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CONES OF EXTINCT CYCADALES FROM THE JURASSIC ROCKS OF YORKSHIRE

By TOM M. HARRIS

Professor of Botany, University of Reading

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[Plates 5, 6]

INTRODUCTION

The Cycadales were throughout the nineteenth century confused with the large fossil family the Bennettiales and thus regarded as a dominant Mesozoic group. Increasing knowledge has, however, led to the inclusion in the Bennettiales of most of the leaf and stem types which had been regarded as fossil cycads; and at the same time it was realized that many of the reproductive organs supposed to belong to this family had been referred to it on superficial evidence and the importance of the Cycads as a fossil family thus seemed very doubtful.

Detailed work on leaf structure has, however, gone far to rehabilitate the fossil Cycadales; it has been shown that several common Mesozoic leaf genera have Cycadean anatomy, though curiously enough not the ones which look most like leaves of living Cycads. Less progress has so far been made with the reproductive organs; apart from a very few critically described specimens, we have only some unsatisfying descriptions.

It may thus be claimed that the species of *Androstrobus* described here are the first Mesozoic male cones in which full Cycadean structure has been proved to exist, even though it may be likely enough that other species were correctly supposed to be Cycadean. Similarly, the female cone *Beania* has been proved to show many fundamental points of agreement with Cycad cones of the *Zamia* type, while of the species of the old-established genus *Zamiostrobus* it can only be said that reinvestigation may provide the necessary anatomical evidence (see Seward 1917, Schuster 1931).

While further work is needed to establish the attribution of the male and female cones described here to their parent plants, there is already evidence that they belong to the same plant as the very abundant leaf *Nilssonia*. Were this proved conclusively, the evidence for referring the whole plant to the Cycadales would be strengthened, but even the isolated organs can be placed in the Cycadales with confidence, so similar are they to those of the Cycads.

The material belongs to the Department of Geology of the British Museum, and was collected by Mr F. M. Wonnacott in 1938 from the famous plant bed of Cayton and Gristhorpe bays, Yorkshire. Its age is Middle Estuarine (Bajocian).

I. MALE CONES

Genus *Androstrobus* Schimper

1872. *Androstrobus* Schimper, p. 199. Type species *A. zamioides*.

Schimper's diagnosis is as follows: 'Amenta cycadacea antherifera, cylindrica, e squamis imbricatis, latere postico antheras sessiles ferantibus efformata.'

Saporta (1875, p. 204) gives a diagnosis in the same sense but different words and also renamed the type species as *A. balduini*, while Seward (1895, p. 109) suggests a more plastic definition.

The present specimens agree fully with Schimper's diagnosis; such additional microscopic features as they show being further points of agreement with the Cycads. The only doubt there may be about the attribution of the present species to *Androstrobus* thus depends on whether Schimper's interpretation of the type-specimen was essentially right. Thus the bodies which Schimper describes and figures as pollen sacs (and certainly look like them) have not been proved to contain pollen and the possibility thus exists that they might be some other organ. However, the type-specimen is as satisfactory as can be expected with a fossil cone known only from its gross form, but this cannot be said of the other species (see Seward 1917, p. 505 for references), none of which is as convincing as the type.

Androstrobus, as described here, agrees in all the observed features with the male cones of the Cycadales. It is a fairly large male cone made up of spirally placed microsporophylls; the broad undersides of the microsporophylls are crowded with sessile pollen sacs which appear to be arranged in small sori. The pollen sacs are shaped as in the Cycadales, have similar wall structure, dehiscence line, and pollen grains. The epidermis of the microsporophyll has been shown to have stomata like those of the Cycadales.

No plant living or fossil is known which shares these features of *Androstrobus* and the Cycadales.

Androstrobus manis sp.nov.

(Plate 5, figures 6–9)

Type-specimen V25900; figure 1 C, F, I, J; figure 9, plate 5.

Diagnosis. Cone at least 5 cm. long, 2 cm. broad; sporophyll very broad, distal part rhomboidal about 5 mm. high, 10 mm. broad, smooth. Pollen grains oval, smooth, typically $36 \times 26 \mu$. Epidermal cells of distal part of microsporophylls finely sculptured with dots, epidermal cells of basal sterile scales showing a broad thickened border. Guard cells sunken, margins concealed by subsidiary cells.

Description of the material.

(1) *Gross form.* There are seven specimens of *A. manis*, four of which are very badly preserved, while the other three are only moderately good. This is surprising, as most fossils in the bed with *A. manis* are beautifully preserved. The coaly substance of

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A. manis has contracted and cracked into minute rectangular blocks which come apart when the fossil is removed from the rock. This is apparently a property of the fossil substance, and is not due to the thinness of its cuticle, for it is the parts of *A. manis* where the coaly substance is thickest that are the most friable, while other fossils in the same bed with just as thin cuticles are coherent. This fact, which has meant that pieces as small as 0.1×0.2 mm. have been used for cuticle preparations, has considerably increased the difficulty of description.

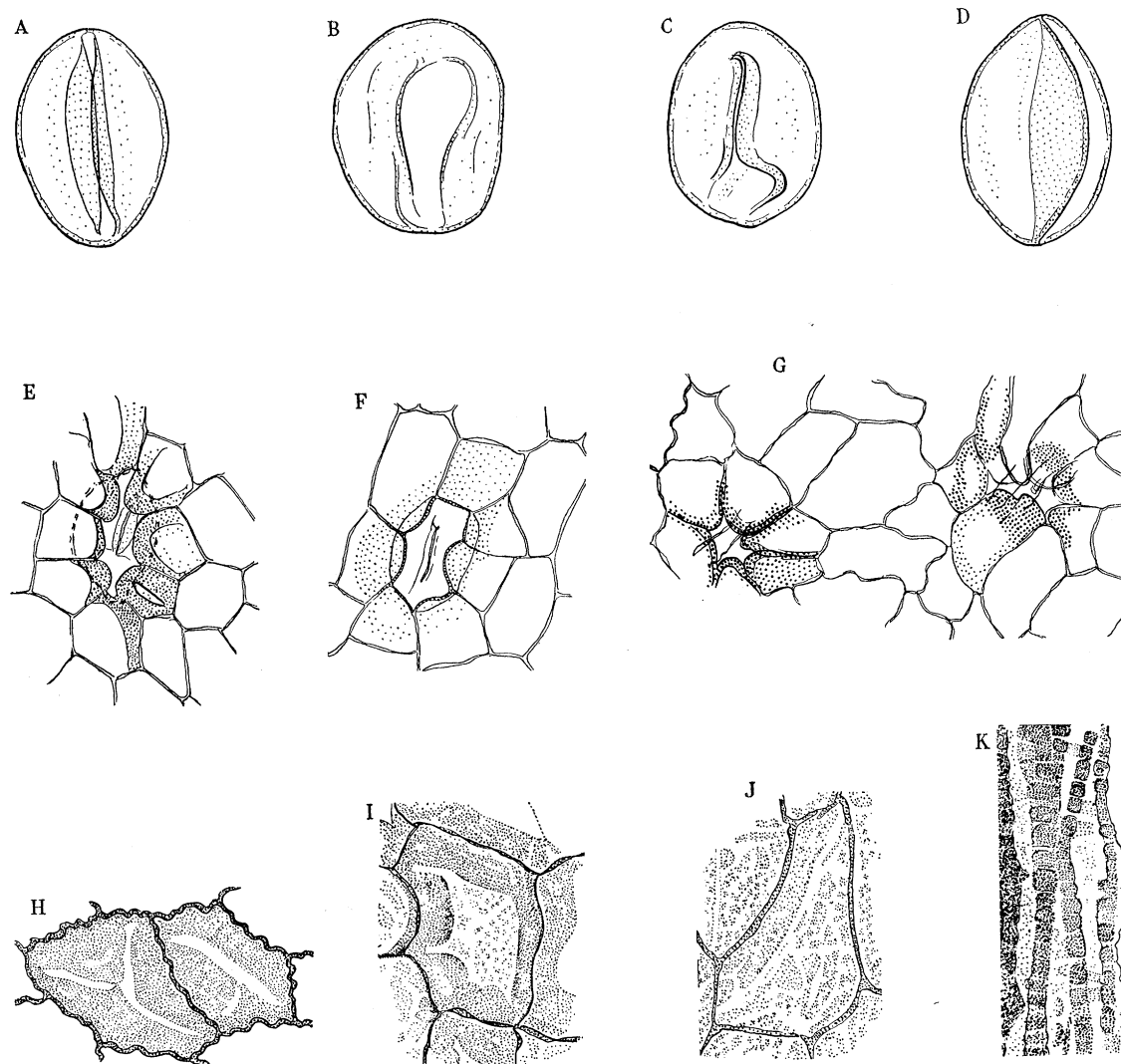


FIGURE 1. *Androstrobilus manis*. A–D, typical pollen grains, $\times 800$; that shown in C was obtained from the type-specimen (V 25900 A), those in A, B, D from V 25899 D. E, typical stoma; V 25899 D, $\times 400$. F, rather exposed stoma from the middle of a scale, type-specimen V 25900 B, $\times 400$. G, rather highly protected stomata; V 25899 C, $\times 400$. H, cells from the outer side of the displaced scale at the right of the type-specimen; V 25900 D, $\times 800$. I, cell from one of the lower scales of the type-specimen; V 25900 C, $\times 800$. J, cell from the middle of a scale of the type-specimen; V 25900 B, $\times 800$. K, part of microsporangium wall, next the aperture, cleared to show the thickening of the cells; V 25899 B, $\times 400$.

The microsporophylls are disposed in a regular spiral. Although it was impossible to determine the spiral; it was noticed that models with the divergence fraction of $\frac{3}{8}$ could be made which agreed well with the specimens, while models of both simpler and more complex fractions were different. It is thus very probable that the phyllotaxis of the cone is a $\frac{3}{8}$ spiral.

Each microsporophyll appears to consist of a horizontal part bearing pollen sacs and an upward pointing distal part. The horizontal part widens very rapidly from the base, the whole underside is covered with sporangia, while the upper side is marked with radiating ridges or oval bulges.

The distal part forms a broad rhomboidal scale; the upper margin projects upwards for some distance and usually conceals the bases of other scales, but the lower margin also appears to be developed and to project downwards to a small extent. The substance of the distal scale becomes progressively thinner towards the upper margin, where it finally becomes a brown film composed of a single epidermal layer. The edge of the lower margin is also thin.

Towards the base and apex of the cone the microsporophylls are smaller, and at the base they are replaced by still smaller sterile scales which also have an obtusely pointed upper margin.

The sporangia are fairly large, and as they are crowded and flattened, it has not been possible to make out the soral arrangement with certainty in this species; though groups of sporangia with apertures facing one another as in sori were noticed. The sporangia are finger-shaped sacs about 1.2×0.7 mm.; all those examined had dehisced, but they still contain plenty of pollen grains.

(2) *Microscopic structure.* The distal parts of the scales have a thin, though fairly well-developed, cuticle over their outer surface, and a much thinner cuticle over the inner surface. The sporangia also yield cuticles, but cuticle is scarcely present over the inner part of the microsporophylls.

Over the outside of the distal part of the scale, the cuticle is $0.25-0.5 \mu$ thick (i.e. thin but not too thin for easy manipulation). Near the top of the scale it shows uniform rectangular or polygonal cells with no stomata; but stomata are present in the middle and lower parts of the scale though not at the very base. The cell outlines are distinct, straight or very slightly sinuous, and sometimes interrupted as though by pits. The surface of the cells is sculptured to produce a mottling of thicker and thinner patches; occasionally these patches form parallel lines. In a few cells a slightly thickened border was seen.

The stomata are scattered at a maximum concentration of 50 or 100 per sq. mm. They are sunken and surrounded by 5-8 subsidiary cells which most often form an elongated or irregular group, but occasionally an almost regular ring. The surface of each subsidiary cell is thickened near the stomatal pit, and occasionally forms a conspicuous, hollow papilla, but more often a mere irregular thickened rim to the pit. The guard-cell surface is very thinly cutinized indeed, but the aperture and the margin of the exposed guard-cell surface can sometimes be seen.

Trichomes do not occur, except perhaps along the upper margin, where occasional cells bulge upwards as a thinly cutinized dome.

The inner surface of the distal part of the scale shows polygonal straight-sided cells and no stomata in the upper part, while no useful preparations were obtained from the lower part.

The sporangia have walls which are fairly coherent and thick enough to be opaque until partly oxidized. They then show a characteristic layer of cells—apparently epidermal—of elongated shape with strongly pitted walls giving them a tracheid-like aspect. The whole of this wall material is soluble on full maceration, apart from the cuticle which merely shows a cell outline. These cells are seen clearly near the aperture, but elsewhere they are partly obscured by deeper layers of cells.

The sporangia yield two cuticles, both very delicate. The outer cuticle shows the very faintly marked outlines of these epidermal cells; the inner (to which pollen grains often adhere) shows obscure outlines of large, broad cells (about $60 \times 30 \mu$), the whole surface being covered by conspicuous granules. This appears to be the innermost cutinized layer of the wall, next the tapetum. (A layer matching this is found in some at least of the living Cycads.)

Although all the pollen sacs had dehisced, the pollen was very imperfectly shed; in fact every sporangium examined yielded some grains, while some sporangia yielded large numbers.

The pollen grains are oval, the mean size is $36 \times 26 \mu$; the longest measured 40μ , the shortest 26μ (these figures omit specimens which appeared crushed). Most of the grains are well preserved, though some show folds in the wall caused by crushing; in all the best specimens a single longitudinal groove is evident, as is shown in various views in figure 1. The exine is almost perfectly smooth, but in favourable specimens can be seen to be very finely mottled.

A. manis is distinguished from *A. wonnacotti* by its larger size, the relatively broader distal region of its sporophylls, its slightly larger pollen grains and its more sunken stomata. The specific name is from *Manis* the pangolin, and refers to the appearance of the scales.

Androstrobus wonnacotti sp.nov.

Type-specimen, figure 2; figures 11, 15, plate 5.

Diagnosis. Cone about 1 cm. broad, at least 5 cm. long; distal region of sporophyll almost square, smooth apart from radiating striae near the margins. Pollen grains typically $29 \times 21 \mu$. Guard cells situated in a shallow pit.

Description. *A. wonnacotti* is represented by the type-specimen alone; the counterpart is missing, and as the specimen is unique no transfer was prepared. Its preservation is just like that of *A. manis* and equally minute pieces had to be used for the preparation of cuticles. In the upper part the plane of rock cleavage has exposed the outer surface of the cone, but elsewhere it has passed close to the cone axis. The base of the cone is indistinct, and possibly it is missing; no sterile bracts were recognized.

As in *A. manis* the phyllotaxis appears to be a $\frac{3}{8}$ spiral. The distal ends of the scales are again rhomboidal, but their width is only slightly greater than their height and the upper margin is fairly substantial, not scarious as in *A. manis*.

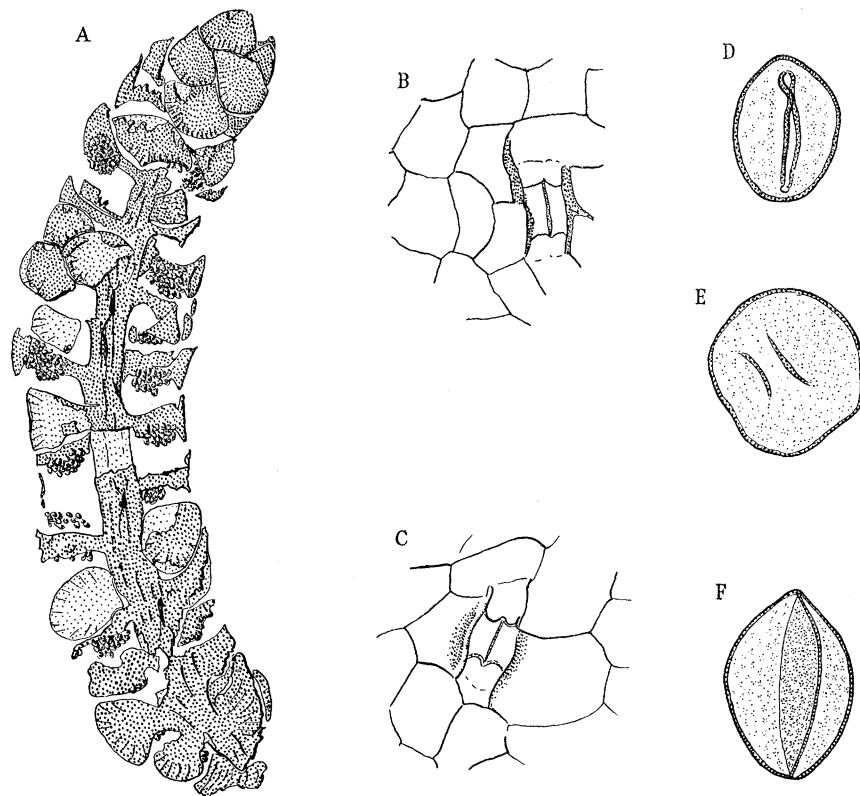


FIGURE 2. *Androstrobus wonnacotti*. A, drawing of type-specimen. The specimen was immersed in xylol and at certain points deeper levels in the fossil are exposed than those seen in figure 15, plate 1; V 25850, $\times 2$. B, C, stomata and epidermal cells from the outer surface of the distal ends of the microsporophylls; V 25850 B, $\times 400$. D, E, F, typical pollen grains; V 25850 A, $\times 800$.

The cuticle of the microsporophyll is rather thin and could only be prepared from the outer surface of the distal part. The epidermal cells have straight, distinctly marked walls and a finely mottled surface sometimes showing parallel striations. The stomata differ slightly from those of *A. manis* in being more exposed. The subsidiary cells form an irregular group, their inner margins (next the stomatal pit) show very little extra thickening and the pit leading to the guard cells is very shallow. The guard cells themselves, however, are better cutinized, the aperture being easily seen, and the central region is marked off from the polar regions of the stoma.

Pollen grains can easily be isolated from the sporangia by long maceration. The number in each sporangium is considerable, certainly amounting to several hundreds. The individual grains are like those of *A. manis* except for having a slightly smaller mean size; and the exine is perhaps a little thicker and more clearly mottled.

A. wonnacotti is named after Mr F. M. Wonnacott, who collected the material described in this paper.

Discussion of the morphology of Androstrobus

Androstrobus zamioides was regarded by Schimper as a cone of similar organization to the male cone of the Cycads: in the species described here this similarity has been proved to exist, and this supports Schimper's interpretation of his species, which is a very similar-looking fossil. *Androstrobus* is a smaller, probably much lighter cone than those produced by most Cycads and has a simpler phyllotaxis, but this may be of little importance from the point of view of comparative morphology.

The form of the microsporophyll is like that of the Cycads in general; it is particularly similar to that of *Encephalartos*, except that it is probably a good deal thinner in substance. In no group but the Cycads is the whole under surface covered with sessile sporangia, and it appears that, as in the Cycads alone, the sporangia are grouped in small sori with their apertures facing one another. An important point of agreement with the Cycads is provided by the very thick wall of the sporangia: in this they agree also with some other groups (Pteridosperms, Bennettitales), but differ from the Conifers, in which the sporangial wall is thin and in fossil specimens reduced to a delicate translucent membrane. The thickness of the wall is largely provided by the heavily thickened epidermal cells, which appear to agree in their strongly pitted walls with those of living Cycads. Another point of agreement with the Cycads is provided by the inner cuticle of the sporangium, which it was found possible to demonstrate also in a recent *Encephalartos* cone; I am unaware of its existence in Conifers; but it is seen also in certain Pteridosperms.

The cuticle of the microsporophyll provides stomata in which the subsidiary cells are arranged in a ring, having a different origin from the guard cells. This type is found in many plants, including nearly all the gymnosperms except the Bennettitales. The thickenings of the surface of the guard cells themselves is also of the general gymnosperm type, but the scattering of the stomata and the rather irregular grouping of the subsidiary cells round the sunken stomata is a good deal more characteristic of the Cycads (and perhaps the Pteridosperms) than of the Ginkgoales or Conifers.

The microspores agree with the type which is found throughout the Cycads, but also in many members of other Gymnosperm families, being what Wodehouse (1935) considers the primitive or generalized condition for this family. Very perfect and fairly complete agreement has thus been established between *Androstrobus* and the Cycad male cone, but differences between it and the reproductive organs of all other families. It is thus clear that *Androstrobus* is to be classified as a Cycadean male cone.

2. FEMALE CONES

Genus *Beania* Carruthers1869. *Beania* Carruthers, p. 98.

Carruthers' diagnosis is as follows: Female fruit composed of scales arranged in loose spikes; scales stalked and peltate, supporting two ovoid sessile seeds, one on each side of the pedicel.

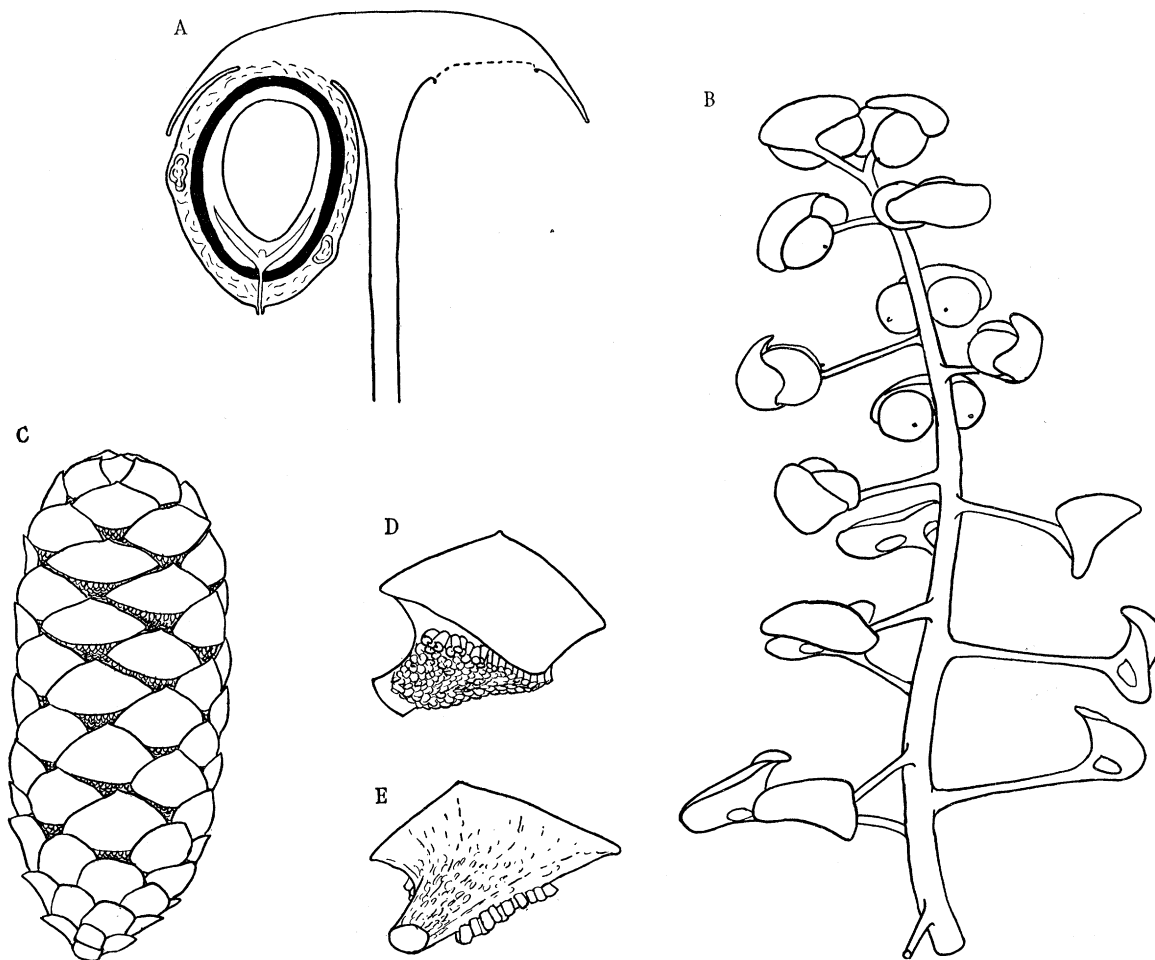


FIGURE 3. Restorations of *Beania gracilis* and *Androstrobus manis*. A, *Beania* sporophyll in L.S. The seed on the left is still attached, the integument shows two resin bodies embedded in the fibrous flesh, and the stone (solid black), inside which is the nucellus and megaspore membrane; \times about 2. B, *Beania* cone, the lower sporophylls have shed their seeds; about natural size. C, *Androstrobus* cone; about natural size. D, E, two views of a sporophyll of *Androstrobus*; \times about 2.

Discussion of nomenclature. Carruthers' type-specimen of *Beania* was a good one, and it was well figured and described. A specimen was, however, figured earlier under the name *Sphaereda paradoxa* by Lindley and Hutton (1835, Pl. 159, fig. 2), but this name refers to Lindley and Hutton's Pl. 159, fig. 1, which is the specimen on which

the main description is based and is certainly distinct from *Beania gracilis*, probably an altogether different type of organ. Another earlier generic name is *Zamiostrobus* Endlicher (published in 1836), which is only distinguished by being a more compact cone. *Zamiostrobus* cannot be considered a satisfactorily founded genus; its diagnosis would appear to refer more to a female cone of *Zamia* than to features proved to exist in any fossil. It is possible that the genus *Stenorrachis* is in part a synonym of *Beania*.

Beania gracilis Carruthers

(Plate 5, figures 10, 12–14; Plate 6, figures 16–28)

1835. *Sphaereda paradoxa* Lindley and Hutton in part; plate 159, figure 2 (not figure 1); Williamson's description on p. 19 which (according to Carruthers) refers to this specimen alone.
1869. *Beania gracilis* Carruthers, p. 97, plate 4, figure 1.
1875. *Beania gracilis* Carruthers, Saporta, p. 63, plate 77, figure 3 (copy of Carruthers' figure).
1875. *Sphaereda paradoxa* L. and H., Phillips, p. 233, plate 8, figure 68.
1900. *Beania gracilis* Carruthers, Seward, p. 279, plate 9, figure 11 (Carruthers' type re-figured).
1917. *Beania gracilis* Carruthers, Seward, p. 502, figure 586 (figure copied from Seward 1900, discussion).
1931. *Beania gracilis* Carruthers, Schuster, p. 183 (discussion).

Carruthers' diagnosis of *B. gracilis* is as follows: Axis of the female inflorescence slender; scales on slender stalks placed at right angles to the axis, peltate, apex of the scale small, scarcely covering the ripe seeds; seeds sessile, ovoid, acuminate at the apex, symmetrically arranged on the two sides of the pedicel, reflexed.

Description of the specimens. Hitherto *Beania* has seemed a rare fossil, but the Wonnacott collection has provided about thirty, half representing the mature cone or seeds, and half being small and immature. The mature cone is described first.

Axis. The mature cone is of considerable size; the longest fragment, figure 22, plate 6, is 10 cm. long, and this specimen though lacking its base may be nearly complete, as its axis reaches the full width of 4–5 mm. The base itself, which is present in other specimens, is abruptly truncate without there being any enlargement or other modification of the axis. Sporophylls arise on all sides of the axis in a very loose spiral; the phyllotaxis could not be determined; the spacing of the sporophylls is irregular in some specimens. In such specimens as that shown in figure 22, plate 2, the sporophylls have been flattened nearly into the horizontal plane and appear to be placed in almost regular alternation, but careful observation always gives evidence that this is a mere effect of distortion. The length of the internode in the mature cone is 4–5 mm.

The surface of the axis is marked with longitudinal ridges which are conspicuous in some, faint in other, specimens. Many of these ridges start on the sporophyll stalks and run up or down from them; as a rule they die out after 1–2 cm. and are replaced by new ones. At the sides of the specimen rock matrix is imprisoned between one ridge and the next, indicating that they were present before compression; their original height being about 0.5 mm., and there being about twenty of these ridges in all (ten

on each surface). The sporophyll stalks arise at right angles to the axis (except at the apex of the cone) and no subtending bract or other organ is found at their base.

The substance of the axis is rather thick, but fragile. Its cuticle is thick. It shows longitudinal rows of rectangular cells with very strongly marked lateral walls. The surface of the cells shows a mottled sculpture; sometimes parallel striations are to be seen and occasionally a broad border is present next to the side walls. Neither hairs nor stomata were observed with certainty.

Sporophyll. The stalk of the sporophyll is straight, and apparently stiff. It is about 1.5 mm. thick and its length varies between 1.5–2.5 cm., being longer in some cones than in others. The surface shows ridges (about twelve in all) like those of the axis. The cuticle of the stalk is like that of the axis.

The distal end of the sporophyll stalk enlarges to form the head. This structure consists of a broadly oval scale, about 18 mm. broad, 6 mm. high. The stalk is attached to the inner side near the base, and beside the stalk, also nearer the lower margin, the two seeds arise. As a rule the head has been flattened in preservation so that its breadth lies parallel with the cone axis, but the striations on the sporophyll stalk show clearly that it has been twisted through about a right angle. In these specimens the free upper margin usually points across the bedding plane and consequently is not seen. The sporophyll then appears to divide into two 1-seeded branches as in *Stenorrachis*. The outer surface of the head is distinctly curved; where seeds are still attached it is convex, but where they have been lost it becomes saddle-shaped, being concave in the horizontal but convex in the vertical plane. Thus in V 23932 (figure 22, plate 6) the sporophylls on the right were exposed by chipping away rock, and it was found that their upper margins overhung the top of the stalk, though this part was removed in preparation. The clearest picture of the shape of the sporophyll head is given by the transfers of young cones, which for some reason are less distorted.

The substance of the head is thin and fairly coherent near its upper margin, but becomes thick and at the same time very friable as the stalk is approached. It shows no sign of veins.

The seeds are attached to an area on either side of the stalk just above the lower margin. In certain specimens this area lies nearly in the bedding plane and so should be scarcely distorted, and in these the scar is not circular but an oval 4.5×2 mm., thus indicating that the base of the seed was flat. The scar shows the presence of scattered thick-walled cells, but the vascular bundle print was not seen. At the margins of the scar the epidermis is obviously broken; originally it would have been continuous with the epidermis of the integument.

The cuticle of the head is difficult to prepare because the substance is friable; it is moderately thick in the lower part, becoming rather thin above. There are some differences between the structure of the inner and outer surfaces. The adaxial side (i.e. inner side where the seeds occur) has often the thicker cuticle and has considerably fewer stomata than the abaxial side. In the lower parts near the seed and

stalk the cells have very prominent walls which are straight or slightly sinuous, while the surface of the cells commonly shows thick bands next the side walls. No trichomes were seen, but a very few stomata occur. In the upper part, near the free margin neither trichomes nor stomata occur and the cells are uniform. The outlines are fine but very distinct and corners of cells are often thickened. The cell surface is finely mottled and the middle is often distinctly thickened, though not to such an extent as to form a papilla.

The abaxial or outer surface shows cells somewhat resembling those of the opposite side, but stomata are rather numerous, occurring in patches rather than being evenly distributed, while in the upper part a few characteristic trichomes occur. In the upper part the cells sometimes show a central thick patch in the middle of which is a thin streak. The stomata show a considerable range of structure, the more exposed types (figure 4 C, E) being found in the upper lightly cutinized part of the scale, while those shown in figure 4 F are normal for the lower part, where the stomatal pit is as a rule all but obliterated.

The trichomes (figure 4 D) consist of a cell with a thickened surface with a thick ring in the middle, apparently representing a compressed hollow papilla. Small trichomes often appear to take their places among the epidermal cells, but large ones like that figured overlap the cells whose outlines can be traced underneath.

Seed. The seed is oval and of rather varied size, the largest are about 16×13 mm.; but some as small as 7×7 mm. were seen which have the same structure and were considered fully developed. Most sporophylls have shed their seeds and isolated seeds are common, but there are plenty of attached ones which serve for identification.

The base of the seed is flat (in the compressed fossil) and some of the rock matrix has often penetrated here, separating the different layers, but higher up none occurs. The apex is mucronate with the minute micropylar papilla, but this part is only seen in favourable specimens. The surface of the seed is marked with obscure lumps and wrinkles, which unlike those on the cone axis are irregular and seldom imprison any rock matrix; at the sides of the seed there are some stronger folds which do imprison rock, so that they must have been present at the time of compression and are possibly a feature present before preservation. The surface of most specimens shows none of the well-defined round lumps which are a conspicuous feature of the seeds of *Beania kochi* and other *Nilssonia* seeds, but in the seed shown in figure 12, plate 5, and in a few other specimens, one or two lumps of this kind are present. It is known in other species that the round lumps are caused by large masses of resin situated in the flesh of the seed coat.

Structure. The structure of the seed is shown by cuticle preparations and by fractured surfaces. Near the base, where mud has penetrated, fractured surfaces give clear evidence of two layers in the seed coat, an outer flesh and an inner stone. The flesh and stone are each about 0.25 mm. thick in a compressed seed whose substance is 1 mm. thick. The flesh appears as a fibrous layer formed by thick-walled bulging cells

which are orientated in different directions, the stone as a homogeneous pitchy material. By clearing the stone in $\text{HNO}_3 + \text{KClO}_3$ and then crushing it, the stone is seen to be composed of many layers of elongated cells with intensely thick, strongly pitted walls—typical elongated stone cells such as occur in the shells of nuts and the hard layer of the coat of many seeds (including Cycads). The flesh seems to have formed a rather firm layer, for at the side of the seed there is no clearly defined thin region flanking the stone, but a gradual decrease in thickness. When the seed coat is softened by soaking in $\text{HNO}_3 + \text{KClO}_3$ the fleshy layer often separates from the stone

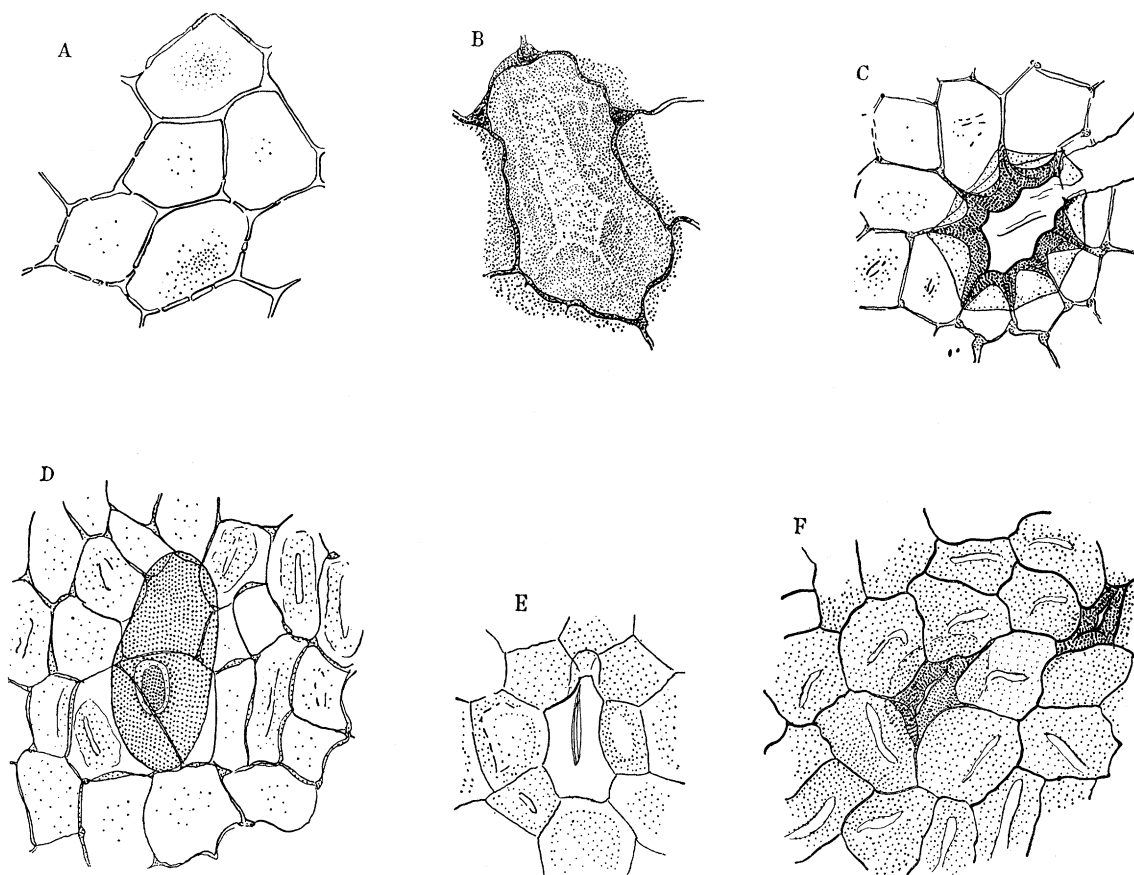


FIGURE 4. *Beania gracilis*, head of megasporophyll. A, cells from inner side of the upper part of the scale showing pitted walls and a faint median papilla; V 23929 C, $\times 400$. B, cell from outer surface of lower part of scale showing thick border; V 26780, $\times 800$. C, stoma from outer surface of scale (the cuticle was torn in preparation); V 23929 A, $\times 400$. D, trichome and epidermal cells from the outer side of the upper part of a scale; V 23929 A, $\times 400$. E, unusually exposed stoma from upper side of scale; V 23929 B, $\times 400$. F, highly protected stomata from outside of lower part of head of scale; V 26780, $\times 400$.

and it is then possible to isolate some of its cells by teasing. These are elongated cells with thick but unpitted walls and occur isolated in more homogeneous matter. These cells appear to correspond to the cells with thick brown walls found in the flesh of recent Cycad seeds: the wall composition has not been determined, but it is easily

shown to be chemically resistant. No vascular tissue was recognized in the flesh, but this must not be considered to indicate its absence.

Fully macerated preparations of the seed yielded a certain amount of resin, which appears to have been derived from the seed coat, though this was not definitely proved. The resin forms numerous small lumps 10–20 μ wide which may have been included in cells, but a seed may also yield one or two very large irregular lumps nearly 1 mm. in diameter. These lumps agree with those of other species and are probably the cause of the occasional round bulges seen on the surface of the seeds of *B. gracilis*.

Maceration methods yield rather disappointing results with most specimens; indeed only two of the ten treated gave really good preparations. Not only do the seeds break up into fragments, but the thickness of the inner layers is extraordinarily variable. The cuticles of the inside of the integument and of the nucellus vary from being moderately thick to very thin indeed; while the megaspore membrane was sometimes found to be quite thick, sometimes non-existent. No considerable differences in the appearance of the seed or of the cutinization of the outside of the integument accompany these internal differences, which are unexplained.

The following cutinized layers are found in the seed:

- (1) Outer cuticle of the integument, which is broken at the base of the seed at the point of its attachment to the sporophyll.
- (2) Lining of the micropylar canal, which is continuous above with the outer cuticle of the integument and below with the inner cuticle of the integument.
- (3) Inner cuticle of the integument, which is continuous with the cuticle of the nucellus below.
- (4) Cuticle of the nucellus (only present round the free part of the nucellus).
- (5) The megaspore membrane, a sac of cuticle extending from within the nucellus to near the base of the seed.

It is a fact readily demonstrated in the seeds of recent gymnosperms that not only is the outside of the integument cutinized but also the micropylar canal, the inside of the integument and the outside of the free part of the nucellus. The nucellus cuticle, however, only extends down to the level where the nucellus unites to the integument, for there its cutinized epidermis bends outwards and becomes the inner lining of the integument. In a fossil seed compression we can therefore determine the extent of the free part of the nucellus by finding how far back its cuticle can be traced: in *Beania gracilis* the cuticle and therefore the free part of the nucellus is confined to the top third of the seed. These layers are now described in detail.

- (1) The outer cuticle of the integument is a hard layer of very thick cuticle (total thickness about 20–30 μ) which is brittle and usually breaks into fragments. The cells are isodiametric, the cell walls project inwards to a remarkable extent, usually covering the whole length of the lateral walls and often much of the basal wall of the epidermal cell; this sometimes makes the cell outline very hard to see, particularly at high magnification. Trichomes are absent, but some scattered stomata occur, in which the

subsidiary cells are so highly thickened that the stomatal pit is all but obliterated by thickening and the guard cells cannot be seen.

In the least thickly cutinized seeds some features of surface sculpture can be seen, taking the form of a broad thickened band along the lateral walls.

(2) Lining of the micropylar canal. In all specimens the canal has entirely flattened and the cuticles of the two sides have stuck together, though it is possible to see the outlines of each set of cells. The cells are more or less rectangular and straight-sided; the walls, which are prominent, project outwards. The micropylar canal widens slightly as it is traced downwards.

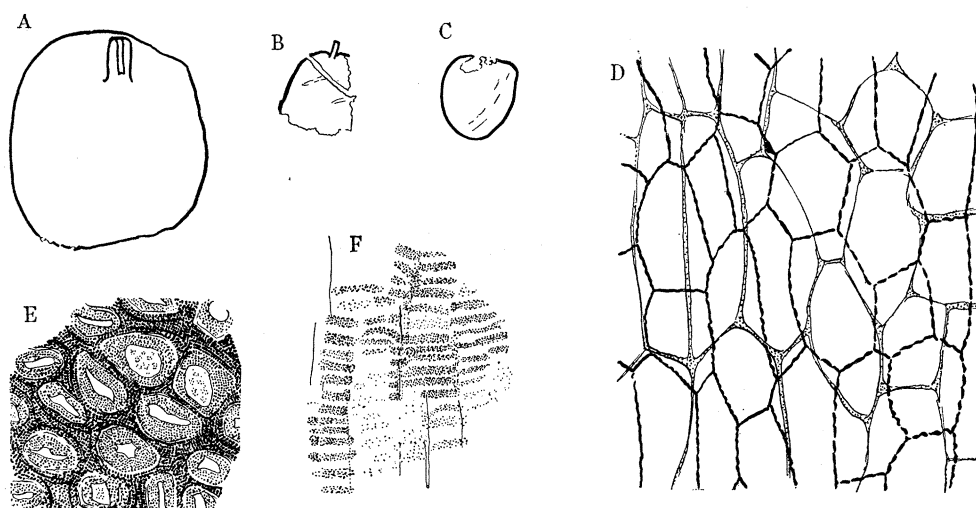


FIGURE 5. *Beania gracilis*, seed. A, B, C, three cutinized membranes from one of the seeds situated underneath the scale shown in figure 21, plate 2; all $\times 10$. A, shows the outer cuticle of the integument and the micropylar papilla and micropylar canal. B, shows the combined inner cuticle of the integument and outer cuticle of the nucellus, and at the apex the inner part of the micropylar canal. C, shows the megaspore membrane; V 23934 B. D, part of the combined cuticles of the inside of the integument (continuous cell walls shaded with stippling), and outer cuticle of nucellus (cell walls appear pitted); V 26781, $\times 400$. E, cells of outer cuticle of integument; V 26778, $\times 400$. F, print of scalariform tracheids on nucellus or inner side of integument; V 26782, $\times 400$.

(3) Inner cuticle of the integument. This layer is thickest at the base of the micropyle, diminishing towards the point of fusion with the nucellus, where it is rather delicate. At the sides, where it extends beyond the nucellus (in the compressed seed), the upper and lower layers of this cuticle stick together, while over the nucellus it is more or less firmly attached to the nucellus cuticle; there may thus be some difficulty in tracing cell outlines in what is nearly always two adherent cuticles. Over most of its extent the cells are isodiametric and show no regular arrangement, but close to the base they are flattened and arranged side by side in groups. The lateral walls are prominent and straight or very slightly sinuous and the corners of cells and sometimes

other points may be locally thickened. The surface of the cells is sometimes unevenly thickened, showing irregular patches which suggest solidified oil drops.

(4) The cuticle of the nucellus is thinner than the inner cuticle of the integument; where that is fairly thick and brown the nucellus is thin and pale or colourless, and where the integument is lined by a thin colourless cuticle, the nucellus is unrecognizable. Its thickness is almost uniform except at the apex, where no cuticle is present, probably as a result of the formation of a pollen chamber. Near the micropyle the nucellus is separated from the inner cuticle of the integument by 1 mm., but farther back the two layers approach and finally join. The cells of the nucellus are distinguished by being both longer and narrower than those of the integument. In some specimens the cell outlines are finely and evenly marked, but in others they show characteristic moniliform thickenings in the upper part, while near the base the fine lateral wall becomes inconspicuous but is accompanied on each side by a conspicuous thick border. The surface of the cells is finely mottled, but does not show the irregular thickened patches often seen on the inside of the integument.

(5) The megaspore membrane is an ovoid sac, the upper end being more pointed. At the sides of the compressed seed it is separated from the nucellar cuticle by about 0.4 mm.—the original thickness of the nucellar tissue. The two layers of the megaspore are easily separable, as there is a small amount of soluble matter enclosed between them, and for the same reason the megaspore is easily separable from the nucellus. The megaspore is a rather thick cuticle—about 10μ thick, but in spite of its thickness it is rather fragile and also more quickly destroyed by over-maceration than the much thinner nucellus or inner cuticle of the integument. The megaspore membrane is non-cellular, but is composed of a spongy mass of very fine granules except for its deepest layer, which appears to be compact. Sometimes the surface shows ill-defined longitudinal marks, which may be the vague impressions of contiguous cells of the nucellus or endosperm.

An unexpected feature shown by one macerated seed consists of distinct traces of vascular bundles superimposed on the adherent cuticles of the nucellus and inside of the integument. The bundles appear to have a vertical, but rather winding course and are 60μ wide and separated by 100μ intervals. They are composed of tracheids showing scalariform bars to the exclusion of other types. Careful focusing suggests that the tracheids are situated in the nucellus rather than in the integument.

The occurrence of vascular strands in this region of the seed is not surprising, but their preservation in a macerated compression is remarkable; possibly the explanation is that oily matter from other parts of the seed had impregnated the tracheids after death and was changed to a resistant resin in fossilization. The scalariform thickening of the tracheids is an important point of agreement with the Cycads.

It may be noted that in this description there is one important gap in the information which a seed preserved as a compression might be expected to yield: no pollen grains have been seen in the micropyle or pollen chamber of the nucellus. It must be

remembered, however, that in two only of the mature seeds were good preparations of this region obtained, so that no significance must be attributed to their absence. In one specimen, however, two well-preserved grains of the *Androstrobos manis* type were found on the surface of the nucellus, near the base of the free part.

Immature specimens. Besides the typical specimens the collection includes a series of smaller ones of precisely similar general organization which indicate their generic identity with *Beania*; there are certain differences in detail which are given below. The possibility was considered, and cannot be said to have been finally excluded, that they might represent other species, but it was thought more likely that they are young specimens of *B. gracilis*, or perhaps specimens of arrested development. The reasons for this are: they seem to be associated with typical *B. gracilis*; they form a series in size ranging between the smallest and typical specimens, and not a circumscribed group; and such differences of structure as they show are just what might be expected to be seen between young and full-grown specimens of *Beania*. The distal scale shows a thinner cuticle with smaller cells in which none of the ridges of thickening on the surface have developed. The stomata are similar in character to those of the mature scale, but have less thickly cutinized subsidiary cells. The seeds are interesting. The integument cuticle is thin and shows small hexagonal cells: it appears that their full number has already been reached in the smallest specimen, and the only further change is mere growth. No resin was found in the seed coat, and it seems that the hard stone layer has not developed. The micropylar papilla is nearly full grown and is already fairly thickly cutinized in the youngest seeds; the nucellus and inside of the integument are already cutinized though not full grown. The youngest seeds provided surprisingly well-preserved megaspore membranes; they are, however, disproportionately small and even softer than in the mature seed.

Comparison with other species. Several other species of *Beania* are known, mostly represented by isolated seeds, and described as 'seeds of *Nilssonina*', but two are known from cones or sporophylls.

Beania carruthersi Nathorst (1902), a cone from the Oolite of Helmsdale, Scotland, agrees very well indeed in its generic characters with *Beania gracilis* and is certainly rightly referred to this genus. The attachment of the seeds to the surface of the head of the scale is clearly shown. In dimensions it is comparable with immature specimens of *B. gracilis*, but it is well distinguished by the regular punctuation of the seeds; it should be noted, however, that Nathorst considered that the seeds were microsporophylls in conformity with his earlier interpretation of other *Nilssonina* seeds.

Beania kochi Harris (1937), first described from Greenland Lower Liassic material as *Nilssonina incisoserrata* seed (Harris 1932), is known from seeds and some rather imperfect sporophylls of similar size to those of *B. gracilis*. The cuticular structure of the sporophylls and seeds is almost the same, but the species is well distinguished by the presence of numerous large masses of resin situated in the flesh and causing bulges in the seed surface. It is discussed in detail below.

A number of isolated seeds have been described (rightly) as seeds of *Nilssonia*. They almost certainly belong to *Beania*, but it would seem best to restrict the name *Beania* to sporophylls and cones, giving a different generic name to the seeds. A form genus for seeds of this general structure has in fact been proposed, *Allicospermum* (Harris 1935), or a separate name might be given to *Nilssonia* seeds, which are further distinguished as a group by the presence of bulging masses of resin in the flesh, and by some other peculiarities.

Discussion of the morphology of Beania

Carruthers, and nearly all subsequent authors, regarded the organization of *Beania* as being essentially like that of a female cone of *Zamia*, and this view is here fully confirmed.

Of the cone axis it merely needs to be said that it agrees with typical stems in bearing its lateral organs on all sides: the possibility that the *Beania* cone might be a compound sporophyll and its central part a rachis is thus excluded on ordinary morphological definitions. It is thus comparable in general with any other cone axis, such as those of Conifers or Cycads. It is a fact that no living Cycad has a lax cone like that of *Beania*, while a few living and fossil conifers have comparable cones, but in view of the fact that plants with even more divergent types of floral structure are included in the main Gymnosperm orders (e.g. *Cycas*, which has no female cone in the ordinary sense), it is clear that this difference is not of sufficient importance to separate *Beania* from the Cycads, though it may well be used to distinguish as a subfamily the Nilssoniae.

The form and structure of the sporophyll is remarkably like that of the genera of the Zamioideae in all respects, and it is unlike the sporophylls of any other group than the Cycads. A comparison was once made between the *Beania* sporophyll and the seed-bearing organ of *Ginkgo* (Seward 1900, p. 275), but its author later gave up this view (Seward 1917, p. 502). This comparison was no doubt suggested by the somewhat T-shaped top of the sporophylls in the type and other specimens, which does appear rather like the branched organ of *Ginkgo*; it was not then known that the specimens showed merely a sort of longitudinal section, and that the end of the sporophyll did not really branch but instead ended in an oval scale unlike any organ produced by *Ginkgo*. On our present slight knowledge of the reproductive organs of the fossil Ginkgoales there is no need to consider further the possibilities that *Beania* might belong to that group.

Among the Conifers, many genera show a pair of ovules placed parallel with the sporophyll stalk and with their micropyles facing the axis, though there does not happen to be any living or fossil genus particularly like *Beania*. In the majority of the Conifers, particularly of the fossil members, there is an important difference however, that the seed-bearing scale is a complex structure composed of 'bract' and 'ovuliferous' scales, which though often of very unequal size are easily recognized as distinct organs. Thus in *Cycadocarpidium*, which was once supposed to be a Cycadean organ,

there is a relatively large bract scale bearing two little triangular appendages to which the seeds are attached. The specimens of *Beania* were carefully examined, but gave no indication of being double; it appears to be a simple sporophyll.

Of the epidermal characters of *Beania*, it is sufficient to say that there is good general agreement with the Cycads, but no fundamental difference in stomatal structure from several other Gymnosperm groups—the Pteridosperms, Ginkgoales and Conifers, though in these groups rather different specialization is often found. From the Bennettiales, *Beania* is sharply distinguished by its stomata.

The seed of *Beania* shows much that is of morphological importance. A fairly full description of the seed of certain species of *Nilssonia* seeds was given by Nathorst (1909); and a somewhat fuller description of the structure of an almost identically similar seed (*Beania kochi*) by Harris (1932), where some different interpretations of the various membranes were given as is shown below.

Nathorst 1909	Harris 1932
Cuticle of integument	(Outer) cuticle of integument
Resin bodies of integument	Resin bodies of flesh of integument
—	Stone layer of integument
Nucellus or 'structureless membrane'	{ Inner cuticle of integument Cuticle of nucellus
Micropylar canal	Micropylar canal
? Spongy layer	Megaspore wall

The best of the present specimens are slightly better than those described by Harris (1932) and, while fully confirming that interpretation, add some further information about the structure of the integument and about the extent of the free part of the nucellus, which is definitely confined to the top third of the seed. The restoration given by Harris (1932, figure 260) shows it extending too far back, but in other respects it is correct. The seed of *B. kochi* is distinguished from that of *B. gracilis* by the presence of far more resin in the flesh, but in the structure of its membranes it is remarkably similar, even agreeing in such details as the presence of waxy droplets on the inner cuticle of the integument and in the beaded character of the cell walls of the nucellus cuticle.

The seed of *Beania* in its general features agrees with other fairly large Gymnosperm seeds—Cycads, Ginkgo, certain Conifers and certain Pteridosperms. In detail it can be stated that it agrees very perfectly with the Cycads and disagrees with many members of the other classes named, though it is not possible to state that it disagrees with all members of these families.

Large seeds with a fleshy layer enclosing the stone are normal in the Cycads, Ginkgo and the Pteridosperms, but in the Conifers they are exceptional. The structure of the stone is typical for that of seeds in general, but the flesh, which includes scattered thick-walled cells, is peculiar, agreeing with the Cycads, but not with any of the other groups known to me. The micropylar papilla too is a feature of most Cycad seeds,

but is absent in many members at least of the other groups, and this is also true of the extremely thick outer cuticle of the integument. The scalariform thickening of the tracheids is an important character in which *Beania* agrees with Cycads (and Pteridosperms) but differs from the Conifers and *Ginkgo*. Another point of agreement with the Cycads is in the free part of the nucellus being confined to the upper part of the seed: in a good many Pteridosperms the nucellus is free to its base. In the general character of the nucellus and megaspore membrane, *Beania* while agreeing perfectly with the living Cycads appears to agree equally well with certain members of other families.

The position may be summarized. *Beania* agrees in every important character with the female cones of typical living Cycads, but it is distinguished by a number of characters from the typical and perhaps indeed from all members of every other Gymnosperm family. In so far therefore as an isolated organ can be classified, *Beania* should be classified in the Cycadales.

ATTRIBUTION OF *BEANIA* AND *ANDROSTROBUS* TO THEIR PARENT PLANTS

There is evidence that both *Beania* and *Androstrobus* belong to the same plants as the leaves of the genus *Nilssonia*. This evidence, as usual with isolated fossil organs, depends partly on repeated association, partly on structural agreement.

(1) *The attribution of Beania to Nilssonia*

Nathorst (1902) was the first to notice the association of certain seeds (which he interpreted as microsporophylls) with a species of *Nilssonia*, *N. pterophylloides*, in the Rhaetic of Sweden. Later (1909) he redescribed them in far greater detail as the seeds of this plant and he described also similar seeds associated with two basal Liassic *Nilssonia* species from different localities in Sweden. Gothan (1914) described a seed of this kind which was associated with a basal Liassic *Nilssonia* in Germany, and the same association probably occurred in the Middle Jurassic flora of Sardinia described by Krasser (1913, 1920). Harris (1932) reported the association of seeds of the same type borne on *Beania*-like sporophylls with a *Nilssonia* leaf in the basal Liassic of Greenland. In this case it can be added that the seeds are confined to a layer where the *Nilssonia* leaves are extraordinarily abundant, but no other species is particularly common. Though I have never collected *Beania* in Yorkshire, I understand from verbal communications with Dr Hamshaw Thomas that it is a very local fossil in the Cayton and Gristhorpe plant bed and strongly associated with *Nilssonia*. Certainly every specimen in the Wonnacott collection is associated with *Nilssonia* leaves—chiefly *N. compta*, but some have the undivided *N. orientalis* as well. The other seed plants associated are: the Conifer *Elatocladus williamsoni*, whose cones are well known; the Caytonian leaf *Sagenopteris phillipsi*, whose fructifications are known as *Caytonia*

nathorsti; the Bennettitalean leaf *Nilssoniopteris vittata*, whose reproductive organ is known as *Williamsoniella coronata*, and finally a very few fragments of *Ctenis sulcicaulis*. *Ctenis* is a leaf thought to be Cycadean on its general epidermal structure, but its reproductive organs are entirely unknown: the precise details of its cuticle is sufficiently distinct to rule out the possibility that it should belong to *Beania*.

The structural evidence relates to the general character of the epidermal cells, stomata and trichomes which may be termed evidence of *generic* agreement; there are features, particularly in the sculpture of the cell walls, which are regarded as showing *specific* agreement with *Androstrobis manis*, but further work is needed to revise the species of the Yorkshire *Nilssonia* leaves before features of exclusive specific agreement with any one can be established. It is thought that this should not be difficult. Evidence supporting the general validity of this method for relating different organs of the same plant will be found in Florin's works (particularly Florin 1933), where a very full comparison is given between the cuticle of leaves and reproductive organs of the same Cycad species.

The general structure of the stomata of *Nilssonia* (see Florin 1920, Thomas and Bancroft 1913) agrees with that of *Beania* and allusion has already been made to the distribution of this type of stoma among the major orders of Gymnosperms. A good many Yorkshire leaves of Ginkgoales and Conifers have stomata agreeing more or less remotely with this type, but if on account of its purely Cycad-like morphology, attention is focused on to Cycad-like leaves, there are very few beside *Nilssonia* which are comparable, namely one species of *Ctenis* and one of *Ctenopteris*, which Thomas and Bancroft assigned with *Nilssonia* to the Nilssoniales. The great bulk of the Yorkshire Cycad-like leaves belong to the Bennettitales, a group sharply distinguished by its peculiar stomata, and certainly unrelated to *Beania*. While *Ctenis sulcata* and *Ctenopteris cycadea* show stomata of the same fundamental type, in each there are peculiar specialized features which distinguish them from *Nilssonia* or *Beania*.

Trichomes just like those of *Beania* are found in *Nilssonia*, and this is valuable supporting evidence, for such trichomes are of by no means general occurrence. So too is the occurrence of resin resistant to maceration, which is found in the leaves of most species of *Nilssonia* and in the seeds and sporophylls of *Beania*: such resin though occurring in other genera is not particularly common.

I was informed verbally of the agreement in structure between *Beania* and *Nilssonia* by Dr Hamshaw Thomas in about 1923 (see also Seward 1917, 1919); the first published account is by Harris (1932) for *Beania kochi* and the leaf *Nilssonia incisoserrata*; it is now reaffirmed for *Beania gracilis*.

Besides referring the seeds of *Nilssonia* to this plant, Nathorst (1909) suggested that *Stenorrachis* was the cone which bore such seeds. Seward (1917, p. 502) appears to be the first to have associated *Nilssonia* with *Beania* on information supplied by Dr Hamshaw Thomas; he pointed out too that *Stenorrachis* somewhat closely resembles *Beania*; though it now appears that they may be rather different after all. Harris

(1932) showed that the seeds described by Nathorst agreed fully in structure with ones borne on *Beania* sporophylls, and this is now established for the type species of *Beania*.

It may thus be claimed that the reasons which led Thomas to suggest that *Beania* belonged to *Nilssonia* have been greatly strengthened by evidence subsequently discovered.

(2) *The attribution of Androstrobus to Nilssonia and Beania*

Androstrobus wonnacotti is represented by a single specimen associated with *Nilssonia orientalis* and the Bennettitalean leaf *Nilssoniopteris vittata* to which it cannot belong. *Androstrobus manis* is represented by five specimens; the associates are *Nilssonia compta* (on every rock specimen), one has the conifer shoot *Elatocladus williamsoni*, two have the Caytonialean leaf *Sagenopteris phillipsi*, one the Bennettitalean leaf *Anomozamites nilsoni*, and one the probably Ginkgoalean leaf *Czekanowskia murrayana*. These last two are plants of unknown reproductive organs, but the precise character of the epidermis makes it exceedingly unlikely that they have anything to do with *Androstrobus*. The general character of the epidermis of the sporophyll of *Androstrobus* is exactly the same as that of *Beania*, indeed apart from having a thinner cuticle there is almost perfect agreement between *Androstrobus manis* and *Beania gracilis*. There is therefore no need to repeat the points in the discussion of its stoma, since everything said for *Beania* applies equally to *Androstrobus*.

There are features which are regarded as indicating specific identity between *Androstrobus manis* and *Beania gracilis*. In addition to the agreement between the stomata of the fossils which indicate generic, rather than specific identity, there is very close agreement between the superficial characters of the epidermal cells. This agreement is most marked between the most thickly cutinized part of *Androstrobus* (that is the outer surface of the sterile basal scales) and the thinner part of the *Beania* scale, that is its upper part. Here the cells show strongly marked peculiarities which are identical. Typical cells of each are of the same size and show nearly straight sides from which a thin ridge of cuticle projects inwards to a considerable extent, making an unusually clear outline. This ridge is distinctly sinuous, especially in its inner part. The surface of the cell shows a strongly thickened border placed parallel with the lateral cell walls, which delimits an angular thin area in the interior. The surface of this thin area appears finely mottled, the result apparently of surface irregularities. In both organs also cells are to be found which differ somewhat from this in the width of the thick border; where it is narrow the whole interior of the cell is mottled, but where it is very broad the thin central area is reduced to a mere narrow strip.

Cells of similar surface characters can be found on the rachis of *Nilssonia compta*, but no other Yorkshire fossil among those I have studied shows it except perhaps *Sagenopteris phillipsi*, and thin regions of the fruit of *Caytonia nathorsti* where the cells approach this condition. In neither *Nilssonia orientalis* nor in *Androstrobus wonnacotti* are such cells seen. This would then appear to be one of those structural peculiarities

which recur in the different organs of a particular species and having as far as can be seen no adaptive physiological significance are all the more valuable for characterizing it as a taxonomic unit. In my opinion this type of cell is sufficiently unusual to provide, when taken in conjunction with the *generic* similarity of the stomata, a very strong reason for believing that *Androstrobos manis* was borne on the same plant as *Beania gracilis*. It will very likely be possible to produce similar evidence that the leaf of the same plant is of the type known as *Nilssonia compta*, though whether *Androstrobos wonnacotti* belongs to the same plant as *Nilssonia orientalis*, with which it is only linked by the association of one specimen and cuticle characters which are mostly negative, is more doubtful, but I feel equally confident that it belongs to a species of *Nilssonia*. The occurrence of *A. manis* pollen in the seed of *B. gracilis* indicates association in life, and if it could be demonstrated repeatedly would provide evidence in support of this conclusion.

DISCUSSION OF THE PLANT BEARING *BEANIA*, *ANDROSTROBUS* AND *NILSSONIA*

This paper does not deal with the leaf *Nilssonia*, for which reference should be made to the very full account given by Florin (1920), who examined afresh both the gross and the minute characters of the leaf and concluded, not only that *Nilssonia* is widely separated from the Bennettiales, but that it should be classified very near the living Cycads. In this conclusion he endorses the findings of previous authors (Thomas and Bancroft 1913), and no one who subsequently examined the leaf of *Nilssonia* has reached any other conclusion.

Evidence has been put forward that *Androstrobos*, *Beania* and *Nilssonia* belong to the same genus. We are thus particularly favourably placed for considering its systematic position, for when the stem is discovered we should have nearly the whole plant. As all three organs show purely Cycadean characters, the evidence that the whole plant is rightly included in the Cycads is overwhelming and may be accepted without reservation.

Within the Cycadales the position is more doubtful. The leaf is constructed on a simply pinnate plan, and though distinguished by certain peculiarities is sufficiently similar to other Cycad leaves to allow the plant to be associated with almost any living genus. It would seem nearest to such leaves as those of *Dioon* and the Zamioideae, in which the leaf segments have numerous almost parallel veins. Its most unusual features for a Cycad are the presence of resin and the delicacy of the substance of its lamina and its cuticle.

The male cone gives no help because throughout the living Cycadales male cone structure is almost uniform, the slightly greater resemblance of *Androstrobos* to the cones of certain genera is thus scarcely significant. The megasporophyll is, however, helpful because it clearly differentiates *Beania* from *Cycas* and *Dioon* while associating it with the remaining genera, where it is smaller and the part beyond the seeds forms

a mere scale or protective head. Comment has already been made on the lax construction of the cone, which as has been said is unique among the Cycads.

It would appear then that the complete plant was a Cycad most closely related to the recent Zamioideae. In view of the extraordinarily loosely constructed cone, it seems wiser at present not to refer it to this subfamily but to place it in a special subfamily, the Nilssonieae, characterized by the wide spacing of the sporophylls of the female cone. With this advance, the class Nilssoniales of Thomas and Bancroft becomes obsolete; it has been suggested that the leaf genera which had been placed in it instead of being classified in families should be referred to as members of the *Ctenis*-series, which consists of leaves resembling those of Cycads, and the *Thinnfeldia*-series, of leaves resembling those of Pteridosperms (Harris 1931, pp. 144–146).

While it is not the purpose of this paper to discuss the general position of the Mesozoic Cycads, it may be pointed out that we have in *Palaeocycas integer* (Nath.) Florin some evidence for the existence in the early Mesozoic of Cycads allied to *Cycas* with several laterally placed ovules on the megasporophyll, and in *Beania gracilis* of Cycads allied to *Zamia*. These two genera are at the opposite extremes of the Cycad series as far as the important female reproductive organs are concerned, and it would thus appear that by Rhaetic times, when both genera occur, the Cycadales had evolved to the full extent. In view of the theory, which seems likely enough, that in the Cycadales the reproductive organs have been reduced from richly branched pinnate organs as in Pteridosperms to mere scales, it is of interest to note that *Beania* and *Androstrobis* are already as advanced as the most advanced recent genera.

REFERENCES

- Carruthers, W. 1869 On *Beania*, a new genus of Cycadean Fruit, from the Yorkshire Oolite. *Geol. Mag.* **6**, 97–99, plate IV.
- Endlicher, S. 1836–1840 *Genera plantarum secundum ordines naturales disposita*. Vindobonae.
- Florin, R. 1920 Über den Bau der Blätter von *Nilssonia polymorpha* Schenk. *Ark. Bot. K. svenska VetenskAkad. Handl.* **16**, no. 7, 1–10, plate 1.
- Florin, R. 1933 Studien über die Cycadales des Mesozokums. *K. svenska VetenskAkad. Handl.* (3) **12**, no. 5, 1–134, plates 1–16.
- Gothan, W. 1914 Die Unter-Liassischen (rhaetische) Flora der Umgegend von Nürnberg. *Abh. naturh. Ges. Nürnberg*, **19**.
- Harris, T. M. 1931 Rhaetic Floras. *Biol. Rev.* **6**, 133–162.
- Harris, T. M. 1932 The Fossil Flora of Scoresby Sound, East Greenland. Part 2. *Medd. Grønland*, **85**, no. 3, 1–112, plates 1–9.
- Harris, T. M. 1935 The Fossil Flora of Scoresby Sound, East Greenland. Part 4. *Medd. Grønland*, **112**, no. 1, 1–176, plates 1–29.
- Harris, T. M. 1937 The Fossil Flora of Scoresby Sound, East Greenland. Part 5. *Medd. Grønland*, **112**, no. 2, 1–114, plate 1, tables 1–3.
- Krasser, F. 1913 *Williamsonia* in Sardinien. *S.B. Akad. Wiss. Wien*, **121**, 1, 943–973, plates 1, 2.

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- Krasser, F. 1920 Die Doggerflora von Sardinien. *S.B. Akad. Wiss. Wien*, **129**, 1, 2. Heft, 3–26.
- Lindley, J. and Hutton, W. 1835 *The fossil flora of Great Britain*, **3**. London.
- Nathorst, A. G. 1902 Beiträge zur Kenntnis einiger mesozoischen Cycadophyten. *K. svenska VetenskAkad. Handl.* **36**, no. 4.
- Nathorst, A. G. 1909 Über die Gattung *Nilssonia* Brongn. *K. svenska VetenskAkad. Handl.* **43**, no. 12.
- Phillips, J. 1875 *Illustrations of the geology of Yorkshire*. Part 1. *The Yorkshire Coast*. 3rd ed. London.
- Saporta, G., Marquis de. 1875 *Paleontologie Française*, ser. 11; *Végétaux—Plantes Jurassiques*, **11** and atlas, Cycadees.
- Schimper, W. P. 1872 *Traité de paleontologie végétale*, **2**. Paris.
- Schuster, J. 1931 Über das Verhältnis der systematischen Gliederung der geographischen Verbreitung und der paläontologischen Entwicklung der Cycadaceen. *Bot. Jb.* **64**, 165.
- Seward, A. C. 1895 *Catalogue of the Mesozoic plants in the Department of Geology, British Museum. The Wealdon flora*, part 2.
- Seward, A. C. 1900 *Catalogue of the Mesozoic plants in the Department of Geology, British Museum. The Jurassic flora*. 1. *The Yorkshire Coast*. London.
- Seward, A. C. 1917 *Fossil Plants*, **3**. Cambridge.
- Seward, A. C. 1919 *Fossil Plants*, **4**. Cambridge.
- Thomas, H. H. 1911 The Jurassic flora of Kamenka in the District of Isium. *Mém. Com. géol., St-Petersb.*, (n.s.) **54**, 71.
- Thomas, H. H. 1933 On some Pteridospermous plants from the Mesozoic rocks of South Africa. *Phil. Trans. B*, **222**, 193–265.
- Thomas, H. Hamshaw and Bancroft, N. 1913. On the Cuticles of some recent and fossil Cycadean fronds. *Trans. Linn. Soc. Lond. Bot.* **8**, 155–204, plates 17–20.
- Walkom, A. B. 1917 Mesozoic floras of Queensland. Part 1 concluded. *Qd Geol. Surv. Publ.* no. 259.
- Wodehouse, R. P. 1935 *Pollen grains*. New York.

DESCRIPTION OF PLATES 5 AND 6

PLATE 5. *Androstrobos*, *Beania*

FIGURE 6. *Androstrobos manis*. Sporangia exposed on the surface of an uncompleted transfer; V 25899 A, $\times 6$.

FIGURE 7. *Androstrobos manis*. Cone lying obliquely across the bedding plane, which thus exposes an oblique transverse section. There is a central axis surrounded by three sporophylls. The corrugated upper surface of the inner part of the sporophylls is seen, while at the sides a few sporangia project. Photograph under xylol; V 25901, $\times 4$.

FIGURE 8. *Androstrobos manis*. Upper part of a cone; V 25898, $\times 2$.

FIGURE 9. *Androstrobos manis*. Type specimen showing the base and middle regions of the cone, and at the side a detached sterile scale. Where the surface is damaged a few sporangia are seen; V 25900, $\times 2$.

FIGURE 10. *Beania gracilis*. Inner membranes of a macerated seed. The dark egg-shaped body is the megaspore membrane, the cap at the top is formed by the cuticles of the nucellus and inside of the integument. The lining of the micropylar canal forms a point at the apex (see figure 14 for details); V 26778, $\times 4$.

FIGURE 11. *Androstrobos wonnacotti*. Under surface of a sporophyll showing the unopened sporangia in which a furrow marking the line of dehiscence is seen. Photograph under xylol; V 25850, $\times 10$.

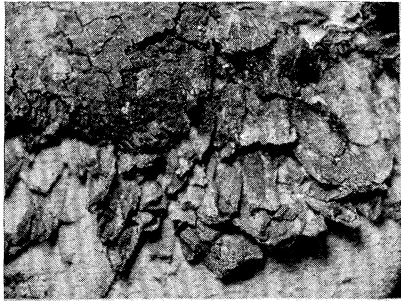
FIGURE 12. *Beania gracilis*. Sporophyll with one seed still attached showing the appearance usually caused by compression. A second sporophyll with a smaller seed lies to the right; V 25861, $\times 2$.

FIGURE 13. *Beania gracilis*. Axis and sporophyll; the sporophyll head shows the scar where the seed was attached, but the rest of it is missing; V 26776, $\times 2$.

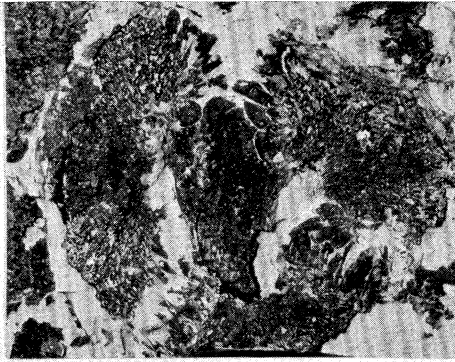
FIGURE 14. *Beania gracilis*. Upper part of the specimen shown in figure 10. Above and outside the black margin of the megaspore membrane is seen the margin of the cuticle of the nucellus, and around that the margin of the inner cuticle of the integument with an apical spike which is the lining of the micropylar canal; V 26778, $\times 10$.

FIGURE 15. *Androstrobos wonnacotti*. Type-specimen (see also figure 2); V 25850, $\times 2$.

Figures 8, 9 are drawings on photographs, the other figures are untouched photographs.



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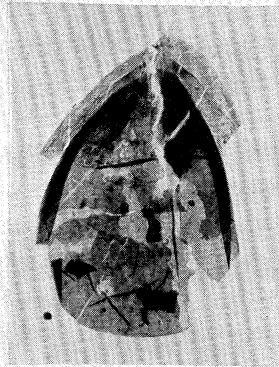
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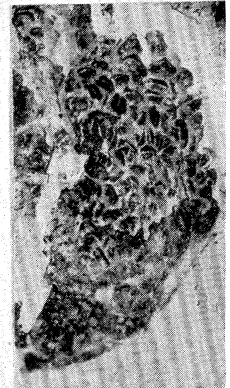
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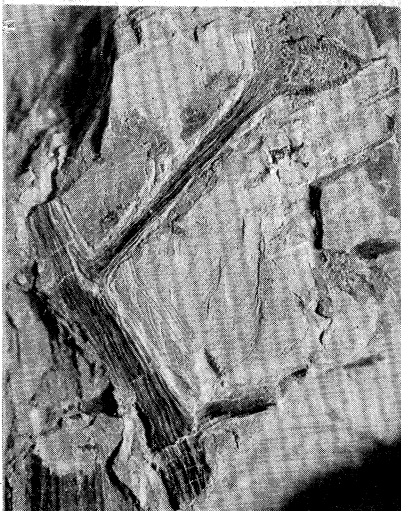
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PLATE 6. *Beania gracilis*

FIGURE 16. Immature cone; V 25862, $\times 1$.

FIGURE 17. Immature cone, the sporophyll on the left shows a print as though caused by the loss of a seed; V 23933, $\times 1$.

FIGURE 18. Smallest immature cone; V 23934, $\times 1$.

FIGURE 19. Transfer of counterpart of figure 18; V 23934 *a*, $\times 1$. Figures 21, 23, 24 were obtained from this specimen during the course of preparation.

FIGURE 20. Heads of sporophylls with immature seeds; V 24716, $\times 1$.

FIGURE 21. Oval head of sporophyll (from the outside). The substance was accidentally chipped near the base; from V 23934 *a*, $\times 6$.

FIGURE 22. Largest mature specimen, showing sixteen sporophyll stalks. Two sporophylls on the right without seeds are shown in figure 28; one sporophyll (on the left) still appears to bear a seed; V 23932, $\times 1$.

FIGURE 23. Seed of immature cone shown in figure 19. The micropylar papilla is labelled *M*; V 23934 *a*, $\times 10$.

FIGURE 24. Lowest sporophyll and seeds shown on the surface of the sporophyll head shown in figure 19. The cone axis is here horizontal. The seed on the right is well preserved but has lost its micropylar papilla, the other is damaged. The sporophyll stalk is seen below the right-hand seed; V 23934 *a*, $\times 10$.

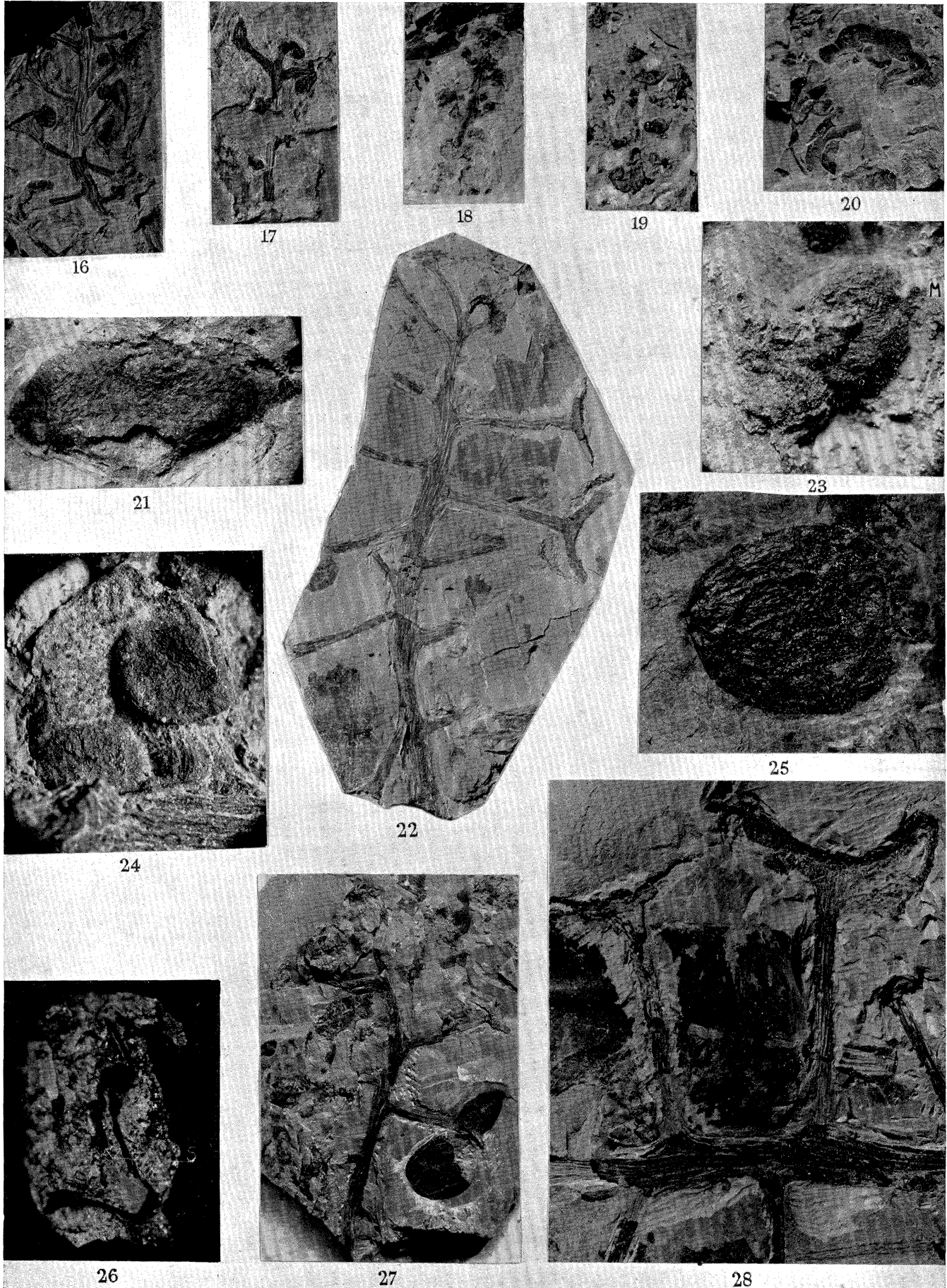
FIGURE 25. Isolated seed; the micropylar papilla is to the left; V 25897, $\times 3$.

FIGURE 26. Fragment from the base of a seed. The split has passed obliquely through the substance exposing the two sides of the stone (*S*) which is enclosed in a layer of flesh in which bulging thick-walled cells are visible; V 26779, $\times 10$.

FIGURE 27. Part of a mature cone. The only well-preserved sporophyll shows a seed (below), while above part of the oval head of the scale is bent into the bedding plane; V 24673, $\times 1$.

FIGURE 28. Details of part of figure 22 under different lighting; V 23932, $\times 2$.

Figures 16, 17, 22 are drawings on photographs, other figures are untouched photographs. The photographs were taken by Mr L. C. Willis.



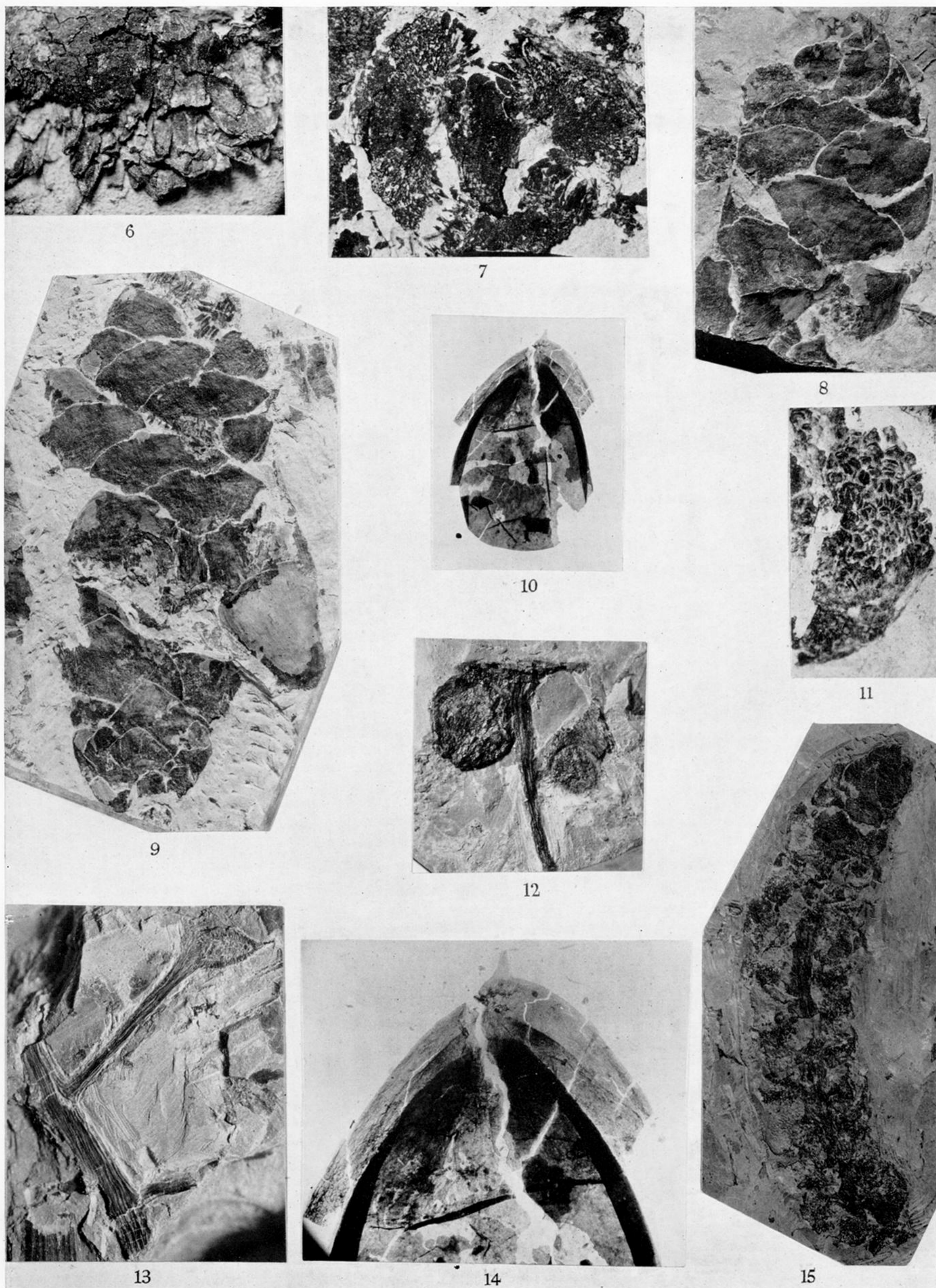


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FIGURE 13. *Beania gracilis*. Axis and sporophyll; the sporophyll head shows the scar where the seed was attached, but the rest of it is missing; V 26776, $\times 2$.

FIGURE 14. *Beania gracilis*. Upper part of the specimen shown in figure 10. Above and outside the black margin of the megaspore membrane is seen the margin of the cuticle of the nucellus, and around that the margin of the inner cuticle of the integument with an apical spike which is the lining of the micropylar canal; V 26778, $\times 10$.

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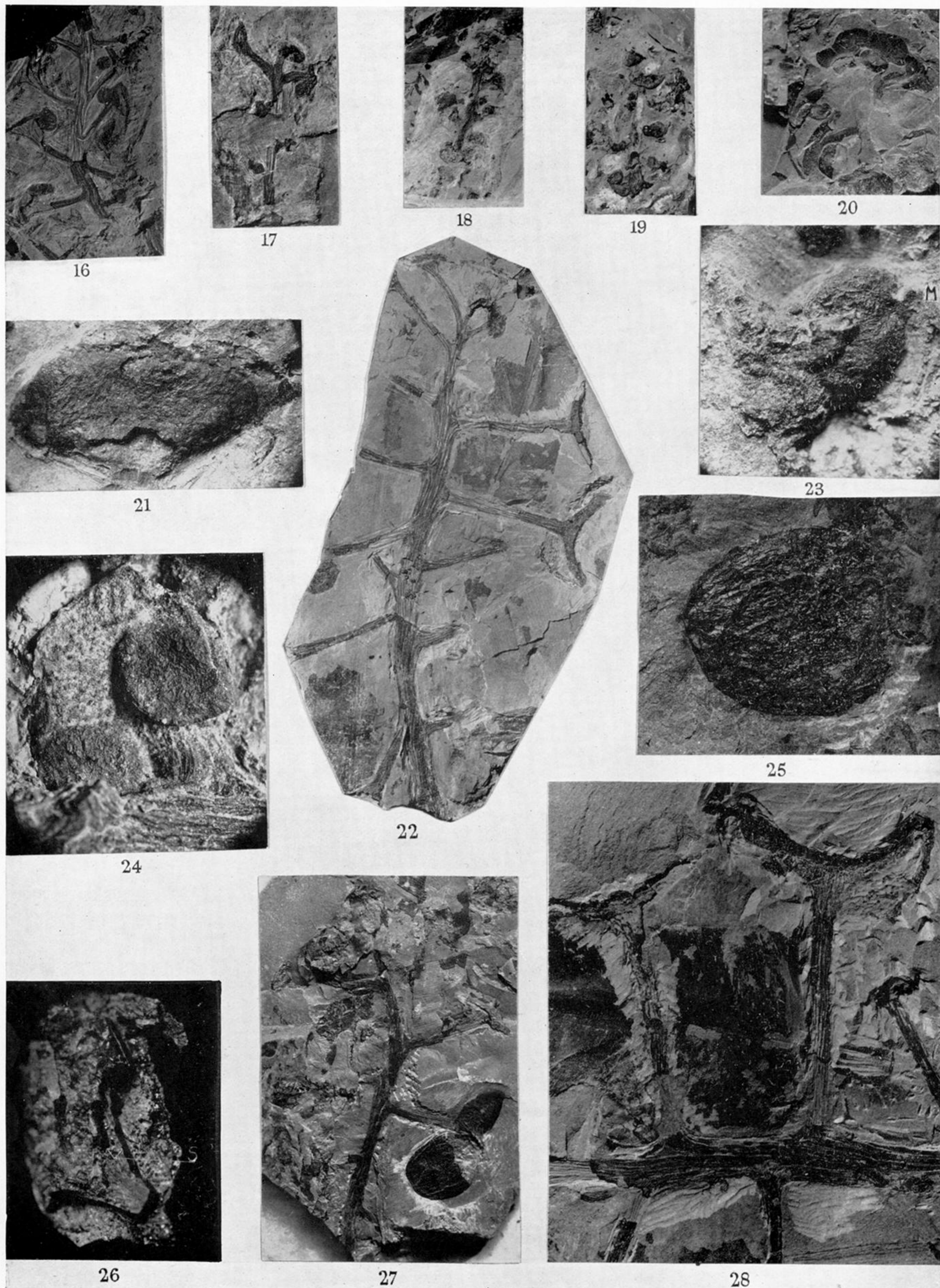


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