On the Structure of the Leaf in Cretaceous Pines.[1]

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With Plates XIII and XIV.

THE leaf in the Gymnosperms has been the subject of many investigations, and it is now recognized that the fibrovascular structures of the foliar organs in this group are phylogenetically important. It is the purpose of the present communication to call attention to certain structural features of the leaves in Cretaceous Pines and allied forms, which appear to have an important bearing on the much disputed problem of the origin of the Coniferales.

It will be appropriate to commence this record with the description of those pine-like leaf remains which appear to present the most primitive characters. Fig. 1, Pl. XIII, shows a magnified external view of a short-shoot or brachyblast of an Abietineous species, which is rather rare in the Kreischerville deposits, from which all the material described in the present connexion has been derived. It will be noticed at once that it differs so strikingly from the fascicular shoots of any living species of *Pinus*, that, judging from external features alone, it might well be doubted whether our specimen was a short-shoot at all. The specimen represented in Fig. 1, Pl. XIII, shows at the base scars of fallen leaves which in this case are not foliage leaves, but are of the nature of bracts. Above the denuded region is a number of bracts still *in situ*. At the very top of the figure the brachyblast presents a truncated appearance and is crowned by the broken bases of a number of true foliage leaves. Fig. 3, Pl. XIII, shows another short-shoot of this species, which is in a much better condition

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of preservation. Much less of the base of the brachyblast is retained, and the sheathing bracts as a result present only a short segment. Above them, however, the foliage leaves are represented by much more elongated bases than in the last-mentioned figure. It may be made out that the fascicular leaves are more numerous than they are in any living Pine. Further, they are not in definite number as is the case in existing species of *Pinus*. The sheath in our specimen is composed of the same loose scales as are found in the sections *Strobus* and *Cembra* among living Pines; but its component bracts, like the fascicular leaves, are much more numerous than they are in any living species of *Pinus*. Moreover they are not deciduous, as is true of the elements of the fascicular sheath in the sections *Strobus*, *Cembra*, &c.

Fig. 2, Pl. XIII, represents a transverse section through the bases of the fascicular leaves in another specimen. The section does not include all of the leaves of the fascicle, since some of these have been removed in process of fossilization. The second projection on the lower left side of the figure represents the growing point of the short-shoot, which, contrary to the conditions found normally in living species of *Pinus*, clearly persists, and in some of our specimens is protected by a covering of thin scale-like bracts. Regarding the remains of the growing-point of the specimen shown in cross-section in the figure as its organic centre, it is clear that there must have been more than twenty-five leaves attached to the uninjured brachyblast. The number appears, however, to vary considerably, so far as we are able to judge from the rather fragmentary specimens at our disposal. As a result of the presence of a large number of leaves in the fascicles, these present, in the case of the internal leaves, a very different contour from those of the normal short-shoots of any living species of *Pinus*; for instead of being bounded by either one or two plane surfaces and one curved one, as is invariably the case in the fasciculate leaves of existing Pines, the internal leaves in these polyphyllous brachyblasts are polygonal in outline and bounded on all sides by plane surfaces. Another feature of contrast to living Pines is presented by their phyllotaxy, for their fasciculate leaves are arranged spirally and not verticillately on the short-shoots.

Before discussing further the internal structure of these interesting short-shoots, it will be well to refer briefly to *impressions* of a somewhat similar appearance described by other authors. Fontaine, in his monograph on the Potomac Flora, figures certain remains which he refers to Heer's Jurassic genus *Leptostrobus* ('The Potomac or Younger Mesozoic Flora', Monographs of U.S. Geological Survey, XV). These he describes as presenting both fasciculate leaves and others, arranged spirally at intervals on the relatively main branches, the latter comparable to the primary leaves found in the seedling, and occasionally as the result of injury in the adult, of living Pines. The leaf-fascicles in Fontaine's species are characterized,

as in our specimens, by the large number of fascicular leaves. In the Kreischerville deposits only short-shoots have been found as yet. Our specimens also strongly resemble *Pinites Solmsi* of Seward (British Museum Reports, Fossil Plants of the Wealden, Part 2). His Fig. 2, Pl. XVIII, shows leafy short-shoots, which must have presented a striking resemblance to our specimens in the living state, since they seem to have had the same long bractigerous base and numerous fascicular leaves.

Turning our attention now to the internal structure of the leaves and axes of these curious brachyblasts, we find in Fig. 4, Pl. XIII, a magnified view of one of the outer leaves shown in Fig. 2. The figure represents the leaf in its morphologically correct position with the xylem uppermost. The wood is only moderately well preserved, and the phloem has entirely disappeared, as is generally the case in Abietineous leaves from the Kreischerville deposits. The remainder of the leaf is composed of sclerified tissues, which contain towards the slightly flattened margins of the leaf two resin-canals. These present a remarkable contrast to those found in the fascicular leaves of living Pines, in the fact that they penetrate to the very base of the leaf and are occluded in this region by tyloses. The latter can be clearly distinguished in the figure. It has not been possible to follow with certainty the foliar resin-canals into the cortex of the short-shoot itself on account of the scantiness of well-preserved material; but it is highly probable that, unlike the fascicular leaves of living Pines, those of *Prepinus statenensis*, as we propose to call our specimens, had their resin-canals continuous with those of their axis and thus resembled the primary leaves of living Pines. The leaf-trace in *Prepinus statenensis* remained undivided in its course through the cortex of the axis of the short-shoot, and in this respect resembled the fascicular leaves of the living species of *Pinus* belonging to the sections *Strobus*, *Cembra* and *Crayopitys*.

An important feature of the leaf-trace in our species is the fact that there is a considerable amount of true centripetal wood present. In Fig. 4, Pl. XIII, this can be distinguished by attentive examination, on the right of the fibrovascular bundle. Fig. 5 shows the bundle of this leaf more highly magnified. The preservation is unfortunately not very good; but nevertheless, on the right hand, radiating masses of xylem tissue, passing away centripetally from the face of the considerable mass of centrifugal wood, can be made out. These masses of centripetal wood, starting with a narrow base, expand in a fan-like fashion towards the upper surface of the leaf. The presence of this well-developed centripetal xylem in the leaf of a Cretaceous Pine-like Conifer appears to be not without significance, since, so far as is known to the writer, it is the first recorded case of the presence of such tissues in a Coniferous leaf, living or extinct. The transfusion tissues are intentionally disregarded in making this statement, since, as will subsequently be shown, these cannot properly be considered as representing

the true centripetal wood, as has been maintained by Worsdell, and more recently by Bernard and others.

Before turning our attention to the structure of the higher portion of the leaf in the species under consideration, it will be well to examine briefly the organization of the axis of the short-shoot. Fig. 8, Pl. XIII, shows the manner in which the large traces of the fascicular leaves pass from the central cylinder of the brachyblast. It is to be noted that they do not divide into two, as is the case in the primary leaves of the seedling even of the *Strobus* group of Pines. This is additional evidence that we have really to do with a short-shoot and its appurtenant leaves. Fig. 6 shows the structure of a section through the woody cylinder of the short-shoot of the same specimen which furnished Figs. 2, 4, and 5. The magnification is not sufficient to show the details of structure; but it is possible to make out that there are islands of sclerenchyma, appearing as dark spots in the pith. This feature is not found in living representatives of the *Strobus* and allied sections of living Pines; but is common among the Hard Pines with three and five fascicular leaves. Fig. 7 shows a portion of the woody cylinder of the short-shoot more highly magnified. Although the enlargement is considerable the tracheids appear small. The most important feature of this figure is the presence of a resin-canal in the upper portion stopped with tyloses. The presence of this phenomenon in the wood of a shoot showing but a single annual ring makes it certain that we can have to do with nothing but the axis of a deciduous shoot or brachyblast. Thus the histological structure of the axis of these curious leafy shoots, which we have named *Prepinus statenensis*, makes it clear that they are brachyblasts of a primitive and somewhat generalized type of Cretaceous Pine-like Conifer.

In view of the general tendency to regard the Araucarians as the most ancient Conifers, the radial pitting of the tracheids of the brachyblasts in this species is of special interest. Fig. 9, Pl. XIII, represents the ends of several tracheids of *Prepinus statenensis* as seen under a magnification of 180. It is to be expected, if the Araucarineae really represent the most primitive type of Conifer, that some evidences of Araucarian structure should be found in the wood of this ancient Pine-like Conifer. The crowded pitting in the ends of the tracheids is purposely chosen for our Fig. 9, since one might expect to find the flattened or angular Araucarian type of pit exemplified under these conditions if at all. It will be noticed, by examining the figure, that the pits do not become more than slightly oval as a result of extreme approximation and in no case show the angularity or flattening of the Araucarian type. Fig. 10 shows the pits very highly magnified, to enforce the truth of this statement. On the left can be seen indications of the presence in the walls of the tracheids of the folds of Sanio between the adjacent pits, especially in the lower part of one

of the tracheids. This is the first occasion on which the author has observed this phenomenon, so common in living Conifers other than the Araucarineae, in a Mesozoic lignite. The entire absence of all indications of a transition towards the Araucarian condition of pitting in the oldest structurally known Abietineous Conifer furnishes a strong argument against the Abietineae having come from an Araucarian stock. On the other hand, in the wood of numerous species of the older Araucarians, which have been investigated for the first time structurally, in the case of leafy branches, by the author, there is a very marked departure from the Araucarian type of flattened or angular pits, towards the rounded bordered pits present in the remaining Coniferales, notably in the Abietineae. This transition towards the Abietineous condition in the radial pitting of the tracheids is paralleled by marked Abietineous characters in the wound reactions, and in some cases by the ray structure found in the case of the older Araucarians of the Cretaceous. It may accordingly be stated, in passing, that there is much better anatomical evidence from the Cretaceous for the Araucarineae having come from the Abietineae than for the opposite view, which is implied by the hypothesis that the Araucarians are the most ancient of living Conifers. Further consideration of this subject may advantageously be deferred until the end of the article.

Fig. 13, Pl. XIII, is a magnified representation of a transverse section of a leaf resembling that of *Pinus*, which is considered, on grounds to be stated below, to belong to *Prepinus statenensis*. The contour of the leaf is very different from that found in any living Pine, for instead of having one curved face and one or two plane surfaces, as is the case in the fascicular leaves of *Pinus*, we find five approximately plane surfaces. Any departure from the planar condition is probably to be explained as the result of the vicissitudes accompanying fossilization. On the margins of the angular leaf are to be seen two resin-canals. The fibrovascular bundle is single, as in the sections *Strobus*, *Cembra* and *Caryopitys*, of living Pines, and entirely lacks the phloem, which has disappeared through decay. The bundle is bounded by a dark zone which completely surrounds it, the like of which has not been found in the fascicular leaf of any living Pine. Outside the dark sheath just mentioned is a thick zone of transfusion tissue, made up of coarsely pitted transfusion cells, without any admixture of parenchyma, such as is found abundantly in the tissues surrounding the leaf-bundle in living Pines. This entire exclusion of parenchymatous elements from among the short tracheid-like cells, which constitute the transfusion tissue, has an interesting parallel in the complete absence of parenchyma (exclusive of that found in the rays) in the secondary wood of the older Gymnosperms, and is probably in both cases to be regarded as a primitive feature. Another remarkable contrast with living Pines offered by our species is the absence of any indication of an endodermal sheath separating the bundle and its associated

transfusion tissues from the mesophyll. Still another noteworthy feature is the presence of strong hypodermal ribs beneath the epidermis. Fig. 11 shows another section of the same leaf still more highly magnified. All the features signalized above can now more clearly be made out. The transfusion tissue is particularly obvious in this figure. Fig. 14 shows the fibrovascular bundle somewhat highly magnified. To the left is a cavity, which marks the position of the phloem, now entirely gone. The dense although not very thick sheath, which surrounds the bundle proper, can be clearly distinguished in this figure. The most interesting feature of the figure, however, is the structure presented by the wood. It can be made out that there is a *large amount of centripetal xylem present.* It will be observed that the centripetal elements, in the centre of the bundle, begin about the middle of a radius drawn through the xylem and pass with a gradual enlargement of their lumen towards the dark sheath already described, upon which as a rule they immediately abut. Fig. 15 shows the central portion of Fig. 14, much more highly magnified. The seriation of the elements is particularly clear in this figure, as well as their relation to the peculiar bundle sheath. The centrifugal xylem is not broken into separate strands as is the centripetal wood. It does not come into direct relation with the thick-walled sheath above mentioned, except on its flanks. In other regions of the xylem the relation between the centrifugal elements and the transfusion tissues is brought about through the centripetal xylem. Fig. 12 shows a longitudinal section through the leaf-bundle somewhat to one side of the centre. The tissues do not appear as well preserved in this plane of section as in the transverse ; but it can nevertheless be made out that typical mesarch structure is present. The ringed and spiral protoxylem elements occupy the centre of the figure, and on the left pass into reticulate elements, which are at once succeeded by pitted tracheids of the centrifugal wood. On the opposite side of the protoxylem are the thinner-walled and less well preserved elements of the centripetal wood, which are entirely pitted tracheids. On the extreme right is to be seen a portion of the very dense bundle sheath. This sheath is so darkly coloured in the fossil that it is almost impossible to resolve its structure even after the prolonged action of such a bleaching agent as chlorine water. It is possible, however, to make out with sufficient pains that it is composed of very thick-walled transfusion elements, with small bordered pits. The elements of the dense transfusion sheath are very much longer and of much narrower lumen than are the more external transfusion cells. They in fact present a certain resemblance to tracheids. The broad zone of transfusion cells surrounding the dense sheath just described is made of cells of much thinner walls and only slightly elongated longitudinally. As has been mentioned at an earlier stage, these are all pitted with bordered pits, which are about twice as broad as those found in the cells of the transfusion

sheath. There is no indication of an endodermis separating the transfusion tissues from the mesophyll as in modern Pines. There is possibly a correlation between the presence of the dense sheath surrounding the bundle and the absence of the endodermis. It is not improbable that the inner sheath, with its thick walls and small bordered pits, may have exercised a beneficial restraining influence in the case of excessive transpiration. Whatever the physiological function of the inner transfusion sheath may have been, we have to go for a parallel to it, significantly enough, to the Cordaites, as will be noted in a subsequent paragraph.

Before proceeding to the discussion of the resemblance of the leaf-bundle in the species which has just been described, to the foliar strands in Cordaites, it will be well to establish the relation of the isolated leaves to the short-shoots which have been considered in earlier paragraphs. From the description of the attached fasciculate leaves of *Prepinus statenensis* given above, it appears that the isolated leaves under discussion agree in the following features: the possession of centripetal wood; the single foliar bundle; the paired resin-canals; and finally, a very important feature, the polygonal outline of the leaf-section, resembling that found in the internal leaves of the brachyblasts of *Prepinus statenensis*. The only very noticeable difference is the presence of transfusion tissue in the case of the isolated leaves, which is absent in the attached bases of the leaves of the short-shoots. This feature is, however, of slight significance, since it is paralleled in the case of *Pinus*, where the transfusion tissue does not appear in the lowermost part of the fascicular leaves. It seems reasonable to conclude from the features of close agreement described above, and especially as *Prepinus statenensis* is unique among the remains of Abietineous Conifers found in the Kreischerville deposits, that the isolated leaves and the short-shoots referred to *Prepinus statenensis* belong together.

A few years ago Miss Stopes described an interesting peculiarity of Cordaitean leaves referred by her to the *Cordaites principalis* of Renault. In Cordaitean leaves, as is well known, the centripetal wood becomes continuous with a zone of transfusionary elements which completely surround the bundle, including the phloem as well as the xylem. Between the protoxylem and the phloem and on the dorsal side of the bundle, there is sometimes present more or less centrifugal wood, which is, however, always less abundant than the centripetal xylem. Miss Stopes (New Phytologist, vol. ii, pp. 91–8, Pl. IX) has shown that in *Cordaites principalis*, what had been taken by Renault for centrifugal wood, was in reality a sheath of elongated transfusion elements, *surrounding the phloem on its dorsal surface* and not interposed *between* the phloem and the centripetal wood, as should be the case were it really centrifugal wood. This sheath she regards as equivalent to the 'primitive transfusion tissue' of Worsdell, the larger-lumined, less prosenchymatous tracheidal sheath external to it being the

counterpart of Worsdell's 'peridesmic transfusion tissue'. Through the kindness of Professor Oliver I have had the opportunity of examining the beautifully preserved material upon which Miss Stopes's observations were made. Fig. 16, Pl. XIV, shows a leaf-bundle from this material somewhat highly magnified. The fibrovascular strand is surrounded by a cordon of large, apparently empty cells, which constitute the outer or 'peridesmic' transfusion tissue. The centripetal xylem lies on the upper side of the bundle, within the 'peridesmic' sheath just described. The bundle illustrated in Fig. 16 presents in essential features a striking resemblance to Fig. 14, the most marked differences being the presence of centrifugal xylem in *Prepinus*, and the fact that the inner sheath of the transfusion tissue does not extend over the posterior region of the xylem in *Cordaites*. In the sections loaned by Professor Oliver there was a good deal of variation in the extent of the inclusion of the centripetal xylem by the inner thick-walled transfusional sheath, in some instances there was only a single tracheid between the mass of centripetal xylem and the large-lumined outer sheath of transfusion tissue. In any case there is a very striking resemblance between the foliar bundles in *Prepinus* and *Cordaites*. This resemblance is none the less significant because of the opinion frequently expressed in recent years by competent investigators, that the Coniferales are descended from the *Cordaites* or from a Cordaitean plexus.

In Fig. 17, Pl. XIV, is shown a section through the basal region of a four-leaved fascicle of a contemporary Cretaceous Hard Pine. The needles are surrounded by the close membranous sheath of the Hard Pines and have the double leaf-trace which is characteristic of that group. By examination it will be seen that the leaves are without resin-canals in the basal region shown in the figure, and in this respect conform to the fascicular leaves of living Pines and differ from *Prepinus statenensis* described above. The double bundles of the leaf-traces are surrounded on the outer side in the region of the vanished phloem as well as in the region of the xylem by a sheath, comparable to that found in *Prepinus statenensis*. This sheath sends off a tongue which is inserted between the two bundles, forming a complete septum of separation. Fig. 18, Pl. XIV, shows the structure of a detached leaf from a Cretaceous Pine with a two-leaved fascicle. It is highly probable, from the presence of double bundle in the leaf in question, that it represents a Hard Pine. In Fig. 19, Pl. XIV, appears in transverse section the leaf of another species of bifoliar Pine which is characterized by the presence of a single fibrovascular bundle and consequently in all probability belongs to the general group of Soft Pines. In both these figures it is to be noted that the transfusion tissue is of the same type as in *Prepinus statenensis*, being composed of an inner dense sheath and a broad zone of outer large lumined transfusion elements.

In the case of Figs. 18 and 19 it is, however, by no means certain that there is no parenchyma intermingled with the outer transfusion elements, although the tracheidal cells are in any case infinitely more abundant than they are in living Pines. In the two species under discussion the endodermis is not clearly marked and may well be absent. The mesophyll is very scanty in amount, and lacks the infolded walls which characterize it in living species of *Pinus*.

Fig. 20, Pl. XIV, shows a somewhat smaller leaf of a Cretaceous Pine than those shown in the two previous figures, but its organization is of the same general type. The state of preservation is more favourable to the differentiation of the inner transfusion sheath than in the foregoing species. It may also be somewhat clearly distinguished, although the magnification is low, that the xylem of the bundle is entirely centrifugal, a condition which we have found to be present in all true Pines from the Middle Cretaceous of Staten Island. Fig. 21, Pl. XIV, shows a highly magnified longitudinal section of the bundle in this species. The inner transfusional sheath appears as very thick-walled, dark-coloured cells, which in the vicinity of the protoxylem are very considerably elongated and possess a very narrow lumen. Passing towards the left in the figure, the transfusion elements become at first more nearly isodiametric and then much thinner-walled. On the extreme left they have suffered disorganization. On the side of the xylem near the inner transfusional sheath are to be made out the somewhat disorganized ringed and spiral elements of the protoxylem. There is no indication whatever of the presence of true centripetal elements, such as are to be found in the foliar bundles of *Prepinus* as described above. Further to the right the centrifugal elements become reticulated and finally pitted, although the latter condition is not clearly shown in the figure.

Fig. 23, Pl. XIV, shows the cross-section of another leaf of *Pinus* belonging to still another Cretaceous species, which, we may judge from the angle made by its two plane surfaces, came from a five-leaved fascicle. In this case the inner sheath of the transfusion tissue has become almost obsolete and appears most clearly on the side of the vanished phloem and between the bundles. Fig. 22 reproduces the transverse section of another leaf, which probably belonged to a three-leaved fascicle. The inner transfusional sheath in this case can be distinguished rather better on the side of the phloem than in the last described species. It has suffered disintegration between the bundles, but again appears at the back of the protoxylem. Fig. 24 shows the transverse view of a very large leaf which has become considerably flattened in process of fossilization. The inner transfusional sheath can be clearly distinguished except on the flanks of the bundles, where in all species it tends to be thin.

It is obvious from the data supplied in the foregoing paragraphs that the leaves of species of true Pines from the Middle Cretaceous of Staten

Island differed from modern Pines, (1) in the better development of the transfusion elements around the bundle; (2) in the differentiation of the transfusion elements into an inner sheath composed of elongated tracheidal elements and an outer, much broader zone made up of more nearly isodiametric elements with thinner walls; (3) in the probable absence of an endodermis; and (4) in the absence of infolding of the walls of the mesophyll. They resembled their modern descendants in possessing a fixed small number of verticillate fascicular leaves for the brachyblasts of each species. The growing-point of the brachyblast in the true Pines of the Cretaceous often persisted, although the author in no case has found it to be as prominent as in *Prepinus*. The wood of the leaf-bundles was entirely endarch. *Prepinus statenensis* differed from other Cretaceous Pine-like Conifers in the possession of true centripetal wood, such as has been described in the leaves of no other Conifer living or extinct. The fascicular leaves were attached in an indefinite large number spirally to the brachyblast, which was deciduous as in the true Pines, but differed from them in having a prominent persistent growing-point covered with protective scales. The transfusion tissue of *Prepinus* has the same general organization as in Cretaceous species of *Pinus*, but it was much more abundant, and the outer zone had no admixture of parenchymatous elements.

Conclusions.

The presence of centripetal wood in *Prepinus* in the present state of our knowledge can scarcely be interpreted in any other way than as the persistence of an ancestral character possessed by the parent stock of the Abietineae. If it be conceded that the centripetal wood which is found in the leaves of *Prepinus* is a vestigial feature, it cannot well be denied that the double transfusionary sheath accompanying it in that genus and still retained in the Middle Cretaceous representatives of the true Pines is susceptible of a similar interpretation. This view of the matter is rendered still more probable because of the close agreement of the presumably primitive Abietineous leaf-bundle with that found in certain Cordaites which are regarded, by those whose studies fit them to judge, as the ancestral stock from which the Coniferales have been derived. If we may venture to depict the phylogenetic development of the Coniferous foliar bundle in the light of the new facts supplied by the study of their Mesozoic representatives, it would appear to be somewhat as follows. The ancestral Conifers, closely allied to the Cordaitales, possessed foliar bundles characterized by the presence of centripetal xylem and transfusion tissue of a complex type, consisting of a double cordon, an inner sheath composed of elongated tracheidal elements, and an outer jacket of ordinary transfusion cells without any admixture of parenchyma. In the course of subsequent

evolution the centripetal wood was the first archaic feature to become blotted out. Its disappearance was complete and occurred at a comparatively early stage of Coniferous history. At a later stage the inner transfusion sheath followed the centripetal wood into oblivion, although even in modern Conifers traces of it may still be found in the region of the protoxylem. As the result of the disappearance of the centripetal wood and the inner transfusional sheath, the centrifugal wood became ultimately directly continuous with the jacket of ordinary transfusion tissue, the outer transfusion sheath of the more ancient Abietineae. The outer or 'peridesmic' transfusion zone in the course of these changes became more and more degenerate and intermingled with parenchyma cells, and came to possess the structure shown in the vegetative leaves of modern Pines. The outer sheath is also persistent to some extent in the leaves of the Araucarineae, but even the older known representatives of this family show no indication of the existence of true centripetal wood or of an inner transfusion sheath.

The new data supplied by present investigation and by other recent researches on living and extinct Coniferales seem to strengthen the hypothesis put forward over two years ago by the author, to the effect that the Abietineae are a very old, if not the oldest, family of the Coniferales. It specially stands out in connexion with these results, that the Abietineae must be considered more primitive than the Araucarineae, which are generally regarded as the ancestral Conifers. The arguments for this view may be summarized as follows:—

1. The possession on the part of the Abietineae of marked vestiges of a double leaf-trace, such as is almost universally characteristic of the older Gymnosperms.

2. The presence of true centripetal wood in the genus *Prepinus*, which may be regarded with a strong degree of probability as the ancestor of the living genus *Pinus*.

3. The marked and detailed resemblance of the foliar bundle in *Prepinus*, not only in the presence of centripetal wood, but also in the complex double sheath of transfusion tissue, to certain *Cordaites*.

4. The persistence of the double transfusionary sheath in the true Pines of the Middle Cretaceous, although no similar structures have been found in numerous representatives of contemporary Araucarineae.

5. The wound-reactions of the older Cretaceous Araucarineae, referred by the author to the new subfamilies Brachyphylloideae and Araucariopityoideae, indicate a derivation of the ancestral Araucarians from an Abietineous stock.

6. The pitting of the older Araucarineae, which still survived in the Middle Cretaceous, showed a marked deviation from that found in *Agathis* and *Araucaria*, and a transition towards the type of pitting found in the Abietineae, while the oldest structurally known type of the Abietineae,

Prepinus, shows no tendency whatever towards the Araucarian type of bordered pits.

In this enumeration no account is taken of anything but sporophytic features. The gametophytes can more conveniently be considered at a later stage, when certain investigations have been completed.

Before summing up the results of the present research, it is necessary to say something in regard to the interpretation of transfusion tissue originally put forward by Worsdell and more recently elaborated by Bernard. In his article on 'Transfusion Tissue' (Trans. Linnean Society, London, vol. v, Part 8, Second Series), Mr. Worsdell makes the following statement: 'Transfusion tissue, which occurs almost universally in the leaves of Gymnospermous plants as an auxiliary conducting-system, has phylogenetically been derived from the centripetally-formed xylem of the vascular bundle, and is thus, morphologically, an integral part of the bundle itself.' The present research strongly supports the general accuracy of Mr. Worsdell's conclusions. It is, however, rendered doubtful if the elongated pitted elements found by this author on the ventral side of the protoxylem of the leaf-bundle in many Conifers can in reality be regarded as vestigial centripetal tracheids. It seems much more highly probable, from the conditions observed in *Prepinus* and in species of Cretaceous *Pinus*, that such elongated elements with bordered pits are in reality vestiges of the ancestral inner transfusional sheath, the real centripetal xylem having disappeared at too early a stage to be represented even vestigially in living Conifers. In any case it will not do to characterize, without qualification, the transfusion tissue which occurs ventrally to the protoxylem in many Coniferous leaves as centripetal xylem, as has been the tendency on the part of recent authors.

Summary.

1. A primitive Abietineous type, closely related to *Pinus* and strongly resembling superficially the *Leptostrobus* of Fontaine and the *Pinites Solmsi* of Seward, has been found in the Middle Cretaceous (Raritan or Upper Potomac) of Kreischerville, Staten Island, N.Y.

2. It is characterized by the possession of short-shoots or brachyblasts of a generalized type, which were deciduous; but bore numerous spirally arranged instead of few verticillate fascicular leaves. The sheath of these short-shoots more nearly resembled that found in the section *Strobus* and allied sections of *Pinus*, but the component scales were not deciduous as in the Soft Pines.

3. The leaves attached to the brachyblasts differed from the fascicular leaves of Pines in having their paired resin-canals continuous to the very base. The leaves further possessed well-marked centripetal xylem. About the foliar bundles was present a complicated double sheath of transfusion

tissue closely related to the centripetal wood and resembling that found in some *Cordaites*.

4. The name *Prepinus* is proposed for this type in the belief that it is the direct ancestor of *Pinus*.

5. Many of the true Pines of the Middle Cretaceous possessed the same double transfusionary foliar sheath as is found in *Prepinus*, but entirely lacked the centripetal wood which is characteristic of that genus.

6. The elongated pitted elements described by Worsdell and others on the ventral side of the protoxylem in existing Coniferous leaves appear rather to be relics of the inner transfusion sheath, which is a feature of Cretaceous Pines, than of true centripetal xylem.

7. The Abietineae are the oldest living family of the Coniferales.

8. *Pinus* is the oldest living representative of the Abietineae, and has in all probability been derived from *Prepinus*, which shows many archaic features.

In closing, the writer wishes to offer his best thanks to Dr. Hollick of the New York Botanic Garden, in whose company most of the material here described was collected. He also wishes to express his indebtedness to Professor F. W. Oliver, of the University of London, for the opportunity of examining unique preparations of Cordaitean leaves.

DESCRIPTION OF PLATES XIII AND XIV.

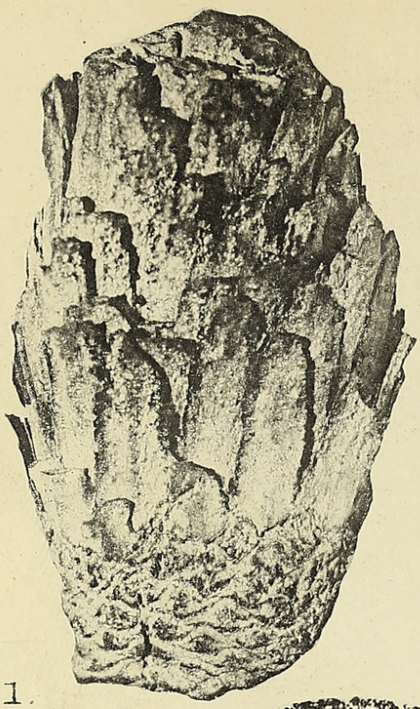
Illustrating Professor Jeffrey's Article on the Leaf of Cretaceous Pines.

PLATE XIII.

Fig. 1. Surface view of a short-shoot of *Prepinus statenensis*. × 10.
Fig. 2. Transverse section of fascicular leaves of *Prepinus statenensis*. × 13.
Fig. 3. Surface view of short-shoot of *Prepinus statenensis*. × 10.
Fig. 4. Fascicular leaf of *Prepinus statenensis*. × 40.
Fig. 5. Leaf-bundle of attached fascicular leaf of the same. × 100.
Fig. 6. Axis of the brachyblast of *Prepinus statenensis*. × 18.
Fig. 7. Part of the wood of the brachyblast of *Prepinus statenensis*. × 180.
Fig. 8. Upper part of the woody axis of a brachyblast of *Prepinus statenensis*. × 20.
Fig. 9. Tracheids of axis of brachyblast of *Prepinus statenensis*. × 180.
Fig. 10. The same. × 500.
Fig. 11. Detached leaf of *Prepinus statenensis*. × 64.
Fig. 12. The same, longitudinal section of the xylem. × 400.
Fig. 13. Detached leaf of *Prepinus statenensis*. × 30.
Fig. 14. Bundle of *Prepinus statenensis* in transverse section. × 140.
Fig. 15. Part of the same. × 500.

PLATE XIV.

Fig. 16. Leaf probably of *Cordaites principalis*. × 180.
Fig. 17. Leaf-fascicle of *Pinus tetraphylla*. × 32.
Fig. 18. Leaf of *Pinus spc.* × 40.
Fig. 19. Leaf of *Pinus spc.* × 40.
Fig. 20. Leaf of *Pinus spc.* × 40.
Fig. 21. Leaf of the same in longitudinal section of bundle. × 180.
Fig. 22. Leaf of *Pinus spc.* × 40.
Fig. 23. Leaf of *Pinus spc.* × 40.
Fig. 24. Leaf of *Pinus spc.* × 33.



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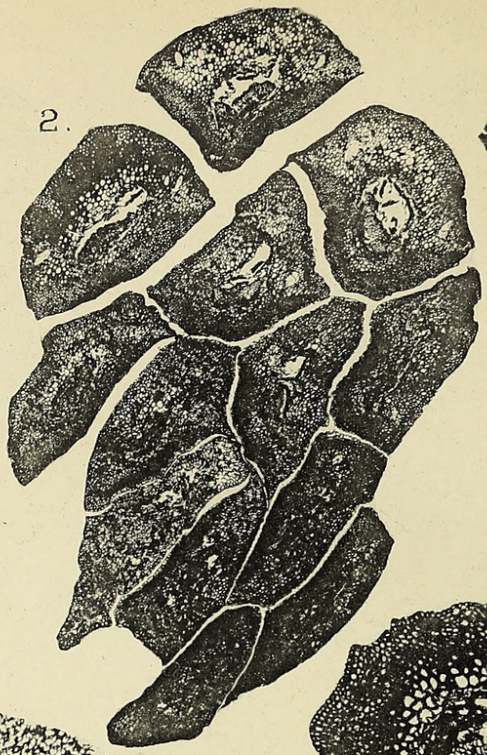

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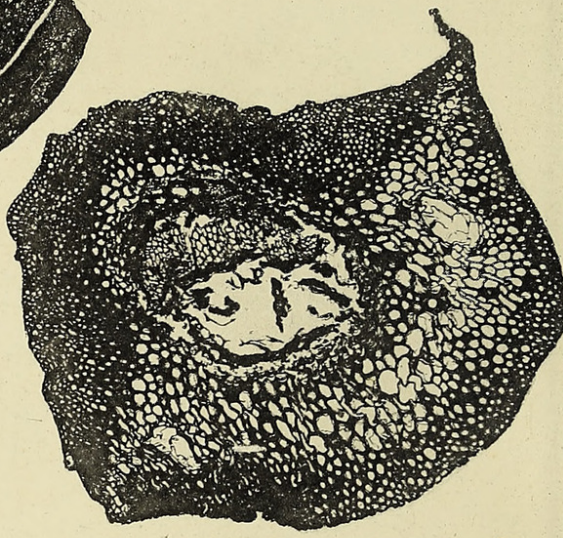

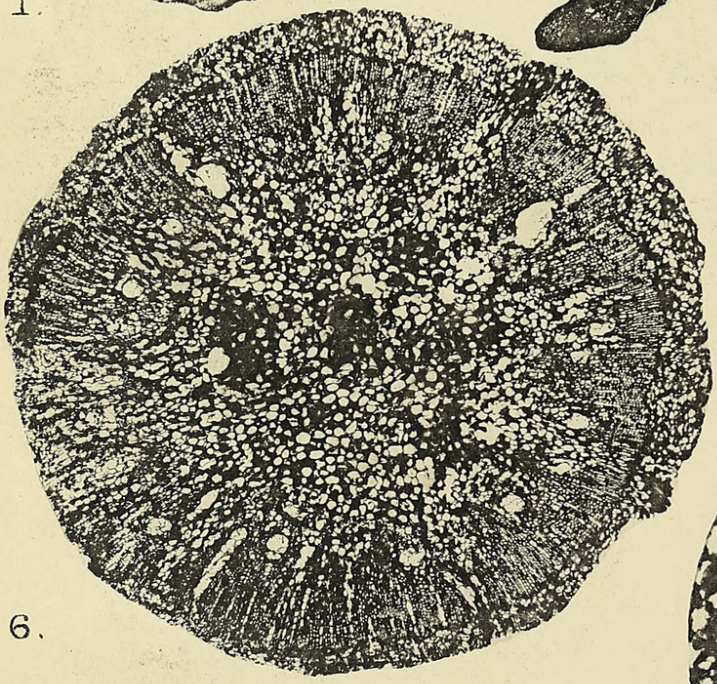

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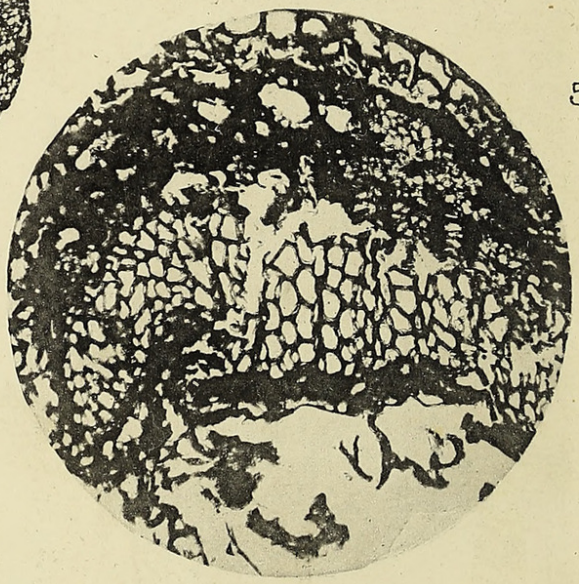

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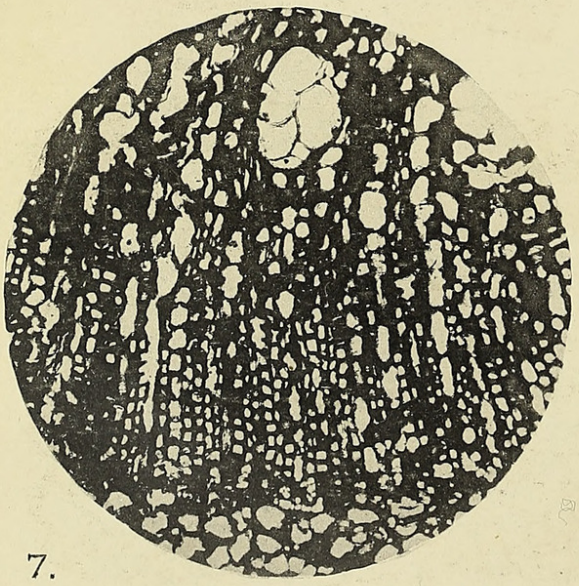

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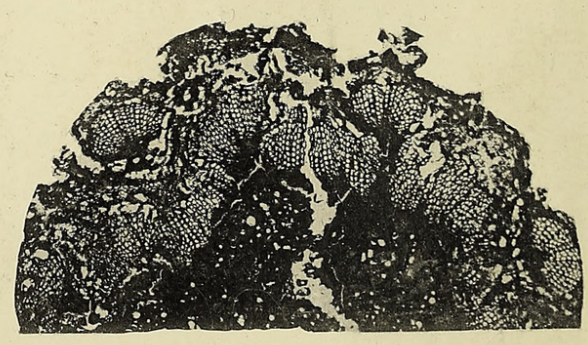

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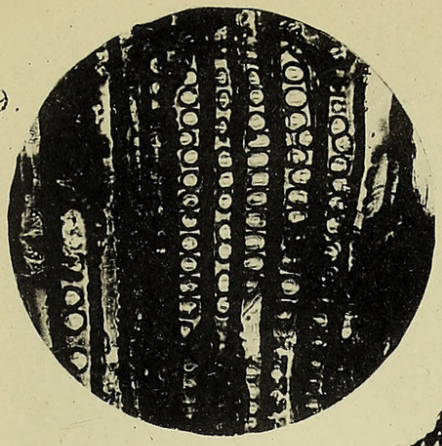

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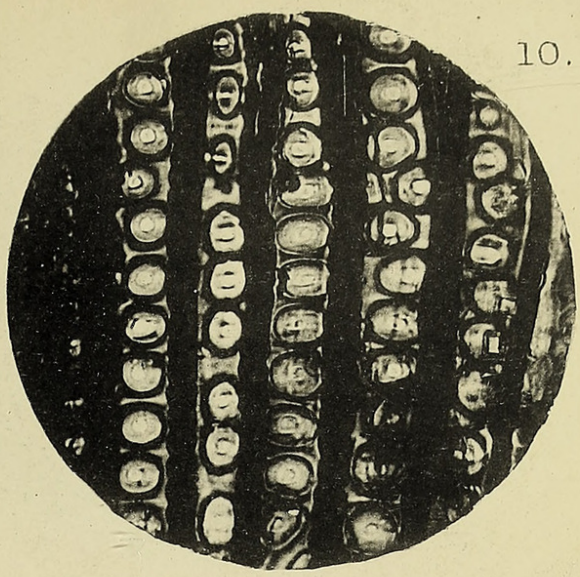

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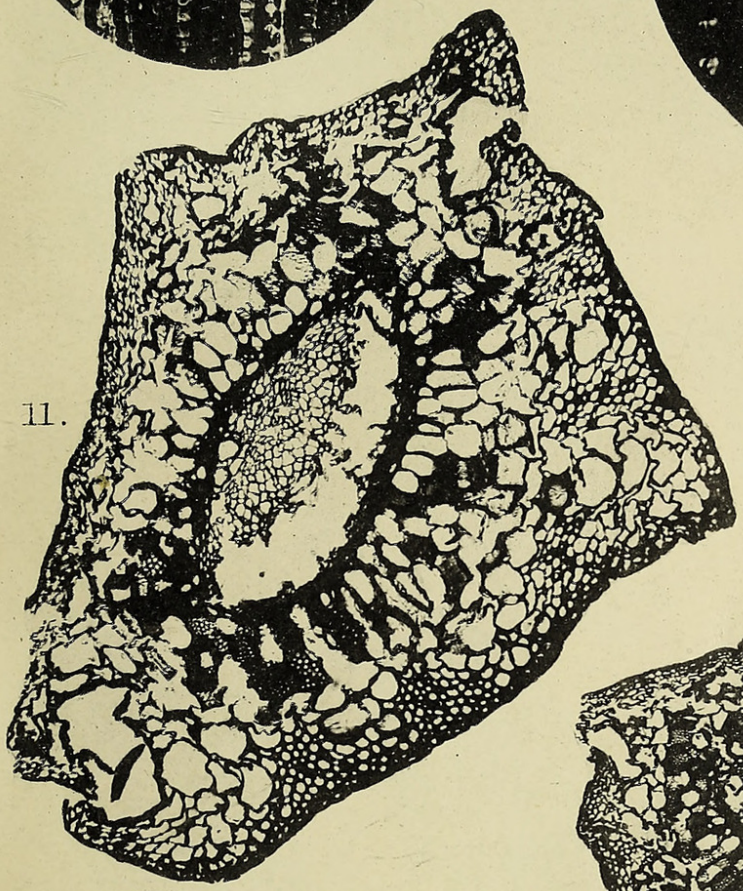

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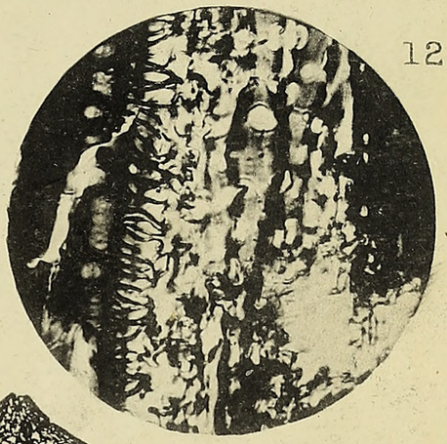

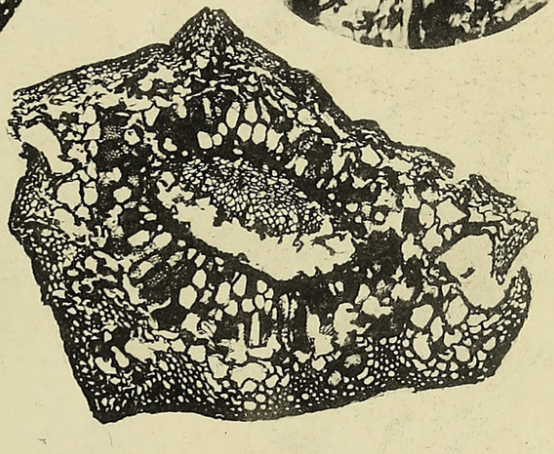

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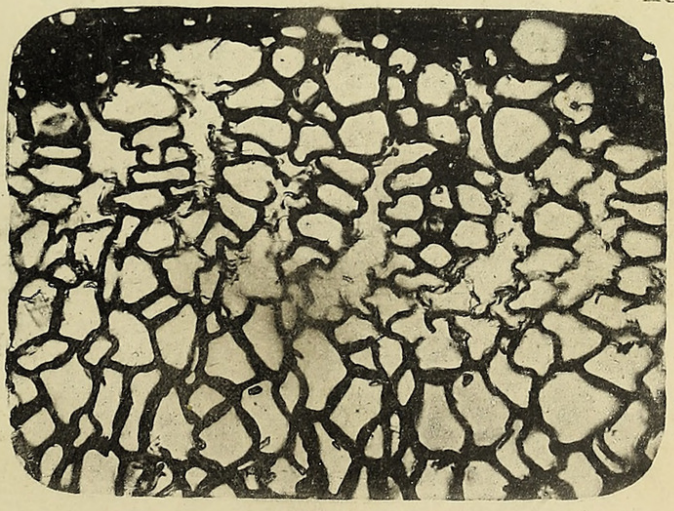

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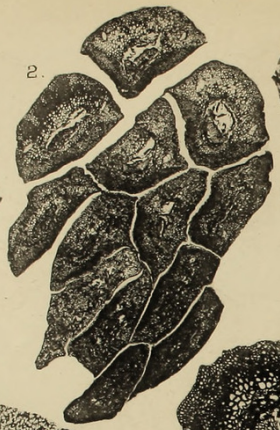

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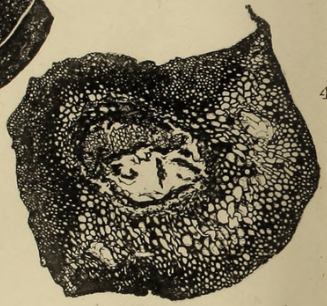

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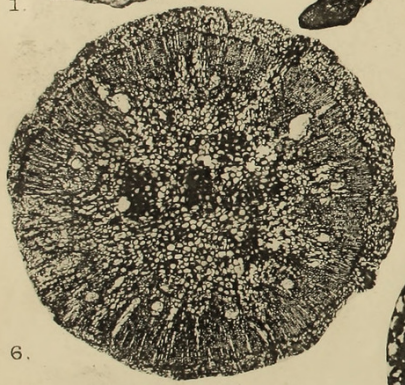

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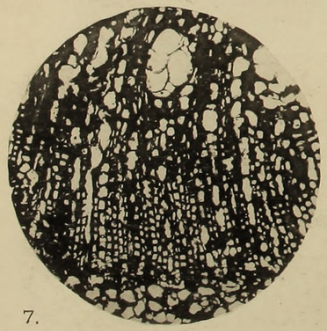

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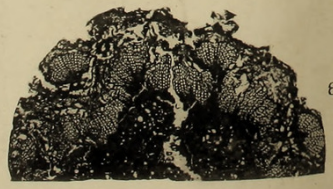

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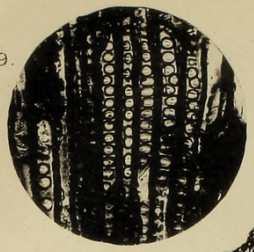

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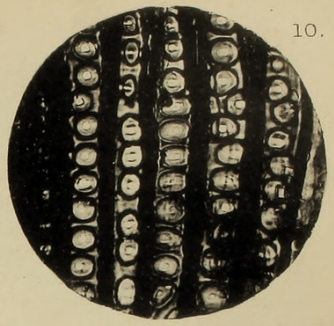

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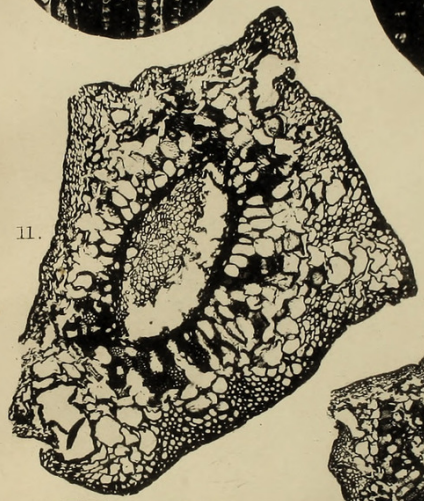

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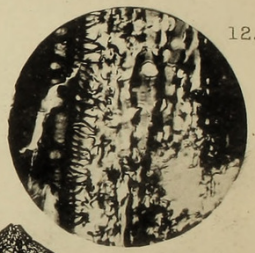

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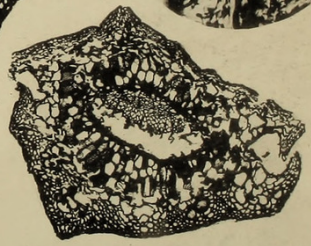

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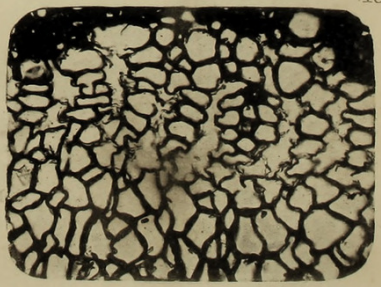

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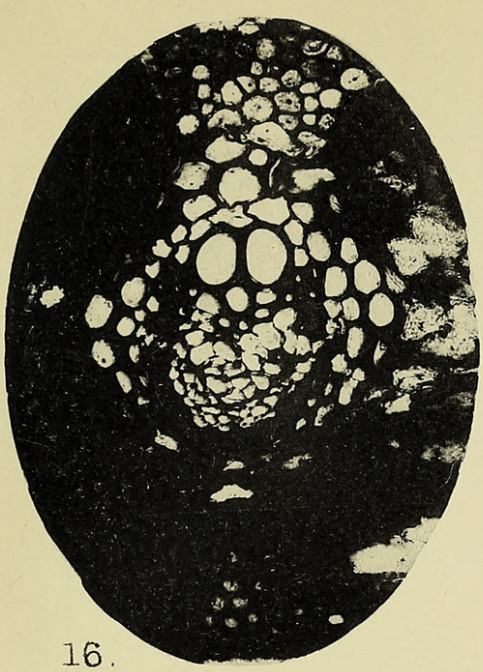

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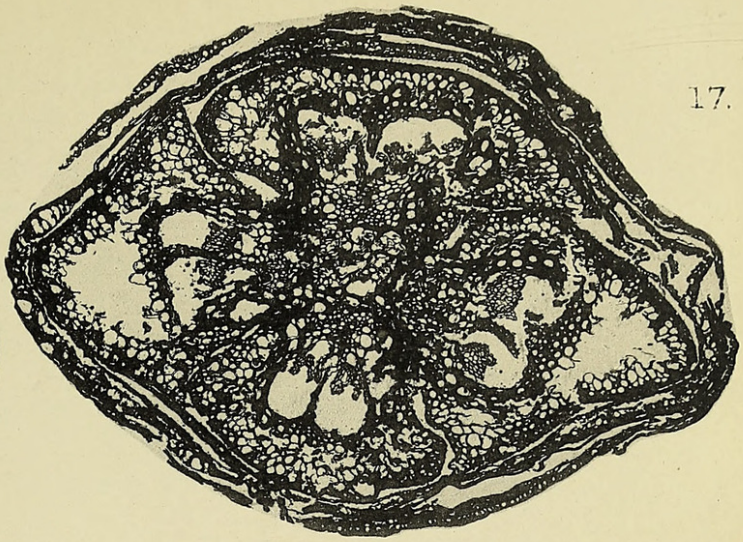

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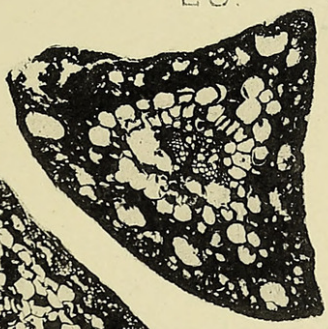

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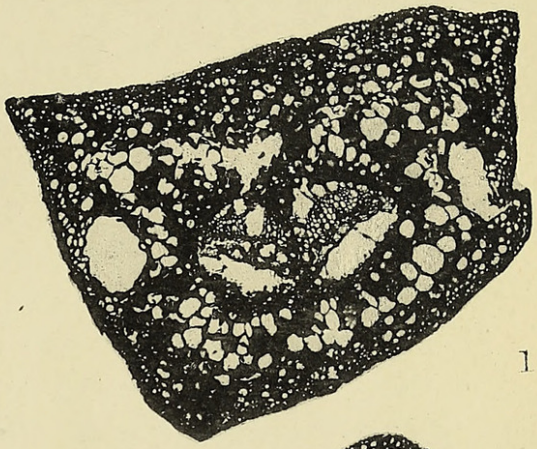

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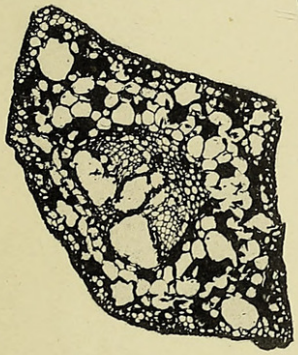

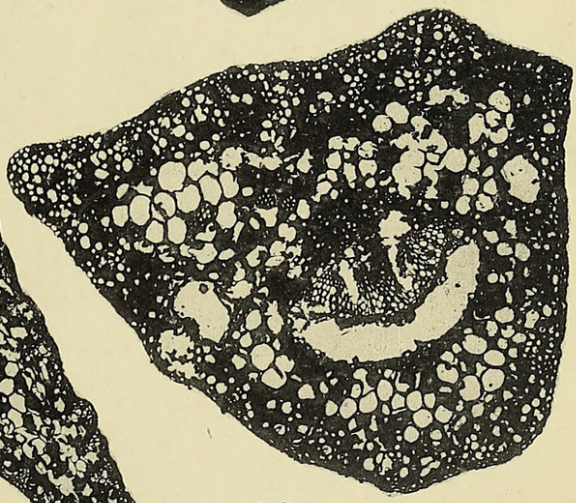

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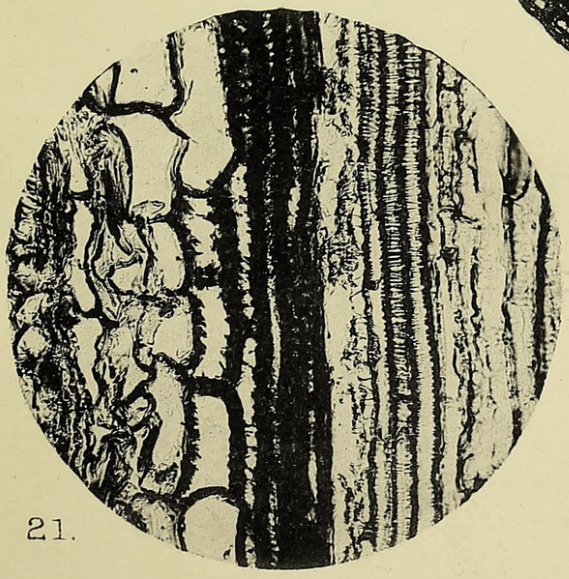

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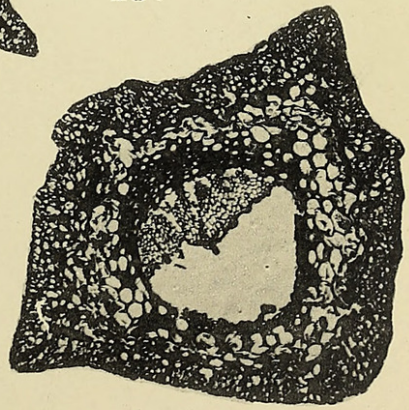

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