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A REVISION OF *WILLIAMSONIELLA*

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(*Communicated by H. Hamshaw Thomas, F.R.S.—Received* 10 *March* 1944)

The various floral organs of *Williamsoniella* are redescribed from new material. It is shown that the flower possessed a perianth like that of Cycadeoidea, that the microsporophylls are pinnately branched and that the pollen is contained in two-valved capsules like those of Cycadeoidea. The seed is shown to have various internal cutinized membranes which are interpreted as indicating a free nucellus. It is concluded that *Williamsoniella* is nearer taxonomically to Cycadeoidea than had been realized.

Introduction

Hamshaw Thomas described the Bennettitalean flower *Williamsoniella* in this journal in 1915. Since then several new methods for investigating such fossils have been devised, making this genus like many others ripe for revision. The material described here, which was collected by Messrs Edwards and Wonnacott between 1932 and 1938 and which is in the Department of Geology of the British Museum, provides the opportunity.

There has been but one important later contribution to *Williamsoniella*, by Zimmermann (1933). He figured a specimen which showed leaves and flowers attached to the stem, thus providing welcome proof of the hypothesis which Thomas founded on circumstantial evidence. He also foreshadowed the altered account of the microsporophyll now put forward. Various authors (including myself) have published speculations about the comparative morphology of *Williamsoniella*, but with the new facts much of this becomes obsolete.

W. coronata Thomas is only known from the Gristhorpe Bed of Cayton Bay, Yorkshire. Its age is Middle Estuarine (part of the Bajocian, Lower Oolite).

The flower as a whole

The flower consists of an axis bearing sterile bracts, an androecium and a gynoecium (text-figure 1). A few specimens show all these parts (figures 19, 20, plate 25), but a good many have lost all the members of one or another category. The bracts were most often lost and their existence was unknown. That they have now been found is not due to new technique, but to the discovery of fortunate specimens.

The flower has a peduncle 2–4 cm. long thickly covered with hair, especially in its upper part. The bracts, probably 20–30 in all, are also hairy and form a perianth of more than one layer. Though probably not forming two distinct whorls—the lower ones indeed arise at slightly different levels—the outer bracts differ from the inner ones in being stouter.

The bracts are succeeded by a whorl of 12–14 microsporophylls which arched over and protected the gynoecium in bud. The gynoecium is of normal Bennettitalean structure, but the axis projects above the seeds to form a characteristically moulded body, the 'corona', against which the tips of the microsporophylls pressed in bud.

Comment is made later on the fact that nearly all the flowers are immature.

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Parts of the flower

(a) *Floral axis*

The peduncle shows the clean-cut base and longitudinal ribs described by Thomas. The ribs do not continue the whole length but die out and are replaced by others and are more likely to be subepidermal fibres than vascular bundles. The fine hairs which cover the peduncle are only seen clearly after immersing the specimen in oil, or in transfers, but Thomas noted their cutinized bases. The hairs are just like those of the bracts described below.

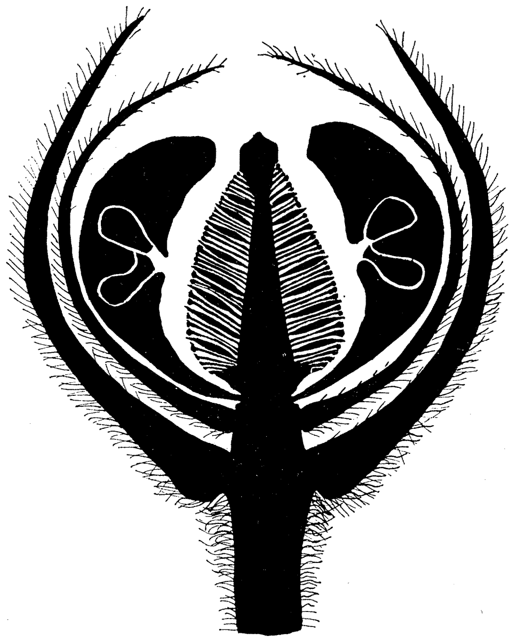

Figure 1. Diagrammatic restoration of flower of *Williamsoniella* in longitudinal section. ×3.

The axis expands slightly at the base of the flower where the bracts arise, and then contracts where the microsporophylls arise and expands again at the base of the gynoecium. The scars of the appendages are hard to see, but those attributed to the lower bracts are sometimes indicated by the sudden end of the hair covering of the peduncle. The lowest bract scars are rhomboidal and nearly as high as broad, the upper ones which are indistinct are of the same width but less high. The whole of this part of the floral axis is covered by the bases of bracts and consequently it has no cutinized epidermis.

The microsporophylls probably sprang from sunken areas just below the gynoecium where there are gaps in the cuticle. It is impossible that they should have arisen higher, because above this level the surface is everywhere covered with a cutinized epidermis.

At the base of the gynoecium is the 'basal flange' which can be regarded as the lower interseminal scales, imperfectly formed and adnate to one another. This flange follows the curve of the gynoecium and is inconspicuous in young fruits, but as the seeds swell it bends back and remains bent back after the seeds and normal scales have fallen off (figure 11, plate 25). In this position it is very apt to be broken by the plane of cleavage (figure 15, plate 25; Thomas 1915, plate 12, figure 8 at *f*). Transfers show it fully, however, and the suggestion that it carried the microsporophylls is disproved when its cuticle is prepared.

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Above this flange, the axis tapers gradually. It is uncutinized and is covered with minute and inconspicuous prints which no doubt represent the seeds and scales. At the top of the gynoecium there are more adnate interseminal scales forming the 'upper flange', and then the thickly cutinized axis projects for 2–3 mm. forming the corona. The present account agrees with that given by Thomas, who regards the flat facets of the corona as the places moulded by the tips of the microsporophylls in bud. The margins of the facets are limited by a mere bend in the cuticle, and their lower margins trespass on the top of the gynoecium and include some of the uppermost scales.

(*b*) *Bracts*

Five flowers show attached bracts clearly; various naked axes show bract scars and there are many isolated bracts forming a varied series. Thomas described some of these isolated bracts but concluded that they were vegetative bud scales and that the flower was normally naked. It is likely enough that some of them are in fact vegetative, but the vegetative buds of this plant are as yet unknown.

The attached bracts are all members of the inner perianth, the outer ones being attributed to it on circumstantial evidence. These attached ones are about 15 mm. long, 1·5–2·0 mm. wide near the base and taper to a point. Their substance is fairly dense, and in the lower part shows some small pimple-like thickenings. The back and margins, and to a less extent the upper side, are covered with fine hairs up to 1 mm. long.

The cuticle (figure 2 A, C) is moderately thick (2–4μ) on both sides and easy to prepare. The upper shows rows of rectangular cells, short in some, long in other specimens. There are no stomata and hairs are frequent in some specimens, rare in others. The cell surface is mottled and often longitudinally striate. The lower side shows less regular cells, hairs are very numerous and stomata are numerous in some specimens but rare in others. The epidermal cells round the stomata have sometimes divided to give unspecialized encircling cells.

The hairs spring from bases of one, two or three small, heavily cutinized cells. The hair itself is a tapering structure consisting, as far as can be seen, of a single cell (figure 2 B, J) which has thick but uncutinized walls.

The isolated bracts form a rather varied series which could not be satisfactorily divided into groups. They are characteristically abundant in shale with leaves and flowers of *Williamsoniella* and not found elsewhere (figure 10, plate 25). Many of them are exactly as described, others are broader and more robust, still others are more delicate. The more robust are believed to belong to the outer perianth because their scars of attachment match the lowest scars on the floral axis. They are about 3 mm. wide, 15–20 mm. long, and their substance is thick and covered with pimples. The scar of attachment is broadly rhomboidal and situated distinctly above the base (figure 21, plate 25). Often the scar shows some glistening bodies which are taken to be stone cells, responsible also for the surface pimples.

The most delicate bracts are smaller, distinctly translucent and have few or no pimples.

The cuticles of all these specimens are fairly similar, but considerable variation was noted in the density of hairs and of stomata, the delicate bracts having particularly few stomata. Some of the robust bracts have very thick *lower* cuticles which may be up to 10μ (measured where the cuticle is folded).

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Thomas figured a bract which carried a small lamina, and the present collection provided a similar one (not figured) in which the cuticle showed an approach to the normal lamina of *Nilssoniopteris vittata*, the foliage of this plant.

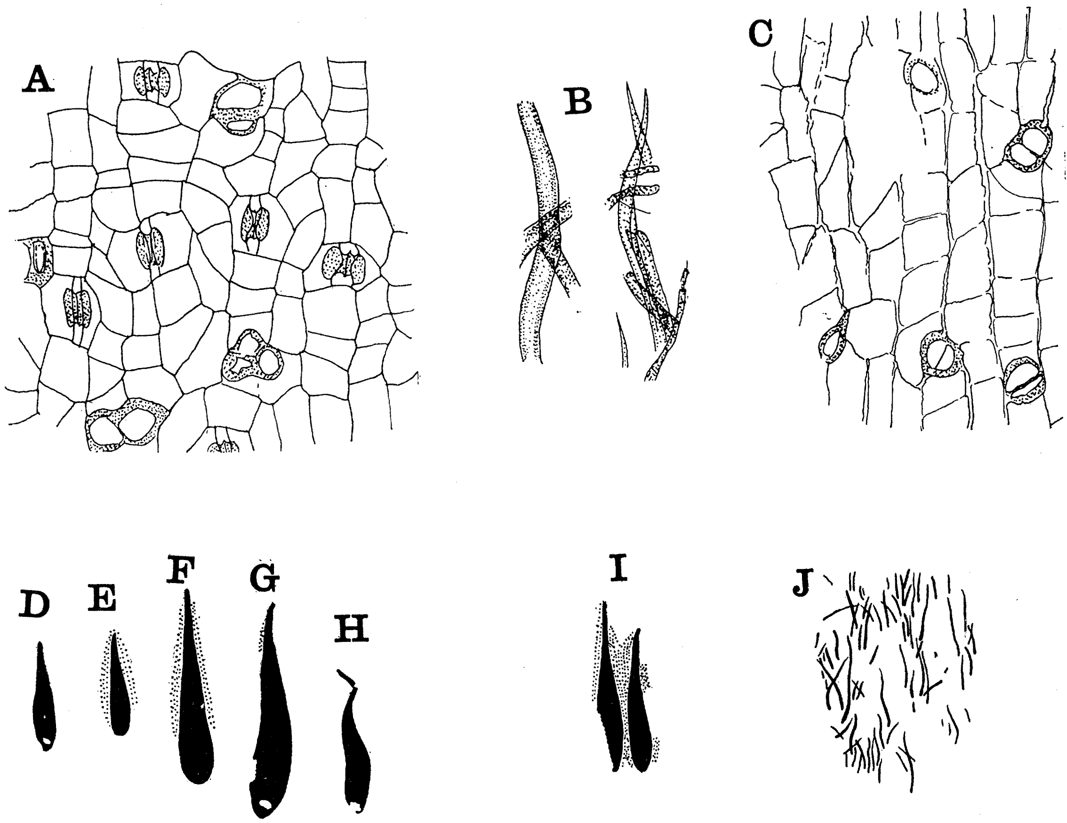

FIGURE 2. Perianth bract. A, lower cuticle showing stomata and hair bases. V25838, ×200. B, hairs seen in transfer from the rock matrix opposite where a bract has fallen off, V25899, ×100. C, upper cuticle showing hair bases, V25838 (the flower shown in figures 8, 11, plate 25, ×200. D–I, isolated bracts: the area covered by marginal hairs is stippled, all ×1. D is V21399, E, F are V25831, G is V23948, H is V21890, I is V23923. J, counterpart of bract, in transfer showing the hairs of the under side. V25899, ×25.

(*c*) *Microsporophylls*

There are a few bud-like flowers showing the microsporophylls in position round the gynoecium (figures 9, 20, plate 25) and many specimens of free-lying microsporophylls identifiable through Thomas's work. This account will be found to modify that given by Thomas in several respects, particularly in the branching of the sporophyll and in the structure of the spore capsule.

The microsporophyll (figure 3 C, E, G) must have been shaped like an orange segment, but with a downward projection of the base to form a short stalk. Thomas recognized that this was their general shape, but it has now been found that they are more elaborate, the thin margin being partly formed by finger-shaped branches with the gaps between them occupied by the pollen capsules. These branches are usually paired and comprise sterile lower ones which point upwards, fertile upper ones which point downwards, approaching or overlapping the lower ones, and finally fertile middle ones which point forwards toward

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the same place as the others. In a specimen where the branches are unpaired, they point irregularly. All these branches appear equally broad in whatever plane they are compressed, so they must have been thick in section, possibly square, as is suggested by the surface ridges in some specimens.

The existence of these segments had not been recognized; they are not easily seen unless the specimen is transferred or mounted in oil. Dissection under paraffin oil of laterally

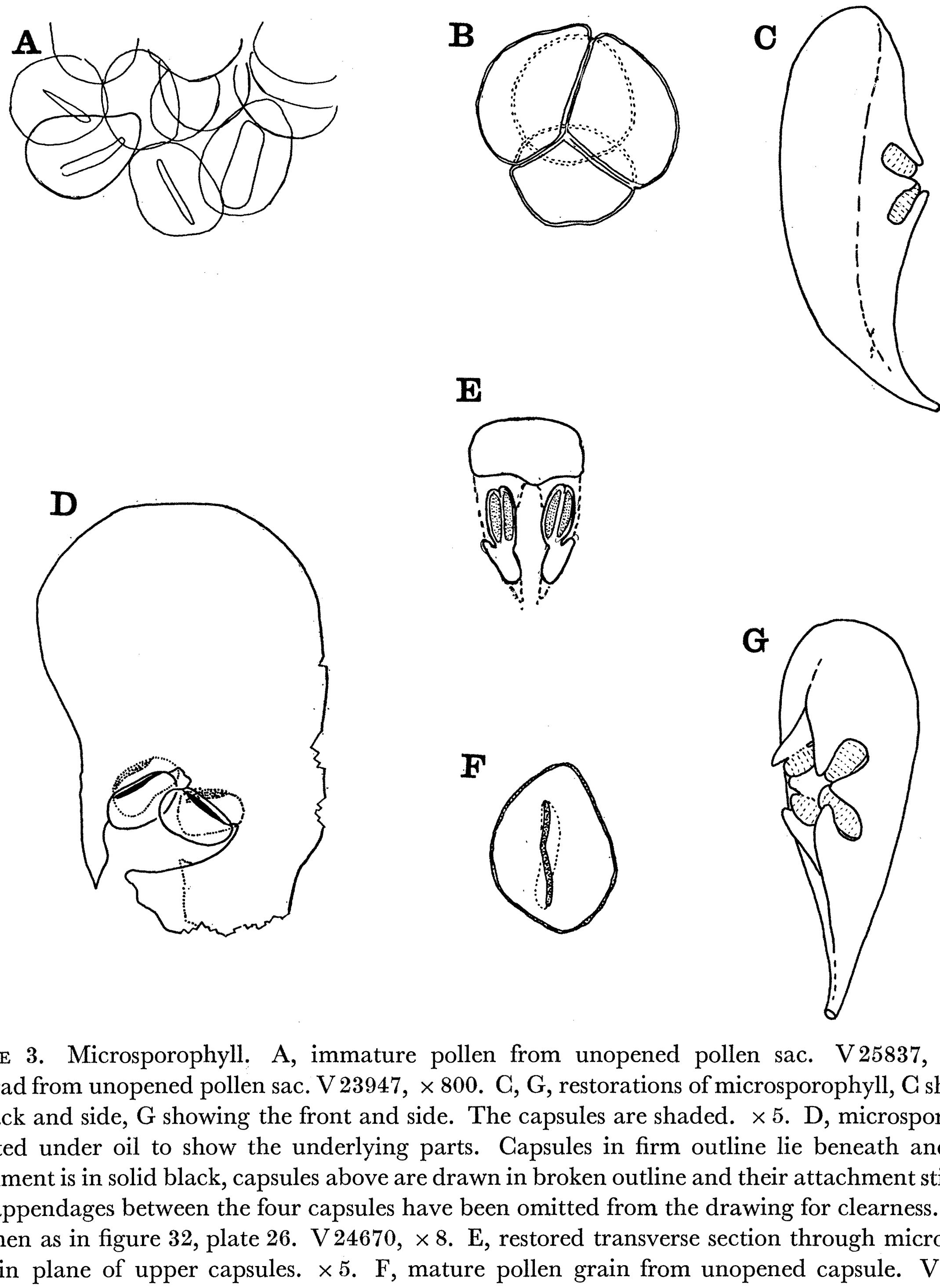

FIGURE 3. Microsporophyll. A, immature pollen from unopened pollen sac. V 25837, × 800. B, tetrad from unopened pollen sac. V 23947, × 800. C, G, restorations of microsporophyll, C showing the back and side, G showing the front and side. The capsules are shaded. × 5. D, microsporophyll dissected under oil to show the underlying parts. Capsules in firm outline lie beneath and their attachment is in solid black, capsules above are drawn in broken outline and their attachment stippled. Two appendages between the four capsules have been omitted from the drawing for clearness. Same specimen as in figure 32, plate 26. V 24670, × 8. E, restored transverse section through microsporophyll in plane of upper capsules. × 5. F, mature pollen grain from unopened capsule. V 23947, × 800. G, see C.

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compressed sporophylls gives convincing proof of their existence. After the carbonaceous matter of the appendages and pollen sacs lying above have been removed a distinct layer of rock matrix is reached, and then similar structures lie underneath.

Most sporophylls in this collection have two pairs of capsules, some have three, none more. It is often difficult to determine their number until the specimen is immersed in oil. The capsules are always attached to the lower sides of the segments.

Surface markings. The back of the sporophyll is covered with pimples which are, as Thomas concluded, caused by compression around locally hard bodies. Maceration destroys these bodies, but a specimen was found which had rotted before preservation, losing part of its upper epidermis and internal substance and so had become translucent. A transfer was made and showed nests of small black cells, like stone cells, occupying the pimples. The adaxial surface of the sporophyll is smoother, but all parts show the epidermal cells.

Cuticle. The cuticle, though not thin, is troublesome to prepare because the underlying substance is fragile. All parts were examined and found to be fairly uniform except for the capsules, but the outer side is distinctly thicker (up to 5μ, measured in folds). The cell walls are straight in some specimens, bent or with jagged thickenings in others, but are never sinuous and hair bases are absent. Thomas has already described the stomata.

Pollen capsules. These organs have been described as synangia by several authors, but the term 'capsule' is preferred because it avoids implying morphological fusion of sporangia (Harris 1942). They are shaped somewhat like scarlet runner bean seeds (*Phaseolus multiflorus*), being flat and broad but not very high, and often slightly curved; but the area of attachment is longer than in the bean. The sporophyll segment usually overlaps the upper edge of the capsule and the attachment is only clearly seen after dissection (figure 32, plate 26; figure 3D). The laterally compressed capsule usually shows no surface features beyond the uniform epidermal cells, but occasionally it shows slight bulges due to sporangia (figure 31, plate 26). The opening is occasionally visible along the adaxial edge, and is easily seen in vertically compressed capsules which show it divided into two equal valves (figure 33, plate 26).

The capsule is particularly fragile, but occasionally yields such preparations as that in figure 30, plate 26, which is part of one valve bearing some sporangia. Its outer cuticle is rather thin and shows rectangular cells with faintly marked outlines. The pollen sacs are distinctly cutinized, their walls are granular and stain deeply, but show no definite cells. The sacs appear to have opened by a slit along their inner sides.

It has not yet been proved that each valve of the capsule bears its own set of sporangia, though this is likely. Sections of young capsules were attempted, but gave no useful results.

Pollen. Ripe oval pollen grains showing a longitudinal furrow lie scattered in pollen sacs and over the sporophylls, and others are found among the hairs of the bracts (figure 3F). Immature pollen, often in tetrads, occurs in the sporangia of many isolated sporophylls, and abnormal pollen was noted (see p. 325).

(*d*) *Gynoecium*

The collection includes a fine series of gynoecia of various sizes. These specimens provide information about general gynoecial development and about the structure of the seed. They show that it reached a rather larger size than had been realized, but even so it remains the smallest yet known in the Bennettitales.

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The gynoecial axis bears some 300 ovules and 1200 interseminal scales. Except at the top and bottom which are sterile, the ovules are spaced very evenly, but by no means all appear to have grown into seeds, many of the upper ones being arrested in development when those in the middle of the gynoecium are mature. No phyllotaxis pattern could be recognized in the seeds and scales, and it was thought that the scales are not entirely definite units, those with two or more apices being produced by adnation or else late dichotomy of initials. Large numbers of slender ramenta lie between the seeds and the stalks of the scales.

Development. Although the gynoecia available seem to comprise similar numbers of scales and ovules, their size differs greatly and they are regarded as a developmental sequence. The cuticles of the gynoecium provide some evidence in support, but there is little relation with the development of the other floral organs (p. 325).

Stage 1. The smallest gynoecium (figure 14, plate 25) is enclosed in young microsporophylls. It has nearly its full length, but is a cylinder only 1·5 mm. wide. It is covered with delicate outgrowths which are thought to be minute interseminal scales with uncutinized heads: ovules were not seen.

Stage 2. The gynoecium is 5 mm. wide and still nearly cylindrical. The interseminal scales have nearly flat heads with cuticles only 1–2μ thick, and the micropyles, though visible, do not project (figure 10, plate 25).

Stage 3. The gynoecium has become inversely pear-shaped and is 6–10 mm. wide (figures 13, 16, 18, plate 25). The interseminal scales have convex heads with cuticles about 4μ thick, and the micropyles are also well cutinized and project; no cuticle is developed, however, on the inner part of the seed. This stage is particularly common and has been figured by Thomas (figures 1, 2, 5, plate 12). It is by no means mature, but only half grown.

Stage 4. The interseminal scales now have cuticles at their mature thickness of 8μ at the apex, and distinct traces of cuticle extend over the protected parts of the seeds which are 1·5 mm. long. The gynoecium has almost certainly enlarged, but its size was not determined because the only specimen was obtained as fragments from maceration (figures 4, 5).

Stage 5. The gynoecium (figure 7, plate 25) has become 15 mm. wide, but its length is not increased. It is thus rounded. The seeds have increased greatly in length and width ($5 \times 0 \cdot 9$ mm.) and the heads of the scales have widened, thus maintaining the complete gynoecial armour. The basal flange of the gynoecium has bent backwards. This stage was represented by two specimens in this collection, and a slightly smaller one is figured by Thomas (plate 12, figure 3). As no fruits with seeds larger than these are known they are presumed to be ripe, but in view of the commonness of abortive gynoecia, the maturity of these too is open to suspicion.

Stage 6. The final stage shown in figures 8, 11, 15, plate 25, is common, and has been figured by Thomas (plate 12, figure 8). All the ovules and scales have been shed leaving the gynoecial axis bare. The basal flange is bent backwards, indicating the previous expansion of the gynoecium, but curiously enough no isolated seeds or scales corresponding to these specimens could be found.

Interseminal scale. In the mature ovary the scale has a stalk 5 mm. or more long but only 0·1 mm. thick, terminating in a bulbous head 0·6 mm. wide. The stalk is compact and shows longitudinal cell striae, but is very thinly cutinized. Near the head, however, the

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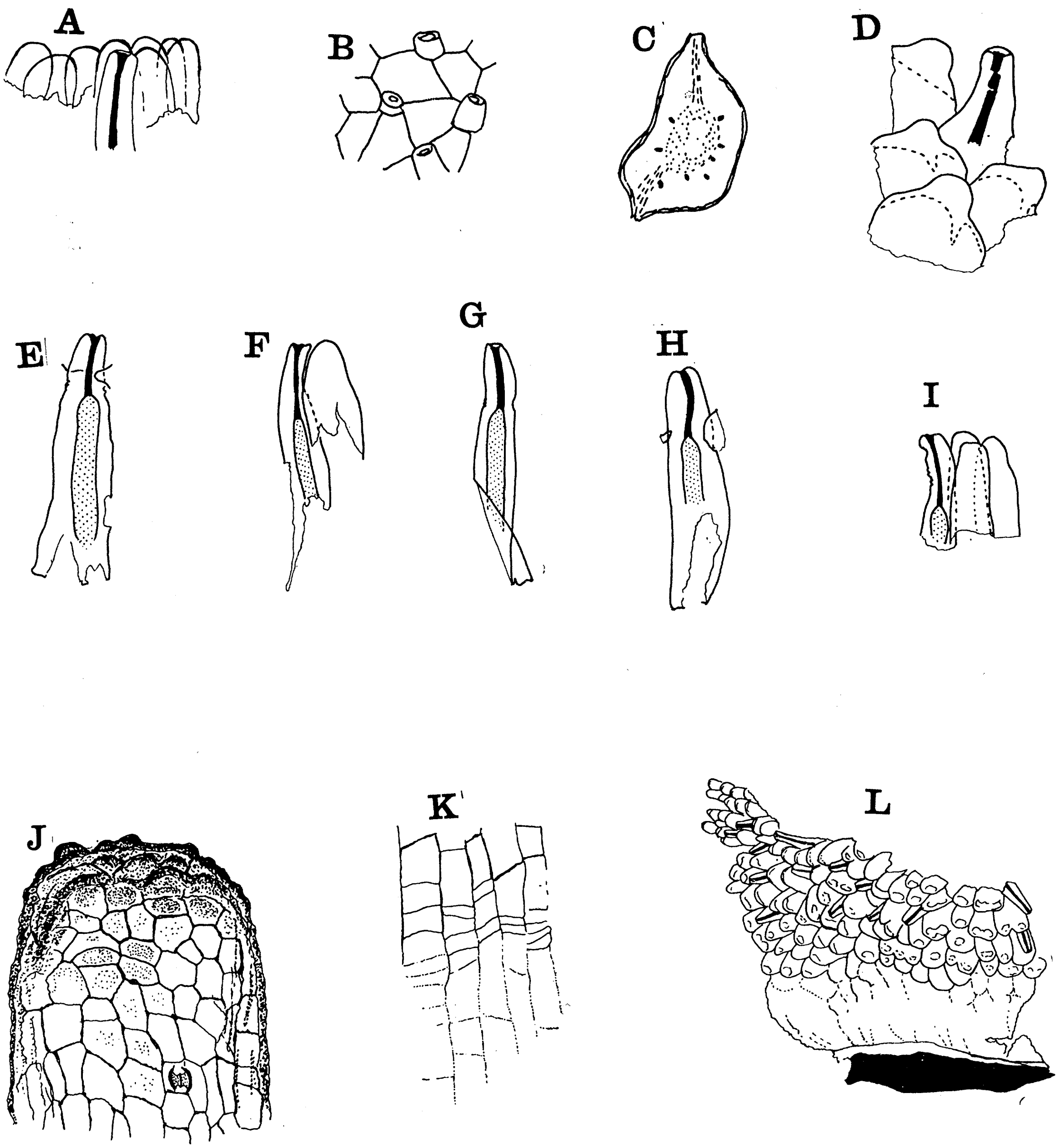

FIGURE 4. Interseminal scale and immature seed. A, B, micropyles and interseminal scales in lateral and in vertical compression from immature gynoecium. V 21387A, V 21387B, ×25. C, ripe interseminal scale in surface showing stomata as large black dots. The smaller stippling represents the raised central area, and striations represent regions of narrow cells. V 25833C, ×25. D, interseminal scales and micropyle from ripe fruit. V 25833D, ×25. E–I, seeds and interseminal scales at stage 4. V 26858, E from slide E, F from slide C, G from slide D, H from slide E, I from slide C, ×25. The micropylar canal is shown in black and the inner cuticles are stippled. Fragments of scales adhere to the bases of the micropyles in E, G, H. J, top of a scale. V 26858D, ×200. K, slightly lower on the same scale showing the meristem-like cells. V 26858D, ×200. L, piece of cuticle from the base of the gynoecium showing many micropyles and interseminal scales which merge into the basal flange. Below the flange is a black mass of corky tissue whence the microsporophylls originate. V 26858A, ×10.

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cuticle thickens and continues to grow thicker to the apex where it reaches 8μ. The robust outer part usually breaks off in preparation, and is easily recognized. In surface view it is polygonal with one or two corners strongly extended; in side view it is a flattish dome with an apical peak, so that it is mammillate (figure 4 C, D). The cells of the apex are isodiametric polygons with very prominent outlines and a thickened surface forming a large, ill-defined papilla. Stomata occur just below the apical peak, and here the cells tend to be rectangular, becoming elongated where extra growth has occurred opposite a micropyle. The inner cutinized parts were not well preserved in these specimens, but are described for the younger ones below.

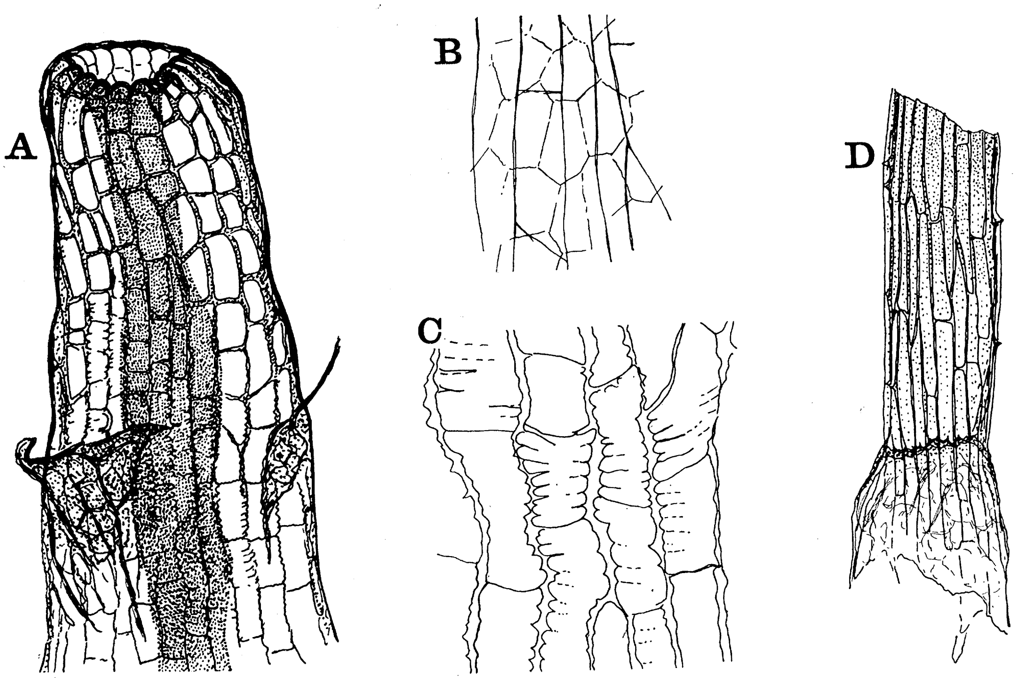

FIGURE 5. Immature seed. A, micropyle with adherent fragments of scales. The shrunken canal is stippled. V 26858C, × 200. B, inner cutinized sac of seed showing two sets of cell outlines. V 26858G, × 400. C, cells of integument at base of micropyle showing surface ribs. V 26858E, × 400. D, micropylar canal dissected out, ending below in the inner cutinized sac. V 26858F, × 200.

Cuticles of the inner parts were ill preserved in these specimens and so are described from the slightly younger gynoecia where they were better seen, though very difficult to prepare. The cells form longitudinal rows and are elongated over the stalk, but just below the head become short, giving the appearance of a meristem (figure 4K).

Growth of scales. The early stages of development were not adequately studied because of lack of material. However, at stage 3 (p. 319) the scales have well-cutinized heads which show full-sized cells at their apices. In surface view the scales form isodiametric polygons and in side view they appear gently rounded (figure 4 A, B). The stomata are concealed in the chinks between adjacent heads.

At stage 4 (figure 4 F, I, J, L) the heads have enlarged and appear much more convex, chiefly because the cuticles of the sides are stiff enough to maintain their form. The enlargement has caused some of the cells of the sides to be drawn on to the top, and the stomata are near the surface and easier to see.

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The mature stage (figure 4 C, D) shows this method of growth continued, with local extension which has the appearance of meeting an emergency (opposite a micropyle which does not contribute to the enlargement of the surface). It is noteworthy that near the apex of the mature gynoecium the scales are less advanced, being at stage 4 or earlier. It seems that the cutinized head at stage 4 is too hard to expand evenly and so forms a peak at stage 5. It is tempting to regard this as being due to a cessation of growth for a period on analogy with *Pinus sylvestris* where a little boss on the middle of the cone-scale represents the exposed surface which endured the first winter and became too hard to grow or alter shape. The same mammillate shape is seen in mature scales of various other Bennettitales.

Ramenta. In the split gynoecium seen in figure 1, plate 25, very delicate elongated bodies can be seen with the microscope (though not in the photograph) on the matrix among the seeds. Some appear to be one cell wide, others are certainly two. Nothing could be made out about their attachment, but the gynoecial axis left by the fall of the seeds and scales shows none.

(*e*) *Seed*

Although it has been possible to find out a good deal about the structure of the seed, less has been learnt than we have a right to expect from compressions because the material is inadequate. Only two ripe gynoecia were available; one was wholly macerated, the other preserved apart from small chips. Had isolated seeds been found, more could have been done.

The reason why the seeds are visible in these ripe fruits is that the surface has split in compression and allowed mud to penetrate between them and the stalks of the scales. No single seed was visible for its full length and the rock was too flaky for successful dissection, but the various parts of different seeds were seen. It is clear, however, that they are spindle-shaped and sessile, about 5–6 mm. long and 0·9 mm. wide in the middle. The surface shows a few longitudinal ribs, the cuticle indicates the presence of about six, and is everywhere marked with longitudinal cell striae. The whole seed is delicate and compressed to a thin but opaque film.

Very small fragments of seeds were detached and macerated, but the best preparations were given by macerating one ripe gynoecium as a whole. Even here they broke into pieces of 1 sq. mm. or less. The integument has a delicate cuticle which gives a most confused picture of elongated cells (figure 6H). This is a single membrane, that is, it cannot be dissected into two layers, but in favourable places the cells can, however, be resolved into (1) a set of slightly broader cells, thought to be the epidermis of the integument, (2) dark bodies forming solidified contents occur in some of these cells. This cell contents is restricted in a way that suggests that the lateral walls were rather thick. Finally, (3) a second set of slightly narrower cells is thought to represent the hypodermal cells, cutinized along their wall of contact with the epidermis.

Near the micropyle the difference between the two sets is more obvious (figure 6J), and in the specimen drawn the cell contents have collected at one end of each epidermal cell forming a comb-like body. This drawing should be compared with that in figure 5C, the same part of a younger seed, where the hypodermal cells are exceedingly faint, if visible at all, and are not shown.

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In the ripe fruit V 25833 the inner tissues of the integument are not preserved, but V 25846 provided much confused matter consisting of elongated casts of fibrous cells. Even the casts of scalariform tracheids were found, but they may have come from interseminal scales. This form of preservation offers distinct promise beyond that of ordinary compressions.

The micropylar region is exactly as in the younger stage (figure 5 A, D). The outer cuticle is very thick (about 4 μ in folds) and shows the strongly marked outlines of the elongated epidermal cells. These cells differ from those of the interseminal scales in having

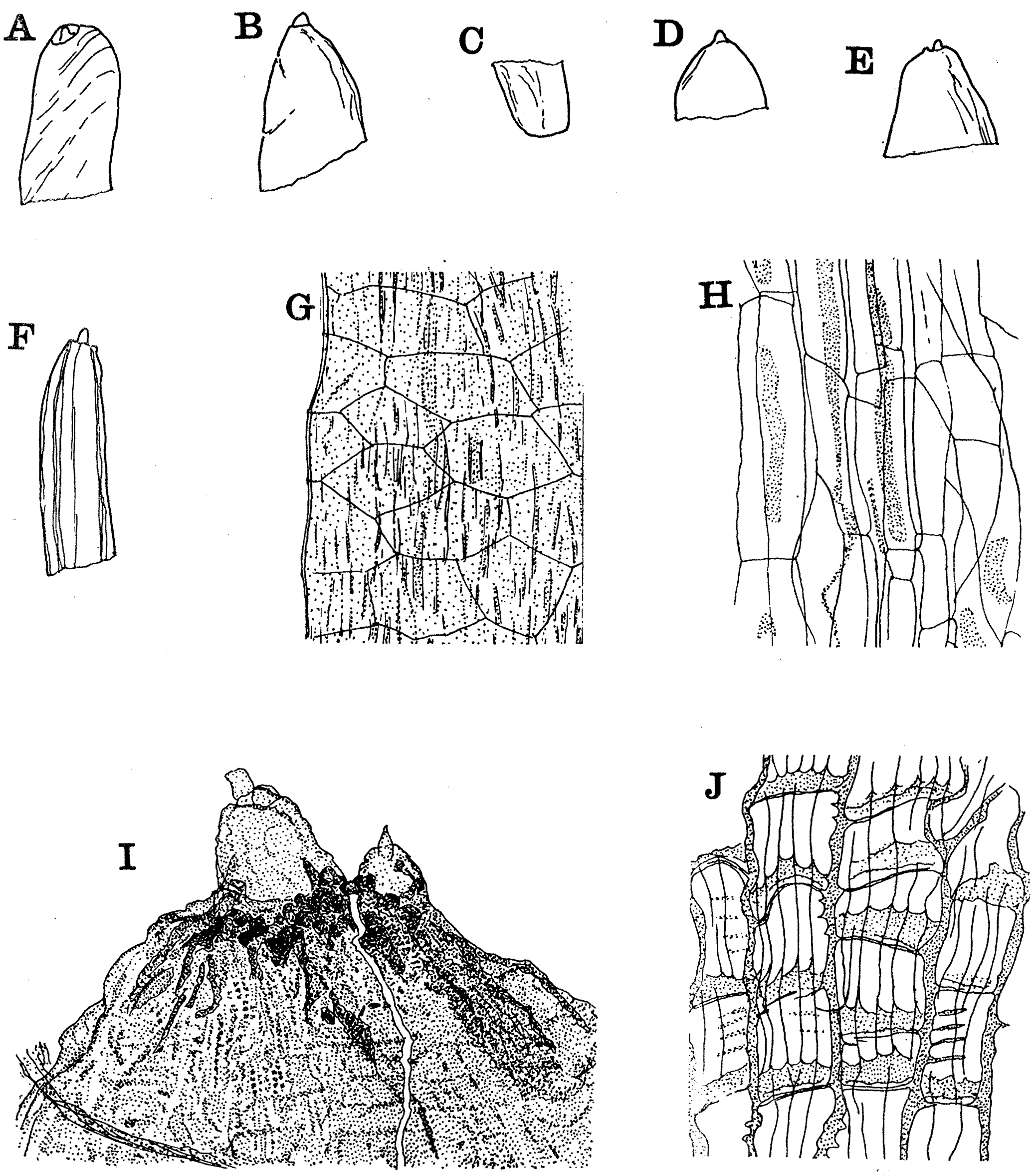

FIGURE 6. Mature seed. A–F, inner cutinized sacs of seeds; C is supposed to be the base, the rest apices, all ×25. A is V 25833F; B, V 25833G; C, V 25833F; D, V 25833B; E, V 25833E; F, V 25833F. G, details of the inner cutinized sac. V 25833E, ×200. H, cuticle of integument. V 25833A, ×400. I, inner cutinized sac apex with two points. The crack is artificial. V 25833G, ×200. J, integument just below the micropyle showing the underlying narrow hypodermal cells and the dark masses of epidermal cell contents. V 25846A, ×400.

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no thickening to form a papilla, and the cuticle is distinctly thinner. Near the base of the micropyle the surface of the cells is sometimes marked with ribs running in from the broad lateral walls.

The cutinized lining of the micropyle is easy to see and to dissect out. It has usually partly collapsed, but that drawn in figure 5D is undistorted, apart from being flattened. It shows the very prominent outlines of narrow, elongated cells, which in the younger seed are readily traced beyond the micropyle over the surface of the nucellus.

At the top of the gynoecium are large numbers of small, abortive seeds which have not changed at all after reaching stage 4. Both ripe fruits yielded fragments of cutinized bodies which certainly came from the interiors of seeds, though they are too much broken to relate exactly to the exterior. This interior cuticle forms an elongated sac 0·6 mm. wide and of considerable length. It is thus nearly as wide as the intact seed and very likely occupies the whole interior below the micropyle. No specimen of this sac shows both ends, but many isolated ends were obtained as fragments. Some of these show conspicuous points (figure 6 A, B, D–F, I), the others (figure 6C) are merely rounded. The rounded end shows no elaborations of interest, its cuticle being thickened and showing cells as elsewhere but even more obscurely. The pointed end, however, shows a thickened zone just below the point, and the point itself has some strongly bulging cells or even sharp spines. A few specimens show a second, smaller point beside the first.

There is no evidence to show whether the pointed or the rounded end faced the micropyle, but the drawings are orientated on the assumption that it is the pointed end. While an upward projection of a megaspore membrane into the micropyle is not surprising, the second, smaller point of certain specimens is unaccountable, and it may be that the points are chalazal outgrowths. Additional material is needed to settle this.

The sac itself is of course double, but the two sides are pressed together and have usually adhered inseparably though they are separable in a few. Evidently there was no appreciable organic matter inside the sac when preserved, suggesting that even in these ripest fruits many of the seeds were empty and abortive. The cuticle of the sac appears to be about 1μ thick where folded.

The sac shows traces of structure, but these are faint and confused because several different cell layers are involved. Different specimens or even different parts of the same specimen show particular cell types more distinctly. The following layers occur:

(1) Elongated cells very indistinctly seen in figure 6G, but which in favourable specimens seem to be about 12μ broad and of considerable length. These cells may belong to the inner epidermis of the integument.

(2) Large cells with finely marked outlines, often 60μ broad, 30μ long. They are very distinct in the specimen shown in figure 6G. These cells are thought to belong to the epidermis of the nucellus.

(3) In occasional specimens there are patches of small isodiametric cells 30μ wide with broad, dark outlines. These cells are distinct from those of group (2) above, which are recognizable in the same specimens, and there is nothing to indicate their nature. The fact that they are as a rule not represented at all suggests that they are not a cutinized layer, but an unresistant layer occasionally impregnated with fat during decay.

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Seed development. In young gynoecia, the only part of the ovule which can be demonstrated is the cutinized apex of the micropyle which is almost fully developed. More of the micropyle is developed in older fruits, and by stage 4 (p. 319) the micropyle has developed fully. At this stage the inner parts of the seed become distinctly cutinized. The whole integument is almost cylindrical, about 0·3 mm. wide and 1·3 mm. long, of which the top 0·3 mm. belongs to the micropyle but is scarcely marked off from the body of the seed below (figure 4E–I). At the base of the micropylar canal is a narrow and delicate cutinized sac which becomes more delicate and finally impossible to prepare towards the base of the seed. This sac shows two sets of cell outlines: elongated ones which are undoubtedly continuous with those of the micropylar canal, and hence should belong to the inner epidermis of the integument, and much less distinct isodiametric polygonal cells which are thought to belong to the nucellus. There are no specimens to illustrate the development of this interior of the young seed to that of the ripe seed.

Discussion

1. *Floral biology*

The sterility of *Williamsoniella* is remarkable: the great majority of the specimens studied have been preserved with one or other essential organ unripe.

About a fifth of the flowers in this collection look like buds, having the young microsporophylls closed over the gynoecium; the remaining four-fifths have shed them, and isolated microsporophylls are correspondingly abundant. Surprisingly, most of these isolated sporophylls retain their pollen, which is often only half grown and at the tetrad stage. One particular pollen sac was noted as containing hundreds of small, immature tetrads (30μ wide) of thin-walled grains, and in addition two tetrads (40μ wide) of normal grains (figure 3B) and a single giant grain (37μ wide).

The only gynoecia which can be regarded as satisfactorily developed are those showing the axis stripped of seeds and scales and these amount to about a fifth of the total.

Another peculiarity is that there is little relation between the stages of development of the different parts. Thus, of the two flowers with bud-like microsporophylls figured on plate 25, that in figure 9 has lost its perianth, and has a gynoecium at stage 1 while that in figures 19, 20 retains the inner perianth and has a gynoecium at stage 3. The young gynoecium (stage 2) in figure 10 has lost perianth and androecium; the ripe gynoecial axis (stage 6) in figures 8, 11 has also lost the androecium, but retains the inner perianth, and both flowers studied at stage 5 are similar to this. All that can be said is that the androecium is always lost before stage 4 or stage 5 of gynoecial development. Careful search was made in micropylar canals for pollen grains, such as are easy to find in various other Bennettitalean seeds, but with negative results although some of the preparations looked suitable.

There is perhaps nothing remarkable in the production of numerous abortive gynoecia. Ovaries may fail to mature because of climate, or merely because they are produced in excess of what can be ripened. This is seen in many, perhaps most, British trees, and in the cultivated apples and plums the development can and often does end prematurely at any stage from flowering to the time of normal fruiting. In apples and plums, however, the

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stamens commonly shed their pollen before falling, and I think that in their prematurely dropped flowers or fruits there would be a fairly definite correlation between the stages of development of the different floral parts. The chaotic relation in this material of *Williamsoniella* implies that a flower was retained and certain parts went on developing long after something had gone wrong with the ovules which became completely arrested. The closest analogy which I can find is one which scarcely helps in providing an explanation, namely, in the Bennettitalean genus *Cycadeoida*. Here it would seem from the American material that the plant had an astonishing chance of dying and being preserved either with all its flowers as buds with unopened pollen sacs; or else as young fruits with unshed but nearly ripe seeds. The fact that our knowledge is based on abnormally developed abortions to some extent makes the relation suggested in figure 1 between the development of androecium and gynoecium a pure assumption.

2. *Comparative morphology and systematic position*

The characters of *Williamsoniella* now known are summarized. Its stems are slender and bore 'Taeniopterid' leaves, now called *Nilssoniopteris vittata* (Brongn.) Florin. The long-stalked flower has a perianth of caducous bracts, free microsporophylls and an essentially normal Bennettitalean gynoecium. The microsporophylls, though small and compact, are still pinnately branched and bear little two-valved pollen capsules which appear to be just like those of *Williamsonia* or *Cycadeoidea* and so is the pollen. The gynoecium is rather peculiar in the apical projection of the axis (though this may be shown in *Williamsonia gigas* and *Cycadeoidea colossalis*), and the seeds differ from those of Cycadeoidea and *Williamsonia* in being sessile, though again they are nearly sessile in *W. scotica*. It is suggested that the long seed stalks of Cycadeoidea are an adaptation allowing a large number of ovules to grow into fairly wide seeds in their peculiar position just within a spherical surface.

It is impossible to extract the full value from comparing the seed of *Williamsoniella* because of uncertainty about fact. *Wielandiella* is known to have possessed an elongated seed which yields cuticles of extremely similar appearance (Harris 1932, p. 86). From the fact that the integument below the micropyle is lined with cuticle and the nucellus is also cutinized, it follows that the nucellus is 'free'. It appears to be free in *Williamsonia scotica* and may well be so in other Bennettitales, but it is difficult to compare the present seed compressions with petrifactions.

The present account has removed what seemed two outstanding peculiarities of *Williamsoniella* which were the absence of perianth and the simple microsporophyll with pad-like pollen capsules. It is now shown to possess a perianth of hairy bracts exactly like those of Cycadeoidea, and the microsporophylls, though simpler than those of any other species, are only slightly reduced from the pinnate type seen in *Cycadeoida colossalis* Wieland. The more complex relation suggested recently (Harris 1942, p. 589) to explain the pad-like form of the capsules in *Williamsoniella* is ruled out now that their two-valved structure has been realized.

Williamsoniella in flower structure, though not in stem or leaf, is perhaps nearest Cycadeoidea, particularly such species as *Cycadeoida colossalis*, and it may occupy a somewhat central position among the known Bennettitales. It has an unspecialized stem and a

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well-developed, normal perianth. The androecium is primitive in being free, but specialized in the reduction of its branches to only six or eight. Its pollen capsules, though possibly not primitive for this group (Harris 1942, p. 589), are of the kind most usual in the Bennettitales. It may be that in its small, sessile seeds it is relatively unspecialized, but we do not know whether the unisexual or the hermaphrodite flower is older in the Bennettitales.

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Description of Plates

Plate 25

Figure 7. Ripe fruit still surrounded with perianth bracts. V 25846, × 2.

Figure 8. Flower with naked gynoecial axis and recurved basal flange, still bearing perianth bracts. Figure 11 same specimen after further clearing. Photos under paraffin. V 25838, × 2.

Figure 9. Flower with no perianth, but bract-scars on floral axis and bud-like microsporophylls. In figure 14 the gynoecium and corona are exposed. V 25837, × 2.

Figure 10. Young gynoecium. No bracts or microsporophylls remain, but several bracts are lying loose close by. V 25869, × 1.

Figure 11. See figure 8.

Figure 12. Axis of gynoecium in transfer, showing the scars of the lower perianth bracts and base of the gynoecium. V 25832, × 4.

Figure 13. Half-grown gynoecium surrounded by bracts. V 25905, × 2.

Figure 14. See figure 9.

Figure 15. Floral axis with one bract still attached. The basal flange of the gynoecium is partly broken by the rock cleavage. V 25834, × 2.

Figure 16. Half-grown gynoecium surrounded by bracts. One of the bracts was afterwards removed to expose the corona. V 25840, × 2.

Figure 17. Margin of bract, showing hairs. Transfer preparation. V 24707, × 20.

Figure 18. Three-quarters grown gynoecium, all other floral parts shed. V 25829, × 2.

Figures 19, 20. Part and counterpart of vertically compressed flower, some of the matrix has been removed in each. In figure 19 the bracts and gynoecium are seen, in figure 20 the bud-like mass of young microsporophylls. V 25904, × 2.

Figure 21. Bases of free lying bracts removed and cleaned with HF. Note the attachment scar above the base. V 26857, × 4.

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PLATE 26

FIGURE 22. Microsporophyll showing the three branches clearly, but the capsules are largely concealed in matrix. V 21891, × 4.

FIGURE 23. Back of obliquely compressed sporophyll (stalk upwards). V 24710, × 4.

FIGURE 24. Laterally compressed sporophyll in which the lower branch projects beyond the upper. V 23924, × 4.

FIGURE 25. Laterally compressed sporophyll in which the upper branch projects beyond the lower. The spore capsules are very distinct. V 25843, × 4.

FIGURE 26. Specimen with a very prominent lower branch. V 25842, × 4.

FIGURE 27. Transfer of obliquely compressed sporophyll; original shown in figure 23. Two capsules are visible. V 24710, × 4.

FIGURE 28. Microsporophyll showing three capsules, the lowest strongly curved. V 25894, × 4.

FIGURE 29. Upper surface of a sporophyll in which the branches and capsules are irregularly placed. Transfer of dorsiventrally compressed specimen. Figure inverted. V 21892, × 4.

FIGURE 30. Fragment of a capsule wall after maceration showing four masses of immature pollen. V 25837, × 40.

FIGURE 31. Part of laterally compressed microsporophyll in which ridges corresponding to sporangia are visible. V 25903, × 10.

FIGURE 32. Partly dissected sporophyll showing attachment scars of the two upper capsules; two others are exposed beneath. V 24670, × 4.

FIGURE 33. Part of specimen shown in figure 29 under different lighting. × 15.

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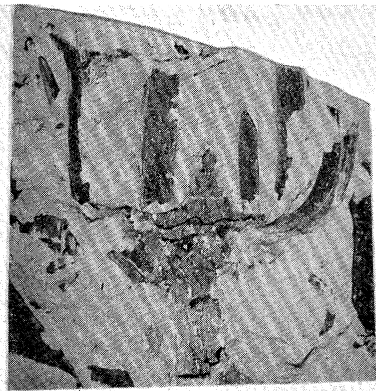

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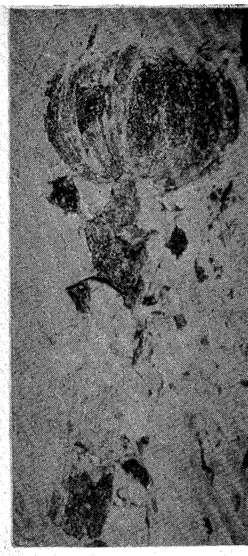

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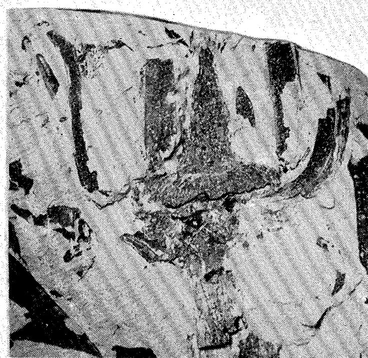

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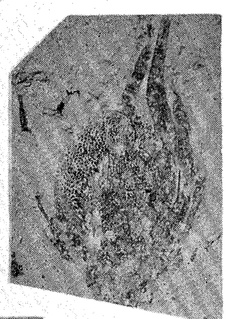

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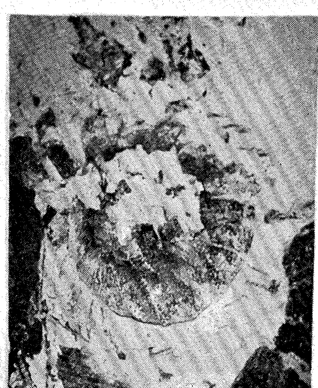

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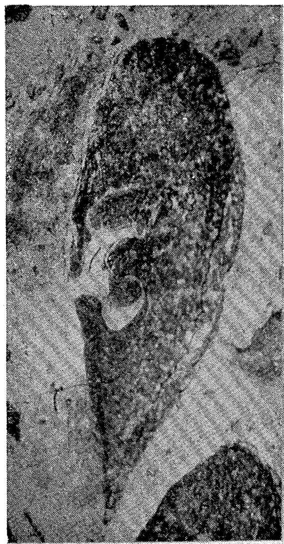

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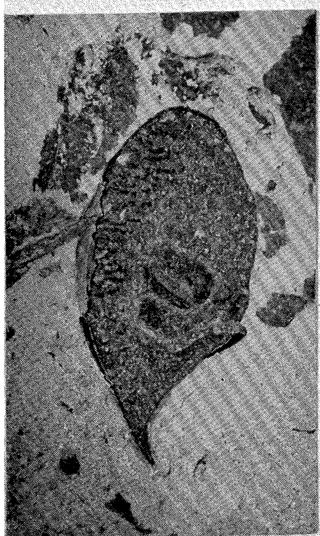

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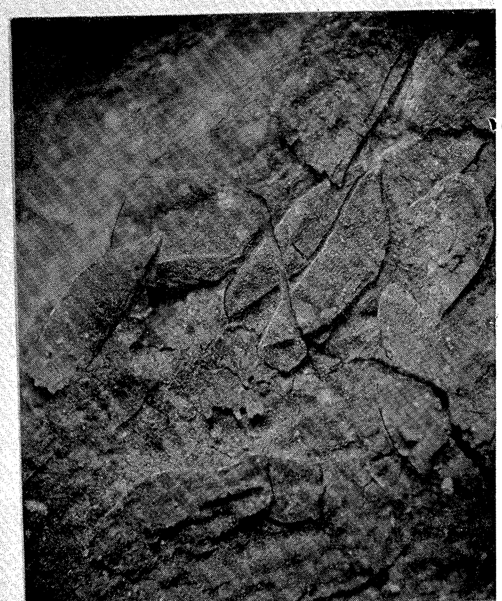

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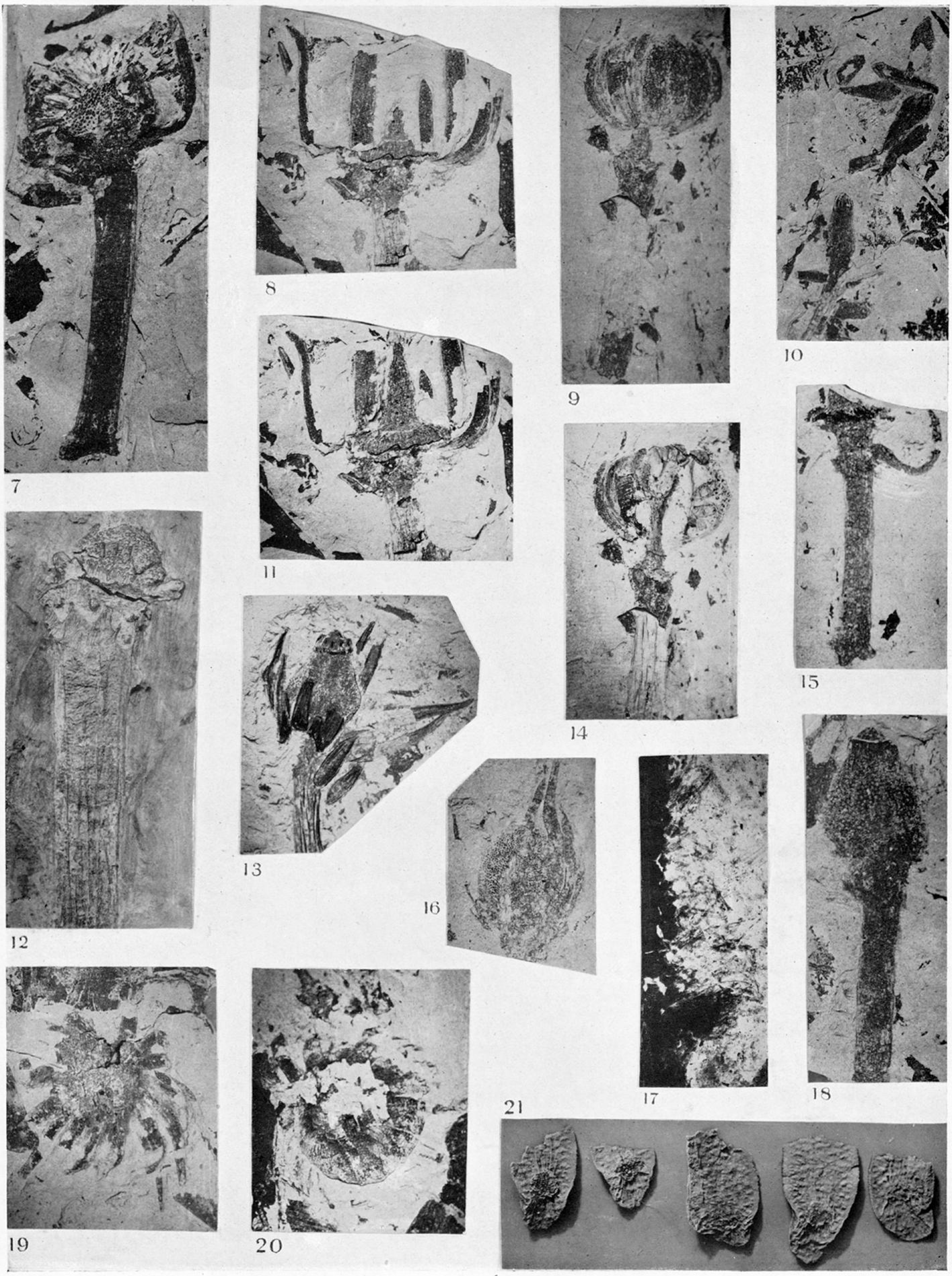

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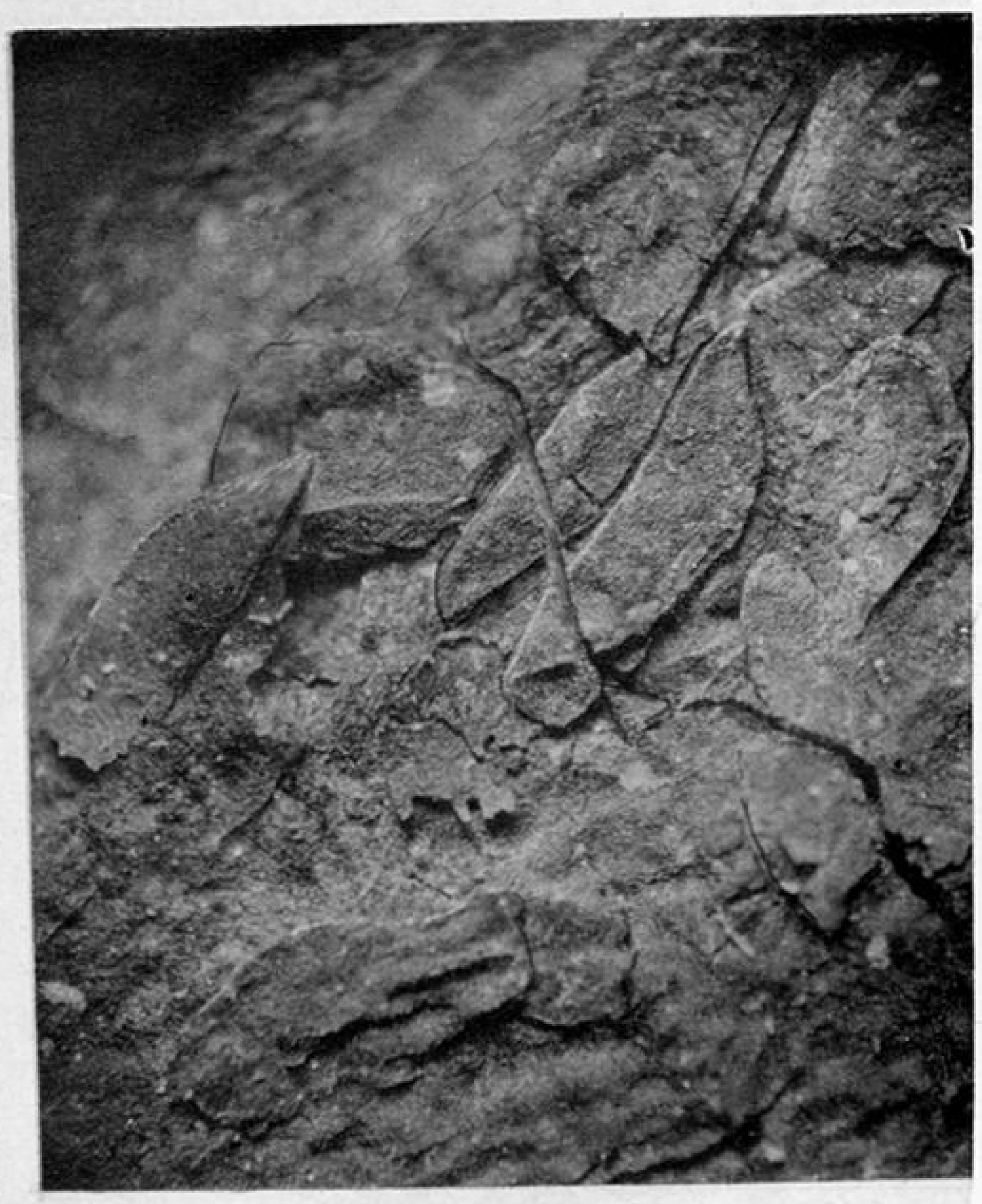

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