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

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THERE is a species of conducting-tissue occurring in the green parts of certain plants which for long has been known by the name of *transfusion-tissue*. It occurs principally in the leaves of Gymnosperms, but is not exclusively confined to this group of plants. It is found most usually in direct connexion with a vascular bundle, and extending out from this among the cells of the surrounding parenchyma, and consists of tracheides, short and parenchymatous in shape, which are often accompanied by bast-cells. It doubtless serves as a secondary conducting-tissue for those leaves whose vascular bundles are few or widely separated, and are not supplied with a complex system of veins such as is found in Dicotyledonous plants. It is most abundantly represented in the leaves of Conifers, where it is universal; it is also found in the leaves of nearly all Cycads. In these two orders of plants the transfusion-tissue occurs almost always in *lateral* connexion with the vascular bundle. But it is also found in a few genera all round the bundle, in others on the outer periphery of the phloem, and in others again opposite the xylem.

As regards the origin of this tissue there are various views: some consider that it forms part of the conducting-tissues of the vascular bundle to which it is attached; others consider that it belongs to the parenchymatous ground-tissue of the leaf; finally, the French botanist, Van Tieghem, maintains that it is part of the pericycle surrounding the bundle. While the latter view may be perfectly correct as far as the ontogenetic origin of the elements composing this tissue is concerned, my own investigations go to show that, phylogenetically, this tissue has an origin agreeing with that assumed by the first of the above views, viz. from the vascular bundle itself, though in a manner very different from what the authors of this view suspected.

I will first of all describe the structure of a bundle from an ordinary foliage-leaf of a Cycad, so as to pave the way for my subsequent remarks. It is well-known that the vascular 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 comes the protoxylem, consisting of narrow, elongated, spirally- or reticulately-thickened elements. Further, 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: this 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. In the petiole the structure of the bundles is the same though their orientation is different.

In all other Gymnosperms and in Angiosperms this tissue is, so far as hitherto observed, completely absent from the vascular bundles. No trace of any such tissue has been found either in the leaves of the Coniferæ or of the Gnetaceæ. In all these cases the whole of the wood has been regarded as centrifugally developed.

In investigating the structure of the *cotyledons* of some seedlings of *Gingko biloba*, grown in the Royal Gardens, Kew, I observed a most interesting point in regard to the minute structure of the vascular bundles, a pair of which traverse each cotyledon. In shape, as seen in transverse section, each bundle was curved, having the form of an arc of a circle. The phloem was very greatly developed. There was a cambium which, on the side of the xylem, had cut off but a very few elements; and to the inside of this lay the small group of protoxylem. On the ventral side of the protoxylem, however, and directly opposite the latter, there were yet other tracheides present, which, by their position and relative development, I determined to be none other than the equivalent of the centripetal xylem as it occurs

* The terms "*centrifugal*" and "*centripetal*," 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 nearer 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 *centripetally* developed. The same terms ("*centrifugal*" and "*centripetal*") are applied to the development of the bundles of the leaf whatever may be their orientation.

in the bundles of the leaves of Cycads. Moreover, these tracheides were very much scattered. In proportion as they receded further from the protoxylem towards either side of the bundle, they attained a greater diameter and, what more especially distinguished them, they were provided with reticulate thickenings on their broad transverse walls. In fact, they presented very much the appearance of the tracheides composing

Fig. 1.

Transverse section of vascular bundle from the upper part of the cotyledon of *Ginkgo biloba*. *ph*=phloem; *px*=protoxylem; *x*¹=centripetal xylem; *x*²=transfusion-tissue.

the transfusion-tissue in the leaves of Coniferae. One or two of these tracheides which most completely resembled transfusion-tissue were situated quite on the side of the bundle and bordering on the phloem. In longitudinal section a most evident transition was seen between those tracheides nearest the protoxylem, which are elongated and narrow in shape, and those farthest removed from the latter, which are short and broad and in every way similar to the elements of the transfusion-tissue in Coniferous leaves.

In the bundles of the petiole of the foliage-leaf of *Ginkgo* there is a great development of the secondary centrifugal wood. But here also, on the inner or ventral side of the protoxylem, were seen two or three small tracheides of centripetal xylem. On the side of the bundle at the level of the phloem a few elements of typical transfusion-tissue were observed.

A study of the structure of the bundles in the cotyledons of *Cycas revoluta* revealed something very similar to the above. 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 could be distinctly seen a transition between the elements nearest the protoxylem, which were quite small, and other tracheides, of great diameter and with bordered pits on their *transverse walls*, which occurred scattered in the ground-tissue, often at a considerable distance from the bundle. It was interesting to see how some of these tracheides extended round towards the phloem.

Fig. 2.

Transverse section of vascular bundle from the upper part of the cotyledon of *Cycas revoluta*. *ph*=phloem; *px*=protoxylem; *x¹*=centripetal xylem.

In the leaves of some of those Coniferæ which approach nearest to *Gingko*, such as *Cephalotaxus* and *Taxus*, I observed tracheides on the ventral side of the protoxylem, which, by their position and general character, may be considered as equivalent to the centripetal xylem in *Gingko* and *Cycas*. After a rather extended investigation, I came upon similar instances in the leaves of *Dammara*, *Araucaria*, *Widdringtonia*, and *Pinus*.

Collating these facts with the structure as we have long known it of the vascular bundles 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 *Gingko*, is clearly an extension, towards the sides of the bundle, of the *centripetal xylem* of the latter. It is the successive, unlimited, centripetal development of the tracheides of this tissue which affords, 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 transfusion-tissue, *e. g.*, of Coniferous leaves 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

Fig. 3. Transverse section of vascular bundle of the leaf of *Taxus baccata*. *ph*=phloem; *px*=protoxylem; *x¹*=centripetal xylem; *x²*=centrifugal xylem.

Fig. 4. Longitudinal section of vascular bundle from the leaf of *Dammara*, and two elements of transfusion-tissue. *ph*=phloem; *px*=protoxylem; *x¹*=centripetal xylem; *x²*=centrifugal xylem; *tf*=transfusion-tissue.

as an important part of the vascular bundle in the ancestors of the plants concerned (for which fossil plants afford ample evidence). But as, in the course of time, the centripetal xylem of the bundle disappeared, as having become a useless tissue, the origin of the transfusion-tissue, which has persisted as a highly useful portion of the bundle, has become almost completely obscured.

[The figures illustrating this paper are drawn quite diagrammatically. At some future time I hope to publish a more detailed investigation of this subject, accompanied by fully-elaborated and accurate figures.

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