Some Points in the Morphology of Phyllocladus alpinus, Hook.

BY

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With Plates XVII and XVIII.

I. INTRODUCTION.

PHYLLOCLADUS is a peculiar and isolated genus belonging to the Taxaceae, and characterized by the reduction of its true leaves to pointed scales, and the expansion of certain of its stem-branches into flattened leaf-like structures. Pilger in his monograph of the Taxaceae [1] places the genus in a sub-family by itself, intermediate between Podocarpoideae and Taxoideae. There are six species confined to New Zealand, Tasmania, and the Indian Archipelago. The isolated systematic position of the genus, its restricted distribution and curious external morphology, added to the fact that little was known of its anatomy or development, suggested to Prof. F. W. Oliver that it might prove an interesting subject for investigation. Accordingly, through the kindness of Dr. L. Cockayne, who had access to *Phyllocladus alpinus*, the Celery Pine of New Zealand in cultivation in the Christchurch Botanic Garden, five gatherings of material were sent to University College during the years 1902, 1903, and 1904, and were handed to me for examination. The following account is based upon this material, supplemented by a supply of the vegetative organs of two other species, *P. rhomboidalis* and *P. trichomanoides*, which Mr. R. I. Lynch, M.A., was so kind as to obtain for me from the Edinburgh Botanic Garden, and which has been very useful for comparison. The material of *P. alpinus*, which was fixed in methylated spirit, was unfortunately inadequate for anything like a complete investigation, and it is greatly to be desired that some one who has access to the genus in its native haunts should give us an exhaustive account of its morphology. I am much indebted to Prof. Oliver for his kind help and advice throughout the work.

[1] R. Pilger, Das Pflanzenreich, iv, 5, Taxaceae, 1903.

[Annals of Botany, Vol. XX. No. LXXIX. July, 1906.]

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II. The Vegetative Organs.

The first extant figure of *Phyllocladus* was published exactly eighty years ago by L. C. Richard [1]; it is an exquisite engraving of *P. rhomboidalis*, the only species then known. The main peculiarity of the vegetative structure, to which I have already referred, is the reduction of the leaves to more or less ephemeral scales, and the development of lateral stem-branches into cladodes (Fig. 1). The cladodes arise in the axils of leaves, and consist not merely of a single flattened lateral axis, but in many cases of a whole system of branches fused edge to edge. In fact, in the words of Bertrand [2], 'le cladode de *Phyllocladus* n'est pas, en général, un rameau unique, aplati en forme d'expansion foliacée, c'est tout un système de rameaux tertiaires et secondaires soudés entre eux et au rameau primaire sur lequel ils sont nés.' The veining of the larger limb of the cladode in Fig. 1 shows the complex nature of the organ; the secondary leaf-traces are easily distinguished from the vascular systems of the tertiary lateral shoots occurring in their axils. The leaves are best studied in sections of the apical leaf-buds, since they soon fall off and are represented only by scars (cf. Fig. 6 and Fig. 1). The leaves are very simple structures, triangular in section, traversed by a single small collateral bundle accompanied by a resin passage. There is no differentiation into spongy and palisade parenchyma, and in our species I have not observed any stomates. Stomates appear also to be absent in the leaves of *P. trichomanoides*, but in *P. rhomboidalis* I have observed a few. In transverse sections of the main axis each leaf-trace is seen to leave the ring of vascular strands accompanied internally by two much larger bundles destined to supply the axillary branch [3] (Fig. 7). If the branch is followed upwards it is found to remain for some little distance fused with the main axis, but the two bundles divide to form a small complete ring, so that a transverse section may show the main vascular rings and one or more subordinate vascular rings side by side with it. If the axillary branch is destined to form a cladode instead of a cylindrical axis it becomes much flattened, and the arrangement of the bundles resembles (in a simple case) that shown in Fig. 2, or some variant on it. The assimilating tissue of the cladode shows a slight differentiation, but this is much more marked in *P. trichomanoides*, where there is a fairly distinct development of palisade parenchyma on one side. The epidermis is strongly cuticularized, and the stomates, which in the three species examined are not confined to one face of the cladode, are well protected (Fig. 5). In the cortex of

[1] L. C. Richard, Commentatio Botanica de Conifereis et Cycadeis, 1826.

[2] C. E. Bertrand, Anatomie comparée des tiges et des feuilles chez les Gnétacées et les Conifères. Ann. des Sci. Nat., v^e^ sér., Bot., t. xx, 1874.

[3] Observed by Th. Geyler, Einige Bemerkungen über *Phyllocladus*, Abhand. der Senckenberg, Naturf. Gesellsch., Bd. xii, 1880.

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both cladode and normal axis there are a number of large lignified pitted elements.

The most interesting point in the anatomy of the cladode is the occurrence in the lateral bundles of *centripetal xylem*. This is remarkably well developed in *P. alpinus*, and also occurs, though less prominently, in *P. rhomboidalis* and *P. trichomanoides*. The centripetal xylem is not found at the base of the cladode, but only appears higher up. It is confined to the cladode, not occurring in the leaf (Fig. 6), the normal more or less cylindrical main axis (Fig. 7), or the axis of the male or female cone (Figs. 10 and 28). It consists of large tracheids which occur on the inner side of the protoxylem and also flank the normal xylem. These tracheids show the sculpturing which one is accustomed to associate with Taxinean wood,—the combination, namely, of scalariform or spiral thickening with bordered pits. The elements of the normal xylem are also marked in this way, though to a less conspicuous extent. Figs. 3 and 4 show radial and transverse sections of a lateral cladode bundle with well developed centripetal xylem. Taxinean sculpturings are not confined to the wood of the cladode, but occur also in that of the leaf, the young part of the main axis, and the axes of the male and female cones. (I have not had an opportunity of examining an old axis.) We will consider the possible significance of these facts later on.

III. The Reproductive Organs.

A. *The female cone.*

The female cone consists of a branch arising in the axil of a scale leaf and bearing a number of succulent bracts in the axil of each of which grows a single erect ovule. The bracts are as a rule, but not always, decussate. The best-developed cones which I examined had two pairs of fertile bracts at the base, succeeded by several sterile ones which had fused with the cone axis into an irregular terminal mass. Often two or three cones are closely clustered together, in which case the number of bracts and ovules in each individual cone is apt to be reduced to two. The stalk of the cone contains a ring of normal collateral bundles (Fig. 10). The appearance and structure of the cone and ovule shortly after pollination (which appears to occur in October) will be understood from Fig. 1 and Figs. 8–16. The nucellus contains the endosperm, surrounded by a well marked megaspore membrane, and is free right down to the base (Fig. 11). It is surrounded by a thick integument which is strengthened by a fibrous layer a little below the surface. After pollination the closure of the micropyle is effected by the growth and tangential division of the epidermal cells (Figs. 12, 13, A and B). The arillus at this stage is a mere ring-like upgrowth round the base of the ovule. No vascular strands enter the integument; they terminate in a tracheal platform below the base of the nucellus.

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Fig. 17, A and B, shows an older cone and seed, while Fig. 18 represents a radial section of the base of such a seed. The arillus is now a conspicuous papery cup. The walls of the fibrous layer have increased to an enormous thickness, and each cell contains a conspicuous crystal (Fig. 21, A and B). The elements composing the tracheal platform have very characteristic Taxinean sculpturing (Fig. 20). Between the tracheal platform and the megaspore is a palisade of long cells with bordered pits (Fig. 19). Unfortunately the preservation of the female cones was too poor and the stages were too few to allow the events within the embryo sac to be followed. Sections of the nucellus of cones gathered two or three months after pollination, such as those shown in Fig. 22, often reveal a small pear-shaped embryo deeply embedded in the endosperm (Fig. 23). The megaspore-membrane at this stage is remarkably clear (Fig. 24).

B. *The male cone.*

The material sent by Dr. Cockayne included three or four male cones gathered just as they were shedding their pollen (Fig. 26). Each sporophyll bears two pollen-sacs on its underside. Sections of a cone which had not dehisced revealed the fact that the ripe pollen-grain was of the Podocarpoid type[1],—winged and containing four nuclei (Fig. 27). Curiously enough, two of the cones sent showed abnormalities. One was hermaphrodite, bearing an ovule at the base succeeded by stamens (Fig. 25), while in a second the axis, instead of being simple, was branched at a point two-thirds from its base.

IV. The Affinities of *Phyllocladus*.

Strasburger (Die Coniferen und die Gnetaceen, 1872) places *Phyllocladus* in the subdivision Podocarpeae of the Taxaceae, but regards it as coming nearer to the Taxeae (Taxus, Torreya, Cephalotaxus, and Ginkgo) than do the other members of the same subdivision. Pilger (Taxaceae, 1903) consigns *Phyllocladus* to the separate group Phyllocladoideae, intermediate between Podocarpoideae and Taxoideae. The difference between these two positions is not a radical one, but my observations make me feel that the earlier view is perhaps the more expressive. The affinity with the Podocarps is undoubtedly the stronger, though there are distinct indications of a Taxoidean relationship as well.

The main points in which *Phyllocladus* resembles the Podocarpoideae and differs from the Taxoideae are as follows :—

1. *Each carpel bears a single ovule.* In the Taxoideae each carpel is bi-ovulate.

[1] W. C. Coker, The Gametophytes and Embryo of Podocarpus. Bot. Gaz., vol. xxxiii, 1902, p. 89.

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2. *The stamens bear two pollen-sacs only.* In the Taxoideae there are more than two pollen-sacs.

3. *The ripe pollen-grains are winged and contain four nuclei.* In the Taxoideae the pollen-grains have one or two nuclei and no wings.

4. *There is a well-marked megaspore-membrane.* In the Taxoideae the megaspore membrane is *never* well-developed, whereas in the Podocarpoideae it is present and well-marked in *Dacrydium*, though absent in *Podocarpus*[1].

The points in which *Phyllocladus* approaches the Taxoideae and differs from the Podocarpoideae are as follows :—

1. *The ovule is erect.* This is a decidedly important point. The ovule of the Podocarps is characteristically inverted, but in certain instances it is erect or nearly so, e. g. *Dacrydium latifolium.*

2. *A symmetrical arillus is present.* The arillus of *Phyllocladus* recalls that of *Taxus* except that it is not succulent. The ovules of the Podocarpoideae, on the other hand, have an 'epimatium' which resembles an arillus, but is characteristically one-sided instead of symmetrical, and is regarded by Pilger (l. c.) as an outgrowth from the carpel, and not homologous with the arillus of the Taxoideae. We must remember, however, that the asymmetry of the epimatium is correlated with the inverted position of the ovule, so that it will not do to lay too much stress on this point, as proving that epimatium and arillus are not homologous.

3. *Centripetal wood occurs in the cladodes.* It is difficult to say what importance, if any, should be attached to the presence of centripetal wood in so specialized an organ as a cladode. May we regard it as suggesting Taxoidean affinity? The Taxoideae show more indications of centripetal wood than the other Coniferae[2]. It has been observed in the leaf and cotyledon of *Cephalotaxus*[2] and *Taxus*[2], and in the cotyledon of *Torreya*[3], and in the stem of *Cephalotaxus koraiana*[4]. The last case is of importance as it is the only instance so far known among recent Coniferae of centripetal xylem in an axial organ. *Cephalotaxus koraiana* is sometimes regarded as merely a fastigiate variety of *C. drupacea*, or *C. pedunculata*, but Rothert is inclined to regard it as a distinct species. It is difficult to determine how much stress to lay on the case of the appearance of centripetal xylem in a single species of a genus, while closely allied species, or it may be even varieties of the same species, are quite normal. But I think its appearance, taken in connexion with the other cases known

[1] R. B. Thomson, The Megaspore Membrane of the Gymnosperms. Univ. of Toronto Biol. Series, No. 4, 1905.

[2] W. C. Worsdell, On 'Transfusion-tissue': its Origin and Function in the Leaves of Gymnospermous Plants. Trans. Linn. Soc., vol. v, 1897.

[3] Edith Chick, The Seedling of Torreya myristica. New Phyt., vol. iii, 1903, p. 83.

[4] W. Rothert, Ueber parenchymatische Trachelden und Harzgänge im Mark von *Cephalotaxus-Arten*. Ber. d. Deutsch. Bot. Gesellsch., Bd. xvii, 1899, p. 275.

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in the family, at least strengthens the presumption that a tendency to the production of centripetal xylem is a hereditary character of the Taxoideae. So I am inclined to believe that the occurrence of centripetal xylem in the cladodes of *Phyllocladus* is quite possibly due to an inherited tendency derived by both *Phyllocladus* and the Taxoideae from some common ancestor, and apt to reappear when a special combination of circumstances renders it appropriate. In the case of *Phyllocladus* the use of the centripetal xylem is not far to seek. As shown in Fig. 2 the cladode is flattened parallel to a plane which would symmetrically divide the lateral bundles, i. e. the latter occupy a position at right angles to that which they would take up if the cladode was a leaf. An extension of the xylem in the plane of flattening of the organ is brought about in leaves by wings of transfusion tissue *lateral* to the bundle (e. g. *Podocarpus*), whereas in *Phyllocladus* an extension of the wood in a corresponding plane necessarily brings centripetal xylem into existence. If we suppose that the centripetal xylem is an ancestral character, one alternative is to imagine that at that remote period when the cladodes were first being evolved the axis and leaves still possessed internal xylem, so that the cladode naturally possessed it as well ; it must then have gradually disappeared from the axis and leaves, while it was retained in the cladode owing to its usefulness. On the other hand, it is, I think, open to us to suppose that the internal xylem was completely lost in stem and leaves before the flattened leaf-like branches were ever developed, but that when the cladode was evolved the need of lateral transmission of water awoke, as it were, a forgotten memory, and the plant once again took up the formation of centripetal xylem.

4. *Taxinean sculpturing occurs in the tracheids.* In *Phyllocladus alpinus* tracheids with the characteristic Taxinean markings (a combination of bordered pits and spiral or scalariform thickenings) occur in the xylem. Tracheids of this kind, though by no means confined to the Taxoideae, are sufficiently characteristic of it to make their appearance in *Phyllocladus* distinctly suggestive of affinity.

V. Summary.

The main result of this investigation is to confirm the view of the systematists that *Phyllocladus* occupies an intermediate position between Podocarpoideae and Taxoideae, but with greater affinity for the former. The existence of winged multi-nucleate pollen-grains ratifies the Podocarpoid affinity, while the presence of centripetal xylem in the cladode is regarded as a 'harking-back' to a hypothetical common ancestor of Taxoideae and Phyllocladoideae which possessed bundles of this type.

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EXPLANATION OF PLATES XVII AND XVIII.

Illustrating Miss A. Robertson's paper on *Phyllocladus alpinus*.

r. = resin passage; *x.* = normal xylem; *cpx.* = centripetal xylem; *ph.* = phloem; *st.* = stomate; *px.* = protoxylem; *b.* = paired bundles going to a branch; *l.t.* = leaf-trace; *l.b.* = leaf base; *sc.* = scar of attachment to cone axis; *ar.* = arillus; *br.* = bract; *o.* = ovule; *pr.* = prothallus; *m.m.* = megaspore membrane; *p.t.* = pollen-tube; *n.* = nucellus; *i.* = integument; *scl.* = sclerized layer of integument; *p.p.* = platform of pitted cells; *p.tr.* = tracheal platform; *emb.* = embryo; *s.* = suspensor; *i.* = idioblast.

PLATE XVII.

Fig. 1. Branch showing ♀ cone shortly after pollination, cladode, leaf-bud, and leaf-scars. × 4 *circa*.

Fig. 2. Diagrammatic transverse section of cladode. × 28.

Fig. 3. Rather young lateral bundle cut radially, from tangential section of a cladode. × 386.

Fig. 4. Transverse section of lateral bundle from a cladode. × 386.

Fig. 5. Stomates from transverse section of a cladode. × 386.

Fig. 6. Transverse section of terminal leaf-bud such as that shown in Fig. 1. × 74.

Fig. 7. Diagrammatic transverse section of an axis. × 28.

Fig. 8. Cone (same age as Fig. 1) cut lengthways. × 3 *circa*.

Fig. 9. Ovule and bract (same age as Fig. 1). × 3 *circa*.

Fig. 10. Diagrammatic transverse section of cone-stalk drawn in Fig. 1. × 28.

Fig. 11. Radial section of ovule and bract shortly after pollination. × 28.

Fig. 12. Transverse section at A, Fig. 11. × 28 and × 74.

Fig. 13. Transverse section at B, Fig. 11, showing closure of micropyle. × 28 and × 74.

Fig. 14. Transverse section at C, Fig. 11. × 28 and × 74.

Fig. 15. Longitudinal section at D, Fig. 11. × 74.

Fig. 16. Longitudinal section at E, Fig. 11. × 74.

Fig. 17 (A and B). Cone and seed somewhat older than that shown in Fig. 1. × 4 *circa*.

Fig. 18. Longitudinal section of base of seed shown in Fig. 17 B. × 28.

Fig. 19. Single pitted cell from palisade below megaspore. See *p.p.* in Fig. 18. × 386.

Fig. 20. Short tracheids from platform at base of seed. See *p.tr.* in Fig. 18. × 386.

Fig. 21. Details of sclerized layer in integument of seed whose base is shown in Fig. 18; A, nearer base; and B, higher up. × 386.

PLATE XVIII.

Fig. 22 (A and B). Two views of cone two or three months older than that shown in Fig. 1. × 5 *circa*.

Fig. 23. Endosperm of cone of age of Fig. 22 showing embryo and suspensor. × 43.

Fig. 24. Edge of endosperm showing megaspore membrane. × 580.

Fig. 25. Hermaphrodite cone. × 7 or 8.

Fig. 26. Normal ♂ cone. × 7 or 8.

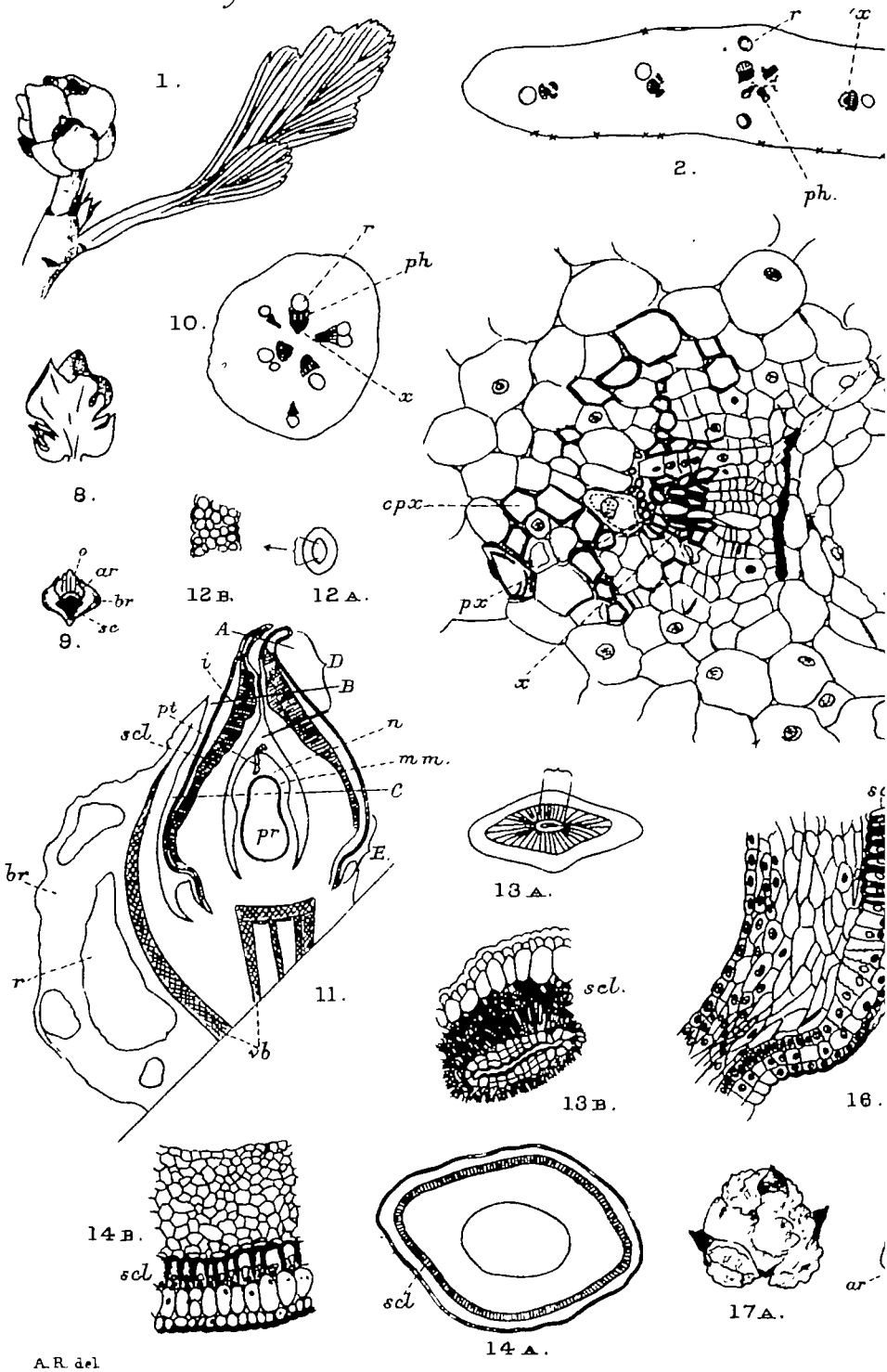
Fig. 27. Ripe pollen-grain. × 580.

Fig. 28. Transverse section axis of ♂ cone below stamens. × 112.

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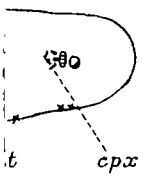
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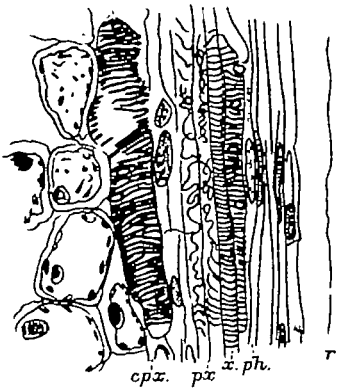
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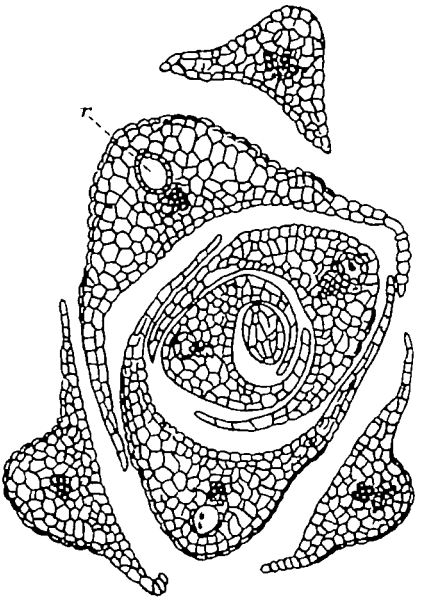
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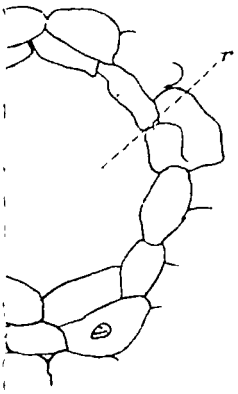




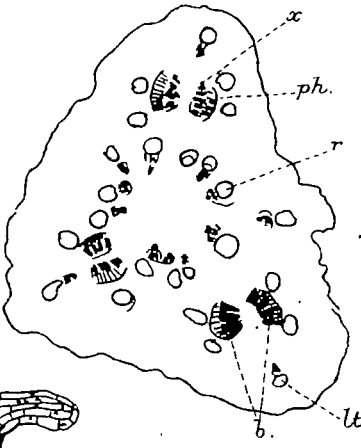
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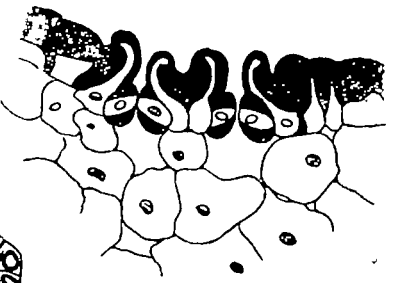
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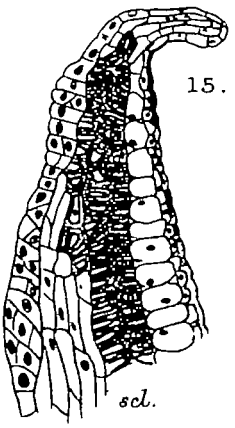
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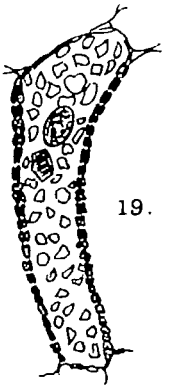
20 A.



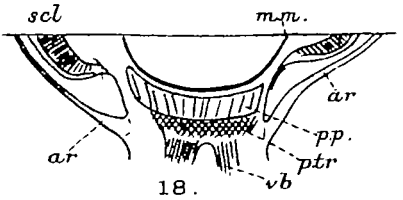
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20.



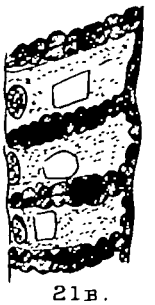
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18.



21 A.



21 B.

Huth, lith. et imp

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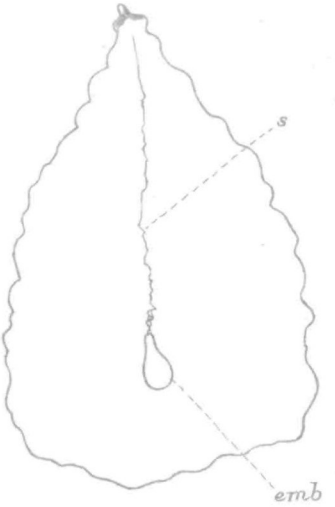
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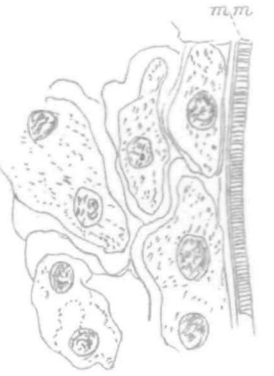
22 A.



22 B.



23.



24.



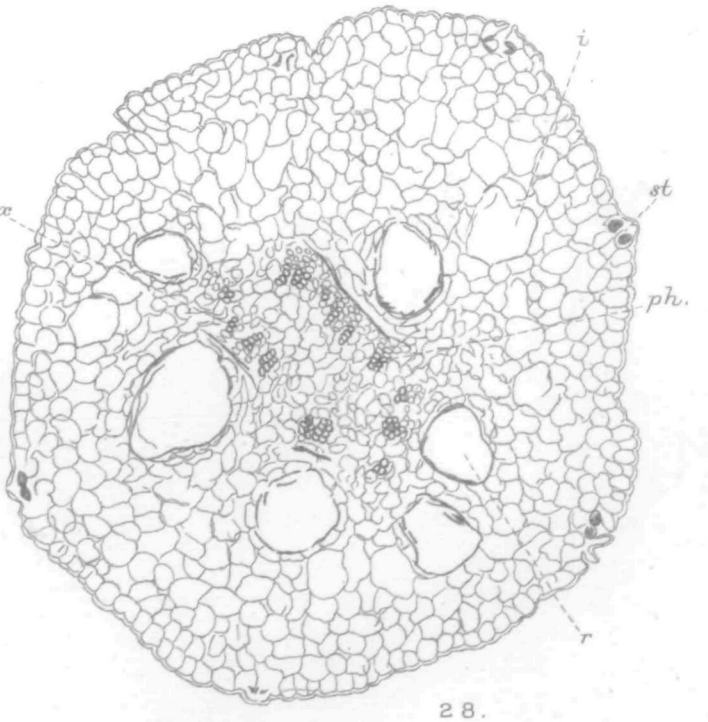
27.



25.



26.



28.

A.R. del.

Huth, lith et imp.

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