XXXIV.—*On the Structure and Affinities of a Lepidodendroid Stem from the Calciferous Sandstone of Dalmeny, Scotland, possibly identical with Lepidophloios Harcourtii* (Witham). By A. C. SEWARD, M.A., F.R.S., University Lecturer in Botany, and A. W. HILL, B.A., University Demonstrator in Botany, Cambridge. (With Plates I.–IV.)

(Read June 19, 1899.)

INTRODUCTORY.*

The unusually fine stem which forms the subject of this paper was found by Mr T. KERR, of Edinburgh, in rocks of Calciferous sandstone age exposed in a railway cutting at Dalmeny, Linlithgowshire. Mr JAMES BENNIE, of the Geological Survey of Scotland, called the attention of Mr KIDSTON to the fossil, and the latter very generously placed part of the specimen in the hands of one of us for investigation.

The photograph reproduced in Pl. I. fig. 1, for which we are indebted to the kindness of Mr J. J. H. TEALL, was taken from a polished slab of the stem in the Museum of Practical Geology, Jermyn Street. A similar specimen is in the Geological Museum, Edinburgh, and the remaining portions of the fossil are in Mr KIDSTON's possession and in the Botanical Laboratory Collection, Cambridge. A preliminary note on the structure and affinities of this Carboniferous plant was contributed to the Cambridge Philosophical Society in November 1898,† but no detailed account of the fossil has been published. A reference to the state of preservation of the tissues has also been made by one of us in a text-book published last year.‡

The specimen consists of a fairly thick piece of a stem, 33 cm. in diameter, and a polished transverse section of the block presents the appearance shown in Pl. I. fig. 1. The peripheral portion consists of a band of unequal thickness of partially disorganised bark; internal to this there is a light-coloured matrix of volcanic ash filling up the hollow trunk, and the detached central cylinder of wood and pith occupies an eccentric position close to the thicker part of the shell of bark. The marked contrast between the dark silicified plant tissues and the buff-coloured volcanic ash renders the specimen one of the most striking examples of a Palæozoic tree that has so far been discovered. The position of the larger angular fragments in the ash and of the central cylinder, point

* The numbers in brackets after the authors' names in the footnotes refer to the year of publication of the works given in the bibliography on page 928; e.g., (99) means that the paper was published in 1899.

† SEWARD and HILL (99).

‡ SEWARD (98), figs. 14, A, B, and 15, p. 83.

to the stem having been preserved in the position in which it is represented in fig. 1. The tree may have been killed by the effects of neighbouring volcanic eruptions; and after the decay and removal of the inner and more delicate cortical tissues, the hollow shell was filled with volcanic ash. Silica was the petrifying medium, and the preservation of the tissues is unusually perfect: in the central cylinder there are numerous spherulitic patches scattered through the matrix; it would seem that silicification was first completed round definite isolated centres, and this was followed by a secondary crystallisation in the matrix, which partially obliterated some of the more delicate structural features.

Several of the photographs show the concentric bands of the circular areas of crystallisation—as in Pl. I. fig. 5 and Pl. II. figs. 13–15.*

The shell of the bark consists in the main of secondary tissue, from 7 to 8 cm. in thickness, for which we shall use Von Mohl's term—Phelloderm; externally this is broken up into irregular patches, as seen in the lower part of fig. 1, by numerous longitudinal fissures, some of which were probably formed during the life of the tree. Decay, previous to the introduction of the silicifying solution, removed the greater part of the cortical tissues, but it will be shown that the lost tissue no doubt consisted of thin-walled parenchyma. The central cylinder has a diameter of 6.5 cm.; the centre is occupied by concentric bands of silica, seen as a white spot in fig. 1; surrounding this is a band of unequal breadth of pith-tissue (fig. 1) about 11 mm. in breadth, succeeded by a ring, 3 mm. in width, of primary wood x' ; beyond this is a broad zone of secondary wood x'' , 2.2 cm. in diameter (*vide* also fig. 33, Pl. IV.). External to the secondary wood some of the tissues have fortunately been clearly preserved.

A. DESCRIPTION OF THE TISSUES.

i. *Pith*.†—The band of pith (fig. 1, Pl. I.) has an irregular inner margin, where it is succeeded in the centre by concentric layers of silica; probably the pith was not quite solid in the old part of the living tree. The cells of this region are parenchymatous in form, and vary considerably in size; those in contact with the innermost tracheids of the primary wood have a more regular arrangement and a more uniform size than those towards the interior (Pl. I. fig. 4, Pl. IV. fig. 25). As we pass towards the centre of the pith, the cells become more irregular in shape, and many of them have the form of long filaments, which show a tendency to grow in a radial and more or less vertical direction, increasing in length by apical growth, and dividing by transverse walls. The general appearance of the parenchyma of the pith, especially the more internal portions, suggests an actively-growing stout hyphal tissue, comparable to the hyphæ in the

* *Vide* SEWARD, *loc. cit.*

† The term "pith" is used for the central tissue of the stele as a matter of convenience, but it would, perhaps, be better to adopt the expression "central conjunctive" [FLOT (93)]. BERTRAND has discussed the morphological nature of this region in his paper on *L. Harcourtii* [BERTRAND (91)].

medullary region of *Fucus* and other genera of large brown seaweeds, which arise as outgrowths of short elements and insinuate themselves between neighbouring cells. This form of tissue is also well known in the middle cortical region of various Lepidodendroid plants, and a similar parenchyma occurs in the cortex of some recent Lycopodiaceæ.* The photograph shown in Pl. I. fig. 4 affords distinct proof of active cell-division taking place in both the smaller external cells and in the larger filamentous cell-rows.† This phenomenon of growth in the pith is referred to in a later part of the paper. It remains to call attention to the existence of numerous elements next the primary xylem, which may be spoken of as short or isodiametric tracheids with fine scalariform and reticulate bands of thickening; these are shown in Pl. IV. fig. 25. A solitary short tracheid was observed at the inner edge of the pith-tissue, similar to those of the peripheral region. These short tracheids are of the same character as the familiar "barred-cells" of WILLIAMSON, scattered through the axial region of the central cylinder of *Lepidodendron vasculare* (Binney).‡

ii. *Primary xylem*.—The limits of the annular band of primary xylem— x' —are readily recognised in Pl. I. fig. 1. This ring of wood consists of scalariform tracheids—about 20 to 30 tracheids in breadth; the narrowest tracheids form the outer limits of the band, and the diameter of the elements increases towards the inner edge of the xylem (Pl. IV. fig. 24). The outer edge of the xylem ring or corona has an undulating outline, prominent tapering teeth, which would appear as ridges in surface-view, and shorter, broader projections alternating with bays or depressions as shown in fig. 24. The two diagrams in fig. 34, Pl. IV., illustrate the general appearance of the outline of the primary wood. The character of the xylem surface appears to agree with that of *Lepidophloios Harcourtii*, as described by BERTRAND.§ The narrowest and most external tracheids, which constitute the protoxylem, have their thickening bands rather farther apart than in the wider elements, and the scalariform type passes in some cases into a spiral form of xylem element. There does not appear to be that well-marked distinction between definite spirally thickened protoxylem elements and the larger scalariform tracheids of the primary xylem, which we find in most recent Vascular Cryptogams. In some ferns, however, the protoxylem tracheids are not clearly differentiated from the rest of the xylem. The broad scalariform pits of the tracheids in both the primary and

* BOWER (93), p. 346.

† The growth and division of pith-cells has been noticed in old coniferous stems. Cf. STRASBURGER (88), p. 88.

‡ This specific name has been adopted, following the example of Solms-Laubach, in preference to that of *Lepidodendron selaginoides* used by CARRUTHERS, WILLIAMSON, and others. In 1862 BINNEY described the internal structure of certain stems, which he named *Sigillaria vascularis* and *Lepidodendron vasculare*; these were afterwards shown to be identical. The structure of the same species was also described by CARRUTHERS [CARRUTHERS (69)], and identified by him with *L. selaginoides* of Sternberg, a determination which WILLIAMSON, who extended CARRUTHERS' account, doubtfully accepted. STERNBERG's species is, however, included by KIDSTON as a synonym of *L. Sternbergii*, Brongn. [KIDSTON (86), p. 151]. The simplest plan would seem to be to adopt BINNEY's name, as we are quite certain as to the characters of the stem to which he gave the specific name of *vascularis*. KIDSTON has included *Sigillaria vascularis*, Binney, as a synonym of *Lepidodendron Harcourtii*, Witham (*loc cit.*, p. 169), but the difference in the anatomical characters is too well marked to render their identity possible.

§ BERTRAND (91).

secondary wood are clearly bordered (Pl. IV. figs. 25, 26 and 29), and the position of the pit-closing membrane is occupied by numerous delicate threads extending from one thickening band to the next; the appearance of these in surface-view is seen in figs. 25 and 26. In tangential longitudinal section the walls of the tracheids have a double contour, and each pit-closing membrane appears to consist of a double series of irregular fine threads, which have probably been formed by the contraction and tearing of the thin membrane which originally connected the scalariform bands. Precisely similar threads occur in *Lepidodendron vasculare* (Binney),* *Lepidophloios Wunschianus* (Will.),† *L. Harcourtii* (Witham),‡ *Lepidodendron mundum* (Will.),§ *L. brevifolium* (Will.),|| *L. squamosum* (Göpp.),¶ and *Stigmaria ficoides*, Brongn.**

Count SOLMS-LAUBACH, in describing the same structure in a Culm species of *Lepidodendron*, speaks of the two sets of delicate threads, which appear as two lines in the drawing of Pl. IV. fig. 29, as probably corresponding to the "grenzhäutchen" of the tracheid wall, the middle lamella of which has disappeared. The same limiting membrane is shown in Pl. IV. fig. 26, and the irregular darker substance in the middle of each thickening band represents the shrunken internal portion of the wall. This histological feature is probably the result of post-mortem changes, and cannot be regarded as of any importance as a specific character.††

In contact with the narrower tracheids, already referred to, in the outer portions of the primary xylem, there are numerous short and more delicate elements characterised by fine spiral and reticulate thickening bands; some of these are shown in fig. 24, Pl. IV., but it is more convenient to deal with this feature in describing the origin and structure of the leaf-traces. At two points in the ring of primary xylem, indicated by . . . in the diagram, fig. 33, Pl. IV., there is an indentation occupied by thin-walled parenchyma and a few fairly large isodiametric tracheids.

iii. *Secondary xylem*.—The broad band of secondary wood consists of radially disposed scalariform tracheids of smaller diameter than the innermost elements of the primary wood. At some points the smaller internal tracheids which compose the inner ends of the rows of secondary xylem are seen in contact with the elongated narrow elements of the projecting teeth of the corona, but for the most part the rows of secondary tracheids are separated from the primary tracheids by a zone of varying breadth consisting of elements of a different type. These intervening cells ‡‡ are short or isodiametric in form, and have spiral or reticulate bands on their walls; they are, in fact, short and delicate tracheids (Pl. II. fig. 13 and Pl. IV. fig. 24). When secondary

* HOVELACQUE (92), p. 42, fig. 6. SOLMS-LAUBACH (92), pl. ii. fig. 6.

† WILLIAMSON (80), pl. xiv. fig. 4.

‡ *Ibid.* (93), p. 20.

§ *Ibid.* (89), pl. v. fig. 14 A.

|| *E.g.*, specimen 511 (Williamson Coll., British Museum).

¶ SOLMS-LAUBACH (92), p. 76.

** *Ibid.*, p. 76.

†† In a specimen of WILLIAMSON'S *Lepidodendron brevifolium*, some of the tracheids show the pit-closing membrane intact, while in others it has the form of fine threads.

‡‡ "Fibres primitives" of BERTRAND. It is probable that these elements described by BERTRAND as cells with smooth walls possessed originally reticulate thickening bands.

thickening began there were some at least of these isodiametric elements present on the surface of the corona, and additional elements of this type were formed during the process of secondary growth; but this question must be considered in more detail in connection with the leaf-traces.*

The rows of secondary tracheids are separated at intervals by bands of one, two or several rows of radially elongated elements characterised by spiral or partially reticulate thickening bands. In the stem before us there appears to be an almost complete absence of any simple unthickened parenchymatous elements in the bands of medullary-ray tissue. The nature of the medullary-ray elements is shown in Pl. I. fig. 6,† which represents the appearance of a broad "ray" as seen in a transverse section of the secondary wood, also in Pl. IV. fig. 24; in figs. 7, 30 and 32, the medullary-ray tissue is seen in longitudinal sections of the wood. In a tangential section of the secondary xylem, the medullary rays are seen to vary considerably in size, consisting of a single row of a few cells deep, or of bands of considerable length and varying breadth (Pl. IV. fig. 30); a leaf-trace may be met with in the broadest rays, as seen in transverse section, on its way through the secondary wood (Pl. I. fig. 7 *lt*, and Pl. IV. fig. 30 *lt*). In the broad medullary ray shown in the slightly oblique tangential section of the wood in Pl. I. fig. 7, it is possible by careful focussing to examine the walls of the tissue, and in every case the elements appear to possess the characteristic thickening bands. In radial section the medullary-ray elements are clearly seen in Pl. IV. fig. 32; this section shows the radially elongated form and other characters of the tissue. The simple nature of the pits in the secondary tracheids which abut on medullary-ray elements is demonstrated in Pl. IV. fig. 29.

There is the same absence of any concentric lines of growth in the secondary tracheids as in Palæozoic stems generally. Here and there, however, the uniformity in the size of the constituents of the wood is interrupted by the occurrence of groups of smaller elements suddenly abutting on the walls of the larger tracheids. This is well shown in Pl. II. fig. 11. Some of the tracheids immediately internal to the patch of smaller elements are seen to have their cavities occupied by thin-walled parenchymatous cells *t*; a similar instance of tullen in the tracheids has also been observed at one place in a longitudinal section of the wood. This local irregularity in the size of the tracheids may, no doubt, be regarded as the expression of some interference with the normal progress of secondary growth.

iv. *Leaf-trace bundles*.—The prominent ridges of the corona, as seen in Pl. IV. fig. 24, gradually detach themselves from the primary wood and constitute the leaf-traces in such manner as BERTRAND and other writers have described in various Lepidodendroid plants. For a short distance a leaf-trace pursues an almost vertical course approxi-

* WILLIAMSON and SCOTT [(94), p. 926], in their account of the secondary thickening in *Sphenophyllum plurifoliatum*, speak of part of the secondary xylem as separated from the primary xylem by a layer of thin-walled tissue.

† Cf. the medullary rays of *Stigmaria ficoides*, *Lepidodendron vasculare* (specimens 362 and 1609, Williamson Coll.), also *L. brevifolium* (No. 489), etc.

mately parallel to the surface of the primary wood. After becoming free it soon bends outwards almost at a right angle, and passes in a horizontal direction through a broad medullary ray until it reaches the limits of the secondary wood ; at this point it again ascends, bending up abruptly and appearing in transverse section just beyond the outermost secondary tracheids (Pl. II. fig. 15 *lt* and Pl. III. 16 and 19).^{*} The projecting ridges of smaller tracheids at the periphery of the primary xylem form a reticulum on the corona as seen in surface-view, and, as BERTRAND has shown in *L. Harcourtii*, the leaf-traces appear to be given off from the lower angle of the meshes. A comparison of the Dalmeny stem with the drawings in BERTRAND'S monograph leads us to consider the mode of attachment of the leaf-traces to the stele identical in the two cases. Each leaf-trace consists of a few primary elongated tracheids, accompanied by numerous thinner walled and shorter spiral and reticulately thickened elements ; these latter elements are shown in fig. 24 in contact with the central projecting leaf-trace group. When seen in a tangential section of the secondary wood, the thicker and larger tracheids of the trace are recognised as a distinct group (Pl. I. fig. 7 and Pl. IV. fig. 30) surrounded by the smaller and more delicate elements which exhibit a more or less regular radiating arrangement. As seen beyond the limits of the secondary wood, a leaf-trace presents a characteristic diploxyloid structure, which on examination reveals certain points of particular interest. There is the well-defined group of long tracheids with the narrowest elements towards the exterior, but not on the edge of the primary elements, and now the radial disposition of the smaller elements, less distinctly shown in the tangential sections previously referred to (Pl. I. fig. 7, Pl. IV. fig. 30), is very striking (Pl. II. fig. 15, Pl. III. figs. 16 and 17). The smallest and somewhat crushed primary elements occupy a position near the outer edge of the primary xylem, the leaf-trace bundle may therefore be described as mesarch (Pl. III. fig. 19 *px*). We have in each leaf-trace a group of primary tracheids partially enclosed by radially disposed rows of secondary tracheids, the latter being characterised by their smaller size and somewhat more delicate structure. The secondary xylem of each leaf-trace has usually the form of a fan, attached to the sides and outer edge of the primary xylem, but the fan-shaped secondary tissue may extend over almost the whole surface, as seen in Pl. III. fig. 16. The secondary thickening of the leaf-trace bundles is effected to some extent during their passage through the secondary wood of the stem, and further additions are made to the trace after it has passed beyond the limits of the wood of the stem. This latter point is illustrated by figs. 16 and 19, Pl. III. *m*, where the external secondary tracheids of the leaf-bundle pass gradually into thin-walled short meristematic cells. In Pl. III. fig. 21 a leaf-trace is seen in radial longitudinal section ; the limit of the secondary wood of the stem is slightly to the right of *c* ; at *a* we have some of the longer and thicker primary tracheids, and at *b* a broad band of the shorter and thinner secondary tracheids. A portion of the same section is more highly magnified in Pl. IV. fig. 28 ; *a* and *b* mark the position of the primary and secondary tracheids respectively. A tangential view of the secondary elements (fig. 21 *b*) is

^{*} Cf. MARKFELDT (85), fig. 3.

afforded by the photograph in Pl. III. fig. 23; in the upper part of the section the more internal secondary elements are shown, with their reticulate, spiral or scalariform bands, and below we have the more delicate recently formed peripheral tracheids. This section shows very clearly the meristematic tissue which has been pointed out in fig. 19; the cells have extremely thin walls and square ends; they are slightly longer than broad, as seen in tangential section (Pl. III. fig. 23 *m, m*). In Pl. III. fig. 17 the transverse section has just missed a leaf-trace, but the accompanying thin-walled meristem is clearly shown, with the cells disposed in a fan-shaped manner.

The presence of undoubted secondary xylem in the leaf-trace bundles is a fact of considerable importance from the point of view of the affinities of the plant, and as proving that the distinction insisted upon by some writers between the *Sigillariæ* of the section *Leiodermaria* and *Lepidodendroid* leaf-bundles cannot be maintained.*

Owing to the absence of the greater portion of the cortex in the Dalmeny stem, the course of the leaf-traces cannot be followed through the cortex, but the partially disorganised tissues of two traces have been met with in the outer cortical tissues. Before passing to the consideration of the outer cortex, the tissues which immediately succeed the secondary xylem, and the question of secondary growth must be dealt with.

v. *Tissues in contact with the xylem; and secondary growth of the central cylinder.*

—The first point to notice in connection with the growth of the secondary wood is the juxtaposition of small tracheids and the most external tracheids of normal size, as in the local patch shown in fig. 11, Pl. II. Instead of finding the large tracheids at the limits of the secondary wood succeeded by thinner-walled elements of the same breadth, which gradually pass into obvious cambium cells, we have a sudden transition from the wide elements (*t'*, Pl. III. fig. 19) to the much narrower elements *t' t''*. It is physically impossible that the latter should ever have been able to alter their form so as to fit on to the older and larger tracheids. It would seem that the constant association of these dissimilar tracheids at the periphery of the wood points to the existence of unfavourable conditions of growth; had the stem continued to grow, the period during which such conditions occurred would be shown by the occurrence of a ring of smaller tracheids; an extension round the whole circumference of such inequalities as are found here and there in the secondary wood (*e.g.*, Pl. II. fig. 11). It may not be unreasonable to suggest that this irregularity in the growth of the wood was due to the harmful effects of neighbouring volcanic activity. Prof. WILLIAMSON has expressed the opinion that the large Arran trees ("*Lepidodendron Wunschianum*") perished probably "in consequence of the mephitic vapours which filled the atmosphere"; the forests grew in a district "as volcanic as Auvergne." †

* In a tangential longitudinal section through the secondary wood of a specimen of *Lepidodendron vasculare* (No. 495) in the Williamson Collection, an outgoing leaf-trace seen in a wide medullary ray shows a tendency of some of the elements to arrange themselves in a fan-shaped manner like that of the secondary tracheids in Pl. I. fig. 7 and Pl. IV. fig. 30.

† WILLIAMSON (96), p. 175.

The occurrence of the narrower tracheids is in all probability merely the expression of the result of harmful conditions, and not an indication that the secondary thickening had reached its maximum extent. It might be suggested that the *Lepidodendroid* stems possessed a limited power of secondary growth, and that the stem before us represents the final stage of wood development; we find, however, that such continuous bands of smaller tracheids occasionally occur in the secondary wood of *Lepidodendron** and *Stigmaria*,† and are succeeded by larger tracheids of the normal size. A section of one of the Arran stems in the Binney Collection shows an almost continuous zone of small tracheids succeeded externally by larger elements near the periphery of the secondary wood. The elements in the region t'' of fig. 19, Pl. III. correspond more closely in size with the large xylem tracheids than do the small elements in contact with the large tracheid a . In forming the small tracheids the segments cut off from the meristem cells must have divided radially; if the radial walls were not formed, the meristem segments would approximate more closely in breadth to the tracheids of normal size. But the mechanics of secondary growth in *Lepidodendroid* stems has still to be satisfactorily explained.

Passing beyond the small tracheids (t' , figs. 16 and 19), we find a few rows of thinner-walled elongated elements, which are succeeded further out by several rows of delicate parenchymatous cells (cm , Pl. II. fig. 10, Pl. III. figs. 16 and 19). The cells composing this band of thin-walled tissue are rectangular, slightly elongated in a tangential direction, and somewhat flattened, as seen in a radial longitudinal section (Pl. II. fig. 10, cm). The thinnest and most recently formed cell-walls in this tissue occupy a radial position. In a few places the band cm may be traced continuously through the more elongated elements t'' to the narrow tracheids, but owing to the delicate nature of the parenchymatous cells the continuity of the tissue is frequently interrupted by tearing.

In Pl. II. fig. 10 we have an oblique radial section of the narrow tracheids and more external tissue; beyond the thicker tracheids t' , corresponding to t' in the transverse sections (figs. 16, 17 and 19), we have shorter and thinner elements t'' (also in the transverse sections, figs. 16, 17, 19, and the radial longitudinal section, fig. 5), which we regard as partially developed tracheids, with transverse or slightly oblique walls, and beyond these the band cm , composed of flattened cells in a state of active division. At mr , in fig. 10, a strand of flatter cells is seen passing across the tracheids: this represents the outward extension of a medullary ray (*vide* Pl. I. fig. 5). This broad band of rectangular cells we regard as the meristematic zone, which is responsible for the growth in thickness of the xylem cylinder. From the examination of the Dalmeny stem and other species of *Lepidodendroid* plants, we are led to the conclusion that, as a general rule, in *Lepidodendron* and *Lepidophloios* there was no well-defined cambium in

* WILLIAMSON (72), pl. xliii. fig. 21.

† *Ibid.* (81), pl. liii. fig. 21. Section No. 1922 H. (Williamson Coll.) shows three complete rings of smaller tracheids in the outer part of the secondary wood. *Vide* also WILLIAMSON (87), pl. iv. fig. 19.

the sense of the typical cambium of recent Gymnosperms and Dicotyledons, or of such Palæozoic plants as Calamites, Sphenophyllum, Lyginodendron, and other genera; but in its place a broader band of meristematic elements, more similar in appearance to the zone of meristem which is formed in the pericycle of certain Monocotyledons or to the meristem zone of Isoetes and other recent plants.

The leaf-trace bundles in their course through the meristematic band, *cm*, are enclosed by an arc of the cambial tissue, *m*, which furnishes additions to the rows of secondary tracheids, and internal to each trace we see some flattened rows of the meristem zone of the stem (Pl. III. figs. 16 and 19). This relation of the leaf-bundles to the cambial tissue, and the arching round them of a special leaf-trace meristem band, may be compared with the behaviour of the petiole stele in *Lyginodendron Oldhamium* (Binney) as figured by WILLIAMSON and SCOTT.*

Beyond the meristem zone *cm* there are preserved portions of a partially disorganised tissue consisting in part of large sacs and smaller, more or less crushed cells (*sc*); this zone is directly continuous internally with the outermost cells of the band *cm*, as shown in Pl. II. fig. 9. This tissue, which may be termed the secretory zone, contains numerous dark and irregular patches which most probably represent the remains of secreted substances. The large circular sacs (*sc*, figs. 9, 15, and 16), which present practically the same appearance in longitudinal as in transverse section, were no doubt secretory in function. The areas bounded by the dark lines shown in fig. 9, *sc*, Pl. II., and fig. 16, *sc*, Pl. III., may enclose some small delicate cells; it is probable that these elements constitute glandular tissues, which gave rise to latex or other products of secretion. External to this secretory zone the tissues have disappeared, and the wide gap which intervenes between this region and the outer cortex is occupied by volcanic ash. The large sac-like spaces in this zone often present the appearance of having been tangentially stretched (figs. 9 and 16).

No tissue has been found which can be described as typical phloem, but to this point reference is made in a later section of the paper. The so-called secretory zone occupies the position of phloem tissue, and may represent it physiologically. The secretory zone may probably be regarded as the outermost tissue of the stelar region.†

vi. *Outer cortex, chiefly phelloderm.*—We now come to the shell of bark already mentioned; a piece of this cortical region is shown natural size in Pl. I. fig. 2. The innermost portion consists of imperfectly preserved large parenchymatous cells of polygonal form (*a* to *b*, fig. 2); the walls of the cells have been partially destroyed, but the angles are more perfectly preserved, and small intercellular spaces occur between the individual elements. At *a* in fig. 2 the remains of a leaf-trace occur, the primary tracheids are seen in slightly oblique transverse view, and the more delicate secondary elements are crushed and displaced. As we follow the parenchymatous tissue outwards,

* WILLIAMSON and SCOTT (95), p. 712, pl. xxii. fig. 6.

† This view is supported by an examination of some unusually perfect specimens of *Lepidophloios fuliginosus* in the Binney Collection. [Since this was written the sections referred to in the Binney Collection, Cambridge, have been figured and described. *Vide* SEWARD (99).]

it is found to gradually pass over, in the region *b* of fig. 2, into regular radially disposed rows of secondary tissue consisting of narrower and more elongated cells. This secondary tissue composes the whole of the outermost cortex from *b* to the surface of the stem. The appearance of the tissue is illustrated by fig. 18, Pl. III.; the cells are of fairly uniform size, but in some rows the elements have been tangentially stretched; intercellular spaces are comparatively large and abundant. The same tissue is seen in radial section in fig. 22, and in tangential view in fig. 20, Pl. III. The regular arrangement and square ends of these elongated cells, as shown in fig. 22, is a characteristic feature of the secondary cortical tissue of *Lepidodendrea* and *Sigillariae*.* The vacuolated cell-contents seen in the tangential section, fig. 20, bear a misleading resemblance to small cells; but the cellular appearance is simply due to the manner of occurrence of the cell-contents, and may be compared with the vacuolated tannin and other substances met with in unhealthy tissues of recent plants. The most interesting feature of the phelloderm is the occurrence of seven or eight fairly regular bands of secretory cell-rows, as seen at *c* in fig. 2, and at *d*, *e*, *f*, and in other parts of the phelloderm. There is a row of distinct secretory groups or canals just internal to the innermost cells of the phelloderm (*b*, fig. 2); each of these secretory patches contains dark indistinct traces of secreted products enclosed by smaller cells lining the cavity.

The row of secretory cells at *c* consists mainly of oval and circular areas, which may be either empty or occupied by portions of thin-walled cells and products of secretion, as shown in fig. 18, Pl. III. At *d* we have a similar row of secretory patches, but in these there is rather more of the secreted material; similarly at *e* and *f* (fig. 2) there are fairly regular bands of such tissue. In these more external rows the disorganisation of the secretory elements is less advanced, and their structure is more clearly seen (Pl. II. fig. 12). The cells forming each secretory strand are much lighter in colour than the neighbouring brown cells which make up the bulk of the phelloderm. It would seem that as the phelloderm was developed from a phellogen, at fairly regular intervals groups of the phelloderm cells underwent further division, and constituted definite strands of secretory cells. In longitudinal section a secretory strand presents the appearance shown in Pl. I. fig. 3; the cells have undergone various transverse and longitudinal divisions, and some of them have become disorganised, and have given rise to dark brown secretory products. A single secretory patch of cells is shown in Pl. IV. fig. 31; this is taken from the region *f* of the phelloderm (fig. 2), and shows a central group of cells deeply coloured by the resinous or other secretion. The method of development of these secretory strands appears to have been lysigenous. The superficial resemblance of the phelloderm with its rows of canals to the wood of resinous Conifers is fairly striking; a figure given by TSCHIRCH† of the resin-ducts in the wood of *Copaifera Langdorffii* also agrees closely with our fig. 18, Pl. III.

* Cf. WILLIAMSON (72), pl. xxix. fig. 42, pl. xxxi. fig. 55; (72), pl. xliii. fig. 17; (78), pl. xxv. fig. 100. Also RENAULT (75), pl. x. fig. 11; RENAULT and GRAND'EURY (75), pls. iii. and v.; BRONGNIART (39), pl. xxvi. figs. 2 and 3; and RENAULT and ROCHE (97), pl. vi. fig. 2.

† TSCHIRCH (89), p. 217, fig. 216.

The phelloderm tissue is continued to the exterior of the fissured surface shown in the lower part of the photograph in Pl. I. fig. 1. In the upper part of the stem this secondary tissue was succeeded by the phellogen layer, and this again by the parenchyma of the leaf-cushions; probably this outermost tissue had been thrown off from the older portion of the stem during the life of the tree.*

Some secretory strands in a state of development are met with also in the neighbourhood of *g* in fig. 2, and beyond this region the phelloderm cells are less clearly preserved, and are characterised by walls of considerable thickness, the lumen being in some cases almost obliterated, and what remains of it is filled with a black substance. It is often difficult in dealing with petrified tissues to distinguish thick-walled tissue from tissue of which the cell-walls have been thickened by mineral deposition or by swelling of the membrane during mineralisation. In the present instance the cell-walls were probably fairly thick, but the thickened mass shown in the cell of Pl. IV. fig. 27 would seem to be the result of swelling of the wall, and this explanation is rendered probable by the fact that the cells of neighbouring rows are more or less flattened by pressure. The outermost portion of the phelloderm is characterised by many of the cells being tangentially elongated, and the occurrence of newly-formed radial walls in some of these elements points to the stretching being the result of growth, and not of mechanical or secondary origin. In a tangential section of the outermost phelloderm there are seen narrow bands of an opaque black substance forming an irregular anastomosing system; these dark lines extending through the imperfectly preserved tissue probably represent resinous or some other mineralised secretion.

There is another point of some interest brought out by the examination of the phelloderm connected with the leaf-traces. Reference has been made to the occurrence of two partially disorganised leaf-traces in the inner part of the outer cortex (region *a*, fig. 2, Pl. I.). In the peripheral part of the outer bark no indication of any leaf-trace xylem elements has been found, but in a radial section of the phelloderm one leaf-trace was met with in the region of the phelloderm indicated by *d* in fig. 2, Pl. I., passing outwards in an approximately horizontal direction; the xylem portion is crushed and imperfect, but sufficiently clear to enable one to easily recognise the tracheids (Pl. II. fig. 14 *tr*). The xylem is accompanied by a large patch of parenchyma composed of cells of varying shape, some of the elements having a hyphal or filamentous form. This mass of parenchyma is in marked contrast to the regular radial rows of phelloderm through which it is passing; there can be no doubt that we have here a portion of the middle cortex which accompanied the leaf-trace as the so-called parichnos (*pr*) of BERTRAND and other writers. The parichnos tissue affords an indication of the character of the lost middle cortex of which it formed a part. In tangential sections of the more external portion of the phelloderm, the mass of fibrous cells of which it consists is

* In a longitudinal section of *Lepidophloios* in the Williamson Collection (No. 1963) there appears to be an indication of an absciss layer of tissue in course of formation at the base of a leaf, suggesting that the leaf-fall was accompanied by the usual phenomenon familiar in the case of recent trees.

occasionally interrupted by the occurrence of an elongated elliptical group of parenchyma, with the cells slightly extended in a radial direction. One of these groups is shown in Pl. I. fig. 8; the cells vary considerably in size and shape, the central region consisting of smaller elements; the group shown in the photograph is about 3 mm. in length, and there is a second similar parenchymatous mass slightly above and to one side of the group shown in the figure. These parenchymatous masses agree in their structural features with the parenchyma accompanying the leaf-trace shown in Pl. II. fig. 14 *pr*, and it is probable that the more external groups like that of fig. 8 are the arms of the parichnos which have been shown by WILLIAMSON* and others to bifurcate in the more external region of the cortex in *Lepidodendroid* stems. In younger stems the two arms of a parichnos would appear on the same level as seen in a tangential section of the outermost cortex, and between them would be found the leaf-trace bundle; in the present instance we are dealing with an old trunk from which the leaves had fallen, and the parichnos arms alone persist, the vascular tissue having been gradually crushed and obliterated. It is well known that in the lower portions of large casts of *Sigillarian* stems the two large elliptical parichnos scars are often seen to lose their regular paired arrangement; one may occur at a higher level than the others, or they may appear as separate areas with no definite order.†

B. AFFINITIES OF THE DALMENY PLANT.

In the foregoing description no reference has been made to the relationship of the stem to other *Lepidodendrea*. The size of the stem and its anatomical characteristics at once suggest a comparison with the famous Arran species described by WILLIAMSON and others. We have no doubt as to the specific identity of the Dalmeny and Arran trees; an examination of the series of sections of the Arran plant in the Williamson Collection (British Museum) reveals an identity in structural features. The Dalmeny specimen is, however, much more perfectly preserved, and enables us to considerably extend the diagnosis of the species.

The fossil trees of Arran were discovered by Mr WÜNSCH‡ in volcanic beds of Calcareous sandstone age at Laggan Bay, and briefly described by him in 1867. He refers to the large stems as apparently *Sigillarian*, containing five or six "internal piths"; the smaller branches he identifies with *Sigillaria*, *Halonia*, and *Lepidodendron*. CARRUTHERS§ afterwards visited the locality and gave a short account of the fossil stems; he speaks of having traced the radiating branches of a *Stigmara* to a large trunk of *Sigillaria*, and describes the internal "piths" of WÜNSCH as young stems which had grown from spores carried into the hollow trunk of a large tree. CARRUTHERS|| proposed the name *Lepidodendron Wünschianum* in 1869 for a species from Arran in

* WILLIAMSON (93), pls. iii. and iv.

† RENAULT (96), p. 770. *Vide* also RENAULT and ROCHE (97), p. 17, where this point is referred to in the description of a silicified *Syringodendron* stem.

‡ WÜNSCH (67), p. 97. *Vide* also LYELL (78), p. 547, and SEWARD (98), p. 89.

§ CARRUTHERS (69), p. 178.

|| *Ibid.* (69), p. 6.

his possession, but no diagnosis of the plant is given. In 1871 BINNEY * described three new *Lepidostrobus* from the Arran volcanic beds, and to one of these, a heterosporous form, he gives the name *Lepidostrobus Wüschianus*. In 1880 WILLIAMSON published an account of the Arran *Lepidodendron*,† in which he described and figured small twigs with a solid "vascular axis" (stele), and larger branches and stems with a parenchymatous axial region enclosed by a ring of wood. He regarded the smaller specimens as representing different stages in the growth of the large trunks, and discussed the evidence in favour of a gradual increase in diameter of the axial tissues, and the conversion of a solid vascular stele to a larger stele with a central parenchyma. In 1883 the same author‡ gave an account of an Halonial branch from Arran which with good reason he referred to the plant previously described. Ten years later WILLIAMSON made a brief reference to BINNEY'S Arran *Lepidostrobus*, and in the second part of his Index,§ published in that year, he speaks of the Laggan Bay plant as *Lepidodendron Wüschianum* (Will.), having hitherto refrained from the use of a specific name in dealing with the "Arran *Lepidodendron*." Finally in 1895 WILLIAMSON || gave a summary of his work on this species, and again discussed the question of growth and modification of the stele during the development of the stem.

SOLMS-LAUBACH ¶ has dealt at some length with WILLIAMSON'S views on the growth of the Arran stems, and points out the physical impossibilities involved in some of the suggested explanations of the conversion of small solid steles into large steles with a wide central parenchyma. We must regard the various forms described by WILLIAMSON as representing, in part at least, branches of different orders, but all belonging to one specific type.

In a footnote to a paper in which some account is given of the Arran species, KIDSTON ** adds that the plant should be referred to the genus *Lepidophloios* and not to *Lepidodendron*, if WILLIAMSON was correct in connecting the Halonial branches which he described in 1883 with the large Laggan Bay trunks.††

It would necessitate an unreasonable extension of the paper to discuss in detail and to illustrate by drawings the numerous points of interest as regards the comparative anatomy of the *Lepidodendreae* which are suggested by an examination of the Dalmeny specimen. There are certain considerations, however, which must be briefly touched on, as they have a direct bearing on the question of the systematic position of the plant. To deal first with the Arran plant, which should be designated *Lepidophloios Wüschianus*.

The large stems represented by various sections in the British Museum ‡‡ and in the Binney Collection, Cambridge, and by a magnificent specimen in the Owens College Museum, agree closely in size as well as in structure with the Dalmeny fossil. There

* BINNEY (71), p. 56, pl. xi.

† WILLIAMSON (80).

‡ *Ibid.* (83), p. 466.

§ *Ibid.* (93), p. 15.

|| *Ibid.* (95), p. 43.

** KIDSTON (97), p. 40.

¶ SOLMS-LAUBACH (91), p. 229. *Vide* also BERTRAND (91), p. 40.

†† For the evidence in favour of the connection between Halonial branches and *Lepidophloios*, *vide* KIDSTON (93), pp. 539 *et seq.*

‡‡ *E.g.*, sections Nos. 451, 452, etc.

are the same hyphal cells in the centre of the stele, the same spirally thickened elements in the medullary rays,* and an identity of structure in the primary and secondary wood. Isodiametric tracheids also occur internal to the primary xylem cylinder, as in the Dalmeny stem.† Unfortunately, the large Arran stems do not afford any positive evidence as to the structure of the leaf-trace after it becomes free from the secondary wood, the tissue in the innermost cortical region having been almost completely destroyed. In one section a leaf-trace with both primary and secondary elements was found close to the edge of the wood, but the fan-shaped group of secondary elements was directed inwards and not outwards as in the Dalmeny stem; as the trace is isolated and not enclosed in tissue, it has no doubt been twisted, and indeed it may not improbably belong to a *Stigmara* and not to the stem with which it is associated.

The phelloderm of the Arran trunks is identical with that which we have described, there are the same rows of secretory strands as in our stem,‡ and in tangential sections of the phelloderm elliptical groups of cells are met with identical with that of Pl. I. fig. 8, which we regard as the parichnos.§ Passing to the smaller specimens, we may first mention the specimen represented in pl. xiv. fig. 5 of WILLIAMSON's tenth Memoir.|| One important fact to notice in connection with this example is the very small amount of secondary xylem in a stem about 12 cm. in diameter. Here, again, there is the closest agreement with the Dalmeny stem as regards the structure of the wood and cortical tissues; the large sac-like cells shown in our Pl. II. figs. 9 and 15, and Pl. III. fig. 16, are clearly seen in WILLIAMSON's figured section. The middle portion of the cortex in WILLIAMSON's specimen presents the characteristic structure which is shown in the parichnos, or portion of the inner cortex accompanying the leaf-trace, represented in our Pl. I. fig. 8. The small twigs described by WILLIAMSON show fairly well-preserved leaf-cushions, and the form of these, as seen in longitudinal section, suggests the *Lepidophloios* rather than the true *Lepidodendron* type. In the smaller axes, 1·2 cm. in diameter, there is no trace of secondary xylem, but each leaf-trace is accompanied by numerous short and spirally thickened tracheids, which in a transverse section of a leaf are seen to be arranged round the strand of elongated scalariform tracheids; their position and appearance recall the transfusion tissue of many recent plants.¶ These short tracheids are well shown also in longitudinal sections of the leaf-trace on the flanks of the tracheal strand.** The solid xylem strand occupying the axis of the small twig may indicate that these are slender shoots of an *Halonial* branch; their stele agrees

* The thin-walled spirally thickened elements accompanying the leaf-traces in their course through the secondary wood are clearly shown also in *Lepidodendron brevifolium*, Will. (cf. especially No. 499), and in *Stigmara*, *L. vasculare*, etc.

† Cf. section 448 A.

‡ These secretory groups of cells are exceedingly well shown in some sections of the phelloderm of the largest Arran stem in the Binney Collection, Cambridge, as well as in British Museum sections. Similar cell-groups have been observed in sections of *L. vasculare*; cf. also HOVELACQUE (92), p. 58, fig. 17.

§ E.g., sections 443, 447, 448, 449 in the Williamson Coll.; cf. also sections of *Sigillaria* (662 and 665).

|| WILLIAMSON (80).

¶ E.g., sections Nos. 431, 432, etc. (Williamson Coll.).

** Cf. section 1955, and several others in the British Museum.

closely with the small vascular strands given off from the stele of the larger *Halonias* described by WILLIAMSON in 1883. In the small twigs the two arms of the parichnos, composed of large thin-walled cells, are found in close proximity to the leaf-trace bundles, as seen in the fleshy leaf-bases.* In the older stems from which the leaves have fallen, and in which a considerable thickness of phelloderm has been developed, the leaf-trace becomes disorganised on its way through the outer cortex, and the parichnos strands lose to some extent their regularity of arrangement; their cells, too, appear to be somewhat compressed by the pressure of the mass of phelloderm, through which the parichnos is passing. The cells in the parichnos figured in Pl. I. fig. 8 are rather smaller and more compact than those in the parichnos arm of a leaf-base.

The Williamson Collection includes one specimen of a piece of rock from Arran (No. 62) which shows imperfect surface markings in the form of lozenge-shaped depressions, which no doubt represent the leaf-bases of a *Lepidodendroid* plant, but the preservation is far from satisfactory, and we have no proof of the connection between this cast and the petrified stems.

There is a specimen of *Lepidophloios Wüschianus* in the fossil-plant gallery of the British Museum, from the Calcareous sandstone of Craigleith (No. 52,625), which represents a stem with two steles 1 cm. in diameter; the stem has been cut across transversely just below the point at which the two branches of the bifurcating axis became free. It is interesting as showing the absence of secondary wood, although the section measures 19 by 14 cm.; this is one of the characters shared by *L. Wüschianus* and the stems known as *L. Harcourtii*.

We may next consider the question as to the possible identity of the Arran and Dalmeny stems with plants described under other specific names. There are many points of resemblance between these stems and the diploxyloid axes from Burntisland, named by WILLIAMSON *Lepidodendron brevifolium*,† but a comparison of the structural features does not lead us to regard the latter form as specifically identical with the Arran and Dalmeny species. There are various characteristics shared by WILLIAMSON'S species, *Lepidophloios fuliginosus* (Will.), and *L. Wüschianus* (Will.), but the former species is no doubt distinct; the nature of its secondary xylem and other features prove it to be a well-defined specific type.

The most interesting comparison‡ is with the species long known as *Lepidodendron Harcourtii* (Witham). The plant bearing this name was first described and figured by WITHAM,§ and afterwards by LINDLEY and HUTTON in their Fossil Flora||; subsequently more accurate figures were given by BRONGNIART¶ in 1837 and 1839.

* Cf. sections 428, 443, etc.

† WILLIAMSON (72), p. 310. In the index (Pt. II.), published in 1893, WILLIAMSON speaks of this species as *Lepidophloios* (p. 10).

‡ For the opinions expressed as to the possible identity of the Dalmeny plant and *L. Harcourtii*, one of us must be held responsible (A. C. S.).

§ WITHAM (32) and (33), p. 51, Pls. xii. and xiii.

|| LINDLEY and HUTTON (33), vol. ii. pls. xcvi. and xcix.

¶ BRONGNIART (37), pls. xx. and xxi.; (39), pls. xxx. and xxxi.

The specimen on which the species was founded was presented by the Rev. C. G. V. Vernon Harcourt to Mr Phillips of York, and the latter forwarded it in 1832 to Mr WITHAM, who named the fossil *Lepidodendron Harcourtii*. It was found, as we are told by the authors of the Fossil Flora, in the roofstone of a bed of coal worked at Hesley Heath, near Rothbury in Northumberland. The seam is considered by LINDLEY and HUTTON to occupy a position "deep in the Mountain Limestone series." * WITHAM published several rather crude figures of the internal structure, and compared the anatomy of the stem with that of *Lycopodium clavatum*; he agreed with BRONGNIART'S conclusion, based on external characters, that the *Lepidodendra* should be regarded as Lycopodiaceous plants. WITHAM'S figures and descriptive text are repeated in his important work of 1833. Other drawings are given in the "Fossil Flora," but these are in many respects far from accurate. ADOLPHE BRONGNIART † afterwards published a few additional drawings in his *Histoire des végétaux fossiles* and in his classic paper on *Sigillaria elegans*. Under the name *Lepidodendron Harcourtii*, BINNEY ‡ described some exceedingly fine specimens from the Coal-measures near Dudley, but these belong most probably to the type since named by WILLIAMSON § *L. fuliginosum*.

WILLIAMSON in his latest paper, published in 1895, || calls attention to the probability that, like *Lepidophloios Wienschianus*, *L. Harcourtii* developed secondary xylem at a comparatively late period of its growth. BERTRAND ¶ has also expressed similar views as to the late appearance of the secondary wood in the latter species.

An exceedingly detailed account of *Lepidophloios Harcourtii* was published in 1891 by Prof. BERTRAND ** of Lille; this author draws attention to the close similarity between this species and the plant figured by CORDA †† in 1845 as *Lomatofloios crassicule*.

The chief characteristic features usually associated with *L. Harcourtii* are (i) the absence or late appearance of secondary wood; (ii) the nature of the leaf-trace bundles, which consist of a strand of xylem tracheids accompanied by a group of "bast fibres"; (iii) the presence of numerous prominently projecting teeth from the surface of the corona; (iv) the usual absence of the middle cortical tissues. In 1887 WILLIAMSON ‡‡ contributed a note to the Royal Society, in which he proposed the name *Lepidodendron fuliginosum* for certain specimens incorrectly described as *L. Harcourtii*; he mentioned the "duplex structure" of the leaf-trace bundle as a special distinguishing feature of WITHAM'S specific type. SOLMS-LAUBACH §§ especially compares *L. Harcourtii* and WILLIAMSON'S *L. fuliginosum*, suggesting for the latter the specific name of *Williamsoni* |||; he refers to the presence of the bast-fibres in *L. Harcourtii* as one of

* LINDLEY and HUTTON, *loc. cit.*, p. 45.

† BINNEY (72), p. 77.

‡ *Ibid.* (95), p. 47.

†† CORDA (45), pl. iii.

||| The change of name suggested by Count SOLMS seems inadvisable, as the older name given to the species by WILLIAMSON has been generally recognised.

† BRONGNIART (37), pls. xx. and xxi.

§ WILLIAMSON (87), *vide also* (93), p. 3.

¶ BERTRAND (91), p. 150.

** *Ibid.* (91).

‡‡ WILLIAMSON (87), p. 7.

§§ SOLMS-LAUBACH (91), p. 226.

the distinguishing features between the two species. There are other differences which need not be considered here, as they are well known and apparently constant. The "bast-fibres" of the leaf-trace are referred to by BERTRAND* as consisting in part of possibly laticiferous tubes, and that they are not bast fibres but brown secretory cells is, we believe, the true explanation. Precisely similar groups of indistinctly preserved cells accompany the leaf-traces of *L. fuliginosum*, and these two are composed of a few partially-disorganised secretory elements. A comparative examination of the species *Lepidophloios Harcourtii*, *L. fuliginosus*, and *L. Wüschianus* shows that in each of these plants there is a fairly broad zone of secretory tissue a short distance beyond the xylem, as shown in several of the photographs of the Dalmeny stem. As the xylem tracheids of a leaf-trace pass into this zone they appear to carry in front of them a patch of the secretory tissue. A leaf-trace bundle when seen immediately external to the primary xylem of the stem has no strand of the so-called fibres accompanying it; but immediately beyond the secretory zone the second strand is present, and it consists, we believe, not of true fibres, but of somewhat crushed or partially-disorganised secretory cells.† This behaviour of the trace is very clearly demonstrated in some sections of *L. fuliginosus*, figured by BINNEY‡ under the name of *L. Harcourtii*, and now in the Woodwardian Museum, also in several sections of *L. Wüschianus*§ and *L. Harcourtii* in the British Museum. A more detailed account will be given of the Binney sections in another place.||

Another point of resemblance between *L. Harcourtii* and the Dalmeny plant is the occurrence of strands of secretory cells in the outer cortical region. In the type-specimen of WITHAM'S species there are a few large canals near the periphery of the partially decorticated specimen; and in the large stem from Airdrie¶ we find large canals just internal to the phelloderm precisely as in the Dalmeny stem, as well as other canals in the phelloderm tissue. In the Dalmeny plant the secretory areas immediately internal to the phelloderm (region *b* Pl. I. fig. 2) are rather larger than those in the phelloderm; in *L. Harcourtii* there is the same slight difference between the more internal and external canals.** BERTRAND†† has figured a secretory area in the cortex of a specimen of *L. Harcourtii* received from M. HOVELACQUE.

The short tracheids which occur in the inner margin of the primary wood of the Dalmeny stem (Pl. IV. fig. 25) are clearly represented in *L. Harcourtii*.‡‡ The margin of the corona in *L. Harcourtii* and in the Dalmeny stem is, we believe, identical, and the leaf-traces apparently become detached from the main mass of xylem in the same manner (figs. 24 and 34). The mesarch structure of the leaf-traces is another character shared by *L. Harcourtii* §§ and the Scotch plant; the same feature is well shown in

* BERTRAND (91), p. 119.

† Cf. specimen 448A, 456A, etc.

‡ BINNEY (72), pls. xiii. and xv. Cf. also specimens 1922A, 384, etc., in the Williamson Collection.

§ E.g., sections Nos. 465, 448A, 428.

|| [Since this was written a description of Binney's specimens has been published in the *Proceedings of the Cambridge Philosophical Society*, vol. x. p. 137; vide SEWARD (99).]

¶ Figured by WILLIAMSON (93), pl. i. fig. 3.

** Cf. specimens Nos. 1593, 380, 381.

†† BERTRAND (91), pl. v. fig. 26.

‡‡ Specimen No. 381.

§§ *Ibid.* (91).

some exceedingly well-preserved sections of *L. fuliginosus*, originally described by BINNEY as *Lepidodendron Harcourtii* and as *Halonina*.*

There are no anatomical characteristics shown in the type-specimen of *L. Harcourtii* nor in the larger stem from Airdrie,† which cannot be matched, more or less exactly, in the Dalmeny and Arran species. This resemblance in structure agrees also with the geological horizon from which the type-specimen of WITHAM was obtained.

We have no precise information as to the geological age of the larger stem of *L. Harcourtii* described by WILLIAMSON from Airdrie; the matrix in which the specimen is embedded bears a close resemblance to that of the Dalmeny tree. There are, however, other examples‡ of what appears to be *L. Harcourtii* from the lower Coal-measures of Lancashire and Yorkshire, but of the identity of these we do not wish to speak with certainty at present. To be consistent with our belief of the specific identity of WITHAM's type and the larger Airdrie stem with the Dalmeny stem, the latter should be spoken of as *L. Harcourtii* (Witham).

The conspicuous gaps accompanying the leaf-trace bundles, as seen in a transverse section of the outer cortical regions of the stems of *L. Harcourtii* hitherto figured, are not present in the large stem which we have described. The size of the parichnos, part of which is shown in Pl. II. fig. 14 *pr*, agrees with the large dimensions of this organ in the smaller specimens, and the absence of the gaps in the phelloderm-band in the Dalmeny stem is in all probability due to the considerable development of phello-derm, which compressed, and to a large extent obliterated, the parichnos tissue of the leaf-traces which were no longer connected with leaves, as the older stems were leafless. The slightly more prominent and obvious tooth-like projections of the corona in the smaller stems may be accounted for by the presence of the broad zone of secondary wood, but the long and narrow prominences shown in Pl. IV. figs. 24 and 34 are indeed very similar to those of the smaller examples of *L. Harcourtii*.

WILLIAMSON's nineteenth Memoir, the last of the splendid series which he communicated as sole author to the Royal Society, concludes with the paragraph: "We have at least arrived at one result from the investigations recorded in the preceding pages; we now know that *L. Harcourtii* was not a distinct form, teaching an independent and special philosophy. So far as its history is now known, it is substantially identical with that of the other known *Lepidodendra*, teaching the same truths, and leading to the same inferences. We only want, in my opinion, to discover it in its arborescent condition to place it side by side with *L. Wüschianum* as a true typical exogenous Lycopod, and with which it has several external close relationships." §

In the Dalmeny stem, and in the much less perfect stems from Arran, we have most probably this "arborescent" form which WILLIAMSON refers to.

* BINNEY (72). [*Vide* also SEWARD (99).]

† Section No. 380 (received by Prof. Williamson from the late Prof. Balfour of Edinburgh).

‡ Specimens No. 1596A, 380B, etc., in the Williamson Collection [*vide* WILLIAMSON (93), pl. i.].

§ WILLIAMSON (93), p. 29.

In considering the affinities of the Dalmeny stem reference must be made to a specimen recently described by RENAULT and ROCHE* from the Culm of Esnost under the name *Syringodendron esnostense*. The petrified block shows several spirally disposed elliptical areas on the weathered surface, which represents the ends of parenchymatous cell-groups, called by the authors *organes aerifères*. Internally there is a segment of a band of secondary wood 20 mm. in diameter, succeeded by portions of an annular zone of primary wood and a large pith. Beyond the secondary wood, and separated from it by a space filled with siliceous material and plant débris, there is a broad band of secondary cortex described as consisting of concentric zones of "suber." In a tangential section of the secondary wood some broad medullary rays are represented containing diploxyloid † vascular bundles passing horizontally outwards, practically identical with our Pl. I. fig. 7. One of the vascular strands is also shown in transverse section immediately beyond the secondary wood of the stem, agreeing closely with the leaf-trace bundles of the Dalmeny stem (e.g., Pl. III. figs. 16 and 19). These bundles are described as passing out to branches, and the true leaf-traces are considered to have been obliterated as the stem had most probably lost its leaves; one small and indistinct bundle is shown in a tangential section of the wood passing through one of the broad rays traversed by a "branch-bundle," which RENAULT and ROCHE speak of as a foliar vascular strand. It would seem, however, much more probable that the diploxyloid xylem strands are the true leaf-traces.

There is, in fact, the closest resemblance between the French and Scotch stems, and if not specifically identical, the two must be very nearly allied. The photograph of the "concentric bands" of secondary cortex suggests a comparison of the fairly regular lines, which break the regularity of the radially disposed phelloderm cells, with the rows of secretory strands in the Dalmeny plant. The elliptical groups of cells visible externally as slightly projecting areas in the French stem agree in structure, except in their somewhat larger dimensions, with the parichnos strands met with in tangential sections of the Arran and Dalmeny stems.

The old name *Syringodendron*, usually regarded as standing for a partially decorticated and old Sigillarian trunk, is used by RENAULT and ROCHE as an autonomous genus on the grounds that the parichnos strands occur singly and not in pairs, and that no evidence has been found suggesting the formation of the single groups by the fusion of two originally separate arms. These reasons seem hardly sufficient for raising *Syringodendron* to generic rank. In *Syringodendron esnostense* we have in all probability an old stem—very closely allied to the Dalmeny species—which was most probably either a Sigillaria, a *Lepidodendron*, or a *Lepidophloios*. To discuss this question would involve us in an examination of the anatomical and other characteristics which distinguish these three genera. The structure of *Lepidodendron* and *Lepidophloios* is

* RENAULT and ROCHE (97).

† The term "diploxyloid" is used by RENAULT to describe vascular tissue consisting of primary (generally centripetal) xylem and secondary centrifugal xylem; he includes under this head the leaf-traces of Cycads, which are now termed Mesarch by many writers; they are not truly diploxyloid in that they consist of primary xylem only.

practically identical, and there are at least some Sigillarian stems * in which we cannot discover any structural features distinct from those of the *Lepidodendreae*. Reasons have already been given for regarding the Dalmeny stem as a *Lepidophloios*, but whether the younger stems and branches of the French stem should be recognised as belonging to *Lepidodendron*, *Lepidophloios*, or *Sigillaria* must remain an open question. This uncertainty as to the respective anatomical characteristics of these three genera is perhaps a reason in favour of retaining such a generic term as *Syringodendron*.

CONCLUSION.

The more important anatomical features of the Dalmeny species may be briefly summarised as follows :—

- i. The diploxyloid and mesarch leaf-trace bundles.
- ii. The numerous canals or secretory strands of parenchyma in the phelloderm.†
- iii. The presence of a fairly regular ring of rather larger secretory strands immediately internal to the secondary cortical tissue (phelloderm).
- iv. The presence of short tracheids on the inner edge of the primary xylem, and the numerous and more delicate short tracheal elements external to the corona.
- v. The delicate and lax nature of the broad inner cortex.
- vi. The parenchymatous pith, which consists in part of elongated cell-filaments, especially in the larger stems; in smaller branches the pith is solid and composed of more regular cells.

The character of the parichnos, the nature of the secondary xylem, the presence of a band of secretory tissue in the innermost cortex and other features are not peculiar to this type of the *Lepidodendreae*. The characters enumerated in the above list must not be regarded as being of specific rank, some at least are certainly shared by allied forms. We are much in need of an exhaustive comparative account of the *Lepidodendroid* species from which to select features common to the various types and others which may serve as specific characters. The apparent absence of typical phloem has been briefly referred to in the above description; this is probably a character shared by other species of *Lepidophloios* and *Lepidodendron*; it would seem that we have as yet no satisfactory evidence in these genera of the existence of tissue possessing the ordinary anatomical characters of phloem, and probably the functions associated with the phloem of

* *E.g.*, a specimen described by CARRUTHERS at the Edinburgh British Association Meeting in 1892; but the account was not published in the Annual Report. [Since the above was written a Sigillarian stem has been described by Prof. BERTRAND which throws fresh light on the anatomy of this genus. Vide *Annals of Botany*, 1899.]

† We have observed similar secretory strands in the phelloderm of *L. vasculare* as well as in other species already referred to. [*Cf.* also a figure by HOVELACQUE (92), in which strands appear to be indicated.]

recent plants must in the Palæozoic types have been carried out by tissues of another kind and of a more primitive character. This question will be dealt with in a forthcoming account of some exceedingly well-preserved examples of *Lepidophloios fuliginosus* (Will.).* It is a remarkable fact that there is no band of tissue which can be spoken of as secondary phloem at all comparable in extent to the secondary xylem. The absence of any well-defined initial meristem layer or typical cambium is another point of general interest. The meristem zone in the Dalmeny stem is separated from the newest tracheids by a comparatively broad band of cells, the elements of which appear to assume more gradually the form of xylem tracheids than is the case with most plants which possess the power of secondary growth; we should speak of a cambial zone rather than a cambium layer as constituting the generative region from which the wood was supplied with new elements.

The thick band of secondary cortex, described as phelloderm, is a character common to the Lepidodendra and Sigillariæ generally. The meristem-zone, which arises just internal to the leaf-cushions, at an early stage in the growth of these plants gives rise to little or no tissue on the outside, but on the other hand produces internally a considerable thickness of radially disposed elongated elements, and some of these cells undergo further divisions to form strands of secretory tissue; from analogy with other plants one may speak of the internal secondary cortex as phelloderm, a tissue with a fairly well-developed aërating system of intercellular spaces. The cork of recent plants, in the sense of an impermeable tissue developed on the outside of the phellogen, is barely represented. It may be noted that WORSDELL has described a thick band of phelloderm in the stems of *Cycas media*, R. Br.,† and *Macrozamia*.‡

When we consider the small diameter of the woody central cylinder, as shown in Pl. I. fig. 1, in comparison with the size of the stem as a whole, the usefulness of the wood as a mechanical support to enable the stem to resist lateral strains would seem to have been extremely small. May we not regard the thick phelloderm of the fossil stem as a tissue of which one of the functions was mechanical; a strengthening band at the periphery of the stem corresponding to the hypodermal stereome or to the peripheral region of secondary wood in recent plants?§

The exact significance of secretory products in recent plants is by no means well understood, and seeing that we cannot determine the nature of the secretions in fossil tissues, we are not in a position to do more than hazard a guess as to the function of the glandular tissue. The abundance of secretory canals in so many of the Palæozoic genera is an interesting fact, and one which, with further data derived from physiological anatomical considerations, may help us to learn something as to the conditions under which these plants grew.

In the outermost stelar region of Lepidodendra the large secretory sacs form a striking feature, and the close connection between strands of this secretory zone and the outgoing leaf-trace reminds one of the large secretory strands which are met with in the

* [SEWARD (99).] † WORSDELL (98), p. 443. ‡ *Ibid.* (96), p. 615. § Cf. HABERLANDT (96), p. 163.

cortex of *Lycopodium inundatum* (Linn.), and other species, and associated with the foliar bundles of some Cycads.* It is possible that the secretory zone of Lepidophloios had some share in the conduction of plastic organic substances, while the secretory tissue of the phelloderm fulfilled a different purpose.

The abundance of short and comparatively thin-walled tracheids is a question which invites speculation as to the possibility of connecting certain anatomical characters with the habit of growth of these Palæozoic Lepidodendrea. Some at least of these elements suggest a comparison with the transfusion tissue † of recent plants, to which reference has already been made, and at the same time there is the possibility that in these short tracheal cells we may have representatives of what have been called "Speichertracheiden." ‡ There are, indeed, indications in the anatomical features of the Dalmeny Lepidophloios that the conditions of growth were such as to require the development of characters usually associated with a xerophytic habit. The existence of striking xerophytic peculiarities in recent plants which inhabit seashore regions, as well as those of arid regions, teaches the need of extreme caution in attempting to deduce from anatomical data conclusions as to the environment of Palæozoic species. On the whole, we are disposed to see in the presence of xerophytic characteristics an indication that some at least of the Carboniferous plants grew in seashore swamps under conditions which necessitated the development of halophytic peculiarities.

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* Cf. WORSDELL (96).

† Vide WORSDELL (97), ZIMMERMANN (80), etc. Short tracheids, similar to those of Lepidophloios, accompanying the petiolar bundles have recently been described by SCOTT in *Medullosa anglica*. An excellent example of transfusion tissue in a fossil conifer has been figured by SOLMS-LAUBACH in *Ullmannia* [SOLMS-LAUBACH (84), pl. iii.].

‡ HABERLANDT (96), p. 354. [In a new genus recently described under the name *Megaloxylon*, the abundance of large short tracheids, which probably served as reservoirs of water, is a characteristic feature. [Vide SEWARD (99).]

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EXPLANATION OF PLATES.

[The photographs reproduced in Pl. I. fig. 6, and Pl. III. figs. 20 and 22, were kindly supplied by Mr Kidston; all the other micro-photographs have been taken by Mr W. Tams, Cambridge.]†

PLATE I.

Fig. 1. Transverse section of the stem. *p*, pith; *x'*, primary wood; *x*, secondary wood. *Circ.* $\frac{1}{4}$ nat. size.

Fig. 2. Portion of the outermost cortex, mainly composed of phelloderm, which extends from *b* to the surface of the stem. *a*, position of a leaf-trace; *b g*, regions referred to in the text. Nat. size.

Fig. 3. Longitudinal section of a secretory strand in the phelloderm. $\times 100$.

Fig. 4. Longitudinal section of the pith, and portions of two xylem tracheids. $\times 100$.

Fig. 5. Longitudinal section through the edge of the secondary wood. *t'*, narrow tracheids; *t''*, thinner and shorter elements representing partially developed tracheids; *mr*, medullary ray. $\times 80$.

Fig. 6. Part of a medullary ray as seen in a transverse section of the secondary xylem. $\times 190$.

Fig. 7. Tangential section of the secondary wood, showing a broad medullary ray and a leaf-trace, *lt*. $\times 90$.

Fig. 8. Tangential section of the phelloderm showing a mass of parenchyma (parichnos) cut through transversely. $\times 80$.

PLATE II.

Fig. 9. Transverse section of the secretory zone. *Sc. cm*, outer portion of the meristematic region. $\times 100$.

Fig. 10. Radial longitudinal section, slightly oblique, of the outermost portion of the secondary xylem and neighbouring tissue. *t'* and *t''*, new and partially developed tracheids; *cm*, meristematic tissue. $\times 80$.

Fig. 11. Transverse section of the secondary wood, showing a group of smaller tracheids. *t*, tullen in the cavities of two tracheids. $\times 120$.

Fig. 12. Transverse section of the phelloderm, with a row of secretory cell-groups. $\times 80$.

Fig. 13. Radial longitudinal section through the junction of the primary and secondary xylem (*x'* and *x''*). $\times 90$.

Fig. 14. Radial longitudinal section through the phelloderm, passing through a leaf-trace with partially disorganised tracheids *tr* and the parichnos *pr*. $\times 60$.

Fig. 15. Transverse section through the stelar region and the outer edge of the secondary wood. *t*, leaf-traces; *sc*, secretory zone. $\times 50$.

PLATE III.

Fig. 16. Transverse section through the secretory zone *sc*, the meristem-zone *cm*, and the edge of the wood; *t'* and *t''*, tracheids; *m*, meristem cells surrounding the secondary tissue of a leaf-trace. $\times 90$.

Fig. 17. From the same region as fig. 16, passing through a fan-shaped group of meristem cells. $\times 90$.

Fig. 18. Transverse section of the phelloderm showing some older secretory canals. $\times 80$.

Fig. 19. Transverse section of the outer edge of the secondary xylem, *t' t''*, the meristem region, *cm*, and a leaf-trace with its cambium arc, *m*. $\times 100$.

Fig. 20. Tangential section of phelloderm cells with vacuolated cell-contents. $\times 80$.

Fig. 21. Oblique radial longitudinal section of a leaf-trace, showing the primary and secondary xylem, *a*, *b* and *c*, region close to the secondary xylem. *sc*, secretory zone. $\times 100$.

Fig. 22. Radial longitudinal section of phelloderm cells. $\times 50$.

Fig. 23. Tangential section of a portion of a leaf-trace. *m*, meristematic cells. $\times 120$.

PLATE IV.

Fig. 24. Transverse section showing the corona (*x'*) and secondary xylem (*x''*). $\times 50$.

Fig. 25. Radial longitudinal section of one of the large innermost tracheids of the primary xylem, with some small isodiametric tracheids in the peripheral region of the pith. $\times 90$.

Fig. 26. Bordered pits with fine threads in the wall of a tracheid. $\times 240$.

Fig. 27. A cell from the phelloderm (outer portion) with thickened wall. $\times 100$.

Fig. 28. Portion of fig. 21, Pl. III., more highly magnified.

Fig. 29. Tangential longitudinal section showing the double bordered pits in the walls of adjacent tracheids, and the single bordered pits between the tracheids and medullary-ray cells. $\times 240$.

Fig. 30. Tangential longitudinal section of the secondary xylem showing a leaf-trace in a medullary ray. $\times 50$.

Fig. 31. A secretory group of cells in the phelloderm. $\times 90$.

Fig. 32. Radial longitudinal section showing a medullary ray traversing the secondary xylem. $\times 50$.

Fig. 33. Diagram of the annular primary xylem *x'*, with remains of pith. The dots . mark the position of two indentations in the ring of wood.

Fig. 34. Diagrams illustrating the external contour of the corona.

SEWARD & HILL: STRUCTURE AND AFFINITIES OF A LEPIDODENDROID STEM
FROM THE CALCIFEROUS SANDSTONE OF DALMENY—PLATE I.

SEWARD & HILL: STRUCTURE AND AFFINITIES OF A LEPIDODENDROID STEM
FROM THE CALCIFEROUS SANDSTONE OF DALMENY.—PLATE II.

SEWARD & HILL: STRUCTURE AND AFFINITIES OF A LEPIDODENDROID STEM
FROM THE CALCIFEROUS SANDSTONE OF DALMENY — PLATE III.

18.

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SEWARD & HILL: STRUCTURE AND AFFINITIES OF A LEPIDODENDROID STEM
FROM THE CALCIFEROUS SANDSTONE OF DALMENY — PLATE IV.