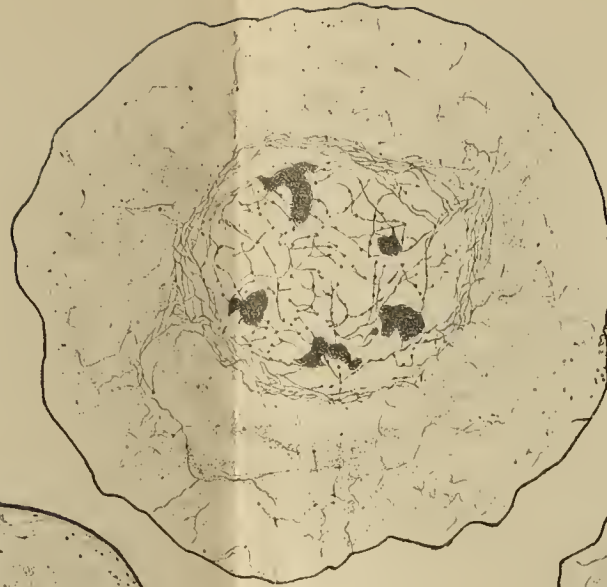


Fig. 13.

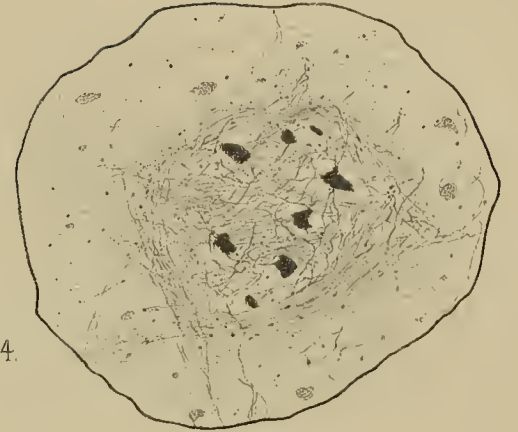


Fig. 14.



Fig. 15.

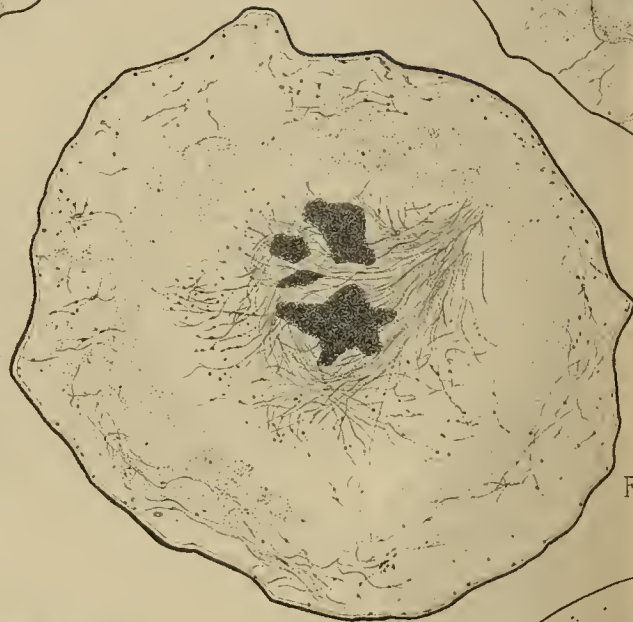


Fig. 16.



Fig. 17.



Fig. 18.



Fig. 20.

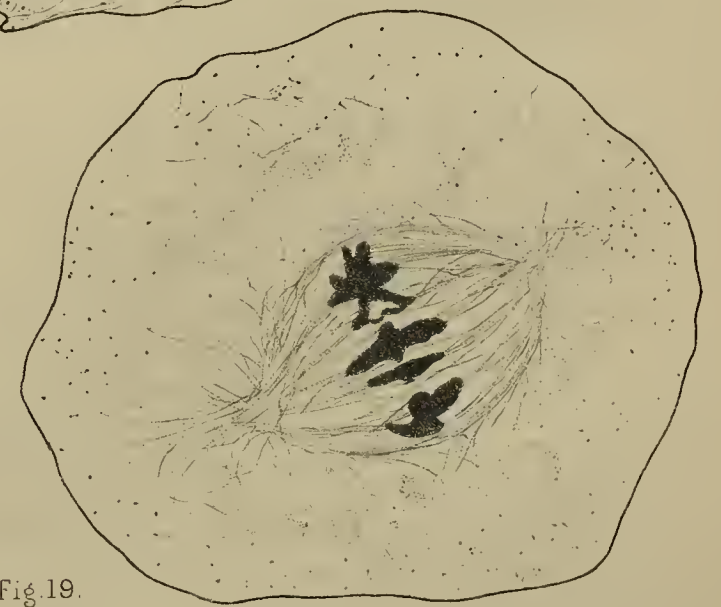


Fig. 19.





# Flowers and Insects in Great Britain.

## PART II<sup>1</sup>.

Observations on the Natural Orders Dipsaceae, Plumbaginaceae, Compositae, Umbelliferae, and Cornaceae, made in the Clova Mountains.

BY

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AND

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IN Part I of this series<sup>1</sup> we described the results of work in the more southern and lowland districts of Britain; the present and following papers deal with the flowers and insects of a definite area in the Eastern Grampians of Scotland, and form a contribution to the study of the problem of the composition, distribution, and origin of the flora of that region and its interdependence with those of the insect fauna. Numerous factors have been active in producing the present phenomena of the vegetation of Northern Europe, and among them the floral ecology of the plants concerned has doubtless been one of much importance; its share may best be determined by comparative work upon limited areas in different parts of Europe.

Our observations were made during vacations spent at Clova between 1894 and 1899. We selected Clova for our

<sup>1</sup> Pt. i, see *Ann. of Bot.*, vol. ix, p. 227, 1895.

[*Annals of Botany*, Vol. XVII. No. LXVI. March, 1903.]

work because it is the focus of the distribution of Alpine plants in Britain, and because of special facilities for our work which the owners of the land there gave us. To them we owe our sincere thanks.

The Clova district as here described means the southern face of the Grampians near Clova in Forfarshire, and includes the upper parts of Glens Clova and Prosen, and the moors of the North Esk above Loch Lee. It comprises about  $103\frac{1}{3}$  square miles, and forms three fairly well defined zones, a zone of straths or valley bottoms (500–1000 feet elevation, 9 sq. miles), a zone of steep hillsides, usually broken by crags above 1,800 feet (1,000–2,500 feet, 74 sq. miles), and a zone of open peaty moors above (2,500–3,000 feet, 20 sq. miles, with  $\frac{1}{3}$  sq. mile above 3,000 feet). The total phanerogamic flora is 363 species, of which eighty-one are alpinines; sixteen other species are maintained by cultivation. Details of these, with discussion of seasonal and altitudinal distribution, are given elsewhere<sup>1</sup>.

The insects which we collected have largely been named by the following entomologists, to whom we are very much indebted.

- G. C. BICKNELL, ESQ., F.E.S. (Parasitic Hymenoptera).
- H. J. BURKILL, ESQ., M.A. (Lepidoptera).
- P. CAMERON, ESQ., F.E.S. (Tenthredinidae).
- E. SAUNDERS, ESQ., F.E.S. (Hymenoptera aculeata).
- D. SHARP, ESQ., M.B., F.R.S. (Coleoptera and others).
- G. H. VERRALL, ESQ., F.E.S. (Diptera).
- C. WARBURTON, ESQ., M.A. (Araneida).

Our observations were distributed as much as possible over the months when flowers occur, August being alone neglected. An account of our visits and a summary of the Flora is given in the Transactions of the Edinburgh Botanical Society, cited below.

Clova stands at about 780 feet above the sea, in a narrow valley between hills which rise rapidly to 2,500 feet, and in

<sup>1</sup> Trans. Edin. Bot. Soc., xxii, 1901, p. 109.

a few instances just exceed 3,000 feet. Crags break the slopes between 2,000 and 2,500 feet. Above the crags stretch peaty moors, which late in the year justify the dreariness attributed to them by Continental writers.

The straths or valley bottoms are as full of flowers and as full of insects as the moors are poor in both. It is part of our purpose to set before the reader a contrast of the two conditions. For the rest we shall compare the conditions of Flower Fertilization at Clova with Flower Fertilization in Germany, the Alps, and elsewhere.

Except on our first two visits we kept a count of individuals visiting, and the record shows more clearly than any lists of visitors the importance of the various species.

The count may be summed as follows, the desirability of the various groups to the flowers being indicated by the type, the larger the type the better suited for fertilizing the flowers<sup>1</sup>:—

<i>Hymenoptera.</i>	{	APIS (APIDAE) . . . . .	430
		BOMBUS AND PSITHYRUS (APIDAE) . . . . .	937
		ANDRENA (66), HALICTUS (1), AND NOMADA (1) (APIDAE) . . . . .	68
		ODYNERUS (5) AND CHRYSIS (1) (= PETIOLATA TUBULIFERA) . . . . .	6
		Vespidae (Wasps) . . . . .	45
		<i>Formicidae and Myrmicidae (Ants)</i> . . . . .	202
		<i>Tenthredinidae (Sawflies)</i> . . . . .	201
<i>Parasitic Hymenoptera (Petiolata parasitica)</i> . . . . .	461		
<i>Lepidoptera.</i>	{	RHOPALOCERA . . . . .	192
		NOCTUIDAE AND GEOMETRES . . . . .	204
		BOMBYCES AND MICROLEPIDOPTERA generally . . . . .	64
		<i>Eriocephala</i> . . . . .	101

*Carried forward* 2,911

<sup>1</sup> Large capitals denote decidedly desirable insects or groups of insects, small capitals denote desirable; small roman letters denote indifferent, and small italics denote injurious visits. The grouping closely agrees with Loew's classification of Anthophilous insects into Eutropous, Hemitropous, Allotropous and Dystropous.



	<i>Brought forward</i>	2,911
Diptera.	SYRPHIDAE . . . . .	712
	EMPIS (411), AND PACHYMERIA (16) . . . . .	427
	Other Empidae . . . . .	129
	Muscidae (in restricted sense), Tachinidae and Sarcophagidae . . . . .	1,083
	Other Diptera . . . . .	10,321
	Coleoptera . . . . .	1314
	<i>Other Insects</i> . . . . .	409
	17,306	

In this part of our paper, taking the Compositae and their allied orders, and the Umbelliferae and their allied order Cornaceae, we shall show what part of the whole available insect fauna these orders with more or less massed flowers may be considered to attract.

The third part will deal with the most highly specialized plants of the Clova Flora; and the fourth will contain an account of the least specialized Entomophilous plants together with a review of the whole results.

#### ABBREVIATIONS.

##### *In references.*

*Brit.* = The British Isles.

*N.C.E.* = North Central Europe (Europe south of the North Sea and Baltic and north of the Alps).

*Arct.* = Arctic regions. Observations chiefly in Greenland and Arctic Scandinavia.

*Pyren.* = Pyrenees.

*Medit.* = Mediterranean countries.

*N.Am.* = North America.

*Scand.* = Lowland Scandinavia.

##### *In lists.*

sh. = sucking honey.

fp. = feeding on pollen.

cp. = collecting pollen.

*And in tables:—*

Hl., Lep.l. = long-tongued Hymenoptera and Lepidoptera respectively.

Hm., Lep.m., and Dm. = mid-tongued Hymenoptera, Lepidoptera, and Diptera respectively.

Hs., Lep.s., and Ds. = short-tongued Hymenoptera, Lepidoptera, and Diptera respectively.

We have found it necessary to modify the literature list which was given in the first part of our paper, but in the new one while we have added and omitted titles we have preserved the numbers used before for all entries that are retained.

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## B' § 1. DIPSACEAE.

57. *Scabiosa Succisa*, Linn. [Lit. *Brit.* 23, 39; Darwin 485; *N.C.E.* 1, 3c, 8, 14, 14a, 18, 21b, 33, 34, 40; De Vries 2460, Magnus 1492.] A *Bombus*-flower at Clova as elsewhere, with abundant visitors among the Syrphidae. We gave figures of the number of insects visiting it on the Scarborough cliffs in the first part of our paper; there the *Bombi* make 55.3 per cent. of the visitors; at Clova they make 38.2 per cent. Long-tongued flies appeared in greater numbers at Clova than at Scarborough.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Polyommatus phloea* L., sh. 13. IX. 95, 700 ft. Heterocera: *Noctuidae*: (2) *Celaena Haworthii* Cuc., 20. IX. 95, 900 ft. (3) *Hydroecia nictitans* Bkh., sh. 13. IX. 95, 700 ft. **Hymenoptera.** Aculeata: *Apidae*: (4) *Apis mellifica* L., sh. 19. IX. 95, 800 ft. (5) *Bombus agrorum* F., sh. 13-24. IX. 95, 7-1,200 ft. (6) *B. lapidarius* L., sh. 15. IX. 95, 800 ft. (7) *B. pratorum* L., sh. 22-23. VI. 95; 13. IX. 95, 7-800 ft. (8) *B. cognatus* Steph., sh. 14. IX. 95, 800 ft. (9) *B. terrestris* L., sh. 13-24. IX. 95, 7-1,200 ft. **Diptera.** *Syrphidae*: (10) *Melanostoma mellinum* L., fp. 16. IX. 95, 800 ft. (11) *Platychirus manicatus* Mg., fp. 23. VII. 95, 800 ft. (12) *P. albimanus* F., fp. 17. IX. 95, 700 ft. (13) *Sericomyia lapponum* L., sh. 13. IX. 95, 700 ft. (14) *S. borealis* Fln., sh. 13-24. IX. 95, 7-900 ft. (15) *Eristalis tenax* L., sh. 13. IX. 95, 700 ft. (16) *E. pertinax* Scop., sh. 13-24. IX. 95, 7-1,000 ft. and once at 2,300 ft. (17) *Heliophilus pendulus* L., sh. 24. IX. 95, 800 ft. *Empidae*: (18) *Empis tessellata* F., sh. 13-22. IX. 95; 11. VII. 96, 7-1,000 ft. (19) *E. grisea* Fln., sh. 15-22. IX. 95, 800 ft. (20) *Pachymeria palparis* Egg., sh. 15-24. IX. 95, 800 ft. *Tachinidae*: (21) *Siphona geniculata* Deg., sh. 13-19. IX. 95, 7-800 ft. *Muscidae*: (22) *Lucilia cornicina* F., sh. 19. IX. 95, 800 ft. (23) *Pollenia rudis* F., 14. IX. 95, 900 ft. *Anthomyiidae*: (24) *Hyetodesia incana* W., sh. and fp. 15-18. IX. 95, 8-1,300 ft. (25) *Drymia hamata* Fln., sh. 14-24. IX. 95, 800 ft. (26 and 27) *Anthomyia* 2 spp., sh. 14-24. IX. 95, 8-900 ft. (28) *Trichophthicus* sp., 13. IX. 95, 700 ft. *Cordyluridae*: (29) *Scatophaga stercoraria* L., 16-23. IX. 95, 9-1,100 ft. **Coleoptera**: (30) *Meligethes viridescens* F., 15-18. IX. 95, 800 ft. **Araneida**: (31) *Xysticus* sp., lying in wait, 13. IX. 95, 700 ft.

B' § 2. PLUMBAGINACEAE, WITH AGGREGATED FLOWERS.

58. *Armeria maritima*, Willd. [Lit. *Brit.* 23; *N.C.E.* 1, 9, 12, 14, 14 a, 15, 21 a, 25, 31, 34, 35; Knuth 1221; MacLeod 1473. *Pyren.* 17.] Only found at 2,890 feet, the flowers are 8-9 mm. in diameter.

*Visitors.* **Diptera.** *Cecidomyiidae*: (1) 1 sp. sh. 2. VII. 96. *Mycetophilidae*: (2) *Sciara* sp.,? sh. 16. VI. 99. *Anthomyiidae*: (3) *Trichophthicus* sp., sh. fairly abundant 2. VII. 96; 16. VI. 99. **Thysanoptera.** (4) *Thrips* sp., 2. VII. 96. All at 2,800 ft.

## B' § 3. BLUE-FLOWERED COMPOSITAE.

59. *Centaurea Cyanus*, Linn. [Lit. *N.C.E.* 1, 3 c, 9, 11, 14, 16, 18, 32, 34, 40.]

*Visitors.* Hymenoptera. Aculeata: *Apidae*: (1) *Andrena analis* Panz., seeking h. *Diptera.* *Anthomyiidae*: (2) 1 sp. Both 11. VII. 96, 600 ft.

59 a. *Lactuca alpina*, Benth. [Lit. *N.C.E.* Loew 1358; *Alps* 2; *Arct.* 36.] At 2,000 ft. The capitula contain 12-20 flowers, and number 16-20. The neighbouring flowers may pollinate each other, but self-pollination by the rolling back of the stigmatic lobes seems not to occur. In this our observations agree with those of Müller. We have had no favourable opportunities for observing visitors.

## B' § 4. PURPLE-FLOWERED COMPOSITAE.

60. *Centaurea nigra*, Linn. [Lit. *Brit.* 23, 39; Marquand 1513; *N.C.E.* 8; *Pyren.* 17.]

*Visitors.* Hymenoptera. Aculeata: *Apidae*: (1) *Bombus terrestris* L., sh. 15-21. IX. 95, 8-900 ft. (2) *B. agrorum* F., sh. 15-21. IX. 95, 8-900 ft. (3) *B. lapidarius* L., sh. 16-22. IX. 95, 800 ft. (4) *B. lapponicus* F., 16. IX. 95, 800 ft. *Diptera.* *Empidae*: (5) *Empis grisea* Fln., sh. 15-21. IX. 95, 800 ft. (6) *Pachymeria palparis* Egg., sh. 16. IX. 95, 800 ft. *Anthomyiidae*: (7) *Hyetodesia incana* W., 16. IX. 95, 800 ft. (8) *Drymia hamata* Fln., sh. and fp. 15-16. IX. 95, 8-900 ft. (9) *Anthomyia* sp., sh. 21. IX. 95, 800 ft. *Coleoptera*: (10) *Meligethes viridescens* F., 15-16. IX. 95, 8-900 ft.

61. *Carduus palustris*, Willd. [Lit. *Brit.* 23; *N.C.E.* 1, 3 c, 8, 16, 18, 34, 40; De Vries 2460; Warnstorf 2507; *Alps* 2, 34.] *Bombus terrestris* and *Empis tessellata* show some measure of constancy in autumn.

*Visitors.* Lepidoptera. Rhopalocera: (1) *Argynnis aglaia* L., sh. 29. VI.-1. VII. 95; 22. VI.-10. VII. 96, 8-900 ft. (2) *Lycaena icarus* Rott., sh. 28. VI. 95, 800 ft. Heterocera: *Noctuidae*: (3) *Hydroecia nictitans* Bkh., sh. 13-21. IX. 95, 7-1,000 ft. **Hymeno-**



ptera. Aculeata: *Apidae*: (4) *Bombus terrestris* L., 16-21. IX. 95, 7-1,400 ft. (5) *B. agrorum* F., sh. 1. VII. 95, 800 ft. (6) *B. venustus* Smith, sh. 26. VI. 96, 800 ft. (7) *B. lapponicus* F., 16. IX. 95, 1,400 ft. (8) *Psithyrus quadricolor* Lep., sh. 19. VI. 96, 1,500 ft. *Formicidae*: (9) *Formica fusca* Latr., 22. VI. 96, 2,300 ft. *Diptera*. *Syrphidae*: (10) *Platychirus manicatus* Mg., sh. 1-6. VII. 95, 800 ft. (11) *Rhingia campestris* Mg., sh. 1. VII. 95, 800 ft. (12) *Volucella bombylans* L., sh. 1. VII. 95, 800 ft. (13) *Eristalis arbustorum* L., sh. 19. VI. 95, 800 ft. *Empidae*: (14) *Empis tessellata* F., sh. 2. VII. 95; 16-21. IX. 95; 19. VI. 96, 8-1,500 ft. *Mycetophilidae*: (15) *Sciara* sp., 21. IX. 95, 1,000 ft. *Anthomyiidae*: (16) *Hyetodesia incana* W., 1. VII. 95; 6. VII. 96, 800 ft. (17) *Trichophthicus* sp., 29. VI.-3. VII. 95; 16. IX. 95, 8-1,200 ft. (18 and 19) *Anthomyia* 2 spp., fp. 26. VI.-1. VII. 95; 21. IX. 95; 19. VI.-1. VII. 96, 8-1,500 ft. *Coleoptera*. (20) *Ceuthorrhynchidius contractus* Marsh, 23. VI. 96, 2,500 ft.

62. *Cnicus arvensis*, Hoffm. [Lit. *Brit.* 23; *N.C.E.* 1, 3c, 8, 11, 14, 14a, 15, 16, 18, 25, 30, 31, 32, 33, 34, 40; De Vries 2460; *Alps* 2, 9, 34; *Pyren.* 17.] At Clova the more specialized visitors deficient.

*Visitors*. *Lepidoptera*. *Rhopalocera*: (1) *Vanessa urticae* L., sh. 21. IX. 95, 1,200 ft. *Heterocera*: *Noctuidae*: (2) *Characae grammis* L., sh. 14. IX. 95, 900 ft. *Hymenoptera*. Aculeata: *Apidae*: (3) *Bombus terrestris* L., 21-24. IX. 95, 9-1,200 ft. *Petiolata* parasitica: *Ichneumonidae*: (4) *Hemiteles politus* Bridgm., sh. 21. IX. 95, 900 ft. (5) a second sp., 17. IX. 95, 900 ft. *Diptera*. *Syrphidae*: (6) *Eristalis pertinax* Scop., sh. 21-24. IX. 95, 9-1,200 ft. *Sarco-phagidae*: (7) *Cynomyia mortuorum* L., sh. 14-24. IX. 95, 9-1,200 ft. *Muscidae*: (8) *Lucilia cornicina* F., sh. 21. IX. 95, 900 ft. (9) *Calliphora erythrocephala* Mg., 24. IX. 95, 1,200 ft. (10) *Pollenia rudis* F., sh. and fp. 14-24. IX. 95, 9-1,200 ft. *Anthomyiidae*: (11) *Hyetodesia incana* W., 21. IX. 95, 900 ft. (12 and 13) *Anthomyia* spp., fp. 17-21. IX. 95, 8-900 ft. *Cordyluridae*: (14) *Scatophaga stercoraria* L., sh. 21. IX. 95, 8-900 ft. *Coleoptera*: (15) *Meligethes viridescens* F., sh. 17-24. IX. 95, 8-900 ft.

63. *Cnicus heterophyllus*, Willd. [Lit. *Brit.* 23; *N.C.E.* 1; Loew 1359; *Arct.* 34; *Alps* 2.]

*Visitors.* **Lepidoptera.** Heterocera: *Noctuidae*: (1) *Plusia chrysochrysa* L., sh. 2. VII. 96. **Hymenoptera.** Aculeata: *Apidae*: (2) *Apis mellifica* L., sh. 3-11. VII. 96. (3) *Bombus terrestris* L., 2. VII. 95. (4) *B. hortorum* L., sh. 29. VI.-11. VII. 96. (5) *B. pratorum* L., sh. 11. VII. 96. (6) *Psithyrus quadricolor* Lep., sh. 22. VII. 95. *Vespidae*: (7) *Vespa norvegica* F., seeking h. 15. VII. 95. **Diptera.** *Syrphidae*: (8) *Platychirus* sp., fp. 22. IX. 95. (9) *Sericomyia borealis* Fln., fp. 8. VI. 95. (10) *Volucella bombylans* L., sh. 11. VII. 96. (11) *Rhingia campestris* Mg., 11. VII. 96. *Empidae*: (12) *Empis* sp., fp. 29. VI. 96. (13) *E. aestiva* Lw., fp. 29. VI. 96. *Bibionidae*: (14) *Scatopse* sp.,? seeking h. 3. VII. 96. *Dolichopodidae*: (15) *Dolichopus* sp., sh. 3. VII. 96. *Anthomyiidae*: (16) *Hyetodesia incana* W., fp. 22. IX. 95; 24. VII. 96. (17) *Hylemyia nigrescens* Rnd., 20. VI. 96. (18) *Anthomyia* sp., 22. IX. 95. *Sciomyzidae*: (19) *Dryomyza flaveola* Fln., 20. VI. 96. *Sapromyzidae*: (20) *Sapromyza* sp., 20. VI. 96. **Coleoptera**: (21) *Meligethes viridescens* F., fp. 15-20. IX. 95; 29. VI. 96. (22) *M. aeneus* F., fp. 3. VII. 96. (23) *Epuraea aestiva* L., fp. 29. VI. 96. (24) *Anthobium sorbi* Gyll., fp. 29. VI. 96. **Hemiptera**: (25) 1 sp., 3. VII. 96. **Thysanoptera**: (26) *Thrips* sp., 3. VII. 96. All at 7-800 ft.

64. *Cnicus lanceolatus*, Scop. [Lit. *Brit.* 23; *N.C.E.* 1, 3c, 8, 11, 14, 14a, 16, 18, 31, 33, 34, 40; De Vries 2460; Warnstorff 2507; *Alps* 2; *Pyren.* 17; *N.Am.* 19 d.]

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus terrestris* L., sh. 21-23. IX. 95, 10-1,300 ft. (2) *B. lapponicus* F., sh. 21. IX. 95, 1,000 ft. (3) *Psithyrus quadricolor* Lep., sh. 21. IX. 95, 1,000 ft. **Diptera.** *Syrphidae*: (4) *Eristalis pertinax* Scop., 13. IX. 95, 700 ft. *Empidae*: (5) *Empis tessellata* F., 21. IX. 95, 1,000 ft. *Phoridae*: (6) *Phora* sp., 17. IX. 95, 700 ft. *Anthomyiidae*: (7) *Hyetodesia semicinerea* W., 21. IX. 95, 1,000 ft. **Hemiptera**: (8) *Aphis* sp., 17. IX. 95, 700 ft.

65. *Saussurea alpina*, DC. [Lit. *Arct.* 36; *Alps* 2, 9.]

*Visitors.* **Diptera.** *Anthomyiidae*: (1) *Trichophthicus hirsutulus* Ztt., fp. 15. VII. 95, 2,400 ft. (2) *Anthomyia* sp., fp. 18. VII. 95, 2,300 ft.

## B' § 5. YELLOW-FLOWERED RAYED COMPOSITAE.

66. *Solidago Virg-aurea*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 11, 18, 33, 34, 40; Warnstorff 2507; *Arct.* 36; *Alps* 2, 34; *Pyren.* 17.]

*Visitors.* **Diptera.** *Tachinidae*: (1) *Siphona geniculata* Deg., fp. 16. IX. 95, 800 ft. *Muscidae*: (2) *Calliphora erythrocephala* Mg., 29. VI. 96, 800 ft. *Anthomyiidae*: (3) *Hyetodesia incana* W., 29. VI. 96, 800 ft. (4) *Anthomyia* sp., fp. 16. IX. 95, 800 ft. (5) *Limnophora solitaria* Ztt., sh. 6-10. VII. 96, 21-2,600 ft.

67. *Tussilago Farfara*, Linn. [Lit. *Brit.* 29; *N.C.E.* 1, 14, 18, 34, 40; *Medit.* 34; *Arct.* 34; *Alps* 2, 9.]

*Visitors.* **Hymenoptera.** *Aculeata*: *Apidae*: (1) *Apis mellifica* L., sh. 12-16. IV. 95, 800 ft. **Diptera.** *Syrphidae*: (2) *Melanostoma quadrimaculatum* Verrall, sh. 12. IV. 95, 800 ft. *Muscidae*: (3) *Lucilia cornicina* F., sh. 12-16. IV. 95, 800 ft. abundant. (4) *Pollenia rudis* F., sh. 12-16. IV. 95, 800 ft. abundant. *Anthomyiidae*: (5) *Anthomyia sulciventris* Ztt., fp. 20. V. 97, 7-16. V. 98, 8-1,200 ft. (6) *A.* sp., fp. 18. V. 97, 19-2,000 ft.

68. *Senecio vulgaris*, Linn. [Lit. *Brit.* 23, 29; A. Bateson 151; *N.C.E.* 1, 3 c, 11, 14, 18, 25, 33, 34.] All observers find it very neglected.

*Visitors.* **Diptera.** *Anthomyiidae*: (1) *Anthomyia* sp., fp. 17-19. IX. 95, 800 ft.

69. *Senecio aquaticus*, Huds. [Lit. *Brit.* 23; *N.C.E.* 8.] Not so abundant as *Senecio Jacobaea*, and very much less visited.

*Visitors.* **Hymenoptera.** *Aculeata*: *Apidae*: (1) *Bombus terrestris* L., sh. 14. IX. 95. **Diptera.** *Syrphidae*: (2) *Eristalis pertinax* Scop., 14. IX. 95. *Empidae*: (3) *Empis tessellata* F., sh. 14. IX. 95. *Tachinidae*: (4) *Siphona geniculata* Deg., sh. 14. IX. 95. *Muscidae*: (5) *Lucilia cornicina* F., sh. 1. VII. 95. *Anthomyiidae*: (6) *Hyetodesia incana* W., sh. 2. VII. 95; 14. IX. 95; 6. VII. 96. (7) *H. variabilis* Fln., sh. 1. VII. 95. (8) *Anthomyia* sp., 13. IX. 95. All at 7-800 ft.



70. *Senecio Jacobaea*, Linn. [Lit. *Brit.* 23, 34, 39; *N.C.E.* 1, 3c, 11, 14, 16, 18, 34, 40; De Vries 2460; *Alps* 34; *Pyren.* 17.] A very conspicuous flower in autumn at low levels, where it attracts the drones of the common Bombi, moths, flies of all sorts and beetles; except the Bombi much in proportion to the then existing prevalence of the various classes; but the Bombi it attracts in less degree.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Polyommatus phloreas* L., sh. 13-14. IX. 95, 7-800 ft. Heterocera: *Noctuidae*: (2) *Hydroecia nictitans* Bkh., sh. 13-21. IX. 95, 8-900 ft. (3) *Celaena haworthii* Cuc., sh. 16-19. IX. 95, 8-900 ft. *Geometres*: (4) *Psodos trepidaria* Hb., sh. 11. VII. 96, 800 ft. (5) *Cidaria immanata* Hw., sh. 13-21. IX. 95, 7-900 ft. *Crambidae*: (6) *Crambus* sp., 14. IX. 95, 700 ft. **Hymenoptera.** Aculeata: *Apidae*: (7) *Bombus terrestris* L., sh. 13-24. IX. 95, 7-900 ft. (8) *B. lapponicus* F., sh. 16. IX. 95, 800 ft. (9) *B. agrorum* F., sh. 13. IX. 95, 700 ft. *Vespidae*: (10) *Vespa norvegica* F., fp. 19. IX. 95, 800 ft. *Formicidae*: (11) *Formica fusca* Latr., 16. IX. 95, 800 ft. Petiolata parasitica: *Ichneumonidae*: (12) 1 sp., sh. 21. IX. 95, 800 ft. *Braconidae*: (13, 14, and 15) 3 sp., 16-7. IX. 95, 7-800 ft. *Cynipidae*: (16) *Eucoela fortinervis* Cameron, 15. IX. 95, 800 ft. *Diptera.* *Syrphidae*: (17) *Platychirus albimanus* F., 16-24. IX. 95, 8-1,000 ft. (18) *P. manicatus* Mg., sh. 10. VII. 96, 800 ft. (19) *Sericomyia borealis* Fln., sh. 21. IX. 95, 800 ft. (20) *Eristalis tenax* L., sh. 13. IX. 95, 8-900 ft. (21) *E. pertinax* Scop., sh. and fp. 14-24. IX. 95, 8-900 ft. (22) *E. rupium* F., sh. 22. VII. 95, 800 ft. (23) *E. arbustorum* L., sh. and fp. 15. VII. 95; 13-22. IX. 95, 7-800 ft. (24) *Helophilus pendulus* L., 21. IX. 95, 800 ft. *Empidae*: (25) *Empis tessellata* F., 13-6. IX. 95, 7-800 ft. (26) *E. punctata* Mg., sh. 22. VII. 95, 800 ft. (27) *E. albipennis* Mg., 21. IX. 95, 800 ft. (28) *Rhamphomyia spinipes* Fln., 14. IX. 95, 800 ft. *Mycetophilidae*: (29) *Sciara* sp., 16-22. IX. 95, 800 ft. *Bibionidae*: (30) *Bibio pomonae* F., fp. 13-22. IX. 95, 7-900 ft. *Chironomidae*: (31) *Ceratopogon leucopeza* Mg., 19-20. IX. 95, 800 ft. *Tachinidae*: (32) *Siphona geniculata* Deg., sh. 14-22. IX. 95, 800 ft. *Sarcophagidae*: (33) *Cynomyia mortuorum* L., 16-24. IX. 95, 9-1,000 ft. *Muscidae*: (34) *Lucilia cornicina* F., 14-24. IX. 95; 10. VII. 96, 8-1,300 ft. (35) *Calliphora vomitoria* L.,? sh. 22. VII. 95, 800 ft. (36) *C. erythrocephala* Mg., sh. 4-22. IX. 95, 8-1,000 ft.

(37) *C. sepulchralis* Mg., 17. VII. 95, 800 ft. and? 14. IX. 95, 900 ft. (38) *Pollenia rudis* F., sh. and fp. 15-22. VII. 95; 14-24. IX. 95, 8-1,300 ft. (39) *P. vespillo* F., 19. IX. 95, 800 ft. (40) *Mesembryna meridiana* L., 21. IX. 95, 800 ft. (41) *Cyrtoneura caesia* Mg., sh. and fp. 16-22. IX. 95, 8-900 ft. *Anthomyiidae*: (42) *Hyetodesia incana* W., sh. and fp. 14-24. IX. 95, 8-1,000 ft. (43) *Drymia hamata* Fln., fp. 14-19. IX. 95, 8-900 ft. (44) *Trichophthicus* sp., 16. IX. 95, 800 ft. (45, 46, and 47) *Anthomyia* 3 spp., sh. and fp. 13-24. IX. 95, 7-1,000 ft. *Cordyluridae*: (48) *Scatophaga stercoraria* L., fp. 16-21. IX. 95, 7-900 ft. (49) Another sp., fp. 16. IX. 95, 800 ft. *Sepsidae*: (50) *Sepsis cynipsea* L., 10. VII. 96, 800 ft. *Phoridae*: (51) *Phora* sp., 21. IX. 95, 800 ft. *Coleoptera*: (52) *Meligethes viridescens* F., sh. and fp. 27. VII. 95; 14-24. IX. 95, 7-1,000 ft. (53) *M. aeneus* F., sh. and fp. 14. IX. 95, 800 ft. (54) *Brachypterus urticae* F., sh. 22. IX. 95, 800 ft. (55) *Homalota* sp., 16. IX. 95, 800 ft. *Hemiptera*: (56) *Anthocoris nemorum* L., sh. 16. IX. 95, 800 ft. *Thysanoptera*. (57) *Thrips* sp., sh. 14-17. IX. 95, 7-800 ft. *Araneida*: (58) *Oligolophus morio* Fabr., 24. IX. 95, 1,000 ft.

#### B' § 6. YELLOW-FLOWERED LIGULATE COMPOSITAE.

71. *Leontodon autumnalis*, Linn. [Lit. *Brit.* 23, 39; *N.C.E.* 1, 3c, 9, 11, 14, 14a, 15, 18, 25, 30, 31, 32, 33, 40; *De Vries* 2460; *Arct.* 34, 36; *Alps* 34; *Pyren.* 17.] This plant ascends (in its var. *pratense*) to considerable elevations, and is one of the most conspicuous of autumn flowers on the moors. Self-fertilization is produced in the way usual in the Compositae by the rolling back of the stigma as the flower ages. Nine-tenths of its individual visitors are short-tongued flies. Visitors of constancy hardly exist, but the circle is wide.

*Visitors.* *Lepidoptera.* *Heterocera*: *Pyralidae*: (1) *Pyrausta?* *alpinalis* Schiff., 4. VII. 95, 2,500 ft. *Hymenoptera.* *Aculeata*: *Apidae*: (2) *Bombus terrestris* L., sh. 24. IX. 95, 1,200 ft. (3) *Andrena coitana* Kirby, sh. 5. VII. 95, 800 ft. (4) *A. analis* Panz., sh. 22. VII. 95, 1,000 ft. *Myrmicidae*: (5) *Myrmica rubra* L., ? fp. 21. IX. 95, 900 ft. *Petiolata parasitica*: (6) 1 sp., sh. 26. VI. 95, 900 ft. (7) a second sp., 17. IX. 95, 800 ft. *Sessiliventres*: *Tenthredinidae*:

(8) *Allantus arcuatus* Forst., 17. VII. 95, 800 ft. **Diptera. Syrphidae:**  
 (9) *Melanostoma mellinum* L., 13. IX. 95, 700 ft. (10) *Platychirus manicatus* Mg., fp. 30. VI.-20. VII. 95, 800 ft. (11) *Syrphus albostriatus* Fln., fp. 20. VII. 95, 800 ft. (12) *S. balteatus* Deg., fp. 13-24. IX. 95, 7-1,000 ft. (13) *S. ? luniger* Mg., fp. 14. IX. 95, 800 ft. (14) *Eristalis pertinax* Scop., sh. 13-24. IX. 95, 7-1,000 ft. **Empididae:**  
 (15) *Empis punctata* Mg., sh. 20. VII. 95, 800 ft. **Mycetophilidae:**  
 (16) *Sciara* sp., fp. 21. IX. 95, 1,600 ft. **Chironomidae:** (17) 1 sp., sh. 30. VI. 95, 800 ft. **Tachinidae:** (18) *Siphona geniculata* Deg., sh. 14. IX. 95, 900 ft. **Muscidae:** (19) *Lucilia cornicina* F., sh. 24. IX. 95, 8-1,200 ft. (20) *Pollenia rudis* F., sh. 14-24. IX. 95, 8-1,200 ft. **Anthomyiidae:** (21) *Hyetodesia incana* W., sh. and fp. 4-20. VII. 95; 16-21. IX. 95, 8-1,600 ft. (22) *H.* sp., fp. 21. VII. 95, 800 ft. (23) *H. semicinerea* W., fp. 21. IX. 95, 1,100 ft. (24) *Drymia hamata* Fln., fp. 14-24. IX. 95, 8-1,400 ft. (25) *Trichophticus* sp., sh. 30. VI. 95, 800 ft. and 2. VII. 96, 2,800 ft. (26) *Hylemyia nigrescens* Rnd., 3. VII. 95, 800 ft. (27, 28, and 29) *Anthomyia* 3 spp., sh. and fp. 13-24. IX. 95, 7-2,000 ft. **Cordyluridae:** (30) *Scatophaga stercoraria* L., 21. IX. 95, 900 ft. **Phoridae:** (31) *Phora* sp., 20. IX. 95, 2,400 ft. **Coleoptera.** (32) *Meligethes viridescens* F., sh. and fp. freq. 26-30. VI. 95; 13-24. IX. 95, 7-1,600 ft. (33) *M. aeneus* F., sh. 14. IX. 95, 800 ft.

**72. *Crepis paludosa*, Moench.** [Lit. *Brit.* 23; *N.C.E.* 3 c, 18; *Alps* 2, 9; *Pyren.* 17.]

**Visitors. Hymenoptera. Aculeata: Formicidae:** (1) *Formica fusca* Latr., 20. VI. 96, 800 ft. **Diptera. Syrphidae:** (2) *Platychirus manicatus* Mg., ? sh. 2. VII. 95, 800 ft. **Anthomyiidae:** (3) *Hyetodesia incana* W., sh. and fp. i. VI. 95, 19. VI.-6. VII. 96, 8-1,700 ft. (4) *Limnophora* sp., sh. 2. VII. 95, 800 ft. (5) *Spilogaster nigrivenis* Ztt., 19. VI. 96, 1,500 ft. (6) *Anthomyia* sp., 14. IX. 95, 800 ft. **Agromyzidae:** (7) *Agromyza* sp., 1. VI. 95, 800 ft. **Coleoptera:** (8) *Meligethes viridescens* F., sh. 2-6. VII. 95; 29. VI.-6. VII. 96, 8-1,700 ft.

**73. *Hieracium pilosella*, Linn.** [Lit. *Brit.* 34; Marquand, 1513; *N.C.E.* 1, 3 c, 11, 12, 14, 16, 18, 25, 30, 31, 33; De Vries 2460; *Arct.* 36; *Alps* 16, 44; *Pyren.* 17.] At Clova fly-visited; in South Germany, the Netherlands and Flanders visited by mid-tongued bees and by several Syrphidae; in



the Alps with a considerable list of Lepidoptera among its visitors. Lindmann saw a butterfly to be a fairly frequent visitor in Norway.

*Visitors. Lepidoptera.* Rhopalocera: (1) *Lycaena icarus* Rott., sh. 28. VI. 95, 800 ft. (2) *Polyommatus phloea* L., sh. 22. VI. 95, 800 ft. *Hymenoptera.* Petiolata parasitica: (3) 1 sp. 14. VI. 95, 700 ft. *Diptera. Syrphidae:* (4) 1 sp., 26. VI. 96, 1,100 ft. *Empidae:* (5) *Tachydromia* sp., ? fp. 24. VI. 96, 800 ft. (6) *Empis chioptera* Flm., 26. VI. 95, 800 ft. *Mycetophilidae:* (7) *Sciara* sp., sh. 18. IX. 95, 800 ft. *Dolichopodidae:* (8) *Dolichopus* sp., sh. 26. VI. 96, 2,200 ft. *Tachinidae:* (9) *Siphona geniculata* Deg., 18. VI. 99, 800 ft. *Muscidae:* (10) *Lucilia cornicina* F., sh. 22. VI. 95, 800 ft. *Anthomyiidae:* (11) *Hyetodesia incana* W., 18. VI. 99, 800 ft. (12) *Limnophora solitaria* Ztt., 28. VI. 95, 1,800 ft. (13) *Hydrotaea* sp., 19. VI. 99, 800 ft. (14) *Hylemyia nigrescens* Rnd., 16-18. VI. 99, 800 ft. (15) *Trichophthicus* sp., 28. VI.-4. VII. 95, 1,800 ft. (16) *Anthomyia sulciventris* Ztt., 25. VI. 96, 2,200 ft. (17 and 18) *A.* spp., sh. and fp. 14. VI.-5. VII. 95; 18-24. IX. 95; 16. VI.-10. VII. 96, 7-2,300 ft. *Coleoptera:* (19) *Meligethes viridescens* F., sh. and fp. 26. VI. 96; 19. VI. 99, 8-1,800 ft. (20) *Brachypterus* sp.?, 26. VI. 95, 800 ft. *Thysanoptera:* (21) *Thrips* sp., 26. VI. 96, 1,800 ft.

74. *Hieracium* (*Archi-Hieracia*) spp. [Lit. *Brit.* 23; *N.C.E.* 1, 3 c, 11, 16, 18, 33, 34, 35, 40; De Vries 2460; Loew 1358; *Arct.* 36; *Alps* 2, 34; *Pyren.* 17.] By the kindness of Mr. F. J. Hanbury and the Rev. E. F. Linton, who examined our specimens of *Hieracia*, we are able to give names to a number of forms. The Clova mountains are very rich in these, and some of them we have studied. The following notes give our observations; we have found it impossible to do otherwise than lump the forms together in enumerating the insect visits. Recognizing in the many forms of *Hieracia* incipient species, we find our chief interest in noting any characters which would promote segregation of the group by preventing indiscriminate hybridisation or crossing. A tendency to flower early or late, a separation in habitat, or a more complete self-pollination than is usual

ought severally to help to isolate forms in which these characters occur.

SPECIES: 1. *H. alpinum*, Linn. Flowers of (a) *H. eximium*, Backh., were carefully observed. On the second and third days after the expansion of the head, the pollen was swept out in the outer florets; on the fourth day the stigmas of these outer florets separated. On the sixth day all the florets were open, and the stigmas of the outermost so recurved as to be self-pollinated. Thus apparently this form secures self-fertilization in the absence of insect visitors. (b) *H. holosericeum*, Backh., growing with the last, is perhaps not self-pollinated to the same extent. (c) *H. alpinum*, the segregate, (d) *H. calenduliflorum*, Backh., and (e) *H. gracilentum*, Backh., are other Clova forms.

SPECIES: 2. *H. nigrescens*, (f) *H. Marshallii*, Linton, (g) *H. senescens*, Backh., (h) *H. chrysanthum*, Backh., and (i) *H. lingulatum*, Backh., are all forms which we have found at Clova. *H. chrysanthum* is rather distinct in its orange-yellow heads, but all the species of insects, seen to visit it, were seen on other species, so that so far as we know the colour causes no selection. The stigmas become slightly revolute, and this brings about self-pollination.

SPECIES: 3. *H. anglicum*, Fries, (j) *H. anglicum*, segregate, (k) *H. iricum*, Fries, (l) *H. clovense*, Linton, (m) *H. cerinthiforme*, Backh., were obtained. Also (n) *H. callistophyllum*, F. J. Hanb., has been gathered at Clova. (F. J. Hanbury, Brit. Hierac., pp. 65, 66.) On the crags at Loch Brandy grow together *H. eximium* and *H. clovense*. The former begins to flower before the latter, but their flowering-periods overlap. Heads of *H. clovense* were kept in a room side by side with *H. eximium*, already described. For five days the behaviour of *H. clovense* was just like that of *H. eximium*, but on the sixth day when the last of the florets of *H. eximium* were open, there were still some florets of *H. clovense* to open, and further the stigma of *H. clovense* never recurved as tightly as that of *H. eximium*, and consequently self-pollination would

appear to be less inevitable. Perhaps of these two associates the earlier flowering of the one, and the less period of time when cross-fertilization is possible, may prevent in a measure the crossing which we believe extremely likely to occur. There are then causes which would help incipient species to become isolated. We have seen more insects on *H. clovense* than on *H. eximium*, but they are of the same or similar species.

SPECIES: 4. *H. murorum*, Linn. (*o*) *H. Schmidtii*, Tausch, (*p*) *H. Leyi*, F. J. Hanb., (*q*) *H. lasiophyllum*, Koch, and (*r*) *H. argenteum*, Fries, were obtained. The second seems very common in some spots. It grows at lower levels than *H. eximium*, *H. chrysanthum*, and *H. holosericeum* for the most part, rarely exceeding 2,250 feet, and where mixed with *H. eximium* flowering like *H. clovense*, a little later than it. The stigma becomes tightly recurved when old. We have also gathered (*s*) *H. pictorum*, Linton, (*t*) *H. murorum*, segregate, (*u*) *H. aggregatum*, Backh., and (*v*) *H. rivale*, F. J. Hanb.

SPECIES: 5. *H. sylvaticum*. (*w*) *H. vulgatum*, Fries, (*x*) *H. euprepes*, F. J. Hanb., (*y*) *H. angustatum*, Lindeb., and (*z*) *H. diaphanoides*, Lindeb., have been obtained at Clova (Linton, in Journ. Bot. 1890, p. 168; Druce, Ann. Scot. Nat. Hist. 1896, p. 126; F. J. Hanb., Journ. Bot. 1893, p. 133). The stigma of these becomes ultimately tightly recurved. With the exception of *H. pictorum* those we have seen all grow intermixed. Other sub-species or varieties of *Hieracia* have been found at Clova, bringing up the total to thirty-one forms. For their names see our paper in the Trans. Edinb. Bot. Soc.

There is a sort of stratification about the *Hieracia*. The sub-species of *H. alpina* grow at the highest levels, next in descending the hills we come to the sub-species *H. Leyi*, *H. clovense*, *H. argenteum*, and similar forms. Lowest come the more richly branched forms, such as *H. anglicum*. One form, *H. vulgatum*, we have found at all heights, from 700-2,900 feet. The others have a much less extensive range. The insects which visit the *Hieracia* are none of them wide-



flying, and there is every probability that a floret if crossed will be fertilized from a very similar plant. This is another cause helping to allow the segregation of the group.

*Visitors.* **Lepidoptera.** Heterocera: *Pyralidae*: (1) *Pyrausta alpinalis* Schiff., sh. (to b, h, j, p) 1-6. VII. 96, 25-2,700 ft. **Hymenoptera.** Aculeata: *Myrmicidae*: (2) *Myrmica rubra* L., (to w) biting flowers, 18. VI. 96, 1,400 ft. Petiolata parasitica: *Cynipidae*: (3) *Cynips* sp., (to w) 16. VI. 96, 700 ft. **Diptera.** *Syrphidae*: (4) *Melanostoma mellinum* L., (to w) fp. 16. IX. 95, 800 ft. (5) *Platychirus manicatus* Mg., (to j, r, w) 1-6. VI. 96, 17-2,700 ft. *Empidae*: (6) *Empis lucida* Ztt., (to w) 4. VII. 95, 1,800 ft. (7) *E.* sp., (to w) 29. VI. 96, 800 ft. (8) *E. aestiva* Lw., (to w) 29. VI. 96, 800 ft. *Mycetophilidae*: (9) *Sciara* sp., (to w) sh. 30. VI. 96, 2,100 ft. *Bibionidae*: (10) *Dilophus albipennis* Mg., (to w) sh. 26. VI. 96, 1,200 ft. *Tachinidae*: (11) *Siphona geniculata* Deg., (to t, w) 18-25. VI. 96, 7-800 ft. *Muscidae*: (12) *Lucilia cornicina* F., (to w) sh. 24. IX. 96, 1,000 ft. *Anthomyiidae*: (13) *Hyetodesia incana* W., (to b, h, j, l, p, r, t, w) sh. and fp. freq. 23. VI.-4. VII. 95, 18. VI.-6. VII. 96, 8-2,600 ft. (14) *H. basalis* Ztt., (to w) sh. 4. VII. 95, 1,200 ft. (15) *Drymia hamata* Fln., (to a, b, c, h, j, l, t) sh. and fp. 26. VI.-2. VII. 96, 17-2,700 ft. (16) *Spilogaster nigrivenis* Ztt., (to w) 19. VI. 96, 1,500 ft. (17) *Trichophthicus hirsutulus* Ztt., (to h, j, p) 6. VII. 96, 17-2,000 ft. (18) *T.* sp., (to a, l, p, w) fp. 20. VI.-6. VII. 96, 18-2,500 ft., 16. IX. 95, 8-900 ft. (19) *Anthomyia sulciventris* Ztt., (to l) 25. VI. 96, 2,000 ft. (20 and 21) *A.* sp., (to b, w) sh. 13. VII. 95, 19. IX. 95, 27. VI. 96, 22-2,400 ft. [and also *Anthomyiidae* to a, g, h, j, l, p, r, w, VI. and VII. 96, 8-2,500 ft.]. **Coleoptera.** (22) *Meligethes viridescens* F., (to p) fp. 26. VI. 96, 2,100 ft. (23) *Anthophagus alpinus* Payk., (to a) ? fp. 10. VII. 96, 2,500 ft. **Hemiptera.** (24) *Aphis* sp., (to k) 22. VI. 96, 2,300 ft.

**75. *Lapsana communis*, Linn.** [Lit. Brit. 23; N.C.E. 1, 3 c, 11, 14, 18; Warnstorf 2507; *Pyren.* 17.] Nowhere, as far as present records go, well visited.

*Visitors.* **Coleoptera.** (1) *Meligethes viridescens* F., sh. 2. VII. 95, 800 ft., nine individuals.

**76. *Hypochoeris radicata*, Linn.** [Lit. Brit. 23; N.C.E. 1, 3 c, 12, 14, 14 a, 16, 18, 25, 34, 40; *Alps* 2; *Pyren.* 17.]

The Clova visitors to this species are a little more specialized than those to *Leontodon autumnale*, the cause being in its earlier flowering. *Andrena* showed some measure of constancy, as also did *Eristalis*. The young flowers close at night and remain closed by day during rain. Mid-tongued bees are the most numerous in the list of North Central Europe and mid-tongued flies stand second.

*Visitors. Lepidoptera.* Rhopalocera: (1) *Vanessa urticae* L., sh. 2. VII. 95, 800 ft. (2) *Lycaena icarus* Rott., sh. 25. VI. 96, 800 ft. Heterocera: *Eriocephalidae*: (3) *Eriocephala calthella* L., fp. 5-6. VII. 95, 8-1,400 ft. *Hymenoptera.* Aculeata: *Apidae*: (4) *Bombus* ? *terrestris* L., sh. 10. VII. 95, 800 ft. once. (5) *Andrena coitana* Kirby, 5-8. VII. 95, 7-800 ft. (6) *A. analis* Panz., sh. 18. VI.-11. VII. 96, 8-1,100 ft. *Formicidae*: (7) *Formica fusca* Latr., 18. VI. 96, 800 ft. Sessiliventre: *Tenthredinidae*: (8) *Allantus arcuatus* Forst., 26. VI.-5. VII. 95, 7-800 ft. fairly freq. *Petiolata parasitica*: *Ichneumonidae*: (9) 1 sp., 26. VI.-6. VII. 95, 26-27. VI. 96, 8-1,000 ft. *Diptera.* *Syrphidae*: (10) *Chilosia fraterna* Mg., 22. VI.-3. VII. 95, 25. VI. 96, 800 ft. (11) *C. antiqua* Mg., sh. 5. VII. 95, 800 ft. (12) *Platychirus manicatus* Mg., sh. 25. VI.-6. VII. 95, 18-25. VI. 96, 800 ft. (13) *Syrphus ribesii* L., fp. 5. VI. 95, 6. VII. 96, 800 ft. (14) *S.* ? *grosulariae* Mg., 1. VII. 95, 800 ft. (15) *Volucella bombylans* L., fp. 2-8. VII. 95, 800 ft. (16) *Sericomyia borealis* Fln., sh. 26. VI.-1. VII. 96, 800 ft. (17) *Eristalis pertinax* Scop., 20. VI. 95, 25. VI.-10. VII. 96, 800 ft. (18) *E. rupium* F., 5. VII. 95, 19. VI. 96, 800 ft. (19) *E. arbustorum* L., 5. VI. 95, 800 ft. *Empidae*: (20) *Empis aestiva* Lw., sh. 5. VII. 95, 800 ft. (21) *Rhamphomyia nigripes* F., 2. VII. 95, 800 ft. (22) *Tachydromia* sp., sh. 5. VII. 95, 800 ft. *Tabanidae*: (23) *Atheryx ibis* F., sh. 1. VII. 95, 800 ft. *Tachinidae*: (24) *Siphona geniculata* Deg., sh. 17. VI.-5. VII. 95, 800 ft. (25) *Tachinid* sp., sh. 6. VII. 95, 1,400 ft. *Muscidae*: (26) *Calliphora vomitoria* L., sh. 2. VII. 95, 800 ft. (27) *C. erythrocephala* Mg., 25-27. VI. 96, 800 ft. *Anthomyiidae*: (28) *Hyetodesia incana* W., sh. and fp. 17. VI.-6. VII. 95, 18. VI.-6. VII. 96, 16-19. VI. 99, 800 ft. (29) *Drymia hamata* Fln., 29. VI.-2. VII. 95, 2. VII. 96, 800 ft. (30) *Trichophthicus hirsutulus* Ztt., 10. VII. 96, 800 ft. (31) *T.* sp., sh. 28. VI.-2. VII. 95, 16. IX. 95, 9-1,500 ft. (32) *Hylemyia nigrescens* Rnd., 22. VI.-3. VII. 95, 800 ft. (33) *Anthomyia sulciventris* Ztt.,

sh. 22. VI. 95, 800 ft. (34) *A. pudica* Rnd., 22. VI. 95, 800 ft. (35 and 36) *A. spp.*, sh. and fp. 14. VI.-5. VII. 95, 17. IX. 95, 16. VI.-11. VII. 96, 7-1,300 ft. (37) *Caricea tigrina* F., 16. VI. 95, 800 ft. (38) *Coenosia* sp., 16. VI.-4. VII. 95, 800 ft. **Coleoptera.** (39) *Meligethes aeneus* F., 16. VI. 95, 800 ft. (40) *M. viridescens* F., sh. and fp. 25. VI.-5. VII. 95, 16-17. IX. 95, 16. VI.-8. VII. 96, 8-1,600 ft. (41) *Phyllobius pomonae* Ol., ? sh. 1. VII. 95, 800 ft. **Thysanoptera.** (42) *Thrips* sp., 5. VI. 95, 800 ft. **Araneida.** (43) *Ysticus* sp., lying in wait, 22. VI. 95, 10. VII. 96, 8-900 ft.

**77. *Taraxacum officinale*, Web.** [Lit. *Brit.* 23, 29, 34; *N.C.E.* 1, 3 c, 11, 14, 16, 18, 25, 31, 34, 35, 40; De Vries 2460; Warnstorf 2507; *Medit.* 34; *Arct.* 34, 36; *Alps* 2, 9, 16, 34; *Pyren.* 17.] All the season visited by abundant Anthomyids. In early spring *Apis* shows a measure of constancy but neglects the flower afterwards; a few butterflies visit the flowers in spring not irregularly. Lists of visitors for North Central Europe are in the most marked contrast; in South Germany, on the Frisian coast, in the Netherlands and in Flanders long and mid-tongued bees are many and mid-tongued flies come next to them. In the Alps Lepidoptera are most numerous, but the bees are hardly less in numbers than the flies. Lindmann, however, observed the flower to be visited by many small or moderately small flies in Norway.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Argynnis selene* Schiff., sh. 14. VI. 99, 1,400 ft. (2) *Vanessa urticae* L., sh. not infreq. 24. V. 96, 19-27. V. 97, 7. V. 98, 6-900 ft. (3) *Pieris napi* L., sh. 22-23. V. 97, 11-16. VI. 99, 6-800 ft. (4) *P. ? rapae* L., sh. 20. V. 97, 800 ft. (5) *Polyommatus phloea* L., sh. 24. V. 96, 800 ft. **Heterocera:** *Geometridae*: (6) 1 sp., 11. VI. 99, 800 ft. (7) a second species, 13-14. VI. 99, 900 ft. *Pyralidae*: (8) *Pyrausta alpinalis* Schiff., sh. 4. VII. 95, 2,700 ft. and 1. VII. 96, 1,800 ft. *Tineidae*: (9) 1 sp., sh. 11. VI. 99, 800 ft. **Hymenoptera.** *Aculeata:* *Apidae*: (10) *Apis mellifica* L., sh. and cp. 20-27. V. 97, 7-15. V. 98, 6-800 ft. (11) *Bombus lapponicus* F., sh. 23. V. 97, 15. V. 98, 800 ft. (12) *Andrena analis* Panz., sh. 25. V. 96, 800 ft. *Petiolata parasitica:* *Ichneumonidae*: (13) 1 sp., sh. 25. V. 96, 800 ft. *Proctotrupidae*: (14) 1 sp., 11. VI. 99, 800 ft. **Diptera:** *Syrphidae*: (15) *Platychirus albimanus* F., 17-



19. IX. 95, 800 ft. (16) *P. manicatus* Mg., sh. and fp. 19. VI. 95, 21. V. 96, 10-11. VI. 99, 7-800 ft. (17) *P. discimanus* Loew, ? fp. 15. V. 98, 800 ft. (18) *Chilosia fraterna* Mg., sh. 11-16. VI. 99, 800 ft. *Empididae*: (19) *Empis tessellata* F., sh. 21. V. 96, 16. VI. 99, 800 ft. (20) *Empis bilineata* Lw., sh. 27. V. 97, 14. VI. 99, 8-900 ft. *Mycetophilidae*: (21) *Sciara* sp., 11. VII. 96, 800 ft. *Bibionidae*: (22) *Scatopse* sp., 11. VII. 96, 800 ft. *Chironomidae*: (23) *Tanytarsus* sp., 11. V. 98, 1,000 ft. *Tachinidae*: (24) *Siphona geniculata* Deg., sh. 21. V. 98, 10. VI. 99, 7-800 ft. *Muscidae*: (25) *Lucilia cornicina* F., sh. and fp. 27. V. 97, 7-13. V. 98, 10. VI. 99, 6-800 ft. (26) *Pollenia vespillo* F., sh. 22-27. V. 97, 10. VI. 99, 6-800 ft. *Anthomyiidae*: (27) *Hyetodesia incana* W., sh. 20. VI.-4. VII. 95, 1. VII. 96, 8-2,700 ft. (28) *Trichophticus* sp., sh. 24. VI.-4. VII. 95, 1. VII. 96, 16-2,700 ft. (29) *Anthomyia radicum* L., 11. VI. 99, 800 ft. (30) *A. sulciventris* Ztt., sh. and fp. very ab. 28. VI. 95, 18-27. V. 97, 12. V. 98, 7-800 ft. and once at 2,000 ft. (31, 32, and 33) *A.* 3 spp., fp. 19. VI.-4. VII. 95, 19. IX. 95, 21-22. V. 96, 6. VI. 96, 19-24. V. 97, 16. V. 98, 10-16. VI. 99, 6-2,600 ft. *Cordyluridae*: (34) *Scatophaga stercoraria* L., sh. and fp. 27. V. 97, 12-13. V. 98, 800 ft. *Phoridae*: (35) *Phora rufipes* Mg., sh. 22. V. 96, 1,100 ft. **Coleoptera**. (36) *Meligethes viridescens* F., sh. and fp. 17-21. IX. 95, 10. VI. 99, 7-800 ft.

#### B' § 7. EYED COMPOSITAE.

78. *Bellis perennis*, Linn. [Lit. *Brit.* 23, 29; *N.C.E.* 1, 3c, 11, 14, 14a, 16, 18, 25, 30, 31, 34; De Vries 2460; Warnstorf 2507; *Medit.* 34; *Alps* 2, 9; *Pyren.* 17.] Visited in spring and less so in summer by great numbers of short-tongued flies, chiefly Anthomyiids.

*Visitors*. **Lepidoptera**. *Rhopalocera*: (1) *Pieris rapae* L., sh. 24. V. 97, 800 ft. (2) *P. napi* L., sh. 11-13. VI. 99, 800 ft. (3) *Lycæna icarus* Rott., sh. 1. VII. 95, 800 ft. (4) *Coenonympha pamphilus* L., sh. 10. VII. 96, 2,500 ft. *Heterocera*: (5) 1 *Microlepidopteron*, 25. VII. 96, 800 ft. **Hymenoptera**. *Aculeata*: *Apidae*: (6) *Apis mellifica* L., 15. IV. 95, 13. V. 98, 800 ft. (7) *Andrena* sp., sh. 20. V. 97, 900 ft. *Myrmicidae*: (8) *Myrmica rubra* L., 23. VI. 95, 900 ft. *Petirolata parasitica*: (9) 1 sp., 27. V. 97, 700 ft. **Diptera**. *Syrphidae*: (10) *Melanostoma* ? *quadrimaculatum* Verrall,

sh. 16. VI. 95, 800 ft. (11) *Platychirus discimanus* Loew, 27. V. 97, 16. V. 98, 800 ft. (12) *P. manicatus* Mg., 10. VI. 99, 700 ft. (13) *P. albimanus* F., 21. IX. 95, 800 ft. (14) *Syrphus vitripennis* Mg., 10-11. VI. 99, 7-1,200 ft. (15) *S.* sp., 10. VI. 95, 2,300 ft. (16) *Eristalis arbustorum* L., sh. 22. VI. 99, 800 ft. (17) *Syritta pipiens* L., 19. VI. 99, 900 ft. *Empidæ*: (18) *Empis tessellata* F., 10. VII. 96, 900 ft. (19) *E. bilineata* Lw., sh. 27. V. 97, 700 ft. (20) *E. ? lucida* Ztt., 23. V. 97, 900 ft. (21) *E. ? vernalis* Mg., sh. 11-12. VI. 99, 11-2,200 ft. (22) *E. opaca* F., sh. 13. VI. 99, 700 ft. (23) *Hilara matrona* Hal., sh. 17. VII. 97, 800 ft. *Mycetophilidæ*: (24) *Sciara* sp., 14-24. IX. 95, 10-1,600 ft. *Dolichopodidæ*: (25) *Hercostomus nigripennis* Fln., 1. VII. 95, 800 ft. *Tachinidæ*: (26) *Siphona geniculata* Deg., sh. 24. VI. 95, 10. VI. 99, 7-1,400 ft. *Muscidæ*: (27) *Lucilia cornicina* F., sh. 16. IV. 95, 18-20. V. 97, 7-8. V. 98, 10. VI. 99, 7-800 ft. (28) *Pollenia vespillo* F., 7. V. 98, 1,700 ft. (29) *P. rudis* F., 15. IV. 95, 30. VI. 95, 800 ft. *Anthomyiidæ*: (30) *Hyetodesia incana* W., fp. 20. VI.-4. VII. 95, 24. IX. 95, 18. VI. 96, 8-1,000 ft. (31) *Spilogaster quadrum* F., 20. VI. 95, 800 ft. (32) *Hylemyia nigrescens* Rnd., 11. VI. 99, 1,200 ft. (33) *Trichophthicus* sp., 14-16. IX. 95, 13-1,600 ft. (34) *Anthomyia sulciventris* Ztt., fp. 18-27. V. 97, 7-12. V. 98, 5-800 ft. very ab. (35, 36, and 37) *A.* 3 spp., sh. and fp. 22. VI.-5. VII. 95, 19-24. IX. 95, 21-22. V. 96, 18. VI.-11. VII. 96, 18-24. V. 97, 10-15. VI. 99, 6-2,300 ft. *Cordyluridæ*: (38) *Scatophaga stercoraria* L., 21. IX. 95, 19. VI. 96, 27. V. 97, 12-14. V. 98, 8-1,400 ft. **Coleoptera.** (39) *Meligethes viridescens* F., fp. 24. IX. 95, 10. VI. 99, 7-1,000 ft. **Hemiptera.** (40) 1 sp., 4. VII. 95, 800 ft. **Thysanoptera.** (41) *Thrips* sp., sh. 26. VI. 96, 1,800 ft.

79. **Chrysanthemum Leucanthemum**, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 3 c, 11, 14, 16, 18, 30, 31, 34, 40; Warnstorf 2507; *Alps* 2, 16, 34; *Pyren.* 17.] Large heads at Clova were found to attain 72 mm. in diameter, the disk being 18 mm. across.

*Visitors.* **Lepidoptera.** Heterocera: *Tortricidæ*: (1) *Tortrix* sp., sh. 2. VII. 95. **Diptera.** *Empidæ*: (2) *Empis* sp., sh. 22. VII. 95. (3) *E. bilineata* Lw., 2. VII. 95. *Tachinidæ*: (4) *Siphona geniculata* Deg., 21. VI. 95. *Anthomyiidæ*: (5) *Hyetodesia incana* W., 29. VI. 96. (6) *Trichophthicus* sp., 30. VI. 95, 16. IX. 95.

**Coleoptera.** (7) *Meligethes viridescens* F., fp. 2. VII. 95, 16. IX. 95.  
**Thysanoptera.** (8) *Thrips* sp., sh. 24. VI. 96. All at 8-900 ft.

**80. *Matricaria inodora*, Linn.** [Lit. *Brit.* 23, 39; *N.C.E.* 1, 3 c, 11, 14, 18, 31.]

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Apis mellifica* L., sh. 22. VII. 95. **Diptera.** *Syrphidae*: (2) *Platychirus albimanus* F., ?sh. 22. IX. 95. (3) *Syrphus vitripennis* Mg., 15. VII. 95. (4) *Ascia podagrica* F., sh. 17. VII. 95. (5) *Eristalis arbustorum* L., sh. 15. VII. 95. (6) *E. rupium* F., sh. 22. VII. 95. (7) *Syrpita pipiens* L., sh. and ?fp. 15-19. VII. 95, 22. IX. 95. *Empidae*: (8) *Rhamphomyia* sp., 5. VII. 96. *Tachinidae*: (9) *Siphona geniculata* Deg., 24. VI. 96. *Muscidae*: (10) *Lucilia sericata* Mg., fp. 15. VI. 95. (11) *L. cornicina* F., sh. 7. VII. 95, 22. IX. 95. (12) *Pollenia rudis* F., sh. and fp. 15. VII. 95, 22-23. IX. 95. *Anthomyiidae*: (13) *Anthomyia* sp., 17. IX. 95, 22. VI. 96. *Cordyluridae*: (14) *Scatophaga stercoraria* L., 22. IX. 95. *Sepsidae*: (15) *Sepsis cynipsea* L., 17. IX. 95, 22. VI. 96. **Coleoptera.** (16) *Meligethes viridescens* F., fp. 17-22. IX. 95. (17) *Amara bifrons* Gyll., ?fp. 3. VII. 95. **Orthoptera.** (18) *Forficula* sp., devouring the ray-florets, 3. VII. 95. **Thysanoptera.** (19) *Thrips* sp., 17. IX. 96. All at 800 ft.

#### B' § 8. WHITE COMPOSITAE.

**81. *Antennaria dioica*, R. Br.** [Lit. *N.C.E.* 14, 18, 25, 33; *Arct.* 36; *Alps* 2, 9; *Pyren.* 17.] Flowers rarely rose pink.

*Visitors.* **Lepidoptera.** Heterocera: *Geometridae*: (1) *Melanippe* sp., sh. 25. VI. 96, 2,200 ft. (2) *Cidaria immanata* Hw., 22. VI. 96, 2,300 ft. **Hymenoptera.** Aculeata: *Vespidae*: (3) *Odynerus trimarginatus* Zett., ?sh. 15. VI. 99, 800 ft. **Diptera.** *Empidae*: (4) *Empis livida* L., sh. 22. VI. 96, 2,400 ft. *Bibionidae*: (5) *Dilophus albipennis* Mg., 15. VI. 95, 900 ft. *Chironomidae*: (6) 1 sp., 6. VI. 95, 2,300 ft. *Muscidae*: (7) 1 sp., 16. VI. 99, 1,500 ft. *Anthomyiidae*: (8) *Drymia hamata* Fln., 26. VI. 96, 2,400 ft. (9) *Trichophthicus hirsutulus* Ztt., fp. 6. VI. 96, 2,100 ft. (10) *Coenosia* sp., 21. VI. 95, 27. VI. 96, 20-2,200 ft. **Coleoptera.** (11) *Meligethes viridescens* F., ?fp. 1. VII. 96, 1,700 ft. (12) *Sericosomus brunneus* F., 16. VI. 99, 1,500 ft.



82. *Achillea Ptarmica*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 3 c, 11, 14, 14 a, 18; Loew 1358.]

*Visitors.* *Diptera.* *Empidæ*: (1) *Empis tessellata* F., sh. 14. IX. 95, 800 ft. *Anthomyiidae*: (2) *Drymia hamata* Fln., 16. IX. 95, 800 ft. (3) *Anthomyia* sp., 15. IX. 95, 800 ft. *Cordyluridae*: (4) *Scatophaga* sp., sh. 20. VII. 95, 800 ft.

83. *Achillea Millefolium*, Linn. [Lit. *Brit.* 23, 34, 39; *N.C.E.* 1, 3 c, 8, 11, 12, 14, 14 a, 16, 18, 25, 31, 33, 34, 40; *Arct.* 36; *Alps* 2, 9; *Pyren.* 17.] Flowers sometimes rose-pink. Müller in his lists unites this species and *A. Ptarmica* together.

*Visitors.* *Lepidoptera.* *Heterocera: Noctuidæ*: (1) *Hydroecia nictitans* Bkh., 14-16. IX. 95, 800 ft. (2) *Dianthecia cucubali* Fuessl., sh. 2. VII. 95, 800 ft. *Tortricidae*: (3) *Tortrix* sp., 2. VII. 95, 800 ft. *Tineidae*: (4) *Glyphipteryx fuscoviridella* Haw., sh. 1-2. VII. 95, 900 ft. *Hymenoptera. Aculeata: Apidae*: (5) *Bombus terrestris* L., sh. 25. VI. 95, 13-14. IX. 95, 7-800 ft. (6) *Andrena analis* Panz., sh. 6. VII. 95, 800 ft. (7) *Halictus subfasciatus* Nyl., 14. IX. 95, 800 ft. *Vespidae*: (8) *Vespa norvegica* F., 13. IX. 95, 700 ft. *Sessiliventres: Tenthredinidae*: (9) *Allantus arcuatus* Forst., sh. 26. VI.-22. VII. 95, 2. VII. 96, 800 ft. *Petiolata parasitica: Ichneumonidae*: (10) *Limneria crassicornis*, 16. IX. 95, 800 ft. (11) *Hemiteles*? *tenebriosus* Grav., 2. VII. 95, 800 ft. (12, 13, and 14) three other spp., 1. VII. 95, 800 ft. *Diptera. Syrphidae*: (15) *Platychirus manicatus* Mg., sh. 26. VI.-3. VII. 95, 10. VII. 96, 800 ft. (16) *P. albimanus* F., fp. 18. VII. 95, 800 ft. (17) *Syrphus*? *vitripennis* Mg., 15. VII. 95, 3. VII. 96, 800 ft. (18) *Syrphus* sp., 13-14. IX. 95, 7-800 ft. (19) *Ascia podagrica* F., 17. IX. 95, 800 ft. (20) *Eristalis pertinax* Scop., 13-18. IX. 95, 7-800 ft. (21) *E. arbutorum* L., fp. 6. VII. 95, 800 ft. (22) *Heliophilus pendulus* L., sh. 21-22. IX. 95, 8-900 ft. (23) *Syritta pipiens* L., 30. VI.-1. VII. 95, 800 ft. *Empidæ*: (24) *Empis tessellata* F., sh. 15-23. VII. 95, 13-16. IX. 95, 2-11. VII. 96, 7-900 ft. (25) *E. punctata* Mg., sh. 19. VI.-17. VII. 95, 800 ft. (26) *E. bilineata* Lw., 28. VI.-5. VII. 95, 800 ft. (27) *E. grisea* Fln., 16. IX. 95, 900 ft. (28) *Pachymeria palparis* Egg., 16. IX. 95, 900 ft. (29) *Rhamphomyia spinipes* L., 30. VI. 95, 16. IX. 95, 8-900 ft. (30) *Hilara martrona* Hal., sh. 17. VII. 95.

800 ft. *Cecidomyiidae*: (31) *Lestremia* sp., 16. IX. 95, 800 ft. *Bibionidae*: (32) *Dilophus albipennis* Mg., 28. VI. 95, 800 ft. *Chironomidae*: (33) 1 sp., fp. 6. VII. 95, 800 ft. *Tachinidae*: (34) *Siphona geniculata* Deg., 16-18. IX. 95, 800 ft. *Sarcophagidae*: (35) *Cynomyia mortuorum* L., 16. IX. 95, 800 ft. *Muscidae*: (36) *Lucilia cornicina* F., fp. 2-6. VII. 95, 13-24. IX. 95, 8-1,600 ft. (37) *L. sericata* Mg., sh. 20. VII. 95, 800 ft. (38) *Calliphora erythrocephala* Mg., sh. 5. VII. 95, 18-21. IX. 95, 800 ft. (39) *C. ? vomitoria* L., 22. VI. 95, 800 ft. (40) *Pollenia rudis* F., sh. 30. VI.-5. VII. 95, 13-24. IX. 95, 8-1,200 ft. (41) *Cyrtoneura caesia* Mg., 16-21. IX. 95, 800 ft. *Anthomyiidae*: (42) *Hyetodesia incana* W., sh. and fp. 26. VI.-15. VII. 95, 16-21. IX. 95, 8-1,800 ft. (43) *H. basalia* Ztt., 17. VII. 95, 800 ft. (44) *Hylemyia nigrescens* Rnd., 2. VII. 95, 800 ft. (45) *Drymia hamata* Fln., sh. and fp. 6. VII. 95, 14-16. IX. 95, 800 ft. (46) *Anthomyia sulciventris* Ztt., fp. 1. VII. 95, 800 ft. (47, 48, and 49) *A.* 3 spp., sh. and fp. 23. VI.-22. VII. 95, 13-21. IX. 95, 16. VI.-11. VII. 96, 7-900 ft. (50) *Trichophthicus* sp., 29-30. VI. 95, 16-18. IX. 95, 8-900 ft. (51) *Coenosia infantula* Rnd., 2. VII. 95, 800 ft. *Cordyluridae*: (52) *Scatophaga stercoraria* L., fp. 6-20. VII. 95, 14-22. IX. 95, 7-900 ft. (53) *S. maculipes* Zett., 2. VII. 95, 800 ft. *Opomyzidae*: (54) *Opomyza germinationis* L., 17. IX. 95, 700 ft. *Chloropidae*: (55) *Oscinis* sp., fp. 6. VII. 95, 800 ft. *Phoridae*: (56) *Phora* sp., 17. IX. 95, 800 ft. **Coleoptera.** (57) *Meligethes viridescens* F., sh. and fp. 14-22. IX. 95, 8-1,000 ft. (58) *M. aeneus* F., 21. IX. 95, 800 ft. (59) *Brachypterus urticae* F., 15. IX. 95, 800 ft. (60) *Thyanis laevis* Duft., ? fp. 27. VI.-1. VII. 95, 800 ft. **Hemiptera.** (61) *Anthocoris nemorum* L., sh. 21. IX. 95, 800 ft. (62) *Lygus campestris* Fabr., 16. IX. 95, 800 ft.

#### A' § 9. UMBELLIFERAE.

84. *Pimpinella Saxifraga*, Linn. [Lit. *Brit.* 23, 39; *N.C.E.* 1, 3 a, 12, 14, 16, 18, 21 a, 30, 34, 40; *Arct.* 36; *Alps* 21 b, 34; *Pyren.* 17.]

*Visitors.* **Lepidoptera.** *Heterocera*: *Noctuidae*: (1) *Miana fasciuncula* Haw., sh. 20. VI. 95. **Hymenoptera.** *Aculeata*: *Apidae*: (2) *Andrena analis* Panz., sh. 23. VI. 95. *Petiolata parasitica*: *Cynipidae*: (3) *Eucoela fortinervis* Cameron, 23. IX. 95. *Ichneumonidae*: (4 and 5) *Hemiteles* spp., 5-20. VII. 95, 22. IX. 95. (6) *Xylo-*

nomus sp., 21. IX. 95. (7, 8, 9, and 10) four other spp., 13 VII. 95, 18. IX. 95, 25. VI. 96. *Braconidae*: (11) 1 sp., ? sh. 17. VII. 95. *Chalcididae*: (12 and 13) 2 spp., 20-23. VII. 95, 13-23. IX. 95, 24. VI. 96. Sessiliventre: *Tenthredinidae*: (14) *Allantus arcuatus* Forst., 8-20. VII. 95, 29. VI.-3. VII. 96. (15) another sp., 12. VII. 95. **Diptera. Syrphidae**: (16) *Chilosia fraterna* Mg., sh. 20. VII. 95. (17) *C. scutellata* Fln., sh. 13. VII. 95. (18) *Syrphus ribesii* L., sh. 20. VII. 95. (19) *S. vitripennis* Mg., sh. 20. VII. 95. (20) *Eristalis pertinax* Scop., 18. IX. 95. *Empidae*: (21) *Empis tessellata* F., sh. 20. VII. 95. (22) *E. punctata* Mg., sh. 23. VII. 95. *Mycetophilidae*: (23) *Sciara* sp., 22. IX. 95. *Bibionidae*: (24) *Bibio pomonae* F., sh. 23. VII. 95, 22. IX. 95. *Chironomidae*: (25) 1 sp., 5. VII. 95. *Tipulidae*: (26) *Pachyrrhina maculosa* Mcq., sh. 17. VII. 95. *Tachinidae*: (27) *Siphona geniculata* Deg., 23. IX. 95. *Muscidae*: (28) *Calliphora erythrocephala* Mg., sh. 12. VII. 95. (29) *Pollenia rudis* F., sh. 16-21. IX. 95. *Anthomyiidae*: (30) *Hyetodesia incana* W., 10-12. VII. 95, 5. VII. 96. (31) *Drymia hamata* Fln., sh. 12. VII. 95. (32) *Trichophthicus* sp., 16. IX. 95. (33 and 34) *Anthomyia* spp., 15-18. IX. 95, 24. VI. 96. (35) *Azelia aterrima* Mg., sh. 17. VII. 95. *Cordyluridae*: (36) *Scatophaga stercoraria* L., sh. 1-17. VII. 95, 13. IX. 95. *Sciomyzidae*: (37) *Tetanocera elata* F., sh. 23. VII. 95. *Sapromyzidae*: (38) *Sapromyza apicalis* Lw., sh. 23. VII. 95. *Sepsidae*: (39) *Sepsis cynipsea* L., sh. 5-20. VII. 35. *Borboridae*: (40) *Borborus geniculatus* Mcq., 5. VII. 95. *Phoridae*: (41) *Phora* sp., sh. 23. VII. 95. **Coleoptera.** (42) *Meligethes viridescens* F., 15-23. IX. 95. All at 7-900 ft.

85. *Conopodium denudatum*, Koch. [Lit. *Brit.* 23; *Pyren.* 17.]

*Visitors. Hymenoptera.* Aculeata: *Acutilingues*: (1) *Apis mellifica* L., 17. VI. 95. Terebrantia: *Ichneumonidae*: (2) *Alomyia debellator* Fabr., 11. VI. 99. (3) *Hemiteles* ? *tenebricosus* Gravenh., sh. 22. VI. 95. (4) *Hemiteles* sp., sh. *Chalcididae*: (5) 1 sp., 18. VI. 96. Phytophaga: (6) *Allantus arcuatus* Forst., lounging and sh. 15-25. VI. 95. (7) *Nematus fallax* Lep., 21. V. 96. **Diptera. Syrphidae**: (8) *Platychirus manicatus* Mg., 17. VI. 95, 16. VI. 99. (9) *Syrphus vitripennis* Mg., 11-16. VI. 99. *Empidae*: (10) *Empis tessellata* F., sh. 15-16. VI. 99. (11) *E. bilineata* Lw., 15-16. VI. 99. *Tipulidae*: (12) *Tipula varipennis* Mg., sh. 16. VI. 99. *Muscidae*: (13) 1 sp., 11. VI. 99.



*Anthomyiidae*: (14) *Hyetodesia incana* W., 17. VI. 95, ? 23. V. 96. (15) *Hylemyia nigrescens* Rnd., 17-30. VI. 95. (16) *Anthomyia sulciventris* Ztt., 18. VI. 96, 10-15. VI. 99. (17) *A. radicum* L., 11. VI. 99. *Cordyluridae*: (18) *Scatophaga stercoraria* L., 17. VI. 95. *Sapromyzidae*: (19) *Sapromyza* sp., 17. VI. 99. **Hemiptera**. (20) *Nabis flavimarginatus* D. and S., 17. VI. 95. **Thysanoptera**. (21) *Thrips* sp., 18. VI. 96, 17. VI. 99. All at 7-900 ft.

**86. Anthriscus sylvestris**, Hoffm. [Lit. *Brit.* 29; *N.C.E.* 1, 3 a, 16, 18, 21 a, 25, 32, 34, 40; *Alps* 16; *Medit.* 34.]

*Visitors*. **Lepidoptera**. *Heterocera*: *Bombycidae*: (1) *Hepialis humuli* L., sh. 23. VI. 95. **Hymenoptera**. *Petiolata parasitica*: *Chalcididae*: (2) 1 sp., 24. VI. 96. *Sessiliventre*s: *Tenthredinidae*: (3) *Dolerus elongatus* Htg., 15-21. VI. 95. (4) *Allantus arcuatus* Forst., 21. VI. 95. **Diptera**. *Syrphidae*: (5) *Syrphus* sp., 26. VI. 95. (6) *Syrpitta pipiens* L., sh. 24. VI. 96. *Empidae*: (7) *Empis bilineata* Lw., sh. 15. VI. 99. (8) *E. punctata* Mg., sh. 24. VI. 96. (9) *Hilara quadrivittata* Mg., 18. VI. 96. *Sarcophagidae*: (10) *Sarcophaga* sp., sh. 24. VI. 96. *Anthomyiidae*: (11) *Hyetodesia incana* W., sh. 19. VI.-17. VII. 95, 18. VI.-11. VII. 96. (12) *Trichophthicus cunctans* Mg., sh. 19. VI. 95. (13) *Trichophthicus* sp., 16. VI. 95, 24. VI. 96. (14) *Anthomyia sulciventris* Ztt., 23. V. 97. (15 and 16) *Anthomyia* spp., 17-19. VI. 95, 24. VI. 96, 19. VI. 99. (17) *Azelia aterrima* Mg., sh. 19. VI. 95. *Cordyluridae*: (18) *Scatophaga stercoraria* L., 15-20. VI. 95, 18-24. VI. 96, 19. VI. 99. *Sciomyzidae*: (19) *Dryomyza flaveola* F., sh. 21. VI. 96. **Coleoptera**. (20) *Meligethes aeneus* F., 24. VI. 96. (21) *Rhagonica limbata* Thoms., 19. VI. 95. **Thysanoptera**: (22) *Thrips* sp., 15. VI. 95. All at 800 ft., except 8 (at 900 ft.) and 15 and 18 also at 700 ft.

**87. Meum athamanticum**, Jacq. [Lit. *Alps* 21 b.] Each small umbel is terminated by an ♀ flower, and has a ring of ♂ flowers outside, the intermediate being ♂; and what is seen in these, is seen also in a modified degree in the large compound umbel; for the intermediate umbels of it have more (usually) ♂ flowers than ♀, the innermost generally and the outermost almost always having more ♀ flowers than ♂.

*Visitors*. **Lepidoptera**. *Heterocera*: *Geometridae*: (1) 1 sp., 15.

VI. 99. *Tortricidae*: (2) 1 sp., 17. VI. 99. *Tineidae*: (3) 1 sp., 17. VI. 99. (4) a second sp., 13. VI. 99. **Hymenoptera**. Aculeata: *Formicidae*: (5) *Formica fusca* Latr., 19. VI. 99. *Myrmicidae*: (6) *Myrmica rubra* L., 16. VI. 95. *Petiolata parasitica*: *Ichneumonidae*: (7) *Alomyia debellator* Fabr., 21. VI. 95. (8) *Hemiteles*?, 14. VI.-1. VII. 95. (9) *Ichneumon* sp., 22. VI. 96. Sessiliventres: *Tenthredinidae*: (10) *Allantus arcuatus* Forst., sh. and devouring flower, 14-26. VI. 95, 18-29. VI. 96, 19. VI. 99. (11) *Dolerus elongatus* Htg., ? sh. 22. V. 96. **Diptera**. *Syrphidae*: (12) *Platychirus manicatus* Mg., 10-19. VI. 99. (13) *Syrphus vitripennis* Mg., sh. 25. VI. 95, 15. VI. 99. (14) *Syritta pipiens* L., 17. VI. 95. (15) *Eristalis arbustorum* L., 14-21. VI. 95. *Empidae*: (16) *Empis tessellata* F., 21-25. VI. 95, 14-16. VI. 99. (17) *E. bilineata* Lw., sh. and preying on flies, 21-22. V. 96, 17. VI. 99. (18) *Rhamphomyia nigripes* F., 22. V. 96. *Bibionidae*: (19) *Dilophus albipennis* Mg., sh. 19. VI. 96. (20) *Bibio nigriventris* Hal., 21. VI. 95, 17-19. VI. 99. *Tabanidae*: (21) *Leptis scolopacea* L., 17. VI. 95. *Tipulidae*: (22) *Tipula varipennis* Mg., ? sh. 22. V. 96. *Tachinidae*: (23) *Gymnochaete viridis* Fln., sh. 22. VI. 96. *Sarcophagidae*: (24) *Sarcophaga* sp., sh. 14-19. VI. 99. *Muscidae*: (25) *Lucilia* sp., 16. VI. 99. (26) *Calliphora sepulchralis* Mg., sh. and fp. 26. VI. 95. (27) *C. erythrocephala* Mg., sh. 16. VI. 99. (28) *Pollenia Vespillo* F., sh. 10-19. VI. 99. (29) *Morrellia simplex* Lw., sh. 22. V. 96. *Anthomyiidae*: (30) *Hyetodesia incana* W., sh. 15-21. VI. 95, 22. V. 96, 18-19. VI. 96, 13-19. VI. 99. (31) *Mydaea* sp., 16. VI. 99. (32) *Spilogaster nigrivenis* Ztt., sh. 19. VI. 99. (33) *Limnophora solitaria* Ztt., 15. VI. 95. (34) *Anthomyia sulciventris* Ztt., sh. and fp. 21. V. 96. (35 and 36) *Anthomyia* sp., 10-19. VI. 99. (37) *Azelia aterrima* Mg., sh. 21. VI. 25. (38) *Coenosia* sp., 13. VI. 99. *Cordyluridae*: (39) *Scatophaga stercoraria* L., sh. 21-22. V. 96, 16. VI. 96, 17. VI. 99. *Sepsidae*: (40) *Sepsis* sp., sh. 21-22. V. 96. *Ephydriidae*: (41) *Hydrellia griseola* Fln., 21. VI. 96. *Chloropidae*: (42) *Ascinis* sp., sh. 21. VI. 95. *Phoridae*: (43) 1 sp., sh. 21. VI. 95. **Coleoptera**. (44) *Meligethes viridescens* F., 22. V. 96, 17. VI. 99. (45) *Epuraea aestiva* L., sh. 22. V. 96. (46) *Tachyporus obtusus* L., 17. VI. 99. (47) *Rhagonycha limbata* Thoms., 17. VI. 99. (48) *Corymbites quercus* Gyll., and its var. *ochropterus* Steph., sh. 21-24. VI. 95, 22. V. 96, 17. VI. 99. **Hemiptera**. (49) 1 sp., 22. V. 96. **Trichoptera**. (50) 1 sp., 17. VI. 99. All at 7-900 ft.

88. *Angelica sylvestris*, Linn. [Lit. *Brit.* 23, 39; *N.C.E.* 1, 3a, 16, 18, 21 a, 34; *Arct.* 36; *Alps* 2; *Pyren.* 17.]

*Visitors.* **Diptera.** *Anthomyiidae*: (1) *Hyetodesia incana* W. **Coleoptera.** (2) *Meligethes viridescens* F. Both 16. IX. 95, 800 ft.

89. *Heracleum Sphondylium*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 3a, 8, 10, 16, 18, 21 a, 31, 34, 35, 40; *Alps* 2, 16, 34.] The secretion of honey continues in a very marked manner after the fall of the petals.

*Visitors.* **Hymenoptera.** *Aculeata: Apidae*: (1) *Apis mellifica* L., sh. 20. VII. 95, 11. VII. 96, 800 ft. *Vespidae*: (2) *Vespa norvegica* F., sh. 15. VII. 95, 800 ft. *Sessiliventre*s: *Tenthredinidae*: (3) *Allantus arcuatus* Forst., sh. freq. 5-25. VII. 95, 24. VI.-11. VII. 96, 7-800 ft. *Petiolata parasitica: Ichneumonidae*: (4) *Hemiteles* ? sh. 6. VII. 95, 25. VI. 96, 7-800 ft., ab. on second date. (5) 1 sp., sh. 22-23. VII. 95, 22. VI.-11. VII. 96, 7-800 ft. and once at 2,300 ft. **Diptera.** *Syrphidae*: (6) *Syrphus compositarum* Verrall, sh. 22. VII. 95, 800 ft. (7) *S. ribesii* L., 17. VII. 95, 11. VII. 96, 7-800 ft. (8) *Eristalis arbustorum* L., sh. 11. VII. 96, 800 ft. *Empidae*: (9) *Empis tessellata* F., 5-23. VII. 95, 7-800 ft. (10) *E. bilineata* Lw., 4. VII. 95, 800 ft. (11) *E. punctata* Mg., sh. 15. VII. 95, 800 ft. (12) *Rhamphomyia* sp., 20-29. VI. 96, 8-900 ft. (13) *Hilara* sp., sh. 5-17. VII. 95, 7-800 ft. *Mycetophilidae*: (14) *Glaphyroptera fascipennis* Mg., 25. VI. 96, 800 ft. *Bibionidae*: (15) *Scatopse* sp., 3. VII. 96, 800 ft. (16) *Dilophus albipennis* Mg., 26. VI. 96, 2,300 ft. (17) *Biblio pomonae* F., sh. 10-11. VII. 96, 8-2,200 ft. *Sarcophagidae*: (18) *Sarcophaga* sp., 25. VI. 96, 800 ft. *Muscidae*: (19) *Lucilia cornicina* F., 5. VII. 95, 700 ft. (20) *Calliphora erythrocephala* Mg., sh. 15. VI.-17. VII. 95, 15-18. IX. 95, 25. VI.-11. VII. 96, 7-800 ft. (21) *C. vomitoria* L., sh. 20-25. VI. 96, 800 ft. (22) *Pollenia rudis* F., sh. 12-15. VII. 95, 15-22. IX. 95, 11. VII. 96; 7-800 ft. (23) *Pyrellia lasiophthalma* Mcq., sh. 24. VI. 96, 800 ft. (24) *Mesembryna meridiana* L., sh. 17-22. VII. 95, 22. IX. 95, 24. VI.-11. VII. 96, 7-800 ft. (25) *Morrellia simplex* Lw., 10. VII. 95, 800 ft. *Anthomyiidae*: (26) *Poletes lardaria* F., sh. 11. VII. 96, 800 ft. (27) *Hyetodesia incana* W., sh. 10-17. VII. 95, 22. VI.-11. VII. 96, 7-900 ft. and four individuals at 2,200 ft. (28) *Limnophora solitaria* Ztt., sh. and fp. 13. VII. 95, 10. VII. 96, 17-2,300 ft. (29) *Trichophthicus* sp., sh. 4-17.



VII. 95, 800 ft. (30) *Anthomyia sulciventris* Ztt., sh. 17. VII. 95, 11.  
 VII. 96, 800 ft. (31 and 32) *Anthomyia* spp., sh. 12-22. VII. 95, 21.  
 IX. 95, 24. VI.-11. VII. 96, 8-2,300 ft. (33) *Azelia Macquarti* Staeg.,  
 sh. 17. VII. 95, 800 ft. (34) *A. aterrima* Mg., sh. 2-17. VII. 95, 3.  
 VII. 96, 800 ft. *Cordyluridae*: (35) *Scatophaga stercoraria* L., 12-20.  
 VII. 95, 25. VI.-3. VII. 96, 7-800 ft. (36) *S. maculipes* Zett., sh.  
 10-17. VII. 95, 800 ft. (37) *S. suilla* Fabr., 10-17. VII. 95, 800 ft.  
*Helomyzidae*: (38) *Tephrochlamys* sp., sh. 10. VII. 96, 2,300 ft.  
*Sapromyzidae*: (39) *Sapromyza* sp., sh. 10. VII. 96, 2,300 ft. *Sep-*  
*sidae*: (40) *Sepsis cynipsea* L., sh. 2-17. VII. 95, 24. VI.-11. VII. 96,  
 7-800 ft. *Ephydriidae*: (41) *Hydrellia griseola* Fln., sh. 12. VII. 95,  
 700 ft. *Chloropidae*: (42) *Chloropisca ornata* Mg., sh. 5. VII. 95, 11.  
 VII. 96, 7-800 ft. *Phoridae*: (43) *Phora rufipes* Mg., 1-13. VII.  
 95, 11. VII. 96, 9-1,700 ft. **Coleoptera**. (44) *Meligethes viridescens*  
 F., sh. 15-21. IX. 95, 22-26. VI. 96, 8-2,300 ft. (45) *M. aeneus* F.,  
 4. VII. 95, 8-900 ft. (46) *Anthobium ophthalmicum* Payk., sh. 10.  
 VII. 96, 2,200 ft. (47) *Epuraea aestiva* L., 4. VII. 95, 800 ft. **Hemi-**  
**ptera**. (48) *Heterocordylus tibialis*, 16. IX. 95, 800 ft. **Thysanoptera**.  
 (49) *Thrips* sp., 26. VI.-10. VII. 96, 8-2,200 ft.

## A' § 10. CORNACEAE.

90. *Cornus suecica*, Linn. [Lit. *N.C.E.* 33.] This plant is little visited, but fruits not infrequently. It has a good deal of asexual reproduction by suckers.

*Visitors*. **Diptera**. *Anthomyiidae*: (1) *Limnophora* sp., 28. VI. 95, 2,300 ft. (2) *Hylemyia nigrescens* Rnd., 13. VI. 99, 2,300 ft.

Out of the whole available anthophilous insect fauna of (for the time of our observations) 17,306 individuals, 6,156 went to Class B', and 1,482 to the massed flowers of Class A, which we may here for brevity call Class A'. The species of plants obtained attention as in Tables IX and X, B' obtained many more of the desirable insects (see p. 315) than A', and very much fewer of the injurious, which could find but small encouragement where the honey is hidden (see Table XI). Class B' is found by our observations to fall very markedly into two divisions: one division contains the plants whose flowers belong to the rose-purple-lilac-blue series, the other

TABLE IX.  
The number of individuals observed on the flowers of Class B'.

	Apis.	Bomb.	Hm.	Tenth.	Parasit.	Ants.	Wasps.	Lep.l.	Lep.m.	Lep.s.	Dm.	Ds.	Col.	Etc.	Total.
57. Scabiosa succisa . . . . .	1	128	—	—	—	—	—	5	—	—	107	74	19	1	335
58. Armeria maritima . . . . .	—	—	—	—	—	—	—	—	—	—	—	10	—	2	12
59. Centaurea cyanus . . . . .	—	—	3	—	—	—	—	—	—	—	—	1	—	—	4
60. Centaurea nigra . . . . .	—	24	—	—	—	—	—	—	—	—	—	35	24	—	91
61. Cnicus palustris . . . . .	—	31	—	—	—	1	—	7	—	—	17	14	1	—	71
62. Cnicus arvensis . . . . .	—	2	—	—	2	—	—	2	—	—	4	40	3	—	53
63. Cnicus heterophyllus . . . . .	—	8	—	—	—	—	1	1	—	—	7	16	6	8	53
64. Carduus lanceolatus . . . . .	—	11	—	—	—	—	—	—	—	—	2	3	—	1	17
65. Saussurea alpina . . . . .	—	—	—	—	—	—	—	—	—	—	—	3	—	—	3
66. Solidago Virg-aurea . . . . .	—	—	—	—	—	—	—	—	—	—	*	9	—	—	9
67. Tussilago Farfara . . . . .	—	*	—	—	—	—	—	—	—	—	—	15	—	—	15
68. Senecio vulgaris . . . . .	—	—	—	—	—	—	—	—	—	—	—	2	—	—	2
69. Senecio aquaticus . . . . .	—	—	—	—	—	—	—	—	—	—	—	17	—	—	17
70. Senecio Jacobaea . . . . .	—	34	—	—	7	1	1	57	1	—	60	474	83	9	727
71. Leontodon autumnalis . . . . .	—	1	2	1	2	1	—	—	2	—	12	411	26	—	458
72. Crepis paludosa . . . . .	—	—	—	—	—	1	—	—	—	—	1	15	19	—	36
73. Hieracium Pilosella . . . . .	—	—	—	—	—	1	—	2	—	—	3	82	4	2	94
74. Hieracium spp. . . . .	—	—	—	—	—	1	—	—	4	—	7	144	2	3	102
75. Lapsana communis . . . . .	—	—	—	—	—	—	—	—	—	—	—	—	9	—	9
76. Hypochaeris radicata . . . . .	—	1	21	54	6	1	—	2	—	3	47	688	30	15	868
77. Taraxacum officinale . . . . .	15	3	2	—	2	—	—	17	5	—	18	1,358	57	—	1,477
78. Bellis perennis . . . . .	1	—	1	—	1	1	—	6	1	—	36	1,101	1	5	1,154
79. Chrysanthemum Leucanthemum . . . . .	—	—	—	—	—	—	—	—	—	—	3	9	2	8	23
80. Matricaria inodora . . . . .	1	—	—	—	—	—	—	—	—	—	11	45	7	9	73
81. Antennaria dioica . . . . .	—	—	—	—	—	—	—	2	—	—	1	10	2	—	16
82. Achillea Ptarmica . . . . .	—	—	—	—	—	—	—	—	—	—	1	5	—	—	6
83. Achillea Millefolium . . . . .	—	4	2	11	8	—	1	3	7	—	47	266	16	2	307
Total . . . . .	24	248	32	66	30	7	3	104	21	3	394	4,847	311	65	6,155
Percentage . . . . .	.39	4.03	.52	1.09	.49	.11	.05	1.69	.34	.05	6.40	78.74	5.05	1.06	

\* April visitors in 1895 when no count was made.

contains those whose flowers belong to the yellow-white series. The latter is visited by less desirable insects than the former, and therefore, as shown in Tables XII and XIII, approaches A'.

TABLE X.

The number of individuals observed on the flowers of Class A'.

	Apis.	Bomb.	Hm.	Tenth.	Parasit.	Ants.	Wasps.	Lep.l.	Lep.m.	Lep.s.	Dm.	Ds.	Col.	Etc.	Total.
84. Pimpinella Saxifraga . . . . .	—	—	2	21	45	—	—	1	—	—	7	98	4	—	178
85. Conopodium denudatum . . . . .	1	—	—	9	11	—	—	—	—	—	15	33	—	2	71
86. Anthriscus sylvestris . . . . .	—	—	—	4	1	—	—	—	1	—	4	111	3	1	125
87. Meum athamanticum . . . . .	—	—	—	34	11	2	—	—	4	—	45	375	16	2	489
88. Angelica sylvestris . . . . .	—	—	—	—	—	—	—	—	—	—	—	2	19	—	21
89. Heracleum Sphondylium . . . . .	2	—	—	18	77	—	3	1	—	—	8	381	70	37	596
90. Cornus suecica . . . . .	—	—	—	—	—	—	—	—	—	—	—	2	—	—	2
Total . . . . .	3	—	2	86	145	2	3	1	5	—	79	1,002	112	42	1,482
Percentage . . . . .	.20	—	.13	5.80	9.78	.13	.20	.07	.33	—	5.33	67.61	7.56	2.85	

TABLE XI.

	Available.		B'.		A'.	
	No.	%	No.	%	No.	%
Distinctly desirable	1,763	10.19	376	6.11	4	0.27
Desirable . . . . .	1,277	7.37	447	7.26	86	5.80
Indifferent . . . . .	12,993	75.08	5,164	83.89	1,117	75.37
Injurious . . . . .	1,273	7.36	169	2.73	275	18.56

Both halves of Class B' as well as Class A' obtain more desirable visitors in North Central Europe than they do at Clova. Whether, as in Tables XIV, XV, and XVI, we contrast Müller's or MacLeod's or Knuth's and Verhoeff's observations with ours, we see in each case that long- and mid-tongued Hymenoptera make far more species visits in Germany or Flanders than they do in Scotland, and that in Scotland



short-tongued flies make far more species visits than they do in Flanders and Germany.

TABLE XII.

	B'.				A'.
	Blue and lilac.	Rose and purple.	Yellow.	Eyed and white.	White, or greenish.
Decidedly desirable	39.53	30.66	3.43	1.03	.27
Desirable . . . .	32.45	12.67	4.82	6.84	5.80
Indifferent . . . .	27.73	51.09	88.94	89.37	75.37
Injurious . . . .	.29	2.67	2.81	2.75	18.56

TABLE XIII.

Percentages of the individual visitors to Class B' arranged by families.

	Apis.	Bomb.	Hm.	Wasps.	Tenth. Parasit. Ants.	Lep.l.	Lep.m.	Lep.s	Dm.	Ds.	Col.	Etc.
Blue and lilac §§ 1 and 3 .	.29	37.76	.89	—	—	1.48	—	—	31.56	22.13	5.60	.29
Rose and purple §§ 2 and 4	2.00	25.33	—	.33	1.00	3.33	—	—	12.67	40.33	11.33	1.67
Yellow flowers §§ 5 and 6 .	.12	.24	.24	.06	1.28	.67	.55	—	6.05	87.60	1.71	1.47
Eyed and white §§ 7 and 8	.39	1.03	.64	.03	2.06	2.01	.31	.08	3.87	82.90	5.93	.75

TABLE XIV.

Species visits in different parts of Europe to the flowers of the Rose-Purple-Lilac-Blue series of B'.

	Apis.	Hl.	Hm.	Hs.	Lep.	Dm.	Ds.	Col.	Etc.	Total.
Clova . . . . . (9 species)	2	22	1	3	9	25	43	8	5	118
Germany—Müller . . (6 ,, )	6	38	66	10	43	51	15	13	—	242
Flanders—MacLeod . (5 ,, )	5	31	24	2	21	45	13	2	—	143
Frisian Coast—Knuth and Verhoeff . . . . (6 ,, )	5	48	21	3	27	37	33	4	1	179
Alps—Müller . . . . (4 ,, )	1	15	5	—	27	7	—	4	—	59
Pyrenees—MacLeod . (2 ,, )	—	21	8	—	30	8	1	1	—	69

By season it can be shown that on flowers of both B' and A' the short-tongued flies decrease in percentage of individual visits towards autumn, while Coleoptera increase on B';

Bombi increase and so do mid-tongued flies on B'; but on A' mid-tongued flies decrease towards autumn. A' owes its large number of long-tongued flies in spring to the genus

TABLE XV.

Species visits in different parts of Europe to the flowers of the Yellow-White series of B'.

	Apis.	Hl.	Hm.	Hs.	Lep.	Dm.	Ds.	Col.	Etc.	Total.
Clova . . . . . (18 species)	3	8	9	29	34	83	184	26	14	390
Germany—Müller . (16 " )	7	63	203	26+	49	110	49	56	4	567+
Flanders—MacLeod . (13 " )	3	18	64	15	41	74	66	18	—	299
Frisian Coast—Knuth and Verhoeff . . . (16 " )	8	87	155	5	29	86	80	11	2	463
Alps—Müller . . . (11 " )	1	25	26	8	101	52	61	22	—	356
Pyrenees—MacLeod (6 " )	—	5	2	1	4	8	13	6	—	39

TABLE XVI.

Species visits in different parts of Europe to flowers of A'.

	Apis.	Hl.	Hm.	Hs.	Lep.	Dm.	Ds.	Col.	Etc.	Total.
Clova . . . . . (7 species)	2	—	1	31	6	27	102	13	7	189
Germany—Müller . . (4 " )	2	5	59	72	7	53	71	67	10	346
Flanders—MacLeod . (4 " )	1	—	9	18	1	28	40	7	1	105
Frisian Coast—Knuth and Verhoeff . . . (5 " )	—	1	21	49	—	32	49	12	—	164
Alps—Müller . . . . (2 " )	—	—	2	8	—	1	5	14	—	30
Pyrenees—MacLeod . (2 " )	—	—	2	11	2	7	19	7	—	48

Platychirus, one of the least specialized of Syrphidae; B' owes its larger number in autumn to highly specialized Empids and Eristalis. Injurious insects are chiefly summer insects. The actual figures recorded are given in Table XVII, the percentages from them in Table XVIII, and the net result in Table XIX.

In conclusion, B' obtained the visits of *Apis mellifica*, of eight species of *Bombus*, one of *Psithyrus*, of one species of *Halictus*, two of *Andrena*, one of *Odynerus*, one of *Vespa*,

of two Ants, and of ten other injurious Hymenoptera; of eighteen of the higher Lepidoptera, of six Microlepidoptera

TABLE XVII.

Individuals visiting by season: Spring = April and May; Summer = June and July; Autumn = August and September.

	Apis.	Bomb.	Hm.	Wasps.	Tenth. Parasit. Ants.	Lep.l.	Lep.m.	Lep.s.	Dm.	Ds.	Col.	Etc.	Total.
<i>Class B'.</i>													
Spring	16	3	1	0	2	14	0	0	12	2,072	0	0	2,120
Summer	7	20	30	1	89	25	20	3	167	1,560	126	48	2,096
Autumn	1	225	1	2	13	65	1	0	215	1,215	185	17	1,940
<i>Class A'.</i>													
Spring	0	0	0	0	4	0	0	0	28	135	8	1	176
Summer	3	0	2	3	218	1	5	0	50	815	46	39	1,182
Autumn	0	0	0	0	11	0	0	0	1	52	58	2	124

TABLE XVIII.

Percentages derived from preceding Table.

	Apis.	Bomb.	Hm.	Wasps.	Tenth. Parasit. Ants.	Lep.l.	Lep.m.	Lep.s.	Dm.	Ds.	Col.	Etc.
<i>Class B'.</i>												
Spring	.75	.14	.05	—	.09	.66	—	—	.57	97.74	—	—
Summer	.33	.96	1.43	.05	4.25	1.19	.96	.14	7.97	74.42	6.01	2.29
Autumn	.05	11.60	.05	.10	.67	3.35	.05	—	11.08	62.63	9.54	.87
<i>Class A'.</i>												
Spring	—	—	—	—	2.27	—	—	—	15.91	76.70	4.55	.57
Summer	.25	—	.17	.25	18.45	.08	.43	—	4.23	68.95	3.89	3.30
Autumn	—	—	—	—	8.87	—	—	—	.81	41.94	46.77	1.61

TABLE XIX.

Insects visiting in different seasons, classed by desirability.

	B'.			A'.		
	Spring.	Summer.	Autumn.	Spring.	Summer.	Autumn.
Decidedly desirable	1.55	2.50	14.92	0.00	0.33	0.00
Desirable . . . .	.62	8.63	11.64	15.91	4.83	0.81
Indifferent . . . .	97.74	81.01	71.90	81.25	73.09	88.71
Injurious . . . .	.09	6.56	1.54	2.84	21.75	10.48



including Erioccephala ; of twenty-two Syrphids, of thirteen species of Empis, of Pachymeria palparis, of five short-tongued Empids, of nine Muscids, one Sarcophagid, two Tachinids, three Cordylurids, of twenty-one Anthomyiids and twenty of other flies ; of twelve Coleoptera, two Hemiptera, and five other insects. A' obtained the visits of Apis mellifica, of one Andrena, of one species of Vespa, of two Ants, and of twelve injurious Hymenoptera ; of one of the higher Lepidoptera (Miana fasciuncula), four short-tongued Lepidoptera, including Hepialis but not Erioccephala ; of eight Syrphids, four species of Empis, four short-tongued Empids, nine Muscids, one Sarcophagid, two Tachinids, three Scatophagids, sixteen of Anthomyiids, and of twenty-three other flies ; of seven Coleoptera, two Hemiptera, and two other insects. 167 species of insects made 6,156 visits to Class B', 104 made 1,482 visits to Class A' ; the average number of visits per insect to Class B' is therefore 36.86, and the average to Class A' is 14.25.



# On the Development of the Sexual Organs and Fertilization in *Picea excelsa*.

BY

K. MIYAKE.

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With Plates **XVI** and **XVII**.

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## INTRODUCTORY.

**I**N spite of the activity which has of recent years been manifested in the study of the fertilization and embryogeny of the Abietineae, the genus *Picea* has been seemingly neglected. In fact, our knowledge on the cytology of the sexual reproduction of *Picea* remained almost stationary for nearly ten years. In the light of the recent studies on the other members of the Abietineae, it is highly desirable that similar investigations should be made in *Picea*. It was with this object that the work described in the present paper was undertaken.

But few investigators have hitherto studied the development of the gametophytes and fertilization in *Picea*. Hofmeister ('51, '58, '62), who made the first careful and extensive studies on the life-history of the Conifers, has only incidentally referred to *Picea*.

Strasburger ('69) in his first work on the fertilization of the Conifers described the structure of the archegonium and the formation of the proembryo in *Picea excelsa* (*P. vulgaris*) with several figures. He traced the pollen-tube into the arche-



gonium, and affirmed Hofmeister's observation regarding the presence of a closed pit at the apex of the tube. Three years later Strasburger ('72) made a further contribution to the embryology of *Picea* by describing the process of embryof ormation in *Picea excelsa*.

In 1878 Strasburger observed two 'primordial cells' in the pollen-tube of *Picea excelsa*, and mentioned that these cells dissolve one after another before fertilization takes place; later, the sperm-nucleus, which, he thought, was formed from the contents of the tube, appears in the upper part of the egg and finally fuses with the egg-nucleus. In his 'Angiospermen und Gymnospermen,' Strasburger ('79) makes the statement that it is the foremost of these two 'primordial cells' in the pollen-tube which becomes active in fertilization. In 1884, by a study of *Picea excelsa*, he confirmed Goroschankin's observation ('83) on *Pinus* as to the passage of both sperm-nuclei into the egg, but pointed out that only the one in advance fuses with the egg-nucleus.

The same author in his work on the pollen of the Gymnosperms ('92), in which he showed that Belajeff's observations ('91) on the development of the pollen-tube in *Taxus baccata* are in general true for other Gymnosperms, gave the results of observations on the germinating pollen of *Picea excelsa*. In the mature pollen-grain just before pollination he observed that the third prothallial cell or central cell<sup>1</sup> has already been divided into the stalk- and generative cells, the two other disintegrating prothallial cells being seen as two slit-like bodies. He also found that the generative cell divides into two sperm-cells before it passes down into the pollen-tube.

In the following year Belajeff ('93), in his second paper on the pollen-tube of the Gymnosperms, described the further development of the pollen-tube in *Picea excelsa*. According to him the generative cell divides into two sperm-cells before it moves down into the pollen-tube; the stalk-cell is broken down and only the nucleus follows the sperm-cells, finally

<sup>1</sup> I take the third prothallial cell as homologous to the central cell of the Pteridophytes, and the latter term is used throughout the paper.

overtaking and passing the latter, and is found near the tip of the tube with the vegetative nucleus.

The material for the present studies was collected from three grown-up trees on the campus of Cornell University, during May and June of 1901 and 1902. The cones of one tree had smooth oval scales, while those of the other two trees had scales somewhat rhomboidal in shape with wavy margins. The three trees looked almost alike in the shape and size of the leaves, and in general appearance. Histologically, at least so far as the structure of the ovule is concerned, I failed to find out any difference between these two forms. As *Picea excelsa* is exceedingly variable, presenting a number of varieties and forms, perhaps little importance should be attached to these individual peculiarities<sup>1</sup>.

Flemming's chrom-osmo-acetic acid solution of the stronger concentration was almost entirely used as the fixing fluid. The material was washed, dehydrated, decolorized, and imbedded in paraffin in the usual way. The sections were cut usually from 8 to 12  $\mu$  in thickness. For staining, Flemming's safranin, gentian-violet, and orange combination was extensively used. Sometimes this stain was used without safranin and gave some good results.

The present studies were conducted in the Botanical Laboratory of Cornell University, and I wish to express here my best thanks to Professor G. F. Atkinson for his kind advice and helpful criticisms.

#### DEVELOPMENT OF THE MALE GAMETOPHYTE.

In the mature pollen-grain, just before pollination, the central cell is usually divided into the stalk- and generative cells, and the disintegrating remains of the first two prothallial cells can be seen merely as two thin and darkly staining bodies between the stalk-cell and the pollen-wall (Pl. XVI, Fig. 6). This fact has already been noticed by Strasburger ('92). According to him *Larix* behaves in the same way as

<sup>1</sup> On the variations of *Picea excelsa* see Schröter, '98.

*Picea*, and differs from *Pinus*, in which the division of the central cell takes place after pollination.

Fig. 1 shows a pollen-grain in which the central cell is still undivided. Several stages of the division of the central cell are shown in Figs. 2-5. Figs. 1-6 are drawn from sections of the anthers, collected a few days before pollination. In the same anther, or even in a single section, I was often able to find out all the different stages figured here. The stalk- and generative cells are almost equal in size and structure when they are formed; they usually contain several nucleoli (Fig. 6). The nucleus of the vegetative or tube-cell is oval or sub-spherical, and is situated very close to the free end of the generative cell. It contains usually two or sometimes more nucleoli (Figs. 1-6).

In the neighbourhood of Cornell University, Ithaca, N. Y., pollination takes place during about the second week in May. The dates varies somewhat by seasons. At the time of pollination, the female cone stands erect, the scales being divergent. It is about one-third or one-fourth the length of the mature cone. After about a week or ten days, the scales are closed and the cone begins to droop downward.

The germination of the pollen-grain seems to take place in a few days after pollination. Soon after the formation of the pollen-tube, the tube-nucleus, which has usually a single nucleolus about this time, moves down towards the tip of the tube (Figs. 9, 10). Both the generative and stalk-cells continue to increase in size (Figs. 7-10). The generative cell enlarges more rapidly, and its nucleus soon assumes a more or less spherical shape with a prominent nucleus; its cytoplasm becomes dense and deeply staining (Figs. 9-11). The cytoplasm of the stalk-cell on the contrary assumes a vacuolate character. Its nucleus grows but slightly, and one or more prominent nucleoli, which were observed in its early stage of development, are now replaced by one or several small granules; sometimes one of the granules is slightly larger and seems to represent a true nucleolus (Figs. 7-11).

In the meantime the stalk-cell is detached from the inner



wall of the pollen-grain, and together with the generative cell moves down into the pollen-tube (Figs. 11, 12). Strasburger ('92) states that in *Picea excelsa* the generative cell divides in the pollen-grain, and of the resulting two cells the one in advance is smaller than the other<sup>1</sup>. Belajeff ('93) also observed in *Picea excelsa* that the generative cell divides into two before it leaves the pollen-grain, and only the naked nucleus of the stalk-cell enters the pollen-tube. Dixon ('94) made a similar observation in *Pinus sylvestris*. Miss Ferguson ('01 a), in her studies on the development of the pollen-tube in several species of *Pinus*, obtained very different results. She found that the generative cell enters the pollen-tube before it divides, and also demonstrated that the whole stalk-cell moves down into the pollen-tube. My observations in *Picea* agree with Miss Ferguson's in both points.

The generative cell, as it passes into the pollen-tube, is more or less elongated and increases much in size; it has no definite cell-wall, and is somewhat irregular in shape (Fig. 12). The stalk-cell, which is attached to the generative cell at its lower side and more or less surrounded by the cytoplasm of the latter, seems to move down the pollen-tube more rapidly; it passes by the generative cell, and soon afterwards is seen at the lower end of the latter (Figs. 13, 14).

Shortly after this the generative cell divides. The process of the division has not been traced very carefully, but judging from several division-figures so far observed, I may say that in general it is very much like that of *Pinus* as studied by Miss Ferguson ('01 a). The mitotic figure, like Fig. 15, suggests that the spindle may very likely be unipolar in origin as in *Pinus*. The cell-plate is formed at the equator of the spindle, but persists only for a short time and finally disappears, as was already noticed by Miss Ferguson in *Pinus* (Figs. 16-20). Soon after the division the two sperm-nuclei are separated from each other by a considerable distance (Fig. 17). Gradually

<sup>1</sup> 'Bei *Picea vulgaris* sieht man die grosse Antheridialzelle sich ebenfalls schon im Pollenkorn theilen. Die vordere generative Zelle ist auch bei *Picea* kleiner als die hintere' (Strasburger, '92, p. 25).

the two nuclei approach each other, or rather the lower nucleus moves towards the upper one, until they come to lie in the uppermost part of the common cytoplasm (Figs. 18-21). The two nuclei are not equal in size, and the upper one seems to be always smaller. This inequality in size could be detected as far back as the formation of the daughter-nuclei (Fig. 16). Miss Ferguson ('01*a*) made a similar observation in *Pinus*. She also demonstrated the fact that in *Pinus* two sperm-nuclei are surrounded by the common cytoplasmic mass; two sperm-cells never being formed as was supposed to be the case by former investigators (Strasburger '92, Belajeff '93, Dixon '94, Coulter '97).

At this time the pollen-tube has reached nearly half way down towards the archegonium. After the formation of the sperm-nuclei the downward growth of the tube is comparatively rapid. The pollen-tube is somewhat sinuous in its course, but I have never observed it to branch, as is often the case in *Pinus*.

The sperm-nuclei increase in size after they are formed, and present a densely granular appearance under a low power, although these granules seem to be somewhat reticularly arranged under a high power. The nuclei, when mature, often stain intensely, taking the violet in Flemming's triple method. They seem to contain several nucleoli, but the latter are often obscured by the other densely staining structures (Figs. 19-22). Fig. 15 shows two mature sperm-nuclei near the tip of a pollen-tube which has reached the lower part of the nucellar cap almost approaching the neck of the archegonium. The stalk-cell with its characteristic nucleus is found at the lower end of the sperm-cytoplasm.

The nucleus of the stalk-cell usually takes the violet stain in the triple method. It is very much like one of the nuclei of the nucellar cap both in its size and staining character throughout its entire history in the pollen-tube. Although Miss Ferguson for the first time clearly established the fact that the stalk-cell remains intact throughout its entire history in the pollen-tube, a careful examination of Strasburger,

Belajeff, and Coulter's drawings<sup>1</sup> leads me to think that they too saw the entire stalk-cell in the pollen-tube ; it was, however, interpreted by them as a mere nucleus.

The tube-nucleus, which is often somewhat irregular in outline and has a prominent nucleolus, is always located near the tip of the pollen-tube (Figs. 10-16, 18-21). This nucleus seems to play an important part in the elongation of the pollen-tube ; it has been observed in *Ginkgo* (Hirase '98) and Cycads (Ikeno '98, Webber '01) that when the tip of the pollen-tube ceases to grow and the other end of the tube begins to elongate, a little while before fertilization, the tube-nucleus migrates to this new growing portion.

The starch-grains, which can usually be observed in the mature pollen-grain, increase much in size and amount after the formation of the pollen-tube. Very often these grains have deeply staining portions, which I have not sketched in my drawings, in their centres. They are probably the cracks or spaces left by the dissolution of some of the starch in the centre of the grain. The starch-grains also appear in the full-grown stalk-cell shortly before its passing into the pollen-tube ; after the cell has entered the tube starch is no longer visible in it (Fig. 11). The stalk-cell with starch-grains was also observed in *Zamia* by Webber ('01).

#### EARLY DEVELOPMENT OF THE ARCHEGONIUM.

The archegonium usually develops from a superficial cell at the apex of the female prothallium. When the prothallium reaches a certain size, some of the cells in the uppermost layer cease to divide, but continue to grow, so that they are distinguished from the adjacent cells by their larger size and larger nuclei. These are the initial cells of the archegonia (Figs. 23, 24). While this archegonial initial is only a few times as large as the adjacent cells it divides, giving rise to a small upper cell, the mother-cell of the neck, and a large lower cell, the central cell of the archegonium (Figs. 25, 26).

<sup>1</sup> Strasburger '92, Figs. 43, 44 ; Belajeff '93, Fig. 16 ; Coulter '97, Fig. 5.



The smaller cell soon divides into two cells by an anticlinal wall; these two cells then divide several times by both anticlinal and periclinal walls and form the neck of the archegonium. The neck of the full-grown archegonium usually consists of four to eight rows of cells, with two to four cells in each row (Figs. 27-36, 41). Strasburger made a similar observation in 1869, and stated that the neck consists of two to four tiers of cells.

The rapid growth of the central cell takes place soon after its formation. The cytoplasm presents a very vacuolate appearance in the early stage of development (Figs. 27-31). But as the central cell continues to grow the cytoplasmic contents become more dense, and the number and size of the vacuoles gradually decrease. When the archegonium reaches its full size only a few small vacuoles are found in the more or less finely granular cytoplasm, and now a few so-called proteid-vacuoles begin to appear (Fig. 32). The nucleus is, from the first, always situated at the apex of the cell just beneath the neck. It has one prominent nucleolus, and sometimes one or two smaller ones may be present (Figs. 26-36). Enveloping the central cell is a layer of cells rich in protoplasm and with large nuclei; these are the sheath- or wall-cells of the archegonium, and correspond to the follicle-cells of the animal egg in their function. These cells are differentiated from the adjacent endosperm-cells very early in the development of the archegonium.

The number of archegonia in each ovule varies from two to seven, the most common number being four. Of over four hundred ovules studied, I kept an account of the number of archegonia in about three hundred of them, and found that about one-half had four archegonia; about one-fourth had three, and about one-fifth had five archegonia, while eight cases were met in which each ovule contained six archegonia. In four cases an ovule was found with two archegonia, and but a single ovule with seven archegonia was met with. This agrees in the main with the observation of Strasburger ('69), who found three to five archegonia in each ovule of *Picea excelsa*.

FORMATION OF THE VENTRAL CANAL-CELL.

As the central cell prepares for division the deeply staining substance, which is coarsely granular, accumulates near the centre of the nuclear cavity, in a condition suggesting synapsis, similar to that observed by Murrill ('00) in *Tsuga*. Soon there appears, along the lower side of the nucleus, a clear court which at first assumes a crescent shape in section, and later approaches to a conical form. Sooner or later delicate fibres make their appearance inside the court; similar fibres also appear on the upper side of the nucleus. These fibres seem to represent the beginning of an extra-nuclear spindle. At the same time the upper and lower sides of the nucleus become more or less irregularly indented (Pl. XVII, Figs. 37, 38). The fibres seem to press the nuclear membrane from both sides, and finally to enter the nuclear cavity by the dissolving away of the membrane, which first takes place where the fibres are attached. Fig. 39 shows a stage in which the nuclear membrane is still intact, except the side close to the fibres where it is beginning to disappear. Chromosomes about twelve in number are found inside the nuclear cavity.

The spindle, when fully formed, is more or less pointed at the lower end and somewhat blunt on the upper side. It seems to lie wholly within the boundary of the original nucleus, so that one who had not seen the earlier stages of division might interpret the origin of the spindle as intra-nuclear (Figs. 40-43). The various stages of the division are shown in Figs. 37-48. The two daughter-nuclei are considerably different in size when they are formed, the nucleus of the egg being several times larger than that of the ventral canal-cell. The process of division is in the main similar to *Pinus* as described by Miss Ferguson ('01 *b*); the only noticeable difference is that no accumulation of chromatic substance has been observed in the early stage of division in *Pinus*. No trace of the dense fibrous mass beneath the

nucleus, from which the lower spindle arises, as described in *Tsuga* by Murrill ('00), has been observed in *Picea*.

The ventral canal-cell shows signs of disintegration very soon after its formation. The nuclear membrane seems to break down very soon, and the nuclear substance becomes scattered throughout the cell. In the mature archegonium ready for fertilization, the ventral canal-cell usually appears as a lenticular or crescent-shaped cap over the top of the egg, with a deeply stained mass of granular substance; and a distinct nucleus is no longer visible in it (Figs. 34, 35, 48). In a few cases a fibrous structure, as observed by Blackman ('98) in *Pinus sylvestris*, was found in the ventral canal-cell of *Picea*. It may probably represent the remains of the spindle-fibres, as suggested by Blackman.

In several preparations showing the division of the central cell, I was able to count the number of chromosomes, and twelve, or approximately twelve, were always found, as already noticed by Blackman ('98) and Miss Ferguson ('01 *b*) in *Pinus*, instead of eight as counted by Dixon ('94). The number of chromosomes in the dividing nuclei of the sheath-cells and other cells of the female prothallium has always been found to be approximately twelve, as already found to be the case in *Pinus* by Blackman ('98), Chamberlain ('99) and Miss Ferguson ('00 *b*), while their number in the cells of the nucellus was invariably more than twenty, the actual number being very likely twenty-four.

#### MATURATION OF THE EGG.

The egg-nucleus, soon after it is formed, begins to increase in size, becoming considerably enlarged before the disappearance of the spindle-fibres (Figs. 47, 48). As the nucleus moves down towards the centre of the egg, it continues to enlarge until the centre is reached (Figs. 34, 35). After the division of the central cell, the few vacuoles, if there are any, in the cytoplasm gradually disappear, and at the same time an increase in the number of proteid-vacuoles takes place. Each proteid-vacuole at first contains a number of granules



often differing in size, and these granules then seem to unite into one or more larger ones. At a later stage, about the time of fertilization, the proteid-vacuoles, each with a single large granule occupying the larger part of the vacuole, are often observed. In addition to the proteid-vacuoles several granules varying in size can be seen scattered all through the egg-cytoplasm. Thus the egg-cytoplasm, which appeared to be finely granular before the formation of the ventral canal-cell, presents a much coarser structure about the time of fertilization (Figs. 33-35, 49-51).

The origin of the proteid-vacuoles is not at all clear, although there is no doubt about their being a kind of nutritive substance. Hirase ('95) observed that the granules in the egg of *Ginkgo* were of nucleolar origin, being derived both from the nucleus of the central cell and from the nuclei of the sheath-cells. Arnoldi ('00 *a*) thought that substantially the same thing takes place in *Cephalotaxus*. Ikeno ('98) observed the passing in of the substance secreted by the nuclei of the sheath-cells, through the numerous pores in the wall of the archegonium, into the egg, and he ascribed to this substance the origin of the proteid-vacuoles. Arnoldi ('00 *b*) described a remarkable migration of whole nuclei from the sheath-cells into the egg in several species of *Pinus*. Murrill ('00) and Miss Ferguson ('01 *b*) have both failed to find such passage of nuclear substance from the sheath-cells into the egg. In careful examination of numerous archegonia in all stages of development, I was not able to find even a single case representing such a passage in *Picea*.

The mature egg-nucleus, situated at or near the centre of the archegonium, usually contains one or more large nucleoli and often several smaller ones; but it is not always easy to distinguish the latter from the chromatic granules in the nuclear reticulum. The reticulum presents a more or less granular appearance and stains violet with the triple stain. The nucleus is usually somewhat oval or elliptical in shape, its average size being  $100\ \mu$  by  $120\ \mu$  (Figs. 35, 49-51).

## FERTILIZATION.

The date of fertilization varies for the same and different trees much as pollination does. In 1901 the earliest date for fertilization was June 15, while in the same tree the conjugating nuclei were observed as early as June 7 in the following year, the process being apparently most active on the 9th or 10th. The difference may largely be ascribed to the unusually early season in 1902, and the condition in 1901 may probably represent that of the normal year. Generally speaking, we may say that in the neighbourhood of Cornell University the fertilization of *Picea excelsa* takes place about the middle of June.

The egg seems to be fertilized about five days or a week after the formation of the ventral canal-cell. The pollen-tube reaches the egg by penetrating the neck of the archegonium, and nearly the whole contents of the lower part of the tube, including the two sperm-nuclei, pass into the egg.

In the mature egg which is ready for fertilization, a vacuole was often observed just beneath the neck. Sometimes a few smaller vacuoles may also be present near the larger one. Miss Ferguson's suggestion about the similar vacuole in *Pinus Strobus* is very instructive; she says that 'this opening in the cytoplasm represents the last act of the egg in its preparation for the reception of the sperm-nucleus.' But I am not quite ready to accept her interpretation without making more careful and extensive observations. The vacuole was sometimes observed in the egg after fertilization (Figs. 51, 52).

The larger sperm-nucleus immediately moves down towards the nucleus of the egg. There is no evidence that the sperm-nucleus increases in size after entering, as was supposed to be the case by some investigators (Coulter '97). The sperm-nucleus is much smaller than the one figured by Strasburger ('84 a), being about one-third the diameter of the egg-nucleus. The sperm-nucleus first comes in contact with the egg-nucleus and soon begins to press itself against the latter. Thus the sperm-nucleus becomes more or less imbedded

in the substance of the egg-nucleus ; but the walls of both nuclei are still intact (Figs. 49-51). Later stages in the conjugation of the sexual nuclei have not been observed. The fate of the second sperm-nucleus, tube-nucleus, and stalk-cell after their entrance into the egg has not been followed in the present studies.

#### DIVISION OF THE FERTILIZED NUCLEUS AND FORMATION OF THE PROEMBRYO.

The fertilized nucleus soon divides into two smaller nuclei. The karyokinetic spindle of this division is shown in Fig. 52. The two daughter-nuclei thus formed increase rapidly in size, and then divide simultaneously. The four free nuclei soon increase in size. When they have reached their full size, they begin to move down toward the base of the egg (Figs. 53, 54). Upon reaching the base of the egg, the four nuclei arrange themselves in a plane, and they are surrounded by a deeply staining mass of protoplasm, which is much more finely granular in structure compared with that of the rest of the egg (Fig. 55).

The four nuclei then divide simultaneously in a plane transverse to the long axis of the egg (Fig. 56). After the complete formation of eight daughter-nuclei walls are formed between them, and a tier of four completely walled cells is cut off below, the upper four nuclei still being freely exposed above to the partially segmented cytoplasm of the egg (Fig. 57). Strasburger ('84*b*) figures the formation of the complete wall in the four-celled stage in *Picea excelsa*, and the figure is repeated in his later publications ('97, '02). Blackman ('98) also describes, in *Pinus sylvestris*, the formation of walls between the four nuclei. According to him, 'the two walls are formed at right angles to one another and to the base of the oosphere ; each nucleus thus lies at the bottom of a kind of shaft which is open above.' Miss Ferguson ('00*b*) failed to find any sign of wall-formation in the four-nuclei stage, and mentions that 'in the five species of Pines which



I have studied, cell-walls do not arise until after eight nuclei have been formed.'

Strasburger ('84*b*), describing the later process of proembryo-formation, states that the lower four of the eight cells divide, and the process is again repeated by the lowest four; thus finally there are three tiers of four cells each, with four free nuclei above them<sup>1</sup>. Coulter and Chamberlain ('01) give a similar description of the corresponding process in *Pinus Laricio*: 'The cells of the single completely walled tier then divide simultaneously, and two tiers are organized. The process is again repeated by the lower tier, and the result is three tiers of four cells each.'

The result of my observations is somewhat different from the above-mentioned process, which seems to be generally accepted. According to my observations, at first, the four nuclei of the upper incompletely walled cells divide simultaneously, and another tier of completely walled cells is formed right above the lower tier (Fig. 58). Then the division is undertaken by the cells of the lowest tier and the formation of the proembryo is accomplished (Fig. 59)<sup>2</sup>. At this stage, therefore, there are four tiers of cells, of four cells each, the upper tier being incomplete since the nuclei are separated from one another by walls, but freely exposed above to the food supply of the egg.

#### ABNORMAL ARCHEGONIA.

Several abnormal archegonia have been observed in the course of the present investigations. The archegonium without a neck was often noticed (Figs. 60-61). This neckless archegonium has probably been originated from a cell below

<sup>1</sup> 'Die das Ende des Eies einnehmenden vier Zellkerne theilen sich in derselben Richtung weiter und die dem Ei-ende näheren wiederholen noch einmal die Theilung. So finden wir schliesslich in dem vom Halstheile abgekehrten Ende des Eies drei Etagen von je vier Zellen und über diesen im Eikörper vier freie Zellkerne' (Strasburger '84*b*, p. 483).

<sup>2</sup> According to Miss Ferguson's unpublished observation, which was kindly submitted to me, the process of proembryo formation of *Pinus* agrees with my result in *Picea*.

the superficial layer of the prothallium. In one of them the ventral canal-cell was found at the side of the egg, instead of the top (Fig. 61). Two archegonia, lying one above the other, were observed several times, and both archegonia were found to be somewhat smaller than the normal one. The lower archegonium, which is usually larger than the upper one, has no neck-cells, but the ventral canal-cell is usually formed.

Fig. 62 shows a double archegonium, in both parts of which the central cell is still undivided. The division of the central cell does not always take place simultaneously. In Fig. 63 the nucleus of the lower archegonium is dividing while that of the upper one remains still undivided. A later stage is shown in Fig. 64; the nuclei of both archegonia are already divided and each egg-nucleus is approaching the centre of the egg. The disorganizing ventral canal-cell, which is somewhat lenticular in shape, is seen on the upper left-hand corner of the lower archegonium; that of the upper archegonium is found in another section, and is not sketched here.

#### SUMMARY.

1. The mature pollen-grain contains the large tube-cell, two smaller generative and stalk-cells, besides two disintegrating prothallial cells. The third prothallial cell or central cell divides into the stalk and generative cells before pollination, as already described by Strasburger. This division seems to take place within a few days before pollination.

2. Pollination takes place, in the vicinity of Ithaca, N. Y., about the second week in May. The pollen-grain germinates in a few days after pollination.

3. Soon after the formation of the pollen-tube, the tube-nucleus leaves the grain, and is found near the tip of the tube. The generative and stalk-cells, which are nearly equal in size and structure when first formed, begin to increase in size, and soon the two cells present very different appearances. The generative cell enlarges more rapidly, and its nucleus assumes a more or less spherical shape with a prominent nucleolus, its

cytoplasm being very dense and finely granular, while the stalk-cell has a smaller nucleus and very vacuolate cytoplasm.

4. About two weeks, or a little more after pollination, the generative cell followed by the stalk-cell moves down into the pollen-tube. The stalk-cell soon passes the generative cell and attaches itself to the lower side of the latter.

5. The generative cell, after passing into the pollen-tube, is more or less elongated and somewhat irregular in its outline. It has no well-defined cell-wall, and the nucleus occupies at the time of its division the upper part of the dense protoplasmic body.

6. The division of the generative cell has not been followed in detail. The process seems to be very similar to that of *Pinus*, as studied by Miss Ferguson. The cell-plate formed at the equator of the spindle later disappears, and two sperm-nuclei, which are unequal in size, remain surrounded by a common mass of cytoplasm.

7. The sperm-nuclei, which are separated by a considerable distance when they are formed, soon come to lie together in the uppermost part of their cytoplasm, and early attain their full size, the lower one being always larger.

8. The archegonium usually originates as a single superficial cell in the micropylar end of the female prothallium. Very early in its development it divides into two cells; the upper smaller one forms the mother-cell of the neck and the lower larger one develops into the egg-cell.

9. The number of archegonia in each prothallium varies from two to seven, the most usual number being four; three and five are the next common numbers; six is less common, while two and seven are extremely rare.

10. The central cell is at first very vacuolate, and its nucleus always remains close beneath the neck-cells. Later, its protoplasmic contents gradually increase, and the vacuoles begin to disappear. When the central cell is fully developed and its nucleus is ready for division, the number and size of the vacuoles become very much decreased, while a few proteid-vacuoles begin to appear in the cytoplasm.



11. In the division of the central cell the spindle-fibres first arise from a clear court along the lower side of the nucleus and grow into the nuclear cavity where they are joined by the fibres from the small upper pole, which also originates outside of the nucleus but without any special court. The spindle, when fully formed, is more or less pointed at the lower end and somewhat blunt on the upper side.

12. The nucleus of the ventral canal-cell when it is formed is much smaller than that of the egg, and very soon shows signs of disintegration. The ventral canal-cell rarely presents the appearance of a normal cell; at the time of fertilization it may usually be seen as a small somewhat lenticular or crescent-shaped, deeply staining body, just beneath the neck-cells.

13. The egg-nucleus, soon after it is formed, begins to increase in size, and moves down towards the centre of the egg. The mature egg-nucleus is more or less oval or elliptical in shape, and presents a deeply staining somewhat interrupted reticulum; its average size is about  $100 \mu \times 120 \mu$ . When the ventral canal-cell is cut off, the vacuoles have nearly disappeared from the cytoplasm of the egg, and the proteid-vacuoles become numerous and prominent. About the time of fertilization the egg-cytoplasm presents a more coarsely granular structure.

14. At the time of fertilization, the greater part of the contents of the pollen-tube including the two sperm-nuclei are discharged into the egg. The larger sperm-nucleus soon moves down and conjugates with the egg-nucleus. The sperm-nucleus first imbeds itself in the side of the egg-nucleus, and both nuclei retain their membranes intact for some time. The further changes in the conjugating nuclei have not been followed. The second sperm-nucleus remains unchanged in the upper part of the egg for some time, and probably disintegrates there finally. The fate of the stalk-cell and the tube-nucleus has not been followed.

15. The fertilized nucleus soon divides into two smaller nuclei. These two nuclei then divide simultaneously, and the four resulting free nuclei soon attain full size and move down

to the base of the archegonium. No wall is formed between these four nuclei, as supposed to be the case by some previous investigators.

16. The four free nuclei at the base of the archegonium divide simultaneously. After eight nuclei are completely formed, the walls are laid down between them, as in the case of *Pinus* described by Miss Ferguson.

17. The upper four nuclei now divide, instead of the lower four as described by previous investigators, and then follows the division in the four cells of the lowest tier. The pro-embryo thus formed consists of three complete tiers of four cells each, and the tier of four nuclei which are separated from one another by walls but freely exposed above towards the main mass of the egg-cytoplasm.

18. Among several abnormal archegonia observed, the archegonium without neck-cells was often noticed. In one of them the ventral canal-cell was seen at the side instead of at the top of the egg. Double archegonia, one archegonium lying above the other, were observed several times. The lower one, which is usually somewhat larger than the upper one, has no neck-cells, while the formation of the ventral canal-cell usually takes place in both of them.

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EXPLANATION OF FIGURES IN PLATES XVI  
AND XVII.

Illustrating Dr. Miyake's paper on *Picea excelsa*.

All figures were drawn with the aid of a camera lucida, using Zeiss's and Bausch and Lomb's microscopes. The abbreviations used are: *g.c.*, generative cell; *s.c.*, stalk-cell; *t.n.*, tube-nucleus; *s.p.<sup>1</sup>*, first sperm-nucleus; *s.p.<sup>2</sup>*, second sperm-nucleus; *v.c.c.*, ventral canal-cell; *e.n.*, egg-nucleus.

PLATE XVI.

Figs. 1-6. Pollen-grains in different stages of development, a few days before pollination. Fig. 1. The central cell is still undivided. Figs. 2-5. Various stages in the division of the central cell. Fig. 6. A stage after the division of the central cell. *p.*, disintegrating prothallial cells; *c.c.*, central cell.  $\times 250$ .

Fig. 7. A pollen-grain about to germinate.  $\times 250$ .

Fig. 8. The same, later stage.  $\times 250$ .

Fig. 9. A pollen-grain soon after germination; the tube-nucleus is just moving down the pollen-tube.  $\times 250$ .

Fig. 10. A later stage; the generative cell is considerably enlarged, and the tube-nucleus is found near the tip of the pollen-tube.  $\times 250$ .

Fig. 11. Upper portion of a germinating pollen-grain, a little before the passage of the stalk- and generative cells into the pollen-tube. Starch-grains are found in the stalk-cell.  $\times 250$ .

Fig. 12. A later stage; showing the passage of the stalk- and generative cells into the pollen-tube.  $\times 250$ .

Figs. 13, 14. Later stages than in the above; the stalk-cell has already passed over the generative cell, and is found at the lower side of the latter.  $\times 250$ .

Fig. 15. Division of the generative cell.  $\times 250$ .

Fig. 16. The sperm-nuclei just after their formation; the spindle with a cell-plate is seen between them.  $\times 250$ .

Fig. 17. Similar stage, but little later; two nuclei are much more separated. The remnants of the spindle are seen near the upper nucleus.  $\times 250$ .

Fig. 18. The two sperm-nuclei are approaching each other; remains of the spindle are still seen.  $\times 250$ .

Figs. 19-21. The sperm-nuclei after all traces of the spindle have disappeared, lying in the upper part of their cytoplasm.  $\times 250$ .

Fig. 22. The full-grown sperm-nuclei near the tip of the pollen-tube; the tube is almost approaching the archegonium.  $\times 250$ .

Fig. 23. An archegonial initial.  $\times 110$ .

Fig. 24. The same, later stage; the nucleus is preparing to divide, being in the spireme stage.  $\times 110$ .

Fig. 25. Nucleus of the archegonial initial is just dividing.  $\times 110$ .

Fig. 26. After the division; the larger central cell and the smaller mother-cell of the neck are formed.  $\times 110$ .

Figs. 27-31. Later stages in the development of the archegonium. Fig. 31

represents an archegonium which has nearly approached to its full size, but its cytoplasm is still quite vacuolate.  $\times 110$ .

Fig. 32. A still later stage, little before the division of the central cell.  $\times 110$ .

Fig. 33. An archegonium showing the division of the central cell.  $\times 110$ .

Fig. 34. An archegonium just after cutting off the ventral canal-cell.

Fig. 35. Mature archegonium; the ventral canal-cell is shown right below the neck-cells.  $\times 110$ .

Fig. 36. Upper portion of an archegonium, showing the nucleus of the central cell shortly before division.  $\times 500$ .

#### PLATE XVII.

Fig. 37. Nucleus of the central cell preparing to divide.  $\times 500$ .

Fig. 38. The same, later stage; a rupture in the upper right-hand corner of the nucleus was probably made during preparation of the section.  $\times 500$ .

Figs. 39-45. Various stages of the division to form the ventral canal-cell.  $\times 500$ .

Figs. 46, 47. Formation of the two daughter-nuclei.  $\times 500$ .

Fig. 48. Early stage in the development of the egg-nucleus, showing also the disorganizing ventral canal-cell.  $\times 500$ .

Fig. 49. Entire egg-cell, showing the first sperm-nucleus approaching the egg-nucleus. The second sperm-nucleus, which is located near the top of the egg, is found in other section.  $\times 110$ .

Fig. 50. A later stage, showing the first sperm-nucleus just coming into contact with the egg-nucleus. The second sperm-nucleus is found in other section near the top of the egg.  $\times 110$ .

Fig. 51. A still later stage; the first sperm-nucleus has partly imbedded itself in the egg-nucleus. The second sperm-nucleus is found in the upper portion of the egg.  $\times 110$ .

Fig. 52. The spindle of the first segmentation.  $\times 110$ .

Fig. 53. The two daughter-nuclei resulting from the first segmentation.  $\times 110$ .

Fig. 54. A later stage, with the four segmentation-nuclei. One of the nuclei is not shown in this figure, being found in other section.  $\times 110$ .

Fig. 55. The four free nuclei at the base of the archegonium; only two of them are shown here.  $\times 110$ .

Fig. 56. Basal portion of an archegonium; the four nuclei are dividing.  $\times 110$ .

Fig. 57. A later stage, showing the eight nuclei of the proembryo; the walls are laid down between the nuclei.  $\times 110$ .

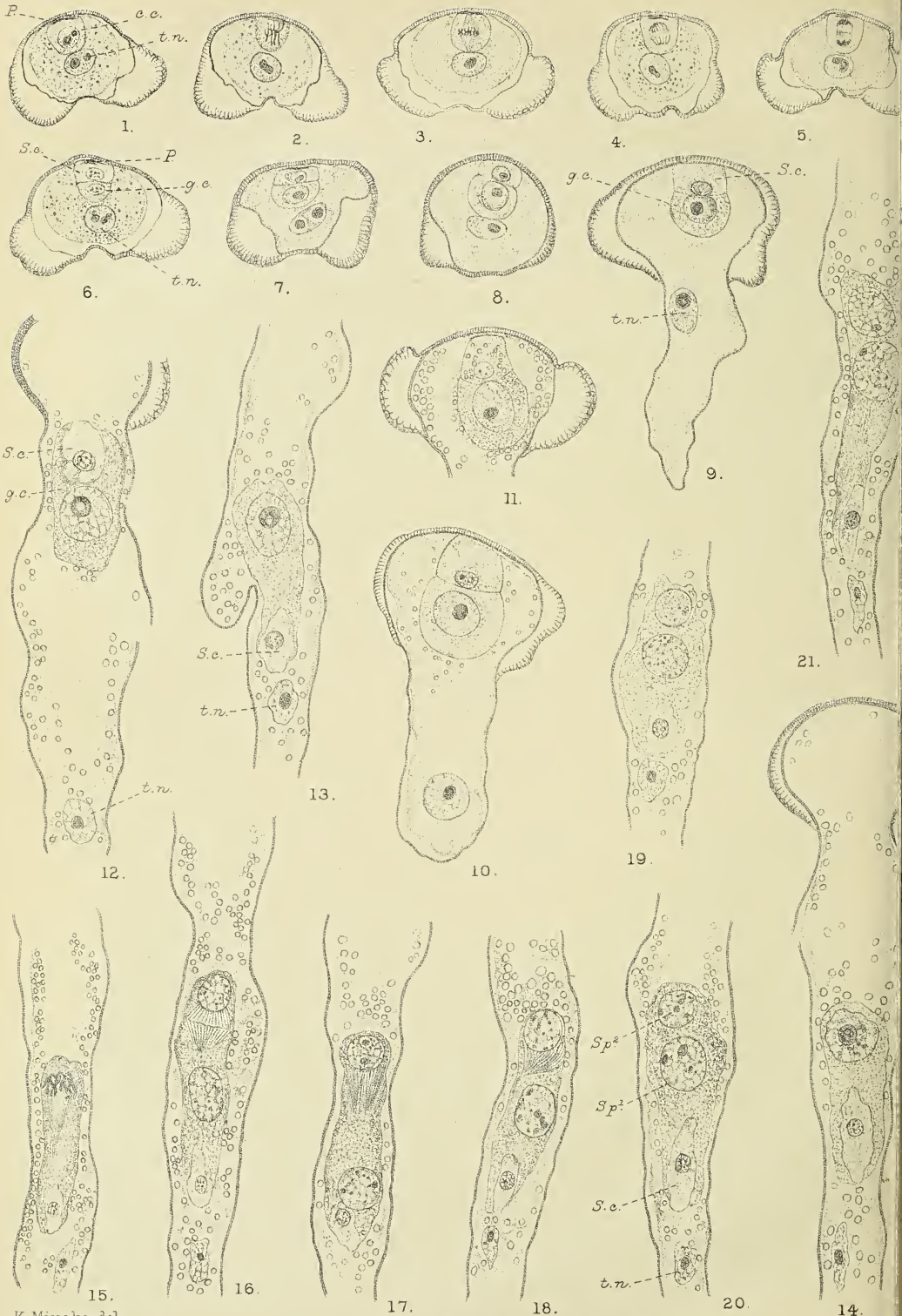
Fig. 58. A still later stage, showing the division of the nuclei of the upper incompletely walled cells.  $\times 110$ .

Fig. 59. Formation of the proembryo is nearly completed; the nuclei of the lower tiers are in the late telophase of division.  $\times 110$ .

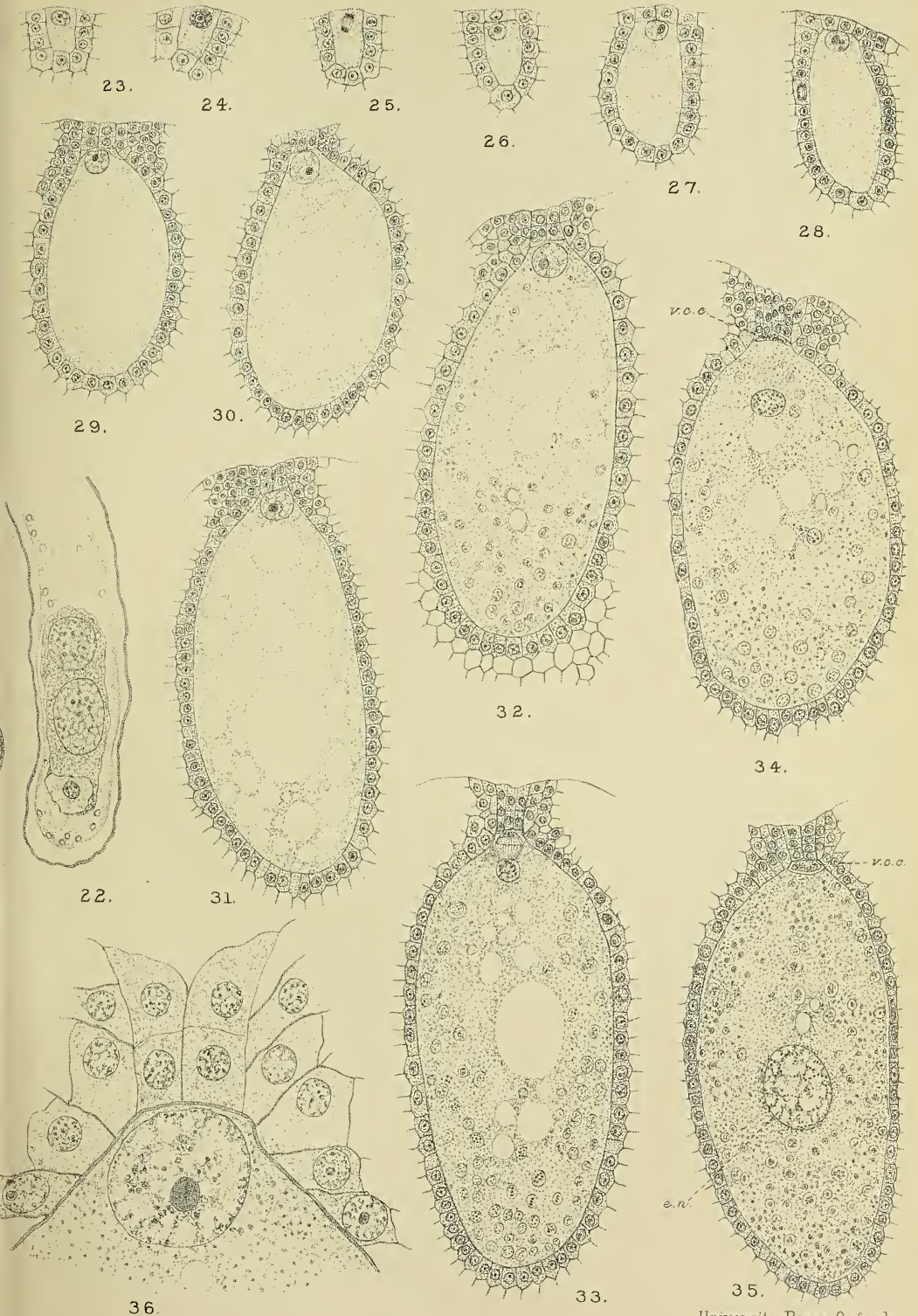
Figs. 60-64. Abnormal archegonia. Figs. 60, 61. Archegonia without neck-cells; in Fig. 61 the ventral canal-cell is formed at the side of the egg instead of the top. Figs. 62-64. Double archegonia in various stages of development.  $\times 110$ .







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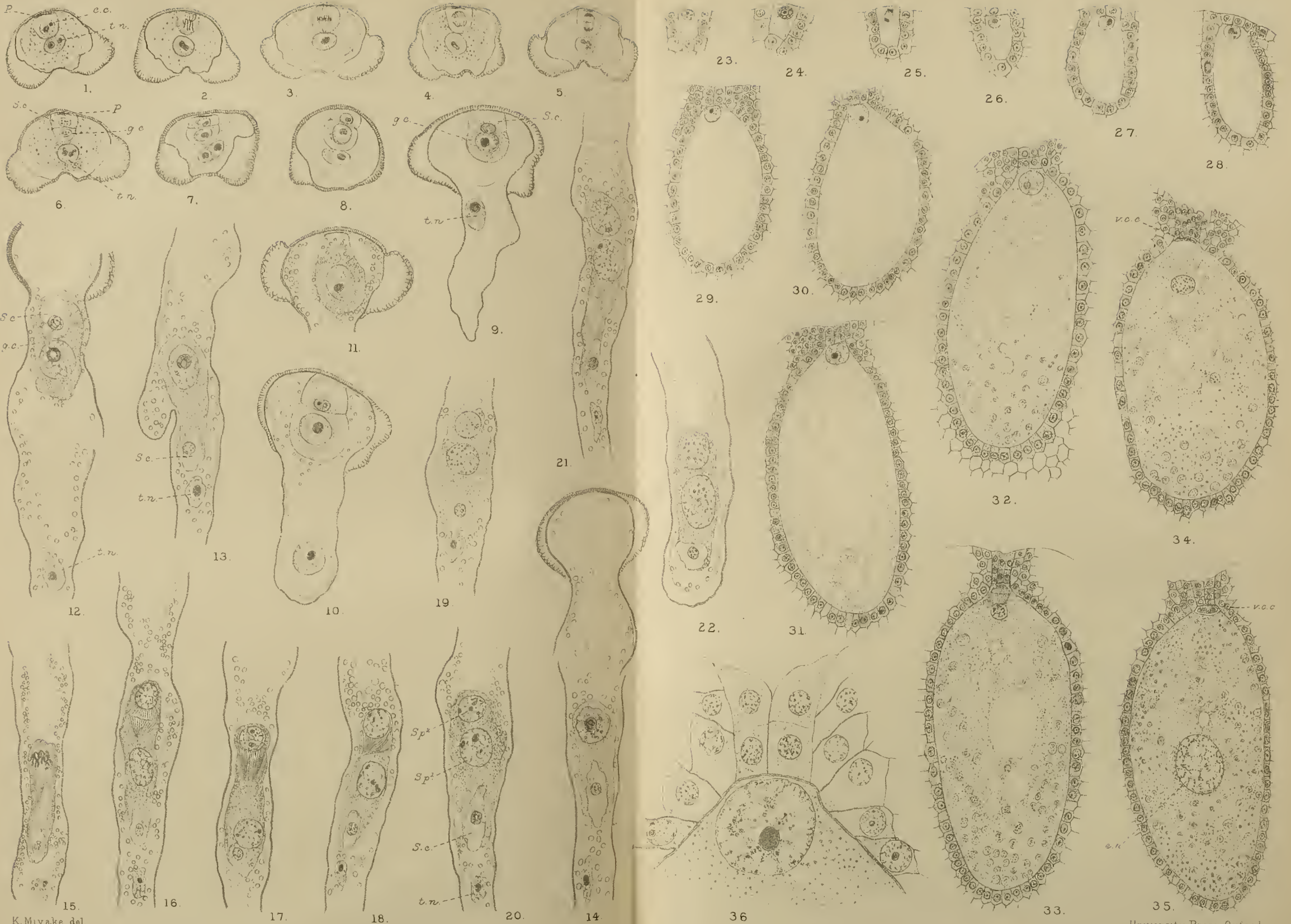
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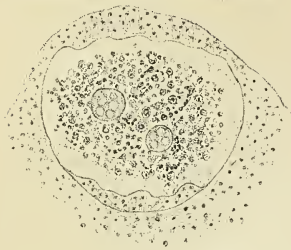


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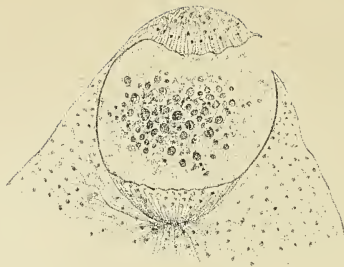




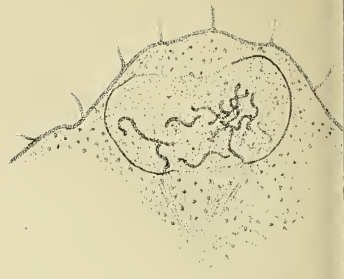




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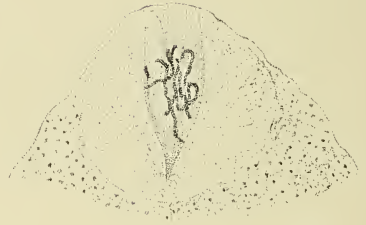
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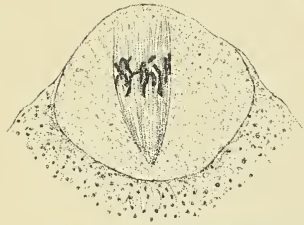
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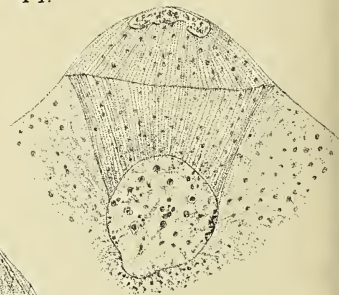
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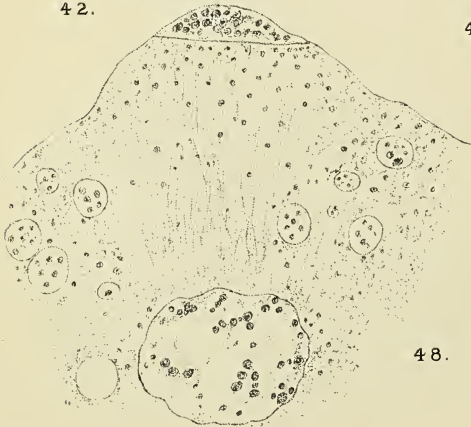
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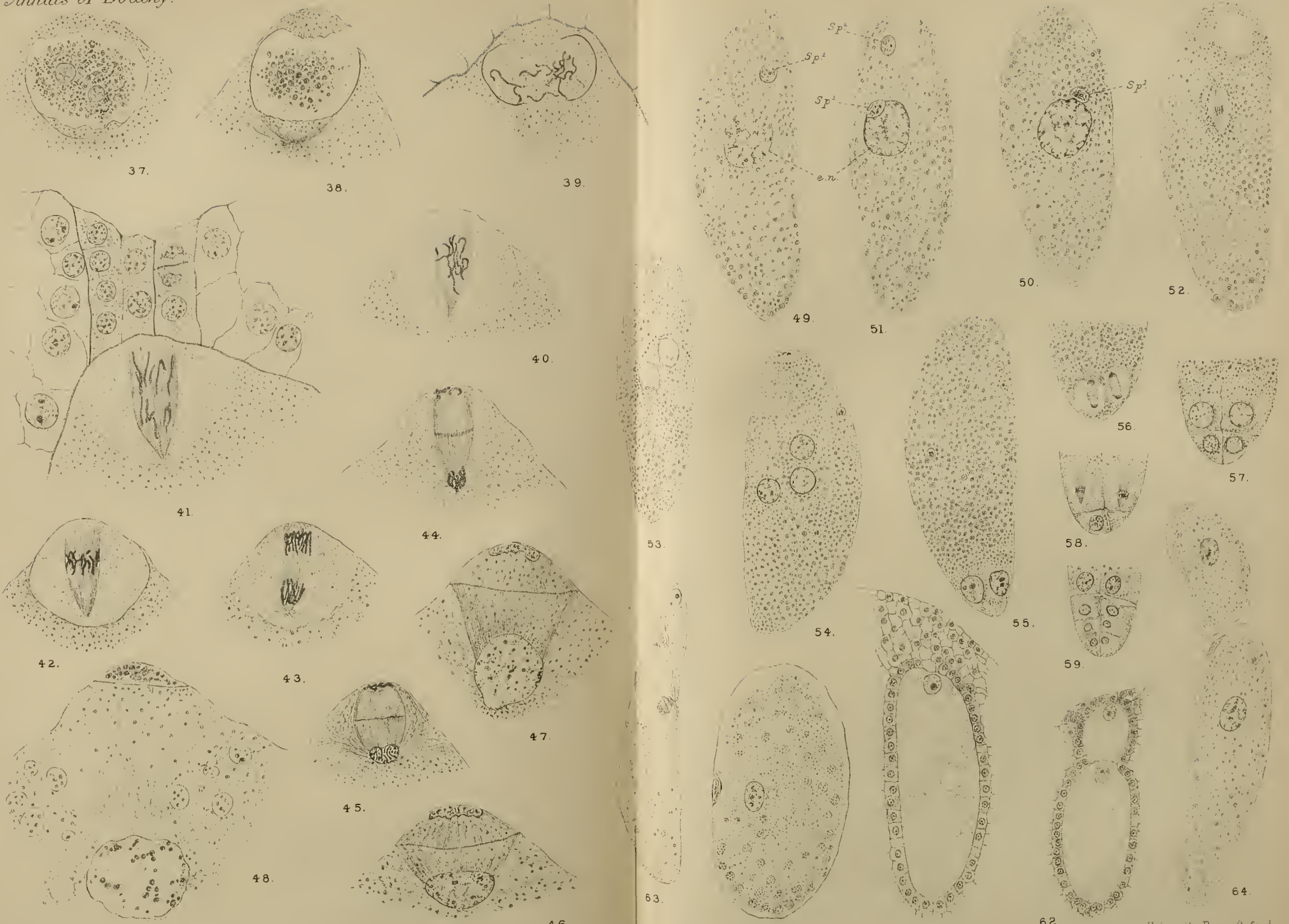
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MIYAKE.— PICEA EXCELSA.

University Press, Oxford.





# On some Diseases of the Sugar-Cane in the West Indies.

BY

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*Late Mycologist to the Imperial Department of Agriculture for the West Indies.*

—♦—  
With Plate XVIII.  
—♦—

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### I. INTRODUCTION.

IN the autumn of 1899 I began an investigation into the life-history of *Trichosphaeria Sacchari*, Masee (5), some of the earlier results of which were published in the 'Annals

of Botany' of December, 1900 (17). The Director of Kew (16) contributed a paper on the sugar-cane disease of the West Indies, in which the literature of the subject is discussed, to the same number of this Journal. Since the publication of these papers I have continued the investigation of this fungus and the 'rind' disease of the sugar-cane, the results of which are given below.

During the last three years my attention has also been directed to a malady of the sugar-cane in Barbados, known among the planters as 'root disease.' Although it was found that this 'root disease' is only a general term covering several apparently distinct diseases of the cane, nevertheless by far the greatest portion which came under my notice proved to be identical in character and to constitute a definite disease. As the facts brought to light in the investigation of this malady have some bearing on the relations between the host and the parasite, and on the influence of the environment on both, an account of this disease may prove of general interest.

## II. THE 'RIND' DISEASE OF THE SUGAR-CANE.

It will be convenient to deal first of all with *Trichosphaeria Sacchari*, Masee, the parasitism of its conidial forms on the sugar-cane, and the part played by these in the 'rind' disease. Afterwards another fungus connected with this disease will be considered.

### 1. The *Melanconium* stage of *Trichosphaeria Sacchari*, Masee.

A species of *Melanconium* has been recorded on dead and diseased canes in almost every country where the sugar-cane is cultivated. Thus in Engler and Prantl (18), *M. Sacchari*, Masee, is recorded on the sugar-cane in the Argentine. Apparently the same form is referred to by Masee (5) on the diseased sugar-canes forwarded to Kew from the West Indies in 1893. Massée (8) also records it as occurring on diseased

canes from Mauritius in 1894, and on specimens of sugar-cane in the Kew Herbarium received from India and Borneo. Cobb (4) describes it in New South Wales under the name of *Strumella Sacchari*, Cooke, as causing a disease of the sugar-cane in the Clarence River district of that colony. Prillieux and Delacroix (11) report its existence from Martinique, Mauritius, and Tonquin, under the name of *Coniothyrium melasporum* (Berk.), Sacc. Went (13) has noted a species of *Melanconium* on dead and badly-diseased canes in Java. Tryon (20) records *M. Sacchari* in Queensland. I have frequently noted the fungus on dead and badly-diseased sugar-canes in many parts of the West Indies.

The conidia of this *Melanconium* are formed under the rind of the sugar-cane in stromata, from each of which a black hair-like filament composed of agglutinated spores is extruded. The resulting appearance of the cane and the germination of the spores are correctly figured by Masee (5), and by Prillieux and Delacroix (11).

The spores germinate in about twenty hours after sowing, and develop a septate branched mycelium in which fusion of the hyphae is extremely common. In about five days one or more stromata are formed in the drop, and after seven days the conidia of the fungus can be detected. This result was almost invariably obtained in hanging drops when the food material consisted of:—

cane extract . . . . .	100 c.c.
gelatine . . . . .	15 grams.
tartaric acid . . . . .	.2 gram.
peptone . . . . .	.5 gram.

Beyond the formation of chlamydo-spores, figured by Went (13), in the hyphae, which were obtained in hanging drops, plate, and flask-cultures, I have never been able to induce this fungus to exhibit any other spore-formation than the conidia started with. Went (13) has described a third reproductive phase of the Java form, namely, large black globose conidia which are formed at the ends of the hyphae.



In my first paper (17) on this subject an experiment is described in which pieces of healthy unsterilized cane were split open and infected with *Melanconium* spores, and with mycelium developed from a pure culture, and in which micro- and macro-conidia developed five days afterwards. On this occasion the control canes showed no such spore-formation. On repeating this experiment several times, however, it was found that micro- and macro-conidia occurred as frequently on the control canes as on those infected with *Melanconium* mycelium and spores, so that no proof of a genetic connexion between these forms, *Melanconium* and the macro- and micro-conidia, can be obtained from the experiment above referred to. Indeed, unless it can be shown that macro- and micro-conidia are developed in sterilized media from a single *Melanconium* spore or its mycelium, these forms must be regarded as two different Fungi.

During the progress of this investigation it appeared interesting to determine what happens if flask-cultures of *Melanconium* spores are made in which macro- and micro-conidia are at the same time intentionally introduced.

Four sterilized flasks, containing the sugar-cane extract food-material mentioned above, were infected as follows (1) with spores obtained from a single-spore hanging-drop culture of *Melanconium*, (2) and (3) with similar *Melanconium* spores to which had been added macro- and micro-conidia from a single-spore hanging-drop culture, and (4) with similar macro- and micro-conidia only. The result was interesting. In two days the liquid in (2), (3), and (4) was filled with colourless mycelium while nothing could be detected in (1). In three days, macro- and micro-conidia, exactly like those started with, were developed in (2), (3), and (4), all three flasks being identical in appearance. On examining (2) the mycelium showed no traces of fusion of the hyphae, so characteristic of *Melanconium*, but the formation of macro- and micro-conidia was extremely abundant. In seven days, stromata of *Melanconium* were evident on the surface of (1), but no formation of these bodies was noted in (3), which was

to all appearances identical with (4). When allowed to compete together for the same food-material the macro- and micro-conidia vanquish the more slowly growing *Melanconium* form.

A corresponding result was obtained when sterile cane-slabs were infected in a similar way to the flasks above. Hence it is evident that if the results of flask-cultures of *Melanconium* spores are to be of any value in showing a genetic connexion between this form and the macro- and micro-conidia, such flasks must be infected from an undoubted pure culture, such as a hanging-drop colony developed from one *Melanconium* spore.

The degree of parasitism of the West Indian *Melanconium* was next investigated. In my previous paper (17), infection experiments on healthy sugar-canes are described, in which spores of this form from a pure culture were found to invade the tissues of a cane to some extent when introduced into fresh wounds, and the conclusion was drawn that this fungus behaves as a parasite and causes the common 'rind' disease of the sugar-cane. This conclusion has been found on further study to be inaccurate. Some of the infected canes in the experiments referred to were kept under observation for three months, when it was found on examination that the fungus had not spread more than 3 inches immediately above and below the wounds, and that it had not penetrated the tissues of the internode to any great extent. In no case could it be traced beyond the internode in which the wounds were made, neither did the canes in question show any of the well-known appearances of the 'rind' disease, such as the drying up of the leaves and the discoloration and shrinkage of the affected areas. On examining the mycelium it was found to have passed into a resting condition. The affected tissues were uniformly bright red in colour.

These results suggested the necessity of further infection experiments with this form. These were made, and the results were as follows:—

1. On November 27, eighteen healthy Bourbon canes were

selected. Six were used as controls and twelve were inoculated at wounds, six with *Melanconium* spores from a pure culture and six with similar spores and food-material. The places where the wounds were made were cleaned with alcohol, and flamed with a spirit-lamp. The holes were cut with a sterile knife, and after inoculation were bound up with sterilized tape which had been soaked in paraffin wax. The control canes were treated in a similar manner, but in this case no spores were introduced. On December 28 these canes were examined. In no instance had the mycelium spread to any extent, except immediately above and below the wound where it reached the nearest nodes. The affected tissues were bright red as before, and the canes exhibited no trace of the 'rind' disease. The controls showed no infection, although the cells round the wound were bright red and the bundles cut through showed gumming in the large vessels. Possibly this formation of gum is an adaptation on the part of the cane to prevent Bacteria and Fungi passing into the vessels where it is wounded.

2. On December 10, four healthy White Transparent canes were inoculated with *Melanconium* spores from a pure culture at wounds made with a sterile knife as above. Four other canes from the same stool were used as controls. Thirty days afterwards the canes were examined. In all cases the tissues were brownish-red above and below the wounds, but no difference was evident between the inoculated canes and the controls in this respect. On examining the inoculated canes it was found that the mycelium of the fungus had in all cases spread in the tissues immediately above and below the wounds as far as the nearest nodes, but it could not be traced beyond the vertical column of tissue containing the wound and bounded by the nodes above and below this aperture. The characters of the invading mycelium were identical with those of the hyphae developed in artificial cultures of *Melanconium* spores. In no case was any mycelium noted in the control canes.

3. On December 19, four healthy White Transparent canes



were doubly inoculated—at wounds in an upper and a lower internode—with actively growing mycelium of the fungus from pure cultures. Four other canes were used as controls. On January 22, the results were almost identical with those obtained above.

4. On December 21, four healthy White Transparent canes were doubly inoculated, at wounds made at an upper and a lower internode, with *Melanconium* spores from a pure culture. On January 27, it was found that the fungus had not penetrated beyond the column of tissue containing the wound and bounded by the nodes above and below. The control canes showed no infection.

These experiments point to the non-parasitic character of the West Indian *Melanconium* towards the sugar-cane. The behaviour of this form, therefore, closely resembles that of the Java *Melanconium* studied by Went (13), and the whole of the evidence points to its being a saprophyte.

A careful examination of a large number of canes attacked by the 'rind' disease showed that after the outer leaves begin to dry up at their margins—the first indication that canes are attacked by this disease—they gradually die in from four to eight weeks. When the leaves are about half dried up, the black filaments of *Melanconium* can be detected bursting through the discoloured areas of the stem. In many cases this is the only fungus which at this stage can be seen on the affected stems. The inoculation experiments described above, however, point to the conclusion that *Melanconium* cannot be regarded as the cause of the 'rind' disease.

The difficulty was solved by the study of another fungus which was found on the affected canes, and which in previous studies of the West Indian 'rind' disease had been overlooked. Before considering this fungus it remains to deal with the macro-, micro-conidial, and the ascigerous phase of *Trichospheria Sacchari*, Masee.

## 2. The macro- and micro-conidial stage of *Trichosphaeria Sacchari*, Masee.

This form is widely distributed throughout the West Indian Islands, and also occurs in Surinam, British Guiana, and Java. It has been described and figured by Went (7, 13, 14), under the name of *Thielaviopsis ethacetica*, Went. This observer found that it gave rise in Java to a disease of cane-cuttings known as the 'pine-apple' disease. Masee (5) has also described and figured it, and has shown that it is parasitic on the cane. The development of both macro- and micro-conidia from a single conidium of these two kinds is described in a previous paper (17).

In addition to the formation of these conidia at the ends of the hyphae, similar spores are also formed inside the vegetative hyphae. In rare instances chlamydospores are formed in the mycelium.

As in Java, the fungus in the West Indies by no means confines itself to the sugar-cane. It is common on bruised fruits such as bananas and pine-apples, and frequently destroys many of the pine-apples sent from Antigua to London during the voyage. It is probable that it gains access to them at bruised surfaces.

As mentioned above, this fungus is principally of importance in Java on account of its causing the 'pine-apple' disease of cane-cuttings, and, as mentioned by Went (13), is not very common on growing canes. Accordingly when examining some of the cane-cuttings which died out or failed to grow at all in Barbados during the planting-seasons in December, 1900 and 1901, and which amount to 25 to 50 per cent. of those planted, depending on the season, this fungus was especially looked for. In a large number of cases *Thielaviopsis* was found in these dead cuttings, and when it did not occur other Fungi were noted which appeared to have something to do with the arrest of growth of the cuttings. It appeared likely, after examining many hundreds of these dead cuttings, that Fungi are instrumental in destroying them. Of these, *Thielaviopsis* was met

with to the greatest extent. The disease of cane-cuttings in the West Indies appeared to be almost identical with that of Java.

It was first of all necessary to prove that the *Thielaviopsis* which attacks standing canes is identical in all respects with that found in diseased cuttings in the ground. The fungus from dead cuttings was cultivated from a single spore, and its development was found to be identical with that of the fungus in growing canes. Next the spores of the former fungus were placed on the cut ends of 100 cuttings before planting. Four weeks afterwards, all these cuttings were destroyed by the fungus, and on being split open were characterized by the odour of ethyl acetate and the development of numerous conidia of the fungus. A like number of uninfected cuttings were planted at the same time, all of which grew normally. Cross inoculation experiments were now made. The fungus from cuttings was found to infect the standing canes and that from the cane to destroy cuttings. Hence it was clear that only one fungus was being dealt with.

A study of the means of protecting cane-cuttings from this fungus (21) showed that dipping the cuttings in Bordeaux mixture and then tarring the ends is an efficient method. Cuttings treated in this way developed readily even after being dipped in water containing the spores of the fungus.

It was next desirable to repeat the experiments described in a former paper (17) on the parasitism of this fungus on the cane. Went (13) states that the fungus can behave as a wound parasite. According to Masee (5), the parasitism of the fungus would appear to be of a more pronounced character. It appeared necessary to find out whether the fungus can easily infect a cane at the old leaf-bases, and also to compare the infection of the cane in the parts rich in cane-sugar with those near the growing-point which are poor in this substance (12). The following experiments were therefore made:—

1. On December 26, four healthy canes were inoculated at wounds, both at an upper and a lower internode, with pure



cultures of this fungus, adopting the precautions described above in the experiments with *Melanconium*. In two of the canes inoculation was made with spores, in the other two with growing mycelium from pure cultures. Four similar canes were used as controls. On January 22, one of each of these canes was examined. At the lower internodes of each of the inoculated canes the mycelium had spread about 12 inches above and below the puncture, and macro-conidia were developed in the hollow centre of the cane. The affected tissues were slightly reddish, and the odour of ethyl acetate was very marked. At the upper part of the cane the fungus had, in each case, completely spread through the infected internodes, the tissues of which were black on account of the development of large numbers of macro-conidia in the cells. The control canes showed no infection. On January 27, the rest of the canes were examined. Both the inoculated canes gave practically the same results as those examined five days earlier.

2. On December 26, spores from a pure culture were placed on the uninjured leaf-bases at upper and lower nodes of two canes. On January 2, one of these canes was examined, when it was found that infection had taken place at the two nodes. At the lower node, the mycelium of the fungus had invaded about 3 feet of the cane. Macro-conidia were developed in the centre, and the odour of ethyl acetate was evident. At the upper node about 6 inches of the stem were infected, and the tissues were black through an excessive development of macro-conidia in the cells. The other cane was examined on January 27, when it was found that infection had only taken place at the upper node, when about 8 inches of the cane were invaded as in the previous case.

3. At the same time spores and food-material were placed on the uninjured internodes of four sound canes and covered up with waxed tape. A month afterwards no infection could be detected.

The result of these experiments leaves no doubt that *Thielaviopsis* is capable of pronounced parasitism on the

sugar-cane, and can infect both at wounds and at old leaf-bases. The contrast between the behaviour of this form and *Melanconium* is most marked.

The fungus has been cultivated in Barbados for two years under a wide range of conditions as regards food-materials, but in no case has any other spore-formation than those mentioned above been detected. Flask-cultures have been kept under observation for eighteen months, but no trace of *Melanconium* spores or perithecia has been observed. These results agree with those obtained by Wakker and Went (14) in Java.

3. The ascigerous stage of *Trichosphaeria Sacchari*,  
Masseé.

Several thousands of rotten canes have been examined in Barbados and other islands during the last three years, but in no case have the perithecia described for this form been found. Several other Ascomycetes, however, have been noted, one of which is distinctly parasitic. The perithecia of this fungus, however, are formed underneath the rind of the cane.

4. The fungus causing the 'rind' disease<sup>1</sup> of the  
Sugar-Cane in the West Indies.

Very characteristic are canes attacked by the 'rind' disease in the West Indies. In Barbados the disease appears about November or December, and increases rapidly in amount up to March and April, when the canes are reaped. It makes its appearance earlier in plant-canes than in ratoons, and attacks sweet canes, like the Bourbon, to a much greater extent than some of the seedlings. I have, however, noted the disease on a large number of the seedling and other canes, which have now almost entirely replaced the Bourbon in Barbados on account of the ravages of this disease. It is quite common on the White Transparent. The first symptom of the malady is the drying up of the leaves, which commences

<sup>1</sup> As contrasted with the disease of cuttings caused by *Thielaviopsis ethacetica*.

at the margins of the older ones and gradually spreads to the centre of the bunch in from four to six weeks. As soon as this drying of the leaves is well marked, the stem of the cane shows a brown discoloration in one or more places, after which the rind shrivels up and the discoloration rapidly extends in all directions. On splitting such canes the tissues are seen to be of a general reddish colour, in which darker red areas can be seen. Very frequently these darker regions contain definite white centres, elliptical in vertical section. The major axis of the ellipse is at right angles to the main axis of the cane stem. The appearance (Fig. 2) coincides exactly with that figured by Went (6, 14) in his writings on the 'Red Smut' disease of Java. Infection seems to take place in many cases at the tunnels made by boring-insects, but in a good many instances it appears to have started at the old leaf-bases. Two Fungi are very common on such diseased canes—the *Melanconium* described above, and a second form which is not very often seen in the earlier stages. This second form occurs as minute, black, velvety patches on the outside of the cane, generally just below the leaf-base, or on the sleeping roots above the node (Fig. 1). These patches are stromata bearing dark hairs. At the base of the hairs, crescent-shaped, unicellular conidia are given off from short basidia. The infected tissue contains colourless mycelium, in which fusion of the hyphae is very common and in which the contents appear as a row of circular oily drops. In the older portions of the affected tissue, brown chlamydospores are to be seen in the hyphae, which also turn darker in colour. All these appearances agree with the fungus causing the 'Red Smut' disease of Java described by Went (6, 14).

In view of the result of the inoculation experiments with *Melanconium*, described above, it appeared desirable to cultivate this second fungus and to study its parasitism. This was done, and hanging-drop cultures containing a single spore were made by Marshall Ward's method (3), using the cane-extract medium given above.



The spores germinate in three hours after sowing by sending out a colourless hypha from one end, after which a second hypha is developed at the other end. These grow rapidly, become septate, branch, and fuse very readily (Fig. 3). When three days old, conidia were developed from the mycelium by a process of budding. These conidia are smaller ( $2.5 \times 2.5 \mu$ ) than those formed at the stromata, and are identical with those produced in great numbers when a piece of fresh cane attacked by the 'rind' disease is split open and placed in a closed chamber. Stages in their formation are shown in Fig. 4. They vary very much as regards shape and size.

When five days old, dark-brown, irregularly-shaped chlamydospores were noted in the hyphae, especially at the ends. They measure  $1.5$  to  $2.5 \mu$  in diameter and are represented in Fig. 5.

When six days old, stromata appeared in the drops, at which sickle-shaped conidia, measuring  $30$  to  $45 \times 5 \mu$ , were formed. Stages are shown in Fig. 6. Only very rarely were the dark-brown hairs, characteristic of the stromata of the fungus on the sugar-cane, noted in these hanging-drop cultures. When they occurred they measured  $100$  to  $150 \times 4 \mu$  and were four to five septate. No further developments were observed in hanging drops.

Next, cultivations of this fungus were made by infecting sterile pieces of sugar-cane with spores from a hanging-drop culture grown from one spore. In three days the slabs were covered with a beautiful white mycelium, and in fifteen days dark-coloured dots were noted, which were found to be stromata bearing dark-brown hairs and numerous conidia exactly like those on the cane.

These cultures were repeated several times, when it was found that the time of appearance of the black stromata varied between five and eighteen days according to the size and character of the cane-slabs.

A similar result was obtained in flask-cultures, using the cane-extract medium. Stromata appeared on the surface of the flasks in from fifteen to twenty days.

In tubes containing 10 c.c. of the cane-extract, a similar development occurred, except that stromata appeared on the surface in from four to five days.

In none of the cultures were any further spore developments noted, and no trace of the formation of any of the phases of *Trichosphaeria Sacchari*, Masee, was detected.

It now remained to perform inoculation experiments with pure cultures of this fungus on healthy sugar-canes. These were as follows:—

1. On December 4, six healthy canes in the same stool were inoculated at wounds made in internodes about the middle of the stem and also at upper leaf-bases, with spores from a pure culture of the fungus. The precautions, described above, to prevent the entry of other spores were taken, and six other canes were used as controls. On December 10, one of the inoculated canes showed that infection was taking place at the wound, but no result was observed at the leaf-base. On December 16, a second cane was examined, when distinct infection was observed in the tissues of the internode where the wound was made and also at the upper leaf-base. On December 26, two more canes were examined. No infection was detected at the leaf-bases, but at the wounds very definite indications of the 'rind' disease were noted. The leaves were beginning to dry in the characteristic manner, and on splitting open the canes infection was apparent in four of the internodes, where the red blotches, with white centres, were evident. The invading mycelium was characterized by its branching and oil-drops, and agreed exactly with that seen in canes attacked by the 'rind' disease. The remaining two canes were also drying at the top and were obviously infected at the wounds. They were used for the experiments with *Melanconium* described below. In this experiment one of the controls became infected with the fungus; the other five gave negative results.

2. On December 10, six canes were inoculated in a similar manner to those in the above experiment, and six others were used as controls. On December 28, one of the inoculated

canes showed infection at the wound, but not at the leaf-base. On January 22, two of the inoculated canes showed that at the wounds the fungus had invaded two of the internodes and had produced the characteristic red blotches with white centres. In one case infection had also taken place at a leaf-base. The other three canes, in which infection at the wounds was very evident, were used for the experiments with *Melanconium* described below. The control canes gave negative results.

3. On December 19, four canes were doubly inoculated at wounds made in an upper and a lower internode, with mycelium from a pure culture of the *Colletotrichum*. As before, controls were employed and precautions taken to introduce only one fungus. The object of this experiment was to determine the comparative effect of the fungus on those portions of the cane which are very rich and very poor in sugar. On January 22, a cane was examined, when it was found that the fungus had invaded 16 inches of the upper part, which showed the characteristic markings, but had not spread beyond the internode at the lower wound. The remainder of the canes were examined five days later. In all cases infection had taken place to about the same extent, the length of cane affected varying from 18 to 24 inches. The characteristic red blotches with white centres were abundant.

4. On December 31, four canes were inoculated with spores from a pure culture of the *Colletotrichum* as follows. In two cases the canes were doubly inoculated at upper and lower leaf-bases, and in the other cases at wounds in upper and lower internodes. Two control canes were also used. On January 22, the canes which had been inoculated at leaf-bases showed that infection had taken place at both the upper nodes and at one of the lower nodes. At the upper part of both canes the stromata of the fungus were abundant on the affected rind at the nodes above and below the point of inoculation. In each case about 9 inches of the cane were affected and the red blotches were abundant. A similar



result was observed in the case of the cane where the fungus had also infected at a lower node but no stromata were evident on the rind. On January 23, the canes inoculated at wounds showed that in all cases infection had taken place, and stromata had formed on the outside at the upper affected regions. From 12 to 18 inches of the cane were invaded at each wound. The controls gave negative results.

The above inoculation experiments were carried out with canes during the ripening period and after active growth in size had ceased. The results obtained, while indicating that the fungus is a wound parasite, nevertheless do not conclusively show that it is capable of overcoming tissues still capable of growth and development. Accordingly, further experiments were made on plant-canes<sup>1</sup> about six months old which were in a vigorous state of growth. In all cases inoculation was performed in developing internodes which were then not more than 1 inch in length. The experiments were as follows:—

5. On June 20, three young canes were inoculated by placing seven days old, actively growing, mycelium, from a pure culture in the sugar-cane extract medium, into wounds made in the centre of a lower internode then about three-quarters of an inch in length. Care was taken to introduce only one fungus and to shut off the apertures from the air by means of sterilized waxed tape. Three similar canes were used as controls. Two months afterwards the canes were examined. In the first case, the infected internode had grown to  $2\frac{1}{2}$  inches in length, and on splitting open the cane this and the internode below were found to be generally reddish in colour with the elliptical white areas, characteristic of the 'rind' disease, well represented. About 4 inches of the cane were invaded by mycelium, which agreed with that of *C. falcatum*. A closely similar result was obtained in the other two inoculated canes, but the controls showed no infection.

<sup>1</sup> The first crop of canes raised from cuttings are known in the West Indies as 'plant-canes.'

6. On June 23, the above experiment was repeated on two similar canes. Two months afterwards two internodes were, in each case, found to be completely invaded by the fungus which had produced all the characters of the 'rind' disease.

7. On June 27, four canes about six months old, growing in tubs, were inoculated with pure cultures of the fungus, three at wounds in the internodes, the other at a leaf-base. On August 19, one of the canes inoculated at a wound exhibited the characteristics of the 'rind' disease in the infected internode, but the other three and the controls gave negative results.

8. On June 23, three vigorous canes about six months old, growing in the field, were inoculated at leaf-bases, from which the adhering green leaves had been torn, with six days' old mycelium from a pure culture. Afterwards the nodes were covered with sterile waxed tape. On August 19, one of the canes gave a negative result, but the other two showed distinct infection. In one case, 5 inches of the cane were invaded, in the other about  $2\frac{1}{2}$  inches.

These experiments show conclusively that the *Colletotrichum* is capable of more than mere wound parasitism. It is able to overcome tissues capable of active growth. At the same time it can thrive readily as a saprophyte in artificial media and pass through its whole development thereon. It occurs in the West Indies every ripening season as a parasite. It would seem to be therefore intermediate between a hemi-saprophyte and a hemi-parasite and not to belong strictly to either of these classes.

Further, it is clear that this fungus and not *Melanconium* is the cause of the 'rind' disease of the sugar-cane.

On referring this fungus to its systematic position it is evident that, in the absence of any higher fructifications than the stromata described, it must be placed in the *Fungi Imperfecti* and that it falls into Corda's genus *Colletotrichum* (18). From its characters and its parasitism on the sugar-cane it evidently agrees with *C. falcatum*, Went (6, 14), a form which causes the 'Red Smut' disease of the sugar-cane in Java.

Thus the 'rind' disease of the West Indies and the 'Red Smut' of Java are identical. This conclusion was strengthened by the examination of specimens of sugar-cane, said to be attacked by 'rind' disease, from other parts of the West Indies and Surinam. In all cases the characters of the disease were identical with those given above, and most of the specimens showed both *Melanconium* and *Colletotrichum*. Further, careful examination of many of the cane-fields of St. Vincent in January, 1902, where the Bourbon is almost exclusively cultivated and where the 'rind' disease makes its appearance every year in December, showed that the disease was identical with 'Red Smut' and that the fungus *Colletotrichum falcatum* was present.

The fungus appears to be widely distributed. In addition to the West Indies it occurs in Java, Madras (19), and also in Queensland (20).

The remedies suggested by Went (13) for the treatment of this disease in Java would seem to apply to the circumstances of the West Indies.

Since *Melanconium* always appears on canes attacked by the 'rind' disease it seemed probable that it must infect the canes after they are diseased. Accordingly the effect of this fungus on a part of a sugar-cane attacked by *Colletotrichum* was compared with its effect on the still healthy portion. The results were as follows:—

1. Two canes which had been inoculated on December 4 with spores of *Colletotrichum*, and which showed from the outside that infection had taken place, were reinoculated on December 21 at the affected region and also near the base, in the still healthy tissue, with spores of *Melanconium* from a pure culture. On January 23, it was found that at the upper part numerous stromata of *Melanconium* had developed, but at the base infection had not taken place.

2. On December 19, three canes, which had been inoculated at the upper parts with spores of *Colletotrichum* nine days previously, were reinoculated with *Melanconium* spores from a pure culture. A second inoculation with these spores was



made at the base of these canes in the still healthy portion. On January 27, *Melanconium* stromata were evident round the upper wounds, but no infection had taken place below.

These experiments show that the part played by *Melanconium* in the 'rind' disease of the sugar-cane is that of a follower of *Colletotrichum*, and that it only invades previously diseased canes.

### III. A ROOT DISEASE OF THE SUGAR-CANE.

Since the rainfall of Barbados and the local agricultural practice have a distinct bearing on the root disease under discussion, some reference to these subjects seems necessary.

There is a well-marked dry season in the spring as will be seen from the following table, in which the mean monthly rainfall at one of the stations is given from 1892 to 1901. The average annual rainfall during this period was 62.85 inches, but the total precipitation on the highlands (above 400 feet) was about 10 inches more than that on the lowlands.

*Mean monthly rainfall from 1892-1901 both inclusive.*

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Rainfall in inches.	3.12	1.65	2.72	2.53	3.42	5.03	6.09	8.24	9.08	7.28	7.88	5.81

Planting is usually carried out in November and December and reaping takes place about eighteen months later, from March to June in the second year after planting. Usually the old stumps are allowed to produce a second crop of 'rattoons,' the growing period of which is about a year. On the red soils in the highlands, two or three of these ratoon crops are obtained, but in the lowlands the canes only ratoon once at the most.

As a rule the first crop of canes is healthy, at any rate till growth is completed and the 'red smut' disease makes its

appearance during the ripening period. Sometimes, however, the young canes do not respond to the early rains of the wet season in June and July, practically making no growth and remaining dwarfed. Instead of the twelve to fourteen broad green leaves of normal canes the affected shoots bear from six to ten pale-green narrow leaves, the oldest showing a tendency to dry up from the apex and margin. Even after rain, when the soil contains much moisture, the young leaves in the centre of the tuft assume the vertical position and partly fold up by the inrolling of the two halves of the lamina, in the manner described and figured by Wakker (9). This device for preventing over-transpiration is only made use of by healthy canes during drought, but in those in question it is constantly apparent and at once suggests water starvation. The stunted canes never recover, but struggle on, throwing up large numbers of shoots from the buds at the base of the stem. These new shoots in turn become affected like the parents and a clump of dwarfed canes results, resembling one of the phases of the 'sereh' disease of the sugarcane in Java (14). The diseased canes occur in circular patches, which, however, are not sharply marked off from the normal areas, but gradually shade off into them.

It is in the second-crop canes or ratoons of the lowland districts especially that the trouble indicated above is to be seen on the large scale. Often the whole field is uniformly affected, and the contrast between it and a neighbouring first-crop field is most striking. In the former case, the narrow, pale-green, erect and partly folded-up leaves are few in number and the clumps of cane do not meet in the rows; in the latter, the leaves are broad, dark-green in colour, and bend to the breeze with the lamina flat and fully exposed to the light. Here the canes meet fully in the rows, and, when viewed from above, look like solid masses of green. The striking difference between first and second crops on the lowland areas is so general that it seems to have been accepted by the planters as part of the ordinary course of things. The general impression seems to be that the soil is not suited

to ratoons. On the red soils in the highland districts this dwarfing of the ratoons, although to be noted here and there in the second crop, is not so general as on the black soils of the lowlands. It makes its appearance, however, to an increasing extent in the third and later crops, and finally leads to the throwing out of the fields. Locally, the red soils of the highlands are known as ratooning soils, while those of the lowlands, although giving very good first crops, are not regarded as specially suitable for a second crop.

The comparative failure of ratoon crops was found on examination to be due, in most cases, to a definite root disease, some account of which is given in the following.

#### **i. Characters of the Disease.**

Apart from the peculiarities of the leaves of the dwarfed canes and their marked tendency to throw up shoots from the base, which have been already referred to, there are other characteristics to be observed on a closer examination. As a rule, a healthy cane sheds its old dry leaves as growth proceeds, but in those in question the leaf-sheaths of the dead lower leaves adhere firmly to the stem, being cemented thereto by a white, musty smelling, fungoid growth. Such canes can moreover be pulled out of the ground with ease, when they are seen to possess very few roots. They are besides very much lighter in weight than healthy canes of the same size. On stripping off the dead leaf-sheaths at the base of the stem, it is found that most of the roots have either not developed or else have ceased to grow when about a  $\frac{1}{4}$  to  $\frac{1}{2}$  an inch in length, when they are brown in colour and corky to the feel. The rind of the cane immediately over the undeveloped roots is marked by brownish or blackish spots. Considerable force is required to remove the leaf-bases from the part of the stem covered by the soil and to clear the nodes, as the white fungoid growth referred to binds the whole into a solid mass. A portion of the lower part of a sugar-cane stem showing the abnormal development of the lower buds and the aborted roots is shown in Fig. 7, while in



Fig. 8 the dwarfed roots from a similar portion of an affected cane are shown on a larger scale. On splitting open the lower portions of the stem, the vascular bundles are often reddish, while towards reaping-time cavities occur in the internodes, in which, when the canes are nearly dead, white mycelium can be detected with the naked eye. The still living leaf-sheaths are covered with a layer of white matted mycelium, and reddish spots are common thereon. Black elliptical areas, surrounded by a reddish border, are also abundant on the leaf-sheaths, which are in some cases slimy to the feel on the inside after rain, when hard, yellowish, spherical bodies, about the size of a small pea, attached to the outside of the leaf-sheaths by whitish threads, are to be seen. Colonies of small, yellowish-white toadstools are to be met with after heavy rains on the lower parts of the diseased shoots (Fig. 9). These persist only for a day under the most favourable circumstances, and for this reason appear to have escaped attention hitherto. Specimens for examination, or for the production of spores, are best collected as soon after day-break as possible, as the sun dries them up very rapidly.

All these characters are to be made out on canes affected by this disease. The matted white mycelium on the dead leaf-sheaths, the reddish areas on those still alive, and the aborted and undeveloped roots are constant characters, while the black elliptical areas, although common, are not always present. The yellow spherical bodies and the slimy leaf-sheaths are comparatively rare.

The white fungoid growth which cements the old leaf-sheaths to the stem proved to be a branched, septate mycelium, very variable in diameter, which exhibited the clamp-connexions chiefly met with among the Basidiomycetes.

A similar mycelium was found around the aborted roots, in fact, these were often imbedded in a thick felted mass of hyphae. It was further detected in great quantity between the still living leaf-sheaths and in the cells of the reddish areas noted on these, and also in the tissues of the aborted roots themselves.

Longitudinal sections of the dwarfed roots showed that the root-cap and cortex were invaded in all directions by a mycelium characterized by clamp-connexions and brown, thick-walled, chlamydospore-like bodies (Fig. 10). These tissues and the whole of the periblem were dead, much disintegrated and dark brown in colour in many places. The pleurome was often invaded by similar mycelium, and the growing-point destroyed. Attempts were frequently made by such roots to branch, but the secondary roots were usually destroyed before the cortex of the parent root was penetrated. The beginning of such attempts is shown in Fig. 11.

The undeveloped roots, which were characterized by brown marks in the rind of the cane immediately over them, were found to be destroyed in a very similar manner to those in which growth had been arrested shortly after penetration of the rind. Longitudinal sections showed that the periblem, and often the pleurome too, were invaded by the above-described mycelium. The root-cap, digestive sac, and growing-points were in all cases destroyed (Fig. 11). The mode of entry of the fungus into the developing root varies. In some cases it passes from the exterior through the digestive sac and root-cap and invades the growing-point tissues direct. In others, it passes between the young root and the surrounding tissue of the stem and invades the periblem from below, passes upwards, and finally overcomes the growing-point.

No matter whether the roots are destroyed just after penetration of the parent stem or before this is accomplished, the result is the same, namely, the loss of a possible means of supplying the cane with water and minerals from the soil. When, as in most cases of this disease, by far the greater number of the roots in the below-ground portion of the stem are destroyed in this way, as well as those for some distance above the ground, it is clear that recovery is out of the question.

If the development of the shoots which arise from the buds at the base of the parent stem is followed, it is found that here too the leaf-sheaths become cemented to the stem by

the white mycelium, and that the majority of the roots are destroyed as before. It sometimes happens that these shoots die off, when they are found to be penetrated by this mycelium in all directions.

The below-ground portions of the older shoots sometimes contain this mycelium and show reddening and extensive gumming of the vascular bundles. As the reaping-period approaches and the supply of water in the soil falls off, large cavities are formed in the centre of the internodes, in which, in cases where the canes are drying up, the white mycelium luxuriates. In a short time such dying canes become infected by the saprophytic fungus *Melanconium* referred to above.

The dark-coloured, elliptical areas on the living leaf-sheaths of many of the canes attacked by this disease were found to be due to the conidiophores and conidia of the fungus *Cercospora vaginae*, Krüger, which is described and figured by Wakker (14) and also by Krüger (15). As in Java, this parasite is extremely common in the West Indies on the leaf-sheaths of the sugar-cane, and is to be met with on both vigorous looking and obviously diseased canes. As it spreads from the older to the younger leaf-sheaths, when these are in contact, with the greatest ease, canes once infected are never able to get rid of this parasite. As the upper portions of the cane embracing the main growing-point ('tops') are generally used as plant-material, and as the leaf-sheaths adhering to the cuttings are often covered with this fungus, it is easy to understand that the young shoots become infected and that this disease is reproduced in every new stand of canes. By following the young shoots arising from the cuttings it can be readily seen that reinfection takes place almost before the young stems are above the ground, and that as far as this disease is concerned, parasite and host are planted together.

The hard, spherical, yellowish, pea-like bodies noted on the leaf-sheaths of some of the diseased canes were found to be sclerotia. Identical structures, accompanied by reddening of the leaf-sheaths and sliminess on the inner side thereof



after rain, were found on other canes not attacked by root disease. In such cases the rind of the cane below the internode was bright red in colour, partly disintegrated and invaded by a mycelium identical with that attached to the sclerotia. The characters of these sclerotia and of their mycelium and the appearance of the affected canes were found to agree in all respects with Went's 'red-rot' disease in Java (14).

The occurrence, therefore, of the sclerotia and of *Cercospora vaginæ* on the leaf-sheaths of the diseased canes is accidental. It is, however, a good example of the simultaneous existence of two or more parasites on the same cane—a frequent circumstance in the cane-fields of the West Indies.

The toadstools noted on the diseased canes are yellowish-white in colour, the pileus varying in diameter from 10 to 18 mm.; the curved stipe being about equal in length to the diameter of the cap (Fig. 9). As these fructifications reach maturity, the pileus becomes flattened, and in some cases depressed to such an extent that the toadstool has the shape of a wine-glass, the gills being on the outside of the cup. The lamellæ run right up to the centrally-disposed stalk, but are not attached thereto. They are arranged in a stellate manner and may branch once or twice towards the margin of the pileus. The spores are milky white in the mass, irregular in shape with one end somewhat elongated. They arise from the basidia in the usual manner, measure 15.5 to 18 by 4.5 to 5  $\mu$ , and, when fresh, contain vacuolated protoplasm and oil-drops. The toadstools dry up quickly and become tough, but they revive when moistened. These characters indicate that this form belongs to Fries' genus *Marasmius*, which, according to Saccardo, includes 450 species, mostly saprophytes of the tropics and sub-tropics.

It appeared probable that there was a genetic connexion between these toadstools and the white mycelium with clamp-connexions found on the old leaf-sheaths, in the aborted roots and in the reddish-coloured portion of the still living leaf-sheaths. Further, there appeared to be some likelihood that

the mycelium referred to was the cause of the non-development of the majority of the roots, and therefore of the root disease under consideration. Since *Cercospora vaginæ* and the sclerotia fungus do not always occur on the diseased canes, but give rise to separate diseases, and moreover as their mycelium does not exhibit clamp-connexions, these fungi could be left out of consideration until the part played by the apparently basidiomycetous mycelium had been investigated. Steps were therefore taken to obtain pure cultures of the toadstool spores and of the white mycelium, and also to perform inoculation experiments therewith on healthy canes.

## 2. Cause of the Disease.

Spores were obtained by placing fresh toadstools in sterilized glass dishes with grooved covers. In a few hours a white spore print appeared on the floor of the chamber, the spores of which were employed in making hanging-drop cultures.

In the cane-extract food-material given above the spores germinated in ninety minutes, sending out a narrow germ-tube, which quickly branched and into which the contents of the spore passed. The earlier stages in the process are shown in Fig. 12. In two days, stellate colonies of colourless, branched, septate mycelium developed, the protoplasm of the apical ends being brilliant and homogeneous. When three days old, the mycelium began to grow down into the air and to exhibit abundant fusion of the hyphae. At this point the formation of clamp-connexions was first noted. Stages in the process, which occupied about an hour, and which agrees with that observed by Brefeld (1) in the case of *Coprinus stercorarius*, are shown in Fig. 13. The development of aërial hyphae continued, until a dense tuft of pure white mycelium resulted. When about seven days old crystals began to be formed at the growing ends of the hyphae, and after twelve days some of the filaments deliquesced into a gelatinous-looking material, which probably explains the cementing

action of the fungus on canes. Several of the drops contained one spore, and this fact and that of the aërial development of the hyphae in the hanging drops enabled pure cultures to be obtained.

These were made on pieces of sterile cane, on bundles of sterile leaf-sheaths, and also with wire baskets of earth containing a portion of a young cane-shoot, the whole having been sterilized. In all cases the results were the same, namely, the production of a brilliant white mycelium, which showed a tendency to collect into feathery strands on the walls of the glass tubes and which, in several cases, produced dark-coloured, branched rhizomorphs when about nine months old (Fig. 14). Portions of these and of the white mycelium in the culture when ten months old were found to be alive, and to develop a growth of white mycelium when transferred to a fresh substratum. Thus the fungus can readily pass into a resting condition, a fact of some significance from the practical standpoint as will appear later.

Cultures were now made with the white mycelium characterized by clamp-connexions found on the leaf-sheaths of diseased canes. By placing some of these leaf-sheaths in a moist chamber the white mycelium thereon produced tufts of hyphae in a few hours, which were used to infect hanging drops. In this way cultures were obtained which were uniform in appearance, and which agreed with those from the toadstool spores. The further results on cane-slabs, cane-trash, and in the sterilized baskets of earth were identical with those obtained above with the hyphae from the toadstool spores. It appeared, therefore, very probable that the toadstools are genetically connected with the white mycelium on the leaf-sheaths of the diseased canes. Complete proof was obtained later when identical toadstools were developed from the mycelium derived from spores and from that on the leaf-sheaths.

The rhizomorphs (Fig. 10) obtained in these cultures were found to have a definite rind made up of dark-brown, thick-walled, septate hyphae arranged somewhat irregularly, which



enclosed a medulla of thin-walled, parallel, septate, colourless mycelium. The dark strands shaded off into loose, white, feathery growths. These latter are very common in cultures and also on cane-cuttings infected with this fungus. They differ markedly from those associated with the sclerotia of Went's 'red-rot' disease.

In no case were toadstools obtained in the above cultures. They were, however, produced in the infection experiments described below.

With one exception three series of inoculation experiments were made in which the infecting material was obtained from different sources in each case. Thus, in addition to using the cultures obtained from a single toadstool spore and those from the white mycelium on the leaf-sheaths, pieces of the leaf-sheath, obtained from diseased canes, were also employed.

*Experiment 1.* In the first instance, three young ratoon shoots, about a foot high, were selected for the experiment. After washing with water, portions of six days' old mycelium (developed from a spore) growing in the cane-extract medium given above, were placed in the axil of one of the lower leaves of two of the shoots and the whole was covered with a clean lamp chimney, cotton-wool being packed around the shoot at the upper end. The third shoot was used as a control. In seven days, the leaf-sheath, on which the mycelium was placed, began to turn yellowish-red, and in fourteen days the whole of this and the next sheath above were covered with a white film of matted mycelium. Reddish areas, where the fungus had invaded and destroyed the tissues, were abundant, and the leaves attached to these sheaths were rapidly drying up. Sections through the red portions of the leaf-sheaths showed that the cells were penetrated by a mycelium, characterized by clamp-connexions and dark-brown, thick-walled, chlamydo-spore-like bodies. The control shoot gave no results. A closely similar set of events followed when culture-mycelium, obtained from the leaf-sheaths of diseased canes, and portions of these leaf-sheaths themselves were employed.

*Experiment 2.* Three two-eyed cuttings were selected from the upper part of healthy White Transparent canes, carefully washed and placed on moist coral sand, previously sterilized, in flower-pots standing in dishes containing water. These served to keep away ants. The pots were then covered with glass bell-jars and placed in a plant shed. Seven days afterwards, when the cuttings had sprouted, two of them were infected at the cut ends with mycelium (developed from a toadstool spore) similar to that used in experiment 1 above, and the buds were also covered therewith. The third cutting was not infected and thus served as a control. The cuttings were now covered with moist sand. In one case, in seventeen days, and in the other in twenty-nine days after infection, small white circular bodies, about the size of a pin's head, were noted at the surface of the sand on the lower leaf-sheaths of a shoot. In forty-eight hours these developed into toadstools identical with those obtained on cane-shoots attacked by root disease. On examining these shoots it was found that the lower leaf-sheaths were dead and cemented closely by white mycelium to those underneath. The outermost of those still living were covered with mycelium and showed numerous reddish areas, where the cells were found to be invaded by hyphae. The control cutting showed no infection. A similar result was obtained with culture-mycelium from the leaf-sheaths of diseased canes, and in one case toadstools appeared three weeks after infection. With portions of the leaf-sheaths from diseased canes a limited amount of infection was obtained, but no toadstools were produced and the shoots seemed to suffer little from the fungus. During this experiment the cuttings were watered, after the appearance of green leaves, with Sachs' solution.

*Experiment 3.* Experiment 2 was next repeated, except that sterile soil was used in the flower-pots, and the cuttings were infected when planted, and watered throughout with boiled tap-water. The developing shoots were found to be attacked by the fungus, but in one case only (when pure culture-mycelium had been employed) were toadstools developed

during the first month, at the end of which the experiment had to be discontinued. No infection was noted in the controls. In one case where pieces of leaf-sheath were used, one of the shoots became badly infected with the sclerotia fungus of Went's 'red-rot' disease. Fourteen days after infection the shoot was killed by the fungus and covered with white thread-like strands and sclerotia. The leaf-sheath employed had evidently been attacked by this fungus.

*Experiment 4.* A small field experiment was next carried out. During planting-time in the early part of December, 1901, the nodes and cut ends of ten healthy White Transparent cuttings were covered with actively growing mycelium, obtained originally from a toadstool spore, and planted in the ordinary way. Eight of these developed normally, but the other two were destroyed by the fungus *Thielaviopsis ethacetica*, Went, the shoots dying off shortly after they appeared above ground. At the present time (August 30, 1902) the shoots from these canes are healthy and vigorous and show no trace of root disease, although white mycelium, characterized by clamp-connexions, can be seen as a matted white coating on the scale-leaves of the buds on the below-ground portions of these canes.

In the early part of February, 1902, ten similarly infected cuttings were planted in the same field, and were watered just sufficiently for germination to take place. After the shoots appeared above ground, the soil around the cuttings was consolidated by treading so as to render root development as difficult as possible. Little growth was made during the dry months of March and April, during which time five of the cuttings died. On examination they and their shoots were found to be penetrated by the fungus in all directions. The remainder showed no response to the rains of May and June, and when examined on August 20 were found to be throwing up shoots from below, and to exhibit all the characteristics of canes attacked by the root disease under consideration. They possessed few roots, the majority having been destroyed, during early development, by the fungus. The



rainfall on the field during this experiment is given in the following table.

*Rainfall from December, 1901, to July, 1902.*

	1901	1902						
	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
Inches of rain.	4.86	.93	.72	.97	.58	3.93	5.80	5.36

In the former case the conditions of growth were distinctly favourable, in the latter unfavourable. The canes planted in December were able to develop rapidly and to establish themselves on their own roots before the dry season. They were able to resist the fungus, although the latter maintained itself on the lower parts of the stem. In the case of the cuttings planted in February, the fungus proved too strong for the canes.

The above results clearly show that the toadstool fungus is a parasite, and that there is a genetic connexion between it and the white mycelium found on the leaf-sheaths of the canes attacked by this root disease. Moreover they serve to complete the life-history of the fungus.

### 3. Some relations between the host and the parasite.

Having established the parasitic nature of the fungus, it became possible to understand the course of the disease more clearly. As already mentioned, the malady, although occurring in first-crop canes, is a much more serious pest among rattoons, especially on the black soils of the lowland districts.

It is a general custom in Barbados to select plant-material from ratoon canes, generally from those of the second crop. The cuttings consist either of the upper part of the stem containing the main growing-point ('tops') or of the next portion, and are generally about a foot in length. The selection of plant-material from this source seems to be based partly on economic considerations, as such rattoons are poor

in sugar, and partly on the fact that these cuttings contain four or five nodes, and thus there is a good chance of one, at least, of the buds developing. As shown in a previous paper (21) it is probable that the greater resistance of such cuttings to fungi like *Thielaviopsis ethacetica* than that of cuttings from the first-crop canes, which are richer in sugar, has been unconsciously found out by experience and has helped to bring about the present practice. It appears, however, likely that planting from the worst canes must eventually lead to the degeneration of cane varieties, and a promising field for investigation seems to be indicated in which the resulting canes from the continued selection of the best and worst cuttings are compared, on an economic scale, for a number of years.

Sometimes the worst canes on the estate are selected for cuttings. In other words, the canes attacked by root disease to the greatest extent are used for the preparation of plant-material. On examining these canes it is found that the leaf-sheaths are firmly cemented to the stem by the mycelium of *Marasmius*, which further covers the scale-leaves of the buds as a whitish coating. The leaf-sheaths around the main growing-point which form part of the 'cane top' generally exhibit the black elliptical spore patches of *Cercospora vaginæ*, Krüger. That both these fungi are alive was proved by cultivating the tuft of white mycelium which arose from the buds when placed in a moist chamber, and by placing the conidia of *Cercospora* in hanging drops. Thus these two fungi are usually planted with the host.

As previously mentioned *Cercospora* can be readily traced from the cutting to the mature canes.

*Marasmius* also follows the cane through its first year's growth, and sometimes, while the young canes suffer from drought, overcomes them and gives rise to root disease. Generally, however, the favourable conditions for rapid growth of the cuttings in December and the high condition of tilth during the first crop, enable the canes to develop normally. During this time the fungus is able to hang on, on the lower

part of the stem, in a resting condition, where it can be seen as a white felted mass on the scale-leaves of the buds.

When, however, the canes are cut in March, and the closely packed condition of the soil combined with extreme dryness prevents anything like rapid growth of the buds at the base of the cane-stumps, the mycelium, after luxuriating in the rich substratum afforded by these stumps, is able to assert itself and master the young shoots, and thus make up for the long period of waiting. As the new shoots develop with great slowness during the dry season, the fungus has time to destroy most of the roots at the base, at the beginning of their development, and thus to give rise to the dwarfed canes so characteristic of the second crop of the lowlands. When the rains come, only a few roots are available for the supply of water and minerals, and, in spite of the liberal application of artificial manures, practically no growth results.

The fact that the fungus is not so destructive to ratoon canes on the red soils of the highland districts as to those on the black soils of the lowlands, seems to be largely due to the much greater rainfall during the dry season in the former districts than in the latter.

We can to a great extent regard the first and second crops of canes on the lowland districts of Barbados as infection experiments on a large scale with the fungus *Marasmius*. In the case of the first crop, conditions favour the cane and there is little disease. In the second crop, everything helps the fungus and at the same time checks the host, consequently a root disease, epidemic in character, often results. Furthermore, it is caused by a fungus which, under ordinary circumstances, can do little damage to the cane, but which, when conditions are against the host, can become a parasite and even overcome meristematic tissue such as that at the growing-point of the cane-root.

We have, therefore, a striking example of the influence of the environment on the result of the struggle between the host and the parasite, and a confirmation of the views brought forward on this subject by Marshall Ward (2).



#### 4. Prophylaxis.

In Java, Wakker (10, 14) described and figured a fungus *Marasmius Sacchari*, n. sp., which destroys cane-cuttings in the 'hatching beds' (Treibbeeten), in which the canes are placed before planting out, and also attacks and destroys mature canes. From his description of the fungus, which he regarded as a wound parasite, and his culture and infection experiments, there can be no doubt that the West Indian and Java forms are identical.

The conditions of cane culture in Java, however, differ markedly from those in the West Indies. In Java, cuttings are raised in special plantations on the hills, from which the cane-fields in the lowlands are planted. Great care is taken in the selection of cuttings and their protection during growth. Further, only one crop of canes is raised from the same stand, so that there are no ratoonings. The fungus in Java, therefore, has less opportunity of causing a widespread root disease than is the case in some parts of the West Indies.

It is clear from the wholesale destruction of the young roots of canes attacked by this disease that there is no hope of a cure. Prevention and the assisting of the host plant as much as possible can therefore alone be aimed at.

The selection of cuttings from healthy canes and their protection during germination, instead of the present system, are essential.

Probably if the fields selected for ratoonings were allowed to remain as late as possible before reaping, there would be less chance of the fungus, if present, overcoming the young shoots. Cultivation of the soil round the old stumps, as the first rains appear, ought to assist new root development. Artificial irrigation during the earlier period of growth and during drought should assist the canes to ward off the fungus.

In Surinam, an ingenious method of starving out the fungus in badly infected fields has been adopted with success by the late Mr. James Mayor. After reaping and digging up and destroying the old stumps, the field is placed under water

for a year or two during which the fungus is destroyed. Afterwards, the water is run off, the soil allowed to dry, and a new crop of canes raised. The soil on this estate is a heavy clay, and in spite of all precautions the fungus makes its appearance in the fields after they have been in canes for four or five years. Where this method is impracticable, rotation crops would serve the same purpose.

The occurrence of rhizomorphs in connexion with this fungus suggests the advisability of isolating diseased areas by a trench from the rest of the canes, as the fungus may travel underground.

In badly diseased fields in Barbados, it is not uncommon to see healthy clumps of canes growing vigorously. Probably if these were continually selected for propagation, more resistant strains than those in use at present might be obtained.

At the present time this disease is by far the most important of the cane pests in Barbados. It also occurs in Antigua and Surinam. In addition to the losses sustained thereby, large sums of money are annually spent on artificial manures for these diseased canes which can obviously have no effect. As time goes on and the significance of the diseases of the cane is realized, reforms will no doubt be made in the local practice. Successful economic experiments on the subject, on a sufficient scale to satisfy the planter, would doubtless greatly hasten these reforms.

In conclusion, I wish to express my indebtedness to Mrs. W. G. Freeman for kindly preparing the drawings of Figs. 1, 2, 7, 8, 9, and 14 which illustrate this paper.

#### IV. SUMMARY OF CONCLUSIONS.

1. The *Melanconium* found on diseased sugar-canes in the West Indies is a saprophyte and is not the cause of the 'rind' disease. The whole of the evidence obtained in these experiments points to this fungus being quite distinct from *Thielaviopsis ethacetica*, Went.

2. The macro- and micro-conidial phase of *Trichosphaeria Sacchari*, Masee, identical with *Thielaviopsis ethacetica*, Went, causes a disease of cane-cuttings in the West Indies which is the same as the 'pine-apple' disease of Java. In addition, it is a parasite on growing canes.

3. The 'rind' disease of the sugar-cane in the West Indies is identical with the 'red-smut' disease of Java, and is caused by the fungus *Colletotrichum falcatum*, Went. It can infect ripening canes at wounds and at old leaf-bases, and can overcome the tissues of young canes which are capable of growth and development.

4. *Melanconium* infects canes easily at points where they have been invaded by *Colletotrichum*.

5. The common root disease of the sugar-cane in Barbados is caused by the fungus *Marasmius Sacchari*, Wakker, the mycelium of which is able, under certain conditions, to overcome the growing-point tissues of the developing roots of the cane.

BARBADOS,

Aug. 30, 1902.

Note added :—Thanks to the kindness of Professor Marshall Ward, I have been able to repeat the culture and inoculation experiments with *Melanconium* and *Thielaviopsis*, described in this paper, at Cambridge. Both these Fungi were grown in pure culture in a cane-extract food-material at a temperature of 75° F., and the inoculation experiments were performed on mature sugar-caness growing in the Lily-house at the Botanical Gardens. No evidence of a genetic connexion between these two forms was obtained, neither did *Melanconium* behave as a parasite towards the cane. On the other hand, the results were identical with those noted in the experiments in Barbados and described in the present paper. Mixed cultures of *Melanconium* and *Thielaviopsis* gave positive results when introduced into healthy canes.

THE BOTANICAL LABORATORY, CAMBRIDGE.

Jan. 3, 1903.



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## EXPLANATION OF FIGURES IN PLATE XVIII.

Illustrating Mr. Howard's paper on Diseases of the Sugar-Cane.

Fig. 1. Portion of a sugar-cane attacked by the 'rind' disease showing stromata of *C. falcatum* above and below the leaf-base. Nat. size. At (a) is a stroma of the fungus as seen under a lens.

Fig. 2. A portion of a sugar-cane, attacked by the 'rind' disease, split in half. A red blotch with a white centre is shown at (a). Nat. size.

Fig. 3. Stages in the germination of a spore of *C. falcatum* in a hanging drop. The sowing was made at 1 p.m., Nov. 29.

$$\left. \begin{array}{l} a = 4 \text{ p.m., Nov. 29} \\ b = 5.40 \text{ ,, ,, } \\ c = 9.10 \text{ ,, ,, } \\ d = 8 \text{ a.m. Nov. 30.} \end{array} \right\} \times 375.$$

$\times 60.$

Temperature throughout 28–31° C.

Fig. 4. Stages in the formation of conidia from the mycelium of *C. falcatum* in a hanging-drop culture. The sowing was made at 1 p.m., Nov. 29.

$$\left. \begin{array}{l} a = 12.45 \text{ p.m., Nov. 30} \\ b = 1.30 \text{ ,, ,, } \\ c = 3.50 \text{ ,, ,, } \end{array} \right\} \times 375.$$

Temperature 29–30° C. throughout.

Fig. 5. Production of chlamydospores on the submerged hyphae of *C. falcatum* in a hanging drop twenty-seven hours after sowing.  $\times 375.$

Fig. 6. Formation of conidia of *C. falcatum* at stromata formed in a hanging drop. The sowing was made at 1 p.m., Nov. 29, the temperature was 30–31° C. throughout, and all are shown  $\times 375.$

$$\left. \begin{array}{l} a = 10.25 \text{ a.m., Dec. 5.} \\ b = 12 \text{ (noon) ,,} \\ c = 5 \text{ p.m. ,,} \end{array} \right\}$$

Fig. 7. A sugar-cane stem attacked by the fungus *Marasmius Sacchari* showing the aborted roots and an abnormal development of the lower buds.

Fig. 8. A portion of the below-ground part of the stem of a similarly diseased cane showing the aborted roots on a larger scale.

Fig. 9. A portion of the lower (above-ground) part of the stem of a diseased sugar-cane showing colonies of the fructifications of *Marasmius Sacchari*.

Fig. 10. Brown, thick-walled, usually terminal, chlamydospores in the mycelium of *Marasmius*.

Fig. 11. Longitudinal section of a developing root of the sugar-cane destroyed by the mycelium of *Marasmius*. The periblem is penetrated by the fungus in all directions, many of its cells being brown in colour and much disintegrated. The root-cap is almost completely destroyed and the shaded portion of the pleurome is filled with mycelium.  $\times 35.$

Fig. 12. Stages in the germination of a spore of the fungus in a hanging drop. The sowing was made at 2 p.m., Dec. 3.

$a = 3.30$  p.m., Dec. 3 }  
 $b = 4.30$  " " }  $\times 375$ .  
 $c = 6$  " " }

Temperature throughout  $29^{\circ}$  C.

Fig. 13. Stages in the formation of a clamp-connexion in a hanging-drop culture. The papilla in (*a*) arose about  $100 \mu$  from the growing-point of a hypha and the arrow indicates the direction of growth. Temperature  $30^{\circ}$  C. throughout. (Zeiss, D D.)

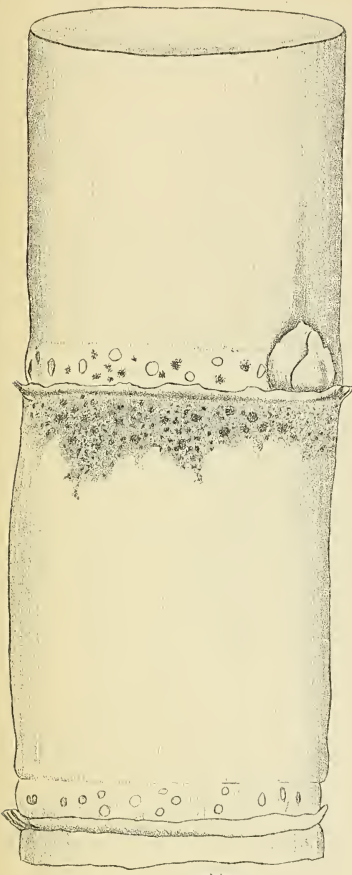
$a = 11.4$  a.m., Oct. 4  
 $b = 11.7$  " "  
 $c = 11.20$  " "  
 $d = 11.25$  " "  
 $e = 11.35$  " "  
 $f = 12.15$  p.m. "

Fig. 14. Production of rhizomorphs on the walls of a culture-tube nine months after infection. Above, these bodies shade off into white feathery mycelial strands.

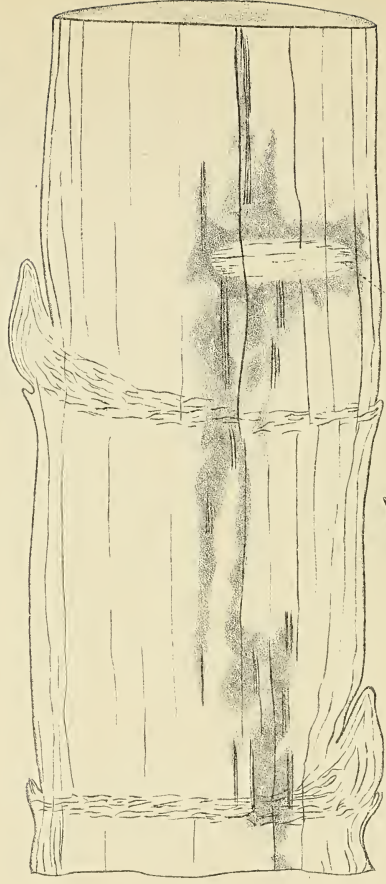








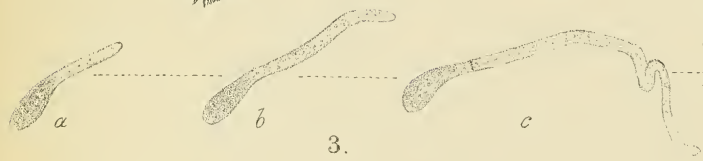
1. a



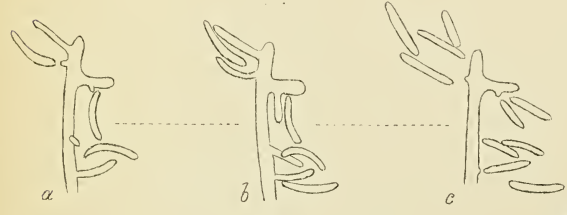
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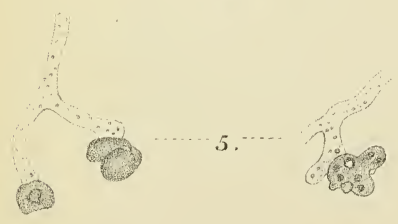
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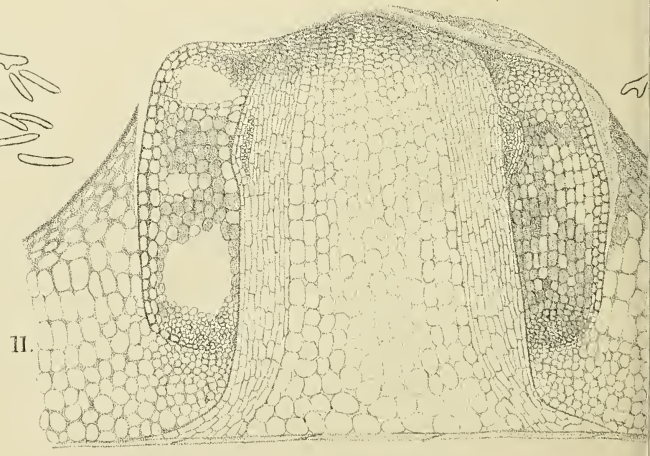
3.



4.



5.



II.











A. HOWARD.— ON SOME DISEASES OF THE SUGAR CANE IN THE WEST INDIES.





# The Root-Structure of *Dioscorea prehensilis*.

BY

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With Plate XIX, and a Figure in the Text.



THE publication of a paper by Dr. D. H. Scott<sup>1</sup> placed botanists in possession of two new examples of spine-bearing roots. Of the plants considered one, *Dioscorea prehendensilis*, Benth., forms the subject of the present communication.

The plant described by Dr. D. H. Scott was grown at Kew, and the tuber was entirely a subterranean organ. It appears, however, that in the natural state the tuberous stem is almost entirely an aërial structure, a fact which is very clearly demonstrated by a photograph of the wild plant, taken by Mr. G. F. Scott-Elliot. The following interesting remarks are quoted from a letter from Mr. G. F. Scott-Elliot to Dr. Scott, which the writer has kindly allowed us to make use of. 'The plant was, I should say, 7 feet high and completely covered by the arched roots. . . . It was photographed and collected in a day's march, and there is not, I think, very much Natural History to be found from such hurried observations. I have an impression that this country has many wild boar who are possibly the enemy. It is not,

<sup>1</sup> Scott, D. H.: On two new instances of Spinous Roots, *Annals of Botany*, vol. xi, 1897.

[*Annals of Botany*, Vol. XVII. No. LXVI. March, 1903.]

I think, a forest district, but it is in the "Acacia zone," i. e. scattered trees of *Acacia* at 20 to 30 feet apart and the colour of the soil showing through a scanty sedge and grass sward. Game is abundant in the neighbourhood, man is absent. The climate is very dry, but there is probably underground water within 20 feet of the surface. There may be no rain for nine months or so.'

In the material at our disposal the thick roots possessed spines which varied in their characters according to the state of their development. The youngest, although often fully grown, were quite soft and gradually tapered off into a fine termination bearing rootlets in the ordinary manner; others were quite hard and sharp. The question which here arises is whether the normal root-ending of some of the softer spines represents a normal condition or not. It will be borne in mind that the large spine-bearing roots are, in the natural state, aërial; and the possibility is not excluded, indeed it is very probable, that under these circumstances the spines when above ground do not terminate in a normal root; this condition only obtaining when the organs are buried.

It is not possible to clear up this point here, inasmuch as the necessary evidence is as yet wanting. However, dealing with the roots at our disposal, it is seen that the absorbing end of the spinous root sooner or later drops off, leaving behind a perfect sharply-pointed spine. This may be explained either on physical or physiological grounds. It was noticed that on dropping into clove oil a spine which had not yet lost its apical region, it immediately curled up at the tip, became brittle, and on being touched separation took place between the absorbent tip and the thick basal part. Something similar to this may occur naturally in the buried roots, although it is much more probable that the absorbent tip shrivels up hopelessly during the dry season. On the other hand the breaking may be due to the cutting off of food-supplies, for the cortex generally has a withered appearance before the actual severance takes place. And further, the sieve-plates in the basal parts of the spinous roots were



invariably blocked by callus, which fact probably points to the conclusion that the cause is physiological rather than mechanical.

The breaking is not effected at any one particular point; there is rather an ill-defined region where the transverse severance may occur.

Sections taken above and below the rupture, where the apical region was preserved, exhibited no anatomical characters such as are found in the separation-layer of a leaf.

The first sign of breaking in a young spine (Pl. XIX, Fig. 1 C) is a slight brown annular discoloration in the region indicated by the line *X-Y*, and sections show that here the softer tissues are withering. The portions of the root nearer the apex appear quite healthy, hence it is obvious that the rupturing is not caused by the mere dying of the tissues from the apex backwards.

In a more developed spine the discoloration-zone is seen to be still more marked and the separation is almost complete, connexion only being maintained by shreds of cortex (Fig. 1 D).

Besides these large spine-bearing roots the tuber also possesses much smaller roots, having numerous lateral rootlets which are clearly absorbent in function. These secondary roots, after dying off, also leave behind a small hard spine similar to those of the larger roots; a fact which has already been pointed out by Dr. Scott<sup>1</sup>. Indeed, it may be stated at once that there is no essential difference either in the morphology or anatomy between the two varieties of roots, the dissimilarity being only in the size.

#### STRUCTURE.

Our knowledge of the anatomy of the roots of the Dioscoreaceae is based chiefly on the researches of Bucherer<sup>2</sup> who, in his work on the anatomy of this natural order, confines

<sup>1</sup> Loc. cit., p. 329.

<sup>2</sup> Emil Bucherer: Beiträge zur Morphologie und Anatomie der Dioscoreaceen, Bib. Bot., Heft 16, iii, 1889.

himself chiefly to the origin, &c., of the roots and the characters presented by their bundle-sheath in species of *Tamus* and *Dioscorea*. Further, he confirms Treub's<sup>1</sup> statements regarding the differentiation of the root-apex of *Tamus communis*, and disagrees with those of Janczewski.

#### Anatomy of the large spine-bearing roots.

These roots attain a diameter of .7 cm. and, as regards their structure, conform to the general monocotyledonous type. There are, however, certain interesting features exhibited which render a brief account of their structure not altogether out of place. The apex is somewhat blunt, and is made up of an enormous number of very small cells. Inasmuch as our material contained but one good and one indifferent apex, it was not possible unfortunately to investigate thoroughly the apical differentiation; however, it appears most probable that there is, in this plant, no definite calyptrogen layer as has already been asserted by Treub<sup>1</sup>, and confirmed by Bucherer<sup>2</sup>, to be the case in the Dioscoreaceae among other Natural Orders.

From a series of transverse sections through the apex it may be seen that the central cylinder is of normal diameter, and before either the phloem or xylem is differentiated a number of canals or vessels are formed in the more central regions, roughly arranged in a circle within the zone which eventually will be occupied by the phloem and xylem. The development of these vessels is extremely remarkable and quite dissimilar to what obtains in other plants as far as is indicated by existing accounts. They are produced not merely by the obliteration of the end-walls of elements situated one above the other, but also by the breaking down of the lateral walls of contiguous cells in a transverse plane. It is not suggested, however, that these structures are formed wholly by such a lateral fusion of elements; for tracing them downwards from the apex it is found that they originate as

<sup>1</sup> Treub: Le méristème primitif de la racine dans les Monocotylédones. Leiden, 1876.

<sup>2</sup> Loc. cit.

a single row of elements somewhat larger than the surrounding cells. Only one case was seen in which the appearance of

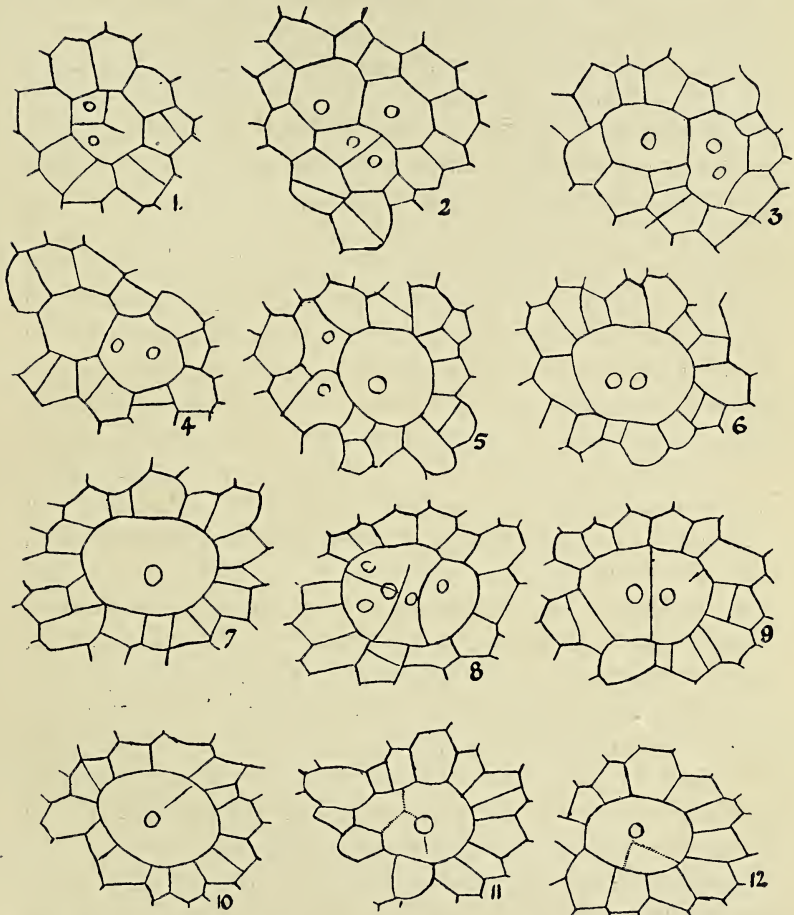


FIG. 19.—1-6 illustrating the origin of one of the central vessels of the large spine-bearing roots. 7-12 showing the cell-walls within the lumen.

the first origin of a central vessel suggested an initial absorption of the lateral walls of contiguous cells (Text-Fig. 19, 1-6). Increase in size takes place, and sooner or later transverse walls, in varying stages of completeness, are seen stretching across the lumen. The majority of these



walls shows signs of disintegration, and their presence may be seen in several successive sections. Further, the nuclei of the cells originally bounded by these walls are very obvious (Pl. XIX, Fig. 2; and Text-Fig. 19, 7-12).

Further back the lumen is again quite clear and contains but few nuclei, but still nearer the base of the root a large number of nuclei, sometimes as many as twelve in a single transverse section, occur at various levels marking the regions where the fusion of a number of cells took place.

The only obvious explanation which will account for the foregoing facts is that these central vessels arise very generally as single rows of elements, but the initial cells of any one vessel may not always be situated immediately one above the other to form a continuous string as in many cases, but are separated by intervening cells the walls of which ultimately break down, and so there is produced a continuous vessel. It sometimes happens that these vessels may not reach a great length, for although many may be traced through, relatively speaking, long distances, some come to an end quite suddenly; this more especially was found to be the case when two had been formed quite close together and separated only by the common wall. Finally they become lignified in common with the other parts, with the exception of the phloem, of the vascular cylinder, and possess bordered pits. Whether or not this curious development is due to the fact that the roots examined were from an abnormally grown plant, cannot be decided at present. It is hoped that more material will be obtained and the matter investigated further.

The structures above described are not the only ones which are multinucleate, for certain of the *inner* vessels of the metaxylem, which are the *first* to originate, together with the larger sieve-tubes, frequently have as many as four or five nuclei at one level<sup>1</sup>. It is doubtful whether these follow the

<sup>1</sup> Since this present paper was written, it has been found that Buscalioni in a recent preliminary communication ('Sull' anatomia del cilindro centrale nelle radici delle Monocotiledoni,' *Malpighia*, 15, 1902) has drawn attention to the fact that the mother-cells of the tracheae of the roots of the Dioscoreaceae and

course of development already described for the central vessels; in the case of the sieve-tubes there is absolutely no evidence to show that such is the case.

Before the differentiation of the xylem and phloem, adjacent cells fuse together at various parts of the cortex to form mucilage reservoirs. These are very numerous; in one transverse section as many as 130 were counted, and they develop rapidly. Eventually they become filled with bundles of raphides, and these may possibly subserve a protective function for the period during which the root remains soft. In longitudinal section these sacs are seen to be long, and they are situated one above the other forming long strings.

The central cylinder increases in diameter, and as it does so the vascular elements are differentiated. As in many roots of Monocotyledons the number of phloem- and xylem-groups is very large, thirty of each being not an uncommon number in the plant under discussion.

Sieve-areas occur on the lateral walls of the larger sieve-tubes, and a well-marked exodermis is present at the periphery of the cortex.

There is nothing further worthy of record until the general lignification of the vascular strand sets in. The first portions to thicken are the regions immediately external to the phloem-groups. This is illustrated in Figs. 3 and 4, from which it may be seen that a crescentic mass of fibres encase the external region of the phloem.

In order to ascertain whether or not this peculiarity obtained in other plants of the Dioscoreaceae, the roots of *Tamus communis* and an unnamed species of *Dioscorea* (labelled Pehio Yam) were examined. In both cases, although the lignification may become general, it was found that the regions external to the phloem-groups were not remarkable in being the first to be so markedly lignified.

Returning to the case of *Dioscorea prehensilis*, induration proceeds inwards towards the centre of the stele, and out-Asparagaceae are multinucleate; he also finds that the development of the xylem is centrifugal.

wards; the tissue external to and opposite the phloem-groups is, however, much thicker-walled.

Finally the cortex withers, and thus are formed roots of a high degree of hardness and bearing spines, the structure of which will be considered below.

For the sake of comparison the smaller and less modified roots, the essential function of which is absorption, were examined. These organs do not depart in any important feature from those of the larger roots as set forth above. Those differences that do obtain are to be solely attributed to the relatively large size of the latter as already described; thus instead of possessing thirty xylem-groups, the smaller roots never exhibited more than eight or ten. As regards histological features there are again no essential features of difference between the two forms, and in both the tissue directly bordering on the outer side of the phloem is the first to become lignified.

Figs. 5 and 6 illustrate the structure of these smaller roots.

#### Anatomy of the large spines.

These thorns originate as very thick lateral roots (Fig. 7), and it is only at the extreme apex that a normal root-structure can be discerned. The phloem and xylem of the spines are connected respectively to the similar tissues of the parent root by a large number of strands. In the case of the phloem these connecting strands are very numerous, being often related to as many as half the total number of phloem-groups present in the parent root (Fig. 7).

A transverse section near the base of a spine shows the phloem to be distributed around the periphery of the central cylinder in small groups isolated one from the other (Fig. 8), the xylem being restricted to two large lateral masses with smaller groups lying between them; these latter are the first to fuse with the xylem of the main root.

The examination of a series of sections from the base to the apex of a thorn shows that the phloem-strands travel in an irregular manner throughout the whole area of the stele.



Their course is sinuous, and as the apex is reached they anastomose with one another; hence just behind the extreme apex of a young spine it is found that there are but few phloem-groups, and these are arranged in quite a normal manner (Fig. 9, *a-e*).

This wide scattering of the phloem, coupled with the numerous connexions with the corresponding tissue of the main root, is probably to be correlated with the induration of the fully developed spine; for it is obvious that during the process of lignification much material, relatively speaking, must be required and must be well distributed for the purpose. The arrangement of the tissue in question is excellently adapted to facilitate such a process of lignification on a large scale.

Tracing the course of the xylem in a similar manner, it has already been stated that at the extreme base of the thorn the xylem is chiefly restricted to two large peripheral (just within the phloem-ring) masses, somewhat crescentic in shape, and that between these, smaller groups—which are the first to be connected with the xylem of the parent root—occur. The junction is effected chiefly by very short tracheides.

Sections cut nearer the main root exhibit longitudinal strands of xylem between the two crescentic masses; these represent the xylem rays of the parent root.

Passing towards the apex of the spine it is found that the xylem is more evenly distributed, and is generally restricted to the more central regions. As the apex is reached it diminishes in amount and gradually takes up a position towards the centre of the stele (Fig. 10). At the extreme apex it is generally aggregated into three or four groups alternating with the phloem in a normal root-like manner.

The abnormalities above described may at first sight appear remarkable, especially when a fully matured spine is examined; but it is to be borne in mind that no induration of the parenchymatous tissue sets in until the lateral root has attained its maximum size. The soft ground tissue of the basal region of the spine is the first to become lignified,

and the peripheral parts of the stele thicken up before the more central.

Fig. 11 illustrates the structure of a spine viewed in transverse section. A mature spine is seen to be made up chiefly of elements with very thick lignified walls, amongst which are scattered small isolated groups of phloem and conducting xylem-elements. The cortex of younger thorns possesses tannin-cells, and sometimes these elements may be found in the stele.

In longitudinal section it is seen that fibres predominate; the phloem pursues an irregular path, and cross-connexions occur between neighbouring groups. Sieve-plates may be observed at rare intervals, and the conducting xylem-elements are much longer in the central regions than those, already described, at the base.

#### SUMMARY.

1. In the natural state the tuberous stem is aërial.
2. The tuber possesses large spine-bearing roots, and smaller roots chiefly absorbent in function. The lateral rootlets of the latter, after dying off, leave behind a small hard spine similar to those of the larger roots.
3. The large spines of the material examined, when in the young state, tapered off into a normal root-ending. This absorbing end of the lateral spinous root eventually separates off, leaving behind a perfect spine.
4. Induration of the vascular cylinder of the thorn does not set in until the maximum size has been attained.
5. The apex of the large spine-bearing roots has no definite calyptrogen layer.
6. The central vessels of these organs are multinucleate and appear to be produced not merely by the obliteration of the end-walls of elements situated one above the other, but also partly by the breaking down of the lateral walls of contiguous-cells in a transverse plane.
7. Certain of the inner vessels of the xylem-rays, the

*development* of which is centrifugal, are also multinucleate, as also are some of the larger sieve-tubes.

It is doubtful whether these structures follow the same course of development as the central vessels.

8. The vascular strands of the spine-bearing roots become very hard, the regions immediately external to the phloem-groups being the first to become lignified.\*

9. The large spines originate as thick lateral roots, and it is only at the extreme apex that a normal root-structure obtains.

10. At the base of these thorns the phloem-groups are arranged in a circle at the periphery of the central cylinder; as the apex is reached it is seen that the phloem-strands travel in an irregular manner throughout the whole area of the stele. Their course is sinuous, and they anastomose with one another; at the extreme apex the phloem consists of but few strands arranged normally.

This arrangement is probably to facilitate the extensive lignification of the spine.

11. At the base of the thorn the xylem is chiefly restricted to two large peripheral masses just within the phloem-ring. Towards the apex the xylem is more evenly distributed, and gradually takes up a position nearer the centre of the stele.



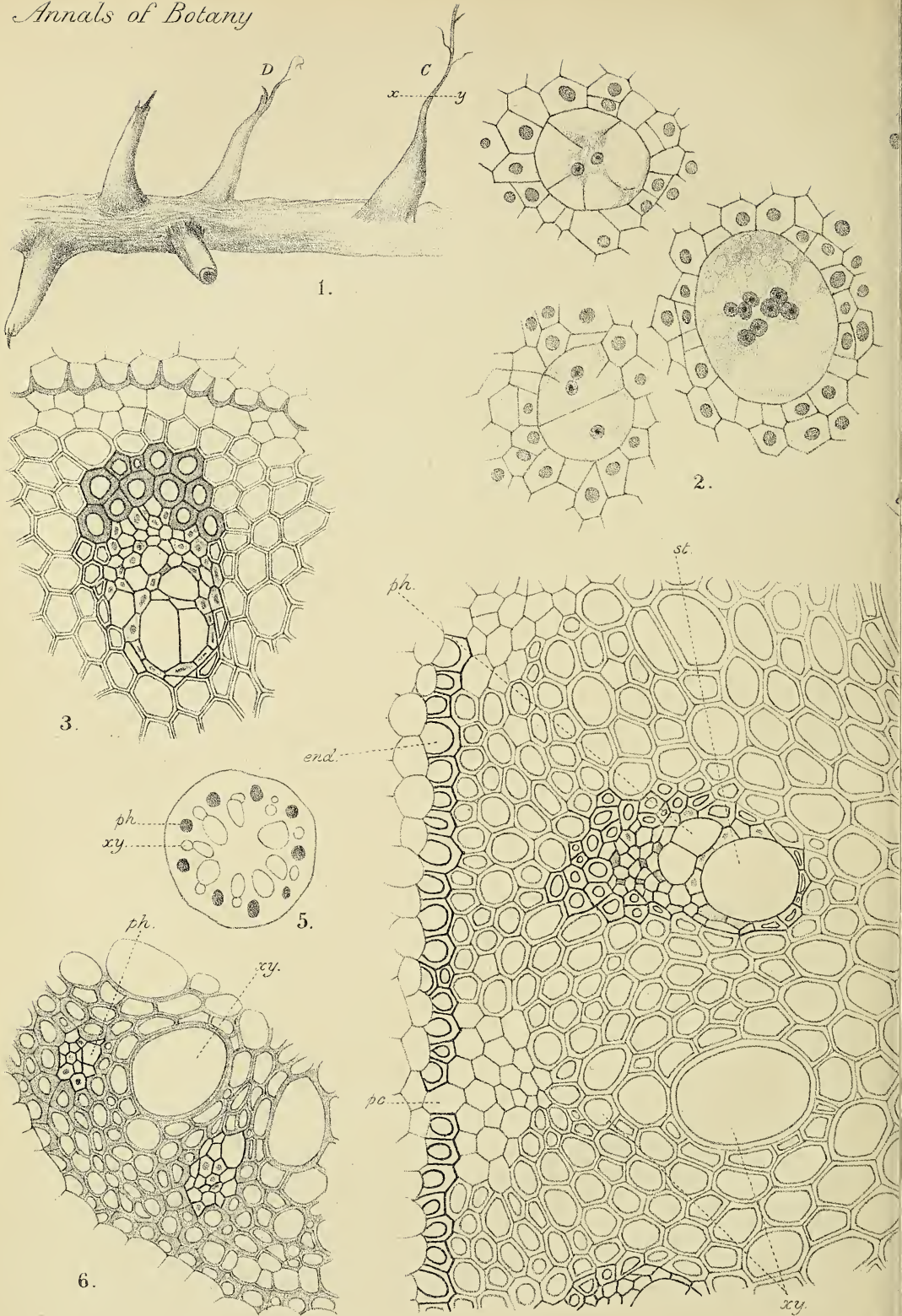
EXPLANATION OF FIGURES IN PLATE XIX.

Illustrating Mr. Hill's and Mrs. W. G. Freeman's paper on *Dioscorea prehensilis*.

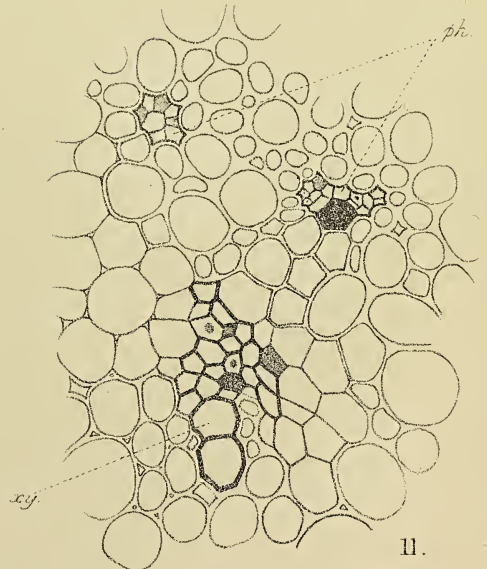
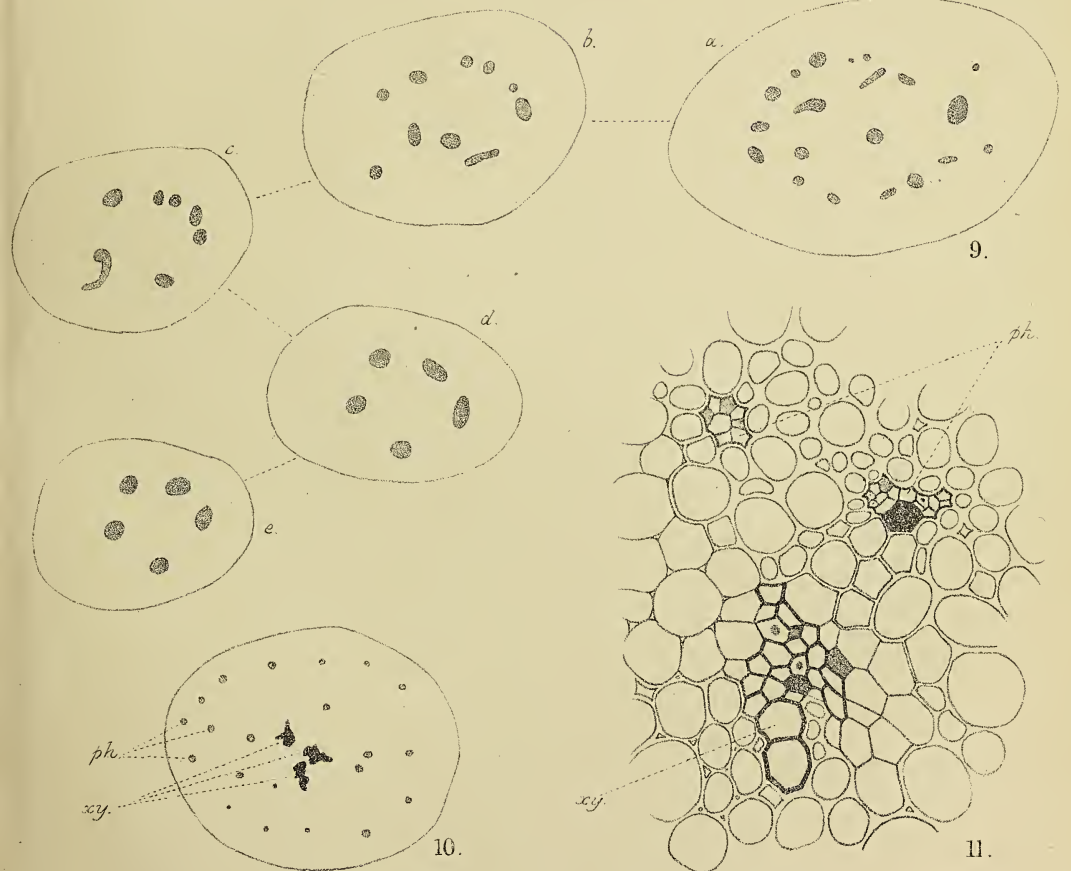
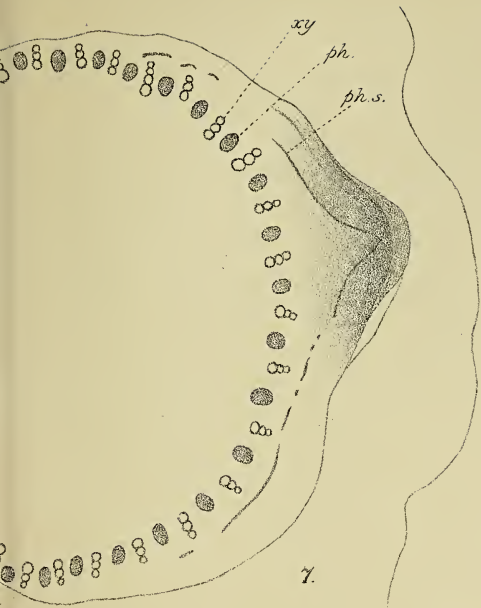
Abbreviations: *end.*, endodermis; *p.c.*, passage cell; *ph.*, phloem; *ph.s.*, phloem-strand; *xy.*, xylem.

- Fig. 1. Portion of a large spine-bearing root.  
Fig. 2. Illustrating the development of the large vessels in the inner regions of the vascular cylinder of a large spine-bearing root.  
Fig. 3. Part of a transverse section of a similar but older root, showing the highly lignified tissue external to a phloem-group.  
Fig. 4. Similar section from an older root.  
Fig. 5. Diagram of a transverse section of one of the smaller absorbent roots.  
Fig. 6. Portion of Fig. 5 in detail.  
Fig. 7. Diagram, showing origin of a large spine.  
Fig. 8. Diagrammatic transverse section near the base of a spine, showing the disposition of the phloem and xylem.  
Fig. 9. Diagrams of a series of transverse sections of a spine, illustrating the gradual fusion of the phloem, from the base (*a*) to the apex (*e*); stele only represented.  
Fig. 10. Diagram of a transverse section of the vascular cylinder of an immature spine.  
Fig. 11. Transverse section of part of the stele of an older spine, but still not fully developed.

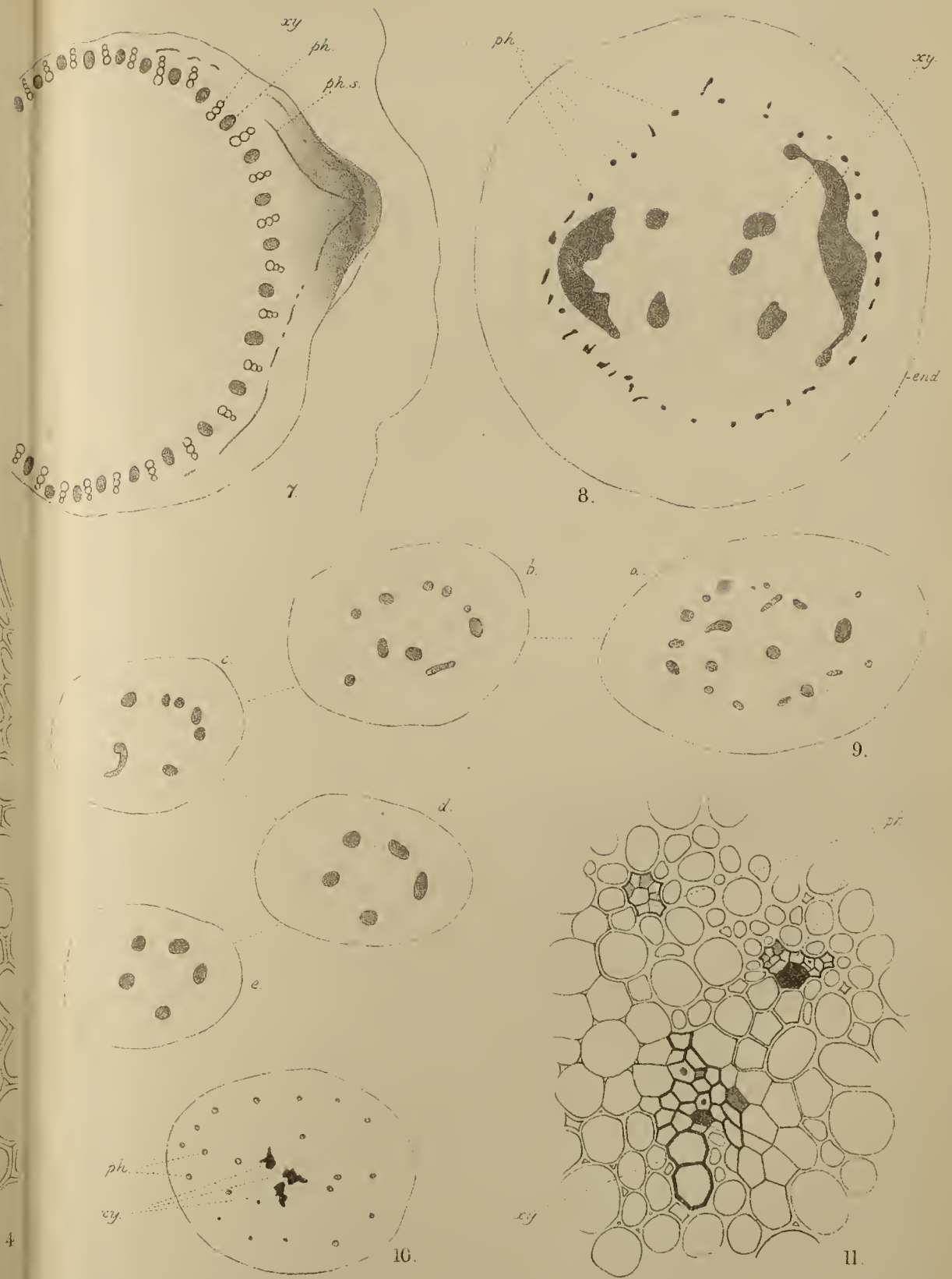
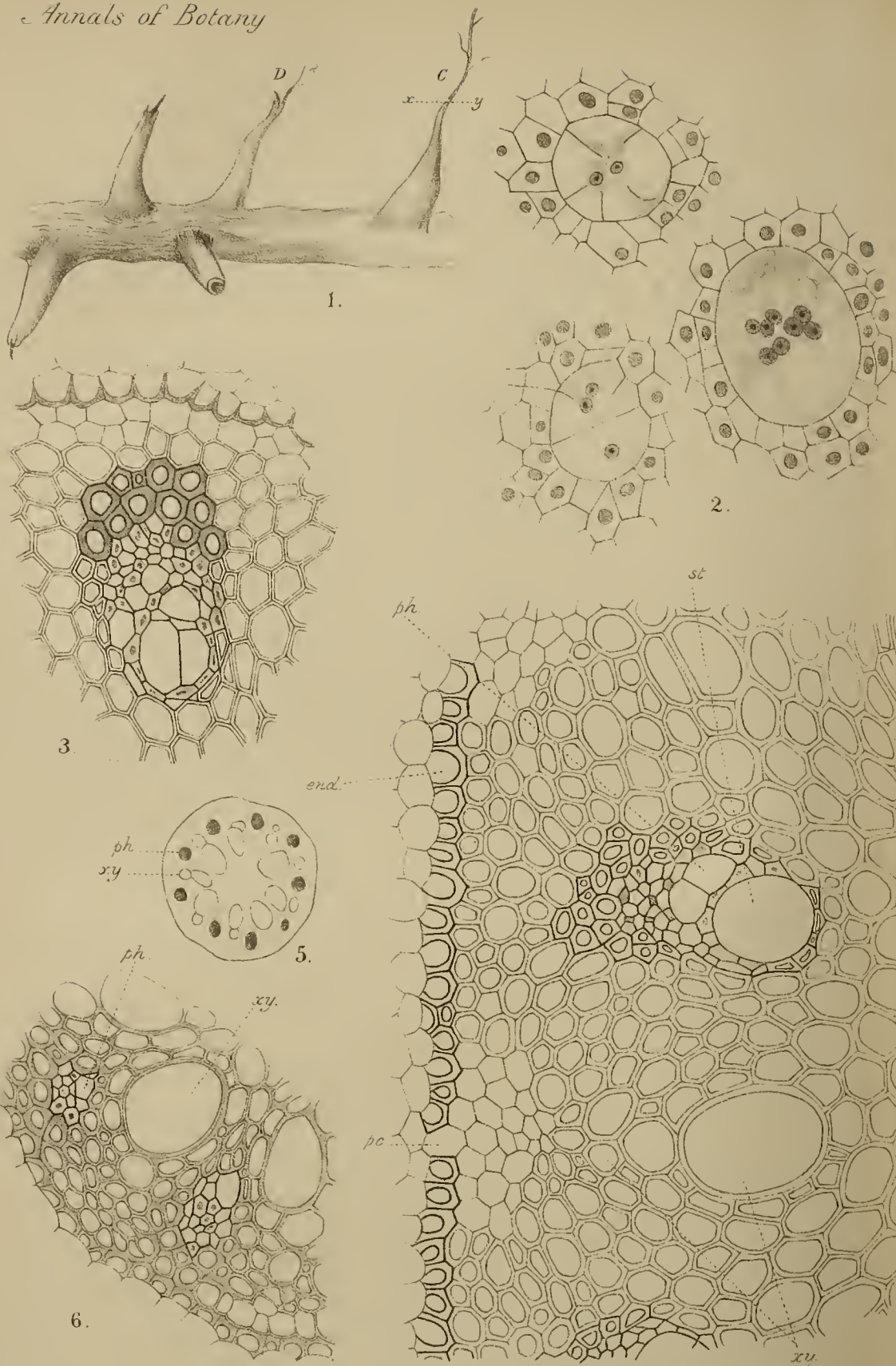
















# On the Roots of *Medullosa anglica*.

BY

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With Plate XX.

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THE first British specimens of *Medullosa*, a genus of Palaeozoic plants belonging to the Cycadofilices, were described by Dr. Scott<sup>1</sup> in a very interesting and complete memoir, published in 1899. Dr. Scott there gave the first account of the structure of the roots of a *Medullosa*.

A short time ago it was found that one of the petrifications belonging to the Binney Collection in the Woodwardian Museum, Cambridge, contained a portion of a stem of *Medullosa anglica*, Scott, with which several roots were associated. No section of this specimen could be found<sup>2</sup>, although the petrification had been cut previous to the presentation of the collection to the University in 1892. So far as I am aware, Binney did not refer to this specimen in any of his papers.

<sup>1</sup> Scott, Phil. Trans. Roy. Soc., Ser. B, vol. cxcI, 1899, p. 81.

<sup>2</sup> A section of *Medullosa anglica* (S. 3533), formerly in the possession of Sir Joseph Hooker, and now in the General Collection of Sections of Fossil Plants in the Geological Department of the British Museum (Nat. Hist.), which was undoubtedly cut from a Binney specimen, may very possibly have been derived from the Cambridge specimen. I am indebted to Professor F. W. Oliver for calling my attention to this section.

There is unfortunately no record of the locality from which the fossil was obtained. Mr. Lomax, however, who has recently made several excellent sections of the stem and the roots, tells me he is certain, from the appearance and preservation of the material, that it was originally obtained from the Lower Coal Measures of Hough Hill Colliery, Stalybridge, Lancashire; the same locality and horizon as the type specimens.

The examination of the structure of the stem, which in the Cambridge specimen is unfortunately incomplete, has added nothing of importance, with one exception, to the very complete account already given by Dr. Scott; which was founded on a study of several different specimens.

In association with the stem, and in one case in continuity with it, several exceptionally well-preserved roots occur. These agree very closely in structure with the roots previously figured<sup>1</sup>, and they undoubtedly belong to *Medullosa anglica*. Some of these are the best-preserved specimens which have yet been found, for the more delicate tissues, especially the phloem, are almost perfect.

A photograph of a transverse section of one of these roots is shown on Pl. XX, Fig. 1 (compare also Fig. 6). The diameter is about 9 mm. The root is triarch, as are all the other roots of *Medullosa* which I have examined. The external tissue consists of a somewhat narrow but well-marked zone of radially seriate elements, the periderm (*p.d.*). As Dr. Scott<sup>2</sup> has pointed out, this periderm is developed centripetally from a phellogen (see Fig. 2, *phg.*) which lies on the inner side of this zone. It was also shown that this periderm is of deep-seated origin, arising, probably, in the pericycle<sup>3</sup>.

Internal to the periderm, there is a somewhat broader zone of thin-walled tissue (*z*), with here and there very conspicuous cells, or groups of cells, with dark-coloured contents. This

<sup>1</sup> Scott, loc. cit., Pl. VIII, photos 19-25; Pl. XII, Fig. 19; Pl. XIII, Figs. 20-4.

<sup>2</sup> Scott, loc. cit., p. 102, Pl. VIII, photo 21.

<sup>3</sup> Scott, loc. cit., p. 104, Pl. XII, Fig. 19.



zone is exceptionally well preserved, and the evidence as to the nature of the tissues composing it is probably more complete than in the specimens which have previously been described. These tissues will be referred to presently in greater detail.

The rest of the root consists of an exceedingly regular triarch strand of xylem. The protoxylem-elements (*p.x.*) lie on the inner margins of three large bays or concavities, which occur at regular intervals in the almost circular outline of the strand. The elements of the primary wood can be seen extending from the protoxylem-groups to the centre of the root.

The secondary wood (*x<sup>2</sup>*) is formed of three large plates of radially disposed elements, with convex outer surfaces. The rays of woody elements composing the plates are generally one or two rows of tracheides, with multiseriate bordered pits on their radial walls. The medullary rays are often perfectly preserved. The parenchymatous cells of the ray are rounded, except where they have become elongated radially, probably as the result of stretching accompanying the increase in the dimensions of the secondary wood.

As a rule no secondary xylem-elements are formed opposite the protoxylem-groups. The vascular system of the secondary roots has, however, its origin in this position, and the xylem-strand, seen in one of the concavities (*r.x.*), is in connexion with a rootlet, which arises at some distance further along the root.

These roots differ somewhat in shape from some of those previously figured. The structure is, however, identical in both cases. Dr. Scott has made out in considerable detail the minute anatomy of the triarch strand, and I have nothing to add to our present very complete knowledge on this subject.

We may now consider in greater detail the structure of the zone of thin-walled tissue lying internal to the periderm, abutting on the convexities of the secondary xylem, and usually filling the concavities opposite the protoxylem-groups.

## THE PHELLODERM AND PERICYCLE.

A portion of a very thin transverse section is figured on Pl. XX, Fig. 2. It shows the thin-walled tissue opposite one of the protoxylem-groups (*p.x.*). The cells are fairly large, polygonal, or somewhat rounded parenchymatous elements, and are not very dissimilar in size or arrangement.

Towards the periphery of the section, in the lower part of the photograph, a small portion of the periderm (*p.d.*) can be seen. Immediately internal to the phellogen (*ph.g.*), some fairly large cells are shown lying on the same radii as the periderm-elements. This is no doubt phelloderm (*ph.d.*), produced by the activity of the phellogenetic meristem. In certain sections in which the preservation is particularly favourable, the origin of these cells can be clearly traced from divisions of the phellogen layer. The thickness of phelloderm is probably quite small. At a short distance from the phellogen the radial arrangement of the cells is lost.

Internal to the phelloderm, there occurs a fairly broad band of parenchymatous tissue (*p.c.*), the cells of which are irregularly arranged. These elements constitute the pericycle.

Conspicuous among the elements of the pericycle, single cells or groups of cells occur, with dark contents. These are regarded as 'secretory sacs'<sup>1</sup>. They appear to be ordinary parenchymatous cells in all the sections of these roots which I have examined. They therefore differ in structure from the gum-canals, which are so abundant in the petiole of *Medullosa*<sup>2</sup>. The 'secretory sacs' occur not only in the pericycle, but among the parenchymatous elements in all parts of the root, including those of the phloem and the primary xylem, as is clearly seen in Figs. 1 and 6. The dark colour of the cells is no doubt due to some organic change which the cell-contents have undergone before, or at the time of, preservation. The distribution of these 'secretory sacs'

<sup>1</sup> The term is used in the same sense as in De Bary's Comparative Anatomy (Eng. edit.), 1884, p. 136.

<sup>2</sup> Scott, loc. cit., p. 99.

rather recalls that of the crystal-containing sacs of certain recent plants, e.g. *Solanum tuberosum*. There is, however, in this case no evidence that these 'secretory sacs' were of a similar nature. In a few cases the cell-contents were found to be much less altered than is usually the case, but even these afforded no clue to the nature of the original substance.

The parenchymatous tissue in the upper portion of the photograph, occupying the concavity on the inner side of which lies the protoxylem-group (*p.x.*), is the very broad main medullary ray (*m.r.*)<sup>1</sup>. Secondary xylem is usually absent in this position. The small xylem-strand (*r.x.*) seen in the photograph belongs to the xylem of a secondary root, which, as already mentioned, has its origin in this position.

#### THE PHLOEM.

The photograph of a transverse section of a root, figured on Pl. XX, Fig. 3, shows a portion of the thin-walled zone of tissue opposite one of the xylem convexities. The tissues seen here include the phloem, which was of course not present in the section just described. At the lower end of the photograph, a few of the elements of the periderm (*p.d.*) and phelloderm are seen. Next comes a broad band of large-celled, irregularly disposed elements, the pericycle (*p.c.*). The 'secretory sacs' with dark contents form large groups in this section.

The upper half of the photograph shows a well-marked tissue, the elements of which are somewhat tangentially elongated. This is the phloem-zone (*b.z.*). The secondary phloem (*b<sup>2</sup>.*) consists of radial groups of rather small cells, the sieve-tubes (*s.t.*), alternating with rays of much larger phloem-parenchyma (*b.p.*). The secondary bast as a whole has much the appearance of that of the stem of *Heterangium tiliacoides*, Will.<sup>2</sup>. The groups of secondary phloem, corresponding to the groups of woody elements in the xylem-

<sup>1</sup> De Bary, loc. cit., p. 474.

<sup>2</sup> Williamson and Scott, Part III, Phil. Trans, Roy. Soc., Ser. B, vol. clxxxvi, 1896, p. 761, Pl. XXIX, Fig. 35.



plate, and separated by dilated parenchymatous rays, are characters common to these two plants. The sieve-tubes are also accompanied by a good deal of conjunctive parenchyma, as in *Heterangium*. In *Medullosa*, however, numerous 'secretory sacs' occur between the elements of the bast, and also among the cells of the parenchymatous rays, as is clearly seen in the photograph.

The sieve-tubes in the root of *Medullosa anglica* are, as far as I can ascertain, without the apparently thickened walls and narrow lumen, which are so characteristic of those of the stem<sup>1</sup>. But, like the sieve-tubes of the stem, they have lateral sieve-plates, similar to those of the phloem of most recent Ferns and Gymnosperms.

On Pl. XX, Fig. 4, a photograph of a drawing of highly magnified sieve-tubes from the *stem* of the Binney specimen is shown. The sieve-plates (*s.p.*) are clearly seen as little patches on the lateral walls.

In the *roots*, lateral sieve-plates also occur, as is shown in the drawing figured on Pl. XX, Fig. 5. It is only fair to add that Dr. Scott, who has examined the Binney sections, and most kindly given me the benefit of his opinion on several points in the anatomy of these roots, first recognized and pointed out to me the occurrence of lateral sieve-plates in the phloem of both stem and roots. I may therefore take this opportunity of expressing my thanks to Dr. Scott for much help in the examination of this material.

Lateral sieve-plates have been previously recognized in the phloem-elements of the stem of *Heterangium tiliaoides*<sup>2</sup>, and by Professor Renault<sup>3</sup> in the stem of *Poroxyton Edwardsi*, Ren. As far as I am aware, this is the first occasion in which they have been distinguished in the root of a fossil plant.

The external margin of the phloem-zone is composed of very tangentially elongated cells without any radial arrangement.

<sup>1</sup> Scott, loc. cit., p. 90, Pl. X, Fig. 3.

<sup>2</sup> Williamson and Scott, loc. cit., p. 762, Pl. XXIX, Figs. 37 and 38 a.

<sup>3</sup> Renault, Étud. Gîtes Minér. Bass. Houill. et Perm. d'Autun, 1896, p. 282, Pl. LXXIV, Fig. 11. Also Bertrand and Renault, Recherches sur les Poroxytons, Arch. Bot. N. France, 1886, Figs. 192-3.

This is no doubt the primary phloem (*b*<sup>1</sup>). It corresponds very closely to the primary phloem in the stem of *Heterangium tiliaeoides*<sup>1</sup>. In this section the primary phloem is very clearly marked off from the outer large-celled tissue, the pericycle.

#### THE SECONDARY ROOTS.

The main points in the structure and origin of the secondary roots of *Medullosa* have been already described by Dr. Scott<sup>2</sup>. The examination of a large series of sections of a root contained in the Binney material has, however, resulted in the elucidation of a few additional details.

The transverse section of a root figured on Pl. XX, Fig. 6, shows the base of a rootlet or secondary root (*r.l.*). The structure of the root itself is precisely similar to that just described (Fig. 1). The particular rootlet shown in the photograph is, however, stunted and abnormal. The xylem-elements are very small, and much less developed than is usually the case, and probably the rootlet never functioned as a typical root.

The lateral roots arise in three rows on the roots, at points opposite the protoxylem-groups. There is apparently, in all the roots which I have examined, some little distance between successive lateral roots in the same row; and only one rootlet is given off in any one transverse plane. The ramification is therefore not so abundant as in certain roots of *Lyginodendron*<sup>3</sup>.

The xylem-strand of the rootlet arises, as we have seen, opposite a protoxylem-group of the triarch root. It then passes outwards obliquely, and not at right angles to the stele of the root, as in *Lyginodendron*<sup>4</sup>. The parenchymatous tissues of the rootlet arise from the divisions of a group of meristematic cells, probably of pericyclic origin, which cause a protrusion of the periderm of the root at some little distance

<sup>1</sup> Williamson and Scott, loc. cit., p. 761, Pl. XXIX, Fig. 35.

<sup>2</sup> Scott, loc. cit., p. 103, Pl. VIII, photos 19 and 21.

<sup>3</sup> Williamson and Scott, loc. cit., p. 740.

<sup>4</sup> *Ibid.*

in front of the point of origin of the xylem-elements. This protrusion becomes more and more marked, until finally the rootlet becomes cut off, and a new growth of periderm completes the outer sheath of tissue of both the root and rootlet. For a short time after it has become free, the rootlet lies in a groove or inflection of the periderm of the root. One of these grooves can be seen in nearly every transverse section (Pl. XX, Figs. 1 and 6, *gr.*), opposite a protoxylem-group.

#### CONCLUSIONS.

The examination of the roots of *Medullosa* in the Binney specimen has resulted in a more complete knowledge of the thin-walled tissues which lie between the xylem and the periderm. The most noteworthy points are, the presence of a thin zone of phelloderm, the structure of the phloem, and the discovery of lateral sieve-plates on the phloem-elements of both the stem and roots. In the phloem of *Medullosa*, we have another point of agreement between *Medullosa* and *Heterangium*. The structure of the root of *Heterangium tiliaeoides* is at present unknown, but the phloem in the roots of *Medullosa anglica* closely resembles that of the stem in the former species.



EXPLANATION OF PLATE XX.

Illustrating Mr. Arber's paper on *Medullosa anglica*.

All the sections (A M 1-A M 29) are in the Woodwardian (Sedgwick) Museum, Cambridge. All the figures, except Figs. 4 and 5, are microphotographs from the actual sections by Mr. W. Tams, Cambridge. Some of these should be examined by means of a hand lens. Figs. 4 and 5 are photographs by Mr. Tams, from drawings by Mr. E. Wilson, Cambridge.

Fig. 1. Complete transverse section of a root. *p.d.*, periderm; *p.x.*, protoxylem; *x<sup>2</sup>.*, secondary xylem; *r.x.*, xylem of rootlet; *z.*, zone of thin-walled tissue, comprising phelloderm, pericycle, and phloem; *gr.*, groove in the periderm.  $\times 11\frac{1}{2}$ . Section A M 18.

Fig. 2. Part of a transverse section of a root, internal to the periderm, and opposite a protoxylem-group. *p.d.*, periderm; *ph.g.*, phellogen; *ph.d.*, phello-derm; *p.c.*, pericycle; *m.r.*, main medullary ray; *p.x.*, protoxylem; *r.x.*, xylem of rootlet.  $\times 75$ . Section A M 24.

Fig. 3. Part of a transverse section of a root, internal to the periderm, and opposite one of the convexities of the secondary xylem. *p.d.*, periderm; *p.c.*, pericycle; *b.z.*, phloem-zone; *b<sup>2</sup>.*, secondary phloem; *s.t.*, sieve-tubes; *b.p.*, bast parenchyma; *b<sup>1</sup>.*, primary phloem.  $\times 75$ . Section A M 15.

Fig. 4. Drawing of sieve-tubes as seen in a longitudinal section of the stem of *Medullosa anglica*. *s.p.*, sieve-plates.  $\times 280$  approximately. Section A M 9.

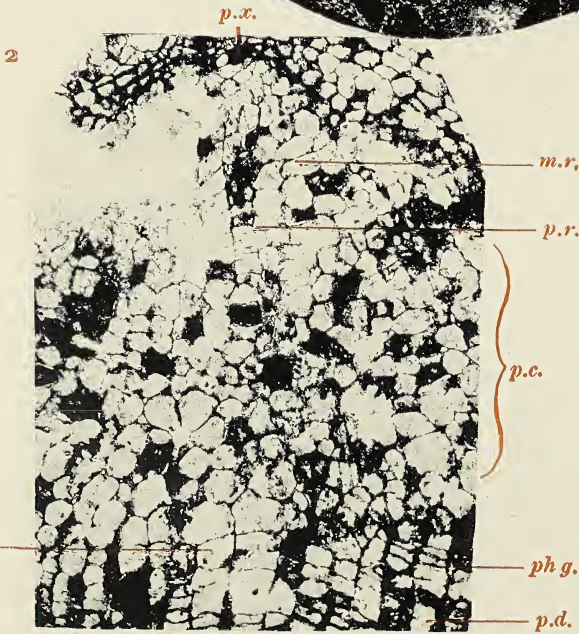
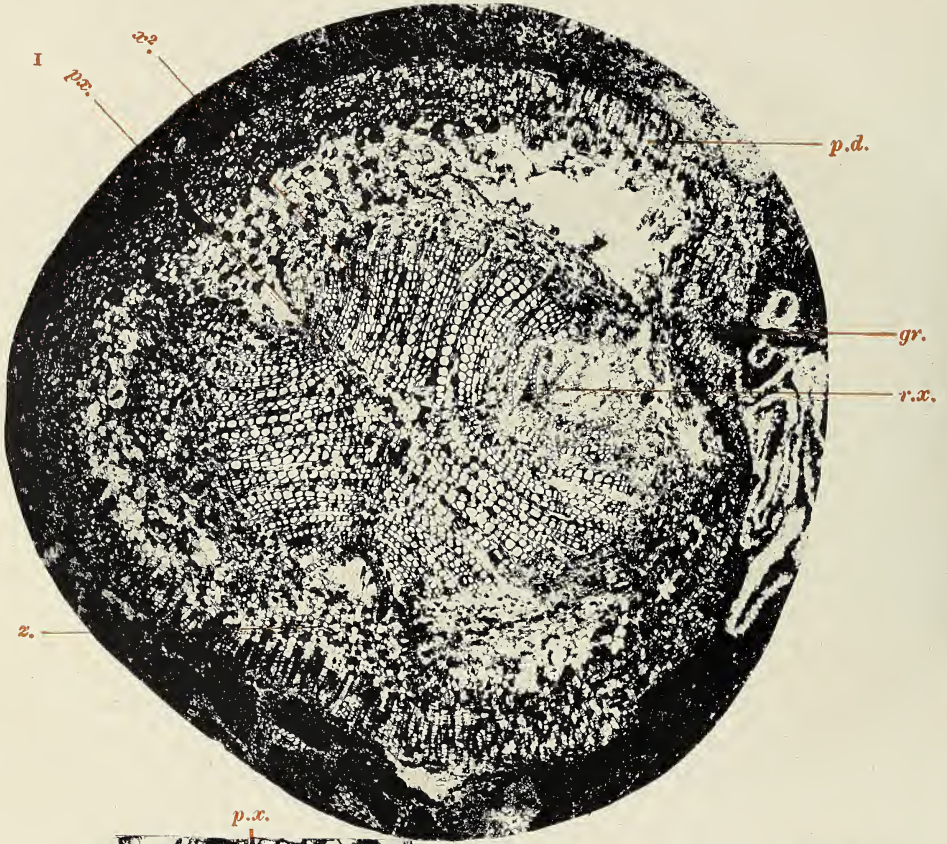
Fig. 5. Drawing of a sieve-tube as seen in a longitudinal section of a root of *Medullosa anglica*. *s.p.*, sieve-plates.  $\times 430$  approximately. Section A M 28.

Fig. 6. Complete transverse section of a root. *r.l.*, lateral root; *gr.*, groove in periderm.  $\times 11\frac{1}{2}$ . Section A M 23.





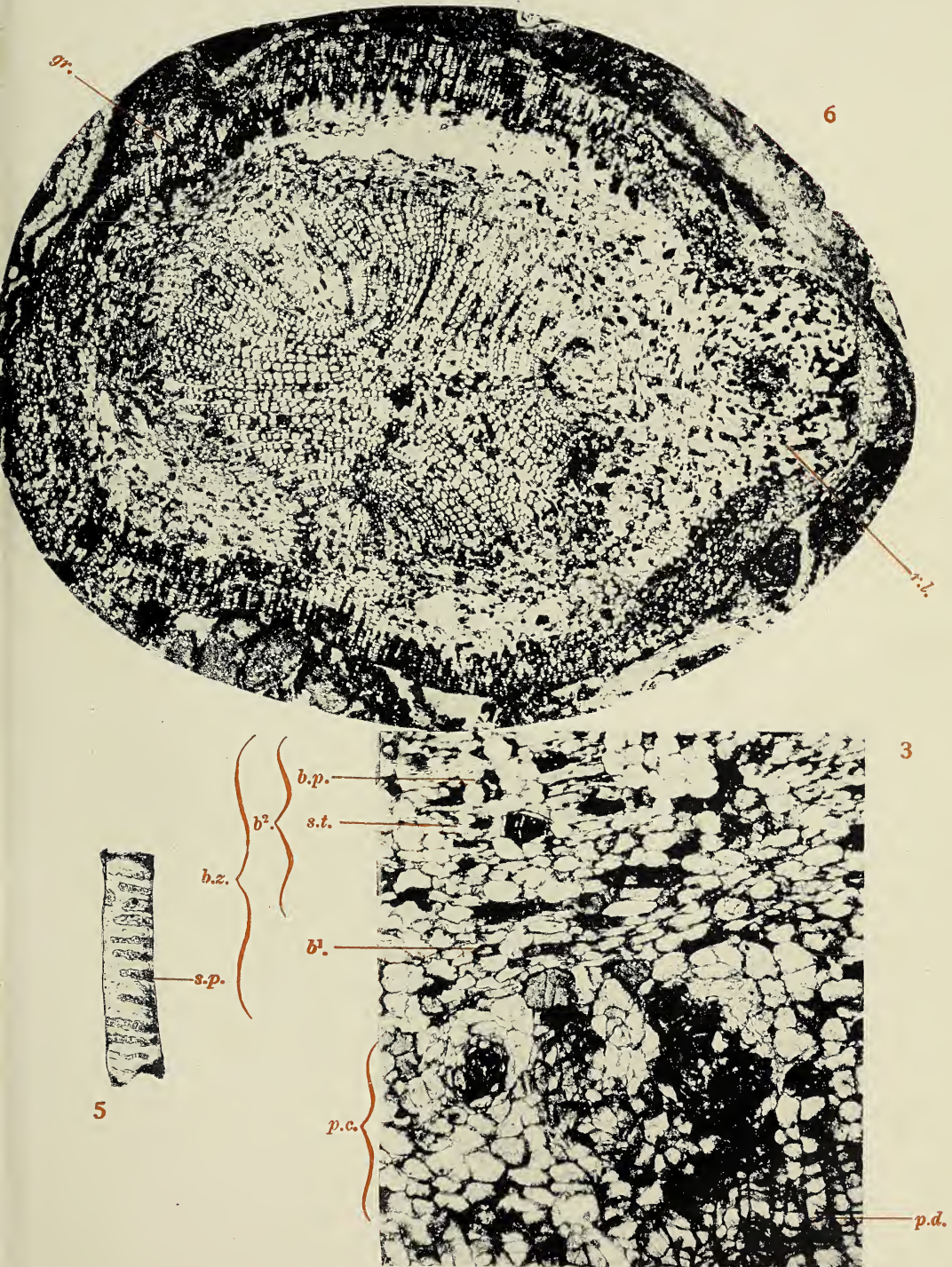




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W. Tams, Microphoto.

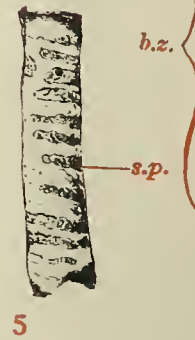
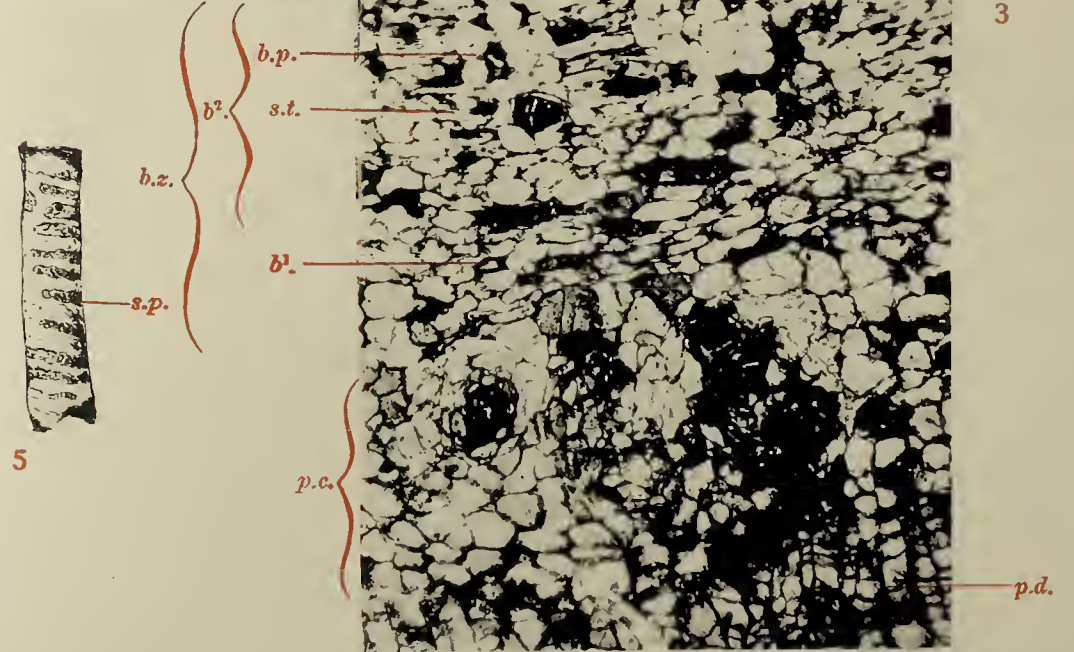
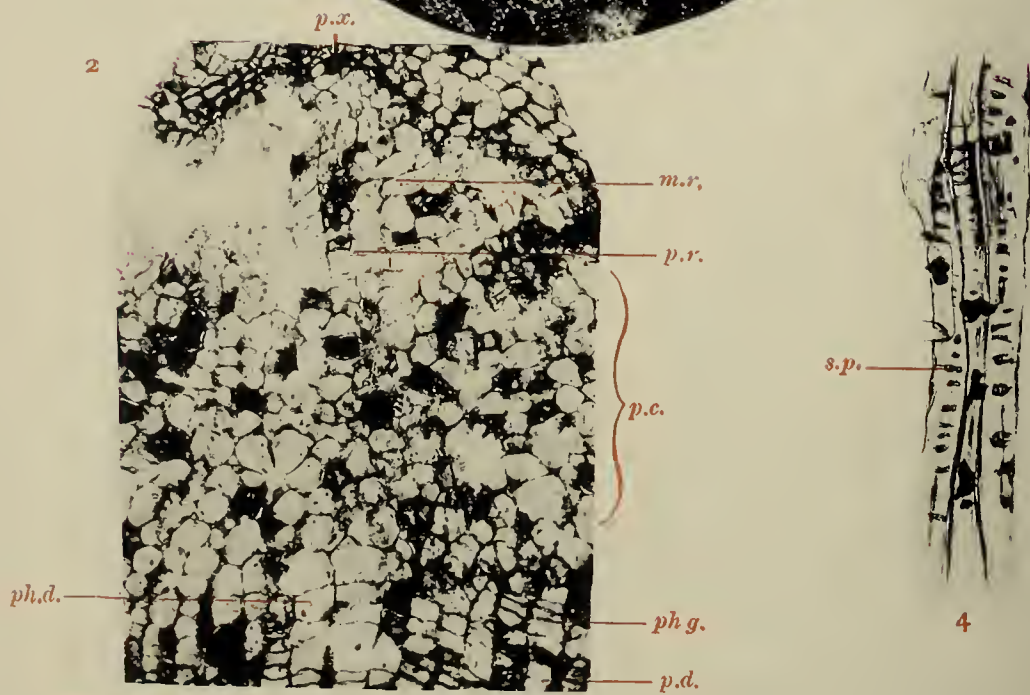
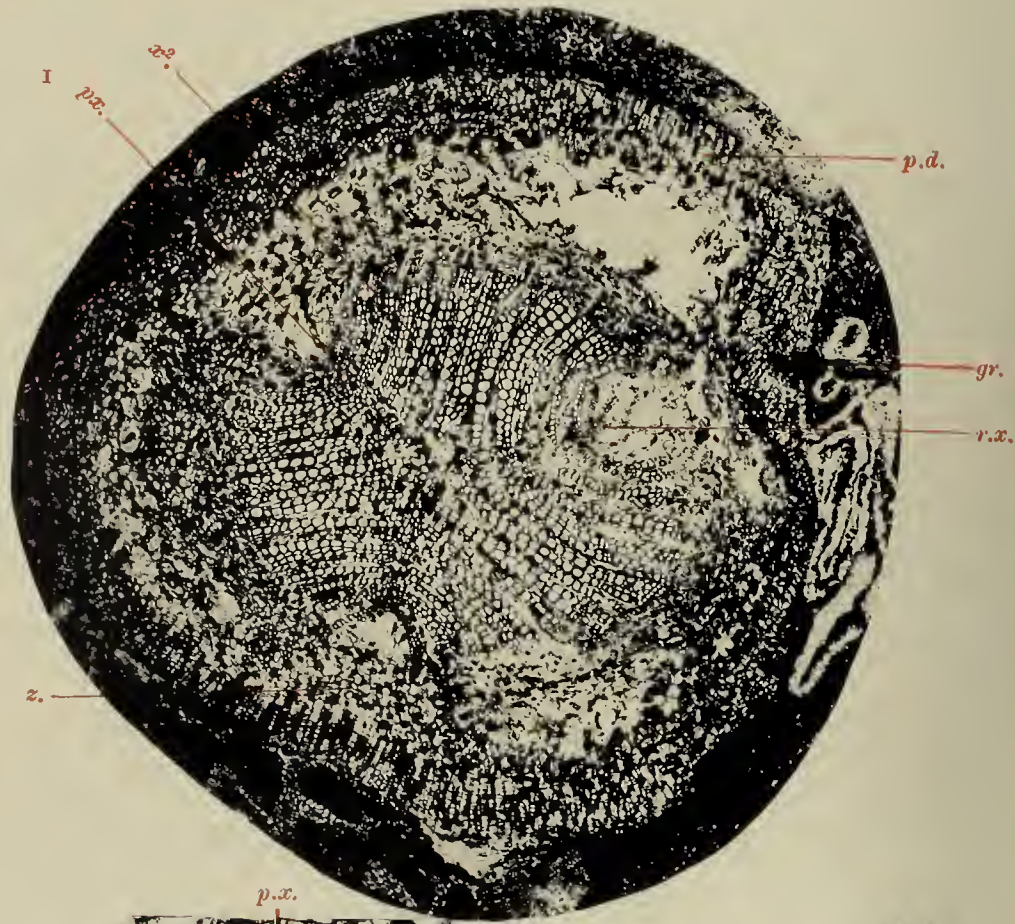




University Press, Oxford.







W. Tams, Microphoto.

University Press, Oxford.





## Morphological Notes.

BY

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With Plates XXI-XXIII.



### IX. A KALANCHOE HYBRID.

WHEN two distinct species are crossed, one would expect, *a priori*, the offspring to exhibit a 'blend' of the parental characters. And this appears to correspond largely with experience. Thus Darwin states: 'As a general rule, crossed offspring in the first generation are nearly intermediate between their parents' (*Variation of Animals and Plants*, ii. 48).

Such cases occur in nature, and before their real origin was understood they were regarded as intermediate species. Thus *Geum intermedium* stands between *G. rivale* and *G. urbanum*. But Bell Salter by crossing these two species proved it to be a hybrid.

The rule is, however, by no means invariable, and Romanes, writing in 1881, remarks: 'Until recently the interest attaching to hybridism was almost entirely of a practical nature, and arose from the fact, which is of considerable importance in horticulture, that hybrids are often found to present characters somewhat different from those of either parent or species' (*Encycl. Brit.*, xii. 422). Darwin states the same

[*Annals of Botany*, Vol. XVII. No. LXVI. March, 1903.]



fact: 'When two races or species are crossed, there is the strongest tendency to the reappearance in the offspring of long-lost characters possessed by neither parent nor immediate progenitor' (loc. cit., ii. 48).

Though such facts are well known to cultivators and are of extreme interest, they have seldom been put on record with much exactness or in a form convenient for reference. It seemed to me, therefore, worth while to illustrate rather fully a striking case which has come under my own notice at Kew.

*Kalanchoe* is a genus of *Crassulaceae* with about fifty species which has its head quarters in Africa, from which, like many types of the African flora, it has spread eastward by way of Arabia and North-west India. Kew has had the good fortune to be able to add to science and to horticulture two striking new species, both of which have been well figured in the Botanical Magazine, and can therefore be readily studied.

*K. flammea* (B. M. 7595), so named from its brilliant orange-red flowers, was raised from seed collected in Somaliland by Mrs. Lort-Phillips and Miss Edith Cole. The flowering plant is about a foot high, with 'obovate or obovate-oblong, thickly fleshy, quite entire or obscurely crenulate' leaves.

*K. Bentii* (B. M. 7765) was raised from seeds collected by the late Mr. Theodore Bent in the Hadramaut district of Southern Arabia. The flowering plant is about three feet high, with thickly fleshy, recurved, 'dagger-shaped,' or rather stiletto-shaped, leaves; the flowers are white, but pinkish when unexpanded.

Both species happening to be in flower together, Mr. W. Watson, the Curator of the Royal Botanic Gardens, a skilful and intrepid hybridizer, attempted to cross them. This was done both ways in June, 1900, and in each case the result was successful.

The results were as remarkable as unexpected. I will briefly summarize them.

1. *K. flammea* ♀ × *K. Bentii* ♂. About fifty seedlings were raised and grew vigorously. The middle figure of Plate XXII represents a young seedling about fifteen months old. It will be noticed that the lower and earliest leaves are intermediate, as was to be expected, between those of the two parents. They are neither flat and obovate nor simply stiletto-shaped, but are thickly fleshy and oblanceolate. Plants of the two parents of about the same age are shown on the same plate, *K. flammea* on the left, *K. Bentii* on the right. The three figures tell their own story.

Very soon, however, the characters of the hybrid entirely changed. The leaves ceased to be entire, but became strongly pinnatisect with segments which were less and less flat and more and more stiletto-shaped. In these characters and in the mode of their development the whole batch of seedlings were absolutely uniform.

On Plate XXIII the details of the leaf-forms of the hybrid and its two parents are shown more in detail. It is to be observed that the earliest leaves of a shoot are always more or less rudimentary. And it is well known that rudimentary structures, not being immediately adaptive, often afford evidence of ancestral influence which is afterwards obliterated. In each case in the plate the rudimentary as well as the mature forms of the leaves are shown. In the case of *K. flammea* (Fig. 2) there is nothing that is not merely ordinary or which calls for remark. In the hybrid (Fig. 3) the earliest leaf may be thought to recall the crenulation of *K. flammea* exaggerated into teeth. But no crenulation will explain the pinnatisect forms into which the dentation is afterwards developed. In the case of *K. Bentii* (Fig. 1) it occasionally, though rarely, happens that one of the rudimentary leaves is strongly two-toothed. It seems possible, therefore, that the extraordinary character of the foliage of the hybrid derives from this parent, in which it was latent.

But I will pass on for the moment to the further development of the hybrid. The plants were grown on, and in their second year attained rapidly a height of about three feet,

rather less or more in individual cases. And they began to flower in May, 1902, when, therefore, about two years old. The appearance they then presented is shown in Plate XXI. This, however, gives only an imperfect idea of the singular appearance of the plants: the leaves were strictly decussate, i. e. each successive pair was set on the stem at right angles to those above and below. And the divisions were so uniform and symmetrical that they exactly corresponded when looked down upon from above.

The flowering of the hybrid was looked forward to with much interest, and when it occurred was a complete surprise. The majority of the plants flowered, and in every case the colour of the flowers was a clear rosy pink, recalling the tint of those of *Erythraea Centaurium*. In the case of a sudden variation or 'break' of this kind it is usual for the colour of the flowers to become highly variable. But in this case it seemed absolutely uniform, and I could not persuade myself that there was any difference between one individual and another.

I must confess that I was completely at a loss to explain how a bright pink could arise from a cross between an orange and a white. The explanation, however, occurred to my friend Dr. Lotsy, who, while staying at Kew, had been much interested in the hybrid. The orange colour of the flowers of *K. flammea* is due to deep yellow chromoplasts immersed in a pink cell-sap. In *K. Bentii* both chromoplasts and cell-sap are colourless. The hybrid has inherited the white chromoplasts of one parent and the coloured cell-sap of the other.

The foliage, however, exhibits in the adult plant no trace of the influence of *K. flammea*. But it is widely divergent from that of *K. Bentii*. *K. laciniata*, which extends from Tropical Africa through India to Java, has deeply pinnatifid leaves with sometimes linear segments. The leaves of *K. Schweinfurthii* from Abyssinia are also similarly divided. The conclusion seems irresistible that we have in the case of the hybrid a reversion to an ancestral character which



exists elsewhere in the genus but is latent in both parents. In attempting to explain how this comes about, I cannot better the theory of Delage: 'Il peut arriver qu'un caractère vraiment latent revienne au jour. Le croisement jette un grand trouble dans l'évolution de l'œuf, par ce rapport d'innombrables gemmules inattendues; certains caractères normaux sont aussi contrariés dans leur développement et des caractères anciens se développent à leur place' (Structure du Protoplasma, 580).

2. *K. Bentii* ♀ × *K. flammaea* ♂. A number of seedlings were raised which at first differed in no appreciable character from seedlings of the same age of *K. Bentii* as represented in Plate XXII. All were exactly alike, and exhibited at first no trace of hybrid origin. But though raised at the same time and subjected to exactly the same treatment as the reverse cross described above (which may be called *K. kewensis*), they at once showed a marked constitutional difference in the extreme slowness of their growth. When *K. kewensis* was three feet high, the plants of the reverse cross had only attained six inches. It is, however, interesting to note that after cultivation for two years and a half they have begun to develop the same pinnatisect leaves which are so characteristic a feature in *K. kewensis*. As none of the plants have yet flowered, what will happen then can only be a matter of conjecture. It is probable, however, that they will resemble those of *K. kewensis*, for as Darwin observes: 'Hybrids raised from reciprocal crosses . . . rarely differ in external characters' (Origin, 6th ed., 244).

It is clear that in the reciprocal crosses the influence of *K. Bentii* has been prepotent. This is in agreement with the facts cited from Gärtner by Darwin in regard to *Nicotiana* (Variation of Animals and Plants, ii. 67).

But *K. kewensis* exhibits in the most striking way a character in the foliage which cannot be attributed to either parent. If I am right in attributing this to reversion, it presents a striking exception to the principle laid down by Gärtner and accepted by Darwin: 'Reversions rarely occur

with hybrid plants raised from species which have not been cultivated, while with those which have been long cultivated they are of frequent occurrence. . . . Max Wichura, who worked exclusively on willows, which had not been subjected to culture, never saw an instance of reversion' (Darwin, loc. cit., 50). I have already quoted Darwin's dictum that: 'As a general rule, crossed offspring in the first generation are nearly intermediate between their parents, but,' he adds, 'the grandchildren and succeeding generations continually revert, in a greater or less degree, to one or both of their progenitors.' It is to this fact, I suppose, that an attempt is made to give expression in what is called Mendel's law. It would have been very interesting to have seen what would have happened to *K. kewensis* in succeeding generations. Unfortunately, so far every attempt to raise seedlings from it has failed. The capsules form with every promise of fertility, but only contain shrivelled rudiments of seeds. But had this been otherwise, it by no means follows that its characters would have shown any dissociation. Wichura 'found in opposition to Naudin that the progeny of hybrid willows retains its hybrid character' (Romanes, loc. cit., 426).

While writing these lines the important paper by De Vries (Comptes rendus, 2 Fevr., 1903, pp. 321-3) comes into my hands. It confirms the suspicion which I have long entertained that Mendel's law is not of universal application. De Vries lays it down that: 'La loi de Mendel s'applique aux caractères dits de variété, tandis que les caractères spécifiques vrais donnent dans leurs croisements des caractères d'hybrides constants.' Such characters 'ne se disjoignent pas; ils restent les mêmes dans les générations successives. J'ai vérifié ce fait par quatre générations d'un hybride entre les *Enothera muricata*, L., et *Æ. biennis*, L., et j'ai étudié à ce point de vue différents autres hybrides, notamment dans le même genre.'

The explanation depends probably on the principle of specific stability, on the importance of which I have elsewhere insisted. From this point of view a hybrid may carry

over the stability of its parents, though it may not necessarily do so. In other words, the resultant of the fused parental characters may be as stable as their components. But when a species is varying, i. e. producing varieties, its stability is for the time lost, and there is nothing to prevent the dissociation of the fused characters and of their constituents, or their recombination in every possible way.

And I am confirmed in this opinion by the statement of Bateson that there is 'one group of cases, definite though as yet not numerous, where we know that the Mendelian principles do not apply' (Principles of Heredity, pp. 34, 35). The remainder of the passage is too long to quote, but may be referred to with advantage by those who are disposed to pursue a fascinating subject.





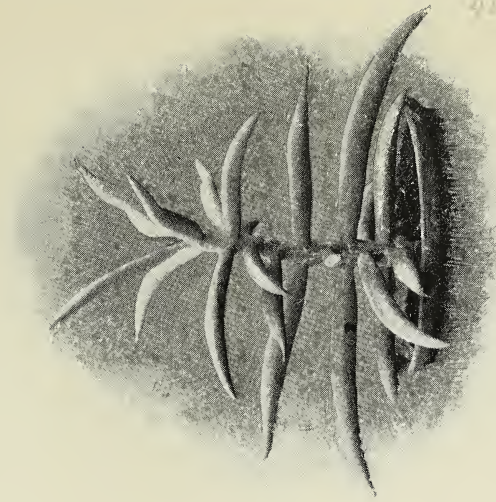
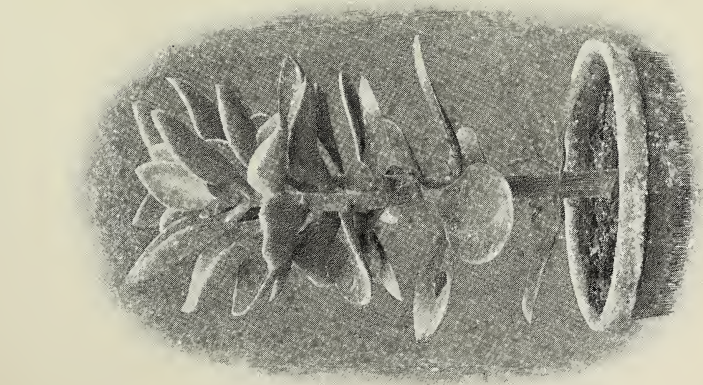
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THISELTON-DYER.—KALANCHOE HYBRID.

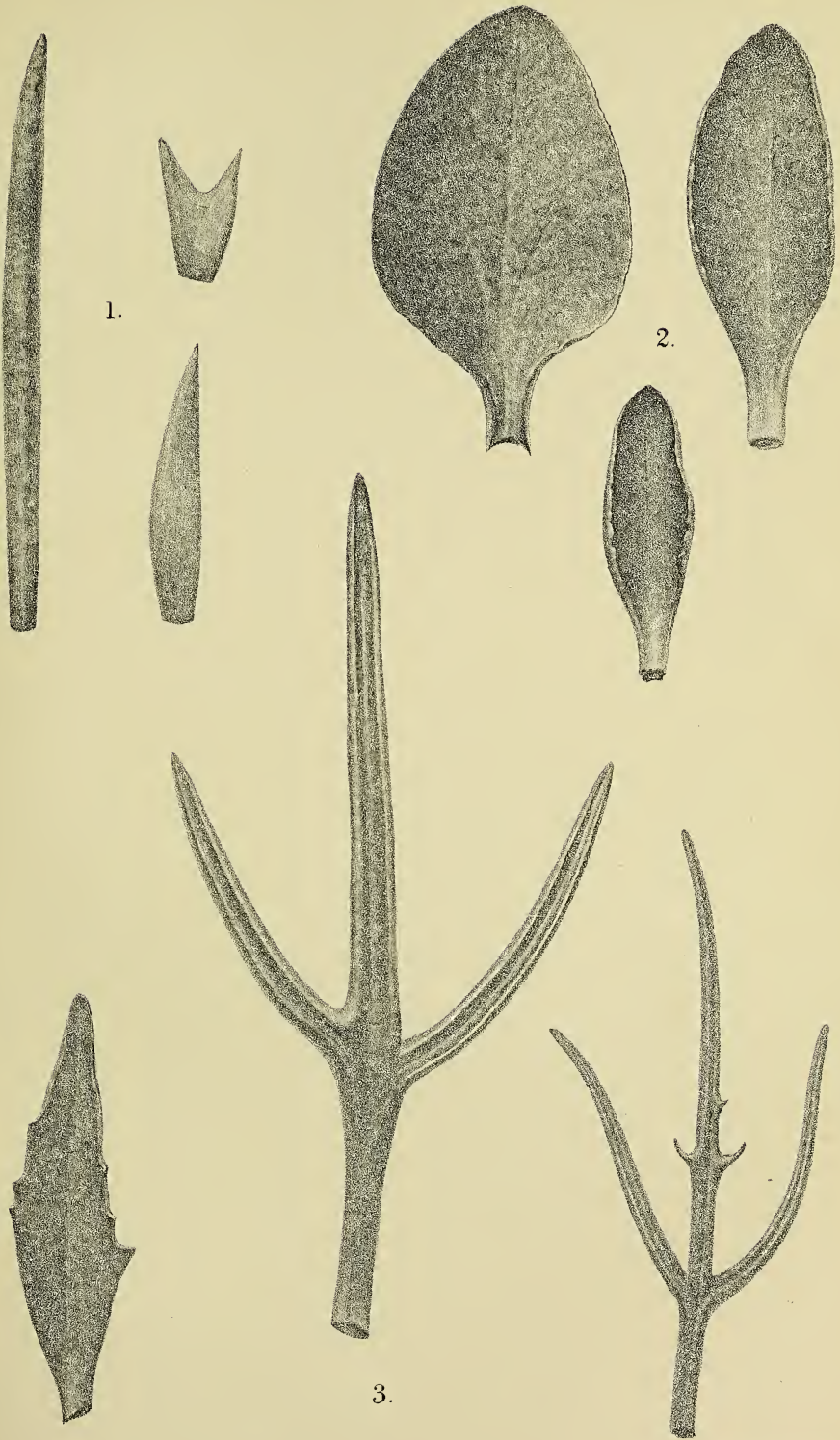






THISELTON-DYER. — KALANCHOE HYBRID.





THISLTON-DYER. — KALANCHOE HYBRID.





## NOTES.

**DIAGNOSES SPECIERUM GENERIS JULIANA, SCHLECHT.,  
AMERICAE TROPICAE.** Auctoribus W. BOTTING HEMSLEY et  
J. N. ROSE.

Arbores mediocres et frutices Mexici et Peruviae incolae, dioicae, adspectu *Burserae* specierum nonnullarum. Folia decidua, alterna, imparipinnata, in apicibus ramorum hornotinorum floriferorum conferta, foliolis oppositis diverse dentatis. Flores masculi parvi, numerosissimi, in amenta vel racemos compositos axillares gracillimos pendentes dispositi; perianthium simplex, tenuissimum, 6-8-partitum, segmentis linearibus acutissimis; stamina isomera, quam perianthii segmenta paullo breviora; gynaecei rudimentum nullum. Flores feminei e solis pistillis constantes, saepius quatuor receptaculo fere clauso inclusi, collaterales (haud concentrici, i. e. circa axin centralem positi), duo exteriores saepissime imperfecti, abortivi. Receptacula parva, per anthesin obscura, circiter semipollicaria, axillaria, pedunculata, gemina singulave, erecta, apice minute paucidentata. Ovarium uniloculare, uniovulatum, stylo tripartito e receptaculi orificio exserto. Fructus cum pedicello plano-compresso dilatato corpus indehiscens apice incrassatum deorsum alatum formans, pendulus; ala e basi cuneata sursum sensim oblique vel aequilateraliter dilatata. Semen unicum, in fundo loculi affixum, perispermo nullo; embryo horizontalis, radícula elongata cotyledonibus plano-convexis accumbente.

*Juliania adstringens*, *Schlecht. in Linnaea*, vol. xvii. (1843), p. 746,  
*Hemsl. in Hook. Ic. Pl.* tab. 2723.

Folia quoad foliolorum numerum, circumscriptionem ac magnitudinem valde variabilia, primum plus minusve hirsuta, demum glabrescentia, nunc in eodem ramo omnia 3-foliolata, nunc in eodem ramo alia 3-foliolata alia 5-foliolata, interdum 5- vel 7-foliolata vel omnia 7-foliolata, cum petiolo communi 2-7 poll. longa; foliola crasse papyracea, sessilia vel brevissime petiolulata, saepius obovata vel oblanceolata, plerumque supra medium latiora et diverse crenata vel serrata, rarissime usque ad basin dentata, basi saepius cuneata, apice

[*Annals of Botany*, Vol. XVII. No. LXVI. March, 1903.]

gradatim vel abrupte acuminata, obtusa, rotundata vel truncata, maxima 3 poll. longa et 2 poll. lata, sed saepius multo minora; venae primariae costae utrinque circiter 10-12. Pedunculi fructiferi brevissimi. Fructus pendulus, oblongus, basi cuneatus, rectus vel plus minusve obliquus, 1-2 poll. longus, tarde glabrescens.—*Hypopterygium adstringens*, Schlecht. in *Linnaea*, vol. xvii. (1843), p. 635. *Amphipterygium adstringens*, Schiede in schedula, ex Schlecht., loc. cit., p. 746.

**Mexico Australis**: Morelos, *Schiede*; alt. 5,000 ped., *Pringle*, n. 7,243 et 8,533; *Rose et Hay*, n. 5,341; Michoacan et Guerrero, *Langlassé*, n. 319 bis; Oaxaca, *Nelson*, n. 1,706 et 1,827.

***Juliania mollis*, Hemsl. in Hook. Ic. Pl. tab. 2722.**

Folia juvenilia omnino albido-villosa, 3- vel 5-foliolata, petiolo communi 2-5 poll. longo; foliola crassa, sessilia vel brevissime petiolulata, oblonga, ovato-oblonga, elliptica, vel terminali distincte petiolulato, interdum fere orbiculari, 1-2 poll. longa, crenato- vel serrato-dentata; venae primariae costae utrinque circiter 10, venis ultimis ob indumentum obscuris. Fructus ignotus.—*Amphipterygium molle*.

**Mexico Australis**: Barranca de Guadalajara, Jalisco, alt. 4,000 ped., *Pringle*, n. 6,871.

***Juliania amplifolia*, species nova.**

Folia juvenilia molliter villosula, adulta glabrescentia, 7- vel 9-foliolata, 6-15 poll. longa, petiolo communi subtereti; foliola mollia, papyracea, crassiuscula, brevissime petiolulata, lanceolata vel ovato-lanceolata, maxima  $3\frac{1}{2}$ - $4\frac{1}{2}$  poll. longa, sed saepius 2-3-pollicaria, acuminata, interdum longe acuminata, acuta vel acutissima, basi saepius rotundata, crenato-serrata vel interdum argute serrata; venae primariae numerosae. Pedunculi fructiferi  $\frac{1}{2}$ -1 poll. longi, validi. Fructus glaber vel cito glabrescens, pendulus, obliquus,  $1\frac{3}{4}$ - $2\frac{1}{4}$  poll. longus, pedicello dilatato usque ad 1 poll. diametro.—*Amphipterygium amplifolium*.

**Mexico Australis**: Jalisco et Durango, *Pringle*, n. 5,002; *Rose et Hough*, n. 2,302, 3,735, 4,755, et 4,819.

***Juliania glauca*, species nova.**

Folia glabra vel cito glabrescentia, subtus glauca, 3- vel 5-foliolata, petiolo communi gracillimo subtereti  $2\frac{1}{2}$ - $3\frac{1}{2}$  poll. longo; foliola papyracea, nisi terminale distincte petiolulatum sessilia, lanceolata, ovato-lanceolata vel oblanceolata, sine petiolulo  $1\frac{1}{2}$ -3 poll. longa, acuta,



basi saepius cuneata, margine leviter incrassata, praecipue supra medium crenulata, vel dentata; venae primariae utrinque circiter 10, venis ultimis minute reticulatis. Pedunculi fructiferi graciles, 1-1½ poll. longi. Fructus pendulus, cum pedicello dilatato circumscriptione pyriformis, 1½-2 poll. longus, glaucus.—*Amphipterygium glaucum*.

Mexico Australis: Jilotlan, Michoacan, *Lumholtz*.

*Juliania Huaucui*, *A. Gray*, *U. S. Expl. Exped.*, vol. i. p. 371.

Folia primum tomentosa demum, saltem supra, glabrescentia, saepissime 7-foliolata, petiolo communi gracili tereti 2-3 poll. longo; foliola mollia, papyracea, sessilia vel brevissime petiolulata, oblonga vel ovato-oblonga, maxima visa vix sesquipollicaria, saepius utrinque rotundata, crenulata; venae primariae utrinque circiter 12, venis ultimis obscuris. Pedunculi fructiferi brevissimi. Fructus pendulus, fere linearis, 2½ poll. longus et medio 4-5 lin. latus, glaber vel glabrescens.—*Amphipterygium Huaucui*.

Peruvia Occidentalis: *A. Mathews*, n. 591; *A. J. Maclean*, sine numero.

#### *Explanatory Note by W. B. H.*

In 1843 Dr. F. L. von Schlechtendal described a Mexican tree at considerable length (*Linnaea*, vol. xvii. pp. 635-8) under the name of *Hypopterygium adstringens*, which he subsequently (op. cit. p. 745) changed to *Juliania adstringens*. In the same place Schlechtendal concludes with the following statement: 'Epitheton adstringens a beato amico [Schiede] in schedula datum verosimiliter vim adstringentem hujus arboris indicat. Amici nomen genericum *Amphipterygium*, quum ala basalis tantum nec cingens adsit, rejecimus<sup>1</sup>.' With regard to its position in the Natural System he could only indicate remote affinities to various orders. Bentham and Hooker (*Genera Plantarum*, vol. i. p. 428) placed it doubtfully at the end of the Anacardiaceae. Engler (*DC. Monogr. Phanerog.* vol. iv. p. 500) places it in the 'genera ex Anacardiaceis excludenda,' adding: 'Quamvis canales resiniferi

<sup>1</sup> It is a pity that Schlechtendal did not adopt Schiede's generic name *Amphipterygium*, especially as he gave publicity to it himself, because both *Hypopterygium* and *Juliania* had already been used, and his objection to Schiede's name is unsound, the fruit being winged on both sides of the axis. As it is not improbable that Schiede's name will be revived by somebody, we have repeated our names under *Amphipterygium*, though we should prefer retaining *Juliania*.

adsint, attamen non tales sunt quales in Anacardiaceis observantur. Planta locus systematicus, cum flores nondum cogniti sint, mihi plane dubius remanet.'

In the Botany of the Biologia Centrali-Americana, having no specimens before me, I could do no more than record the name; and it was not till 1901, when Kew acquired specimens of the male of my *J. mollis*, and fruiting specimens of what I take to be the original *J. adstringens*, that I was able to throw a little more light on the subject by publishing (Hooker's *Icones Plantarum*, t. 2722 et 2723) figures of the structure, so far as the material permitted. This was done with the idea of directing attention to this singular genus, and of obtaining better specimens. It resulted in Dr. J. N. Rose, Assistant Curator of the Botanical Collections of the United States National Museum at Washington, generously offering to procure for me the privilege and advantage of examining the whole of the material belonging to that Institution, collected partly by himself, partly by Messrs. Pringle, Nelson, Lumholtz, Hay, Langlassé and Hough, together with his notes. At the present time we are engaged on a fully illustrated monograph of the genus, including an account of its anatomy and organogeny by Dr. F. E. Fritsch; and in that we shall fully discuss its affinities. This preliminary communication, it is hoped, will bring us further material of some of the species; more female flowers especially are wanted to enable us to complete our researches. I may add that Dr. A. Engler, of Berlin, Dr. C. Mez, of Halle, and Dr. A. Zahlbruckner, of Vienna, have failed to find any of the original specimens collected by Dr. C. J. W. Schiede, the discoverer.

**NOTE TO ARTICLE IN THE ANNALS OF BOTANY, VOL. XVI, NO. 63, SEPTEMBER, 1902, ON 'THE "SADD" OF THE UPPER NILE.'**

*Grasses of the 'Sadd.'*

At p. 501 of the *Annals of Botany*, in the article above cited, Sir William Garstin, the Under-Secretary to the Government of Egypt, in the Public Works Department, was quoted by me as saying that a specimen of the 'umsoof' grass, *Vossia procera*, which had been sent to the British Museum, was there identified as *Phragmites communis*. And Sir William did not mention it anywhere in his report as being one of the components of 'Sadd'; nor, so far as I had

observed, did Dr. Schweinfurth mention it in the works I quoted from. But it was difficult to believe that the botanists of the British Museum could have made the mistake imputed to them. After the article was published I read Sir Harry Johnston's 'The Uganda Protectorate,' and found in it a description of the 'Sadd,' in which, after describing the growth of the Papyrus plant, he says:—

'A long *Phragmites* reed, with fluffy-like plumes like the Pampas grass, grows out into the shallow water, and builds barriers into the stream which arrest the floating islands of papyrus; or this reed may form floating islands of its own. Papyrus may prosper so much on the floating islands, composed mainly of its own roots, that these roots may reach the thickness of a man's leg, and grow downwards twenty feet below the top of the floating islands.'

Next, my attention was drawn to the paper on 'The Botany of the Speke and Grant Expedition,' published in the Transactions of the Linnean Society, London, vol. xxix, in which, at p. 173, was found the following:

'19. *Phragmites communis*, Trin.; Kunth, Enum. Pl. i, 25. *Arundo phragmitis*, L., App. Speke's Journ. 653. Hab., from 4° 55' N. lat. and northward, Col. Grant! A cosmopolitan species.

'[Reed in Unyoro marshes, 21st Sept. 1862. Not in flower. 8 feet high, erect, round stem, tubular between the joints. Leaves 2 spans long, 2 inches broad at their bases, stiff, smooth, not filed at their edges or on their surfaces, alternate, their bases clasp the stem, and grow regularly in one plane from the right and left sides only.

'Native name and uses: "Mataetae." The flutes and whistles of the Waganda are made of this reed. It is said to grow as thick as the arm in Nyassa, 11° S. lat., where the natives make a fence of it. . . . It extends in one great sea for 1,100 miles north of 4° 55' N. lat.—J. A. G.]'

From all this it is clear that Sir William Garstin, or the officer under him who collected the specimens of the 'Sadd' plants which were sent to the British Museum, possibly owing to absence of inflorescence, failed to distinguish between the two large grasses which probably were growing together in the same 'Sadd.'

*Phragmites communis* is the largest grass indigenous to Britain; and in the Dehra Dún district, and other parts of British India, it covers square miles of swampy ground, and is commonly called Elephant or Tiger grass, from its size, 15 to 20 feet in height, or,



perhaps, from affording shelter to those large animals. The vernacular name in the Dehra Dún is *nál*. It there grows on land which is submerged during floods as well as in actual swamp; and amongst it I have seen, drawn up by its shelter and support, the fern *Asplenium* (*Anisogonium*) *esculentum*, Presl., 9 to 12 feet high, with a subarborescent caudex, 6 to 12 inches high. This is not the usual habit of the fern, which in the same locality, outside the *nál*, grows in clumps 3 to 4 feet high. Elsewhere in the Dún, it is a hedge-and-ditch-row plant.

‘*Sudd*’ v. ‘*Sadd*.’

As to the pronunciation and spelling of the word ‘*sudd*’ or ‘*sadd*,’ the following is found in Sir Harry Johnston’s book, vol. i. p. 149. ‘The “*Sudd*” (which should really be spelt “*sadd*”<sup>1</sup>—Schweinfurth first refers to it as “*satt*” or “*sett*”) is, as most untravelled people now know, an extraordinary floating vegetable obstruction which collects in the waters of these equatorial lakes and rivers where the lake surface is sheltered from rough winds, and where the current of the river is sluggish. Papyrus clumps become detached by the action of the waves or floods, and, driven by the breeze into little groups, these roots become united below the surface of the water by the accretion of water-reed and other vegetable substances, so that in time a peaty mass is formed just below the surface of the water, from which the Papyrus continues to grow as from a soil.’ (Then follows the passage quoted above, showing the part *Phragmites communis* plays in the formation of a ‘*Sadd*’ block.)

Though Sir Harry Johnston explained that the word ‘*Sadd*’ is Arabic, and said how it is to be pronounced, he did not tell us what it really means, or how it is otherwise used. But this has lately become known to people who are not acquainted with Arabic from contributions to the Press in connexion with the completion of the great dams across the Nile, which were alluded to at the outset of the article in the Annals of Botany to which this is a supplement. In a description of the works which were found necessary in the construction of the great dam at Assuan, I find mention of the considerable work ‘done in connexion with *sadds* (*sic*) or temporary dams across three out of the five deep channels which cross the

<sup>1</sup> ‘It is an Arabic word pronounced like the “*sud*” “in soapsuds”; but this is really a short sound of the vowel “*a*” in phonetic spelling.’

line of the dam and carry the supply of the Nile during summer and winter. . . . The method adopted for dealing with these deep channels was to construct "sadds" across them upstream and downstream of the site of the dam; these sadds were then made sufficiently watertight to allow of the area between them being laid dry by pumping. It was necessary to make the sadds on one side of the dam of stones so as to stand the great rush of water: these sadds were made before the great rush of water, to a level of 5 mètres below high Nile, and on the north side of the dam. Thus, when the flood was subsiding, still water was easily obtained upstream of the sadd, and a sandbag sadd was commenced on the other side, so that the three channels were cleared by the end of the year.' And the word 'sadd,' as meaning a temporary or subsidiary dam, of earth or stone work, is found in other parts of the article now being quoted from. It seems probable the use of the word 'sadd,' as the name for the vegetable obstructions in the Upper Nile, was taken from the ordinary use of the word on lower parts of the river where irrigation has long been in vogue. The smallest kind of sadd is the two or three spadeful of earth with which the cultivator (in India at least) turns canal or rain water from one compartment of a field into another.

*The Clearing of the 'Sadd.'*

A recent number of the Geographical Journal contains a paper on the 'Sadd' of the White Nile, by Dr. Edward S. Crispin, explaining the method of opening up the true river bed employed by Major Matthews, who commanded the Sadd Expedition of 1901-2. The first difficulty is to find the position of the river bed; this is done by probing, the depth suddenly increasing to 15 to 20 feet. Next, the top growth, consisting mostly of Papyrus, is cut down or burnt. Men are then landed on the cleared surface, and the sadd cut along the river banks with saws; next transverse cuts are made, dividing the sadd into blocks convenient for the steamer to tear out. The bows of the steamer are run into the block, and the loop of a steel hawser, both ends of which are made fast to the steamer, is passed over the bows and trodden into a trench cut on the surface of the block. The steamer then goes full speed astern, men standing on the hawser to keep it in position, and after a number of trials the block is torn away and cast adrift to float downstream, where it is gradually disintegrated.

*Plants allied to the Ambatch.*

From The Botany of the Speke and Grant Expedition; Trans. Linn. Soc. vol. xxix, p. 58, the following may be taken:—

'36. *Æschynomene Schimperii*, Hochst., in Hb. Schimp. Abyss. No. 202; A. Rich. Fl. Abyss. i. 202; Baker in Fl. Trop. Africa, ii. 146.

'*Hab.* By the Nile, Nov. 1862, Col. Grant. This is a form of the Abyssinian plant, from which it may possibly prove distinct when more ample material shall have been obtained.

[. . . 'A wide-spreading branched tree, 20 feet high, in or by water at Unyoro, with the Papyrus. . . . The wood is white, and streaked with black longitudinally. It is so remarkable for lightness that I measured a log  $4\frac{1}{2}$  feet long and 15 inches in mean circumference, and it weighed only  $2\frac{1}{2}$  pounds. It is a most useful wood to the inhabitants, as they make floats, levers for carrying their loads, blocks to cut upon, bolts for their doorways; and for shields no wood can equal it for toughness and lightness, two qualities requisite in the shield of the Uganda people. It would make admirable sun hats.—J. A. G.]

'37. *Æ. indica*, Linn.; DC., Prod. ii. 320; Baker in Fl. Trop. Africa, ii. 167; Wight Ic. t. 405.

'*Hab.* Unyoro, Sept. 1862, Col. Grant! Widely spread in Trop. Africa and Asia.

[Native name "m'neenge" (Zanzibar). Plentiful everywhere: at 5° S. lat.; in the dry season (September) its dead stem was prostrate on the dried mud; but at 2° N. lat., in the same month it was in leaf and fruit. Though only growing straight to 6 or 7 feet high, the thickest part of the stem measures large in proportion, 16 inches in circumference.—J. A. G.]

C. W. HOPE.



# The Ovules of the older Gymnosperms<sup>1</sup>.

BY

F. W. OLIVER.

—♦—  
With Plate XXIV and a Figure in the Text.  
—♦—

THE seeds of most recent Conifers are fully siphonogamous, and their organization exhibits an adaptation in complete harmony with this type of fertilization—the most perfect that has been evolved by aërial plants. But if there is any conclusion in phylogeny on which we may confidently rely, it is that the method of fertilization by pollen-tubes has been evolved from zoidiogy, the type of fertilization characteristic of an aquatic ancestor. The discovery of motile spermatozoids in the Cycads and in *Ginkgo* indeed places a coping-stone on the edifice of Hofmeister's generalizations.

The pollen-tube of the Conifer affords so simple and direct a means of effecting fertilization that we recognize that an ovule of relatively simple construction offers adequate facilities for the accomplishment of this process. But the instant we turn to *Cycas* or *Ginkgo*, where zoidiogy prevails, the ovule is seen to be much more complex. Not only do we find a special chamber excavated in the apex of the nucellus for the reception of the pollen, but the ovule is also provided

<sup>1</sup> This article is based on a lecture delivered by the writer before the Botanical Section of the British Association for the Advancement of Science at its meeting in Belfast, September, 1902.

with a fairly complicated vascular system. When we pass from these most archaic of living Phanerogams to the various Gymnospermous seeds found in the palaeozoic rocks, seeds which there is every reason to believe possessed an even less specialized type of zoidiogamy than obtains in recent Cycads, we are struck with the importance and dimensions of the pollen-chamber and with the very complicated vascular system which embraces the body of the nucellus. These older seeds needed to be complex to neutralize the disadvantages of their ancestry. In them, whilst the macrospore is retained, the microspore still liberates spermatozoids on the nucellus. The arrangement, viewed in the light of what we find in more recent plants, may be a clumsy makeshift, but it was probably an essential link in the evolution of more perfect arrangements. The central principle of zoidiogamy is still there, hedged about by contrivances so that it may be carried out, independent of chance water-supply, by land-growing plants. With the appearance of siphonogamy these contrivances became obsolete, and the modern ovule is a reduced and comparatively simple structure from which traces of the ancestral history have in large degree vanished.

The object of the present paper is to draw attention to the details of some of these older seeds, and to trace the modifications that seem to have occurred *pari passu* with the evolution of more perfect methods in the transportation of the male cells. And in so doing it is hardly possible to ignore certain other changes that have taken place in the structure of the ovule, changes involving an enlargement of its functions so that it has become as well a temporary resting-place or brood-chamber for the embryo. The discussion in the following pages will include a consideration (1) of the ordinary palaeozoic types of seed so well represented in the French permo-carboniferous and described by Brongniart and Renault; (2) of *Lagenostoma*, a peculiar type found in the lower coal-measures of Lancashire and Yorkshire, and standing somewhat apart from the French palaeozoic seeds; (3) of recent Cycads; and (4) of *Torreya*, a remark-

able genus of Taxaceae, which though siphonogamous yet appears to retain marked traces of those contrivances which usually became obsolete when siphonogamy appeared. Finally we can hardly close this article without some allusion to such elementary seed-like structures as have been described, with a view to linking up the Seed Plants with the true Pteridophytes. But in this department, though facts that will be of the greatest value hereafter have already come to light, some time must elapse before we are able to realize step by step the manner of origination of the earliest seeds.

#### 1. ORDINARY PALAEOZOIC SEED TYPES.

These in their simplest form are represented by *Stephanospermum*<sup>1</sup>, a small unassigned seed some 10 mm. in length, 5 mm. in diameter, and circular in transverse section. This seed may be taken as the type of a group of radially symmetrical seeds—many with ridges and other excrescences often fantastic in character. For convenience all such forms were ranged together provisionally by Brongniart, and for the sake of easy reference may be termed the Radiospermeae (= Brongniart's Group B)<sup>2</sup>, in contradistinction to the flattened seeds or Platyspermeae (= Brongniart's Group A) of which a few are known to belong to the Cordaiteae.

The members of these two provisional groups differ in other respects than in their form. Whilst the Radiospermeae, with rare exceptions<sup>3</sup>, possessed a bony integument only, the Platyspermeae were in all cases provided with an additional external fleshy layer, the sarcotesta. And there were further differences in the internal organization of these two groups, though they are not of such a character as to upset the broad general resemblance that embraces all these seeds. In the briefest possible manner a type from each group may now be

<sup>1</sup> Cf. Brongniart, *Les graines fossiles silicifiées*, Pl. XVI.

<sup>2</sup> Brongniart, *loc. cit.*, p. 20.

<sup>3</sup> *Trigonocarpus pusillus*, Brongniart, and *Tripterosperrum*, in the sense of Brongniart. Cf. *loc. cit.*, p. 26, footnote. These had a sarcotesta in addition to a bony sclerotesta.



described, *Stephanospermum* as a Radiosperm, *Cardiocarpus* as a Platysperm.

*Stephanospermum* is a small cylindrical seed with sharply-pointed apex. It consists of a straight nucellus enclosed in a hard bony integument. The chalaza is at the base, the micropyle at the apex. Its general organization may be apprehended by reference to Pl. XXIV, Fig. 10. This diagram is drawn for another purpose, but if the outer light layer of the integument and the red strand which runs along its inner margin be ignored, and the entering chalazal bundle be regarded as quite simple (as it is in Fig. 1), then we have an ordinary Radiosperm. A special study of *Stephanospermum* seems to show that the nucellus stands up freely within the integument, and though this is a point of some importance it is one that has been definitely ascertained in relatively few of these seeds. The apex of the nucellus is occupied by an extensive pollen-chamber which is accurately centred to the micropyle, with which its perforated apex seems to have engaged. The body of the nucellus is occupied by the macrospore and its contained prothallium. The chalazal strand of tracheides expands at the base of the nucellus into a tracheal plate, the margins of which are continued in the wall of the nucellus right up to the pollen-chamber, the floor of which is paved with tracheides. The contained macrospore is thus completely invested in a thin mantle of tracheides. This mantle is exposed in Fig. 10, and is represented by a wash of red. Whilst some of the Radiosperms resembled *Stephanospermum* in possessing a continuous tracheal mantle, there were others in which the tracheides had become segregated into distinct strands<sup>1</sup> (as shown in the nucellus of Fig. 1).

The pollen-chamber often contains a number of large pluricellular pollen-grains that had been sucked into it no doubt in the ordinary way. Here it would seem they underwent a

<sup>1</sup> This was the case in *Tripterosperrum*, *Gnetopsis*, *Codonospermum*, and *Aetheotesta*. In *Polylophospermum*, the intermediate condition of a coarse-meshed reticulum is sometimes found, perhaps the result of an enlargement of the nucellus.

period of maturation, and in due course liberated free-swimming spermatozoids. It is true spermatozoids have never been certainly recognized in these seeds, but that is a matter of small importance. The apex of the nucellus of *Cycas* and *Ginkgo* is similarly organized as a pollen-chamber, and in these cases it is well known that spermatozoids were liberated. But *Stephanospermum* is an older seed and exhibits more primitive characters than do the Cycads. Were fertilization effected by pollen-tubes the whole structure of the seed would be a contradiction. Whether or no the discharge of spermatozoids was accompanied by pustule-like projections from the surface of the grain is an open question. Such projections, very small in relation to the diameter of the pollen-grain, have been occasionally observed. The stage at which almost all these seeds have been preserved is that just preceding fertilization; only occasional specimens being met with in a slightly earlier stage of development. In referring to them the term *seed* is usually employed, though in recent Gymnosperms the corresponding stage would be called an unfertilized ovule. This usage in terminology has doubtless arisen from the appearance of maturity which their integumentary tissues present, a maturity which seems to preclude all possibility of subsequent expansion. In course of evolution, probably, the time of hardening of the integument was postponed till embryonic stages had set in, so that well-marked ovular and seed phases became recognizable; but in the palaeozoic seeds known to us such a distinction can hardly be drawn.

Whatever their differences in detail, the Radiosperms agree in that the nucellus is invested in a tracheal mantle or a number of tracheal strands, which, arising from the chalazal bundle, meet below the pollen-chamber, the floor of which they seem to have paved. Nor does their function seem difficult of interpretation. It was that of a mechanism for bringing water to the pollen-chamber. This would be important during the period of pollen-maturation and vital to the transport of motile spermatozoids at fertilization.

The pollen-chamber shows every indication of having been

excavated in the apex of the nucellus through a mucilaginous breakdown of the tissue there; and should the watery mucilage tend to concentrate through desiccation, fresh supplies of water would be drawn up from the tracheal system. Ultimately there is reason for supposing that the way to the archegonia (which lie much as in *Cycas*) was cleared for the passage of the spermatozoids by a further mucilaginous breakdown in that portion of the tracheal sheath which overlaid the summit of the macrospore; but in the tracheides outside the area of the pollen-chamber no such change is indicated. Whether it may not have happened in allied seeds that the nucellar tracheides stopped short from the first at the margin of the pollen-chamber, so that the necessity for their solution prior to fertilization did not arise, is a question difficult to answer. For it must be borne in mind that it would be difficult to discriminate between such a case, and one in which the tracheides had been locally absorbed. That is, of course, unless the state of preservation were remarkably good and the appropriate developmental stages forthcoming.

As regards the number of pollen-grains usually present in a pollen-chamber, it is impossible to speak other than broadly in consequence of the fact that even when a series of sections is obtained there is a considerable loss as a result of cutting and grinding. In the case of *Stephanospermum*, from twelve to twenty does not seem too generous an estimate; and if each of the twenty cells or so of which each pollen-grain consists be regarded as producing a single spermatozoid, that would allow from 240 to 400 of the latter. The distance to be traversed in the passage from the pollen-grain to the archegonium varies in this seed from .5 to .85 mm.

It will have been gathered from the foregoing that whilst the problem of water-supply in relation to free-swimming spermatozoids stood on a satisfactory footing, there still remained room for advance in the direction of greater precision in the mechanism as a whole. We still appear to have the promiscuous liberation of motile spermatozoids reminiscent of a heterosporous Pteridophyte.



Turning now to the Platysperms, we may take *Cardiocrarpus* as their type. It is characterized by its flattened, heart-like form, and by the possession of a sarcotesta. As the supply-bundle enters at the chalaza and traverses the sarcotesta, it gives off a pair of bundles which run along the inner limit of that layer to the micropyle (as in Fig. 1). The plane in which these two bundles run is the plane of flattening, generally designated the principal plane of the seed<sup>1</sup>. The main bundle continues to the base of the nucellus, where it expands into the tracheal plate. From the margins of this plate a number of nucellar strands pass off peripherally in the wall of the nucellus and extend a variable distance in the direction of the pollen-chamber. And now we come to a difficulty not infrequent in the investigation of fossil seeds, the inadequacy of the preservation. In the first place there is some uncertainty as to the extent of freedom that obtained between nucellus and integument, and secondly as to the actual extent of the nucellar vascular system. If we turn to the works of the French investigators who have described these seeds, the impression gained is that the lower part of the nucellus is fused with the testa and that the tracheal strands travel upwards in the plane of fusion, ceasing where the nucellus becomes free. Brongniart's figure of one of these seeds, *Taxospermum Gruneri*<sup>2</sup>, shows very clearly that the fusion in this case involved the basal fifth of the nucellus, but unfortunately the tracheides are not represented in his plate. Renault makes some allusion to the question, and speaks of the nucellar bundles reaching up to about one-third the height of the nucellus<sup>3</sup>. So that as far as the data are available it would seem quite probable that a certain

<sup>1</sup> In others of the Platyspermeae the entering bundle passes unbranched to the tracheal plate, the margins of which supply the nucellus in the usual way. The bundles for the sarcotesta, however, are inserted upon the under face of the tracheal plate, and running outwards and backwards penetrate the sclerotesta and curve round into the sarcotesta. This type is only a slight modification of that figured, and the two types occur in seeds so nearly resembling one another as to have been included by Brongniart under the same genus.

<sup>2</sup> Brongniart, loc. cit., Pl. XV, Figs. 1 and 2.

<sup>3</sup> B. Renault, Cours de bot. fossile, I, 1881, pp. 100-1c.

amount of fusion obtained amongst the Platysperms, and that the internal vascular system was restricted approximately to that zone. But it would be interesting to know, should the preservation permit of it, whether, and if so to what extent, the tracheal elements passed beyond the line of separation of nucellus and integument. For the structure of the seeds and the relations of the bundles recall in a very marked degree Cycadean characters (cf. Figs. 4 and 6). It is known that in certain Cycads (e.g. *Bowenia* and *Stangeria*<sup>1</sup>) the inner system of bundles does not lie quite in the plane of fusion of nucellus and integument, but that the bundles exhibit a centrifugal tendency and actually lie outside the arbitrary province of the nucellus, as determined by the downward continuation of the plane of separation of the free regions of nucellus and integument. Renault has noticed this centrifugal tendency in Brongniart's seed *Cardiocarpus Augustodunensis*, and in view of this point of contact with certain Cycads he has founded the new genus *Cycadinocarpus* for its reception<sup>2</sup>.

In other respects, too, the Platysperms exhibit Cycadean features, among which may be mentioned the relatively small pollen-chamber as compared with the Radiosperms, whilst often, as W. H. Lang has pointed out, the cells of the beak of the nucellus are thickened in a corresponding manner<sup>3</sup>. The pollen in the pollen-chambers of these seeds is generally smaller in size than the elliptical multicellular pollen so frequently associated with the Radiosperms. Here, too, there is an internal cell-group, but it by no means fills the entire grain. That it was antheridial in nature, as suggested by D. H. Scott<sup>4</sup>, rather than a vegetative prothallium, seems very probable. Whether spermatozoids were liberated directly from these pollen-grains, as has been suggested in the case of *Stephanospermum*, or whether they were led part of the way to the archegonia in tubes, as in recent Cycads, is a question

<sup>1</sup> I am indebted to Dr. W. H. Lang for much information concerning these and other Cycadean ovules.

<sup>2</sup> *Flore fossile d'Autun et d'Épinac*, pt. ii, p. 385.

<sup>3</sup> W. H. Lang, *Annals of Botany*, vol. xiv, p. 286.

<sup>4</sup> D. H. Scott, *Studies in Fossil Botany*, 1900, p. 436.

that cannot be considered, owing to the lack of data. It is just possible, of course, in view of the distinctly Cycadean tendencies of the Cordaitean seeds themselves, that this parallelism also involved the pollen; or, on the other hand, as D. H. Scott points out, the pollen-grains of *Cordaites* may have been a stage nearer the Cryptogamic microspore than those of *Cycas* or *Ginkgo*<sup>1</sup>.

From what has been stated above it is evident that the Platyspermic (or Cordaitean) seeds must be carefully discriminated from the Radiospermic. The former show a marked approach to a parallelism with the ovules of recent Cycads, whilst the latter appear to exhibit more general and perhaps more primitive characters. That all these seeds belonged to plants of common or remote ancestry there can be little reasonable doubt in view of their general striking unity of organization. The types of seed possessed by these remote ancestors may have to a certain extent combined the characters of both these groups, as in the hypothetical Figures 1 and 10. Actually the seeds represented in these figures are symmetrical about a principal plane, but that modification has been introduced for purposes of comparison with certain recent seeds; here, regarding them as possible ancestral forms of the Radiospermeae and Platyspermeae, this implied flattening may be disregarded.

## 2. LAGENOSTOMA.

This seed, belonging to the lower coal-measures, was in point of time considerably earlier than Brongniart's seeds from the French permo-carboniferous. Nevertheless, it shows marked and unusual peculiarities, and evidently stands somewhat apart from the generality of palaeozoic seeds. In consequence, it seems fitting to treat it apart from the other seeds of the primary rocks, though regarding it as a type analogous to the Cycad in certain respects.

The general organization of this seed is known from Wil-

<sup>1</sup> D. H. Scott, loc. cit., p. 435.



Williamson's description of *Lagenostoma ovoides*<sup>1</sup>. It is a small seed, some  $4\frac{1}{2}$  mm.  $\times$   $2\frac{1}{2}$  mm., circular in transverse section, and belonging to the type with adnate integument and nucellus. These parts are free from one another in the region of the pollen-chamber alone, about one-fifth the whole length of the seed. The relations of the parts in median longitudinal section are given diagrammatically in Fig. 9. The free apex of the nucellus, the 'lagenostome' of Williamson, is transformed into a pollen-chamber (Fig. 9, *pc.*). The nucellar epidermis persists as the wall of the chamber (*pcw.*), the cavity of which has arisen by the separation of the central tissue from the wall. This central mass stands up freely from the floor as a cone of tissue (*cc.*), so that the actual pollen-chamber, in which numerous pollen-grains frequently occur, is a crevice that may be likened to the true cavity of a 'Sachsian bell-jar.'

Surrounding the pollen-chamber is the very complicated integument, of which only the general relations are seen in the longitudinal section. In the transverse section of the apex of the seed, represented in the adjacent text-figure, the integument is seen to consist of an outer zone *t.*, which is circular in transverse section, and an inner zone of (in the case figured) nine symmetrically disposed chambers which are separated from one another by strong radial plates. The internal angle of each chamber is convex, and their internal containing-walls form collectively a fluted membrane (*c.*) which was termed by Williamson the 'canopy.' The convexities of the canopy engage with corresponding concavities of the pollen-chamber wall. The space *g.* between the two membranes is the natural gap between nucellus and integument. The chambers which formed the canopy were occupied by soft parenchyma, whilst in each chamber a single tracheal strand ran longitudinally (*v.*, Text-fig. 20). These strands were direct prolongations of the system of strands which diverged from the entering supply-bundle of the chalaza, and ran up near the plane of 'fusion' of nucellus and integument

<sup>1</sup> On the Organization of the Fossil Plants of the Coal-Measures, pt. viii, Phil. Trans. 1877, pp. 233-43, and Figs. 53-75.

(Fig. 9). The seed appears to lack a sarcotesta, and so far agrees with such members of the Radiospermeae as had distinct nucellar bundles. But the chambered apex of the seed with its vascular prolongations constitutes an organ unique amongst the palaeozoic seeds. The peculiar form of the pollen-chamber is correlated with the distribution of the archegonia, which seem to have occupied a ring immediately beneath the bell-shaped crevice (as suggested in Fig. 9).

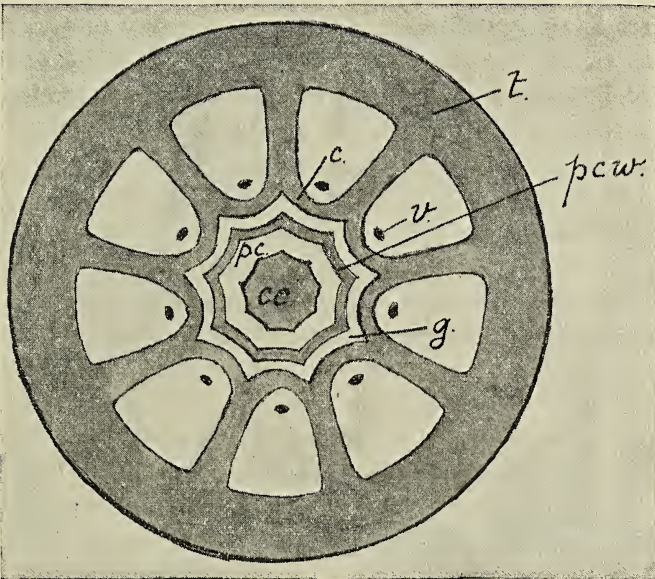


FIG. 20.—Transverse section of *Lagenostoma* cut near the apex at *v* in Fig. 9 (Pl. XXIV). The section traverses the pollen-chamber *pc.*, enclosed in its wall *pcw.*; *cc.* is the central cone of nucellar tissue; *t.* testa; *c.*, the fluted 'canopy'; *v.*, vascular strands running in the chambers of the 'canopy'; *g.*, chink between canopy and pollen-chamber wall.  $\times 30$  (From the 'New Phytologist'.)

Compared with the ordinary palaeozoic type of seed, *Lagenostoma* seems peculiar in the lack of tracheal supply beneath its pollen-chamber. Assuming that this deficiency is real and not due to imperfect preservation, there are at least two possibilities open in respect of the course of events in the pollen-chamber. The pollen-grains themselves, though

not yet fully studied, seem to have been filled with a tissue as in the well-known case of *Stephanospermum*<sup>1</sup>. They would in that case belong to the old type, and it may reasonably be suspected that they liberated spermatozoids. A consideration of the relations of this pollen-chamber at one time suggested that perhaps the pollen-grains formed haustorial attachments in the central cone of parenchyma and behaved somewhat as in Cycads, but the best specimens give no support to such an hypothesis, which must accordingly be rejected. Another view is based on the peculiar relations of the micropyle. As shown in Fig. 9, the micropyle is plugged by the summit of the nucellus, so much so that if this condition obtained at pollination the intervention of a micropyle would be dispensed with. If, now, there were any reason for believing that the apices of the chambers of the canopy were porous, if the tracheal strands could be supposed to end in hydathodes, all the essentials of a contrivance for supplying the pollen-chamber with water would be present. For whatever may have been the natural position of the seed (pendent or erect), a drop of water at the summit would inevitably be drawn into the narrow crevice of the pollen-chamber. The specimens convey the impression that the wall of the pollen-chamber was so tightly jammed in the micropyle as to exclude the siphoning of water into the space *g*. (Fig. 9) which lies between the canopy and the true pollen-chamber. As yet no sections are available which fully elucidate the mode in which the strands end at the micropyle; but the preservation of this seed occasionally reaches such a high standard of excellence as to encourage the hope that such sections may eventually be forthcoming.

Sufficient has been said regarding *Lagenostoma* to show that whilst it resembled Cycads in the considerable area of 'fusion' that obtains between the nucellus and testa, as well as in the presence of vascular strands in the plane of 'fusion,' it is yet marked by peculiarities all its own. The confined form of the pollen-chamber marks an advance in precision on the open type of the ordinary palaeozoic seed,

<sup>1</sup> Cf. Renault, Cours de bot. fossile, IV, Pl. XXI, p. 99.



whilst in the canopy we seem to have a structure whose homology, like its function, is at present obscure. It would be premature to enter into any discussion as to the relations of this seed until its structure has been more fully elucidated.

### 3. CYCADS.

The ovule in this group offers so general an agreement with the usual palaeozoic type that any view of its affinities seems inadmissible which excludes relationship with the Radiospermeae and Platyspermeae. The main difference is found in the fact that only at the apex are nucellus and integument free from one another.

The pollen on its entry into the pollen-chamber becomes rooted by haustorial attachments in the wall of the chamber. It thus obtains adequate nourishment for its further development. In due course the pollen-grain extremities of these tubes undergo a stretching, so that the sperm-cells are brought down close to the necks of the archegonia. Here they are liberated, the necessary fluid for their swimming being supplied, in some cases at any rate, from the tubes as they burst<sup>1</sup>.

The distribution of the vascular system in the Cycadean ovule demands some consideration. Though the general plan is fundamentally the same throughout the group, there is considerable variation in detail in the different genera and even species. The case here set forth is that of *Cycas Rumphii*<sup>2</sup> (Figs. 4-8). The common supply-bundle gives off the branches to the integument before its actual entry into the ovule (Fig. 4 *sb.*), and then continues its course into the chalaza (*cb.*). The integumental bundles are two in number and run in the sarcotesta undivided to the micropyle. The plane in which they run is known as the principal plane of the ovule. Before these integumental bundles pass beyond the chalazal region, however, each gives off an internal

<sup>1</sup> H. J. Webber, *Spermatogenesis and fecundation of Zamia*, 1901.

<sup>2</sup> I have to acknowledge much assistance from Miss Edith Chick, in the study of the structure of Cycadean ovules.

bundle (*nb'*) which constitutes the nucellar supply in the regions adjacent to the principal plane. The nucellar ring of bundles is completed by the strands which originate from the central chalazal bundle. Fig. 4 is a section in the principal plane, Fig. 5, in the plane at right angles to the principal plane. The nucellus is thus invested in a system of bundles of double origin. One portion, and here the chief portion, of the bundles has its origin in the central chalazal cord; whilst on the flanks, i. e. adjacent to the principal plane, a limited number of bundles is supplied from the strands of the integument. These relations are fully exposed in Fig. 6, which represents an ovule with the integument of one side dissected away so that the nucellar bundles are laid bare. The principal plane is indicated by the line *p*., consequently the relations shown by this dissection are those that would obtain if Fig. 5 be imagined built up into a solid figure and not merely a section. For the sake of clearness the main supply-bundle (*sb.*) and the two groups of nucellar bundles which arise directly from its continuation are drawn in *black* in this figure (the same holds in Figs. 7 and 8), whilst those nucellar bundles that take their origin from the integumental bundle on the exposed side are coloured *red*. The point of insertion of the integumental bundle on the main supply-bundle is shown as a red spot (*ib.*), but the intervening connexions with the nucellar bundles *nb'*. (readily understood from Fig. 4) are for obvious reasons not represented. The transverse sections cut at the levels *A* and *B* (in Fig. 6) show that the series of bundles from the central cord (black in Figs. 8 and 7) reach nearer the pollen-chamber than those inserted upon the integumentary bundles (red in those Figs.). This disparity in the upward extension of the nucellar bundles is correlated with the fact that the groove between the free nucellus and integument extends considerably further down in the neighbourhood of the principal plane than it does elsewhere (cf. Fig. 6). The significance of this peculiarity in the course of the groove (which recurs also in *Torreya*, see p. 468) is obscure.

The arrangement of the strands in *Cycas Rumphii* is in close agreement with that shown by Warming to exist in *Cycas circinalis*<sup>1</sup>. But many other different types obtain according to the manner of joining up of the vascular strands at the chalaza. Thus in *Zamia* sp. (a complex case) the ovular supply is constituted from two bundles, each of which forks and joins again as they pass into the chalaza. Of these two reunited bundles, one supplies one-third of the integument and nothing more; the other gives off two bundles which supply the remaining two-thirds of the integument, whilst its continuation breaks up, supplying two-thirds of the nucellus. The remaining one-third of the nucellar ring is derived, relatively high up, from one of the two integumental bundles which arose lower down from this same system.

These varying types of chalazal branching seem consistent with the assumption that the whole of the body of the ovule, below the level at which the nucellus becomes free, is phylogenetically younger than its apical parts—that between the original ovule and its insertion a new region has been intercalated. This suggestion is embodied in Figs. 1, 2, and 3. In Fig. 1 is shown the conjectured ancestral palaeozoic type as described in the first section, but so far modified by the assumption of a plane of symmetry as to bring it in touch with a Cycadean ovule such as that of *C. Rumphii*. In Fig. 2 the possible mode of intercalation of a new zone is indicated by the broken lines (included under the bracket *b.*), all the structures of nucellus and integument being continued across this new zone. As the zone of stretching lies below the insertion of the nucellus, the gap between nucellus and integument finds no place in the new insertion. For the rest, however, it is a mere extension of the tissues of integument and nucellus. An ideal case is represented in Fig. 2, perhaps never realized, in which the bundles are all connected at the chalaza exactly as in the palaeozoic type (Fig. 1). With the basal extension of the ovule fresh distributions of the

<sup>1</sup> E. Warming, *Recherches et remarques sur les Cycadées*, 1877, p. 21 and Pl. III, Figs. 6–12.



bundles could take place, and in an instance like *Cycas Rumphii* it is readily comprehensible that a certain number of the nucellar strands in the neighbourhood of the principal plane might have joined up with the integumental bundles as shown in Fig. 3. In other cases, as in *Stangeria* where nucellar and integumental bundles appear to arise in common, the whole of the nucellar bundles may have undergone this change of insertion; whilst even in the complex *Zamia* it is possible to understand that the growing basal zone gave opportunity for the production of the anastomoses outlined above. But of course no attempt is made to offer a special explanation for each several case—that is out of the question. The suggestion made is a general inference from the facts, and its validity must depend on the degree in which it renders the structure of the Cycad ovules more intelligible than it was before. The main significance of this intercalation is probably nutritive—the provision of a suitable brood-chamber for the nursing of the embryo.

The other point that calls for notice here is the retreat of the nucellar bundles from the pollen-chamber (cf. Figs. 1, 2, and 3). In the Cycadean ovule they are no longer needed so urgently as in the palaeozoic seeds (especially the Radiosperms), mainly because the pollen effects haustorial attachments in the nucellar tissues, obtaining thus the water required in further development, and even for the swimming of the spermatozoids in their brief journey to the archegonium. In part, perhaps, the broader surface of continuity of the tissues of nucellus and integument (a result of the basal extension) would be a contributing factor in the decline of the water-excreting tracheal contrivance which was so conspicuous in palaeozoic times.

#### 4. TORREYA.

The facts of the vascular anatomy in the seeds of this genus of Taxaceae are peculiar and isolated among recent plants, and in the light of palaeozoic seeds would mark it as an archaic type even were *Torreya* not recognized as far back as

the lower Cretaceous. In the apparent retention of old features it exceeds either *Taxus* or *Cephalotaxus*, and its inaccessibility as an object of detailed investigation has left a regrettable lacuna in our knowledge of the Taxaceae. Whilst all details are reserved for treatment in a special memoir<sup>1</sup>, certain of the facts of its ovular morphology may be outlined here.

Already in the winter buds the rudiments of nucellus and integument are discernible. By the beginning of May the latter overtops the former. Towards the end of this month basal stretching ensues, so that nucellus and integument are raised up slightly from the enclosing scales. From this intercalated zone a circular cushion projects, this is the future arillus. At the beginning of June the buds open, exposing the micropyles, and pollen is collected in the usual way. The arillus now grows rapidly and meets above the micropyle before the end of July. By this time pollen-tubes have developed, and these reach the embryo-sac early in September. Before the winter resting-period pro-embryos have been formed in the archegonia, whilst the base of the young seed has undergone considerable expansion. This expansion and further embryonic development is continued in the following spring. The most striking phase is that shown in July, when enormous expansion of the seed-base is manifested. This is followed by the differentiation of the stone, and by the autumn the drupe-like seed ripens and falls. During this second year a marked rumination of the endosperm develops, but this feature need not be described here.

The vascular system, indicated in the first year by strands of desmogen, undergoes no marked degree of differentiation till the approach of seed-ripening. Its distribution is indicated in red in Fig. 12. This diagram is a longitudinal section of a ripening seed cut in the principal plane, but the central light-red area must be regarded as convex as it represents the exposed surface of the nucellus. At the top of the figure

<sup>1</sup> For some time I have, in conjunction with Miss Edith Chick, been occupied upon an investigation of this genus, and it is with her sanction that I am enabled to utilize some of our results here.

are seen the free arillus (*a.*) and integument (*i.*) covering the free portion of the nucellus. The wall of the nucellus is thin, and the contained embryo-sac and endosperm are continued towards the base of the seed, as also are the arillus and integument. Two bundles enter the seed at the base, and whilst each may divide into two or more branches<sup>1</sup> in passing upwards, these branches unite again below the level at which arillus and integument are free from one another in the principal plane of the seed (*f.*). At this point the central portion of the reunited bundle dips suddenly inwards, penetrating the stony layer at a special shield-like area.

The two shield-like areas, right and left of and a little below the micropyle, form characteristic marks on the stone of the ripe seed when stripped of its fleshy arillus. The view of the stone in Fig. 13 shows one of these shields with the foramen (a dot) perforating it. The crescent-shaped area at the top of the seed, often covered by a thin translucent membrane, represents the outer surface of the integument where it is free from the arillus. It is noticeable that this area attains its greatest downward extension in the plane at right angles to the principal plane, whilst in the principal plane (*p.*) (i. e. the one which traverses the foramina) it is much narrower. Identical relations obtain between nucellus and integument.

After its passage through the stony layer of the integument, and as it traverses the soft tissue which lies between the internal aperture of the foramen and the base of the groove between nucellus and integument, the tracheal strand forks, the branches turning sharply away from the principal plane of the seed. These branches direct their course towards the groove between the nucellus and integument, striking the furrow of the groove a little below its highest point. These relations are somewhat elucidated in Fig. 14, a nearly transverse section across the seed at the level of the foramina. Outside is the arillus, then the stone (shaded dark) with a lining of soft parenchyma. The bridge which traverses the figure vertically is the nucellus joined to the integument above

<sup>1</sup> This branching is very marked in *T. nucifera*.



and below. The semicircular gaps (*g.*) on either side owe their existence to the fact that the nucellus is not at this level wholly merged in the integument. The bundle (red) is seen (below) traversing a foramen. The subsequent forking of the strand and the direction taken by its two branches are shown as though happening in one plane. On the other side (above) the section is so drawn as to show what happens at a slightly lower level. The integumental bundle is cut below the foramen of that side, whilst within the stone the descending branches of the strand that has penetrated the foramen (in a higher plane) are represented as red dots (*x*) in contact with the furrow between nucellus and integument.

It has been explained that the groove corresponding to the line of separation of nucellus and integument is highest opposite the foramen, lowest in the plane at right angles to the principal plane<sup>1</sup>. Here in the nearly ripe seed the bundle seems to lose itself in the curious hypoderm of the nucellus. Though the bundle at this stage cannot be traced further, in a younger seed (May of the second year), when only desmogen is present and tracheides are as yet not differentiated in the upper part of the seed, the desmogen-strands may be traced close to the angle of the groove right across till they meet the corresponding branches from the opposite side. The course followed by these desmogen-strands may be compared to that of the side ropes of a hammock, the two poles from which the hammock is suspended standing for the two main bundles of the seed which run outside the stone. In other words the strands from the foramina encircle the base of the free apex of the nucellus (cf. Fig. 12, the horizontal red line passing across). But true lignified tracheides do not seem to differentiate in these strands much beyond the point of forking of the primary strand, i. e. only quite a short distance within the interior aperture of the foramen. And in development differentiation comes late in the region of the foramen—coinciding with the hardening of the stone. As the summer advances there comes a period when tracheides are well shown in the bundle

<sup>1</sup> In *Cycas* this groove dips in the principal plane, see Fig. 6.

outside the foramen, but it was only by the middle of August of the second year that these elements could be recognized in the actual foramen and continuing to the place of forking.

A seed freshly picked at this stage and stood with its cut base in a watery solution of eosin sucked up the eosin by its xylem, and the pigment was drawn right through the foramina and a little distance further, i. e. up to the limit of differentiation of tracheides.

It has been stated that the desmogen-strands run right across from one foramen to the other, encircling the base of the free nucellus, but in the nearly ripe seed they can no longer be traced all the way. Running in the hypoderm of the nucellus in the angle of the groove between nucellus and integument they become merged in the peculiar hypoderm of the nucellus which becomes prominent in July. This tissue consists of large, thick-walled, mucilaginous, pitted cells of remarkable appearance which first arise in the nucellus adjacent to the trough, but ultimately appear in the downward continuation of the nucellus, everywhere enclosing the prothallium in a continuous sheath or mantle. This layer is very characteristic, and its protoplasm becomes filled with oily granules. Its actual signification is obscure without special investigation, but its appearance suggests that it serves in some way as a go-between in respect of food that is being transferred from the green assimilating layer of the arillus to the prothallium. Perhaps it may be termed provisionally a 'digestive layer.' It is in this layer that the strands from the foramina become lost. Indeed as a strand is followed from the forking-place the tracheides slowly die out and large mucilage cells begin, the impression gained from a study of these transition regions being that the mucilage cells and tracheides mutually exclude one another—that they are produced from identical structures.

For the completion of this brief account of the vascular system of the seed in *Torreya* one point remains to be added. It was stated at p. 468 that only the central portion of the reunited bundle turned sharply inwards and traversed the

foramen (cf. Fig. 12, *f.*). The flanks continue their course for an appreciable distance in the pulp outside the stone, and end in a mass of transfusion-tracheides at a point a little below the level at which the arillus becomes free from the integument (Fig. 12, *t.*).

The remarkable course of the bundles shown in this seed suggests a comparison with that found in Cycads and the palaeozoic seeds. At first sight *Torreya* seems so different that such a comparison must be vain. But bearing in mind the conclusion reached in the section dealing with the Cycads, as to the probability of the lower part of the seed being phylogenetically younger than the apex where nucellus and integument are free, and applying the same principle to *Torreya*, it seems possible to describe the latter in terms of the palaeozoic seed. For the purposes of this elucidation it is convenient to start with a form slightly modified from the supposed ancestral palaeozoic seed as in Fig. 10, a form differing from the type (Fig. 1) in that, instead of a single supply-bundle entering at the chalaza, we assume that there is a pair. Such a seed is shown cut longitudinally in the principal plane in Fig. 10. It resembles that given as the starting-point of *Cycas* in all other respects, except that the nucellar investment of tracheides is rendered as a continuous mantle and not as discrete bundles. (The red shade over the nucellus is to be regarded as representing the surface of the nucellus covered with its tracheal mantle.) From such a type *Torreya* may be derived by supposing that, at the time when a basal stretching of the ovule set in, this was accompanied by a marked rotation of the bundles which immediately connected with the tracheal plate at the base of the nucellus, so that one was carried some  $80^\circ$  to the right and the other a similar amount to the left. This process is sufficiently represented in the transitional Fig. 11, where the intercalated zone (under the bracket *b.*) is drawn in broken lines. It may be said that a marked feature of the evolution of this seed was the transverse expansion of the inner part of the chalaza which accompanied the general basal extension.



Concurrently the embryo-sac has extended down (as represented by arrows in Fig. 11) and occupied all the available space. To interpret the facts literally the tracheal plate (at the base of the nucellus in Fig. 10) has become stretched and split into a ring, and the embryo-sac has obtained an outlet by extending right through this ring (Fig. 11). In the seed of *Torreya* the tracheal plate may be still represented by the desmogen-strands which appear in development reaching from one foramen to the other (Fig. 12). Here then we have a seed in which the stone ends blindly below, and the water-supply for the nucellus is brought up round the outside and led through the foramina to the base of the free apex. These two foramina represent the ancestral chalaza, which by a strange evolutionary freak now finds itself close to the apex of the orthotropous seed<sup>1</sup>!

As for the integumental bundles of the ancestral type, these have dwindled down in *Torreya* and are represented by the spurs *t.* (Fig. 12).

Finally, there is a temptation to wonder whether the peculiar 'digestive layer' of the nucellus which invests the embryo-sac may not be the palaeozoic tracheal mantle modified to meet present requirements. Its pitted, mucilaginous character indicates that it probably performs some transfusion function in connexion with the water supplied by the tracheal strands which penetrate the foramina, whilst the nature of its contents suggests that it also plays a part in some metabolic process. Though the surface of the nucellus is coloured red in Fig. 12, thus emphasizing this view, the suggestion is necessarily of the most tentative character.

From what has been written it would seem possible to derive the very dissimilar seeds of a Cycad and *Torreya* from something approximately identical with the supposed ancestral

<sup>1</sup> The actual relations of base and apex in the seed of *Torreya*, as well as some matters of minor detail, would appear to have been misapprehended by former writers. Cf. C. E. Bertrand, *Ann. des sciences nat., Bot.*, 6<sup>e</sup> sér., tom. vii, pp. 72, 76, and Pl. XI, Figs. 1-6; also *Bull. Soc. Bot. de France*, 1883, p. 293. The same assertions appear in Renault's *Cours de bot. fossile*, IV, 1885, p. 77.

palaeozoic type. If this be true, it should be possible to realize at every stage in the evolution the factors that have led to a modification of the ancestral type or to the persistence of some of its characters. In the case of the Cycads this is beset with less difficulty. The chief factors suggested above were the attachment of the pollen-grains to the wall of the pollen-chamber by haustoria and the need for increased space for the nutrition of the embryo. In *Torreya*, however, the factors are less evident, though the presence of the enlarging embryo midway between the foramina just as the stone is hardening (end of July) may not be without significance (cf. Fig. 14, *c.*). The retention of the nucellar tracheal sheath as a mucilage layer (if it be homologous with the palaeozoic mantle) may be correlated with the exiguous nature of the water-supply, whilst its possible digestive function may also have a bearing. Otherwise the interior of the seed might become prematurely isolated from water-supplies. For, being completely siphonogamous like the other Taxaceae (*Taxus* and *Cephalotaxus*), its retention here cannot be attributed to the requirements of spermatozoids.

As for the other Conifers, they have lost their nucellar vascular systems, whilst the pollen-chamber is either quite obsolete or represented by the merest pouch. The base of the ovule has, however, generally undergone a marked extension.

The problem of the limit of the real ovule in Gymnosperms is not a new one. Strasburger made some allusion to the question years ago<sup>1</sup>.

In another place I have emphasized the distinction drawn between the original ovule and the phylogenetically younger intercalation by proposing the terms *Archisperm* and *Hyposperm* to designate these regions. The phylogenetic history of a gymnospermous ovule may be compared to the case of an island rising out of the sea which becomes an inhabited centre of activity. As the elevation continues the original island becomes a remote mountain summit, whilst the newly-won

<sup>1</sup> Die Angiospermen und die Gymnospermen, pp. 124 and 134.

ground in its turn becomes the scene of active operations. In time the summit is little more than a land-mark, and is ultimately denuded away.

Whilst the consideration of these seeds from the palaeozoic rocks, together with those of recent Cycads and Taxaceae, tends to confirm the view that is held on many hands as to their common origin, it is evident that even the oldest forms show a marked advance on the condition that probably obtained in their pteridophytic ancestors. Whilst the work of recent years has tended to carry the lower limit of the Gymnosperms deep down into the Ferns, we are still in search of fern-sporangia exhibiting a tendency or capacity for seed-like adaptation. Along the line of the Lycopodineae such structures have become known to us in *Lepidocarpon*, the evident strobilus of a *Lepidodendron* bearing seed-like structures<sup>1</sup>. But in view of the probable Filicinean affinities of the Cycads and of the other Gymnosperms, *Lepidocarpon* is only of value for the moment as an analogy. It cannot be supposed that the Gymnosperms were evolved from the Lycopodinean phylum. A structure standing in the same relation to the probable fern-like ancestors of the Gymnosperms as *Lepidocarpon* does to the Lycopodineae has yet to be discovered. Whether the transverse section of an unidentified sporangium<sup>2</sup> showing a belt of tracheal elements between the sporangial wall and the mass of developing spores is likely to furnish a clue must await the identification of that sporangium. In any case the condition of vascularity in a fern-sporangium, which this specimen proves to have actually existed, may have been an important antecedent to the evolution of the vascular nucellus that played so considerable a part among the earlier Gymnosperms, and from which it may be reasonably supposed the ordinary Coniferous type of nucellus has been derived.

UNIVERSITY COLLEGE, LONDON,

*January, 1903.*

<sup>1</sup> D. H. Scott, The Seed-like Fructification of *Lepidocarpon*. Phil. Trans., 1901, p. 291.

<sup>2</sup> A Vascular Sporangium, The New Phytologist, Vol. i, p. 60.



EXPLANATION OF THE FIGURES IN  
PLATE XXIV.

Illustrating Professor F. W. Oliver's paper on the Ovules of Gymnosperms.

In all cases red colour indicates tracheal tissues.

Fig. 1. A conjectural synthetic type of seed embodying the characters of such a seed as *Stephanospermum* with those of a *Cardiocarpus*.

Fig. 2. Hypothetic stage connecting the Cycadean ovule with the palaeozoic type. *b.*, the supposed intercalated younger zone.

Fig. 3. Ovule of *Cycas Rumphii*, cut in the principal plane. The dotted lines beneath the pollen-chamber indicate the shrinkage of the original nucellar strands.

Fig. 4. Section of ovule of *Cycas Rumphii* cut in the principal plane. *sb.*, main supply-bundle; *nb.*, insertion of nucellar bundles on the main strand; *nb'*, nucellar bundle inserted on an integumental bundle; *ib.*, integumental bundle; *st.*, stone or sclerotesta.

Fig. 5. The same ovule cut in the plane at right angles to the principal plane. References as in Fig. 4.

Fig. 6. Ovule of *Cycas Rumphii* dissected so as to show the vascular system of the nucellus. The dotted line *p.* indicates the position of the principal plane of the ovule. The nucellar bundles (*nb.*) that arise from an integumental bundle are alone coloured red. *ib.*, place of insertion of integumental bundle on the main supply-bundle. *AA.*, *B.B.*, heights at which the transverse sections represented in Figs. 8 and 7 respectively were cut. Other references as in Fig. 4.

Figs. 7 and 8. Transverse sections of the ovule represented in Fig. 6 at the heights *B* and *A*. The red dots in the nucellar circle of bundles in Fig. 7 are those which are inserted upon the integumental bundles. They have died out at the height at which Fig. 8 is cut.

Fig. 9. Diagrammatic median longitudinal section of *Lagenostoma. pc.*, pollen-chamber containing pollen-grains; *pcw.*, wall of pollen-chamber; *cc.*, the central cone of nucellar tissue in the pollen-chamber; *g.*, space between pollen-chamber wall and canopy; *c.*, canopy; *v.*, tracheal strand here running in a chamber of the canopy; *t.*, testa; *a.*, archegonium. The unshaded cavity of the chambers contained a soft parenchyma; the tissue within the shaded layer of the testa in the body of the seed was probably of the same character.

Fig. 10. Median longitudinal section of palaeozoic seed type for comparison with *Torreya*. The light red shade on the nucellus is to indicate a continuous tracheal mantle. Beneath the nucellus is the tracheal plate (dark red), and two supply-bundles each of which originates an integumental bundle.

Fig. 11. Transitional type connecting with *Torreya*. At *b.* the broken lines indicate the position of the supposed intercalated zone. The dark red horizontal stripe across the nucellus is the stretched tracheal plate, now a ring. The arrows show the downward extension of the nucellus and embryo-sac.

Fig. 12. Median longitudinal section of seed of *Torreya* through the principal plane. *a.*, arillus; *i.*, integument becoming hardened; it is continued as a dark shaded layer right round the seed; *f.*, foramen perforating sclerotesta and allowing

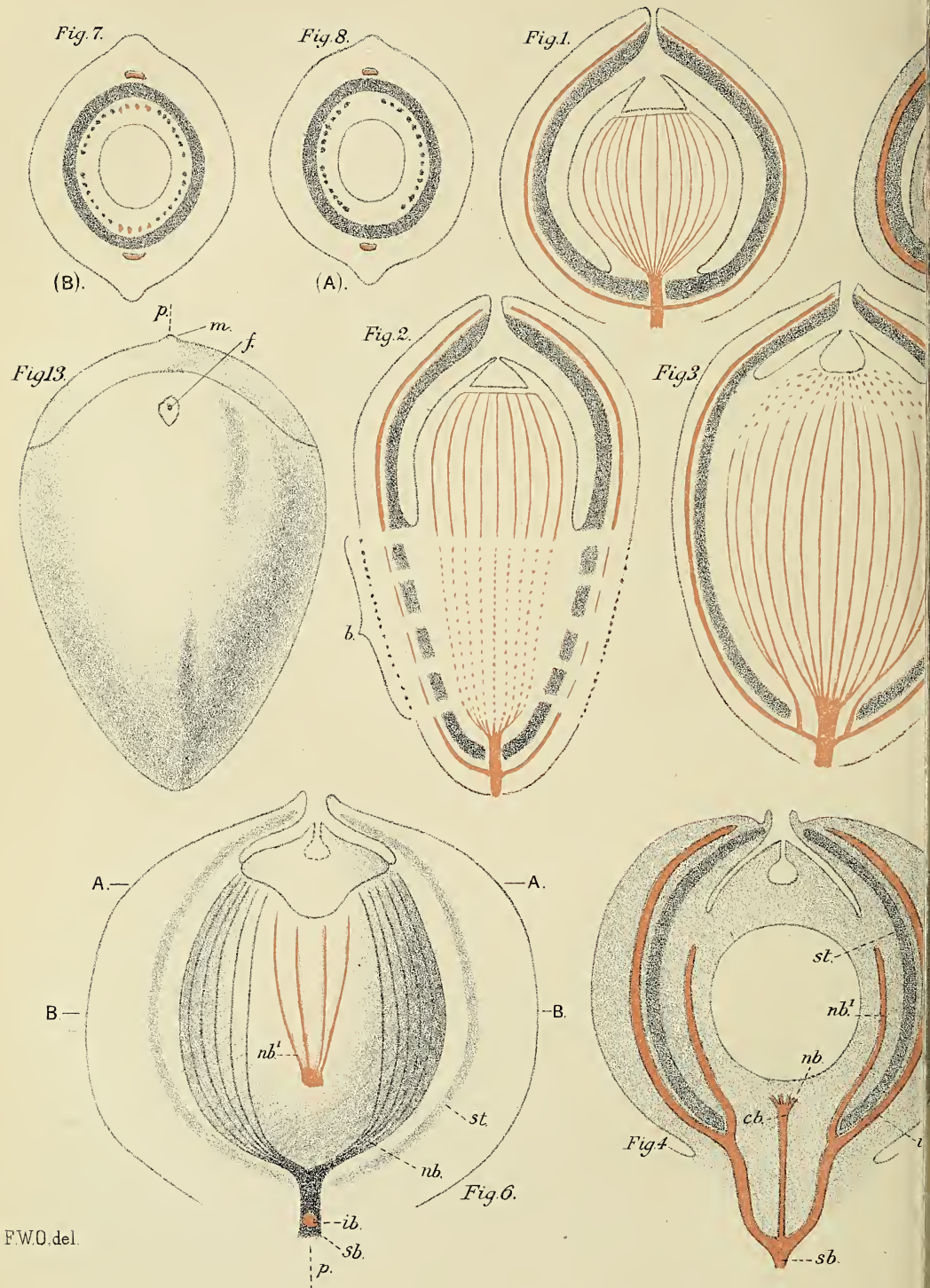
vascular strand to pass to the base of the nucellus; the dark red stripe joining the two foramina represents the supposed traces of the tracheal plate; *z*, mass of transfusion-tracheides; the old integumental bundles are supposed to be reduced to these spurs.

Fig. 13. View of stone of *Torreya Myristica* stripped of its fleshy arillus. The shield with foramen (*f*.) is near the apex; *m*., micropyle; *p*., principal plane.  $\times 2$ .

Fig. 14. Cross-section of seed of *Torreya Myristica* so cut as to lie in the plane of one foramen (towards the bottom of the figure) and to pass *below* the other. The section is consequently not quite transverse. The red T (below) is the bundle traversing the foramen and its two branches which pass right and left in the direction of the furrows of the gaps (*g*.) here present on the flanks between nucellus and integument. The foot of the T represents the portion of the bundle which remains outside the stone (= *t*., Fig. 12). On the other side of the seed the bundle is cut through a little below the foramen. The two detached red spots are the cross-sections of the strands which follow the groove. As these strands sag a good deal they can only be followed from *x* to *y* by examining a series of transverse sections. *e*., embryo; *p*., prothallium; *ml*., coloured pale red, represents the mucilage-layer of the nucellar wall; *z*., integument, the dark shaded ring is the stone (sclerotesta), the lighter ring within it is also a part of the integument but of soft parenchyma (endotesta); *a*., arillus. Had the section been cut a little nearer the apex, gaps would have appeared right and left between the integument and arillus.  $\times 2$ .







F.W.O. del.

Fig.10.



Fig.11.

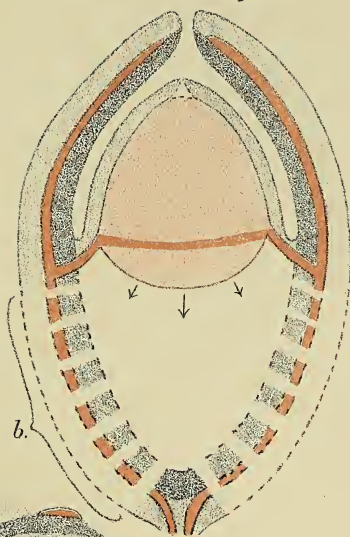


Fig.12.

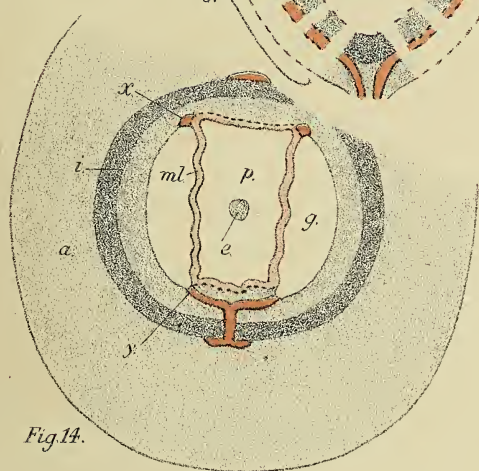
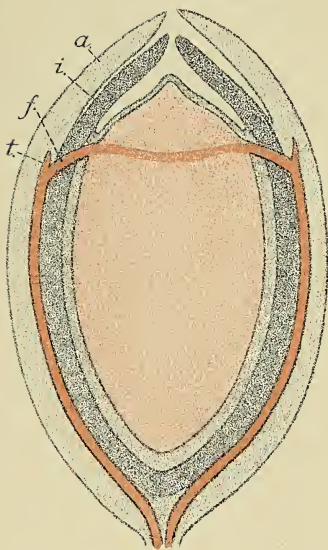


Fig.14.

Fig.9.

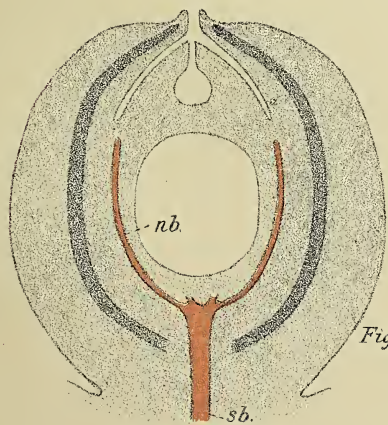
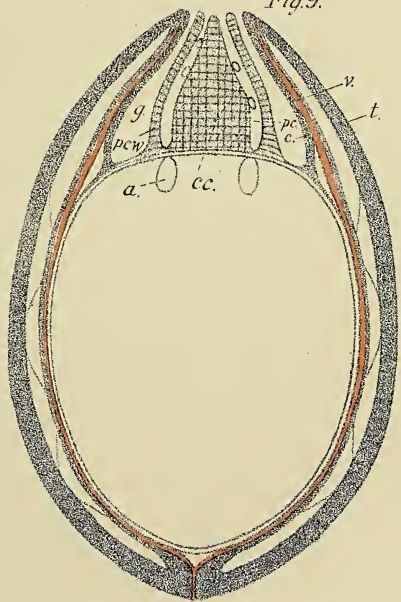
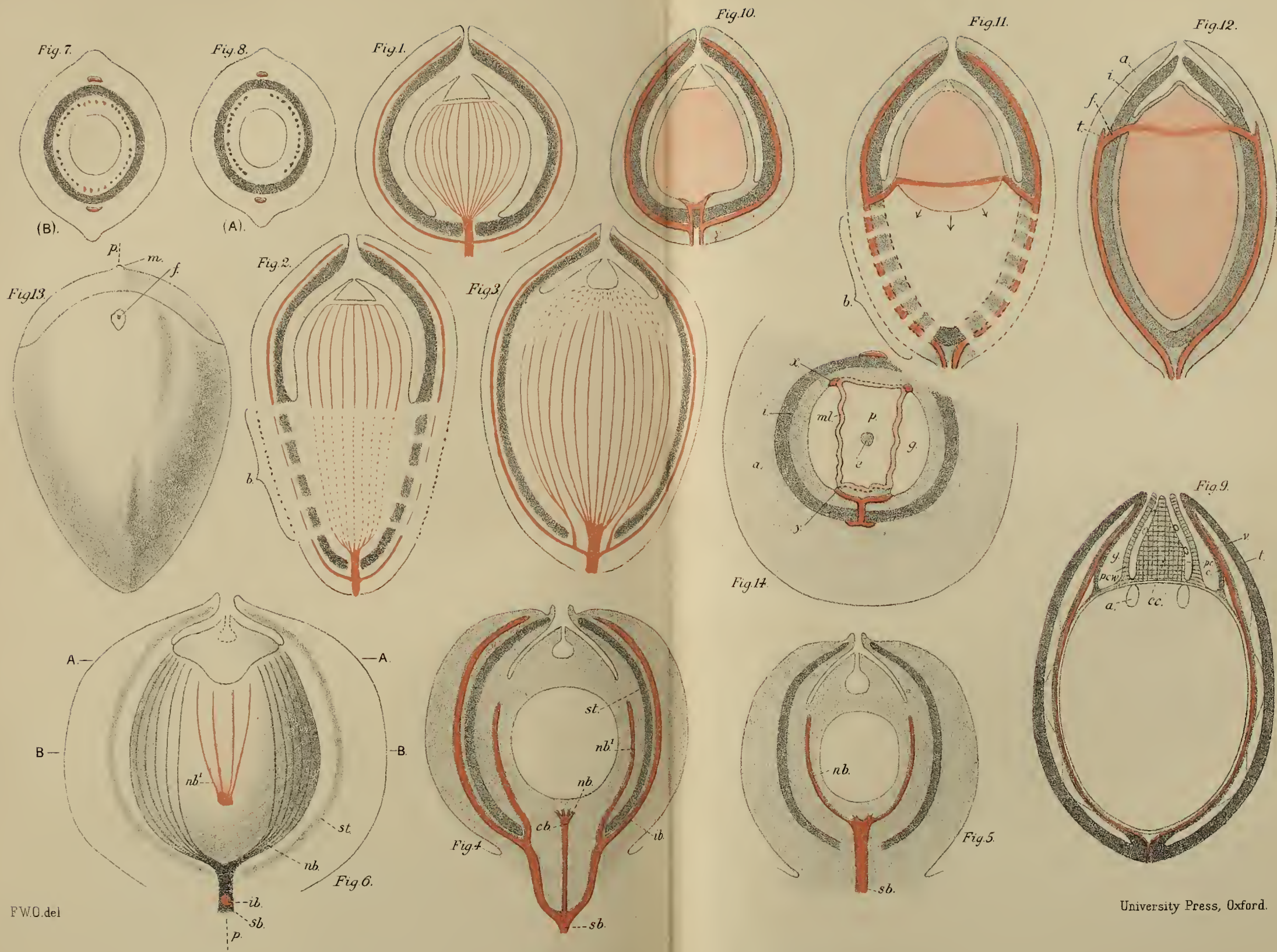


Fig.5.







FWO.del

University Press, Oxford.



# The Origin of the Archegonium<sup>1</sup>.

BY

BRADLEY MOORE DAVIS.

—♦—

With two Figures in the Text.

—♦—

THE gap between the Thallophytes and those groups of higher plants which may collectively be called the Archegoniates is perhaps the most difficult of all to bridge when one attempts to trace the evolution of the plant kingdom. The problems chiefly concern the relation of the sexual organs in the two groups, or more precisely the origin of the archegonium and antheridium of the Bryophytes.

The presence of a well-defined sporophyte generation in the Bryophytes, while an important distinguishing character, gives less difficulty, because studies among the Thallophytes in recent years have indicated the possibility of a very general tendency towards the development of a sporophyte in this group. It is probably shown at low levels of the Confervales (*Ulothrix*), in the Conjugales and the Oedogoniaceae, while *Coleochaete*, the Rhodophyceae, and perhaps the Ascomycetes, present sporophyte generations that in complexity may fairly be compared with the simplest Bryophytes.

But the archegonium and antheridium have no parallel in the sexual organs of the higher Thallophytes, i. e. those groups

<sup>1</sup> Contributions from the Hull Botanical Laboratory, No. 48.



which have advanced to the level of sexual evolution termed heterogamy.

The sexual elements of heterogamous Algae are almost universally formed in single cells. These cells are generally called oogonia when they contain eggs, and antheridia if they produce antherozoids or sperms. Sometimes a collection of sperm-producing cells, with or without accompanying sterile tissue, is called an antheridium. This term has therefore ceased to have exact morphological value, and is applied to structures widely different in their degree of complexity, some being unicellular and some multicellular.

This vagueness in terminology has led to a recent protest by Vuillemin<sup>1</sup>, especially with reference to the term 'sporangium,' which is now applied to any organ bearing spores, regardless of its structure, whether multicellular or unicellular. Vuillemin suggests a terminology that will clearly show the morphology of the reproductive organs of Thallophytes in contrast to conditions among the higher plants. He proposes the following names for unicellular reproductive organs:—

Sporocyst,	an unicellular structure,	producing asexual spores.
Gametocyst,	" "	" gametes.
Oocyst,	" "	developing eggs.
Antherocyst,	" "	" antherozoids or sperms.

These unicellular structures may then all be removed from the group of multicellular reproductive organs, which will then retain the old terms of—

Sporangium,	a multicellular organ,	producing spores.
Gametangium,	" "	" gametes.
Archegonium,	" "	peculiar to higher plants, developing eggs.
Antheridium,	" "	developing antherozoids or sperms.

The question of terminology may seem to some a minor

<sup>1</sup> Vuillemin, Bull. d. l. Soc. Bot. d. France, xlix, 16, 1902.

matter, but it becomes of utmost importance when it rests on a clear morphological basis. It seems to the writer that the peculiarities of the reproductive organs of most Thallophytes justify a most careful consideration of the above suggestions, and he will employ the terminology throughout this paper as the best means of making clear the fundamental distinctions between the archegonium and antheridium of the Bryophytes and the reproductive organs of most Algae.

There are of course no archegonia in the Thallophytes, and antheridia in the narrower use of the expression (i. e. multicellular organs) are only represented by such structures as are found in the Characeae, and less conspicuously in groups of sperm-producing cells occasionally found among the green and brown Algae (e. g. *Oedogonium*, *Dictyota*).

Logically, the term 'antheridium' should be strictly reserved for such multicellular structures as have clearly developed from a single cell whose activities produce tissues with a definite form and function. The antheridium of *Chara* is such an example, and the antheridia of all plants above the Thallophytes illustrate clearly the point. On the contrary, many so-called antheridia of Algae, especially among the Rhodophyceae, are simply groups of antherocysts, independent cells that happen to be associated together but are not tissues.

The antheridia of Bryophytes present clearly the distinctions between the antherocyst, a single cell, and the tissue with definite form whose co-operating cells establish an organ. The method of development of the antheridium is the basis of these fundamental distinctions. A superficial cell generally begins the process by several oblique divisions, which frequently result in the differentiation of a terminal cell that plays an important part in defining the form of the structure. This apical cell, if present, cuts off segments that build up the antheridium from above. If there is no clearly differentiated apical cell, the structure increases in size by various cell-divisions in its mass. Finally, periclinal walls separate a sterile layer of cells on the exterior from a central group. The latter divide by walls at right angles to one another into small cubical cells,

each of which develops a sperm. The antheridium is then a capsule of sterile tissue enclosing a mass of fertile cells.

The archegonium presents peculiarities of form and certain structural features that obscure its fundamental agreement in structure with the antheridium, but a close study of its development makes the homology of these organs clear. The archegonium, like the antheridium, arises from a single superficial cell, which divides in such a manner that a growing point is generally established, sometimes with a single apical cell, sometimes terminated by a group. This growing point, acting as a whole, builds up the archegonium, which is thus a unit from its earliest inception. At maturity the archegonium is a long narrow capsule, whose outer layer of cells encloses a central group. This central mass is a line of cells, sometimes numerous, running the entire length of the structure. Of these only the lower cell develops a gamete, its contents rounding off as an egg. The other cells (canal-cells) break down.

Generally the cells of the central mass form a single row, but Mr. G. M. Holferty has recently found among the Mosses that there may be two or more rows of canal-cells at various levels of the archegonium, but especially near the tip. His results have not yet been published, but their bearings on the present problem are so important that I have asked the privilege of announcing them in advance. Such conditions are identical with certain stages in the development of the antheridium, and establish clearly the homologies between these sexual organs. It seems almost certain that the canal-cells at one time produced gametes, and are therefore homologous with one another and also with the cell that develops the egg. The entire group, canal-cells and the egg, is homologous with the mass of sperm-producing tissue of the antheridium.

The archegonium is therefore a gametangium which has passed through an evolution characterized by such extensive sterilization of the reproductive cells that finally only one gamete is formed in the structure. The sterilization was progressive from the terminal region backwards, so that



the selected egg lies at the bottom of the capsule in the position most favourable for its own nourishment and for the protection and assistance offered to the young sporophyte.

The primitive archegonium and antheridium, then, agree in all essentials of structure, and are homologous. They are both multicellular from the beginning, the form is generally determined by a growing point, and the final result is a sterile capsule enclosing a mass of gamete mother-cells, very numerous in the antheridium, but so reduced in the archegonium that only one gamete matures.

It is not necessary in this discussion to consider the changes that come over the archegonium and antheridium in the higher groups of the Pteridophytes and in the Spermatophytes. The general trend is always towards the simplification and reduction of cell structure until many features of the primitive organs are lost. We are not concerned with these later conditions, but only with the older, more generalized form of organ, best illustrated to-day among the Liverworts and Mosses.

A comparison of the archegonium with the sexual organs of heterogamous Algae brings out great and fundamental differences. *Chara* and *Coleochaete* are the forms naturally considered in this connexion, because their sexual organs become invested with a cellular envelope, so that the eggs either before or after fertilization lie in a capsule. But the development of these organs shows clearly that the final structure is not a unit, but a composite of several independent elements. The eggs are produced in oocysts after the method usual to Algae. The enveloping capsules are formed of independent filaments which, arising from cells below the oocysts, have absolutely no organic relation to the latter.

The conditions in the Charales are further complicated by the peculiar small cells (*Wendungszellen*) that are cut off from the egg-cell before its maturity. The significance of these accessory cells has long been a matter of conjecture. There appears to be no reduction of the chromosomes with their

development. Götz<sup>1</sup> believes them to stand for the walls of a reduced archegonium, thus removing this sexual organ of the Charales from the category of the gametocyst and regarding it as a degenerate archegonium plus the enveloping whorl of filaments that surrounds the egg and forms the crown. Götz calls the Charales Phycobryophytes, and does not consider them to be directly connected with the Algae. This is a very interesting suggestion, although objections present themselves in the complexity of the processes required to bring about the degeneration of such a well-established organ as the archegonium and its displacement by an equally elaborate envelope of filaments. It seems to the writer that the accessory cells (Wendungszellen) may be nothing more than the final and somewhat irregular expression of the vegetative activities of a growing point that is about to become transformed into a sexual organ. In any event all botanists will probably agree with Götz and others that the female sexual organ of the Charales is not a primitive archegonium.

There seems to be, then, no sexual organ of the heterogamous Algae from which the gametangium (multicellular) of the Bryophytes could have arisen. We are forced to seek for clues in other groups and among other structures than these gametocysts (unicellular).

The structure of the archegonium and antheridium would suggest a derivation from some multicellular organ, a sporangium or gametangium. But unfortunately few structures of this character are known among the Chlorophyceae, that group of Thallophytes which naturally is considered nearest to the Bryophytes. We should be forced to assume a more extensive existence of such multicellular structures in groups, now extinct, which were much nearer the main line of ascent to the Bryophytes than any surviving Algae.

To what extent would we be justified in placing all the heterogamous green Algae far away from such a main line, and in recognizing a region of extinct groups with sexual

<sup>1</sup> Götz, Ueber die Entwicklung der Eiknospe bei den Characeen. Bot. Zeit. lvii, 1, 1899.

organs unlike any existing Thallophytes? The justification could only be the theoretical working-out of a very plausible series of stages in types whose previous existence, while entirely speculative, would do no violence to the position and arrangement of existing groups of Algae.

The assemblage of plants called the Thallophytes is much better understood with the advances of recent years. Although correlative with three other branches of the plant kingdom (Bryophytes, Pteridophytes, and Spermatophytes), the Thallophytes are peculiar in quite lacking common morphological characters of the sort that make these assemblages of higher plants very natural groups. The bonds of union in the Thallophytes are negative characters. Its members do not have the various positive marks of the higher groups. The association of the Thallophytes together because the vegetative structure is generally undifferentiated into stem, root, and leaf, is very similar to that old grouping of several independent branches of the animal kingdom under the head Invertebrata because they lacked the character of the highest subdivision.

The Thallophytes include an immensely more diverse assemblage of subclasses and orders than any other great class of plants. These groups are in certain regions so distantly related to one another that the gaps can only be bridged by assuming the previous existence of whole orders now entirely extinct or represented only by an occasional stray remnant. And the ages that brought about this fragmentary condition, with its remarkable forward developments in various directions, have left us in the structure of the surviving forms little or no evidence of the exact steps in the process. It is necessary to state this standpoint with respect to the Thallophytes so that the reader will clearly understand the possibilities of the theory that will be discussed presently, and which perhaps demands such preliminary explanation to justify its speculations.

The Chlorophyceae, as we have said, present no multicellular organs from which the archegonium or antheridium can be easily derived. But one region of the Thallophytes



gives us a structure that may throw some light on our problem. This structure is the plurilocular sporangium, and it is found in a number of the lower groups of the Phaeophyceae. The lower Phaeophyceae are represented by a number of families whose vegetative structure is diverse, but which agree in having one or both of two types of reproductive organs. There is the unilocular sporangium, a sporocyst, whose products are asexual zoospores; and there is the plurilocular sporangium whose products, likewise biciliate zoospores, are known to be sexual in many forms.

The sexuality of the plurilocular sporangium, while well established in certain types, is nevertheless far from universal in the group. It is well known from studies among the Ectocarpaceae that the zoospores from plurilocular sporangia may germinate without conjugation, and the external factors that determine sexuality are in part understood. So in considering the plurilocular sporangium we are dealing with a very simple and primitive type of sexual organ. The plurilocular sporangium is plainly a modified filament or branch. It consists at first of a row of cells, but shortly most or all of these begin to divide by walls in three planes, until the space originally occupied by one large cell is divided up into very many small cubical compartments (loculi), which give the structure a curious checkerboard-like appearance. A biciliate zoospore or gamete is formed in each of these compartments. Certain cells generally remain undivided at the base of the branch, constituting a stalk; and sometimes the tip remains sterile as a hair-like continuation of the axis.

Such is the structure of the simplest plurilocular sporangium. The higher types of this organ present some important modifications. The sterile tip is transformed entirely into reproductive tissue, so that the structure has less the appearance of a modified branch and more that of a specialized reproductive organ. There is also presented in certain forms (best known from studies among the Ectocarpaceae) a wide range of variation in the size and number of the compartments. Some of the sporangia have rather large compartments, and their

products are well-developed zoospores, deeply coloured by the brown chromatophores. The compartments of other sporangia are much smaller, and develop minute zoospores that are sometimes almost colourless. These conditions are shown in Fig. 21, a. Between these extremes there is frequently a sporangium with medium-sized cells whose products strike an average between the large and small zoospores.

The large and medium-sized zoospores may germinate directly if the conditions are not favourable for sexuality. The small zoospores have been known to settle down and germinate, but the results were feeble sporelings that could not live long. When sexuality is present the conjugation is usually between the large and small zoospores. The large gametes swim much more slowly than the small, and in certain forms (*Ectocarpus siliculosus*, *E. secundus*, and *Cutleria*) settle down as motionless cells which are fertilized by the small motile gametes. The latter have evidently reached a stage in their differentiation very similar to sperms both as to structure and behaviour.

It is evident that the plurilocular sporangium was not established from the first as a gametangium, because there is such a large amount of parthenogenetic development among its products. The structure at the outset was probably asexual. But it is evident that with sex once established the evolutionary direction is along lines exactly parallel with the history, so well understood, for several divergent and independent lines of Algae. Briefly stated, we observe the tendency to differentiate the gametes as to size resulting in small male and large sluggish female cells. The latter even behave like eggs in certain forms at the time of fertilization, when they are motionless. Although the type of sexual reproduction is isogamous, because the gametes are identical in form at the time of their discharge from the gametangia, still the conditions at the moment of fertilization are physiologically those of heterogamy.

Another peculiarity of the plurilocular sporangium should

be noted, and then we shall be ready to consider it in relation to our problem of the origin of the archegonium. The zoospores or gametes from plurilocular sporangia escape in various ways. There is extensive dissolution of the walls forming the compartments, and the zoospores are in this manner set free. But it has been observed in some species that the zoospores make their exit from the tip of the structure. It seems that the walls in the interior of the sporangium may break down more rapidly than those on the outside, so that the zoospores come to lie almost free in the interior, and are therefore able to escape from the opening first formed, which is generally at the tip.

We shall now take up some speculations on the fate of such a structure as the plurilocular sporangium under certain environmental conditions and in relation to the principles of sexual evolution. We shall try to show that the archegonium and antheridium might have been derived from such a structure.

It should be clearly understood that this is not stating a belief that the Phaeophyceae were the progenitors of the Bryophytes. We are using the plurilocular sporangium of the brown Algae simply as an illustrative type of a reproductive organ. To relate such an organ to the archegonium and antheridium we shall probably have to assume the existence of groups of green Algae with plurilocular sporangia of which no trace is left among living forms. This point will be considered later.

However, it is well to point out that a few Chlorophyceae have structures identical with the very simplest types of plurilocular sporangia, although with nothing approaching the complexities of the higher conditions. In *Schizomeris Leibleinii* portions of a filament, at times terminal, may become transformed into a thickened region several cells in diameter, all of which develop zoospores. And again, in *Draparnaldia* and some related forms the reproductive cells of lateral branches sometimes divide longitudinally to produce a branch which departs from the structure of a single row of



cells, and, since the cells develop zoospores simultaneously, strikingly resembles a plurilocular sporangium. The conditions among the lower Ectocarpaceae, especially in *Pylaiella*, are no more complex than in *Schizomeris*; so we have in the Chlorophyceae structures that might readily be the forerunners of well-differentiated plurilocular sporangia.

A plurilocular sporangium is subject to two sets of factors that may influence its form and structure, together with the character of the sexual cells. There are, first, the general laws underlying all sexual evolution in its advance from isogamy to heterogamy. And in addition to these developments there are the changes possible in any multicellular organ, because it is a cell-complex, and may be differentiated into tissues. A gametocyst (single cell) is by its simplicity barred from the complications possible to a gametangium.

The differentiation of the gametes into eggs and sperms is readily understood along the line that we have already suggested, which is a well-known path of development, and has been travelled by many groups of Algae. We know that the gametes vary in size, and that the larger female elements are sluggish and tend to settle down before fertilization as quiescent cells, to which the male gametes are attracted. Should the sluggishness of the female gametes be intensified some of them might not be able to leave the gametangium, but would remain there as eggs, retained on the parent plant, to which the male gametes must make their way. It is not at all uncommon for zoospores of various Algae to be mechanically held within a parent sporangium and, unable to escape, to germinate there. Such habits on the part of female gametes of plurilocular sporangia would finally result in heterogamy, with the retention of the eggs within the parent gametangium.

What are the possibilities of modifications in form and structure of the plurilocular sporangia themselves? These would depend on two important factors, first the sterilization of portions of the structure, and second the differentiation of regions of exit or entrance for the gametes. Modifications

of the first sort are very significant, those of the second would be readily understood in relation to them.

Sterilization of reproductive tissue is a well-known tendency among plants. It results in the sacrifice of certain reproductive cells or tissues, either in relation to environmental conditions, or through the conservation of food-material by which certain cells are favoured in their nourishment at the expense of others. The latter condition is illustrated very extensively in the asexual reproductive tissue of the sporophyte, and among sexual cells notably by the sacrifice of the nuclei in the oocysts of the Fucaceae (e.g. *Pelvetia*), and during oogenesis in certain Phycomycetes (e.g. *Albugo*, *Peronospora*, &c.). It is of course a fundamental principle in oogenesis among animals. If, as seems very probable, the canal-cells in the archegonium are degenerate gamete mother-cells, this principle finds an admirable illustration, for they are sacrificed with obvious advantage to the egg at the bottom of the structure, not only for its nourishment but also in relation to the mechanics by which the neck of the archegonium is opened and the sperms brought to the egg.

Sterilization of reproductive tissue in relation to environmental conditions implies such changes as are obviously a response to external factors. They are frequently involved at the same time with the conservation of food, but this is of secondary importance. The most powerful external factor affecting an organ is the medium in which it lies. If this be air the structure must provide itself with effective protective coverings, for the drying action of the atmosphere is perhaps the most serious difficulty with which the land plant contends. Desiccation must have been the chief danger that aquatic plants faced when they left the water, and very little advance in internal structure could have been possible until this problem was solved by the development of suitable external coverings.

Now let us consider what would happen to plurilocular gametangia of aquatic Thallophytes if such forms should gradually adopt terrestrial habits. The general protection

against desiccation demanded by the plant would sooner or later affect the details of structure. The plurilocular sporangia would respond to the conditions and become modified with other organs of the plant. Probably the first change would be the differentiation of an external protective tissue. This would require the sterilization of the outer layer of gamete mother-cells which would form a capsule enclosing the remainder of the tissue. The structure of such an organ is diagrammed in Fig. 21, b. An advance of this character would place the plurilocular sporangium in the same group of organs as the antheridium and archegonium.

After such a modification of the plurilocular sporangium the more special peculiarities of the archegonium and antheridium would seem insignificant. The structure would of course all along have been under the influence of the principles that regulate the evolution of sex. The gametes might already have reached some degree of sexual differentiation; or, if not, they would constantly tend in that direction; and the results would eventually be heterogamy, with the continued specialization of male and female organs. The female gametangium would retain its gametes as eggs, and the male would discharge its sperms under the proper conditions of moisture. The highest development would be attained in the female organ when, through the sterilization of the gamete mother-cells, all but one were sacrificed to the advantage of a specialized egg (see Fig. 21, c).

And in this connexion we may again refer to Mr. Holferty's unpublished observations upon the archegonium of Mosses. When the canal-cells form two or more rows at various levels in this structure, we have conditions exactly like those diagrammed in Fig. 21, b and c. So these important stages in the evolution of the archegonium which we have assumed as necessary to the hypothesis are actually present, except of course that in the archegonium the canal-cells normally do not develop gametes<sup>1</sup>. But the evidence that the canal-cells are

<sup>1</sup> Since the above was written, W. C. Coker has described and figured (*Botanical Gazette*, XXXV, 136, 1903) an archegonium with two eggs, lying one above the



degenerate gamete mother-cells can hardly be stronger, apart from the actual existence of such a series of organs as we have postulated.

To complete the agreement between such structures and the archegonium and antheridium we have only to understand the manner in which the terminal openings of these organs would be differentiated. These points of exit and entrance are conveniently situated, but there are probably more important reasons for their selection. The apex of the plurilocular sporangium is the situation where the gametes first mature and from which they first escape. And this would probably lead to the choice of such a point of dehiscence if the archegonium and antheridium were derived from this structure.

We have, naturally, very little direct evidence bearing on such evolutionary processes as we have just discussed. But the writer can see nothing in the structure, development, or behaviour of the archegonium, antheridium, or plurilocular sporangium that offers serious objections to the hypothesis presented. The difficulties are in the absence of intermediate stages, which cannot of course be presented unless forms exist that illustrate these conditions. The value of the hypothesis lies largely in its suggestiveness for further research, but it seems to the writer to offer an explanation far more acceptable than other views. Attempts to relate the archegonium to the oocysts of heterogamous Algae do violence to the fundamental character of their organization, as was shown at the beginning of the paper. This hypothesis, which carries the origin of the archegonium much farther back in point of time, seems safe in its reasoning and thoroughly consistent with the evolutionary principles of sex and tissue-differentiation.

To make the chief points in this paper clearer, and also as a summary, we have constructed diagrams (Fig. 21) illustrating

other and each with a ventral canal-cell. It was evident that the upper egg had developed from the lowest canal-cell. Such abnormalities are to be expected, according to our theory of the archegonium. Mr. Holferty has observed similar examples.

the evolutionary stages required by this theory of the origin of the archegonium and antheridium. And at the end (Fig. 22) we have arranged certain groups of Algae in relation to one another and to a problematical region of extinct forms which are supposed to have existed and been directly responsible for the Bryophytes.

The families Ulothricaceae, Chaetophoraceae, and Coleo-

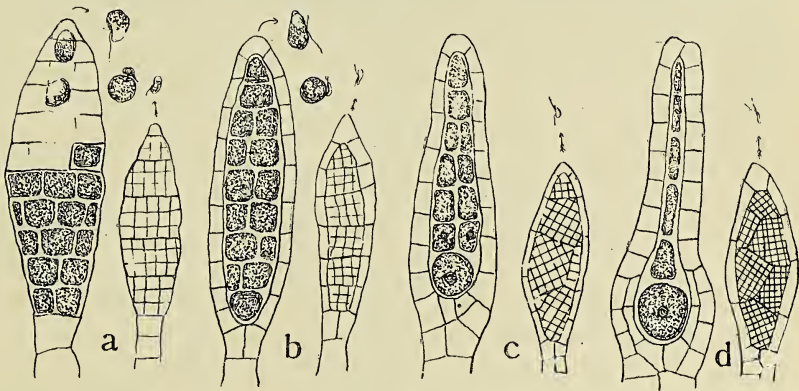


FIG. 21.—Diagrams illustrating the possible evolution of the archegonium and antheridium from the plurilocular sporangium. *a.* Plurilocular sporangia, with large and small gametes discharged from the apex, after the habit found in certain Phaeophyceae (e. g. *Chilionema Nathaliae*<sup>1</sup>, *Ectocarpus virescens*<sup>2</sup>, &c.). *b.* Plurilocular gametangia of a hypothetical algal type which has adopted terrestrial habits. The outer layer of gamete mother-cells has become sterilized as a protective capsule enclosing the fertile tissue. The gametes are differentiated in sex but both are still motile. *c.* Plurilocular gametangia of somewhat higher hypothetical forms at the level of heterogamy. Sterilization has proceeded so far in the female gametangium that only a few gametes are matured at the base of the organ, and these are eggs. *d.* Simple types of archegonium and antheridium. The female gametes are reduced to one, while the number of male gametes is greatly increased, and these cells are smaller and more highly specialized than in the earlier conditions.

chaetaceae of the Confervales are closely related to one another and seem to constitute a line of ascent. Among the lower representatives of these families are several forms (*Schizomeris*, *Draparnaldia*, &c.) whose zoospores are pro-

<sup>1</sup> Sauvageau, 'Sur quelques Myrionémacées.' Ann. d. Sci. Nat., 8<sup>e</sup> sér., v, 103, 1898.

<sup>2</sup> Id., 'Sur l'*Ectocarpus virescens*, Thuret.' Jour. d. Bot., x, 17, 1896.

duced in special regions of the filaments, sometimes considerably thickened, which resemble the simplest types of plurilocular sporangia. The presence of such structures among the Chlorophyceae is important, since it tends to overcome the difficulties in our assumption of a region of extinct green Algae with plurilocular sporangia which we have supposed to be the ancestors of the Bryophytes.

The Rhodophyceae may have arisen close to the Coleochaetaceae.

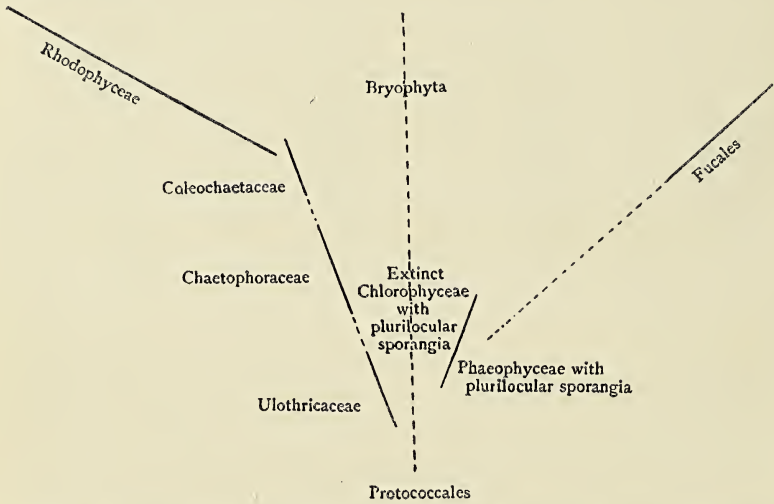


FIG. 22.—Diagram showing the position of a hypothetical group of extinct Chlorophyceae with plurilocular sporangia, supposed to be the progenitors of the Bryophytes, in relation to the algae most intimately concerned with this discussion.

The lower Phaeophyceae can hardly be supposed to have given direct origin to the Bryophytes, although this is conceivable. They have been arranged at the side of a hypothetical region of extinct Chlorophyceae. The Fucales are far to one side. Their sexual organs are gametocysts, and must have had their origin from unilocular sporangia.



# On the Structure of *Schizaea malaccana*.

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With Plates XXV and XXVI and a Figure in the Text.



THE Schizaeaceae are certainly one of the most interesting families of Ferns from the point of view of their stelar anatomy. Within the limits of a very natural group of but four genera they appear to exhibit all the principal stages which recent theory has distinguished in the evolution of the stele—protostely with a solid xylem in *Lygodium*, and with a parenchymatous pith in *Schizaea*, solenostely in *Anemia* § *Anemiorhiza*, and dialystely in the majority of the species of *Anemia* and in *Mohria*. There seems at present no reason for taking any other than the simple view that these four types represent progressive stages in the evolution of the stelar system, according to the general theory of Jeffrey<sup>1</sup> and Gwynne-Vaughan. But in a case of this kind, where we have such a wide range of structure in a single family of but few genera, it is of importance to examine the anatomy of every

<sup>1</sup> Professor Jeffrey, however, considers that *Schizaea* represents a degeneration-stage from a siphonostelic type. See 'The Structure of the Stem in the Pteridophyta and Gymnosperms,' *Phil. Trans.*, B, 1902.

species, so as to obtain all possible evidence as to the relations of the different types of structure exhibited.

The present species shows some interesting features which seem worthy of record, partly by way of supplement to Boodle's excellent comparative account of the family in a recent number of this Journal<sup>1</sup>, and partly because they suggest a discussion of the phylogenetic problems involved<sup>2</sup>.

The sequence of cell-divisions at the apex of the stem, so far as our rather scanty knowledge of the meristems of Ferns goes, is quite exceptional, and is a striking example of the impossibility of considering histogenetic distinctions as trustworthy guides to the morphology of adult tissues.

#### GENERAL DESCRIPTION AND SPORANGIA.

*Schizaea malaccana*, Baker, is a fairly well distributed species of the Malayan region. It is very common on the upper part of Mount Ophir (Johore), where our material was gathered in January, 1901. The plants commonly grew several together, with their sub-erect stems embedded in leafy liverworts or in humus. The stem is short, none of the specimens in our material attaining an inch and a half in length. It is normally unbranched, yet in two or three cases we have found a branch arising close to the apex. In one instance at least this was merely owing to the death of the apical meristem; but in another specimen there was a regular dichotomy, one branch dichotomizing again almost immediately. The apical growth is probably very slow, and the tissues at the hind end of the stem die off gradually as growth proceeds. The surface of the stem is densely covered with the bases of fronds and with roots, which together form a thick matted investment, and give the stem a diameter of 3 mm. or more.

The fronds are well described in the Synopsis Filicum as

<sup>1</sup> Boodle, Anatomy of the Schizaeaceae. Ann. of Bot., June, 1901.

<sup>2</sup> The above was written before the discovery by Mr. Boodle in *Schizaea dichotoma* of similar features to those indicated. Mr. Boodle's paper containing an account of them will be found in the present number of this Journal.

'4-8 inches long, weak, flexuose, subterete.' They are also said to be 'channelled,' but this is probably mainly due to drying, as the transverse section of the frond is oval-oblong usually with no distinct groove, though there is sometimes a slight concavity on the morphologically upper surface. There is no differentiation into petiole and lamina, the whole length of the frond being perfectly uniform externally. The fertile fronds bear at the apex a few crowded fertile pinnae, the two rows standing out on one side parallel to one another and nearly at right angles to the axis of the frond, forming a kind of double comb (Pl. XXV, Fig. 1). When ripe the pinnae frequently come to stand out on each side of the axis in one plane (Figs. 1 and 2). The sporangia are borne on the inner (morphologically lower) side of the pinnae, and lie in two acropetal rows, one on either side of the midrib of each pinna. In structure and development they correspond so closely with those of *S. Pennula* as described by Prantl<sup>1</sup>, that it has not seemed worth while to give details.

Four countings were made of the number of spores in a sporangium, and the results were 90, 110, 112, 115. These come fairly close to the typical number 128, and agree well with Professor Bower's results for the order<sup>2</sup>.

#### THE ANATOMY OF THE STEM.

The plan of structure of the stem in the present species is usually on a smaller scale than in the other species that have been described (*S. Pennula* by Prantl<sup>3</sup>, *S. digitata*, *dichotoma*, and *fistulosa* by Boodle<sup>4</sup>).

The cortex, apart from leaf-bases, is only four or five to eight cells thick. It consists of rather large, not particularly thick-walled cells, which are frequently packed with starch grains, and always contain a good deal of mucilage.

<sup>1</sup> Untersuchungen zur Morphologie der Gefässkryptogamen. Heft 2. Die Schizaeaceen, 1881.

<sup>2</sup> Studies in the Morphology of Spore-producing Members. IV. The Leptosporangiate Ferns, Phil. Trans., 1900. Professor Bower found 128 the typical number for one species of *Lygodium*, for *Anemia* and for *Mohria*.

<sup>3</sup> Op. cit.

<sup>4</sup> Op. cit.



The stele has a rounded or oval outline, a shape which is frequently distorted by the departure of the leaf-traces. Apparently the leaves normally have a  $\frac{2}{3}$  divergence, but the vertical distance between the exits of successive traces is very variable, so that some transverse sections show two in process of leaving the stele, while others pass across the exit of only one, and others again show the stele entirely undisturbed in this way. In a few cases the insertion of leaves and leaf-traces appears to be quite irregular. The endodermis is composed of cells which have usually less than half the diameter of the cortical ones, with an average of about 30-40 on the circumference. The cells are filled with dense mucilage. Their outer walls, separating them from the cortex, are thick and brown; the radial walls are suberized in the usual way.

The cells of the pericycle, which has but a single layer, are of about the same size as, and correspond accurately with their sister-cells of the endodermis. Occasionally a pericycle-cell is divided by a tangential wall.

Immediately inside the pericycle comes the phloem, consisting of a one- or two-layered, almost complete zone of very small sieve-tubes, with practically no phloem-parenchyma. The number of sieve-tubes abutting on the pericycle is two or three times as great as that of the pericyclic cells. The breadth of the sieve-tubes is frequently twice as great in the tangential as it is in the radial direction. The tracheids of the xylem are often in immediate contact with the sieve-tubes of the phloem, i.e. there is no intervening layer of parenchyma such as Mr. Boodle has described in *S. digitata*, a layer almost universally present in Ferns. Occasionally, however, a few scattered parenchymatous cells are present between the xylem and phloem (a good many in Fig. 5), and in some of the larger steles this layer is constant and continuous. Sometimes the layer of sieve-tubes is itself interrupted, so that in places the tracheids abut directly on the pericycle (Figs. 3 and 4). The tracheid-ring is one to two—very rarely more than two (Fig. 5)—cells thick, and, like the

phloem, has practically no nucleated cells between its elements. The tracheids themselves are narrow; their thickening is scalariform or slightly reticulate. There is no trace of spiral elements anywhere in the stem.

The centre of the stele inside the xylem is one of the great features of interest in this species. In the simplest case there is a homogeneous 'pith' consisting of living thin-walled parenchymatous cells, of about the same, or rather greater, diameter than the tracheids, and of approximately the same length as the latter, seen in longitudinal section. This tissue has nothing in common (except its position) with the tissue enclosed by the internal endodermis of a solenostele. It is undoubtedly an 'intra-stelar pith,' as Russow and Prantl held.

Sometimes, though rather rarely, there appears in the midst of this central parenchyma a strand, or more seldom two strands, of tracheids, rarely more than two or three in a strand as seen in transverse section, and quite distinct from the xylem-ring (Fig. 4, *int. tr.*). Followed up in a series of sections, it is found that these strands are sometimes quite isolated, and sometimes connected at one end with the xylem-ring, while the other end has a blind termination in the parenchyma. The arrangement of these strands appears to have no relation whatever to the leaf-traces, and in fact to be quite capricious. The tracheids themselves are quite normally developed, and are identical in structure with those of the xylem-ring. These internal tracheids are only found in the larger steles where there is a comparatively bulky pith. In one specimen from Perak, kindly given us by Mr. R. H. Yapp, a considerably larger number of internal tracheids occurred at a certain level, forming an almost complete band across the pith (Fig. 5). Higher up, the stem dichotomized, but the phenomenon in question had no direct connexion with this, for the internal tracheids all disappeared before the stele began to divide<sup>1</sup>.

<sup>1</sup>The discovery of internal tracheids in the pith of the stele of *Schizaea* was made by Mr. Boodle in *S. dichotoma* before we found them in the present species.

In other cases, and far more frequently, there appears, also embedded in the central parenchyma, an internal endodermis. Such an endodermis may consist of a ring of as many as thirteen endodermal cells (Fig. 3), having all the characters of those belonging to the external endodermis, and enclosing one or more cells considerably smaller than, but otherwise possessing the characters of the cells of the cortex. On following such an internal endodermis upwards (towards the apex of the stem), it is found to be continuous with the ordinary external endodermis at the 'axil' of the next leaf-trace, while the enclosed cells are continuous with those of the cortex, in exactly the fashion characteristic of a solenostelic Fern. Traced downwards, the internal endodermis ends blindly, usually in the region of the node next below the one to which it belongs. In one case only was a blind termination found also at the upper end. In that case the internal endodermis had no connexion whatever with the exterior of the stele. Frequently, however, the internal endodermis, for the whole or for part of its course, encloses no cells, but simply consists of a solid strand, which may be reduced to a single row of endodermal cells. Many of the leaf-traces, however, have no internal stelar endodermis in connexion with them, the endodermis of each being continuous at the 'axils' simply with the external stelar endodermis (second node in Fig. 23).

Fig. 23, p. 499, gives a diagrammatic view of a median longitudinal section through an actual stem, showing the behaviour of the endodermis at the insertion of three successive leaf-traces. [These insertions are represented as distichous so that they may all three be shown in one plane. In reality they are not so. See p. 496.] When, as is not unfrequently the case, one or more strands of central tracheids coexist with an internal endodermis, the two have no connexion whatever.

#### PHYLOGENETIC SIGNIFICANCE OF THE STELAR ANATOMY.

The bearing of these new facts on the question of the phylogenetic position of the *Schizaea*-stele are not entirely clear, and must be considered at some length.



In the first place, we take it, they confirm the idea that the normal central parenchyma of the stele of *Schizaea* is part of the system of primitive intra-stelar parenchyma, here forming a distinct pith. If we believe, as apparently we must believe, that the 'protostele' (Jeffrey) with solid central xylem, as seen in *Gleichenia* and *Lygodium*, is the primitive type among Ferns, then we are naturally led to suppose that in *Schizaea* the central tracheids of such a stele are normally replaced by parenchyma, just as is the case in most species of *Lepidodendron* whose structure is known. Such a change might take place as the result of an increase in the circumference of the whole stele unaccompanied by a corresponding increase in the total amount of xylem, so that the centre of the stele becomes, as it were, vacant as regards conducting tissue, and is filled with parenchyma; or it might happen, and this is more probable in the case of *Schizaea*, that while the stele remains of the same diameter, or at any rate is not increased in size, the demand of the plant for water-conduction decreases considerably, and that, as a result, the central tracheids are no longer developed, but are replaced by parenchyma, among which a few ancestral tracheids still occasionally appear. The fact that the species of *Schizaea* are all comparatively small plants, mostly living in the humus of deeply shaded forests, and with a strikingly small transpiring surface

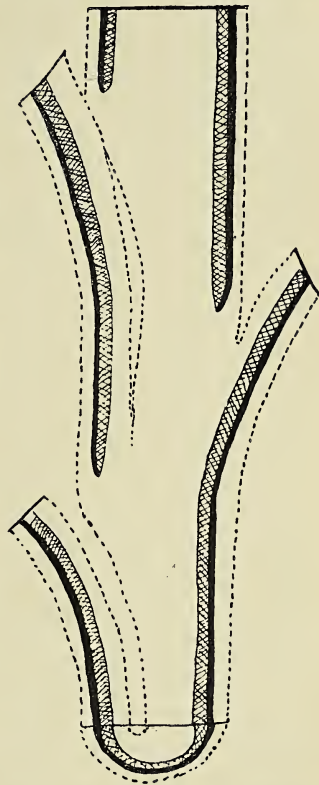


FIG. 23.—Schematic longitudinal section of part of an actual stem. *Endodermis* represented by dotted lines; *xylem* cross-hatched, *phloem* black.

even relatively to the diameter of the stele, makes it exceedingly likely that such a change would take place if we suppose an ancestor of the genus to have had a stele of the type which we find in the allied genus *Lygodium*.

But these phenomena are distinctly complicated by the occurrence of the internal endodermal pouches and rods in connexion with the leaf-traces, bringing *Schizaea* into relation with solenostelic forms. Are we to regard these endodermal structures as a progressive modification, constituting an advance on the medullated protostelic type, or as vestiges of a former solenostelic condition?

The main difficulty of the former hypothesis is to see how these endodermal structures, in their present condition, can be of any use to the plant. The same difficulty occurs in considering the downward extension of an internal endodermis from the node of *Gleichenia*<sup>1</sup> and *Lindsaya*<sup>2</sup>. Perhaps it may be partly met by the following suggestion. Suppose the diameter of a protostele be increased for any reason while the demand for intra-stelar (i. e. conducting) tissue is not increased; or suppose, as we are doing for *Schizaea*, that the diameter remains constant or is only slightly diminished, while the demand for intra-stelar tissue is considerably diminished. The lessened demand for conducting-tissue should affect the intra-stelar parenchyma as much as it will affect the xylem and phloem, since we have reason to believe that the main function of the parenchyma is to conduct carbohydrates. Certainly the proportion of intra-stelar parenchyma in *Schizaea*, in places where no internal endodermis is present, considerably exceeds the proportion ordinarily found in fern-steles. The central parenchyma here may be directly compared with that found in the roots and stems of some Phanerogams where this central parenchyma or pith is relatively narrow, and does not differ very markedly from the small-celled active tissue immediately connected with

<sup>1</sup> Cf. Boodle, The Anatomy of the Gleicheniaceae, Ann. of Bot., Dec. 1901.

<sup>2</sup> Cf. Tansley and Lulham, On a new type of Fern-stele, &c., Ann. of Bot., March, 1902.

the vascular bundles—in other words, where there is no very clear differentiation between the ‘internal’ and ‘external conjunctive’ of Flot. Such a central parenchyma will tend to become functionless for conducting purposes. In Phanerogams, when the stele is further dilated, this central tissue takes on the characters of typical ‘pith,’ i. e. its cells are short and broad, frequently entirely passive to all appearance, and sometimes even destroyed by the rapid growth of the surrounding tissues of the vascular ring. Such a pith obviously forms no functional part of the stele, though it is not separated from the vascular ring by a differentiated endodermis. But the corresponding tissue in Ferns, which is either used for the storage of starch or is sclerotic, is always separated from the vascular ring by a definite endodermis, and it is the origin of this state of things that is perhaps illustrated in *Schizaea*. The mass of the intra-stelar parenchyma is greatest at the point of departure of a leaf-trace, and here consequently we get the beginnings of its replacement by a physiologically extra-stelar tissue which is definitely non-conducting. This takes the form of what has been described as an ‘intrusion’ of cortical tissue into the stele, or, as we should prefer to say, of the development of a strand of tissue in connexion with the cortex, penetrating into the stele; and since the boundary of extra- and intra-stelar tissue is always marked by an endodermal layer, such a strand is always bounded by an endodermis, or may even consist of a mere rod of endodermal cells. *In this way the balance of the different intra-stelar tissues is readjusted.* So long as the stele does not increase in diameter we have these first beginnings of the development of physiologically extra-stelar tissue within the stele, remaining in the inconstant and irregular condition met with in *Schizaea*. If the stele were to increase in diameter, however, these pouches of extra-stelar tissue would increase in diameter with it, would meet and open into one another at the nodes, and an ‘ectophloic siphonostele’ (Jeffrey) would be formed. The ectophloic siphonostele is, however, the exception in Ferns. The more usual course of evolution apparently involves the development of internal phloem



as the first definite advance on the protostele with solid xylem. This is the condition found in *Lindsaya*. With further dilation the extra-stelar pouch appears at the node, just as in *Schizaea*, only here it replaces phloem instead of intra-stelar parenchyma. The meeting and fusion of the pouches, which is in process of happening in *Microlepia pinnata*, will then result in the formation of the typical 'amphiphloic siphonostele' of Jeffrey or 'solenostele' of Gwynne-Vaughan<sup>1</sup>.

The alternative, and as some will perhaps think, the more natural hypothesis, is that the *Schizaea*-stele has been derived by reduction from a siphonostelic type, the occasional internal endodermis being a vestige of this former condition. There is no *a priori* objection to such a view. It must be remembered, however, that no vestiges of internal phloem have been found in a considerable amount of material, and that the ectophloic siphonostele is a rare type in Ferns, no evidence of its existence being forthcoming in any of the allies of *Schizaea*. Further, the considerable amount of persistent central intra-stelar parenchyma, with its occasional tracheids, is difficult to understand on this hypothesis. If *Schizaea* were really derived by degeneration from an ectophloic siphonostelic type we should rather expect the remains of the internal endodermis to be always close to the xylem-ring. Thus it appears that the hypothesis we have put forward is really the simpler and more natural one, provided the general view of the factors governing the formation of physiologically extra-stelar tissue within the stele be accepted.

#### THE ANATOMY OF THE LEAF-TRACE AND LEAF.

The leaf-trace (Figs. 3 and 4) consists simply of a section of the stele of the stem which gradually passes off through the cortex at a slight angle with the long axis of the stem. It is therefore strictly collateral and remains so throughout the leaf. It is made up of a short band of phloem, separated by a single sometimes incomplete row of parenchyma from a short band of xylem, the whole surrounded by a peridesm composed of a single layer of rather large cells—those on the outer side

<sup>1</sup> Cf. Tansley and Lulham, *op. cit.*

continuous with the pericycle of the stele, those on the inner with the outer cells of the pith—and by an endodermis like that of the stem-stele. The characters of the xylem and phloem are also exactly like those of the stem-stele, spiral tracheids being quite absent. The meristele retains these characters for some millimetres up the leaf, but at a distance of 1 cm. from the leaf-insertion practically all the characters of the leaf-bundle have been acquired.

The leaf-bundle (Fig. 6) is circular or rather oval in outline, situated rather nearer the lower than the upper leaf-surface, and surrounded by an endodermis and pericycle exactly like those of the stem. The xylem has the form of a crescentic strand enclosing three or four large parenchymatous cells (which have strikingly large, elongated nuclei) and the band-shaped strand of sieve-tubes between its horns. The body of the xylem crescent is occupied by two large scalariform tracheids, side by side. Between these and the periderm is a little group of spiral protoxylem-elements (Fig. 7, *px.*), which in the adult leaf are crushed and often nearly obliterated (Fig. 6, *px.*)<sup>1</sup>. The sides of the crescent are occupied by a few narrow scalariform tracheids (*tr.*), and at each horn, between these lateral tracheids and the sieve-tubes, is a group of fibres (*s. t. f.*) such as Boodle has described in a similar position in *S. digitata*. As in that plant, they are, pretty clearly, thickened and lignified sieve-tubes, their end walls bearing sieve-plate-like structures (Fig. 7, *s. t. f.*). The whole bundle in fact, except for the existence of the two large central tracheids, is simply a smaller edition of that found in the other species. In the last few millimetres below the fertile pinnae the spiral elements are not formed, and the parenchyma-cells between the xylem and phloem are smaller. Just below the lowest fertile pinnae the bundle is considerably enlarged, the tracheids increasing to thirty or more in number.

As has already been said there is no distinction between petiole and lamina. For the first few millimetres from the

<sup>1</sup> There is no trace of the two lateral groups of spiral tracheids described by Prantl in the larger species *S. Pennula* and *S. elegans*.

base the epidermis and cortex of the leaf resemble those of the stem, but at 1 cm. up, the characteristic mesophyll and leaf-epidermis make their appearance. The mesophyll is distinctly peculiar (Figs. 6 and 8). It consists of very long cells running parallel to the axis of the leaf, with rows of lateral lobes coming off horizontally and joining the similar lobes of other cells so as to leave rounded or angular lacunae between the cells. The lobes sometimes have two arms and are irregular in size and shape, so that they enclose a very irregular network of lacunae (Fig. 6), though they themselves form fairly even longitudinal rows, each row containing eight or ten lobes (Fig. 8). All the mesophyll cells are alike in structure and contents.

The epidermal cells are thick-walled, broad, and of considerable length. The stomata are arranged in two longitudinal rows on the morphologically lower surface of the leaf. In each row every alternate cell becomes the mother-cell of a stoma. The guard-cells project slightly from the general surface of the leaf. Their length is three or four times as great as their transverse diameter. The inter-stomatic cells (*i. st. c.* in Figs. 6 and 8) of the stomatiferous rows are shorter and deeper than the ordinary epidermal cells.

#### THE ANATOMY OF THE ROOT.

This corresponds with Prantl's description and illustration of *S. Pennula*<sup>1</sup>, but we have thought it well to figure a transverse section of the stele (Fig. 9), as the cells of the phloem are not shown by Prantl.

#### DEVELOPMENT OF TISSUE-SYSTEMS AT THE APEX OF THE STEM.

The growing-point of the stem of this plant is rather variable in form. The free apical surface is always flattish, and sometimes forms a perfectly plane surface at right angles to the long axis of the stem. More usually it is slightly convex. There is a well-defined apical cell of an approxi-

<sup>1</sup> Prantl, *op. cit.*, p. 38, Taf. IV, fig. 59.



mately tetrahedral shape, about twice as deep as it is broad (Fig. 10); in longitudinal section its side-walls appear nearly parallel to one another towards the free surface, and this character is correlated with the flatness of the apex. Sometimes the apical cell and its immediate products occupy a projection or papilla in the centre of the flat meristematic surface. This appears to be the case when growth is very feeble or at a standstill; the products of segmentation are then much divided, and the resting apical cell has pushed out in front of the general meristematic surface. The apex is protected by numerous mucilage-producing hairs (*h.*, Fig. 10), which grow out from the cells of the meristematic surface quite close to the apical (the fourth or fifth cell from the apical has often already produced its hair), and bend inwards, usually quite covering the apex. Every one of the peripheral cells of the meristematic surface produces such a hair. Leaves are formed, together with adventitious roots, at a very early period, and one of the former often projects from the shoulder of the growing-point. The sequence of cell-divisions and the origin of the stem-tissues are not altogether easy to follow. This is due partly to the early origin of leaves and roots, the dividing tissues of whose rudiments sometimes force the stem-apex out of the central axis, and disturb the regular arrangement of the initials of the stem-tissues, and partly to the somewhat inconstant and irregular sequence of divisions in these last; microtome-series are not easy to obtain, owing to the packing of the early-differentiated cortical cells with large starch-grains preventing thorough impregnation with paraffin and consequently causing the sections to break up under the knife. Owing to one or other of these causes we have comparatively few sections in which the whole course of histogenesis is perfectly clear, in spite of the considerable amount of material at our disposal; but by carefully comparing a number of series, we have arrived at conclusions of whose correctness we have no doubt. We have figured a section in which the course of histogenesis is particularly clear (Fig. 10).

Each segment cut off from the apical cell divides first by

a periclinal wall into an outer segment (*o.*) and an inner (*i.*). The latter then divides by another periclinal wall giving rise to an innermost cell (*i'*.) and a middle cell (*m.*) of the anticlinal series of three into which the original segment has now divided. Of these *o.* is a cortical initial, *m.* an initial of the endodermis, pericycle, phloem and xylem, and *i'* an initial of the pith. The divisions of these initials are not entirely constant. The outer cell may divide at once anticlinally, or it may remain undivided for a time and then divide periclinally (commonly into two and almost immediately into four). The middle cell divides by a periclinal wall, which in most cases separates an initial (*me.*) of the endodermis and pericycle from an initial (*mi.*) of the xylem and phloem. The innermost cell undergoes various divisions, largely horizontal, and the innermost daughter-cells differentiate very shortly into pith-cells, which are formed so early that they are often only separated from the apical by two or three meristematic cells<sup>1</sup>.

To return to the fate of the segments of the middle cell (*m.*): on a level with the young pith, at a distance of .14 mm., and separated by about six cells from the apical in the apex figured in Fig. 10, the inner (*mi.*) of its two segments divides by a periclinal wall into two narrow cells, elongated in the direction of the axis of the stem, the inner of which (*x.*) is a xylem initial, and the outer (*ph.*) a phloem-initial. Both of these elongate, divide by radial and tangential walls, and very soon give rise to tracheids and sieve-tubes. Shortly after the division of *mi.* into *x.* and *ph.*, the outer segment (*me.*) divides tangentially into *e.* and *p.*, initials of the endodermis and pericycle respectively. Outside these the cortex is now about eight cells thick, but is often disturbed by a leaf-rudiment.

Detailed information as to the course of histogenesis at the

<sup>1</sup> The appearance of the resting nuclei of the pith-cells is quite different from that of the meristematic cells which give rise to them. The nuclei are smaller and look more homogeneous in our material (fixed in ordinary methylated spirit). They take up haematoxylin much less readily than do those of the meristematic cells, in which chromatin granules are quite obvious. Later on, however, the pith-cells divide again to a certain extent and their nuclei reacquire the meristematic appearance.

stem-apex in Ferns is very scanty, but it appears from the general statements of Van Tieghem that the first-formed tangential walls generally mark the external limit of the stele or ring of steles, the sheath-layers (pericycle and endodermis) usually arising in common with the cortex outside these early tangential walls. On this ground Russow<sup>1</sup>, believing that histogenesis should be used as a basis for the morphological classification of tissues, proposed to exclude these sheath-layers from the vascular system. Strasburger<sup>2</sup>, as is well known, proposed the name 'phloeoterma' for the innermost layer of the cortex, using this last term for the belt of tissue external to, and clearly separate from, the young stelar system during histogenesis. In this sense the pericycle and endodermis of monostelic fern-stems nearly always arise from the phloeoterma, and it might be supposed that this layer had a widespread morphological value. But the present case, even should it prove an isolated one<sup>3</sup>, in which the sheath-layers arise, with the vascular ring, from a single initial layer, would appear to destroy this supposed morphological value, for we can hardly imagine that the sheath-layers are not homologous (that is phylogenetically identical) throughout the monostelic Ferns. This is a particularly striking instance of the untrustworthiness of histogenetic differences as guides to the morphological correspondence of different regions, a conclusion which can be reached on various grounds<sup>4</sup>.

It is now, we believe, generally accepted by those who concern themselves with the phylogeny of tissues, that single criteria cannot be employed, the only sound method of procedure being a careful comparative consideration of the structures as a whole from every point of view, the adult struc-

<sup>1</sup> Vergleichende Untersuchungen, 1872, p. 195.

<sup>2</sup> Bau und Verrichtungen der Leitungsbahnen, Hist. Beitr., IV. p. 310.

<sup>3</sup> From appearances observed by Mr. Boodle in transverse sections of the stem of *Schizaea*, it is probable that the type of histogenesis described may be found in other species of the genus.

<sup>4</sup> We cannot enter here into the intricacies of the actual relation of histogenesis to the morphology of the adult tissues, but it is proposed to publish shortly a detailed historical and critical account of the whole subject.



ture, as representing the current state of evolution of the plant body, naturally forming the starting-point of the investigation.

#### DIFFERENTIATION OF TISSUES BEHIND THE APEX.

The further development and differentiation of tissues below the point at which the initials *x.* and *ph.* are derived from *mi.* can best be followed in a series of transverse sections (Figs. 11-13). From these it is seen that the radial and tangential divisions in the layer of xylem- and phloem-initials is by no means constant and regular. The new longitudinal walls are formed in various orders, and division is much further advanced at some places on the circumference of the stele than it is at others. The three zones of stem-tissue derived respectively from *o.*, *m.*, and *i'*., are extremely obvious in Fig. 11. The cortical and pith-cells have thicker and darker walls, the nuclei of the former and some of the latter (those to the left) having already lost their meristematic appearance, while the intermediate zone comprising the initials of the vascular ring and sheath-layers is still markedly meristematic. A stage in which there are twice as many xylem- and twice as many phloem-initials as there are pericyclic cells is common, and there are often no further radial divisions in the initials of the vascular ring, but tangential divisions continue irregularly till the ring is four or five cells thick. In spite of this frequent irregularity in division, the common origin of a given endodermal and pericyclic cell with the adjacent xylem- and phloem-initials is often very obvious (e. g. at A in Fig. 12). The endodermis differentiates before the other tissues derived from *m.*, early acquiring the mucilaginous contents which give it such characteristic staining reactions. Meanwhile the first sieve-tubes are developed from the outermost phloem-initials at scattered spots on the circumference of the stele (Fig. 12). This differentiation continues till there is a fairly complete ring of phloem, and then isolated tracheids begin to develop abutting on the pith (Fig. 13). Hence the xylem is technically *endarch*, though whether this has any morphological significance is perhaps doubtful. It may, however, be noted that the stem-

protoxylem corresponds in position with the spiral elements of the leaf-bundle. At the point where a leaf-trace is leaving the stele the tracheids are first formed in the stele above the point of departure of the trace at a higher level than in the trace itself. The tracheids likewise increase in number till they form a fairly complete ring, normally one or two cells thick.

The endodermal and pericyclic cells occasionally divide by additional walls, either radial or tangential. The increase in the number of cells on the circumference of the stele is, however, comparatively small from the period of the separation of endodermis and pericycle initials right up to the period when differentiation of all the tissues is complete.

#### EXPLANATION OF PLATES XXV AND XXVI.

Illustrating the paper by Mr. Tansley and Miss Chick on *Schizaea malaccana*.

Fig. 1. Plant of *Schizaea malaccana*, half natural size.

Fig. 2. Pinnae of a fertile frond seen from below.  $\times 4$ .

Fig. 3. Transverse section of stele of stem of rather small plant (stem .8 mm., stele .2 mm. in diameter) showing departure of a leaf-trace, two endodermal cells, *end. r.*, continuous above with inner part of endodermis of leaf-trace; and endodermal pouch, *end. p.*, enclosing four cells of same histological character as cortex and continuous with cortex at departure of next leaf-trace above.  $\times 232$ .

Fig. 4. Transverse section of stele of larger stem (stem 1 mm., stele .3 mm. in diameter) showing departure of leaf-trace; one-sided endodermal pouch, *end. p.*, belonging to it, and enclosing two cells of same histological character as cortex; endodermal rod, *end. r.*, consisting of seven cells, belonging to next leaf-trace above; and internal tracheids, *int. tr.*, part of a strand continuous with edge of leaf-gap above and ending blindly below.  $\times 270$ .

Fig. 5. Transverse section of stele of large stem (stem 1.5 mm., stele .54 mm. in diameter) showing unusually rapid departure of leaf-trace and closure of gap in xylem-ring. *Int. tr.*, internal tracheids forming almost complete band across the pith.  $\times 100$ .

Fig. 6. Part of transverse section of leaf passing through the two stomatic rows on the lower surface; on the left a large inter-stomatal cell (*i. st. c.*); on the right a stoma (*st.*). In the meristele the two lateral groups of fibres (*s. t. f.*) lie between the sieve-tubes (*s. t.*) and the lateral tracheids (*tr.*). *Px.*, obliterated protoxylem.  $\times 150$ .

Fig. 7. Longitudinal section passing through side of meristele of leaf. Letters as in Fig. 6.  $\times 200$ .

Fig. 8. Longitudinal section passing through side of leaf showing a stomatal row with the alternation of stomata and inter-stomatal cells, and the armed longitudinally elongated mesophyll cells.  $\times 60$ .

Fig. 9. Transverse section of stele of root with inner layer of cortical cells. *Px.* protoxylem, *ph.* phloem, *per.* pericycle, *end.* endodermis.  $\times 200$ .

Fig. 10. Median longitudinal section of apex of small stem showing apical cell and common origin of endodermis, pericycle, xylem and phloem from middle segment (*m.*) of the anticlinal series of three formed by division of primary segments of apical: *o.* outer, *m.* middle, *i', i'.* anticlinally divided inner segment, formed by periclinal division of primary segment of apical cell; *me.* external segment of *m.* (= common mother-cell of endodermis and pericycle), *mi.* internal segment of *m.* (= common mother-cell of xylem and phloem), *e.* endodermis, *p.* pericycle, *ph.* phloem, *x.* xylem, *h.* mucilage-forming hair.  $\times 200$ .

Fig. 11. Transverse section of stele of large stem in meristematic region, close behind the apex, showing clear differentiation of the three layers, derived from the three series of cells shown in Fig. 10. The central cells, forming the young pith, *p.*, have mostly completed their divisions. The nuclei of those to the left (unshaded) have already entered the resting condition in which they take up haematoxylin much less readily. The middle zone, which is the initial zone of the vascular ring and its sheath, is thin-walled, and its inner division, *v. r.*, still often only two cells thick, corresponds to the mother-layers of xylem and phloem. At *l.* and *r.* the middle zone is thicker owing to the formation of a leaf-trace and of a root respectively. The outer division of the middle zone is the sheath-layer, or coleogen, *col.*, the mother-layer of endodermis and pericycle. This is still undivided except about the line *l.* Its cells are thin-walled and have darkly staining nuclei. Their common origin with the mother-layer of the vascular ring is extremely obvious. The outer zone, of which only the inner layers are shown, of larger thick-walled cells with resting (unshaded) nuclei, forms the young cortex, *cor.* Its divisions are practically complete.  $\times 200$ .

Fig. 12. Transverse section of young stele of same stem further back than in Fig. 11, showing coleogen divided into endodermis, *end.*, and pericycle, *per.*, and origin of sieve-tubes. The cells of the young phloem, *ph.*, whose walls are darkly shaded, already show the peculiar light blue colour with fuchsin-iodine-green characteristic of the walls of sieve-tubes in this plant. Some of them still possess nuclei. At *A* the differentiation of the stele is not so far advanced, and the accurate radial seriation of the mother-cells of endodermis, pericycle, xylem and phloem is well seen. This seriation can also be traced in other parts of the section where the mother-cells of xylem and phloem have already divided.

*e.r.*, *e.r.*, two endodermal cells belonging to two endodermal rods (proving the early differentiation of the internal endodermal structures) one of which dies out almost at once, while the other is continuous with an internal endodermis also dying out below.  $\times 240$ .

Fig. 13. Transverse section of stele of same stem further back than in Fig. 12, showing completed differentiation of pericycle and endodermis and of phloem-ring, broken by departure of a leaf-trace; also progressing differentiation of xylem-ring, *x.*, exhibiting its *endarchy*. *end. p.*, endodermal pouch, enclosing here one file of cells. *l. t.*, leaf-trace with xylem not yet differentiated.  $\times 175$ .







Fig. 1.  $\times \frac{1}{2}$

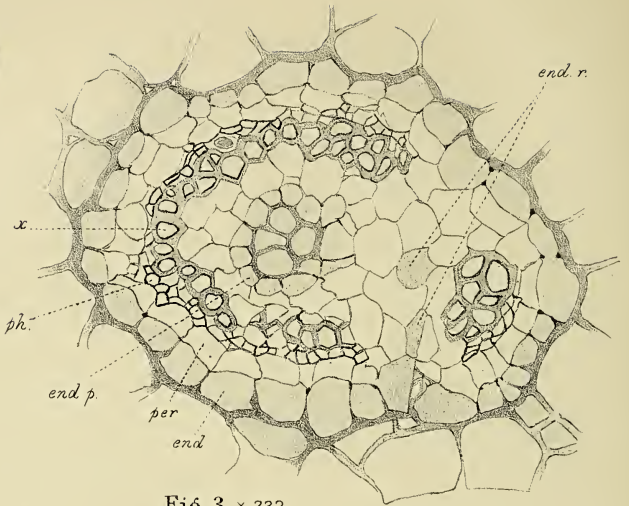


Fig. 3  $\times 232$ .

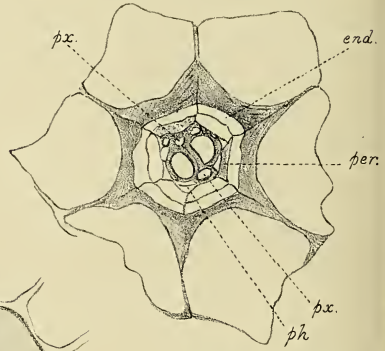


Fig. 9.  $\times 200$ .

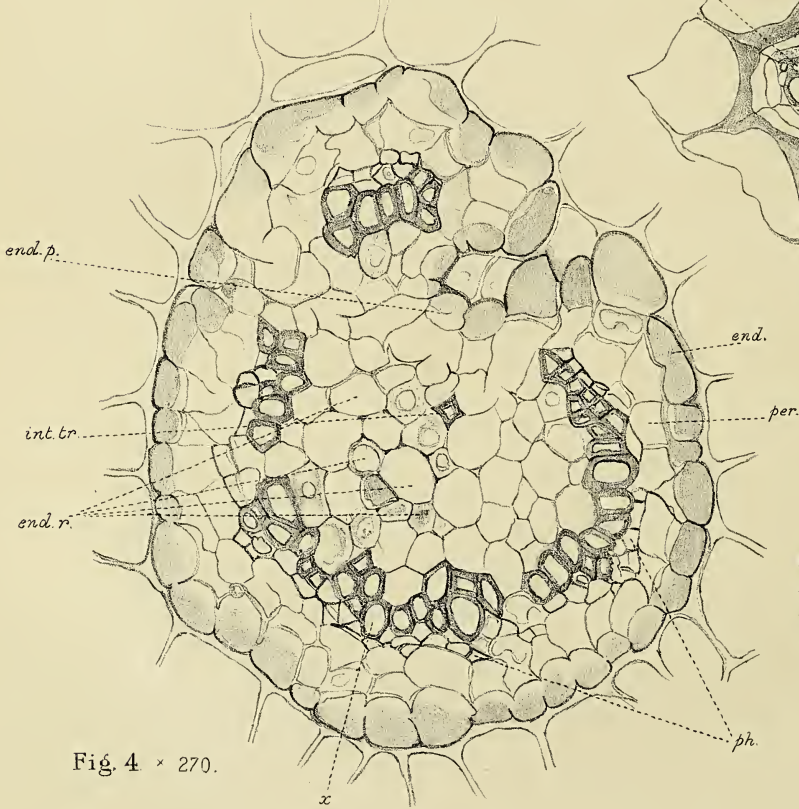


Fig. 4  $\times 270$ .



Fig. 2.  $\times 4$ .

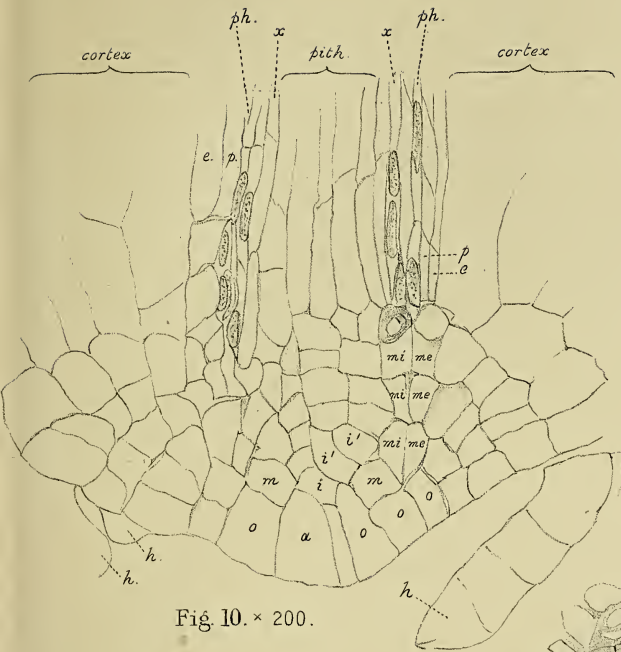


Fig. 10. × 200.

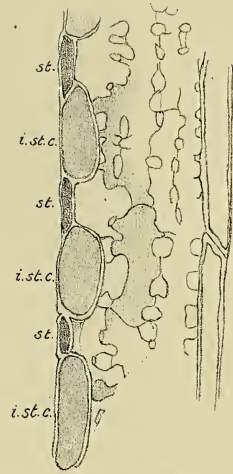


Fig. 8. × 60.

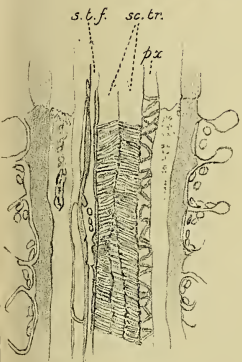


Fig. 7. × 200.



Fig. 5. × 100.

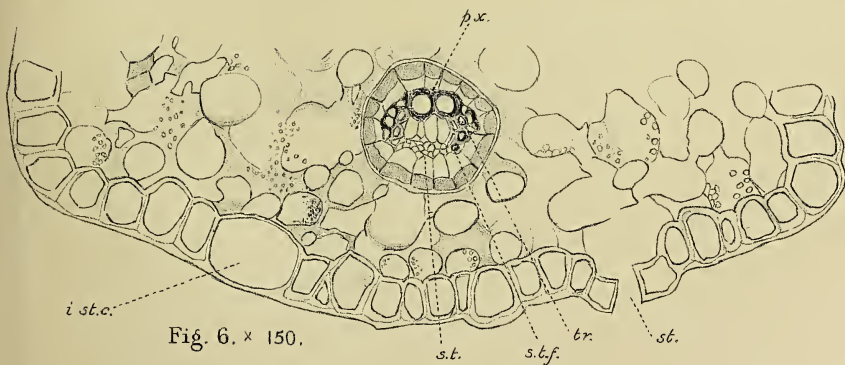


Fig. 6. × 150.





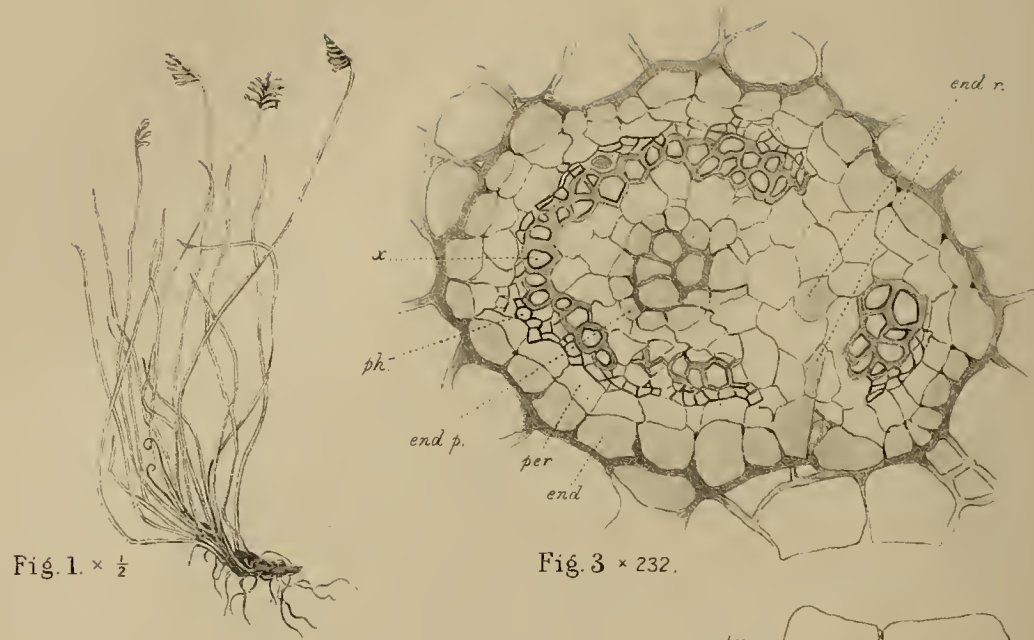


Fig. 1.  $\times \frac{1}{2}$

Fig. 3.  $\times 232$ .

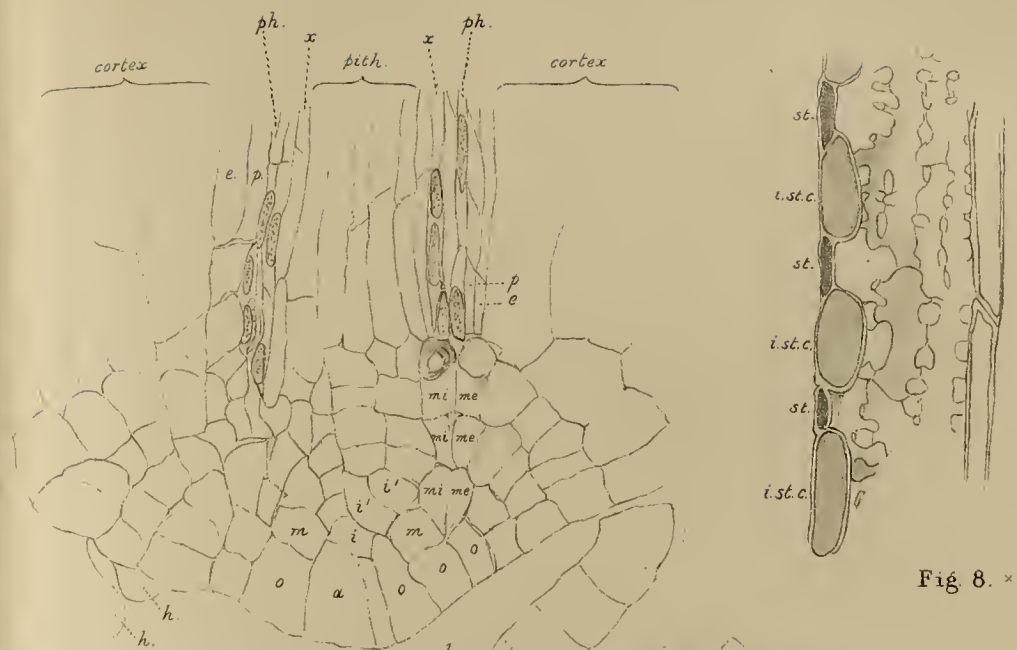


Fig. 8.  $\times 60$ .

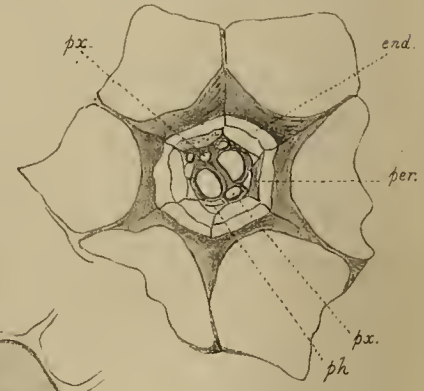


Fig. 9.  $\times 200$ .

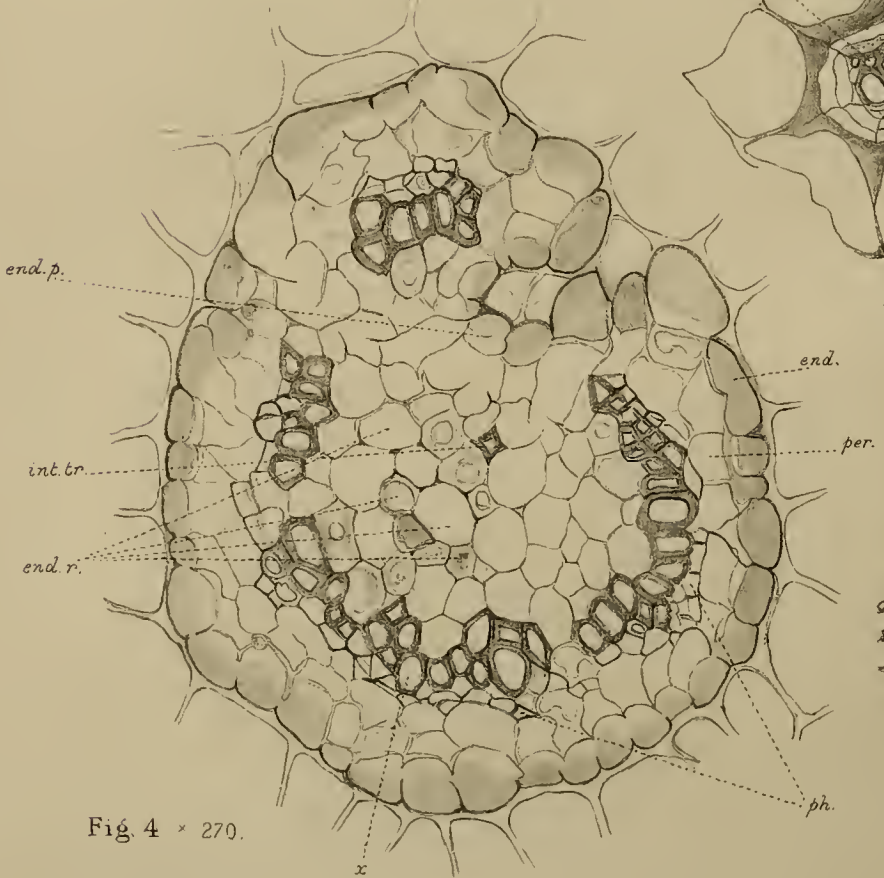


Fig. 4.  $\times 270$ .



Fig. 2.  $\times 4$ .

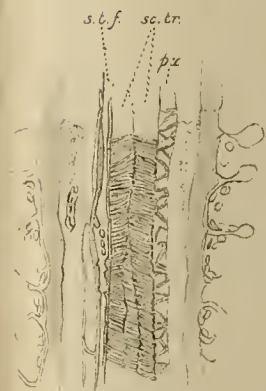


Fig. 7.  $\times 200$ .

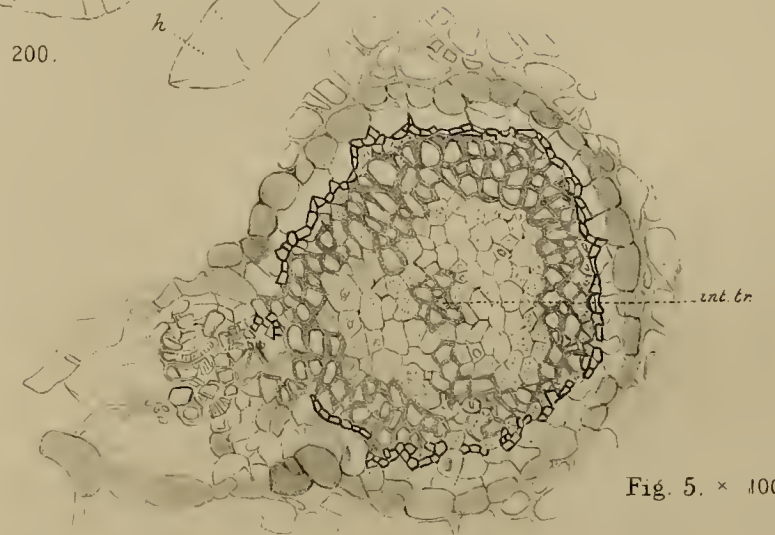


Fig. 5.  $\times 100$ .

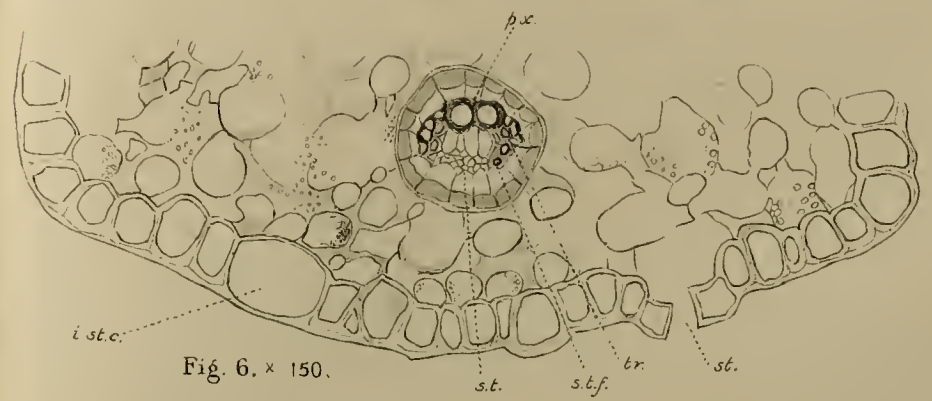
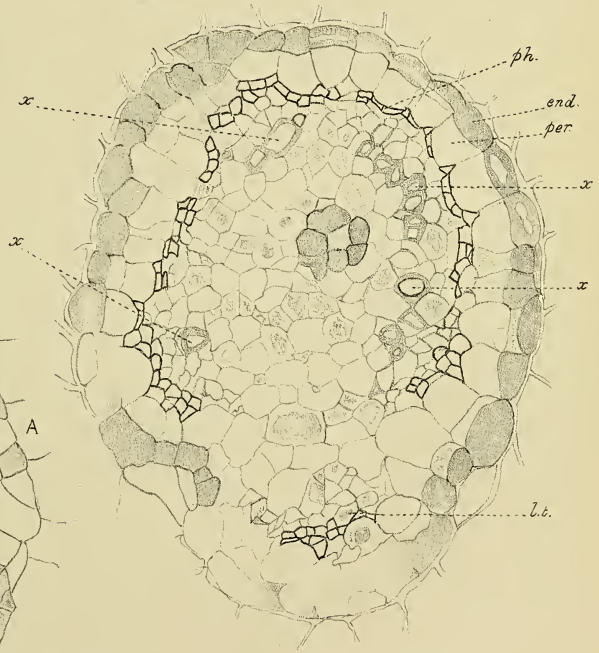
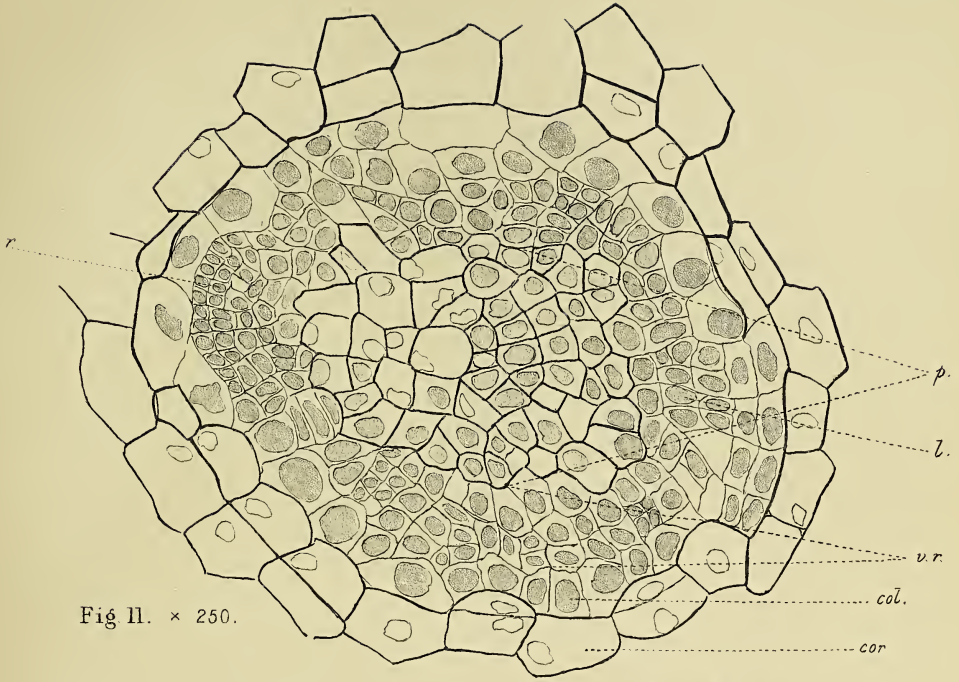
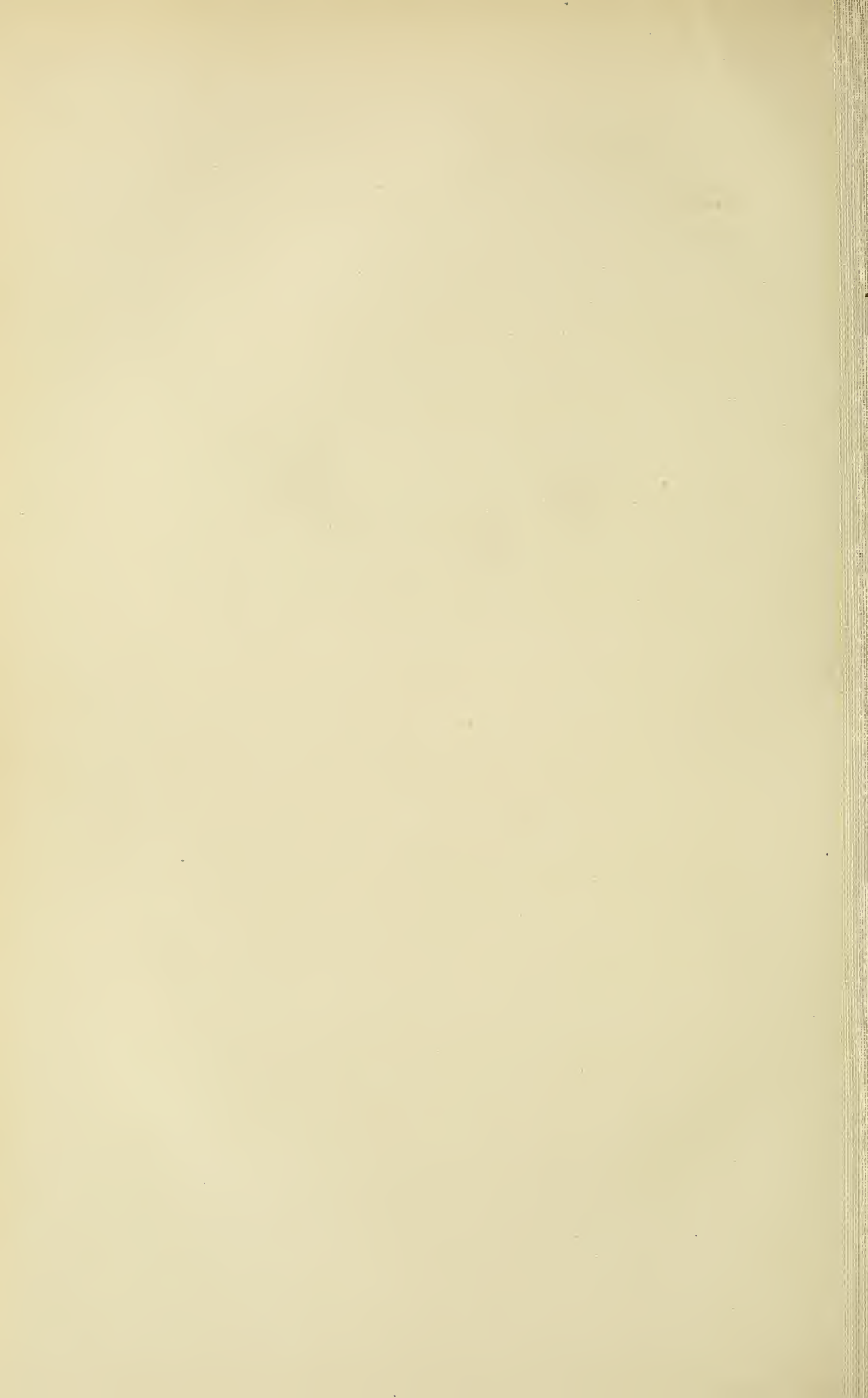


Fig. 6.  $\times 150$ .









# Comparative Anatomy of the Hymenophyllaceae, Schizaeaceae and Gleicheniaceae.

## IV. Further observations on Schizaea<sup>1</sup>.

BY

L. A. BOODLE, F.L.S.



With three Figures in the Text.



IN a previous paper on the anatomy of the Schizaeaceae (Boodle, 1901, p. 373) the vegetative structure of *Schizaea digitata*, Sw., was treated at some length, and a few observations were added regarding *S. dichotoma*, Sw., and *S. fistulosa*, Labill. The two latter species could not be dealt with fully, as small pieces of the dried rhizome formed the whole of the available material.

Further material of *Schizaea* has since been examined, namely, additional specimens of *S. digitata*, several plants of *S. dichotoma*, and of *S. bifida*, two specimens of a small form of *S. dichotoma*, and some seedling-plants of *S. pusilla*, Pursh. The structure observed in these species will now be described.

### SCHIZAEA DICHOTOMA.

The general structure of the rhizome of *S. dichotoma* has already been referred to (Boodle, '01, p. 378, Pl. XIX, Fig. 11, and Pl. XX, Fig. 15), but certain important features, which occur locally in parts of the stem of this species, call

<sup>1</sup> From the Jodrell Laboratory, Royal Botanic Gardens, Kew.



for special description. These are: dichotomous branching, nodal endodermal pockets, internal endodermis, and internal tracheides.

1. **Branching.** Among the specimens of *S. dichotoma* there were two or three with branched rhizomes. The branching has every appearance of being dichotomous, both on external examination and also in the behaviour of the stele. When

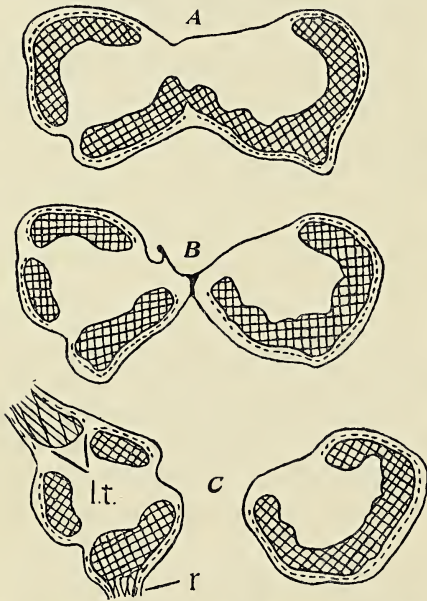


FIG. 24.—Dichotomy of the stele of *S. dichotoma*. *A, B, C*, three stages in acropetal order.  $\times 9$ . Endodermis represented by bounding line; xylem cross-hatched; phloem shown as a broken line. In *C*, leaf-trace and root at *l.t.* and *r.*

preparing for dichotomy the stele becomes elongated in the horizontal plane and then divides into two in a simple manner<sup>1</sup>. Three stages of its division are shown in Fig. 24. In this series, after the elongation of the stele, a leaf-trace is given off on the upper side leaving a gap in the xylem and phloem, which becomes very wide (Fig. 24, *A*); the lower part of the band of xylem and phloem splits in the median plane; the endodermis becomes constricted and fuses in the same plane (Fig. 24, *B*), producing an hour-glass-shaped double stele, which then separates

into two by fission of the endodermal bridge at the neck. The dichotomy of the stele is thus complete (Fig. 24, *C*). No branching other than apparent dichotomy was observed.

The mode of division of the stele (assuming that the latter

<sup>1</sup> Internal endodermis and internal tracheides may be present in the region of dichotomy, but do not affect the mode of division of the stele.

is bounded by the endodermis) resembles the dichotomy of the stele of *Lygodium* (Boodle, '01, p. 365), and the behaviour of the phloem in the region of branching gives no evidence for reduction from solenostely. Attention is drawn to this, because in *Osmunda cinnamomea* the special behaviour of the phloem in the region of forking (viz. the presence of internal phloem there and its continuity at times with the outer phloem) has been used by Faull ('01, p. 411 et seq.) and by Jeffrey ('02, p. 126) as one of their grounds for regarding the present structure of *O. regalis*, &c., as derived from a solenostelic (amphiphloic siphonostelic) type.

Without giving any very decided opinion as to the origin of the stellar structure of *Osmunda*, the writer wishes to emphasize: firstly, the importance, in any case where phylogenetic consideration of structure is concerned, of examining a large number of specimens of a given species—as was done by Faull in *O. cinnamomea*, &c.—so as to obtain any individual structural variation that occurs within the species; and secondly, the necessity of a very careful scrutiny of the results in the light of all available evidence suggestive of reduction on the one hand or advance on the other. Complication of structure restricted to a region of branching, just like complication at a node, should be accepted with great caution as a primitive structure, unless it be supported as such by weighty independent evidence.

While acknowledging the excellence of the observations detailed in Faull's paper, it may be pointed out as a serious omission that the seedling-stem of *Osmunda cinnamomea* is not described in greater detail. One gathers from the statements on pp. 396 and 410 of Faull's paper, and on p. 125 of Jeffrey's paper (Jeffrey, '02), that internal phloem is not present in the transitional region of the stem, but only occurs near the region of branching of the stem<sup>1</sup>. This being so, a grave difficulty arises, for we have two alternative views.

<sup>1</sup> In *Osmunda regalis* Leclerc du Sablon ('90) found in the transitional region a pith with no internal phloem, and Seward ('03, p. 241) found the same in *Todea hymenophylloides*.

(1) If we accept the evidence derived from the seedling as thoroughly reliable, the absence of internal phloem in it proves that *Osmunda* has not been derived from an amphiphloic siphonostelic form, and that the local occurrence of internal phloem in the mature stem has been entirely misinterpreted by Faull and Jeffrey.

(2) If, on the other hand, one accepts their interpretation of the internal phloem, occasionally present in the mature stem, as a primitive structure, then the absence of a stage in the seedling showing similar structure proves that the ontogeny is not reliable as an index of structural phylogeny. This would strike at the root of Jeffrey's whole generalization (which is chiefly founded on ontogeny) as to amphiphloic siphonostely being the type of structure which succeeded protostely in Ferns, and gave place in certain cases to medullated monostely by reduction<sup>1</sup>. For if the seedling-stem is at all dependable in repeating the structural history of the mature stem, one might of necessity count on *Osmunda cinnamomea* to show clear ontogenetic evidence of the previous existence of internal phloem, as, on our present assumption, it is a plant so little removed from the solenostelic condition that certain individuals of the species actually produce, by reversion in their mature stems, well differentiated local solenostelic structure. Thus it appears that either the basis of Jeffrey's theory, referred to above, is unsound, or the structure of *Osmunda* does not bear out Jeffrey's interpretation of it, and this genus forms an exception to his generalization.

The disagreement between Jeffrey's deductions from the anatomy of the mature plant and the evidence derived from the seedling, has already been pointed out by Scott ('02, p. 209) in a review.

The case of *Osmunda* has been referred to thus fully, because evidence of a similar nature has to be dealt with below in the case of *Schizaea*.

<sup>1</sup> There is certainly no sufficient evidence for regarding an inner endodermis as proving, in cases where it occurs, the previous existence of internal phloem.



2. Endodermal pockets. These are formed in connexion with some of the leaf-traces. One is seen in the transverse sections of the node represented by diagrams *A-D* in Fig. 25, which are arranged in acropetal order. In *A* two small endodermal pockets are shown cut transversely ( $e_1$ ). They

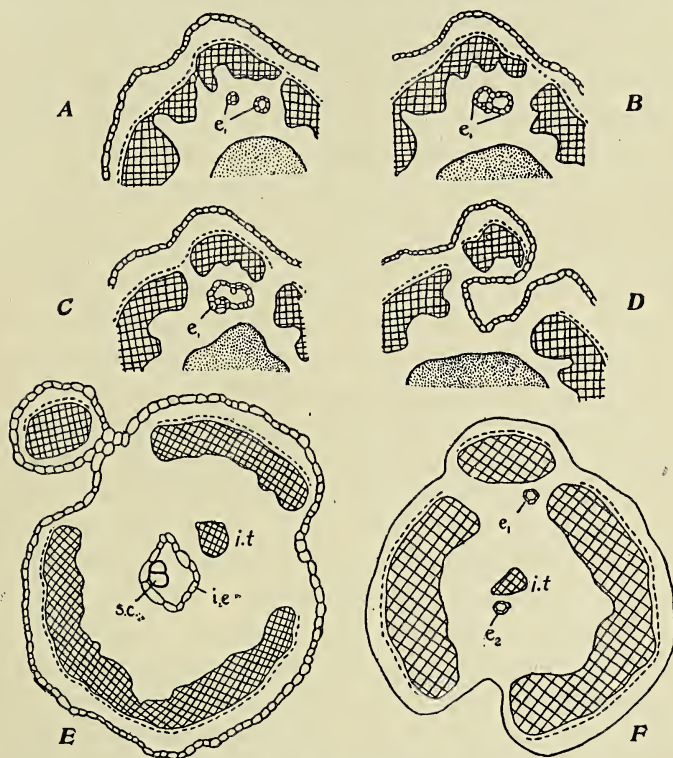


FIG. 25.—*Schizaea dichotoma*. *A*, *B*, *C*, and *D*, diagrams showing endodermal pocket ( $e_1$ ) connected with departing leaf-trace. Position of sclerotic tissue shown by dotted area. *E*, stele showing internal tracheides (*i.t.*) and internal endodermis (*i.e.*); *s.c.*, two sclerotic elements. *F*, stele showing internal tracheides (*i.t.*), nodal endodermal pocket ( $e_1$ ) and probably a second pocket ( $e_2$ ). All  $\times$  about 23.

soon fuse to form one, two stages of the fusion being shown by diagrams *B* and *C*. In *C* the mass of xylem belonging to the leaf-trace has become detached, while in *D* it has moved further outwards, and the endodermal pocket has

become connected with the outer endodermis, so as to form an involution of the latter, the tissue contained in the pocket thus becoming continuous with the cortex. A little higher up the loop of endodermis, thus formed, becomes connected with the outer endodermis across the other gap in the xylem, i. e. on the left of the leaf-trace, which then becomes free from the stele. After the separation of the leaf-trace the endodermis may remain 'invaginated' for a short time, e. g. as shown by a diagram in the previous paper (Boodle, '01, Pl. XX, Fig. 15). The length and obliquity of the nodal pockets<sup>1</sup> vary greatly; occasionally one of them may pass inwards some little distance towards the centre of the stele ( $e_2$  in Fig. 25, *F*, may be an extreme case of this, but the series of sections did not extend far enough to prove it); at other nodes, where the leaf-trace passes off more nearly at right angles to the stele, there may be no endodermal pocket. The nodal pockets of endodermis in *Schizaea dichotoma* are similar to those found by Tansley and Lulham in *Lindsaya orbiculata*, as represented in Fig. 10 accompanying their description of that species (Tansley and Lulham, '02), and to those occurring in *Anemia coriacea* (Boodle, '01, Pl. XV, Figs. 41 and 42 *e'*). A comparison between the structure of *Schizaea dichotoma* and that of *Anemia coriacea* will be made later.

**3. Internal endodermis.** Besides endodermal pockets connected with the nodes, an isolated internal endodermis is occasionally met with, e. g. a hollow spindle of endodermis tapering and closed both above and below, and lying vertically in the central tissue of the stele. Thus in Fig. 25, *E*, there is an inner endodermis (*i. e.*), which encloses a group of soft-walled cells (left blank) and two brown sclerotic elements

<sup>1</sup> The form of an ordinary endodermal pocket may be pictured by supposing a conical-tipped rod of cortical parenchyma provided with a sheath of endodermis to be pushed into the stele obliquely inwards and downwards from what may be called the axil of stele and leaf-trace, the endodermal sheath mentioned being continuous with the outer endodermis, which sheathes stele and leaf-trace. The endodermal pocket shown in Fig. 25 differs from the form above described in that it is forked at its base.

(*s.c.*). The inner endodermis in this case remains near the centre of the stele throughout its course, and only for a short distance encloses 1-2 sclerotic elements, resembling cells of the outer cortex; elsewhere it surrounds soft-walled cells only, like those forming the inner part of the cortex. Another case of a well-developed internal endodermis should be referred to. It differs from the one just described in the following characters: it attains a greater size, and, in the region where it is best developed, contains a fairly large group of brown sclerotic elements (a maximum of about 15) together with a certain amount of thin-walled tissue; for the greater part of its course it lies not far within the xylem-ring, and opposite a gap in the latter; for a certain distance it lies *in* this gap, and at one point a bridge of 1-2 endodermal cells connects this inner endodermis with the outer endodermis of the stele. There is, however, no communication between the ordinary cortical tissue and the parenchyma or sclerenchyma contained within the inner endodermis. Although the following fact probably has little importance, it should be mentioned that, in this series of sections, the phloem curved slightly round one of the ends of the open xylem-band, and that, when the gap in the xylem became closed, two or three sieve-tubes were shut in, but only persisted in the periphery of the pith for a short distance.

Deductions from the mode of occurrence of internal endodermis, &c., will be reserved until the internal tracheides have been described.

Internal endodermis in *Schizaea* was first discovered by Professor Tansley, viz. in *S. malaccana*; the inner endodermis of *S. dichotoma* was found by the writer subsequently.

4. **Internal tracheides.** The remaining peculiarity of *S. dichotoma* is the occurrence, in certain parts of the mature stem, of internal tracheides<sup>1</sup>, of which two examples are

<sup>1</sup> There is no constant relation of internal tracheides either to nodes or to the branching of the stem. In two cases of dichotomy some internal tracheides were present, and in one of these an inner endodermis also, in the region of forking, but in other cases, where internal tracheides were present, there was no branching near.



represented in Fig. 25, *E* and *F* (at *it.*). The group of tracheides and the adjacent endodermal ring, shown diagrammatically in Fig. 25, *F*, are represented in detail, with the adjacent parenchymatous cells, in Fig. 26, *G*. Internal tracheides are not often found. When present, they may behave in different ways, as will be seen from the two following cases. The strand of tracheides, represented in Fig. 25, *E*, was followed through a series of sections and was found to become gradually reduced to only two or three elements, and then to disappear both above and below, the tracheides being at no time very far from the centre of the stele. In the second case, there were a few tracheides at some little distance within the ring of xylem, but when followed in the acropetal direction they were found to decrease in number to one or two, which then passed outwards and joined the xylem-ring just where a gap in the latter became closed. In both these cases, in the region where the tracheides are most numerous, they form a solid strand, but, when the tracheides are reduced in number, they become separated from one another by parenchymatous elements (this separation has begun in Fig. 26, *G*).

Thus the internal tracheides may or may not have a connexion with the tracheides of the ring.

**5. Deductions from the anatomy of the mature plant.** We may now enter into a discussion of the conclusions to be drawn from the occurrence of internal endodermis and tracheides.

Jeffrey ('02, p. 129), applying the conclusions he reached in the Osmundaceae to the Schizaeaceae by analogy, regards it as probable that the type of central cylinder found in *Schizaea* is derived by reduction from that which is characteristic of *Mohria* and *Anemia* (i. e. from dialystelic structure). This view is not accepted here (though the theory put forward by the writer is similar in some respects), firstly, because the case of *Osmunda* is not admitted as proved, and secondly, on account of the nature of the structural evidence derived from *Schizaea* itself.

Endodermal pockets, if they occurred alone, need not, according to our present knowledge, affect the question of the phylogenetic history of the stelar structure, for they may penetrate a solid stele as in the case of *Lindsaya*, described by Tansley and Lulham and referred to above. That is to say, so far as one knows, they need not be vestigial structures, but might perhaps arise for mechanical reasons<sup>1</sup>. Thus no certain conclusion can be drawn from the presence of endodermal pockets alone.

The isolated internal endodermis, however, is difficult to explain except as a reduced structure. An argument which is practically based on the apparent impossibility of attributing a function to a given structure in its present condition is naturally inconclusive, but absence of function is also suggested by the apparently hap-hazard occurrence of the structure in question (without definite relation to nodes or branching).

Under these circumstances the following views are brought forward, while fully recognizing the tentative nature of some of them.

1. The internal endodermis described above, being isolated and apparently functionless, is probably reduced from some better developed structure.

2. Where the internal endodermis is best developed, it may be regarded as least reduced. And, as in that case it encloses two kinds of elements similar to the cells of the inner and outer cortex respectively, there is some probability that these two tissues were at one time (in the phylogenetic history) continuous with the cortex<sup>2</sup>, on the ground that continuity

<sup>1</sup> It is conceivable that certain strains, liable to occur in the leaf-trace (perhaps before the sclerification of the cortex), might be capable of tearing the endodermal sheath of the vascular system at its 'axillary' point, while the elongation of this part of the endodermis as a hollow tapering tube dipping into the stele might prevent rupture between endodermal cells. The fact that leaf-traces, which leave the stele nearly at right angles instead of at a more acute angle, do not have well-developed endodermal pockets, may have some such significance, though it would not, on the other hand, be incompatible with a vestigial nature of the endodermal pockets.

<sup>2</sup> Such continuity would prove nothing as to the homology of the tissues concerned.

generally goes hand in hand with physiological and structural identity. On the other hand, it is just possible that the presence of cortex-like elements within the inner endodermis may be due to a certain correlation in tissue-development<sup>1</sup>, the formation of an endodermis leading to the production, on its inner side, of elements similar to those on the outer side of the outer endodermis.

3. Comparison with *Anemia* (which belongs to the same Order) is of considerable value. Certain forms of that genus (in Prantl's sub-genus *Aneimiorrhiza*), which have a creeping rhizome and solenostelic structure, appear to form a series of reduction, the more xerophilous forms, some of which are adapted to growth on rocks, having thinner rhizomes. It is highly probable that the structure of the latter should be regarded as reduced from the type found in the larger forms of this series. To take two examples, which were partially investigated, *Anemia mexicana* has solenostelic structure, and central sclerotic tissue continuous with the cortex through the leaf-gaps, while *A. coriacea*, which is a plant with a smaller rhizome than that of *A. mexicana*, has in its stele a central core of sclerotic tissue surrounded by an inner endodermis, and also has endodermal pockets (see Boodle, '01, Pl. XXI, Figs. 41 and 42, e'), which are independent of the inner endodermis<sup>2</sup>. The most natural conclusion is that the endodermal pockets in *A. coriacea* are reduced remnants of previous funnel-like connexions between outer and inner endoderms at each node, i. e. of typical foliar gaps, such as are found in species with a thicker rhizome, e. g. in *A. mexicana*. Now as the two structural features just referred to in *A. coriacea* are paralleled in *Schizaea dichotoma*

<sup>1</sup> The writer hopes to publish at a later date some facts, which probably find their explanation in a correlation of this kind. As an example of correlation of a different kind, but also apart from function, one may quote the dorsiventrality of the floral organs of certain Podostemaceae as explained by Willis ('02, p. 438).

<sup>2</sup> These facts are based on the examination of a small amount of dried material, so it cannot be said whether important variations of structure may not occur within these two species, but the occurrence of the structure described in them is sufficient for our present purpose.



by the quite similar endodermal pockets and the internal endodermis enclosing sclerotic tissue (although of local occurrence), and as the form of the inner endodermis in *S. dichotoma* suggests reduction from a more extended tissue, the most satisfactory explanation of the facts is that the stelar structure of *S. dichotoma* is due to reduction from a type in which the endodermis had the same distribution as in *Anemia mexicana*. This view does not involve reduction from solenostely, but only from ectophloic siphonostely, because there is no sufficient evidence that *Schizaea* or its ancestors ever had internal phloem. Nor does it directly touch the question of the morphology of the central tissues. That, on the present supposition, could only be attacked by an examination of forms (if such were extant) transitional in structure between a protostelic type and the supposed 'siphonostelic' ancestor of the *Schizaeas*.

The structure of *S. dichotoma* is, however, of interest in relation to the general question of the morphology of tissues. For, if one attempts to assign morphologic value to the endodermis as would be implied by using the word 'phlooterma,' the natural inference is that the spindle-shaped sheath of inner endodermis, referred to above, contains cortical tissue, that in Fig. 25, *E*, where this endodermis is present, the bulk of the central tissue (that between inner endodermis and xylem) is stelar, and that, where the inner endodermis, after thinning off, comes to an end, *all* the central tissue must be regarded as stelar. It is difficult to see how an exponent of the morphological importance of the endodermis can avoid this conclusion.

The writer's view may be stated here: (1) that the local complications of structure in the rhizome of *S. dichotoma* are reversional phenomena occurring at certain periods in the life of the plant, probably when nutritive conditions were at their best, as indicated by Thomas ('02, p. 344 et seq.), in the case of local reversional complication of sporophylls in *Tmesipteris*; (2) that the structure of *Schizaea* has probably been derived from protostelic structure by the following stages, (*a*) appear-

ance of a parenchymatous pith, (*b*) differentiation from part of this parenchyma of a central strand of sclerotic tissue surrounded by an endodermis and continuous with the cortex at the nodes<sup>1</sup>, (*c*) reduction in size of the central core of sclerotic tissue, and severing of its connexion with the cortex, leaving endodermal pockets as a vestige of the previous connexion between inner and outer endodermis, (*d*) disappearance of brown sclerotic tissue and of inner endodermis, leaving a parenchymatous pith, (*e*) transformation of the latter into sclerotic tissue (as found in most parts of the stem of *S. dichotoma* and always (?) in *S. digitata*).

If one now turns to a consideration of the internal tracheides, it is important to remember their relation to the inner endodermis. The two best-developed strands of tracheides were associated with the two best-developed examples of internal endodermis. One tracheide-strand, being quite unconnected with the xylem-ring, appears to be a vestigial structure; the association with the inner endodermis also points to the same conclusion, for the tracheide-strand is an added structure in a part of the stem, which is presumably reverting to earlier characters.

The exact significance of the tracheide-strands must be left an open question, but one may say that they probably indicate that the tissue within the xylem-ring (exclusive of the area taken up by the inner endodermis) is potentially xylem-tissue. This is suggested also by the fact that, apart from these definite strands of tracheides, one or two tracheides sometimes branch off from the inner face of the xylem-ring and pass a short way into the pith. This and other features often cause an indefiniteness of demarcation between the xylem-ring and the central parenchyma, such as impressed Prantl ('81, p. 24) in *S. Pennula*, and gave one of his reasons for regarding the central parenchyma or sclerenchyma of *Schizaea* as belonging to the 'bundle,' and not representing a 'true pith.' His other reason was the absence of an endo-

<sup>1</sup> The change described in (*b*), and possibly in (*a*) also, might begin at the nodes and spread to the internodes.

dermis separating this tissue from the xylem, and this fact also determined Russow ('72, p. 97) and De Bary ('77, p. 344) to regard the central tissue as belonging to the bundle-tissue.

#### STRUCTURE OF THE MATURE PLANT IN OTHER SPECIES.

*Schizaea bifida* need not be specially described. In structure it resembles *S. dichotoma*, but its parts have smaller dimensions. Endodermal pockets are present, but neither inner endodermis nor internal tracheides were found. Further material of *S. digitata* has also been examined, but none of the complications of structure shown by *S. dichotoma* were present in the specimens sectioned.

#### YOUNG PLANT OF SCHIZAEA PUSILLA.

The life-history of this species has been described by Britton and Taylor ('01). A figure of the mature stem (in transverse section) of this species is given by these authors ('01, Pl. V, Fig. 80), but the transitional region is not dealt with. Seedling-plants of *S. pusilla* were sectioned with the microtome. The largest of these plants, examined in an acropetal series of sections, shows the stele becoming immature between the fourth and fifth leaf, but previously the mature type of structure usual in the genus had been practically attained, so a description of the series is worth giving.

The main root appears to be diarch; the transition to protostelic stem-structure takes place in the usual way, the tracheides becoming more uniform in size and surrounded by phloem (Fig. 26, A). When the first leaf-trace separates from the stele, it leaves only three tracheides; on the separation of the second leaf-trace 6-8 tracheides remain in the stele; these increase, after the attachment of the second lateral root, to about 15, the xylem of the stele being still solid. Parenchymatous cells next make their appearance in the xylem (at first only two of them), and they and some of the tracheides undergo change of position, so that the parenchyma-cells are sometimes completely shut in, sometimes not. When the xylem of the third leaf-trace separates



(Fig. 26, *B*), it leaves a horseshoe-shaped mass of xylem in the stele. The xylem becomes nearly closed again and the fourth leaf-trace passes off; after which the stele possesses a fair-sized group of central parenchyma surrounded by a ring of tracheides (Fig. 26, *C*), thus agreeing with the structure of the mature stem in other species of the genus. The xylem is now not quite mature, lignification not being complete in the two tracheides with dark walls in the diagram. One of the central parenchymatous elements in the same diagram is shown with dotted contents to represent mucilage. This cell differs from the other cells of the central parenchyma in possessing mucilage, and in this resembles the cells of the endodermis. It may quite possibly be a rudimentary vestige of a nodal endodermal pocket. Or probably a more correct statement of this supposition would be to say that this cell may represent part of an endodermal pocket, but has been differentiated (owing to correlation) in connexion with a node in a region of the stem, which probably never possessed complete endodermal pockets.

The central parenchyma in the part of the seedling we have been considering, gives no indication of being of the nature of phloem, so that from the young plant we obtain no suggestion of reduction from solenostely.

The petiolar bundles of the first and second leaf of *S. pusilla* are shown in Fig. 26, *E* and *D* respectively. The bundle of the first petiole, in the basal region of the latter, has two or three sieve-tubes and is collateral, but higher up (Fig. 26, *E*) sieve-tubes are not present. Fig. 26, *D*, is the collateral petiolar bundle of the second leaf. Thus there is no indication in the early leaves of the collateral bundles of the leaf having been derived from concentric ones by reduction in this phylum.

Britton and Taylor ('01) give three figures of leaf-bundles. The structure of the largest of these appears to be of the same type as that found in other species of the genus, and fibres appear to be present in the usual position.

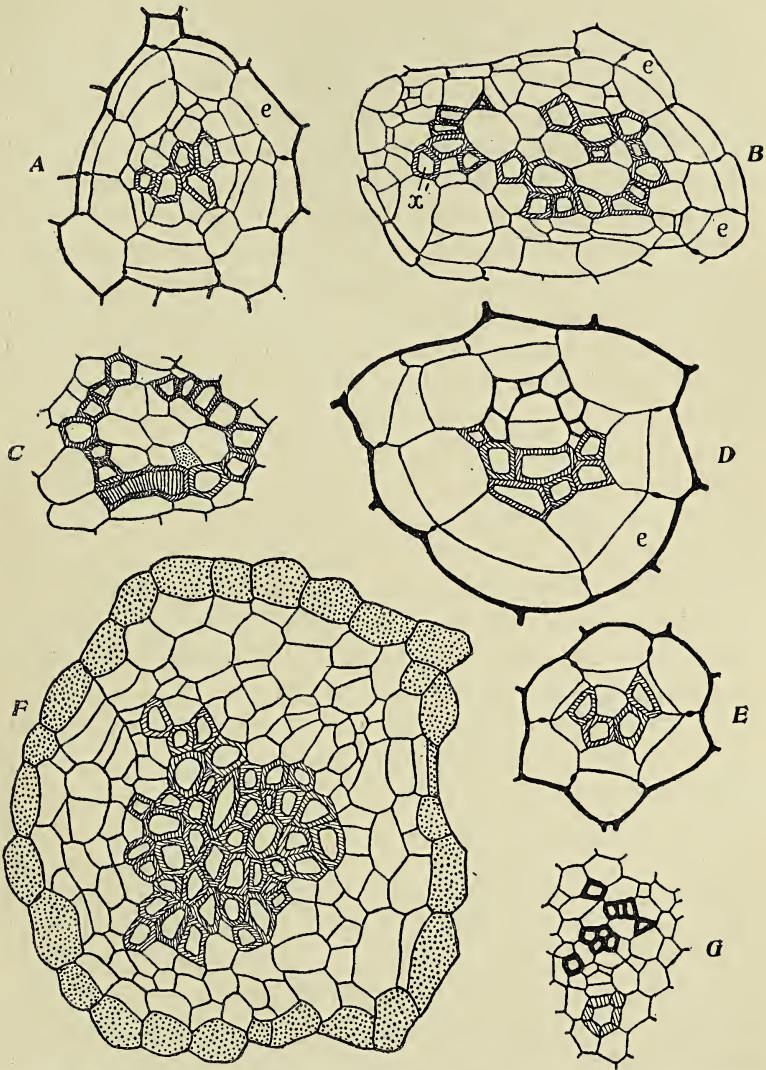


FIG. 26.—A-C, transverse sections of the seedling-stem of *Schizaea pusilla*: A, close above the primary root and before the separation of the first leaf; B, separation of the third leaf-trace ( $x'$ , xylem of the latter); C, after departure of the fourth leaf-trace. D and E, petiolar bundles of second and first leaf respectively of *S. pusilla*. F, *S. dichotoma*, small form, protostelic region of the stem. G, central tracheides and endodermis of *S. dichotoma* from Fig. 25, F. A, B, C, F, G,  $\times 260$ ; D, E,  $\times 600$ .

## SCHIZAEA DICHOTOMA, SMALL FORM.

Two plants, collected by Mr. R. H. Yapp and determined by him as a small form of *S. dichotoma*, will now be described. One of these plants bore two *fertile* leaves, but from the structure of the stem it is probable that both specimens were young plants<sup>1</sup>; the primary root, however, was not present in either. Fig. 26, *F*, illustrates a protostelic stage near the base of one of the specimens. Higher up one finds the transition to the mature type of structure. It takes place in much the same manner as in seedlings of *S. pusilla*, but the dimensions are greater than in the latter species. Only a few details need be given. In both specimens two or three parenchymatous cells appear in the xylem and soon increase to form a fair-sized pith, which shows no trace of internal phloem. In one specimen a very small endodermal pocket was formed in connexion with an early leaf-trace (i. e. not far above the protostelic region), while at a roughly corresponding level in the other specimen a small isolated tube of endodermis appeared in the central parenchyma. One slightly later node in each specimen was remarkable for the small difference in size between leaf-trace and stele, and the resemblance in shape of their respective xylem-masses, the shape being flattish-crescentic<sup>2</sup>.

## DEDUCTIONS FROM THE ONTOGENY.

If the transitional region of the stem of *S. pusilla* be compared with that of *Anemia Phyllitidis*, it is seen that, in these two plants<sup>3</sup>, the behaviour of the xylem and the mode of occurrence of soft-walled elements within it are very similar, but the nature of the soft-walled elements is different. In *Anemia* they comprise sieve-tubes at an early stage, while in *Schizaea pusilla* this is not the case. Nor does phloem occur

<sup>1</sup> They may be simply young plants of the typical *S. dichotoma*.

<sup>2</sup> One of these nodes when first examined was taken for a dichotomy.

<sup>3</sup> Examination of the structure of older seedlings of *S. pusilla* than that described in the present paper, and of known seedlings of *S. dichotoma*, is of course highly desirable.



in the pith of the supposed seedling-plants of *S. dichotoma*. These facts do not suggest a solenostelic ancestry for *Schizaea*, nor derivation from the *Lindsaya*-type.

The first two petiolar bundles are collateral ; hence there is no ontogenetic evidence for the petiolar bundles of *Schizaea* being reduced from the concentric type, and this fact favours the conclusion that the stem-structure has not been derived from a solenostelic type.

If one brings the supposed seedlings of *S. dichotoma* into consideration, the early appearance in them of small endodermal pockets and of rudiments which may represent an inner endodermis, while internal phloem is absent, would favour the view of reduction from ectophloic phyllosiphony.

#### ONTOGENY AND STRUCTURE OF MATURE PLANT.

The structure of the young plant of *Schizaea* has been insufficiently examined owing to lack of material, but such data as were obtained, are in agreement with the view derived from a consideration of the typical mature structure together with its variations in *S. dichotoma*. This is stated before giving an opinion as to what relative importance should be attached to different kinds of evidence.

A few words may now be said on this subject. Firstly, a study of the development of the tissues from the apical region, as Schoute ('02, p. 90 et seq.) has shown, does not give a morphological criterion. Secondly, the structure of the seedling-stem *may* give a clue to the phylogenetic origin of the mature structure, but probably what is found in the seedling requires great care in interpretation. Assuming that the transitional region of the stem repeats to some extent the phylogenetic history of the mature structure, it is extremely likely that there may be disturbing factors, which would at times make the evidence quite misleading. Thus certain kinds of reduction in the structure of the mature stem might be attained by one of the stages of the transitional region being continued unchanged in the mature stem, so that the plant would be a kind of permanently embryonic form

If this were to take place the ontogeny would give no clue to reduction. On the other hand a correlation in development, that is to say a tendency to uniformity of structure at all nodes<sup>1</sup> or in all parts of the stem, may cause the appearance of certain tissues precociously (i. e. at too low a level in the seedling-stem). Thus it is possible that in plants, where the possession of internal phloem is a well-established character in the mature stem, the internal phloem may spread downwards below its proper ontogenetic level. If this were to take place, all deductions from the seedling as to phylogenetic priority of internal phloem as compared with a pith would be quite unreliable<sup>2</sup>. To turn to the Dicotyledons for an illustration, the presence of internal phloem in the pith of the primary root of *Asclepias obtusifolia* (see Scott and Brebner, '90, p. 272) is almost certainly due to a downward extension (speaking metaphorically) of the inner phloem of the hypocotyl, and it is not an improbable assumption that the internal phloem in the lower part of the hypocotyl itself has originated in a similar way; otherwise, on ontogenetic grounds, one would have to assume that the ancestry of the plant in question did not include forms devoid of inner phloem.

Having pointed out one or two reasons for doubting the value of evidence derived from the stem-structure of the young plant, it will be as well to state what class of data appear to the writer to be important in elucidating a problem like that presented by *Schizaea*. The following is the method suggested:—

1. Any variations in the different parts of the mature stem or in the stems of different individuals should be noted.
2. Special attention should be paid to the structure of the node (because complications of advance or reversion, or more correctly retention, are to be sought here).

<sup>1</sup> Some features in the seedlings of some plants seem to point to the existence of such correlation.

<sup>2</sup> The writer does not wish to imply that in every case pith preceded internal phloem. Uniformity in this respect in different phyla is perhaps improbable on general grounds.

3. The structure of nearly allied species should be carefully compared with that of the species dealt with.

4. The structure of the young plant should be examined, chiefly to see whether it gives evidence of reduction not indicated by the mature plant, in the form of tissues not represented in a corresponding position in the mature stem.

5. In interpreting all such data obtained, both internal evidence and also independent clues should be sought as tests of advance or reduction.

#### GENERAL THEORY.

In the previous paper on the Schizaeaceae, as the forms included in that Order were found to possess features of special interest in relation to the stele, a discussion of some of the points at issue was given (Boodle, '01, p. 403 et seq.). It will be well to put together some further considerations on this subject and to restate others.

Tansley and Chick ('01) deduce, from their researches on some of the Bryophyta and from the probability of similarity of physiological requirements in the unknown primitive ancestors of the Pteridophyta, that in the latter the stem possessed a solid central strand of conducting tissue of the protostelic type and having acropetal development, that leaf-traces were developed independently of this protostele, and that their connexion with it was only a secondary phenomenon. This view appears well founded on theoretical grounds, and receives a certain amount of support from the fact that most cases of protostelic stems are found among the more primitive Ferns, and that as one passes from the lower to the higher forms the leaf-trace appears to exert more and more influence on the structure and development of the stele (cf. Gwynne-Vaughan, '01, p. 87). If one adopts this view, the tissues of the stele and leaf-trace are not strictly homologous<sup>1</sup>.

<sup>1</sup> Hence the writer prefers to retain the terms 'leaf-trace' and 'petiolar bundle,' rather than replace them by the word 'meristele,' suggested by Brebner ('02, p. 523) for use in an extended sense.



Starting with a small protostele and a simple type of petiolar bundle, the following appears a probable course of advance in structure among the Ferns. Increased leaf-surface necessitated increase in sectional area of stele and petiolar bundle. But this was achieved in two different ways, viz. simply by greater diameter in the case of the protostele, and by elongation into a band-shaped structure in the case of the petiolar bundle<sup>1</sup>. For mechanical reasons the peripheral part of the petiole had to be occupied by sclerenchymatous tissue; so, to avoid too great diameter in the petiole, the band-shaped bundle became arched. To admit of the insertion of a number of large arched bundles, the stele increased its diameter beyond the size required by the exigencies of water-conduction, and the central part of the xylem of the stele was transformed into parenchyma or other tissues. Such central tissue might be parenchymatous or sclerenchymatous at its origin and remain so in certain phyla (especially where the leaf-traces were collateral); in other cases it might be parenchymatous at first, and afterwards have its peripheral part converted into phloem; or inner phloem and pith might arise simultaneously; or possibly inner phloem might be produced without an ordinary pith (see Tansley and Lulham, '02).

To return to the petiole, its arched bundle was able to increase its sectional area<sup>2</sup> by an incurving of its ends, thus producing the horseshoe-type, which is of such frequent occurrence among Ferns as pointed out by Gwynne-Vaughan ('01, p. 95), and as seen by reference to the table of diagrams given by Parmentier ('99, p. 340). The division of the petiolar bundle into two or more portions, as found in many Polypodiaceae, &c. (see Bertrand et Cornaille, '02, pp. 53, 207, &c.), may be connected with the downward extension of the leaf-gap in the stem, or may have originated for mechanical reasons, because a large petiolar bundle would be subjected to consider-

<sup>1</sup> Convenient for the insertion of numerous distichous branch-bundles. Whether the primitive petiolar bundle was concentric or collateral must be left an open question, but probably both types existed at a fairly early stage.

<sup>2</sup> Without increasing the diameter of the petiole.

able strains unless the petiole possessed almost complete rigidity, and the latter would be unsuitable for positions exposed to wind.

Thus the theory suggested with regard to the origin of a bundle-system like that found in the petiole of *Pteris aquilina*, is that a band-shaped primitive bundle became arched and afterwards convoluted and divided<sup>1</sup>.

We therefore arrive at a different view as to the origin of the vascular bundles in the petiole of *Pteris aquilina* from that which the writer would suggest for the vascular system of the stem of the same species<sup>2</sup> (see Jeffrey, '00, pp. 10-11).

Jeffrey in his recent paper ('02, p. 143) states that it is not easy to see why on the views put forward (Boodle, '01) 'the same view [that applied to the bundles in the adult stem of *Pteris aquilina*] should not be taken of the equally complex arrangement of bundles in the petiole.' What has been said above explains the writer's view<sup>3</sup>. It should be pointed out that, when one is dealing with a question of morphology and comparing the tissues in two different organs, it is necessary to form a definite theory as to the phylogenetic history of the tissues in *both* organs before formulating their morphological relations.

#### FURTHER ANATOMICAL DETAILS.

The resistance to strong sulphuric acid shown by cell-walls in the cortex, pith, &c., of *Schizaea digitata* has already been

<sup>1</sup> A petiolar bundle of the horseshoe-type may also become closed (presumably by the conversion of the tissue between its ends into vascular tissue), e. g. in some species of *Gleichenia* (Boodle, '01 a, Pl. XXXIX, Fig. 19). In this case the central tissue of the bundle is regarded as belonging to the historically non-vascular portion of the petiole, which has been invaginated; so the view corresponds to that held by Jeffrey for the solenosteles in stems.

<sup>2</sup> For the stem the theory suggested is that if one could follow the stages in the evolution of its structure, one would find a protosteles converted into a solenosteles by the replacement of its central tissue by parenchyma and phloem (the two tissues appearing successively or simultaneously), and then by the conversion of part of the central parenchyma into vascular strands.

The non-stelar nature of the petiolar bundle is not insisted on here, but simply the theoretical view that the centrally placed parenchyma in the petiole has not been directly derived from vascular tissue.

mentioned (Boodle, '01, p. 376). *S. dichotoma* was found to behave in a similar way. A transverse section of the rhizome was placed in strong sulphuric acid, with a section of *Cucurbita* as a control. Some time after the greater part of the cellular tissue in the control had swelled up and disappeared, a very different result was seen in the section of *Schizaea*. The walls of the tracheides were considerably swelled, but sharply outlined walls remained representing practically all the rest of the cells. Previous boiling of the material in water did not alter the effect of the acid.

The differentiation of the xylem, as seen in a microtome-series of sections of the stem-apex of *S. dichotoma*, is irregular. Thus, taking one particular part of the stele as an example, no tracheides were differentiated except one at the extreme outside and one at the extreme inside of the young xylem-ring, while, in other parts of the ring of xylem, tracheides in an intermediate position may be the first to differentiate. The differentiation may also be much further advanced on one side of the stele than on the other, in relation to the nearest leaf-trace.

The sieve-tubes of *S. dichotoma* appear to be of a fairly normal Fern-type.

The petiolar bundle of *S. dichotoma* is of a similar type to that of *S. elegans* figured by Prantl ('81, Taf. IV, Fig. 40). Fibres are present in the usual position, and protoxylem appears to lie at two points on the upper side. In the leaf the stomata are placed in two neat longitudinal rows, just as in *S. pusilla* (Britton and Taylor, '01, p. 14). In the flattened part of the leaf the bundle is similar to that of the petiole, the epidermal cells are very thick-walled, and the stomata are raised.

#### RECENT WORKS TREATING OF THE MORPHOLOGY OF TISSUES.

Reference should now be made to certain views regarding the stele and the morphology of tissues, which have been recently published. Farmer and Hill ('02, pp. 396 and 400)



regard the pith as not belonging to the stele. They recognize the difficulty in estimating the morphological nature of a tissue, and state that 'our criteria only become applicable as the adult condition is reached' or approached.

A thoroughly consistent and strictly morphological treatment of tissues is probably an impossibility, and in any case the subject is rather elusive, but in many cases one can draw an opinion from the position of a certain tissue, though suppositions as to the exact mode of its first origin may become necessary. Two cases may be brought forward in which the morphological nature appears fairly certain. The cortical sieve-tubes of *Cucurbita* must be regarded as derived from cortical cells; morphologically they are part of the cortex. Secondly, the trabeculae in the sporangium of *Isoetes* have probably been derived from the sporogenous tissue and, morphologically speaking, represent part of it, —not ingrowths of the surrounding tissue.

We will now turn to the stele. It is exceedingly probable that the solid protostele was the universal primitive type, that the more complicated types were moulded from it, and that it never passed through a stage of flattening and rolling round, such as is assumed by the writer for the petiolar bundle of many Ferns. Consequently, whatever tissue is found within the xylem is presumably morphologically stelar. Assuming an exarch protostele, a pith may have originated by incomplete differentiation of the xylem-mass. At any rate if one regards the pith or other central tissue as having arisen in the first place by the transformation of potential tracheides into other tissue elements, these latter should be treated morphologically as part of the stele.

The different types of stem-structure in Ferns have probably been derived by a differentiation of the protostele into vascular and non-vascular parts, hence, although the possibility of there being exceptions is kept in view, the writer agrees with Schoute's conclusion ('02, p. 163) as a provisional generalization that a single type of stele is found in the stem and root of the vascular plants, viz. monostely; that is to say, taking

'stele' and 'monostely' in a morphological sense, applying as strict morphology as is possible in the case of tissues, and working on the hypothesis set forth in the present paper.

As a consequence of this conclusion the description and classification of different types of stelar structure have at present no morphological basis, but only a physiological one, because they refer to specializations of tissue within the morphological unit with which we started.

Brebner ('02, p. 548) recognizes the physiological nature of the descriptive terms, which he applies to different types of stelar structure. In the writer's opinion, also, terms defined as referring to definite types of tissue-arrangement within the stele are useful, and in some cases necessary, but a constant morphological distinction between the different kinds of tissue concerned is not upheld. As to the terms to be employed many already in use are sufficiently suitable. Thus 'solenostele' as defined by Gwynne-Vaughan ('01, p. 73) describes a special arrangement of tissues; its derivation signifies 'tube-stele,' and whether one regards the stele itself as being tubular, or the vascular part of the stele as being tubular, does not interfere much with the appropriateness of the term.

Farmer and Hill ('02, p. 398, &c.) decide to take the vascular strand as their unit for comparative considerations, both pith and the parenchyma forming the leaf-gaps of a solenostelic or dialystelic type being excluded. This is excellent as a physiological treatment of the tissues, but, in accordance with the views adopted in the present paper, the writer holds that it obscures the homologies of the tissues concerned. Leaf-gaps are held to have been originally formed by the replacement of vascular tissue by ordinary parenchyma, the first stage possibly consisting in the incomplete differentiation of the tracheides in the region afterwards occupied by the leaf-gap; and the same view is held with regard to the pith<sup>1</sup>. To exclude part of a given tissue as soon as it changes its structural nature does not appear to be a morphological treatment.

<sup>1</sup> Cf. the case of arrested roots, &c., in *Gleichenia* (Boodle, '01 a, p. 732).

SUMMARY.

The mature rhizome of *Schizaea dichotoma* exhibits apparent dichotomy. In the region of dichotomy the stele (as seen in transverse section) undergoes elongation, constriction, and fission. The ring of xylem is open during the process, but no internal phloem is present.

In the mature rhizome of *S. dichotoma* endodermal pockets are often present at the nodes; an isolated internal endodermis is occasionally found and may contain brown sclerotic elements; isolated internal tracheides sometimes occur.

In the stem of the young plant of *S. pusilla* no internal phloem is present in the transitional region.

In two specimens of a small form of *S. dichotoma*, which are probably seedling-plants, and at any rate have protostelic structure in their basal region, no internal phloem was present in the transitional region, but endodermal pockets or rudiments of them were present early in the medullated stage.

The deduction, which appears most natural, in the light of the various facts recorded, is that the inner endodermis is a vestigial structure, and that *S. dichotoma* owes its typical (or more usual) structure to reduction from a medullated form with inner endodermis ('ectophloic siphonostelic'). The same would probably be true for the other species of *Schizaea*. There is no evidence for the previous presence of an internal phloem.

CONCLUSION.

It is likely that a further structural examination of sufficiently numerous specimens of *S. dichotoma* and of other specimens of *Schizaea* may give more safe grounds, than were obtainable from the material examined, for elaborating a theory as to the phylogenetic history of the stele of *Schizaea*; and this may be helped by an extended comparison with certain species of *Anemia*, when their structure also has been examined in a large number of individuals. Both genera will



probably be productive of further data, useful in considerations on stelar morphology<sup>1</sup>.

I wish to express my thanks to Dr. D. H. Scott, F.R.S., to whom I am indebted for many valuable suggestions. I am also indebted to Mr. Maiden, Mr. R. H. Yapp, Mrs. Britton, Mr. E. S. Salmon, and Mr. J. C. Willis, for material of different species kindly placed at my disposal.

<sup>1</sup> The writer hopes shortly to be able to publish some further observations on two or three species of *Anemia* and on *Gleichenia pectinata* in continuation of the present series.

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# Flowers and Insects in Great Britain.

## PART III.

### Observations on the most Specialized Flowers of the Clova Mountains.

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WE now publish our observations on the fertilization, about Clova in the Eastern Grampians, of the flowers specially adapted for the visits of bees and butterflies<sup>1</sup>. The next part of our paper will complete the series, and will terminate with a general review.

#### CLASS F § II. SUITED FOR DIURNAL LEPIDOPTERA.

91. *Silene acaulis*, Linn. [Lit. *Brit.*, Wilson 2567; *Arct.* 7, 34, 36, 38; Aurivillius 78; Axell 81; *Alps* 2, 9, 21 b, 34; Ricca 2071; *Pyren.* 17.] A marked Lepidoptera-flower at Clova as in the Alps and Pyrenees, Bombs having only been recorded as visiting it in Arctic regions. The flowers are polygamo-trioecious, the hermaphrodite condition being common, and fruit ripening very abundantly. The perfect flowers are proterandrous. The larger flowers have a breadth

<sup>1</sup> Pt. I (Lowland flowers), *Ann. of Bot.* 1895, p. 227; II (Clova), do. 1903, p. 313.

[*Annals of Botany*, Vol. XVII. No. LXVII. June, 1903.]

of 10 mm. and a depth of 8 mm. Two points call for mention: (1) the apparently greater separation of the sexes on the continent, and (2) the more accessible honey in a form of the species found in Greenland.

*Visitors.* **Lepidoptera.** Heterocera: *Geometridae*: (1) *Thera variata* Schiff., 8. VII. 94, 4. VII. 95, 22. VI. 96, 23-2,700 ft. (2) *Larentia salicata* Hb., 8. VII. 94, 2,400 ft. *Pyralidae*: (3) *Scopula alpinalis* Schiff., sh. 4. VII. 95, 26-2,700 ft. **Hymenoptera.** Aculeata: *Apidae*: (4) *Bombus jonellus* Kirby, sh. 22. VI. 96, 2,300 ft. **Diptera.** *Empidae*: (5) *Empis tessellata* F., sh. 22. VI. 96, 2,300 ft. *Chironomidae*: (6) *Chironomus* sp., ? sh. 6-13. VII. 95, 2,000 ft. **Coleoptera.** (7) *Anthophagus alpinus* Payk., sh. 4. VII. 96, 22. VI. 96, 25-2,700 ft. (8) *Meligethes* sp., sh. 15. VI. 99, 1,900 ft. **Thysanoptera.** (9) *Thrips* sp., sh. 4. VII. 95, 2,700 ft.

92. *Habenaria conopsea*, Reichb. [Lit. *Brit.* 23; Darwin 483; *N.C.E.* 1, 4, 16, 44; *Arct.* 36; *Alps* 2, 9, 21 b.] A Lepidoptera-flower known to be fertilized by moths and butterflies in North Norway, Scotland, England, and the Alps. Some differences in the length of the spur are to be noted; it is recorded as 10-11 mm. long in North Norway, 15 mm. in South Sweden, 13-14 mm. in the Alps, and is 10-12 mm. long at Clova. We have watched flowers at night without observing insects to visit them.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Argynnis aglaia* L., sh. 25. VI. 95, 900 ft. once. (2) *Lycaena icarus* Rott., sh. 1. VII. 95, 900 ft. once. Heterocera: *Crambidae*: (3) *Crambus* sp., sh. 2. VII. 95, 900 ft. *Erioccephalidae*: (4) *Erioccephala calthella* L., 8. VI.-2. VII. 95, 8-900 ft. **Diptera.** *Tachinidae*: (5) *Siphona geniculata* Deg., 22. VI. 95, 800 ft. once. *Anthomyiidae*: (6) *Anthomyia* sp., 2. VII. 95, 900 ft., 26. VI. 96, 1,100 ft.

#### CLASS F § 12. SUITED FOR NOCTURNAL LEPIDOPTERA.

93. *Lonicera Periclymenum*, Linn. [Lit. *Brit.* 23, 39; *N.C.E.* 1, 3c, 8, 11, 14, 14a, 18, 31, 33; Knuth 1234; Warnstorf 2508; *Alps* 9.] A moth-flower but somewhat visited by bumble-bees. *Apis* was seen to lick the stigma.

*Visitors.* **Lepidoptera.** Heterocera: *Noctuidae*: (1) *Plusia pulchrina* Haw., sh. 22. VI. 95. **Hymenoptera.** Aculeata: *Apidae*: (2) *Apis mellifica* L., cp. and seeking h. 20-22. VI. 95. (3) *Bombus hortorum* L., sh. 22. VI. 96, 18. VI. 99. **Diptera.** *Empididae*: (4) *Empis punctata* Mg., seeking h. 21. VI. 96. *Anthomyiidae*: (5) *Trichophthicus* sp., fp. 20-23?. VI. 95. All at 800 ft.

CLASS H § 13. LYCHNIS TYPE.

94. *Lychnis diurna*, Sibth. [Lit. *Brit.* 23, 39; White 2548; *N.C.E.* 1, 11, 21 a, 34; De Vries 2460; *Arct.* 36; *Alps* 2, 9, 16.] This flower is little visited at Clova, where the tube is 10-15 mm. long. In the Alps many butterflies seem to go to it.

*Visitors.* **Diptera.** *Syrphidae*: (1) *Platychirus manicatus* Mg., ? fp. 15. VI. 99, 900 ft. (2) *Rhingia campestris* Mg., sh. 25. VI. 95, 800 ft. **Coleoptera.** (3) *Meligethes viridescens* F., sh. and fp. 25. VI.-4. VII. 95, 15. VI. 99, 8-900 ft.

95. *Lychnis flos-cuculi*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 3 b, 14, 16, 18, 21 a, 21 b, 25, 34; De Vries 2460; *Alps* 9.] A bee and Lepidoptera-flower, with (at Clova) a tube 7-9 mm. long.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Lycaena icarus* Rott., sh. 26. VI. 95, 800 ft. **Hymenoptera.** Aculeata: *Apidae*: (2) *Bombus lapponicus* F., seeking h. 26. VI. 95, 800 ft. (3) *B. agrorum* F., sh. 21. IX. 95, 900 ft. **Diptera.** *Syrphidae*: (4) *Rhingia campestris* Mg., sh. 26. VI.-1. VII. 95, 800 ft. (5) *Platychirus manicatus* Mg., seeking h. and fp. 23. VI.-4. VII. 95, 800 ft. *Empididae*: (6) *Empis tessellata* F., sh. 1. VII. 95, 800 ft. *Anthomyiidae*: (7) 1 sp., 23. VI. 95, 800 ft.

96. *Lychnis alpina*, Linn. [Lit. *Brit.* 26; *Arct.* 36, 38; Axell 81; *Alps* 9, 34; Kirchner 1185.] The following account is drawn up from Clova specimens. The flower is strongly proterandrous. After the dehiscence of the anthers, the stamens bend outwards; then the styles elongate and separate, bending so as eventually to be at right angles to the ovary across the mouth of the flower. Ultimate autogamy is possible by



means of anthers still adhering to their filaments, and seems to take place, fruiting being regular. The flowers are 12–14 mm. in diameter; the petals have a claw 3 mm. long and a limb 4 mm. notched to halfway. As the internode between sepals and petals is about 1 mm. long, the honey at the base of the flower is about 4 mm. removed from the mouth, a distance a little less than the width of the mouth. Thus the tube is rather funnel-shaped than tubular. The flowers are very variable in the number of parts, six petals being frequently, seven occasionally, present. It is possible that the flower should be regarded as belonging to Class B.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Psithyrus quadricolor* Lep., sh. 2. VII. 96, once. **Diptera.** *Chironomidae*: (2) 1 sp., 2. VII. 96. *Anthomyiidae*: (3) *Trichophthicus* sp., sh. 27. VI.–2. VII. 96. **Thysanoptera.** (4) *Thrips* sp., 2. VII. 96. All at 2,850 ft.

97. *Primula vulgaris*, Huds. [Lit. *Brit.* 23, 29; Christy in *Trans. Essex Field Club*, iii. p. 195; Darwin 470 and 485; Briggs 290; Scott 2253; *N.C.E.* 1, 33.] One of us gave some account of the fertilization of the Primrose (see lit. 29) a few years ago, showing how the conditions of its fertilization are hardly known. Since then we have noticed that it is very abundantly visited at Kew by a bee, *Anthophora acervorum*, and is visited also by it in Essex (see Miller Christy, loc. cit.). This insect does not occur at Clova. We have seen few visitors in our district. The tube is 12.5–16 mm. long there; it is longer in England and Germany. We found certain long-styled flowers with the style dwarfed, probably in deformity, and in them the *Anthomyiids* were able to push their way down the throat to the stamens.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus hortorum* L., sh. 20. V. 97, 800 ft. once. **Diptera.** *Anthomyiidae*: (2) *Anthomyia sulciventris* Ztt., fp. and seeking h. 20–22. V. 97, 6–1,200 ft. freq. (3) *Hylemyia* sp., fp. 20. V. 97, 900 ft. **Coleoptera.** (4) *Meligethes* sp., fp. 22. V. 97, 10. VI. 99, 700 ft. **Araneida.** (5) *Xysticus* sp., lying in wait on the corolla, 22. V. 97, 600 ft.

## CLASS H § 14. CROCUS TYPE.

98. *Crocus aureus*, Linn. [Lit. *Brit.* 29.] In cultivation.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Apis mellifica* L., sh. and cp. 2-15. IV. 95, very ab. **Diptera.** *Muscidae*: (2) *Pollenia rudis* F., fp. 2. IV. 95, freq. (3) *Lucilia cornicina* F., fp. 2. IV. 95, freq. All at 800 ft.

## CLASS H § 15. VIOLA TYPE.

99. *Viola palustris*, Linn. [Lit. *Brit.* 23; *N.C.E.* 14.] Reproduction is largely by runners. The flowers are insignificant, with a spur only 2 mm. long and with little honey. The stigma projects beyond the stamens. They are neglected by insects, so that we have only seen three individuals on them; the fourth (*B. lapponicus*) was observed on the flowers by the father of one of us, Mr. I. H. Burkill, sen. Knuth observed no visitors in the North Friesian Islands.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus lapponicus* F., sh. 19. V. 98, 1,400 ft. once. **Diptera.** *Empidae*: (2) *Empis lucida* Ztt., sh. 12. VI. 99, 17-2,500 ft. *Anthomyiidae*: (3) 1 sp., 18. V. 98, 800 ft.

100. *Viola canina*, Linn., and *V. sylvatica*, Fries. [Lit. *Brit.* 23, 29; Bennett 219; *N.C.E.* 1, 3 b, 14, 18, 25, 33, 40; MacLeod 1471; *Alps* 2.] Pronounced bee-flowers, but not well visited at Clova. The spur of *V. sylvatica* sometimes attains the length of 8 mm., that of *V. canina* (segregate) is about 5 mm. long. Once in the first-named it was found bitten through. The butterflies abroad in spring visit the flowers on the continent as at Clova; *Bombi* are recorded as visitors in Dumfriesshire and Yorkshire. The chasmogamic flowers seem to set little seed (cf. Linton in Bot. Exchange Club Rep. 1890, p. 284). Cleistogamic flowers follow them.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Pieris napi* L., sh. 21. V. 96, 23. V. 97, 15. VI. 99, 6-1,000 ft. (2) *Argynnis selene* Schiff., sh. 15-16. VI. 99, 900 ft. **Hymenoptera.** Aculeata: *Apidae*: (3)

*Bombus agrorum* F., sh. 22. V. 97, 600 ft. **Diptera.** *Tachinidae*: (4) *Siphona geniculata* Deg., 21. V. 96, 800 ft. *Anthomyiidae*: (5) *Anthomyia sulciventris* Ztt., fp. 20–27. V. 97, 7–800 ft. **Araneida.** (6) *Xysticus* sp., lying in wait inside a flower, 21. V. 97, 800 ft.

**101. *Viola tricolor*, Linn.** [Lit. *Brit.*, Bennett 209; Darwin 482; Kitchener 1197; *N.C.E.* 1, 3 b, 9, 11, 14, 18, 25, 35, 40; *Scand.*, Wittrock 2592; *Alps* 9, 34; *Pyren.* 17.] The following statement shows it to be at Clova a neglected bee-flower; it is not abundant, and owes its position high up the glen perhaps to cultivation. Verhoeff points out the possibility of self-pollination in the Friesian islands and the frequency with which the spur is bitten through for its honey.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Pieris napi* L., sh. 17. VII. 95, 800 ft. **Diptera.** *Anthomyiidae*: (2) *Hyetodesia incana* W., 19. VI. 95, 800 ft.

**102. *Viola lutea*, Smith.** [Lit. *Brit.* 39; *Scand.* 34.] A neglected bee-flower. Bombi and butterflies are recorded as visiting it near Stockholm. On the hundreds of thousands of flowers seen by us at Clova, but fifty insects have been recorded, representing sixteen species, mostly flies which sit on the flower licking the hairs at the mouth of the tube or feeding on pollen. Four species of *Lepidoptera* were seen on the flowers, each once. The flowers are almost always wholly yellow, and all turn towards the south. The spur is 5–6 mm. long.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Pieris napi* L., 24. V. 96, 800 ft. (2) *Lycaena icarus* Rott., sh. 18. VII. 96, 800 ft. Heterocera: *Tineidae*: (3) *Glyphipteryx fuscoviridella* Haw., sh. 2. VII. 95, 900 ft. *Erioccephalidae*: (4) *Erioccephala calthella* L., 2. VII. 95, 800 ft. **Hymenoptera.** Aculeata: *Apidae*: (5) *Andrena analis* Panz., 22. VI. 96, 1,000 ft. **Diptera.** *Syrphidae*: (6) *Sphaerophoria* sp., 6. VII. 94. *Bibionidae*: (7) *Dilophus* sp., 19. V. 97, 800 ft. *Muscidae*: (8) *Pollenia rudis* F., licking the hairs at the mouth of the tube, 21. V. 96, 800 ft. *Anthomyiidae*: (9) *Drymia hamata* Fln., sh. 4. VII. 95, 800 ft. (10) *Hyetodesia incana* W., 21. VI. 95, 800 ft. (11) *Anthomyia sulciventris* Ztt., seeking h. and fp. 19–27. V. 97, 16. V. 98,



7-800 ft. (12 and 13) *A.* 2 spp., fp. 4. VII. and 21. IX. 95; 10. VI. 99, 7-1,500 ft. (14) *Coenosia* sp., 1. VII. 95, 900 ft. *Cordyluridae*: (15) *Scatophaga stercoraria* L., 4. VII. 95, 800 ft. (16) 1 sp., 2. VII. 95, 800 ft.

CLASS H § 16. ORCHIS TYPE.

103. *Orchis maculata*, Linn. [Lit. *Brit.*, Darwin 483; *N.C.E.* 1, 3 a, 14, 18, 34, 40; Warnstorf 2506; *Alps* 2.] A bee-flower apparently much neglected about Clova. The spur contains no free honey and requires a breaking of the tissues to yield any sweet juice.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Pieris napi* L., seeking h. 19. VI. 96, 1,500 ft. **Diptera.** *Anthomyiidae*: (2) *Hylemyia variata* Flh., seeking h. 21. V. 95, 800 ft. (3) *H. nigrescens* Rnd., sitting on flower, 16. VI. 99, 800 ft.

104. *Orchis mascula*, Linn. [Lit. *Brit.*, Darwin 483; *N.C.E.* 1.]

*Visitors.* **Diptera.** *Anthomyiidae*: (1) One sp., 22. VI. 95, 1,400 ft. *Cordyluridae*: (2) *Scatophaga stercoraria* L., 5. VII. 94, 800 ft.

CLASS H § 17. TROPAEOLUM TYPE.

105. *Tropaeolum speciosum*, Poepp. and Endl. In cultivation.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus agrorum* F., sh. 19. IX. 95, 800 ft.

CLASS H § 18. PINGUICULA TYPE.

106. *Pinguicula vulgaris*, Linn. [Lit. *N.C.E.* 14; Buchenau in *Bot. Zeitung*, 1865, p. 95; Hildebrandt 1041; *Arct.* 36, 38; Warming 2498; *Alps* 2, 9.] A self-fertilizing flower, abundant, but as neglected by insects about Clova as elsewhere. Lindman remarks the great rarity of visitors. Sprengel, Kerner, and Warming describe the way in which the stigma rolls back on to the anthers, and in sections of the flower we have seen the pollen-tubes passing into the stigmatic tissue. Abnormal flowers are very common; in these it is usual for the number

of lobes of the corolla to be increased. Lindman speaks of it being frequently abnormal, and he also notices the occurrence in the Dovrefjeld of flowers which are almost cleistogamic. At Clova it is very frequently abnormal, generally by the addition of extra lobes to the corolla.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Pieris napi* L., sh. going from flower to flower, 15. VI. 99, 800 ft. **Hymenoptera.** Aculeata: *Apidae*: (2) *Bombus lapponicus* F., settled on a flower but did not stay to sh. 1. VII. 96, 2,000 ft. **Diptera.** *Anthomyiidae*: 1 sp., seen settled on flowers on five occasions, 27. VI. 96, 10. VI. 99, 8-2,500 ft.

CLASS H § 19. PEDICULARIS TYPE.

107. *Pedicularis sylvatica*, Linn. [Lit. *Brit.* 23; Ogle 1904; *N.C.E.* 1, 3 c, 4, 12, 14, 18, 21 b, 34.] The position of the flowers of this species is constant, the hood always above and vertical. The tube is 14-16 mm. long.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Pieris napi* L., sh. 19. VI. 96, 15. VI. 99, 8-1,500 ft. **Hymenoptera.** Aculeata: *Apidae*: (2) *Bombus lapponicus* F., seeking h. 11. VII. 96, 800 ft. once. (3) *B. jonellus* Kirby, ? sh. 22. VII. 95, 1,200 ft. once. **Diptera.** *Anthomyiidae*: (4) *Anthomyia sulciventris* Ztt., seeking h. or p. 23. V. 97, 900 ft.

108. *Pedicularis palustris*, Linn. [Lit. *Brit.* 23; *N.C.E.* 4, 8, 14, 16, 18, 21 a; *Arct.* 36; *Alps* 2.] The position of the flowers is not constant. No one has seen this plant richly visited.

*Visitors.* **Diptera.** *Syrphidae*: (1) *Rhingia campestris*, Mg., sh. 2. VII. 95, 800 ft.

109. *Melampyrum pratense*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 3 c, 4, 16, 18, 21 b, 32, 33, 34, 40; *Alps* 9.] A flower distinctly suited to Bombi, but not much visited.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus lapponicus* F., sh. 27. VI. 95, 2,100 ft.

## CLASS H § 20. 'LABIATE' TYPE.

110. *Euphrasia officinalis*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 3 c, 4, 14, 18, 21 b, 30, 40; Wettstein 2539; *Arct.* 36, 37 c, 38; *Alps* 2, 9, 21 b, 34; Wettstein 2539; *Pyren.* 17.] The flower varies considerably in size, but the mechanism does not change. In the glen the tube is usually 2.5 mm. long.

*Visitors.* Hymenoptera. Aculeata: *Apidae*: (1) *Apis mellifica* L., sh. 15. IX. 95, 800 ft. once. Diptera. *Syrphidae*: (2) *Platychirus manicatus* Mg., fp. 14. IX. 95, 800 ft.

111. *Nepeta Glechoma*, Benth. [Lit. *Brit.* 23, 29, 34; Bennett 212; Marquand 1513; *N.C.E.* 1, 3 c, 4, 16, 18, 21 a, 21 b, 33, 34, 40; De Vries 2460; *Alps* 34; *N.Am.* 19 c.] Gynodioecious; the tube of the flower is 4 mm. long.

*Visitors.* Hymenoptera. Aculeata: *Apidae*: (1) *Apis mellifica* L., sh. 20. V. 97, 800 ft. Diptera. *Anthomyiidae*: (2) *Anthomyia* sp., fp. 20. V. 97, 800 ft.

112. *Prunella vulgaris*, Linn. [Lit. *Brit.* 23, 39; Ogle, 1904; *N.C.E.* 1, 3 c, 4, 11, 14, 14 a, 16, 18, 21 a, 21 b, 30, 32, 34; De Vries 2460; MacLeod 1473; *Arct.* 34; *Alps* 2, 16, 21 b, 34; *Pyren.* 17; *N.Am.* 19 c.] The tube of the decidedly proterandrous flower is usually 9-10 mm. long. We found, however, a larger-flowered form on the crags at 2,000-2,800 feet.

*Visitors.* Hymenoptera. Aculeata: *Apidae*: (1) *Bombus hortorum* L., sh. 11. VII. 96, 800 ft.

113. *Stachys palustris*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 3 c, 4, 8, 11, 18, 21 b, 32, 33; *Alps* 16; *Pyren.* 17.]

*Visitors.* Hymenoptera. Aculeata: *Apidae*: (1) *Bombus agrorum* F., sh. 2. VII. 95. Diptera. *Syrphidae*: (2) *Rhingia campestris* Mg., sh. and fp. 2-6. VII. 95. All at 800 ft.

114. *Galeopsis Tetrahit*, Linn. [Lit. *Brit.* 23, 39; *N.C.E.* 1, 3 c, 4, 18, 21 b, 33, 40; *Alps* 2, 9, 34; Briquet 293; *Pyren.* 17.] The form with rose flowers is very rare.

*Visitors.* Lepidoptera. Rhopalocera: (1) *Lycaena icarus* Rott.,



sh. 5. VII. 95, 800 ft. (2) *Coenonympha pamphilus* L., sh. 5. VII. 95, 800 ft. each once. **Hymenoptera.** Aculeata: *Apidae*: (3) *Bombus terrestris* L., sh. 16-17. IX. 95, 7-800 ft. (4) *B. agrorum* F., sh. 5. VII. and 13. IX. 95, 7-800 ft. **Diptera.** *Syrphidae*: (5) *Melanostoma mellinum* L., fp. 22. IX. 95, 800 ft. (6) *Platychirus albimanus* F., fp. 16-17. IX. 95, 800 ft. (7) *P. manicatus* Mg., fp. 5. VII. 95, 800 ft. *Muscidae*: (8) *Calliphora erythrocephala* Mg., fp. 5. VII. 95, 800 ft. *Anthomyiidae*: (9) *Anthomyia* sp., fp. 17. IX. 95, 800 ft. (10) *Trichophthicus* sp., fp. 16. IX. 95, 800 ft. **Coleoptera.** (11) *Meligethes viridescens* F., 16-17. IX. 95, 800 ft.

115. *Lamium purpureum*, Linn. [Lit. *Brit.* 23, 29, 34; Bennett 212; *N.C.E.* 1, 3 c, 4, 11, 14, 16, 18, 21 b, 34, 40; De Vries 2460; *Alps* 34.] The flower is proterandrous; the stigma gradually passes above the stamens to a point beyond them, but not so much as to make self-fertilization impossible.

*Visitors.* **Diptera.** *Syrphidae*: (1) *Platychirus discimanus* Lw., ? fp. 15. V. 98, 800 ft.

116. *Lamium maculatum*, Linn. [Lit. *N.C.E.* 1, 3 c, 4, 21 b, 33, 34, 35; *Alps* 2, 34.] This plant has been established since at least 1840 without spreading to any extent. Some *Bombus*, not seen by us in the act, bores the corolla, and *Apis* makes use of the holes.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Apis mellifica* L., cp. 20. V. 97, and sh. through holes in corolla and cp. hanging under hood, 7-15. V. 98. (2) *Bombus hortorum* L., sh. 22. V. 97. (3) *B. agrorum* F., sh. 23. V. 97, 11. VI. 99. **Diptera.** *Syrphidae*: (4) *Platychirus* sp., fp. 23. V. 97. *Muscidae*: (5) *Lucilia cornicina* F., 7. V. 98. *Anthomyiidae*: (6) *Anthomyia* sp., fp. 16. V. 98. All at 800 ft.

117. *Ajuga reptans*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 3 c, 4, 16, 18, 21 a, 21 b, 33, 40; *Alps* 2, 34; *Pyren.* 17.]

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus agrorum* F., sh. 24. VI. 95, 10. VI. 99, 7-800 ft. **Diptera.** *Anthomyiidae*: (2) 1 sp., fp. 10. VI. 99, 700 ft.

## CLASS H § 21. EXPLOSIVE LEGUMINOUS TYPE.

118. *Genista anglica*, Linn. [Lit. *N.C.E.* 1, 3 b, 14, 14 a, 34, 40.] A species little visited at Clova, where the genera of mid-tongued Hymenoptera observed on it by Müller, Alfken, and Höppner are poorly represented.

*Visitors. Hymenoptera. Aculeata: Apidae:* (1) *Apis mellifica* L., cp. 2. V. 97, 7-800 ft. (2) *Bombus terrestris* L., cp. and seeking h. 25. V. 97, 800 ft. (3) *B. lapponicus* F., seeking h. 22. V. 97, 700 ft. *Diptera. Anthomyiidae:* (4) *Anthomyia sulciventris* Ztt., fp. and seeking h. 20-22. V. 97, 8-900 ft.

119. *Ulex europaeus*, Linn. [Lit. *Brit.* 23, 29; Ogle 1905; *N.C.E.* 8, 14, 18, 33.] *Apis* is a more frequent visitor than the *Bombi*, but both genera are regular visitors in Scotland and in England. *Apis* visits the flowers abundantly in Flanders. After explosion a variety of flies find pollen enough to attract them. Many times we have seen the *Bombi* and *Apis* thrusting their proboscis into the base of the flower seeking for honey.

*Visitors. Hymenoptera. Aculeata: Apidae:* (1) *Apis mellifica* L., cp. and seeking h. 21. V. 96, 20-22. V. 97, 7-16. V. 98, 10. VI. 99, 6-900 ft. (2) *Bombus terrestris* L., cp. and seeking h. 20-27. V. 97, 10-19. VI. 99, 7-800 ft. (3) *B. lapponicus* F., seeking h. 20-27. V. 97, 7-800 ft. (4) *B. agrorum* F., 27. V. 97, 800 ft. *Diptera. Syrphidae:* (5) *Syrphus* sp., fp. 20-27. VI. 97, 800 ft. *Muscidae:* (6) *Pollenia vespillo* F., fp. 27. V. 97, 800 ft. *Anthomyiidae:* (7) *Anthomyia sulciventris* Ztt., fp. 19-27. V. 97, 7-900 ft. (8) *A.* sp., fp. on exploded flowers, 16. V. 98, 700 ft. *Thysanoptera.* (9) *Thrips* sp., 21. V. 97, 800 ft.

120. *Cytisus scoparius*, Link. [Lit. *Brit.* 23, 34; Henslow 990; Darwin 991; *N.C.E.* 1, 3 b, 14, 16, 18, 25, 33, 34, 40; De Vries 2460.] The flowers are very well visited, the bees (*Apis* and *Bombi*) proceeding from flower to flower regularly. *Apis* is more abundant than the *Bombi*: second in abundance is *Bombus terrestris*; *Anthomyiids* and *Meligethes viridescens* are very common on exploded flowers. It is obvious, as

Müller remarks, that the flower is more sure of advantage from the visits of Bombi than of Apis; but at Clova, in Flanders, Westphalia, &c., the latter is the more abundant visitor.

*Visitors. Hymenoptera. Aculeata: Apidae:* (1) *Apis mellifica* L., cp. and seeking h. 19. VI. 95, 21-22. V. 96, 24. V. 97, 10. VI. 99, 7-800 ft. freq. (2) *Bombus terrestris* L., cp. and seeking h. 21-22. V. 96, 22-27. V. 97, 16. VI. 99, 7-800 ft. freq. (3) *B. lapponicus* F., sp. and seeking h. 23. VI. 96, 800 ft. once. (4) *B. agrorum* F., seeking h. 21. VI. 95, 800 ft. once. (5) *B. pratorum* L., 10. VI. 99, 800 ft. once. *Myrmicidae:* (6) *Myrmica rubra* L., seeking h. 23. VI. 95, 800 ft. once. *Formicidae:* (7) *Formica fusca* Latr., seeking h. 23. VI. 95, 800 ft. once. *Diptera. Syrphidae:* (8) *Syrphus* ? *ribesii* L., seeking h. 17-23. VI. 95, 800 ft. and ? the same once at 2,300 ft. *Muscidae:* (9) *Calliphora* sp., 17. VI. 95, 2,300 ft. *Anthomyiidae:* (10) *Hyetodesia incana* W., seeking h. 17. VI. 95, 2,300 ft. (11) *Anthomyia* sp., fp. 19-23. V. 97, 16. VI. 96, 20-26. V. 97, 10. VI. 99, 7-800 ft. (12) *Trichophthicus* sp., fp. 19-23. V. 97, 7-800 ft. (13) *Azelia aterrima* Mg., seeking h. 17. VI. 95, 2,300 ft. *Sapromyzidae:* (14) *Lauxania cylindricornis* F., 23. VI. 95, 800 ft. (15) *L. elizae* Mg., 23. VI. 96, 800 ft. *Coleoptera.* (16) *Meligethes viridescens* F., fp. 15. VI. 95, 24. VI. 96, 10. VI. 99, 800 ft. (17) *M. aeneus* F., 15. VI. 95, 800 ft. (18) *Anthobium torquatum* Marsh., seeking h. 23. VI. 95, 24. VI. 96, 800 ft. (19) *Ceuthorrhynchidius* sp., ? sucking the juice of the flower, 24. VI. 96, 800 ft. *Hemiptera.* (20) *Heterocordylus tibialis* Hahn., 19-23. VI. 95, 8-900 ft. freq.

#### CLASS H § 22. LEGUMINOUS TYPE.

**121. *Cytisus Laburnum*, Linn.** [Lit. *N.C.E.* 1, 9, 33, 40.]  
In cultivation. As honey is obtained by boring the tissues the range of visitors is narrowed considerably, for none but *Apis* and *Bombi* find how to obtain it.

*Visitors. Hymenoptera. Aculeata: Apidae:* (1) *Apis mellifica* L., ab. (2) *Bombus terrestris* L. (3) *B. lapidarius* L. All sucking the juices of the flower, 21. V. 96, 800 ft.

**122. *Trifolium pratense*, Linn.** [Lit. *Brit.* 23; Darwin 482; *N.C.E.* 1, 3 b, 11, 14, 14 a, 15, 16, 18, 21 b, 25, 30, 31,



32, 33, 34, 40; De Vries 2460; *Arct.* 36; *Alps* 2, 34; *Pyren.* 17; *N.Am.* 19 a.] Contrasting it with *T. repens* the effect of the greater length of the tube in inviting long-tongued Hymenoptera and Lepidoptera is evident. According to Verhoeff insects on the Friesian coast require tongues 11–12 mm. long, and to Müller 9 mm. long; at Clova 8 mm. would suffice. *Apis* and some of the shorter-tongued *Bombi* and other Hymenoptera are recorded as obtaining honey by perforation of the calyx. A honey-bird visits it in the United States. Our observations need extending.

*Visitors. Hymenoptera. Aculeata: Apidae:* (1) *Bombus terrestris* L., sh. 22. IX. 95, 800 ft. (2) *B. venustus* Smith, sh. 11. VII. 96, 700 ft. *Diptera. Bibionidae:* (3) *Bibio pomonae* F., seeking h. 11. VII. 96, 700 ft. *Muscidae:* (4) *Lucilia cornicina* F., fp. 5. VII. 95, 700 ft. *Anthomyiidae:* (5) *Anthomyia sulciventris* Ztt., fp. 2. VII. 95, 900 ft. (6) *A. sp.*, fp. 22. IX. 95, 800 ft. *Coleoptera.* (7) *Meligethes viridescens* F., cp. and fp. 23. VI. 95, 800 ft. Each once.

123. *Trifolium hybridum*, Linn. [Lit. *N.C.E.* 3 b, 9, 33, 34; Kirchner 1183.] Cultivated, and well visited by *Apis*.

*Visitors. Hymenoptera. Aculeata: Apidae:* (1) *Apis mellifica* L., sh. 5. VII. and 22. IX. 95, 25. VI. 96, 7–800 ft. *Diptera. Muscidae:* (2) *Lucilia cornicina* F., fp. 5. VII. 95, 700 ft.

124. *Trifolium repens*, Linn. [Lit. *Brit.* 23; Darwin 468 and 482; Marquand 1513; *N.C.E.* 1, 3 b, 4, 11, 14, 14 a, 15, 16, 18, 25, 30, 31, 32, 33, 34, 40; De Vries 2460; *Arct.* 34, 36; *Alps* 2, 34; *Pyren.* 17.] A *Bombus*-flower which by the accessibility of the honey attracts *Apis* in great numbers. In Arctic Norway *Bombi* are its only recorded visitors; they are the most abundant visitors in the Alps and in the Pyrenees. In North Central Europe and in Britain where bees are kept *Apis* is perhaps more frequent than the *Bombi*. Darwin demonstrated in England the need of insect aid in pollination.

*Visitors. Lepidoptera. Rhopalocera:* (1) *Coenonympha pamphilus* L., sh. 22. VI. 95, 800 ft. (2) *Lycaena icarus* Rott., sh. 26. VI.–I. VII. 95, 10. VII. 96, 800 ft. *Heterocera: Geometridae:* (3) *Cam-*

ptogramma?, sh. 11. VII. 96, 700 ft. **Hymenoptera.** Aculeata: *Apidae*: (4) *Apis mellifica* L., sh. 24. VI.-22. VII. 95, 5-11. VII. 96, 7-800 ft. (5) *Bombus pratorum* L., sh. 4. VII. 95, 800 ft. (6) *B. lapponicus* F., sh. 20. VI. 95, 18. VI.-10. VII. 96, 8-2,300 ft. (7) *B. agrorum* F., sh. 22. VI.-6. VII. 95, 800 ft. (8) *B. venustus* Smith, sh. 26. VI. 95, 800 ft. **Diptera.** *Empidae*: (9) *Empis tessellata* F., sh. 5. VII. 95, 800 ft. *Bibionidae*: (10) *Biblio pomonae* F., ? fp. 11. VII. 96, 700 ft. *Cordyluridae*: (11) *Scatophaga maculipes* Zett., ? fp. 2. VII. 95, 800 ft.

125. *Lotus corniculatus*, Linn. [Lit. *Brit.* 23, 34; Farrer 653; *N.C.E.* 1, 3 b, 11, 12, 14, 14 a, 15, 16, 18, 21 b, 25, 30, 32, 33, 34; Warnstorf 2507; *Alps* 2, 9, 16, 34; *Pyren.* 17; *Medit.* 34.] A *Bombus*-flower, fertilized at Clova by *B. lapponicus* and *B. agrorum*. The butterflies, which visit, are to it robbers. The tongue of *Apis* is hardly long enough to reach the honey. Kerner speaks of dark-coloured flowers occurring at high levels; once we found such at 2,400 ft.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Argynnis aglaia* L., sh. 23. VI. 95, 900 ft. once. (2) *Lycaena icarus* Rott., sh. 22. VI.-8. VII. 95, 18. VI.-10. VII. 96, 7-1,000 ft., the male much more freq. than the female. Heterocera: *Geometridae*: (3) *Fidonia atomaria* L., 15. VI. 99, 1,100 ft. (4) Another sp. 15. VI. 99, 12-1,500 ft. **Hymenoptera.** Aculeata: *Apidae*: (5) *Apis mellifica* L., sh. 16. VI. 95, 700 ft. (6) *Bombus terrestris* L., sh. 1-8. VII. 95, 800 ft. (7) *B. pratorum* L., 26. VI. 95, 800 ft. (8) *B. lapponicus* F., cp. and sh. 26. VI.-1. VII. 95, 22. VI.-10. VII. 96, 19. VI. 99, 8-2,300 ft. (9) *B. lapidarius* L., sh. 6-11. VII. 96, 800 ft. (10) *B. agrorum* F., sh. and cp. 25. VI.-23. VII. 95, 14-15. VI. 99, 8-1,100 ft. (11) *B. venustus* Smith, sh. 16. VI.-11. VII. 96, 700 ft. (12) *B. hortorum* L., sh. 15. VI. 99, 800 ft. Petiolata tubulifera: *Vespidae*: (13) *Odynerus pictus* Curt., 25. VI. 95, 800 ft. **Diptera.** *Tachinidae*: (14) *Siphona geniculata* Deg., seeking h. 16. VI. 99, 800 ft. *Muscidae*: (15) *Calliphora* sp., seeking h. 15. V. 95, 900 ft. *Anthomyiidae*: (16) *Hyetodesia incana* W., 22. VI. 95, 800 ft. (17) *Drymia hamata* Fln., 26. VI. 96, 2,300 ft.

126. *Oxytropis campestris*, DC. [Lit. *Arct.* 7; *Alps* 2, 16.] The flower is usually creamy white with two yellow

patches on the standard and a purple tip to the keel, not pure white as stated in *Trans. Bot. Soc. Edin.*, xviii. 391; but it is whiter and larger than the usual form of the Eastern Alps. The colour varies from this creamy white to a pale lemon-yellow or a pale violet. The flower has a sweet scent and abundant honey. The calyx-tube is 7 mm. long, and its teeth an additional 2 mm., and is rather thin, so that it offers but little resistance to the insects which rob the honey by biting through it. The narrow part of the flower is 10 mm. long. The passages to the honey between the bases of the stamens are very long. The stigma stands 1 mm. above the stamens, and is touched by its own pollen. Rubbing appears to be necessary to make it receptive. The rough areas on the petals, which afford a foothold to insects, have been fully described by Loew for *O. pilosa* (*Flora*, 1891, p. 84). In plants from Clova they are distributed as follows: standard very smooth below, less so above on the inner face; wings very rough on the surface directed upwards, especially towards the interlocking processes; keel slightly rough on both sides towards the tip, perfectly smooth below, and rather smooth along the middle line. The plant fruits very freely.

*Visitors.* **Hymenoptera.** *Aculeata*: *Apidae*: (1) *Bombus lapponicus* F., sh. 26. VI.-2. VII. 96, 2,300 ft. *Formicidae*: (2) *Formica fusca* Latr., seeking h. 26. VI. 96, 22-2,300 ft. *Petiolata parasitica*: (3) 1 sp., seeking h. 26. VI. 96, 2,200 ft. **Diptera.** *Bibionidae*: (4) *Scatopse* sp., fp. 26. VI. 96, 22-2,300 ft. *Anthomyiidae*: (5) *Limnophora solitaria* Ztt., seeking h. 26. VI. 96, 2,200 ft. *Sapromyzidae*: (6) *Sapromyza* sp., seeking h. 2. VII. 96, 2,300 ft. **Coleoptera.** (7) *Meligethes aeneus* F., seeking h. 2. VII. 96, 2,300 ft. (8) *M. viridescens* F., fp. 26. VI. 96, 22-2,300 ft. **Thysanoptera.** (9) *Thrips* sp., 22. VI.-2. VII. 96, 22-2,300 ft. very ab.

127. *Vicia Cracca*, Linn. [*Lit. Brit.* 23; *N.C.E.* 1, 3 b, 8, 14, 18, 21 b, 32, 33, 34, 40; De Vries 2460; *Arct.* 36; *Alps* 2, 9, 16, 21 b; *Pyren.* 17.] A *Bombus*-flower with honey attainable to all the *Bombi*, but not readily to *Apis*; rare at Clova. The calyx is sometimes bitten through. The tubular part of the flower is 5-6 mm. long.



*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus terrestris* L., sh. 11. VII. 96, 700 ft. **Diptera.** *Sarcophagidae*: (2) *Sarcophaga* sp., sh. through boring in the calyx, 11. VII. 96, 700 ft.

128. *Vicia sylvatica*, Linn. [Lit. *Brit.* 23.] The flowers are so massed together that the plant is very conspicuous, and there is a sweet scent. The petals are veined with mauve. The stigma projects a trifle beyond the anthers, and the style has a long brush of sweeping hairs. If rubbed the stigma leaves a sticky streak, and does not become self-fertilized in the absence of insect visitors. Hence the mechanism of the flower seems to be that suggested for the genus by H. Müller. The petals are 16–18 mm. long, and the narrow part of the flower 10–12 mm. The honey is secreted in the position usual for the genus. We have seen the calyx with a hole bitten through it. Schulz, in error, states that Darwin observed bees to bite through the calyx; the plant referred to is, however, *Lathyrus sylvestris*. Scott Elliot observed *Bombus muscorum* and *B. hortorum* as visitors.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus lapponicus* F., seeking h. and cp. 10. VII. 96, 2,300 ft. *Petiolata tubulifera*: *Vespidae*: (2) *Odynerus* sp., sh. through borings in calyx, 10. VII. 96, 2,300 ft. **Diptera.** *Bibionidae*: (3) *Dilophus albipennis* Mg., sh. through borings in calyx, 26. VI. 96, 2,300 ft. *Anthomyiidae*: (4) 1 sp., seeking h. 2. VII. 96, 2,300 ft. *Sapromyzidae*: (5) *Sapromyza* sp., sh. through borings in calyx, 10. VII. 96, 2,300 ft. **Coleoptera.** (6) *Meligethes viridescens* F., 26. VI. 96, 2,300 ft. (7) *M. aeneus* F., seeking h. 10. VII. 96, 2,100 ft. **Thysanoptera.** (8) *Thrips* sp., 26. VI. 96, 2,300 ft.

129. *Vicia sepium*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 3 b, 11, 16, 18, 21 b, 33, 34, 40; De Vries 2460; *Alps* 2, 9, 34; *Pyren.* 17.] *Vicia sepium* is, as Müller points out, a *Bombus*-flower in which the honey is too difficult of access for *Lepidoptera*, and to *Bombus terrestris* is most readily obtained by a biting through of the calyx. We have found bitten flowers at Clova; and they have been noted abundantly by Müller, Schulz, Knuth, and Alfken in Germany, and by MacLeod in

Flanders. *Myrmica rubra* was seen (24. VI. 95) on the stipules apparently on account of the honey there.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus venustus* Smith, sh. **Diptera.** *Anthomyiidae*: (2) *Hyetodesia incana* W., seeking h. *Sepsidae*: (3) *Sepsis cynipsea* L., seeking h. All at 800 ft. 18. VI. 96.

130. *Lathyrus pratensis*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 3 b, 14, 14 a, 18, 21 b, 32, 34, 40; *Arct.* 36; *Alps* 2, 34; *Medit.* 34.] A bee-flower, but not freely visited. Fertilization is, however, dependent on insect visits.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Apis mellifica* L., sh. 11. VII. 96, 700 ft. once. **Diptera.** *Anthomyiidae*: (2) *Anthomyia* sp., fp. 4-5. VII. 95, 800 ft. **Hemiptera.** (3) *Anthocoris* ? *nemorum* L., seeking h. 16. IX. 95, 900 ft.

131. *Lathyrus macrorrhizus*, Wimm. [Lit. *Brit.* 23; *N.C.E.* 14, 21 b, 34, 40; Loew 1358; *Pyren.* 17.] A *Bombus*-flower needing insect aid for fertilization, and, as it is not freely visited by insects, commonly sterile.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Pieris napi* L., sh. 10. VI. 99, 700 ft. **Hymenoptera.** Aculeata: *Apidae*: (2) *Bombus lapidarius* L., sh. 21. V. 96, 800 ft. (3) *B. agrorum* F., 1. VI. 97, 19. VI. 99, 800 ft. **Diptera.** *Anthomyiidae*: (4) *Anthomyia sulciventris* Ztt., seeking h. 24. V. 97, 800 ft.

132. *Polygala vulgaris*, Linn. [Lit. *Brit.*, Hart. 933; *N.C.E.* 1, 3 b, 14, 18, 21 b, 34; *Pyren.* 17.] *Polygala vulgaris* is another neglected bee-flower. *Apis* and *Bombi* are recorded—the one or the other—as frequent visitors by Müller in Germany, by MacLeod in the Pyrenees, and (to *P. deprena*) by MacLeod in Flanders; both have been observed on *P. vulgaris* by Knuth in the North Friesian islands. At Clova spontaneous self-fertilization is the rule. Self-fertilization likewise is common on the Continent. At Clova the wings are usually bright blue, and, when the flower is open, 7 mm. long. A tongue 4 mm. long is sufficient to reach the honey.

*Visitors.* **Diptera.** *Muscidae*: (1) 1 sp., 6. VII. 94, about 2,000 ft.

## CLASS H § 23. DIGITALIS TYPE.

133. *Digitalis purpurea*, Linn. [Lit. *Brit.* 23, 39; Ogle 1904; Darwin 482; *N.C.E.* 1, 4, 21 b, 30, 32, 33, 34; *Alps* 9.] Bees and beetles visit this plant. Contabescence was observed.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus terrestris* L., sh. 25. IX. 95, 800 ft. and ? 29. VI. 95, 1,100 ft. (2) *B. agrorum* F., cp. and sh. 5. VII. 95, 800 ft. once. (3) *B. venustus* Smith, sh. 18. VI. 96, 800 ft. once. **Diptera.** *Anthomyiidae*: (4) *Drymia hamata* Fln., 25. VI. 95, 800 ft. (5) *Anthomyia* sp., seeking h. 21. IX. 95, 800 ft. **Coleoptera.** (6) *Meligethes viridescens* F., 2. VII. and 21. IX. 95, 800 ft., 29. VI. 96, 11–1,500 ft. freq. **Thysanoptera.** (7) *Thrips* sp., sh. 21. VI. 96, 1,500 ft.

134. *Mimulus Langsdorffii*, Donn. (*M. luteus*, auctorum anglorum). [Lit. *N.C.E.* 1, 9; Batalin 147.] Self-pollination occurs in the fall of the corolla by the anthers sliding up the style to the stigma. The stigma is very sensitive. The flower is obviously suited to *Bombus*-like insects; but the throat is rather low for our British *Bombi*. We have not seen them to visit.

*Visitors.* **Diptera.** *Anthomyiidae*: (1) *Anthomyia* sp., sh. 22. VI. 96, 800 ft.

## CLASS H § 24. ERICA TYPE.

135. *Arctostaphylos Uva-ursi*, Spreng. [Lit. *N.C.E.* 34; *Arct.* 36, 37 a; *Alps* 2, 9; *Pyren.* 17.] As the snows melt the young inflorescences can be found in the newly cleared patches of ground. The first flowers open in early May, and at mid May the plant is in full flower. These flowers are strongly scented, and are entirely visited by *Bombi*, chiefly *B. lapponicus*, which runs along the ground eagerly from bunch to bunch, sucks hanging back downwards, and then flies or crawls off to another plant. A bee, probably *Bombus terrestris*, often bites the corolla. Seed is freely formed, and ripens in September.

*Visitors.* **Hymenoptera.** Aculeata: *Apidae*: (1) *Bombus terres-*



tris L., sh. 20-23. V. 97, 15-1,900 ft. not infreq. (2) *B. lapponicus* F., sh. 20-23. V. 97, 8-1,900 ft. ab.

136. *Vaccinium myrtillus*, Linn. [Lit. *Brit.* 23, 29, 39; *Ogle* 1905; *N.C.E.* 1, 4, 16, 18, 33, 34, 40; *Arct.* 34, 36; *Alps* 2, 34; *Pyren.* 17.] A very typical bee-flower, attracting *Bombus lapponicus* in great quantity and other *Bombi* also. The honey is particularly abundant, and drops appear on the bell within the reach of insects which cannot obtain it from the nectary. Fruit may ripen very abundantly.

*Visitors.* **Lepidoptera.** Heterocera: *Geometridae*: (1) *Larentia salicata* Hb., sh. 25. VI. 95, 2,300 ft. twice. **Hymenoptera.** Aculeata: *Apidae*: (2) *Bombus terrestris* L., sh. 16. VI.-17. VII. 95, 22-23. V. 96, 18-27. V. 97, 12. VII. 99, 7-2,300 ft. (3) *B. pratorum* L., sh. 19. VI. 95, 2,000 ft. (4) *B. lapponicus* F., sh. 16-25. VI. 95, 18-25. V. 97, 12. VI. 99, 7-2,400 ft. very ab. (5) *B. hortorum* L., sh. 17. VI. 99, 2,500 ft. *Formicidae*: (6) *Formica fusca* Latr., seeking h. 18. V. 97, 1,900 ft. and inside a flower, the edge of which had been eaten, 12. V. 98, 800 ft. **Diptera.** *Empidae*: (7) *Empis lucida* Ztt., 24. V. 97; 12. VI. 99, 1,600-2,300 ft. *Anthomyiidae*: (8) *Anthomyia sulciventris* Ztt., seeking h. 25. VI. 95, 2,300 ft.

137. *Vaccinium Vitis-idaea*, Linn. [Lit. *Brit.* 23, 26; *N.C.E.* 14, 33, 34, 40; *Arct.* 7, 36, 37 a, 38; *Alps* 2, 9.] Bees and hemitropous flies visit this flower. Fruit is set abundantly.

*Visitors.* **Lepidoptera.** Heterocera: *Noctuidae*: (1) *Triphaena* sp., 19. VI. 95, 2,000 ft. **Hymenoptera.** Aculeata: *Apidae*: (2) *Bombus terrestris* L., sh. 24. IX. 95, 1,200 ft. (3) *B. lapponicus* F., sh. 19-27. VI. 95, 20-2,100 ft. (4) *Nomada ruficornis* L., sh. 12. VI. 99, 1,000 ft. **Diptera.** *Syrphidae*: (5) *Melanostoma quadrimaculatum* Verrall, sh. 19. VI. 95, 2,000 ft. *Empidae*: (6) *Empis lucida* Ztt., 19. VI. 95, 13. VI. 99, 19-2,000 ft. (7) *E. livida* L., sh. 19. VI. 99, 2,000 ft.

138. *Erica Tetralix*, Linn. [Lit. *Brit.* 23, 29, 34, 39; *N.C.E.* 1, 3 c, 11, 12, 14, 14 a, 18, 21 a, 30, 35, 40.] *Bombi* are the chief visitors. By flowering just after midsummer, when butterflies are numerous, it obtains a certain number

of visits from them. *Apis* visits it freely. A species of *Bombus*, probably *B. terrestris*, bites through the corolla. Abnormally, more or less polypetalous flowers (such as Sigerson described in Proc. Royal Irish Acad., 1871, Ser. II, vol. i, and Price in Proc. Bot. Soc. Edinb., xi, p. 256) are not uncommon in certain seasons.

*Visitors. Lepidoptera.* Rhopalocera: (1) *Argynnis selene* Schiff., sh. 23. VI. 95, 900 ft. (2) *A. aglaia* L., sh. 15-25. VI. 95, 1. VII. 96, 9-1,000 ft. (3) *Polyommatus phloea* L., sh. 1. VII. 95, 800 ft. Heterocera: *Noctuidae*: (4) *Celaena haworthii* Curt., sh. 23. IX. 95, 1,100 ft. *Geometridae*: (5) *Cidaria* sp., sh. 2. VII. 95, 1,100 ft. **Hymenoptera.** Aculeata: *Apidae*: (6) *Apis mellifica* L., sh. 17-21. VII. 95, 9-1,200 ft. (7) *Bombus terrestris* L., sh. 23. VI.-23. IX. 95, 22. VI.-9. VII. 96, 8-1,400 ft. ab. (8) *B. lapponicus* F., sh. 23. VI.-19. IX. 95, 8-10. VII. 96, 8-1,500 ft. (9) *B. jonellus* Kirby, cp. and sh. 21-22. VII. 95, 11-1,200 ft. (10) *B. agrorum* F., sh. 5. VII. and 23. IX. 95, 8-900 ft. (11) *B. venustus* Smith, sh. 22. VI. 95, 1,100 ft. *Vespidae*: (12) *Vespa norvegica* F., sh. by means of borings, 21-22. VII. 95, 11-1,200 ft. **Diptera.** *Syrphidae*: (13) *Eristalis pertinax* Scop., 20. IX. 95, 9-1,000 ft. *Muscidae*: (14) *Pollenia rudis* F., sh. and fp. 22-23. IX. 95, 9-1,110 ft. *Anthomyiidae*: (15) *Hyetodesia incana* W., 20. IX. 95, 9-1,100 ft. *Ortaliidae*: (16) *Pteropaectria frondescens* L., seeking h. 6. VII. 95, 900 ft. **Coleoptera.** (17) *Meligethes viridescens* F., sh. by means of a boring, 23. IX. 95, 1,100 ft.

139. *Erica cinerea*, Linn. [Lit. *Brit.* 23, 26, 29, 34, 39; Ogle 1905; Powell 2020; *N.C.E.* 14, 14 a, 15, 16, 18, 21 a, 21 b.] *Apis* visits this plant more freely than it does *E. Tetralix*. *Bombi* are however the chief visitors, one of them, *B. terrestris*, often bites through the corolla in order to obtain the honey. *Vespa* and other short-tongued insects afterwards take advantage of the borings.

*Visitors. Lepidoptera.* Rhopalocera: (1) *Argynnis aglaia* L., sh. 18. VI. 96, 800 ft. (2) *A. selene* Schiff., sh. 23. VI. 95, 900 ft. (3) *Coenonympha pamphilus* L., sh. 26. VI. 95, 800 ft. (4) *Polyommatus phloea* L., sh. 15. IX. 95 and 18. VI. 96, 800 ft. **Hymenoptera.** Aculeata: *Apidae*: (5) *Apis mellifica* L., sh. 17-22. VII. 95,

9-1,200 ft. freq. (6) *Bombus terrestris* L., sh. in the proper manner and biting through, 23. VI.-24. IX. 95, 18. VI.-9. VII. 96, 8-1,700 ft. very ab. (7) *B. jonellus* Kirby, sh. 21-22. VII. 95, 11-1,300 ft. (8) *B. lapponicus* F., sh. 25. VI.-14. IX. 95, 18. VI.-10. VII. 96, 8-2,300 ft. freq. (9) *B. smithanus* White, 14. IX. 95, 800 ft. (10) *B. pratorum* L., sh. 27. VI. 95, 800 ft. (11) *Psithyrus quadricolor* Lep., sh. 22. VII. 95, 1,700 ft. *Vespidæ*: (12) *Vespa norvegica* ? F., sh. by means of borings, 21. VII. 95, 11-1,200 ft. twice. **Diptera.** *Syrphidæ*: (13) *Volucella bombylans* L., sh. 23. VI. 95, 900 ft. once. *Muscidæ*: (14) *Pollenia rudis* F., sh. by means of a boring, 14. IX. 95, 900 ft. once.

CLASS H § 25. SIMPLE PENDULOUS TYPE.

140. *Geranium phaeum*, Linn. [Lit. *Brit.*, Darwin 482; *N.C.E.* 1, 21 b, 33, 34; Errera 633; Loew 1358; *Pyren.* 17.] Errera found it in Belgium to be a very characteristic bee-flower. At Clova *Bombus agrorum* is a regular visitor, but Syrphids are not infrequent.

*Visitors.* **Lepidoptera.** Heterocera: *Noctuidæ*: (1) *Habrostola urticae* Hb., sh. 14. VI. 99, 800 ft. *Tineidæ*: (2) *Gelechia* sp., sh. 26. VI. 95. **Hymenoptera.** Aculeata: *Apidæ*: (3) *Bombus agrorum* F., sh. 16-21. VI. 95, 10-12. VI. 99, fairly constant. (4) *B. terrestris* L., sh. 22. VI. 96, 12. VI. 99. *Petiolata tubulifera*: *Vespidæ*: (5) *Odynerus trimarginatus* Ztt., sh. 22. VI. 96. **Diptera.** *Syrphidæ*: (6) *Platychirus manicatus* Mg., sh. 10. VI. 99. (7) *Rhingia campestris* Mg., 17. VI. 96. *Empidæ*: (8) *Empis* sp., sh. 22. VI. 96. (9) *E. punctata* Mg., 22. VI. 96. *Tachinidæ*: (10) *Siphona geniculata* Deg., sh. 18. VI. 96. *Anthomyidæ*: (11) *Anthomyia* sp., sh. 19-22. VI. 96. All at 800 ft.

141. *Prunus avium*, Linn. [Lit. *N.C.E.* 1, 3 b, 16, 18, 33.] This tree is very well visited by *Bombus lapponicus*.

*Visitors.* **Lepidoptera.** Rhopalocera: (1) *Pieris rapae* L., sh. 22. VI. 97, 600 ft. (2) *Vanessa urticae* L., sh. 21. V. 97, 600 ft. **Hymenoptera.** Aculeata: *Apidæ*: (3) *Apis mellifica* L., sh. 21. V. 97, 800 ft. (4) *Bombus lapponicus* F., 21-25. V. 97, 800 ft. freq. **Diptera.** *Syrphidæ*: (5) *Syrphus punctulatus* Verrall, sh. 21. V. 97,



800 ft. (6) *P. discimanus* Lw., fp. 21. V. 97, 800 ft. *Empidae*: (7) *Rhamphomyia cinerascens* Mg., sh. 24. V. 97, 800 ft. *Anthomyiidae*: (8) *Anthomyia sulciventris* Ztt., 21-25. V. 97, 6-800 ft. *Thysanoptera*: (9) *Thrips* sp., in base of the flower, 16. V. 98, 800 ft.

142. *Rubus Idaeus*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 16, 18, 32, 34, 40; MacLeod 1473; *Alps* 2, 9.] We found moths frequent visitors; MacLeod observed the same in Belgium.

*Visitors. Lepidoptera.* Heterocera: *Bombycidae*: (1) *Hepialis humili* L., sh. 27. VI.-3. VII. 95, 800 ft. *Noctuidae*: (2) *Apamea gemina* Hb., sh. 27. VI. 95, 800 ft. (3) *Dianthecia cucubali* Fues., sh. 24-27. VI. 95, 800 ft. (4) *Xylocampa areola*, Esp., sh. 27. VI. 95, 800 ft. (5) *Habrostola tripartita* Hufn., sh. 27. VI. 95, 800 ft. (6) *Plusia chrisitis* L., sh. 27. VI.-6. VII. 95, 800 ft. (7) *P. festucae* L., sh. 27. VI. 95, 800 ft. (8) *P. pulchrina* Haw., sh. 27-30. VI. 95, 800 ft. *Geometridae*: (9) *Cabera pusaria* L., sh. 27. VI. 95, 800 ft. (10) *Thera variata* Schiff., sh. 27. VI. 95, 800 ft. *Hymenoptera.* Aculeata: *Apidae*: (11) *Apis mellifica* L., sh. 20-23. VI. 95, 800 ft. (12) *Bombus terrestris* L., 27. VI. 95, 800 ft. (13) *B. pratorum* L., 27. VI. 95, 800 ft. (14) *B. lapponicus* F., sh. 3-6. VII. 96, 21-2,300 ft. (15) *B. agrorum* F., sh. 20. VI.-2. VII. 95, 19. VI. 99, 800 ft. freq. *Vespidae*: (16) *Vespa norvegica* F., sh. 29. VI. 96, 800 ft. (17) *Vespa sylvestris* Scop., 27. VI. 95, 800 ft. *Diptera.* *Syrphidae*: (18) *Sericomyia lapponum* L., sh. 23. VI. 95, 800 ft. (19) *Eristalis arbustorum* L., sh. 23. VI. 97, 800 ft. *Anthomyiidae*: (20) *Hyetodesia incana* W., sh. 21-23. VI. 95, 26. VI. 96, 8-1,000 ft. (21) *Anthomyia* sp., sh. 23. VI. 95, 800 ft. (22) *Hydrotaea* sp., sh. 19. VI. 99, 800 ft.

143. *Geum rivale*, Linn. [Lit. *Brit.* 23; *N.C.E.* 1, 16, 21a, 21b, 33, 34; Warnstorff 2507; *Arct.* 34; *Alps* 2, 9.]

*Visitors. Hymenoptera.* Aculeata: *Apidae*: (1) *Bombus lapponicus* F., sh. 6. VII. 95, 20. VI.-6. VII. 96, 23-2,500 ft. (2) *B. agrorum* F., sh. 24. VI. 95, 800 ft. (3) *Psithyrus quadricolor* Lep., sh. 20. VI. 96, 2,400 ft. *Diptera.* *Anthomyiidae*: (4) *Anthomyia* sp., fp. 6. VII. 96, 2,400 ft. *Coleoptera.* (5) *Meligethes viridescens* F., sh. 20. VI. 96, 2,400 ft.

## CLASS H § 26. PYROLA SECUNDA TYPE.

144. *Pyrola secunda*, Linn. [Lit. *N.C.E.* 1, 4, 34; *Alps* 9.] The stigma protrudes from the opening bud, and the stamens seem to force their way between the petals. The openings of the anthers are turned away from the stigma.

*Visitors.* Hymenoptera. Aculeata: *Apidae*: (1) *Bombus lapponicus* F., sh. Coleoptera. (2) *Meligethes aeneus* F., sp. (3) *Epu-raea aestiva* L., ? fp. All 6. VII. 96, 1,900 ft.

145. *Ribes sanguineum*, Pursh. [Lit. *Brit.* 29; *N.C.E.* 3 a, 40.] In cultivation.

*Visitors.* Hymenoptera. Aculeata: *Apidae*: (1) *Bombus terrestris* L., sh. 14. V. 98, 800 ft.

## CLASS H § 27. GALANTHUS TYPE.

146. *Galanthus nivalis*, Linn. [Lit. *N.C.E.* 1, 9, 18, 33, 34; Knuth 2871.] In cultivation.

*Visitors.* Hymenoptera. Aculeata: *Apidae*: (1) *Apis mellifica* L., 15. IV. 95, 800 ft.

## CLASS H § 28. CAMPANULA TYPE.

147. *Campanula rotundifolia*, Linn. [Lit. *Brit.* 23, 34, 39; Marquand 1513; *N.C.E.* 1, 11, 14, 14 a, 16, 18, 30, 32, 34, 35; *Arct.* 36, 38; *Alps* 2, 34; *Pyren.* 17.] A flower in a measure specialized for *Melitta*, *Eriades*, and *Halictoides*, and a shelter-flower to small flies, which are abundant in its bells, and also sometimes a shelter-flower to *Andrena*. *Bombi*, *Apis*, *Melitta*, *Cilissa*, *Eriades*, *Halictoides*, and other similar bees visit the flower in Germany and the Alps; *Bombi* have been seen on it in Scandinavia and the Pyrenees, and *Bombus terrestris* in Southern Scotland; it is worth remark that we have seen no bees in the flowers except two species of *Andrena*. Insects with a tongue of 3 mm. and upwards can reach the honey.

*Visitors.* Lepidoptera. Heterocera: *Pyralidae*: (1) *Scopula alpi-*

TABLE XX.  
Individuals visiting the different species.

	Apis.	Bomb.	Hm.	Phyt.	Entom.	Ants.	Wasps.	Lep.l.	Lep.m.	Lep.s.	Dm.	Ds.	Col.	Etc.	Total.
91. <i>Silene acaulis</i> . . . . .	—	1	—	—	—	—	—	24	3	—	1	6	13	2	50
92. <i>Habenaria conopsea</i> . . . . .	—	—	—	—	—	—	—	2	1	2	—	3	—	—	8
93. <i>Lonicera Periclymenum</i> . . . . .	3	—	—	—	—	—	—	3	—	—	1	6	—	—	16
94. <i>Lycchnis diurna</i> . . . . .	—	—	—	—	—	—	—	—	—	—	2	—	—	—	7
95. <i>Lycchnis flos-cuculi</i> . . . . .	—	2	—	—	—	—	—	1	—	—	5	—	5	—	9
96. <i>Lycchnis alpina</i> . . . . .	—	1	—	—	—	—	—	—	—	—	—	3	—	4	8
97. <i>Primula vulgaris</i> . . . . .	—	1	—	—	—	—	—	—	—	—	—	17	5	1	24
98. <i>Crocus aureus</i> . . . . .	*	—	—	—	—	—	—	—	—	—	—	*	—	—	*
99. <i>Viola palustris</i> . . . . .	—	*	—	—	—	—	—	—	—	—	2	1	—	—	3
100. <i>Viola canina and sylvatica</i>	—	1	—	—	—	—	—	8	—	—	—	11	—	1	21
101. <i>Viola tricolor</i> . . . . .	—	—	—	—	—	—	—	1	—	—	—	1	—	—	2
102. <i>Viola lutea</i> . . . . .	—	—	1	—	—	—	—	2	1	1	—	45	—	—	50
103. <i>Orchis maculata</i> . . . . .	—	—	—	—	—	—	—	1	—	—	—	2	—	—	3
104. <i>Orchis mascula</i> . . . . .	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
105. <i>Tropaeolum speciosum</i> . . . . .	—	2	—	—	—	—	—	—	—	—	—	—	—	—	2
106. <i>Pinguicula vulgaris</i> . . . . .	—	1	—	—	—	—	—	1	—	—	—	5	—	—	7
107. <i>Pedicularis sylvatica</i> . . . . .	—	2	—	—	—	—	—	2	—	—	—	2	—	—	6
108. <i>Pedicularis palustris</i> . . . . .	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
109. <i>Melampyrum pratense</i> . . . . .	—	2	—	—	—	—	—	—	—	—	—	—	—	—	2
110. <i>Euphrasia officinalis</i> . . . . .	1	—	—	—	—	—	—	—	—	—	1	—	—	—	2
111. <i>Nepeta Glechoma</i> . . . . .	1	—	—	—	—	—	—	—	—	—	—	1	—	—	2
112. <i>Prunella vulgaris</i> . . . . .	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
113. <i>Stachys palustris</i> . . . . .	—	3	—	—	—	—	—	—	—	—	—	—	—	—	4
114. <i>Galeopsis Tetrabit</i> . . . . .	—	1	—	—	—	—	—	—	—	—	3	—	—	—	4
115. <i>Lamium purpureum</i> . . . . .	—	7	—	—	—	—	—	2	—	—	7	8	7	—	31
116. <i>Lamium maculatum</i> . . . . .	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
117. <i>Ajuga reptans</i> . . . . .	—	7	—	—	—	—	—	—	—	—	1	—	—	—	14
118. <i>Genista anglica</i> . . . . .	—	2	—	—	—	—	—	—	—	—	—	2	—	—	4
119. <i>Ulex europaeus</i> . . . . .	35	17	—	—	—	—	—	—	—	—	3	8	—	—	64





nalis Schiff., sh. 27. VI. 95, 2,000 ft. once. *Tineidae*: (2) *Glyphipteryx fuscoviridella* Haw., sh. 27. VI. 95, 800 ft. once. *Erioccephalidae*: (3) *Erioccephala calthella* L., 23. VII. 95, 800 ft. **Hymenoptera**. Aculeata: *Apidae*: (4) *Andrena analis* Panz, cp. 17. VII. 95, and sh. 10. VII. 96, 800 ft. (5) *A. coitana* Kirby, sh. freq. and sheltering (?), 2-23. VII. 95, 800 ft. Petiolata parasitica: *Cynipidae*: (6 and 7) 2 spp., 16. VI. and 23. VII. 95, 800 ft. **Diptera**. *Syrphidae*: (8) *Rhingia campestris* Mg., sh. 10. VII. 96, 800 ft. once. (9) *Platychirus manicatus* Mg., sh. 3-17. VII. 95, 800 ft.; 8. VII. 96, 2,400 ft. (10) *Melanostoma mellinum* L., 3. VII. 95, 800 ft. *Tachinidae*: (11) *Siphona geniculata* Deg., sh. 26. VI. 95; 13-16. IX. 95, 7-800 ft. *Muscidae*: (12) *Calliphora erythrocephala* Mg., sh. 10. VII. 96, 800 ft. *Anthomyiidae*: (13) *Drymia hamata* Fln., fp. 2. VII. 96, 2,100 ft. (14) *Anthomyia* sp., 16. VI.-23. VII. 95, 8-1,800 ft. (15) *Trichophthicus hirsutulus* Ztt., 6. VII. 96, 2,000 ft. (16) *Trichophthicus* sp., sh. and fp. 17-23. VII. 95, 800 ft. **Thysanoptera**. (17) *Thrips* sp., sh. 22. IX. 95, 800 ft.

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We have had under observation the following flowers of Classes F and H, but have seen no insects visiting them:—

*Polygala serpyllacea*, Weihe, *Anthyllis vulneraria*, Linn., *Rubus saxatilis*, Linn., *Vaccinium uliginosum*, Linn., *Gentiana campestris*, Linn., *Rhinanthus Crista-galli*, Linn., *Habenaria albida*, R. Br.; however, from the last-named the pollinia were observed to be regularly removed at night. We have seen in flower at Clova, but have not had suitable opportunities for watching: *Lobelia Dortmanna*, Linn., *Primula veris*, Linn., and *Utricularia minor*, Linn. *Silene Cucubalus*, Wibel, *Vicia hirsuta*, Koch, *Arctostaphylos alpina*, Spreng., and *Scrophularia nodosa*, Linn., are other Clova plants of Class H which we have not seen in our district, although we have every reason to believe that they have been observed. *Symphytum officinale*, Linn., we have observed just outside our limits at 500 feet to be diligently visited by *Bombus agrorum*.

Out of the whole available anthophilous insect-fauna of (for the time of our observations) 17,306 individuals, 1,507 went to

Classes F and H. It is not worth while to separate the two classes here; for there are but three species assigned to F, and of them only one (*Silene acaulis*) appeared as a true Lepidoptera-flower. The species of plants obtained attention as in Table XX. The decidedly desirable insects showed their marked preference; and nearly one half of the total number of individuals of them, which we observed to visit, went to flowers of these two classes, and made 57·73 per cent. of their visitors.

TABLE XXI.

	Available.		F and H.	
	No.	%	No.	%
Distinctly desirable	1,763	10·19	870	57·73
Desirable . . . .	1,277	7·37	87	5·77
Indifferent . . . .	12,993	75·08	413	27·41
Injurious . . . .	1,273	7·36	137	9·09

We found that in Class B' the blue-lilac flowers attracted the best of the insects, that the rose-purple came next, that yellow followed, and that white or eyed flowers came last. Experience with Classes F and H is different, and our figures are as follows: with white at the top, rose-purple second, yellow third, and lilac-blue last.

TABLE XXII.

	Lilac and blue.	Rose and purple.	Yellow and scarlet.	White.
Decidedly desirable	16·66	74·67	46·26	76·55
Desirable . . . .	12·35	5·95	1·77	7·24
Indifferent . . . .	60·31	16·50	32·75	15·86
Injurious . . . .	10·67	2·88	19·22	·34

In the table which follows and which amplifies XXI, we have kept *Campanula* apart, for it certainly is a peculiar type;



but still the lilac-blue flowers remain those which get fewest of the decidedly desirable insects.

TABLE XXIII.

	Apis.	Bomb.	Hm.	Phyt. Entom. Ants.	Wasps.	Lep.l.	Lep.m.	Lep.s.	Dm.	Ds.	Col.	Etc.
Campanula . . . . .	—	—	12.82	1.71	—	—	1.71	.85	4.27	63.25	—	15.39
Other blue-lilac flowers .	1.45	13.04	1.45	—	—	18.84	1.45	2.90	2.90	44.93	8.70	4.35
Rose-purple . . . . .	12.09	54.13	.19	.38	2.30	8.45	.77	—	4.99	7.10	7.10	2.50
Yellow . . . . .	17.24	19.02	.39	.98	—	10.00	.20	.20	1.18	25.69	6.86	18.24
White . . . . .	27.93	30.00	.34	—	1.03	18.62	—	—	6.90	8.97	5.86	.34

In our enumeration of visitors, and in Table XX, we have taken the flowers of Class H in such order that first come those with erect actinomorphic flowers, secondly those with horizontal zygomorphic flowers, and thirdly, those with pendent actinomorphic flowers. We may add to them the three flowers of Class F—one erect actinomorphic and two horizontal zygomorphic—whereupon we get:—

1. Six erect actinomorphic in which to reach the honey a tongue 4–16 mm. long is required, average 10 mm.

2. Thirty-eight horizontal zygomorphic in which to reach the honey a tongue 4–20 mm. long is required, average 8 mm.

3. Thirteen pendent actinomorphic in which to reach the honey a tongue 1–7 mm. long is required, average 4.5 mm.

It is very easy to show that a greater exclusion of the undesirable or little desirable insects is effected by the simple inversion of the flower than by lengthening the tube.

TABLE XXIV.

Effect of the position of the flower upon the groups of the visitors.

	Apis.	Bomb.	Hm.	Entom. Phyt. Ants.	Wasps.	Lep.l.	Lep.m.	Lep.s.	Dm.	Ds.	Col.	Etc.
Erect . . .	—	5.10	—	—	—	25.51	3.06	—	8.16	27.55	23.47	7.14
Horizontal .	23.57	19.01	.39	.65	—	9.04	.26	.39	2.29	22.01	7.81	13.28
Pendent . .	8.11	50.55	2.65	.62	2.34	9.83	.47	.16	4.37	16.07	1.87	2.96

TABLE XXV.

Effect of the position of the flower upon the desirability of the visitors.

	Erect.	Horizontal.	Pendent.
Decidedly desirable . . . . .	30.61	52.22	68.49
Desirable . . . . .	11.22	3.64	7.49
Indifferent . . . . .	51.02	30.21	20.44
Injurious . . . . .	7.14	13.93	3.58

The pendent flowers thus, despite the shallowness of their honey, are seen to get the greater proportion of distinctly desirable insects, this proportion being chiefly made up by Bombi.

It happens that the majority of the white flowers are pendent, all the lilac-blue flowers, except *Campanula rotundifolia*, are horizontal, and most of the yellow flowers also, while the rose-purple flowers are divided.

TABLE XXVI.

Colour and position of flowers of Classes F and H.

	Lilac-Blue.	Rose-Purple.	Yellow-Scarlet.	White.
Erect . . . . .	0	4	2	0
Horizontal . . . . .	14	10	11	3
Pendent . . . . .	1	5	1	6

But the observation recorded by means of Tables XXII and XXIII, that white and rose-purple flowers of Classes F and H get the best of the insects is, however, not entirely due to so many of the pendent flowers being white or rose-purple; and if we take the horizontal flowers by themselves, the result remains the same, but the differences are somewhat lessened.

By season the distinctly desirable insects get fewer towards autumn, the indifferent get a little fewer, while the desirable and injurious increase, especially the latter.

TABLE XXVII.

Desirability of visitors to the various colours of the horizontal zygomorphic flowers.

	Lilac and Blue.	Rose and Purple.	Yellow and Scarlet.	White.
Decidedly desirable	33.33	52.08	47.69	79.53
Desirable . . . .	5.80	6.25	1.89	7.09
Indifferent . . . .	56.52	34.37	29.83	13.39
Injurious . . . .	4.35	7.29	20.04	0.00

TABLE XXVIII.

Visitors to Classes F and H by season.

	Spring.		Summer.		Autumn.	
	No.	%	No.	%	No.	%
Distinctly desirable	211	65.94	605	56.23	54	48.65
Desirable . . . .	10	3.12	68	6.32	9	8.11
Indifferent . . . .	93	29.06	291	27.04	29	26.13
Injurious . . . .	6	1.88	112	10.41	19	17.12
Total . .	320	—	1076	—	111	—

The actual numbers and percentages in the different groups are as follows:—

TABLE XXIX.

Visitors to Classes F and H by season.

	Apis.	Bomb.	Hm.	Phyt. Entom. Ants.	Wasps.	Lep.l.	Lep.m.	Lep.s.	Dm.	Ds.	Col.	Etc.	Total.
Totals. {	Spring	62	141	—	2	—	8	—	10	91	2	4	320
	Summer	168	285	20	7	15	152	8	40	189	83	105	1076
	Autumn	3	49	—	—	—	2	—	—	9	19	10	111
Percentages. {	Spring	1.38	44.06	—	.62	—	2.50	—	3.13	28.44	.62	1.25	—
	Summer	1.61	26.49	1.86	.65	1.39	14.13	.74	3.71	17.56	7.71	9.76	—
	Autumn	2.70	44.14	—	—	—	1.81	—	8.11	17.12	9.01	17.12	—



As the flowers of the classes under consideration set themselves apart almost completely for the larger Apidae, we give here the seasonal distribution of these bees:—

TABLE XXX.

Seasonal distribution of Bees. The sequence is the sequence of their tongue-lengths.

Name.	Spring (23 days).	Summer (88).	Autumn (12).	Total.
<i>Bombus hortorum</i> . . . . .	3	12	—	15
<i>B. agrorum</i> . . . . .	5	49	44	98
<i>B. venustus</i> . . . . .	—	9	—	9
<i>B. smithianus</i> . . . . .	—	—	1	1
<i>B. cognatus</i> . . . . .	—	—	2	2
<i>B. lapidarius</i> . . . . .	3	—	3	6
<i>B. lapponicus</i> , with <i>B. pratorum</i> . . . . . <i>B. jonellus</i> , and . . . . . <i>B. scrimshiranus</i> . . . . .	182	163	11	356
<i>Psithyrus quadricolor</i>	—	10	1	11
<i>Bombus terrestris</i> . . . . .	77	76	240	393
<i>Bombi</i> (unidentified)	2	43	1	46
<i>Apis mellifica</i> . . . . .	160	266	4	430
Total . . . . .	432	628	307	1367

We may class these bees by their tongue-lengths: *Bombus hortorum* to *B. cognatus* first, *B. lapidarius* and *B. lapponicus* second, *Psithyrus quadricolor* and *Bombus terrestris* third, and *Apis* last.

TABLE XXXI.

Bees in season by their tongue-lengths.

	Spring.		Summer.		Autumn.	
	No.	Percentage of total insects.	No.	Percentage of total insects.	No.	Percentage of total insects.
Tongue 15 mm. and over . . . . .	8	.19	70	.72	47	1.41
Tongue 10-15 mm. long . . . . .	185	4.41	163	1.67	14	.42
Tongue 7-10 mm. long . . . . .	77	1.83	86	.88	241	7.25
Tongue 6 mm. long . . . . .	160	3.81	266	2.72	4	.01

It remains now to compare our results with those of other observers, and the table which follows does this. As in the case of B' and A', we again find Müller's observations very closely supported by those of Knuth, Verhoeff, Alfken and others on the coast of North Germany. Again we see the Alps showing an abundance of Lepidoptera, and our own country an abundance of short-tongued flies. Further comment is reserved.

TABLE XXXII.

Comparison of species-visits to Clova flowers of Classes F and H in various parts of Europe.

	Apis.	Hl.	Hm.	Hs.	Lep.	Dm.	Ds.	Col.	Etc.	Total.
Clova . . . . . (57 plants)	17	85	3	14	56	36	95	19	12	337
Germany—Müller . (35 ,, )	25	230	78	2	73	46	1	10	2	476
Flanders—MacLeod (25 ,, )	10	74	15	10	46	12	7	8	—	182
Friesian Coast—Knuth, Verhoeff, &c. . . (37 ,, )	23	293	66	8	54	32	12	6	1	495
Alps—Müller . . . (23 ,, )	3	90	2	1	179	10	1	6	2	294
Pyrenees—MacLeod. (11 ,, )	—	41	2	—	21	9	1	1	—	75

In conclusion, Classes F and B obtained the visits of *Apis mellifica*, of nine species of *Bombi* (all in the district except *B. cognatus* and *B. scrimshiranus*), of *Psithyrus quadricolor*, of two species of *Andrena*, of a *Nomada*, and two species of *Odynerus*, of two species of *Vespa*, of two kinds of ants, and of two species of ichneumons, of eight butterflies, of twelve of the Noctuid moths which are almost entirely crepuscular or nocturnal, of five geometers, of five ordinary Micro-lepidoptera, including *Hepialis humuli*, and also of *Eriocephala calthella*; among Diptera, of thirteen Syrphidae including *Rhingia campestris*, of five species of *Empis*, of one *Rhamphomyia*, of four Muscids, of one *Sarcophaga*, and of *Siphona geniculata*, of eight Anthomyiids including *Drymia hamata*, of two Scatophagids, and of eleven other flies; of six Coleoptera, of two Hemiptera, of Thrips and of a spider.

Thus 109 species of insects visited the two classes, making 1,507 individual visits, the average constancy being 13.83.

# Observations on Gymnoascaceae.

BY

MISS E. DALE.



With Plates XXVII and XXVIII.



## INTRODUCTION.

IN May, 1901, Professor Marshall Ward handed to me for investigation three species of *Gymnoascus*, which had been received by him from Mr. Masee, who had collected them on the substrata referred to below. The species were (1) *G. Reessii* (Baranetzky), growing on dung, of what kind could not be determined; (2) *G. setosus* (Eidam), on an old bee's nest; and (3) *G. candidus* (Eidam), *Arachniotus candidus* (Schroeter), on dead grass. Subsequent examination showed that all three species were growing together on the old nest.

The total number of species of *Gymnoascus* actually known is probably about a dozen. Winter<sup>1</sup>, in Rabenhorst's Kryptogamen-Flora, describes *G. Reessii*, *G. ruber*, and *G. uncinatus*. Masee<sup>2</sup> mentions *G. Reessii* and *G. ruber* (van Tieghem), but does not notice any other species as found in Britain.

Fischer<sup>3</sup> mentions five species, viz. *G. Reessii*, *G. setosus* (Eidam), *G. durus* (Zukal), *G. umbrinus* (Boudier), and *G. Bourqueloti* (Boudier). Saccardo<sup>4</sup>, in 1889, describes six species

<sup>1</sup> Band I. 2. Pilze, p. 15 (1887).

<sup>2</sup> British Fungus Flora, vol. iv, p. 18 (1895).

<sup>3</sup> Engler und Prantl, Pflanzenfamilien, I. 1, p. 294 (1897).

<sup>4</sup> Syll. Fung., vol. viii, p. 823 (1889).



of *Gymnoascus*, viz. *G. Reessii*, *G. ruber*, *G. aurantiacus* (Peck), Sacc. (*Gymnascella aurantiaca*, Peck), *G. uncinatus* (Eidam), *G. reticulatus* (Zuk.), and *G. setosus* (Eidam).

In three later volumes he adds seven other species, viz. *G. Zuffianus* and *G. Eidami*<sup>1</sup>; *G. Bourquelotii*, *G. umbrinus*, *G. luteus*, and *G. myriosporus*<sup>2</sup>; and *G. ossicola*<sup>3</sup>.

During the present year (1902) a new species of *Gymnoascus* has been described, but not figured, by Klöcker<sup>4</sup>, under the name of *G. flavus*. Schroeter<sup>5</sup>, in treating of the *Gymnoascaceae* in general, founded two new genera, *Arachniotus* and *Amauroascus*, by breaking up the original genus *Gymnoascus* into three. He did not describe any new forms, but only reclassified those already known. Eidam's *Gymnoascus candidus* belongs to the genus *Arachniotus*, according to Schroeter's classification, which has been generally adopted. It is the one which has been accepted by Matruchot and Dassonville, whose results, as will be seen later (page 590), appear to be confirmed by the work about to be described.

#### HISTORICAL.

The three species may first be considered briefly from the historical point of view.

1. *Gymnoascus Reessii* (Baran.) was first described in 1872 by Baranetzky<sup>6</sup>, who founded the genus on this species. He made cultures of the fungus, and worked out its life history in as great detail as was possible with the histological methods then available. His conclusions were afterwards disputed by subsequent workers, who, however, do not seem to have gone into the matter as thoroughly as Baranetzky.

According to Baranetzky the fructifications are formed in the following manner: two swellings arise side by side on a single

<sup>1</sup> vol. x, p. 71 (1892).

<sup>2</sup> vol. xi, p. 437 (1895).

<sup>3</sup> vol. xiv, p. 824 (1899).

<sup>4</sup> Bot. Cent., Bd. lxxxix, No. 22, p. 626 (1902), and Hedwigia, Bd. xli, Heft 2, pp. 80-8 (1902).

<sup>5</sup> Cohn's Kryptogamen-Flora von Schlesien, Bd. iii, zweite Lieferung, zweite Hälfte, p. 210 (1893). See also Saccardo, l. c., vol. xi, p. 438 (1895).

<sup>6</sup> Entwicklungsgeschichte des *Gymnoascus Reessii*, Bot. Zeit., p. 145 (1872).

hypha, one on each side of, and quite close to, a transverse wall. These swellings grow out into little branches, which twist spirally round one another and become club-shaped. At this stage Baranetzky observed that the two cells cannot be separated, but he says 'a true copulation does not occur since both cells remain completely closed.' They each become cut off by a wall from the hypha on which they arose. The free end of one cell swells, and becomes cut off by a transverse wall from the part below it. The other cell puts out from its free end a thin cylindrical projection, which is also cut off by a side wall. This cell gives rise to the ascogenous hyphae, and may therefore be called the *ascogenous cell*, while the other may be distinguished as the *sterile cell*. The cylindrical projection lays itself round the swollen end of the sterile cell, and encircles it once by annular growth. It becomes segmented into almost isodiametric cells. Certain of these cells, generally not more than two, grow out into hyphae, which branch copiously without increasing much in length. In consequence there arise thick tufts with many short branches which swell at their ends and form asci. From the base of the sterile cell, meanwhile, grow out thin vegetative hyphae.

The results of the work about to be described, in most of the essential points, confirm those obtained by Baranetzky, but, by the use of modern methods, they have been extended.

In 1877 van Tieghem<sup>1</sup> described under the name *Gymnoascus ruber*, a species which he compared with *G. Reessii*. His account of the development of the reproductive organs is very short, and he gives no figures. This species belongs to Schroeter's genus *Arachniotus*.

In 1883 Eidam<sup>2</sup> described *G. Reessii* as it occurred on a pupa of *Sphinx Galii*. He did not find the reproductive organs described by Baranetzky, but gives the origin of the coiled hyphae as follows: below the dividing wall of a mycelial hypha a lateral branch arises which coils closely round

<sup>1</sup> (1) Sur le développement de quelques Ascomycetes. Bull. de la Soc. Bot. de France, vol. xxiv, p. 159 (1877).

<sup>2</sup> (1) Beitrag zur Kenntniss der Gymnoasceen. Cohn's Beiträge, p. 267 (1883).

the parent hypha or one which is adjacent. After winding round in a close coil for about eight or ten times it becomes loose and septate, and then grows out into branches which are the ascogenous hyphae. Eidam further states that Baranetzky says the method of reproduction described by him only occurs in weak mycelia.

I can find no such statement in Baranetzky's paper; in fact, he distinctly says that his cultures were perfectly normal and strong.

Eidam<sup>1</sup> also cultivated *G. ruber* (*Arachniotus ruber*), and in this species he found the kind of reproductive organs described by Baranetzky in *G. Reessii*, but only the early stages were described. Cell-fusion was not seen, although he sought specially for it, because he had already discovered it in *Eremascus*<sup>2</sup>. Perhaps the stages seen were too young, or the cultures not strong enough, as the ripe fructifications were never formed. In *G. uncinatus*, described by Eidam<sup>1</sup> as a new species, the early stages also agreed with Baranetzky's account of *G. Reessii*. The fungus occurred spontaneously on sparrow-dung, but here again the ripe asci were not obtained in culture.

In 1891 *G. Reessii* was again described by Brefeld<sup>3</sup>, who declares that the ascogenous hyphae arise from *solitary* branches, each of which coils itself into a spiral, from which the ascogenous hyphae are produced by branching. Baranetzky figures a few such solitary branches, but regards them as anomalous cases which do not develop farther. Brefeld confirms Baranetzky's account of the formation of the asci on the ascogenous hyphae.

2. *Gymnoascus setosus* (Eidam) was first described by Eidam<sup>4</sup> as a new species at a meeting of the Botanical section of the *Schlesische Gesellschaft für vaterländische Cultur*, in January, 1882. Its habitat was an old wasp's nest. Eidam, in a very

<sup>1</sup> loc. cit. (1), p. 273.

<sup>2</sup> (2) Untersuchungen über die Familie der Gymnoascaceen: Bericht über die Thätigkeit der bot. Section der Schlesischen Gesellschaft, p. 164 (1886).

<sup>3</sup> (1) Ascomyceten, ii, Heft x, p. 158 (1891).

<sup>4</sup> (3) Ueber Entwicklungsgeschichte der Askomyceten: Jahresbericht der Schlesischen Gesell., p. 175 (1883), and Bot. Cent., vol. x, p. 107 (1882).



brief description, says that the mode of origin of the coil which precedes the formation of the asci is the same as in *G. Reessii*. No detailed life-history of this species has yet been given.

3. *Gymnoascus candidus* (Eidam) (*Arachnietus candidus*, Schroeter) was first described in 1886 by Eidam<sup>1</sup>, who gives an account of the mature fructifications as found by him growing spontaneously on cooked rice. It was subsequently separated from *Gymnoascus* and placed in a new genus, *Arachnietus*, by Schroeter<sup>2</sup>, who at the same time founded the genus *Amauroascus* on other species previously included in the genus *Gymnoascus*. The two new genera both agreed in having a peridium of very thin-walled, similar hyphae; whereas, according to Schroeter's limitations, *Gymnoascus* has a peridium of thick-walled hyphae which branch copiously and form a kind of trellis. *Arachnietus* differs from *Amauroascus* in having colourless, red, or yellow ascospores, while in *Amauroascus* the ascospore-wall is brown or brownish-violet.

In the genus *Arachnietus* Schroeter places three species, *Gymnoascus candidus* (Eidam), *G. ruber*<sup>3</sup> (van Tieghem), and *G. aureus* (Eidam<sup>4</sup>). Schroeter describes mature asci and conidia, but the life-history has not been worked out until now, as Eidam's cultures were unsuccessful and he saw no conidia.

#### METHODS OF CULTURE AND PREPARATION.

The three species were isolated by means of plate cultures, and the colonies thus obtained were transferred to one of the following culture media:—sterilized horse-dung in tubes, extract of horse-dung in 2 per cent. agar-agar, or beer-wort in 2 per cent. agar-agar. The agar was sterilized in test-tubes. The most convenient method was found to be to grow, fix, and harden the fungus on the agar in the tube, as the species grew equally well on any of the media<sup>5</sup>. The material thus obtained was imbedded in paraffin, and the sections were

<sup>1</sup> (2) loc. cit., p. 5 (1886).

<sup>2</sup> loc. cit., p. 210. See also Saccardo, Syll. Fung., vol. xi, p. 438 (1895).

<sup>3</sup> See p. 573.

<sup>4</sup> loc. cit. (2).

<sup>5</sup> As a fixing reagent Flemming's weak solution was used.

stained in various ways. The best results were obtained with Flemming's triple-stain-safranin, gentian violet and orange G, and with toluidine blue and eosin. The latter stain is somewhat uncertain, but when successful the results are very good. The eosin stains the nucleoli red, while the toluidine blue stains the protoplasm blue.

A very useful stain for these Fungi is brazilin<sup>1</sup>, which differentiates the nuclei very clearly. Its special advantages are that its effects are very certain, and there is no over-staining. The results seem to be equally good, whether the material is stained before or after cutting.

#### I. THE LIFE-HISTORY OF GYMNOASCUS REESSII.

The original material consisted of little brick-red balls, made up of thick-walled septate hyphae, freely branching and anastomosing, and enclosing a mass of ripe ascospores, spherical in form and of a pale brown colour. These spores were for the most part isolated, but some were still contained in the spherical asci (Pl. XXVII, Fig. 1).

The thick-walled hyphae branch in a peculiar manner, the branches arising almost at right angles to the axis which bears them. Thus anastomosis is facilitated, and also the dense growth which results in the spherical mass of hyphae surrounding the groups of asci. The branches are said by Fischer<sup>2</sup> to be covered with 'short, straight, or slightly bent spines, 10-15  $\mu$  long.' Both in the original material and in the cultures subsequently made from it, the ends of the hyphae were blunt (Fig. 1 *a*). The hyphae were either empty or contained a greater or less amount of protoplasm. None of the asci was attached to any hyphae.

The ascospores readily germinated in various nutritive media. Those chiefly used were beer-wort, or horse-dung extract, made up with 10 per cent. or 15 per cent. of gelatine. Colonies were afterwards transferred either to sterilized horse-

<sup>1</sup> Hickson, Q. J. M. S., vol. 44, p. 469 (1901).

<sup>2</sup> Engler und Prantl, loc. cit., p. 294.

dung, or to beer-wort, or horse-dung extract, made up with 2 per cent. agar-agar, placed in test-tubes and sloped. In all these media the fungus grew well, and produced an abundance of ripe ascospores from which other cultures were made.

The ascospore germinates by the bursting of the outer wall and the growing out of the germ-tube (Fig. 2 *a-d*). The germ-tube soon branches close to the spore and becomes septate. Some of the branches grow almost parallel to the main axis in one direction, while adjacent ones grow in a completely opposite direction (Fig. 2 *d*). In some cases the mycelium branches little, and grows straight on; and in other cases the hyphae branch and curve considerably. In many mycelia, but not in all, the hyphal segments are swollen close to, and on one side of, each septum. This fact has been pointed out by Baranetzky, Brefeld, and others as characteristic of the family. Irregular knots of hyphae appeared in a hanging drop culture, but came to nothing. Apparently these were pathological, and due to the starved condition of the mycelium in the small drop. Similar irregular masses of hyphae have also been observed by Eidam<sup>1</sup> in *Ctenomyces*, a genus closely allied to *Gymnoascus*, and were by him also regarded as pathological.

In cultures on horse-dung the mycelium had completed its first fructifications, and ripe ascospores were obtained, by the first week in July, that is, in about two months from the sowing of the spores.

The vegetative mycelium varies greatly in external appearance according to the nature of the medium on which it is grown. If the fungus is growing on the surface of a dry medium, it forms a very small aërial mycelium, which is soft, flocculent, and perfectly white (Fig. 3). On it the fructifications soon arise as little white bodies which become yellow and then brick-red. But if the medium is wet at the surface, or if the mycelium is sunk in it, e.g. in gelatine or agar, the aërial hyphae cling together in bundles and grow up in strands which stand erect and taper to a point (Figs. 4

<sup>1</sup> loc. cit. (1), pp. 286, 287.



and 6). After a while the hyphae at the ends of the strands separate from one another (Figs. 5, 7, and 8) and grow out into a flocculent mycelium like that grown on a drier medium. On this the fructifications arise. The plants grown under the latter conditions have a much longer period of vegetative growth and are much larger and stronger than the former. In fact the two types would not be taken for the same species they differ so greatly.

So far as could be discovered none of the cultures of *G. Reessii* produced any conidia.

The origin of the coils, which precede the formation of asci, takes place exactly as Baranetzky has described<sup>1</sup> and figured, and, although hundreds of sections were examined, no structures were seen like those described by Eidam<sup>2</sup> and by Brefeld<sup>3</sup>. In every case *two* branches arise from a single hypha, one on each side of a septum. These two branches grow upwards, at right angles to the hypha which bears them, and twist round one another once or twice. Their free ends swell up into club-shaped heads (Fig. 9), each of which now becomes cut off by a transverse wall as a separate cell (Fig. 10). The cells become very closely applied to one another, and soon the wall between them breaks down, and the two cells fuse. The fusion can be seen in specimens stained whole, but much more clearly in microtome sections (Figs. 11, 12, 26-29). At this stage there is usually no differentiation whatever between the two cells. But in some cases a differentiation may be noticed even before conjugation. One cell, that called by Baranetzky the 'sterile cell,' is larger than the other, the 'ascogone' of Baranetzky. The sterile cell is almost straight, whereas the ascogone is longer, smaller in diameter, and is coiled round the sterile cell (Fig. 13). After conjugation the sterile cell grows larger and more spherical, so that the ascogone often comes to lie on its side, some distance from its apex (Fig. 14). The ascogone soon puts out a prolongation, which winds round the sterile cell (Figs. 13, 15, and 16). If the conjugating

<sup>1</sup> loc. cit.<sup>2</sup> loc. cit. (1).<sup>3</sup> loc. cit.

cells are of approximately the same size and shape, so that the apex of the ascogone and of the sterile cell are at the same level, the prolongation winds loosely and irregularly round the two cells (Fig. 15); but if the sterile cell is larger, so that the point of fusion lies some distance from its apex, the prolongation of the carpogone, at least at first, winds closely round the sterile cell (Fig. 14).

After forming a considerable coil round the original conjugating cells the prolongation of the ascogone becomes segmented, as may be seen in solid preparations (Figs. 17 and 19) and also in longitudinal and transverse sections (Figs. 18, 29 *c*). From most of these segments, not merely from one or two, short thick branches grow out, and soon themselves branch (Fig. 18) and form a dense mass of hyphae (Figs. 19 and 20). These are the ascogenous hyphae, and their ends swell up into the rounded asci.

From below the sterile cell, and possibly from below the ascogone also, there eventually grow out a few vegetative hyphae which are longer, thinner, and straighter than the ascogenous hyphae (Fig. 21), but they do not arise till a considerably later stage in the development is reached.

With regard to the behaviour of the nuclei the following facts have been observed. When the two hyphae forming the coil are still quite small each contains a single nucleus of considerable size, in which may usually be seen a nucleolus surrounded by a nuclear zone (Figs. 22 and 23).

At the time of conjugation, however, *both cells contain large numbers of nuclei*, which, at least in certain stages, have each a distinct nucleolus and nuclear zone (Figs. 27 and 28). These nuclei must apparently have arisen by division from the original single nucleus, and cases were noticed, which seem to be intermediate stages, in which there were several, but far fewer, nuclei (Figs. 24, 25, and 26). As the nuclei divide they become smaller in size, because the growth of the divided nuclei does not keep pace with division. When division is completed the nuclei grow until they attain their permanent size. The cells themselves are usually completely

filled with dense protoplasm, but in some stages, apparently the later stages, the protoplasm is vacuolated.

At the time of fusion a considerable portion of the wall between the two cells breaks down, and the nuclei and protoplasm become mingled. Doubtless a nuclear fusion now takes place, but this has not been determined with certainty (Figs. 27 and 28). The nuclei pass over from the sterile cell into the ascogone (Fig. 28), and later into the prolongation of the ascogone (Fig. 16). Evidently they ultimately pass into the ascogenous hyphae, for, within a mass of ripening asci are to be seen ascogenous hyphae containing many nuclei, while the conjugating cells, though retaining their original shape and size, and often showing very distinctly the point of fusion, are completely empty (Fig. 29 *a*, *b*, and *c*). The numbers of nuclei in the ascogenous hyphae are so large that it would seem as if nuclear division occurred in these hyphae, more especially if we consider the enormous numbers of asci produced from one pair of conjugating cells. The small ascogenous hyphae generally show one nucleus, with a nucleolus and nuclear zone, lying in the apex of the hypha, before it has begun to enlarge (Fig. 30 *a*). At a later stage when the apex is beginning to swell (Figs. 30 and 31) we find first two and then four nuclei which are smaller in size than the original nucleus, and apparently have no nuclear zone.

In the stage with two nuclei, the nuclei in some cases lie one above the other (Fig. 30 *b'*), and in other cases side by side (Fig. 30 *b''*), recalling the figures and descriptions given by Harper<sup>1</sup> and others of the development of the asci in the higher Ascomycetes. In *Gymnoascus* also the arrangement of the nuclei in two different planes may indicate that the nucleus has undergone two divisions.

At a still later stage the ascus becomes larger and almost spherical, while, instead of being filled with dense protoplasm, it has a large central vacuole, so that the protoplasm and the eight nuclei it now contains, come to lie on the wall,

<sup>1</sup> Sexual Reproduction in *Pyronema confluens* and the Morphology of the Ascocarp, *Annals of Botany*, Sept. 1900, vol. xiv, p. 363.



usually, but not always, near the apex (Fig. 31 *b*). The nuclei now increase in size, and the protoplasm also seems to become more abundant, so that the vacuole disappears and the developing spores fill the ascus (Fig. 31 *c*).

At different stages in their development the young spores behave very differently towards stains. At first they are oval in shape and, with the toluidine blue method (cp. p. 576), their nuclei stain a deep pink with the eosin. In some young spores there are two deeply staining bodies (Fig. 32 *a*); in others a single elongated body, which in some cases is thickened at each end (Fig. 32 *b*), and in other cases is thickened in the centre (Fig. 32 *c*). These observations suggest a nuclear fusion in the spores like that in the spores of Uredineae. At a later stage the spores become larger and rounder, and their contents stain more diffusely and not so deeply (Fig. 32 *e*). Finally the spores attain to their full size and become spherical. In this stage they remain colourless with the toluidine blue method (Fig. 32 *f*).

With the triple stain, on the other hand, the ripe spores stain more deeply than those which are still immature. They become strongly coloured by the safranin.

Amongst the ascogenous hyphae are a few thinner, slenderer hyphae, which often contain many small nuclei. These hyphae appear to be vegetative, and may either be those of the ordinary mycelium or those arising from the base of the coil.

Some of the ordinary vegetative hyphae become changed into the thick-walled hyphae described above (p. 576, Fig. 1), which envelop the asci.

## II. GYMNOASCUS SETOSUS.

The original material of this species also consisted of ripe ascospores and vegetative hyphae. The hyphae were so thick-walled, and coloured such a deep brown, that, except at their ends, they were opaque (Fig. 33). Their branching is peculiar, and both the main and the lateral branches end in sharp spines or bristles. They occurred in masses enclosing numbers of spindle-shaped colourless spores, either isolated or still

within the spherical asci. The hyphae do not anastomose, although they branch considerably.

The ascospores germinate by putting out one or two germ-tubes, which soon branch and form conidia by budding (Figs. 34-36). The end of a branch swells into an almost spherical knob, which is a conidium (Fig. 34). Immediately below it other conidia grow out. Branches, usually very short, and either spherical or oblong, arise, chiefly at the septa, but also at other points, and bud out at the top into conidia, which are formed in rapid succession (Figs. 34 and 35). These branches may be thrown off, and then frequently begin a yeast-like budding. The conidial form of this species resembles those of some of the higher Ascomycetes, e. g. *Nummularia*, *Xylaria polymorpha*, &c., as figured by Brefeld<sup>1</sup>. The conidia germinate at once, but their behaviour varies under different conditions. If many conidia are sown in a small hanging drop they begin to bud at once, and the buds fall off as they do in a yeast (Fig. 37). In this connexion it may be noted that Klöcker<sup>2</sup> states that yeast formation does not occur in the Gymnoascaceae, and draws conclusions therefrom in discussing the affinities of the Gymnoascaceae.

If a few conidia are sown in a drop a small mycelium is formed (Fig. 36). Similar differences occur in streak-cultures of conidia. If the spores be grown on 2 per cent. beerwort agar scarcely any mycelium is formed, and the culture soon consists of nothing but a dense white powdery mass of budding conidia (Fig. 38). But sometimes, apparently if the agar has become drier and more concentrated, a mycelium is first formed (Fig. 39), which, however, soon becomes smothered in the enormous quantities of conidia which it produces. On such a mycelium the conidia-bearing branches somewhat resemble a *Verticillium*, since they are produced, one or more together, chiefly at the 'nodes' of the hyphae, i. e. where the cross-walls occur (Fig. 35). Van Tieghem<sup>3</sup> has described a similar verticillate form in *G. ruber*, but Eidam<sup>4</sup> doubts the

<sup>1</sup> loc. cit. (2), Pl. IX.

<sup>2</sup> loc. cit.

<sup>3</sup> loc. cit. (1), p. 160.

<sup>4</sup> loc. cit. (e), p. 164.

accuracy of this statement, and thinks that van Tieghem may have had a true *Verticillium* in his cultures. The conidial form is always pure white.

This species has now (December, 1902) been kept in culture for a period of eighteen months, but so far it has never produced any other kind of spore but conidia, although it has been grown under various conditions on different media. The cultures are still being continued in the hope of obtaining ascospores. As will be noticed below, other species are known which have only produced conidial forms in artificial cultures.

### III. GYMNOASCUS CANDIDUS.

The original material again consisted of a mass of ripe asci and ascospores, and a few slender, colourless, almost unbranched hyphae, which had no connexion with the asci (Fig. 40). Hyphae, asci, and spores were all completely devoid of colour, and, to the naked eye, appeared as small, dense, and perfectly white masses.

The ascospores germinate readily, and ripe fructifications are formed in a few weeks.

On germination the minute ascospores swell considerably, and produce a mycelium of very thin and delicate hyphae. The young coils which precede the asci were first observed about three weeks after the sowing of the spores. Each coil consists of a central club-shaped hypha, the 'sterile cell' (to retain Baranetzky's terminology), surrounded by a thinner hypha, the 'ascogone,' which coils round it in a close, symmetrical spiral (Fig. 41).

The two hyphae may or may not arise from the same hypha; more usually they appear not to do so. Nor do they arise simultaneously, as in *G. Reessii*; for the 'sterile cell' is first formed, and the 'ascogone' afterwards grows round it, as far as the apex, and here, after each has been cut off by a transverse wall (Fig. 43), the two cells fuse with one another (Figs. 44, 45, and 46). The ascogone now segments (Figs. 46-48), and the greater number of the segments thus formed grow out into short thick hyphae (Figs. 46-48), which branch



repeatedly and form round the coil a dense mass of ascogenous hyphae (Fig. 49). Besides the ascogenous hyphae a few vegetative hyphae seem to grow out from the base of the coil, as in *G. Reessii* (Fig. 50).

The development of the asci and ascospores seems to take place exactly as in *G. Reessii*, except that the occurrence of a large vacuole is not so constant. But the exceeding minuteness of the asci and their spores makes the details of their development very difficult to follow, even with the highest available magnification. For the same reason the behaviour of the nuclei is difficult to observe. There is no doubt, however, that the conjugating cells about the time of fusion both contain numbers of small nuclei (Fig. 45), whereas in the youngest stage, as in *G. Reessii*, there seems to be but one large nucleus in each cell (Fig. 43 *a*).

The young asci also appear at first each to have one large nucleus, with a nuclear zone, in the dilating end of the ascogenous hypha (Fig. 51 *a*). This evidently divides into two (Fig. 51 *b*), then into four, and finally into eight (Fig. 51 *c*), which are small after division, but increase in size when the divisions are all completed. Certain slender hyphae, filled at the apex with small nuclei, are apparently vegetative hyphae like those occurring in *G. Reessii* (Fig. 51 *e*). As is the case in *G. Reessii*, the remains of the empty coil may be seen within the mass of ripening asci (Fig. 52). Besides ascospores this species also produces abundant oidia. Each colony produces either oidia or ascospores, or both.

With the naked eye the ascogenous parts of the colonies are of a chalky whiteness and consistency, because the dense masses of minute asci cover up the small cushion of delicate hyphae which is first formed. In cultures grown from single ascospores each colony forms a white circular mass, a centimetre or more in diameter, which usually produces asci at the centre and oidia round the periphery (Figs. 53 and 54). The hyphae forming the oidia are usually erect and branching, and form masses which, to the naked eye, are somewhat flocculent.

As in *G. Reessii* and *G. setosus* the habit of the colonies

differs under different conditions. For example, oidia were sown in plates of beer-wort gelatine. The sowings were made from a pure culture, and yet two different kinds of colonies were formed—a dense kind and a loose kind. This difference was due simply to the fact that the dense colonies were submerged, while the loose form was growing on the surface of the medium.

Microscopic examination of the oidium-bearing hyphae shows that they consist of erect hyphae branching dichotomously with great regularity (Figs. 55–57). When more highly magnified the protoplasm in these branches is seen to be collecting into regular squarish masses, each containing a large vacuole (Fig. 55 *c*). Finally, walls appear between the masses of protoplasm, and the walls break up into oidia (Fig. 56 *a*), which are at first flat at the ends, but which later become rounded (Fig. 57). Each oidium (Fig. 57) is larger than an ascus. The oidia readily germinate and form cultures indistinguishable from those grown from ascospores<sup>1</sup>.

Amongst the vegetative hyphae of the oidium-bearing mycelium may often be seen thicker hyphae, which, however, bear branches of varying thickness (Fig. 58). Some of the thicker hyphae show the pyriform swellings (Fig. 59), the cyst-like ends to some hyphae, and the beaded appearance of other hyphae (Fig. 60), which are characteristic of the genus *Gymnoascus* and which have also been observed in other genera, e. g. in *Onygena equina*<sup>2</sup>.

Besides the erect hyphae oidia may occur on the ascus-bearing mycelium, between the layer of sexual coils and the vegetative hyphae imbedded in the nutritive medium, but lying on the surface between the medium and the ascogenous layer.

<sup>1</sup> The mycelium of another species of *Gymnoascus*, still under culture, behaves in a similar manner.

<sup>2</sup> Marshall Ward, *Onygena equina*, Willd., a horn-destroying fungus, Phil. Trans., series B, 175, vol. cxci, pp. 269–291, Pl. XXI, Figs. 11 and 12, Pl. XXII, Fig. 13 (1899).

THE VARIOUS KINDS OF REPRODUCTION OBSERVED IN  
THE GYMNOASCACEAE.

The occurrence of asexual spores has not been observed in all species of *Gymnoascus*. Some species, e. g. *G. Reessii*, seem to reproduce themselves exclusively by means of ascospores. On the other hand, there are species which, at least under certain conditions, produce nothing but asexual spores. As examples may be noted the case of *G. setosus* just described, for, though Eidam<sup>1</sup> succeeded in obtaining the young coil, his cultures did not produce any ascospores. Another case is that of a species cultivated by Matruchot and Dassonville<sup>2</sup>, who do not, however, give its name.

The majority of the Gymnoascaceae, however, produce in culture both sexual spores and also various kinds of asexual spores. Frequently these are of the type of chlamydospores, as, for example, in *G. uncinatus*<sup>3</sup>. In *G. setosus* (p. 582), and perhaps in *G. ruber*<sup>3</sup>, the conidia arise in a verticillate manner on erect subaërial hyphae. In *G. setosus* conidia may also arise by budding from a germinating conidium (p. 582).

In *G. candidus* (pp. 584, 585) the asexual spores are oidia, resulting from the breaking up into spores of subaërial hyphae, which may either lie horizontally upon the substratum, or, more usually, stand erect and branch copiously.

CONCLUSIONS.

The investigations just described leave no doubt as to the occurrence of a sexual process in the Gymnoascaceae, if not in every species, at least in *Gymnoascus Reessii* and in *G. candidus*. Such a process has not before been described, though it was assumed by Baranetzky<sup>4</sup>, who, however, expressly states that

<sup>1</sup> loc. cit. (2).

<sup>2</sup> (1) Sur le Champignon de l'Herpès (Trichophyton) et les formes voisines, et sur la classification des Ascomycètes. Bull. Soc. Myc. de France, tom. xv, p. 250 (1899).

<sup>3</sup> Eidam, loc. cit. (1), p. 298.

<sup>4</sup> loc. cit., pp. 148 and 156.



he saw no fusion between the two cells, so that 'fertilization' must take place by means of 'transfusion' through the wall between them.

Eidam<sup>1</sup> also takes a sexual process for granted in the species he cultivated, viz. *G. Reessii*, *G. uncinatus*, and in the closely allied genus *Ctenomyces*.

On the other hand, van Tieghem<sup>2</sup>, Zukal<sup>3</sup>, and Brefeld<sup>4</sup> emphatically deny the occurrence of any sexual process whatsoever. Van Tieghem, indeed, denies that sexuality occurs in any Ascomycete, on account of what he calls the 'monocarpous Ascomycetes,' i. e. Ascomycetes in which, according to him, the asci arise from a solitary original branch<sup>5</sup>. The cases where actual fusion has been seen he regards as examples of purely vegetative union, comparable to ordinary anastomosis.

Brefeld, according to whose observations the coils in *G. Reessii* are formed from a *single* branch, also, for this reason, considers that any idea of sexuality is quite out of the question. Some cases which he saw of coils made up of two hyphae, like those described by Baranetzky, he regards as pathological.

But undoubted cases of fertilization in which has been seen the union, not only of the conjugating cells, but in some cases of their nuclei also, have now been recorded amongst the Ascomycetes, e. g. in *Sphaerotheca Castagnei*<sup>6</sup> and *Pyronema confluens*<sup>7</sup> by Harper, and also in *Eremascus albus*<sup>8</sup> by Eidam,

<sup>1</sup> loc. cit. (1), p. 300.

<sup>2</sup> loc. cit. (1), p. 96.

<sup>3</sup> Ueber einige neue Pilzformen und über das Verhältniss der Gymnoascen zu den übrigen Ascomyceten: Berichte der Deutschen Bot. Gesellschaft, Bd. viii, p. 295 (1890).

(2) Sur le développement du fruit des *Chaetomium* et la prétendue sexualité des Ascomycètes. Ann. des Sci. Nat., 6<sup>e</sup> sér., vol. ii, p. 364 (1875).

<sup>4</sup> loc. cit. (1), p. 159.

<sup>5</sup> (3) Sur le développement du fruit des *Ascodesmis*, genre nouveau de l'ordre des Ascomycètes. Bull. de la Soc. Bot. de France, vol. xxiii, p. 271 (1876).

<sup>6</sup> Die Entwicklung des Peritheciums bei *Sphaerotheca Castagnei*: Ber. der Deut. Bot. Ges., Bd. xiii, p. 475 (1895).

<sup>7</sup> Sexual reproduction in *Pyronema confluens*, and the morphology of the Ascocarp. Annals of Botany, vol. xiv, p. 321 (1900).

<sup>8</sup> (3) Zur Kenntniss der Entwicklung bei den Ascomyceten. Cohn's Beiträge, vol. iii, p. 385 (1883).

and in *Monascus* by Barker<sup>1</sup>, though not in those forms which are most nearly related to *Gymnoascus*.

The affinities of the Gymnoascaceae have gradually become apparent, as our knowledge of the family has increased by the addition of new genera and species. The investigations which have been recorded above seem to throw some further light on this interesting question.

One of the forms most nearly allied to *Gymnoascus* is *Ctenomyces serratus*. *Ctenomyces serratus* was first described by Eidam<sup>2</sup>, and bears a most striking resemblance to *Gymnoascus candidus*; in fact, the description given by Eidam of the development of the coil and of the ascogenous hyphae and asci in *Ctenomyces* would serve equally well for *G. candidus*. Eidam, however, did not see any cell-fusion, or any nuclei in *Ctenomyces*. The only difference between *Ctenomyces* and *G. candidus* is that whereas the former (like most other species of *Gymnoascus* hitherto described) has hard, thick-walled hyphae round the asci, the mycelium of *Gymnoascus candidus* consists exclusively of extremely thin and delicate hyphae.

The resemblance between the two species extends to the asexual spores, but in *Ctenomyces* these are conidia, budded off laterally from the hyphae, while in *G. candidus* they are oidia.

Another closely allied species is *Eidamella spinosa*, a parasite growing on the skin of a dog. Matruchot and Dassonville<sup>3</sup>, who founded the genus, made pure cultures which produced asci. The original coil arises exactly as in *Ctenomyces* and in *Gymnoascus candidus* from two branches, which sometimes grow out from one hypha, sometimes from two. But occasionally an anomalous case occurs, in which a single branch coils round the hypha from which it sprang. It is interesting to note that this is what Eidam observed in *G. Reessii*, and what he also records as an occasional occurrence in *Ctenomyces*. *Eidamella* also produces chlamydospores. This species is particularly

<sup>1</sup> Morphology and Development of the Ascocarp in *Monascus*. Ann. of Bot., Jan. 1903.

<sup>2</sup> loc. cit. (1), p. 271.

<sup>3</sup> (2) *Eidamella spinosa*, Dermatophyte produisant des périthèces. Bull. de la Soc. Myc. de France, tom. xvii, p. 123 (1901).

interesting, as the authors point out, because it is the first dermatophyte which has produced asci under artificial culture.

The life-history of *Gymnoascus Reessii* shows affinities in other directions, some of which have already been pointed out by previous investigators. Attention has been drawn to the fact that, though the young coils in this species always consist of two cells which are at first identical, certain variations may occur later which seem to indicate affinities with other genera and species. For example, when the two cells are of the same size and shape at the time of conjugation, they exactly resemble the similar stage which Eidam has described and figured in *Eremascus albus*<sup>1</sup> (cp. Figs. 9-11 with Eidam's figures on his Pl. XIX).

*Eremascus* was originally placed by Eidam amongst the Gymnoascaceae, and was by him regarded as forming a link between the Mucorineae and the Ascomycetes.

In connexion with the possibility of a connexion between the Gymnoascaceae and Zygomycetaceae it is interesting to remember that the sexual reproductive organs described and figured by Eidam in *Basidiobolus ranarum*<sup>2</sup> originate exactly in the same way as in *Gymnoascus Reessii*, namely, by the outgrowth of two adjacent cells, close to the septum which divides them from one another, and that these two cells fuse together as in *Eremascus* and *Gymnoascus*.

Schröter, in Engler and Prantl<sup>3</sup>, however, places *Eremascus* amongst the Endomycetaceae, which, together with the Saccharomycetaceae, form the group of the Protoascineae.

If, on the other hand, the sterile cell in *Gymnoascus Reessii* grows more rapidly than the ascogone, the latter grows round the former in a manner suggesting *G. candidus*, *Ctenomyces*, and *Eidamella*.

Such a variation which, as it were, unites the type of *G. Reessii* and that of *G. candidus* also very closely agrees with the descrip-

<sup>1</sup> loc. cit. (3).

<sup>2</sup> (4) *Basidiobolus*: eine neue Gattung der Entomophthoraceen. Cohn's Beiträge, Band iv, Heft ii, p. 181 and Taf. xi (1887).

<sup>3</sup> loc. cit., p. 152.



tion and figures drawn by Eidam of the early stages in *Aspergillus* (*Sterigmatocytis*) *nidulans*<sup>1</sup>. The fate of the two hyphae was not determined with certainty, but asci were ultimately formed from the coil.

Another species of *Aspergillus*, e. g. *A. herbariorum* (Wiggers), of which figures are reproduced by Engler and Prantl<sup>2</sup>, does not resemble the Gymnoascaceae nearly so closely as *A. nidulans*. In view of recent work on the sexuality of the lower Ascomycetes it would seem worth while reinvestigating, by means of modern histological methods, the life-histories of *Aspergillus* and *Penicillium*.

The obvious resemblances between the early stages of the coil of *Penicillium* and that of *Gymnoascus Reessii* have been noticed by previous investigators, and have led to the families of the Aspergillaceae and the Gymnoascaceae being included, with others, amongst which may be mentioned the Onygenaceae, in the group of the Plectascineae<sup>3</sup>.

Previous to their discovery of *Eidamella*, Matruchot and Dassonville had drawn attention to the possibility of a relationship between the Gymnoascaceae and certain dermatophytes<sup>4</sup>, especially *Trichophyton*<sup>5</sup>, on account of the similarity in the asexual reproduction. The life-history of *Eidamella* confirmed their view, which now seems also to be strengthened by the likeness between *Gymnoascus candidus* and *Eidamella*. These authors place the Gymnoascaceae between the Endomycetaceae, on the one hand, and the Onygenaceae on the other, and give the following classification<sup>5</sup> :—

1. Endomycetées. *Endomyces*.
2. Gymnoascées. *Gymnoascus*, *Ctenomyces*, *Trichophyton*, *Achorion* (?), *Microsporium* (?), &c.
3. Onygénées. *Onygena*.

<sup>1</sup> loc. cit. (3), p. 406 et seq., Pl. XXI, Figs. 8-14.

<sup>2</sup> loc. cit., p. 301, Fig. 214.

<sup>3</sup> Engler und Prantl, loc. cit., p. 293.

<sup>4</sup> loc. cit. (1), p. 240. (3) Sur le *Ctenomyces serratus*, Eidam, comparé aux champignons des Teignes. Bull. Soc. Myc. de France, tom. xv, p. 305 (1899). (4) Sur une forme de reproduction d'ordre élevé chez les *Trichophyton*. Bull. Soc. Myc. de France, tom. xvi, p. 201 (1900).

<sup>5</sup> (1) p. 251.

Later they place *Eidamella* amongst the Gymnoasceae<sup>1</sup>, near to *Myxotrichum*.

With regard to *Endomyces decipiens*, no sexual organs have been found, but the life-history of *G. candidus* tends to confirm the views of Matruchot and Dassonville. In neither *G. candidus* nor *Endomyces decipiens* are there any thickened hyphae, but in both the asci are completely naked and borne on delicate colourless hyphae. In both the mycelium breaks up into oidia<sup>2</sup>. The life-history of *Endomyces* would probably repay reinvestigation, with a view to ascertaining the presence or absence of sexual organs before the production of asci. The chief difference between these two species is that in *Endomyces decipiens* each ascus contains only four ascospores, whereas in *Gymnoascus candidus* there are eight spores in each ascus.

Van Tieghem<sup>3</sup> also compares *Gymnoascus* with *Hypomyces* (*Endomyces*) on the one hand, and on the other with *Penicillium*.

Boudier<sup>4</sup>, as well as Matruchot and Dassonville, regards the Gymnoascaceae as having close affinities with *Onygena*. Indeed, he considers that the Gymnoascaceae do not differ essentially from the sessile species of *Onygena*.

Matruchot and Dassonville claim that Marshall Ward's recent work on *Onygena*<sup>5</sup> confirms their views as to the relation between the Gymnoascaceae and the Onygenaceae. Though no definite coil was seen by this author, the resemblances between the two families are very strong. In both the ascus formation is preceded by a coil, and the asci and ascospores develop in the same way. In both families there are chlamydo-spores; in both pyriform swellings and cyst-like swellings at the ends of the hyphae occur in the vegetative mycelium. But since definite sexual organs are unknown in *Onygena*, its exact systematic position is uncertain.

<sup>1</sup> loc. cit. (1), p. 128.

<sup>2</sup> loc. cit., p. 155, Fig. 135.

<sup>3</sup> loc. cit. (1), p. 161.

<sup>4</sup> Description de deux nouvelles espèces de *Gymnoascus* de France. Bull. Soc. Myc., tom. viii, p. 43 (1892).

<sup>5</sup> loc. cit.

A comparison of the habitats of the various genera included in the Gymnoascaceae and Onygenaceae is also very suggestive in considering their affinities. For example, many species of *Gymnoascus* live either on the excrements of animals or on various parts of dead or living animals. *G. ossicola* and *G. aurantiaca* have been found growing on old bones. Eidam found *G. Reessii* growing on the dead pupa of *Sphinx Gallii*. *G. umbrinus* has been found on a dead cockchafer, *G. candidus* on the feathers of owls, *G. setosus* on an old bee's nest and on an old wasp's nest, which probably both contained excrements; *G. reticulatus* was found on the decaying horn of a cow, and *G. myriosporus* on the surface of the claws of birds of prey, and also on the excrements of these birds; *Ctenomyces* grows on feathers, *Onygena* on horn; *Eidamella* was obtained from the skin of a live dog, and is, according to Matruchot and Dassonville, related to other dermatophytes, e. g. *Trichophyton*. Moreover, the genera and species included in the Endomycetaceae, the Gymnoascaceae, and the Onygenaceae fall into a series in which there is a gradually increasing complexity in the structure of the fructification.

In *Endomyces decipiens* the asci are naked and solitary, and are produced on the ends of branching hyphae and show a tendency towards aggregation.

In *Gymnoascus candidus* the asci, while still completely without investment, are aggregated together in dense masses, each mass being produced from a single pair of conjugating cells. In other species of *Gymnoascus*, in *Ctenomyces*, and in *Eidamella* the groups of asci are more or less enclosed in a loose investment of thick-walled, branching, and, in most cases, anastomosing hyphae.

In *Aspergillus* and *Penicillium* the still more compact groups of asci are each surrounded by thick-walled hyphae, which form a continuous wall of pseudo-parenchyma—the peridium. In *Onygena* also the asci are enclosed in a complete investment, which in some respects is more differentiated than that of the Aspergillaceae.

In comparing the sexual organs of the forms under con-



sideration *Endomyces* and *Onygena* must be omitted, because in them such organs are unknown. But in all the other species the asci are the product of ascogenous hyphae arising from two cells which in every case are in close contact with one another, and which in two species, *Gymnoascus candidus* and *Gymnoascus Reessii* have been seen to actually fuse. Thus the probability of a sexual process in the allied genera is increased.

Evidently, then, the normal origin of the reproductive organs in this series is by means of two cells arising as branches, either from the same hypha or from two adjacent hyphae. But anomalous cases occur, like those described by Eidam in *G. Reessii* (p. 572) and in *Ctenomyces* (p. 588), in which a single branch coils round the parent hypha. Still more abnormal cases, which are undoubtedly pathological, are the irregular coils like those seen by Eidam in *Ctenomyces* and by the present writer in a starved drop culture of *G. Reessii* (p. 577). Such coils never produce asci, but soon degenerate.

It seems, therefore, as if this series of forms was natural, and based, not upon mere resemblances, but upon real affinities.

DESCRIPTION OF FIGURES IN PLATES  
XXVII AND XXVIII.

Illustrating Miss Dale's paper on the Gymnoascaceae.

Figs. 1-32. *Gymnoascus Reessii.*

Fig. 1 *a.* Part of the original material, consisting of hard thick-walled hyphae and loose ascospores. (2.F.)

Fig. 1 *b.* The spores more highly magnified. (4.F.)

Fig. 2 *a-d.* Germinating ascospore.

Fig. 3. Photograph of young colonies growing on a dry substratum in a culture plate.

Fig. 4. Photograph of similar colonies on a wet substratum.

Fig. 5. Photograph of older colonies in which the upper part of the mycelium grown on a wet substratum is becoming flocculent.

Fig. 6. Drawing of a mycelium on a wet substratum.

Fig. 7. An older stage of the same, in which the aërial hyphae are separating from one another.

Fig. 8. Still older stage of the same.

Fig. 9. Early stage in the formation of the sexual organs.

Fig. 10. The sexual organs more twisted round one another.

Figs. 11 and 12. Surface views of conjugating sexual cells. In 11 the two cells are of the same shape and size, in 12 one is larger; but both are coiled.

Fig. 13. A similar stage where one cell is much straighter than the other.

Fig. 14. A later stage of a form like that in Fig. 13. *a*, the outgrowth of the 'ascogone.'

Fig. 15. Two coiled cells after conjugation, showing the outgrowth *a*.

Fig. 16. Section of a similar stage, showing nuclei.

Fig. 17. Section of the segmented outgrowth round the end of the 'sterile cell.'

Fig. 18. The segments of the outgrowth forming branches which are the ascogenous hyphae.

Fig. 19. Surface view of segmented and branching outgrowth, *a*, vegetative hyphae.

Fig. 20. Group of ascogenous hyphae produced from a pair of sexual cells.

Fig. 21. Section showing vegetative hyphae springing from the base of the sexual organs.

Fig. 22. Section of young sexual cells, each containing a single nucleus.

Fig. 23. Later stage, after nuclear division and the formation of a dividing wall below the 'sterile cell.' The nuclei have increased in size, and show a distinct nucleolus and nuclear zone.

Fig. 24. A later stage in which the nuclei have undergone division.

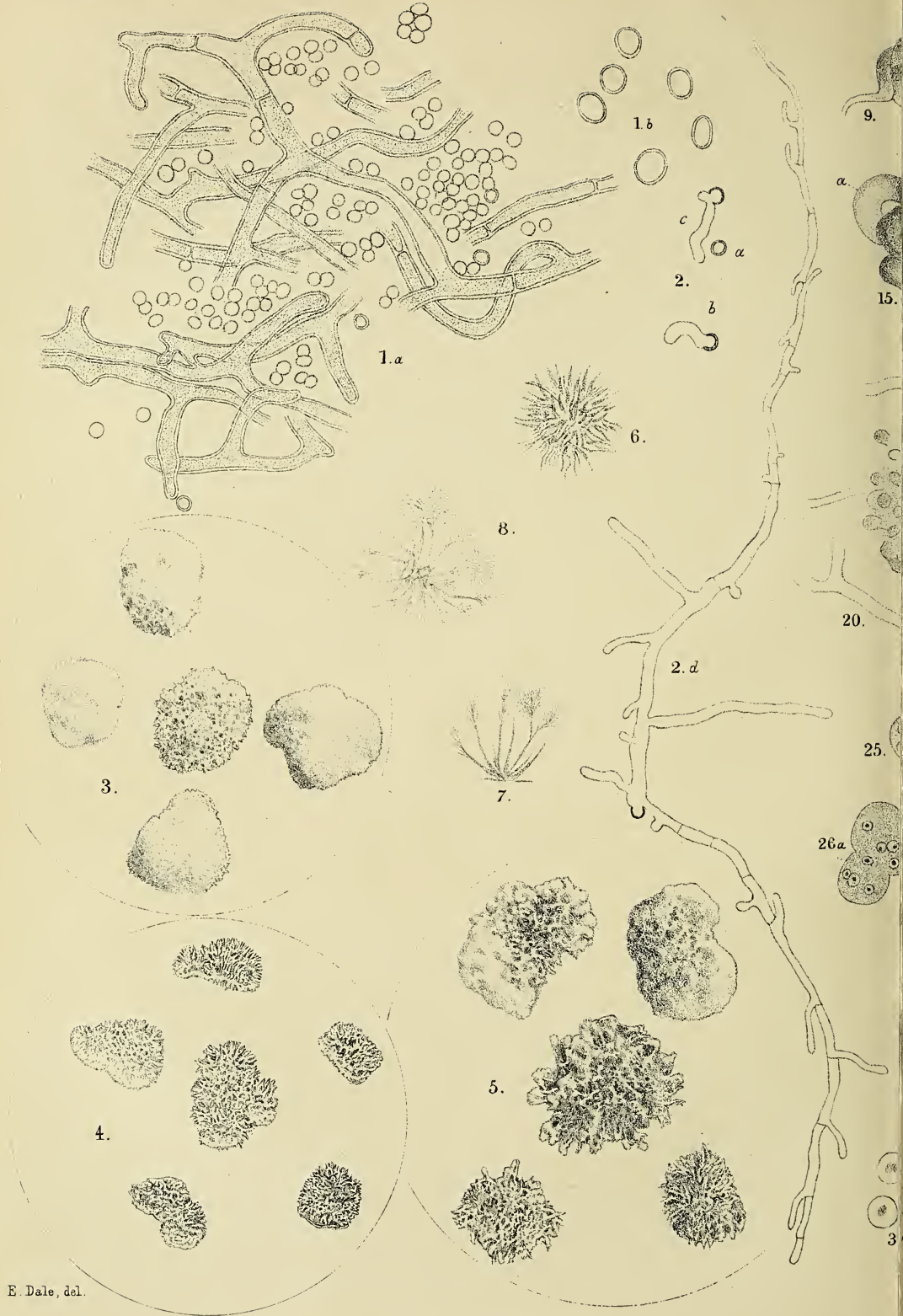
Fig. 25. A still later stage in which the nuclei are more numerous and smaller.

Fig. 26 *a, b, c.* Conjugating sexual cells in transverse section.

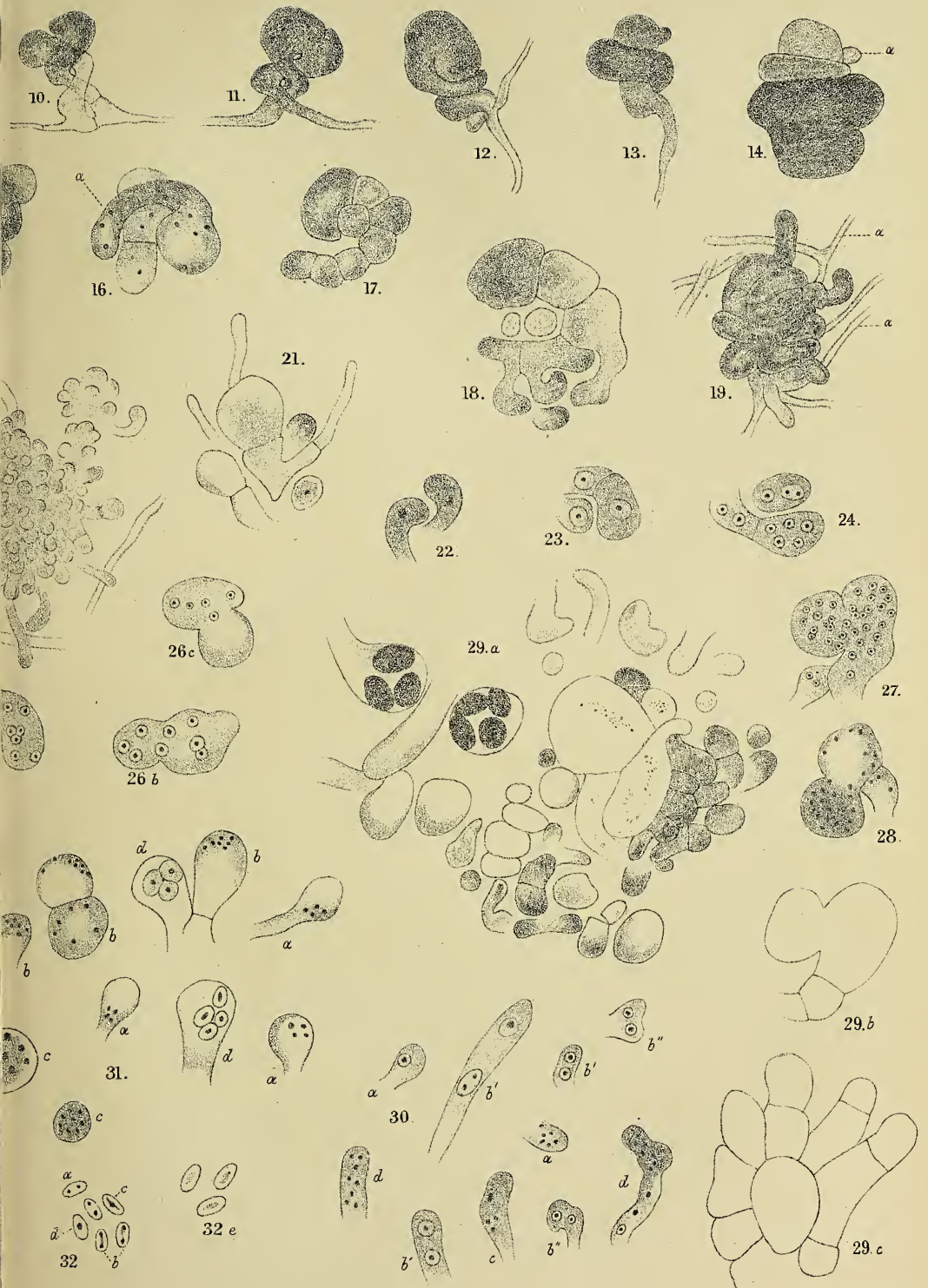
Fig. 27. The same in longitudinal section, showing many small nuclei.





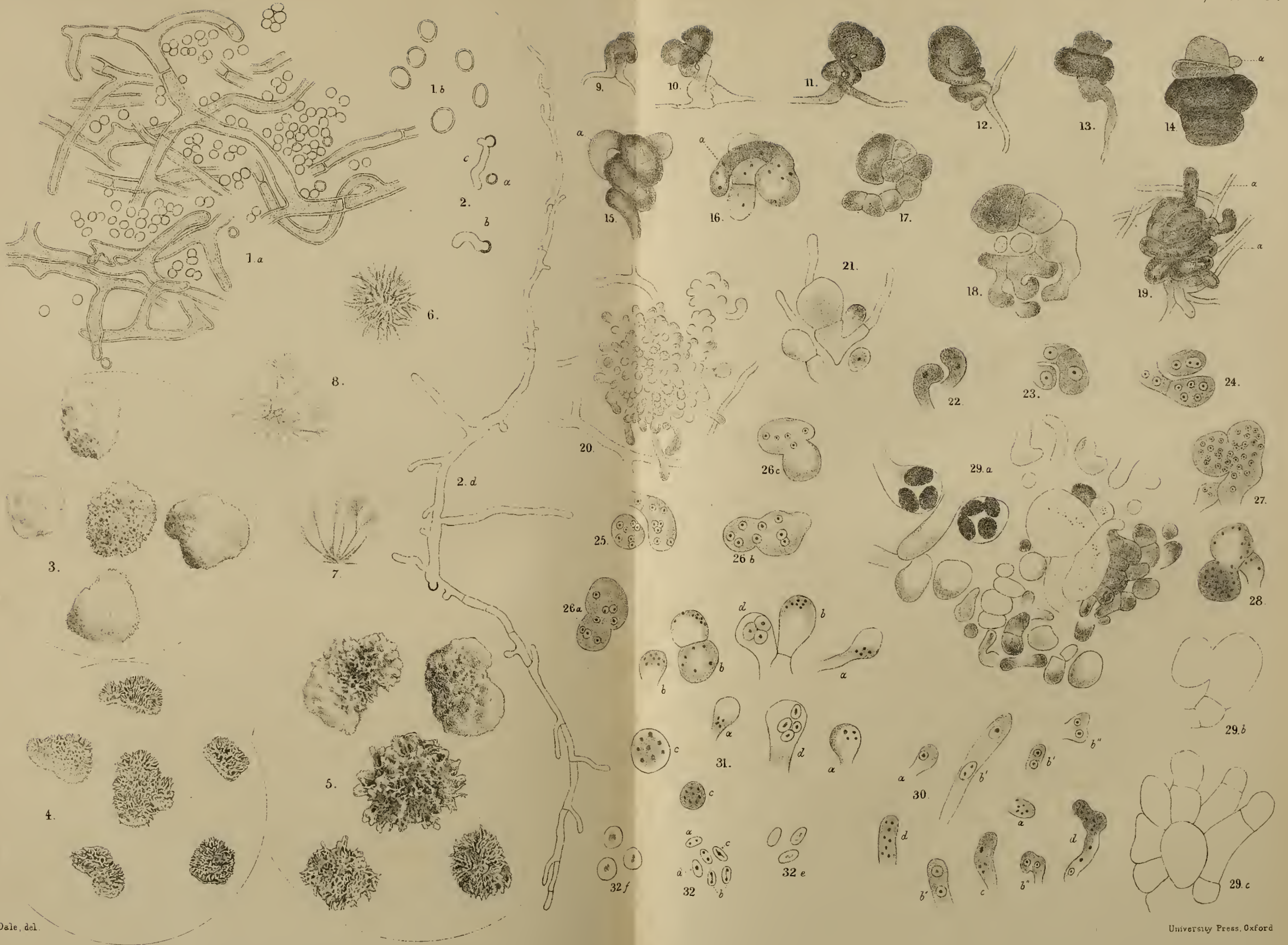


E. Dale, del.







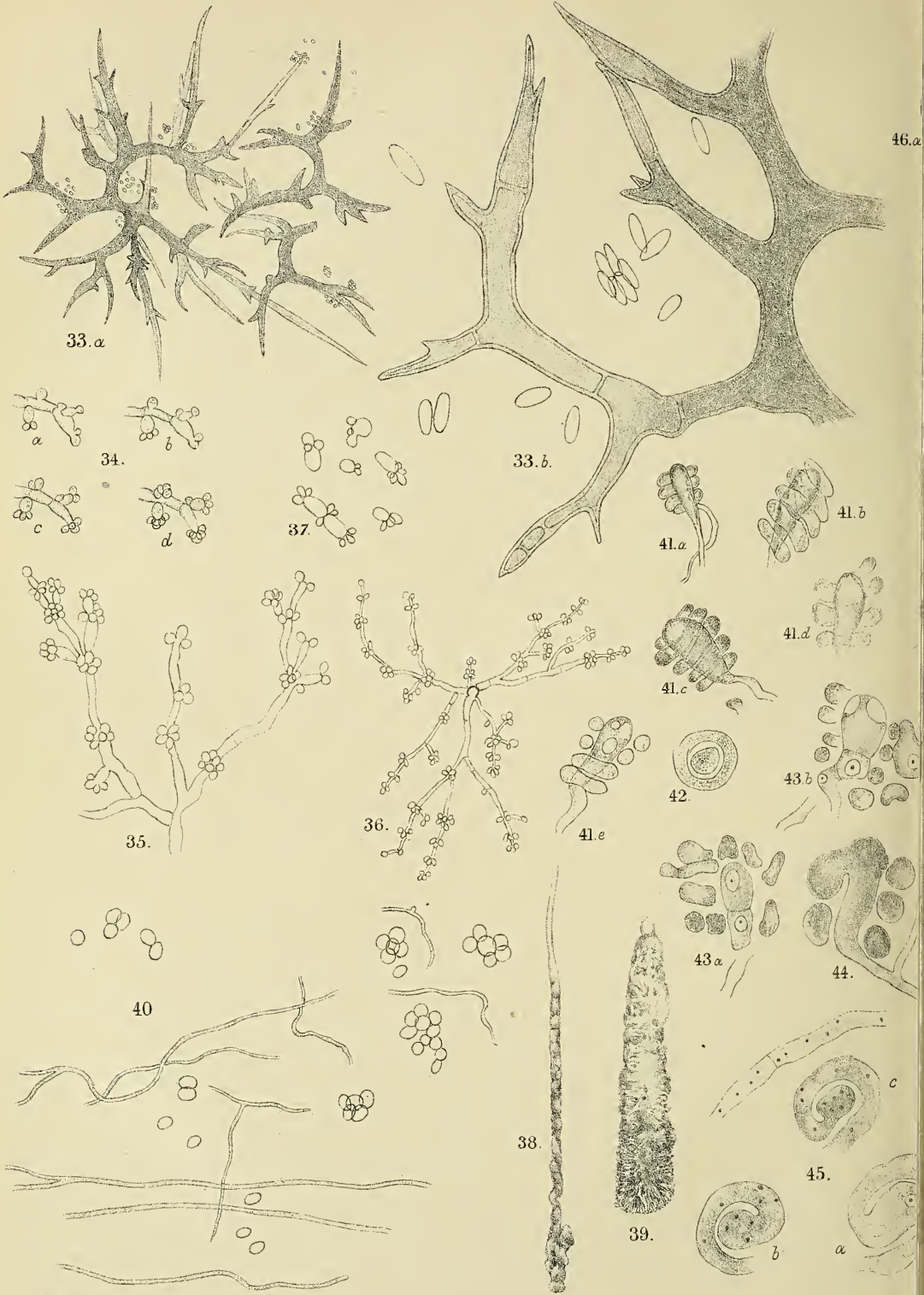


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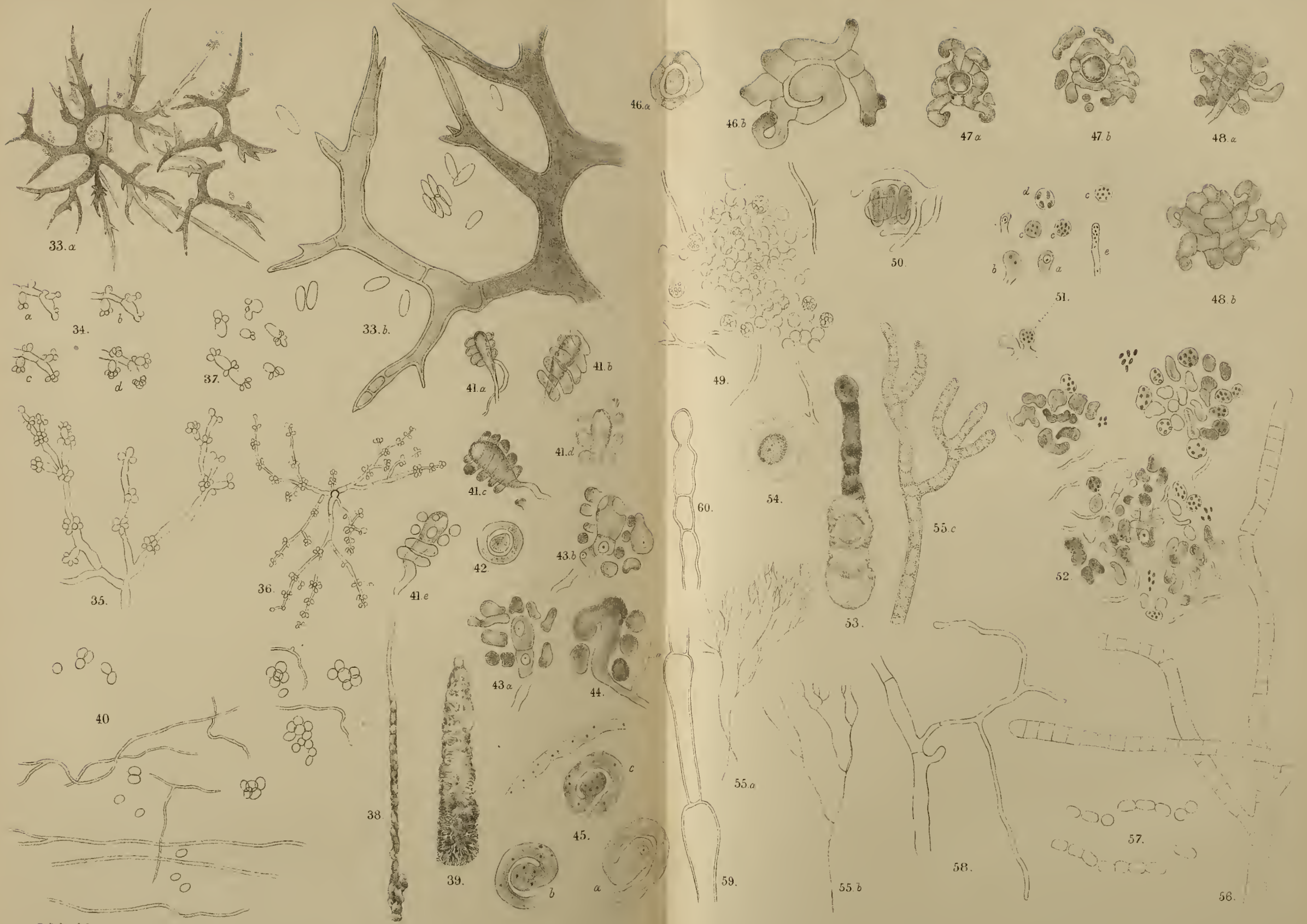


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Fig. 28. Conjugating cells, showing the passage of nuclei from the 'sterile cell' into the 'ascogone.'

Fig. 29 *a, b, c*. Sections of the old sexual cells as they occur in the centre of the ascocarps after their contents have passed into the ascogenous hyphae. 29 *a* shows ascogenous hyphae, vegetative hyphae, and developing asci. 29 *c* shows the segmented outgrowth of the ascogone with some of its branches.

Fig. 30 *a-d*. *Development of asci*. *a*. Young ascus with a single large nucleus. *b*. Older ascus with the nucleus divided into two. The nuclei sometimes lie in one plane, *b'*, sometimes in another, *b''*. *c*. Stage with four nuclei. *d*. Stage with eight or more nuclei.

Fig. 31 *a-d*. *Development of ascospores*. *a*. Stage with four nuclei and a large vacuole. *b*. Stage with eight nuclei and a large vacuole. *c*. The eight nuclei enlarged in size, and surrounded by so much protoplasm that the vacuole has almost disappeared. *d*. The young spores surrounded by their walls.

Fig. 32 *a-f*. *Ascospores*. *a*. Ascospore with two deeply staining bodies, *b*, the two bodies united by a stained protoplasmic strand. *c*. Spore with a densely stained central body with stained protoplasmic strands at each end of it. *d*. Spore with deeply stained central body. *e*. Larger spores diffusely stained. *f*. Mature spores.

Figs. 33-39. *Gymnoascus setosus*.

Fig. 33 *a*. Part of the original material showing thickened spiny hyphae and loose ascospores (2.D). 33 *b*. Part of the same more highly magnified. (4.F.)

Fig. 34. Formation of conidia. (4.F.)

Fig. 35. Conidial branches. (4.F.)

Fig. 36. Conidium producing a small mycelium bearing other conidia.

Fig. 37. Conidia budding. (4.F.)

Fig. 38. Streak culture consisting almost exclusively of masses of conidia.

Fig. 39. Streak culture consisting of a mycelium bearing conidia.

Figs. 40-60. *Gymnoascus candidus*.

Fig. 40. Part of the original material showing conidia and vegetative hyphae.

Fig. 41 *a-c*. Young stages of the young coil, consisting of a thick straight cell surrounded by a thin coiled hypha. Longitudinal sections or surface view.

Fig. 42. The same in transverse section.

Fig. 43 *a* and *b*. Longitudinal section of an older stage showing the central cell cut off by a transverse wall.

Fig. 44. Conjugating cells in longitudinal section. *a*. Vegetative hyphae.

Fig. 45. Conjugating cells in transverse section.

Fig. 46 *a*. Central cell surrounded by the ascogone divided into segments.

Fig. 46 *b*. Conjugating cells with the ascogone segmented and branching.

Fig. 47 *a, b*. Transverse section of central cell surrounded by segmented and branching ascogone.

Fig. 48 *a*. Longitudinal section of central cell surrounded by the segmented and branching ascogone.

Fig. 48 *b*. The same in surface view.

Fig. 49. Group of young asci developed from a pair of conjugating cells.

Fig. 50. Young sexual coil showing origin of vegetative hyphae.

Fig. 51 *a-e*. Development of asci.



Fig. 52. Group of developing asci.

Fig. 53. Photograph of a streak culture on beer-wort agar.

Fig. 54. Sketch of a colony bearing asexual spores round the circumference, and ascospores in the centre.

Fig. 55. A branch in which the protoplasm is dividing into masses.

Fig. 55 *a*. Part of a mycelium about to break up into oidia. 55 *b*. Part of the same more highly magnified.

Fig. 56. A branch breaking up into oidia.

Fig. 57. Mature oidia.

Figs. 58, 59, 60. Parts of the old vegetative mycelium.

(Figs. 9-32 and 41-52 were drawn with the camera lucida, the lenses used being Zeiss 1.5 oil immersion objective and no. 4 eye-piece.)

## Proteolytic Enzymes in Plants (II).

BY

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IN the January number of the present volume (1) I published some observations tending to show that proteolytic enzymes are of very general occurrence in plants. Whilst it had previously been implicitly assumed by physiologists that this was probably the case, the first experimental demonstration of the fact was, I believed, that contained in my paper. It turns out, however, that I was mistaken. My attention has since been directed to a paper by Buscalioni and Fermi (2), published in 1898, which somewhat anticipates my results: but though our conclusions are concordant on the whole, our methods were widely different. The method of Buscalioni and Fermi is an adaptation of the gelatine-culture of Bacteria. A layer of gelatine, with carbolic acid (.5-1 %) as the antiseptic, covers the floor of a Petri-dish, and upon this are placed the objects (seeds, portions of leaves, &c.) whose proteolytic action is to be determined; the test being, of course, the liquefaction of the gelatine. By this simple method the authors were able to detect more or less marked proteolytic activity in many Fungi, but by no means in all those tried; in some Algae (*Codium tomentosum*, *Padina Pavonia*, *Chara* sp., *Dictyota dichotoma*, *Ceramium* sp.); and in some Lichens: but the experiments with a Moss (*Funaria hygrometrica*), a Liverwort (*Lunularia vul-*

garis), with *Equisetum* sp. (rhizome), and with the leaves and rhizomes of various Ferns, all gave negative results.

Turning to the Phanerogams, the authors give first their results with laticiferous and resinous plants, and these are rather conflicting. They found no digestive action in the liquids of the various Fumariaceae (*Corydalis lutea*), Papaveraceae (*Papaver somniferum*, *P. Rhoas*, *Argemone mexicana*), and Compositae (*Crepis setosa*, *Sonchus tenerrimus*, *Taraxacum officinale*, *Lactuca sativa*) that they investigated. On the other hand, positive results were obtained with all the Urticales tested, viz. *Ficus Carica* and *F. elastica*, *Morus alba* and *tatarica*, *Broussonetia papyrifera*, and *Maclura aurantiaca*. In the remaining orders, some species were, whilst others were not, found capable of liquefying the gelatine; for instance, in the Euphorbiaceae, *Euphorbia Lathyris*, *E. Tirucalli*, *E. canariensis*, *E. balsamifera*, *E. coerulescens*, *E. grandidens*, and *Poinsettia pulcherrima* were active, whilst *Euphorbia tigridis* and *dulcis*, *Homalanthus populifolius*, and species of *Croton* were not: similarly in the Convolvulaceae, *Convolvulus sylvaticus* and *Calonyction (Ipomoea) macrantholeucum* were active, but not *Convolvulus arvensis* and species of *Ipomoea*: in the Asclepiadaceae, *Tweedia neerifolia* and *Asclepias curassavica* were found to be active, but not *Hoya carnosa*: in the Apocynaceae, *Tanghinia venenifera* and *Plumeria alba* were active, but not *Vinca minor*, *Acokanthera spectabilis*, nor *Echites flavescens*. It is interesting to note that the resin of *Pinus halepensis* showed some activity, if only weak, as did also the secretion of *Nelumbium speciosum*.

Of juices expressed from the plant, but few were active, namely those obtained from the young leaves of *Agave mexicana* and *A. americana*, from the young stems of *Phytolacca dioica*, from the stems of *Anagallis arvensis*, from the apices of the shoots of *Glycine sinensis*. Amongst the considerable number of inactive juices were those obtained from old leaves of *Agave mexicana*, and from adult branches of *Phytolacca dioica*; hence it would appear that young tissues are more likely than old ones to contain the protease.



The action of sections of stems and leaves was next investigated: and here again the number of positive results is much smaller than that of negative. Out of a list including about fifty species, only a few were markedly active; namely, sections of the leaf of *Dyckia princeps*, of young shoots of *Phytolacca dioica*, of *P. abyssinica*, and of *Portulaca oleracea*. In the case of *Phytolacca abyssinica*, it is specially noted that sections of young tissues acted much more powerfully than those of older parts.

In the case of roots, those which proved to be active were about equal in number (28) to those that failed to act, though in many cases the activity was slight. The most active roots were those of *Amorphophallus Rivieri*, of *Aspidistra elatior*, and of an undetermined Bromeliad. The authors contrast the more general distribution of the enzyme in the roots with its more restricted distribution in the green parts, where its presence seems to be especially associated with rapid growth. At the same time they find reason for doubting if the penetration of the tissues of the parent member by endogenously developing roots is due in any degree to the action of the proteolytic enzyme; in fact they assert that the 'poche digestive' of van Tieghem has no significance so far as the solution of proteids is concerned. In this connexion they mention that their researches were carried on in the month of July, when conditions were most favourable for ferment action.

The number of bulbs, tubers, and tuberous roots examined was but small, only twelve, and the positive and negative results were equally divided. The tubers of *Tamus communis* and of *Dioscorea bulbifera*, as also the tubercular roots (containing *Anabaena*) of *Cycas revoluta* were found to be most active, whilst the root-tubercles of the Leguminosae acted but feebly. The bulbs examined were those of *Allium sativum*, *Cepa*, and *Porrum*, but they were not found to be active; nor were the tuberous roots of *Beta* and of *Dahlia*. From these facts the conclusion, which seems to me to be hardly justified by the facts, is drawn that of these organs those that are

modified roots are more generally active than those that are modified shoots: for of the three cases in which vigorous liquefaction was observed, one only (*Cycas*) is a true root, whilst the organs of the other two are of cauline origin; this is certainly true of the tuber of *Tamus communis*, and I believe it is also true of *Dioscorea bulbifera*.

Next come the experiments with flowers and fruits, of which about sixty are recorded. Of the various parts of the flower, the stamens and the pollen proved to be by far the most active. Only three experiments were made with pollen (*Hedychium maximum*, *Hibiscus speciosus*, *Cucurbita maxima*), and in all three liquefaction was marked. A considerable number of fruits was tested, among others the Grape, the Orange (epicarp), the Lemon (unripe), the Red Currant, the Peach, the Apricot, the Cherry, and the Strawberry, but with invariably negative result.

These are followed by the experiments with seeds. A few unripe seeds were investigated, and of these only a small number gave positive results, one of them being *Phaseolus multiflorus*. Among a number (22) of ripe seeds, those of *Sorghum cernuum*, *Cannabis sativa*, *Linum usitatissimum* (especially the seed-coat), and *Anagallis arvensis*, were found to be active. Contrary to what might have been anticipated, the authors found that many germinating seeds, whether albuminous or exalbuminous, were quite inactive.

Some observations were also made on parasitic Phanerogams. The presence of a protease was indicated only in the haustoria of *Orobanche Hederae* and of *Cuscuta*, the other parts of these plants apparently containing none of it: nor was any trace of it detected in *Viscum album* or in *Loranthus europaeus*.

Finally, attention was directed to 'insectivorous plants.' The results obtained with *Drosera* were sometimes positive, sometimes negative. The investigation of *Nepenthes* was effected by placing pieces of the pitcher upon the gelatine, some having the inner and some the outer surface in contact with it: in the former case the gelatine was liquefied, but not

in the latter. The liquefying action of both *Utricularia* and *Aldrovanda* was but slight, as was also that of *Sarracenia purpurea*.

The memoir concludes with some general considerations as to the action of heat and light upon the enzyme, and as to the influence of the reaction of the medium upon its activity. With regard to the latter point, the general conclusion arrived at is that in the large majority of cases the presence of acid increases the activity of the enzyme, the presence of alkali diminishes it. The acids employed were chiefly organic, the citric, tartaric, and oxalic, in 1% solutions: in a few instances 1% HCl was used, and was found to promote liquefaction by *Ficus* and *Phytolacca abyssinica*, but more frequently its effect was unfavourable. In only one case, that of *Tuber aestivum*, was liquefaction limited to an alkaline medium (3%  $\text{Na}_2\text{CO}_3$ ). In certain others, however, such as the style and stigma of *Hibiscus speciosus*, the latex of *Ficus Carica*, and the unripe seeds of *Phaseolus multiflorus*, experiments of 24 hours' duration in the alkaline medium showed vigorous liquefaction. It is not impossible that these results may have been due to Bacteria; the authors themselves do not seem to attach importance to them.

I have thought it necessary to give this rather full account of the researches of Buscalioni and Fermi, because their work is not, I believe, as well known as it deserves to be, at least among English botanists; and also because a certain amount of detail is necessary for the discussion of the relation of their results to those that I have obtained by an altogether different method. I am glad to find that our conclusions are in agreement so far as general principles are concerned. The demonstration of the wide distribution of a proteolytic enzyme in the plant-body, is the outcome of their experiments as of my own. There is, not unnaturally, some divergence in matters of detail. For instance, they found such laticiferous Composites as the Lettuce and the Dandelion to be inactive, whereas I found them to be active, and I have since found the leaves of the Endive to be active. The same divergence



exists with regard to the Beet-root, and to the epicarp of the Orange. These divergences probably depend to some extent upon seasonal differences in the material examined, upon the higher temperature which I employed, and perhaps to an even greater extent upon the antiseptics used in the different experiments. Buscalioni and Fermi used exclusively carbolic acid; whereas I have never done so, but have used chiefly hydrocyanic acid or chloroform-water. In subsequent pages of this paper, I propose to consider the relation of various antiseptics to proteid-digestion in some detail.

Further, we are in agreement in the general conclusion that the vegetable proteases are most active in an acid medium. But as regards the products formed in digestion we necessarily part company: for it was not possible by the gelatine-method to obtain the information afforded by the tryptophane-method. Buscalioni and Fermi mention, indeed, that in certain cases they obtained the biuret-reaction, indicating the presence of albumoses or peptones, in the liquefied gelatine, but they did not attempt to pursue the subject further. The advantage of the tryptophane-method adopted by me, is that it throws light upon this fundamental question, and that any kind of proteid matter can be subjected to experiment. Whilst the gelatine-experiments of Buscalioni and Fermi were the first to indicate the wide distribution of proteases in plants, my tryptophane-experiments demonstrated that these widely-diffused substances are completely proteolytic in action, so far as they have been investigated.

#### PROTEASES AND ANTISEPTICS.

I have already suggested that such divergences as exist between the observations of Buscalioni and Fermi and my own are probably due, at any rate to some extent, to the fact that we respectively made use of different antiseptics. This suggestion is based on results that I have obtained tending to show that the same protease is affected differently by different antiseptics, as also that different proteases are diversely affected by the same antiseptic. In the following paragraphs

I give an account of my experiments in this direction, so far as they have gone.

In March, 1902, I published in this periodical a paper (3) which dealt, among other topics, with the digestive properties of papain. I there adduced evidence to prove that this protease proteolyzes fibrin and Witte-peptone, and is more active in acid than in neutral or alkaline liquids, as indicated by the tryptophane-reaction. As regards its proteolytic action, my results confirmed those of Martin (4), who had found leucin and tyrosin among the products of digestion. After my MS. had left my hands, I received a paper on the subject by Mendel and Underhill (5), which contains observations apparently disproving the proteolytic activity of papain, and suggesting that it can only peptonize the higher proteids. This was followed, after an interval of several months, by a second paper (6), which, without adducing fresh experimental evidence, restates the conclusions of the previous paper, criticizing also the view, to which I have more than once given expression, that all known vegetable proteases decompose the proteid molecule into leucin, tyrosin, tryptophane, &c., that is, are completely proteolytic.

The facts upon which Mendel and Underhill rely, are that in over sixty trials made with four different samples of papain, and with casein, fibrin, coagulated egg-albumin, and boiled muscle-tissue as the material to be digested, they failed to detect leucin, tyrosin, or tryptophane. Only with fresh, unboiled muscle were these products obtained, a result that these authors attribute to the self-digestion (autolysis) of the tissue. In all the experiments, sodium fluoride (NaF 1%) was the antiseptic employed. On this evidence they conclude that papain is an enzyme differing from both pepsin and trypsin. 'While the products of the papain digestion of proteids resemble quite closely those of pepsin, . . . the enzyme differs from animal pepsin in that it acts readily in both neutral and alkaline media. On the other hand, although papain is comparable with trypsin in exerting a solvent action in fluids of various reactions, the failure to form leucin, tyrosin,

or tryptophane in appreciable quantities—at least under conditions in which they are readily formed in large quantities by the other tryptic enzymes—places it in a class of its own for the present.'

In endeavouring to account for the wide divergence between their conclusions and my own, I was at first inclined to question the activity of the papain employed by Mendel and Underhill; but the numerical results which they give show conclusively that a considerable amount of the proteid supplied (as much sometimes as 70%) was dissolved, and the peptonization of casein was definitely proved. Hence there is evidence that the papain was active. This being so, the only remaining difference in the material of the two sets of experiments lay in the antiseptics employed, sodium fluoride in theirs, hydrocyanic acid in mine. I had already drawn attention to the fact that papain-digestion is promoted by HCN, and I thought it not improbable that this might prove to be an important factor in the problem. I accordingly instituted the following comparative experiments, in which NaF and HCN were the respective antiseptics, with results that fully realized my anticipation.

In the first instance I made use of Witte-peptone as the digestible material, and sodium fluoride (NaF), hydrocyanic acid (HCN), and chloroform-water as the antiseptics, the solutions being neutral, acid, or alkaline. The result proved that the proteolysis, as indicated by the tryptophane-reaction, was much more marked in the acid liquid containing HCN than in any of the others: it was less marked in the chloroform-water liquids, and scarcely perceptible in those containing NaF.

The details of the experiment were as follows: 5 grms. of papain ('purified papain,' Christy) were extracted for 3 hours with 250 cc. distilled water; the liquid was then filtered: the filtrate was a clear brownish liquid, distinctly acid, giving good biuret-reaction but no tryptophane-reaction. 10 grms. of Witte-peptone were similarly extracted with 250 cc. dist. water: on filtration a yellowish, neutral solution was obtained giving no tryptophane-reaction.



25 cc. of each of these solutions were then placed in each of 10 stoppered bottles: the contents of 3 of these were acidified by the addition to each of .25 gm. of citric acid (= 0.5%), the contents of other 3 made alkaline by the addition to each of 0.12 gm. of  $\text{Na}_2\text{CO}_3$  (= .25%), whilst to the remaining 3 neither acid nor alkali was added: the contents of the last 3 were slightly acid, but they are distinguished below as 'neutral.'

To an acid, an alkaline, and a neutral bottle, 0.5 gm. of NaF was added (= 1%): to a similar set, HCN was added to 0.2%: to a third set of 3, chloroform was added to 0.5%.

A control bottle contained 25 cc. of boiled papain-solution, with 25 cc. of Witte-peptone solution.

After 18 hours' digestion at 40°C., the tryptophane-reactions were as follows:—

	<i>HCN.</i>	<i>Chlorof.</i>	<i>NaF.</i>
<i>Acid</i>	very strong	marked	distinct
<i>Alkaline</i>	distinct	faint	faint
<i>Neutral</i>	distinct	faint	faint.

The control bottle gave a scarcely perceptible reaction.

These results indicate to how great an extent the activity of papain is affected by the antiseptic employed; and more especially that sodium fluoride exerts a strong inhibitory influence. Moreover, the advantage of an acid over an alkaline or a neutral medium is apparent.

In order to more definitely establish these conclusions, the experiment was repeated with fibrin instead of Witte-peptone: each bottle contained 1 gm. of fibrin, otherwise the contents were the same as in the preceding experiment, except that the percentage of  $\text{Na}_2\text{CO}_3$  in the alkaline bottles was increased to 0.5%. After eighteen hours' digestion, at 40°C., the results were:—

	<i>HCN.</i>	<i>Chlorof.</i>	<i>NaF.</i>
<i>Acid</i>	{ fibrin quite disintegrated marked tryptophane	scarcely attacked faint trypt.	distinctly attacked faint trypt.
<i>Alkaline</i>	{ fibrin quite disintegrated faint tryptophane	scarcely attacked doubtful trypt.	scarcely attacked doubtful trypt.
<i>Neutral</i>	{ fibrin nearly all gone distinct tryptophane	distinctly attacked faint trypt.	mostly disintegrated faint trypt.

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24 hours later, the results were :—

	<i>HCN.</i>	<i>Chlorof.</i>	<i>NaF.</i>
<i>Acid</i>	{ fibrin as before strong tryptophane	as before faint trypt.	mostly disintegrated faint trypt.
<i>Alkaline</i>	{ fibrin as before faint tryptophane	as before doubtful trypt.	as before doubtful trypt.
<i>Neutral</i>	{ fibrin quite disintegrated marked tryptophane	about half gone distinct trypt.	mostly disintegrated faint trypt.

The contents of all the bottles gave a good biuret-reaction at the close of the experiment. The alkaline bottles retained their reaction throughout.

The results with fibrin not only serve to confirm those with Witte-peptone, but they give valuable information as to the nature of the action not only of the antiseptics but also of the reaction of the medium. With regard to the first point, it appears that neither chloroform nor NaF inhibits the peptonizing action of papaïn, but that they both (especially NaF) impede further proteolysis with the formation of tryptophane. With regard to the second point, it is clear that the presence of acid is altogether favourable, whilst the presence of alkali is as distinctly unfavourable, impeding even peptonization in the bottles containing either chloroform or NaF.

These results suffice to make clear the reason of the failure to obtain the tryptophane-reaction in the experiments of Mendel and Underhill, and they establish the accuracy of my previous observations. They strikingly demonstrate the remarkably favourable effect of the presence of HCN upon the proteolytic activity of papaïn, as also the inhibitory effect of NaF.

In view of these results, I thought it worth while to make comparative experiments with a number of the antiseptics in general use for these purposes. In the first series, Witte-peptone was the digestible material; in the second, fibrin.

*Experiment with Witte-peptone.*

A clear solution (2 grms. in 200 cc. dist. water) of papaïn, and a clear solution of Witte-peptone (2 grms. in 200 cc. dist. water), were prepared: in the latter .1 gram. of citric acid was dissolved. 25 cc. of

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each solution were placed in each of 8 bottles, and to each (except one, the control) one of the following antiseptics was added: NaF, 1%; Salicylic acid, 1%; thymol, .5%; chloroform, .5%; toluol, .5%; formalin, .8%.

After 7 hours' digestion at 40° C., the tryptophane-reactions were:—

Distinct; HCN bottle.

Faint; thymol, toluol, control, chloroform.

None; Salicylic acid, NaF, formalin.

17 hours later, the reactions were:

Strong; HCN.

Distinct; thymol, toluol, control.

Faint; Salicylic acid, chloroform.

None; NaF, formalin.

A similar series of experiments, in which fibrin (2 grms.) replaced the Witte-peptone, and in which a stronger solution of papaïn (4 grms. extracted with 200 cc. dist. water) was used, gave confirmatory results.

*Experiment with Fibrin.*

The same antiseptics in the same strength as before. After 7 hours' digestion, the results were:—

HCN; fibrin completely disintegrated; distinct tryptophane reaction.

Salicylic acid; fibrin unaffected; no tryptophane.

Thymol; fibrin slightly attacked; no tryptophane.

NaF; fibrin partly disintegrated; no tryptophane.

Chloroform; fibrin unaffected; no tryptophane.

Toluol; fibrin gelatinous; no tryptophane.

Formalin; fibrin unaffected; no tryptophane.

Control; fibrin largely disintegrated; distinct tryptophane.

19 hours later, the results were essentially similar: the fibrin was rather more attacked in one or two cases, but it had not been completely disintegrated in any but the HCN and the control bottles, and these were still the only bottles the contents of which gave any tryptophane-reaction, strong in the HCN bottle, distinct in the control. The contents of all the bottles gave good biuret-reaction.

In these experiments the influence of HCN in promoting proteolysis by papaïn is very evident. In order to determine



that HCN does not exercise any direct proteolytic action, the following experiment was made:—

30 cc. of a papain solution like the above were placed in each of 2 bottles, that in one of the bottles having been previously boiled: to each bottle were added 1 gm. Witte-peptone, .25 gm. citric acid, and 20 cc. dist. water containing HCN so that the percentage of HCN in the mixture was 0.2. After 18 hours' digestion, the unboiled contents of the one bottle gave strong tryptophane-reaction, whilst the boiled contents of the other gave none.

I then proceeded, for purposes of comparison, to make a similar experiment with the juice of the Pine-apple.

50 cc. of expressed juice were placed in each of 7 bottles, with 1 gm. of moist fibrin: in 5 of the bottles the juice was of natural acidity, and to each of these antiseptics were added respectively as follows: 0.2 % HCN, 1 % NaF, 0.5 % thymol, 0.5 % toluol, 0.5 % chloroform: the juice in the sixth bottle was neutralized and then made distinctly alkaline by the gradual addition of 1.7 gm.  $\text{Na}_2\text{CO}_3$ , when 0.2 % HCN was added: no antiseptic was added to the seventh bottle.

After 24 hours' digestion at 40°C., the results were as follows. The fibrin had been quite or almost completely dissolved in all the bottles: least in the NaF and chloroform bottles. The tryptophane-reactions were:—very strong in NaF, thymol, toluol, and chloroform bottles; marked in the toluol bottle and in the alkaline HCN bottle; less marked in the acid HCN bottle and in the bottle without antiseptic.

These results are altogether contradictory to those obtained with papain: for in this case proteolysis was most active in the presence of NaF, and least active in the presence of HCN. It seems natural to infer that the difference in the behaviour of the two proteases with the two antiseptics indicates a fundamental diversity in their properties. It is generally agreed that bromelin is a more active protease than papain, though no digestion-experiments have been made with equivalent weights of the pure substances; and until that has been done, there is no real basis for comparison. There can, however, be little

doubt that the undiluted juice used in this series of experiments contained a much higher percentage of protease than did the extracts of papain in the previous series; and it seemed possible that the diverse results might be due rather to the relative amount of the proteases in the solutions than to a difference in their properties. With this possibility in view, I instituted the following experiments with papain-extracts of different strengths, and with diluted and undiluted Pine-apple juice, NaF and HCN being the antiseptics employed.

*Papain.*

50 cc. of 4 % watery extract were placed in each of two bottles, together with 0.2 gm. citric acid and 1 gm. of moist fibrin: to one bottle 0.5 gm. NaF (= 1%) was added, to the other 2.5 cc. of 4 % HCN (= 0.2 %).

Two exactly similar bottles were prepared in which, however, the strength of the papain-extract was 2 %.

After 18 hours' digestion at 40° C., the fibrin was completely dissolved in both the HCN bottles; only partially dissolved in the NaF bottles. The tryptophane-reaction was strong in the bottle containing the 4 % extract and HCN; distinct in the bottle containing the 2 % extract and HCN; faint in both the NaF bottles.

30 hours later, the fibrin was completely dissolved, except for a small residue, in all the bottles. The tryptophane-reaction was strong in both the HCN bottles; faint in both the NaF bottles.

*Bromelin.*

50 cc. of undiluted Pine-apple juice were placed in each of 2 bottles with 1 gm. moist fibrin: to the one 0.5 gm. NaF (= 1 %) was added, to the other 2.5 cc. 4 % HCN (0.2 %).

Two exactly similar bottles were prepared in which the juice had been diluted with an equal volume of distilled water.

After 18 hours' digestion, the fibrin was mainly dissolved in all the bottles. The tryptophane-reaction was strong in the bottle containing undiluted juice and NaF; marked in the bottle containing diluted juice and NaF; distinct in that containing undiluted juice and HCN; faint in that containing diluted juice and HCN.

30 hours later, the fibrin was dissolved in all the bottles. The tryptophane-reaction was very strong in the NaF bottle with undiluted

juice, strong in the NaF bottle with diluted juice, marked in both the HCN bottles.

From these experiments it is clear that the influence of such antiseptics as NaF and HCN on proteolysis depends, not upon the amount of the protease present, but upon the nature of the protease, probably upon its chemical constitution.

The general conclusion to be drawn from all these experiments with various antiseptics is that these substances exert a considerable influence, greater than is usually supposed, upon proteolytic processes. It is, I think, made clear that in investigating the action of any protease, it is necessary that experiments should be conducted with more than one antiseptic before any conclusion as to the properties of the enzyme is arrived at. I am also justified in reasserting that all vegetable proteases, so far as they have been investigated, are essentially proteolytic; and that no merely peptonizing protease has yet been discovered.

I may incidentally mention here an experiment upon the action of Pine-apple juice at the ordinary temperature of the laboratory instead of in the incubator: that is, at about 17° C. instead of 40° C. The results show that proteolysis is effected under these conditions, but more slowly than at the higher temperature.

50 cc. of Pine-apple juice were placed in each of two bottles, with 1 gm. moist fibrin; to the one 0.5 gm. of NaF (= 1%) was added, to the other 2.5 cc. of 4% HCN (= 0.2%).

After 19 hours' digestion the fibrin was quite disintegrated in both: the NaF bottle gave distinct tryptophane-reaction, the HCN bottle gave no reaction.

29 hours later, the NaF bottle gave strong tryptophane-reaction, the HCN bottle a distinct reaction.

#### DAHLIA VARIABILIS.

The tuberous roots of the Dahlia have long been the subject of investigation on account of their peculiar chemical contents. They have largely provided the material for the



study of inulin, though the discovery of the enzyme *inulase* was made by Green (1887) in the tubers of the Jerusalem Artichoke (*Helianthus tuberosus*). But the fact of more immediate interest in connexion with the subject of the present paper is that Leitgeb (7) found the roots, in a state of rest, to contain considerable quantities of asparagin and tyrosin as nitrogenous reserve-material. On this ground the Dahlia-roots seemed likely to be promising material for digestion-experiments, which I have accordingly made, together with some incidental observations on the presence of tyrosin.

The expressed juice of the tuberous roots immediately assumes a dark colour owing to the action of the oxidase which Bertrand (8) found to be present, and which he termed *tyrosinase*, upon the tyrosin in solution. On filtration, a brown, opalescent, distinctly acid liquid is obtained, which gives strong xanthoproteic reaction, strong Hofmann's reaction with Millon's reagent, and oxidase-reaction with guaiacum, but no biuret-reaction: it gives a tryptophane-reaction which is not easy to perceive on account of the brown colour of the liquid. On boiling the juice there is a considerable precipitate: the clear filtrate gives the same Hofmann's and xanthoproteic reactions as the unboiled liquid.

These reactions, especially the Hofmann's reaction with Millon's reagent, in which a brilliant pink colouration appears on heating, followed by the formation of a similarly coloured precipitate, indicate the presence of tyrosin in considerable quantity. More definite evidence is afforded by the application of Mörner's (9) test. As this reagent is not yet well known, I give its preparation. It is a mixture of 1 vol. of formalin (40%) with 45 vols. of distilled water, and 55 of concentrated sulphuric acid. Heated with tyrosin, a striking green colour is produced. I found that on adding some of this reagent to Dahlia-juice, the green colour was developed without heating; the effect of heating was to give rise to a brown colour, due probably to the action of the  $H_2SO_4$  on the inulin present.

Turning now to the question of the proteolytic activity of the juice, I may mention that Buscalioni and Fermi found the tuberous roots of the Dahlia to be proteolytically inactive, but this is not in accordance with my results. I made experiments (*a*) with the juice alone (autolysis); (*b*) with Witte-peptone added; (*c*) with fibrin added; in all cases there was distinct evidence of proteolysis. The material used was the root in the resting condition, and the experiments were carried on at intervals from January to March.

#### *Autolysis.*

40 cc. of slightly diluted expressed juice were placed in each of 4 bottles: to (1) nothing was added; to (2) HCN 0.2%; to (3) citric acid 0.5%; to (4) HCN 0.2%, and citric acid 0.5%.

After 21 hours' digestion at 40°C., the contents of (1) and (2) gave a distinct tryptophane-reaction, those of (3) and (4) a marked reaction. 30 hours later, (1) and (2) still gave the same reaction, whilst that of (3) was marked, and that of (4) had become strong.

#### *Proteolysis of Witte-peptone.*

In each of four bottles were placed 50 cc. of expressed juice diluted with equal vol. of dist. water, and 0.5 gm. Witte-peptone: the further additions to the bottles were precisely as in the preceding experiment.

After 4 hours' digestion at 40°C., the tryptophane-reaction was strong in the bottle containing citric acid, and in that to which neither citric acid nor HCN had been added; marked in the citric acid and HCN bottle; distinct in that to which HCN but no citric acid had been added.

19 hours later, the reactions were essentially the same.

#### *Fibrin.*

4 bottles were prepared precisely as those in the preceding experiment, except that 1 gm. moist fibrin was substituted for the Witte-peptone.

After 19 hours' digestion at 40°C., the fibrin had become shrivelled and stringy in all the bottles, and did not appear to have been at all dissolved. The tryptophane-reactions were:—distinct in the citric acid and HCN bottle, as also in the bottle with HCN but no citric

acid, and in the bottle to which neither citric acid nor HCN had been added; marked in the bottle with citric acid but without HCN.

48 hours later, the fibrin presented the same appearance, and the tryptophane-reactions were:—marked in all the bottles except the one containing HCN but no citric acid, where it remained distinct.

I have further succeeded in preparing a proteolytically active glycerin-extract from the roots. 100 grms. of the root, cut into small pieces, were macerated in strong alcohol for twenty-one hours, and then dried at room-temperature: the dried material, which weighed only 13 grms., was well triturated with 50 cc. glycerin, and left to stand for three days. The mass was then strained through muslin, yielding a turbid brownish extract, the activity of which was tested as follows:—

30 cc. of the glycerin-extract were mixed with 130 cc. chloroform-water, and 40 cc. of the mixture were placed in each of 4 bottles. To the liquid in No. 1, which was slightly acid, 0.2 gm. Witte-peptone was added: to No. 2, 0.2 gm. Witte-peptone, and 0.2 gm. citric acid (= 0.5%): to No. 3, 0.2 gm. Witte-peptone and 0.2 gm.  $\text{Na}_2\text{CO}_3$  (= 0.5%) so that the reaction was distinctly alkaline: to No. 4 nothing was added.

After 4 hours' digestion at 40° C., the contents of Nos. 1, 3, and 4 gave a faint tryptophane-reaction; those of No. 2, a distinct reaction. 19 hours later the tryptophane-reaction was distinct in No. 1, marked in No. 2, faint in Nos. 3 and 4.

From these experiments it is clear that the tuberous root of the Dahlia contains an enzyme which proteolyses the proteids of the root; that it also proteolyses Witte-peptone is shown by the rapid development of a more or less strong tryptophane-reaction when this material is presented to it. There is, however, no evidence that the protease attacks fibrin, for in no case did there appear to be any definite solution of it; the tryptophane-reactions given by the contents of the bottles in the fibrin-experiments were so nearly the same as those given by the bottles in the autolysis-experiments that they do not appear to have been to any extent due to the presence of the fibrin.



## HELIANTHUS TUBEROSUS.

I have already stated (1) that the tissue of the tuber of this plant proteolyses Witte-peptone. I have since ascertained that the expressed juice of the tuber proteolyses Witte-peptone, as also its own proteids.

In view of the presence of inulin in this tuber, I thought it worth while to determine whether or not the inulin were accompanied by tyrosin, as is the case in the tuberous root of the Dahlia. I found that there was no such storage of tyrosin in this plant.

The expressed juice is a brown, turbid, slightly acid liquid; it gives the oxidase-reaction with guaiacum, and strong xanthoproteic reaction. On boiling there is a dense precipitate; the clear filtrate gives faint tryptophane-reaction, no biuret, only a faint Millon's reaction, and none with Mörner's reagent for tyrosin, in striking contrast to the juice of the Dahlia-root.

## CRAMBE MARITIMA.

The etiolated shoots of the Sea-kale occurred to me as probably interesting material for investigation. The expressed juice is a yellow acid liquid, giving good peroxidase but no oxidase-reaction with guaiacum; it also gives weak xanthoproteic and Millon's reactions. A precipitate is formed on boiling; the filtrate gives no biuret, but faint tryptophane-reaction. Digestion-experiments showed that autolysis is feeble, but the proteolysis of Witte-peptone is active.

50 cc. of expressed juice, diluted with an equal vol. of dist. water, were placed in each of 4 bottles: to (1) only a little thymol was added; to (2) a little thymol and 0.5 grm. Witte-peptone; to (3) thymol, 0.5 grm. of Witte-peptone, and 0.25 grm. citric acid (= 0.5%); to (4) 0.5 grm. Witte-peptone, 0.25 grm. citric acid, and HCN to 0.2%.

After 19 hours' digestion at 40°C., (1) gave faint tryptophane-reaction; (2) a strong reaction; (3) and (4) a marked reaction.

The action of the juice upon fibrin was then investigated. Inasmuch as in the previous experiment the activity of the juice had been found to be greatest in the bottle to which no acid had been added, no acid was added in this case: but the contents of the bottles were very distinctly acid at the close of the experiment. The result indicates that the juice does not act upon fibrin.

40 cc. of expressed juice, diluted with an equal vol. of dist. water, were placed in each of 3 bottles, with some thymol: to (1) nothing further was added; to (2) 0.5 gm. of Witte-peptone; to (3) 1 gm. of moist fibrin.

After 29 hours' digestion at 40° C., (1) and (3) gave distinct tryptophane-reaction, (2) a strong reaction. The fibrin in (3) did not appear to have been attacked to any extent, so that the tryptophane-reaction was due to autolysis.

Inasmuch as neither the enzyme of the Sea-kale, nor that of the Dahlia acts upon fibrin, they are to be referred, like those of many other plants (see my previous paper, 1), to the erepsin-group of proteases.

#### BETULA ALBA.

I happened to have the opportunity of investigating the sap poured out by a 'bleeding' Birch-tree.

The sap is a clear, yellowish, neutral liquid: it gives the peroxidase- but not the oxidase-reaction with guaiacum, also faint xanthoproteic and Millon's reaction, no tryptophane or biuret-reaction, but strong sugar-reaction with Fehling's solution.

Digestion-experiments were made with and without added proteid (Witte-peptone and fibrin), the sap being acidified with citric acid or made alkaline with  $\text{Na}_2\text{CO}_3$ , also with or without the addition of a few drops of HCN solution as an antiseptic, but in no case was any tryptophane-reaction observed, even when digestion was prolonged to forty-eight hours. The sap apparently contains no protease.

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## NOTES.

**THE DOUBLE PITCHERS OF DISCHIDIA SHELFORDII, sp. nov.**—A previous paper contained an imperfect account, founded upon herbarium material, of the double pitchers of four species of *Dischidia*, viz. *D. complex* from Malacca, the Phillipine *D. pectenoides*, and two undescribed Bornean species <sup>1</sup>.

Mr. R. Shelford, M.A., Curator of the Sarawak Museum, has been so kind as to interest himself in the subject, and as a result of his endeavours complete herbarium material, as well as spirit specimens of a double-pitchered species from Kuching, have been received at Kew. These belong to a species not hitherto described, and are identical with Haviland's specimen from the Kuching Lake, bearing the number 2015 <sup>2</sup>. Upon these specimens is founded the description of the species which I have the pleasure of naming after Mr. Shelford, who has been the first to send to me the material which rendered a knowledge of the species possible.

*DISCHIDIA SHELFORDII*, sp. nov. *Planta* epiphyta, volubilis, glabra. *Folia* normalia pauca, opposita, breviter petiolata, late triangularia vel suborbiculare, basi truncata, apice rotundata vel breviter apiculata, crassiuscula, arcte nervata,  $\frac{1}{3}$ – $\frac{1}{2}$  in. long. *Ascidium* maturum brevissime petiolatum, videtur solitarium in nodo,  $1\frac{1}{2}$  poll. longum, 1 poll. latum,  $\frac{3}{4}$  poll. crassum; exterius late reniforme, colore lurido-purpureo suffusum, venis ramosis purpureis instructum (speciminibus in vini spiritu conservatis), apice invaginante introrsum et formante ascidium interius parvum. *Cymae* capituliformes, terminales in ramis axillaribus, 3–6-florae. *Flores* albidæ (?), pedicellis brevissimis glabris crassiusculis suffulti. *Calyx* alte 5-lobatus; lobi membranacei, oblongi, apice rotundati, carinati, glaberrimi, persistentes, circ.  $\frac{1}{16}$  poll. longi. *Corollae* tubus urceolatus, quinquangularis, glaber, circ. 1 lin. longus; lobi lanceolati, acuti, sub anthesin erecti, glabri, marginibus crassis,

<sup>1</sup> Pearson, Journ. Linn. Soc. Bot., xxxv, 1902; pp. 375–390, with Plate IX.

<sup>2</sup> Pearson, loc. cit., 376 (and footnote), 378, 379.

circ.  $\frac{1}{2}$  lin. longi. *Coronae* squamae, 5, angustae, tubo stamineo affixae, membranaceae, apice alte 2-fidea, lobis longiusculis recurvis. *Antherae* erectae. *Stigma* complanatum, obsolete 2-lobatum, vix ex antheris exsertum. *Folliculi* tenues, teretes, leves, acuminati,  $1\frac{1}{2}$ - $2\frac{1}{2}$  poll. longi. *Semina* pilis longis albidis sericeis coronata.

Borneo: Kuching, *Shelford*, near Kuching Lake, *Haviland* 2015.

Mr. Shelford states that his specimen is epiphytic on a tree which he believes to be a species of *Ficus*.

H. H. W. PEARSON.

**STUDIES IN THE MORPHOLOGY OF SPORE-PRODUCING MEMBERS. NO. V. GENERAL COMPARISONS, AND CONCLUSION**<sup>1</sup>.—This concluding Memoir contains a general discussion of the results acquired in the four previous parts of this series, and of their bearing on a theory of sterilization in the sporophyte. The attempt is made to build up the comparative morphology of the sporophyte from below, by the study of its simpler types; the higher and more specialized types are left out of account, except for occasional comparison. It is assumed for the purposes of the discussion that alternation of generations in the Archegoniatae was of the antithetic type, and that apogamy and apospory are abnormalities, not of primary origin.

After a brief allusion to facts of sterilization in the sporogonia of Bryophytes, the similar facts are summarized for the Pteridophytes. It has been found that examples of sterilization of potentially spore-genous cells are common also in vascular plants, while occasionally cells which are normally sterile may develop spores. Hence it is concluded that spore-production in the Archegoniate plants is not in all cases strictly limited to, or defined by, preordained formative cells, or cell-groups. A discussion of the archesporium follows, and though it is found that in all Pteridophyta the sporogenous tissue is ultimately referable to the segmentation of a superficial cell, or cells, still in them, and, indeed, in vascular plants at large, the segmentations which lead up to the formation of spore-mother-cells are not comparable in all cases; in fact, that there is no general law of

<sup>1</sup> Abstract of a paper read before the Royal Society on February 12, 1903, reprinted from the Proceedings.

segmentation underlying the existence of that cell or cells which a last analysis may mark out as the 'archesporium'; nor do these ultimate parent-cells give rise in all cases to cognate products. Therefore it is concluded that the general application of a definite term to those ultimate parent-cells which the analysis discloses has no scientific meaning, beyond the statement of the histogenic fact.

Further, it is shown that the tapetum is not a morphological constant, but varies both in occurrence and origin; that even the individuality of the sporangium is not always maintained. All that remains then as the fundamental conception of the sporangium in vascular plants is the spore-mother-cell, or cells, and the tissue which covers them in, for such cells are always produced internally. The definition of the sporangium may then be given thus: 'Wherever we find in vascular plants a single spore-mother-cell, or connected group of them, or their products, this with its protective tissues constitutes the essential of an individual sporangium.' From the point of view of a theory of sterilization such sporangia may, at least in the simplest cases, be regarded as islands of fertile tissue which have retained their spore-producing character, while the surrounding tissues have been diverted to other uses. It will be seen later how far this view will have to be modified in the more complex cases.

In a second section of the Memoir the variations in number of sporangia in vascular plants are discussed; the methods of variation may be tabulated as follows, under the heads of progressive increase and decrease:—

#### I. *Increase in Number of Sporangia.*

- (a) By septation, with or without rounding off of the individual sporangia.
- (b) By formation of new sporangia, or of new spore-bearing organs, which may be in addition to, or interpolated between those typically present.
- (c) By continued apical, or intercalary growth of the parts bearing the sporangia.
- (d) By branching of the parts bearing the sporangia.
- (e) Indirectly, by branchings in the non-sporangial region resulting in an increased number of sporangial shoots; this is closely related to (c) and (d).



II. *Decrease in Number of Sporangia.*

- (*f*) By fusion of sporangia originally separate.
- (*g*) By abortion, partial or complete, of sporangia.
- (*h*) By reduction or arrest of apical or intercalary growth in parts bearing sporangia.
- (*i*) By fusion of parts which bear the sporangia or arrest of their branchings.
- (*j*) Indirectly, by suppression of branchings in the non-sporangial region, resulting in decreased number of sporangial shoots ; this is closely related to (*h*) and (*i*).

We are justified in assuming that (subject to the possibility of other factors having been operative, of which we are yet unaware) the condition of any polysporangiate sporophyte as we see it is the resultant of modifications such as these, operative during its descent.

The problem will, therefore, be in each case to assign its proper place in the history to any or each of these factors.

It is pointed out that in homosporous types, which are certainly the more primitive, the larger the number of spores the better the chance of survival, and hence, other things being equal, increasing numbers of spores and of sporangia may be anticipated ; but in the heterosporous types reduction in number both of spores and of sporangia is frequent. The former will accordingly illustrate more faithfully than the heterosporous forms the story of the increase of complexity of spore-producing parts. The general method put in practice here is to regard homosporous forms as in the upgrade of their evolution, as regards their spore-producing organs, unless there is clear evidence to the contrary. The *onus probandi* lies rather with those who assume reduction to have taken place in them.

A summary of evidence of variation in number of sporangia by any of these methods is then given for the Lycopodiaceae, Psilotaceae, Sphenophylleae, Ophioglossaceae, Equisetineae, and Filicineae; followed in each case by a theoretical discussion of the bearing of that evidence on the morphology of the spore-producing members. The general result is that all of them, including even the dorsiventral and megaphyllous types, are referable to modifications of a radial strobiloid type ; progressive elaboration of spore-producing parts, followed by progressive sterilization, and especially by abortion of sporangia in them, of which there is frequent evidence, together with the acquire-

ment of a dorsiventral structure, may be held to account for the origin of even the most complex forms. But the vegetative organs once formed may also undergo elaboration and differentiation *pari passu* with the spore-producing organs, a point which has greatly complicated the problem, especially in the higher forms; all roots are probably of secondary origin; facts of interpolation of additional sporangia, especially in Ferns, and of apogamy and apospory, are also disturbing influences, which have probably been of relatively recent acquisition.

A comparison is drawn as regards position, physiological and evolutionary, in the sporophyte, between the fertile zone in certain Bryophytes and the fertile region of certain simple Pteridophytes, e.g. the Lycopods; though no community of descent is assumed, the relation of the reproductive to the vegetative regions is the same. In the Bryophytes that region is regarded as a residuum from progressive sterilization; it is suggested that the same is the case for a strobiloid Pteridophyte, such as *Lycopodium*. The theory of the strobilus, based on this comparison, is that similar causes would lead to the decentralization of the fertile tissue in the primitive Pteridophytes as in the Bryophytes, and result in the formation of a central sterile tract, with an archesporium at its periphery; that such an archesporium, instead of remaining a concrete layer as it is in the larger Musci, became discrete in the Lycopods; that the fertile cell-groups formed the centres of projecting sporangia, and that they were associated regularly with outgrowths, perhaps of correlative vegetative origin, which are the sporophylls.

Whether or not this hypothesis of the origin of a Lycopod strobilus approaches the actual truth, comparison points out the genus *Lycopodium* as a primitive one, characterized by more definite numerical and topographical relation of the sporangia to the sporophylls than in any other type of Pteridophyta.

Then follows, as a consequence of comparison, the enunciation of a theory of the sporangiophore, a word which is here used in an extended sense to include not only the spore-producing organs of Psilotaceae, Sphenophylleae, Ophioglossaceae, and Equisetaceae, but also the sori of Ferns. The view is upheld that all these are simply placental growths, and not the result of 'metamorphosis' of any parts or appendages of prior existence; that the vascular supply, which is not always present, is not an essential feature; that they are seated at

points where, in the ancestry, spore-production has been proceeding on an advancing scale; hence they do not occupy any fixed and definite position. It seems probable that at least a plurality of sporangia existed on primitive sporangiophores, and that where only one exists that condition has been the result of reduction.

The above theories are then applied to the several types of Pteridophyta. The Lycopods, Psilotaceae, Sphenophylleae, and Ophioglossaceae may be arranged as illustrating the increased complexity of the spore-producing parts, and of the subtending sporophylls; the factors of the advance from the simple sporangium to the more complex sporangiophore are, septation, upgrowth of the placenta with vascular supply into it, and branching, with apical growth also in the Ophioglossaceae. But even in the most complex forms the sporangiophore may be regarded as a placental growth, and not the result of transformation of any other member.

In the case of *Helminthostachys* the marginal sporangiophores are regarded as amplifications from the sunken sporangia of the *Ophioglossum* type; in *Equisetum* they are regarded as being directly seated on the axis, and having originated there by a similar progression; they would thus be non-foliar. It is pointed out that though a foliar theory would be possible for *Equisetum* itself, it is not applicable to the facts known for the fossil Calamariaceae, which are so naturally related to it. Thus the strobilus of the Equisetineae is of a rather different type from that of the Lycopods, Psilotaceae, or even the Ophioglossaceae, in all of which there is a constant relation of the spore-producing parts to the leaves; in the Equisetineae no such constant relation exists; the leaves and sporangiophores may be in juxtaposition, as in *Calamostachys*, without exactly matching numerically; or the sporangiophores may occur in larger numbers and in several ranks, between successive leaf-sheaths, as in *Phyllothea* and *Bornia*; or without any leaves at all, as in *Equisetum*. Thus, on a non-phyllome theory the latter may be held to be only an extreme case of what is seen in certain fossils.

The Ferns, notwithstanding their apparent divergence of character from other Pteridophytes, may also be regarded as strobiloid forms, with greatly enlarged leaves; the primitive sori of the Simplices resemble the sporangiophores of other Pteridophytes; the more complicated soral conditions of the Gradatae and Mixtae were probably derivative from these, the chief difference being due to the interpolation



of new sporangia, an innovation which is in accordance with biological probability, as well as with the palaeontological record.

The effect of the results thus obtained on the systematic grouping of the Pteridophytes is then discussed; it is pointed out that the Lycopods, Psilotaceae, Sphenophylleae, Ophioglossaceae, and Filices illustrate lines of elaboration of a radial strobiloid type, with increasing size of the leaf. The division of Pteridophyta by Jeffrey, on anatomical characters, into small-leaved Lycopsidea and large-leaved Pteropsida is quoted; but it is concluded that the anatomical distinction of Jeffrey does not define phylogenetically distinct races, but is rather a register of such leaf-development as differentiated them from some common source. It is contended that the Ophioglossaceae and Filices, which constitute Jeffrey's Pteropsida, are not necessarily akin on the ground of their large leaves, and consequent phyllosiphonic structure; but that they probably acquired the megaphyllous character along distinct lines. The opinion of Celakovsky is still held, 'that the Lycopods are probably of living plants, the nearest prototypes of the Ophioglossaceae.' The more recent investigations of Jeffrey and of Lang have shown, however, that in the gametophyte of the Ophioglossaceae there is an assemblage of 'Filicinean' characters, which differ from those of *Lycopodium* itself. But Celakovsky's comparison is *with the Lycopods, not with the genus Lycopodium*; so far as the facts go, increasing 'Filicinean' characters of the gametophyte follow in rough proportion to the larger size of the leaf; thus from *Isoetes* we learn that a combination of cross-characters is found in a megaphyllous Lycopod type. What we find in the Ophioglossaceae is that in conjunction with their more pronounced megaphyllous form, still retaining, however, the Lycopodinous type of the sporophyte, they show more pronounced 'Filicinean' characters of the gametophyte and of the sexual organs. It is unfortunate that the facts relating to the gametophyte of the Psilotaceae and Sphenophylleae are not available in this comparison.

What the meaning is of this parallelism between leaf-size and characters of the sexual organs it is difficult to see; a further difficulty in its interpretation lies in the fact that for the Equiseta the parallelism does not hold; there 'Filicinean' characters of the gametophyte accompany entirely non-Filicinean characters of the sporophyte, the latter showing nearer analogy to the Lycopods than to the Ferns. Such cross-characters are difficult to harmonize with any phylogenetic

theory; on account of them, the Equisetineae are placed in an isolated position, and in the same way, though with less pressing grounds, a separate position should be accorded to those types which lie between the extremes of Lycopods and Ferns, in proportion as the cross-characters are more or less pronounced.

On this basis the Isoetaceae would probably best take their place as a sub-series of the Lycopodiales, Ligulatae; the Psilotaceae and Sphenophylleae would constitute a series of Sphenophyllales, separate from, but related to, the Lycopodiales. The Ophioglossaceae would form an independent series of Ophioglossales, more aloof than the Sphenophyllales from the Lycopodiales, but not included in the Filicales. The actual connexion of these series by descent must remain open; it is quite possible that some or all of them may have originated along distinct lines from a general primitive group, which may be provisionally designated the Protopteridophyta; these were probably small-leaved strobiloid forms, with radial type of construction, and with the sporangia disposed on some simple plan. The grouping arrived at in these Memoirs may be tabulated as follows:—

#### PTERIDOPHYTA.

##### I. LYCOPODIALES.

###### (a) Eligulatae.

Lycopodiaceae.

###### (b) Ligulatae.

Selaginellaceae.

Lepidodendraceae.

Sigillariaceae.

Isoetaceae.

##### II. SPHENOPHYLLALES.

Psilotaceae.

Sphenophyllaceae.

##### III. OPHIOGLOSSALES.

Ophioglossaceae.

##### IV. FILICALES.

###### (a) Simplices.

Marattiaceae.

Osmundaceae.

Schizaeaceae.

Gleicheniaceae.

Matonineae.

###### (b) Gradatae.

Loxsomaceae.

Hymenophyllaceae.

Cyatheaceae.

Dicksonieae.

Dennstaedtiinae.

Hydropterideae (?).

###### (c) Mixtae.

Davalliaceae.

Lindsayaeae.

Pterideae, and other Poly-podiaceae.

##### V. EQUISETALES.

Equisetaceae.

Calamariaceae.

F. O. BOWER.

ON LAGENOSTOMA LOMAXI, THE SEED OF LYGINODENDRON<sup>1</sup>.—The existence in Palaeozoic times of a group of plants (the Cycadofilices of Potonié) combining certain characters of Ferns and Gymnosperms, has been recognized for some years past by various palaeo-botanists<sup>2</sup>. The group in question embraces a number of genera, among which *Medullosa*, *Heterangium*, *Calamopitys*, and *Lyginodendron* may be mentioned; the fern-like foliage of these plants is placed according to its external characters in the form-genera *Alethopteris*, *Neuropteris*, *Sphenopteris*, and others.

The evidence for the intermediate position of the Cycadofilices is extremely strong, but at present it is drawn entirely from a detailed comparison of their vegetative organs, especially as regards their anatomical characters. In no case, as yet, is the fructification of any member of the group known with certainty; such indications as have hitherto been detected are still in need of corroboration. Thus, the suggestion has been made that the large seed, *Trigonocarpon olivaeforme*, may have belonged to some member of the genus *Medullosa*<sup>3</sup>; and in the case of *Lyginodendron* itself there is fairly strong reason to believe that one form of fructification (in the light of the observations to be described below, presumably the male), may have been of the *Calymmatotheca* type<sup>4</sup>, a type, however, of which the organization is not yet fully understood. In the absence of satisfactory data as to the fructification, so high an authority as M. Zeiller has expressed a doubt whether the Cycadofilices were, after all, anything more than a specialized group of Ferns<sup>5</sup>.

A re-examination of the seeds, placed by Williamson in his genus *Lagenostoma*, has revealed unexpected points of agreement between the structure of the envelopes of certain of these seeds on the one hand, and that of the vegetative organs of *Lyginodendron* on the other.

<sup>1</sup> Read before the Royal Society on May 7, 1903; reprinted from the Proceedings.

<sup>2</sup> Williamson, Organization of the Fossil Plants of the Coal-measures, Pt. XIII, Phil. Trans., B, vol. clxxviii, p. 299, 1887; Solms-Laubach, Fossil Botany, 1887, Engl. ed., pp. 141, 163; Williamson and Scott, Further Observations on the Organization of the Fossil Plants of the Coal-measures, Pt. III, Phil. Trans., B, vol. clxxxvi, p. 769, 1895; Potonié, Lehrbuch der Pflanzenpalaeontologie, p. 160, 1899; Scott, Studies in Fossil Botany, pp. 307, 514, 1900.

<sup>3</sup> G. Wild, On *Trigonocarpon olivaeforme*, Trans. Manchester Geol. Soc., vol. xxvi, 1900.

<sup>4</sup> Scott, Studies, p. 334; Miss Benson, The Fructification of *Lyginodendron Oldhamium*, Ann. of Bot., vol. xvi, p. 575, 1902.

<sup>5</sup> Zeiller, Éléments de Paléobotanique, 1900, p. 370.



Two species of *Lagenostoma* (*L. ovoides* and *L. physoides*) were described by Williamson<sup>1</sup>; a third species, the subject of the present note, was left undescribed by him, though in his MS. catalogue he named it, after its discoverer, *Lagenostoma Lomaxi*, a name which we here provisionally adopt. This seed occurs in calcareous nodules of the lower Coal-measures, and chiefly at Dulesgate, in Lancashire.

In general structure the seed *L. Lomaxi* agrees with *L. ovoides*.

It is an orthotropous seed, circular in transverse section, and broadest midway between base and apex. The height of the seed slightly exceeds the diameter, and in general form it may be compared with a Jaffa orange. Its height in full-sized specimens is about  $5\frac{1}{2}$  mm., the diameter at the equator  $4\frac{1}{4}$  mm. Many of the specimens that have passed through our hands show signs of having become detached through the agency of a layer of separation and bear a low conical papilla centrally placed at the chalazal end, beneath which the actual layer of abscission was situated.

In the most general relations of its organization the seed approaches the Gymnosperm type in that the integument and nucellus are distinct from one another in the apical region only, whilst the body of the seed, which contains the large single macrospore with traces of prothallial tissue, shows complete fusion of the integumental and nucellar tissues. But in other respects the seed is remarkable. The free portion of the nucellus which stands above the macrospore is conical in form, its base is about 0.75 mm. across, and its height somewhat greater. The tapering apex reaches to the exterior, plugging the micropylar aperture like a cork. The whole of this structure, the 'lagenostome' of Williamson, constitutes a pollen-chamber, owing to the separation of the nucellar epidermis from the underlying parenchymatous body of the free part of the nucellus. The pollen-chamber thus has the form of a bell-shaped cleft situated between the persistent epidermis and the central cone of nucellar tissue. Access to the chamber is gained at the apex, which is open, and pollen-grains are found in its lower part. The integument, which is a simple shell where fused with the nucellus, becomes massive and complicated in its free part which corresponds to the upper fifth of the seed. In this region it is usually composed of nine chambers radially disposed around

<sup>1</sup> Organization, Pt. VIII, Phil. Trans., vol. clxvii, p. 233, Figs. 53-75, and 77-79, 1877; Pt. X, Phil. Trans., Pt. II, 1880, p. 517, Figs. 61-63. See Oliver, New Phytologist, vol. i, no. 7, 1902.

the micropyle. The existence of these chambers is indicated on the outside surface of the seed by the presence of nine little ridges disposed like the rays of a star around the micropyle, but dying out almost at once. These ridges over-lie the partitions of the chambered portion of the integument just as do the stigmatic bands the septa of a poppy capsule. The whole structure from within is like a fluted dome or canopy, the convexities of which correspond to the chambers, and actually engage with broad low grooves on the surface of the wall of the pollen-chamber.

The vascular system of the seed enters as a single supply-bundle at the chalazal papilla, and branches, a little below the base of the macrospore, into nine radially-running bundles. Each of these bundles passes, without further branching, to the apex of the seed, running outside the macrospore and a little distance below the surface. At the canopy the bundles enter the chambers and end at the tips.

*Lagenostoma Lomaxi* was thus a seed or seed-like structure detached as a whole and containing pollen-grains in the remarkable cleft-like pollen-chamber; the integument in its free part, when compared with that of Williamson's *Lagenostoma physoides*, suggests a number of originally free arms or processes that have become laterally fused into a complex chambered organ.

The seed, *L. Lomaxi*, is in some cases still attached to its pedicel<sup>1</sup>; the great peculiarity of this seed, as compared with other members of the genus, is that when young, and sometimes even at maturity, it is found enclosed in an envelope or cupule, springing from the pedicel just below the base of the seed, and extending above the micropyle—at least in young specimens. The cupule appears to have been ribbed below, and deeply lobed in its upper part; in form it may be roughly compared to the husk of a hazel-nut—of course on a very small scale.

The pedicel and cupule bear numerous capitate glands, of which some are practically sessile, others shortly stalked, while in others again the stalk is of considerable length. The head, or secreting portion of the gland, which is spherical in form, is almost invariably empty, only the multicellular wall persisting. The tissue of the stalk of the gland, consisting of many layers of cells, is preserved, though in a somewhat disorganized state.

These cupular glands present the closest agreement in size, form,

<sup>1</sup> Cf. Williamson, loc. cit., Pt. VIII, Fig. 68 (*L. ovooides*).

and structure with the glands which occur on the vegetative organs of *Lyginodendron Oldhamium*<sup>1</sup>, and which are especially abundant on the particular form of that plant found in association with *Lagenostoma Lomaxi*. Both on petiole and cupule the majority of the glands are short, those which are not sessile being commonly about 0.4 mm. in height. Long-stalked glands, exceeding a millimetre in height, sometimes occur both on the vegetative organs and on the cupule. The dimensions of the head of the gland agree exactly on cupule and petiole, the diameter averaging about 0.2 mm. in each case. In both, the stalk is usually somewhat narrower than the head, except at the base, where it is often considerably enlarged. On the stem, as might be expected, the glands are usually somewhat larger than on petiole or cupule.

As a rule, the structure of the glands on the vegetative organs is well preserved, the secretory tissue in the head being perfect. But occasionally the vegetative glands are found in the same state of preservation as those on the cupule, with the head hollow, owing to disappearance of the secretory mass. Where we thus have the two organs in a corresponding state of preservation, the agreement between the vegetative glands of *Lyginodendron* and those on the cupule of *Lagenostoma Lomaxi* is found to be exact.

There is no other known plant from the Coal-measures with glands at all similar to those described, nor is it likely that any unknown Gymnosperm should so exactly resemble *Lyginodendron* in these characters. On the ground, then, of the glandular structure we are led to the conclusion that the seed *Lagenostoma Lomaxi* can have belonged to no other plant than *Lyginodendron Oldhamium*, and more particularly to the glandular form of that type with which the seed is associated.

The state of preservation of the glands and of the cupule as a whole, indicates clearly that this organ, as we find it, was in an effete condition, having, no doubt, already discharged its functions while the seed which it protected was still quite young.

The vascular system of the cupule was well developed, and is very fairly preserved. A number of bundles branched off from the main strand of the pedicel, and traversed the cupule throughout its whole

<sup>1</sup> It has long been realized that the name *Lyginodendron Oldhamium* characterizes a type rather than a species. It is probable that the very glandular form occurring at Dulesgate may deserve specific rank.



extent. The structure of the large bundle, seen in the pedicel, agrees with that of a petiolar strand in *Lyginodendron*. The minute characters of the tracheides are also in close agreement with those observed in the xylem of the foliar organs of the same plant.

Hence, characters presented by the internal anatomical structure strengthen the conclusion drawn from a comparison of the glands, and thus further support the attribution of *Lagenostoma Lomaxi* to *Lyginodendron*.

The evidence thus indicates that in a transitional type, such as *Lyginodendron Oldhamium*, with leaves wholly fern-like in structure and form, but with decided Cycadean as well as Filicinean characters in the anatomy of stem and root, the seed habit had already been fully attained, as fully, at any rate, as in any known Palaeozoic Gymnosperm. *Lyginodendron* retains, so far at least as its vegetative structure is concerned, the intermediate position already assigned to it, but whereas the fern-like characters have hitherto seemed to preponderate, the discovery of the seed inclines the balance strongly on the Gymnospermous side. It is not likely that *Lyginodendron* stood alone in this; we must now be prepared to find, what has long been recognized as a possibility, that many of the plants grouped under Cycadofilices already possessed seeds, and thus that a considerable proportion of the so-called 'fern-fronds' of the Palaeobotanist really belonged to Spermophyta. It is at present impossible to say at what stage in the evolution of the Fern-Cycad phylum the great change in reproductive methods came, whether it followed in the wake of general anatomical advance, or *vice versa*. The discovery of further evidence as to the reproductive processes of these ancient plants is likely to yield interesting results.

The authors are much indebted to Miss Marie Stopes for her valuable aid in the examination of the numerous sections in the Williamson and various other Collections.

Mr. J. Lomax deserves high praise for his good judgement and skill in collecting and preparing the material for the investigation.

A full account of the fossils dealt with in the present note is in preparation, and will shortly be submitted to the Royal Society.

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## Further Observations on the Phytoplankton of the River Thames.

BY

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THE present year, with its unusually great rainfall and consequent heavy floods, has not been very favourable for comparative investigations of the river Plankton. The disturbing influence due to the height of the water and the strength of the current has been very noticeable in some of the samples collected, especially in those of May 2. The speed of the current on that day was quite four times the usual one, and it is a well-known fact that the quality of the Plankton is considerably dependent on the rate of the stream (cf. Zacharias, '98, p. 46; Zimmer, '99, p. 7); a continuation of such conditions for several days would probably have a very considerable effect on the composition of the Plankton, and this would most likely last for some time after the restoration of the normal state of affairs. It is therefore probable that, although the main features of the periodicity are sufficiently evident, observations under more normal conditions would have disclosed a number of minor points which have been obscured this year. The object of the present paper is primarily to touch upon the main points in the periodical development of the Plankton of the River Thames.

Detailed investigations of the periodicity of river Plankton as yet scarcely exist, although Schröder has examined the



Oder to some extent from this point of view, and observations of this kind are at present being carried out on the river Volga (cf. Zytkoff, '02, p. 60). With regard to the Oder at Breslau, Schröder ('98, p. 525, '99, pp. 22-23), gives the following data :—

I. December-February:—nothing or exceptionally *Synura* and *Eudorina*.

II. March-May :—*Synedra* and a few brown Flagellates.

III. June-August:—*Asterionella*; a few green and occasional blue-green forms.

IV. September-November :—*Synedra* and a few brown Flagellates.

During the winter months the only living elements occurring in the Plankton are a few Rotifers, intermingled with large quantities of organic detritus and muddy particles, whilst Algae are almost alone represented by detached portions of filamentous forms. During March *Melosira varians* and *Fragilaria virescens* appear in some quantity, but near the end of the month *Synedra delicatissima* is the most abundant form; only a few specimens of green Algae (*Chlamydomonas tingens*, *Pandorina morum*, *Eudorina elegans*, and *Volvox minor*) occur, whilst Flagellates are rather commoner at this time of the year (*Synura uvella*, *Uroglena Volvox*, *Dinobryon sertularia* and *Chrysomonas ovata*). In the summer months *Asterionella* plays an exceedingly important part, and is accompanied by a quantity of other Diatoms (*Diatome tenue*, *Fragilaria capucina* and *F. crotonensis*, *Melosira granulata*, *Stephanodiscus Hantzschianus*); of the green forms *Actinastrium Hantzschii*, var. *fluviatile*, and *Dictyosphaerium Ehrenbergii*, alone are at all abundant. As the autumn comes on the Plankton again acquires the spring character, and by a decrease in number of individuals gradually merges into that of the winter months.

In the Danube, the Plankton of which has been examined by Brunthaler ('00, pp. 310-311), the periodicity is somewhat different. In the clear water, occurring during the winter months, life is almost entirely wanting. In February *Synedra*

appears, and at the same time a few individuals of *Melosira*. In the next months *Melosira* and *Fragilaria* increase in numbers, whilst the prevalent *Asterionella* of the succeeding summer months is as yet only slightly represented. In the height of the summer this latter form is accompanied by *Ceratium*, *Dinobryon*, *Clathrocystis*, and *Fragilaria*, in subordinate numbers. With the autumn a decrease in number of individuals again becomes noticeable. Green forms only occur in any considerable amount during the summer months.

To come now to the River Thames (see table), an important difference in contrast to the two rivers just discussed at once appears. There is a well-marked living Plankton all the year round! The Diatoms, which form such a very large percentage of the organic life of the Thames, are always present in appreciable numbers, even though from December to February about two-thirds of the individuals are dead and only represented by an empty frustule. At the same time, however, more or less abundant living representatives of all the species mentioned in the table for these months were observed, and samples, when examined under the microscope, always exhibited a number of live Diatoms in the field of view. This difference in the Thames Plankton as opposed to that of the Oder and Danube may most probably be ascribed to the mildness of our winter in contrast to the continental one; for the sample collected on February 4, 1903 a few days after the cessation of a heavy frost, showed no change in the living element in the river, and it is only rarely that we exceed the degree of cold attained on this occasion. It is easy to understand how a frost of long duration, converting the backwaters and other sources of the river's Plankton into a thick sheet of ice, would reduce the organic life in the river to a minimum by the temporary congelment of the reservoirs, from which it is in the main derived; this is undoubtedly the case with the continental rivers, and it will be interesting to see what effect a protracted frost (of say three to four weeks), as occasionally occurs, will have on the Plankton of the Thames.

The following observations on the periodicity of the Thames Plankton were all made on the stretch of river lying between Teddington Lock and Kingston, and were carried out on seven separate occasions, from October to the beginning of July, at intervals of from one to two months. More frequent visits would have been desirable, but were prevented by the state of the river; unfortunately it is also impossible to undertake any further investigations during this year, and I have therefore added the results of my dredging in July of last year (Fritsch, '02), to complete the table to some extent. These latter were obtained from the river below Teddington Lock, the Plankton of which, however, shows no marked difference from that above the lock. All the samples were taken from the surface-layers only.

In the samples, collected in October, abundant life was still present; in addition to a number of green forms, of which *Pandorina morum* and *Pediastrum Boryanum* were most frequently met with, the Diatoms, *Melosira varians* and *Fragilaria virescens*, were exceedingly common. The three species of *Surirella* and *Stephanodiscus Hantzschianus* are also very characteristic of the Plankton at this time of the year, whilst other rather abundant forms are *Synedra Ulna*, *Nitzschia sigmoidea*, and *Pleurosigma attenuatum*. On the whole it is scarcely possible at this time to point out any one species as preponderating considerably over the others, although perhaps the two filamentous Diatoms are the most striking forms in the samples collected in this month. In December the green and blue-green forms had become exceedingly rare, whilst the Diatoms, as already stated above, although still occurring in appreciable numbers, are to a considerable extent present as empty frustules. *Melosira varians* is still very abundant, whilst *Fragilaria virescens* is less evident, and the species of *Surirella* are decreasing in numbers. The most noticeable point about the Plankton at this time of the year, however, is the appearance of *Asterionella gracillima* in small numbers; no trace of it was observed in the October samples. In February the Plankton practically



Table illustrating periodicity of Thames Plankton<sup>1</sup>.

	Oct. 11, 1902; t = 12°C.	Dec. 4, 1902; <sup>2</sup> t = 4.75°C.	Feb. 4, 1903; t = 5.5°C.	Mar. 14, 1903; t = 7.5°C.	May 2, 1903; <sup>3</sup> t = 12°C.	June 3, 1903; t = 17°C.	June 29, 1903; <sup>4</sup> t = 21.5°C.	July 11, 1902; <sup>4</sup> t = 20°C.
I. CHLOROPHYCEAE.								
<i>Scenedesmus quadricauda</i> (Turp.), Bréb. . . . .	r.	r.	i.	—	i.	—	r.	rc.
<i>Pediastrum Boryanum</i> (Turp.), Men. . . . .	rc.	r.	i.	vr.	i.	rc.	rc.	c
" <i>pertusum</i> , Ktz. . . . .	rr.	—	—	i.	—	rc.	rr.	c.
" <i>pertusum</i> , var. <i>clathratum</i> , Braun	rr.	—	—	—	—	rr.	rr.	—
<i>Chlamydomonas Braunii</i> , Gorosch. . . . .	r.	—	—	—	—	rc.	—	—
<i>Eudorina elegans</i> , Ehrb. . . . .	rc.	—	—	vr.	—	rr.	r.	r.
<i>Pandorina morum</i> , Ehrb. . . . .	c.	—	—	i.	—	—	r.	rc.
<i>Gonium pectorale</i> , Müll. . . . .	—	—	—	—	—	—	vr.	—
II. CONJUGATAE.								
<i>Closterium acerosum</i> (Schrank), Ehrb. . . . .	r.	—	—	—	—	—	—	vr.
" <i>moniliferum</i> (Bory), Ehrb. . . . .	rr.	—	—	—	—	rc.	—	vr.
III. BACILLARIALES.								
<i>Coccinodiscus radiatus</i> , Ehrb. . . . .	vr.	—	—	—	—	—	—	rc.
<i>Stephanodiscus Hantzschii</i> , Grun. . . . .	c.	rr.	rc.	—	—	—	rc.	?
<i>Melosira moniliformis</i> (Müll.), Ag. . . . .	rr.	rr.	rc.	rc.	rc.	rr.	r.	rc.
" <i>varians</i> , Ag. . . . .	vc.	vc. <sup>5</sup>	c. <sup>5</sup>	c.	a.	a.	rc.	c.
<i>Campylodiscus noricus</i> , Ehrb. . . . .	rc.	rr.	r.	rc.	rc.	rr.	r.	rc.
<i>Surirella biseriata</i> , Bréb. . . . .	c.	c.	rc.	rc.	rr.	rr.	r.	rc.
" <i>ovalis</i> , Bréb. . . . .	c.	c.	rr.	rc.	rr.	r.	r.	c.
" <i>splendida</i> (Ehrb.), Ktz. . . . .	c.	rc.	rr.	rc.	rr.	rc.	r.	r.
<i>Cymatopleura Solea</i> (Bréb.), Sm. . . . .	rr.	r.	r.	r.	r.	rr.	—	r.
<i>Cymbella gastroides</i> , Ktz. . . . .	r.	rr.	rr.	rr.	—	—	—	rc.
<i>Amphora ovalis</i> , Ktz. . . . .	rr.	rr.	rr.	rc.	rr.	rr.	r.	rc.
<i>Fragilaria virescens</i> , Ralfs . . . . .	vc.	c.	rc.	c.	rc.	rc.	r.	c.
<i>Grammonema spec.</i> (long cell = 16 μ) . . . . .	rc.	rc.	rc.	r.	—	—	—	—
<i>Pleurostaurum acutum</i> (Sm.), Rabenh. . . . .	r.	r.	rc.	rc.	—	—	vr.	—
<i>Synedra Acus</i> , Ktz. . . . .	—	—	—	rc.	rr.	rr.	a.	?
" <i>Acus</i> , var. <i>delicatissima</i> , Sm. . . . .	—	—	—	rc.	rr.	—	c.	—
" <i>Ulna</i> , Ehrb. . . . .	c.	c.	rc.	rc.	c.	c.	a.	rc.
<i>Asterionella gracillima</i> , Heib. . . . .	—	rc.	c.	r.	—	—	—	—
<i>Nitzschia sigmoidea</i> (Nitzsch), Sm. . . . .	c.	c.	c.	rc.	rc.	rc.	r.	rc.
<i>Pinnularia viridis</i> (Ehrb.), Rabenh. . . . .	—	—	—	r.	—	—	vr.	—
<i>Pleurosigma attenuatum</i> (Ktz.), Sm. . . . .	c.	c.	c.	rc.	rc.	rc.	r.	rc.
" <i>Fasciola</i> (Ehrb.), Sm. . . . .	—	—	—	rr.	—	—	—	—
<i>Tabellaria fenestrata</i> , Ktz. . . . .	—	—	—	rr.	rr.	r.	—	—
IV. SCHIZOPHYCEAE.								
<i>Microcystis marginata</i> (Men.), Kirchn. . . . .	—	i.	—	—	—	—	—	—
<i>Merismopoedia glauca</i> (Ehrb.), Näg. . . . .	r.	vr.	—	—	—	—	—	—
V. FLAGELLATAE.								
<i>Euglena viridis</i> , Ehrb. . . . .	—	vr.	—	i.	—	—	—	rc.
<i>Phacus pleuronectes</i> , Nitzsch . . . . .	r.	vr.	—	—	—	—	—	r.
<i>Synura Volvox</i> , Ehrb. . . . .	—	—	—	vr.	—	—	rc.	r.

<sup>1</sup> a. = abundant ; vc. = very common ; c. = common ; rc = rather common ; rr. = rather rare ; r. = rare ; vr. = very rare ; i. = isolated.

<sup>2</sup> The weather had only just become cold the day before, having been mild and foggy previously ; so that not too much stress should be laid on this temperature.

<sup>3</sup> River high and current very strong.

<sup>4</sup> Added in order to complete table as far as possible, cf. text.

<sup>5</sup> With auxospores.

consisted of Diatoms only; the green species, mentioned in the table, were both only observed once, groups of green Pleurococoid cells being somewhat more frequent. Of the Diatoms observed, about two-thirds of the individuals were dead; *Melosira varians*, *Fragilaria virescens*, and the species of *Surirella*, had decreased very much in amount, whilst *Asterionella gracillima* is far commoner, being very characteristic of the Plankton at this stage. Its reign is apparently short, however, for samples collected in the middle of March showed a very great decrease in the number of individuals of this species; otherwise the Plankton remains very much the same, the two filamentous Diatoms still preponderating over the others. At the same time *Synedra Acus*, var. *delicatissima* is present in sensible numbers (cf. foot-note, p. 637). In May there is no trace of *Asterionella*, whilst *Melosira varians* is present in extreme abundance, large numbers of the chains of this Diatom always lying in the field of view under the microscope; *Fragilaria* is relatively far less abundant. The only other common species is *Synedra Ulna*, the green forms being just as rare as in March. This latter feature may in part be due to the strong current in the river on this occasion, owing to the heavy rains (cf. p. 631). Samples collected a month later (June 3, 1903) showed an increase in the green forms (species of *Pediastrum*, *Chlamydomonas Braunii*, *Closterium moniliferum*), whilst the relative number of individuals of Diatoms occurring is approximately the same as before, *Melosira varians* being by far the most abundant species. In the next month two species of *Synedra* (*S. Ulna* and *S. Acus*, as well as its var. *delicatissima*) develop to an extraordinary extent, *Melosira* being almost lost in contrast to the numerous needles of these species. Two months before we had a *Melosira*-Plankton; in July we have an excellent example of a *Synedra*-Plankton. The green forms are now rather abundant, and *Synura Volvox* is also frequently met with.

Stated briefly, the relative development of the Plankton of the Thames at different times of the year is thus as follows: In October, *Melosira*, *Fragilaria*, *Surirella*, &c., in almost

equal numbers, being accompanied by a development of *Asterionella gracillima* about the time of the New Year; in May a very abundant development of *Melosira varians*, succeeded in the summer months again by a great increase in species of *Synedra*; in the height of the summer and the autumn considerable prevalence of any particular form is not noticeable (according to last year's results, see Fritsch, '02). This periodicity in the course of a year may be summarized thus:—

mixed Plankton (with *Asterionella*-phase) → *Melosira* →  
*Synedra* → mixed Plankton.

*Asterionella*, it should be observed, cannot be said to individualize the Plankton to the extent that *Melosira* and *Synedra* do in later months. In the past season, at least, it merely formed a minor phase in the development of the river's Plankton, and the characteristic outward form of this species alone makes its occurrence so striking and readily noticeable; there are probably a number of such minor phases<sup>1</sup>, which are not great enough to give a definite stamp to the Plankton, and most of which would be overlooked in the course of a single year's observations (cf. also p. 631).

If we compare the periodicity of the Plankton of the Thames with that of the Oder and Danube, which was mentioned above, it will at once be perceived that, although we have the same dominant forms, their distribution in the different seasons of the year is not at all identical. *Synedra*, which is a spring and autumn form in the two continental rivers, attains its maximum during the summer in the waters of the Thames; whilst *Asterionella*, which plays some part in the winter-Plankton of the latter, abounds in the Oder and Danube during the summer months, a time at which it is not at all or scarcely represented in the Thames. According to Brunnthaler, *Melosira* (but together with *Fragilaria*) abounds in the Danube in spring, that is to say, at the same time as it does in the Thames; apparently this Diatom does not occur

<sup>1</sup> The relative abundance of *Synedra Acus*, var. *delicatissima* in March may possibly turn out to be another such minor phase.



to such an extent as to characterize the Plankton of the Oder at any particular period. *Melosira*, being well provided with chloroplasts, would be likely to be able to assimilate freely before forms like *Synedra*, *Fragilaria*, &c., with far smaller chloroplasts, were capable of doing so, and its great development during the spring months may be explained on these grounds (cf. Zacharias, '99, p. 27). To some extent *Asterionella* and *Synedra* may be said to have exchanged places in the Thames Plankton with regard to that of the continental rivers. It remains to be seen whether other European rivers show the same periodicity as the Oder and Danube, and whether other British rivers will follow the lines of the Thames Plankton. Our present scanty knowledge of the conditions of life of the Plankton of rivers makes it impossible to account for this divergence; it may be that the difference of climate, already referred to above, has something to do with the matter. It does not seem likely that the height of the water at some times during this year will have had any effect on the general features of the periodicity of the Plankton, although the minor points may have been to some extent obscured. From what I have seen I do not consider it impossible that different portions of the river's course, sufficiently distant from one another, may show variations in the periodicity of the Plankton, a point which I hope to examine more carefully next year.

A few points regarding the Plankton of this part of the river still deserve mention. In addition to collecting samples from the main river, on several occasions some were also taken from a side-arm of the river between Tatham's Island and the Middlesex bank. Those taken from this arm in last October contained a number of individuals of *Bacillaria paradoxa*, Gmel., in a healthy condition, the concertina-like movement of the individuals of the colony taking place in rapid succession. This was not the only marine form observed here at the time, *Pleurosigma Fasciola* (Ehrb.), Sm. and *Navicula amphibaena*, Bory being also represented in small numbers. The peculiar point about their occurrence here is that a diligent search did

not reveal them in the main river itself, although *Bacillaria* was found in samples taken from below the lock at Teddington. Possibly the salinity of the water in the shallow arm is greater than in the main river, although *Pleurosigma Fasciola* was observed in a sample taken from the latter at a later date. The first two of the above-named Diatoms have also been observed by Zacharias ('98, p. 44) in the Unter-Eider (near Rendsburg), the waters of which at this point are of a brackish nature. I have never met with *Bacillaria* before or after in the river. *Stephanodiscus Hantzschianus*, a common constituent of the Plankton in the warmer months and in the autumn, was frequently observed to be provided with numerous elongated needle-like processes at its margin; such have been already described and figured by Schröder ('97, p. 488 and Pl. XXV, Fig. 1), although in the cases observed by me they were relatively far more numerous than Schröder's figures indicate. They undoubtedly serve to heighten the floating capacity of the individual. The individuals of *Nitzschia sigmoidea*, which were very common in some samples, were frequently covered by large numbers of epiphytic specimens of *Amphora minutissima*, whose occurrence in the Plankton is thus due to its attachment to a larger form. Finally the occurrence of *Gonium pectorale* in the samples of June 30 is noticeable, it not having been observed in the river before this.

In the following portion of this paper I propose to give an account of the flora of some of the backwaters of the Thames between Chertsey and Teddington, of which on the whole there is a remarkably small number. I have already previously pointed out (Fritsch, '02, p. 578), that the Plankton such as we find it in the main stream, although capable of a certain amount of multiplication, must to a great extent be stocked from other places, namely from the backwaters and slow-flowing tributaries of the river's course. The presence of these backwaters is of immense importance from the point of view of the fisheries, for it is on the Plankton that the smaller fish, which furnish the food for the larger

ones, must rely for sustenance. Zimmer ('99, p. 7) remarks as follows on this important subject: 'Die verschwindende Planktonmenge eines Flusses kann als Fischnahrung ganz und gar nicht in Betracht kommen. Die Fische, die auf das Plankton des Gewässers als Nahrung angewiesen sind, also namentlich die junge Brut, würden in fließendem Wasser einfach verhungern, sie müssen sich ihre Nahrung da suchen, wo sie zahlreicher vorhanden ist, d. h. einmal in den Stellen zwischen den Bühnen und dann in den Altwässern und den stromlosen Uferbuchten. Da aber zwischen den Bühnen das Plankton quantitativ immer noch ausserordentlich spärlich auftritt, so können diese Stellen die Altwässer durchaus nicht ersetzen.' This sufficiently indicates the value of the backwaters of a river in relation to the production of fish in the same, and the importance of leaving them undisturbed in their natural condition cannot be sufficiently emphasized. The quantity of individuals in the Plankton of a backwater is in most cases very much greater than that in the main stream, although the number of different species is often less (cf. also Fritsch, '02, p. 584).

(i) *Backwater just below Molesey Lock (June 3, 1903).*

	Head of backwater.	Mouth of backwater.	Main river just outside backwater.
<i>Melosira moniliformis</i> (Müll.), Ag. . .	rc.	rc.	rr.
„ <i>varians</i> , Ag. . . . .	c.	c.	a.
<i>Campylodiscus noricus</i> , Ehrb. . . . .	rr.	rr.	rr.
<i>Surirella biseriata</i> , Bréb. . . . .	rr.	rc.	rc.
„ <i>ovalis</i> , Bréb. . . . .	rc.	r.	r.
„ <i>splendida</i> (Ehrb.), Ktz. . . . .	rc.	rc.	rc.
<i>Cymatopleura Solea</i> (Bréb.), Sm. . . . .	—	r.	rr.
<i>Amphora ovalis</i> , Ktz. . . . .	—	—	rr.
<i>Fragilaria virescens</i> , Ralfs . . . . .	—	—	rc.
<i>Synedra Ulna</i> , Ehrb. . . . .	—	rc.	c.
<i>Nitzschia sigmoidea</i> (Nitzsch), Sm. . . . .	rc.	rc.	rc.
<i>Pleurosigma attenuatum</i> (Ktz.), Sm. . . . .	—	rc.	rc.
<i>Tabellaria fenestrata</i> , Ktz. . . . .	r.	r.	r.
<i>Scenedesmus acutus</i> , Meyen. . . . .	rr.	rc.	—
<i>Pediastrum Boryanum</i> (Turp.), Men. . . . .	r.	r.	rc.
„ <i>pertusum</i> , Ktz. . . . .	rc.	rc.	rc.
<i>Chlamydomonas Braunii</i> , Gorosch. . . . .	rc.	rc.	rc.
<i>Eudorina elegans</i> , Ehrb. . . . .	rc.	rc.	rr.
<i>Closterium acerosum</i> (Schränk), Ehrb. . . . .	rc.	rc.	—
„ <i>moniliferum</i> (Bory), Ehrb. . . . .	r.	r.	rc.



This backwater has a winding course, and penetrates between 100-150 yards into the land up to Hampton Court railway station ; it is deep enough to admit of rowing along its entire length. The banks are fairly thickly wooded, pollard willows being especially common. This is the only case I have as yet observed, in which the Plankton of a backwater is relatively poor as compared with that of the main river<sup>1</sup>, although the percentage of green forms present in the former is even here greater. To some extent also there is a difference in the constitution of the Plankton of the backwater and the main stream ; *Synedra Ulna*, which is common in the latter at this time of the year, is entirely wanting in the backwater, as is also the case with *Fragilaria virescens* and *Pleurosigma attenuatum*; on the other hand *Scenedesmus acutus* and *Closterium acerosum* were both only found in the backwater, whilst the other species of *Closterium* is far commoner in the main river. Animals are also considerably more abundant in the backwater. As far as I am aware, the River Mole is in some way connected with this backwater ; and the Plankton of the former, except for the occurrence of a number of blue-green forms (*Microcystis marginata*, *Merismopedia glauca*), is quite identical with that of the backwater just discussed, being rich in green forms and poor in Diatoms relative to the main river.

(ii) *Backwater near Sunbury* (May 23, 1903).

This backwater, except in quantity of individuals, differs very slightly from the main river. It is very shallow, and communicates with the stream by means of a short arm about halfway along its length. At this time of the year there is little vegetation in it ; *Nymphaea* is just commencing to appear. It has a rich Diatom flora, green forms in correspondence with the time of the year being rare. Amongst the Diatoms *Pleurosigma Fasciola* and *Asterionella gracillima*

<sup>1</sup> Bacteria were rather abundant in some parts of this backwater, which seems to indicate that refuse of some kind has access to it. This may possibly account for the paucity of its Plankton.

were observed in very small numbers. On the same day a slow-flowing arm a little further down the river was examined; here the green forms were rather more abundant, and in correspondence with this animal life more frequent than in the main stream. *Asterionella gracillima* was again observed here, and even in rather greater quantity than in the backwater; it would thus appear as though some of the forms, which are already wanting in the main stream, manage to maintain their existence for a somewhat longer period in some of the backwaters and slow-flowing arms on the river's course (cf. also the small backwater at Walton, discussed below).

The two backwaters at Walton, except perhaps for the one at Shepperton, are the most typical of those examined this year. The first (the 'Sale') is a broad pond-like arm of the river just below the bridge at Walton; its connexion with the main river is about 5 to 6 yards in breadth, but a very little way inside it broadens out very considerably. It is deep enough to allow of easy rowing, and in part was filled with a growth of *Nymphaea*, &c. In no part of the river was such a diversity of green forms and Flagellates found as here, whilst blue-green forms, curiously enough, were entirely wanting. It is unnecessary to especially mention any of these forms, as they are sufficiently evident from a glance at the following table; the latter also shows how the large majority of them are wanting in the main river. In the case of a form like *Synura Volvox*, which is abundant in the backwater, the entire absence in the river itself is very noteworthy. On the other hand *Gonium pectorale*, which is occasionally met with in the river at this point, was not observed in the backwater. In this latter, however, the first member of Peridineae that I have as yet found in the Thames was observed, but even then only scanty in number of individuals. With regard to the Diatoms, *Melosira* and the two species of *Synedra* are represented in rather equal numbers, whereas the latter are the prevalent forms in the river outside. The almost entire absence of *Campylodiscus noricus* and the species of *Surirella*

in the backwater, as contrasted with their occurrence in the main river, is also of interest.

A little below Walton Bridge on the opposite (Middlesex) side of the river there is a short, very narrow backwater, which, perhaps owing to its origin in a small bay, formed

(iii) *Backwaters at Walton* (July 1, 1903).

	The 'Sale' at Walton Bridge; t = 23°C.	Backwater a little lower down; t = 21.5°C.	Main river at Walton; t = 21.5°C.
<i>Stephanodiscus Hantzschianus</i> , Grun. . . . .	rc.	rc.	rc.
<i>Melosira moniliformis</i> (Müll.), Ag. . . . .	r.	—	r.
<i>varians</i> , Ag. . . . .	c.	a.	rc.
<i>Campylodiscus noricus</i> , Ehrb. . . . .	—	—	r.
<i>Surirella biseriata</i> , Bréb. . . . .	—	—	r.
<i>ovalis</i> , Bréb. . . . .	—	r.	rr.
<i>splendida</i> , Ehrb. . . . .	r.	—	rr.
<i>Cymbella gastroides</i> , Ktz. . . . .	r.	—	—
<i>Fragilaria virescens</i> , Ralfs. . . . .	rc.	c.	rr.
<i>Synedra Acus</i> , Ktz. . . . .	rc.	rc.	c.
<i>Ulna</i> , Ehrb. . . . .	rc.	rc.	c.
<i>Nitzschia sigmoidea</i> (Nitzsch), Sm. . . . .	r.	—	—
<i>Pleurosigma attenuatum</i> (Ktz.), Sm. . . . .	vr.	—	vr.
<i>Pleurosigma acutum</i> (Sm.), Rabenh. . . . .	rc.	—	—
<i>Scenedesmus quadricauda</i> (Turp.), Bréb. . . . .	rr.	—	r.
<i>acutus</i> , Meyen. . . . .	r.	—	vr.
<i>Pediastrum Boryanum</i> (Turp.), Men. . . . .	rr.	—	r.
<i>pertusum</i> , Ktz. . . . .	rc.	r.	rc.
<i>pertusum</i> , var. <i>clathratum</i> , Braun	rc.	r.	rc.
<i>Eudorina elegans</i> , Ehrb. . . . .	rc.	—	—
<i>Gonium pectorale</i> , Müll. . . . .	—	r.	r.
<i>Pandorina morum</i> , Ehrb. . . . .	rc.	r.	r.
<i>Richteriella polychaete</i> , Fritsch. n. sp. <sup>1</sup> . . . . .	r.	—	—
<i>Closterium moniliferum</i> (Bory), Ehrb. . . . .	r.	—	—
<i>Cornu</i> , Ehrb. . . . .	r.	r.	—
<i>acerosum</i> (Schranck), Ehrenbg. . . . .	vr.	—	—
<i>Staurastrum paradoxum</i> , Meyen. . . . .	rr.	—	—
<i>Ceratium cornutum</i> , Clap. et Lachm. . . . .	vr.	—	—
<i>Synura Volvox</i> , Ehrb. . . . .	c.	r.	—
<i>Dinobryon sertularia</i> , Ehrb. . . . .	rc.	—	—
<i>Phacus longicaudus</i> , Dujard. . . . .	r.	—	—

<sup>1</sup> This new species is very closely related to *Richteriella botryoides*, Lemm., the only well-marked difference lying in the occurrence of numerous hyaline processes on each cell of the colony; further investigation may show such differences to only warrant the establishment of a variety. Figures and full description will be given in a later publication.



by the river, and its consequent removal from the current, showed a well-marked Plankton of its own. This is chiefly interesting because of the abundance of *Melosira varians* present, which is quite the most prominent form; this backwater as it were is at present in the phase of Plankton-development, found in the main river about two months ago. The *Melosira* completely eclipses the species of *Synedra* in numbers, whilst it is accompanied by a relatively abundant development of *Fragilaria virescens*. Green forms are rare here, some of them not being even as common as in the main river. The main mass of the Plankton of this backwater is thus constituted by Diatoms.

(iv) *Backwater just above Shepperton (June 6, 1903).*

	Backwater ; t = 18°C.	Main river ; t = 18°C.
<i>Stephanodiscus Hantzschianus</i> , Grun. . .	rc.	rc.
<i>Melosira moniliformis</i> (Müll.), Ag. . .	—	rc.
" <i>varians</i> , Ag. . . . .	a.	c.
<i>Campylodiscus noricus</i> , Ehrb. . . . .	—	rr.
<i>Surirella biseriata</i> , Bréb. . . . .	—	r.
" <i>ovalis</i> , Bréb. . . . .	—	r.
" <i>splendida</i> (Ehrb.), Ktz. . . . .	rr.	rc.
<i>Cymatopleura Solea</i> (Bréb.), Sm. . . . .	rr.	r.
<i>Cymbella gastroides</i> , Ktz. . . . .	r.	—
<i>Amphora ovalis</i> , Ktz. . . . .	r.	r.
<i>Fragilaria virescens</i> , Ralfs . . . . .	a.	c.
<i>Synedra Acus</i> , Ktz. . . . .	rr.	rc.
" <i>Ulna</i> , Ehrb. . . . .	rr.	rr.
<i>Nitzschia sigmoidea</i> (Nitzsch), Sm. . . . .	c.	r.
<i>Pleurosigma attenuatum</i> (Ktz.), Sm. . . . .	r.	rr.
<i>Tabellaria flocculosa</i> , Ktz. . . . .	rc.	—
" <i>fenestrata</i> , Ktz. . . . .	r.	r.
<i>Scenedesmus quadricauda</i> (Turp.), Bréb. . . . .	r.	r.
" <i>acutus</i> , Meyen. . . . .	r.	—
<i>Pediastrum Boryanum</i> (Turp.), Men. . . . .	rr.	r.
" <i>pertusum</i> , Ktz. . . . .	rc.	rc.
<i>Eudorina elegans</i> , Ehrb. . . . .	rc.	—
<i>Pandorina morum</i> , Ehrb. . . . .	rc.	—
<i>Richterella polychaeta</i> , Fritsch, n. sp. . . . .	rr.	—
<i>Closterium moniliferum</i> (Bory), Ehrb. . . . .	vr.	—
<i>Synura Volvox</i> , Ehrb. . . . .	rc.	—

This backwater is of no very great length, and is sufficiently deep to admit of rowing all along it. The flora shows well-

marked differences from the main river outside ; the Plankton in the first place is very much richer in number of individuals. The Diatom flora is mainly composed of *Melosira varians* and *Fragilaria virescens*, the latter species especially being far commoner here than in the main river. Further, the Plankton of the backwater is characterized by the occurrence of large numbers of splendid specimens of *Nitzschia sigmoidea* (frequently bearing *Amphora minutissima*), which are almost absent from the river itself at this point. Green forms were better represented in the backwater, whilst a number of them (notably *Pandorina morum* and *Eudorina elegans*) were entirely wanting in the Plankton of the river ; however, the relative abundance of the green forms with regard to the main river is not so noticeable in this as in some of the other backwaters. It is the Diatom-flora here, as in the case of the smaller backwater at Walton, that affords the characteristic feature. The Plankton of the Wey, which was cursorily examined on this occasion, does not differ noticeably from that of the Thames at this point, except for a rather frequent occurrence of *Closterium acerosum*.

The most important features of the backwaters are thus :—

(i) Relative abundance of the Plankton in individuals as compared with that of the main stream.

(ii) Relative greater development of green and blue-green Algae and of the fauna, compared with the river itself.

(iii) An often very noticeable difference in the entire specific constitution of the Plankton.

On the whole, though however much the Plankton of the backwaters examined may differ from that of the actual Thames, its nature is still very different from that of the Plankton of a pond, and, so to say, always bears the stamp of a river Plankton. As an example, the results of some dredging carried out on the Brentford Reservoir near Hendon towards the end of October of last year may be mentioned. The chief mass of the Plankton consisted of animals, whilst Diatoms were only represented by a species of *Stephanodiscus* and a few isolated individuals of *Surirella ovalis*. A con-

siderable number of other Algae are common, however, *Clathrocystis aeruginosa* being most abundant. The following other forms were observed:—*Pediastrum Boryanum*, *P. pertusum*, *Scenedesmus quadricauda*, *S. acutus* with vars. *obliquus* and *dimorphus*, *Chlamydomonas Braunii*, *Lemmermannia emarginata*, *Closterium gracile*, *C. striolatum*, *Staurastrum paradoxum*, *Gomphosphaeria aponina*, *Phacus longicauda*.—It seems probable, however, that longer backwaters may at their head show less of the character of a river Plankton than those discussed in the present paper; the backwater at Molesey (see table, p. 640) even showed a greater contrast from the river in the Plankton from its head as compared with that from its mouth.

The following are the main points brought out by the present paper:—

(i) The Thames has a well-marked living Plankton all the year round.

(ii) The periodicity of the Plankton (mixed Plankton—*Melosira*—*Synedra*—mixed Plankton) differs rather markedly from that observed in continental rivers; *Asterionella* forms a minor phase during the winter months.

(iii) The backwaters, although differing very markedly in quality and quantity of the Plankton from the river itself, always bear the stamp of a river Plankton.

It is hoped during the next year to make a more complete study of the periodicity and also of the Plankton of the backwaters of the higher parts of the river's course.

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Two Fungi, parasitic on species of Toly-  
porthrix (*Resticularia nodosa*, Dang. and  
*R. Boodlei*, n. sp.).

BY

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With Plate **XXIX.**



THE researches of the last twenty years have shown that there are a considerable number of Fungi which infest algal hosts and generally cause considerable havoc amongst them. Lemmermann ('01) has recently enumerated 193 such forms, which belong chiefly to the Chytridineae and the Ancylistaceae. With a member of this latter order we are concerned in the present paper.

The genus *Resticularia* was first established by Dangeard in 1890 for a Fungus, parasitic in *Lyngbya aestuarii*. Since that time no further contribution towards our knowledge of the genus has, as far as I am aware, been published. Dangeard's genus has been accepted by Fischer ('92, p. 84) and by Schröter ('93, p. 92), both authors placing it next to the genus *Ancylistes* of Pfitzer.

Dangeard's *Resticularia nodosa* (Dangeard, '90) assumes the form of a straight tube, which is frequently appreciably enlarged within each cell of the Alga, so that in its entirety



the parasitic mycelium presents a moniliform appearance. The mycelium, although as a rule simple, is occasionally somewhat branched; and by means of such branches, emerging from the algal threads into the surrounding medium, infection from one filament to another readily takes place<sup>1</sup>. Occasionally uniciliate zoospores of relatively large size and moving actively are produced; these ultimately come to rest on the Alga and germinate immediately. According to Dangeard's view, a sexual process also takes place, leading to the formation of thick-walled zygospores, which are generally spherical but sometimes elongate-elliptical in shape, and which are often formed in considerable numbers in the same algal filament. The germination of these zygospores was not observed.

I have observed a species, which is probably identical with the *Resticularia nodosa* of Dangeard, although differing in a number of points from the author's original description. Further, a new species from the Pen Ponds, Richmond Park, will be described, which I have great pleasure in naming after its collector, Mr. L. A. Boodle, F.L.S.

#### I. RESTICULARIA NODOSA, DANGEARD (?).

This Fungus was first observed in a species of *Tolypothrix*, growing on rocks in the *Nepenthes*-house at Kew, in October of last year. At this time many of the filaments of the Alga were infested by the parasite (Figs. 19-23). The latter formed long chains of cells within its host, each link of the chain generally occupying one of the algal cells. The successive cells in the chain were separated from one another by true transverse walls, which seem, however, to arise after the constriction of the fungal hypha has taken place. The shape of the cells of the parasite is very varied, and it appears more or less to adapt itself to the size of the surrounding algal cell. Usually each segment of the Fungus has an elongated elliptical outline (Figs. 19-21), frequently with one or both ends considerably dilated; the cells may, however, also be oval or

<sup>1</sup> Dangeard does not figure any such infection.

almost spherical (Fig. 26). Usually the constrictions, and therefore also the transverse walls of the Fungus correspond in position with the dividing septa of the algal filament; this is due to the narrowing down of the fungal hypha, when it has to pass through a wall of the Alga. Not infrequently the Fungus branches within the host (Figs. 24, 25) and a very complicated tangle may sometimes be formed in this way (Fig. 26).

The contents of the fungal segments are colourless, and consist of vacuolar protoplasm with one or more bright granules of some oily substance. I was not able to make out nuclei. The effect on the cell-contents of the Alga was in the first place decolourizing. It would appear that the action of the Fungus does away with the special colouring-matter of the *Tolybothrix*-cells, so that those which have been recently attacked have a dirty yellowish-green colour. But even this soon disappears, and ultimately the entire cell-contents, as well as the dividing-walls of the Alga, are dissolved away. In the earlier stages of this process the contracted protoplasm forms a kind of granular sack round the fungal cell (Figs. 19, 20).

The most striking point about this Fungus, and a point in which it differs from the species to be described below, is the frequent occurrence of thick-walled dark brown cells in the course of the parasitic hyphae; such cells are to be seen in all my figures of this species. These spores were formed in considerable numbers in the course of each hypha; they were most commonly single (Figs. 21, 24), often in twos (Figs. 22, 23), and sometimes aggregated together in large numbers. Apparently any cell of the Fungus could develop into one of these spores, but there seemed a great tendency for their formation inside the heterocysts of the Alga (Fig. 20), probably because the conditions of nourishment are worse there than in the other cells of the filament. The heterocysts present a considerable obstruction to the passage of the Fungus, and in many cases the latter was observed to terminate at these points (Fig. 19); sometimes these terminations

were marked by the formation of a group of the thick-walled spores, abutting directly on the heterocyst.

These spores arise in the following way: a single segment of the Fungus increases somewhat in size and acquires a thicker wall. This is followed by the appearance of one or two large oily granules in its homogeneous contents (Fig. 27). Ultimately the wall differentiates into two layers and acquires a dark brown colour, and the number of oily granules present generally increases (Figs. 20, 26). The spores have very much the same shape as the fungal segment, from which they arise; generally a slight rounding-off takes place in their formation. These thick-walled cells are of the nature of chlamydo-spores; ultimately the remainder of the Fungus disappears and they alone remain, lying within the empty algal sheath (Fig. 22). They probably undergo a long period of quiescence before germination takes place.

Occasionally hyphae are formed as branches on the parasitic mycelium, which emerge from the Alga into the surrounding medium (Fig. 25). They are generally very delicate and show no trace of septation, although drops of oily matter, which to some extent simulate partition-walls, frequently occur in their course. I have no doubt that they serve to infect other (healthy) algal filaments, although I have been unable to obtain figures of such cases.

Except for the absence of zoospore-formation, the Fungus I have just described is in most essentials similar to the *Reticularia nodosa* of Dangeard. The latter observer considers the thick-walled spores<sup>1</sup> to have arisen by a sexual process; he remarks (Dangeard, '90, p. 98): 'La reproduction sexuelle se fait de la manière suivante: sur le trajet d'un même filament le protoplasma se condense par place comme le montrent les figures 29 et 30; on ne saurait faire aucune distinction entre le protoplasma mâle et le protoplasma femelle, bien qu'il y ait souvent l'une des portions un peu plus grosse que la seconde; le filament mycélien sur lequel se forment ces zygosporés ne paraît pas se cloisonner; du moins,

<sup>1</sup> Dangeard does not remark that the walls of the spores take on a brown colour.



nous n'avons jamais réussi à voir une cloison quelconque<sup>1</sup>. Dangeard's figures 29 and 30 give no indication of a fusion between protoplasmic masses or nuclei in the formation of the spores (with the possible exception of Fig. 30), nor does he state that he has seen anything of the kind. His assumption that they are sexually-formed zygosporoes is based on a comparison with Maxime Cornu's and with Zopf's figures of *Myzocyttium* and *Lagenidium* respectively; and he adds that ' nous devons noter toutefois que la différenciation sexuelle est bien faible et que, dans beaucoup de cas, il devient impossible de la saisir ' (loc. cit., p. 99).

Fischer ('92, p. 85) remarks that, according to Dangeard's description, ' die Sexualorgane in der Weise entstehen, dass in einem aufgeschwollenen Fadenstück das Protoplasma sich in zwei gleiche Theile verdichtet, die mit einander verschmelzen und die Dauerspore (Zygospore) erzeugen.' Dangeard says nothing about a fusion, although, by his calling the thick-walled cells zygosporoes, he tacitly assumes its occurrence.

I can see no reason for regarding these spores as having been sexually produced. They are merely formed by an increase in size of a part of the ordinary mycelium, and the fact of their sometimes being formed in groups of three, four or five together alone speaks against their sexual origin; for there are no traces of empty antheridial cells between the individual spores in such cases. It is true that the young stages often have a sort of pear-shaped form, so that there are apparently a large and a small swelling side by side (cp. Fig. 18 of *R. Boodlei*); but in these cases the fully-developed spore has the same shape (Figs. 20, 21), and I was unable to detect a differentiation into two protoplasmic masses in the earlier stages.

There is one further point, which I think speaks very strongly against the sexual origin of these spores. I have already mentioned that some branches of the parasitic hyphae

<sup>1</sup> It is not quite plain to me, whether Dangeard is referring to the entire hypha, in whose course the spore is formed, or to the non-occurrence of a division-wall between the assumed sexual organs; if the former is the case, this is a point of difference between *R. nodosa* and the form I am describing.

can leave the host and emerge into the surrounding medium. In some cases this external mycelium becomes very much branched, and spores, in all respects similar to those formed on the internal hyphae, are developed on it by a kind of budding-process. Short lateral branches of the unseptate mycelium swell up apically, thus becoming capitate (Fig. 27). In these swellings, as they increase in size, large oily granules appear, whilst the thickened membrane finally becomes differentiated into two layers and takes on a dark brown colour; the fully-developed chlamyospore is separated by a transverse wall from the mycelium on which it is borne (Fig. 28). The spores, formed in this way, are usually absolutely spherical and are attached by a short stalk—the unaltered portion of the lateral branch—to the mycelium. Such spores were formed in great numbers during the previous month; undoubtedly they go through a resting-period, but of what duration I am unable at present to say. A comparison of the figures will show that these spores differ in no respect from those formed internally, and here it is certainly impossible to assume the occurrence of a sexual process.

Although I have at present preferred not to give the Fungus just described a new name, it may turn out to be specifically distinct from *R. nodosa*, Dangeard. In this latter species branching is scarce, the spores contain a single large oil granule<sup>1</sup> and are apparently only formed singly, and zoospore-formation is apparently common. The dimensions of the spores agree fairly well.

I give the following measurements of the Fungus described :

Diameter of internal (parasitic) mycelium =  $\cdot 004$ – $\cdot 006$  mm.

„ „ external mycelium =  $\cdot 0005$ – $\cdot 001$  mm.

„ „ chlamyospores =  $\cdot 006$ – $\cdot 009$  mm.

## 2. RESTICULARIA BOODLEI, NOV. SP.

This species was found parasitic in the filaments of a *Tolyptothrix*, which formed the most characteristic feature

<sup>1</sup> Dangeard found that the spores of *R. nodosa* later came to contain a number of oily granules (loc. cit., p. 98); he interprets this as a stage preceding germination.

of the algal vegetation in the lower of the two Pen Ponds, Richmond Park, last November; since then the Alga has practically disappeared.

In the material collected in November, 1902, all the algal filaments presented a healthy appearance, and the only indication of the presence of the Fungus was to be found in the occurrence of numbers of colourless spores of relatively large size between the threads of the *Tolybothrix*. These spores had rather thin walls generally differentiated into two layers, and possessed clear, homogeneous contents (Fig. 1); many of them had grown out at one or more points, giving rise to unseptate hyphae, which frequently followed the course of the algal filaments externally, not rarely enveloping them in a perfect mycelial web, which, however, remained purely epiphytic. In germination the external layer of the membrane is ruptured, and the contents surrounded by the internal layer grow out. One curious feature observed at this date remains to be mentioned. Some of the spores appeared to lie *within* the external layer of the *Tolybothrix*-sheath, a position for which I am unable to account (Fig. 1).

In samples of the same Alga, collected a month later, it was at once apparent that some change had taken place. In many places the dark green colour of the *Tolybothrix* had given way to a dirty greenish-yellow, and all transitions between these two colours could be observed with the naked eye. A microscopic examination showed that now, in addition to the abundant epiphytic mycelium of the Fungus, large numbers of hyphae had penetrated into the interior of the Alga<sup>1</sup>; Fig. 2 shows a germinating spore, the hypha from which has pierced the sheath and grown for a short distance inside the host. Once successfully inside, the Fungus makes rapid progress, and large numbers of the algal filaments were found to contain long moniliform hyphae, like the one shown

<sup>1</sup> It is curious that a diligent search revealed no traces of parasitic hyphae a month before. Possibly the Fungus is only able to penetrate into the Alga, when the latter is in a low state of vitality. The way in which the filaments of the latter are enveloped by the epiphytic mycelium might alone tend to produce such a state; and thus ultimately make it possible for some hyphae to penetrate into the host.



in Fig. 3. This moniliform shape of the parasitic hypha is due to the same cause as in *R. nodosa*, Dangeard; that is to say, the Fungus expands considerably within each cell of the Alga, narrowing down each time it has to penetrate one of the transverse walls of the latter. The Fungus itself at this stage either presents no partition-walls whatever, or they only occur at very rare intervals; this is readily discerned with a high power of the microscope. As the parasite grows on in front, it generally dies off behind, and the posterior portion is then cut off from the living anterior part by the successive formation of transverse walls; these generally arise at the points where the constrictions occur (Figs. 8, 10). The living portion of the Fungus has perfectly homogeneous contents of an opaque white appearance, occasionally interrupted by small drops of oily matter of a highly refractive nature (Figs. 3, 7). Nuclei were not observed. The segments are most commonly ovate, but occasionally spherical. The Fungus only rarely pursues a straight course within the Alga; generally it is more or less zigzag or spiral<sup>1</sup>.

The Fungus has the same effect on the cell-contents of the Alga as the species first described; in both cases no deformation of the algal filaments, such as Dangeard describes as occasionally occurring in the *Lyngbya* attacked by *R. nodosa* (cp. Dangeard, '90, p. 96), was observed. Fig. 3 shows the protoplasmic contents of the algal cell contracted around the segments of the parasite, whilst Figs. 4, 7, 8, &c., show stages in which the Fungus alone remains within the sheath of the *Tolypothrix*.

Usually only a single fungal hypha is to be seen in each algal filament; in a very few cases branching was observed to take place, both branches continuing to live inside the host. On the other hand, external branches, i. e. branches which penetrate the sheath of the Alga and emerge into the surrounding water, are very common. Figs. 3 and 4 show early stages in the development of such branches, whilst Figs. 5, 6, and 7

<sup>1</sup> In passing from one homogonium of the Alga to another the hypha narrows down and presents no constrictions (Fig. 8); cp. also Dangeard, loc. cit., p. 97.

show them in the fully-developed condition. These external branches are generally somewhat narrowed down at the point where they pass through the algal sheath, expanding again as soon as they enter the water. Except for the absence of the regular constrictions, they in every way resemble the internal mycelium; transverse walls occasionally occur in their course. They are frequently branched and ramify in all directions in the water. The vegetative cells of the internal mycelium, from which they arise, are in no way especially modified.

When these hyphae come into contact with another healthy algal filament they frequently penetrate its sheath, and give rise to a parasitic mycelium within (Figs. 10, 11). Such infecting hyphae ('Ansteckungshyphen') are one of the chief means of propagation of the Fungus, and constitute a strong point of resemblance to the genus *Ancylistes*, in which they occur abundantly. It should, however, be remarked that these hyphae were often seen to come into contact with a healthy filament of the Alga without attacking it. In some cases the hyphae arising from the parasite all grow out in one and the same direction, as though there were some stimulus regulating their formation and direction of growth.

The thick-walled heterocysts of the Alga (which in this species occurred in groups of 4-9 together), again presented a considerable obstruction to the passage of the Fungus, and not rarely seemed to form an unsurpassable barrier. Further, the Alga protects itself by the formation of thick transverse walls some little way in front of the momentary position of the Fungus<sup>1</sup>. Apparently these also form considerable obstacles to the growth of the latter, and in some few cases the Fungus was observed to emerge from the filament at such a point and to come in again on the other side (Figs. 13, 14), finding it easier to pass through the thick sheath than through the protecting wall formed by the Alga. To the difficulty of passing through a heterocyst must also be

<sup>1</sup> Such protecting-walls were also, but rarely, seen in the case of the first-described species.

attributed the fact that the Fungus so frequently leaves the main filament for a branch at the points, where branching of the *Tolypothrix* occurs; it thus avoids the heterocyst, which is situated immediately above the point of branching.

A few anomalous cases were observed in connexion with the external mycelium. Thus Fig. 12 shows a hypha which has just emerged and has formed a number of branches, one of which is again penetrating into the same algal filament, whilst Fig. 15 shows a case where the mycelial branch has re-entered the Alga and fused with the hypha from which it arose.

I have already mentioned that the external mycelium may be very much branched. In some cases it attains a great development and proceeds to form large numbers of spores. The mycelium then becomes septate and develops numerous lateral branches, which generally do not reach any considerable length. In these branches transverse walls are formed, so that they come to consist of a row of thin-walled cells. These increase in size, at the same time assuming an elliptical shape (Fig 16), and develop into the thin-walled spores, which were first seen in November last. In some cases the lateral branches are very short and only develop into a single spore, which is thus formed in a way very similar to the chlamydospores of the first described species.

In other cases the mycelium proceeds to form these spores immediately after emerging from the Alga, as is seen in Fig. 17; here the entire external mycelium has been transformed into spores. This is frequently the case, and when spores are thus formed from a strongly-branched and extensive mycelium we get enormous masses of them, many of which still show their origin from a row of cells. The spores are oval and generally slightly drawn out at one or both ends, owing to their previous position in a moniliform thread (cp. Fig. 16). When occurring in extensive masses the shape of the individual spores is often very curious, probably owing to mutual pressure in their crowded position. These spores can germinate almost at once, sending out one



or two hyphae in various directions (Figs. 5 and 9), relatively only a few of which are successful in penetrating an algal filament. Fig. 5 shows a spore which has rather thicker walls than is usual in this species; such spores are occasionally to be found.

As already mentioned, this mode of formation of the spores does not account for their occasional position within the layers of the *Tolybothrix*-sheath (Fig. 1). Such a position can be accounted for by assuming spore-formation to have taken place on a mycelial branch, ramifying in the sheath of the Alga. Such mycelial branches undoubtedly occur, but I have never observed a formation of spores in them.

In a few individuals certain parts of the parasitic hyphae were seen to be very much more swollen than others (Fig. 18); such swollen portions may possibly develop into internal spores, analogous to those of *R. nodosa*, Dang., but I have as yet been unsuccessful in following up their further fate. They were especially observed in material grown in a solution of cane-sugar. Since the spores usually formed by *R. Boodlei* are relatively thin-walled and incapable of existing for a long period, it would seem natural that they should only be formed on the external and not on the internal mycelium. For spores, formed in this latter position, must be surrounded for a long time by the empty sheath of the *Tolybothrix*, and months would ordinarily elapse before this latter would decay and leave the spores lying freely in the water. It is true that the fungal hyphae normally have to penetrate the sheath of the Alga, but it is questionable whether a young, just-formed hypha is capable of doing this.

I have had the species described under observation for several months, and have seen no indication of zoospore-formation.

The life-cycle of *R. Boodlei* may be briefly summarized as follows: Mycelial branches, emerging from the internal parasitic hyphae, give rise to large numbers of thin-walled spores. These germinate almost at once, giving rise to one or more hyphae, which attack the host and penetrate into

its interior. Branches of the internal mycelium also serve to convey the Fungus from one individual to another.

I give the following measurements of this species:—

Diameter of the internal mycelium =  $\cdot 005 - \cdot 008$  mm.

„ „ external „ =  $\cdot 0015 - \cdot 005$  mm.

„ „ spores =  $\cdot 012 - \cdot 015$  mm.

A few remarks may be added on the bearing of the facts, described in this paper, on the systematic position of the genus *Resticularia*. As far as I am aware, the formation of spores on external branches of the parasitic mycelium is a feature as yet unobserved in the Ancylistaceae; and in the two species under consideration this is evidently a common method of propagation. Whereas the species, which I have provisionally united with *R. nodosa*, Dangeard, forms thick-walled chlamydospores, *R. Boodlei* has thin-walled spores, incapable of standing a long resting-period. Undoubtedly this latter species also forms chlamydospores of some kind, enabling it to pass through unfavourable external conditions; and it remains to be seen whether *R. nodosa* does not also form thin-walled spores at some period in its life-history.

Since the observations contained in the preceding pages tend to cast considerable doubt on the sexuality of *R. nodosa*, one of the chief links connecting the genus in question with *Ancylistes* is removed. According to Pfitzer's description ('72, p. 379), there are undoubted dioecious sexual organs in this latter genus.

In many respects, however, *Ancylistes* and *Resticularia* are similar to one another, and it will be best for the present to leave them side by side; although further observations may make it advisable to place the latter genus in a separate section of the Ancylistaceae<sup>1</sup>. Renewed observations may

<sup>1</sup> Quite recently v. Deckenbach has published an interesting treatise on a new Fungus parasitic in marine species of *Calothrix* (*Coenomyces consuens*, nov. gen. nov. spec., Flora, Bd. xcii, 1903, pp. 253-83, Pl. VI and VII), which further contains a lengthy discussion of the phylogenetic relationships of the Fungi. *Coenomyces* possesses a well-developed septate mycelium, and is propagated by means of uniciliate zoospores (the only method of reproduction observed); owing to the occurrence of these two characters side by side, which are considered as

also make it advisable to separate *R. Boodlei* generically from Dangeard's species.

The following is a brief description of the genus *Resticularia* and its two species:—

*Resticularia*, Dangeard (emend.).

Mycelium in part endophytic, in part ectophytic. Endophytic mycelium moniliform, with or without transverse septa, occasionally forming chlamydospores; ectophytic mycelium with or without septae, generally strongly branched and forming thin- or thick-walled spores. Other portions of the ectophytic mycelium act as infecting-hyphae. Sporangia formed in the endophytic mycelium, the contents of which are protruded to the outside through the wall of the host and there split up into a small number of zoospores, the latter rather large and uniciliate.

*R. nodosa*, Dangeard (emend.).

Endophytic mycelium (diam. 4–6  $\mu$ ) usually septate, and forming numerous chlamydospores (diam. 6–9  $\mu$ ), ectophytic mycelium very fine (diam. .5–1  $\mu$ ), much branched, forming numerous chlamydospores, singly on lateral branches. Infecting-hyphae rare. Endophytic mycelium commonly branched. Zoospores occasionally formed. In the filaments of *Lyngbya aestuarii* (Dangeard!) and *Tolypothrix* sp. (mihi!).

*R. Boodlei*, Fritsch, n. sp.

Endophytic mycelium (diam. 5–8  $\mu$ ), with occasional septa; ectophytic mycelium relatively broad (diam. 1.5–5  $\mu$ ), much

characteristic of the higher and lower Fungi respectively, a new division, Coenomycetes, is established for the reception of the genus *Coenomycetes*, and to this *Aphanistis* must probably also be referred. This division is thought to occupy an intermediate position between Phycomycetes and Eumycetes, although originating from an independent stock. The space at my disposal does not allow of a detailed discussion of these views, but the existence or non-existence of transverse walls in a fungal mycelium does not appeal to me as a point of great importance. In *Resticularia nodosa*, Dang., for instance, the internal mycelium is distinctly septate, whilst in *R. Boodlei* septation only occurs in connexion with the dying out of the hyphae; in this latter species, however, the external mycelium at the time of spore-formation is distinctly septate. I have not yet observed the zoospores of these two species (cf., however, Dangeard for *R. nodosa*), but their discovery would seem to me to necessitate the inclusion of this genus in the *Coenomycetes*, if further investigation warrants the maintenance of this group. (Note added July 6, 1903.)



branched, forming numerous large thin-walled spores (diam. 12–15  $\mu$ ), generally in a chain on lateral branches. Infecting-hyphae abundant. Endophytic mycelium rarely branched. Zoospores not observed. In the filaments of *Tolyptothrix*, sp.

It only remains for me to acknowledge the kind assistance of a friend in the preparation of the figures for this paper.

UNIVERSITY COLLEGE, LONDON.

March 6, 1903.

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DESCRIPTION OF FIGURES IN PLATE XXIX.

Illustrating Dr. Fritsch's paper on Fungi parasitic on *Tolythrix*.

Figs. 1-18. *Resticularia Boodlei*, n. sp.

Fig. 1. Two spores, lying in the membrane of the *Tolythrix*, from which epiphytic hyphae have arisen.  $\times 600$ .

Fig. 2. A spore has germinated, giving rise to a short endophytic mycelium.  $\times 600$ .

Fig. 3. Fully-developed parasitic hypha, showing moniliform constrictions; at  $\alpha$ , an external branch is developing.  $\times 750$ .

Fig. 4. The same; shows a further stage in the development of the external branch.  $\times 750$ .

Fig. 5. A spore has germinated at both ends; one of the hyphae thus formed has penetrated a filament of the Alga, giving rise to a parasitic, moniliform hypha in both directions. From the internal mycelium an infecting-hypha has branched off.  $\times 750$ .

Fig. 6. A spore has germinated; the parasitic mycelium has formed three infecting-hyphae.  $\times 750$ .

Fig. 7. Oily granules are seen in the mycelium; also an infecting-hypha.  $\times 750$ .

Fig. 8. The Fungus has died off behind and has become septate in the dead portion; in front the mycelium is not constricted, but forms a straight tube.  $\times 750$ .

Fig. 9. Spore germinating; the penetrating hypha has spread out in both directions along the algal filament. The latter has formed thick protecting-walls, a little way in front of the present position of the parasite.  $\times 750$ .

Figs. 10, 11. Infection from one individual of the host to another. The dead posterior portion of the parasite has become septate.  $\times 750$ .

Fig. 12. Reinfection of same filament; see explanation in text.  $\times 750$ .

Figs. 13, 14. Evasion of the protecting-walls formed by the Alga.  $\times 750$ .

Fig. 15. Reinfection and fusion; see explanation in text.  $\times 750$ .

Fig. 16. Formation of spores on the external mycelium, early stages. The arrow indicates the point at which the main hypha continued and joined on to the endophytic mycelium.  $\times 750$ .

Fig. 17. The same; further advanced stage. The entire external mycelium has given rise to spores.  $\times 560$ .

Fig. 18. At *sp.* internal spores are possibly developing.  $\times 750$ .

Figs. 19-29. *Resticularia nodosa*, Dangeard (?).

Fig. 19. This shows the ordinary appearance of the parasitic mycelium, which terminates at one of the heterocysts of the Alga. The cell-contents of the latter are contracted about the Fungus.  $\times 600$ .

Fig. 20. The same; a chlamydospore has developed within the heterocyst.  $\times 600$ .

Fig. 21. A chlamydospore is developed in the course of the internal mycelium.  $\times 600$ .

Figs. 22, 23. Show chlamydospores; in Fig. 22 they alone remain.  $\times 600$ .

Fig. 24. The internal mycelium branched ; a chlamyospore has been formed on the simple portion.  $\times 600$ .

Fig. 25. Internal mycelium branched ; an infecting-hypha has been developed.  $\times 760$ .

Fig. 26. Two chlamyospores are growing out to form long external hyphae.  $\times 750$ .

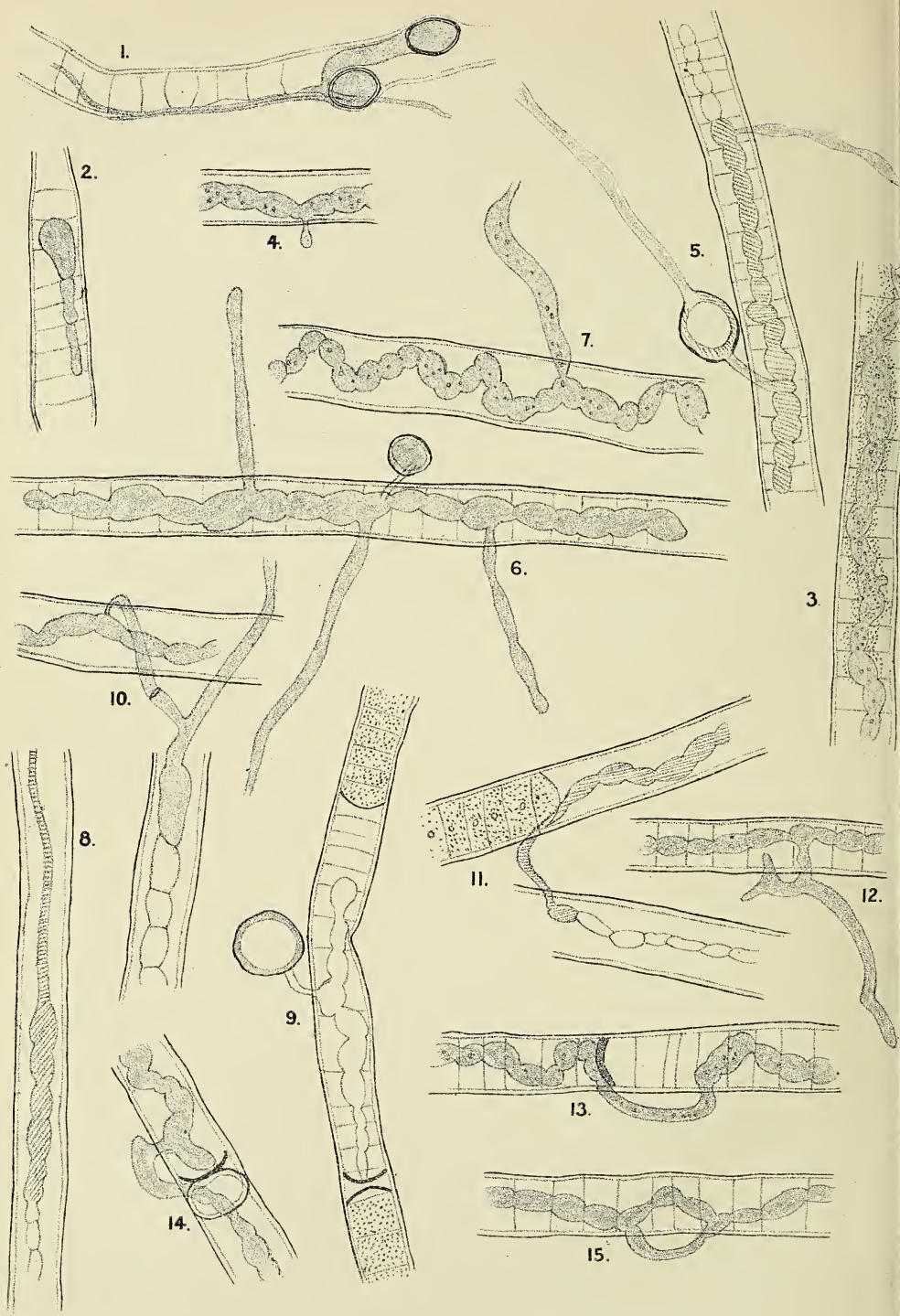
Fig. 27. Young stages in the formation of external chlamyospores.  $\times 750$ .

Fig. 28. Later stages in chlamyospore-formation.  $\times 750$ .

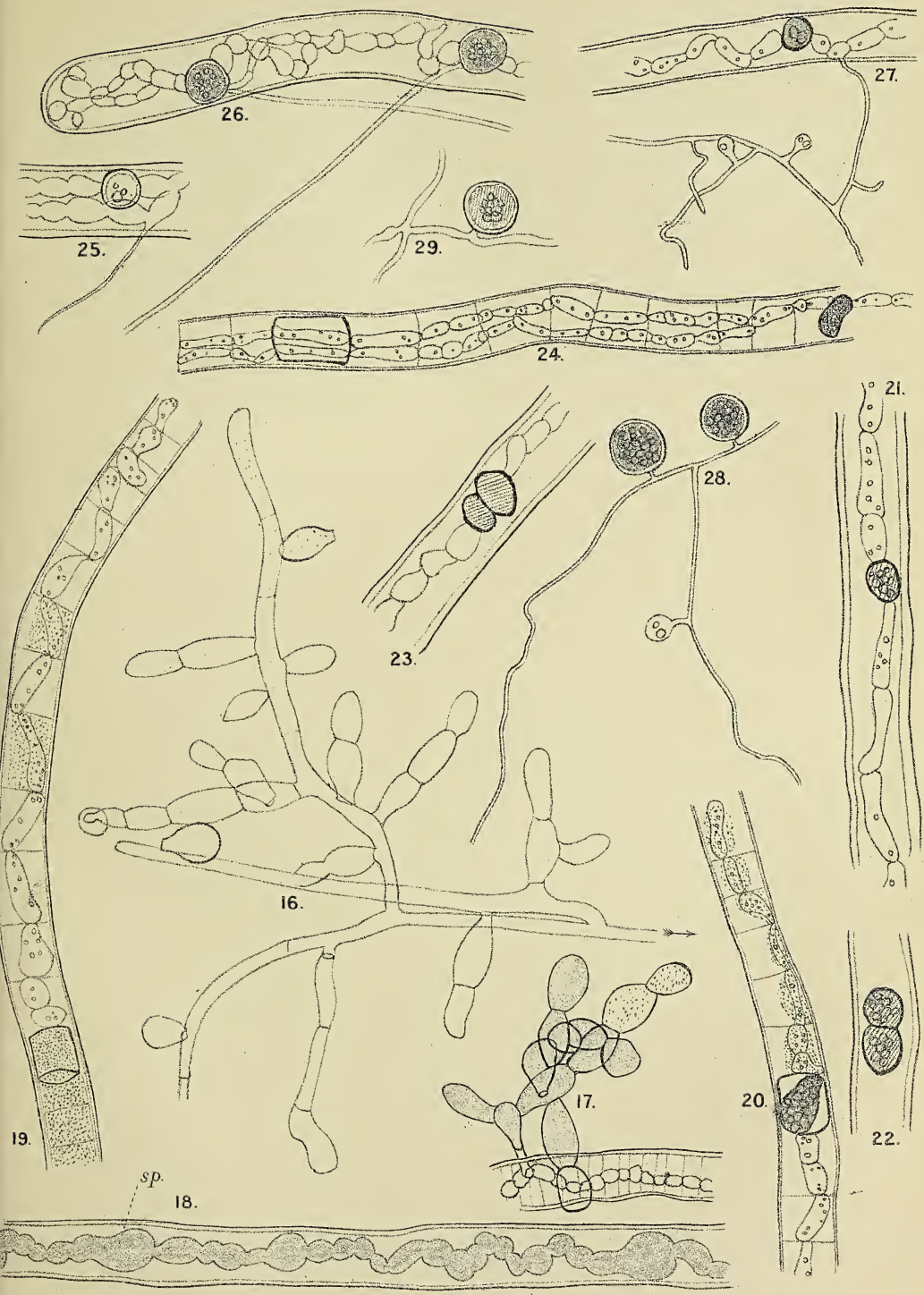
Fig. 29. An isolated chlamyospore with a portion of the external mycelium.  $\times 760$ .





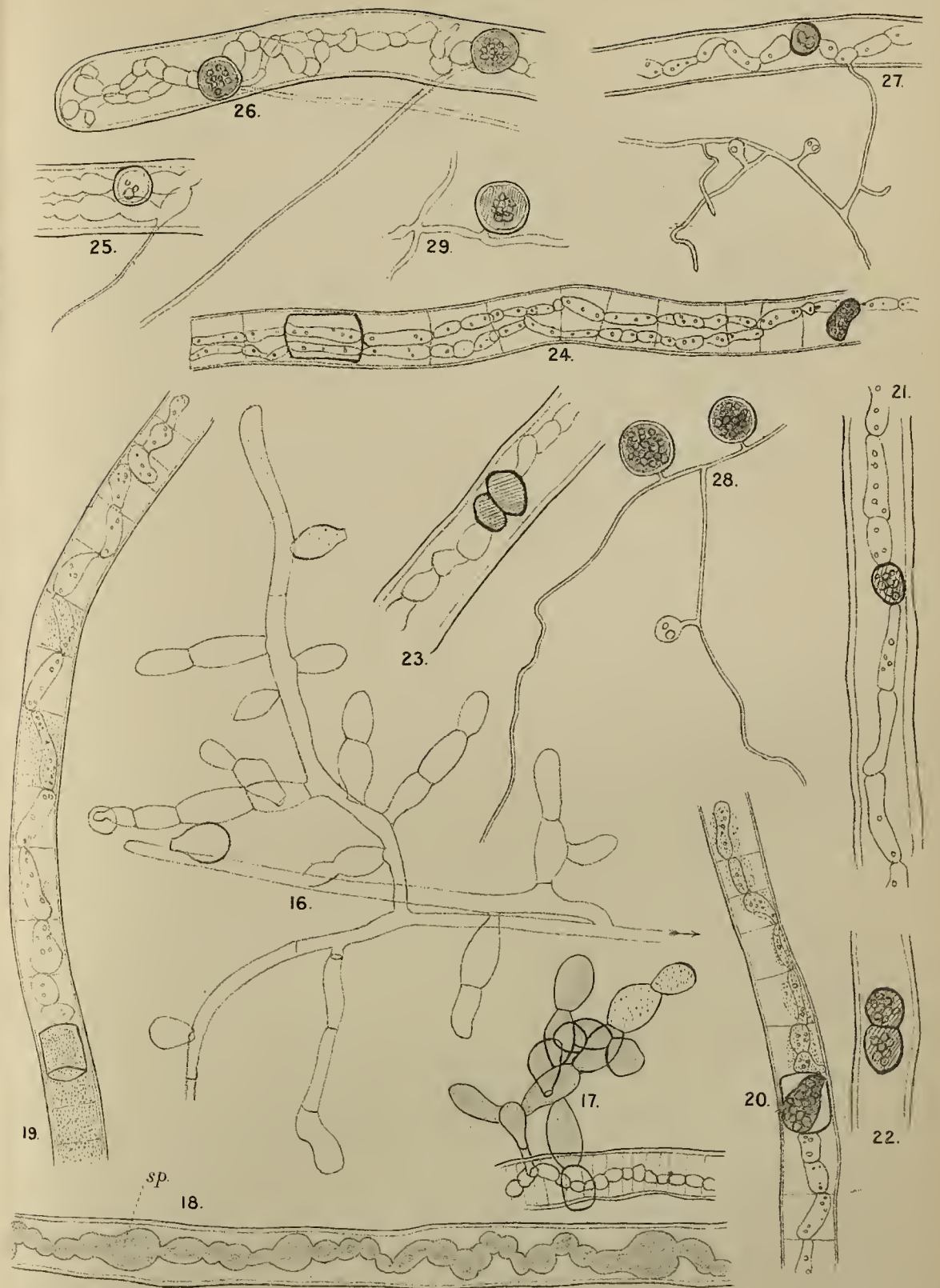
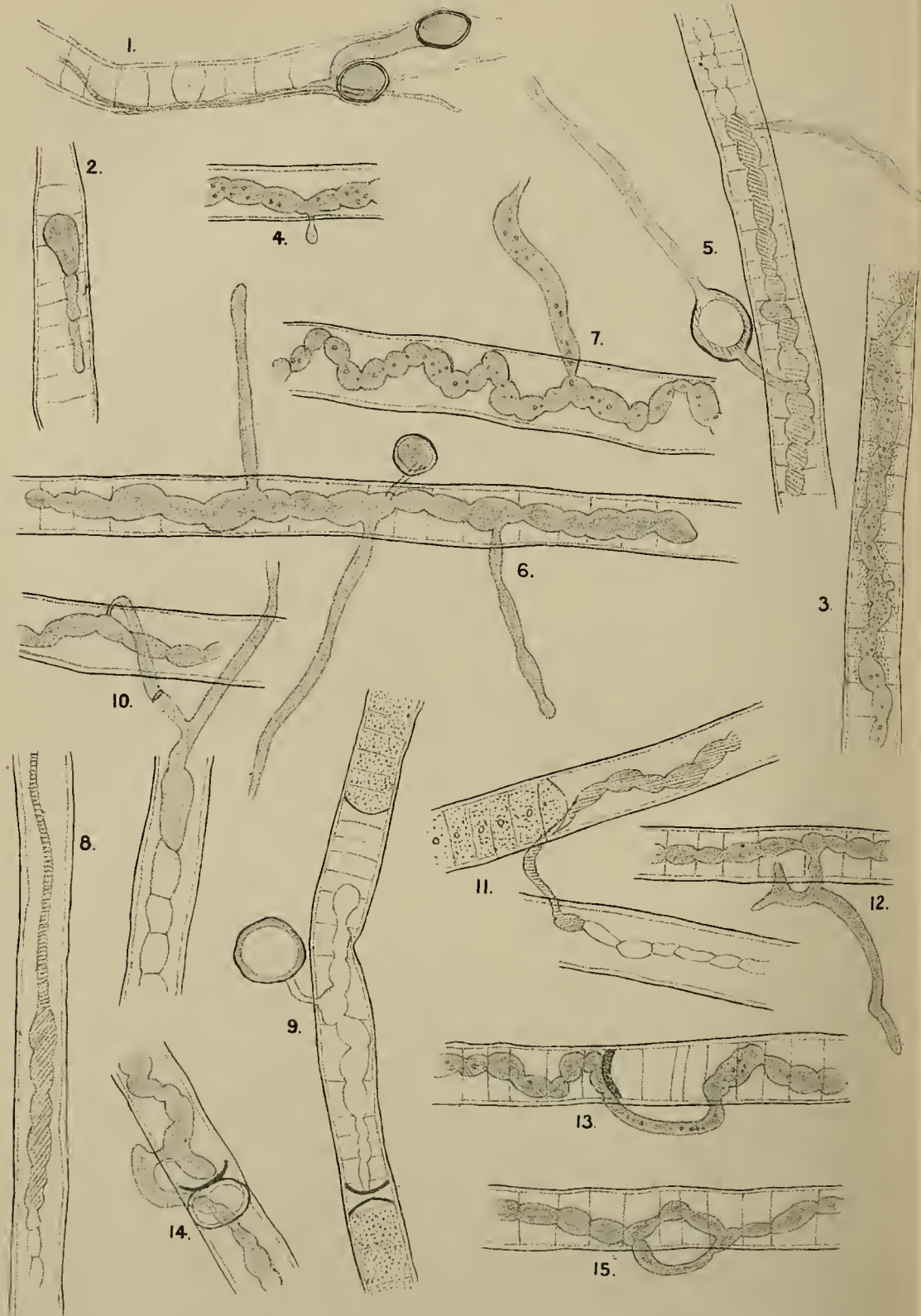


H.L. and F.E.F., del.









HL and FEF, del





## Studies on the Araceae.

The Embryo-sac and Embryo of *Aglaonema* and  
*Spathicarpa*.

BY

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With Plates XXX, XXXI, and XXXII.



SEVERAL years ago a series of investigations were undertaken upon the development of the embryo-sac and embryo in the Araceae. Some of the results of these studies have already been published<sup>1</sup>, but the investigations were interrupted for a time owing to pressure of other work, and have but recently been resumed. The present paper deals for the most part with two species, *Aglaonema commutatum*, Schott, and *Spathicarpa sagittaeifolia*, Schott.

The earlier literature upon the development of the Araceae has been referred to in the writer's previous papers, and will not be repeated here. A paper by Caldwell upon *Lemna*<sup>2</sup> was omitted, but except for this the writer has seen no further contributions to the subject.

The materials upon which the present paper is based were collected at the Royal Botanic Gardens at Kew, in August, 1899. Through the kindness of the director, Sir W. Thiselton-Dyer, it was possible to obtain complete series of a number of species from the rich collection of Aroids in the greenhouses at Kew. Some of the material still remains to be investigated.

<sup>1</sup> Annals of Botany, xiv, March, 1900.

<sup>2</sup> The Life History of *Lemna minor*, Bot. Gazette, xxvii, Jan. 1899.

Nearly all the Araceae that have been studied show certain anomalies in the character of the embryo-sac, and this makes it all the more desirable that further investigations should be made upon this interesting family. Both of the species especially treated in the present paper show more or less marked deviations from the ordinary angiospermous type. It is hoped that further study of other genera of the Araceae may not only add to our knowledge of this family, but may also throw light upon the character and origin of the embryo-sac of the lower Monocotyledons.

Among other forms collected in Jamaica in 1897, was a species of *Aglaonema*, probably *A. commutatum*, cultivated under the name *Dieffenbachia Aglaonema*, which showed some puzzling abnormalities; but the material was too incomplete to make a thorough study of these possible. What was apparently the same thing was found flowering freely at Kew, and a good supply was secured which served for the basis of the work now recorded. Much the same peculiarities of the embryo-sac noted in the Jamaican specimens were found, and a fairly complete study was made of the species.

The other form to which special attention has been given was *Spathicarpa sagittaeifolia*, which was flowering and fruiting very freely in the Kew greenhouses.

Owing to the large amount of mucilaginous matter secreted by the ovules in many Araceae, they are especially difficult to fix properly, and even with the greatest precautions much of the material was very unsatisfactory. On the whole, the best results were obtained by the use of a concentrated alcoholic solution of corrosive sublimate. Aqueous fixing fluids were useless in most cases. Some good results were also obtained by the use of alcohol, to which ten per cent. of acetic acid was added. This was not specially satisfactory for fixing nuclei, but otherwise often gave very good results. Fleming's triple stain was used with success in some cases, but very good preparations were also made by staining with alcoholic Bismarck-brown and aniline-safranin.

Most of the Araceae that have been examined show various

peculiarities, both in the formation of the endosperm, and in the behaviour of the antipodal cells. Some of them, like *Arisaema triphyllum*<sup>1</sup>, differ also from the usual angiospermous type, in the character of the archesporium. The archesporium in this species shows in cross-section from two to four or five cells, which, according to Mottier, are the product of the division of a single primary archesporial cell. It seems probable, however, that sometimes, at least, these cannot all be traced back to the division of a single primary archesporial cell, but arise from two or more independent sub-epidermal cells. A similar archesporium has been found by the writer in *Aglaonema commutatum*, and it is quite probable that further research will show the same thing in other Araceae.

Hofmeister<sup>2</sup> showed that in nearly all the Araceae examined by him the endosperm at an early period fills the embryo-sac with a continuous tissue, or in some cases leaves a greater or smaller portion of the cavity permanently empty<sup>3</sup>. He however misunderstood the process of cell-division by which the endosperm is formed, and supposed that in all cases there was a 'free cell-formation' preceding the formation of the solid endosperm. It is true that in *Pothos longifolia* he found frequently an early division by a transverse cell-wall; but he infers that the subsequent endosperm formation, which he says is confined to the upper and larger of the two primary cells, is formed by 'free cell-formation,' and not by successive cell-divisions, as is probably the case. A type of endosperm formation somewhat similar to that of the Araceae has been described by Strasburger<sup>4</sup> for *Ceratophyllum*. In this case, however, the first division-wall in the embryo-sac divides it into equal parts.

Hofmeister called attention to the large size of the antipodal cells in some species of *Arum*, and the writer has found in *Lysichiton* a remarkable development of the antipodal cells

<sup>1</sup> Mottier, Bot. Gazette, 1892.

<sup>2</sup> Neue Beiträge zur Embryobildung, &c.; Monocotyledonen. Leipzig, 1861.

<sup>3</sup> l. c. p. 704.

<sup>4</sup> Ein Beitrag zur Kenntniss von *Ceratophyllum submersum*, Pringsheim's Jahrb. für wiss. Botanik, xxxvii. 564, 1902.



subsequent to fertilization, and much the same thing occurs in *Spathicarpa*, and probably in other Araceae as well. On the other hand, in *Aglaonema commutatum*, it was often impossible to demonstrate certainly the presence of any antipodal cells, although in the apparently closely related species, *A. pictum*, they seem to be always present.

The development of the embryo in the two species under consideration does not show anything specially noteworthy. In *Spathicarpa* the embryo remains small, and there is a largely developed endosperm in the ripe seed; in *Aglaonema* the mature embryo nearly fills the embryo-sac.

The very considerable variation shown in the types of Araceae already studied make it highly desirable that as many types as possible should be investigated in order to determine the affinities of the family. It is to be hoped that the characteristic genera of the eastern United States may be examined by some of the botanists who are interested in the morphology of the embryo-sac, and have access to material of our native Araceae.

#### AGLAONEMA.

The genus *Aglaonema*<sup>1</sup> comprises about ten species of the East Indies and Malayan region. Several species, including *A. commutatum*, are in cultivation. The latter species was flowering freely at Kew in August, 1899, and apparently the same plant was collected at the Hope Gardens, near Kingston, Jamaica, in the summer of 1897. A second species, *A. pictum*, was also flowering at Kew, and material of this species was collected.

The flowers are unisexual, the pistillate flowers being borne at the base of the thick spadix, the crowded staminate ones occupying the upper portion. No perianth is developed, but there is a conspicuous white spathe, partially enwrapping the base of the spadix.

The pistillate flower consists of a single carpel, with a

<sup>1</sup> Engler and Prantl, *Die natürlichen Pflanzenfamilien*, 11. Th., 3. Abth., p. 135.

large solitary anatropous basal ovule. The nearly globular ovary is crowned with a large discoid sessile stigma, slightly depressed in the centre, where it joins the very short canal leading to the ovarian cavity.

While *A. commutatum* and *A. pictum* agree closely in their structure, the former, owing to its larger nuclei, as well as from the peculiarities of the embryo-sac, was especially studied, and, unless otherwise stated, the account here given refers to this species.

The ovule from the first is very massive, and while the integuments are developed at an early period, they remain short, the chalazal region of the ovule being very large—a not uncommon feature in other Araceae as well. The short funiculus is also very thick.

The nucellus is relatively small. In the youngest stage observed (Pl. XXX, Fig. 1) the young embryo-sac was already evident, an elongated cell with a large nucleus. Whether in this case the embryo-sac arose directly from a hypodermal cell, or whether it was the product of the division of a primary archesporial cell, could not be positively ascertained.

The lateral tissue of the young nucellus consists of two or three layers of cells, while at the summit the cells are somewhat larger, and persist as a cap of tissue after the lateral tissue of the nucellus is destroyed. This occurs at an early stage, so that the embryo-sac soon comes into contact with the inner integument.

In a number of cases observed, and this evidently is not unusual, the archesporium consisted of two or three large cells, all of which were apparently potential embryo-sacs. These ovules (Figs. 5, 7) much resemble those of *Arisaema triphyllum*.

As the embryo-sac enlarges the lateral tissue of the nucellus is soon crowded upon, and finally becomes quite obliterated. The apex of the nucellus, as in many other similar cases, persists as a conical cap above the apex of the embryo-sac.

There is so much variation in the behaviour of the embryo-sac in its earlier stages that it is difficult to say what may be

considered the normal development. No tapetal cells were observed in any case, and the single archesporial cell, or each of the two or three cells where more than one embryo-sac mother-cell is present, develops at once into the embryo-sac. Where two or three young embryo-sacs develop, they may be separated by an obliquely transverse wall (Fig. 7), or more commonly by oblique or longitudinal walls (Fig. 5).

Where a single embryo-sac only is present, it enlarges rapidly, and the nucleus divides as usual, the two daughter-nuclei sometimes at least occupying approximately the micropylar and antipodal ends of the young sac (Fig. 4). With the crowding upon the nucellar cells, their nuclei become extraordinarily flattened, assuming the form of thin discs, in which the nuclear network is extremely conspicuous (Fig. 4, *c*). After the second nuclear division in the embryo-sac, the nuclei may be in pairs at the end of the sac, but this is not always the case. In the specimens shown in Fig. 6 the four nuclei were close together at the apex of the sac, and from other cases examined it is clear that the polarity, so marked in the embryo-sac of most Angiosperms, is in this case very slight or quite absent. Even where the nuclei are in two groups they are more often placed laterally than at the extremities of the sac. This is especially true of the group from which the egg-cell develops. So far as could be determined from the examination of a large number of ovules, the characteristic structures of the typical angiospermous embryo-sac, the egg-apparatus, polar nuclei, and antipodals are never clearly differentiated in *Aglaonema commutatum*.

While the number of nuclei is probably eight in most cases, there are frequently deviations from this number. In the specimen shown in Fig. 8, *c, d, e*, there were twelve nuclei, in three groups of four; Fig. 18 shows a sac with ten nuclei, six in one group and four in the other; in Fig. 9 is shown a sac in which the nuclei were only four, although something like an egg-apparatus was evident at the micropylar end of the sac.

Where the archesporium consists of more than one cell,



each is a potential embryo-sac, and its nucleus may undergo the first divisions; but in no case observed was more than one complete embryo-sac seen. The secondary embryo-sac, where two are present, may persist, however, until the definitive embryo-sac has reached its full development; indeed it is quite impossible sometimes to be certain whether the structures present at the time of fertilization are all the products of a single embryo-sac, or of two (see Fig. 11). Where two or three embryo-sac mother-cells are present, they are often quite similar, and as the nucleus may divide once or twice in all of them, it is impossible to determine which is destined to become the definitive embryo-sac. In Fig. 5 is shown an ovule where there are two entirely similar young embryo-sacs, each of which contains four nuclei. In another case observed (Fig. 7) there were three young embryo-sacs separated by oblique walls. In the upper one (*a*) there was a single large nucleus; in the second (*b*) there were eight nuclei, in two groups of four, and the members of each group partially fused, in a manner entirely similar to the ordinary fusion of the polar nuclei. The lower sac (*c*) was apparently the definitive embryo-sac. There were eight (possibly nine) nuclei in this. Four of the nuclei were enclosed by delicate membranes, and formed a group of cells suggesting an egg-apparatus, or possibly a group of antipodal cells. Near these was a nearly hemispherical cell (*d*) whose nucleus was preparing to divide. This was near the upper end of the sac, but at one side. Near the base of the sac was a group of large nuclei, partially fused together, and presumably giving rise to the endosperm-nucleus. Three nuclei were very plainly seen, and there was possibly a fourth one, but this could not be certainly determined. Whether the two groups of nuclei in the second embryo-sac (*b*) were destined to take part in the endosperm formation, could not, of course, be determined.

In the embryo-sac shown in Fig. 10 there were eight nuclei. Four of them were at one side of the sac near the apex, and there was some indication of the differentiation of

an egg-cell. The other four were at the antipodal end of the sac, but there were no clearly indicated antipodal cells, nor was there, at this stage, any indication of polar nuclei. A second embryo-sac, containing two nuclei, accompanied this one.

Fig. 23, which shows an embryo-sac taken from the Jamaican specimens, differs from any cases found in the material collected at Kew. At the micropylar end of the sac was a well-marked egg-apparatus, consisting of two clearly defined synergidae and an egg-cell. At the chalazal end were two large nuclei surrounded by a mass of granular cytoplasm, and evidently in the early prophases of division. It would certainly seem that in this case no polar nuclei could be developed, and from older specimens from the same plant (Fig. 24) it looks very much as if the basal nuclei assumed at once the rôle of endosperm nuclei, proper antipodal cells being quite suppressed.

The specimen figured as Fig. 18 showed ten nuclei. Four of these were at the base of the sac, where there was developed a group of four cells, one of which projected into the cavity of the sac, and may have been the egg-cell, but it is possible that this group of four cells may have been antipodal cells. Nearly opposite these were six free nuclei, but no further differentiation could be discerned, and what the further history of the sac would have been could only be conjectured.

In the embryo-sac shown in Fig. 12 there were twelve nuclei. In this case the pollen-tube could be seen, but it was not certain which were the generative nuclei. Above the sac was a second one, in which were two conspicuous nuclei, which may possibly have been the generative nuclei derived from the pollen-tube, but they were much more probably the nuclei of the second embryo-sac. The apex of the lower embryo-sac contained no nuclei. At the lower end were four nuclei (*b*) with delicate membranes between them, and probably to be considered as antipodal cells. Near them was a second group of four cells, which may have represented the egg-apparatus, and on the opposite side of the sac were four

free nuclei, apparently in process of fusion (*c*), presumably to form the endosperm-nucleus.

The specimen drawn in Fig. 13 showed a group of four cells at the apex of the sac. Of these, two lying side by side (*o*, *o'*) were hemispherical, and probably one of them was the egg. In contact with this group of cells was the enlarged end of the pollen-tube, containing a nucleus, which was probably one of the generative nuclei. The second generative nucleus was not clearly visible. Nothing resembling antipodal cells could be seen, but four free nuclei (Fig. 14) were seen in the cavity of the embryo-sac. Two of these were larger, and in close contact. The other two showed some indications of disorganization.

Fig. 15 shows a very peculiar case, which was probably abnormal. There were apparently three embryo-sacs, two smaller ones above and the larger definitive one below. The two upper ones showed signs of degeneration. In the lower one, the chalazal end of the sac was occupied by two very large irregular nuclei (Fig. 16) having every appearance of being composed of several nuclei fused into one. Two other nuclei were present, one of which (Fig. 17) also looked as if it were compound.

In Fig. 11 is shown a puzzling case. Separated from a large cell below, were two distinct cells which may have been derived secondarily from a division of the primary embryo-sac, or may perhaps represent two other embryo-sacs. There was no sign of degeneration in these, and with the large lower cell they seemed to form one structure. Traces of the pollen-tube could be seen, and in one of the cells two nuclei could be seen which were possibly the generative nuclei. Besides these nuclei, two others were present, and in the second of the upper cells there were three nuclei. In the lower cell were two large nuclei in close apposition.

It is very evident that in *Aglaonema commutatum* we have to do with an extraordinarily variable plant. The not infrequent increase in the number of the embryo-sac nuclei, and the imperfect differentiation of the usual structures of the



embryo-sac, are worthy of note, as is also the absence of marked polarity in the arrangement of the nuclei. The frequent occurrence of multiple nuclear fusions is also interesting, as in this respect this species furnishes a condition intermediate between that found in *Peperomia* and that occurring in the typical Angiosperms. A similar condition has been found to exist also in the peculiar genus *Gunnera*<sup>1</sup>.

Where the egg-cell was evident it was usually hemispherical, and was either at the apex of the sac or, more often, laterally placed. While the pollen-tube was seen in a few cases, the fertilization was not satisfactorily made out, and it is possible that some of the apparently abnormal appearances encountered may have been due to lack of fertilization.

The development of the embryo is slow at first, and it remains very small until the endosperm is well advanced in its development. It is not rare to find the embryo-sac filled with a solid mass of endosperm, without any certain evidence of an embryo being present at all.

#### THE ENDOSPERM.

It is not probable that the formation of the endosperm is entirely uniform in *Aglaonema commutatum*. To judge from the frequency with which multiple fusions of the nuclei of the embryo-sac are encountered, it is likely that in such cases the primary endosperm-nucleus results from such fusions, although it also probably may arise from the fusion of two nuclei, as in most Angiosperms. The definitive endosperm nucleus was not seen, nor was it possible to find the first division: but to judge from a comparison with *Spathicarpa* and *Anthurium*, in which the young endosperm presents much the same appearance, it is probable that the first division is accompanied by a wall which cuts off a relatively small cell from the base of the embryo-sac. This is followed by a similar division in the cavity of the embryo-sac, and

<sup>1</sup> Schnegg, Beiträge zur Kenntniss der Gattung *Gunnera*, Flora, Bd. 90, pp. 161-208 (1902).

a second cell is cut off from its base, in contact with the first one. In this way the formation of a solid endosperm proceeds from the base upwards (Fig. 21) until the whole cavity is filled. These cells later undergo further divisions, but in all cases, apparently, nuclear divisions are accompanied by cell-formation.

Not infrequently a group of cells, differing somewhat in appearance from the endosperm-cells, can be seen at the base of the embryo-sac (Figs. 27, 32). These may be possibly antipodal cells, but this point was not satisfactorily proven, and it is not impossible that in some cases, at least, they are merely somewhat modified endosperm cells.

The embryo-sac shown in Fig. 23 was found in some of the Jamaican material referred to this species, but perhaps not correctly determined. In this case, as we have already stated, besides the egg-apparatus, there were but two nuclei, situated at the base of the embryo-sac, and evidently in the early prophase of division. A somewhat older embryo-sac (Fig. 24), evidently of the same type, was found, and from a comparison with these, it appears that the endosperm formation results directly from the further division of the two basal nuclei found in the younger sac. This may be a further development of the type shown at Fig. 9, where the three apical nuclei were already arranged like an egg-apparatus, while but a single nucleus occupied the base of the sac. The complete absence of antipodal cells and polar nuclei in these instances, and the development of endosperm without the preliminary nuclear fusion, is certainly noteworthy.

The embryo-sac in *Aglaonema* becomes strongly bent as it grows. The peculiar mass of cells referred to, differing in appearance from the endosperm-cells (Figs. 27, 32), while in some cases to be interpreted as a mass of antipodal cells, may possibly be an embryo in some instances, as unmistakable young embryos have been found at the chalazal end of the sac; and in some of these embryo-sacs of large size, and already filled with endosperm, no trace of an embryo can be detected at the micropylar end.

The embryo-sac in the ripe seed occupies relatively a small part of its bulk. The large development of the integuments and chalazal part of the ovule suggests the perisperm formation of the Piperaceae or Cannaceae.

#### THE EMBRYO.

The embryo may occupy the usual position at the micropylar end of the sac, but more commonly it is at some distance from the apex of the sac, corresponding to the lateral or even basal position of the egg-cell.

The first divisions (Fig. 24) are probably always transverse, but no well-defined suspensor is developed, this doubtless being associated with the early filling up of the sac with endosperm, which completely invests the young embryo. The cell next the wall of the embryo-sac may be regarded as a suspensor cell, but it does not become enlarged, nor give any other evidence of being functionally important.

The subsequent divisions of the embryo do not show an absolute regularity. The strikingly pointed form of the young embryo shown in Fig. 26 recalls the embryos of some Grasses; but this does not appear to be by any means always characteristic of the young embryo of *Aglaonema*.

As the embryo grows it assumes an elongated form, but for a long time there is no differentiation of the external parts, nor are the tissues at all clearly defined. The enlarging embryo encroaches rapidly upon the endosperm, and fills almost completely the upper part of the embryo-sac. The greater part of the embryo is composed of the cotyledon, which becomes somewhat club-shaped and expanded at the end, which crowds into the enlarged chalazal part of the embryo-sac, destroying the endosperm as it grows, and leaving but a small part of it intact (Fig. 33). The tissues of the embryo are almost perfectly uniform, and the boundaries of the different organs very vaguely defined. The hypocotyl is very short, and although a median section of the root-end of the embryo (Fig. 31) shows some slight differentiation of the primary tissues, this is very imperfect. In the older embryo



(Fig. 34 *a*), a single layer of root-cap cells could be seen, but the tissues of the root-apex show very little evidence of a definite arrangement, and the same is true of the stem-apex (*b*), whose exact position it is impossible to determine.

#### AGLAONEMA PICTUM.

A brief examination was made of *A. pictum*, which closely resembles in general appearance *A. commutatum*, but which shows notable differences in the development of the ovule. The cells of the ovule are decidedly smaller, with correspondingly small nuclei, so that the two species are readily distinguishable in this way. More important, however, is the marked difference in the development of the embryo-sac. So far as one can judge from an examination of a considerable number of mature embryo-sacs of *A. pictum*, this species shows none of the variability so characteristic of *A. commutatum*. In all the specimens examined, the embryo-sac was not essentially different from other typical Angiosperms. The hemispherical egg-cell was accompanied by two large and conspicuous synergidae. Small but perfectly characteristic antipodal cells were at the base of the sac, and a single large endosperm-nucleus, evidently the product of the fusion of two polar nuclei, was conspicuous. Numerous starch granules were present in the sac, especially around the endosperm-nucleus—a not unusual feature of the embryo-sac in some other Araceae, e. g. *Dieffenbachia*. Except for the slightly lateral position of the egg-apparatus, *A. pictum* conforms entirely to the ordinary angiospermous type, and it is very remarkable that the apparently closely related *A. commutatum* should show such an extraordinary difference in the development of the embryo-sac.

The ripe pollen-spores of *A. pictum* contain two generative nuclei, in which respect they differ from those of *Dieffenbachia seguine*, where there is but a single generative nucleus. *Symplocarpus*<sup>1</sup> also shows but a single generative nucleus in the ripe spore.

<sup>1</sup> Duggar, Bot. Gazette, xxix, Feb. 1900.

## SPATHICARPA SAGITTAEFOLIA.

The genus *Spathicarpa*<sup>1</sup> includes four very characteristic South American Aroids. The flowers, which are of the simplest possible structure, are borne directly upon the upper surface of the green leaf-like spathe, no spadix being developed. The flowers are arranged in rows, staminate and pistillate flowers being intermingled. The staminate flower consists of a peltate synangium borne upon a stalk, and closely resembles the peltate sporophyll of *Equisetum*. The pistillate flower (Fig. 35) consists of a single peg-shaped carpel, terminating in a small stigma. No perianth is present, but between the flowers are numerous small nearly sessile staminodia.

The great simplicity of the flowers suggested that the embryo-sac might possibly show correspondingly primitive characters, but this was not found to be the case, although there were some interesting peculiarities which will be considered presently.

The material used, like that of *Aglaonema*, was collected at Kew, and all belonged to one species, *S. sagittaeifolia*. A brief reference to the structure of the embryo-sac in this species has already been published<sup>2</sup>, but a mistake was made in the interpretation of certain structures, which has since been corrected.

The peg-shaped carpel of the exceedingly simple flower is tipped by a small stigma composed of the usual papillate cells. The short style merges gradually into the ovary, which is completely filled by the single basal orthotropous ovule (Fig. 35). Both integuments are well developed, and, as in *Aglaonema*, the young embryo-sac soon destroys the lateral tissue of the nucellus, and thus comes into direct contact with the inner integument.

The earliest stages of the embryo-sac were not seen, but from the youngest ones which could be found it is evident

<sup>1</sup> Engler and Prantl, l. c., p. 145.

<sup>2</sup> Campbell, *American Naturalist*, Oct. 1902.

that there is no marked departure from the usual course of development. Whether the embryo-sac mother-cell arises at once from the primary archesporial cell, or is formed after division of the latter, could not be determined.

The apical part of the nucellus persists as in *Aglaonema*, but is perhaps a little larger, relatively. In the youngest case met with (Fig. 36) the primary nucleus of the embryo-sac had already divided, and the daughter-nuclei, which were placed at opposite ends of the sac, were dividing, the division of the two taking place simultaneously, and the embryo-sac at this stage presented the usual appearance.

No attempt was made to follow in detail the development of the sac up to the time of fertilization, as it was evident that it was in no way peculiar. The three cells of the egg-apparatus are nearly similar, and taper into the narrowed micropylar end of the sac. The polar nuclei are just above the three antipodal cells (Fig. 39), and their fusion into the endosperm nucleus is completed some time before fertilization takes place. In most cases observed, the fusion was complete. The antipodal cells are surrounded by distinct membranes, and while not noticeably conspicuous, are readily demonstrable.

Owing to the small size of the nuclei the plant does not offer special facilities for studying the phenomena of fertilization, and no attempt was made to follow these in detail, although in several cases the sexual nuclei were observed in process of fusion. The process is evidently slow, and before it is complete the egg has increased perceptibly in size, and the pollen-nucleus, which is smaller than the egg-nucleus, becomes much flattened against the latter, with which it finally merges completely (Figs. 41, 44). The fusion-nucleus is not noticeably rich in chromatin, but has a conspicuous nucleolus. In the cytoplasm of the egg there are formed numerous small starch-grains which become larger before the first division occurs in the young embryo. These starch grains disappear during the early cell-divisions in the embryo, and are probably used in the formation of the cell-walls.



In the specimen figured in Fig. 37 one of the synergidae was conspicuous, while the second one was smaller, with a smaller nucleus; whether this inequality is frequent in *Spathicarpa* was not determined.

#### THE ENDOSPERM.

The endosperm-nucleus increases a good deal in size before its first division. It lies just above the antipodal cells, and is imbedded in a mass of granular cytoplasm, which exhibits a more or less reticulate appearance in sections, probably indicating a vacuolate structure in the living state. The endosperm-nucleus has a conspicuous nucleolus, and is much richer in chromatin than the egg-nucleus. The first division of the nucleus was not seen, but from the appearance of the very young endosperm there is little question that the first division results in the cutting off of a basal endosperm-cell from the embryo-sac. The youngest stage observed (Fig. 40) consisted of three basal endosperm-cells, with exceedingly delicate membranes, and a fourth nucleus lying free in the base of the undivided portion of the embryo-sac. From a study of older stages, it is clear that the development of the endosperm proceeds from the base toward the apex of the sac, which soon becomes entirely filled with the cellular endosperm. The large, thin-walled primary endosperm-cells divide further, so that the cells of the endosperm become smaller and their membranes thicker.

#### THE ANTIPODAL CELLS.

The three small antipodal cells present at the time of fertilization are stimulated into active growth and show an extraordinary development. Not infrequently, in somewhat later stages, four or occasionally more antipodal cells are present, but it is probable that the increased number is due to a division of one or more of the original antipodal cells, subsequent to fertilization. The small compressed antipodal cells of the embryo-sac at the time of fertilization elongate

rapidly to many times their original dimensions, and show every indication of extremely active growth. The cytoplasm is abundant, and the small nuclei enlarge rapidly, becoming extremely conspicuous. At this period (Fig. 42) the enlarged antipodal cells so closely resemble the young endosperm that they were at first mistaken for them, and this led to the erroneous statement made in a former article.

The walls of the antipodals become thicker, and they ultimately reach gigantic dimensions, being easily seen in sections by the naked eye (Fig. 56). This enlargement is accompanied by a corresponding growth of their nuclei, which become many times larger than those of the endosperm-cells. At first they show a perfectly normal structure, but later there are evidences of disintegration. The nucleoli become immensely enlarged (Fig. 59), and finally very irregular in form, and the reticulate structure of the active nucleus becomes more or less completely broken down, and shows many evidences of disintegration.

From their close resemblance to the active young endosperm-cells, there can be no doubt that the antipodals function as endosperm during the early development of the fertilized embryo-sac.

The great enlargement of the antipodal cells is not peculiar to *Spathicarpa* among the Aroids. Hofmeister<sup>1</sup> figures enlarged antipodal cells in *Arum orientale*, and the writer has noted the same phenomenon, accompanied by increase in their number, in *Lysichiton*. In the latter there is also the great enlargement and subsequent degeneration of the nuclei of the antipodal cells. It is highly probable that a similar condition will be found in other genera.

#### THE EMBRYO.

The fertilized egg increases slowly in size, but there is no division of the embryo until the embryo-sac is nearly or quite filled with endosperm, so that almost from the first the embryo is completely surrounded by the endosperm-tissue,

<sup>1</sup> l. c., Pl. VII, fig. 4.

and, as might be anticipated, the suspensor is very rudimentary.

The first division is transverse and cuts off a small pointed basal suspensor-cell, which, however, undergoes very little further growth. The next divisions are probably not always exactly the same. Usually the second wall is vertical (Fig. 45) and divides the embryonal cell into two nearly equal parts. Sometimes before this vertical wall is formed an oblique wall may cut off a small cell (Fig. 46) in contact with the suspensor-cell. The latter does not always show the pointed form which usually distinguishes it. Following the first vertical wall in the embryonal cell, there are usually two transverse walls, intersecting it and dividing the embryo into nearly equal quadrants, and these may be divided into octants, although it is not probable that this is always the case. Figs. 49-52 represent nearly median sections of embryos of about the same age, showing the variation in form as well as in the cell-arrangement and the character of the rudimentary suspensor.

For a long time there is no evidence of the development of the external organs, nor is it possible to trace any definite relation between these and the earlier divisions of the embryo. The stem-apex arises in a lateral depression at a point a little below the middle of the embryo, the region below developing the hypocotyl and root, the part above, the cotyledon (Fig. 53). In the origin of the organs of the embryo, *Spathicarpa* does not differ essentially from the commonest type of the Monocotyledons. The tissues of the embryo remain almost perfectly homogeneous, and even in the root, where the arrangement of the tissues is most regular, the limits of the different tissue systems are very imperfectly defined. At the root end, in the most advanced embryo, there may be seen the rudimentary suspensor, and although the tissues are somewhat better defined than in the embryo of *Aglaonema*, still they are rather vague. The root-cap is not clearly delimited, nor are the meristems below it at all clearly defined. Some evidences of a central strand can be made out, above which



is a layer of meristem, which probably serves as the initial for all the outer tissues.

The epidermal cells of the stem-apex are narrower than the ordinary epidermal cells (Fig. 55), but otherwise the stem-apex is indistinguishable, except from its position. The cotyledon constitutes the greater part of the embryo, and its base partially encloses the inconspicuous stem-apex, as is so often the case among Monocotyledons.

None of the permanent tissue elements were recognizable in the oldest embryos which were available, and only the slightest traces of the young vascular bundles could be detected. The embryo in the ripe seed occupies only a small portion of the large embryo-sac, which is filled with the endosperm-tissue (Fig. 56).

As the seed approaches maturity the endosperm-cells develop numerous small starch-granules. The growing embryo uses some of this, so that the cells immediately surrounding the embryo contain but little starch, while those in the central part of the sac (Fig. 58) contain a great deal. The basal cells of the endosperm become much larger than the upper ones, and their walls are much thickened, so that they show a certain likeness to the enlarged antipodal cells. Like the latter, their nuclei are also enlarged, although not nearly to the same degree, and show some evidences of disintegration.

#### SUMMARY.

1. In both *Aglaonema* and *Spathicarpa* the pistillate flower consists of a solitary carpel containing a single basal ovule, probably of axial origin.
2. The embryo-sac of *Aglaonema commutatum* shows many deviations from the usual type. These consist first in a varying number of embryo-sacs, ranging from 1 to 3. Where two or three are formed, this may be from a division of a common archesporial cell, but in some cases it looks as if these originated independently from hypodermal cells. All of these embryo-sacs usually undergo the first nuclear divisions, but probably only one ever becomes fully developed. The

second peculiarity is the extraordinary variation in the number of nuclei in the embryo-sac, and in the character of the structures developed in it. The number of nuclei ranges from 4 to 12, and the polarity is usually but slightly indicated. Multiple nuclear-fusions are of common occurrence, and it is often impossible to be certain which of the structures represent the egg-apparatus, and which the antipodal cells.

3. In specimens of an undetermined species (*Dieffenbachia Aglaonema* Hort.), perhaps identical with *A. commutatum*, the endosperm may arise from the direct division of two nuclei (or possibly a single one) at the base of the sac, without any formation of polar nuclei.

4. *A. pictum* does not depart to any marked extent from the usual angiospermous type. The pollen-spore of this species has two generative nuclei.

5. The embryo of *Aglaonema*, although reaching a large size, shows little differentiation of its external parts, and its tissues are almost perfectly homogeneous. In the ripe seed it almost completely fills the embryo-sac. The nucellus is relatively small, but the integuments and base of the ovule are very massive, and comprise the greater part of the seed.

6. In *Spathicarpa* the development of the ovule and embryo-sac are of the usual type. After fertilization the antipodals become very greatly enlarged, and one of them may divide, so that there are often four antipodals present. The nuclei of the antipodal cells become enormously enlarged.

7. The embryo of *Spathicarpa* remains small in the ripe seed. The external organs are indicated, but the tissues remain but slightly developed.

8. The development of the endosperm in both *Aglaonema* and *Spathicarpa* proceeds gradually from the base of the sac until it is completely filled. It is probable that this is the ordinary method of endosperm-formation in the Araceae.

EXPLANATION OF FIGURES IN PLATES  
XXX, XXXI, AND XXXII.

Illustrating Professor Campbell's Studies on the Araceae.

PLATE XXX.

All figures refer to *Aglaonema commutatum*. Figs. 1, 7, 15, Leitz, oc. 3, obj. 3. Figs. 12, 13, 14, 16, 17, Leitz, oc. 1, oil imm. 1/16; the other figures, Leitz, oc. 1, obj. 7.

Fig. 1. Median longitudinal section of young ovule, showing the young embryo-sac, *m*, and the two integuments *in*<sub>1</sub>, *in*<sub>2</sub>.

Fig. 2. The nucellus and embryo-sac, more highly magnified.

Fig. 3. Oblique section of the nucellus, showing two young embryo-sacs, apparently derived from the division of a common mother-cell.

Fig. 4 *a*, *b*. Two sections of young embryo-sac with two nuclei. *c*, Nuclei from the lateral cells of the nucellus, more enlarged, showing the very much compressed form.

Fig. 5. Section of a nucellus with two young embryo-sacs; each contains four nuclei.

Fig. 6. Embryo-sac containing four nuclei, all at the micropylar end. (Three only shown in the section.)

Fig. 7. Nearly median section of an ovule with three embryo-sacs.

Fig. 8. The details of the sacs shown in Fig. 7, more highly magnified. *a*, contains a single nucleus; *b*, eight nuclei in two groups, partially fused; *c*, *d*, and *e*, the details of sac *c*: *d*, antipodals (?), *e*, egg (?), *c*, fusing endosperm nuclei.

Fig. 9. Sections of embryo-sac with four nuclei, three at the micropylar end, a single one, *b*, at the chalazal end.

Fig. 10. Sections of a sac with eight nuclei, in two groups of four; no definite polar nuclei recognizable.

Fig. 11. Two sections of an ovule with three large cells (embryo-sacs?), but probably abnormal. The largest of the three cells contained but two nuclei (*c*). What looked like a pollen-tube, *p. t.*, occupied the micropyle, above the apex of the nucellus.

Fig. 12 *a*. Upper part of nucellus, showing the pollen-tube, *p. t.* The cell with the two nuclei probably represents a second, imperfect embryo-sac. The lower embryo-sac contained twelve nuclei, in three groups. *b*, the four antipodal nuclei. *c*, four nuclei fusing, presumably to form the endosperm-nucleus.

Fig. 13. Two sections of the apex of a sac, with what seemed to be a very broad pollen-tube, *p. t.*, containing a generative nucleus, *g*. There were four cells at the apex, of which two hemispherical ones, *a*, *d*', were much alike. One of these is probably the egg-cell.

Fig. 14. Nuclei from the cavity of the embryo-sac shown in Fig. 13. There were four nuclei, two in process of fusion, and two (only one shown in the section) which were apparently disintegrating. No antipodal cells were present.

Fig. 15. Section of a group of three embryo-sacs; the two upper ones degenera-



ting. At the base of the lower one were two very large nuclei, and there were two free nuclei in the cavity of the sac.

Figs. 16, 17. Nuclei from the lower sac shown in Fig. 15 more highly magnified.

## PLATE XXXI.

Figs. 18, 22, 28 and 31 refer to *Aglaonema commutatum*, the others to a very similar, but possibly different, species grown at the Hope Gardens, Kingston, Jamaica, under the name *Dieffenbachia Aglaonema*. Figs. 19, 25, 28, 32, Leitz, oc. 3, obj. 3; 33, about 20 diameters; the others Leitz, oc. 1, obj. 7.

Fig. 18. Embryo-sac with ten nuclei, four at the chalazal end (*a*), the other six in a group at one side of the sac (two only shown in the section *b*).

Fig. 19. Section of a fertilized sac, showing the forming endosperm at the base.

Fig. 20. Young embryo, from near the chalazal end of the same embryo-sac.

Fig. 21. Young endosperm of the same sac.

Fig. 22. Group of four [antipodal (?)] cells from the same sac.

Fig. 23. Embryo-sac with egg (*o*) and two synergidae (*c*), at the apex, and two nuclei, preparing to divide, at the antipodal end.

Fig. 24. A similar embryo-sac, after fertilization. At the apex a young embryo, surrounded by large celled endosperm, apparently derived from the division of the basal nuclei shown in Fig. 23.

Fig. 25. An older embryo-sac, with young embryo, *em*.

Fig. 26. Two sections of an older embryo, *sus*, suspensor-cell.

Fig. 27. Base of an older embryo-sac, with mass of tissue different from the endosperm, and possibly representing the embryo, as no other evidence of an embryo can be found. Above this mass was an elongated body (*p. t. ?*), which may possibly have been the pollen-tube.

Fig. 28. Section of embryo-sac, with older embryo, *em*.

Fig. 29. Micropylar (root-)end of an older embryo.

Fig. 30. Apex of the cotyledon of the same embryo.

Fig. 31. Root-end of an embryo, showing slight differentiation of the tissues.

Fig. 32. Embryo-sac, with mass of cells, perhaps an embryo, at the chalazal end. No embryo was present at the apex of the sac.

Fig. 33. Section of older ovule, the embryo filling most of the embryo-sac end, the basal endosperm.

Fig. 34. *a*, root-end; *b*, central portion of the embryo shown in Fig. 33, *st*, the future stem-apex.

## PLATE XXXII.

All figures refer to *Spathicarpa sagittae-folia*. Figs. 35, 53, Leitz, obj. 3, oc. 3; Fig. 56, about 8, Fig. 57 about 45 diameters; Figs. 36, 37, 41-44, Leitz, oil imm. 1/16, oc. 1; the others, Leitz, obj. 7, oc. 1.

Fig. 35. Longitudinal section of mature pistillate flower of *Spathicarpa sagittae-folia*; *m*, embryo-sac.

Fig. 36. Young embryo-sac; the second nuclear division is taking place; the chalazal nucleus was also dividing.

Fig. 37. *a*, egg-apparatus; *b*, endosperm-nucleus from a mature embryo-sac.

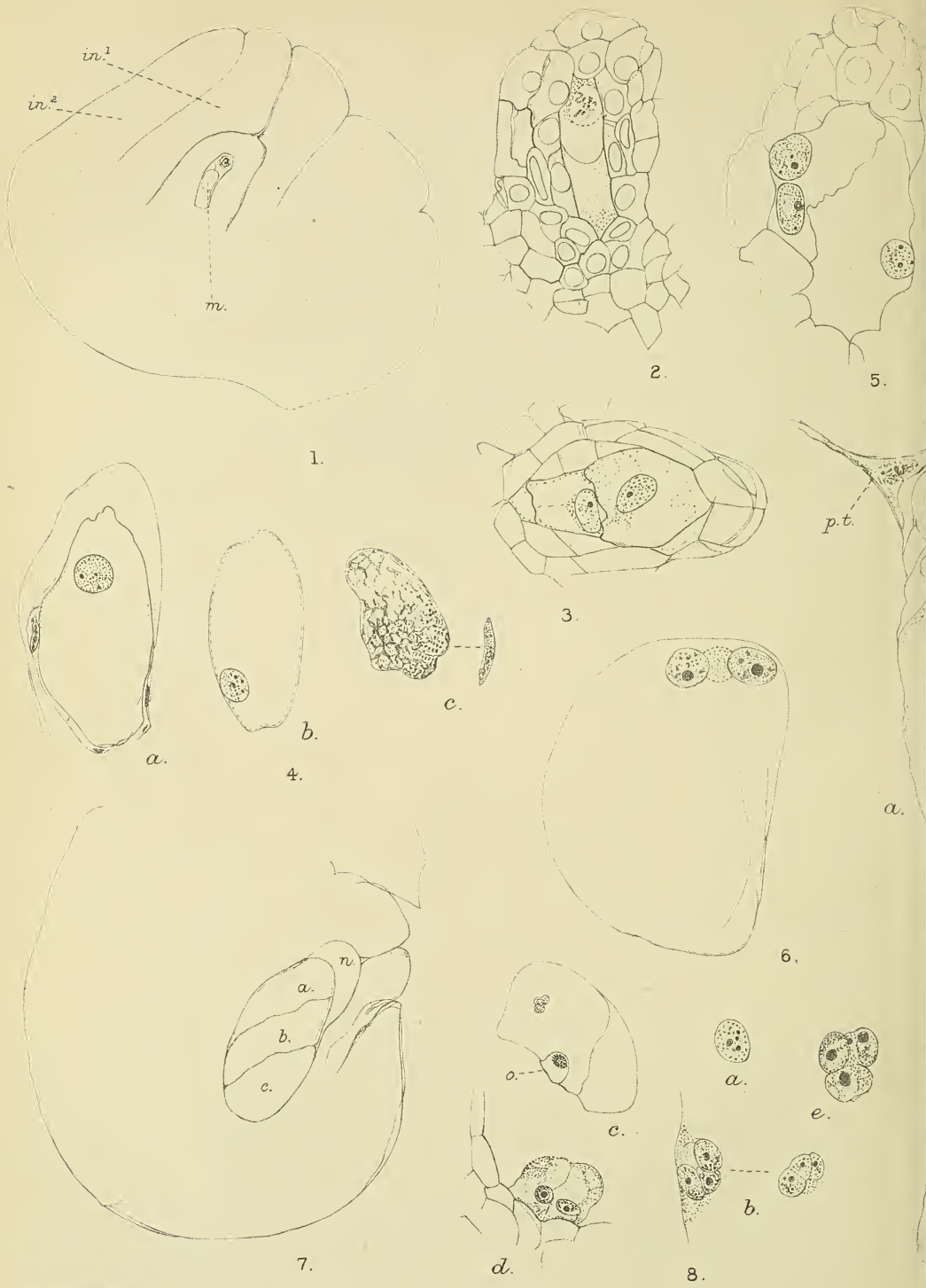
Fig. 38. Antipodal cells and endosperm-nucleus, from an embryo-sac of about the same age as Fig. 37.

- Fig. 39. Antipodal cells and polar nuclei from a younger sac.  
Fig. 40. Embryo-sac after fertilization. The sexual nuclei are fusing in the egg-cell, and the endosperm formation has begun.  
Fig. 41. Fertilized egg of Fig. 40, more enlarged, showing conjugation of the sexual nuclei.  
Fig. 42. Chalazal end of the same sac, more highly magnified, showing the enlarged antipodal cells and young endosperm.  
Fig. 43. Chalazal end of an older embryo-sac.  
Fig. 44. Egg-cell, with fusion of the sexual nuclei almost completed. One of the synergidae is clearly evident.  
Figs. 45-47. Young embryos, *sus*, suspensor.  
Fig. 48. Young embryo surrounded by endosperm.  
Figs. 49-52. Median longitudinal sections of older embryos, showing the variation in form, and in the development of the suspensor.  
Fig. 53. Three longitudinal sections of an older embryo; *a*, a nearly median section; *st*, stem-apex; *r*, root; *col*, cotyledon.  
Fig. 54. Nearly median section of the root portion of the same embryo as Fig. 53, more highly magnified.  
Fig. 55. Central region of the same embryo showing the stem-apex, *st*.  
Fig. 56. Longitudinal section of a nearly full-grown seed, showing the small embryo, *em*, and the large antipodals, *ant*; enlarged about eight times.  
Fig. 57. The lower part of Fig. 56, more enlarged.  
Fig. 58. Endosperm cells from a nearly ripe seed.  
Fig. 59. Nucleus from one of the antipodal cells.

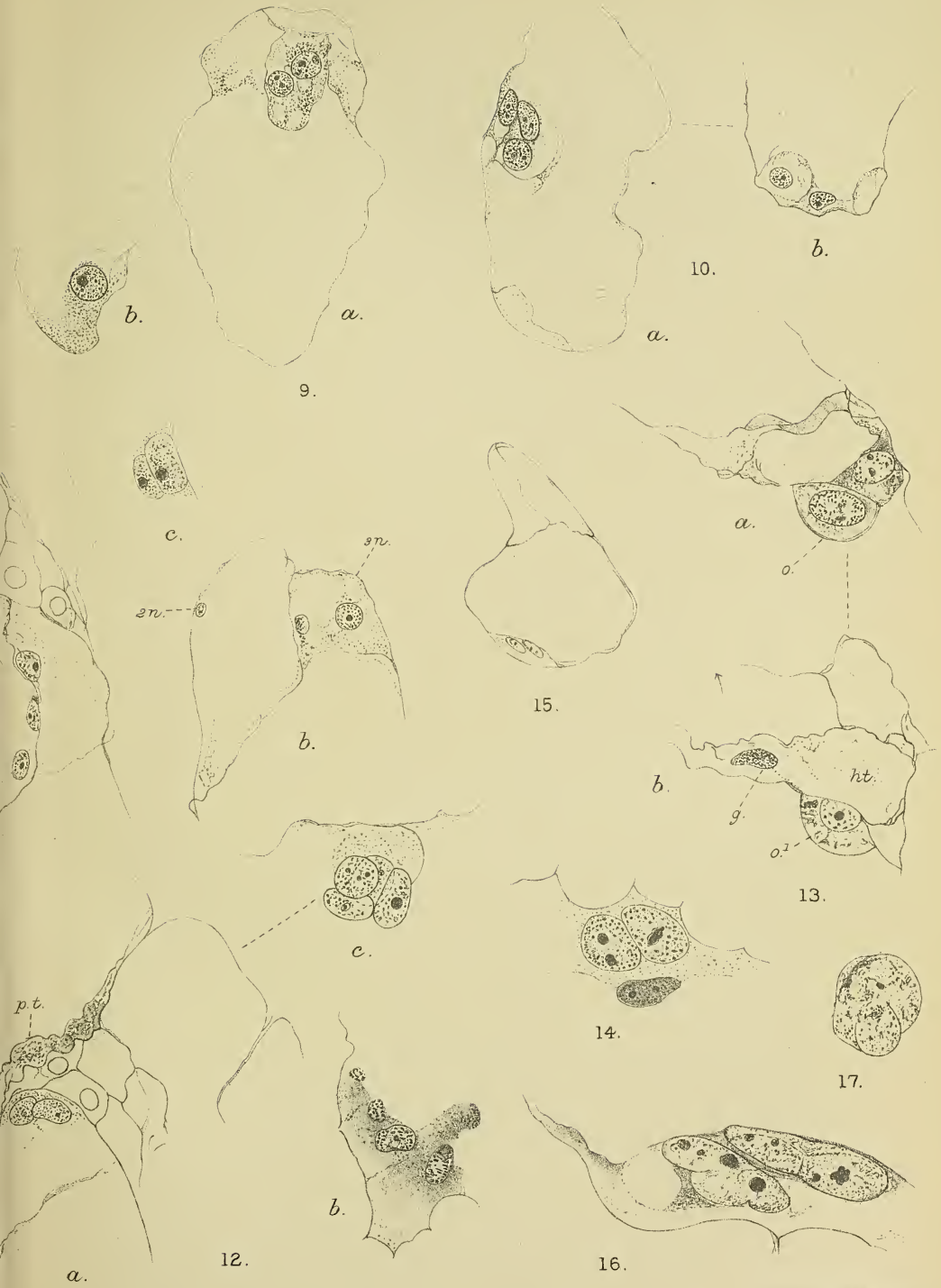






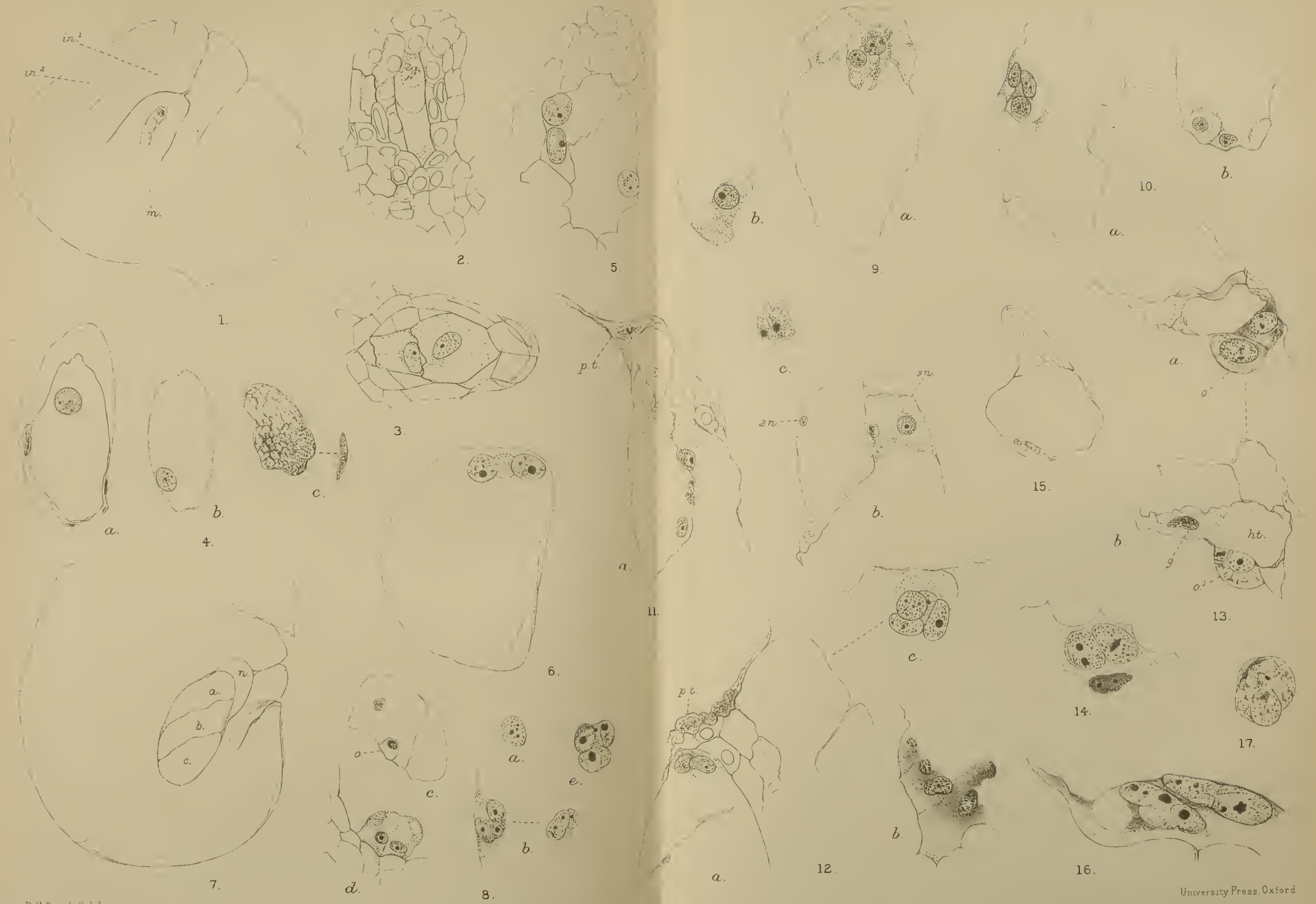


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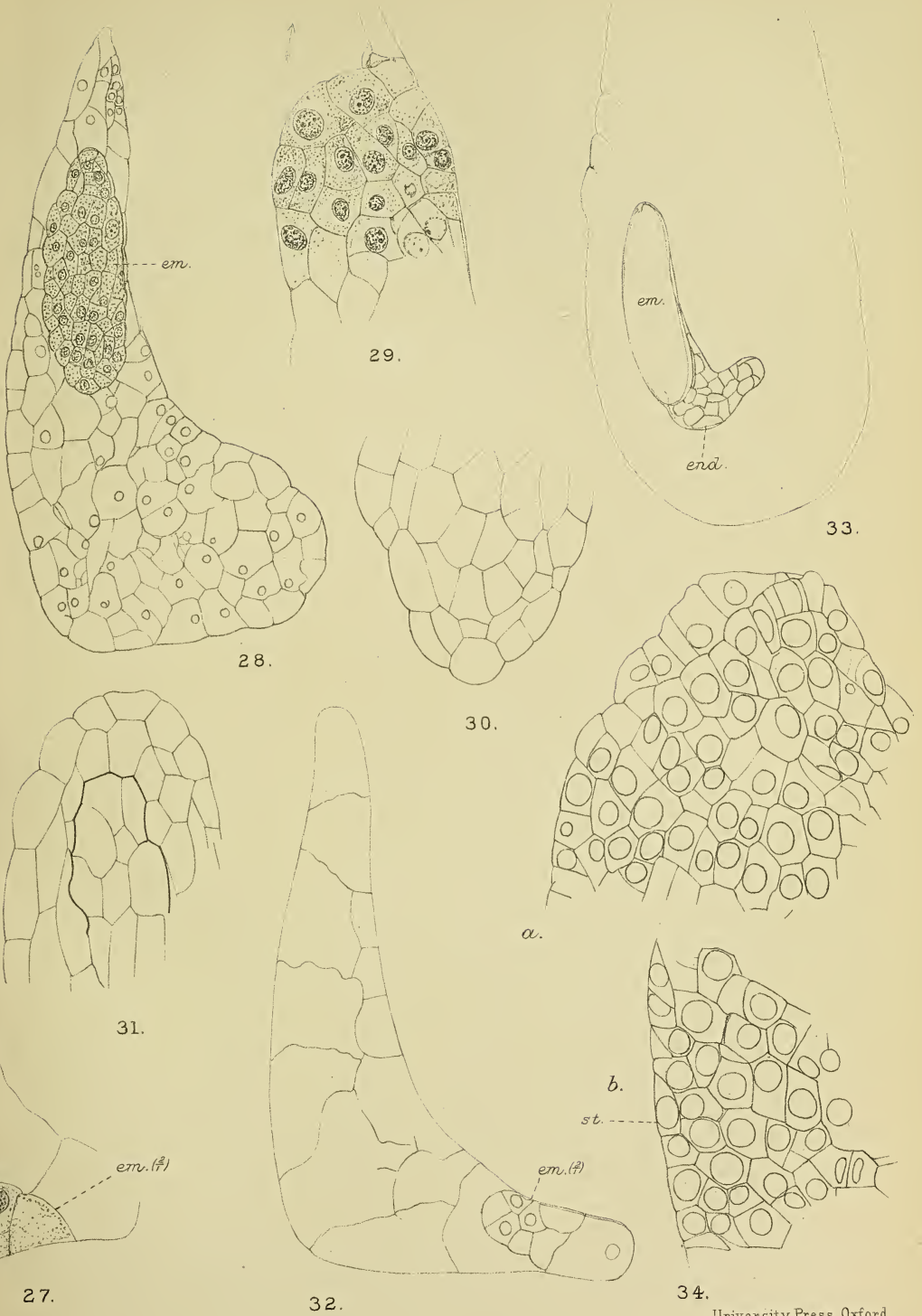






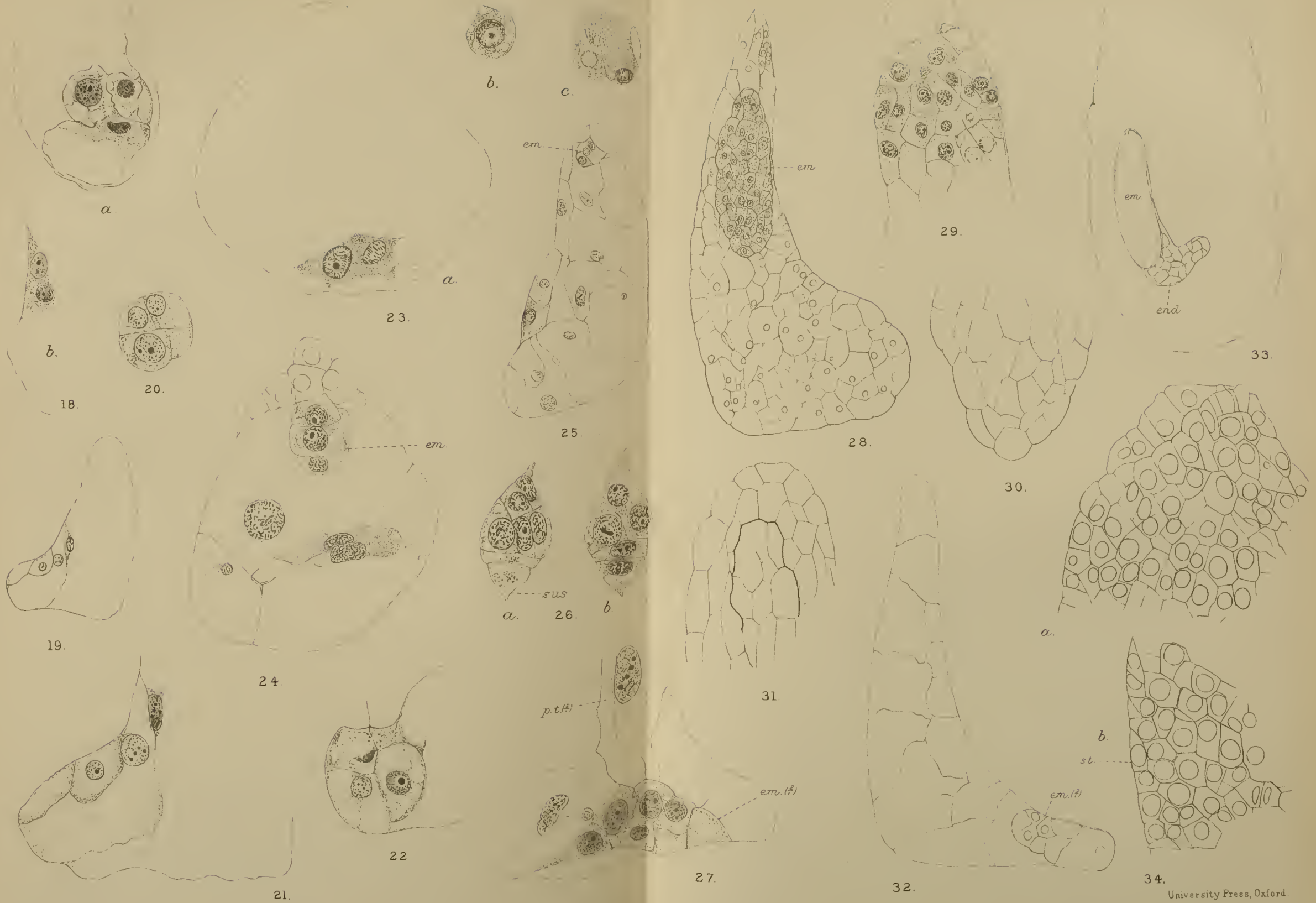


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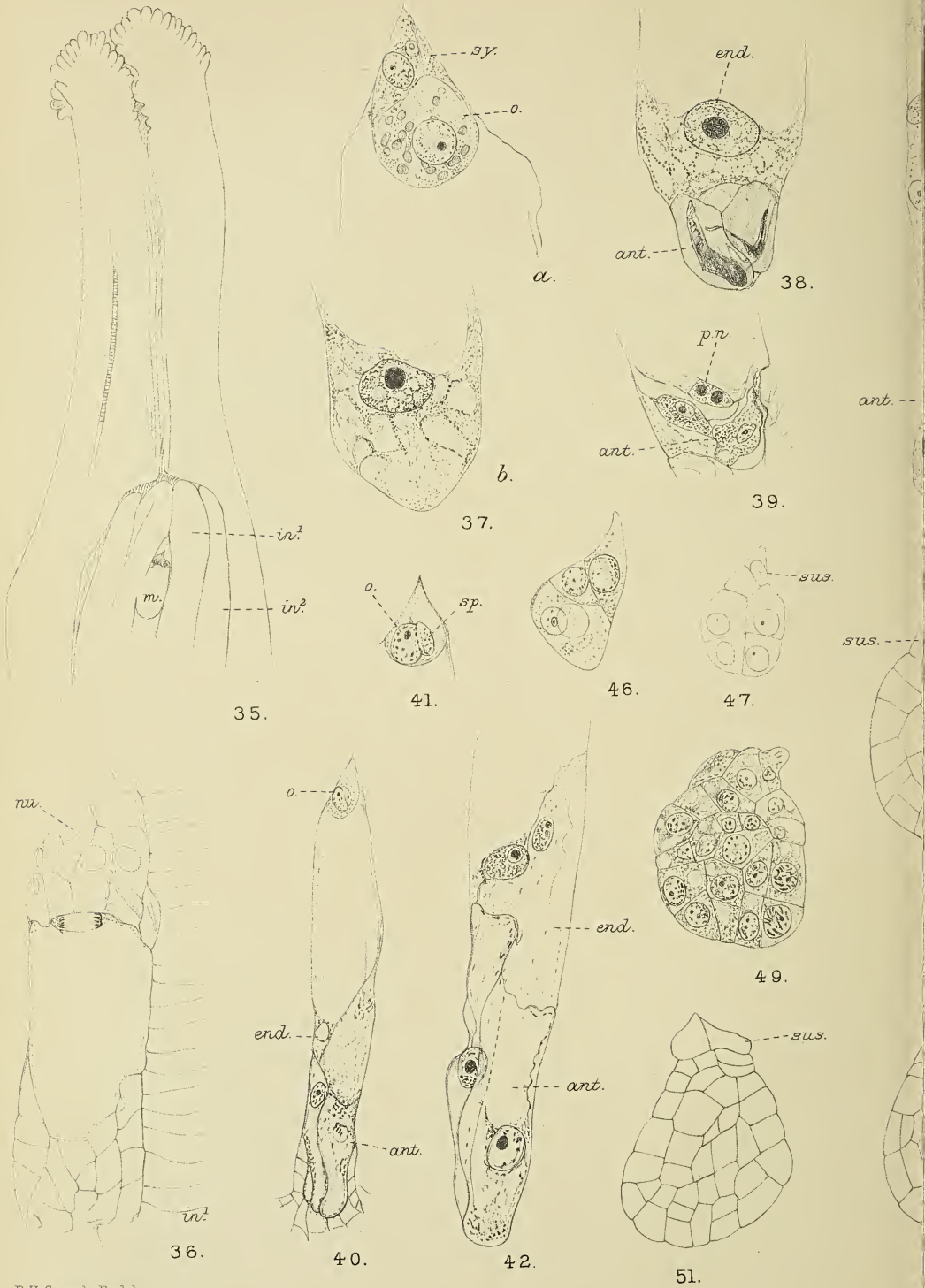
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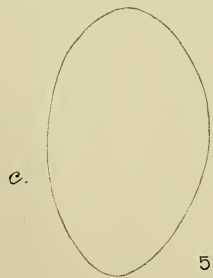
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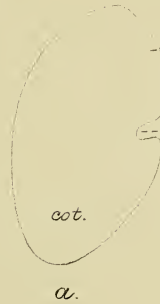
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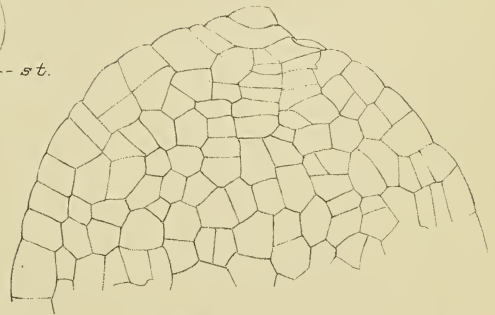


c.



cot.

a.

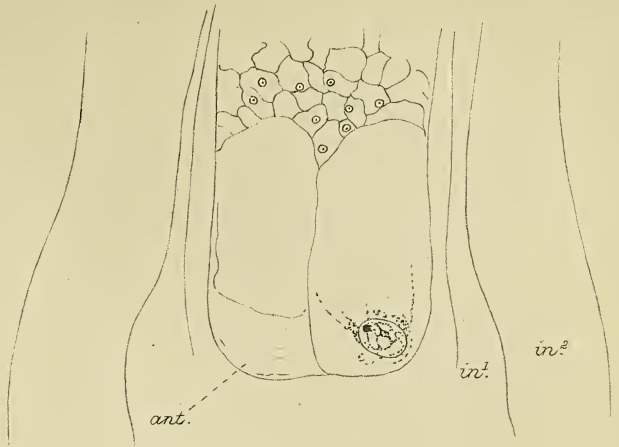


54.



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in.<sup>2</sup>

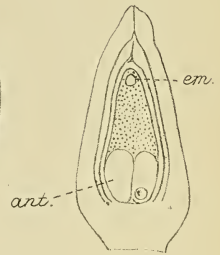
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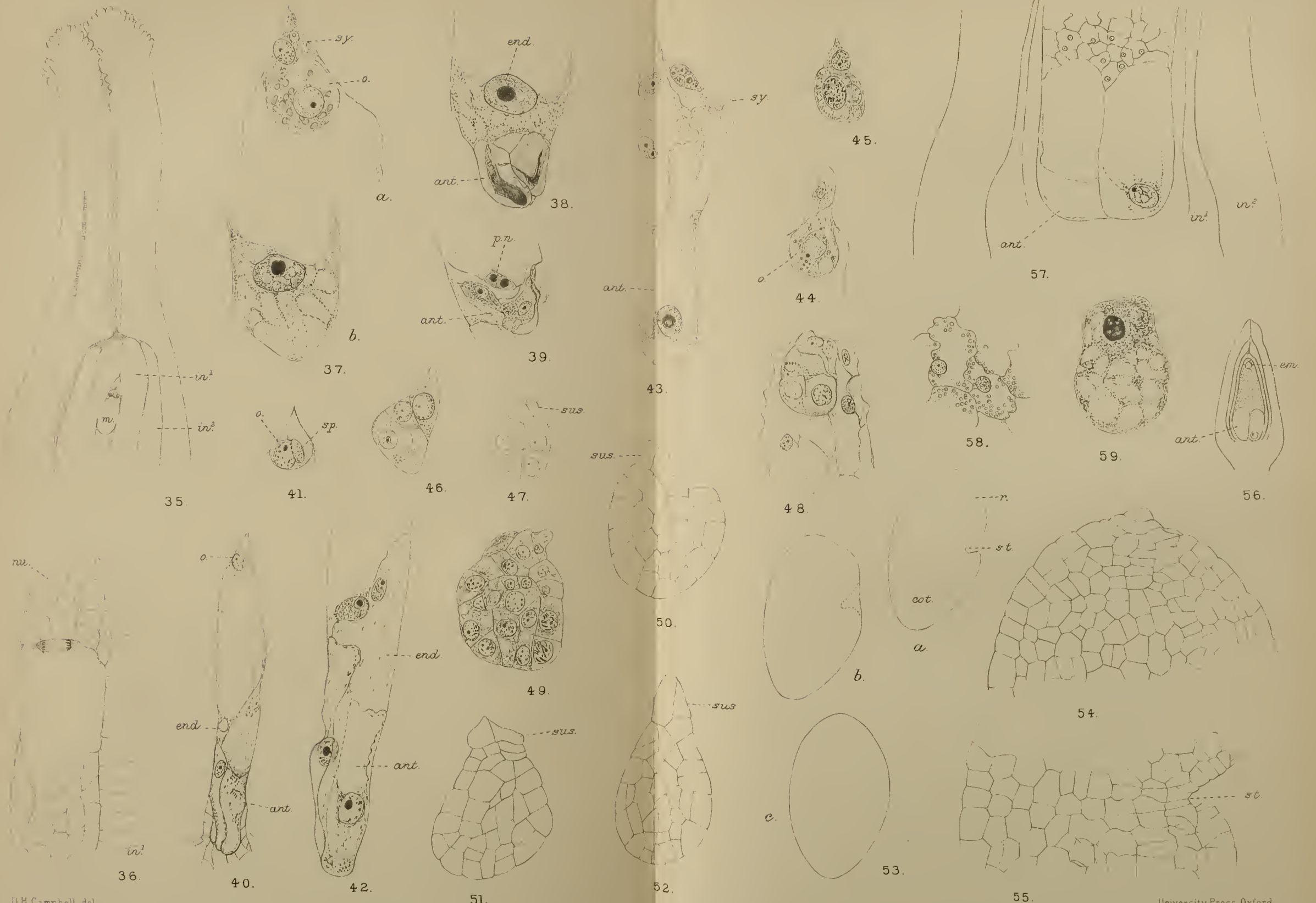
em.

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56.







D.H Campbell del.





# Observations on the Anatomy of Solenostelic Ferns.

## Part II.

BY

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—♦—  
With Plates XXXIII, XXXIV, and XXXV.  
—♦—

THE terms used to indicate the different types of vascular arrangement in plants have recently become so numerous and varied that before going on to the descriptive part of this paper it is necessary to explain why some of those employed in it were chosen. So far as the Cyatheaceae and Polypodiaceae are concerned it is no longer advisable to make use of Van Tieghem's term 'polystely' for those cases in which the single central cylinder of the young plant becomes divided up into several separate portions, because it is now quite clear that none of the so-called 'steles' that result can properly be regarded as equivalent to the original central stele. It has therefore been decided to adopt the term 'dictyostele,' recently proposed by Brebner<sup>1</sup>, for the tubular network of vascular tissue that arises by the occurrence and overlapping of gaps in a solenostele. The separate portions into which

<sup>1</sup> Brebner, On the anatomy of *Danaea* and other Marattiaceae, *Annals of Botany*, vol. xvi, no. lxiii, p. 523, 1902.

the original central stele has in this manner become broken up will be called 'meristeles.'

The most primitive type of vascular system that occurs in the Filicineae is probably the single protostelic central cylinder of the mature stem of *Lygodium*, the most important characteristic of which is that the continuity of the central xylem mass is not interrupted by the subsidence of the external tissues, cortical or vascular, at the departure of the leaf-traces. Such a structure has not yet been found in the mature stem of any of the Cyatheaceae or Polypodiaceae, although it is sometimes to be met with at the very base of the young plant. The solenostele holds an intermediate position between this simple protostelic type and the more complicated dictyostelic arrangements most frequently exhibited by these two orders, and it is chiefly due to this fact that the solenostele becomes a structure of particular interest.

The earliest reference to the solenostelic type of structure was made in 1838 by Robert Brown<sup>1</sup>, who noted the presence of a complete ring of *vasa scalariformia* in *Polypodium Horsfieldii*, R. Br. (*Dipteris conjugata*, Reinw.). A similar structure has since been recorded by various botanists in a large number of different Ferns, although many of their so-called 'pith-containing wood-cylinders' have proved upon investigation to be really dictyosteles and not solenosteles. Most of the examples included in this paper have already been mentioned at one time or another, and although most of the previous descriptions have been more or less inadequate or incorrect, those given by Karsten<sup>2</sup> and Mettenius<sup>3</sup> can hardly be improved upon. The true solenostele is not of very general occurrence, although it is to be met with in several different genera, e. g. *Dicksonia*, *Davallia*, *Lindsaya*, *Hypolepis*, *Pteris*,

<sup>1</sup> Horsfield, *Plantae Javanicae*, p. 2.

<sup>2</sup> *Die Vegetationsorgane der Palmen*. Abhandl. d. K. Acad. d. Wissensch. z. Berlin, p. 186, 1847.

<sup>3</sup> *Über den Bau von Angiopteris*. Abhandl. d. K. Sächs. Gesellsch. d. Wissensch., Bd. VI, p. 531, 1864.

*Pellaea*, *Polypodium*, and *Famesonia*. However, in these and other genera (*Cheilanthes*, *Nothochlaena*, *Adiantum*, *Gymnogramme*, *Antrophyum*, and *Vittaria*) a number of transitional types related to the solenostele are to be found, which will also have to be taken into consideration. So many different species taken from several different genera have been examined that it is impossible to deal with them individually. It would also be very inconvenient to treat each genus separately, because their anatomical characteristics do not, for the most part, run parallel with their systematic position. Therefore, in the first part of this paper, where the general vascular arrangement in the stem is described, the plants will be dealt with in groups which will, as far as possible, lead up to the more interesting results that have come to light during the investigation. A few points of interest relating to the structure of the vascular bundles of the petiole, the lateral shoots, and the roots will be mentioned, and the histology of the vascular system will also be considered, but only in a very general manner.

#### TYPICAL SOLENOSTELES.

A perfectly solenostelic vascular system was found in the stems of all the species included in the following list<sup>1</sup>: *Davallia hirsuta*, *marginalis*, *strigosa*, *platyphylla*, *hirta*, *Speluncae*, *Novae-Zelandiae*, *Lindsaya retusa*, *Dicksonia apiiifolia*, *cicutaria*, *scabra*, *punctiloba*, *davallioides*, *Pteris scaberula*, *incisa*, *ludens*, *Pellaea atropurpurea*, *falcata*, and *Famesonia imbricata*. All these Ferns have a creeping, more or less dorsiventral rhizome with the leaves arranged in two rows on the upper surface, and their solenosteles differ from each other and from that of *Loxsona*, as described in Part I of this paper<sup>2</sup>, in so slight a degree that the same description

<sup>1</sup> For the sake of uniformity the nomenclature of Hooker's 'Synopsis Filicum' will be adopted as far as possible throughout. It will therefore be unnecessary to give the authorities for the names, unless they are not recognized as such in the 'Synopsis Filicum.'

<sup>2</sup> Annals of Botany, vol. xv, no. lvii, 1901.



will serve for them all. The gaps formed in the solenostele by the departure of the leaf-traces never overlap. The xylem-ring is surrounded, both externally and internally, by a complete ring of phloem and pericycle, and the whole is delimited from the ground-tissue on both sides by a well-marked endodermis. The leaf-trace departs from the solenostele of the stem as a single continuous vascular strand, usually curved so that it has a section similar in form to a horse-shoe or an arch. This curved strand is so attached to the solenostele that its concavity faces the median dorso-ventral plane of the rhizome, either directly, as in *Dicksonia punctiloba* (Pl. XXXIII, Fig. 1), *Pteris incisa*, &c., or else more or less obliquely, as in *Dicksonia apiifolia* (Fig. 2), *Davallia Speluncae* (Fig. 3), &c. In *Pteris ludens* and *Famesonia imbricata* the leaf-trace faces directly towards the apex; a position it also occupies in *Loxsonia* (Part I<sup>1</sup>, Fig. 4); in this Fern, however, the leaves are inserted along the upper surface in a single median row. For some time before it actually departs, that portion of the solenostele destined to form the leaf-trace is usually well defined as a protrusion which is somewhat thinner than the rest of the vascular ring (Figs. 2 and 3). The leaf-gap generally closes up at the same time as the acroscopic flange of the leaf-trace departs, or immediately afterwards. It may, however, remain open for a short distance above the leaf, as in *Davallia Speluncae* (Fig. 3), *Pteris ludens*, *Famesonia imbricata*, and others. The free margin of the leaf-gap is usually of the same thickness as the rest of the solenostele, but in some cases it becomes more or less enlarged: *Dicksonia apiifolia*, *cicutaria*, *Davallia hirta*. The enlargement is entirely due to the increased thickness of the xylem-ring in this region; in the two *Dicksonias* it is often twice as thick as elsewhere in the stele, so that the free margin of the leaf-gap projects markedly towards within. This marginal thickening is a feature of considerable interest, and those Ferns in which it reaches a more conspicuous development will be treated separately later on. When

<sup>1</sup> Ann. of Bot. vol. xv. Pl. III.

lateral shoots are borne by any of the above Ferns they are always inserted upon the base of the petiole, and their vascular systems are joined on to one or the other margin of vascular strand of the petiole (cf. Figs. 4, 5, and 6).

A perfect solenostele is also present in the stem of *Hypolepis tenuifolia*, *millefolium*, *distans*, and *repens*, but certain additional peculiarities occur in relation to the insertion of the leaf-trace which will require especial description. The stem is a dorsiventral rhizome, as in the Ferns mentioned above, with the leaves arranged in two rows upon the upper surface. The leaf-trace becomes definitely marked off from the rest of the solenostele some distance before it actually departs as such, and the gap formed by its departure runs forward a considerable distance before it is closed up again. The leaf-trace consists of a single curved strand in all cases except in *H. tenuifolia*, where it departs as two separate pieces, and later on in the petiole breaks up into several. One or more lateral shoots are given off from the base of each leaf in all four species. If only one is present it always arises from the basiscopic margin of the leaf-trace, if there are two or more, then the lowest on the basiscopic side is always stronger and further developed than the others (Fig. 6). In order to form the vascular system of a lateral shoot the margin of the leaf-trace curls inwards on to itself, and the curved portion eventually separates off as a gutter-shaped stele which rapidly closes up into a complete cylinder.

Reference to Figs. 4, 5, and 6 will show how this takes place, and also how the presence of the lateral shoots affects the form of the leaf-trace and the manner of its departure. At the very base the leaf-trace is very irregular in form, and its concavity is directed towards the apex of the stem, but once it has become free from the steles of the lateral shoots it exhibits the customary form of an arch, the concavity of which faces the median dorsiventral plane of the rhizome.

The structure of the node in these Ferns is still further complicated by the appearance of certain small vascular strands which connect up the free margins of the leaf-trace,

shoot-stele, and stem-stele with each other. In my specimens two such strands were usually present. The most constant of these was one running from the free margin of the gutter-shaped stele of a lateral shoot to that margin of the leaf-trace from which the shoot in question arose (*a* in Figs. 4, 5, and 6). The other strand, which was sometimes wanting, ran either from the free margin of the gutter of the basiscopic shoot to the opposite (acrosopic) margin of the leaf-trace (*b* in Figs. 4 and 6), or it started from the free margin of the leaf-gap itself and ran to the acrosopic margin of the leaf-trace (*c* in Fig. 5).

A perfect solenostele of almost exactly the same nature as that described in the above species of *Hypolepis* was also found in *Polypodium punctatum*. The lateral shoots arose in the same way, and, what is even more interesting, the small additional strands in the neighbourhood of the leaf-gaps were also present. In my specimen they had the same position and course as those marked *a* and *c* in the diagrams of *Hypolepis*.

Several other cases of solenostely were met with in different plants, which possess special features of such importance that it will be more convenient to deal with them separately later on.

#### TRANSITIONAL TYPES.

Vascular systems were found in a large number of Ferns belonging to several different genera which seem to represent a series of stages transitional, or intermediate, between solenostely and dictyostely. The examination of these forms makes it quite clear that the dictyostely of the Cyatheaceae and Polypodiaceae is primarily due simply and solely to the overlapping of the leaf-gaps in a solenostele; although it is not to be denied that gaps may sometimes occur in the vascular cylinder which are not in any way related to the insertion of the leaves. It appears also that two different factors may be concerned in bringing about this overlapping of the leaf-gaps. In the first place, it is evident that if the



leaf-gaps remain open long enough after the departure of the leaf-trace they will eventually overlap; again, the same result will also be obtained if the leaves be crowded sufficiently close together, although the leaf-gaps may close up comparatively rapidly.

In some of the intermediate forms the leaf-gaps only overlap now and then, so that the stem, to a certain extent, still remains in a solenostelic condition. In others again the overlapping is more general, and a complete stelar cylinder is only to be found at rare intervals. It will therefore be understood that cases sometimes arise where it is impossible to say definitely of the vascular system of the plant as a whole that it is either solenostelic or dictyostelic.

The investigation of these forms shows that the distinction drawn by De Bary<sup>1</sup> between the dorsiventral and the radial type of vascular arrangement in dictyostelic Ferns is one of considerable value, because it will be seen that the structural features of the two types depend upon the different methods by which they are derived from the solenostele.

The transition from solenostely to dictyostely in a dorsiventral rhizome with two rows of leaves, one on either side of the upper surface, will be first considered. A reference to the diagrams (Figs. 7 and 8) will show the effect of closely crowded leaves, or of long persisting leaf-gaps upon the solenostele. It is seen that the dorsal internodal portion of the solenostele has become so reduced that it is now no more than a mere strand running across between each leaf-insertion from one margin of the large ventral portion of the solenostele to the other. A structure such as this may be found in the rhizomes of *Nothochlaena Marantae* (Fig. 7), *trichomanoides*, *ferruginea*, *Pellaea rotundifolia* (Fig. 8), *andromedaefolia*, *Adiantum trapeziforme*, *Kaulfussii*, and *Gymnogramme vestita*. A similar type appears also to be present in *Antrophyum reticulatum*, but it is a little exceptional and will be referred to again later on. Transverse sections of the stems of these Ferns will in most cases exhibit a single large gutter-shaped

<sup>1</sup> Comparative Anatomy, pp. 284 and 287 (Engl. ed.).

meristele, but in some a small additional dorsal one will also be present.

Bearing in mind the structure just described one is now in a position to understand the somewhat aberrant form of solenostely found in the dorsiventral Ferns *Cheilanthes lendigera* and *microphylla*. So far as the endodermis and pericycle are concerned each leaf-gap in the stele is closed up before the next above is formed, but the leaf-gap in the xylem-ring remains open until it overlaps the gap formed in the xylem by the departure of the leaf-trace next above. In this manner a small separate xylem-strand is produced *within the stele* which crosses over between each leaf-insertion from one side of the open xylem-ring to the other; having precisely the same course and origin as the free dorsal meristele in the forms described above.

In the more perfectly dictyostelic Ferns the dorsiventral type of vascular arrangement becomes much more complicated, but, in most cases, the manner of its origin from the solenostele is essentially similar to that already described, although it may differ considerably in detail. For instance, in *Asplenium scandens* the internodes are long, and the course of the dorsal meristele as it runs across from one side of the ventral portion of the solenostele to the other is a very oblique one; moreover, since the two rows of leaves are on exactly opposite sides of the stem, the dorsal meristele is almost as large as the ventral. In a dissection of the stem, therefore, two fairly large meristeles are to be found, very similar to each other in form and size, and between each two leaf-insertions the dorsal meristele is seen to cross slowly over from one side of the ventral meristele to the other.

If the dorsal meristele were to pursue a straight course, and instead of coming into bodily contact itself with the ventral meristele, as in *Asplenium scandens* and the cases mentioned above (Figs. 7 and 8), it were to keep up its connexion with it at the same points as before by means of short transverse strands or sutures, a structure would then result essentially

similar to that described and figured by Mettenius<sup>1</sup> and De Bary (loc. cit.) in several different dorsiventral Ferns. All the Davallias of the section *Humata* that were examined belong to this type, and also most of those belonging to the sections *Eudavallia* and *Leucostegia*. In some of these Ferns, however, the actual state of affairs is a little obscured by the fact that several separate leaf-traces are given off to each leaf, which run forward for some distance in the ground-tissue of the stem before they turn out into the petiole, also the two meristemes of the stem are often so similar to these in form and size that they are scarcely to be distinguished from them.

Attention should also be drawn at this point to the vascular arrangement described by Mettenius (loc. cit., p. 552) in a number of dorsiventral Ferns, of which *Platyserium alaicorne* may be quoted as an example. In these the dorsal meristeme seems to be present as usual, but the ventral one appears to be broken up into an irregular meshwork of strands, the gaps in which bear no relation whatever to the leaf-insertion.

In Ferns which have their leaves arranged radially in several rows all round a prostrate or an erect stem three or more leaf-gaps usually overlap at the same level, and the solenostele is broken up into just as many more or less equivalent meristemes arranged in a ring around the axis.

If the structure is still but little removed from solenostely it may happen that two leaf-gaps only overlap at any one level, and then the vascular arrangement, when seen in transverse section, generally consists of a large gutter-shaped meristeme with another small one lying across its opening (Figs. 9 and 10). Although this structure is very similar in appearance to that presented by the simpler forms of the dorsiventral type, it is really to be regarded as quite distinct, because the relative positions of the two steles change in accordance with the radial arrangement of the leaves. The following Ferns were found to be radially dictyostelic, but still remain very close to solenostely: *Dicksonia Barometz* (Fig. 17), *Pteris tremula*, *cretica*, *flabellata*, *heterophylla*

<sup>1</sup> l. c., Taf. vii, viii.



*pellucida*, *Taenitis blechnoides*, *Gymnogramme calomelanos* (Fig. 9), *Hemionitis palmata*, *Adiantum lunulatum*, *Lomaria semicordata* (*Plagiogyria biserrata*, Met.) (Fig. 10). No particular form of leaf-trace is especially related to the simpler intermediate forms of dictyostely, either dorsiventral or radial. However, it generally consists of a single strand, as in *Nothochlaena Marantae* (Fig. 7) and *Pteris tremula*, or else it is divided into two separate portions, as in *Adiantum trapeziforme* and *Gymnogramme calomelanos* (Fig. 9).

Whenever more than two rows of leaves are found upon the stem of a Fern they are nearly always arranged radially all round the axis, even though it may be a creeping or prostrate rhizome. There are, however, a few in which they are inserted in several rows all upon the upper surface, and in these the rhizome is dorsiventral in structure, e. g. *Pellaea cordata*. It seems probable that they originally belonged to the radial type, and have become dorsiventral in a secondary manner in consequence of the prostration of the stem. It is also possible that they have been derived from a dorsiventral type with two rows of leaves by the intercalation of additional leaves between those already present. However, their anatomy has not yet been thoroughly investigated, and the question must be left open.

#### SOLENOSTELES WITH INTERNAL ACCESSORY VASCULAR STRANDS.

Attention has already been drawn to the fact that the free margin of the leaf-gap in *Dicksonia apiifolia* and other solenostelic Ferns is considerably thicker than the rest of the solenostele, owing to an increase in the amount of xylem present at that point. In *Dicksonia adiantoides* this feature becomes so conspicuous and important that it requires especial description; particularly so because it appears to give an explanation of certain complex modifications of the vascular system that occur in a number of other Ferns. *Dicksonia adiantoides* has a dorsiventral rhizome with leaves in two rows on the upper surface, and a perfectly solenostelic vas-

cular system. The leaf-trace consists of a single curved strand inserted so that its concavity faces the median dorsiventral plane of the rhizome, and the leaf-gap closes up at the same time as the acroscopic flange of the leaf-trace departs. The enlargement of the leaf-gap margin is so pronounced that it projects markedly towards the interior, and, what is more important, this projection is not confined to the limits of the open leaf-gap, as in the previous examples, but is continued as a ridge upon the internal surface of the solenostele throughout the whole length of the internode, running from one leaf-gap margin to the other (Fig. 11). In the immediate neighbourhood of the leaf-gap the additional xylem-elements that cause the internal projection of the margin are in more or less complete continuity with the rest of the xylem-ring, just as in *Dicksonia apiifolia*, &c., but in the internodes they become separated off as a distinct strand (Fig. 12), which may even be surrounded by a phloem-ring of its own distinct from that of the solenostele. This separate strand of xylem generally attains its greatest independence in the upper part of the internode, and is most closely fused with the xylem-ring of the solenostele towards the top of the leaf-gap. In my specimens the separate strand of xylem never became free from the endodermis and pericycle of the solenostele, but in a stout example it seems probable that along part of its course it may become completely isolated in the central parenchyma. The protoxylem-elements of the solenostele are located in definite endarch or mesarch strands; a similar protoxylem-group is sometimes to be found in the internal xylem-strand (Fig. 12).

The insertion of the leaf-trace in this Fern is further complicated by the presence of lateral shoots and of one or two small vascular strands which run across the leaf-gap very much in the same way as those already described in *Hypolepis*. In this case they start from the internal surface, or from the basicopic margin of the leaf-trace (Fig. 11), and run forwards to the free margin of the leaf-gap. The marginal thickening and the transverse strands were found at nearly all the leaf-

gaps, but occasionally, both in the main axis and in the lateral shoots, one or the other, or even both of these features may be wanting.

Seward and Dale<sup>1</sup> have described a thickening of the margins of the leaf-gaps in *Dipteris conjugata* (Reinw.) which should probably be regarded as of the same nature as that in *Dicksonia adiantoides*, only a step more advanced. For in this case it appears that the free xylem-strand has almost separated off from the solenostele altogether, being connected with it only at two points, between which a tongue of ground-tissue has inserted itself.

From the description given by Boodle<sup>2</sup> it appears that a structure very similar to this is also to be found at the margin of the leaf-gaps of *Gleichenia pectinata*, and it is suggested that here again we have to deal with the same phenomenon as in *Dipteris conjugata* and *Dicksonia adiantoides*. One point of difference, however, is to be noted in the two last cases, which is that both flanks of horse-shoe-shaped leaf-trace depart at the same time, and both sides of the leaf-gap are similarly thickened.

Before going on to describe the internal vascular strands that occur in the stem of *Dicksonia rubiginosa* it is necessary to point out certain very exceptional features that are also presented by the ordinary vascular cylinder of this plant. The habit of the rhizome and the insertion of the leaf-traces are essentially the same as in *Dicksonia adiantoides*. The leaf-gaps close up directly after the leaf-trace departs (Fig. 13), but nevertheless the vascular system cannot be regarded as a solenostele, because in addition to the leaf-gaps other lacunae occur in the stelar cylinder which have no relation to the leaf-insertion whatever. These lacunae occur somewhat irregularly, but chiefly along two lines on opposite sides of the creeping rhizome. They are sometimes comparatively short, but more

<sup>1</sup> Structure and Affinities of *Dipteris*, &c., Phil. Trans., Series B, vol. cxciv, p. 499, and Fig. 4, 1901.

<sup>2</sup> On the Anatomy of the Gleicheniaceae, Annals of Botany, vol. xv, no. lx, p. 730, 1901.



often they form long splits interrupted by small meristeles passing across the lacuna from one side to the other. Although a completely closed vascular ring is sometimes to be met with in transverse sections of the internode, the most frequent appearance is that of two large curved meristeles, one dorsal and one ventral, with or without one or two smaller ones lying between their margins. In this plant, therefore, an entirely exceptional kind of dictyostely has been attained without relation to the overlapping of the leaf-gaps; indeed so far as that is concerned the vascular structure may still be regarded as solenostelic. So far as I am aware, in this respect *Dicksonia rubiginosa* stands unique among the Ferns.

The accessory vascular strands found within the ordinary stelar cylinder vary in number from point to point. There were never more than three present in my specimen, and sometimes they all fused up to a single large curved strand. In their course through the internode they may branch and anastomose with each other, but they never come into contact with the internal surface of the ordinary stelar cylinder except in the neighbourhood of the nodes. At each node a single internal strand approaches the free margin of the leaf-gap, and gradually fuses with it until the two xylems are perfectly continuous, presenting an appearance exactly as in *Dicksonia adiantoides*. As soon as the leaf-trace has departed it separates off again and passes on as a free internal strand into the internode above. One internal strand at least was present in all parts of the specimen examined, even at the base of the narrow lateral shoots. Distinct mesarch protoxylem groups are to be found in them, which, however, do not appear to be in any way related to those of the leaf-trace. In this plant, again, the vascular systems of lateral shoots are usually to be found departing from the margins of the petiolar strand, and, as in *Dicksonia adiantoides*, small vascular strands are sometimes to be met with which run forward from the internal surface of the leaf-trace to the free margin of the leaf-gap.

A still more conspicuous system of internal vascular strands

is to be found in the stem of *Pteris elata*<sup>1</sup> which is an erect or oblique rhizome with the leaves arranged radially all round. The vascular system is perfectly solenostelic, and the leaf-gap closes up immediately after the departure of the leaf-trace. The curved leaf-traces are inserted with their concavities facing directly towards the apex, which, moreover, appears to be always the case in all Ferns in which the stem grows erect. The appearance of the internal vascular system will vary according to the dimensions of the plant, and to the position of the section relative to the nodes (Fig. 14). In a rhizome of average thickness the internal system usually has the form of a large gutter-shaped strand or of a completely closed cylinder, the latter being generally present for some distance below each of the nodes. As the leaf-gap is approached from below a fairly large flat strand is seen to separate off from the internal vascular cylinder, which, travelling forwards and outwards, ends by fusing completely and finally with the anterior margin of the leaf-gap in the outer solenostele; just as the latter becomes closed up again. The lacuna thus produced in the internal vascular cylinder converts it into a gutter which, however, gradually closes up in the internode above, so that a complete cylinder is again formed, usually for some distance before the next leaf-insertion is reached. Sometimes, on the other hand, two such gaps in the internal vascular system may overlap, so that two separate internal strands are occasionally to be met with.

In large and especially well-grown rhizomes a second internal vascular system is to be found lying within the first. It is not, however, very highly developed, but consists of a single small free rounded strand. This central strand fuses with the margin of each of the lacunae in the first internal cylinder, but usually separates off again after a little while. In fact, it behaves towards the first internal vascular system in exactly the same way as the internal vascular strand of *Dicksonia rubiginosa* behaves to the ordinary stelar cylinder.

<sup>1</sup> *Pteris elata*, var. *Karsteniana*, Kz., a variety not mentioned by Hooker, was the plant actually investigated.

More rarely, it is not the central strand itself that goes to fuse with the margin of the lacunae, but a branch given off from it; in which case it terminates there and does not separate off again. Even in rhizomes of medium size indications of this second internal system are not wanting, for it is often to be observed that one of the margins of the lacunae in the first internal vascular cylinder is considerably thickened, and projects inwards in a manner similar to the margins of the leaf-gaps in the solenostele of *Dicksonia adiantoides*. The solenostele at the base of the lateral shoots (which arise from about the middle of the back of the petiolar strand, and not from its margin) is perfectly typical and without any internal strands. I have no doubt that a series of stages intermediate between this and the complex structures described above are to be found in weak rhizomes, or, at any rate, in the young plant.

Judging from the description given by Seward<sup>1</sup> the vascular system of *Matonia pectinata* seems to be essentially similar to that of *Pteris elata*, both as regards the arrangement of the internal accessory strands, and also in their relation to the leaf-insertion. Miss Wigglesworth's<sup>2</sup> account of the same plant serves to strengthen this opinion, although it appears that in her specimen the complexity of the internal systems is carried a step further still. For the third and most central system, which in *Pteris elata* consists of a small rounded strand only, is represented by a large gutter-shaped strand, or even by a completely closed cylinder.

From the description of *Dicksonia Plumieri* (*Saccoloma adiantoides*, Sw.) given by Mettenius<sup>3</sup> it is clear that in this plant again the vascular system is constructed upon exactly the same plan, and, moreover, it appears that a still higher degree of complexity is reached than in the *Matonia* of

<sup>1</sup> The Structure and Affinities of *Matonia pectinata*, Phil. Trans. Roy. Soc., Lond., Series B, vol. cxci, p. 171, 1899.

<sup>2</sup> Notes on the rhizome of *Matonia pectinata*, The New Phytologist, vol. i, no. vii, p. 157, 1902.

<sup>3</sup> l. c., p. 531.



Miss Wigglesworth. For not only are there two concentric vascular cylinders lying within the ordinary solenostele, but a small central strand is present in addition, which may be regarded as an indication of a third.

It is evident that in all these cases the ordinary typical vascular cylinder is represented by the outermost vascular system. The internal vascular system is an accessory development, and from the consideration of the facts brought forward above it appears that, even in its most complex form, it is to be derived from the ordinary stelar cylinder by the progressive elaboration of a local thickening of the xylem-ring at the leaf-gap margin. The initial stage of such a development would be a simple marginal thickening something like that in *Dicksonia apiifolia*. The first step in advance would be the further development of this thickening into an internal ridge resembling that in *Dicksonia adiantoides*. Very little is wanting to separate off this ridge so as to give rise to a free internal strand similar to those in *Dicksonia rubiginosa*. The internal strand might then become converted into a more or less closed cylinder, like that found in *Pteris elata*, in two different ways: either by enlarging and at the same time curving round so that its two ends eventually meet, or as it enlarged it might also branch, and the branches eventually fuse up into a ring. It is difficult to decide which of these two methods is the more probable, indeed, it is possible that both may occur. If the same series of changes were to take place in the first internal ring a second would be produced, and thus again a third, one lying within the other, as exemplified by *Pteris elata* and *Matonia pectinata*.

It must at once be understood that the order in which these Ferns have been placed in order to illustrate this theory is not intended to represent a phylogenetic series. All that it is necessary to assume is that their relationship is sufficiently close for the various modifications of structure that they present to be taken in explanation of one another. According to the theory outlined above a strong distinction must be drawn between the internal vascular cylinders and the original

external one, because the former are not only different in origin, but also later in development. In this it differs essentially from the suggestion put forward by Seward<sup>1</sup> and Boodle<sup>2</sup>, according to which it would appear that the internal vascular cylinder was split off as a whole from the original solenostele. It is to be regretted that young plants of none of these Ferns were available for examination, for no doubt they would provide much valuable information upon this question.

#### THE CYATHEACEAE.

The first observations upon the anatomy of this order were made about a hundred years ago by Plumier, who describes the appearance of the cut end of a stem of a *Cyathea*. The history of the subsequent attempts to arrive at a more satisfactory knowledge of their structure is unusually interesting, in that it discloses how the successive results were damaged and impeded by the interference of preconceived ideas based upon currently accepted theories. For instance, it is evident that the opinions held by most of the earlier anatomists upon the nature of the Fern stem in general were really the outcome of a statement made by Cesalpino so long ago as 1583<sup>3</sup>. Having first come to the conclusion that Ferns do not possess true seeds, Cesalpino proceeded to deduce the fact that they cannot possess true stems either. Hence, in the earlier part of the last century, we find that Brisseau-Mirbel<sup>4</sup>, Link<sup>5</sup> and Hanstein<sup>6</sup> all firmly refuse to recognize a true stem in the Ferns, insisting that their caudex is merely a symposium of leaf-bases. Indeed, the authority of Cesalpino does not seem to have lost all its influence even

<sup>1</sup> The structure and affinities of *Matonia pectinata*, Phil. Trans. Roy. Soc. Lond., Series B, vol. cxci, p. 180, 1899.

<sup>2</sup> On the anatomy of the Gleicheniaceae, l. c., p. 739.

<sup>3</sup> De plantis, lib. I, cap. 14.

<sup>4</sup> Éléments de botanique, vol. i, p. 122, 1815.

<sup>5</sup> Einige Bemerkungen über den inneren Bau der holzigen Farnkräuter, Linnaea, p. 414, 1826; also, Über den Bau der Farnkräuter, Abhandl. d. K. Acad. d. Wissensch. z. Berlin, p. 375, 1834, and 1835, p. 82.

<sup>6</sup> Plantarum vascularium folia, caulis, &c., Linnaea, p. 65, 1848.

at the present time. For his conclusion lies essentially at the base of the various theories of 'phytons,' 'rejuvenescence,' and 'segmentation' that have been advanced by Gaudichaud, C. H. Schultz, Delpino, and others. The most recent modification of these theories is that set forth by Celakovský<sup>1</sup> in his paper upon the segmentation of the stem. He also arrives at the same conclusion as Cesalpino, from very different premises, but by an analogous process of deduction. So far as the Ferns are concerned, it is fairly clear that any apparent segmentation that may occur in this group is to be regarded as a late development rather than a primitive feature, because it is becoming more and more probable that the dictyostelic species, in which the so-called segmentation is most obvious, are to be derived from solenostelic forms, and these in turn from forms with a solid central cylinder. That is to say, so far as the structure of the stem is concerned, there is less indication of segmentation in the primitive types than in the more advanced. Von Mohl<sup>2</sup>, with his habitual freedom from external influences, was the first to establish the cauline nature of the vascular system of the Tree-fern stem; the leaves being supplied by branches given off from the stem system. He admitted that the vascular strands in the 'pith' of the stem ran out directly through the leaf-gap into the centre of the petiole, but in spite of this, he utterly rejected the comparison of the Tree-ferns with the Monocotyledons which had hitherto been advanced with enthusiasm by Link and others. From now on the controversy settled upon the nature and course of these central strands of the leaf-trace. Karsten<sup>3</sup>, who next investigated them, observed that their course in the stem was similar to that of the central vascular bundles of a Palm, and in consequence revived the Monocotyledonous comparison, rendering it so much support that it continued to exercise

<sup>1</sup> Die Gliederung der Kaulome, Bot. Zeit., Bd. lix, p. 79, 1901.

<sup>2</sup> Über den Bau des Stammes der Baumfarne, Vermischte Schriften, p. 108. Tübingen, 1845. First published in Martius' 'Icones plantarum cryptogamicarum Braziliae,' 1833.

<sup>3</sup> Die Vegetationsorgane der Palmen, Abhandl. d. K. Acad. d. Wissensch. z. Berlin, p. 186, 1847.



a marked influence upon many subsequent investigations. Stenzel<sup>1</sup>, however, was entirely unaffected by it, and was the first to declare that even the central strands of the stem were cauline, although he admits that branches are given off from them which run out into the centre of the petiole. The Monocotyledonous comparison was also rejected by Mettenius<sup>2</sup>, although he still describes the central strands of the stem as running out direct into the petiole, sending branches to the margin of the leaf-gap as they pass through. The point was carefully reinvestigated by Trécul<sup>3</sup> in 1869, who reverts to the opinion of Stenzel, and concludes that none of the central strands of the stem pass out as such into the petiole, and that therefore all the vascular bundles of the leaf-scar arise from the margin of the leaf-gap. De Bary, in his text-book (l. c., p. 291), follows Mettenius, so that the question may be regarded as still an open one.

*Cyathea Brunonis*, a Tree-fern with comparatively simple once-pinnate leaves, was examined by me, and will serve as a good example in which to describe the relations that exist between the internal accessory strands and the leaf-traces. In this plant the ordinary stelar cylinder is a dictyostele consisting of two or three large band-shaped meristeles separated by relatively small leaf-gaps. A large number of separate leaf-traces arise from the outwardly turned margin of each leaf-gap, and these are so arranged in the petiole that a figure is produced in transverse section easily recognizable as a modification of the outline given by the gutter-shaped trace so often met with in Fern petioles. In this case, however, the margins of the gutter are strongly curved towards within, and there is also a deep tuck or fold along each of its sides (Fig. 15). In consequence of this, certain of the petiolar strands come to lie some distance within the others, and these are the central strands, the origin and

<sup>1</sup> Über Verjüngungserscheinungen bei den Farnen, Verhandl. d. Deutsch. Acad. d. Naturforsch., Bd. xxviii, p. 18, 1861.

<sup>2</sup> l. c., p. 525.

<sup>3</sup> Remarques sur la position des trachées dans les Fougères, Ann. des Sc. Nat., 5<sup>e</sup> sér., vol. xii, p. 274, 1869.

course of which is under dispute. To return to the stem; the internal strands are small and round, and about twenty or thirty of them are scattered in the ground-tissue within the ordinary stelar cylinder. At each leaf-insertion four of them approach the margin of the leaf-gap and join on to it exactly at the points of departure of certain of the leaf-traces (Figs. 15 and 16). The first pair join on to the traces *a, a*, the next pair divide each into two branches, which join on to the traces *b, b* and *c, c*, respectively. In their course from the leaf-gap margin down the stem the internal strands run first of all towards the centre, and then, turning more directly downwards, they travel obliquely towards without, diminishing as they do so, and finally ending blindly without coming into contact with the external stelar cylinder. The leaf-trace protoxylems are all endarch, but they gradually become mesarch as they pass down the stem; those of the leaf-traces that abut upon internal strands are continued down the internal strands; those of the others run down the margin of the leaf-gap, joining on to each other as they do so, and rapidly disappearing after the leaf-gap has closed. In other species (*C. arborea* and *C. glauca*) Trécul has shown that matters are much more complicated and obscure, because the number of internal steles related to each leaf-insertion is greater, and those leaf-traces that abut upon the internal strands often stand away from the leaf-gap margin, remaining connected with it only by a short horizontal strand, or they may even be altogether free from it.

Considerable light is thrown upon the nature of the central strands of the petiole by the structure of *Dicksonia Barometz*. There are no internal vascular strands at all in the stem of this Fern, but only the ordinary stelar cylinder. The leaf-gaps are very small and close up rapidly, nevertheless they occasionally overlap each other, and therefore the structure must be regarded as dictyostelic, although it is very near solenostely. The leaf-trace departs as a single piece, but sooner or later it breaks up into a large number of separate strands. The point at which the disintegration

takes place varies from one leaf to another; sometimes it breaks up almost immediately upon its departure from the stelar cylinder of the stem, and sometimes not until it has reached the free petiole (Fig. 17). While the leaf-trace remains a single continuous strand it has the form of a gutter with deeply incurved margins and a fold along each of its sides. After it has become broken up into separate portions these still keep the same conformation, so that some of the strands, chiefly those of the incurved margins, come to occupy a central position exactly as they do in *Cyathea Brunonis*. In this case, however, all the separate strands clearly arise from the leaf-gap margin, and from the leaf-gap margin only.

It may be mentioned in passing that lateral shoots are of frequent occurrence in *Dicksonia Barometz*, and like those of *Pteris elata* they arise not from the margin but from the back of the leaf-trace, just before it begins to break up. Sometimes two may arise upon the same petiole.

These observations all tend to prove that Trécul was quite correct in maintaining that the internal strands of the stem are strictly and essentially cauline, and this being granted, the idea is at once suggested that they are essentially similar in nature and origin to those of *Dicksonia rubiginosa*, *Pteris elata*, &c. It will be seen that this suggestion receives strong support from the manner in which the internal strands first appear in the young plant of *Alsophila excelsa*.

I have been able to examine a number of young plants of *Alsophila excelsa* that were grown from the spore, and since the vascular system of the young plant of the Cyatheaceae has not yet been dealt with in detail, it is perhaps advisable to describe their structure at some length. Although the course of the development of the vascular system was practically the same in all the specimens examined, yet the rapidity with which the different stages are passed through varies considerably according to the conditions of growth. It must be understood, therefore, that the description given here is a more or less generalized one, and that it must not



be expected to hold good rigidly from leaf to leaf in every specimen. This statement applies in particular to the diagram given in illustration (Fig. 18). With this reservation, however, it is believed that the diagram will serve to represent the course of development of the vascular system, not only in the Cyatheaceae, but also in most of the solenostelic and dictyostelic Ferns up to the particular stage that they retain when mature.

The young plant of *Alsophila excelsa* has its leaves arranged radially all round the axis, and it probably grew erect. At the very base of the stem the single central cylinder possesses a small central strand of xylem, usually with a few xylem-parenchyma cells intervening between the tracheides. The first leaf-trace may depart without in any way altering the structure of this stele or of its xylem-strand, but usually the phloem on the adaxial surface of the leaf-trace is prolonged a short distance downwards into the substance of the central xylem. At the departure of the subsequent leaves this feature is much more pronounced, and the phloem thus decurrent runs down through the whole length of the internode to meet with that decurrent from the leaf below. In the second leaf, however, it often falls short of the point of departure of the first leaf and ends blindly in the internode. From this point, therefore, up to the third or fourth leaf the centre of the xylem-strand is occupied by a core of phloem. At the departure of about the third or fourth leaf the pericycle follows the phloem down into the internode below, so that a few pericyclic cells are now to be found in the centre of the core of phloem. At the fifth leaf (or sometimes at the fourth) the endodermis also is decurrent, giving rise at first to a few cells only in the centre of the pericycle which usually disappear before the node below is reached. Higher up it is continuous from node to node, and surrounds a progressively increasing amount of ground-tissue which is now decurrent with it. The vascular system has, in fact, at length become a solenostele. This stage, however, does not last long, for the leaf-gaps begin to overlap after the departure of about the eighth leaf,

and above this point it becomes more and more dictyostelic, although at first a complete vascular ring is occasionally to be met with. The leaf-trace of the first five or six leaves consists of a single curved strand. Above this point two or three separate strands are given off to each leaf, and at about the tenth leaf four such strands are present, two arising from each side of the leaf-gap.

The first indication of internal steles that occur in the mature plant is to be found at about the tenth leaf. Just below one or both of the two upper (adaxial) traces of this leaf the xylem of the stem-stele is seen to project slightly towards within, so as to form a small ridge on its internal surface, which is often continued as such for some distance down the stem. Sometimes, however, it separates off completely so as to produce a small xylem-strand lying free within the phloem of the stele, which either ends blindly below, or eventually fuses up again with the main xylem-strand. These free xylem-strands are always present at the subsequent leaf-gaps, and although still remaining enclosed by the same endodermis, they become more and more distinct from the main xylem-strand of the stele. Later on they may even separate off from the stele altogether in the upper part of their course, only fusing with it again at a point lower down. The separation of the small xylem-strands from the main stele finally becomes complete throughout, and from their starting-point they run as small independent vascular strands ending blindly in the central ground-tissue, having no further communication with the main stele, except sometimes by a small branch near their point of origin.

It seems, therefore, that the internal vascular strands of *Alsophila excelsa* owe their existence to the same initial phenomena as do those of *Dicksonia rubiginosa*. That is to say, they are probably derived from the elaboration of a local thickening of the xylem-ring at the margins of the leaf-gaps in the ordinary stelar cylinder. The earlier stages of their development also proceed along essentially the same lines, although it is to be admitted that there are certain marked

differences. Thus in *Alsophila excelsa* the internal strands of one leaf-gap are not related to any of the other leaf-gaps, nor are the internal strands of succeeding leaf-gaps in any way joined up or connected with one another. It should also be noted that in this plant the internal strands do not appear at all until the ordinary stelar cylinder has become more or less dictyostelic.

The real nature of the accessory cortical strands that occur in certain Cyatheaceae (*Cyathea arborea*, *Alsophila armata*, &c.) is not as yet known with certainty. Two concentric rings of vascular strands are also present in the stems of *Acrosticum scandens* and *A. tenuifolium* (*Lomaria fraxinifolia*). According to Bertrand and Cornaille<sup>1</sup> the leaf-traces arise from both of these two rings, but which of the two is to be regarded as the typical stelar cylinder has not yet been decided.

In the stem of *Davallia immersa*, again, two concentric series of vascular strands are present. The central ring alone gives off the leaf-traces, and probably represents the typical stelar cylinder. My material was not sufficient to determine the nature of the small peripheral strands. It is possible, however, that they are merely root-steles that run forwards for a long distance in the ground-tissue of the stem before turning outwards.

#### DAVALLIA ACULEATA AND D. PINNATA.

The stem of *Davallia aculeata*, like those of the other solenostelic Davallias, is a dorsiventral rhizome with the leaves inserted in two rows upon the upper surface, but the solenostele itself differs so much in structure from those already described that it deserves especial mention. Instead of surrounding a central mass of ground-tissue as a hollow vascular cylinder, the wall of which is of the same breadth throughout as in the previous examples, the ventral region of the soleno-

<sup>1</sup> Étude sur quelques caractéristiques de la structure des Filicinées actuelles. Mémoires de l'Université de Lille, tom. x, no. 29, p. 136, 1902.



stele in *D. aculeata* is more than twice as broad as the dorsal region. In consequence of this the enclosed ground-tissue is displaced so as to occupy an excentric position near the dorsal surface (Fig. 19). The extra breadth of the ventral half of the solenostele is entirely due to the increased amount of xylem present in that region, because the sheath of phloem and pericycle is of approximately even thickness throughout, both on the inside and on the outside of the stele (Fig. 20). No definite protophloem is to be made out on the inside of the stele, although it forms a fairly distinct layer on the outside. The absence of an internal protophloem is, however, sometimes to be observed even in typical solenosteles, e.g. *Lindsaya retusa*. The leaf-trace departs from the narrow dorsal region of the solenostele as a single curved strand with its concavity directed toward the median dorsiventral plane of the rhizome. In passing outwards it gradually loses its curvature, and in the free petiole has the form of an equilateral triangle with rounded angles and sides; the xylem-strand, however, still remains V-shaped. The leaf-gap is very small and is closed up at the same time as the acroscopic margin of the leaf-trace is set free.

In *Davallia pinnata* the habit of the stem and the insertion of the leaves is exactly the same as in *D. aculeata*. The appearance presented by the vascular system also, at least in sections taken just below a leaf-insertion, is very similar in both. It has at these points the form of a hollow vascular cylinder, the wall of which is very much broader in the ventral region than it is in the dorsal, and the ground-tissue enclosed within the stele is displaced, as in *D. aculeata*, so as to lie excentrically near the dorsal side (Fig. 21). On the other hand, the extra breadth of the ventral half of the vascular ring in *D. pinnata* is not entirely due to the xylem alone as it was in *D. aculeata*. The internal phloem also takes part in its production, there being a much greater quantity of this tissue on the ventral side of the enclosed ground-tissue than on the dorsal (Fig. 22). The anatomy of this plant has already been described by

Tansley and Lulham<sup>1</sup>, and the following observations confirm their account. The leaf-trace departs as a single strongly curved strand with the concavity, as usual, facing towards the median dorsiventral plane of the rhizome. The leaf-gap closes up at the same time as, or even slightly before, the leaf-trace is quite free. The sclerenchymatous ground-tissue lying in the concavity of the leaf-trace passes down with it into the substance of the stem-stele. In this manner it produces the leaf-gap itself, and also accounts for the stout strand of sclerenchyma, surrounded by endodermis and pericycle, that lies within the stele, near its dorsal side, in regions just below the nodes. If the strand of ground-tissue thus enclosed be followed downwards through the internode to the node below, it is seen to diminish gradually in size until finally it disappears altogether, usually a short distance before the leaf-gap next below is reached. So that in the lower part of each internode the whole space within the xylem is occupied by internal phloem alone (Fig. 21). Occasionally, however, the strand of ground-tissue may persist until that decurrent through the leaf-gap next below is also enclosed in the stele. In the specimens examined the ground-tissue decurrent through one leaf-gap was never found to be continuous with that decurrent through the gap below. Just before it disappears the enclosed strand sometimes breaks up into two or three small branches.

The line of delimitation between the internal phloem and the xylem is not quite an even one, because small teeth of phloem project irregularly here and there between the peripheral elements of the xylem. The sieve-tubes of the internal phloem are unusually small and angular, and are scattered throughout the whole of its mass. They occur in greatest abundance towards the dorsal side, but no definite protophloem is to be distinguished.

The stem branches frequently in a dichotomous manner. As the stele of the main axis approaches the point of branching

<sup>1</sup> On a new type of Fern stele and its probable phylogenetic relations. *Annals of Botany*, vol. xvi, no. lxi, p. 157, 1902.

it flattens out dorsiventrally and finally divides into two by constricting in the middle. The constriction usually takes place in such a manner that there is no communication between the tissues within the xylem-ring and those without it. Sometimes, however, a leaf-trace is given off at the same time as the stem-branches, and then the leaf-gap occurs just between the two branch steles and the ground-tissue is decurrent through it in the ordinary manner. The sclerenchymatous ground-tissue enclosed within the stele is always in direct continuity with that decurrent through the leaf-gaps, except a few very small strands which occasionally occur in the neighbourhood of the branchings. These strands are completely surrounded by their own endodermis and appear to be quite isolated. The leaf-trace departs as a single strongly curved strand, and the curvature increases as it passes out, until sometimes the margins of the gutter meet adaxially and fuse up so as to enclose a small mass of ground-tissue (Fig. 21). This completely closed ring is only to be found over a very short distance; it may never even be formed at all. In either case the leaf-trace eventually divides into two separate halves.

#### DAVALLIA REPENS.

The peculiar nature of the vascular system of *Davallia repens* was first observed by Trécul<sup>1</sup> in 1885, but in his account the most interesting feature of its structure was unfortunately overlooked. However, the same type of stele has recently been discovered in certain Lindsayas by Tansley and Lulham (l.c.), who have given it a perfectly correct interpretation. *Davallia repens* is referred to here because it is necessary to complete the series begun by *D. aculeata* and *D. pinnata*; for the structure of its stele throughout the whole stem is similar to that found in *D. pinnata* at the base of the internodes only. In fact there is no ground-tissue to be found

<sup>1</sup> Observations sur la structure du système vasculaire dans le genre *Davallia*, et en particulier dans le *Davallia repens*. Comptes rendus, tom. ci, p. 1453, 1885.



within the stele of *D. repens* at any point whatever. The xylem-ring is about ten times broader in the ventral region of the stele than it is in the dorsal, and the mass of enclosed phloem occupies in consequence a very excentric position (Fig. 23). The dorsal portion of the xylem-ring is very thin and forms a kind of bridge resting on the ventral mass, and arching over the enclosed phloem. The xylem-strand of the leaf-trace departs from this bridge, giving rise to a small gap, through which the internal phloem comes into contact with the external. The endodermis and pericycle which surround the external surface of the stele are not in the least decurrent through the leaf-gap; they pass evenly across it, or at most only dip very slightly inwards. The leaf-gap closes up before even the xylem of the leaf-trace has yet separated off from that of the stem-stele. The structure of the internal phloem is quite normal, and the whole of it is probably to be regarded as metaphloem. The sieve-tubes nearest the bridge are somewhat smaller than the rest, but no definite protophloem can be distinguished, nor does the external protophloem dip in through the gap in the xylem of the bridge. The leaf-trace departs as a single strand, more or less cordate or reniform in section.

The steles of *Davallia tenuifolia*, *Parkeri*, *hymenophylloides* and *clavata* were found to be precisely similar to that of *D. repens*, apart from slight differences in the relative thickness of the ventral mass of xylem and the dorsal bridge, and in the amount of internal phloem present. The same type of stele is also to be found in fifteen or more different species of *Lindsaya*, but since a paper upon the anatomy of this genus is in preparation by Tansley no further reference need be made to them here. This type of vascular system has been called the *Lindsaya*-type by Tansley and Lulham, and since it is so characteristic of that genus it will be referred to in this paper by the same name. It should be noted, however, that there are at least two solenostelic species of *Lindsaya*. One of these, *Lindsaya retusa*, is perfectly typical and has already been mentioned. The solenostele of the other,

*Lindsaya cultrata*, is very small and thin, and, moreover, the leaf-trace departs as two separate strands and not as a single piece.

Tansley has suggested that the two types of stele exhibited by *Davallia repens* and *D. pinnata* represent structures intermediate between protostely and dictyostely. I thoroughly agree with this, and consider that the type of stele found in *D. aculeata* may now be added to this series. The almost exactly parallel stages passed through by the vascular system in the young plant, even in such an advanced dictyostelic Fern as that described on p. 710, appear to me to give the suggestion a high degree of probability. As I understand the facts, the idea is that as the leaf and the leaf-trace increased in importance relative to the stem, the phloem lying on the adaxial side of the leaf-trace became extended downwards into the substance of the xylem of the protostele. Gradually reaching further down through the internode this internally decurrent phloem at length came into contact with that decurrent from the leaf-trace below, and a continuous solid core of phloem was thus formed within the stele. Then the ground-tissue lying in the adaxial concavity of the leaf-trace also began to extend downwards into the stele, forming at first a prolongation that ended blindly in the core of phloem, but eventually it reached down from one leaf-trace until it met with that decurrent from the leaf-trace below. In this manner an internal strand of ground-tissue was formed which is continuous throughout the stem, and the stele has become a solenostele. Now if such a series of changes were to take place in a dorsiventral rhizome with the leaves inserted only on the dorsal surface, it is extremely probable that the phloem and ground-tissue decurrent from the leaf-traces would not at first occupy the very centre of the stele, but would lie nearest to the dorsal surface on which the leaves are inserted, and hence the ventral portion of the xylem-ring would be broader than the dorsal, as is actually the case in *Davallia repens*, *D. pinnata*, and *D. aculeata*. What is not so easy to understand is why the xylem-ring should

ever become of even thickness all round in such a dorsiventral rhizome.

Judging from the *Davallias* and *Lindsayas* alone, it would seem that a continuous core of phloem was already present in the stele before the ground-tissue began to be decurrent at all. On the other hand, from Boodle's<sup>1</sup> description of the structure of the node in certain *Gleichenias* (*G. dichotoma*, *G. flabellata*), it appears that both the ground-tissue and the phloem are decurrent together and for a short distance only into the substance of the xylem. If this may be regarded as the first step in another series of modifications similar to those described above, it follows that in this case a solenostele could be reached without passing through a stage with a solid core of phloem, because both ground-tissue and phloem would be decurrent contemporaneously.

The whole theory is, of course, open to the inevitable criticism that the series of forms in question is perhaps one of reduction, and not one of advance. It seems to me, however, that the increased thickness of the lower region of the xylem-ring forms an insuperable objection to the general application of any reduction hypothesis to this series. That the vascular system actually has undergone reduction in a number of different Ferns is well known, but although it must be admitted that in some cases structures have resulted which bear a strong superficial resemblance to those described above, it may nevertheless be shown that there are crucially important differences between them. For instance, in *Vittaria stipitata*, which possesses a dorsiventral rhizome and leaves in two rows on its dorsal surface, the stele is very small and the xylem-ring is only one or two elements thick. Each leaf is supplied with two separate traces, one of which departs from each side of the leaf-gap, and the ground-tissue is decurrent through the leaf-gaps into the stele. So far as the stele itself is concerned each leaf-gap is closed up again before the next above is formed, but the gaps in the xylem-ring remain open long enough to overlap, so that in this respect the stele resembles

<sup>1</sup> On the anatomy of the Gleicheniaceae, l. c., p. 720.



that of *Cheilanthes lendigera* (cf. p. 696). At the level of the leaf-gap the internal ground-tissue is fairly voluminous, but it rapidly decreases as it passes down the internode until only a small strand is left lying close to the dorsal side of the stele. In my specimens this also eventually disappears, so that the decurrent ground-tissue is not continuous from one leaf-gap to another. The stele, therefore, in its general appearance resembles that of *Davallia pinnata*, but on closer comparison some very important differences come to light. In the first place the xylem-ring of *Vittaria stipitata* is equally narrow on all sides of the stele, and secondly, as the internal ground-tissue disappears it is not replaced by phloem but by pericycle. Only a slight amount of internal phloem is present at the most; it is even completely wanting on the ventral side of the stele, being replaced by parenchyma.

A number of plants identified as *Vittaria elongata* were also investigated, and in some of them the stele possessed exactly the same structure as in *V. stipitata*. In others the ground-tissue did not pass in through the leaf-gaps at all, so that, apart from the thin internal sheath of phloem, the whole of the centre of the stele was occupied by pericyclic parenchyma, even at the level of the leaf-gap itself. In several other specimens, again, the vascular system proved to be distinctly dictyostelic and of the simple dorsiventral type described on p. 695. According to Poirault<sup>1</sup> no internal phloem whatever is to be found in this species; and Jeffrey<sup>2</sup> states that both the internal phloem and the internal endodermis are wanting, but a certain amount of internal phloem was present in all the specimens that I examined, although it is replaced by parenchyma on the ventral side. It is rather surprising to find so wide a variation in the vascular anatomy of one and the same species, and since it is very difficult to be quite sure about the identification of some of the *Vittarias*

<sup>1</sup> Recherches anatomiques sur les cryptogames vasculaires, Ann. des Sc. Nat., 7<sup>e</sup> sér., t. xviii, p. 179, 1895.

<sup>2</sup> The structure and development of the stem in the Pteridophyta and Gymnosperms, Phil. Trans. Roy. Soc. Lond., Series B, vol. cxlv, p. 132, 1902.

it is quite possible that some of the specimens examined were wrongly named.

In *Antrophyum plantagineum*, another dorsiventral Fern with a reduced stele, the ground-tissue is not decurrent through the leaf-gaps into the stele at all. The centre of the stele is occupied by a mass of pericyclic parenchyma as in certain specimens of *Vittaria elongata*. The internal phloem is very scanty, and as stated by Jeffrey (loc. cit., p. 132) it is altogether absent on the ventral side of the stele. I can also confirm this author upon the absence of the internal phloem over the same region in *Antrophyum reticulatum*, but while he says that the internal endodermis is also absent, my specimens are distinctly and definitely dictyostelic; the plant has already been mentioned as such on p. 695.

If these cases be taken as illustrating the effect of reduction upon the different tissues of the stele in a dorsiventral rhizome, it is seen that, in spite of the dorsiventrality, the xylem is equally affected on all sides of the stele. The phloem, on the other hand, experiences greater reduction on the ventral side of the stele than on the dorsal. The pericycle does not appear to be reduced at all, being, in fact, relatively more highly developed than in an unreduced stele. It will now be remembered that none of these indications of reduction are to be found in the stele of *Davallia pinnata*, or in the *Lindsaya*-type of stele.

The effects of reduction upon the stele of an erect stem with the leaves inserted in several rows all round it are essentially the same as those described above, allowance being made for the difference in habit. A good example of such a structure is provided by *Adiantum Aethiopicum*. The leaf-traces depart as small, very slightly curved arcs, leaving very small leaf-gaps which, so far as the stele itself is concerned, close up at once. The leaf-gaps in the xylem-ring, however, persist long enough to overlap, so that in a transverse section two or three separate strands of xylem may be found enclosed within the stele. The endodermis and ground-tissue as a rule do not dip in through the leaf-gaps at all, and even if they are

slightly decurrent they disappear almost immediately below. The centre of the stele is occupied almost entirely by a large mass of pericyclic-tissue, the internal phloem being very much reduced, although it is still continuous all round.

According to Jeffrey (loc. cit., p. 132) a reduced stele, which he describes as a tubular central cylinder with a parenchymatous pith, but with no internal phloem or endodermis, is also to be found in *Davallia stricta*. The authority for the name of the plant on which he made his observations is not given, and I am in doubt as to which species he refers to. In *Davallia tenuifolia*, var. *stricta* (Hort.) the structure is exactly the same as in *Davallia tenuifolia* itself.

#### THE VASCULAR SYSTEM OF THE PETIOLE.

The *Lindsaya*-type of stele is found to be regularly associated with a single very simple vascular strand in the petiole. Seen in section this strand is subrotund or cordate in outline, and contains a xylem-strand shaped like a  $\wedge$  with the base directed towards the axis of the stem (Fig. 24). The protoxylem groups are distinct and endarch; one occurs at the end of each arm of the  $\wedge$ , and sometimes a third is also present at its apex. The arms of the xylem-strand are sometimes prolonged past the two lateral protoxylems, curving inwards towards the plane of symmetry of the petiole so as to form two small hooks (Fig. 25). These hooks are included in the phloem of the bundle, which is perfectly continuous all round the xylem-strand. According to Bertrand and Cornaille (loc. cit., p. 99) these hooks are always to be considered as present in theory, although they are often so reduced as to be practically obsolete. Using the terminology introduced by these authors in their recent elaborate and exhaustive researches upon the leaf-traces of the Ferns, the trace with two protoxylems would be expressed as a binary chain of divergents, and that with three protoxylems as a ternary chain: the latter resulting from the fusion of two binary chains and the reduction of the median bipolar thus formed to zero. Both cases are considered by Bertrand and Cornaille to be derived



by reduction from a more complicated type. Vascular strands of exactly the same structure are also to be found in the upper regions of many different petioles, which lower down possess a more complicated vascular system, e. g. *Loxsonia Cunninghamii*<sup>1</sup>, *Dicksonia apiifolia*, *Davallia ciliata* and *D. hirsuta*. According to Bertrand and Cornaille these also may be regarded as reduced structures.

It may be objected, however, that there is hardly any evidence that can be brought forward in support of a theory of reduction in any of these cases. There certainly does not seem to be any general reason why the vascular system at the top of the petiole should ever have been at any time in a more advanced condition than it is at present. It is clear that in any leaf the whole brunt of an increase in the leaf-surface must be felt in its entirety by the vascular system of the lower part of the petiole, and especially at or near its extreme base, where the water-current running directly upwards in the stem has to be diverted into the leaf. For this reason any advance towards greater efficiency in the water-conducting apparatus would probably make its first appearance in this region, and I have found, in many cases, that this actually does occur. On the other hand, the water-conducting apparatus that formerly supplied the whole leaf would still suffice for the amount of leaf-surface lying beyond it, provided that it was situated at a point sufficiently high up in the rachis. Apart from the disturbance due to the branching, the vascular system would therefore experience less incentive to modify its form as you pass upwards towards the apex of the leaf, and on this account it would seem preferable to regard the simplicity of its structure in this region as due to the retention of primitive features rather than to reduction. The same simple type of petiolar bundle is, moreover, characteristic of the earlier leaves of the young plants of *Dicksonia apiifolia*, *D. antarctica*, and even of *Cyathea excelsa*, in which, especially in the latter, the mature petioles possess a very elaborate vascular system.

<sup>1</sup> Gwynne-Vaughan, l. c., p. 89, and Fig. 8.

Upon the whole, therefore, I am inclined to regard this type of leaf-trace as relatively primitive, and as one from which the various more complex forms found in the Cyatheaceae and Polypodiaceae may be derived. Further, I agree with Bertrand and Cornaille in their important conclusion that, except in *Acrosticum tenuifolium* and *A. sorbifolium* (in which the petiole seems to possess accessory peripheral strands not derivable from the ordinary system)<sup>1</sup>, every modification undergone by the vascular system of the petiole in these two orders takes place in pursuance of a single main design. As the petiolar bundle increases in size the curvature of the xylem is followed by the vascular strand as a whole. The strand thereby takes up the form of an arc or an  $\cap$  (Fig. 26), and as it increases further in size and curvature it comes to assume different forms of gradually increasing complexity, which when seen in section give rise to various different outlines, suggesting an arch, horse-shoe, amphora, &c. Later on the single strand may break up into separate portions, but these always remain so related to each other that it is still possible to determine the sectional outline of the strand from which they were derived. It has already been stated that a single cordate petiolar bundle is generally related to stems with the *Lindsaya*-type of stele. The petioles of solenostelic stems also usually contain a single strand, but of varied and often complicated outline. In stems with advanced dictyostelic structure the petiolar bundle is generally broken up into two or more portions; although when the structure is but little removed from solenostely a single strand is often to be found.

According to Bertrand and Cornaille (loc. cit., cap. iii) there are two main regions to be distinguished in the vascular system of a Fern petiole. In that of *Cyathea Brunonis*, for instance (Fig. 15), there is a large folded curve extending abaxially from *c* to *c*, and there are two adaxial arcs, one on either side, extending from *c* to *b*. In petioles of a simpler structure, such as those of *Davallia tenuifolia* (Fig. 25)

<sup>1</sup> l. c., p. 133 (*Polybotrya Meyeriana* and *Lomariopsis fraxinifolia*).

and *Davallia speluncae* (Fig. 26), &c., the abaxial curve forms practically the whole of the strand, the adaxial arcs being reduced to small inflected hooks at the ends of the arms. In view of this suggestion it is interesting to find that whenever a petiole branches a vascular strand is always given off to the branch from the point where the adaxial arc or the xylem hook joins on to the abaxial curve. In many of the cases examined a single strand alone passes into the petiolar branch, but in others a second strand is also present, which invariably departs from the abaxial curve itself at the point where it is folded inwards (*x* in Fig. 15).

#### LATERAL SHOOTS.

In most of the solenostelic and in many dictyostelic Ferns lateral shoots are frequently to be found growing out from the bases of the petioles. Their vascular systems are usually connected up with the adaxial margins of the leaf-trace, rarely, as in *Pteris elata* and *Dicksonia Barometz*, with the middle of its abaxial curve. The vascular system at the base of the lateral shoot is often a completely closed cylinder, even when the main axis is perfectly dictyostelic, e.g. *Adiantum trapeziforme*. Sometimes a single central cylinder with a solid mass of xylem is present. As this stele passes through the cortex of the main axis a core of phloem appears in the centre of the xylem, then a solenostele is formed, and finally it may become more or less dictyostelic, as in *Dicksonia Barometz*. A similar structure is also to be found in the lateral shoots of *Dicksonia adiantoides*, but here the change from the solid central cylinder into the solenostele takes place very rapidly, and the solenostele is afterwards permanent. In this plant, and also in *Pteris elata*, the internal vascular strands do not occur in the lower part of the lateral shoots. In *Dicksonia rubiginosa*, however, they are usually present, even at the very base. So far as my investigations went on this point they may be summed up generally by stating that the ontogeny of the vascular system of the plant as a whole is very fre-



quently repeated, although more or less imperfectly, in the development of its lateral shoots.

In *Davallia gibberosa* two separate vascular strands run out from the stem into each lateral shoot, and the structure at the base of the shoot is similar to that described on page 695 as the simplest form of dorsiventral dictyostely. The lateral shoots are very numerous, but only a few of them ever become properly developed; all the others remain abortive and form no visible projection upon the surface of the stem. These suppressed shoots, however, are still utilized for the purpose of bearing the roots. A number of these arise upon the lower or ventral meristele of the shoot, which now functions merely as a special radiciferous strand.

I am inclined to believe that the radiciferous strands described by Trécul<sup>1</sup> and Lachmann<sup>2</sup> in *Blechnum brasiliense*, *Scolopendrium officinale*, D.C., *Asplenium Serra*, and others, should also be regarded as the vascular vestiges of suppressed lateral shoots. In the first two examples they consist, according to Lachmann, of a single solid vascular strand, but in *Asplenium Serra*, Trécul describes them as cylindrical vascular tubes. It has just been shown above that there are a number of Ferns the lateral shoots of which, if arrested at the right stage of their development, would present both these kinds of structure.

In all the Polypodiaceae that I examined the xylem-strand of the true root-stele was invariably diarch. Its long axis was generally tangential to a radius of the stem in the transverse plane, but it was so often oblique, or even parallel to it, that this distinction is evidently of no great value. In their course through the cortex of the stem the root-steles sometimes run directly outwards, more often they run obliquely forwards, or they may even take a zigzag course, running first of all towards the apex and then turning abruptly backwards before reaching the surface of the stem, as in *Dicksonia*

<sup>1</sup> Remarques sur la position des trachées dans les Fougères, l. c., p. 228.

<sup>2</sup> Contributions à l'histoire naturelle de la racine des Fougères. Thésis présentée à la faculté des Sciences de Paris, Sér. A, No. 116, p. 102, 1889.

*rubiginosa*. I agree with Lachmann (l. c., p. 130) in thinking that the course of the root-stele depends chiefly upon the different tensions set up in the cortex of the stem, incident upon the varying energy of its terminal growth at the time of the development of the root.

The most striking feature relating to the root-stele is that it possesses no cortex of its own during the greater part of its course through the ground-tissue of the stem. The cortex of the stem runs without break or interruption right up to the endodermis of the root. According to Van Tieghem<sup>1</sup> this is due to the fact that the definitive apical cell of the root arises in the endodermis so very near to the apex that the cortical tissue lying without it has at that point only attained three or four layers in thickness. The apical cell is subsequently kept in this position by divisions in the subjacent pericycle, which keep pace with the expansion of the surrounding cortex and result in the formation of a 'root-pedicel.'

#### HISTOLOGY OF THE VASCULAR SYSTEM.

In the Cyatheaceae and Polypodiaceae the endodermis is always exceptionally well-marked and characteristic. It always stands out with great clearness in sections treated with phloroglucin, because the radial walls of its cells are lignified and stain red. In all cases examined the endodermis and pericycle on both sides of the stele appear to arise from the division of a common cell-layer. The first-formed elements of the xylem in the petiolar bundles are small annular or spiral tracheides, and they are always grouped into well-defined strands situated on the morphologically internal side of the xylem (Figs. 24, 25, 26, *prx.*). The metaxylem sometimes closes up in front of the protoxylem elements, so that they appear to be immersed in the substance of the xylem; but nevertheless, as regards these two orders, it may be taken as a general statement that the protoxylems in the petiole

<sup>1</sup> Van Tieghem et Duliot, *Recherches comparatives sur l'origine des membres endogènes*, Ann. des Sc. Nat., Sér. 7, t. viii, p. 540, 1888.

are primarily and essentially endarch. In many Ferns, both solenostelic and dictyostelic, the individual protoxylems of the leaf-trace are continued downwards into the stem, so that the xylem of the stem is also differentiated from a number of definite endarch or mesarch centres, just as that of the petiole, e. g. *Dicksonia rubiginosa*, *D. davallioides* (Fig. 27, *prx.*), *D. adiantoides* (Fig. 12), *Hypolepis repens*, *Davallia Novae-Zelandiae*, *Pteris incisa*, *Dicksonia culcita*, *Asplenium scandens*, &c. On the other hand, there are a large number of Ferns in which the protoxylems of the petiolar bundles gradually die out towards the base of the leaf-trace, disappearing entirely before, or immediately after, its insertion upon the stele of the stem. No definitely localized protoxylem strands are to be found in the stems of these Ferns, nor are there any spiral or annular tracheides present. The first-formed elements of the xylem either form a fairly continuous layer all round the external periphery, so that the differentiation is more or less centripetal; or else they appear without order here and there throughout the whole xylem mass, so that the differentiation is quite irregular. In the former case, the small peripheral tracheides may be regarded as forming an exarch protoxylem, although they are all scalariform and differ from those of the metaxylem only in their smaller size and earlier development. In the latter case, there is no difference whatever between the first-formed elements of the xylem and those formed later on, so that a protoxylem as distinct from the metaxylem can hardly be said to exist. A continuous exarch protoxylem was found in several solenostelic Ferns, *Loxsona Cunninghamii*<sup>1</sup>, *Dicksonia apiifolia* (Fig. 28), *Davallia platyphylla*, *D. speluncae*, *D. hirta*, *D. marginalis*, &c. In some dictyostelic Ferns also the peripheral elements are smaller, and upon the whole develop earlier than the rest, but the subsequent differentiation is usually rather irregular, as in *Gymnogramme japonica*, *G. vestita*, *Adiantum trapeziforme*, *Dicksonia Barometz*, &c. In the *Lindsaya*-type of stele the large ventral mass of xylem seems always differentiated more or less

<sup>1</sup> Gwynne-Vaughan, l. c., p. 79, Fig. 3.



irregularly (Fig. 23). In *Cyathea Brunonis*, *Alsophila excelsa*, *Dicksonia culcita*, and in several other dictyostelic Ferns with large meristeles, the leaf-trace protoxylems are decurrent along the margins of the leaf-gaps and even for some distance below the gap itself, but the differentiation of the main mass of xylem is irregular, or sometimes more or less centripetal.

These observations are of course not exhaustive, but, so far as they go, it appears that whenever definite protoxylem strands consisting of spiral and annular elements do occur in the stem they are in relation, directly or indirectly, to the decurrent protoxylems of the leaf-trace. On the other hand, the small scalariform tracheides, which are the first to be formed at the periphery of the xylem of the stem, may in many cases be regarded as constituting a definite exarch protoxylem proper to the stem itself.

The phloem is generally separated from the xylem by a continuous layer of parenchyma (the 'vasal-parenchym' of Strasburger), although sieve-tubes are occasionally to be found in direct contact with the tracheides. The parenchymatous cells of the phloem generally contain less starch and more proteid matter than those of the xylem or those of the above-mentioned 'xylem-sheath.' This distinction, however, is very variable, and seems to depend upon such factors as the season, the condition of growth, &c. In the case of the Ferns, therefore, it seems advisable to give no greater importance to the terms phloem-parenchyma, xylem-parenchyma, and xylem-sheath than as indicating certain definite topographical regions in a common vascular ground-tissue. Cavity-parenchyma is very generally present in the petioles of the Cyatheaceae and Polypodiaceae, occurring at points just in front of the protoxylem strands (Figs. 24, 25, 26). It consists of rather large cells, the longitudinal walls of which are transversely plicate on the side facing the xylem. These cells have living contents and thin cellulose walls, except in *Loxsonia Cunninghamii*<sup>1</sup>, where they become reticulately thickened and lignified. In *Dicksonia apiifolia*, *Davallia hirta*, and *D. Novae-Zelandiae*,

<sup>1</sup> Gwynne-Vaughan, l. c., p. 87, Fig. 11.

it is clearly shown that the formation of cavity-parenchyma is really due to a kind of thylosis. At a certain stage in the development of the young petiole the cells of the xylem-sheath bordering upon the protoxylem strands increase rapidly in size, and send protrusions in between the rings and spirals of the first-formed elements, so as partly to fill up their cavities (Fig. 29). The protoxylem elements at maturity are almost completely disintegrated, and these protrusions give rise to the irregularly folded appearance of the longitudinal walls. Sometimes, when the leaf-trace protoxylems are decurrent down the steles of the stem their cavity-parenchyma also accompanies them, as in *Dicksonia davallioides* (Fig. 27), *Davallia Novae-Zelandiae*, *Hypolepis repens*, &c.

A number of irregularly shaped siliceous nodules are to be found in the cells of the xylem-parenchyma of *Davallia repens*, *D. tenuifolia*, *D. hymenophylloides*, and in most of the *Lindsayas* with the same type of stele. They have exactly the same form and appearance as those described by Boodle<sup>1</sup> in *Lygodium dichotomum*. In *Davallia repens* and *Lindsaya lobata* they also occur in the phloem-parenchyma.

The first-formed elements of the external phloem are always more or less distinct from the rest, and constitute a fairly definite protophloem. In most cases a definite protophloem is also to be found on that side of the internal phloem furthest away from the xylem, but in the *Lindsaya*-type of stele (Figs. 22 and 23) and also in several solenosteles, *Davallia platyphylla*, *D. strigosa*, *D. hirta*, *Lindsaya retusa*, &c., no internal protophloem can be made out at all. It has already been mentioned that internal phloem is altogether absent from the ventral side of the stele in *Vittaria stipitata*, *Antrophyum plantagineum*, *A. reticulatum* and *A. semiconstatum*.

The petiolar bundle of the Cyatheaceae and Polypodiaceae is essentially concentric throughout. The phloem is most plentiful on the abaxial side of the xylem, but at the same

<sup>1</sup> On the anatomy of the Schizaeaceae, *Annals of Botany*, vol. xiv, no. lviii, pp. 364 and 402, 1901.

time it is never altogether absent from the adaxial side (Figs. 24, 25, 26). The protophloem is always quite distinct on the abaxial side, and it is nearly always to be found on the adaxial side as well. Indeed when the petiole contains a single strand only, the protophloem can often be followed all round its adaxial concavity. Whenever the xylem strand of the petiole is prolonged into a hook, the protophloem, if present, always passes straight across over the bay that lies between the hook and the main strand (Fig. 26). It appears, therefore, that the sieve-tubes situated within the bay itself must be regarded as belonging to the metaphloem. In most cases the sieve-tubes within the bay of the hook are quite normal (Figs. 25, 26), but in a good many Ferns they exhibit a special kind of structure. Their walls are unusually thick, and when unstained have a swollen pearly appearance. The additional thickening is all cellulose, and consists of two fairly distinct layers, the innermost of which is broader, softer, and less refractive than that next the middle lamella. They have rather more contents than the ordinary sieve-tubes, and the deeply staining granules characteristic of typical Fern sieve-tubes are rarely if ever to be found in them. For all that they do not seem to be essentially different from typical sieve-tubes, although it is doubtful whether they continue to function as such. One form of sieve-tube graduates insensibly into the other; indeed, towards the base of the petiole the thick-walled sieve-tubes are nearly always replaced by the typical form. The thickened sieve-tubes may also occur all round the adaxial side of the leaf-trace; especially near the protoxylems, and again on the abaxial side of the strand on the flanks of the xylem. They are especially well shown in the petioles of *Dicksonia adiantoides*, *D. culcita*, *D. punctiloba*, *Davallia aculeata*, *D. platyphylla*, and *D. davallioides*. These modified sieve-tubes occupy exactly the same position as the lignified 'phloem-fibres' in the leaf-traces of *Loxosoma Cunninghamii*<sup>1</sup> and of certain species of *Aneimia*<sup>2</sup>, and

<sup>1</sup> Gwynne-Vaughan, l. c., p. 83, Figs. 5 and 6.

<sup>2</sup> Eoodle, On the anatomy of the Schizaeaceae, l. c., p. 400.



I have no doubt that these also represent metamorphozed sieve-tubes.

Attention must finally be drawn to the very remarkable mucilage ducts or vessels that are to be found in the external phloem of the petiolar strands of *Dicksonia Barometz*. They occur in the metaphloem, and are easily distinguished from the rest of its elements by their greater size and their dense, deeply staining mucilaginous contents. The structure of these elements was not investigated in detail, but it appears that they are formed by a number of elongated cells arranged in vertical series, the walls of which have become reabsorbed at certain points where they are contiguous, so that their contents are continuous throughout the series. In position they correspond to the inmost sieve-tubes of the metaphloem, but the perforations appear to be true perforations, and they are much too wide to resemble the sieve-plates. Whether they are to be regarded as metamorphozed sieve-tubes or not was not decided. From a figure given by Bertrand and Cornaille (loc. cit., p. 58, Fig. 30) similar structures appear to be present in the petiole of *Dicksonia regalis*.

#### THE SYSTEMATIC VALUE OF THE VASCULAR ANATOMY.

No really satisfactory conclusion upon the degree of importance that ought to be assigned to the vascular anatomy as a factor in the classification of the Polypodiaceae can be arrived at until the structure of at least a majority of the species of the various genera has been correctly described. The facts already at our disposal, although not so extensive as one might wish, are still sufficient to show that the characters brought to light by the study of the vascular anatomy will probably prove to be of great assistance in constructing a natural classification, and they must certainly be taken into account by the systematists. The anatomy of so many species, even in the genera especially dealt with in this paper, is still unknown, that the tentative nature of any conclusions drawn from the results obtained must, in the first place, be thoroughly understood.

If the solenostele and the *Lindsaya*-type of stele are to be regarded as the most primitive types of vascular arrangement in the Polypodiaceae, as suggested above (p. 717), it must at the same time be admitted that these primitive characters do not run parallel with Professor Bower's division of the order into Gradatae and Mixtae. Bower himself, however, supports the view that several different lines of descent may be represented within the Polypodiaceae alone<sup>1</sup>, and it is very probable that a more or less similar primitive type of vascular arrangement might occur in the primitive members of each line of descent. It follows that those genera in which the solenostele, or the *Lindsaya*-type of stele, is predominant may be regarded as relatively primitive, at any rate within their own particular family. The prevalence of the primitive types of stele in the various genera and subgenera may be summed up as follows.

All the species of *Dennstaedtia* (regarded by Hooker in the 'Synopsis Filicum' as a section of *Dicksonia*) that have hitherto been examined prove to be essentially solenostelic. It must be noted, however, that in *D. rubiginosa* the solenostele is not quite typical, and that additional internal vascular strands are also present.

*Microlepia*, including *Saccoloma*, is placed in the 'Synopsis Filicum' among the Davallias, and, apart from the fact that additional internal vascular strands are present in the Saccolomas (cf. p. 703), all the species that have been examined are typically solenostelic with two exceptions only. Of the exceptions, *Davallia ciliata* is dorsiventrally dictyostelic, and is clearly out of place among the Microlepias<sup>2</sup>. It is placed by

<sup>1</sup> Bower, Studies in the morphology of spore-producing members, no. 4, Phil. Trans. Roy. Soc. London, Series B, vol. cxcii, p. 123, 1899.

<sup>2</sup> Professor Bower has been kind enough to examine the sorus of this species for me, and he finds that 'the receptacle is almost flat, and the sporangia of various ages are intermixed; successive ones being interpolated without order between those already there. The older sporangia are long stalked, so as to raise their heads above the younger. There appears to be no regularity of orientation. The annulus is vertical. All these characters stamp it as one of the Mixtae, and it should find its place elsewhere than among the Microlepias.'

J. Smith<sup>1</sup> in the section *Leucostegia* under the synonym of *L. hirsuta*, and this arrangement is quite in accordance with its vascular structure. The other exception is *Davallia pinnata*, the stele of which exhibits a structure intermediate between a solenostele and the *Lindsaya*-type of stele. This plant has been removed from *Microlepia* by H. Christ<sup>2</sup> and given a section to itself: *Wibelia*. The anatomy agrees with this separation, and indicates a closer relationship to the *Lindsayas* than to *Microlepia*. *Davallia Novae-Zelandiae* (*Leptolepia*, Met.) is regarded by J. Smith and H. Christ as a species of *Microlepia*, but in the 'Synopsis Filicum' it is included in the section *Leucostegia*. Since, however, it proves to be typically solenostelic, and the section *Leucostegia* itself is a predominantly dictyostelic one, the anatomy gives unqualified support to the two former authorities.

Probably all the species of the genus *Hypolepis* are solenostelic, although the four species mentioned in this paper are the only ones in which the anatomy has been sufficiently described.

Prantl<sup>3</sup>, in 1892, proposed to divide the Polypodiaceae into four great tribes: the Aspidieae, the Asplenieae, the Pterideae, and the Polypodieae. At the same time he founded the sub-tribe *Dennstaedtiinae* to include the genera *Dennstaedtia*, *Microlepia*, *Leptolepia*, *Saccoloma* and *Hypolepis*, which he regards as containing all the most primitive species of his first tribe, the Aspidieae. It has been shown above that essentially the same type of primitive vascular system is to be found in every species of this sub-tribe in which the anatomy is known. Therefore, as regards the primitive nature of the sub-tribe as a whole, Prantl receives strong support from the anatomy, but to decide whether all these genera belong to the base of one and the same line of descent, or not, is another and a very difficult question; as he himself acknowledges. *Dennstaedtia* and *Microlepia* certainly appear

<sup>1</sup> *Historia Filicum*, 1875.

<sup>2</sup> *Die Farnkräuter der Erde*. Jena, 1897.

<sup>3</sup> *Das System der Farne*, Arbeiten aus dem K. Bot. Gart. z. Breslau, Bd. i, Heft i, 1892.



to go together, and they both come under Bower's division of Gradatae. It seems probable also that the genus *Loxsonia* should be regarded as more nearly allied to these two genera than to any others. The development of the sorus in *Leptolepia* and *Saccoloma* is not known, but *Hypolepis* belongs to the Mixtae. According to the anatomy *Leptolepia* goes with the Microlepias, but it may prove that a distinction should be made between *Saccoloma* and *Hypolepis* and the rest of the group, and also between each other. As a secondary character of the Dennstaedtiinae Prantl states that, except in *Saccoloma*, hairs are present instead of paleae throughout the group. So far as the species that I examined are concerned this certainly holds true.

The *Lindsaya*-type of primitive stele has been found in all the species of that order hitherto examined, except in *L. retusa* and *L. cultrata*, which possess solenosteles. The same type of stele is also characteristic of the sections *Odontoloma* and *Stenoloma*, which are placed by Hooker in the genus *Davallia*. The anatomy, therefore, agrees with H. Christ in removing these two groups from *Davallia* and placing them among the Lindsayas. J. Smith also places *Odontoloma* in his tribe Lindsaeae. The section *Stenoloma* he removes from the Davallias, but places it in his tribe Saccolomeae under the synonym of *Odontosoria*. It should be mentioned that *Davallia* (*Stenoloma*) *aculeata* is somewhat exceptional, in that it exhibits a type of solenostely peculiar to itself. H. Christ has given it a section of its own: *Lindsayopsis*. It has already been stated that according to the anatomy *Davallia* (*Microlepia*) *pinnata* should be included with the Lindsayas rather than with the Microlepias. The most primitive genera in Prantl's second tribe, the Asplenieae, were considered by him to be *Lindsaya*, *Lindsayopsis*, *Wibelia* (*Davallia pinnata*), *Odontosoria* (*Stenoloma*) and *Davallia*. If the last genus, *Davallia*, be excluded he finds here again support from the anatomy, since all the species in the four remaining genera possess a primitive vascular system, and, with three exceptions only, they all possess the same type of stele. Finally they all

belong to Bower's division of Mixtae. The presence of paleae instead of hairs is given by Prantl as a secondary characteristic of this group, and it held good in all the examples examined by me.

Of the genus *Davallia* there now remain to be discussed the sections *Humata*, *Eudavallia*, *Leucostegia* and *Loxoscaphe*. All the species that were examined in these sections proved to be perfectly dictyostelic, with the single above-mentioned exception of *Davallia* (*Leucostegia*) *Novae-Zelandiae*. The vascular arrangement was dorsiventral in every case, except *Davallia Emersoni* and *D. contigua* which are radially symmetric. These two species form the sub-section *Prosaptia*, which, according to J. Smith, should be removed from the *Davallias* altogether. Upon the whole the anatomy of the above sections would agree better with the *Polypodi* than with the rest of the genus *Davallia*.

Only a few species of *Pteris* are known to be solenostelic. One of these, *P. incisa*, is isolated with its varieties as the section *Histiopteris* both by Smith and H. Christ. Another, *P. scaberula*, together with *P. viscosa*, the anatomy of which is as yet unknown, form, according to Christ, the separate section *Paesia*. *Jamesonia* is solenostelic, and so also are two species of *Pellaea*. All these belong to Prantl's third tribe, the *Pterideae*, the most primitive genera of which he considers to be *Lonchitis*, *Pteridium*, and *Paesia*. It appears, therefore, that the agreement of the anatomy with his arrangement is not so complete in this as in the two previous tribes.

In his fourth tribe, the *Polypodieae*, solenosteles are still more rare. It is true that the *Polypodiums* of the section *Dipteris* are solenostelic, but Seward and Dale<sup>1</sup> have shown that it must be removed from the *Polypodiums* altogether. They even go so far as to give it a family to itself, apart from the *Polypodiaceae*. The only other case of solenostely that I am aware of in this group is in *Polypodium punctatum*, and here the vascular system so very closely resembles that of *Hypolepis* that, since Hooker himself has remarked that this

<sup>1</sup> On the structure and affinities of *Dipteris*, l. c., p. 502.

plant (l. c. p. 312) 'is very closely related to *Euhypolepis*,' it may confidently be removed to that genus.

Upon the whole, therefore, Prantl receives considerable support from our results, since nearly all of the genera regarded by him as relatively primitive in their respective family branches also prove to be characterized by the possession of a primitive vascular structure, especially as regards his first two tribes. Nevertheless, this must not be taken to mean that each, or even any, of his tribes actually represent separate single lines of descent. Much further research is necessary on all sides before this question can be satisfactorily faced, and the above discussion merely serves to point out the fact that anatomical considerations must play an important part in coming to any conclusion.

#### CONCLUSION.

The stelar theory has undergone many modifications under the hands of different authors since it was first introduced by Van Tieghem, and the exact meaning of the word 'stèle' as now used is getting somewhat obscure. It is, however, becoming more and more apparent that the chief value of the conception lies in its ontogenetic and phylogenetic significance, whereby the stèle of the stem may be regarded as the central cylinder of the young plant and all those tissues of the mature axis that result from its modification, or, as Farmer and Hill<sup>1</sup> would prefer to have it, the central cylinder of the young plant and all those *vascular* tissues of the mature axis that result from its modification. As a consequence of the first point of view it must also be held that there exists a regional distinction of primary importance between the stelar tissue and the cortex. Therefore, when considering a vascular arrangement such as a dictyostele or a solenostele it becomes impossible to neglect the question, whether the central parenchyma is to be regarded as stelar, and therefore morphologi-

<sup>1</sup> On the arrangement and structure of the vascular strands in *Angiopteris evecta* and some other Marattiaceae, *Annals of Botany*, vol. xvi, no. 62, p. 392, 1892.



cally distinct from the cortex ; or as cortical, in which case the stele, or the separate portions of it, must possess a definite internal as well as an external limit. Supposing the central parenchyma in question to be really stelar, then it must have come into existence by the substitution in the stele of parenchymatous elements for those that were previously vascular. To take the case of the Cyatheaceae and Polypodiaceae in particular ; if the course of development actually did take place in the manner suggested above (p. 717), then each cell of the central parenchyma must have belonged in previous generations successively to the xylem, phloem, pericycle and endodermis before attaining its present condition. On the other hand, if the central parenchyma be regarded as cortical, then the stelar elements at certain points in the stele through successive previous generations must have undergone fewer and fewer divisions as they developed, while the divisions in the cortex opposite these points must have correspondingly increased. Therefore the cortical tissue at these points would eventually encroach upon the vascular, and would in time come to occupy the greater part of the centre of the stele.

It has been very generally assumed that if the distinction between stele and cortex is really a morphological one, the two regions must of necessity be marked off from one another by the earliest cell-divisions at the apex, or by the so-called histogenetic layers. But recent researches upon apical meristems<sup>1</sup> have shown that the earlier tangential divisions in the segments of an apical cell, and even the histogenetic layers of Hanstein, are not only very inconstant and unreliable, but also that they bear no invariably fixed relations to any of the subsequent tissue-differentiations in the mature regions of the plant, and that in consequence they have little or no general value as morphological criteria. It does not appear to me that the regional significance of the stele is in any way bound up with the maintenance of these distinctions. The consideration of the morphology of the stele can only begin when

<sup>1</sup> Schoute, *Die Stelärtheorie*, Groningen, 1902 : also Tansley, *Proceedings of the Linnean Society*, Nov. 20, 1902.

that region is definitely and satisfactorily delimited. It is not directly concerned with any question as to which particular segment it is in which the tangential wall appears that first of all delimits it. All that is required is that a definite delimitation should actually be possible at one point or another during the course of its development in a majority of cases sufficiently great to render the statement general.

According to the view taken by Farmer and Hill the attention is concentrated upon the vascular tissue alone, and therefore the stele as a whole is deprived of any regional distinction. I quite agree with them that it is inconvenient, from a descriptive point of view, to draw theoretical distinctions that have no histological expression between different regions of the general ground-tissue. But at the same time I hold that it would be a great mistake to give up all attempts to discover the phylogenetic history, and the precise method of origin, in each particular case of such tissues as the central parenchyma, and even as the much abused endodermis. Full information upon such points is bound to be of considerable value, and the ability to state of two plants presenting the same type of structure whether they reached this condition by passing through the same, or through different series of changes would throw light upon many interesting problems which might otherwise remain obscure. For instance, in the Cyatheaceae and Polypodiaceae, it has been suggested above that, whether by the intrusion of the cortex, or by the metamorphosis of stelar tissue, the first appearance of the internal parenchyma must have taken place at the periphery of the protostele, and at points just above the departure of the leaf-traces. This displacement, or transformation, of the vascular tissue then advanced gradually inwards from these points until even the most central region of the stele was affected by it. The internal parenchyma, therefore, from the moment of its first appearance, was always in contact with the cortical parenchyma.

Now several other methods of procedure might also have taken place by which a similar result could be attained. For

instance, the first appearance of internal parenchyma might take place in the centre of the xylem of the protostele. The xylem-ring thus formed might subsequently become interrupted by the departure of the leaf-traces, and finally a structure resembling a solenostele might be attained by the gradual differentiation of phloem and endodermis through the leaf-gaps and all round the inside of the xylem-ring. Again, an internal endodermis might be differentiated within the internal parenchyma before the xylem-ring is interrupted, in which case the phloem alone would have to extend around the inside in order to bring about the above-mentioned structure. Finally, the internal phloem and endodermis might both be differentiated within the internal parenchyma before ever the xylem-ring is interrupted, and then the formation of leaf-gaps would do no more than set the internal tissues in continuity with the external. Although the first of these methods alone has been ascribed to the Cyatheaceae and Polypodiaceae above, it is very probable that the others may occur in other orders. Indeed Boodle<sup>1</sup> has already made some suggestions on similar lines in relation to the Schizaeaceae.

In a vascular system arising according to the two last methods it is evident that there can be no two opinions regarding the stelar origin of the central parenchyma. In the first two cases, however, it is possible to conceive of the intrusion of the cortex into the stele in the manner previously explained. It is difficult to see where any conclusive evidence upon this point, one way or another, is to be sought for. It is, however, reasonable to suppose that if the young plant of such a Fern as *Davallia pinnata* be examined at different stages in its development, some light may be thrown on the matter by the comparison of the state of affairs at those regions of the apex where the distinction between stele and cortex first becomes evident: or, perhaps, even by the comparison of the same region in the mature plant with that in a typically solenostelic Fern.

<sup>1</sup> On the anatomy of the Schizaeaceae, l. c., p. 407, and Further observations on Schizaea, Annals of Botany, vol. xvii, no. lxxvii, p. 530, 1903.



The simplest way of getting over the matter would be to accept the stelar origin of the central parenchyma in all cases, and to regard the internal endodermis as never strictly homologous with the outer. But still the other alternative is theoretically possible, and should not at once be rejected as inherently improbable.

In conclusion I have to thank Professor Bower and Dr. Lang for the assistance they have given me in obtaining material, and for their valuable advice upon various points in relation to my work. I have further to express my gratitude to the Director of the Royal Gardens, Kew, the Director of the Royal Gardens, Calcutta, and to Mr. Hemsley of Darjeeling, for their kindness in providing me with much useful and valuable material.

EXPLANATION OF FIGURES IN PLATES  
XXXIII, XXXIV, AND XXXV.

Illustrating Mr. Gwynne-Vaughan's Paper on Solenostelic Ferns.

Figs. 12, 20, and 22 to 28 are from photographs; a more or less under-exposed print being used as a camera-lucida drawing. All the other figures, except Fig. 29, are diagrams. Fig. 29 was drawn from the section. The following lettering is used throughout; *L.T.*, leaf-trace; *e.*, external endodermis; *e'*, internal endodermis; *P.*, external pericycle; *P'*, internal pericycle; *ph.*, external phloem; *ph'*, internal phloem; *pph.*, external protophloem; *pph'*, internal protophloem; *prx.*, protoxylem.

Fig. 1. *Dicksonia punctiloba*. Diagram of vascular system of rhizome including a node and the base of a leaf-trace. The upper surface of the rhizome would face the observer.

Fig. 2. *Dicksonia apiifolia*. Ditto.

Fig. 3. *Davallia Spelunca*. Ditto.

Fig. 4. *Hypolepis millifolia*. Ditto: *l.sh.*, lateral shoot arising from basiscopic margin of leaf-trace; *a.*, vascular strand running from free margin of lateral shoot to proximal margin of leaf-trace; *b.*, a similar strand running to distal margin of leaf-trace.

Fig. 5. *Hypolepis tenuifolia*. Ditto: *l.sh.* and *a.* as in Fig. 4; *c.*, vascular strand running from free margin of leaf-gap to acroscopic margin of leaf-trace.

Fig. 6. *Hypolepis repens*. Ditto: *l.sh.*, *a.* and *b.* as in Fig. 4; *l.sh'*, lateral shoot arising from acroscopic margin of leaf-trace.

Fig. 7. *Nothochlaena Marantae*. Diagram of vascular system of rhizome including two nodes and the bases of the departing leaf-traces. The upper surface of the rhizome faces obliquely towards the top of the plate.

Fig. 8. *Pellaea rotundifolia*. Ditto.

Fig. 9. *Gymnogramme calamelanos*. Ditto. The stem is radial.

Fig. 10. *Plagiogyria biserrata*. Diagram of transverse section of the vascular system. The steles are unshaded; the dark masses *sc.e.* and *sc.i.* represent sclerenchyma respectively external and internal to the stelar ring.

Fig. 11. *Dicksonia adiantoides*. Diagram of vascular system of rhizome, including a node and the base of a leaf-trace: *l.sh.*, lateral shoot arising from basiscopic margin of leaf-trace; *i.s.*, ridge upon internal surface of solenostele. The upper surface of rhizome would face the observer.

Fig. 12. *Dicksonia adiantoides*. Transverse section of the free margin of a leaf-gap in the solenostele: *i.s.*, the free xylem-strand forming a projection on the internal surface.

Fig. 13. *Dicksonia rubiginosa*. Diagram of the vascular system of the rhizome including a node and the base of a leaf-trace: *l.sh.* and *i.s.* as in Fig. 11; *L.*, lacunae in the solenostele not related to the departure of a leaf-trace. The upper surface of the rhizome would face the observer.

Fig. 14. *Pteris elata*, v. *Karsteniana*. Ditto. A piece is supposed to be cut out of the side of the solenostele so as to show the internal vascular system. Note that a small strand lying within the second vascular ring is also present. The stem is radial.

Fig. 15. *Cyathea Brunonis*. Diagram showing the arrangement of the vascular strands in the petiole: *a*, *b*, and *c* indicate those below which the internal vascular strands of the stem are inserted.

Fig. 16. *Cyathea Brunonis*. Diagram of one side of the acroscopic half of a leaf-gap; seen from within, and showing the insertion of the internal strands of the stem, *a*, *b*, and *c*.

Fig. 17. *Dicksonia Barometz*. Portion of the vascular system of the stem; seen from within, and showing the departure of three leaf-traces.

Fig. 18. *Alsophila excelsa*. Diagram of vascular system of a young plant in median longitudinal section. The xylem is black, the phloem lightly shaded and the endodermis is indicated by a dotted line. The ground-tissue is left white.

Fig. 19. *Davallia aculeata*. Diagram of vascular system of rhizome including a node and the base of a leaf-trace: *ph'*, internal phloem. The external phloem is not indicated. The upper surface of the rhizome would face the observer.

Fig. 20. *Davallia aculeata*. Transverse section of the stele of the rhizome in the middle of an internode: *scl'*, sclerenchymatous internal ground-tissue.

Fig. 21. *Davallia pinnata*. Diagram as in Fig. 19. The vascular system is supposed to be curved so that the two cut ends face the observer more or less obliquely: *ph'*, internal phloem.

Fig. 22. *Davallia pinnata*. Transverse section of the stele of the rhizome in the upper part of an internode: *scl* and *scl'*, sclerenchyma belonging respectively to the external and internal ground-tissue.

Fig. 23. *Davallia repens*. Transverse section of the stele of the rhizome at a point immediately above the leaf-gap. The petiolar bundle has not yet become free.

Fig. 24. *Davallia repens*. Transverse section of the vascular bundle of the free petiole.

Fig. 25. *Davallia tenuifolia*. Ditto: *Hk.*, adaxial hook of the xylem.

Fig. 26. *Davallia Speluncae*. Ditto: *Hk.*, as in Fig. 25; *Cp.*, cavity-parenchyma.

Fig. 27. *Dicksonia davallioides*. Portion of a transverse section of the solenostele: *Cp.*, cavity-parenchyma.

Fig. 28. *Dicksonia apiifolia*. Portion of a transverse section of the solenostele.

Fig. 29. *Dicksonia apiifolia*. Cells of the cavity-parenchyma sending protrusions into a disintegrating protoxylem element of a young petiole.





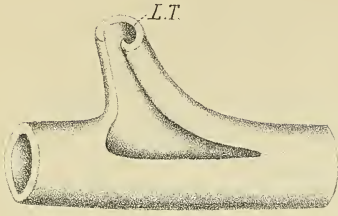


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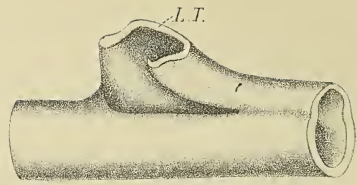


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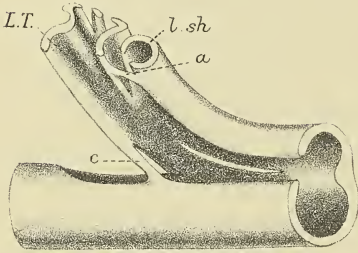


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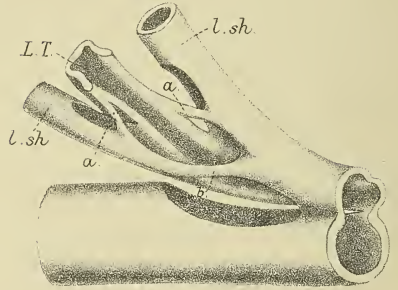


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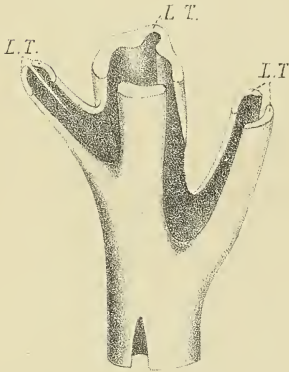


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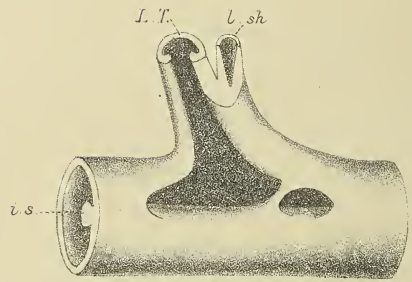


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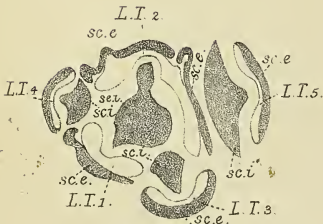


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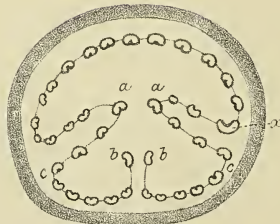


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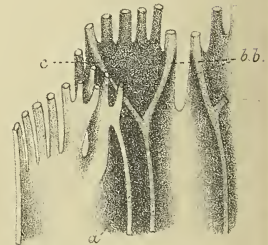


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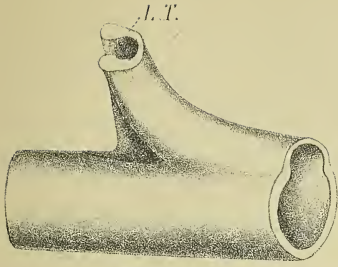


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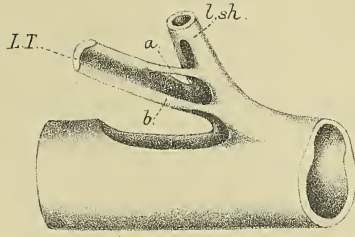


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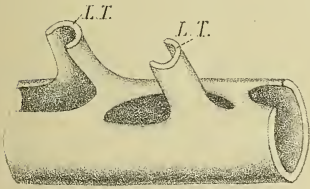


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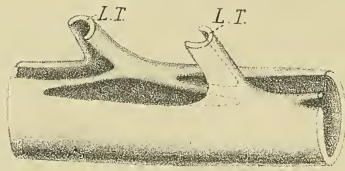


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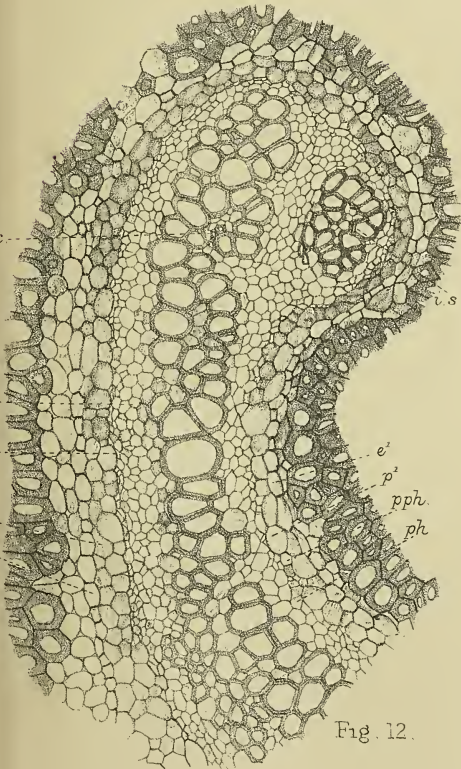


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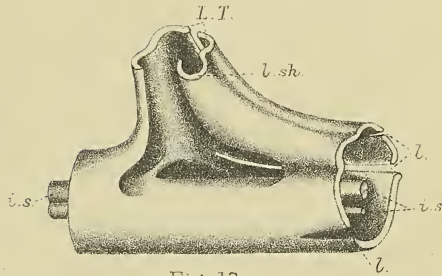


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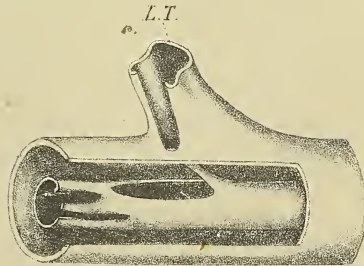


Fig. 14.





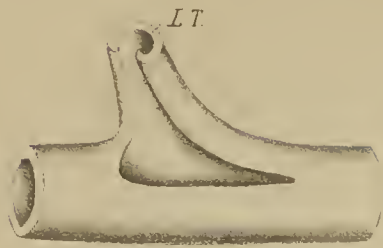


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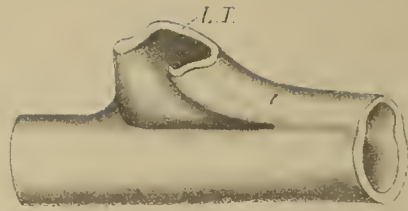


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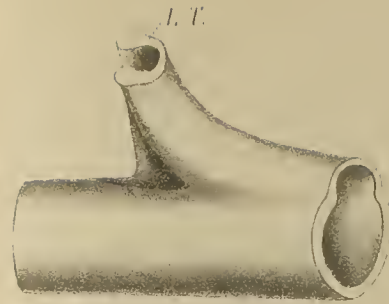


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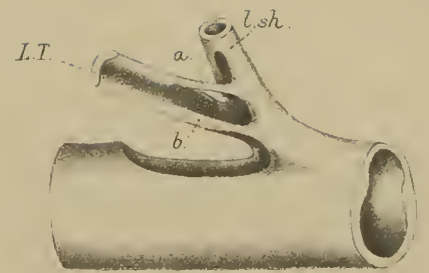


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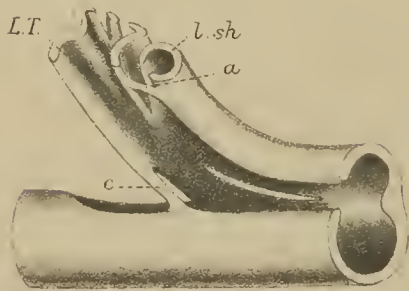


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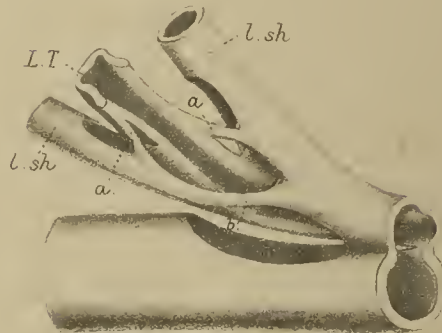


Fig. 6.



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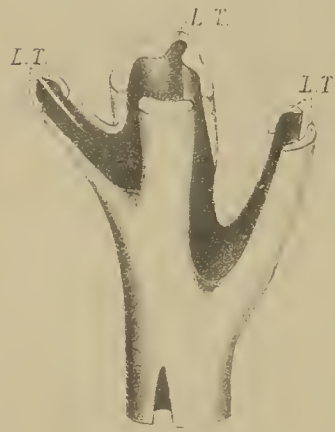


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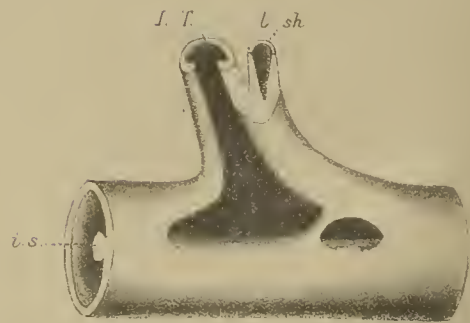


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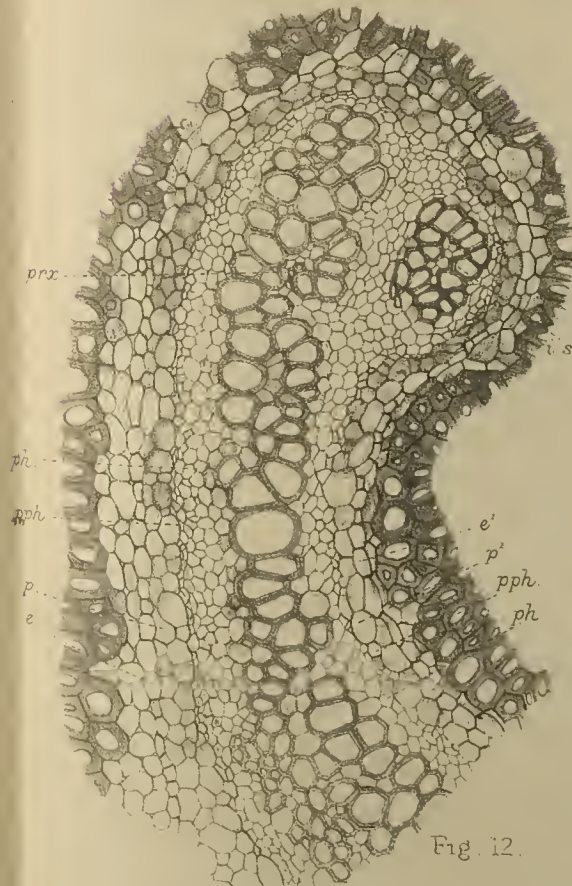


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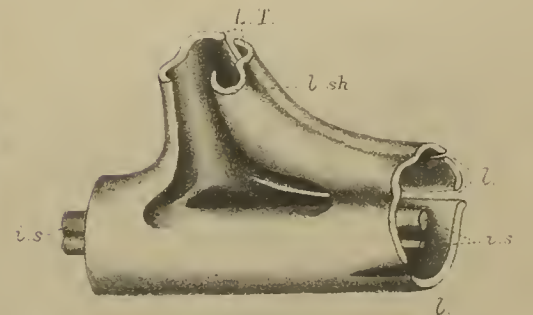


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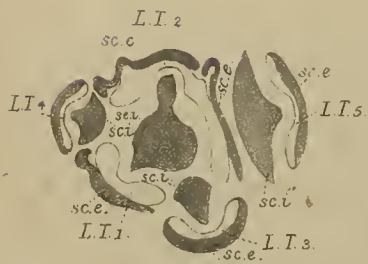


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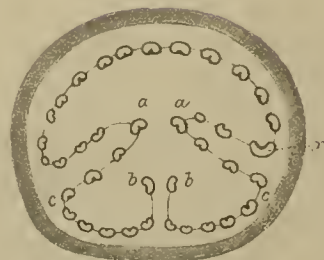


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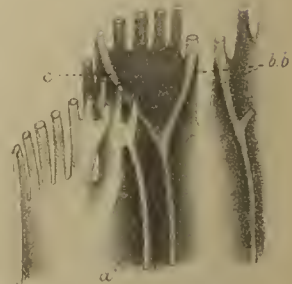


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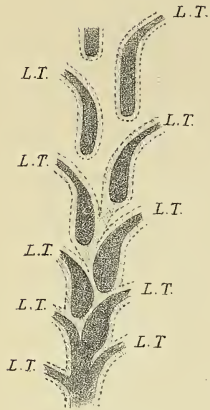


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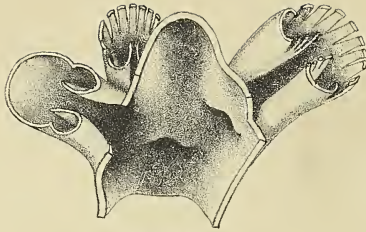


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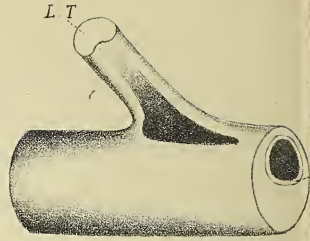


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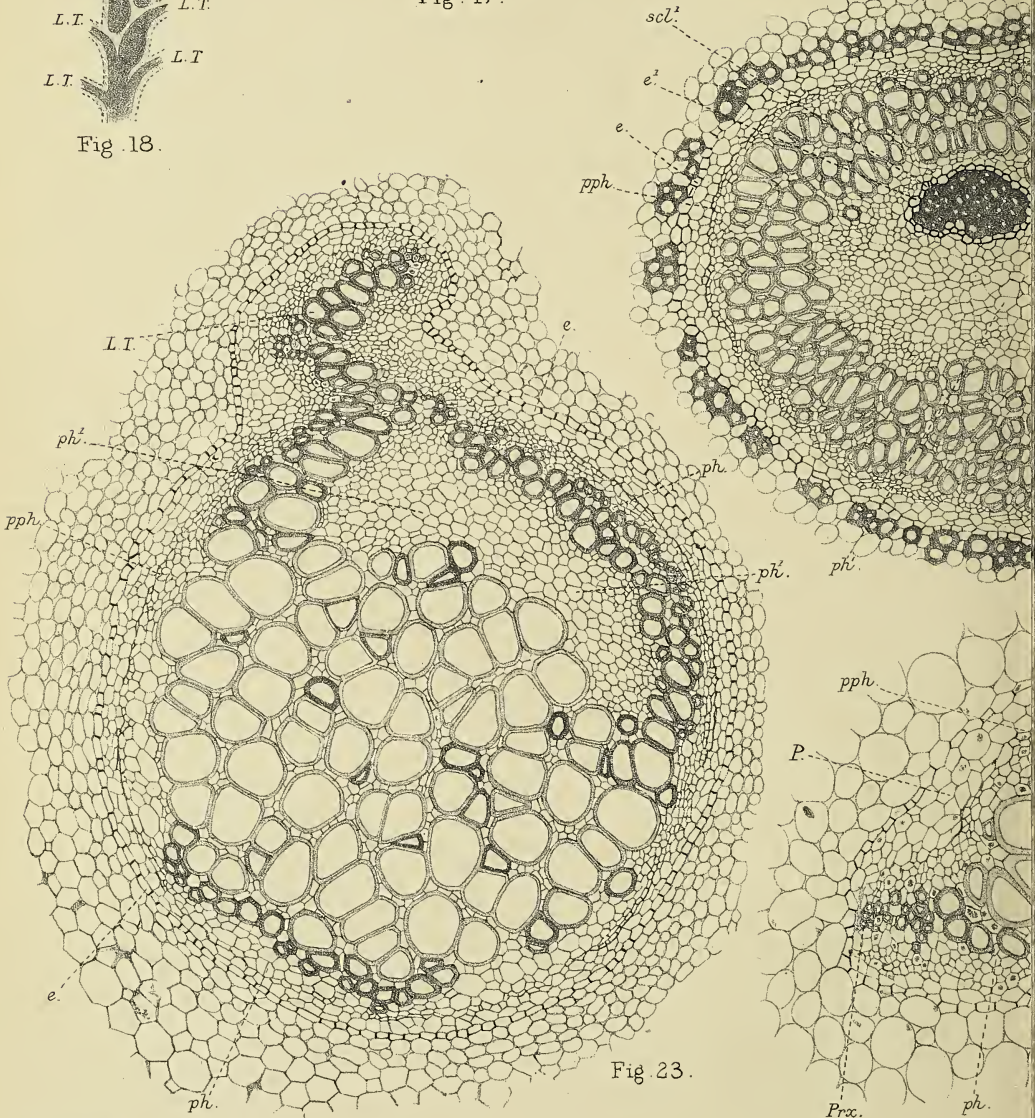


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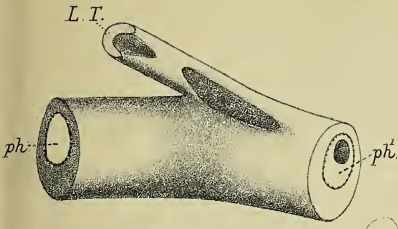


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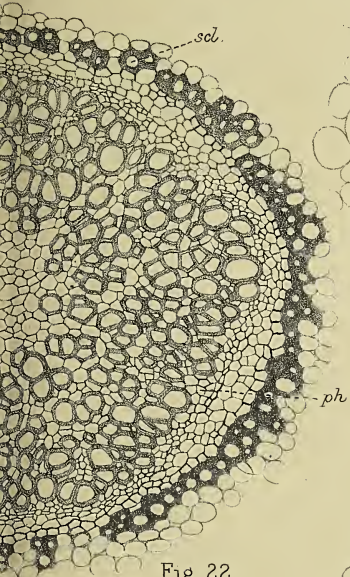


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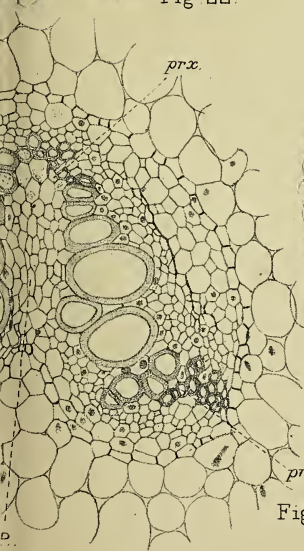


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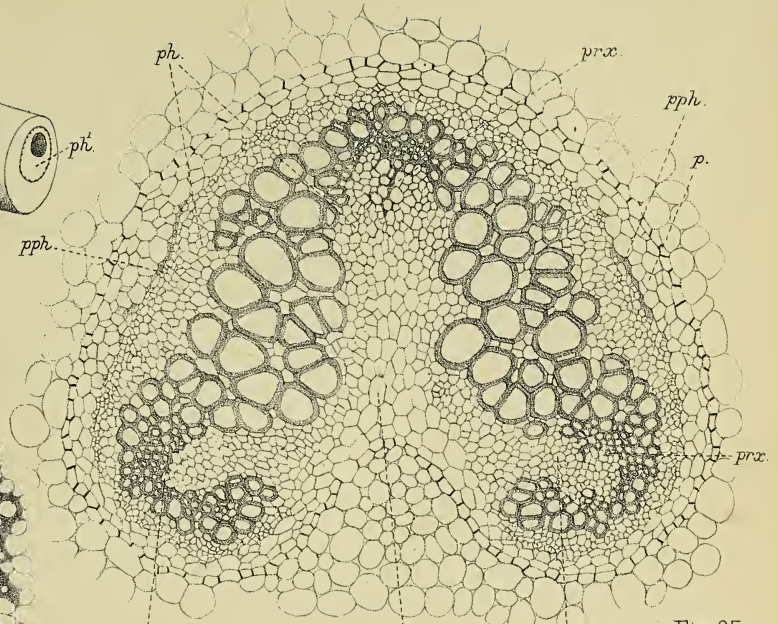


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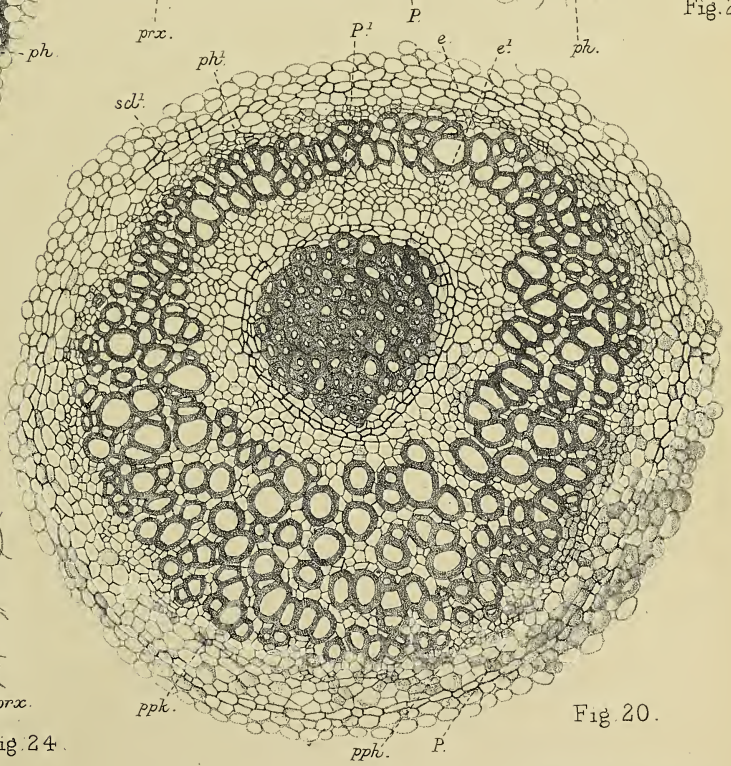


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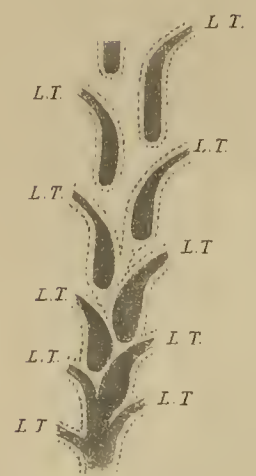


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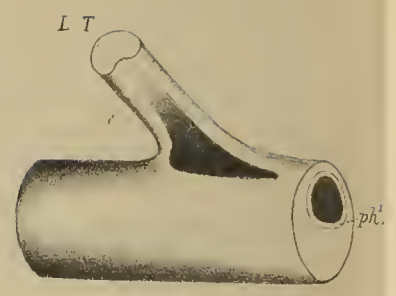


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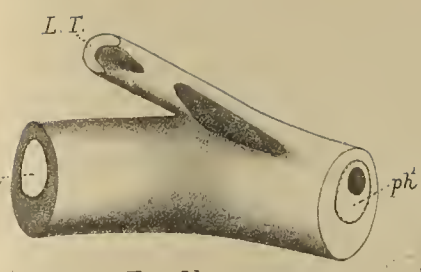


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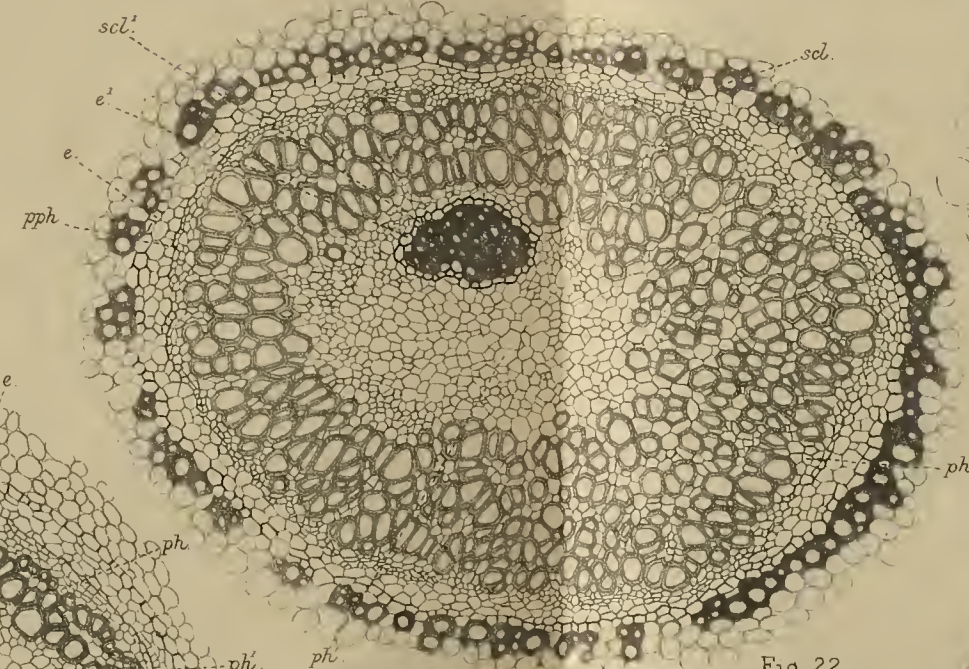


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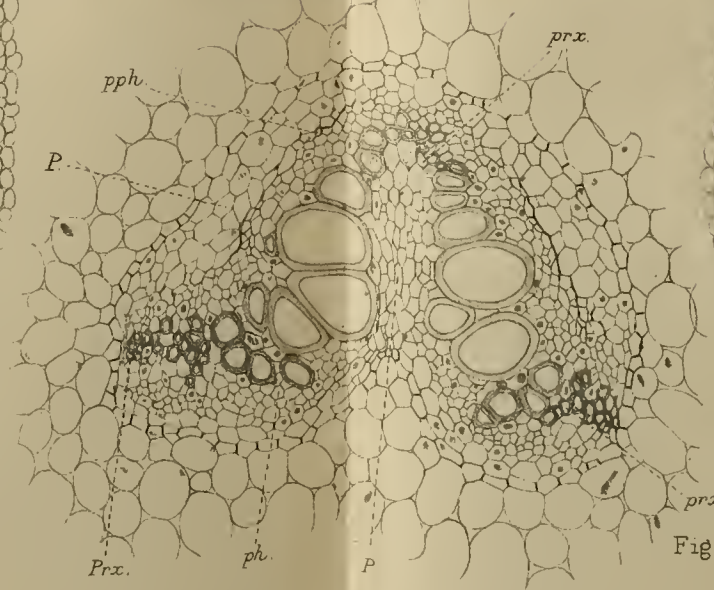


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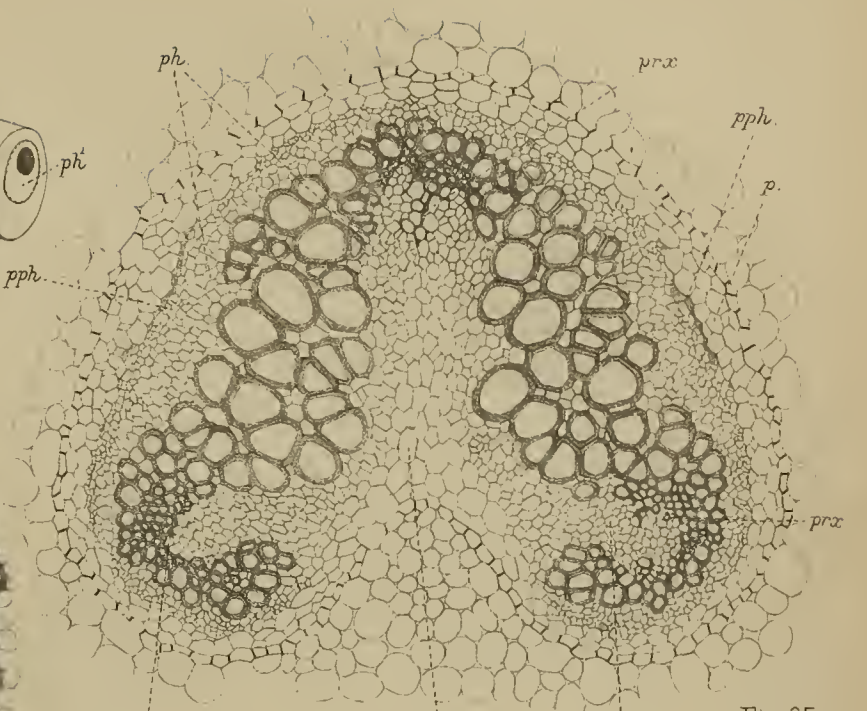


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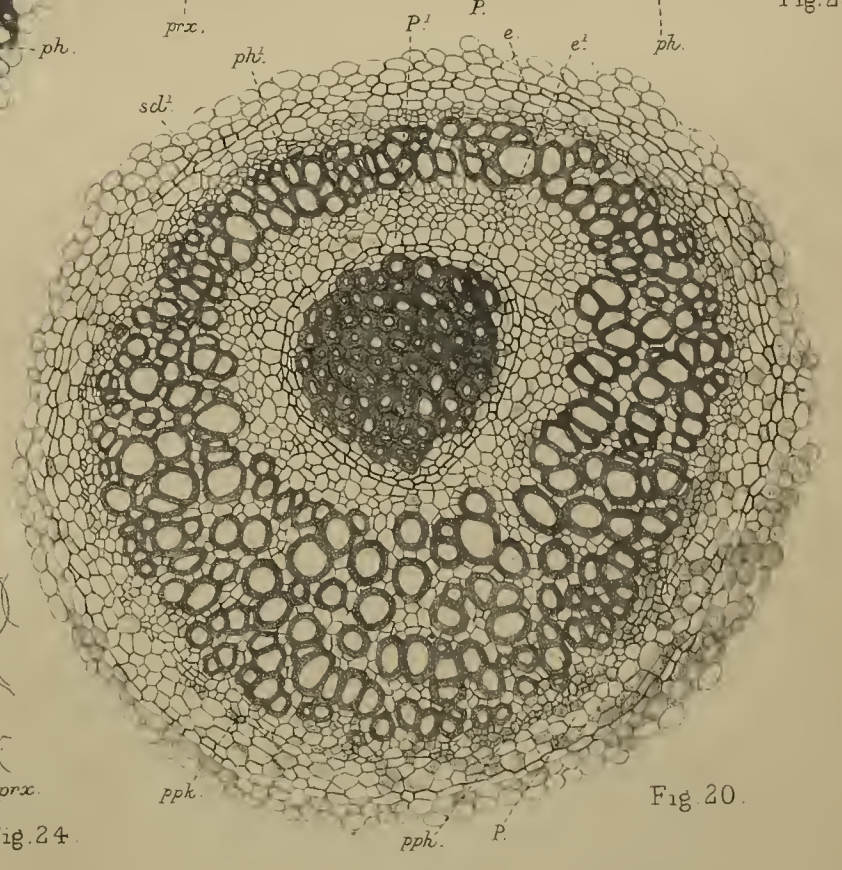


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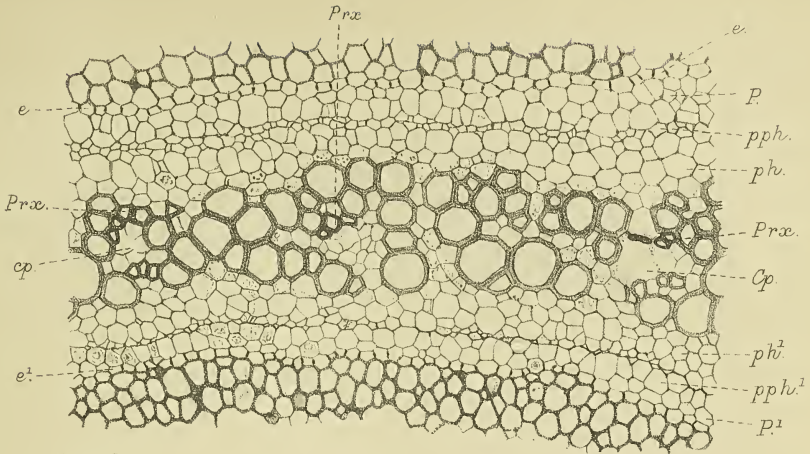


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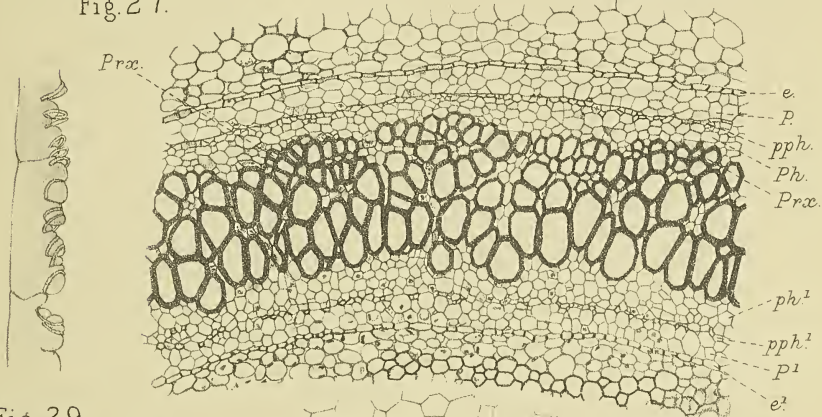


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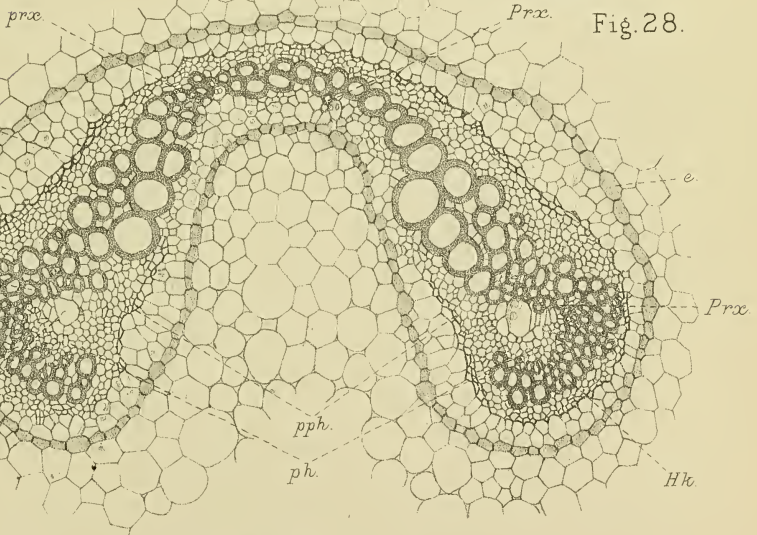


Fig. 28.

Fig. 26.

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# On the Genus *Corynocarpus*, Forst., with Descriptions of two New Species.

BY

W. BOTTING HEMSLEY, F.R.S., F.L.S.,  
*Keeper of the Herbarium and Library, Royal Botanic Gardens, Kew.*

—♦—  
With Plate XXXVI, and two Figures in the Text.  
—♦—

## BOTANICAL HISTORY.

**C**ORYNOCARPUS was established by the Forsters (Char. Gen. Pl. Ins. Mar. Austr., p. 32, t. 16) in 1776, and although the description is incomplete, and the figures of the parts of the flower inaccurate, there can be no question about the tree intended. It was described from specimens collected in New Zealand on Cook's second voyage (1772-75), and the perfect fruit seems to have been unknown to the Forsters, or they would hardly have given it a name signifying club-fruit<sup>1</sup>.

But Sir Joseph Banks and Dr. Solander, who were the botanists on Cook's first voyage (1768-71), also brought specimens of this tree to England, and it was described and figured by them under the name of *Merretia lucida*<sup>2</sup>, though not published. The authorities of the Botanical Department of the British Museum have obligingly furnished me with

<sup>1</sup> They were evidently unaware, too, that the fruit of *Corynocarpus* is edible, or it would have been included in G. Forster's 'De Plantis Esculentis Insularum Oceani Australis.'

<sup>2</sup> In memory of Christopher Merrett, M.D., author of 'Pinax rerum naturalium Britannicarum,' 1666.



a copy of the description, which is very full and accurate in most of the details. The most important point in which it differs from what I have observed and what other authors have described, or figured, is the shape of the petaloid staminodes. They describe them as ‘apice tricuspidata, cuspidate intermedio duplo maiore.’ As may be seen from the accompanying figures, the staminodes of *C. similis* and *C. dissimilis* are acutely toothed at the apex, whilst those of *C. laevigata* are irregularly and minutely toothed from about the middle upwards and around the top. There can be no doubt about Banks and Solander’s specimens having been brought from New Zealand, because exact localities are given, and because Cook did not visit the New Hebrides on his first voyage. On the second voyage he touched at several of the islands; but the Forsters record their *Corynocarpus* from New Zealand, and their figures and description of the staminodes convey no information whatever beyond the presence of such bodies in the flower. Banks and Solander also describe a fully developed fruit in the following terms: ‘Drupa oblongo-ovalis, glaberrima, lutea, magnitudine Olivae Hispanicae ( $1\frac{1}{3}$  unc.), substantia carnosa, lutea sesquilineam crassa edulis.’ They further describe the ‘nucleus’ [seed] as ‘amarissimus.’

Unfortunately Banks and Solander’s specimens in the British Museum only bear two imperfect flowers, and therefore it is almost, or quite, impossible to test the accuracy of their drawing and description, though there is no reason to doubt it, except the fact that the staminodes are different from those figured and described by others. Forsters’ specimens in the British Museum bear a number of flowers, and in one examined the staminodes are of the usual form of those of *C. laevigata*. It is quite probable, however, that there is considerable variation in this organ in all three species, as, in *C. similis*, they vary from three- to nine-toothed at the apex.

The earliest writers, subsequent to the Forsters, attempted the classification of *Corynocarpus* from the description and figures of the latter. Scopoli (1777) placed it in his ‘Nomadeae,’ the definition of which I have not mastered.

Jussieu (1789), who had more definite ideas, included it in his 'Berberides.' In this he was followed by St. Hilaire in 1805, and Roemer and Schultes in 1819.

In 1823, according to various horticultural authorities, it was in cultivation in this country, but I have not succeeded in finding any published exact record of its introduction.

I have some doubts, however, about this date being correct, because I have found evidence of its having been introduced to Kew in 1824. In the Kew collection there are three coloured drawings of barren branches of *C. laevigata*. The earliest is dated Feb. 1825, and is endorsed as having been made from a living plant sent by Mr. Allan Cunningham from New South Wales in 1824, and a reference is given to the page of the 'inwards book' of that date, where it is recorded that the plant was dispatched from New South Wales in February, and received at Kew in June, 1824. There is also a record of another living plant having been received from the same source in 1830.

In 1832 A. Richard (Voyage de l'Astrolabe ; Essai d'une Flore de la Nouvelle Zélande, p. 365) gave a somewhat fuller description of the genus, 'e manusc. Forst.,' but he adds nothing of importance. He places it under 'Genera incertae sedis vel quoad ordines dubia.'

G. Don, 1837 (Gen. Syst. iv, p. 23) appears to have examined specimens, and refers the genus to the Myrsinaceae. He also mentions that it had been in cultivation since 1823.

A. Cunningham, in 1840 (Florae Insularum Novae Zelandiae Precursor, in 'Annals of Natural History,' iv, p. 260), gives a Latin description of all the parts except the fruit, and cites Banks and Solander's manuscript name. He is also the first, so far as I am aware, to explain the process by which the Maoris got rid of the poisonous properties of the seeds, and rendered them edible.

A. de Candolle (Prodromus, viii, p. 145), in 1844, refers to the genus under the Theophrastaceae as 'forsan praesentis ordinis sed corolla polypetala dicitur et placentatio ignota.'

In 1848 Sir William Hooker figured *C. laevigata* from

cultivated specimens in the 'Botanical Magazine,' t. 4379, where the stamens are represented and described as alternate with the petals; and the plant is doubtfully referred to the Myrsinaceae. In 1852 Sir Joseph Hooker described it in greater detail (*Flora Novae Zelandiae*, i, p. 48) and discussed its affinities, with the result that he placed it in the Anacardiaceae, 'though unable to indicate direct affinity with any plant of that order, except perhaps with *Mangifera*.' He, also, describes the stamens as alternating with the petals. This was followed by Bentham and Hooker in 1862 (*Genera Plantarum*, i, p. 425), where it is placed in the Anacardiaceae, without any remark on its anomalous structure, except that under 'Formae Abnormes' it runs: 'Stamina cum squamulis alternantia in *Corynocarpo*.' Sir Joseph Hooker, in 1864, (*Handbook of the New Zealand Flora*, p. 46) still held the same view of its affinities.

In 1889 Kirk's 'Forest Flora of New Zealand' appeared, and it contains (p. 171, t. 88) a figure and description of *Corynocarpus laevigata*, but the figure is crude and the description faulty, and one can only suppose they were made from imperfect, dried specimens. The enlarged parts of the flower give no idea of structure, and the ripe fruit, unusually small, is represented as erect.

In 1897 Engler (*Die natürlichen Pflanzenfamilien, Nachträge*, p. 215) redescribed and figured *C. laevigata* as the type of a new order (Corynocarpaceae), partly from fresh material cultivated in the Berlin Botanic Garden. His description does not agree in some particulars with what I have observed, but I have no fresh material before me to test certain characters, which may disappear or become very obscure in the dried state. For example, he describes the sepals and petals as 3-5, ciliate, the former deciduous, and the disk as rather broadly annular with five short lobes. Among the numerous flowers I have examined, none was trimerous nor even tetramerous, and the sepals never free and deciduous.

Dr. Engler is the first and only writer, so far as my researches go, who has observed and described two styles to



the gynaecium. He also describes and figures a second cell containing the rudiment of an aborted ovule. But, although I have found a second rudimentary style in all three of the species described here, I have not succeeded in finding a trace of a second cell or cavity in any one of the three.

Dr. Engler agrees that *Corynocarpus* belongs to the Sapindales, but the absence of resin-ducts, in his opinion, excludes it from the Anacardiaceae, and the peculiar structure of the androecium from all the orders of the group; hence, he says, it must be regarded as the type of an independent order, to be called Corynocarpaceae.

He places it in his Subseries Celastrineae, characterized by having no resin-ducts. This Subseries includes the Cyrillaceae, Pentaphylaceae, Corynocarpaceae, Aquifoliaceae, Celastraceae, Hippocrateaceae, Stackhousiaceae and Staphyleaceae.

On the whole I am in favour of giving certain isolated, aberrant genera ordinal rank, rather than placing them at the end of other orders, from which they differ as much as most neighbouring orders do from each other. I think the absence of connecting links does not justify the latter course, and the existence of a certain type may be overlooked in a synopsis of orders that does not cover the peculiarities of its structure. Of course it would be inconvenient to unduly increase the number of orders; but how far it is desirable to go I will not attempt to discuss here. With regard to the genus *Corynocarpus*, I am not sure that the reasons given for separation from the Anacardiaceae are strong enough. Apart from the absence of resin-ducts, there is nothing of importance, in my opinion, to keep it out of that order. But Engler (Natürl. Pflanzenf., Nachträge, p. 217) adds: 'Zudem ist die Entwicklung des Andröceums bei *Corynocarpus* so, wie sie weder bei den Anacardiaceen, noch einer anderen Familie der *Sapindales* angetroffen wird.' I venture to suggest that *Pentaspadon*, Hook. f., as figured by the author (Trans. Linn. Soc. xxiii, t. 24) and by Engler himself (DC. Monogr. Phanerog. iv, t. 9, figs. 30-36), presents an analogous androecium and disk, and differs in the shape and relative

position of the parts of the flower rather than in any fundamental character. Both genera are pentamerous up to the gynaecium, but the position of the fertile stamens and the drumstick-shaped staminodes of *Pentaspadon* is the reverse of what it is in *Corynocarpus*, and the continuous disk is 10-lobed, instead of consisting of five free bodies.

The oblique or unsymmetrical, imperfectly 2-celled gynaecium of *Corynocarpus* is analogous to that of *Cotinus* as figured by Engler (op. cit. t. 12, Figs. 29, 30), where he represents an immature drupe, similar to Figures 23 and 24 in our plate (after Engler), but without any trace of a second cell. The gynaecium of the genus *Trichoscypha*, Hook. f., has three styles, but the drupe is one-celled and one-seeded. Sometimes, however, a second cell is partially developed, as shown by Engler (op. cit. t. 11, Figs. 11 and 12), though without any trace of a second ovule. The fibrous endocarp of the fruit of *Corynocarpus* has a parallel in *Mangifera*, and the minute radicle of a large embryo is repeated in *Bouea*, *Holigarna* and other genera.

The general aspect of *Corynocarpus* is so similar to that of *Mangifera*, and some species of *Buchanania*, that one would naturally, without examination, sort specimens into the Anacardiaceae, or perhaps into the Myrsinaceae.

#### ANATOMICAL CHARACTERS.

Coming to the anatomy of *Corynocarpus*, it is true that there is a total absence of resin-ducts, and Engler lays great stress on this fact. He states (DC. Monogr. Phanerog. iv, p. 173) 'Omnium Anacardiacearum rami atque ramuli in sectionibus transversalibus circulum phloëmati interiori proprium canalium succum resinosum continentium extusque libri semicirculis circumdatorum, insuper stratum sclerenchymaticum hypodermatis exhibent.' This being so, and I suppose no one could write on the subject with more authority than Engler, it seems almost a pity to admit an exception, yet as there is nothing that correlates with it, and

having regard to the divergent anatomical characters in some of the most natural of natural orders, I prefer following Sir Joseph Hooker and others in placing *Corynocarpus* in the Anacardiaceae. Baillon (*Histoire des Plantes*, v, p. 327) retains it in the Terebinthaceae, under which, however, he includes the Burseraceae, Olacaceae (in the widest sense), as well as the Anacardiaceae.

I am indebted to Dr. F. E. Fritsch and Miss H. Lasker for the following description and illustrations of the anatomical characters of *C. laevigata*.

Anatomy of the Leaf. (Fig. 27.)

The leaf-structure is bifacial. The epidermal cells of both sides of the leaf are polygonal in surface view. Those of the upper side are somewhat larger than those on the lower side and have only a very slight altitude in transverse section (*ep*). Their outer walls are very strongly thickened, and the cuticle

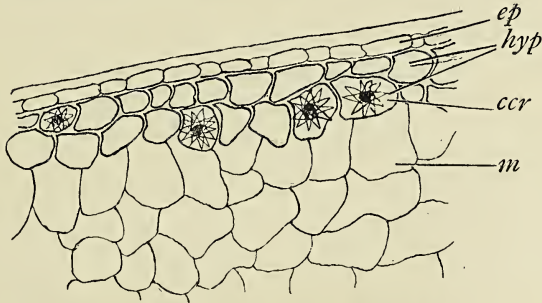


FIG. 27. Small portion of a transverse section of leaf, showing upper epidermis (*ep*), 2-layered hypoderm (*hyp*), clustered crystals (*ccr*), and a small part of the mesophyll (*m*). (x 320).

is smooth. The stomata are confined to the lower side, and are provided with a pair of subsidiary cells placed parallel to the pore. Beneath the upper epidermis a 1 to 2-layered hypoderm (*hyp*) exists, the cells of which are polygonal in surface view and 2-3 times the size of the epidermal cells; their lateral walls are slightly thickened. The lowermost layer of the spongy tissue frequently forms a kind of hypoderm



beneath the lower epidermis, which shows up in the shape of loosely arranged polygonal cells in surface view. The palisade tissue consists of two layers of almost isodiametric cells, and is not very well differentiated from the loose spongy tissue, the cells of which appear more or less transversely elongated in a transverse section of the leaf. Altogether the spongy tissue occupies about four times as much of the diameter of the leaf as the palisade tissue. The vascular bundles of the veins are all embedded in the mesophyll (*m*), and the larger ones are accompanied, both above and below, by rather wide-lumened sclerenchyma. A characteristic feature of the leaf-structure is the abundance of large clustered crystals (*ccr*); these occur especially in the two layers of hypoderm on the upper side of the leaf and also in the hypoderm-like, lowermost cell-layer of the spongy tissue. Very frequently also they occur in specially enlarged cells of the mesophyll, arranged in an interrupted line in about the middle of the leaf. Cork-warts occur in small numbers on the lower epidermis.

#### Anatomy of the Axis. (Fig. 28.)

In a transverse section of the stem the primary bundles (*pb*) project more or less considerably into the pith (*p*). The vessels of the wood are not very abundant and not very wide-lumened. The main mass of the wood is made up of prosenchyma, part of which is thick-walled and part thin-walled (*x*), the two kinds of cells lying in approximately tangential bands. The medullary rays (*mr*) are rather broad, as much as 6-seriate, and their walls are simply pitted. The pith consists of large, rounded, thin-walled, non-pitted cells, many of which contain large clustered crystals (*ccr*). The pericycle contains isolated groups of rather wide-lumened bast-fibres (*bf*), placed opposite the primary bundles. The cortex (*pr.c*) abounds in clustered crystals, and these also occur in the secondary bast (*s*) opposite the medullary rays. The cork (*c*) arises in the second cell-layer beneath the epidermis; the cells are thin-walled, flat or somewhat elongated radially.

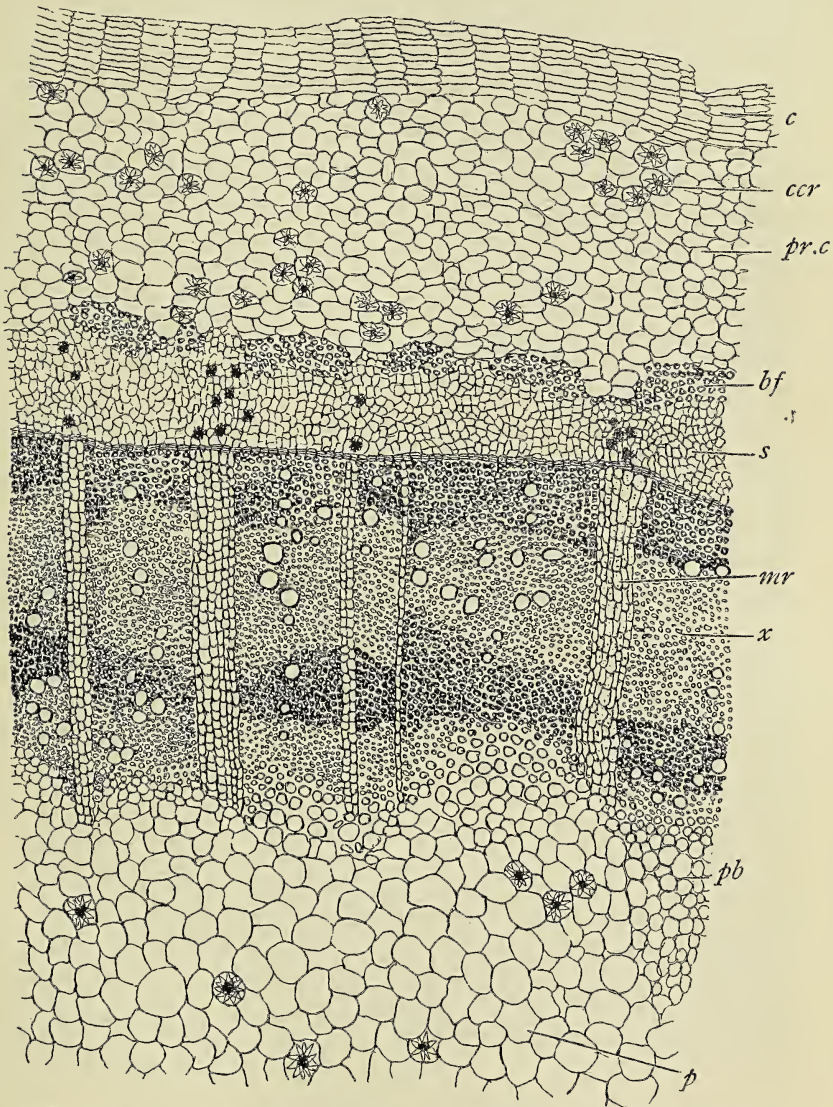


FIG. 28. Portion of transverse section of stem, showing cork (*c*), clustered crystals (*ccr*), primary cortex (*pr.c*), bast-fibres of pericycle (*bf*), secondary bast (*s*), medullary rays (*mr*), xylem (*x*), primary bundles (*pb*) and pith (*p*). ( $\times 120$ .)



## DESCRIPTIONS.

**Corynocarpus, Forst. Character Generis.**

(Hic emendatus et amplificatus.)

Calyx inferior, subcarnosus, alte 5-lobus (sepala 3-5, decidua, ex Engler); lobi petaloidei, inaequales, duobus exterioribus minoribus, ovati vel fere orbiculares, concavi, valde imbricati. Petala subperigyna, calycis lobis similia, isomera, paullo maiora. Stamina 5, petalis opposita et breviora; filamenta plana, deorsum leviter dilatata, petalis ima basi adnata; antherae dorsifixae, biloculares, rima longitudinali dehiscentes, pollinis granae minimae, circiter  $25\mu$  diametro. Staminodia 5, petaloidea, a medio sursum denticulata vel apice acute 3-9-dentata, petalis alternantia. Nectaria (vel disci glandulae) 5, inter se libera, ovoidea vel ellipsoidea, solida, staminodiis opposita et iis basi leviter adnata. Gynaecium liberum, sessile, nunc uniloculare, stylo unico, nunc imperfecte biloculare (nonnunquam perfecte biloculare et biovulatum?) stylis 2 valde inaequalibus (interdum fere aequalibus, ex Engler); ovulum unicum, pendulum, anatropum. Fructus drupaceus, anguste ovoideus, unispermus, endocarpio fibroso. Semen pendulum, loculo conforme; testa membranacea, tenuis, venoso-reticulata, loculi pariete adhaerens; perispermium nullum; embryo loculum implens, cotyledonibus planoconvexis, radícula minima hilo proxima supera, plumula haud evoluta.

Arbores mediocres vel parvae, sempervirentes, haud resinosae, omnino glabrae, Australasiae incolae. Folia alterna, simplicia, integerrima, exstipulata. Flores hermaphroditi, parvi, albo-viridi, inodori, in paniculas terminales vel subterminales quam folia breviores vel aequantes dispositi, in ramulis solitarii vel saepius ternatim fasciculati, brevissime pedicellati, bracteis bracteolisque minutis. Fructus drupaceus, pulpo eduli, endocarpio fibroso; semen exalbuminosum, amarissimum, venenatum.

**Descriptiones Specierum.**

**Corynocarpus laevigata**, Forst. Char. Gen. Pl. Ins. Mar. Austr. (1776), p. 32, t. 16, floris partes cum fructu valde imperfecto; Fl. Ins. Austr. Prodr. (1786), p. 19.



Arbor fructifera spectabilis, usque ad 15 m. alta, trunco 30–60 centim. diametro, sed saepius dimidio minor, interdum frutex a basi ramosus, undique glabra. Ramuli floriferi crassi, teretes, leves, internodiis brevissimis. Folia breviter crasseque petiolata, crassa, valde coriacea, saturate viridia, glaberrima, supra nitidissima, oblongo-lanceolata, oblanceolata vel interdum elliptica, interdum usque ad 2.5 decim. longa sed plerumque minora, apice saepissime rotundata, basi cuneata vel subcuneata; costa valida, infra elevata, venis immersis obscuris. Paniculae densae, per anthesin quam folia saltem dimidio breviores, ramulis ac pedicellis brevissimis crassis subcarnosis. Flores circiter 6–7 millim. diametro; bracteae bracteolaeque vix acutae. Sepala fere orbicularia, 2–3 millim. lata, quam petala paullo breviora. Petala obovato-spathulata, margine obscure eroso-denticulata. Stamina oblongo-spathulata, apice rotundata, margine praecipue supra medium obscure eroso-denticulata ('apice tricuspidata, cuspidate intermedio duplo maiore,' Banks et Solander, manuscr.), quam petala circiter dimidio breviora. Fructus drupaceus, anguste ovoideus vel ellipsoideus, saepe leviter obliquus, plerumque 2.5–4 centim. longus, sed interdum usque ad 5.7 centim. longus, primum atroviridis, demum aurantiacus, levis, glaber, nitidus.—Bot. Mag. lxxiv (1848), t. 4379, quoad positionis stamina falsa; Gard. Chron. n. s. xx (1883), p. 397, fig. 61, ramus foliifer fructiferque; Kirk, For. Fl. N. Zeal. (1889), p. 171, t. 88, quoad flores mala; Featon, Art Album of the New Zealand Flora (1889), p. 100, t. 2, flores et fructus; Harris, New Zealand Berries, t. 4, fructifer; *Corinocarpus laevigata*, Lam. Encyc. Bot. ii (1786), p. 107, et Tabl. Encyc. ii (1793), p. 128, t. 143 (descr. et fig. ex Forster); *Merretia lucida*, Banks et Solander, descriptio cum icone colorata inedita in Mus. Brit.

New Zealand: common in North Island from North Cape to Cook Strait, especially in littoral districts; rare in South Island, where it is restricted to a few localities in the Nelson, Marlborough and Canterbury Districts. The highest southern localities are in Banks's Peninsula. Chatham Islands: common on the main island. Kermadec Islands: plentiful on Sunday Island.

*Corynocarpus similis*, Hemsl., species nova, ad aspectu *C. laevigatae*, a qua differt foliis basi obliquis latioribusque, inflorescentia folia aequantibus vel superantibus, et staminodiorum forma.

Arbor usque ad 12 m. alta (fide Cominsii) ramulis floriferis crassis.

Folia distincte petiolata, crasse coriacea, oblongo-lanceolata vel elliptica, usque ad 15-20 centim. longa, maxima 8 centim. lata (4, plus minusve imperfecta, visa) apice subacute acuminata. Panicula (unica tantum visa) per anthesin folia aequans, laxa, ramulis patentibus. Flores circiter 10 millim. diametro, distincte pedicellati, pedicellis bractea bracteolisque duabus basi suffultis. Sepala fere orbicularia, quam petala paullo breviora. Petala obovato-spathulata, margine obscure irregulariterque denticulata. Stamina ligulata, petala fere aequantia, apice saepissime acute 5-7-dentata. Fructus edulis (fide Cominsii).

Northern New Hebrides: Torres Island, Banks's Group, Archdeacon Comins, 343, herb. Kew.

The fruits belonging to this and some other specimens were by some means misplaced, and none have been found that could possibly belong to *Corynocarpus*.

***Corynocarpus dissimilis***, Hemsl., species nova, a *C. laevigata* et *C. simili* foliis minoribus multo tenuioribus graciliter petiolatis et floribus minoribus recedit.

Arbor, vel frutex, minus robusta quam species supra citatae. Folia vix coriacea, elliptica vel oblongo-lanceolata, cum petiolo 6-12 centim. longa et 5-6½ centim. lata (specimen unicum visum ramulorum duorum cum foliis paucis et inflorescentiis duabus sistens), apice obtusissima, basi subrotundata, venis inconspicuis. Paniculae quam folia breviores. Flores 4-5 millim. diametro, distincte pedicellati, pedicellis basi bractea et bracteolis duabus minutis suffultis. Sepala elliptico-rotundata. Petala obovato-rotundata, margine irregulariter eroso-denticulata. Stamina sursum dilatata, apice saepius acute tridentata, dente intermedio longiore. Fructus ignotus.

New Caledonia: Vallée de la Tihouaca, près Wugap, Vieillard, 2244, in herb. Kew.

Since the foregoing description was written, I have found a reference to a New Caledonian species in Baillon's *Histoire des Plantes*, v (1874), p. 327: 'Species forte duae, quarum altera Austro-Caledonica, altera autem *C. laevigata*, Forst.' In all probability it is the same as that described above, but there is no description and no indication of how it differs from the original species.

ECONOMIC HISTORY.

*Corynocarpus laevigata* occupies, among plants, a prominent position in the history and traditions of the Maoris of New Zealand and the Morioris of the Chatham Islands. It is one of the few trees of the country yielding an edible fruit, and it was of great importance to the aboriginal inhabitants as an article of food. One of the most interesting points connected with it is the tradition, both in New Zealand and the Chatham Islands, that the immigrant ancestors of the Maoris introduced this tree from the unknown island of Hawaiki. Geographers are not agreed as to the position of this island, and the fact that the genus *Corynocarpus* was unknown outside of the New Zealand region made it difficult to accept this tradition. But the discovery of a species in New Caledonia, and of another, very closely allied to the New Zealand species, in the still more distant New Hebrides, removes the difficulty. Indeed, it seems quite probable that *C. laevigata* may yet be found in some of the islands of Western Polynesia, but not in Eastern Polynesia, where most geographers have placed the Hawaiki island of Maori traditions. The eastern islands have been more or less thoroughly explored botanically, and the presence of such a distinct and conspicuous tree would hardly have been overlooked. On the other hand, New Caledonia, the New Hebrides, and the Solomon Islands are still, to a great extent, unexplored. *C. laevigata*, both in a wild, and formerly cultivated state, thrives only in the warmer parts of the New Zealand region. Kirk (Forest Flora, p. 173) states that it is very rare in the South Island, being restricted to a few localities in the Nelson, Marlborough and Canterbury Districts. So it may be inferred that it is probably a native of a warmer country, generally, than New Zealand. Featon (Art Album of the New Zealand Flora, p. 100) regards all the localities in the South Island as the remains of cultivation.

The Morioris of the Chatham Islands represented to



Mr. H. H. Travers (Trans. New Zealand Institute, iv, p. 64) that their Maori ancestors came originally to New Zealand from Hawaiki, and when they migrated to the Chathams they took with them the *kumera* (*Ipomoea tuberculata*) and the *karaka* (*Corynocarpus laevigata*), but the former did not thrive owing to the moistness of the climate. Travers found the *karaka* growing abundantly in the immediate neighbourhood of the various old settlements, but not in the general bush of the island, which gives colour to the statement of its comparatively recent introduction. This, however, does not quite accord with Mr. L. Cockayne's more recent experience (Trans. New Zeal. Inst., xxxiv, p. 277), for he states that *Corynocarpus laevigata* is the predominating tree in the 'Lowland Forest,' by which he means all below the tableland. The Chatham Islands are about 450 miles east of New Zealand in about the same latitude as Banks's Peninsula. *C. laevigata* is also abundant in Sunday Island, one of the Kermadec group, which is situated about midway between New Zealand and the Tonga group; but I have found no historical records in this connexion. Cockayne goes on to state 'that according to Mr. A. Shand the aborigines of Chatham Islands . . . did not cultivate the ground at all. The only vegetable foods they made use of were the rhizome of *Pteris esculenta* [*P. aquilina*] and the fruit of *Corynocarpus laevigata*.' Whether this means that they did not even plant the seeds of the latter is uncertain.

Some writers, however, regard it as almost certain that Hawaiki was the name of one of the islands of the Navigators' or Samoan group and that the migration was by way of Rarotonga; but the botany of this group and the neighbouring Tonga or Friendly Islands is so well known that it is extremely unlikely that the genus *Corynocarpus* exists in either of these groups. And Mr. T. F. Cheeseman, a well-known New Zealand botanist, has recently botanically explored the island of Rarotonga<sup>1</sup> almost exhaustively, so far as the vascular

<sup>1</sup> Transactions of the Linnean Society, 2nd series, Botany, vi, pp. 261-313, tt. 31-35.

plants are concerned, without discovering any tree of this affinity.

Who first published the Maori tradition of the origin of the *karaka* in New Zealand, I have not ascertained with certainty, but I believe it was Sir George Grey<sup>1</sup>, and it is repeated by Dr. A. S. Thomson<sup>2</sup>, W. Colenso, Hochstetter, Skey, Kirk, and many other writers.

#### THE KARAKA AS AN EDIBLE FRUIT.

Although *Corynocarpus laevigata* was cultivated in this country as early as 1824, Allan Cunningham appears to have been the first to publish (Ann. Nat. Hist. iv, 1840, p. 260) its Maori name together with some particulars of the fruit and seed and the preparation of the latter for eating.

The flesh of this fruit could be regarded as edible only in the absence of more palatable and luscious kinds. In the first place it is very thin, only a line and a half ( $\frac{1}{8}$  in.) in thickness according to Banks and Solander's description, and not good-flavoured what there is of it. Featon describes it as having a 'sweet, insipid flavour, which is much appreciated by the Maoris but rather distasteful to Europeans.' He adds that even to this day (1889) the natives collect it in large quantities. But the large seeds were the important part. As already stated, they contain a highly poisonous principle in the fresh state, which is removed by baking or steaming and steeping in salt water. Thus prepared they constituted one of the principal and most valued articles of food. They were collected, prepared, and stored in a methodical manner.

The intensely bitter, poisonous principle is described by Mr. W. Skey (Transactions of the New Zealand Institute, iv, 1872, p. 316), who names it karakine. Chemical treatment of the extract proved that the principle does not contain nitrogen and is not of an alkaloidal nature, and that it is closely allied to digitaline. 'Its deportment with sulphate of copper and potash is strikingly similar to that of digitaline

<sup>1</sup> Poems, Traditions and Chaunts of the Maories, 1853.

<sup>2</sup> The Story of New Zealand, 1859.

to the same tests. Both give green precipitates of a tint very similar to arsenite of copper. . . . Taking all these facts into consideration I am inclined to believe that the bitter of the *karaka* nut is a glucoside, and that digitaline falls into the same class, though I have not known this character imputed to it before.'

Skey failed to find any alkaloid body in the nut (seed), and came to the conclusion that the bitter substance is the poisonous part, but he did not establish this by experiment. He also found that the inner bark of the tree is bitter, probably from the presence of karakine, whilst the outer bark is not bitter but astringent, from the presence of tannin. The leaves, the wood, and the sap are sweet.

Kirk (*Forest Flora*, p. 171) states that the leaves are greedily eaten by horses and cattle, and its value as fodder has led to its almost total extirpation in districts where it was formerly plentiful.

In all the recent works cited or quoted, *karaka* is the only Maori name given; but Bennett (*Gatherings of a Naturalist*, 1860, p. 346) mentions *kopi* as an alternative name. Possibly this may be the name of a certain part. Bennett also states that the colonists called it the 'cow-tree,' on account of the fondness of cattle for the foliage. The Forsters record no vernacular name, and Banks and Solander write it *chalacha*. This spelling may be attributable to Solander alone, as an Englishman would almost certainly have employed k's instead of ch's for the hard sound.

In conclusion I have the pleasure of thanking Miss M. Smith for the great care she has taken in drawing the dissections; Sir William Thiselton-Dyer and the Bentham Trustees for defraying the cost of the drawings; Dr. F. E. Fritsch for the anatomical details; Mr. G. Masee for drawing the pollen; and Dr. O. Stapf for kind assistance throughout.

I also have to thank Mr. Wyndham Fitzherbert, of Kingswear, S. Devon, for his wide-seeking, though unsuccessful attempts to procure fresh flowers of *C. laevigata* in the West of England.



EXPLANATION OF THE FIGURES IN  
PLATE XXXVI.

Illustrating Mr. Hemsley's paper on the genus *Corynocarpus*, Forst.

*C. laevigata*, Forst.

- Fig. 1. A flower and portion of a branch of an inflorescence. Enlarged.  
Fig. 2. A flower. Natural size.  
Fig. 3. Floral diagram, showing pentamery up to gynaecium. The stamens are opposite the petals, and the glands or nectaries, and the petaloid staminodes are opposite the sepals.  
Fig. 4. A flower laid open, showing a portion of a sepal on the left, the petals, the staminodes, the stamens and the nectaries. Enlarged.  
Fig. 5. A petal and its superposed stamen. Enlarged.  
Fig. 6. A staminode and its superposed nectary. Enlarged.  
Fig. 7. A sepal and its superposed staminode, copied from a drawing in the Banksian Collection at the British Museum. Enlarged.  
Fig. 8. A stamen, front view. Enlarged.  
Fig. 9. A stamen, back view. Enlarged.  
Fig. 10. Pollen, magn. 400.  
Fig. 11. A gynaecium. Enlarged.  
Fig. 12. A gynaecium, showing indications of a second carpel or style. Enlarged.  
Fig. 13. Longitudinal section of ovary, showing the solitary pendulous ovule. Enlarged.  
(Figs. 1-6 and 8-13 are from Lyall's specimens collected in Massacre Bay, Collingwood, South Island, New Zealand.)  
Fig. 14. Section of a flower, showing two nearly equal styles. Enlarged. After Engler.  
Fig. 15. A ripe fruit. Natural size.  
Fig. 16. A fruit from which the flesh has been removed, showing the fibrous endocarp. Natural size.  
(Figs. 15-16 are from fruits collected by G. Oliver.)  
Fig. 17. A seed from a smaller fruit with reticulated testa corresponding to the fibrous cords of the endocarp. Natural size.  
Fig. 18. Embryo from which the testa has been removed, showing the slightly unequal cotyledons with a cap-like growth on the radicular end, which is apparently a second undeveloped embryo. Natural size.  
Fig. 19. Another view of the same.  
Fig. 20. Rudimentary second embryo. Enlarged.  
Fig. 21. Cross section of rudimentary embryo, showing the vascular bundles which radiate from a single basal cord. Much enlarged.  
Fig. 22. Inner face of a cotyledon and minute plumule and radicle. Enlarged.  
(Figs. 17-22 are from specimens cultivated at Tresco Abbey, Scilly Isles, in 1883.)  
Fig. 23. An immature fruit. Natural size. After Engler.  
Fig. 24. A longitudinal section showing remains of a second cell and aborted ovule. Natural size. After Engler.

760 *Hemsley*.—*On the Genus Corynocarpus, Forst.*

*C. similis, Hensl.*

Fig. 25. Flowers and portion of a branch of an inflorescence. Enlarged.

Fig. 26. A flower. Natural size.

Fig. 27. A flower laid open showing petals, staminodes, stamens, nectaries and gynaeceum with two unequal styles. Enlarged.

Fig. 28. A petal and a stamen. Enlarged.

Fig. 29. A staminode and a nectary. Enlarged.

Fig. 30. A 5-toothed staminode. Enlarged.

Fig. 31. A gynaeceum. Enlarged.

Fig. 32. A longitudinal section of the same, showing the solitary pendulous ovule. Enlarged.

(Figs. 25-32 are from a specimen collected by Archdeacon R. B. Comins in Torres Island, Northern New Hebrides.)

*C. dissimilis, Hensl.*

Fig. 33. A flower and portion of a branch of an inflorescence. Enlarged.

Fig. 34. A flower. Natural size.

Fig. 35. A portion of a flower laid open, showing part of a sepal and three petals, staminodes, stamens and nectaries. Enlarged.

Fig. 36. A petal and a stamen. Enlarged.

Fig. 37. A staminode and a nectary. Enlarged.

Fig. 38. A gynaeceum with one style. Enlarged.

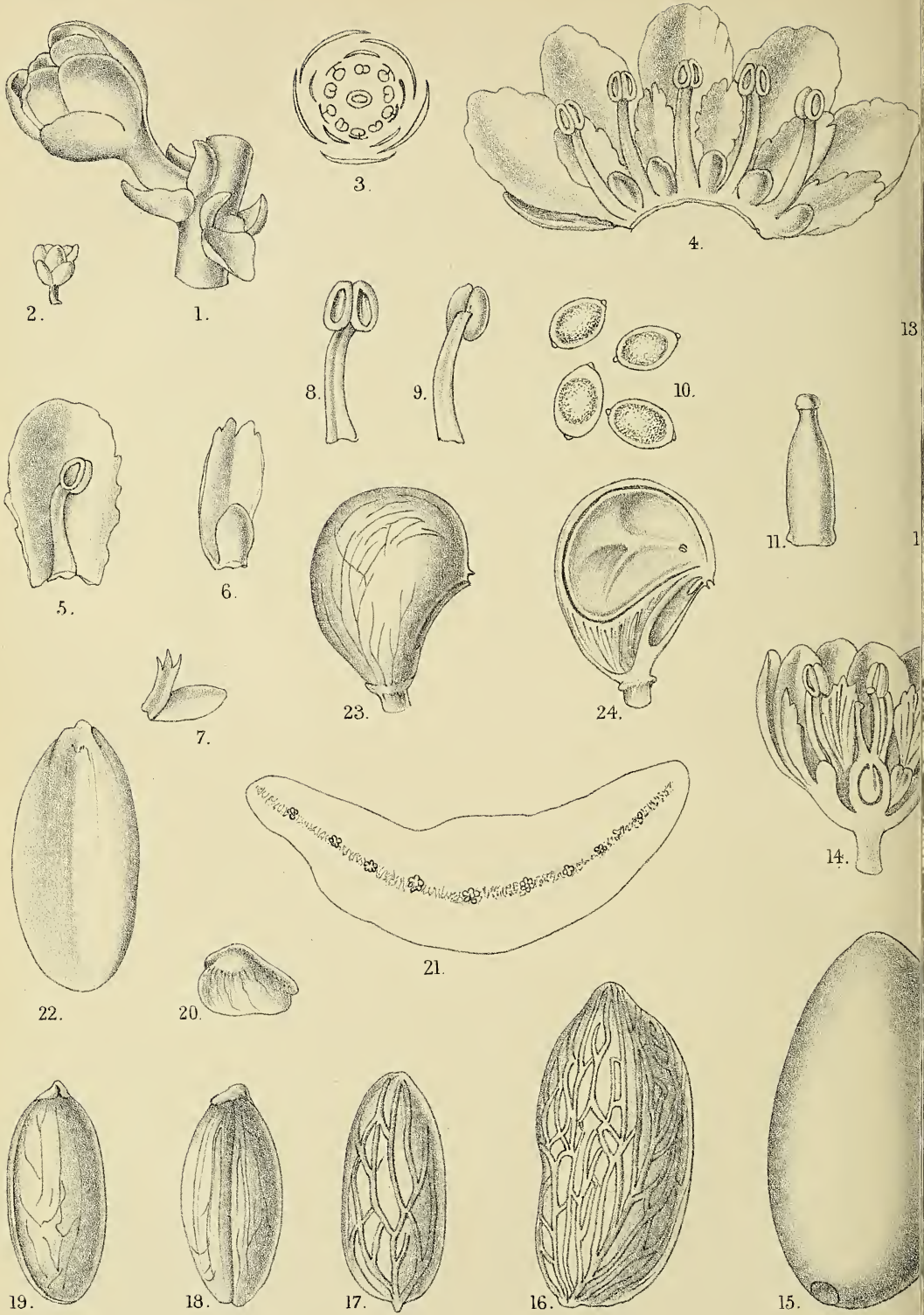
Fig. 39. A gynaeceum with two unequal styles. Enlarged.

Fig. 40. A longitudinal section of ovary showing single cell and ovule. Enlarged.

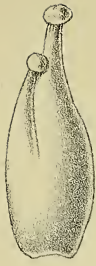
(Figs. 33-40 are from a specimen collected by Vieillard in New Caledonia, n. 2244.)



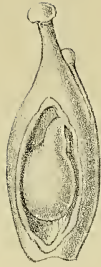




M. Smith, del.



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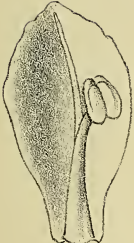
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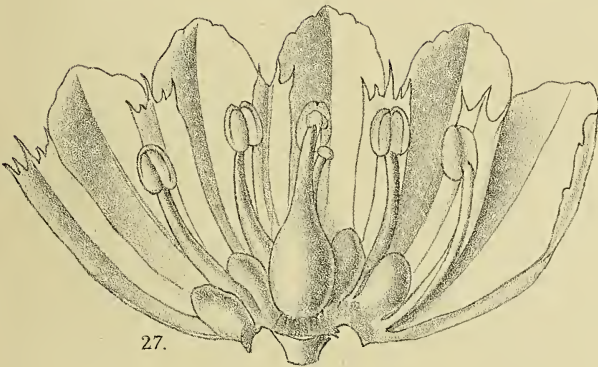
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37.



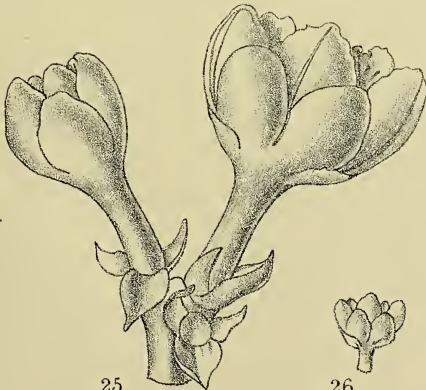
36.



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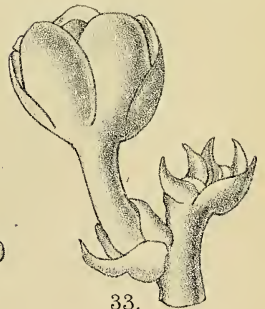
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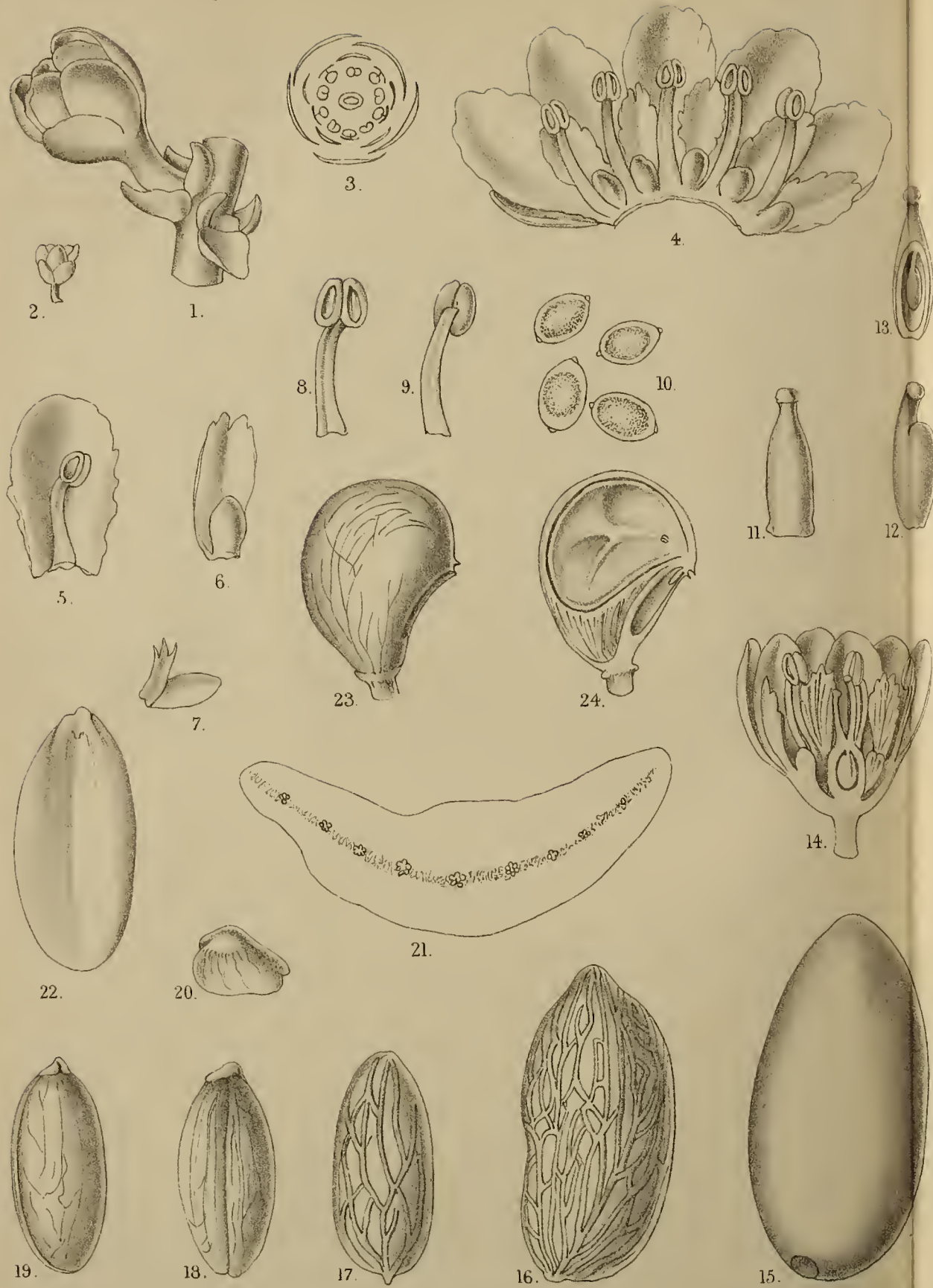
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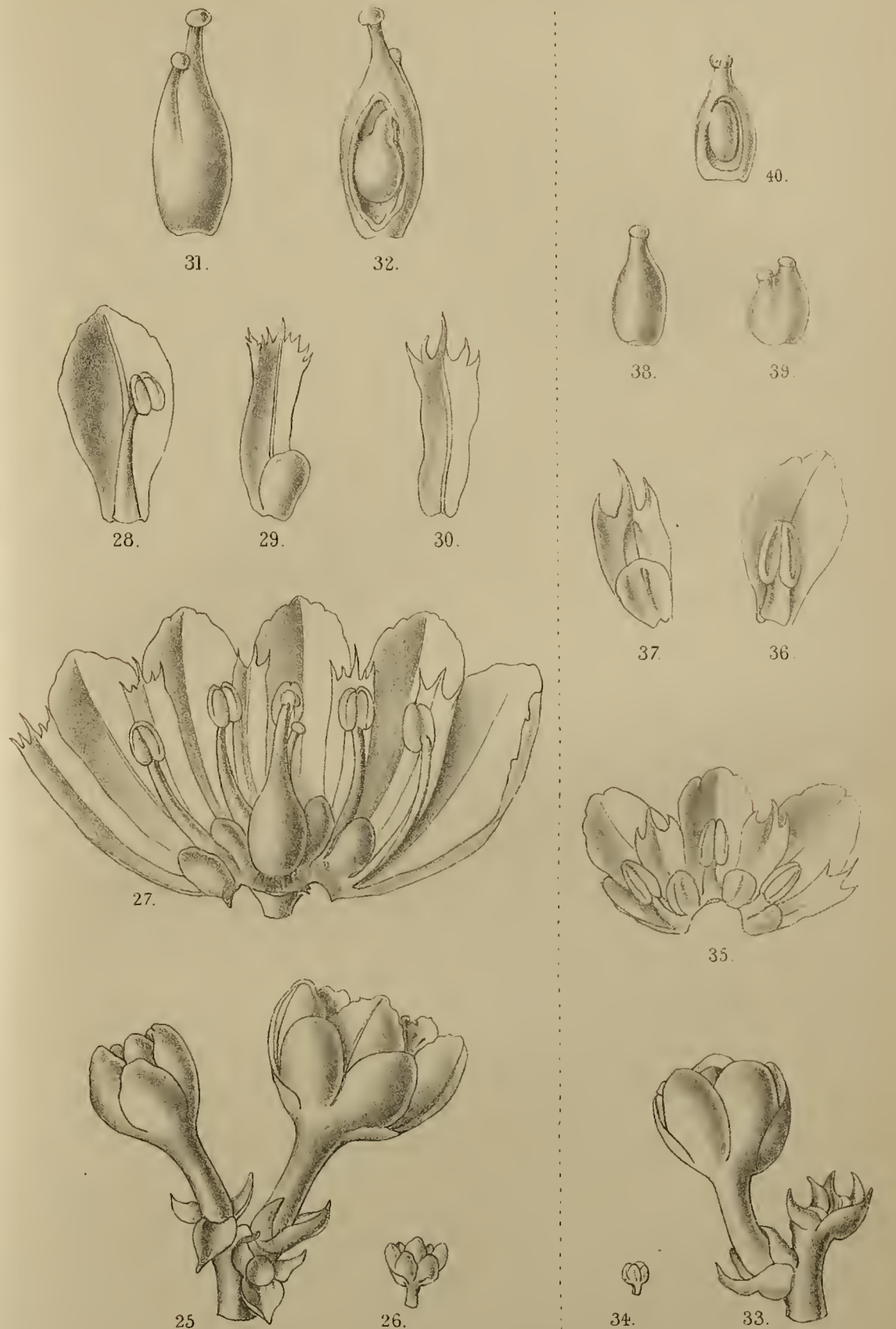






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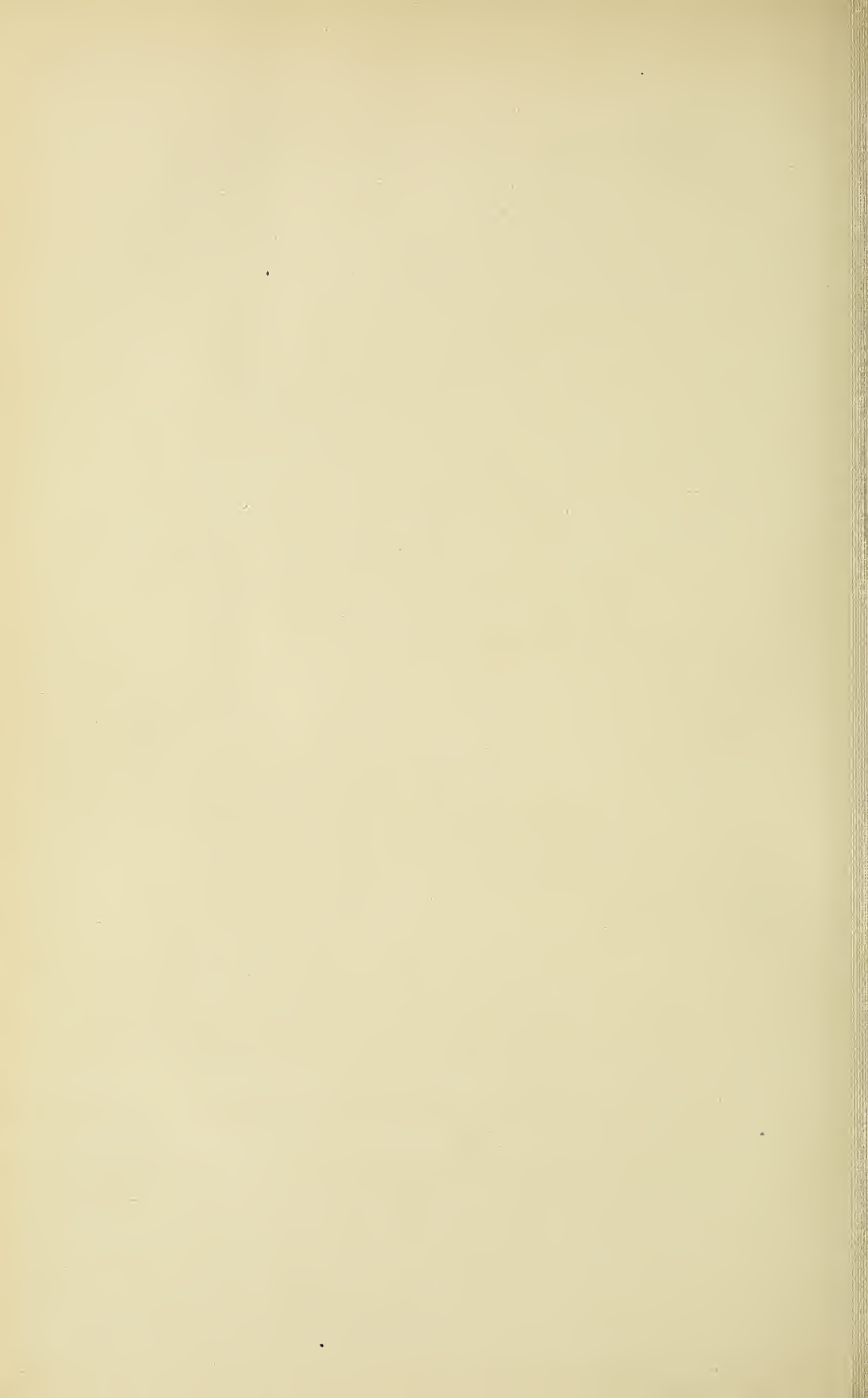
CORYNOCARPUS LAEVIGATA, Forst.



C. SIMILIS, Hemsl.

C. DISSIMILIS, Hemsl.

University Press Oxford.



# On the Movements of the Flowers of *Sparmannia africana*, and their Demonstration by means of the Kinematograph.

BY

RINA SCOTT.

—+—  
With Plates XXXVII, XXXVIII, and XXXIX.  
—+—

*SPARMANNIA africana* is a common greenhouse plant, which was introduced from the Cape into Europe as early as 1790. It was named after Dr. Sparmann, a Swedish botanist, who accompanied Captain Cook on his second voyage round the world.

It belongs to the order Tiliaceae; there are three species: *S. abyssinica*, *S. palmata*, and the subject of the present paper.

It is well known to the botanist on account of the curious movements of its stamens, which, when touched, gradually move away from the style, leaving the stigma exposed and ready for fertilization by bees.

A paper was written on the subject as early as 1841 by Charles Morren<sup>1</sup>.

*S. africana* is found wild in many parts of S. Africa, occurring about the Knysna district and from thence East, but always at no great distance from the coast. It attains a height of about 15 feet, ripening its seeds towards the end

<sup>1</sup> Mém. de l'Acad. Roy. de Bruxelles. Ch. Morren, 1841, vol. xiv.



of October or beginning of November and again in March. It is found at the edges of forests outside the tree belt.

All my investigations were made on plants growing in a greenhouse. In its natural state the day temperature during flowering rises to a maximum of 92° F. (33° C.); but it is seldom more than 80–87° F. (27–30.5° C.), and the nights average about 60–65° F. (15.5–18.5° C.), seldom falling lower than 57° F. (14° C.)<sup>1</sup>.

The whole plant is covered with hairs, which protect it during the cold nights on its native mountains round the Cape. The young buds are themselves covered with dense hairs, and are sheltered at an early age by the hairy leaves above them (Fig. 13).

*Sparmannia africana* is an exceptionally favourable plant on which to study reaction to stimulus, as so many of its parts are sensitive. The most strikingly sensitive organs are the stamens: these are arranged in four groups, having an outer circle of staminodes. Both stamens and staminodes are provided with curious tooth-like outgrowths, few in number on the stamens, but becoming more and more numerous and conspicuous as the outer staminodes are reached. All of these are sensitive to touch; if only one stamen be touched, the stimulus spreads until all the stamens and staminodes have moved outwards away from the stigma.

These movements have been described in great detail by various writers<sup>2</sup>.

Then the petals and sepals respond to the stimulus of light, and lastly the flower as a whole is capable of special movements, regulated not merely by the curvature of the pedicel, but by the action of the pulvinus or joint situated at a short distance below the flower.

The following observations, which extend over two seasons, are principally on the movements of the flower bud and flowers up to the time of the setting of the fruit.

Three complete inflorescences from bud to fruit were drawn

<sup>1</sup> I am indebted to Mr. Harry Bolus, of Cape Town, for these details.

<sup>2</sup> Haberlandt, *Sinnesorgane im Pflanzenreich*, pp. 46–51. Leipzig, 1901.

every day and night, and from these data the following results were obtained :

The inflorescence is an umbel. At first the buds hang all on one side of the main peduncle, both buds and pedicels are densely hairy. The pedicel of each bud is jointed. This curious joint or pulvinus is situated at an average distance of about 1 cm. from the bud, and will be found to be much swollen on the side away from the bud. The swelling becomes more noticeable as the bud grows older and the functions of the joint come into play.

This joint, which is present in all three species of *Sparmannia*, bears in its action and structure some resemblance to the pulvinus found on such leaves as those of the sensitive plant (*Mimosa pudica*), and helps to regulate the position of the bud, flower or fruit at different times of its development. It is capable of causing the most delicate movements of the bud or flower, and responds readily to the stimulus of light.

The greenhouse plant is specially favourable for the study of the joint. Owing to the fact that *Sparmannia africana* is used as a winter flowerer here, the flowers open much less readily than they do in their natural state. This can be easily seen, if a dried wild specimen be compared with one from a greenhouse. In the specimens in the Kew Herbarium one frequently finds flowers and ripe fruits of which some have already fallen on the same umbel, and very often (see Pl. XXXVII, Fig. 14) an umbel has nine or ten open flowers at a time, while in the greenhouse specimen quite frequently days pass without a fresh flower opening, while in one umbel drawn, the last flower lost its petals on March 19 and the first fruit was not ripe till April 25. So that a joint, which under natural conditions might only be used for a few weeks, will in a greenhouse specimen have to remain active for as many months.

Thus the joint develops by use, and, after a cold month, when the temperatures have been too low to admit of the flowers opening, becomes quite a conspicuous feature of the plant.

The peduncle circumnutates and grows during flowering on an average  $1\frac{3}{4}$  inches ( $4\frac{1}{2}$  cms.) in height, and the flower-bud rises 3 inches ( $7\frac{1}{2}$  cms.) in height.

These results were arrived at by means of a diagram made by careful daily measurements on a cylindrical glass enclosing the inflorescence.

Figs. 1-12 represent stages in the development of an inflorescence, and are drawings selected from a continuous series beginning on March 6 and ending July 23, 1902, drawn every day and every night during flowering.

If Fig. 1 is first examined, three buds will be seen moving up into the flowering position; we will first follow the behaviour of bud 3, in Figs. 1, 2, and 3, as this has only just started from the pendent position parallel to the main peduncle. The first drawing of bud 3 was made at 11 a.m. March 6, temp.  $63^{\circ}$  F. ( $17.5^{\circ}$  C.) on a fine sunny day, and the movement of the pedicel was very rapid; the amount of movement attained by 4 p.m. is shown by the dotted lines in Fig. 1. Here it will be seen that the whole pedicel is straightening itself; it continues to rise in this way all through the night (Fig. 15 represents the position of a similar bud at 4.30 a.m.), until on March 7, 10 a.m. it had attained the position shown in Fig. 2. The pedicel then makes a sharp bend as seen in Fig. 3 (or better in Fig. 31) the bud is dropped into the vertical position ready for flowering by the movement at the joint (see Fig. 5 where 3 is in flower), and in Figs. 1 (bud 1), 52, 55, 58. The exactness of the vertical position attained is very remarkable; no doubt the opening bud has its stamens protected from injury till the last minute before opening by this means, and, if rain falls, the hairy sepals are in the position of an umbrella, ready to throw it off, without injury to the more internal parts of the flower. We must now follow the opening of the bud. (Figs. 22-25, 30-39, 58-64 show this process.)

The bud on a hot day begins to open as a rule a short time before sunrise. For instance, on the morning when the sun rose at 6.32 a.m. March 8, at 5.45 a.m. I found the buds



breaking open on all sides temp.  $50^{\circ}$  F. ( $10^{\circ}$  C.), till at sunrise they had attained the position shown in Figs. 35 and 59. Up till now the stamens have not been exposed; now for the first time a few of the staminodes raise themselves and begin to show between the petals (see Figs. 23, 24, 56 and diagram), and the rapidity with which the flower opens from this stage depends on the temperature. If it is sunny and has reached about  $60^{\circ}$  F. ( $15.5^{\circ}$  C.) by then the process of unfolding is so rapid that it is difficult to draw the different stages (an example of this rapid opening is shown in Figs. 22-25) where the time interval between 23 and 24 is only ten minutes; but if, on the other hand, the temperature remains low, these little hooked staminodes, which are now raised into the position in which they will be in an open flower, appear to be peculiarly sensitive, and from observations made later seem to transmit a message to the other parts of the flower, causing it to finish opening as soon as the temperature is right. They are a most conspicuous feature in a flower during the critical moments of its opening and closing, but even when a flower is opening rapidly, if carefully watched, one can see that these staminodes are raised first.

The flower continues to open gradually, the petals becoming less and less crumpled, the sepals and petals rising one by one (see Fig. 24) until eventually on a sunny day the sepals are pressed tightly back and the petals raised to the utmost, exposing the stamens (Figs. 5 (2 and 3), 25, 39, 64). The style is at first shorter than the stamens, but by the following day has grown to their length. If very cold weather prevails, and the flower is prevented from opening for some days, then the style is found to be its full length as soon as the flower opens.

The opening is generally complete by about 9 a.m. The flower remains wide open during sunlight; as the sun's power diminishes, the flower-stalk moves from the joint until the flower again reaches the vertical position (Fig. 4), the petals close over the stamens one by one (see Fig. 15, one flower has one petal closed, the other two and Figs. 16-20), then the

sepals close too, and the flower shuts for the night (see Fig. 4 (2), where the flower 2 in Fig. 3 is seen closed and the older flower 1 has just been dropped into the vertical position preparatory to closing. Also Fig. 6, where flower 3 in Fig. 5 is closed).

The first day then the flower is small, has a short style, and generally closes about 6 p.m. (see Figs. 25, 53, and 63).

On the second day the flower begins opening much earlier than on the first occasion—5 a.m. (when sunrise is 6.32 a.m.), and opens so rapidly that it is difficult to follow its movements. The style has grown as long as the stamens, which are now very sensitive, and at the slightest touch move rapidly away from the stigma. The flower is closed by 9 p.m. (see Figs. 54 and 64).

The third day the flower again opens as before, the stamens are still sensitive, but the flower is *very late* going to sleep. At 10.30 p.m. the petals had fallen into the flat open position (Fig. 4, 1), at 11.30 one petal was closed, and it was not until 4.30 a.m. that the flower was completely shut.

The fourth day the flower is flat open, and again goes to sleep late. The fifth day the flower does not open so widely, and the stamens are no longer sensitive. At the time when the other flowers are shutting for the night, it shuts slightly but never reopens. Gradually it closes more and more, and during this time it is gradually attaining the vertical position (see Fig. 5, Flower 1, which in Fig. 6 has shut and will not reopen.) In Fig. 7 it has almost attained the vertical position.

As the flower withers, if bees have not been plentiful the pollen is mechanically extruded from the stamens. This is the usual course of a flower's life, when fertilization has not taken place. It varies to a certain extent according to weather conditions. For instance, sometimes a flower does not reopen in the position of the second day, but at once takes up the flat open position of the third day.

The progress of the flowers from day to day is very difficult to watch accurately. The flower of to-day takes up the position occupied by yesterday's flower. This was well brought out

by plotting the flowers as explained on p. 764, where it was found that the flowers in succession occupied one another's places, so that unless each flower be accurately drawn daily it would be very easy to confuse the identity of the individuals.

I will now describe the progress of a fertilized flower, Fig. 8, Flower 9.

This opened first at 2 p.m. on March 12.

Closed 6 p.m.

Second day. Bees were introduced into the greenhouse, and the flower was fertilized (Fig. 21). Stigma as long as the stamens.

Began going to sleep 8.45, March 13.

The flower continued to open and close on the 14th, 15th, not beginning to close on the 15th until 10 p.m. After this it gradually closed its petals, whilst moving up into the vertical position. On March 18, six days after it first opened, the whole pedicel moved down from the vertical into the horizontal position (Fig. 9, Flower 9); the flower was turned up vertically by movement at the joint. The fertilized flowers always behave in this way, thus getting out of the way of the buds and open flowers.

On March 19 the flower still opened a little, the pollen was ripe and plentiful, and the pedicel was gradually moving up again. The petals now fell off, the stamens withered and the fruit swelled. It was ripe in June (Fig. 11). A layer of periderm is formed at the joint, and it is here that the fruit detaches itself when ripe (Fig. 14, a figure drawn from a herbarium specimen). The seed was sown on June 22, and the seedling came up and was figured on July 23 (Fig. 12).

The ovules are capable of being fertilized in cold weather also. I have one example of a fertilized ovule (Jan. 8) with endosperm, but the fruit cannot ripen under these conditions. Temperature about 40° F. (4.5° C.).

If we now review the general movements of the umbel, we shall see that the arrangement is such as to ensure an even distribution of the flowers and afterwards of the fruits over the sphere of the umbel, so that each flower or fruit is



separated from its fellows and is exposed to the best advantage to the sun's rays. The buds when young hang down close to the peduncle out of the way. As the flowers open they rise, and again move out of the way into a close vertical cluster after fertilization. Then the fertilized flowers move down one by one into the horizontal position, and gradually rearrange themselves equally over the sphere during ripening; the last fruit remaining in the vertical position.

The whole development from bud to seedling thus occupied four months; this is no doubt a very much slower process than it would be under natural conditions. As the flowers only open well during sunlight with a temperature of about 60° F. (15.5° C.) and the plant is flowered in our early spring, one often gets only one flower at a time on an inflorescence, and many days may elapse before another has the opportunity of opening, while on a hot day one may get three or four fresh flowers opening at the same time.

The plant flowers again six months later, in September, though it is seldom given the opportunity here, as the usual treatment is to cut it back after the early flowering.

The opening of a normal bud has now been described, but the weather conditions make very considerable alterations in the habits of the bud.

The opening is retarded by fog, probably principally because fog tends to keep down the temperature, which must be about 60° F. (15.5° C.) for a flower to open. The bud will not go on opening if for any reason the temperature falls.

One bud (Figs. 42 and 43) began opening at 10.50 a.m. temp. 72° F. (22.5° C.) on a bright sunny day. At 11 a.m. it put up two sepals (Figs. 44 and 46); at 12.10, temp. 66° F. (19° C.), it was putting up a third (Figs. 47 and 48) when a hailstorm reduced the temperature below 60° F. (15.5° C.)<sup>1</sup>. This is the stage at which in the normal opening the stamens

<sup>1</sup> The hailstorm no doubt reduced the temperature much more than would have been the case in the open, as the glass of the greenhouse was made wet and cold by the falling hailstones, and the evaporation afterwards tended still further to make the temperature fall.

begin to expand, but here only a few staminodes were protruded and erected from between the petals (Fig. 50).

This happens so constantly when a flower is checked in opening (see Fig. 56) that it seems as if in some way the delicate projections from the filament must be more sensitive to temperature changes than the rest of the flower, and are perhaps able to send a message to the other parts. At 12.40 p.m. the temperature again rose above 60° F. (15.5° C.), and it put up a third sepal (Figs. 49 and 50) at 2.20 p.m. Another hailstorm so reduced the temperature that the flower closed for the night (Figs. 51 and 52). Figs. 53 and 54 show it open the next and following mornings. In Fig. 53 the style will be seen to be short, while in Fig. 54 (drawn the following day) it had grown to the length of the stamens.

Another flower (Fig. 55), which began opening at 10 a.m., kept one sepal up (Figs. 55-57) till 12.30 p.m., and then a hailstorm lowered the temperature, and it closed for the night (Fig. 58).

I watched one flower on Nov. 20, which had been trying to open for three days; this had developed the most conspicuous joint, which I ever observed.

On warm sunny days the buds go on developing, and one sometimes has the good fortune to be able to watch the whole process of opening without getting up before sunrise. Figs. 22-25 show a flower, which began opening at 12 p.m. and was full open at 2.5 p.m., closed at 6 p.m. Note in Figs. 23 and 24 the staminodes rising above the first opened petal.

The so-called 'sleep' of these flowers is a very interesting and variable process, and probably has some connexion with their fertilization, as the flowers no longer close well after the stamens have ceased to be sensitive. The plant is very active at night. The buds move upwards and outwards in the most vigorous way all night, and the style also grows in length during the night, so that a one-day-old flower, which had a short style on closing about 6 p.m., has on opening the following morning a full-grown style as long as the stamens.

## EFFECT OF RAIN ON THE FLOWER.

Kerner describes the effect of rain on the flowers of *Sparmannia africana*<sup>1</sup>. He says: 'The flowers are inverted and their anthers are turned towards the ground and covered over by the petals. When the flower is open, however, the petals are slightly tilted back, i. e. upwards. The margins of the petals overlap one another, and their outer surfaces, which in consequence of the inverted position of the flower are uppermost, thus form a basin open to the sky. When it rains this basin placed above the anthers fills with water, thus adding to the weight borne by the stalk, and as drop after drop increases the strain upon the latter, a point is at length reached when the basin tips over, letting the water flow over its edge, without wetting the stamens suspended beneath it.'

I have repeated this experiment; Fig. 26 shows the position of the flower before the rain-shower, Figs. 27 and 28 after the rain has begun. For a long time the cup fills and empties, shooting out the water in the direction of the arrow in Fig. 28 in a most perfect manner, and the stamens remain perfectly dry. The long, dense hairs of the sepals which form the cup also help to throw off the water rapidly. But if the rain is long continued or very heavy, the stamens eventually get wetted, as seen in Figs. 27 and 28, where the drops can be seen running off the stamens, which are hanging together in groups. Fig. 29 represents the same flower shutting up at 7 p.m. I found that if the stamens were once wetted the flower did not reopen, though if they kept dry they opened as usual the following day.

## CHLOROFORM EXPERIMENTS.

One flower was chloroformed for a few seconds; the stamens were no longer sensitive, but recovered their sensitiveness again after a short lapse of time.

<sup>1</sup> Kerner von Marilaun, A., Eng. Ed. 1895, vol. ii, p. 119.



A young inflorescence with all flowers in bud was chloroformed next, and the results watched. No apparent change took place, but the development of the inflorescence was very curiously affected.

The drooping buds went straight up into the vertical position, the position which the flower assumes after fertilization. The open flowers behaved in various ways: One took up the vertical position, whilst others moved down into the horizontal position, as in Fig. 9, 9. Some of the buds did not open at the usual time, but the style grew in length, as would have been the case normally the day after the opening of the flower. These buds presented the most abnormal appearance, with the stigma hanging out, though the sepals were quite closed. One bud measured 1 cm., and the style projected 6 mms. from it. In some cases, after a few days, the flowers fell off at the joint.

The effect of the chloroform seems to have been to make the buds and flowers lose all count of time. A bud, after recovering from chloroform, often missed out several stages of its development, another would grow a long style as if it were a two-day-old flower, while an open flower would take up the position of a fruit, or fall off at the joint, as if it were a ripe fruit.

The difficulty in carrying out these experiments is that it is so very easy to give too much chloroform and poison the inflorescence so that it never thoroughly recovers; in these cases other inflorescences are generally affected too.

#### KINEMATOGRAPH EXPERIMENTS.

It struck me that the inflorescence of *S. africana* would be admirably adapted for an experiment with the kinematograph.

The inflorescence could be photographed at intervals while young, so as not only to show the opening and the closing of the flowers and the movements of the stamens, but also the development of the inflorescence from bud to fruit. The

series of photographs taken could then be projected with the lantern on the screen, and the development of the inflorescence, which in reality takes several months, could be watched in progress and could pass before the spectators on the screen in a few minutes, until the buds first shown had become fruits.

The difficulty of trying this experiment was principally one of expense.

Professor Pfeffer<sup>1</sup>, of Leipzig, has made many successful botanical demonstrations with a kinematograph and has devised a very perfect apparatus for class demonstration, but the expense of his apparatus (exclusive of the cost of his original experiments) is too great to make it possible for use by the private investigator; one of the most serious items being the cost of production of each film, which amounts, Prof. Pfeffer tells me, to ninety marks (£4 10s.), while the apparatus for taking the photographs cost £45 (exclusive of the kinematograph and lantern for demonstration).

I at first experimented with a small film kinematograph, but the results were not satisfactory, as the machine was not suitable for making time exposures, and the makers were unwilling to help adapt their machine for scientific work. Also the life of the films when obtained was so short. The following experiments were made with a machine called the Kammatograph, in which the photographs are taken on a glass disc instead of on a film. In the use of this machine I have received every possible help from the inventor<sup>2</sup> of it, who has done his best to adapt it in every way for the work.

A short description of the machine will first be necessary to those who have not seen it. A glass disc of 12 inches in diameter is suspended in a metal ring; this disc is coated with a sensitive emulsion, and is in fact a large circular dry plate ready for use in photography, capable of taking 350 photographs. (Half one of these plates, after the photographs have been taken on it, is shown in Fig. 65, Pl. XXXIX.)

<sup>1</sup> Jahrbuch f. wiss. Bot., 1900, vol. xxxv, p. 38.

<sup>2</sup> Messrs. Kamm & Co., 27 Powell Street, E.C.

This glass disc, when ready for use, is put into a light-proof box, and by means of a handle at the side can be spirally rotated, so that every part of it is in turn exposed before the small oblong opening in front of the lens. In ordinary kinematograph work the handle is rotated at a uniform speed, and a series of snapshots are produced, but for the work now required it is necessary to take time exposures, as the light in a greenhouse would seldom, if ever, be good enough for instantaneous photography, and also, if it were possible, the number of photographs thus obtained would be unnecessarily large; as a large number are only required when rapid movement, such as that made by the stamens when touched or when a bud is opening, is taking place. For many parts of the day a photograph taken every quarter of an hour is sufficient.

The practical difficulties were very great; the principal ones were:

(1) To obtain absolute rigidity of the apparatus.

(2) Uniform exposure for each photograph, as photographs had to be taken at all times of the day and night and in all weathers.

(3) The difficulty of having some one always watching the plant.

(4) Compensating accurately for the growth in length of the inflorescence, so that the part of interest is always in the field.

The first difficulty was removed by the construction of a heavy metal tripod stand.

The second was soon removed by the use of an accurate actinometer, which must, however, be used for almost every photograph to ensure perfect results. The night photographs can be taken by means of a magnesium wire, accurately measured in lengths, or better still, by those who have electric light installed, with an arc light.

For the third difficulty I am afraid there is no solution but the adoption of an elaborate and costly automatic mechanism. This has been done by Professor Pfeffer.



It certainly would be a great advantage to be able to take photographs mechanically through the night, as unfortunately this plant, so far from following the human habit of sleeping through the night, seems to be peculiarly active between the hours of 1 and 5 a.m.

For the overcoming of the fourth difficulty I am indebted to Mr. Kamm, who constructed a very accurate sight to the machine, by the use of which the elevation could be readjusted every morning.

I will give a brief account of the kinematograph picture illustrated, Fig. 65. It was begun at 8.30 a.m. March 6, 1903. As many photographs as possible were taken of the bud while opening; then it remained more or less stationary for some time, and photographs were only taken at half-hour intervals until the flower began to go to sleep, when regular photographs were again taken with longer and longer time exposures as the light decreased, and then by means of magnesium wire. The following morning photographs were taken by magnesium wire from 4.30 a.m. until sunrise (see Fig. 66), when time exposures were again taken. To show the movements of the stamens when touched, instantaneous photographs were taken by turning the handle of the machine as in ordinary kinematograph work.

After two days' work another difficulty arises—the flower-stalk elongates, so that if a new adjustment is not made one finds the future photographs show only the stalk. This is remedied by raising the stand of the Kammatograph with the help of a very accurate sight adjustable for any distance above 9 inches, and then starting again. Of course one loses the growth of the flower-stalk, but this is inevitable, unless a much larger photograph is taken, which would involve a much more costly machine.

The sensitized plate is then removed and developed just like an ordinary plate, and when dry the positive is printed from it in a few minutes.

I must here state the one drawback to the use of this machine: there is no means of remedying a mistake.

With the film kinematograph over- or under-exposure, or a photograph which has been spoilt by accidental movement, has only to be missed out when printing, or if necessary the next photograph can be printed twice.

On the other hand this machine has great advantages. The developing of the whole series of 350 photographs only takes the same time as that required for developing any ordinary sensitive plate, and printing is also perfectly simple, as the negative is simply placed on a positive plate exposed for a definite number of seconds to the light of a lamp and then fixed. Any number of positives can thus be made by an ordinary photographer with a very small expenditure of time. The cost of producing each negative is 3*s.* 6*d.* and each positive costs the same amount, so that each subject taken costs 7*s.*

My experiments with both kinematographs extend over more than a year, and I have only quite recently succeeded in producing fairly good results ; but I think that most of the principal practical difficulties are now surmounted, and that the machine is in a fit condition for experimental work.

I have used it successfully for other subjects, such as climbing plants, to show the movements of the leaves of the sensitive plant.

I believe these are the first kinematograph experiments under natural conditions, daylight being used and artificial light only resorted to at night. It was thus possible to leave the plant undisturbed throughout the time of observation.

I am indebted to Miss M. Smith, of Kew, for kindly drawing two figures for me from photographs.

I am making microscopical investigations of the parts of the plant connected with movement, which promise some interesting results, but have thought it better to defer this to another paper, which I hope to publish shortly in conjunction with Miss Richards of the Royal Holloway College.

DESCRIPTION OF FIGURES IN PLATES XXXVII  
XXXVIII, AND XXXIX.

Illustrating Mrs. Scott's paper on *Sparmannia africana*.

- Fig. 1. March 6, 60°, 11 a.m., sun out, dotted lines, 60°, 4 p.m., sun out.  
 Fig. 2. „ 7, 57°, sun out, 10 a.m.  
 Fig. 3. „ 8, 57°, sun out, 9.30 a.m.  
 Fig. 4. „ 8, 55°, 8.50 p.m.  
 Fig. 5. „ 9, 70°, sun out, 10 a.m.  
 Fig. 6. „ 9, 62°, 9.15 p.m.  
 Fig. 7. „ 10, 56°, dull, 10 a.m., flower 3 shut, 10 p.m.  
 Fig. 8. „ 15, 68°, sun out, 11 a.m.  
 Fig. 9. „ 18, 58°, „ 2 p.m.  
 Fig. 10. April 25, 68°, „ 3 p.m.  
 Fig. 11. June 22, 7.30 p.m.  
 Fig. 12. July 23, 1902, seedling sown June 24, 1902. G-G level of ground.  
 Fig. 13. Shows buds covered by leaf, from photograph.  
 Fig. 14. Drawing of ripe fruit from Kew Herbarium of wild *Sparmannia*.  
 Fig. 15. Drawing from kinematograph photograph, showing bud rising at night while flowers are closing.  
 Fig. 16. Sleep position, 7.30 p.m., 56°, 2 petals shut.  
 Fig. 17. „ „ 8.30 p.m., 55°, 1 petal shut.  
 Fig. 18. „ „ 9.10 p.m., 54°.  
 Fig. 19. „ „ 7.30 p.m., 56°.  
 Fig. 20. „ „ 9.10 p.m., 54°.  
 Fig. 21. Bees fertilizing flowers, 11 a.m., 65°, March 13, 11.40 a.m., 65°, flower bud began opening.  
 Fig. 22. 12 p.m., 70°, March 25.  
 Fig. 23. 12.50 p.m., 69°.  
 Fig. 24. 1 p.m., 70°.  
 Fig. 25. 2.5 p.m., 72°, asleep 6 p.m.  
 Fig. 26. Position of flower 12 p.m., 55°, before rain.  
 Fig. 27. „ „ after rain, March 4, 1902.  
 Fig. 28. „ „ „ „  
 Fig. 29. Same flower at 7 p.m., 52°, „  
 Fig. 30. 1 b, 10 a.m., March 22, 60°, sun out.  
       1 c, „ „ 22, „ „  
 Fig. 31. 2 b, 1 p.m. „ 22, 63° „  
       2 c, „ „ 22, „ „  
 There was a hailstorm at this time, and the flowers did not open further.  
 Fig. 32. 3 b, 6.45 a.m., March 23, 48°, sun out.  
       3 c, „ „ 23, „ „  
 Fig. 33. 4 b, 7.20 a.m., „ 23, 50°, „



- Fig. 41. 4 c, 7.20 a.m., March 23, 50°, sun out.  
 Fig. 34. 5 b, 9 a.m., ,, 23, 55°, ,,  
           5 c, ,, ,, 23, ,, ,,  
 Fig. 35. 6 b, 9.5 a.m., ,, 23, ,, ,,  
 Fig. 36. 7 b, 9.10 a.m., ,, 23, ,, ,,  
 Fig. 37. 8 b, 9.20 a.m., ,, 23, ,, ,,  
 Fig. 38. 9 b, 9.30 a.m., ,, 23, ,, ,,  
 Fig. 39. 10 b, 9.45 a.m., ,, 23, 60°, ,,  
 Fig. 40. 11b, 11.50 a.m., ,, 25, 55°, ,,  
           6 c, ,, ,, 25, ,, ,,  
 Fig. 42. 1, 10.50 a.m., ,, 21, 72° ,,  
 Fig. 43. Other view, ,, 21, ,, ,,  
 Fig. 44. 2, 11 a.m., ,, 21, ,, ,,  
 Fig. 45. 3, 11.20 a.m., ,, 21, 68°, ,,  
 Fig. 46. Other view.  
 Fig. 47. 4, 12.10 p.m., ,, 21, 66°, ,,  
 Fig. 48. 5, 12.40 p.m., ,, 21, 66°, ,, other view.  
 Fig. 49. 6, 2.20 p.m., ,, 21, 60° (violent hailstorm).  
 Fig. 50. Other view, ,, 21 ,, ,,  
 Fig. 51. 7, 8.30 p.m., 52°.  
 Fig. 52. ,, ,, ,,  
 Fig. 53. 8, 10 a.m., March 22, 60°.  
           1 a, ,, ,, 22, ,, ,,  
 Fig. 54. 9, 1 p.m., ,, 22, 63°.  
 Fig. 55. 2 a, 11.30 a.m., March 22, 68°.  
 Fig. 56. 3 a, 12.30 p.m., ,, 22, 63°.  
 Fig. 57. 3 a, ,, ,, ,, other view of 56.  
 Fig. 58. 4 a, 8.30 p.m., ,, 22, 58°?  
 Fig. 59. 5 a, 6.40 a.m., ,, 23, 48°.  
 Fig. 60. 6 a, 6.45 a.m., ,, 23, ,,  
 Fig. 61. 7 a, 7 a.m., ,, 23, ,,  
 Fig. 62. 8 a, 7.10 a.m., ,, 23, 50°.  
 Fig. 63. 9 a, 7.35 a.m., ,, 23, 51°.  
 Fig. 64. 10 a, 9 a.m., ,, 23, 55°. (Sunrise March 23, 5.58 a.m.).  
 Fig. 65. Half circle of kinematograph plate reduced.  
 Fig. 66. 5 successive photographs enlarged, the first four, from below upwards,  
 taken by magnesium light.

The lettered numbers, e.g. 1 a-10 a, indicate series of figures taken from the same flower-bud.

The figures 1-64 were drawn natural size and reduced to  $\frac{3}{4}$ .









R. Scott. del.









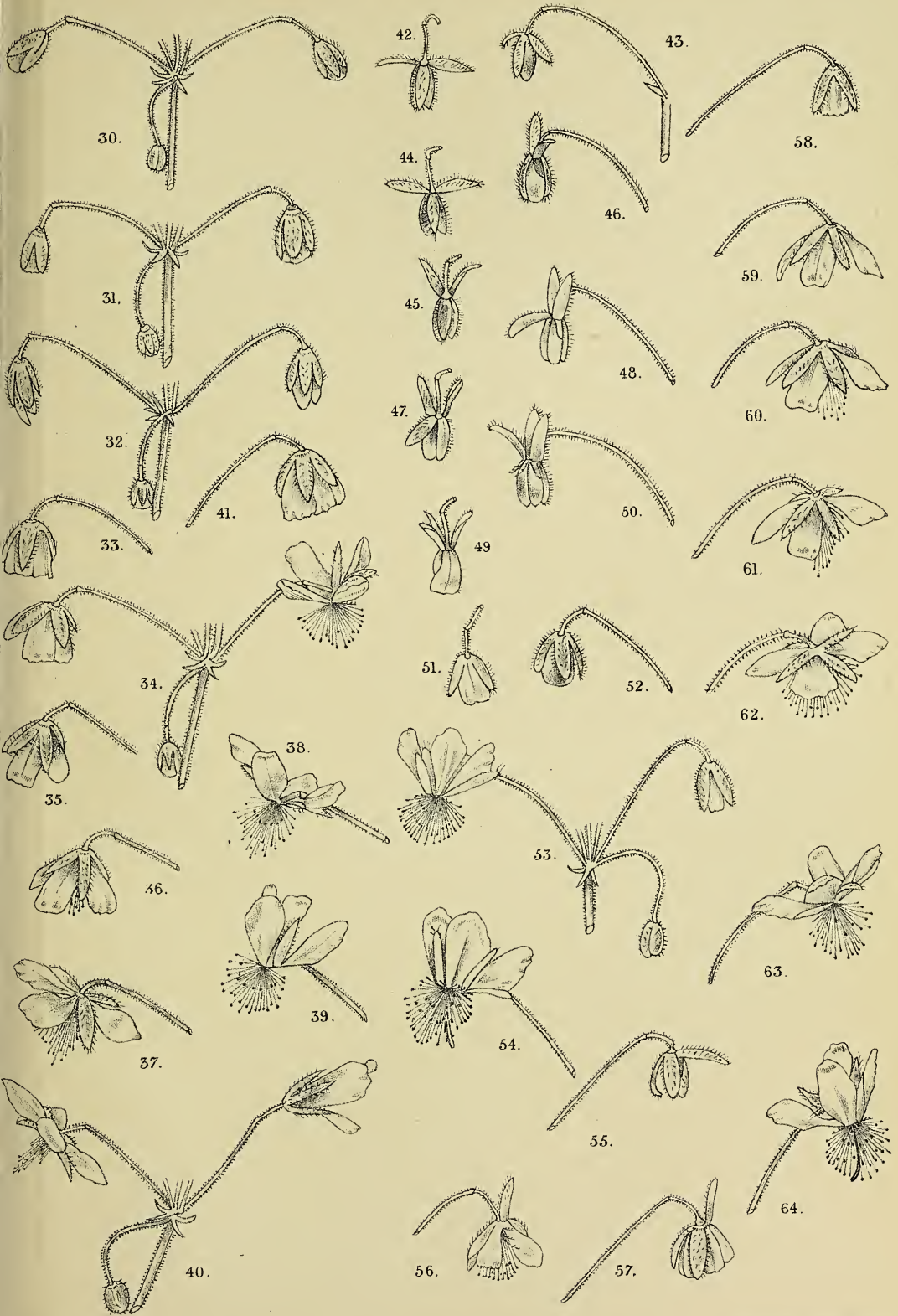
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R. SCOTT — SPARMANNIA AFRICANA.







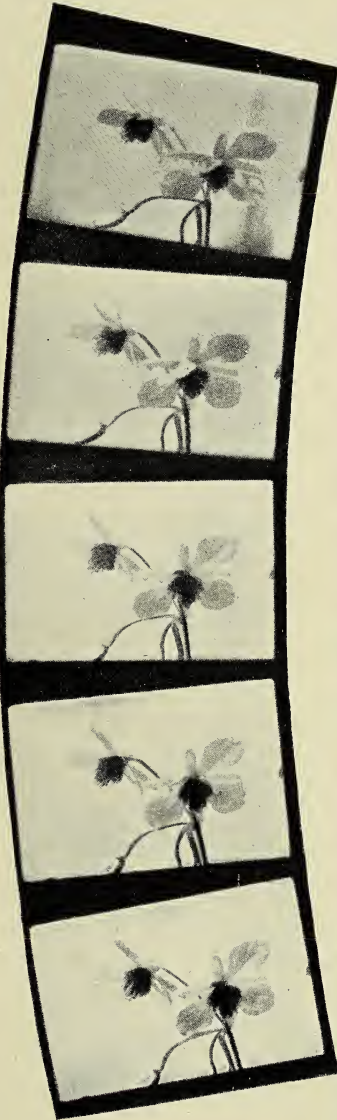
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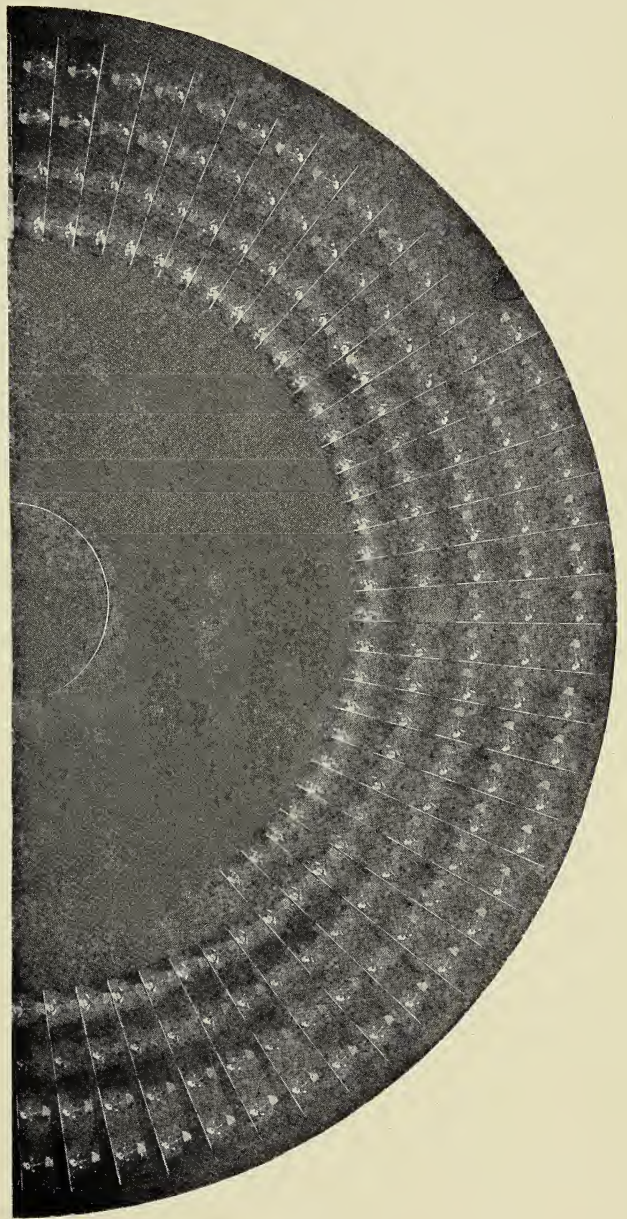




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R. SCOTT, Phot.





## Morphological Notes.

BY

SIR W. T. THISELTON-DYER, K.C.M.G., C.I.E., F.R.S.,

*Director, Royal Botanic Gardens, Kew.*



With Plate XL.



### X. A PROLIFEROUS PINUS CONE.

THE specimen described in this note has perhaps a little more than a scientific interest. It was brought from Spain by the late H. R. H. the Comte de Paris in 1894 and sent by him to me not many months before his death, which took place on September 8 of that year.

Its history is given in the following letters:—

PALACIO DE VILLAMANRIQUE,  
PROVINCIA DE SEVILLA (ESPAÑA),  
*April 27, 1894.*

SIR,

I have in my possession what I consider as a very curious botanical phenomenon, and I would gladly present it to the Kew Museum, or send it to you for inspection, if you thought it worth of it.

It is a frondiferous cone of the *Pinus Pinea*, out of the upper end of which has grown a young tree just as a pine-apple grows out of the crown of this fruit. Generally these cones fall only after having thrown away their seeds. This one fell on the ground (how I do not know) with the seeds or almonds still encased in it. It was picked up in a large *Pinar* or pine forest which I own in this neighbourhood, by

[*Annals of Botany*, Vol. XVII. No. LXVIII. September, 1903.]

one of my keepers a day I was out shooting. The young tree was then about six inches long. The woodmen of this country say they never saw anything like it.

I took the cone home and left it alone on a table, about the middle of February. It went on growing for a month, made a stem more than a foot long with three branches, and even threw out new shoots. About the end of March, although it was watered, it ceased to grow and dried, although the needles did not fall and preserve their colour.

Will you kindly send your answer to Stowe House, Buckingham, where I shall be in a few weeks, as a letter sent to Spain would be too late to reach me.

Believe me, &c.,

PHILIPPE COMTE DE PARIS.

STOWE HOUSE, BUCKINGHAM,

*May 19, 1894.*

DEAR SIR,

I have just received your letter of yesterday, and I hasten to thank you for it.

I send you at once the curious growth out of the cone of *Pinus Pinea* which I mentioned to you in my first letter. If it can be of any interest I shall be glad to present it to the Kew Museum.

As I wrote to you, this cone was found on the ground in the Pinar de los Lobos on my estate of the Coto del Rey near Seville, by one of my keepers a day I was out shooting in February, 1894. The growth then was only six inches long and single, and quite fresh. I took it home and put it on a shelf in my study where it went on growing and dividing in branches for about a month. Then it suddenly stopped, dried up, and nothing could induce it to start again: very likely the stock of sap which the cone contained was exhausted.

Believe me, &c.,

PHILIPPE COMTE DE PARIS.

STOWE HOUSE, BUCKINGHAM,

*June 11, 1894.*

DEAR SIR,

I learn from your letter, with the greatest pleasure, that the botanical specimen which I had sent you a fortnight ago has been most fortunately discovered, and the foolish idea of the

railway expeditor in Buckingham who labelled the parcel containing this specimen as an empty box, has had no serious consequences. I only regret very much the trouble which this absurd mistake has caused you, and I beg to apologize for it. It would indeed have been very unfortunate if this curious and anomalous growth had been lost for ever under a heap of old empty boxes.

I thank you very much for the interesting lecture given in your letter upon the physiological characters of pine-cones. What struck me most in that specimen is the following fact: when it was picked up it must not have been lying on the ground more than two or three weeks, perhaps less. The young single shoot was not six inches long. It went on growing very rapidly, throwing off branches and showing all the appearances of an ordinary strong and healthy branch, without being ever fed in any way. After about six weeks it had attained its present size, and then the growth suddenly stopped and the needles, losing their dark green appearance, began to wither. It was in vain that I put the cone in a wet cloth, nothing could restore life in it. This shows evidently that there was a certain quantity of sap in the cone sufficient to insure this anomalous growth up to a given size, and that when this store of food was exhausted the autonomous life of this cone became extinct.

Excuse me for making this remark, and believe me, &c.,

PHILIPPE COMTE DE PARIS.

The total length of the specimen is  $19\frac{1}{2}$  inches. The figure is therefore reduced to rather more than a third.

The cone belongs to the 'Stone Pine' (*Pinus Pinea*, L.). As is well known the seeds are edible, hence the Comte de Paris writes of them as 'almonds': strung together they are sold in the market at Lisbon. Examples may be seen in the Kew Museum, where the specimen is also preserved.

I have failed to find any record of terminal proliferation in a *Pinus* cone, and Dr. Masters, F.R.S., who is an accepted authority on the *Coniferae*, kindly informs me that he knows of none.

Normal cones of *Pinus Pinea* are usually about 6 inches long. That now described is only  $3\frac{1}{2}$  inches. It is therefore a small cone. But as the apex of the largest scales



measures an inch across, which is the normal size, the smallness of the cone is due to its having fewer scales and not to its being immature.

The morphological interpretation of the female cone in the *Abietineae* is a subject upon which the most divergent views have been held. As is well known a cone is composed of seminiferous scales (which become greatly enlarged in *Pinus*) and these are apparently axillary structures subtended by the primary reduced leaves of the axis of the cone, the so-called bract-scales.

In *Larix* proliferation of the female cones is not uncommon. But the passage from cone to shoot is not, as in the present case, abrupt, but gradual. Masters has shown conclusively (*Gardeners' Chronicle*, N.S., xvii. pp. 112, 113) that in such cases the bract-scales pass into ordinary foliage leaves with which they are serially continuous. The fact admits of no dispute and the interpretation is generally accepted.

So far we seem to be on solid ground: whatever be the explanation of the seminiferous scale it is at any rate 'subtended' by the bract-scale, which is undoubtedly a modified foliar organ and is not seminiferous.

This state of things is in sharp contrast to that which obtains in the *Cycadeae*. In a former note (*Annals*, xv. pp. 548-550) I have shown from the study of a proliferous *Encephalartos*, that the carpophylls or seminiferous scales are homologous with the ordinary foliage leaves and therefore with the bract-scales in the *Coniferae*, as both belong to the primary axis.

No one would I suppose now deny that the Gymnosperms stand in an intermediate position between the Phanerogams and the Cryptogams. Few things in vegetable morphology are more remarkable than the reluctance with which this has been admitted.

Nothing can of course be simpler than the fundamental generalization which is applied to both. An *Anther* is a modified leaf which produces microsporangia: a *Carpel* is a modified leaf which produces macrosporangia. Of the latter

the carpophyll of *Cycas* is the simplest we know: we fold it like a sheet of note-paper, and we get an arrangement which does not differ essentially from a pea-pod. But in the majority of Phanerogams, a carpel of this simple type is lost sight of in the complexity of adaptive arrangements, and a subsidiary structure—the placenta—is called into existence to bear the ovules.

It seems to me that the Gymnosperms having assisted us to grasp the generalized structure underlying the complex arrangements of the Phanerogams, we must use great caution in the attempt to find in the former the specialized structures developed in the latter. Nevertheless the history of Gymnospermous morphology shows a constant attempt to bring it forcibly into line with that of Phanerogams.

The most recent view as to the nature of the seminiferous scale in *Abietineae* proper is that of Goebel (*Outlines of Classification and Special Morphology*, p. 328). He lays stress on the fact that in *Abies* 'the seminiferous scale arises as a protuberance on the base of the so-called bract-scale and therefore is not axillary.' I must confess, however, that vegetable morphology presents us with so many cases of similar dislocations that the mere fact taken alone does not strike me as of great importance. I am disposed to agree with Van Tieghem that it merely depends on 'intercalary growth' such as 'separates a dialypetalous corolla from a gamopetalous one.' If this is the correct view, as I believe it to be, Goebel's theory that 'the seminiferous scale' must 'be regarded as a *placenta* of large dimensions growing out of a carpellary leaf' seems to be without a valid argument to support it. And in *Pinus*, where the seminiferous scale is truly axillary, Goebel admits that it cannot be considered an outgrowth, though he still thinks it may be considered a placental growth.

If the seminiferous scale is not a placenta or outgrowth from the bract-scale, which in that case would be a carpel, it must be some kind of foliar organ. Lindley was satisfied 'that the scales of the cones really are metamorphosed leaves'

(Vegetable Kingdom, 3rd ed. 227). And this view seemed to him conclusively supported by a monstrous cone of *Picea excelsa* figured by Richard (Mémoire sur les Conifères et Cycadées, t. 12, f. 3). Unfortunately this was not a cone at all, but a 'false cone' or gall. Schleiden, whose boisterous criticisms may still be studied with advantage, insisted that the seminiferous scale was the equivalent of an axillary bud:—'l'écaille, considérée par R. Brown comme un ovaire ouvert, n'est autre chose que le bourgeon axillaire de la feuille carpellaire, placé sous l'écaille, et, par cette raison seule, ne saurait être un organe foliaire, parce que *folium in axilla folii* est chose sans exemple dans tout le monde végétal (Ann. d. sc. nat., 2<sup>o</sup> sér., xii. 374). Schleiden's theory was developed by Braun, Caspary, and at first Eichler: they regarded the seminiferous scale as a short axis which has coalesced with its two carpels; Von Mohl as 'a coherent structure formed of the leaves of an undeveloped branch.'

The latter view derives some support from the ingenious argument which Masters has founded on a proliferous cone of *Sciadopitys*, first figured in Veitch's Manual of Coniferae (Gardeners' Chronicle, l.c.). According to a note by Van Volxem in the same volume (p. 155) this is 'the most common form . . . . in the neighbourhood of Yokohama.' Masters finds that in this case the bract-scale remains unchanged, while the seminiferous scale is replaced by a normal 'leaf.' He remarks that 'whatever be the nature of the so-called 'leaf' of *Sciadopitys* it must be essentially the same as that of the seed-scale of the *Abietineae*.' The argument is, however, doubtful. *Sciadopitys* does not belong to the *Abietineae* proper, and its 'leaf' has itself been regarded as a shoot formed by the coalescence of a pair of leaves such as occur in *Abietineae*.

Van Tieghem has adopted a view of which I have given an account in a note to Sachs' Textbook (1st ed. pp. 453-4). He regards the seminiferous scale 'as the first and only leaf of an axis which undergoes no further development.' This reconciles the views of Schleiden and Lindley.



The position, however, becomes more complicated when we consider the remarkable case of a monstrous cone of *Pinus lemoniana* (P. Pinaster), described by Parlatore, from the Gardens of the Royal Horticultural Society at Chiswick (Ann. d. R. Mus. di St. nat. di Firenze, 1884). In this the seminiferous scale is replaced by a limited branch or fascicle of ordinary foliage leaves. The facts:—‘dimostrano chiaramente come ne conviene lo stesso Signor Eichler, che nell’organo squamoso o squama interna, secondo ch’egli lo chiama, delle Abietinee, debba scorgersi non un asse soltanto secondo l’opinione di Schleiden, nè un carpello come comunemente si crede, ma un ramo raccorciato con gli organi fogliacei.’

An important paper by Stenzel (Nova Acta, xxxviii, 1876) I have not had the opportunity of seeing. But it has been carefully summarized by the late Professor McNab (Journ. Bot. 1877, pp. 26–7). It was based on abnormal scales of the spruce (*Picea excelsa*, Lk.) in which the seminiferous scale was replaced by an axillary bud. ‘The two lateral bud-scales . . . are well developed, hard, brown, with the margin irregular and quite of the texture of the scales of the cone. By further tracing these abnormal buds it is found that at last all trace of the bud except the two lateral bud-scales disappears, and these become soldered more or less completely. . . . Farther down, the scales show no trace of a suture, and pass into the ordinary bifid scales of the cone.’

The conclusion arrived at was that the fruit-scale of the spruce, and also of the other true *Abietineae*, consists of the first two leaves of a suppressed bud developed in the axil of a bract. This is in agreement with the view of Von Mohl (1871).

Latterly Eichler changed his views, according to a note in the Gardeners’ Chronicle (l.c. pp. 264–6). ‘In his opinion the seed-scale is only an excrescence from the outer scale or bract, so that the two really constitute one leaf, and the bud or branch in the axil of the bracts in proliferous cones are not to be considered as transformed seed-scales, but as axillary buds to the composite leaf.’ If this were the true explana-

tion one would expect to find some trace of the seminiferous scale persisting, even in the presence of an axillary bud. But it is clear that this is not the case. In the *Abietineae* with membranous cone-scales (possibly also in *Sciadopitys*) it seems to me that the view of Von Mohl, supported by the researches of Stenzel, is probably correct, and that the seminiferous scale is complex in its origin. But I am not clear that this is the case when the cone is woody, as in *Pinus*. It does not follow because the seminiferous scale is replaceable by a fascicle of leaves that all potentially take part in its development. The general resemblance of a cone of *Pinus* to one, say, of *Encephalartos* is obvious at a glance. In each case we have a 'carpophyll' enlarged above into an hexagonal apophysis with an 'umbo' on its external surface. However violent may seem the transformation, I have clearly demonstrated that the carpophyll in *Encephalartos* is a modified leaf belonging to the primary axis: in the *Abietineae* it appears to me equally demonstrable that it belongs to a secondary one. As Van Tieghem has remarked:—'This establishes a fundamental distinction between *Cycadeae* and *Coniferae*.' But, as in *Encephalartos*, the umbo seems to me clearly the dilatation of the atrophied apex of a foliar organ.

Returning to the specimen now described, I have already noticed that, unlike what takes place in the proliferous shoots of *Larix*, there is an abrupt discontinuity between the reproductive and vegetative regions of the axis. This reminds one in fact of *Callistemon*, where the same axis serves alternately one or the other purpose: an even closer analogy would be found in *Cycas* if the carpophylls were persistent.

The explanation of the fact that a cone is not proliferous is to be found in physiological necessity. The upward stream of food is diverted and absorbed by the developing carpophylls, and the growing point of the cone is arrested in its further development practically by starvation. The upper seminiferous scales share the same fate and become mere woody rudiments. Meanwhile the growth of the cone in diameter sets up a passive tension which would, by mechanical pressure,

in ordinary cases effectually suppress any extension of the growing point. It is, however, to be remarked that in *Pinus Pinea* the cone is often not quite symmetrical; there is a sort of apical appendix, as if terminal growth were not relinquished without a struggle.

I have already noticed that the cone now described is below the normal size. It may be supposed that the food-supply directed towards it was in excess of its needs. The growing point was therefore started into activity. That this was not, however, accomplished without a struggle is proved by the deep constriction between the shoot and the cone. The passive tension of the apex of the cone prevented any increase in the diameter of the shoot till it was entirely free from it.

The age at which the specimen came into my hands had obliterated any trace of external morphological continuity between its two parts. But it seems impossible to shut one's eyes to the fact that the fascicles of leaves in the upper part must correspond to the carpophylls or seminiferous leaves in the lower.

One or two other points remain to be mentioned. Why the cone was shed, seeing that it was actively vigorous, is difficult even to conjecture. When first found the shoot was six inches long; it is now sixteen: it therefore grew at least ten inches after separation from the parent tree. The cone is probably figured in about its normal position: the strong curvature of the shoot is no doubt due to geotropism.

The shoot was entirely dependent on the cone for its supply of both constructive material and water. It is a striking illustration of the power possessed by rapidly-growing tissues of not merely diverting nutriment from others which are less active, but of actually robbing them. But in the absence of roots the supply was bound sooner or later to come to an end. Probably the actual cause of death was, notwithstanding the pains of the Comte de Paris, the failure of a water supply to maintain the transpiration current.

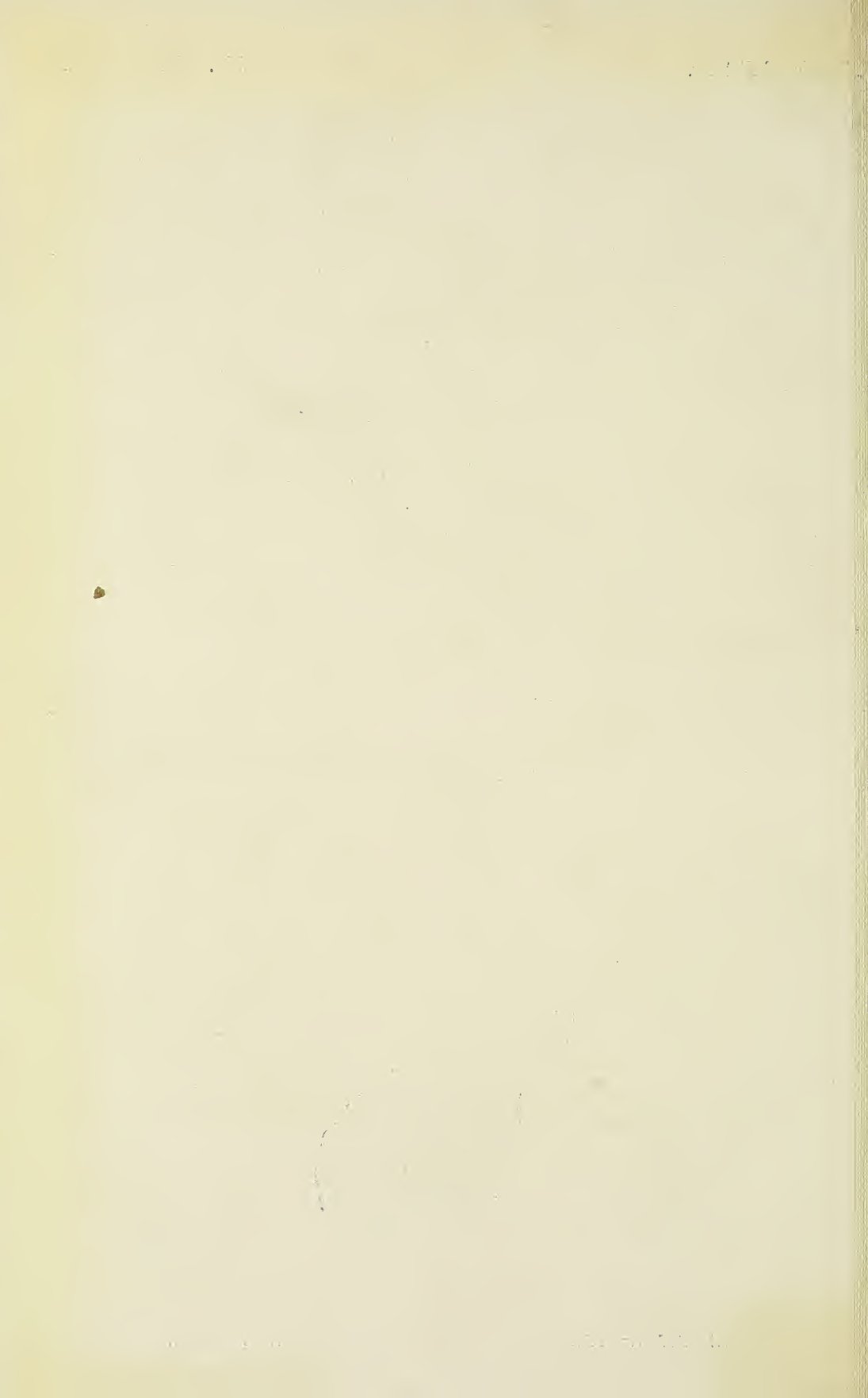






University Press, Oxford

THISLTON-DYER—PROLIFEROUS CONE OF *PINUS PINEA*.





## NOTES.

**THE COTYLEDONS OF GINKGO BILOBA AND CYCAS REVOLUTA.** Mr. Lyon, in discussing the phylogeny of the cotyledon in the journal *Postelsia* (1901), has come to the conclusion that the so-called cotyledons of the Pteridophyta and Gymnosperms, with the probable exceptions of *Ginkgo* and the Cycads, are true foliage leaves.

The foliar nature of the 'cotyledons' of *Ginkgo* and the Cycads would seem from this still open to discussion. The alternative would be the interpretation of these cotyledons as feeders, the term applied by Prof. Bower to the absorptive organs of the Gnetaceae.

Apart from the obvious double structure of the absorptive organs in *Ginkgo* and *Cycas*, which clearly distinguishes them from the feeders of the Gnetaceae, and would suggest their foliar nature, there are other features which may, I think, be taken to indicate that they are much modified foliar organs. Among these characters one I have recently observed is the occurrence of stomata on these cotyledons.

In *Ginkgo* the cotyledons are surrounded by endosperm but not fused with it. Their inner surfaces are closely pressed together so that each appears semi-circular in transverse section; sometimes only the margins meet, and then the cotyledons appear almost crescentic in transverse section.

Stomata are found chiefly on the upper surface, while in the foliage leaves they occur on the lower side only. This may be explained either by supposing those on the under surface of the cotyledons to have disappeared owing to the absorptive function of that part of the cotyledons, or, if we assume that the cotyledons were at a former period in the history of the plant expanded above ground, the stomata on the upper surface may have been protected by closing movements of the cotyledons similar to those of *Cucurbita*.

The guard-cells, which are smaller than the other epidermal cells, lie flush with the surface of the cotyledon; they contain large, deeply staining nuclei. In surface view they appear crescent-shaped, enclosing a small, round or slightly oval pore in the centre (Fig. 29 A). In transverse section it is seen that the pore opens into a small intercellular space which in some cases appears to be filled with loose-celled tissue.

The guard-cells are oval in transverse section and obliquely inclined towards one another at the surface, their walls are thicker than those of the neighbouring cells but do not seem to be cuticularized.

In *Cycas revoluta* the cotyledons are much thicker and narrower than those of *Ginkgo*; they are more closely connected with the surrounding endosperm and their inner flattened surfaces are fused together, so that the junction of the two can only be distinguished near the margin, where the epidermal layers are still marked out, and by the thickening of the cell-walls of a few smaller cells here and there in the central part.

In spite of this very considerable alteration which the cotyledons have undergone stomata are still recognizable in a transverse section of the cotyledon.

The guard-cells here are much smaller than the neighbouring cells, and of characteristic shape. They contain large, deeply staining nuclei, and their walls are very much cuticularized on what would be their outer surface if the cotyledons were not fused. A well-marked pore leads into an intercellular space below (Fig. 29 B).

It is evident from the position of the stomata in *Cycas revoluta* that they cannot possess any functional value; probably they only indicate an ancestral condition when the cotyledons came above ground and functioned as ordinary foliage leaves.

In *Ginkgo*, however, where the cotyledons are not fused, there would be a layer of air between the two cotyledons, between which there often exists a considerable space, and here they might possibly have a respiratory function.

At all events, whether functional or not, their presence suggests that at one time the cotyledons of *Ginkgo* were withdrawn from the testa and expanded above ground, as is the case in most Gymnospermous seedlings.

There seems, therefore, good reason to regard the cotyledons of Cycadaceae and Ginkgoaceae as true foliage leaves, which have

become hypogeal like those of *Araucaria brasiliana*, *A. imbricata* and *A. Bidwillii*.

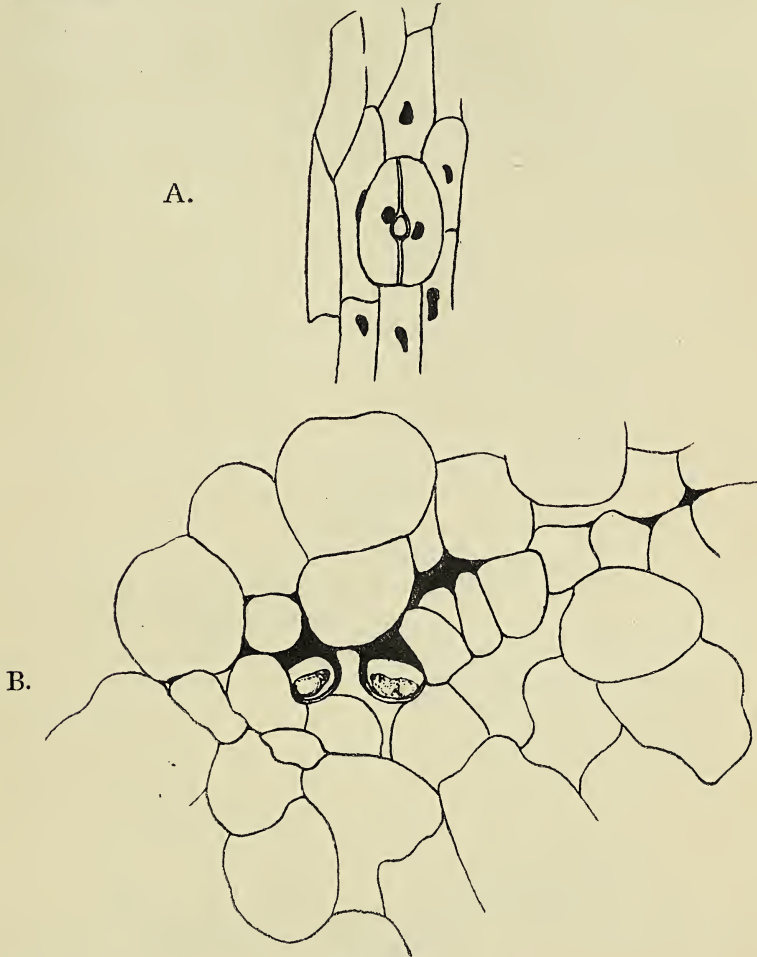


FIG. 29.

A. Portion of the upper surface of the cotyledon of *Ginkgo*, showing a stoma with distinct pore.

B. Portion of a section across the fused cotyledons of *Cycas*. The two guard-cells of the stoma are distinctly separated and their outer walls are cuticularized. Cuticular thickening at other points indicates the line of junction of the two cotyledons.

GRACE WIGGLESWORTH.

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**THE 'EPIDERMOIDAL' LAYER OF CALAMITE ROOTS.—**

The bounding layer of young calamite roots consists of cells with thick outer membranes. These are in no way specially remarkable, being cells which have 'the structure of a thick-walled epidermis, and appear to correspond in all respects with the epidermoidal layer described by Olivier in many recent roots'<sup>1</sup>. As is seen from the published figures<sup>2</sup> they are much the same size as the cells of the

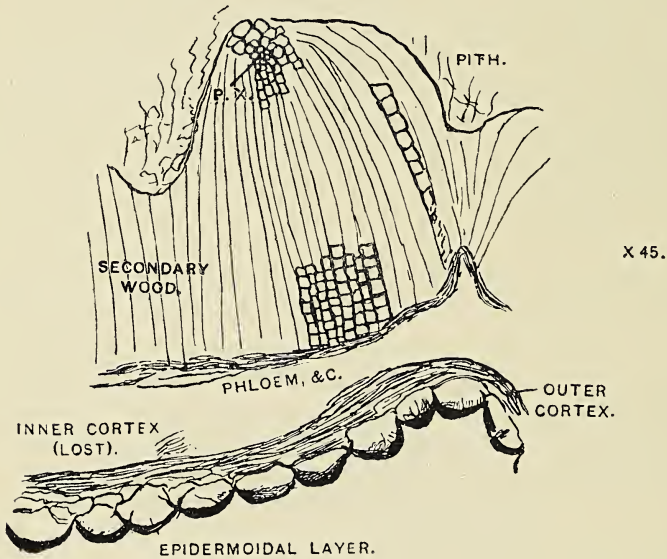


FIG. 30.

cortex (diameter about  $\cdot 08$  mm.), and do not stand out from them in any very remarkable way, except in the thickness of the external wall.

In foreign specimens of older roots a periderm of nine to twelve layers has been described by M. Renault<sup>3</sup>, but the outermost layer does not appear to have differed from the ones below it. No such definite periderm has been described for English roots. In the above

<sup>1</sup> Williamson and Scott, Further Observations, II, Phil. Trans., 1895, p. 694.

<sup>2</sup> loc. cit., Pl. XV, Phot. 5, Pl. XVII, Figs. 7 and 8.

<sup>3</sup> Genre *Astromylon*, Ann. des Sci. Géol., 1885, vol. xvii, Fig. 2, Pl. VII.

quoted memoir<sup>1</sup> the authors draw attention to a section in which the outer layer appeared two cells in thickness, and which 'suggested that we have here a peridermic formation' even although the cells lacked the clear definition of a well-developed periderm.

The object of this note is to place on record what appears to be an undoubted peridermic formation in roots from the lower coal-measures of England, which also show a highly specialized 'epidermoidal layer.' The slides from which the present descriptions and sketches have been taken are S. 4014 and 4015, from the series S. 4013-7, continued in S. 3556-8, in the general collection of the geological department of the British Museum (Nat. Hist.).

The root appears to have had a diameter of about 15 mm., but it is impossible to be quite accurate as the pith is not well preserved, and the stele is somewhat compressed and split by stigmarian rootlets. The preservation of the inner and middle cortex is poor, but there is sufficient evidence of continuity between these layers and the outer cortex, which is crushed against the well-preserved 'epidermoidal layer,' continuous round the root, see Fig. 30.

The individual epidermoidal cells are very large, ranging from .175 to .2 mm. in diameter, and considerably exceeding any other tissue in the root. The outer membrane of each cell is thick, and from it fibrous fragments project into the cell-cavity, Fig. 31; it is not possible to ascertain the minute structure of these fibres, and I am not aware of any similar appearance in recent plants that would throw light on their nature.



X 100.

FIG. 31.

The epidermoidal cells appear to originate as the enlarged outer layer of the periderm, see Fig. 32 A and B, and it seems probable that they took the outermost position with some irregularity, as in most cases the linear arrangement of the periderm cells has been disturbed,

<sup>1</sup> Will. and Scott, *loc. cit.*, Pl. XVII, Fig. 11, and p. 694.

and cells such as *a* in Fig. 32, A are common, where a periderm cell below the outer layer is beginning to take on the epidermoidal characters; this explains the lack of linear continuity between the periderm as such and the outer layer, as the enlarging cell pushes the others to one side. In Fig. 32, B the linear arrangement is not disturbed, and we also get the remains of a layer outside the present functional one.



FIG. 32.

It appears, therefore, that, at least in the English specimens, when periderm formation takes place, the primary epidermoidal layer of the young root is replaced by the specialized outer layer of periderm which is irregularly reinforced from the cells beneath.

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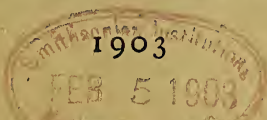
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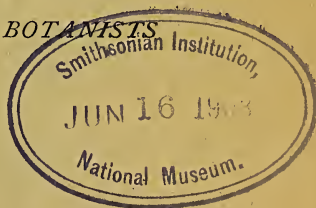
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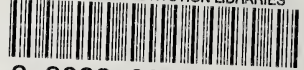








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