VII.—*On the Structure and Affinities of* Acmopyle Pancheri, PILGER.*

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(*Communicated by Prof.* A. C. SEWARD, *F.R.S.*)

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[PLATES 9–11.]

CONTENTS.

INTRODUCTORY.

Our knowledge of the monotypic New Caledonian genus *Acmopyle* is practically confined to incomplete descriptions of the external features by A. BRONGNIART and GRIS (1869), Sir J. D. HOOKER (1902), and PILGER (1903). The only other accounts of the plant are brief references in the 'Genera Plantarum' (BENTHAM and HOOKER, 1883), the 'Kew Bulletin' (1892), and 'The Gardeners' Chronicle' (MASTERS, 1892). I therefore gladly welcomed Prof. SEWARD's suggestion that I should undertake an investigation of some material collected in New Caledonia by Prof. R. H. COMPTON, M.A., during his expedition to that island in 1914.† My very sincere

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† A preliminary account of this work was read before the Cambridge Philosophical Society on May 20, 1918. See 'Nature,' vol. 101, p. 299.

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thanks are due to Prof. COMPTON for his generosity in allowing me to work at this rare material.

To Prof. SEWARD I owe a debt which I cannot adequately express; besides affording me the opportunity for carrying out this research, he showed an unfailing and kindly interest in the work, which, with his advice and able criticism on difficult theoretical questions, was quite indispensable to me. I am also deeply grateful to him for the privilege of consulting the proofs of the fourth volume of his work on Fossil Plants, the publication of which is shortly expected.

New Caledonia shares with many other islands in the Pacific the possession of a large number of endemic species. So far as the Podocarpineæ are concerned, PILGER (1903, p. 36) has already drawn attention to the peculiarities of the New Caledonian flora, which includes at least nine species of Podocarpineæ hitherto recorded only from that island. With the exception of *Acmopyle*, all of these plants are being investigated by Mr. C. P. DUTT, of Queen's College, Cambridge. Mr. DUTT was kind enough to allow me to examine his preparations for comparison—a fact which helped me considerably in my work on *Acmopyle*. In particular, I would like to thank him for allowing me to reproduce in this paper a photograph (Plate 11, fig. 31), of the stone of a new species of *Podocarpus* discovered by Prof. COMPTON in New Caledonia.

The material of *Acmopyle* was originally preserved mostly in formalin, but was subsequently transferred to a mixture of alcohol and glycerine. It consisted of vegetative shoots bearing twigs with pectinately arranged leaves; a stouter piece of stem with about twenty well marked growth rings; male cones in two stages of development; and over a dozen megastrobili. At the time of collection, March 10, 1914, the ovules had all reached the stage when they contain young embryos at the ends of the tortuous suspensor tubes; they had evidently received the last year's pollen. The fact that most of the male cones collected were nearly mature, suggested that younger ovules (in a stage shortly before pollination) would also be present, but there were none such in the material at my disposal. It is hoped that this unfortunate gap will soon be filled up when more material becomes available.

Through the courtesy of the Director I obtained from the Royal Botanic Gardens, Kew, some material of roots and leaves from two young plants growing in the Temperate House. I would also like to thank Mr. L. A. BOODLE for facilities to fix this material at the Jodrell Laboratory.

Besides the two young plants at the Kew Gardens there is another at the Glasnevin Garden, Dublin, from which, through the great kindness of the Director, Sir F. MOORE, I received a fresh twig which has been very useful for comparison.

This research was aided by a Research Studentship at Emmanuel College, Cambridge, and by a grant from the Dixon Fund of the University of London. To both these bodies I am thankful for the financial help.

HISTORICAL.

In 1869 A. BRONGNIART and GRIS described under the name *Dacrydium Pancheri* some specimens collected in New Caledonia and sent to them by PANCHER. In the notes attached to his specimens the latter had named the plant *Podocarpus pectinata,* a designation which apparently still persists in nurseries. Whereas this name is fully justified by the *Podocarpus*-like habit, and by the form and arrangement of the largest leaves, which are quite distinct from those commonly associated with *Dacrydium*, the position of the micropyle led BRONGNIART and GRIS to transfer the plant to the latter genus. Here it was supposed to occupy a peculiar position, firstly, on account of the drupaceous character of the seed—another feature that justifies PANCHER'S reference to *Podocarpus*—and, secondly, because of the entire absence, as the joint authors believed, of the structure now generally known as the epimatium. The brief account by BRONGNIART and GRIS, based only on vegetative material and immature seeds, was unaccompanied by figures.

In 1902 Sir J. D. HOOKER published, for the first time, figures of a shoot bearing male cones, and of stamens showing the dehiscence of the pollen-sacs. Following the Genera Plantarum he placed the plant in the genus *Podocarpus* (§ Dacrycarpus). HOOKER, though unable, in the absence of female flowers and ripe fruit, to fix the generic position of the plant, suggested the possibility that it might prove to be an independent genus.

In 1903 PILGER transferred the plant to a new genus of doubtful affinity, and called it *Acmopyle Pancheri,* the generic name having reference to the position of the micropyle, which, however, is not strictly apical. He was the first to describe the ripe seed, in which the micropyle is according to him hardly visible. In the absence of young ovules he leaves undecided the question as to the existence of an epimatium and, with it, the problem as to whether the entire thickness of the seed-coat is formed by the integument alone. His description is on the whole correct, but the biseriate disposition of the leaves on the terminal shoots, although mentioned in the text, does not appear in the figure. In his dried material, moreover, PILGER appears to have missed the curved ridge at the back of the seed.

COULTER and CHAMBERLAIN (1917, p. 353) have recently referred *Acmopyle** to the Taxineæ, thus placing it nearer to *Taxus* than to *Podocarpus.* This is evidently due to oversight, for the little that is known about the plant points clearly to an affinity with *Podocarpus* rather than with *Taxus.*

In the published literature the plant is first mentioned as having been introduced into England in 1891, when the Royal Gardens at Kew ('Kew Bulletin,' p. 105) received a living specimen from the Sydney Botanic Garden. This plant flowered at Kew in 1902, only male flowers being produced, so far as I can ascertain ; it is the original of HOOKER'S figures (1902), the first ever published. MASTERS (1892) also

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* And also *Polypodiopsis,* which has long been known as a synonym of *Podocarpus vitiensis,* A. BRONGN. See BERTRAND, 1874, p. 65.

drew attention to a plant having been discovered at the Orchid Nurseries of Messrs. Sanders, of St. Albans, England.

DESCRIPTIVE.

A. *Distribution and Habit.*

PILGER mentions *Acmopyle* as being peculiar to New Caledonia. There is, however, at the Royal Herbarium, Kew, a specimen which although unfortunately sterile, in its vegetative features, external and internal, agrees so closely with *Acmopyle* that it is undoubtedly to be referred to this genus.* The specimen is labelled :

"Fiji Islands, Coll. J. Horne, 1877–78. Received March, 1879,"

but HORNE in his book "A Year in Fiji" (1881) does not mention it, possibly because he had no flowers. On the other hand it is, of course, possible that there was an error in labelling the specimen as coming from Fiji. But considering that *Podocarpus elata* R. Br. remained unnoticed in Fiji till 1907 when it was first recorded by Miss L. S. GIBBS† (1909, p. 183) it would not be astonishing if in the absence of flowers *Acmopyle* has escaped detection.

The photograph on Plate 9, fig. 1, is from the older of the two plants at the Royal Gardens at Kew, and was taken with the kind permission of the Assistant Director, Mr. A. W. HILL. Although this plant is only a few feet high, while the tree in its native habitat is said to attain a height of 17–20 metres, it gives some idea of the rather yew-like habit of the dorsi-ventral terminal shoots, with their leaves arranged like the pinnæ of a pectinate leaf—a feature which no doubt suggested the specific name adopted by PANCHER. There is a wide variation in the number of leaves on each side of these shoots, and local departures from the pectinate arrangement are frequent; this is especially the case in the shoots bearing the male cones, at least so far as can be judged from the available material. Possibly the male shoots are more often held erect, although this is not the impression given by HOOKER's figure (1902).

B. *Root.*

The roots of the Podocarpineæ (except *Pherosphæra* and *Acmopyle*) have formed the subject of a recent paper by Miss SPRATT (1913). My material, as already stated, was from the plants growing at Kew, and consisted of young roots up to about 2 mm. thick, with hardly any secondary xylem. As expected, tubercles were present, though only in small numbers. None of them appreciably exceeded the roots in

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[*] I wish to express here my appreciation of Dr. STAPF's kindness in sending me a portion of this specimen, which enabled me to examine it anatomically, and also to thank him for advice concerning the identity of the specimen in question. Dr. STAPF, who kindly examined my sections, does not consider it likely that the Fiji specimen is specifically identical with *Acmopyle Pancheri*, but he agrees to the generic identity.

[†] I am also much indebted to this lady, who has an intimate knowledge of the flora of Fiji, for her kind advice on the above question.

diameter; several of them had proliferated, having continued their growth distally into normal rootlets (Plate 9, fig. 2), a fact which supports VAN TIEGHEM'S view (1889, p. 352) that the tubercles are modified rootlets. In some material collected at a later date no tubercles were present; this may be due to all the tubercles having grown out into normal rootlets.

The stele of the tubercle, like that of the root, is diarch, and lies in the same plane, at least at its point of origin. Root-hairs were altogether absent in my material, both on the root and tubercles.

In the root the cells of the inner cortex show pronounced local thickenings which, in the form of hoops, girdle the cells in different planes. Similar thickenings have been described by NOELLE (1910) in the Araucarineæ, Taxodineæ and Cupressineæ. In section (Plate 9, fig. 3) these thickenings appear like beads, and turn yellow in SCHULTZE'S solution. EICHLER (1889, p. 34) also describes delicate spiral thickenings in the outer cortical cells in the roots of *Sequoia gigantea*, *Cryptomeria*, *Chamæcyparis*, and in *Podocarpus*, *Phyllocladus* and *Torreya*. The endodermis consists of 2–3 layers of tabular cells which are in radial seriation and give a bright yellow reaction with SCHULTZE'S solution; the outer tangential walls of the outermost layer are much thickened and dark brown. The pericycle, 5–6 layers thick at the sides of the xylem-plate, thins down to 2–3 layers opposite the protoxylems.

The structure of the tubercles presents few features not already noticed by Miss SPRATT in *Podocarpus*. The infected cells lie in an ill-defined zone about half-way out in the cortex (Plate 9, fig. 2); the bars of thickening in the cortical cells are very inconspicuous and sometimes hardly visible, probably because of the young stage of the material.

C. *Stem.*

The stem anatomy closely resembles that well known in *Podocarpus*. A section across a young twig before secondary growth shows the usual ring of collateral end-arch strands, each with a mucilage canal outside it.* At this stage the pith and cortex cells are all thin-walled, some of them filled with a homogeneous, brown, resinous-looking substance.† In branches a few years old stone-cells appear in the pith and cortex, while the colourless thin-walled cells become starch-laden. In the oldest shoot available (with about twenty growth-rings in the wood), the secondary phloem contains much-elongated fibres which in transverse section are rectangular; they appear exactly like the flattened "autumn" tracheides, and conform to the radial seriation of the xylem and phloem elements. These fibres are comparable

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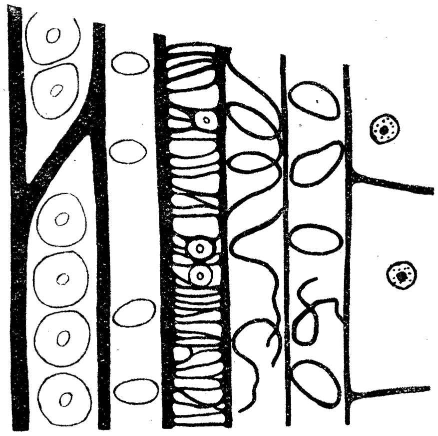
[*] The contents of these canals become white and opaque in strong alcohol, are slow in taking up stains, show a finely granular or alveolar structure, and usually include deep-staining tabular crystals of different sizes, varying in shape between triangles, squares and hexagons. See fig. 10, Plate 10.

[†] Although this substance, so commonly present in the Podocarpineæ and other Conifers, usually passes for resin, it is not soluble in alcohol. The only justification for the use of the word resin is convenience of description.

with the sclerites described by TISON (1909, p. 140) in the secondary phloem of *Saxegothœa*. The secondary phloem also contains abundant "resin"-cells, which are arranged in discontinuous rings concentric with the woody cylinder.


TEXT-FIG. 1.

The secondary wood is so similar to that of *Podocarpus* that it is needless to describe it, but attention must be drawn to the sculpturing of the tracheides composing the protoxylem and the metaxylem adjacent to it. Although the narrower protoxylem elements are of the ordinary spiral or annular type, many of the wider ones are scalariform, and also possess circular or oval pits with or without a border, thus closely resembling the transfusion tracheides in the leaf (see below). Some of the earlier-formed metaxylem elements, even in regions not in contact with medullary rays, show large uniseriate borderless pits (Eiporen) at long intervals, instead of the usual bordered pits (text-fig. 1). Exactly the same type of pitting is seen also in the early metaxylem of the leaf-strand.

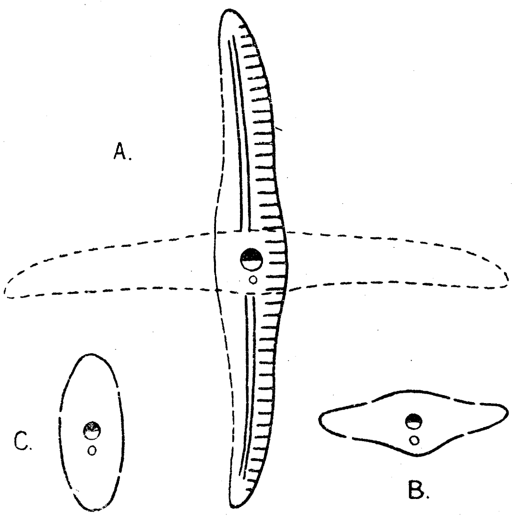
D. *Leaf.*

The polymorphism of the leaf in the Conifers has for a long time drawn the attention of botanists (MASTERS, 1891). In *Acmopyle* at least six types of leaves occur in different regions of the plant :—

1. The large triangular scale-leaves on the thicker branches.
2. The minute imbricate scales on the peduncles of the megastrobili.
3. The chief assimilating leaves, further described below.
4. Small laterally compressed leaves with an isobilateral structure, forming the transitions from 1 to 3 and 3 to 2.
5. The sterile bracts on the fleshy receptacle.
6. The fertile bracts.

The leaves on the dorsi-ventral pectinate shoots deserve special mention, for they afford a striking illustration of the direct influence of the orientation of an organ upon its internal structure. The rather fleshy, linear, obtusely pointed leaves have their smooth and shining, slightly convex, upper surfaces directed towards the light (Plate 11, fig. 22*b*), while the shaded under sides present, on each side of the faint midrib, a broad glaucous band to which the stomata are usually confined, but which is not wide enough to extend to the leaf-edge. A transverse section shows a rather unexpected feature : the plane passing through the xylem, phloem, and the associated mucilage canal, instead of being perpendicular to the leaf surface as in all ordinary leaves, is here parallel to it (Plate 9, fig. 4, and text-fig. 2).

Since there is no sign of a torsion in the decurrent leaf-base it is obvious that the leaf is expanded in the antero-posterior plane, so that the middle lines of the actual upper and lower surfaces represent the margins of an ordinary leaf. The whole anatomy of the leaf, except the vascular strand, has, so to speak, been shifted through an angle of 90°. It is clear, also, that this shifting has taken place in opposite directions in the leaves respectively on the right and left sides of the shoot, for the palisade layer is on the morphologically left side in the right-hand series of leaves, and on the morphologically right side in the left-hand series. As BERNARD (1904, p. 256) points out, leaves thus constituted contradict LIGNIER'S view that the accessory transfusion tissue is the remnant of a former system of veins.



TEXT-FIG. 2.—Diagrams to show the organisation of three different types of leaves in *Acmopyle.* In A the palisade tissue is indicated as short transverse lines, and the accessory transfusion tissue as long parallel lines; the broken line shows the position of the lamina in an ordinary leaf (expanded in the horizontal plane). *Xylem,* black; *phloem,* unshaded.

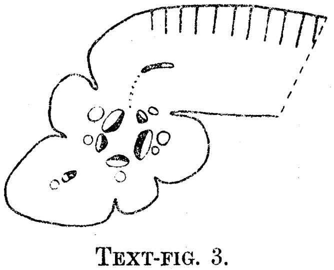
Towards the base and apex of the pectinate shoot, but especially in the latter region, are frequently seen a few smaller leaves, which indicate the manner in which this peculiar structure has been attained. They show all transitions, both in orientation and anatomical structure, between the linear leaves already described and the spirally placed scale-leaves by which they are distally succeeded. Text-fig. 2, C, shows the lenticular transverse section of one of these transitional leaves, expanded in the radial plane, devoid of palisade cells, and with the stomata evenly distributed on the two faces. Leaves expanded in the radial plane, and having an isobilateral structure, are also met with in the New Caledonian species *Dacrydium taxoides,* and probably in several other Podocarpineæ (see MAHLERT, 1885, p. 279, and VAN TIEGHEM, 1891, pp. 169, 171).

It is well known that, in the horizontal shoots of *Taxus* and many other plants, the apparently distichous arrangement of the leaves is brought about by a torsion in the leaf-bases, some of which at the same time bend round the axis of the shoot, so as to occupy approximately the same (horizontal) plane as the leaves arising from the right and left sides of the axis. In *Acmopyle,* however, no trace of a torsion is seen in any of the leaves; these are all attached by a narrow longitudinally extended base from which the lower edge of the leaf can be followed a considerable distance backwards as a straight decurrent ridge. That here, as in *Taxus,* the leaves arise spirally is seen from the leaf-traces and from the salients caused by the decurrent bases in the outline of a transverse section of the shoot. Since, however, the leaves are already expanded in the radial plane, a simple bending (unaccompanied by torsion) suffices to bring them into the horizontal position (text-fig. 3), and even this bending is dispensed with in the case of the leaves arising from the sides of the axis.

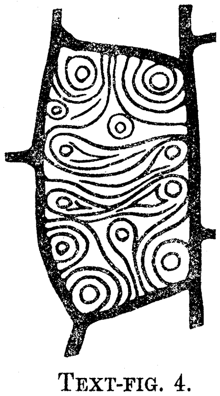
Examples of leaves which show the closest resemblance in principle to those of *Acmopyle* also occur in *Podocarpus imbricatus* Bl. and *P. dacrydioides* A. Rich., a fact noticed in a passing reference by BERNARD (1904, p. 256), but not elucidated by figures.

Prof. GOEBEL has recently (1913, pp. 238–247, 289) described rather similar adaptations in other Conifers (*Thujopsis*, etc.) and some Vascular Cryptogams (*Lycopodium complanatum*, *L. volubile*, *Tmesipteris*). See also BOODLE (1900).

Plate 9, figs. 4–7, and text-fig. 4, illustrate the minute structure of one of the leaves on the pectinate shoot of *Acmopyle.* The thick upper and lower cuticles, the sunken stomata, and the fleshy character of the leaf, are features consistent with the xerophytic habitat of *Acmopyle.* The plant grows, according to PILGER, in rocky places in the south of New Caledonia.* There is the usual palisade layer on the upper side, and the spongy parenchyma below. Sections cut parallel to the leaf surface present a mosaic of large thin-walled mucilage cells, which probably store water, and are responsible for the fleshy nature of the leaf, and groups of much smaller dark-staining palisade cells with abundant interspaces (Plate 9, fig. 5). Hypodermal fibrous elements occur in small numbers on both faces of the leaf, but are confined to the region of the midrib. Between the two mesophylls lies a loose network of transversely elongated cells (Plate 9, fig. 6), several layers thick, extending in the horizontal plane from the median vein to either edge of the leaf. This network consists of (1) thin-walled cells with living contents; (2) dead cells with thick, simply pitted walls ("accessory transfusion tissue," WORSDELL).



TEXT-FIG. 3.



TEXT-FIG. 4.

The transfusion tissue proper, which is as a rule clearly separated from the accessory by a layer or two of parenchyma, is further distinguished by its elements

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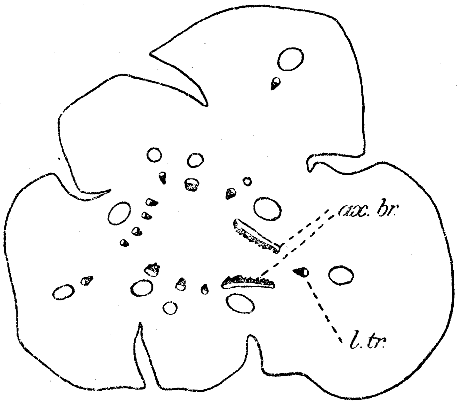
* I have to thank Prof. COMPTON for the following additional information regarding the habitat of *Acmopyle.* The typical situation in which *Acmopyle* grows is in mixed forest containing many species of conifers, on serpentine rocks above 3000 feet altitude. Here it is associated with *Podocarpus minor*, *P. sp.* (unpublished), *Dacrydium taxoides*, *D. lycopodioides*, etc. The majority of arboreal plants in this association show some xerophilous features.

having all their walls provided with crowded bar thickenings, as well as small borderless or narrowly-bordered pits (text-fig. 4). These transfusion tracheides are of two types, one long and narrow, the other considerably broader and nearly isodiametric, but intermediate shapes are also met with. The sculpturing on all is of the same type. The narrower elements are almost all on the side nearest to the protoxylem. In the median plane the transfusion tissue is also separated from the protoxylem by one or two layers of parenchyma, but, laterally, it is often contiguous with the wood. The protoxylem and centrifugal xylem of the leaf show the same types of pitting as described above for the corresponding tissues in the stem.

The epidermal cells, which in the non-stomatiferous regions are longitudinally extended, have straight (as opposed to sinuous) walls, which show moniliform thickenings (Plate 9, fig. 7). The lumina are almost completely filled up by a homogeneous dark brown substance, but the nucleus invariably lies in a pocket in the latter. The stomata are of the usual Gymnospermous type, and the figures on Plate 9, figs. 7*a*–*d*, will suffice to describe them.

E. *The Vascular Supply of the Axillary Branch.*

For reasons stated below, attention is particularly directed to the vascular supply to the axillary branch, which originates as two strands (*ax.br.*), one from each side of the gap in the main cylinder, caused by the subtending leaf-trace (*l.tr.*), (text-fig. 5). Before passing into the branch, the strands turn round, so as to face each other by their xylem ends. It may also be mentioned that this mode of origin is of wide occurrence among Conifers (GEYLER, 1867; STRASBURGER, 1872).



TEXT-FIG. 5.

F. *Microstrobilus.*

The male cones are terminal, and either solitary, or more frequently in groups of 2–5 or 6 (Plate 10, fig. 12), on short peduncles covered with scales. When in a group they are borne on a branched system of peduncles. Each sporophyll bears two spherical abaxial pollen-sacs, except at the base of the cone, where sporophylls with one and three sacs are of frequent occurrence. The longitudinal section given in Plate 9, fig. 8, shows at × the organic apex of the axis, and at ✻ the terminal sporophyll, which is distinctly peltate. The development of all the sporangia in the cone appears to take place almost simultaneously. Neither in the structure of the cone-axis, nor in that of the sporophylls, is there any important difference from *Podocarpus*; a reference to the figures, and the explanations attached to them, will suffice (Plates 9, 10, figs. 8–12).

As in *Podocarpus* and *Dacrydium*, the pollen-grains have two wings, with reticulate markings (Plate 10, fig. 11). Unfortunately, the contents of the pollen-grains are badly shrunken in all the material, so that the structure of the male gametophyte cannot be definitely ascertained. Not more than one nucleus can with certainty be made out in each pollen-grain, but it is highly improbable that no more are produced.

Another feature, perhaps of little significance, in which *Acmopyle* resembles *Podocarpus*, is the thick-walled character of the pollen-tube (STILES, 1912, p. 483, *P. macrophyllus*).

G. *Megastrobilus.*

The field notes accompanying the material are not explicit as to whether *Acmopyle* is monœcious or diœcious, but the probability is in favour of the latter, for none of the published accounts or figures show both sexes as being represented on the same plant.

External Features.

The megastrobili occur terminally on the pectinate shoots;* as a rule solitary, they sometimes occur in pairs (Plate 11, fig. 22), and, according to BRONGNIART and GRIS (1869, p. 330), even in threes. Each strobilus is borne directly on a long peduncle, and consists of a large fleshy receptacle, ending in a single plum-like seed.† The photographs on Plate 11, figs. 22, 23, are natural size. At the stage represented, the peduncle is strongly curved, sometimes almost into a semicircle; it is completely covered with adpressed scale-leaves, each consisting of a basal cushion adnate to the axis, and a free triangular apex provided with a faint abaxial keel. The peduncle tapers slightly towards the base, for the cushions of the leaves diminish in size, while the keels become more prominent.

The receptacle, sharply marked off from the peduncle by a sudden increase in diameter, is 10–18 mm. long and 8–10 mm. in diameter, being slightly thicker distally. From its remarkably verrucose or tuberculate surface project the thick scale-like tips of a few distant sterile bracts. These bracts are probably in serial continuation with the scales on the peduncle, although their arrangement is obscured by the much greater length and swollen character of the internodes; at the base of the receptacle the sterile bracts are of a size and form transitional to the leaves on the distal part of the peduncle.

A feature worth noting is that in the axils of many of the sterile bracts the surface of the receptacle is raised into a more or less prominent hump (text-fig. 6), usually distinguishable from the swollen base of the bract. The entire receptacle is thus composed of the swollen axis, the swollen bract bases, and these axillary humps, which, to judge from their vascular supply, are probably vestigial axes (see p. 267).

Attention must be drawn to a curious fact constantly observed in the material at

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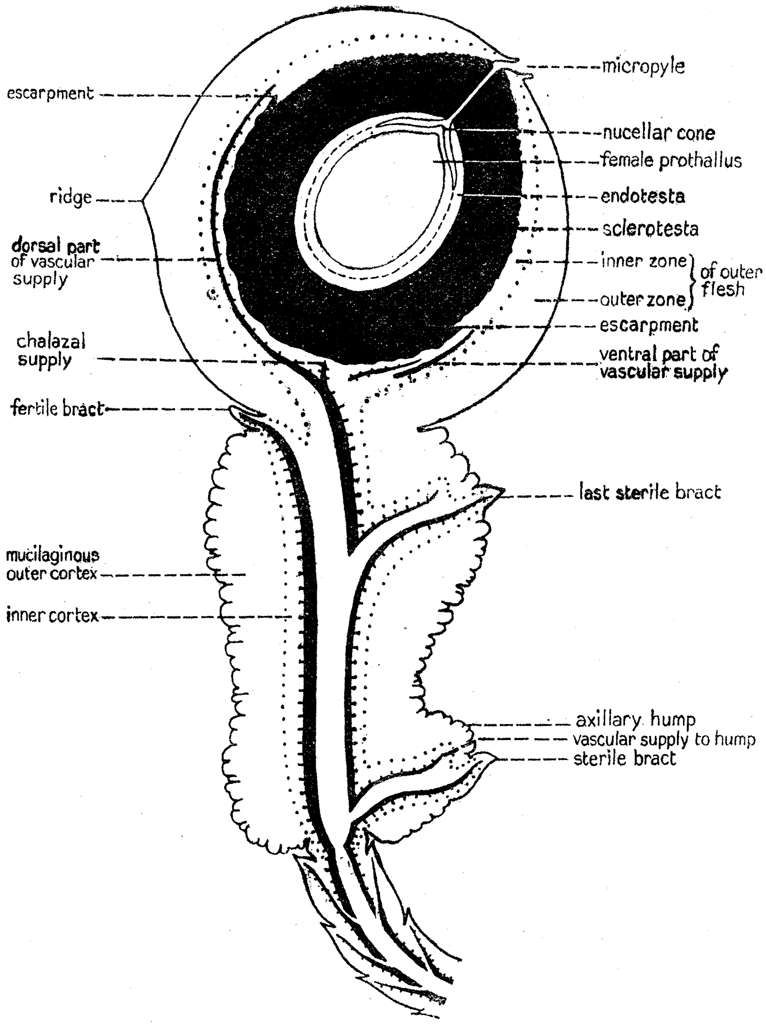
* PILGER also records strobili in the axils of the distally situated smaller leaves.

† PILGER records 1–2 fertile bracts on each receptacle.

my disposal, namely, that the most distal sterile bract of each receptacle differs from the others in two respects. Firstly, the tip of the bract is awl-shaped instead of scale-like ; secondly, the cushion bearing this free tip is considerably larger than the swollen bases of the other bracts, and is always circular with the bract-tip projecting from the centre (Plate 11, fig. 23, text-fig. 6). One face of the receptacle, conveniently called the dorsal, is usually free of sterile bracts (Plate 11, fig. 22*a*, is the only exception in my material) ; this is the side on which is situated, at the distal end of the receptacle, the single, smooth, broadly rotundate, fertile bract (Carpidium, PILGER), easily distinguished from the sterile bracts by its shape and, of course, by the fact that it subtends the seed. In Plate 11, fig. 22*a*, the fertile bract is seen wedged in between the receptacle and the seed. The most distal sterile bract is



TEXT-FIG. 6.—Diagrammatic longitudinal section, in the dorsi-ventral plane, of the peduncle, receptacle, and seed of *Acmopyle* (compare Plate 11, fig. 22*c*). The vascular bundles in the axils of the bracts are shown in the figure, although, being pairêd, they would not actually be visible in a median section. The *xylem* strands are shown as thick longitudinal lines, the *phloem* as short transverse lines.

always placed on the ventral side of the receptacle, directly, or almost directly opposite to the fertile bract.

Although in the absence of young material a definite opinion cannot be expressed, I rather incline to the view that the large round elevation on the ventral face of the receptacle is the organic apex of the strobilus, pushed aside and overtopped by the developing seed. The fertile bract would thus be not the most distal leaf on the receptacular axis. This conclusion is based chiefly on analogies in *Podocarpus* and *Dacrydium*. (See especially PILGER's figure of *D. Bidwillii* (1902, p. 47) and STRASBURGER's account of *Podocarpus chinensis* (1872, p. 20, and Plate 2, fig. 38)). Miss Gibbs also states (1912, p. 539) that in *P. spicatus* the apex of the strobilus is always distinguishable beyond the last fertile bract.

A similar pushing aside of a primary apex by an enlarging seed has been well known in *Taxus* since VAN TIEGHEM discovered it in 1869 (*loc. cit.*, p. 303, and Plate 16, fig. 91; see also STRASBURGER's well-known figure, 1872, Plate 1, fig. 5).

The unripe seed is an almost perfect sphere, sessile on the apex of the receptacle, with its axis inclined to that of the receptacle at an angle of about 45°. It thus presents a strong contrast to the condition in *Podocarpus*, but approaches that in some species of *Dacrydium*.

The seeds figured by PILGER (1902, p. 117) are all very nearly erect; this fact may quite possibly be due to his material being slightly older than that examined by me, and may suggest that the young ovule is horizontal or even further inclined, as in some species of *Dacrydium*. However, in the absence of younger material, these remarks can only be taken as conjectures. (See also p. 285, below.) It is worth mentioning that the seeds here described were collected in March, 1914, on Mount Mou.

The surface of the drupaceous seed is covered with bloom and is smooth except for a slight ridge passing obliquely round the base of the seed, but not forming a complete circle. If the seed is viewed from the ventral side (Plate 11, fig. 23), the ridge is hardly visible.

The micropyle is distinctly two-lipped, the upper lip adpressed, the lower projecting and transversely extended.

Anatomy.

The Peduncle.—It was mentioned above that at the stage represented in Plate 11, fig. 22, the peduncle is strongly curved. The plane in which the curvature lies is by no means fixed with regard to the dorsal and ventral faces of the receptacle. In text-fig. 6 it *happens* to coincide with the dorsiventral plane. A section across the distal region of the peduncle shows a striking peculiarity: the strands composing one-half of the vascular ring are much stouter than the rest. This asymmetry was at first suspected to have a relation to the plane of curvature of the peduncle as a mechanical adaptation, either the convex or the concave side having the better developed strands. However, sections through peduncles curved in different planes soon showed that this is not the case: the best developed strands were invariably found to lie along the line which if produced distally would pass along the dorsal face of the receptacle and through the fertile bract. It will later be seen that this want of symmetry in the vascular system is continued right through the receptacle itself, and that it is no doubt connected with the needs of the developing ovule.

The Receptacle.—(a) *Non-Vascular Tissues.*—The ground-tissue is rather sharply marked off into two concentric regions. The central area comprises the pith, medullary rays, and a few of the inner cortical cell-layers; it is characterised by the small size of the thin-walled longitudinally extended cells, by the entire absence of mucilage cells, and by the presence of small scattered "resin"-cells. The peripheral zone differs in the much larger size of the cells, which, moreover, are mostly radially elongated, and especially in the great preponderance of huge mucilage cells, which form the bulk of the outer cortex, and are responsible for the fleshiness of the receptacle. The large amount of mucilage in the receptacle and in the outer flesh of the seed very probably serves as food to birds, which no doubt disperse the seed. Hand-sections of the receptacle, when placed in water, swell up markedly in their peripheral region, while the central portion remains unaltered. The clear contents of the mucilage cells become white and opaque in strong alcohol; they are slow in taking up stains, and show a granular or alveolar structure. "Resin"-cells are also present in the outer cortex; they are larger and more abundant than in the pith, and, like the mucilage cells, are radially elongated, frequently forming radial chains (Plate 10, fig. 13).

Fig. 13, Plate 10, shows the rather deeply lobed appearance of the tuberculate surface of the receptacle. A specially thick cuticle covers the spherical ends of the lobes, and the small-celled epidermal layer is exceedingly rich in the dark-brown "resinous" matter. No stomata were observed on any part of the receptacle.

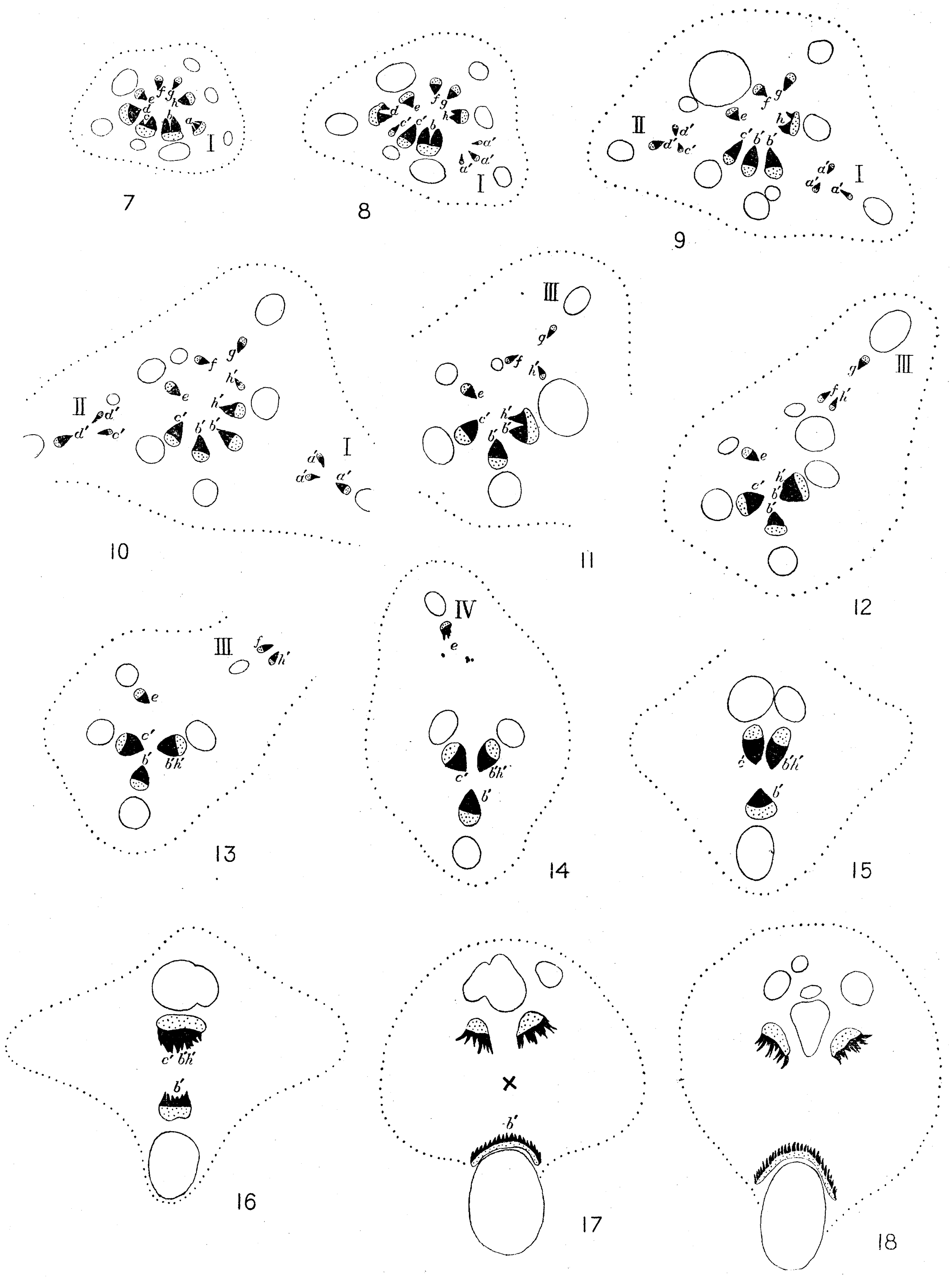
The free tips of the sterile bracts have a thick cuticle perforated by a few stomata on both faces of the bract. In the fertile bract the lower cuticle is considerably thicker than the upper, both being pierced by irregularly distributed stomata.

(b) *Vascular Anatomy of the Receptacle.*—Of all the known Podocarpineæ the vascular system of the receptacle is the most complex in *Acmopyle.* In broad outline it may be described as a dictyostele from which a simple leaf-trace is given off to supply each of the bracts, and in typical cases two strands come off from the sides of the leaf-gap to supply the humps in the axils of the bracts.

The following account is based chiefly on complete series of transverse sections of three whole receptacles and portions of two others. Of these one was embedded in paraffin after most of the cortex had been removed, and was microtomed from base to apex.

A description will first be given of one of the receptacles, then the more important variations observed in the others will be dealt with.

Serial sections cut from the distal end of the peduncle and carried up into the base of the receptacle show at the junction between the two regions a slight constriction in



TEXT-FIGS. 7–18.—Vascular anatomy of the receptacle of *Acmopyle*, as revealed in serial transverse sections from the base upwards. *Xylem*, black; *phloem*, dotted. The peripheral dotted line represents approximately the limit between the inner and outer cortex. In all the figures the dorsal (posterior) side of the receptacle faces the foot of the page. Further explanation in the text.

the pith, which suddenly expands again distally, though not in proportion to the enormous increase in diameter of the receptacle as compared with the peduncle Text-fig. 7, from the base of the receptacle, shows a ring of about eight collateral endarch strands of which those lying on the posterior side are distinctly the largest. Surrounding the strands is a ring of seven mucilage canals, one outside each strand, except for one of the strands which is without a canal.

The receptacle in question had four sterile bracts; three of these had each a well-developed axillary hump; the fourth and most distal arose, as already described, from the summit of a relatively large circular prominence on the ventral face of the receptacle. In the figures the Roman numerals refer to the vascular supplies of these sterile bracts in acropetal order. It is not always easy to speak, in definite terms, of the exact number of strands in the axial cylinder for, as the diagrams show, several of them are in different stages of fusion and disintegration; but it is hoped that the letters adjoining them will enable the reader to identify the strands, or their components at different levels, without unnecessary reference to the text.

Sterile Bract I: Strand *a* comes off bodily from the ring, causing in the latter a gap which closes up in text-fig. 11. The strand immediatelly splits up radially into three pieces which soon arrange themselves fanwise, the canal of the original strand being at the back of the middle piece. This arrangement is brought about by the two lateral pieces turning away from the median with their protoxylem ends as pivots. As we trace the little system obliquely upwards through the cortex of the receptacle the two lateral strands continue their turning movement till they have almost completely reversed their orientation (fig. 10). While the normal median strand with its canal enters the free tip of the sterile bract, there ending in a mass of transfusion tracheides, the two inverted strands end blindly in the mass of small-celled tissue forming the core of the axillary hump. Between the paired inverted strands supplying the axillary hump and those supplying a normal vegetative axillary branch (text-fig. 5) there is such a close resemblance that the hump appears without doubt to be a reduced axillary shoot. See also p. 293 below.

Sterile Bract II: The supply to this bract comes off at only a slightly higher level than that to the first. As before, one of the strands in the ring (*d*) passes out bodily, but in this case it splits up into two unequal pieces (*d′*, *d′*) of which the larger enters the bract-tip. The supply to the axillary hump is in this case formed partly by the smaller piece, and partly by a branch (*c*) from one of the strands of the axial ring. The behaviour of the pair of axillary strands is precisely the same as that already described under Sterile Bract I.

Sterile Bract III: At this stage we have reached a level in the receptacle midway between its base and apex; meanwhile the remaining strands of the ring have undergone considerable re-arrangement which will be clear from the lettering in the figures.

The strand *g* passes out from the ring (fig. 9) and without dividing enters the bract-tip. The supply to the axillary hump consists as before of two strands (*f*, *h'*). Of these one (*h'*) arises, as in the case of the second bract, by the splitting of one of the strands at the sides of the leaf-gap; the other is constituted by the entire strand (*f*), flanking the other side of the leaf-gap. These two axillary strands behave exactly like those in the axils of Bracts I and II, except that, being appreciably larger than the former, each of them at the same time carries out with it a mucilage canal (fig. 12). These two canals very soon fuse into one (fig. 13).

Sterile Bract IV: We are now near the apex of the receptacle; there is a ring of four strands, three of them much the largest. The smallest of these (*e*), occupying the ventral side of the ring, forms the supply to the fourth sterile bract and its associated hump, which, it will be remembered, is larger than the other humps. The strand passes out undivided through about half the thickness of the cortex, and then gives off from its upper surface two minute strands whose orientation it was not possible to determine (fig. 14). The subsequent behaviour of these strands leaves little doubt as to their homology with the inverted axillary strands above described (see text-fig. 10).

Fertile Bract: There are now three very large strands in the axis (fig. 15). If we trace these strands or their components downwards to the base of the receptacle, we find that the posterior one (*b'*), which is the trace of the fertile bract, has all along preserved its original orientation (text-figs. 7–9). On the other hand, the components of the other two strands (which in fig. 13 face each other, lying in the right-left plane) originally formed part of a more open ring.

As we proceed distally (towards the base of the seed), the two opposing strands continue their turning movement till they come to lie parallel to each other, diametrically opposite both in position and orientation to the third strand. These "inversely orientated" strands compose the vascular supply of the seed; their further behaviour will more appropriately be described later, but attention may be directed to their obvious homology with the paired strands in the axils of the sterile bract-traces. Their relatively huge size is evidently connected with the nutrition of the seed, which may be said to exercise a basipetal influence, which is felt as far back as the peduncle, and results in the asymmetrical development of the entire vascular cylinder.

Shortly before entering the fertile bract, the trace becomes much extended tangentially, and tends to spread round the large mucilage canal, narrow "medullary" rays at the same time breaking it up into a number of thin plates. In the distal part of its course, transfusion tracheides appear in large quantities.

Variations Observed in other Receptacles.—(1) In each of the other two receptacles, which were sectioned from base to apex, the trace of the first sterile bract was not accompanied by any axillary strands.

(2) The last sterile bract of one of these receptacles possessed two unusually large axillary strands, each of which became inversely orientated during its outward

passage, and carried out with it the associated mucilage canal. The two canals did not fuse into one, as described above under Sterile Bract III, but ended blindly shortly before the strands themselves.

(3) The last sterile bract of the other receptacle had only one axillary strand, of medium size, and accompanied by a canal. The behaviour of this single axillary strand was exactly the same as if it were one of a pair, for it did not occupy a median position, and, during its outward course, rotated through an angle of nearly 180°.

In order to check the results obtained from transverse sections, portions of the fourth and fifth receptacles were embedded in paraffin for longitudinal sections, as well as for sections cut transversely to the oblique course of the bract and axillary strands. An axillary strand, as seen in longitudinal section, is shown in text-fig. 6. Turning slightly upwards, in the distal part of its course, it ends blindly in the midst of the small-celled core of the hump.

The Seed. (a) *Non-vascular Structures.*—Text-fig. 6 shows a median section of the unripe seed along the dorsi-ventral plane, which is the only plane of symmetry. The oblique curved ridge on the back of the seed is crossed by this plane about two-fifths of the way up from the fertile bract to the micropyle. The surface of attachment to the receptacle is considerably broader than appears from PILGER'S fig. 24*b* (1903, p. 117). PILGER, moreover, figures the seed as being very nearly erect (see his fig. 24*c*) ; the stony layer is shown proportionately much thicker than it is in any of the seeds examined by me, while the outer flesh is represented as little more than a skin covering the stone, probably because PILGER examined dried material.

The fleshy outer coat of the seed has a roughly uniform thickness of about 2–2·5 mm., except near the apex of the seed. Here it rather abruptly thins to about 0·5 mm., and forms the distal one-third of the micropylar canal. This part of the canal is peculiar in its curved horn-like shape (text-fig. 6), the curvature being in the plane of the section figured. Moreover, this part of the canal traverses the seed-coat very obliquely, being bent at a considerable angle (over 60°), to the straight inner part of the canal, which is bounded by the sclerotesta.

A very thick cuticle forms a smooth protective covering pierced by stomata, which are consequently more deeply sunk than those on the leaf. The distribution of the stomata, which are, as a rule, placed longitudinally, does not show any regularity, except that they are, on the whole, perhaps fewer towards the micropylar end. The lumina of the epidermal cells are small, and nearly always filled with the brown substance above mentioned. At the micropyle the epidermis dips inwards, to line the horn-like part of the canal, the cuticle at the same time gradually becoming thinner.

The fleshy outer coat of the seed is roughly divided into a thick outer zone exceedingly rich in mucilage cells and devoid of vascular tissue, and a thinner layer immediately covering the sclerotesta. This zone appears much darker than the outer, because it almost entirely consists of "resin"-cells. *The vascular system of the seed is confined to the inner zone.*

The stony layer has a thickness about equal to that of the outer flesh at the seed-base, and encloses a cavity whose diameter almost equals the combined thickness of the stony and outer fleshy layers.

The inner surface of the stone is smooth, but the outer is carved into a pattern which although complex is essentially constant. The photographs on Plate 10 (figs. 15–19) will give a better idea of the sculpturing than will be obtained from a lengthy description. They represent different views of one seed from which most of the flesh was scraped off. The darker lines and patches correspond to the depressions in the surface, from which the remains of the "resinous" inner zone of the flesh could not easily be removed. The surface of the stone is sharply marked off into two regions, an apical and a basal, by a line which may be described as an escarpment facing the micropylar end. (See the sectional view in text-fig. 6.) It will be noticed that while the apical region is characterised by a uniformly granular surface, the basal region shows a series of thick dark lines diverging from the chalaza and ending abruptly at the escarpment. These irregular lines are due to grooves in the stone, and represent the course of the more important vascular strands in the inner region of the outer flesh.

The "escarpment," as seen in the sectional view (text-fig. 6), rather suggests the so-called "crown" which forms the most obvious distinctive feature of the palæozoic seed, *Stephanospermum*. The resemblance is not so clear with *S. akenioides*, Brongn., as with *S. caryoides*, Oliver, where the crown being much less developed, the peri-micropylar trough is shallower (OLIVER, 1904, p. 380, text-fig. 2). The comparison is, however, only permissible so far as the longitudinal section is concerned, for while in *Stephanospermum* the edge of the crown forms a complete circle which lies in a single plane transverse to the seed-axis, in *Acmopyle* the line of the escarpment forms two wide loops, one on the ventral face of the stone, the other on the dorsal. These loops, of which the ventral is considerably the deeper, are only narrowly connected together at the micropyle.

It will be seen from text-fig. 6 that the position of the escarpment has no relation either to the ridge on the external surface of the seed, or to the line of separation of the nucellus from the integument.

Prof. OLIVER (1903, Plate 24, fig. 13) also figures in *Torreya* a rather similar line on the surface of the stone, but this, as he states (p. 468), marks the line of separation of the integument from the arillus.

According to SPRECHER (1907, p. 123, fig. 123), in *Ginkgo biloba* the line of separation of the nucellus and integument is marked by a circular groove on the outer surface of the stone at a level below that of the equator. I am, however, unable to confirm this observation in some material of this plant from Montpellier.

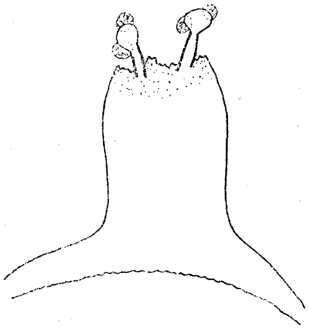
In its symmetry, so far as I know, the stone of *Acmopyle* is unlike that of any other Gymnospermous seed hitherto described. The two faint ridges on the right and left sides (Plate 10, figs. 18, 19), correspond to those on a bicarinate seed of *Ginkgo* or *Taxus*, in which genera they lie in the plane of principal symmetry; but in *Acmopyle* the plane in which the ridges lie is not flat but distinctly curved with the convexity facing the dorsal side (see the side view, Plate 10, fig. 18). An examination of the photographs will show that the chalaza of the stone—if one may employ this term for the point from which the strands radiate—is not situated exactly at the broad end of the stone, so that the straight line joining the micropyle with the chalaza does not represent the greatest length of the stone. The eccentric position of the chalaza is well demonstrated by Plate 10, figs. 15 and 17, which are respectively ventral and basal views. In a view from the dorsal side (fig. 16) the chalaza is not visible. Thus it happens that what in numerous other Gymnospermous seeds corresponds to the plane of principal symmetry, is in *Acmopyle* not a plane of symmetry at all. As is the case with the entire seed, the median dorsi-ventral plane is the only plane of symmetry.

Viewed from either the front or the back the stone has an almost circular outline, there being hardly any trace of a micropylar beak. A section across the middle is isodiametric (Plate 11, figs. 20, 21); the cavity of the stone is here nearly circular, but it is noteworthy that the plane of dehiscence does not traverse it symmetrically, the ventral valve being distinctly larger than the dorsal (text-fig. 32). This asymmetry tends to disappear towards the distal part of the stone. A section across the apical region is lemon-shaped (text-figs. 33, 34), the stone being here slightly flattened in the right-left plane, and produced at each side into a blunt ridge. The portion of the micropylar tube bordered by the sclerotesta is about 2·5 mm. long; throughout this region it is a narrow slit-like passage, flattened in the dorsi-ventral plane (text-fig. 34), and immediately lined by one layer of "resin"-cells continuous with the epidermal lining of the more distal portion of the canal. Meeting this slit at right angles, and joining together the two ridges on the stone are two faint lines representing the plane along which the stone probably dehisces during the germination of the seed.

The cells composing the stone are generally isodiametric, except those along the plane of dehiscence which are flattened in that plane, and those along the cavity of the stone which are flattened tangentially. Their walls are pierced by numerous fine branched canal-like pits which as usual correspond in position on the opposite sides of the middle lamella. In SCHULTZE's solution the main substance of the wall becomes yellow, but the innermost lining of the cell—which in surface view presents a sieve-like appearance—as well as the lining of the pits, gives the cellulose reaction.

As in *Podocarpus* the inner fleshy layer is for the most part fused to the nucellus (text-fig. 6). The limit between the two is difficult to make out in the fused region, except for the presence, in the inner flesh, of scattered "resin"-cells which increase in number towards the sclerotesta, and even encroach upon the adjacent regions of the latter. The innermost layer of the free portion of the inner flesh consists largely of "resin"-cells, and is continuous with the rather similar lining of the micropylar canal which may hence be regarded as representing the inner flesh in that region.

The free portion of the nucellus is dome-shaped, and its apex is produced as in *Podocarpus* into a distinct receptive cone or column traversed by several rather thick-walled empty pollen-tubes (text-fig. 36). The nucellar cone, as well as the upper part of the dome upon which the cone is perched, appears white in contrast to the lower part of the dome, whose superficial layer of cells is rich in "resin" (Plate 11, fig. 25). A definite layer of cuticle protects the entire free region of the nucellus except the very tip of the nucellar cone where the cells are crushed and disorganised (text-fig. 36).



TEXT-FIG. 36.—The receptive column of the nucellus of *Acmopyle*, with germinating pollen-grains. The shaded apical portion of the nucellus has become disorganised.

The apex of the female prothallus forms a blunt conical process which lies against the base of the nucellar cone (text-fig. 6 and Plate 3, fig. 26), suggesting the so-called "tent-pole" of *Ginkgo*, *Cordaites*, and other archaic Gymnosperms (BRONGNIART, 1881, Plate 2, fig. 2; Plate 3, fig. 8; Plate 6, fig. 9; Plate 11, fig. 4; Plate 12, fig. 2). The pro-embryo has already been formed; no traces are seen of any aborted archegonia. From the position of the single pro-embryo it may be inferred that the parent archegonium opened a little to one side of the central axis (Plate 11, fig. 26). It may be stated that one prothallus showed an embryo exactly in the axis. In the distended condition of the archegonial wall jacket cells, if there were any in the young archegonium, are not visible.

The structure of the pro-embryo and suspensor tubes presents no features of special interest, being practically identical with that in *Podocarpus*. I am unable to say whether there is a sterile cap to the embryo, such as SINNOTT describes in some species of *Podocarpus* (1913, p. 60).

PILGER (1903, p. 33) records unusually long suspensor tubes in some species of *Podocarpus* (*P. amarus*, 30 mm.). In *Acmopyle* the tubes when stretched out reach a length of over 15 mm.

As in most species of *Podocarpus*, too, the megaspore membrane is poorly developed (Plate 11, fig. 28), although it is possible to distinguish two layers, of which the outer is a film of cuticle. On the conical apex of the megaspore the membrane is particularly thin, the cuticle being absent, or at any rate extremely thin.

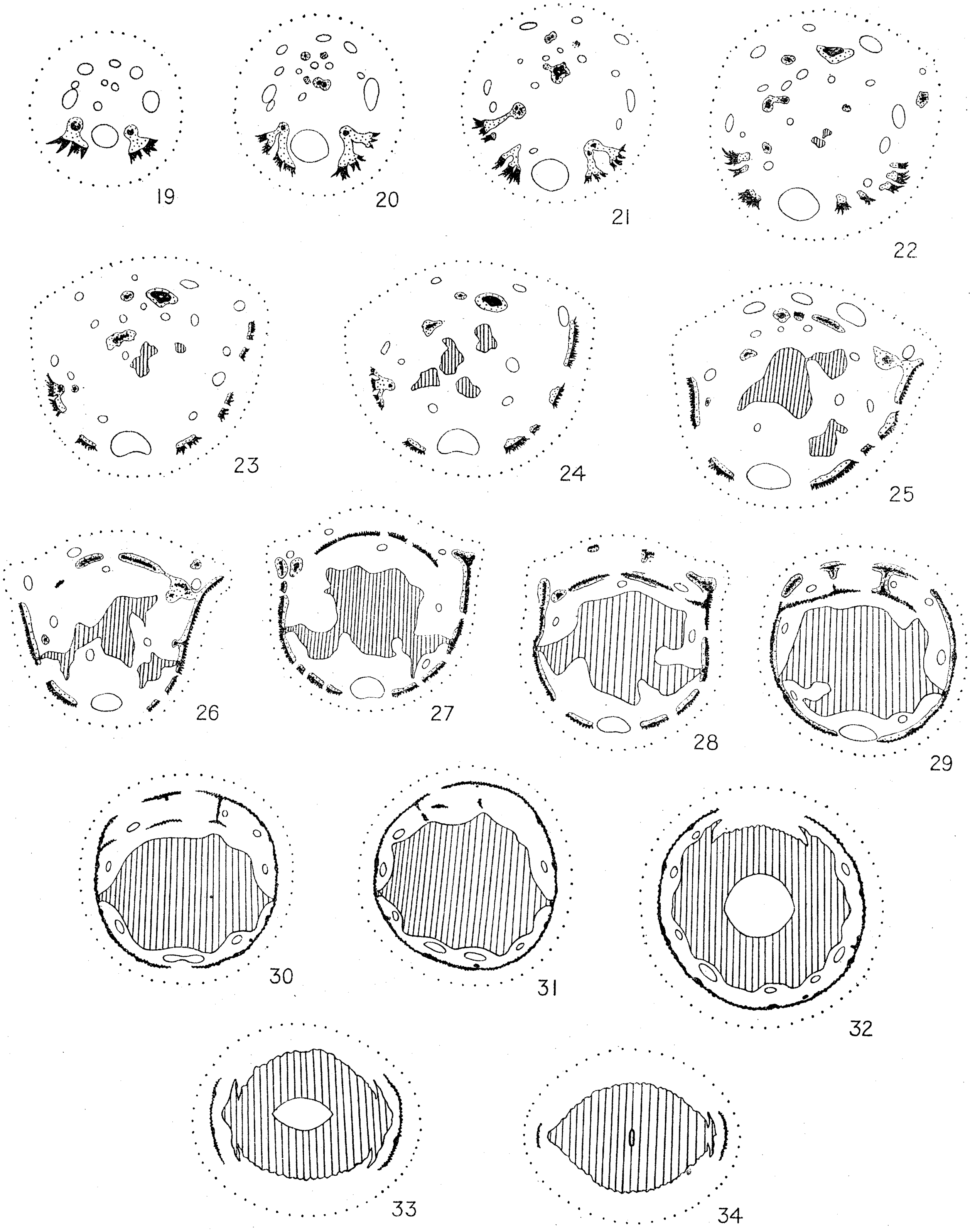
Plate 11, fig. 28, shows a longitudinal section of the superficial region of the female prothallus; the small multi-nucleate cells (see Plate 11, fig. 29) composing the peripheral layer of the prothallus have their anticlinal walls slightly thickened in the regions adjacent to the megaspore membrane. In the last-mentioned figure, which is a surface view of this layer, these walls are seen traversed by straight pits.

All the remaining cells of the prothallus are thin-walled and most of them are multi-nucleate; those forming the axis of the prothallus in front of the advancing embryo are distinguished by their small size, elongated shape and abundant starch-content. No tracheides were seen such as those described by Miss GIBBS (1912, p. 546, Plate 51, figs. 42–3) in *Podocarpus polystachya* and by COKER (1902, p. 97) in *P. coriacea.*

(b) *Vascular Anatomy of the Seed.*—In broad outline the vascular structure of the seed may be described as a tracheal cupule (Plate 11, fig. 24) stiffened by a network of strands and exactly covering the basal region of the stone which, as already mentioned, is limited distally by the "escarpment." A vascular system internal to the stone is not present, but besides two concentric strands terminating against the chalazal end of the stone, a number of other strands come off at different levels from the inner surface of the cupule, and end before reaching the sclerotesta. In the right-left plane the tracheides of the cupule are for some distance in organic connection with the stone cells.

The vascular system will now be described in detail (text-figs. 19–34). Text-fig. 35 shows the approximate levels at which the sections drawn in text-figs. 19–34 were cut. Serial transverse sections were cut of two seeds, and the results confirmed by dissections and longitudinal sections of two others. A reference to fig. 15, p. 266, will show that at the apex of the receptacle there were two very large strands lying parallel to each other and with an orientation inverse to that of the fertile bract-trace. We shall now examine the further behaviour of these strands, for it is chiefly by the disintegration of these that is produced one of the most complex vascular systems known among Gymnospermous seeds.

Immediately above the level where we left them on p. 268 these two strands completely fuse together, xylem with xylem and phloem with phloem, while their mucilage canals may also fuse into one (text-fig. 16). However, the resulting large strand immediately breaks up again into two (text-fig. 17); at the same time the two mucilage canals (or one in case of fusion) are replaced by several canals of different sizes which lie in two roughly concentric rings (text-fig. 19). At this level an important change has taken place in the aspect of the cross-section; whereas at first the centre of the figure was towards the xylem side of the strands (at × in fig. 17) it has now shifted suddenly to the phloem side, and lies in the middle of the group of mucilage canals (fig. 19). The cells among which the canals lie are distinguished from the surrounding tissue by their small size, and by the fact that they are nearly all filled with "resin." We are now at the chalazal end of the seed, and these cells constitute the dark internal zone of the fleshy seed-coat, of which the outer limit is

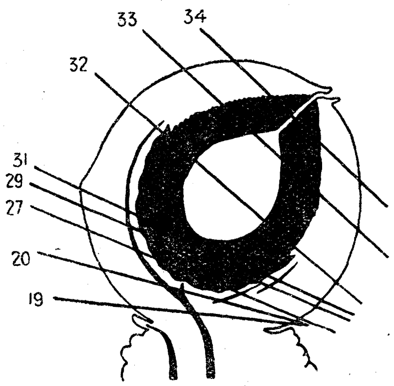


TEXT-FIGS. 19–34.—Vascular anatomy of the seed of *Acmopyle*, as revealed in serial transverse sections. *Xylem*, black; *phloem*, dotted. The peripheral dotted line represents the limit between the two zones of the outer flesh. In all the figures the dorsal (posterior) side of the seed faces the foot of the page. *For the approximate levels at which the different sections were cut, see the corresponding numbers in text-fig.* 35.

marked in the figures by means of a dotted line. Nevertheless, it must be made clear that the boundary is by no means a sharp one.

As we trace the two strands upwards, they diverge from each other, especially by their xylem ends, and at the same time become tangentially extended. One or more radial splits soon appear in the xylem, so that for a time each of them consists of an unbroken mass of phloem facing the centre, and a forked mass of xylem directed outwards.

At about this stage two fairly large concentric strands come off, one from the inner face of each, but they soon dwindle in size, and, before they have proceeded very far towards the centre, they end blindly near the chalazal end of the stone. They are probably the reduced homologues of the two strands in *Ginkgo* which, lying in the principal plane of the seed, penetrate the base of the sclerotesta.



TEXT-FIG. 35.—Index-figure to text-figs. 19–34.

The splits in the xylem of the two large original strands rapidly extend to the phloem, and result in the formation of several distinct strands, which in turn become tangentially flattened, and split up radially into a large number. These tend to envelop the central tissue, including the mucilage canals, amongst which by now the first traces of the stony layer have also appeared (text-figs. 22, 23). This process of fragmentation, accompanied by tangential flattening of the strands, ultimately gives rise to the thin but nearly continuous vascular arc, which, at the level shown in text-fig. 27, covers the dorsal two-thirds of the cross-section.

The similar arc forming the ventral one-third of the vascular ring in the same figure has originated independently of the dorsal arc. In order to trace its mode of origin, we must again refer to the series of sections in text-figs. 19–27. In text-fig. 20 it will be noticed that there is, besides the large dorsal strands, a group of small mostly concentric strands on the ventral side of the section. In the small amount of material examined I could not trace any connection at the chalazal end between the dorsal and the ventral groups. As this fact was subsequently found to be of some theoretical importance (see p. 283, below) in the interpretation of the seed of *Acmopyle*, it was considered worth while to confirm it by means of paraffin sections of the basal region of a third seed (in addition to the two sectioned by hand); no trace of a connection was observed. The ventral strands are in two batches, one inside the inner ring of canals, the other in the space between the two rings. Those of the inner batch terminate after only a short upward course; those of the outer batch, on the contrary, increase in number, and, becoming markedly flattened in the tangential direction, ultimately form the ventral arc seen in text-fig. 27.

Thus, at the level of the figure just referred to, the stone is almost completely enveloped by two vascular arcs. The ends of the dorsal arc become distinctly curved outwards (text-figs. 26–28), and it is noteworthy that these reflexed ends correspond in position to the ridge on the outer surface of the seed. The dark internal zone of the fleshy seed-coat also shows distinct bulges over these curved ends. So far as I could ascertain, no other disturbance is caused by the ridge in the internal structure of the seed.

As we proceed distally, new strands make their appearance outside the ventral arc, and these establish connections both internally with the ventral arc and laterally with the free ends of the dorsal arc (text-figs. 28–30). For a short distance upwards there are thus two interrupted ventral arcs, which are connected together by radial commissures, and which at their ends converge into the single dorsal arc (text-figs. 29–30). The inner ventral arc now rapidly breaks up and dies out, while the outer at the same time becomes more substantial, with the result that the stone is soon enveloped by a single, practically unbroken, vascular ring (text-fig. 31). In this ring the local thickenings are the transverse sections of the compressed, ill-defined strands, which may be said to form a supporting network for the vascular cupule shown in surface view in Plate 11, fig. 24.

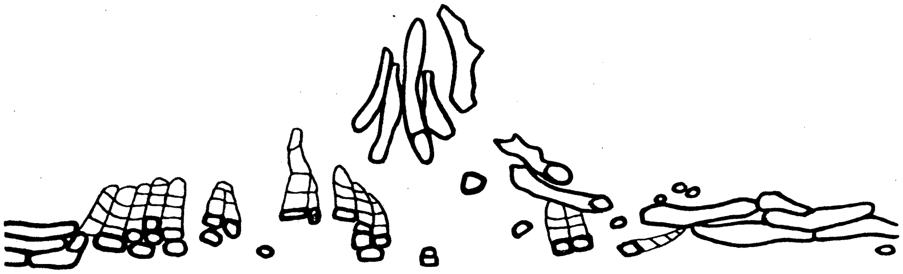
The figure just referred to is from a slightly enlarged photograph of the left half of a seed, from which the outer portion of the fleshy seed-coat was carefully shaved off, so as to expose the tracheal cupule. The photograph was taken with the seed immersed in alcohol, for the cupule then assumed a white colour, and stood out clearly against the dark inner zone of the flesh. At the base are the two large strands forming the main supply. A comparison with the side view (Plate 10, fig. 18) of the naked stone shows that the edge of the cupule closely follows the line of the escarpment. This correspondence is well seen in the sections shown in text-figs. 32–34. As we proceed towards the distal end of the seed, two successive gaps appear in the cupule: first, a gap corresponding to the ventral (deeper) loop of the escarpment (text-fig. 32), and, at a higher level, another corresponding to the dorsal loop (text-fig. 33). The gaps rapidly enlarge, so as to reduce the cupule to two lobes, opposite to the right and left ridges of the stone. These lobes extend up to within a short distance of the micropyle, becoming narrower and narrower as they approach the apex of the seed (text-fig. 34).

At various levels the inner surface of the vascular envelope gives off minute strands towards the sclerotesta, but all of these die out before actually reaching it. Plate 11, fig. 21, is a photograph of a section cut at about the level of text-fig. 32.

Text-figs. 26–33 show a feature worthy of special note, whose importance will be seen in the theoretical part of the paper (p. 286): along two lines which lie in the right-left plane of the seed, the cells composing the stone are for some distance in intimate contact with the tracheides of the cupule. This liaison between the vascular system and the sclerotesta, coupled with the porous structure of the latter, suggests that the sclerotesta may to some extent serve to keep up a supply of water to the developing female prothallus and embryo. This view seems all the more probable in the absence of a vascular system internal to the sclerotesta. In *Ginkgo*, where there is no vascular system outside the sclerotesta, SPRECHER (1907, p. 137, fig. 150) has drawn attention to the remarkably tracheide-like character of the superficial cells of that layer.

Fig. 27, Plate 11, gives some idea of the different shapes and sizes of the tracheides composing the cupule. While the majority of the tracheides are long, narrow, and generally placed lengthwise, some are broader and nearly isodiametric. The sculpturing is difficult to describe, being of various types grading into each other, but the general impression gained is that of the transfusion tissue of the leaf. Special mention may be made of the occurrence of spiral tracheides, some of which have several bands crossing each other; minute round pits may also be present on these, as they may be on all the remaining types of tracheides composing the vascular investment.

Before closing the description of the seed, it must be stated that in the vascular cupule the position of the phloem with regard to the tracheides could not always be determined with certainty, and that for this reason it was considered best to omit the phloem altogether from some of the drawings (text-figs. 30–34). In text-figs. 28, 29, too, the amphi-phloic nature of the ventral strands is by no means certain. The exceedingly hard sclerotesta makes thin sections impossible, while the preponderance of "resin"-cells tends to obscure the vascular tissues embedded among them.



TEXT-FIG. 37.—Part of transverse section of vascular cupule from the seed of *Acmopyle*. The outer face of the cupule corresponds to the lower edge of the figure. The thick-walled cells are tracheides, the thin-walled cells phloem, the latter being mostly internal to the xylem. In the middle of the figure some tracheides are coming off from the inner face of the cupule. Sculpturing of tracheides not shown.

It appears likely, however, that the major portion at least of the cupule has only an internal lining of phloem—a condition which would be in harmony with the inverted orientation of the ovular supply in *Podocarpus* (see text-fig. 37).

Finally, it may be noted that the mucilage canals—one of which elsewhere in the plant generally accompanies each strand—in the seed have a distribution which is at present not reducible to a definite principle, except that in the distal half of the seed, at least, they all lie in a ring between the sclerotesta and the cupule. Their position inside the cupule is in conformity with their usual association with the phloem side of strands.

Theoretical.

From the foregoing description of *Acmopyle* it will be agreed that the plant shows some obvious resemblances to *Podocarpus*, the genus to which the discoverer, PANCHER, originally assigned it. The points of resemblance are indeed so numerous and far-reaching that to some systematists it may even appear doubtful whether a generic separation is justified.

Thus the habit, as well as the stem and root structure, including the wood-anatomy and the presence of root-nodules characteristic of the family, are features common to the two genera. The intimate correspondence shown by the two genera in the habit and structure of the male cones and microsporophylls, as well as in the outward form of the pollen-grain, fully justifies the presumption that the same will be found to be the case with the male gametophyte, an important structure which shows, so far as known, a remarkable constancy of plan throughout the Podocarpineæ. In the female organs, too, the thick fleshy receptacle, and especially the drupaceous seed, with the semi-inferior nucellus and the structure of the pro-embryo, find their exact counterparts in *Podocarpus.*

Although the receptacle of *Acmopyle* shows the most complex organisation known among the Podocarps, it does not present a single feature of importance not also met with in *Podocarpus;* and in this respect, so far as I have been able to ascertain, the nearest approach to *Acmopyle* is seen in the § *Dacrycarpus.* On a minute scale, the receptacle of *P. imbricatus*, Bl. (= *P. cupressinus*, R. Br.) recalls that of *Acmopyle*, both in the verrucose or tuberculate surface (Plate 11, fig. 30) and in the vascular anatomy.*

There is at the base a vascular cylinder composed of strands which as in *Acmopyle* are best developed on the side from which at a higher level the ovular supply originates. Paired axillary strands are also associated with some of the spirally disposed bract-traces; the members of each pair after their departure from the axial cylinder execute the familiar rotatory movement, but before completely reversing their orientation end blindly in the axil of the subtending bract. Strands which are no doubt homologous with these have been observed also in *P. spinulosus* (BROOKS and STILES, 1910, Plate 21, fig. 12); in *P. sinensis* (VAN TIEGHEM, 1869, Plate 15, fig. 82); and an unnamed species of *Eupodocarpus* (AASE, 1915, p. 303, fig. 173).

Here we may also mention that the superficial sculpturing of the stone of *Acmopyle* is very similar in pattern to that in a hitherto unpublished New Caledonian species of *Podocarpus* discovered by Prof. R. H. COMPTON. The photograph on Plate 11, fig. 31, will show that, as in *Acmopyle*, the surface of the stone is divided by an escarpment into two areas, although in this case the loops of the escarpment are

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* To judge from herbarium specimens and published figures of the external features, *P. dacrydioides* would probably be essentially similar.

deeper than in *Acmopyle.* In a deep-lying structure a resemblance of this kind, apparently of no biological significance to the plant, cannot easily be explained away on the view of parallel development.

Next to *Podocarpus*, *Dacrydium* is the genus which most nearly approaches *Acmopyle,* for several of the above-mentioned *Podocarpus*-like features of *Acmopyle* are also met with in *Dacrydium.* The most obvious point in which the two last-named genera agree is, of course, the sub-erect position of the seed, which is at the same time a notable difference from *Podocarpus,* and it is significant that BRONGNIART and GRIS regarded *Acmopyle* as a species of *Dacrydium.*

Only three characters stand out prominently in *Acmopyle* as being distinct from *Podocarpus.* But they are all of sufficient importance to deserve careful attention, for upon their interpretation largely depends the position of *Acmopyle* within the family :—

Firstly, the vascular structure of the seed is peculiar.

Secondly, the ultimate posture of the ovule is different from that in *Podocarpus.*

Thirdly, the rather perplexing fact that there is, to all appearance at least, no sign of an epimatium.

These points will now be discussed in some detail.

A. *The Interpretation of the Structure of* Acmopyle *in Relation to its Affinities.*

1. *The Epimatium.*

The reader will have noticed that in the descriptive section of this paper no mention was made of an epimatium. This was not because an epimatium is lacking in *Acmopyle,* but because it does not figure as a distinct structure and, consequently, its existence is only inferred from a comparison with related genera. The obvious resemblance to *Podocarpus* and *Dacrydium* naturally lead one to seek a place for *Acmopyle* in the vicinity of those genera, and there is no escape from the conclusion that an epimatium must be present in this genus ; the real problem is to define its limits.

Before we attempt this in the case of *Acmopyle* it is necessary to be clear as to the limits of the epimatium in *Podocarpus* itself. It is well known that in a median longitudinal section (see Plate 11, fig. 30) the ovule of *Podocarpus* shows on the dorsal* side, near the micropyle, a distinct lobe (the free portion of the epimatium), of which there is no counterpart on the ventral (fused) side. The question arises as to whether :

(*a*) The "ovular stalk," adnate to the ventral side of the ovule, should be regarded

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* To avoid confusion, it may here be stated that if the ovule of *Podocarpus* is conceived of as being adnate by its entire length to a stalk, the ventral face of the ovule is naturally understood to be that by which the ovule is fused to the stalk. This terminology is consistent with that applied above in describing *Acmopyle,* and may be extended to the other Conifers with inclined or inverted ovules, and even to the anatropous ovules of Angiosperms.

as a part of the epimatium, and the latter therefore as completely surrounding the ovule (PILGER, 1903, p. 16; TISON, 1909, p. 147; SINNOTT, 1913, p. 41; GIBBS, 1912, p. 527; STILES, 1912, p. 472); or

(*b*) The "ovular stalk" should be regarded as a structure distinct from the epimatium, in which case the latter does not completely surround the ovule.

On the first view the epimatium is homologous with the ovuliferous scale of other conifers; on the second view only the "ovular stalk" with its distal continuation the "apical knob" (SINNOTT) is homologous with the ovuliferous scale. It is not easy to choose between the two views. In the absence of a histological differentiation between the stalk and the epimatium (in the restricted sense), it would be simpler to regard the entire structure in question as an ovuliferous scale whose margins have become arched over the seed so as completely to enclose the latter. But for convenience of description it is here considered preferable to employ the term epimatium in the restricted sense.*

While it may be immaterial whether the epimatium is regarded as completely surrounding the ovule, it is of real importance to have some idea as to the boundary between the integument and the epimatium which overlies it. The importance of this enquiry becomes apparent when we realise that STILES regards the vascular system of the seed of *Podocarpus* as being entirely epimatial rather than (in part at least) integumental, and that he denies its homology with the vascular system of the other Gymnosperms (STILES, 1912, p. 477).

Since this question is intimately connected with the morphological status of the vascular supply, the full discussion will be given at a later page. Here I will merely state that I consider it more natural to regard the inner part of the outer flesh, which contains all the descending strands, as an integral part of the integument. The epimatium of *Podocarpus* is on this view only the peripheral portion of the flesh and contains no vascular supply.

We are now in a position to attempt an interpretation of the seed of *Acmopyle* in terms of that of *Podocarpus*, its nearest ally. Two views present themselves; one of them tends to relate *Acmopyle* more to *Dacrydium*, the other to *Podocarpus*:—

(*a*) The epimatium exists in the form of a broad concave scale, similar in shape and position to the epimatium in most species of *Dacrydium* (that is, forming a small asymmetrical cup at the base of the seed), but different in being fused to the integument by its entire inner surface. Its presence is outwardly indicated only by its margin, which forms the ridge (see Plate 11, fig. 22*a*) obliquely girdling the seed-base.

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* This restricted use of the term epimatium would, indeed, be a necessity, if it is shown that the close analogy between the ovule of *Podocarpus* and the anatropous ovule of the Angiosperms is based on a homology of the different parts. For, the outer integument of the angiospermous ovule (which would then be homologous with the epimatium), is naturally regarded as a structure distinct from the funiculus, being frequently distinguishable also on the ventral side of the ovule, between the funiculus and the inner integument.

The semi-erect posture of the seed, which may be regarded as an important point of contact with *Dacrydium*, lends countenance to this view, and in virtue of its several *Podocarpus*-like features, *Acmopyle* deserves an independent generic position, bridging the gap between *Dacrydium* and *Podocarpus*. It is significant in connection with this view, that BRONGNIART and GRIS (1869, p. 330), regarded the plant as the only species of *Dacrydium* provided with a drupaceous seed but devoid of an epimatium.

(*b*) The epimatium forms an almost complete investment to the ovule, as in *Podocarpus*, but differs in being entirely fused with the integument, even in the region of the micropyle, in the formation of which it takes part. Thus, as in *Podocarpus*, the "outer flesh" of the seed consists peripherally of the epimatium and internally of the sarcotesta, an integral part of the integument.

The ovular stalk is here represented by the broad concave scale, of which the distal margin forms the curved ridge passing obliquely round the base of the seed. This ridge corresponds to the "apical knob" in *Podocarpus*. Except for the greater fusion of the epimatium *Acmopyle* is practically a *Podocarpus* with a semi-erect and highly vascular seed. So far as the epimatium is concerned the three genera form a linear series with *Podocarpus* in the middle.

The second view is preferable on all hands; it does not involve the assumption of any new morphological combination but fits in with the conditions already existing in *Podocarpus*, the differences being to a large extent traceable to the orientation of the seed. Moreover, the persistence with which the so-called "apical knob" (SINNOTT, 1913, p. 42) occurs both in *Dacrydium* and *Podocarpus* leads to the suspicion that it carries a deep morphological significance; and it is difficult to set aside the obvious similarity of the curved ridge on the back of the seed in *Acmopyle* to that described by Miss GIBBS in *P. vitiensis* (1912, fig. 14). This is no doubt the same structure which in *D. taxoides* (PILGER, 1903, p. 47, fig. 4),* in *D. falciforme* (GIBBS, 1914, p. 192, fig. 8) and in *P. andinus* (PILGER, 1903, p. 65, fig. 10) develops into a long horn-like process, especially in the young ovule, but which in *P. Nagi* and § *Eupodocarpus* is either reduced to an insignificant tip or is completely merged in the scale. There is no doubt, too, that this organ is the homologue of the distal end of the ovuliferous scale of other Conifers (see SINNOTT, 1913, p. 75).

2. *The Orientation of the Seed.*

With its erect seed *Acmopyle* clearly resembles *Dacrydium* rather than *Podocarpus*, and the question arises whether this feature has been retained from a *Dacrydium*-like ancestor, or whether it is a secondary acquirement.

In *Dacrydium* the final position of the ovule varies from the nearly erect (*D. Fonkii*, *D. laxifolium*, etc., see PILGER, 1903, p. 49, fig. 5) to the nearly

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* As Miss GIBBS points out (1914, p. 192), PILGER'S figs., H–L, on p. 47 of his 'Monograph,' are erroneously referred to *D. falciforme*.

horizontal (*D. taxoides*, see PILGER, 1903, p. 47, fig. 4) while the completely inverted seed is confined to *Podocarpus*.* SINNOTT (1913, p. 71), who has propounded the reduction theory of Podocarpineæ, regards the inverted seed of *Podocarpus* as the more primitive condition, from which he derives the more erect seed of most species of *Dacrydium*. In accordance with this view he regards as a case of recapitulation the resemblance between the final stage of *Podocarpus* and the young stage of *D. colensoi* and *D. intermedium*, in which the ovule is inverted and the epimatium overtops the integument (SINNOTT, p. 49).†

However, it has long been known through the work of STRASBURGER (1872, Plate 2, figs. 39 *ff*) and of BAILLON (1873, Plate 8) that the ovule of *Podocarpus chinensis* executes during development a movement in the opposite direction, namely, from a nearly horizontal to a completely inverted position. STILES (1912, p. 470) records a similar movement in *P. latifolius*, and Miss GIBBS' photograph (1912, fig. 79) of a comparatively young ovule of *P. elata* leads to the same conclusion.

These facts about *Podocarpus* are not here cited as reminiscences of a dacrydioid ancestry; but they at least indicate the uncertainty attending the interpretation of the juvenile stage of *Dacrydium*.

As regards the posture of the young ovule of *Acmopyle* a definite statement is naturally at present out of the question, but even if it is found to be inverted, it would be difficult to argue that the sub-erect position of the ripe seed is the expression of a dacrydioid affinity, for in the only other points in which *Acmopyle* departs from *Podocarpus* it does so in a direction opposite to that of *Dacrydium*. As already concluded above from a consideration of the epimatium the three genera probably form a linear series with *Podocarpus* in the middle; the nearly erect position of the seed of *Acmopyle* is therefore probably to be regarded as a recent secondary acquirement. If the reduction theory is to be maintained—a view to which I do not subscribe—*Acmopyle* must be the most primitive member of the family, both in view of the total fusion of the epimatium and of the great complexity of the entire female reproductive organs.

3. *The Vascular Structure of the Seed.*

This complexity is perhaps most clearly seen in the vascular supply of the seed, which is the best developed not only among the Podocarps but among all known Conifers.

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* PILGER states that the three New Zealand species of *Dacrydium* (*D. Bidwillii*, *D. Kirkii*, *D. biforme*) have their seeds completely inverted, as in *Podocarpus*; they have for this reason been regarded as showing an interesting transition between the latter genus and the remaining species of *Dacrydium* (SINNOTT, 1913). I have, however, found evidence to show that *D. Bidwillii*, and probably also the other two species, belong properly to the genus *Podocarpus*, of which they would probably form a distinct section. (SAHNI, 1918A, p. 219.)

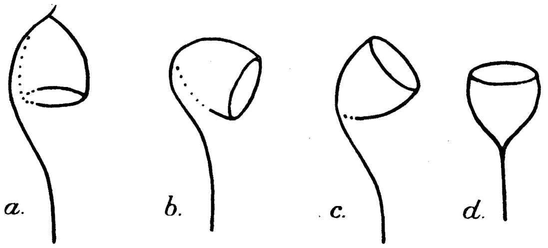
† The same inverted condition is seen in the young ovules of *D. cupressinum* (PILGER, 1903, p. 54, fig. 6), *D. taxoides* (PILGER, p. 47, fig. 4), and *D. falciforme* (GIBBS, 1914, p. 192, fig. 8); on the other hand, some young ovules of *D. laxifolium*, on which I hope soon to publish notes, are only slightly inclined from the erect position, the ripe ovules being perfectly erect.

Apart from the presence in *Acmopyle* of a more or less continuous vascular network (cupule) in place of the separate strands of *Podocarpus*—which is only a matter of degree of development—the differences in the distribution of the vascular supply in the two genera are no doubt to be traced chiefly to the different posture of the seed. This view is illustrated in text-fig. 38 by means of a series of purely diagrammatic sketches of the vascular skeleton. For the sake of simplicity, the descending portion of the ovular supply in *Podocarpus* (text-fig. 38, *a*) is also shown as a continuous vascular mantle, as in *Acmopyle* (text-fig. 38, *c*).

The series of diagrams may be read in either direction according to the view adopted as to the relative antiquity of the two genera. Assuming for the sake of argument, that the ovule of *Podocarpus* is more primitive than that of *Acmopyle*, as the ovule gradually erects itself, its ventral surface would become free from the "ovular stalk," and would thus be left with a gap in the vascular supply originally occupied by the ascending strands. We could then reasonably expect that the existing strands would tend to distribute themselves more evenly round the circumference of the ovule wherever the latter is free from the "stalk," so as to ensure a supply to the ventral side as well. This ventral completion of the vascular ring would begin at the micropylar end (which would be the first to become free) and gradually extend towards the chalaza as the ovule was tilted up. At an inclination of about 45° a condition would be reached not very unlike that actually seen in *Acmopyle*. It is now easy to see the significance of the fact—which at first was rather puzzling—that there is no direct connection, at the chalazal end of the seed of *Acmopyle*, between the strands on the ventral side and those on the dorsal (see p. 275 and text-fig. 20).

The next stage, shown in text-fig. 38, *d*, is hypothetical, and shows the presence of such a connection in the final phase of erection. The stage shown in text-fig. 38, *b*, is also hypothetical.

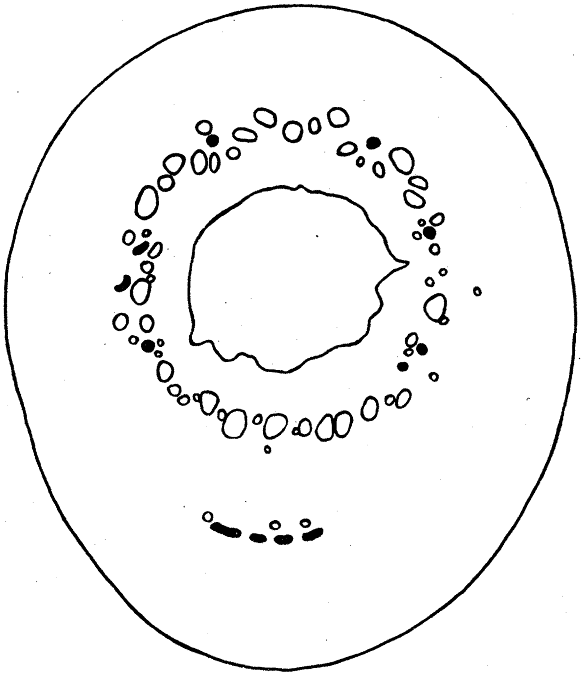
Arguing in the reverse direction—that is, if the seed of *Acmopyle* is regarded as more primitive than that of *Podocarpus*—one would expect that, as the ovule gradually became more and more inclined and its mid-ventral surface became fused to the "stalk," the vascular strands on that side would tend to become atrophied, for they would be superfluous in the proximity of the ascending strands of the "stalk." This atrophy would naturally begin at the chalazal end, and gradually work its way towards the micropyle.



TEXT-FIG. 38.—Diagrams. See text above.

If the above interpretation is correct, it is apparent that in *Podocarpus* the ascending and the descending strands do not properly belong to one and the same system, for the descending strands (which I think belong strictly to the integument, and not to the epimatium) represent a cup-like system pendent from the distal region of the ascending system.

It is of some interest to find a little confirmation of this view in the adjoining figure of *P. bracteata*, BLUME* (text-fig. 39). The section passed through a level about midway between the micropyle and the equator. It will be noticed that the ring of descending strands is incomplete on the "stalk" side, and, what is more important, that the line bridging the gap leaves the row of ascending strands an appreciable distance outside the ring.† The disposition of the mucilage canals, too, which form a complete circle of their own apart from the canals of the ascending strands, is probably not without significance. At a higher level the ascending strands approach the gap and finally themselves occupy the gap. A section from a level between the chalaza and the equator therefore gives the misleading impression that all the strands in the ring belong to the same system. (See STILES's fig. 4, *e*, *f*, p. 471, for *P. macrophyllus*, which will do equally well for the closely allied *P. bracteata*.)



TEXT-FIG. 39.—*Podocarpus bracteata*, BLUME. Transverse section of seed at a level midway between the micropyle and the equator. The vascular bundles are shown solid black.

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* Synonymous with *P. neriifolius*, DON.

† I have observed the same feature in one other (unidentified) species of *Podocarpus* (§ *Eupodocarpus*), and consider it very probable that it occurs in several other species. The fact that STILES does not figure or describe the phenomenon in *P. macrophyllus*, a species closely allied to *P. bracteata*, may be due to his sections not having passed through the region to which this condition appears to be limited.

The conception of a cup-like vascular system pendent from the chalaza occurred to **Favre** (1865, p. 381) as early as 1865 from his study of *Podocarpus chinensis*, but, so far as I am aware, no one has followed up his suggestive idea.

In homologising the vascular system of the female organs of *Podocarpus* with that in *Acmopyle*, it must be recognised that what in *Podocarpus* is known as the "ovular stalk," adnate to the whole length of the seed and forming a distinct bulge in the transverse section, is in *Acmopyle* flattened out into a thin, curved lamina, so completely fused to the basi-dorsal surface of the seed that except for the curved ridge indicating its margin it would be impossible to detect its presence. The ascending strands of *Podocarpus* would correspond not only to the pair of large inverted basal strands in *Acmopyle*, here of very short length, but also to a portion of the dorsal valve of the cupule into which they distally expand. The distal limit of the "ascending system" of *Acmopyle* would probably be marked by the reflexed strands in text-fig. 26 which, as stated on p. 276, lie just under the ridge. That portion of the dorsal valve of the cupule which lies beyond the ridge would thus correspond to the "descending system" of *Podocarpus*. The ventral part of the cupule of *Acmopyle* must be regarded as a new acquisition, related in origin to the semi-erect position of the seed.

Although in broad outline, the above suggestion seems to afford a reasonable interpretation of *Acmopyle* in terms of *Podocarpus*, there remains one difficulty, which must at present remain unexplained, namely, the double nature of the cupule on the ventral side of the seed. Is it that the erection of the seed from the *Podocarpus*-like condition took place in two distinct stages, so that first the outer ventral arc was acquired and then the inner? The fact that of the two arcs the inner extends to a point nearer the chalaza (see text-fig. 6) than does the outer at any rate does not contradict this hypothesis. In this connection an examination of younger material would be of some interest. On the other hand, it may of course be that the process of erection is not merely ontogenetic, but is spread over the phylogeny of *Acmopyle*. In that case a *Podocarpus*-like form must have existed with a horizontal seed intermediate between these two genera.

We shall now consider **Stiles**'s theory that the elaborate vascular system of the seed of *Podocarpus* is not homologous with that in the older Gymnosperms. As stated on a previous page, I prefer to draw the line between the integument and epimatium just outside the ring of descending strands, considering only the peripheral portion of the flesh as the epimatium, and the inner region (containing the descending strands) as an integral portion of the integument. **Stiles**, on the other hand, draws the line at the outer limit of the stony layer (1912, p. 475, and figs. 6, 7), thus assigning the descending as well as the ascending strands to the epimatium, and implying the absence of a sarcotesta proper to the integument. If the broken line in the figures cited were, indeed, the limit between the integument and epimatium, it is clear that **Stiles**'s theory would follow as a corollary, for the epimatium, being homologous with the ovuliferous scale, is not an integral part of the ovule; its vascular supply cannot therefore be homologised with that of the Cycads, which is strictly ovular.

STILES, however, arrived at his conclusions by a different route. Arguing that the vascular system of the *Podocarpus* ovule is an elaboration of the rudimentary system in the more primitive members of the family, he concludes that the ovular system of the Podocarpeæ has been evolved within the family, and is therefore not homologous with that in the older Gymnosperms.

But I consider it possible that, during its evolutionary history, an organ may become much reduced, and subsequently attain a considerable development along different lines. Thus I regard the vascular system of the ovule of *Acmopyle* as homologous with that in the Cordaitalean ancestor, although in the modern genus the outer set of bundles has become well developed, while the inner has disappeared.

Unfortunately, the question is one that does not admit of a solution by positive histological evidence of any value. So far as I know, the descending strands have not been traced into the epimatium beyond its point of separation from the integument; on the other hand, it is equally true that they have not been traced into the free micropylar region of the integument.*

In the absence of direct evidence, therefore, we are left to whatever indirect evidence may be available from comparisons with other Gymnosperms. Perhaps the strongest argument against the theory advanced by STILES lies in the fact that the seeds of the Podocarpineæ, and, in fact, of all the Conifers, conform to the fundamental plan of structure of the typical platyspermic seed, and that, for this reason, such an important difference as that involved in the theory would be a *primâ facie* improbability.

Thus, two basal main supply strands, situated in the right-left plane, are an invariable rule throughout the Podocarps, as they are in the Cordaitales, *Ginkgo*, and the Taxineæ. When there is an inner or an outer system of strands (or when both systems are present), the strands, if unbranched, always lie in the plane of the carinæ (right-left plane), in the Cordaitales, *Ginkgo*, the Taxineæ, and in the only Pinaceæ in which they have been recorded, viz., *Abies* and *Cedrus* (RADAIS, 1894, Plates 2 and 6). In those species of *Podocarpus* in which there are only two descending strands, *e.g.*, *P. ferrugineus* and the species commonly known as *Dacrydium Bidwillii*, these always lie in the plane of the carinæ, and in *P. ferrugineus* they are actually in contact with the latter (SINNOTT, 1913, text-fig. 3, p. 46). In *Acmopyle*, too, it is significant that it is the carinal portions of the vascular cupule that reach nearest the micropyle.

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* Miss GIBBS (1912) has given very useful figures of longitudinal sections of several species of *Podocarpus*, but from their diagrammatic character it is difficult to be sure of the correct positions of the strands. In any case they lie very near the limit. This author does not go into the question under discussion.

The correspondence, in the vascular organisation of the seed, between the Podocarpineæ and the remaining Gymnosperms, is so close that, unless there are strong reasons to the contrary, it is natural to recognise the homology of the different parts of the vascular system. It may therefore be concluded that the inner region of the fleshy seed-coat, which contains the "descending" strands, is really a part of the integument proper.

As regards the inter-relationships of the remaining genera of the Podocarpineæ, this subject has been admirably dealt with by STILES (1912, pp. 489–496), the main trend of whose argument appears to be convincing. I would only like to suggest that the genus *Dacrydium*, instead of forming a side line from *Microcachrys* (see the scheme on p. 496 of STILES's paper), may probably lie in a direct line, leading to *Podocarpus*, *Microcachrys* itself lying at the base of *Dacrydium*, as already indicated by STILES. It is rather surprising that, in the scheme proposed by STILES, *Dacrydium* does not appear as a link between *Microcachrys* and *Podocarpus*, for, from *Dacrydium Bidwillii* (as the plant was then known) to *Podocarpus*, the transition is so much more gradual than it is from *Saxegothœa* to *Podocarpus*.

Further, although I agree with STILES that *Saxegothœa* and *Pherosphœra* are two of the most primitive Podocarpineæ, I would not commit myself to any definite view as to their connections with the other genera of the family, especially as our knowledge of *Pherosphœra* is exceedingly meagre. The position of *Saxegothœa* is so clearly intermediate between the Podocarps and Araucarians (STILES, NORÉN, TISON, THOMSON) that it raises the question as to whether it would not be advisable to place this genus in a separate tribe, *Saxegothœœ*, linking together the other two. It is significant that TISON (1909, p. 156) proposed the inclusion of *Saxegothœa* in the phylum Araucariales instituted by Prof. SEWARD and Miss FORD (1906, p. 398).

Phyllocladus appears to represent a branch leaving the main stem at about the level of *Dacrydium*, to which, apart from its specialised vegetative characters, it appears to show more resemblance than to any other Podocarp. The symmetrical nature of the epimatium would thus appear to have been secondarily acquired, for the ovule is erect throughout its development. Mrs. ARBER has already suggested that there is a correlation between the symmetry of the epimatium and the posture of the ovule.

B. *The Systematic Position of the Taxineœ.*

We may enter now upon the wider question of the affinities of the Podocarpineæ to the other groups of Conifers and the ancestry of the Conifers themselves. Since the discussion is intimately bound up with the inevitable question of the morphology of the ovuliferous scale, it is advantageous to make the latter a starting point.

But before dealing with this subject it is necessary to point out that I have ventured to exclude from the phylum Coniferales the genera *Taxus*, *Cephalotaxus*, and *Torreya*. Both the general morphology and the internal structure of the fructifications lead me to the conclusion that the family Taxineæ is too distinct to occupy a place among the Conifers, and that it should rank as an independent phylum, Taxales,* related to *Ginkgo*, to the Cordaitales, and to the Coniferales as here defined.

In LINDLEY'S 'Vegetable Kingdom' (1853, p. 231), the Order Taxaceæ, which included the Yews and Podocarps† as well as *Ginkgo*, appeared as a group of equal rank with the Cycadaceæ, Gnetaceæ, and Pinaceæ. The latter group was also named Coniferæ, a term which has since acquired a wider significance, for it now covers both the Pinaceæ and Taxaceæ of LINDLEY, with the exception of *Ginkgo*.

In the most up-to-date general work on Gymnosperms (COULTER and CHAMBERLAIN, 1917) these two groups appear as equivalent orders of the phylum Coniferales. However, as Dr. SCOTT (1911, p. 172) has remarked, "it is doubtful whether even this first grouping is natural, for the Podocarps among the Taxaceæ seem to have little to do with the Yews."

The opinion that the relation between the Yews and the Podocarps is not a close one dates at least as far back as 1838, when BENNETT and BROWN (1838, p. 36) wrote as follows: "It is singular that so unessential a character as the general solitary position of the ovuliferous scale should have induced all the authors who have attempted an arrangement of the Coniferæ to separate *Podocarpus* and *Dacrydium* from the true Pines and to associate them with the Yew." PILGER expressed exactly the same view in 1903 (pp. 25, 38). In 1910, BROOKS and STILES (p. 316) observed: "The points of similarity between the Podocarpeæ and the Taxeæ do not seem to us to be very striking;" and in 1912, STILES (498–499) wrote: "It is at least safe to say that there is as yet little evidence of any near connection of the Taxeæ and Podocarpeæ," at the same time enumerating several important structural features in which the two groups show a "marked contrast."

Remembering that LINDLEY was unaware of the presence of motile sperms in *Ginkgo*, his placing that genus in relation to *Taxus*, *Cephalotaxus*, and *Torreya* may be regarded as a natural step; but in including *Dacrydium* and *Podocarpus* in the same Order as *Taxus*, he was probably unduly impressed by the tendency in all these genera towards a fleshy development of some parts of the female fructification, which may not necessarily be homologous. The Yew berries, for example, closely resemble the dry seed of *Dacrydium laxifolium* perched upon the delicate fleshy receptacle composed of swollen bract bases.

In 1906, Mrs. AGNES ARBER (Miss ROBERTSON, 1906, p. 101), expressed the opinion that "the general morphology of the female 'flower' of *Taxus* more closely recalls that of *Cordaites* than that of any other known plant." At the same time *Ginkgo*, itself showing strong Cordaitean features, has long been known as an ally of *Cephalotaxus*—an alliance which, as Dr. SCOTT observes (1906, p. 143), was

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* A name previously employed by LOTSY (1911, p. 160), but not in the sense of a group equal in rank with the Coniferales.

† With the exception of *Pherosphæra*, *Saxegothæa*, and *Microcachrys*. In his 'Natural System' too (1836, p. 317) LINDLEY had associated *Taxus* with the genera *Podocarpus*, *Dacrydium*, *Phyllocladus*, and *Ginkgo*.

established before the discovery of the motile sperms. If we agree with Dr. SCOTT that the Yews have little to do with the Podocarps, it may confidently be added that they have still less to do with any other Conifers.

Had it not been for the genus *Phyllocladus* which chiefly on account of its symmetrical epimatium, appears to link the remaining Podocarps with the genus *Taxus*, it is extremely probable that the Order Taxaceæ would not so long have preserved its integrity. It is, therefore, of importance critically to examine the evidence upon which *Phyllocladus* claims a Taxinean affinity.*

It is noteworthy that with the exception of PILGER, who placed *Phyllocladus* in a tribe intermediate between the Taxineæ and Podocarpineæ, nearly all the modern writers on the subject have definitely expressed the view that the affinities of the genus are clearly with the Podocarps, and have considered it unnecssary to retain the intermediate tribe (KILDAHL, 1908, p. 465; YOUNG, 1910, p. 91; BROOKS and STILES, 1910, p. 316; STILES, 1911, p. 346; STILES, 1912, p. 445).

Mrs. AGNES ARBER (Miss ROBERTSON, 1906)—who was the first to investigate this interesting genus in detail—while fundamentally agreeing with this view, appears to have been impressed, rather more than the other authors, by certain features in which *Phyllocladus* seemed to approach the Taxineæ rather than the Podocarpineæ. However, at the time when Mrs. ARBER wrote her lucid paper on *Phyllocladus* our knowledge of the Podocarpineæ was very meagre: in the light of facts which have since been observed, out of the few characters which were then suggested as being Taxinean rather than Podocarpean, all except one appear to lose much of their value.

(i) *Presence of Centripetal Wood in the Cladodes.*—Mrs. ARBER herself does not lay much stress on this point, and I think justly. It is still a moot point whether transfusion tracheides found in the vicinity of the protoxylem, and often separated from it by parenchyma, should be reckoned as true centripetal xylem. But whatever view be adopted on this point, the tissue referred to in *Phyllocladus* is found in numerous other Conifers (including *Dacrydium*, *Podocarpus*, *Acmopyle*) in exactly the same relative position, and without leaving any doubt as to its identity with it.

Although in *Phyllocladus alpinus* Mrs. ARBER records the presence of this tissue only in the lateral bundles of the cladode, in my preparations of *P. aspleniifolius* and *P. trichomanoides* (the latter closely allied to *P. alpinus*) it occurs not only in all the strands of the branch-system of the cladode, but also in the scale-like leaves of the unmodified shoot.

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* In all the following features it differs from the Taxineæ, while at the same time resembling the Podocarps:—The form and structure of the male cones and stamens; winged pollen; male gametophyte; the general morphology of the female cone with each ovule always clearly subtended by a bract; free nucellus (entirely absent in the Taxineæ, but present in some Podocarps); presence of spongy tissue and a thick two-layered megaspore-membrane (a feature of doubtful value; although conspicuously absent in the Taxineæ it is also absent in some Podocarps); general vegetative anatomy, such as the presence of root tubercules and entire absence of bar thickenings in the secondary wood; and, finally, the southern distribution of the genus (the Taxineæ being chiefly northern forms, the Podocarpineæ chiefly southern).

(ii) *Taxinean Sculpturing.*—Mrs. ARBER discovered that the tissue just referred to, for which I prefer the non-committal name of transfusion tracheides, showed in *Phyllocladus* a peculiar type of sculpturing, which combined small scattered narrowly bordered pits with band-shaped thickenings; the latter passed round the cells in various directions, specially when the cells were iso-diametric. A rather similar type of ornamentation was recorded in the "normal" xylem. By the latter term I understand that only the primary xylem is meant; for in the two species examined by me (one of which, as already stated, is very similar to *P. alpinus*) I could not discover any trace of band-like thickenings in the secondary wood, and it would be surprising if these were found in *P. alpinus.**

It is doubtful whether we can justly refer to this feature as true Taxinean sculpturing, which is rather different in appearance and *is always present in the secondary wood.* Moreover, it is important to mention that I have observed exactly the same type of tracheides as those recorded in *Phyllocladus*, in the primary xylem of *Acmopyle* (see text-fig. 1), in two species of *Podocarpus* and in *Dacrydium laxifolium.* In none of the members of this family, however, does the secondary wood show any band-like thickenings at all.

(iii) *The Erect Posture of the Seed.*—As Mrs. ARBER herself states, a nearly erect seed is also found in *Dacrydium laxifolium*† and, we may add, on the authority of PILGER, in *D. Fonkii*, *D. Franklinii* and, of course, *Acmopyle.* In some ripe material of *D. laxifolium* and *D. cupressinum* examined by me the seeds are perfectly erect; the same condition is figured by KIRK in *D. intermedium* (1889, Plate 87B), and also in the two former species.

However, the seed is in these cases not erect in the same sense as in *Taxus* where the nucellus is evidently from the very outset the direct continuation of the seminiferous axis. The condition in *Taxus* is more readily compared with *Cordaites* and *Ginkgo* than with any of the Podocarps.

(iv) *The Symmetrical Epimatium.*—It cannot be denied that this character is more Taxinean than Podocarpean, but there appears to be some reason for the view that the symmetry of the epimatium of *Phyllocladus* has been secondarily acquired (see above, p. 287). This feature, as suggested by Mrs. ARBER, is probably correlated with the erect position of the seed, exception being made, of course, in those cases where an inclined ovule with an asymmetrical epimatium subsequently becomes erect, as in *Dacrydium.* In *Acmopyle*, too, the epimatium is symmetrical, at least in the major portion of the seed—a fact which, by the way, would seem to suggest that the young stage of the ovule is probably not much more inclined than the ripe seed, or at least not completely inverted.

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* Since the above was written I have been able to confirm their absence in this species from Mrs. ARBER'S original preparations, which she most generously placed at my disposal for comparison.

† The spelling of the specific name as "latifolium," repeated by Miss KILDAHL (1908, p. 465) is evidently a misprint.

Mrs. ARBER justly observed that it would not do to lay too much stress upon the usually asymmetric nature of the epimatium of the Podocarpeæ, as showing that this organ is not homologous with the aril of *Taxus* and *Torreya*. At the same time, the symmetrical epimatium of *Phyllocladus* and *Acmopyle* does not necessarily indicate a homology with the aril of *Taxus*, for any extra seed-coat would tend to develop symmetrically if subjected to uniform surroundings, such as obtain in the case of erect ovules. It would seem, therefore, that the symmetry of the epimatium of *Phyllocladus* speaks neither definitely for nor against its homology with the aril of *Taxus*.

The Taxales stand apart from the Coniferales in the general organisation of their ovuliferous shoots and in the retention of obviously primitive characters in the seed (OLIVER and CHICK, 1902; OLIVER, 1902) and seedling (CHICK, 1903). They are the only living Gymnosperms which, having relinquished the zoidiogamic mode of fertilisation, still linger behind the others in preserving the vanishing traces of an internal vascular system in the seed (OLIVER, 1903). The male cones are very distinct from those of the Conifers, especially in the habit and in the frequent presence of bracts between the groups of stamens. The importance of the presence of bracts (*cf.* Cordaitales) is probably very great. The individual stamen, too, is in *Taxus* totally unlike that in any Conifer, although in *Torreya* there are unmistakable signs of progress in that direction by a gradual departure from the peltate form. In spite of this, however, the mode of insertion and general appearance of the branched bracteate male cone of *Cephalotaxus* remains strikingly different from that of any known Conifer.

The entire absence of vegetative prothallial cells in the male gametophyte may also be reckoned as a feature of some importance in distinguishing the Taxales, for although it is found also in the Taxodineæ and Cupressineæ, these two tribes are in most other respects so markedly different from the Yews that this resemblance can hardly be traced to a near relationship. A similar argument applies to the so-called "taxinean sculpturing" in the secondary wood, for it occurs in some of the Abietineæ (*Pseudotsuga*, *Larix*, *Picea*; see GOTHAN, 1905, p. 98)—a tribe of Conifers which probably has very little to do with the Taxales.

It is difficult to say what significance can be attached to ROTHERT'S discovery of so-called "parenchymatous tracheides" in the pith of a species (or perhaps only a variety) of *Cephalotaxus* (1899, p. 275). From ROTHERT'S account and from some preparations which Mrs. ARBER very kindly allowed me to examine, these tracheides do not essentially differ from the familiar transfusion tracheides associated with the leaf-strand in numerous Conifers. In their presence in an axial organ they are certainly unusual, but not unique, for similar elements occur also in the branch system of the cladode of *Phyllocladus* (see p. 289). Mention may also be made of the fact that the presence of secretory canals in the pith of the stem—a very uncommon feature in which the genera *Ginkgo* and *Cephalotaxus* agree—has been emphasised by VAN TIEGHEM (1891A, p. 189), as a sign of affinity.

The position adopted by several writers, such as R. B. THOMSON (1905, pp. 45 and 54), LAWSON (1907, p. 20), COULTER and CHAMBERLAIN (1917, p. 418), and BLISS (1918, p. 56), that the Yews represent a relatively modern group, appears to be untenable in view of the evidence from the morphology of the male and female organs, specially the presence of bracts in the male cone and the structure of the seed.

The absence of a thick megaspore membrane has been employed by Prof. THOMSON (1905) in support of the view that the Taxineæ are a recent group. This author examined *Taxus canadensis* and states (p. 45): "The later stages of *Taxus* up to maturity of the seed gave no indication of the presence of a megaspore-coat." However, in *T. baccata* a species closely allied to, if not identical with *T. canadensis*, I found that, although the megaspore membrane is really a "negligible feature" at the early free-nuclear stage of the prothallus, at the time of embryo formation it is of appreciable thickness. While the thick membrane of the Cycads and *Ginkgo* is thoroughly in accord with their primitive nature, the value of this criterion in the other groups is still doubtful, specially in the Podocarpineæ, among which both thick and thin megaspore membranes occur. In particular I may mention that in my preparations this variation is even seen within the genus *Podocarpus*, which, so far as I am aware, has hitherto been known only to have a poorly developed membrane, in contrast to *Dacrydium*. Thus the two species of *Podocarpus* hitherto known as *Dacrydium Bidwillii* and *D. Kirkii* (see p. 282, footnote*), as well as *Podocarpus alpinus* (§ *Eupodocarpus*) have each a well-developed megaspore membrane like that of *Dacrydium* or *Phyllocladus* (ROBERTSON, 1906). One other species belonging to § *Eupodocarpus* shows a medium thickness.

Prof. OLIVER'S work has conclusively shown that *Torreya* possesses one of the most primitively organised seeds among living Gymnosperms. From his study of the seed of *Cephalotaxus*, WORSDELL (1900, pp. 317–18) has come to a similar conclusion with regard to this genus. The resemblance in the general morphology of the female shoot of *Taxus* and *Cordaites* has also been widely recognised. These considerations impelled me to search for possible archaic features in the mature seed of *Taxus*, and to attempt to describe it in terms of *Torreya*, which, according to Prof. OLIVER'S well-known theory, is not difficult to derive from a type like *Cardiocarpus*. The result of this search has been to convince me that the seed of *Taxus* is in some respects even more primitive than that of *Torreya*, appearing, in fact, to form the terminal link in a remarkable chain of seed-types, leading from *Cardiocarpus* through *Cycadinocarpus*, *Rhabdospermum*, *Mitrospermum*, and *Taxospermum*, to the living genus *Taxus*.

It would take us too far here to discuss the relations between the different stages of this series, which, although not by any means suggested as representing the actual course of evolution, yet appears to illustrate progression along certain well-marked tendencies, which would seem to bridge up the structural gap between the seeds of the Cordaitales and those of the Taxales. I hope shortly to deal with this subject in a separate paper.*

C. *The Ovuliferous Scale of Conifers.*

In the entire domain of plant morphology, there is no structure which has exercised so wide an influence upon our views on the phylogeny of a group as the ovuliferous scale of Conifers. Out of the mass of literature, dating from nearly a hundred years ago, two rival theories stand out prominently: (1) the Brachyblast Theory; (2) the Ligular Theory.

The question is so wide, and has so often been handled by experts, that I cannot pretend to deal with the entire evidence. I shall, however, venture to go into some detail with regard to the evidence from the vascular anatomy, which, I may say beforehand, appears to me to be conclusively in favour of the Brachyblast Theory.

(a) *Evidence from Vascular Anatomy.*—The most striking fact that emerges from a general survey of the literature† is that, at its origin, the supply to the ovuliferous scale is fundamentally similar to that to a vegetative axillary branch, while sometimes the resemblance is so close that a distinction appears impossible. The similarity between the vascular supplies of the ovuliferous scale and vegetative axillary bud was frequently urged by STRASBURGER in his classical work on the Conifers and Gnetaceæ (1872, frequent statements scattered over pp. 25–75, in connection with *Biota*, *Juniperus*, *Araucaria*, *Agathis*). More recently, EAMES (1913, p. 21) has laid emphasis on the same feature. But no author has illustrated this point so clearly as Miss AASE (1915) has quite recently done in a detailed paper on the vascular anatomy of the megastrobili of Conifers. A comparison of her figures, specially of *Pinus maritima* and *P. Banksiana* (pp. 286, 287), besides numerous others, is alone sufficient to demonstrate the identity of the vascular relations; in both the ovuliferous scale and the vegetative axillary bud the supply comes off typically from the sides of the foliar gap in the axial cylinder.

The vascular structure of *Acmopyle*, too, shows the fundamental similarity between the supply to the ovuliferous scale (or its vestige) and the vegetative axillary shoot (see above, pp. 267, 268, and text-figs. 5, 7–18). In this connection, a comparison of text-figs. 5 and 10 of the present paper with Mrs. ARBER's (Miss ROBERTSON's) figure of the vegetative stem of *Phyllocladus* (ROBERTSON, 1906, Plate 17, fig. 7) and STRASBURGER's figure of *Sciadopitys* (1872, Plate 26, fig. 5) is particularly illuminating.

From such data as these, the axial nature of the ovuliferous scale appears to be clearly demonstrated.

Soon after its origin, the supply to the scale becomes arranged in the form of an

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* This paper has, since the above was written, been published in the 'Annals of Botany,' vol. 34, pp. 117–133, January, 1920.

† See especially the extensive researches of VAN TIEGHEM (1869), STRASBURGER (1872), RADAIS (1894), AASE (1915).

arc, having an orientation inverse to that of the subtending bract-trace.* This inverse orientation of the vascular supply, while being intelligible on the brachyblast view, is an obstacle in the way of the ligular theory. EICHLER (1881, p. 1026) states that the inverted orientation is a property of the supply to all excrescences of the leaf, whether they come off from the upper or from the lower face, but it is doubtful if this statement is at all of general application. It fails, as EAMES has already pointed out, in the irregular orientation (most often concentric) of the ovular strands in many of the Conifers studied by RADAIS (1894, p. 286; see especially his figures of *Abies*, *Tsuga*, and *Sciadopitys*). Miss AASE (1915, p. 287) also records concentric ovular supply strands in *Keteleeria Fortunei*. Since EAMES has already dealt with THOMSON'S (1909) statement relating to the alleged two inversions (one for the ovuliferous scale and one for the ovules), I will here only express my complete agreement with the former author.

As already noticed, in the majority of the cases on record, the ovuliferous scale supply showed a striking agreement with the supply to a vegetative axillary bud; it had an independent origin from the sides of the gap in the cone-axis cylinder. In other (comparatively few) instances the ovuliferous scale supply was described as branching off from the bract supply, and these instances have been employed in support of the ligular theory. Until recently, except for one or two genera, such as *Araucaria* and *Microcachrys*, there were no cases on record in which both these modes of origin were known in the same genus, nor was it generally realised that the relative sizes of the two parts of the cone-scale are subject to considerable variation, even in different regions of the same cone.

Thus THOMSON (1909) was led to believe that while in the Abietineæ (and, by inference, in the Taxodineæ and Cupressineæ) the cone-scale was evidently a double structure and the ovuliferous organ a modified axillary shoot, in the Araucarineæ and Taxaceæ (incl. Taxineæ and Podocarpineæ) the scale was simple, and the ligule of *Araucaria* and the epimatium of *Podocarpus* were mere excrescences of the upper surface. He thus founded two great groups of Conifers, the Diplosporophyllous and the Aplosporophyllous forms. This step has appropriately been criticised by EAMES (1913, p. 33).

More recently, Miss AASE (1915) has published facts which are of value in this connection, showing that the classification proposed by THOMSON is not tenable. A glance at her fig. 1, p. 283, will show that, according to THOMSON'S classification, the scales in the proximal region of the cone are aplosporophyllous, while those higher up in the same cone are diplosporophyllous. In *Pinus maritima*, *P. Banksiana*, *Keteleeria fortunei*, *Cupressus Benthamii* Miss AASE describes both types of vascular

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* The vascular cylinder of the brachyblast is to be conceived of as having a gap opposite to the subtending bract, as is usually the case with the vascular cylinder of the vegetative axillary shoot in its basal region, not only in the Conifers but also in many Ferns. If the ovuliferous scale is really a branch, it is evident that, strictly speaking, there is no sense in describing, as inverted, the strands on the side opposite to that on which the bract is placed.

supply (independent and joint) in different parts of the same cone. After reading her paper, I found the same feature in *Pinus silvestris;* I have also described it above in *Acmopyle* ('Vascular Anatomy of Receptacle,' p. 265 *ff*).

It is interesting to remark that almost all the different vascular relations between the ovuliferous scale and bract of Conifers are paralleled among the Ferns by those of the axillary branch and its subtending leaf; the analogy is indeed so close that the condition in the Ferns may throw light upon the morphology of the ovuliferous scale in Conifers. Those cases among Conifers in which the scale supply appears to originate partly or entirely in the trace of the subtending bract are analogous to the condition in the Hymenophyllaceæ and numerous other Ferns, in which the branch (whether adaxial or abaxial to the associated leaf) may be adnate to the petiolar base for a variable distance. In such cases it is entirely out of the question to regard the branch as an outgrowth of the leaf. As pointed out elsewhere (SAHNI, 1917, p. 19), the basal undivided portion of the vascular supply must be regarded as having a dual nature, partly axial, partly foliar. STRASBURGER (1872, p. 69) has also drawn attention to somewhat similar analogies among Angiosperms, of which the adnate inflorescence of *Tilia* affords the most familiar instance.

The fact that the supply to the ovuliferous scale appears to arise from the supply to the bract, therefore, does not necessarily indicate that the one organ is morphologically an excrescence of the other.

(b) *Degree of Development of the Ovuliferous Scale as an Index of Affinities.*—Considerable importance has been attached by several authors to the degree of development of the ovuliferous scale as an index of affinity or of relative antiquity. While the exponents of the ligular theory have naturally interpreted the poorly developed ovuliferous scale of *Araucaria* and *Agathis* as signifying primitiveness, Prof. JEFFREY and his pupils, who believe in the brachyblast theory and in the Abietineous origin of the Conifers, have made use of the fact that in *Pinus* and allied genera the ovuliferous scale (in the middle region of the cone) appears more nearly to resemble an axillary shoot than it does in *Araucaria.* Finally, against those who advocate a Cordaitean ancestry for the Conifers, the criticism has been made (SEWARD and FORD, 1906, p. 393) that as we pass backwards in geological time we do not find an increasing development of the ovuliferous scale, which would bring the older Conifers (Araucarineæ) more nearly into line with *Cordaites.*

We have seen, however, that the degree of development of the ovuliferous scale is variable, not only within narrow circles of affinity (EAMES, 1913, on *Athrotaxis* spp.), but even in different regions of the same cone (AASE, 1915). Keeping in view the analogy with the Ferns, where, as we know, the relative development of the branch and its associated leaf does not bear any definite relation to the systematic position of the plant, one is naturally inclined to ask whether even among the Conifers too much importance has not been attached to the degree of development of the ovuliferous scale as an index of relative primitiveness.

D. *The Ancestry of the Conifers.*

(a) *Relative Antiquity of Abietineæ and Araucarineæ.*—If we exclude the Taxineæ, as suggested in this paper, there remain two groups, the Abietineæ and the Araucarineæ which, respectively, according to two rival schools of thought, claim to be the oldest living Conifers. It would be superfluous to repeat the evidence adduced by the two sides—both claim the support of the fossil record as well as that of the structure of living plants, and the controversy is certainly a beautiful example of the way in which practically the same data can be construed in diametrically opposite directions.

While the palæontological evidence (SEWARD and FORD, 1906) places beyond doubt the existence of Araucarians in the Palæozoic, the existence of Carboniferous and Permian Abietineæ has been shown to be without any proof. Of two fossil woods supposed by JEFFREY and CHRYSLER (1906) to belong to Palæozoic Abieteneæ, one has been shown to be not Abietineous and the other is equally certainly not Palæozoic. THOMSON and ALLIN (1912) have clearly demonstrated that the supposed horizontal resin-canals of the wood named by PENHALLOW *Pityoxylon chasense* (from the Permian of Kansas) are really the persistent leaf-traces of a *Dadoxylon* devoid of annual rings. The other wood, *Pinites Conwentzianus*, Goepp., the Abietineous nature of which Prof. SEWARD has confirmed by an examination of the original sections, was believed by GOEPPERT to be of Carboniferous age. The fossil was, however, found on a rubbish-heap, so that its correct age is extremely doubtful, and Prof. SEWARD has recently obtained further confirmation of this doubt (SEWARD, 1919, p. 220).

Both from the structural and from the historical side, the balance of evidence is at present decidedly in favour of the Araucarineæ being the more primitive group, and the resemblances which the latter group shows to the Cordaitales (BURLINGAME, 1915) are in accord with the view that they are more primitive than the Abietineæ. However, the facts at our disposal do not appear definitely to indicate that the one group is necessarily derived from the other. An independent origin from a common source is, at any rate, a safe hypothesis.

(b) *Fossil Podocarpineæ.*—Unfortunately, the fossil history of the Podocarpineæ—the family with which we are here more intimately concerned—is very imperfectly known. This is probably because, as BURLINGAME has hinted (1908, p. 175), "we know but little of the plant-remains of those parts of the world in which their remains would be most likely to be found." The probability of a relation with the Araucarians justifies the hope that undoubted Podocarpineæ may be discovered in the Mesozoic rocks, but it is for the future to show whether this group can at all rival in age the Araucarineæ.

Apart from abundant petrified wood of the *Podocarpus* type, numerous impressions have provisionally been referred to the Podocarpineæ.* Of these impressions, one

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* The literature has been well summarised by STILES (1912, pp. 486–89); a more complete account is given in the fourth volume of Prof. SEWARD'S 'Fossil Plants.'

of the oldest, and also the most interesting, is the Rhaetic genus *Stachyotaxus*, NATHORST (1908, p. 11, Plates 2, 3), whose correct systematic position it is of great importance to ascertain, for it may, as hinted by Prof. NATHORST (p. 15, footnote), form a link between the Cycadophyta and the Conifers. The resemblance of this genus to *Cephalotaxus* is perhaps, on the whole, more striking than that to *Dacrydium*, in view of the paired ovules, symmetrical cup at the base, and the biseriately arranged leaves. But, as Prof. NATHORST says (*loc. cit.*, p. 15), the habit of the vegetative shoot is strikingly suggestive of *Podocarpus imbricatus.**

The large two-winged pollen-grains discovered by Prof. NATHORST (1908, Plate 2, figs. 53–55) in the Triassic rocks of Sweden, and compared with pine-pollen, may equally well belong to extinct Podocarpineæ, for we are at present without any knowledge as to the contents.

A passing reference was made on a preceding page to a faint resemblance between the sculpturing of the sclerotesta of *Acmopyle* and that of the Palæozoic seed *Stephanospermum caryoides*, Oliver. Although this can only be regarded as a distant analogy, it was considered worth while to give detailed figures of the stone of *Acmopyle*, in view of the possibility that seeds with a similar pattern may be discovered in a fossil condition from the southern hemisphere.

It is also difficult to say what justification there may be for homologising with the "tent-pole" of *Ginkgo* and *Cordaites* the cone-like projection at the apex of the female prothallus of *Acmopyle* (see text-fig. 6). In order to see how far this feature is repeated in other members of the family, a search was made of the few published figures, showing the apex of the female gametophyte. Miss GIBBS (1912, Plate 49, fig. 6) figures a distinctly pointed apex in *Podocarpus imbricatus.* Miss YOUNG's figure of *Phyllocladus* (1910, Plate 6, fig. 36) shows a condition particularly suggestive of *Ginkgo* and *Cordaites*, for there is a distinct central projection, surrounded by what looks like a deep trough, into which the archegonia open, but, in the absence of figures of transverse sections, I am unable to say if the archegonial depressions pass completely round the central peg.

(c) *Ultimate Origin of Conifers as a Whole.*—Whether the Conifers arose ultimately from megaphyllous (Pteropsid) or microphyllous (Lycopsid) ancestors is a question which cannot yet be regarded as settled, although it has engaged the attention of a number of eminent botanists for many years.† The more closely one tries to examine the evidence, the more distant does the solution appear to become, and I find it impossible to express a definite opinion. It goes without saying, that our knowledge of the older vegetations of the world is yet far from satisfactory ; in the Devonian, or, it may be, in even older rocks, probably still lies buried the

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* The figures (NATHORST, 1908, plate 2, figs. 19–24) also make it probable that *Stachyotaxus elegans* at least shares with *P. imbricatus*, *Acmopyle*, and *Dacrydium falciforme*, etc., the peculiar laterally compressed leaf-blade, for there appears to be no twist in the leaf-base.

† The discussion has recently been well summarised by BURLINGAME (1915).

answer to the question: Is the division of vascular plants into Pteropsida and Lycopsida so fundamental that it existed at their very origin from the non-vascular plants, or was the one class derived from the other? Naturally, if the megaphyllous forms have ultimately originated from microphyllous ones, the apparently divergent views as to the origin of the Conifers can to some extent be reconciled with each other. Thus, I believe it may be stated with confidence that the relatively near ancestors of the Conifers were forms like the Cordaitales. But the possibility of a remote Lycopsid connection,* without the intervention of true ferns or fern-like seed-plants, may not perhaps be entirely excluded, although at present there does not appear to be much evidence of a positive nature in support of such a connection.

As is well known, Dr. SCOTT (1909, pp. 650–652) has emphasised certain points of resemblance between the Cordaiteæ and the Pteridosperms, in support of the conclusion already expressed by him in 1902 (SCOTT, 1902) that the Cordaiteæ sprang from a Pteridosperm stock. In the first place, the seed in the two groups is constructed on the same general plan; secondly, by a gradual loss of centripetal xylem the stem anatomy of certain Pteridosperms passes into that of the typical Cordaiteæ. A number of Cordaitean stems are also known which approach the Pteridosperms in the possession of centripetal wood. In recent years the evidence for such an anatomical transition in the stem has been steadily increasing, and to express their intermediate structure, some of these Cordaitean stems were grouped by SCOTT and MASLEN (1910) under the genus *Mesoxylon*, of which several species have now been described (SCOTT, 1912, 1918, 1919; MASLEN, 1911).

So far as present knowledge goes, the Pteridosperms undoubtedly represent the nearest approach to the hypothetical ancestors of the Cordaitales. At the same time, there are important points of difference between the two groups, which have, of course, been recognised by Dr. SCOTT, but which may perhaps deserve as much emphasis as he has justly laid upon the resemblances. I wish to guard against the impression that I consider an origin of the Cordaitales from a Pteridosperm stock as improbable, but the wide differences between the two phyla, at any rate as we know them at present, do not readily fall in with this view.

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* Naturally, an affinity so remote as may here be implied can hardly be expected to find expression in detailed structural resemblances: as may be inferred from my above-expressed belief in the brachyblast theory of the ovuliferous scale of Conifers, I do not agree with SCHUMANN (1903, p. 71) in regarding the ligule of the Heterosporous Lycopods as being homologous with the organ so named in *Araucaria*. If such a homology existed, it might be reasonable to expect that the latter genus should preserve a trace of the ligule on the microsporophyll as well, if not on the vegetative leaf, in order to materialise the comparison with the Heterosporous Lycopodiales, which are never devoid of a ligule, even in the vegetative leaves. SCHUMANN (1903, p. 70), who believes in the Lycopod origin of all Conifers, is so deeply impressed by the resemblances between the *Lepidocarpon* and the ovuliferous organ of the Conifers, that he considers it by no means certain that the Lepidodendreæ have correctly been assigned to the Pteridophyta. But the ligule of the Heterosporous Lycopods appears still to be a morphological enigma.

A review of the entire Gymnospermous series shows that there are two great divisions, based primarily upon the manner in which the seed is borne, whether upon the leaf or directly upon the axis. In the Pteridosperms and Cycads the seeds are always clearly borne upon the leaves, while in the Cordaitales (so far as known) and in the Ginkgoales, Taxales, and Coniferales they are borne either clearly upon an axis, or upon a structure which is probably some modification of an axis.* This differentiation of the Gymnosperms into two divisions, which I here propose to refer to as the Phyllosperms (with leaf-borne seeds) and Stachyosperms (with stem-borne seeds), respectively, appears to be very old, for, as far as I am aware, there is among the Pteridosperms no sign of a transition from the phyllospermic to the stachyospermic condition: a sharp differentiation is seen as far back as the available fossil records can take us. There could scarcely be a greater contrast in this respect than there is between RENAULT's well-known figure of *Cordaianthus Williamsoni* (see SCOTT, 1909, p. 540) and the equally familiar figure of *Lyginopteris Oldhamia*, which forms the frontispiece of Dr. SCOTT's 'Studies.' .

Combined with this fact there are other important features, in which, as Dr. SCOTT points out (1909, p. 650), the Cordaiteæ and the fern-like seed-plants are as far apart as two groups of Gymnosperms very well can be. The strap-shaped parallel-veined leaves of *Cordaites*, and in fact the leaves of any known Stachyosperm, living or fossil, are entirely different from the much-divided fern-like fronds of the Pteridosperms or the almost equally complex leaves of the Cycads. The result is that in habit the two groups are totally distinct, and it is not easy to picture a Pteridosperm frond reduced into the simple Cordaitean leaf—at any rate, no intermediate form is yet known. Our knowledge of Cordaitean and Pteridosperm leaves is by no means complete, and transitional forms may yet be discovered; but until these are forthcoming it seems necessary to give due importance to the sharp contrast between the two types.

It is difficult to say whether we can extend to *Cordaites* the so-called phyllode theory of the leaf, originally applied to the monocotyledonous leaf. According to this theory, the typical monocotyledonous leaf represents only the proximal non-laminated region of the typical dicotyledonous leaf. Quite recently Mrs. AGNES ARBER (1918, p. 472) has published a paper of unusual interest, in which she brings forward convincing anatomical evidence which I think places the theory upon a firm basis, so far as the monocotyledons are concerned. In the leaves of *Cordaites* and the Conifers, however, similar anatomical evidence appears to be lacking. Nevertheless, I

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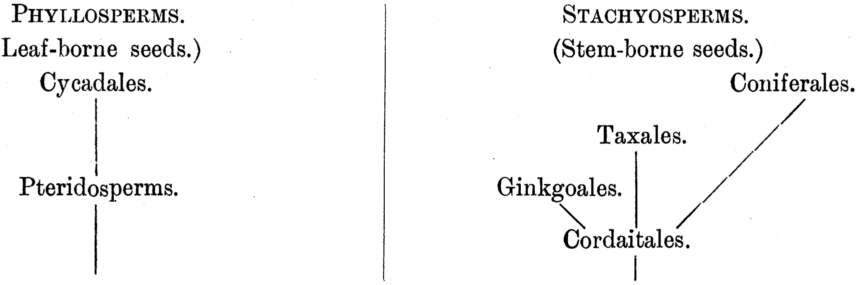
* The importance of this difference between the Cyads and the Conifers was emphasised by STRASBURGER as long ago as 1879 (p. 139). As to the Gnetales and Bennettitales, further investigation is needed to show clearly whether they belong to the first category or to the second. STRASBURGER placed the Gnetales among the former class. On the other hand, in view of the far-reaching resemblances, in vegetative characters, of the Bennettitales with the Cycadales, the rather sharp contrast in the reproductive organs is disconcerting. The view has, however, been expressed (SEWARD, 1917, p. 382) that the seed-bearing pedicels of the Bennettitales are morphologically of a foliar nature.

consider it likely that the cupressoid type of leaf may have been produced by reduction from a taxoid leaf, and the latter from the multinerved type found in *Cordaites*, particularly as leaves similar to that of *Cordaites* also occur in the Araucarineæ. But the difficulty appears to lie in deriving the Cordaitean or Araucarian leaf from the much-divided fern-like frond, and this, it will be agreed, is the crux of the question. It is gratifying to learn that Mrs. ARBER hopes to return to this aspect of the phyllode theory, and her results may be awaited with interest, for light may be thrown upon the important question as to whether the apparent microphylly of the Conifers is due to reduction from a Pteridosperm-like condition or a reduction merely within the Conifers.

In the male organs, too, there is no clear resemblance between the Cordaitales and the Pteridosperms, the latter, as Dr. SCOTT points out, having no definite "cones." There appears to be hardly a comparison—except a rather distant one in form—between the "epaulets" of *Crossotheca* and the "stamens" of *Cordaites*. The one represents a minute portion of a dissected leaf; the other, according to the view which appears the most plausible, is itself an entire foliar organ, attached directly to the axis.* Each "epaulet" of *Crossotheca* may possibly be compared to a sorus on the microsporophyll of a Cycad, but not with the "stamen" of *Cordaites*; the latter organ is probably homologous with the microsporophyll of the Taxales, in which group the presence of interstitial sterile bracts in the male cone (*Cephalotaxus*) may considerably enhance the resemblance with *Cordaites*.

If the Stachyosperms and the Phyllosperms have had a common origin from megaphyllous ancestors it is clear that we must await the discovery of forms which show a transition from the leaf-borne to the stem-borne seed, as well as a reduction of the much-divided fern-like frond to the simple leaf invariably found in the Stachyosperms. A rather similar reduction must also be visible in the male organs. So long as these important links are missing there is at least some strong negative evidence against the megaphyllous theory.†



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* If it is held, with SOLMS-LAUBACH, that the structure here called a stamen is a male flower (see SCOTT, 1909, p. 537), the above comparison would be still less valid.

† Since the above was written Dr. SCOTT (SCOTT, 1920) has read a paper bearing on the ultimate origin of the Pteridosperms, and expressed the view that they "have always been distinct from any of the known phyla of vascular Cryptogams . . . parallel in important respects to the ferns, but of unknown and remote origin." Unfortunately, my knowledge of this paper is still limited to the brief reference in 'Nature.'

Much has recently been accomplished in connecting up the Cordaiteæ with certain Pteridosperms by means of Cordaitean forms showing an intermediate stem-anatomy, but light has still to be thrown upon the nature of the fructifications borne by these plants. The most recent work on the subject (SCOTT, 1919) makes it quite probable that one of these Cordaitean stems (*Mesoxylon multirame*) bore the seeds previously described by Mrs. ARBER (1910) as *Mitrospermum compressum*, but there is no indication that these seeds make a closer approach, either in their structure or in their mode of attachment, to those of the Pteridosperms, than do those of the other Cordaiteæ.

SUMMARY.

A description is given of the anatomy of *Acmopyle Pancheri*, Pilger, based chiefly on material from New Caledonia, the native habitat of the plant. Reasons are given for the view that the genus also occurs in the Fiji Islands.

So far as characters of generic rank are concerned, *Acmopyle* does not differ from *Podocarpus* in any of the following features: vegetative anatomy of root, stem and leaf; drupaceous character of the seed, megaspore membrane, female prothallus and young embryo, structure of male cone, microsporophyll, pollen-grain and probably male gametophyte. As is generally the case in *Podocarpus*, the seed is borne on a thick fleshy receptacle composed of the swollen axis and bracts.

The surface of the receptacle is tuberculate, and is raised into more or less prominent humps in the axils of the sterile bracts. The vascular supply to these axillary humps is in the form of paired strands inversely orientated with respect to the subtending bract-traces; the humps are therefore concluded to be vestigial axillary shoots, the entire receptacle being regarded as a reduced branch system. The vascular supply to the ovuliferous organ in the axil of the fertile bract does not differ, except in its much greater degree of development, from that to the humps in the axils of the sterile bracts; the ovuliferous organ is hence regarded as a brachyblast, and homologised with the ovuliferous scale of other Conifers.

Acmopyle differs from *Podocarpus*:

(1) In the nearly erect posture of the adult seed;

(2) In the complete fusion of the epimatium to the integument, even in the region of the micropyle, in the formation of which the epimatium takes part;

(3) In the much greater development of the vascular system of the seed, which forms a nearly continuous cup-like tracheal investment covering the basal two-thirds of the stone.

Taking into consideration the entire structure of *Acmopyle*, the genus is concluded to be the most highly specialised of the Podocarpineæ; there appears to be no support for the view that the family is a reduction series with *Podocarpus* as one of its most primitive genera.

The theoretical part of the paper also deals with other controversial questions, namely, the systematic position of the Taxineæ, the morphology of the ovuliferous

scale of Conifers, and the origin of the Conifers. With regard to the first of these questions, the conclusion arrived at is that the structure of the genera *Taxus*, *Torreya*, and *Cephalotaxus* is sufficiently distinct to justify their being placed in a separate phylum, for which the name Taxales is proposed, and which would be equivalent in rank and related to the Ginkgoales and Coniferales. The relations oi the Taxales are, it is believed, closer with *Ginkgo* and the Cordaitales than with the Conifers, as here defined.

Concerning the ovuliferous scale of Conifers, the conclusion is in favour of the brachyblast theory.

No definite conclusion is expressed on the question as to whether the Conifers ultimately arose from microphyllous or megaphyllous (fern-like) ancestors, for, although the author confidently believes that they arose from Cordaitalean ancestors, the origin of the Cordaitales themselves from a megaphyllous (fern-like) stock is still considered to be " not proven " on the existing evidence.

Emphasis has been laid upon certain facts of a negative character, which are—pending further evidence—regarded as obstacles in the way of an unqualified acceptance of the megaphyllous theory. Of these facts, special importance is attached to a sharp differentiation that exists between those Gymnosperms (Cycadales, Pteridosperms) in which the seed is clearly borne upon a leaf, and those (Cordaitales, Ginkgoales, Taxales, Coniferales) in which it is either clearly borne directly upon an axis (Cordaitales, *Taxus*), or upon an organ which is probably some modification of an axis (Conifers, *Ginkgo*, etc.). For these two divisions of Gymnosperms, the author proposes the names Phyllosperms (with leaf-borne seeds) and Stachyosperms (with stem-borne seeds) respectively. It is argued that the Cordaitales, being Stachyosperms, cannot have arisen from Phyllosperm ancestors, unless there existed forms which bridge up this and other apparently wide gaps between the two divisions ; and of the existence of these intermediate forms there is at present no evidence.

At the same time, it is fully recognised that the meagre evidence of a positive nature that is available at present, is distinctly in favour of a common megaphyllous origin for the Cordaitales and Pteridosperms.

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EXPLANATION OF PLATES.

Plate 9. *Acmopyle Pancheri.*

Fig. 1.—Photograph showing habit. About $\frac{1}{6}$ nat. size.

Fig. 2.—Longitudinal section of young root-tubercle growing out into normal rootlet. Shaded cells in cortex forming an ill-defined infected zone. About × 17.

Fig. 3.—Transverse section of young diarch root. Hoop-like thickenings on inner cortical cells, in section appearing like beads. About × 45.

Fig. 4.—Transverse section of leaf. Compare text-fig. 2, A. *x.*, xylem; *p.*, phloem; *c.*, mucilage canal. About × 28.

Fig. 5.—Section of leaf cut parallel to dorsal surface, showing mosaic of large thin-walled mucilage cells and small crowded palisade cells. About × 100.

Fig. 6.—Section of leaf cut along plane of expansion, showing accessory transfusion tissue. The vascular bundle of the leaf lies not far from the lower edge of the photograph. The upper edge of the photograph shows the leaf margin. About × 25.

Fig. 7.—Camera-lucida drawings of stomata. About × 375.

a. Section of leaf cut very nearly parallel to stomatal surface. The stoma towards the lower end of the series was cut very near the cuticle, and shows the deep-staining dorsal lignified lamellæ, and the thickenings of the septa between the guard-cells. The stoma at the upper end was sectioned along a plane midway between the dorsal and ventral lamellæ. The sinuous lines over the septal thickenings are cellulose layers. The walls of the epidermal cells show moniliform thickenings; the cell-contents have been omitted. There is usually one polar subsidiary cell common to two consecutive stomata, and 2–4 lateral subsidiary cells to each stoma. The lateral subsidiary cells of each stoma touch those of the stomata in front and behind.

b. Transverse section through middle of stoma, showing dorsal and ventral lignified lamellæ.

c. As we proceed towards the end of a stoma (fig. 7, *c*), the ventral lamellæ gradually vanish, their place being taken by the median septal thickenings; the dorsal lamellæ here stand almost perpendicularly instead of almost horizontally as in the middle region of the stoma.

d. Nearly median longitudinal section of stoma. Of the lignified portions only the septal thickenings are seen, besides the lining of the stomatal pore.

Fig. 8.—Median longitudinal section of microstrobilus. ×, organic apex of axis; ✱, peltate terminal stamen, the sterile "shield" forming a (?) protective cap. About × 17.

Fig. 9.—Transverse section of male cone axis, with well-defined epidermal layer of "resin"-cells, and ring of mucilage canals round a circle of strands. The light patches in the canals are coagulated masses of mucilage, one of which contains a deep-stained tabular hexagonal crystal. About × 40.

PLATE 10. *A. Pancheri.*

Fig. 10.—Transverse section of stamen. × ×, points of dehiscence; the figure 10 points to the mucilage canal of the sporophyll strand; the strand itself is not preserved in this section. On the abaxial (lower) side there is a λ-shaped air space between the sporangia. About × 32.

Fig. 11.—The same, further enlarged to show reticulate markings on the wings of the pollen-grains, and the thin septum between the sporangia. About × 175.

Fig. 12.—Male inflorescences. Natural size.

Fig. 13.—Transverse section of outer cortex of a receptacle, showing the thick cuticle covering the rounded tubercles; the large clear mucilage cells, and smaller "resin"-cells. About × 35.

Fig. 14.—Part of transverse section of a receptacle, showing the trace of a sterile bract (to the right of the black cross), and two smaller inverted strands (left of the cross) destined to supply an axillary hump. About × 35.

Fig. 15.—Ventral view of stone. The large white spot near the lower end is the eccentric chalaza. The ventral loop of the "escarpment" is not far from the chalaza. About × 3.

Fig. 16.—Dorsal view of stone. The chalaza is invisible from this side, and the dorsal loop of the "escarpment" is nearer the micropyle than it is in fig. 15. About × 3.

Fig. 17.—Basal view of stone, showing the eccentric chalaza and the radiating marks corresponding to the strands in the flesh. About × 3.

Fig. 18.—View of stone from the left side. One arrow points towards the chalaza, the other away from the micropyle. A curved faintly prominent ridge connects the two points. Note the relative positions of the two loops of the " escarpment " with respect to the chalaza. About × 3.

Fig. 19.—Apical view of stone. The micropyle is just visible as a minute black spot in the centre. About × 3.

PLATE 11. *A. Pancheri.*

Fig. 20.—Part of transverse section of seed, at about the level of text-fig. 32 (compare index-figure on p. 275). *o.o.f.*, outer zone of outer flesh; *i.o.f.*, inner zone of outer flesh; *scl.*, sclerotesta; *cup.*, vascular cupule; just inside this point a strand is seen coming off from the inner face of the cupule.

The horizontal line indicates the plane of dehiscence of the stone. Note that the ventral (upper) valve is considerably larger than the dorsal. The arrow points to one of the carinæ of the sclerotesta. About × 5½.

Fig. 21.—Transverse section of seed, cut at about the level of text-fig. 32 (see also text-fig. 35). The vascular cupule is seen in section as a faint white line with moniliform thickenings. Slightly larger than natural size.

Fig. 22.—Megastrobilus. *a.* Oblique dorsal view of two strobili on a forked, strongly curved peduncle. The curved ridge on the back of the seed, the tuberculate surface of the receptacle with the sterile bracts, and the broad fertile bract wedged in between the receptacle and seed, are clearly seen. Nat. size.

b. Ventral view of a strobilus attached to a pectinate shoot. In the natural position of the organs, if the shoot is seen from the upper side (as in our photograph) the fruit would be concealed beneath it. In order to expose it to the view, the fruit has been moved out of its natural position. The sub-apical micropyle is well seen, but the curved ridge is invisible from this side. Nat. size.

c. Median longitudinal section of fruit. Nat. size.

Fig. 23.—Ventral view of a megastrobilus, showing (1) the large round hump on the receptacle, with the most distal sterile bract projecting from its centre (just below the seed); and (2) three other sterile bracts (two right and left and one in the middle below), each with an axillary hump. Nat. size.

Fig. 24.—View from left side of a seed from which the outer zone of the outer flesh was shaved off so as to expose the vascular cupule, stiffened by a network of strands. The two basal strands are also exposed. Comparison with Plate 2, fig. 18, shows that the cupule does not extend beyond the " escarpment."

The seed was photographed while immersed in alcohol, for then the xylem appeared white and showed up well against the "resinous" inner zone of the flesh. Slightly larger than natural size.

Fig. 25.—The dome-shaped free portion of a nucellus, flattened out under a coverslip after removal of the nucellar cone, of which the scar is indicated by an arrow. Round this scar is a broad areole of light colour, which contrasts well with the dark peripheral part rich in "resin"-cells. About × 20.

Fig. 26.—Apical part of megaspore, with a pro-embryo to one side of the axis. The coiled suspensor tubes are seen cut in different planes. The apex of the megaspore is produced into a blunt process which may (?) be likened to the "tent-pole" of *Ginkgo*. About × 11.

Fig. 27.—Drawings to show the different types of tracheides in the vascular cupule of the seed.

Fig. 28.—Superficial cells of megaspore, with poorly developed megaspore membrane, and anticlinal walls specially thickened next to the membrane.

Fig. 29.—Surface view of superficial layer of megaspore. The multinucleate cells have their thickened anticlinal walls perforated by straight pits which impart a prismatic appearance to the walls.

Podocarpus imbricatus.

Fig. 30.—Longitudinal section of receptacle and micropylar region of seed. As in *Acmopyle* the receptacle has a tuberculate surface (compare Plate 11, figs. 22*a*, 23). At × there was a sterile bract (in a position corresponding to that of the last sterile bract of *Acmopyle*, see Plate 11, fig. 23), but this was removed before the section was prepared. About × 17.

Podocarpus sp.

Fig. 31.—Stone of a new species discovered by COMPTON in New Caledonia. The sculpturing shows a general similarity to that in *Acmopyle* (see Plate 10, fig. 15). Slightly enlarged.

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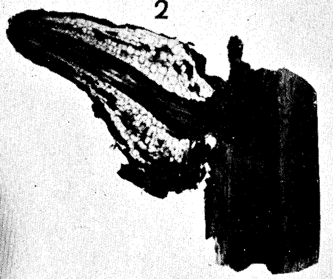

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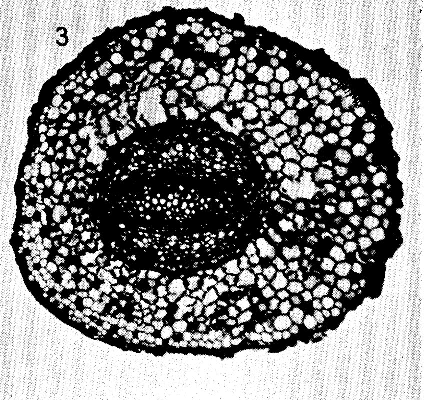

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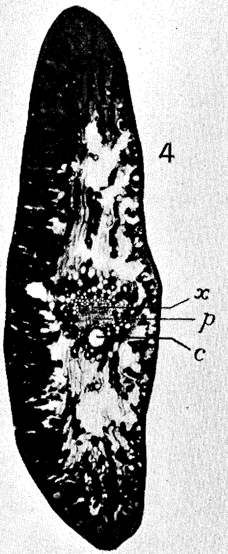

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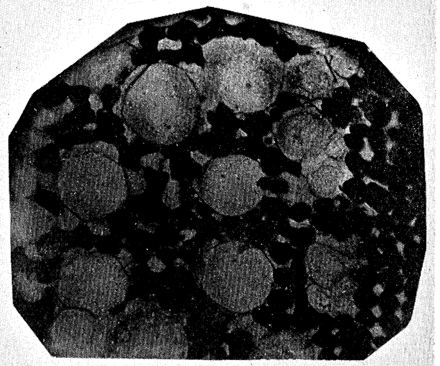

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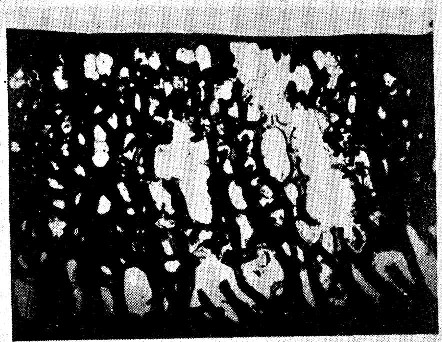

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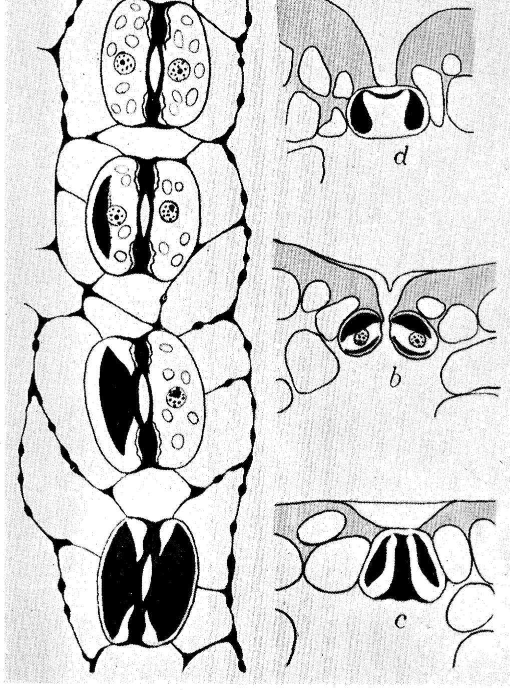

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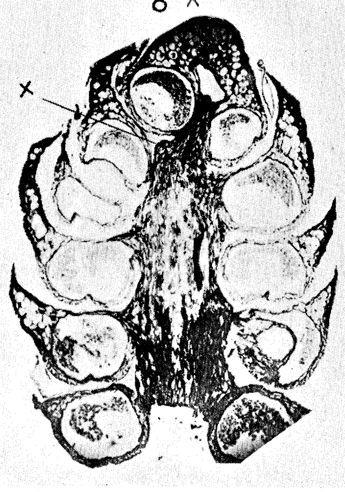

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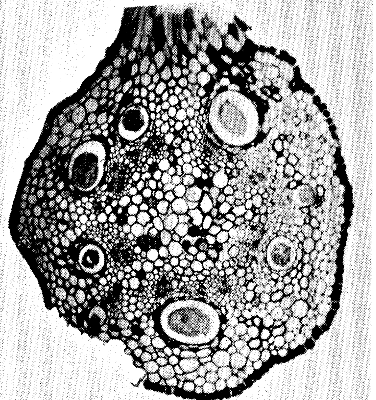

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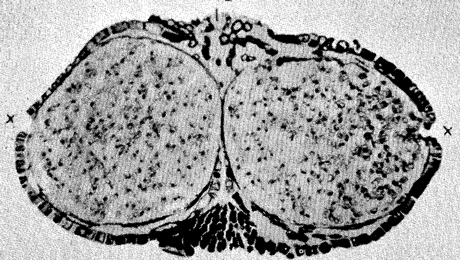

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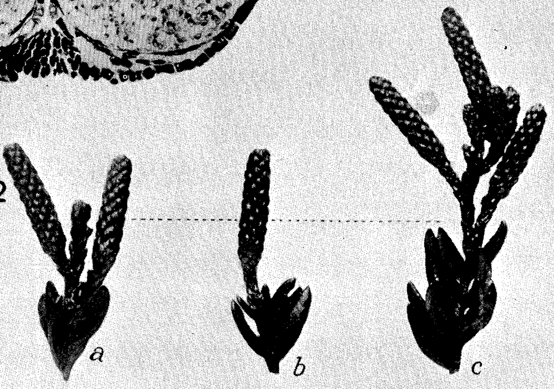

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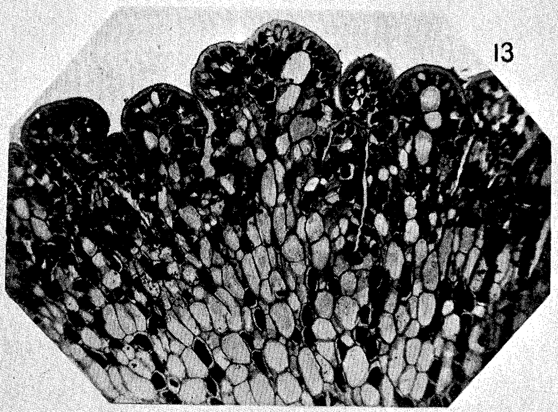

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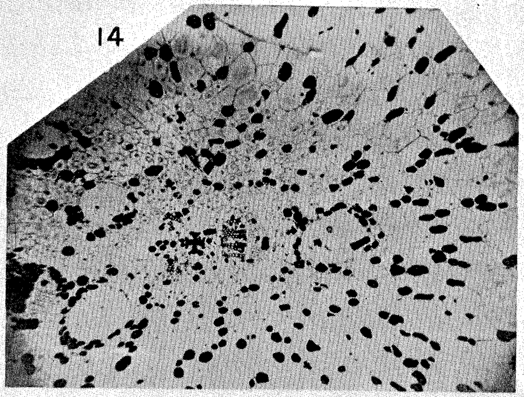

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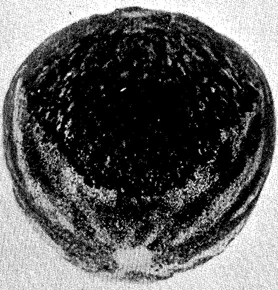

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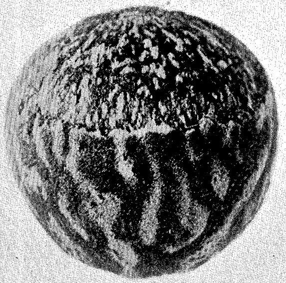

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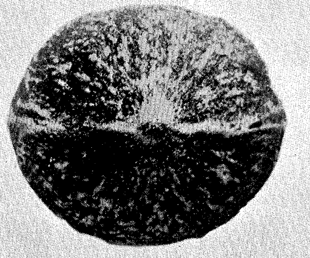

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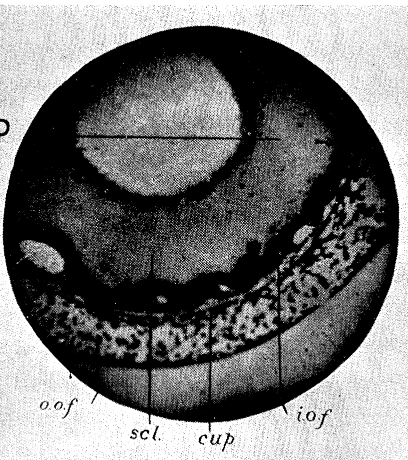

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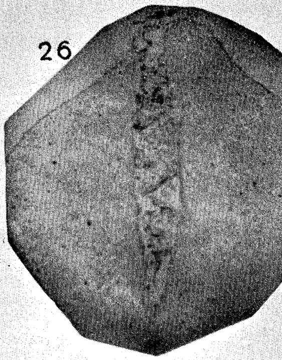

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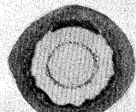

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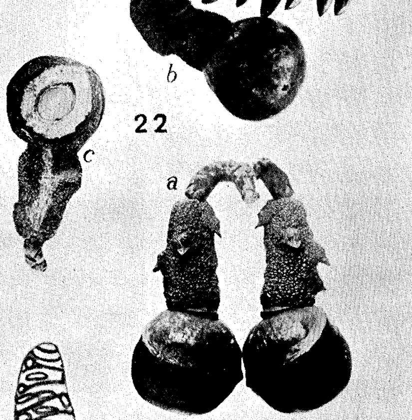

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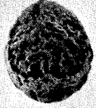

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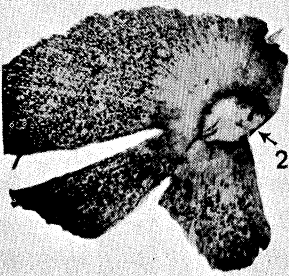

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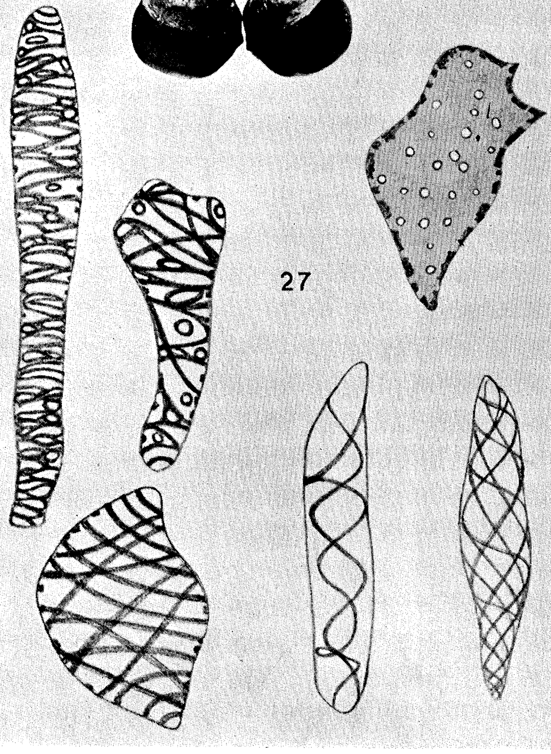

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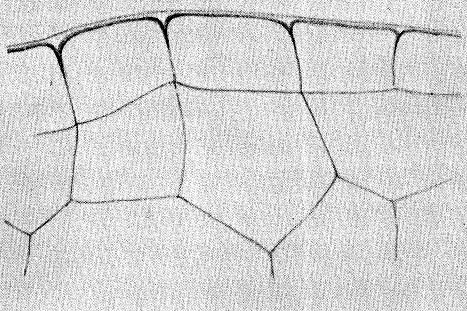

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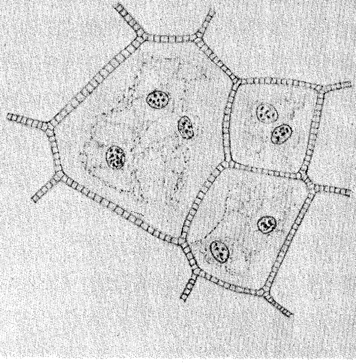

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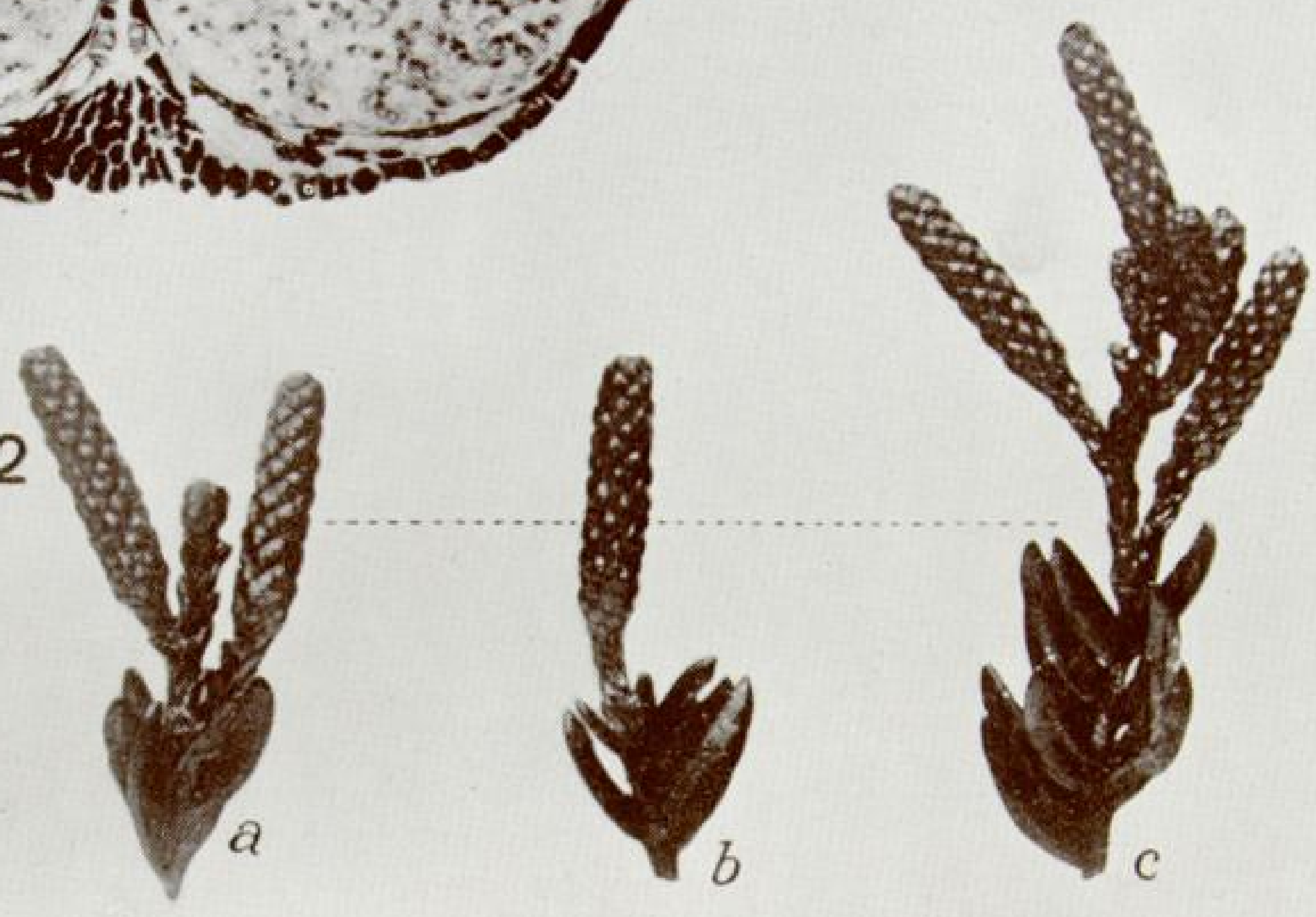

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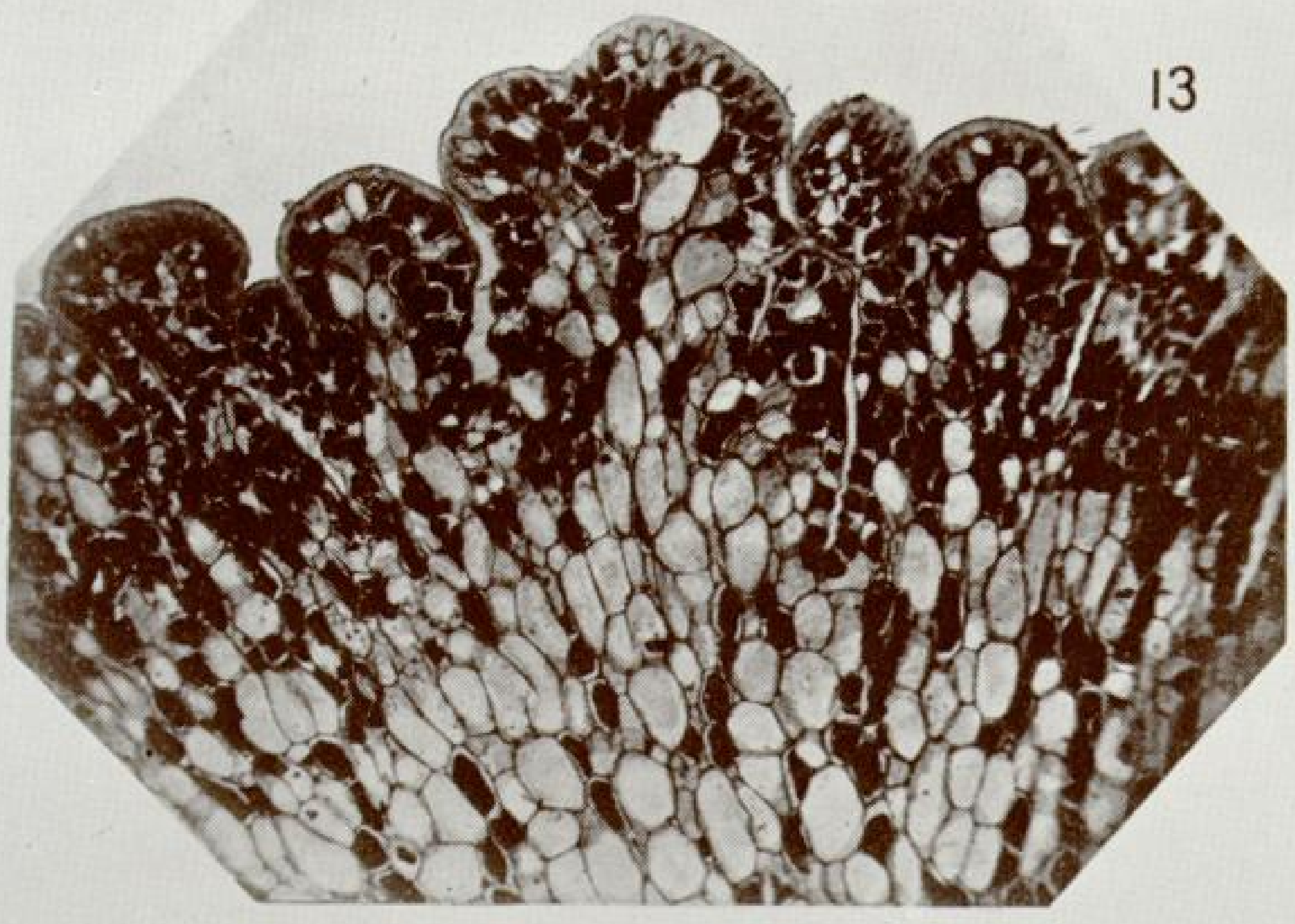

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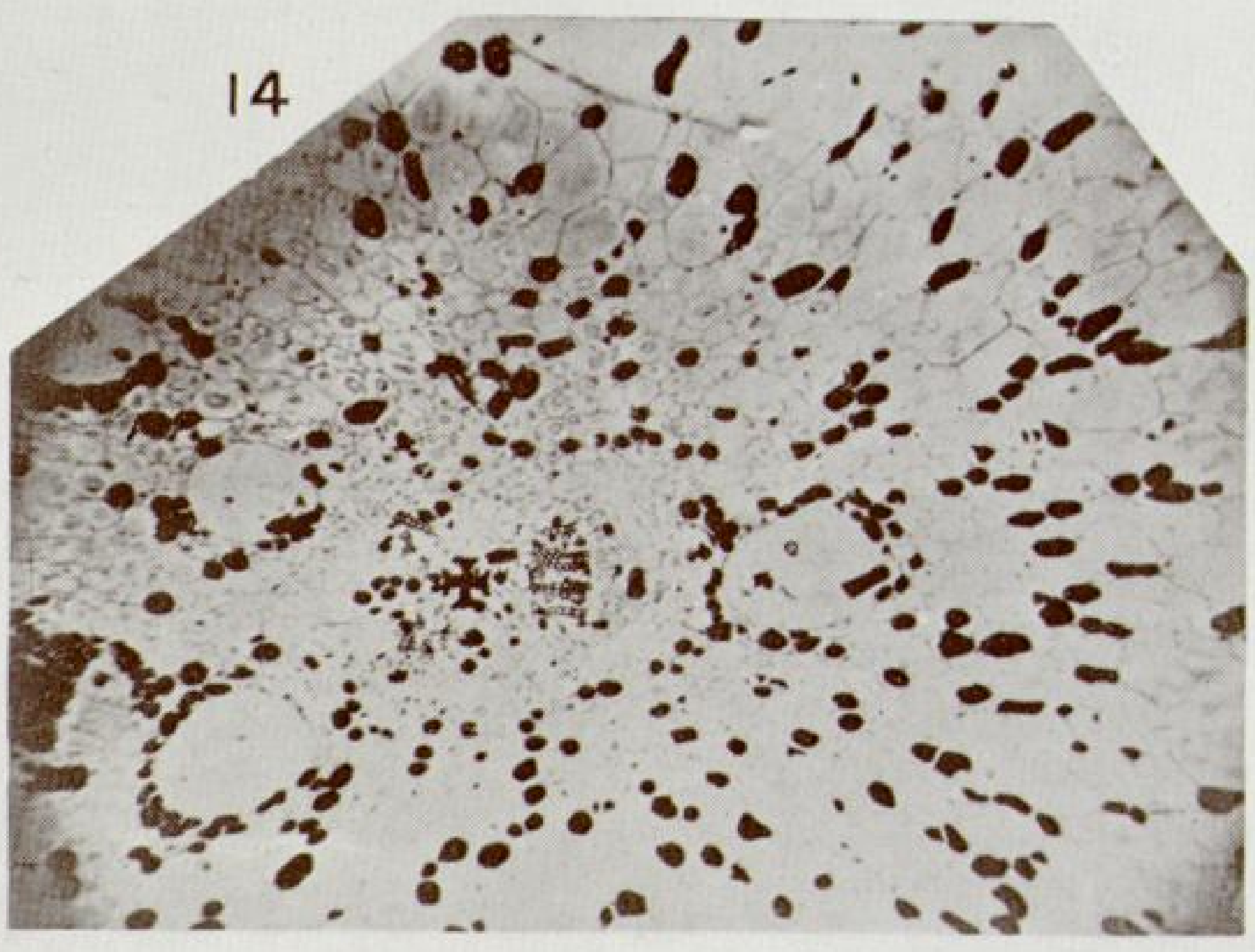

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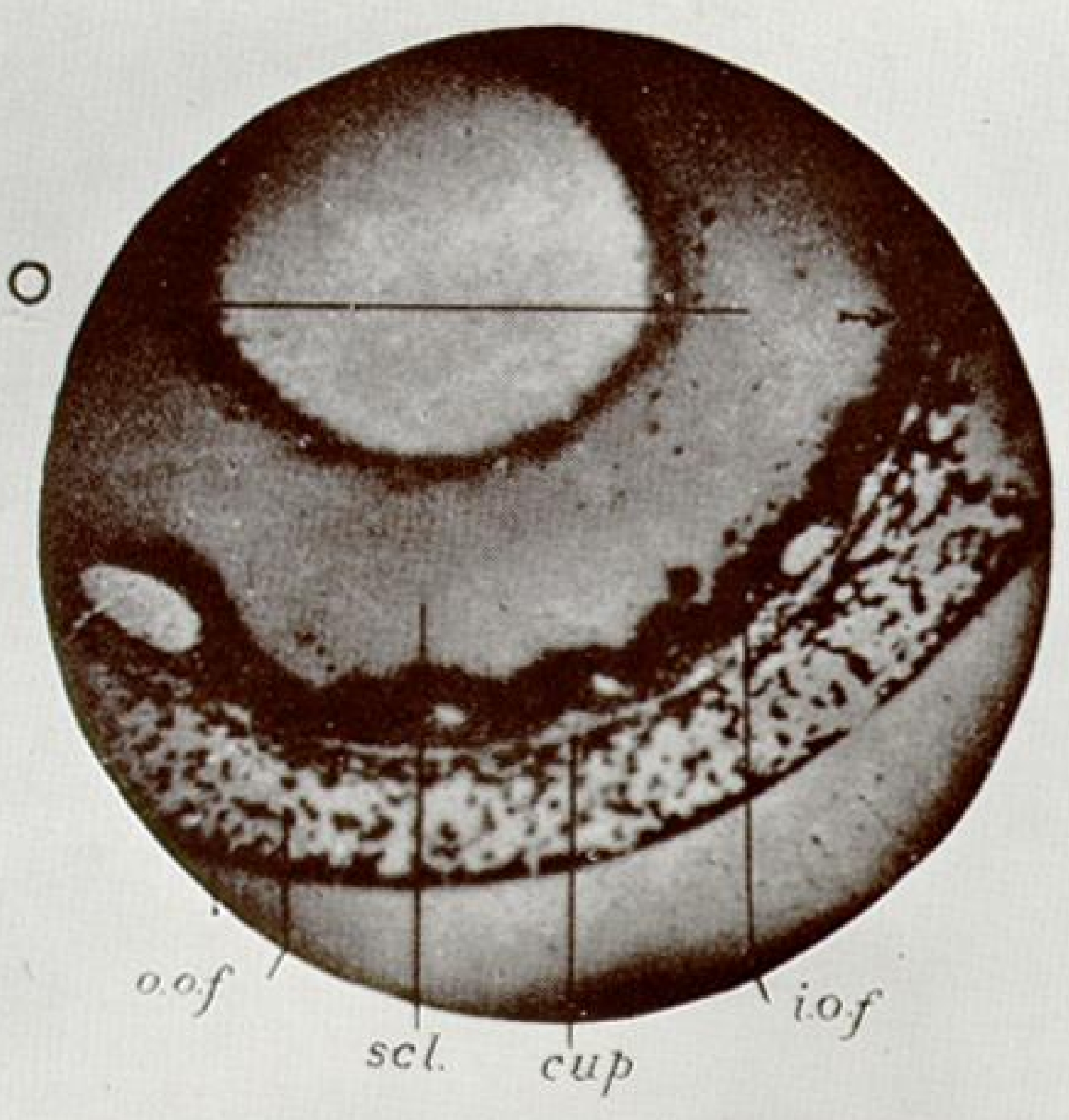
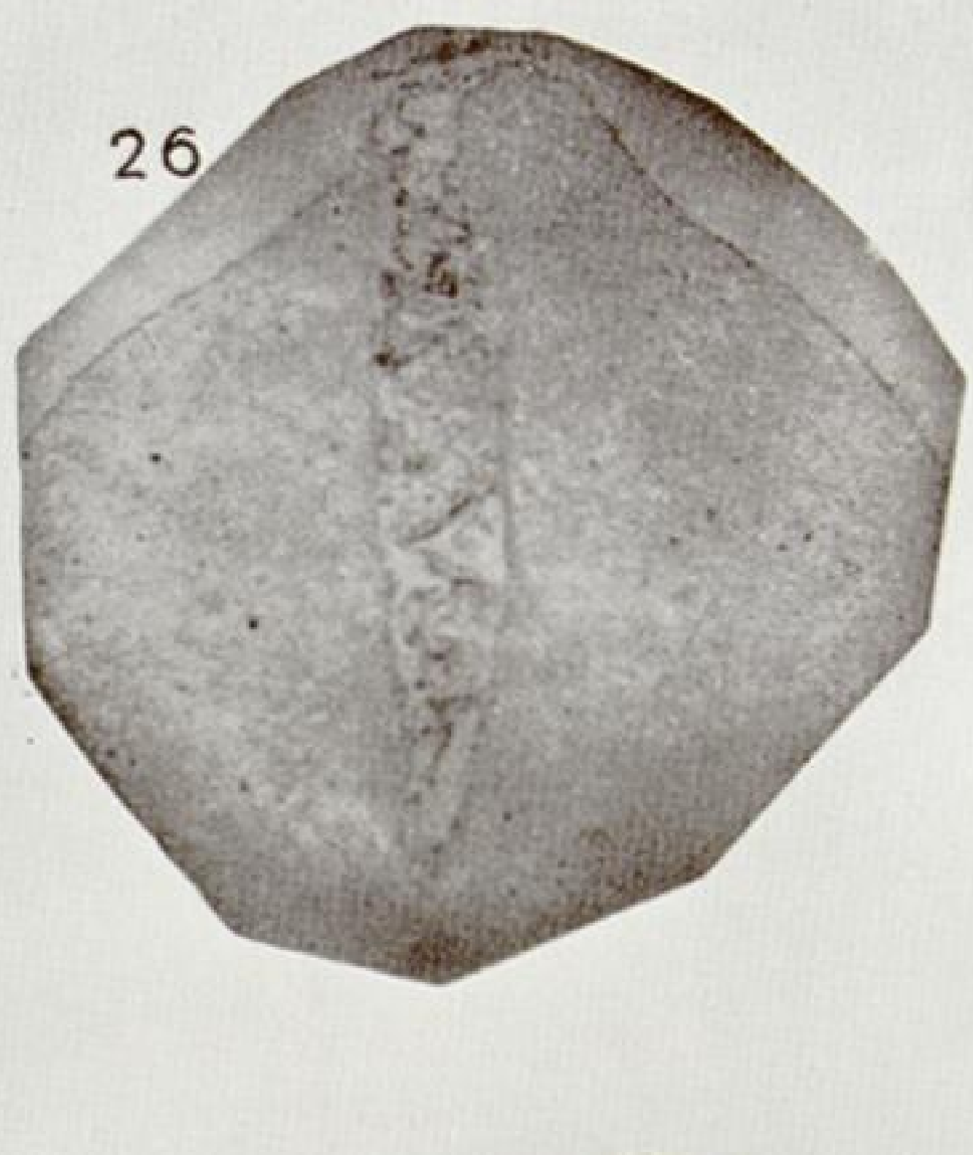
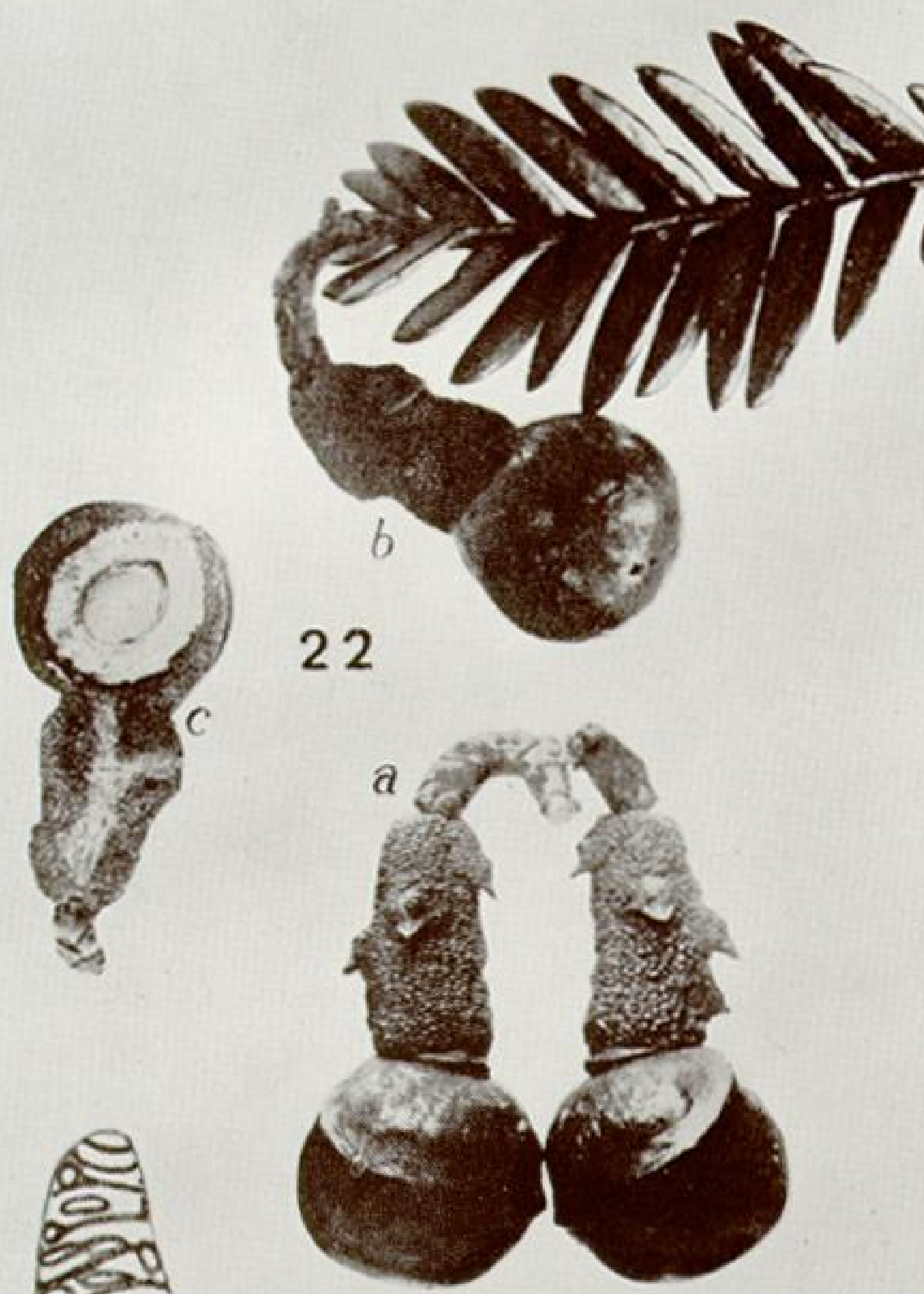
Fig. 17.—Basal view of stone, showing the eccentric chalaza and the radiating marks corresponding to the strands in the flesh. About × 3.

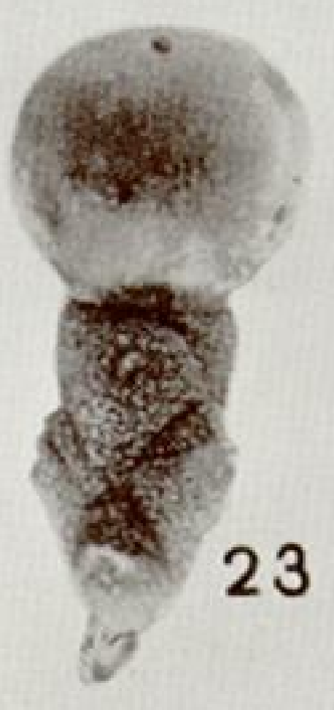
Fig. 18.—View of stone from the left side. One arrow points towards the chalaza, the other away from the micropyle. A curved faintly prominent ridge connects the two points. Note the relative positions of the two loops of the "escarpment" with respect to the chalaza. About × 3.

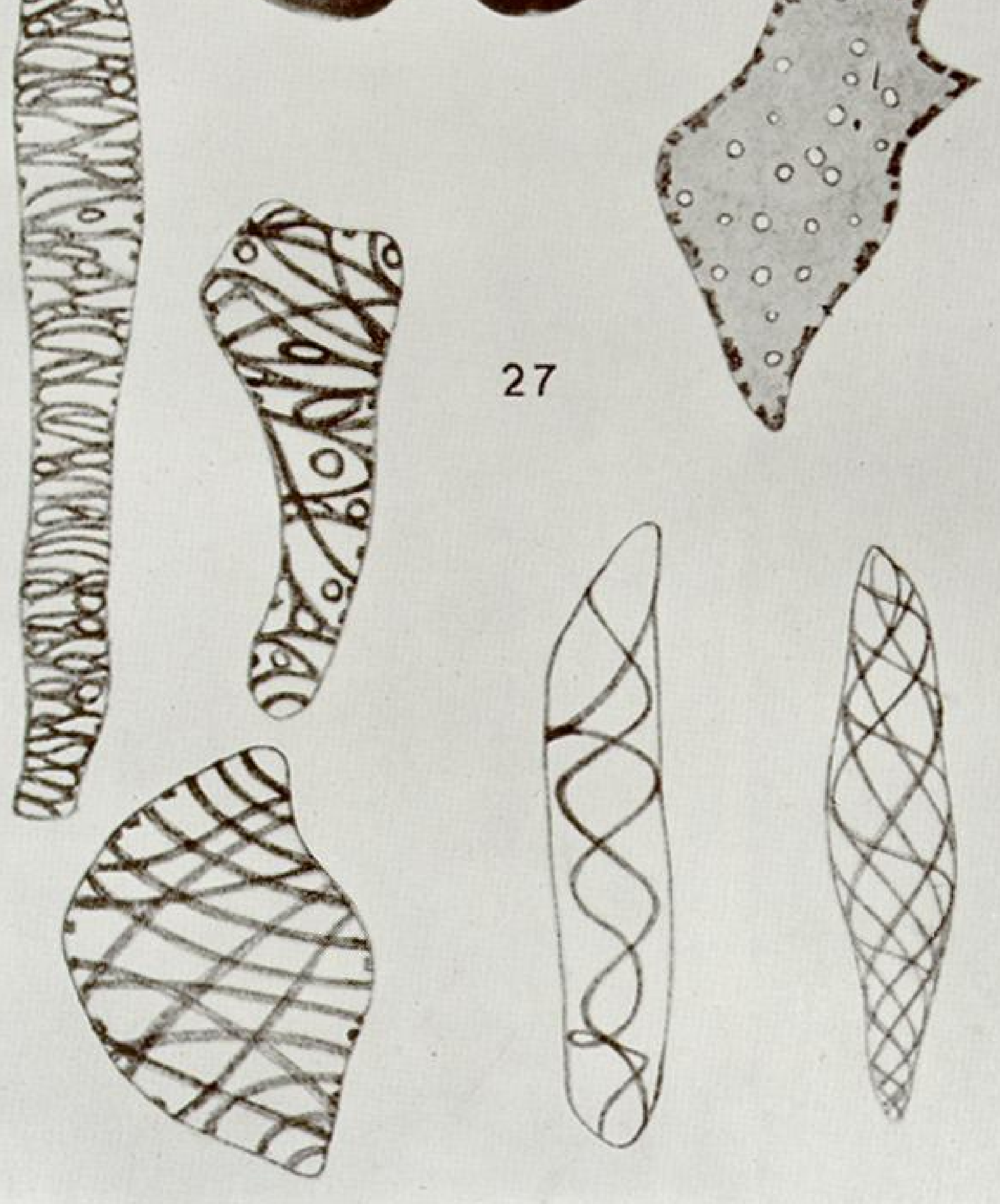
Fig. 19.—Apical view of stone. The micropyle is just visible as a minute black spot in the centre. About × 3.

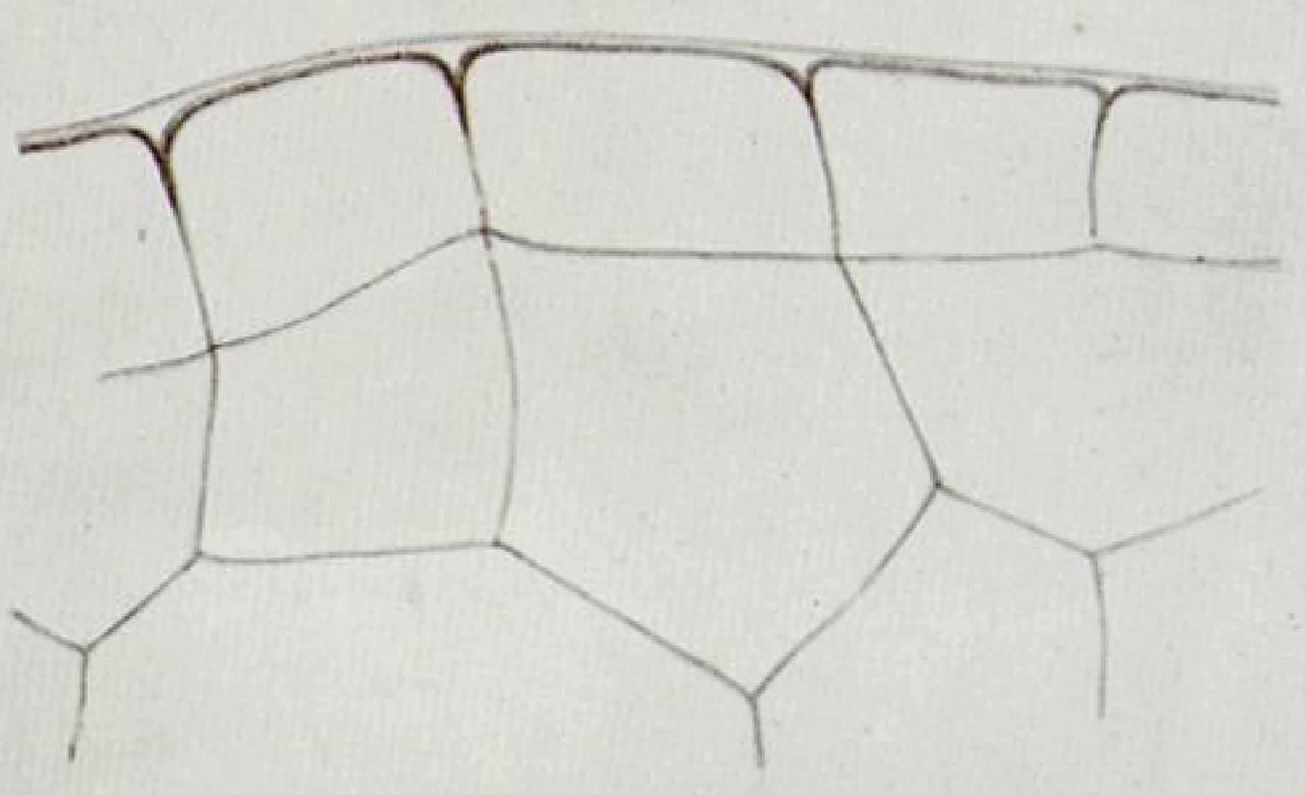












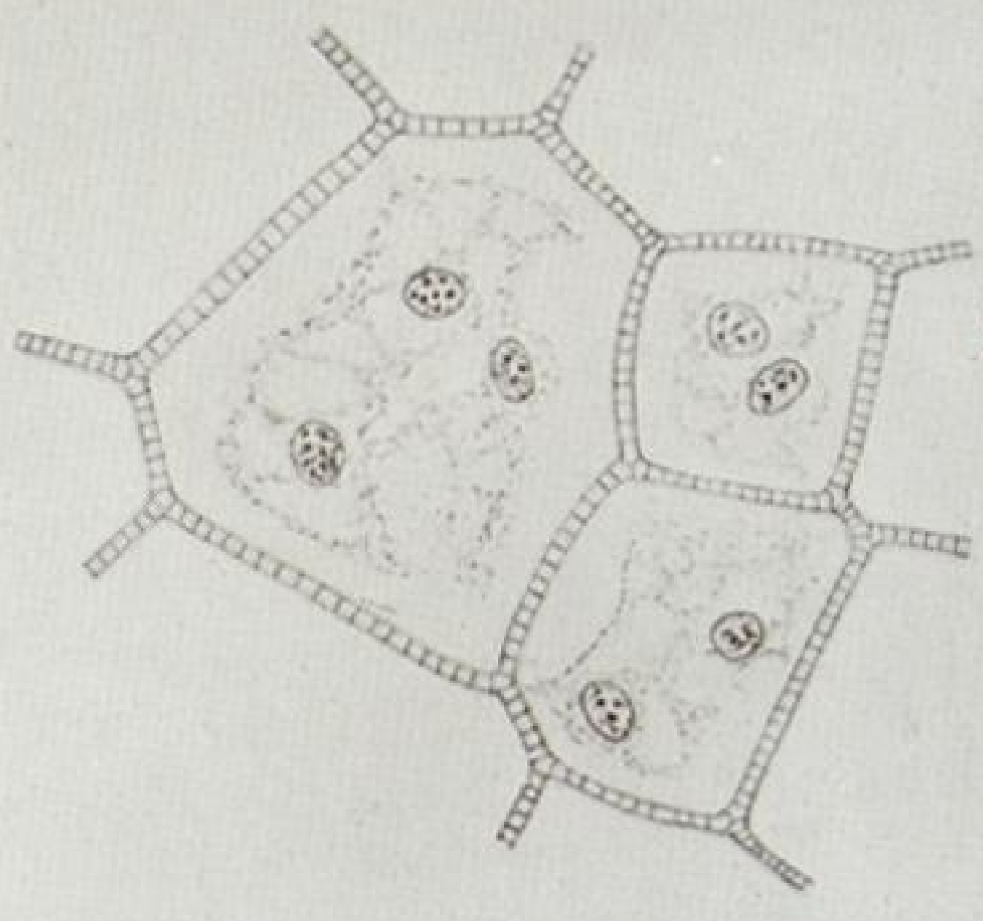


PLATE 11. *A. Pancheri.*

Fig. 20.—Part of transverse section of seed, at about the level of text-fig. 32 (compare index-figure on p. 275). *o.o.f.*, outer zone of outer flesh; *i.o.f.*, inner zone of outer flesh; *scl.*, sclerotesta; *cup.*, vascular cupule; just inside this point a strand is seen coming off from the inner face of the cupule.

The horizontal line indicates the plane of dehiscence of the stone. Note that the ventral (upper) valve is considerably larger than the dorsal. The arrow points to one of the carinæ of the sclerotesta. About × 5½.

Fig. 21.—Transverse section of seed, cut at about the level of text-fig. 32 (see also text-fig. 35). The vascular cupule is seen in section as a faint white line with moniliform thickenings. Slightly larger than natural size.

Fig. 22.—Megastrobilus. *a.* Oblique dorsal view of two strobili on a forked, strongly curved peduncle. The curved ridge on the back of the seed, the tuberculate surface of the receptacle with the sterile bracts, and the broad fertile bract wedged in between the receptacle and seed, are clearly seen. Nat. size.

b. Ventral view of a strobilus attached to a pectinate shoot. In the natural position of the organs, if the shoot is seen from the upper side (as in our photograph) the fruit would be concealed beneath it. In order to expose it to the view, the fruit has been moved out of its natural position. The sub-apical micropyle is well seen, but the curved ridge is invisible from this side. Nat. size.

c. Median longitudinal section of fruit. Nat. size.

Fig. 23.—Ventral view of a megastrobilus, showing (1) the large round hump on the receptacle, with the most distal sterile bract projecting from its centre (just below the seed); and (2) three other sterile bracts (two right and left and one in the middle below), each with an axillary hump. Nat. size.

Fig. 24.—View from left side of a seed from which the outer zone of the outer flesh was shaved off so as to expose the vascular cupule, stiffened by a network of strands. The two basal strands are also exposed. Comparison with Plate 2, fig. 18, shows that the cupule does not extend beyond the "escarpment."

The seed was photographed while immersed in alcohol, for then the xylem appeared white and showed up well against the "resinous" inner zone of the flesh. Slightly larger than natural size.

Fig. 25.—The dome-shaped free portion of a nucellus, flattened out under a coverslip after removal of the nucellar cone, of which the scar is indicated by an arrow. Round this scar is a broad areole of light colour, which contrasts well with the dark peripheral part rich in "resin"-cells. About × 20.

Fig. 26.—Apical part of megaspore, with a pro-embryo to one side of the axis. The coiled suspensor tubes are seen cut in different planes. The apex of the megaspore is produced into a blunt process which may (?) be likened to the "tent-pole" of *Ginkgo*. About × 11.

Fig. 27.—Drawings to show the different types of tracheides in the vascular cupule of the seed.

Fig. 28.—Superficial cells of megaspore, with poorly developed megaspore membrane, and anticlinal walls specially thickened next to the membrane.

Fig. 29.—Surface view of superficial layer of megaspore. The multinucleate cells have their thickened anticlinal walls perforated by straight pits which impart a prismatic appearance to the walls.

Podocarpus imbricatus.

Fig. 30.—Longitudinal section of receptacle and micropylar region of seed. As in *Acmopyle* the receptacle has a tuberculate surface (compare Plate 11, figs. 22*a*, 23). At × there was a sterile bract (in a position corresponding to that of the last sterile bract of *Acmopyle*, see Plate 11, fig. 23), but this was removed before the section was prepared. About × 17.

Podocarpus sp.

Fig. 31.—Stone of a new species discovered by COMPTON in New Caledonia. The sculpturing shows a general similarity to that in *Acmopyle* (see Plate 10, fig. 15). Slightly enlarged.