VII. *On some Pteridospermous Plants from the Mesozoic Rocks of South Africa.*

By H. HAMSHAW THOMAS, *M.B.E., Sc.D., University Lecturer in Botany and Fellow of Downing College, Cambridge.*

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INTRODUCTION.

This paper forms a further contribution towards the elucidation of the nature of the floras of Mesozoic times and of the affinities and systematic position of the plants composing them. When the author commenced work on this subject in 1910, a number of form genera of leaves had for many years been considered to represent the remains of ferns, though no fertile specimen had ever been found. It has since been shown that one of the most ubiquitous form genera, *Tæniopteris*, included several species which were the fronds of bennettitalean seed plants (THOMAS, 1915). Subsequently the form genus *Sagenopteris* was shown to be the leaf of a primitive angiospermous type, the Caytoniales, and not a fern frond (THOMAS, 1925). We now come to deal with a group of plants whose leaves have been known for a long time under the names of *Thinnfeldia* and *Lepidopteris*. Here again we have evidence that these somewhat fern-like leaves belonged to seed-bearing plants.

We are thus slowly approaching the time when we can make a closer estimate of the nature and affinities of the Mesozoic floras, but there are still many forms whose position remains to be ascertained but about which evidence is being accumulated. In this endeavour great importance attaches to the work of Dr. T. M. HARRIS (1926, 1932) on his collections from East Greenland. He has not only discovered several new reproductive structures, but his material has enabled him in many cases to confirm or to correct the conclusions of the present author, based on the somewhat earlier floras of South Africa and on the later floras from the Jurassic rocks of Yorkshire.

The advances, which have recently been made, are due to two modes of work—firstly, intensive and continued collection of material in the field by the investigator. In the past the field work has mainly been done by collectors, or stratigraphical geologists, who have frequently neglected the small and inconspicuous reproductive structures; these have consequently escaped attention, though really of the greatest interest.

The second line of advance has come from the detailed investigation of the cuticularized remains of fossil plants and the comparison of fossil and recent cuticles. All the evidence yet collected shows that the epidermal cells of the higher plants furnish us with characters which may be of equal value with other specific or in some cases generic features. As is shown by Dr. FLORIN'S (1931) great work on the recent conifers, the shapes of the epidermal cells and stomata are not developed at random, but are the outcome of the specific constitution of the plant, just as are the forms of the leaves or of the flower.

Owing to a recent paper (ODELL, 1932) on the use of cuticule characters in palæobotany, it must be observed that such features are not however more important than the other morphological characters of a plant. No diagnosis can be made on the evidence of a single feature whether vegetative or reproductive, but in comparing plants or plant structures it is important to find the maximum number of characters on which a comparison can be based. Although each individual feature, *e.g.*, the shape of the epidermal cells, may vary within wide limits, yet the coincidence in two plants of a number of characters which may vary independently indicates a high probability of relationship. Moreover, while floral characters differ in their diagnostic importance according to whether we are seeking to institute varietal, specific, or generic comparisons, so also must the different cuticle characters be used with discrimination.

The study of cuticle characters is of especial importance when we come to the work of assembling the different fragments of one original species found in a deposit of fossil plants. A long range of leaves of varying external outline with identical cuticles can be safely taken to represent the various leaves of a single species, while leaves of similar external shape with totally dissimilar cuticles must be regarded as specifically or generically distinct. Where we have leaves and reproductive structures the form of the epidermal cells, and especially the shape of the guard cells and their relation to the surrounding cells, often provides strong evidence of their origin from plants of the same type.

The Pteridospermæ formed one of the chief constituents in the vegetation of Upper Palæozoic times, but are usually regarded as having become extinct or almost extinct at the close of that period. The results described in this contribution show that similar plants formed an important element in the Triassic floras of the Southern Hemisphere.

The first suggestions that the group persisted into the Mesozoic period seems to have been based on the discovery in Jurassic rocks of strongly cutinized leaves, which were somewhat fern-like in shape, but which have never been found in a fertile state, although they have been collected in some abundance in many localities. SCHENK (1867) seems to have been the first to found the view that *Thinnfeldia* was probably intermediate between the ferns and the gymnosperms, while SEWARD (1910) grouped *Thinnfeldia, Lomatopteris, Cycadopteris, Dichopteris, and Callipteris* with form genera of the palæozoic pteridosperm fronds. Dealing with *Thinnfeldia,* in which he included the forms now known as *Dicroidium,* he remarked that it was by no means improbable that many of the species are closely allied to the Palæozoic pteridosperms, and that search should be made for fertile specimens and for evidence as to the association of fronds with seeds. When the cuticular structure of Mesozoic plants came to be systematically examined, it became clear that some of the European plants described as *Thinnfeldia, Cycadopteris,* and *Lepidopteris* had cuticles which were as thick and resistant as those of modern Gymnosperms, and so could scarcely have been derived from fern plants, whose cuticles, so far as is known, are always thin and little resistant to acid-oxidizing solutions. The details of the stomatal structure have not yet been fully described for this group, but GOTHAN (1912) has pointed out that there are some important differences between the cuticle structure of the Northern and Southern forms of the *Thinnfeldia* type. In the South African fronds the guard cells are but slightly sunken and show a structure which is comparable with that of some modern gymnosperms. The later work of ANTEVS, FLORIN, HIRMER, and HARRIS shows that at least a section of these well-known fronds may be regarded as more closely allied to gymnosperms than to the ferns.

One of the earliest discoveries of seed-like structures which seemed to be connected with fronds like *Thinnfeldia* was made by the author in 1915 near Roseberry Topping, in Yorkshire, but the early specimens were very difficult to interpret, and it was not until 1928 and 1929 that more complete examples were found. These structures will be described in the near future, but they must still be regarded as somewhat problematical.

We have now, however, obtained in South Africa seed-bearing branches which can be connected with the *Dicroidium* fronds (formerly known as *Thinnfeldia*) and a series of allied leaves. These structures, while unique in some of their morphological characters, seem generally similar in structure to such Palæozoic pteridospermous structures as *Lagenostoma* or to the forms described by CARPENTIER (1929) and BERTRAND (1926) as *Sphenopteris striata.* On examining them in detail it would appear that probably more than a dozen species are represented, which testifies to the importance of such plants as an element in the flora.

The seed-bearing branches are accompanied by structures bearing numerous microsporangia in which characteristic winged pollen grains were produced, and we have good reasons for considering them as the microsporangia of the same group. Here again we have a variety of forms, some similar in general appearance to the Palæozoic *Crossotheca,* one comparable with the type known as *Potoniea,* and others of a new form, but all variants on the *Crossotheca* or *Telangium* type of structure. As with the seed-bearing structures we are without evidence as to the mode of origin of these fertile branches, and it seems unlikely that they were borne on the ordinary vegetative fronds. Thus, while we have a group of plants comparable to the typical pteridosperms in their fern-like fronds, in their cupulate seeds and in their tufts of pollen sacs, they may have differed, according to our present ideas, in at least one important respect from the typical pteridosperms.

The Pteridospermæ, as at present understood, include a very comprehensive assemblage of forms, and the class may be further extended to receive all the plants which combined gymnospermous reproduction with the possession of compound fern-like fronds. A plant of this description is the Triassic form *Lepidopteris,* which also occurs in the Molteno beds of South Africa. A study has been made of the frond and seed-bearing structure of the Southern species of this type, which possesses some features of exceptional interest.

The author wishes here to acknowledge indebtedness to his wife, who was responsible for the collection in the field of the greater part of the material of the *Corystospermaceæ*, and who assisted in the preparation of this paper, and also to Mr. J. W. B. MacLean, the owner of the farm on which most of the material was collected, for his hospitality and valuable assistance. Dr. A. L. Du Toit gave invaluable advice and assistance in the arrangement of the collecting expedition, and the present paper is mainly due to his initial discovery of the Upper Umkomaas locality. A few months after we had made our collections this locality was also visited by Mr. O. A. Høeg, Keeper of the Botanical Section of the Trondheim Museum, who obtained another fine series of specimens. The author has been kindly allowed to examine these specimens, which include several of the forms described below and other new species of the same genera, which will be described later by their discoverer. The author wishes to record his grateful thanks to Mr. Høeg, Dr. T. M. Harris, Mr. W. N. Edwards, and especially to Professor Seward, for information and help of various kinds. Mr. W. L. Cuttle, of Downing College, has kindly suggested some of the new generic names here employed.

Part of the expenses of the journey to the Upper Umkomaas were defrayed by a grant from the Worts Fund of the University of Cambridge.

The specimens and slides figured in this paper are being added to the collections of the Geological Department of the British Museum (Natural History).

The Locality and Age of the Plants.

The material to be described was mainly collected from the Molteno beds of Natal. These beds lie at the base of the Stormberg Series, the uppermost division of the Karroo System, and include sandstones, grits, dark grey and black shales, together with oil shales and impure coal. Fossil plants appear to be locally abundant in the dark shales, but in many places are represented only by moulds, the original plant material having disappeared after leaving an impression in the fine-grained sediment. In a few localities, however, the altered plant tissue is still to be found in an exceptionally good state of preservation, and one of these was discovered by Dr. A. L. du Toit in the Upper Umkomaas Valley, on the slopes of the Natal Drackensberg. A small series of plants was collected and described by Du Toit (1927), and the author paid a visit to the district in 1929 for the initial purpose of getting further information about the plant described as *Sagenopteris longicaulis* Du Toit. The whole of the short time available during the visit was spent in collecting from the locality called by its discoverer "The Waterfall," which is now included in Mr. J. W. B. MacLean's farm named Burnera, situated at about 18 miles from Himeville. At this locality a stream runs over an exposure of black shales some 7 feet in thickness which underlie a bed of oil shale. The black shales are in places crowded with plant remains, and although a very limited volume of rock was examined, several hundreds of specimens of leaves, with some seeds and reproductive structures, were obtained. A much larger collection could have been made had it not been for the difficulties of transporting it from the remote spot.

The locality has been mapped and described by Du Toit (1916), who correlates the horizon of the oil shale with that of the Molteno and Cyphergat seams of the Stormberg in the Cape Province; the plants must therefore belong to a level somewhere near the middle of the Molteno Series.

The age of the Molteno beds has been recently discussed by Du Toit (1926, 1927), who concludes that its flora must be regarded "as essentially of Upper Triassic-Keuper age, but containing an element of Permian aspect . . . an element from the local Glossopteris flora, and a fairly large fraction mostly Filicales and Ginkgoales which migrated northwards to form a component of the Rhaetic assemblages of the Northern Hemisphere."

It must be noted, however, that the species which Du Toit regards as Rhaetic in type are mainly forms which cannot be identified with any great certainty at the present time from their external form, *e.g.*, species of *Cladophlebis* in a sterile condition, species of *Tæniopteris*, *Marattiopsis*, and *Pterophyllum*. After studying my own collection, and that of Du Toit in the Cape Town Museum, I consider that his *Thinnfeldia rhomboidalis* is almost certainly a *Dicroidium*, a type not found in the Northern floristic region, and his *Sagenopteris* is a *Glossopteris*. While it is true that the general aspect of the flora has some resemblance to that of the Upper Triassic of Europe and that several of the genera occur in Upper Triassic or even in Jurassic deposits in the Northern Hemisphere, there is little evidence that the Molteno beds were homotaxial with the Rhaetic or even with the Keuper of Europe. On the other hand, it now seems that the commonest elements in the flora were pteridosperms, and these are not very different from some of the forms from the Hermit Shale, Arizona, which White (1929) places near the top of the Lower Permian.

It may be asserted with confidence that the flora of the Molteno beds is Triassic in character, but it is very doubtful whether it is safe to go beyond this. Probably the vertebrate fossils in the Beaufort beds below, and in the Cave Sandstone beds above the Molteno series, afford a more exact means of dating this part of the Karroo series, and Professor D. M. S. Watson in a letter to the author suggests that from such evidence the Molteno beds should be regarded as Middle Triassic in age.

The Material.

The material from our collections which is here described consists of about 30 specimens of seed-bearing structures, 25 specimens of pollen-bearing structures, and a considerable number of isolated seeds. Each piece of the matrix containing a specimen has been given a number, in several examples part of the remains of the plant is divided between one hand-specimen and its counterpart. The plant remains are almost invariably well preserved as brittle black structures lying in the fine grained shaly matrix. They have undergone a certain amount of compression and the surfaces are often somewhat wrinkled, but they are very little decayed, and the shapes of the epidermal cells can often be seen with the aid of the binocular microscope. In most specimens the plant remains were more or less embedded in the matrix below the surface of the hand specimen, but by carefully dissecting away the matrix with very finely pointed needles it was possible to expose most of the external structure. This process of laying bare the plant remains by removing successive particles of the matrix is a laborious one, but it may result in a specimen which was almost as complete as though it had been dried and glued on to an herbarium sheet. The remains of the plant tissue could usually be detached readily from the matrix, though sometimes where the cuticle was thin WALTON'S transfer method has been used. Treatment of the fragments so obtained with potassium chlorate and strong nitric acid followed by an alkaline solution, resulted in the liberation of the cuticularized membranes. Preparations were made of the stalks from all except one of the forms, of the inner and outer epidermis of the cupules, of the seeds, and of the microsporangia, the best of these preparations have been photographed and the figures given below have been made by tracing over the cell outlines seen on the photographic prints with waterproof ink and subsequently bleaching out the print.

We have thus exceptionally good material for the study of these new structures, and the generic characteristics can be established with certainty. The forms studied are now associated in a new family.

FAMILY—CORYSTOSPERMACEÆ.*

Seed plants with forking fronds of varying character; inflorescences unisexual, 2–6 cm. in length, consisting of a main axis with lateral branches; seed bearing inflorescence with lateral branches produced in the axils of bracts and pedicelate cupules; cupules recurved, campanulate or bivalved, containing one seed; seeds ovoid or elliptical with a curved bifid micropyle projecting from the cupule; branches of male inflorescences without subtending bracts, enlarged towards their apices and bearing numerous pendulous synangia, containing winged microspores.

General characters.—The male and female structures are associated for the following reasons:—(1) They occur closely associated in the same bed, and they are comparable in size, though the microspore bearing branches are smaller and less heavily cutinized; (2) one of the characteristic seeds was found to contain within it, in the position which would be occupied by the pollen chamber, at least eleven of the pollen grains characteristic of the male structures; (3) the cuticular characters of the axis and branches of the male and female structures are closely comparable, and in some specimens almost

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* From Greek *κορυστής* = a helmet wearer. This name is chosen instead of one derived from the generic name of a single organ because the family includes form genera of various kinds, *i.e.*, leaves, male organs and seed-bearing structures.

identical except for the amount of thickening; (4) the characteristic microspores are frequently found adhering to hairs on the inside of the cupules.

The reproductive structures are associated with the fronds on account of their close association, and because of the similarity between the cuticles of the cupules and those of the foliar lamina and between the cuticles of the petioles and seed bearing branches.

The Female Inflorescences.

These may be described as the fertile branches, whose ultimate divisions terminate in recurved cupular structures containing seeds. The remains of the seeds are not seen in all cupular structures, for sometimes the specimen has probably shed its seeds before preservation, while in others they may have aborted, but it seems clear that these structures are all of the same type. The more complete specimens show a main axis often bearing a pair of bracts near the base and giving off branches right and left in one plane. These branches appear at first sight like the pinnæ of a sporophyll, but they are generally seen to arise in the axils of bracts. They either fork at their apex into equal halves, or bear a terminal cupule, in some species they bear a pair of bract-like structures which will be termed bracteoles, and they often give rise to further branches lying in the same plane, which are not subtended by bracts and which may have an opposite or alternate arrangement. These ultimate divisions terminate in cupules. The complete structure must then be described as an inflorescence, but it resembles a sporophyll both in the restriction of the lateral branches and appendages to one plane, and also in the fact that the epidermal cells of the axis, as indicated by the cuticle preparations, often differ on the two sides. The exact structure of the cupules is difficult to determine. Nearly all the specimens have been compressed and flattened out in the plane of the branching and they appear to have been basin-shaped, campanulate, or urceolate structures springing from the ultimate branches or pedicels with their mouths or openings facing the base of the inflorescence. In some specimens there are indications of one or two lateral clefts, obscured owing to the flattening, but which probably divided the cupule into two valve-like parts. Each cupule apparently contained one seed, whose mode of attachment is not known. When young the micropyle projected from the opening of the cupule, it was bifid and displayed a characteristic lateral curvature which no doubt facilitated pollination. The mature seeds projected farther from the cupules, they were probably ovoid or ellipsoidal structures generally about 5 mm. long. They were probably flattened before preservation. The seeds are often found isolated, but can be readily identified by their curved micropyle which is more or less bifid at the tip.

Some of the cupules were probably fleshy, their external surface shows a series of wrinkles, while their cuticles are comparatively thin and the remains of the vertical walls of the epidermal cells indistinct, but in others the surface is smooth and the cuticle thick, its cellular structure being very distinct. Cuticle preparations show that stomata are fairly numerous on the external surface and occasionally occurred on the inner surface.

The stomata are surrounded by from four to six unspecialized subsidiary cells, one of which occurs at each pole, while there may be one or two at each side. The guard cells are often slightly sunk below the surface, but the pore can usually be clearly seen, and it is bordered by areas where the cuticle is extremely thin. This thin area is bounded by bands or lines of cutinized material; they have a somewhat characteristic shape, and probably represent the cuticle from the sides of the rectangular cavity in which the stomata are sunk. On either side of the pore this material usually forms a well-defined crescentic band tapering to a fine point at each end; in some specimens the ends of the adjacent points appear joined by a transverse line of cutin, while at times a thin line appears to connect the crescentic bands across the guard cells just to the inside of the ends of the pore, fig. 24.

The appearance of the stomata is generally similar to that figured by FLORIN (1931) for *Callipteris conferta* Br., and it would be explicable on the assumption that the original stomata had a structure resembling that figured by FLORIN for *Lyginodendron Oldhamium* (BINNEY) (FLORIN, 1931, p. 505, text-fig. 107).

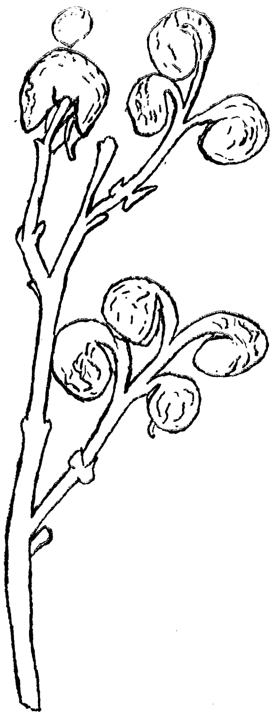

FIG. 1.—*Umkomasia Macleani* sp. nov. Inflorescence. No. U11. × 2.

In two genera the epidermis from the inside of the cupules had a very delicate cuticle on which there are few stomata and no traces of hairs. In the cupules of another genus the inner epidermis had a fairly thick cuticle plentifully covered with the bases of the simple hairs which must have formed a felt-like covering, stomata were also present.

Range of Structure.

In the suite of specimens available there is considerable variation in almost every part. The idea first entertained that we were dealing with one genus (THOMAS, 1931)* had to be abandoned when a detailed examination of the material was made, and it is clear that we have a number of forms, but the separation of these forms is a matter of considerable difficulty. Some of the forms are very distinct in almost every character and are placed in separate genera, others are less well marked and appear to be connected by intermediates. Since all the plants from which the material was derived probably grew together, it is quite possible that some of the specimens represent hybrids or segregates resulting from the crossing of original more

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* P. 663, fig. 8. In this first communication all the forms were included in the genus *Umkomasia*.

distinct parent species. The chief characters which may be used in the separation of species are, (*a*) the form of the cupules; (*b*) general habit and mode of branching; (*c*) the form of the epidermal cells as revealed by cuticle preparations; (*d*) the form and arrangement of the bracteoles and bracts. We have no idea of the extent to which any of these characters may have varied on a single plant or within a single species, but in comparing the different forms with regard to their general habit and mode of branching it must be remembered that we are here dealing with inflorescences and not with vegetative structures. Consequently, we may consider that differences in the mode of branching, in the length of the pedicels and internodes, and in the development of the bracts will more probably be indications of specific differences than of differences in the physical conditions of the environment of each form. As all the forms were found together within the space of a few feet of rock, it is likely that they grew together in the same habitat. For the same reason we have grounds for considering that such differences as occur in the cuticle structure are not habitat variations. Our inflorescences are the remains of mature structures probably produced in an exposed position on the plant, and are therefore not merely sun and shade forms of the same structure. Within one species there was no doubt some variation in the elongation of the branches and in the size of the epidermal cells, while the cuticle structure in different parts of the same organ may have varied, but when we meet with simultaneous variations in *all* the diagnostic characters it becomes unlikely that the specimens showing them were derived from plants of the one and the same type.

The variation in form may be appreciated by comparing the different specimens side by side, and to facilitate comparison the figures accompanying the subsequent descriptions are drawn on the same scales. The complete specimens are shown twice magnified, while the drawings of individual cupules show them enlarged five times. With a few exceptions, the figures of the cuticles were made directly from photomicrographs with a magnification of 120 diameters.

The present state of our knowledge of cuticle structure certainly indicates that distinct differences in the form of the epidermal cells may be taken as an indication that we are dealing with distinct forms of plants, but these differences do not show whether such forms are to be regarded as distinct genera, species, or varieties.

In view of the fact that a considerable number of different forms of leaves occur in the same bed which must be regarded as derived from the same type of plants which furnished our female inflorescences, it would appear likely that we have to deal with a number of species. The best plan seems therefore to describe as separate species those forms which appear to be readily distinguishable and are represented in my collection by fairly complete material, and to add notes on the other specimens which are not so complete or so well defined.

It is proposed to divide the specimens in the present collection into three genera, distinguishable by the form and character of the cupules; the study of the cuticle structure of the axis and cupules supports this division. *Umkomasia* has a two-lobed cupule without a lining of hairs, *Spermatocodon* has a campanulate cupule also without hairs, while *Pilophorosperma* has a hood-like cupule thickly lined with hairs on its inner surface.

Description of new Genera and Species.

Umkomasia gen. nov.

Diagnosis.—Inflorescence branching in one plane, with pedicelate cupules enclosing seeds ; cupules deeply divided into two lobes by clefts in the plane of branching ; inside of cupules without hairs or hair bases.

Type species *Umkomasia Macleani.*

Umkomasia Macleani sp. nov., fig. 56, Plate 23, and figs. 1–4.

Diagnosis.—Main axis elongated, with distant alternate branches, lateral branches with two opposite small saccate bracteoles, dichotomously forked at the apex into two pedicels bearing cupules and producing one or two stalked cupules just below ; pedicels short and strong ; cupules ellipsoidal, bivalved with a well-marked fissure extending up to the pedicel and another on the opposite side of the cupule ; margin of cupule entire ; surface of cupules much wrinkled, smooth between the ridges ; seeds with long tapering micropyle ; cuticle of the axis stout, differing noticeably on the two sides ; axis and cupules glabrous.

Type-specimen No. U11.

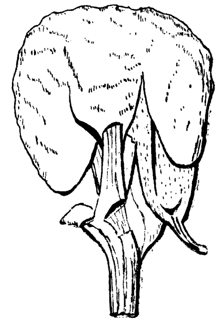

FIG. 2.—*Umkomasia Macleani* sp. nov. Cupule and seed seen from the side of the pedicel. No. U11. × 5.

Description.—This species is founded on the well-preserved specimen shown in fig. 56, Plate 23, and fig. 1. The main axis, 3·5 cm. long, gave cuticular preparations which suggests a distinctly dorsiventral structure, figs. 3 (*a*), (*b*). Small bracts, 1 mm. long, subtend the alternate lateral branches and remains of a pair of similar structures occur on the main axis. The lateral branches bear a pair of small bracteoles with saccate bases, fig. 4, and two pairs of cupules borne on short thick pedicels.

The elliptical cupules are well preserved ; the form of the epidermal cells from the outer and inner surfaces is shown in fig. 3 (*c*), (*d*). Stomata occur on both sides, and there are no traces of papillæ or hair bases. The bi-valved form of the cupule can be made out owing to the slight relative displacement of the two halves in some places. The cupule, fig. 2, shows part of an enclosed seed with its curved micropyle ; the testa is smooth, but has a prominent longitudinal ridge, which may indicate that the seed was originally flattened.

This species is readily distinguishable and is named after Mr. MacLean, the owner of the locality, and the collector of the first specimen seen by the author.

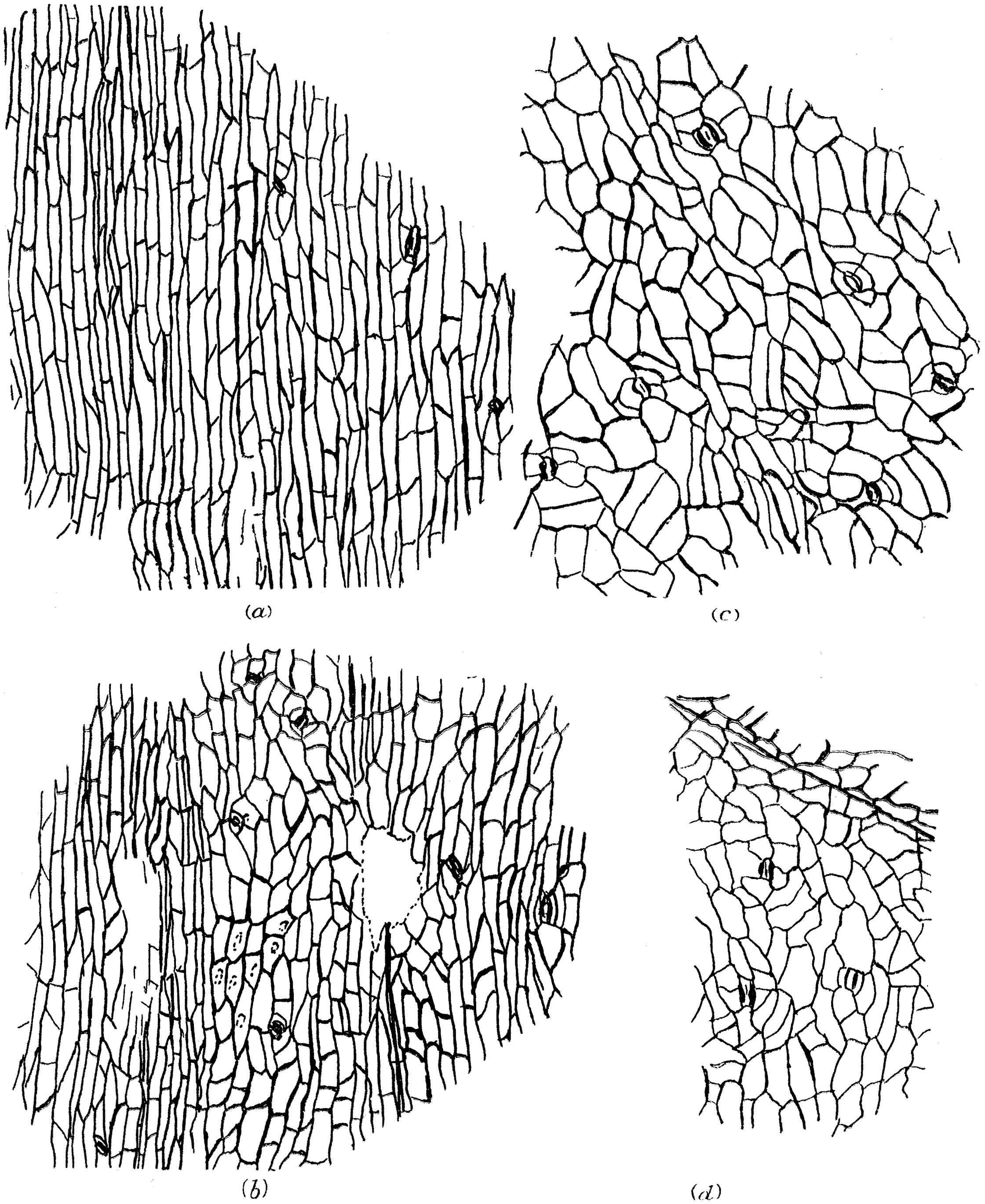

FIG. 3.—*Umkomasia Macleani* sp. nov. Epidermal cells seen in cuticle preparations from :—Axis (upper side), *a* ; axis (lower side), *b* ; cupule outer epidermis, *c* ; cupule inner epidermis, *d* ; all × 120. *a* and *b* slide No. 7, *c* No. 6, *d* No. 5.

Umkomasia verrucosa sp. nov. fig. 57, Plate 23, and figs. 5–8.

Diagnosis.—Main axis stout, apparently divided above into two more or less equal branches, branching profuse towards the apex; pedicels short and stout; cupules forming two valves united at their base but with deep fissures on either side, spherical to ovoid, external surface verrucose; cuticles of stalk with alternating bands of narrow and wider cells; few sunken stomata; outer epidermis of cupule with very numerous stomata, inner epidermis very thin.

Type-specimen No. U140 and 144 (counterpart).

Description.—This form has the characteristic habit shown in fig. 57, Plate 23, and fig. 5, with an axis 2·5 mm. broad. A pair of sub-opposite bracts occurs on the axis, and its cuticle is illustrated in fig. 7 (*b*), the gap in the centre of this figure represents the lateral margin of the stalk. The branching is very distinct from that of the preceding species. A bract subtending a lateral branch is shown in fig. 8, this appears to have a thick base passing into a toothed spathulate structure about 3 mm. long, similar to that seen in *Pilophorosperma natalense*. No trace of bracteoles can be found. A cuticle from a pedicel with sunken stomata is shown in fig. 7 (*a*).

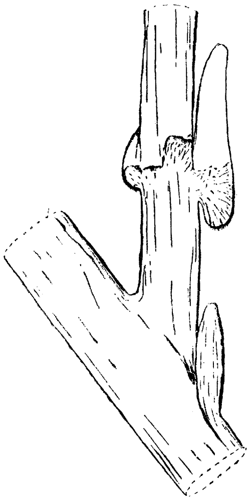

Fig. 4. — *Umkomasia Macleani* sp. nov. Main axis with base of lateral branch showing subtending bract and bracteoles. No. U11. × 10.

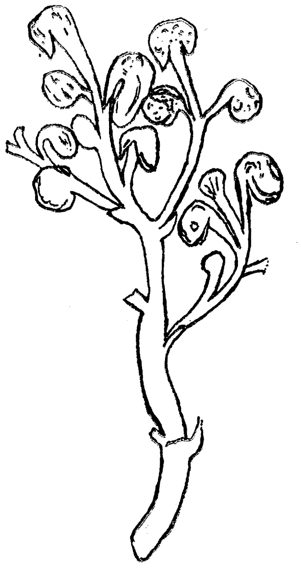

Fig. 5.—*Umkomasia verrucosa* sp. nov. Inflorescence. No. U140. × 2.

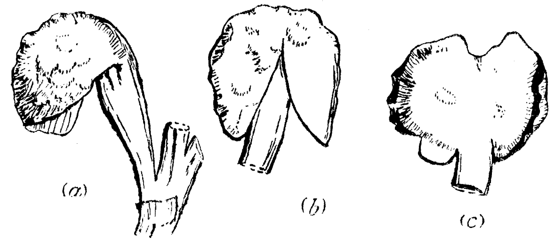

Fig. 6.—*Umkomasia verrucosa* sp. nov. Cupules seen from different sides. *a*, normal appearance. *b*, side view. *c*, interior, the seed has been shed. *a* and *b* from No. U140, *c* from No. U144. × 5.

The remains of the cupules are thick rounded structures of the form shown in fig. 6, many of them are broken. They must have been ovoid or spherical, with a verrucose surface and the two valves are often clearly seen. In one place the inside of the cupule, is seen, fig. 6 (*c*), but there is no certain trace of the seed. The external cuticles from the cupules are thick and give good preparations, fig. 7 (*c*), while the inner cuticle is extremely thin, fig. 7 (*d*).

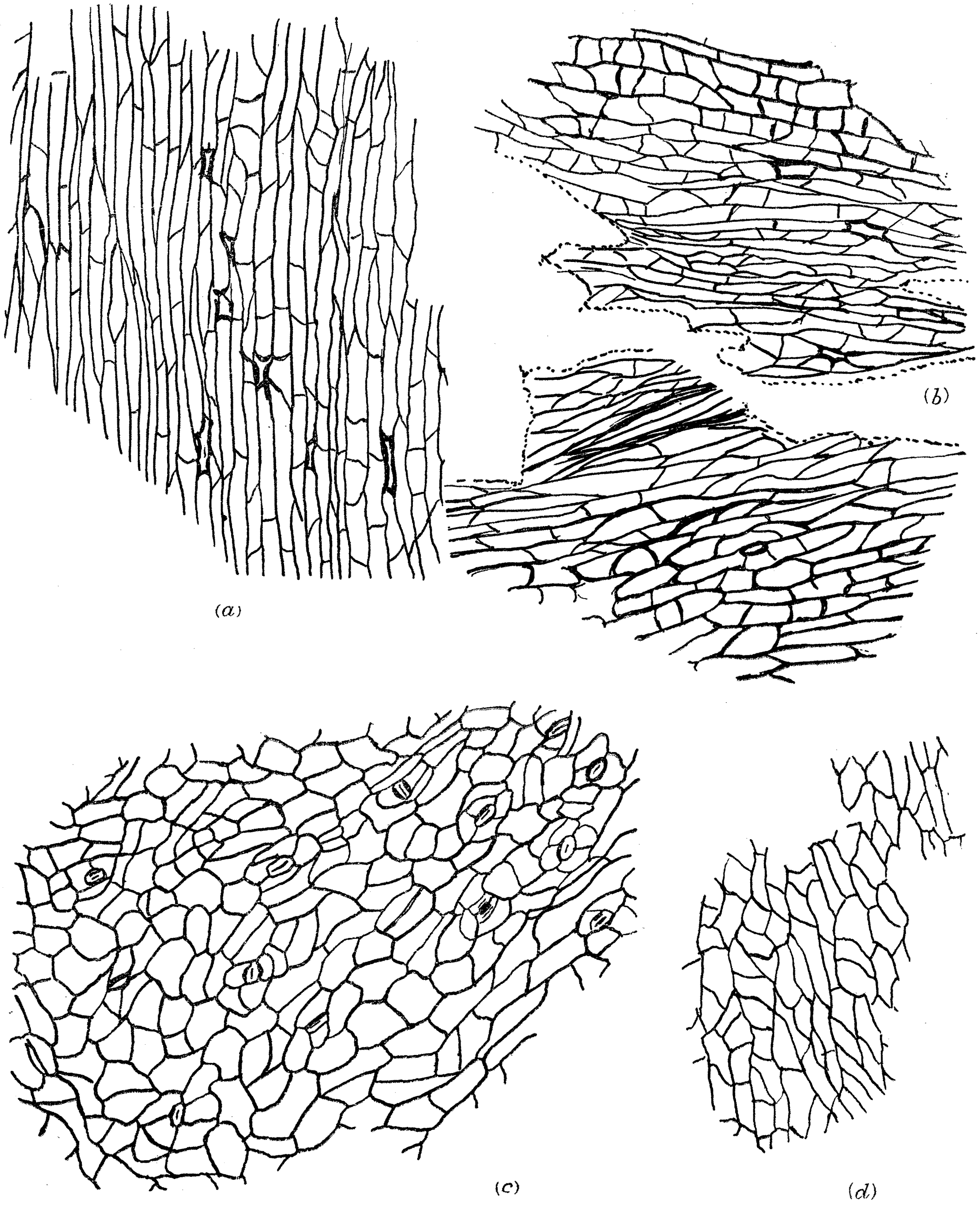

FIG. 7.—*Umkomasia verrucosa* sp. nov. Epidermal cells. *a*, from pedicel. *b*, from axis. *c*, cupule, outer side. *d*, cupule, inner side. All × 120. *a*, slide No. 4, *b*, No. 3, *c* and *d*, No. 1.

This species resembles *Umkomasia Macleani* in the form of its cupules and in the absence of hairs from the inner epidermis of the cupules. It differs markedly from that species in its habit, in the mode of termination of the lateral branches, and the bracts. The cuticles are distinguishable but have several features in common.

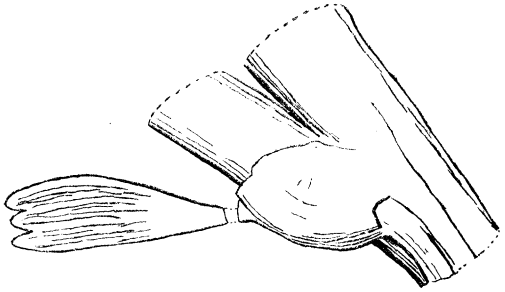

FIG. 8.—*Umkomasia verrucosa* sp. nov. Main axis with lateral branch in the axil of bract. × 10. No. U140.

*Pilophorosperma** gen. nov.

Diagnosis.—Inflorescences with branches in one plane, bearing recurved, helmet-shaped or campanulate cupules ; cupules often with one cleft on the side adjacent to the pedicel ; inner surface of cupule covered with hairs arising from thickened bases.

Type species *Pilophorosperma granulatum.*

Synopsis of the species of *Pilophorosperma.*

I.—Branches spreading, lateral branches with three or more pedicellate cupules.

(*a*) Bracteoles conspicuous.

P. granulatum, cupules semicircular, cuticles with abundant papillæ.

P. natalense, cupules circular or elliptical, cuticles with short hairs, papillæ few.

(*b*) Bracteoles absent (or small).

P. geminatum, cupules in partly fused pairs.

P. burnerense, cupules small, single, basally attached to pedicels.

II.—Branches few, lateral branches dichotomizing at the apex to form the pedicels of the cupules.

P. gracile, pedicels short, cupules circular.

P. paucipartitum, pedicels long, cupules hoodlike.

III.—Branches very short, cupules crowded, each with a thicker and a thinner portion.

P. crassum, cuticle very thick, cells papillate, cupules large.

P. costulatum, cuticles thin with small papillæ and hairs, ridged seeds remaining long in the cupules.

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* From Greek πιλοφόρος = wearing a hair-lined helmet.

Pilophorosperma granulatum sp. nov., fig. 58, Plate 23, and figs. 9–11.

Diagnosis.—Branching sparse; lateral branches bearing two lateral and a terminal cupule on long pedicels; bracts and bracteoles conspicuous; bracteoles falcate; cupules elliptical to semicircular, their longer axis at a wide angle to the pedicel to which they are attached laterally, surface granular, margin of opening undulating; seed smooth, micropyle strongly curved and bifid; outer surface of stem and cupule covered with minute papillæ borne on almost every cell; inner surface of cupule with long pointed hairs.

Type-specimen No. U91. Para-type No. U4.

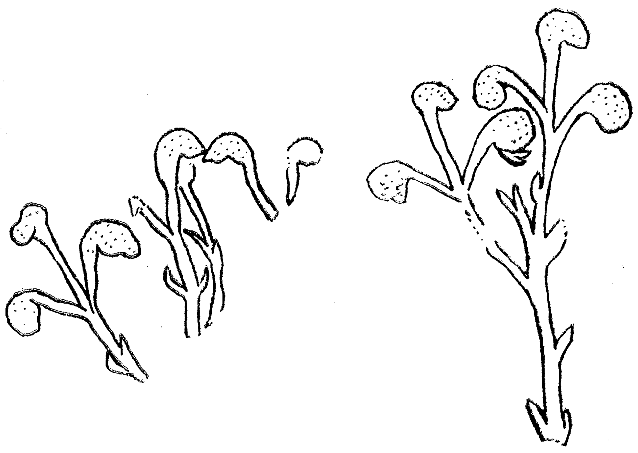

(*a*) (*b*)

FIG. 9.—*Pilophorosperma granulatum* sp. nov. Inflorescences. *a*, No. U91. *b*, No. U4. Both × 2.

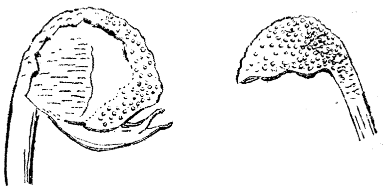

(*a*) (*b*)

FIG. 10.—*Pilophorosperma granulatum* sp. nov. Cupules, showing mode of attachment to pedicels. *a*, specimen No. U4, with projecting micropyle. *b*, No. U91. Both × 5.

Description.—The type specimen, fig. 58, Plate 23, and fig. 9 (*a*), shows parts of four lateral branches with cupules in a good state of preservation, while specimen No. U4, fig. 9 (*b*), shows a specimen with the main axis 17 mm. long, and remains of a seed, but the preservation is not so good. At the base of the axis is a pair of bracts, while the apex appears to be also terminated by a pair of smaller bracts. The falcate bracteoles, 2 mm. long, which occur on the branches are a characteristic feature. The pedicels are relatively long and slender (3 mm. long, 0·5 mm. broad).

The surface of the axis was composed of cells with strongly convex surfaces and blunt papillæ. The cuticle structure is shown in fig. 11*a*, *b*; most of the cells were well cutinized and papillate, but a band of thinner, less regular cells including stomata occurs (11*b*).

The cupules are more or less semicircular when well preserved, fig. 10, their surface is granular. Their outer epidermis, fig. 11 (*c*), was composed of isodiametric cells with microsinuous walls and short thickened papillæ, among which stomata are but few. The inner epidermis shows microsinuous walls, frequent bases of hairs and

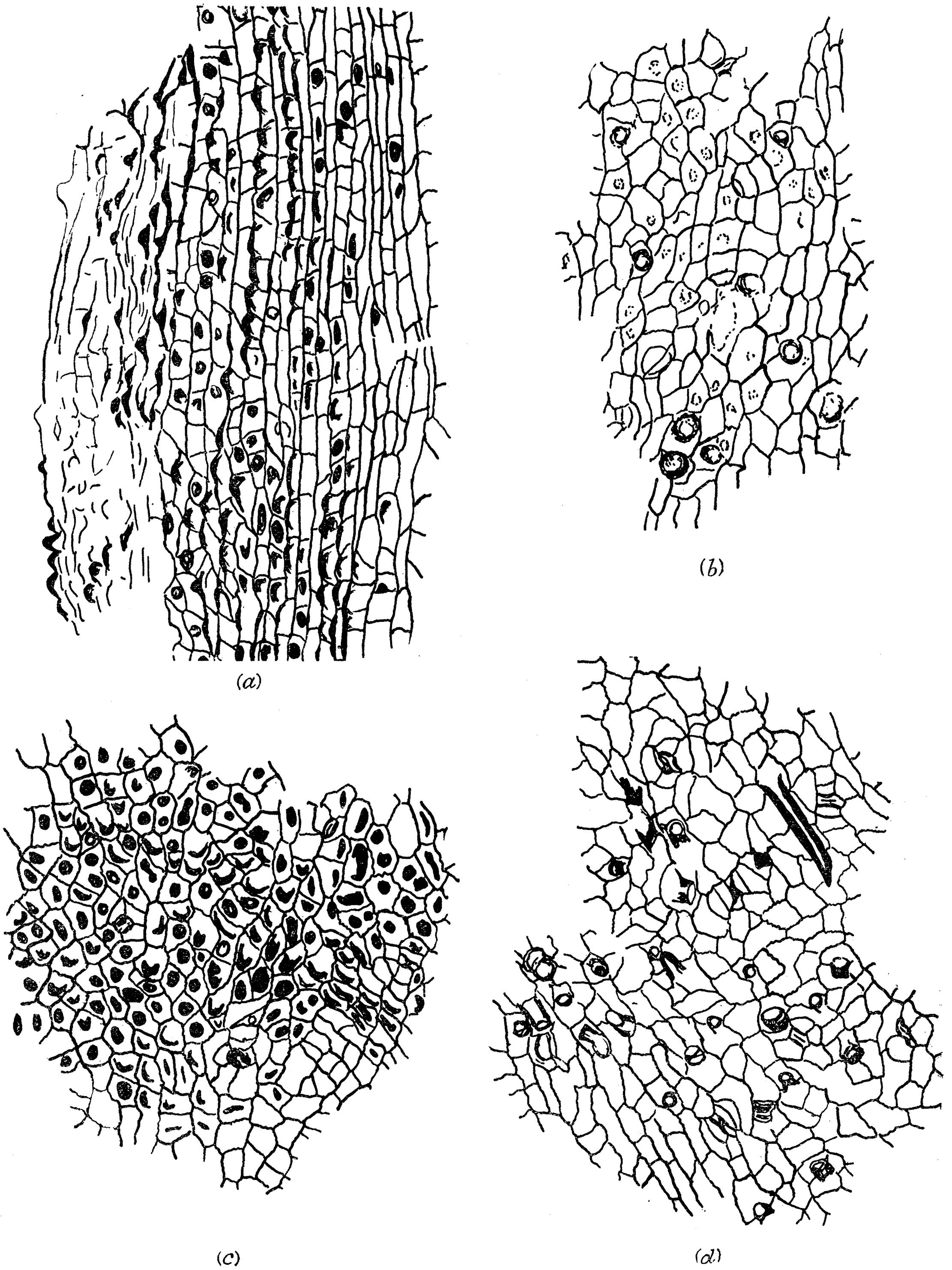


Fig. 11.—*Pilophorosperma granulatum* sp. nov. Epidermal cells. *a*, usual type found on the axis. *b*, part of stomatal band on axis. *c*, outside of cupule. *d*, inside of cupule. All × 120. *a*, slide No. 30. *b*, No. 25. *c*, No. 24. *d*, No. 26.

occasionally an attached pointed hair, fig. 11 (*d*). Part of a seed is seen in U4, with a characteristic micropyle, fig. 10 (*a*).

This species can be readily distinguished by its bracteoles, by its papillate epidermis and the form of its cupules.

Pilophorosperma gracile sp. nov., fig. 59, Plate 23, and figs. 12, 13.

Diagnosis.—Main axis straight and slender, bearing two pairs of sub-opposite lateral branches in the axils of falcate bracts ; lateral branches forking apically to form short pedicels ; cupules circular, occurring only at the apex of the lateral branches ; margin of opening smooth or sinuolate ; cuticle of axis thin, cells elongate, mostly rectangular and with small papillæ ; outer cuticle of cupule thin, wrinkled, cells polygonal, mostly, with short pointed hairs or papillæ ; stomata numerous.

Type-specimen No. U123 and U115 (counterpart).

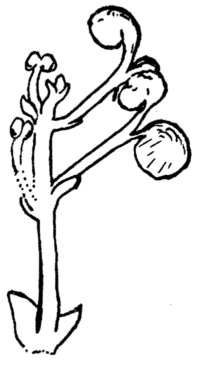
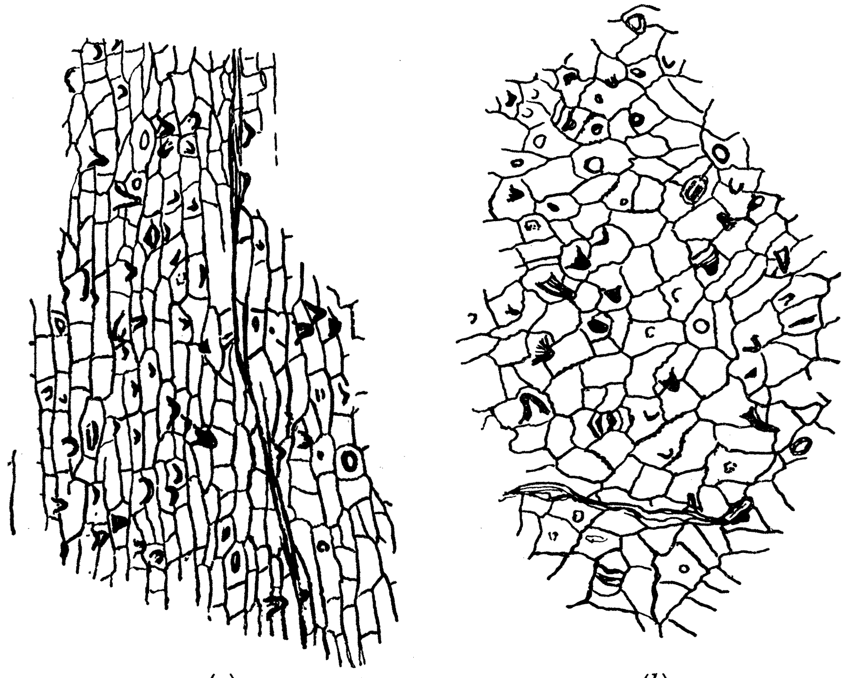


FIG. 12. — *Pilophorosperma gracile* sp. nov. Inflorescence showing aborted branches on one side No. U123. × 2.



(*a*) (*b*)

FIG. 13.—*Pilophorosperma gracile* sp. nov. Epidermal cells showing papillæ. *a*, axis ; *b*, outside of cupule. × 120. *a*, slide No. 12. *b*, No. 11.

Description.—The habit of this specimen, fig. 12, is characteristic, but the branches on one side appear to be aborted and terminate in pairs of sessile rudimentary cupules. The main axis is 2 cm. long, and has a pair of broad triangular bracts at its base, while there appears to be a bud-like structure with a pair of bracts at the apex, though the details are not clearly visible. The cuticle of the axis is shown in fig. 13 (*a*).

The lateral branches are about 7 mm. long, and the pedicels of the cupules not more than 2 mm. long. The mature spherical cupules are 4 mm. in diameter, their surface is slightly wrinkled ; their outer cuticle is illustrated in fig. 13 (*b*), some of the walls are minutely sinuous, short papillæ and numerous stomata are seen. No seeds are visible.

This species is distinguishable by its habit and by its thin papillate cuticles.

Pilophorosperma geminatum, sp. nov., fig. 14.

Diagnosis.—Axis with many elongated slender branches, which terminate in pairs of sessile cupules ; subtending bracts broad, their apices blunt ; cupules more or less

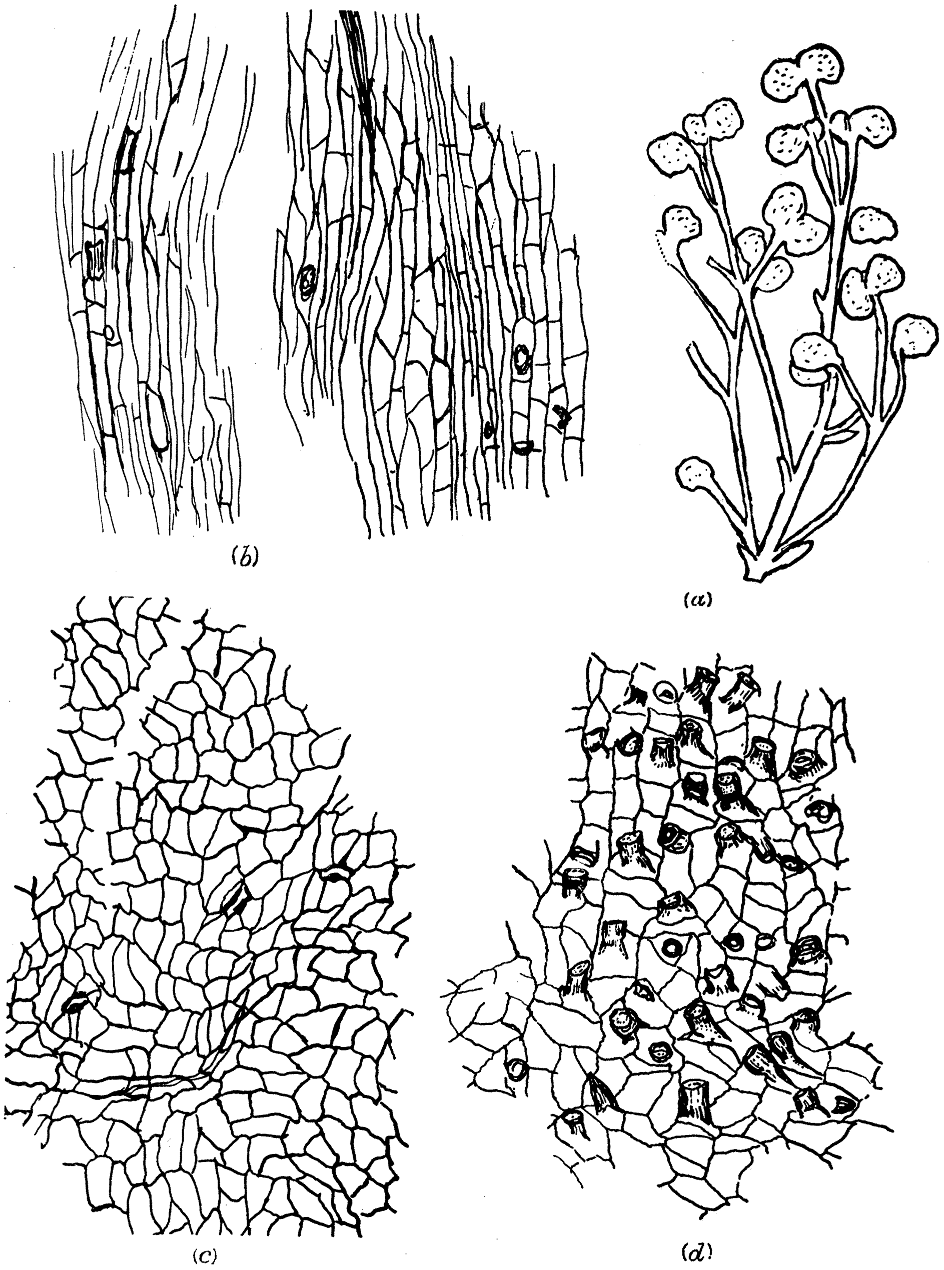


FIG. 14.—*Pilophorosperma geminatum* sp. nov. *a*, inflorescence, × 2. *b*, delicate cuticle of axis. *c*, cuticle from outside of cupule. *d*, cuticle from inside of cupule with large bases of hairs. × 120. *a*, specimen No. U109. *b*, slide No. 20. *c*, No. 22. *d*, No. 21.

circular with large opening; cuticle of stalk very thin, cells mostly narrow and much elongated, some stomata and circular hair bases; outer epidermis of cupule composed of small cells, inner epidermis with very numerous hair bases and some short acutely pointed hairs.

Type-specimen No. U109.

Description.—This form has the very distinct habit shown in fig. 14 (*a*). The branches are relatively long and slender. The fracture of the main axis sometimes reveals a central core with a striated surface, probably the remains of the stele. The outside of the axis shows fine longitudinal ridges and grooves, probably the result of contraction. The cuticle was exceptionally thin and it was impossible to get good preparations. Fig. 14 (*b*) shows a fragment with cells of varying width, a few stomata and some hair bases. The lateral branches are subtended by bracts about 4 mm. long and 1 mm. wide, but no traces of bracteoles are seen.

The cupules appear to have been produced in pairs at the ends of the branches, but their structure cannot be made out so readily as in the other forms, and no seeds were seen. The cuticle of their outer epidermis, fig. 14 (*c*), is without papillæ or hairs, and stomata are few. The inner epidermis has microsinuous walls, a few stomata and very numerous thickened bases of large hairs, fig. 14 (*d*).

The pairs of cupules, the habit and the cuticle structures are the distinguishing characters of this form.

Pilophorosperma paucipartitum, sp. nov., fig. 63, Plate 23, and figs. 15–17.

Diagnosis.—Main axis slender; lateral branches short, forking to form two long pedicels; bracts on main stem with rectangular cells having sinuous walls; cupule helmet-shaped; outer cuticle of cupule showing cells with minutely sinuous walls and small thick superficial spots, stomata few; hair bases on inner cuticle numerous.

Type-specimen No. U143.

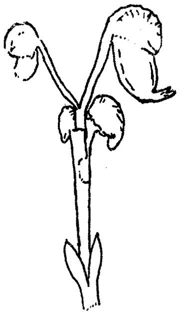


FIG. 15.—*Pilophorosperma paucipartitum* sp. nov. Inflorescence. No. U143. × 2.

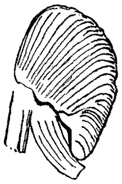


FIG. 16.—*Pilophorosperma paucipartitum* sp. nov. Small cupule with young seed. No. U143. × 5.

Description.—The type specimen shown in fig. 63, Plate 23, and fig. 15 is clearly incomplete, but shows features which distinguish it from other forms. The branching is distinctive, for the lateral branch appears to be very short before forking to give a

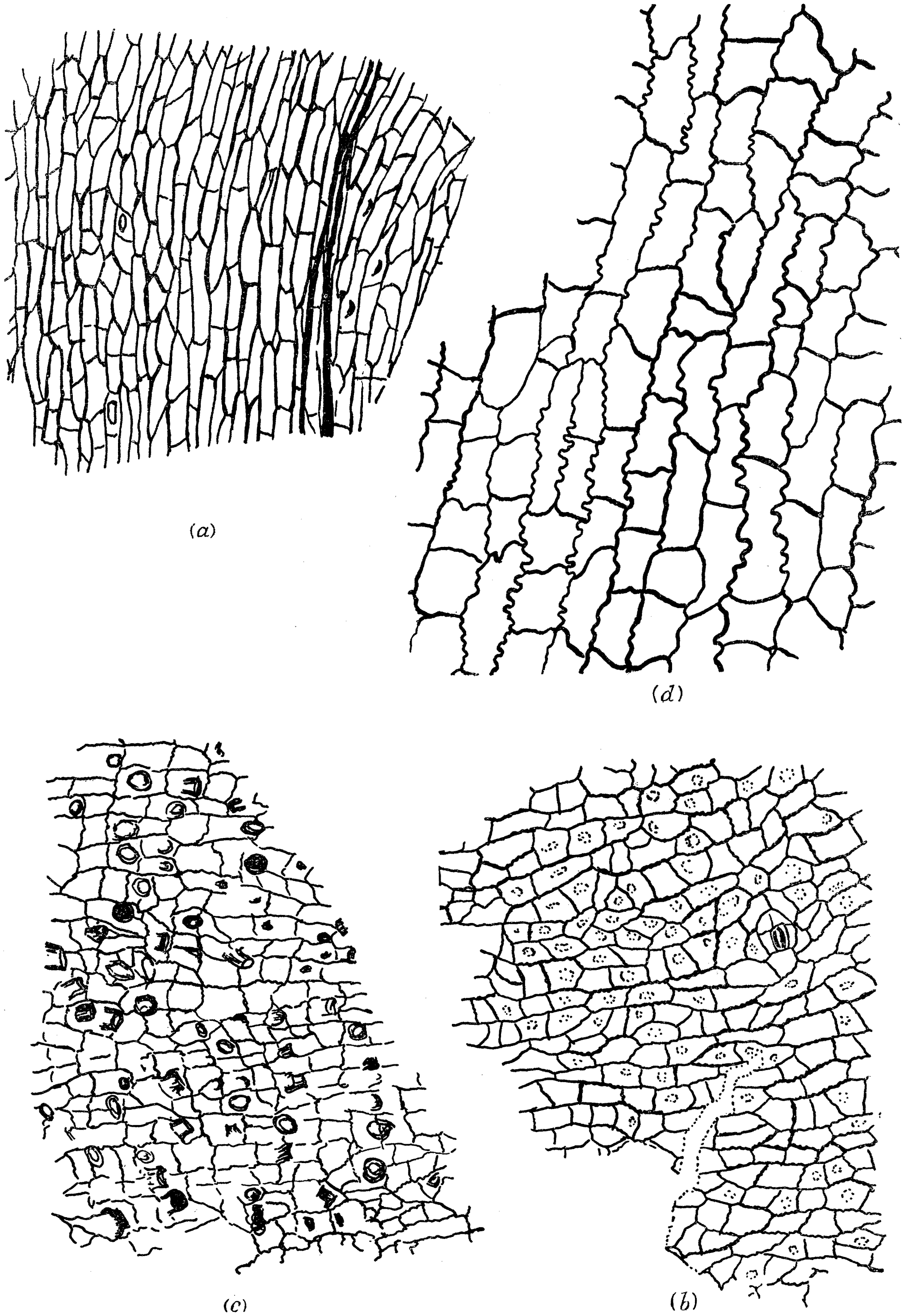


FIG. 17.—*Pilophorosperma paucipartitum* sp. nov. Epidermal cells. *a,* from axis. *b,* cupule outside. *c,* cupule inside. All × 120. *d,* from basal bract. × 300. *a,* slide No. 13. *b, c,* No. 9. *d,* No. 14.

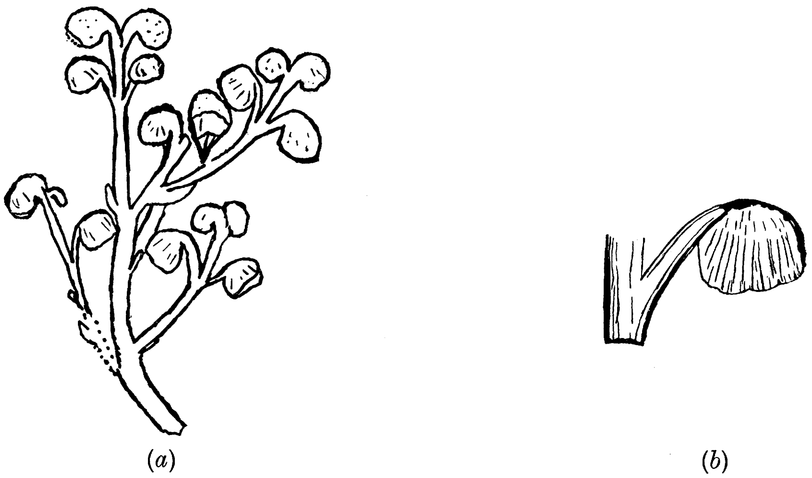
pair of long slender pedicels 7 mm. long. The pair of bracts with sheathing bases, seen at the bottom of the specimen, had an epidermis of rectangular cells, some of which had the very sinuous walls shown in fig. 17 (*d*). The cuticle of the main axis and pedicel was stout and mainly composed of fusiform cells, fig. 17 (*a*). The cupules have a helmet-like form, one of them still encloses a large seed, while another, fig. 16, shows part of a micropyle. The surface of the cupule is smooth, and gives good preparations, fig. 17 (*b*) and (*c*). The walls are microsinuous and most of the cells from the outside have a dark central spot, on the inner epidermis small hair bases are numerous, and a few complete sharply pointed hairs are seen.

The seed is 6·5 mm. long and 3·5 mm. broad; it has a tapering form and shows clearly the sharply curved bifid micropylar tube.

Pilophorosperma burnerense sp. nov., fig. 60, Plate 23, and figs. 18, 19.

Diagnosis.—Branching spreading, main axis giving off lateral branches bearing two pairs of cupules on short pedicels; cupules small, basin-shaped, attached to pedicels near centre; seed about 5 mm. long, conical with rounded base; epidermal cells of main axis short, in longitudinal rows, often slightly papillate or with hairs; cell wall of stems, pedicels and cupules minutely sinuous.

Type specimen No. U94.



(*a*) (*b*)

FIG. 18.—*Pilophorosperma burnerense* sp. nov. *a*, inflorescence. × 2. *b*, single cupule divided through the centre. × 5. Specimen No. U94.

Description.—The type of this form is very well preserved and is shown in fig. 60, Plate 23, and fig. 18 (*a*). Its total length is 3 cm. and four lateral branches are seen, with subtending bracts but no bracteoles. The axis has a very delicate cuticle, and only fragments could be obtained, parts of which are shown in fig. 19 (*a*). Most of the surface was composed of short cells with convex outer walls and papillæ. The cells of the pedicels have microsinuous walls, hair bases, and stomata are numerous. Each lateral branch bears four cupules on short pedicels. The cupules are small and fig. 18 (*b*) shows one in longitudinal section, the inner surface is striated. The cuticles of the cupules are stout and are shown in fig. 19 (*c*), (*d*). The outer epidermis had a few sunken stomata and almost all the cells have conspicuous central dark spots, representing a short papillæ, seen in profile in fig. 19 (*e*), these spots are absent from the inner epidermis. In

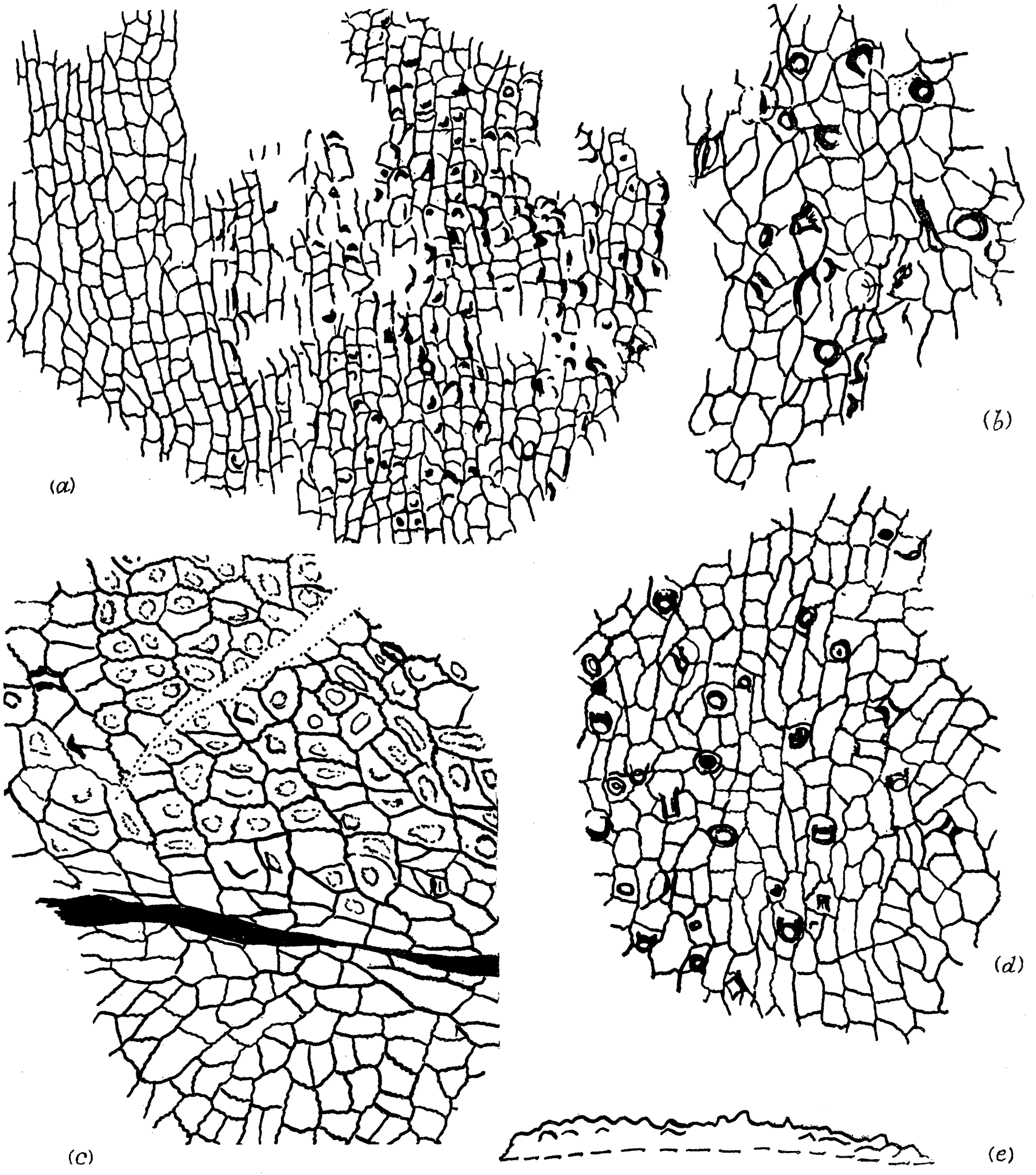


Fig. 19.—*Pilophorosperma burnerense* sp. nov. Epidermal cells. *a*, axis. *b*, stomatal band on pedicel. *c*, margin of cupule, outer epidermis above, inner epidermis below. *d*, inside of cupule. *e*, outer epidermis seen from the side showing papillæ. All × 120. *a*, slide No. 15. *b*, No. 10. *c* and *d*, No. 16. *e*, No. 23.

one place a small seed 4·5 mm. long is seen, its connection with the inflorescence cannot be established with certainty, though it lies in the position in which a seed might be expected to occur. While approaching *P. granulatum*, the cupules, pedicels, and cuticles are distinct and no bracteoles are seen.

Pilophorosperma crassum sp. nov., fig. 62, Plate 23, and figs. 20–21.

Diagnosis.—Habit compact; stout main axis with short lateral branches bearing cupules which are almost contiguous or overlapping; lateral branches terminate in a pair of cupules; pedicels very short; compressed cupules almost circular with a distinct thick basal portion having a rounded termination on the distal side and a thinner portion enclosing the seed; surface wrinkled; seeds ribbed; cuticle of stems thick, cells almost isodiametric, strongly papillate; outer cuticle of cupule composed of cells with slightly sinuous walls, often papillate.

Type specimen No. U214.

Description.—The type specimen is unfortunately broken through the middle, but it and the other small specimens of this type are distinguishable by their thick (probably fleshy) cupules and by their cuticles. The axis is stout (1·7 mm. wide) and produces several branches close together, it had a thick cuticle, with a characteristic appearance, fig. 21 (*a*), occasional stomata with oblique orientation and thin-walled subsidiary cells are seen. The bracts also have papillate cells and a few stomata. The remains of the cupules are rather broken, probably owing to their thickness, and their interpretation is rather difficult, especially as many of them are represented only by moulds. Fig. 20 (*b*) shows the remains of one of them in which the short pedicel merges into a thick wrinkled portion *a* with a rounded termination on the distal side, below this the part labelled *c* appears to be thinner, with some internal striations, a carbonized layer in the centre of the cupule may represent the broken remains of a seed.

(*a*) (*b*)

Fig. 20. *Pilophorosperma crassum* sp. nov. *a*, inflorescence, showing crowded cupules. × 2. *b*, remains of a cupule, showing thicker part *a*, and thinner part *c*. × 5. No. U214.

Cuticle preparations from the outside, fig. 21 (*b*), show minutely sinuous walls, small central papillate spots and some stomata. The inner cuticles are stout, with numerous stomata and conspicuous rounded papillæ, fig. 21 (*c*). In one preparation pollen grains are found still adhering to the inner cuticle.

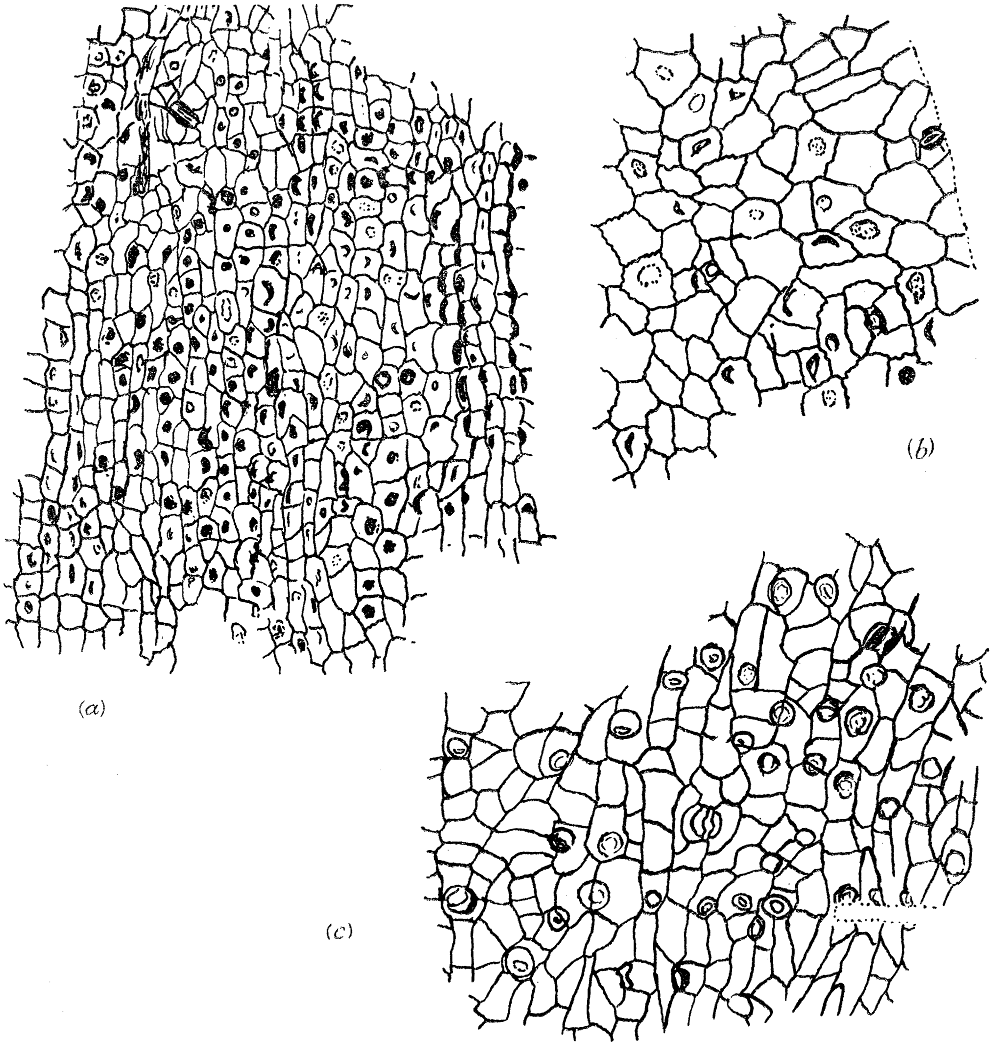


FIG. 21.—*Pilophorosperma crassum* sp. nov. Cuticles from :—Axis, *a*. Outer epidermis of cupule, *b*. Inside of cupule, *c*. All × 120. *a*, slide No. 29. *b*, No. 28. *c*, No. 40.

A fragmentary specimen (No. U201) referable to this type, shows several portions of seeds in close proximity to its cupules, one of these pieces, nearly 4 mm. long, shows a slightly curved micropyle and traces of longitudinal ribs.

It is possible that this type, together with the form next to be described, should be placed in a separate genus on account of the peculiar form of the cupules.

Pilophorosperma costulatum, sp. nov., figs. 22–24.

FIG. 22. *Pilophorosperma costulatum* sp. nov. Specimen showing ribbed seeds. × 2. No. U207.

Diagnosis.—Axis bearing short alternate branches some of which terminate in a pair of cupules; pedicels very short; cupules wrinkled showing two parts, a distal crescentic portion and a cup-like portion surrounding the base of the seed; margin of cupules with slight undulations; seeds with smooth testa bearing several distinct ridges running up to the bifid, sharply curved micropyle; cuticles of stalk thin, composed of cells of varying lengths, polygonal or rounded in outline, including stomata and isodiametric cells bearing the bases of large papillæ; surface

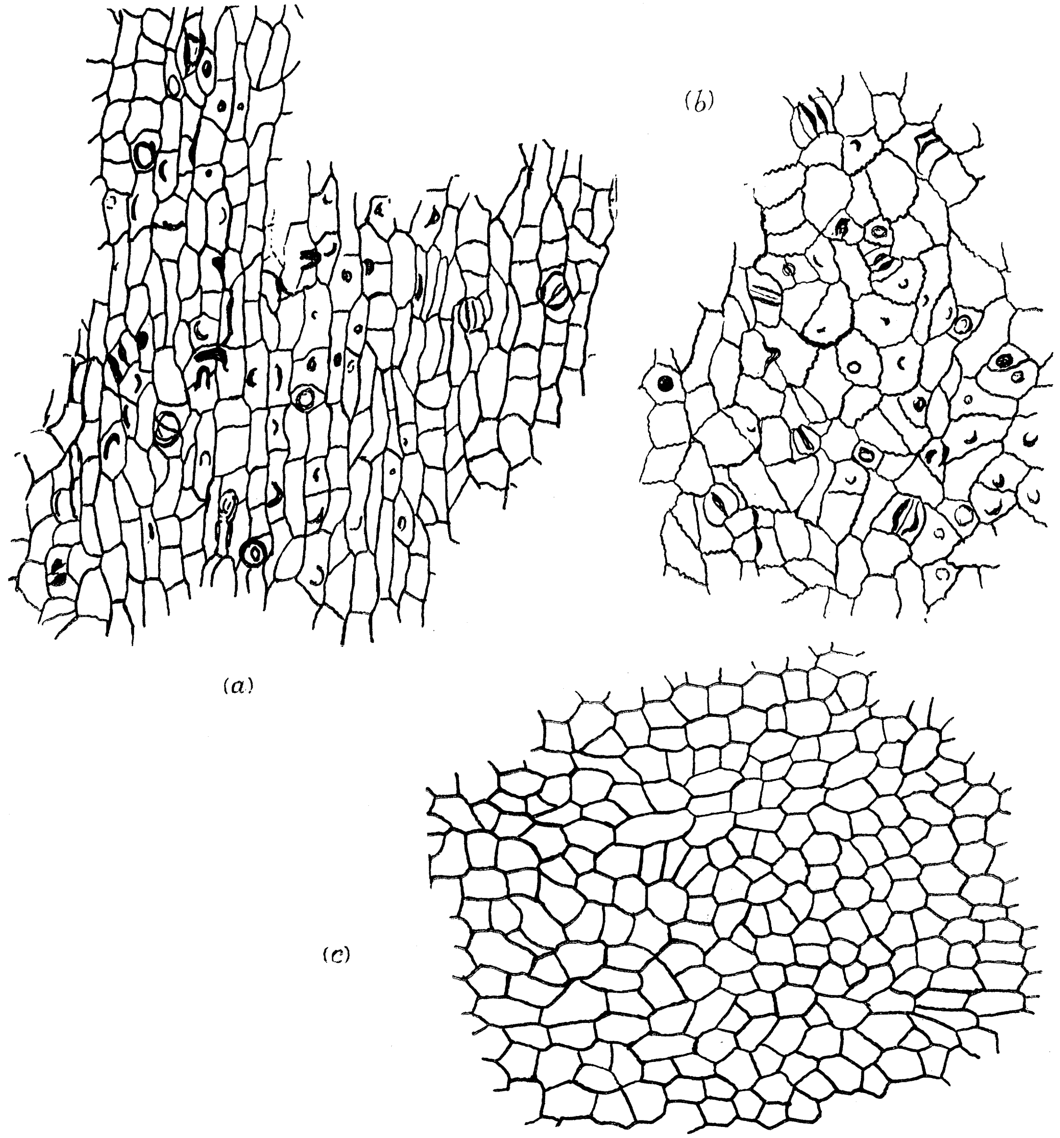


FIG. 23.—*Pilophorosperma costulatum* sp. nov. Cuticles from :—Axis, *a*. Outside of cupule, *b*. Testa of seed, *c*. All × 120. *a*, slide No. 41. *b*, No. 42. *c*, No. 43.

walls of cells generally smooth, a few with short thickened mammilate projections; cuticle of outside of cupule thin, cells polygonal with minutely sinuous walls and small thickened spots in centre of the superficial walls, some cells bear long thickened papillæ. Cuticle of inside thin with a few hairs.

Type-specimen No. U207.

Description.—This species is founded on a single specimen and more material is needed to confirm the diagnosis given, but it has several features of interest and while showing close affinities to *P. crassum*, it has some distinguishing characters. The specimen, fig. 22, shows two well-preserved branches bearing cupules on short pedicels. The cuticles are distinct, the epidermal cells of the axis, fig. 23 (*a*), were elongated and their walls but thinly cutinized, some minute mamillæ or hair bases are seen, and stomata are numerous. The walls are microsinuous, and the whole structure seems to differ markedly from that of *P. crassum.* The cupules are interesting in that each still encloses a seed, they are thinner than in the previous species, but show a thicker wrinkled basal portion and a thinner part around the seed. A cuticle of the outside of the cupule is shown in fig. 23 (*b*) and fig. 24. The cell walls are distinctly microsinuous, numerous stomata and some short papillæ are present. Hair bases were less numerous on the inner epidermis.

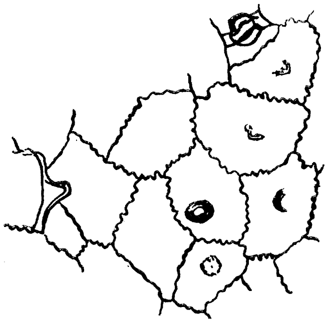


FIG. 24. — *Pilophorosperma costulatum* sp. nov. Cuticle from outside of cupule showing microsinuosity of cells, small papillæ and a stoma. × 200. Slide No. 42.

The most complete seed is 6 mm. long and 3 mm. broad at its widest part. The well-preserved testa has several longitudinal ridges and the epidermal cells can often be seen under the microscope. The cuticle of the testa is very thick and is formed from regular polygonal cells, fig. 23 (*c*).

Pilophorosperma natalense sp. nov., figs. 25, 26.

Diagnosis.—Main axis elongate, bearing sub-opposite lateral branches; lateral branches with a terminal cupule and two or three pedicellate cupules near the apex, the lower part of the branch bearing only bracteoles; some of the bracteoles elongated and expanded at their tips to a ligulate structure with several fine apical teeth; cupules almost circular, probably fleshy, open margin smooth and entire, terminal cupule laterally expanded; cuticles of axis thin, showing regular rows of rectangular cells with few papillæ and hair bases on one side, and smaller less regular cells with numerous short hairs on the other side; cuticles of outer epidermis of cupule very thin and wrinkled, composed of small polygonal cells, some of which bore short thickened hairs, and including numerous small stomata; cuticle of inner epidermis of cupule thicker, with microsinuous walls and many thickened bases of small hairs.

Type-specimen No. U44.

Description.—The type specimen, fig. 25, is fairly complete and lies across the type specimen of *Pteruchus papillatus.* Its axis is 2 mm. broad at the base, about 35 mm. long, and has two or three distinct longitudinal ridges. The cuticle of the axis is thin and appears to vary in structure on the two sides, fig. 26 (*a*), (*b*) ; one side has short hairs and stomata. The cupules seem to have been confined to the distal parts of the lateral branches, which also bore bracteoles. One of these, B, fig. 25, is similar in form to the subtending bract of *U. verrucosa*, fig. 8, but lacks the enlarged base seen in that form.* The shape of these bract structures, showing no approach to the form of a foliage

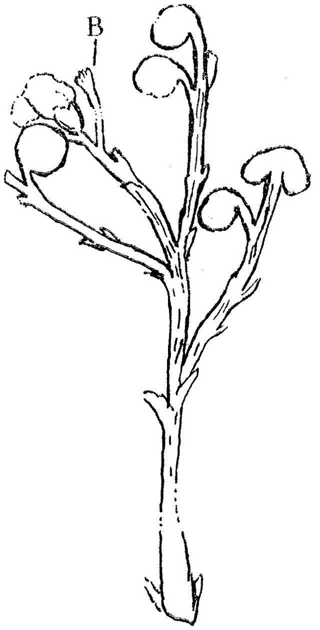


FIG. 25. — *Pilophorosperma natalense* sp. nov. Inflorescence showing characteristic branching, ligulate bracteole at B. × 2. No. U44.

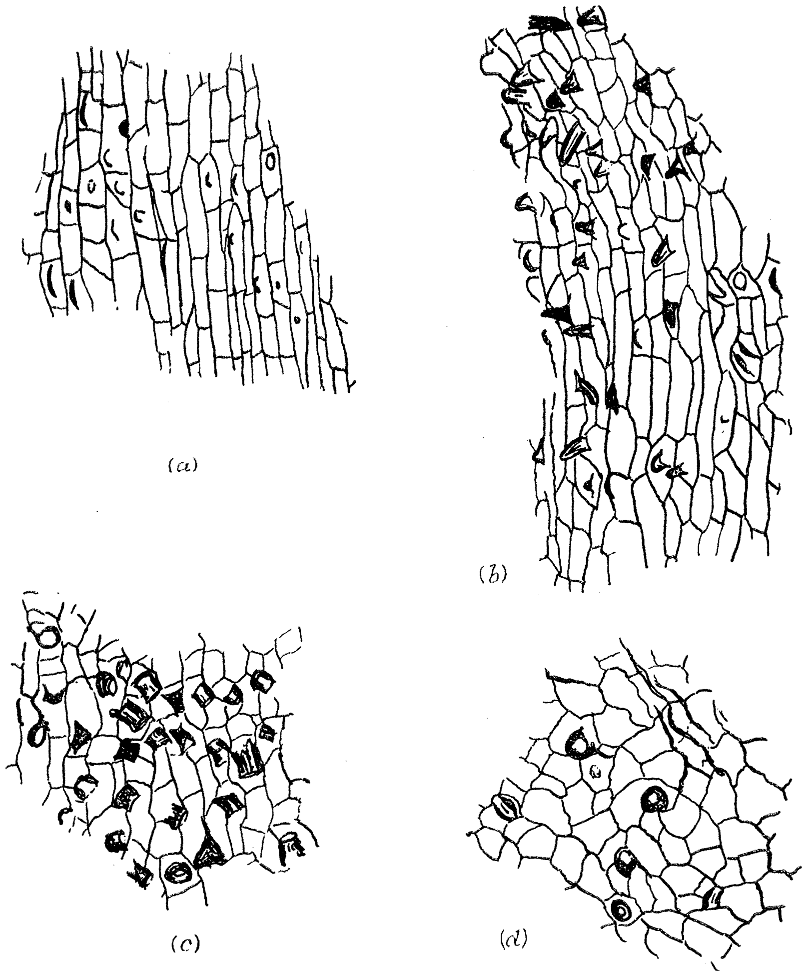


FIG. 26.—*Pilophorosperma natalense.* Portions of cuticles from the main axis, *a*, *b* ; from the outer epidermis of the cupule, showing circular hair bases, *d* ; from the inner epidermis of the cupule with numerous hair bases, *c*. All × 120. Slides No. 44, *a*, *b*. No. 45, *c*, *d*.

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* SHIRLEY (1898), p. 13, in describing *Pteruchus* (*Stachyopitys*) *annularioides* states that occasionally at the base of the peduncle are seen bract-like ginkgoid leaflets, in miniature resembling those of *G. bidens.* He also records a small bract like an undivided Ginkgo leaflet in connection with *Pteruchus* (*Stachyopitys*) *Simmondsi.*

leaf, invites speculations as to their morphological nature. It is possible that they represent the aphlebiæ of the Zygopterid ferns and primitive microphylls.

The laterally-expanded terminal cupule shown on the right of fig. 25 is an interesting feature, it has been carefully examined and its shape is not due to an accident of preservation. The cuticles from the outside of the cupules were thin and had many irregular wrinkles and folds obscuring the cell outlines except near the open margin. Small stomata and some hair bases are seen, fig. 26 (*d*). The inner cuticle is stouter and shows very numerous thickened hair bases. One cupule contains the remains of a smooth seed 4 mm. long.

Notes on fragmentary specimens probably representing other species.

In addition to the specimens described above our collection contains some other fragments which do not agree closely with any of the species recognized, but which are not sufficiently complete to be regarded as the types of new species. Some of these are worthy of mention.

Pilophorosperma sp., Type A. fig. 65, Plate 24, fig. 27, fig. 64, Plate 23.

Specimens No. U151, 152 (counterpart).

The material shows the end of a well-preserved branch with a terminal and two lateral cupules, which lies on top of a frond of *Stenopteris elongata* (Carr.) as shown in fig. 65. The branch is about 1 cm. long, at the base of which lie the remains of a pair of opposite bracteoles, and at the apex is a terminal cupule ; the lateral cupules are alternate but lie close together, their pedicels are 4 mm. long, slightly striated and attached to the central parts of the cupules. The compressed cupules are approximately circular, with a relatively smooth surface, the margin of the opening is entire or slightly sinuous, one of the cupules contains a seed with a curved micropyle 1 mm. long projecting from it. The terminal cupule is somewhat different in shape, it is broader than long and appears to curve over on either side of the pedicel, as is also seen in *P. natalense* ; it shows no traces of a seed.

The preservation of the axis is so good that the cell outlines of its surface can be seen, and it was well cutinized. Part of the cuticles of both sides is shown in fig. 27, the position of the margin being indicated by the arrows. There is little difference between the two sides, but on one side the cells are slightly more elongated. The more important features of these preparations are the distinctly elongated and often rectangular shapes of the cells ; the presence of files of long narrow cells and the smooth and evenly thickened superficial walls ; the scarcity of papillæ. A few stomata are seen lying in longitudinal position. The cupules also give excellent preparations. The cuticles of the inner and outer surfaces of the cupule near its margin are shown in fig. 64, Plate 23, where the central dark part represents the slightly sinuous margin. The outer cuticle came from cells with rather thick, slightly sinuous walls, a few of them had small central papillæ and they included a few scattered stomata. The guard cells were very little thickened and lie between a pair of slightly thickened subsidiary cells. The inner cuticle is characterized by the abundance of large circular hair bases, which almost cover the surface of the cells ; frequently the hairs are still seen attached to their bases ; they were 0·2 mm. long and were somewhat different from other cupular hairs in their large diameter, their length and their blunt apices.

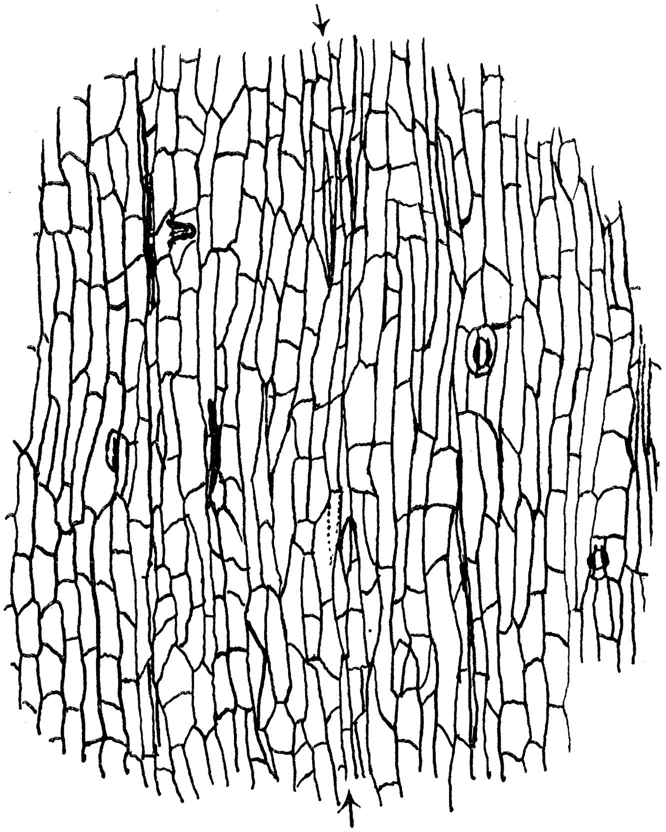

FIG. 27. *Pilophorosperma* A. Cuticle of the axis. The small arrows above and below show the position of the margin of the compressed stalk before the cuticle was flattened out. × 120. Slide No. 33.

While this type bears some resemblance to *P. natalense* in the form of its cupules it is clearly distinguishable in the structure of its cuticles. The characters of the cells both from the axis and from the cupules are quite distinct, and the differences observed can scarcely be attributed to differences in habitat, age, or preservation. It also seems to differ from the next form to be described.

Pilophorosperma sp., Type B. figs. 28, 29.

Specimens No. U205, U205A (counterpart).

This is the lower part of a branching inflorescence. A main axis gives off branches subtended by bracts and bearing cupules on short pedicels, but only the lower parts of the branches are seen. Fig. 28 shows a well-preserved portion with a gradually expanding pedicel, and an elliptical cupule having a rounded lower margin. The cupules appear to have been thin, they are slightly granular on the outside and finely striated on the inside. No attached seeds are seen, but an isolated seed lies across one of the branches, fig. 33 (*e*); there is no proof that it belonged to this type, but its characters may here be mentioned. The body of the seed is 3·5 mm. long and pear-shaped with a rounded base, it tapers gradually towards the micropylar tube which is about 1 mm. long, sharply curved and slit down one side. This seed is smaller and rather different in outline from the isolated seeds more commonly found.

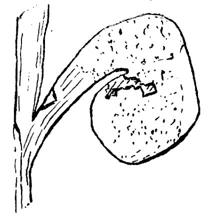

FIG. 28.—*Pilophorosperma* B. Single cupule showing rounded form and gradually expanding pedicel. × 5. No. 205.

The cuticles which are illustrated in fig. 29 have some distinctive features. The short irregular cells from the axis include a few hair bases often borne on isodiametric cells and small stomata with slightly thickened subsidiary cells. The cuticles from the cupules are thick, the outer epidermis, fig. 29 (*b*), has minutely sinuous walls, and many of the cells have a dark central spot, which is occasionally enlarged into a papilla. Stomata

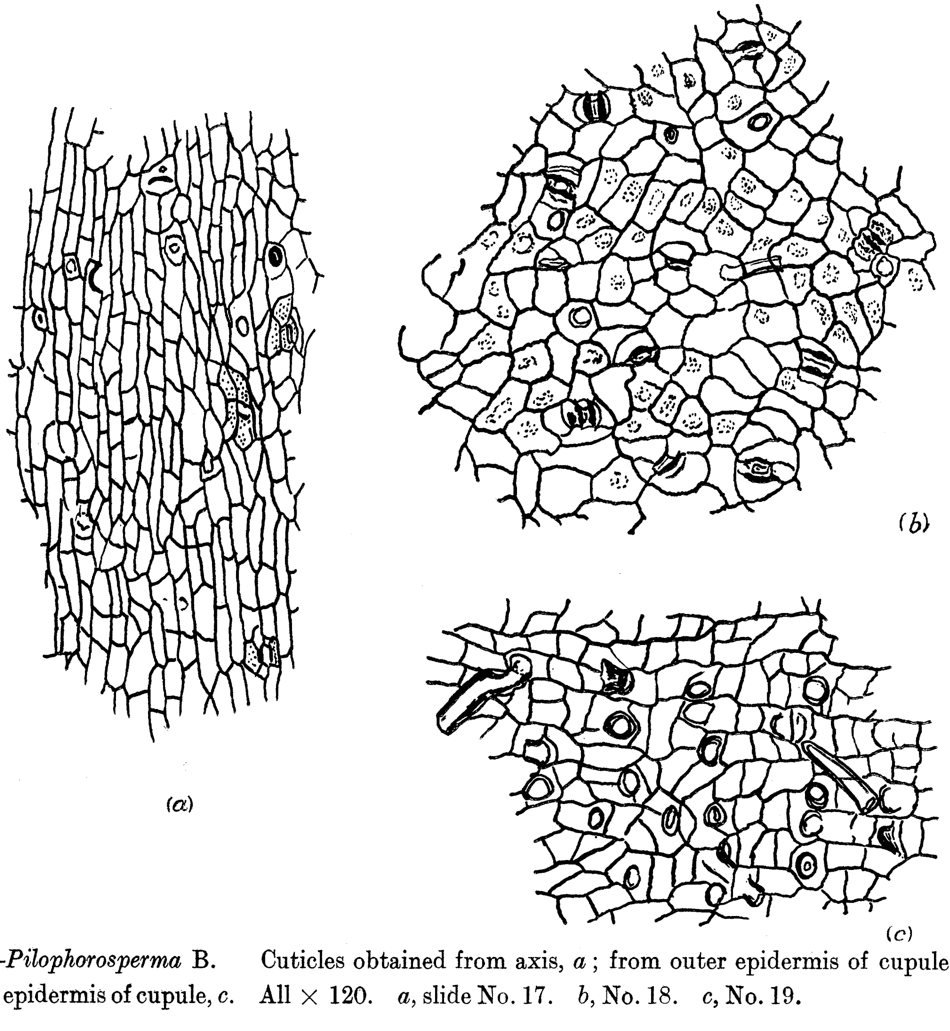

FIG. 29.—*Pilophorosperma* B. Cuticles obtained from axis, *a*; from outer epidermis of cupule, *b*; from inner epidermis of cupule, *c*. All × 120. *a*, slide No. 17. *b*, No. 18. *c*, No. 19.

are abundant and well preserved, they seem to vary somewhat in appearance, the pore is very clearly seen, with a thin area on either side, this is bounded by a pair of lateral crescentic thickenings attenuated at the ends to fine points, which reach the walls of the polar subsidiary cells, delicate projections from these thickenings meet across the guard cells at the poles of the pore. In one case we seem to see the dorsal walls of the guard cells in addition to the thickenings.

The cells of the inner epidermis, fig. 29 (*c*), tended to be arranged in rows, their walls were straight or occasionally microsinuous. Many bases of thickened hairs, and a few complete hairs are seen, but there are few stomata on this surface.

Pilophorosperma sp., Type C. fig. 30 (*a*).

A single specimen (No. U100) shows a very fragmentary portion of an inflorescence. The preservation of the fragments is fairly good, but probably owing to the very delicate cuticle the original structure has become much broken up. The axis, which is about 1 mm. wide, appears to give off several short branches; its surface was composed of small papillate cells arranged in longitudinal series. Cuticle preparations are very difficult to obtain, but show the papillæ, which are thicker than the rest of the cuticle and occur on practically every cell. One of the main branches terminates in a pair of cupules badly preserved, below is a pair of opposite cupules borne on very short pedicels. The cupules are helmet-like in shape, about 3 mm. long and broad, the opening is somewhat flattened. In one case a well-preserved seed, shown in fig. 30 (*a*), is seen projecting about 2 mm. from the cupule. It has several well-marked ridges and a sharply curved micropyle. The cuticle of the cupule, like that of the stem, is delicate, most of its cells possess a short papillæ on their surface, while the inner cuticle has very

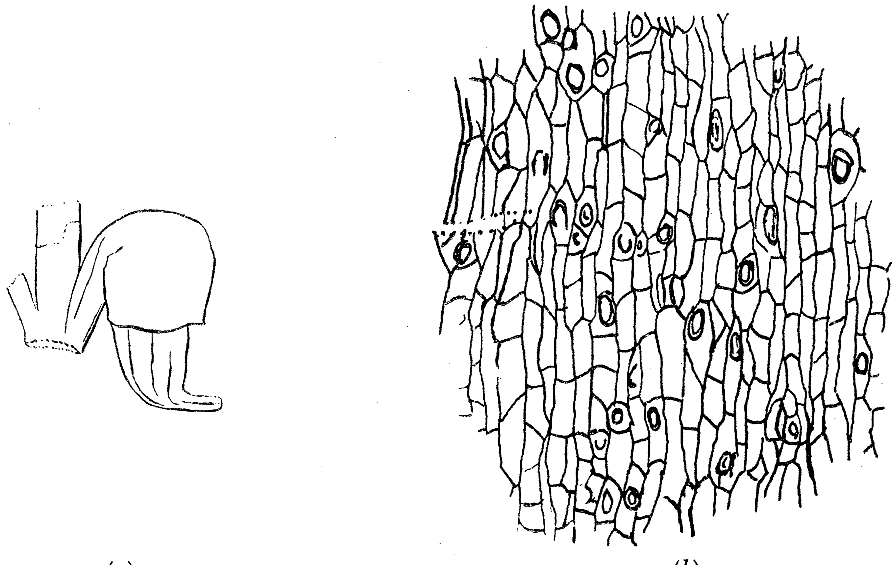
(*a*) (*b*)

FIG. 30. *Pilophorosperma* spp. *a*, type C cupule with seed × 5. No. U100. *b*, cuticle from axis of specimen No. 209, showing numerous hair bases. × 120. Slide No. 46.

numerous hairs. This form is probably another distinct species, but the material is not sufficiently complete to furnish a definite diagnosis.

Pilophorosperma spp.

Among other fragments which cannot be confidently assigned to any of the above species is that shown in fig. 61, Plate 23. Here we have a stout axis giving off long lateral branches with axillary bracts, and bearing elliptical cupules. The cuticle of the axis is characterized by the presence of numerous bases of large hairs or large blunt papillæ, fig. 30 (*b*), and it differs noticeably from the cuticles obtained from other species. The seeds also had remarkably long curved micropyles, one of which is seen at M, fig. 61, Plate 23.

There are other fragments which also belong to the same genus, but which cannot be accurately matched in their cuticle characters or their general form with the more complete specimens. My examination of Mr. Høeg's collection shows that several other types probably existed in the same bed, and it is therefore advisable to await further investigation before describing these fragments. As suggested above, it is possible that some of the types described may be hybrids. If we could assign leaves to each type we should probably be in a better position to judge the status of the various forms which have been described, but for the present the only available course is to present an account of the material studied.

Spermatocodon gen. nov.

Diagnosis.—Inflorescence with some spiral branching ; axis with thick cuticle differing slightly on the two sides ; cupules campanulate, inner surface without hairs.

Type-species *Spermatocodon Sewardi.*

Spermatocodon Sewardi, sp. nov., fig. 66, Plate 24, and figs. 31, 32.

Diagnosis.—Inflorescence apparently racemose, upper cupules much smaller than lower ones ; axis with thick cuticle in which the cells of one side are somewhat shorter and are less regularly arranged than those on the other side ; axis and cupules glabrous ; pedicels short ; cupules smooth, spherical when young, campanulate-globular with some striations when older ; margin of older cupules with three-four small lobes.


(*a*) (*b*)

FIG. 31. *Spermatocodon Sewardi* sp. nov. *a*, the most complete specimen. × 2. *b*, largest cupule. × 6. No. U206.

Type-specimen No. U206.

Description.—Although this species is based on two fragments only, they are very well preserved and appear to possess very distinct characters ; more material, however, is needed to complete the diagnosis and description of the genus and species.

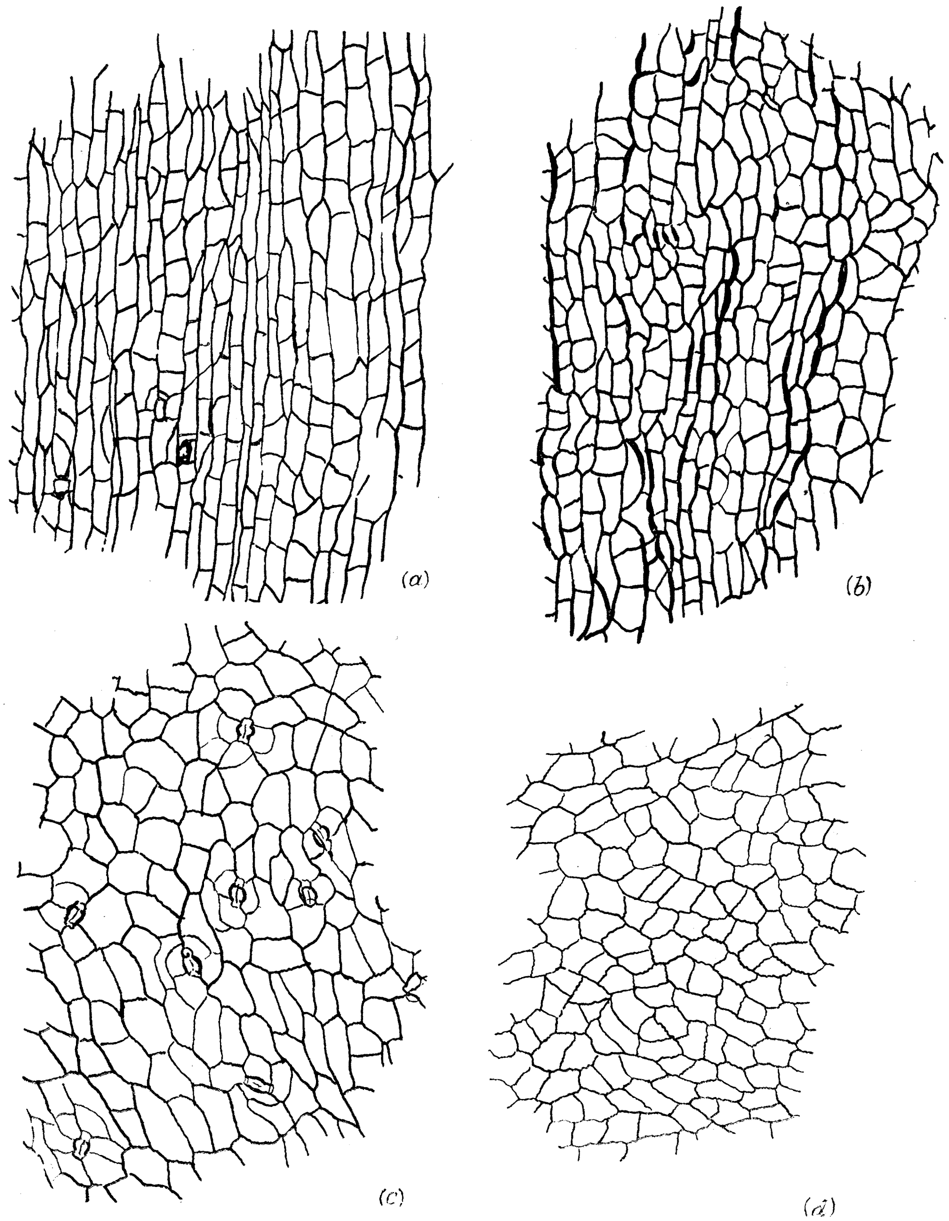

FIG. 32. *Spermatocodon Sewardi* sp. nov. Cuticles from the two opposite sides of the axis, *a*, *b* ; from outside of cupule, *c* ; from inside of cupule, *d*. All × 120. *a* and *b*, slide No. 50. *c*, No. 51. *d*, No. 52.

The fragments examined represent parts of terminal or lateral branches of the inflorescence ; they come out of the matrix very cleanly, probably owing to their thick cuticle. The axis of the type specimen is 1 cm. long and about 0·7 mm. broad near the base. It is unbranched in the lower 5 mm., but bears traces of a bract close to the base. The apex is apparently bud-like, but not very clearly seen. The most characteristic feature is the racemose type of the structure. In all other species there is little or no difference between the appearance of the apical and the basal cupules, while in several the apices of the branches are terminated by a pair of equal and well-developed structures. In this form a small, and almost sessile, cupule lies near the apex, succeeded alternately by three others, which as we pass down the stem steadily increase in size, having longer pedicels and separated by an increasing internodal space.

This is almost the only species of which it has been possible to obtain a complete and unbroken specimen of the cuticle of a whole piece of the stalk, an indication of the stout nature of the cuticle, which is almost as thick as that of *P. crassum.* We see that the axis possessed some dorsiventrality, for the epidermal cells on one side differ in shape, arrangement, and cuticular thickness from those of the other. The form of the epidermal cells in the centre of each side is shown in fig. 32 (*a*), (*b*). There are a few stomata on each side but no papillæ.

The cupules have short pedicels; the lowest cupule is 3·5 mm. across and shows no trace of a seed, but micropyles project from the younger ones. The outer epidermis of the older cupule has a stout cuticle, fig. 32 (*c*), from polygonal cells with slightly sinuous anticlinal walls. Stomata with subsidiary cells having thin walls are numerous and clearly visible. The subsidiary cells occasionally divide to form additional encircling cells. The inner epidermis has a very delicate cuticle without any hairs, fig. 32 (*d*).

This form certainly represents a distinct species, and differs sufficiently from the other types to be placed in a separate genus.

Isolated Seeds, figs. 67, 68, Plate 24, and fig. 33.

A number of isolated seeds are found in the same bed as the specimens just described. They may be regarded as belonging to the Corystospermaceæ owing to their similarity in form with attached seeds, and especially in their curved bifid micropylar tubes. It seems certain that in our collection we have the seeds of several species, for while there is a considerable general similarity, differences in size, shape, in surface appearance, and in the form of the micropyle may be noticed. Fig. 33 shows a series of these seeds drawn to the same scale. They vary from 3·5 to 7 mm. in length, and from 2·2 to 5 mm. in breadth. We have no certain indications of their original form, but they may have been flattened or platyspermic owing to the fact that almost all the specimens when found show the curvature of the micropyle; had they been symmetrical ellipsoids or pear-shaped we should have expected that in a large percentage of specimens the bifid micropyle would be found projecting upwards or downwards into the matrix as in fig. 33 (*g*), where the micropyle has been broken away. In this specimen, which was transferred from the matrix, a prominent ridge is seen running down one surface of the seed, and in another example a similar ridge is seen in a central position, suggesting that this form may have been more or less triangular in section.

The surface of the tissue which remains is usually quite smooth, though in (*f*) we have some fine ridges representing folds in the epidermis owing to contraction. It would seem that the testa was originally hard and stony, and this is supported by the thickness of its cuticle in most of the forms. In some, *e.g.* (*b*), the outlines of the original cells of the testa can be seen, and in (*b*) there are also slight lumps and depressions near the micropylar end. The small example (*e*) occurs in U205 and has been already described (p. 223). Four specimens, removed whole by WALTON's method and macerated, provided some important information.

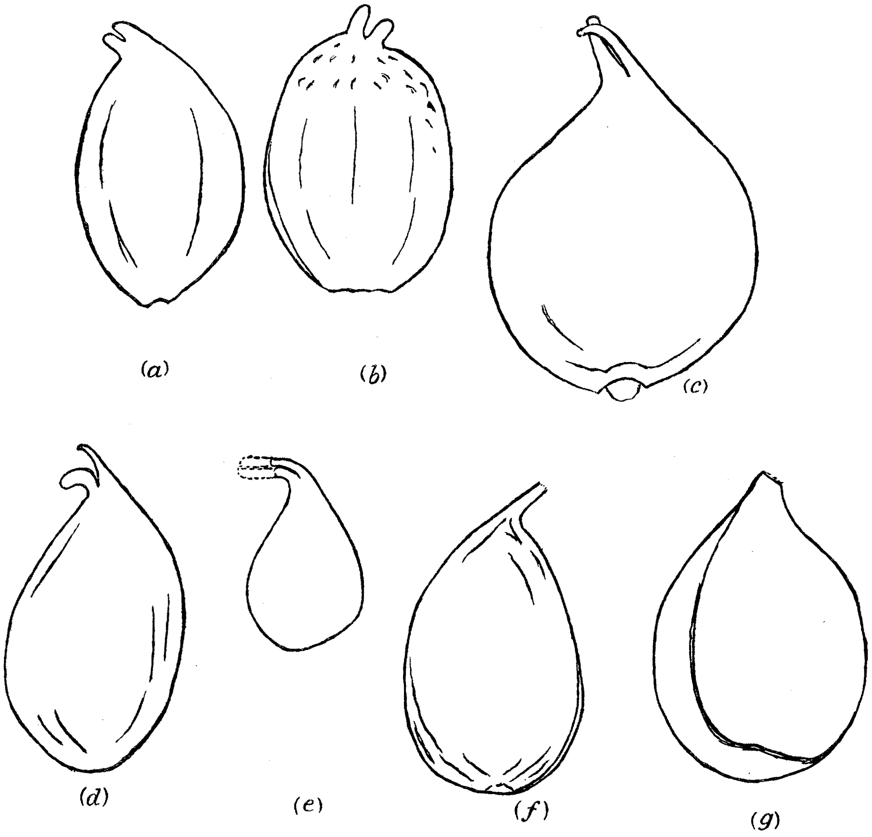

FIG. 33.—Outline drawings of isolated seeds showing shapes and sizes of the various types. All × 7. *a*, No. U221. *b*, No. U222. *c*, No. U229. *d*, No. U225. *e*, No. U205.

The seeds all possessed a well-cutinized testa, but no signs of fibrous integumentary tissue was observed, like that found in the seeds of *Caytonia*. An exceedingly delicate inner membrane was sometimes seen during the clearing process as the oxidized material dissolved away, but only the most minute fragments showing cellular outlines could be obtained in the mounted preparations. In two cleared seeds a small cutinized cylinder 0·5 mm. long was noticed lying inside the testa below the micropyle, near where the apex of the nucellus would be expected; at the top of this cylinder and surrounded by the remains of a very delicate membrane lay a number of very characteristic winged microspores. After staining and mounting one of these objects, fig. 70, Plate 24, five spores still remained attached, while six others floated off but were retained on the slide; it is probable that a number of others were lost during the process of solution and staining. Most of these spores are ruptured and several look as though they may have germinated prior to preservation, but the large lateral wings with a sculptured surface are quite characteristic. These spores measure about 0·1 mm. across the wings and 0·07 mm. deep. It seems probable that they represent the contents of a pollen chamber, and must have been caught and sucked into the micropyle by a drop mechanism. There is, of course, little to indicate the structure of this pollen chamber, though we may note that the cutinized cylinder, to which the spores are attached, is thicker in its upper half than its lower, and the abrupt change in thickness appeared to be caused by the presence of an additional cuticularized layer; this appearance is compatible with the suggestion that the original pollen chamber had the form of a lagenostome.

The discovery of these spores, which are similar in form to some examples found inside one of the cupules as well as to those lying on certain leaves in the plant bed, provides some evidence as to the identity of the microsporangia of these plants (see p. 233).

The cuticular preparations from the testas provide additional evidence for the existence of several species among these isolated seeds, and further evidence is found for the view that some of the seeds were platyspermic when living. The four examples which were transferred from the matrix and macerated show differences in the shapes of the cells composing the outside of the testa. A seed similar to that shown in fig. 33 (*f*) had a fairly uniform cuticle of cells arranged in longitudinal rows. The shape of the cells is very varied and in the middle of each side the longitudinal arrangement is lost over an elliptical area; the surface walls are somewhat thinner than those of some other species and the majority of the cells show a dark spot in the centre of their superficial walls, which stains more deeply. The external cells of the seed represented in fig. 33 (*g*) show a very different character; they were elongated, more or less rectangular, and arranged in longitudinal rows, the anticlinal walls appear thick and show a well-marked microsinuosity. As the micropyle of this form is not shown there is some uncertainty as to whether it belonged to the group of plants now under consideration. A seed similar to that shown in fig. 33 (*d*) has a testa with cells of very varied shapes and sizes, they have neither the regularity of arrangement found in the (*f*) form, nor the uniformity of shape as figured in fig. 23 for *P. costulatum*.

The preparation made from the seed similar to that figured at (*a*), fig. 33, from which the pollen grains were obtained, shows the testa near the base of the micropyle. Here the central part of the surface consists of isodiametric polygonal cells showing little regularity of arrangement, near the margin, however, there is a marked change in the form and arrangement of the cells, they become smaller, rectangular, and are arranged in definite longitudinal rows. It seems impossible to explain the occurrence of these cells on any other assumption than that the seed was originally flattened, and that the edge in the seed, as found to-day, was the original margin of the platyspermic seed.

Comparison with other forms.

(*a*) *Mesozoic Types.*—The existing descriptions of Triassic floras contain few references to any reproductive structures comparable with *Umkomasia*, but it seems most probable that the objects from the Ipswich Series from Queensland and from the Hawkesbury Series, New South Wales, are closely allied if not identical structures. The Queensland forms were described by SHIRLEY (1898) as *Beania geminata*, while WALKOM (1917) later figured them under the heading of Gymnospermous seeds. The figures show rounded structures, which their authors identified as seeds, or in some of SHIRLEY's forms as bifid scales, borne in pairs on recurved pedicels which arose by the dichotomy of a slender axis. In certain specimens the seed-bearing stems are shown as branches of a main axis, thus they are apparently similar in form to my *P. gracile* but somewhat larger. They do not appear to have been very well preserved, and no traces of a micropyle were seen or figured, while only in one specimen does SHIRLEY show any bracteoles. In the earlier description, however, certain points are noticed, the significance of which may now be explicable. SHIRLEY states that "the fruits when intact were brownish, and as if originally covered with coarse brown hairs; occasionally they show an inner coat (aril) which has a convoluted surface; usually they are broken in half, just as the seed of a broad bean can split, and show a system of vessels curving from the fruit stalk round the circumference of the (?) seed coat. The ovule is apparently anatropous. With the seeds are peculiar bifid scales, each half presenting a convex surface." Each half of the scales was believed to carry a seed. It seems probable that SHIRLEY had before him corystosperm structures in several states, some with empty cupules, which generally split into two halves when the rock is broken, and which he interpreted as the seed-bearing scales; in other specimens the seed was probably present, possibly in some, surrounded by hairs from the inside of the cupule. The system of vessels curving round the circumferences of the specimen split into two halves, was perhaps the fractured section of the cupule. Thus some of the points noticed by SHIRLEY which seem fantastic when applied to *Beania*, are quite in harmony with the identification of the structures as species of *Umkomasia* or *Pilophorosperma*. WALKOM in describing the forms from the same locality adds no further significant details except that many of the seeds (?) have a surface with a wrinkled appearance, a point seen in the cupules of several species described above.

The structures figured by WALKOM (1925 Plate, 31, figs. 6, 9, 11) from the Hawkesbury Series of New South Wales also suggest that the Corystospermaceæ occur in the Triassic beds of Australia, and good specimens will probably be found if thorough search for them be made.

(*b*) *Palæozoic Types.*—The comparison of the Corystospermaceæ with the seed-bearing parts of Palæozoic pteridosperms should be of considerable interest as indicating the evolutionary tendencies of the group, but unfortunately the nature of the material does not allow a very close comparison to be made. The present specimens can yield little information which is valuable in connection with the Palæozoic seeds showing structure, while the mummified Carboniferous and Permian forms are still incompletely known and await study by modern methods. Certain features, however, are noteworthy.

(1) *Position of the seeds.*—The seeds of *Lagenostoma,* and possibly of all the Lyginopterideæ, were borne at the tips of slender branches. These branches seem to have formed the ultimate ramifications of a structure devoid of sterile pinnules in the immediate vicinity of the seeds in *Calymmatotheca Stangeri* (JONGMANS, 1930, figs. 1, 2) and *Lagenostoma Sinclairi* (E. A. N. ARBER, 1905, fig. 7, Plate 2), and probably branched only in one plane. They were thus somewhat similar to the inflorescence of *Umkomasia,* which can also be compared with figures of the inflorescence of *Sphenopteris striata.* In the form known as *Aneimites fertilis* the seeds were terminal on slender branches with sterile foliar pinnules below, and a similar structure is seen in *Diploimema.* GRAND EURY (1906), who briefly described several forms of fertile structures, considered that the majority of the Upper Palæozoic pteridosperms bore their reproductive organs on separate inflorescences. From the analogy of the Psilophytales and the earliest known ferns, *e.g.*, *Botryopteris* and *Stauropteris,* we must consider the terminal position of the seed as the more primitive, and our observations suggest that this habit continued in at least one group in Mesozoic times. On the other hand, Dr. SCOTT has pointed out that in *Neuropteris heterophylla* the seeds were borne terminally on a vegetative frond which was but slightly modified (1923), while in *Pecopteris Pluckeneti* they were borne on ordinary pinnules. More recently Professor HALLE (1929) has drawn attention to the fact that in the Permian ferns *Alethopteris Norinii, Sphenopteris tenuis,* and *Emplectopteris triangularis* the seeds were borne on the surface of ordinary pinnæ or pinnules.

It would thus seem that the pteridosperm seeds show a close parallel to the sporangia of the ferns (BOWER, 1928); in the course of evolution some became superficial, but, on the other hand, in the Corystospermaceæ the terminal position has been retained and the inflorescence has not developed into an expanded frond.

(2) *Structure of the seeds.*—Our evidence from the Corystospermaceæ is meagre, but some of the Mesozoic species may be regarded as having been flattened like certain of the Palæozoic forms. The elongated micropyle of certain species, *e.g.*, *U. Macleani,* may be compared with the corresponding structure in *Trigonocarpus,* but the curvature of the micropyle seems without parallel. The mode in which the pollen grains were retained at the base of the micropyle and the columnar structure from this region suggest the presence of a pollen chamber, or lagenostome, of a type comparable with that of *Trigonocarpus.* There may have been a similarity also in the firm and strong character of the outer part of the integument which is sometimes ribbed.

(3) *Form and structure of the cupule.*—Some of the Lyginopterideæ seem to have had a cupule which was divided up into several distinct arms or segments united at the base, though in *L. Sinclairi* (ARBER, E. A. N., 1905, fig. 8, Plate 2) the segments are shown as united together round the seed. It may well be that this type of structure

was developed from a form in which the lobes of the cupule were free almost to the base as is suggested in some of the figures of *Calymmatotheca*, and of the seeds attributed to *Sphenopteris striata* Gothan (BERTRAND (1926), CARPENTIER (1929)). In *Gnetopsis elliptica* Renault the cupule is divided into two main lobes each of which is divided into about five teeth above. In *Umkomasia Macleani* and *U. verrucosa* the cupule is divided into two lobes, while in *Pilophorosperma* the cupule appears to have formed a basin-like envelope without any definite lobing, though the blunt teeth of *Spermatocodon Sewardi* may represent the vestiges of the original lobes.

The only other points in which a noteworthy comparison can be made is the presence of hairs inside the cupule. These are recorded for the cupules of *Lagenostoma Lomaxi* and *Gnetopsis elliptica* (OLIVER and SALISBURY, 1911, p. 34), while they occur in the species of the *Pilophorosperma.*

There are thus several points of general structure and of detail which suggest that the structures described above were generally similar to the seed-bearing structures of the Palæozoic pteridosperms, and that differences such as in the shape of the cupule, may be due to the course of evolution of this structure proceeding in the same direction as the development of sympetaly in the flowering plants.

Male Inflorescences.

The microspores of the Carboniferous pteridosperms of the *Lyginopteris* type were borne in sporangia hanging in clusters from shortly stalked spathulate laminæ of a fertile frond (*Crossotheca*). Several other forms have been described from the Carboniferous and Permian rocks by KIDSTON (1923), WALTON (1931), GOTHAN (1927), and others, which consist of tufts of elongated microsporangia borne on the ends of branches which probably belonged to plants of the same group.

ANTEVS (1914) described specimens under the name of *Antholithus Zeilleri,* from the Upper Trias of Sweden, consisting of groups of elongated sporangia borne in clusters at the ends of short forked lateral branches on a pinnate structure, and brought forward evidence for their connection with the large fern-like fronds *Lepidopteris Ottonis*, which we now have further reasons for considering as a pteridosperm (see p. 251).

In the present collection we have twenty-five specimens of a type which is closely comparable with *Crossotheca* in its general construction, and for this reason may be regarded as derived from pteridospermous plants. There are probably several species represented, but they all agree in having within their sporangia winged microspores of a characteristic form, similar to that previously found in the Caytoniales. These microspores are of the type which was found inside the corystospermous seed described above, while similar spores have been seen inside the cupules, as well as resting on the stalks, of *Umkomasia* inflorescences, and they have often been found on the surfaces of *Dicroidium* leaves. The microsporangiate structures are found closely associated with the female inflorescences, thus there is a high degree of probability that they belonged to the same family of plants.

A structure comparable to those under consideration was described by Seward (1903, Plate 9, figs. 2, 2*a*), from the Stormberg rocks of Kenigha River, South Africa, under the name of *Stachyopitys sp.* and compared with a form from the Argentine described by Geinitz (1876, Plate 2, figs. 23, 24) under the name of *Sphenolepsis rhætica.* Shirley (1898, Plate 18) described two forms from Queensland as *Stachyopitys annularioides* and *S. Simmondsi,* which are almost certainly allied to my structures. They were found in beds containing fronds of the same genera, which I now associate with the reproductive structures here described, and also structures superficially comparable with *Umkomasia.*

Before proceeding to the description of the present specimens, it is necessary to decide on their name. Justification may be found for employing each of the names *Crossotheca, Antholithus,* and *Stachyopitys,* but each is open to objection. If the generic name is merely to signify a type of structure *Antholithus* might be the most convenient, though in the forms hitherto described under this name the axis has exhibited dichotomous branching to a greater or less degree, but if the name is to indicate the male organs of a natural group of plants *Antholithus* should be avoided since it has been used for the microsporophylls of *Lepidopteris,* and previously—probably incorrectly—for the anther-bearing branches of the Caytoniales (Thomas, 1925, p. 327). *Stachyopitys* is a recognized name for structures of the type now in question, but this name was instituted by Schenk (1867, p. 185, Plate 44, figs. 9–12) for structures from the Rhætic of Franconia, described as axes bearing short lateral appendages terminating in oval bodies which open at maturity into 10–12 spreading lobes. This description would scarcely be applicable to the present specimens, and there can be little doubt that the type specimens from Franconia belonged to some genus of plants distinct from those of the southern hemisphere. Thus, it is impossible to continue to use Schenk's name, and future confusion may be avoided if a new generic name is instituted. The name *Pteruchus** is therefore proposed as the generic designation of the microspore-bearing structures from the southern hemisphere of the type described below.

Pteruchus gen. nov.

Diagnosis.—Branched structures bearing microsporangia in groups, branching dichotomous, alternate, or opposite; each ultimate branch narrow or expanded into a delicate circular, elliptical, or star-shaped lamina generally bearing a considerable number of small oblanceolate synangia on one side; synangia consisting of uniform delicate elongated cells, not showing any definite dehiscence line, and probably dehiscing by a terminal pore-like opening; synangium before dehiscence containing a mass of microspores probably produced in two loculi; microspores having a central cell, and two lateral wings symmetrically placed.

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* Greek πτέρυξ = a wing-like thing.

Type species of the genus *Pteruchus africanus*.

General Description.—The microsporangial branches of the African forms are all small structures not more than 3 cm. long overall, but judging from SHIRLEY'S figures —which do not agree very well with some of the few dimensions given in his description— the Australian species may be somewhat larger. Branches in most cases appear to arise in one plane, opposite or alternate, while *Pteruchus annularioides* (SHIRLEY) Thomas is described as having alternate branches forking once or twice. Lateral branches are usually short, not much more than 2–8 mm. long. Some specimens may possibly have been unbranched. Main axis, about 1·5 mm. broad at the base, is thin and delicate; small bracts were produced near its base in some forms, but the lateral branches do not appear to have had subtending bracts. Lateral branches gradually expand into a delicate lamina, which varied in shape in different species. In some specimens its margin is very ill-defined and was probably very thin since the outlines of the sporangia are visible through it. In others the margin which can be seen more clearly, was slightly lobed. The lamina was more or less circular or elliptical, 3–7 mm. in diameter. The sporangia appear to have been produced all over the under surface of the lamina, their number varies in the different forms but could seldom have been less than 12 in each group. In this respect the African forms differ from the Queensland species, since WALKOM (1917, Plate 4, fig. 6), re-describing SHIRLEY'S forms, states that there are about twelve obovate bodies (sporangia) in a cluster in *S. annularioides* and not more than six in *S. Simmondsi*. But we do not know whether he was able to see the whole of the group or only those sporangia which projected beyond the margin of the lamina.

The sporangia vary in length from about 1 mm. to 4 mm., they are obovate or oblanceolate in shape, and from 0·4 to 0·75 mm. broad at their widest part. Their form is well seen in fig. 73, Plate 24. Their apices are pointed or bluntly rounded. They were composed of elongated cells whose walls give the appearance of longitudinal striations. No signs of a dehiscence line is to be seen, nor do any sporangia show a longitudinal fissure. On the other hand, some specimens have a small notch at their apex suggesting the presence of an apical pore, and one of these was found to contain only two spores when macerated. In several cases groups of five or six sporangia apparently attached together at the base were found lying alone in the matrix of the bed, fig. 73, and this may indicate that they were produced in groups, though only one specimen shows any indication of the grouping of sporangia in the large clusters in which they originated.

All the synangia macerated contained some remains of winged microspores, large numbers usually being seen. The evidence is not yet clear as to whether these were produced in one or in two loculi. In cases like this the presence of two or more loculi filled with spores may often be detected in mummified material for the ground tissue of the synangium dissolves away on maceration leaving the separate masses of spore coats clearly visible, and they may even float out as separate groups in the preparation. If, however, the sterile tissue separating the loculi is thin the spore groups may remain in close contact and appear only as one solid mass, though it may be possible to distinguish the edges of the two adhering masses under the microscope. In most of the preparations made from the present material there seemed to be a single mass of spores in the sporangium, but in several the spores seemed to form two superposed groups, while in another preparation two masses of spores floated out from a sporangium after solution of the soluble material and the removal of the thin cutinized remains of the sporangium wall.

Some of the preparations show the spores in various stages of development. Sometimes the spores appear almost circular or elliptical in outline, and of fairly uniform thickness, the characteristic wings are not expanded, and there is a single linear scar across the centre of the spore, probably indicating development of the spores in two pairs from the spore mother cell. As development proceeded the wings appear to have gradually become drawn apart, leaving the central body of the spore clearly distinguishable by its smooth and apparently thinner wall. The wings often have a finely granular or reticulate appearance, fig. 77, Plate 24, owing to the uneven distribution of the cuticular thickening. The fully-expanded microspores measure from 0·1 to 0·07 mm. across the wings, and about 0·05 mm. across the body.

Preparations have been made from several specimens to show the structure of the cuticule of the main axis and of the heads bearing sporangia. These show certain well-defined differences, which support the view that several species are represented in the collection. In all, however, the structures are delicate and but lightly cuticularized. The cuticles of the axis show very little difference on the two sides. Their cells are more or less arranged in regular longitudinal rows, and stomata are present, in some forms in abundance. The preparations from the fertile heads often show a wrinkling, such as is associated with a fleshy structure, and numerous small stomata. The form and thickenings of the stomatal structures are identical with those seen in certain species of *Pilophorosperma*, and this provides further good evidence for the association of these male and female structures.

In view of the variety of forms of female inflorescences found in the bed and also of fronds, we should expect that several species of microsporangiate structures would be represented. Unfortunately, many of the specimens in our collection are fragmentary and few complete examples are seen; this renders the recognition of specific differences less easy. It seems fairly safe, however, to divide the present collection of forms into seven or eight groups, in which we have definite characters that seem likely to be of specific importance, and these will be made the types of species. Notes are added concerning some other forms.

Pteruchus africanus, sp. nov., figs. 71, 72, Plate 24, and figs. 34, 35.

Diagnosis.—Main axis with fine superficial striations, epidermal cells generally long and narrow with some short thicker cells bearing circular hair bases and a few elongated stomata with longitudinal orientation; slender lateral branches arising at an acute angle to the axis, bending sharply and becoming expanded into elliptical heads 3–5 mm. long and 2–3 mm. broad ; fertile heads with very thin cuticles, bearing very numerous synangia, the whole group about 9 mm. long and 6 mm. broad ; individual synangia spathulate with bluntly pointed apex, 2–3 mm. long.

Type-specimen No. U244.

Description.—All the specimens are incomplete, the best, shown in fig. 71, Plate 24, and fig. 34, is 24 mm. long, but is broken at the base and the origin of the lower lateral branches is not seen. The axis is 1·2 mm. wide at the base, it narrows slightly above and appears to terminate in a tuft of synangia. Some of the lateral branches are very clearly seen in this and other specimens ; they have been studied by means of transfer preparations.

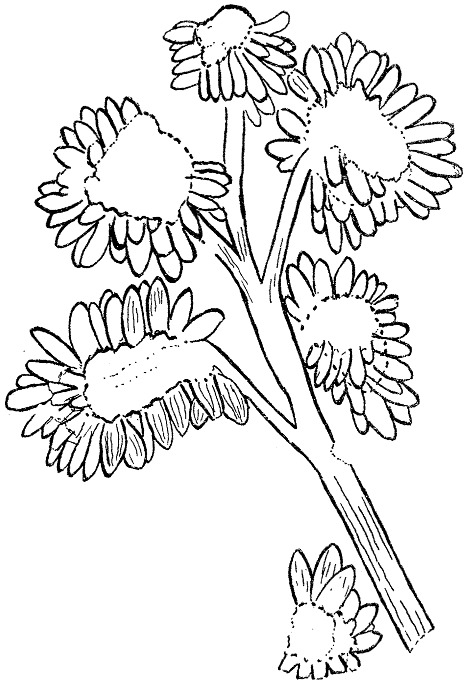

FIG. 34.—*Pteruchus africanus* sp. nov. Specimen showing branching, elongated fertile heads and synangia. × 3·5. No. U244.

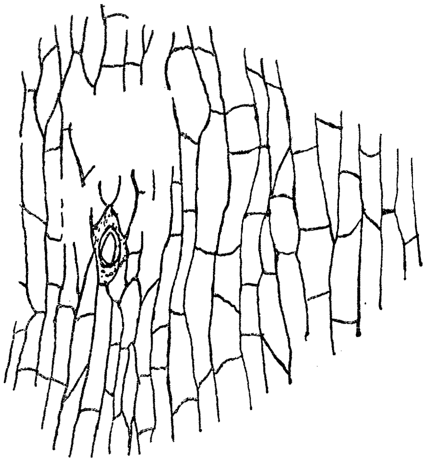

FIG. 35.—*Pteruchus africanus* sp. nov. Cuticle of axis with characteristic hair base. × 120. Slide No. 53.

The cuticles of the axis were delicate and only fragments were obtainable. It is possible that the axis was originally somewhat flattened and had elongated epidermal cells near its margins with shorter and broader cells near the centre. A few circular hair bases are seen, as shown in fig. 35. The elliptical fertile heads are characteristic, their lamina is very thin at the margins, which are ill-defined and allow the outlines of the synangia below to be seen. The synangia are well preserved and their loculi were filled with spores in masses about half a millimetre wide. Individual spores were ·075 mm. across the wings. The specimen No. U145, fig. 72, Plate 24, is associated with this species, though shorter and more compact ; at its base are a pair of ovate pointed bracts 3 mm. long; above two large fertile heads lie on top of the axis, while another, 7 mm. long, lies to one side and shows about twenty synangia. In another specimen (U247) the lower side of a fertile head is seen with synangia radiating out from a central line; they are more than 3 mm. long, and taper gradually to their base.

The shape of the fertile heads and the cuticle distinguish this species.

Pteruchus papillatus sp. nov., figs. 36, 37.

Diagnosis.—Axis with short alternate lateral branches; epidermal cells of axis mostly rectangular or polygonal, not more than twice as long as broad, many with a small central papillate projection, including numerous stomata with pore and guard-cells transversely placed, subsidiary cells slightly thickened; lateral branches curve rapidly and expand into a thin circular head 3 mm. in diameter bearing numerous synangia which often completely cover the lower part of the branches and overlap the central axis; synangia 2·5–3 mm. long, 0·4–0·5 mm. broad, oblanceolate, tapering gradually to a blunt point.

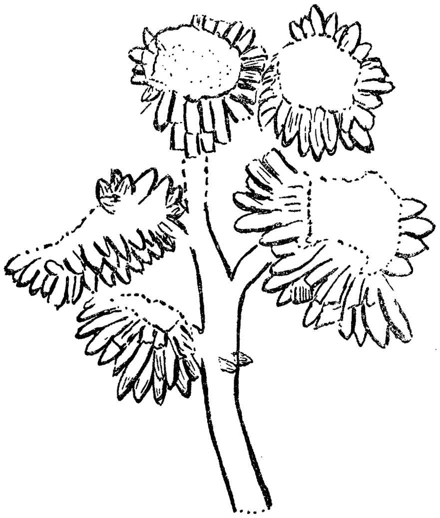

Fig. 36.—*Pteruchus papillatus* sp. nov. No. U44. × 3.

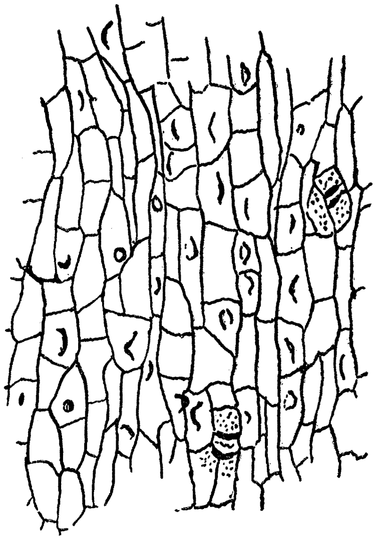

Fig. 37. *Pteruchus papillatus* sp. nov. Cuticle of axis, showing characteristic papillæ and stomata with thickened subsidiary cells. × 120. Slide No. 54.

Type-specimen No. U44.

Description.—The forms with circular heads show certain differences in their general appearance, but are difficult to separate without reference to cuticular structure. The specimen shown in fig. 36 yielded some good cuticle fragments by Walton's transfer method, and the preparations, fig. 37, show distinctive features. The more or less rectangular cells with their small thickened spots or papillæ and the stomata with their oblique or transverse orientation suggest a connection with a form like *Pilophorosperma granulatum.*

The short lateral branches are mostly obscured by the overlapping synangia. It is uncertain how they were attached to the fertile heads, though they were probably peltate. The margins of the heads are very thin, about twenty synangia are seen round the circumference, though there were more synangia below. The synangia were rather more fusiform than in *P. africanus.* A cuticle preparation was made from one of the circular heads and shows polygonal cells, some of which were papillate, small stomata were also present. The width of the microspores was 0·1 mm. and the wings have a reticulate thickening.

Pteruchus peltatus sp. nov., figs. **38, 39**.

Diagnosis.—Axis smooth, with opposite short lateral branches, producing peltate fertile heads which are markedly convex; epidermal cells of axis elongate, including stomata longitudinally arranged; fertile heads 3–5 mm. in diameter; synangia numerous, 1·5–2 mm. long.

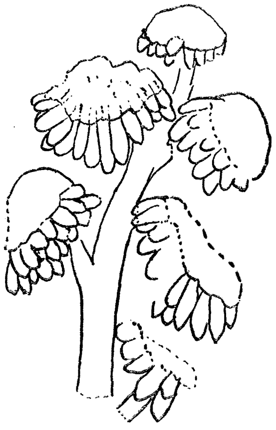

FIG. 38.—*Pteruchus peltatus* sp. nov. No. U58. × 3.

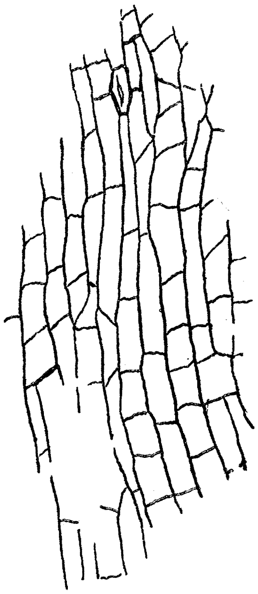

FIG. 39.—*Pteruchus peltatus* sp. nov. Cuticle of axis showing stoma. ×120. Slide No. 55.

Type-specimen No. U58.

Description.—This type is represented by a single very well-preserved specimen, fig. 38. The fertile heads were concave and apparently peltate with the synangia attached below and a thin membraneous margin. In spite of the good preservation of the specimen it is very difficult to determine exactly where the margin lies, for the outlines of the synangia can be seen through it for a distance of about 1 mm. The individual synangia were spathulate in shape with a rounded apex and contained spores of the usual type. The smooth axis has a thin cuticle showing cells that are mainly elongated and rectangular in form, fig. 39. A few stomata with longitudinal orientation show their pore and thin guard cells, they seem to have been slightly sunk. While it is possible that this specimen is only a younger form of one of the other types, its cuticular structure and general form merits separate description.

Pteruchus Hœgi sp. nov., fig. 75, Plate 24, and figs. 40, 41.

Diagnosis.—Axis with basal sterile portion bearing one or more bracts in the lower 10 mm., with short alternate fertile branches above and a terminal fertile head; surface of the axis shows fine longitudinal striations, cuticle of axis composed mainly of elongated cells in longitudinal rows with a central band of irregular more or less isodiametric cells, stomata with thickened subsidiary cells; fertile heads circular, probably peltate, about 6 mm. across, with thin central lamina; numerous fusiform synangia 2·5–3 mm. long, arranged radially round centre of lamina.

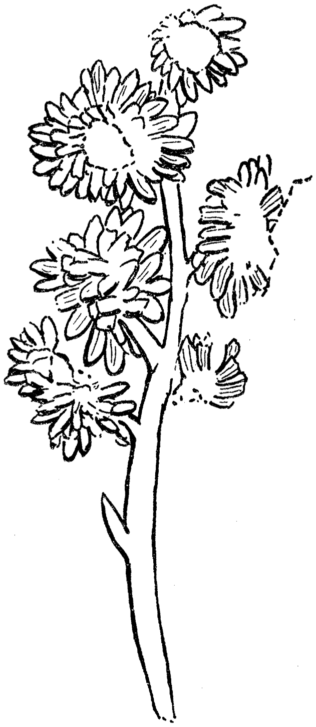

FIG. 40.—*Pteruchus Hœgi* sp. nov. No. U23. × 3.

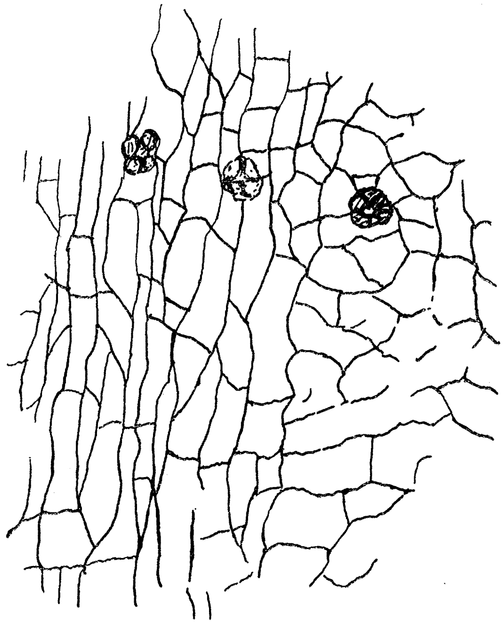

FIG. 41.—*Pteruchus Hœgi* sp. nov. Cuticle of axis. × 120. Slide No. 56.

Type-specimen No. U23.

Description.—The specimen shown in fig. 75, Plate 24, and fig. 40, is 30 cm. long, the lower part of the axis is unbranched and bears a bract. The cuticle of the axis is very thin and most of the fragments obtained were derived from the marginal parts where the cells were elongated, but some of the preparations show also the remains of irregular cells lacking the longitudinal arrangement, fig. 41. These are regarded as parts of stomatal bands comparable with the structures seen in *Umkomasia Macleani*, but stomata occur elsewhere, they appear to have raised thickened subsidiary cells and so approach the Lepidopteris structure. The fertile heads are rather small and little can be seen of their lamina. The synangia are numerous and radiate out from a central point; they seem to have a fusiform shape; in several cases there is a small notch at their apex and on maceration the loculi were almost empty while the walls showed rather stronger cuticularization than usual. This may indicate that dehiscence took place by a terminal pore. A few winged microspores were found in the synangia, indicating that the species cannot be associated with *Lepidopteris*.

Pteruchus Edwardsi sp. nov., fig. 74, Plate 24, and fig. 42.

Diagnosis.—Axis more than 4 cm. long, with spirally arranged branches about 5 mm. long; branches terminating in small circular peltate heads, which bear a single whorl of 10–12 sporangia or synangia arranged round their periphery; synangia (?) 2–3 mm. long, 0·7 mm. broad, of curved form.

Type-specimen No. V20911 in the collection of the Geological Department of the British Museum.

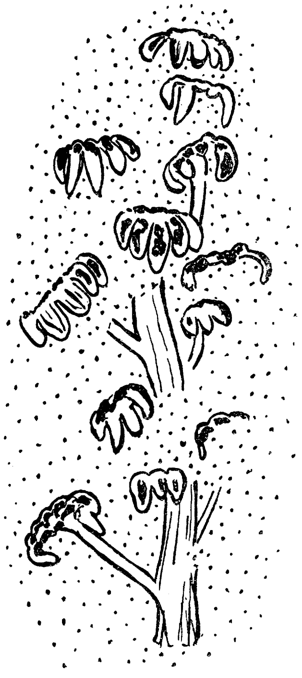

FIG. 42.—*Pteruchus Edwardsi* sp. nov. Diagrammatic drawing of type specimen from Elliot. No. V20911. (B.M.) × 3.

Description.—This species is founded on a specimen which differed from all the other forms described in this work in its place of origin and mode of preservation. It was collected by Mr. W. N. EDWARDS at Koning's Kroon, near Elliot, from beds which, like those of the waterfall at Burnera, are probably of Middle Molteno age, but the plant remains are only moulds in a fine grained matrix from which all the actual plant tissue has disappeared. The structures had undergone very little compression before the mould was formed, and so their original form is clearly seen, but it is impossible to obtain any information about the cuticles or the spores. The surface of the mould is covered by a whitish brown deposit of mineral matter which facilitates the photography of this form, fig. 74, Plate 24, but the white colouring invades the darker matrix to some extent round the remains of the plant structures. In the absence of spores and cuticle we cannot be certain of identity of this form with the genus *Pteruchus*, though its general structure makes this highly probable.

The whole structure seems to have been distinctly longer than any of the other forms. The central axis is only seen in two places, but the remains of the branches cover a length of 3·5 cm. The axis was 1·4 mm. broad, and the branches produced from it are spirally arranged, remains of about twenty fertile heads are seen and they appear to have been borne on slender branches, 0·4 mm. wide, which spring from the axis at an angle of about 45°. They were about 5 mm. long in the middle and upper part of the specimen. These branches appear to have terminated in small peltate heads, about 2·5 mm. in diameter, around which was a single ring of sporangia or synangia. The remains of the sporangia are seen as small sausage-shaped cavities 2–3 mm. long and about 0·7 mm. broad. There were 10–12 only on each head, a number which is comparable with that seen in the specimens described by SHIRLEY (1898) and WALKOM (1917) for *Pteruchus* (*Stachyopitys*) *annularioides*, and by SEWARD (1903), but which is very distinct from that seen in our other species. The remains of the sporangia show a well-marked cavity which was probably filled with spores, and a terminal pointed portion, which was probably thinner and more delicate in the original structure.

This form appears to be quite distinct in the spiral arrangement and number of lateral branches, and in the form of the fertile heads with their smaller number of sporangia. It occurs in close association with fronds of *Dicroidium* of the type named by DU TOIT (1927, p. 332), *Thinnfeldia lancifolia* Morris.

Pteruchus stormbergensis sp. nov., fig. 43.

Diagnosis.—Axis with opposite branches separated by internodes about 7 mm. long; branches in lower part of structure long, with small fertile heads bearing large tufts of pendulous sporangia; epidermal cells of axis much elongated and arranged in longitudinal rows; fertile heads of branches with granular surface; synangia oblanceolate, 2–3 mm. long.

Type-specimen No. U240 and counterpart.

Description.—The specimen shown in fig. 43 differs noticeably from the other species in its general form and in its slender axis and branches. Its epidermis seems to have been composed of elongated cells. The mode of attachment of the small fertile heads to the branches is not clearly seen, though it appears to be lateral. The lamina of the heads appears to be somewhat granular in appearance, while its cuticles are thin and wrinkled with numerous small stomata. Maceration indicated that many of the spores had been shed, though a few remained inside the loculi. The preparations show the long narrow shape of the outer walls of the synangia and also traces of other membranes, possibly from inside the loculi.

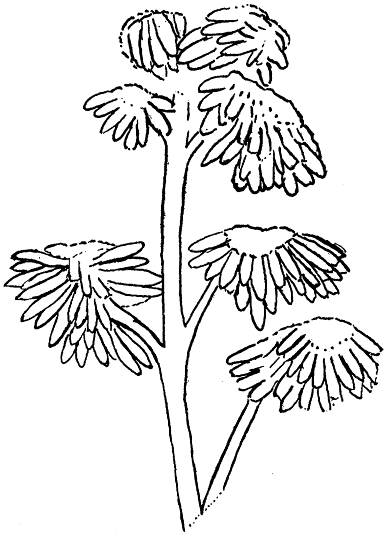

FIG. 43.—*Pteruchus stormbergensis* sp. nov. No. U240. × 3.

Pteruchus dubius sp. nov., figs. 44, 45.

Diagnosis.—Fertile branches bearing sporangia along a length of 7 mm. from the apex without any well-defined fertile head; cuticle of stalk thin; epidermal cells rectangular in longitudinal rows; stomata on stalk very numerous, longitudinally or transversely arranged, with fusiform thickenings on either side of pore and slightly thickened subsidiary cells; synangia grouped along the sides in upper part of stalk, most abundant towards the apex, where the stalk expands somewhat; synangia spathulate, 1–0·8 mm. long, with rounded apex.

Type-specimen No. U248 (and counterpart U241).

Description.—The specimen, fig. 44, shows a distinct type of grouping of synangia along an axis, which shows no signs of branching, though it may well represent a detached lateral branch of a much larger structure. Its cuticle is most distinctive, fig. 45, owing to the presence of very numerous stomata with thickened subsidiary cells; these generally have a longitudinal orientation, though a few are transverse; the epidermis was uniform in structure on both sides of the axis. The individual synangia were distinctly shorter than those of the other species and were elliptical to spathulate in shape with a rounded apex; they contained winged microspores of the usual type.

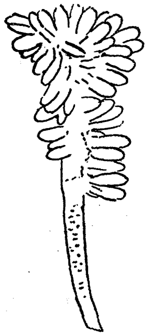

FIG. 44.—*Pteruchus dubius* sp. nov. No. U241. × 3.

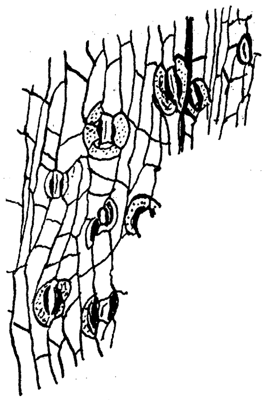

FIG. 45.—*Pteruchus dubius* sp. nov. Cuticle of axis showing numerous stomata with thickened subsidiary cells. × 120. Slide No. 57.

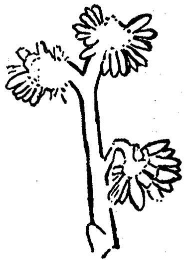

FIG. 46.—*Pteruchus minor* sp. nov. No. U125. × 3.

Pteruchus minor sp. nov., fig. 76, Plate 24, and fig. 46.

Diagnosis.—Axis slender 0·6–0·8 mm. wide, terminating in a pair of fertile branches; lateral branches alternate, short, terminating in small tufts of synangia 4 mm. in diameter; heads of fertile branches probably deeply lobed, about 1·5 mm. in diameter; synangia relatively few, 1·5 mm. long, spathulate in shape, rounded at apex.

Type-specimen No. U125.

Description.—The small specimen shown in fig. 46, and fig. 76, Plate 24, is fairly well preserved, but incomplete. It appears as though the axis forked at the apex, but this is not quite certain owing to the presence of a small projection near the base of one of the branches. The branches and fertile heads are very small, and their lamina is not very clear, but seems to show pointed lobes in some places. The synangia appear to radiate out from a centre, and about twenty occur in each tuft; they are smaller than those of the other species with circular heads. The form and size of the specimen suggest that it is specifically distinct.

Pteruchus sp. Type X. figs. 47, 48.

Specimen No. U129 is interesting because it shows more clearly the vegetative portion of one of the fertile heads. The remains of five fertile heads can be made out, but the synangia attached to them are only seen in a few places, where, however, they are well preserved and show typical forms. The uppermost head appears to have been attached centrally to its pedicel, and shows eight distinct radial ridges ; its margin was indented opposite to the ridges. Cuticle preparations made from the lamina, fig. 48, were thin but showed numerous stomata, which can be closely compared with preparations made from cupules of female inflorescences. The cuticle of the axis seems to have been composed of isodiametric cells. The spores were of the normal type, but not fully developed.

FIG. 47.—*Pteruchus* Type X. No. U129. Showing the stouter fertile heads with radiating ridges and grooves. × 3.

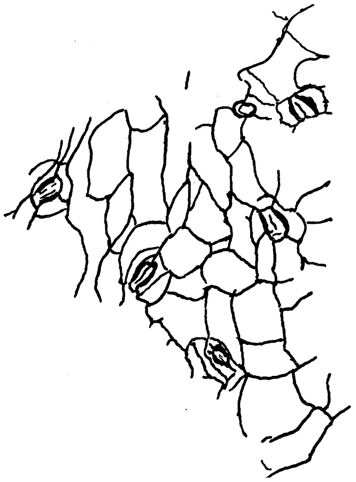

FIG. 48.—*Pteruchus* Type X. Cuticle of fertile head showing stomata. × 120. Slide No. 58.

This specimen shows that the synangia were produced on the under side or inside of a somewhat cup-shaped structure or lamina which can be compared with the seed-bearing cupule.

Pteruchus. Type Y.

A fragmentary specimen, No. U131, may be mentioned, since it indicates the probability that other species had considerably larger fertile heads. Nothing is seen of the axis or branches, but we appear to have two heads more or less superposed. One of these has a wrinkled lamina broken at the edges with a diameter of at least 7 mm. The remains of numerous synangia project from it and occupy a zone about 5 mm. broad, so that the whole fertile head is about 17 mm. in diameter. The other head shows a mass of synangia overlapping one another and with a general radial arrangement. The individual synangia were probably 4 mm. or more long; they seem for the most part to be empty. The lamina of the head was more strongly cutinized than in the other species and the remains of polygonal cells were clearly seen. The walls of the latter showed microsinuosity in places, and there were also numerous stomata, accompanied by thickenings extending over the subsidiary cells, as seen in other species of the Corystospermæ.

General Comparisons.

The similarity of *Pteruchus* to the Queensland forms described by SHIRLEY has already been mentioned and it would be well to include provisionally his two species, *annulari-oides* and *simmondsi* in the genus *Pteruchus*. Before their generic identity can be regarded as established we need to know whether the Australian forms possessed winged microspores and had similar cuticle characters. The Tasmanian forms which JOHNSTON (1888, Plate 27, figs. 2*d* and *e*) figured may be similar structures. It is more doubtful whether the specimens from the Argentine which GEINITZ (1876) described should also be included; it is probable that they should, but the published figures furnish insufficient evidence.

An interesting comparison can be made with the male fructifications of the Carboniferous pteridosperms. So far as our knowledge goes, these were generally groups of elongated sporangia or synangia. The Lower Carboniferous forms *Telangium, Diplotheca,* and *Calathiops*—in which GOTHAN (1927) includes the types described by KIDSTON (1924) as *Schuetzia* and *Alcicornopteris*—possessed erect tufts of sporangia terminating short branches which arose by the dichotomy of a main stalk. KIDSTON described the branches of *Telangium* as terminating in a disc to which the unilocular sporangia were attached, this disc reached about 3 mm. in diameter in *T. bifidum* and was regarded as directly derived from the rachis and not from the modification of a pinnule. This type of structure may be regarded as the primitive form.

When we come to the Upper Carboniferous, we find a considerable variety of forms. The axes bearing the tufts of sporangia no longer show equal dichotomies, but the branching is monopodial, the sporangial groups being borne on side branches of the main axis or rachis. The fertile disc may still be small, as shown in BERTRAND'S (1926) figure of *Sphenopteris striata,* and HIRMER'S (1930) *Crossotheca pinnatifida,* or it may be somewhat enlarged, so that it is possible to compare it with a fertile pinnule, as in *Crossotheca.* The sporangia may be united in their lower parts to form a synangium of 6–12 members as in *Telangium Scotti*, or partially united and surrounded with a cupular envelope as Professor HALLE (1931) has found in *Whittleseya* and the type called *Aulacotheca* (*Holcospermum*) *elongata* Kidst. In the *Potoniea* type (KIDSTON, 1914, p. 113) we have a bell-like structure with numerous sporangia on the inner surface, the individual sporangia being apparently small and separate. Then we have a further group of forms, in which the sporangial groups are no longer free but have become involved in the fusion of branches to form a lamina, they still terminate vascular strands, the sporangia may retain their original form or tend to be united at their bases. In this group we may place *Dactylotheca* and possibly some of the varied forms of *Asterotheca*, if, indeed, these are pteridosperms as suggested by KIDSTON (1925, p. 538). In *Zeilleria* the tufts of sporangia were still terminal structures, but lamina formation had taken place between them and the rachis.

Thus the historical sequence of forms shows precisely the same course of evolution as BOWER has outlined in his great work for the ferns, we have the evolution of marginal and superficial synangia along the same lines as have been indicated above for the seeds. It may also be suggested that the evolution of the *Potoniea* and *Whittleseya* types from the Lower Carboniferous may be compared with the evolution of perigynous and epigynous flowers from the hypogynous forms.

Pteruchus seems to show the persistence of the *Crossotheca Kidstoni* (= *C. Hœninghausi*) type into the Mesozoic epoch. *P. africanus* might be called a *Crossotheca* had not the specimens been so well preserved and the winged spores found. It must also be compared with the Permian form called by GOEPPERT *Dictyothalamus schrollianus*, and with the specimen recently figured by CARPENTIER (1930) which was compared with that form. Some of KIDSTON'S (1923, Plate 89, figs. 6–8) figures of *Crossotheca Schatzlarensis* are suggestive when compared with our *Pteruchus peltatus* and *Pteruchus Edwardsi*. Though we cannot yet be absolutely certain that these forms had peltate fertile heads, the mode of attachment of the pedicel to, what KIDSTON called, the limb of the pinnule suggests how a peltate structure might have arisen from a form like *C. Crepini* (KIDSTON, 1923, fig. 27, p. 345).

Often in the Palæozoic forms the microsporangial branches were borne on naked branches, which formed part of a large frond. The Lower Carboniferous *Diplopteridium teilianum* (KIDSTON) was found by WALTON (1931, p. 349) to possess a fertile branch system springing from the point of forking of the rachis of the frond. This suggested that the inflorescence of the Corystospermæ and of *Pteruchus* might be borne in a similar position, but no evidence of such a structure can be found, and in some specimens it seems out of the question owing to the large size of the fertile axis compared to the size of the rachis of the associated leaves. If we assume, in the absence of definite evidence, that the microsporangial branches of all the Palæozoic pteridosperms were produced on the same rachis as bore foliar pinnæ, it is, nevertheless, likely that the fertile structures of the Corystospermaceæ were borne on special branches, or inflorescences, since here the sterile fronds have become so much reduced in size.

Foliage of the Corystospermaceæ.

While the general structural features of the reproductive organs of the Corystospermaceæ are so comparable with those of the palæozoic pteridosperms as to leave little doubt about their affinities, this identification is confirmed by the results of a general survey of the leaves occurring abundantly with them.

The flora of the black shales exposed in the waterfall on Mr. MACLEAN'S farm is a rich one, and, as usual, the great majority of the plant remains are leaves, mummified and very well preserved. The forms represented include a series of types, unlikely to be connected with the reproductive structures here described, such as *Cladophlebis sp.*, forms of *Baiera,* coniferous twigs and Cycadean or Bennettitalean forms such as *Moltenia*, *Pterophyllum*, and *Pseudoctenis*. But the most abundant leaves are types with a somewhat fern-like character having a resistant cuticle and including those identified by DU TOIT, WALKOM, and others as *Thinnfeldia* Ett (= *Dicroidium* Gothan), *Stenopteris, Pachypteris, Taeniopteris, Lepidopteris,* and *Glossopteris.* This group most probably includes the species whose reproductive organs have now been described.

The leaf from this locality which DU TOIT (1927, p. 326, text fig. 4) identified as *Sagenopteris longicaulis* is almost certainly the same as the form which he describes as *Glossopteris Browniana.* Its identification as Sagenopteris depended on the single specimen in which a group of leaves appeared to spring from a common point of origin, though this point was not seen in the original hand specimen. We were fortunate in finding a more complete specimen having leaves of the type figured by DU TOIT attached in whorls to a slender stem, parts of two whorls 5 cm. apart being seen. There is now evidence (WALTON and WILSON, 1932, p. 201) from other sources to show that in at least some species of *Glossopteris* the leaves were arranged in whorls. The investigation of the cuticle structure of these *Glossopteris* leaves renders it improbable that they were connected with the fertile structures described in this paper, for though they evidently possessed a lightly cuticularized epidermis the cuticle was exceedingly thin and delicate.

In the other Mesozoic localities which have been studied in detail, reproductive structures are usually found associated with an abundance of the leaves of the plants on which they were borne. Thus strobili of *Williamsoniella* and *Williamsonia* are only found in spots where leaves of *Tæniopteris vittata* and *Ptilophyllum spp.* respectively are abundant. *Caytonia* and *Gristhorpia* only occur with great quantities of *Sagenopteris* leaves (THOMAS, 1925, p. 332). The plant bed containing the *Corystospermaceæ* contains a very considerable mass of fronds of the forked *Dicroidium* and *Stenopteris* types (some typical forms are shown in figs. 49–51), and they are by far the most abundant forms in the locality. Both of these have been identified, by several authors, with plants occurring in Europe, but in the light of modern knowledge this view seems incorrect. GOTHAN (1912) instituted the name *Dicroidium* for fronds like those of figs. 49, 50, from the Southern Hemisphere which had previously been called *Thinnfeldia*, on the grounds of their characteristic forking rachis and their cuticle structure. All our recent observations on South African forms of this type confirm GOTHAN'S view. In the form of the epidermal cells, the mode of the distribution of the stomata, the form of the stomatal openings and their relation to the surrounding cells, the cuticles of *Dicroidium* are quite different from those of the European *Thinnfeldia.* The forked rachis is seen in every reasonably complete frond from South African localities, and fairly perfect fronds whose ultimate segments are similar to those described by

Du Toit as *Thinnfeldia rhomboidalis* (Du Toit, 1927, p. 340) are now found to have been forked.

The leaves described by Seward, Du Toit, Walkom, and others as *Stenopteris** also have forking axes, fig. 51, and they may be connected by a series of forms with the *Dicroidium* type. In their cuticle structure also they show an unmistakable similarity (*cf.* fig. 52). There is no evidence of forking in the fronds from the Northern Hemisphere to which Saporta's (1873) name of *Stenopteris* was originally applied. Harris (1932) has identified this Northern type in his Greenland collections and finds that it had cuticles which were completely different from the corresponding leaves of the Southern Hemisphere. The name " *Stenopteris* " will be retained, however, in the present work.

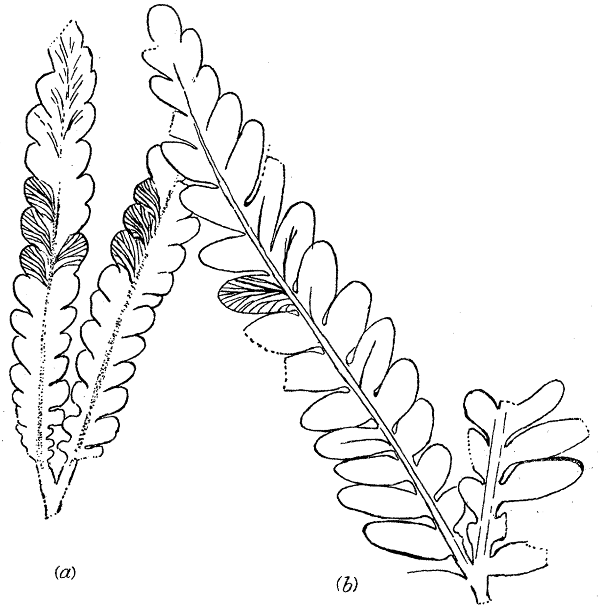

Fig. 49.—(*a*) *Dicroidium odontopteroides* (Morris) ; (*b*) *Dicroidium sp.* cf. *lancifolia* (Morris). To show form of frond and nervation. Nat. size. Specimen No. U162.

On the basis of external form it seems very difficult to draw any sharp line between the genera *Dicroidium*, *Pachypteris*, and " *Stenopteris*," though it may prove to be possible on the basis of cuticle structure. It is highly probable that these three form-genera belonged to the same group of plants, while *Johnstonia*, which also had a forking frond, is probably allied to them. *Pachypteris* and " *Stenopteris* " have exceptionally thick and resistant cuticles, while in *Dicroidium* the cuticles all resist acid oxidizing agents, but vary in thickness. The form usually known as *D. odontopteroides* (Morris) has a rather delicate cuticle, while some of the bi-pinnate forms—probably similar to those identified by Du Toit as *Thinnfeldia Feistmanteli* Johnst.—have a thick cuticle like that of " *Stenopteris*." Whereas Du Toit (1927, p. 307) identified seven species of *Thinnfeldia* (= *Dicroidium*), two species of *Pachypteris* and two species of *Stenopteris* from the Molteno beds, there were probably a larger number of species present.

* For references see Du Toit (1927), p. 362.

Leaves of the *Lepidopteris* type are present in the bed at the Waterfall, but they need not be considered when discussing the Corystospermaceæ, since their characteristic stomatal structure has enabled their seed-bearing structures to be identified with some certainty. Thus the facts of association are strongly in favour of the hypothesis that *Umkomasia*, *Pilophorosperma*, *Spermatocodon*, and probably *Pteruchus* belonged to the plants which bore leaves of the *Dicroidium* and " *Stenopteris* " type.

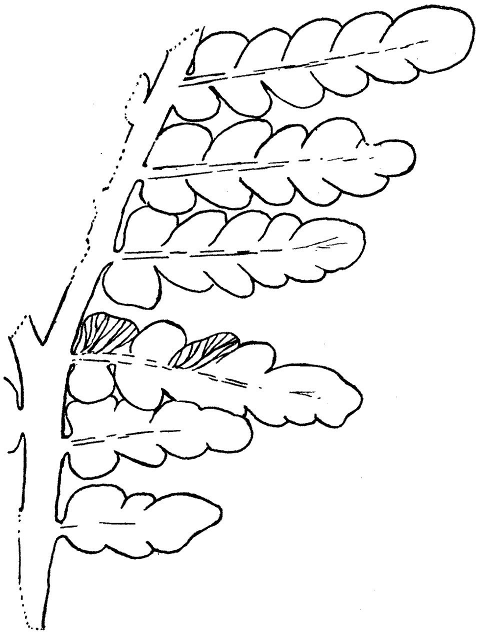

Fig. 50.—*Dicroidium sp.* cf. *Feistmanteli* (Johnston). A bipinnate form with papillæ on the epidermal cells. No. U100. Nat. size.

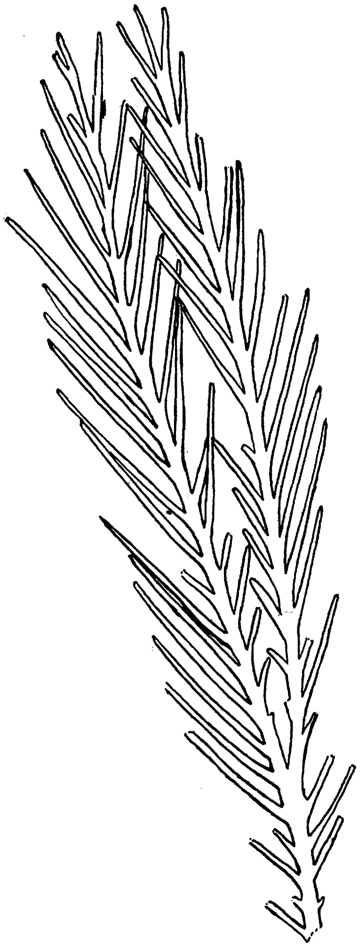

Fig. 51.—" *Stenopteris* " *densifolia*, Du Toit. No. U76. Nat. size.

Another, and probably more reliable, source of evidence is provided by the comparative study of the cuticle structures. The epidermal cells from different parts of the same plant usually show considerable similarity in their cuticle structures (Florin, 1931, p. 142), and so a demonstration that the cuticles of the cupules resembled those of certain leaves in their more important features, while those from the fertile axes showed some resemblance to those from the leaf petioles, would provide substantial evidence for the association of leaves with their reproductive structures. The detailed examination of the cuticles of all the forms of *Dicroidium* and " *Stenopteris* " is not yet complete, but sufficient progress has been made to show that there is considerable correspondence between them and the cuticular structures described above (cf. fig. 52 with figs. 7, 11, 24, etc.).

A few of the more important features may here be summarized.

(*a*) *General structure.*—The lamina of *Dicroidium* was composed of cells which were more or less isodiametric; of irregular shapes in the centre, becoming more regular in arrangement close to the margin. In " *Stenopteris* " the shapes of the cells are irregular in the centre of the lower part of the leaf, but become elongated near the margins. The cells of the cupules of the *Corystospermaceæ* are similar in these respects. In petioles and seed bearing axes the cells are more definitely elongated.

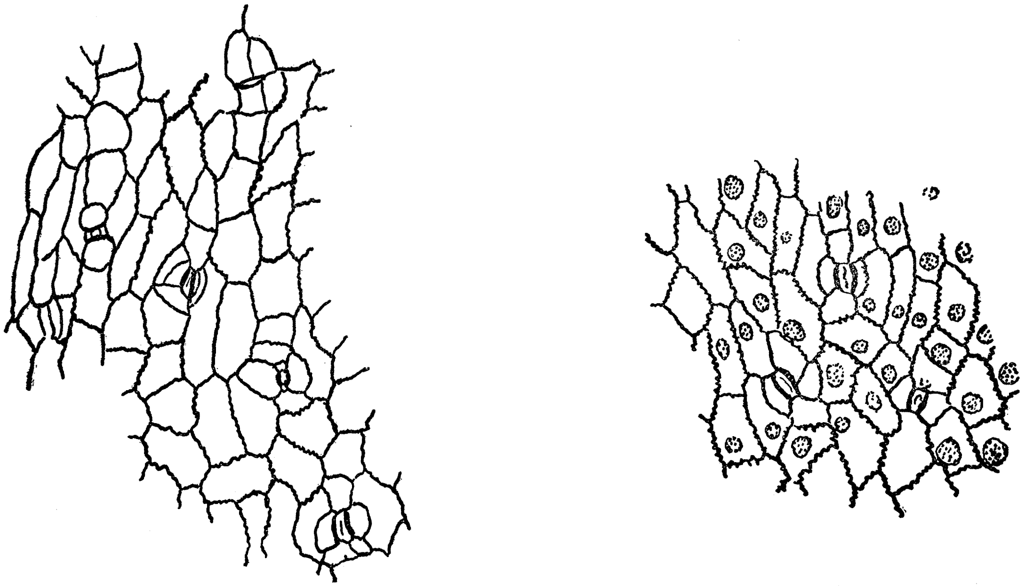
(*a*) (*b*)

FIG. 52.—Cuticles from lower epidermis of " *Stenopteris* " *densifolia* (*a*) and *Dicroidium sp.* cf. *Feistmanteli* (*b*); showing form of epidermal cells and stomata. × 120. (*a*), slide No. 62. (*b*), slide No. 63.

(*b*) The anticlinal walls of the epidermal cells in *Dicroidium* show the minutely sinuous walls which GOTHAN (1912) regarded as characteristic and we have the same character in the lower epidermis of " *Stenopteris*." The degree of sinuosity varies in different species and it is sometimes comparable with that seen in the cupules and bracts of some species of *Pilophorosperma* (figs. 24, 17 (*d*)).

(*c*) The periclinal (surface) walls of the epidermal cells of several forms of *Dicroidium* possess a small dark central spot representing a thickened mound or rudimentary papilla arising from the surface of the cell, fig. 52 (*b*). These spots are also present on the axes and cuticles of some species of *Pilophorosperma* (cf. figs. 11 and 21), but are absent in others.

(*d*) The stomata provide one of the most important features for comparison. In both the *Dicroidium* and the " *Stenopteris* " leaves they occur on both the upper and the lower epidermis with approximately the same frequency, and they likewise occur both on the inside and the outside of the cupules. In all these genera they lack any regularity of arrangement or orientation, the lateral subsidiary cells are slightly differentiated in shape and are somewhat thicker than the adjacent epidermal cells, while the polar subsidiary cells show little or no differentiation. There may be a pair of lateral subsidiary cells in some, while in others one or both may be divided into two by a wall running out radially from the guard cells; occasionally a division by a wall more or less parallel to the guard cells separates off cells like the "Krantz" cells of FLORIN (= encircling cells of HARRIS (1932, p. 81)). The surface walls of the guard cells were very thin, the pore is usually clearly visible, though it lacks any special cuticularization. The guard cells seem to have been sunk slightly below the surface in a shallow more or less rectangular cavity whose sides show a definite outline owing to the extra thickness of cuticle, which varies somewhat in the different species. The stomata on the leaves resemble those on the cupules in all these characters, and the slight variations seen in the different species of the *Corystospermaceæ* seem to have their counterparts in the different species of the leaves which have been examined. It seems probable that when all the forms of leaves have been examined we shall be able to match at least a number of them with species of *Umkomasia*, etc., by comparison of the details of their stomata and epidermal cells.

In view of all these facts it appears highly probable that the plants which bore the fertile structures of the corystospermous types also produced leaves of the type of *Dicroidium*, "*Stenopteris*," *Johnstonia* or perhaps of the forked *Pachypteris*, the cuticles of which have not yet been so carefully examined; it is very much more probable that these leaves belonged to pteridospermous types than to plants of filicinean affinities.

FAMILY PELTASPERMACEÆ.

This name is proposed for the plants whose characteristic fronds were designated *Lepidopteris* by SCHIMPER. Their pollen bearing structures have been identified and studied by ANTEVS and HARRIS, while the seed-bearing organs have now been discovered both in Greenland and Natal. These plants appear to be related to the pteridosperms and it is desirable to give them a family name which indicates that they were seed plants rather than ferns.

Lepidopteris SCHIMPER.

The specimen shown in fig. 53 can be closely compared in all its principal characters with the specimens figured by SCHIMPER (1869, Plate 34, fig. 1), ANTEVS (1914, Plate 1, figs. 1–3) and HARRIS (1932, p. 58, Plate 5, fig. 16; Plate 6, figs. 2, 10). Dr. DU TOIT (1927, p. 400, Plate 28) records this genus from the uppermost Beaufort beds at Aliwal North, but his specimens were preserved in sandstone and show little beyond the general form of the fronds, so that their identification with *Lepidopteris stuttgardiensis* (Jaeg.) is very uncertain; in fact, we cannot be certain that they belong to the genus.

The plant found at the Waterfall locality is distinct from the European forms previously described, but is close to *Lepidopteris Ottonis* (Goepp.) Schimp. It differs from this form in having a rachis which is comparatively smooth, especially in the upper part of the frond, and lacks the characteristic blister-like swellings in the lower part, while the epidermal cells show sinuous anticlinal walls which are very marked in some of the specimens. A point of particular interest is the occurrence in my collection of a specimen of a seed-bearing branch which can be referred to this genus. The stomatal structure of the fronds is very characteristic, and this led to the identification with them of a structure in which seeds were borne on peltate branches having stomata of the same type. While the present work was in progress HARRIS (1932, p. 65) found in his material from East Greenland specimens, which he has described as "cupulate discs," and isolated seeds which he was able to identify with *Lepidopteris Ottonis* owing to their cuticle structure. The complete structures, as restored by HARRIS, agree closely with my specimens from South Africa, though differing somewhat in size and in details.

The present work seems, then, to afford conclusive proof of the view that *Lepidopteris* was a seed-bearing plant, and it is of interest because very few natural genera have yet been found to be common to the Mesozoic floras of the Northern and Southern floristic regions.

Lepidopteris natalensis sp. nov., fig. 78, Plate 24, and figs. 53–55.

Diagnosis.—Fronds bipinnate, with fairly stout rachis having an uneven surface at the base, becoming more smooth above; uppermost pinnæ shortening rapidly towards the apex; one or two pinnules on the rachis between the pinnæ; pinnules linear lanceolate, margins of larger pinnules broadly serrate; secondary veins arising at a narrow angle from the well-marked midrib and forking once or twice; cuticles showing sinuous anticlinal walls, superficial walls often with a central thickened spot; stomata numerous on both sides. Female inflorescence with axis 1 mm. wide having fine longitudinal striations and spirally arranged branches; lateral branches with peltate heads 4–5 mm. diameter, much wrinkled, with recurved margins and bearing several seeds; small (immature) seeds 1 mm. long and 1 mm. broad near base, triangular-cordate in outline, larger seeds (mature) smooth, 4 mm. long, 2·5 mm. broad tapering to slightly curved micropyle; cuticle of axis and branches with some large thickened, rounded papillæ and small stomata; cuticle of inner (lower) side of disc thin without stomata; cuticle of outer (upper) side of disc thick with numerous small stomata.

Type Specimens, Frond, No. U59. Inflorescence, U138 and 141 (counterpart).

Description.—Little need be added to the above diagnosis, which probably includes some points which are common to this species and *L. Ottonis.* The largest specimen which shows most of a frond is shown in fig. 53; it is about 19 cm. long, and the longest pinnæ are about 9 cm. long. The length of the lower pinnæ gradually decreases, as usual in this genus. The longer pinnules, which are 20 mm. long, have markedly serrate margins and an acute apex, but the small pinnules of the basal pinnæ are entire and have a blunt rounded apex; in larger pinnules the midrib and secondary veins may be

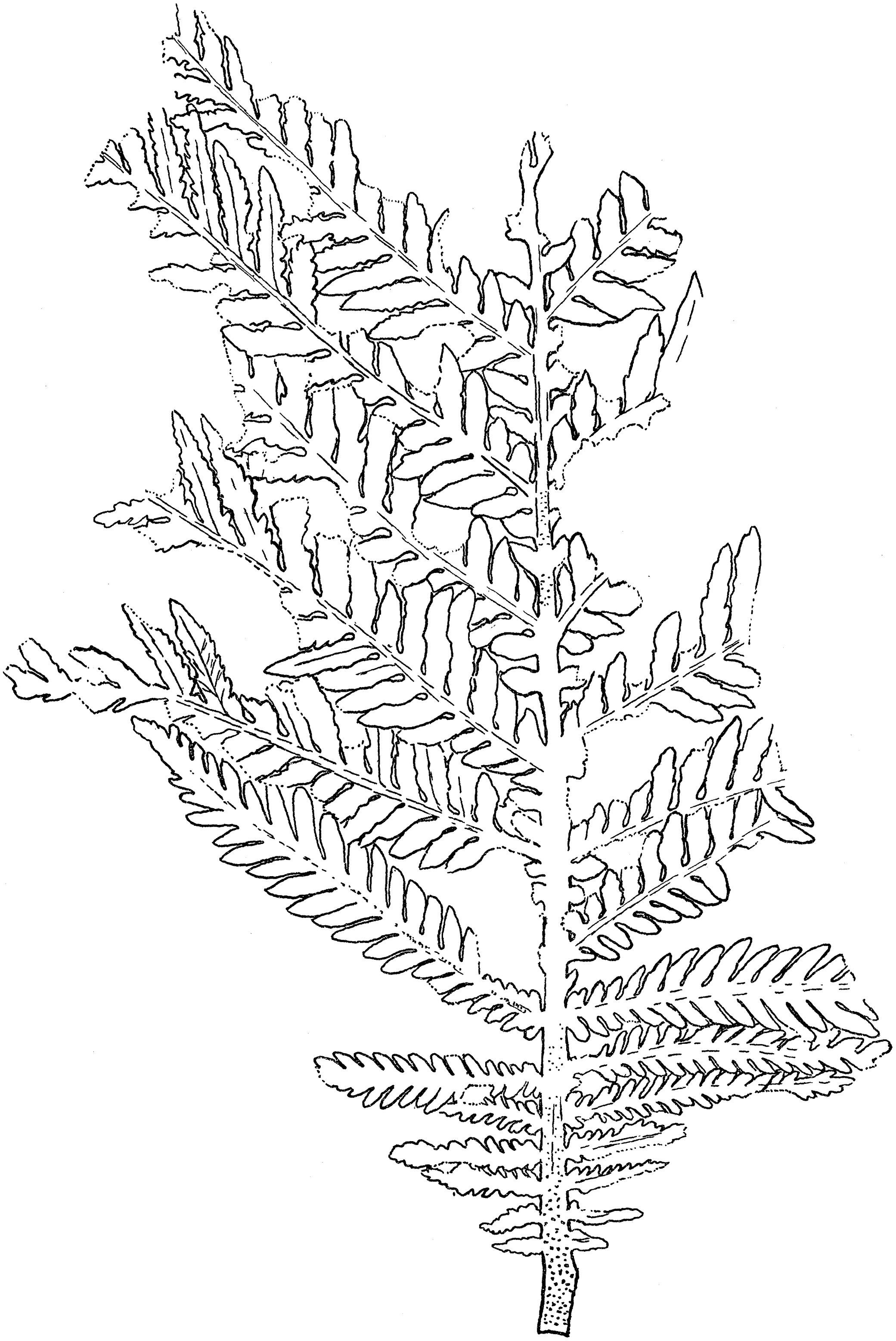

Fig. 53.—*Lepidopteris natalensis* sp. nov. Frond showing the characteristic shape of the lower portion, but lacking its apical part. No. U59. Nat. Size.

clearly seen. The base of the rachis has a rough surface owing to the presence of numerous small protuberances, but they are much less prominent than those of *L. Ottonis*; towards the top of the rachis the surface is almost smooth, but bears small transverse humps like those seen in some species of *Dicroidium*, these become larger and more numerous as the base of the frond is approached. The cuticles of this frond show but little difference on the two sides, the cells show sinuous walls, fig. 54, and there are very numerous stomata, but the courses of the veins and the sinuosity of the walls is more marked on the lower side. Small dark thickened spots are present on many of the cells.

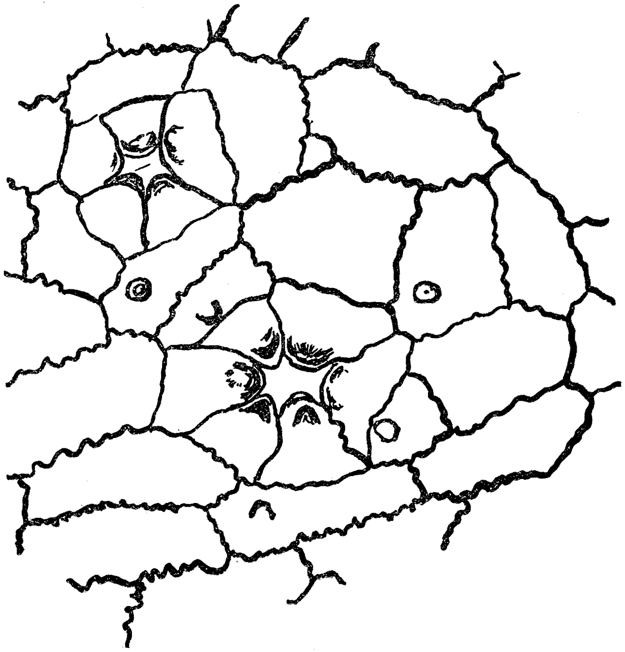

FIG. 54.—*Lepidopteris natalensis* sp. nov. Cuticle from lower epidermis of a pinnule, showing characteristic stomatal openings, sinuous walls and papillæ. × 390. Slide No. 64.

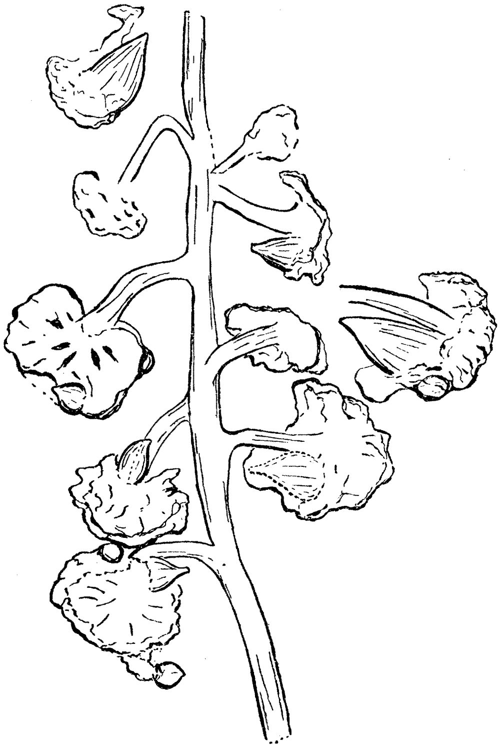

FIG. 55. *Lepidopteris natalensis* sp. nov. Seed bearing structure seen in Nos. U138 and 141. × 3·5.

In other specimens the apex of the frond is seen, the pinnæ are here produced at an angle of about 40° to the rachis and they rapidly diminish in size, the pinnules and eventually the pinnæ become united near the acute apex. The rachis here has a distinct central ridge, but is otherwise almost smooth.

In all specimens the cuticles have the typical *Lepidopteris* stomata which have been figured by HARRIS (1926), p. 67, text fig. 8*c*, *d*, and (1932), p. 60, text fig. 27 *a* and *b*. The guard cells are sunk in a cavity formed by the overarching of a circle of five or six subsidiary cells, each of these bears a papilla on its upper surface, which projects more or less over the stomatal cavity, fig. 54. The stomata occur on both the pinnules and the rachis, and they can be very closely compared with the stomata on the seed-bearing structure.

The seed-bearing structure is shown in fig. 78, Plate 24, and fig. 55, which was traced from superposed photographs of the main specimen and its counterpart. The whole specimen is 27 mm. long, but neither apex nor base is seen, the axis shows some slight longitudinal striations like the upper part of the rachis of some of the fronds. Its cuticle was thin and was composed of more or less rectangular cells, some of which are enlarged to form thickened elliptical papillæ ; few stomata are present. The lateral branches are borne spirally and not in one plane as in *Umkomasia*, they are 2·5–5 mm. apart, are 3–5 mm. long, and 0·7 mm. broad ; the peltate seed-bearing heads (or cupulate discs of Harris) are only one-third of the size of the Greenland structures. Several seeds were borne on or near the margin of each head and appear to have been sessile, probably only one reached maturity. The mature seeds were about half the size of the Greenland examples, they were probably conical with a rounded basal part. On account of the small amount of material, their structure has not yet been investigated. The cuticles of the head differed considerably on the two sides. The cuticle of the outside or top of the head is much wrinkled and folded, while that of the lower or inner side is more smooth ; this suggests that the head may have had a thick or even somewhat fleshy structure. The outer cuticle is fairly thick and the epidermis was composed of small polygonal cells among which were a number of stomata of the same type as found on the fronds, with five or six thick papillose cells overarching the stomatal cavity. The cuticle of the lower side of the head was composed of uniform isodiametric polygonal cells with somewhat thick remains of the anticlinal walls ; no stomata have been seen on this side. There are no traces of the marginal spikes or of the radial ridges seen on the lower surfaces of the Greenland forms. In one case the lower surface of one of our discs shows a series of slight irregular depressions radially arranged, but the peltate heads are clearly different in detail. No traces of the pollen-bearing structures *Antholithus Zeilleri* Nath. have yet been found.

MORPHOLOGICAL CONSIDERATIONS.

The discovery of new Mesozoic reproductive structures is especially interesting at the present time, when the morphological study of the higher plants in the light of recent palæobotanical discoveries is beginning to reveal the weakness of the foundations of the old-established theories of plant morphology. Ever since 1790, when Goethe elaborated the view that stamens and style could be considered as modified leaves, it has generally been held that reproductive structures represent fertile foliage leaves. Subsequent to Hofmeister's great work and the study of the pteridophyta, it has been considered that the sexual organs of the seed plants have been derived from fertile leaves comparable with those of the ferns. The *sporophyll* has almost assumed the importance of a morphological category, and the use of the term sporophylls for the stamens and carpels of the flowering plants has become a commonplace. Consequently the interpretation of the fertile structures of seed plants has often become unnecessarily complicated and their relationships have been greatly obscured. In several instances such as in the Gnetales, where the seed is obviously a terminal structure, it has been necessary to postulate the former existence and subsequent disappearance of the original sporophylls. But all recent work on the ferns goes to show that their sporangia were originally terminal structures and that the inclusion of sporangium in a leafy lamina is not an early feature. Thus, even assuming their derivation from the same stock, the seed plants were probably differentiated long before this inclusion took place. In the early land plants the differentiation of the sporangia at the tips of the segments of the thallus probably preceeded the differentiation of expanded foliar structures, while the evolution of the micro- and mega-sporangia proceeded independently to that of the leaves. Palæobotanical evidence affords strong support to TANSLEY's view* that large leaves almost certainly developed from branch systems, while the sporangiophores may be regarded as organs " sui generis " as suggested by BOWER (1908, p. 153). These hypotheses have been upheld by the recent discoveries of the Psilophytales and have been developed by ZIMMERMAN (1930).

Such opinions on the origin of reproductive structures must lead us to a reconsideration of the whole question of the concept of the sporophyll, and it is very doubtful whether the use of this term should be continued for seed plants unless it is defined simply as a lateral fertile structure of limited growth. It should be recognised that the chief, if not the only, arguments for the view that the stamens and carpels represent altered leaves (rather than branches) are that apparent transitions can be observed between vegetative leaves, sepals, petals, stamens, and carpels, and that in abnormal flowers all the parts may become foliar. But such arguments are not supported by the evidence of vascular anatomy or by any objective criteria. On the other hand, the interesting theory of irreversibility in evolution put forward by DOLLO and recently elaborated for plants by Mrs. ARBER (1919) strongly contests the validity of conclusions based on abnormal forms. According to this view the phylloidy of stamens and carpels is not a reversion, but a change in which the primordium of the original branch, or potential branch system, has for the first time become foliar.†

In considering these problems the palæobotanical evidence is the most trustworthy. If we try to determine whether, in reviewing the past history of a group, the organs bearing the micro- and mega-sporangia become more leaf like when we pass from the later to the earlier forms, we find that there is no group in which the earlier " sporophylls " should be regarded as more leaf like, though in many cases they were compound, and not simple structures. The early pteridospermous seeds certainly terminated branches,

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* TANSLEY (1908), p. 6. This idea had been previously put forward by LIGNIER (1908) on general grounds, but TANSLEY produced good anatomical evidence to substantiate it.

† GRÉGOIRE (1931) has arrived at the same conclusion on other evidence.

even though these may be regarded as segments of large foliar structures, but when we come to consider the morphology of the inflorescence of the Corystospermaceæ we find facts of considerable interest. The seed-bearing structures of this group have been described above as inflorescences instead of as sporophylls, though they were mainly branched in one plane and often show a slight difference between the cuticles on the upper and lower sides. But in the Angiosperms and other seed plants, structures which are subtended by leaves or bracts are always regarded as branches rather than leaves, and in the Corystospermaceæ the seed-bearing structures are constantly subtended by bracts. Thus the only parts which might be described as sporophylls are the lateral pedicels bearing the cupules, and the plane of branching and cuticle structure of the *main* part of the inflorescence have no morphological significance. But there is no reason why these pedicels should be regarded as foliar structures, especially since the apex of each lateral branch subtended by a bract is, in several species, terminated by a cupule. So the obvious and simplest interpretation is to regard the whole structure as a branch system. The evidence of the Corystospermaceæ suggests that the concept of the seed-bearing leaf is an illusion, and this also affects *Pteruchus* in which no subtending bracts are yet known.

The morphology of *Pteruchus* is somewhat speculative, owing to the uncertainty of the exact structure of some of the forms. It is clear, however, that *P. africanus* has the structure of a *Crossotheca* and may be regarded as a group of sessile micro-synangia produced on a more or less cuplike or spathulate structure. It must be noticed that in no species are the sporangia marginal productions, and they may be regarded as forming a terminal group on each lateral branch. The cup-like structure may be interpreted either as the expanded receptacle or head of the branch, or as a cupule which has grown up round the original group of sporangia and on to which the sporangia have spread. Probably the best interpretation is the combination of these two views, namely, that the sporangia were produced on an expanded receptacle surrounded with a small cup-like envelope. This would make each group of sporangia correspond in position to the one ovule of the Corystospermaceæ. This explanation, however, does not fit all the species, for in some, especially *P. Edwardsi*, there seems to be little doubt that the ultimate branches bear peltate fertile heads. It would seem from the comparison with the palæozoic forms that this may be due to a secondary development along a line similar to that which has led to the evolution of the micro-sporangiophores of *Taxus*.

The peltate fertile branches of *Lepidopteris* are very different from any structure previously found in the pteridosperms, but they may be compared with a peltate species of *Pteruchus* in which the sporangia are much reduced in number and in which the microsporangia are replaced by seeds. It is possible that the peltate head, the cupulate disc of HARRIS, is similar in nature and origin to the cupules of the Corystospermaceæ, but it seems to be preferable to regard it as originating from a fused group of megasporangia-bearing branches.

The Corystospermaceæ and the Gymnosperms.

The morphological views elaborated above not only affect our conceptions of the morphology of the pteridosperms, but also our views on the "sporophylls" of the other gymnosperms. It is possible that the female inflorescences of the Corystospermaceæ represent a very primitive type of structure similar to that from which the seed-bearing structures of the Ginkgoales, Gnetales, Cycadales, and Coniferales have been derived. They are not very different from the structure postulated by ZIMMERMANN (1930, p. 290, fig. 209, 6) as the "Urform" from which the seed-bearing organs of Conifers have been derived. Without entering into this question in detail a few points may be noticed.

The ovules of *Ginkgo biloba* normally appear as terminal structures on short branches, the apex of the branch generally appears to fork and bears a pair of ovules, of which only one develops into a seed. The base of the ovules is enclosed in a shallow cup or collar which has been compared with the cupule of *Lagenostoma* (SHAW, 1908), and may be compared with the cupules of the Corystospermaceæ. Often the axis bearing the ovules gives off branches, as many as eight being occasionally found (SAKISAKA, 1929, p. 227). There is clearly a similarity between these structures and the corystospermous inflorescence, while their vascular structure indicates a cauline rather than a foliar nature, and it is reasonable to regard them as morphologically similar. The male structures in *Ginkgo* are comparable with *Pteruchus.*

The Gnetales may be regarded as forms in which the branches of the female inflorescence and the pedicels have usually become greatly shortened and reduced, so that instead of a pair of dichasia, as seen in *Ephedra altissima*, we may have a whorl of sessile ovules. In some species of *Ephedra* the ovules are produced in pairs, but in *Welwitschia* they are solitary. The view which regards "the nucellus in the Gnetales as the real prolongation and termination of the floral axis" is undoubtedly the simplest, as PEARSON (1929, p. 53) remarks, and it would probably be unchallenged but for morphological preconceptions. The nature of the outer coverings of the ovules in the Gnetales has been much debated.* It may be here suggested that the outer covering, in at least some of the forms, represents the cupule of the Corystospermaceæ, for in *Gnetum* it also becomes fleshy and its epidermis bears stomata unlike the normal testa.

The Bennettitales possess female strobili which are very uniform in character, the ovules are clearly terminal structures on the ends of crowded branches of the axis. Towards the base of the ovules is an external layer of elongated cells, thinning out near the middle of the ovule, which LIGNIER called the "enveloppe tubuleuse" and WIELAND (1906, p. 120) has described as a cup-shaped basal husk; this probably represents the pteridosperm cupule.†

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* Cf. PEARSON (1929) for references.

† SCOTT (1923) describes the structure as forming "a kind of cupule round the seed." HARRIS (1932 *a*) has recently brought forward evidence of the presence of a distinct cupule in *Vardekloeftia,* one of the earliest known members of the group.

In the Cycadales the ovule bearing structures are flattened and have been used as the strongest evidence in support of the sporophyll concept. They may, however, be equally well regarded as derived by fusion and reduction from a complex of branches like the inflorescence of *Pilophorosperma granulatum.* The aggregation into cones, which (assuming the *Dioon* type to be derived from the *Cycas* type) seems to have resulted in the loss of fertility of many of the branches of each seminiferous structure, might perhaps be correlated with the change of form. Very little is known of the fossil history of the Cycadales proper. Probably the seed bearing structure known as *Beania* belonged to this group, for different species have been connected with fronds of the genus *Nilssonia* by the author and by HARRIS (1932, p. 52), on material from Yorkshire and Greenland from independent investigations. In *Beania,* the seed bearing branches of the main axis were widely separated and each bore a pair of seeds in a manner comparable to the ovules of *Ginkgo.* This structure invites comparison with a form like *Pilophorosperma gracile.* There seems to be little trace of a cupule in the cycads, but in *Cycas* and other forms the ovule and seed is situated in a basin-like hollow in the tissue of the " sporophyll " which may be extended to form a rim round the base of the seed. This structure is comparable to the collar of Ginkgo and was regarded by SHAW (1908, p. 92) as the relic of a cupule.

The Coniferales seem at first sight very remote from the Corystospermaceæ, but we have a large range of forms from the Taxus type to the Abietineæ, through the Podocarps in which the ovules are recurved and seem to be borne on short lateral branches. ZIMMERMANN (*loc. cit.*) and SAHNI (1920, p. 293) have recently reconsidered the morphology of these structures and their views merit careful consideration. It seems as though a very good case can be made out for the view that the ovules represent terminal structures produced on a system of branches of the type seen in the Corystospermaceæ with bracts and in some forms bracteoles. The pairs of ovules described and figured by Mrs. ARBER (Miss Robertson) (ROBERTSON, 1907, p. 98, Plate 1, figs. 4*a*, 5*a*) for *Taxus* and *Torreya* would agree with this idea, and the recurved position of the podocarp ovules may well be a primitive feature. Professor SEWARD has drawn my attention to the question of the epimatium of the Taxaceæ. The nature of this envelope has always seemed very problematical, but it can certainly be compared with the cupules of the Corystospermaceæ in its position, in the facts that it often becomes fleshy, and that, unlike the testa, its outer epidermis possesses numerous stomata. The early origin of the cone habit in the Abietineæ and Araucarineæ may be correlated with the evolution in these groups of ovuliferous structures which seem very remote from what is here regarded as a primitive inflorescence, but WALTON'S (1928) recent discovery of a bract scale, together with the form of the ovuliferous scale in *Voltzia,* renders the suggested connection more probable. It would seem, then, that the new female inflorescences now described are not so incompatible with the ovuliferous structures of the Gymnosperms as they might at first appear. They may represent the primitive form of gymnospermous seed-bearing branches.

The ancestry of the Caytoniales.

The Caytoniales (Thomas, 1925, p. 299) constitute a distinct group of plants in which the ovules were produced in a closed or nearly closed ovary. In the Jurassic forms fertilization was preceded by the reception of the pollen grains on a specialized stigmatic surface developed near the stalk of the ovary. This group existed in the Northern Hemisphere from the Rhaetic probably to the Lower Cretaceous period. The recent discoveries of Harris in Greenland (1926, 1932 *a*) show that the group existed not very long after the time when the Corystospermaceæ flourished in the Southern Hemisphere.

There is considerable general similarity between the lateral branches of forms like *Umkomasia Macleani* and the structures described as the sporophylls of Caytoniales, but in the former we have pediculate cupules containing one seed while the Caytoniales have stalked ovaries enclosing several seeds. In Corystospermaceæ the cupule is open while in the Caytoniales the envelope of the ovary, which superficially resembles the cupule, has become closed with a stigmatic surface, and the ovules and seeds are included within it.

When the Caytoniales were first described their derivation from the palæozoic pteridosperms was suggested on account of the similarity in seed structure, but at the time no form of pteridospermous fructification which bore any general resemblance to the *Caytonia* "sporophyll" was known. We now, however, have forms which though typically gymnospermous may be regarded as probably similar to ancestors of the Caytoniales. In making this suggestion we must not minimize the great distinction between an angiospermous and a gymnospermous structure, but it is not unreasonable to suggest that the *Caytonia* ovary may have been evolved by the closing of the cupule round the micropyle of the contained seed, and the formation of a stigmatic surface at the point of closure, possibly by the specialization of hairs or papillæ like those which line the cupule, followed by the failure of the micropyle to project to the exterior. It may well be that the Caytonias from Greenland represent a stage in this process, where the stigma is formed but the pollen grains can still find their way into the micropyles. There is some general similarity between *Pteruchus* and the anther bearing branches of the Caytoniales, but in the latter the tips of the fertile branches are not expanded, while the synangia have four loculi instead of two. Both groups produced similar winged microspores. The proof of the pteridospermous nature of *Lepidopteris* is important, as the fertile branches *Antholithus Arberi* resemble those of its microsporophylls or male inflorescences (formerly known as *Antholithus Zeilleri*). We have, then, some further grounds for deriving the Caytoniales from the palæozoic pteridosperms.

The Pteridosperms and the Flowering Plants.

In a recent paper (Thomas, 1931, p. 665) the author has suggested the derivation of the modern angiosperms from the pteridosperms, and the present communication adds some new facts which support this view. It is now clear that two groups of plants allied to the Palæozoic pteridosperms existed in the Mesozoic period immediately prior to the time when the Caytoniales first appear, and at a period when the earlier stages in the evolution of the flowering plants must have been accomplished. In these groups the seeds and pollen grains were borne on special branch systems or inflorescences, some suggesting dichasial cymes, others apparently racemose in character. This fact suggests a modification in our usual concepts of the characters of the Pteridospermæ, and removes the difficulty which was felt in suggesting the derivation of the flowering plants from forms in which the seeds were isolated on the margins of large multipinnate fronds.

Axilary branching is a characteristic of the flowering plants and was previously known to occur in only one of the pteridosperms *Lyginopteris oldhamia*, where its presence had been demonstrated by Brenchley (1913, p. 354). It is a constant feature in the Corystospermaceæ, while the fertile branches of several species in this group possessed bracteoles.

The author's hypothesis is that the flowering plants have sprung from several distinct groups of pteridosperms ; that in each case the first step was the closure of the cupule and the development of a stigma, as indicated by a consideration of the Caytoniales ; that the number of cupules on each lateral branch became reduced to two or three and that these became fused together to form the carpels. The flower was considered to have evolved by the aggregation at the apex of a branch of a number of micro- and megaspore bearing appendages, but the structure of *Pteruchus* suggests that some flowers may represent primitive terminal groups of sporangia.

We have some evidence for the postulated idea of the fusion of the cupules, or their derivative ovaries, in the structure of *Pilophorosperma geminatum* and in the aborted branches of *P. gracile*, where the usual pedicels are absent and the cupules are more or less fused. If such a fusion occurred in forms like *Umkomasia Macleani* or *Pilophorosperma granulatum* it would result in the production of an inflorescence bearing bracts with axilary structures comprising two bracteoles and a terminal carpel. If this were accompanied by a male inflorescence derived from *Pteruchus*, with a considerable number of synangia (stamens) springing from a shortly stalked cup-shaped receptacle, we should have a plant with flowers referable to the Amentiferæ, and not far different from *Populus*.

The male "sporophylls" or inflorescences of the Caytoniales suggested that the typical stamen of a Ranunculus or Magnolia may have been derived by reduction from a branching structure, but the present range of structures grouped in the form genus *Pteruchus* suggests that the male flowers of certain diclinous plants may have had a different origin. The vascular system of the Poplar flowers supports this idea. Thus the Corystospermaceæ offer some new lines of thought for investigation in floral morphology.

While making the above comparisons it must be remembered that the leaves which are attributed to the Corystospermaceæ show few or no tendencies to develop in a direction leading to the flowering plants, and it is clear that we must not regard them as actual flowering plant ancestors. But we may suggest that they were possibly similar in certain features to such hypothetical ancestral forms. In relation to leaf form there is, however, one point worth notice. The Palæozoic pteridosperms usually had large highly divided fronds, which must be regarded as derived from branch systems through types like the Devonian *Aneurophyton* or the Lower Carboniferous *Sphenopteris affinis*. But in contrast to the large Upper Carboniferous *Sphenopteris* or *Neuropteris* fronds, the Mesozoic species of pteridospermous type such as *Dicroidium odontopteroides* (see fig. 49) had leaves comparable in size to those of the modern flowering plants. The consideration of leaf form in relation to time leads to the view that in the megaphyllous seed plants simple leaves have probably been evolved from compound types.

SUMMARY.

1. The reproductive structures described were found by the author in Natal in the Molteno beds, belonging to the upper part of the Karroo Series of rocks. They are regarded as probably of Middle Triassic age. They are exceptionally well preserved in a mummified condition.

2. The collection includes a variety of seed-bearing branches, and male inflorescences, together with characteristic isolated seeds all of which are grouped together in a new family the Corystospermaceæ, allied to the Palæozoic Pteridospermæ.

3. The seeds are gymnospermous, borne in cupules on the ends of branches forming an inflorescence; the larger branches are borne in the axils of bracts, and bracteoles are also present in some forms.

4. Three genera of seed bearing structures are distinguished, *Umkomasia* with two species, *Pilophorosperma* with eight species and several other types which may be specifically distinct but are represented only by fragments, *Spermatocodon* with one species.

5. The genera and species are distinguished by the form of their branching and by their cupules, also by the characters of their epidermal cells, as shown in cuticle preparations from the branches and cupules.

6. The cupules of *Pilophorosperma* were lined with hairs, a feature previously recorded for the Palæozoic genera *Lagenostoma* and *Gnetopsis*.

7. The isolated seeds of this group can be distinguished by their curved bifid micropyles; they show some variety in size and form and were probably platyspermic.

8. From macerated seeds evidence was obtained suggesting the presence of pollen-chambers of the lagenostome type. Eleven characteristic winged microspores were found in one of these structures.

9. *Umkomasia* can be compared with structures previously described from the corresponding beds in Australia under the name of *Beania*.

10. The comparison of the seed-bearing structures of the Corystospermaceæ with those of the Palæozoic pteridosperms indicates that the lobes of the earlier cupules may

have become fused in Mesozoic times. Considerable interest centres around the question of the position in which the seeds were borne on the pteridosperm plants. It is suggested that the seeds were originally separate from the lamina of the fronds and became restricted to distinct inflorescences in the Triassic forms, though in some Permian types they became closely connected with the expanded lamina of the fronds. A comparison is made with the probable evolution of the ferns as regards the position of the sporangia.

11. The male inflorescences are described under the generic name of *Pteruchus*, and eight species have been distinguished. Their association with the seed-bearing structures is based on similarity of form, of cuticle structure, and on the occurrence of their characteristic microspores within a seed.

12. The symmetrically winged microspores of *Pteruchus* are very comparable with those of the Caytoniales, and with spores which have been found in beds of Lower Beaufort or Upper Ecca age.

13. The form of the type species of *Pteruchus* is essentially similar to that of the Palæozoic genus *Crossotheca*, while other species approach the type formerly known as *Potoniea*. Comparable forms have also been described from the Triassic beds of Australia.

14. A preliminary survey of the leaves associated with the reproductive structures indicates that the forms from the Southern Hemisphere known as *Dicroidium*, "*Stenopteris*," *Pachypteris*, and probably *Johnstonia* are to be regarded as the leaves of the Corystospermaceæ. This view is based mainly on the study of the gymnospermous cuticles of these forms and also on the facts of association.

15. A new species of *Lepidopteris*, nearly related to *Lepidopteris Ottonis* of Greenland and other Triassic localities in Europe, is described with its seed-bearing branches. The family Peltaspermaceæ is instituted for the reception of this form.

16. The morphological significance of these discoveries is considered. It is suggested that gymnospermous seeds must be regarded as terminal structures formed at the ends of branches, and not as marginal structures borne on a typical foliar organ. The frequent use of the term sporophyll as applied to the seed plants is considered to be misleading. The seed bearing organs of all other gymnosperms can be considered as derived from structures somewhat similar to those of the Corystospermaceæ, and traces of a cupule can be detected in all the major groups.

17. The present studies suggest that the Caytoniales were probably derived from the pteridosperms by the closing of the cupule, they also provide further fragments of evidence supporting the hypothesis of the derivation of the modern angiosperms from the same group.

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DESCRIPTION OF PLATES.

(Photographs by the Author.)

PLATE 23.

FIG. 56.—Type specimen of *Umkomasia Macleani* showing main axis and lateral branches bearing cupules. × 2. (No. U11.)

FIG. 57.—*Umkomasia verrucosa* showing difference in habit and stout axis. × 2. (No. U140.)

FIG. 58.—*Pilophorosperma granulatum.* Terminal portions of branches showing bracteoles and stalked cupules. × 3. (No. U91.)

FIG. 59.—*Pilophorosperma gracile.* Showing main axis with lateral branches bearing pairs of cupules. Part of frond of *Dicroidium odontopteroides* (Morr.) showing venation is also seen. × 2. (No. U123).

FIG. 60.—*Pilophorosperma burnerense* showing habit of this more delicate form. × 5/3. (No. U94.)

FIG. 61.—*Pilophorosperma sp.*, showing stout axis and lateral branch subtended by a small bract (B). Parts of rounded cupules are seen near the top of the branch and a long curved micropyle (M) projects from one of them. × 4. (No. U209.)


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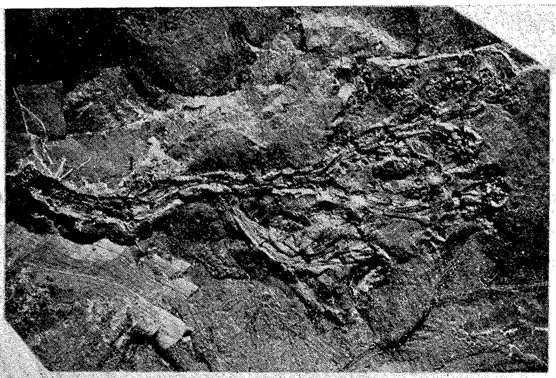
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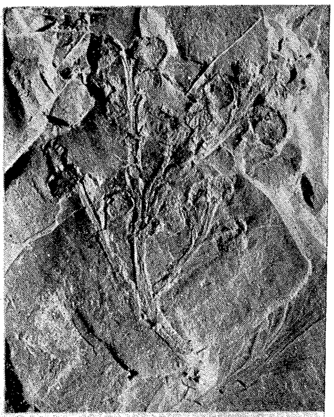
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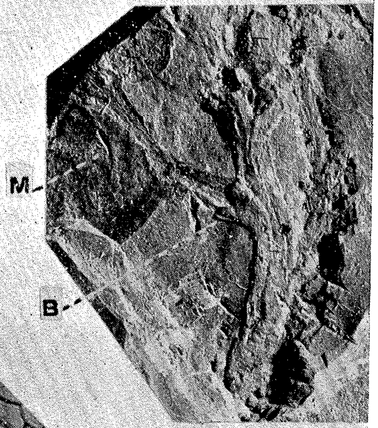

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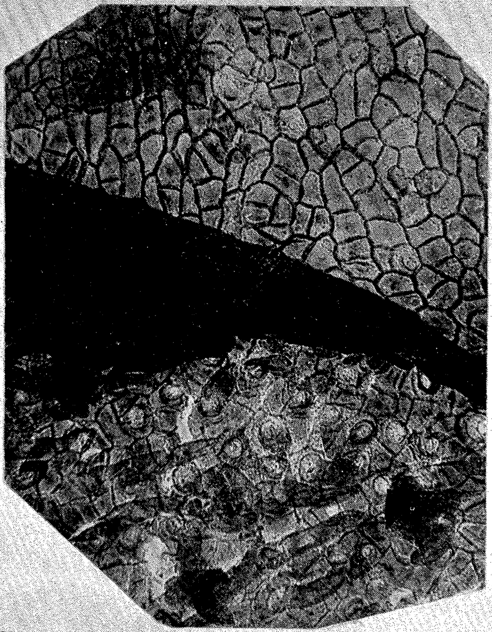
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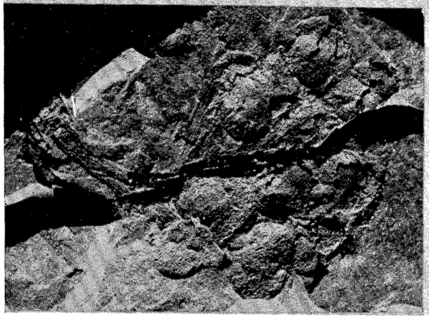
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Umkomasia, Pilophorosperma.


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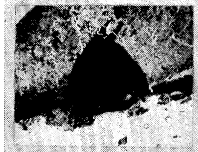
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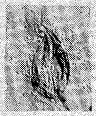
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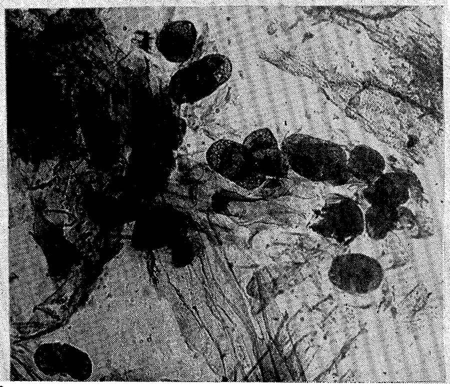
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Pteruchus, Lepidopteris, Spermatocodon, &c.

FIG. 62.—*Pilophorosperma crassum* showing the remains of the thick cupules crowded together. × 2. (No. U214.)

FIG. 63.—*Pilophorosperma paucipartitum.* The axis is seen with bracts (or bracteoles) at the base, above the long slender pedicels of the cupules are visible, and the large seed attached to one of the cupules is shown. × 2. (No. U143.)

FIG. 64.—*Pilophorosperma, sp.* type A. Photograph of part of a cuticle preparation of a cupule. The dark part in the centre of the figure represents the marginal portion of the opening, the cuticle of the outer epidermis is seen above, the cuticle of the inner epidermis below. Note the remains of the hairs and their large circular bases on the inner epidermis. × 120. (Prep. No. 40. A. from specimen No. U151.) The figures of cuticles, in the text, were made from similar photographs.

PLATE 24.

FIG. 65.—*Pilophorosperma sp.* type A. Apex of a branch showing three cupules, the left-hand one containing a seed with projecting micropyle. The specimen is lying upon a frond of "*Stenopteris*" *densifolia* Du Toit. × 2. (No. U152.)

FIG. 66.—*Spermatocodon Sewardi.* Branch with cupules of varying sizes. × 2. (No. U206.)

FIGS. 67, 68.—Isolated Corystospermous seeds showing form and curved bifid micropyle. × 2. Fig. 67. No. U221, is a seed of elliptical form. Fig. 68. No. U225, tapers towards the micropyle. *Cf.* fig. 33 (*a*) (*d*).

FIG. 69.—Isolated Corystospermous seed transferred from matrix to a slide and photographed with transmitted light to show the remains of the small bifid micropyle. × 4.

FIG. 70.—Apical portion of nucellus from a macerated seed, probably a structure of the lagenostome type. The remains of four or five characteristic pollen grains are seen at the apex while six others washed out in the course of staining and mounting.

FIGS. 71, 72.—*Pteruchus africanus*, showing the large fertile heads with crowded synangia. In fig. 72 the remains of bracts at the base of the axis are seen, and on the right a fertile branch compressed laterally. × 3. (Fig. 71. No. U244; fig. 72, No. U145.)

FIG. 73.—*Pteruchus sp.*, group of isolated synangia showing their form. × 15. (No. U169.)

FIG. 74.—*Pteruchus Edwardsi.* Specimen showing moulds of branches terminated by peltate sporangiophores, each with a single circle of pendulous synangia. In the top left-hand corner the remains of a *Dicroidium* frond are seen. × 2. (British Museum specimen No. V20911, from Kronings Kroon, nr. Elliot.)

FIG. 75.—*Pteruchus Hœgi*, showing small circular groups of synangia. × 2. (No. U23.)

FIG. 76.—*Pteruchus minor.* Small type, showing groups of synangia. × 2. (No. U125.)

FIG. 77.—Preparation made by macerating synangia of *Pteruchus papillatus* (No. U44), showing characteristic winged microspores and the remains of the synangia walls. × 120. Slide No. 60.

FIG. 78.—*Lepidopteris natalensis.* Fertile axis, showing peltate branches bearing seeds. Some other branches were dissected out of the matrix after this photograph had been taken. × 2. (No. U138.)


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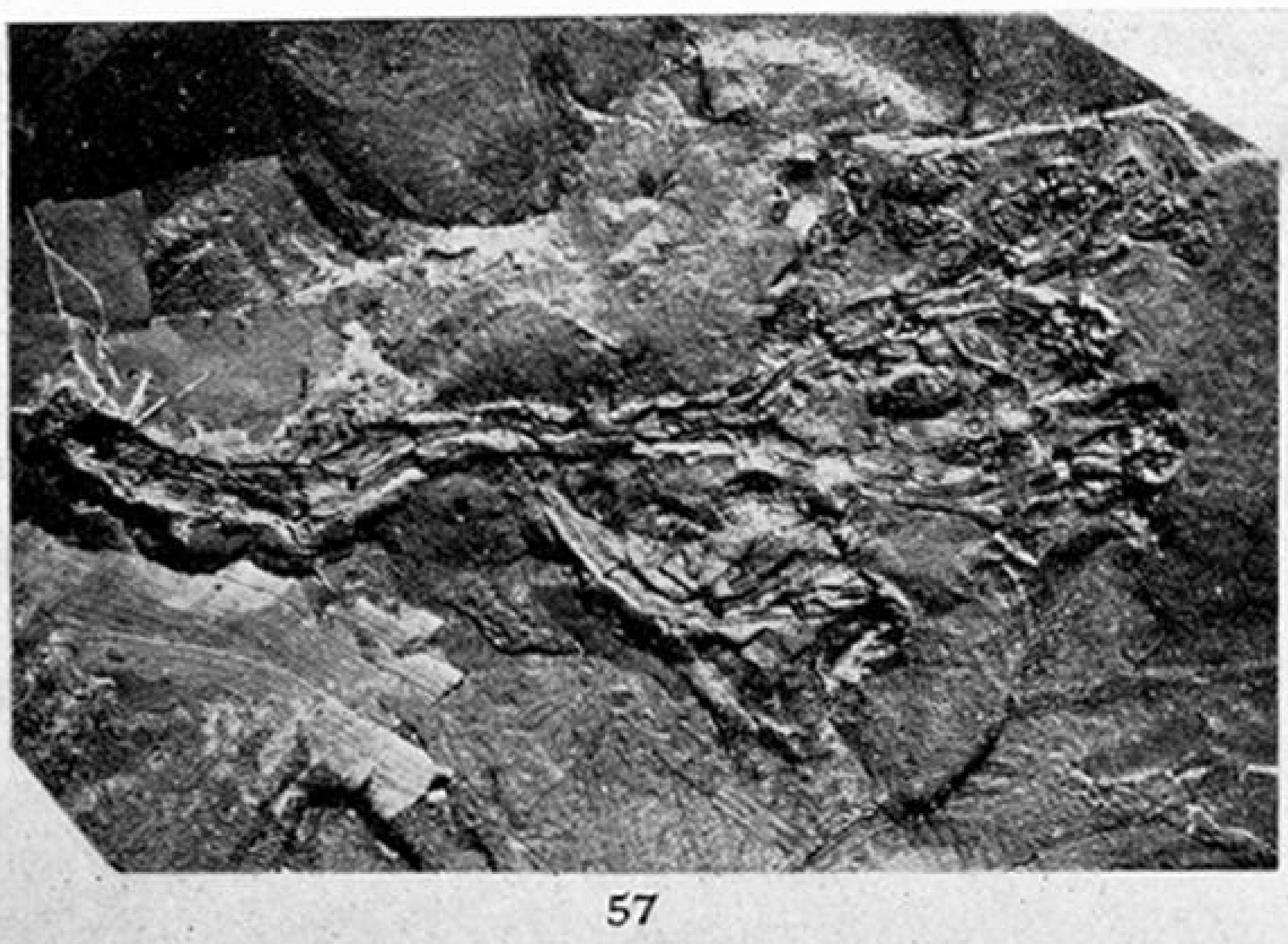
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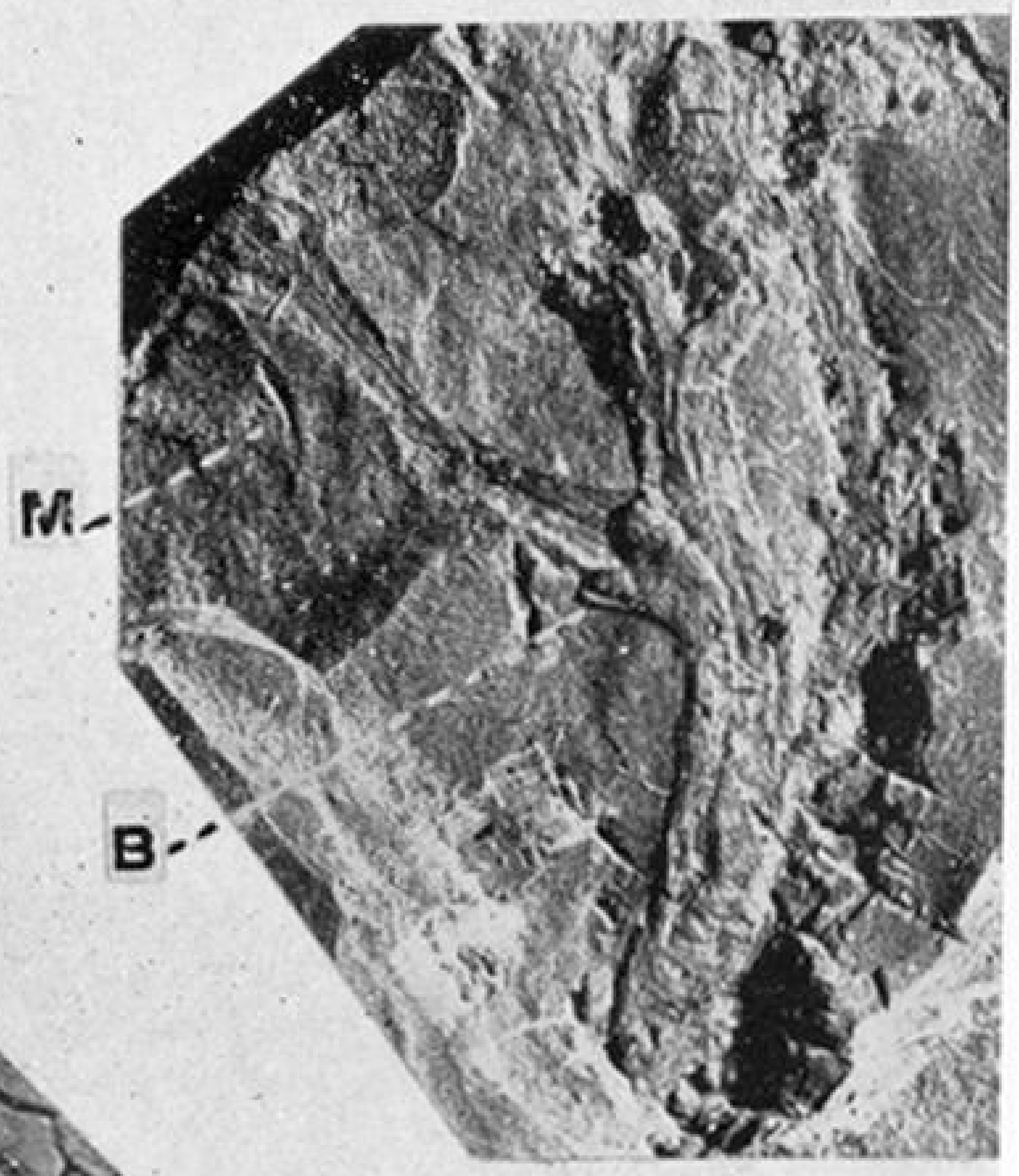

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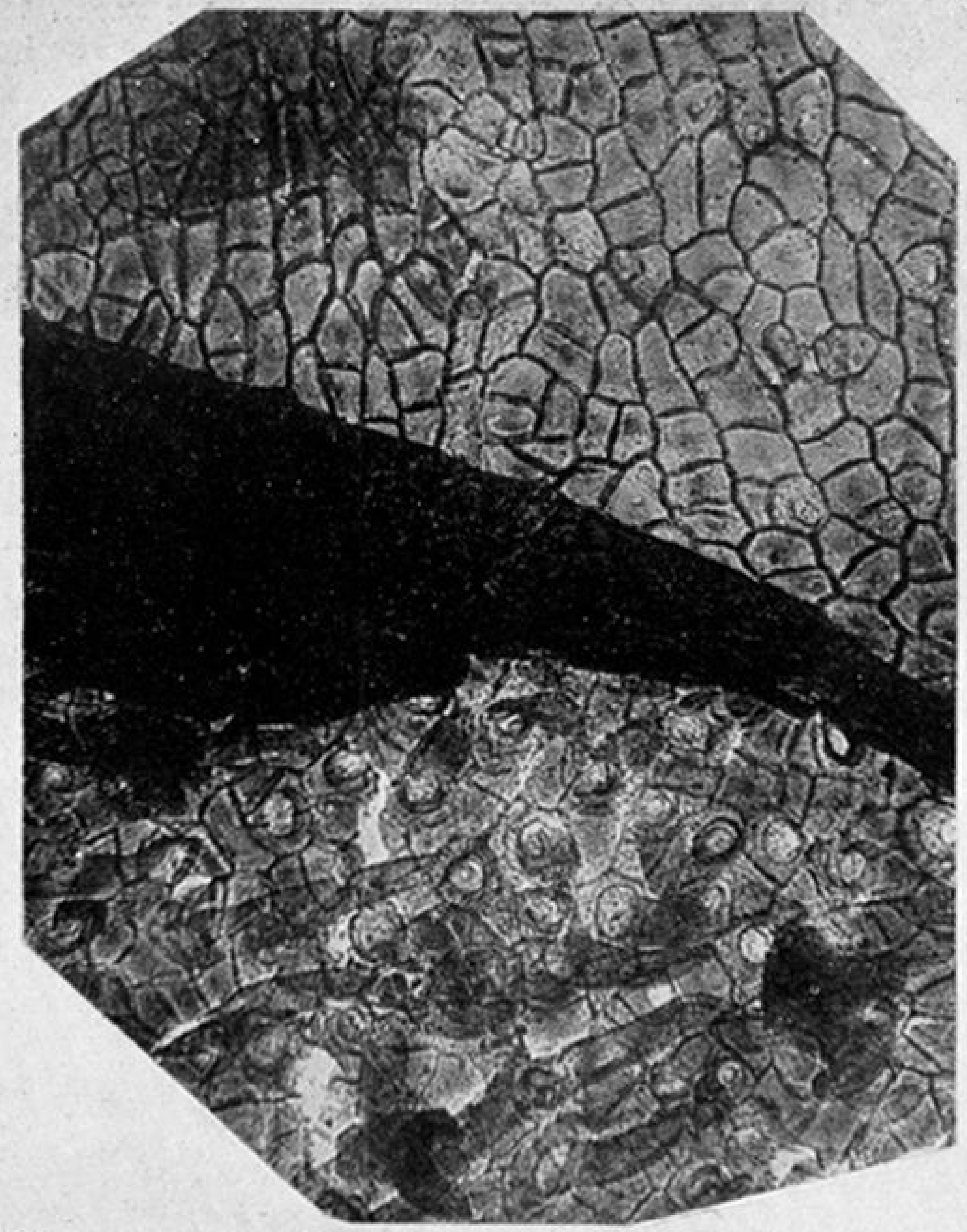
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Umkomasia, Pilophorosperma.

PLATE 23.

FIG. 56.—Type specimen of *Umkomasia Macleani* showing main axis and lateral branches bearing cupules. × 2. (No. U11.)

FIG. 57.—*Umkomasia verrucosa* showing difference in habit and stout axis. × 2. (No. U140.)

FIG. 58.—*Pilophorosperma granulatum.* Terminal portions of branches showing bracteoles and stalked cupules. × 3. (No. U91.)

FIG. 59.—*Pilophorosperma gracile.* Showing main axis with lateral branches bearing pairs of cupules. Part of frond of *Dicroidium odontopteroides* (Morr.) showing venation is also seen. × 2. (No. U123).

FIG. 60.—*Pilophorosperma burnerense* showing habit of this more delicate form. × 5/3. (No. U94.)

FIG. 61.—*Pilophorosperma sp.*, showing stout axis and lateral branch subtended by a small bract (B). Parts of rounded cupules are seen near the top of the branch and a long curved micropyle (M) projects from one of them. × 4. (No. U209.)

FIG. 62.—*Pilophorosperma crassum* showing the remains of the thick cupules crowded together. × 2. (No. U214.)

FIG. 63.—*Pilophorosperma paucipartitum.* The axis is seen with bracts (or bracteoles) at the base, above the long slender pedicels of the cupules are visible, and the large seed attached to one of the cupules is shown. × 2. (No. U143.)

FIG. 64.—*Pilophorosperma, sp.* type A. Photograph of part of a cuticle preparation of a cupule. The dark part in the centre of the figure represents the marginal portion of the opening, the cuticle of the outer epidermis is seen above, the cuticle of the inner epidermis below. Note the remains of the hairs and their large circular bases on the inner epidermis. × 120. (Prep. No. 40. A. from specimen No. U151.) The figures of cuticles, in the text, were made from similar photographs.


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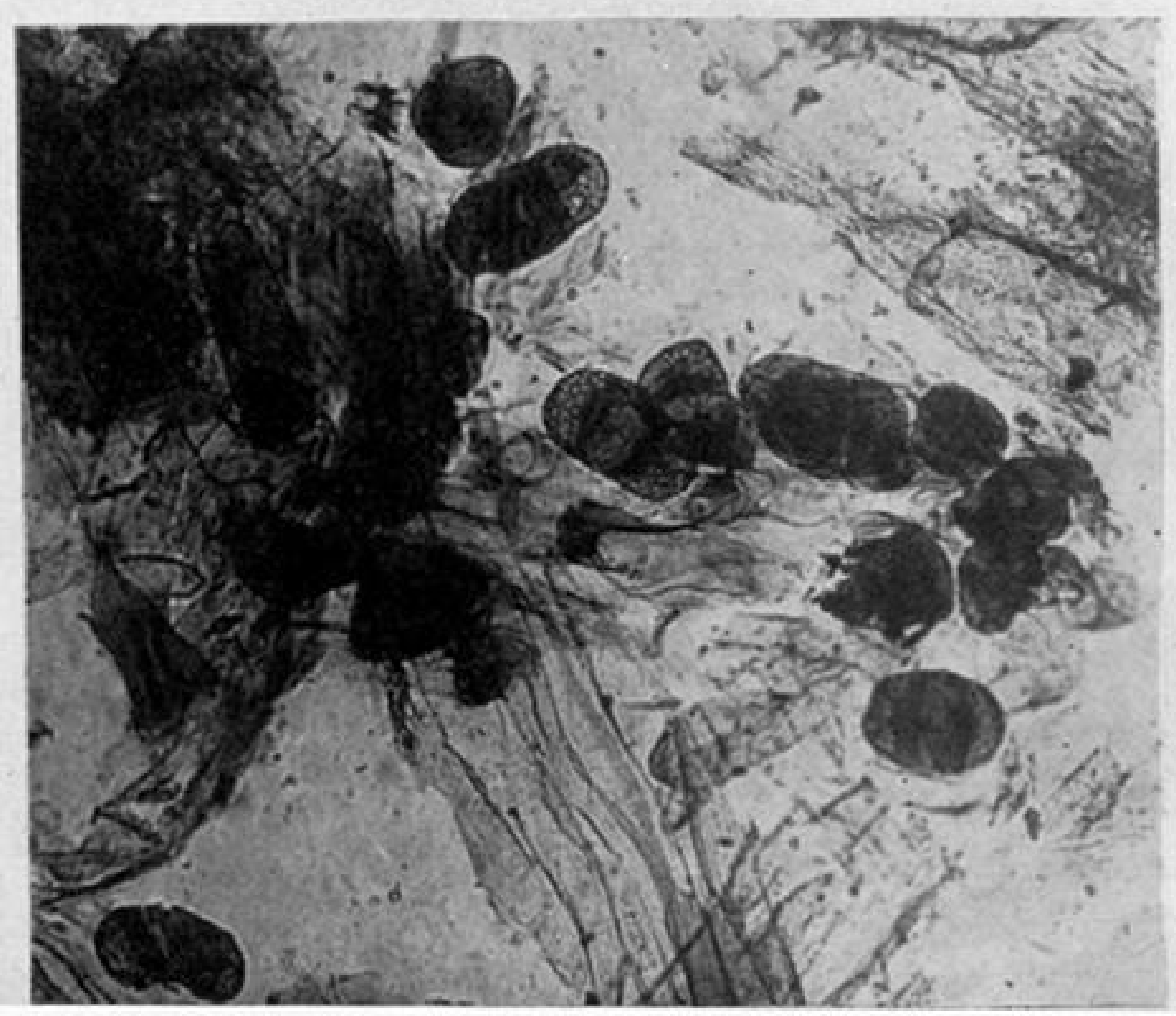
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Pteruchus, Lepidopteris, Spermatocodon, &c.

PLATE 24.

FIG. 65.—*Pilophorosperma sp.* type A. Apex of a branch showing three cupules, the left-hand one containing a seed with projecting micropyle. The specimen is lying upon a frond of "*Stenopteris*" *densifolia* Du Toit. × 2. (No. U152.)

FIG. 66.—*Spermatocodon Sewardi*. Branch with cupules of varying sizes. × 2. (No. U206.)

FIGS. 67, 68.—Isolated Corystospermous seeds showing form and curved bifid micropyle. × 2. Fig. 67. No. U221, is a seed of elliptical form. Fig. 68. No. U225, tapers towards the micropyle. *Cf.* fig. 33 (*a*) (*d*).

FIG. 69.—Isolated Corystospermous seed transferred from matrix to a slide and photographed with transmitted light to show the remains of the small bifid micropyle. × 4.

FIG. 70.—Apical portion of nucellus from a macerated seed, probably a structure of the lagenostome type. The remains of four or five characteristic pollen grains are seen at the apex while six others washed out in the course of staining and mounting.

FIGS. 71, 72.—*Pteruchus africanus,* showing the large fertile heads with crowded synangia. In fig. 72 the remains of bracts at the base of the axis are seen, and on the right a fertile branch compressed laterally. × 3. (Fig. 71. No. U244; fig. 72, No. U145.)

FIG. 73.—*Pteruchus sp.*, group of isolated synangia showing their form. × 15. (No. U169.)

FIG. 74.—*Pteruchus Edwardsi*. Specimen showing moulds of branches terminated by peltate sporangiophores, each with a single circle of pendulous synangia. In the top left-hand corner the remains of a *Dicroidium* frond are seen. × 2. (British Museum specimen No. V20911, from Kronings Kroon, nr. Elliot.)

FIG. 75.—*Pteruchus Hœgi*, showing small circular groups of synangia. × 2. (No. U23.)

FIG. 76.—*Pteruchus minor*. Small type, showing groups of synangia. × 2. (No. U125.)

FIG. 77.—Preparation made by macerating synangia of *Pteruchus papillatus* (No. U44), showing characteristic winged microspores and the remains of the synangia walls. × 120. Slide No. 60.

FIG. 78.—*Lepidopteris natalensis*. Fertile axis, showing peltate branches bearing seeds. Some other branches were dissected out of the matrix after this photograph had been taken. × 2. (No. U138.)