

On the Prothallus and Embryo of *Danaea simplicifolia*, Rudge.

BY

GEORGE BREBNER.

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With Plate IX.
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A LARGE number of young plants of *Danaea simplicifolia*, Rudge, were forwarded to the Royal Gardens, Kew, in the spring of 1895, by G. S. Jenman, Esq., F.L.S., Superintendent of the Botanic Gardens, British Guiana. At the suggestion of Dr. D. H. Scott, F.R.S., Honorary Keeper of the Jodrell Laboratory, I undertook the examination of the material.

Among the youngest plants a few prothalli were found, which showed an abundance of adult, as well as degenerating, archegonia, and also afforded sufficient material of healthy young and adult antheridia to enable their structure and development to be satisfactorily followed. Some of the archegonia contained embryos.

The fact that hitherto the prothallus and embryo of *Danaea* have not been described, makes the present opportunity rather a fortunate one, on account of the large amount of attention which is being given at present to the study of both the sporophyte and the gametophyte of the Marattiaceae.

PROTHALLUS.

In its essential characters the prothallus of *Danaea simplicifolia* agrees with that of the other genera of the

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Marattiaceae, in being more than one cell thick except at the margin, in having the archegonia distributed on a median cushion and the antheridia almost anywhere on the lower or upper surface. In general appearance the prothallus is somewhat different from that of *Angiopteris* and *Marattia* (cf. Figs. 1 and 2 with the prothalli figured by Jonkman¹, Farmer², and Campbell³).

The prothallus may, or may not, be deeply notched at the anterior growing margin (cf. Figs. 1, 2, and 3), and has evidently great capacity for long-continued growth, as in the other genera (cf. Figs. 3, 4, and 5). In some cases the prothalli attached to the young plants were nearly twice the diameter of those bearing embryos. As already indicated, the archegonia usually occur on a median cushion, the limits of which are not sharply defined. In one instance a small cushion, with a few archegonia, was found on one of the heart-shaped lobes quite remote from the median line and apical margin. This agrees with Prof. Campbell's statement, that⁴, in the Marattiaceae, 'the sexual organs of the lobes are *mainly* (the italics are mine) antheridia.'

The antheridia are truly ubiquitous, occurring freely on the under and upper surfaces of the main part of the prothallus, on the lobes, and also, but more sparingly, on the median cushion amongst the archegonia. Marginal cushions are not uncommon; they are literally studded with antheridia in such a manner that some of the antheridia open on the edge of the prothallus. The occurrence of antheridia on the lateral portions of the prothallus agrees with Luerssen's observations on *Angiopteris*⁵, which Jonkman was not able

¹ Jonkmann, H. F., La génération sexuée des Marattiacées. Archives Néerlandaises, T. xv. p. 199.

² Farmer, J. B., On the Embryogeny of *Angiopteris evecta*, Hoffm. Annals of Botany, Vol. vi. No. XXIII. October, 1892.

³ Campbell, D. H., (a) Observations on the development of *Marattia Douglasii*, Baker. Annals of Botany, Vol. viii. No. XXIX, March, 1894; (b) The Structure and Development of the Mosses and Ferns. Macmillan and Co., 1895, p. 254 et seq.

⁴ Loc. cit. (b), p. 258.

⁵ Luerssen, Ueber die Entwicklungsgeschichte des Marattiaceenvorkeims. Bot. Zeit. 1775; Medicinisch-pharmaceutische Botanik, Bd. I. p. 581.

to confirm in the prothalli examined by him¹; neither observer, however, found them on the actual margin. Even after the cotyledon of the young plant has completed its development, antheridia may still be found in process of formation on the prothallus (cf. Fig. 3 at *an.*).

Perhaps the most notable point about the prothallus of *D. simplicifolia* is that the rhizoids are septate, three or four transverse walls being readily observable (cf. Fig. 6). Prof. Campbell² mentions, with regard to the other genera of the Marattiaceae, that the 'root-hairs' of the prothallus are unicellular³. These rhizoids of *Danaea* remind one not a little of the protonema of a Moss.

ANTHERIDIUM.

The antheridia agree in every respect with those of *Angiopteris* and *Marattia*, at least with those which may be considered as of the normal type (cf. Fig. 12 with the corresponding figures of Jonkman and Campbell's papers). The figures for one genus would do almost as well for either of the other two. A modification in the usual mode of development, which has not been described for either *Angiopteris* or *Marattia*, was, however, noticed in *D. simplicifolia*, although there is no reason why it should not occur in these genera also. The usual process, to quote Prof. Campbell⁴, is as follows:— 'The antheridium arises from a single superficial cell, which first divides into an inner cell, the mother-cell of the sperm-cells, and an outer cover-cell. The latter divides by several curved vertical walls which intersect, and the last wall cuts off a small triangular cell, which is thrown off when the antheridium opens and allows the sperm-cells to escape. Before these are completed, however, cells are cut off from the adjacent cells of the prothallium, completely enclosing the mass of sperm cells.' The peculiarity observed in *Danaea*

¹ Loc. cit., p. 211.

² Loc. cit. (b), p. 257.

³ I was able to confirm this statement with regard to *Angiopteris*, Prof. J. B. Farmer having very kindly placed prothalli bearing young plants at my disposal.

⁴ Loc. cit. (a), p. 5.

is that not infrequently the formation of the curved intersecting vertical walls, even down to the last, may precede the horizontal wall, which cuts off the mother-cell of the sperm-cells (cf. Figs. 7, 9, and 10). All these figures were taken from antheridia developing on the prothallus, in which the mother-cells involved had already reached, or nearly reached, their adult condition before commencing to form the antheridia. In the case of the two latter figures, a developing antheridium of this type is represented, as seen from below (Fig. 9) and from above (Fig. 10). As far as the drawings permitted, corresponding walls have been lettered alike; but to realize the point clearly it might be as well to make a tracing of Fig. 10, and then turn it over and superpose it on Fig. 9, when the relation of the walls would at once become obvious. In Fig. 9 the two cells which will ultimately give rise to the spermatozoids are still quite young and merismatic, whereas in Fig. 10 the cover-cells have already reached their adult condition. This condition differs considerably from that represented by Prof. Campbell's Figs. 8, 9, and 10¹, where the growth of the antheridium as a whole goes on *pari passu* with that of the prothallus. As a result of the exceptional mode of development, in the most extreme case—and such was actually observed—there may be only a single vertical row of four spermatozoid-mother-cells visible in one plane, whereas in a normal case (e.g. Fig. 12) five vertical rows, each of four spermatozoid-mother-cells, may occur. Jonkman noted the fact that the number of spermatozoids formed in *Angiopteris* and *Marattia* was very variable, and gave as observed numbers 20–500 or even more².—This exceptional state of matters in *Danaea* can only be looked upon as a further reduction due to late development.

ARCHEGONIUM.

Material was not available for following the development of the archegonia, but the adult structure is essentially the

¹ Loc. cit. (a), Pl. I.

² Loc. cit., p. 214.

same as that of *Angiopteris*, as figured by Jonkman and Farmer¹, as also of *Marattia Douglasii*, Baker, figured by Campbell². Jonkman pointed out the fact that in *Angiopteris* the number of neck-cells in two of the vertical rows is frequently three, while in the other two it is four, sometimes four and five, rarely two and three respectively³. The last of these three conditions occurs most frequently in the case of *Danaea simplicifolia*, in which there are only two cells in two of the vertical rows and three in the other two. Jonkman likewise noted the variability in the formation of the accessory cells (*m.*), which are cut off from the cells adjacent to the developing archegonia. In *D. simplicifolia* this variability seems to be carried further, so that comparatively rarely were archegonia seen with the full complement of these cells. The corresponding cells of the antheridium (cf. Figs. 9 and 12, *m.*) are much more constant, a fact which is readily understood, since they are doubtless functional in aiding the discharge of the spermatozoids at maturity. In Fig. 13 the structure marked *sp.* is in all probability a spermatozoid, *ov.* is the ovum. In Fig. 14 the condition of the neck, already referred to, is quite obvious, there being only two neck-cells on one side and three on the other. In the case of Fig. 13 it was seen that the two rows behind, which could not be figured, consisted each of three neck-cells⁴.

EMBRYO.

Embryos in the earlier stages of development were not found, the youngest being represented in Fig. 15. It was obtained from the prothallus of Fig. 2, and forms a good sequel to Prof. Campbell's Fig. 22⁵. Most of the divisions of the latter are still fairly readily recognizable in the former. This figure was taken from a hand-section, and its exact

¹ Loc. cit., Fig. 1.

² Loc. cit. (a), Fig. 16.

³ Loc. cit., p. 216.

⁴ For theoretical considerations concerning the affinities of the Marattiaceous archegonium, see Campbell, loc. cit. (a), p. 7.

⁵ Loc. cit. (a).

position could not be determined, although there is every reason to believe that it was not far off the median line¹.

Prof. Farmer², and likewise Prof. Campbell, states that it is the anterior epibasal octants which give rise to the cotyledon. The embryos of Figs. 16 and 18 agree with their observations in this respect, as they were in both cases presumably developed near the growing apex of the prothallus, at least for the time being, the cotyledon being anterior. With regard to the embryo of Fig. 16, it was impossible to say which was the original axis of growth, as the development of the prothallus had been exceedingly erratic. The embryo of Fig. 18 was from the prothallus of Fig. 1, in which its position is indicated by the black dot. With regard to Fig. 15 from the prothallus of Fig. 2, the direction of the growing margin is indicated by the arrow; but as this section is not median, it is impossible to decide which epibasal octants are giving rise respectively to stem and to cotyledon. With a view to try and settle this point for *Danaea simplicifolia*, as embryos were not available, a young plant which had only expanded its first leaf, or cotyledon, was microtomed along an axis at right-angles to the growing edge, as there was some doubt about the attached prothallus being entire; in fact, it was probably only a large lobe with an adventitious cushion. Be that as it may, this series showed without a doubt that the cotyledon must have been developed from the *posterior epibasal* octants, and the stem-apex from the anterior, unless there had been subsequent rotation. This seems to indicate that in *Danaea*, at least, the orientation of the embryo is not constant. Seeing that the embryo penetrates vertically through the prothallus, any definite orientation as regards its epibasal octants becomes unimportant, so long as they are turned towards the upper side. This consideration gives the clue to the inconstancy observed³.

¹ Careful re-examination of the sister-section, which is rather thick, has shown that it contains the apical cell (or cells?) of the stem and cotyledon, and that in it the line II . . . II divides the embryo more nearly into two equal halves.

² Loc. cit., p. 267.

³ This question cannot be considered as really settled till a far greater number

COTYLEDON.

The adult cotyledon is a very simple spatulate leaf without stipules¹ (cf. Figs. 3 and 4), and the venation is monopodial in its branching, thus agreeing with *Angiopteris*² and differing from *Marattia Douglasii*³.

The vascular bundle is very simple, consisting sometimes of only two or three tracheids and a small amount of phloem. It may be considered collateral, but this depends on whether the layer of parenchymatous cells towards the upper surface is to be looked upon as phloem or otherwise. Certain it is that phloem, with recognizable sieve-tubes, occurs only on the underside and flanks of the bundle.

THE STEM.

The primary stem, which is comparatively short, has a small concentric bundle, or stele, of the ordinary Marattiaceous type, and is somewhat elongated in the same plane as the diarch xylem-plate of the root, the stele of which merges so gradually into that of the stem that it is impossible to determine where the one ends and the other begins. With regard to the phloem, the transition first shows itself by a gradual increase in the number of the thin-walled elements at the poles of the xylem-plate of the root, so that the protoxylem no longer abuts directly on the endodermis, or is separated from it by

of embryos have been examined under conditions more favourable for determining their orientation.

¹ *Danaea* agrees with the other genera of the Marattiaceae in having well-developed stipules to the older fronds, and, moreover, the sclerenchyma of the petiole, &c. is of the usual Marattiaceous type. Holle in his paper '*Ueber die Vegetationsorgane der Marattiaceen*' (Sitzung der Königlichen Gesellschaft der Wissenschaften zu Göttingen, Jan. 8, 1876), made a mistake in these two respects, which was subsequently corrected by Kühn (*Ueber den anatomischen Bau von Danaea*, Flora, 1890), who pointed out that *Danaea* differs anatomically in no essential respect from the rest of the Marattiaceae. There is little doubt, as Kühn suggests, that Holle had incorrectly-named specimens to deal with. I myself have had the opportunity of verifying Kühn's statements in several species of *Danaea*.

² Farmer, loc. cit., Fig. 19.

³ Campbell, loc. cit. (a), p. 11 and Fig. 27.

only one thin-walled element. Passing upwards, the thin-walled tissue in question increases in amount till it becomes recognizable as part of the phloem of the primary stem. With regard to the xylem, the details of the junction of the stele of the root with that of the stem could not be made out with anything like certainty; this was also the case with regard to the transition from the xylem of the stem to that of the cotyledonary trace. All that can be safely said is that in both cases the elements in the transitional region seem to be exclusively scalariform tracheids¹. The stele of the primary stem has a well-marked endodermis (Fig. 20, *en.*), and in this *Danaea* agrees with *Angiopteris*², but differs in not having a central mass of parenchymatous tissue. Fig. 20 shows the stele just about to divide to form the traces of the cotyledon and of the second leaf. In some cases, as already mentioned, the xylem of the cotyledon consists of only two elements, arranged side by side in the tangential plane. In such a case it is obviously impossible to speak of a protoxylem as distinguished from a later formed xylem. In cotyledons with more vigorous bundles, protoxylem is readily enough recognizable on the inner (axial) side; it is not, however, composed of spiral elements, but of delicate tracheids of narrow calibre with wide scalariform pits. The arrangement of the steles in the stem of young and older plants need not be discussed here³, but the mode of succession of the first three leaves is exactly the same as in *Angiopteris*, as described by Prof. Farmer⁴, and thus the first part of the spiral is laid down; the anatomy, however, becomes subsequently much complicated by anastomoses of the steles. The adventitious roots seem to arise much later than in *Angiopteris*, in which the *second* leaf already has its accompanying adventitious root

¹ The series of microtome-sections obtained through the parts in question were not very successful, and the young plants were not at the best stage for the purpose.

² Leclerc du Sablon, *Recherches sur la tige des fougères*. Ann. des Sciences naturelles, 1890, T. ii.

³ This question will be more fully treated in a paper on the comparative anatomy of the Marattiaceae, which is in process of preparation.

⁴ Loc. cit., p. 270.

which emerges just beneath the cotyledon¹. In plants of *Danaea simplicifolia*, in which several leaves had already expanded, there was no external evidence of adventitious roots. These, when they do appear, come out through the bases of the leaves next below those to which they belong, and for a long time, at any rate, there is only one root to each leaf.

The ground tissue of the primary stem is composed of ordinary parenchyma being fairly bulky. Tannin-sacs² of the ordinary Marattiaceous type early make their appearance, but the mucilage-canals do not do so till comparatively late, there being no sign of them in the first few leaves at any rate.

THE ROOT.

The primary root has a simple diarch stele, the xylem-plate lying in approximately the same plane as the bundles of the first two leaves. The phloem occupies the usual position, and is of the kind characteristic of the group. *Danaea* agrees with *Angiopteris*³ in having a diarch xylem-plate, but differs from *Marattia Douglasii*, which has usually a tetrarch stele⁴. There is a well-marked endodermis, and again in this respect *Danaea simplicifolia* agrees with *Angiopteris* and differs from *M. Douglasii*⁵.

The primary root emerges from the prothallus long before the cotyledon (cf. Fig. 8). The embryo of this figure was, it is true, the only one sufficiently advanced to show this; but there is no reason to regard this as other than the normal case. Moreover, two of the embryos figured by Prof. Farmer show a tendency in the same direction⁶. This seems to completely nullify the importance attached to the converse condition, found in *M. Douglasii*, by Prof. Campbell⁷.

It is rather interesting to note that the root-hairs of the primary root are of exactly the same type as the rhizoids of

¹ Farmer, loc. cit., p. 270.

² Farmer, loc. cit., p. 269.

³ Leclerc du Sablon, loc. cit.

⁴ Campbell, loc. cit. (a), p. 14.

⁵ Loc. cit. (a), p. 14.

⁶ Loc. cit., Figs. 9 and 10.

⁷ Loc. cit., p. 14.

the prothallus, viz. long narrow hairs with a few transverse walls, the component cells being distinctly uni-nucleate. The figure of the rhizoid of the prothallus would do just as well for a root-hair of the young sporophyte.

APICAL GROWTH.

The vexed question of the apical growth in stem, root, and cotyledon is not much cleared up by the stages secured in *D. simplicifolia*. The stem of the embryo, represented in Fig. 16, seems to have a well-marked single apical cell at *st*. This is represented on a larger scale in Fig. 17. There is probably a certain amount of obliquity in this section, as the young bundle is not seen passing into the cotyledon at this point, but in the fourth preceding section of the series. This much is certain, however, that the cell in question is absolutely the largest anywhere near the apex of the stem, and likewise possesses the largest nucleus. On account of its size, and of its position in relation to the cotyledon, it is practically certain that it is the apical cell. With regard to the embryo of Fig. 18, there is probably still a single apical cell in the growing-point of the stem, but rapidly approaching the time when it will be merged in a group of equivalent initials. It is already hardly, if at all, larger in size than one or two of the adjacent cells, but its nucleus is undoubtedly the largest and at the same time richest in chromatin (cf. Fig. 19); hence, in all probability, it is the apical cell. In a series of transverse sections of a plantlet, in which only the cotyledon had expanded, and of which the second leaf was still quite young, the stem had a single apical cell with a four-sided base. The cotyledon of this plantlet was the one already referred to as having a very feebly developed bundle, the xylem consisting of only two elements. In somewhat more advanced plantlets it was quite impossible to fix on any particular cell as the apical cell, and in these cases there would be little doubt that the apical meristem consisted of a small number of equivalent initials.

With regard to the cotyledon, the somewhat late stages

available showed no definite single apical cell, and Prof. Campbell found the same to be the case with *Marattia Douglasii*¹. A plantlet was investigated in which, besides the cotyledon and a quite young second leaf, there was the earliest rudiment of a third; but this rudiment seemed already to have a two-celled apex, one of the cells being in the last stage of karyokinesis, although the new anticlinal wall had not been formed. Hence it is exceedingly probable that in the case of the cotyledon and the subsequent leaves, if at any time there is a single apical cell it can only be of exceedingly transitory duration.

The root presented the same difficulty; the only promising young embryo, Fig. 16, did not show any cell, or cells, which could be recognized as constituting the growing-point of the future root. The root of Fig. 8 might have shown the condition at a later stage, but it unfortunately got broken off before imbedding and was sectioned by hand. It does not show anything decisive. Attempts were made to study the primary roots of young plants, but these were nearly all either actually injured, or in such bad condition at the tip as to make otherwise successful microtome-sections useless. In one case, however, a longitudinal section (one of a microtome-series) was obtained which showed a remarkably large cell which, judging from its position and the condition of the adjacent tissues, seemed to be the apical cell, although it was not quite axially median. Sections of the adventitious roots left no doubt that, in their case at least, the growing-point consisted of a few equivalent initials, in one case a well-marked group of four.

SUMMARY.

The genus *Danaea*, as exemplified by *Danaea simplicifolia*, Rudge, is found to agree very closely with *Angiopteris* and *Marattia*, both in the gametophyte and in the embryo-sporophyte. Perhaps the most important point of difference is the presence of septate, or multicellular, rhizoids in the former

¹ Loc. cit., p. 11.

genus, whereas they are unicellular in the two latter genera. It is possible this may be found to have phylogenetic importance, and strengthen the view that the Eusporangiate Ferns and the Mosses had a not very remote common ancestor.

The exceptional mode of development of the antheridia, in certain cases, resulting in the formation of a very small number of spermatozoids, is probably due to the antheridium as a whole being developed from a cell which was nearly, or quite, adult.

The archegonia present no features which are not likewise characteristic of *Angiopteris*, *Marattia*, and presumably *Kaulfussia*.

The structure of the growing-point of the stem of *Danaea* seems to be very much in the same condition as in the other two genera which have been studied. It appears in fact to be still in the transition stage from a single apical cell to a group of equivalent initials. It is interesting to note that *Danaea*, which is usually placed lowest in the scale among the Marattiaceae, is the genus which presents the clearest indications of a single apical cell. There can be little doubt, in view of the results obtained, that the Marattiaceae are descended from an ancestor whose growing-point presented a well-marked single apical cell, that being really the primitive type of growing-point throughout for the great Fern-series.

The apical meristem of the cotyledon and subsequent leaves does not seem at any time to obviously possess an apical cell, and in this also there is agreement with the other genera.

The primary root, until further evidence is forthcoming, may be considered to have a single apical cell; but the subsequent adventitious roots have a group of equivalent initials, sometimes clearly four.

The stele, both of the stem, and of the root, has a distinct endodermis, agreeing in this with *Angiopteris* at any rate. The root-stele merges directly in that of the stem, the latter

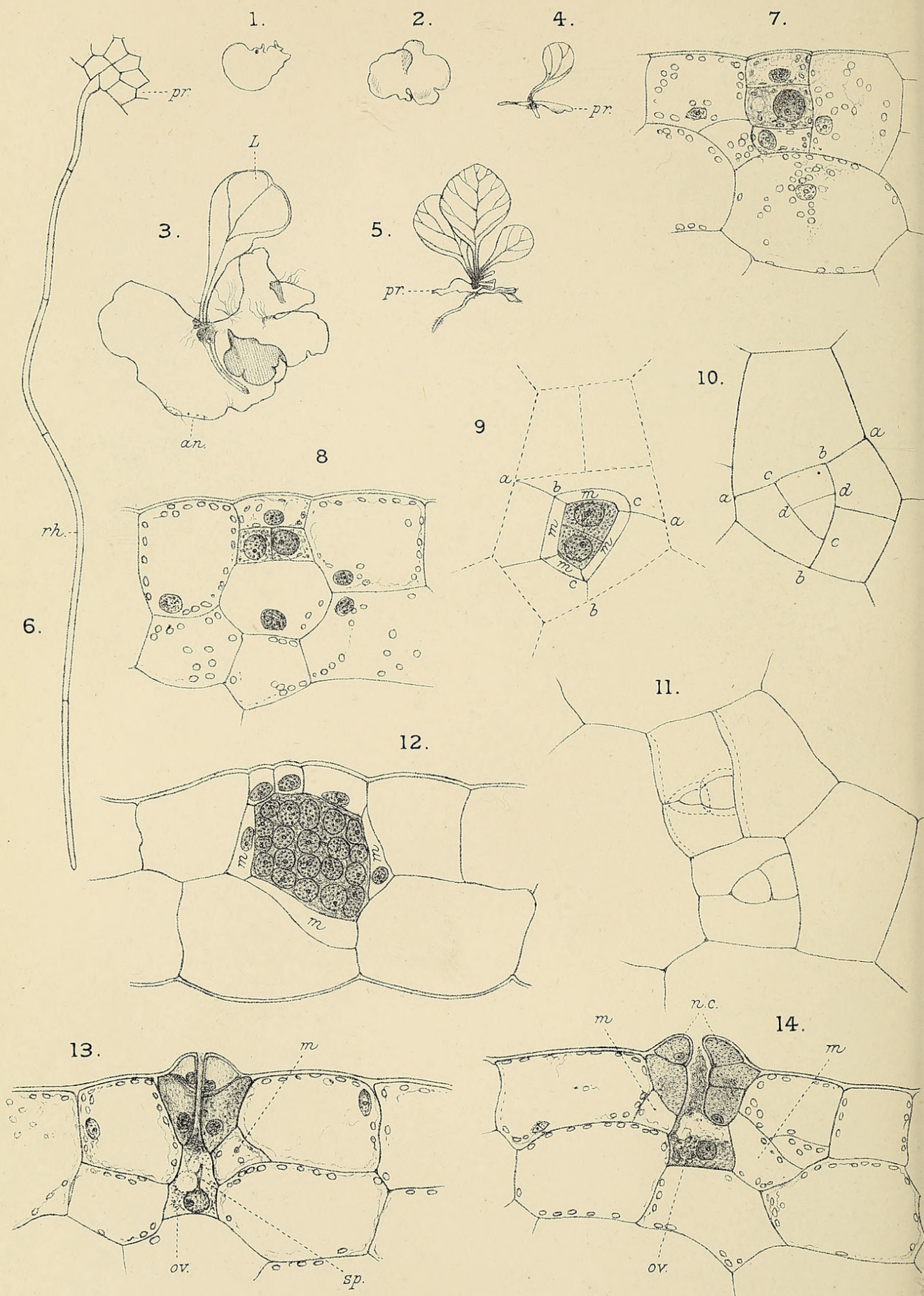
(i. e. stele of the stem) of course consisting of the leaf-trace-bundle of the cotyledon until complications arise through the addition of the subsequent leaf-traces. The junction is effected by ordinary scalariform tracheids.

Note.—In No. 15 of the *Botanisches Centralblatt* for 1896 (Band LXVI, p. 49), Jonkman has a preliminary communication on the embryogeny of *Angiopteris* and *Marattia*, the special interest of which lies in the fact that the embryos were obtained by cultivation. He, so far, does little more than confirm previous observations; the most important point, however, being that he finds that the growing-point of the embryonic stem consists of a few initials, and that of the root of four. This agrees in the main with the results of previous observers; but Jonkman is disposed to consider these conditions as constant, whereas Prof. Campbell and, in the present paper, myself are of the opinion that there is a certain amount of inconstancy, and that occasionally, if not frequently, the embryonic stem, as also the root, has a single apical cell. It is somewhat interesting that Jonkman finds in *Angiopteris* and *Marattia* a group of four equivalent initials in the growing-point of the primary root, a number which was found in the young adventitious roots of *Danaea simplicifolia*, although the condition of the primary root was not satisfactorily made out in the latter. Prof. Farmer had come to the conclusion, with regard to *Angiopteris evecta*, Hoffm., that in the embryonic root there is a single apical cell, which has a very transitory existence as such.

EXPLANATION OF FIGURES IN PLATE IX.

Illustrating Mr. Brebner's paper on the prothallus and embryo of *Danaea simplicifolia*, Rudge.

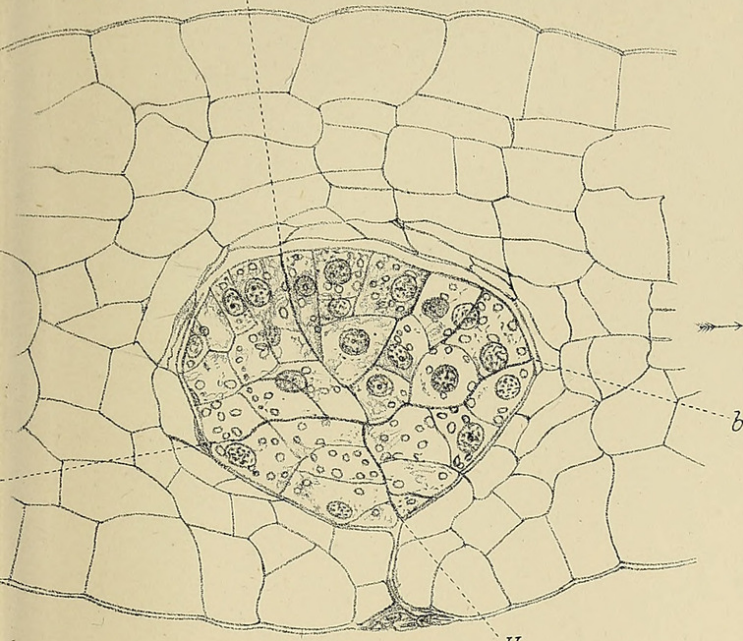
- Figs. 1 and 2. Prothalli. Nat. size.
Fig. 3. Young plant attached to prothallus, with only the cotyledon expanded: *an.*, developing antheridia. $\times 2\frac{1}{2}$.
Fig. 4. Similar to preceding: *pr.*, prothallus. Nat. size.
Fig. 5. Young plant still attached to prothallus, *pr.*, showing three young leaves and the bases of the two first. Nat. size.
Fig. 6. Rhizoid, *rh.*, of prothallus, *pr.* $\times 50$.
Fig. 7. Young antheridium originating from adult cell of prothallus. $\times 350$.
Fig. 8. Young antheridium, slightly older than the preceding, and showing the first division of the mother-cell of the sperm-cells. $\times 350$.
Fig. 9. Young antheridium, similar to preceding, seen from below: *m.*, peripheral cells. $\times 350$.
Fig. 10. Cover-cells of preceding, seen from above. $\times 350$.
Fig. 11. Cover-cells of empty antheridia, seen from above. The dotted lines in one of the sets indicate the thickness of the cells seen in perspective. $\times 350$.
Fig. 12. Nearly mature antheridium: *m.*, peripheral cells. $\times 350$.
Fig. 13. Mature archegonium: *ov.*, ovum; *sp.*, probably a spermatozoid. $\times 350$.
Fig. 14. Mature archegonium: *ov.*, ovum; *n.c.*, neck-cells. $\times 350$.
Fig. 15. Vertical section of a youngish embryo, not quite median: *b.b.* basal wall; *ll. ll.*, transversal wall. Arrow indicates direction of growing-point of prothallus. $\times 250$.
Fig. 16. Vertical section of an older embryo: *st.*, growing-point of stem; *L.*, cotyledon. $\times 200$.
Fig. 17. Growing-point of stem of the same. $\times 400$.
Fig. 18. Vertical section of a still older embryo: *st.*, growing-point of stem; *L.*, cotyledon; *r.* root. $\times 100$.
Fig. 19. Growing-point of stem of the same. $\times 400$.
Fig. 20. Transverse section of stele of the stem at junction of first and second leaf-traces: *L. b.*, cotyledon bundle; *en.* endodermis. $\times 400$.



G. Brebner del.

15.

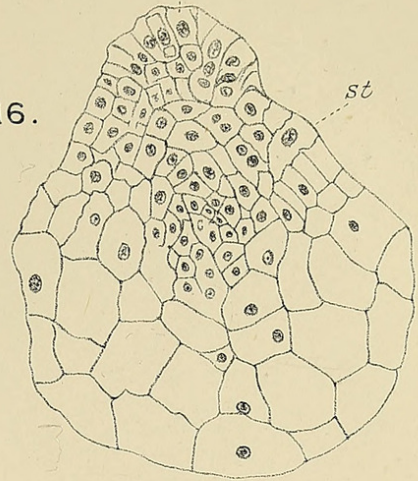
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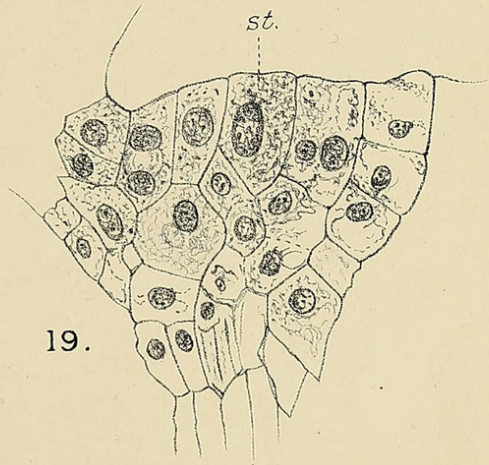
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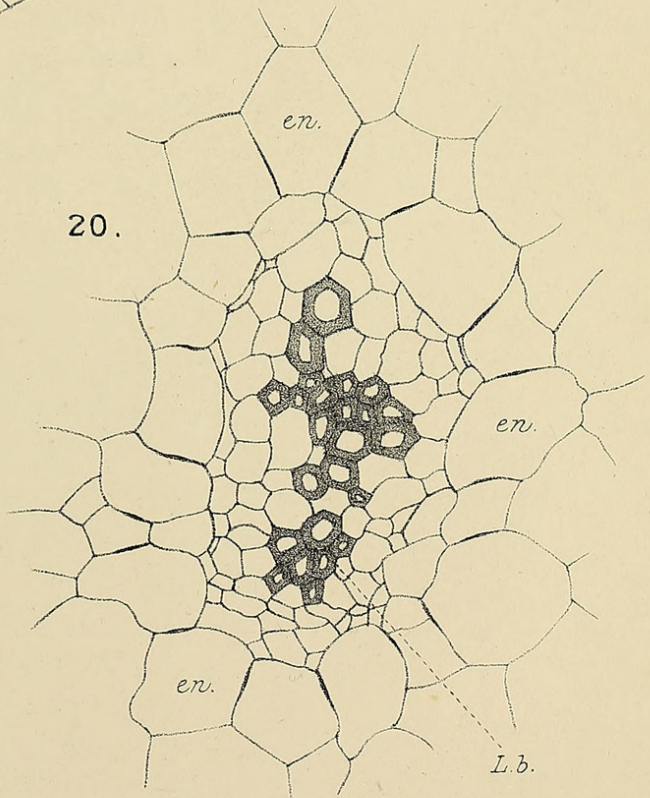
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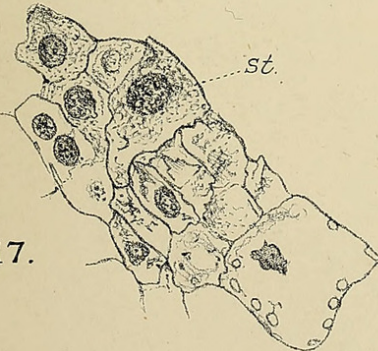
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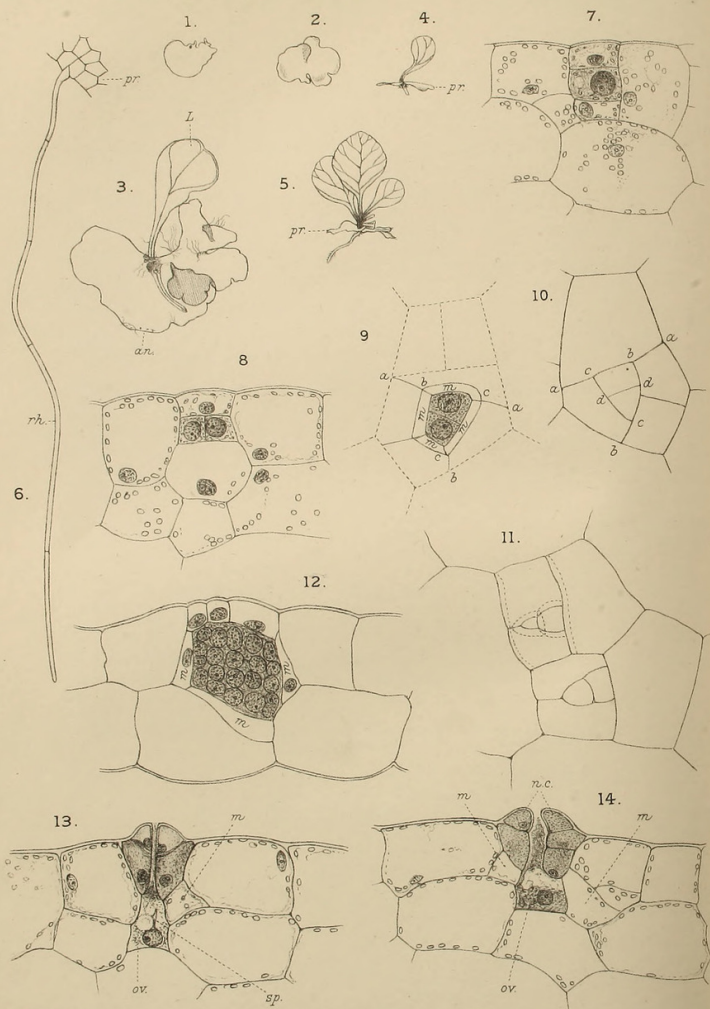
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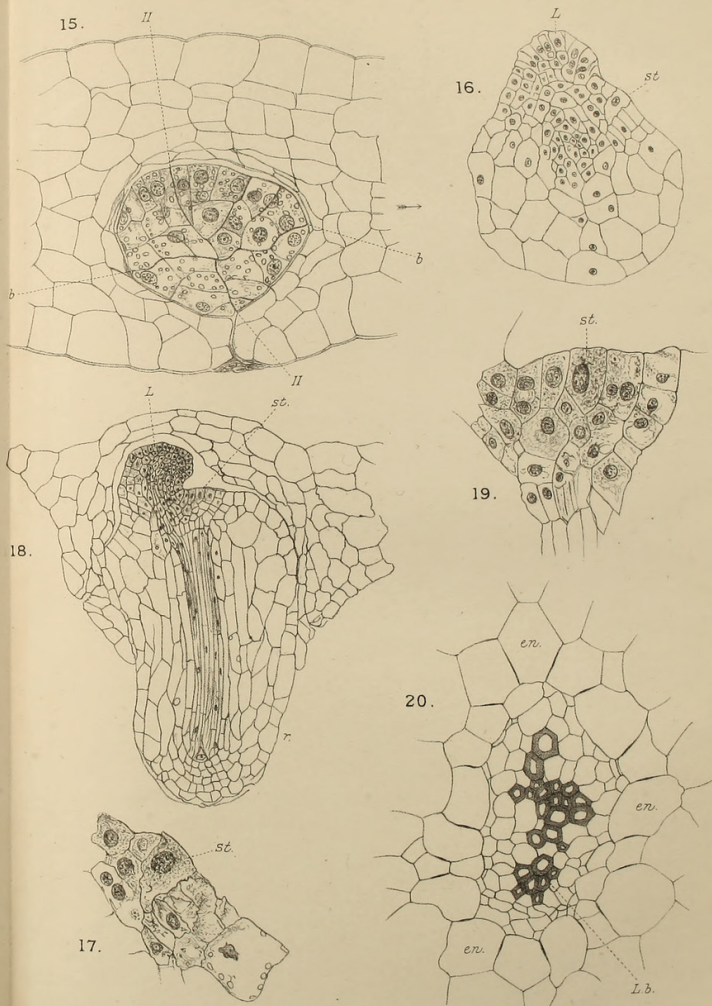
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BREBNER. — DANAEA.



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