

A NEW FERTILE LYCOPOD FROM THE LOWER CARBONIFEROUS OF SCOTLAND

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ABSTRACT. The morphology and anatomy of the leafy stems and cone are described and attributed to *Oxroadia gracilis* gen. et sp. nov. The leaves were recurved and show no evidence of abscission. The plant was probably herbaceous. Comparison is made with other lycopods based on petrifications and also with forms based on compressions. Megaspores closely associated with the cone are described under *Triletes subpalaeocrisatus* sp. nov.

THE material upon which this study is based consisted of a single limestone block containing the petrified remains of several vegetative stems and a fertile axis belonging to a hitherto unknown lycopod. The block was collected from the shore at Oxroad Bay, East Lothian, Scotland. The matrix of the block resembles that of similar blocks collected from the volcanic ash cliffs at the same locality (Gordon 1938, Barnard 1959). There is no reason to doubt that the block came originally from the cliffs. The outcrop belongs to the Cementstone Group of the Calciferous Sandstone Series.

The preservation is generally rather poor. Much crystalization of the matrix has occurred and iron pyrites has been precipitated round many of the plant remains. However, the xylem is usually very well preserved, and so too very often is the epidermis, especially the cutinized outer walls; small portions of certain other tissues are occasionally fairly well preserved.

The material has been studied mainly by close serial peel sections prepared by the now well-known method of Joy, Willis, and Lacey (1956).

SYSTEMATIC DESCRIPTION

Genus OXROADIA gen. nov.

Diagnosis. Lycopod with dichotomously branched stems without distinct leaf cushions but with more or less decurrent leaf bases. Stem protostelic, exarch; leaf traces mesarch. No secondary thickening. Leaves spirally arranged (but longitudinal ranks also well marked), eligulate, dorsi-ventrally flattened, with single median vein; attachment to stem narrow, round; no leaf abscission; no parichnos. Stomata in two bands on the lower surface. Sporophylls in a terminal strobilus, spirally arranged, eligulate. Sporangium elongated, attached to the horizontal basal part of the sporophyll by an elongated attachment; sub-archesporial sterile pad present.

Oxroadia gracilis sp. nov.

Plates 32, 33, 34, figs. 1-5; text-figs. 1, 2, 3A-D

Diagnosis. Stem (2.5-)5.0(-6.5) mm. in diameter. Leaves arranged in 2/11 spiral. Leaf bases somewhat decurrent giving the transverse section of the stem an approximately hexagonal outline. Stem protostele solid, typically with eleven protoxylem points. Leaf

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traces arising successively from every alternate protoxylem point. Tracheids of metaxylem scalariform with reticulate fibrils between the bars. Outer part of cortex consisting of compactly arranged, non-seriated cells, round or polygonal in transverse section, rectangular in longitudinal section. Epidermal cells (surface view) 70–100 μ long and 20–30 μ broad, walls 3.5 μ thick, generally with asymmetrical, bluntly pointed ends. Leaf recurved, ovate-lanceolate, 6–8 mm. long, expanding to about 3 mm. broad at the widest part from about 1 mm. at its attachment; margin smooth. Mesophyll without a palisade. Xylem strand surrounded by a zone of transfusion tracheids. Stomata arranged in irregular longitudinal rows in the stomatal bands. Stoma surrounded by (5–)6(–7) polygonal cells not different from the other epidermal cells within the stomatal bands. Epidermal cells of the midrib region more elongated and lying in longitudinal rows. Cells of upper epidermis polygonal.

Strobilus at least 4 cm. long, about 1 cm. in diameter. Axis 1–1.5 mm. in diameter, with solid or hollow exarch protostele. Sporophyll with horizontal basal portion 4 mm. long with narrow attachment to the axis but expanding to about 2 mm. broad and thickening to about 1 mm. at the 'heel'; upturned part about 3 mm. long. Sporangium borne on an elliptical attachment about 2.0 \times 0.7 mm. Xylem strand becoming lost in numerous transfusion tracheids towards the end of the horizontal part of the sporophyll.

Locality and horizon. Oxroad Bay, East Lothian, Scotland. Cementstone Group (Upper Tournaisian), Calcareous Sandstone Series, Lower Carboniferous.

Holotype Material. British Museum (Natural History), Palaeontology Department, V 51512–13.

Detailed description

Morphology of the vegetative shoot. Something of the external features of the shoot can be seen from the specimen exposed on a broken surface of the block and illustrated in Plate 32, fig. 1. One leaf is seen attached on the left and the stem surface shows a number of leaf bases indicating quite well the leaf arrangement. The surface here appears quite smooth, but this is not the genuine external surface of the stem. The epidermis is situated in the outermost dark layer just beyond the thin light layer seen in the cross-section at the bottom of the figure. Judging from peel sections (Pl. 32, fig. 2), however, the external surface of the stem was in fact smooth except for about six obtuse angles representing the decurrent leaf bases; these were not separated by furrows.

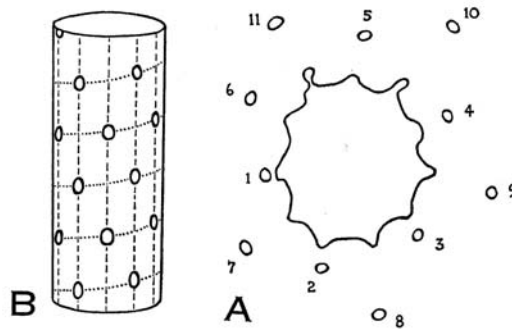
The phyllotaxis is of interest. From series of transverse sections it is evident that leaf traces are given off from the protoxylem points of the stem stele successively from every alternate one. As there are eleven points which persist, it follows, provided that the points run vertically, that the phyllotaxis is a 2/11 spiral. Evidence that this is so can

EXPLANATION OF PLATE 32

Figs. 1–7. *Oxroadia gracilis* gen. et sp. nov. 1, Shoot exposed on broken surface of the block showing leaf bases and one attached leaf. The surface of the stem does not represent the genuine external surface but a layer several cells below the epidermis. Specimen V51512a. \times 5. 2, Transverse section of stem. Slide V51513a. \times 14. 3, The stem stele with protoxylem points and leaf traces and part of a band of preserved cortical tissue. Slide V51513b. \times 60. 4, Portion of the protostele enlarged showing the departure of a leaf trace. Slide V51513b. \times 240. 5, Single leaf trace from stem cortex. Slide V51513b. \times 240. 6, Portion of a tracheid in longitudinal section showing the reticulate fibrils between the scalariform bars. Slide V51513c. \times 1200. 7, Cuticle (top), epidermis and hypodermis (bottom) of the stem in surface section. Slide V51513r. \times 120.

also be obtained from isolated transverse section (text-fig. 1A). Moreover, that there are about eleven ranks of leaves can also be determined by dividing the stem circumference by the measured distance apart of adjacent ranks in the specimen in Plate 32, fig. 1. The diagram in text-fig. 1B is based on this same specimen.

The $2/11$ spiral itself is remarkable in that it is not one of the Fibonacci fractions. Apart from this, the phyllotaxis is of interest because it gives not only very apparent longitudinal rows of leaves, but also alternating pseudowhorls formed by the turns of the rather flat spiral (text-fig. 1B). It would appear that this sort of leaf arrangement was



TEXT-FIG. 1. *Oxroadia gracilis* gen. et sp. nov. A, Camera-lucida drawing of stele and leaf traces in transverse section; numbers indicate the order in which the traces have arisen from the protoxylem points. Slide V51513q. $\times 60$. B, Diagrammatic reconstruction of part of the stem showing the leaf arrangement; dotted lines indicate the turns of the spiral (= pseudowhorls); broken lines, the vertical ranks or orthostichies.

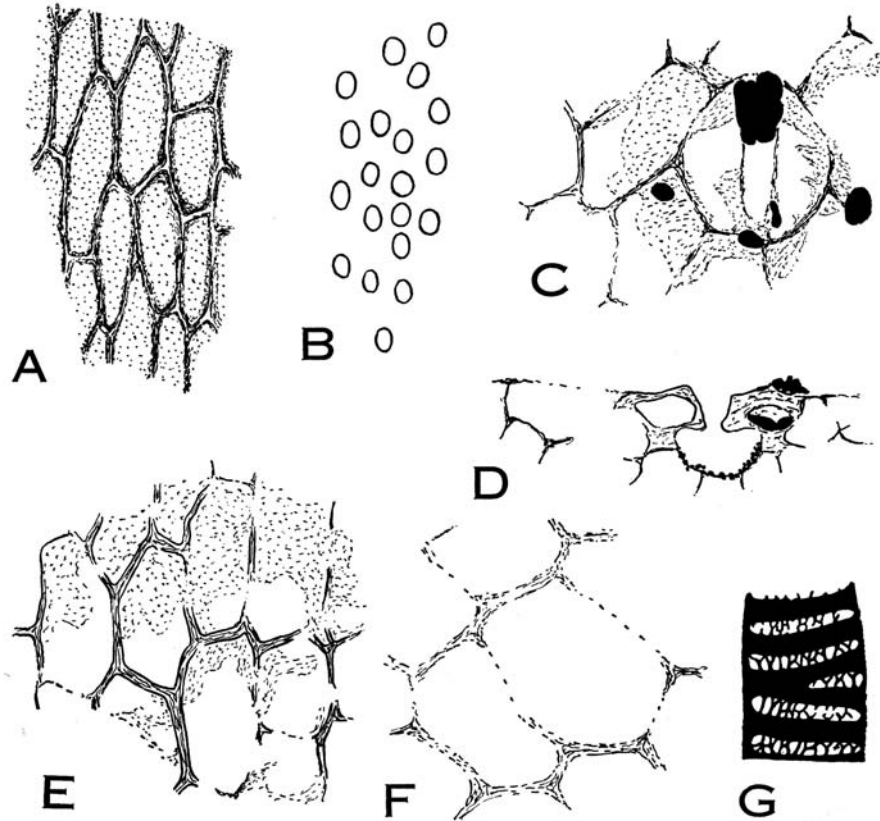
frequent amongst early lycopods. It also occurs in *Lycopodium*. This is discussed further below.

The leaves are strikingly recurved so that the extreme leaf tip is approximately parallel to the stem (Pl. 33, fig. 1). The base of the leaf is about 1.0 mm. wide and round or oval in section, but the leaf expands into a flattened lamina 3 mm. broad before tapering to a point. The base of the leaf just beyond its attachment is generally very badly preserved (Pl. 33, fig. 1). However, careful examination of many leaf bases has revealed no evidence of a ligule.

Anatomy of the stem. The most striking feature of the transverse section is the central protostele (Pl. 32, figs. 2, 3). The solid xylem strand possesses typically eleven protoxylem points from which the mesarch leaf traces are given off (Pl. 32, fig. 4).

The metaxylem consists of scalariform tracheids mainly $30\text{--}50\mu$ in diameter. The protoxylem elements also appear to be scalariform, or possibly more or less reticulate. Between the bars of thickening of probably all tracheids, including transfusion tracheids, there is a network of fibrils (Pl. 32, fig. 6; text-fig. 2G) resembling basically that found in many fossil lycopods. As reported by Smith (1962) in certain arborescent forms, the fibril reticulum together with a narrow strip of material along the edges of the

scalariform bars appears to consist of a different, more translucent material from that of the bars themselves. An indication of this is seen in the photograph (Pl. 32, fig. 6); no attempt has been made to show it in the drawing (text-fig. 2G).



TEXT-FIG. 2. *Oxroadia gracilis* gen. et sp. nov. A, Stem epidermis in surface view. Slide V51513r. $\times 280$. B, Distribution of stomata in stomatal band. Slide V51513s. $\times 65$. C, D, Stoma. Slide V51513v. $\times 465$ (solid black represent mineral). E, Lower epidermis of leaf in midrib region. Slide V51513t. $\times 465$. F, Upper epidermis of leaf. Slide V51513u. $\times 465$. G, Portion of tracheid showing reticulate fibrils between the scalariform bars. Slide V51513d. $\times 1100$.

Outside the xylem in the best-preserved specimens there is a narrow zone containing the remains of a delicate tissue which may reasonably be assumed to represent the phloem (Pl. 33, fig. 4). This is enclosed by a ring of larger-celled, better-preserved tissue which is interpreted as part of the inner cortex. In most specimens the phloem is entirely absent and except for a narrow belt of inner cortex (Pl. 32, fig. 3) there is nothing

between the xylem and the outer part of the cortex (Pl. 32, fig. 2). The outer cortex itself is nearly always conspicuous as a dark zone, although its preservation, except for a narrow belt of cells on the inside (bordering the space) and some of the superficial cells, is poor. These alternating zones of preserved and unpreserved tissues are a peculiar feature of most of the stems in the material. Occasionally, however, the preservation is different and the tissues are more continuous (Pl. 33, fig. 4). I believe that the cortex was originally differentiated into two zones, an outer consisting of compact parenchyma, possibly rather thick walled, and an inner zone of delicate parenchyma. Even in the best-preserved specimens the inner cortex is never well preserved and sometimes there is a suggestion that this region may have been aerenchymatous (Pl. 33, fig. 4). However, no definite aerenchyma has been observed. The alternation of preserved and unpreserved regions probably resulted from the early breakdown of the softest tissues, i.e. phloem and inner cortex, and the penetration of these spaces by petrifying mineral. This mineral preserved the immediately adjacent tissues, i.e. the xylem and the narrow strip of cortical tissue close to the stele and just inside the dark outside zone; the epidermis and hypodermis were presumably penetrated and preserved by mineral external to the stem. The intervening outer cortical tissue were then destroyed to give the dark residual material seen in most specimens.

There is no indication of any radial seriation of cells in the cortex, and thus no suggestion of secondary activity.

The epidermis is usually remarkably well preserved (Pl. 32, fig. 7; text-fig. 2A). The outer walls seen in surface section have a striking yellowish-brown colour due presumably to the presence of a fairly thick cuticle.

The leaf traces pass through the cortex rather steeply so that as one trace departs from a protoxylem point the last one in the same orthostichy has not yet entered its leaf. Indeed, the trace departs at a level corresponding to about two leaves below the one into which it eventually passes, a distance of about 11 mm. The trace remains mesarch with rather more centrifugal than centripetal metaxylem. Nothing is preserved of the trace except the xylem of which there are generally some twenty tracheids. As the trace passes through the preserved regions of the cortex it is accompanied by a small space which presumably represents the phloem (Pl. 32, fig. 5).

Branching. Three specimens have been observed showing evidence of branching. The best one was traced through the block for a distance of some 7 cm. during which it dichotomized once (Pl. 33, figs. 2, 3). The distance between these two sections is approximately 1.5 cm. The dichotomy is evidently equal. The protostele of the parent axis divides into two equal portions by a median suture (Pl. 33, fig. 3). Five or six new protoxylem points arise along the metaxylem adjacent to the suture in each of the daughter steles. The specimen illustrated in Plate 33, fig. 4, contains two steles of somewhat different appearance suggesting that this may represent a kind of unequal dichotomy. However, in a distance of some 4 mm. this specimen shows no perceptible change and there is no proof that the two steles have arisen by division. One side of this specimen (top of photograph) was broken and the inner cortex was open to the outside.

Anatomy of the leaf. The leaves are generally very poorly preserved except for the vascular strand and the epidermis (Pl. 33, fig. 1).

At the base of the leaf the vascular trace is small and compact resembling the leaf

trace in the stem cortex, but as the leaf expands the strand acquires a sheath of transfusion tracheids.

The mesophyll is very badly preserved except for small patches close to the epidermis or at the extremities of the leaf (Pl. 33, fig. 5). It was apparently more or less uniform in structure.

The essential features of the epidermis including the stomata are given in the specific diagnosis and illustrated in text-fig. 2B-F.

The strobilus. It is believed on the evidence of anatomy as well as association that the single badly distorted fertile axis found in the same block as the vegetative shoots belongs to the same plant.

The fertile axis is more slender than the smallest vegetative stem; its diameter decreases from 1.5 mm. at the proximal end to only 1.0 mm. at the distal end. It has been traced through the block for a total distance of about 4 cm. The fact that the axis is small and decreases upwards suggests that it represents a terminally borne strobilus rather than an intercalary fertile region.

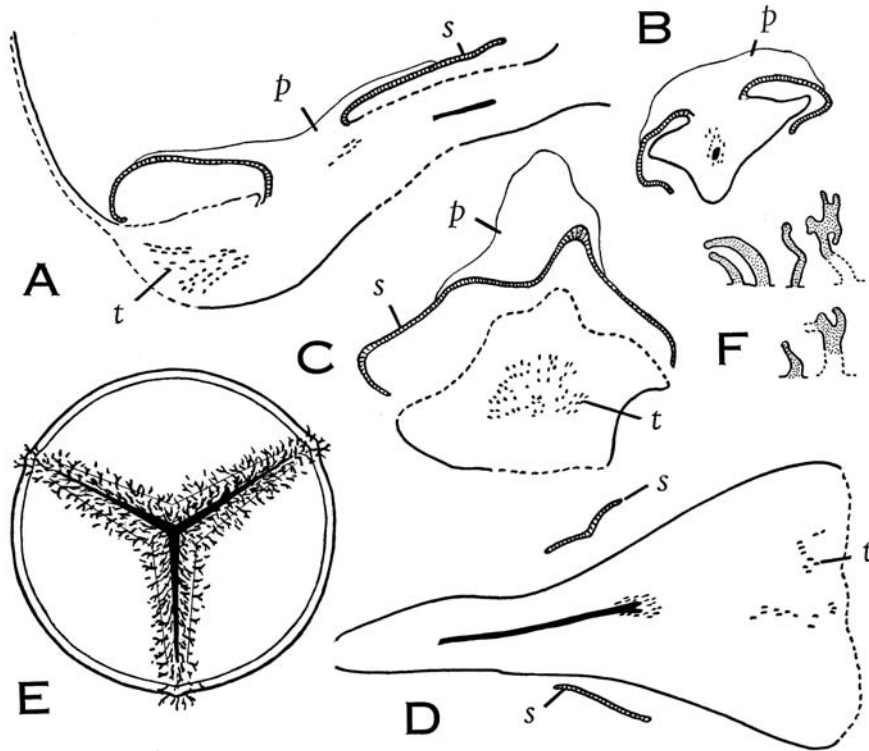
At the thicker end of the axis a transverse section shows a solid protostele exactly similar to that of a vegetative stem. Through the greater part of the axis, however, the protostele is hollow (Pl. 34, fig. 2). There is no evidence of parenchyma at the centre: possibly the central tracheids failed to mature. There are about eleven protoxylem points, and the sporophyll traces arise from them in a similar manner to leaf traces in the stem. The traces themselves are similar (Pl. 34, fig. 3). The pitting of the tracheids is identical to that in the stem. The cortex, though much less massive than in the stem, is probably similar in structure; there is always a space inside the preserved outer region (Pl. 34, fig. 2).

Sporophylls are rather infrequently found actually attached to the axis; they mostly lie in a rather distorted mass around it. The form of the sporophyll has been elucidated by tracing individual examples through serial peels. It consists of a lower, horizontal or possibly somewhat descending portion about 4 mm. long carrying the sporangium on its upper side, and an upturned distal portion which is always very badly preserved so that its exact size and shape is uncertain. The sporangium-bearing portion is slender at the base but gradually expands both in breadth and thickness into a massive 'heel' beyond the sporangium (text-fig. 3A-D). As the expansion occurs, the slender vascular bundle becomes surrounded by a mass of transfusion tracheids until eventually in the 'heel' the strand itself seems to become entirely lost (text-fig. 3C). Only a few transfusion tracheids appear to enter the upturned portion. Beneath the sporangial attachment, some transfusion tracheids pass towards the sporangium but do not enter it (Pl. 34, fig. 5; text-fig. 3B).

All the sporangia have dehisced. Generally the remains of the sporangial wall have

EXPLANATION OF PLATE 33

Figs. 1-5. *Oxroadia gracilis* gen. et sp. nov. 1, Longitudinal section of stem with attached leaves. Slide V51513d. $\times 5$. 2, Transverse section of stem at point of dichotomy. Slide V51513e. $\times 9$. 3, Section of the stele of the same specimen as in fig. 2 below point of dichotomy. Slide V51513f. $\times 45$. 4, Transverse section of a stem with a better preserved but broken cortex and two steles. (For further explanation see text.) Slide V51513g. $\times 40$. 5, Longitudinal section through the base of a leaf showing upper epidermis, apparently homogeneous mesophyll and the vascular strand. Slide V51513h. $\times 60$.



TEXT-FIG. 3. A-D, *Oxroadia gracilis* gen. et sp. nov. E, F, *Triletes subpalaeocristatus* sp. nov. A, Nearly radial longitudinal section through a sporophyll. Slide V51513w. $\times 20$. B, Vertical section through a sporophyll passing through sporangial attachment. Slide V51513o. $\times 20$. C, Somewhat oblique vertical section distal to sporangial attachment near the sporophyll 'heel' showing distribution of transfusion tracheids. Slide V51513x. $\times 20$. D, Longitudinal section through horizontal portion of sporophyll in dorsi-ventral plane showing part of the vascular system and portions of the wall of the dehiscent sporangium. Slide V51513y. $\times 20$. E, Reconstruction of *Triletes subpalaeocristatus* sp. nov. (proximal view). F, Hairs from the trilete ridge. Slide V51513m, n. $\times 215$. *p*, subarchesporial pad; *s*, wall of sporangium; *t*, transfusion tracheids.

recurved round the basal portion of the sporophyll (text-fig. 3B-D). I estimate that the sporangium was about 4×1 mm. The attachment, which in text-fig. 3 appears short, is in fact elongated radially. This is because the section is not perfectly radial and does not pass through the whole length of the attachment. The elongated form of the attachment has been demonstrated by following through serial peels.

A striking feature of the sporangium is the massive pad of parenchyma forming a short, wide columella extending up into the sporangium from the sporophyll. This tissue also spreads along the sporangial wall where it resembles inner layers of wall cells.

The tissue appears homogeneous and consists of large, thin-walled cells. The outermost layer of the sporangial wall is always conspicuous. It is about 25μ thick, palisade-like in cross-section, and in section parallel to the surface it resembles collenchyma, the polygonal cells having thickenings in the corners. Such a wall structure is common amongst fossil lycopods. Indeed, in no structural feature, except for the apparent absence of a ligule, is the strobilus significantly different from *Lepidostrobus*.

There is no evidence concerning the microspores that the cone may have borne. A sample of the block containing a portion of the cone was macerated and numerous microspores were obtained. There were, however, some twelve different kinds of spores present, and no preponderance of any one kind. Most abundantly represented were spores belonging to the genera *Punctatisporites*, *Convolutispora*, and *Apiculatisporites*. There is evidence of association that the megaspore described below may have been borne by the cone.

Genus TRILETES Bennie and Kidston ex Zerndt

Triletes subpalaeocristatus sp. nov.

Plate 34, figs. 6-7; text-fig. 3E-F

Diagnosis. Megaspore spherical; mean diameter $1,355\mu$ (range $1,250$ – $1,460\mu$ for three spores measured). Wall about 35 – 45μ thick, undecorated except near the trilete ridge; arms of trilete ridge extending the whole radius of the spore; ridge up to about 150μ high. Lips of trilete ridge bearing a crest of simple and variously branched hair-like appendages up to about 150μ long and (3.5) – 6.5 – $(13.0)\mu$ thick; hairs often with small ball-shaped tips; crest of hairs about 250μ in total breadth.

Holotype. Sectioned spore in slides V51513m-p, British Museum (Natural History), Palaeontology Department (Pl. 34, figs. 6, 7).

Locality. Oxroad Bay, East Lothian, Scotland.

Further description. Altogether six megaspores have been seen in the block: four were in the immediate vicinity of the cone, i.e. more or less within the region of sporophylls (Pl. 34, fig. 1), another was within a distance of 2 cm. and the sixth was elsewhere in the block, remote from the cone. This last spore showed evidence of being a different kind of spore from the other five; its wall showed a membranous outermost layer not apparent in the others which were probably all similar to one another although their preservation varied. This close association is impressive but is the only evidence that this new spore was borne by *Oxroadia*.

EXPLANATION OF PLATE 34

Figs. 1–5. *Oxroadia gracilis* gen. et sp. nov. 1, Cross-section of strobilus showing the axis (top left of centre), portions of sporophylls and dehisced sporangia and four associated megaspores (*m*). Slide V51513i. $\times 13$. 2, Strobilus axis. Slide V51513j. $\times 45$. 3, Part of protostele of strobilus axis and two sporophyll traces. Slide V51513k. $\times 240$. 4, Portion of wall of a sporangium. Slide V51513k. $\times 120$. 5, Sporophyll in oblique vertical section through the horizontal part showing dehisced sporangium with its subarchesporial pad (top) and transfusion tracheids in the 'heel' region. Slide V51513l. $\times 27$. Figs. 6, 7. *Triletes subpalaeocristatus* sp. nov. 6, Section of the holotype passing through the summit of the trilete ridge. Slide V51513m. $\times 27$. 7, Section of the trilete ridge (near the summit) showing hairs. Slide V51513n. $\times 120$.

Of the five spores seen only one was complete, the others all having lost portions in saw cuts. This whole spore (the holotype) was also fortunately the best preserved, and is represented in a series of peel sections. The holotype was the largest of the three measurable spores. The reconstruction in text-fig. 3E is based on this spore.

The spore shows no indication of an equatorial flange or of arcuate ridges. The wall is uniformly thick except at the lips of the trilete ridge where it thickens to about 50μ . The arms of the ridge are nearly 900μ long, so that in a view of the proximal face they would be seen to extend the whole radius of the spore. The hair-like appendages are often quite elaborately branched (Pl. 34, fig. 7; text-fig. 3F). The whole crest of hairs is probably about 150μ high (excluding the height of the ridge itself).

Discussion. This spore is strikingly similar to one described by Chaloner (1954) under the name *Triletes cristatus* (later changed to *T. palaeocristatus* Chaloner (1956) to avoid synonymy) from the Beaver Bend Limestone of the Indiana Mississippian. This American spore differs from the new species only in its somewhat larger size ($1,700$ – $2,200\mu$) and rather thicker wall (50μ). It is, however, younger, its horizon being correlated with the Lower Chesterian in the American succession or Upper Dinantian of the European.

It is convenient at present to follow Winslow (1959, 1962) in using the name *Triletes*, as this spore does not fall readily into any of the more narrowly defined genera into which fossil megaspores are now usually classified. Potonié (1958) classified *T. palaeocristatus* in his Turma *Barbates*, a group which comprises mainly a number of Mesozoic spores with hairs or processes along the trilete ridge. The hair-like appendages of the new spore, in being frequently branched, are similar to those in Carboniferous megaspores of the *Setosiporites* kind, such as *T. globosus* Arnold and *T. praetextus* Zerndt; this is in contrast with the generally simple appendages in spores of the section *Lagenicula*, such as *T. subpilosus* Schopf, Wilson, and Bentall and *T. horridus* Schopf, Wilson, and Bentall. In both of these groups, however, the distribution of the appendages is quite different from that in *T. palaeocristatus* and *T. subpalaeocristatus*; other important differences lie in the presence of apical prominences and generally also arcuate ridges.

GENERAL DISCUSSION

The view that *Oxroadia gracilis* represents a herbaceous lycopod rather than the ultimate branchlets of a woody arborescent form is based mainly on the absence of secondary activity in either the vascular system or the cortex. The absence from the block, and indeed from the Oxroad Bay flora as far as it is at present known, of any woody lycopod axis to which these shoots could have been attached lends a little support to this view. The absence of any indication of rooting organs, on the other hand, suggests that the plant was not at any rate a creeping herb. However, although Zimmermann (1930) reported roots in the Upper Carboniferous *Eleutherophyllum mirabile*, roots are rare amongst the remains of early Palaeozoic herbaceous lycopods.

Oxroadia differs from most fossil lycopods known from petrifications in the absence both of distinct leaf cushions and of a ligule. One of the few with which it shares these characters is *Levicaulis arranensis* Beck (1958). However, *Levicaulis* has a protostele with an almost smooth surface due to the very small and probably much more numerous protoxylem points. It has a very similar, though usually slightly more complex, system of reticulate fibrils between the scalariform bars. Although secondary activity in the

cortex appears to begin at an early stage, only one specimen was reported in which there was secondary wood. There were fibrous strands in the cortex.

Of interest in the comparison between *Oxroadia* and *Levicaulis* is the general similarity between the strobilus of *Oxroadia* and the fructification *Lycostachys protostelicus* Pant and Walton (1961) which, on the evidence of both structure and association, was tentatively referred to *Levicaulis*. The sporophylls of the two fructifications are very similar in structure, differing only in certain details such as the absence of any tracheids in the subarchesporial tissue and of any indication of trabeculae in *Oxroadia*. The attachment of the sporangium to the sporophyll, which Pant and Walton claim was short in the radial direction, was, I believe, probably elongated as it is in *Oxroadia* or, for that matter, in *Lepidostrobus*. If the sporophyll illustrated in text-fig. 2F in Pant and Walton's paper is interpreted as curved so that the longitudinal section passes through the attachment twice, this attachment was at least as long as the distance apart of these 'two attachments'. However, *Lycostachys* is considerably larger than the strobilus of *Oxroadia*; moreover, the axis contains a solid protostele (throughout its length?) with smaller and more numerous protoxylem points. If the strobilus of *Oxroadia* were known only as an isolated fructification, it would probably be classifiable in the genus *Lycostachys*. It should be pointed out, however, that both *Lycostachys* and the *Oxroadia* strobilus appear to differ from *Lepidostrobus* only in the absence of a ligule. If the megaspores associated with the strobilus of *Oxroadia* are accepted as belonging to it, this would constitute a very important difference from any species of *Lepidostrobus* in which the megaspores are known, and probably also from *Lycostachys*. No megaspores were found inside the sporangia of *Lycostachys*, but those found in close association had a well marked equatorial flange and processes on the distal face.

With *Paurodendron* Fry (1954), a genus of herbaceous lycopods represented in both the Lower and Upper Carboniferous, *Oxroadia* shares a number of features. The cortex has a similar two-layered structure, though the outer layer is probably more fibrous, and the stele is a solid exarch protostele with the number of points varying with the species. However, important differences from *Oxroadia* include the presence of a ligule, the unequal dichotomy and the usually non-anastomosing nature of the fibrils between the scalariform bars.

As it has been possible to determine the general external morphology of *Oxroadia*, it is worth attempting a comparison with certain fossil lycopods represented by compressions.

According to the classification of Kräusel and Weyland (1949), *Oxroadia* would fall into the Protolpidophytales and might fit in either the Protolpidodendraceae or the Eleutherophyllaceae. It is clearly distinct from the genera *Protolpidodendron* and *Colpodexylon* on account of the simple leaves, although in passing, it is worth noting the general anatomical similarity to *Protolpidodendron gilboense* Grierson and Banks (1963). It is much more comparable with certain species of *Lepidodendropsis* Lutz which Kräusel and Weyland also classify in the Protolpidodendraceae. This genus has recently been redefined by Danzé-Corsin (1958*a* and *b*) who place it in a separate subfamily (Lepidodendropsidaceae) of their Ulodendraceae within the Lepidophytales. It is generally typified by its leaf cushions which are arranged in 'verticilles alternes' (= pseudowhorls), also by the lack of a distinct leaf scar, parichnos and ligule, and the attachment of the leaf at or near the top of the cushion. The conception of the genus

is, however, still wide and it includes species which were relatively massive and perhaps with secondary thickening, e.g. those described by Jongmans, Gothan, and Darrah (1937), Jongmans (1939), and Jongmans and van der Heide (1955), as well as some which were relatively slender and perhaps herbaceous, e.g. *L. recurvifolia* Lacey (1962). The resemblance between the Lower Carboniferous *L. recurvifolia* and *Oxroadia* is in fact considerable. Both are of similar size with similarly recurved leaves, though the leaves are a little larger in *L. recurvifolia*. The phyllotaxis, judging from Lacey's figures, is probably the same. The one important difference lies in the presence in *L. recurvifolia* of distinct leaf cushions. These cushions, however, do not taper at the bottom, but represent the decurrent leaf bases running down the stem to the pair of leaves next below. The surface of the cushion has the same epidermal structure as have the narrow strips of stem between adjacent cushions, suggesting that they were simply ridges on the stem. This is in contrast to a larger stemmed species, *L. jonesi* Lacey, where the leaf cushion and stem surface are quite different in epidermal structure. The stem epidermis in *L. recurvifolia* consists of elongated cells of similar width but rather longer than those in *Oxroadia*; in *L. jonesi* these cells are irregular and thick walled and quite different. Although *L. recurvifolia* and *Oxroadia* have much in common and may have been closely related, they are certainly not identical; apart from small differences in size and proportions, the decurrent leaf base was evidently much more strongly developed in *L. recurvifolia*.

Comparison may also be made with the genera *Eleutherophyllum* and *Zimmermannia*, with both of which, incidentally, Lacey compares his *Lepidodendropsis recurvifolia*. Grierson and Banks (1963) give the bifid leaf as being a characteristic feature of *Eleutherophyllum*, although the Namurian *E. drepanophyciforme* Remy and Remy (1960) is described as having a simple lanceolate leaf. The leaf arrangement too in this species appears to be very similar to that in *Oxroadia*, but a difference lies in the extension of the leaf base up the stem above where the free part of the leaf is attached. A similar type of leaf base, rather resembling the base of a rose thorn, is also characteristic of the early lycopods *Drepanophycus*, *Protolpidodendron*, *Colpodexylon*, and *Archaeosigillaria* (Banks 1960, Grierson and Banks 1963). Another important point of difference lies in the reproductive parts of *Eleutherophyllum drepanophyciforme*; there were no distinct cones and the sporangia were attached by a non-elongated attachment to the upper surface of the fertile leaves. *E. waldenburgense* (Stur) Zimmermann has a larger number of leaves in the pseudowhorl than *Oxroadia*. The Upper Devonian *Zimmermannia eleutherophylloides* Gothan and Zimmermann (1932) agrees with *Oxroadia* in size as well as in the recurved leaves, but the leaves appear to be arranged in true whorls.

The herbaceous lycopod described by Kräusel and Weyland (1937) as *Lycopodites oosensis* from the Upper Devonian bears some resemblance to *Oxroadia*. The stem surface and leaf base were probably very similar and the authors remark that the leaves, although spirally arranged, often have the appearance of being in alternating whorls and, where more widely separated, of being in longitudinal rows. But it was a smaller plant than *Oxroadia* and had upturned falcate leaves. Its sporophylls were borne on fertile branchlets (presumably strobili), but although microspores were found, there was no evidence of heterospory.

The anomalous phyllotaxis of *Oxroadia* in comparison with most living plants has already been referred to. From published accounts of various other fossil lycopods,

however, it appears highly likely that many of them had a comparable phyllotaxis. Thus, the leaves of such genera as *Lepidodendropsis*, *Eleutherophyllum*, *Protolepidodendron*, *Archaeosigillaria*, *Colpodexylon*, and *Drepanophycus* would appear to be arranged in a spiral $2/x$, where x is a relatively high, odd number. In all of these the leaf arrangement can generally be interpreted in terms of spirals, pseudowhorls, or longitudinal rows. Similarly, even many of the larger lepidodendroids such as *Omphalophloios*, *Sigillaria*, *Lepidophloios* spp., and *Lepidodendron* spp., where the leaf cushions are arranged in more or less obvious vertical ranks, may have a fundamentally similar phyllotaxis. In the living *Lycopodium* I found a $2/15$ spiral in a specimen of *L. clavatum*, although elsewhere on the same plant there was no traceable spiral but rather irregular alternating whorls. Similar alternating whorls were found in *L. annotinum*, *L. selago*, *L. lucidulum*, and *L. obscurum*. In a specimen of *L. alpinum*, the erect shoots had opposite decussate leaves, but the main creeping shoot, a very irregular spiral; in no instance was a regular spiral of the Fibonacci series observed.

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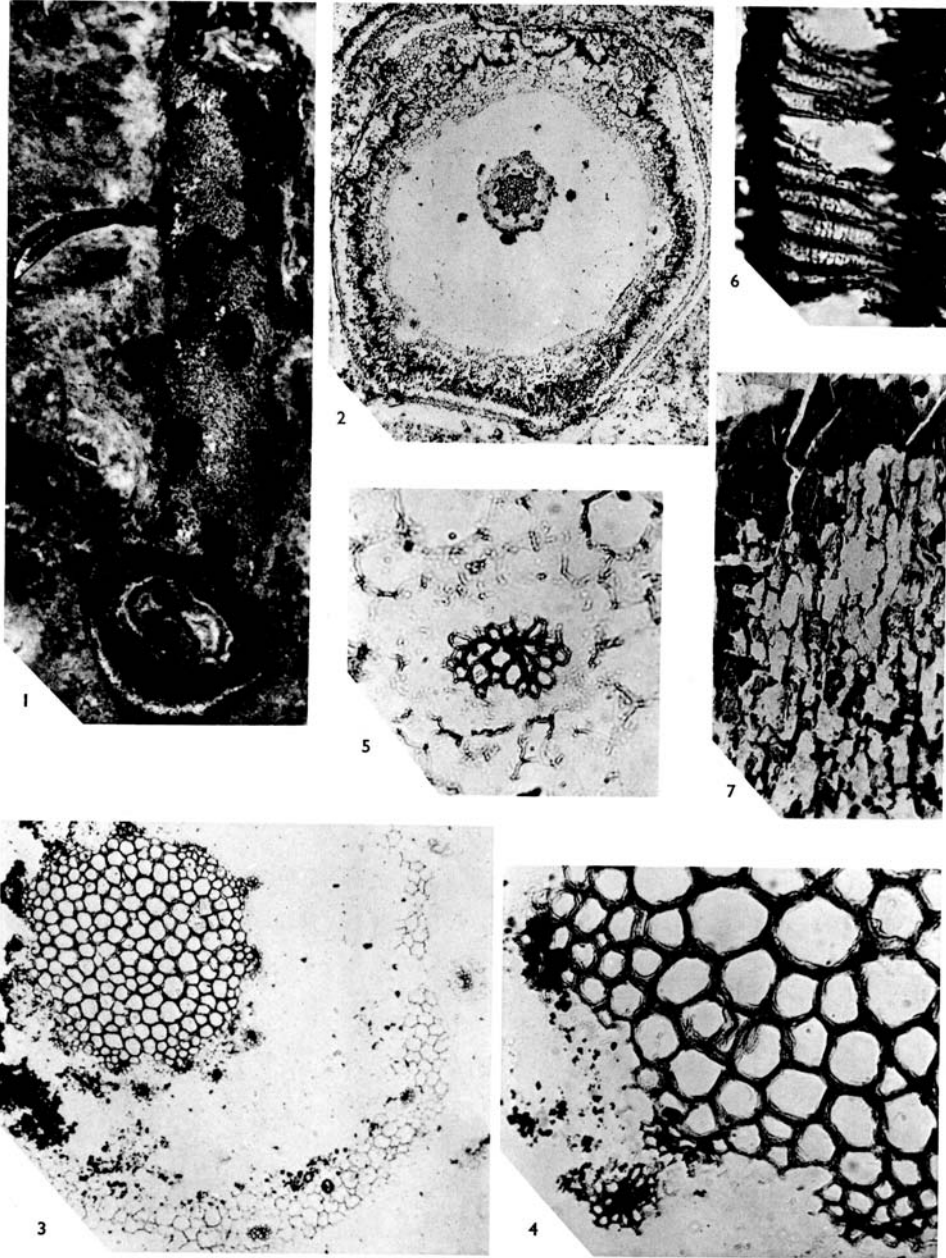
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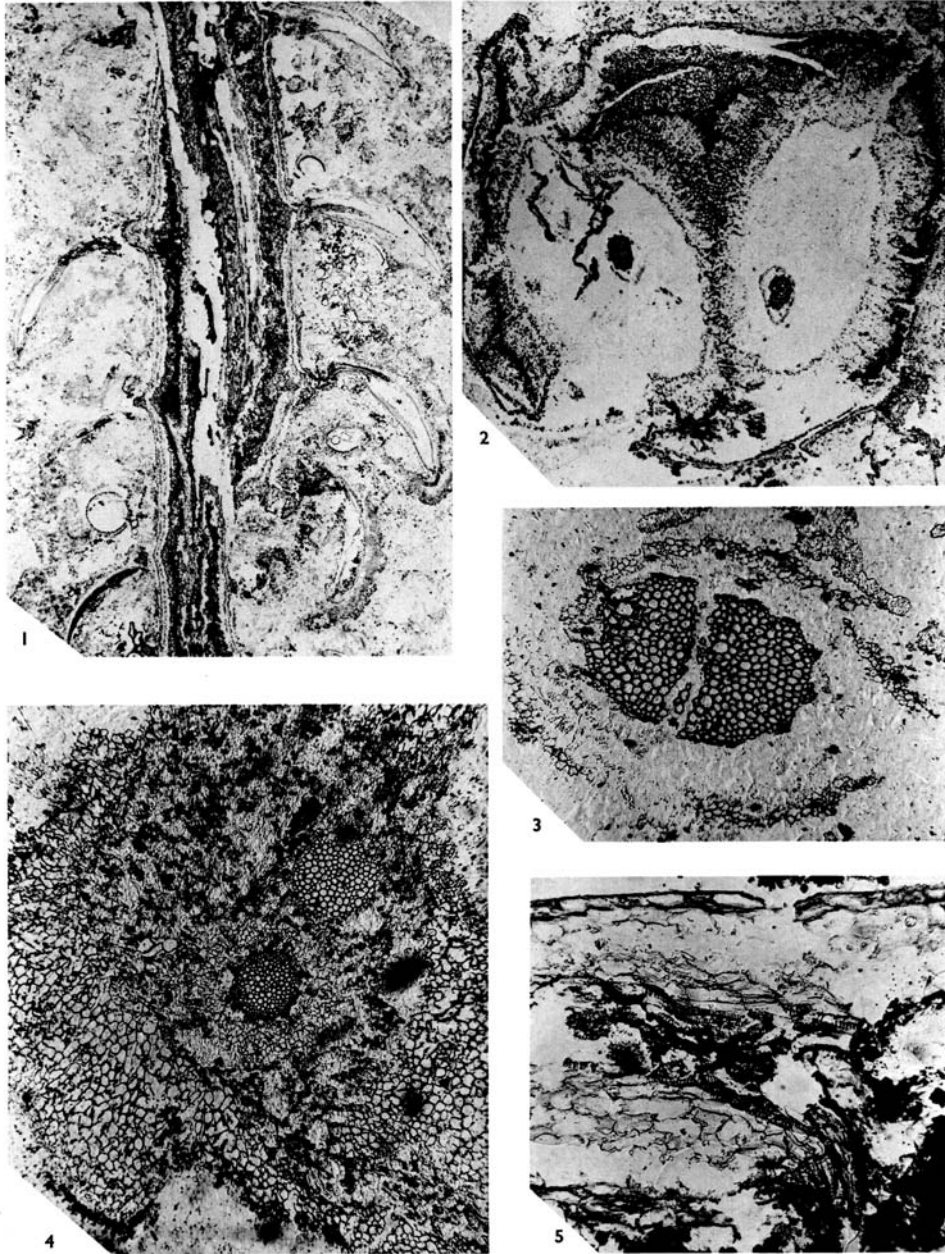
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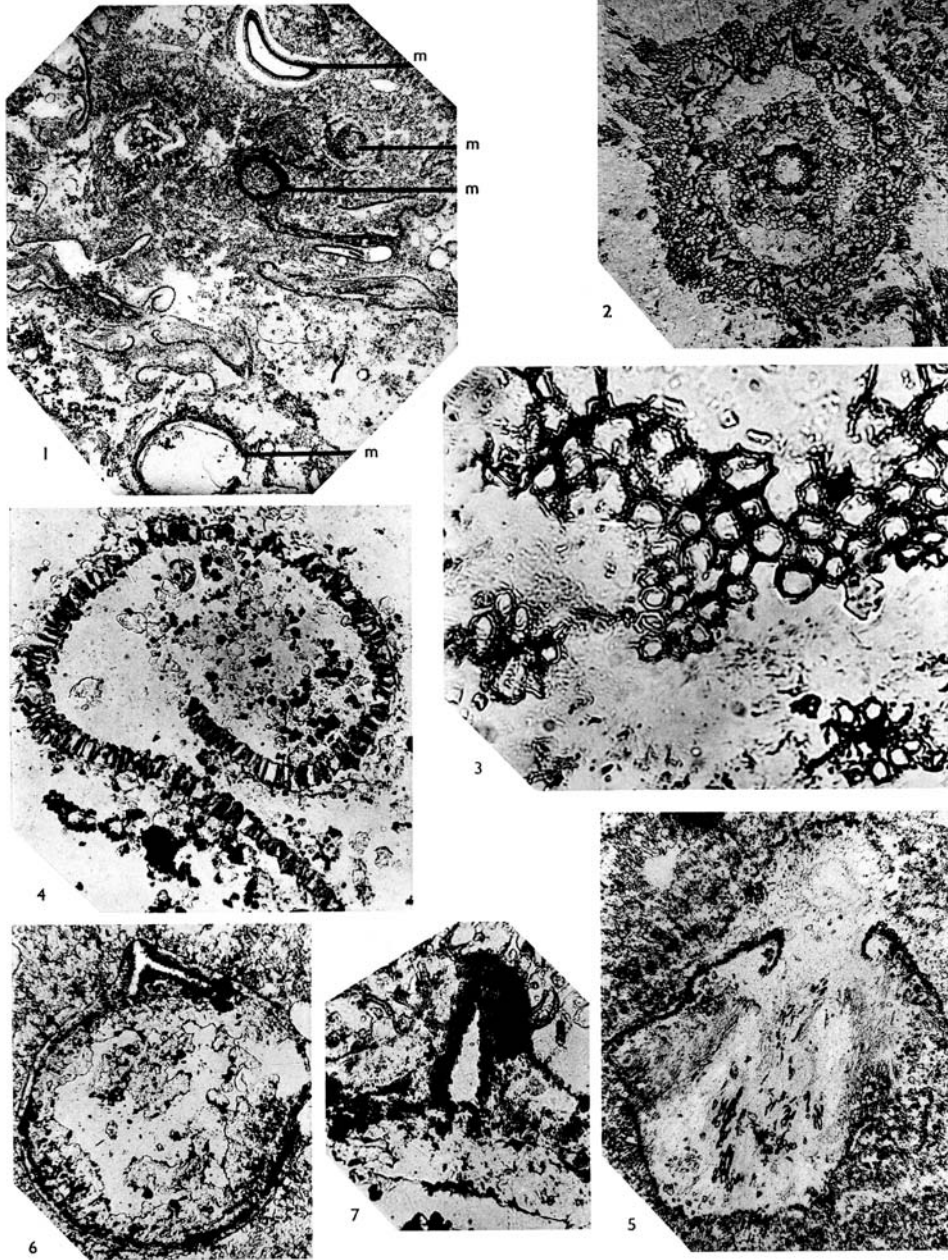
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