VIII. *On "Transfusion-tissue": its Origin and Function in the Leaves of Gymnospermous Plants.* *By* W. C. WORSDELL. (*Communicated by* D. H. SCOTT, *Ph.D., F.R.S., F.L.S., Hon. Keeper of the Jodrell Laboratory, Royal Gardens, Kew.*)

(Plates XXIII.–XXVI.)

Read 4th November, 1897.

THIS paper, which has been preceded by a short preliminary thesis, presenting only the chief facts (Journ. Linn. Soc., Bot. vol xxxiii. pp. 118–123), furnishes a more detailed and elaborate account of the subject therein dealt with. It treats at some length of the origin and distribution of transfusion-tissue in the foliar organs of Gymnospermous plants.

This tissue is well known to be universally present in the leaves of Conifers; it occurs generally in the leaves of Cycads, and in those of *Ephedra* and *Welwitschia* among the Gnetaceæ. Among Angiospermous plants it is known to occur here and there in leaves and stems, but in these cases in a more or less modified form.

No one, however, as yet, has been able to give a satisfactory account of the origin and homology of this important and striking tissue. This I hope to be able to do in the following pages.

Historical Survey.

The first discoverer of "transfusion-tissue" was the German botanist Frank, who, in an important paper*, describes it in connection with the vascular bundle of the leaf of *Taxus baccata*, Linn. As regards its origin, he considers it to arise from the bundle, having noticed transitions in the shape and size of the tracheides from the ordinary xylem of the bundle outward to the transfusion-tissue at its side.

Thomas † mentions transfusion-tissue in the leaves of three genera of Conifers. He believes it to be parenchymatous in origin.

A paper by Kraus ‡, "Ueber den Bau der Cycadeenfiedern," dealing with the minute structure of the leaves of various Cycadean genera, does not mention the transfusion-tissue proper, but describes, in the genus *Cycas* (probably for the first time), the tracheides of the "accessory transfusion-tissue" running at right angles to the midrib towards the margin of the leaf, and which are characteristic of, and peculiar to, this genus.

In 1871 Mohl published an interesting paper § on the structure and morphology

* "Ein Beitrag zur Kenntniss der Gefässbündel," Bot. Zeit. 1864.

† "Zur vergl. Anat. d. Coniferen Laubblätter," Pringsh. Jahrb. Band iv. 1865.

‡ Pringsh. Jahrb. 1865.

§ "Morph. Betrachtung der Blätter von *Sciadopitys*," Bot. Zeit. 1871.

of the leaf of *Sciadopitys*. He is the first author to use the word "transfusion-tissue," applying it to the tracheides found in the tissue around the xylem of the bundle in this plant. He agrees with Thomas that it belongs to the parenchymatous tissue of the leaf, and not to the bundle.

Bertrand*, in a general sketch of the anatomy of the stems and leaves in the Gnetaceæ and Coniferæ, describes and figures transfusion-tissue in several genera, but does not enter into much detail concerning it.

De Bary† affords us the completest and clearest account given by any author of the transfusion-tissue as it occurs in the leaves of Gymnosperms, and illustrates his description by two very good figures of leaf-bundles of *Cunninghamia* and *Juniperus communis*, Linn. He does not attempt, however, to explain its origin.

Zimmermann's description‡ of transfusion-tissue is one of the best and fullest. He rightly argues that a sharp distinction must be made between the large elongated tracheides running out to the margin of the leaf in *Cycas* and *Podocarpus* (which are specially modified from the parenchyma) and the real transfusion-tissue at the side of the bundle.

There is an excellent paper by Scheit§, entitled "Die Tracheidensäume der Blattbündel der Coniferen," which is worthy of special notice. He made a minute investigation into the character of the bordered pits and thickenings of the tracheides of the transfusion-tissue in many genera of Coniferæ. Of the transfusion-tissue of the Cycadeæ he does not say much, but finds it to agree entirely in most points with that of the Coniferæ. He makes an interesting study, with regard to this tissue, of the Gnetaceæ. He regards the reticulate venation of the foliage-leaf of *Gnetum* as a transition between the rudimentary venation of *Ephedra* and Conifers and the complex venation of Dicotyledons. But it is very questionable whether he is right in regarding the short tracheides which occur at the point of branching of the bundles and at their final endings as equivalent to the transfusion-tissue of Coniferæ. It is, however, of the greatest interest to find that the *bracts* of *Gnetum Gnemon*, Linn., which externally resemble the foliage-leaves of *Ephedra*, have the same rudimentary venation (though here consisting of five to six bundles), and also well-developed transfusion-tissue accompanying the bundles. He appears to be the first author to thoroughly investigate transfusion-tissue from the physiological point of view. At the opening of the paper the tracheidal nature of its elements, ascertained by reference to their mode of thickening, watery contents, and the closed character of the bordered pits, is fully discussed; at the close he considers the factors which determine the mode of thickening of the transfusion-tracheides and the development of the tissue as a whole. The chief factor determining the character of the wall appears to be the greater or less exposure to the turgescence of the surrounding parenchyma-cells; in the former case reticulate and other thickenings are present on the wall, in

* 'Bibliothèque de l'École des Hautes Études,' tome xii., art. no. 1, 1875.

† 'Comp. Anat. of Phanerog. and Ferns,' p. 380, 1877 (Engl. ed. 1884).

‡ "Ueber das Transfusionsgewebe," Flora, 1880.

§ Jenaische Zeitschr. f. Naturwiss., Band xvi. 1883.

the latter these tend to disappear and bordered pits to be alone present. The development of the tissue as a whole he considers to depend on the amount of transpiration to which the leaf is subjected—this, again, depending on the habitat.

As regards the origin of the transfusion-tissue, he approaches nearer to the truth than any other author. These are his words:—"Wherever, in the mature condition, the transfusion-tissue is found surrounding the phloem or the xylem, or both, *its origin lies in the xylem, as it completely passes over into the latter.*" This is, nevertheless, a vague statement, and not very much value can be attached to it.

The paper, as a whole, is extremely suggestive, and, I think, has been rather overlooked by subsequent writers.

A dissertation by Vetters *, entitled 'Die Blattstiele der Cycadeen,' gives a most minute and thorough description of the structure of the petioles, and the course of the bundles in the pinnæ, of all Cycadean genera. There is a careful and accurate account of the "accessory transfusion-tissue" in *Cycas*; and he also notifies the occurrence, though under varying forms, of the normal transfusion-tissue on the side of the bundles of the pinna.

The most accurate and thorough investigation of transfusion-tissue, as it occurs in the group Abietineæ, which has hitherto been made is that by Daguillon †. He is the first to define the exact tissue of the leaf in which, in this group, the tracheides occur, viz. the pericycle. He is careful to notice the various positions with regard to the bundle which the tracheides of the transfusion-tissue occupy respectively in the cotyledon and foliage-leaf. He finds that in the cotyledon of *Pinus sylvestris*, Linn., they occur opposite the protoxylem; in the foliage-leaf, on the contrary, chiefly round the phloem; an intermediate stage is presented in the "primordial" ‡ leaf, where the pericyclic sclerenchyma, which he holds to be homologous with the transfusion-tissue, extends round both xylem and phloem, being most abundant round the latter. His figures illustrating these points are the clearest and finest ever published.

A great authority on the subject, Van Tieghem §, describes the occurrence and the varying positions of transfusion-tissue in the leaves of Conifers. He recapitulates the statements of Frank, Mohl, and De Bary as to its origin, concluding that the views of these authors are inadmissible, and that the transfusion-tissue, from his own observation, belongs morphologically to the *peridesm* (pericycle) of the bundle.

Lignier ‖, the latest author dealing with the subject, discusses the homology of the transfusion-tissue in the pinna of *Cycas*, and finds that the tracheides of the "accessory transfusion-tissue" which traverse the mesophyll to the margin of the leaf merge

* Inaugural Dissert., Leipzig, 1884.

† "Recherches sur les Feuilles des Conifères," Revue générale de Bot. tome ii. 1890.

‡ The "primordial" leaves are the first-formed leaves of the seedling, which succeed the cotyledons, and occur singly and scattered around the stem; they possess a flattened lamina with a single bundle, thus differing considerably from the later-formed "needles."

§ "Sur les Tubes criblés extralibériens et les Vaisseaux extraligneux ('needles')," Journ. de Bot., 1891.

‖ "La Nervation ténioptéridée des Folioles de *Cycas* et le Tissu de transfusion," Bulletin de la Soc. Linn. de Normandie, sér. IV. tome vi. fasc. 1.

insensibly into the tracheides of the normal transfusion-tissue immediately adjoining the bundle, and that there is thus no real distinction to be made between the two. He considers the transfusion-tissue in the leaf of *Cycas* and of all Gymnosperms, not as a later structure than the bundle, but as the remnant of a dichotomously-branched venation which was a common feature in their ancestors, and is still found in the allied genus *Stangeria* and in some Ferns.

In another important and interesting paper * he establishes the fact that the vascular bundle-system in the pinnæ *of all Cycads* is really dichotomous, though, owing to the fact that the branching of the bundles sometimes takes place in the very base of the pinna or on the outermost edge of the rachis, this feature, though often obvious even to superficial observation, has not been recognized as generally characteristic of the order.

Strasburger † describes fully the position and structure of the transfusion-tissue in the leaves of Gymnosperms, especially those of Coniferæ and Cycadeæ; his book is certainly the best compendium for a general and accurate account of the anatomy of Gymnospermous leaves.

General Considerations.

Transfusion-tissue consists of short tracheides, parenchymatous in shape, and with reticulate or other thickenings or bordered pits, on all the walls (Pl. XXIII. fig. 1). Its usual position is at the sides of the bundle in the pericyclic region; but it may frequently extend, as in *Araucaria* and *Libocedrus*, in an arc round the protoxylem, or it may, as in *Picea* and *Pinus*, completely encircle the bundle. Its evident function, as has been rightly inferred by various authors, is to supplement, in the leaves of these plants, what must be considered a rudimentary conducting-system. In a number of Conifers the leaf is traversed by but a single bundle (in some Abietineæ by two closely-contiguous bundles); in others, and in most Cycads, by a number of widely-separated, parallel bundles. In all these plants there is an entire absence of the complex, reticulate system of conducting-tissue, such as is met with in Dicotyledonous plants, and which must be considered the highest type of venation in the vegetable kingdom. In order to compensate, therefore, for the lack of an efficient conducting-system in the leaf, recourse has been had to the development of these peculiar tracheides (often accompanied by bast-cells of similar shape), now known as "transfusion-tissue." In *Cycas* and many species of *Podocarpus*, in which the broad pinnæ or leaves are traversed by a single bundle, in addition to the normal transfusion-tissue, a new and accessory system has been developed, running from the bundle to the margin of the leaf. This, however, as will be shown later on, is a purely secondary modification of the mesophyll-cells, and bears only a functional relation to the normal transfusion-tissue, having therewith no homology whatever. In the pinna of *Stangeria* a dichotomizing system of *closely-placed* veins springs from the large central midrib. In the pinnæ of all other Cycads, and in

* "La Nervation des Cycadées est dichotomique," Assoc. Française pour l'Avancement des Sciences. Congrès de Caen, 1894.

† 'Ueber den Bau und die Verrichtungen der Leitungsbahnen,' Jena, 1891.

Podocarpus Nageia, R. Br., *Dammara*, and *Araucaria*, among Conifers, a system of parallel venation prevails, and here transfusion-tissue is markedly developed.

The leaves of most Conifers are very narrow, and are traversed by a single bundle, which, in all cases, is provided with well-developed transfusion-tissue.

Ginkgo differs widely from all other Conifers in having a dichotomizing system of bundles traversing its large, fan-shaped leaf, and has transfusion-tissue present in connection with its rather widely-separated bundles, though more feebly developed than in most Conifers.

In order to prepare the way for my subsequent remarks, I will first of all describe the structure of the vascular bundle in the lamina of an ordinary foliage-leaf of a Cycad. It is well known that the bundles of the leaf of Cycads have a structure peculiar to this order and not found in any other living group of plants. Towards the dorsal (lower) surface of the lamina is placed the phloem; next comes the ordinary xylem, which is formed by the cambium in a centrifugal * manner; on the inner side of the secondary wood there may or may not be a few elements of primary centrifugal wood, and then follows the protoxylem, consisting of narrow, elongated, spirally- or reticulately-thickened elements. Farther, beyond the protoxylem, *i. e.* between this tissue and the ventral (upper) surface of the leaf, occurs another strand of xylem, primary in origin, and of much greater development than that of the centrifugal wood; it is *centripetal* in development, *i. e.* its elements are formed successively from the protoxylem towards the ventral (upper) surface of the leaf; it is characteristic of the Cycadeæ. Typical transfusion-tissue occurs at the side of the bundle, and this is seen to be in intimate connection with the centripetal xylem (Pl. XXIII. fig. 2). In the petiole the structure of the bundles is the same, though their orientation is different. In other Gymnosperms and all Angiosperms this tissue is, so far as hitherto observed, absent from the vascular bundle. No trace of any such tissue has previously been observed either in the leaves of the Coniferæ or of the Gnetaceæ. According to existing observations, the structure of the bundle in these two latter groups of plants, as in all Angiosperms, is *endarch*, in contradistinction to that of the leaf of Cycadean plants, which is *mesarch* †.

Original Observations.

An investigation into the structure of the *cotyledons* of some seedlings of *Ginkgo biloba*, Linn., grown in the Royal Gardens, Kew, revealed a most interesting and novel structure. The cotyledons, as in the Cycadeæ, are rudimentary, hypogeal structures.

* The terms "centripetal" and "centrifugal," applied to the development of the parts of the bundle, are used with reference to the centre of the stem, in such a way that, in the case of the xylem starting from the first-formed tracheæ (protoxylem), elements formed successively near the phloem, *i. e.* towards the outside of the stem, are called "centrifugal," and those formed successively in the direction away from the phloem, *i. e.* towards the centre of the stem, are said to be developed "centripetally." The same terms ("centripetal" and "centrifugal") are applied to the development of the bundles in the leaf, whatever may be their orientation.

† The term "mesarch" was first suggested by Solms-Laubach (Introd. to Fossil Bot., Engl. ed. p. 257) to define the mode of development of the xylem of the bundle in Cycadean plants. In such plants the protoxylem occupies a central position in the xylem of the mature bundle. This term was first definitely adopted by Williamson and Scott in describing the structure of the stem-bundles in the fossil plants *Lyginodendron* and *Heterangium* (Phil. Trans.

They are thick and fleshy in consistence, bearing little, if any, resemblance to leaves, and are closely adpressed by their ventral faces, though not completely connate, as in the Cycadeæ. The tip of each is slightly notched. The cotyledons are traversed each by two bundles which in shape, as seen in transverse section, are curved in the form of an arc of a circle. There is a great development of the phloem of the bundle. The centrifugal part of the xylem is but very feebly developed; some of its elements can be seen to be secondary and cut off by the cambium, some of the smaller and innermost are probably primary. To the inside of the latter lies the small group of protoxylem. On the ventral side of the protoxylem, however, and directly opposite the latter, there are yet other tracheides present with densely spiral thickenings, which, by their position and relative development, I determined to be none other than the equivalent of the centripetal xylem as it occurs in the bundles of Cycadean leaves. These tracheides are very much scattered (Pl. XXIII. fig. 3). A row of three, however, more compactly grouped, show clearly the nature of the bundle, to which the term "mesarch," as descriptive of the bundle of Cycadean leaves, may fitly be applied. The remaining tracheides occupy various positions. In proportion as they recede farther from the protoxylem towards either side of the bundle, they attain a greater diameter and are provided with reticulate bars of thickening on their transverse walls; they moreover assume a perfectly angular outline as seen in transverse section. In fact, they present very much the appearance of the tracheides composing the transfusion-tissue in the leaves of Coniferæ. One or two of these tracheides which most completely resemble transfusion-tissue are situated quite on the side of the bundle and bordering on the phloem (fig. 3). In longitudinal section of the bundle, a most evident and interesting transition is seen between the tracheides nearest the protoxylem, which are elongated and narrow in shape, much resembling the elements of the latter, and those which are farthest removed from the protoxylem, which are short and stout, thus entirely different from the former tracheides, and in every way similar to the elements of the transfusion-tissue of Coniferous leaves (fig. 4). In the bundles of the lamina of the *foliage-leaf* of *Ginkgo*, tracheides, to the number of one or two, are usually present on the ventral side of the protoxylem, but, compared with the cotyledon, the centripetally-formed xylem is here very much reduced. There is typical transfusion-tissue at the sides of the bundle, consisting of wide tracheides with conspicuous reticulate thickenings and bordered pits (Pl. XXIII. fig. 5). In the bundles of the petiole there is a great development of the secondary centrifugal xylem; consequently, the number of elements of the centripetal xylem is exceedingly reduced, the tracheides being very inconspicuous and scattered (Pl. XXIV. fig. 6). Fig. 7 shows a good

---

Roy. Soc. vol. 186 (1895) B, pp. 703–779). The term "endarch," kindly suggested to me by Dr. D. H. Scott, is employed here for the first time to define the structure of a bundle in which, as in the stems of the great majority of Phanerogams, the whole of the later-formed xylem is centrifugal, *i. e.* is developed towards the phloem, the protoxylem always occupying the innermost portion of the bundle. Van Tieghem (Traité de Bot. pp. 763 & 764) uses the two terms *perixylic* and *centroxylic*; the former would include the terms "mesarch" and "exarch," the latter would be the equivalent of "endarch."

example of such a tracheide in longitudinal section. In this part of the leaf the transfusion-tissue is also but little developed.

A study of the structure of the bundles in the cotyledons of *Cycas revoluta*, Thunb., revealed something very similar to what was found in those of *Ginkgo biloba*, Linn. There are a number of bundles in each cotyledon, arranged somewhat in the form of a triangle. Here, as in *Ginkgo*, there was a relatively small development of the centrifugal, but a great development, on the contrary, of the centripetal xylem. Here also, in the latter tissue, could be distinctly seen a transition between the elements nearest the protoxylem, which were elongated and of small diameter, and other elements which were short, of great diameter, and possessing conspicuous bordered pits on their transverse walls, which occurred scattered in the ground-tissue, often at a considerable distance from the bundle and chiefly in a lateral direction. It was interesting to see how some of these tracheides extended round towards the phloem, exactly as occurs in the bundles of the mature foliage-leaf (figs. 8 & 9). In fig. 10 is represented a longitudinal section of a similar bundle.

I will now proceed to consider the structure of the vascular bundles of the foliar organs of Gymnosperms generally. This may be deemed, perhaps, a rather useless task, as botanists may assert that the structure of the leaves of these plants is already well known. Nevertheless, I hope, before the close of this paper, to exhibit a feature of considerable importance which has hitherto apparently been unsuspected by all investigators.

I will begin with the order Cycadeæ. These plants are known to be intermediate in their general structure between Conifers on the one hand and the great Fern-group on the other. In the structure and general appearance of the leaf *Stangeria* certainly approaches nearest to the Ferns. The broad, elongated pinnæ of the leaf are traversed by a single thick midrib; from this a dense venation of dichotomizing bundles radiates out on either side to the margin of the leaf. The vascular bundle, as in all Cycads, possesses centripetal, as well as centrifugal, xylem. Transfusion-tissue, though inconspicuous and of small development, is present at the sides of the bundles. It is conceivable that *Cycas*, in the structure of its leaf, may be a nearer relative than any other Cycad to *Stangeria*. The pinnæ, while retaining the single midrib in much reduced form, have become, relatively to their length, very much narrower, as a consequence of which the lateral veins, typical of *Stangeria*, have completely disappeared, leaving the pinnæ provided with but a single vascular strand, the remnant of the bundles traversing the much thicker midrib of the pinna of *Stangeria*. Of the tissues composing the bundle in the midrib of *Cycas*, the centrifugal xylem is, as in all Cycads, but feebly developed, and is secondarily formed by the cambium. The centripetal xylem, on the contrary, is extremely well developed, and consists of tracheides increasing in diameter as they extend towards the ventral side. The transfusion-tissue, forming a dense group of tracheides at the sides of the bundle, is that typical of all Cycads. In the intermediate pericyclic region there extends in an oblique direction a group of tracheides connecting the main part of the centripetal xylem with the

transfusion-tissue at the end of the phloem. In this group of tracheides could be observed, both in transverse and longitudinal sections, a most interesting transition in the character of the elements. Starting from the large tracheides of the main part of the centripetal xylem, we first come to the small tracheides of the connecting group, which approximate in size to the tracheides of the centrifugal wood, and pass from these to the elements of the transfusion-tissue, in which, at first, a gradual thickening of the walls can be noticed, then a shortening in length and an increase in diameter of the elements, until they merge into the ordinary parenchyma-shaped tracheides which form the bulk of the transfusion-tissue (Pl. XXIII. fig. 2). These tracheides sometimes occur among the stone-cells of the endodermal ring; in other cases it appears that communication takes place between the tracheides in the pericycle and those in the mesophyll through a stone-cell of the endodermis, which (and this is invariably the case) at this point *has no contents*, while the stone-cells on either side contain numerous crystals.

But I now have to deal with a tissue in the leaf of this plant which is unique among Cycads. Stretching amidst similarly elongated cells in the central region of the mesophyll of the leaf, from the midrib to the margin, is a band of conspicuous tracheides, narrow and elongated in shape and with bordered pits on their walls. These bordered pits are mostly of a rather rudimentary type, with wide slit-like pores, but in many of the tracheides nearest the vascular bundle they are more typical in appearance. These tracheides are in intimate connection, by means of their wide, expanded ends, with the small tracheides of the transfusion-tissue. They form a loose complex of tissue extending along the whole length of the leaf in a plane parallel to its two surfaces (Pl. XXIV. fig. 11). Lignier * has attempted to account for this tissue by regarding it as the remnant of a lateral system of dichotomizing bundles such as that found in the leaf of *Stangeria*. He appears to offer no special reason for this assumption, but founds it merely on the general structure and appearance of these strands of tracheides. Now, to my mind, the general arrangement and structure of this tissue are precisely the characters which prevent any such origin as that proposed by Lignier being attributed to it. It is almost impossible to suppose that the regular venation of a leaf like that of *Stangeria*, with distinct and conspicuous intervals between the veins, could have been transformed into the irregular strands of anomalous tracheides which occupy the entire middle portion of the leaf, with the exception of the mesophyll-cells, narrow and elongated like themselves, which lie scattered among them. Far more probable does the explanation seem that these tracheides are a later modification of the mesophyll-cells of the leaf, which has been adopted *since* the narrowing of the leaf and the loss of the lateral veins. Lignier also considers the normal transfusion-tissue, as found in Gymnosperms generally, to be a remnant of such a lateral system of venation. That this idea is equally false I hope to show clearly before the close of this paper. If it can be proved that the normal transfusion-tissue is in no wise such a remnant as he supposes, but is an independent formation, then this would be an additional proof that the anomalous transfusion-tissue

* Bulletin de la Soc. Linn. de Normandie, sér. IV. tome vi. fasc. 1.

of *Cycas* is also an independent formation, as how otherwise can one account for the intercalation of the normal transfusion-tissue between the midrib and this "bundle-remnant"? This "accessory transfusion-tissue," as I propose calling it, is, as Lignier rightly says, an extension of the transfusion-tissue proper, the latter being, as it seems to me, an older formation, acquired by the ancestors of the plant soon after the lateral veins were dropped, and the former, as it were, an afterthought to ensure a more perfect supply of water to the distant cells of the broad lamina of the leaf; there may also be much truth in Zimmermann's view, that this tissue serves the mechanical purpose of strengthening the leaf, in the same way as would a system of lateral veins.

In all other Cycads a *dichotomous* system of venation prevails without any midrib whatever. This dichotomy is sufficiently evident and conspicuous in the broad pinnæ of *Bowenia* and *Zamia*, and may also be seen pretty clearly at places in the lamina of *Ceratozamia*. In those genera with narrower pinnæ, such as *Dioon* and *Macrozamia*, the dichotomy is quite obscured and hidden from superficial observation owing to the fact that, as Vetters and Lignier showed, and as I have myself since verified, the branching of the bundles takes place low down in the very base of the pinna, or in the extreme edge of the rachis; as, subsequently, no further branching occurs higher up in the pinna, the result is a series of parallel veins of equal strength traversing the mesophyll. In all these other genera normal transfusion-tissue is present at the sides of the bundle, as in *Cycas*. But the elements composing it are always inconspicuous and scarcely recognizable as transfusion-tissue such as it is seen in *Cycas*. They are often clearly seen in connection with the centripetal xylem extending along the sides of the bundle. It is only occasionally that these elements exhibit bordered pits or reticulations on their transverse walls (Pl. XXV. fig. 12). Vetters, while recognizing the presence of these tracheides, refused to regard them as equivalent to the transfusion-tracheides of *Cycas*; but I have no doubt that he was wrong in this respect.

In the order Coniferæ there obtains a far greater diversity in the conformation of the foliage-leaf than in the order we have just been considering. *Ginkgo* stands entirely alone both as regards the shape and the venation of its leaf, and clearly indicates a much less modified and more primitive type of structure than is found in any other genus of the order. The broad fan-shaped lamina and dichotomous venation sufficiently prove this to be the case.

As I have already dwelt upon the structure of the vascular bundle in the foliar organs of *Ginkgo*, I will now pass on to its nearest allies among the Coniferæ, viz. the Taxineæ. In these the leaves are much reduced and in no wise resemble those of *Ginkgo*.

Cephalotaxus drupacea, Sieb. & Zucc.—In the *cotyledon* of this plant the bundles, which are the least varying parts of the leaf, present a structure strikingly similar to what obtains in *Ginkgo*. Transfusion-tissue is scarcely to be distinguished, and is only represented by some tracheides at the corner of the centrifugal xylem. The *centripetal xylem*, on the other hand, as seen in transverse section, is very well developed, forming a nearly continuous band along the ventral side of the bundle, and consisting of

large round tracheides, the smaller of which lie towards the protoxylem of the bundle. This protoxylem stretches right across the intervening space between the centrifugal and centripetal parts of the xylem, the latter tissue having even some protoxylem elements attached to it (Pl. XXV. fig. 13). The centrifugal xylem has a fair development, an active cambium being present. This bundle is therefore extremely interesting as forming in its structure a connecting-link between that of the cotyledonary bundles of *Ginkgo* and of other Coniferæ.

Cephalotaxus Fortuni, Hook.—In the *cotyledon* and *leaf*, as seen in transverse section, the transfusion-tissue, as in all Coniferæ, is very well developed at the sides of the bundle; but in addition to this, there are nearly always a variable number of tracheides of much smaller diameter on the *ventral* side of the xylem. They lie scattered, in various positions, among the parenchyma-cells of this region, and are quite distinct and separate from either the protoxylem or the transfusion-tissue. In longitudinal section of the bundle these tracheides are very clearly shown on its ventral side, directly opposite the oldest, spiral elements of the protoxylem, and separated from these by one, two, or three layers of cells. In shape they are somewhat elongated, with square or tapering ends, and reticulate thickenings, with or without bordered pits, on their walls (fig. 14); those nearest the protoxylem have reticulations alone, those farthest away in the ventral direction have bordered pits intercalated between the thickenings. These tracheides, seen thus in both sections, as in the above species, are constituents of the *centripetal* xylem and equivalent to the tracheides observed on the ventral side of the bundle in both the cotyledon and leaf of *Ginkgo*.

Taxus (2 species).—In the cotyledon and leaf I was able to discover similar tracheides, though they appeared in this genus scarcely so conspicuous as in *Cephalotaxus*. These elements, of which, in one transverse section, I observed three, were separated from the protoxylem (whose limit on the ventral side was well defined) by a single layer of cells. From their superiority in size to the elements of the protoxylem they could not possibly be outlying members of that tissue. The finely-developed transfusion-tissue at the side of the bundle showed in places an interesting transition in the size of its elements from its extreme outer side, where the tracheides were large in diameter and conspicuously pitted, to its innermost part, nearest the protoxylem, where the final tracheide, in one instance observed, much resembled, in size and in the character of the wall, the elements of the centripetal xylem above-mentioned (fig. 15). In longitudinal section of a leaf-bundle short, reticulate tracheides were observed here and there on the ventral side of the protoxylem, which appeared to occupy the same position with regard to the latter tissue as did those seen in transverse section; they were also of about the same diameter. Thus in the leaf of this plant also we find a conspicuous instance of centripetal xylem.

Podocarpus chilina, Rich.—This plant has long, pointed, and rather broad leaves, provided with a single median vein or midrib. At the side of this bundle the normal transfusion-tissue is remarkably conspicuous, constituting a group of large, pitted tracheides (fig. 16). In a horizontal section of the leaf, *i. e.* one made parallel to its

surfaces, it can be seen that the transfusion-tissue is bordered, on the side away from the bundle, by a single layer of parenchyma-cells similar in shape to its own tracheides. Immediately abutting on these, however, by their expanded ends are to be seen strands of lignified elements which, starting from this region, run out through the mesophyll to the margin of the leaf (fig. 16). In arrangement, shape, and general appearance they resemble extremely the strands of "accessory transfusion-tissue" in *Cycas*. But the individual elements present a remarkable difference from those of the "accessory transfusion-tissue" in *Cycas*, from the fact that they possess narrow, slit-like *simple* pits in their walls without the remotest trace of any border. From the thickness and consistence of their walls, the simple pits, and the scattered arrangement of these latter, they have very much more the appearance of stone-cells than of tracheides, and it is possible that they are analogous to the tracheides occupying the same position in *Cycas* only in so far as the mechanical function of strengthening the broad lamina of the leaf is concerned, and that they therefore do not possess in any way a conducting function.

Podocarpus Totara, G. Benn.—In the much shorter and narrower leaf of this species it is interesting to note the complete absence of this tissue in the leaf. Here the central mesophyll-cells are elongated in the direction of the margin of the leaf, but are thin-walled and unpitted. I was able to determine, however, the presence of a very slight lignification of their walls.

P. alpina, R. Br.—In the still smaller and evidently much reduced leaf of this species the same entire absence of this tissue was to be seen. Here and there, however, in the central region of the leaf, and occupying the same position as the thick-walled, pitted elements of *P. chilina*, Rich., occurred one or two large stone-cells. One of these abutted directly, by its narrower end, on the cells immediately adjoining the normal transfusion-tissue. Another was seen to be in intimate connection with an assimilating cell of the parenchyma. Except for their greater diameter, these cells looked exactly like the elements above described in *P. chilina*, Rich. I am tempted to regard them as a relic and last vestige of the well-developed tissue as seen in *P. chilina*, Rich., the latter, owing to the great reduction of the leaf in breadth, as well as in length (probably from its exposed habitat on the mountains), having become no longer necessary. As regards the structure of the leaf of *P. Totara*, G. Benn., it may possibly also be a reduction from the type of *P. chilina*, Rich., but it is impossible to be certain of this. The stone-cells, in the two species examined, are devoid of contents.

In this genus there appeared no sign of centripetal xylem attached to the bundle, as in other Taxineæ.

Araucaria excelsa, R. Br.—Having at my disposal a seedling with four cotyledons, I was able to thoroughly investigate the structure of the latter. Each cotyledon is oblong in shape, with a broad lamina traversed by about six vascular bundles and a number of hypodermal resin-canals. It is denticulate at the apex. A transverse section showed

large-celled transfusion-tissue occurring chiefly at the sides of the bundle, but also very frequently indeed on the ventral side of the xylem. A longitudinal section showed that the tracheides of the transfusion-tissue, both at the sides of the bundle and on its ventral side, were of various lengths, some being very long, others shorter; there is also considerable variation in their breadth, which is usually rather great. Here and there very long and comparatively narrow ones occur opposite the protoxylem, though not directly opposite its main part where the annular vessels occur. In one place, however, opposite such an annular vessel, a short, broad tracheide was observed. The parenchymatous elements immediately abutting on the protoxylem are, many of them, extremely narrow and of great length, tapering very much at the ends, owing to their having undergone a great amount of sliding-growth. The pitting of the tracheides of the transfusion-tissue and centripetal xylem is very interesting. These elements, at least those on the ventral side of the xylem, have very much the appearance of thin-walled sclerotic cells, and are in many cases almost, if not quite, indistinguishable therefrom, owing to the fact that the pits of many appear to be quite simple. It appears that a degeneration of the bordered pits has taken place such that the borders have become gradually obliterated, so that in most cases only a slight swelling of the wall around the pit has remained (Pl. XXVI. fig. 17). This slight thickening can be readily seen both in a sectional and a surface view of the wall. It is in some cases much more distinct than in others, and in such a definite border is seen. It is by means of these latter transitional cases that the real tracheidal nature of all these elements can be determined, and also that none of them are sclerotic cells. The cross-walls are often horizontal, but also very frequently rather oblique. I think there is but little doubt that these tracheides have all been derived from the centripetal xylem which once existed in normal form in the position in which these tracheides now occur, and that the latter have been since extremely modified.

Araucaria Bidwillii, Hook.—In a transverse section of the *cotyledon* the bundles are seen to be united into long bands. There is a great development of transfusion-tissue consisting of elements of various shapes, rounded or angular, reticulated or pitted, often of considerable size, on the ventral side of the protoxylem and immediately abutting on it; they may also be seen running out into the parenchyma. There are sometimes smaller tracheides next the protoxylem, which are rounded and appear like normal tracheides of the bundle, though larger. These constitute the *centripetal xylem*.

In a transverse section of the *leaf* a number of parallel bundles are observed traversing the broad lamina. Each of these has transfusion-tissue largely developed on all sides of the xylem, consisting of wide, angular tracheides with small bordered pits. But, abutting on the protoxylem, and connecting the latter with these large tracheides, are smaller ones with rounder, smoother walls, forming a transition between the protoxylem and the transfusion-tissue, and evidently representing *centripetal xylem*. In longitudinal section of the leaf there are no transitional elements between protoxylem and transfusion-tissue in direct connection with the main part of the former, *i. e.* where the elements with annuli and long-drawn-out spirals are situated. But a little to the

side of this, and still directly opposite spiral elements of the protoxylem, evident transitional elements are seen which represent centripetal xylem; these sometimes abut directly on the protoxylem, in other cases lie a short distance away from the latter. These tracheides are sometimes *of great length* and quite narrow, having the same shape as a tracheide of the protoxylem. They possess transitional characters in their walls, where rudimentary bordered pits with wide openings and large borders occurred in the midst of very fine and delicate, but regular and close, spiral or reticulate markings. Farther away from the protoxylem, in a radial direction, the tracheides gradually become shorter and stouter, this also happening in a tangential direction towards the sides of the bundle.

Araucaria imbricata, Pav.—In a transverse section of the *leaf* a number of small, parallel bundles are seen. At the sides of each bundle well-developed transfusion-tissue occurs; in many cases it curves round so that a group of its tracheides frequently comes to lie, by itself, opposite some part of the protoxylem; in such a case the tracheides of the group nearest the protoxylem are smaller than the others. In some cases, directly opposite the main part of the protoxylem, are seen one or two *small, round* elements of *centripetal xylem.* They afford a very clear instance of a remnant of this latter tissue (fig. 18).

Dammara sp.—A number of parallel bundles traverse the broad lamina, as in *Araucaria.* In transverse section the transfusion-tissue is seen to extend on all sides of the xylem, and there are also other smaller tracheides abutting directly on the ventral side of the protoxylem (fig. 19). In longitudinal section one or two of these latter elements are seen to be elongated tracheides with pointed ends and spiral thickenings situated immediately on the ventral side of the elements of the protoxylem with loose spirals. They thus exhibit an undoubted case of *centripetal xylem.* The transfusion-tracheides are of quite a different appearance and quite typical in character (fig. 20).

Sequoia gigantea, Lindl. & Gord.—In a transverse section of the *cotyledon* the single bundle possesses a very conspicuous development of the secondary centrifugal xylem. Only one or two elements of transfusion-tissue are present at the sides of the bundle. There are no tracheides on the ventral side of the xylem. In a similar section of the *foliage-leaf* there is seen to be a very much smaller amount of secondary centrifugal wood. The transfusion-tissue, on the other hand, has reached a greater development than I have seen in any other Conifer; its outermost tracheides being of very great diameter, nearly equalling that of the entire xylem of the bundle. The innermost are very much smaller. The nearest approach to centripetal xylem in this plant that I found was one of the innermost transfusion-tracheides, smaller than most of the others, which was situated in an intermediate position between these and the protoxylem.

Widdringtonia Whytei, Rendle.—In a transverse section of the *cotyledon* the transfusion-tracheides, which are of various shapes, both small and rounded and also very

large and angular, are scattered on all sides of the xylem, sometimes appearing in contact with the protoxylem. In longitudinal section they are seen to be short, broad elements with spiral thickenings and bordered pits. In a similar section of the *plumular leaf* it is interesting to note that the transfusion-tissue is confined to the sides of the bundle; there are no tracheides opposite the protoxylem, as in the cotyledon. This is what one would expect to find in passing from the more primitive to the more modified organ.

Libocedrus decurrens, Torr.—In a transverse section of the *cotyledon* the transfusion-tissue is seen to extend on all sides of the xylem of the single bundle, and there also appear to be transitional elements between the protoxylem and the transfusion-tissue. In a similar section of the *plumular leaf* the transfusion-tissue is seen to be present only at the sides of the bundle, and entirely absent from the region opposite the protoxylem. In a longitudinal section of the *cotyledon* it is seen that undoubted transitional stages between the protoxylem and the transfusion-tissue exist opposite the former, consisting of *elongated* tracheides with both spiral thickenings and bordered pits. To the outside of these the tracheides become shorter and have exclusively bordered pits. On the sides of the bundle the transfusion-tracheides are very much shorter and have either bordered pits or reticulate-spiral thickenings. They are usually greater in diameter than those opposite the protoxylem. In a longitudinal section of the *plumular leaf* the centripetal xylem, of *long* elements with reticulate-spiral thickenings, is seen to occur on the ventral side of the protoxylem, and there are transitions from these to the transfusion-tracheides, which are shorter and stouter.

Juniperus bermudiana, Linn.—In a transverse section of the *cotyledon* the transfusion-tissue of the small bundle is seen extending from the lateral position round to the ventral side of the protoxylem, where its tracheides are larger and also scarcely lignified; in some sections they are absent from this part. In a longitudinal section of the cotyledon a vertical row of rather short tracheides was observed opposite the protoxylem. In a transverse section of the *leaf* the transfusion-tissue occurs in a lateral position and is only somewhat inclined towards the ventral side of the xylem, not extending so far round in that direction as is the case in the cotyledon. This is interesting, as showing the gradual modification which has taken place in the more recent organ.

In the great group of the Abietineæ the transfusion-tissue is very characteristic and has been well figured and described by Daguillon *. It consists of tracheides of the usual shape, with very transparent walls and well-defined, circular, bordered pits. These occur in the pericyclic region, and usually extend completely round the bundle, forming a kind of cylinder of transfusion-tissue. In some it is chiefly found around the xylem, in others, again, chiefly around the phloem. Daguillon cites the case of *Pinus sylvestris*, L., where, in the bundles of the *cotyledon*, the transfusion-tissue occurs on the ventral side of the xylem, in the *foliage-leaf*, on the contrary, chiefly round the phloem. This, again, is a very suggestive and interesting case. In a transverse section of the *cotyledon* of *Pinus*

* Rev. gén. de Bot. ii. (1890).

Thunbergii, Parl., which I examined, I could, however, find no trace of transfusion-tissue anywhere.

Pinus Pinaster, Soland.—In a transverse section of the *foliage-leaf* the transfusion-tissue occurs all round the bundle. But besides these elements, there were observed immediately on the ventral side of the protoxylem, a group of thin-walled, irregularly-shaped, rather small-celled elements with lignified walls. In a longitudinal section the parenchymatous elements abutting on the protoxylem appeared very much elongated, with either oblique or horizontal walls, and had undergone a great amount of sliding-growth. Among them were found tracheides with very small, but distinct, bordered pits; but in many of these thin-walled tracheides, which are of the same diameter and length as those of the protoxylem, the bordered pits are almost obliterated, and, in a great many, are entirely gone. It seems to me that these tracheides represent the last lingering remnant of the centripetal xylem, which is gradually becoming resolved into the parenchymatous elements above mentioned. Outside one of these tracheides just described were seen two tracheides of the transfusion-tissue, of which it is to be noted that the innermost is much more elongated and narrower than the other one, this latter representing the more normal form of these tracheides (Pl. XXVI. fig. 21).

The following plants afford additional instances in which I have observed centripetal xylem in the bundle of the leaf:—*Cupressus torulosa*, D. Don; *Cunninghamia sinensis*, R. Br.; *Saxegothea conspicua*, Lindl.; *Prumnopitys elegans*, Phil.; *Torreya californica*, Torr.; and *T. nucifera*, Sieb. & Zucc.

General Results.

Collating all these facts with the structure, as we have long known it, of the vascular bundle of the leaves of Conifers and Cycads generally, it appears to me that there is a clue to be found as to the origin of the transfusion-tissue in these plants. This tissue, as seen in the cotyledonary bundles of *Cycas* and *Ginkgo*, is clearly an extension towards the sides of the bundle of the *centripetal xylem* of the latter. As this tissue began to extend itself irregularly both in a ventral and in a lateral direction away from the protoxylem, the tracheides forming its lateral extension were finally fixed, and, occurring as they did at the sides of the bundle, bordering on the surrounding mesophyll of the leaf, were eventually made use of as a permanent and useful auxiliary conducting-system, this latter being found necessary on account of the inadequate distribution of the bundles in the mesophyll of the leaf. In the case of Conifers, where the centrifugal xylem has considerably increased in amount, the centripetal xylem, as such, tends to disappear, but persists in a modified form when of use as an auxiliary conducting-system. An objection to this view of the origin of the tissue in question has been raised on the ground that tracheides, such as those of the transfusion-tissue, may be formed anywhere, at any time, and from any tissue of the plant. The transfusion-tracheides, it is urged, may have been developed quite independently of the centripetal xylem, and have become directly continuous with its lateral region, from the fact that this part of the xylem is the most convenient for the attachment of the transfusion-tissue. I quite admit the possibility

of such an origin for a transfusion-tissue, and a conspicuous instance thereof is found in the stem of *Casuarina* *, where transfusion-tissue, consisting of tracheides with simple pits and lignified walls, is formed directly from the parenchyma-cells immediately surrounding the cortical bundles, and, of course, here quite independently of any centripetal xylem, a tisssue which these bundles never possessed. But what I maintain is that in Gymnospermous plants the transfusion-tissue is nothing more or less than a direct extension of the centripetal xylem. This could scarcely be decided upon from an examination of the foliage-leaves of either Cycads or Conifers, but was conclusively revealed by an investigation of the cotyledons of these plants. The *transitions* in size and other characters which take place, both in a ventral and in a lateral direction, between the elements of the centripetal xylem directly opposite the protoxylem and those of the peripheral transfusion-tissue, left no doubt as to the truth of the above inference. Had the tracheides of the transfusion-tissue been formed independently from the pericyclic or mesophyll-cells around the bundle, I see no reason why there should have been found such easy and delicate transitions in size, &c., between these and the centripetal xylem. It is true that there is a difference in size, both of diameter and length, between the cells of the mesophyll and those of the pericycle; but this, though it might possibly account for the transitions in size and shape above mentioned, yet would not account for the transitions in the characters of the cell-wall which are frequently met with, nor, indeed, for the fact that in the cotyledonary bundles the transfusion-tissue is better developed on the *ventral* than on the lateral side of the bundle. In the cotyledonary bundle of *Ginkgo*, as indicating the place of its origin, the tracheides of the transfusion-tissue are frequently seen to be mingled with the ordinary tracheides of the centripetal xylem, and, in one case, an element of the former, with reticulations on its transverse wall, was seen jammed in between two elements of the latter tissue. Again, if the transfusion-tissue were a distinct and independent formation, it would, I imagine, not be so conspicuous in the cotyledons, *e. g.* of *Ginkgo*, as is in reality the case. In these organs it can have but little function to perform. In the foliage-leaf, on the contrary, of *Ginkgo*, where the importance of its function is obvious, it is but very sparingly present as compared with its occurrence in the cotyledon of this plant. The *raison d'être*, then, of its having an origin independent of the centripetal xylem in this case falls to the ground, while my own view, that the transfusion-tissue is a modification of the centripetal xylem, is clearly supported by these facts.

That in those cases, of which there are several, where the transfusion-tissue is in direct connection with the *centrifugal* xylem, there are seen to be transitions in size between the elements of the two tissues, does not affect my position when it can be shown that this is a purely secondary result, for in the cotyledonary bundles of *Ginkgo* and *Cycas*, and in several other plants which I have examined, the transfusion-tissue is always to be seen extending out from the region on the ventral side of the protoxylem. The transition just mentioned is due, doubtless, to the difference in size between the parenchyma-cells immediately adjoining the bundle, viz. those of the pericycle, and those, belonging to the ground-tissue of the leaf, lying farther away.

On the whole, then, I think the facts justify my position, viz. that the normal

* "On the Comparative Anatomy of the Casuarinæ," etc., Ann. Bot. vol. viii. (1894).

transfusion-tissue (not the "accessory transfusion-tissue"), as at present known in the foliar organs of Gymnosperms, is not an outlying tissue of no morphological value with regard to the vascular bundle to which it is attached, but that it has a distinct and definite origin in this bundle, viz. from the centripetal xylem; that it was *the successive, unlimited, centripetal development* of the tracheides of this latter tissue which, generations back, afforded, as it were, *the first start*, which has eventually culminated, in more modern plants, in the characteristic transfusion-tissue at the side of, or in various positions around, the vascular bundle. The albuminous cells or "phloem transfusion-tissue," called by Strasburger "Uebergangszellen," appear to arise, on the contrary, quite independently, from the parenchyma-cells immediately flanking the phloem. Though evidently similar in their function of conducting substances between the cells of the surrounding mesophyll and the bundle, the two kinds of transfusion-tissue have, nevertheless, a very different origin, the one springing from the vascular tissues of the bundle itself, the other from the parenchyma lying outside these vascular tissues. The former, the xylem transfusion-tissue, is not, as some have supposed, a distinctly new tissue derived from the parenchyma of the ground-tissue of the leaf, or even of the pericyclic cells; nor is it again, as others have imagined, the equivalent of a lateral vein or branch of the bundle. The conclusion at which I have arrived is that this tissue is *a direct derivative of the centripetal xylem* which normally occurred as an important part of the vascular bundle in the ancestors of the Coniferæ (for which fossil plants afford ample evidence), and which still occurs in full development, along with the transfusion-tissue, in modern Cycads. But as, in the course of time, the centripetal xylem of the bundle, in the case of the Coniferæ, disappeared, as having become a useless tissue, the origin of the transfusion-tissue, which has persisted as a highly useful portion of the bundle, though still perceptible in Cycads, has, in the Coniferæ, become almost completely obscured.

Summary.

The chief points to be gathered from the investigation into the subject of this paper are the following:—

1. The universal presence of transfusion-tissue in the *leaves* of Gymnosperms whose venation is of a reduced or rudimentary character, and where the complex reticulate or dichotomous venation of the Ferns or the higher Angiosperms is lacking.
2. The conspicuous development of *centripetal xylem* in the vascular bundles of the foliage-leaves of all modern *Cycads*, without exception, where it constitutes the most important part of the xylem of the bundle. This is a point which has long been familiar to botanists.
3. The discovery, for the first time, of a *mesarch* structure of the vascular bundle in the leaves of Coniferæ. In the cotyledonary bundles of *Ginkgo biloba*, Linn., where this was first observed, the *centripetal* xylem forms the chief part of the woody strands and is very conspicuously developed. In the bundles of the cotyledons and mature leaves of all other Coniferæ which were examined the centripetal xylem is extremely reduced, this reduction having, in most cases, corresponded with a greater development of the *centrifugal* xylem. It is most obviously present in

those genera which approach nearest to *Ginkgo* in general relationship, such as *Cephalotaxus* and *Taxus*. In many genera, however, no trace of this tissue could by discovered, at least in the sections examined, though it is not improbable that isolated remnants of it may occur here and there along the course of the bundle through the leaf.

4. The occurrence, in the cotyledonary bundles of *Ginkgo biloba*, Linn., and *Cycas revoluta*, Thunb., of an intimate union and gradual transition between the tracheides of the centripetal xylem on the one hand and those of the transfusion-tissue on the other; whence it may be justly inferred that the latter tissue owes its origin, wherever it may subsequently be found, directly to the former. Though in the leaves of the majority of Coniferæ this origin is by this time almost entirely obscured, owing to the more or less complete obliteration of the centripetal xylem, it is still often evidenced by the presence of transfusion-tissue on the ventral side of the xylem, by the very frequent extension of the lateral transfusion-tissue *towards the ventral side of the bundle*, and by the transitions in the characters of the tracheides between those most externally placed and those nearest the protoxylem. In the foliage-leaves of *Cycas* the connection between the two tissues is obvious.
5. The final inference, that transfusion-tissue, which occurs almost universally in the leaves of Gymnospermous plants as an auxiliary conducting-system, has been phylogenetically derived from the centripetally-formed xylem of the vascular bundle, and is thus, morphologically, an integral portion of the bundle itself.

I am indebted to Mr. C. P. Robertson-Glasgow for the use of some excellent preparations of the cotyledons, leaves, &c., of various Coniferous plants. My best thanks are also due to Dr. D. H. Scott for many invaluable criticisms and much kind assistance during the progress of my work.

[The important discovery, quite recently made by the two Japanese botanists, Hirase and Ikeno, of spermatozoids in the pollen-tubes of *Cycas revoluta*, Thunb., and *Ginkgo biloba*, Linn., and still more recently by Webber in a species of *Zamia*, bridges over in a striking manner the gulf, hitherto supposed to exist between flowerless and flowering plants, between Ferns or Fern-like plants and Gymnosperms. The relation between the two great groups of plants had already been partly indicated by the Fern-like foliage of such a Cycad as *Stangeria*.

One of the most important of the facts brought forward in the present paper, viz. the occurrence of centripetal xylem in the cotyledonary bundles of both *Ginkgo biloba*, Linn., and *Cycas revoluta*, Thunb., seems to me (especially in view both of the external characters and anatomical structure of such fossil forms as the *Medulloseæ*, *Lyginodendron*, and *Nœggerathia*) to strongly support the above conclusion that *Ginkgo* and the Cycads hold an intermediate position between some primitive group or groups of Fern-like plants and modern Gymnosperms.

1st October, 1897. W. C. W.]

EXPLANATION OF THE PLATES.

PLATE XXIII.

Fig. 1. Two tracheides of typical Gymnospermous transfusion-tissue. × 390.
Fig. 2. Transverse section of a bundle from the pinna of *Cycas circinalis*, Linn., showing centripetal xylem and transfusion-tissue. × 130.
Fig. 3. Transverse section of a bundle from the cotyledon of *Ginkgo biloba*, Linn. × 390.
Fig. 4. Radial section of ditto. × 390.
Fig. 5. Transverse section of bundle from lamina of foliage-leaf of *Ginkgo biloba*, Linn. × 390.

PLATE XXIV.

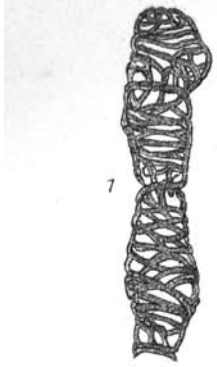
Fig. 6. Transverse section of bundle from petiole of foliage-leaf of *Ginkgo biloba*, Linn. × 130.
Fig. 7. Radial section of bundle from petiole of foliage-leaf of *Ginkgo biloba*, Linn. × 390.
Fig. 8. Transverse section of bundle from lamina of cotyledon of *Cycas revoluta*, Thunb. × 85.
Fig. 9. Transverse section of bundle from stalk of cotyledon of *Cycas revoluta*, Thunb. × 390.
Fig. 10. Radial section of bundle from lamina of cotyledon of *Cycas revoluta*, Thunb. × 390.
Fig. 11. Tangential section of portion of pinna adjoining the bundle of *Cycas circinalis*, Linn., showing the "accessory transfusion-tissue." × 130.

PLATE XXV.

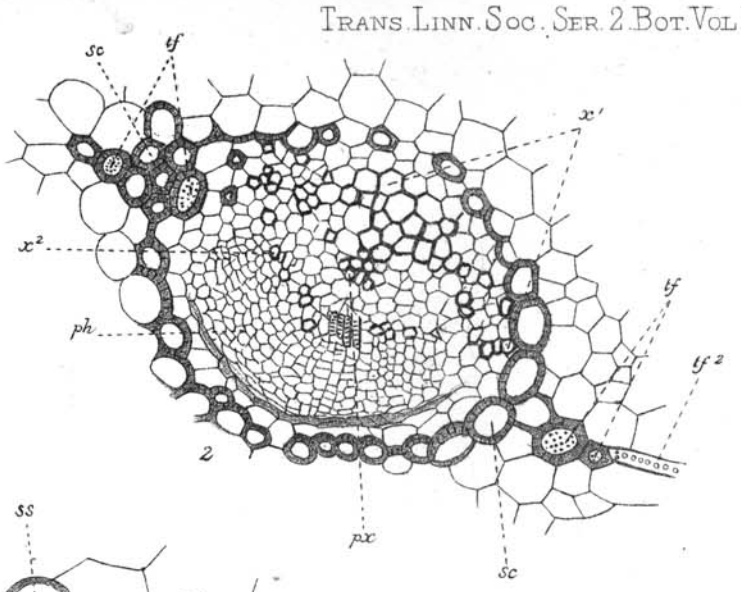
Fig. 12. Transverse section of bundle from pinna of *Ceratozamia mexicana*, Brongn. × 390.
Fig. 13. Transverse section of bundle from cotyledon of *Cephalotaxus drupacea*, Sieb. & Zucc. × 390.
Fig. 14. Radial section of bundle from cotyledon of *Cephatolaxus Fortuni*, Hook. × 390.
Fig. 15. Transverse section of bundle from leaf of *Taxus baccata*, Linn. × 390.
Fig. 16. Transverse section of leaf of *Podocarpus chilina*, Rich., showing accessory stone-cell tissue. × 85.

PLATE XXVI.

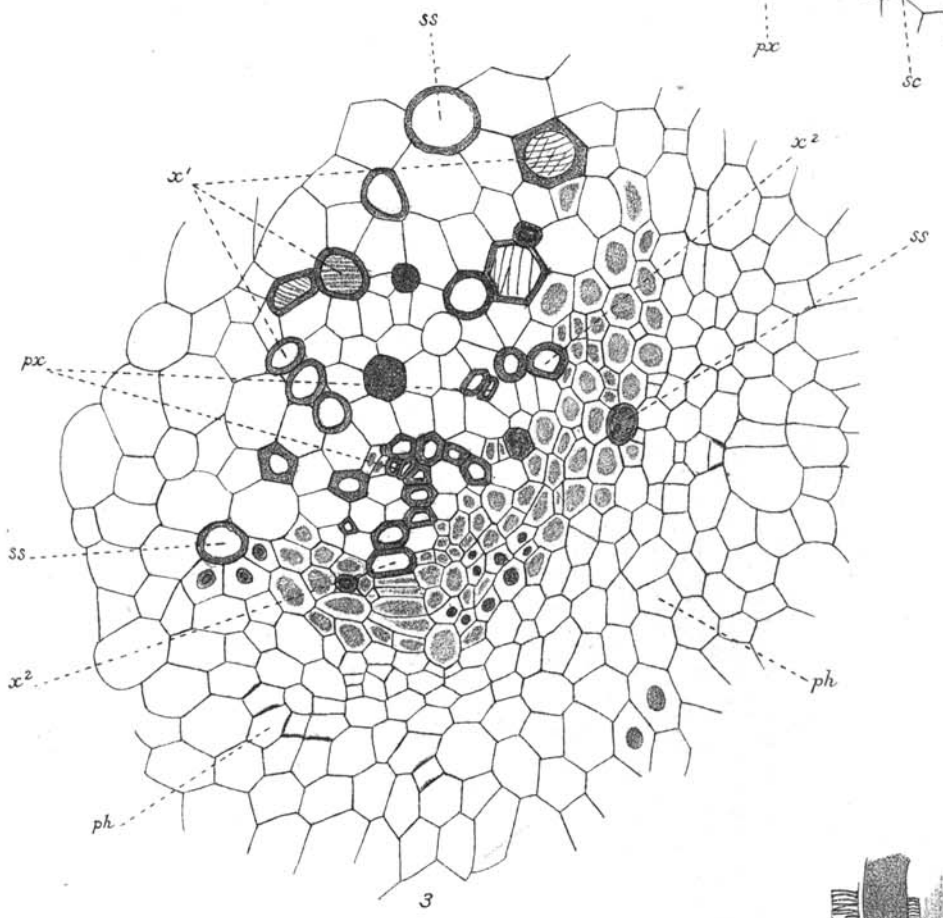
Fig. 17. Radial section of bundle from cotyledon of *Araucaria excelsa*, R. Br. × 390.
Fig. 18. Transverse section of bundle from leaf of *Araucaria imbricata*, Pav. × 390.
Fig. 19. Transverse section of bundle from leaf of *Dammara* sp. × 390.
Fig. 20. Radial section of ditto, and two tracheides of transfusion-tissue from the side of the bundle. × 390.
Fig. 21. Radial section of leaf of *Pinus Pinaster*, Soland. × 390.



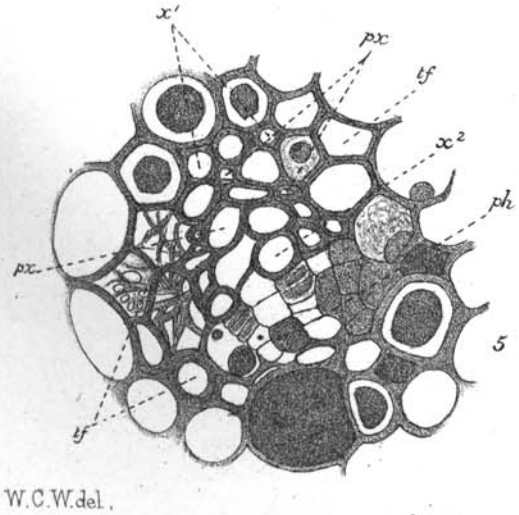
1



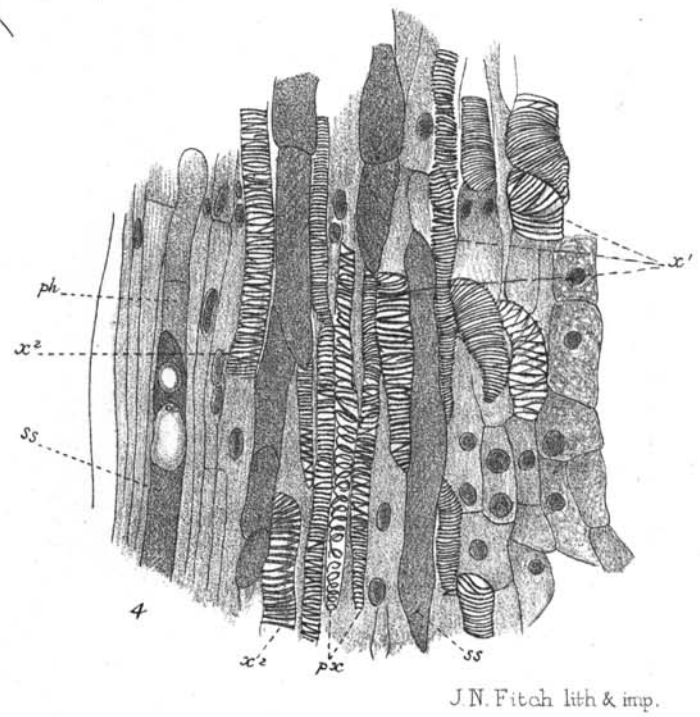
2



3



5

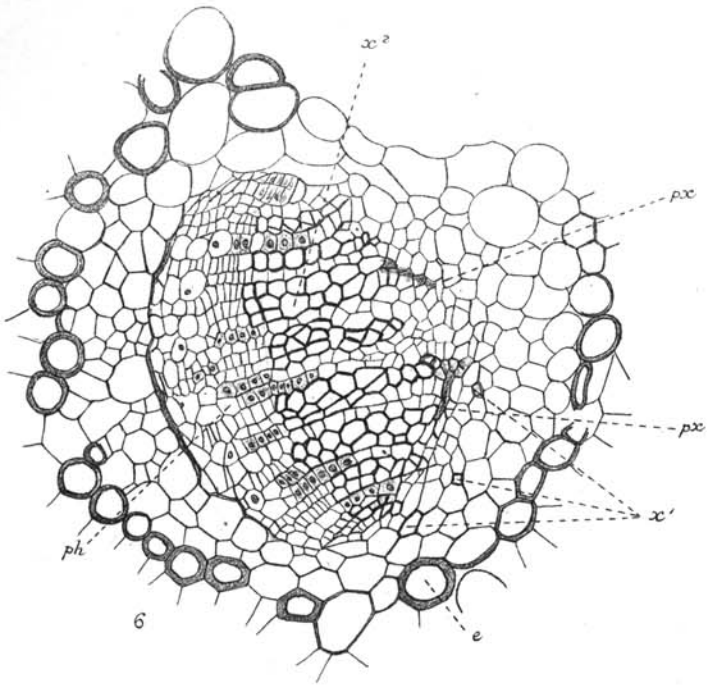


4

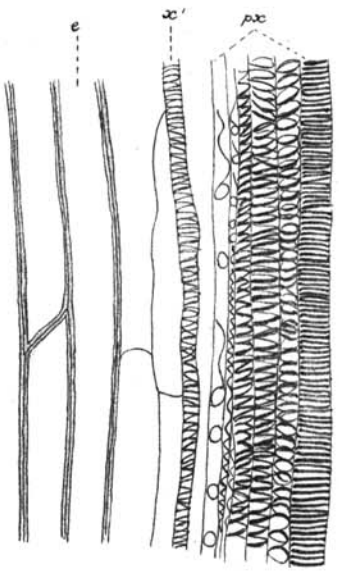
W.C.W.del.

J.N.Fitch lith & imp.

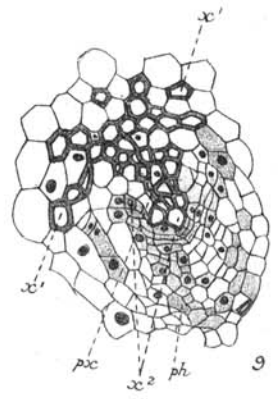
GYMNOSPERMOUS TRANSFUSION TISSUE.



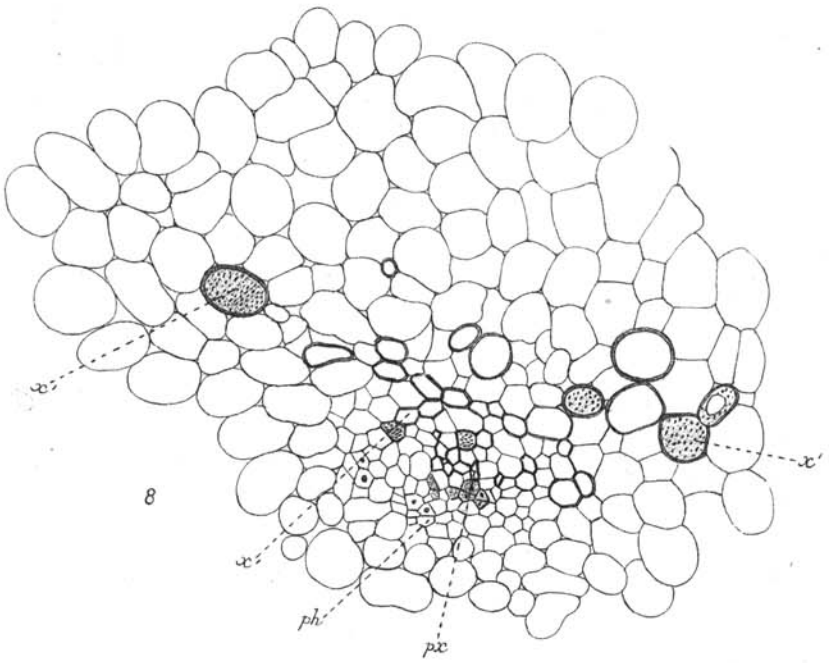
6



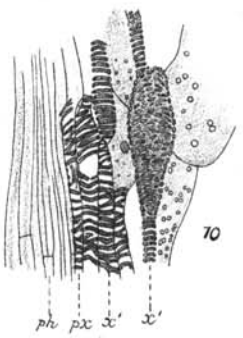
7



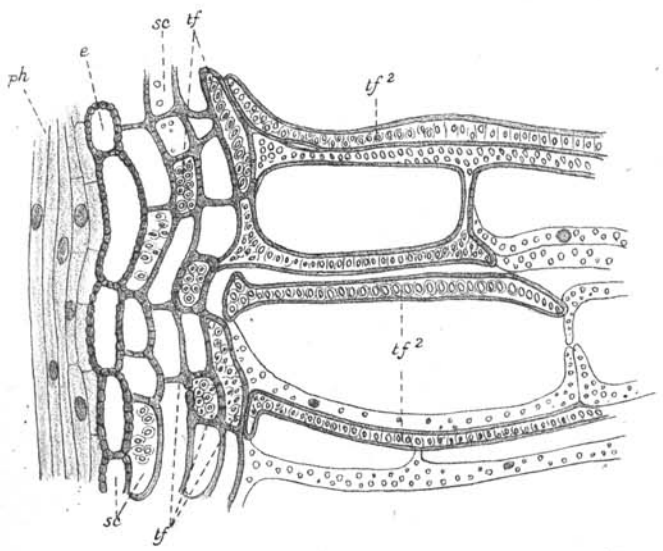
9



8



10

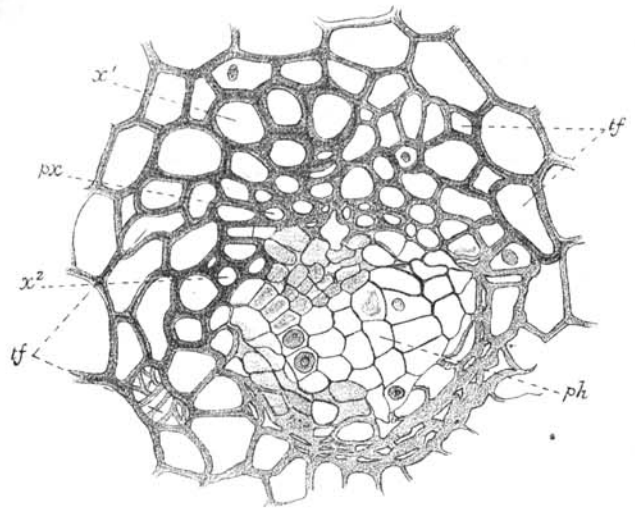


11

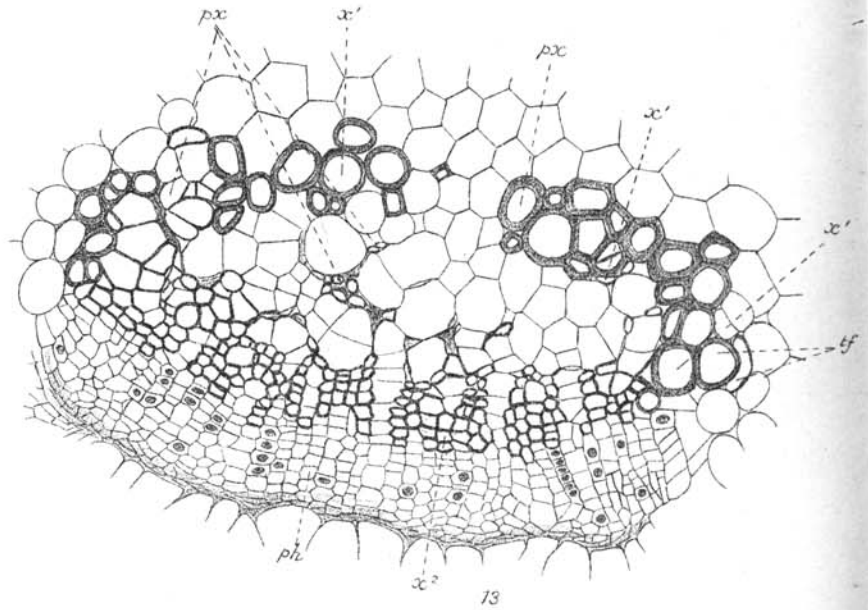
W.C.W. del.

J.N. Fitch lith & imp.

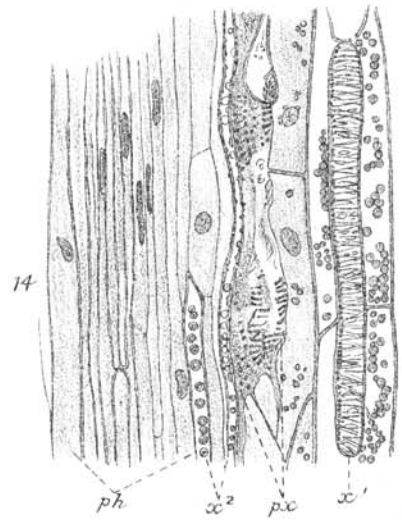
GYMNOSPERMOUS TRANSFUSION TISSUE.



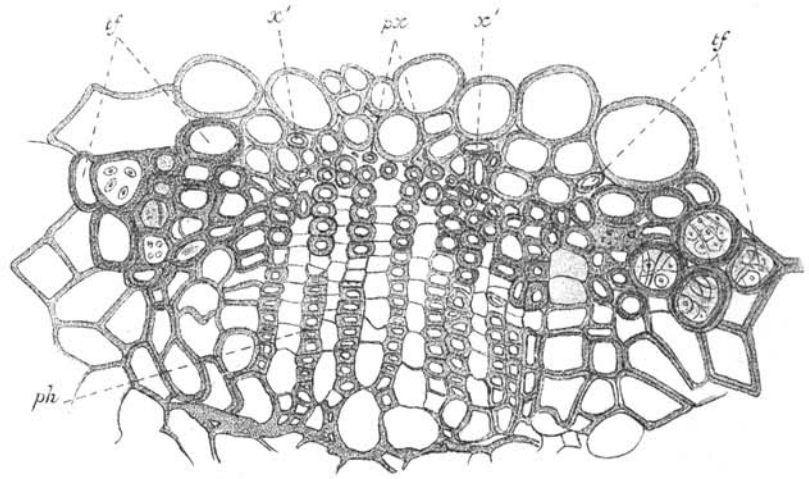
12



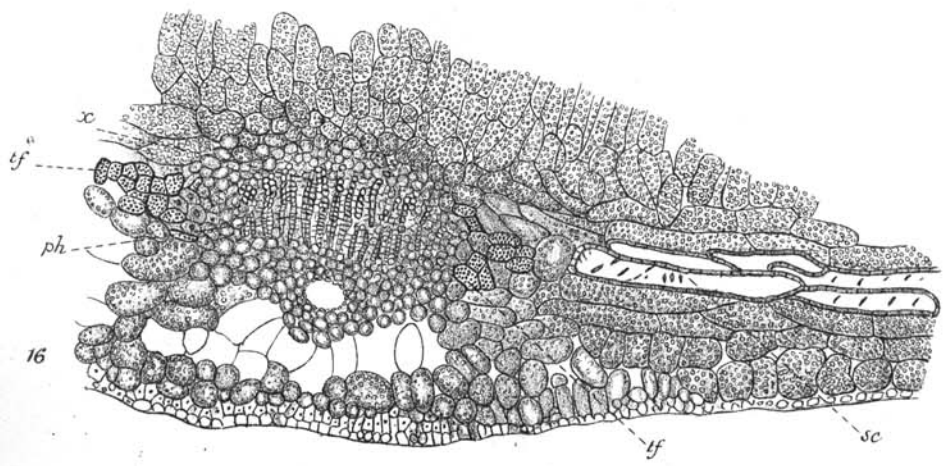
13



14



15

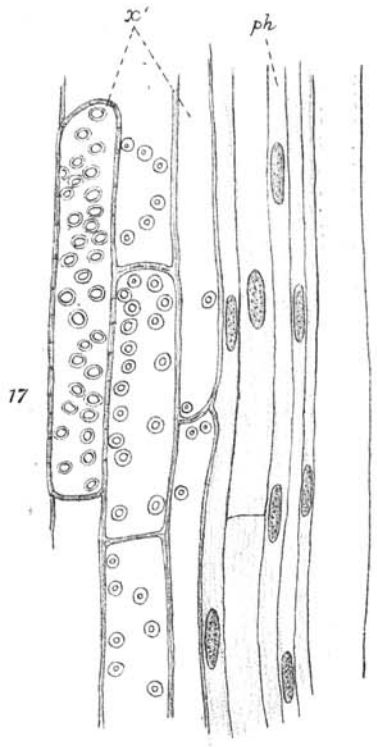


16

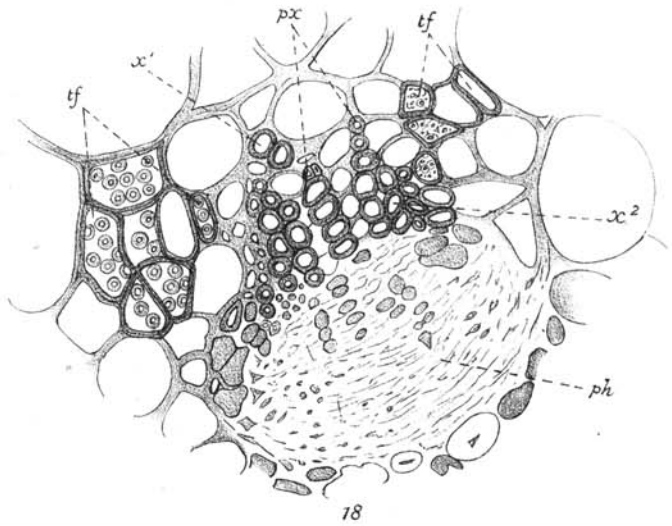
W.C.W. del.

J.N.Fitch lith & imp.

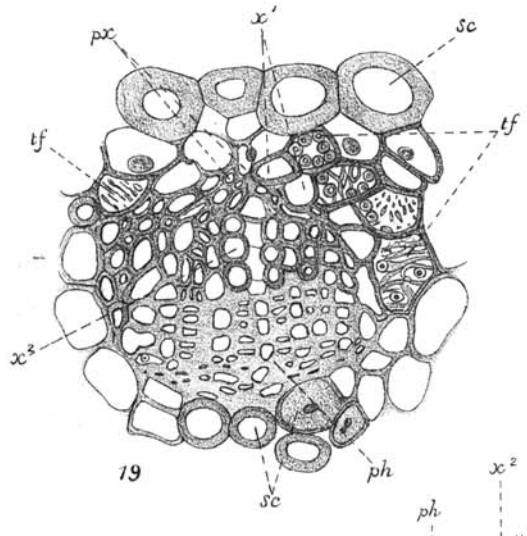
GYMNOSPERMOUS TRANSFUSION TISSUE.



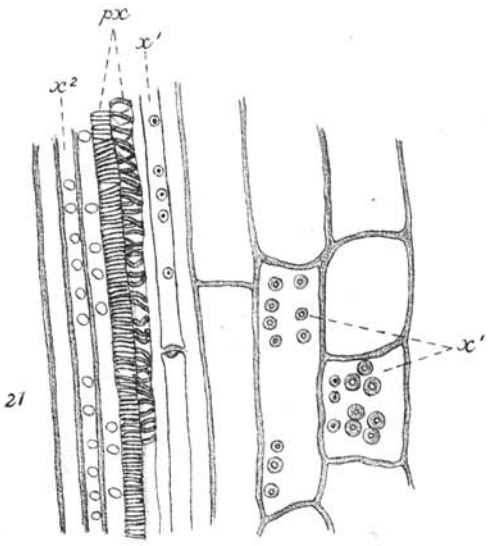
17



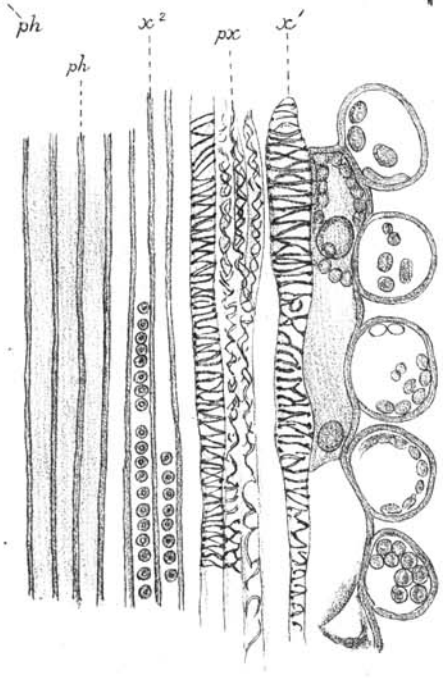
18

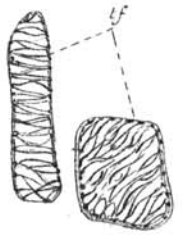


19



21





20

W.C.W. del.

J.N. Fitch lith & imp.

GYMNOSPERMOUS TRANSFUSION TISSUE.