

A Contribution to the Study of the Marattiaceae.

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With Plates **XXI** and **XXII** and thirty-three Figures in the Text.

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INTRODUCTION.

JUDGING from the geographical distribution of the modern representatives of the Marattiaceae, it would seem that this group of Ferns occupied a far more prominent position in the flora of the past. The palaeontological record lends support to this hypothesis. Moreover, it has long been recognized that in these Ferns the stelar system has attained to a stage in complexity far in advance of that of any other modern group of Vascular Cryptogams. It is therefore not surprising that these plants have formed the subject of repeated investigations. But many difficulties are encountered whenever an attempt is made to reconcile the statements of previous writers respecting even the more important details of the structure and development of the vascular tissues in this interesting group of Ferns. And it can safely be said that, with the possible exception of *Angiopteris*, there is still not a genus of Marattiaceae of which we possess a complete account.

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For this reason, the opportunity of throwing fresh light on several points which were in dispute, and of adding to our knowledge of the adult sporophyte of the hitherto little-known genus *Danaea*, was welcomed by the present writer, who desires at the outset to express his indebtedness to Dr. S. E. Chandler, F.L.S., for his kindness in supplying him with a large number of plants of *Danaea alata*, Sm., and of *Danaea nodosa*, Sm., which were collected by him during a recent visit to the West Indies.

MATERIAL AND METHODS.

Apart from the complete series of plants of *Danaea alata*, Sm., and of *Danaea nodosa*, Sm., already mentioned, material of *Angiopteris evecta*, Hoffm., *Kaulfussia aesculifolia*, Bl., *Danaea simplicifolia*, Rudge, and of several species of *Marattia*, including a large specimen of *Marattia Cooperi*, Mre., was available for investigation.

In order to facilitate the elucidation of the complicated arrangement of the vascular strands in these ferns, a number of wax models of the vascular tissues were built up. The method described by Farmer and Hill (29, p. 375) was adopted with a few modifications.¹ Although this method is very laborious, it has many advantages, inasmuch as every detail of the complicated branching and anastomosing of the vascular strands, both in the stem and in the leaf-bases of the adult plant, can readily be determined.

For the histological work, a number of stains and reagents, including safranin, Kleinenberg's haematoxylin, eosin, gentian violet, Bismarck brown, iodine, phloroglucin + HCl, chlor-zinc-iodide, KOH, and concentrated H₂SO₄, were employed. Prolonged staining in a saturated alcoholic solution of safranin, followed by rapid staining in Kleinenberg's haematoxylin, was found most satisfactory for demonstrating the presence of an endodermis.

Most of the preparations were mounted in Canada balsam or in glycerine jelly, but a few were mounted in euparal (46, p. 247). Euparal has a low index of refraction ($n = 1.483$), and shows up the endodermis, when present, even in the regions where its histological characters are otherwise difficult to observe.

¹ Owing to their large size and extreme complexity, it was found necessary to strengthen these models (1) by introducing into the wax long pieces of copper wire bent to the required shape, and (2) by giving them several coats of enamel, which, on drying, formed a rigid covering to the wax and effectively prevented its gradual subsidence during hot weather. Electro-plating with copper was found impracticable owing to the uneven deposition of the metal, which resulted in the formation of numerous centres of weakness and did not add materially to the strength of the models whilst greatly increasing their weight.

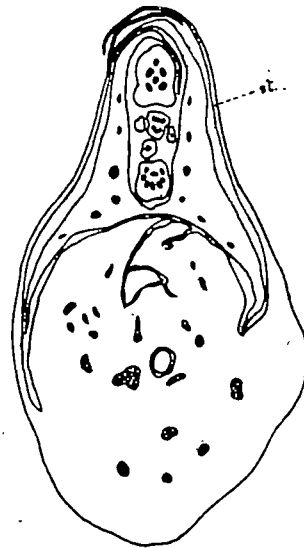
MORPHOLOGY.

I. *Danaea*.

The very young sporophyte of both species of *Danaea* examined by the present writer exhibits a perfectly radial symmetry (Pl. XXI, Fig. 4), the first few leaves being arranged in a rough spiral on the stem, which is relatively elongated as compared with sporelings of *Angiopteris*, *Macroglossum*, or *Marattia*¹ of similar age.

In the case of *Danaea*, we find within the limits of a single genus two distinct trends of organization. Whereas in *Danaea nodosa*, Sm., the radial symmetry is maintained in the adult plant, in *Danaea alata*, Sm., the shoot-apex very soon bends through an angle of approximately 90° (Pl. XXII, Fig. 9, A and B), and continues its growth in the horizontal plane. The stage at which this change in the direction of growth of the shoot takes place varies slightly in different plants, but it always occurs very early. As a result, the adult plant of *Danaea alata* exhibits well-marked dorsiventrality, the leaves, which are simply pinnate, arising from the dorsal and lateral surfaces of the horizontal rhizome, as is shown in Pl. XXI, Fig. 2. Very occasionally, however, a leaf arises from the ventral surface of the rhizome.

All the leaves grow more or less vertically upwards, the bend taking place in the region of the basal pulvinus of the petiole. The roots, which branch freely in a monopodial manner,² arise in no very definite order from all sides of the rhizome, but there is usually one to each leaf of the adult plant. Prominent stipules with distinct commissures occur at the base of the petioles and provide a most efficient means for protecting the growing apex, the stipule of any leaf completely enveloping the next younger leaf whilst the latter is at an early stage in its development (Pl. XXI, Figs. 5 and 6; Text-fig. 1). Moreover, numerous peltate hairs or scales occur on the petiole. It is worthy of note that those Ferns which bear relatively few leaves at a time generally possess highly developed protective devices (e.g. Ophioglossaceae; and cf. Campbell, 20, pp. 191-2).



TEXT-FIG. 1. *Danaea alata*, Sm. Transverse section through the apex of an old plant, showing bud-protection. *st.* = stipule. $\times 4$

¹ The young plants of *Marattia fraxinea*, Sm., investigated by Kühn (42) appear to be exceptional.

² It is difficult to reconcile this fact with Kühn's (43, p. 149) statement that in the case of *Danaea alata* 'die Wurzeln scheinen normal unverzweigt zu sein'.

On the other hand, the adult sporophyte of *Danaea nodosa*, Sm., which is a much larger plant than *Danaea alata*, Sm., has a very different habit. The stem, upon which the leaves are inserted in an irregular spiral, is constructed on a radial plan, but in a few of the specimens examined the axis had assumed an oblique position relatively to the ground-level; the change in the direction of growth of the stem apparently has no effect upon the arrangement and position of the leaves, which adapt themselves to the altered conditions by bending in the region of the basal pulvinus, whilst the long robust roots, which are equally numerous on all sides of the stem and which bear no definite numerical relation to the leaves, grow more or less vertically downwards, branching freely in a monopodial manner, often at a considerable distance from the stem. This gives a curious appearance to the larger specimens of *Danaea nodosa*, such as that represented in Pl. XXII, Fig. 8, the caudex of which had attained a diameter of 4 cm. and a length of more than 40 cm.



TEXT-FIG. 2. *Danaea nodosa*, Sm. Part of the caudex of an adult sporophyte, showing a young adventitious bud (adv. b.). Nat. size.

In this species also, stipules with distinct commissures occur near the base of the petioles.

The stem was unbranched in every specimen examined; what at first sight appeared to be a lateral branch on one of the stems on closer examination proved to be an adventitious bud, which had arisen from one of the old leaf-bases (Text-fig. 2).

This method of vegetative propagation is not uncommon in *Angiopteris* and *Marattia*, and it is a general practice among fern-growers to propagate these two genera by means of their adventitious buds, which are often produced in large numbers (cf. Buchanan, 16; also Hofmeister, 33, p. 255).

Gwynne-Vaughan (30, p. 266) called attention to masses of meristematic tissue which he observed in the leaf-bases of *Archangiopteris* and of *Kaulfussia*, and suggested that they might represent the rudiments of adventitious buds. The present writer has noticed the occurrence of similar masses of meristematic tissue in the leaf-bases of *Kaulfussia* and of two species of *Danaea* (Text-figs. 10, A, and 8, B), but only in the case of *Danaea nodosa* has their ultimate development into leafy shoots been observed.

Vascular Anatomy. Apart from the scanty observations of the earlier botanists (Brongniart, 13, p. 439, Pl. XXXIII, Figs. 2 and 3; Karsten, 40, p. 198, Pl. IX, Fig. 10; Mettenius, 49, p. 524; Kühn, 43, p. 147), practically nothing was known of the arrangement of the vascular strands in the genus *Danaea* until 1902, when Brebner (12) published a full account of the

development of the vascular system in the young sporophyte of *Danaea simplicifolia*, Rudge.

Jeffrey (36) very briefly described the arrangement of the vascular tissues in young stems of *Danaea*, in which he observed a tubular central cylinder interrupted by foliar gaps, and a single medullary strand which fused with the wall of the stelar tube above the foliar gaps. According to this investigator, the medullary strand later develops into a tube or a series of strands; finally, the stelar system is further complicated by the appearance of another series of strands. This arrangement of the vascular strands was compared with that which obtains in *Matonia*.

In his monograph on the Psaronieae and Marattiaceae, Rudolph (51) described the course of the vascular strands in a small piece of an old stem of an unidentified species of *Danaea* from Brazil. This stem showed a radial organization, but unfortunately the lower portion was missing. A series of outline drawings of transverse sections of this stem, in which the individual bundles were numbered (l. c., Taf. III, Figs. 5-14, 16), illustrated the description; such a method, however, is most unsatisfactory because the extreme complexity of the structures concerned leads to confusion in the mind of the reader.

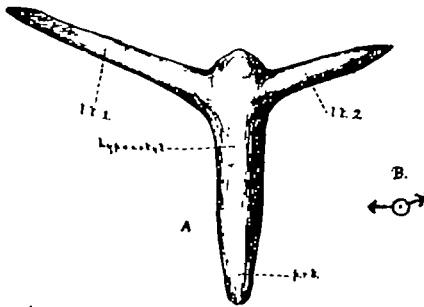
Campbell (20) has recently published a critical study of the development and arrangement of the stelar tissues in three species of *Danaea* (*D. jamaicensis*, *D. Fenmani*, and *D. elliptica*). This botanist puts forward the view that the stele of the very young sporeling consists of a sympodium of leaf-traces which below merge insensibly into the diarch primary root, and suggests that in these young sporelings there is no stem in the strict sense. Only a passing reference is made to the vascular anatomy of the adult plant, which, apart from an increase in the number of leaf-traces and commissural strands, is assumed to be essentially similar to that of the young plant (l. c., p. 175).

Thus, it is evident that no satisfactory account of the stelar anatomy of the adult sporophyte of *Danaea* has yet been published. Since this is the only genus of Marattiaceae at present known which includes both radial and dorsiventral species, it seemed that a comparative study of the development and arrangement of the stelar tissues in *Danaea alata* and *Danaea nodosa* respectively might yield both useful and interesting results. With this end in view, three wax models (Text-figs. 3 and 4, A; Pl. XXI, Fig. 1 A), showing clearly the transition from the simple stelar system of the young sporeling to the highly complex arrangement of vascular strands in the adult plant, were built up.¹ These models, although constructed from three plants, form what is practically a continuous scheme of the stelar system in the rhizome of *Danaea alata*, Sm., and for this reason the following description of the vascular anatomy of the genus *Danaea* is mainly

¹ Unfortunately the actual specimens from which these models were built up were not sketched before being cut up; however, Pl. XXI, Fig. 2, and Pl. XXII, Fig. 9 B, respectively represent plants of about the same age as those from which the two larger models were made.

based upon a study of these models. But, owing to the difficulty of manipulating thin layers of wax of uneven thickness with any degree of accuracy, the curvature of the basal portion of the adult rhizome is not represented in the large model (Pl. XXI, Fig. 1A). For a similar reason, the slight curvature of the apex of the small rhizome, which was about to assume its horizontal growth, is not shown in the model represented in Text-figs. 4, A, and 5.

Danaea alata, Sm. The present writer's observations on the development of the vascular tissues in a large number of very young sporelings of *Danaea* for the most part confirm the account given by Campbell (20) as regards this genus. The vascular strand of the embryo plant is formed



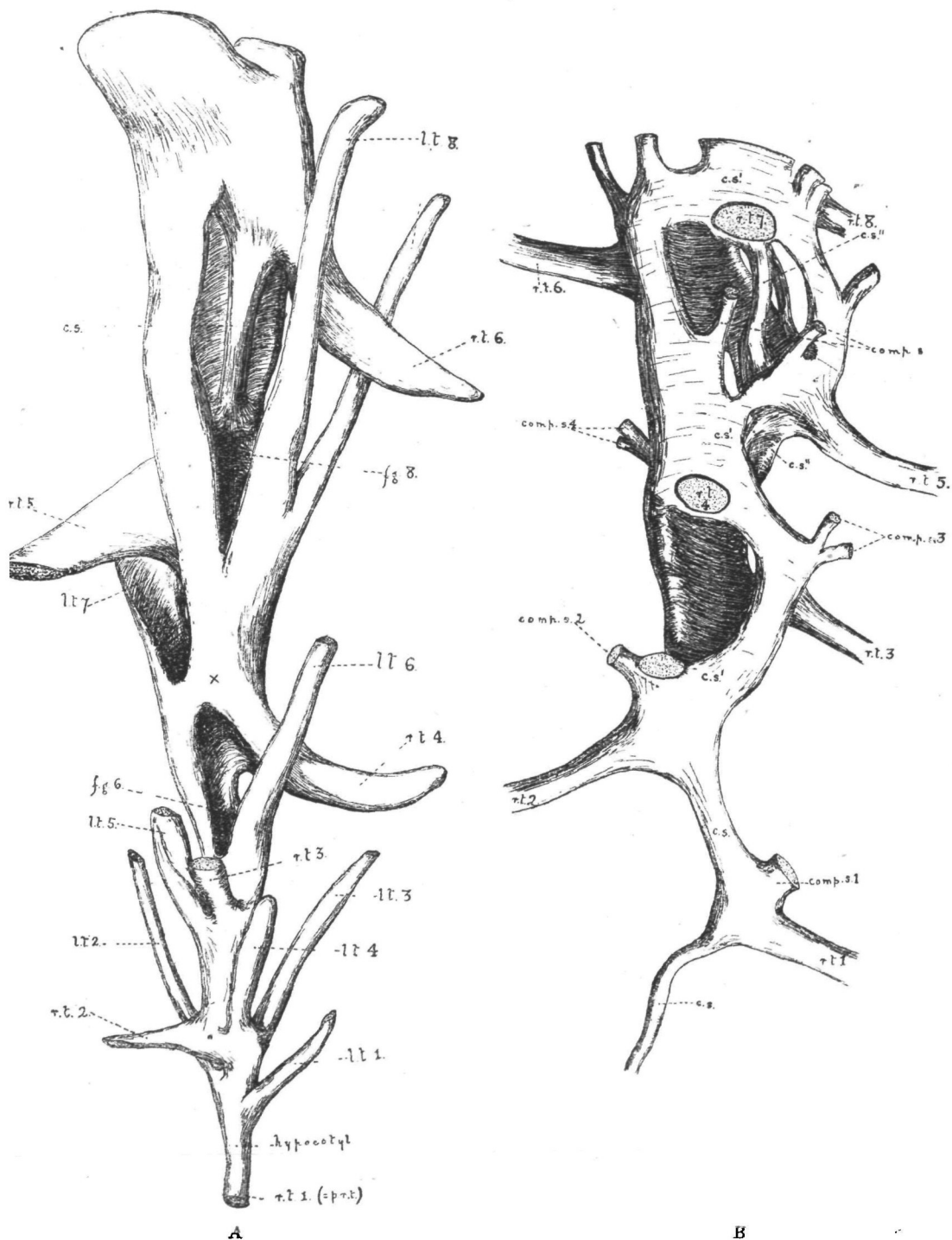
TEXT-FIG. 3. A. *Danaea alata*, Sm. Model of the stelar system of a very young sporeling. Side view. Lt. 1, Lt. 2, leaf-traces. B. Diagram showing divergence of the first two leaves.

very early, being first differentiated in the cotyledon; tracheides make their first appearance at the junction of cotyledon and primary root, and from thence the development of the tracheides works upwards and downwards until a simple vascular strand, continuous from the tip of the cotyledon to the apex of the primary root, is produced. The trace of the second leaf, which arises nearly opposite the cotyledon (Text-fig. 3, B), unites with the primary vascular strand in the so-called hypocotyledonary region.

As Campbell (20) rightly points out, the strands belonging to the first two leaves of the young sporophyte are quite distinct in this region, being separated from one another by a very irregular layer of small parenchymatous cells. Lower down, however, they appear to form a single more or less oval strand (as seen in transverse section) which merges insensibly into the diarch bundle of the primary root. A model of the vascular system of a young plant which had attained to approximately this stage of development is represented in Text-fig. 3, A. It will be noticed that there is as yet no sign of a second root.

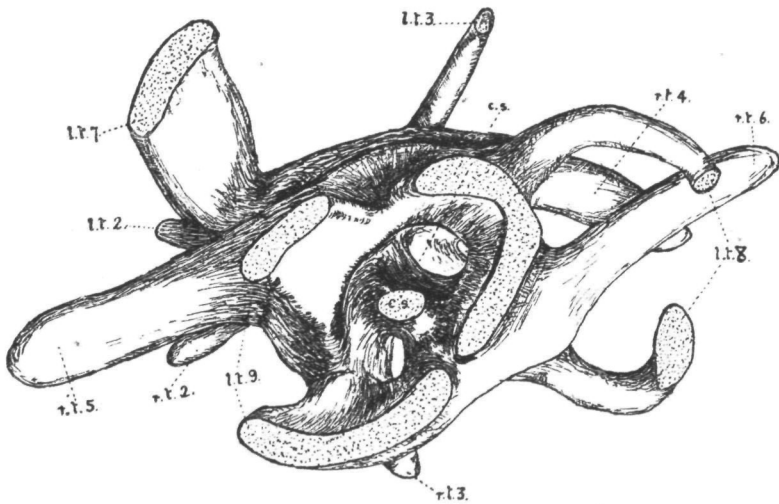
Text-figs. 4, A, and 5 represent a model of the stelar system of a rather older sporophyte which had developed eight leaves. Traced downwards, the simple traces belonging to the third and fourth leaves (Text-fig. 4, A, Lt. 3 and Lt. 4) gradually approach and finally coalesce, and still farther down join the trace of the second leaf close to its union with the vascular strand of the first leaf or cotyledon. The trace of the first adventitious root (Text-fig. 4, A, r.t. 2) joins the stem-stele¹ near the point where the traces of the third and fourth leaves become united. Thus, in the young

¹ The convenient descriptive term 'stem-stele' is here employed for the common vascular tissue produced by the close association or union of the earlier leaf- and root-traces.



TEXT-FIG. 4. A. Model of the stelar system of the rhizome of a young sporophyte of *Danasa alata*, Sm., viewed from below. B. Model of the internal stelar system of the rhizome of an old sporophyte of *Danasa alata*, Sm., viewed from above. *c.s.*, commissural strand; *c.s'*, internal stelar system arising out of the commissural strand; *c.s''*, commissural strand of the internal stelar system; *comp.s.*, compensating strand; *f.g.*, foliar gap; *lt.*, leaf-trace; *p.r.t.*, trace of the primary root; *r.t.*, root-trace.

sporophyte of *Danaea*, the stelar system is not complicated so early by the influence of the adventitious roots as in the case of *Angiopteris*, in which the first adventitious root is given off nearly opposite the first leaf (cf. Farmer and Hill, 29, Pl. XVI, Fig. 1, with Text-fig. 3, A, of the present paper). In a similar way the simple traces of the fifth and sixth leaves (Text-fig. 4, A, *lt.* 5 and *lt.* 6) traced downwards appear to approach one another and ultimately enter into close association, giving rise to a single strand, which is more or less crescent-shaped in section. This strand at a still lower level becomes united with the fused traces of leaves 3 and 4. The trace of the third root joins the stem-stele close to the point of fusion of the traces of the fifth and sixth leaves.



TEXT-FIG. 5. *Danaea alata*, Sm. Front view of the model represented in Text-fig. 4, A. *c.s.*, commissural strand; *lt.*, leaf-trace; *rt.*, root-trace.

Up to this point, the description of the earlier stages in the development of the vascular system in the genus *Danaea* as given by Campbell (20, p. 174) so closely agrees with the arrangement of the bundles as I have found them in the species studied by me, that I cannot do better than quote his summary word for word:

‘The vascular system in the young sporophyte of *Danaea* begins as a single axial strand, which is continuous through the cotyledon and root. At a very early period a second vascular bundle or stele is formed in the second leaf connecting with the primary strand, and this is followed by a similar single strand or stele in each succeeding leaf, up to about the seventh. Up to this time, except for the steles of the secondary roots, the whole vascular system is built up of united leaf-traces and there is no cauline bundle in the strict sense of the word, although we may speak of the bundle, or stele of the stem, as soon as there is a solid central strand formed below

the junction of the earlier leaf-traces. This primary stele never has the form of a true protostele, however, as the xylems belonging to the separate leaf-traces can be recognized and the compound nature of this central bundle is unmistakable.

It has already been pointed out that the sporeling of *Danaea alata* is radial in structure; correlated with this fact, we find that the sympodium of leaf- and root-traces which together make up the vascular system of the young sporophyte is likewise based on a radial plan, the traces of the first few leaves being arranged in a rough spiral.

It may be noted in passing that the vascular tissue of the embryo plant of other megaphyllous Vascular Cryptogams (e. g. Ophioglossaceae, *Isoëtes*) may consist solely of a system of leaf- and root-traces, hence it is not surprising that a similar condition should obtain in the remarkable megaphyllous Marattiacean Ferns.

A distinct leaf-gap is formed by the trace of the sixth leaf, above the point of insertion of which the stem-stele is definitely crescentic in transverse section. Campbell(20) maintains that the stem-stele in this region still consists solely of leaf- and root-traces, but the present writer is of the opinion that part, at least, of the vascular tissue of the 'siphonostele' with large leaf-gaps (cf. Text-fig. 4, A) which marks the next stage in the elaboration of the stelar system of *Danaea*, is made up of elements which have a truly cauline origin and serve to connect up adjacent leaf-traces.

A root-trace (Text-fig. 4, A, r.t. 4) joins the stelar cylinder above the gap formed by the trace of the sixth leaf; in this region the siphonostele forms a complete cylinder (= solenostele) uninterrupted by leaf-gaps (the region indicated by a x in Text-fig. 4, A). The first commissural strand arises by proliferation of the vascular tissues on the inner surface of the stelar tube opposite the point where the trace of root 4 joins the stem-stele (above leaf-gap 6 in Text-fig. 4, A); considered from the point of view of water-conduction, this strand forms a direct continuation of the root-trace. Traced upwards, this strand passes across the medullary ground-tissue from the upper end of one leaf-gap to the apex of the next leaf-gap above, which it helps to close, and since, generally speaking, a root-trace joins the outer surface of the stem-stele at these points, the commissural strand at first forms an auxiliary internal conducting system of cauline origin, which continues to connect up the points of insertion of the relatively large and important root-traces. During these earlier stages, the commissural strand obviously fills a relatively subordinate position, as compared with the main-stelar cylinder, but, as Brebner (12, p. 536) rightly pointed out, the special advantage of such an arrangement is obvious, since any root probably does not reach the soil until after the related leaf has unfolded.

Now, whereas the trace of the seventh leaf consists of a single strap-shaped strand which splits into two whilst still within the stem-cortex, the

eighth leaf-trace dichotomizes near its base (Text-fig. 4, A, *l.t.* 8), whilst the traces of later leaves depart as two distinct strands, which, instead of arising from the base of the gap, as in the case of the single trace of the earlier leaves, arise from the sides of the gap, usually at different levels (Pl. XXI, Fig. 1 A, *l.t.* 1-4). Further branching and occasional anastomosing of the strands of the leaf-trace occur in the cortex of the stem.

The siphonostelic condition is maintained for a short time only; sooner or later, owing to the crowding of the spirally arranged leaf-traces, the gap above one leaf-trace fails to be repaired till after the exit of the trace of the next leaf; in this way a simple dictyostele is produced (Pl. XXI, Fig. 1 A).

The change in the direction of growth, to which reference has already been made, takes place in the specimen under discussion at the level of the apex of the gap made by the departure of the traces of the third leaf represented in the large model; this region is indicated in Pl. XXI, Fig. 1 A, by the two arrows.

Correlated with the change in the direction of growth there is an important difference in the organization of the vascular tissues, the radial configuration of the stem-stele being replaced by one in which dorsiventrality is well marked. This change is indicated at an early date by the formation of a large gap (*v.g.* in Pl. XXI, Fig. 1 A) in a position where one would expect to find a gap formed by the departure of the traces of leaf 5. However, the traces of this leaf, instead of continuing the spiral in which the earlier leaf-traces are arranged, depart from the stem-stele at a point almost opposite the exit of the preceding leaf-trace. In this connexion it is interesting to find that the commissural strand, after leaving the inner surface of the vascular cylinder above the gap of leaf 4, *takes a sharp bend* (indicated by a \times in Pl. XXI, Fig. 1 A) *towards the upper end of this large ventral gap* before continuing its course towards the apex of the next leaf-gap above (*i. e.* the gap made by the departure of the traces of the fifth leaf), which it helps to close. A root-trace (Pl. XXI, Fig. 1 A, *r.t.* 1) fuses with this commissural strand immediately below the point where the latter joins the inner surface of the stelar cylinder.

The stem, meanwhile, steadily increases in diameter, the dictyostele opening out to a corresponding degree; at about this stage the latter becomes fractionated, perforations, other than leaf-gaps, occurring in the stelar cylinder.

On the dorsal and lateral surfaces of the dictyostele the leaf-traces become more crowded and more complex, frequently leaving the stem-stele as six or more separate strands, among which the two main laterals can readily be recognized by their stronger development (*cf.* Farmer and Hill, 29, p. 378). The strands of the leaf-trace depart from the basal and lateral margins of the foliar gaps, anastomosing at irregular intervals with the strands which can still be regarded as belonging to the original dictyostele

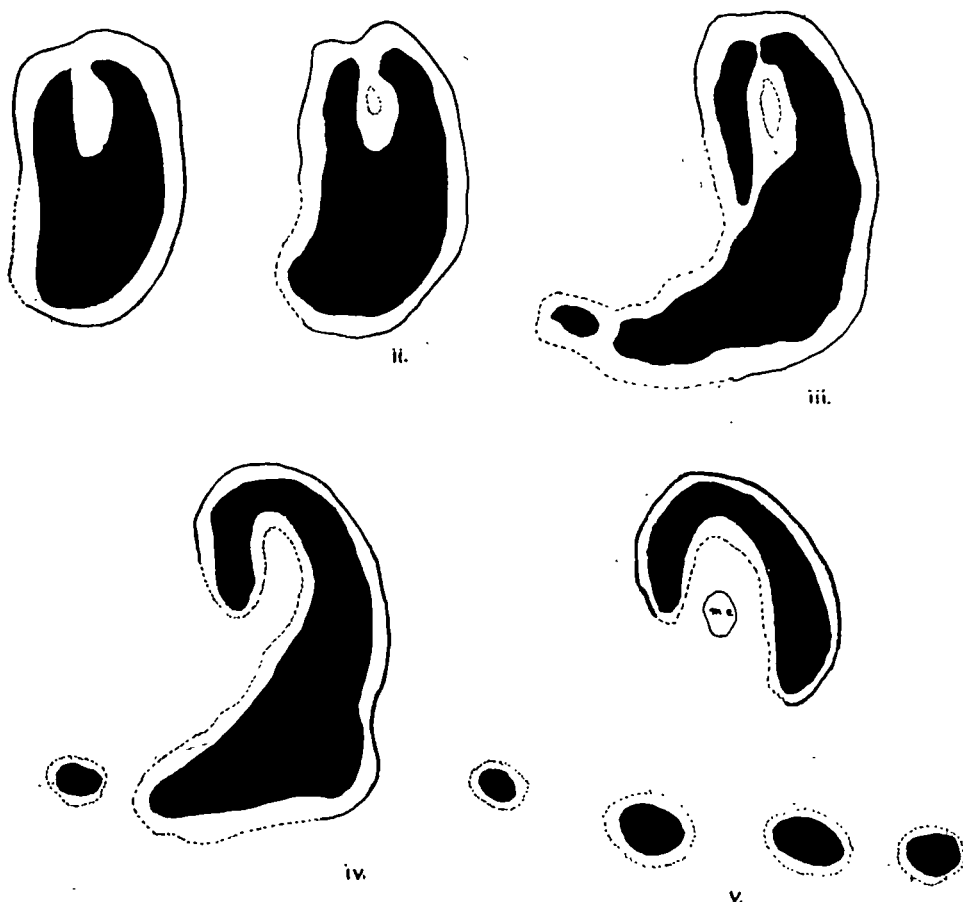
as well as with one another. On the other hand, in accordance with its dorsiventral organization, only a single weakly developed leaf-trace (i. e. *Lt.* 8 in Pl. XXI, Fig. 1 A, and Pl. XXII, Fig. 7) takes its origin from the ventral surface of the stem-stele, although a number of large diamond-shaped gaps, closely resembling leaf-gaps, occur in this part of the stele.

In *Danaea* the *internal* vascular cylinder arises by the gradual elaboration of the original commissural strand. In its development the internal vascular system passes through a series of stages strictly analogous to those of the original vascular cylinder. For comparison, Text-figs. 4, A and 4, B, which represent respectively a model of the stelar system of the rhizome of a young sporophyte of *Danaea alata* and a model of the *internal* stelar system of the rhizome of an adult plant of the same species, are placed side by side.

It has already been stated that the commissural strand (Fig. 1, A, *c.s.*) at first consists of a small solid vascular bundle which pursues a somewhat zigzag course through the medullary ground-tissue, fusing with the main stelar system at the apex of the leaf-gaps, which it helps to close; in other words, this commissural strand itself functions as a compensating (*Ersatz*) strand. Traced upwards, this strand rapidly gains in importance, and instead of fusing directly with the outer stelar cylinder at the apex of the leaf-gap (i. e. the gap made by the departure of *Lt.* 5 in Pl. XXI, Fig. 1 A), it gives off a branch (Text-fig. 4, B, *comp.s.* 1) which functions as the compensating strand. The commissural strand then crosses over towards the upper end of the next leaf-gap above; meanwhile, the number of its vascular elements are considerably augmented by the addition of those of a root-trace (Text-fig. 4, B, *r.t.* 2) which passes through this foliar gap and fuses with the commissural strand. In this way a large solid mass of vascular tissue, more or less oval in transverse section, is produced. A short massive compensating strand (Text-fig. 4, B, *comp.s.* 2) leaves this vascular mass and, anastomosing right and left with bundles of the external cylinder, assists in closing the gap formed by the exit of the meshed segment, which at this stage constitutes the leaf-trace. The departure of this compensating strand produces a distinct gap, comparable with a leaf-gap, in the central stelar system, which now opens out to form an incomplete cylinder of vascular tissue. Text-fig. 6, i-v, represents a successive, but not consecutive, series of transverse sections of this transitional region (indicated by a \times in Pl. XXI, Fig. 1 A); it is seen that a well-marked 'pocket' is produced, at first phloem (Text-fig. 6, i) and then characteristic ground-tissue parenchyma (Text-fig. 6, ii, iii) appearing in the centre of the xylem core.

The subsequent stages in the development of the internal stelar system proceed along lines essentially similar to those of the original solenostele; in brief, the *internal* vascular cylinder, thus inaugurated, increases in size *pari passu* with the widening of the outer cylinder and of

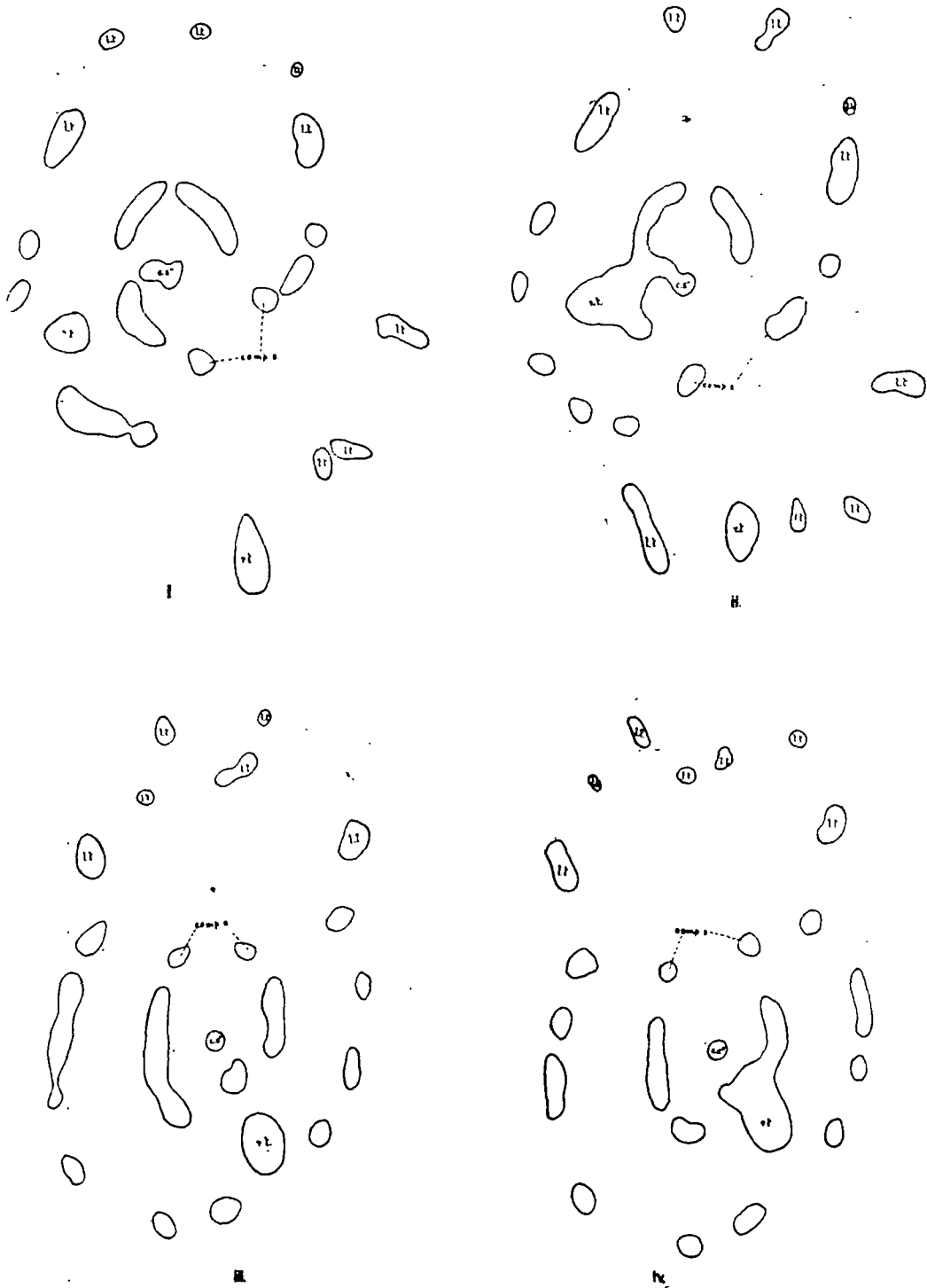
the stem, further complications resulting from the increasing importance and crowding of the compensating strands. Sooner or later, the gap above one compensating strand fails to be repaired until after the exit of the next, with the result that the internal vascular cylinder becomes broken up into a typical dictyostele, or, more strictly speaking, a 'perforated' dictyostele (cf. Tansley, 64, p. 65), since a few relatively small



TEXT-FIG. 6. i-v. *Danaea alata*, Sm. The diagrammatic figures illustrate in successive, but not consecutive, transverse sections the changes that occur in the internal vascular system of the rhizome of an adult plant at the transitional region (marked by a \times in Fig. 1 A, Plate XXI). The smooth contours denote the endodermis, while the dotted contours mark the outer limits of the phloem. The shaded areas = xylem. *m.c.*, mucilage canal.

gaps, other than those formed by the departure of the compensating strands, occur in the internal cylinder.

An interesting parallel may also be drawn between the leaf-traces and the compensating strands, which respectively pass through an ontogenetic series of stages starting with a simple single strand, passing through



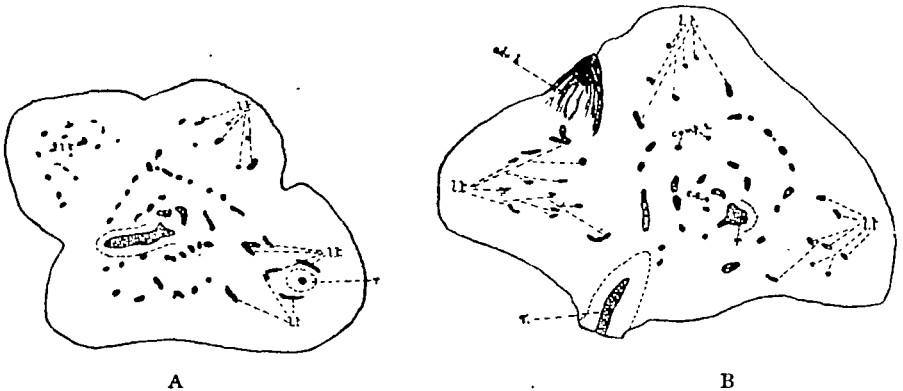
TEXT-FIG. 7. i-iv. *Danaea alata*, Sm. Diagrams illustrating transverse sections of the rhizome of an old plant at successively higher levels. They are in fairly close sequence, but are not consecutive. The contours mark the outer limits of the phloem. *cs.*, commissural strand of the internal stelar system; *comp.s.*, compensating strand; *l.t.*, leaf-trace; *r.t.*, root-trace.

an intermediate condition where the strand forks near its base, and ending with two independent strands which originate, not from the base, but from the lateral margins of their respective gaps (Text-fig. 4, A and B).

The root-traces are inserted directly upon the outer surface of the *internal* vascular cylinder of the stem (Text-fig. 4, B).

Eventually a commissural strand (Text-fig. 4, B, *c.s.*) is differentiated from the inner surface of the internal stelar system, to which it bears exactly the same relation as the original commissural strand (Text-fig. 4, A, *c.s.*) does to the external stelar system.

In the specimen of *Danaea alata* under discussion, the commissural strand of the internal stelar system leaves the inner surface of the cylinder near the insertion of a root-trace (Text-fig. 4, B, *r.t.* 4), and above the gap formed by the exit of a compensating strand (Text-fig. 4, B, *comp.s.* 2)



TEXT-FIG. 8. A and B. *Danaea nodosa*, Sm. Transverse sections of the stem of a large plant, showing three concentric zones of bundles and a central strand. *adv.b.*, adventitious bud; *c.s.*, commissural strand; *comp.s.*, compensating strand; *l.t.*, leaf-trace; *r*, root.

passes slowly across the central ground-tissue to the point of insertion of the next root-trace (Text-fig. 4, B, *r.t.* 5) above the gap of the next compensating strand (Text-fig. 4, B, *comp.s.* 3), and thus forms an accessory conducting system, which serves to connect up the points of insertion of the root-traces. Further complications arise later by the branching and anastomosing of the original commissural strand of the internal stelar system and by the appearance of a second strand, whilst weak commissures are differentiated across the central ground-tissue and serve to join up the two main commissural strands.

Even in the largest specimens of *Danaea alata* and of *Danaea nodosa* examined by the present writer, no distinct third vascular *cylinder* was present, the innermost stelar system (if we are entitled to designate it as such) consisting only of a few weakly developed anastomosing and branching commissural strands (Text-fig. 8, A and B).

Danaea nodosa, Sm.

In its development, the stelar system of *Danaea nodosa* passes through a series of stages in elaboration identical with those described above for *Danaea alata*, while the stele of the adult rhizome differs from that of *Danaea alata* only in its larger proportions and perfectly radial symmetry, the leaf- and root-traces being given off equally all round the stem-stele; a detailed description of the structure and development of the vascular system of *Danaea nodosa* is therefore unnecessary.

However, an examination of the vascular anatomy of an ill-nourished adult specimen yielded interesting results. Judging from its slender elongated rhizome, on which definite internodes could be distinguished, this specimen had fallen upon evil days.

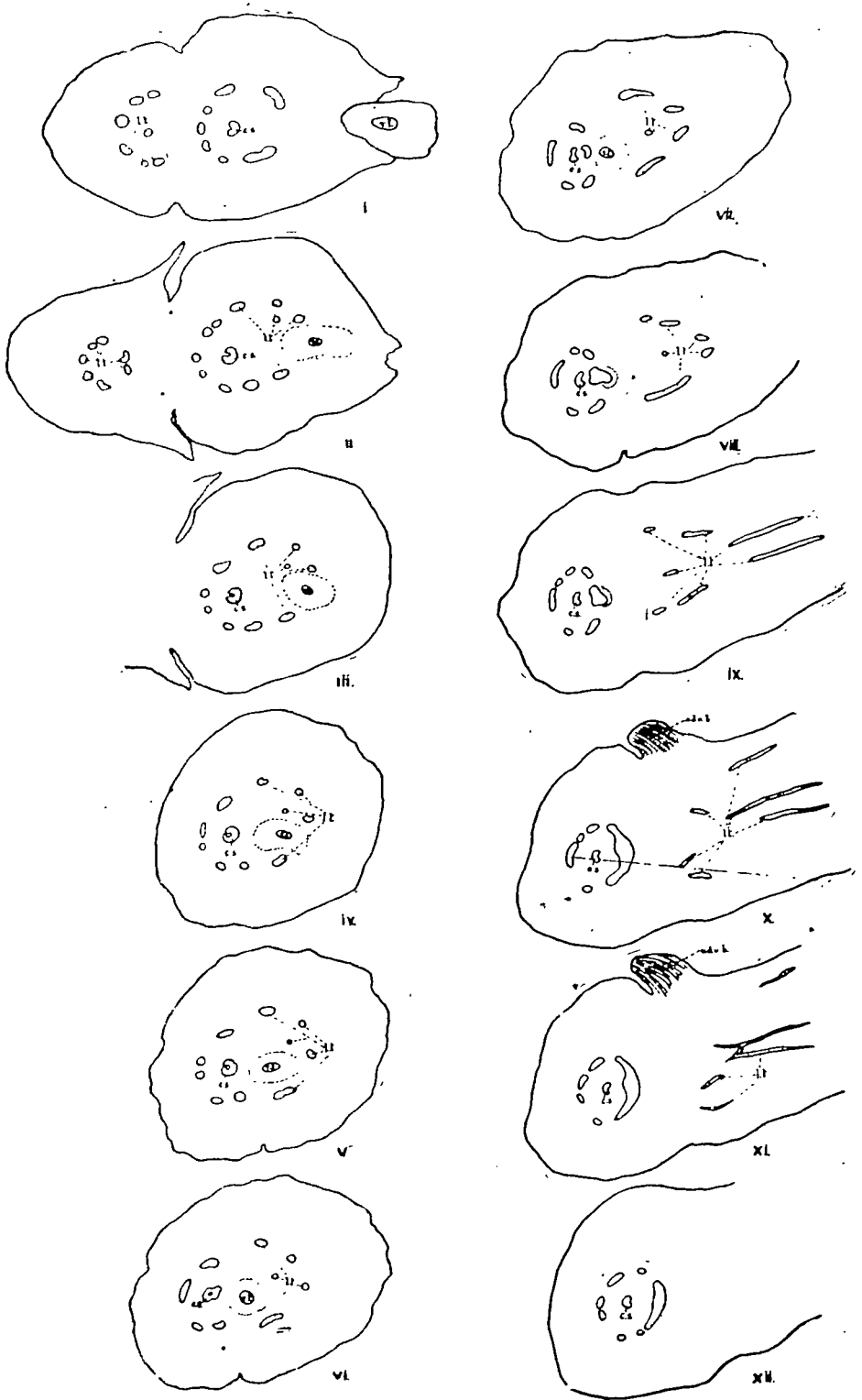
The stele of this rhizome consisted of an outer network of vascular strands enclosing a ground-tissue parenchyma which was traversed by a single strongly developed commissural strand (Text-figs. 9, i, and 14, A). The leaf-traces, which are made up of several (4-6) strands, pass off from this outer network of bundles leaving large foliar gaps. But since the insertions of the spirally arranged leaves are widely separated from one another, the foliar gaps seldom overlap. In the internodes the commissural strand opens out into a solenostele (Text-fig. 9, ii-vi) and below each leaf-gap in turn branches into two almost equal parts, one of which functions as a compensating strand, joining on to the strands bounding the leaf-gap and closing it in front, whilst the other passes slowly across the central parenchyma towards the next leaf-gap above, where the same sequence of events is repeated.

A root-trace usually joins the commissural strand in the internodal region and plays an important part in the formation of the solenostele, but sometimes the root-trace joins the outer lattice-work of bundles at the point where the compensating strand fuses with the main vascular cylinder, as is shown in Text-fig. 9, viii-x.

Thus we find that the stem of this ill-nourished adult sporophyte of *Danaea nodosa* not only approximates in size to that of the sporeling, but it permanently retains a type of stelar organization which marks only a passing phase in the development of the vascular system of the normal sporophyte (cf. Lang, 44, p. 51).

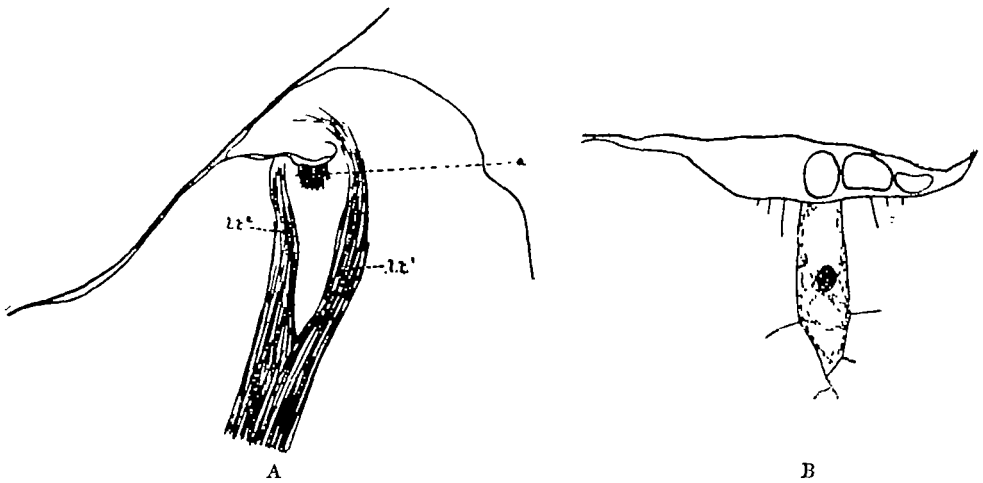
It is possible that the ontogenetic evolution of the stelar system is here arrested at an earlier phase than usual, the requirements of the plant having become simpler.

Adventitious Buds. In *Danaea nodosa*, Sm., adventitious buds arise from a group of meristematic cells situated at the extreme base of, and towards one side of the swollen leaf-base of the parent plant (Text-figs. 8, B, and 10, A). It has already been pointed out by Lang (45, p. 7c6) that



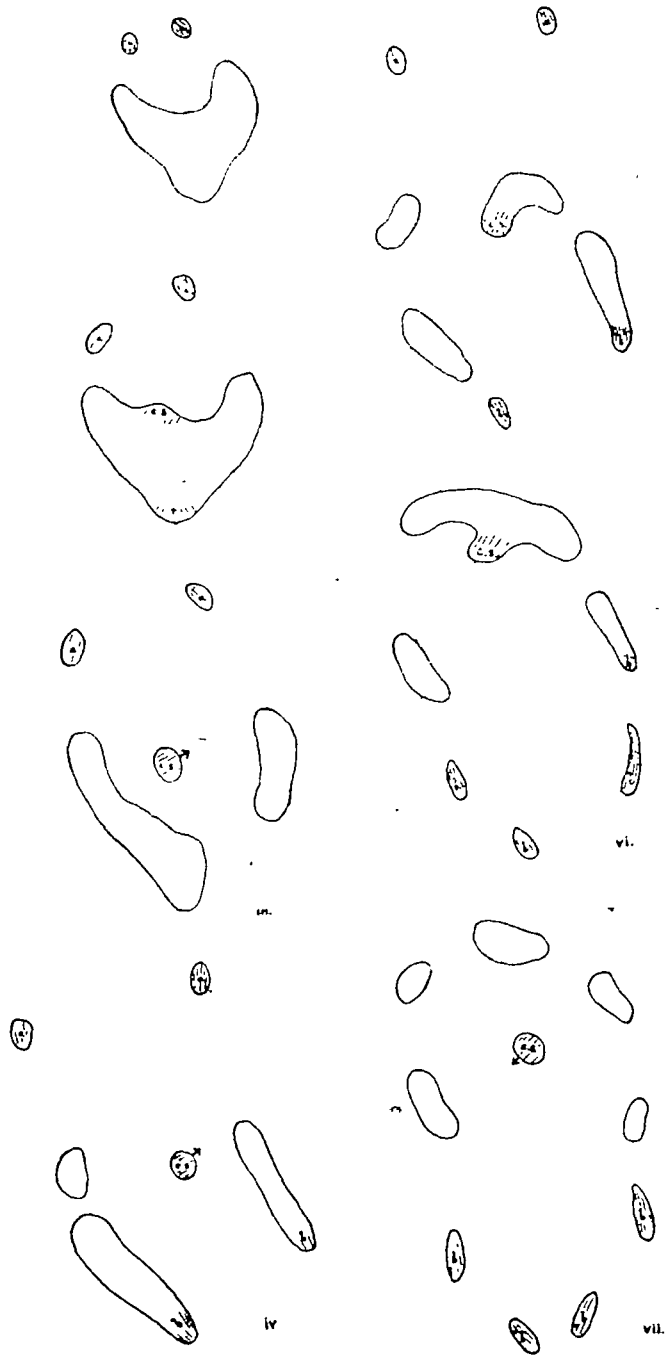
TEXT-FIG. 9. i-xii. *Danaea nodosa*, Sm. These diagrammatic figures illustrate in successive, but not consecutive, transverse sections the changes and rearrangements that take place in the vascular system of an ill-nourished adult rhizome. For description see text. *adv.b.*, adventitious bud; *c.s.*, commissural strand; *l.t.*, leaf-trace; *r.t.*, root-trace. $\times 3$.

vegetatively produced plants tend in their development to pass through stages in elaboration similar to young plants which take their origin from a zygote (cf. Jones, 37, p. 27). This statement also holds good for the adventitiously produced plants of *Danaea nodosa*. At the apex of the stem of the adventitious bud there is a single elongated initial cell, similar in every respect to that found at the stem-apex of the sporophyte (cf. Text-fig. 10, B, with Text-figs. 20, B, and 21, B). Moreover, the second leaf of the adventitious bud is formed almost exactly opposite to the first leaf (cf. Text-fig. 10, A, with Text-fig. 3, B). Not only does the adventitious bud actually arise upon the basal pulvinus of the petiole (although very close to the stem), but its vascular supply is derived directly from one of the foliar traces (Text-fig. 8, B); it cannot therefore be regarded as a *branch* of the parent stem.



TEXT-FIG. 10. A. Median longitudinal section through the apex of an adventitious bud of *Danaea nodosa*, Sm. a., apical cell of the stem; lt.¹, lt.², traces of the first and second leaves respectively. × 8. B. Apical cell of same more highly magnified. × 360.

Vascular Anatomy. In the vegetatively produced plant the vascular tissue differs in its origin from that of the sexually produced plant, inasmuch as it arises as a simple strand from one of the numerous leaf-traces of the parent plant; also, the earlier stages are hurried over or absent altogether, a fact which may be correlated with the relatively greater importance of the first leaf of the adventitious bud and with the early development of the commissural strand. Otherwise the stages in the elaboration of the stelar system are almost identical with those described above for the sporophyte. The protostele at once becomes crescentic after the departure of the first leaf-trace; the latter departs from the stem-stele as two strands which branch whilst still within the cortex of the stem. The trace of the first root fuses with the stem-stele opposite the point of departure of the first leaf-trace, whilst immediately above this point the commissural strand (Text-fig. 11, c.s.) arises by proliferation of the vascular tissues. A relatively



TEXT-FIG. 11. i-vii. *Danaea nodosa*, Sm. The diagrams illustrate transverse sections of a hand-cut series of an adventitious bud at successively higher levels. They are in fairly close sequence, but are not consecutive. The contours mark the outer limits of the phloem. *a*, meristele of first leaf-trace; *b*, meristele of second leaf-trace; *c s.*, commissural strand; *r*, root.

large leaf-gap is formed by the departure of the trace of the second leaf from the convexity of the crescent-shaped stem-stele; this leaf-trace consists of four strands which pass off at various levels from the margins of the foliar gap. (Text-fig. 11, v-vii). The stem-meristeles meanwhile branch and anastomose, and the commissural strand pursues a roughly spiral course through the central ground-tissue, fusing with the stem-meristeles above the foliar gaps. In this way, then, the protostele becomes directly transformed into a typical dictyostele without the intervention of a solenostelic stage. The subsequent stages are essentially similar to those described by Brebner (12) for the sporeling of *Danaea simplicifolia*, Rudge, and by the present writer for the young sporophyte of *Danaea nodosa*, Sm., the radial symmetry being retained throughout.

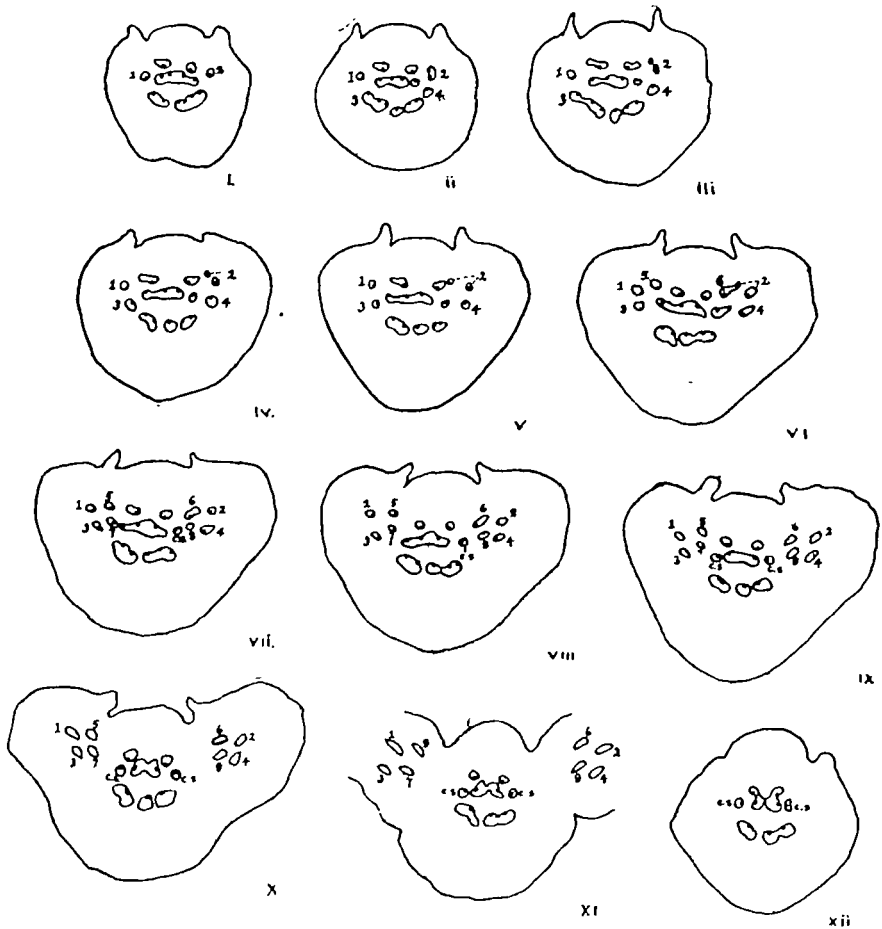
Vascular Anatomy of the Petiole of the Adult Sporophyte. The leaf-trace,¹ both in *Danaea alata* and in *Danaea nodosa*, is made up of an abaxial arc of several strands and of adaxial wings derived from the two strong lateral strands which generally branch two or three times whilst still within the cortex of the stem (Pl. XXI, Fig. 1, A). No strands from the inner cylinder contribute directly to the leaf-trace, but a varying number of internal accessory strands, similar in every respect to those described by Gwynne-Vaughan (30) for *Kaulfussia* and for *Archangiopteris*, arise from the strands of the abaxial arc near the base of the petiole, travel across the ground-tissue, and unite with the terminal strands of the primary ring. The presence of these so-called internal strands of the leaf-trace is a very characteristic feature of this group of Ferns. Above the region of the basal pulvinus the strands of the horseshoe curve anastomose repeatedly; sometimes the terminal (i. e. adaxial) strands fuse together to form a single large strand with adaxially directed protoxylem groups (Text-fig. 12, i-ix).

The vascular supply of the pinnae is interesting, but since a considerable variation in the number and shape of the vascular strands was found among the specimens examined, two typical cases are described in some detail below.

Case I. The arrangement of the strands represented in Text-fig. 12, i, was found a short distance below the point of insertion of the lowermost pinnae. Each leaflet of the lowermost pair receives four strands; three of these (numbered 1, 3, 5 and 2, 4, 6 respectively) proceed from the flank of the horseshoe curve, while the fourth (numbered 7 and 8 respectively) arises from the edge of the large strand which is formed by the fusion of the terminal (i. e. adaxial) strands of the petiolar curve with the internal accessory strands of the basal pulvinus. Occasional branchings and anastomosing occur in these pinna-traces (Text-fig. 12, ii-viii). Branches arising

¹ For a brief, but comprehensive, summary of previous work on this subject consult Tansley, A. G.: *Evolution of the Filicinean Vascular System*. Reprint from *New Phytologist*, vols. vi and vii, 1907-8.

from the ends of the large terminal strand (Text-fig. 12, vii-xii, *c.s.*) assist in repairing the gaps made in the petiolar curve by the departure from its flanks of strands 1, 3, 5 and 2, 4, 6 respectively, and their function is therefore strictly analogous to that of the compensating (= *Ersatz*) strands in the stem-stele. Finally, the terminal strand divides into two, the



TEXT-FIG. 12. i-xii. *Danaea alata*, Sm. The figures illustrate in successive, but not consecutive, transverse sections the changes and rearrangements that occur in the vascular strands of the rachis, including the region of the lowermost pinnae. The position of the protoxylem groups is denoted by the black areas. *c.s.*, compensating strand. $\times 6$. For description see text.

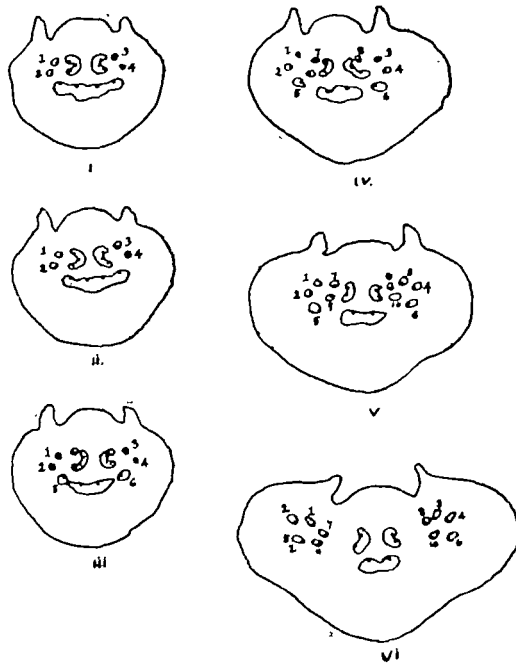
respective halves fusing with the two adaxial strands of the curve, as shown in Text-fig. 12, x-xii. The petiolar curve at a level immediately above the point of insertion of the lowermost pair of pinnae is represented in Text-fig. 12, xii.

³ *Case-II.* In the second case the arrangement of the petiolar strands at a level immediately below the point of insertion of the lowermost leaf-

lets is essentially similar to that described above, except that in this case the terminal strands of the curve do not fuse to form a single strap-shaped strand (Text-fig. 13, i). Five strands pass to each leaflet, viz. four strands (numbered 1, 2, 5, 7 and 3, 4, 6, 8 respectively in Text-fig. 13) from each flank of the horseshoe curve and a strand (numbered 9 and 10 respectively) from the incurved end of each of the terminal (i. e. adaxial) strands. It will be noticed that in this case no compensating strands are produced; the arrangement of the strands of the petiole at a short distance above the point of insertion of the pinna-traces is shown in Text-fig. 13, vi.

Thus it would appear that the vascular supply of the pinnae is based on the same lines in every genus of Marattiaceae in which this point has been investigated (cf. Gwynne-Vaughan, 30, p. 262 et seq.).

Several pulvinoid swellings or 'nodes' are normally present on the petioles of adult plants of *Danaea alata* and *Danaea nodosa*. These structures have been interpreted as representing the position of abortive pinnae (cf. Brebner, 12, p. 537), but this interpretation has up to the present been based on poor evidence. In the course of the above investigation, however, a single case was noticed where a rudimentary vascular strand left the main petiolar curve on one side only in the region of one of these nodes. This strand soon petered out, ending blindly in the parenchymatous ground-tissue of the petiole.



TEXT-FIG. 13. i-vi. *Danaea alata*, Sm. The figures illustrate in successive, but not consecutive, transverse sections the changes and rearrangements that occur in the vascular strands of the rachis below the point of attachment of the lowermost pinnae. The position of the protoxylem groups is denoted by the black areas. $\times 6$. For description see text.

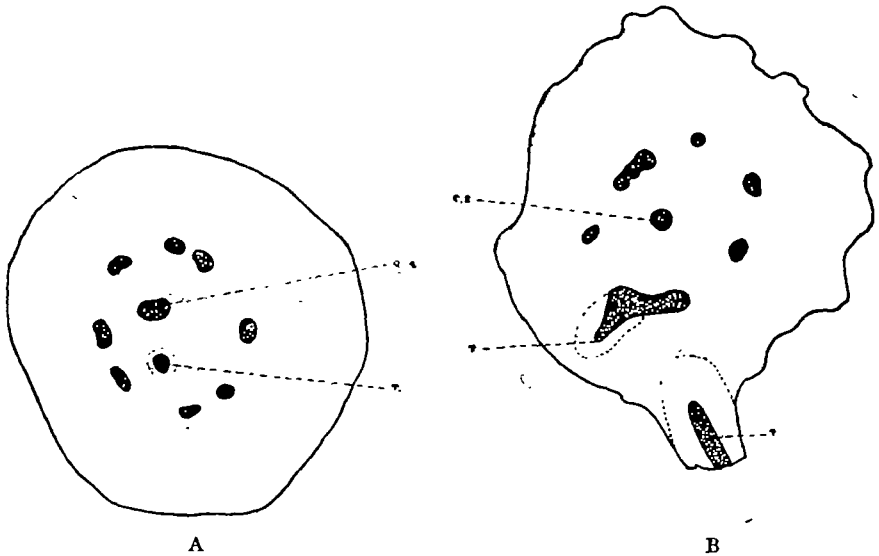
2. *Kaulfussia*, Blume (= *Christensenia*, Maxon).¹

The genus *Kaulfussia*, of which only one distinct species (i. e. *Kaulfussia aesculifolia*, Bl.) is at present known, possesses a relatively slender prostrate rhizome with a very well-marked dorsiventral configuration. According to Kühn (42, p. 462), lateral branching of the rhizome some-

¹ Carl Christensen, Index Filicum, 1906.

times occurs, but the rhizome was unbranched in every specimen examined by the present writer. The numerous roots which arise from the ventral surface and flanks of the rhizome greatly outnumber the leaves, which form two ranks on the dorsal side of the rhizome. The leaves of *Kaulfussia* are not crowded, consequently distinct internodes can be distinguished (cf. the ill-nourished specimen of *Danaea nodosa* described above [p. 375] and cf. Text-fig. 14, A with 14, B).

The development and arrangement of the vascular strands in the very young sporophyte have been carefully studied by Campbell, who, in his monograph on the 'Eusporangiatae', maintains that the vascular system of *Kaulfussia* is at first essentially similar to that of *Danaea*, consisting of a sympodium of the traces of the earlier leaves. He states, however, that

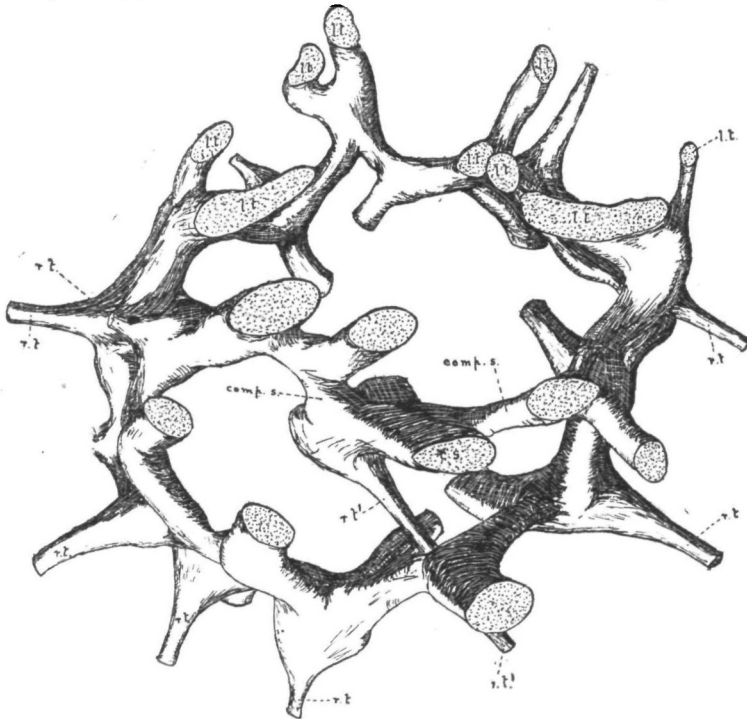


TEXT-FIG. 14. A. *Danaea nodosa*, Sm. Transverse section of the rhizome of an old (ill-nourished) specimen. $\times 5$. B. *Kaulfussia aesculifolia*, Bl. Transverse section of the rhizome of an old specimen. $\times 4$. *c.s.*, commissural strand; *r.*, root.

the marked dorsiventrality of the adult plant has already impressed itself on the morphology and vascular anatomy of the young sporophyte, a distichous arrangement of the leaves being evident from the beginning, while the traces of the first and of all succeeding leaves are inserted upon the same side of the stelar system. Between the solid stele found in the very young stem and the dictyostelic cylinder of the older rhizome, Campbell (20, p. 184, Fig. 168, J, K) observed a transitional siphonostelic condition.

The vascular anatomy of the adult plant of *Kaulfussia* has already been investigated by Kühn (42), Farmer and Hill (29), and Gwynne-Vaughan (30). However, for comparison with that of the dorsiventral species of *Danaea*, the present writer examined the stelar system of the adult rhizome and petiole.

In the internodal regions of the adult rhizome of this fern there is a single ring of branching and anastomosing bundles, from five to twelve in number, surrounding a single commissural strand (Pl. XXI, Fig. 3; Text-figs. 14, B, and 15). The leaf-traces, which consist of several strands, pass off as large meshed segments from the dorsal region of the stelar system, leaving wide foliar gaps (Pl. XXI, Fig. 3; Text-fig. 15). The commissural strand (*c.s.* in Pl. XXI, Fig. 3, and in Text-fig. 15), which in this genus, according to Campbell (20, p. 184), arises late in the development of the vascular system, pursues a somewhat sinuous course through the central



TEXT-FIG. 18. *Kauffussia aesculifolia*, Bl. Front view of a model¹ of the stelar system of a portion of the rhizome of an old plant. *c.s.*, commissural strand; *comp.s.*, compensating strand; *l.t.*, leaf-trace; *r.t.*, root-trace (cf. Pl. XXI, Fig. 3).

ground-tissue, and below a leaf-gap gives off either a single strand, which immediately dichotomizes, or, more often, two separate strands, which, fusing with bundles of the peripheral ring, help to close the foliar gap (Pl. XXI, Fig. 3, and Text-fig. 15, *comp.s.*).

A root-trace (Pl. XXI, Fig. 3, and Text-fig. 15, *r.t.*) usually joins the commissural strand immediately before the latter gives off a branch (or two branches) to close the leaf-gap; the great majority of the root-traces, however, are inserted indiscriminately upon any of the stem-meristemes and apparently bear no intimate relation to the number and position of the leaf-traces. In the oldest specimens examined, the stelar anatomy had

¹ This model, now in the Botanical Museum of the Imperial College, was prepared by Mr. T. G. Hill.

not increased in complexity beyond this stage, hence it would appear that in the genus *Kaulfussia* the arrangement of the vascular strands in the adult rhizome is *simpler* than in *Danaea*.

Vascular Anatomy of the Petiole. The arrangement of the vascular strands in the petiole of *Kaulfussia* has already been dealt with at some length by Bertrand and Cornaille (2) and by Gwynne-Vaughan (30); according to the last-named botanist (l. c., p. 263), several (1-5) internal strands leave the abaxial strands of the arc, pass across the central ground-tissue, and unite with the adaxial terminal strands of the horseshoe curve; hence they are not continued up as separate strands beyond the region of the pulvinus. The two terminal strands sink in towards the centre of the petiole and eventually fuse together across the median plane to form a single large strand; this is the arrangement of the vascular strands as seen in a transverse section taken at some distance below the point where the petiole branches (Text-fig. 16, i; and cf. Bertrand and Cornaille, l. c., Fig. 86, p. 169). But in the region immediately below the point where the petiole branches, the large central bundle divides into six strands (Text-fig. 16, iv); of these six strands, two pass into each of the three main branches accompanied by three strands from the peripheral ring of bundles (Text-fig. 16, v-vii); these together form an anastomosing ring of strands in each of the three primary branches of the petiole. Two or more strands leave the ring of bundles to supply the secondary branches of the petiole (Text-fig. 16, viii-x).

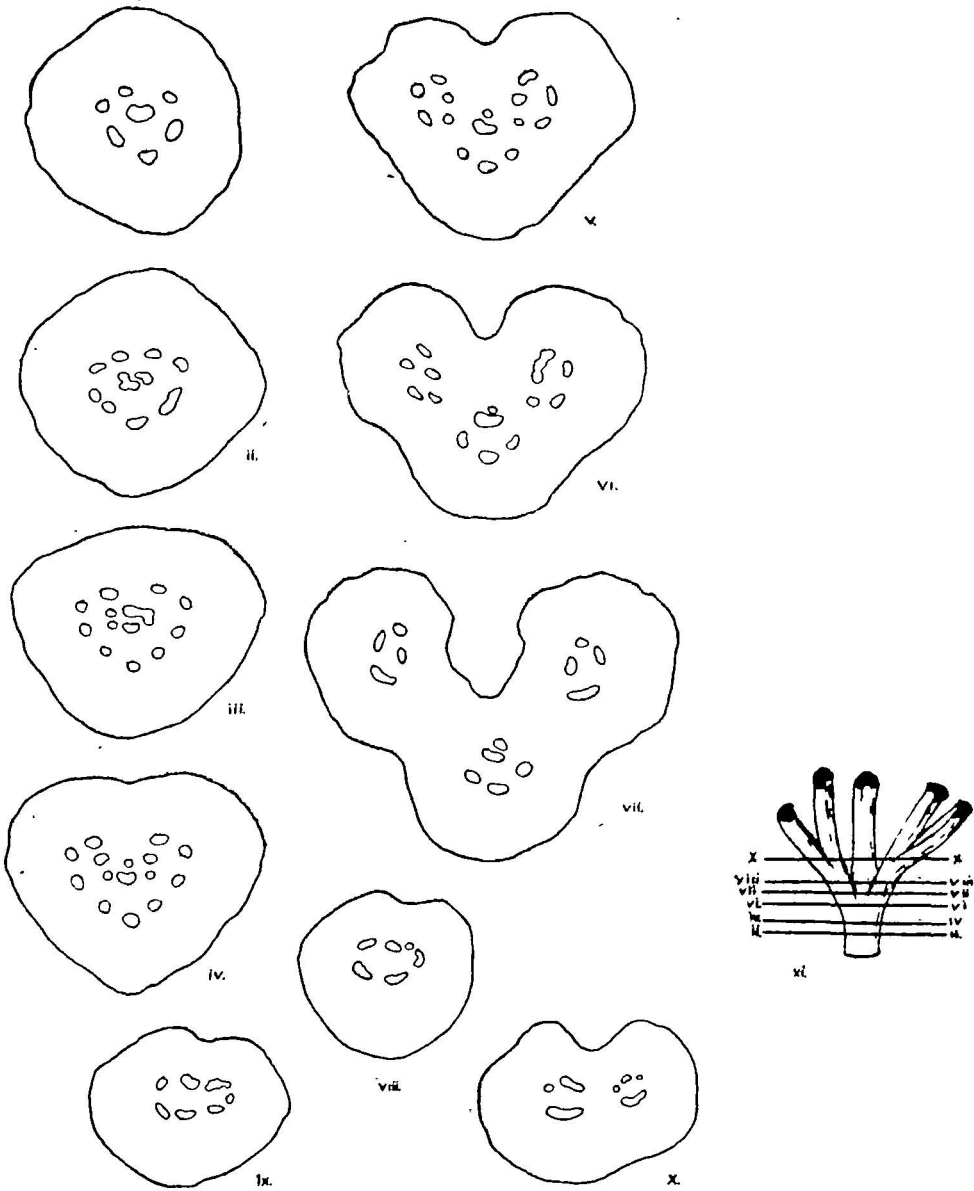
3. *Archangiopteris*.¹

Our knowledge of the general morphology of this monotypic genus is still far from complete, and it is impossible to decide from the information available whether the stem of the *adult* plant has a radial or a dorsiventral organization. Gwynne-Vaughan (30), who investigated the anatomy of the petiole and of a small fragment of the stock, states that the arrangement both of the leaves and of the vascular strands in the stem indicates a radial symmetry. An examination of herbarium specimens by the present writer lends support to this view.

Archangiopteris Henryi has simply pinnate leaves and closely resembles the larger species of *Danaea*.

According to Gwynne-Vaughan (30, p. 261), the vascular system of the stem consists of a single dictyostelic ring of two to four small strands, which anastomose with each other in a somewhat irregular manner; in addition there is usually a small internal (= commissural) strand which runs free in the central ground-tissue through the greater part of its course, and from time to time approaches the dictyostelic ring, fusing with those

¹ For information regarding the morphology of the frond of *Archangiopteris Henryi*, the reader is referred to Pteridographische Notizen, published by H. Christ and K. Giesenhagen in Flora, Bd. lxxxvi, 1899.



TEXT-FIG. 16. i-x. *Kaulfussia aesculifolia*, Bl. These diagrammatic figures illustrate in successive, but not consecutive, transverse sections the changes and rearrangements that take place in the vascular system of the petiole of an adult plant in the regions indicated on xi. $\times 6$. xi, nat. size.

meristemes that are about to close a foliar gap. This central strand soon separates off again and passes on across the central ground-tissue to the next leaf-gap above, which it helps to close up (cf. the young sporophyte of *Danaea*); root-traces arise from the external surface and sides of the stem-meristemes, a root-trace invariably arising from the point where the

central strand fuses with a meristele of the dictyostelic ring (cf. 30, Plate X, Fig. 6). In this way a direct water-channel is formed between a root and the next leaf above.

Two strands only are given off to supply the petiole, but as they pass outwards through the cortical region of the stem, they divide into several (eight or nine) strands, which, at the base of the petiole, are arranged in a typical horseshoe curve (cf. 30, Pl. X, Fig. 12).

The vascular anatomy of the petiole closely resembles that of *Kaulfussia* and of *Danaea*, internal accessory strands being found in the region of the basal pulvinus of all three genera.

Also, the manner in which the pinnae obtain their vascular supply from the rachis is essentially similar in these three plants.

4. *Marattia*.

The adult sporophyte of *Marattia* possesses an upright, tuberous, more or less conical stem surmounted by a rosette of large pinnate leaves; the remainder of the stem surface is almost entirely covered by the huge leaf-bases. Numerous stout adventitious roots anchor the stem to the soil.

Apart from a passing reference by Holle (34), the vascular anatomy of this genus was first studied by R. Kühn (42), who found in the stem of comparatively young plants of *Marattia fraxinea* a peripheral ring of anastomosing vascular strands surrounding a single axile bundle (l. c., Taf. XVIII and XIX, Fig. 22). In rather older stems of the same species this investigator showed that the stelar system was further complicated by the appearance of a second zone of anastomosing strands (l. c., Taf. XVIII and XIX, Figs. 30–32). His account of the arrangement of the vascular strands is rather difficult to follow, but he seems to show that compensation for the departure of the leaf-traces from the outer zone of bundles is provided for by two strands which leave the inner zone and, passing obliquely outwards, help to close up the foliar gap. The central strand likewise gives off two branches which assist in closing the gap formed in the inner zone. It will be noticed that Kühn describes for the comparatively young plant of *Marattia fraxinea* a type of stelar structure which is fundamentally similar to that of the adult sporophyte of the radial species of *Danaea* (e. g. *Danaea nodosa*, Sm.).

Farmer and Hill (29) gave a brief account of the development of the vascular system in the sporeling of this same species of *Marattia*, and showed (l. c., pp. 378–9) that the protostele found at the base of the stem of the young sporophyte opens out to form a siphonostele with extremely large foliar gaps (l. c., Pl. XVII, Figs. 20 and 21). Sooner or later commissural strands of an attenuated form are developed within the siphonostele. The earlier leaf-traces are single, but those subsequently formed fork once in the stem-cortex; the dichotomy extends farther

back in the successively produced leaves, till it is obvious at their first origin at the base of the foliar gap.

Lotsy (47, p. 681) briefly states, with reference to *Marattia sambucina*, that 'Der Stamm hat eine weniger komplizierte Dictyostele als *Angiopteris*'.

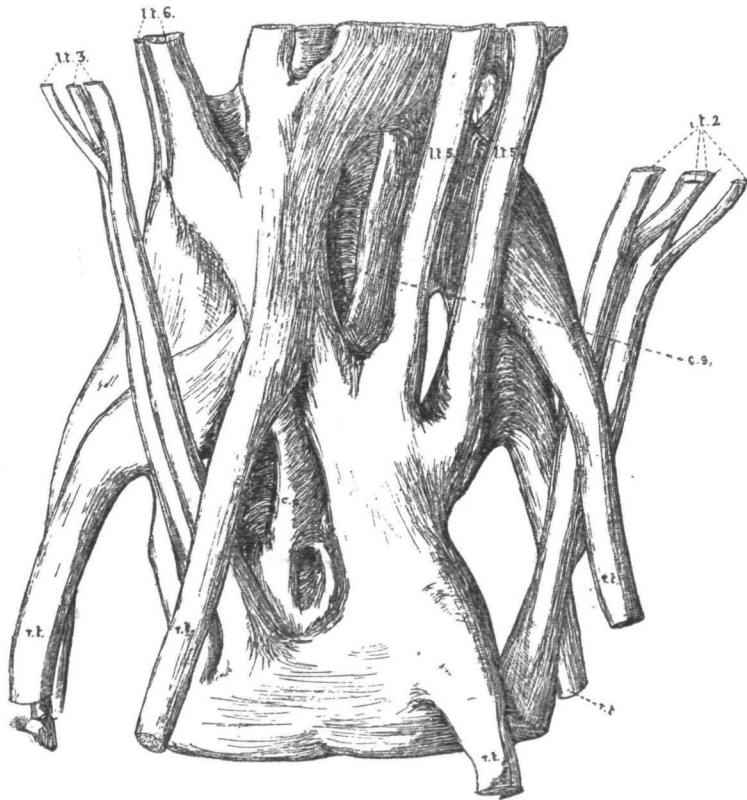
Campbell (20), as a result of his investigations upon the vascular anatomy of young sporophytes of *Marattia Douglasii* and *Marattia sambucina*, brings this genus into line with *Danaea* and *Kaulfussia* by maintaining that the solid strand which occurs at the base of the stem is composed of the united traces of the earlier leaves. This botanist also describes (20, pp. 191-3) the anatomy of the stem of a small adventitiously formed plant of *Marattia alata*; his description of the stelar system of this species agrees essentially with that given for *Marattia fraxinea* by Farmer and Hill (l. c.).

The most recent and complete account of the development of the stele in this genus, however, was published by Charles (23), who had the great advantage of working with abundant material of *Marattia alata*. At the base of the young sporeling this observer finds (l. c., p. 97) a protostele from which the transition to a solenostele takes place suddenly and without the intervention of a distinct medullated monostelic stage. Later, a medullary strand arises, and at first behaves like the commissural strand in the young sporophyte of *Danaea*, but as the leaf-traces become more crowded, the medullary strand divides into a number of branches, which join the stelar cylinder above the leaf-gaps. Eventually, however, a second cylinder is produced by anastomosing and branching of the medullary strands (l. c., p. 92, Fig. 3). The main root-supply joins the external system, the medullary system having only a few small roots.

The model represented in Text-figs. 17 and 18 was built up from a series of transverse sections of the caudex of an adult plant of *Marattia Cooperi*, Mre., the base of which had unfortunately completely decayed away. A transverse section of the existing basal region of this specimen showed a ring of strap-shaped bundles surrounding a single central bundle (Text-fig. 19), whilst a similar section taken just below the apex of the same plant showed two concentric zones of strands (Text-fig. 18). The region of the stelar system at which the transition between these two conditions takes place is represented in this model, from a study of which it is seen that the stem-stele of this plant is made up of a simple dictyostelic cylinder with extremely large foliar gaps (cp. Farmer and Hill, l. c., p. 379) and an internal accessory system which at first consists of a single commissural strand, a short branch from which assists in closing the foliar gap. Subsequently, however, further elaboration of the internal conducting system takes place by branching and anastomosing of the original commissural strand, whereby an internal vascular cylinder is produced (Text-fig. 18). Only a single compensating strand (Text-fig. 18, *comp.s.*) leaves this inner cylinder to assist in closing the gap formed in the outer cylinder by the departure of

the leaf-trace. No gaps other than leaf-gaps occur in the external vascular cylinder.

The double leaf-traces, which are arranged in a fairly regular spiral,¹ leave the outer cylinder from near the base of the leaf-gaps and at first pass out to their respective leaves so gradually, branching meanwhile in the cortical ground-tissue (Text-figs. 17 and 18), that the traces of a number of leaves appear in a transverse section of the stem and present an appear-



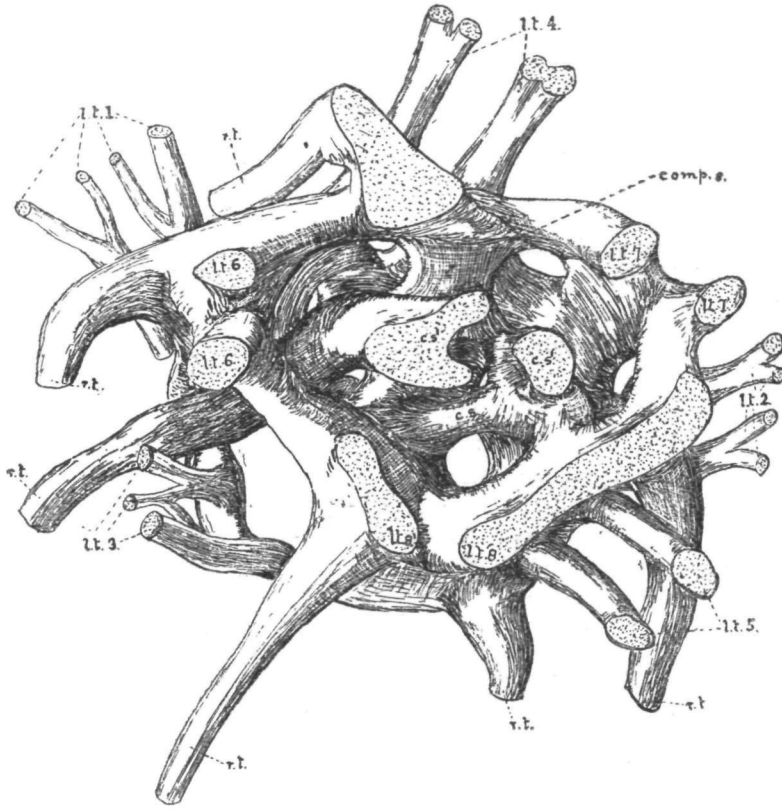
TEXT-FIG. 17. *Marattia Cooperi*, Mre. Model of the stelar system of the caudex of an adult plant, viewed from one side. *c.s.*, commissural strand; *lt.*, leaf-trace; *r.t.*, root-trace.

ance very similar to that of the outermost ring of bundles of the stem-stele in *Danaea*, with which at first sight they may very easily be confused. However, the model clearly demonstrates their true foliar nature; anastomosing between adjacent leaf-traces never take place.

Usually a root-trace fuses with the main vascular cylinder just below the point of departure of the leaf-trace (Text-fig. 17), and there is generally one root to each leaf, as Holle (34) pointed out long ago. Other root-traces join the central stelar system at irregular intervals (Text-figs. 17 and 18).

No third cylinder was developed in the specimen examined. It

¹ The leaf-divergence = 144° approximately.

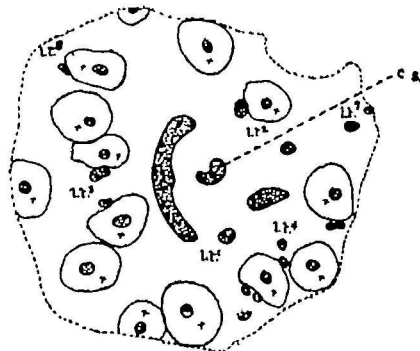


TEXT-FIG. 18. *Marattia Cooperi*, Mre. Model of the stellar system of the caudex of an adult plant, viewed from above. *c.s.* = commissural strand; *c.s.*' = central cylinder; *comp.s.* = compensating strand; *l.t.*, leaf-trace; *r.t.*, root-trace (cf. Text-fig. 17).

is probable that further complications arise in the stellar system of the huge tuberous stems of very old plants, but, unfortunately, no very old plant of *Marattia* was available for investigation.

Vascular Anatomy of the Petiole.

Gwynne-Vaughan (30, pp. 264-5) found a large number of internal strands within the typical ring of bundles just above the basal pulvinus of a petiole of *Marattia fraxinea*; traced upwards, these internal strands decreased in number by a succession of fusions, which, however, take place so gradually that a number of the



TEXT-FIG. 19. *Marattia Cooperi*, Mre. Transverse section of the basal region of the stem of an old plant, showing numerous roots (*r.*) and leaf-traces (*l.t.*) embedded in the ground-tissue. The leaf-bases had been artificially removed. The leaf-traces are numbered consecutively, *l.t.*¹ being the youngest shown. *c.s.*, commissural strand. × 1.5.

internal strands continue their course from the pulvinus far up into the region of the rachis, where, according to Bertrand and Cornaille (2, pp. 162 and 212), the primary branches of the petiole are supplied direct with strands from the internal system, in addition to those they obtain from the outer ring.

5. *Angiopteris*.

The adult sporophyte of *Angiopteris*, which closely resembles in size and in habit that of most species of *Marattia*, also has a bulky tuberous caudex surmounted by a rosette of huge leaves, which are usually twice-pinnate.

The first account of the vascular anatomy of the genus *Angiopteris* was published in 1853 by Harting (De Vriese and Harting, 27), who found that the vascular system of the stem consisted of a confused network of bundles which traversed the ground-tissue in all directions. This investigator, however, not only failed to distinguish the foliar traces from those of the intracortical roots, but made no attempt to trace out the actual course of individual vascular strands.

In 1864 Mettenius (49) published an important monograph in which the course of the bundles in the stem and leaf-bases of an old plant of *Angiopteris* was described in great detail. He showed that the very numerous vascular strands of the tuberous stem form a number of concentric cylinders of anastomosing bundles each having the general form of an inverted cone. Meshed segments leave the outermost cylinder to supply the leaves; the gaps in this cylinder formed by the departure of the leaf-traces are compensated by corresponding segments from the next inner zone. In a similar manner segments from the third cylinder compensate for the gaps produced in the second, and so with successive inner cylinders. Mettenius (l. c., p. 590) also stated that strands from the second cylinder sometimes contribute directly to the leaf-trace.

De Bary (1) pointed out that the stem-stele of a young plant of *Angiopteris* consisted of a 'Bündelrohr' with foliar gaps, while Leclerc du Sablon (54) gave a brief account of the vascular anatomy of the young plant as it appeared in a series of transverse sections of the stem.

Shove (58) described the vascular anatomy of a large specimen of *Angiopteris* and in most of the important details confirmed the results obtained by Mettenius. This plant, however, exhibited a dorsiventral structure which was especially well marked towards its base, where the lower surface was quite destitute of leaves, but thickly covered with roots. This observer (58, p. 505; Pl. XXVIII, Figs. 5 and 6) found that, correlated with the external dorsiventrality of the plant, the meshes of the vascular network were much longer on the ventral root-bearing side than on the dorsal leaf-bearing side. All the strands of the leaf-trace were derived solely from the outermost

ring of bundles at the time being, no strands from the second cylinder contributing directly to the leaf-trace.

The year 1902 was marked by a great advance in our knowledge of the stelar system in this genus, when Farmer and Hill (29) published a full account of the arrangement and development of the vascular tissues in *Angiopteris evecta*; this paper was illustrated by means of a series of wax models representing the stelar skeleton of this plant at various stages in its development. In this way, a most accurate description of the successive stages in the elaboration of the complicated vascular system of the adult plant was obtained. A gradual transition was traced from the solid axile rod of vascular tissue (= protostele) of the very young sporeling to a hollow cylinder or siphonostele, and with perforations corresponding to foliar gaps enclosing a core of pith, which they regarded as distinct from the now tubular stele. Sooner or later, the gap above one leaf fails to be repaired until after the exit of the traces of the next leaf; in this way a typical dictyostele is produced. Meanwhile commissural strands are differentiated across the central parenchyma and serve to connect the opposite sides of the stelar cylinder. 'Finally (l. c., pp. 377-8) the siphonostele opens out to a considerable width (l. c., Pl. XVI, Fig. 6), whilst the axile commissures assume an ever-growing importance forming a sort of sympodial column. . . . The leaf-traces also become more complex, and anastomoses take place at irregular intervals with the strands which can still be recognized as the relics of the original siphonostele, as well as with one another. Irregularities also begin to become apparent as to the relative height at which the two members of the leaf-traces become freed from the plexus of tissue, and a stage is thus reached at which the vascular skeleton appears to consist of a stout axile strand surrounded by upwardly diverging zones of steles which ultimately pass out above to the leaves. The complexity and obscurity is primarily due to the commissural strands which connect up the margins of siphonostelic foliar gaps, and the whole arrangement is to be correlated with the presence of the bulky parenchyma of the stem.' According to these observers, the roots of *Angiopteris* sometimes unite with the more central strands, though far more commonly with those peripherally situated, but Shove (l. c., p. 506) states that the majority of the roots originate from the inner zones, although a few arise from the outer ones, usually at the points where the strands anastomose.

In his monograph on the 'Eusporangiatae', Campbell (20, p. 200) states that 'in the early stages *Angiopteris* appears to agree closely with the other Marattiaceae in the development of its vascular system, but the single central stele without leaf-gaps is retained much longer than in the other genera, and it also becomes much larger and has a better-developed xylem, and the open dictyostele, formed from the anastomosing of the early single leaf-traces, characteristic of *Danaea* and *Marattia*, is not present'.

Thus it is seen that the anatomy of this genus has already been

carefully elucidated; the present writer's investigations on this genus, although covering most of the ground, merely confirm previous results.

*Vascular Anatomy of the Petiole.*¹ The vascular anatomy of the petiole of *Angiopteris* appears to differ from that described above for *Marattia* only in the larger number of internal strands which arise from the strands of the abaxial arc; as many as five separate concentric rings of bundles were counted by the author in a transverse section of the base of a petiole of an old plant.

6. *Macroglossum.*

This recently discovered genus resembles *Marattia* and *Angiopteris* both in size and in the form of its upright, nearly globular, bulky stem, upon which the leaves are spirally arranged (cf. Copeland, 26; also cf. Campbell, 21). In the form of its simply pinnate leaves, however, it more closely resembles *Danaea*,² whilst its sporangia are very similar to those of *Archangiopteris*.

We are indebted to Campbell (21) for the only account of the anatomy of *Macroglossum* that has yet appeared. According to his account (l. c., p. 661), no true cauline stele is developed in the young sporophyte, the vascular system of the axis of which is at first composed only of leaf- and root-traces. A single root is formed for each of the early leaves.

Sections of the basal region of the stem of a rather older specimen showed a type of stelar structure not far removed from that of the young sporophyte. In the centre there were five strands; of these five strands, one was comparatively large and somewhat crescentic in transverse section, whilst the remaining four bundles, which were of smaller size, were arranged in pairs; the latter probably represent the double leaf-traces.

It is to be regretted that the author (l. c., pp. 662-3) only briefly refers to the anatomical features exhibited by the adult plant, which, as indicated above, unites within itself certain characters of four other genera of Marattiaceae.

APICAL MERISTEMS.

1. *Stem.*

The structure and arrangement of the generative tissues at the apex of the massive stem and roots of the Marattiacean Ferns has been for many years the subject of much divergence of opinion.

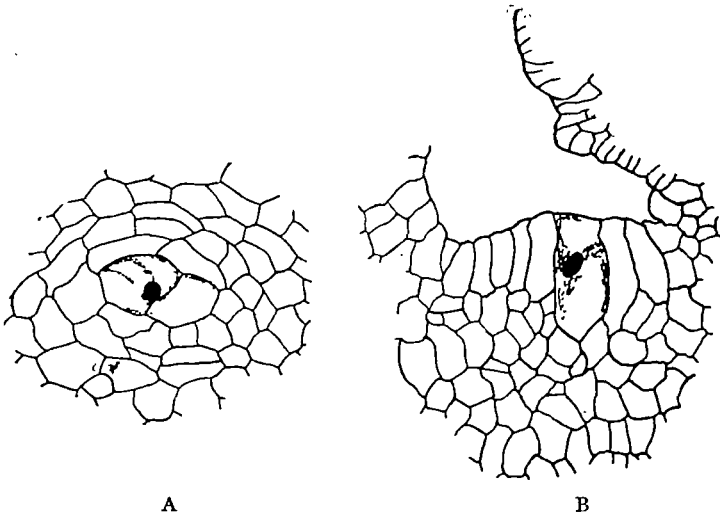
¹ For an exhaustive account of the arrangement of the vascular strands in the petiole of *Angiopteris*, *Marattia*, and *Kaulfussia*, the reader is referred to Bertrand, C. E., et Cornaille, F.: *Études sur quelques caractéristiques de la structure des Filicinaées actuelles*, in *Trav. et Mém. de l'Université de Lille*, t. x, Mém. 29, 1902.

² Moreover the gametophytic characters of *Macroglossum* and *Danaea* agree in (1) the structure of the spermatozoids and in (2) the presence of a large suspensor (cf. Campbell, 21).

As long ago as 1857 Hofmeister (32 and 33) ascribed a three-sided apical cell to the stem of all known Vascular Cryptogams, and referred to *Marattia cicutaefolia* as an example of the Marattiaceae.

Holle (34, p. 218; 35, p. 21) found a four-sided, long-drawn-out initial cell at the apex of the stem of *Marattia cicutaefolia*, and believed that a similar condition obtained in the stem of *Angiopteris evecta*; but he admitted that in the latter genus the origin of the cells at the stem-apex cannot with certainty be traced back to the divisions of a single cell.

Jonkman (38 and 39), on the other hand, described and figured (39, p. 225; Pl. VI, Figs. 13 and 18) a small-celled meristem at the apex of the stem of young sporophytes of *Marattia* and of *Angiopteris*, while Shove (58, p. 522) satisfactorily demonstrated several initial cells in the apical region of an old plant of *Angiopteris*.



TEXT-FIG. 20. *Danaea alata*, Sm. A. Transverse section of stem-apex of a very young sporeling showing the apical cell. B. Longitudinal section of stem-apex of a very young sporeling showing the apical cell. $\times 350$.

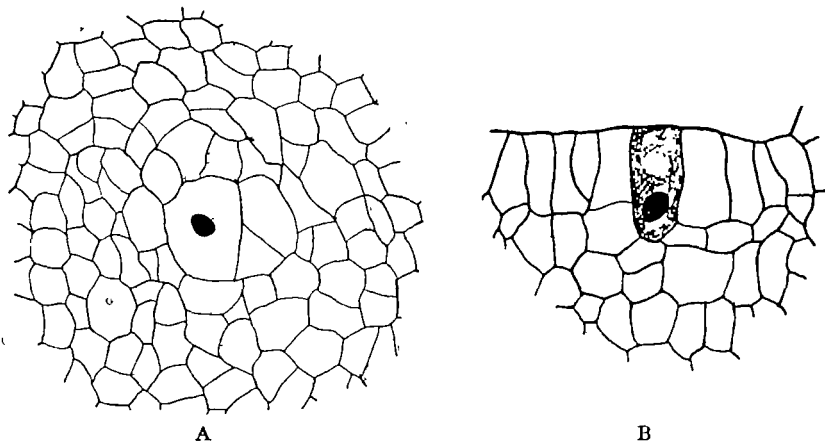
According to Brebner (10), Farmer and Hill (29), and Charles (23), a single initial cell occurs at the apex of the stem of sporelings of *Danaea simplicifolia*, *Angiopteris evecta*, and *Marattia alata* respectively. A similar view is held by Campbell (18, 19, 20, and 21), who also includes in this category the genera *Kaulfussia* and *Macroglossum*.

For our knowledge of the cell-divisions at the apex of the stem of adult sporophytes, we are indebted to the investigations of Bower and of Charles. In an earlier communication, Bower (4, p. 579) stated that his observations on a well-grown plant of *Angiopteris evecta*, var. *pruinosa*, Kuntze, pointed clearly to the existence of a wedge-shaped apical cell, which was represented in Pl. XXXVII, Fig. 9 of that work. This botanist (7, p. 327), however, subsequently arrived at the conclusion that in strongly

grown plants of *Marattia fraxinea* and of *Angiopteris evecta*, the stem-apex is devoid of an apical cell, the meristem being referable, in some cases at least, to a group of four or five initials of exactly similar size and shape, which meet at the intersection of two more or less perpendicular lines.

Charles (23), working on *Marattia alata*, gave a full account of the series of stages of increasing complexity which lead up to the formation of a meristem of several cells at the stem-apex of the older plant.

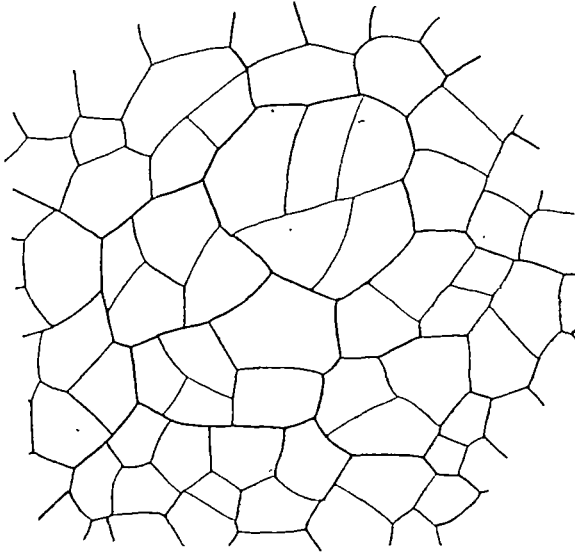
The present writer's observations on the structure of the stem-apex in a large number of young sporelings of *Danaea alata*, Sm., and of *Danaea nodosa*, Sm., confirm Campbell's (20) account of the apical growth in young plants of this genus, a single very distinct apical cell being found at the apex of the stem of every specimen examined. This apical cell varies consider-



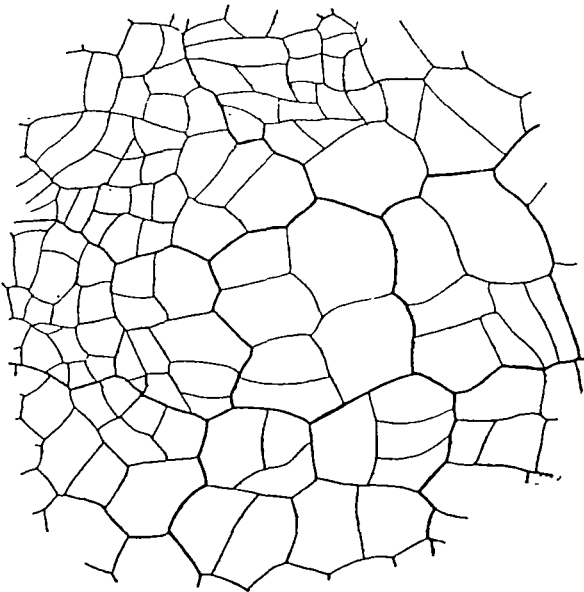
TEXT-FIG. 21. *Danaea nodosa*, Sm. A. Transverse section of stem-apex of a very young sporeling showing the apical cell. B. Longitudinal section of stem-apex of a very young sporeling showing the apical cell. $\times 350$.

ably in shape, but generally has an irregular triangular outline in transverse section (Text-figs. 20, A, and 21, A), whilst in longitudinal sections it appears as an elongated cell which may be either pointed or truncate below (Text-figs. 10, B, 20, B, and 21, B).³ In slightly more advanced sporelings, the apical cell appears roughly four-sided in transverse section, and is generally more or less truncate below. At a later stage one or more lateral segments of the apical cell do not pass over into permanent tissue, but retain their meristematic condition indefinitely, and thus become the equivalents of, and assume a similar function to, the original apical cell. In other words, each of these cells contributes to the slow growth in length of the stem by dividing periclinally; consequently, at the apex of large well-grown stems, a meristematic region, such as that represented in Text-figs. 22 and 23, is found.

Campbell (20) states that in *Kaulfussia* the apical cell of the young rhizome is roughly triangular in transverse section, and oblong with a broadly truncate base in longitudinal section, but gives no account of the



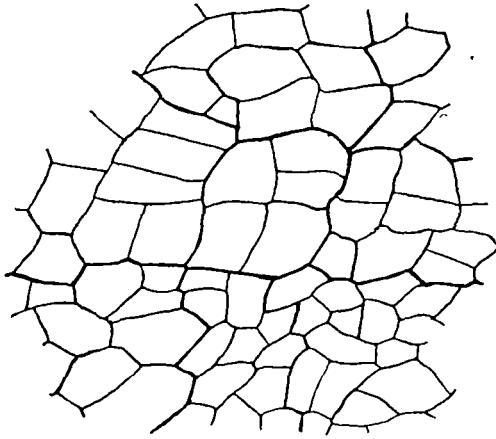
TEXT-FIG. 22. *Danaea alata*, Sm. Transverse section of stem-apex of a large sporophyte showing three meristematic blocks. $\times 220$.



TEXT-FIG. 23. *Danaea nodosa*, Sm. Transverse section of stem-apex of a large plant showing meristematic region. $\times 220$.

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structure of the apex of the older rhizome. The present writer has found that a meristematic region, similar in all essentials to that described above for *Danaea*, occurs at the apex of the old rhizome of *Kaulfussia aesculifolia* (Text-fig. 24).



TEXT-FIG. 24. *Kaulfussia aesculifolia*, Bl. Transverse section through the apex of an old rhizome showing initial cells. $\times 180$.

The stem-apex of *Marattia* and of *Angiopteris* was not examined by the writer, since Charles (23) for the former, and Bower (4, 5, 7, 9) for the latter, have already published a full account of the changes which take place at the apex of the stem in these genera, and have shown that whilst the apical growth of the young sporeling may be traced back to the segmentation of a single initial cell, in older plants a

group of equivalent initials constitute the apical meristem.¹

2. Roots.

Russow (54, p. 107, Taf. VIII, Fig. 158) expressed the opinion that the apical growth of the roots in the Marattiaceae takes place by means of several (*Marattia* = 7-10; *Angiopteris* = 12-18) relatively large prismatic or pyramidal initial cells, the outermost of which give rise to the cortex and epidermis, whilst the more central form the axile vascular tissue and the tissues of the root-cap.

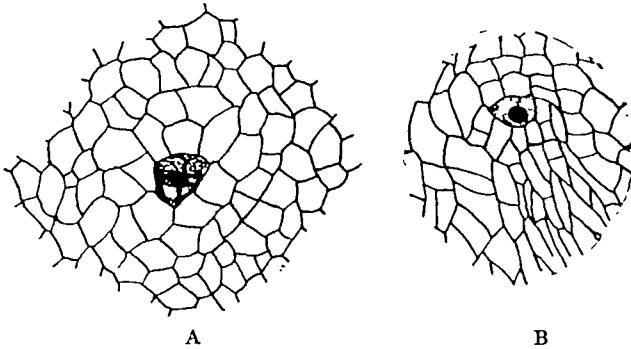
Holle (34, p. 217) gave a brief account of the apical growth of the roots of *Marattia cicutaeifolia* and of *Angiopteris evecta*, in which he stated that the number of initials at the root-apex was correlated with the size and strength of the roots, a single four-sided apical cell being found only in the weaker roots. Schwendener (56, Taf. VI, Figs. 3 and 4) described and figured four initial cells at the apex of the roots of *Angiopteris evecta* and of *Marattia Kaulfussii*.

Van Tieghem and Douliot (66) briefly referred to the apical growth of the lateral root in *Angiopteris Durvilleana* and in *Marattia laevis*, and figured (l. c., Pl. XXVI, Fig. 407) a lateral root of *Marattia* with a single large triangular apical cell.

¹ Several initial cells are found at the apex of the stem of other Vascular Cryptogams in which the shoot is relatively bulky; e.g. *Lycopodium* (Russow, 53; Strasburger, 61), *Phylloglossum* (Bower, 6), *Isoetes* (West and Takeda, 71), and certain species of *Selaginella* (Russow, 53; Bruchmann, 14, 15).

Bower concluded (7, p. 315) that his own observations on roots of *Marattia fraxinea* and of *Angiopteris evecta* bore out Schwendener's conclusions rather than those of Russow. Farmer (28, p. 268) stated with reference to the root of the embryonic plant of *Angiopteris evecta*, that 'the apical cell, which is at no time very clear, is subsequently replaced in most cases by a group of initials', and suggested that some connexion may exist between the robust condition of the root and the structure of its apex.

In a long paper devoted to the subject of apical growth in roots, Koch (41) put forward the view that no *persistent* apical cell is present in roots of *Angiopteris*, the function of the apical cell being temporarily assumed by one of four particularly large cells that are found at the apex of the roots of this genus.



TEXT-FIG. 25. *Danaea alata*, Sm. A and B. Apex of small roots in transverse and longitudinal section respectively, showing the single initial cell. $\times 200$.

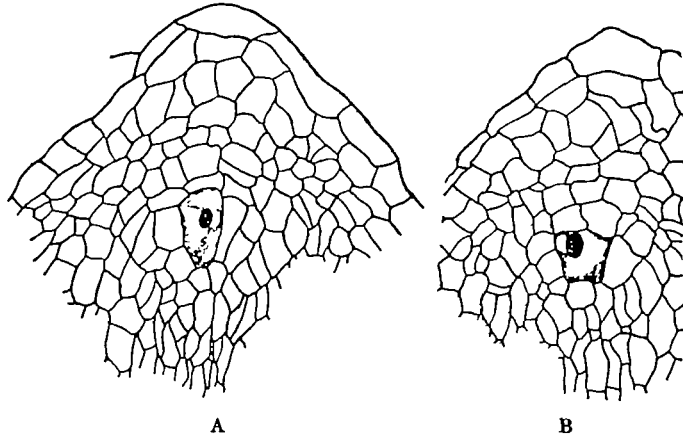
According to Jonkman (39, p. 224), the apical meristem of the primary root of *Marattia* and of *Angiopteris* consists of 'un groupe de quatre cellules environs' (l. c., Pl. VI, Figs. 15 and 16).

Brebner (10, p. 119) concluded that a single initial cell was present at the apex of the primary root of *Danaea simplicifolia*, but that the adventitious roots possessed a group (sometimes four) of equivalent initials.

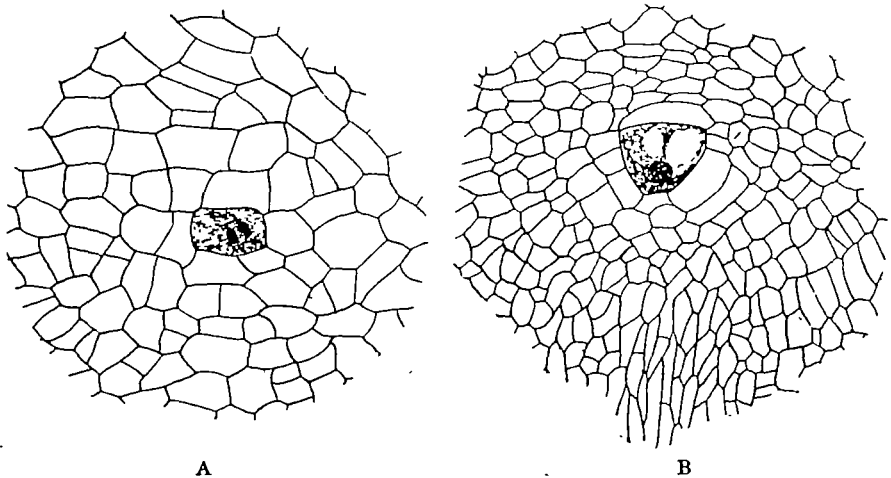
The most important contribution to this subject is the recent comparative work of Campbell (20 and 21), who finds a single initial cell at the apex of the primary root of *Angiopteris*, *Danaea*, *Kaulfussia*, *Marattia*, and *Macroglossum*; this botanist adds, however, that in the later roots of *Danaea*, *Marattia*, and *Macroglossum*, the single apical cell is replaced by a group of apparently equivalent initial cells which are wedge-shaped in longitudinal section.

The present writer, working on *Danaea alata*, *Danaea nodosa*, *Angiopteris evecta*, *Kaulfussia aesculifolia*, and *Marattia Cooperi*, has obtained results on the whole very similar to those of Campbell. A single apical cell of moderately large dimensions and of variable shape is found at the apex of the primary and earliest adventitious roots of the above-named genera and

species (Text-figs. 25, A and B, 26, A and B, 27, A and B). At the apex of later roots of moderate size a block of about four equivalent initial cells is found (Text-fig. 28), but the largest and most bulky adventitious roots possess a definite apical meristem (Text-figs. 29, 30, A and B), consisting

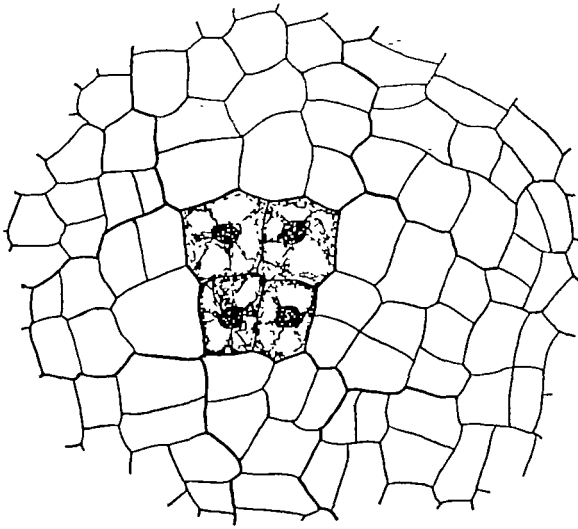


TEXT-FIG. 26. *Danaea nodosa*, Sm. A and B. Longitudinal sections of small roots showing variation in shape of the single initial cell. $\times 180$.

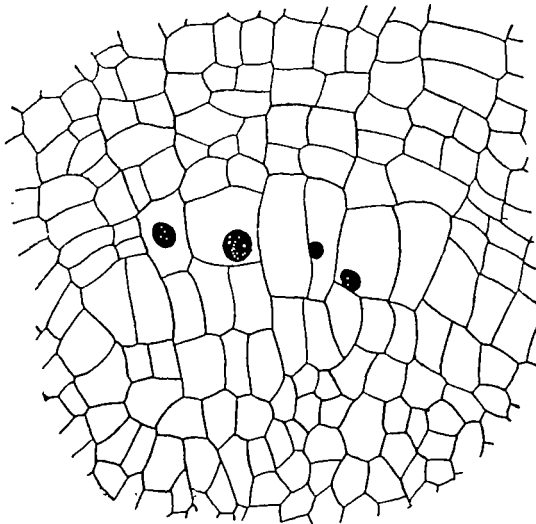


TEXT-FIG. 27. *Marattia Cooperi*, Mre. A. Transverse section of the apex of a small root showing a single initial cell. B. Longitudinal section of the apex of a similar root showing the single initial cell. $\times 180$.

of a number of independent, usually wedge-shaped initials, which in median longitudinal sections of the roots in question appear to be arranged in a fan-shaped manner as described and figured by Campbell (20, p. 177, Fig. 162). Hence it would appear that in the case of the Marattiacean roots, the number of initial cells found at the apex depends upon the bulk, and



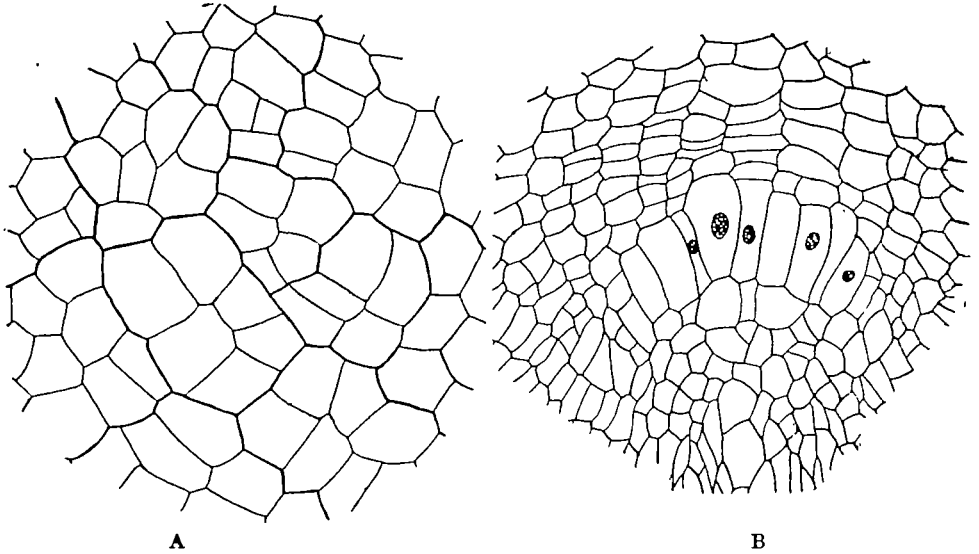
TEXT-FIG. 28. *Danaea nodosa*, Sm. Transverse section of the apex of a large root showing four equivalent initial cells. $\times 240$.



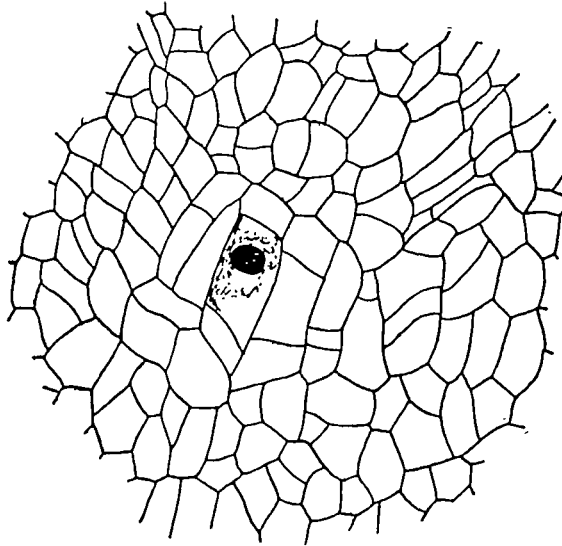
TEXT-FIG. 29. *Danaea alata*, Sm. Longitudinal section of the apex of a large root showing meristematic region. $\times 220$.

not necessarily upon the age of the roots in question; the stronger and more robust the root, the larger the number of equivalent initials which constitute the apical meristem.

The adventitious roots of *Danaea* and of *Kaulfussia* originate from the undifferentiated stelar tissues in the very young region of the stem (also cf.



TEXT-FIG. 30. *Marattia Cooperi*, Mre. A. Transverse section of the apex of a large root showing meristematic region. B. Longitudinal section of the apex of a large root showing meristematic region. $\times 180$.



TEXT-FIG. 31. *Kaulfussia aesculifolia*, Bl. Transverse section of the apical region of the rhizome, showing early origin of a root from the vascular meristem. $\times 240$.

Bower, 5, p. 90 and Pl. IX, Fig. 30; and Farmer and Hill, 29, p. 391, for *Angiopteris*; Charles, 23, p. 96, for *Marattia*). In the first instance there appears to be a single initial cell of elongated prismatic form, from which segments are cut off parallel with its long axis (Text-fig, 31). In the larger

roots certain of these lateral segments assume a function equivalent to that of the mother-cell from which they have arisen (cf. Bower, 5, Pl. IX, Figs. 30, 31, and 32). Segments are also cut off from the distal end of these cells; these apparently go to form the root-cap.

HISTOLOGICAL NOTES.

The histological details of the structure and development of the vascular tissues in the young sporophyte have already been critically examined by Campbell (20 and 21); recapitulation of the facts by the present writer, whose observations, extending over several hundred serial sections of young sporelings of *Danaea alata*, Sm., and *Danaea nodosa*, Sm., entirely confirm those of Campbell, would therefore be quite superfluous. However, since several points of interest have arisen from the present investigation on the histology of *Danaea*, especially with reference to the older sporophyte, a few notes on the more important details are set forth below.

As in all other known genera of this family, the anomalous position of the protophloem, first pointed out by Shove (58, p. 522, Pl. XXIX, Fig. 28), was very obvious in every species of *Danaea* examined by the present writer.

The protoxylem of the stem-meristemes is generally mesarch, occasionally endarch, whilst in the leaf-trace meristemes it invariably occupies an endarch position.

Even in quite old plants of *Danaea* the cells of the ground-tissue are capable of reassuming meristematic activity; this fact was clearly shown in the case of an adult plant of *Danaea alata* in which the conducting tissues of one of the stem-meristemes had completely decayed away, probably as the result of fungal attack working up from the decayed basal region of the rhizome. The cells immediately surrounding this meristeme had become actively meristematic, and had produced around it a continuous layer of periderm-like cells, the walls of which, however, were unsubserved.

1. *Endodermis.*

Whilst it is not proposed to attempt to enter upon a lengthy discussion of the real significance of the endodermis in the Marattiaceae, a few remarks upon the peculiar distribution of this morphological layer in the genus *Danaea* may not be out of place, especially as certain botanists (e.g. Jeffrey) have assigned to it far-reaching importance in questions of stelar anatomy.

For the sake of brevity, the statements which have already been published as to the presence or absence of this layer in the various genera of Marattiaceae are briefly summarized in the following table :

<i>Genus.</i>	<i>Examined by.</i>	<i>Stem-stele.</i>	<i>Leaf-trace.</i>	<i>Root-stele.</i>
<i>Danaea</i>	Kühn (43)	+		
	Brebner (11)	+*	-	+
<i>Kaulfussia</i>	Kühn (42)	-	-	+
	Farmer and Hill (29)	+		
	Campbell (20)	+*		+
<i>Archangiopteris</i>	Gwynne-Vaughan (30)	-	+	+
<i>Marattia</i>	Russow (53)	-	-	
	Holle (34)	-	-	+
	Thomae (65)	-	-	
	Kühn (42)	-	-	+
	Farmer and Hill (29)	+		
<i>Angiopteris</i>	Charles (23)	+	+	+
	Sachs (65)	-	-	
	Holle (34)	-	-	+
	de Bary (1)	-	-	+
	Thomae (65)	-	-	
	Shove (58)	-		+
	Farmer and Hill (29)	+		+

+ denotes presence of an endodermis; - denotes absence of an endodermis; * = not recognizable in older rhizomes.

According to Jeffrey (36, p. 122), the phlooterma (=endodermis) of the Marattiaceae is characteristically present in the stem of the young plant even when it is absent in the adult. He adds that the primitive medullary strand is generally surrounded by a well-marked phlooterma.

Leclerc du Sablon (54) remarks, with reference to *Angiopteris*, that 'Le peu de netteté de l'endoderme est le caractère spécial'.

Such wide differences of opinion would suggest that in this group of Ferns the distribution of an endodermal layer is most erratic, and that there is very little constancy in the position of histologically differentiated endodermal cells. The present writer's observations on *Danaea* spp. have shown that this is actually the case. When present, the endodermis is very conspicuous,¹ and can readily be recognized in sections stained with safranin and haematoxylin, especially when they are mounted in euparal. A very distinct endodermis surrounds the stele of the young sporophyte, being easily distinguished in the stem and petiole as well as in the root. But in older plants no general rule can be laid down as to its distribution; for instance, all attempts to demonstrate its presence in the leaf-traces and petiole met with no success; on the other hand, an endodermis is invariably found in roots of all ages.

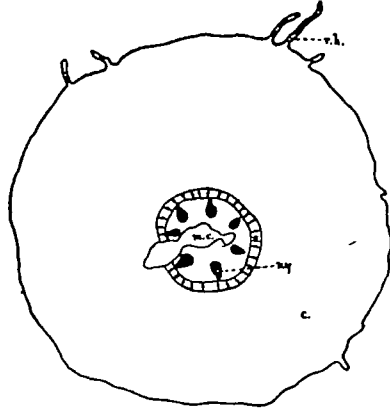
Occasionally an endodermal layer can be observed completely surrounding a stem-meristele (the central strand, or strands, are included in this category), but more frequently this layer is incomplete, or absent altogether.

No trace of an endodermis could be demonstrated round the stem-meristemes of a number of sections which were carefully examined after treatment with concentrated H₂SO₄.

¹ According to Rumpf (52, p. 24, Taf. II, Fig. 4S), the endodermal cells of the Marattiaceae belong to his *primary* type.

2. Mucilage Canals, Tannin Cells, and Tannin Ducts.

A comparative account of the structure and development of the various secretory tissues found in the Marattiaceae was published by the present writer (68) in a recent number of this journal, to which the reader is referred. Since the publication of that paper, however, the writer has observed in a moderately large root of *Marattia Cooperi* a mucilage canal traversing the endodermis (Text-fig. 32). When it is remembered that in the roots of this plant the mucilage canals arise very early just behind the growing point, it becomes apparent that, apart from the cells of the ground tissue, others, which would normally become endodermal cells, may be concerned in the formation of the canal. Moreover, stelar tissues in the strict sense also take part in the formation of the canal.



TEXT-FIG. 32. *Marattia Cooperi*, Mre. Transverse section of a root showing a mucilage canal (*m.c.*) traversing the endodermis (*e.*). *c.*, cortex; *r.h.*, root-hair; *xy.*, xylem. $\times 30$.

3. Secondary Thickening.

No trace of secondary thickening, such as that described and figured for *Angiopteris* and for *Marattia* by Farmer and Hill (29, p. 388, Pl. XVIII, Figs. 26, 28), was observed in the stem of either species of *Danaea* examined by the present writer; neither was it found in the rhizome of *Kaulfussia aesculifolia*; but regular tangential division of the pericyclic parenchyma was noticed in old roots of *Marattia Cooperi*, Mre. The cells which exhibit this secondary activity appear to be sister cells of the endodermis (cf. Farmer and Hill, 29, p. 388).

4. Mycorrhiza.

The Fungi which are normally associated with the roots of this group of Ferns have recently been described by the writer (69 and 70). Further reference to the mycorrhiza of the Marattiaceae is therefore unnecessary.

5. Cavity Parenchyma (= Tyloses).

Cavity parenchyma was frequently met with in both species of *Danaea* examined. Series of intrusive thin-walled cells of the ground-tissue, similar in appearance to those described by Brebner (12, p. 544, Pl. XXIII, Fig. 22) for *Danaea simplicifolia*, and by McNichol (48, p. 408, Pl. XXV,

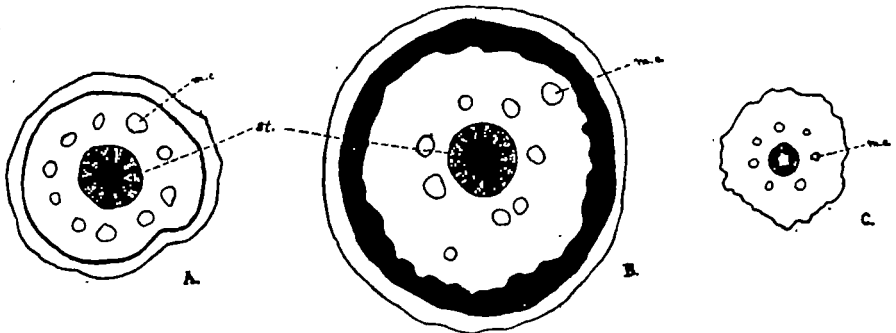
Fig. 13) for *Angiopteris* and *Marattia*, were frequently found completely blocking the lumen of the protoxylem elements of the vascular strands both in the stem and in the petiole.

6. Leaf Structure.

The adult leaf of *Danaea nodosa* and of *Danaea alata* has a leathery texture, and exhibits histological characters which are generally associated with a xerophytic habit. In other words, the leaf is provided with a thick cuticle, whilst the ground-tissue of the lamina exhibits differentiation into a palisade layer and spongy mesophyll; large intercellular spaces occur in the latter. Numerous stomata are found on the lower surface of the leaf; as Campbell (20, p. 152) has already pointed out, each fully developed stoma is surrounded by a series of accessory cells, which are more or less spirally arranged.

7. Root Structure.

The general anatomical structure of the root, which is identical throughout the family, is already well known and needs no further



TEXT-FIG. 33. Diagrammatic transverse sections of roots of (A) *Danaea alata*, Sm., (B) *Danaea nodosa*, Sm., and (C) *Kauffussia aesculifolia*, Bl. *m.c.* = mucilage canal; *st.* = stereome. All $\times 10$.

description. However, a comparative study of the distribution of stereome in the roots of the first order in the various genera and species of Marattiaceae is of interest, since it can readily be correlated with the general habit of the plant.

In the principal roots of *Danaea nodosa* and of *Danaea simplicifolia*, two of the radial species, the stereome forms a fairly wide zone near the periphery of the cortex, whilst lignified tissue (excluding the tissues of the xylem) also occurs in an axile position (Text-fig. 33, B). Considered from the point of view of mechanical efficiency, this distribution of the stereome would enable these roots to withstand effectively both crushing and pulling strains. Now, although the basal portion of the massive more or

less upright caudex of these species rests upon the soil (often consisting of loose forest humus), the greater part of its weight is supported by the roots, which apparently function in much the same way as the so-called prop roots of certain mangrove plants, e.g. *Rhizophora*. In this connexion it should be remembered that the stem of all known genera of Marattiaceae is characterized by the complete absence of sclerenchyma.¹

On the other hand, the main roots of *Danaea alata*, which is a much less bulky plant with a horizontal rhizome (Pl. XXI, Fig. 2), differ from those described above in the much feebler development of the peripheral zone of stereome (cf. Text-fig. 33, A, with 33, B). Whereas in the roots of *Danaea alata* this zone is frequently only a single layer of cells in thickness, in the roots of *Danaea nodosa* and of *Danaea simplicifolia* as many as six layers were observed. A corresponding difference was noticed by Campbell (20, p. 179) between the roots of *Danaea jamaicensis* (= dorsiventral species) and of *Danaea elliptica* (= radial species) respectively.

If we except the 'stone'-cells which occur sparingly in the cortex of roots of *Angiopteris*, this peripheral zone of stereome is entirely wanting from the main roots of all the other known genera of Marattiaceae (Text-fig. 33, C), the adult plants of which possess either a strictly dorsiventral rhizome (e.g. *Kaulfussia*) or a massive conical stem (e.g. *Angiopteris*, *Macroglossum*, and *Marattia*). In both cases the entire weight of the plant is borne by the substratum, the stem therefore requiring anchorage only; this need is well supplied by the main roots, which act as stays, their anatomical structure being well fitted for withstanding a pulling strain.

DISCUSSION.

Two main points of theoretical interest emerge from the statements found in the preceding pages. Firstly, the question as to whether the radial or the dorsiventral type of symmetry is primitive in the Marattiaceae, and secondly, the question as to whether the results derived from a comparative study of the morphological, anatomical, and histological characters in this group of Ferns give any clear indication of the probable affinities of this family.

We will now briefly consider the first question. According to Campbell (20), the organization of the embryonic plant (excepting *Kaulfussia*) is from the very beginning of its development strictly radial, the vertical growth of the young sporeling being initiated by the primary segmentation (or basal) wall of the fertilized ovum; this wall in all genera of Marattiaceae is always transverse, with the result that the first leaf, or cotyledon, arising from the half of the embryo which is turned away from the

¹ 'Stone'-cells are sometimes found near the periphery of the cortex of the rhizome of *Danaea alata*.

archegonium, grows straight upwards and eventually pierces the prothallium, emerging on its upper surface (cf. Campbell, 20, p. 138, Fig. 108, A). The root, which in this family is a strictly endogenous structure, as soon as its apex is established, rapidly increases in length, and with the cotyledon, which in the meantime has been growing actively upward, forms almost a straight line, so that the young sporophyte may be described as bipolar (cf. Campbell, 20, p. 145). Thus the evidence derived from a consideration of the Marattiacean type of embryogeny points clearly to a radially organized ancestry for this group of Ferns.

Strong evidence in favour of this view can also be derived from a comparative study of the structure and development of the skeletal framework in this family. In every genus and species, with the exception of *Kaulfussia*, the shoot of the young sporophyte, for a time at least, is radially organized, the earliest leaves forming an irregular spiral around the stem, and in the case of *Marattia*, *Macroglossum*, certain species of *Danaea* (e. g. *D. nodosa*, *D. elliptica*, and *D. simplicifolia*), and probably *Archangiopteris*, this radial organization of the shoot is permanently retained. However, in other species of *Danaea*, as for example *D. alata*, *D. Fenmani*, &c., the apex of the shoot sooner or later bends over and growth proceeds horizontally, the leaves being for the most part confined to the dorsal and lateral surfaces of the rhizome whilst the roots arise from all sides of the stem.

Lastly, we have in *Kaulfussia* a plant in which a dorsiventral structure is indicated at a very early stage, the second leaf arising quite close to the cotyledon and on the same side of the stem-apex (cf. Campbell, 20, p. 156; 19, p. 79). The distichous arrangement of the leaves, thus early initiated, is retained permanently on the slender creeping rhizome of this genus. Campbell (l. c., p. 218) maintains that *Kaulfussia* is probably the most primitive of the living representatives of the Marattiaceae; in the opinion of the present writer, however, this view is untenable, since not only is this genus the most aberrant type externally, but the comparatively simple type of vascular anatomy found in the adult rhizome is to be regarded as a derived or specialized condition correlated with the habit of the plant.

I have omitted *Angiopteris* from the series traced above because there has been considerable divergence of opinion with regard to the symmetry of the axis of this plant. According to the observations of Campbell (20, p. 201), plants of *Angiopteris* growing upon level ground are always strictly radial in structure.

Farmer and Hill (29, p. 380) remark that 'both *Marattia* and *Angiopteris* also exhibit a tendency to dorsiventrality, but it is not very marked in young plants', while Shove (58, p. 521) states that the stem of *Angiopteris* examined by her presented definite dorsiventrality. Charles

(23, p. 84) found that the tendency to dorsiventrality shown by older *Angiopteris* stems did not appear in *Marattia*, although the specimens of *Marattia* which she examined were gathered from steep banks (23, p. 83).

An examination of a very considerable number of plants of *Angiopteris evecta* of all ages and sizes was undertaken by the present writer in order to decide this question, with the result that of thirty-six specimens examined twenty were found to possess a strongly dorsiventral stem (cf. Pl. XXII, Fig. 10),¹ six had an obliquely ascending axis, whereas only ten exhibited a strictly radial configuration of the stem. The present writer was therefore led to the opinion that the genus *Angiopteris* does show a marked tendency towards dorsiventrality, especially in older plants. Against the view that the change in direction of growth of the stem depends entirely upon the slope of the ground, it can be urged that several of the large plants of *Danaea nodosa* examined by the author were gathered by Dr. Chandler from a very steep bank, and yet they exhibited a strictly radial symmetry.

The statements of Miss Charles (23, pp. 83-4) with reference to *Marattia alata* also show that the configuration of the shoot is quite independent of the position of the plant. No signs of dorsiventrality were observed in *Marattia*.

In the case of the genera and species with upright radial axes, the skeletal framework is developed more or less uniformly all round, and, if we except the leaf-insertions, it is usually so, also, in the horizontal rhizomes of the adult sporophytes of *Danaea alata* and of *Angiopteris evecta*; however, Shove (58, p. 521) asserts that the specimen of *Angiopteris* which she examined presented definite dorsiventrality, not only in its external morphology, but also in its vascular anatomy, the meshes of the stelar lattice-work on the lower (= ventral) surface being long drawn out and with few anastomoses between the strands.

The present writer agrees with Farmer and Hill (29, p. 380) that the occurrence of large diamond-shaped gaps, similar in many respects to leaf gaps, upon the ventral surface of the skeletal framework of the markedly dorsiventral adult rhizomes of *Danaea alata* and of *Kaulfussia* indicates that the dorsiventrality, which these plants now exhibit, was probably acquired from a radially formed ancestor, the interior anatomical characters corresponding to such a disposition having been to a varying extent retained.

In the following table the degree of dorsiventrality exhibited by young and old plants respectively of all the genera and species of Marattiaceae at present known is summarized in convenient form :

¹ In the specimen of *Angiopteris* figured, which was quite an old plant, the bases of only two weakly developed leaves were found on the ventral surface of the stem; the roots, on the other hand were restricted to the ventral surface.

	Young Sporophyte.		Adult Sporophyte.	
	Orientation of Shoot.	Organization of Shoot.	Orientation of Shoot.	Organization of Shoot.
<i>Marattia</i>	Vertical	Radial	Radial	Radial
<i>Macroglossum</i>	"	"	"	"
<i>Archangiopteris</i>	" (!)	" (!)	" (!)	" (!)
<i>Angiopteris</i>	"	"	} Obliquely ascending, or horizontal	} Dorsiventral
<i>Danaea simplicifolia</i>	"	"		
" <i>nodosa</i>	"	"	} " or Obliquely ascending	} "
" <i>alata</i>	"	"		
<i>Kaulfussia</i>	"	Dorsiventral	"	"

Two main factors can be recognized as having played an important part in the evolution of the wide range in form of the Marattiacean stem, namely (i) the remarkable megaphylly of these plants and (ii) the complete absence of stereome (other than isolated 'stone'-cells) in their stem-tissues. In every genus the adult fronds are relatively large and require a large surface for their attachment, although it should be remembered that in many species comparatively few leaves are unfolded at once, and that these leaves are confined to the apical region of the stem. In this respect the Marattiaceae and Ophioglossaceae show close agreement.

In order to support, and also to supply sufficient surface for the attachment of the large fronds, it would be necessary for an upright stem to become greatly elongated, in which case a development of stereome (such, for example, as we find so well exemplified by the V-shaped bands of sclerenchyma that occur in the stem of certain tree-ferns) would be essential. It is probably for this reason that none of the existing Marattiacean Ferns has adopted the 'tree' habit. The nearest approach to this type of stem is found in *Danaea nodosa* and *Danaea elliptica*, where the comparatively massive shoot assumes either a vertical or an obliquely ascending growth, and largely depends upon the stout adventitious roots for its mechanical support (Pl. XXII, Fig. 8).

While still retaining a strictly radial organization of the shoot, three genera of Marattiaceae (e.g. *Angiopteris*, *Marattia*, and *Macroglossum*) have adopted the squat, massive type of stem, which not only offers an extensive superficial surface for the attachment of the leaves and roots, but also relegates to the substratum the task of bearing the greater part of its weight. In these genera the roots act as stays and assist in keeping the plant anchored to the soil.

The most economical solution of this problem, however, is found in the relatively slender horizontal rhizome; here again the soil to a great extent relieves the stem of the necessity for supporting the weight of the leaves. This type of stem occurs in most species of *Danaea* (e.g. *D. alata*, *D. Fenmani*, &c.), in *Kaulfussia*, and sometimes in *Angiopteris*. With

reference to the last-named genus, it is interesting to note that the majority of the stems which exhibit pronounced dorsiventrality are generally more elongated and less bulky than the radial ones.

The general conclusions which may be drawn from a comparative study of the morphological, anatomical, and histological characters of the Marattiaceae may be briefly summarized as follows :

1. The modern representatives of the Marattiaceae, as exemplified by the six genera *Angiopteris*, *Archangiopteris*, *Danaea*, *Kaulfussia*, *Macroglossum*, and *Marattia*, undoubtedly form a very natural and homogeneous group, as is shown by the following characters which they share in common :

- i. Arrangement of the vascular strands in the stem.
- ii. Structure of the vascular strands in the stem ; e.g. anomalous position of the protophloem ; structure and irregular distribution of the endoderms ; position of the protoxylem ; structure of the xylem and phloem elements.
- iii. General morphology of the frond.
- iv. Arrangement of the vascular strands in the petiole.
- v. Absence of sclerenchyma from the stem-tissues.
- vi. Bud-protection devices.
- vii. Anatomy of the root.
- viii. Presence of an endotrophic mycorrhiza (West, 70).
- ix. Apical meristems of stem and root.
- x. Presence of lysigenous mucilage canals (West, 68).
- xi. Presence of tannin cells or tannin ducts (West, 68).

These genera also show a striking similarity with regard to their

- xii. Spore-producing members, e.g. the radiate uniseriate type of sorus (cf. Bower, 8).
- xiii. Embryogeny (cf. Campbell, 17, 18, 19, 20, 21).
- xiv. Gametophytic structures, e.g. prothallia, sexual organs (cf. Campbell, 17, 19, 20, 21).

2. The Marattiacean Ferns occupy an isolated position among modern Vascular Cryptogams.

Considered from the point of view of their morphological, anatomical, and histological characters, as summarized above, the Marattiacean Ferns are very sharply marked off from all other modern groups of Vascular Cryptogams, with the possible exception of the Ophioglossaceae. But whilst admitting with Campbell (20, p. 218) the possibility of a common origin for the Marattiaceae and Ophioglossaceae from the same primitive stock, the present writer is of the opinion that these two families have proceeded along widely divergent lines from this common plexus, with the result that by comparing *individual* surviving genera from these two families

it is impossible to demonstrate any satisfactory evidence of phyletic relationship.

The geographical distribution of the living genera of Marattiaceae suggests that these plants represent the remnants of a much larger group, which, according to the available evidence derived from what is provisionally believed to be their palaeontological record, dates back to the lower coal measures.

A considerable number of fern-like fructifications, e.g. *Ptychocarpus* (Renault, 50), *Cyathotrachus* (Watson, 67), *Scolecopteris* (Strasburger, 63), *Danaeites*, &c., bearing a striking superficial resemblance to the sporangia or synangia of the modern genera of Marattiaceae, have been described from palaeozoic strata. Among these fossil fructifications are found types which closely resemble the spore-producing members of each of the surviving genera; this fact in itself would indicate that the modern genera of Marattiaceae are of equal antiquity, and suggests their possible multiple derivation from some primitive stock or plexus. As Bower (8, p. 73) pertinently remarks, perhaps no feature in the Marattiaceae is more remarkable than the persistence of type from the remote past to the present day.

Unfortunately, however, we cannot at present fix upon any links from strata of more recent geological eras, and, moreover, it is quite possible that all, or most, of these fern-like fossil fructifications which have been referred to the Marattiaceae are in reality the male fructifications of Pteridosperms; this evidence should therefore be accepted with reservation.

The doubts cast upon the hitherto generally accepted view of the Marattiacean affinities of the fossil genus *Psaronius* by Farmer and Hill (39, pp. 382-3) have been materially strengthened by the recent observations of Solms-Laubach (60) on the anatomy of this genus.

SUMMARY.

1. A comparative account of the structure and development of the stelar system in the Marattiaceae, with special reference to the adult sporophyte of *Danaea*, is given, and the question of the symmetry of the sporophyte in this group of Ferns is discussed. A primitive radially symmetrical type of shoot is distinctly suggested.

2. The single apical cell found in the apex of the stem of the young sporeling is later replaced by a group of equivalent initial cells or by a meristematic region.

3. A single large apical cell occurs at the apex of the primary and earliest adventitious roots. At the apex of the later adventitious roots of moderate size a group of about four equivalent initial cells is found, while the more robust roots generally possess a definite meristem consisting of a number of independent initial cells. In brief, the number of initial

cells found at the apex of the Marattiacean roots is clearly related to the bulk, and not necessarily to the age of these roots.

4. The six genera which comprise the Marattiaceae show remarkable uniformity in their morphological, anatomical, and histological characters, and constitute a very homogeneous and natural family, which probably occupies an isolated position amongst modern Vascular Cryptogams.

In conclusion, the author wishes to express his sincere thanks to Professor J. B. Farmer, F.R.S., not only for suggesting that this work should be undertaken, but also for his constant help and valuable advice throughout the course of this investigation; to Dr. S. E. Chandler, F.L.S., who supplied him with much valuable material of *Danaea*; and to Mr. C. H. Wright, A.L.S., for help in the identification of material.

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EXPLANATION OF FIGURES ON PLATES XXI AND XXII.

Illustrating Mr. West's paper on *Marattiaceae*.

ABBREVIATIONS.

c.s., commissural strand; *c.s.*', central stelar system; *c.s.*'', commissural strand of the central stelar system; *comp.s.*, compensating strand; *l.t.*, leaf-trace; *p.*, prothallium; *p.r.t.*, trace of the primary root; *r.t.*, root-trace; *st.*, stipule; *v.g.*, ventral gap.

PLATE XXI.

Fig. 1 A. *Danaea alata*, Sm. Model of the stelar system of the rhizome of a moderately large specimen, viewed from below. In this model the transition from the simpler vascular structure of the young sporophyte to the more complicated vascular structure of the adult sporophyte is clearly shown. The leaf- and root-traces are consecutively numbered in order of priority. An unusual feature of this plant was the absence of adventitious roots from the basal region of the rhizome; it was probably due to this abnormality that the older portion of the rhizome had so far successfully resisted decay; there is normally one root to each leaf of the young sporophyte. (N.B. The natural proportion between the length and breadth is here exaggerated in the ratio 1 : 2.)

F f 2

Fig. 1 B. Transverse section of the stele in the plane α, β , of the same model, showing almost perfect solenostelic structure.

Fig. 2. *Danaea alata*, Sm. Rhizome of an adult plant, showing the well-marked dorsiventrality. Nat. size.

Fig. 3. *Kaulfussia aesculifolia*, Bl. Model of the stelar system of a portion of the rhizome of an old plant, viewed from below (cf. Text-fig. 15).

Fig. 4. Sporeling of *Danaea alata*, Sm. Nat. size.

Figs. 5 and 6. Bud-protection in *Danaea alata*, Sm. The stipules (*st.*) of the young leaf completely envelop the next younger leaf. Slightly enlarged.

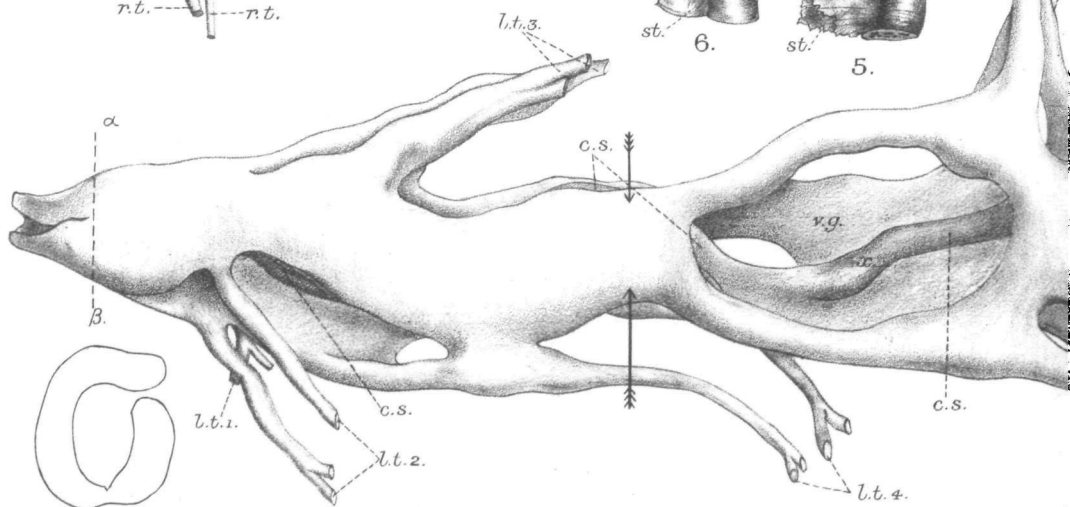
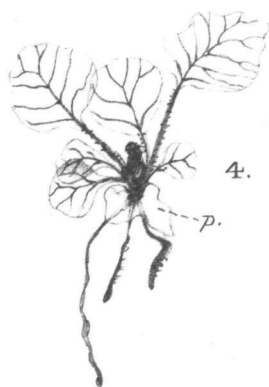
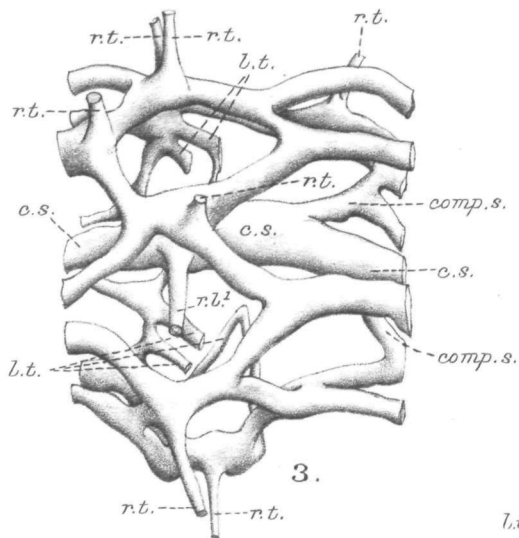
PLATE XXII.

Fig. 7. *Danaea alata*, Sm. Front view of the model represented in Fig. 1 A.

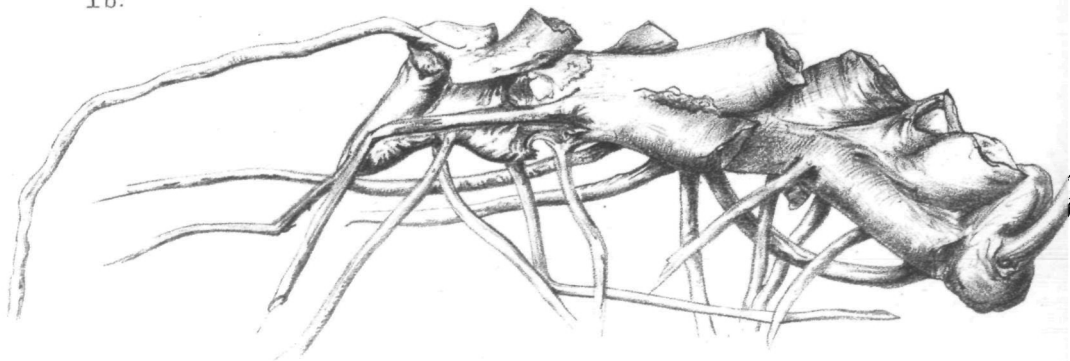
Fig. 8. *Danaea nodosa*, Sm. Large sporophyte, showing habit. The leaves had been artificially removed. $\times \frac{1}{2}$.

Fig. 9. A and B. Sporelings of *Danaea alata*, Sm., showing the inception of the dorsiventral habit. $\times \frac{1}{2}$.

Fig. 10. *Angiopteris evecta*, Hoffm. Rhizome of a moderately large plant, showing well-marked dorsiventrality. $\times \frac{1}{2}$.



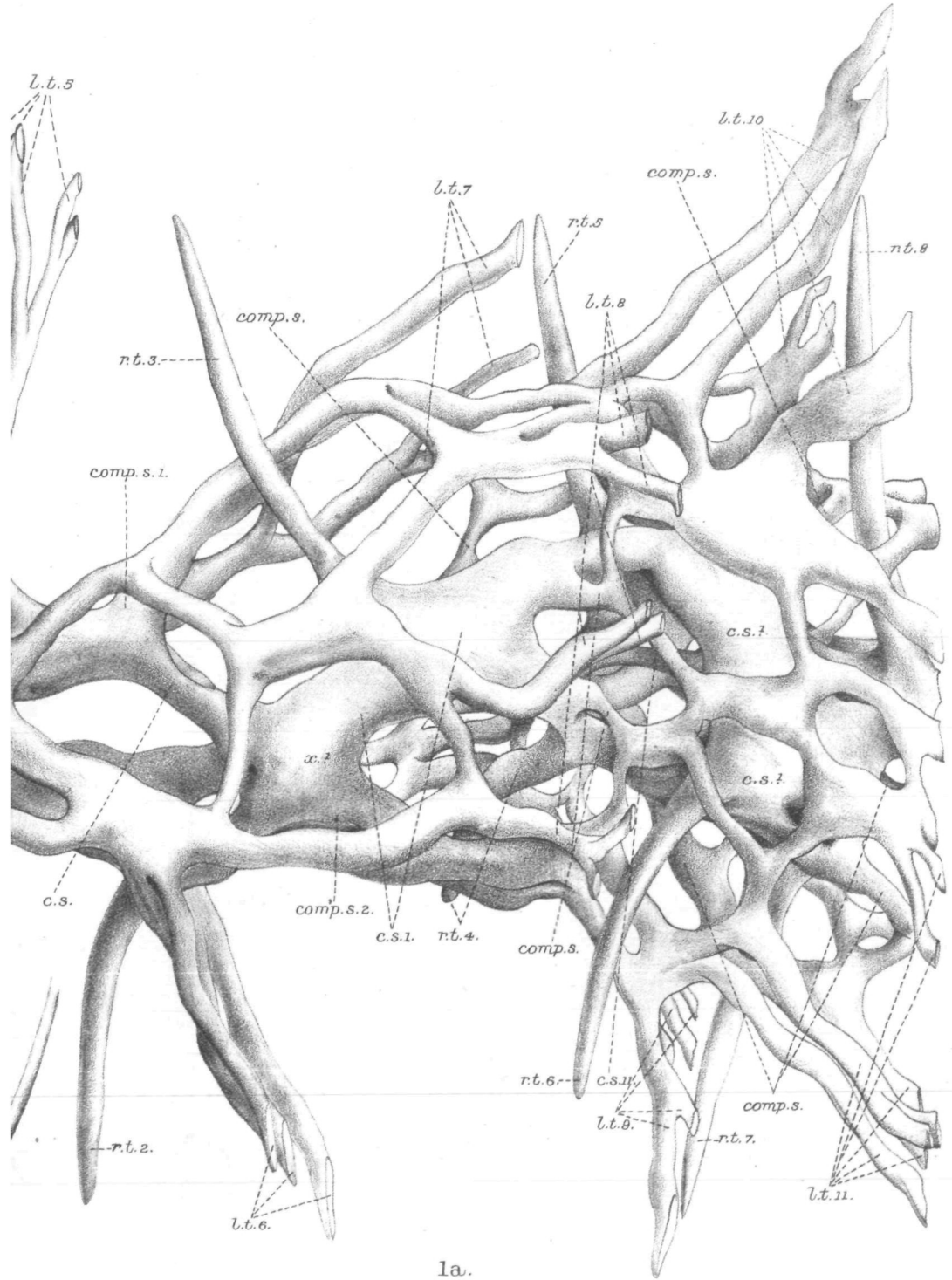
1b.



2.

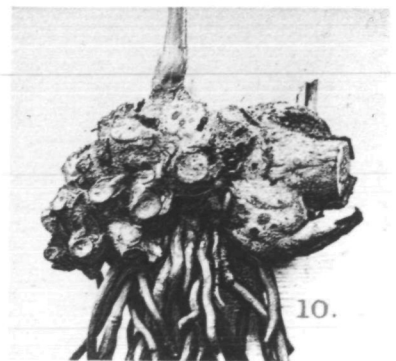
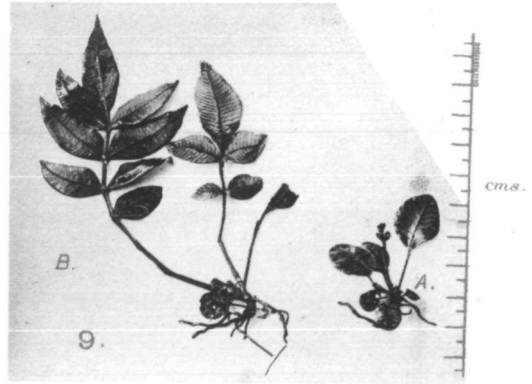
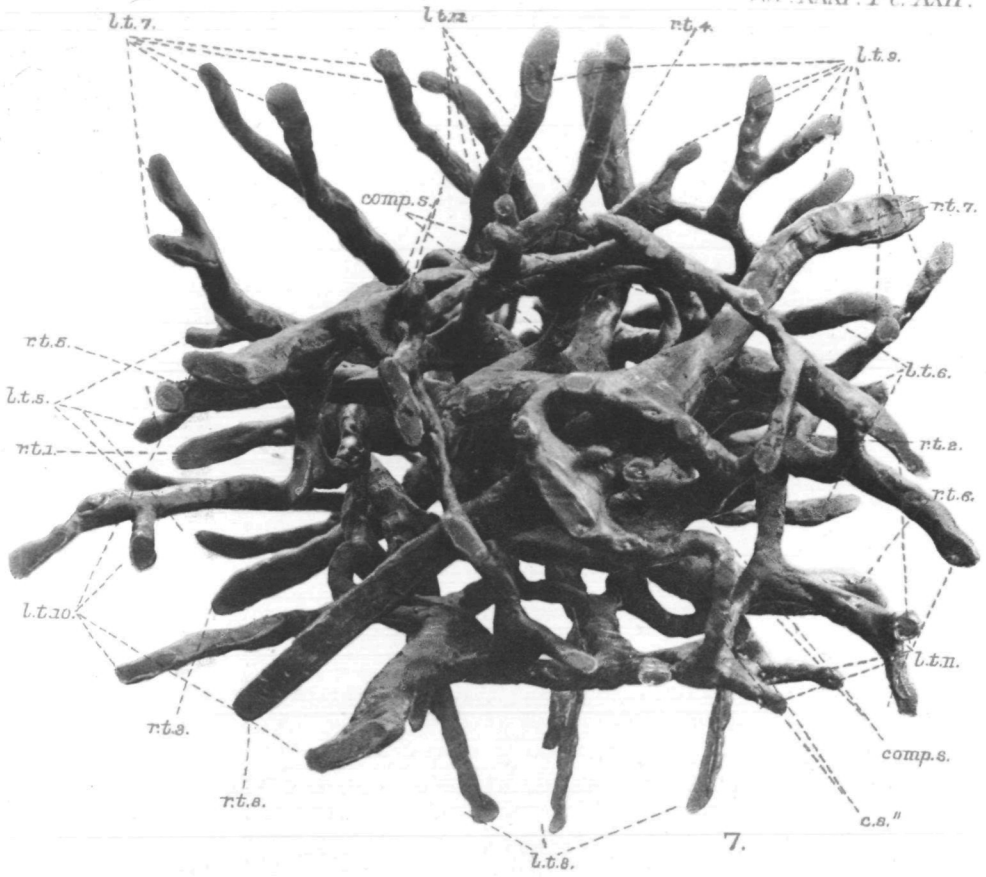
C. West del.

WEST — MARATTIACEAE:



1a.

Huth lith et imp



C.W. Photo

WEST-MARATTIACEAE.

Huth, coli.

