

III. *A Petrified Williamsonia from Scotland.*By A. C. SEWARD, *F.R.S., Cambridge.*

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[PLATES 9–12.]

INTRODUCTORY.

The account of Scotch Jurassic floras given by HUGH MILLER in the ‘Testimony of the Rocks’* deals chiefly with plants from the neighbourhood of Helmsdale, on the coast of Sutherland, and from Eathie, near Cromarty. The Sutherland species have recently been described in a paper published by the Royal Society of Edinburgh,† which includes also a description of the majority of the Eathie specimens. Some of the latter were, however, reserved for separate treatment. It is the most interesting of these that forms the subject of the present communication.‡

MILLER referred the Helmsdale plants to the Oolitic series, and those from Eathie he regarded as Liassic. The great majority of the Sutherland plants are from rocks now recognised as Kimmeridgian, and there is no reason to suppose that the Eathie specimens are not, approximately at least, of the same age, though the limestone nodules in which they are preserved indicate by their weathered appearance and by the occurrence of pits made by boring organisms that they were picked up on the beach, and not found *in situ*.

The fossil dealt with in the following pages, for which the name *Williamsonia scotica* is proposed, is figured by MILLER, and described by him as follows:—“With the leaves of the Eathie *Zamia* [fronds recently re-described and figured under the name *Pseudoctenis eathiensis* (RICH.)]§ we find . . . cones of a peculiar form, which, like the leaves themselves, are still unfigured and undescribed, and some of which could scarce have belonged to any coniferous tree. In one of these (fig. 138) the ligneous bracts or scales, narrow and long, and gradually tapering till they assume nearly the awl-shaped form, cluster out thick from the base and middle portions of the cone, and, like the involucreal appendages of the hazel nut,

* MILLER ('57).

† SEWARD ('11).

‡ A short account of the Eathie *Williamsonia* (described as *Williamsonia* sp.) was given at the Portsmouth meeting of the British Association (‘Rep. B. A., Portsmouth, 1911,’ p. 570, London, 1912. See also ‘Nature,’ 1911, vol. 88, p. 59). A description of the remaining Eathie plants is now in preparation.§ SEWARD ('11), Plate 10, fig. 45; MILLER ('57), fig. 138.
(296.)

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or the sepals of the yet unfolded rose-bud, sweep gracefully upwards to the top, where they present at their margins minute denticulations."* The drawing of the cone, rather less than half natural size, published in the 'Testimony of the Rocks,' gives a fairly accurate representation of the specimen which for many years has been preserved in the Royal Scottish Museum, Edinburgh, with the other plants collected by HUGH MILLER. The counterpart of this fossil (text-fig. 1), in the



TEXT-FIG. 1.—Portion of the Strobilus in surface-view. Nat. size.
British Museum. Peach Coll. V. 3944.

Geological Department of the British Museum, consists of impressions and petrified portions of numerous bracts lying in a slight concavity which fits on to the convex surface of the Edinburgh specimen (fig. 28, Plate 12).

Several years ago, when examining the Miller collection, I made a note that the cone appeared to be a *Williamsonia*, and my friend Prof. NATHORST tells me that he came to the same conclusion. Through the courtesy of the Director of the Royal Scottish Museum it has been possible to investigate the anatomy of MILLER'S cone. The specimen has necessarily suffered in the process of cutting, but a cast was taken before the original was handed to me, and the sections will be incorporated in the Miller collection.

* MILLER ('57), p. 480.

The leaves spoken of by MILLER as associated with the cone were not found in the same nodule, and there is no special reason for supposing them to have any connection with the fertile shoot. They were named by RICHARDS *Zamites eathiensis*,* and have since been placed in a new genus *Pseudoctenis*† because of their close resemblance in habit and in the venation of the pinnæ to the pinnate fronds of *Ctenis*. The species *Nilssonia orientalis* Heer is also recorded from Eathie.‡ From a more northerly locality (Brora) CARRUTHERS described a *Bennettites* stem, *B. Peachianus*, and other Cycadean stems referred by him to the genera *Yatesia* and *Bucklandia*.§ There is, however, no evidence as to the nature of the foliage or stems of the plant which bore MILLER's cone, beyond the occurrence of small lateral segments on two of the longer bracts (fig. 28, α and β ; figs. 29, 30), suggesting a reduced form of a pinnate frond such as that of *Pseudoctenis eathiensis*, and similar types.

An imperfectly preserved specimen from the Sutherland Kimmeridgian beds has been described as *Williamsonia* sp.|| but, even assuming the correctness of this determination, the species does not agree at all closely with that from Eathie.

DESCRIPTION OF THE SPECIMEN.

The complete strobilus (text-fig. 1; fig. 28, Plate 12) is 11 cm. long, measured from the tip of the longest bract, and has a maximum breadth of 6 cm. In speaking of the linear leaves surrounding the strobilus I use the term bract as indicating a contrast from the foliage leaves, which were probably much larger pinnate structures, and in preference to the term perianth-segments on the ground that the appellation perianth, as used for the corresponding members of *Bennettites* by ARBER and PARKIN,¶ implies a smaller collection of foliar organs more restricted in their association with sporophylls than are the bracts of the Eathie strobilus. The cone resembles a bud enclosed in linear bracts converging and gradually decreasing in breadth towards the apex. Most of the bracts in the lower part of the fossil are broken across obliquely, showing broadly triangular fractured surfaces. The "minute denticulations" spoken of by MILLER (fig. 28, α and β ; figs. 29, 30) are small obliquely placed lateral appendages, forming a single series on one side of the apical portion of the bracts. The single appendage (fig. 28, α , and fig. 29) has a forked axial ridge, V, which may be a vascular strand. Two sections were cut transverse to the bract β by Mr. Hemingway, of Barnsley, which throw some light

* RICHARDS ('84).

† SEWARD ('11), p. 692.

‡ *Ibid.*, p. 695.

§ CARRUTHERS ('70), Plate 55, figs. 1, 7-9; Plate 62. The strata at Brora are slightly lower in the Jurassic series than the Kimmeridgian.

|| SEWARD ('11), p. 691, Plate 5, fig. 99; text-fig. 12B.

¶ ARBER and PARKIN ('07).

on the anatomical features. The epidermis of the appendages is composed of thick cells with a strong cuticle, agreeing closely with the epidermal layer of the bracts: there is a sub-epidermal layer of small and apparently thick-walled elements succeeded by a few crushed mesophyll cells, and in one section there are indications of a xylem strand. The structure, though imperfectly petrified and only partially revealed by the section, is such as one would expect in small, more or less cylindrical, leaflets or reduced and modified pinnæ borne on bracts having the structure described below.

A noteworthy feature of the strobilus is the absence of any clean-cut base, such as would be formed by the separation of the cone along an absciss-layer. This apparent absence of a well-defined basal line (fig. 2, Plate 9, *x, h*) is probably due to a slight obliquity in the position of the strobilus in relation to its supporting axis; it suggests also that the diameter of the peduncle was narrower near the base than in the upper part.*

Fig. 31 shows more accurately than fig. 28, Plate 12, the lower left-hand edge of the strobilus in surface-view. The oblique fractured surface of the slightly ridged and contracted bract A is seen at S; on the surface of the bract B, as in the case of several others, part of the surface, *α*, is dark brown while the rest, *β*, raised a little above *α*, is lighter in colour. The darker surface, as shown by sections, is no doubt the epidermis of the bract, while the lighter portion consists of a dense mass of tubular hairs.

Fig. 32 shows the transverse section (very slightly enlarged) exposed on the upper face of fig. 31 and cut approximately at the level ii in fig. 28. A few shrivelled bract-bases are seen in organic connection with the axis *ax*, while the rest of the section consists of transverse or obliquely transverse sections of free portions of bracts embedded in a mass of hairs filling the unshaded portions of the drawing (*cf.* fig. 6, Plate 9). Fig. 33 represents a slightly diagrammatic drawing, approximately natural size, of the surface exposed by a transverse cut at the level iv, fig. 28. On the left is part of the main axis, *ax*, with its surrounding bracts; the alteration in the disposition of the smaller bracts at B is the result of their connection with a lateral axis, the apex of which, though not actually seen, is immediately below the centre of the concentric series of slender bracts. There is no indication of the existence of this lateral axis on the surface of the strobilus. The lateral branch, or bud, is given off almost at right angles to the axis of the strobilus as shown by the section, fig. 34, cut 6 mm. below that shown in fig. 33 and at the level v, fig. 28. At the edges and base of the branch B the xylem is cut in oblique longitudinal section (*x*), and several bracts, one of which is attached, are seen in oblique transverse section at the distal end of the axis; a comparison of the sections shown in figs. 33, 34 demonstrates that the branch bends rather sharply upwards at the apex. In the larger axis a few collateral vascular strands occur at *x'*.

* *Cf.* WIELAND ('06), figs. 59, 67, pp. 113, 133, for examples of fertile shoots with a narrow base.

A transverse section close to the tip of the branch is reproduced in fig. 13, Plate 10 (*cf.* B, fig. 33); the axis of the bud is not seen, but the concentric disposition of the bracts points to its proximity. The centre of the bud consists of transverse sections of imperfectly preserved and shrunken bracts, or possibly small foliage leaves, embedded in a matrix of long hairs, the sweeping curves of which, as shown in fig. 13A (an enlargement of *x*, fig. 13), illustrate the approximate boundaries of the woolly coverings of these young organs. These central leaves are characterised by a V-shaped section suggesting a comparison with fronds in veneration. The outer part of the bud is composed of slightly curved and flat bracts also embedded in a dense packing of hairs.

The occurrence of this partially developed branch may mean that the strobilus itself is a lateral shoot, the main axis being represented by the bud B, figs. 33, 34, which has been pushed to one side. The evidence can hardly be regarded as demonstrating, but rather suggesting, the existence of a sympodium. In this connection it is relevant to refer to bract-covered fertile shoots of *Williamsonia* from the Inferior Oolite beds of Yorkshire in the Yates collection, Paris,* and in English collections.† Graf zu SOLMS-LAUBACH speaks of the occurrence in *Bennettites Gibsonianus* of spadices in close association differing in length, and adds: "I could not resist the impression that the new [that is the shorter] spadices were lateral branches which projected further from the axis."‡ A section in Dr. SCOTT's collection§ shows a fully developed flower with a shorter one at its side which may be compared morphologically with the bud of *Williamsonia scotica*.

A brief statement at this stage of the salient morphological and anatomical features of the strobilus may facilitate the more detailed description of the several parts. The axis, which reaches a diameter of 1.5 cm., bears in the lower portion (fig. 2) a number of linear bracts, some of which extend considerably above the apex of the central region; the surface of the upper part of the axis (fig. 1, *s*, *s'*) is covered with short and narrow appendages, both sterile and fertile (interseminal scales and megasporophylls) and its conical form agrees closely with the axis of the fertile shoot of *Cycadeoidea dacotensis* and other species described by WIELAND,|| as also with NATHORST's English species *Williamsonia pyramidalis*.¶ The bracts are clothed with numerous long and narrow hairs which form a dense packing in the inter-bracteal spaces and take the place of the ramental scales of other Cycadean strobili hitherto described from Mesozoic strata.

* Part of this collection has recently been acquired by the University of Yale; WIELAND ('11), p. 436.

† SEWARD ('97); WIELAND ('08, '11).

‡ SOLMS-LAUBACH ('91), p. 430.

§ I am indebted to my friend Dr. D. H. SCOTT for the loan of some of the sections in his possession, which were cut from the piece of the type-specimen preserved at Kew and described by SOLMS-LAUBACH.

|| WIELAND ('06).

¶ NATHORST ('11), p. 25, fig. 7.

The strobilus was in all probability borne on a branch which extended beyond the region of the main trunk occupied by the persistent bases of the fronds, as in *Williamsonia gigas*.

Axis of Strobilus.—The longitudinal section reproduced in fig. 2, though approximately median, shows part of a bract with its ramental hairs, *h*, at the base, and cannot, therefore, be median in regard to the axis of the peduncle. The centre is occupied by imperfectly preserved and crushed parenchymatous tissue with occasional groups of secretory sacs full of dark contents, and patches of xylem in longitudinal, oblique, and transverse section, composed of scalariform tracheæ. The axis as a whole presents an appearance suggestive of partial disorganisation prior to petrification. At the base of the section there are more continuous patches of xylem forming part of a peripheral vascular cylinder (*x*, *x'*). The tracheæ are for the most part of the scalariform type with occasional inclination towards reticulate pitting; the xylem appears to consist entirely of radially arranged elements associated with numerous medullary rays (fig. 3, an enlarged piece of *x'*, fig. 2). The tracheæ in this section are not sufficiently well preserved to show the pitting very clearly except in a few places where the radial walls have short transversely elongated pits with occasional tendency to reticulation. The xylem is succeeded externally by narrow elongated elements, doubtless imperfectly preserved phloem, and next to these occur some fairly large parenchymatous cells where the axis passes into the bases of the bracts.

In the upper half of the strobilus (fig. 1, cut at vi, fig. 28) the tissues of the axis are very much disorganised and contiguous radially disposed interseminal scales and associated megasporophylls, *s*, *s'* (fig. 4, *s*), replace the bracts; the truncated distal ends of these appendages, 2 mm. in length, abut on the ramental hairs, *h*, which are succeeded by longitudinally cut bracts, *b*, and their accompanying hairs, *h*, *h'*. The apical portion of the axis is not preserved, the space at its summit being partially occupied by strands of bracteal hairs, *h''*, *h''*. Part of another longitudinal section, cut close to that shown in fig. 1, is diagrammatically represented in fig. 35, Plate 12; the interseminal scales and megasporophylls, *s*, extend rather nearer the apex of the strobilus. An interesting feature is the occurrence of three vascular strands, *x*, in longitudinal section, accompanied by secretory tissue; these are portions of the conducting cylinder, which appears to have become reduced in diameter in the upper region of the axis. It is clear, from the section shown in fig. 2, that, in the lower part of the strobilus, the vascular tissue occupied a peripheral position, but the imperfect state of preservation of the more internal tissues precludes any complete description of the vascular supply. There is no reason for supposing that the vascular tissue was not mainly confined to the peripheral region of the axis of the strobilus (as shown in fig. 2), though, as indicated in fig. 35, *x*, the cylinder may have contracted slightly in the apical region. The very incomplete state of this tissue is a difficulty in the way of fuller description: in fig. 36, *x* (cut at II, fig. 28), it is

represented by a few well-defined bundles having the structure shown in fig. 39; the xylem, which appears to be all centrifugal in development, contains a relatively large proportion of medullary-ray parenchyma. In the transverse section reproduced in fig. 6, Plate 9, a few bundles of conducting tissue occur at *x*. The circular form of the axis and its rather broader diameter are shown in fig. 4, where it is completely enclosed by a zone of uniform diameter of interseminal scales and megasporophylls, *s*.

Bracts and Hairs.—As seen in figs. 4, 5, 6, Plate 9, the bracts nearest the axis are much more shrivelled and contracted than those further away, a circumstance connected with the greater development of hypodermal stereome in the latter.* The anatomical features of the bracts may be summarised as follows: The epidermis consists of a layer of thick-walled cells, with a strongly developed cuticle (fig. 43), which occasionally separates itself as a curved strip from the rest of the layer (fig. 38). The cells, as seen in surface-view, are oblong in shape, and have straight walls. In many of the sections of bracts, the superficial tissue is detached from the hypoderm (fig. 4, *a*; figs. 5, 7; 37, *e*). Stomata occasionally occur in the outer (lower) epidermis in fairly deep pits and agree closely with those of recent Cycads. Below the epidermis, in the more external bracts, is a broad band of short sclerenchymatous cells, with their thick walls traversed by numerous pit-canals (figs. 10, 14, 15, 44; *sc*).† The broad thickening layer of these cells is frequently detached from the thin outer membrane (fig. 15). In the case of some of the outer bracts, the hypodermal stereome is almost confined to the external surface, and, as seen in figs. 5 and 7, where this tissue occurs on both sides, it is broader and composed of rather larger cells on the outer edge. The much less regular form of the inner bracts is due partly to the obliquity of the sections, and in part to the greater contraction of the tissues, which are much poorer in mechanical elements. The inner ground-tissue consists of large thin-walled parenchyma, very rich in broad secretory sacs, almost filled with a dark brown substance (fig. 7, the dark patches; fig. 15, *se*; figs. 37, 44, *se*).

The vascular bundles are of the collateral type, and the xylem is mainly centrifugal, though there are indications of the presence of a few centripetal elements; the preservation is, however, not such as to enable one to recognise with accuracy the position of the protoxylem. In the single strand shown in fig. 37*a* (the bundle represented in fig. 37 at *a*), the crushed phloem is seen at *ph*, and on the outside are two thick-walled elements, *sc*. The usual distribution of the conducting strands is most clearly seen in fig. 37, which shows a bract, with its inner (upper) side towards the top of the plate; there are two strands, *v'*, on the inner side, and five, *v*, near the outer surface. Some of the vascular bundles are shown also in fig. 7, *v, v*.

The hairs borne by the epidermis of the bracts and on the surface of the lower

* Cf. WIELAND ('06), Plate 40, figs. 73, 75; pp. 146, 150, &c.

† WIELAND ('06), Plates 38, 40; LIGNIER ('94), Plate 5, fig. 59.

part of the strobilus axis are a very striking and important feature. They arise as outgrowths of single epidermal cells; the thickly cuticularised outer wall of an epidermal cell forms a dark ring round the lower end of a hair (fig. 40), which consists of a short basal cell, succeeded by a cell of great length, and in most cases, at least, without transverse septa; or from the summit of the basal cell there may be formed a group of small cells, each of which forms the starting-point of one of the long tubular cells (figs. 41, 42). A few hairs are shown in organic connection with the epidermis in fig. 10, *h*, *h'*. The free portion of a hair has a diameter of approximately 0.025 mm., and a fairly thick wall, the thickening ring being frequently detached from the limiting membrane (fig. 45, *h*). In surface-view, this thickened wall sometimes presents the appearance shown in fig. 8, the dark spiral bands being no doubt the expression of a partial destruction by enzyme action of the thick cellulose wall, a feature reminding one of the etching of tracheal elements in recent Conifers by partial solution along the lines of striation. It is difficult to estimate the length of these hairs, but their occurrence as long strands of woolly threads, as seen in fig. 1, *h''*, at a considerable distance from their points of origin, and an examination of them in other sections, lead me to believe that they reached a length of several centimetres.

Interseminal Scales and Megasporophylls.—The two longitudinal sections reproduced in figs. 1 and 2, Plate 9, include almost the whole of the strobilus, but unfortunately neither section shows a transition from the bracts and hairs of the lower part of the axis to the appendages of the upper part. The transverse section reproduced in fig. 4 was the first one cut and in its preparation the boundary between the sterile and fertile regions must have been involved. In view of the fact that the vertical distance between the two longitudinal sections is represented by the amount of material destroyed in cutting the transverse section, it is clear that the bract-bearing region was succeeded abruptly by the fertile region of the strobilus, and there cannot have been any whorl of microsporophylls between the two as there is in the American strobili described by WIELAND. The appendages to the upper part of the axis no doubt originally extended to the conical apex, the actual summit of which is not preserved (figs. 1, 35); they form a compact zone, 2 mm. broad, completely surrounding the axis (figs. 4, 5, *s*). For the most part the proximal ends of the appendages end freely, having been separated by decay and shrinkage from the peripheral tissue of the axis (fig. 5, *s*, shows a crushed piece of axis at *c*), but in some places the imperfect bases of the appendages are in organic connection with the peduncle (fig. 11, *s*, text-fig. 2, A, *ax*). The appendages at first sight appear to be all of the same type, but a closer inspection reveals the occasional occurrence of rather narrower organs having the attributes of ovules. The latter are spoken of as megasporophylls, and the former, which are very much more numerous, are referred to as interseminal scales. The small portion of a transverse section of the fertile part of the strobilus reproduced in fig. 11, Plate 10, shows one megasporophyll, part of which is enlarged in

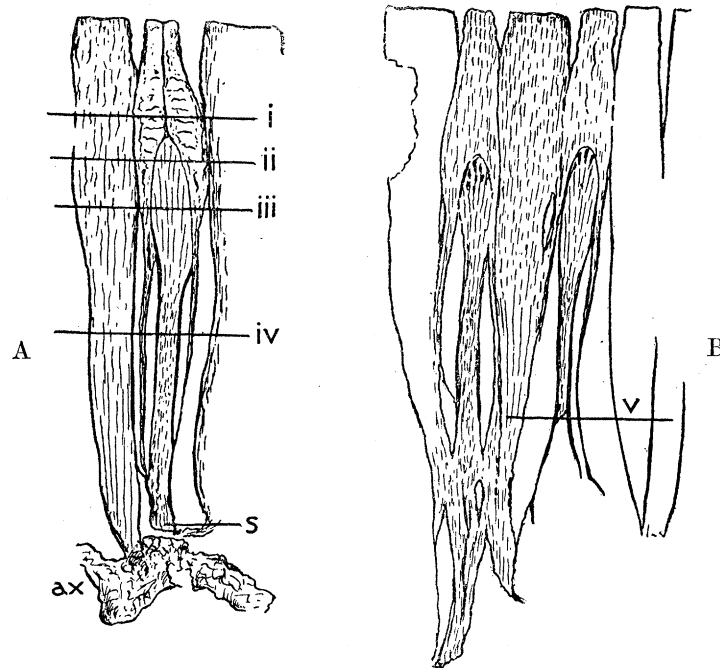
fig. 12. In fig. 19, Plate 11, the upper part of an ovule, that is the apex of a megasporophyll, is seen in lateral contact, except at the distal end, with an interseminal scale. The breadth of the truncate and slightly funnel-shaped end of a megasporophyll is 0.15 mm. while the flatter distal end of an interseminal scale is approximately 0.23 mm. across. Owing to the uniformity in the length of these organs their truncate tips, separated for a short distance from one another, form an almost straight boundary-line between the appendages and the mass of hairs beyond (figs. 4, 5). Fig. 9 illustrates the arrangement of the interseminal scales and megasporophylls as seen in a section tangential to the zone *s* of figs. 4 and 5. The small patches of tissue lying in clear circular spaces show the position of the megasporophylls and the smaller number of these organs in proportion to the interseminal scales.

Interseminal Scales.—The term scale is perhaps not very appropriate for the organs so designated, but as the name has become well established for the corresponding structures in other species it is convenient to adopt it here, particularly as it carries no definite morphological significance. The interseminal scales are polygonal in section and five or six surround a single megasporophyll (figs. 24, 27, Plate 11). A thick-walled and cuticularised epidermis covers the truncate, flat, or very slightly concave distal end (fig. 45) and extends along the sides, the dark brown surface-membrane forming a fairly conspicuous boundary between adjacent appendages, though the actual cells may be partially destroyed (figs. 11, 17, text-fig. 3, E). The epidermal cells in the free upper part of the interseminal scales are often papillose and the short cuticularised projections loosely interlock with similar teeth from the surface of the adjacent megasporophyll (fig. 24). In the distal portion of a scale the epidermis is succeeded by short thinner-walled parenchymatous cells (fig. 19, *s*, fig. 45) while the greater part of the tissue consists of vertically elongated parenchymatous elements (fig. 19) which in the lower region of each scale assume a long tubular form. The elongated form of the cells is diagrammatically indicated by the longer lines in text-fig. 2, A and B: the unusually large proportion of shorter elements in the upper two-thirds of the scale shown in fig. 2, B, is due to the more superficial plane of the section. Fig. 24, Plate 11, shows the contrast between the rather narrower internal cells and the longer hypodermal elements in transverse sections of interseminal scales a short distance below their apices. In only one longitudinal section of a scale have I detected any vascular tissue, represented by a very slender strand of two or three tracheal elements near the proximal end. In a few cases some secretory sacs occur parallel to the elongated cells of the scale-tissue.

The preservation of the outer edge of the strobilus axis and the bases of the interseminal scales is not sufficiently good to show the origin of the scales with any completeness. Fig. 26, Plate 11, represents a transverse section near the proximal ends of the scales, *s*, and shows also two megasporophylls, *n*, *n*. The scales appear as polygonal areas bounded by dark lines and occupied by imperfectly preserved tissue. A diagram of a similar section is seen in text-fig. 3, A, the shaded areas marking the

position of the scales: one of these, enlarged in fig. B, has a central strand of thin-walled and clear tissue which is probably an immature vascular strand, enclosed in ground tissue composed of thin and partially destroyed parenchymatous elements with a few thick-walled cells. The diameter of this scale close to its base is 0.14 mm. The manner of origin of the interseminal scales appears to be very similar to that of the bracts: the superficial tissue of the axis grows outwards and the individual cells become very considerably elongated to form the tubular elements composing the lower part of each scale. It has not been possible to discover any connection between the conducting tissue of the axis and the central, apparently immature, strand in the interseminal scales.

Megasporophylls.—As already stated, and as the sections reproduced in figs. 9, 24, 27, demonstrate, the megasporophylls are scattered regularly among the interseminal scales, each forming the centre of a group of five or sometimes six scales. One of the most complete megasporophylls is seen in fig. 11, and is diagrammatically drawn in text-fig. 2, A. At the proximal end it consists of a slender column of crushed parenchymatous tissue, *s*, closely associated with the strobilus axis (text-fig. 2, A, *ax*).



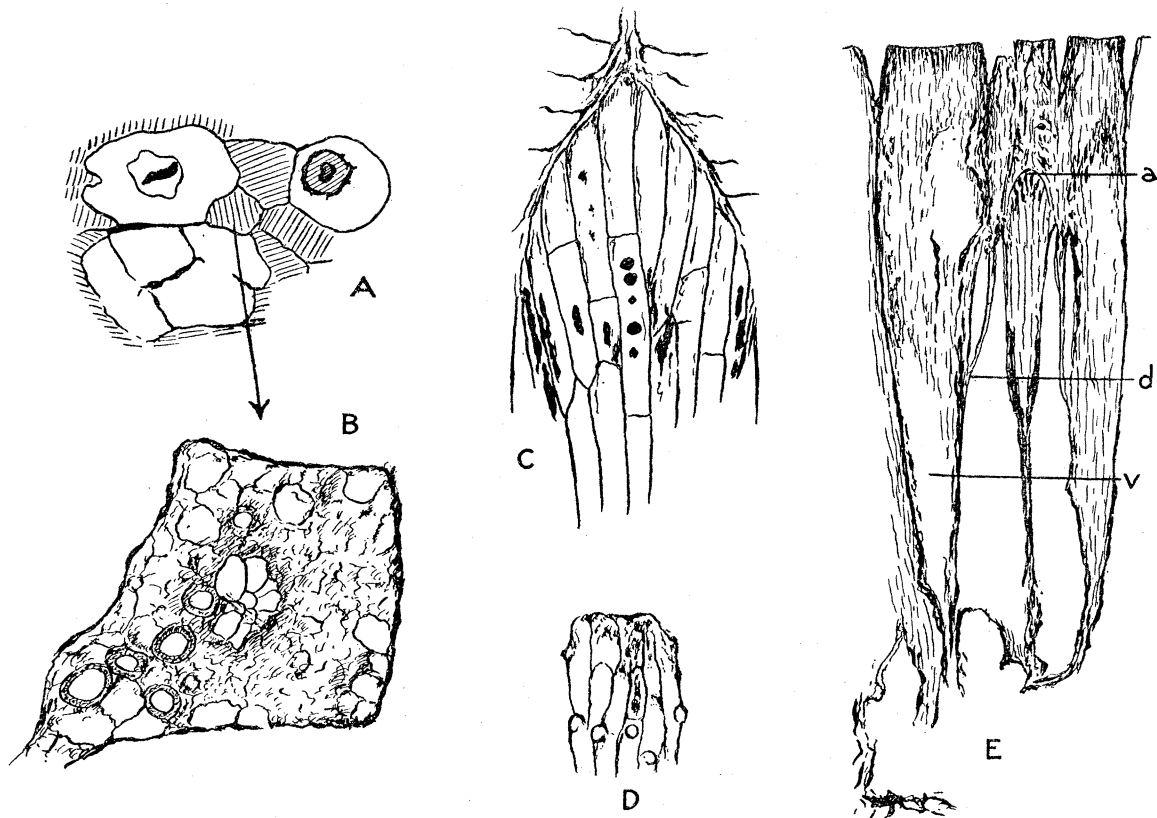
TEXT-FIG. 2.—Sketches of Interseminal Scales and Megasporophylls.

s, base of axis of megasporophyll; *ax*, crushed tissue of strobilus peduncle; i-v, levels of transverse sections. Actual length of scales, 2 mm. (Fig. A, section E; fig. B, section D*.)

This column passes up for about half the length of the organ; its external cells have darker contents, but there is no indication of an epidermis. From this column and near the base are detached two imperfectly preserved strips of indistinct thick-walled and short cells which have no epidermis and are almost certainly portions of a tissue which was originally broader, and may have filled the spaces between the

central column and the detached strips. At a higher level the column gradually expands and the short cells become rather larger and much longer, and are also distinguished from the lower tissue by their much better state of preservation. These elongated cells (fig. 12, *b*; text-fig. 3, E) accommodate themselves to the slightly increased diameter of the distal region of the central column, which ends in a conical apex, by a tendency to slope a little towards the summit away from the median line. The form of the apex of the central column is shown in text-fig. 3, C, and in this, as in many other examples, some of the cells in the apical region are rendered conspicuous by the presence of globules and patches of a dark substance.

Text-fig. 2, A, B; text-fig. 3, E; figs. 12, *a*, 16, *a*, and figs. 17–19, illustrate the structural features of this part of the megasporophylls. The upper portion of the



TEXT-FIG. 3.—A, section (diagrammatic) near the proximal ends of scales and megasporophylls (Section 10); B, transverse section of one of the interseminal scales shown in A (Section 10); C, apex of nucellus; D, surface-view of micropylar tube showing bases of papillæ (Section E); E, interseminal scales and megasporophyll (partly diagrammatic); *a*, apex of nucellus; *d*, union of peripheral tissue of megasporophyll with interseminal scales (Section E).

central region, characterised by the elongated cells and conical apex, is considered to be the nucellus, while the lower and narrower column of shorter and less distinct cells is referred to as the pedicel. The pedicel, as seen in text-fig. 3, E, is sometimes represented by still narrower and crushed strands of tissue, such as is shown in

fig. 26, *n*, and at iii, fig. 17, also, in a less contracted form, in figs. 20, 22, 23, where it is surrounded by a loose envelope of tissue. The appearance presented by the transverse sections reproduced in figs. 20, 22 (cut about level iv in text-fig. 2, A, and at ii, fig. 17) suggests a differentiation into an axial strand and an enclosing zone of crushed parenchyma. I have not been able to recognise any tracheal elements, though it is highly probable that in older specimens such would occur in the centre of the pedicel, as indicated in figs. 20, 22.

Returning to text-fig. 2, A; the loose strips of tissue belonging to the cylinder of tissue surrounding the central column (*cf.* fig. 23) become adherent to the nucellus, and the investing tissue now closely embraces the wider central column as an integument distinguished by its smaller, shorter, and less distinctly preserved cells from the larger elements of the nucellar region. At the shoulders of the nucellus the cells of the integument become larger and slightly extended in a horizontal direction (figs. 12, 18, 19), and as the integument increases further in breadth and overtops the nucellus, these cells become larger and constitute a conspicuous palisade layer which occupies the greater part of the breadth of the integument. This distal end of the megasporophyll is clearly a broad micropylar region, ending in a wide-open V-shaped apex (figs. 12, 18, 19; text-fig. 2, A), the centre of which leads to a very narrow canal, probably slit-like rather than circular in section, extending to the summit of the nucellar cone. This micropylar canal is exceedingly narrow and is represented by a very small space between the tips of the palisade cells. In fig. 18 and in other sections there are indications of a very slender upward extension of the nucellus into the micropyle, suggesting a shrivelled beak-like prolongation. The micropylar region is bounded externally by an epidermal layer with strongly cuticularised outer walls which project as short and blunt teeth like those described on the epidermis of the interseminal scales (figs. 12, 16, 18, 24; also, in surface-view, text-fig. 3, D). It is noteworthy that this epidermis does not extend below the region where megasporophylls and scales come into contact laterally, but it seems to die out near the shoulder of the nucellus. Next the epidermis there is a layer of similar small cells, not very clearly shown, and this is succeeded by the radially elongated palisade elements. The ovule seen in fig. 18 shows very clearly the integument partially separated from the nucellus.

The morphological features of the megasporophyll are further illustrated by the series of transverse sections reproduced in Plate 11, figs. 21–27. The section reproduced in fig. 27 and the smaller piece more highly magnified in fig. 24 show the cylindrical micropylar tube above the apex of the nucellus (level i, text-fig. 2, A): the thick cuticle and projecting teeth are clearly seen, also the radially elongated cells, some of which have dark contents, meeting or very nearly meeting at the centre. Fig. 21 shows the apical part of the nucellus, *n*, surrounded by the integument in which the lower and shorter palisade cells are seen at *c*: portions of the adjacent interseminal scales are in contact with the outer edge of the integument.

This section was cut about the level ii, text-fig. 2, A. At a slightly lower level (i, fig. 17, Plate 11) the nucellus is rather broader and the dark cell-contents characteristic of the apical cells are no longer seen: the broad integument is now composed of smaller cells. In fig. 23, cut at ii, fig. 17, the closely investing integument of fig. 25 is replaced by a loose and more ragged sheath of torn tissue, and at a still lower level (figs. 20, 22: cut at iii, fig. 17; iv, text-fig. 2, A) the central column or pedicel is further reduced in breadth. The outer cells of the loose envelope in figs. 20, 22, 23 are torn, and there is no indication of the epidermal layer shown in fig. 21. Passing nearer the proximal end, transverse sections (cut about the levels v, text-fig. 2, B; text-fig. 3, E; and iii, fig. 17) show a still narrower and more crushed axial column with its ragged detached sheath separated by fairly large spaces from the interseminal scales. Such sections are shown in the more central part of fig. 9, the edges of which show the megasporophylls cut nearer their apical ends, also in fig. 26 and in text-fig. 3, A. It is by no means improbable that the large spaces between the loose sheath and the interseminal scales (figs. 20, 22, 23, 26, etc.) are the result of the disappearance of loose tissues such as LIGNIER, SOLMS-LAUBACH, and WIELAND have described in the seed-peduncles of Bennettitean strobili; but further reference is made to this possibility on a later page.

A reference to text-fig. 3, E, *d*, illustrates a common feature in the megasporophylls, namely, the intimate association, and in some cases apparently organic connection, between the loose cylinder of cells and the tissue of adjacent interseminal scales. This fact, in conjunction with other features already alluded to, points to an absence of a well-defined limiting layer in the pedicels of the ovules and reminds one of the absence of a normal epidermis in the seed-peduncles of Bennettites.*

COMPARISON WITH OTHER TYPES.

Bracts and Hairs.—The bracts of the Eathie species agree generally with those of *Bennettites Gibsonianus* Carr. and *B. Morierei* (Sap. and Mar.), as also with the corresponding structures in American examples of Cycadeoidea. The great abundance of secretory sacs, the occurrence of thick-walled hypoderm, and, so far as can be ascertained, the structure of the vascular bundles are features common to all. The ground-tissue cells in *B. Gibsonianus* have all thick walls with scalariform thickening,† while in *Williamsonia scotica* this tissue consists only in part of sclerous cells and not of scalariform elements. In *B. Morierei*‡ the ground-tissue cells are described by LIGNIER as more or less sclerous, some having narrow canals while others show transversely elongated pits in their walls. WIELAND also calls

* LIGNIER ('94).

† SOLMS-LAUBACH ('91), p. 432; CARRUTHERS ('70), Plate 40, figs. 8-10.

‡ LIGNIER ('94), p. 20, Plate 1, fig. 17.

attention to the occurrence of transverse markings in the cells of **American species**.* The hypodermal tissue in *Williamsonia scotica* characterised by the thick and pitted walls (fig. 14) of the cells agrees closely with similar elements in some of the previously described species and must have rendered the bracts exceedingly tough and resistant, giving them a texture comparable with that of the pinnæ of some species of *Encephalartos*. Similarly the very thick cuticle and the sunken stomata are characters denoting special protection. LIGNIER† records stomata in *B. Morierei*, and a few were noticed by Dr. BARBER in *Bennettites Gibsonianus*,‡ but WIELAND has not described any in the bracts of American strobili.§

It is the substitution of long hairs for the multicellular scales of other species that constitutes the most striking peculiarity in the vegetative structures in *Williamsonia scotica*. In *Cycadeoidea nigra* WIELAND|| describes the ramental scales as one cell in thickness, but in most species, e.g., *Bennettites Gibsonianus*, *B. Morierei*, *Cycadeoidea gigantea*,¶ and in the majority of American species, particularly in the genus *Cycadella*, the scales are often several cells thick in the middle. The hairs of *Williamsonia scotica* agree fairly closely with those of recent Cycads, such as *Dioon edule*,** species of *Encephalartos*, and other genera : while they differ from the ramenta of the majority of recent ferns.

In the arrangement of the vascular bundles the bracts of the Scotch type resemble most closely *B. Morierei*. The branching of the vascular strands in the upper region of the bracts in the French species led LIGNIER†† to describe the bracts as incomplete and as representing the basal portions of larger organs. The mutilated distal ends of the bracts in the French specimen and the general absence of the tips in WIELAND'S strobili preclude any definite statement as to the nature of the terminal portions of these protecting leaves. The occurrence of lateral appendages on the distal parts of two of the longest bracts of *W. scotica* affords some support to LIGNIER'S contention, though in the Scotch type the bracts are pinnate, and not palmate as LIGNIER believed to be the case in the French species. These bracts may be regarded as homologous with pinnate vegetative fronds, and they afford an illustration of the slender dividing-line between foliage leaves and bracts analogous to that between carpellary leaves and fronds described by THISELTON-DYER‡‡ and WIELAND§§ in *Encephalartos* and *Zamia* respectively.

* WIELAND ('06), p. 115 ; fig. 60, C.

† LIGNIER ('94), p. 18.

‡ SCOTT ('09), p. 571.

§ WIELAND ('06), p. 115.

|| *Ibid.*, p. 52.

¶ SEWARD ('97²).

** *Ibid.*, Plate 3, fig. 6.

† LIGNIER ('94), pp. 23-25.

‡‡ THISELTON-DYER ('01).

§§ WIELAND ('02).

Peduncle.—The bract-bearing lower portion of the fertile shoots of several American species agrees closely with the sterile half of the Eathie fossil as regards the narrow diameter of the axis, the peripheral position of the vascular cylinder, and the scalariform pitting of the tracheæ.*

Interseminal Scales and Megasporophylls.—Comparison with other species of *Williamsonia* is necessarily restricted owing to the absence of petrified specimens. The interseminal scales of the Yorkshire species described by NATHORST† from preparations of the cuticular membranes, and those of *Williamsonia* from Mexico, figured by WIELAND,‡ agree closely with the scales of *W. scotica*, and there is no reason for supposing that the interseminal scales and megasporophylls of *Williamsonia* differed essentially from those of *Bennettites*. The length of both fertile and sterile appendages in *Williamsonia* is less than in *Bennettites Gibsonianus* and *B. Morierei*; but in American strobili, in which the receptacle has the form of an elongated cone instead of the hemispherical cushion of the French and English species, the scales and seed-peduncles are no longer or even shorter than those in *Williamsonia*. The micropylar region of *Williamsonia*, as described by NATHORST, appears to be broader than in *Bennettites*, and this difference is well illustrated by *W. scotica*. Between the micropylar tube of *W. pecten*,§ as represented by the mummified cuticle, and that of *W. scotica*, there is a striking resemblance, which extends to the papillose outgrowths of the epidermal cells. A comparison of the structure of the micropylar integument of the Scotch specimen with that described by LIGNIER, SOLMS-LAUBACH, and WIELAND points to certain differences, such as the greater breadth in *W. scotica*, and the large transversely elongated cells, which may be of generic importance.

The much simpler structure of both interseminal scales and megasporophylls in *W. scotica* is an obvious peculiarity distinguishing them from their highly differentiated homologues in *Bennettites*.|| This raises the question as to the possibility of this difference being due to immaturity. The relative disposition of sterile and fertile appendages is similar in all cases; in American strobili each micropylar tube is the centre of a rosette of six, or in some cases, eight or ten interseminal scales, and in *W. pecten* NATHORST shows the tube surrounded by six scales. In *Bennettites Gibsonianus* and *B. Morierei* the distal ends of the interseminal scales are considerably swollen and enormously exceed in breadth the micropylar tubes, presenting in this respect a marked contrast to the almost equal breadth of the two kinds of organs in *Williamsonia scotica*. In *B. Gibsonianus*

* WIELAND ('06), fig. 59, p. 113; Plates 39, 40, etc.

† NATHORST ('09), Plates 3, 4.

‡ WIELAND ('11), fig. 14, p. 457.

§ NATHORST ('09), Plate 3, figs. 6, 7.

|| I use this name in a wide sense as including the strobili described by WIELAND in species of *Cycadeoidea*. The question of *Cycadeoidea* or *Bennettites* as the more appropriate designation for the plant as a whole need not be raised.

the tips of some of the interseminal scales are 2·8 mm. broad, the micropylar tube being only 0·25 mm. wide; in *W. scotica*, on the other hand, the diameters are respectively 0·23 and 0·15 mm. In the latter species both scales and megasporophylls are clearly young structures and, as previously stated, there are indications of feebly marked differentiation in the axial regions which suggest early stages in the development of conducting strands. But, making due allowance for further development, it is difficult to believe that the strongly cuticularised superficial tissue of the interseminal scales of *W. scotica* could admit of any substantial increase in size of the distal ends of these organs. Whatever further differentiation and growth may have been in store for the scales, it is hardly conceivable that their distal ends could have reached dimensions comparable with those of Bennettites. WIELAND* describes some interseminal scales of a species of *Cycadella* as young organs, 0·75 mm. long and 0·15 mm. broad, consisting of "thick-walled" and "scalariform" elements, but such tissue suggests rather a partially aborted scale than one capable of further growth.

No young megasporophylls like those of the Scotch species have been fully described by WIELAND, and anything more than a superficial comparison with the mature seed-peduncles of Bennettites is exceedingly difficult.

The mature seed-stalks of *Bennettites Morierei*, taking that species as the type, are characterised by a high degree of differentiation: a transverse section through the middle of a seed-stalk shows a broad enclosing zone of loose tubular cells surrounding a layer of cells with coloured contents ("l'assise colorée"), parenchymatous ground-tissue, and a concentric conducting strand. This internal tissue, that is the tissue internal to the tubular envelope, undergoes no appreciable change in the length of the seed-stalk. The tubular envelope, on the other hand, decreases a little in breadth nearer the proximal end, that is as the strobilus-axis (receptacle) is approached, though the individual cells increase in number and are reduced in size. Still lower, the envelope is converted into a tissue of large parenchymatous cells, and each of these cells corresponds to a group of tubular elements.† In the other direction, near the base of the seed, the diameter of the tubular envelope decreases, the diameter of the individual cells increasing until the zone is reduced to two layers: (i) a tubular layer; (ii) a folded layer ("l'assise plissée"). The former extends over the sides of the seed as isolated or grouped tubes and the cells of the second layer, at about half the length of the seed, become radially extended and abut on the epidermis of the interseminal scales. These cells continue to elongate transversely as the layer is followed towards the apex of the seed, and their walls become thicker; in this region LIGNIER speaks of the layer as "l'assise rayonnante." In the micropylar region the two layers of the tubular envelope undergo a complete change. The outer layer assumes the rôle of an epidermis and the radially extended cells

* WIELAND ('06), p. 175.

† LIGNIER ('94), p. 37.

form a sub-epidermal layer. LIGNIER shows that this tubular envelope arises from a single epidermal layer, and he considers that these two superficial layers in the micropylar region have the same origin. From the base of the micropyle and over the whole of its surface the cells of the tubular layer are completely transformed; they now form a compact layer of sclerous elements. The sub-epidermal layer, which is continuous with the radially elongated layer, in the micropylar region is formed of short isodiametric cells with thick walls. The inner epidermal layer, lining the inside of the micropyle, consists of narrow radially elongated cells.*

On the stalks bearing atrophied seeds LIGNIER records the occurrence of an epidermis at their lower end identical with that of the interseminal scales. Next to this is a zone of parenchymatous ground-tissue consisting of young and partially developed cells enclosing a small axial vascular strand. Passing up the stalk almost up to the base of the seed, there is differentiated below the epidermis and at the expense of the parenchymatous ground-tissue a coloured layer ("l'assise colorée") and at the same time the epidermal cells become modified, being transformed into tubular elements. Still higher up the stalk the epidermal cells form a loose tissue, each tube being isolated from its neighbours; the cells become divided longitudinally and so a broad tubular envelope is produced which replaces the original epidermis. This alteration of the epidermis, which begins at the base of the seed, extends to the proximal end of the peduncles. From a study of the mature and partially atrophied megasporophylls, LIGNIER is led to the conclusion that the seed-stalks were very short in the earlier stages of development and were covered with a normal continuous epidermis. At a later stage the epidermal cells were considerably elongated and changed into tubular elements, and in a more advanced stage they divided longitudinally and separated from one another as cylindrical tubes.

Returning to the megasporophylls of *Williamsonia*; the results arrived at by LIGNIER suggest certain comparisons. The radially extended cells lining the micropyle of *B. Morierei* are directly comparable with the relatively larger cells in the Scotch species. Similar cells are described by WIELAND in the micropylar tube of *Cycadeoidea Wielandi*.† It is, however, the absence of an epidermis of the usual type in the seed-stalks of Bennettites that suggests a possible clue to the interpretation of the anatomical features exhibited by *Williamsonia scotica*. The column of short-celled parenchyma below the broader upper region, which has been spoken of as the nucellus, may correspond to the "internal tissues" of LIGNIER's peduncles; that is the central tissue in figs. 20, 22, 23, may be correlated with the axial conducting strand and the surrounding parenchyma in the peduncle of *B. Morierei*; and the space beyond it, which becomes enlarged towards the proximal ends of the megasporophylls (fig. 26; text-fig. 3, E, etc.) may have been originally occupied by LIGNIER's tubular envelope. This comparison is by no means complete,

* LIGNIER, *loc. cit.*, p. 45.

† WIELAND ('11²), p. 141, fig. 3, C.

and there are difficulties in regard to detailed correlation, but it offers a possible interpretation of the absence of a typical epidermis from the megasporophylls except in the region where the integument begins to assume the structural features which it exhibits in the micropylar region. The nucellus appears to have been petrified at a stage in development anterior to the differentiation of a megaspore, and there is no indication of any pollen-chamber. The integument is in comparison much more advanced and the appearance of its tissue does not suggest the possibility of further growth; at the base of the micropylar tube the integument closely invests the conical apex of the nucellus and then passes downwards as a narrow sheath of smaller cells into the loose and ragged cylinder (figs. 20, 22) which it is suggested may represent a portion only of the axial column, the spaces internal and external to the sheath having been originally occupied by delicate tissue. The megasporophyll as a whole has the form of a long and narrow organ bearing an apical megasporangium closely invested and overtopped by an integumentary extension of the peripheral region of the supporting column or pedicel. In the long and prominent micropylar tube the young ovules bear a fairly close resemblance to those of certain Conifers about the time of pollination. The long micropylar tube of *Fitzroya* with its broad funnel-shaped apex affords a striking illustration of such resemblance.

Williamsonia scotica does not furnish decisive evidence as to the homologies of interseminal scales and stalked ovules, but the close resemblance between the two kinds of appendages, already emphasized by previous writers, receives further support. No new reasons are supplied in favour of the view that scales and ovules are not strictly homologous. Both are believed to be leaves; in the one case, leaves transformed into cylindrical organs bearing terminal integumented megasporangia, and, in the other, sterile, or sterilised—whichever term is preferred—sporophylls. There are two additional points suggested by the structure of the fertile portion of the strobilus, namely, the possibility that the megasporophylls are arrested rather than immature organs, and, secondly, the method of pollination. In regard to the first point, there would seem to be no adequate reason for doubting the correctness of the view that the megasporophylls are in an immature condition, and are potentially perfect ovules.

The dense woolly covering of hairs closely investing the surface of the interseminal scales and megasporophylls reminds one of an inflorescence of *Æsculus hippocastanum* wrapped up in its winter fur, and hardly suggests a collection of ovules accessible to microspores. In all probability, at a later stage of development, the protecting bracts would bend outwards, carrying with them their felt of hairs, leaving exposed the receptive micropyles.

SYSTEMATIC POSITION OF THE STROBILUS.

In a paper on the leaves of *Williamsonia*, published in 1897, I wrote: "Although we have not as yet discovered any examples of *Williamsonia gigas* showing internal

structure, there are many reasons for believing that this Lower Oolite fossil represents an inflorescence very closely allied to that of *Bennettites Gibsonianus*.* The recent work of Prof. NATHORST,† so far, at least, as regards the female organs, and it is these with which we are alone concerned, has not revealed any facts necessitating a modification of this opinion. It is by no means easy to decide between *Williamsonia* and *Bennettites* as the more appropriate generic designation for the Scotch fossil. The question of *Bennettites versus Cycadeoidea* is hardly germane to the present discussion, as we are dealing with a detached fertile shoot, and, whatever force there may be in the arguments advanced by WARD and WIELAND in favour of the latter and older name for Mesozoic trunks bearing fertile branches, the use of BUCKLAND'S genus (*Cycadeoidea*) would be inappropriate in the case of a single strobilus. The difficulty might be shirked, not altogether without reason, by adopting the *pis aller* of instituting a new genus on the ground of the substitution of long hairs for the usual multicellular scales, hitherto regarded as characteristic of Mesozoic *Bennettiales*; but, in view of the meagreness of our knowledge of the structure of undoubted *Williamsonias*, which we know have hairy bracts—and the hairs may be of the type represented by *Williamsonia scotica*—it is impossible to estimate the degree of morphological difference between the Scotch strobilus and the Yorkshire *Williamsonias*.

The bi-sporangiate character of WIELAND'S strobili affords a definite distinction between the Lower Cretaceous and Jurassic American species and the new type. On the other hand, it would seem practically certain that some of the *Williamsonias* recently investigated by NATHORST are, as he maintains, unisexual. In the arrangement and form of the bracts some of the English specimens of *Williamsonia*, especially certain strobili in the Yates collection, closely resemble the Eathie species, but the same remark may be made as regards *Bennettites* strobili. In its elongated conical axis, *Williamsonia scotica* agrees with the English *Williamsonias* and with some of WIELAND'S species, while in *Bennettites Gibsonianus* and *B. Morierei* the axis is of the short hemispherical type, which, as WIELAND suggests, probably represents a later stage in evolution.

The definitions of the flowers of *Bennettites* and *Williamsonia* given by Mr. CARRUTHERS, the author of both names, necessarily require modification in the light of recent research, but there are some generic distinctions recognised by him which it is important to notice. The stems of *Williamsonia* are described as cylindrical, covered with rhomboidal scars of deciduous petioles and bearing terminal flowers. In *Bennettites*, the stem is stated to be elliptical in transverse section, covered with the persistent bases of petioles, and bearing fruits on secondary axes "not projecting beyond the bases of the petioles."‡ The circular or elliptical form of

* SEWARD ('97), p. 373. See also ('95), pp. 146 *et seq.*

† NATHORST ('11), p. 28.

‡ CARRUTHERS ('70), pp. 691, 694.

the stem is probably a character of no taxonomic importance. The supposed distinction between *Williamsonia* and *Bennettites* as regards the persistent or deciduous nature of the petioles rests on very slender evidence; in the few specimens of stems described by WILLIAMSON and other authors from material associated with fronds of *Zamites gigas*, the external features are entirely consistent with the view that, in *Williamsonia*, as in *Bennettites*, the stem was covered with an armour of old leaf-stalks. There remains the distinction, probably a valid one, based on the position of the strobili. In *Bennettites*, the fertile shoots are lateral and axillary, the strobili being partly enclosed by the adjacent petiole-bases, or at most projecting very slightly beyond the surface of the trunk, while in *Williamsonia* the main trunk bore comparatively long fertile shoots in the apical region. The best specimens of such shoots are in the Yates collection* already referred to, and other examples may be seen in the museums of Leeds, Whitby, Scarborough, and in the British Museum. These branches bear numerous hairy bracts, and the terminal strobili are covered with similar imbricating leaves.

The morphological features of the Eathie strobilus do not throw any fresh light on the interesting question as to the grounds on which the Bennettitean type of flower has been spoken of as affording the "key to the Angiosperms."† One difficulty in the way of regarding the strobilus of *Williamsonia* or *Bennettites* as closely related to the Angiospermous flower is the great difference between the carpel of a Dicotyledon and Monocotyledon and the naked ovule with its encircling rosette of interseminal scales. In view of this morphological contrast, apart from other considerations, the statement that "we seem justified in the conclusion that of all known plants the Bennettiteæ were the most nearly akin to the Angiosperms,"‡ serves not only to express a definite point of view in regard to the most promising connecting line between the Angiosperms and Gymnosperms, but it also emphasizes the comparative isolation of the Angiospermous type. Recent comparisons between seeds of *Gnetum* and those of *Bennettites* by Miss BERRIDGE§ and Mrs. THODAY|| reveal a close similarity. Prof. PEARSON's figure of the long micropylar tube of *Welwitschia*¶ may be quoted as a further illustration of the resemblance between a Gnetalean ovule and those of the Bennettitales. It is, however, difficult to estimate the degree of relationship between the Gnetales and the Bennettitales.

Comparisons between the Bennettitales and Gnetales and Ginkgoales are dismissed by COULTER and CHAMBERLAIN as "too slight to merit serious discussion."** The

* SEWARD ('97); WIELAND ('11).

† OLIVER ('06).

‡ SCOTT ('11), p. 88.

§ BERRIDGE ('11).

|| THODAY ('11).

¶ PEARSON ('09), Plate 23, fig. 11.

** COULTER and CHAMBERLAIN ('10), p. 86.

difference between a Maidenhair-tree and Bennettites or Williamsonia is undoubtedly considerable; but, it may be urged, the differences between these extinct types of Gymnosperms and the Angiosperms are also considerable. In the normal female shoots of *Ginkgo* two sessile ovules are borne on a naked axis; on the other hand, examples are by no means rare in which the peduncles bear several stalked ovules, the slender pedicels of which are homologous with leaf-petioles. Jurassic fossils described by HEER* from Siberia as male flowers of *Ginkgo* or *Baiera*,† and recorded by other authors from different localities, bear a close resemblance to certain abnormal female shoots of *Ginkgo biloba*; they consist of an axis, which was clearly a fairly stout structure and much larger than that of the male flower of a recent *Ginkgo*, bearing numerous spirally disposed slender stalks given off at a wide angle and terminating in a small distal swelling. The swollen tips were identified by HEER as microsporangia; but no undoubted microspores have been discovered. An examination of some of HEER's specimens borrowed from St. Petersburg through the kind offices of my friend Prof. ZALESSKY, failed to provide support to HEER's view as to the male character of these fossils. I have elsewhere discussed‡ the nature of these supposed male flowers, suggesting that they are more likely to be shoots bearing carpellary leaves. If the axis of one of these Jurassic species, for which I have adopted SAPORTA's name *Stenorrachis*,§ employed by NATHORST|| for ovuliferous shoots of a similar type, bore sterile scale-leaves interspersed with the fertile organs, or if leaves were added to the axis of an abnormal flower of *Ginkgo biloba*, the resemblance to the Bennettitean type would be fairly close. This comparison, though resting on a basis which may be reasonably criticised as inadequate, is perhaps not unworthy of consideration. The morphology of the Bennettitean flower is still a problem to be solved, and the attractive hypothesis that would have us regard this dominant group of the Mesozoic era as a guide to the evolution of the class which now occupies the pre-eminent position in the vegetable kingdom, requires to be substantially strengthened before it can claim to have solved the mystery of the origin of the flowering plants.

DEFINITION.

Williamsonia scotica sp. nov. (Type-specimen in the Royal Scottish Museum, Edinburgh). Strobilus ovoid, covered with numerous linear bracts, some of which bear short lateral appendages or reduced pinnæ; axis cylindrical with a maximum diameter of 1.5 cm. bearing in the lower region bracts and long hairs, and in the upper conical and gradually tapered portion interseminal scales and megasporophylls.

* FUJII ('96); SEWARD and GOWAN ('00); SPRECHER ('07).

† HEER ('77), Plates 4, 6, 11; ('78), Plate 6.

‡ Particularly in a paper on Mesozoic plants from Afghanistan, now being published by the Geological Survey of India (May, 1912).

§ SAPORTA ('75).

|| NATHORST ('02).

Strobilus in all probability borne on a lateral branch, either terminally or as an axillary shoot, and extending well beyond the zone of persistent leaf-bases which, it is assumed, enclosed the parent stem. The overlapping series of bracts are embedded in a dense woolly mass consisting of very long tubular hairs given off from the epidermis of the bracts and the lower part of the axis of the strobilus. The interseminal scales, 2 mm. long and 0.23 mm. in breadth at the truncate unexpanded distal ends, are polygonal in section and arranged as a rosette of 5-6 round each megasporophyll. Megasporophylls, which are immature, are of the same length as the interseminal scales; they consist of a cylindrical axis bearing a terminal megasporangium enclosed by a single integument prolonged as a micropylar tube above the conical end of the nucellus and characterised by a slightly funnel-shaped apex.

BIBLIOGRAPHY.

- ARBER, E. A. N., and PARKIN, J. ('07). "On the Origin of Angiosperms," 'Journ. Linn. Soc.,' vol. 38, p. 29.
- BERRIDGE, EMILY M. ('11). "On some Points of Resemblance between Gnetalean and Bennettitean Seeds," 'New Phytologist,' vol. 10, p. 140.
- CARRUTHERS, W. ('70). "On some Fossil Cycadean Stems from the Secondary Rocks of Britain," 'Trans. Linn. Soc.,' vol. 26, p. 675.
- COULTER, J. M., and CHAMBERLAIN, C. J. ('10). 'Morphology of Gymnosperms,' Chicago.
- FUJII, K. ('96). "On the Different Views hitherto proposed regarding the Morphology of the Flowers of *Ginkgo biloba* L.," 'Bot. Mag. Tokyo,' vol. 10, p. 7.
- HEER, O. ('77). 'Flora Fossilis Arctica,' vol. 4 (ii) 'Beiträge zur Jura-Flora, &c.,' Zürich.
- Idem* ('78). *Ibid.*, vol. 5.
- LIGNIER, O. ('94). "Structure et Affinités du *Bennettites Morierei* Sap. et Mar. sp." 'Mém. Soc. Linn. Normandie,' vol. 18.
- MILLER, HUGH ('57). 'The Testimony of the Rocks,' Edinburgh.
- NATHORST, A. G. ('02). "Beiträge zur Kenntniss einiger Mesozoischen Cycadophyten," 'K. Svensk. Vetenskapsakad. Hand.,' vol. 36, No. 4.
- Idem* ('09). "Paläobotanische Mitt. 8. Über *Williamsonia*, &c.," 'K. Svensk. Vetenskapsakad. Hand.,' vol. 45, No. 4.
- Idem* ('11). "Paläobot. Mitt. 9," *ibid.*, vol. 46, No. 4.
- OLIVER, F. W. ('06). "Pteridosperms and Angiosperms," 'New Phytologist,' vol. 5, p. 232.
- PEARSON, H. H. W. ('09). "Further Observations on *Welwitschia*," 'Phil. Trans. Roy. Soc.,' series B, vol. 200, p. 331.

- RICHARDS, J. T. ('84). "On Scottish Fossil Cycadaceous leaves contained in the Hugh Miller Collection," 'Proc. Roy. Phys. Soc. Edinb.'
- SAPORTA, LE MARQUIS DE ('75). 'Paléontologie Française,' sér. 2, vol. 2, Paris.
- SCOTT, D. H. ('09). 'Studies in Fossil Botany,' (edit. 2), vol. 2, London.
- Idem* ('11). 'The Evolution of Plants,' London (N.D.).
- SEWARD, A. C. ('95). 'Catalogue of the Mesozoic Plants in the Department of Geology, British Museum (Nat. Hist.),' "The Wealden Flora, II," London.
- Idem* ('97). "On the Leaves of Bennettites," 'Proc. Camb. Phil. Soc.,' vol. 9, Pt. V, p. 273.
- Idem* ('97²). "On *Cycadeoidea gigantea*, a new Cycadean stem from the Purbeck Beds of Portland," 'Quart. Journ. Geol. Soc.,' vol. 53, p. 22.
- Idem* ('11). "The Jurassic Flora of Sutherland," 'Trans. R. Soc. Edinburgh,' vol. 47, Part IV, p. 643.
- SEWARD, A. C., and GOWAN, J. ('00). "The Maidenhair Tree (*Gingko biloba* L.)," 'Ann. Bot.,' vol. 14, p. 109.
- SOLMS-LAUBACH, H. GRAF ZU ('91). "On the Fructification of *Bennettites Gibsonianus* Carr.," 'Ann. Bot.,' vol. 5, p. 419.
- SPRECHER, A. ('07). 'Le *Gingko biloba* L.,' Geneva.
- THISELTON-DYER, Sir W. T. ('01). "The Carpophyll of *Encephalartos*," 'Ann. Bot.,' vol. 15, p. 548.
- THODAY, MARY G. ('11). "The Female Inflorescence and ovules of *Gnetum africanum*, with notes on *Gnetum scandens*," 'Ann. Bot.,' vol. 25, p. 1101.
- WIELAND, G. R. ('02). "Notes on living Cycads," 'Amer. Journ. Sci.,' vol. 13, p. 331.
- Idem* ('06). "American Fossil Cycads," 'Carnegie Inst., Washington.'
- Idem* ('08). "Historic Fossil Cycads," *ibid.*, vol. 25, p. 93.
- Idem* ('11). "On the Williamsonia Tribe," *ibid.*, vol. 32, p. 433.
- Idem* ('11²). "A Study of some American Fossil Cycads, Part V," *ibid.*, vol. 32, p. 133.

EXPLANATION OF PLATES.

All the specimens figured are in the Royal Scottish Museum, Edinburgh. Photographs by Mr. Tams, Cambridge.

PLATE 9.

- Fig. 1.—Longitudinal section (cut along the line vi, fig. 28) of the upper part of the strobilus. *b*, bracts; *s*, interseminal scales and megasporophylls; *h*, *h'*, *h''*...hairs. *Ca.* × 3. Section 6.
- Fig. 2.—Longitudinal section of the lower part of the peduncle. *x*, *x'*, secondary xylem; *h*, hairs. *Ca.* × 2. Section 3.
- Fig. 3.—Part of the secondary xylem shown at *x'* in fig. 2. Section 3.
- Fig. 4.—Transverse section. *s*, scales and megasporophylls; *a*, bract showing detached superficial tissue on the inner side. *Ca.* × 2. Section D.
- Fig. 5.—Part of a transverse section more highly magnified (cut at i, fig. 28). *c*, piece of tissue of strobilus axis. × 10. Section 7.
- Fig. 6.—Transverse section of the peduncle at a lower level (iii, fig. 28). *x*, portions of vascular cylinder; *h*, hairs attached to axis; *a*, bract with partially detached epidermis. Section C.
- Fig. 7.—Transverse section of bract. *v*, *v*, vascular bundles. × 10. Section D.
- Fig. 8.—Part of a hair showing dark spiral lines. Section 9.

PLATE 10.

- Fig. 9.—Tangential section through the zone of interseminal scales and megasporophylls, showing the edges of this zone on the right and left margin. *m*, micropylar tube; *h*, hairs. × 10. Section 8.
- Fig. 10.—Longitudinal section of bract. *h*, hairs attached to epidermis; *sc*, sclerous cells below the thick epidermis of the outer side. *Ca.* 90. Section 6.
- Fig. 11.—Longitudinal section of part of the zone of scales and megasporophylls. *s*, attachment of scale and megasporophyll to axis. × 20. Section E.
- Fig. 12.—The distal part of the megasporophyll of fig. 11 more highly magnified. *c*, transversely elongated cells of micropylar tube; *a*, apex of nucellus; *b*, long cells of nucellus. *Ca.* × 100. Section E.
- Fig. 13.—Transverse section of lateral bud borne on axis of strobilus. *x*, bract and hairs shown in fig. 13A. *Ca.* × 6. Section B.
- Fig. 13A.—Bract *x* of fig. 13. *Ca.* × 40. Section B.
- Fig. 14.—Sclerous cells of bract in longitudinal section. × 300. Section 6.
- Fig. 15.—Sclerous hypoderm of bract in transverse section. *se*, secretory sacs and dark contents; *sc*, sclerous cells. *Ca.* × 100. Section 7.

Fig. 16.—Tip of micropylar tube, showing funnel-shaped apex and some papillose epidermal cells on the integument and on the adjacent interseminal scale. *a*, apex of nucellus. *Ca.* × 100. Section E.

PLATE 11.

Figs. 17–19.—Megasporophylls and scales in longitudinal section. i–iii, fig. 17, levels of sections described in the text. *a*, apex of nucellus; *c*, transversely elongated cells of micropylar tube; *s*, hypodermal tissue of scale (*cf.* fig. 24). Fig. 17, *Ca.* × 50, Section D; fig. 18, *Ca.* × 100, Section E; fig. 19, *Ca.* × 100, Section E.

Figs. 20–23.—Transverse sections at different levels of megasporophylls. *c*, as in fig. 19; *n*, nucellus. *Ca.* × 120. Section 8.

Fig. 24.—Transverse section near the distal end of a micropylar tube and surrounding scales. *Ca.* × 100. Section 8.

Fig. 25.—Transverse section (level i, fig. 17) showing nucellus and integument. *Ca.* × 120. Section 8.

Fig. 26.—Transverse section in lower part of zone of scales, etc. *s*, interseminal scales; *n*, lower part of nucellus. *Ca.* × 120. Section 10.

Fig. 27.—Transverse section, a portion of which is more highly magnified in fig. 24. *m*, micropylar tube. *Ca.* × 50. Section 8.

PLATE 12.

Fig. 28.—Strobilus in surface-view. I–VII, levels at which sections were cut. *a*, *β*, distal parts of bracts with appendages. Natural size.

Figs. 29, 30.—Enlarged distal portions of bracts *α*, *β*, in fig. 28. V, ? vascular strand. × 7.

Fig. 31.—Piece of strobilus (left-hand lower edge of fig. 28), showing:—A, ridged surface and broken transverse face, S, of bract; also *α*, *β*, surface and hairy covering of bract B.

Fig. 32.—Part of transverse section of axis, *ax*, and bracts, near base of strobilus. Slightly enlarged.

Fig. 33.—Transverse section showing part of main axis, *ax*, and lateral bud, B (level iv, fig. 28). Slightly enlarged.

Fig. 34.—Transverse section of part of main axis with vascular strand, *x'*, and axis of bud bearing bracts, with xylem, *x*, in oblique-tangential section (level V, fig. 28). $1\frac{1}{4}$ natural size.

Fig. 35.—Longitudinal section of upper part of strobilus. *x*, xylem; *s*, scales, etc. Natural size. Section D*.

Fig. 36.—Transverse section of part of strobilus-axis with bracts and pieces of vascular cylinder, *x* (cut at level III, fig. 28). Slightly enlarged. Section 4.

Fig. 37.—Transverse section of bract. *e*, detached epidermis; *sc*, hypodermal sclerous tissue; *v*, *v'*, vascular bundles; *a*, bundle enlarged in fig. 37*a*.
×14. Section 7.

Fig. 37*a*.—Bundle *a*, *v'*, of fig. 37. *ph*, phloem; *sc*, thick-walled elements.
Section 7.

Fig. 38.—Cuticle detached from epidermis of bract. Section C.

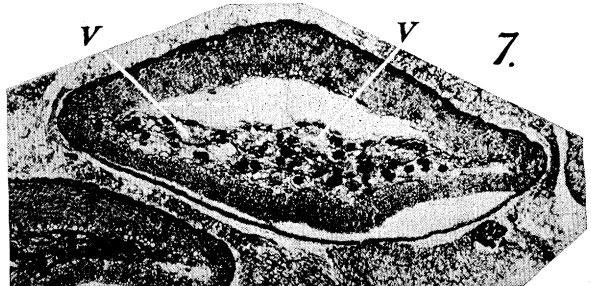
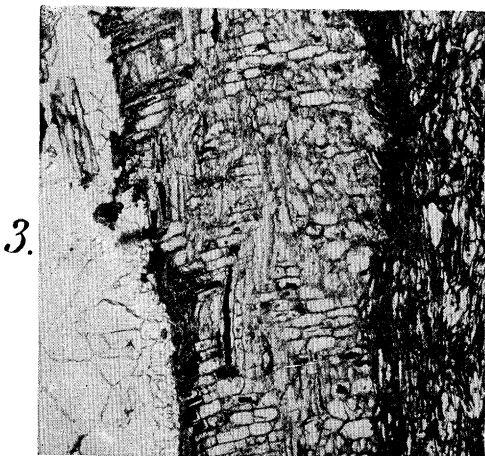
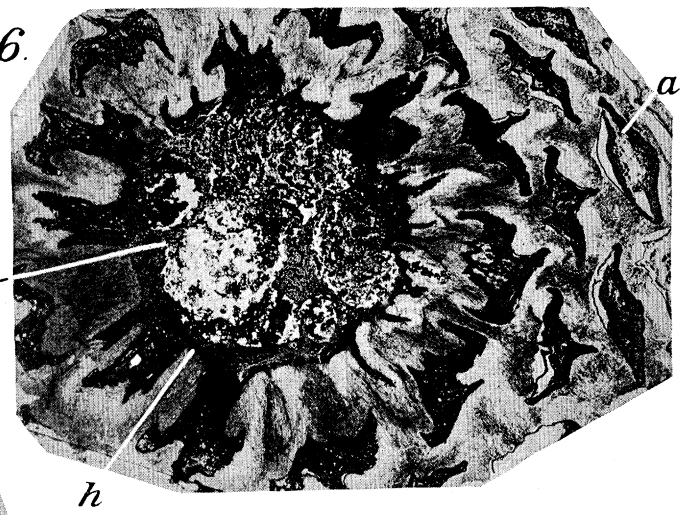
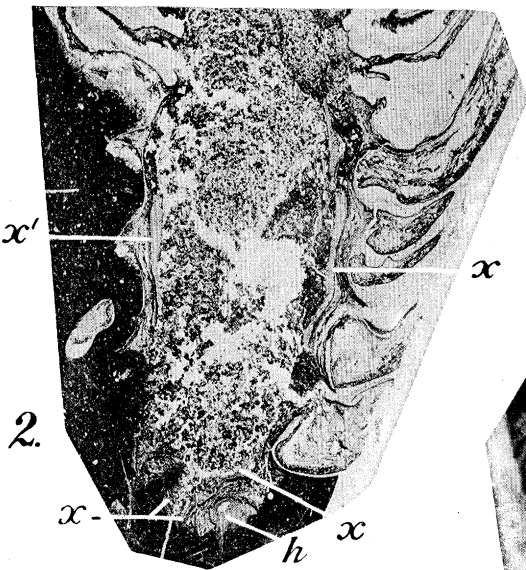
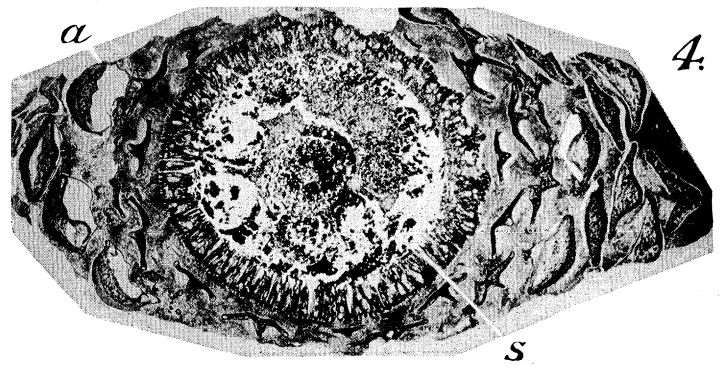
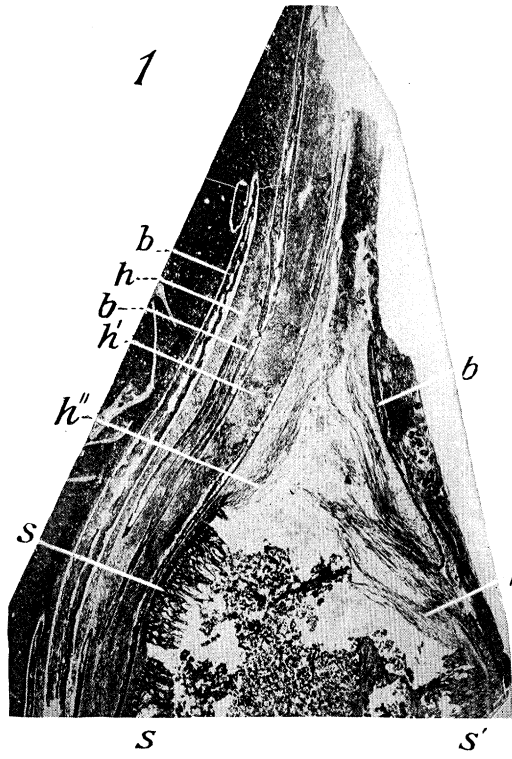
Fig. 39.—Transverse section of secondary xylem, crushed phloem, and medullary rays, *m*, from vascular cylinder of peduncle shown in fig. 36. Section 4.

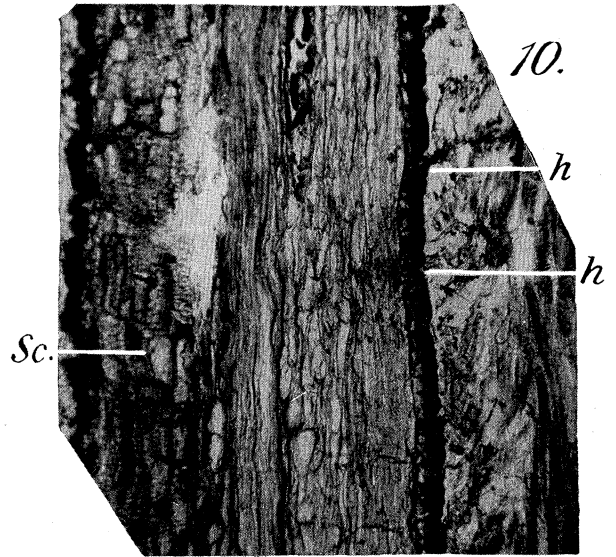
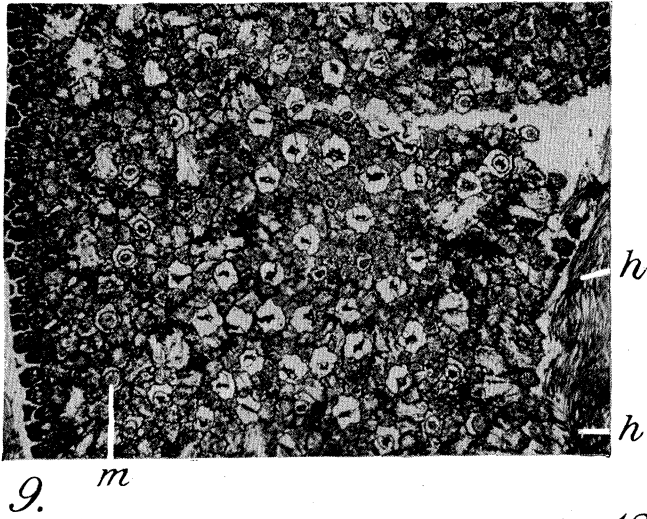
Figs. 40–42.—Attachment of hairs to epidermis of bracts. Fig. 40, Section 6;
figs. 41, 42, Section 9.

Fig. 43.—Epidermis of bract. Section 7.

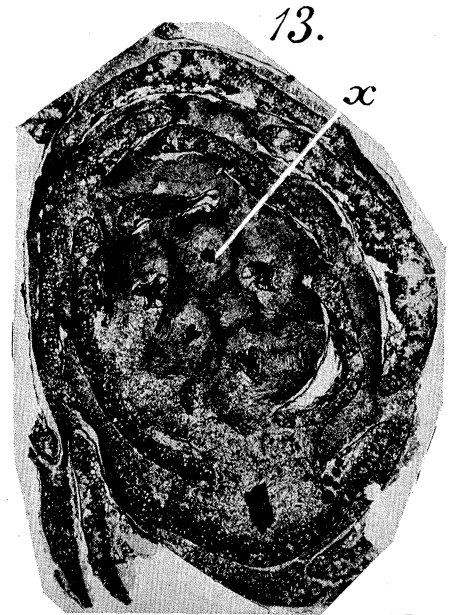
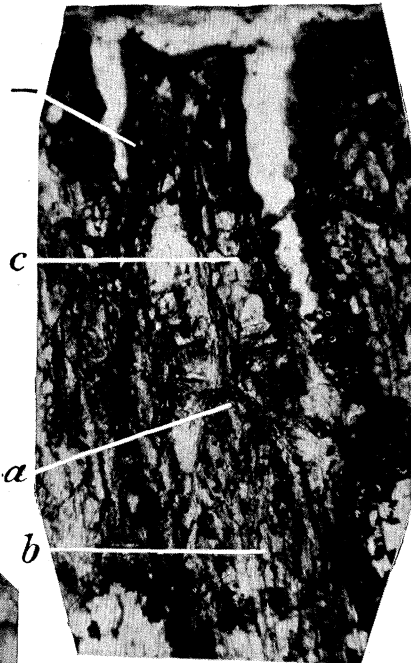
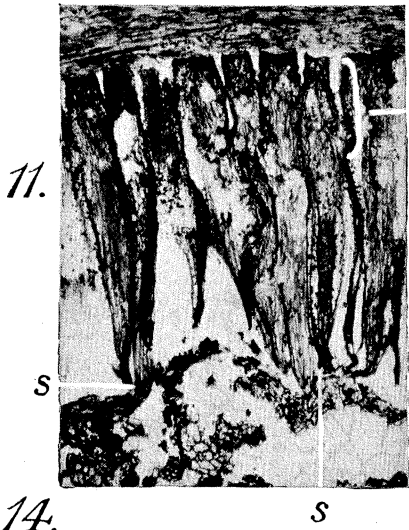
Fig. 44.—Part of a bract in transverse section. *sc*, sclerous tissue; *v*, vascular bundles. Section 7.

Fig. 45.—Part of interseminal scale, showing truncate and thick-walled apex.
h, hairs in transverse section. Section 7.

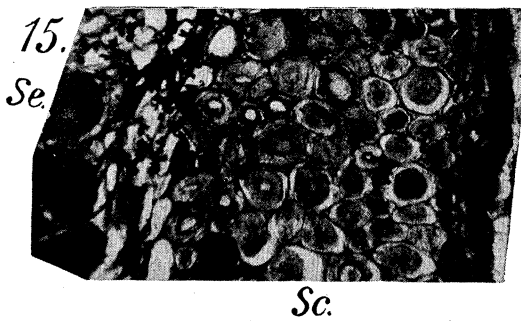
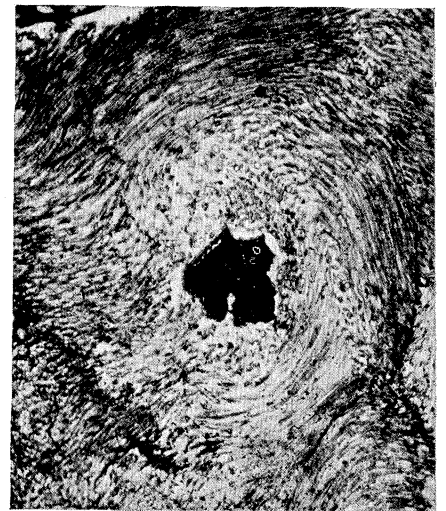
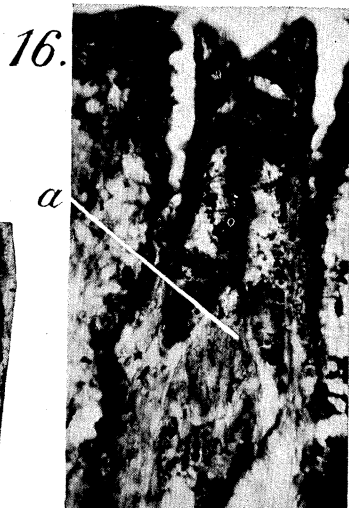


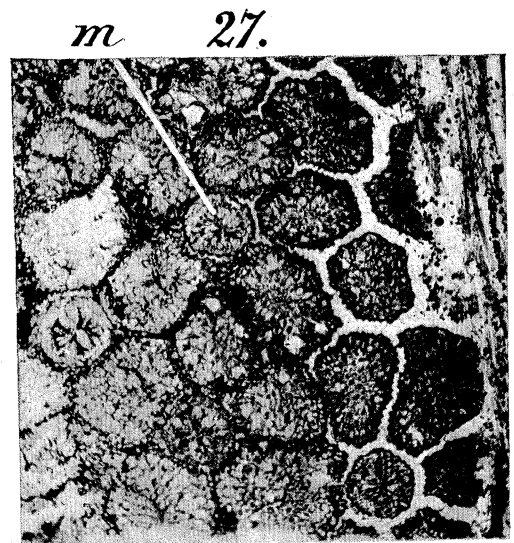
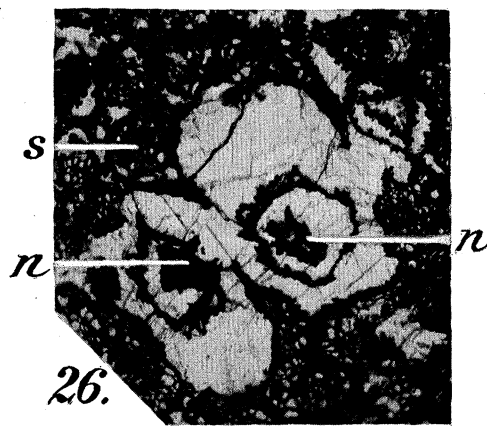
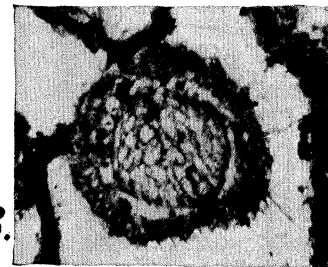
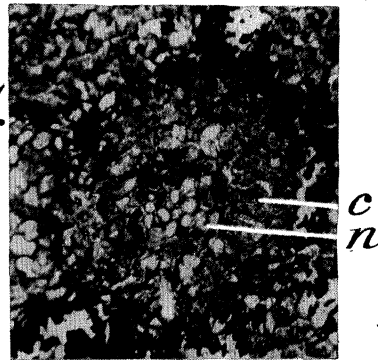
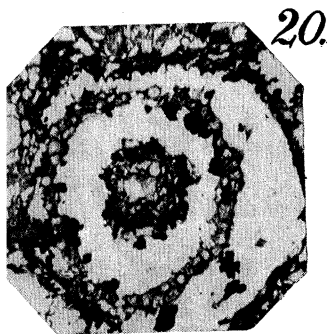
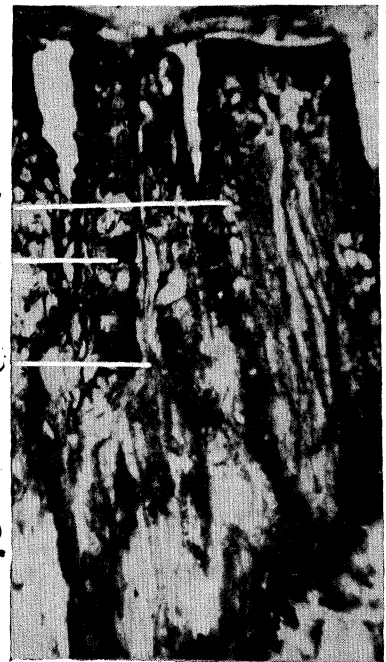


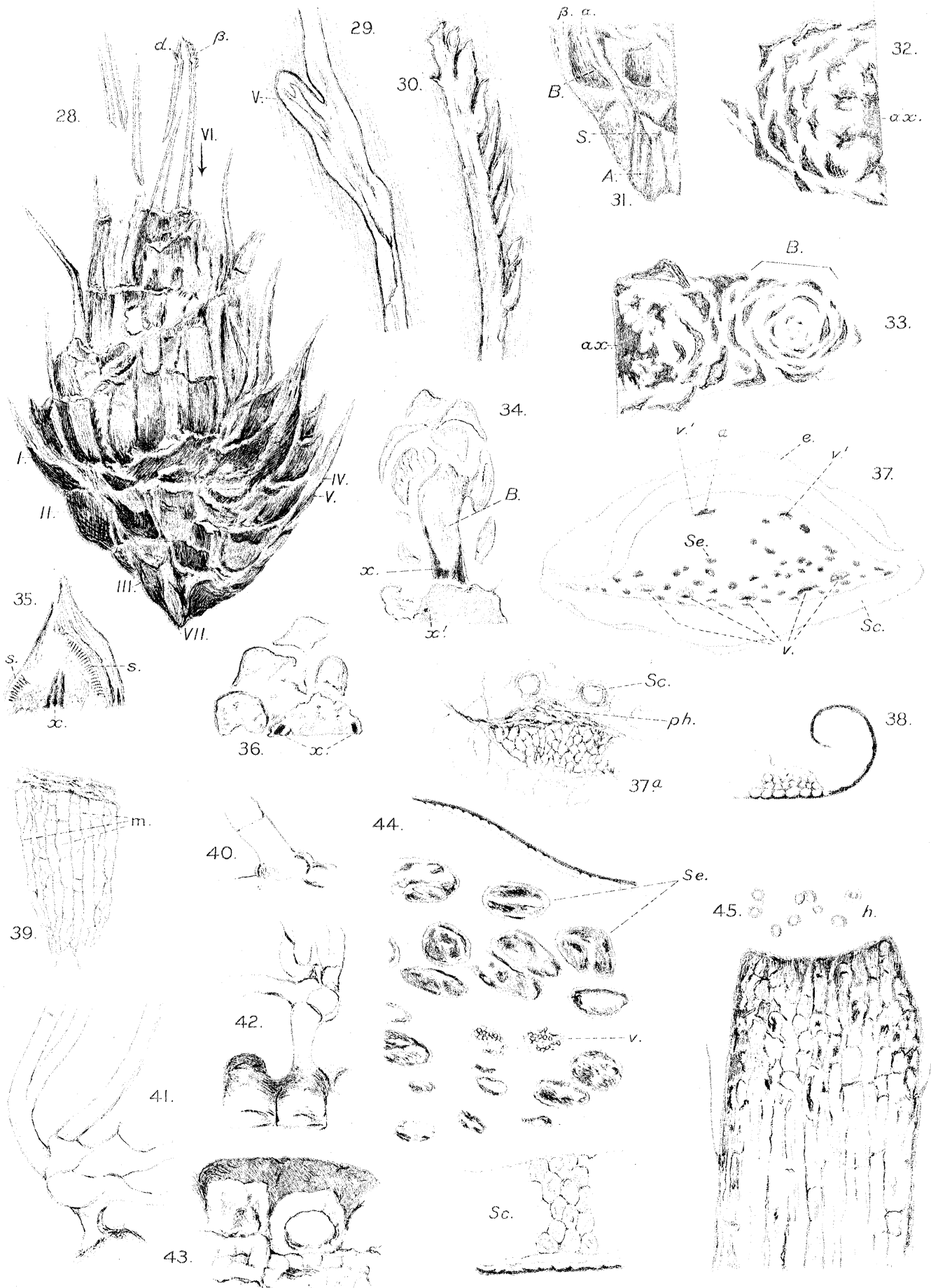
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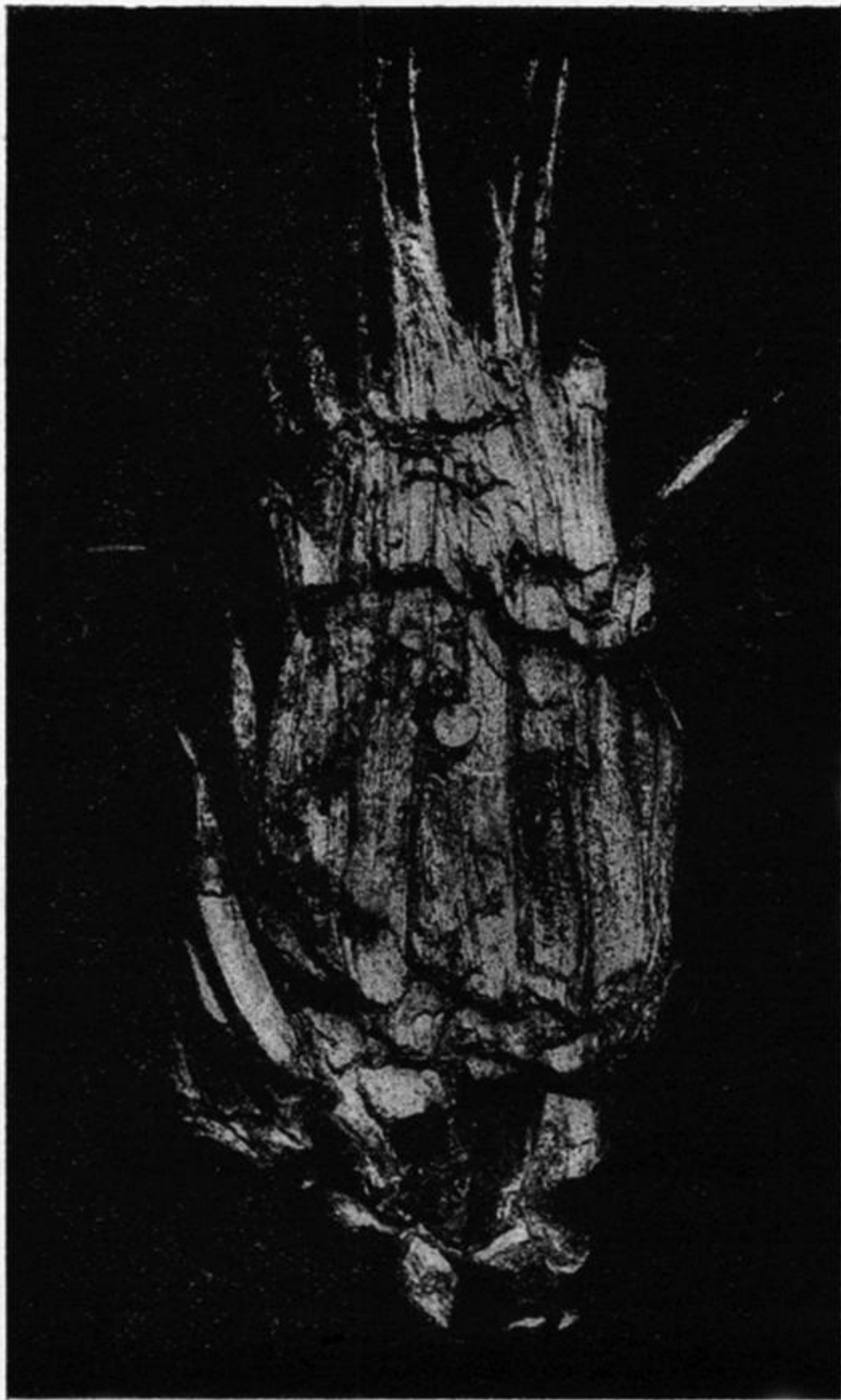


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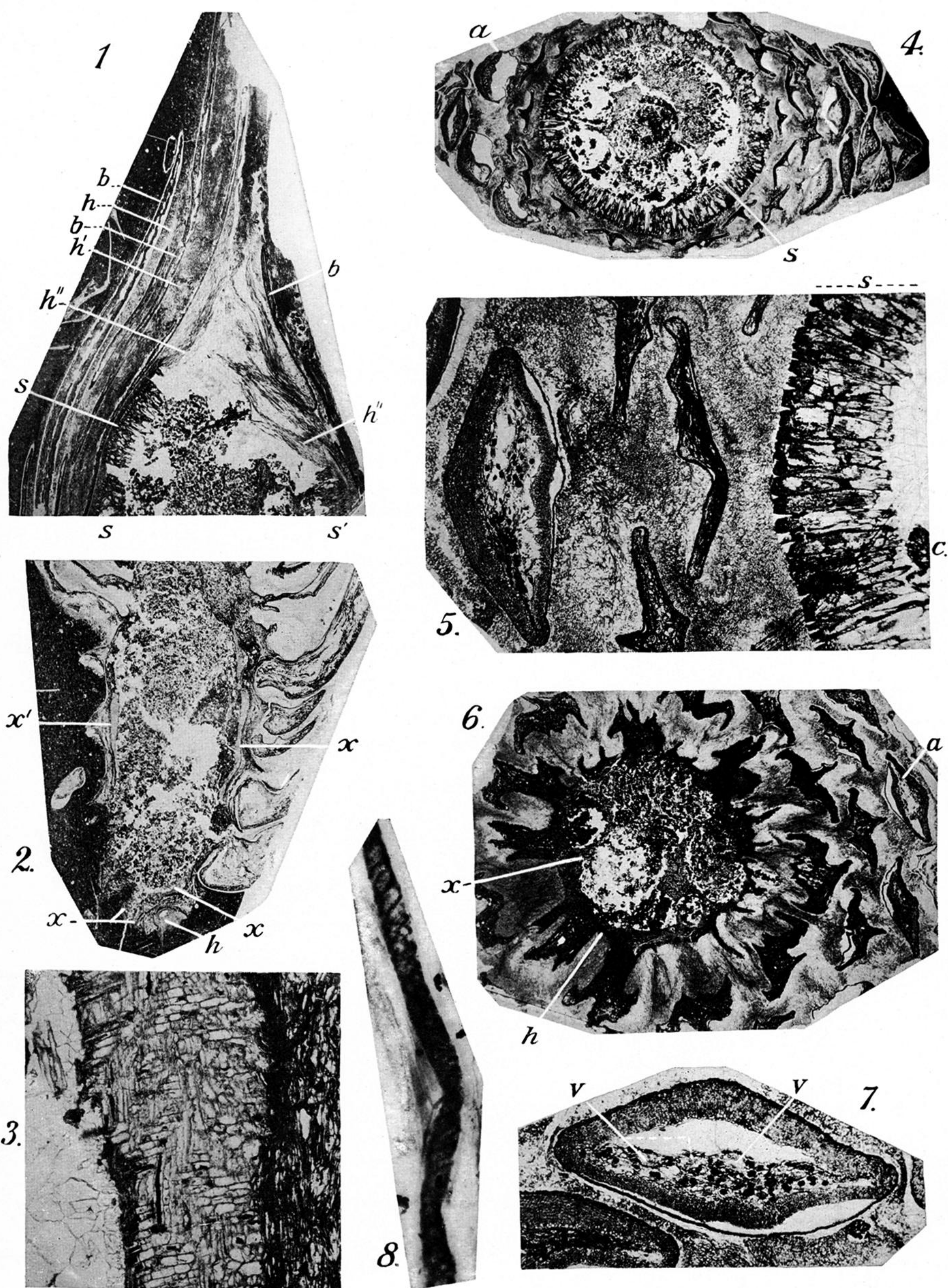








TEXT-FIG. 1.—Portion of the Strobilus in surface-view. Nat. size.
British Museum. Peach Coll. V. 3944.



WILLIAMSONIA SCOTICA.

PLATE 9.

Fig. 1.—Longitudinal section (cut along the line vi, fig. 28) of the upper part of the strobilus. *b*, bracts; *s*, interseminal scales and megasporophylls; *h*, *h'*, *h''*...hairs. *Ca.* × 3. Section 6.

Fig. 2.—Longitudinal section of the lower part of the peduncle. *x*, *x'*, secondary xylem; *h*, hairs. *Ca.* × 2. Section 3.

Fig. 3.—Part of the secondary xylem shown at *x'* in fig. 2. Section 3.

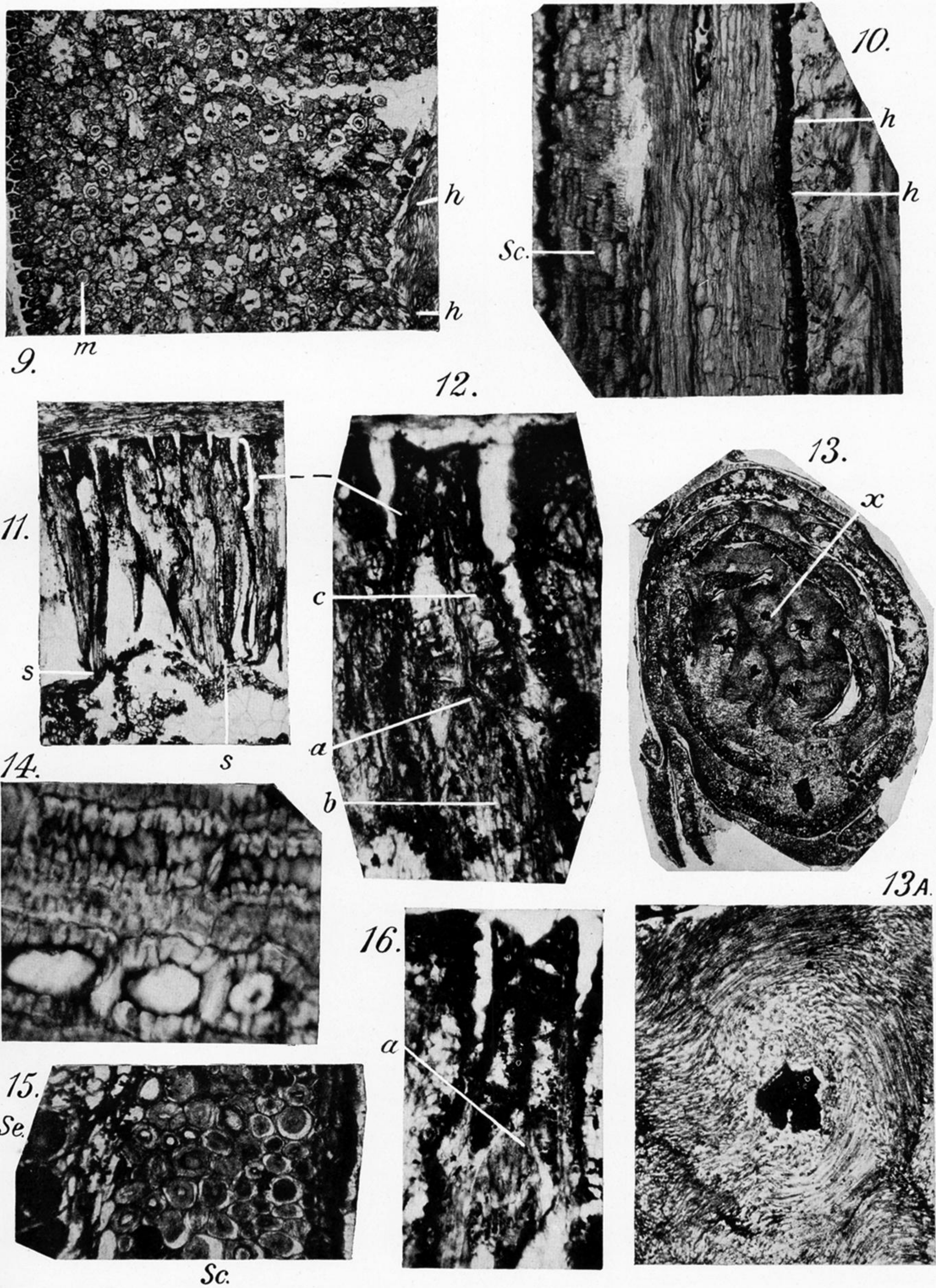
Fig. 4.—Transverse section. *s*, scales and megasporophylls; *a*, bract showing detached superficial tissue on the inner side. *Ca.* × 2. Section D.

Fig. 5.—Part of a transverse section more highly magnified (cut at i, fig. 28). *c*, piece of tissue of strobilus axis. × 10. Section 7.

Fig. 6.—Transverse section of the peduncle at a lower level (iii, fig. 28). *x*, portions of vascular cylinder; *h*, hairs attached to axis; *a*, bract with partially detached epidermis. Section C.

Fig. 7.—Transverse section of bract. *v*, *v*, vascular bundles. × 10. Section D.

Fig. 8.—Part of a hair showing dark spiral lines. Section 9.



WILLIAMSONIA SCOTICA.

PLATE 10.

Fig. 9.—Tangential section through the zone of interseminal scales and megasporophylls, showing the edges of this zone on the right and left margin. *m*, micropylar tube; *h*, hairs. $\times 10$. Section 8.

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Fig. 11.—Longitudinal section of part of the zone of scales and megasporophylls. *s*, *s*, attachment of scale and megasporophyll to axis. $\times 20$. Section E.

Fig. 12.—The distal part of the megasporophyll of fig. 11 more highly magnified. *c*, transversely elongated cells of micropylar tube; *a*, apex of nucellus; *b*, long cells of nucellus. *Ca.* $\times 100$. Section E.

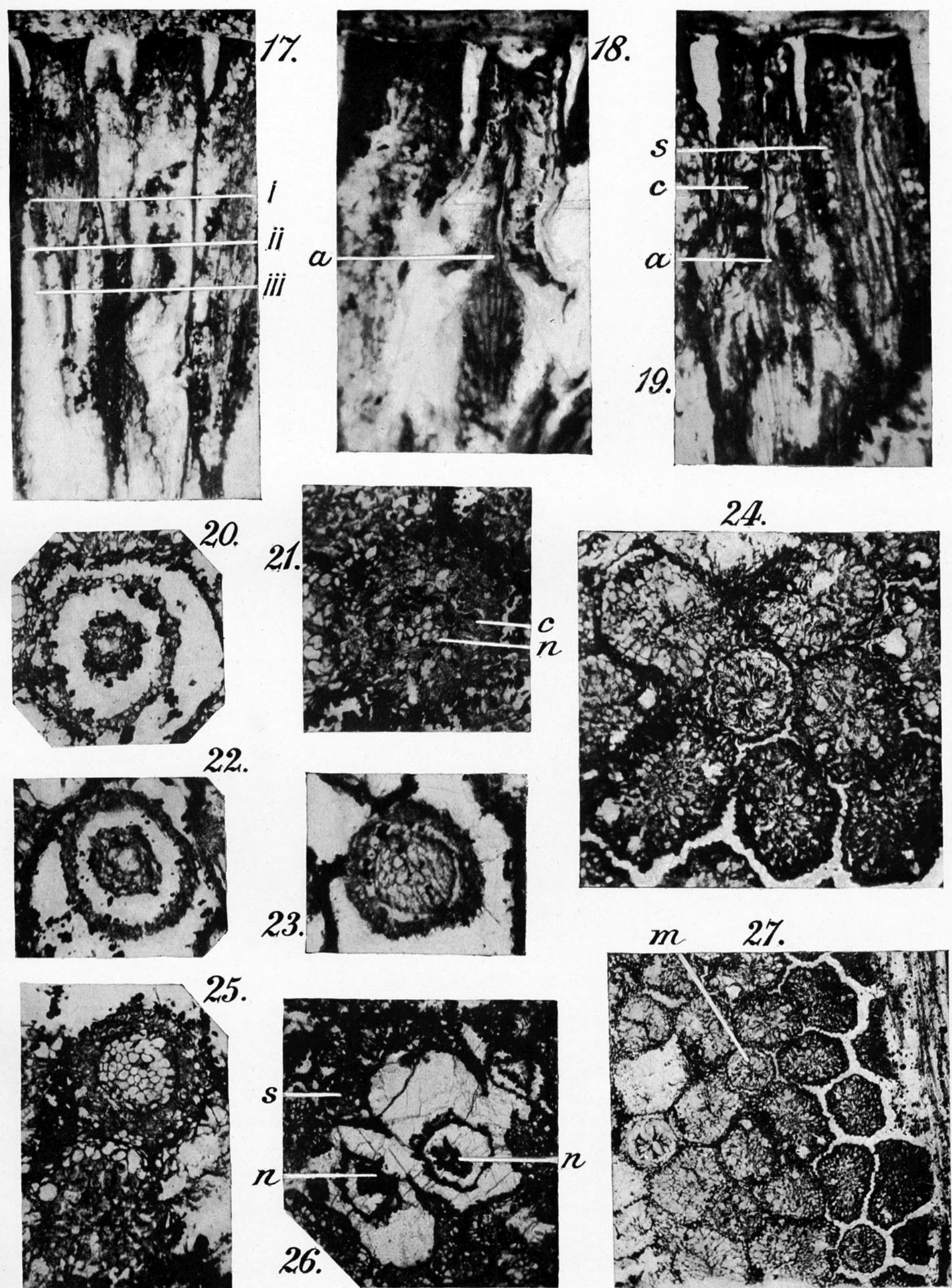
Fig. 13.—Transverse section of lateral bud borne on axis of strobilus. *x*, bract and hairs shown in fig. 13A. *Ca.* $\times 6$. Section B.

Fig. 13A.—Bract *x* of fig. 13. *Ca.* $\times 40$. Section B.

Fig. 14.—Sclerous cells of bract in longitudinal section. $\times 300$. Section 6.

Fig. 15.—Sclerous hypoderm of bract in transverse section. *se*, secretory sacs and dark contents; *sc*, sclerous cells. *Ca.* $\times 100$. Section 7.

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WILLIAMSONIA SCOTICA.

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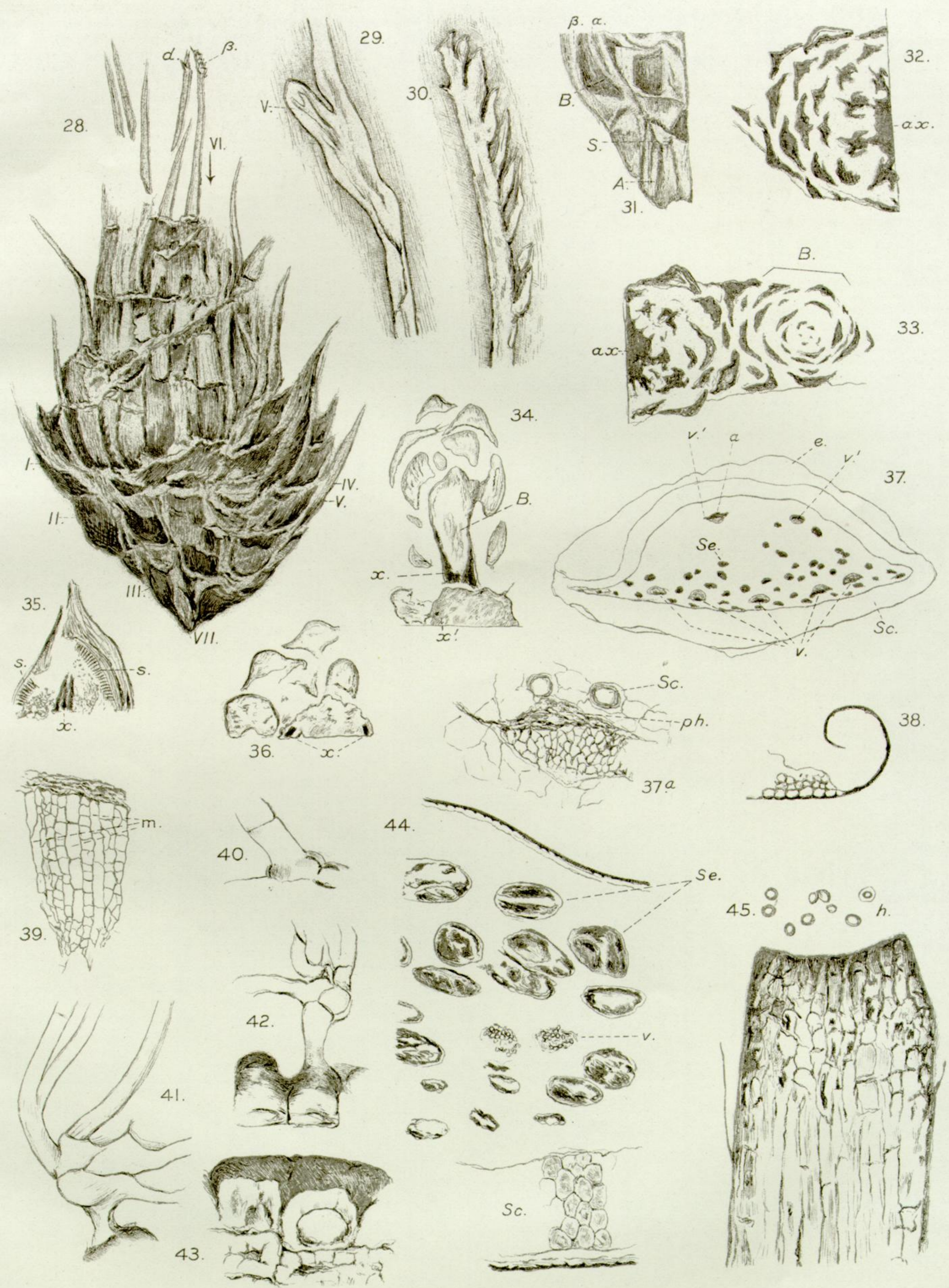
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Williamsonia scotica.

PLATE 12.

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Fig. 36.—Transverse section of part of strobilus-axis with bracts and pieces of vascular cylinder, *x* (cut at level III, fig. 28). Slightly enlarged. Section 4.

Fig. 37.—Transverse section of bract. *e*, detached epidermis; *sc*, hypodermal sclerous tissue; *v*, *v'*, vascular bundles; *a*, bundle enlarged in fig. 37*a*. $\times 14$. Section 7.

Fig. 37*a*.—Bundle *a*, *v'*, of fig. 37. *ph*, phloem; *sc*, thick-walled elements. Section 7.

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