THE LOWER CARBONIFEROUS FLORA

OF THE

KILPATRICK HILLS

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DAVID L. SMITH

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INTRODUCTION

The Clyde Plateau Lavas form the main mass of two ranges of hills in the west of Scotland. They are the Campsie Fells in Stirlingshire and the Kilpatrick Hills in Dunbartonshire. The Lavas are part of the Calciferous Sandstone Series of the Lower Carboniferous formation. According to J.G.C. Anderson (in Richey, 1938) the following succession holds good on the Dumbarton side of the Kilpatrick Hills:-

Clyde Plateau Lavas

Basaltic Ash

Spout of Ballagan Sandstone
Ballagan Beds

The Ballagan Beds overlie, without apparent unconformity, the Upper Old Red Sandstone. They consist largely of greyish or greenish shales and nodular cementstones, interbedded with thin layers of sandstones. Fish scales and teeth occur in the shales. The Spout of Ballagan Sandstone is a fairly massive white or yellow sandstone, sometimes gritty but not pebbly.

Overlying the Spout of Ballagan Sandstone is a considerable thickness of basaltic ash, which, immediately under the lavas, becomes more sedimentary in charagter and includes ashy sandstones,

shales, fireclays and thin coal seams. At two points where these sedimentary rocks outcrop beds containing plant remains have been discovered. Previously these plant beds and their associated ashes were considered to be interbedded in the Lavas but further investigation has suggested that more likely they belong to the pre-laval position, repeated by faulting. They are thus attributable to the basal part of the Calciferous Sandstone Series and are probably the equivalent of the Cementstone Group.

The first plant bed to be discovered was in Glenarbuck, near Bowling. There does not appear to be any record of its discovery but most probably it was found by the Geological Survey about 1870. A number of petrified specimens of Stigmaria ficoides Brongn. and one of lepidodendroid secondary cortex in the Hunterian Museum Palaeobotanical Collection of the University of Glasgow are labelled "Glenarbuck, Bowling, 1872", but there is no indication as to the identity of the collector. Three were presented to the Museum by Professor A. Dickson; two by a Mr. John Young; and one by Professor F.O. Bower. About 1930 Mr. Robert Brown drew to the attention of Professor John Walton the occurrence of petrified plant remains in these beds and further search yielded a large number of calcareous nodules containing petrifications and also a number of plants

preserved in the form of compressions. According to Mr. Brown (MS., 1937), "the section . . . . consists of beds of coal, shale, carbonaceous clays and tuffs, among volcanic ash. In the upper part . . . . there is a bed of coal which has been burned by the overflowing lava. In the underlying beds of tuff the petrifications are found, their position usually marked by coaly streaks in the strata. The petrifications have been formed by the infiltration of calcium carbonate and other minerals . . . . About 30 feet below the level of the bed where the petrifications were collected there is a bed of dark chert with shrinkage cooling cracks on the surface. No plant remains have been found in it. Its occurrence in these beds may indicate hot spring conditions . . . . and the hot water from these springs, carrying gas and minerals may have been the cause of the fine preservation of the plant remains."

Most of the plant remains in the bed are petrified, but preserved as compressions are several small lepidodendroid twigs and a number of fragments of fronds of Aneimites acadica Dawson. The only new species previously described from the bed is Lyginorachis brownii Calder.

The following is a complete list of the species previously described or recorded from the bed:-

FILICALES

Botryopteris antiqua Kidston — Walton et al., 1938.

? PTERIDOSPERMAE

Lyginorachis brownii Calder — Calder, 1935.

Aneimites acadica Dawson — Walton et al., 1938.

?CORDAITALES

Endoxylon zonatum Scott — Lacey, 1953.

The other plant bed in the Kilpatrick Hills is in an outcrop of sedimentary rocks in a shallow gorge cut by a small tributary on the south side of the Loch Humphrey Burn, about half way between Loch Humphrey and Greenside Reservoir. Apparently the first record of fossil plants from this locality is in a letter dated 12th February, 1886, from a Mr. James Bennie of the Geological Survey, Edinburgh to Mr. Robert Kidston. It mentions the Loch Humphrey Burn locality as being the source of the fossil plants enclosed with the letter, but it gives no clue as to their identity. In a paper on Araucarioxylon (now Eristophyton) fasciculare Scott (1899) records that the specimen was given to him by Mr. Kidston. It came from near the Loch Humphrey Burn where it was found by Mr. James Renwick in 1898.

Its horizon is given as that of the Calciferous Standstone Series. Later, Scott (1924) described Calamopitys radiata and Bilignia resinosa from the same locality. Both specimens were found in "beds of coarse ash agglomerate on the south side of Loch Humphrey Burn". Although both specimens were from the same bed he attributes the former to the Oil Shale Series and the latter to the Calciferous Sandstone Series, Cementstone Group! Kidston (1923) records a number of species preserved as compressions from the "escarpment on south side of Loch Humphrey Burn where stream with waterfall enters, about ½ mile below the Loch".

Following their discoveries in Glenarbuck Mr. Brown and Professor Walton extended their search to the Loch Humphrey Burn area. Just before the tributary enters the main burn it falls down a cliff of volcanic ash about 80 feet high and most likely it was from the foot of this cliff that the plants described by Scott were obtained. Further investigation by Mr. Brown and Professor Walton (Walton, 1949a) resulted in the discovery at the top of the cliff of a "small but rich bed of fine sandstone . . . . in the shales overlying the bed of coarse volcanic ash in which the earlier discoveries of petrified plants had been made." Probably the compressions

recorded by Kidston came from this bed. According to Tyrrell (Walton, 1949a) the sandstone consists "of a mixture of angular quartz grains and fragments of basalt minerals, and the plants are preserved in a mixture of this material in a base of calcium carbonate. He is of the opinion that the sandstone was not directly deposited ash but was probably ash which had been first deposited on a land surface and then washed, together with other sandy and silty material, into a pool or small lake in which the plant fragments also accumulated."

The following is a complete list of the species previously described or recorded from the beds:-

CALAMITALES:

Archaeocalamites göppertii Solms.	Walton, 1949b.
A. radiatus - Brongn.	Walton, 1949b.

FILICALES:

Etapteris tubicaulis Göpp.	Walton et al., 1938.

PROTOPITYALES:

Protopitys scotica Walton	Walton, 1957.

PTERIDOSPERMAE:

Lyginorachis trinervis Calder	Calder, 1935.
Calathospermum scoticum Walton	Walton, 1940, 1949,a.
Alcicornopteris hallei Walton	Walton, 1949, c.

FILICALES ET PTERIDOSPERMAE INCERTAE SEDIS:

Rhacopteris inaequilatera Göpp.	Kidston, 1923.
R. lindsaeformis Bunb.	Kidston, 1923.
R. petiolata Gopp.	Walton, 1957.
R. robusta Kidston	Walton et al., 1938.
Rhodea spp.	Walton, 1957.
Spathulopteris ettingshausenii.	Walton et al., 1938.
S. obovata	Walton et al., 1938.
Spenopteridium pachyrachis	Walton et al., 1938.
Telangium affine L. & H.	Kidston, 1923.
T. bifidum L. & H.	Kidston, 1923.

? CORDAITALES:

Calamopitys radiata Scott	Scott, 1924.
Bilignia resinosa Scott	Scott, 1924.
Eristophyton fasciculare (Scott) Zal.	Scott, 1902, 1918.
E. waltonii Lacey	Lacey, 1953.

MATERIALS AND METHODS

All the material from the Glenarbuck beds was collected by Professor John Walton and Mr. Robert Brown between 1930 and 1935. Recent investigation of the locality by the present author yielded some more material but it was badly weathered and of little use for structural investigation. Most of the specimens are petrified in calcite but occasionally other minerals, such as pyrite, are also present. Except where stated otherwise the material was investigated by means of peel sections prepared by the recent modified technique described by Joy, Willis and Lacey (1957). Dilute hydrochloric acid (1 part acid to 30 parts water) was employed as the mordant. Transfer preparations and nitrocellulose 'pulls' were made from compressed specimens of Aneimites acadica and the lepidodendroid twigs but as they did not reveal any structure, even on maceration, they were rejected.

Most of the Loch Humphrey Burn material was among that obtained by Professor Walton and Mr. Brown during the same period as they collected in Glenarbuck. All their specimens were placed in the Hunterian Museum Palaeobotanical Collection, which is housed in the Botany Department, University of Glasgow. Additional material from this locality was collected by the author.

Unlike those from Glenarbuck the petrifications from the Loch Humphrey Burn beds are not preserved entirely in calcium carbonate. Frequently some cells of a specimen are filled with calcite while adjacent cells contain silica, pyrite or, occasionally, other materials. Successful peels were made from most specimens, however, by etching first in dilute hydrochloric acid (1 part of acid to 30 parts of water) for 45 to 60 seconds and then in concentrated hydrofluoric acid for about the same length of time. In the case of Geminitheca scotica some petrological sections were used.

The compressions were investigated by means of transfer preparations and 'pulls', many of which were later macerated in either nitric acid or Schulze's fluid (concentrated nitric acid and potassium chlorate), followed by treatment with very dilute ammonia or other alkali. For epidermal structures 'pulls' were usually found to be quite adequate, which was rather fortunate as it was found that the cuticles disintegrated in acids. The most successful results in the investigation of ovulate fructifications were obtained by macerating transfers by the method described by Harris (1944). After maceration in nitric acid, on a slide, under a cover-slip, the specimen was washed in water and then treated with a weak alkali, in this

case a phosphate buffer of pH 7.8. The reaction was watched carefully through the microscope and when the desired stage was reached the reaction was stopped by adding a strong solution of sodium chloride. By this method some cell structure, e.g., in the nucellus and integument, is rendered visible, which would be destroyed by the use of strong alkalis.

In the case of petrified sporangia, e.g. Alcicornopteris hallei and Protopitys scotica, spores were obtained by dissolution of small fragments of the specimen in dilute hydrochloric acid. The suspension so obtained consisted largely of spores. It was washed in water and then a drop was mounted in glycerine jelly. Some spores were mounted in corn syrup, without a cover-slip, a method described by Radforth (1938), but there is no obvious advantage over glycerine jelly.

The use of hydrofluoric acid after hydrochloric acid, even after repeated washing, usually resulted in the formation of a fine precipitate, probably of calcium fluoride, which obscured detailed structure of spores. It was eliminated, at first, by the bromoform : acetone flotation method outlined by Frøy (1951). Later it was found that a solution of zinc bromide of specific gravity 2.3 was more suitable than the bromoform/acetone mixture, because it is miscible with water.

All peels and other preparations used in the investigation have been placed in the Figured Slide Collection and all hand specimens in the Hunterian Museum Palaeobotanical Collection. Both collections are housed in the Botany Department, University of Glasgow. Throughout this work the abbreviation 'F.S.C.' refers to the Figured Slide Collection and 'Pb' to the Hunterian Museum Palaeobotanical Collection.

PART I.

THE FLORA OF THE GLENARBUCK BED

The following species are here described:-

Lepidophloios kilpatrickensis sp. nov.

Lepidodendron solenofolium sp; nov.

L. brevifolium Williamson

L. cf. brevifolium Will.

Lepidocarpon wildianum Scott

Dineuron ellipticum Kidston

Heterangium grievii Williamson

Pteridosperm 'seed'

The following species are here recorded from the bed for the first time, but are not mentioned further:-

Protocalamites cf. pettycurensis Scott ex Lotsy

Stigmaria ficoides Brongniart

Metaclepsydropsis duplex Williamson

cf. Mittagia seminiformis Lignier

LEPIDODENDRALES

Lepidophloios kilpatrickensis sp. nov.

The new species, Lepidophloios kilpatrickensis, is based on a number of petrified axes collected from Glenarbuck bed. The axes which can with certainty be ascribed to this new species range from under 5 mm. to over 2 cm. in diameter and most of the fragments are 2 cm. to 4 cm. long. All the axes are calcified. Numerous peel sections have been made from all the specimens, and using the Croft Parallel Grinder Mr. C.A. Hopping prepared three series of sections, two longitudinal and one transverse. These were particularly useful in tracing the origin of the leaf-traces and in reconstructing the leaf cushions. The following petrological sections were prepared from a specimen with halonial branching: one longitudinal section through the main axis and both side-branches, two transverse sections of the main axis, and three transverse sections of one of the side-branches. The following description is based largely on these six sections.

DESCRIPTION

In the general arrangement of its tissues L.kilptrickensis agrees closely with other lepidodendroid species (pl. 1 fig. 1). Many of the axes show branching by unequal dichotomy. Usually only one branch is present in each specimen but in some cases two sub-opposite branches are present. Branching occurs by the separation of the xylem cylinder into unequal columns which soon become rounded off.

The stele:- The xylem cylinder is protostelic with exarch protoxylem. In no specimen has any secondary xylem been observed. The protoxylem forms more or less projecting groups of small tracheids, 4 μ to 20 μ in diameter, and arranged at fairly regular intervals round the surface of the xylem cylinder. These projecting protoxylem groups are frequently referred to collectively as the 'corona' of the xylem cylinder. The protoxylem tracheids have usually scalariform but occasionally spiral thickening. The leaf-traces are derived directly from the protoxylem groups and consequently, in transverse section, the extent to which the protoxylem groups project from the surface of the cylinder depends upon the level of the section relative to the outward passage of the leaf-traces (Pl. 1 fig. 2).

Usually the whole protoxylem group passes off from the stele as a leaf-trace, leaving a groove in which a new protoxylem group eventually arises. Occasionally a much larger protoxylem group is present and in such cases only a part of it passes off to form the leaf-trace. Since each new protoxylem group is formed in the groove left by the departure of a leaf-trace at a lower level the leaves must be arranged in vertical series.

The largest metaxylem tracheids, at the centre of the stele, are up to 210 μ in diameter, while the smallest, at the periphery, may be as small as 25 μ. The longest tracheid which it was possible to measure is 1.8 mm. long. The tracheids have the scalariform thickening characteristic of the Palaeozoic lycopods. The bars are about 3 μ broad and 8 μ apart. Occasionally some of the bars fork and in a few tracheids there is a transition to reticulation. The pits appear to be narrowly bordered. The better preserved specimens show the double series of fine threads, sometimes known as "Williamson's striations", bridging the pits and connecting the adjacent bars. In longitudinal section of the tracheids the nature of the apparently bordered pits is clearly seen.

The bordering is due to the fact that the bars themselves are double structures, a feature which has already been described and illustrated by several authors, e.g. Borghoorn and Scott (1958). Each half of the bar is connected to the corresponding half of the adjacent bars by a thread system. That the thread system is double is clearly shown at "a" in Pl. 1 Fig. 3. The arrangement of the threads in this species appears to be somewhat similar to that described by Calder (1953) in Lepidodendron brownii Unger sp. The threads do not join directly on to the scalariform bars but are attached to a continuous strip of material, apparently of the same composition as themselves and extending the full length of the bar (Pl 1, Fig. 3). That it is not a tertiary layer of thickening completely surrounding the bar, as was tentatively suggested by Calder, is quite obvious in longitudinal section, and in specimens where degradation has progressed further. In the latter case the threads and the strip of material to which they are attached are often detached from the bar (Pl. 1 Fig. 4), while in more extreme cases the bar itself has almost disappeared, though the threads are still present. This feature is dealt with more fully in the discussion. The threads anastomose frequently. They are

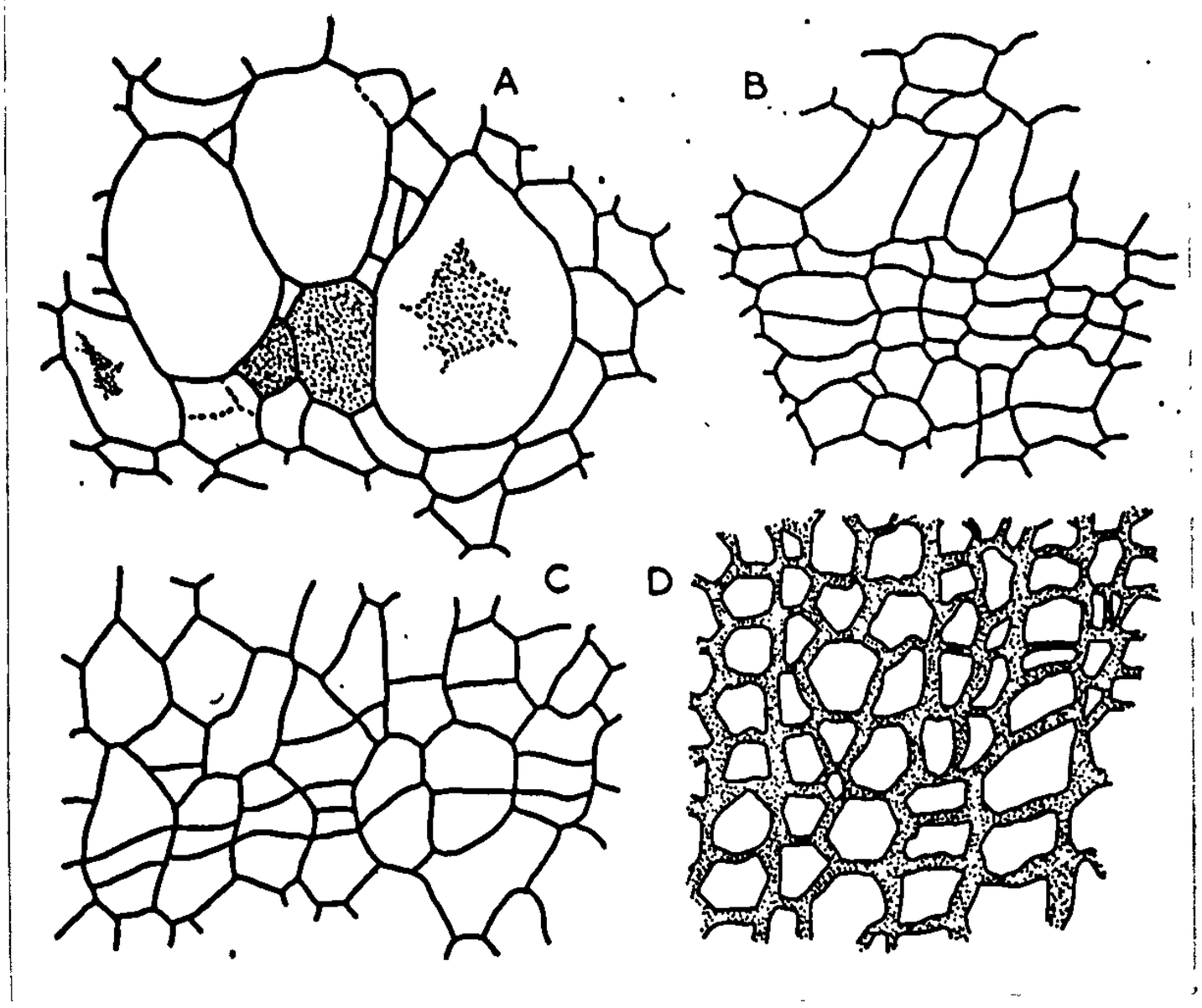
about 1 μ in diameter but they broaden, in the plane of the bars of thickening, to 2 μ to 3 μ where they join on to the continuous strip.

In most of the axes there is a gap between the xylem cylinder and the cortical tissue. The exceptions to this are one small twig and the smaller branches of branching axes. The following description of the phloem and the inner cortex is based on the petrological sections, mentioned previously, through such a branching specimen. It is possible that the side branches are cone peduncles and are, therefore, not typical. This seems unlikely as most are over 1 cm. in diameter and possess a well developed secondary cortex.

Immediately external to the xylem cylinder is a layer, three to four cells wide, of parenchymatous tissue (Pl. 1 Fig. 5). In transverse section the cells appear to be more or less isodiametric, and of fairly uniform size. They are quite small, being only 20 μ to 25 μ in diameter. They are arranged in vertical series and have transverse end walls. Their length varies from 20 μ to 50 μ. They have dense cell contents. External to this layer is the tissue which has been referred to by various authors as 'phloem' or 'secretory tissue'. It is here called phloem. It consists

of from one to three layers of large, thin-walled cells interspersed with a few smaller cells, of which some have dark contents (Pl. 1 Fig. 5 and Text-fig. 1A). The largest cells are of considerable size and extend for the full width of the zone (Pl. 1 Fig. 5). The vertical dimension of the cell is usually the shortest, and the end-walls are usually transverse. They tend to occur in vertical series but often their arrangement is very irregular. There is no evidence of any break-down of the end-walls such as has been described in other species of the genus (Walton, 1953, p. 52). The lumen of the cells is filled with a clear yellowish green substance, and there are frequently granular cell contents present in the centre of the cell.

The primary cortex:- The primary cortex is composed of three layers which are clearly demarcated from one another. The inner cortex, adjacent to the phloem, consists of a layer, up to ten cells wide, of small, thin-walled, axially elongated, radially seriated cells (Pl. 1 Fig. 5, and Text-fig. 1B). The tangential dimension is greater than the radial. The middle cortex consists of thin-walled parenchymatous cells which tend to be rather elongated tangentially (Pl. 1 Fig. 5). Towards the outside of the zone this elongation becomes more pronounced



Text-fig. 1. L.kilpatrickensis. A, transverse section of the phloem, x 100; B, transverse section of part of the inner cortex, x100; C, transverse section of part of the outer cortex showing the initiation of the secondary cortex, x 60; D, transverse section of the secondary cortex, x 100. (A, B & C drawn from slide F.S.C. 658; D, drawn from slide F.S.C. 1340).

and in the two or three outermost layers periclinal divisions have frequently occurred. Occasionally, as a result of this division, the outer layers are radially seriate. Throughout the zone the cells are loosely packed and there are large intercellular spaces. Only one fragment of an axis has been found in which at least part of the middle cortex was not preserved. The outer cortex consists of large celled parenchyma, the cells towards the inside being thin-walled and more or less isodiametric, and the cells towards the periphery relatively thick-walled and slightly elongated axially. In the older axes the cells of the outer cortex, external to the secondary cortex, show frequent evidence of both anticlinal and periclinal division (Pl. 2 Fig. 6).

The secondary cortex:- The term "secondary cortex" is here used in place of the more usual but inaccurate "periderm". Several authors, e.g. Beck (1958) have pointed out that the secondary cortex of the Lepidodendrid must have been a living tissue and therefore could not have resembled a periderm. In most axes the secondary cortex is well developed and only from the smallest, which are under 5 mm. in diameter is it completely absent. Most of the smaller branches show an early stage in its initiation. At about the middle of the outer cortical zone a discontinuous layer of cells, one to three cells

wide, shows a number of periclinal divisions (Text-fig. 1C). In slightly older specimens further division has resulted in the formation of short radial files of cells (Pl. 2 Fig. 7). Some of the files extend for the full width of the secondary zone, but many do not. At this stage the cells are relatively thin-walled. In the oldest axes found the secondary cortex is forty to fifty cells wide and the cell walls are heavily thickened (Text-fig. 1D). In transverse section the cells are rather irregular in shape but there is a tendency for them to be square to rectangular. They are axially elongated and in radial view appear to have transverse end-walls; in tangential view the ends of the cells are tapered. Most of the radial files of cells extend for the full width of the secondary zone, but many do not extend to the inner margin of the zone, while a few do not reach the outer margin; a few short files of ten to fifteen cells do not reach either margin. The number of cells along the outer margin of the zone is greater than the number along the inner margin by almost 10% in a stem of diameter approximately 2 cm. The outermost cells tend to be larger and to have relatively thin walls, but there is no evidence of the presence of a definite cambial layer. Some of the short files of cells are obviously the result of radial division in some of the initial

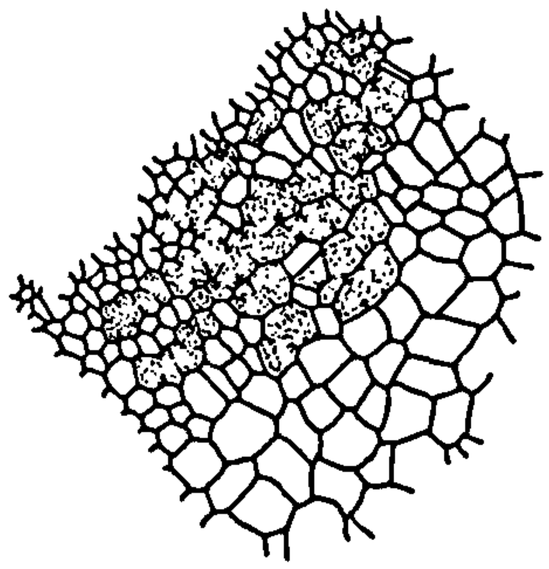
files, while others appear to have been interposed (Text-fig. 1D).

Secretory ducts:- A tangential series of secretory ducts is present in the outer zone of the primary cortex immediately inside the secondary zone. In many cases they do not appear to be true ducts because the centre of each is occupied by large, irregular, apparently convoluted cells, with clear yellow contents. Presumably these cells are in process of dissolution because in many of the ducts in the larger axes only a few remains of cell walls are present in the ducts. They are surrounded by an irregular layer of very small cells derived from the adjacent cortical cells by division in all planes (Pl. 2 Fig. 8). In transverse view the ducts are usually circular though in some the tangential diameter may be up to three times the length of the radial one. There is considerable variation in vertical extent: most ducts are from three to five times as long as broad, but a few are more or less isodiametric and some may be ten tofifteen times as long as broad. As in the specimens of Lepidophloios wunschianus Carr. described by Walton (1935) there is a definite correlation between the secretory ducts and the leaf-traces. The usual situation is that the leaf-trace passes

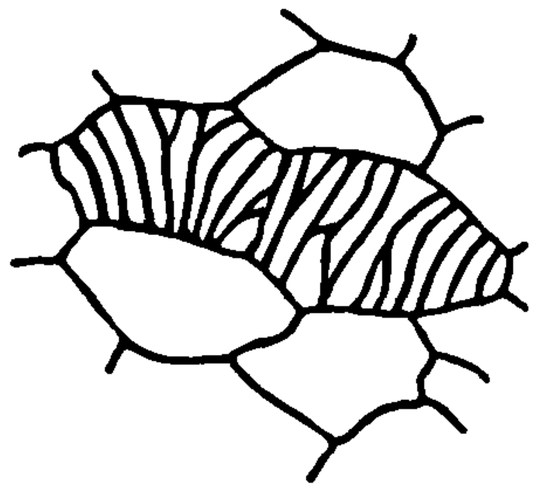
between two ducts, which converge on it and become united with the phloem of the trace. Sometimes only one duct is associated with a trace and occasionally a trace may have no associated ducts.

In the secondary cortex there are frequently occurring pockets where many of the radial and some of the tangential walls of the cells have disappeared, giving the appearance, in transverse section, of tangentially elongated cells with papillate walls (Text-fig. 2). These pockets are filled with a clear yellow substance similar in appearance to that in the secretory ducts in the outer primary cortex. The pockets are not of any great vertical extent. Since there does not appear to be any disturbance or distortion of the surrounding tissues it seems that they were a natural feature and that they performed some secretory function.

Secretory canals have been described in the secondary cortex of several species of lepidodendrid, but there is some doubt as to whether they are true lysigenous canals or whether they are merely the result of poor preservation of parenchymatous tissue. Seward and Hill (1900) proposed the former view, which has been disputed by Arnold (1940). In any case it is certain that the canals, if such they really are, have developed



Text-fig. 2. L.kilpatrickensis. Transverse section of part of the secondary cortex, showing the break-down of some of the cell-walls, x 50. (Drawn from slide F.S.C. 652)



Text-fig. 3. L.kilpatrickensis. Transfusion tracheids in the leaf cushion, x 320. (Drawn from slide F.S.C. 1332).

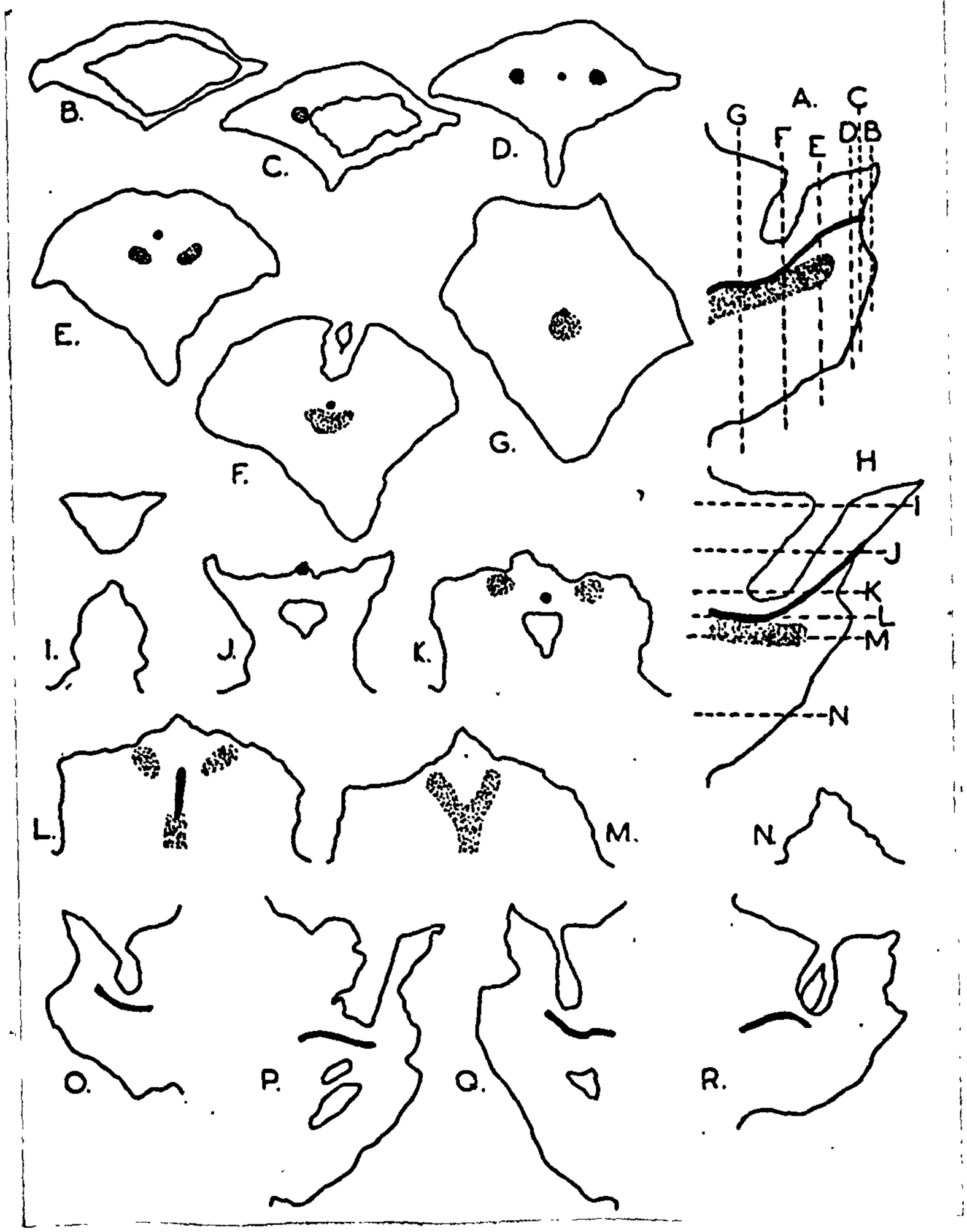
from bands of parenchymatous tissue, and are not comparable with those of L.kilpatrickensis, though in all probability they performed a similar function.

The leaf-traces:- The size of the leaf-trace, as would be expected, varies with the size of the stele, e.g. in transverse section the traces arising from a stele of diameter 0.35 mm. contain six to twelve trabheids; from a stele 0.62 mm. in diameter the traces contain nine to eighteen tracheids; and from a stele 2 mm. in diameter they contain from sixteen to twenty-eight tracheids. The tracheids seldom exceed 25 μ in diameter and the trace appears to consist entirely of protoxylem elements, the smallest being at the centre of the trace. By the time the trace reaches the secondary cortex, however, larger tracheids up to 50 μ in diameter are frequently present. They have scalariform thickening and are presumably metaxylem elements. On becoming detached from the xylem cylinder the leaf-trace continues to rise very steeply through the tissue immediately surrounding the xylem and through the phloem. It appears to cross the phloem on a bridge of the inner tissue. The exact behaviour of the strand in this region is not very clear in the material available, but a strand of very small phloem elements, also with clear cell contents, appears to accompany the strand on the abaxial side, and the trace acquires

a sheath of slightly elongated parenchymatous elements. Exactly where this sheath is developed is not quite clear, but it is present when the strand enters the inner cortical layer. It may be derived from the inner parenchytous layer surrounding the xylem cylinder. In the inner cortex the angle of the trace decreases to about 45° and this angle remains fairly constant until the trace reaches the secondary cortex. On entering the outer cortex an abaxial strand of loosely packed, isodiametric parenchymatous cells accompanies it on the abaxial side (Pl. 2 Fig. 9). This is the parichnos strand, which remains in close association with the leaf-trace until after it has entered the leaf cushion. The course of the parichnos strand and the leaf-trace through the secondary cortex is horizontal and all their cells are very much elongated radially. The horizontal course through the secondary cortex is a result of the rapid radial expansion of that tissue, as also, presumably, is the elongation of all the elements of the trace and its associated tissues. In the outer layer of the primary cortex, external to the secondary cortex, the cells regain their original dimensions, and the leaf-trace again rises at an angle of about 45° to the horizontal. At about the level where it enters the leaf cushion there is a marked development of transfusion tissue round

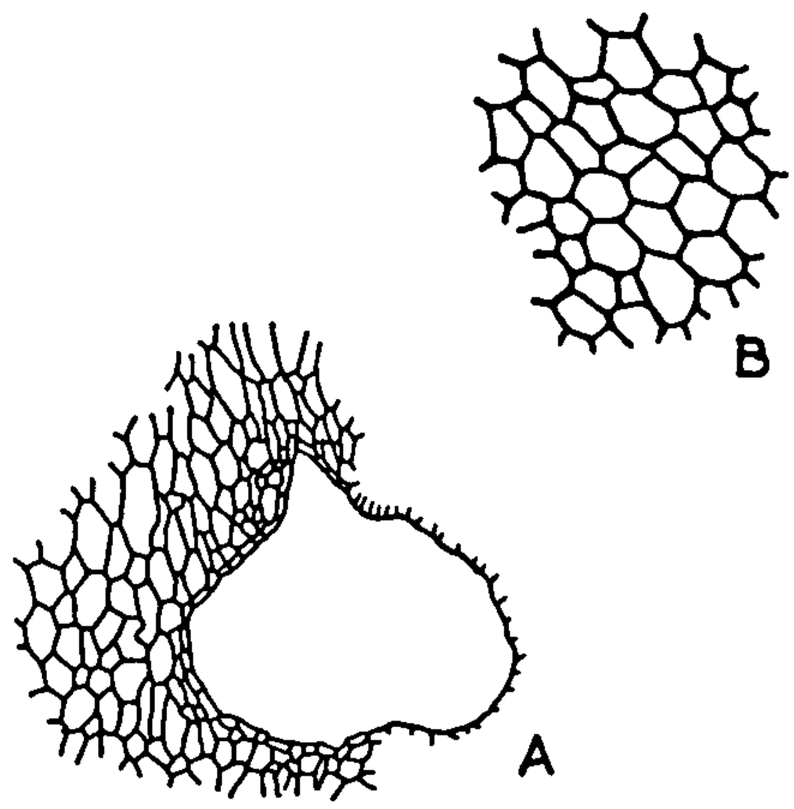
the trace. The transfusion tracheids are short and broad, with transverse end-walls. All the walls have a well developed reticulate thickening (Text-fig. 3).

The leaf cushions:- The leaf cushion is composed mainly of large celled parenchyma with intercellular spaces. The cells towards the outside of the cushion tend to be smaller than those at the centre. In tangential section through the base the cushions are roughly diamond-shaped (Text-fig. 4G), with, usually, the horizontal measurement slightly greater than the vertical, though there is considerable variation in this; sometimes in one cushion the vertical dimension is the greater, while in an adjacent cushion the horizontal dimension is the greatest. The cushion is strongly keeled from its point of attachement to the stem to the base of the leaf-scar, which is situated at the upper end of the cushion and is usually almost three times as broad as it is high (Text-fig. 4B). There does not appear to have been a definite abscission layer and the withered remains of the leaf are often still present, even in the larger axes. The cells of the leaf are much smaller than those of the cushion and the transition between the two tissues is very sudden. Abscission usually occurred at this point. Most often the scar is about the same width as the



Text-fig. 4. L. kilpatrickensis. A, radial section of a leaf cushion reconstructed from tangential sections, B-G; H, radial section of a leaf cushion reconstructed from transverse sections, I - N; O - R, radial sections of leaf cushions to show the variation in size and shape. Vascular tissue black, parichnos strand stippled. All sections x 12. (B - G drawn from slides F.S.C. 1269 - 71, 1274, 1277, 1281; I-N from F.S.C. 1327, 1328, 1330, 1332, 1334, 1338; O - R from F.S.C. 701, 701, 1309, 805.

cushion at its point of attachment to the stem, and the cushion attains its greatest width at about two-thirds of the way from the stem to the scar, tapering slightly in both directions. The cushion often sags slightly at the base (Text-Fig. 4 O-R). The centre of the leaf-scar is slightly concave and the leaf-trace forms a slight projection at or just below the mid point of the scar. The branches of the parichnos strand form two small depressions, one on each side of the leaf-trace (Text-fig. 4). The ligule pit is rather variable in shape, but on the whole it tends to be rather short and broad. The pit opening is directly above the broadest part of the cushion, and the pit slopes backwards towards the axis. The canal is narrower than the base of the pit. In transverse section the pit is broadly, rounded triangular, with the base of the triangle slightly concave, and the apex directed towards the axis (Text-fig. 5A). At the broadest point of the pit the apex of the triangle is often prolonged to form a sort of sinus, which is seen in longitudinal section in text-figure 4P. Towards the base the pit tends to become more rounded in section (Pl.2 Fig. 11). The epidermis of the pit consists largely of rather flattened cells (Text-fig. 5A), which are more or less isodiametric in surface view (Text-fig.5B). It has a thick cuticle. The



Text-fig. 5. L. kilpatrickensis. A, transverse section of the ligule pit, x 90; B, tangential section of the epidermis of the ligule pit, x180. (A drawn from slide F.S.C. 1328; B from slide F.S.C. 701).

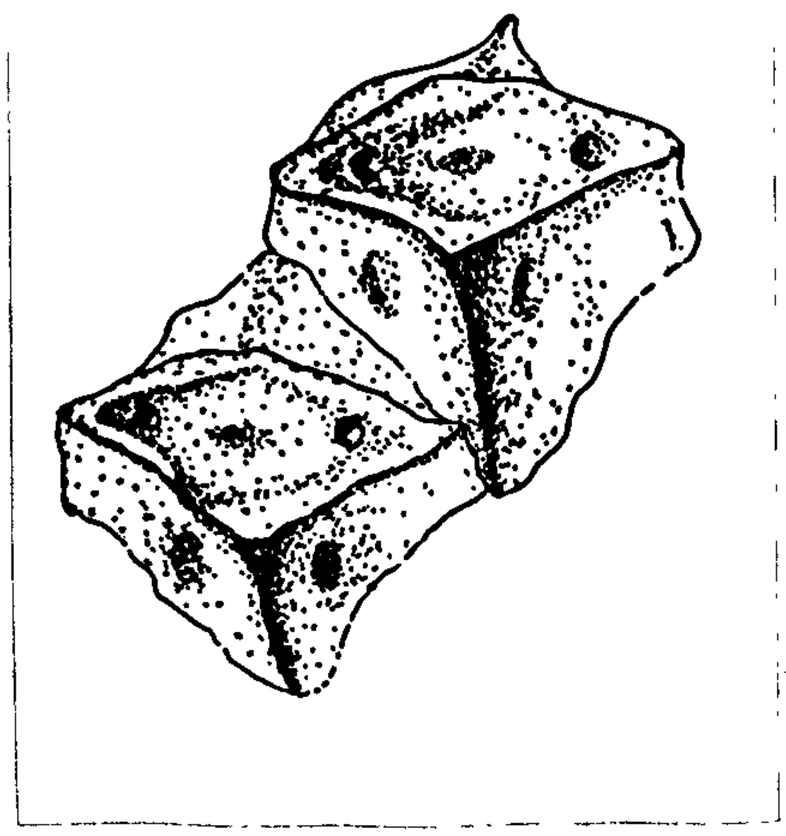
ligule is occasionally well preserved. It is rounded triangular in transverse section and is quite short and fat. It tapers to an acute apex which does not project out of the pit. It is composed of a uniform tissue of small, isodiametric, thin-walled cells, frequently with dense contents (Pl. 2 fig. 11).

The leaf-trace enters the cushion usually at an angle of about 45°. It dips slightly as it passes under the ligule pit, and then rises steeply to the leaf-scar. The parichnos strand does not divide until after the trace has passed under the pit. The two branches of the parichnos dip slightly away from the trace, and then run up parallel to the surface of the cushion until they reach the leaf-scar. They do not become attenuated as they approach the scar, and in tangential section through the cushion, immediately behind the scar, they are seen as circular depressions lying one on each side of, and at about the same level as, the vascular strand. Thus in a compression they would most probably be represented by two small indentations. The tissue lying between the branches of the parichnos and the surface of the leaf cushion has a columnar arrangement with numerous elongated air spaces running from the parichnos strand to the surface (Pl. 2 Fig. 10).

Though the preservation of the epidermis is rather poor and consequently it is impossible satisfactorily to decide the point, it seems likely that these air spaces did not communicate directly with the surface but were closed by stomata. In some the large-celled parenchyma lying below the parichnos strand has broken down to form usually a number of small air cavities, but occasionally a single large one. In some cases the parichnos strand itself has broken down.

As mentioned previously, within the leaf-cushion there is a considerable development of transfusion tissue round the leaf-trace. It is confined mainly to the lateral and adaxial sides of the trace, and its greatest development is between the trace and the base of the ligule pit. None has been found in the ligule itself, however.

A reconstruction of two leaf-cushions as they would most likely appear in a compression is shown in Text-fig. 6. It is based on a series of tangential longitudinal sections. The most important features are that the scar is at the apex of the cushion and is transversely elongated, that the cushion is strongly keeled, that the branches of the parichnos strand leave small identations, one on each side of the vascular trace,



Text-fig. 6. L.kilpatrickensis. Two leaf cushions reconstructed from serial tangential sections, x 12.

and that the opening of the ligule pit is hidden behind the leaf-scar.

SPECIFIC DIAGNOSIS

Lepidophloios kilpatrickensis sp. nov. :-

Branch fragments of an arborescent lycopod. Branches, at least those up to 2.5 cm. in diameter, with a solid protostele and no secondary xylem. Protoxylem forming more or less projecting ridges on the surface of the xylem cylinder. Leaf-traces derived directly from the protoxylem groups. Primary cortex three-layed, inner radially seriate, two outer layers parenchymatous. Secondary cortex of thick-walled, vertically elongated cells, arranged in radial files. Leaf cushions usually rhomboidal, with horizontal and vertical axes more or less equal, strongly keeled, not imbricating. Leaf-scar transversely elongated, rounded-rhomboidal, at apex of cushion. Scars of leaf-trace and branches of parichnos at or slightly below the mid-line of the leaf-scar. Ligule pit short and wide, sub-triangular in section.

Syntypes:-

Specimens Pb3319a,b,c,d,e,f in the Hunterian Museum Palaeobotanical Collection, and the slides made from them, F.S.C. 652-710, 738-740, 804-806, 1269-1340, in the Figured

Slide Collection, both in the Botany Department, University of Glasgow.

SYSTEMATIC POSITION AND COMPARISON WITH OTHER SPECIES.

The distinguishing features between the two genera Lepidodendron and Lepidophloios have for long been the subject of much controversy. Anatomically they appear to be indistinguishable and therefore the generic separation is based almost entirely on the form of the leaf cushions. Some writers, e.g. Scott (1920), consider that the major distinction is that in Lepidophloios the horizontal measurement of the cushions is greater than the vertical, whereas in Lepidodendron the vertical measurement is the greater. Others, e.g. Weiss (1902), consider that in Lepidophloios, as well as being horizontally elongated, the leaf-cushions imbricate, over-lapping from above downards. Neither of these characters will suffice to distinguish all species. Kidston (1893), in his monograph on the British species of Lepidophloios, gave a diagnosis of the genus, from which the following extracts have been taken:- "scale-like leaf-cushions, at or near whose summit it placed the leaf-cicatrix"; "leaf-cushions imbricated, upright or deflexed"; "leaf-cicatrices transversely oval, rhomboidal or rhomboidal-elongate". Watson (1907) selected

as the most significant character in this diagnosis the fact that the leaf cushions imbricate, and he based his separation of the two genera on this single feature. His rule is that "if a normal radius of the stem can be drawn so as to cut more than one leaf cushion, the specimen is a Lepidophloios". That this character is in itself insufficient is obvious from the fact that the leaf-cushions of some undoubted species of Lepidodendron are imbricated, e.g. L.brevifolium (Williamson, 1872, Pl. XLI, Fig. 1). Arnold (1947) says that in Lepidophloios the transverse diameter of the leaf cushion exceeds the vertical and that the leaf-scar is below the mid-line of the cushion. That this is not always the case has been clearly shown by Kidston (1893) in twigs of L.scoticus Kidst. In this species the leaf cushions on small twigs are directed upwards, whereas in older twigs the cushions are directed downwards and the scar actually hangs below the base of the cushion. An even clearer demonstration was given by Walton (1935) who showed both stages to occur in a single twig of L.scoticus.

The only conclusions that cen be drawn from these varied views is that to some extent Lepidodendron and Lepidophloios grade into each other and that they cannot be

separated by any single character, as many authors have attempted. L. ~~weltonii~~ kilpatrickensis is somewhat intermediate between the two, but the balance of evidence indicates that it is nearer to Lepidophloios. The following are the reasons for accommodating it in that genus:-

1. The leaf cushions tend to be transversely elongated.
2. The leaf-scar is situated at the apex of the cushion.
3. The leaf-scar is more or less rhomboidal and is over twice as broad as it is high.

The only criterion in which L. kilpatrickensis differs materially from Kidston's diagnosis is that the leaf cushions do not imbricate, but as mentioned previously this does not appear to be a critical feature since imbricating leaf cushions are present in some species of Lepidodendron.

The erection of a new species of Lepidophloios seems to require some justification, and for this reason fairly detailed comparisons have been made with all possibly similar or related species of Lepidodendron and Lepidophloios. It is unlikely that L.kilpatrickensis could be closely allied to any Upper Carboniferous species, and therefore detailed comparisons have been restricted

mainly to axes of similar size, from the Lower Carboniferous and the Upper Devonian. Table I summarises the differences between L. ~~waltonii~~ kilpatrickensis and other species of Lepidodendron. In making comparisons as many as possible of the following features were taken into consideration:-

1. The stele - whether or not a medulla was present.

2. The corona and the method of departure of the leaf-traces. Calder (1934a) has pointed out that in Lepidodendron and Lepidophloios there are at least two methods of formation of the leaf-traces. In one type, worked out in detail for Lepidodendron harcourtii Witham by Bertrand (1891), each trace is derived from the inner tracheids of a coronal ridge which splits into two to permit the outward passage of the trace. This type is usually found in species with a medullated stele. In the other type the leaf-trace arises, according to Scott (1920), "directly from the angles of the primary wood"., and this is the type found in L.kilpatrickensis.

3. The phloem, which unfortunately is usually poorly preserved or completely destroyed, and the secretory ducts in the outer cortex.

4. The zonation of the primary cortex.

5. The secondary cortex.

6. The leaf cushions.

Three species have been recorded from the Pettycur Limestone,, which has been ascribed to the Calciferous Sandstone Series and is therefore of approximately the same age as the Glenarbuck beds. These species are Lepidodendron pattycurense Kidston, L.brevifolium Williamson, regarded by some authors, e.g. Hirmer (1927), as being identical with L.veltheimii Sternberg, and Lepidophloios scottii Gordon. Kidston (1907) described L.pettycurense from a single axis, which is protostelic and has a well developed ring of secondary wood. As these are the only features described it is impossible to make a detailed comparison, but what evidence is available indicates that there was probably very little resemblance between the two species. The following measurements are taken from Kidston's type specimen, slide No. 544 in the Kidston Collection. The total diameter of the xylem cylinder of L.pettycurense was about 10 mm, while the primary wood itself measured only 2 mm., which is roughly the same as the diameter of the primary xylem cylinder of the largest specimen of L.kilpatrickensis. Beck (1958) has pointed out that there is really no definite proof that L.pettycurense is in fact a Lepidodendron. In the case of the other two species

detailed descriptions are available. L.scottii, described by Gordon (1908), differs from L.kilpatrickensis mainly in the structure of the stele and in the leaf cushions. Even in axes of 2.5 cm. or less in diameter the stele is either completely medullated or has a mixed pith. The leaf-traces arise like those of L.harcourtii. The leaf cushions differ markedly from those of L.kilpatrickensis. They are elongated horizontally and have a considerable sag, so that they overlap from above downwards. The ligule pit opens far back from the leaf-scar and the canal is oval in section, whereas that of L.kilpatrickensis is subtriangular. L.brevifolium, described by Williamson (1872, 1893), also differs from L.kilpatrickensis in being solenostelic, but the method of formation of the leaf-traces is similar in the two species. The leaf-cushions have lateral wings, so that they imbricate, and their height greatly exceeds their width.

Lepidophloios wunschianus Carruthers is another species recorded from the Calciferous Sandstone Series, at Dalmeny (Seward and Hill, 1900) and at Laggan, Arran. A complete account of the trunks and branches of the Arran specimens has been given by Walton (1935). L.wunschianus is similar to L.kilpatrickensis in having protostelic branches but it differs

in the method of departure of the leaf-traces from the stele. The organisation and arrangement of the secretory ducts in the outer cortex is the same in both species and the leaf cushions appear to differ only in minor details. In L.wunschianus the two branches of the parichnos strand become attenuated as they approach the leaf-scar, and therefore they would most likely not be visible in a compression. This is not so in L.kilpatrickensis. Also the ligule pit of L.wunschianus is very long and narrow (Walton, 1935, Text-fig. 6) while that of L.kilpatrickensis tends to be short and broad.

The only other Scottish Lower Carboniferous species preserved as a petrification is Lepidodendron brownii Unger sp., described by Calder (1933) from the Lower Limestone Group of the Carboniferous Limestone Series, at East Kilbride, Lanarkshire. It differs from L.kilpatrickensis in being solenostelic and in the fact that the cells of the outer cortex have well developed longitudinal ribs of thickening. There is little possibility of its being confused with L.kilpatrickensis and so it will not be considered further.

Renault described two species of Lepidodendron with protostelic branches from the Culm of France. They are L.rhodumnense Renault (1879) and L.esnostense Renault (1896). Any confusion

of L.kilpatrickensis with either of these two species is precluded on account of the very characteristic development of their secondary cortex. In both species it consists of anastomosing plates of thick-walled elongated cells, forming a network which is occupied by large parenchymatous cells.

Of the Devonian species Lepidodendron caracubense Schmalhausen and Lepidodendron saalfeldense Solms-Laubach (1896) are known from small protostelic axes. According to the description by the Zalesskys (1921) the secondary cortex of L.caracubense is like that of Renault's two species, though they do not show this very clearly owing to the poor preservation of their material. In L.saalfeldense the leaf cushions and the outer layers of the cortex are not preserved. The main distinguishing feature appears to be that the cells of the secondary cortex have unevenly thickened walls. The cells of the outer part of the middle cortex tend to be arranged in radial rows, a feature also shown by some specimens of L.kilpatrickensis. Beyond this the comparison cannot be carried.

The only compression species of Lepidophloios to be considered is L.scoticus Kidston, which is of very frequent occurrence in the Calciferous Sandstone Series of Scotland.

According to Kidston (1893) the leaf-cushions on young axes are directed upwards and are not keeled. The branches of the parichnos strand, and the leaf trace are represented by three small depressions a little below the centre of the leaf-scar. In the specimen figured by Walton (1935, Text-fig. 8) and in several specimens in the Hunterian Museum Palaeobotanical Collection, Glasgow University, Botany Department, however, the cushions are definitely keeled, and only the remains of the leaf-trace are visible on the leaf-scar. This latter type seems to be the usual form and it is on this that the comparison is based. The probable appearance of the leaf cushions of L.kilpatrickensis in a compression has already been described. The cushions would be strongly keeled and the branches of the parichnos, and the leaf-trace, would show on the leaf-scar. Probably lateral pits would be present below the scar owing to the collapse of the columnar tissue running between the branches of the parichnos and the surface of the cushion. These are not present in L.scoticus. In the shape of the leaf cushions, the shape and position of the leaf-scar, and in the fact that the ligule pit ishidden behind the scar, there is a strong similarity between the two species, suggesting a possible, fairly close, relationship between them. Still, it is possible

that the similarity is merely superficial and that anatomically they were widely different. According to a manuscript note by Bower in a copy of Gordon's paper on L.scottii (No. Q.G. 136 in the Pamphlet Collection, Glasgow University, Botany Department) Kidston himself believed L.scottii to be identical with his species L.scoticus, though he was unable to prove it.

In conclusion, although L.kilpatrickensis bears a strong similarity to L.scoticus it does not seem likely that the two are identical. They are possibly closely related, but the proof of such a relationship is impossible on the available evidence. Of the species known as petrifactions L.wunschianus is the closest to L.kilpatrickensis.

DISCUSSION OF CERTAIN MORPHOLOGICAL FEATURES.

(a) The pits of the tracheids.

The nature and origin of the double series of fine 'threads' connecting adjacent scalariform bars in the tracheids of many of the Palaeozoic lycopods has for long been the subject of much controversy. They were acutally first mentioned and figured by Witham (1833, Pl.8, Fig. 10), but they were first described in detail by Williamson (1869), who appears to have considered them as part of the secondary wall. Seward and

and Hill (1900) advanced the theory that each series of 'threads' represented the remains of a pit-closing membrane which had become torn due to contraction. Most other authors, Solms-Laubach (1892), Duerden (1933), Pannel (1942), Wesley and Kuyper (1951) and Fry (1954) have interpreted them, in some way or other, as being secondary wall structures. Calder (1933), after an examination of L.brownii, tentatively suggested that tertiary thickening had occurred in the tracheids, and that the vertical 'threads' were part of a tertiary deposit. Barghoorn and Scott (1958) interpret the threads as constituting part of the primary wall. Beck (1958) agrees with them, and, in fact, their view is the most convincing yet put forward. They coin for the 'threads' the term 'fimbrils', which will be used hereafter.

As has previously been mentioned, the scalariform bars and the fimbril systems connecting them are double. Consequently any theory interpreting the fimbrils as being secondary or tertiary implies the total removal of the primary wall and the middle lamella. Barghoorn and Scott point out that this interpretation is contrary to the normal degradative sequence. Barghoorn (1952) has shown that in the anaerobic degradation of wood there is a uniform and consistent sequence

of degradative changes showing a fundamental relationship to the lamellar structure of the cell wall. The order of break-down is as follows:-

1. The central layers of the secondary wall.
2. The innermost layers of the secondary wall.
3. The outermost layers of the secondary wall.
4. The primary wall.

According to Barghoorn and Scott, if the normal sequence of degradation has occurred in the lepidodendrid tracheids the residues must consist of primary wall remains, perhaps occasionally associated with the outermost layers of the secondary wall. Consequently the fimbril system must represent part of the primary wall. Also the lepidodendrids must have had a thicker primary wall than is usually found in the tracheids of the vascular plants.

The most likely interpretation of the peculiar tracheid structure of L.kilpatrickensis in which the fimbril system has apparently become separated from the scalariform bar (Pl. II Fig. 4) is that delamination of the primary wall has occurred. This view is supported by Barghoorn (personalcommunication), who points out that a similar feature can be readily seen in living plants in the bordered pits of some conifers. Delamination

occurred perhaps because of the break-down of pectic compounds within the thick primary wall.

(b) Features of the cortex.

It has usually been assumed that the space surrounding the stele in many of the Palaeozoic lepidodendrids is due merely to poor preservation of delicate parenchymatous tissue. This has recently been questioned by Beck (1958) who has suggested that the space may be a true circumstelar lacuna. In his species Levicaulis arranensis he postulates that the lacuna was formed as a result of circumferential growth during the development of the secondary cortex; since there was no compensating growth in the inner cortex it was pulled outwards from the stele and eventually tears occurred in its inner margin. He suggested further that the same process might occur in other species. As evidence for this theory in the case of Levicaulis he shows that the ratio of the width of the primary cortex to the diameter of the primary xylem is more or less constant (0.765 to 0.876) and is independent of the presence of a gap around the stele. Had the gap been merely the result of poor preservation this ratio would not be constant. This is a very plausible theory and might well apply to Levicaulis but unfortunately it cannot apply to L.kilpatrickensis for the following reasons:

1. The ratio of the preserved primary cortex to the diameter of the stele is not constant. The figure obtained for a number of stems varied from 0.18 to 3.00, a marked contrast to the figures obtained by Beck.

2. The relative amount of primary cortex preserved varies from one specimen to another, e.g., in an axis of diameter 4.2mm. only about 0.1 mm. of primary cortex was preserved, and yet in an axis 8 mm. in diameter all the tissues are perfectly preserved.

3. In axes where a circumstelar space is present there is no trace of the phloem or of the delicate radially seriate tissue of the inner cortex.

4. The cells of the inner layer of the preserved cortex correspond in size and shape with those of the middle cortex of completely perserved axes.

Clearly these facts do not accord with Beck's suggestion and so it is unlikely that a lacuna could have been formed here by the method he supposes. On the other hand it is possible that a lysigenous circumstelar lacuna could have been developed by dissolution of the inner and part of the middle cortex. This view is supported by the fact that the inner margin of the preserved cortex is always clearly demarcated (Pl.I fig. I and

Pl. II fig. 9). Had the circumstelar space been merely the result of decay one would expect the cortex to be progressively less well preserved towards its inner margin.

The nature and origin of the secondary cortex have been extensively discussed by several authors, notably Kisch (1913) and Beck (1958) and it is not proposed to go further into the matter here. It is sufficient to state that the numerous short radial files of cells present in the secondary cortex add further proof to Beck's theory that the secondary cortex has originated by the development of a succession of zones of meristematic activity rather than from a single zone analogous to a phellogen, as was previously thought.

A further interesting feature of the primary cortex is the frequent evidence of cell division in all of its three layers: the inner cortex is radially seriate, periclinal divisions occur frequently in the outer part of the middle cortex, and in the outer cortex external to the secondary zone most of the cells show evidence of anticlinal division (Pl. 2 fig. 6). The obvious conclusion which can be drawn from this is that the primary cortex remained in a meristematic state for a considerable part of the life of the plant. This would in part account for the large size attained by the plants

in spite of their relatively small secondary development. The division of the outer cortex must have occurred in response to the great circumferential expansion of the axis due to the development of the secondary cortex.

Lepidodendron solenofolium sp. nov.

Two specimens of lepidodendroid twigs have been referred to Lepidodendron solenofolium sp. nov., One is represented by a series of four longitudinal sections through a small twig 2 to 3 mm. in diameter, the other by three transverse sections of a badly crushed axis which was probably 12 to 15 mm. in diameter. All the sections are peels. Both specimens are structurally fairly well preserved and both are still bearing leaves, which are the most interesting feature of the plant.

DESCRIPTION

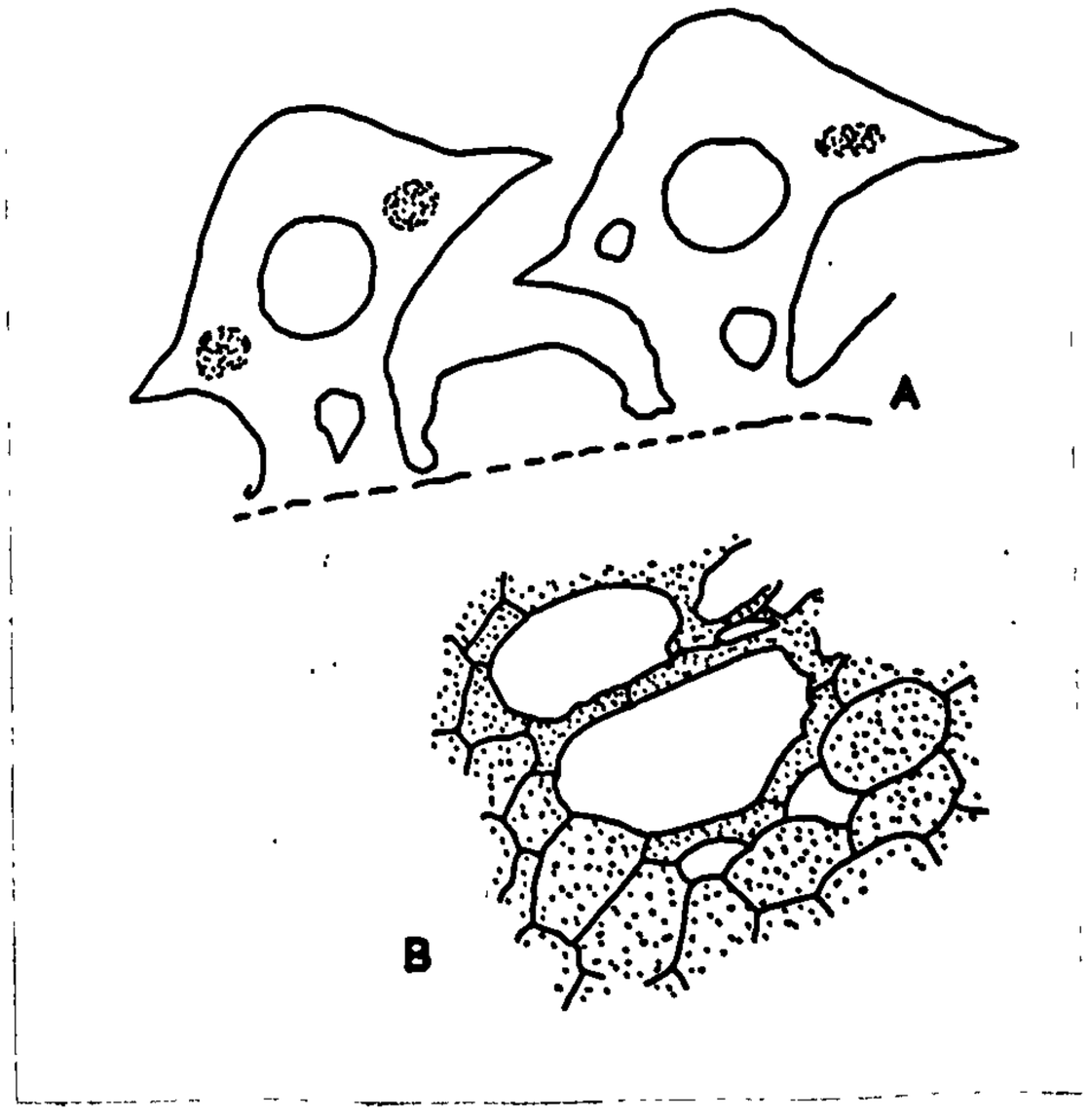
The stem:- The xylem cylinder is very similar to that of Lepidophloios kilpatrickensis. It is protostelic with exarch protoxylem. No secondary xylem is present. The protoxylem groups form characteristic coronal ridges arranged at irregular intervals round the surface of the xylem cylinder, exactly as in L.kilpatrickensis. It differs from that species in that the ridges anastomose occasionally. Although the mode of origin of the leaf-traces cannot definitely be determined from the three transverse sections available it most probably resembles that of L.kilpatrickensis, i.e., the traces are derived directly from the protoxylem points. There is no evidence of any relationship between

the anastomosis of the protoxylem ridges and the departure of the leaf-traces, such as was demonstrated in L.harcourtii Witham by Bertrand (1891). Undoubtedly spirally thickened tracheids are present in the protoxylem groups and in the leaf-traces. The metaxylem tracheids have the usual scalariform thickening and show the same double fimbril system as already described in detail for L.kilpatrickensis. The metaxylem tracheids vary from about 25 to 200 μ in diameter, the largest being at the centre of the stele. The walls of the larger tracheids are not as thick as those of the smaller tracheids at the periphery.

The phloem and inner cortical layers are not preserved in either specimen. The outer cortex is parenchymatous, the cells tending to be slightly elongated axially. No secondary cortex is present in either stem. In this respect L.solenofolium resembles L.brevifolium Will. rather than L.kilpatrickensis. In L.brevifolium the secondary cortex is frequently lacking even in stems 2 cm. in diameter. In L.kilpatrickensis it is present in stems under 1 cm. in diameter. The cortex is unusually narrow.

The leaves: All the leaves are still attached to the stems. In transverse view of the stem the leaf cushions are keeled and have well developed lateral wings, which imbricate slightly (Text-fig. 7A). The cushion is composed of a fairly uniform parchenchymatous tissue. The ligule pit (Pl.3 Fig. 1) is long and narrow, widening slightly towards the base, where the ligule is situated. The ligule is fairly small, more or less tongue-shaped, and composed of a uniform small-celled parenchyma (Pl. 3 Fig. 1).

Above its point of attachment to the stem the leaf becomes rather irregularly rhomboidal in section (Pl.3 Fig. 2). It has a thickened hypodermal layer, from one to six cells wide. The cells of both the ground parenchyma and the hypodermal layer tend to be arranged in longitudinal series. The centre of the leaf is occupied by a cavity (Pl.3 Fig. 2) which is continuous with the circumstelar space. It is possible that both are lysigenous lacunae. The arguments for and against this hypothesis as it concerns the stem have been dealt with in discussing the circumstelar cavity of L.kilpatrickensis. In the case of the leaves, supporting the view that the cavity is a true lacuna and not merely the result of poor preservation of



Text-fig. 7. L.solenofolium. A, transverse section of the leaf cushion, partly reconstructed, x 20; B, transverse section of the parichnos strand, showing the armed parenchyma, x 210. (Both drawn from slide F.S.C. 732).

delicate tissue is the fact that the other delicate tissues of the leaf, the ligule, the arm parenchyma of the parchnos strands, and the aerenchyma between the parichnos and the epidermis, are quite well preserved. Against it is the fact that, although the cavity is very regular in shape, being almost circular in section, there does tend to be a progressive deterioration in the state of preservation of the tissues towards the centre of the leaf. As in the case of the circumstelar cavity insufficient evidence is available to decide this point but what evidence there is tends to support the view that the central cavity of the leaf is a true lacuna.

The position of the leaf-trace varies considerably, but usually it lies on the abaxial side of the cavity, projecting slightly into it (Pl.3 Fig. 2), while at irregular intervals round the cavity are scattered transfusion tracheids. This appears to be the only development of such tissue in the leaf, an unusual situation in a lepidodendrid. The parichnos strand forks after it has passed under the ligule pit, and the two branches diverge and pass up the abaxial side of the leaf (Pl.3 fig.2). They extend almost to the tip of the leaf. The parichnos tissue is quite well preserved.

It consists of armed parenchyma cells with prominent intercellular spaces (Pl.3 Fig. 2; Text-fig. 7B). Between each branch of the parichnos strand and the epidermis there is a longitudinal strip of parehchymatous tissue with large intercellular spaces (Pl. 3 Fig. 2). Probably two longitudinal stomatal bands coincide with these strips of aerating tissue. Unfortunately tangential sections of the leaves at this point are not available.

DIAGNOSIS

Lepidodendron solenofolium sp. nov.:

Branch fragments of an arborescent lycopod. Small branches protostelic, with no secondary xylem. Protoxylem groups forming more or less projecting ridges along the surface of the xylem cylinder. Leaf-traces dervied directly from these ridges. Secondary cortex not developed in twigs up to 12 mm. in diameter. Leaves persistent, keeled, with lateral wings, imbricating slightly. Ligule pit long and narrow, broadening near the base, rounded triangular to circular in transverse section. Ligule small, tongue-shaped. Leaves with central longitudinal cavity, around which are scattered transfusion tracheids. Leaf-trace on abaxial side of cavity, often projecting slightly into it. Parichnos strands, consisting of armed parenchyma, persisting through

almost whole length of leaf. Aerating tissue present between parichnos strands and epidermis.

Syntypes:- The two specimens represented by slides number F.S.C. 732, 785, 786, and F.S.C. 733 - 736, in the Figured Slide Collection, Glasgow University Botany Department.

DISCUSSION AND COMPARISONS

The important characters on which the new species is founded are the structure of the xylem cylinder, particularly the corona, the shape and structure of the leaf cushions and the structure of the leaves. No other species has apparently been described which has both protostelic branches and leaf cushions with prominent lateral wings. Only six other lepidodendroid species with protostelic branches have been described from Lower Carboniferous horizons, and in none of these do the leaf cushions resemble those of L.solenofolium. They are:-

Lepidophloios kilpatrickensis sp. nov.

L.wunschianus Carruthers - Walton (1935)

Lepidodendron caracubense Schmal. - Zalesskey & Zalesskey (1921)

L.esnostense Renault (1896)

L.pettycurense Kidston (1907)

L.rhodumnense Renault (1879)

As the main distinguishing features of the last five species have already been discussed when comparing them with L.kilpatrickensis detailed comparisons are not necessary here and it will suffice to mention briefly the characteristics in which they differ from L.solenofolium. L.kilpatrickensis and L.wunschianus differ in the shape and structure of the leaf cushions and in the broad cortex. L.pettycurense differs in that even in the smallest branches known secondary xylem is present. In L.caracubense, L.esnostense and L.rhodumnense the secondary cortex has a very characteristic reticulate structure and is present even in the smaller twigs. So there is little possibility of confusion between these species and L.solenofolium. The differences between L.kilpatrickensis and other lepidodendroid species are summarised in Table I.

In his comprehensive survey of the leaves of the aborescent lycopods Graham (1935) recognises eighteen types, about half of them undoubtedly belonging to species of Lepidodendron and Lepidophloios, and three further types were described by Reid (1941). The leaves of L.solenofolium do not fit in with any of these types. The main difference is in the arrangement of the vascular tissue around a central lacuna (or possibly a central strand of very delicate parenchyma),

and in the parichnos strand. Usually the branches of parichnos strand are absent from the greater part of the length of the leaf, e.g. Lepidophyllum minor Graham (1935, p. 596), or are present as two narrow abaxial, subhypodermal strips of aerating tissue, e.g. L.brevifolium. In L.solenofolium the parichnos strands are well developed almost to the tip of the leaf and comprise typical armed parenchyma. So far as is known no other lepidodendroid species has been described in which the parichnos itself consists of such tissue, though it is present in the leaf cushions of some species, e.g. L.vasculare Binney (Seward, 1910), lying between the parichnos and the surface. Thus L.solenofolium possess a further type of leaf hitherto unknown among the arborescent lycopods.

Lepidodendron brevifolium Williamson.

Lepidodendron brevifolium was first described by Williamson (1873) from petrified axes found in the Pettycur Limestone at Burntisland, Fife. These beds are part of the Calciferous Sandstone Series. Two other petrified axes have been tentatively attributed to this species, one from the Calciferous Sandstone Series of Berwickshire, described by Calder (1934), and one from a Lower Carboniferous horizon in New South Wales, Australia, by Barnard (1928). Both of these specimens possessed the Diploxylon type of structure and were completely decorticated. Solms-Laubach (1892) described and figured twigs of a Lepidodendron which he considered to be specifically identical with the plant from Burntisland. Though he did not name it he could only be referring to L.brevifolium because at that time it was the only lepidodendroid species described from the locality. So far as is known this is the only record of small branches or twigs other than those from Burntisland.

Dawson, in a letter to Williamson (1873, p. 310), expressed the view that the Burntislandspecies is identical with the impression species L.veltheimii Sternberg. This view has been supported by several later authors, including Hirmer (1927).

Jongmans (1929, pp. 130-131) has strongly criticised this identification and has retained the name L. brevifolium for structurally preserved specimens.

Two small fragments of axis have been found in the Glenarbuck beds which can with certainty be attributed to L.brevifolium - specimens Pb3361a and b in the Hunterian Museum Palaeobotanical Collection. The smaller axis is about 1.5 mm in diameter (including the leaf-cushions). The larger is rather oval in section, the shorter diameter being about 8 mm. and the longer 13 mm. Neither axis has any secondary tissue, either xylem or cortex. Several transverse peel sections were prepared from both axes, and longitudinal peel sections were made from the larger specimen.

Both axes have been compared in detail with sections, in the Kidston Collection, of twigs of L.brevifolium from Burntisland and with the original description by Williamson (1873). The following are the features on which the identification with L.brevifolium is based:

1. The stele:-

The xylem cylinder (Pl. 3, Fig. 3 and 4) is solenostelic and has exarch protoxylem, but in neither specimen is the medulla preserved. It is possible, though very unlikely, that at least in the smaller axis the apparent presence of a medulla is due

to the fact that at the time of preservation the xylem had not completely differentiated, and that consequently the gap in the centre of the xylem cylinder is the result of a lack of preservation of the immature metaxylem elements. There is considerable evidence against this. Many twigs of considerable size from Burntisland specimens of L.brevifolium have a well preserved medulla. In species with protostelic branches, e.g., L.kilpatrickensis and L.wunschianus, the xylem is fully differentiated even in the smallest twigs known, which in the case of L.kilpatrickensis are less than 5 mm. in diameter. A further point is that in both of the new specimens the largest metaxylem tracheids are situated at the middle of the xylem ring (Pl. 3 Fig. 3), whereas if the stele was merely an immature protostele the largest tracheids would be expected to occur at the inner margin of the ring. The xylem of the three steles figured by Williamson (1873, Pl XLI, Figs. 3, 4 and 8) show exactly the same arrangement as do the two Glenarbuck specimens. Thus it seems reasonable to conclude that the stele actually was meduallated.

There is no clear distinction between the metaxylem and the protoxylem. The protoxylem tracheids are aggregated into rather ill-defined groups which appear as small, very obtuse projections, irregularly spaced round outside of the xylem cylinder (Pl. 3 Fig. 3; cf. Williamson, 1873, Pl. XLI, Fig. 8). There is no well defined corona. The origin of the leaf-traces

has not been worked out in detail, but they appear to arise directly from the protoxylem groups in much the same way as do those of L.kilpatrickensis. This is the method of origin of the leaf-traces of L.brevifolium as recorded by Calder (1934, p. 57). No undoubted spirally thickened tracheids have been observed in the protoxylem groups or in the leaf-traces. All the metaxylem tracheids show the typical lepidodendroid type of scalariform thickening, with an occasional transition to reticulation. This also has been recorded in L.brevifolium by Calder (1934). The tracheids show the double fimbril structure, which is similar in appearance to that already described in L.kilpatrickensis. Although Williamson does not mention the presence of the fimbrils in L.brevifolium they are present in most of the sections of that species in the Kidston Collection (e.g. Slides 497^{1-9}), and their occurrence has been recorded by Seward and Hill (1900), Barnard (1928) and Calder (1934).

The phloem is not preserved in either specimen.

2. The cortex:-

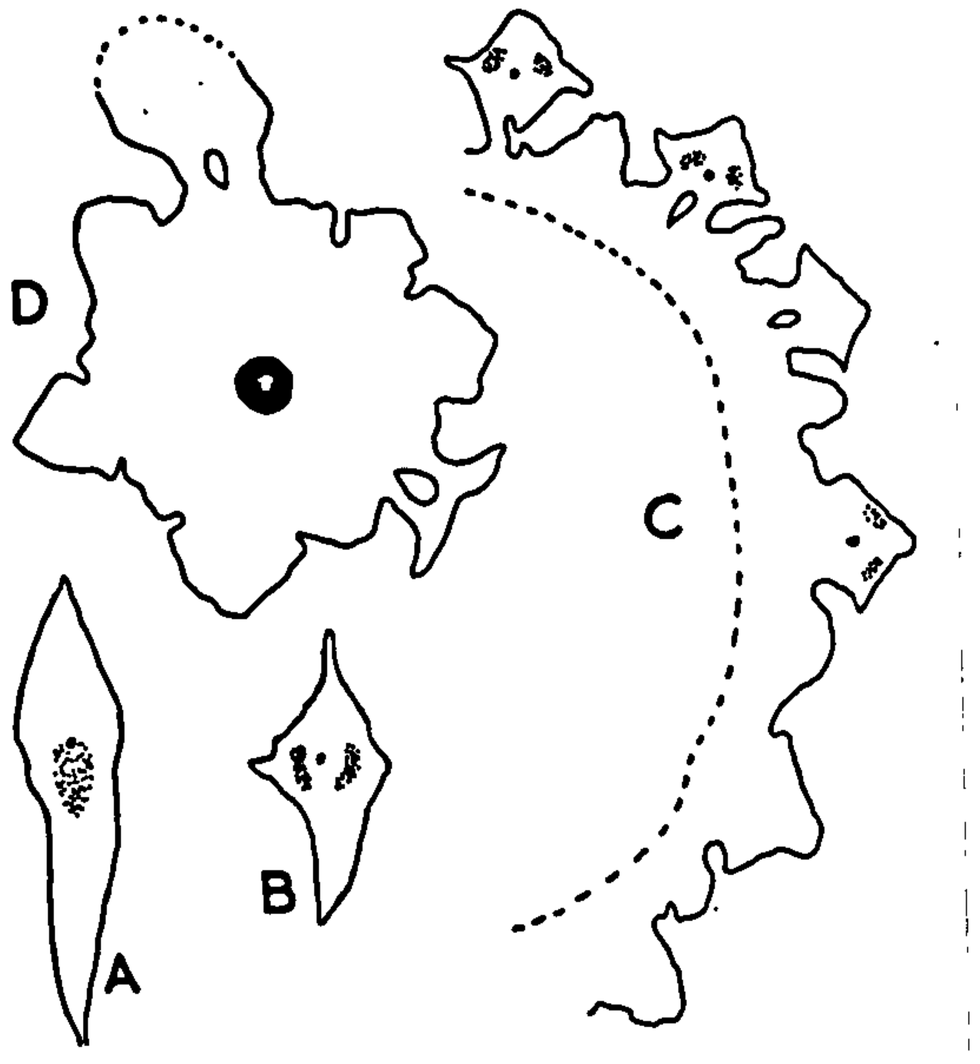
The cortex is poorly preserved in the smaller axis and almost completely lacking in the larger, a layer only about 0.3 mm. wide, immediately inside the leaf cushions, being preserved. In the smaller axis the cortex appears to have been a fairly uniform

parenchymatous tissue. There is no evidence of any definite zonation of the cortex such as is usually found in the axes of lepidodendrids. This lack of zonation is a conspicuous feature of the smaller twigs of L.brevifolium (cf. Williamson, 1872, Pl.XLI, fig. 2). The almost complete lack of preservation of the cortex of the larger specimen indicates that it was probably of a very soft parenchymatous nature, especially since most of the leaf cushions are still intact. Consequently it is unlikely that a secondary cortical zone could have been present in the axis, as such a tissue would almost certainly have been more resistant to decay than would the parenchymatous leaf cushions. Williamson (1873, p. 290 and Pl.XLII, fig. 9) comments on the usual lack of preservation of the greater part of the cortex of L.brevifolium: "the tissue is usually limited to the outer-most part, viz. to the subepidermal parenchyma and a small portion of the subjacent prosenchyma". Examination of sections of twigs of L.brevifolium has revealed that frequently axes of 10 to 20 mm. in diameter possess a similar narrow region of preserved cortical tissues to the Glenarbuck specimens, and in axes where the entire cortex is preserved (though invariably compressed) the secondary cortex is either sparsely developed or completely lacking. Initiation of the secondary cortex appears to have occurred at about the same time as, or perhaps slightly before, the development of the secondary xylem.

3. The leaf cushions:-

Williamson barely mentioned the leaf cushions and leaves in his original description of L.brevifolium, though he includes sections of both in his figures. No complete description is available and therefore comparisons have been made largely from Kidston's sections.

The leaf cushions of the larger Glenarbuck stem are very much elongated axially (Text-fig. 8A,B). They have well developed lateral wings, so that to some extent they are imbricated (Text-fig. 8C). Most of the cushions shown in transverse section in Text-Fig. 8C can be closely matched by leaf cushions in one of the sections figured by Williamson (1873, Pl. XLII, fig. 9) and all are closely comparable with sections from Burntisland specimens. The leaf-trace and the parichnos strand behave in the manner usual for species of Lepidodendron. The ligule pit is fairly long and narrow, and more or less oval in section, with the longer diameter orientated radially to the axis. Often the inner side of the pit is rather acute in section (Text-fig. 8 C,D). The ligule is small, rather oval in section, and tapers gradually to an acute apex. It is composed of a uniform, small-celled parenchyma (Pl. 3 fig. 5). The ligule and ligule pit of L.brevifolium were described by Solms-Laubach (1892). Incidentally, this and the almost simultaneous description of it in L.selaginoides



Text-fig. 8. L. brevifolium. A & B, tangential sections of leaf cushions, x 10; C, transverse section of part of the larger axis, showing the leaf cushions, x 10; D, transverse section of the smaller axis, x 18. (A & B drawn from slide F.S. C. 1342; C from slide F.S.C. 1341; D from slide F.S.C. 744).

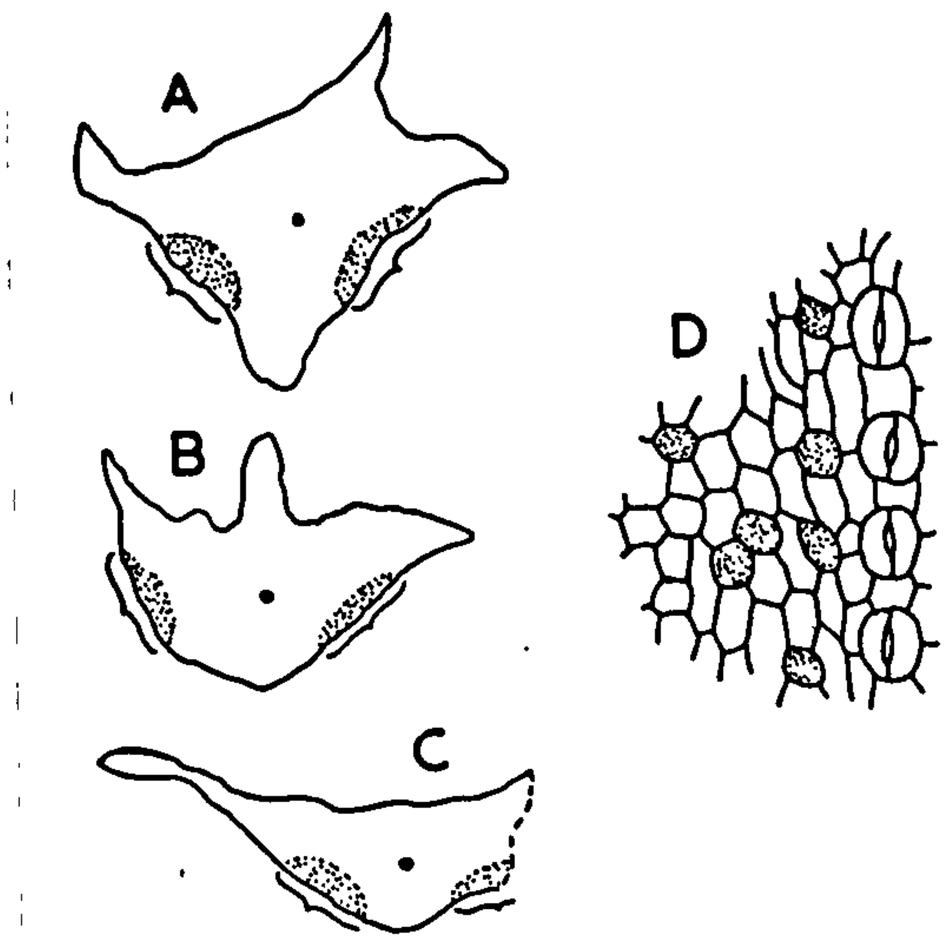
Sternberg by Hovelacque (1892), was the first demonstration of the presence of a ligule in the Lepidodendraceae. The ligule and its pit figured by Solms-Laubach (1892, Fig. 2) are rounded triangular in section, as are a few in Burntisland specimens. However, in so far as they are preserved, the ligule and its pit in most axes of L.brevifolium are similar in size and shape to those of the Glenarbuck stems.

4. The leaves:- All the leaves are still present on the smaller Glenarbuck axis but as only a few transverse sections were prepared little information is available concerning their structure. In the case of the larger axes many of the leaves are still attached but their preservation is unsatisfactory, especially towards the apex. Nevertheless they are sufficiently well preserved for their gross structure to be determined.

The leaves of L.brevifolium have been described by Graham (1935). The leaves of the Glenarbuck axes are rather different in cross section from that figured by Graham (1935, Fig. 1), but this is of little significance as the same applies to many of the leaves of twigs from Burntisland. The reason for this, as Graham himself indicates, is that the shape of the leaf in section varies with the relative position of the section. In

transverse view near the cushion the leaf is rather irregularly rhomboidal (Text-fig. 9A). Further up the abaxial side becomes more rounded and the adaxial side tends to become concave, apart from a curious dorsal ridge (Text-fig. 9B), which gradually peters out towards the middle of leaf. At about the middle the leaf has the appearance shown in Text-fig. 9C. Many of the leaves of Burntisland twigs follow this pattern, but there is considerable variation, even in the leaves on a single twig. In some cases the adaxial side of the leaf remains convex, like that figured by Graham (1935, Text-Fig. 1).

Anatomically the Glenarbuck leaves coincide more or less with those described by Graham. The leaf has a well developed, thickened hypodermis, about two cells wide, but owing to poor preservation it is impossible to determine whether or not it extends completely round the leaf, and it does in Graham's specimens. Abaxially, on each side of the central vascular strand, is a sub-hypodermal strip of parenchymatous tissue with numerous air spaces (Text-fig 9A,C, and this seems to be a continuation of the parichnos strand. The stomata (Text-fig. 9D) are confined to two longitudinal strips which coincide with the aerating tissue (Text-figs. 9A-C). They are very simple and do not appear to have any definite subsidiary cells. They are not sunken but are level with the other epidermal cells and are orientated parallel with the axis. They are arranged in



Text-fig. 9 L.brevifolium. A, B & C, transverse sections of leaves, at increasing distances from the leaf cushion x 30; D, surface section of part of the leaf epidermis showing papillae (stippled) and a row of stomata, x 180. In A, B & C the branches of the parichnos strand are stippled and the extent of the stomatal strips is indicated by brackets. (A, B and C drawn from slide F.S.C. 1341; D, from slide F.S.C. 1346).

regular longitudinal rows and there are four to six rows in each stomatal region. In the non-stomatal region the epidermis consists of two types of cell: fairly regular cells which tend to be slightly elongated axially, and small, rounded papillae (Text-fig. 9D). The arrangement of the stomata is more regular and the alternation of the elongated cells and papillae more irregular than in Graham's leaf, but this can be explained by individual variation. Twigs of L.brevifolium from Burntisland show a similar variation.

Taking into account all the evidence listed above there can be little, if any, doubt that the two twigs from Glenarbuck are specifically identical with L.brevifolium from Burntisland.

Lepidodendron cf. brevifolium Williamson

Three fragments of a completely decorticated axis, from the Glenarbuck bed, have tentatively been ascribed to Lepidodendron brevifolium Williamson. All are of the Diploxylon type, i.e., they have a central medulla surrounded by a ring of primary xylem and a broad ring of secondary xylem. Almost certainly the fragments are parts of a single axis, as in all three a vein of a reddish-bbown mineral runs through the medulla, and corresponding parts of the secondary wood of each are pyritised, the rest being calcified. As each fragment is about 10 cm. long the original fragment was about 30 cm. in length.

There has been slight compression of the fragments, so that they are slightly oval in transverse section; the shorter diameter is about 3.2 cm., the long 4 cm. Neither the pith nor the extraxylary tissues are preserved.

DESCRIPTION.

The primary xylem:- The pith is approximately 1.4 cm by 0.7 cm. in diameter and is surrounded by a ring of primary xylem 1 mm. to 2.5 mm. wide. The tracheids of the primary xylem are rather distorted. The protoxylem elements are not clearly differentiated from the metaxylem and the protoxylem groups do not form well marked coronal ridges. In transverse section the

outer margin of the primary xylem has a slightly undulating outline, the protoxylem groups forming small and rather illdefined, obtuse projections (Pl. 4 Fig. 1). Although the origin of the leaf-traces has not been worked out in detail it is fairly certain that the traces arise directly from the protoxylem groups, in a similar fashion to those of L.kilpatrickensis. No short, isodiametric tracheids (the 'barred' cells of Williamson) have been observed at the periphery of the primary xylem.

Between the primary and secondary xylem there is a discontinuous layer of apparently parenchymatous tissue, comprising more or less isodiametric cells. Only the protoxylem groups appear to be directly in contact with the secondary xylem. No short tracheids, like those described by other authors (e.g. Barnard, 1928, p. 668) have been discerned in this region, but quite possibly this is because of the very poor state of preservation here.

The secondary xylem:- The secondary xylem cylinder is 9 mm. to 12 mm. thick. The tracheids tend to be rather square in transverse view, and they are much narrower than those of the primary zone (Pl. 4 Fig. 1). Towards the inner margin of the secondary xylem there is a marked decrease in diameter of the tracheids, and as a consequence the radial rows taper sharply

(Pl. 4 Fig. 1). The numerous rays are uniseriate for the greater part of their length, and most are from one to four cells deep. The exceptions to this are the very broad rays carrying the leaf-traces. The rays increase to up to six cells wide and about the same in depth as they approach the primary xylem. The tissue of the ray eventually becomes continuous with the layer of parenchyma lying between the primary and secondary wood (Pl. 4 Fig. 1). The cells of the rays are thin-walled and radially elongated.

The tissues of this axis are more degraded than those of L.kilpatrickensis, L.solenofolium and L.brevifolium already described and consequently the tracheids of both the primary and secondary xylem show even more clearly the structure of the double fimbril system. The fimbrils and the strip of wall material to which they are attached are frequently completely separated from the scalariform bars (Pl. 4 Fig. 2), while in many instances the bar itself has almost disappeared.

The leaf-traces:- As already mentioned, the leaf-traces appear to arise directly from the protoxylem groups. After it has become detached from the primary xylem cylinder the trace continues to rise steeply, almost parallel to the primary axis, for a short distance. It then makes an almost right angled bend and

passes on a more or less horizontal course, through a broad ray (Pl. 4 Fig. 3) to the periphery of the xylem. The only elements of the trace which have been preserved are very narrow, apparently spirally thickened, protoxylem tracheids, and a few undoubtedly scalariform tracheids at the periphery of the trace. The smallest elements are at the centre of the trace (Pl. 4 Fig. 3). Occasionally a small strand, consisting, in transverse view, of only one or two elements, accompanies the trace on its abaxial side (Pl. 4, Fig. 3). It consists of short, more or less isodiametric tracheids with scalariform thickening on the walls. These appear to be identical with the 'transfusion' tracheids occurring in the leaves and between the primary and secondary wood of most lepidodendroid species.

Branching:- The axis shows two vertical series of branches arising alternately, on the longer diameter of the axis (Pl. 4 Fig. 4). Branching occurs by the separation from the outer part of the primary xylem cylinder of a small column of xylem which gradually becomes rounded off as it pursues a steep course upwards through the layer of secondary wood. The branch does not leave a gap in the primary xylem ring.

DISCUSSION OF AFFINITIES.

The stems of only two Lower Carboniferous lepidodendrids have been described in the diploxyploid state. They are Lepidophloios wunschianus Carr. and Lepidodendron brevifolium Will. Comparison of the anatomy of the Glenarbuck axis with these two species demonstrates a closer similarity to L.brevifolium. The major difference from L.wunschianus and, as far as has been determined, from all known Upper Carboniferous species is in the lack of prominent ridges in the corona of the primary xylem cylinder. L. brevifolium appears to be the only species described from which these ridges are absent. There is a further similarity in the structure of the leaf-traces and the fact that they pass almost horizontally through the secondary wood. The only significant difference between the Glenarbuck axis and the diploxyloid axes of L.brevifolium is in the conjunctive tissue between the primary and secondary xylem, and quite possibly this is merely the result of poor preservation in the former. In L.brevifolium this tissue consists of two types of element: parenchymatous cells and 'transfusion' tracheids, and it is the latter which have not been found in the Glenarbuck stem. However, since they are sometimes present in the rays, in association with the leaf-traces, it is quite possible that initially they were present and that their apparent absence is merely due to lack of preservation.

It is possible that this axis represents the secondary state of a species at present known only in the primary condition, e.g., L.kilpatrickensis. The only objection which can be raised to its belonging to L.kilpatrickensis is that in the smaller branches of that species the corona of the primary xylem has well marked ridges. Nevertheless, it is possible, though rather unlikely, that coronal ridges were present in the small branches but absent from branches with secondary thickening.

Insufficient evidence is available to make a definite decision on this point, and so the axis is tentatively referred to L.brevifolium, the only known species with which it agrees in coronal structure. This identification is supported by the fact that twigs undoubtedly of L.brevifolium occur in the same bed.

Lepidocarpon wildianum Scott

Atrributed to Lepidocarpon wildianum Scott is a single specimen from the Glenarbuck bed, represented by one peel section (R.S. fig. 1), in the Figured Slide Collection, Glasgow University Botany Department. Only two British species of Lepidocarpon have been described from petrified material. They are L.lomaxii Scott, described by Scott (1901) from the Coal Measures, and L.wildianum Scott from Burntisland, described in the same paper.

The section of the Glenarbuck specimen appears to be in a rather oblique, tangential plane, through the distal part of the 'seed'. ~~The reason for assuming this is that the micropyle appears in the section (Pl. 5 Fig. 1) but the base of the sporophyll is very narrow, and the sporangium is not at that point attached to it. Also, there does not appear to be a vascular strand in the sporophyll, which further suggests that the section is from the distal end.~~ The megaspore membrane shows the typical fibrillar structure (Pl. 5 Fig. 2) of Cystosporites giganteus Zerndt (figured by, e.g. Dijkstra, 1956), the isolated fertile megaspore of species of Lepidocarpon. As far as the structure is concerned the new specimen adds nothing to our knowledge of Lepidocarpon.

The attribution of the Glenarbuck specimen to L.wildianum is based on negative rather than on positive evidence. In size, shape and general appearance it bears a closer resemblance to L.wildianum than it does to L.lomaxii. Also the Glenarbuck bed is of approximately the same age as, and has several species in common with, the Burntisland beds, from which L. wildianum was described, whereas L.lomaxii has been found only in Upper Carboniferous horizons. It is possible, of course, that the Glenarbuck specimen belongs to a yet undescribed species of Lepidocarpon,

but the differences between it and the Burntisland specimens described by Scott are so slight that they could easily be accounted for by individual variation, and they certainly do not warrant the erection of a new species.

FILICALES

Dineuron ellipticum Kidston

A short length of petiole represented by a number of transverse sections in the Figured Slide Collection has been ascribed to Dineuron ellipticum Kidston. Kidston (1909) described this species from a single transverse section of a petiole from Pettycur, Fife.

DESCRIPTION.

The arrangement of the tissues (Pl.5 Fig. 3) is exactly as described by Kidston. The outer cortex consists of thickened cells, which tend to be smaller and thicker walled towards the periphery, larger and thinner walled towards the inner margin of the zone. The inner cortex is not preserved; presumably it consisted of delicate parenchyma. What is apparently the endodermis surrounds the remains of the pericycle and phloem - a delicate tissue of small, thin walled cells.

The xylem is more or less elliptical in outline and is composed of large tracheids. No parenchyma is present. At one side of the stele there is a circular opening surrounded by protoxylem elements; at the opposite side (Pl. 5, fig. 3) there is a semi-circular sinus. At about the middle of the outer

cortical region, opposite the sinus, is a pinna trace. It consists of a narrow crescentic band of small tracheids surrounded by the remains of a delicate small celled tissue (Pl. 5, Fig. 3). Unfortunately the series of sections does not include the point of departure of the trace.

DISCUSSION.

Kidston's section did not include a pinna trace. He suggested that in D. ellipticum the origin of the traces was similar to that of Metaclepsydropsis (Zygopteris) duplex Will.: a crescentic band of tracheids was cut off alternately from each side of the xylem to supply the pinna traces. This is confirmed by the new specimen. He thought further that the trace probably divided into two in its course through the cortex, as in M.duplex. The evidence provided by the new specimen does not support this view.

PTERIDOSPERMAE

Heterangium grievii Williamson

Two short lengths of stem, represented by a number of transverse sections in the Figured Slide Collection, have been attributed to Heterangium grievii Williamson. Both are about 2 mm. in maximum diameter. They consist only of the stele, surrounded by the remains of the cortex and a few leaf-traces (Pl. 5, Fig. 4). No secondary xylem is present. The leaf-traces are single.

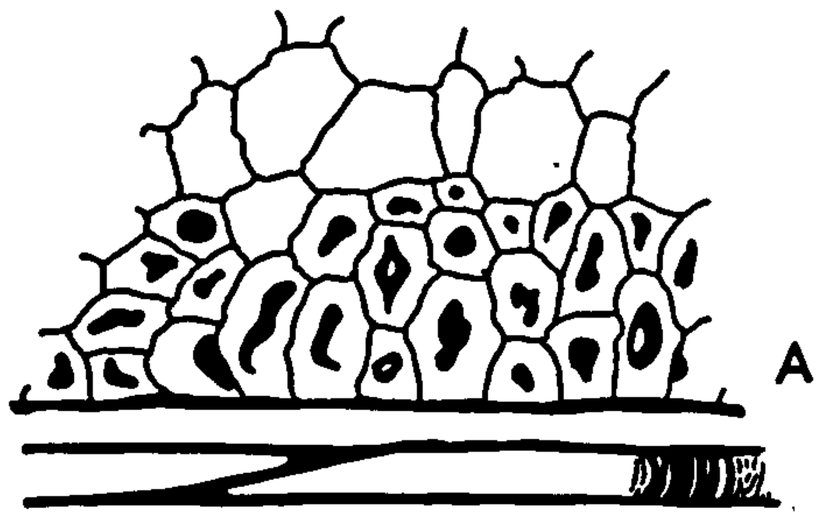
These stems are attributed to H.grievii for two reasons: first, because H.grievii is the only known Lower Carboniferous species; second, because H.grievii is the only species having a single vascular strand in the petiole, all other species having two.

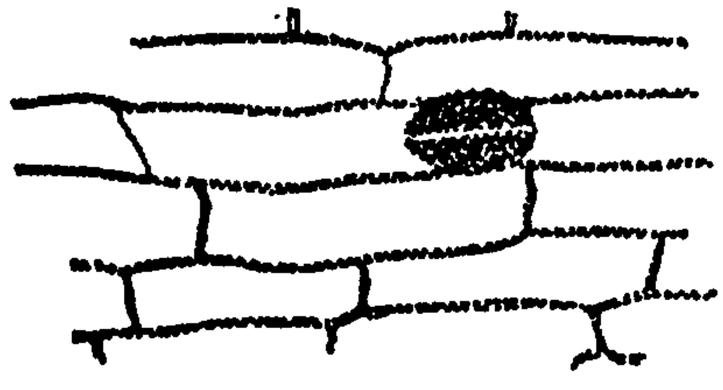
H.grievii has been recorded from Pettycur, Fife, by Williamson (1873) and from Gläzisch-Falkenberg by Solms-Laubach (1892).

Pteridosperm 'seed'

The pteridosperm 'seed' is represented by three oblique longitudinal sections in the Figured Slide Collection. One of them is illustrated in Pl.5, fig. 5. On first examination the seed appears to have a well developed integument and a large prolongation of the nucellar apex, which passes between the integumantary lobes. Closer examination shows that the 'nucellar apex' is in fact another lobe of the integument seen in tangential section. Of the nucellus little remains except a fragment of megaspore membrane attached to a narrow layer of indeterminate tissue. The structure of the membrane is not clear. It probably had a least two layers, one of which had some sort of fibrillar or reticulate structure (Pl. 5 Fig. 6).

The integument consists of three layers of tissues(Text fig. 10A); an inner layer, up to five cells wide, of thick-walled, elongated cells, probably of a fibrous nature; a narrow middle layer of thin-walled, isodiametric cells with dark contents; and an outer parenchymatous layer. Small scalariform or reticulate tracheids are present in the middle layer. The outer part of the parenchymatous layer is mssing. The inner epidermis is badly preserved. In tangential section (Text-fig. 10B) only the vague outline of the cells is visible. They tend to be slightly





Text-fig. 10. Pteridosperm seed. A, longitudinal section of the integument, slightly simplified, showing the three main layers, x 100; B, tangential section of the inner epidermis of an apical lobe of the integument, x 140. (Drawn from slide F.S.C. 1358).

elongated polygonal in shape. A few darker, rounded cells may represent papillae or stomata.

DISCUSSION.

Since nothing is known of the structure of the nucellus of this 'seed' very little can be decided as to its relationships. It is probably a member of the Lagenostomales. The free lobes of the integument suggest affinities with Physostoma and Sphaerostoma rather than with Lagenostoma or Conostoma, in which the integumentary lobes are joined together. The integument/in structure differs from the integuments of all four genera, so that a close relationship is unlikely.

PART II

THE FLORA OF THE LOCH HUMPHREY BURN BED.

The following species are heredescribed:-

cf. Pothocites sp.

Protopitys scotica Walton

Geminitheca scotica gen. et sp. nov.

Calathiops trisperma sp. nov.

Staphylotheca kilpatrickensis gen. et sp. nov.

Alcicornopteris hallei Walton

The following species is here recorded from the bed for the first time but is not mentioned further:-

Stigmaria ficoided. Brongniart.

CALAMITALES

cf. Pothocites sp.

The specimen shown in Pl.6 Fig. 2 has tentatively been ascribed to the genus Pothocites Paterson. It was found among the material collected by Professor Walton and Mr. Brown.

The stobilus and spores:- The specimen is a compression consisting of a strobilus about 1 cm. in diameter. It is borne on a naked pedicel which has broken about 2 mm. from the base of the strobilus. The distal part of the strobilus is missing. Its length from the pedicel to the edge of the rock is about 3 cm. At the distal end, near the edge of the rock the strobilus tapers sharply and it is possible that the break has occurred near the apex of the specimen. Alternatively it is possible that the strobilus was segmented, as in P.calamitoides Kidston, and that the break occurred just below the first node. Scattered linear leaves are present in the strobilus; there is no evidence that they were borne in whorls and possibly they represent sterile parts of the sporophylls.

Maceration of small fragments of the strobilus has yielded numerous spore masses. Their shape varies considerably but most are 2 to 5 times as long as they are broad. This suggests that

they were borne in rather narrow, elongated sporangia.
The spores unfortunately are immature and repreated attempts to isolate single spores from spore masses have been unsuccessful. They are of the Calamospora type. They are round, 30 to 40 μ in diameter. The spore coat is thin and completely smooth. Apart from the triradiate mark they are absolutely featureless. In most cases the triradiate mark is rather indistinct; in a few it is clearly visible (Text-fig. 11). The rays extend for about one third of the diameter of the spore.

DISCUSSION:

The new specimen has been placed, with some hesitation, in the genus Pothocites Paterson for negative rather than positive reasons. It was felt that insufficient data were available to justify the creation of a new genus and of the existing genera of fructifications attributed to the Articulatae Pothocites was apparently the nearest to the new specimen. It is possible, though unlikely, that it is not referable to the Articulatae but to some unknown group of plants.

Of the species of Pothocites enumerated by Kidston (1883) only one has leaves on the strobilus. It is P.calamitoides Kidston. It differs from the new specimen in that it is undoubtedly segmented and that the leaves are borne only in whorls at the nodes.

Text-fig. 11. cf. Pothocites sp. Spores at the edge of a spore-mass. The trilete mark is visible in the spore in the centre, x 500. (Drawn from slide F.S.C. 1367).

Insufficient is known of the new specimen to compare it adequately with species described from petrifications. It probably had a complex structure and may have resembled to some extent Cheirostrobus pettycurensis Scott, which is of the same age. The spores of Cheirostrobus, however, differ from those just described.

Kidston (1883) regarded species of Pothocites as being the fructifications of Archaeocalamites (Bornia) species, while Cheirostrobus is probably attributable to the Sphenophyllales. Although stems of Archaeocalamites are common in the Loch Humphrey Burn Bed there is no evidence of any connection with the new frutification. So its precise relationships must for the present remain undecided.

PROTOPITYALES

Protopitys scotica Walton

Two new specimens referrable to Protopitys scotica Walton have been found. The first to be described was collected from the Loch Humphrey Burn bed by the author; the other was among the material collected by Professor Walton and Mr. Brown.

SPECIMEN A.

This specimen adds little to what has already been described of P.scotica by Walton (1957). It consists of a fragment of stem with a broad ring of secondary xylem (Pl.6 Fig. 2). In the type specimen there was a very narrow zone of secondary xylem in the stem bearing the sporophylls (Walton, 1957, Pl. I Fig. 3). The arrangement and structure of primary wood in the new specimen agrees with that described for the type specimen. It is interesting, however, in that the ring of secondary wood is excentric and has a single growth ring. It is unlikely that this could be a seasonal effect as other axes (e.g. Eristophyton waltonii Lacey) from the same bed do not show it. It is possibly due to a temporary inundation with volanic ash, or some similar catastrophe.

SPECIMEN B.

The type specimen of P.scotica was apparently not quite mature as the sporophylls had not unfolded and the sporangia had not dehisced. From the evidence available Walton (1957, p. 355) concluded that the sporophylls were arranged alternately on opposite sides of the stem and that "the branching of the sporophyll was mainly dichotomous but the smaller rachides which bore the sporangia were branched in a pinnate manner". Apparently the sporophylls were entirely fertile.

The specimen collected by Professor Walton and Mr. Brown is a compression of a plant fragment fitting the above description of a sporophyll of P.scotica (Pl.6 Fig. 3). It consists of a dichotomising rachis bearing at the tips of its four branches a number of irregular branches arranged more or less pinnately. This pinnate arrangement is clearly derived from a dichotomous structure.

Several nitrocellulose 'pulls' were prepared from this specimen; some of these were mounted on slides directly; others were macerated in Schulze's solution. From an examination of the mounted 'pulls' it was obvious that the ultimate divisions of the rachis bore sporangia, but unfortunately dehiscence had occurred prior to fossilisation and few spores were present in them.

The sporangium wall was reasonably well preserved in some cases and it does not appear to differ from that of the type specimen of P.scotica figured by Walton (1957, Pl. III Fig. 19). Two stomata were also observed on sporangium walls and these too agreed with those of P.scotica (Walton, 1957, Pl. III, Fig. 18).

The residue from the maceration of two 'pulls' was mounted on a single slide. It contained about 50 spores of which about 40 were of one type, though they showed an enormous size range of over 150 μ. Some of them were surrounded by a curious, discrete membrane.

In order to carry out a complete comparison spores were isolated from the type specimen of P.scotica. A small fragment was detached, treated first with dilute hydrochloric acid and then with concentrated hydrofluoric acid. After washing half of the residue was mounted in glycerine jelly; the other half was first macerated and then mounted. There was no appreciable difference between the two batches of spores so obtained, and, more important, they were identical with those obtained from the new specimen. It was concluded, therefore, that the new specimen is specifically identical with P.scotica and that it confirms Walton's deductions about the structure of the sporophyll.

The spores:- The two most interesting features of P.scotica arising from this further investigation using maceration techniques are the structure and the range in size of its spores. Walton (1957, p. 337) stated that three size of its spores were present. Most sporangia had small spores (diameter 82 μ); some had large spores (147 μ); while some had spores of an intermediate size (98 μ). An examination of the type slides by the author confirmed this view, but an examination of the spore samples obtained by maceration strongly contradicated it. The histogram shown in text-fig. 12 was obtained by plotting the number of spores against their diameter in microns. It shows an almost continuous variation in size. 261 spores were measured; they shows a size range from 75 μ to 355 μ, with a mean of 125 μ. About 70% of the spores were in the range 90 to 150 μ.

An attempt was made to isolate the spores from a single sporangium but it was unsuccessful. As far as can be determined from peel sections the range in size of the spores within any sporangium is fairly small. This is what would be expected. 20 spores in one sporangium had a mean size of 102 u, the range being from 95 to 107 μ. In another sporangium 20 spores had a mean size of 147 μ, the size range being 137 to 160 μ.

It is almost certain that the results obtained as regards the number of larger spores (i.e., above 200 μ) is inaccurate. Many of those measured were damaged and the number of fragments present suggests a rather higher number of large spores than is shown by the counts. It is quite possible that a second peak should be present in the histogram somewhere between 240 and 270 μ. Repeated attempts to obtain more undamaged large spores have been unsuccessful.

In many cases the spore is surrounded by a discrete, cutinised membrane (Pl. 7 Fig. 1). It appears to be a sort of 'perispore' rather than a true air bladder such as is found, e.g., in species of Glomospora B & W., since in most cases the spore is free inside it. In some cases, however, it appears to be attached to the spore along the rays of the trilete mark. Detached 'perispores' are quite common in the maceration and many of them show the trilete mark quite clearly (Pl. 7, Fig. 2). Even so it is likely that they functioned as air bladders in spore dispersal since spores with 'perispores' still attached have been found among the sporae dispersea of the bed. The margin of the 'perispore' is rather irregular. The surface is smooth to microreticulate.

The spore itself (Pl. 7, Fig. 3) is more or less circular in equatorial outline. The margin is smooth. The spore coat is fairly thin and is usually folded. It is usually perfectly smooth though occasionally it appears to be slightly roughened. The trilete mark is prominent. The rays, which are straight, extend for about half the length of the radius. The ratio of the length of the ray to the radius of the spore is fairly constant and is independent of the size of the spore. The suture is narrow and simple. The lips are prominently raised.

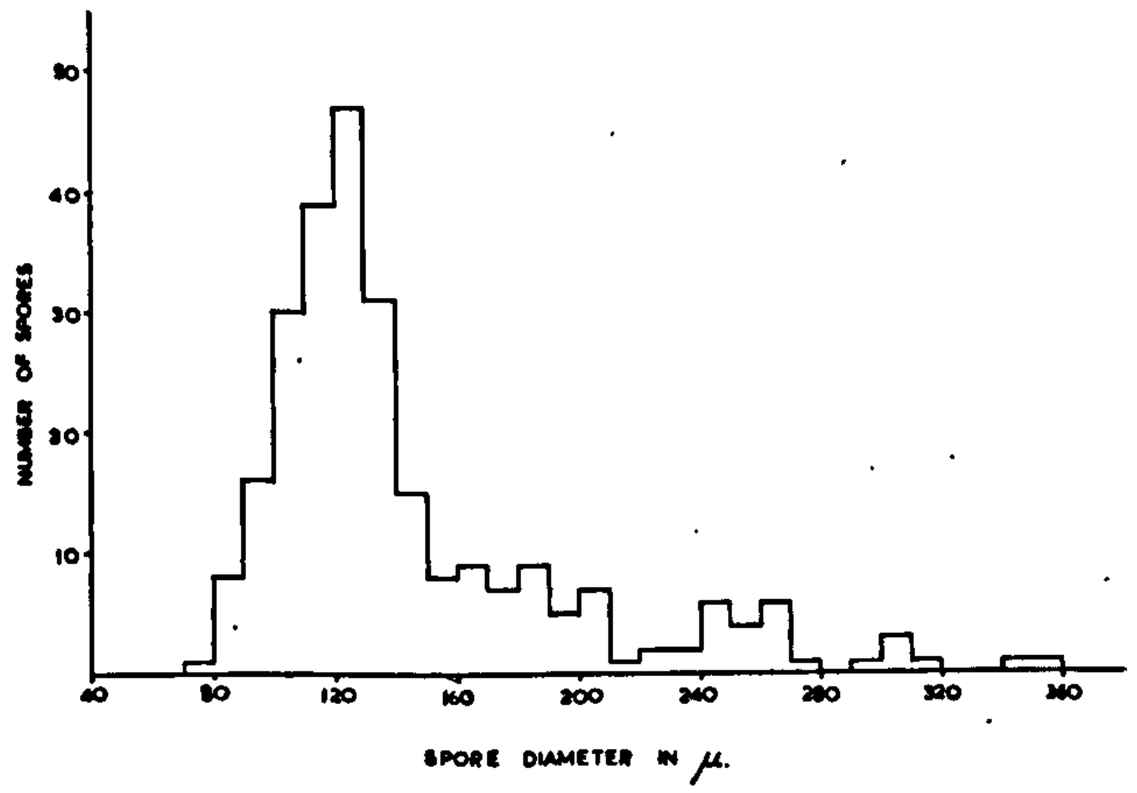
Diagnosis of the spores:- Spores more or less rounded in equatorial outline, approximately 75 to 355 μ in diameter. Spore coat thin, laevigate, usually folded. Trilete mark prominent; rays straight, extending for half length of radius. Lips prominently raised; sutures narrow and simple. Spore initially enclosed in thin, cutinised 'perispore'.

Discussion: - The spores of P.scotica, as obtained by maceration, are of very great interest. The two most outstanding features are the range in size and the possession of a 'perispore'. The term 'perispore' is used here with some hesitation. As defined by Bower (1923, p. 259) the perispore is a tapetal deposit on the outside of the spore wall, appearing like a loose sac. It is laid down after the division of the spore mother cells and one would

not expect it to show any sign of the trilete mark, though possibly it might. It is possible that in this case the 'perispore' is homologous with the air sac of some monosaccate spores and pollen. The non-comittal term, perine, as used by Erdtman (1952) should perhaps be used.

Walton (1957) has already suggested that P.scotica probably represents a stage in the evolution of heterospory, though as the histogram in Text-fig. 12 shows it is impossible at this stage to divide the spore population into micro- and megaspores.

Had the spores been encountered as sporae dispersea those which had shed their perispores would without doubt have been placed in the genus Calamospora Schopf, Wilson and Bentall. Had the 'perispore' still been present the classification of the spore is doubtful. They would probably have been related to a monosaccate type such as Remysporites B. &.W., whose only species, R. magnificus (Horst) B.&.W. is the pollen of Paracalathiops stachei Remy (Butterworth & Williams, 1957). Species of Calamospora as the name implies are thought to be the spores of calamites. Many species are distinguished solely by their size and the spores of P.scotica would probably be placed in one or other of the



Text-fig. 12. Protopitys scotica. Histogram showing the range of spore size.

following species, according to their size:

C. liquida Kosanke	76 - 94 µ
C. perrugosa (S., W. &.B.) Loose	130 - 160 µ
C. laevigata (S., W. &.B.) Ibrahim	250 - 500 µ

PTERIDOSPERMAE.

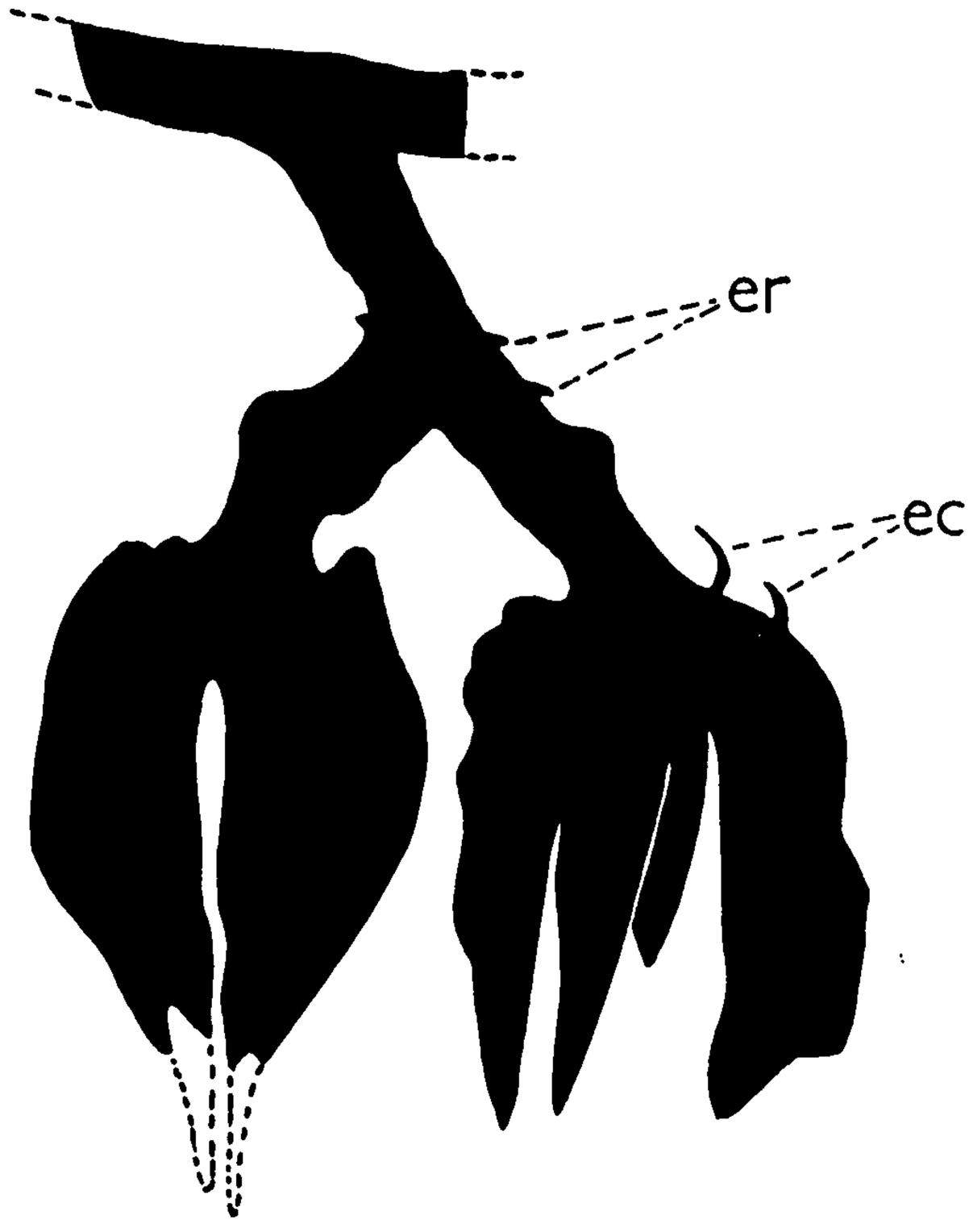
Geminitheca scotica gen. et sp. nov.

Among the plant remains found in the Loch Humphrey Burn bed there are several specimens of two small fructifications preserved as petrifications, semi-petrifications and compressions. One fructification consists of small paired cupules, each containing two ovules; the other consists of bunches of paired microsporangia and is undoubtedly the male organ of the same species. They have been named Geminitheca scotica gen. et sp. nov.

Four petrological sections of a petrified group of empty cupules were prepared by the late W.N. Croft, and for the rest several series of peel sections have been made using the Croft Parallel Grinder. The compressions were investigated largely by means of transfer preparations and nitrocellulose 'pulls', many of which were macerated in Schulze's solution.

DESCRIPTION

The paired ovulate cupules are united at the base for about a quarter of their length (Text-fig. 13) and are borne in large bunches at the tips of naked dichotomising rachides.



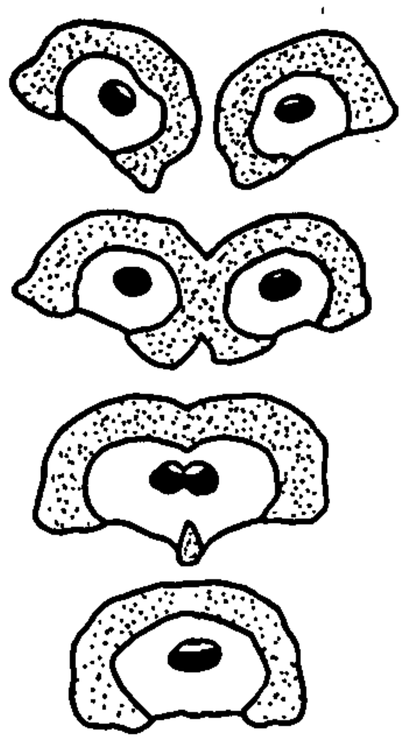
Text-fig. 13. G.scotica. Silhouette drawing of two pairs of ovulate cupules, x5. The pair on the right is damaged. ec, emergence on cupular lobe; er, emergence on rachis. (Drawn from Hunterian Museum specimen Pb2674).

While several isolated specimens consisting of one or two pairs of cupules have been found both as compressions and as petrifactions in most of the compressions and in one petrification there are three successive dichotomies of the rachis, resulting in a bunch of eight pairs of cupules. A few specimens are still larger, probably containing sixteen cupule pairs; in two instances two such bunches are lying adjacent to each other, in the same bedding plane, suggesting that they were borne on the same rachis (Pl. 8 Fig. 1). Usually the larger bunches of cupules are compressed vertically (i.e. the vertical axis of the cupules is foreshortened), with the rachis projecting upwards into the overlying rock, and only one specimen has been found in which a large bunch of cupules is compressed laterally (Pl. 8 Fig. 2). This and the fact that the cupules, although of rather massive construction, are carried at the tip of a relatively slender rachis suggests that they were most likely borne pendulously on the parent plant, as depicted in Text-fig. 13. When compressed vertically the cupule pairs show considerable distortion and it is impossible to determine their original shape (Pl. 8 Fig. 1). When compressed laterally they appear more or less pear-shaped in outline (Text-fig. 13.). They vary from 9 mm. to 12 mm. in length and each cupule attains a maximum diameter of from 2 mm. to 4 mm. at about a third of the way from the base.

The rachis:- As stated above, in the most complete petrified specimen there are three successive dichotomies of the rachis. Below the first the rachis has a greatest diameter of 2.5 mm. and a shortest of 1.6 mm.; above the ultimate dichotomy it measures 2.0 mm. by 1.2 mm. (Pl. 8 Fig. 3). The cortex of the rachis is divided into two distinct zones: a sclerotic outer cortex composed of elongated cells, apparently of a fibrous nature, and an inner cortical zone consisting of axially elongated parenchymatous cells, which are about twice as long as they are broad and which frequently have dense, dark brown contents. The outer cortical zone is crescent-shaped in transverse view and does not extend completely round the rachis (Pl. 8 Fig. 3). The side of the rachis from which it is absent is slightly concave, possibly as a result of shrinkage of the parenchymatous tissue, though it may be a natural feature as it occurs in all the rachides which have been found. In the smaller rachides the cells towards the periphery of the inner cortex have slightly thickened walls and do not have dark cell contents. In the centre of the rachis there is a single collateral vascular strand with apparently three protoxylem groups consisting of small irregularly spiral tracheids. The protoxylem is orientated towards the gap in the outer cortical tissues.

In the smaller rachids the metaxylem tracheids are predominantly of a type showing a transition from scalariform to reticulate thickening. In the larger rachides there is a further transition to tracheids with from one to five rows of bordered pits with transverse elliptical apertures. This is especially clear in 'pulls' of some of the compressions (Pl. 8 Fig. 4). The remains of a small-celled, thin-walled tissue adjoining the metaxylem presumably represents the phloem.

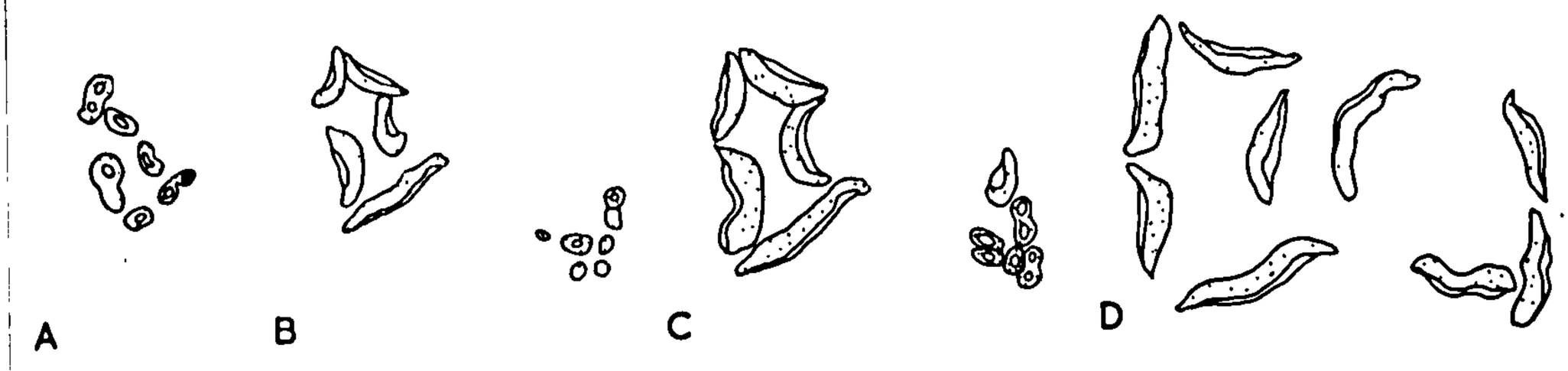
The rachis has a very characteristic mode of branching which is illustrated diagrammatically in Text-fig. 14. Below the fork a group of sclerotic cells is developed in the middle of the gap in the sclerotic outer cortex. After the division of the vascular strand a further development of sclerotic tissue between the two daughter strands results in the formation across the centre of the rachis of a complete strip of mechanical tissue. Separation of the two branches is effected by a division along the centre of this tissue. This type of branching, in which forking of the vascular strand is accompanied by the development of sclerotic tissue between the two daughter strands and the subsequent divergence of the two branches by cleavage of this tissue, is repeated in all dichotomies of the rachis, and, as demonstrated below, it occurs in a modified form in the cupules



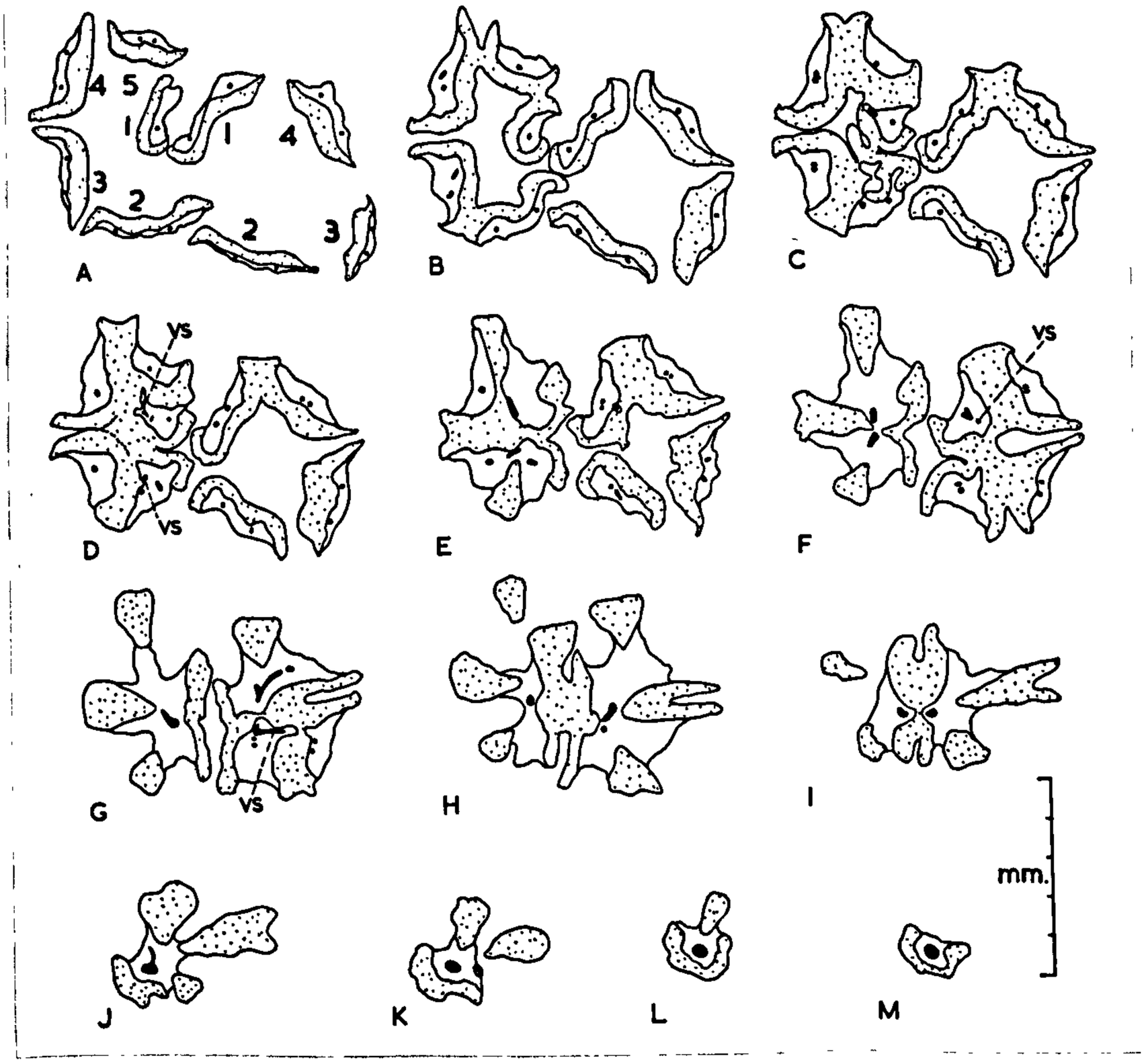
Text-fig. 14. G.scotica. Diagrammatic series of sections through a dichotomy of the rachis.

themselves. The branching of the rachis is very regular. The branches diverge at an angle of 120° and the plane of the dichotomy is at an angle of about 120° to the parent rachis. In the cupule lobes the angles of divergence of the vascular strands are not constant.

The cupules:- Immediately below the base of the cupule-pair four peripheral groups of sclerotic tissue arise successively in the gap in the outer cortical tissues of the rachis (Text-figs. 16, I-L). The outer cortex becomes reduced in size and divides into two parts, so that altogether there are six peripheral groups of sclerotic tissue. When the vascular strand forks in the base of the cupule pair two of these groups on opposite sides of the base are connected by a further development of sclerotic tissue between the two daughter strands. The two cupules become separated by a division down the centre of this tissue (Text-fig. 16, G-I). This division is approximately at right angles to the ultimate dochotomy of the rachis. In many cases the groups of sclerotic tissue form processes which project backwards from the base of the cupule (Text-fig. 13); so that in a transverse section through the base of the cupule pair many of the sclerotic groups are not in contact with the main mass of tissue. This feature is shown by all the cupules examined, both compressions and petrifications, and appears to be a natural phenomenon,



Text-fig. 15. G. scotica. Drawings of a series of sections through the apex of a pair of empty cupules. Sclerotic tissue stippled. (Drawn from slides F.S.C. 583, 585, 586 and 588).



Text-fig. 16. G.scotica. Drawings of a series of sections through the base of the same cupule-pair as in text-fig. 15; sclerotic tissue stippled; vascular tissue black; vs, vascular strand to an ovule. The lobes are numbered for convenience in description. (Drawn from slides F.S.C. 1182, 1185, 1187, 1188, 1190, 1192, 1194, 1197, 1200, 1204, 1208, 1210.)

not the result of decay or shrinkage of ths tissues. The point at which the groups of sclerotic tissue arise varies considerably in different cupule pairs. In the pair illustrated in Text-fig. 16 one group is not formed until after the division of the vascular strand (Text-fig. 16, I). After the two cupules separate, in the base of each a further group of sclerotic cells arises at the periphery; so that in transverse section near the base the cupule has a central vascular strand surrounded by a tissue of thin-walled cells, frequently with dark contents, corresponding to and continous with the inner cortex of the rachis, and four unequal, peripheral groups of sclerotic tissue (Text-fig. 16, G,H).

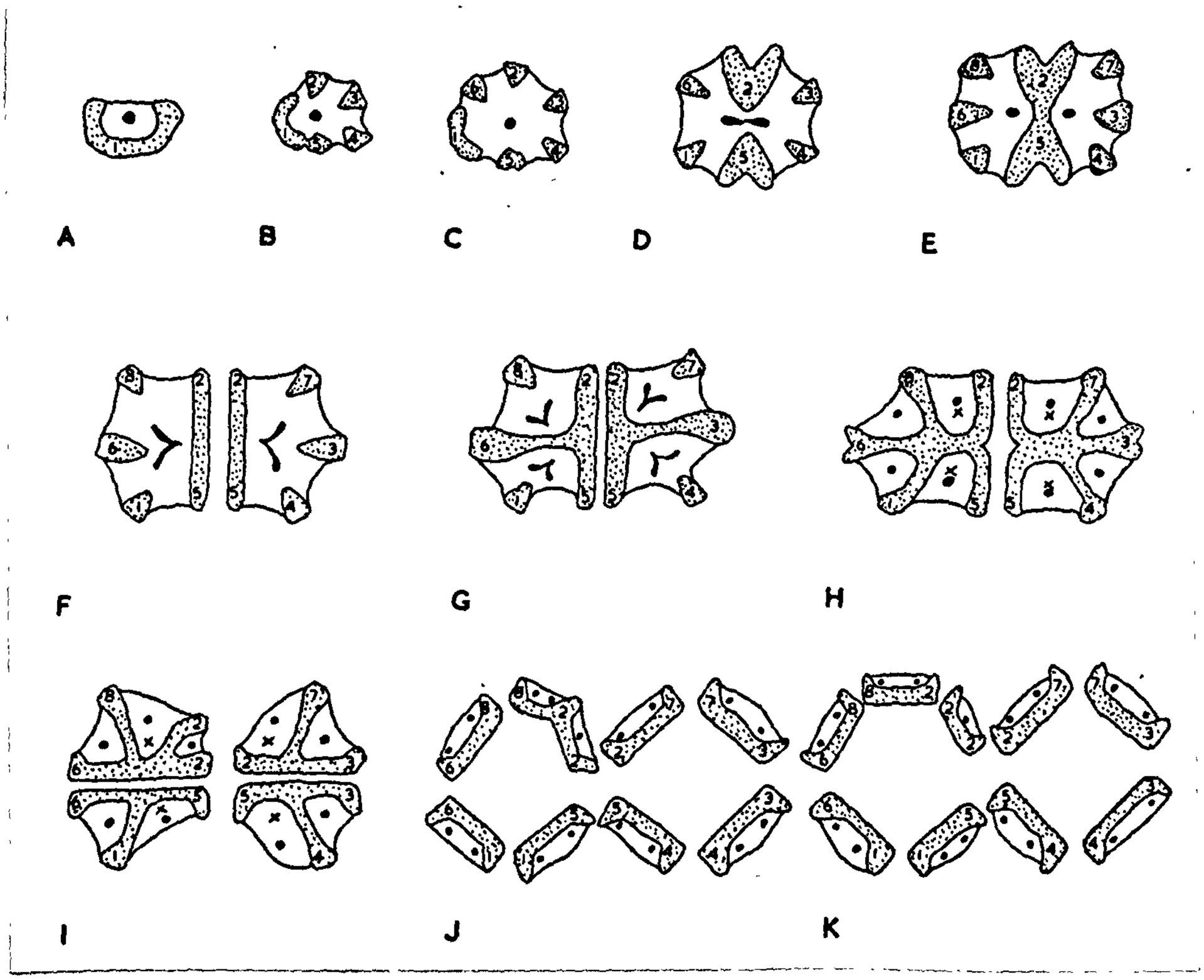
In the right-hand cupule of the pair illustrated two successive dichotomies of the vascular strand, accompanied by the development of sclerotic tissue and subsequent cleavage, have resulted in the separation first of two and then of four cupular lobes, each initially with a single vascular strand. In lobes 1 and 2 a further division of the vascular strand occurs; in each case one branch enters the base of an ovule and the other supplies the lobe. Thus in effect the two ovules are borne on cupular lobes. (Text-fig. 16, F,G). In the left-hand cupule of the pair illustrated the situation is more

complex owing to the presence of a fifth lobe. One branch of the main cupular vascular strand supplies lobes 2 and 3, and the other lobes, 4,5 and 1. The latter strand divides: one branch supplies lobe 4, while the other branch forks, one strand passing into one of the two ovules and the other dividing to supply lobes 5 and 1. The vascular strand of the other ovule arises as a branch of the strand which supplies lobe 2.

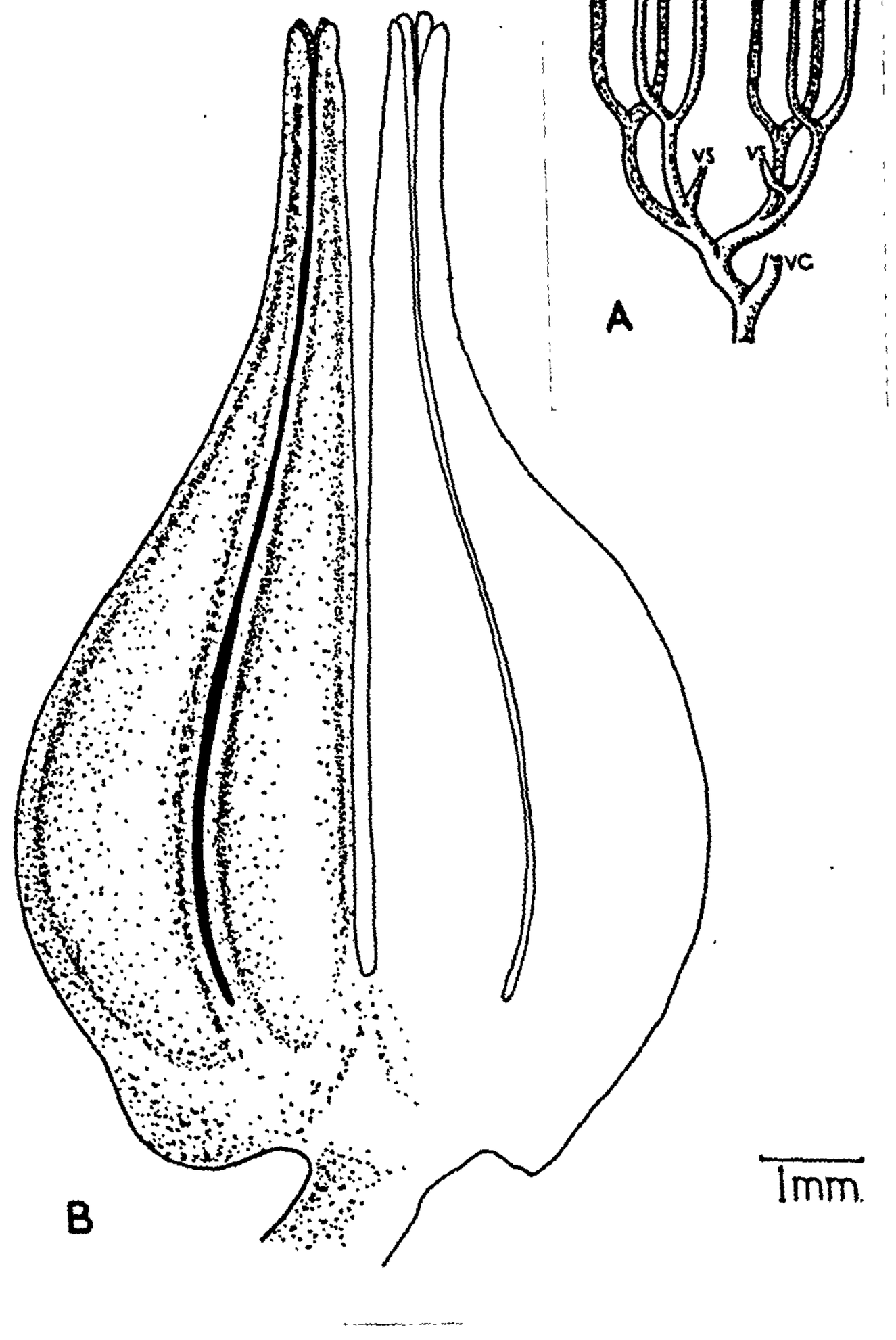
At and above the point where the lobes become free each has a layer of sclerotic tissue directed towards the cupular axis and an abaxial layer of parenchymatous tissue identical with the inner cortical tissue of the rachis. The edges of the sclerotic layer are curved outwards (Pl. 8 Fig. 5). In the base of each lobe the vascular strand forks and the two daughter strands pass up the abaxial layer. An exception to this is lobe 1 of the left-hand cupule of the illustrated pair, where the strand remains undivided. Since the divisions in the cupule follow the same pattern as the dichotomy of the rachis it would be expected that the phloem of the cupular vascular strands would be orientated towards the sclerotic layer of the cupular lobes, i.e., towards the cupular axis. This is, in fact, the case (Pl. 8 fig. 5). In transverse section the xylem of the cupular strands consists of eight to twelve tracheids (Pl. 8 Fig. 6).

Theyshow a transition from scalariform to reticulate thickening. A few tracheids with biseriate bordered pitting are present in some cases. The division of the strand in the lobe differs from all other divisions of the vascular strand in that the associated development of sclerotic tissue is delayed. At the apex of most lobes the edges of the adaxial sclerotic layer becomes increasingly recurved and at the same time sclerotic tissue develops between the two vascular strands. The final result is that each strand, surrounded by parenchymatous tissue, is completely enclosed by sclerotic tissue (Text-fig. 15A). Division then occurs along the centre of the sclerotic tissue between the two strands, thus completing the dichotomy. In a few lobes there is no development of sclerotic tissue between the strands and the dichotomy is never completed. In other cases further forking occurs at the tips of the lobes. In all cases the ultimate tips of the lobes are composed entirely of sclerotic tissue (Text-fig. 15B).

A diagrammatic representation (not drawn to scale) of the divisions in the base of a cupule pair similar to that shown in Text-fig. 16 is illustrated in Text-fig. 17. Text-fig. 18A is a diagrammatic illustration of the vascular system in the base



Text-fig. 17. G.scotica. Diagrammatic series of sections showing the divisions in the base of a cupule-pair. The sclerotic tissue is stippled; vascular tissue is black. The masses of sclerotic tissue are numbered in the order in which they arise.



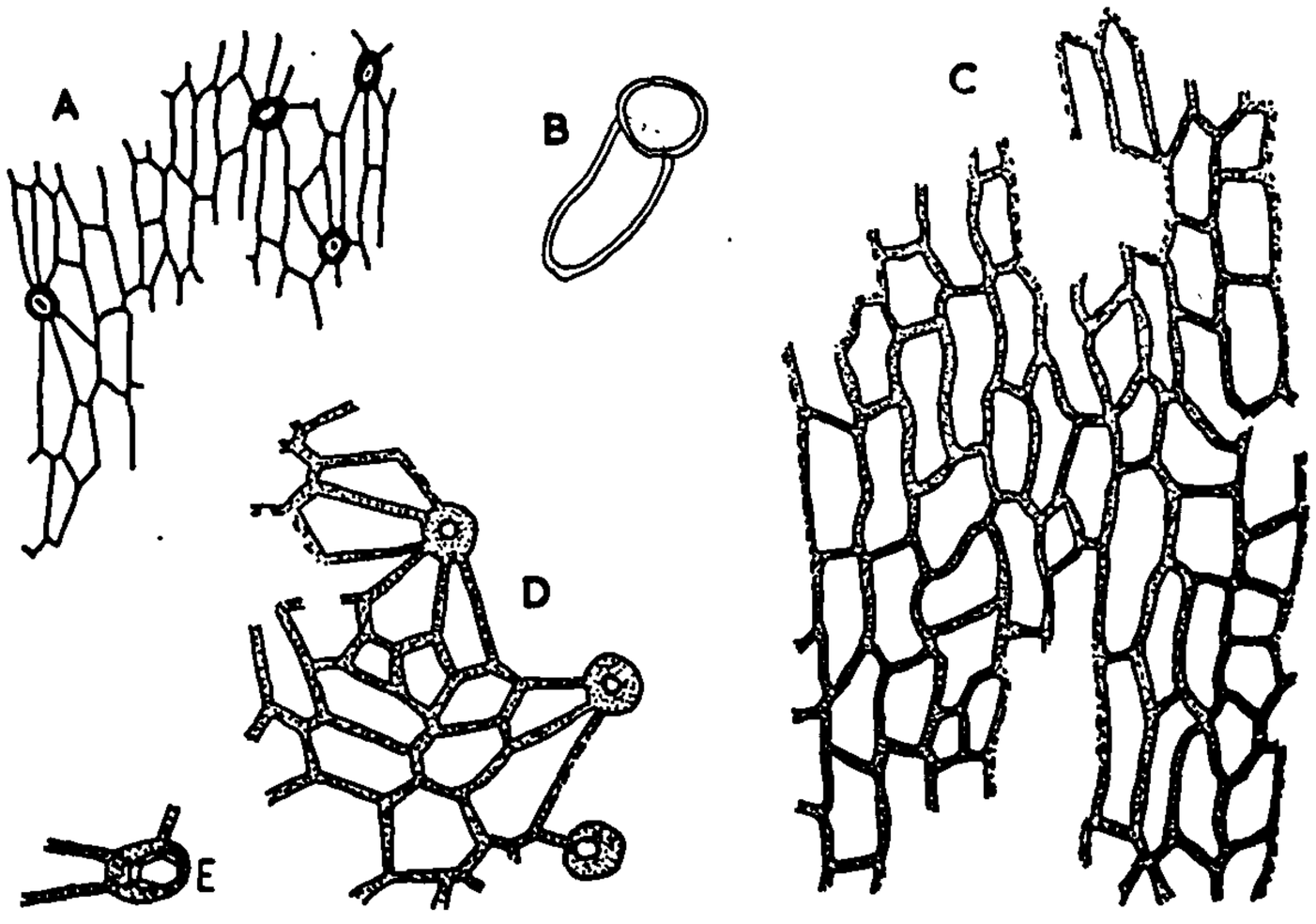
Text-fig. 18. G. scotica. A, diamgrammatic reconstruction of the vascular system in the base of a single cupule. vc, vascular strand to the other cupule; vs, vascular strand to an ovule. B, partial reconstruction of a cupule-pair.

of a single four-lobed cupule. A diagrammatic reconstruction of one cupule of a pair is shown in Text-fig. 18,B.

Epidermal structures of the rachis and cupules:-

In the compressions small fragments of the epidermis of the rachis and cupules are preserved but as they are partly petrified they disintigrate in acids and therefore the cuticles cannot usually be isolated by maceration techniques. However, reasonably satisfactory observations have been made by means of nitrocellullse 'pulls' of small areas of the compression. All the epidermal structures figures are from the specimen illustrated in Pl.8 Fig. 2.

The epidermal cells of the rachis are axially elongated, with thin, moderately straight walls, and are interspersed with numerous hair bases, each consisting of a small, rounded, thick-walled cell (Text-fig. 19,A). Each hair base is surrounded by six to eight elongated, polygonal cells which radiate out from it in a characteristic manner. Thehair, which frequently is still present, either compressed vertically on the base or lying detached nearby, consists of an elongated stalk cell bearing a rounded apical cell (Text-fig. 19, B). The stomata, which are orientated longitudinally, are very sparsely scattered and of the few found only one is reasonably complete



Text-fig. 19. G.scotica. A, epidermis of the rachis, x130; B, bicellular hair from the rachis, x260; C, inner epidermis of cupular lobe, x130; D, outer epidermis of cupular lobe; E, hair base from outer epidermis, showing thin-walled, polygonal basal cell, x260. (Drawn from nitro-cellulose 'pulls' of specimen Pb2711: Pl.8, Fig. 2)

(Pl. 9 Fig. 1). In it lateral subsidiary cells have been cut off from the neighbouring epidermal cells but there is no sign of any anticlinal division in the polar cells. The outline of the sunken guard cells is discernable below the subsidiary cells. All the stomata found are apparently on the side of the rachis from which the sclerotic cortical tissues are absent. Apart from this feature the epidermis overlying the parenchymatous cortical tissue does not appear to differ in any way from that overlying the sclerotic layer.

In 'pulls' of the cupules six distinct cutinised membranes are recognisable. They have been interpreted as follows:-

1. The outer cuticle of the cupule
2. The inner cuticle of the cupule
3. The outer cuticle of the integument
4. The inner cuticle of the integument
5. The cuticle of the nucellus
6. The megaspore membrane

The outer epidermis of the cupule (Text-fig. 19, C) is composed of rather irregular, polygonal cells, showing considerable variation in size and shape. Numerous hair bases are present. They have fairly regularly arranged, somewhat elongated, polygonal cells radiating out from them. In some compressions these hair

bases and their associated cells are the only epidermal features preserved. Usually part of the hair is compressed on to the base, so obscuring its structure, but in some cases where the hair appears to have been broken off before fossilization the base is visible as a small, thin-walled, polygonal cell (Text-fig. 19, D). The hairs appear to be of two types. The hairs borne on the bases just described are long, multicellular and uniseriate. They are fairly numerous, especially between the cupules (Pl. 9 Fig. 2) and have been found in both compressions and petrifications. The other type of hair is short, bicellular and capitate and is closely similar to the type borne on the rachis. However, it has proved impossible to determine the nature of its base as so far it has been found only in petrifications. All the bases found in compressions appear to belong to the multicellular hairs.

The inner epidermis of the cupule consists of irregular, more or less rectangular cells, which tend to be arranged in short vertical rows, possibly preserving the outline of the original meristematic cells (Text-fig. 19,E). The cell walls are fairly uniformly thickened. In some cupules the cuticle and the cell walls are not preserved but the outline of the cells is demarcated by the dense, dark brown cells contents.

These contents are visible in some of the petrified cupules, e.g. Pl. 9 Fig. 2.

No stomata have been seen in either of the epidermises of the cupule.

The other four cutinised membranes will be dealt with in the description of the ovules.

The emergences on the rachis and cupules:-

Two types of emergence are present, one on the outside of the cupular lobes (Pl. 8 Fig. 5) and one on the side of the rachis from which the sclerotic outer cortex is absent (Pl. 9 Fig. 3). Those on the cupular lobes are usually about 2.0 mm. long, 0.1 mm. in diameter for most of the length, but broadening suddenly at the base to 0.5 mm. or more. They are composed throughout of small, elongated, thick-walled cells, indicating that they were quite stiff, rigid structures. Those on the rachis are 0.5 mm. to 0.8 mm. long, 0.5 mm. broad at the base and curved upwards at the tip. The base, which is covered by a continuation of the epidermis of the rachis with several hair bases, is parenchymatous but there is a rapid gradation towards the apex, where the cells are small, thick-walled and elongated, resembling those of the cupular emergences. Most of the emergences on the rachis are flattened or rather irregular at

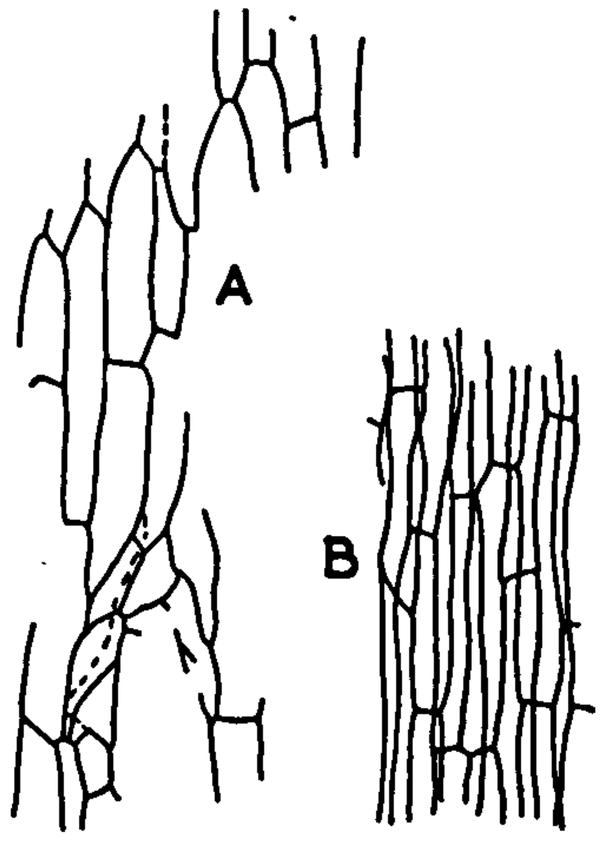
the apex (Pl. 9 Fig. 3), suggesting that the tip has been broken off and that initially they may have borne some resemblance to those on the cupular lobes.

The ovules:- So far only two pairs of petrified cupules have been found which still contain ovules. In both cases, as preservation is rather poor, very little detailed structure is visible, especially at the base of the ovules. The outstanding feature of the ovules is a cupule-like integument which, on the evidence stated below, is free from the nucellus except at the extreme base. Apart from this feature they bear a strong resemblance to the ovules of Salpingostoma dasu Gordon (1941) and Calathospermum scoticum Walton (1949a).

The ovule is borne on a very short pedicel attached near the base of a cupular lobe. It has usually four but in one case three prominent longitudinal ridges. The integument is divided into usually eight lobes which become free from one another at about the level of the base of the lagenostome (Pl.9 Fig. 5). In some ovules the number of integumentary lobes is not clear owing to poor preservation, but it appears to vary from six to nine with eight as the commonest number. The integument is composed of a uniform tissue of thin-walled, much elongated cells.

Each lobe possess a single, central vascular strand but it is impossible in the present material to determine its orientation. As seen in transverse view the xylem of the strand consists of two or three small tracheids. They have irregularly spiral or scalariform thickening. The nucellus is represented, in petrifications, merely by a thin layer of small, badly preserved cells with dark contents. It does not appear to have possessed any vascular tissue. The megaspore membrane is well preserved both in compressions and in petrifications.

In compressions all that is usually preserved of the outer epidermis of the integument is the dark cell contents, and only a very few small fragments of cuticle, showing cell walls, have been found (Text-fig. 20, A). The cells are thin-walled, long and narrow. At the basal end of one of the fragments the cells are rather irregularly shaped, appearing as if several anticlinal divisions had occurred, as a result possibly of a wound or the presence of an emergence. The inner cuticle of the integument and the nucellar cuticle are inseparably fused together to form a double membrane on which the outlines of both sets of epidermal cells are clearly visibly (Text-fig. 20, B). The presence of these two fused cuticles is taken as clear evidence that the integument and nucellus are free from each other.



Text-Fig. 20. G.scotica. A, outer epidermis of integument, x130; B, fused inner cuticle of integument and nucellar cuticle, x130. (Drawn from 'pulls' of specimen Pb 2711: Pl.8, fig. 2).

According to Harris (1926), where the nucellus and the integument are continuous there is no cutinised membrane between the outside of the integument and the megaspore membrane. As the fused cuticles will not withstand maceration in acids and as they are covered by a thick layer of coaly matter it has proved impossible to isolate them. The largest fragments wereobtained in nitrocellulose 'pulls'. In both cuticles the cells are extremely long and narrow but because very few transverse walls are present in the fragments examined (Text-fig. 20, B) the outline of a complete cell has not been found.

With the megaspore membrane maceration has been successful and one complete one and several fragments have been isolated from transfers of cupule-pairs. The complete membrane obtained (Pl. 10 fig. 1) is 4.9 mm. long and has a maximum diameter of 1.2 mm. at about the centre. Several fragment of macerated membranes have been embedded and sectioned on a microtome. The sections reveal that the membrane is composed of two distinct layers: an inner homogeneous layer and an outer granular layer. Each layer is about 3μ in thickness at the middle of the membrane. The membrane becomes thicker towards the ends. There is no trace of a large cuticularised reticulum on the outer surface of the membrane, such as has been described in other

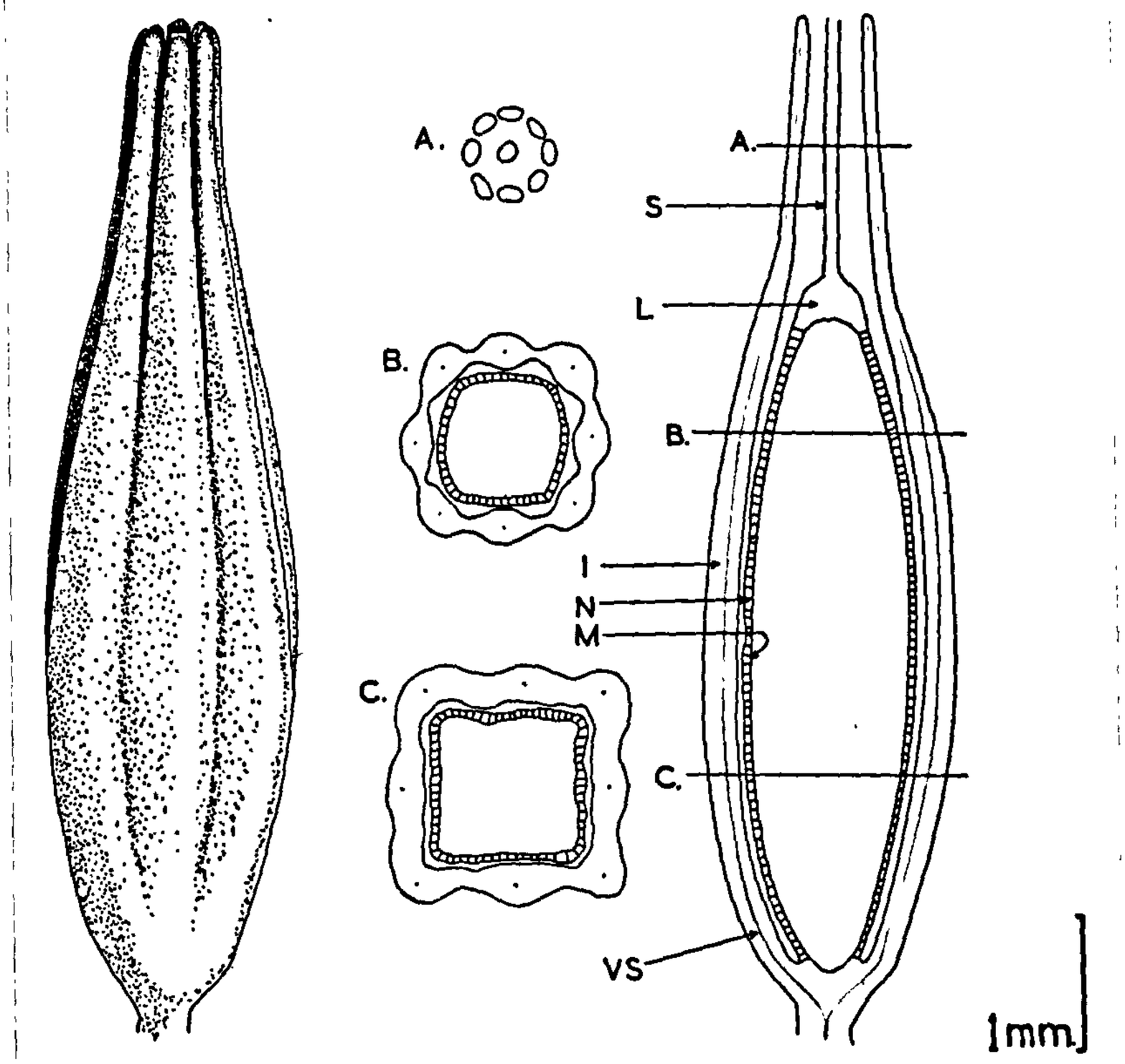
species, e.g. by Arnold (1948) and Barnard (1959). In several specimens, including that illustrated, irregularly distributed perforations are present. That they are not a constant feature suggests that they are of secondary origin, probably a result of bacterial or fungal activity before fossilisation. Small spherical bodies resembling fungal spores are frequently present in the ovules and occasionally also in the tissues of the cupules. No openings have been found, near the apex of the membrane, such as are present, e.g. in the cycads, in association with archegonia. In one petrified ovule, inside the membrane and just below its apex, there is a small mass of tissue showing very little cell structure, which must be the remains of the prothallus. Within it are two rather rounded, conical bodies which show no cell structure and which appear to be archegonial eggs (Pl. 9 Fig. 4).

From some compressed cupules the megaspore membranes which have been isolated differ from the type described above (Pl. 10 Fig. 2). They resemble the usual type in shape but are much smaller, being usually about 1.0 mm. long and 0.2 mm. to 0.3 mm. in diameter. They are also composed of two distinct layers, an inner homogeneous layer and an outer granular layer, but in this case each layer is about 5 μ in thickness. The most likely interpretation of these structures is that they are the megaspore membranes of abortive ovules.

The ovule has a large lagenostome, or pollen chamber, with a dome-shaped roof composed of small, elongated cells with dark contents. The apex of the lagenostome is prolonged into a tubular salpynx (Pl. 9 Fix. 4) which extends for at least 2 mm., reaching almost to the tip of the cupule lobes. The megaspore membrane, apparently forming the floor of the lagenostome, projects for some distance into the cavity. The free lobes of the integument extend upwards as long slender processes surrounding the salpynx and at least equalling it in length. Microspores are present in the lagenostome and salpynx of all the petrified ovules found. In one lagenostome, of which a rather oblique longitudinal section is illustrated in Pl. 10 Fig. 3, as many as twenty-two spores are present. Of these, twenty-one are all of the same type and spores of this type are the only ones found in other ovules. Similar spores have been isolated from the small microsporangiate fructifications described below. The 'contaminant' in the lagenostome figured is of an entirely different type and appears much darker than the other spores in the photograph.

Text-fig. 21 shows a diagrammatic reconstruction of an ovule, together with diagrammatic sections in various planes.

<u>The microsporangia and microspores</u>:- Only two compressions of the microsporangiate fructification have so far been found but



Text-fig. 21. G. scotica. Reconstruction of an ovule.

I, integument; L, lagenostome; M, megaspore membrane; N, nucellus; S, salpynx; VS, vascular strand.

there is some evidence that a small petrified bunch of microsporangia from the same locality, represented by three peel sections in the Figured Slide Collection, of Glasgow University Botany Department, is of the same species.

The tassel-like bunches of sporangia (Pl. 10 Figs. 4 and 5) bear a superficial resemblance to the fructification of Telangium Benson (1904) and it is quite likely that they were included in the T. affine Kidston recorded by Kidston (1924) from the "Escarpment on south side of Loch Humphrey Burn". They differ from Telangium as described by Benson (1904) and Kidston (1924) in the smaller size of the sporangia which are completely free from one another and are not united together at the base to form a disk of sterile tissue.

In the compression illustrated in Pl. 10, Fig.4. the rachis forks five times; so that each of the two bunches theoretically contained sixteen sporangia. Owing to the effects of compression the exact number cannot be counted. Although on the whole preservation of the compressions is rather poor a certain amount of detailed structure is visible, particularly in the rachis, which is semi-petrified. The epidermis of the rachis, with its numerous hair-bases and sparsely scattered stomata, is indistinguishable from that of the rachis of the

ovulate cupules, and it is largely upon this evidence that the specific identity of the ovulate cupules and the microsporangia is based. The outer cortex of the rachis is composed of elongated sclerotic cells, apparently like the cells of the outer cortex of the rachis of the ovulate organs. Whether or not it extends completely round the rachis cannot be determined. The inner cortex is parenchymatous and surrounds a central vascular strand. The only tissues of the strand which have been preserved are small scalariform tracheids.

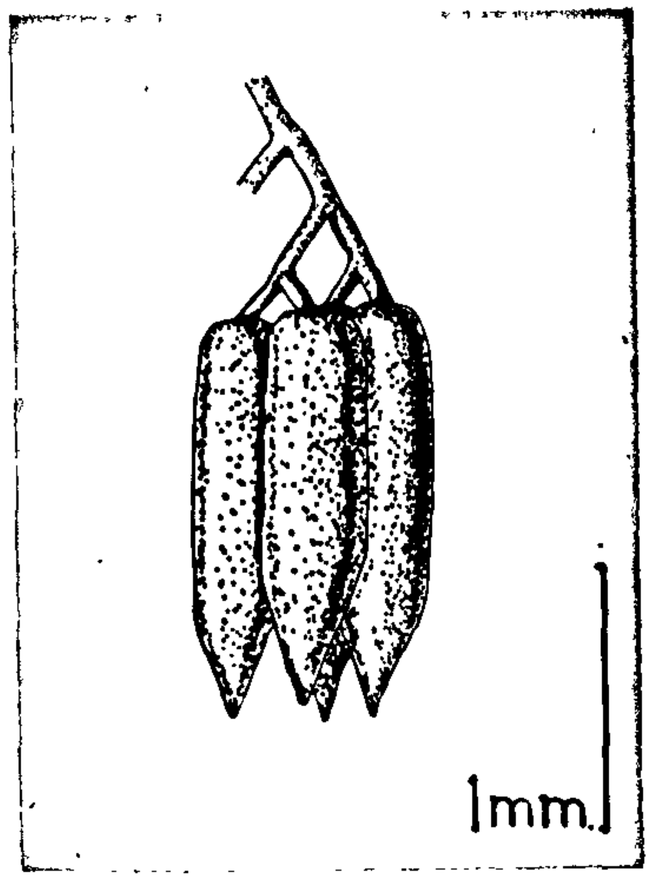
As most of the sporangia have been compressed closely together it has proved rather difficult to determine with any accuracy their original size and shape. They appear to be approximately 1.5 mm. long, 0.5 mm. in diameter for about three-quarters of their length and then tapering off to an acute apex. They are completely free from one another and are borne terminally in pairs, since the ultimate dichotomy of the rachis occurs very near the tip. The sporangium wall is composed of more than one layer of elongated cells, frequently with dark contents. The petrified sporangia (Pl. 11 Fig. 1) agree in size and shape with those occurring as compressions, the average dimensions of eight sporangia being: length 1.5 mm., maximum diameter 0.4 mm.

Owing to poor preservation of the petrification no structure is visible in the sporangium wall.

A diagrammatic reconstruction of part of a bunch of microsporangia is illustrated in Text-fig. 22.

Although most of the sporangia, both in compressions and in petrifications, have shed their spores there is no indication of the method of dehiscence. A few spores resembling those present in the lagenostomes of the ovules occur inside and in assocation with the petrified sporangia but their number is too small to establish beyond doubt that they originated there.

In a transfer of one of the compressions, however, it was clear that two of the sporangia had failed to open and so to shed their contents. On maceration each of these sporangia yielded a mass of several hundred spores. One of the spore masses is illustrated in Pl. 11 Fig. 2. In the other compression (that shown in Pl. 10, Fig. 5) all the sporangia appeared to have dehisced, though a number of them still contained a few spores and some of these have successfully been isolated. One of them is illustrated (Pl. 11 Fig. 3).



Text-fig. 22. G. scotica. Reconstruction of part of a bunch of microsporangia.

In equatorial outline the spores are rounded triangular to circular with a size range of approximately 45 μ to 58 μ, mean 50 μ. They have a cingulum which varies from 1.5 μ to 3.0 μ in width, even in the same specimen; the narrowest regions are usually opposite the rays of the trilete mark. The spore coat is thin; the ornamentation is irregularly punctate. The rays of the trilete mark are straight and extend for about two-thirds of the radius; the sutures are narrow with simple margins. There is no evidence of the presence of any germinal mechanism other than the triradiate mark.

The spores present in the lagenostomes of the petrified ovules are somewhat distorted and poorly preserved, and even when isolated their true shape and surface features are not clear, though the cingulum is always distinct (Pl. 10, Fig. 3). The twenty-five spores measured gave a size range of approximately 48 μ to 60 μ, with a mean of 52μ. In spite of the lack of a detailed comparison it seems reasonable to conclude that the spores present in the lagenostomes are identical with those isolated from the microsporangia. The question as to whether these microspores are in fact the required pollen is discussed in more detail later.

DIAGNOSES

Geminitheca scotica has been placed in a new order, the Geminithecales. The reasons for this are given in the discussion of affinities.

Geminithecales ord. nov. :-

Pteridospermous ovules or seeds in which the integument is free from the nucellus except at the base and in which there is no vascular tissue within the nucellus. A cupule may or may not be present.

Type genus: Geminitheca gen. nov.

Geminitheca gen. nov. :-

Ovulate cupules united in pairs. Cupule divided into two primary lobes, each subdivided into two or three lobes; lobes free almost to base. Cupular vascular strands with abaxial xylem. Two ovules contained in each cupule, borne on short pedicels on cupular lobes. Apex of nucellus differentiated into large lagenostome with salpynx. Integument free from nucellus, cupule-like, lobed, lobes becoming free at level of base of lagenostome and forming long apical processes.

Microsporangia elongated, borne in pairs, but not fused together.

Type species: G. scotica gen. et sp. nov.

G. scotica gen. et. sp. nov.:-

Ovulate cupules borne in bunches containing sixteen cupule-pairs, terminally on naked, dichotomising rachides. Cupule-pairs 9 mm. to 12 mm. long, united for about a quarter of their length. Maximum diameter of each cupule 2 mm. to 4 mm. Each cupular lobe with adaxial sclerotic and abaxial parenchymatous layers. Usually two vascular strands passing up the abaxial layer. Ovules with three or four prominent, longitudinal ridges. Integument six to eight lobes.

Microsporangia about 1.5 mm. long, 0.5 mm. broad for three quarters of their length, tapering to an acute apex. Borne in bunches of about sixteen sporangia, terminally on naked dichotomosing rachides. Microspores rounded triangular to circular in equatorial outline, 45 μ to 58 μ, mean 50 μ. Cingulum 1.5 μ to 3.0 μ broad. Spore coat thin; ornamentation irregularly punctate. Rays of trilete mark straight, extending for about two-thirds of radius; sutures narrow with simple margins.

Syntypes:-

Ovulate organs:- Specimens Pb2674 and Pb2680 in the Hunterian Museum Palaeobotanical Collection; slides F.S.C. 584-589, 766-768 and 1181-1240 in the Figured Slide Collection.

Microsporangiate organs:- Specimen Pb2697; slides F.S.C. 1241-1243. Both collections are housed in the Department of Botany, University of Glasgow.

DISCUSSION

(a) The cupules and ovules:- From a consideration of Text-fig. 16 and the accompanying description it is quite apparent that the cupules of Geminitheca scotica are bilaterally symmetrical and their structure is such that they cannot have been derived by the partial concrescence of a true whorl of foliar segments. However, the single collateral vascular strand in the rachis suggests that almost certainly the whole bunch of cupules has been derived from a frond or a part of a frond which had attained some sort of dorsiventrallity, though not necessarily possessing a lamina. In fact it is rather unlikely that a lamina was present. The most obvious and at the same time the most likely explanation of the origin of the cupules is that they arose by the modification of a system of dichotomising rachides, very similar to those on which they are now borne, in order to enclose terminal ovules. The

evidence in favour of this view may be summarised as follows:-

1) There is a strong anatomical resemblance between the rachis and the cupular lobes. The sclerotic outer cortical zone of the rachis corresponds in structure and distribution to the adaxial layer of the cupular lobes, while the inner cortex of the rachis is identical to and continuous with the parenchymatous abaxial layer of the lobes.

2) The successive divisions which occur in the base of the cupule pair and again in the base of the individual cupules and in the cupular lobes all follow the same pattern as the dichotomies of the rachis. This is less obvious in the cupular lobes, where the development of sclerotic tissue which usually accompanies the division of the vascular strand is delayed and does not occur until the apex of the lobe.

3) Throughout all the divisions of the vascular strand the phloem always remains orientated towards the part of the sclerotic tissue which was developed last. Consequently, as would be expected if the cupules were derived from rachides, the vascular strands of the lobes are apparently inverted.

4) The number of cupular lobes is not constant.

5) Further dichotomy occurs at the apex of many of the lobes.

6) The ovules are borne on cupule lobes.

It is fairly certain, then, that the cupules are merely condensed systems of dichotomising rachids. Since each lobe contains usually two vascular strands it probably represents a segment of rachis which has developed into a broad, somewhat flattened structure owing to the fact that although the dichotomy was initiated in the usual manner, by the division of the vascular strand, in the base of the lobe, the accompanying development of sclerotic tissue and subsequent cleavage have been delayed. Although the dichomtomy is usually completed at the lobe apex the fact that in some cases this does not happen indicates that further reduction must have been in progress.

It appears that no other Palaeozoic cupules, ovuliferous or sporangiate, have been described as invariably possessing vascular strands with adaxial phloem. In the very irregular cupule of Lagenostoma lomaxii (Williamson MS) Oliver & Scott (1904, p.222 and Pl.8., fig. 15) the authors show that some of the vascular strands are so orientated but they point out that this is very infrequent and that while the orientation may really

have varied the inversion of the bundle may have been due to some displacement, possibly as a result of decay; the cupule is riddled with fungal hyphae and spores. In this feature, therefore, the cupule of Geminitheca scotica stands alone and it can only be concluded that it must have evolved along a different line from other, previously described cupules. From this evidence, then, it appears that cupules generally have been evolved along at least two independent lines, and judging by the diversity in cupule shape and structure there were most probably several lines.

Halle (1933, 1937) suggested that the seed cupules and pollen synangia of the Palaezoic pteridosperms are morphologically equivalent structures. He pointed out that although they show radial symmetry they were probably borne on leaves and he suggested that they were formed by the lateral fusion of bunches of cyclically arranged telomes, sterile in the case of a cupule, fertile in the case of a synangium (Halle, 1933, p. 66). Walton (1953, a, p. 139 and fig. 111b) has supposed that cupules and integuments, and synangia of the Whittleseya or Aulacotheca type could be formed by the inrolling of part of a frond consisting of several pinnules; had they been fertile a synangium would have resulted; had they been sterile a cupule or integument would have been formed. He considered that the cupule of Calathospermum

scoticum, which is bilaterally symmetrical, provides further evidence in favour of this theory.

These theories may each eventually be found to be true in part but at present they can only be accepted with certain reservations. Apart from Calathospermum, Lagenostoma and now Geminitheca nothing (or at least not enough) is known of the structure of ovulate cupules or of synangia of the Whittlesya or Aulacotheca type, since most of the material discovered so far has been preserved in the form of compressions. It is quite feasible that when more evidence is forthcoming it may be possible to show that some cupules and synangia have evolved along lines similar to those outlined above while others have originated as dichotomous structures in a manner similar to the cupules of Geminitheca.

In the differentiation of the cupular lobes into an adaxial layer of fibrous tissue and an abaxial parenchymatous layer the cupule of Geminitheca scotica shows a development closely parallel to that of Calathospermum scoticum and presumably the opening mechanism suggested for Calathospermum by Walton (1949a) would also apply to Geminitheca. In dry conditions the parenchymatous outer layer of the cupule would contract to a greater extent than the fibrous inner layer and as a result the

cupular lobes would become reflexed, thus exposing the ovules for pollination or liberating the fertilised ovules or seeds. Unlike the cupule of Calathospermum, in which the lobes fitted closely together when the cupule was closed, the cupule of Geminitheca was never a tightly closed organ for there are considerable gaps between the lobes, especially at the base between the two primary lobes (Text-fig. 16). There is no evidence that the pedicel of the ovule of Geminitheca elongated at any stage as did that of Calathospermum and it is assumed that at maturity the seed merely became detached from its very short pedicel since the remains of the latter are present in the empty cupules.

The ovules of Geminitheca scotica bear some resemblance to those of Calathospermum scoticum and Salpingostoma dasu Gordon (1941). All three are similar in being rather spindle shaped and in the fact that the apical part of the nucellus is differentiated to form a large lagenostome prolonged at the apex into a tubular salpynx. They differ, however, in one very important feature. In the ovule of Geminitheca the integument is cupule-like and free from the nucellus except at the base whereas in the other two species the integument and nucellus are continuous. In this respect Geminitheca is the most primitive. It is obvious from the description that there is a marked similarity between the cupule and the integument of Geminitheca, suggesting the possibility that the integument originated by a process analogous to that which resulted in the

formation of the cupule. In this case the ultimate ramifications of the rachis system would have become aggregated round a terminal sporangium. Later, or perhaps simultaneously, when further modifications resulted in the development of the cupule, the integumentary lobes must have become much simplified in structure and eventually become fused for about half their length to form the cupule-like integument possessed by the ovule at the time of fossilisation. It is unfortunate that the base of the ovule is not in a better state of preservation as it is quite likely that the vascular strands there would still show some dichotomous branching. Further reduction of the integumentary lobes and progressive fusion of the integument to the nucellus would result in the development of an ovule closely comparable with that of Calathospermum or Salpingostoma.

The ultimate tips of the rachis, i.e., those which surrounded the sporangium, may all have been initially sterile but the analogy between the hypothetical ovule as described above and the microsporangiate organs suggests that they may have been fertile and that sterilisation occurred as they assumed a protective function. Another possibility is that sterilisation occurred simultaneously with the development of heterospory and the assumption of a protective function by the now sterile telomes followed as a consequence of this. This latter theory seems to be the most

probable and it recalls the synangial hypothesis of the origin of the integument put forward by Benson (1904) in her paper on Telangium scottii. She supposes that in a synangium of the Telangium type the peripheral sporangia became sterile and were retained as a protective envelope. The main difference between this view and the one outlined above is that here Benson supposes that fusion of the sporangia preceded sterilisation whereas above it is suggested that sterilisation preceded fusion. The latter view seems the more probable, but as insufficient evidence is available finally to decide this point the question must be suspended until more is forthcoming.

The free integument of Geminitheca adds considerable support to the view that the integument and cupule are fundamentally homologous. This idea was first put forward by Oliver and Scott (1904, p. 232) in their monograph on Lagenostoma lomaxii. They commented on the "possible multiple character of the integument in its free part, as suggested by the chambering of the canopy". With regard to the origin of the seed they stated that, "we have in Lagenostoma a megasporangium which has been enclosed in two successive, concentric, indusium-like structures, of which the inner has become an integral portion of a new organ, the seed. The outer is probably of later

origin . . . . . It is quite possible that the two enclosures have originated very similarly, i.e., as peltate, lobed structures, and that the present integument was once a comparatively unspecialised cupule-like indusium". The work of Oliver and Scott also received strong support from work on the integument of the Cycadales independently by Matte (1904) and Stopes (1905). Both of these authors concluded that the integument of the cyads is a double structure, each part having its own vascular supply.

In Geminitheca we have an earlier stage than, e.g. Lagenostoma or Calathospermum, in the evolution of the ovule (or seed), where the integument to some extent at least is still a "comparatively unspecialised, cupule-like indusium". In this respect the ovule of Geminotheca scotica is the most primitive yet described. Other primitive features which it possesses are the large lagenostome and the salpynx. As Walton (1953) has already demonstrated, in the evolution of the ovule there has been a progressive reduction in complexity of the nucellar apex as its pollen-catching function has gradually been assumed by the integument.

In conclusion, Geminitheca scotica adds very strong support to the statement by Walton (1953b) that "there is clear evidence that the integument and cupule in the pteridosperms have each been derived by concrescence of a number of foliar divisions". Whether these "foliar divisions" were sterile or fertile is still open to discussion.

(b) The microsporangia and microspores:- The reasons for assuming that the spores present in the lagenostome and salpynx of all the petrified ovules found are identical with the spores isolated from the microsporangiate have already been stated. The evidence that these spores are in fact the required pollen may be summarised as follows:-

1) The cuticle of the rachis bearing the microsporangia is identical with that of the rachis of the ovulate cupules. In fact, by accident the lable of a slide containing a fragment of the cuticle of a rachis became detached and was lost, and it is now impossible to tell from which type of fructification the cuticle came. This evidence seems fairly convincing.

2) With one exception all the spores discovered inside or in association with ovules are of the same type.

3) This piece of evidence may at first seem rather irrelevant but the reasons for its importance will be obvious later;

lycopod remains of any type are vary scarce in the Loch Humphrey Burn bed. The only lycopodeaceous macrofossils are two compressions of fragments of Stigmarian axes. A single megaspore and microspores of the Endosporites type have also been found.

There can be no doubt that the spores found in the microsporangia actually originated there. In the transfer of one of the compressions it was possible to see the microspore masses inside two of the sporangia, through breaks in the sporangial wall. Each sporangium was macerated separately on a slide under a cover-slip. So it can safely be concluded that without doubt the microspores concerned are the required pollen.

Florin (1937) recognised two basic types of pteridosperm pollen. They are:-

1) Round, trilete, with ~~out~~ or without germinal furrow, e.g., Potoneia pollen, spores of Crossotheca.

2) Ellipsoidal, with germinal furrow and longitudinal tetrad mark e.g., Whittleseya pollen.

On the basis of more recent research Remy (1954) recognises four basic types, which he designates as follows:-

1) Round with trilete mark and germinal furrow

2) Round with trilete mark and saccus, e.g., pollen of Paracalathiops.

3) Ellipsoidal with germinal furrow and longitudinal tetrad mark.

4) Rounded-ellipsoidal with saccus, e.g, Thruingia pollen.

It is obvious that Remy's types 1 and 3 correspond more or less to Florin's ~~type~~ two types. But Remy further points out that no one has as yet definitely established that any undoubted pteridosperm pollen grain did not possess some germinal mechanism other than the tetrad mark. The evidence on which Crossotheca is attributed to the Pteridospermae is purely circumstantial and as its spores are trilete but do not possess a germinal furrow he does not consider it to be a pteridosperm. However, the pollen grains of Geminitheca scotica, which is undoubtedly a pteridosperm, do not possess a germinal furrow, and so to some extent at least Remy's conclusions are erroneous. Another feature in which the Geminitheca pollen differs from any of the above types is in the possession of a well developed cingulum. Clearly then it does not fit in with any of the above types and so it represents a further type of pteridosperm pollen hitherto ynkown in the group.

It is possible that the spores (or pollen) of Crossotheca McLuckii described by Andrews and Mamay (1948) had a cingulum. The authors do not mention this feature but their photographs suggest its possible presence.

Had the pollen grains of Geminitheca scotica been encountered as sporae dispersae probably they would have been classified as belonging to the form genus Lycospora. They conform closely to the diagnosis of the genus given by Pontonie and Kremp (1954) and are only exlcuded by their slightly larger size from the genus as defined by Kosanke (1950). He defines the upper size limits of the genus as 45 μ whereas the limits of the measured specimens of Geminitheca pollen are 45 μ to 58 μ. All species of Lycospora which have been traced to the parent plant have proved to be the microspores of arborescent lycopods. They have been isolated frommany species of Lepidostrobus. Other spores with a cingulum, e.g., Endosporites which have been traced to the parent plant have proved to belong to plants of lycopodiaceous affinity and consequently it has been assumed by many palynologists that all spores possessing a cingulum were borne only by lycopods. The pollen of Geminitheca clearly contradicts this assumption, hence the necessity to establish its identity beyond any shadow of doubt.

Spores apparently identical with Geminitheca pollen have been found by Dr. M.A. Butterworth (personal communication) from the Cross Borehole of N. Ireland, probably from a horizon near the top of the Oil-Shale Group.

The presence of pollen grains inside the lagenostome and salpynx raises the question of the pollination mechanism. Presumably pollination occurred by means of a pollination drop exuded from the tip of the salpynx. But there is no indication as to how it was ensured that only (or almost only) the required pollen reached the pollen chamber. Whatever it was the method must have been very efficient.

DISCUSSION OF AFFINITIES AND COMPARISON WITH OTHER SPECIES.

It is quite evident that Geminitheca scotica is of pteridospermous affinities but, although its ovulate and polliniferous organs agree in general morphology with those of other Palaezoic pteridosperms, it does not appear to be closely related to any previously described species. The fact that it possesses both a free integument and a cupule separates it from all known groups. The Palaeozoic pteridospermous seeds and ovules are usually divided into two major groups, the Lagenostomales and the Trigonocarpales. According to Seward (1917) the main differences between these groups are that in the Lagenostomales the nucellus is united to

the integument, usually up to the level of the base of the pollen chamber, and there is no development of vascular tissue in the nucellus, whereas in the Trigonocarpales the nucellus is free within the integument and the peripheral zone of the nucellus is supplied with vascular tissue. Walton (1953) has put forward a theory which is gaining much support in the light of recent researches on Carboniferous ovules and seeds. He supposes that the so-called integument of the Trigonocarpales is morphologically equivalent to the cupule possessed by at least some of the members of the Lagenostomales and that the outer part of the nucellus, containing the vascular tissue is actually a much reduced integument which has fused with the nucellus. Stopes's (1905) work on cycad ovules supports this view, as she showed that the 'nucellar' vascular system in cycads is actually in the inner layer of the integument. In terms of Walton's theory Geminitheca is more closely related to the Lagenostomales than to the Trigonocarpales but it differs in the important respect that the integument is free from the nucellus except at the base. Therefore it must represent an earlier stage than the Lagenostomales in the evolution of the ovule and it appears that a new order will have to be created to accommodate it and similar but still undescribed types. As Geminitheca is at present the only known member the

order must be named the Geminithecales.

It is important to bear in mind that these orders are created purely for convenience and that it is unlikely that many of their constituent genera are closely (if at all) related. It is obvious from what has already been said about them that although they show several features in common a close relationship is most unlikely between Geminitheca and Calathospermum. As more knowledge is obtained of the detailed structure of the pteridosperms it is becoming increasingly obvious that they form a very heterogeneous group and that almost certainly, as with heterospory, the seed habit was evolved separately in a number of distantly related (or possibly unrelated) groups of pteridophytic plants. The three orders Geminithecales, Lagenostomales and Trigonocarpales represent stages in the evolution of the ovule or seed and are no indication of any natural affinity.

Another possible member of the order Geminithecales is Calymmatotheca kidstonii Calder(1938) at present being reinvestigated by Mr. A.G. Long (personal communication) who has discovered further material. He has placed it in a new genus Genomospermum and has divided it into two species G.kidstonii and G.latens. In both species the integument is free from the nucellus but there is vascular tissue at the base of the nucellus.

A number of other fructifications have been described as consisting of paired cupules. Among them are Xenotheca devonica Arber & Good (1915), Lagenospermum imparirameum Arnold (1939) and one to which no name has been given, described by Arnold (1935) and occurring in association with fronds of Archaeopteris in the UpperDevonian of Pensylvania. It is not the fructification of Archaeopteris and belongs to an unknown plant. The cupules are very similar in shape to those of Geminitheca but they are distinctly stalked. Unfortunately nothing is known of the contents of the cupules and so it is impossible to carry the comparison any further. X. devonica and L.imparirameum are both of Lower Carboniferous age, the former being from Devon, the latter from Pensylvania and Virginia. In both species the cupules are borne on short stalks and are not fused together, though in some specimens of L.imparirameum (Arnold, 1939, fig.3) the stalks are so short that the cupules appear as a single unit. Each cupule of L.imparirameum apparently contains a single seed but there is no indication as to the nature of the contents of the cupules of Xenotheca. Although np structure was described for either species and so it is impossible to make satisfactory comparisons neither of the fructifications bears much superficial resemblance to Geminitheca and it is unlikely that they were closely related. Yet certain comparisons may be made between

them and Geminitheca and Gnetopsis elliptica Renault (1885). In all the specimens of Xenotheca figured by Arber & Goode (1915) and in Arnold's Upper Devonian fructifications all the cupules are distinctly stalked. In L.imparirameum the cupules are stalked but there appears to be a tendency towards a reduction in the length of the stalks to form a single, compound structure (Arnold, 1939, Fig. 3). In Geminitheca the cupules are completely united at the base and each contains two ovules. In Gnetopsis elliptica there is a single primarily bi-lobed cupule which contains four ovules (Renault, 1885, Pl. 21. fig. 1). It is not suggested that this is a phylogenetic reduction series but the bi-lobed cupule of Gnetopsis is strongly suggestive of an origin from twin cupules by a progressive reduction along similar lines to the above. It is quite possible that at some stage in their evolution cupules of Geminitheca were quite separate and that their present state was attained by reduction. Further reduction could result in the development of a primarily bi-lobed cupule containing four ovules apparently with central placentation, which, so far as is known, is the case with Gnetopsis. That the cupule of Gnetopsis did not originate as a dichotomous structure in the same way as that of Geminitheca is obvious from the vascular strands of the cupule, which are orientated with the protoxylem

towards the cupular axis. But it is easy enough to visualise other ways in which dichotomising rachides could become condensed to form cupules. It is suggested, then, that these other paired cupules and also the bi-lobed cupule of Gnetopsis could also have arisen by the modification of a system of dichotomising rachides, though not necessarily in exactly the same way as has been suggested for Geminitheca.

The compression described under the name of Pterispermostrobus? wanderianus by Florin (1926) bears a slight resemblance to some species of G.scotica and also to both L.imparirameum and G.elliptica. Again, unfortunately, no detailed structure has been described and an adequate comparison cannot be made.

Other fructifications which bear a superficial resemblance to the ovulate cupules of Geminitheca are some species of Calathiops Göppert and Scheutzia Geinitz but they have not been sufficiently well described to make a comparison possible.. The polliniferous fructification bears some resemblance to species of Calathiops and to Telangium. The differences from Telangium have already been noted.

Calathiops trisperma sp. nov.

Calathiops trisperma sp. nov. is represented by two specimens; one was collected by Professor Walton and Mr. Brown, the other by the author.

Description:- The fructification consists of small ovulate cupules which are borne on naked dichotomising rachides (Pl. 11, Fig. 5). The rachis forks irregularly and the cupules are borne singly at the tips. The number of cupular lobes is not constant but varies considerably. The range observed is from five to nine. The lobes are 4 to 5 mm. long and about 0.5 mm. broad. They are represented merely by a structureless film of coal. Transfers were prepared from the two counterparts of one cupule and both were macerated on a slide, under a coverslip, by the method described by Harris (1944). No structure was revealed in the cupular lobes but two halves of megaspore membrane were isolated from one counterpart, and one from the other. The maceration was stopped when traces of cell outlines appeared on the surface of the membrane.

The half membranes vary from 1.2 to 1.5 mm. in length and are 0.7 mm. in diameter at the broadest part. The complete membrane was probably about 2.5 mm. long. As all three membranes were orientated in the same direction it was assumed that they belong

to three ovules. The best preserved membrane (Pl. 11, fig. 6) has three longitudinal folds, possibly indicating that the ovule was ~~prominently~~ three ridged. Alternatively they may be an effect of fossilisation. On the surface of the membrane there are traces of small elongated cells which must be the remains of the nucellus and integument. A few narrow scalariform tracheids are also present, presumably in the integument. The membrane is very thick at its apex, 25 μ in some cases. At the thinnest part, near the break, it is only 5 to 6 u thick. Although it has not been sectioned it seems to be similar in fine structure to that of Geminitheca scotica.

There is no indication as to whether the integument was fused to or free from the nucellus.

Diagnosis:-

Calathiops trisperma sp. nov.

Ovulate cupules borne singly at the tips of naked, dichotomising rachides. Dichotomy irregular. Cupules up to 5 mm. long, consisting of 5 to 9 linear lobes. Each cupule containing usually three ovules. Ovules elongated, about 2.5 mm. long.

Type Specimen:- Pb3326 and the slides prepared from it: F.S.C. 1374-6.

Discussion:- The genus Calathiops was instituted by Göppert (1864) for fructifications of Lower Carboniferous age from Lower Silesia. The fructifications included in the genus were described as consisting of small bunches of linear scale-like appendages borne on the ends of naked, dichotomising rachids. He did not demonstrate whether they were microsporangia or ovulate cupules. Benson (1935) emended the genus to include only ovulate fructifications, and her view is followed here.

C.trisperma is certainly the female organ of a pteridosperm but its affinities are not clear. It probably represents some hitherto unknown group and provides some evidence in favour of the theory that the seed habit has been evolved separately in a number of perhaps unrelated plants. It does not resemble any of the structurally preserved species described so far. Of the species described from compressions it resembles most closely Calathiops bernhardti Benson (1935). This species differs from C.trisperma in that it is larger and contains more ovules, which are about the same length as those of C.trisperma but are much broader.

Staphylotheca Kilpatrickensis gen. et. sp. nov.

This new species is based on a single compression collected from the Loch Humphrey Burn bed by Professor Walton and Mr. Brown.

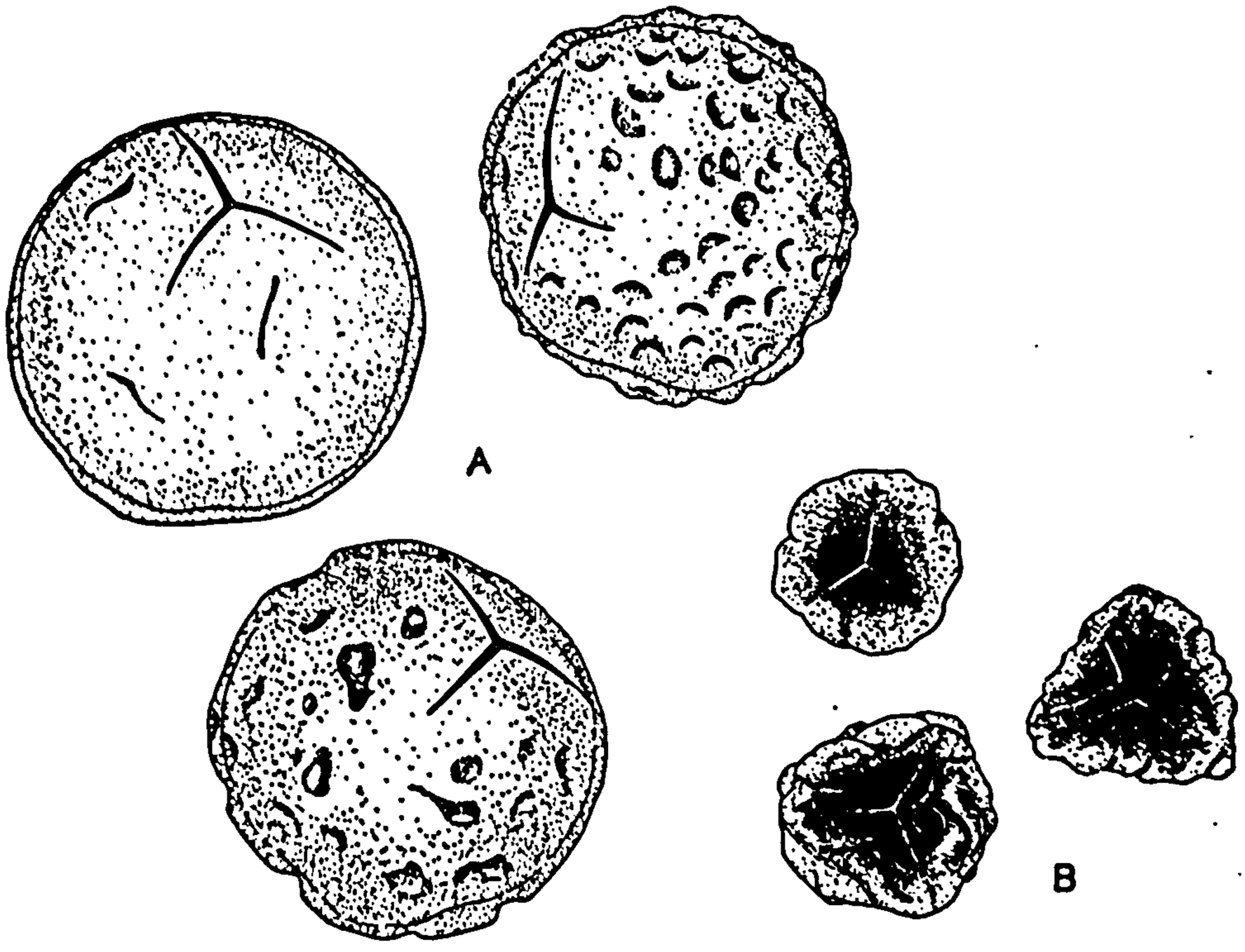
Description:- On the surface of the rock all that was initially visible of the plant was a curious rachis with a single dichotomy (Pl. 12 Fig. 1). A second rachis of similar appearance arose from under one of the branches but was separated from it by about 1 mm. of rock. The rachis has undulate margins; so that in appearance it rather resembles a compressed string of tightly packed beads. Whether it was flat or rounded in nature is impossible to decide, but as the film of coal is fairly thick it must have been a fairly massive structure. Several 'pulls' of the rachis have failed to yield any details of its structure.

Hanging on short slender pedicels from the underside of the rachis are several bunches of linear sporangia. They were uncovered by making two sawcuts across the rachis and carefully chipping away the intervening matrix. Transfers were prepared from the rock chips; these were later macerated and yielded large numbers of spores.

The sporangia are aggregated in bunches of an indefinite number. There at least ten in each bunch, possibly even twice that number. It is impossible to decide whether they are free from one another or whether they are fused at the base. Most of them are 7 to 10 mm. long and about 0.5 mm. in diameter. Again, 'pulls' and transfers failed to reveal any structural details of the sporangium wall.

Several thousand spores were obtained from the fructification. They are of two main types which occur in the same sporangia:

Type A (Pl. 12, fig. 2) is by far the commoner type. These spores are more or less circular in equatorial outline. They vary from 78 to 100 μ in diameter, mean 87 μ. At the distal end the spore coat is 4 to 5 μ thick; at the proximal end it is about 2 u in thickness. A number of indentations or punctations are present over most of the spore surface, though usually they are absent from the contact faces. They are usually 4 to 10 μ in diameter and up to 3 μ deep. They vary considerably in shape; most are circular or sub-circular in outline but in some spores they are elongated or irregular. Text-fig. 23 A shows several spores isolated from a single sporangium. They illustrate very well the complete range of variation which does occur. The rays of the trilete mark extend for slightly over half



Text-fig. 23. S.kilpatrickensis. A, fertile spores, x500; B, abortive spores, x500. All the spores are from one sporangium. (Drawn from slide F.S.C. 1378).

the radius. In most cases the spore appears to have split along the trilete mark. The lips are not raised. The suture has simple margins.

Type B (Pl. 2, fig. 3) is much smaller than type A. The spores are rounded triangular in equatorial outline. The margin is irregular. They vary in size from 42 to 57 μ, mean 45 μ. The spore coat is very thick. The ornamentation is rather irregular; it consists of a number of depressions separated by more or less convolute ridges. The trilete mark is very narrow and in some spores is barely distinguishable. The rays extend for over three-quarters of the radius. Text-fig. 23, B shows the variation in this type within a single sporangium.

Diagnoses:-

Staphylotheca gen. nov.:-

Dichotomising rachides with undulate margins; bearing on under surface bunches of linear sporangia.

Type species: S.kilpatrickensis gen. et sp. nov.

S. kilpatrickensis gen. et sp. nov:-

Sporangia in bunches of 10 to 20; 7 to 10 mm. long, 0.5 mm. in diameter. Spores round, 78 to 100 u, mean 87 u. Spore coat up to 5 u thick distally, 2 u thick proximally. Ornamentation, round to linear indentations, 4 to 10 u long,

up to 3 μ deep. Rays of trilete mark straight, extend for over half radius; suture with simple margins; lips not raised.

Type specimen:- Specimen Pb335 in the Hunterian Museum Palaeobotanical Collection, and the slides prepared from it, F.S.C. 1377 and 1378 in the Figured Slide Collection.

Discussion:- There seems to be little doubt, from the vary heavily cutinised walls of the type B spores that they are abortive. The fact that both types occur in the same sporangia strongly supports this view.

In its arrangement of bunches of sporangia hanging from the undersides of dichotomising rachides S.kilpatrickensis resembles Alcicornopteris hallei Walton. Here, however, the resemblance stops. They differ markedly in the shape of the rachides and in the structure of the spores. The bunches of sporangia are similar to species of Calathiops Göppert and Scheutzia Geinitz. The distinctive rachis and spores of the present specimen exclude it from the former genus which was emended by Benson (1935) to include only ovulate cupules borne on simple rachides. The genus Scheutzia is ill-defined and may include both ovulate cupules and microsporangia.

As regards the affinities of the genus nothing definite can be decided owing to a lack of knowledge of the structure of the plant. Fructifications of this type are usually considered to be the male organs of pteridosperms but in many cases there is no direct evidence in support of this view and quite possibly they may have belonged to plants superficially similar to pteridosperms but with a pteridophytic method of reproduction.

As sporae dispersae type B would probably have been placed in the genus Convolutispora H.S.&.M. Type A does not appear to resemble any previously described spore type. Certainly the two types would have been widely separated. They would probably have been regarded as fern spores. It is likely that type A would have been split into two species.

Alcicornopteris hallei Walton

Among the specimens collected by Professor Walton and Mr. Brown there are several compressions which had been referred tentatively to Alcicornopteris hallei Walton. In order to establish whether or not this identification was correct spores were isolated from them by treating small fragments with hydrochloric acid and then with hydrofluoric acid. The residue consisted largely of spores. Some spores were mounted directly in glycerine jelly; others were macerated before mounting. Several small fragments of the type specimen were treated in the same way. The spore samples obtained from all specimens were identical and it was concluded that the identification was correct. The spores obtained by this method, however, showed features which were not visible in sections.

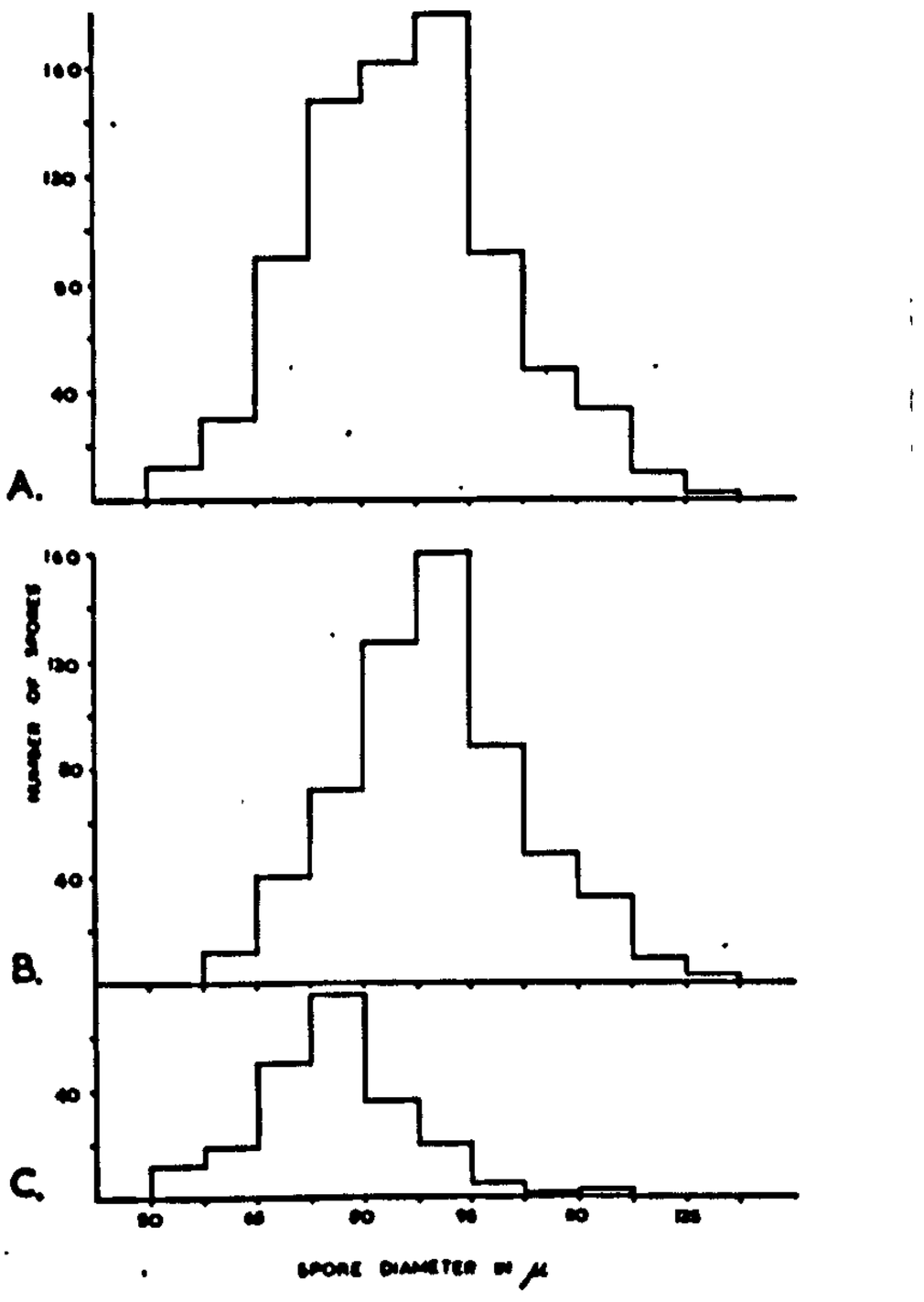
The spores:- As Walton (1949, c) pointed out the spores in most of the sporangia are not well preserved and probably they are immature and not completely cutinised. The spores at the periphery of the nodule are well preserved. He also observed that the well preserved spores at the periphery are smaller than the spores towards the centre of the nodule.

Maceration has yielded a wide variety of spores, which for convenience have been divided into four basic types:

Type A (Pl.13, fig. 1) is found only in unmacerated samples; it disappears on maceration and so it is uncutinised and immature. Most of the spores occurring towards the centre of the nodule are of this type. They are colourless. They are more or less round and range in size from about 60 to 130 μ. The spore wall is thin and featureless in many cases but in some a reticulate thickening has been developed (Pl.13, fig. 2). In all cases the trilete mark is very broad and extends to the periphery of the spore. Intermediates occur between this type and spores of type B.

Type B (Pl.13, fig. 3) is light yellowish brown in colour and is well cutinised. It, too, occurs towards the centre of the nodule. The spores are round and similar in size to those of type A. They have a well developed reticulate ornamentation; the trilete mark is distinct; the suture is narrow. The rays extended to the circumference of the spore.

Type C (Pl. 13, fig. 4) is brown in colour and heavily cutinised. The spores are more or less circular in equatorial outline and range in size from 50 to 95 μ, mean 73 μ. The spore coat is thick and has an irregularly punctate ornamentation.



Text-fig. 24. A.hallei. Histograms showing the range of spore size. A, total spore population; B, spore types A and B; C, spore types C and D.

The punctations are very fine. There is also a large but very faint reticulate ornamentation. The rays of the trilete mark are often slightly sinuous. They extend for almost the full length of the radius. The trilete mark is slightly raised; the suture is narrow and has simple margins. In unmacerated samples fragments of a granular substance, presumably tapetal residues are commonly found adhering to the wall. They dissolve on maceration. In sections the granules appear to be part of the spore wall, giving the appearance of an apiculate ornamentation. This has been commented on by Walton (1949, c, p. 448).

Type D (Pl. 13, fig. 5) . Spores of this type are the least common. They are brown in colour and well cutinised. They are usually rather irregular in outline. They vary from 60 to 120 μ in diameter. The spore is thin and the spore coat is usually folded. The ornamentation is similar to that of type C but the reticulate thickening is much better developed; irregular thin areas are also present. The trilete mark is not prominent. It is represented merely by a narrow slit. The rays seldom extend for more than half the radius. Intermediates occur between this type and type C.

The following facts may usefully be summarised:

1. A and B occur towards the centre of the nodule.
2. Intermediates occur between A and B.
3. C and D occur at the periphery of the nodule.
4. Intermediates occur between C and D.
5. No spores have been found which could be interpreted, as being intermediate between B and C or between B and D.

The histograms shown in text-fig. 24 show the frequencies of the spore types. A and B, and C and D have been grouped together. Of 812 spores measured 72.9% are of type A or B; 27.1% are of type C or D. The observed size range of A + B is 61 to 128 μ; of C + D, 50 to 118 μ.

Discussion:- It can reasonably be assumed that type A is a developmental stage of type B. No completely satisfactory explanation of C and D has been found. It is not likely that either could be an immature form of the other as they differ in the size of the trilete mark. It is unlikely that either is abortive. A reasonable explanation is that they represent variations of a single spore type, C being the commoner.

As regards the relationship between B and C a number of possibilities have been considered, none of which is entirely

satisfactory. The two most feasible are dealt with here.

1. B could be a developmental stage of C. This is the most likely explanation though it is difficult to see how a spore with reticulate ornamentation could develop into one with finely punctate ornamentation. Knox (1948) has shown that in living archegoniate plants the sculpturing is usually initiated while the tetrad of spores is still contained within the wall of the spore-mother cell. In all cases the final ornamentation is foreshadowed at an early stage and there is no suggestion of difference of form during development. Radforth (1938, 1939) has shown this to be the case in the fossil Senftenbergia. On the other hand C does show a faint reticulum and it is possible that the fine punctations represent the smaller meshes of the reticulum which have to some extent been filled in. There remains the fact that the type B spores are larger than those of type C. As both are cutinised it is unlikely that a change in size could have occurred during maturation. The only possible explanation, if B is an immature form of C, is that the spores at the periphery of the bunch, i.e., those at the periphery of the nodule, were smaller and matured earlier than those in sporangia at the centre of the bunch.

The histogram of the total spore population obtained from the type specimen suggests a single type of spore.

2. The plant could be heterosporous with two types rather than two sizes of spore. This type of arrangement has not yet been recorded for either living or fossil plants but there is no reason why it should not exist. However, it is not considered that the available evidence is sufficient to prove this and the question must be left open.

Walton regarded A.hallei as being the pollen-bearing organ of a pteridosperm. He based his conclusion on the exannulate sporangia, the position of the thickening on the cells of the sporangial walls, the presence of sclerotic nests in the rachides, and the structure of the vascular strands. It is not felt that the new information regarding the spores is sufficient to contradict this view.

It is not known how the spores would have been classified as sporae dispersae since none of the three cutinised types agrees closely with any described spore genus.

GENERAL DISCUSSION OF THE TWO FLORAS

It is obvious from Table II that on present knowledge at least the floras of the Glenarbuck and the Loch Humphrey Burn beds have no species in common (except Stigmaria ficoides, which can be discounted). The Glenarbuck flora consists predominantly of lepidodendrids, with a relatively minor element of calamites, ferns, pteridosperms and possibly cordaites. The Loch Humphrey Burn flora, on the other hand, judging by the fructifications, probably consisted mainly of pteridosperms. Cordaites may have been fairly common. Calamites, although present were relatively rare and lepidodendrids were almost entirely absent.

As both floras are of approximately the same age and the beds are only about a mile apart the differences between them must be due to ecological conditions rather than to major differences in climate. The abundance of lepidodendroid remains in the Glenarbuck bed and the presence of coal seams in association with it suggest that the vegetation was a swamp forest similar to those of the coal measures. There is no direct evidence as to the ecological status of the Loch Humphrey Burn flora. It was probably a forest dominated by pteridosperms, occupying the drier ground, at a higher level, behind the swamp.

The comparison of these two floras with others of similar age has been carried out only briefly. There are two reasons for this. The first is that insufficient is known of other Lower Carboniferous floras to make such a comparison worth while. The second is that it is considered that the basis upon which species of such genera as Rhacopteris, Sphenopteridium and Spathulopteris are separated is unsound. Specific separation is based upon the gross morphological features of the frond and while many species may be perfectly sound, many intergrade. There is a diversity of opinion as to which features are of importance and consequently most species are inadequately described. The same applies to such types of fructification as Calathiops and Scheutzia.

The following five floras are compared briefly with those of Glenarbuck and Loch Humphrey Burn in Table II. As far as possible the floras are listed in geological sequence. The sources of the information are also given.

1 and 2. Glenarbuck and Loch Humphrey Burn respectively.

3. Pettycur, Fife: Scott (1901, 1920), Williamson (1872, 1873, 1883), Kidston (1909).

4. Glätzisch-Falkenberg, Silesia: Solms-Laubach (1892).

5. Cementstone Group, Scotland: Kidston (1923-1925).

6. Oilshale Group, Scotland: Kidston (1923-1925).

7. Lower Limestone Group, Scotland: Kidston (1923-1925).

8. Upper Black Limestone, N. Wales: Walton (1931).

The first five floras are of approximately the same age; the other three are younger.

It is clear that the three floras known from petrifications, Glenarbuck, Pettycur and Glätzisch-Falkenberg, are fairly similar. The flora of Pettycur has eight species, that of Glätzisch-Falkenberg four species in common with that of Glenarbuck. It is interesting that Etapteris tubicaulis and Protopitys occur in the floras of Glätzisch-Falkenberg and Loch Humphrey Burn but not in that of Glenarbuck. In this respect the Loch Humphrey Burn flora is intermediate between the other two. Aneimites acadica, which occurs in Glenarbuck, has only been recorded from the Cementstone Group.

The Loch Humphrey Burn flora is similar to the other Cementstone Group floras of Scotland but its affinities appear to lie more with the Oilshale Group and younger floras, and so it is probably best regarded as transitional between the two types. It is much richer in species than any other known Cementstone Group Flora.

TABLES I AND II.

TABLE I

	Main differences from *L. kilpatrickensis* & *L. solenofolium*.	Stele of branches
L. harcourtii With. *wunschianus* Carr.	departure of leaf trace	PROTOSTELIC
caracubense Schmal. *esnostense* Ren. *rhodumnense* Ren.	structure of secondary cortex	
fuliginosus Will. *intermedium* Will. *macrophyllus* Will. *vasculare* Binney	structure of leaf cushions	
aculeatum Sternb. *laricinus* Sternb. *obovatum* Sternb. *scottii* Gordon	departure of leaf trace	SOLENOSTELIC
brownii Unger *scleroticum* Pannel	structure of primary cortex	
hickii Watson *brevifolium* Will. *hallii* Evers *serratum* Felix	structure of leaf cushions	
pettycurense Kidston *pachydermatikos* A. & M. *johnsonii* Arnold	known only as solenostelic axes with secondary xylem	

TABLE II

	1	2	3	4	5	6	7	8
CALAMITALES								
Protocalamites pettycurensis	x		x					
Archaeocalamites göppertii		x						
A. radiatus		x		x	x	x	x	x
cf. Pothocites sp.		x			G	G		
LEPIDODENDRALES								
Lepidophloios kilpatrickensis	x							
Lepidodendron solenofolium	x							
L. brevifolium	x		x	x				
Lepidocarpon wildianum	x		x					
Stigmaria ficoides	x	x	x	x	x	x		x
FILICALES								
Metaclepsydropsis duplex	x		x	x				
Etapteris tubicaulis		x		x				
Dineuron ellipticum	x		x					
Botryopteris antiqua	x		x					
PROTOPITYALES								
Protopitys scotica		x		G				
PTERIDOSPERMAE								
Heterangium grievii	x		x	x				
Lyginorachis brownii	x							
Lyginorachis trinervis		x						
Calathospermum scoticum		x						
Geminitheca scotica		x						
Calathiops trisperma		x					G	
Staphylotheca kilpatrickensis		x						
Alcicornopteris hallei		x			G	G		

	1	2	3	4	5	6	7	8
GENERA INCERTAE SEDIS								
Aneimites acadica	x				x			
Rhacopteris inaequilatera		x			x	x	x	
R. lindsaeformis		x				x	x	x
R. petiolata		x				x	x	x
R. robusta		x				x	x	x
Rhodea spp.		x			x	x	x	x
Spathulopteris obovata		x				x		
S. ettingshausenii		x				x		x
Sphenopteridium pachyrrachis		x			x	x	x	x
Telangium affine		x				x		
Telangium bifidum		x				x		
Calamopitys radiata		x						
Bilignea resinosa		x						
Endoxylon zonatum	x							
Eristophyton waltonii		x						
E. fasciculare		x						

x indicates the presence of the species

G indicates the presence of the genus

1, Glenarbuck.
2, Loch Humphrey Burn.
3, Pettycur, Fife.
4, Glätzisch- Falkenberg, Silesia.
5, Cementstone Group, Scotland.
6, Oilshale Group, Scotland.
7, Lower Limestone Group, Scotland.
8, Upper Black Limestone, N. Wales.

SUMMARY

1. Two beds of sedimentary rock of Lower Carboniferous age, in the Kilpatrick Hills, Dunbartonshire, have yielded fragments of fossil plants.

2. Lepidophloios kilpatrickensis sp. nov., and Lepidodendron solenofolium sp. nov., from the bed in Glenarbuck, are described in detail and compared with other lepidodendroid species of similar age.

3. Other species recorded from the bed are Lepidodendron brevifolium Will., Lepidocarpon wildianum Scott, Dineuron ellipticum Kidston and Heterangium grievii Will.

4. The spores of Protopitys scotica Walton, from the Loch Humphrey Burn bed, are described.

5. An account is given of the morphology of the ovulate cupules and microsporangiaof Geminitheca scotica gen. et sp. nov., a new type of pteridosperm. The cupules are united in pairs and are borne in bunches at the tips of naked dichotomising rachids. Evidence is put forward to show that the cupules are probably derived from a system of dichotomising rachides modified to enclose terminal ovules. Each cupule contains two ovules similar in form to those of Calathospermum scoticum Walton, but differing in that the integument

and cupule are homologous structures. The elongated microsporangia also are borne in terminal bunches. The microspores have a cingulum.

6. Brief descriptionsare given of Calathiops trisperma sp. nov., a fructification consisting of small cupules, each containing three elongated ovules, and Staphylotheca kilpatrickensis gen. et sp. nov., a spore-bearing organ containing fertile and abortive spores.

7. The spores of Alcicornopteris hallei Walton are described.

8. The two floras are compared briefly with other Lower Carboniferous floras.

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PLATES.

PLATE 1.

Lepidophloios kilpatrickensis sp. nov.

Fig. 1. Transverse section of a branch (x 2.5)

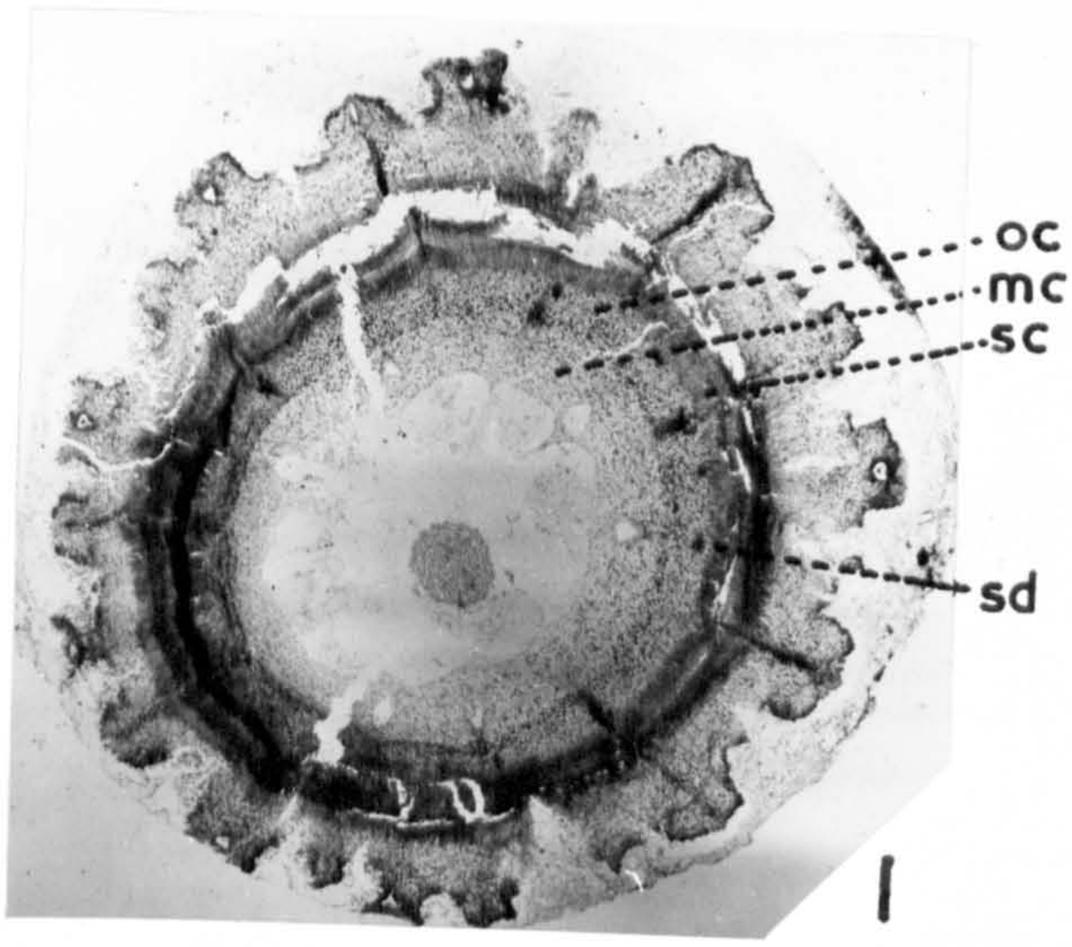
Fig. 2. Transverse section of the xylem of a small branch (x 50) F.S.C. 738.

Fig. 3. Longitudinal section of a metaxylem tracheid showing the fimbrils. The double nature of the fimbril system is clearly visible at 'a'. (x 1000) F.S.C. 1317.

Fig. 4. Longitudinal section of a metaxylem tracheid. The fimbril system is detached from the bar of thickening at 'b' (x 1000) F.S.C. 1317.

Fig. 5. Transverse section of part of a small branch (x 50) F.S.C. 658.

Abbreviations: ic, inner cortex; lt, leaf-trace; mc, middle cortex; oc, outer cortex; p, phloem; sc, secondary cortex; sd, secretory 'duct'; xy, primary xylem.



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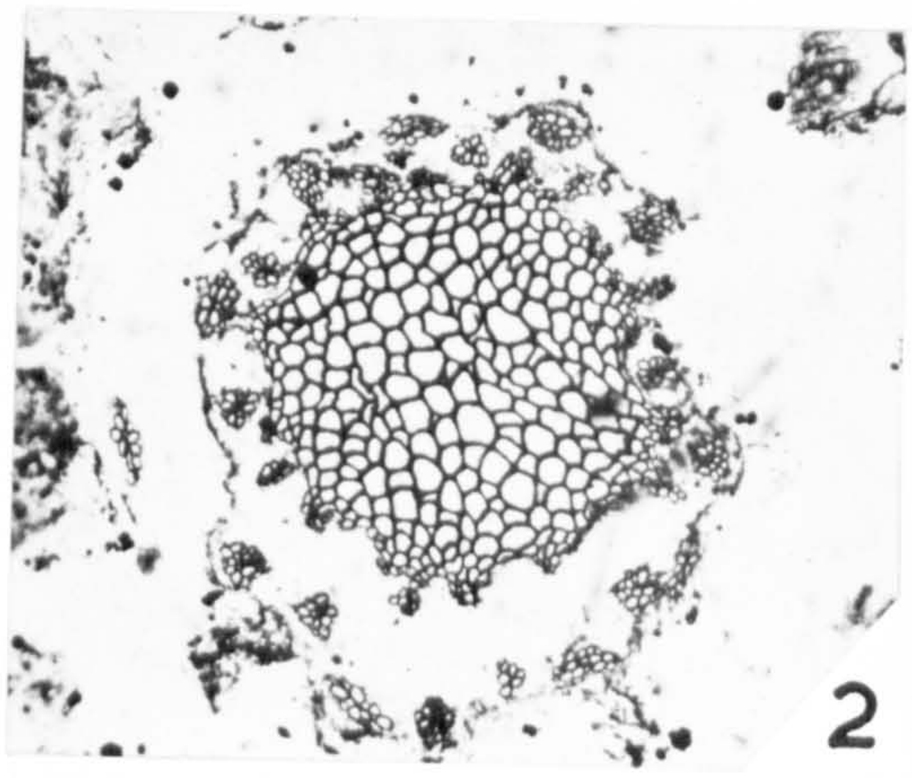

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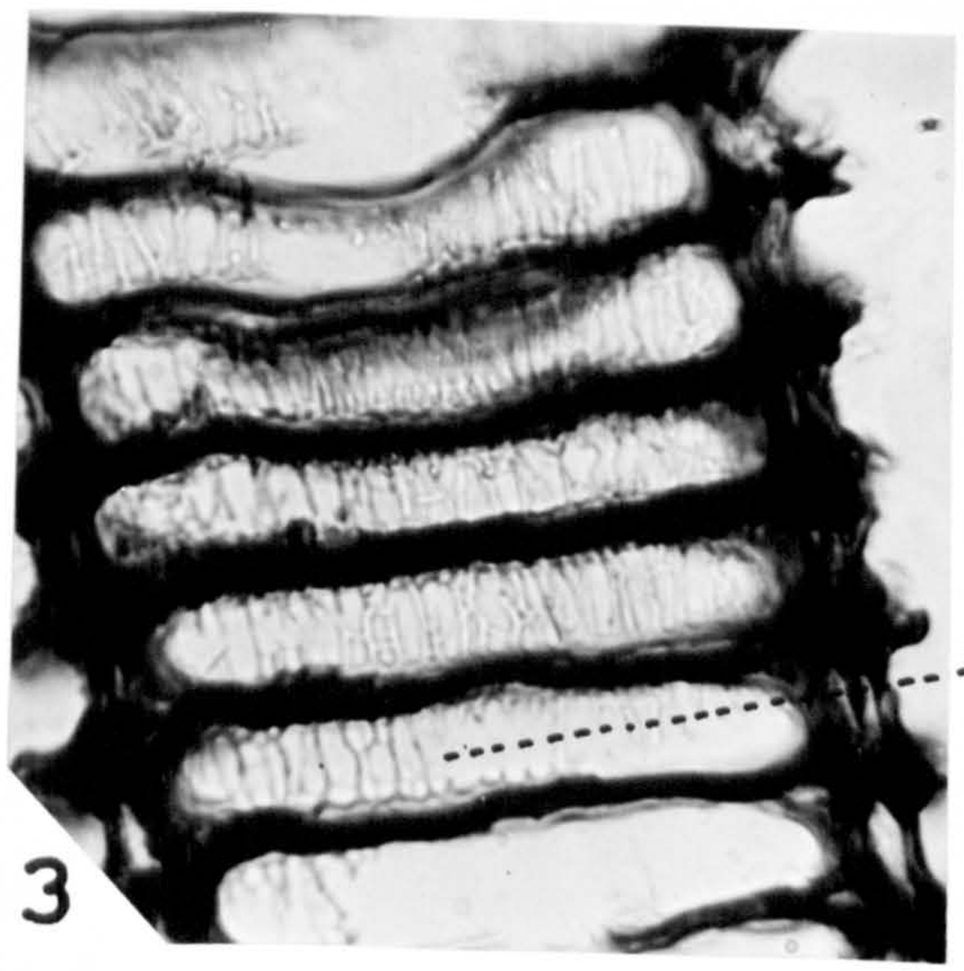

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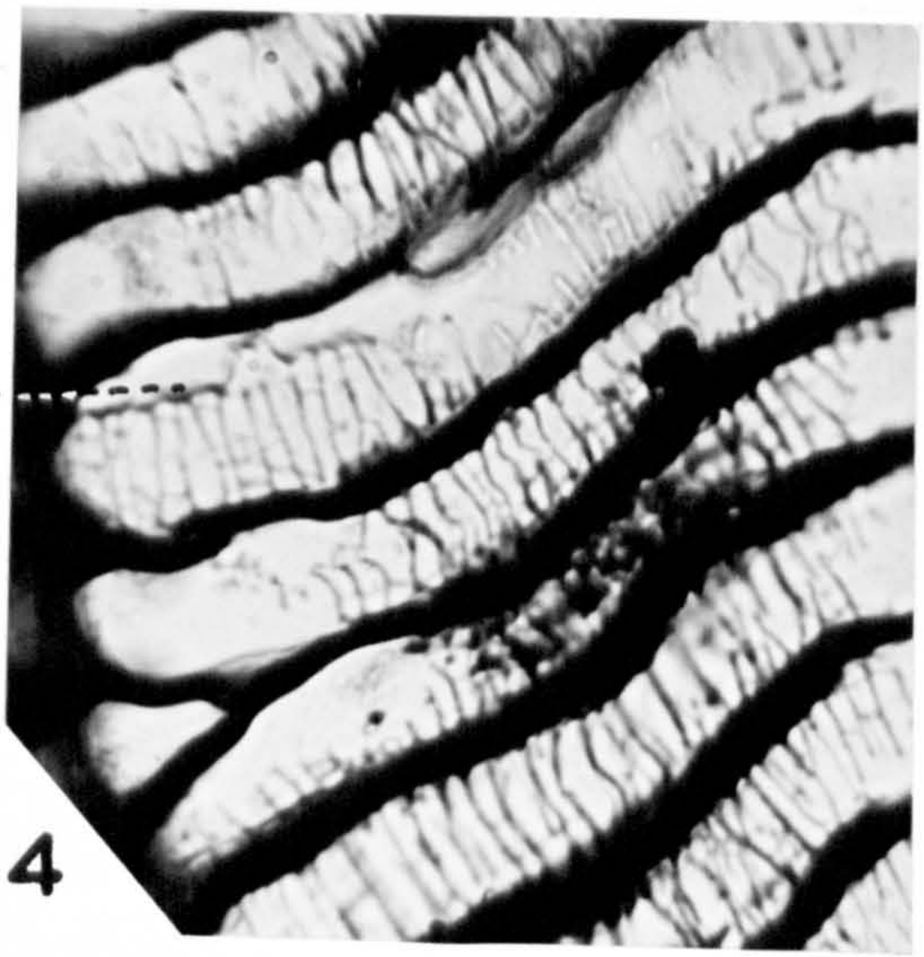

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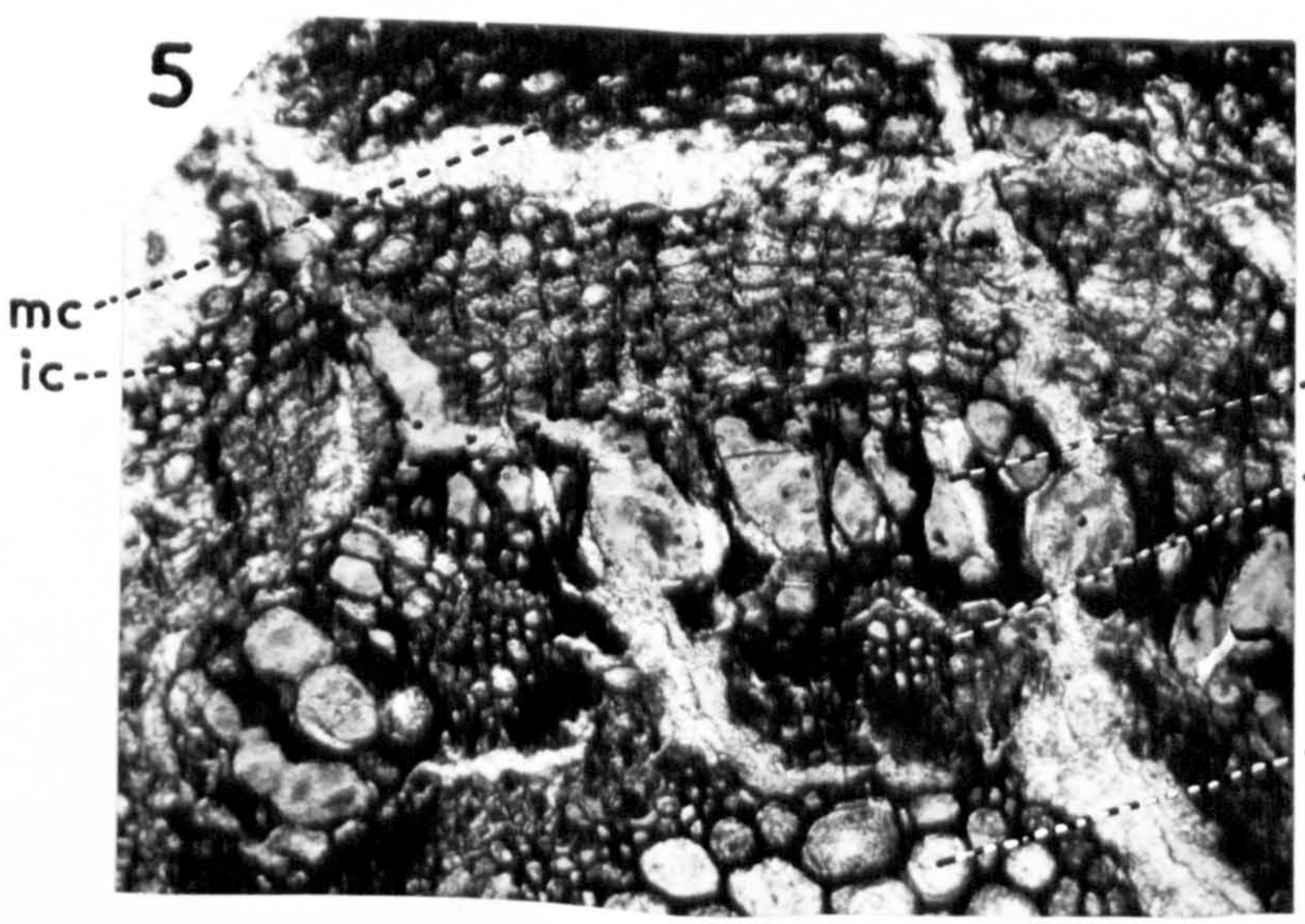


PLATE 2.

Lepidophloios kilpatrickensis sp. nov.

Fig. 6. Transverse section of the outer cortex external to the secondary cortex, showing the radial division of the cells. (x 50) F.S.C. 652.

Fig. 7. Transverse section of the secondary cortex at an early stage in its development (x 150). F.S.C. 653.

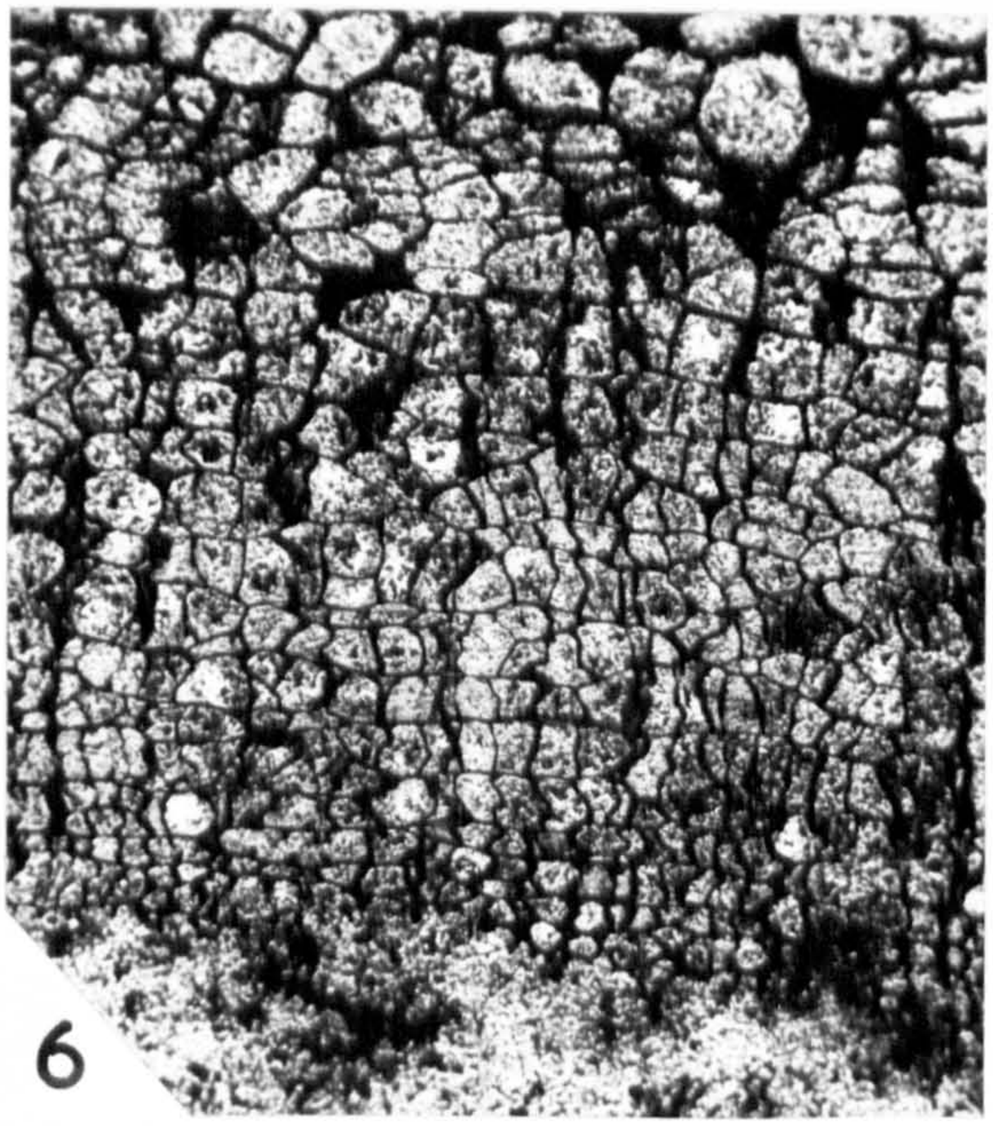
Fig. 8. Transverse section of a secretory 'duct' (x 250). F.S.C. 683.

Fig. 9. Radial longitudinal section of the middle and outer cortical zones showing the leaf-trace and accompanying parichnos strand. (x 20) F.S.C. 1316.

Fig. 10. Longitudinal section of the base of a leaf-cushion showing the columnar tissue with elongated air-spaces (x 30). F.S.C. 1313.

Fig. 11. Transverse section of the ligule and pit (x 100). F.S.C. 1331.

Abbreviations: lt, leaf-trace; mc, middle cortex; oc, outer cortex; p, parichnos strand.



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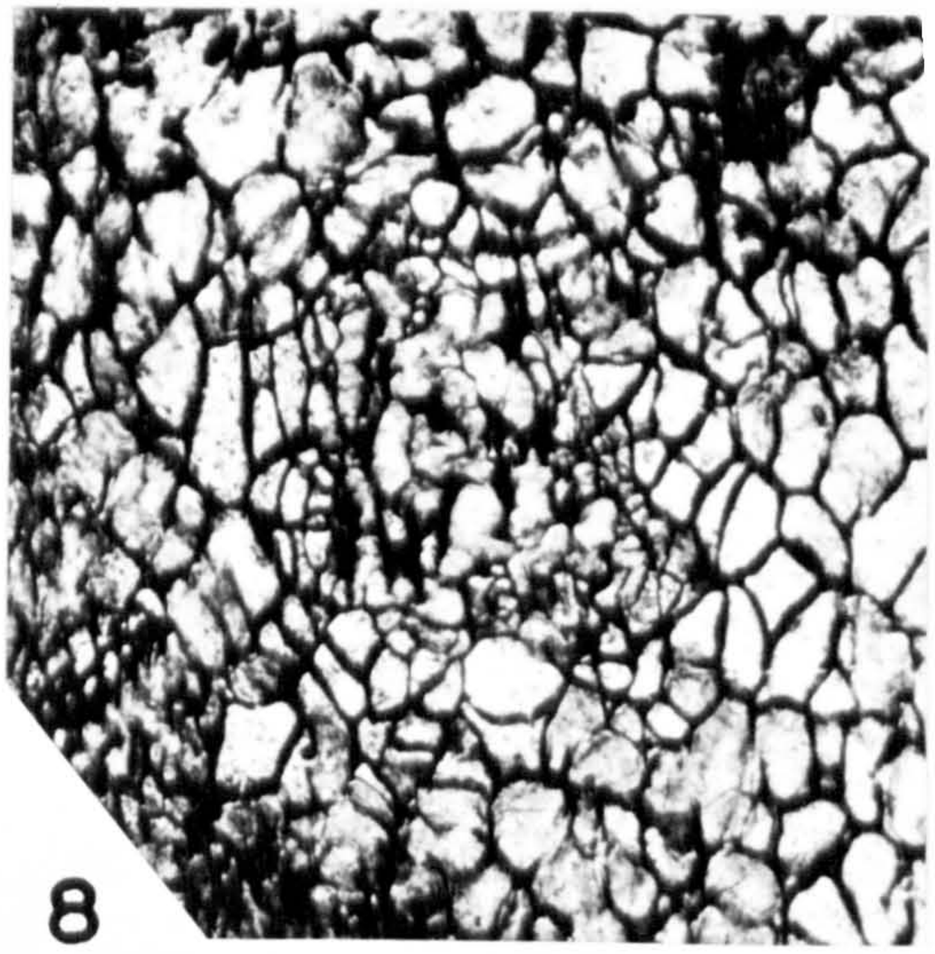

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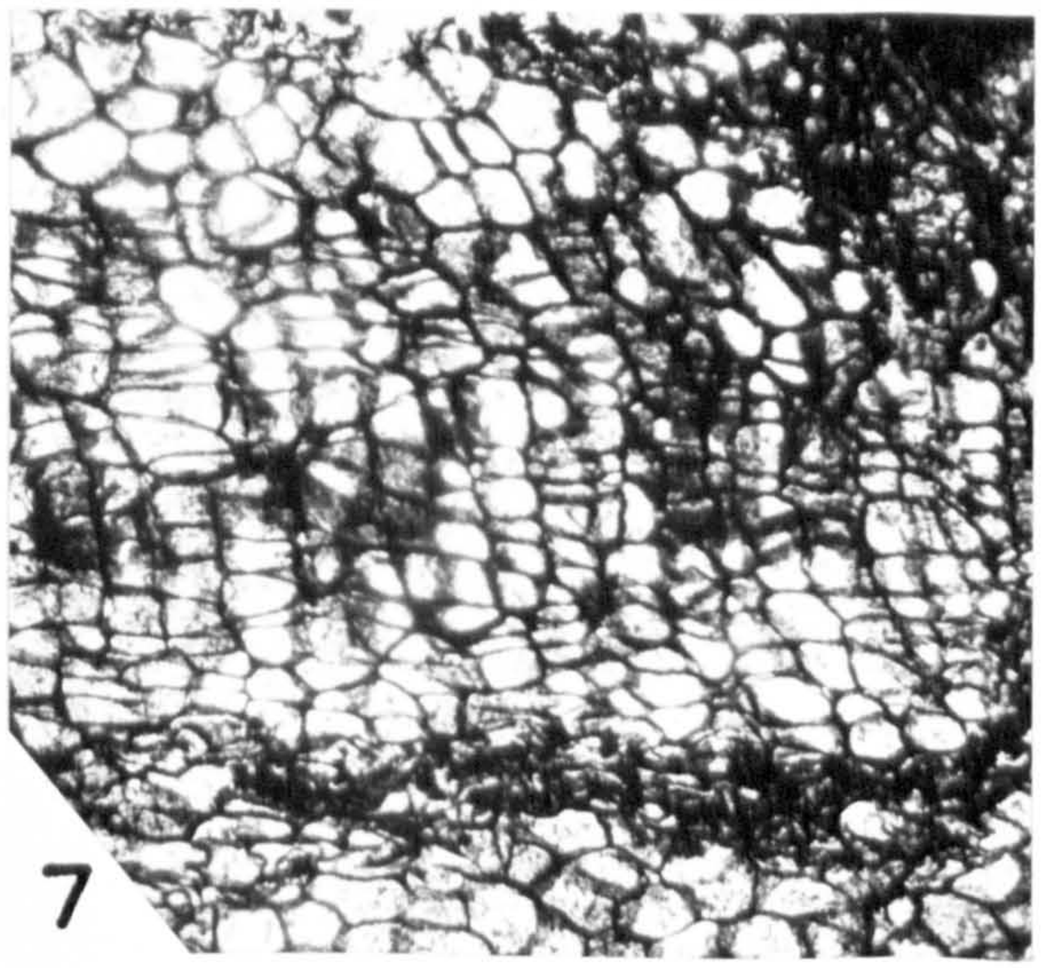

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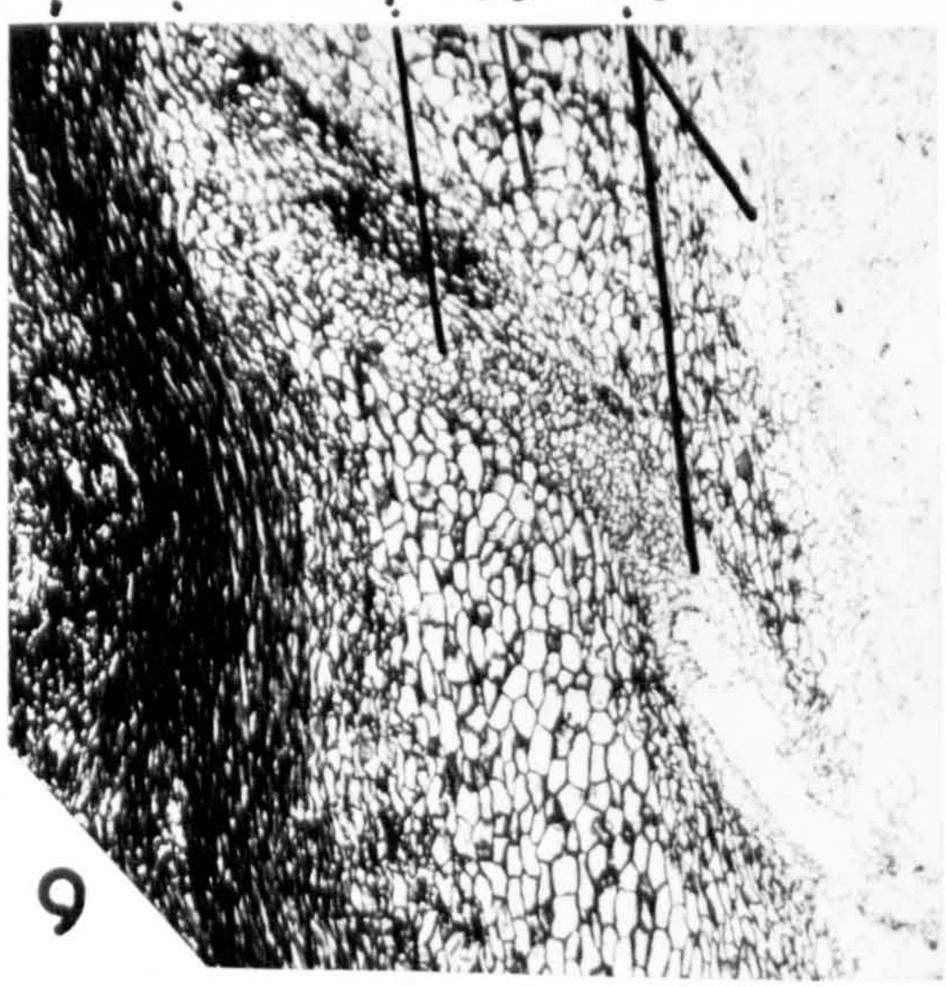

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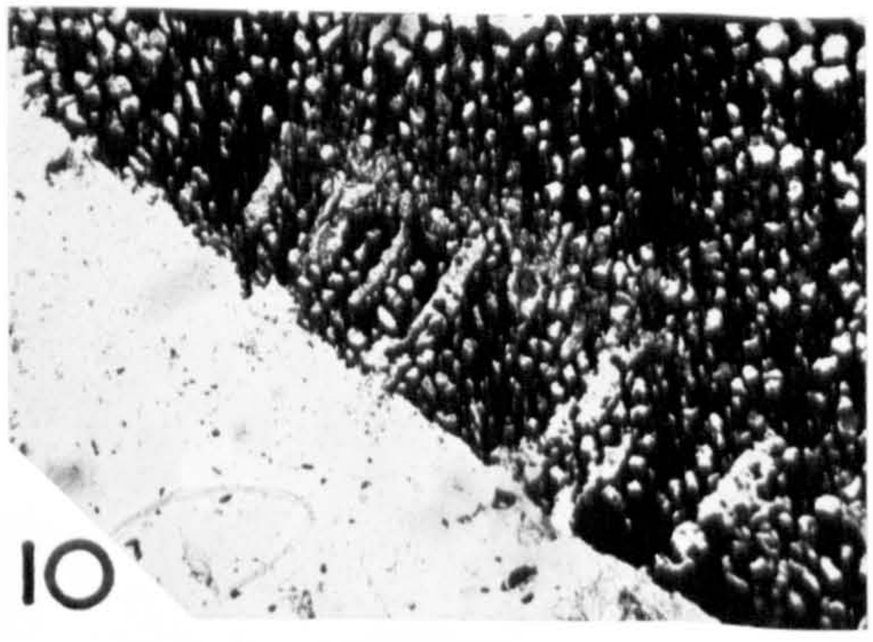

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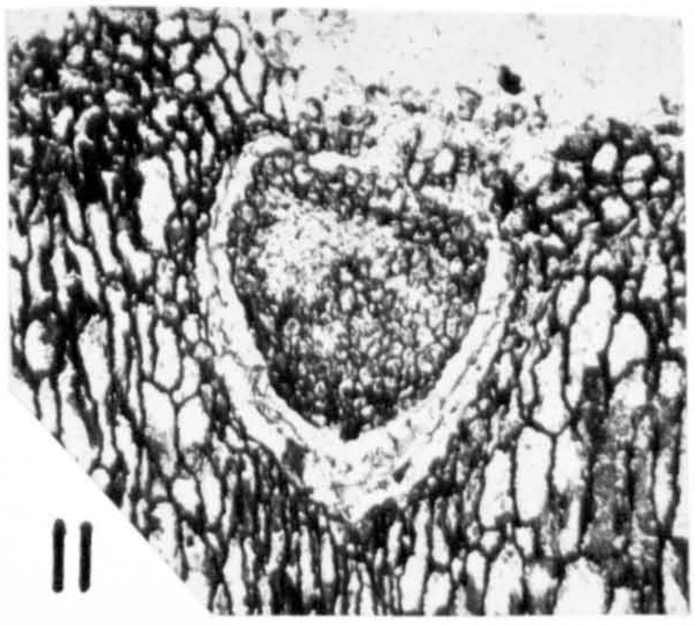

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PLATE 3.

Lepidodendron solenofolium sp. nov.

Fig. 1. Oblique section of the ligule and pit (x 100) F.S.C. 733.

Fig. 2. Transverse section of the leaf (X 60) F.S.C. 732.

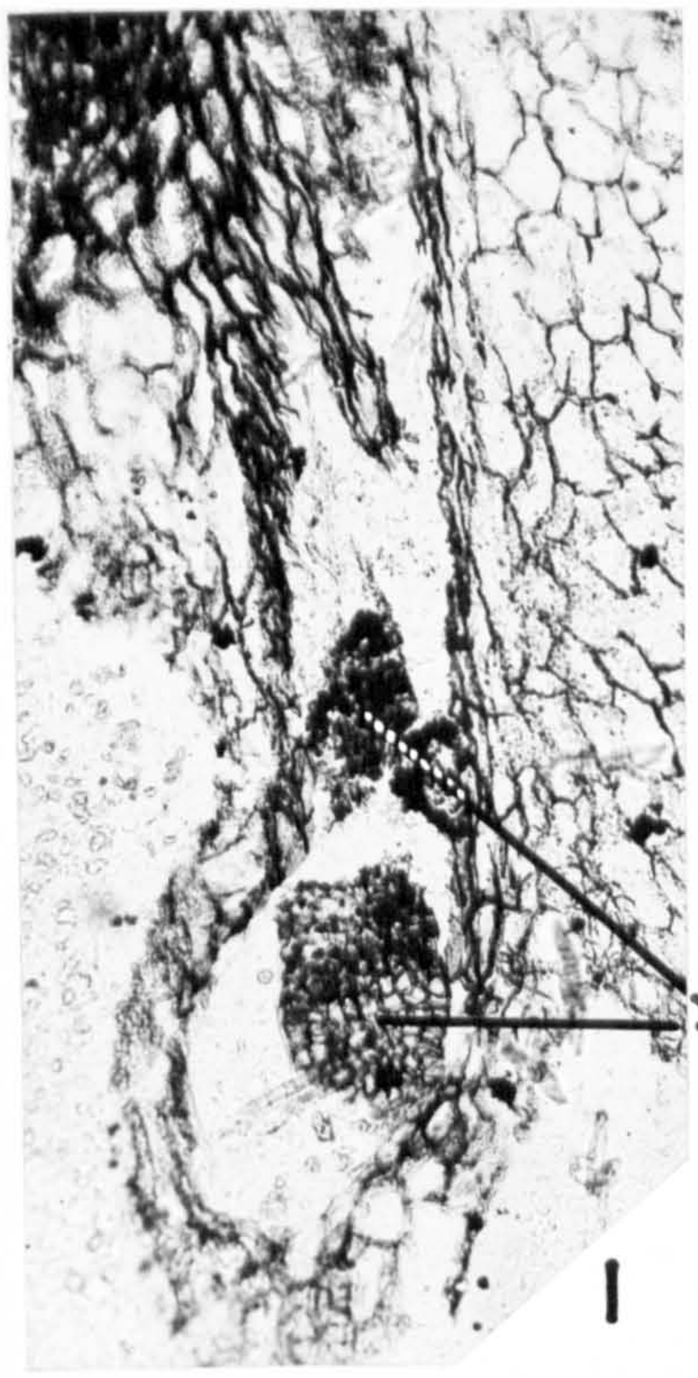
Lepidodendron brevifolium Will.

Fig. 3. Transverse section of the xylem of the larger specimen. (x 30) F.S.C. 1341.

Fig. 4. Transverse section of the xylem of the smaller specimen (x 100) F.S.C. 744.

Fig. 5. Tangential longitudinal section of the leaf cushion through the ligule and pit. (x 100). F.S.C. 1343.

Abbreviations: a, aerating tissue; c, central cavity; l, ligule; lt, leaf-trace; p, parichnos strand; tt, transfusion tracheids.



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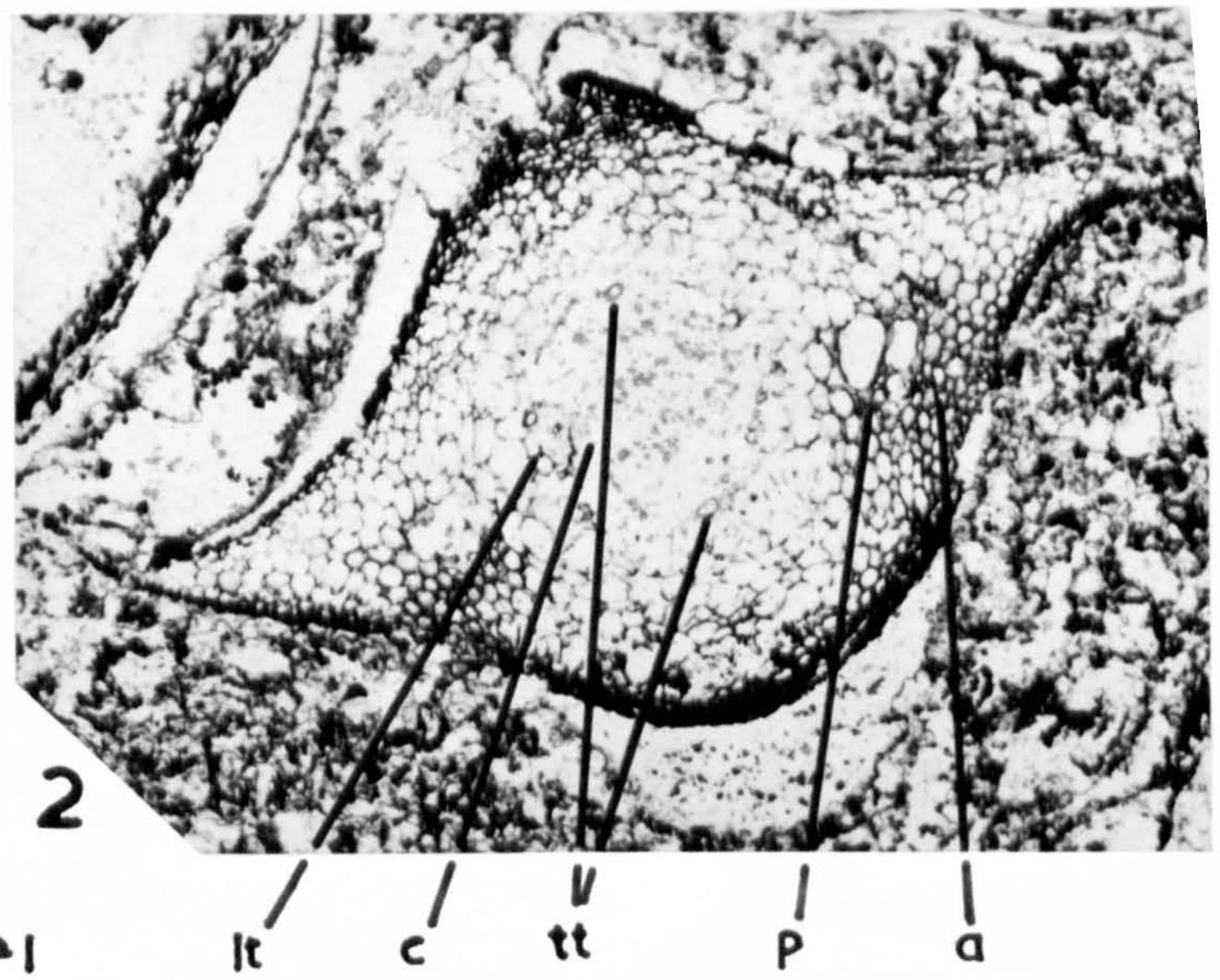

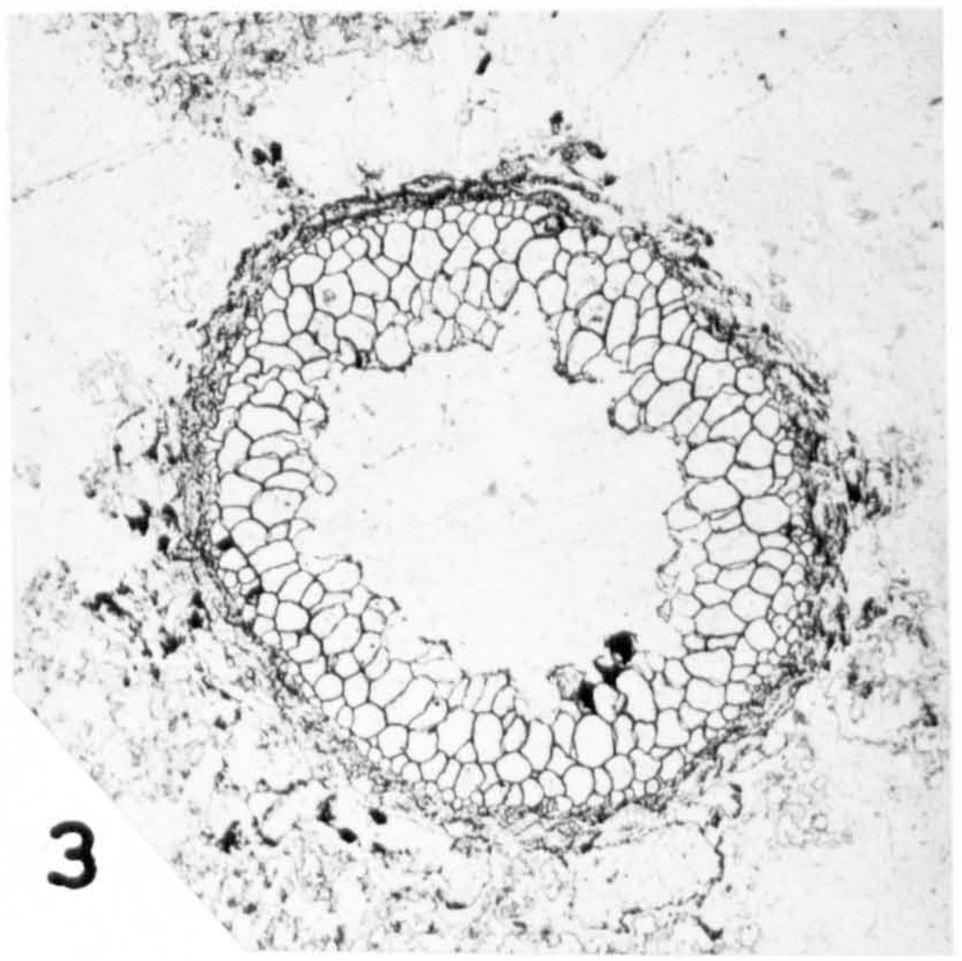

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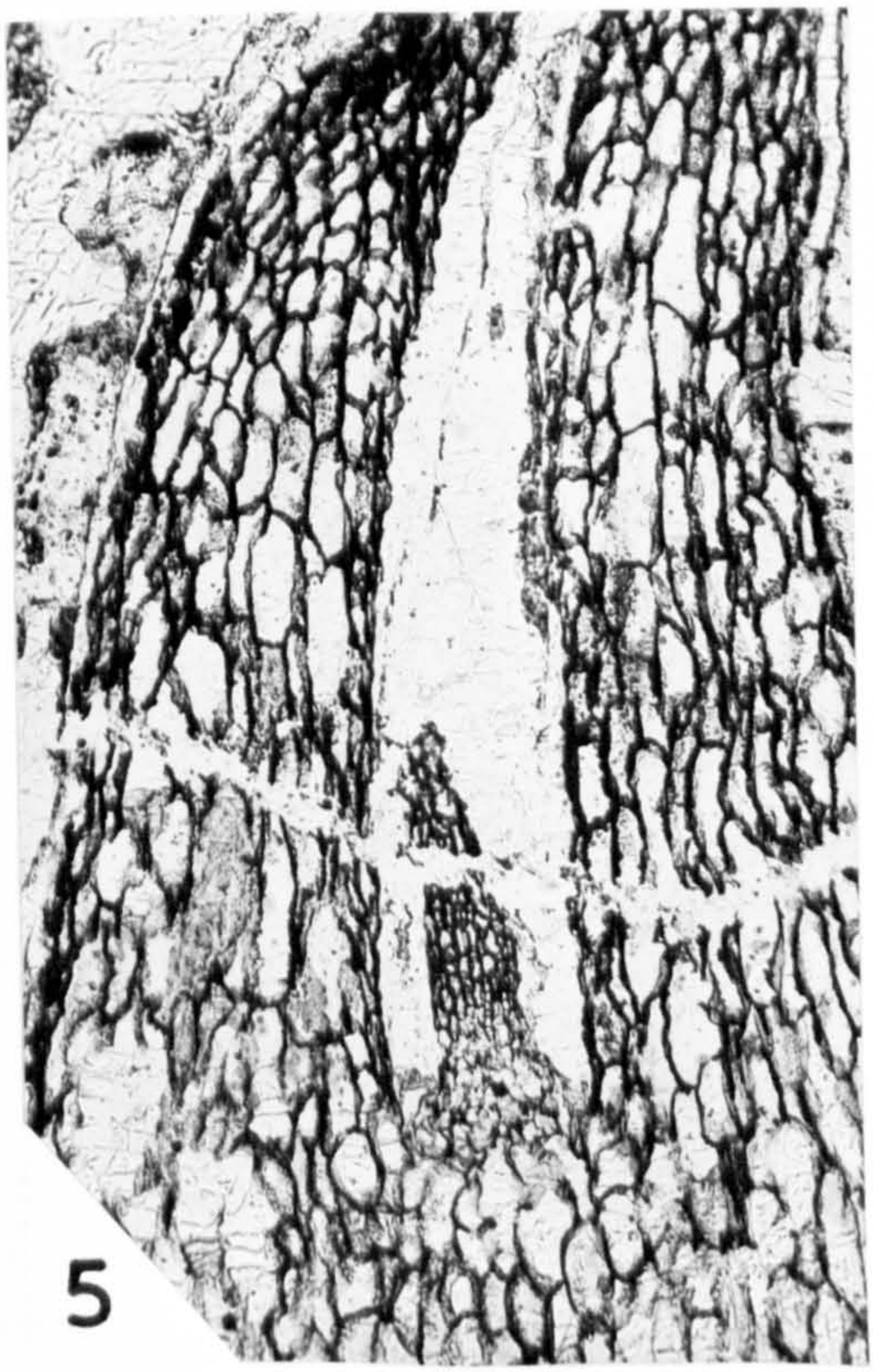

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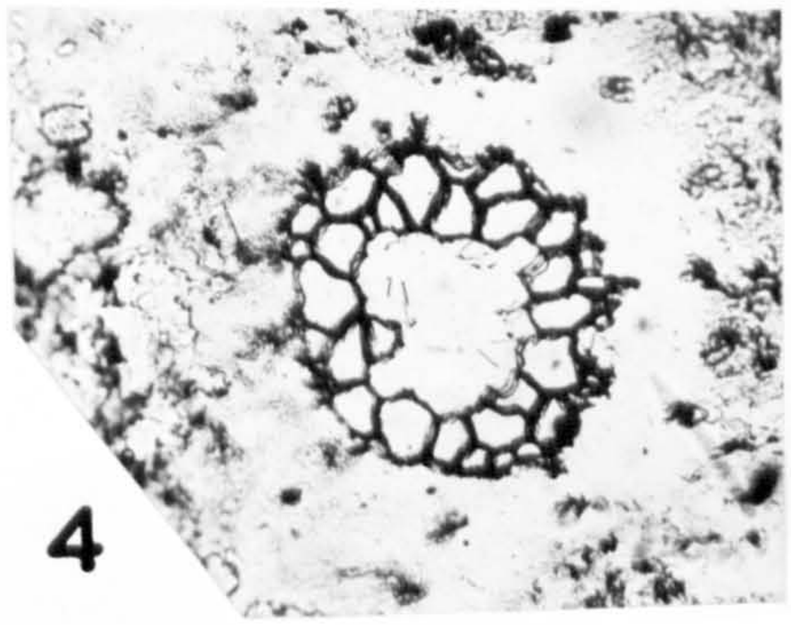

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PLATE 4.

Lepidodendron cf. brevifolium Will.

Fig. 1. Transverse section of the junction of the primary and secondary xylem (x 30) F.S.C. 1347 .

Fig. 2. Longitudinal section of a degraded tracheid of the secondary xylem, showing the fimbril system detached from the bar of thickening. (x 500) F.S.C. 1351.

Fig. 3. Tangential longitudinal section of the secondary xylem showing a ray containing a leaf-trace.

Fig. 4. Departure of a branch trace from the primary xylem. (x 15) F.S.C. 1347.

Abbreviation: tt, transfusion tracheids.

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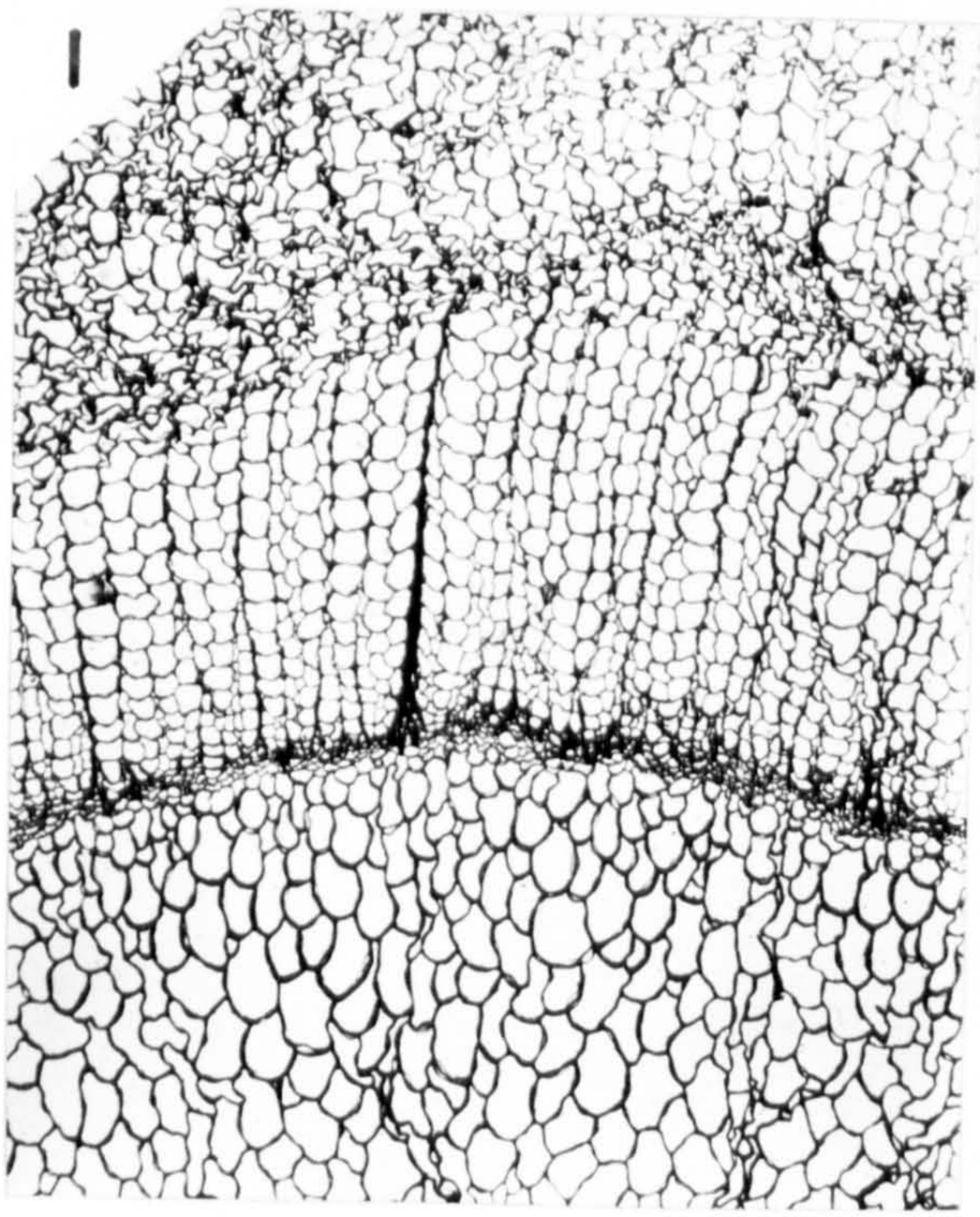

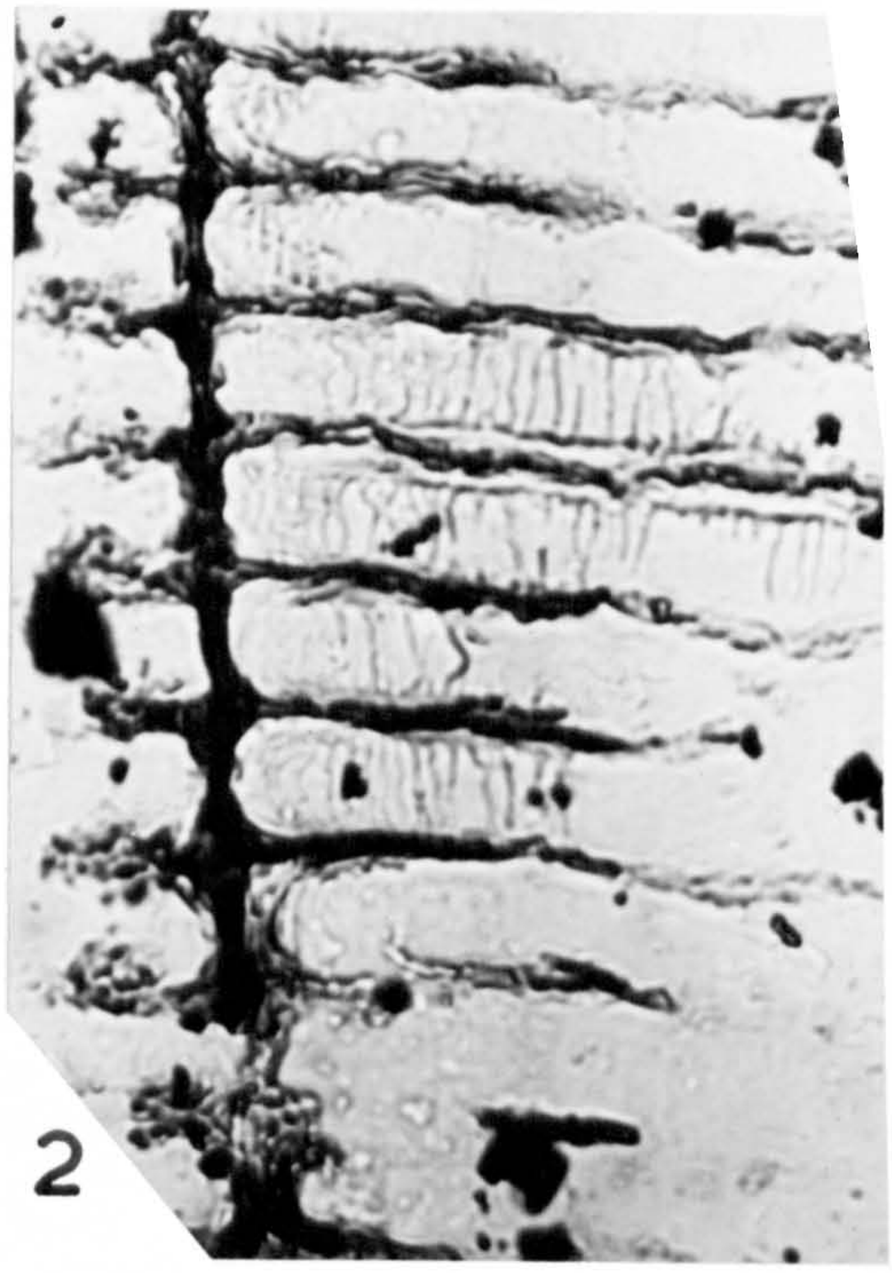

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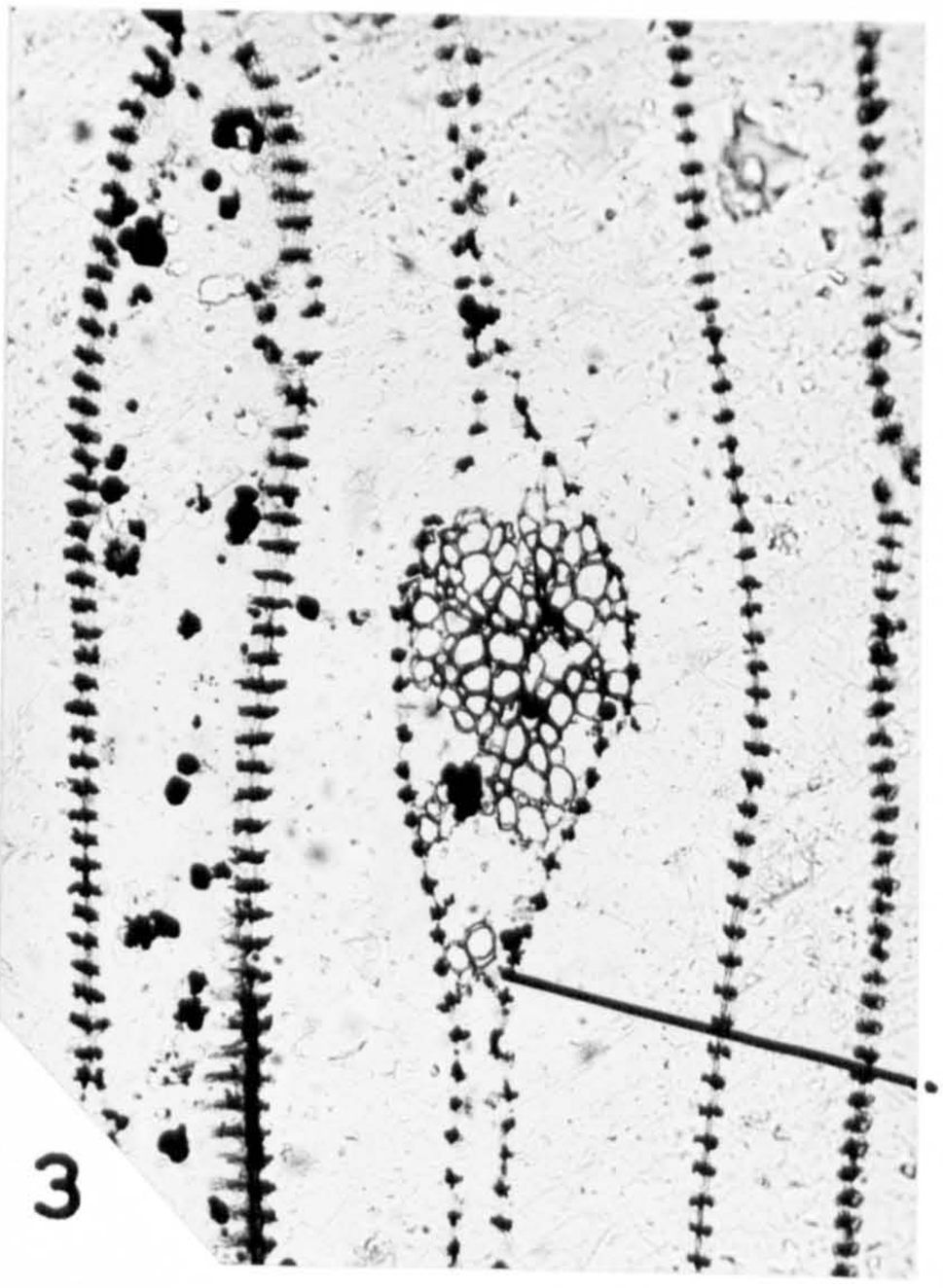

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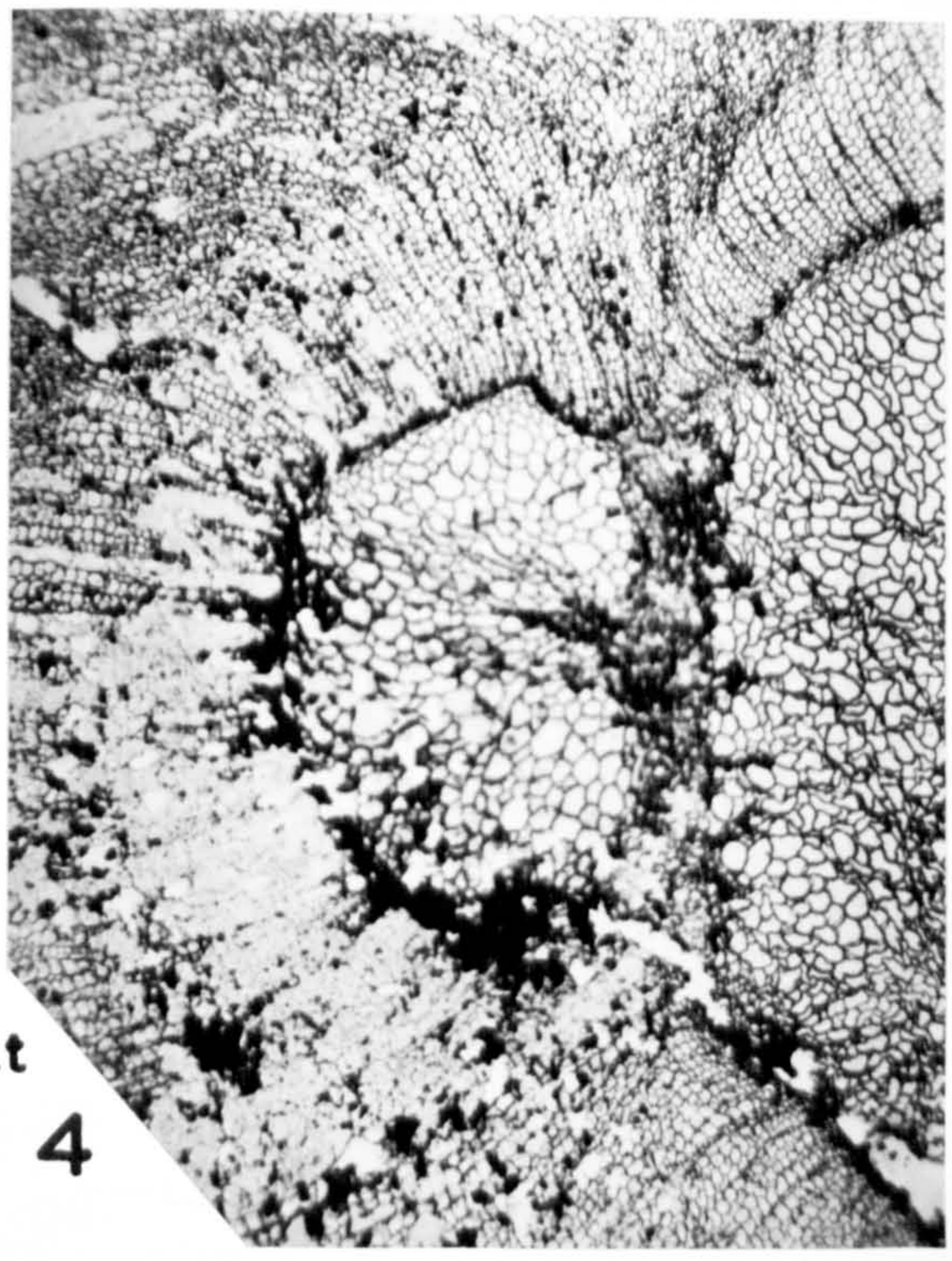

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PLATE 5.

Lepidocarpon wildianum Scott

Fig. 1. Tangential section of the 'seed'. (x30) F.S.C. 1353.

Fig. 2. Fragment of the megaspore membrane in the above section, showing its fibrillar structure. (x 500) F.S.C. 1353.

Dineuron ellipticum Kidston

Fig. 3. Transverse section of part of the rachis with a pinna-trace. (x 50) F.S.C. 1366.

Heterangium grievii Will.

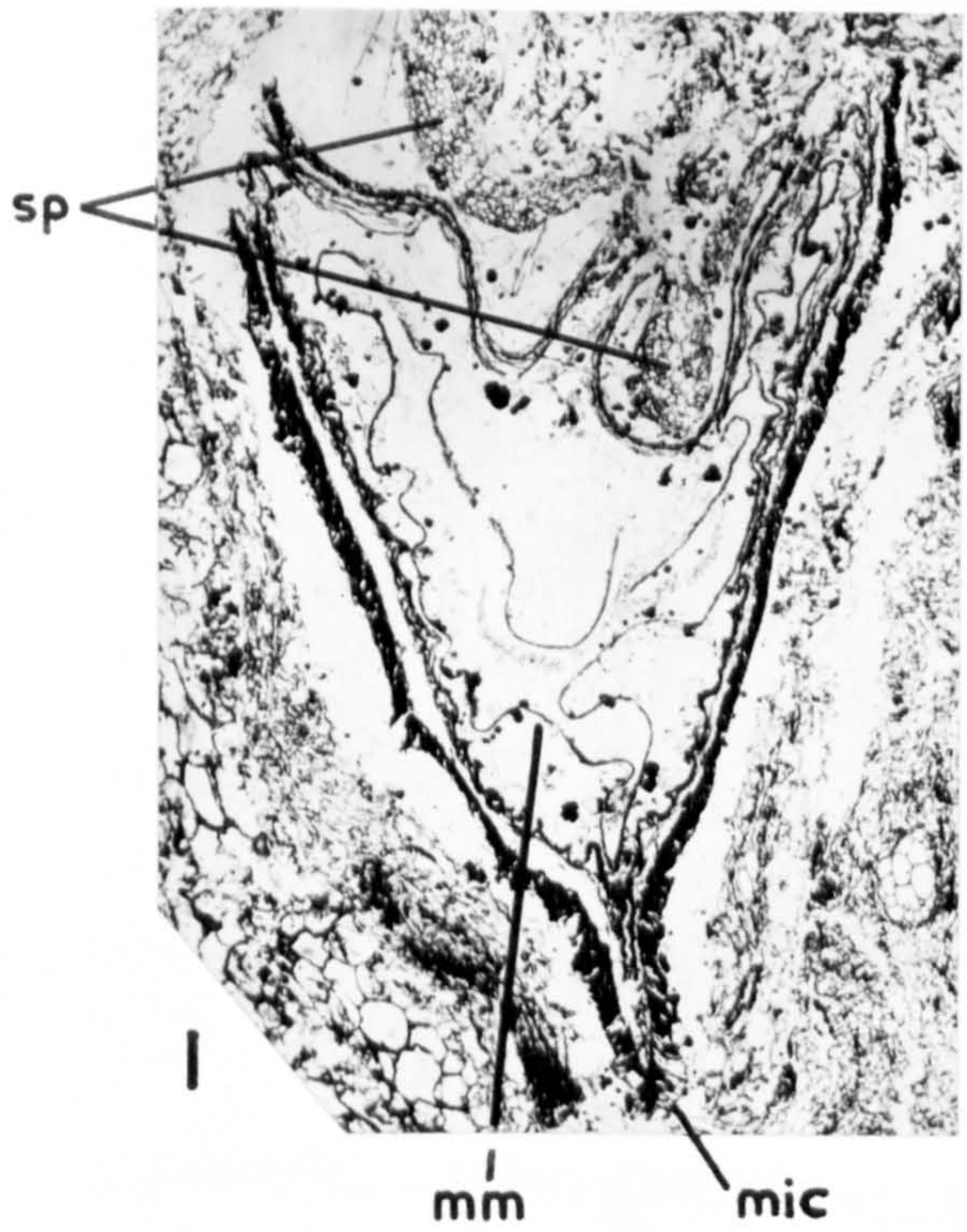
Fig. 4. Transverse section of a small stem. (x 25)

Pteridosperm 'seed'

Fig. 5. Longitudinal section (x 5) F.S.C. 1358.

Fig. 6. Fragment of the megaspore membrane (x 500) F.S.C. 1357.

Abbreviations: e, endodermis; i, integument; mm, megaspore membrane; oc, outer cortex; ph, ?phloem; pt, pinna-trace. mic, micropyle ; sp, sporophyll.



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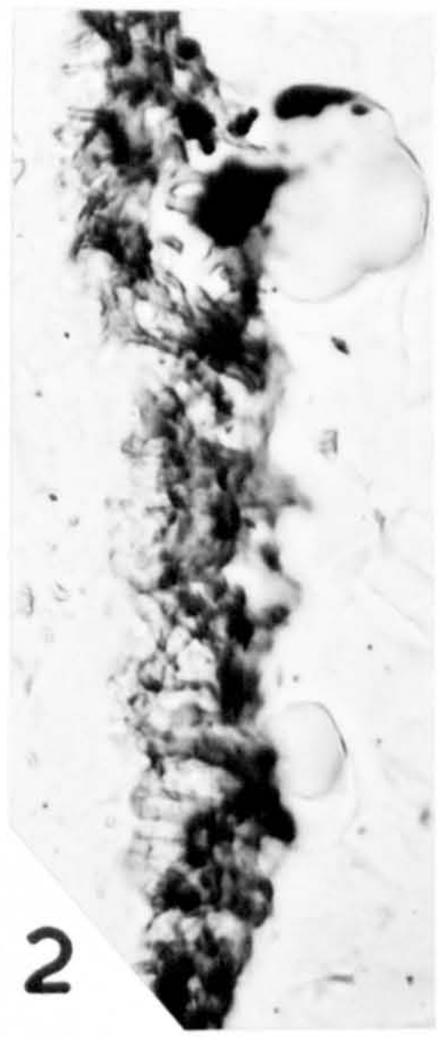

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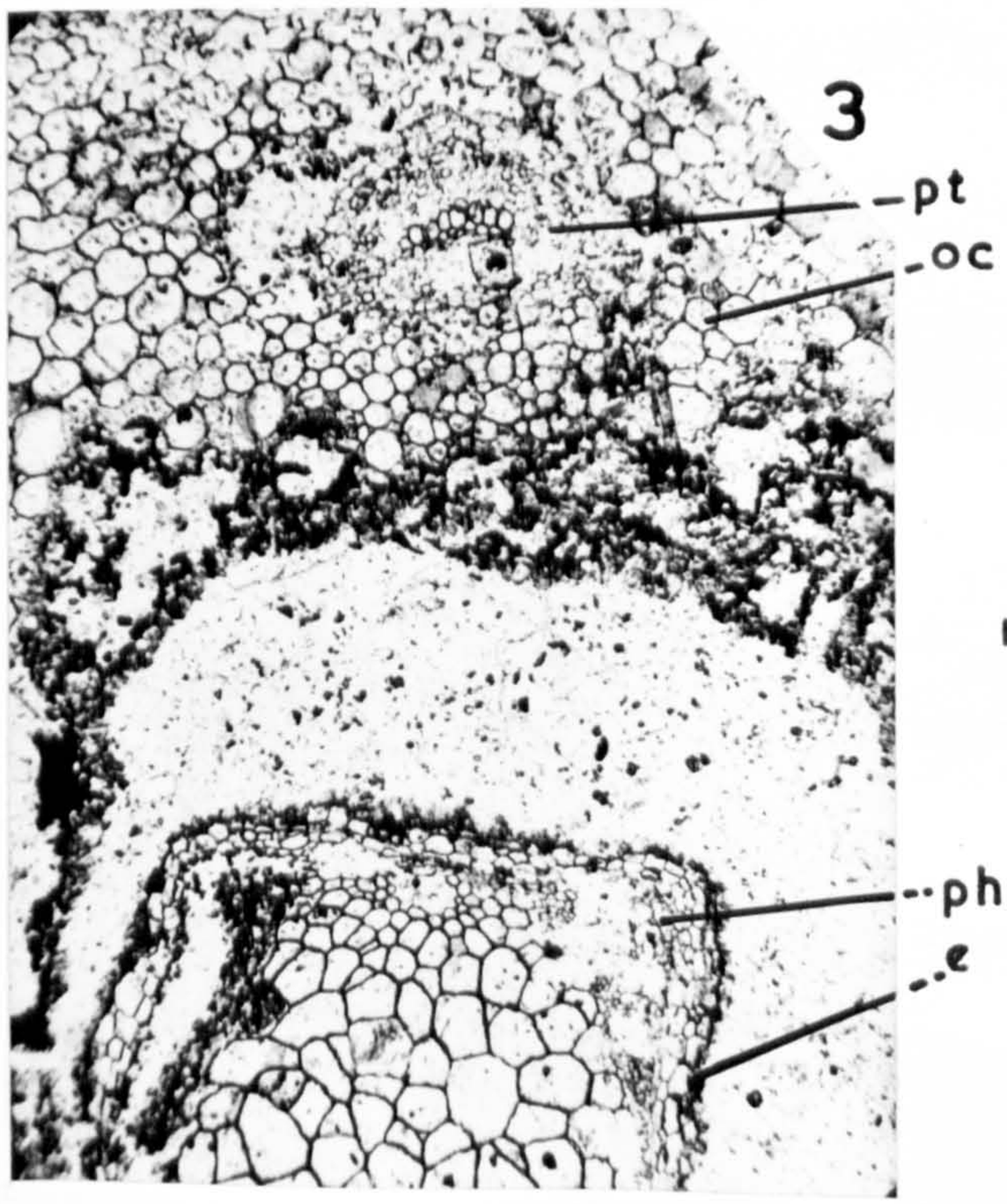

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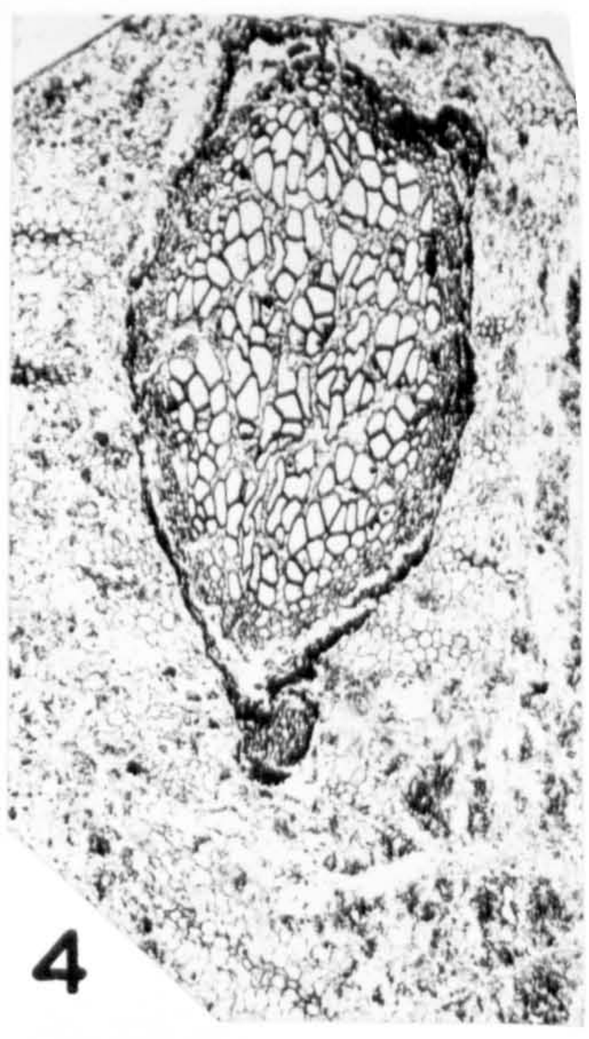

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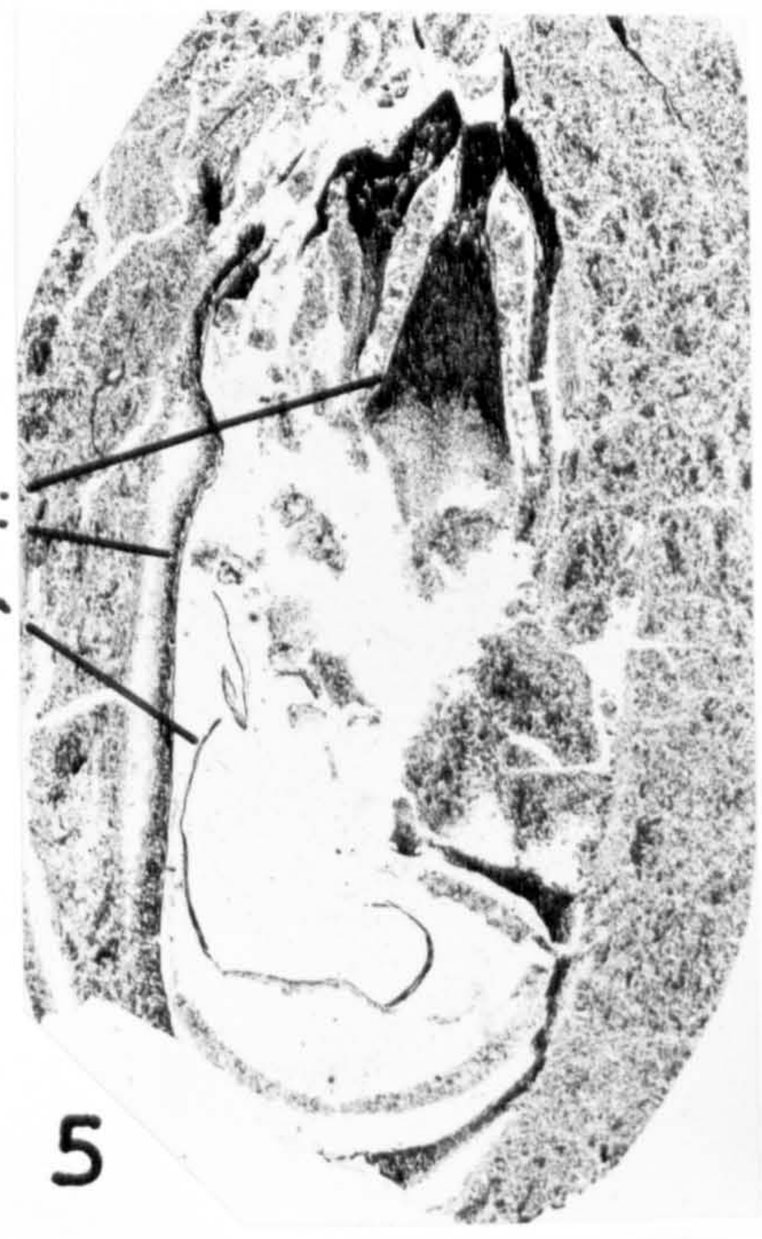

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PLATE 6.

cf. Pothocites sp.

Fig. 1. Compression of the fructification. (x2) Pb 2556.

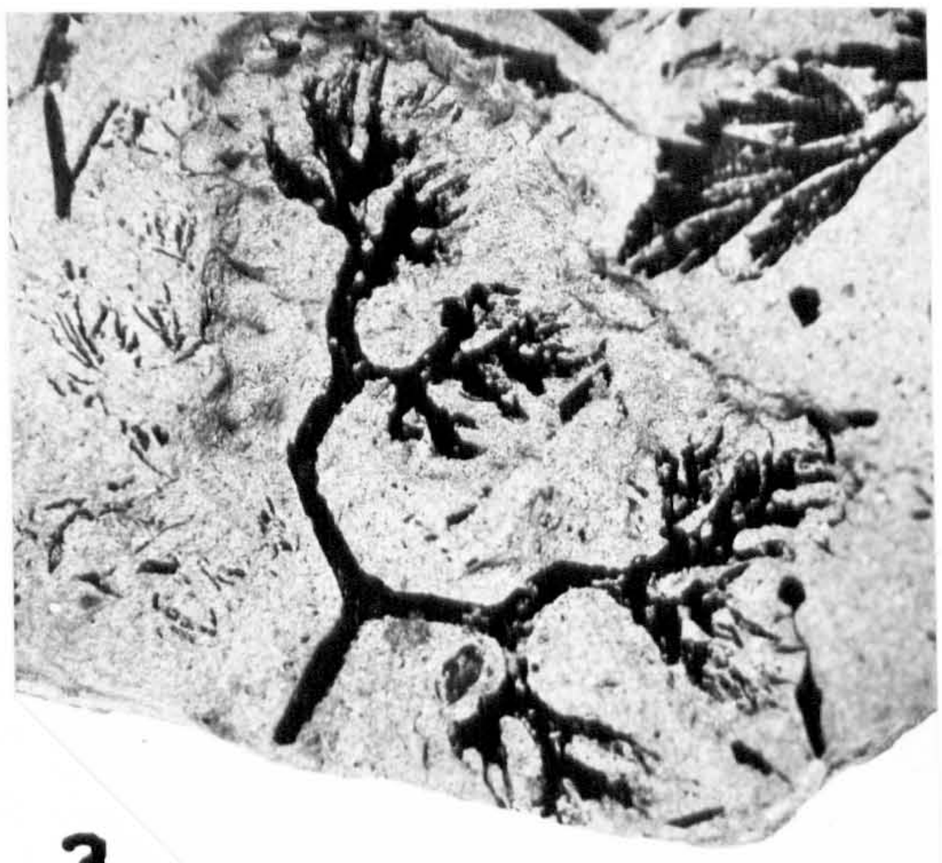
Protopitys scotica Walton

Fig. 2. Transverse section of the stem. (x 50) F.S.C. 1370.

Fig. 3. Compression of a sporophyll. (x1) Pb 2696.

Abbreviations: mx, metaxylem; px, protoxylem; sx, secondary xylem.

1



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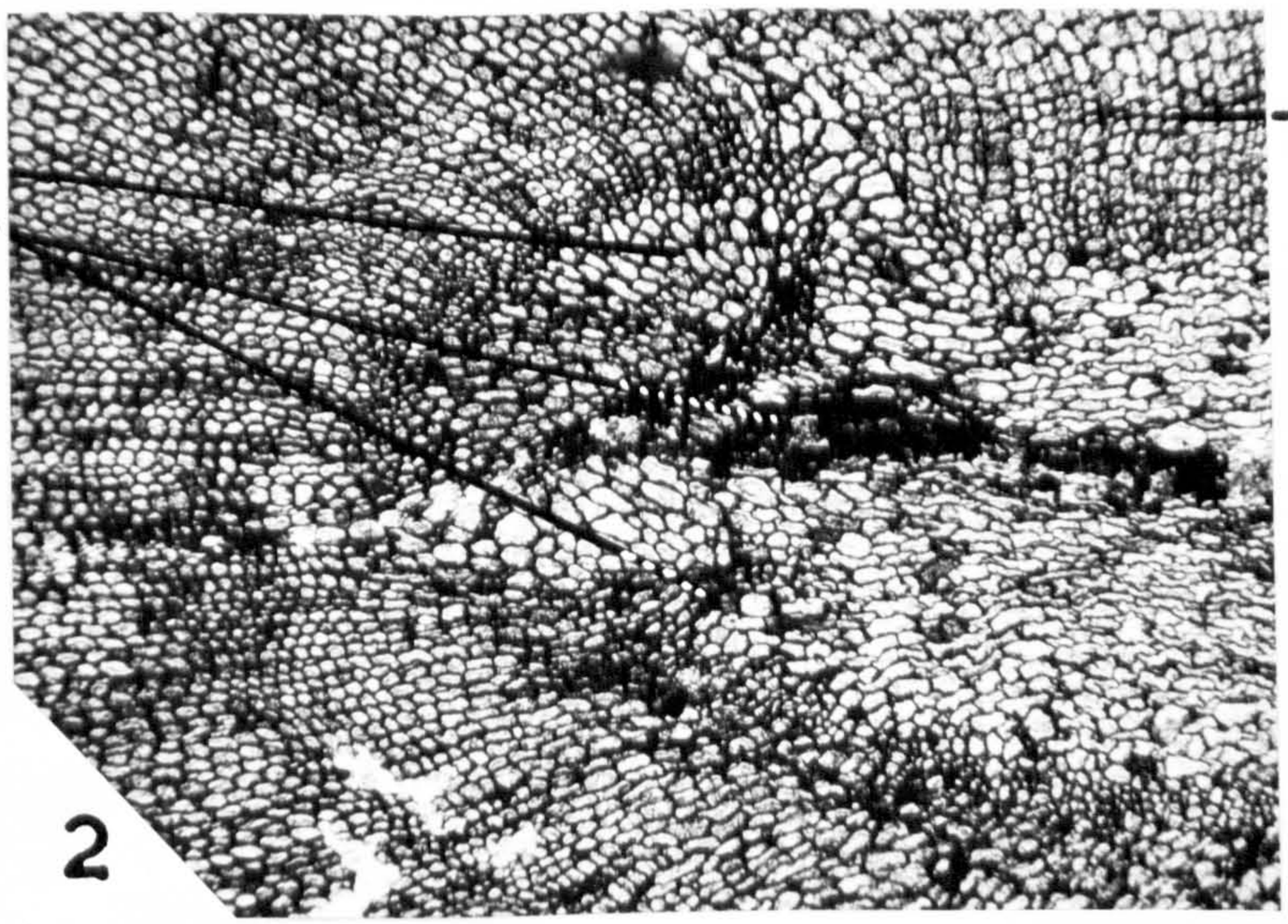

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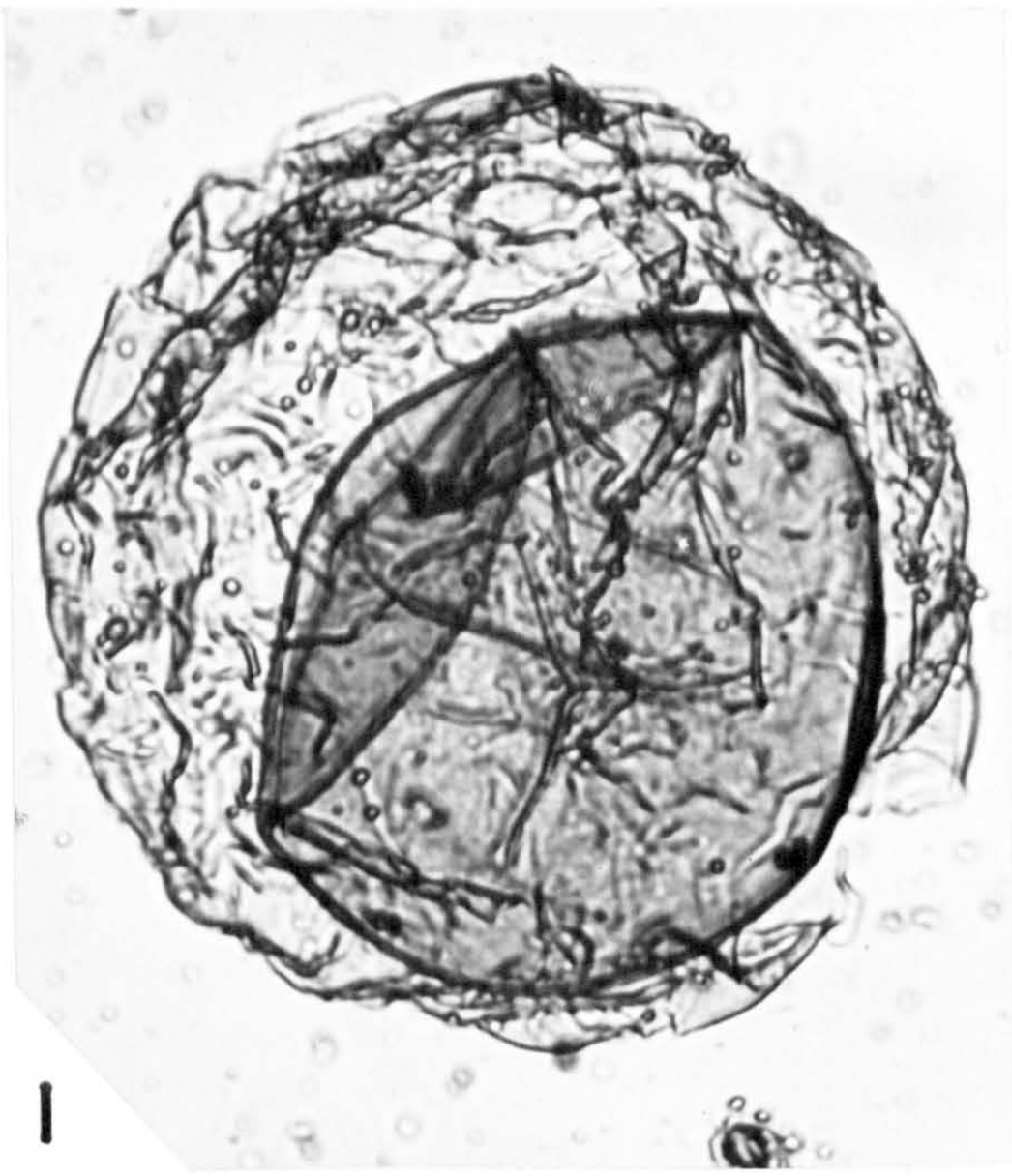
PLATE 7.

Protopitys scotica Walton

Fig. 1. Spore complete with 'perispore'. (x 500) F.S.C. 1372.

Fig. 2. Detached 'perispore' showing trilete mark (x 500) F.S.C. 1371.

Fig. 3. Spore which has shed its perispore. (x 500) F.S.C. 1371.



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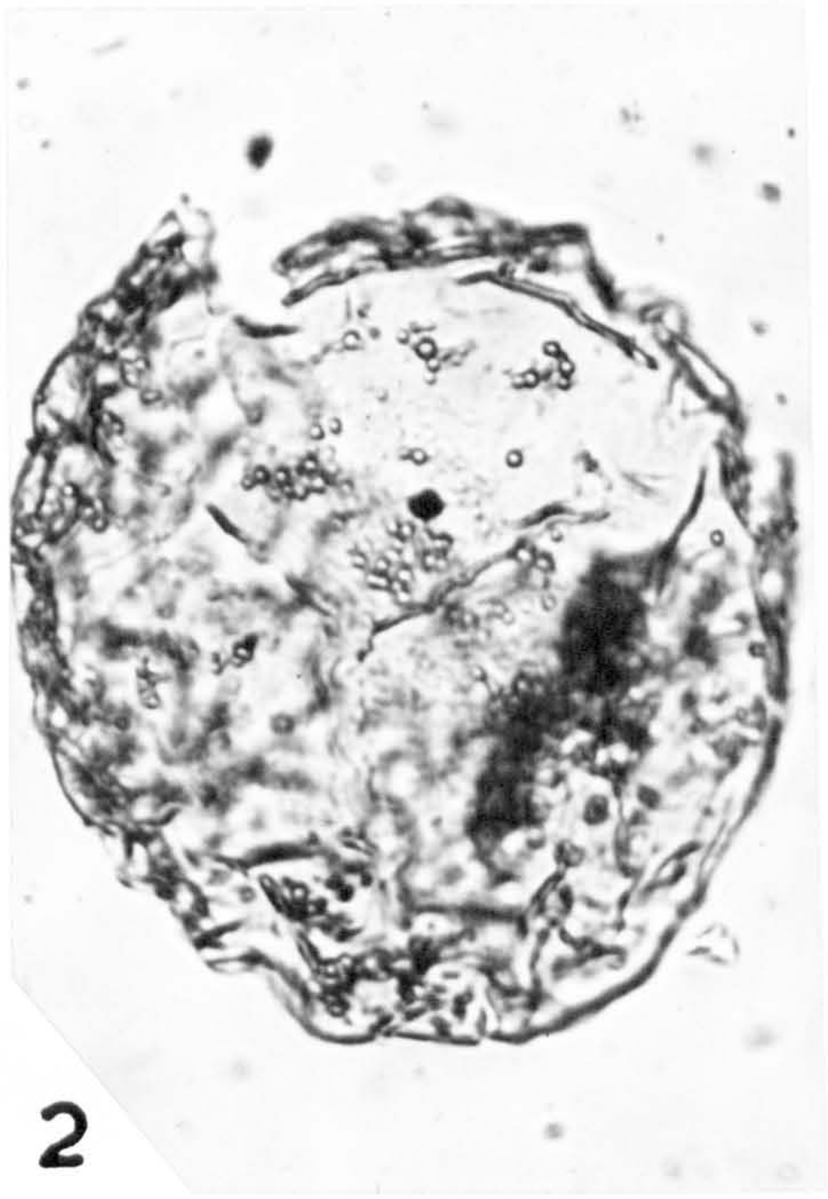

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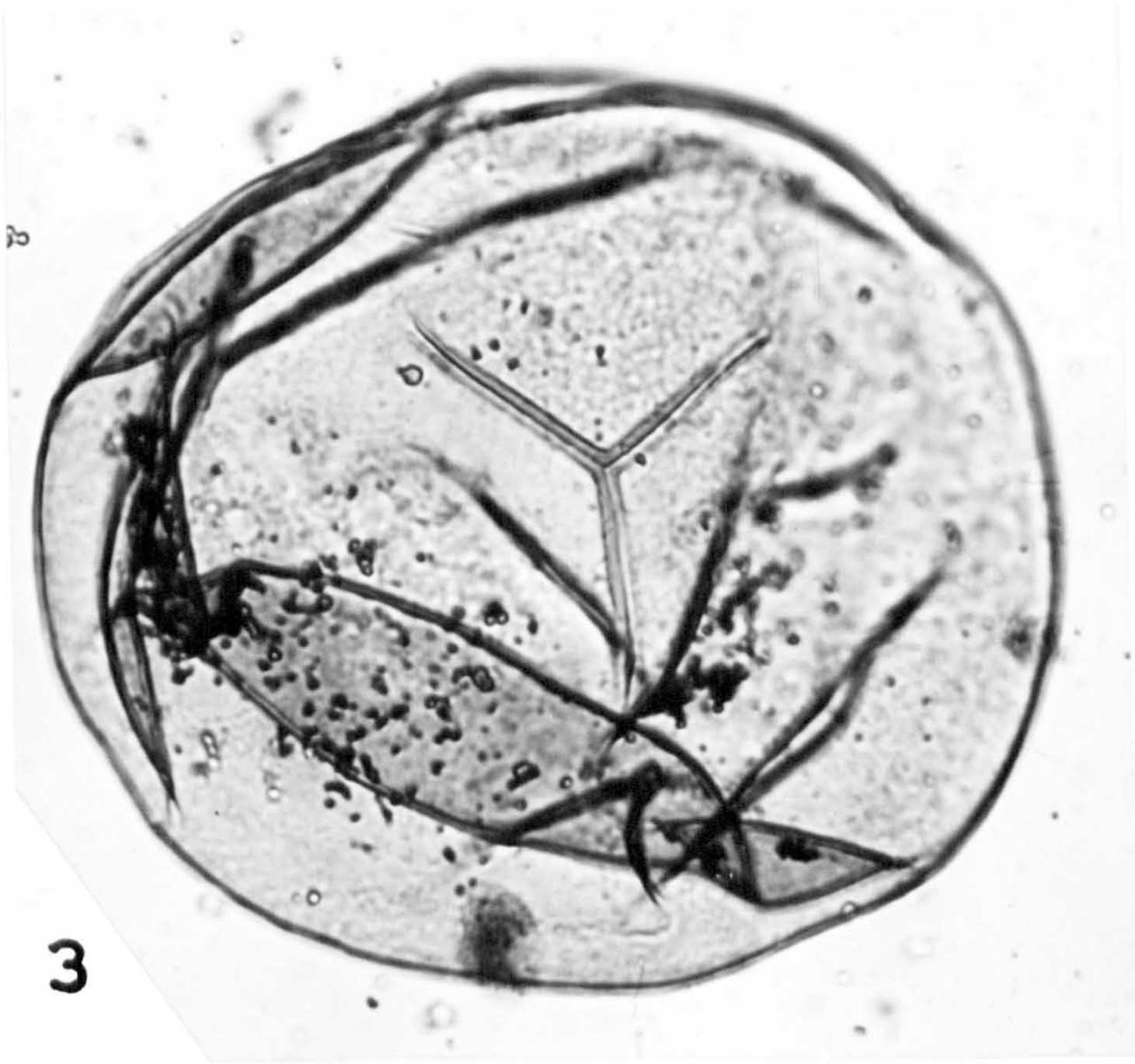

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PLATE 8.

Geminitheca scotica gen. et sp. nov.

Fig. 1. Bunch of ovulate cupules compressed more or less vertically. (x2).

Fig. 2. Bunch of ovulate cupules compressed laterally. (x1) Pb 2711.

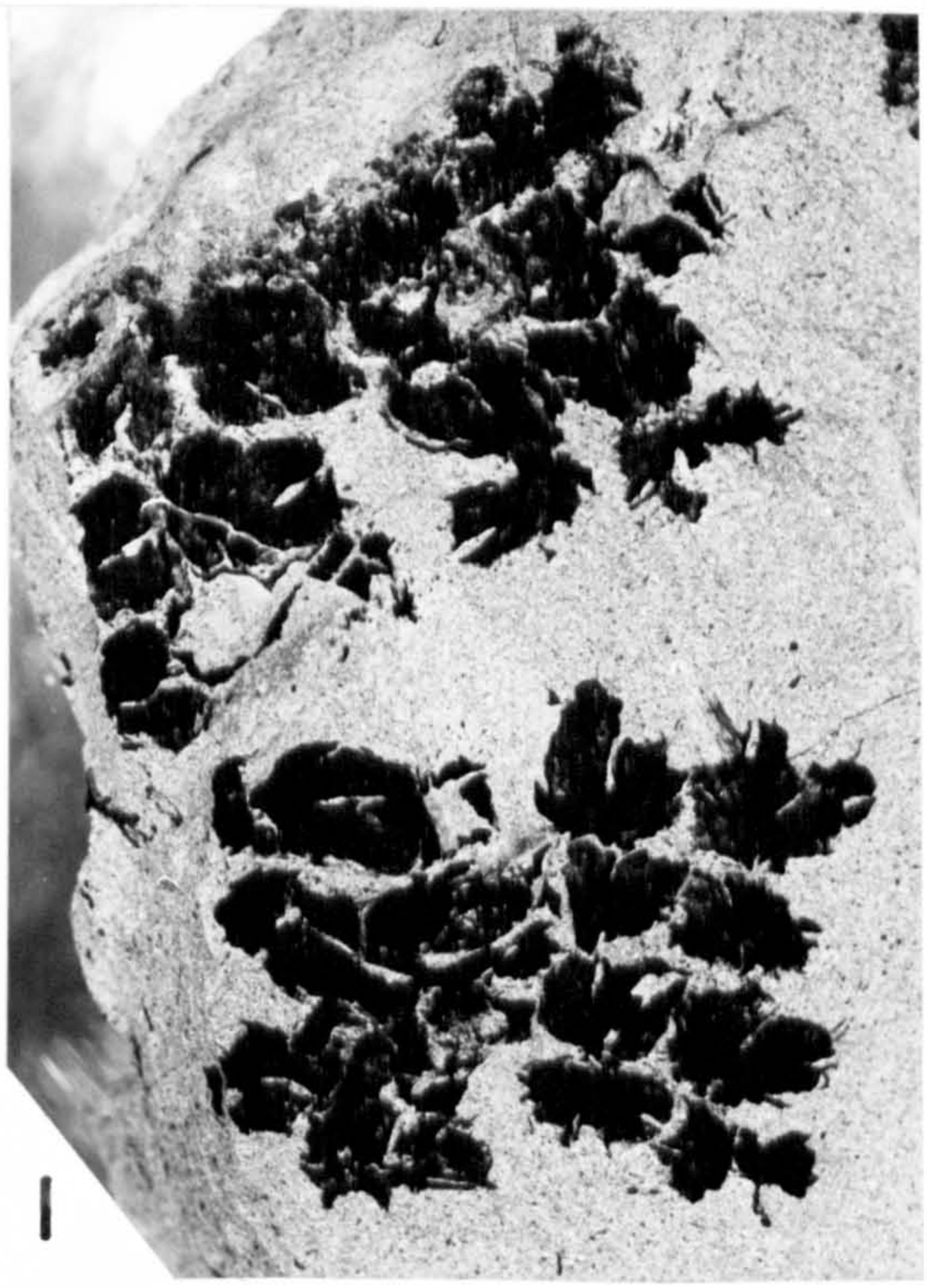
Fig. 3. Transverse section of the rachis immediately below a cupule-pair. (x 30). F.S.C. 1210.

Fig. 4. Pitted tracheids in a rachis: 'pull' of Pb 2711. (x 310) F.S.C. 1219.

Fig. 5. Transverse section of part of a cupular lobe with an emergence (x 30) F.S.C. 1181.

Fig. 6. Transverse section of the vascular strand in the above cupular lobe. (x 200) F.S.C. 1181.

Abbreviations: ec, emergence on abaxial side of cupular lobe; ic, inner cortex; oc, outer cortex; par, parenchymatous layer of cupular lobe; scl, sclerotic layer of lobe; vb, vascular strand of lobe.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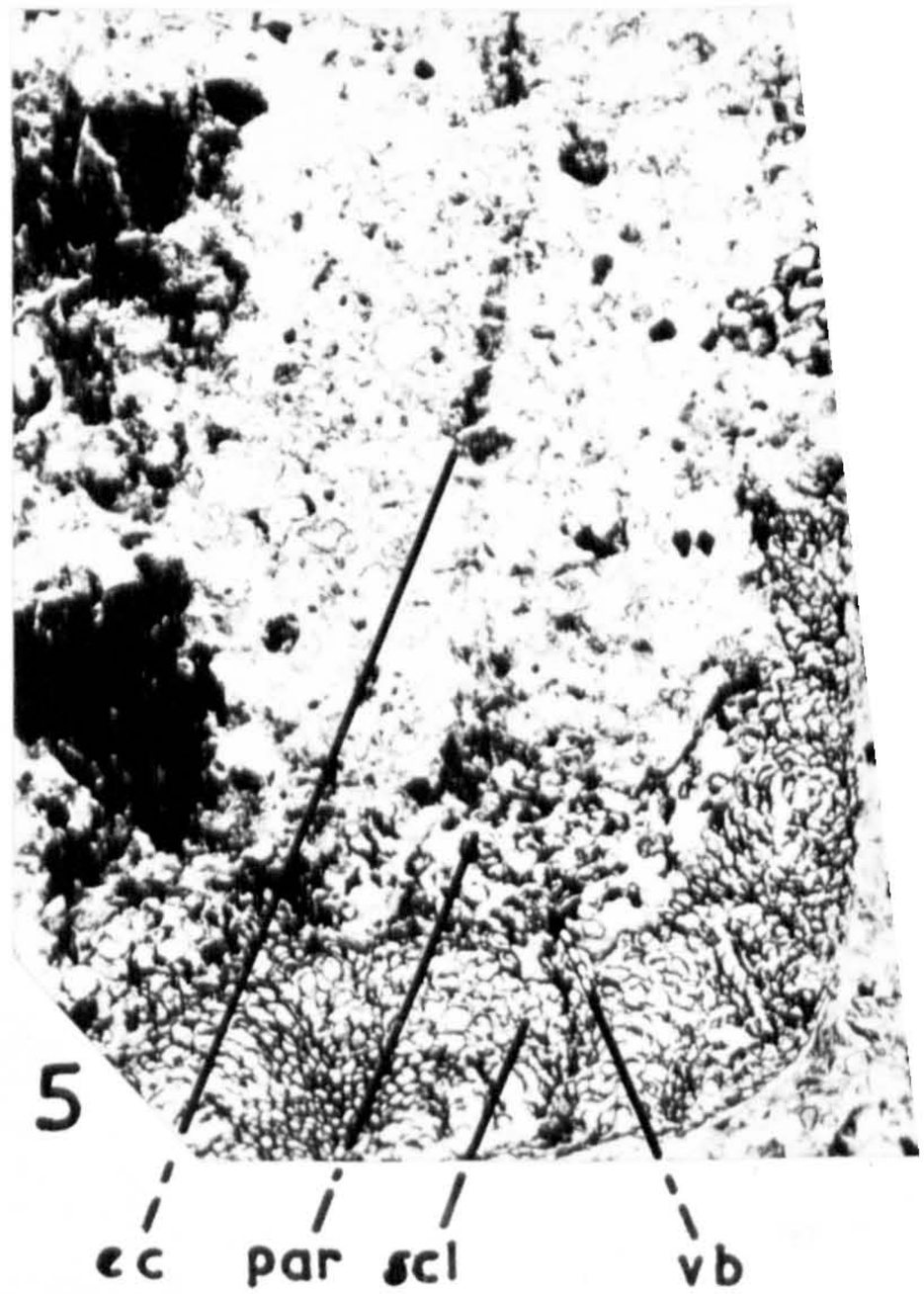


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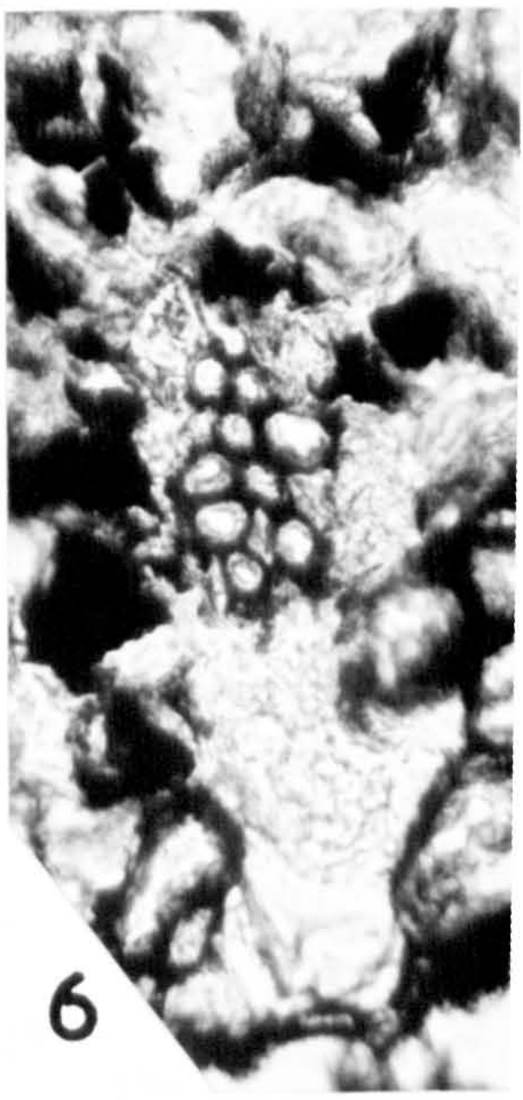
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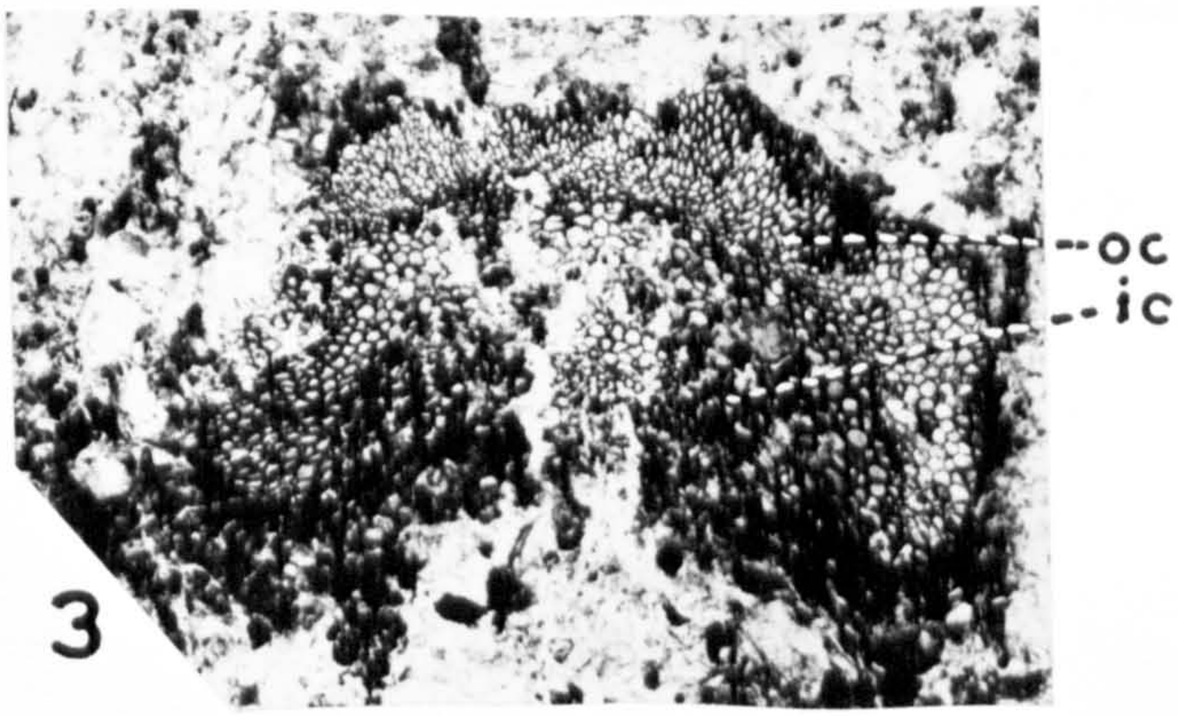

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PLATE 9.

Geminitheca scotica gen. et sp. nov.

Fig. 1. Stoma on rachis: 'pull' of Pb 2711. (x 380) F.S.C. 1220.

Fig. 2. Transverse section of the junction of the cupule-pair, showing the hairs. (x90) F.S.C. 1200.

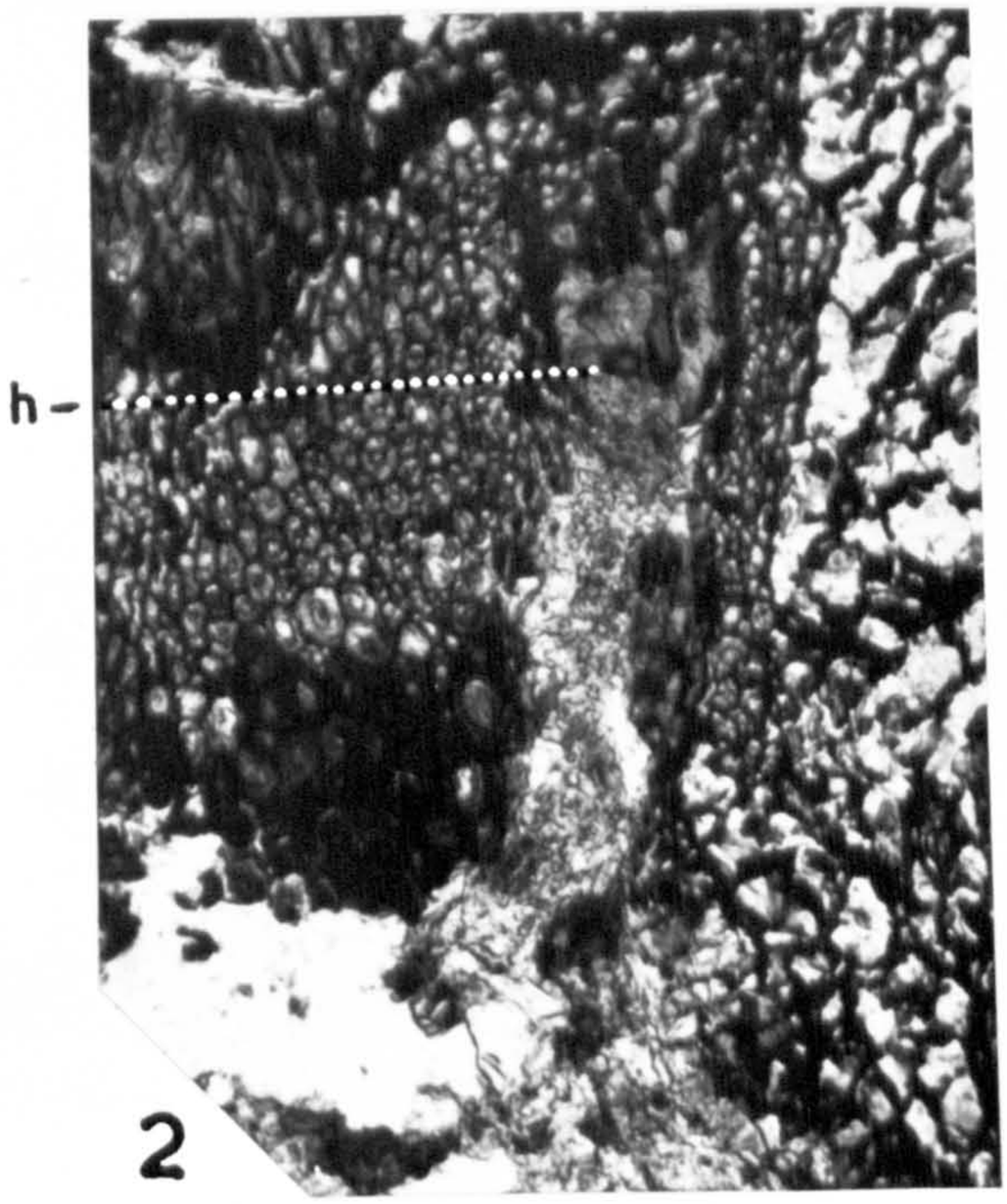
Fig. 3. Longitudinal section of an emergence on the rachis. (x 50) F.S.C. 1211.

Fig. 4. Longitudinal section of the apical part of an ovule. (x 34) F.S.C. 1228.

Fig. 5. Transverse section through the base of the lagenostome. (x 40)

Abbreviations: h, hair; hb, hair-base; la, lagenostome; mm, megaspore membrane; pr, apical process of integument; ps, remains of prothallus with ?archegonial eggs; sa, salpynx; scl, sclerotic layer of cupular lobe.

1



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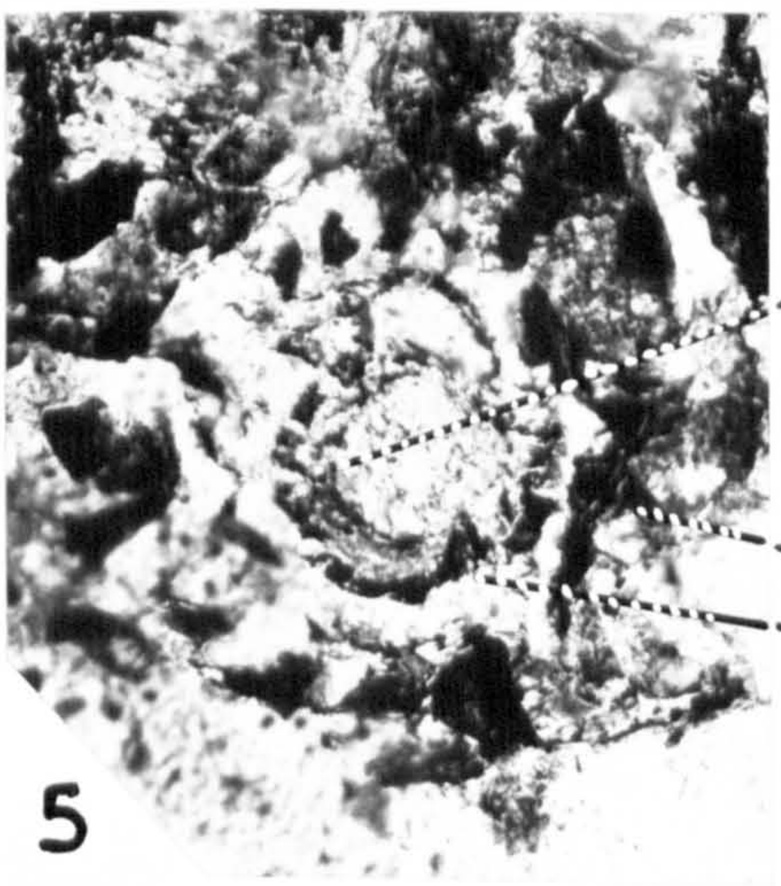

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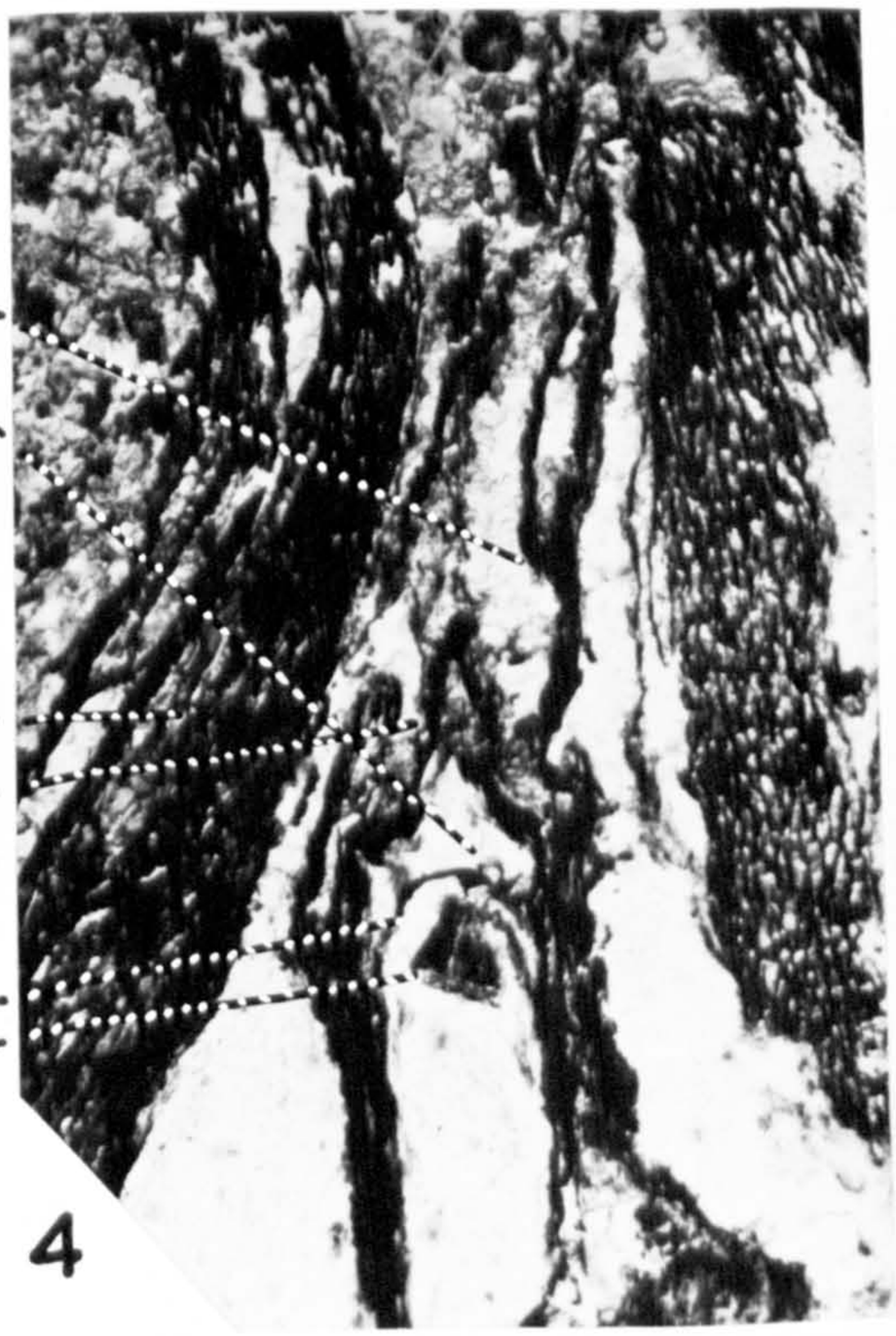

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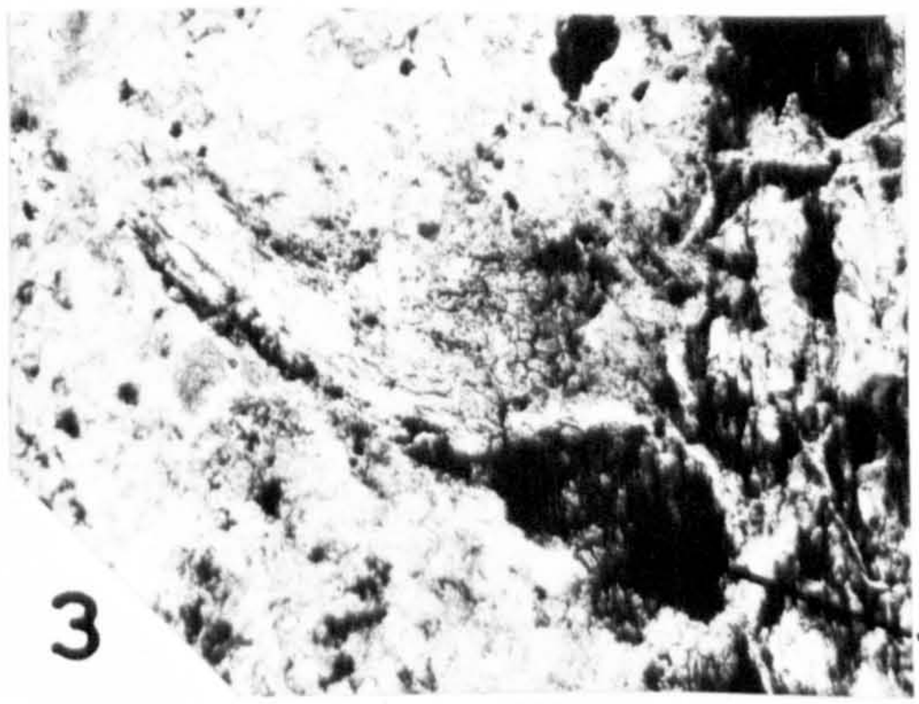

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PLATE 10.

Geminitheca scotica gen. et sp. nov.

Fig. 1. Megaspore membrane. (x 17) F.S.C. 1221.

Fig. 2. Megaspore membrane of an abortive ovule, with part of the nucellus still attached. (x 20) F.S.C. 1373.

Fig. 3. Oblique section of a lagenostome containing pollen. (x 170) F.S.C. 1223.

Fig. 4. Compression of two bunches of microsporangia. (x 1) Pb 2697.

Fig. 5. Compression of several bunches of microsporangia (x2)

Abbreviation: c, contaminant spore.


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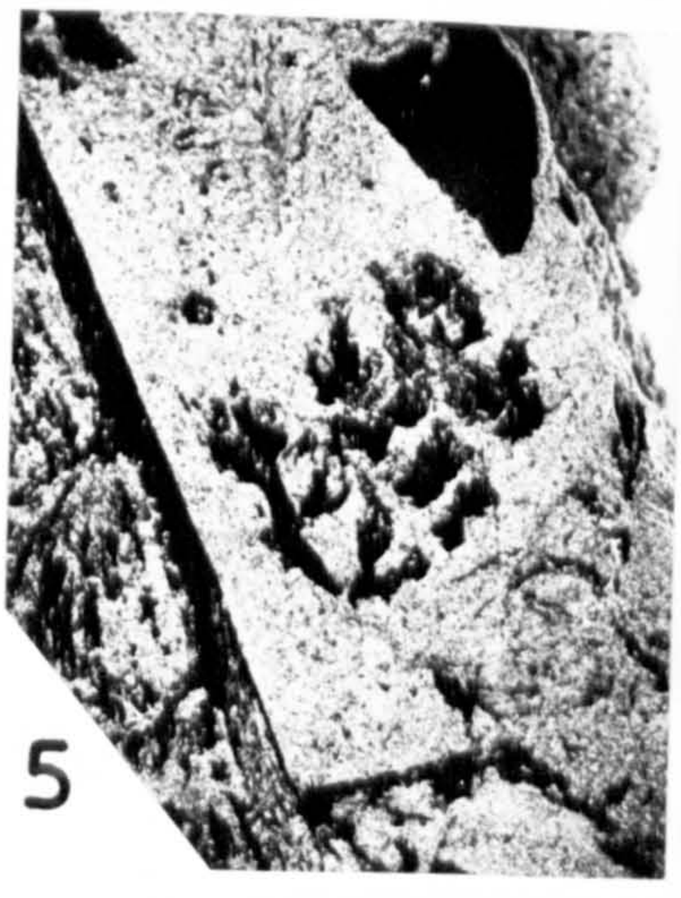
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PLATE 11.

Geminitheca scotica gen. et sp. nov.

Fig. 1. Longitudinal section of a bunch of empty microsporangia. (x 25) F.S.C. 768.

Fig. 2. Pollen mass isolated from the fructification illustrated in Pl. 10, fig. 5. (x 70). F.S.C. 1242.

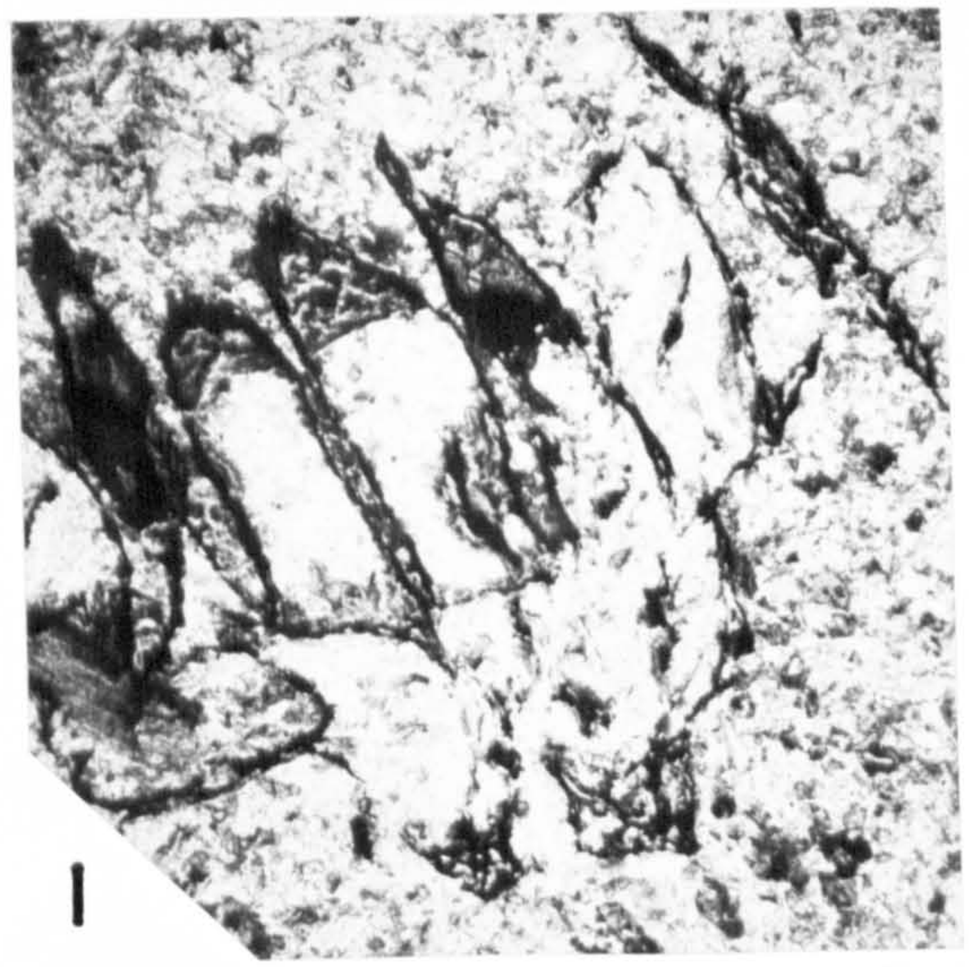
Fig. 3. Pollen grain isolated from specimen Pb 2697 (Pl. 10, fig. 4). (x 500) F.S.C. 1243.

Calathiops trisperma sp. nov.

Fig. 4. Group of ovulate cupules. (x 1) Pb 3326.

Fig. 5. Part of above group. (x 2) Pb 3326.

Fig. 6. Apical part of a megaspore membrane isolated from above specimen. (x 40) F.S.C. 1374.



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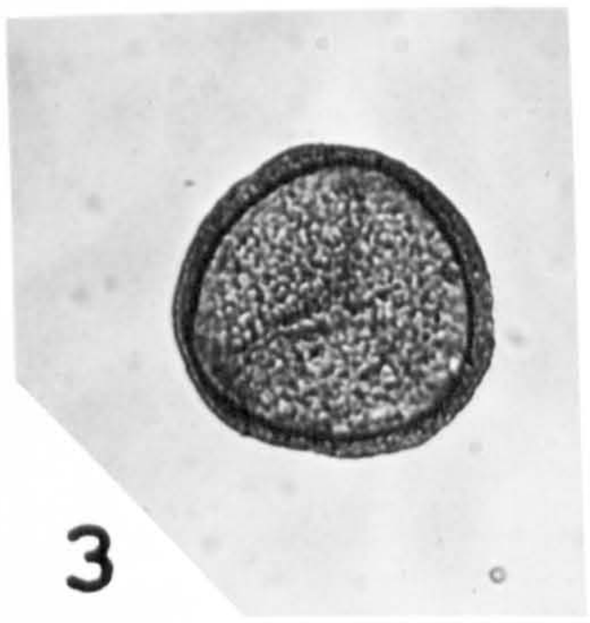

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PLATE 12.

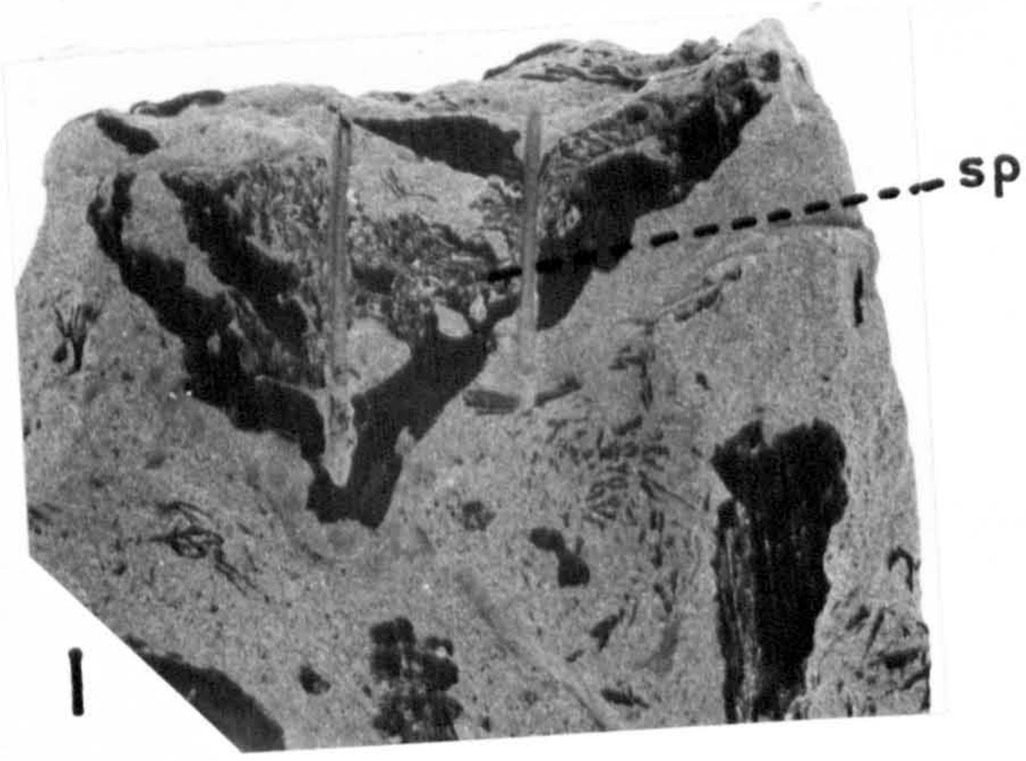
Staphyllotheca kilpatrickensis gen. et sp. nov.

Fig. 1. Compression of rachis bearing bunches of sporangia (x 1) Pb 335.

Fig. 2. Fertile spore from above specimen (x 500) F.S.C. 1377.

Fig. 3. Abortive spore from above specimen (x 500) F.S.C. 1377.

Abbreviation: sp, bunches of sporangia.



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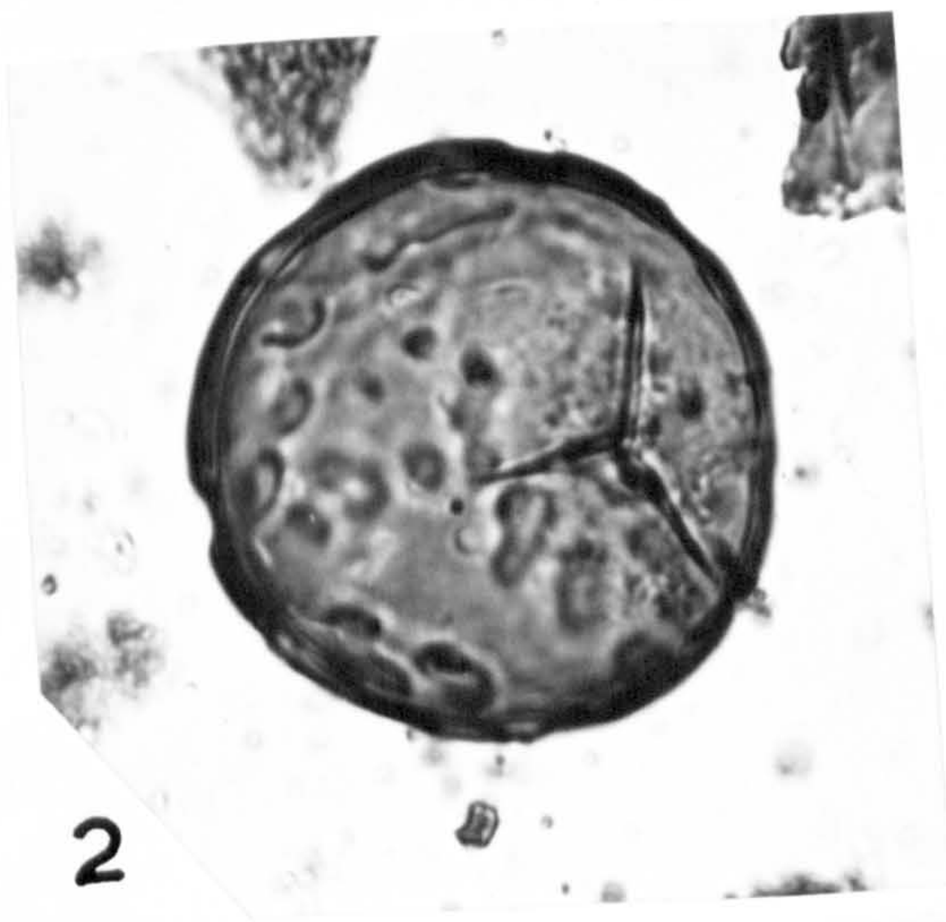

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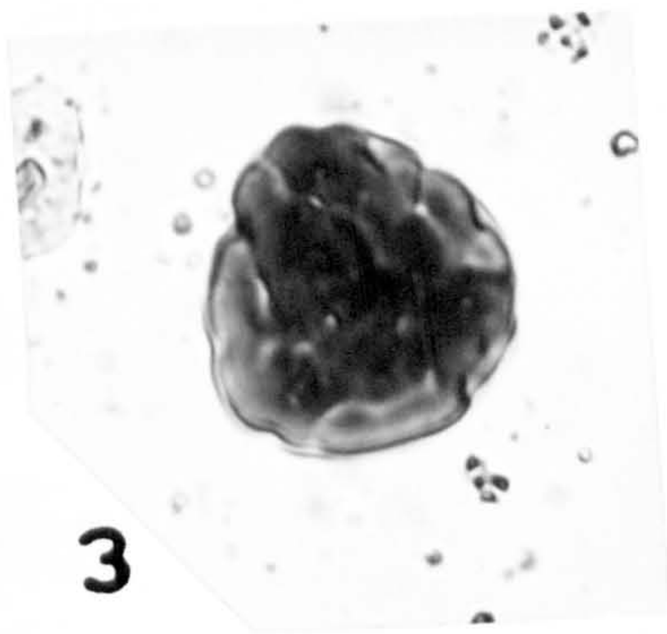

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PLATE 13.

Alcicornopteris hallei Walton

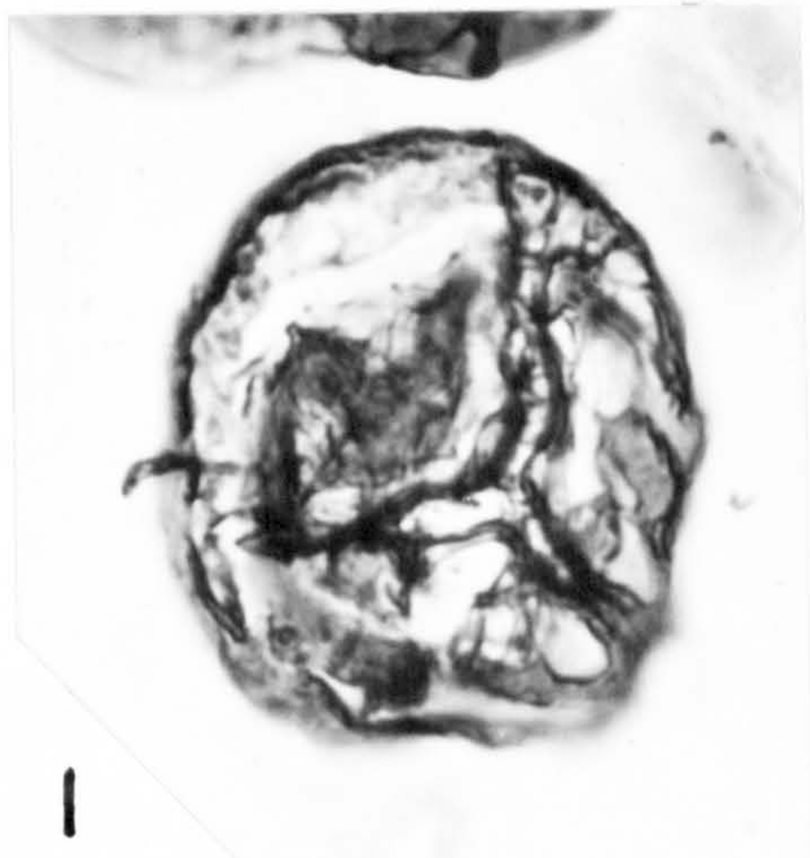
Fig. 1. Spore, type A. (x 500) F.S.C. 1380.

Fig. 2. Distal surface of a spore of type A, showing the reticulate ornamentation. (x 1000) F.S.C. 1380.

Fig. 3. Spore, type B. (x 500) F.S.C. 1380.

Fig. 4. Spore, type C. (x 500) F.S.C. 1380.

Fig. 5. Spore, type D. (x 500) F.S.C. 1380.



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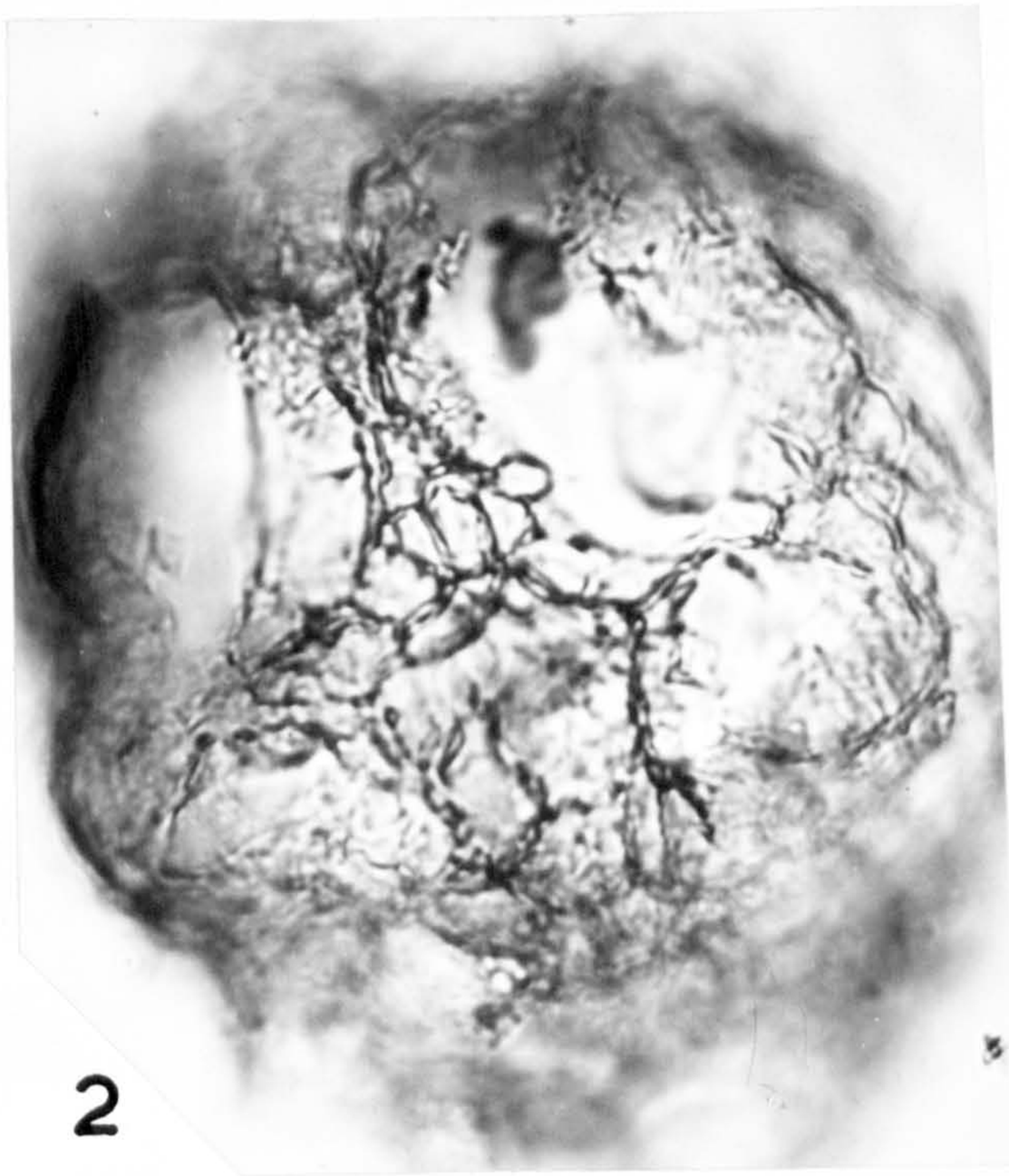

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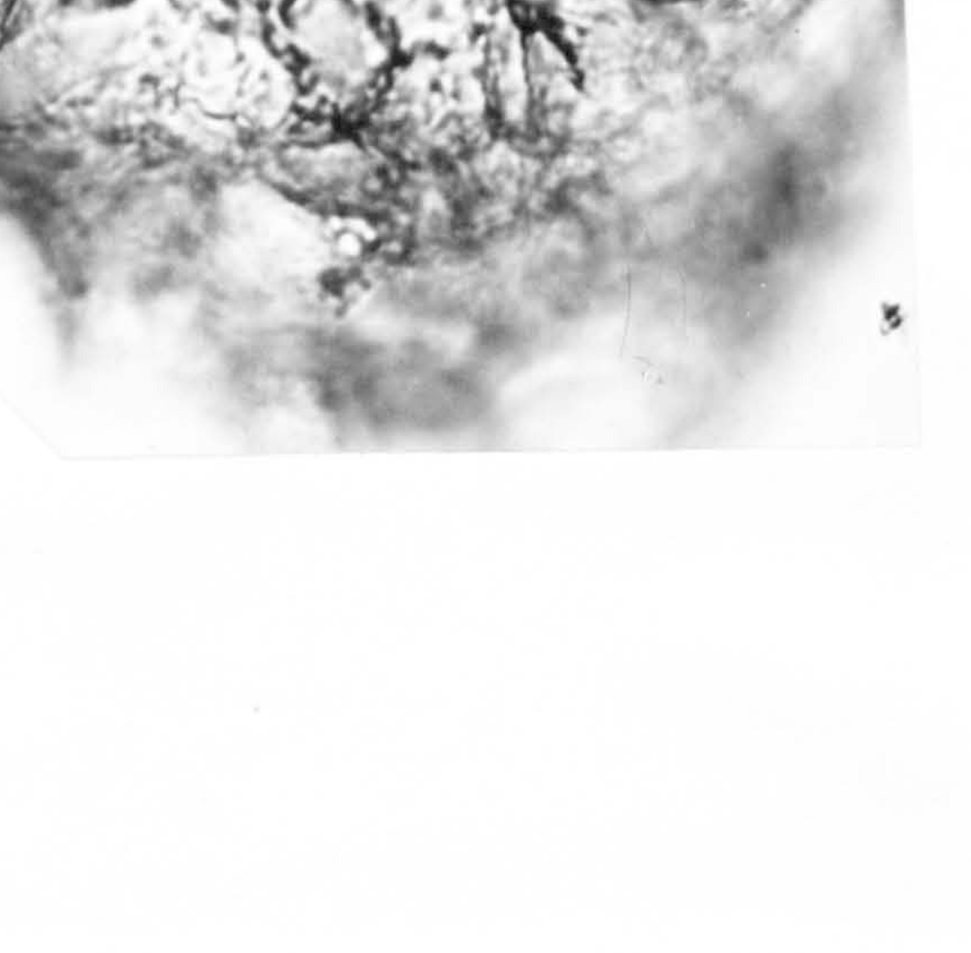

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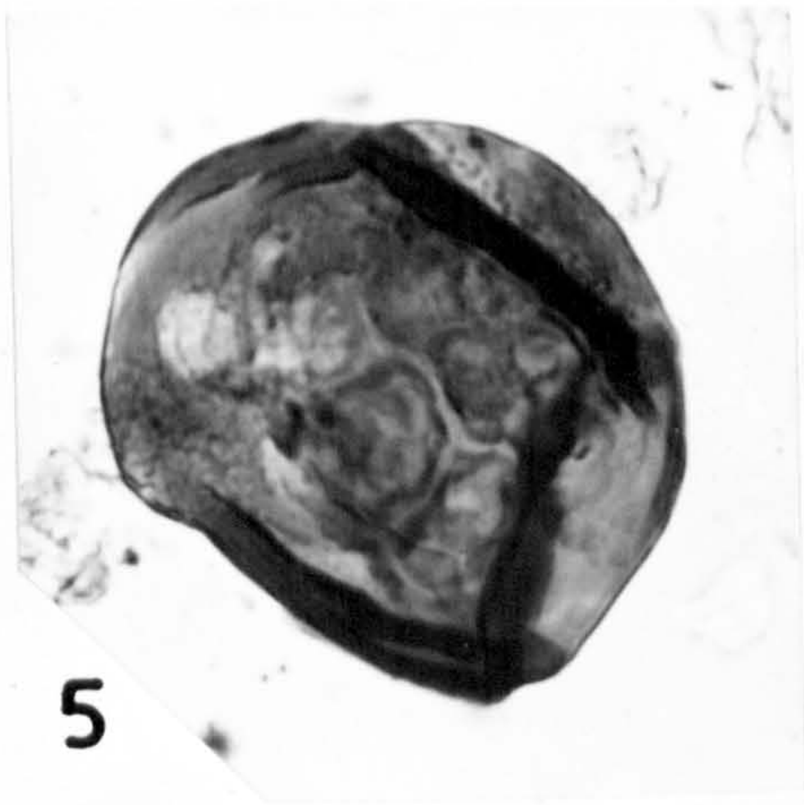

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