

XXIX.—On *Rhetinangium arberi*, a new genus of Cycadofilices from the Calciferous Sandstone Series. By W. T. Gordon, M.A., B.A., D.Sc., Lecturer in Palæontology, Edinburgh University. Communicated by Professor JAMES GEIKIE, D.C.L., LL.D., etc. (With Three Plates.)

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During the past few years probably no group of fossil plants has received more attention from palæobotanists than that of the Pteridospermeæ. Many fern-like impressions, derived from Carboniferous rocks, have proved to be members of this division of the vegetable kingdom; while many more may ultimately be removed from the Filicales and included in the Pteridospermeæ. Specimens, however, in which the internal structure is preserved, may, as a rule, be correctly referred to their respective class, but among those included in the latter group there is considerable diversity of organisation, and recently described genera have tended to increase the diversity of type rather than to indicate relationships among the forms already known. In fact we seem so far to have obtained only a very few examples of what must have been an exceedingly diversified plant family in late Palæozoic times.

Yet certain genera—*Sutcliffia*, *Stenomyelon*, etc.—exhibit anatomical characters which place them in an intermediate position between the polystelic *Medulloseæ* and the monostelic *Lyginodendreaæ*. These recently discovered forms, while helping to link up the extreme types, cannot be included in the same genus; their anatomy, indeed, seems to indicate several different lines of evolution within the group.

The first petrification described from the Calciferous Sandstone rocks of Pettycur, namely, *Heterangium grievii*, was one of the simpler pteridospermous* forms, and the specimens were so abundant and so well preserved that the structure of this species is exceedingly well known. It has marked fern affinities, while cycadean characters are also present in the loose form of the secondary wood. No other Pteridosperm was obtained from the Pettycur rocks until about four years ago, when I collected what appeared to be a new species of *Heterangium*.† Subsequent investigation has shown that it differs markedly from *Heterangium* and also from all known genera of the *Pteridospermeæ*, though it undoubtedly belongs to the *Cycadofilices*. I have been compelled, therefore, to make it the type of a new genus. In the choice of a name I have been guided by a characteristic feature of the anatomy, namely, the great development of what appear to be secretory sacs and ducts. At the same time *Rhetinangium*—the name adopted—suggests affinities with *Heterangium*. The specific name was given in

* Classed as a Pteridosperm on structural evidence only. SCOTT, *Studies in Fossil Botany*, 1909.

† *Heterangium arberi*, Gordon: Thesis, *On the Fossil Flora of the Pettycur Limestone*. University Library, Cambridge (1910), Edinburgh (1911).

honour of Dr E. A. NEWELL ARBER, to whom I was much indebted for his kindly criticism and advice while conducting my research work at Cambridge.

DESCRIPTION OF THE SPECIMENS.

As already stated, the first specimen was obtained about four years ago, and the structure determined as far as possible; but a second example was discovered more recently at the same locality; while a third, which may be specifically identical with these two, was collected by Dr KIDSTON on the bank of the Whiteadder Water near Edrom, Berwickshire. All three specimens were derived from rocks of Lower Carboniferous age and probably from similar horizons. The Berwickshire stem was obtained several years ago, but was so indifferently petrified that it could not be described. The following description has therefore been based on the remains from Pettycur, which are, on the whole, well preserved, though not uniformly so. This variable preservation is very noticeable in the shorter of the two specimens, and, unfortunately, the best portion lay exposed on the surface of the limestone block, with the result that it had been partially weathered away. When followed further into the mass this stem was poorly petrified and finally disappeared. Its total length did not exceed $5\frac{1}{2}$ inches.

The second example was nearly twice as long (10 inches), and it passed completely through the block in which it was embedded. From both specimens series of transverse and longitudinal sections have been prepared. These number about 120, and a very fair idea of the anatomy of the plant has been obtained from them.

Several petioles were also discovered, either in organic continuity with the stems or closely associated with them, while a root was obtained attached to one of the specimens.

GENERAL STRUCTURE.

A transverse section of the stem is represented in Pl. I. fig. 1, and, although the central xylem cylinder is not particularly well preserved in this specimen, a good general idea of the anatomy may be obtained by an examination of the figure. The actual measurements of the stem are 2.5 cm. \times 1.5 cm., but the flattening is entirely due to compression prior to fossilisation. This is proved by the fact that the cortical tissues at the ends of the longer diameter are crushed together. The stem in the living plant would therefore be circular in section and probably about 2 cm. in diameter.

In the centre of the specimen is the vascular axis, which consists of an internal zone of primary wood (x^1), and an external one of secondary wood (x^2). Surrounding the xylem cylinder is the phloem and inner cortical tissues, while enclosing the whole is a thick layer of outer cortex with a well-marked hypodermal zone of anastomosing sclerotic strands. A general resemblance to the stem of *Heterangium* will at once be noticed, but a more detailed examination will disclose several differences between *Rhetinangium* and that genus.

As the vascular axis is not well petrified in the example figured (Pl. I. fig. 1), we shall turn to the other stem from *Pettycur* in order to examine that part more closely. In this specimen the xylem cylinder is about .7 cm. in diameter, and sections of it are represented in Pl. I. figs. 2 and 7. As in the former example, two regions may be noted in the xylem—the inner, primary wood, and the peripheral secondary zone (Pl. I. fig. 2, x_1 and x_2 respectively). The primary wood consists of anastomosing groups of tracheides scattered in a parenchymatous ground tissue (Pl. I. figs. 3 and 5, x^1). In the parenchyma numerous secretory sacs and ducts may be seen, their deeply coloured contents imparting a dark appearance to this central zone (Pl. I. fig. 7, *s.s.*). Surrounding the primary xylem is a zone of secondary wood with its radially distributed elements, and, in both specimens, this tissue attains a fair thickness (Pl. I. figs. 1 and 2, x_2). It is traversed by medullary rays which vary greatly in height and breadth. These rays sometimes spread out when they enter the phloem region as they do in *Heterangium tiliaoides*.

The various tissues which succeed the wood externally are each well preserved at one or other part of the specimen. In one stem the phloem is seen to consist of elongated elements, but sieve-plates have not been detected with certainty. No pericycle or endodermis can be separated from the inner cortex, which appears to have been a zone of rather delicate tissue containing numerous resin ducts and cells with dark contents (Pl. II. figs. 10 and 11, *i.c.*). These latter elements may have acted as storage or even mucilage cells, and this would account for their dark colour. No stone cells or other strengthening elements occur in the inner cortex. The outer cortex, on the other hand, contains numerous strengthening fibres, and these give a characteristic appearance to the whole zone. Pl. II. fig. 15 gives an excellent idea of this tissue; in the inner part a rather thick-walled parenchyma is seen, but the hypodermal part contains a reticulum of elongated sclerotic bands or threads. The meshes of the reticulum are narrow but they are exceedingly long. Associated with the fibres themselves are long secretory ducts.

The general outer surface of the stem is rendered irregular by the decurrent petioles. These swell out enormously at their junction with the stem, their outer cortex loses its sclerotic fibres, and so the cortex of the leaf base consists entirely of a mass of uniform small-celled parenchyma through which the petiole-trace passes to join the central axis (Pl. I. fig. 4, *pet. b.*). As a result, the petioles are readily torn from the stem, and this, no doubt, accounts for the fact that the outer cortex often appears broken up into separate segments. Usually three petiole-traces are seen departing from the stem in any transverse section. They show a succession in their development, but the stems are so crushed that the phyllotaxy has not been determined.

When the petiole-trace leaves the xylem axis it is rather peculiar in form and does not resemble the trace in any known genus of the *Pteridospermeæ*. The xylem consists of a more or less continuous, corrugated mass while still in the cortex of the stem. In the free petiole the xylem still appears continuous though the outline is

irregular (Pl. III. fig. 19), and even in the smallest divisions of the petiole observed the same irregular outline may be seen in the trace (Pl. III. fig. 20).

One example of an adventitious root has been discovered in organic continuity with the stem, but the preservation leaves much to be desired. The root-trace is represented in transverse section in Pl. II. fig. 12.

HISTOLOGY OF THE STEM.

Although both specimens are to some extent crushed, yet the preservation is sufficiently perfect to allow of a minute examination of the tissues. Starting with the primary wood, we find that there is conjunctive parenchyma between the anastomosing xylem strands, and this ground tissue is interesting on account of the numerous secretory ducts and sacs contained in it (Pl. I. fig. 7, s.s.). The ducts may result from the fusion of several sacs or they may be elongated sacs. The former notion seems to be supported by the fact that the dark contents do not occur as continuous masses but are, in every case, broken up into small pieces (Pl. III. fig. 25, s.s.). This appearance, however, may be explained otherwise, for the resinous contents may have contracted prior to fossilisation, and the fragments have been subsequently separated by the petrifying medium. The whole duct would thus seem to contain a series of dark coloured bodies in its interior, and appear to result from the fusion of separate cells. In transverse section the ducts may be clearly seen in Pl. I. fig. 7, s.s.; the dark contents are here seen contracted into the centre of the lumen. Taking all available data into account, however, it seems more probable that these ducts are produced by the elongation of single elements. No epithelium has been noticed surrounding the secretory elements.

The primary wood consists of tracheides, on the walls of which multiseriate pits are arranged in a reticulate manner (Pl. I. fig. 5, x^1). These elements vary in size from 130μ to 150μ in diameter, and are united in groups of from twenty to sixty. The number of tracheides in each group is thus much greater than in the corresponding groups in *Heterangium*. There are, however, fewer xylem groups in the primary wood of *Rhetinangium* than in the former genus.

Round the periphery of the primary wood the xylem groups contain much smaller tracheides. These are the protoxylem elements, and they are seen in longitudinal sections to have scalariform or sub-spiral thickenings on their walls (Pl. I. fig. 6, *prx.*). They are *exarch* in position and not *mesarch* as in *Heterangium*.

Each peripheral group of the primary xylem is bounded externally by a wedge of secondary wood, and so the principal medullary rays are in direct communication with the ground tissue of the central primary wood. The elements of the secondary zone are much smaller than those of the primary xylem, being from 45μ to 85μ in diameter, and they are arranged, as usual, in radial rows. Secondary medullary rays occur in each wedge, and usually a ray occurs between each two or three rows of xylem, though

sometimes they occur between every two rows (Pl. I. fig. 8, *m.r.*). In one specimen, after the development of some fourteen rows of tracheides, there is a sudden change to much smaller elements (Pl. I. figs. 8 and 9, *w.r.*). Just such a change, indeed, as is seen between the spring and autumn wood in living trees. About three rows of small elements are formed and then the larger tracheides are again developed. The change occurs simultaneously all round the stem and not irregularly, as has been occasionally observed in some fossil stems. It is not suggested, however, that this proves seasonal alternation at that early time in the earth's history, though probably some external influence had caused a temporary check to the growth. When, however, the conditions became favourable again, large elements were developed as before.

Immediately beyond the xylem cylinder there occur, in certain places, patches of phloem in a fair state of preservation. The elements comprising this tissue have thin walls and are considerably elongated. No sieve plates were observed on their walls, but the light brown contents of the cells may have obscured them. Secretory sacs and ducts are sometimes seen in this region.

Passing outwards from the phloem the cortical zone is reached, and it can easily be separated into two layers—the inner and outer cortex. No hard and fast line, however, can be drawn between the pericycle and the inner cortex. In transverse section the latter tissue may be seen in Pl. II. fig. 10, *i.c.*, and there the delicate cell walls of the parenchyma may easily be observed. Numerous secretory cells (*s.c.*) and sacs (*s.s.*) are also clearly visible. In longitudinal tangential section a great number of these elongated sacs (*s.s.*) are shown, while the small secretory cells are also very distinct (Pl. II. fig. 11, *s.s.* and *s.c.* respectively). The secretory elements with their dark contents are so numerous that they impart a peculiar appearance to the whole inner cortex. One would almost imagine that the whole tissue was of a mucilaginous nature.

Towards the periphery of this region the cells appear tangentially elongated (Pl. II. fig. 10, *c.p.*), but that is due to the outer cortex being crushed down upon the inner zone. As a result there is a well-defined junction between inner and outer cortex, but the junction is less marked where there has been little crushing (Pl. II. fig. 15, *i.c.*). The great number of secretory elements in the inner cortex at once distinguishes it from the innermost layers of the outer cortex.

The outer cortical region constitutes one of the most distinctive features of the genus, and in both specimens it is very well preserved. Three zones may be noticed. The innermost consists of a thick-walled parenchyma and is free from secretory elements. The second (hypodermal) zone consists of a parenchymatous ground tissue in which anastomosing groups of sclerotic fibres are set. These fibres are closely associated with secretory ducts. The ground tissue of this cortical layer is peculiar. In a transverse section of the stem the parenchyma is seen to contain elements which are elongated radially with respect to the nearest sclerotic group (Pl. II. fig. 15, *e.o.c.*). In any other direction they resemble the rest of the cortical cells in size. The elongation takes place towards the sclerotic groups as centres (Pl. II. fig. 15). In some cases the

elongation of the cell has been so great that it divides into two cells (Pl. III. fig. 23, *c.w.*). Although this elongated parenchyma is very marked in some cases, yet it is not always constant over the whole hypodermal region. In Pl. II. fig. 15 it is a marked feature over the whole area, particularly towards the inner part of the hypoderma, but in Pl. II. fig. 14, while present on the right-hand side, it is almost absent on the left-hand side of the figure. A similar phenomenon is shown in longitudinal section in Pl. III. fig. 23 (marked elongation at α) and in Pl. II. fig. 13 (no elongated parenchyma).

The sclerotic strands, which are not uninteresting in themselves, consist of groups of vertically elongated elements in which the lumen has been almost entirely closed by deposition of material on the cell walls. The number of these cells in each strand varies greatly. The strands unite tangentially at various levels and hence a reticulum results. They only unite, however, at considerable distances, so that the meshes of the reticulum are long and narrow. Each strand may also divide radially into two or three smaller groups (Pl. II. fig. 15). Between the sclerotic strands the ordinary cortical parenchyma is found, while associated with these fibrous groups, or partly or completely sunk in them, are long secretory ducts (Pl. II., figs. 13, 14, and 15, *s.s.*). These ducts are about 100μ in diameter, and are clearly seen among the smaller-celled cortical parenchyma and sclerotic fibres.

In some cases the hypodermal sclerenchyma abuts directly on the surface of the stem, but, as a rule, there are about three layers of small-celled parenchyma external to the hypoderma. In certain parts, however, there is an enormous development of parenchyma beyond the sclerotic zone (Pl. I. fig. 4, *pet. b.*), and sometimes the fibrous outer cortex disappears entirely at these places. This takes place at the junction of the petiole with the stem, and will be considered later.

HISTOLOGY OF THE PETIOLE.

In the centre of the petiole is the vascular strand, and it is quite unlike the corresponding strand in other *Pteridospermeæ*. In the more complex members of that group a great number of small strands pass into the petiole, while in the *Lyginodendreae* the trace consists of a single or double bundle. In *Rhetinangium*, however, the petiole-trace appears to consist of several U-shaped xylem groups aggregated into one long corrugated band. Usually three such traces are seen round the stem in any transverse section, and these are in different stages of development. In Pl. I. fig. 2 one trace has just been emitted at A, a second is completely differentiated from the stem at B, while the third is only forming at C. The first thing to be noted about this last trace is that it appears to consist of several peripheral strands of the primary wood. As will also be noted, it has passed about half-way through the zone of secondary wood. The second trace B has emerged from the secondary xylem, and the various groups are more or less U-shaped and connected together either directly or by conjunctive parenchyma. The protoxylem groups are on the external edge and are fairly numerous

(Pl. III. fig. 16, *prx.*). The trace B is shown at a lower level in Pl. III. fig. 17, and at a still earlier stage in Pl. III. fig. 18. In this last figure the trace is just leaving the zone of secondary wood; a few of the elements of the latter tissue still may be seen on the outer margin of the trace (Pl. III. fig. 18, x^2). The peculiar fashion in which the xylem of the petiole strand is connected together is clearly shown in Pl. III. fig. 17. The trace passes slowly outwards as we ascend, but unfortunately the soft nature of the inner cortex of the stem has allowed the latter to be easily crushed, and the petiole-traces have suffered disintegration along with the inner cortex. All that can be said of the petiole-trace in this region is that it certainly does not divide into small strands during its passage through the cortex into the free petiole. The protoxylem elements lie abaxially in the trace (Pl. III. figs. 16 and 17, *prx.*).

Opposite the point of emission of a petiole-trace from the central axis of the stem, the sclerotic hypoderma thins out and finally disappears. Concurrently as the hypoderma dies out, the external part of the cortex becomes enormously developed until it becomes almost as large as the stem itself (Pl. I. fig. 4, *pet. b.*). In the figure shown the petiole base is detached from the stem, and in fact this section is cut some distance above the point where the trace enters the petiole. It indicates, however, the great development of buttressing tissue round the petiole base.

It will also be noticed that at this point the petiole has no sclerotic hypoderma. This fibrous zone, however, again appears higher up the petiole, but at that level the diameter of the whole rachis is much reduced. In other words, the base of the petiole is greatly dilated, and in that region the sclerotic outer cortex disappears. As a result of the soft nature of the petiole base the rachis is almost always torn from the stem or laterally displaced. The petiole shown in Pl. I. fig. 4 really departed opposite the gap seen at A in the outer cortex of the stem. The dilatation of the petiole base occurred both on the upper and under sides.

It is interesting to note that certain fern-like impressions of Carboniferous age have similar dilatations where the pinnæ join the rachis, and this also happens where the latter join the stem. (A similar type of structure may be seen in recent *Marattia* and *Angiopteris* pinnæ where they joined the petiole.)

Only one petiole was actually traced into the stem, but several have been followed until the hypoderma disappears and the trace was seen surrounded by a uniform, parenchymatous cortex. A similar disappearance of the sclerotic fibres has been seen in longitudinal section. Behind the departing petiole the sclerotic hypoderma closes in and ultimately fills the gap. Thus the departure of the petiole causes a temporary gap in the fibrous zone of the cortex.

The trace in the free petiole is represented in Pl. III. fig. 19, and although there is considerable crushing, one can easily observe that it consists of a continuous flat band of xylem with abaxial protoxylem groups. Even in the smallest branch discovered, the trace is continuous but with a convoluted outline (Pl. III. fig. 20). In no case does the trace break up into a number of small strands.

The cortical tissues in the petiole are quite similar to those in the stem. The inner cortex is a delicate parenchyma with secretory sacs and ducts, while the outer zone contains the sclerotic hypoderma with its secretory ducts.

HISTOLOGY OF THE ROOT.

One example of an adventitious root has been found in organic connection with the stem, and several similar detached roots have been noted. The root-trace seems to leave the stem close to the point of emission of the petiole-trace, or it may be that it comes from the petiole-trace itself. This particular specimen occurs at a part of the stem where the outer cortex has been stripped off and the root is seen in the inner cortex. Although the trace is not very well preserved, one can see that it was probably tetrarch. A considerable amount of secondary wood has been developed round the primary xylem (Pl. II. fig. 12, x_1 and x_2 respectively).

There are still some points in connection with the anatomy of the petiole and root which require further elucidation, and it is to be hoped that additional well-preserved examples may be discovered.

There is no indication in the specimens of their foliage or fructifications.

SUMMARY.

Rhetinangium arberi had a stem of considerable length, and was probably of scrambling habit, with adventitious roots at intervals on the stem. Petioles were emitted in spiral sequence, and three of them may be seen intersected at different levels in any transverse section.

The vascular axis is protostelic, the primary wood is of the *Heterangium* type, but the protoxylem is exarch, and many secretory sacs and ducts are present in the conjunctive parenchyma. The secondary wood is of cycadean type. The protoxylem elements have scalariform or sub-spiral thickenings on their walls; the other tracheides are reticulately pitted. The phloem consists of elongated elements and parenchyma, while the inner cortex is formed of a zone of delicate tissue with numerous secretory bodies scattered through it. The outer cortex is made up of thick-walled parenchyma, and contains a sclerotic hypodermal zone round which the cortical parenchyma is much elongated radially.

The leaf-trace is peculiar in form and is produced by the union of several peripheral groups of the primary xylem. The protoxylem elements are on the lower (abaxial) surface of the trace and continue throughout in that position. In no case does the petiole-trace divide up into numerous small bundles. Even in the smallest division noticed the trace is a single strand. The cortical tissues are similar to those of the stem.

Close to the emission of a petiole-trace an adventitious root has been observed to leave the stem.

DIAGNOSIS.

Rhetinangium, gen. nov.

The characters of this new genus are, meanwhile, those of the only recorded species, *R. arberi*.

Rhetinangium arberi, sp. nov.

Stem 2 cm. in diameter, circular in transverse section and surrounded by spirally developed leaves. Central vascular axis protostelic, consisting of anastomosing groups of tracheides in a parenchymatous ground tissue with secretory ducts. Protoxylem exarch, and with scalariform or sub-spiral thickening. Xylem (primary or secondary) of long, reticulately thickened, porose tracheides. Medullary rays broad and high. Phloem and inner cortex with many secretory cells and ducts. Outer cortex of thick-walled parenchyma. Hypodermal zone of sclerotic anastomosing fibres associated with elongated secretory ducts.

Petiole-trace an aggregate of several peripheral xylem groups loosely attached together to form a corrugated band. Protoxylems abaxial. Leaf-bases without sclerotic hypoderma, but outer cortex enormously expanded. Diameter of petiole beyond base not abnormally large compared with stem but showing reappearance of sclerotic outer cortex. Roots tetrarch; secondary wood well developed.

Foliage and fructifications unknown.

Localities.—Pettycur, Fife, Scotland, and Edrom, Berwickshire, Scotland.

Horizon.—Calciferos Sandstone Series (= Culm).

AFFINITIES AND GENERAL CONSIDERATIONS.

The primary wood in *Rhetinangium* is similar in its general structure to the xylem cylinder in certain living protostelic ferns, and, in particular, since the xylem is exarch, to that of *Lygodium*. At the same time the type of the secondary wood, with its numerous broad and high medullary rays, is distinctly cycadean. The structure of the axis thus places *Rhetinangium* in an intermediate position between ferns and cycads. In any case, the new genus possesses all the characters necessary for its inclusion in the group of the *Cycadofilices*.

Although its fructification is unknown, it is quite admissible to refer this new plant to the *Pteridospermeæ* on anatomical grounds alone, but its structure does not indicate any very obvious relationship with other members of that group. The genus, however, is not a perfectly isolated one, since there are marked resemblances between its anatomy and that of certain other forms. The primary xylem recalls the corresponding tissue in *Megaloxyton*, *Heterangium*, *Medullosa*, and in a less degree that in *Sutcliffia*. The exarch nature of the xylem, however, at once separates this new type from *Heterangium* and *Medullosa* (which latter, as far as its vascular axis is concerned, is really a polystelic *Heterangium*). With *Megaloxyton*, on the other hand, the affinities are much closer: apart from the difference in size, indeed, the primary wood in both is

similar when viewed in transverse section. In each case we find a mixture of tracheidal and parenchymatous tissue in the axis, while secretory cells are also seen in the parenchyma. In longitudinal section, on the contrary, marked differences are at once visible. It is true that the peripheral groups of scalariform or sub-spiral elements are similar in position in each, but here the similarity ends. The remainder of the tracheidal tissue in *Megaloxylon* consists of short, broad elements with multiseriate bordered pits on their walls, while the secretory cells are also short. In *Rhetinangium* the tracheides are long, reticulately thickened, elements, and the secretory bodies are either short cells or long ducts (Pl. III. fig. 25, *s.c.* and *s.s.*). The distinction between the primary wood in these two genera, then, consists essentially in the type of tracheide.

The secondary xylem is of a similar type in each case, but in the new genus it appears to be less compact than in *Megaloxylon*. An interesting point is the clearly marked ring of narrow elements in the secondary wood. Professor SEWARD records the sporadic occurrence of such tracheides in a similar position in his genus.

Although the leaf-trace in Professor SEWARD's plant is not known outside the zone of secondary xylem, yet its resemblance, in that area, to the stem of *Heterangium* (except for the exarch xylem) is not without interest, for the trace in *Rhetinangium* under the same conditions would have a similar form. In Pl. I. fig. 2, C, the departing trace in *Rhetinangium* is merely a group of xylem strands, with conjunctive parenchyma as in the stem of *Heterangium*, and there cannot be any doubt that if the two ends of the trace B in that figure or in those shown in Pl. III. figs. 16, 17, and 18, were bent inwards until they met, it would also form a leaf-trace similar to the stem of *Heterangium*. (The position of the protoxylem groups, of course, is different.) It is just possible, also, that the breadth of the zone of secondary xylem and its compact nature in *Megaloxylon*, may account for the rounding off of the petiole-trace in that genus, while it is traversing this tissue, and that when the trace became free it would flatten out in a similar fashion to the trace in *Rhetinangium*. In both forms several adjacent exarch strands coalesce to produce the trace, the protoxylem groups being situated abaxially. All these structural resemblances in the two stems show that they were probably related, but *Megaloxylon* appears to be the more specialised type. The peculiar short tracheides in the primary wood of the latter are, no doubt, as Professor SEWARD has pointed out, an adaptation for water-storage.

The affinities of *Rhetinangium* with other members of the *Pteridospermæ* are not so obvious. The type of the primary xylem cylinder and the monostelic character of the stem, at first sight, suggest affinities with *Heterangium*, but the detailed structure of the stele and also of the petiole-trace proves that the resemblances are more apparent than real. In the primary vascular cylinder of the new genus the tracheidal groups are large and few in number, while in *Heterangium* (Pl. III. fig. 22) the reverse is the case. Then, again, the exarch xylem and the numerous secretory elements in *Rhetinangium* at once distinguish it from *Heterangium*. It must be borne in mind, however, that certain species of the latter genus have protoxylem elements situated much nearer the

periphery than in others, and that secretory sacs occur in *H. tiliæoides* in the medullary rays and in the inner cortex. One characteristic feature of *Heterangium*—the sclerotic discs in the inner cortex—finds no parallel in *Rhetinangium*, while the peculiar outer cortex of the latter is not seen in the former.

As far as the petiole-trace is concerned the two types are distinct, yet there seems to be some connection between them. In Pl. III. fig. 21 an exceedingly well-preserved petiole-trace of *Heterangium grievii* is shown; it is sub-triangular in shape, and the protoxylem is mesarch (Pl. III. fig. 21, *prx.*). The petiole-trace in *Rhetinangium*, as we have seen, is much more complex and it is exarch, yet it looks, to some extent, like an aggregation of several traces, each similar to a *Heterangium* trace in which the base of the triangular xylem has disappeared. Now, in *Heterangium* the petiole-trace gradually assumes a U shape as it is followed outwards, though it has always mesarch protoxylem in two groups, one in each arm of the bilobed (U-shaped) trace.

Relationships with the more complex pteridosperms are not very evident, but the peculiar form of the undivided petiole-trace appears to indicate a transition from the simple type so characteristic of the *Lyginodendreae* to the much divided type in the *Medulloseae*. The outer cortex of the stem and petioles, in transverse section, is partly of the *Myeloxylon landriotii* and partly of the *M. radiata* type, both of which are common in the *Medulloseae* though not confined to that group. But in longitudinal section the sclerotic fibres are occasionally seen to join, thus forming a reticulum. The exarch xylem of *Rhetinangium* suggests affinities also with *Sutcliffia* and *Stenomyelon*.

The nearest relative seems to be *Megaloxylon*, though that genus is more highly specialised in at least one direction. The difference between the two seems exactly parallel to what occurs among the *Osmundaceae*, and the explanation that the short tracheide is probably a specialisation for water-storage has also been adopted by KIDSTON and GWYNNE-VAUGHAN in their memoirs on the *Fossil Osmundaceae*.*

Taking the *Cycadofilices* as a whole, the more ancient types show a simpler structure, and, since *Rhetinangium* occurs at a lower horizon than *Megaloxylon*, we would expect it to show a relatively simpler organisation. The primary wood in the former genus contains long tracheides and is much smaller in diameter than is the case in *Megaloxylon*, and it may be argued that the inner tracheides in the latter stem would be too far from the periphery to perform the function of water conduction except near the apex of the stem. They therefore appear to have terminated their growth and become modified for water-storage, whereas those in *Rhetinangium* retain their primary function throughout.

In concluding this paper I desire to express my thanks to Dr ARBER, Dr KIDSTON, F.R.S., and Dr SCOTT, F.R.S., for their unfailing kindness and valuable suggestions whenever difficulties arose, and also for the readiness with which they placed specimens from their collections at my disposal.

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EXPLANATION OF PLATES.

(Figures all taken from untouched negatives by the author. Unless otherwise stated, the figured specimens are in the author's collection.)

PLATE I.

Rhetinangium arberi.

Fig. 1. Transverse section of stem. x^1 = primary wood; x^2 = secondary wood; *i.c.* = inner cortex; *sc.o.c.* = sclerotic hypoderma. Slide 1045. $\times 3.7$ diameters.

Fig. 2. Transverse section of central vascular axis. x^1 = primary wood; x^2 = secondary wood; *i.c.* = inner cortex; *o.c.* = outer cortex; A, B, C, = points of emission of petiole-traces. Slide 1000. $\times 8.5$.

Fig. 3. Longitudinal section of stem. x^1 = primary wood; x^2 = secondary wood; *m.r.* = medullary ray; *ph.* = phloem; *i.c.* = inner cortex; *o.c.* = outer cortex; *sc.o.c.* = hypoderma. Slide 984. $\times 9$.

Fig. 4. Transverse section of stem and petiole base. x^1 = primary wood; x^2 = secondary wood; *sc.o.c.* = sclerotic hypoderma; *pet. b.* = petiole base; A = point of emission of petiole-trace from the cortex. Slide 1003. $\times 2.3$.

Fig. 5. Longitudinal section to show tracheides. x^1 = primary wood; *c.p.* = conjunctive parenchyma of primary cylinder; x^2 = secondary wood; *m.r.* = medullary ray; *ph.* = phloem; *i.c.* = inner cortex. Slide 984. $\times 23$.

Fig. 6. Longitudinal section of primary cylinder to show protoxylem. x = primary xylem; *pr.x.* = protoxylem (exarch). Slide 986. $\times 170$.

Fig. 7. Transverse section of primary wood to show secretory sacs. x^1 = primary wood; x^2 = secondary wood; *s.s.* = secretory sacs. Slide 1007. $\times 19$.

Fig. 8. Transverse section of part of axis to show structure of wood. x^1 = primary wood; *prx.* = protoxylem; x^2 = secondary xylem; *m.r.* = medullary rays; *w.r.* = ring of small tracheides. See also Pl. III, fig. 24. Slide 1005. $\times 19$.

Fig. 9. Section similar to fig. 8. x^1 , *m.r.*, *w.r.* as in that figure. Slide 1006. $\times 19$.

PLATE II.

Rhetinangium arberi.

Fig. 10. Transverse section of part of stem. x^2 = secondary wood; *ph.* = phloem; *i.c.* = inner cortex; *c.t.* = crushed cells at exterior of inner cortex; *o.c.* = outer cortex; *s.s.* = secretory sacs in inner cortex; *s.c.* = secretory cells in inner cortex. Slide 1006. $\times 30$.

Fig. 11. Longitudinal section of inner cortex. Lettering as before. Slide 1077. $\times 14$.

Fig. 12. Transverse section of root-trace. x^1 = primary xylem; x^2 = secondary xylem; *prx.* = protoxylem. Slide 1037. $\times 70$.

Fig. 13. Longitudinal section of part of outer cortex. *p.o.c.* = parenchymatous outer cortex; *sc.o.c.* = sclerotic outer cortex; *s.s.* = secretory sacs. Slide 986. $\times 36$.

Fig. 14. Transverse section of part of outer cortex. *e.o.c.* = elongated outer cortex; *sc.o.c.* = sclerotic outer cortex; *s.s.* = secretory sacs. Slide 1003. $\times 36$.

Fig. 15. Transverse section of cortex. *i.c.* = inner cortex; *e.o.c.* = elongated outer cortex; *sc.o.c.* = sclerotic outer cortex; *s.s.* secretory sacs. Slide 1048. $\times 23$.

PLATE III.

Rhetinangium arberi and *Heterangium grievii*.

Fig. 16. *R. arberi*. Transverse section of petiole-trace while attached to the axis of the stem. x^1 = primary xylem; x^2 = secondary xylem; *prx.* = protoxylem of leaf-trace; *lt.* = leaf-trace. While transferring this section a crack appeared in the specimen, and although the trace is still complete it has parted from the rest of the section near one end. Slide 994. $\times 19$.

Fig. 17. *R. arberi*. Transverse section of petiole-trace at a slightly lower level. $x^2s.$ = secondary wood of stem; *prx.* = protoxylem groups of petiole-trace. Slide 999. $\times 34$.

Fig. 18. *R. arberi*. Transverse section of petiole-trace at a still lower level. $x^2s.$ = secondary wood of stem; x^2 = secondary wood on back of petiole-trace; *prx.* = protoxylem groups of petiole-trace. Slide 1003. $\times 34$.

Fig. 19. *R. arberi*. Transverse section of petiole-trace in free petiole. Slide 1048. $\times 16$.

Fig. 20. *R. arberi*. Transverse section of trace in smallest observed division of the petiole. *lt.* = trace; *prx.* = some of the protoxylem groups. Slide 1005. $\times 60$.

Fig. 21. *Heterangium grievii*. Transverse section of petiole-trace while still joined to central axis of stem. (Compare with *R. arberi*, fig. 16.) *lt.* = petiole-trace; x^1 = primary xylem of stem; x^2 = secondary xylem of stem; *prx.* = protoxylem. Scott Collection 1016. $\times 60$.

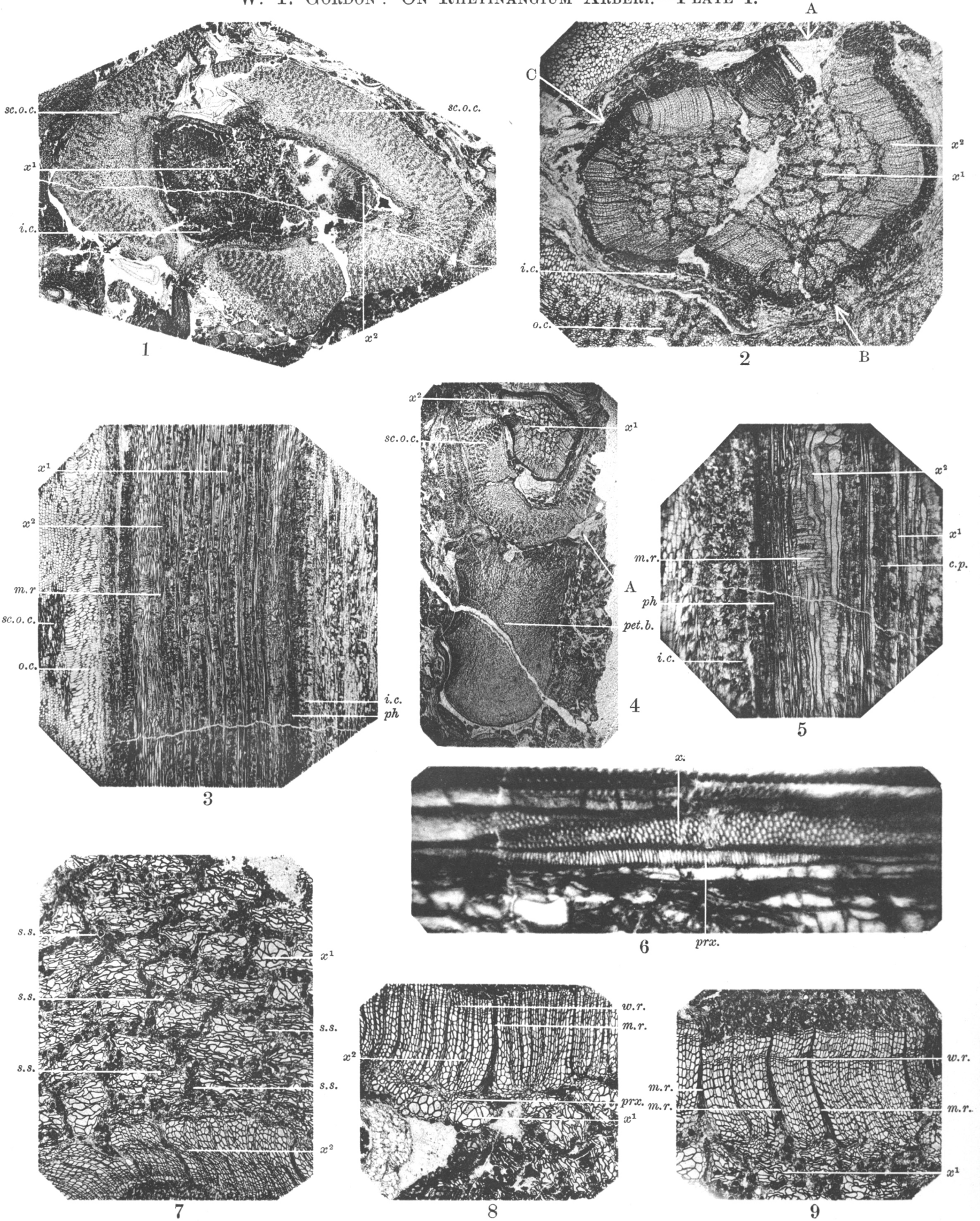
Fig. 22. *Heterangium grievii*. Transverse section of stem. (Compare with *R. arberi*, Pl. I, fig. 2.) KIRSTON Collection 512. $\times 8.5$.

Fig. 23. *R. arberi*. Longitudinal section of outer cortex showing radial elongation and the occasional division of the inner cortical parenchyma. *p.o.c.* = parenchymatous outer cortex; *sc.o.c.* = sclerotic outer cortex; *a* = radially elongated parenchyma; *c.w.* = wall dividing elongated cells into two. Slide 984. $\times 36$.

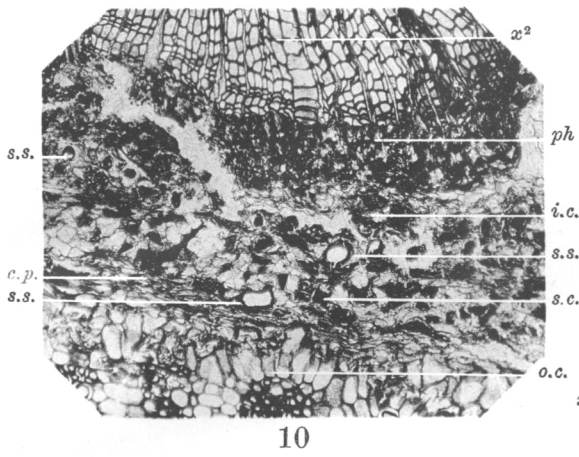
Fig. 24. *R. arberi*. Transverse section of peripheral primary wood to show position of protoxylem. Part of section shown in Pl. I, fig. 8. The photographs are reversed in position. x^1 = primary wood; *prx.* = protoxylem; x^2 = secondary wood; *c.p.* = conjunctive parenchyma of primary wood; *m.r.* = medullary ray. Slide 1005. $\times 85$.

Fig. 25. *R. arberi*. Longitudinal section of primary xylem cylinder to show secretory sacs and cells. x^1 = primary xylem group; *c.p.* = conjunctive parenchyma; *s.s.* = secretory sacs; *s.c.* = secretory cells. Slide 984. $\times 45$.

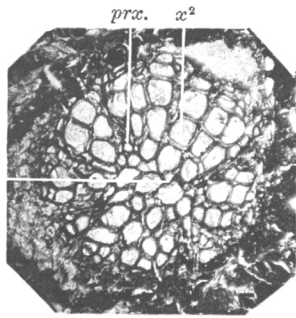
W. T. GORDON : ON RHETINANGIUM ARBERI.—PLATE I.



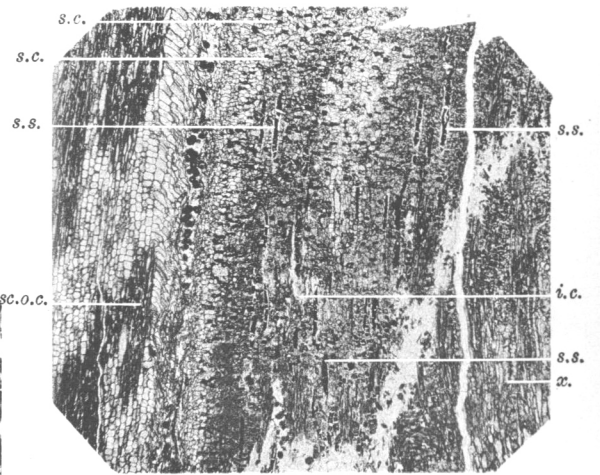
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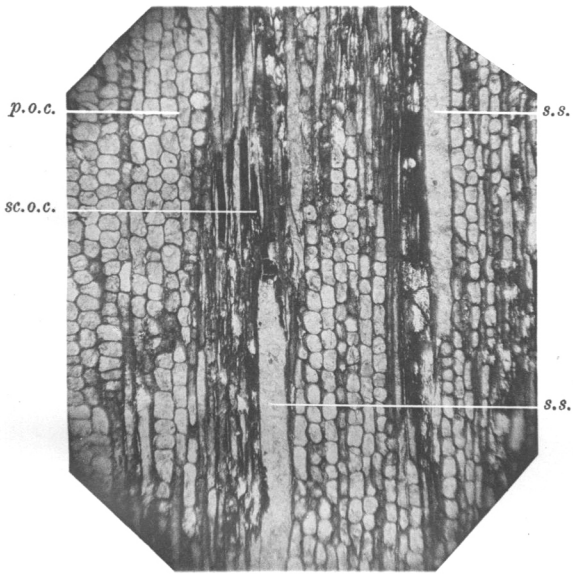
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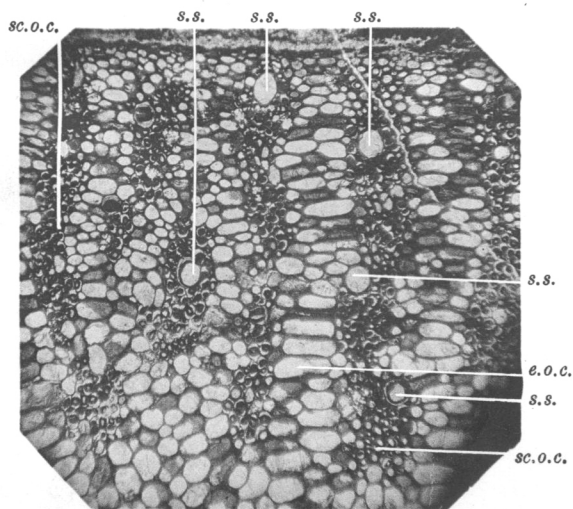
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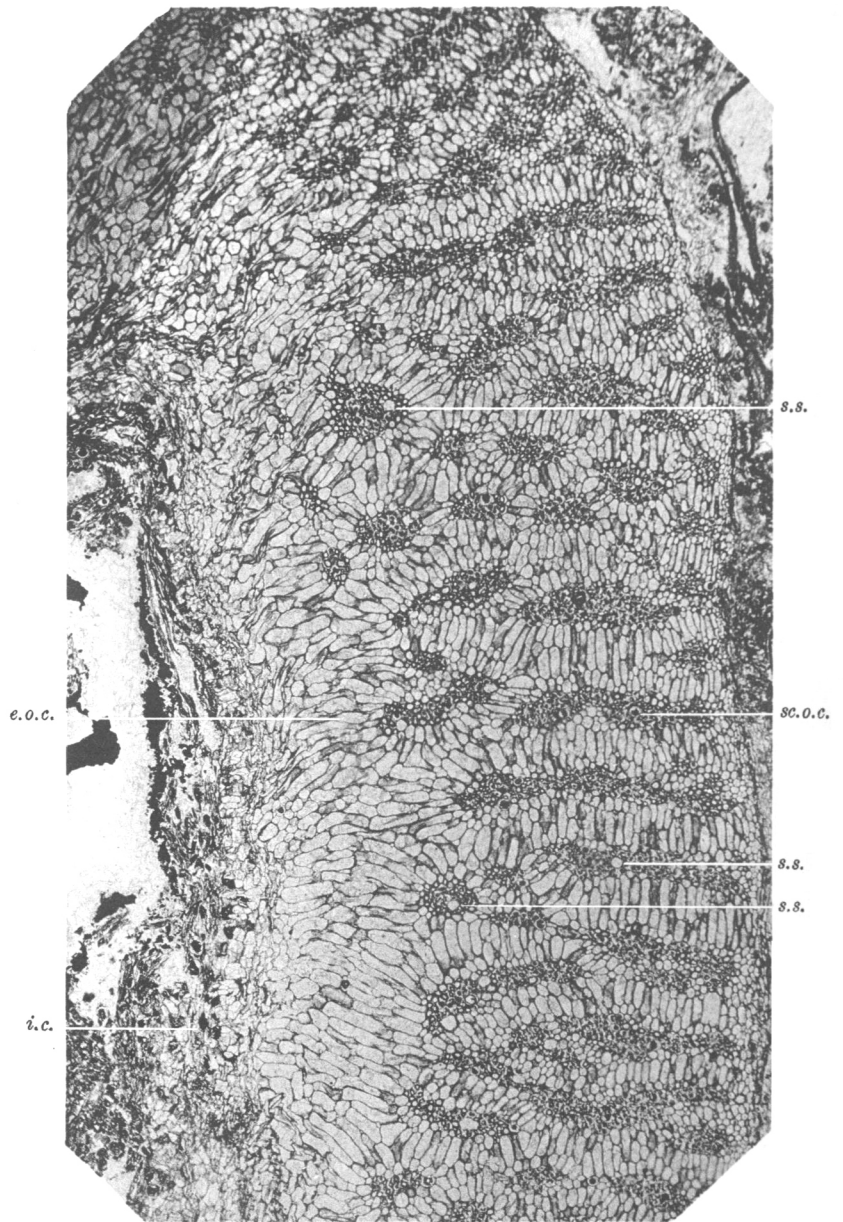
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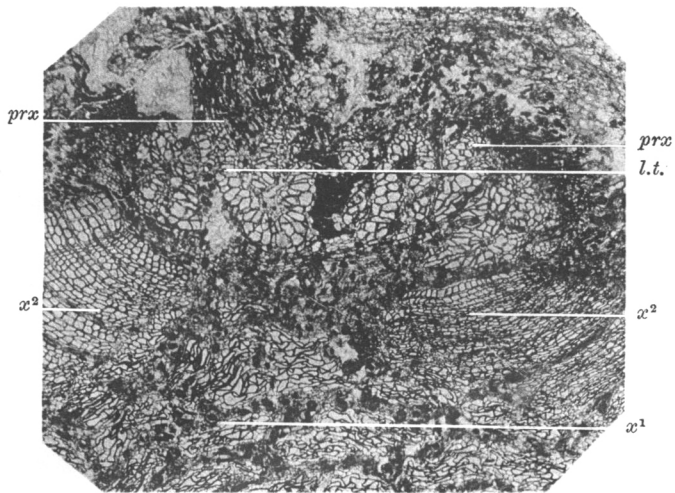


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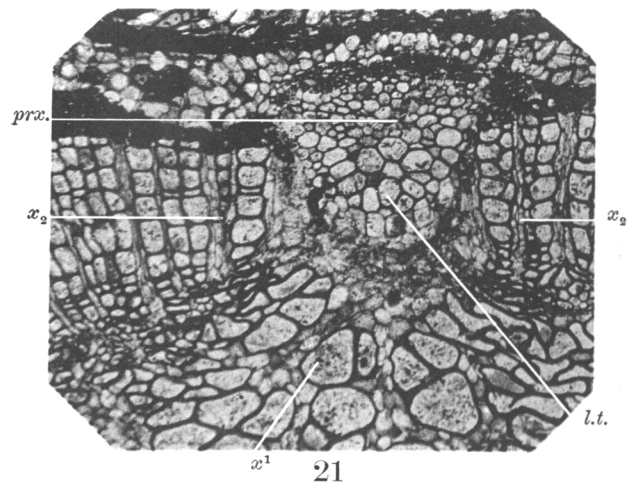


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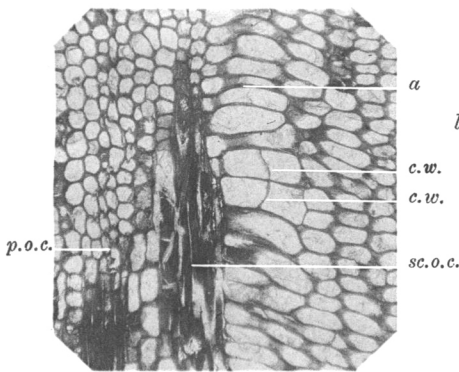
W. T. GORDON : ON RHETINANGIUM ARBERI.—PLATE III.



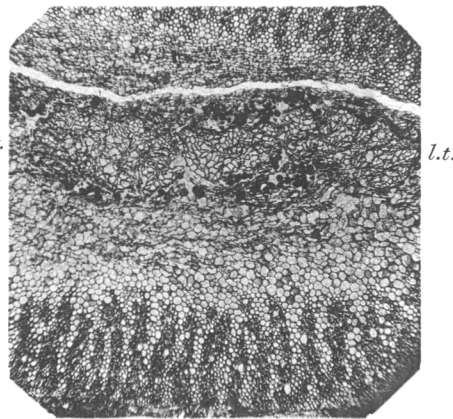
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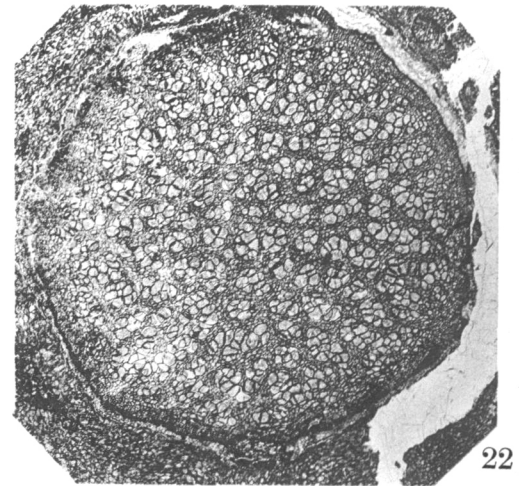
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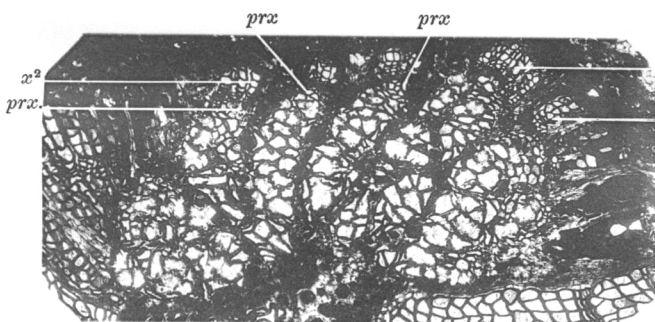
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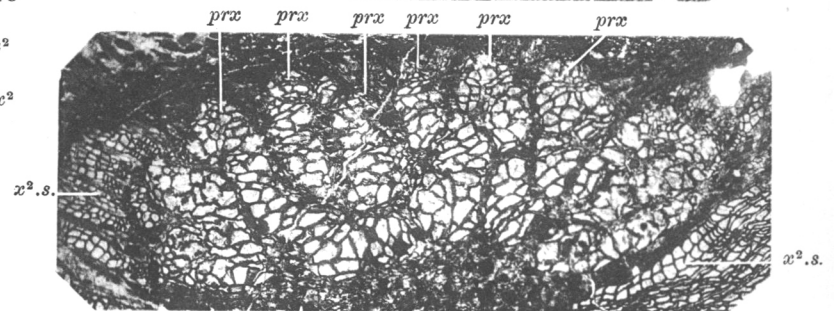
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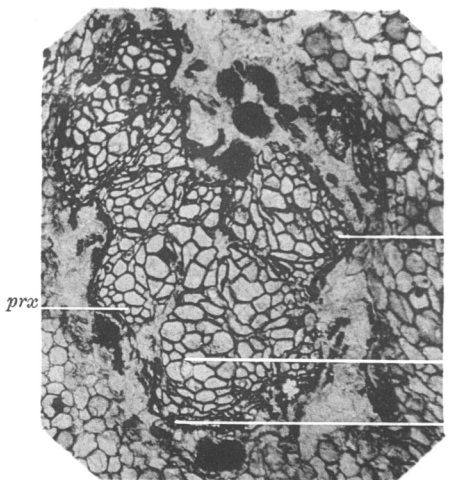
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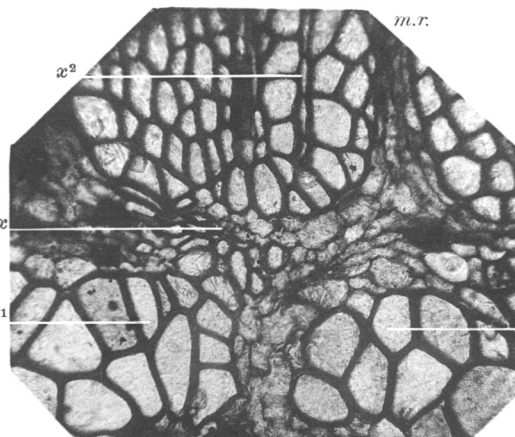
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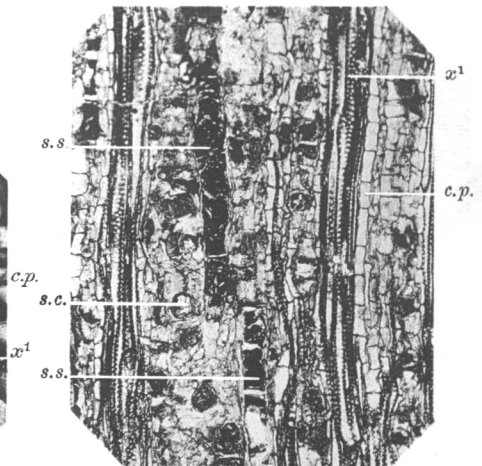
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