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VII—On the Factors which Influence the External Form of Fossil Plants; with Descriptions of the Foliage of Some Species of the Palaeozoic Equisetalean Genus *Annularia* Sternberg

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[PLATES 31 AND 32]

I—ON THE FACTORS WHICH INFLUENCE THE EXTERNAL FORM OF FOSSIL PLANTS

Most writers of general treatises on Palaeobotany give an introductory chapter on fossilization, and this as a rule includes an account of the various kinds of fossil plants and the circumstances under which plants may become incorporated in sediments. The differences between the external form of the fossil and the original plant fragment are not often mentioned in relation to the factors which operate in the production of a fossil. It is often implied that fossil plants of the “incrustation” or “impression” type are produced in much the same way as herbarium specimens. That such a crude analogy does not satisfactorily explain the forms found among fossil plants of this type is obvious to those who have applied transfer methods to the examination of such fossils. In the writer’s opinion, the reason why so little precision has been given to descriptions of fossil-plant forms is that insufficient attention has been paid to the properties of sediments and the role played by the matrix. While many writers recognize that the differences in shape between a fossil and the original plant are due to the compressibility of the plant tissues the writer is not aware of any reference in the literature to the importance of the compressibility of the matrix in determining the form of a fossil embedded in it. It will be shown that the alteration in shape of a plant in undergoing fossilization in many cases may be best described as the result first of the collapse of the plant tissues and second of a more or less uniform vertical strain of the fossil and the surrounding matrix together.

The relative compressibility of the sedimentary matrix and the plant substance in a mass such as coal has been realized as an important factor by KENDAL (1918, p. 463), who has used it to explain the form of shale or sandstone “partings” in coal-seams. As the result of his study of these structures he was led to assume “that in the consolidation of the coal-bearing strata coal itself—in the change from the condition of peat to the hard mineral—undergoes a very much greater reduction in volume than does a sand bed or well compacted mud bed”. He gives good reasons

for believing that in the transformation from peat to coal there may be a compression to one-twentieth the original thickness (KENDAL, 1923, p. 65).

In the discussion of KENDAL's theories it has been suggested by one geologist (*see* under KENDAL, 1918, p. 476) that water-logged peat could not possibly be compressed to such an extent for water is practically incompressible. The incompressibility of water has, however, no bearing on the question, for the mud or sand matrix is porous and the water is probably free to rise up between the particles. The layers of sediment overlying a coal seam may be most aptly compared with a porous piston in which the pores are sufficiently large for the water to escape from the compression chamber but not sufficiently large to allow the particles of sand or mud to escape.

KENDAL (1923, p. 63) points out that freshly deposited mud may contain 90% water and when reduced to the condition of shale may still contain 20% interspace. Thus, according to him, a mud may be reduced at least to one-third its original thickness. On the other hand, a bed of sand deposited in water may suffer scarcely any loss in bulk once it has passed the quicksand stage. Obviously mixtures of sand and mud will have contractions which range between these limits, and muds with a high percentage of organic content will exhibit even greater contractions.

KENDAL (1923, p. 65) showed that owing to the differential compressibility of plant substance and matrix the shape of a mass of sediment enclosed in a coal seam may undergo notable changes in form.

It will be shown that similar principles may be applied to the explanation of the form of fossil plants which may often be regarded as small coal seams enclosed in a sandy or shaly matrix.

Fossil plants may be classified as follows :—

1 *Petrifactions*—(Plantes minéralisées, ZEILLER 1900, p. 9.) The external form, the internal cellular structure, and sometimes the carbonaceous substance of the original plant, is preserved, *e.g.*, coal-balls, silicified plants.

2 *Incrustations* in a restricted sense ("Moules," ZEILLER, 1900, p. 11). The external form of the plant is preserved in the form of a cast. The internal structure is not preserved and usually the carbonaceous substance is completely replaced by inorganic matter, *e.g.*, casts of plants in tuffs (ZEILLER, 1900, pp. 10, 11).

3 *Compressions*—External form of the plant modified by the vertical pressure of the sediment with which it is surrounded. Vertical dimensions of the plant fragment reduced, but the horizontal dimensions usually unchanged. The substance of the plant is usually preserved in the form of coaly matter which sometimes retains some of the original cutinized membranes and a certain amount of the original structure.

4 *Impressions*—The form impressed by the fossil plants of the incrustation and compression type on the matrix are usually termed impressions.

5 *Compactions*—Masses of plant fragments without intervening matrix such as are found in peat. They are compressed by vertical pressure and *deformed by the pressure of one fragment against another*. *E.g.*, Peat, lignite, and coal in seams. A large proportion of the solid substance of the plant is preserved in the form of carbonaceous

residues and may retain some of the original membranes and a certain amount of structure.

This discussion deals with the compression-type of fossil plant. Most fossil plants are in the form of thin sheets of carbonaceous matter which when viewed normally to the bedding plane bear a very close resemblance to the original leaves, stems, roots, and fructifications, but which are, as regards relief, profoundly modified. This type of fossil is usually found in sandstones or shales which have been formed by the consolidation of sediment under its own weight in water. Fossil plants of this type, for which I suggest the name *compressions*, have in the past been named plant-impressions, Pflanzenabdrücken, or impressions végétales. Several palaeobotanists have pointed out the misleading nature of these terms, and Dr. H. HAMSHAW THOMAS has suggested the use of the description mummified plants. While mummified plants is perhaps the best expression so far proposed, it does not suggest the considerable distortion in form which is characteristic of this type of fossil. In a mummy the alteration is generally in the nature of a uniform shrinkage due to the drying up of the soft tissues.

A Theory to Account for the Form of Fossil Plants of the Compression-type

It may be supposed that in the formation of fossil plants of the *compression-type* the plant fragments are embedded in silt or sand under the surface of the water. It is obvious that a plant fragment for dynamic reasons will come to rest in a position in which its centre of gravity is lowest and its shortest axis vertical. The most extended surface will be extended in the bedding plane.

The plant fragments are then covered and surrounded by further deposit of mud. The rate at which this deposit occurs will undoubtedly influence the form of the fossil. If the rate of covering is slow, oxidation and decay processes may remove a large part of the less resistant tissues and little but the cuticle may remain. If sedimentation is rapid, the loss of organic substance is checked, and if the mud contains fine particles such as clay the plant fragments may be very effectively sealed up and their organic substance retained within the epidermal cuticle.

Before considering the further changes that may take place in the form of the plant fragments, it is necessary to consider the changes that take place in the mud. As KENDAL has shown, freshly deposited mud may contain as much as 90% water and may be reduced by partial elimination of its water to one-third its original thickness. This contraction of the mud may be produced by drying, but under the conditions postulated here in a mass of mud of indefinite horizontal extent the water is removed by displacement upwards. If we consider an average particle of solid material in the mud and the forces acting on it we see that the sum of the horizontal components of the forces acting on it due to the water and the surrounding particles is zero. If there is a clear water space below it will sink owing to its own weight in water and the pressure due to particles weighing on it above. Its resultant movement will be a vertical downward movement and water is displaced upwards.

If we now consider the mud deposit as a whole we may regard the solid part of the mud as a sponge. The mud is deposited in a basin formed by an estuary or lake the sides of which support the mass, and any lateral thrust forces are taken up and counterbalanced by the backward pressure of the sides of the basin. Under these conditions it is clear that a spherical mass of sediment will, as it is buried deeper and deeper, assume the shape of a spheroid and, moreover, the major axis of the spheroid will be horizontal and equal to the diameter of the original sphere (fig. 1) as there can be no lateral displacements.

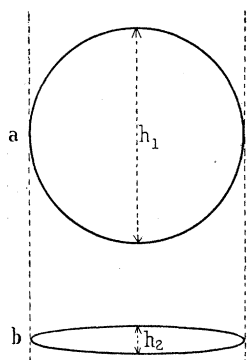


FIG. 1.—Diagram to illustrate the change in shape of a spherical portion of a large deposit of mud in an estuarine or lacustrine basin. The change in shape is due to the weight of the spongy mass of solid particles and to the upward displacement of water. The sphere becomes spheroidal in shape and its major diameter is horizontal and is equal to the original diameter of the sphere.

It is probable that a mud may be compressed ultimately to considerably less than one-third of its original thickness. If the mud consists largely of vegetable particles the first water to be displaced upwards will be the water held in the interspaces between the particles, then as the pressure increases one would expect that the water held by the colloidal particles would tend to be forced out and finally there would be a loss of bulk from the vegetable carbohydrates as the vegetable material approached coal in character and contained a greater proportion of hydrocarbons.

If a relatively large organic fragment such as a leaf is embedded in mud its shape is altered as the mud becomes converted in course of time into shale. From a study of fossil plants in shale it is obvious that the dimensions of the plant fragments normal to the bedding plane are considerably reduced. There is usually no evidence of alteration of dimensions in directions parallel to the bedding plane. This is what one would expect if the plant fragment possessed the same spongy properties as the mud in which it was embedded. As a matter of fact, a leaf may contain as much as 90% of water, and even a relatively solid plant tissue such as wood is exceedingly porous and, when rotten, spongy in character. We might therefore be led to expect that a spherical fragment of plant tissue embedded in mud would become spheroidal just as the spherical element of mud.

Taking as an example of a woody structure a cylinder of wood we may consider the change in shape that will occur when it is embedded with its long axis horizontal in a compressible matrix. If the compressibility of the wood is the same as that of the matrix, the cylinder will finally have an elliptical section when cut transversely to its axis (fig. 1). The major axis of the ellipse will be equal to the original diameter of the cylinder. The writer has measured a number of lignitized *Gleichenia* rachises from the Cretaceous rocks of Greenland which are elliptical in cross-section. The rachises varied from 3 mm to 15 mm in breadth but the ratio of breadth to thickness in all of them lay between the limits 1 : 0.14 and 1 : 0.2. The rachises were

extracted from a mass of fine vegetable debris which would represent a highly compressible matrix.

As another illustration we may take a hollow cylinder of fairly compressible tissue embedded in a less compressible matrix which also fills the hollow of the cylinder. The result which is suggested in fig. 2, *b* is not an unknown type of fossil. The hollow stems of *Calamites*, particularly those with a considerable development of secondary wood, are found in this form (*e.g.*, *Calamites approximatus* BGT. SEWARD, 1898, p. 370, fig. 100). The pith cast covered with a layer of carbonaceous material stands up in relief while at the sides is a border of carbonaceous material representing the wood and other tissues which did not underlie or overlie the pith cavity.

If, on the other hand, we consider the fossilization of a leaf which contains perhaps more than 80% of water we find that another factor comes into play. The examples so far considered have similar upper and lower surfaces when they have acquired their final form. The fossil is convex on both sides and both sides have suffered the same degree of alteration. With a leaf, however, the result is different, the contours of the upper surface are usually more changed than those of the under surface. The soft tissues of the leaf would collapse under the weight of the overlying sediment more readily than the surrounding matrix, and as a result the upper surface of the leaf would sink as the water in the leaf was displaced upwards. Under these circumstances the surface of the matrix underneath the leaf is subjected at first to very little pressure and its form does not alter to any considerable degree during this part of the process. In other words, the upper surface of the leaf subsides as the water is pressed out of it and the substance of the leaf forms a layer over the surface of the matrix which formed a cast of the lower surface of the leaf. (Fig. 3, A and B.) After this stage is reached the compressibility of the concentrated material of the leaf will approximate to that of the matrix and the whole leaf-matrix system may have a uniform compressibility. Subsequent compression due to added deposition of sediment may further change the shape of the leaf by the production of a uniform vertical deformation in the leaf and the surrounding matrix.

The process of fossilization of a leaf from the point of view of its external form may therefore take place in two stages; in the first the leaf collapses on to the matrix surface below it by loss of water, in the second it undergoes with the matrix a practically uniform vertical deformation. The shape of the resulting fossil is principally based on the form of the lower surface of the original plant fragment. Thus the leaf represented in vertical section in the sediment in fig. 3 A_1 first collapses

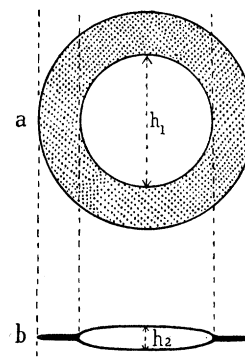


FIG. 2—Diagram to illustrate the approximate result of compression in a sediment of a hollow cylinder or sphere of highly compressible material filled with the sediment. The sediment has undergone a compression to about one sixth its original depth. The core of sediment would only be approximately elliptical in section as the less resistant material round it might allow of some lateral bulging.

to form what is seen in A_2 and then all the vertical dimensions undergo a reduction to about one-quarter, a figure representing the compressibility of the matrix.

It is evident that under the postulated conditions a lateral expansion of the fragment is impossible when the matrix is uniform round about it. The tendency for the fragment to bulge out at the sides under the pressure of the overlying matrix will be prevented by the resistance of the matrix at the sides. The pressure at the sides will always be greater than that on top of the leaf owing to the greater depth at the sides.

The compressibility of a sediment will depend on the size and shape of its particles and the amount of water and compressible organic particles contained in it. A sandy matrix will be relatively incompressible, but a mud or silt containing much water and a high organic content will be very compressible. Corresponding to

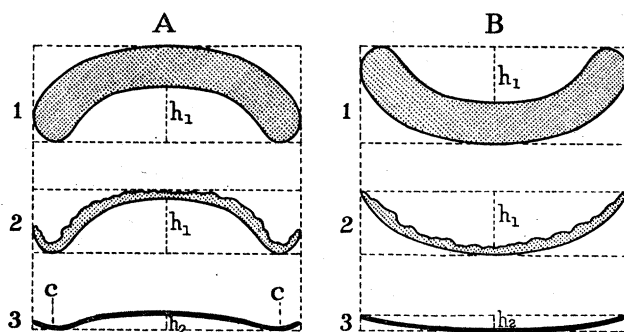


FIG. 3—Diagrams representing the compression in a sediment of a leaf with a concavo-convex lamina. In A_1 the leaf is buried with the convex surface up and in B_1 with the concave surface up. A_2 and B_2 represent the effect of the collapse of the soft tissues as the water in them is displaced upwards and A_3 and B_3 the final form of the fossil after the vertical compression of the sediment is complete. A compression border (c) is formed in A_3 .

these differences in the nature of the matrix we usually find a relatively high degree of relief in fossils preserved in sandy rocks or in rocks with a low percentage of organic or humic material, while in fine muds with a large amount of organic matter the greater compressibility usually results in the fossils having a low degree of relief. This is illustrated in fig. 3, A and B, where it is obvious that the greater the compressibility of matrix the smaller h_2 will be and the flatter the resulting fossil.

The following examples illustrate peculiarities exhibited by some fossil plants of the compression type which may be most readily explained by supposing that fossilization has taken place in the manner suggested by the above theory.

1 *The Shape of Leaf Margins*—In compressions of leaves belonging to the form-genera *Alethopteris*, *Neuropteris*, and *Pecopteris* the lamina of a leaflet was, we must suppose, often convex or concave in shape and there is frequently a narrow, flat border round the margin in the fossils. This border is of the same carbonaceous substance as the rest of the lamina and is surrounded by the cuticle. It is set at an

angle to the curved part of the lamina and may be termed a *compression border*. It will be seen by reference to fig. 3 (A and B) that it is most likely to form if the original leaflet was orientated in the bedding plane with its convex surface uppermost. This border would probably not be formed if the leaflet was situated with the convex surface underneath. If a hand specimen of rock has a leaf on it showing this border it should be possible to determine the upper and lower side of the specimen in relation to the bed of rock from which it had been extracted. If such a fossil were found in position in the rock stratum it would be possible to determine whether the stratum was normally orientated or whether as a result of geological disturbances had been inverted. Moreover, the width of the border on a fossil leaf is a measure of the thickness of the original leaf-lamina.

Another example of a compression border is found in inrolled leaves. The writer

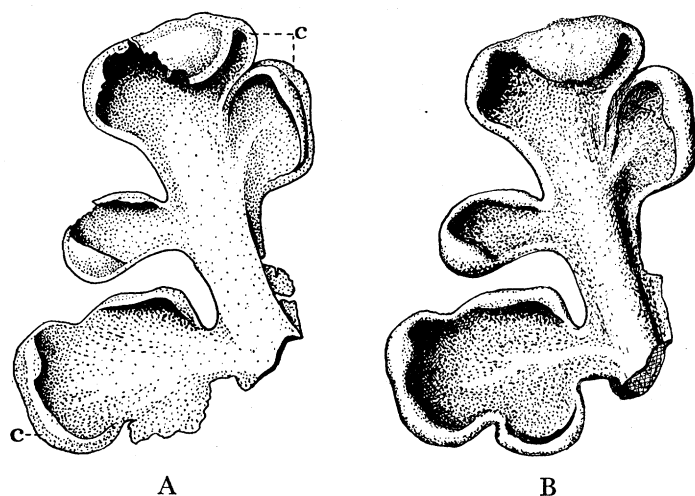


FIG. 4—A, drawing of part of a transfer preparation of *Sphenopteris nummularia* (Walton Collection 35) showing a clearly defined compression border at c, c. B, reconstruction of the same specimen before fossilization.

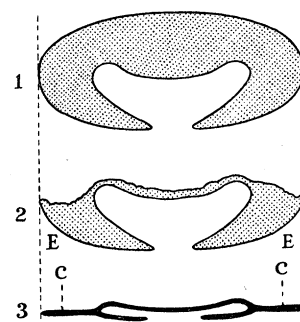


FIG. 5—Diagram to illustrate the effect of vertical compression in sediment on a leaf with inrolled margins. c, compression border.

has in his collection a transfer preparation of *Sphenopteris nummularia* (fig. 4A) in which the leaflets have in vertical section approximately the form seen in fig. 5₃. From the appearance of the specimen the leaflets undoubtedly belonged to an immature frond with inrolled leaf margins. The presence of the flat border (c, c, figs. 4 and 5) can be best explained as the result of vertical compression of a leaf such as that shown in fig. 5₁. Here, however, after the upper part of the leaf had collapsed the pressure of the overlying matrix was transmitted by the core of sediment in the hollow of the leaflet to the matrix below the centre of the leaflet. This was pressed downwards so that the matrix on either side at E and E rose relatively and compressed the leaf to the form seen in fig. 5₃.

Other examples of leaf forms modified in fossilization will be given in the descriptions of species of *Annularia* which follow.

II—DESCRIPTIONS OF THE FOLIAGE OF SOME SPECIES OF *Annularia* STERNBERG*

Although in the living genus *Equisetum* the leaf is small and ineffective as a photosynthetic organ in the Palaeozoic representatives of the Equisetales the leaves were well developed and undoubtedly represented the main photosynthetic part of the plant. Of the three more important form-genera of Palaeozoic Equisetalean plants which are based on the form of the leaf and leafy shoot, *Asterophyllites*, *Annularia*, and *Lobatannularia*, *Annularia* is the most abundant. It reaches its maximum abundance in the Upper Carboniferous where it is a familiar constituent of most Coal-Measure floras.

A large number of species of *Annularia* have been founded on the outline form of the leaves and shoots of specimens preserved in the form of compressions. The shape of the leaves and their manner of arrangement on the shoot are practically the only criteria which have been used in distinguishing one species from another. As a result some of the species are exceedingly ill defined and the nomenclature and synonymy of the species in the genus are very involved. A good deal of confusion is due to the fact that in the fossil Equisetales as in the fossil Lycopodiales the leaves on the different orders of branches on one and the same plant may show considerable differences. The leaves on the main axis or large branches of *Annularia sphenophylloides* ZENKER are quite different in size and shape from those found on the ultimate branches. The best account of the genus *Annularia* and the systematic relations of its species is given by JONGMANS (1911 and 1914, pp. 5, 235).

Of the internal structure of plants belonging to this genus practically nothing is known. CARPENTIER (1924) has described some structurally preserved leaves from the Permian of Autun or the Stephanien of Grand Croix (Loire) which he compares with an *Annularia* of the *stellata* type. HOLDEN (1935, p. 239) is, however, of the opinion that these leaves may not belong to Equisetalean plants in view of the absence of lignified bars on the stomatal guard cells. Certain authors have described as surface features certain structures which, as will be shown later, are expressions of internal structures. Our knowledge of *Annularia* falls far behind our knowledge of the genus *Asterophyllites*, the internal structure of which has been worked out in considerable detail in some species by HICK (1895, p. 179) and later by THOMAS (1911, p. 51).

Lobatannularia is only known from incrustations.

JONGMANS (1911, p. 235) describes the genus *Annularia* as follows: "Leaves linear, lanceolate, or spatulate, uninerved at the base and fused to a more or less distinct sheath. The individual leaves do not all make the same angle with the stem but lie in the same plane with the branches and the stem. The leaves of a whorl may not always be of the same size, the lateral leaves may be longer than the upper and lower ones." He points out that it is not always possible to say for certain

* A preliminary account of some of the forms described in this memoir was given at the meeting of the British Association in 1925.

that a particular species of *Annularia* represents the foliage of only one type of Calamitean stem and that the recognized species of *Annularia* are in most instances probably merely type-assemblages.

JONGMANS and other authors state that in *Asterophyllites* the leaves are attached separately at the node and that in *Annularia* they are joined to a sheath, but Dr. JONGMANS has told the writer recently that this distinction is not reliable and that it is possible that there is no sharp separation in this respect between the two genera *Annularia* and *Asterophyllites*. In some species of *Asterophyllites* the swollen node when flattened in a compression closely resembles a sheath, while in some species of *Annularia* it is impossible to distinguish a distinct sheath. The form of the leaf-mosaics found in these Palaeozoic genera has been fully discussed by HALLE (1928, p. 230) and will not be dealt with here. Recently a new genus *Carpannularia* has been proposed by ELIAS (1931, p. 116) for some American examples of the species *Annularia stellata* Schl. with which he found associated structures which he has interpreted as seeds. Some of these seed-like bodies he found attached to the specimens he describes. He raises the question as to the possibility of these structures being tubers but finally decides that they are seeds. The writer does not consider that the evidence justifies him making this decision. There is in the first place no evidence apart from their ovoid shape to support the view that they are seeds and they do not form part of a cone, as one might have expected on morphological grounds in a seed-bearing Equisetalean plant. On the other hand, they bear a very close resemblance to the tubers of *Equisetum* and they are borne in a corresponding position on the shoot. It is well known that the shoot of *Equisetum* is exceedingly easily influenced by environmental conditions; branches and roots which would not normally develop on an aerial shoot beyond the stage of a small bud at the base of a leaf sheath may be caused to develop by burying the shoot in the soil or enclosing it in a damp atmosphere. The description by ELIAS of the "seeds" as having the form of thin shell of carbonaceous matter is very reminiscent of the exhausted tubers of *Equisetum maximum* L. It is by no means inconceivable that shoots of *Annularia stellata* might have responded to burying or to the influence of a damp atmosphere by producing tubers from dormant buds at the nodes. Similar tuber-like bodies are found associated on the same slab of shale with *Annularia stellata* in a specimen in the Kidston Collection (No. 310) in the Geological Museum at South Kensington.

The investigation, of which the results are given here, was undertaken in an attempt to get more precise information about the form and structure of the leaves and shoots of *Annularia*. Some interesting and hitherto unobserved features of some of the common species have been discovered, but it has been found in addition that some of the forms that have been included under one specific name are certainly aggregates of very diverse forms.

During the course of this investigation a consideration of some of the forms assumed by leaves as a result of the factors which influence the shape of a plant fragment during fossilization led the author to make certain generalizations as to

the manner in which forces, to which plant fragments are subjected during sedimentation and fossilization, determine the shape of the resulting fossils (*see above*, p. 221).

During the last ten years the writer has had frequent opportunities of obtaining specimens of *Annularia* and has pleasure in acknowledging the friendly assistance which he has received from Professor Dr. P. KUKUK of the Westfälische Berggewerkskassen, Bochum, Dr. R. CROOKALL, and Dr. EMILY DIX. Some of the material which they have provided has been of great value in this investigation. The material which the writer has been able to obtain from various sources has been subjected to detailed examination by means of the transfer method (WALTON, 1923, p. 379) and infra-red photography (WALTON, 1935, p. 265). As the result of these investigations it has been possible to increase our knowledge of the peculiar morphological features of the leaves of this genus and to revise and improve considerably the definitions of some of the more important species.

Description of Species of Annularia

1—*Annularia sphenophylloides* ZENKER—(Figs. 8, 9, Plate 31.) The writer accepts the synonymy of this species given by JONGMANS (1914, p. 35) without criticism. It is one of the easily identified species and no one will doubt the correctness of the identification with it of the specimens described here. They are quite normal examples of the species. The ultimate branches and leaf whorls illustrated in figs. 8 and 9, Plate 31, represent portions of the main photosynthetic system of the plant. The leaves which were attached to the stems and perhaps larger branches were of a different type, lanceolate and with long points (JONGMANS and KUKUK, 1913, p. 47). The leaf-whorls on the ultimate branches consist of from 12 to 18 spatulate leaves 3 to 10 mm long and from 1 to 3 mm wide at the widest part. The apex of each leaf is rounded but bears a distinct mucro. The leaves are all arranged in the plane of the branch and thus form with it a dorsiventral shoot. In examples of this species the leaf lamina is rarely flat, it is usually convex or concave. Owing to the dorsiventral orientation of the leaves on the shoot they are all spread out in one plane and, judging from all the specimens so far examined, the convex surfaces of all the leaves on a shoot faced the same way. It is impossible to decide from the evidence whether the convex surface represents the abaxial surface or not. This concavity (or convexity) of the leaf blade must have been a very pronounced feature in the living plant for even in the fossils preserved in shale which have been subjected to considerable vertical compression the concavity is still quite pronounced.

In transfer preparations (fig. 9, Plate 31) further details may be observed. There is a distinct, narrow midrib at the base of the leaf which in the broadest part of the translucent, brownish lamina widens out to form a very characteristic expansion (fig. 9, *t*, Plate 31). This feature sometimes appears as a concavity on the convex side of the leaf on the rock and, as a result, if the leaf has been only partly freed from the matrix the apex of the leaf appears to be emarginate (*e.g.*, JONGMANS and KUKUK, 1913, fig. 7, Plate 21). ZEILLER (1888, p. 388), no doubt misled by this,

states that the leaves of this species are sometimes acuminate, sometimes emarginate. The concavity in these cases is no doubt the result of the collapse of the tissues constituting the vein expansion. The expansion of the midrib diminishes at the apex of the leaf and the vein appears to be continuous with the mucro. There is evidence that occasional simple hairs were present on the leaf, particularly round the apex (fig. 9, *h*, Plate 31). The bases of such hairs may be seen as small projections on the sides of the midrib expansion (fig. 9, *h*₂, Plate 31). Some small lighter coloured spots are present on the lamina (fig. 9, *s*, Plate 31) and it is possible that they may represent the positions of stomata. In other specimens of possibly the same species which were no doubt subjected to somewhat different conditions during decay and during fossilization, the lamina is not uniformly translucent and in transfer preparations examined by transmitted light small elongated darker coloured bodies are visible (fig. 10, *c*, Plate 31) which give the leaf a hairy appearance. It is highly probable that the "hairs" described by HALLE (1928, p. 239; Plate I, figs. 7, 8, 9) in a specimen of *Annularia sphenophylloides* are a slightly different expression of the same structural peculiarity. This hairy appearance which is seen on several species when examined even without transfer will be discussed later in relation to some other species in which the nature of these structures is more evident.

Such pronounced expansions of the vein or midrib are not found in the other species of *Annularia* which have been examined in this way. It will be noticed, however, that there is a slight expansion of the end of the vein in a specimen of *Annularia stellata* shown in fig. 29, Plate II, and in the specimen of *Annularia pseudostellata* POTONIÉ figured by JONGMANS and KUKUK (1913, fig. 4, Plate 21) the presence of such an expansion is suggested by the appearance of the ends of the leaves. In living plants similar expansions are also found; they are not uncommon in the Ferns, and it is to be particularly noted that there is a distinct expansion in the strand of tracheids in the free part of the leaf in *Equisetum limosum* L. (other species of *Equisetum* have not been examined for this feature). Terminal expansions of veins are usually associated with the excretion of water in drops through special stomata. In the early morning shoots of *Equisetum* may often be found with a drop of water on the tip of each leaf. It is probable, therefore, that the expansions of the veins in *Annularia sphenophylloides* were related to hydathodic activity.

2—*Annularia galioides* LINDLEY and HUTTON sp. (fig. 11, Plate 31)—This species has a similar leaf mosaic to *A. sphenophylloides*, but there are larger gaps between the ends of the leaves owing to the more lanceolate shape of the leaf. There are as a rule about eight leaves in a whorl. In some specimens with small leaves the leaves are so broad that they are almost circular in outline. A mucro has never been observed on the rock. In transfer preparations the lamina is partly translucent and elongated darker structures are present which appear to be of a similar nature to those seen in some specimens of *A. sphenophylloides*. These darker inclusions in the lamina for the most part run parallel to the margin of the leaf or to its long axis and are most concentrated along the centre of the leaf. They converge in the tip of

the leaf and seem to form a short rather ill-defined mucro which did not apparently lie in the plane of the leaf for it does not appear in hand specimens. These observations confirm JONGMAN's suggestion that the apparent hairiness of this species might not be due to hairs but to some internal cell network (JONGMANS, 1911, p. 258).

The specimen figured here (fig. 11, Plate 31) came from approximately the same locality as Lindley and Hutton's type of the species (LINDLEY and HUTTON, 1833, Vol. I, p. 79, fig. 2, Plate 25).

3—*Annularia Jongmansii* sp. nov. (fig. 6, and figs. 12, 13, 14, 15, Plate 31)—This species is fairly common in the Upper Carboniferous of the Central Valley of



FIG. 6—*Annularia Jongmansii* sp. nov. Part of a penultimate branch bearing part of several ultimate branches. Nat. size. (Pb. 1131, Hunterian Museum, University of Glasgow.)

Scotland. I have also seen a specimen from a boring from the Dutch coal-fields in the Kidston Collection, and Dr. JONGMANS tells me that he has found it frequently in the Dutch Limburg coal-field. He has recorded it in manuscript under the name *Annularia radiata* forma *hirsuta*. In outline form the leaves and shoots are closely similar to those of *Annularia radiata* BGT. and more especially with *Annularia fertilis* STUR and *Bechera dubia* STERNB. which most authors regard as the same species as *A. radiata* BGT. It is probable that several of the plants recorded in the literature of fossil-plants as *A. radiata* belong to *A. Jongmansii* which may have a very extended geographical distribution in the Upper Carboniferous. One other quite distinct type of leaf which from its appearance on the rock would have in the past been identified as *A. radiata* will be described later. It is clear, therefore, that *A. radiata* can now only be used as a group name for specimens

which have the outline form of the plant which has been called *A. radiata*.

In *Annularia Jongmansii* (fig. 6, and figs. 12, 13, 14, 15, Plate 31) the penultimate branches have inter-nodes about 20 mm long and the ultimate branches are arranged distichously. The inter-nodes on the ultimate branches are about 9 mm in length. In fig. 6 a specimen with parts of six ultimate branches is shown in outline. It is clear from the regularity of the branches and leaves that the ultimate branches and leaves were originally in one plane, the foliage forming a characteristic mosaic. The leaves vary from 4 to 10 mm in length and from 1 to 2 mm in width at the broadest part, and are arranged in whorls of from 9 to 13. Each leaf is slightly spatulate with a median midrib. A mucro is rarely seen on the stone.

In transfer preparations the leaf is usually partly translucent (figs. 12, 13, Plate 31) and the "hairy" appearance is most pronounced. The specimen shown in the figure was originally on black coaly shale and showed the "hairy" appearance on its surface even before transfer. From a study of several transfer preparations of this species it is clear that in all probability each leaf bore a distinct mucro (figs. 12, 13, Plate 31). In the relatively translucent lamina is a conspicuous system of elongated darker structures of cellular dimensions which are obviously homologous with the dark inclusions found in the lamina of *A. sphenophylloides* and *A. galioides*. It is these darker bodies in the substance of the lamina which cause the carbonaceous film of the lamina to be thicker where they are present and appear to be covered with hair-like structures. These dark bodies in the lamina have never been found projecting beyond the translucent part when the margin is complete (fig. 13, Plate 31), they are never separated by matrix from the lamina at any part of the leaf, and have not as yet been found lying loose in the matrix. If fig. 15, Plate 31 is examined, it will be seen that they have blunt ends and that they are usually grouped in series. The form and arrangement of these structures clearly suggests that they are for the most part not on the surface of the lamina but are internal. They are almost certainly to be regarded as cell inclusions. True hairs occur on the plant and they are present on the internodes (fig. 13, *h*, Plate 31) and at the nodes (fig. 14, Plate 31). All these undoubted hairs are, however, of a translucent brown colour and not like the structures in the lamina of the leaf.

Dark coloured carbonaceous cell contents of a similar shape to those found in the leaf of *Annularia Jongmansii* occur in the leaves of *Asterophyllites* found in petrifications (THOMAS, 1911, pp. 60–80). In *Asterophyllites*, according to THOMAS, these dark inclusions are found in a few of the epidermal cells, which are elongated in a direction parallel to the long axis of the leaf, in elongated cells of the mesophyll which are orientated with their axes at right angles to the long axis of the leaf, and in large numbers in the elongated cells forming the bundle sheath of the leaf. If now the specimen of *Annularia* sp., of which a transfer preparation is shown in figs. 16, 17, Plate 31, be considered it will be noticed that the distribution of dark cell contents in the flattened incrustation corresponds very closely with the arrangement found in *Asterophyllites*. In other words, if a leaf of *Asterophyllites* was vertically compressed the cells with dark contents would form a similar pattern to that seen in fig. 17, Plate 31.

The leaves in *A. Jongmansii* appear to be united to a short collar or sheath at the node (fig. 14, Plate 31). In some transfer preparations the rings of thickening of the protoxylem tracheids in the inter-nodes are visible (Walton Collection, Slide 429).

Annularia Jongmansii sp. nov.

Diagnosis of Species—Leaves spatulate, from 10 mm to 5 mm in length, and from 1.3 mm to 0.5 mm broad, mucronate. The leaves number from 9 to 13 in a whorl and lie in the same plane as the branch which bears them. The leaves in a whorl are of approximately equal length. The ultimate branches of the plant are borne distichously on the penultimate branches. The branches are indistinctly

ridged longitudinally. The inter-nodes on the ultimate branches are about 9 mm long, on the penultimate branches they are about 20 mm long. Simple hairs are present on the inter-nodes and nodes. Under certain conditions of preservation a pronounced reticulum of dark cell contents is visible in the lamina of the leaf.

Westphalian Series, Upper Carboniferous :

Western Europe

Type Specimen ; Walton Collection, Slide 423

4—*Annularia radiata* BGT. forma (figs. 16, 17, Plate 31)—The specimen, of which the transfer is shown in fig. 16, consists of an ultimate branch showing part of four leaf whorls. The leaf is lanceolate and mucronate. The reticulum of dark cell contents is very conspicuous and reference has been already made to it in the account of *A. Jongmansi*.

This plant evidently falls into the *radiata* group on the basis of the outline of the leaf. It seems to be distinct from *A. Jongmansi* in which the leaf is slightly spatulate. Westphalian Series. Scotland.

5—*Annularia fimbriata* sp. nov. (figs. 18–21, Plate 32)—It is highly probable that this species may be at a later time recognized in specimens which have been referred to *Annularia radiata* BRONGNIART and that without the preparation of a transfer it may be impossible to distinguish it from the forms usually placed in BRONGNIART'S species solely on the strength of outline form. The description of this new species is based on two sets of specimens one from Lancashire given to me by the late Dr. KIDSTON as specimens of *A. radiata* BRONGNIART "vera," the other from near Bristol, given to me by Dr. CROOKALL.

When examined on the rock these specimens appeared to possess simple, nearly linear leaves with a smooth surface. Judging from the somewhat fragmentary material, there must have been about fifteen leaves in the whorl. The leaves narrow slightly at the base and taper off towards the apex. No complete leaf tips were represented in the Lancashire specimens, but in the Bristol specimens a distinct mucro is present on the complete leaves. In transfer specimens these characters are seen very distinctly (fig. 18, Plate 32), and it appears as if the leaves were joined to a narrow collar or sheath at the node (fig. 18, *s*). This collar might be merely the flattened cortical tissues of the slightly swollen node.

The surface of the leaf exposed by the transfer process is, however, very different from that seen on the untransferred specimen. In the transfer there is a shallow median groove about one-third the breadth of the leaf which extends from near the base up to near the apex. Attached to the two sides of the groove and extending over it are short hairs (fig. 19, *r, r*, Plate 32) the edges to which the hairs are attached slightly overhang the groove. The floor of the groove is slightly convex, the convexity representing the midrib of the leaf. One specimen was obtained which had been exposed by the matrix splitting over the grooved surface of the leaf. The edges of the groove with their rows of hairs were removed on one-half of the matrix and the

rest of the leaf consisting of the greater part of the lamina on the other part of the matrix. A transfer preparation from the part of the matrix with the edges of the groove was made (fig. 20, Plate 32). It shows the edges of the groove and the two rows of hairs (*rr*) and in places small fragments of the coaly lamina. Occasional hairs were present on the surface of the floor of the groove (fig. 21, *h*₂, Plate 32). All these hairs appear to be unicellular.

The simplest way to interpret these compressions is by supposing that the original leaf was gutter-shaped and had a cross-section like that suggested in fig. 5. It should be noted that in fig. 19, Plate 32, there are flat borders (*ff*) on the outer sides of the rows of hairs, the significance of this feature is discussed on p. 225.

Annularia fimbriata sp. nov.

Diagnosis of Species—Leaves linear, lanceolate, terminating distally in an acute apex which is prolonged into a distinct mucro. The edges of the leaf are inrolled and each edge has a series of short simple hairs which project over the concave surface of the leaf. Simple hairs are also found occasionally on the surface of the concave side of the leaf and at the nodes. The leaves are between 7 and 15 mm in length and from 1 to 2 mm broad and number from 15 to 20 in each whorl. The leaves lie in the same plane as the ultimate branch which bears them.

This species has so far only been recognized in specimens from the Westphalian Series in the Bristol and Lancashire coal-fields.

Type Specimen ; Walton Collection, Slide 396

6—*Annularia stellata* Schlotheim. sp. (figs. 24–29, Plate 32).

(For synonymy see JONGMANS, 1914, p. 41. *Carpannularia americana* ELIAS is also a synonym.)

Annularia stellata, judging by the figures which have been published by many authors, is a very variable species. It is probable that several of the forms are merely different types of preservation of the same species. In order to understand how such variety in form is found in fossils belonging to possibly the same species of plant the suggestions made in the first part of this paper (p. 224) should be considered.

A typical example of *A. stellata* SCHLOTH is shown in fig. 24, Plate 32. Parts of two leaf whorls are shown. The leaves are convex with a slightly sunken groove down the centre (fig. 25, Plate 32). The surface of this depression is flat and is marked with small projections (not shown in the figure) which probably represent the points of attachment of hairs (*cf.* POTONIÉ, 1893, Plate XXIV, fig. 6). By cutting into the shale it was possible to see the form of the cross-section of the compression. A transfer preparation was made from three of the leaves shown in fig. 25. As one would have expected from the cross-sectional view, the surface so exposed was concave with a slight median elevation corresponding to the groove seen on the original specimen (fig. 25). In addition, there is a small projecting ridge on each side of the central elevation. The transfer preparation which was opaque and black was then photographed by transmitted, infra-red light (fig. 26, Plate 32). The infra-red

photograph shows three dark lines in the lamina; the central one is evidently a structure which is not revealed elsewhere and is undoubtedly the vascular strand of the leaf, or perhaps the xylem strand, while the lines on each side of it are the ridges to which reference has already been made. The hypothetical reconstruction of the cross-section of the leaf is shown in fig. 7, and it will be noticed that the suggestion is made that the ridges of carbonaceous material which appear on each side of the vein represent the sides of the midrib as distinct from the vein itself. An almost complete leaf apex is shown in figs. 25, 26, Plate 32, and there appears

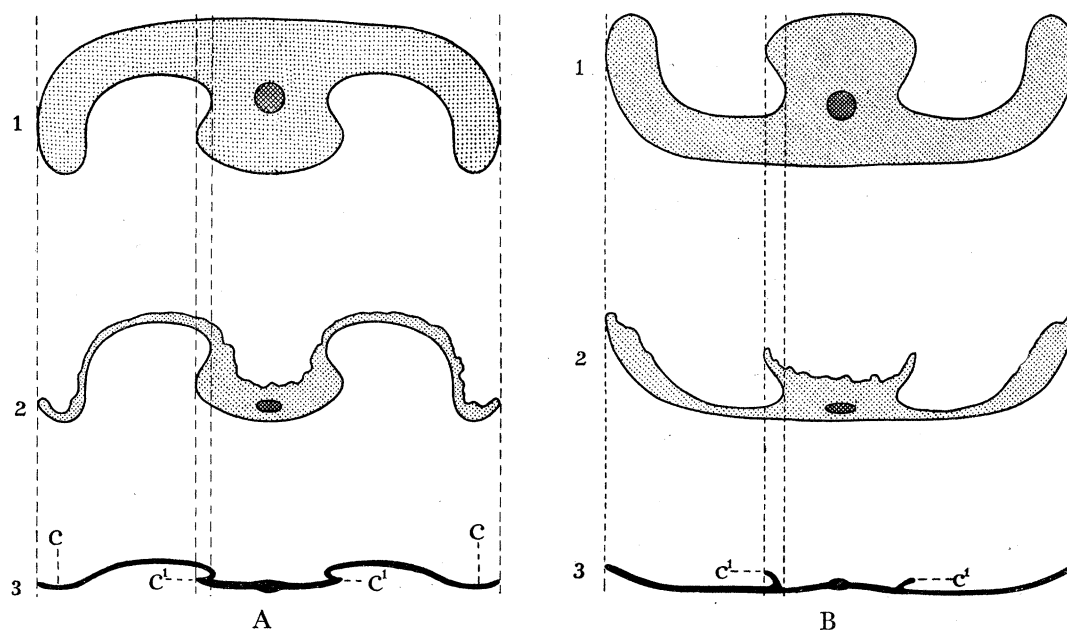


FIG. 7 (A and B)—Diagrams to represent the effect of vertical compression on a concavo convex leaf-lamina with a well-developed midrib with overhanging sides. Explanation as for fig. 3. *c*, compression border of leaf and *c*¹, compression borders of midrib.

to be a slight expansion of the vein and traces of a mucro. In another specimen from the Bassin du Gard, France (figs. 27, 28, Plate 32), two grooves (fig. 28, *gg*) appear on the surface of the leaf and a close comparison may be drawn between this form and that described by POTONIE (1893, p. 162, Plate XXIV, figs. 1–6) in that there are flat borders (*säume*) on each side of the leaf (fig. 28, Plate 32). The original form of leaf which may have given rise to this type of incrustation is suggested in fig. 7A 3. The only difference between this form of *Annularia stellata* and that described above is that here there was probably a greater curvature of the lamina giving a pronounced inrolling of the edges of the leaf. The reconstruction of this form closely resembles the actual form of the petrified leaves or bracts described by CARPENTIER (1924, p. 241) which he considers belong to a species of *Annularia* closely related to *A. stellata*. Professor HOLDEN, on other grounds, is inclined to believe that these petrifications may not belong to Equisetalean plants (*see* p. 226).

A third form of *Annularia stellata* is known in which the leaf has a more or less plane surface with a single ridge down the centre representing the midrib or vein. In completely preserved specimens a distinct mucro is shown. In the transfer preparation (fig. 29, Plate 32) of a leaf of this type from Shropshire the lamina evidently contains dark coloured inclusions similar to those found in some of the other species of *Annularia*. Here, however, their rather small size and regular arrangement suggests that they may have been contained in the epidermal cells. The resemblance between these leaves and those of the plant figured by ELIAS under the name *Carpannularia americana* is most striking. There is no doubt that the "shagreened" appearance of the Shropshire leaf and the American leaves are due to the same structure. The feathery appearance of the leaves on the penultimate branches of *Carpannularia americana* (ELIAS, 1931, p. 132, Plate 13, fig. 1a, 1b) might also be due to the same type of structures which cause the "hairiness" of the leaves in other species of *Annularia*. The original form of the cross-section of this type of *Annularia stellata* is suggested in fig. 3, B.

6—*Annularia* sp. (figs. 22, 23, Plate 32)—This plant, which comes from the South Wales coal-field, differs from *Annularia stellata* in being more lanceolate in shape and in possessing a relatively long mucro (fig. 23, Plate 32). The substance of the lamina is black and anthracitic and no internal structure is visible, so that a closer comparison with the preceding forms is impossible.

SUMMARY

I—Certain peculiarities (Compression borders, etc.) in the external form of fossil plants are described and a theory is proposed which accounts for some of the forms found.

It is suggested that there may be two stages in the process of fossilization of a plant organ. (a) The plant collapses under the weight of the overlying sediment, and, losing water, forms a layer of organic material over the surface of the matrix which formed a cast of its lower surface. (b) The compressibility of the organic material approximates to that of the sediment, and the plant and matrix together may undergo further compression with the production in them of a uniform vertical deformation.

The horizontal dimensions of the plant undergo no change, but all the vertical dimensions are more or less uniformly reduced. It is shown that the fossil formed from a thick leaf embedded with its concave surface up is not necessarily similar to a fossil produced from a leaf of the same form embedded with its convex side up.

II—An account is given of the results obtained from a detailed examination of the following species of *Annularia* by the transfer method.

The use of infra-red photography was found to be of considerable value in finding out the position of the vascular tissue in one specimen.

- Annularia sphenophylloides* ZENK.
 „ *Galioides* LINDLEY and HUTTON sp.
 „ *Jongmansi* sp. nov.
 „ *radiata* forma.
 „ *fimbriata* sp. nov.
 „ *stellata* SCHLÖTH sp.

In *Annularia sphenophylloides*, *A. galioides*, *A. Jongmansi*, *A. radiata* forma, and *A. fimbriata* the apex of the leaf has a distinct mucro. In *A. stellata* a mucro has not been demonstrated in all the forms examined. A system of dark coloured cellular inclusions has been found in the lamina of all the species investigated with the possible exception of *A. fimbriata*, although it is probable that this may be due to the condition of preservation of the specimens of *A. fimbriata* which were examined. Reasons were given for supposing that these cell inclusions correspond to the black cell inclusions found in petrified examples of *Asterophyllites*. The presence of these cell inclusions is shown to be responsible for the "hairy" appearance of various species of *Annularia*. In *A. sphenophylloides* there is a pronounced terminal expansion of the vein, a feature which is shown to a lesser degree in *A. stellata*. It is suggested that this structure might have been connected with hydathodic activity. In *A. fimbriata* the lamina of the leaf is inrolled and bears on its margins rows of short hairs. In all the species examined it has been possible to increase considerably our knowledge of their detailed structure and to show that there is very considerable range in form in the leaves of species belonging to this genus.

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DESCRIPTION OF PLATES

PLATE 31

- FIG. 8—*Annularia sphenophylloides* ZENK. Transfer on Canada balsam. There are parts of two ultimate branches shown in the photograph. $\times 2$. Tynning Pit, Radstock. Horizon : Radstockian Series, Upper Carboniferous. (WALTON Collection, Slide 403.)
- FIG. 9—*Annularia sphenophylloides* ZENK. Transfer on Canada balsam. Parts of two leaf whorls are shown. *m*, midrib of leaf; *t*, terminal expansion; *p*, mucro of leaf; *h*, hairs or hair-bases; *s*, stomata. Same locality and horizon as for fig. 8. $\times 13$. (WALTON Collection, Slide 405.)
- FIG. 10—*cf. Annularia sphenophylloides* ZENK. Transfer on balsam. Parts of two leaves are shown. Dark cell-contents are shown at *c*. Other lettering as for fig. 9. $\times 13$. Bradford Colliery, Manchester. Yorkian Series, Upper Carboniferous. (WALTON Collection, Slide 404.)
- FIG. 11—*Annularia galioides* L. and H. sp. Transfer on balsam. Parts of about a dozen whorls are shown. $\times 2$. Moncton Main Colliery, Barnsley. Horizon : Barnsley Thick Coal, Yorkian Series. (WALTON Collection, Slide 409.)
- FIG. 12—*Annularia Jongmansii* sp. nov. Transfer on balsam of two leaf whorls. Lettering as for fig. 9. $\times 3$. Devon Tower Colliery, 1 mile S.W. of Tillicoultry, Clackmannanshire. Westphalian Series. (WALTON Collection, Slide 423.)
- FIG. 13—Part of the specimen shown in fig. 12 at greater magnification. *h*, hairs on the inter-node. Undamaged margin shown at *x*. $\times 12$.
- FIG. 14—Part of the same specimen showing part of the node, the nodal sheath *s*, and hairs *h*. $\times 30$ (approx.).
- FIG. 15—Part of a leaf of the same specimen at greater magnification. Showing a series of dark, cell-contents in the lamina at *c*. $\times 60$.
- FIG. 16—*Annularia* sp. Transfer on cellulose of an ultimate branch with parts of four-leaf whorls. *p*, *p*, mucro. $\times 7$. Brucefield Colliery, Clackmannanshire. Westphalian Series. (WALTON Collection, Slide 426.)
- FIG. 17—Part of the specimen shown in fig. 15 at greater magnification. The mucro, *p*, is shown. Long, dark cell-contents oriented parallel to the axis of the leaf and shorter, dark cell-contents oriented at right angles to the axis are also shown. $\times 39$.

Walton

Phil. Trans. B, vol. 226, Plate 31.



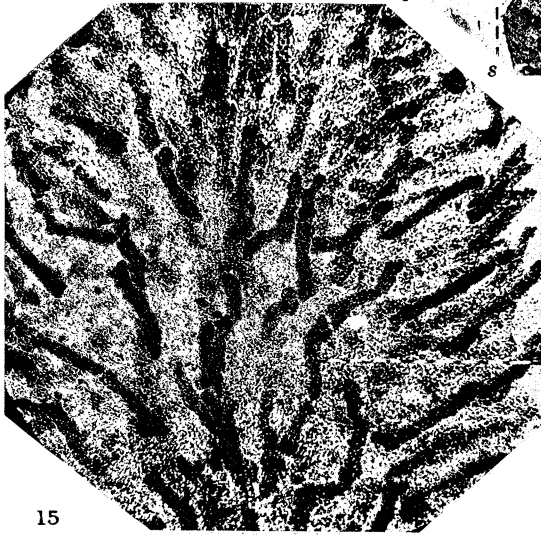
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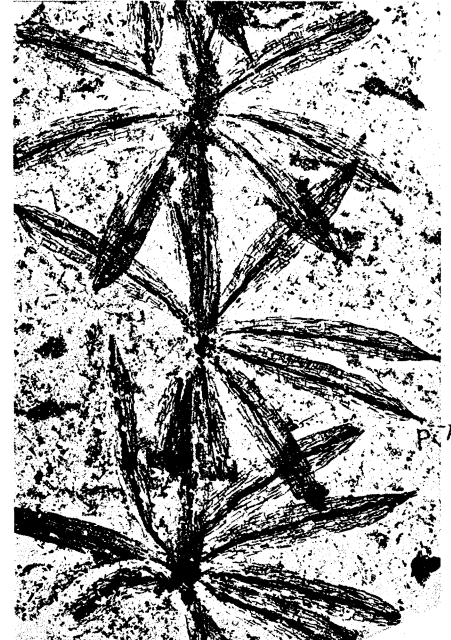
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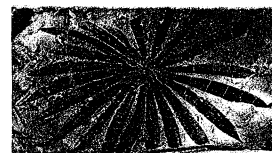
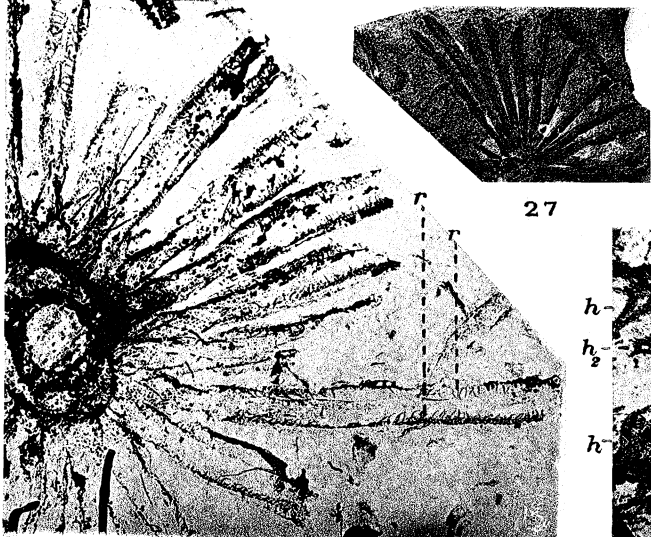
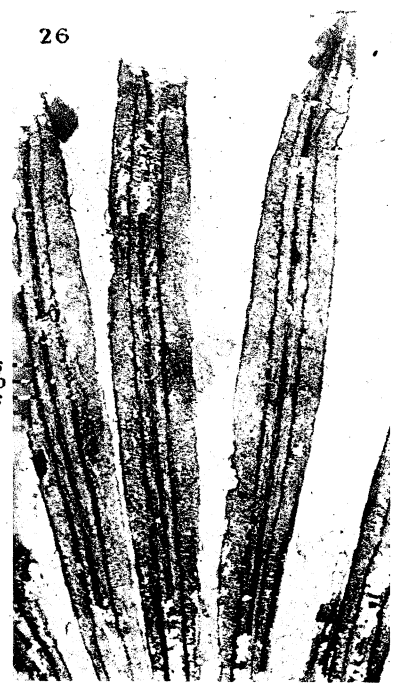
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PLATE 32

- FIG. 18—*Annularia fimbriata* sp. nov. Transfer preparation on balsam of four incomplete leaf-whorls. *p*, mucro. *s*, sheath or collar. $\times 3$. Coalpitheath Colliery, Gloucestershire. Horizon: Farrington Series. (WALTON Collection, Slide 395.)
- FIG. 19—*Annularia fimbriata* sp. nov. Transfer preparation on balsam photographed by reflected light showing parts of two leaves with inrolled margins. The two marginal rows of hairs are seen at *r* and *r* flattened borders of leaf *ff*. $\times 13$. Lea Green Colliery, $\frac{3}{4}$ mile S.S.E. from Thatto Heath Station, Lancashire. Horizon: Potato Delf Seam. Westphalian Series. (WALTON Collection, Slide 392.)
- FIG. 20—*Annularia fimbriata* sp. nov. Transfer preparation on balsam. Almost the whole of the substance of the leaf lamina has been removed on the counter part of the specimen and on this transfer only the margins of the leaves with their hairs are represented. Marginal rows of hairs most clearly visible at *r* and *r*. $\times 6$. Deep Pit, Kingswood near Bristol. (WALTON Collection, Slide 396.)
- FIG. 21—Part of the same specimen at *m*, fig. 13, to show the two margins of one leaf. *h*, *h*, marginal hairs. *h*, hair from surface of lamina. $\times 35$.
- FIG. 22—*Annularia cf. radiata* BGT. Transfer preparation on balsam. Nat. size. Gannoch No. 3 Colliery near Swansea, Wales. Hor. Five Feet Seam. (WALTON Collection, Slide 417.)
- FIG. 23—Part of the same specimen at greater magnification. $\times 3$. *p*, mucro.
- FIG. 24—*Annularia stellata* SCHLOTH. Leaf whorl on shale matrix. Nat. size. Camerton Colliery, Radstock, Somerset. Hor. Great Vein, Radstock Series. (Hunterian Museum, Univ. of Glasgow, No. Pb. 1132.)
- FIG. 25—Part of the same specimen. $\times 4$.
- FIG. 26—Part of the same specimen shown in fig. 24. Transfer preparation on Canada balsam of parts of three leaves, photographed on an infra-red sensitive plate using an infra-red light filter. *vb*, vascular bundle of midrib. *s*, *s*, slides of midrib. $\times 4$.
- FIG. 27—*Annularia stellata* SCHLOTH. Specimen on shale matrix of one-leaf whorl. Nat. size. Fontane, Couche 4, Lower Molières Series, Bassin du Gard, France. (Miss E. DIX.)
- FIG. 28—Transfer on Canada balsam of part of the same specimen photographed by reflected light. Showing the presence of two grooves in the substance of the lamina at *gg*. $\times 3$. (WALTON Collection, Slide 402.)
- FIG. 29—*Annularia stellata* SCHLOTH. Transfer preparation on cellulose. Terminal parts of two leaves. *p*, *p*, mucro. $\times 7$. Right Bank (S.W.) of Borle Brook, 700 yds. N.E. of Billingsley Hall Farm, $\frac{1}{2}$ mile E.N.E. of the church, Billingsley, Shropshire. Horizon: Staffordian Series. (WALTON Collection, Slide 421.)



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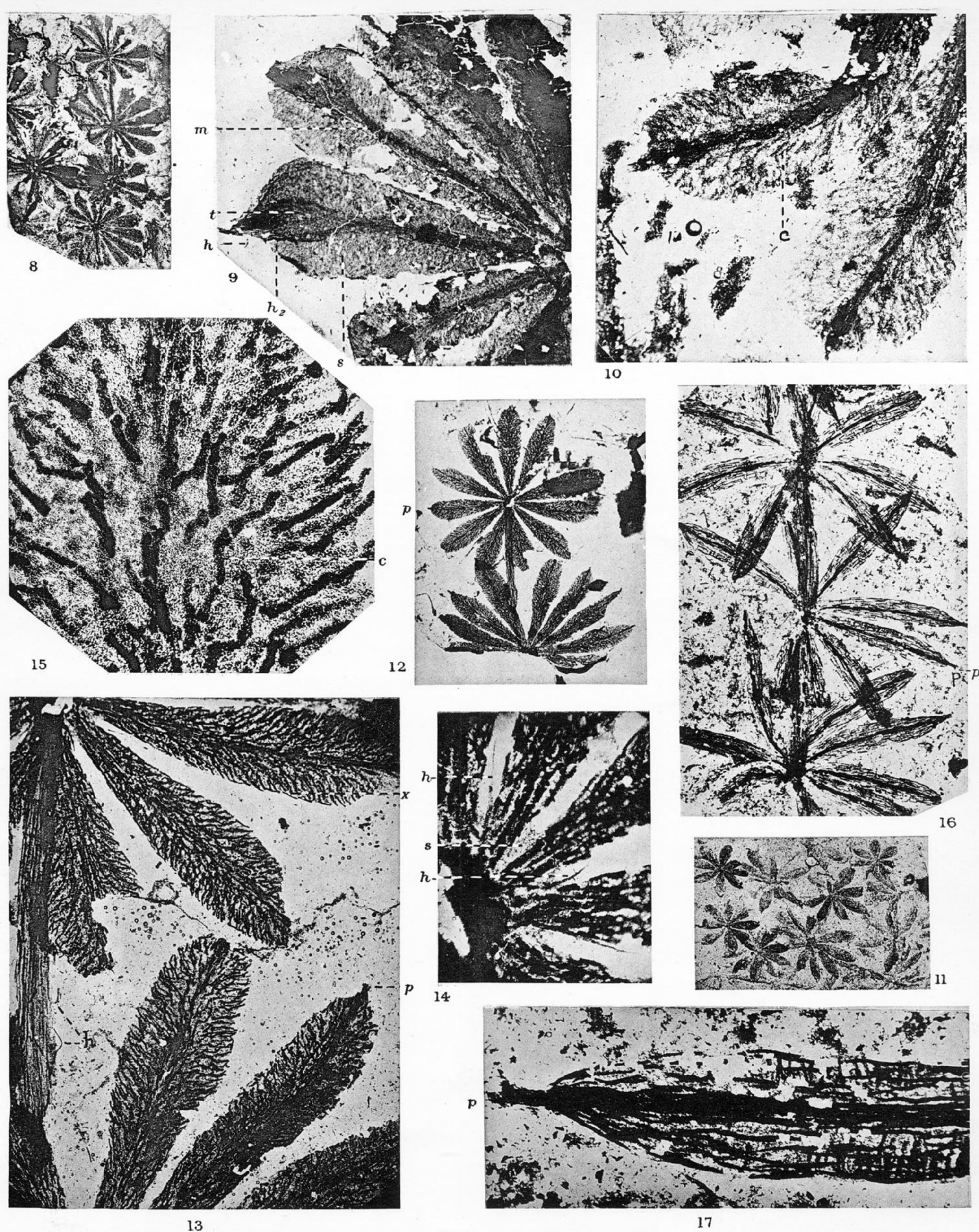


PLATE 31

FIG. 8—*Annularia sphenophylloides* ZENK. Transfer on Canada balsam. There are parts of two ultimate branches shown in the photograph. $\times 2$. Tynning Pit, Radstock. Horizon: Radstockian Series, Upper Carboniferous. (WALTON Collection, Slide 403.)

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FIG. 11—*Annularia galioides* L. and H. sp. Transfer on balsam. Parts of about a dozen whorls are shown. $\times 2$. Moncton Main Colliery, Barnsley. Horizon: Barnsley Thick Coal, Yorkian Series. (WALTON Collection, Slide 409.)

FIG. 12—*Annularia Jongmansii* sp. nov. Transfer on balsam of two leaf whorls. Lettering as for fig. 9. $\times 3$. Devon Tower Colliery, 1 mile S.W. of Tillicoultry, Clackmannanshire. Westphalian Series. (WALTON Collection, Slide 423.)

FIG. 13—Part of the specimen shown in fig. 12 at greater magnification. *h*, hairs on the inter-node. Undamaged margin shown at *x*. $\times 12$.

FIG. 14—Part of the same specimen showing part of the node, the nodal sheath *s*, and hairs *h*. $\times 30$ (approx.).

FIG. 15—Part of a leaf of the same specimen at greater magnification. Showing a series of dark, cell-contents in the lamina at *c*. $\times 60$.

FIG. 16—*Annularia* sp. Transfer on cellulose of an ultimate branch with parts of four-leaf whorls. *p*, *p*, mucro. $\times 7$. Brucefield Colliery, Clackmannanshire. Westphalian Series. (WALTON Collection, Slide 426.)

FIG. 17—Part of the specimen shown in fig. 15 at greater magnification. The mucro, *p*, is shown. Long, dark cell-contents oriented parallel to the axis of the leaf and shorter, dark cell-contents oriented at right angles to the axis are also shown. $\times 39$.

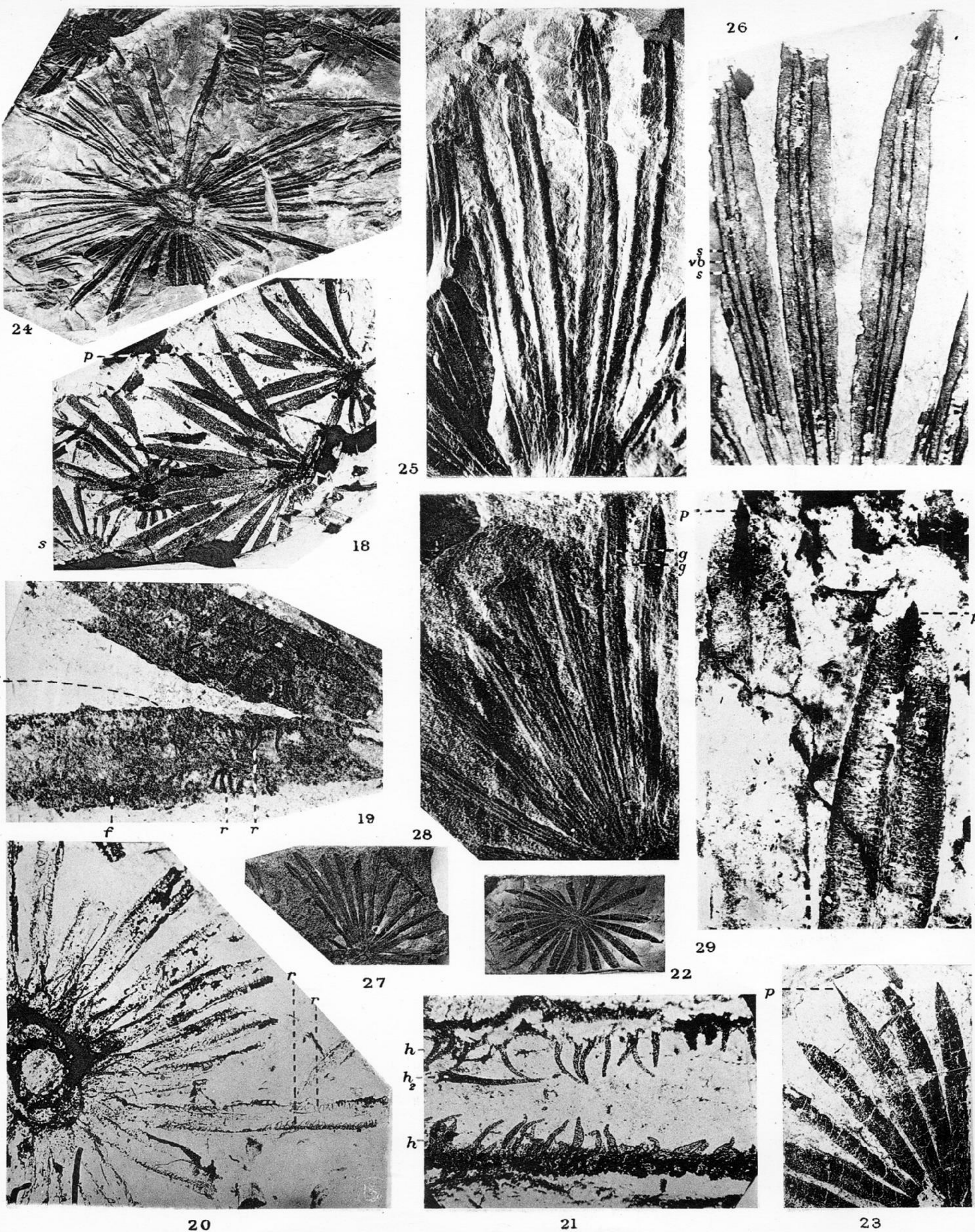


PLATE 32

FIG. 18—*Annularia fimbriata* sp. nov. Transfer preparation on balsam of four incomplete leaf-whorls. *p*, mucro. *s*, sheath or collar. $\times 3$. Coalpitheath Colliery, Gloucestershire. Horizon: Farrington Series. (WALTON Collection, Slide 395.)

FIG. 19—*Annularia fimbriata* sp. nov. Transfer preparation on balsam photographed by reflected light showing parts of two leaves with inrolled margins. The two marginal rows of hairs are seen at *r* and *r* flattened borders of leaf *ff*. $\times 13$. Lea Green Colliery, $\frac{3}{4}$ mile S.S.E. from Thatto Heath Station, Lancashire. Horizon: Potato Delf Seam. Westphalian Series. (WALTON Collection, Slide 392.)

FIG. 20—*Annularia fimbriata* sp. nov. Transfer preparation on balsam. Almost the whole of the substance of the leaf lamina has been removed on the counter part of the specimen and on this transfer only the margins of the leaves with their hairs are represented. Marginal rows of hairs most clearly visible at *r* and *r*. $\times 6$. Deep Pit, Kingswood near Bristol. (WALTON Collection, Slide 396.)

FIG. 21—Part of the same specimen at *m*, fig. 13, to show the two margins of one leaf. *h*, *h*, marginal hairs. *h*, hair from surface of lamina. $\times 35$.

FIG. 22—*Annularia cf. radiata* BGT. Transfer preparation on balsam. Nat. size. Gannoch No. 3 Colliery near Swansea, Wales. Hor. Five Feet Seam. (WALTON Collection, Slide 417.)

FIG. 23—Part of the same specimen at greater magnification. $\times 3$. *p*, mucro.

FIG. 24—*Annularia stellata* SCHLOTH. Leaf whorl on shale matrix. Nat. size. Camerton Colliery, Radstock, Somerset. Hor. Great Vein, Radstock Series. (Hunterian Museum, Univ. of Glasgow, No. Pb. 1132.)

FIG. 25—Part of the same specimen. $\times 4$.

FIG. 26—Part of the same specimen shown in fig. 24. Transfer preparation on Canada balsam of parts of three leaves, photographed on an infra-red sensitive plate using an infra-red light filter. *vb*, vascular bundle of midrib. *s*, *s*, slides of midrib. $\times 4$.

FIG. 27—*Annularia stellata* SCHLOTH. Specimen on shale matrix of one-leaf whorl. Nat. size. Fontane, Couche 4, Lower Molières Series, Bassin du Gard, France. (Miss E. DIX.)

FIG. 28—Transfer on Canada balsam of part of the same specimen photographed by reflected light. Showing the presence of two grooves in the substance of the lamina at *gg*. $\times 3$. (WALTON Collection, Slide 402.)

FIG. 29—*Annularia stellata* SCHLOTH. Transfer preparation on cellulose. Terminal parts of two leaves. *p*, *p*, mucro. $\times 7$. Right Bank (S.W.) of Borle Brook, 700 yds. N.E. of Billingsley Hall Farm, $\frac{1}{2}$ mile E.N.E. of the church, Billingsley, Shropshire. Horizon: Staffordian Series. (WALTON Collection, Slide 421.)