Contributions to the Anatomy of Mesozoic Conifers.

No. I. Jurassic Coniferous Woods from Yorkshire.¹

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With Plates XXXIX and XL.

DURING the last few years, a large number of Cretaceous woods have been investigated anatomically, and found to throw considerable light on the inter-relationships of the various families of Conifers. Structurally preserved material from the Jurassic is comparatively rarer and less known, but seems to be of even greater value than the Cretaceous from this standpoint. Especially interesting are those specimens described by Professor Seward from Yorkshire, England (1), by Gothan from King Karl's Land (2) and the island of Spitzbergen (3), and by Lignier from Normandy (4). The woods to be described in this article are all from the Jurassic of Yorkshire. They are in two conditions of preservation—petrified and lignitic. With a few exceptions, the petrified material was sent by Mr. James Lomax to Professor Jeffrey, to whom the writer is indebted for an opportunity to study it. All the lignite, on the other hand, and a small number of petrified specimens, were obtained by the writer from various localities on the Yorkshire coast. All the sections from Mr. Lomax, and representative ones of the lignitic material, are now at the University Museum, Harvard College, Cambridge, Massachusetts.

Before entering on the descriptive part, it will be apposite to consider briefly those features which have been found to be of greatest significance in diagnosing woods, especially in differentiating between the two great groups of Conifers—Araucarian and non-Araucarian, or Abietineous. The earliest classification, that of Kraus (5), was based entirely on the character of the radial pitting of the tracheides—the pits being alternating and compressed in the Araucarineae, and opposite and separated in the Abietineae and other tribes. This is the criterion used by both Seward and Lignier. Jeffrey (6), however, has shown that in the Cretaceous there were woods which combined the Araucarian type of pitting with that characteristic of

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the Abietineae. In this type, which he called *Brachyoxylon*, some of the pits are closely compressed and flattened, while others are scattered and circular. Further (7), he has shown that in the seedling of both living Araucarian genera—*Araucaria* and *Agathis*—this *Brachyoxylon* type persists. Since there is this marked departure from the so-called Araucarian pitting even in living forms, it seems to follow that this type of pitting will be even less constant in forms which are now extinct. Accordingly it appears to be unsafe to employ this criterion exclusively in diagnosing fossil woods.

Gothan also considers of little importance the character of the tracheary pitting, for he describes as Abietineous a number of fossils with typical Araucarian pitting. His criterion is the nature of the medullary ray cells—any Conifer whose rays have thick, heavily pitted walls is Abietineous, no matter what its other structural peculiarities may be. Neither Lignier nor Jeffrey follows him here, for both have described as Araucarian specimens with pitted rays—*Cormaraucarioxylon crasseradiatum*, Lignier (op. cit.), and *Araucariopitys americana*, Jeffrey (8). Moreover, the last-mentioned writer has shown that in the cone axis of *Agathis australis*, and in traumatic wood of both *Araucaria* and *Agathis*, there are typical Abietineous rays. It seems evident that in living forms the character of the rays is as inconstant as that of the pitting of the tracheides, and is accordingly as little to be relied on in fossil forms.

The only feature which holds absolutely is the occurrence of certain cellulose¹ thickenings, embedded between the pits in the substance of the cell wall itself. These are the so-called 'bars of Sanio', which are present in all woods of Abietineous affinities—Abietineae, Cupressineae, Taxodineae, Podocarpaceae, and Taxineae (9)—but are invariably absent in those of Araucarian affinities, *except in the first few secondary tracheides of the cone axis of Araucaria and Agathis* (7). Since this is the only character which is perfectly constant in those Conifers existing at the present day, it appears to be the safest to choose in diagnosing fossil forms. The most striking case where this feature alone has been considered sufficient to decide the affinities of a wood is that of *Paracedroxylon*, Sinnott (10), which its founder calls Araucarian in spite of scattered pits, resin canals, and thick, pitted rays (both these last two features, however, are traumatic). It has been suggested that 'bars of Sanio' are structures too delicate to be preserved in petrified material. Such is not the case, for in many silicified specimens they are as unmistakable as in living forms. Owing to the fact that they are composed of cellulose, which speedily disappears in the course of fossilization,

¹ By cellulose is meant giving the ordinary cellulose reactions, e.g. a dark blue stain with iodine and sulphuric acid. Whether they are called 'bars of Sanio', or, as Professor Groom prefers, 'rims of Sanio,' is a matter of absolutely no importance as long as it is understood that they contain cellulose, and that they are embedded in the cell wall.

they appear as white lines between the pits. It is this feature which has been used in the following descriptions to differentiate between Araucarian and Abietineous woods.

ARAUCARINEAE.

Xenoxylon phyllocladoides, Gothan (Pl. XXXIX, Figs. 1-4).

Wood of this type composed the greater part of the lignite from Scarborough, and is, as a whole, in a perfect state of preservation. Its general character may be observed in Fig. 1; the annual rings are well marked, with but a small amount of summer wood, there is an abundance of ray parenchyma, but no wood parenchyma. The nature of the rays is shown in Fig. 2, or better, in the more highly magnified view of Fig. 4. The horizontal and end walls are thin and unpitted, while on the vertical wall communicating with the tracheides there are large 'Eiporen'. Usually there is but one, rarely two, to each cross-field. The character of the tracheary pitting is evident from Figs. 2 and 3. The pits are large, usually remote (though rarely compressed and flattened), and, instead of being circular, are elongated in a horizontal direction. When in more than a single row, they are usually opposite, but sometimes alternate. In Fig. 3 a dark spot may be seen in the centre of the mouth of each pit. In radial section it looks like a small torus, but tangential sections show that this appearance is due to a particle of dirt having become lodged there. The exceedingly large 'Eiporen' indicate that this wood is a species of *Xenoxylon* and the character of the tracheary pitting exactly resembles *Xenoxylon phyllocladoides*, Gothan. The only difference between the two consists in the shape of the ray. According to Gothan, the rays of *Xenoxylon phyllocladoides* are much higher than wide, so that in tangential section they appear oval. Such is distinctly not the case here. Figs. 1 and 2, both photographed at the same magnification, show them to be of approximately the same dimensions in the two planes, and their circular outline in tangential section proves the point. This wood seems also to be identical with *Cupressinoxylon Barberi*, Seward, from the Jurassic of Whitby, though lacking the resiniferous tracheides of that specimen. In regard to the affinities of *Xenoxylon phyllocladoides*, Gothan (2, p. 38) states that it is 'without analogy in living or fossil gymnospermous woods'. The absence of bars of Sanio, however, shows that it belongs among the Araucarian Conifers, a conclusion borne out by the occasional compressed and flattened condition of the pits, though among living Araucarian forms there are none with similar pitting of the rays.

Locality : Scarborough.

Horizon : Oolite.

Xenoxylon latiporosum, Gothan (Figs. 5 and 6).

Sections of this type were cut from a block of petrified wood found on the Yorkshire coast, a short distance north of Robin Hood's Bay. Fig. 5 shows a typical radial section. Like *Xenoxylon phyllocladoides*, the wood consists entirely of tracheides and rays, and the rays have one large pit which covers the entire cross-field. Unlike the former, the tracheary pits are invariably flattened and closely compressed. The extreme compression has resulted in the appearance of pits which are fully twice as wide as high (Fig. 6). When two-ranked, the pits are always alternating (Fig. 6). In every respect this specimen is identical with *Xenoxylon latiporosum*, Gothan, and must be included among the Araucarineae, both on account of the absence of bars of Sanio and the presence of alternating pitting.

Locality: Robin Hood's Bay.

Horizon: Lias.

Paraphyllocladoxylon eboracense (Figs. 7-9).

Figs. 7-9 show the character of this lignite. The radial pits of the tracheides are usually scattered and circular (Fig. 7), but are never separated by cellulose bars of Sanio. Tangential pitting is abundant (Fig. 9). The rays are smooth-walled, with one, rarely two, large pits to each cross-field (Fig. 8). These pits are, however, conspicuously smaller than those of *Xenoxylon* (cf. Fig. 4). In Fig. 9 several of the tracheides have dark cross-walls which give the appearance of wood parenchyma. The character of the partition shows that it is a resin plate, due to the fact that certain tracheides become filled with resin. That this resinous substance is derived from the rays is shown by the dark content of one tracheide in the centre of the field, which lies immediately next the ray. Jeffrey (7, p. 538) has referred to similar resinous exudations in the wood of living and fossil Araucarians, and suggested that this is the explanation of the apparently thick-walled tracheides situated next the rays in some of Lignier's specimens. This wood closely resembles the *Phyllocladoxylon* described by Gothan from King Karl's Land. It would seem better, however, to reserve the generic name *Phyllocladoxylon* for podocarpineous forms with these large 'Eiporen', and to use the name *Paraphyllocladoxylon* for similarly characterized Araucarians. Since this specimen is from Yorkshire, it is proposed to call it *Paraphyllocladoxylon eboracense*.

Locality: Scarborough.

Horizon: Oolite.

Paraphyllocladoxylon araucarioides (Fig. 10).

This material was among the specimens sent by Mr. Lomax to Professor Jeffrey. As shown in Fig. 10 the rays closely resemble those of the last-described wood. The tracheary pits, on the other hand, are

quite different, being always closely compressed and flattened. On that character it is proposed to call this specimen *Paraphyllocladoxylon araucarioides*.

Paracupressinoxylon cedroides (Figs. 11-14).

The sections included under this head were sent by Mr. Lomax. Fortunately, a considerable amount of material was available, so that it is possible to present a fairly complete account of this interesting wood. The pith is homogeneously parenchymatous, without any sclerotic cells or diaphragms such as occur very commonly in Mesozoic forms, both Abietineous and Araucarian (Literature 4, 6, 7, 8, and 12). The wood consists of tracheides, rays, and resiniferous elements. The tracheides are small, and rarely have more than one row of pits on the radial wall. In such cases they are alternate and compressed. When uniserial, the pits are usually scattered and circular, though often flattened (Fig. 13). In no case was there any indication of cellulose bars of Sanio. There are also abundant tangential pits. The rays are highly resinous, and—an unusual feature in Araucarian woods—thick-walled and heavily pitted. Fig. 14 shows this character clearly. On the wall next the tracheide the pits are small and piciform, ranging from two to several to each cross-field. The resiniferous elements are of two sorts—true wood parenchyma, which is scattered throughout the year's growth, and resin-filled tracheides. The phloem is less well preserved, but there seem to be no alternately recurring zones of hard and soft bast, such as occur in the Cupressineae, for example. In the outer bark there are clusters of stone cells, and on the outside a layer of periderm.

It is evident from a study of the normal tissues that we are dealing with an Araucarian Conifer presenting a new combination of Araucarian and Abietineous features. Under these circumstances it is extremely fortunate that it is possible to investigate its traumatic reaction. One of the sections shows, at a short distance from the pith, a distinct wound-cap, from which rows of resin canals extend on each side (Fig. 11). These canals persist for some distance around the stem and then die out. The nature of this abnormal tissue may be ascertained from Figs. 11 and 12. Each duct is very wide tangentially, communicates freely with its neighbours, is constricted at short intervals, and is surrounded by a jacket of thick-walled parenchyma cells. The structure of these canals is paralleled exactly by those formed after wounding in the genera *Abies* or *Tsuga*, and indicate beyond doubt that their appearance here is an instance of traumatic reversion. It is in the vicinity of the wound that the rays are most highly resinous, and the resiniferous elements most abundant.

The affinities of this wood are not difficult to infer. The absence of cellulose bars of Sanio vouches for its Araucarian nature, and its Abietineous features show it to be another of those transitional forms so abundant

in the Mesozoic. In the formation of traumatic resin canals, it resembles *Brachyoxylon* (6), *Paracedroxylon* (10), *Araucariopitys* (8), and *Araucarioxylon Lindleyi* (1). Its resemblance to *Araucariopitys* is indeed very close, since, in addition to wound resin canals, both have heavily pitted rays. *Araucariopitys*, however, lacks the wood parenchyma of this specimen, and also contains sclerotic diaphragms in the pith. With some of Lignier's specimens, also, it has much in common, but those, like *Araucariopitys*, have sclerites in the pith. *Araucarioxylon Lindleyi* seems to be the nearest, but differs in that Professor Seward's specimen has exclusively terminal wood parenchyma. To denote an Araucarian *Cedroxylon* Mr. Sinnott founded the genus *Paracedroxylon*. Since this wood bears almost the same relation to *Cupressinoxylon* as his to *Cedroxylon*, it is proposed to call this type *Paracupressinoxylon*. To emphasize the fact that this wood differs from most *Cupressinoxyla* in the possession of thick-walled heavily pitted rays, such as occur in the cedars, it may be called *Paracupressinoxylon cedroides*.

Paracupressinoxylon cupressoides (Figs. 15 and 16).

The sections photographed for Figs. 15 and 16 are also from Mr. Lomax. This wood has *Brachyoxylon* tracheary pitting, with no cellulose bars of Sanio, thin-walled highly resinous rays, and abundant wood parenchyma scattered throughout the year's growth. Though its wound reaction is unknown, it is evident that it belongs to the genus *Paracupressinoxylon*. Since it differs from the last-described wood in the possession of thin and unpitted, rather than thick and pitted rays, it may be called *Paracupressinoxylon cupressoides*.

Metacedroxylon araucarioides (Pl. XL, Figs. 17-21).

This type of wood seems to be comparatively abundant in the Jurassic of Yorkshire, Mr. Lomax having sent several specimens, and the writer having procured a considerable amount of lignite of this variety from the Oölite of both Whitby and Scarborough, and some petrified material from the Lias of Robin Hood's Bay. The sections used for Figs. 17 and 18 are from Mr. Lomax, and have already been figured by Professor Jeffrey (7). There is a great deal of variety in the pitting of the tracheides. When uniserial the pits are often widely scattered and circular in outline, but equally often they are compressed and flattened. When more than one row occurs in a tracheide, they are at times typically Araucarian—alternate and angular, while at others they are in distinctly opposite pairs, or in groups of three or four (Fig. 17). It is often noticeable that the pits, however Araucarian in arrangement, are not so in outline,—the close approximation and consequent compression are absent, and instead, the pits are free and circular. The ray structure is shown in Fig. 18. It is obvious that the ray

cells, where in contact with each other, are heavily pitted, precisely as in the Abietineae. The pits from ray to tracheide are piciform, usually one or two to each cross-field. There is never any wood parenchyma. Figs. 19, 20, and 21 are of a lignite from Scarborough, showing similar structure. It differs in that the tracheides are smaller, the radial pits are uniserial, and always closely approximated, and usually the rays have but one pit to each cross-field. The most striking feature of this specimen is the large number of tyloses in the tracheides (Figs. 20 and 21). Several lots of this material were found, and in all the tyloses are present.

From the absence of cellulose bars of Sanio in all the specimens of this type, it is evident that we are dealing here with another Araucarian Conifer, which in view of the ray pitting must be transitional between that group and the Abietineae. The wood is indeed identical with that described by Jeffrey as *Araucariopitys*, and by Gothan as *Protocedroxylon araucarioides*, even to the tyloses in the tracheides. Jeffrey considers this an Araucarian type, while Gothan, from the structure of the rays, considers it Abietineous. As pointed out above, such thick-walled pitted rays are present in the cone axis of the living genus *Agathis* and may be recalled as a result of wounding in both *Araucaria* and *Agathis*. Since the cone axis has been shown repeatedly to retain ancestral conditions, and traumatic tissue to recall them, it seems entirely logical to conclude that the living Araucarineae are derived from ancestors which had thick-walled pitted rays. If so, there can be no doubt that this Jurassic wood under consideration is one of these ancestors. Since the term *Protocedroxylon* implies Abietineous affinities, it seems better to change it to *Metacedroxylon*, though retaining the original specific name of Gothan, and to call this wood *Metacedroxylon araucarioides*. It is interesting to note that Lignier (op. cit.) has described as Araucarian several similar specimens, with Abietineous pitting of the rays. His diagnosis depends on the character of the tracheary pitting. As mentioned above, approximated and flattened pitting are not invariably characteristic of the living *Araucaria* and *Agathis*, being replaced in the seedling by the scattered and circular pits which constitute the *Brachyoxylon* type. Since the seedling, like the cone axis, has in numerous instances been shown to perpetuate ancestral conditions, it seems justifiable to assume that flattened pitting is not the primitive condition for the Araucarineae, and will be less and less reliable as a diagnostic feature in progressively older geological horizons. Thus by a process of elimination, we are led to adopt the cellulose bars of Sanio as the only sure criterion for diagnosing coniferous woods. Accordingly, *Metacedroxylon araucarioides* cannot be other than an Araucarian Conifer.

Locality: Whitby and Scarborough.

„ Robin Hood's Bay.

Horizon: Oolite.

„ Lias.

Metacedroxylon latiporosum (Figs. 22–24).

Another closely allied species is shown in Figs. 22–24. The lack of wood parenchyma, presence of thick-walled, heavily pitted rays, and Araucarian pitting of the tracheides clearly affiliate it with *Metacedroxylon*. In many places the ordinary compressed tracheary pitting becomes accentuated, until a condition is reached like that shown in Fig. 24. This type is similar to that of *Xenoxylon latiporosum*, and on that account it is proposed to call this wood *Metacedroxylon latiporosum*. In *Xenoxylon* it seems evident that the large pits of the tracheides are formed by the extreme compression of a single row of approximated pits. In this specimen, however, the not infrequent substitution of a pair of small opposite pits for a single large one indicates another mode of origin. In fact, there seems to be no reason why such pits could not have been formed in two ways—either by the horizontal enlargement of a single pit, or the fusion of a pair of opposite pits.

Brachyoxylon sp. (Figs. 25 and 26).

Among both the lignites and petrified material, there were numerous specimens conforming more or less closely to the *Brachyoxylon* type. Figs. 25 and 26 show the structure of one of the lignites. A noticeable peculiarity of this wood is the angle at which the rays cross the tracheides (Fig. 25). This feature seems to be constant, since it was found in several specimens. It is evident that the rays are smooth and unpitted on horizontal and end walls, with one or two piciform pits on each radial wall. The tracheary pits are either circular and scattered or flattened and compressed (Fig. 26). Not infrequently they occur in sub-opposite pairs, but in no instance is there any indication of cellulose bars of Sanio.

Another variety of *Brachyoxylon* is shown in Fig. 27. This specimen has scattered pits and thin-walled rays, but is unique in the possession of large numbers of septate tracheides at the beginning of each annual ring. The significance of these cells it is difficult to infer. Whether they represent incipient parenchyma, or are related to an injury, it is impossible to say, but the latter supposition is rendered improbable by their appearance in several successive years, and the lack of any twist in the grain which would indicate proximity to a wound.

Of the other specimens of *Brachyoxylon* none presented any especial features of interest, beyond the fact that in one there were medullary stone cells.

Araucarioxylon sp. (Fig. 28).

Among the lignites was one clearly defined *Araucarioxylon*. This is shown in Fig. 28. The tracheides have one or two rows of closely compressed, flattened pits, the rays are low, thin-walled, and highly resinous,

with two to five small piciform pits to each cross-field. Whether this *Araucarioxylon* represents the wood of the Araucarineae or not, it is impossible to say. If so, it must be almost the oldest fully developed specimen of that family. It seems much more probable that it belongs to *Cordaite*s, whose presence in the Lias is vouched for by Lignier's description of *Artisia* from that horizon (op. cit., ii, p. 135).

Locality: Scarborough.

Horizon: Oolite.

ABIETINEAE.

Protobrachyoxylon eboracense (Figs. 29 and 30).

This specimen is among the most interesting lignites from Scarboro. The general features of the wood—small tracheides with predominately uniserial pits, thin-walled ray cells, and absence of wood parenchyma—may be seen in Fig. 29. When examined carefully, the radial pits of the tracheides are found to present certain peculiarities of structure quite unique in Coniferous woods. As stated above, the pits are usually in one row; when two-ranked, as is not uncommon in the larger tracheides formed in the spring, they are always opposite. The uniserial pits are often scattered and circular, but equally often approximated and compressed. An example of the latter condition is shown in Fig. 30. Between the uppermost pit of the series and the one immediately below it may be seen on each side, but especially well on the left, a small white knob-like structure. Similar structures, though less well marked, may be observed below the next pit, and below the third they are quite evident again. Such appearances, which are exceedingly common in the best-preserved tracheides, can be interpreted as only one thing—degenerate bars of Sanio. To those who believe that the Abietineae are the ancestors of the Araucarineae, it is easy to see how these structures arose. As the pits of a Conifer like *Pinus*—remote, circular, and separated by bars of Sanio—become approximated, the bar is necessarily eliminated. It naturally disappears first in the centre, where the pits first come into contact with each other. As the pits become more crowded, only the ends of the bar persist. Such a condition is shown in Fig. 30. Occasionally, when the pits are not as closely approximated as usual, it is possible to make out a faint white line, connecting the knobs on the end. Such dumb-bell-like bars are very rare. In other places the centre of the bar is completely gone, but the ends, instead of being knob-like, are long and narrow. It is remarkable that these bars should persist when the pits are closely compressed, and not when they are scattered, but such is the case. In view of the fact that all transitional Araucarians, such as *Brachyoxylon*, &c., are descended from such a form as this, it is appropriate that it be called *Protobrachyoxylon eboracense*—the specific name to mark the place where it was found.

The presence of these degenerate bars has a not unimportant bearing on the diagnostic significance of bars of Sanio in general. As pointed out above, their extreme constancy in living forms has led to their adoption as the *sine qua non* of an Abietineous Conifer. Such has been the assumption of Sinnott in the case of *Paracedroxylon*, of Jeffrey in *Brachyoxylon* and *Araucariopitys*, and of the writer in these Jurassic woods. Gothan (op. cit., p. 32) has questioned the cogency of such reasoning. He denies that there is a phylogenetic principle involved in their distribution, and inclines to the opinion that their appearance is correlated with the amount of available space,—i. e. when the pits are remote, the bar is present; and when they are crowded, the bar is absent. There are two facts militating against the soundness of this view. In the first place, as Jeffrey has pointed out (7), the pits in the seedling of *Araucaria* and *Agathis* are as remote as in *Pinus*, and yet the bars are always absent; in the second, the pits in the specimen now under consideration are as crowded as those of any Araucarian, and yet the bars are clearly present. From these considerations it seems evident that Gothan's explanation is inadequate, and that, on the other hand, the diagnostic significance of cellulose bars of Sanio cannot be over-emphasized.

Locality: Scarborough.

Horizon: Oolite.

Podocarpoxylon sp. (Figs. 31 and 32).

This lignite is also from the vicinity of Scarborough. The rays are thin-walled, with one or two piciform pits to each cross-field. Usually the tracheary pits are uniserial, but double rows are not infrequent, in which case the pits are opposite. Between several of the pits shown in Fig. 31 may be seen white lines. These are bars of Sanio. They are very common, and show all the variations present in living genera, such as Pine. Frequently they are double, in places they fork at the ends, occasionally they are curved, following the contour of the pit, and when the pairs of pits are not strictly opposite the bars are at a distinct angle, until rarely they become almost vertical. The thin-walled rays exclude this specimen from the genus *Cedroxylon*, and the absence of parenchyma from *Cupressinoxylon*; the best place for it seems to be in the genus *Podocarpoxylon*, Gothan.

The wood of Fig. 32 came from Mr. Lomax. It is less well preserved than that last described, but its Abietineous affinities are unquestionable. The rays are thin-walled, there is well-marked wood parenchyma at the end of the annual ring, and the radial pits of the tracheides are scattered, or, when two-ranked, opposite. Bars of Sanio may often be observed. Like the last-described wood, this is probably an ancestral Podocarp, and should be placed in the genus *Podocarpoxylon*, Gothan.

CONCLUSIONS.

There are several interesting conclusions to be drawn from these Jurassic woods of Yorkshire. The most important is the bearing of such transitional forms on the relative antiquity of the Abietineae and Araucarineae. From a study of the comparative anatomy of living representatives, Jeffrey (7) seems to have demonstrated beyond logical doubt that the Araucarineae are descended from ancestral forms which had, in the mature wood, resin canals, heavily pitted rays, wood parenchyma, and Brachyoxylon pitting. Such hypothetical ancestors are materialized in *Metacedroxylon*, *Paracupressinoxylon*, *Paracedroxylon*, &c. Fossil evidence is not of course always perfectly clear, for in many cases the Abietineous features of an Araucarian Conifer may, with equal reason, be interpreted either as persisting from a typical Abietineous form which is on the reduction path to the Araucarineae, or as incipient in an Araucarian which is on the upward way to the Abietineae. On the other hand, whenever experimental evidence is available for the study of extinct forms, such ambiguity is not possible. Thus, when these fossil Araucarian Conifers, on wounding, give rise to traumatic resin canals it seems evident that in its primitive condition the Araucarian stock had resin canals normally, and that the series is a reduction one from Abietineae to Araucarineae. There is, however, no possibility of a double interpretation in the evidence furnished by those Conifers existing at the present day. Under these circumstances the explanation which is universally applicable—both to living and extinct forms—appears beyond doubt the correct one.

Another fact leading to the same conclusion may be obtained by comparing the transitional forms of different geological horizons. In the Cretaceous the majority of these intermediate forms were of the *Brachyoxylon* type, with thin-walled rays, and a mixture of Araucarian and Abietineous pitting. In the Jurassic, on the other hand, as shown by the investigations of Gothan, Seward, Lignier, and others, the majority had thick-walled pitted rays, with a distinctly less Araucarian type of tracheary pitting. In other words, the farther back geologically we go, the more like the Abietineae do the transitional forms become.

If it be granted that the Araucarineae were derived from the Abietineous Conifers which were characterized by the possession of resin canals, wood parenchyma, and thick-walled rays, it is easy to understand how, in the course of reduction, different combinations of these features should be found in early Araucarians. Thus *Protopiceoxylon*, Gothan, is probably an Araucarian Conifer which has not yet lost its resin canals; while *Paracupressinoxylon* retains its wood parenchyma, and *Metacedroxylon* its pitted rays. Whether *Paraphyllocladoxylon* should be interpreted as a *Phyllo-*

cladoxylon in which the 'Eiporen' persist, is doubtful. There are many features in which the Araucarians and Podocarps are alike, but it still seems unlikely that it is from forms like *Phyllocladus* that the Araucarians have been derived. It seems more probable that large 'Eiporen' are in the nature of sports, without diagnostic significance. Their occurrence in forms as widely separated phylogenetically as *Pinus*, *Sciadopitys*, and *Phyllocladus* indicates such to be the case.

SUMMARY.

1. There were present in the Jurassic of Yorkshire a few typically Abietineous woods, a few typically Araucarian, and a large number intermediate between the two.

2. The character of these transitional woods corroborates other evidence—both palaeobotanical and comparative anatomical—pointing to the conclusion that the Abietineae are the oldest Conifers, and ancestral to the Araucarineae.

3. Comparative examination of living and fossil forms leads to the rejection of all criteria except cellulose bars of Sanio as an infallible test for tribal affinities. That these bars are of real diagnostic significance, and not simply incidental to the spacing of the pits, is indicated by their absence in the seedling stem of *Araucaria* and *Agathis*, where the pits are as remote as in *Pinus*, and their presence in *Protobrachyoxylon*, where the pits are as crowded as in *Araucaria* or *Cordaites*.

In conclusion, I wish to express my thanks to Professor Jeffrey for material and advice in connexion with this investigation.

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DESCRIPTION OF PLATES XXXIX AND XL.

Illustrating Miss Holden's paper on Jurassic Coniferous Woods from Yorkshire.

PLATE XXXIX.

- Fig. 1. *Xenoxylon phyllocladoides*, transverse section. × 60.
- Fig. 2. Same, radial longitudinal section. × 60.
- Fig. 3. Same, to show tracheary pitting. × 250.
- Fig. 4. Same, to show ray structure. × 250.
- Fig. 5. *Xenoxylon latiporosum*, radial section. × 40.
- Fig. 6. Same, to show tracheary pitting. × 250.
- Fig. 7. *Paraphyllocladoxylon eboracense*, radial section. × 60.
- Fig. 8. Same, to show pitting of rays. × 250.
- Fig. 9. Same, tangential section. × 60.
- Fig. 10. *Paraphyllocladoxylon araucarioides*, radial section. × 60.
- Fig. 11. *Paracupressinoxylon cedroides*, transverse section to show traumatic resin canals. × 40.
- Fig. 12. Same, radial section, showing resin canal. × 40.
- Fig. 13. Same, radial section, showing tracheary pitting. × 60.
- Fig. 14. Same, showing ray pitting. × 325.
- Fig. 15. *Paracupressinoxylon cupressoides*, transverse section. × 60.
- Fig. 16. Same, longitudinal section, showing wood parenchyma. × 60.

PLATE XL.

- Fig. 17. *Metacedroxylon araucarioides*, radial section to show radial pitting of tracheides. × 125.
- Fig. 18. Same, to show pitted rays. × 250.
- Fig. 19. Similar wood from Scarborough, transverse section. × 60.
- Fig. 20. Same, radial section, showing compressed pits and tyloses. × 60.
- Fig. 21. Same, tangential section. × 60.
- Fig. 22. *Metacedroxylon latiporosum*, transverse section. × 40.
- Fig. 23. Same, radial section. × 40.
- Fig. 24. Same, radial section, showing large pits. × 125.
- Fig. 25. *Brachyoxylon* sp., showing ray pitting. × 80.
- Fig. 26. Same, showing Araucarian tracheary pitting. × 325.
- Fig. 27. *Brachyoxylon* sp., showing septate tracheides. × 60.
- Fig. 28. *Araucarioxylon* sp., showing tracheary pitting. × 60.
- Fig. 29. *Protobrachyoxylon eboracense*, showing thin rays. × 60.
- Fig. 30. Same, showing degenerate bars of Sanio. × 325.
- Fig. 31. *Podocarpoxylon* sp., showing bars of Sanio. × 325.
- Fig. 32. *Podocarpoxylon* sp., radial section, showing terminal parenchyma. × 60.

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