

On the Seedling Structure of Gymnosperms. I.

BY

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With Plate XXXV and eight Figures in the Text.

THE study of seedlings was commenced by one of us seven years ago, but the work, occupying a secondary place as an investigation, made but slow progress. The appearance of the results obtained by Miss Sargent¹ rendered it desirable to modify the original scheme, and it was decided to ascertain, as far as possible, the precise value of the transition-phenomena in questions relating to the phylogeny of the higher plants. With this end in view, it was considered advisable to examine as large a number of species as possible in well-marked cycles of affinity, and the Gymnosperms, Piperales, Centrospermae, and those Natural Orders of the Tubiflorae more directly related to the Scrophulariaceae were selected as being likely to afford the evidence required.

Whether this somewhat extensive programme will be completed remains to be seen ; it is probable that the work on the Scrophulariaceae will not be continued, for, in the light of the knowledge gained of the groups mentioned, together with others, it appears possible that the expenditure of so much time and labour may not be necessary.

The work on the Gymnosperms is fairly well advanced, and it has been decided to publish the results obtained from the study of the Taxaceae, the Cupressineae, and the Taxodiinae of the Abietineae.

As regards methods, little need be said. In nearly all cases the seedlings were microtomed. The staining of the sections presented some initial difficulty ; those excellent stains haematoxylin and safranin not only

¹ Sargent, E. : A Theory of the Origin of Monocotyledons, founded on the Structure of their Seedlings (*Annals of Botany*, xi).

require much time, but they also give, for this particular work, a very poor differentiation. The method finally pursued was as follows:—

The sections were stained on the slip for about half an hour in a saturated solution of gentian violet in 50 % alcohol and were then, without washing, transferred to a saturated alcoholic solution of vesuvian brown for a few seconds; the excess of stain was then washed out in a mixture of absolute alcohol and xylol, and the sections rinsed, when necessary, very rapidly in absolute alcohol. They were finally cleared in xylol and mounted in balsam. If the process is properly performed, the lignified tissues are coloured a very bright violet, while the phloem stains brown, and the ordinary parenchyma a light brown.

The number of seedlings of one species prepared varied according to the supply. The usual course was to cut up at least three individuals whenever possible, and more when necessary.

This work would have been impossible except for the kindness of many in supplying material. As we still have hopes of obtaining further contributions, we propose to postpone the expression of our indebtedness until our results are in a more forward state of publication.

Finally, it may be remarked that our general conclusions will not be stated until the whole of the facts and the immediate conclusions derived therefrom have been published.

TAXACEAE.

Cephalotaxus pedunculata, Sieb. & Zucc. On germination the seed is carried up above the level of the soil by the two cotyledons, which remain embedded within the endosperm and function as organs of absorption until the tissues of reserve are depleted, by which time the plumule is well advanced. Ultimately the seed is dropped, and the seed-leaves perform an assimilatory rôle (Figs. 1 and 2, Plate XXXV).

The structure of the cotyledon requires but a brief description. The epidermis is covered by cuticle which is poorly developed, excepting over the guard-cells, where it is very thick. The mesophyll consists of an undifferentiated mass of parenchyma with fairly abundant intercellular spaces. Cells, which appear to be of a secretory nature, with dense and deeply-staining contents, occur within the mesophyll, being situated especially in the hypodermal region of the dorsal surface of the leaf and on the dorsal side of the vascular bundle.

Each cotyledon has a single vascular strand which is somewhat tangentially elongated. Directly abutting on to the soft bast is a mass of rather wide and long cells, fibrous in nature, which, when mature, are devoid of contents, closely packed together, and unligified.

The xylem exhibits a pronounced mesarch structure; the centripetal

elements, however, are not very numerous. This feature has already been described by Worsdell,¹ and, to save reiteration, it may here be remarked that Worsdell describes the occurrence of mesarch structure in *Taxus*, *Ginkgo*, and other plants, and the presence of transfusion tracheides in *Cephalotaxus*, *Taxus*, *Sequoia gigantea*, *Widdringtonia Whytei*, *Libocedrus decurrens*, &c.

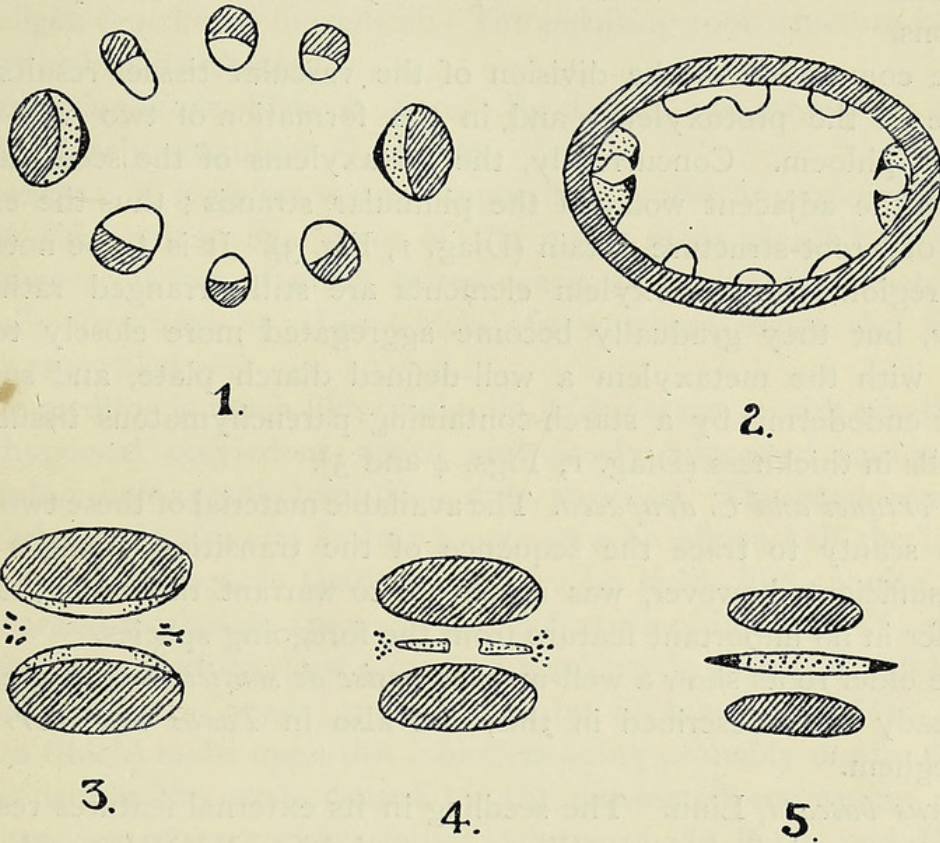


DIAGRAM I. *Cephalotaxus*. In this, and in all the following text-figures, the protoxylem is indicated by the black areas, the metaxylem by dots, and the phloem by diagonal shading.

Transition. At the cotyledonary node the bundles retain their undivided nature and gradually pass inwards towards the central region of the hypocotyl, during which passage the centripetal wood dies out. The arrangement of the vascular bundles at the top of the hypocotyl is, roughly, elliptical; the two seed-leaf-traces occupy the foci of the ellipse, and there are two groups of plumular strands, three in each group, placed at right angles to the cotyledonary plane (Diag. 1, Fig. 1). On tracing the bundles downwards, they undergo a centripetal displacement, so that they soon form a continuous vascular ring by the coalescence of the phloem-masses (Diag. 1, Fig. 2).

The abundant protoxylem of the cotyledonary bundles still occupies an

¹ Worsdell. : On Transfusion Tissue: its Origin and Function in the Leaves of Gymnospermous Plants (Trans. Linn. Soc. London, 2nd ser., vol. v).

endarch position. Very soon the phloem-ring becomes thinner and breaks at the two points opposite the protoxylems of the seed-leaf-traces ; but, before this rupture is actually accomplished, each xylem-mass derived from a cotyledon bifurcates, and the protoxylem undergoes a certain amount of rotation, which, however, is not very pronounced and is unequal in degree in different instances ; in fact the movement results in nothing much further than the concentration of the protoxylem units in the plane of the cotyledons.

The completion of the division of the vascular tissues results in the exposure of the protoxylems, and in the formation of two well-defined masses of phloem. Concurrently, the metaxylems of the seed-leaf-traces fuse with the adjacent wood of the plumular strands ; thus the essential features of a root-structure obtain (Diag. 1, Fig. 3). It is to be noted that, at this region, the protoxylem elements are still arranged rather tangentially, but they gradually become aggregated more closely together, forming with the metaxylem a well-defined diarch plate, and separated from the endodermis by a starch-containing parenchymatous tissue about seven cells in thickness (Diag. 1, Figs. 4 and 5).

C. Fortunei and *C. drupacea*. The available material of these two species was too scanty to trace the sequence of the transition changes in any detail ; sufficient, however, was made out to warrant the assumption that they differ in no important feature from the foregoing species.

The older roots show a well-marked *assise de soutien*, a character which has already been described in this, and also in *Taxus* and *Torreya* by Van Tieghem.¹

Taxus baccata, Linn. The seedling in its external features resembles *Cephalotaxus* and *Podocarpus* (Figs. 3, 3a, 3b, Plate XXXV) ; and, further, the structure and transition-phenomena resemble those of *Cephalotaxus*, and have already been described by Strasburger,² so that it is only necessary to draw attention to a few minor characters.

The single bundle of each cotyledon exhibits a mesarch structure, but the number of centripetal elements are very few indeed (Fig. 6, Plate XXXV). The rearrangement of the vascular tissues begins at the level of the cotyledonary node by the xylem taking on a V-like arrangement with the protoxylem occupying the apex which is directed outwards ; this is quickly followed by the division of the phloem into two parts. During the inward journey these changes become more marked, and, as the metaxylem travels inwards more quickly than the protoxylem, the latter for a time is mesarch in position (Diag. 3, Fig. 4). A continuous vascular ring is not formed as in the case of *Cephalotaxus*. The separate phloem-masses of each coty-

¹ Van Tieghem : Recherches sur la symétrie de structure des plantes vasculaires (Ann. Sci. Nat., Bot., xiii, 1870-1).

² Strasburger : Die Coniferen und die Gnetaceen (Jena, 1872).

ledon-trace immediately effect a junction with the corresponding tissue of the plumular strands, and concurrently the metaxylem of the same traces move towards, and fuse with, the wood of the epicotyledonary bundles. Thus the protoxylems of the seed-leaves are left exposed; there is no definite rotation of this tissue; its exarch position is attained chiefly by the movements of the metaxylem; but, at a lower level, there may be made out a rather indefinite rearrangement of the protoxylem elements coupled with a slight centrifugal movement. The resulting root-structure is exactly the same as in *Cephalotaxus*.

Taxus cuspidata, Sieb. & Zucc. So far as our inadequate material indicates, closely resembles *T. baccata*.

Torreya. It is unfortunately impossible to offer any original observations on this genus, since none of the many seeds planted germinated. This, however, is not of much consequence, as the seedling-anatomy has been fully described by Miss Chick,¹ from whose paper the following remarks are culled:—

The seedling is much like *Ginkgo* in its appearance, with two thick and fleshy hypogeal cotyledons which are closely adpressed and may fuse together by their morphologically upper surfaces. The seed-leaves show much variation in size and in form; one may be about half the length of the other, and, as regards shape, they may be sickle-like, tubular, or with a well-marked spatulate apex. Another feature of interest is found in the fact that the cotyledons show a marked tendency to lobing, which has been described also for Cycads and *Ginkgo* by Strasburger.² Mrs. Tansley (*née* Miss Chick) looks upon this lobing as being probably due to the space relations within the seeds caused by the ruminated endosperm, and she cites other cases of seeds with a similar endosperm, viz. Palms and *Myristica*, which also have lobed cotyledons; but at the same time it is pointed out that the cotyledons of *Anona* show no tendency to lobing, although the endosperm is ruminated. We shall offer an alternative explanation later on.

As regards the anatomy of the cotyledons, the main features are as follows: Each has a single vascular bundle, which exhibits centripetal wood and transfusion elements. When the seed-leaf is lobed a branch of the bundle enters the lobe, and in some instances the vascular strand showed a tendency to branch.

The transition is, on the whole, fairly rapid. 'The root protoxylem dies out below the cotyledonary node; and the protoxylem which accompanies the cotyledon-trace outwards would seem to have a double origin, one portion . . . which is directly inserted upon the root metaxylem, and the other seeming to belong more intimately to the cotyledon-trace. . . . A possible explanation of the "dying-out" of the root protoxylem is that

¹ E. Chick: The Seedling of *Torreya Myristica* (New Phytologist, vol. ii, 1903).

² Strasburger, loc. cit.

the xylem connexion between the root and the cotyledons was made at a time when, and in a region where, elongation had ceased, and possibly growth in thickness was taking place. This would account for a region devoid of spiral and annular elements.'

The root is diarch, with many fibres in the secondary phloem; also an *assise de soutien* obtains. It is thus seen that, as regards the number and structure of the cotyledons and the anatomy of the root, there is a marked similarity to *Cephalotaxus*; and, further, a study of the figures illustrating the above account leads to the opinion that the transition-phenomena of *Torreya* are also comparable to those of *Cephalotaxus*, although masked by the occurrence of secondary thickening.

PODOCARPEAE.

Podocarpus chinensis. The young seedling is illustrated in Figs. 4 and 4a, Plate XXXV. The chief feature to be noted is that the two cotyledons are intra-seminal, and carry the seed up above the level of the ground; the resemblance to the corresponding stages in *Cephalotaxus* and *Taxus* is close, but, as only one seed out of a large number germinated, we have no observations to make regarding the phases later than the one figured.

The general structure of the cotyledons, except with regard to the vascular strands, is like that of *Taxus*. Each seed-leaf of *Podocarpus* has two bundles endarch and collateral throughout the whole length of the leaf, and, relatively, widely separated one from the other. Histologically, the vascular bundles are quite normal; there are no fibres as in *Taxus* and *Cephalotaxus*, and the cambium is fairly active, judging from the crushed appearance of the outer phloem elements (Fig. 7, Plate XXXV). No centripetal wood has been observed; there are, however, a number of transfusion tracheides generally forming lateral expansions from the metaxylem.

Transition. At the level of the cotyledonary node the pair of bundles of each seed-leaf become orientated in such a manner that their xylem-masses become directed obliquely towards one another (Diag. 2, Fig. 1). This orientation becomes more marked during the inward passage. As the central cylinder is reached, the bundles of each pair approach and become connected, one with the other, by a strand of cambiform cells, which are, in all probability, immature phloem elements (Diag. 2, Fig. 2), on the inner side of which a few tracheae may be seen. There is, however, no direct connexion between the corresponding xylem-masses of each pair of seed-leaf-traces. This bridge of phloem speedily disappears, and at the same time the protoxylem elements of each pair of cotyledon-bundles commence to rotate towards each other and outwards, so as to occupy the exarch position. The traces derived from the seed-

leaves now occupy a position at right angles to the plane of the cotyledons, and the metaxylem and phloem of each strand fuse with the adjacent corresponding vascular tissues derived from the plumule (Diag. 2, Fig. 3).

The completion of these rearrangements results in the formation of a diarch root, the further changes, at lower levels, merely consisting of an increase in the number of protoxylem elements and the constitution of a diarch plate (Diag. 2, Fig. 4).

The main feature of difference between this plant and the other

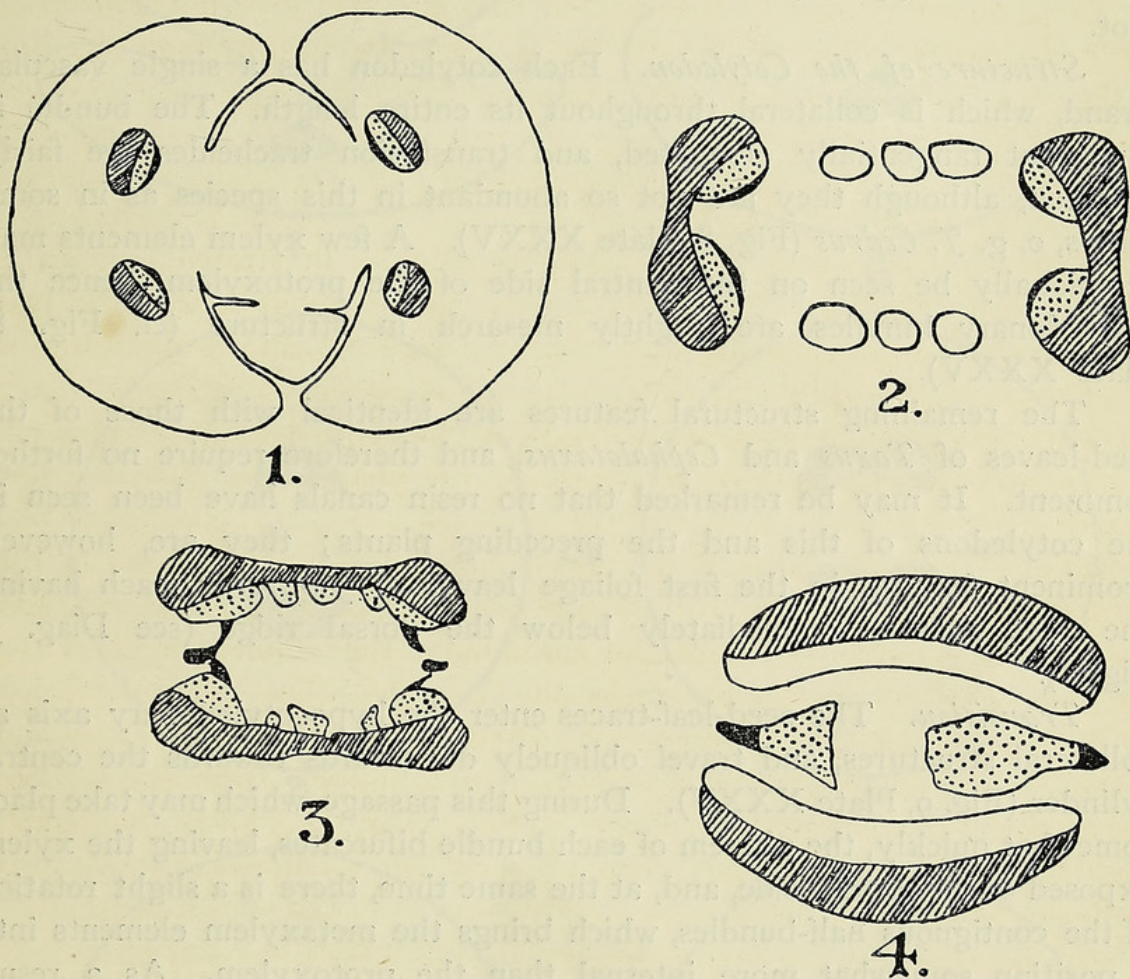


DIAGRAM 2. *Podocarpus*.

members of *Taxaceae*, so far as they have been examined, is found in the cotyledons, each having two bundles, which together form one pole of the diarch root. As will be seen later on, this feature is characteristic of certain *Gnetales*.

Owing to failure in obtaining material, it is impossible to say whether the features described above also obtain in the seedlings of other genera of the *Podocarpeae*. There is, however, a strong indication that such may be the case, for Geyler¹ has pointed out that *Phyllocladus trichomanoides*

¹ Geyler, H. Th.: Einige Bemerkungen über *Phyllocladus*. Abhand. Senckenberg. Naturforsch. Gesellsch., xii, 1881.

has two cotyledons, each of which is traversed by two vascular strands, and Van Tieghem² indicates that the primary root of *Phyllocladus* is diarch in structure.

CUPRESSINEAE.

Juniperus virginiana, Linn. The morphology of the seedling in this, and also in the other species examined, calls for no special comment. The epigeal cotyledons are two in number, ligulate in shape, and inserted on the slender hypocotyl, which is continued downwards into the primary root.

Structure of the Cotyledon. Each cotyledon has a single vascular strand, which is collateral throughout its entire length. The bundle is somewhat tangentially elongated, and transfusion tracheides are fairly common, although they are not so abundant in this species as in some others, e. g. *J. Cedrus* (Fig. 8, Plate XXXV). A few xylem elements may occasionally be seen on the ventral side of the protoxylem, hence the cotyledonary bundles are slightly mesarch in structure (cf. Fig. 8, Plate XXXV).

The remaining structural features are identical with those of the seed-leaves of *Taxus* and *Cephalotaxus*, and therefore require no further comment. It may be remarked that no resin canals have been seen in the cotyledons of this and the preceding plants; they are, however, prominent features in the first foliage leaves of *Juniperus*, each having one duct situated immediately below the dorsal ridge (see Diag. 3, Fig. 1).

Transition. The seed-leaf-traces enter the hypocotyledonary axis as collateral structures, and travel obliquely downwards towards the central cylinder (Fig. 9, Plate XXXV). During this passage, which may take place somewhat quickly, the phloem of each bundle bifurcates, leaving the xylem exposed on the dorsal side, and, at the same time, there is a slight rotation of the contiguous half-bundles, which brings the metaxylem elements into a position somewhat more internal than the protoxylem. As a result of this, when the central cylinder is just about reached, each cotyledon-trace has a central mass of xylem, bounded on each side by two separate groups of phloem elements, which lie in a position at right angles to the plane of insertion of the seed-leaves (Diag. 3, Fig. 3).

The protoxylem is almost in an exarch position, but not quite; it is still covered externally by a few metaxylem elements. In other words, the protoxylem, for a time, is in the mesarch position (Diag. 3, Figs. 4 and 5, and Figs. 9 and 10, Plate XXXV). The protoxylem finally becomes exarch by its own somewhat indefinite efforts, aided by the inward movement of the metaxylem. Concurrently, the opposing masses

¹ Van Tieghem, loc. cit.

of phloem of the cotyledonary bundles fuse together either directly, in the case of younger seedlings with no differentiated epicotyledonary

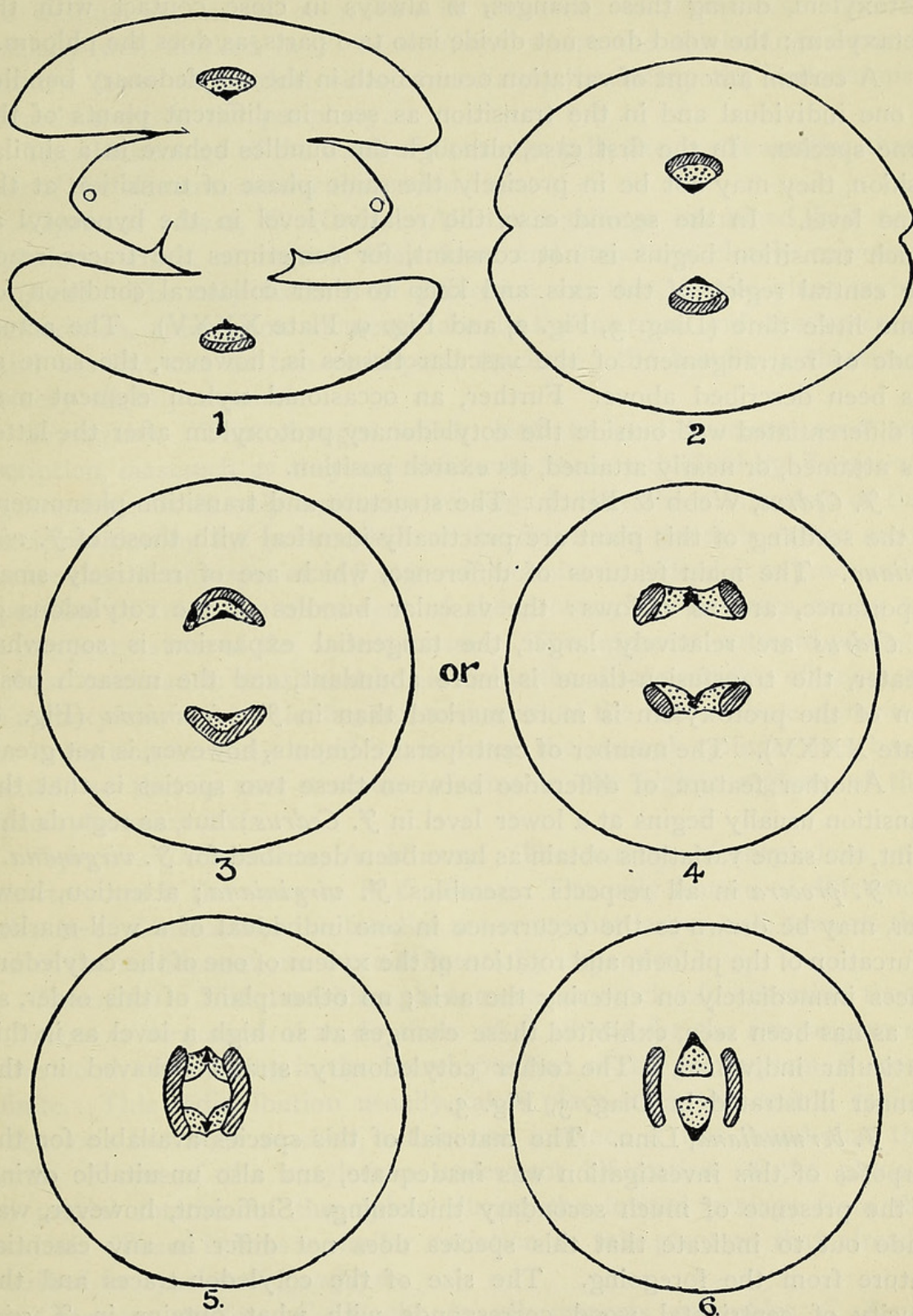


DIAGRAM 3. *Juniperus virginiana*.

traces; or indirectly, by their junction with the intervening plumular bast, as in the case of older seedlings. A diarch root-structure is thus

arrived at in the upper region of the hypocotyl; the endodermis, however, does not appear until the collar is reached. It is to be observed that the protoxylem, during these changes, is always in close contact with the metaxylem; the wood does not divide into two parts, as does the phloem.

A certain amount of variation occurs both in the cotyledonary bundles of one individual and in the transition as seen in different plants of the same species. In the first case, although the bundles behave in a similar fashion, they may not be in precisely the same phase of transition at the same level. In the second case, the relative level in the hypocotyl at which transition begins is not constant, for sometimes the traces reach the central region of the axis and keep to their collateral condition for some little time (Diag. 3, Fig. 2, and Fig. 9, Plate XXXV). The actual mode of rearrangement of the vascular tissues is, however, the same as has been described above. Further, an occasional xylem element may be differentiated well outside the cotyledonary protoxylem after the latter has attained, or nearly attained, its exarch position.

J. Cedrus, Webb & Benth. The structure and transition-phenomena of the seedling of this plant are practically identical with those of *J. virginiana*. The main features of difference, which are of relatively small importance, are as follows: the vascular bundles of the cotyledons of *J. Cedrus* are relatively larger, the tangential expansion is somewhat greater, the transfusion-tissue is more abundant, and the mesarch position of the protoxylem is more marked than in *J. virginiana* (Fig. 8, Plate XXXV). The number of centripetal elements, however, is not great.

Another feature of difference between these two species is that the transition usually begins at a lower level in *J. Cedrus*; but, as regards this point, the same variations obtain as have been described for *J. virginiana*.

J. procera in all respects resembles *J. virginiana*; attention, however, may be drawn to the occurrence in one individual of a well-marked bifurcation of the phloem and rotation of the xylem of one of the cotyledon-traces immediately on entering the axis; no other plant of this order, so far as has been seen, exhibited these changes at so high a level as in this particular individual. The other cotyledonary strand behaved in the manner illustrated in Diag. 3, Fig. 3.

J. bermudiana, Linn. The material of this species available for the purposes of this investigation was inadequate, and also unsuitable owing to the presence of much secondary thickening. Sufficient, however, was made out to indicate that this species does not differ in any essential feature from the foregoing. The size of the cotyledon-traces and the paucity of centripetal wood corresponds with what obtains in *J. virginiana*, while the abundance of transfusion elements is in close agreement with *J. Cedrus*. It is, however, not desired to lay any particular stress on this last point, for it is a feature which may vary with the age of the leaf.

Before passing on, attention may be drawn to another feature of resemblance to *Cephalotaxus* and *Taxus* which is found in the presence of a well-marked *assise de soutien* in the roots of *Juniperus*. This is especially well marked in *J. bermudiana*, where the thickenings extend from the layer of cortical cells immediately bounding the endodermis, outwards towards the periphery.

The thickenings of the walls of the outer cells are much smaller than those of the elements nearer the endodermis.

Cupressus obtusa, C. Koch. All the seedlings examined had two cotyledons, which, as regards their form and structure, closely resemble *Juniperus*. The only features of difference are that, in the plant under consideration, transfusion elements are less numerous and the vascular strand has but one or two centripetal tracheae; the bundle is, therefore, but very slightly mesarch.

Transition. The changes which lead to root-structure need no description, inasmuch as they are similar to those exhibited by *Juniperus virginianum*. It is only necessary to remark that the attainment of the exarch position by the protoxylem of the cotyledon-traces is rather more obscure than in any species of *Juniperus* examined; indeed, it is practically impossible to trace the movement of the protoxylem elements, owing to the compact nature of the xylem-masses. The apparent outward passage of these tracheae is considerably aided by the disappearance of some of the metaxylem, and by the inward movement of the rest of these elements. The transition is fairly rapid when once the central cylinder has been reached, so that a root-structure obtains in the higher regions of the hypocotyledonary axis.

Cupressus Lawsoniana, A. Murray. The number of cotyledons and their structure is the same as in *C. obtusa*. The only feature of difference is that in *C. Lawsoniana* the bundles are somewhat larger and, towards the base of the seed-leaves, are more tangentially expanded.

Transition. The transition-phenomena more closely resemble those of *Juniperus virginiana* than do those of *C. obtusa*, for the rearrangement of the wood, culminating in the exarch position of the protoxylem, is more definite. This redistribution usually takes place after the central region of the axis has been reached, but in one instance it was found that the bundle of one of the cotyledons underwent bifurcation of the phloem and partial rotation of the xylem during the inward passage from the seed-leaf. There is thus a similar variation in this plant to that already described for species of *Juniperus*.

Cupressus pisifera, C. Koch., in all respects resembles *C. Lawsoniana*.

Cupressus torulosa, D. Don. The number of cotyledons varies from three to five; thus out of twelve plants, nine had three, two had four,

and one had five seed-leaves. The structure of the cotyledons does not differ from that of the preceding species.

Transition. Considering first an example with three seed-leaves, it

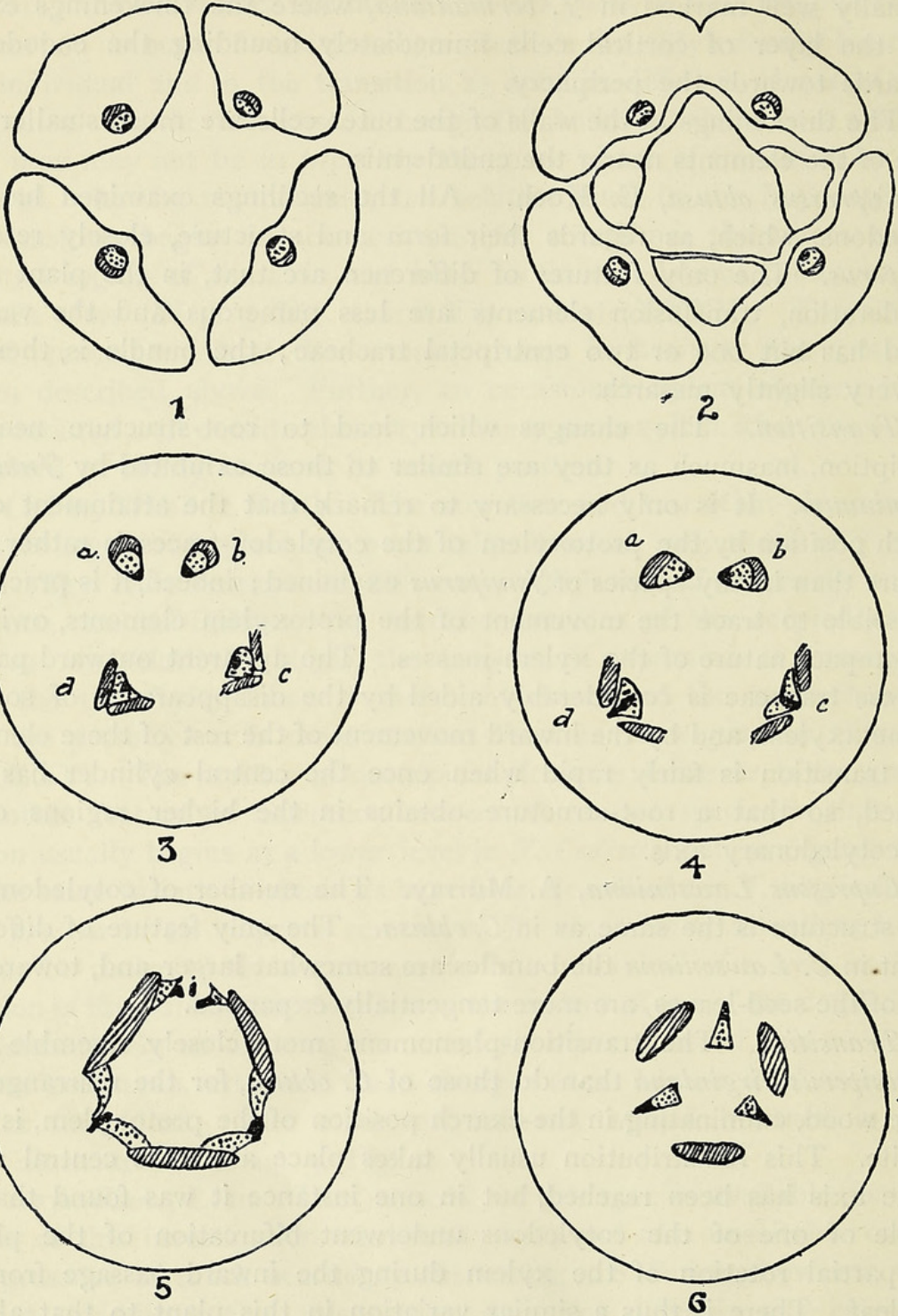


DIAGRAM 4. *Cupressus torulosa*. For the sake of clearness the vascular bundles of the plumule seen in Fig. 2 have been omitted in the later figures.

is found that there is a marked resemblance to the *Juniperus*-type; and, further, there are the same variations as regards the phases of the different bundles at the same level in one and in different individuals.

In the case of a seedling with four cotyledons (Series C) the accompanying illustrations (Diag. 4) render a long description unnecessary. The first figure shows four cotyledons in transverse section; of which two are considerably smaller than the others.

Just above the region of insertion of the seed-leaves upon the axis the two smaller cotyledons fuse together (Diag. 4, Fig. 2). The four traces enter the axis as collateral structures, and during the inward passage *a* and *b*, the bundles of the smaller cotyledons, move towards one another while the phloems of *c* and *d* bifurcate (Diag. 4, Fig. 3). At a slightly lower level (Diag. 4, Fig. 4) *a* and *b* are orientated in such a manner that their protoxylems face one another, and *c* and *d* are seen to behave in a way already described above. The remaining figures, together with Fig. 11, Plate XXXV, show that the strands *a* and *b* act together in the

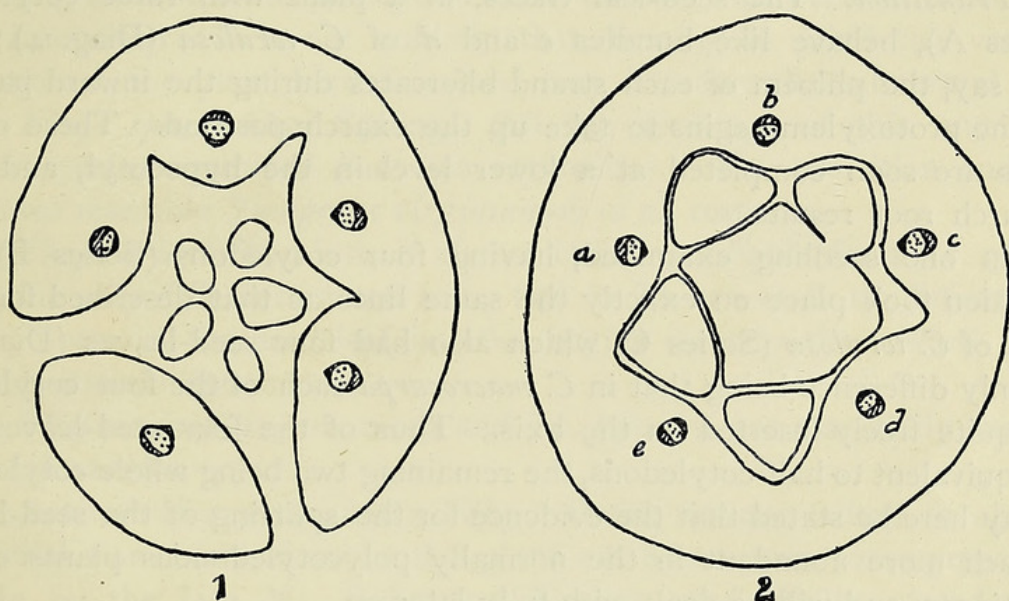


DIAGRAM 5. *Cupressus torulosa*. Transverse sections of the cotyledons at different levels of the proximal region.

same way as does either *c* or *d* separately, and form one pole of the triarch root.

The consideration of these facts leads to the inference that the two smaller seed-leaves may have been derived from a single pre-existing one; in fact, that each represents a half-cotyledon. And this is confirmed by the one seedling of this same species which possessed five cotyledons (Series D). In this plant the seed-leaves were free at the tip, but towards the proximal end four of them joined together in the manner indicated by the first figure in Diag. 5. Just above the cotyledonary node, the fifth one entered and completed the ring. The fused whorl has five bundles, corresponding to the seed-leaves, which are indicated alphabetically in the second figure.

The transition, although very much slower, followed the course

already indicated; the bundle marked *a* formed one pole of the root, *b* and *c* formed the second, while the two remaining bundles, *d* and *e*, formed the third.

The strands *b* and *c*, and *d* and *e*, acted in the same fashion as the bundles *a* and *b* in the seedling with four cotyledons (Diag. 4). It may therefore be concluded, from the behaviour of the vascular bundles, that of the five seed-leaves one (*a*) represents a whole cotyledon, while the rest are half-cotyledons, although a second complication has been introduced by the fusion of several of the seed-leaves.

Cupressus macrocarpa, Hartweg. The number of seed-leaves is three or four; their structure is the same as in the foregoing species, but they are very much narrower, their shape in transverse section being similar to that of the half-cotyledons of *C. torulosa* (Diag. 4, Fig. 1).

Transition. The seed-leaf traces, in a plant with three cotyledons (Series A), behave like bundles *c* and *d* of *C. torulosa* (Diag. 4); that is to say, the phloem of each strand bifurcates during the inward passage and the protoxylem begins to take up the exarch position. These movements are soon completed at a lower level in the hypocotyl, and thus a triarch root results.

In one seedling examined, having four cotyledons (Series B), the transition took place on exactly the same lines as that described for that plant of *C. torulosa* (Series C) which also had four seed-leaves (Diag. 4), the only difference being that in *C. macrocarpa* each of the four cotyledons was quite freely inserted on the axis. Thus of the four seed-leaves, two are equivalent to half-cotyledons, the remaining two being whole cotyledons. It may here be stated that the evidence for the splitting of the seed-leaves is much more abundant in the normally polycotyledonous plants of the Abietineae, and will be dealt with fully later on.

Libocedrus decurrens, Torr. Two seedlings only were available for the purposes of this investigation, and of these one alone was suitable for the study of the transition-phenomena, owing to the presence of extensive secondary thickening in the other. The older of these had two cotyledons, while the younger, which is considered below, had three (Fig. 5, Plate XXXV); Professor Lawson informs us, however, that the usual number of seed-leaves is two.

Although the structure and transition is of the same type as has been described above, the transition from stem to root-structure is very much slower than in any of the preceding plants. The upper part of the hypocotyledonary axis exhibits stem-structure, and the rearrangement of the vascular tissues is very gradual. The phloem of any one bundle diverges on each side of the wood and fuses with the corresponding masses of bast derived from the adjacent bundles; hence a radial arrangement of the essential tissues results. The redistribution of the elements of the

xylem groups, to bring the protoxylem into an exarch position, is very slow. The protoxylem lies buried in the centre of the metaxylem for some distance downwards, and the metaxylem elements slowly take up a more internal position; but this does not bring the protoxylem, which is gradually becoming less in amount, into the desired position, owing to the differentiation of new xylem elements outside it, which addition is much more marked than that described for *Juniperus virginianum*. Indeed, a careful study of these tracheae downwards towards the root apex, warrants the conclusion that in *L. decurrens* the protoxylems of the cotyledons die out and that new protoxylems are organized in an exarch position, which means that the protoxylems of the root are not directly continuous with those of the seed-leaves.

A similar state of affairs has been described in *Torreya Myristica*¹, but at present it is not possible to state whether this occurrence is normal for *Libocedrus*; it is not unlikely that, bearing in mind the variations mentioned, the plant here described may be somewhat abnormal.

Thuja sphaeroidea, Spreng. All the seedlings of this and of the other species examined had two cotyledons. The transition and other features resemble *Juniperus virginianum* in all respects.

Thuja orientalis, Linn., is almost indistinguishable from *Th. sphaeroidea*, the only difference noted being that in *Th. orientalis* the bifurcation of the phloem of the seed-leaf bundles begins directly the inward passage of the strands commence.

Thuja orientalis var. *aurea* and *Th. japonica* are essentially similar to *Th. sphaeroidea*.

Actinostrobus pyramidalis, Miq. Owing to our failure in obtaining material, our observations on this plant are based upon some preparations made by the late Mr. Robertson Glasgow, and kindly placed at our disposal by Dr. D. H. Scott.

Actinostrobus pyramidalis resembles *Thuja orientalis*; the difference between them may be looked upon as one of degree rather than of kind. The bundles of the cotyledons, which are two in number, are single collateral structures throughout the whole length of each seed-leaf, but directly the axis is entered each trace divides into two half-bundles, the division being in the cotyledonary plane. This bifurcation extends not merely through the phloem but also affects the metaxylem. Rotation takes place around the protoxylem, so that the latter tissue is practically in an exarch position as soon as the central region of the hypocotyl is reached (Diag. 6, Fig. 1), the metaxylem and phloem-masses being placed on either side. Fusion of the opposing groups of vascular elements, other than protoxylem, takes place, thus resulting in the formation of a diarch root (Diag. 6, Fig. 2).

¹ Chick, E., loc. cit.

Callitris. All the species of this genus examined had two cotyledons and a primary diarch root.

Callitris Muelleri, Benth. & Hook. resembles *Thuja orientalis*. The transition-phenomena are identical, and, as regards the structure of the cotyledons, there is the same indication of a few centripetal xylem elements in the vascular strands of some individuals; these elements, both in this and in other species, are very poorly marked indeed. Transfusion tissue in all the species examined is fairly abundant.

Callitris calcarata, R. Br., is like the foregoing species, but the phloem of each cotyledon-bundle bifurcates towards the base of each seed-leaf. The protoxylem assumes the exarch position in the same manner as obtains in *Juniperus*, i.e. the metaxylem passes inwards more rapidly than does the protoxylem, and there is a disappearance of some of the

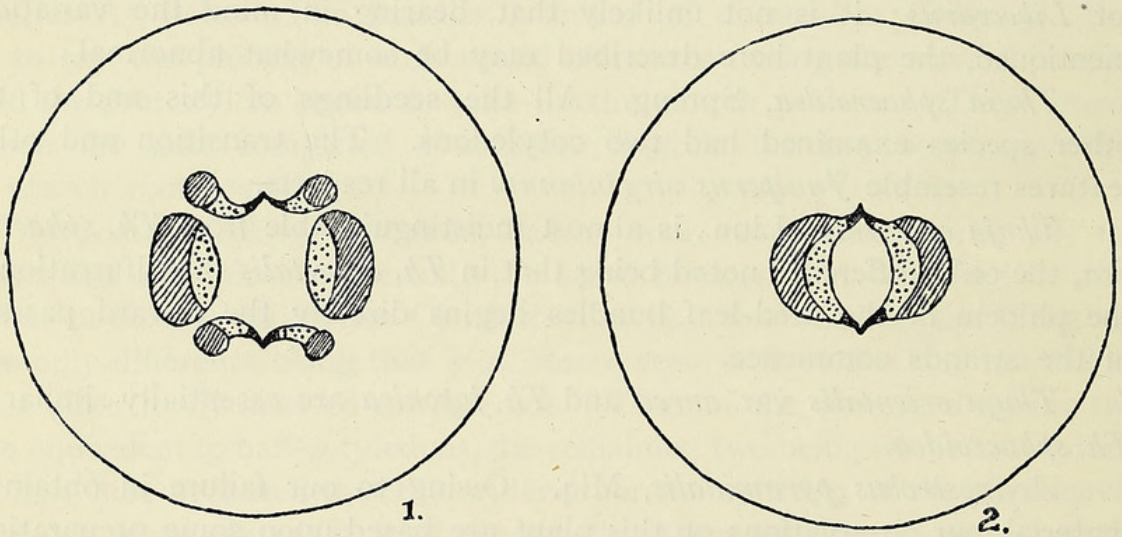


DIAGRAM 6. *Actinostrobus pyramidalis*.

more externally situated metaxylem elements. The assumption of the exarch position of the protoxylem, both in this and in the above species, takes a relatively long time.

Callitris robusta, R. Br., closely resembles *C. calcarata*. The vascular strand of a cotyledon of one individual showed not only a bifurcation of the phloem, but also a division of the wood, accompanied by a certain amount of rotation of the protoxylem to take up the exarch position, while the bundle was still contained within the seed-leaf. The trace of the other cotyledon behaved in the manner described for *C. calcarata*.

In all the species of *Callitris* examined there are the same variations regarding the difference in the phase of each seed-leaf bundle at the same level in the same and in different individuals that have already been mentioned in the case of *Juniperus* and *Cupressus*.

A minor point connected with the foliage leaves may here be remarked upon.

It has been seen that in *Cupressus torulosa* and *C. macrocarpa* there

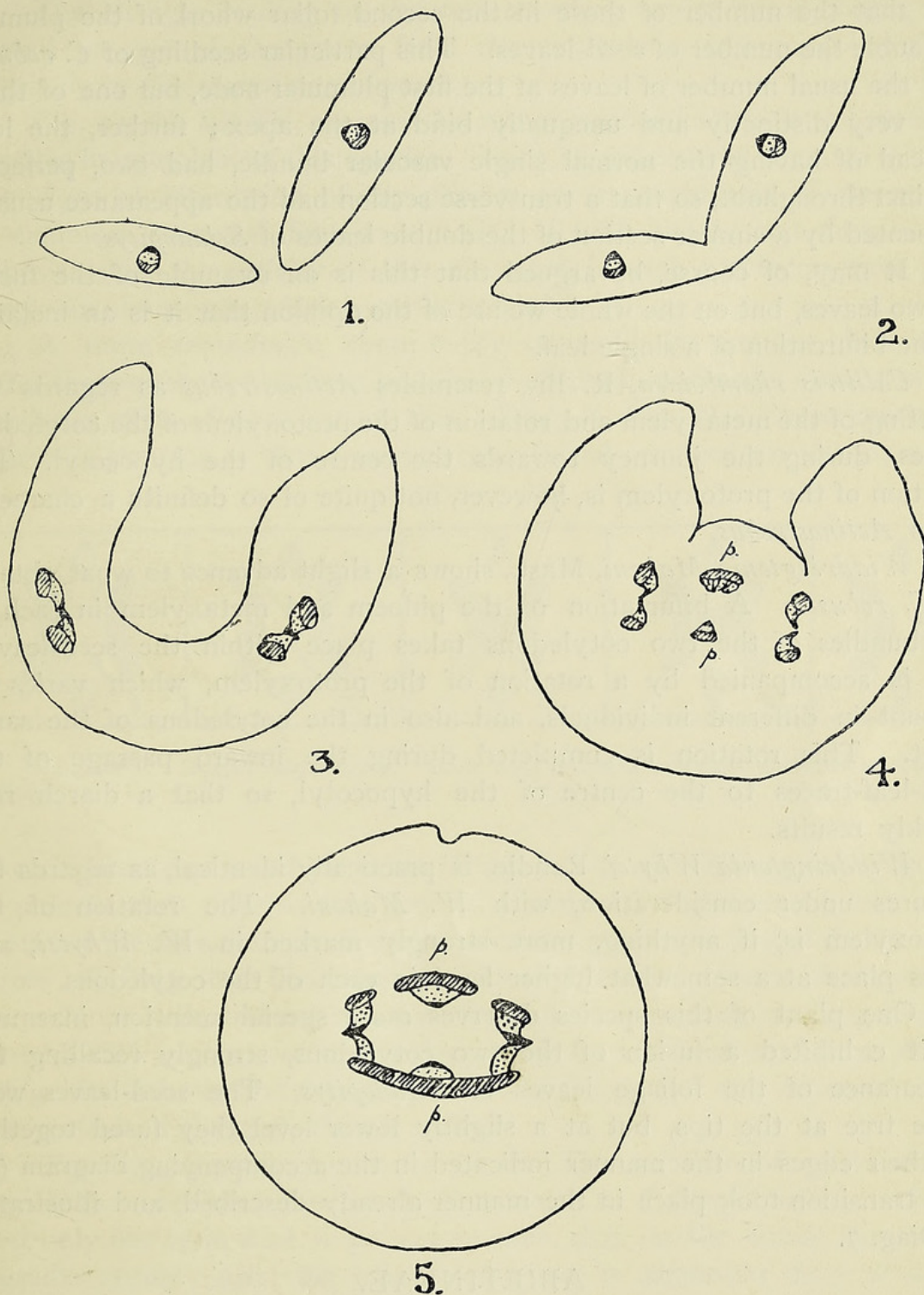


DIAGRAM 7. *Widdringtonia Whytei*. A specimen showing fusion of the cotyledons. The bundles marked *p* are plumular traces.

is evidence which leads to the conclusion that some of the seed-leaves really represent half-cotyledons; one plant of *Callitris robusta* showed

a similar state of affairs in the first whorl of foliage leaves. In this, and in the other plants dealt with, the general rule is that the number of the leaves in the first foliar whorl is equal to the number of cotyledons, and that the number of those in the second foliar whorl of the plumule is double the number of seed-leaves. This particular seedling of *C. robusta* had the usual number of leaves at the first plumular node, but one of them was very distinctly and unequally bifid at the apex; further, the leaf, instead of having the normal single vascular bundle, had two, perfectly distinct throughout, so that a transverse section had the appearance usually presented by a similar section of the double leaves of *Sciadopitys*.

It may, of course, be argued that this is an example of the fusion of two leaves, but on the whole we are of the opinion that it is an instance of the bifurcation of a single leaf.

Callitris rhomboidea, R. Br., resembles *Actinostrobus* as regards the splitting of the metaxylem and rotation of the protoxylem of the cotyledon-traces, during the journey towards the centre of the hypocotyl. The rotation of the protoxylem is, however, not quite of so definite a character as in *Actinostrobus*.

Widdringtonia Mahoni, Mast., shows a slight advance to what obtains in *C. robusta*. A bifurcation of the phloem and metaxylem in each of the bundles of the two cotyledons takes place within the seed-leaves, and is accompanied by a rotation of the protoxylem, which varies in amount in different individuals, and also in the cotyledons of the same plant. This rotation is completed during the inward passage of the seed-leaf-traces to the centre of the hypocotyl, so that a diarch root quickly results.

Widdringtonia Whytei, Rendle, is practically identical, as regards the features under consideration, with *W. Mahoni*. The rotation of the protoxylem is, if anything, more strongly marked in *W. Whytei*, and takes place at a somewhat higher level in each of the cotyledons.

One plant of this species deserves more special mention, inasmuch as it exhibited a fusion of the two cotyledons, strongly recalling the appearance of the foliage leaves of *Sciadopitys*. The seed-leaves were quite free at the tips, but at a slightly lower level they fused together by their edges in the manner indicated in the accompanying diagram (7). The transition took place in the manner already described, and illustrated in Diag. 7.

ABIETINEAE.

TAXODIINAE.

Sequoia sempervirens, Endl. The number of cotyledons, as far as has been seen, is two; and structurally they do not differ in any marked degree from those of the foregoing plants, excepting in the fact that, in

this plant, each seed-leaf has three resin ducts situated just below the epidermis, one at each end of the leaf, and the other immediately above and dorsal to the vascular bundle.

The changes leading to the root-structure are initiated during the inward passage of the traces from the cotyledons, and resemble those obtaining in *Juniperus virginianum*.

Fig. 12, Pl. XXXV, represents a rather curious feature in the seed-leaf bundles in one plant of this species. Each strand entered the axis without any signs of bifurcation of the phloem or rearrangement of the xylem. A cambium extended first on one side of each bundle and then on the opposite side, the activity of this meristem, in each cotyledon-trace, gave rise to an almost concentric vascular strand.

A more remarkable abnormality occurred in another individual. After the transition had been practically effected, meristems arose towards the inner sides of each xylem mass (Diag. 8, Fig. 1). These cambiums effected a junction so that a semi-circular strand occurred on the inner side

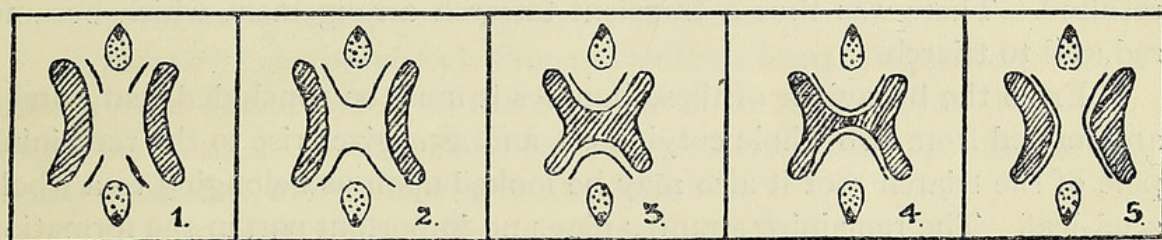


DIAGRAM 8. *Sequoia sempervirens*. Black lines represent cambium, the other markings, as before.

of each bundle of wood-elements (Diag. 8, Fig. 2). The opposing groups of phloem then underwent a gradual centripetal displacement, met in the centre of the axis, and gave rise to an arrangement indicated in the third figure of Diag. 8. The cambium formed a few phloem elements and parenchyma cells, but not in a quantity sufficient to cause crushing (Fig. 13, Plate XXXV). On tracing the tissues still further downwards, the phloem bridge thinned out, and finally broke; thus the normal disposition of tissues was reattained (Diag. 8, Figs. 4 and 5).

Sequoia gigantea, Lindl. & Gord. The number of seed-leaves is usually three or four; structurally they resemble *S. sempervirens*, excepting that only one resin duct is present in each, that on the dorsal side of the vascular strand; also, the transfusion tissue is somewhat more abundant than in *S. sempervirens*.

Taking first a tricotyledonous specimen, it was found that the transition was identical with what obtains in *Widdringtonia Whytei*, the main feature being that bifurcation of the phloem and rotation of the xylem to assume the exarch position, takes place while the bundles

are still contained within the seed-leaves. A triarch root-structure therefore is formed at a very high level of the hypocotyledonary axis.

A plant with four cotyledons gave rise to a tetrarch root in the same manner, although three of the seed-leaf bundles did not start the re-arrangement of their vascular tissues until entry into the axis had been gained, and, further, the rotation of the xylem was not nearly so well marked as in the plant of this species first considered.

Another individual with four cotyledons (Series C), afforded further evidence of the splitting of these structures. For the sake of clearness in description the bundles of these seed-leaves may be termed *a*, *b*, *c*, and *d*. *a* underwent bifurcation of the phloem and partial rotation of its xylem while still within the seed-leaf, and ultimately gave rise to one pole of the triarch root. *b* performed in a similar fashion, but did not start the re-arrangement of the vascular tissues until its entry into the axis; it also formed one pole of the root. *c* and *d* followed on the same lines as *b*, but the protoxylem of *c* died out, its metaxylem effected a junction with the metaxylem of *d*, the isolated phloem-masses fused, so that a triarch root resulted. There was thus a transient tetrarch arrangement which became reduced to triarch.

From the behaviour of these bundles it must be concluded that *a* and *b* are derived from two whole cotyledons, and as *d* gives rise to the remaining pole of the triarch root it also may be looked upon as belonging to a whole seed-leaf. The remaining strand *c* plays no important part in the formation of the root-structure, and therefore falls into the category of seed-leaves which we have termed subsidiary cotyledons.¹ It is to be observed, however, that this bundle at first behaved in such a fashion as to lead one to suppose that it would form a pole of the root; for bifurcation of the bast and a certain amount of rearrangement of the wood took place. This occurrence is not uncommon and is more especially found in species of *Pinus* for instance; the explanation of it may perhaps be left until these other examples have come under consideration.

Cryptomeria japonica, D. Don. The number of seed-leaves varies from two or three, each has two resin ducts situated one at each end of the leaf.

The transition takes place in the same manner as in the plants already described, resembling *Juniperus virginianum* pretty closely.

All the tricotyledonous plants examined had triarch primary roots.

Sciadopitys verticillata, Sieb. & Zucc., is constant in its number of seed-leaves, never more than two having been observed; they resemble in structure those of *Sequoia sempervirens*, although there is a larger number of transfusion tracheides present; in fact this tissue is more abundant in this plant than in any of the foregoing.

¹ Hill and de Fraine: British Assoc., Section K, York, 1906.

The transition is the same as in *Sequoia gigantea*; a diarch root is, however, always formed.

It may also be remarked that the same variations in the phase of transition of the cotyledonary bundles at the same level occur in this plant as have already been described above for species of *Juniperus*, *Cupressus*, *Callitris*, and *Sequoia*. This is illustrated by Figs 14 and 15, Plate XXXV.

SUMMARY AND CONCLUSIONS.

COTYLEDONS.

1. As regards the number of cotyledons, the following plants have two:—*Taxus*, *Cephalotaxus*, *Podocarpus*, *Juniperus*, *Cupressus obtusa*, *C. Lawsoniana*, *C. pisifera*, *Thuja*, *Actinostrobus*, *Callitris*, *Widdringtonia*, *Sequoia sempervirens*, and *Sciadopitys*.

The following have 2-3:—*Libocedrus decurrens* and *Cryptomeria japonica*.

The following have 3-4:—*Cupressus macrocarpa* and *Sequoia gigantea*.

The following has 3-5:—*Cupressus torulosa*.

2. Some of the polycotyledonous seedlings form a short cotyledonary tube by the lateral union of the seed-leaves in the proximal region, e. g. *Cupressus torulosa*. Occasionally the two seed-leaves fuse laterally to form a single member, e. g. *Widdringtonia Whytei*.

3. Resin ducts, as far as has been seen, are absent in the seed-leaves of *Cephalotaxus*, *Taxus*, *Podocarpus*, *Juniperus*, *Cupressus*, *Libocedrus*, *Thuja*, *Actinostrobus*, *Callitris*, and *Widdringtonia*. They are present in the cotyledons of *Cryptomeria*, *Sequoia*, and *Sciadopitys*.

4. With the exception of *Podocarpus* and *Cupressus torulosa*, the seed-leaves each contain a single vascular strand.

Podocarpus has two bundles, entirely separate, in each cotyledon, and the same may occur in *Cupressus torulosa*, which is due, in this particular plant, to the splitting of certain of the seed-leaves.

5. The cotyledon-bundles have a pronounced mesarch structure in *Cephalotaxus*; the phenomenon is much less obvious in *Taxus* and *Juniperus*; and is merely indicated by one or two centripetal xylem elements in *Cupressus obtusa*, *C. macrocarpa*, and *Callitris*.

6. Transfusion tracheides are generally present.

7. Elements of a fibrous nature occur in the bast of *Cephalotaxus*, *Taxus*, and *Thuja*.

TRANSITION-PHENOMENA.

8. The transition of the majority of the Taxaceae and Cupressineae follows Van Tieghem's Type 3. That is to say, the single vascular strand of each seed-leaf undergoes bifurcation of the vascular tissues accompanied

by a rotation of the xylem in order that the protoxylem may be situated in an exarch position. Finally, the opposing phloem-masses unite in pairs; thus a diarch root-structure obtains.

9. There is, however, some variation. There is frequently no definite rotation of the protoxylem, the exarch position being gained rather by the movement of the metaxylem elements, e.g. *Taxus*, *Juniperus virginiana*, *J. Cedrus*, *Cupressus obtusa*, *C. pisifera* *Libocedrus*, and *Callitris*.

The remaining plants considered exhibit a more definite rotation of the protoxylem.

These variations differ in degree in the several plants, and they merge one into the other. Further, it may happen that the trace of one cotyledon shows practically no movement, of a definite nature, of the protoxylem, while the same tissue of the other seed-leaf may exhibit a well-defined rotation e.g. *J. procera*.

There is also a well-pronounced variation, more especially in the Cupressineae, in the level at which the transition begins, and this not only in different species of the same genus, but in individuals of the same species. The transition-phenomena may start in the cotyledons themselves; or, in the topmost part of the hypocotyl, before the traces have reached the central region; or, finally, it may be further postponed and take place at different levels of the hypocotyl. It is obvious that, in the first two cases, a root-structure obtains practically throughout the whole of the hypocotyledonary axis.

10. The transition-phenomena in some of the polycotyledonous forms described (*Cupressus torulosa*, *C. macrocarpa*, and *Sequoia gigantea*) follow the same general course as is summarized above, but showing certain variations which are due to the increased number of seed-leaves. The consideration of these leads to the inference that some of the cotyledons probably represent the halves of single pre-existing seed-leaves; in other words, that the dicotyledonous condition is the more primitive, and that polycotyledony has been derived from it.

11. *Podocarpus*, and possibly also other plants of the Podocarpeae, differ from the other members of the Taxaceae and the Cupressineae, inasmuch as each of the two cotyledons have two vascular bundles, which together form one pole of the primary diarch root.

ROOT.

12. An *assise de soutien* occurs in the roots of *Cephalotaxus*, *Taxus*, and *Juniperus*.

13. The following table shows the relations, in the plants examined, between the number and nature of the cotyledons and the root-structure.¹

¹ Van Tieghem (loc. cit.) states that the primary root of the Taxaceae and Cupressineae is diarch, and is in agreement with the number of cotyledons. Occasionally, when the number of seed-leaves is three, the tap-root is triarch.

Plant.	Series.	Cotyledons.			Root.
		Total.	Whole Cots.	Half Cots.	
<i>Cephalotaxus pedunculata</i>	all	2	2		2-arch
" <i>Fortunei</i>					
" <i>drupacea</i>					
<i>Taxus baccata</i>					
" <i>cuspidata</i>	all	2	2		2-arch
<i>Podocarpus chinensis</i>					
<i>Juniperus Cedrus</i>					
<i>J. bermudiana</i>					
<i>J. virginiana</i>					
<i>J. procera</i>					
<i>Cupressus obtusa</i>					
<i>C. Lawsoniana</i>					
<i>C. pisifera</i>	A	3	3		3-arch
<i>C. torulosa</i>					
"					
"					
"	B	3	3		3-arch
"	C	4	2	2	3-arch
"	D	5	1	4	3-arch
<i>C. macrocarpa</i>	A	3	3		3-arch
"	B	4	2	2	3-arch
<i>Libocedrus decurrens</i>	A	3	3		3-arch
<i>Thuja sphaeroidea</i>	all	2	2		2-arch
<i>Th. orientalis</i>					
" <i>var. aurea</i>					
<i>Th. japonica</i>					
<i>Actinostrobus pyramidalis</i>					
<i>Callitris Muellerei</i>					
<i>C. calcarata</i>					
<i>C. robusta</i>					
<i>C. rhomboidea</i>	A	3	3		3-arch
<i>Widdringtonia Mahoni</i>					
<i>W. Whytei</i>					
<i>Sequoia gigantea</i>					
" "	B	4	4		4-arch
" "	C	4	3	I	4 → 3-arch
<i>S. sempervirens</i>	all	2	2		2-arch
<i>Cryptomeria japonica</i>	all	3	3		3-arch
<i>Sciadopitys verticillata</i>	all	2	2		2-arch

EXPLANATION OF FIGURES IN PLATE XXXV,

Illustrating Mr. T. G. Hill's and Miss de Fraine's paper on the Seedling Structure of *Gymnosperms*.

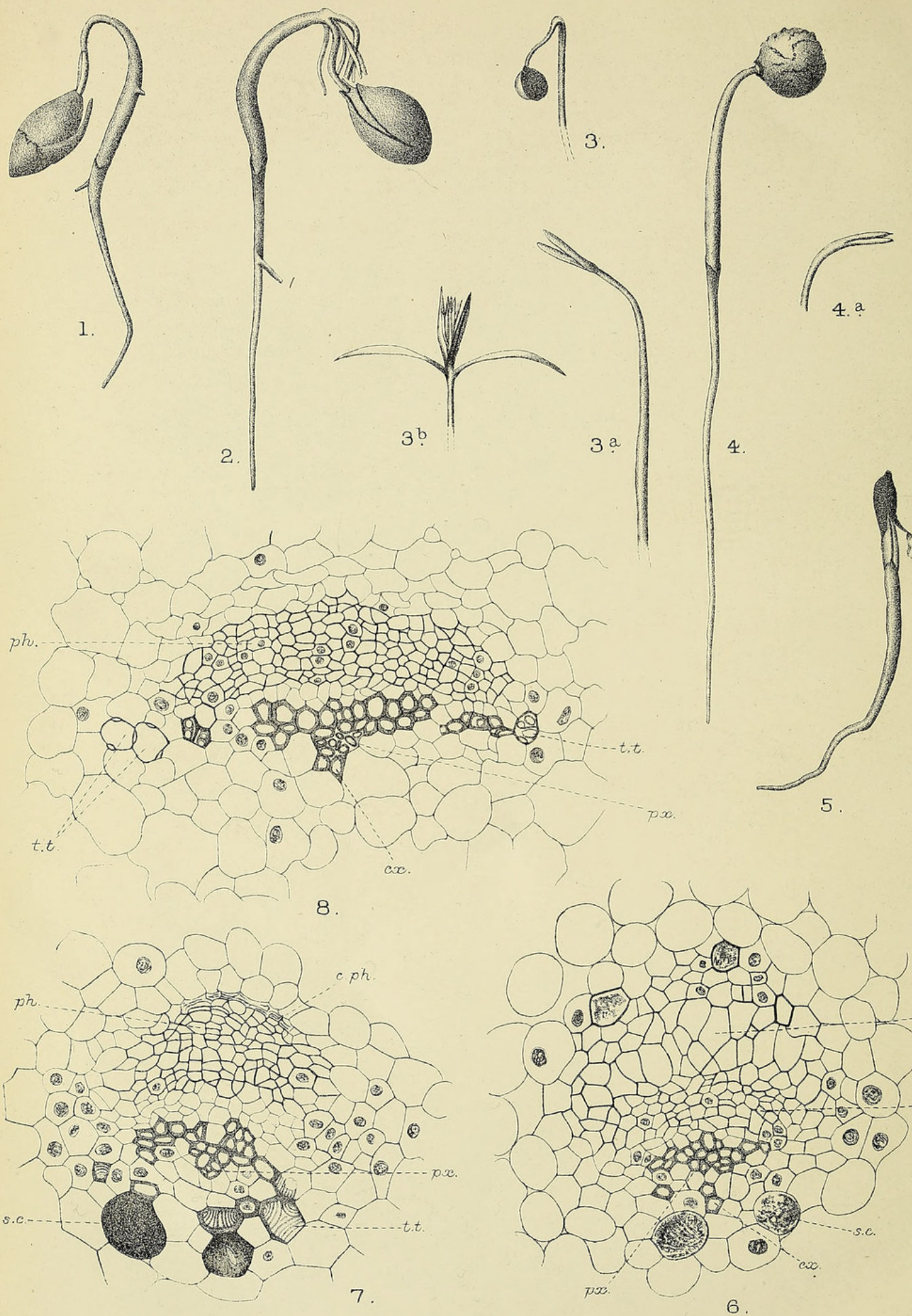
Abbreviations used:—*c.*, cambium; *c. ph.*, crushed phloem; *c. x.*, centripetal xylem; *mx.*, metaxylem; *f.*, fibres; *ph.*, phloem; *px.*, protoxylem; *s. c.*, secretory cells; *T. S.*, transverse section; *t. t.*, transfusion tracheides.

Figs. 1–5 natural size.

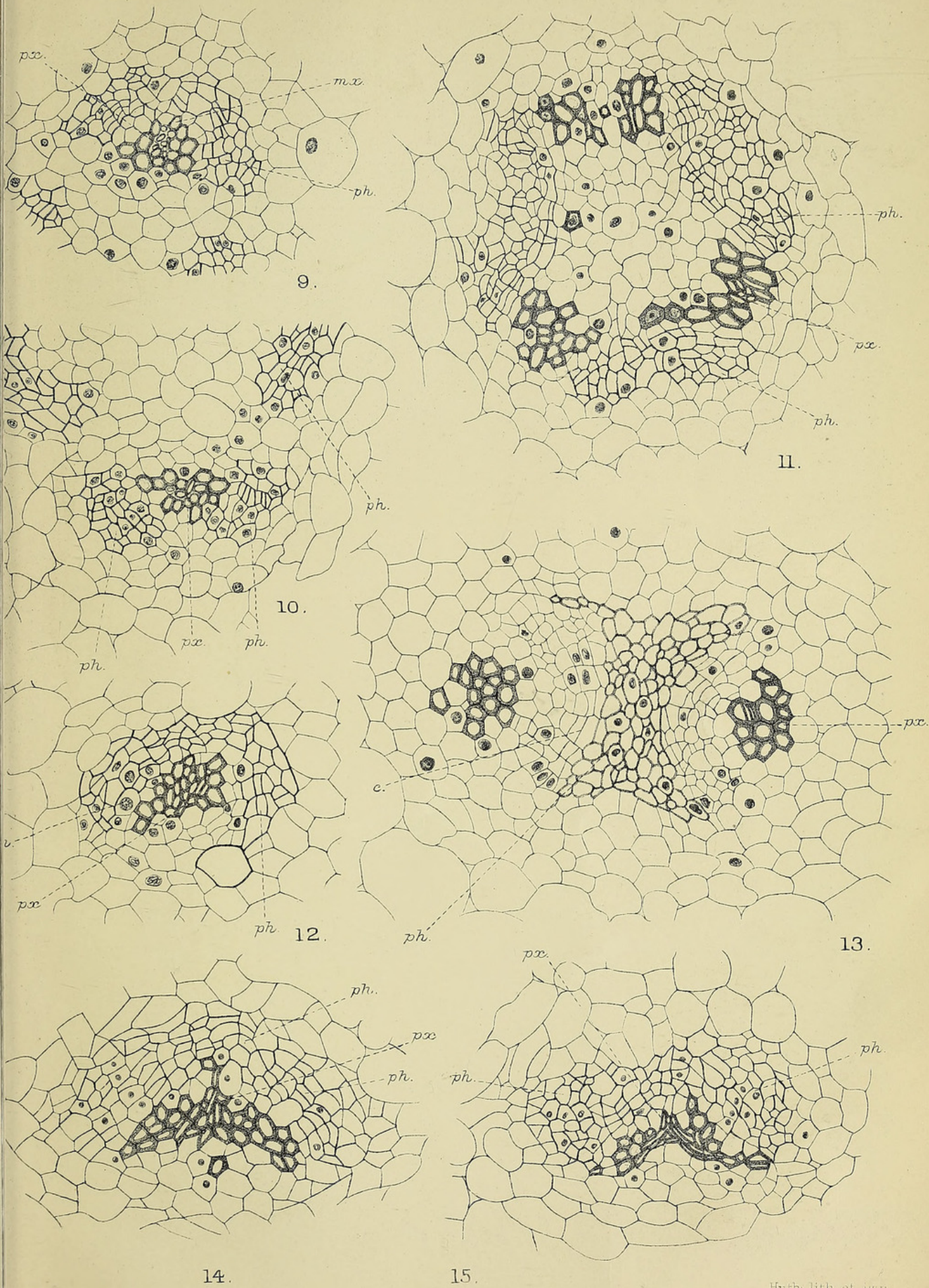
- Fig. 1. *Cephalotaxus pedunculata*. Young seedling.
- Fig. 2. *Cephalotaxus pedunculata*. Older seedling.
- Fig. 3. *Taxus baccata*. Upper region of young seedling; cotyledons still enclosed within endosperm.
- Fig. 3a. *Taxus baccata*. Older seedling; cotyledons free.
- Fig. 3b. *Taxus baccata*. Still older seedling with plumule.
- Fig. 4. *Podocarpus chinensis*. Seedling with cotyledons enclosed within seed.
- Fig. 4a. *Podocarpus chinensis*. The same seedling showing cotyledons.
- Fig. 5. *Libocedrus decurrens*. Young seedling; cotyledons still contained within seed.

Figs. 6–15 $\times 240$.

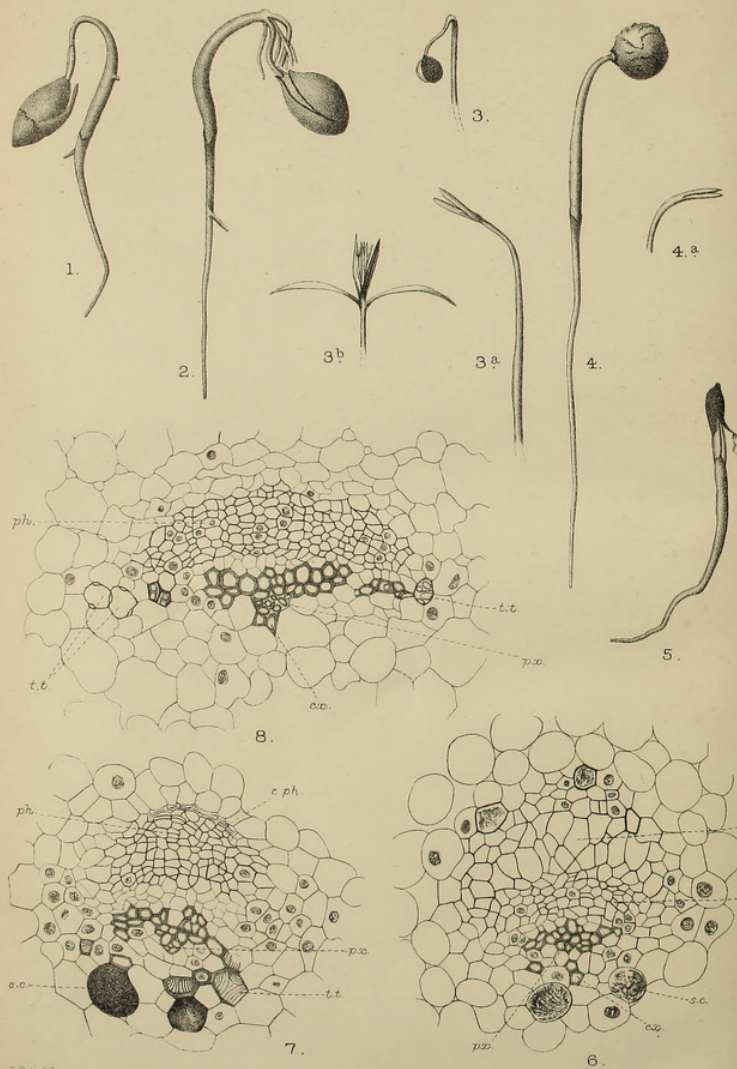
- Fig. 6. *Taxus baccata*. T. S. cotyledon-bundle.
- Fig. 7. *Podocarpus chinensis*. T. S. cotyledon-bundle.
- Fig. 8. *Juniperus Cedrus*. T. S. cotyledon-bundle.
- Fig. 9. *Juniperus virginiana*. T. S. hypocotyl showing seed-leaf-bundle immediately before its bifurcation.
- Fig. 10. *Juniperus virginiana*. T. S. hypocotyl, showing the bifurcated cotyledon-bundle nearing the central region of the axis.
- Fig. 11. *Cupressus torulosa*. T. S. upper region of hypocotyl.
- Fig. 12. *Sequoia sempervirens*. T. S. cotyledon-bundle.
- Fig. 13. *Sequoia sempervirens*. T. S. hypocotyl.
- Fig. 14. *Sciadopitys verticillata*. T. S. cotyledon-bundle at the extreme base of the seed-leaf.
- Fig. 15. The same in another seedling.



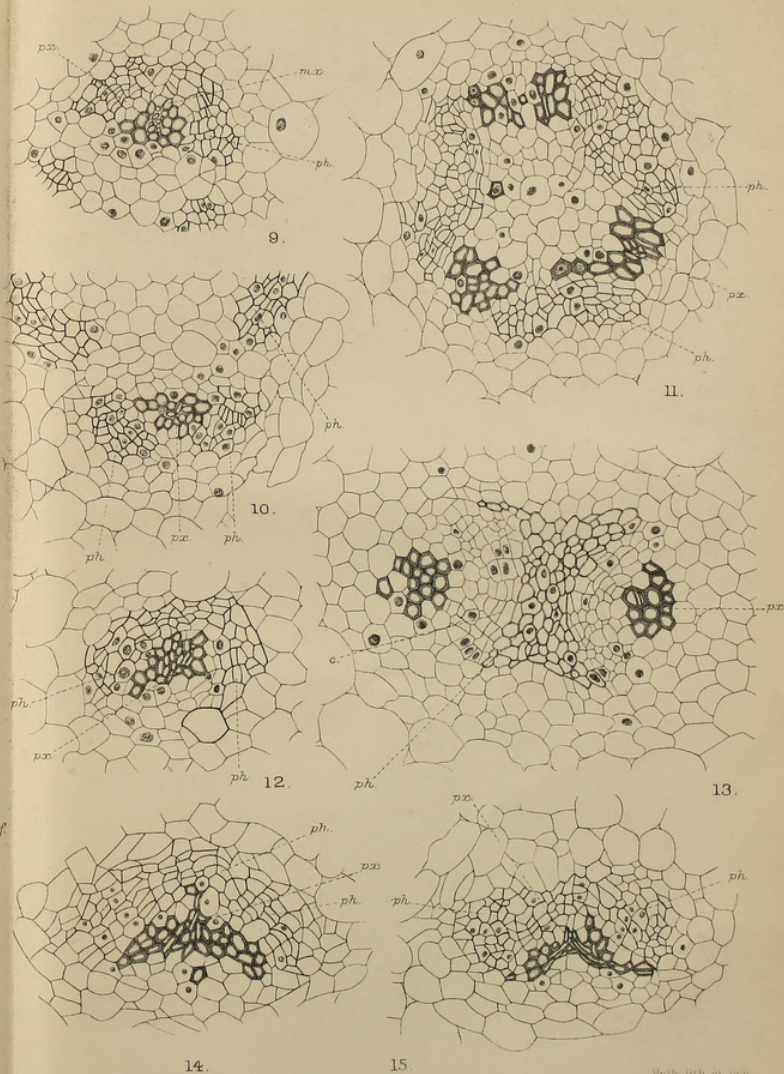
T. G. H. del.



Huth, lith. et imp.



T.G.H. del.



Hill, lith. et imp.



Hill, T. G. and De Fraine, E. 1908. "On the seedling structure of gymnosperms. I." *Annals of botany* 22, 689–712.

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