IV. *On the Structure of* Sigillaria scutellata, Brongn., *and other Eusigillarian Stems, in Comparison with those of other Palæozoic Lycopods.*

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[Plates 14–16.]

Contents.

1. Introduction.

Among the fragments of plant remains, the structure of which is preserved for us in the coal balls of the Lower Coal Measures of Lancashire and Yorkshire, Sigillarian stems have hitherto proved to be extremely infrequent. This fact has not escaped notice.

WILLIAMSON,* in 1872, remarked that "considering the abundance of Sigillariæ in the Coal-measures, it is marvellous that *indisputable* specimens displaying their internal organisation should be so rare; but such is the case." Dr. SCOTT, in 1900, suggested that the rarity of such stems in the petrified state may be due to the infrequent occurrence of branching, "for, of course, it is in the case of small branches, rather than of great trunks, that petrifaction, such as to preserve the tissues, is most likely to have occurred.†

The recent reopening of a coal working at Shore-Littleborough, in Lancashire, rich in calcareous nodules containing plant petrifactions, a mine which is now, thanks to the liberality of Mr. W. H. SUTCLIFFE, F.G.S., being worked solely for the coal balls, has, however, resulted in the discovery of several well-preserved stems of ribbed Sigillarias of the *Rhytidolepis* type, which are described here. These specimens have been obtained by Mr. LOMAX, one by one, as the result of a special search for this material, extending from July 1904 until the beginning of the present year (1907).‡ Our thanks are due to him for the trouble he has taken to obtain the petrifactions, and for the skill with which he has prepared the sections.

The classification of Sigillarian stems, at present adopted, is the twofold system instituted by the German Palæobotanist, the late Professor C. E. WEISS,§ in 1889, and is based on their external morphology.

In the Eusigillarian type, the stems are ribbed; in the Subsigillarian type there are no ribs. In each case two subdivisions of these groups have been generally recognised.

Eusigillariæ.—Stems ribbed.

Rhytidolepis.—Ribs separated by straight, vertical furrows. Leaf-bases usually distant, as broad as, or narrower than, the ribs.

Favularia.—Ribs separated by zig-zag, or flexuous furrows. Leaf-bases often approximate, and as broad as the ribs.

Subsigillariæ.—Stems without ribs.

Clathraria.—Leaf-scars borne on approximate leaf-bases, which are separated one from the other by oblique furrows.

Leiodermaria.—No leaf-bases. Leaf-scars distant.

It is now well known that impressions have been found which combine the characters of some of these sub-groups, or may even show a transition from the Eusigillarian to the Subsigillarian type of stem. While, therefore, it is recognised that this classification has little intrinsic value, it is still retained as a useful method of roughly grouping many of the commoner species of Sigillarian stems.

* WILLIAMSON ('72), p. 212.

† SCOTT ('00), p. 196.

‡ See Bibliography, —— ('06), —— ('07).

§ C. E. WEISS ('89), p. 379.

It is satisfactory to record that, including the present communication, we are now acquainted with the structure of stems belonging to all four of these sub-groups. The following account completes the list by the first, full description of a Eusigillarian stem of the *Rhytidolepis* sub-group, in which the external features are sufficiently well preserved to permit of specific determination.

We would here express our sincere thanks to Dr. D. H. Scott, F.R.S., for valuable suggestions, and for the loan of several sections from his collection. We would also record our indebtedness to a grant from the Committee on "the Structure of Fossil Plants," of Section K, of the British Association, whereby the cost of obtaining the material has been defrayed.

2. Historical.

The specimens of Sigillaria which have been previously described and which show internal structure, are very few in number. The earliest account is that, by Brongniart,* of a stem, now referred to *Sigillaria Menardi*, Brongn., a member of the Clathrarian sub-group. In 1875, Renault and Grand'Eury† described *Sigillaria spinulosa* (Rost), a Leiodermarian stem.

Until 1905, when Mr. Kidston‡ published a paper on the structure of *Sigillaria elegans*, Brongn., a Favularian species not to be confounded with the specimen which Brongniart also described by mistake under this name, no complete memoir on a Eusigillarian stem had appeared.

Though the present paper contains the first, full account of a Sigillarian stem of the Rhytidolepis sub-group, there have, however, been published previously short notes on specimens of ribbed Sigillarias by several authors. The evidence which was presented was, in all cases, very incomplete. Passing over Dawson's§ attribution of a petrified stem to this genus, which, with very little doubt, was of Cordaitean affinity, we may notice that Williamson‖ figured, in addition to some Diploxylons, two specimens showing the bark of a ribbed Sigillaria, probably belonging to the Rhytidolepis section. We may disregard the first¶ of these, but the second,** which Williamson described as unmistakably referable to the "group of *S. Saulii*, *S. Schlotheimii* and *scutellata*," is undoubtedly a species belonging to this sub-group, in which the leaf-scars are distant from one another. This petrifaction will be further described in the present paper.

* Brongniart ('39), Corda ('45), Renault ('79), p. 262; ('80), p. 143; ('96), p. 200.

† Renault and Grand'Eury ('76); also Renault ('79), p. 264; ('80), p. 138; ('96), p. 208.

‡ Kidston ('05[1]).

§ Dawson ('71), pp. 147 and 149, Plate 10.

‖ Williamson ('72).

¶ Williamson ('72), p. 212, Plate 29, figs. 35 and 36; Plate 28, figs. 37 and 38.

** Williamson ('72), p. 213, Plate 29, figs. 39, 40, and 42; Plate 30, fig. 41.

Some years later, WILLIAMSON* briefly noted that two sections from Halifax in his collection (Nos. 651, 652) were referable to a ribbed species, *Sigillaria reniformis*, but these specimens were never described. It is exceedingly improbable that WILLIAMSON was correct as regards the specific identification, for, as KIDSTON has pointed out, this species of *Sigillaria* is unknown from as low an horizon as the Lower Coal Measures, from which the petrifaction was derived. Certainly an examination of the two sections mentioned by WILLIAMSON does not confirm his conclusion, and these specimens need not be further considered here.

In a short communication, without figures, published in 1899, Professor BERTRAND† described a Sigillaria of the Rhytidolepis sub-section, derived from the Hardinghen district of the Pas-de-Calais Coalfield. It was regarded as probably identical with *Sigillaria elongata*, BRONGN. This important note will be further discussed at a later stage.

In 1900, Dr. SCOTT‡ published a figure of a transverse section of an English stem of the Rhytidolepis sub-group with a brief description. The whereabouts of this section is unknown to us, but we think it not improbable that it was cut from the petrifaction described here as Specimen C.

The above-mentioned references complete the list of the previous literature on the structure of Sigillarian stems of the Rhytidolepis type. We have, however, received from Mr. KIDSTON,§ just as the present paper was completed, a copy of a short preliminary note on the structure of *Sigillaria mamillaris*, BRONGN., and *S. scutellata*, BRONGN.

3. THE MATERIAL.

The more important specimen described here (Specimen A) consists of a petrifaction containing two well-preserved Sigillarian stems, lying side by side. They are both capable of specific determination. In addition, several other examples have been obtained from various sources, all of which contain stems of a Sigillaria of the Rhytidolepis section, and belong to a species or species with distant leaf-scars like Specimen A. It is not, however, possible to determine the actual species in any instance. But the structure of these petrifactions agrees so exactly with the example on which our description is chiefly based, that we have not hesitated to make use of them to amplify or to illustrate the evidence which it presents.

It may be well here to briefly enumerate the various specimens, which form the material of our description.

Specimen A.—*Sigillaria scutellata*, BRONGN.
(Plate 14, figs. 1–4, 6; Plate 16, figs. 2, 4, 5, 10.)

This specimen, one of the last to reach us, was received from Mr. LOMAX on April 20, 1906. It was found at Shore-Littleborough, Lancashire. Mr. LOMAX was

* WILLIAMSON ('93[1]), p. 36, and also p. 35.

† BERTRAND ('99).

‡ SCOTT ('00), p. 207, fig. 80.

§ KIDSTON ('07).

fortunately able to uncover the external surface of the ribs of both stems (Plate 14, figs. 2 and 4), and these agree specifically with the impressions known as *Sigillaria scutellata*, Brongn. This specimen will be fully described at a later stage.

Specimen B.—*A Eusigillarian Stem of the Rhytidolepis Type.*

(Plate 15, figs. 1, 2, 4, 6.)

On March 1, 1906, we received from Mr. Lomax a beautifully preserved Sigillarian stem, also derived from Shore. An attempt had been made to uncover the external surface of the ribs (Plate 15, fig. 4), but with much less success than in the case of Specimen A. It is impossible to determine the species in this instance, but there is little doubt that the leaf-scars were fairly distant from one another, and that the stem belonged to the Rhytidolepis section.

Specimen C.—*A Eusigillarian Stem of the Rhytidolepis Type.*

(Plate 14, fig. 5; Plate 15, figs. 3, 8, 10; Plate 16, fig. 9.)

The third specimen described here is one which Professor Boyd Dawkins informs one of us he obtained from the Lower Coal Measures, near Oldham, more than thirty years ago. The petrifaction later found a home in the Botanical Department of the British Museum (Nat. Hist.), from which it was more recently transferred to the Geological Department, where it is now incorporated in the "General Collection of Sections of Fossil Plants." It is represented by a small fragment of the original petrifaction (Reg. No. V. 8935) and five sections in different directions (Reg. No. V. 10981–5). A few years ago three additional sections (Reg. No. V. 8931–3) were cut from the same specimen. Some of the older sections are labelled *Sigillaria Saulii*?

The existence of this specimen has been long known, and though it has never been fully described, it has been referred to by several writers. Renault,* in 1879, mentioned a specimen showing a fragment of the bark of *S. Saulii* and also a detached vascular cylinder, obtained from the neighbourhood of Manchester by M. Grand'Eury, the structure of which he states is analogous to that of Brongniart's *Sigillaria elegans* (= *S. Menardi*, Brongn.). It is possible, though by no means certain, that Renault is here referring to some of the earlier sections made from the present specimen.

Williamson and Hartog,† in 1882, mentioned a *Sigillaria* with the bark of *S. Saulii* in Mr. Carruther's cabinet, and this reference again probably relates to our Specimen C. Solms‡ also noted the existence of this fossil.

* Renault ('79), p. 238.

† Williamson and Hartog ('82), p. 342; see also Williamson ('93[1]), p. 35.

‡ Solms ('91), p. 254.

The section figured and described by SCOTT* in 1900 was also derived from this specimen, but the actual section is unknown to us, and those which we have been able to trace as having been cut from this petrifaction do not agree at all exactly with the one he figures.

The external surface of the present specimen has been exposed, but the only portion of the petrifaction which we have seen is too fragmentary to permit of specific determination. There is no doubt, however, from the existing radial and tangential sections, that this Sigillaria is of the Rhytidolepis type, and belongs to a species with distant leaf-scars.

Specimens showing only the Bark of Sigillarias of the Rhytidolepis Section.

Specimen D (Plate 16, fig. 8).

This specimen was obtained from Shore-Littleborough. We received several tangential and radial sections from it in August, 1904.

Specimen E (Plate 15, fig. 5; Plate 16, fig. 11).

This specimen, of which the external surface of the ribs is exposed (Plate 15, fig. 5), reached us on February 23, 1905. It was obtained from Dulesgate, Lancashire, and is probably identical with *Sigillaria scutellata*.

Specimen F (Plate 15, fig. 11; Plate 16, figs. 6, 7).

The sections from Oldham, figured by WILLIAMSON (see p. 135) in his second memoir on p. 213, Plate 29, figs. 39, 40, 42, and Plate 30, fig. 41 (Nos. 653, 654 in the WILLIAMSON Collection) has been re-examined by us. The petrifaction from which these sections were cut is unknown, but from the longitudinal section there is little doubt that the stem bore distant leaf-scars, and was of the Rhytidolepis sub-group.†

Specimen G (Plate 15, fig. 9; Plate 16, fig. 3).

Among the petrifactions belonging to the BINNEY Collection of the University of Cambridge, one has been found to contain some well preserved bark of a Sigillaria of the Rhytidolepis section with distant leaf-scars. Sections‡ from this material were made in August, 1907.

* SCOTT ('00), p. 207, fig. 80.

† There is, in the General Collection of Sections in the Geological Department, British Museum (Nat. Hist.), another petrifaction (Reg. No. V. 8937) of the bark of a ribbed Sigillaria, the external surface of which is very well preserved. Only a single transverse section of the ribs apparently exists, and the history of the specimen is unknown to us. It did not appear to us to be necessary to have longitudinal sections made from this petrifaction, for the structure of the bark is amply illustrated by our own material.

‡ Nos. AN 8–AN 19, Sedgwick Museum, Cambridge.

Specimen H.—*A Eusigillarian Stem of the Rhytidolepis Type* (Plate 15, fig. 7).

This specimen, also derived from Shore, Lancashire, was one of the earliest received by us, in July, 1904.

4. The Structure of *Sigillaria scutellata*, Brongn.

We now pass to a detailed account of the structure of Specimen A, the external surface of which is referable to the species *Sigillaria scutellata*, Brongn., supplementing the evidence by that afforded from the other specimens of ribbed stems belonging to the Rhytidolepis section with distant leaf-scars.

(*a*) *The External Surface.*

The petrifaction contains two stems lying side by side, which are seen in transverse section on Plate 14, fig. 1. The upper one (*a*) shows about nine ribs on each side, and also a fragment of the stele. The lower (*b*) exhibits about the same number of ribs, and the stele (*st.*) though crushed, is fairly well preserved on the upper side. It is probable that these two stems belonged to different plants, for branching is believed to have been comparatively rare in this genus. The external surface of the ribs of the upper stem (*a*) is seen on Plate 14, fig. 2, where three ribs, bearing well-preserved leaf-scars, are figured. These are identical in character with the impressions of *Sigillaria scutellata*, Brongn., such as are figured on Plate 14, figs. 7 and 8.

The external surface of the lower stem (*b*) is figured on Plate 14, fig. 4. The preservation here is much less perfect, but on one or two of the ribs the leaf-scars can be made out, and there is little doubt that the stem belongs to the same species, *S. scutellata*, Brongn. The internal structure, at any rate, is identical with that of the other stem.

(*b*) *The Stele.*

The stele consists of a ring of primary, centripetal wood, surrounded by a zone of secondary, centrifugal xylem. There was a well-marked pith, but the tissue in this region is not preserved in any of the specimens which we have seen, and the pith cavity is usually obliterated by the lateral crushing which the stem has undergone. In the lower stem (*b*) of Specimen A, a portion of which is shown enlarged four times on Plate 14, fig. 3, the stele, which measures 1·5 cm. along its greater axis, is badly crushed laterally. The ring of primary wood is seen at x^1. The secondary wood (x^2) is well seen on the upper side, but is very fragmentary below. Only the inner part of this tissue is preserved, the outer portion, as well as the phloem, being absent.

The primary wood in all the Sigillarias, attributed to the Rhytidolepis sub-group, which we have seen, forms a perfectly continuous ring. Mr. Kidston* has found

* Kidston ('05[1]).

that this is also the case in his specimen of *S. scutellata*,* and also in *S. mamillaris* and *S. elegans*, the latter a Favularian type. We know, however, that in some Sigillarias belonging to the Subsigillariæ, the primary wood was aggregated in isolated strands. In the present specimen (Plate 14, fig. 6) the breadth of the ring is about 1 mm. The elements consist entirely of scalariform tracheides, usually somewhat hexagonal in transverse section, the largest being midway between the inner and outer margins of the ring. Those abutting on the grooves of the corona tend to be rather more radially arranged than those in proximity to the teeth. We have not detected any well-marked annular or spiral elements in the protoxylem (Plate 15, fig. 3).

The outer margin of the primary wood is crenulate, the protoxylem groups forming the ridges (Plate 14, figs. 5, 6, Plate 15, fig. 1). This corona is not very distinct, for the ridges are only of moderate prominence, and, in comparison with those of a *Lepidophloios*, might be termed blunt. Mr. KIDSTON† has pointed out that in his specimen also "the outer margin of the primary xylem is very feebly crenulated." This region is well seen on Plate 14, fig. 6, a photograph of a transverse section of Specimen A in the possession of Dr. SCOTT (No. 2300), which he has most kindly lent to us. With this may be compared Plate 14, fig. 5 (Specimen C), and Plate 15, fig. 1 (Specimen B). A radial section cut from Specimen C is seen on Plate 15, fig. 3, which shows the primary (x^1) and secondary wood (x^2) as well as the protoxylem (*px.*).

The secondary wood, a tissue present in all the specimens of Eusigillarian stems which we have examined, forms a well-developed zone, only part of which is preserved in Specimen A (Plate 14, fig. 6, x^2). It consists of elongated tracheides arranged in radial rows. These elements are seen in radial section on Plate 15, fig. 3 (Specimen C), and in tangential section on Plate 15, fig. 6 (Specimen B). They are precisely similar to those of the primary wood, but are of smaller diameter. The outer margin of this tissue is preserved in Specimen C, and is distinctly crenulated, the ridges of the primary wood corresponding with the ridges of the secondary. The secondary zone here measures 4·5–5 mm. in diameter.

The medullary rays, both primary and secondary, are numerous, and generally consist of a single row of cells of varying height (see Plate 14, fig. 6, Plate 15, fig. 3, and Plate 15, fig. 6, *m.r.*). Some of the walls of the rays, as seen in transverse section, are transversely thickened. Mr. KIDSTON has also observed the occurrence of these thickenings in the case of *S. elegans*.

(*c*) *The Periderm.*

All the thin-walled tissues external to the secondary xylem, including the cambium, phloem, and primary cortex, as well as the leaf-traces in the latter region,

* KIDSTON ('07).

† KIDSTON ('07), p. 205.

have perished in every specimen of the ribbed Sigillarias which we have seen. The external tissues of our Sigillarian stems invariably consist of a well-marked periderm of greater or less extent. We have not obtained any example of a very young stem, in which this secondary tissue is absent. For reasons which will be discussed somewhat later, we think it highly probable that even the young stems possessed ribs.

In a transverse section of the ribs, the periderm (*pd.*) and the leaf-bases (*l.b.*), formed of parenchymatous elements, are easily recognised, where, as is usually the case, the section passes through one or more of the latter (compare Plate 14, fig. 3, Plate 15, figs. 2 and 8). Where no parenchymatous cushion appears at the outer margin of the rib and the periderm almost extends to the surface, the section has been cut between the leaf-bases borne on that rib.

The question of the exact origin of the thick-walled, secondary cortical tissue is a difficult one. This has also proved to be the case with regard to the bark of *Lepidodendron*. HOVELACQUE* concluded that, in *Lepidodendron selaginoides*, this tissue was of the nature of cork formed externally to a phellogen. SCOTT† has, however, pointed out that the meristematic zone occurs outside the periderm, and, therefore, the bark is really of the nature of phelloderm.

The latter appears to be true of *Sigillaria*, though we have not been able to distinguish any definite cambial layer in any of our specimens, and the internal margin of the thick-walled tissue is invariably badly preserved. That the secondary tissue found here is really of the nature of phelloderm we think extremely probable for the following reasons. Although there is no definite cambium outside the phelloderm, there are often some cells to be found (Plate 15, fig. 8) in the parenchymatous tissue immediately bordering on the secondary cortex which have the appearance of having recently divided. Further, the tangential walls of the outer of the radially arranged elements of the periderm are often much closer together than those lying more internally, and, further, they are distinctly thinner.

It would thus appear likely, so far as the imperfect evidence will permit us to judge, that the secondary tissue is really phelloderm, and that the phellogen was of a periodic nature and not a persistent tissue. The latter conclusion is supported by the fact that, in some transverse sections of the phelloderm, definite rings of growth can be seen, like those found in the bark of some Lepidodendrons. This is well seen in the periderm of Specimen H.

The elements of the phelloderm are thick-walled prosenchyma, usually somewhat elongated longitudinally, and prismatic in shape. They are seen in transverse section on Plate 15, fig. 8 (Specimen C), Plate 15, fig. 9 (Specimen G), in radial on Plate 16, fig. 6 (Specimen F), and Plate 15, fig. 11 (Specimen E), and in tangential

* HOVELACQUE ('92), p. 56, fig. 16.

† SCOTT ('00), p. 139.

section on Plate 16, fig. 5 (Specimen A), and fig. 8 (Specimen D). Plate 15, fig. 7 (Specimen H), shows the entire depth of a rib. Some of these fibres, especially in the deeper portions of the phelloderm, are chambered. The radial arrangement of the cells is usually very marked. The breadth of the periderm varies from about 5 mm. in Specimen E to 3·5 mm. in Specimen A.

(*d*) *The Leaf-bases.*

Before describing the structure of the leaf-bases, we may inquire into the exact morphological nature of the ribs, a point on which we differ from some previous authors.

Solms* states that "the longitudinal ribs of the stem of Rhytidolepis originate in the coalescence of the leaf cushions which stand vertically one above another." Also that "an indication of the separate leaf cushions which have united to form the ribs is very often shown in the serpentine course of the furrows, which is due to the circumstance that the cushions are broadest at the insertion of the leaves and narrow downwards, so that every leaf-scar lies on a knot-like swelling of the rib."

Renault† says "dans les Sigillaires cannelées, *Favularia tessellata*, *Fav. Saulii*, les côtes longitudinales dues à de vraies cannelures sont très appréciables sur la surface interne de la zone subéreuse."

Scott,‡ in his "Studies," concludes that "the ribs may be looked upon as representing a series of fused leaf-bases, a view which is supported by the fact that the ligular pit, which must clearly have belonged to the leaf-base, is placed on the rib immediately above each leaf-scar."

The structure of the ribs of a Sigillarian stem of the Rhytidolepis section with distant leaf-scars, such as *Sigillaria scutellata*, Brongn., is fully illustrated by the material described here. The leaf-bases, consisting of parenchymatous elements, form, in the uncrushed condition, bracket-shaped projections from the surface of the rib, the sloping shelf of the bracket bearing the leaf-scar and also the ligular pit (see text-fig. on next page). Apart from the projecting leaf-bases the greater portion of the thickness of the rib is formed by the phelloderm. External to the phelloderm, both in the case of the ribs and the grooves between them, a thin layer of primary cortical tissue persists. This forms the actual surface of the rib both above and below the successive leaf-bases, for the latter, in *Sigillaria scutellata*, are neither confluent with, nor even approximate to, each other.

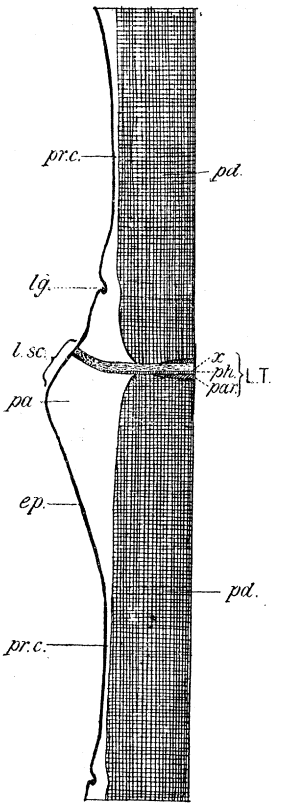
The structure of the ribs may be best illustrated by a comparison of radial sections of the petrifactions (see text-fig. on next page and Plate 15, fig. 7) with *impressions* of the stem of this species, and with the external surface of the ribs of the upper stem

* Solms ('91), pp. 242–3.

† Renault ('96), p. 202.

‡ Scott ('00), p. 191.

of Specimen A (Plate 14, fig. 2). In many impressions, such as that from Newcastle,* figured on Plate 14, fig. 8, the leaf-bases, before or during preservation, have become greatly compressed, and, further, the whole series of ribs have been flattened by pressure. One cannot here distinguish the leaf-bases. The shape of the leaf-scars of this species, however, is well seen. In others, such as the impression figured on Plate 14, fig. 7, from the Middle Coal Measures of Dudley, South Staffordshire,† the ribs have escaped crushing, and are seen in the natural condition (*cf.* Plate 14, fig. 2). This specimen, although slightly decorticated in places, is very instructive in comparison with the petrifactions described here.



TEXT-FIG.—Diagrammatic representation of part of a rib of *Sigillaria scutellata*, BRONGN. *ep.* = epidermis; *pr. c.* = primary cortex (unshaded); *pd.* = periderm; *pa.* = parenchyma of leaf-base; *l.sc.* = position of leaf-scar; *lg.* = ligular pit; L.T. = leaf-trace; *x.* = xylem of leaf-trace; *ph.* = phloem of leaf-trace; and *par.* = parichnos.

The leaf-bases stand out prominently, and though the parenchymatous tissues of the greater part of the leaf-scar, and of the leaf-base immediately above the leaf-scar, are not preserved, the limits of the leaf-base below each scar are roughly but clearly indicated by the extent of the smooth surface. The fibrous-looking appearance of other portions of the ribs represents the phelloderm, which is here exposed by the slight decortication which the stem has suffered, whereby the thin layer of primary cortex between the leaf-bases, and also part of the upper portion of each leaf-base, has been removed.

Thus we see that the ribs are formed of cortical tissues and persistent leaf-bases, the thickness of the rib being greatest at the external angle of each bracket-shaped leaf-base, and least at the short interval between the upper limit of one leaf-base and the lower limit of the next above it on the same rib.

It is doubtful whether, strictly speaking, the leaf-bases can be regarded as forming part of the rib in a morphological sense. They may, perhaps, be better looked upon simply as bracket-like projections from it, for the following reasons. It would seem quite probable that the stem was ribbed at a much younger stage than is seen in any of the specimens described here, and before the secondary cortical tissues had begun to appear. It may, indeed, be imagined that, at the growing point of the stem, before

* No. 751. Carbon. Plant Coll., Sedgwick Museum, Cambridge.

† V. 1232, Geological Department, British Museum (Nat. Hist.).

even the leaf primordia arose, the outlines of the ribs would be laid down in the dermatogen. As the leaves developed the ribs became more clearly marked out, and the leaf primordia only arose on the ribbed portion of the stem. Further, the base of the leaf was strongly decurrent. It is also conceivable that the leaf was fully developed before secondary cortical tissues were formed. At this stage we should find a ribbed stem, the outer tissues of which no doubt consisted of a thin-walled primary cortex, protected by an epidermal layer externally. The ribs would bear long, linear, or lanceolate leaves, with decurrent leaf-bases, arranged in vertical rows.

Next we have the beginnings of secondary cortical tissue, laid down by a periodic, perhaps at first a persistent, meristematic zone. It is conceivable that at this period the leaves were still attached to the stem, but whether that was the case or not is really immaterial to the argument. For, when the leaf fell, the point of detachment was not at the surface of the rib, but at some slight distance from it, and the decurrent leaf-base persisted. It is, however, important to remember that there is every indication that the phellogen only gave origin to secondary tissues on the *inner* side, *i.e.*, to phelloderm. Thus while increase in the diameter of the stem was provided for, the primary tissues external to the meristem remained practically unchanged. For the phellogen did not arise in the external layer of the primary cortex, but in the hypoderm, at a short distance from the surface. Thus the ribs, like the grooves, consisting originally of primary cortical tissues, are in the specimens described here largely formed of phelloderm, and a few layers of the primary cortex, which lay external to the secondary meristem, and which have persisted. The leaf-bases which clothe the ribs cannot, therefore, be regarded as forming the ribs any more than they form the grooves between the ribs.

This interpretation is supported by the following considerations. The position of the secondary meristem forming the phelloderm is indicated by the curved or sinuate external boundary of that tissue, whether viewed in transverse (Plate 15, fig. 2) or in radial section (Plate 15, fig. 7). It is thus obvious that this cambium arose in close relation to the ribs and grooves, which already existed on the external surface of the stem. Even in the grooves (Plate 15, fig. 2, ribs on lower side), the primary tissues still persist outside the phelloderm, and between the consecutive leaf-bases of a rib (Plate 15, fig. 7, *p.c.*) this is also the case. Further, the phellogen arose in a position in conformity with the form of the decurrent leaves or leaf-bases, as is plainly seen by the sinuate external limit of the phelloderm, concave to the leaf-base, shown on Plate 15, fig. 7.

Thus we are not surprised to find in stems like Specimen B (Plate 15, fig. 2), where the phelloderm development has been slight, that the ridges and grooves are as pronounced as in those where the secondary cortex is much more highly developed.

We have dwelt upon this point in some detail for, as we have seen, other interpretations have been put upon the structure of the ribs of Sigillarias of the Rhytido-

lepis section. Before we discuss it further, it may be well to compare briefly the external features of the Rhytidolepis species, *Sigillaria scutellata*, BRONGN., with those of Sigillarias belonging to other sub-groups. In the Subsigillareæ, *e.g.*, *Sigillaria Menardi*, BRONGN., and *S. spinulosa* (ROST) the stems are not ribbed, but in the former species a periderm occurs, which is apparently similar to that of the species described here. In *Sigillaria spinulosa*, however, the structure is very different, especially in the arrangement of the periderm elements, which form an open network. In this species, also, definite leaf-bases are absent, though they are present in *S. Menardi*, BRONGN.

In Eusigillarian stems of the Favularia section, the ribs are formed of cortical tissues in much the same way as in *Sigillaria scutellata*. As regards *Sigillaria elegans*, Mr. KIDSTON* has recently concluded that the ribs must "probably be regarded as composed of the confluent persistent leaf-bases and a small portion of the underlying periderm." We have also examined a Favularian species, but with a somewhat different result. In such a stem the leaf-bases, instead of having a bracket-like form, are roughly hexagonal, and sometimes broader than long. Further, the successive leaf-bases borne on the same rib are closely approximated, though in our specimen they do not appear to be united to one another. Thus each rib is closely set with an armour of broad, persistent leaf-bases, throughout its entire length, and no portion of the rib is exposed externally. While this close investment of leaf-bases adds greatly to the apparent thickness of the rib, a real rib is present, quite distinct from the leaf-bases, as any transverse section through a rib, cut between two leaf-bases, will show. The structure of the periderm in the Favularian stem appears to be identical with that which we have described here, and we therefore regard the ribs and grooves also as being of similar origin, although owing to the great difference in the form and arrangement of the leaf-bases, the external appearance is very different.

Thus the subdivision of Sigillarian stems into ribbed and non-ribbed appears to us to be a natural one, since the ribbing is quite independent of the leaf-bases. We know, however, from the evidence of impressions that transitions from the Eusigillarian to the Subsigillarian type may occur. It may be that in certain species of the latter group, belonging to the Clathrarian section, the proximate leaf-bases partially fuse to form ribs, closely resembling those of Favularian Sigillarias, but not homologous with them. Or again, a stem may be ribbed in one part and not in another; a more unlikely probability, as it seems to us. Until, however, the internal structure of these interesting specimens is known, it is hardly possible to offer a full explanation of the occurrence of species apparently combining features common to these two subdivisions.

We may now turn to the anatomy of the leaf-base. The parenchyma of the leaf-base is thin-walled, and is of the loose polygonal type (Plate 15, fig. 8; Plate 16, figs. 3 and 4). The walls of the external layers are thickened (Plate 16, figs. 2 and 3).

The leaf-base is unsymmetrically triangular in radial section, the leaf-scar being

* KIDSTON ('05[1]), p. 543.

situated on the upper and shorter face (text-fig. on p. 143 and Plate 15, fig. 7, *l.s.*). As will be shown later, the parichnos and the leaf-trace pass somewhat obliquely downwards through the leaf-base until they reach the phelloderm (Plate 15, fig. 11).

In well-preserved impressions of this and many other species of *Sigillaria* belonging to the Rhytidolepis section, the lower, outer face of the leaf-base bracket is ornamented by numerous short transverse striæ or shallow grooves, either linear or angular in form (Plate 14, fig. 8). In tangential and radial sections through this region, such traces of the "ornament" as can be found appear to point to its being of an entirely superficial nature, and due to the presence of little bands of cells, specially thickened, lying just beneath the epidermis (Plate 16, fig. 10).

(*e*) *The Ligule.*

In many well-preserved impressions of Eusigillarian stems, a small print can be recognised in the median line of the rib, above the leaf-scar. This was first noticed many years ago by STUR,* who described it as the pit of the ligule, homologous with that which occurs so constantly on stems of Lepidodendreæ. It has been often referred to by various authors as the "ligular pit," or "ligule scar." The ligule of *Sigillaria* has not, however, been described so far from petrified material. In the recent account of *Sigillaria elegans* by Mr. KIDSTON, no mention of this organ is to be found.

In the bark of one of our Sigillarias (Specimen G) we believe we can trace the ligular pit and the remains of the ligule, though its structure is poorly preserved.

The upper surface, or "shelf" of the bracket-like leaf-base is only in part occupied by the leaf-scar (text-fig. on p. 143). Above that scar, but still situated on the leaf-base, and thus conforming to the position indicated by Dr. SCOTT in the passage quoted on p. 142, there may be seen, in such sections as pass through both the median line and surface of the rib, a shallow superficial groove, in which a small peg-like body is situated. This groove is shown in radial section on Plate 16, fig. 3, and in transverse section on Plate 15, fig. 9. In the latter figure, the conical body (*l.*) lying in the pit is no doubt the remains of the ligule. We cannot, however, determine its precise form or structure.

(*f*) *The Leaf-traces in the External Tissues.*

The leaf-trace, as it enters the stem from the leaf, is shown on Plate 16, fig. 2, a tangential section of Specimen A through the external surface of a rib. It enters near the apex of the leaf-scar (Plate 14, fig. 8). The bundle is collateral, and without secondary wood. There are two xylem groups (*x.*), clearly separated from one another. The thin-walled tissues of the bundle are not preserved, but above the

* STUR ('77), p. 293.

xylem strands, some remains of the transfusion tissue can just be made out. Around the bundle the thick-walled elements of the external surface of the leaf-base are seen, and one strand of the parichnos is also visible at *par.*

The course of the leaf-trace, through the leaf-base and phelloderm, is well seen in the radial section figured on Plate 15, fig. 11 (Specimen F). The bundle on entering the leaf-base passes through it, not horizontally, but inclined slightly downwards, though in the phelloderm the direction becomes almost horizontal. The elements of the xylem consist of scalariform tracheides, as may be seen by magnifying Plate 15, fig. 10. The thickening seen on the walls here, although apparently spiral, is in reality scalariform.

The form of the trace, as seen in tangential section at a somewhat deeper level in the leaf-base than that figured on Plate 16, fig. 2, is shown on Plate 16, fig. 4 (Specimen A). The two xylem groups are still quite distinct, and a few cells of the transfusion tissue are preserved. Between and below the two xylem groups, the remains of the phloem can be made out. At this level the parichnos forms two broad, crescent-like strands, on either side of the trace, one of which is seen at *par.*

In the photograph on Plate 16, fig. 5 (Specimen A), the leaf-trace is seen at a deeper level still, and is now in the phelloderm. The two xylem groups have united to form a single strand. The elements of the xylem can be distinguished, but the preservation and the thickness of the section will not permit us to discriminate between the other tissues. The large size of the parichnos strands is well seen in this photograph.

At a deeper stage in the phelloderm (Plate 16, fig. 11, Specimen E), the single xylem group is seen, and the bundle as a whole is smaller. The parichnos is here much closer to the bundle, and the two strands have nearly met below, and are on the point of uniting. At a slightly deeper level they fuse completely.

The deepest stage in the phelloderm to which we can follow the leaf-trace is shown on Plate 16, fig. 9 (Specimen C). It is here completely surrounded by the parichnos. The xylem elements can just be distinguished in the section, but the other tissues of the bundle cannot be discriminated.

In the absence of the inner cortex and phloem, the next point at which we meet with the leaf-traces is in the secondary wood. Before, however, passing to this region, we may give some account of the bundle of the leaf of Sigillaria, and describe the parichnos in greater detail.

(*g*) *The Leaf.*

No specimen of a petrified *Sigillaria* is at present known, in which the leaves are still in continuity with the stem. Mr. KIDSTON* has, however, found leaves

* KIDSTON ('07), p. 206.

possessing "the double vascular trace of *Sigillariopsis*" in association with his stem of *Sigillaria scutellata*, but he does not describe the structure of the leaf-traces in his preliminary note. Our discovery of the double xylem strands in the leaf-traces of the same species, when passing through the leaf-bases of the stem, naturally led us to a comparison with the leaves described by RENAULT, and more recently by SCOTT, under the name *Sigillariopsis*. This genus was instituted by RENAULT* in 1879, for a single known specimen of a stem (*S. Decaisnei*) surrounded by several detached leaves, apparently belonging to the same plant. The stem, the bark of which apparently was not ribbed, differs remarkably from all the Sigillarias whose structure is known. Some of the elements of the secondary wood were pitted. The leaves possessed a double leaf-trace, which, however, became single towards the apex of the leaf. Both primary and secondary xylem occur in the trace. In 1880, RENAULT† included *Sigillariopsis* under the Poroxylæ on the grounds that it formed a transition from the Sigillariæ to that group.

In 1904, Dr. SCOTT‡ published a preliminary note on the structure of two specimens, one from Shore-Littleborough (*Sigillariopsis sulcata*, SCOTT), the same locality as that from which our specimen of *Sigillaria scutellata* was derived, showing detached leaves, which he identified as falling within RENAULT'S genus *Sigillariopsis*. Dr. SCOTT stated that "at present no stem is known with which these leaves can be correlated."

Dr. SCOTT has very kindly afforded one of us an opportunity of examining these specimens, and, as he suggested, it was at once apparent that the structure of the foliar bundle of these leaves corresponded almost exactly with that of the leaf-trace in the leaf-bases of *Sigillaria scutellata* as described above. So close is the resemblance that it is clear that his specimens are the leaves of a ribbed Sigillaria, and may have even belonged to this very species. We understand that Dr. SCOTT is about to describe these leaves in detail, so we do not propose to enter into the subject here at all fully. Dr. SCOTT has, however, with great generosity, permitted us to figure one of his sections of *S. sulcata*, to show the correspondence between the structure of the leaf-trace and the leaf-bundle. This figure will be found on Plate 16, fig. 1, which may be compared with the tangential section through a leaf-base of *Sigillaria scutellata*, figured on Plate 16, fig. 4, *cf.* also fig. 2. This section has already been briefly described by Dr. SCOTT, so we need only indicate here the main features of its anatomy. On the lower surface it will be noticed that there are two furrows (*st.*), in which no doubt the stomata were placed. The vascular bundle shows the two xylem groups (*x.*) widely separated, and each is surrounded by a tissue of thin-walled elements, the precise nature of which is not very evident. There is no indication of the secondary xylem which occurs in RENAULT'S specimen.

* RENAULT ('79), p. 270, Plate 12, figs. 15–19; Plate 13, figs. 1–4.

† RENAULT ('80), p. 117; ('96), p. 245.

‡ SCOTT ('04), p. 520.

(*h*) *The Parichnos.*

The strands of delicate thin-walled tissues, which are termed the parichnos, accompanying the trace through the leaf-base and phelloderm, are well seen in some of the figures to which we have already drawn attention in describing the leaf-trace. At the external margin of the leaf-base (Plate 16, fig. 2, *par.*, Specimen A) they are not of very large size, and were probably covered over by the thickened cells of the external layers of the leaf-base.

At the deeper stage, shown on Plate 16, fig. 4, *par.* (Specimen A) the strands are slightly larger, and they lie nearer to the trace. At the next level, more internal still, and just inside the phelloderm, they are very much larger and closer, and each is becoming more or less club-shaped, the broadest part being below the bundle (Plate 16, fig. 5).

Deeper still, this broadening below the trace continues, and the two lower extremities begin to curve in towards the median plane of the rib, until they nearly meet, as is seen on Plate 16, fig. 11 (Specimen E).

A further stage, after the union of the lower margins of the parichnos, is shown on Plate 16, fig. 8 (Specimen D). The two upper portions of the strands are here seen beginning to bend inwards. At a still deeper level in the phelloderm, the parichnos forms a complete ring round the trace (Plate 16, fig. 9, Specimen C).

The cells of the parichnos are frequently preserved in our specimens. They are thin-walled, delicate elements (Plate 16, fig. 4, *par.*, fig. 7, *par.*, and fig. 9, *par.*; Plate 15, fig. 11, *par.*). As seen in radial section (Plate 16, fig. 7, and Plate 15, fig. 11), the appearance of the elements suggests that their walls may have possessed some form of delicate thickening. On the other hand, we have not observed any indications that this tissue was differentiated into two zones, as in *S. spinulosa.*

It is well known that among impressions of ribbed Sigillarian stems, specimens of a more or less highly decorticated nature frequently occur, in which often the phelloderm is exposed. These are sometimes distinguished as examples of the *Syringodendron* state of *Sigillaria.* It is interesting to find that in many of them the form and size of the parichnos at different levels may be used as an index of the degree of decortication. Practically all the conditions of the parichnos which are met with as we pass from the external surface to the interior of the rib can be distinguished on such decorticated impressions, including the stage in which the parichnos surrounds the leaf-traces completely. The form and size of the parichnos, however, varies in different species. It is exceptionally large, for instance, in *Sigillaria reniformis,* Brongn., while in other species it may be comparatively small.

The badly preserved petrifaction from Shore, Lancashire, recently figured by Miss Coward,* consists of a highly decorticated stem of a Sigillaria in the Syringodendron state. The ribs of this specimen apparently exhibit more than one

* Coward ('07).

degree of decortication. Those which possess only a single row of parichnos scars are more decorticated than those where a double row is found. The variation in the size of the scars is also explained by the description of the parichnos of *Sigillaria scutellata* given here. Further, we have not been able to distinguish, in any of our sections through the parichnos, the two kinds of cells which Miss COWARD figures as occurring in this region. Nor can we detect the presence of any definite secretory elements in this tissue such as RENAULT* found to occur in the case of *S. spinulosa*.

(*i*) *The Leaf-traces in the Central Cylinder.*

In the absence of the inner cortex, we next meet with the leaf-traces in their course through the secondary wood. They pass along a medullary ray, at first bending sharply downwards obliquely, at an angle of about 60° to the vertical, and then suddenly pursue an almost horizontal course (Plate 15, figs. 1 and 6, *l.t.*) until near the inner margin of the secondary wood. Here they again bend sharply downwards, parallel to the primary xylem, and eventually unite with it (Plate 14, fig. 5). The elements are scalariform (Plate 15, fig. 1) and about a dozen or more in number (Plate 14, fig. 5). The traces invariably leave the secondary wood opposite the grooves of the corona. There is no secondary wood associated with the trace.

We are unable to determine whether the number of leaf-traces and grooves of the corona correspond to the number of ribs, as Mr. KIDSTON decided to be the case in *Sigillaria elegans*. The inner cortex is not preserved, and therefore it is impossible to decide whether the bundles divided or not in this region.

5. THE STRUCTURE OF *Sigillaria scutellata*, Brongn., IN COMPARISON WITH OTHER PALÆOZOIC LYCOPODS.

(*a*) *Other Sigillarias.*

The genus *Sigillaria*, representing a great plexus of Palæozoic Lycopods, attained to its maximum development at a much later geological period than either *Lepidodendron*, *Bothrodendron*, or *Lepidophloios*. While *Bothrodendron* and *Lepidodendron* are among the earliest plants known to us, and occur in Devonian rocks, *Sigillaria* is not met with until we reach the Lower Carboniferous sediments, and even then it is but scantily represented. It was only in Upper Carboniferous and Permian times that this group became a highly developed and extremely abundant factor in the Palæozoic flora.

At the present moment there is not sufficient evidence to indicate which of the two types of Sigillarian stems is geologically the older. The Eusigillariæ, however, reach their maximum period of differentiation before the Subsigillariæ. The former

* RENAULT ('96), p. 225, Plate 41, fig. 5.

are extremely abundant in the Westphalian* division of the Upper Carboniferous, the latter in the Stephanian and Permian.

We may now compare briefly *Sigillaria scutellata* with the other Sigillarias, showing structure, which have previously been described.

The Clathrarian type, *S. Menardi*, originally described by BRONGNIART under the name *S. elegans*, differs from our stem in the absence of ribs, and in the fact that the leaf-bases are approximate, and more or less fused together. Internally, an important distinction is found in the fact that the primary wood does not form a continuous ring with a crenulated outer margin, but is aggregated into a large number of distinct strands, quite free laterally from one another. These, with the secondary wood, constitute definite vascular bundles. The leaf-traces have also secondary wood, as RENAULT† has shown. They do not possess double xylem strands.

On the other hand, *S. Menardi* agrees closely with our species in the structure of the elements of the periderm, and of the primary and secondary wood, with the exception that we have not recognised, beyond doubt, the occurrence of spiral tracheides in our stems.

The Leiodermarian species, *S. spinulosa*, has neither ribs nor leaf-bases. The well developed periderm composed of fibres, forming a network which encloses a tissue of thin-walled elements, is quite unlike that of *S. scutellata*, though the form of the individual thick-walled fibres offers a close comparison. The primary wood consists of groups of centripetally developed xylem, either quite free from one another laterally, or, as SOLMS‡ has shown, united in groups as continuous strands for some little distance. The leaf-traces are also diploxylic, the secondary wood being well developed.

Yet *S. spinulosa* agrees with *S. scutellata* in the fact that the secondary xylem is less clearly differentiated into bundles than in *S. Menardi*, and in the form of the elements of the primary and secondary wood.

In *S. spinulosa*, as in *S. Menardi*, part of the parenchymatous inner cortex, and the leaf-traces in that region, are preserved.

Passing to Eusigillarian stems, the Favularian species, *S. elegans*, described by Mr. KIDSTON, differs from *S. scutellata* in the shape and close approximation of the leaf-bases. The anatomy, however, appears to correspond very closely. The structure and course of the leaf-traces through the wood are practically identical. We have, however, no information in the case of *S. elegans* as to the structure of the traces in the periderm and leaf-bases, and especially as to whether, in the latter region, the xylem was or was not separated into two distinct strands. Mr. KIDSTON'S material apparently did not permit of a detailed study of the leaf-trace in the more external tissues of the stem, nor do we yet know the precise form of the parichnos in this

* This term is used here in the wide sense, generally adopted, and not in the sense of a restricted zone as advocated recently by Mr. KIDSTON ('05[2]).

† RENAULT ('79), p. 264; ('80), p. 144; ('96), p. 205.

‡ SOLMS ('91), p. 252.

region. The primary and secondary xylem, and the periderm appear to present almost identical features in both species. We have not, however, recognised any parenchymatous elements associated with the primary wood on its inner margin.

The detailed structure of *Sigillaria elongata*, a Rhytidolepis stem, so far as one can judge from the brief note by Professor BERTRAND, agrees very closely with that of *S. scutellata*. The teeth of the corona of the primary xylem appear, however, to be more prominent in the former, and we have not recognised any spiral elements in the wood of our specimens.

It is interesting to find that in all the three species of Eusigillarian stems, in which the structure is now known, the primary xylem forms a continuous ring with a crenulated outer margin, a feature which may or may not occur in Subsigillarian species. Further, the leaf-traces have no secondary wood.

(*b*) *Lepidodendron, Lepidophloios, and Bothrodendron.*

The internal structure of *Sigillaria scutellata*, BRONGN. may be compared with that of a *Lepidodendron* or a *Lepidophloios*. The anatomy of three Upper Carboniferous species of *Lepidodendron* is now known, viz., *L. selaginoides*, STERNB.,* *L. obovatum*, STERNB.,† and *L. aculeatum*, STERNB.‡ Many other petrified stems, of which the specific, or even the generic, characters of the external surface have yet to be determined, have also been referred to this genus, but it remains to be proved whether their external morphology is really in generic agreement with the impressions on which STERNBERG founded the genus.

As regards *Lepidophloios*, the evidence for a correlation of the external features with internal structure is even less satisfactory. One type of petrified stem (*L. fuliginosus*) alone has been shown to possess leaf-bases generically identical with those exhibited by impressions referable to STERNBERG'S genus. Yet this type of internal structure, which at one time was regarded as probably characteristic of the genus, has recently been shown to be common to, at least, two species of *Lepidodendron*.§ Hence it follows that the internal structure of some Lepidodendrons was almost identical with that of some members of the genus *Lepidophloios*, and *vice versâ*. Thus the relationship between these two genera is a close one.

The species of *Lepidodendron* known from the Lower and Upper Carboniferous rocks, *e.g.*, *Lepidodendron selaginoides*, STERNB., in which the stele is solid, the central portion consisting of centripetal xylem, appear to be the more remote anatomically from the ribbed *Sigillarias*, so far as the vascular cylinder is concerned. But, in the general structure of the periderm, a somewhat close comparison is

* CARRUTHERS ('69); F. E. WEISS and LOMAX ('05).

† SCOTT ('06).

‡ SEWARD ('06).

§ SCOTT ('06); SEWARD ('06).

afforded to the Sigillarias described here. The same is also true as regards the elements of the xylem, whether primary or secondary.

In such petrifactions as the Lower Carboniferous species *Lepidodendron brevifolium*, WILL., a stem whose external surface has not yet been described, where a definite pith is present, and the centripetal xylem is aggregated in the form of a ring, though the external margin is not however crenulated, we seem to see an intermediate stage to our next type of structure. The stems of *Bothrodendron*,* so far as they are known, also belong here.

In *Lepidodendron obovatum*, STERNB., and *L. aculeatum*, STERNB., as well as in some petrifactions which belong to the genus *Lepidophloios*, we have an anatomical structure, which is described as the *Lepidophloios fuliginosus* type, this latter species being one founded on internal morphology alone. There is a distinct pith and a well-marked zone of primary wood, which is crenulated externally—the crenulations being spoken of as the corona. The leaf-trace bundles arise in the grooves between the angles of the corona. So far the structure may be closely compared with that of a Eusigillarian stem. But the secondary vascular tissues in these plants were anomalous, whereas in *Sigillaria scutellata* they are of the normal type.

Probably the nearest approach to the Sigillariæ, from an anatomical point of view, is to be found in the Lower Carboniferous stems from Arran and Dalmeny. The Arran trunk was referred by WILLIAMSON† to the genus *Lepidodendron* as *L. Wunschianum*. Others have admitted the possibility that it may have been a *Lepidophloios*, but it must be remembered that the external features of this tree have never been observed, and that these opinions are arrived at entirely from the internal structure. The importance of bearing these facts in mind is emphasised by the recent discoveries that at least two Lepidodendrons possessed the type of structure hitherto regarded as characteristic of *Lepidophloios*. The Dalmeny stem was described by SEWARD and HILL‡ as possibly identical with *Lepidophloios Harcourtii* (WITHAM). Here again the external features are unknown.

In both the Arran and Dalmeny trunks, the primary wood, which is crenulated externally, forms a ring bounding a well-marked pith. The leaf-traces arise from the grooves of the corona, and secondary wood of the normal centrifugal type is present. So far the comparison with the Sigillarias described here is close. The leaf-traces, however, in the Dalmeny stem where they leave the secondary wood, are diploxylic. This feature is unknown in either of the two ribbed Sigillarias so far fully described, but it does occur, as has been pointed out, in the Subsigillariæ (*S. Menardi* and *S. spinulosa*). Thus on the whole these great trunks from Arran and Dalmeny stand closer anatomically to the ribbed Sigillarias than any of the other known types

* Described as *Lepidodendron mundum* by WILLIAMSON ('89), p. 197.

† WILLIAMSON ('80), Plate 14.

‡ SEWARD and HILL ('00).

of structure exhibited by *Lepidodendron* or *Lepidophloios*. The structure of some of the Subsigillariæ, in which the primary xylem is, in whole or in part, aggregated into separate strands or bundles, seems to suggest a more remote relationship with *Lepidodendron* and *Lepidophloios* than is the case with the Eusigillariæ.

The Eusigillariæ are distinguished from *Lepidodendron* and *Lepidophloios* by the fact that the stem is ribbed, and by the form and arrangement of the leaf-bases, as well as the shape of the leaf-scar. Thus so far as the external morphology is concerned the differences are great. When, however, we turn to the anatomical structure, the comparison is closer. The phelloderm of *Sigillaria scutellata* corresponds very closely to that of *Lepidodendron selaginoides*. The elements of the primary and secondary wood are like those of any known *Lepidodendron*, which has secondary thickening of the normal type. The presence of a corona, and the point of origin of the leaf-traces are further resemblances to be matched among certain Lepidodendrons, and are also found in a *Lepidophloios*. It is true that the teeth of the corona in *Sigillaria scutellata* are much shorter, and less pointed, than those of the primary wood of the *Lepidophloios fuliginosus* type of stem, but this is a difference of little value in such a comparison, and may vary with the species in question. In the Rhytidolepis species *S. elongata*, the teeth are described by BERTRAND* as "very prominent." The breadth of the ring of primary wood may be often rather less in the case of a *Sigillaria* than a *Lepidodendron* or a *Lepidophloios*, but this by itself hardly appeals to us as a character of real importance in this connection.

The double xylem strands of the leaf-trace, when passing through the leaf-base, and of the foliar bundle of the leaf, are, however, very distinctive features not as yet met with elsewhere among Palæozoic Lycopods, if we regard *Sigillariopsis* as closely allied to, if not identical with, *Sigillaria*.

Thus the present study has confirmed the previous conclusion that the structure of the ribbed Sigillarias lies very close to that of certain *Lepidodendreæ*. In the absence of the bark it would appear impossible to distinguish the vascular cylinders of the one from certain types of stele possessed by the other, at least not with any certainty.

(*c*) The Genus *Diploxylon*, CORDA.

The present inquiry renders advisable a brief consideration of the genus *Diploxylon*, some species of which may be closely compared with the Sigillarias described here. In 1845, CORDA† published some excellent figures of a petrifaction, which he had previously described a few years earlier (1840) under the name *Diploxylon elegans*, CORDA. Since then other authors have attributed fossils to this genus, but of these we shall only mention the British species, *D. cycadoideum*,

* BERTRAND ('99), p. 608.

† CORDA ('45), p. 36, Plate 10; Plate 11, figs. 1–3.

BINNEY, described by BINNEY,* in 1865, from the Lower Coal Measures of Lancashire.

CORDA's plant was a decorticated trunk, in which the vascular tissues were alone preserved. It showed both centripetal and centrifugal wood, and the primary wood formed a continuous ring, with a crenulate, rather than sinuous, outer margin. The elements of the wood agree somewhat closely with those subsequently found in true members of the genus *Sigillaria*.

BINNEY's plant† was also decorticated, and, further, the secondary wood, which is of considerable thickness, is very badly preserved except on the inner margin. The teeth of the corona are here quite sharp and long.

During the present investigation a number of decorticated stems showing only the steles, which, in some respects, are like those of a Sigillaria, have come under our observation. Some of them closely resemble BINNEY's plant. Although CORDA instituted a new family, the Diploxyleæ, for his fossil, BINNEY, like BRONGNIART,‡ regarded the Diploxylons as being probably decorticated Sigillarias, a conclusion which has since been generally current. The presence of a corona, as well as of secondary wood, seems to have been the basis of this opinion. We have not, however, obtained any specimen, agreeing closely with BINNEY's *Diploxylon cycadoideum*, which furnishes additional evidence to show that this large stem is in reality a true *Sigillaria*.§ The form of the corona is much more like that of a *Lepidophloios* than a *Sigillaria*. While decorticated specimens of true Sigillarias may occur in the petrified state, yet we are led to the conclusion that stems of other plants, in all probability generically distinct from *Sigillaria*, possessed a vascular cylinder in some respects, especially in the presence of a corona, which is liable to be confused with that of a true Sigillaria, where the cortical tissues are not preserved.

Thus the genus *Diploxylon* is not only still obscure, but one of doubtful value. If we continue to speak, as a matter of convenience, of decorticated stems under this name, the stele of which more or less resembles that of a ribbed *Sigillaria*, it must be at the same time recognised that the stems of several genera are in all probability being included, if only temporarily, under one name.

6. GENERAL CONCLUSIONS AND SUMMARY.

Our object in the present communication has been not only to elucidate the structure of one particular species of *Sigillaria*, but to gain as full a knowledge as possible of the anatomy of stems of the Rhytidolepis section, in which the leaf-bases of the ribs are comparatively distant from one another.

* BINNEY ('65), p. 582, Plate 30.

† BINNEY ('65).

‡ BRONGNIART ('49).

§ Sections of this fossil are in the Sedgwick Museum, Nos. E 1–E 10, and in the British Museum (Nat. Hist.), General Collection of Sections (Geol. Dept.), V. 7730–3, V. 7747. Part of the type specimen is also to be found in No. 1 Museum at the Royal Gardens, Kew.

In such stems we have not met with any indications of branching, either externally or in the steles. It would thus seem probable that the specimens described here are, in reality, the upper portions of stems, not very remote from the apices, for we know that the trunks of many Eusigillariæ attained to a very considerable diameter.

The fact that the stems were ribbed, and that the ribs are in reality of cortical origin and quite independent of the leaf-bases, suggests that, despite apparent exceptions, the two-fold classification proposed by WEISS, namely, Eusigillariæ and Subsigillariæ, may be a natural one.

The presence of a ligule tends to emphasise still further the close relationship of the Sigillariæ to other Palæozoic Lycopods. This view is now so generally accepted that it is unnecessary here to combat BRONGNIART'S* correlation of this genus with the Gymnosperms. Nor is it possible to agree with RENAULT'S† conclusion that, while the Eusigillariæ were Cryptogamic, the affinities of the Subsigillariæ lie closer to the Cycads than to any other group. The comparison made here between these two types of stem may serve to emphasise their very close relationship.

The chief characteristics of the Eusigillariæ, so far as they are known anatomically, as opposed to the Subsigillariæ, are four in number. The stems were ribbed, and the primary xylem always formed a perfectly continuous ring. Thus the woody tissues as a whole are not marked out into definite vascular bundles. The leaf-traces were monoxylic, and, in the leaf, the bundle divided into two distinct xylem groups, which persisted in the leaf-bases, but united again in the phelloderm of the rib.

Further, the Eusigillariæ may be closely compared anatomically with certain Lower Carboniferous trunks, believed to belong to the genus *Lepidodendron*, and in some respects they also show clear relationship to *Lepidophloios*. With the genus *Bothrodendron* the anatomical relationship is more remote, and the evidence does not support the inclusion of this genus with the *Sigillariæ*, as advocated by WEISS and STERZEL.

So far as the internal structure is concerned, there is little to support the view that *Bothrodendron* may be assigned "a position intermediate between *Lepidodendron* and *Sigillaria*."‡

Passing to the leaf-traces, the parichnos accompanying the bundle of Sigillaria appears to differ somewhat in form from that described in the case of other Palæozoic Lycopods. In *Lepidodendron*§ and *Lepidophloios*‖ the two strands, as they pass through the leaf-base, fuse on the lower side of the trace. In *Sigillaria scutellata*, however, the parichnos completely surrounds the trace, for the two arms unite above

* BRONGNIART ('39).

† RENAULT ('96), p. 245.

‡ KIDSTON ('01), p. 89.

§ HOVELACQUE ('92), text-figs. 47–50; F. E. WEISS ('07).

‖ WILLIAMSON ('93²), Plate 4, figs. 31–37.

it, as well as below, in the region of the phelloderm. Thus the parichnos of *Sigillaria* differs markedly from any hitherto described among Palæozoic Lycopods,* and still more from the so-called parichnos of living Lycopods. Our specimens, further, do not support Mr. T. G. HILL'S† recent conclusion that this organ, when mature, had the form of an empty canal.‡ In many of our sections the parichnos tissue is fairly well preserved, and where it is absent in others the fact may be accounted for by the delicate nature of the walls of the elements.

Perhaps the most interesting point brought to light by the present study is the fact that the xylem of the leaf-trace, when passing through the leaf-base, divides into two distinct strands. In the secondary cortical tissue, which is regarded here as being of the nature of phelloderm, the two xylem groups unite, and continue as a single strand during their passage through the wood. The form of the leaf-trace in the more external tissues of the stem has enabled us to identify the detached leaves, named by SCOTT, *Sigillariopsis sulcata*, as being the leaves of a Sigillarian stem closely allied to *S. scutellata*, perhaps even identical with that species. Thus, while no petrifaction is as yet known in which the leaves can be seen actually in continuity with a Sigillarian stem, there is now clear evidence which enables us to recognise some of them, even when detached.

Apparently all Sigillarian leaves did not possess this peculiarity. If RENAULT§ was right in attributing certain leaves to the stems of *S. Brardi* and *S. spinulosa* with which they were associated, then some of the leaves of the Subsigillariæ possessed a diploxylic leaf bundle, of quite different construction to that of a Eusigillarian leaf.

This question involves some further discussion of the affinities of the genus *Sigillariopsis*, which was regarded by RENAULT as an intermediate link between the Sigillariæ and the Poroxyleæ. We have already enumerated (p. 148) the principal features of his unique specimen, *Sigillariopsis Decaisnei*. On our view, the discovery of the double xylem strands of the leaf-traces of *Sigillaria scutellata* shows emphatically that, not only do the detached leaves described by SCOTT as *Sigillariopsis sulcata* belong to a Eusigillarian stem, but that the stem associated with the leaves figured by RENAULT, which he included under the name *S. Decaisnei*, was also a Sigillarian stem. If this is so, then it probably belonged to the Subsigillariæ, for the bark is apparently not ribbed. The great difficulty in the way of this conclusion is that some of the elements of the wood of the stem in question are not scalariform, but pitted. While this is no doubt a very important feature, it does not seem to us that it outweighs the whole of the other evidence, pointing strongly in the direction of the Sigillariæ. On this view, we recognise that some of the elements of the wood of certain Sigillarias may have been pitted, and not scalariform, just as the

* F. E. WEISS ('07).

† HILL ('06), p. 268.

‡ See also F. E. WEISS ('07), p. 5.

§ RENAULT ('80), p. 145; ('96), p. 198, Plate 41, figs. 12–24.

Dictyoxylon type of cortex may occur, though in most cases the periderm is closely analogous to that of a *Lepidodendron*.

The following is a summary of the chief features in the anatomy of *Sigillaria scutellata*, and of the conclusions arrived at here :—

The *pith* was large, but this tissue is not preserved, and the pith cavity is often obliterated by the lateral crushing which the stem has undergone.

The *primary xylem* forms a continuous ring of large scalariform tracheides, of about 1 mm. in breadth. The outer margin of the centripetal wood was crenulated, but the teeth of the corona are, in this species, short and bluntly rounded. The protoxylem groups form the teeth of the corona, and consist of scalariform elements without, so far as we can ascertain, any spiral tracheides.

The *secondary xylem* consists of a well developed zone of scalariform tracheides, of rather smaller size than those of the primary wood, and radially arranged, the rows being separated by primary or secondary medullary rays. The outer margin of this zone was also crenulated, the ridges and grooves corresponding in position to those of the corona of the primary wood. The medullary rays consist of a single row of cells of varying height, the walls of which are usually thickened transversely. The phloem, and inner cortex of thin-walled tissues are not preserved in any of our specimens.

The *periderm* consists of a broad band of phelloderm, or secondary cortical tissue, arising internally to a meristematic zone. No definite cambial layer is present in any of the stems examined, and it is suggested that the meristematic activity in this region was of a periodic nature. The elements of the phelloderm are prosenchymatous, thick-walled prismatic cells, resembling fibres, and were often chambered.

The *ribs* are formed by the cortical tissues, and consist chiefly of phelloderm, with the addition of a small thickness of persistent primary cortex, which probably lay outside the zone of secondary meristematic activity. The stem was no doubt ribbed before periderm formation commenced. The leaf-bases merely form bracket-like projections of thin-walled tissue from the surface of the rib, and those of the same vertical series were probably free from each other above and below. The ribbing of the stem appears to us to be a natural feature of importance in classifying the Sigillariæ.

A *ligule* lying in a ligular pit has been detected for the first time in petrified material. It lies on the leaf-base above the leaf-scar.

The *leaf-traces* pass down through the leaf-bases inclined at an angle to horizontal plane of the rib, and then continue through the phelloderm almost horizontally. The bundle is collateral, and without secondary wood. While the bundle is passing through the leaf-base the xylem is aggregated in two distinct strands, which, however, unite in the region of the phelloderm. The structure of the trace in the leaf-base is almost identical with that of the foliar bundle of the leaf described by Scott as *Sigillariopsis sulcata*, which is obviously simply the leaf of a Eusigillarian stem, possibly of the same species as that described here.

The *parichnos* consists of a thin-walled tissue, showing traces of a delicate thickening on the walls. The two strands, which near the exterior of the rib are comparatively small, increase in size as they are traced inwards. Further, the two lower extremities of the strands bend towards one another and finally fuse, and, at a deeper level in the phelloderm, the upper portions behave in a like manner, so that eventually the trace is entirely surrounded by a broad zone of this tissue.

The course of the leaf-trace through the secondary wood is at first at an angle of some 60° to the vertical, but it soon becomes almost horizontal, until near the inner margin, where it again bends sharply downwards. It eventually unites with the primary wood in one of the grooves of the corona.

The structure of the Eusigillariæ is compared with that of the Subsigillariæ, and it is found that there are four main points which distinguish them. In the Eusigillariæ the stems are ribbed, and the primary xylem always forms a perfectly continuous ring. The leaf-traces are monoxylic, as opposed to the diploxylic traces of the Subsigillariæ. Further, the leaf-trace, when traversing the leaf-base, divides into two distinct xylem strands, which persist independently in the leaf as part of the foliar bundle until near the apex of the leaf. If, however, we include RENAULT'S genus *Sigillariopsis* among the Subsigillariæ, a conclusion which seems inevitable, then this characteristic is common to some members of both groups, though in the Subsigillariæ it is combined with the diploxylic structure.

The Eusigillariæ are compared with the various types of structure assigned to *Lepidodendron* and *Lepidophloios*, with the conclusion that they correspond most closely to the Lepidodendroid trunks of the Lower Carboniferous of Arran and Dalmeny. Anatomically they appear to be remote from *Bothrodendron*, so far as the structure of that genus is known. It is found that, in the absence of the cortical tissues, it is not possible to distinguish the stele of a Eusigillarian stem by any definite characters from that of some Lepidodendreæ. The genus *Diploxylon* is discussed in this connection, and it is shown that it is by no means certain that all the decorticated stems which are classed under this name belong to the Sigillariæ. It is more probable that the stems of several distinct genera are here grouped together, if only as a temporary expedient.

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EXPLANATION OF THE PLATES.

The photographs, with two exceptions, are by Mr. W. Tams, of Cambridge. The figures need to be examined with a hand-lens in some cases.

PLATE 14.

Sigillaria scutellata, BRONGN.

Fig. 1.—Specimen A. Transverse section of a petrifaction containing two stems belonging to this species. The upper stem (*a*) shows nine ribs on each side, and a small portion of the stele (*st.*), which is badly crushed. The lower (*b*) exhibits the same number of ribs. The stele (*st.*) is better preserved. × $\frac{4}{3}$.

Fig. 2.—Specimen A. External surface of three ribs, showing the leaf-scars, belonging to the upper stem (*a*) seen in transverse section on fig. 1. Natural size.

Fig. 3.—Specimen A. Part of a transverse section of the lower stem (*b*) seen on fig. 1, showing the primary (x^1) and secondary wood (x^2). On the upper side the ribs are decorticated, and only the more internal portion of the periderm (*pd.*) is seen. On the lower, there are three ribs, the middle one showing a small portion of a leaf-base (*l.b.*). The stem has undergone some distortion before or during preservation, with the result that the grooves between the ribs on the lower side are now very much broader than they probably were in the living state. × 4.

Fig. 4.—Specimen A.—External surface of five ribs, showing traces of leaf-scars, belonging to the lower stem (*b*) seen in transverse section on figs. 1 and 3. Natural size.

Fig. 5.—Specimen C. Transverse section through a leaf-trace bundle (*l.t.*) in a groove of the corona formed by the crenulated outer margin of the primary wood (x^1). The secondary wood (x^2) and two protoxylem groups (*px.*) are also seen. Section V. 8931, General Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 95.

Fig. 6.—Specimen A. Transverse section of the stele of the lower stem (*b*) shown on figs. 1 and 3. On the right is seen the secondary wood (x^2), the elements of which are radially arranged, and often separated by medullary rays (*m.r.*). On the left, the larger, and less regularly disposed elements of the primary wood (x^1). The corona (*c.*), formed by the crenulated outer margin of the primary wood, and numerous protoxylem (*px.*) groups at the angles of the corona, are also shown. Scott Coll., No. 2300. × 40.

Fig. 7.—*Impression* of the ribs of a specimen from the Middle Coal Measures of Dudley, South Staffordshire. The leaf-bases (*l.b.*) are here seen in the natural condition, and form bracket-like organs projecting from the surface of the ribs. They are slightly decorticated, especially above the leaf-scars (*l.s.*). The smooth surface of the leaf-bases, which in the living state occupied a larger area both above and below the leaf-scars, gives a rough idea of the extent of the parenchymatous tissue forming the leaf-base. The striæ of the ribs are due to the periderm being laid bare through a slight decortication of the more external thin-walled tissue. The prints of the leaf-trace, and the parichnos (*par.*) of the leaf-scars are well seen. No. V. 1232, Geol. Dept., Brit. Mus. (Nat. Hist.). Johnston Coll. Natural size.

Fig. 8.—*Impression* of the ribs of a specimen from the Coal Measures of Newcastle, Northumberland. The ribs and leaf-bases are here compressed and flattened,—a common condition among such impressions. This photograph should be carefully compared with fig. 7. The form of the leaf-scars, typical of this species, is well seen, as also the ornamentation of the leaf cushion below the scar (*cf.* Plate 16, fig. 10). No. 750, Carbon. Plant Coll., Sedgwick Museum, Cambridge. × $\frac{6}{5}$.

Plate 15.

Sigillaria, sp.

Fig. 1.—Specimen B. Transverse section through the stele, showing the primary wood (x^1), the corona (*c.*), the secondary wood (x^2) and a leaf-trace (*l.t.*) passing through the secondary wood. The scalariform tracheides of the leaf-trace are seen in oblique longitudinal section. × 40.

Fig. 2.—Specimen B. Transverse section showing the ribs and the stele. Five ribs are seen on the upper side, the middle one showing a gap (*l.t.*) marking the position at which a foliar bundle entered the leaf-base. The primary xylem (x^1) has become almost entirely free from the secondary wood (x^2) through some accident in the preservation, and thus the sinuous outline of the corona (*c.*) is clearly seen. The pith cavity (*p.*) is much less compressed than in Specimen A. On the lower side the ribs are less well preserved. The parenchymatous tissue external to the periderm is, however, seen to be continuous from one rib to another. × $\frac{3}{2}$.

Fig. 3.—Specimen C. A radial section through the primary xylem (x^1), the protoxylem (*px.*) and the secondary xylem (x^2). The section passes through a medullary ray at *m.r.* No. V. 8932, General Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 40.

Fig. 4.—Specimen B. External surface of the ribs, which are not well enough preserved to permit of specific determination. Traces of the leaf-scars (*l.s.*) can, however, be seen, and these were fairly distant from one another. The transverse section of this petrifaction is shown on fig. 2 of this plate. Natural size.

Fig. 5.—Specimen E. External surface of three ribs of a petrifaction with distant leaf-scars (*l.s.*), showing only the bark of a ribbed Sigillaria. Natural size.

Fig. 6.—Specimen B. Tangential section through the secondary wood, showing medullary rays (*m.r.*) and a leaf-trace (*l.t.*) passing through the wood. × 40.

Fig. 7.—Specimen H. Radial section through a rib, showing the form of the leaf-base (*l.b.*) which is not cut here quite in the median plane. The position of the leaf-scar is indicated by *l.s.* This section is interesting as showing that the rib is formed largely of phelloderm (*ph.*). The position of the secondary meristematic zone is indicated by the curved line bounding externally the dark coloured prosenchymatous tissues of the phelloderm. Below the leaf-base, a small area of parenchymatous tissue is seen at *p.c.*, which is probably part of the primary cortex which has persisted, external to the secondary meristem. The leaf-base forms a bracket-shaped excrescence of parenchymatous elements on the surface of the rib. Compare text-figure on p. 143. × 5.

Fig. 8.—Specimen C. Transverse section of a rib passing through a leaf-base (*l.b.*). The radially arranged elements of the phelloderm (*ph.*) are seen in the lower half of the photograph. There is no definite cambial zone on the outer margin of this tissue, but, in this position (*m.*), several of the parenchymatous cells appear to have recently undergone divisions. In the upper part of the figure the parenchymatous elements of the leaf-base (*l.b.*) are well seen. No. V. 8931. General Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 40.

Fig. 9.—Specimen G. Transverse section through a rib just above the leaf-scar, showing the ligule (*l.*) lying in its pit, the leaf-base (*l.b.*), and the phelloderm of the rib (*ph.*). × 18.

Fig. 10.—Specimen C. Radial section through a rib, showing the xylem of a leaf-trace, passing through a leaf-base. The tracheides (*tr.*), which appear to be spiral, are in reality scalariform. No. V. 10,983, General Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 100.

Fig. 11.—Specimen F. Radial section of a rib and a leaf-base, passing through the median plane of the rib. The external surface is slightly decorticated in the neighbourhood of the leaf-scar. The parenchyma of the leaf-base is seen at *l.b.*, which is near the angle of the leaf-base below the leaf-scar. The phelloderm (*ph.*) is here of considerable thickness. One of the

xylem strands of the leaf-trace is seen at *l.t.*, below the parichnos (*par.*), which is represented below by a large gap, though above by thin-walled elements on either side of the trace, but at some little distance from it. No. 654, Williamson Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 18.

Plate 16.

Sigillaria, sp.

Fig. 1.—The *Sigillariopsis sulcata* of Scott. Transverse section of the leaf of a Eusigillarian stem. The two xylem strands (*x.*) of the bundle are here very distinct. The stomatiferous furrows (*st.*) are also shown. No. 2268, Scott. Coll. × 27.

Fig. 2.—Specimen A. Tangential section through the surface of a leaf-scar. This photograph shows the thick-walled cells which form the external limit of the leaf-base. The two xylem groups (*x.*) of the leaf-trace are clearly seen. One of the strands of the parichnos is shown at *par.* × 35.

Fig. 3.—Specimen G. Radial section of a rib passing through the pit of the ligule. The cells of the leaf-base are here cut somewhat obliquely. × 37.

Fig. 4.—Specimen A. A tangential section of a leaf-base, at a slightly deeper level than that shown on fig. 2. The two xylem strands of the leaf-trace can be seen, and one arm of the parichnos (*par.*) is shown on the left-hand side. × 40.

Fig. 5.—Specimen A. A tangential section at a still deeper level in the rib than that shown in the last figure, and cut near the external margin of the phelloderm. The structure of the bundle is here obscure. The large size of the parichnos strands, below the bundle, is especially noticeable. × 30.

Fig. 6.—Specimen F. A radial section through the phelloderm (*ph.*) and leaf-base (*l.b.*) of a rib. No. 654, Williamson Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 35.

Fig. 7.—Specimen F. A radial section through a rib, showing the tissue of a parichnos strand (*par.*). No. 654, Williamson Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 18.

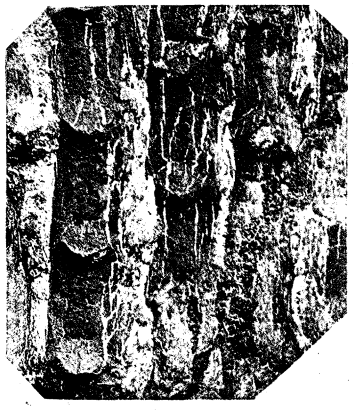
Fig. 8.—Specimen D. A tangential section at a deeper level in the phelloderm than that shown on Fig. 5. The xylem strand (*x.*) of the leaf-trace is here single. The two arms of the parichnos (*par.*) have met and coalesced below, and are beginning to approach one another above the bundle. × 20.

Fig. 9.—Specimen C. A tangential section of a rib passing deep in the phelloderm. The structure of the leaf-trace is here obscure. The parichnos (*par.*), at this level, completely surrounds the trace. No. V. 10,984, General Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 35.

Fig. 10.—Specimen A. An oblique tangential section through the external layers of the leaf-base below the leaf-scar, showing, on the right, the ornamentation (*cf.* Plate 14, fig. 8) formed by short, transversely placed bands of thick-walled elements. To the left the thickened cells, limiting the leaf-base externally, are seen. × 20.

Fig. 11.—Specimen E. A tangential section through a rib, passing through the phelloderm at a level intermediate between that of the sections figured on figs. 5 and 8. The two arms of the parichnos have met below, but the fusion is as yet slight. × 35.

[All the specimens and sections figured, unless the contrary is stated, are for the present in the care of the senior author of this paper.]



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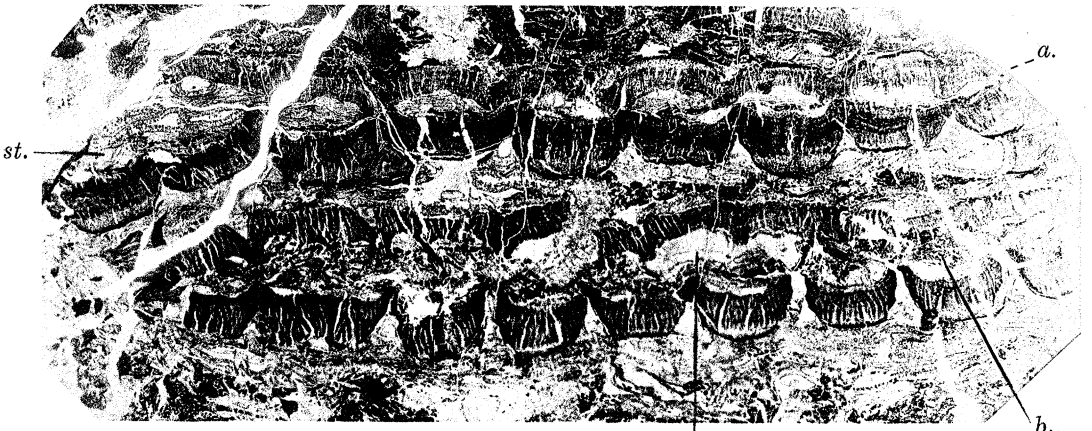

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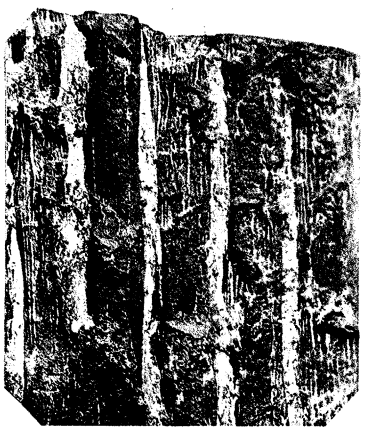

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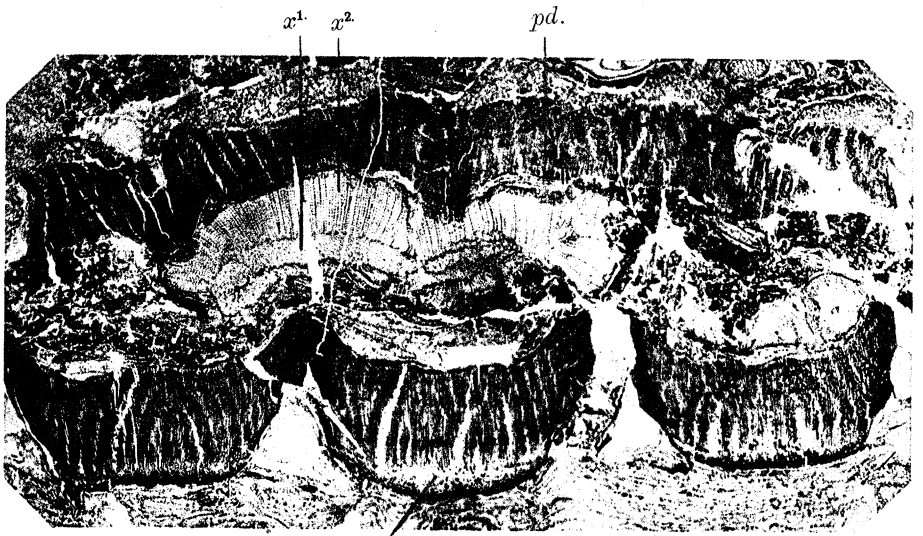

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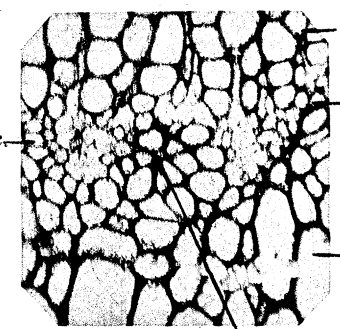

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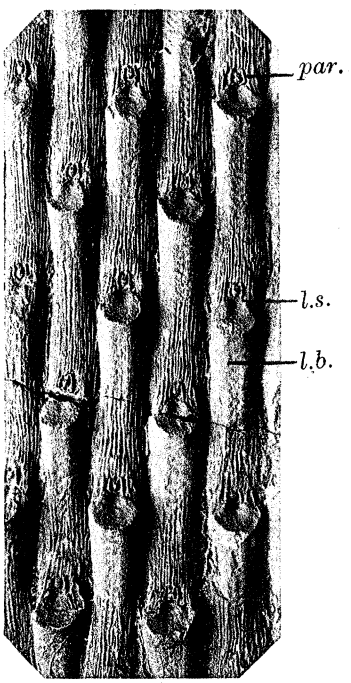

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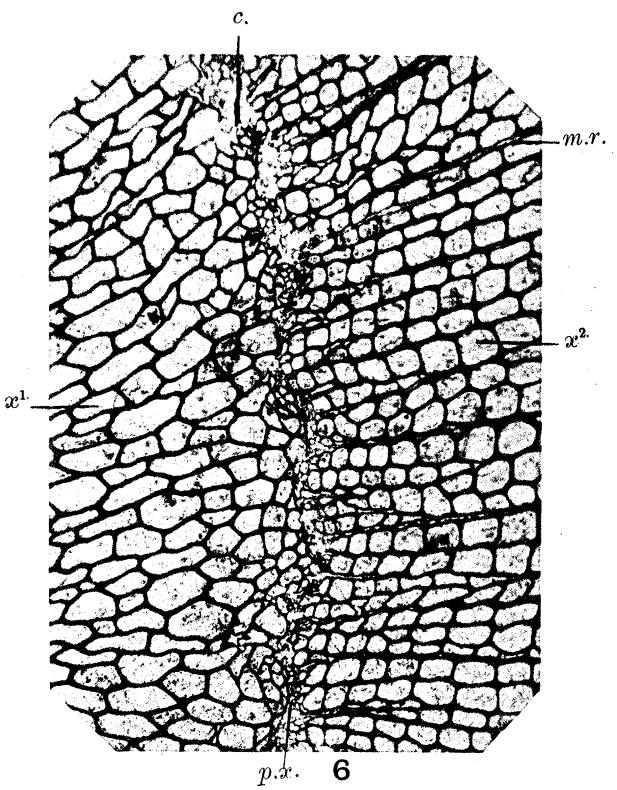

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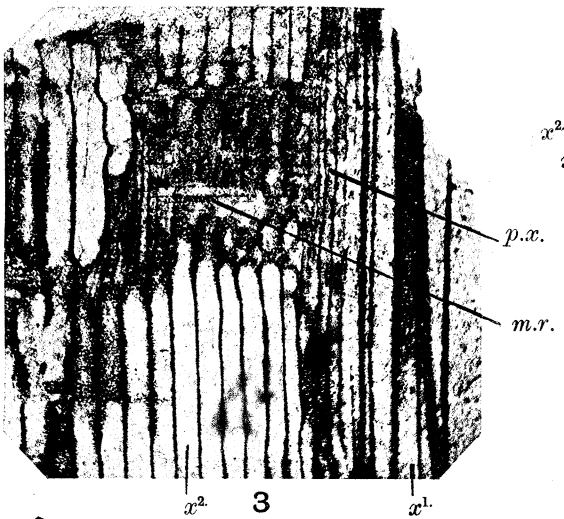
W. TAMS. PHOTO.

London Stereoscopic Co. imp.

SIGILLARIA SCUTELLATA BRONGN.



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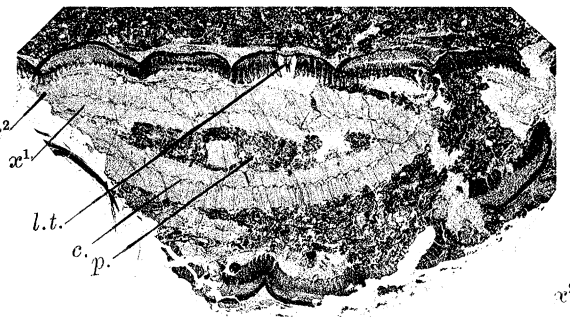

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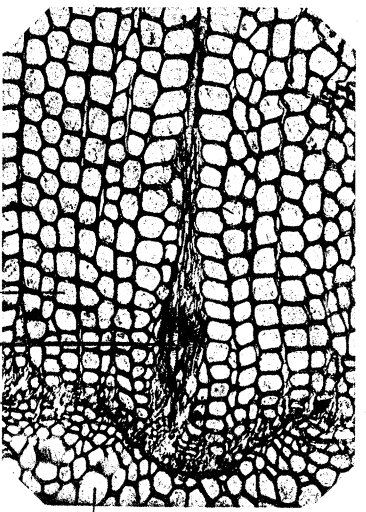

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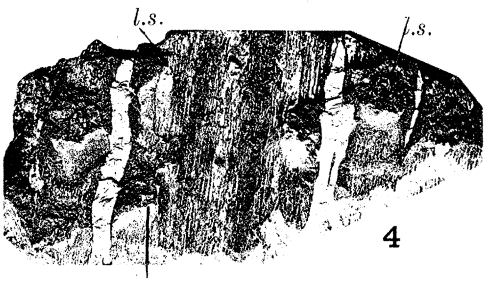

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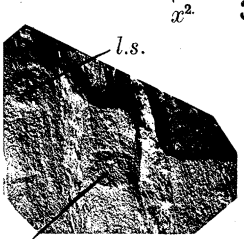

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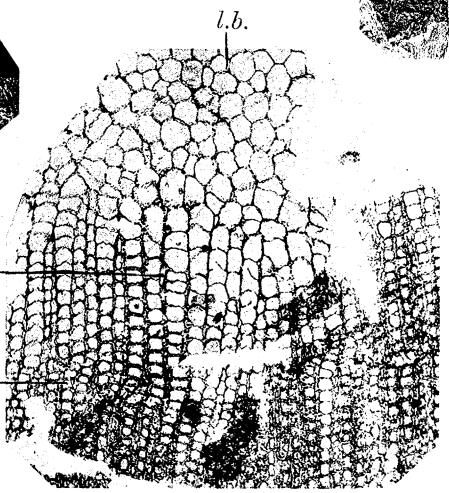

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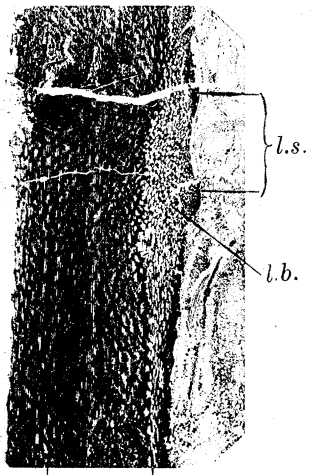

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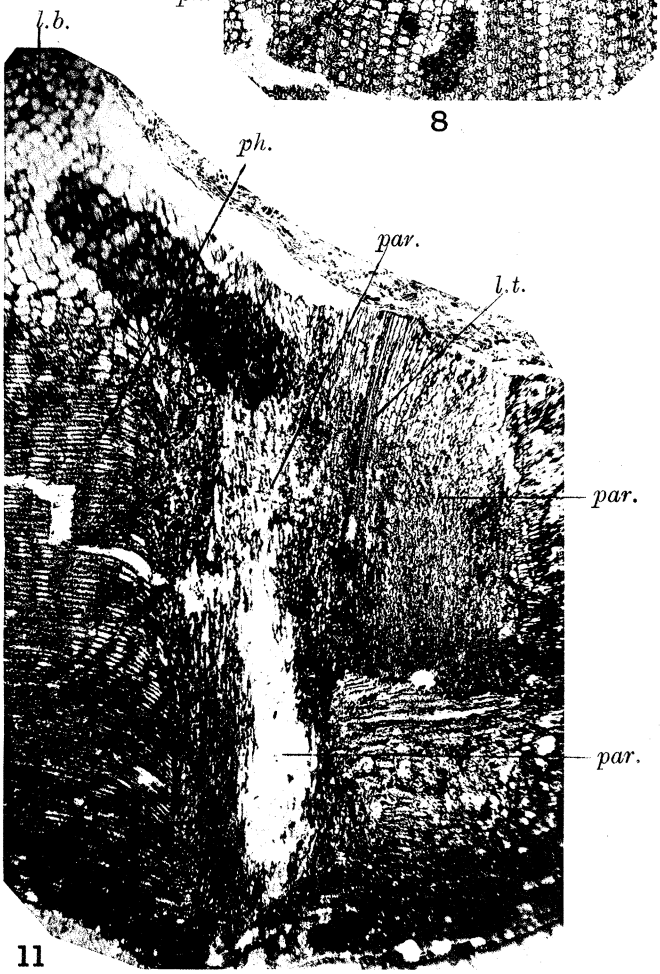

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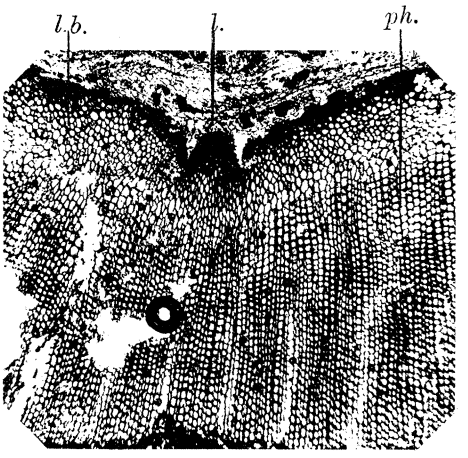

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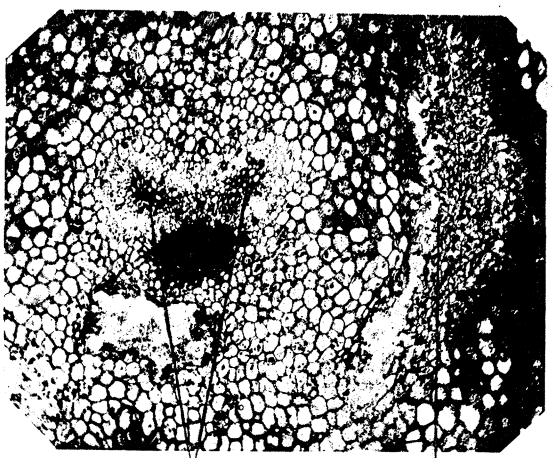

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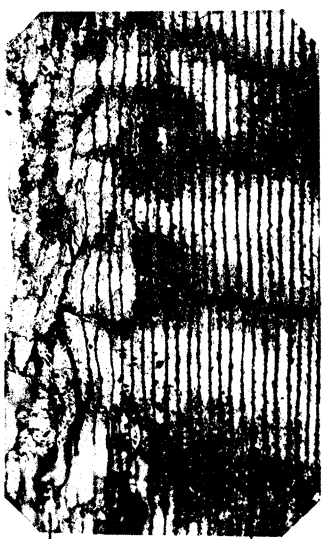

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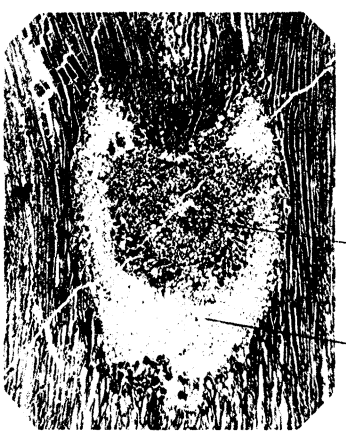

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W. TAMS. PHOTO.

London Stereoscopic Co. imp.

SIGILLARIA SP.

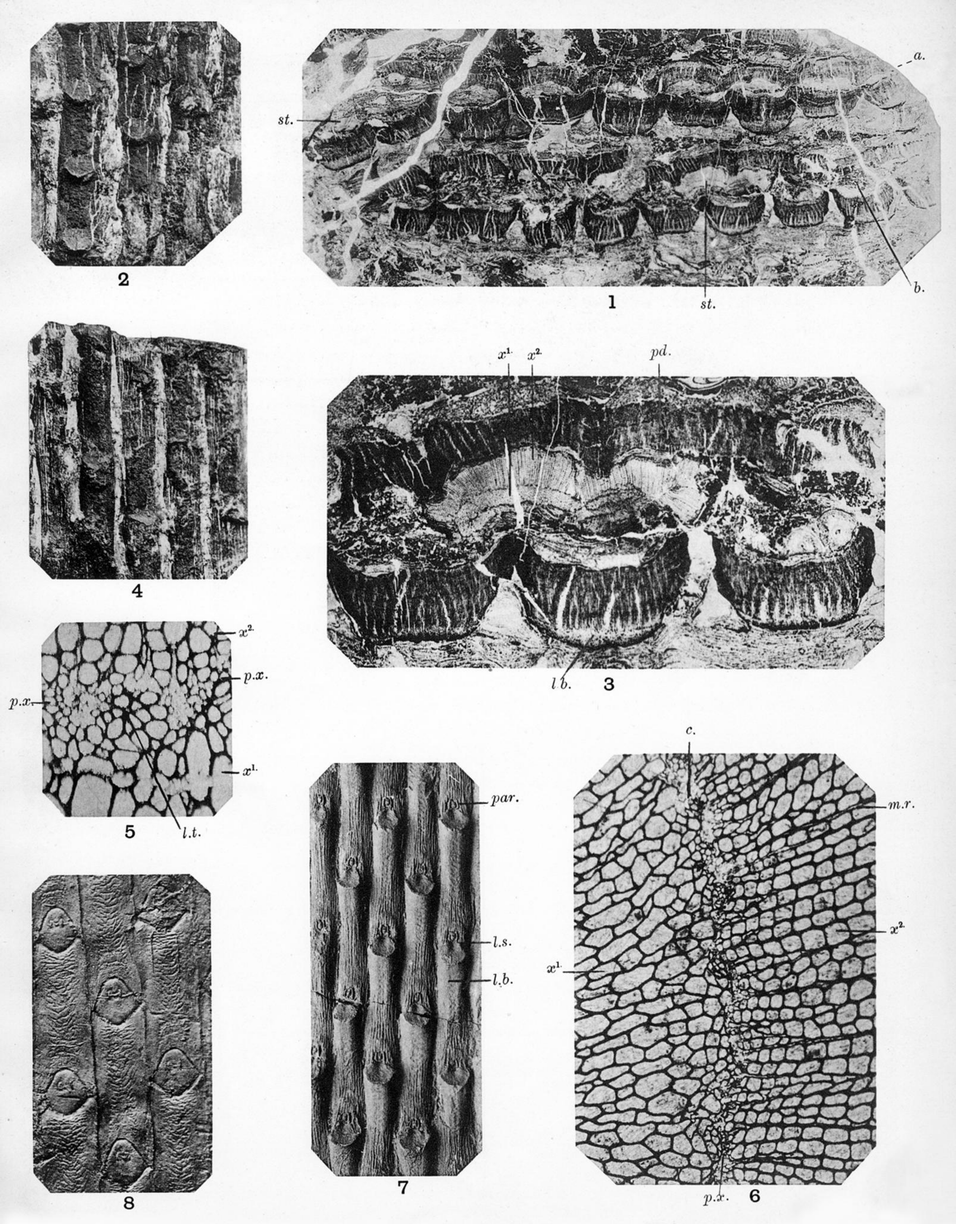

PLATE 14.

Sigillaria scutellata, BRONGN.

Fig. 1.—Specimen A. Transverse section of a petrifaction containing two stems belonging to this species. The upper stem (*a*) shows nine ribs on each side, and a small portion of the stele (*st.*), which is badly crushed. The lower (*b*) exhibits the same number of ribs. The stele (*st.*) is better preserved. × $\frac{4}{3}$.

Fig. 2.—Specimen A. External surface of three ribs, showing the leaf-scars, belonging to the upper stem (*a*) seen in transverse section on fig. 1. Natural size.

Fig. 3.—Specimen A. Part of a transverse section of the lower stem (*b*) seen on fig. 1, showing the primary (x^1) and secondary wood (x^2). On the upper side the ribs are decorticated, and only the more internal portion of the periderm (*pd.*) is seen. On the lower, there are three ribs, the middle one showing a small portion of a leaf-base (*l.b.*). The stem has undergone some distortion before or during preservation, with the result that the grooves between the ribs on the lower side are now very much broader than they probably were in the living state. × 4.

Fig. 4.—Specimen A.—External surface of five ribs, showing traces of leaf-scars, belonging to the lower stem (*b*) seen in transverse section on figs. 1 and 3. Natural size.

Fig. 5.—Specimen C. Transverse section through a leaf-trace bundle (*l.t.*) in a groove of the corona formed by the crenulated outer margin of the primary wood (x^1). The secondary wood (x^2) and two protoxylem groups (*px.*) are also seen. Section V. 8931, General Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 95.

Fig. 6.—Specimen A. Transverse section of the stele of the lower stem (*b*) shown on figs. 1 and 3. On the right is seen the secondary wood (x^2), the elements of which are radially arranged, and often separated by medullary rays (*m.r.*). On the left, the larger, and less regularly disposed elements of the primary wood (x^1). The corona (*c.*), formed by the crenulated outer margin of the primary wood, and numerous protoxylem (*px.*) groups at the angles of the corona, are also shown. Scott Coll., No. 2300. × 40.

Fig. 7.—*Impression* of the ribs of a specimen from the Middle Coal Measures of Dudley, South Staffordshire. The leaf-bases (*l.b.*) are here seen in the natural condition, and form bracket-like organs projecting from the surface of the ribs. They are slightly decorticated, especially above the leaf-scars (*l.s.*). The smooth surface of the leaf-bases, which in the living state occupied a larger area both above and below the leaf-scars, gives a rough idea of the extent of the parenchymatous tissue forming the leaf-base. The striæ of the ribs are due to the periderm being laid bare through a slight decortication of the more external thin-walled tissue. The prints of the leaf-trace, and the parichnos (*par.*) of the leaf-scars are well seen. No. V. 1232, Geol. Dept., Brit. Mus. (Nat. Hist.). Johnston Coll. Natural size.

Fig. 8.—*Impression* of the ribs of a specimen from the Coal Measures of Newcastle, Northumberland. The ribs and leaf-bases are here compressed and flattened,—a common condition among such impressions. This photograph should be carefully compared with fig. 7. The form of the leaf-scars, typical of this species, is well seen, as also the ornamentation of the leaf cushion below the scar (*cf.* Plate 16, fig. 10). No. 750, Carbon. Plant Coll., Sedgwick Museum, Cambridge. × $\frac{6}{5}$.

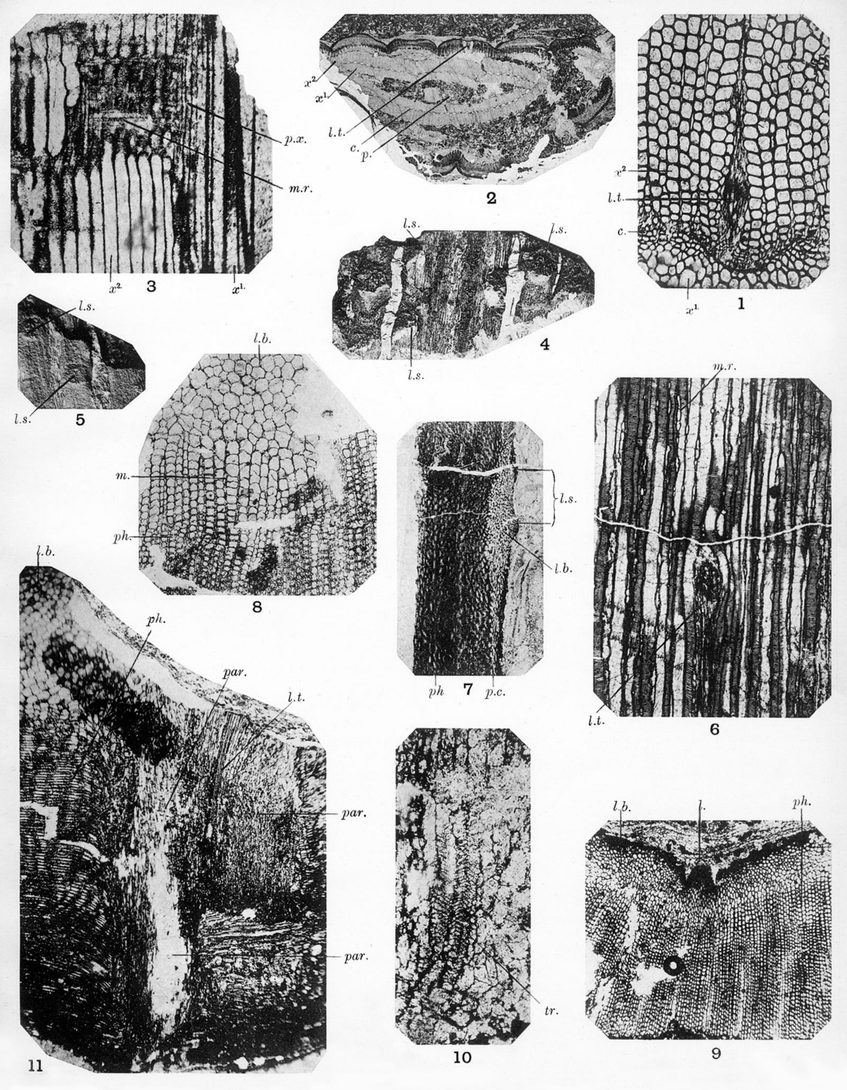

PLATE 15.

Sigillaria, sp.

Fig. 1.—Specimen B. Transverse section through the stele, showing the primary wood (x^1), the corona (*c.*), the secondary wood (x^2) and a leaf-trace (*l.t.*) passing through the secondary wood. The scalariform tracheides of the leaf-trace are seen in oblique longitudinal section. × 40.

Fig. 2.—Specimen B. Transverse section showing the ribs and the stele. Five ribs are seen on the upper side, the middle one showing a gap (*l.t.*) marking the position at which a foliar bundle entered the leaf-base. The primary xylem (x^1) has become almost entirely free from the secondary wood (x^2) through some accident in the preservation, and thus the sinuous outline of the corona (*c.*) is clearly seen. The pith cavity (*p.*) is much less compressed than in Specimen A. On the lower side the ribs are less well preserved. The parenchymatous tissue external to the periderm is, however, seen to be continuous from one rib to another. × $\frac{3}{4}$.

Fig. 3.—Specimen C. A radial section through the primary xylem (x^1), the protoxylem (*px.*) and the secondary xylem (x^2). The section passes through a medullary ray at *m.r.* No. V. 8932, General Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 40.

Fig. 4.—Specimen B. External surface of the ribs, which are not well enough preserved to permit of specific determination. Traces of the leaf-scars (*l.s.*) can, however, be seen, and these were fairly distant from one another. The transverse section of this petrifaction is shown on fig. 2 of this plate. Natural size.

Fig. 5.—Specimen E. External surface of three ribs of a petrifaction with distant leaf-scars (*l.s.*), showing only the bark of a ribbed Sigillaria. Natural size.

Fig. 6.—Specimen B. Tangential section through the secondary wood, showing medullary rays (*m.r.*) and a leaf-trace (*l.t.*) passing through the wood. × 40.

Fig. 7.—Specimen H. Radial section through a rib, showing the form of the leaf-base (*l.b.*) which is not cut here quite in the median plane. The position of the leaf-scar is indicated by *l.s.* This section is interesting as showing that the rib is formed largely of phelloderm (*ph.*). The position of the secondary meristematic zone is indicated by the curved line bounding externally the dark coloured prosenchymatous tissues of the phelloderm. Below the leaf-base, a small area of parenchymatous tissue is seen at *p.c.*, which is probably part of the primary cortex which has persisted, external to the secondary meristem. The leaf-base forms a bracket-shaped excrescence of parenchymatous elements on the surface of the rib. Compare text-figure on p. 143. × 5.

Fig. 8.—Specimen C. Transverse section of a rib passing through a leaf-base (*l.b.*). The radially arranged elements of the phelloderm (*ph.*) are seen in the lower half of the photograph. There is no definite cambial zone on the outer margin of this tissue, but, in this position (*m.*), several of the parenchymatous cells appear to have recently undergone divisions. In the upper part of the figure the parenchymatous elements of the leaf-base (*l.b.*) are well seen. No. V. 8931. General Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 40.

Fig. 9.—Specimen G. Transverse section through a rib just above the leaf-scar, showing the ligule (*l.*) lying in its pit, the leaf-base (*l.b.*), and the phelloderm of the rib (*ph.*). × 18.

Fig. 10.—Specimen C. Radial section through a rib, showing the xylem of a leaf-trace, passing through a leaf-base. The tracheides (*tr.*), which appear to be spiral, are in reality scalariform. No. V. 10,983, General Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 100.

Fig. 11.—Specimen F. Radial section of a rib and a leaf-base, passing through the median plane of the rib. The external surface is slightly decorticated in the neighbourhood of the leaf-scar. The parenchyma of the leaf-base is seen at *l.b.*, which is near the angle of the leaf-base below the leaf-scar. The phelloderm (*ph.*) is here of considerable thickness. One of the xylem strands of the leaf-trace is seen at *l.t.*, below the parichnos (*par.*), which is represented below by a large gap, though above by thin-walled elements on either side of the trace, but at some little distance from it. No. 654, Williamson Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 18.

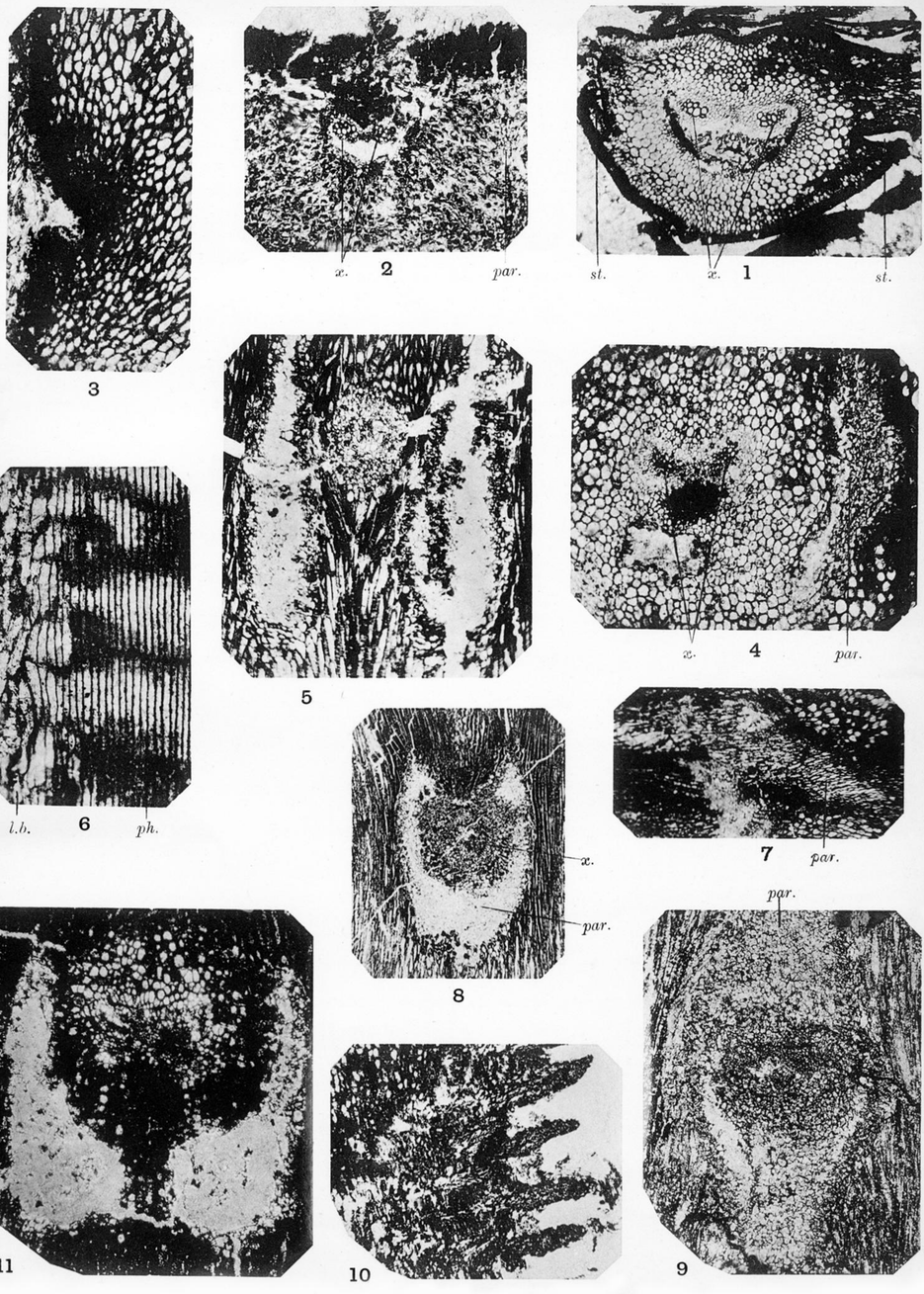

PLATE 16.

Sigillaria, sp.

Fig. 1.—The *Sigillariopsis sulcata* of Scott. Transverse section of the leaf of a Eusigillarian stem. The two xylem strands (*x.*) of the bundle are here very distinct. The stomatiferous furrows (*st.*) are also shown. No. 2268, Scott. Coll. × 27.

Fig. 2.—Specimen A. Tangential section through the surface of a leaf-scar. This photograph shows the thick-walled cells which form the external limit of the leaf-base. The two xylem groups (*x.*) of the leaf-trace are clearly seen. One of the strands of the parichnos is shown at *par.* × 35.

Fig. 3.—Specimen G. Radial section of a rib passing through the pit of the ligule. The cells of the leaf-base are here cut somewhat obliquely. × 37.

Fig. 4.—Specimen A. A tangential section of a leaf-base, at a slightly deeper level than that shown on fig. 2. The two xylem strands of the leaf-trace can be seen, and one arm of the parichnos (*par.*) is shown on the left-hand side. × 40.

Fig. 5.—Specimen A. A tangential section at a still deeper level in the rib than that shown in the last figure, and cut near the external margin of the phelloderm. The structure of the bundle is here obscure. The large size of the parichnos strands, below the bundle, is especially noticeable. × 30.

Fig. 6.—Specimen F. A radial section through the phelloderm (*ph.*) and leaf-base (*l.b.*) of a rib. No. 654, Williamson Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 35.

Fig. 7.—Specimen F. A radial section through a rib, showing the tissue of a parichnos strand (*par.*). No. 654, Williamson Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 18.

Fig. 8.—Specimen D. A tangential section at a deeper level in the phelloderm than that shown on Fig. 5. The xylem strand (*x.*) of the leaf-trace is here single. The two arms of the parichnos (*par.*) have met and coalesced below, and are beginning to approach one another above the bundle. × 20.

Fig. 9.—Specimen C. A tangential section of a rib passing deep in the phelloderm. The structure of the leaf-trace is here obscure. The parichnos (*par.*), at this level, completely surrounds the trace. No. V. 10,984, General Coll., Geol. Dept., Brit. Mus. (Nat. Hist.). × 35.

Fig. 10.—Specimen A. An oblique tangential section through the external layers of the leaf-base below the leaf-scar, showing, on the right, the ornamentation (*cf.* Plate 14, fig. 8) formed by short, transversely placed bands of thick-walled elements. To the left the thickened cells, limiting the leaf-base externally, are seen. × 20.

Fig. 11.—Specimen E. A tangential section through a rib, passing through the phelloderm at a level intermediate between that of the sections figured on figs. 5 and 8. The two arms of the parichnos have met below, but the fusion is as yet slight. × 35.