Palaeo-botany. — *"Etapteris Bertrandi Scott, a new Etapteris from the Upper Carboniferous (Lower Coal-Measures) from England, and its bearing to stelar-morphological questions."* By O. POSTHUMUS. (Communicated by Prof. J. W. MOLL.)

(Communicated at the meeting of October 27, 1923).

Remains of this plant have been found in a coal-ball from Shore, Lancashire; only the petiole is known, of which a series of transverse sections has been cut by J. LOMAX. Of this series 3 sections are present in the Palaeo-botanical collection of the Mineralogical-Geological Institute of the Groningen University (N°. 140—142); besides I have seen 6 other sections in the collection of Dr. SCOTT in the British Museum (Natural History) in London (N°. 2835—2840). The species has been mentioned by Dr. SCOTT in his catalogue of the collection as Etapteris Bertrandi, and is distinguished, as he remarks, from the other species of the genus by the well developed sinus in the xylem of the vascular bundle of the petiole.

The sections in the Groningen collection, though less in number, show some features which are not present in the British Museum specimens, and enable us to form an opinion of the relation of the species to its nearest allies.

The following description is chiefly derived from the sections present in the Groningen collection.

The order of the sections is 140—141—142; I cannot give with certainty the exact place in the series of the British Museum sections, but of the series the end is in Groningen. They are all transverse sections of the petiole, which is about $2^1/_2$ mm. thick.[1])

The epidermis is wanting; it could not be made out whether assimilating tissue with intercellular spaces had existed under the epidermis, but it is unlikely from analogy with allied species. Under these missing layers we find sclerotic tissue: thick-walled cells with a narrow lumen without intercellular spaces. In its innermost part the thickness of the cell-walls decreases and the lumen is wider. The inner cortex consists of thin-walled parenchymatous tissue without intercellular spaces; it is only preserved at the extremities

[1]) The other dimensions are shown in the microphotographs which are enlarged 45 times.

of the vascular bundle near the pinna-bar; it contains scattered cells, slightly larger than the others and with a black content. In the space caused by the destruction of the inner cortex, the pigment derived from these cells, is also scattered.

The tissue surrounding the vascular bundle has been partially preserved with it. It is thin-walled without intercellular spaces; its elements, though often very indistinct, possess a narrow lumen; they are more clearly shown in some places near the pinna-bar; there the peripheral elements seem to be smaller in size than the inner ones; this tissue may be considered as phloem. It is separated from the inner cortex by a continuous double layer of tangentially elongated cells, the endodermis.

The arrangement of the xylem-tissue of the vascular-bundle in the petiole is characteristic. Its structure is in agreement with the symmetry of the petiole and its appendices. The pinnae are placed in alternating pairs, their position to the petiole is similar to that of a leaf to an erect branch: their upper side is turned towards the petiole.

A pair of pinnae is symmetrical to a plane going through the axis of the petiole and passing between the pinnae.

The vascular bundle is symmetrical to the same plane. The structure at one end of the vascular bundle will be found at a higher or lower level to be on the opposite side. This is caused by the alternation of the pairs of pinnae. It is evident by comparing analogous structures at one end with those at the other side, that the pairs of pinnae had not quite alternated, but approached the subopposite position, often also present in the fronds of existing Ferns.

In section 142 the pinna-bundles are clearly shown, passing the cortex and lying halfway between the periphery and the vascular bundle. They are surrounded by an endodermis. The xylem-tissue is nearly round, with the narrower elements (protoxylem) lying at the inner side. The outer row of trachieds seems not to be fully differentiated yet. When followed in their downward course, the two pinna-bundles fuse, thus forming the pinna-bar, a tangentially elongated reniform bundle, with two protoxylems at its inner side. This bundle is seen at different levels in section 141, 140 and 142. At a somewhat lower level it becomes more flattened, approaches the petiolar bundle and its endodermis fuses with that of the petiolar bundle. The xylem of the latter shows in transverse section the H-form, so characteristic in this genus. From a middle band, the apolar, which is slightly thickened in its middle part and consists

of relatively large elements, two arms, the antennae, are given off at each side; they are slightly recurved and prominent at the outer side at their insertion into the apolar. Thus a more or less well developed sinus is formed. The endodermis but slightly incurves on both sides of the vascular bundle.

When followed in its downward course, the pina-bar fuses with the petiolar bundle; the ends of the xylem of the pinna-bar fuse with the two prominences on both sides of the sinus (N°. 140). Thus an elliptical mass of parenchymatous, or at any rate thin-walled tissue, is enclosed. At a lower level, as seen in section 141, the pinna-bar has wholly fused with the petiolar bundle; the enclosed parenchyma has diminished in size, especially in breadth. The peripheral loop, the downwards prolongation of the pinnabar has diminished in thickness and is but a few elements thick in its middle part.

At a still lower level its continuity is interrupted; now on the surface of the rather flat xylem a deep sinus is seen, which is bordered on both sides by prominent ridges of tracheides. These become more rounded at a lower level, and the original condition is reached again.

The continuity of the peripheral loop which is formed by the fusion of the pinna-bar with the petiolar bundle occurs in 2 of the sections of the Groningen collection. It is not shown in the London specimens. But in these the well developed sinus is clearly shown; in this feature they differ much from the other species of the genus. It is on these grounds that Scott distinguishes in his Catalogue this form from the other species; it is shown here that the deeper sinus is not an independent character but caused by the fusion of the pinna-bar, when still continous, with the petiolar bundle; a feature which is aberrant from that usual in the genus.

If one tries to make a stereometrical model of this structure, the result is shown in fig. 4. In the other species of Etapteris e.g. E. Scotti Bertrand, the pinnae-bundles are also placed in pairs and fuse on their downward course in the cortex. But at a slightly lower level before their fusion with the petiolar bundle, the pinna-bar is split up, and the two bundles resulting from this division fuse independently with the vascular bundle of the petiole. An amount of parenchyma is thus never enclosed by the fusion of the petiolar bundle with the vascular tissue coming from the pinnae. That this difference with the features in E. Bertrandi is but a relative one is shown by comparing the model of the structure of E. Scotti (fig. 5) with that of the former species. Here we see the pinna-bar

fusing with the petiolar bundle. At a somewhat lower level the continuity of the peripheral loop formed by this fusion is disturbed. The interruption thus formed is limited on both sides by the downward continuation of the halfs of this peripheral loop. The xylem of the next pinna-bar fuses with the two ridges at its extremities.

In E. Scotti we see the pinna-bar approaching the petiolar bundle too. But just before its fusion with the latter it is split up in its middle part; thus two separate bundles are formed, which fuse with the petiolar bundle. We see here the same fusion with the petiolar bundle and the same interruption in the pinna-bar; but in E. Bertrandi the highest point of the interruption is below the fusion of the pinna-bar with the petiolar bundle and in E. Scotti it lies above this point.

The interruption, the height of which is different in these two species, is always limited below by the next pinna-bar. It lies above the insertion of the pinna-bar. The relative length of the interruption to the distance between two pairs of pinnae determines the condition of the transverse section. In E. Scotti the distance between two successive pairs of pinnae is but small, often the bundles of two pairs of pinnae are shown on the same side in one and the same transverse section.

Thus the structure of Etapteris Bertrandi Scott enables us to explain the features in other more complicated species of Etapteris. On the other hand it has many points in common with simpler forms, e.g. Diplolabis Römeri (Solms) Bertrand. In this plant an interruption above the insertion of the pinna-bar is present too.

If the petiolar bundle is followed here in its downward course, which Gordon's [1]) researches enable us to do, it can be shown, that the lowest pinna-bar encloses at its inner side an amount of parenchyma by the fusion of the pinna-bar with the two sides of the interruption. At a lower level the two protoxylems which are situated on both sides of the parenchyma fuse. The parenchymatous tissue diminishes in size and ends blind below.

But throughout its course to its lowest point it is in contact with the protoxylem; it seems as if the lowest part of the parenchymatous tissue follows the course of the protoxylem when penetrating into the tracheides of the metaxylem.

It is remarkable that in these plants the protoxylems are always associated with parenchyma except in the lowest part; this parenchyma, or at any rate thin-walled tissue, is situated at the adaxial

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[1]) W. T. Gordon, 1911.

side of the protoxylem. If we assume that the protoxylem was originally wholly immersed in the metaxylem, but that afterwards the development of tracheidal elements has been arrested at the inner side, except in the very lowest part, we can explain the existence of the interruption above the insertion of the pinna-bar. For when the pinna-bar approaches the petiolar bundle and fuses with it, the parenchymatous tissue at its adaxial side is enclosed. The parenchyma associated with the protoxylems of the next pinna-bar approaches in its downwards course the peripheral loop formed by the pinna-bar next above, and as the development of the procambial cells into tracheids has been arrested, a break is formed in the loop. Through this interruption the parenchyma at the inner side of the pinna-bar is connected with that enclosed by the fusion of the pinna-bar next above with the petiolar bundle. The parenchyma which is enclosed and that which lies in the sinus is formed by the fusion of the strands of parenchyma lying adaxially to the protoxylems of successive pinna-traces. These interruptions in the peripheral loop show some resemblance to the leaf-gaps in the stele of many Ferns. Here, too, parenchyma situated adaxially to the protoxylems of the leaf-trace penetrates into the xylem of the stem, either connecting the softer tissue in the interior of the stele with that without, or hollowing the xylem of the stem by the fusion of these parenchymatous formations of successive internodes. In the first case a little strand of parenchyma, ending below blindly, can be found some distance below the insertion of the leaf-trace; in the other case this funnel in the xylem is absent. The parenchyma enclosed inside the peripheral loop may be compared with the pith, formed after the second method, but the connection of the successive parenchyma-strands of successive pinna-traces is not caused by reduction in tissue which was present before (in phylogenetical sense). This structure, caused by the peculiar symmetry of the bundle, is present on both sides.

This species agrees in the form of the antennae with E. Scotti Bertr.,[1]) but differs from it by the simpler structure of the pinnae-bundles, its smaller dimensions, and the more scattered position of the idioblasts in the inner cortex. It differs from E. shorensis Bertr.[2]) by having another form of the apolar. In this species the continuity of the pinnabar is maintained for a rather long distance, but the presence of a peripheral loop has not yet been noted. A continuous

[1]) P. Bertrand, 1909, p. 140—147, 209, pl. XVI, fig. 111, 112.
[2]) P. Bertrand, 1911, p. 30—38, pl. II, fig. 23—31, 34, 35.

peripheral loop however has been found once in E. Tubicaulis Göppert sp.[1]) from Lower Carboniferous strata of Silezia, but in many other respects it is very different from the species under discussion. Perhaps E. Bertrandi may turn out to be really a portion, e.g. the highest portion of the petiole, never before observed, of some species already known, e.g. E. Scotti or E. shorensis. By its aberrant structure however it seemed to me desirable to describe this form.

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EXPLANATION OF THE PLATE.

Fig. 1—3. Etapteris Bertrandi Scott. Transverse section of the petiole; N°. 140, 141, 142 respectively.

Fig. 4. Etapteris Bertrandi Scott. Model of the xyleem tissue of the petiolar bundle (the sides of the sinus are too sharply accentuated).

Fig. 5. Etapteris Scotti Bertrand. Model of the xylem-tissue of the petiolar bundle.

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[1]) P. BERTRAND, p. 206.

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O. POSTHUMUS: "Etapteris Bertrandi Scott, a new Etapteris from the Upper Carboniferous (Lower Coal-Measures) from England, and its bearing to stelar-morphological questions".

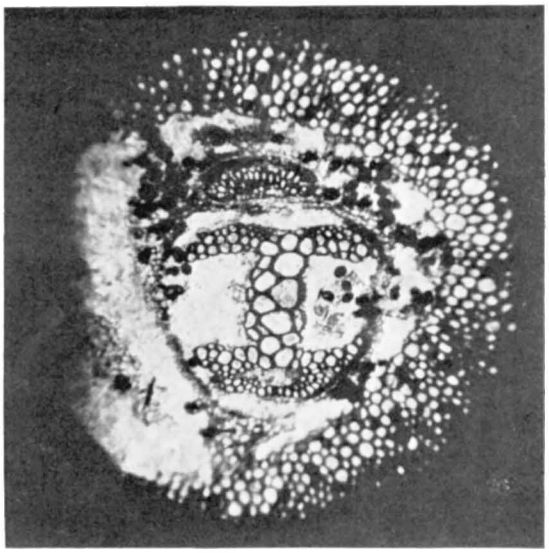

Fig. 1.

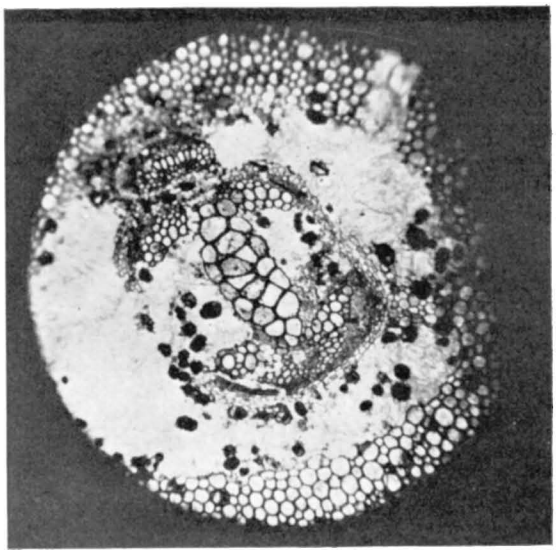

Fig. 2.

Fig. 4.

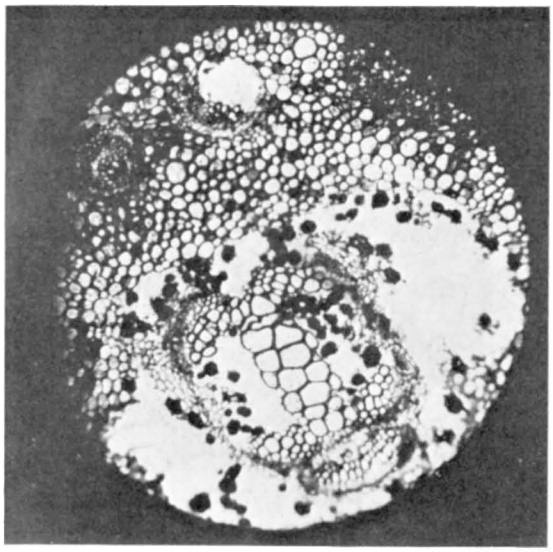

Fig. 3.

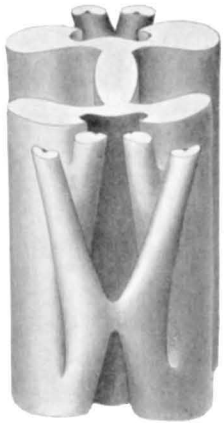

Fig. 5.