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H. Hamshaw Thomas

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III. *On Williamsoniella, a New Type of Bennettitalean Flower.*

By H. HAMSHAW THOMAS, M.A., F.G.S., Fellow of Downing College, Cambridge,
and Curator of the Cambridge Botanical Museum.

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[PLATES 12–14.]

INTRODUCTION.

It is now generally recognised that the Bennettiales occupied a dominant position in the vegetation during part of the Mesozoic period, and the elucidation of their reproductive structures is therefore of special importance. An additional stimulus has been given to the study of their remains by the suggestion, on the part of some botanists, that in the morphological features of these plants we may find a solution of the problem of the origin of the Angiosperms. The Estuarine beds of North East Yorkshire which had provided some of the earlier specimens had remained for a long time unexplored until the chance discovery of the beautiful *Williamsonia spectabilis* flower by Prof. NATHORST. Subsequently to NATHORST'S discovery I commenced a systematic examination of the Jurassic plant-beds of Yorkshire, and Dr. HALLE paid a visit to the coast in 1910 which resulted in the discovery of many important specimens. The previously described specimens belonging to the genus *Williamsonia* were found in the Lower Estuarine beds near Whitby, Runswick and Marske, while other well preserved examples were derived from the Middle Estuarine beds at Cloughton Wyke. The examples now to be described were obtained from the famous Gristhorpe plant-bed, which had not previously—so far as I know—yielded any examples of fertile structures clearly referable to the Bennettiales.

The Gristhorpe bed is a layer of bluish-grey shaly clay, 1–3 feet thick, and containing very beautifully preserved plant remains. It is exposed on the shore at the northern end of Gristhorpe Bay, which lies between Scarborough and Filey; it runs up into the cliff (Red Cliff) towards the north, but is here covered by Boulder Clay and unworkable. About four or five hundred yards farther it descends again and is found on the shore at the extreme southern (or south-eastern) end of Cayton Bay, but soon runs out to sea once more. It would appear that most of the fine specimens collected in former days by WILLIAMSON, BEAN and other workers from this locality were obtained on the Gristhorpe Bay side, and this may perhaps account

for the non-discovery of such recently discovered genera as *Williamsoniella*, *Eretmophyllum* and *Caytonia*.* We must also remember that coast-erosion is proceeding at a rapid rate in Yorkshire, and that the parts of the bed now exposed may well contain new plants, for in a distance of a few yards the assemblage of forms may change completely. It is unnecessary to describe the strata in which the plant-bed occurs, but it has been shown by WILLIAMSON that they belong to the Middle Estuarine Series of the Middle Jurassic.†

It may be noted here that although previous observers do not seem to have distinguished any of the remains of the "flowers" now to be described, yet they sometimes encountered isolated male sporophylls. In the British Museum Collection a specimen (V 39219) shows a frond of *Taniopteris vittata* Br., with a sporophyll near it; while the collection in the Scarborough Museum possesses one or two similar examples, labelled in one case "Impression of a fruit from Gristhorpe."

The plant-beds at Cloughton, Hayburn Wyke and Marske, which have yielded many other forms, have not as yet afforded any examples of *Williamsoniella*. I have not myself found any specimen at Whitby, but Prof. NATHORST has described a small flower-bud‡ from this locality, which must probably be included in the genus. At Roseberry Topping, in the Cleveland district, one specimen of an unopened bud was found, and I have also seen a poor specimen which was perhaps a separate male sporophyll.

The mode of occurrence of the specimens described in this paper presents some features of interest. As indicated above, the assemblage of plant remains in the Gristhorpe bed varies in every four or five yards. In one place there is little else but *Taniopteris vittata* Br.; farther along this form is very scarce, but the bed is full of *Pagiophyllum Williamsoni* (Brongn.). Working up nearer the cliff we come to an abundance of *Sagenopteris Phillipsi* (Br.), *Caytonia* and *Marchantites*; next we find a place where *Nilssonia compta* Phill., *Todites Williamsoni* Br., and *Beania gracilis* Car. are plentiful, while farther on *Nilssonia orientalis* Hen., *Czekanowskia Murrayana* (L. and H.), *Eboracia lobifolia* (Phil.) are dominant, together with *Eretmophyllum pubescens* Thomas and *Pagiophyllum Williamsoni* (Brongn.). It is suggested that a distribution of this type, in which the plants are more or less sorted and not indiscriminately mixed, furnishes some ground for connecting any leaves and fructifications which may occur abundantly together at more than one place and which do not occur separately in any abundance in intermediate places. It has been noted that *Williamsoniella* always occurs most abundantly in those parts of the bed which are full of *Taniopteris vittata* Br.

The state of preservation of the plant here described is a point of importance. The specimens obtained are the remains of the actual plants and not merely casts or

* THOMAS ('12), p. 569.

† Cf. FOX-STRANGWAYS ('92), p. 217; PHILLIPS ('75), p. 113.

‡ *Williamsonia* ? *Lignieri*, see below, p. 134.

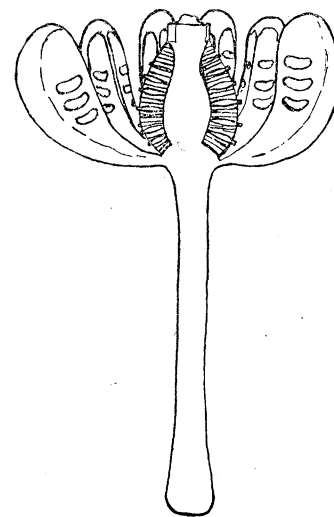
moulds in the shale; the greater part of the tissue has become converted into a carbonaceous substance, but the cuticularised portions still remain and can be obtained as membranes by treatment with Schultze's solution. Unless they are very delicate, the plants can be removed intact from the rock, and may perhaps be best described as mummified.* These remains must, however, be distinguished from petrified plants, as, with the exception of cuticularised membranes, no part of the internal structure seems to have been preserved.

The material on which the present description is based consists of a large number of separate male sporophylls, about 25 examples of female strobili free from the male sporophylls, six or seven young unopened buds and two specimens of more or less mature flowers, showing the male sporophylls still attached; many examples of stems, fronds, etc., have also been collected and examined.

DESCRIPTION OF MATERIAL.

Williamsoniella coronata, gen. et sp. nov.

General.—The fertile shoots, for which the name of *Williamsoniella*† is proposed, and which for convenience are referred to as flowers, consist of a central axis or peduncle, near the top of which the sporophylls are situated (text-fig. 1, Plate 12, fig. 1). The axis extends to the summit of the flower, where it has a characteristic crown-like appearance; below this is a small pear-shaped mass of closely packed elongated structures, the ovules and interseminal scales, which are probably smaller than in any mature form of Bennettitalean flower previously known, the whole group having a diameter of 6 mm. and being 1 cm. high. Towards the base of the ovulate region the axis expands slightly, and the interseminal scales are shorter and point obliquely downwards. Just beneath the lowest interseminal scales the male sporophylls were produced; they seem to have been more or less wedge-shaped structures, free from each other to their narrow bases and arranged in a regular hypogynous manner; each sporophyll bore five or six pollen-sacs, reniform in shape, like the synangia of *Williamsonia* but lacking the conspicuous transverse septa of the latter. There is no satisfactory evidence for the presence of any bracts outside of or below the male sporophylls.



TEXT-FIG. 1.—Diagrammatic section through a mature flower, showing the probable relationships of the various parts. ($\times Ca. 2$)

* The conditions of preservation are further discussed in an article on "The Thinnfeldia Leaf-bed of Roseberry Topping," THOMAS ('15).

† I am indebted to Prof. NATHORST for suggesting this name.

Although only a single mature specimen has been found which shows clearly the male sporophylls still attached to the axis below a mature female cone, this is fortunately a very good one (see Plate 12, fig. 1).

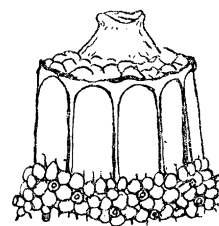
But a number of unopened buds have also been found, showing the external appearance of the sporophylls closely packed round the central portions. By clearing one of these buds with acid the central female strobilus and the remains of many masses of pollen-grains were disclosed. The bisexual nature of the flower is thus clearly established.

The Axis.—The peduncles on which the flowers were borne were stout structures about 3 mm. in diameter and attaining a length of 3.5 cm. In one or two examples the bluntly rounded base is probably seen, though the method of attachment to the original stem is not shown. The peduncle has the appearance of being somewhat expanded towards the base, but higher up it shows a number of irregular longitudinal wrinkles or furrows, such as would be produced by the compression of a soft and somewhat succulent living stem (see Plate 12, fig. 2). Cuticular preparations have been obtained from the peduncle, showing that it had a strongly thickened epidermis of rectangular cells forming long rows; these seem to have a large irregular deposit of cutin on the radial epidermal walls, and in some places there are traces of a hypodermal layer of cells. No stomata are recognisable, but in a few examples globular papillæ were apparently produced from the corners of some of the epidermal cells. At the base of the flower the axis expands and forms the receptacle, which is more or less conical in form. On the lower part of the receptacle of most of the specimens there is little trace of the insertion of the male sporophylls, which were, however, delicate in structure and could scarcely be expected to leave very conspicuous scars; in some cases, however, there is a series of small humps which may have some value in this connection, while in other forms there is a slight groove running round the receptacle at the base of the interseminal scales. An approximately median section shows that the receptacle narrows towards the top of the ovulate region, but seems to expand again to form the apical coronate structure—a characteristic feature. The form of the receptacle is, however, shown very clearly in a favourably preserved specimen from which not only the microsporophylls but also the interseminal scales and megasporophylls have disappeared (Plate 12, fig. 8). The peduncle is not seen: at the base of the receptacle is a collar-like outgrowth, on which the microsporophylls were probably originally situated (see fig. 8, *f*). Above this the substance of the receptacle has disappeared, but a cast is left showing that it was about 3 mm. in diameter, and became slightly enlarged and then tapered again. Fortunately all the upper part of the axis still remains, showing that at 2 mm. below the apical disc it narrowed to a diameter of about 1.7 mm., and then again expanded until it reached the size of the apical disc (4 mm. in diameter). Its surface shows no traces of the scars of the interseminal scales and megasporophylls, having only fine longitudinal striations. Just below the apical disc a few of the interseminal scales (fig. 8, *s*) have

remained, forming a slight flange-like group which has a somewhat irregular junction with the apical disc. The stalks of these scales must have been much shorter than those on the lower part of the axis. The apical disc itself is clearly seen, with its crinkly conical apex and longitudinal ribs.

The structure just described is of considerable interest in connection with the curious axis of the flower of *Wielandiella* described by NATHORST.* My specimen certainly shows that in some circumstances, if not usually, the appendages of the receptacle may have fallen away, leaving it as a naked skittle-like structure without any trace of the original megasporophylls and interseminal scales. Had the apical disc been absent and the appendages continuous over the surface as in *Williamsonia Leckenbyi* and *pyramidalis* Nath., and probably in *Wielandiella*, the receptacle would have presented an appearance exactly similar to that figured by NATHORST for the latter genus, but without the conspicuous "Palisadenring" at the base. The place of the latter is taken by the collar-like structure which bore the microsporophylls; this, as seen in some other examples, was probably more or less striated. A suggestion which presents itself is that the "palisaden-ring" of *Wielandiella* might also represent the basal swelling of the receptacle on which microsporophylls were originally inserted, rather than a group of actual reduced microsporophylls, but Prof. NATHORST'S cuticular preparations seem to negative this idea.

The curious structure at the apex of the axis which is probably characteristic of the species now described, is clearly shown in several of the figures (see text-fig. 2, Plate 12, figs. 1, 3, 6, 8). Its general outline is not unlike that of a royal crown, as indicated in the diagrammatic figure. In most specimens the uppermost interseminal scales are seen to be immediately succeeded by a flattened, originally cylindrical, band (corona), 1-2 mm. high, and possessing 12-16 vertical ridges. The spaces between the ridges are clearly marked, and were produced by the pressure of the tips of the microsporophylls in bud. Above this band the apex tends to become more or less horizontally flattened, but a further small hump or projection usually occurs in the centre of the flattened portion, forming the true vertex. While the vertical ridged band is usually quite smooth, the part above it is generally mottled or irregularly wrinkled, probably owing to shrinkage and pressure effects. The apical view of an unopened flower bud (Plate 12, fig. 9) at once indicates the mode of formation and the interpretation of this structure. The tips of the 12 sporophylls are closely pressed against the sterile apical corona; in the centre is seen the horizontally flattened portion with a small crater-like hump in the middle. The small specimen shown in Plate 12, fig. 6,



TEXT-FIG. 2.—Apical portion (corona) of the ovulate strobilus. The apical projection shown here is often not so prominent. (\times Ca. 5)

* NATHORST ('02) and ('09).

also shows the apex clearly, and the sharp delimitation of the ridges of the corona.*

Cuticular preparations of this apical structure show that its epidermal cells were the same in form and arrangement as those forming the heads of the interseminal scales, but as we pass upwards their walls become thicker. This thickening is more especially seen at the corners of the cells and produces the appearance of sections through collenchymatous tissue. The individual cells are irregularly polygonal in form and neither papillæ nor stomata have been detected. At its lower edge the corona possesses a series of projecting lobes which fit in between the uppermost interseminal scales (*cf.* Plate 13, fig. 12). The form of the junction, as indicated in the photograph, gives a strong indication that the apical corona was formed, at least in part, from fused functionless interseminal scales, for at frequent intervals we see apparently normal scales fused along two or more of their sides to the coronal structure.

This apical structure is more fully considered later, but we may here notice two points, (*a*) that in several genera of the Bennettitales the apex of the female axis is completely fertile (*Williamsonia Leckenbyi*), and (*b*) that in some species a sterile apical structure is found which is closely comparable with the present one. This is especially the case in a new type of female *Williamsonia* strobilus from Whitby, not yet described, but which possesses a smooth sterile apex showing about 22 sharp vertical ridges.

The Microsporophylls.—The microsporophylls clearly seen in the unopened buds (see Plate 12, figs. 9 and 10) seem to have usually numbered 12 or 14 in each flower. When young they closely invested the ovulate portion, but opened out later, becoming free from each other and uncovering the interseminal scales and micropylar



TEXT-FIG. 3. -- Diagrams of a single microsporophyll as seen in surface-view and in section; the dotted structures represent the synangia. ($\times Ca. 3$)

tubes, as shown in the figure of the mature flower (Plate 12, figs. 1 and 5). It seems probable that immediately after shedding their pollen the microsporophylls fell from the axis, for most of the ovulate strobili show no traces of them, while separate sporophylls are frequently found, and few of these have any spores left in their synangia.

Separate sporophylls are shown in Plate 12, fig. 7.

They usually show a more or less semicircular outline, the distal end being rounded and the proximal end somewhat elongated towards the point of attachment (text-fig. 3).

* The term *corona* is here employed in a sense slightly different from that in which it was originally used by WILLIAMSON [(70), p. 669]. He used the word for the terminal part of the axis only, and his *pyramidal axis* separated the corona from the upper interseminal scales. The structure which I have designated the corona thus corresponds to the corona plus the pyramidal axis on WILLIAMSON'S terminology, but the good descriptive nature of the term and the impossibility of drawing a morphological distinction between the pyramidal axis part and the portion above it, justify my usage in this matter.

The flattened side is the adaxial one, while the curved side has the appearance of being originally thickened, and a slight ridge can often be distinguished which seems to separate the enlarged portion from the thinner upper part to which the synangia are attached. The small rounded projections which are very characteristic of the microsporophylls in bud are seen chiefly on the enlarged portion of the separate sporophylls; they form a useful feature for identification. The examination of numerous separate more or less flattened microsporophylls and the comparison with their appearance in bud indicate clearly that each sporophyll must have had a wedge-like section. The sides of adjacent microsporophylls were in contact in the bud; the adaxial side extended upwards in a tapering wedge-like form, and this bore the synangia. The form is indicated in the diagrammatic figures (text-fig. 3). This type of structure, though at first sight rather unusual, is quite comparable with that described by Prof. NATHORST for *Williamsonia* and *Weltrichia*, but shows a marked extension of the median ridge in a plane at right-angles to the theoretical surface of the sporophyll (see later, p. 138, and text-fig. 6).

The sessile synangia were borne on either side of the adaxial extension of the sporophyll. They sometimes appear as if slightly sunken in the tissue. Some synangia can be made out in the photograph (Plate 12, fig. 7), but it is usually difficult to determine their number or exact arrangement owing to the confusion of the impressions of those lying on the two sides of the sporophyll.

In most cases there seem to be three synangia on each side, but two or four may also be present. Each synangium was flattened and reniform. The synangia lie in a fairly regular position; they were about 2.3 mm. long and 1.5 mm. broad, and were probably attached by a considerable length of the concave side at right-angles to the axis of the sporophyll, for the rounded side of the synangium may face either the apex or base of the structure on which it grows. It was at first thought that the synangia differed from those of previously described types in the absence of transverse septa, for there are no external indications of the transverse bands which are clearly seen in the synangia of *Williamsonia*. It was found, however, as the result of macerating young synangia, more especially those from unopened flower buds, that the spores before maturity were very clearly separated off in distinct masses. Some of these masses are shown in the photographs (see Plate 13, figs. 13, 14). On clearing some of the carbonised remains many of the spore-masses were found in their original positions lying in a parallel series; these examples seem to show that each synangium originally contained a large number of loculi, probably about 20. The original septa extended transversely across the synangium at frequent intervals, and the spore-masses consequently possess what must be practically the outline of a transverse section through a synangium; the mass figured (Plate 13, fig. 14) shows clearly that one end is pointed and the other more or less obliquely rounded; the latter would probably correspond to the side of the synangium by which it was attached to the sporophyll. The small thickness of these spore-masses indicates that

the synangium contained a large number of loculi, a feature that has also been directly observed.

In the unopened bud from which the spore-masses shown in figs. 13-15, Plate 13, were obtained, the microspores were evidently almost mature. Under a high power the outlines of individual spores can just be made out (fig. 13), but they are very crowded and confused; their walls must have been well cutinised before preservation. In one case it is possible to make out clearly a tetrad of spores. In another case a tetrad of spores had remained in an older sporangium after all the rest had disappeared, and so the method of formation of the spores is established, although the usual tetrad-scar can seldom be seen on mature spores. Individual mature spores were more clearly seen in a preparation from an isolated sporophyll shown in Plate 13, fig. 11. They appear circular or elliptical and were probably flattened spheres; their walls were thin and they were about 0.02 mm. in diameter. Many preparations made from synangia on isolated sporophylls showed that these were devoid of spores, which may have been shed before the fall of the sporophylls. In these cases no indications could be detected of the line of dehiscence of the synangia, and the probability is that it was apical. The wall of the synangium was very lightly cuticularised and little can be made out as to its structure.

The epidermal cells of the sporophylls were somewhat lightly cuticularised, but fairly satisfactory preparations could be made from them: the investigation of these cuticles is a matter of very great importance as affording evidence of the affinities of the present flower.

The best examples came from unopened flower-buds, but other fragmentary cuticles were obtained from isolated sporophylls. It was found that the mottled appearance of the abaxial surface has no obvious effect on the cuticular structure; this suggests that the mottling is the expression of some sub-epidermal structural feature. There seems to be some difference between the cuticles of the outer swollen part of the sporophylls (Plate 13, fig. 19) and the inner part near the synangia (Plate 13, fig. 18), the cell walls of the latter being less cuticularised, more irregularly angular and possessing few stomata. This is to be expected from the greater exposure of the abaxial surface in bud, and is probably also an expression of the morphological difference between the upper and lower sides seen in most of the Bennettitalean fronds, a difference which shows itself even in the bracts, as will be indicated later.

It is important to notice that the walls of the epidermal cells of the sporophylls are typically straight and not sinuous. The feature of greatest interest in these cuticular preparations is the presence of stomata showing a characteristic structure (Plate 13, fig. 20); these occurred in some numbers, especially in the distal portions of the abaxial surface. They are never quite so much thickened and so distinct as in the fronds from the same bed, but their characters can be easily made out. They are

clearly of the type recently described as characteristic of the Bennettitales* and show the usual crescentic thickening patches.

The special characters of these stomata (Plate 13, fig. 20, A-E) are the presence of what I have described as outer and inner thickening patches and of unthickened subsidiary cells.

The outer thickenings have sharply pointed ends and are shorter than the subsidiary cells when measured in a direction parallel to the slit. The inner thickening patches are smaller and thinner and not so well defined. The subsidiary cells are unthickened and seem to underlie the outer thickenings of the guard-cells; they are apparently separated from the polar parts of the latter by distinct walls which often appear like polar continuations of the pointed ends of the thickenings.

It has recently been shown† that each genus of Bennettitalean frond had a characteristic stomatal form. The stomata of the two genera *Anomozamites* and *Taniopteris* are comparable with those just described, possessing unthickened subsidiary cells, which are broader than the guard-cell thickenings, and whose inner walls often appear continuous with these pointed thickenings. Among other leaves examined those of *Otozamites Feistmanteli* possess somewhat similar stomata. The stomata of *Anomozamites* are nearly identical with those described here, but it may be noted that in that genus the central thickening patches on either side of the slit are as thick or thicker than the outer spindle-like or crescentic patches and are sharply marked off from them, while in *Taniopteris*, as in the present case, they are more often thinner than the outer patches and their limits are very indistinctly defined.

A comparison of a number of stomata on the sporophylls with those from fronds of *Taniopteris vittata* occurring in the same bed, seems to indicate that these structures are almost identical in form and structure, though the ordinary epidermal cells of the sporophylls have straight walls instead of the sinuous ones seen in the fronds.

I have, however, noticed some cases where the walls of the sporophyll epidermal cells show a tendency to become sinuous. Mention may also be made of two cases in which preparations were made from part of a sporophyll which showed after clearing some fragments of cuticle with very sinuous walls; these could be identified without hesitation as fragments of a *Taniopteris* frond. The exact point of origin of these fragments was indeterminable, and they may probably have been derived from an unobserved fragment of a frond accidentally lying beneath the sporophyll and pressed into intimate connection with it. On the other hand, in both cases they were marginal fragments, and it is possible that the sporophylls occasionally possessed a more typical leaf-lamina structure at their apices. This view is suggested by the structure of some isolated bracts which we shall notice later.‡

* THOMAS and BANCROFT ('13).

† *Ibid.*

‡ See below, p. 125.

The Ovuliferous portion.—Immediately above the place of insertion of the microsporophylls there is a mass of ovules and interseminal scales possessing the same general structure as the female strobili in the Bennettitalean flowers already known. So far as can be ascertained, *Williamsoniella* only differs from the other types in the sterile apex of the axis and in the apparently sessile ovules.

The inverted pear-shaped mass of ovules and interseminal scales is shown in the figures (Plate 12, figs. 1, 2, 5; Plate 14, fig. 29). It has a diameter of 6·9 mm. at the base, tapering to 2·7–4·5 mm. at the apex, having a length of about 10 mm. inclusive of the apical corona. In surface-view the rounded heads of the interseminal scales with the micropylar tubes projecting among them are clearly seen.

The whole surface sometimes possesses a number of longitudinal ridges corresponding with the ridges of the apical corona, and apparently produced by the pressure of the microsporophylls when in a young condition; in these specimens, which may have been less mature at the time of preservation, the interseminal scales are more or less flattened and hexagonal and the micropylar tubes do not project much above them. In some examples the tubes project more in the lower than in the upper portion of the strobilus, possibly indicating that the ovules ripened in acropetal succession; micropylar tubes are seen in all specimens, though in the younger ones they scarcely project above the interseminal scales and can only be distinguished by the canal in their centre. There are few ovules in the lowest millimetre of the strobilus. The scales are all alike and do not show the rosette-like arrangement round the micropylar tubes, which is seen in some forms of Bennettitalean strobilus.* In many cases the micropylar tubes project far beyond the scales and are very conspicuous, while their canals, filled with matrix, are very distinct (*cf.* Plate 12, fig. 2A).

One specimen has been found which shows a fortunate state of preservation and provides some information as to the structure of the strobilus. The specimen seems to have been broken in half longitudinally before it was embedded in the matrix, and it shows the outline of the axis with its appendages (Plate 12, fig. 3). The section was not quite median near the apex, and the corona is seen below some of the appendages.

The axis is a somewhat conical structure rather more than 3 mm. in diameter; projecting outwards from it are the appendages which appear as striated structures, 3–4 mm. long. At first sight they appear to be all alike, but towards the exterior it is easy to distinguish the megasporophylls or ovules, with their micropylar tubes, from the interseminal scales with more rounded or flattened heads. The exact outlines of the scales cannot be definitely made out, but they seem to be club-shaped structures, thickest about 0·5 mm. from their apices and tapering gradually towards their bases.

* *Cf. Wielandiella*, figd. NATHORST ('09), Taf. 6, figs. 4 and 8, and *Williamsonia Leckenbyi*, Nath., figd. NATHORST ('02), Taf. 2, fig. 32.

The megasporophylls were perhaps not quite fully developed, for the micropylar tubes do not project far beyond the interseminal scales. When traced downwards a gradual expansion occurs below the tubes so that the ovules are about 0·7 mm. broad at a distance of 1–2 mm. from the surface; they then taper again very gradually towards the base.

The surfaces of both the megasporophylls and the interseminal scales are finely striated, the result possibly of shrinkage before preservation. The most noticeable features of these structures are (1) the close similarity in appearance between the megasporophylls and the interseminal scales; (2) the fusiform shape of the former and the absence of a distinct elongated pedicel. In the latter character they differ considerably from the corresponding structures in *Cycadeoidea*, where the ovules possess long stalks, and they resemble more closely those of *Williamsonia scotica* Sew.* In the latter species the outline of the microsporophyll was probably somewhat similar to that of the present structures, though their basal portions are not well defined owing to shrinkage; there, too, the cone was undoubtedly in a young state, and a more marked pedicel may have developed later, but in the present instance there is little doubt that the cone was approaching maturity.

Very good preparations can be made of the cuticularised portions of the structures described above, the rounded distal ends of the interseminal scales and the exposed portions of the micropylar tubes showing very clearly the form of their epidermal cells. The irregularly hexagonal interseminal scales are seen to surround the micropylar tubes in the usual way, five to six surrounding each tube; they present a less regular appearance in surface-view than in several other forms. The epidermis was composed of thin-walled polygonal and more or less isodiametric cells, but they appear to have been more strongly thickened at the margins where they abutted on the other scales (*cf.* Plate 13, figs. 12, 17). An interesting feature presented by some scales is the presence of a ring of thickening material in the centre with a flat top of their cells, and forming a little circular disc-like projection above the general surface. These structures are reminiscent of the flat-topped interseminal scales of *Williamsonia scotica*, Seward, and suggest the top of an aborted ovule. One of the best examples occurs near the top of a strobilus in a position in which we should expect to find a megasporophyll, and seems to indicate a type of structure intermediate between a megasporophyll and an interseminal scale, incidentally lending support to the homology of these two structures.

In one case an interseminal scale seems to possess a single stoma; in the centre of a somewhat enlarged cell two small crescentic thicker patches are seen, which look exactly like the thickening patches of a guard-cell, and these are connected to adjacent cells by fine walls or thickenings. Though the structures seen are very small, they are clearly visible and could scarcely be the result of some chance injury or accident of preservation. In their size and relations to the surrounding cells these

* SEWARD ('12).

stomatal thickenings appear to have been very similar to those figured by NATHORST in a membrane from *Williamsonia Lignieri*.*

The micropylar tubes are usually clearly seen in preparations from mature female strobili, though they cannot be clearly made out among the scales in the preparations from the young unopened bud. In some of my slides they have a length of 0·8 mm., but were often longer when fully extruded. They were composed of very regular rectangular epidermal cells, rather more strongly cutinised than the epidermal cells of the interseminal scales (see Plate 13, figs. 16, 17). They had a plain cylindrical form with almost straight sides without the slight contraction which is seen near the top of the tubes of *W. Leckenbyi* (= *W. pecten*).† The characteristic papillæ of the latter form are also absent from the present specimens, which agree in this respect more closely with *Wielandiella angustifolia*.‡ Most of the tubes in my slides are slightly curved, probably as the result of bending during mounting. The apex of the tube seems to have had a rounded edge, and the inside is well cuticularised; it appears as though the walls of the tube were originally fairly thick, and this must have enabled them to remain in their original upright position during preservation, as shown in Plate 13, fig. 16.

Buds and Young Flowers.—Three specimens show young flower-buds which had presumably become detached from their peduncle before preservation, and are seen lying in the matrix apex upwards. They appear as small circular structures 8–12 mm. in diameter, with the top of the apical disc surrounded by closely packed microsporophylls which are so tightly pressed against the disc that they appear, at first sight, as if joined to it (*cf.* Plate 12, fig. 9). On closer inspection a groove can be seen marking the boundary between the microsporophylls and the apical disc, but the latter shows few traces of the ridges which form so characteristic a feature in older examples, and these no doubt represent the regions between the adjacent sporophylls of the bud. In one specimen the edge of the disc at the junction of the sporophyll seems to have a distinct dentate form with ridges between the successive apices of microsporophylls.

The top surface of the apical disc or corona shows in one specimen a few fine radiating striations, but in another is irregularly wrinkled as if it had contracted during drying. The latter example shows, however, a very distinct central raised projection about 1 mm. in diameter at the top, and having a cup-shaped depression in the middle (*cf.* fig. 9, Plate 12). This projection, referred to in the description of the apical disc of the mature flower (see p. 117), has probably no special significance, but is interesting in comparison with the apex of the flower of *W. gigas* (L. and H.). In the other specimens the apical projection, though present, is not quite so well defined. The sporophylls in the only complete bud number 15 or, possibly, 16, while

* NATHORST ('09), Taf. 4, fig. 9.

† *Ibid.*, Taf. 3, figs. 6 and 7.

‡ NATHORST ('09), Taf. 6, figs. 4–7.

in another well-preserved specimen there are about seven in half the circumference. The outer surface of the sporophylls is characterised by the small rounded projections seen on the abaxial side of the separated examples.

Three or four other specimens show buds or young flowers flattened out sideways (Plate 12, fig. 10); in one case the peduncle is seen, but in the others the base of the flower is not visible. These specimens also have a more or less circular form, four to six microsporophylls are seen closely packed together; they are divided from each other by a fine groove and only become free at their apices; they show the usual roughened surface very clearly (fig. 10).

In one of the examples which shows the peduncle, the outer surface of the basal portion has been removed in some way and in the broken carbonaceous material exposed, a number of well-defined ridges are seen running upwards from the peduncle into the sporophylls and occasionally bifurcating. These may perhaps represent the vascular bundles which supplied the microsporophylls, though no other example shows any trace of similar structures.

A cuticular preparation was obtained from one of the young flowers of this second group which proved conclusively the bisexual nature of the flower. Part of the apex of the entire bud was cleared in the usual way, after which all the cuticularised membranes became visible; in the centre of the bud was found the apical disc with interseminal scales below it, and surrounding these were the epidermes of the microsporophylls adhering very closely to the apical disc by their terminal portions. From the interior of the bud a large number of spore-masses were set free from the synangia borne on the unopened microsporophylls. Thus the bud contained both the characteristic micro- and mega-sporangial features. Since this observation is one of considerable importance, it has been thought desirable to add a photograph of part of one of the original preparations (Plate 13, fig. 15). This shows a mass of fragmentary material exactly as it appears after treating with Schultze's solution and ammonia and before any attempt has been made to separate or clean the membranes. At *p* in the photograph two pollen-masses are seen, while at *s* some interseminal scales can be made out.

The possibility of thus obtaining valuable knowledge of the internal structure of an apparently structureless mass of carbonaceous material, indicates clearly the great utility of the maceration method in palæo-botanical research.

Bracts.—Most of the previously described Bennettitalean flowers were probably more or less surrounded by sterile bracts. In *Williamsonia gigas* there were a large number of them, as also in *W. scotica*, and various species of *Cycadeoidea*. In *Wielandiella* and *W. scotica* these bracts were flattened lanceolate structures, and, morphologically, modified petioles, for they often bear at their tips greatly reduced laminæ of the ordinary foliage-type. From the present flowers, however, sterile bracts are typically absent. Had bracts of the *Williamsonia* type been present originally, some trace of them would certainly have remained round some

of the buds which have been preserved, or some scars would be seen on the pedicels.

But while in other forms the bracts form a protecting layer investing the young developing female strobili, here the tightly packed microsporophylls, with their apices fitting closely against the apical corona, must have formed a highly efficient protection for the more delicate internal organs. The stoutly cuticularised epidermis and numerous stomata on the outer surface of the young microsporophylls may also be taken as an indication that these were freely exposed and not enclosed by an investing covering of bracts. In the layers of shale where the flowers are found, bract-like structures are of extremely rare occurrence; a few have, however, been found and present some features of interest.

The most noteworthy specimen is shown in the photograph (Plate 14, fig. 22) and is closely comparable with the examples described and figured by Prof. NATHORST* in *Wielandiella*. It consists of five small bracts lying close together in the matrix and parallel to each other. They were lanceolate structures about 15 mm. long, and 2–3 mm. broad near the base, rather thin in texture and tapering gradually towards the apex, which in two cases is pointed. In three of the bracts the apex is expanded to form a small oval lamina about 3 mm. broad and 4 mm. long, which shows a midrib and several dichotomising lateral veins, and which almost certainly represents a reduced lamina of the *Taniopteris vittata* type. Another isolated fragment of a small lamina of the same type has also been seen.

A cuticular preparation made from the expanded basal part of one of these bracts (shown in the photograph, Plate 14, fig. 23) shows that its cuticles were very thin, and differed on the two sides. The cuticle from one side, probably the adaxial one, is seen to be composed of clearly defined cells arranged in regular rows, and having a more or less rectangular outline. The cell walls are thin and usually straight, but sometimes show a slightly sinuous form. A number of thickened places occur which are arranged fairly regularly and probably represent stomata, though in no case can the guard-cell thickenings be clearly made out; they may indeed only be papillæ. The cuticles of the other surface, probably the abaxial one, are much obscured by dirt, but they are noticeably different. The cells are slightly more strongly cuticularised and they have a much more rounded shape, the cell-walls are thin, but an important feature is the presence of the remains of numerous stomata, which are almost as abundant as on the leaf-lamina. The thickenings of their guard-cells are not so clearly defined but are fairly distinct; in several cases they seem to have been identical in form with those seen on the microsporophylls of the flower just described. The outer thickenings of the guard-cells show a crescentic or hemispherical form, with fine walls apparently connecting their poles to the adjacent cells; the inner thickenings are not clearly defined.

It is very interesting to find that the expanded petioles of these bracts had such

* NATHORST ('02), Taf. 1, figs. 28–34.

relatively thin cuticles, with a distinct difference between the upper and lower sides, numerous stomata on one side, and taking on a structure like that of the leaf-lamina, but without the sinuous cell-outlines. Their thin cuticles may indicate that they were comparatively ephemeral structures, and the stomata may point to the adoption of photosynthetic activity consequent upon their flattening. The cuticles indicate that a comparison may be drawn between these expanded petioles and the microsporophylls, for in both cases we have dissimilar inner and outer membranes with stomata of exactly similar pattern. The form of the stomata being exactly similar to that of the microsporophyll stomata and belonging to a structure which is certainly a modified *Tæniopteris vittata* leaf, provides evidence that these bracts belonged to the flower above described and that this flower was borne on the plant whose leaves have been long known as *Tæniopteris vittata*, Br.

These bracts are no doubt similar structures to those figured by NATHORST for *Wielandiella*, where a much reduced segmental lamina of the *Anomozamites* type was sometimes present. One or two further examples of structures which may have been bracts with pointed apices have been noticed but, as mentioned above, they are very rare when compared with the numbers of microsporophylls which are found.

Two questions then arise: (1) Did these structures belong to the plant whose flowers have been just described, and (2) if so, in what position were they originally produced? I have little doubt that an affirmative answer must be given to the first of these questions. In addition to the evidence from the cuticular and stomatal structure mentioned above, the structures in question occur in the layers of shale in which the floral structures are found and which are also full of leaves of *Tæniopteris vittata*, Br. The flowers were very probably produced on the plants which bore these leaves, as shown by constant and close association, as well as by the form of the stomata on the microsporophylls. The flowers of *Wielandiella* were enclosed by and associated with very similar structures which combine the characters of simple protecting bracts and foliage-leaves, and it is therefore reasonable to suppose that the present structures were originally connected with the flowers. This being so, there are two possible alternatives as to their mode of origin and growth. In the first place, only a few of these bracts are found, and they are somewhat delicate in structure, their bases are not seen, but must have been quite thin; we may then suppose that in exceptional cases a few sterile bracts were produced in a loose fashion on the peduncle just below the microsporophylls, their points of attachment being very narrow and leaving no scar.

A second and more probable explanation is that they were of the nature of bud-scales—and, in fact, their general form is identical with that of the bud-scales of the Horse-Chestnut. They may have been produced more particularly round the bud from which the flower grew, but of which we at present know little, since a flower has not yet been found in connection with a main stem.

Leaves.—It has already been pointed out that the remains of the flowers which

have just been described are constantly found in association with leaves of the type previously known as *Taniopteris vittata* Br. I do not think that I have any specimen of the female part of the flower which does not show some portions of a frond of this type in the same block, and the same is true in regard to the majority of the separate male sporophylls. In some blocks, however, which contain male sporophylls, I have observed *Nilssonia compta* Phil., *N. orientalis* (Heer) = *tenuinervis* Nath., *Eretmophyllum pubescens* Thomas, *Pagiophyllum Williamsoni* Br., *Sagenopteris Phillipsi* Br., and *Todites*, but these are only occasionally present. We may thus state the evidence of association as follows: (a) the remains of the flowers *Williamsoniella coronata* are only found where leaves of *Taniopteris vittata* are abundant; (b) no remains of flowers, with the possible exception of a few male sporophylls, are found in other parts of the bed where *Taniopteris* fronds are less abundant than the fronds of other types.

The fronds or leaves under consideration were described by BRONGNIART* in 1828 as *Taniopteris vittata*. PHILLIPS, in the following year, described them as *Scolopendrium solitarium*, but in later editions of PHILLIPS' work, BRONGNIART'S name was employed, as also in LINDLEY and HUTTON'S 'Fossil Flora.'† SCHIMPER substituted the generic name of *Oleandridium*, while BORNEMANN‡ was one of the first to recognise their possible Cycadean affinities and instituted the generic name of *Stangerites*. Subsequent writers have for the most part used BRONGNIART'S name, though the attribution of the leaves to fern-like plants was recognised as uncertain. A complete list of references to the species is given in Prof. SEWARD'S British Museum Catalogue,§ with a description and figure.

The fronds may be shortly described as follows (some examples are seen in the photographs, Plate 14, figs. 27, 28):—Simple lanceolate structures of varying size from 7 mm. to 3 cm. broad, and from 6 cm. to perhaps 20 cm. long. The larger types pass into the other species, e.g., *T. major* (L. and H.), which can usually be distinguished easily in examples from this locality by the wide separation of the veins. The average specimens are about 17 mm. broad and perhaps 12 cm. long; a few short and broad examples have been noticed which had an almost elliptical lamina. The margin of the lamina is usually entire, but not always so; occasionally we see on one or both sides a few irregular indentations of the lamina, sometimes reaching the midrib and giving the leaf the same outline as in *Nilssonia polymorpha* figured by SCHENK,|| and also as in *Nilssonia orientalis* from the Gristhorpe bed.

Curiously irregular leaves of another kind show a number of rounded hollows in

* BRONGNIART, 'Prodrome,' p. 62; BRONGNIART ('28), 'Hist. vég. foss.,' p. 263, Plate 82, figs. 1-4.

† LINDLEY and HUTTON, Plate 62.

‡ BORNEMANN ('56), p. 59.

§ SEWARD ('00), p. 157, Plate 16, fig. 1.

|| SCHENK ('67), Plate 29, figs. 3, 4, 8.

the margin, which has sometimes been very much cut away. These leaves had, no doubt, been partially eaten by animals of some kind before preservation.

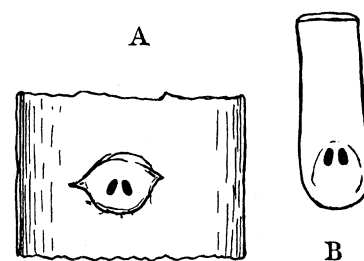
The apex of the lamina was usually retuse, often with the top of the midrib projecting as a small point in the centre of the notch; some specimens, however, have a bluntly rounded apex; towards the base the margins usually narrow and then terminate in rounded lobes, which are usually unequal.

The petiole of the frond is continued upwards as a broad stout midrib, on the upper side of which the lamina is produced; the two sides of the lamina do not meet on the top of the midrib, but are separated by a space of about 0.5 mm. or more towards the base of the frond. This feature provides one of the characters distinguishing these fronds from the *Nilssonias*, but the insertion of the lamina is almost identical with the insertion of the pinnæ in *Ptilophyllum* and with the insertion of the lamina of *Anomozamites*.

The secondary veins are numerous and almost parallel to each other, usually forked near the midrib and sometimes bifurcating again nearer the margin; they are 0.3–0.5 mm. apart.

The petioles are fairly distinctive, below the lamina they are usually 2–3.5 mm. broad, gradually widening a little when traced downwards and rounded off at the base in a very regular fashion; they are 1.5–2.5 cm. long and are sometimes straight but more usually are curved near their bases, suggesting that the lamina originally had a horizontal position on a vertical stem; the curvature is sometimes irregular and often oblique, and it frequently results in causing the actual base of the petiole to become obscured by the matrix. The petiole usually shows a number of rather indistinct longitudinal ridges or grooves, on the upper side two ridges run down in a line with the place of insertion, and the lower side sometimes shows traces of having had originally a well-marked median ridge.

Only one or two specimens have been found lying in a position in which we might expect to see the scar of attachment to the stem (*cf.* Plate 14, fig. 28, *p*). In several cases the region of attachment has a small irregular mass of carbonaceous substance adhering to it as though the abscission were not very sharp, but in one example a perfectly clean surface is presented on which two small humps rather less than 1 mm. apart are seen, at a distance of 2 mm. from the end (Plate 14, fig. 26). These, no doubt, represent the traces of the vascular bundles which supplied the leaf and are interesting in connection with the humps of similar size seen on the leaf-scars on some of the stems which I believe to have borne these leaves (*cf.* text-fig. 4). The width of the petioles at their base was 2–3 mm.



TEXT-FIG. 4.—A, diagram of leaf-scar of stem, showing bundle traces (*cf.* Plate 14, fig. 25). B, diagram of attachment-surface of petiole of *Tainiopteris vittata* frond, showing bundle scars (*cf.* Plate 14, fig. 26). (\times Ca. 4)

The appearance of a clean-cut face at the point of attachment of the petioles of these leaves suggested to Prof. SEWARD* a comparison with the recent fern *Oleandra neriiiformis* Cav., where the petiole becomes detached by the formation of a well marked absciss-layer. In spite of the irregularities noted above, it is extremely probable that an absciss-layer was formed. A full description of the cuticular structure of the lamina of these fronds is published elsewhere,† and the figures given may be compared with those shown on Plate 13, fig. 20. The cuticular structure shows clearly that these fronds belong to the Bennettitalean group, being most nearly allied to *Anomozamites*. The study of the external form of the fronds given above and the occurrence of divisions in the lamina also point to their relationship with *Anomozamites*; as is pointed out later, the similarity between the plant reconstructed in this paper (text-fig. 5), and *Wielandiella* (whose leaves were of the *Anomozamites* type) was probably very close.

I regard *Teniopteris* as a form-genus including fronds of uncertain affinities and either filicinean or cycadean, and as such the generic name must be retained in dealing with detached fronds.

Adopting Prof. NATHORST's views,‡ I think it best to use the separate generic name for the flower and in speaking of the whole plant here described, in the same way that the name *Williamsonia* is employed for floral structures, some of which were borne on the plants whose leaves may be called *Ptilophyllum* or *Zamites*. It is less clear how we should treat the specific name *vittata*—whether or not this name, instituted long ago for the leaves, should also be employed for the whole plant and the flowers. Against this course it may be urged (*a*) the evidence for the connection of the leaves and flowers, though strong, is not absolutely conclusive, and (*b*) the limits of this form-species are rather indefinite, and probably many fronds have been described from other localities which had quite distinct reproductive structures. My view is that the two names *Williamsoniella coronata* and *Teniopteris vittata* should be retained as referring to flowers and leaves respectively, until further discoveries have been made, especially in other areas where fronds of this type occur.

At Whitby, where the type-specimen of *Williamsoniella Lignieri* (Nath.) was found, fronds of *Teniopteris* are also very common. Most of these fronds can be distinguished from the typical *T. vittata* by their more oval outlines and by the less regular and rather more distinct veins.

Since the flowers from Gristhorpe and Whitby are specifically distinct, it is probable that some at least of the fronds from Whitby may have belonged to a plant specifically distinct from the Middle Estuarine type, on which the present paper is principally based.

Stems.—While the evidence in favour of connecting the flowers of *William-*

* SEWARD ('00), p. 158.

† THOMAS and BANCROFT ('14), p. 188; Plate 19, figs. 10–12; Plate 20, figs. 6, 7.

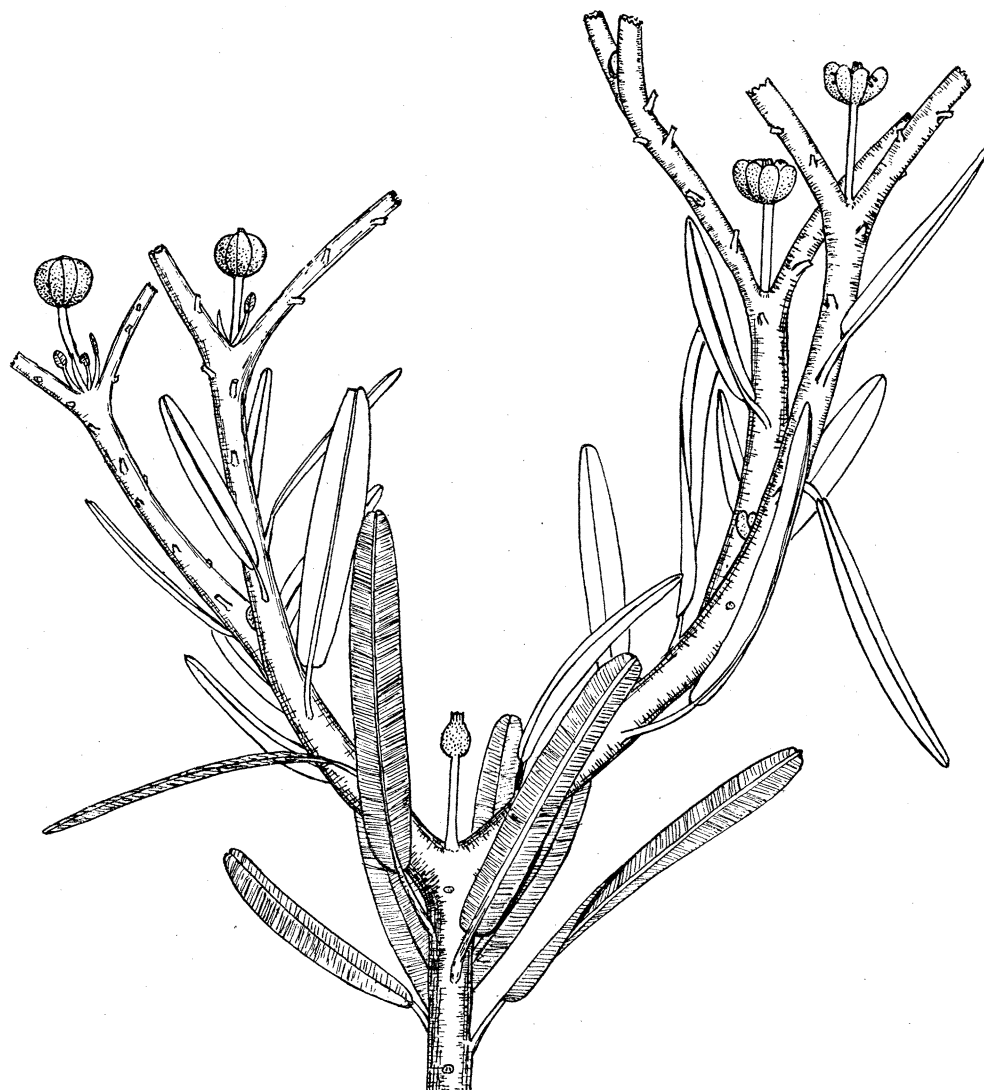
‡ NATHORST ('13).

soniella with the fronds *Taniopteris vittata* is fairly strong, it is nevertheless entirely indirect. The evidence for assigning the flowers to certain stems in my collection is still less direct, but nevertheless it presents some satisfactory features, and the whole plant, when restored in accordance with the examples recently found, agrees so closely with *Wielandiella* that it affords strong support to my contention.

But so long as the direct evidence of organic connection is not forthcoming, any conclusions we may reach must be to some extent speculative. In the places and levels in the Gristhorpe bed where the leaves are so abundant and where the flowers are found, a number of fragments of stems are also present (see Plate 14, fig. 28). These were originally cylindrical structures, varying in diameter from 7 mm. to 2 cm., and frequently branched, though no specimen is large enough to show more than one node. The branching was of a forking type, but in most cases the base of the V between the two unequal arms is not clearly visible. In one specimen, however (Plate 14, fig. 24), the point of forking is fairly clear, and to one side of it a small raised projection can be made out. This structure is like a small raised platform with striated sides, and a rather irregular lumpy top; though not completely preserved, it seems to have a diameter of about 4 mm. It almost certainly represents the place of attachment of the flower, for the average diameter of the peduncles at the base was 4–5 mm. The flowers of *Wielandiella* were borne at the forking of very similar stems, and the frequent occurrence of detached pedunculate flowers in our bed indicates that their stalks became readily detached from the stems which bore them. Assuming that the flowers were borne in this way, the type of branching must be regarded as a kind of false dichotomy, possibly referable to an original decussate type.

The surface appearance of the stems is fairly clearly seen when the substance of the branch has remained as a mass of carbonaceous material: it may well have been covered with bark, which in the older examples appears irregularly cracked and wrinkled, but in the smaller specimens the surface was fairly smooth and the outlines of the cells are just visible. The best preserved examples of younger stems show a number of irregular longitudinal ridges, perhaps due to the compression of an originally soft and yielding structure. The leaf-scars or leaf-bases are clearly seen as projecting humps, but they are somewhat irregular in form, and the details of their structure are not very clearly seen; they have frequently been broken in extraction from the matrix. No regular arrangement seems to be presented, and in some cases the projecting leaf-bases appear to be of two kinds, either small and oval or larger and transversely widened. The small projections are the more numerous, sometimes occurring close together in the same vertical line; they appear to have a central hump surrounded by a furrow which may possess a spar-like extension at one end. One may, perhaps, regard them as the bases of aborted or incompletely developed leaves. The larger leaf-bases show some variation; in the best preserved examples (*cf.* Plate 14, fig. 25) a clearly defined projection about 3 mm. broad is seen,

with a groove and ridge below it; almost in the centre two distinct depressions may be observed—they lie side by side in a slightly inclined position and correspond in size and in their distance apart with the two humps which represent the vascular bundle-scars on the leaf-bases of *Tæniopteris* described above.* The whole leaf-scar on the stem has approximately the same size as the base of the petiole in that



TEXT-FIG. 5.—Diagrammatic restoration of part of a plant of *Williamsoniella coronata*, about $\frac{2}{3}$ natural size. The upper leaves are shown as having been removed.

species (*cf.* text-fig. 4 and figs. 25 and 26, Plate 14). In some cases the bundle-scars on the stem are represented by two humps with a groove between them; in other cases only a single central hump is seen.

We see, then, that the scars on the petioles of *Tæniopteris vittata* can be fairly exactly matched with the leaf-scars on the associated stems, the two scars or leaf-

* See p. 129.

trace bundles are seen on both, the size of the scars and petiole-bases was about the same, viz. 1–4 mm., while both the stem scars and the petiolar bases were rounded. We may reasonably assume that where the stems occur they would probably be associated with the leaves borne on them, and everything points to the stems being the axis of "*Tæniopteris*." We may carry the argument a step farther by inquiring if other fronds occur in the Gristhorpe bed which might have been borne by these stems.

The following species are fairly abundant in the bed :—*Nilssonina compta*, *Nilssonina orientalis*, *Ptilophyllum pecten*, *Anomozamites Nilssoni*, and *Ctenis falcata*, besides *Tæniopteris vittata* and *Tæniopteris major*. We may assume that it is very unlikely that the stems are not Cycadean or Bennettitalean. Now of the above, the *Nilssonias* had large expanded bases, while *Ctenis* had also a very large rachis. The bases of *Ptilophyllum* fronds were also transversely expanded, and this form is rare in the part of the bed from which the stems come. We are thus left with *Anomozamites* and *Tæniopteris*. The former genus is uncommon at the place where the stems were found, while the latter abounds and many examples are found in every block containing stems.

There is, then, a very strong presumption that our stems and *Tæniopteris vittata* fronds belonged to the same plant, for fronds of *T. major* are very sparingly found. This being the case, the connection which has been traced between *Tæniopteris* and the *Williamsoniella* flowers, and the similarity to *Wielandiella*, whose structure is well known, point to the conclusion that all the remains described above formed parts of the same plants.

Williamsoniella roseberriensis, *sp. nov.*

In the Spring of 1914 was discovered a fairly good specimen of an unopened bud in one of the beds of fine dark shale exposed on Roseberry Topping. This example was obtained from some of the fallen material near the eastern end of the "slip," and though the place from which it came could be fairly accurately located the condition of the rocks above made it unsafe to carry on any further excavations at that point. The beds at this place are rich in plant remains which are well preserved: the block containing the bud shows parts of the fronds of *Nilssonina orientalis* and *N. compta* (?), and a species of *Tæniopteris*, while specimens of *Tæniopteris* were found in close proximity. Though many of the species closely resemble forms found at Gristhorpe,* there can be no doubt that these beds belong to a much earlier date; they lie just above the Upper Liassic shales, which seem to pass into them without any marked break, and the presence of abundance of *Thinnfeldia* fronds would seem to indicate that the flora belongs to a transitional period between the formation of the Lias and Oolite.

* A short description of the beds and a provisional list of species was given in the 'Naturalist,' 1913, p. 198. See also THOMAS ('15), p. 7.

The only specimen of *Williamsoniella* obtained unfortunately broke while it was being extracted, but was put together again and is shown in fig. 4, Plate 12. It seems to be a bud which was flattened out in the same way as that previously described and figured (Plate 12, fig. 9) and now shows the apical portion. It is rather larger than the buds of *W. coronata*, having a diameter about 20 mm. It has 13 microsporophylls, which are slightly separated from each other at the edges. Each sporophyll is 3–4 mm. broad near its central portion and tapers gradually to a point at its apex, its surface has the same series of small humps giving the mottled appearance noted for the foregoing species, but these are absent for a distance of about 2 mm. from the apex and the comparatively smooth sporophyll tips provide a point of distinction from the Gristhorpe species. Another very important point—if it can be relied on from our example—is the absence of any trace of the apical disc which characterises *W. coronata* and into which the more bluntly rounded ends of the microsporophylls fit.

While there appears to be little doubt as to the generic identity of this specimen with *Williamsoniella*, its larger size, the smooth and more pointed tips of microsporophylls, and the apparent absence of an apical “corona,” would appear to indicate that a specific distinction from *W. coronata* may be based on external form. A portion of the bud was removed from the rock and treated with clearing agents, but unfortunately its central portion appeared to be full of the muddy matrix and no spores or interseminal scales could be found. The cuticle of the outer surface of the sporophylls was obtained, and a portion of it is shown in the photograph (Plate 14, fig. 21). It showed very clearly the outlines of the epidermal cells and some stomata (at S). The cuticle appeared to be thicker than that of *W. coronata* but the cells had a similar irregular outline and straight walls. The stomata were also of the type already described; their large subsidiary cells are unthickened, while the guard-cell thickenings are fairly clearly seen, the inner thickening patches are thinner than the outer but the polar diameters of the thickenings and subsidiary cells are more nearly the same. These stomata, however, come very close to the examples shown in Plate 13, fig. 20.

Thus the general form, the size, and the epidermal structure of this example seem to justify our regarding the Roseberry specimen as a second species of *Williamsoniella* to which the specific name of *roseberriensis* is given.

An isolated specimen was found near Little Roseberry which had the appearance of a flattened male sporophyll, but it was badly preserved and little importance can be attached to it.

Williamsoniella Lignieri (Nathorst).

1909. *Williamsonia* (?) *Lignieri*, NATHORST, ‘Paläobotanische Mitteilungen’ (8), p. 20, Taf. 4.

Prof. NATHORST has described a small flower-bud found at Whitby, different in type from the flowers of *Williamsonia*, but apparently similar to some of the

unopened buds already figured. The bud was flattened in a horizontal plane, and shows a number of microsporophylls (or bracts), which are somewhat more numerous, and appear more pointed than in my specimens. No details of structure were visible on the exterior, but preparations revealed many interesting features. The cuticular membranes from the sporophylls were delicate, and some of them possessed small stomata, occurring inside ordinary cell-outlines. These stomata, as far as can be ascertained, appear to be of the *Teniopteris* type, and, though similarly produced structures are not commonly seen in my flowers, one or two comparable cases have been observed. The flower-bud contained spores, of the same size as those in *Williamsoniella*, but Prof. NATHORST believed that the female parts were absent; he figured some membranes from the interior of the flower, which he regarded as derived from fused microsporangia. I believe, however, that these membranes came from the tops of interseminal scales; they evidently were composed of portions with a more or less hexagonal outline (NATHORST'S Taf. 4, figs. 3, 4, 5), and appear to have been thickened or turned at the edges. In figs. 7 and 8 they are also seen to have a circular, thickened portion in the centre, as frequently seen on the tops of interseminal scales. Each portion seems to have had a diameter of about 4 or 5 mm., while my scales were 2 to 4 mm. across. In all my specimens the cuticular membranes of the microsporangia were extremely thin and fine, and were only obtained in fragments, while the membranes in question had quite a stout texture, much more like that of the interseminal scales. No micropylar tubes were seen, but these are absent or indistinct among the interseminal scales obtained from my unopened flower buds. Though, of course, it cannot yet be definitely proved, it is very probable that *W. Lignieri* was bisexual. The two types of membranes from the microsporophylls and the form of the stomata are points of comparison with *Williamsoniella*, and, taken with the general form and size of specimen, it appears probable that NATHORST'S species may be reasonably regarded as a third species of the genus *Williamsoniella*.

We may notice here that it is possible that some of the smaller bud-like structures, or spherical groups of sporophylls, described by other authors as problematical *Williamsonia* flowers, may possibly be other examples of this genus. For example, the form figured by HOLLICK,* under the name of *Williamsonia problematica* (Newb.), may be compared with the buds of the flowers here described. But, in the absence of further evidence, no useful purpose can be served by transferring these doubtful remains to my genus.

COMPARISON WITH OTHER BENNETTITALEAN GENERA.

The Bennettitalean genera already fully known appear to fall into two main groups: (a) the Bennettiteæ, including *Bennettites* and *Cycadeoidea*—if, indeed,

* HOLLICK ('06), p. 107, Plate 5, fig. 31.

these genera can be reasonably separated, and (b) the Williamsoniæ, including the two main types, *Williamsonia* and *Wielandiella*. We know something of the flowers, stems, and leaves of all these types, but, in addition, there are other isolated flowers whose position cannot be so clearly defined, such as *Cycadocephalus*, several species of *Williamsonia*, and perhaps *Weltrichia*.

Dealing first with general characters we may, without hesitation, place *Williamsoniella* in the sub-class *Williamsoniæ*, in a position intermediate between *Williamsonia* and *Wielandiella*, its closest affinity being with the latter of these two genera.

(a) *Comparison with Wielandiella.*

The plants here described, if the restoration represented is correct, were similar to *Wielandiella** in many respects. The general habit and mode of branching were probably identical in both forms, but the stalked flower in *Williamsoniella* may, perhaps, emphasise the idea that this mode of branching must be regarded as false dichotomy, the main axis being terminated by a flower as seen in the inflorescences of *Welwitschia*. It cannot now be ascertained whether the main branches which continued the growth of the stem arose in an original axillary position.

In Prof. NATHORST'S genus the leaves were apparently restricted to the portion of the stem near the nodes, while in the present specimens they were more or less evenly arranged all over the stem, and the leaf-scars remain as projecting structures.

The leaves of the *Taniopteris* type, as has already been pointed out, come very near to those of *Anomozamites*, in general outline, in the relations of the lamina to the midrib, in nervation, in the petiole, the structure of the stomata and epidermal cells, and, to some extent, in the form of the apex. Moreover, some *Taniopteris* leaves have been found with an irregularly incised lamina. The bracts found in connection with the two forms can be very closely matched. The flowers of *Wielandiella* were sessile and not pedunculate as in *Williamsoniella*; they present, moreover, considerable differences in structure. Reference to Prof. NATHORST'S descriptions shows that these flowers are known in two forms, or stages, one which exhibits the female strobilus with micropylar tubes and interseminal scales surrounded by bracts, the other shows only a pyriform axis with the "Palisadenring" at its base. The first form, as indeed all the other *Williamsonia* female strobili, can be compared with the inner ovular part of my flower; it differs in size, in the absence of a sterile apex, and in the possession of surrounding bracts. The second form presents a more interesting comparison. Prof. NATHORST is of the opinion that the pyriform structure represents the axis of the female strobilus after the fall of the appendages, and the somewhat similar but coronate axis described above (fig. 8, Plate 12) strongly supports this view. How, then, are we to regard the "Palisadenring"? Pollen-grains were obtained from these structures, and the view was put forward that they represented fused microsporangia, or sporophylls which developed after the ripening

* See NATHORST ('02) and NATHORST ('09).

and fall of the seeds. With this I am in partial agreement. Had it not yielded pollen-grains I should have homologised it with the flange-like expansion at the base of my flower-axis, to which the male sporophylls were probably attached, but the presence of pollen-grains is probably a certain indication that the "Palisadenring" was, indeed, composed of sporophylls.* We may get some help in the question by comparing a figure of one of my unopened buds showing the outer surface of male sporophylls fitting close together (*cf.* Plate 12, fig. 10). If we imagine one of these buds greatly reduced in length, composed of a greater number of sporophylls and with the axis projecting above, we should have a structure closely comparable with the "Palisadenring," and I should therefore homologise the elements of this peculiar structure with my male sporophylls, but at the same time regarding it as a much reduced and perhaps functionless structure, rather than one with a late (protogynous) development. In spite of the presence of numerous small spores I should regard *Wielandiella* as showing a transition between the truly bisexual type of flower seen in *Williamsoniella* and the unisexual flowers seen in *Williamsonia scotica*, and probably all other known species of *Williamsonia*. Thus, on this view, the flowers of Prof. NATHORST's genus are not so unlike those here described as appears at first sight, but on the contrary are very closely homologous.

(b) *Comparison with Williamsonia.*

The stems of *Williamsonia* were occasionally branched but much stouter, and covered with foliage-leaves in a manner very different from my specimens. I do not think that at present any valuable comparison can be drawn as to the place of origin of the peduncles. Passing over the leaves, whose cuticles have been already compared,† and the scale-covered peduncles, we come to the flower. Here the presence of numerous ensheathing bracts presents a point of difference, though the bracts in *W. scotica* were morphologically similar to those here described.‡ There seems to be no trustworthy evidence that the flowers of *Williamsonia* were bisexual, and in this we have an important point of difference.

The male flowers of *Williamsonia* were very much larger and had a much greater pollen output than the present flower, a fact which may, perhaps, be correlated with the unisexual nature of that plant. We may, following Prof. NATHORST,§ arrange the male sporophylls in a series with the pinnate sporophylls of *W. spectabilis* at one end, followed by the large synangiate form of *Cycadocephalus*, the smaller synangiate types of *Weltrichia* and *Williamsonia whitbiensis*; the sporophylls of the present

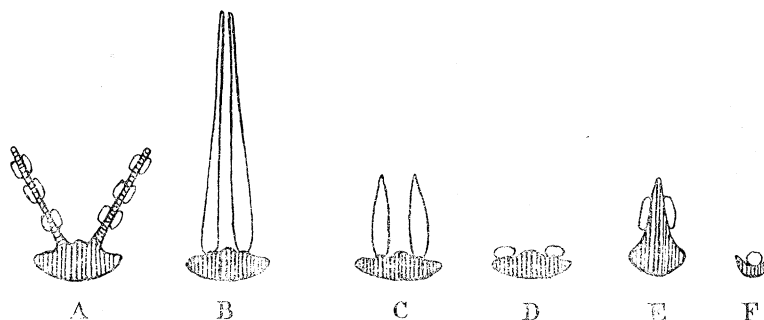
* We may notice that the outer epidermis of the "Palisadenring" was somewhat strongly cuticularised, which points to its being composed of fused sporophylls rather than of fused sporangia, but apparently stomata were absent, as would be expected in a structure so reduced.

† THOMAS and BANCROFT ('14).

‡ See above p. 125, Plate 14, fig. 22.

§ NATHORST ('12), p. 7.

flower form the next term of the series, with the much reduced unopened sporophylls of *Wielandiella* at the lower end. These structures are shown diagrammatically in the figures (text-fig. 6). The reduced nature of the *Williamsoniella* microsporophylls is further emphasised by the fact that not only are their synangia smaller in size than those of *W. whitbiensis*, but also we only get four to six synangia in each of our sporophylls as against, perhaps, 12 per sporophyll in NATHORST'S species.



TEXT-FIG. 6.—Diagram showing comparative structure of the microsporophylls of various members of the Williamsonian alliance. The series shows reduction in the number of synangia on each sporophyll. A, *Williamsonia spectabilis*, Nath.; B, *Cycadocephalus Sewardi*, Nath.; C, *Weltrichia mirabilis*, Fr. Braun.; D, *Williamsonia whitbiensis*, Nath.; E, *Williamsoniella coronata*, Thomas; F, *Wielandiella angustifolia*, Nath. Figs. A–D after NATHORST.

With regard to the structure of the sporophyll, we may notice that in *W. spectabilis*, and, in fact, in all the species described by NATHORST, the middle line of the sporophylls is somewhat thickened, and the synangia arise from this enlarged portion. In the present genus, however, this enlargement seems to have assumed gigantic proportions, and the sporophylls are thereby converted from tangentially flattened almost to radially flattened structures.

The different types of synangia, as seen in cross-section, are shown in text-fig. 6, the first four figures of which are copied from Prof. NATHORST'S papers.*

The structure of the synangia of *Williamsoniella* seems to be identical with that in *Williamsonia*, but, as regards size, the new genus again shows reduction. The sporophylls also are free in my genus, and not united in the cup-like structure so clearly seen in *W. spectabilis* and *W. whitbiensis*, but in both genera they seem to have been deciduous.

The female strobilus in all the Bennettitalean genera possesses essentially the same structure. The pyriform axis here described is similar in section to that of *Williamsonia gigas*, but differs from *W. Leckenbyi* and *W. pyramidalis* in the presence of a sterile apical structure. As the whole flower in the present instance is smaller than most of the previously described forms, so the ovulate portion has very much smaller dimensions than any of the above-mentioned species. Its diameter of 5–6 mm. is remarkably small when compared with such forms as *W. gigas*,† whose diameter was

* NATHORST ('12), figs. 7–9.

† LIGNIER ('03).

about 4 cm., and the sizes of the interseminal scales and ovules are correspondingly smaller, though they are quite mature and apparently functional. While slight differences in detail are seen in the thickenings of the cuticles of the various forms, the principal point to be noticed is that in *Williamsoniella* the ovules are apparently almost sessile, and not on long stalks as in many of the other types. The comparison may perhaps be drawn between the form of the ovules here described and those of *Williamsonia scotica** described by SEWARD. Here the peduncles of the ovules were much less distinct, and, allowing for a certain amount of contraction, it would appear as if they formerly had the same external outline as those shown in fig. 3, Plate 12. The actual nucellus, however, according to SEWARD, was limited to the upper part of the centre of the megasporophylls, and it may be that in *Williamsoniella* also the nucellus was small and embedded in the centre of the cylindrical ovule whose basal portion was composed of sterile tissue. Sessile ovules of this type may, perhaps, be correlated with the small size of the flower and of its ovuliferous portion; they certainly lend no support to the view which regards the ovules as axial structures.

A further point of comparison between my genus and *W. scotica* is the similarity between the outlines of the ovules and the so-called interseminal scales. The ovules can only be distinguished in the section figured in Plate 12, fig. 3, by the presence of distinct micropylar tubes at their apices.

We have here a further suggestion of the view put forward by Prof. SEWARD and other authors that the scales and ovules are homologous organs, and the existence of scales near the sterile part of the strobilus which had an apical cuticularised ring, together with the irregularity in the arrangement of ovules and scales in the apical and basal regions lead me to support this view.

A comparison must now be drawn between the apical structure of the female strobilus of the various types. We may note that the apex in *Wielandiella* and in *Williamsonia Leckenbyi* is completely fertile; *W. pyramidalis* may also have been completely fertile, but some difference is noticeable in its apical appendages, but possibly this is due to the plane in which it was flattened. In *Williamsonia gigas*, however, the apex was sterile, and the same is true of the present genus. The exact structure of the apex in the specimens of *W. gigas* described by WILLIAMSON† and by LIGNIER‡ has given rise to some discussion, and it may be that the examples here described may be useful in elucidating the problem. Reference to the works of the authors just mentioned shows that the appendages to the ovulate strobilus terminated towards the apex in a more or less flat horizontal surface on which the impressions of interseminal scales were still visible; from this surface there arose a central projection which, as it sloped gradually upwards, was seen to bear a series of

* SEWARD ('12), p. 110.

† WILLIAMSON ('70).

‡ LIGNIER ('03).

distinct ridges. This ridged structure again terminated abruptly with a flange and the summit of the axis was occupied by a small conical projection. One of the best specimens showing these apical features is a cast in the Paris Museum, of which a mould has been figured by WIELAND,* who dissents from the interpretation placed upon the example by LIGNIER.† WIELAND holds that the specimen was formed from the tips of microsporophylls with synangia, but this can only be conjecture, and there are strong grounds for comparing it with WILLIAMSON'S original examples of strobilar apices.

Now above the megasporophylls of *Williamsoniella* there was also a sterile ridged structure, the ridges being due to the presence in bud of appressed microsporophylls. We are then entitled to interpret the ridges on the *Williamsonia* axis as also due to the pressure in bud of the surrounding bracts, for this species was almost certainly unisexual.‡ The top of the corona in my specimens was somewhat flattened, but with a central irregular terminal hump, which seems to be closely comparable with the terminal structures figured by WILLIAMSON.§ LIGNIER'S restoration places a large cup-like appendage (appendice terminal infundibuliform) at the apex, and if this is correct a very different type of structure would have been presented, but there appear to be no conclusive grounds for placing this large cup-like structure in an apical position. In any case the sterility of the apex of *W. gigas* and *Williamsoniella coronata* provide grounds for comparison.

The closest resemblance to *Williamsoniella* is possessed by the apical part of a new species of female strobilus of *Williamsonia* from Whitby as yet undescribed.

A note may be added as to the leaves of our form. At first sight the entire linear or elliptical leaves of the *Taniopteris* type appear considerably different from the pinnate fronds of *Ptilophyllum* or *Zamites*. The relation of the lamina to the petiole, and especially the position of the lamina on the upper side of the main axis, present important points of comparison. The *Anomozamites* form of leaf provides a link connecting up the *Taniopteris* type of lamina, which is usually entire, but rarely segmented in an irregular way, with the constantly pinnate types where the pinnæ are distinctly separated from each other. The dichotomising secondary veins are a feature characteristic throughout the group. But, in the structure of the cuticle and stomata, we possess the most important diagnostic character, which clearly demonstrates the alliance of the *Taniopteris* type with the other Bennettitalean forms.

* WIELAND ('11), p. 463, fig. 18.

† Cf. also LIGNIER ('07).

‡ In the Paris Museum there is an ironstone cast of the male flower of most probably the same species which seems to be nearly identical with NATHORST'S *W. spectabilis*. The microsporophylls, whose synangia are clearly seen, were united in a cup-like structure, its shape indicating a free development unsurrounded by bracts. I believe that this specimen, which forms part of the Yates Collection, has been overlooked by previous workers. See THOMAS ('15²).

§ WILLIAMSON ('70), Plate 53, figs. 6-9.

(c) *Comparison with Bennettites (Cycadeoidea).*

The relation between the Bennettitean and the Williamsonian sections of the Bennettitales presents several features of interest, and the discovery of an indisputably bisexual flower in the latter group adds considerably to the homologies of these forms. The presence in the Bajocian beds of a form like *Williamsoniella*, which exhibits reduction in the size of the flower, and especially in the number of synangia and in the spore-output, is of considerable importance when contrasted with the large flowers of *Bennettites*, with their complex male sporophylls and enormous spore-output, which come in the much newer Lower Cretaceous beds. It probably points to wide separation of the lines of descent, embracing on the one hand *Williamsonia*, *Williamsoniella*, and *Wielandiella*, and on the other hand the various forms of *Cycadeoidea*.

In the group which includes the last-named forms we find a general reduction in the length of the stems, resulting in the formation of small ovoid or tufted groups of branches, which are thickly covered with an armour of contiguous leaf-bases. The examples of *Ænothera* stems without internodes, described by GATES,* seem to indicate that stems of the *Cycadeoidea* type may be produced under special cultural conditions from plants with the normal type of elongated internodes, and we are then justified in assuming that the great difference in habit between the *Cycadeoideas* and *Williamsonias* is not of such fundamental importance as one might at first sight imagine. A further noteworthy point is the probability that the short form of stem was evolved from the more elongated type.

Passing over the leaves, which present little difference in the two groups, we come to the flowers. The almost sessile flowers of *Cycadeoidea*, produced among the leaf bases, offer the first point of contrast. We may then notice that, while for the most part the flowers of the American and English forms were large, yet WIELAND has described† some small flower buds of *Cycadeoidea Marshiana*, whose dimensions were comparable with those of *Williamsoniella*.

It may be claimed that the flowers here described are the only undoubtedly bisexual Bennettitalean flowers apart from the American *Cycadeoideas*. We may also remark that in the present flower the ripening of the micro- and mega-sporangia seem to have been less separated in time, and that both of them were functional, while in the American forms the megasporophylls are very small and undeveloped in the flowers containing micro-sporophylls and I have not seen any direct evidence that the male and female parts of the same flower were functional. There is, of course, strong presumption that the micro-sporophylls were shed and that then the megasporophylls became mature, but the separation in time of the ripening of the parts did not allow mature organs of both sexes to be preserved. *Williamsoniella* does then add materially to our knowledge of the morphology of the whole group.

* GATES ('12), Plates 2 and 3.

† WIELAND ('12), p. 76.

The contrast between the small six-synangiate microsporophylls described above and the immense microsporophylls of *Cycadeoidea dacotensis* or *C. ingens* has already been mentioned, but the individual synangia do not seem to have been very different in form or size. I am inclined to think, however, that these synangia differed in structure, and from the shape and size of the spore-masses I believe that the septa in *Williamsoniella* extended from one side of the synangium to the other, giving a single, rather than a double, row of loculi.*

It is in WIELAND's newly described form *Cycadeoidea colossalis* that we find microsporophylls more comparable with those of *Williamsoniella*, and this interesting flower may probably be regarded as showing a parallel development in the *Cycadeoidea* group to that outlined for the *Williamsonias*. *C. colossalis*† flowers occur as small buds, comparable in size to those of *Williamsoniella* and characterised by the presence of massive microsporophylls which in the young state form a closely sheathing covering round the female strobilus, not very unlike that which I have described. When they opened, these sporophylls presented a very different appearance to mine, and, moreover, they were apparently fused at the base, but the number of synangia borne by them was reduced to about six pairs.‡ They were thus simple and pinnate in the fertile region, only giving off a single pair of appendages above, and consequently very distinctive as regards their apical parts.

The ovulate part of the flowers seems to have been young and rudimentary, with a very minute and limited seed zone and a large sterile region above. While in the absence of further details of structure we cannot draw a very full comparison, we may say that this form shows us that small flowers developed among the *Cycadeoideas* which had massive incurved microsporophylls with a relatively increased amount of sterile tissue and a decreased number of synangia comparable to *Williamsoniella* in the *Williamsonian* group.

The ovulate cones of almost all of the *Cycadeoideas* show an important point of difference which has already been mentioned, and that is in the well-developed seed pedicels which they exhibit and in the length of the stalks of both the ovules and the interseminal scales. Another point of contrast is the more flattened shape of the axis of the female strobili, though in the flower of *C. colossalis* we have an axis of the flower which is closely comparable to that described here.

We see, then, that *Williamsoniella* seems to take its place very naturally among the *Williamsonias*, showing agreement with their main features and forming a term in a series indicating the gradual simplification and reduction of the microsporophyll. This evolutionary tendency seems to be leading away from the type of structure of the newer flowers of *Cycadeoidea dacotensis*, etc., but the discovery of the flower of *C. colossalis* demonstrates the occurrence in that group of the same tendencies

* Cf. WIELAND ('06), fig. 81, p. 157.

† WIELAND ('14), p. 121.

‡ No information is given as to the exact number, but about six pairs are figured.

towards the reduction of the male sporophylls and the limitation of the area of production of the megasporophylls.

These facts seem to further strengthen the solidity of the Bennettitalean group, which is so remarkably uniform in the form and structure of its female reproductive structures. They are also of considerable theoretical interest, especially in connection with the theories of the "Bennettitalean" ancestry of the Angiosperms. ARBER and PARKIN* and other exponents of this view postulated the gradual reduction of the microsporophylls of their hypothetical Hemiangiosperm, and the observation of actual reduction to microsporophylls, bearing as few as four synangia, in the parallel Bennettitalean line may be considered as affording support to this view.

We must, however, remember that though in *Williamsoniella* a reduction in the number of synangia has taken place, yet the pollen-grains are still produced in synangia with very distinct septation, and that a sporophyll with two synangia would still be very distinct from a typical angiosperm stamen. It might, on the other hand, be regarded as comparable with the microsporophyll of *Welwitschia*.

But when we consider the female part of the flowers here described we may be struck with the lack of any evidence in support of even a remote connection between the Bennettitales and Angiosperms. Throughout the whole of the group here considered we see no departure from the essentially gymnospermous type of ovule, and the similarity between the interseminal scales and megasporophylls noticed above emphasises this character. The evolutionary tendencies which we have noticed, while pointing to the sterilisation of the apex of the axis, and perhaps to the production of ovules borne in a radial manner on a cylindrical axis, do not show the slightest indication towards the formation of an angiospermous carpel.

Until some evidence is forthcoming as to the mode of origin of the carpel no great reliance can be placed on any theory connecting the Angiosperm ancestors with the Bennettitales, and the bisporangiate type of strobilus must be regarded as developed along parallel but not closely related lines.

On the other hand, I believe that evidence is accumulating in support of the view which relates the Bennettitales with the Gnetales, though the connection is somewhat remote.

SUMMARY.

Williamsoniella, gen. nov., is founded upon specimens obtained from the Middle and Lower Estuarine rocks of Yorkshire.

The best known species *Williamsoniella coronata*, sp. nov., occurs in local abundance in the Gristhorpe plant-bed near Scarborough, and is of Middle Estuarine age. It is represented by buds, mature flowers, detached microsporophylls and female strobili. The flowers were bisexual and pedunculate, they were very small in size. Each flower had 12-16 wedge-shaped microsporophylls bearing 4-6 synangia apiece. The synangia

* ARBER and PARKIN ('07), p. 67.

had many septa and the pollen-grains were small and tetrahedrally formed. The deciduous microsporophylls were arranged round a small female strobilus of the usual Bennettitalean type. The ovules were sessile and very similar in external appearance to the interseminal scales, the micropylar tubes were long when mature. The apex of the strobilus was sterile and terminated in a characteristic corona-like structure, with characteristic ridges produced by the pressure of the microsporophylls when in bud. Bracts were typically absent from the flower. Under certain conditions the ovules and interseminal scales were also deciduous.

The flowers were probably produced from stems which had forking branches and were borne at the point of bifurcation. These stems were similar to the stems of *Wielandiella*, but the arrangement of the leaves was more uniform. The leaf-bases show a double bundle-trace.

The leaves known as *Teniopteris vittata*, Br., were also probably borne on these stems, and their stomata agree in structure with those produced on the microsporophylls. Some small bracts with a tiny *Teniopteris* lamina and expanded petioles have been observed. The leaves of this species also possessed a double bundle.

A flower-bud probably of the same genus has been found in the Lower Estuarine beds at Roseberry Topping. It has been described under the name of *Williamsoniella roseberriensis*, sp. nov. It possessed pointed microsporophylls having a somewhat different cuticular structure.

The form already described by Prof. NATHORST as *Williamsonia* ? *Lignieri* was also probably bisexual and belonged to this genus.

The structure of *Williamsoniella* is compared with that of other Bennettitalean genera. It is probably most closely related to *Wielandiella*, but shows points of similarity with *Williamsonia*. The male sporophylls form a term in the reduction series which may be traced in this group. The apical structures are compared with the curious arrangement seen in *Williamsonia gigas* (L. and H.).

The constancy of form of the ovules and interseminal scales throughout the Bennettitales is very marked. No tendencies towards the formation of carpels can be noted.

In conclusion the author wishes to express his thanks to Prof. A. C. SEWARD, at whose suggestion the work on the Yorkshire Jurassic Flora was recommenced. The writer is particularly indebted to Prof. SEWARD, not only for constant help and advice, but also for relieving him, during absence from Cambridge on military service, of much of the work of seeing this paper through the press.

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EXPLANATION OF PLATES.

All the specimens figured are in the Museum of the Botany School, Cambridge. Drawings on Plate 12, figs. 1–4, by Mr. T. A. Brock. Photographs by the author.

PLATE 12.

Williamsoniella coronata, sp. nov.; figs. 1–3 and 5–10.

- Fig. 1.—Drawing of the most complete mature flower, showing peduncle, ovulate strobilus, corona, and microsporophylls still attached. The specimen is also shown, natural size, in the photograph, fig. 5. $\times 2$.
- Fig. 2.—Ovulate strobilus showing long peduncle. The micropylar tubes were very conspicuous in the example and are shown in fig. 2A. The microsporophylls had fallen off. $\times 2$.
- Fig. 2A.—Small part of the ovulate part of 2, enlarged to show projecting micropylar tubes and interseminal scales. $\times 8$.
- Fig. 3.—Drawing of a specimen showing a section through the centre of the ovulate strobilus. At the apex the corona is seen; in the centre the axis is shown, with its closely set appendages, the ovules and interseminal scales. The ovules are recognisable by their micropylar tubes and are club-shaped. $\times 4$.
- Fig. 4.—*Williamsoniella roseberriensis*, sp. nov. Drawing of the flower-bud on which this species is founded. On the left-hand side the pointed tips of the microsporophylls can be made out. $\times 2$.
- Fig. 5.—*W. coronata*. Photograph of the flower, natural size. Compare with fig. 1.

- Fig. 6.—Photograph of apical part of strobilus or corona. The characteristic vertical ridges are well seen, also the wrinkled projecting hump at the apex. Below, the interseminal scales can be made out. Compare with text-fig. 2. $\times 4$.
- Fig. 7.—Two separate microsporophylls, as commonly found in the bed. Their outline is clearly seen, while at *S* two synangia may be distinguished. $\times 3$.
- Fig. 8.—Axis of a flower after the fall of the various appendages. At the top the corona is seen, terminated by an apical hump. A few interseminal scales are still adherent below (at *S*). At the base the remains of the flange on which the microsporophylls were probably seated is seen at *f*. The portion between *S* and *f* bore the ovules and interseminal scales. $\times 4$.
- Fig. 9.—A young flower-bud seen from above. The closely packed microsporophylls with their characteristic roughened appearance are shown, while in the centre the top of the corona, with its central projecting hump, is visible. $\times 4$.
- Fig. 10.—A young flower-bud pressed out sideways. Shows the external appearance of the microsporophylls. $\times 4$.

PLATE 13.

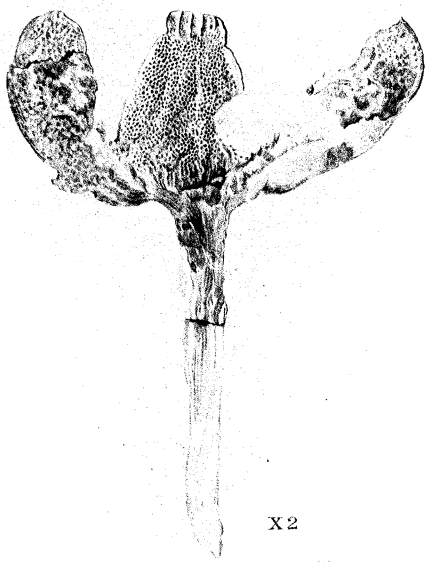
Williamsoniella coronata, sp. nov.

- Fig. 11.—Microspores adhering to a fine membrane, which is the remains of the wall of a synangium. $\times 200$.
- Fig. 12.—Preparation showing the lower part of the epidermis of the corona and the upper interseminal scales. Note the way in which the scales fit into the corona. $\times 40$.
- Fig. 13.—A mass of microspores which formed the contents of a single loculus of a synangium. $\times 200$.
- Fig. 14.—An entire mass of microspores similar to that shown in fig. 13. This probably indicates the form of the interior of one loculus. Obtained from a preparation of an unopened flower-bud. $\times 40$.
- Fig. 15.—Part of a preparation made by treating an unopened flower-bud similar to that shown in fig. 10. The photograph was made from a slide in which the contents of the bud were mounted without any separation or cleaning. At *p* masses of pollen-grains, similar to those shown in figs. 13 and 14, are seen, while the mass of dark membranes at *S* were the cuticles of interseminal scales. $\times 33$.
- Fig. 16.—Two separate micropylar tubes, showing their outer surface, apex, and part of the inner surface strongly cuticularised. $\times 38$.

- Fig. 17.—Preparation showing the tops of interseminal scales with micropylar tubes projecting among them. $\times 34$.
- Fig. 18.—Cuticular membranes from the epidermal cells of a microsporophyll. This preparation is made from the inner side of the microsporophyll and shows the remains of very lightly cuticularised cells. A few stomata can be made out. $\times 200$.
- Fig. 19.—Cuticular membranes from the outer surface of a microsporophyll, showing more strongly thickened and more rounded cells. Stomata were present, but are not clearly shown. $\times 200$.
- Fig. 20.—Drawings of stomata from the epidermis of microsporophylls. Showing the guard-cell thickenings of characteristic form and the unthickened subsidiary cells. \times about 400.

PLATE 14.

- Fig. 21.—Cuticular preparation from the outside of a microsporophyll of *Williamsoniella roseberriensis*, showing more strongly thickened epidermal cells with stomata (*S*). $\times 175$.
- Fig. 22.—Photo of bract-like structures, possessing a thin expanded petiole and a much reduced lamina of the *Teniopteris vittata* type. $\times \frac{7}{3}$.
- Fig. 23.—Cuticular preparation made from one of the petioles of the bracts, showing cells with straight walls, which are rectangular on the inner epidermis, but rounded on the outer. Numerous stomata are present. $\times 40$.
- Fig. 24.—One of the best preserved specimens of stems. At the point of forking a small raised scar was present, which was probably the place of origin of a flower. A *Teniopteris* leaf is also shown. $\times \frac{4}{3}$.
- Fig. 25.—Part of a stem showing leaf-bases. At *T* two small bundle-scars can be made out. $\times 4$.
- Fig. 26.—Base of the petiole of a frond of *Teniopteris vittata* Br., showing the point of attachment. Two small raised humps representing the scars of vascular bundles can be made out. This specimen is also seen at *p* in fig. 28. $\times 4$.
- Fig. 27.—Leaves of *Teniopteris vittata* Br., showing form and venation of the lamina. Natural size.
- Fig. 28.—A typical block of the material from the Gristhorpe bed, showing the association of the various parts of the *Williamsoniella* plant. Many leaves of the *Teniopteris vittata* are seen, also stems at *S*. A petiole (shown in fig. 26) occurs at *p*. At *m* fragments of microsporophylls are shown, while at *O* a portion of the female strobilus remains. (The preparation shown in fig. 17 was made from this structure.) $\times \frac{5}{8}$.
- Fig. 29.—Female strobilus showing external appearance with micropylar tubes and interseminal scales. $\times 5$.



X2

1



X22

2



X4

3

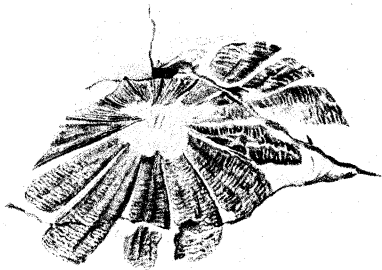


X8

2 a



6



X2

4

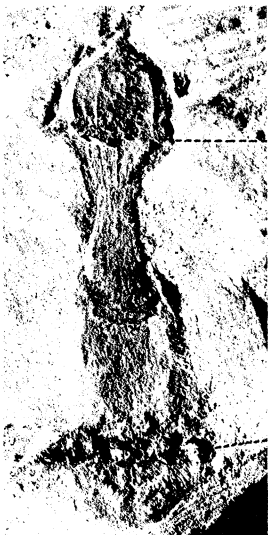


5



S

7



S

f

8



9



10



11



12



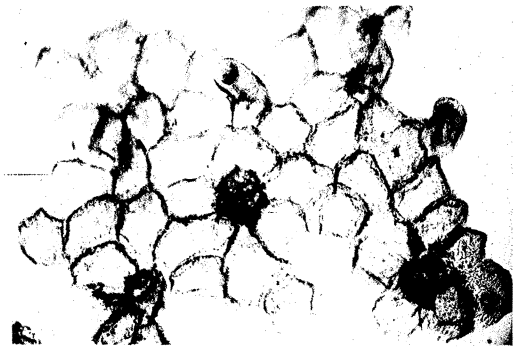
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15



13



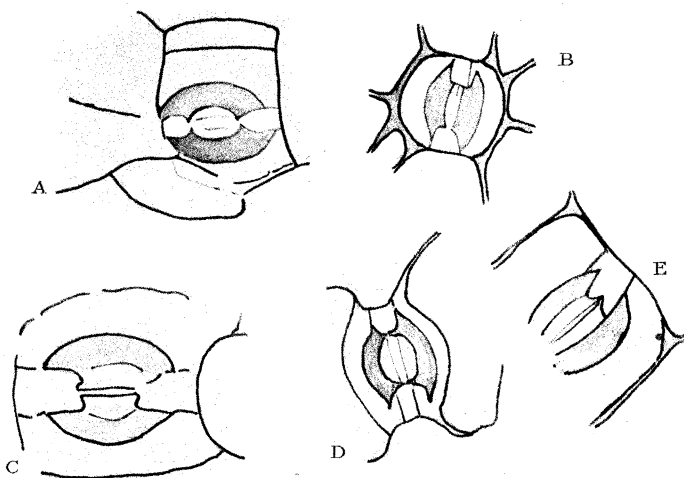
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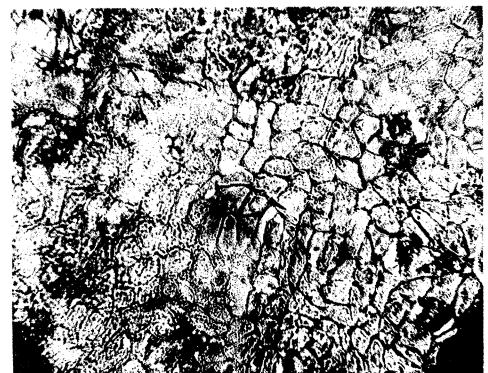
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19



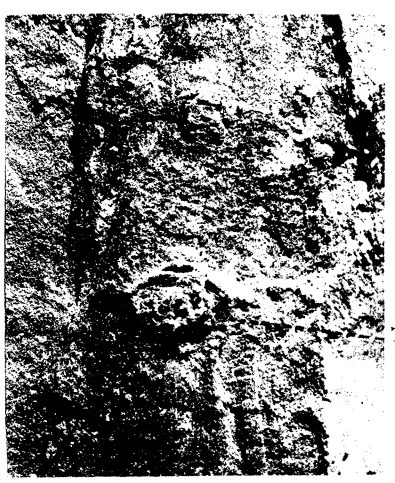
21 S



22



24



25 T



23



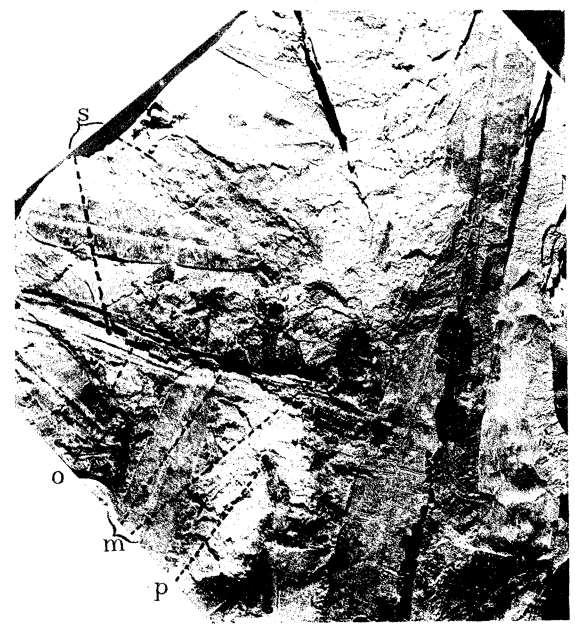
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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY OF BIOLOGICAL SCIENCES

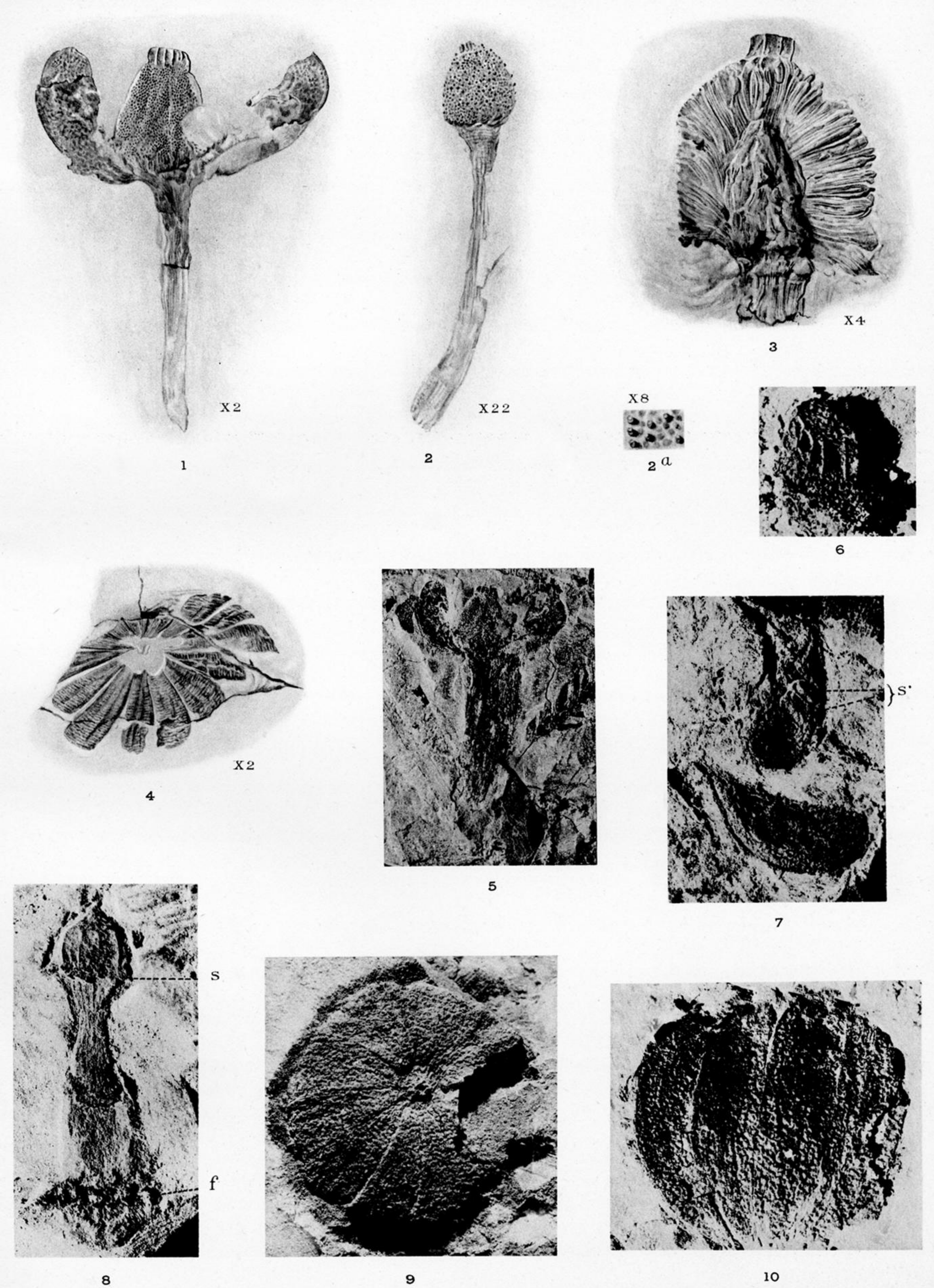


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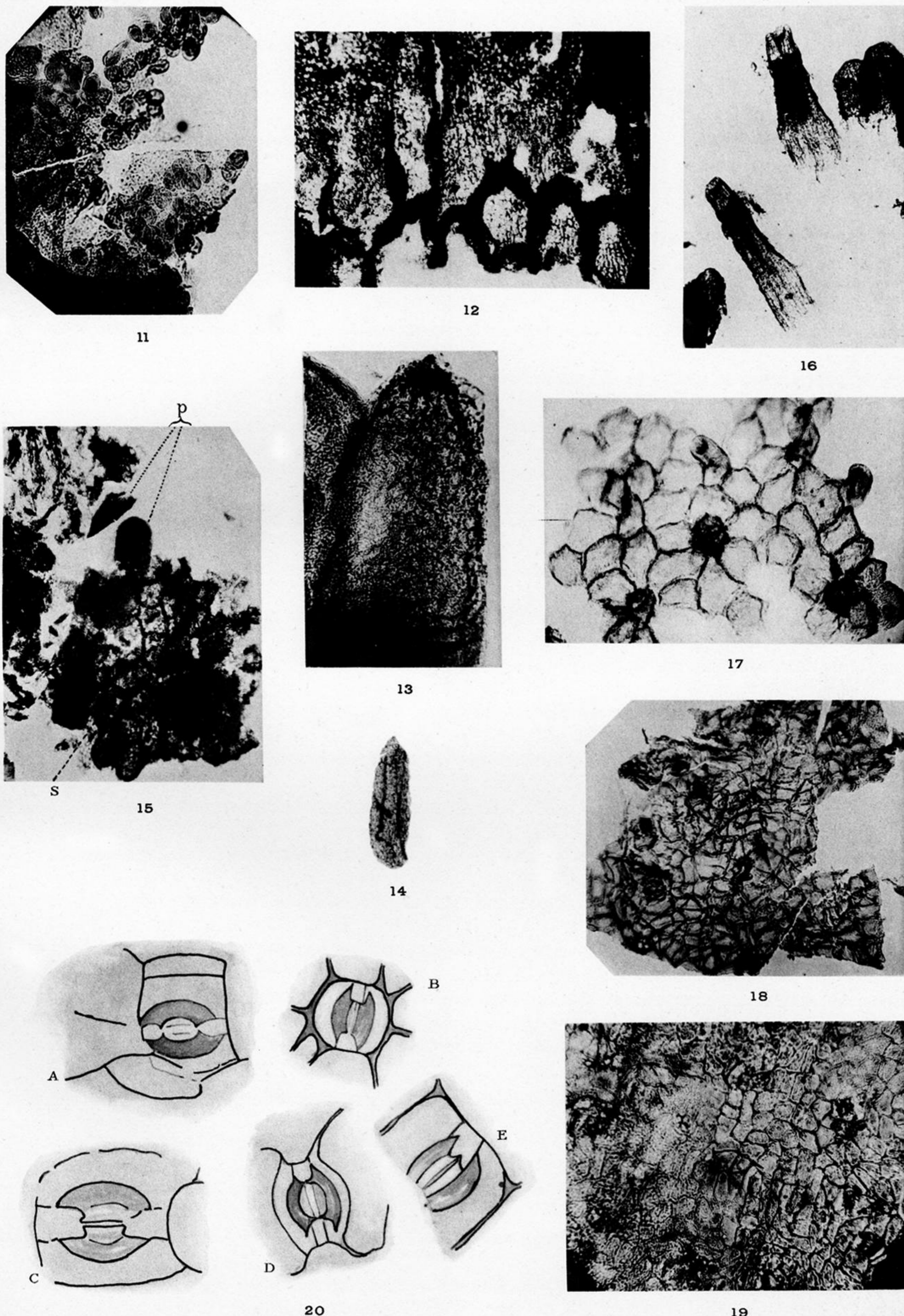


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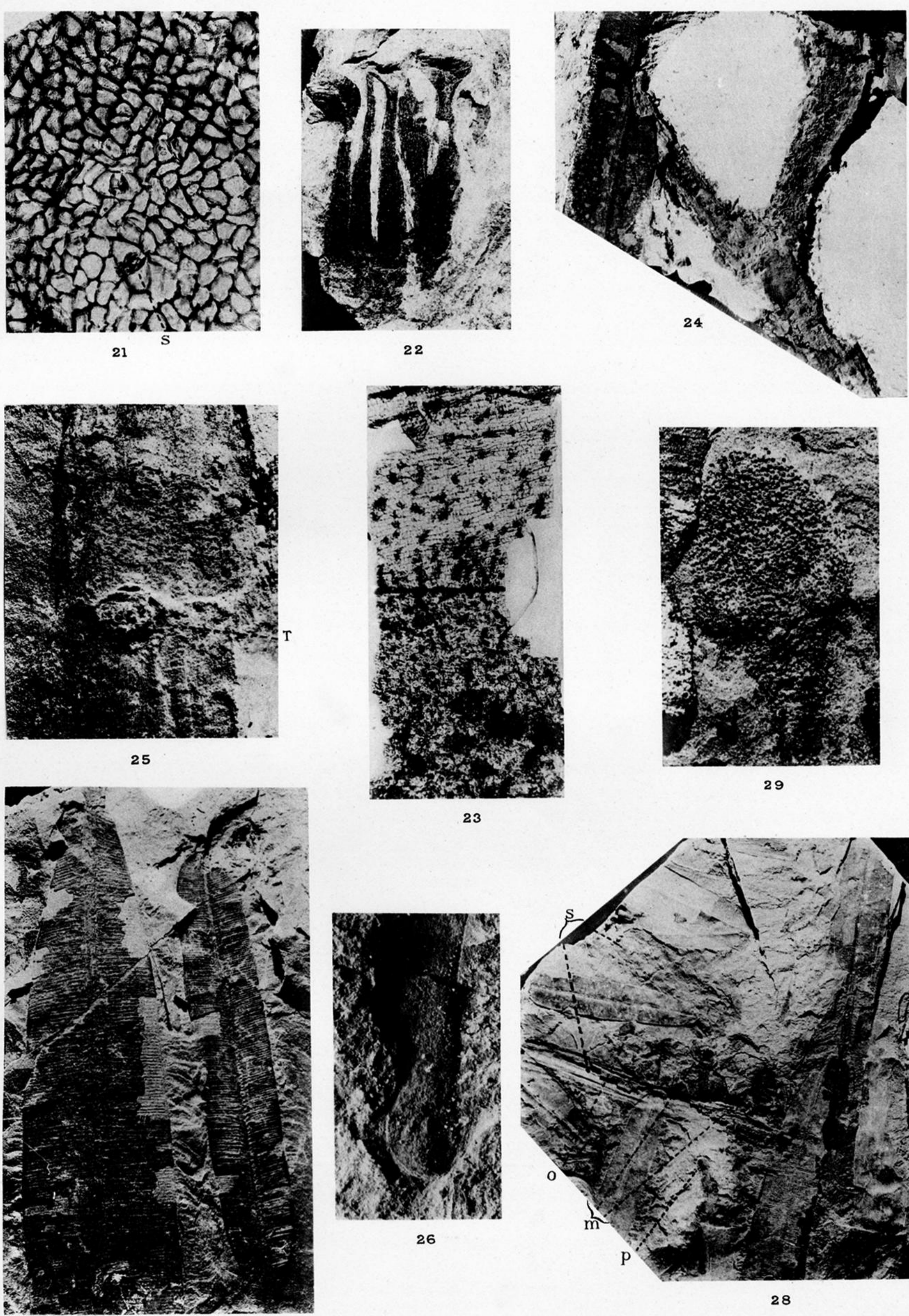
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WILLIAMSONIELLA CORONATA, ETC.

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