VIII. *On the Structure and Affinities of Stephanospermum, Brongniart, a Genus of Fossil Gymnosperm Seeds.* By F. W. OLIVER, M.A., D.Sc., F.L.S., Quain Professor of Botany, University College, London.

(Plates 41-44.)

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INTRODUCTION.

THE last of many notable contributions to Fossil Botany by Adolphe Brongniart was a general account of the morphology of a large series of silicified seeds from the pebbles of Grand' Croix, near St. Etienne. Originally published in 1874*, this contribution was re-issued in 1881 with numerous beautiful plates some years after his death as a memorial volume†. Of seeds having what may be termed a Cycadean organisation, Brongniart enumerates seventeen genera, a number which has been increased since. In the years that have elapsed since Brongniart's time many of these forms have been elaborated in greater detail by his followers, especially Renault, and in rare instances it has been possible to produce adequate evidence for referring a certain number to the plants to which they belonged. To this day the great bulk of the French seeds found in the later Palæozoic rocks, as also the less numerous forms from the English Coal-Measures, are known as detached structures, and their real affinity is a matter of conjecture. Notwithstanding this limitation, that we know these seeds only as detached structures, so important a portion of the plant is the seed that a detailed knowledge of the organisation of fossil seeds cannot fail to be a useful adjunct in unravelling the intricate phylogenetic history of recent plants.

It was in connection with one of these fossils—*Stephanospermum*—that Brongniart

* Ann. Sc. Nat., Bot. 5^e sér. t. xx. (1874) pp. 234-265, pls. 21-23.

† 'Recherches sur les Graines fossiles silicifiées,' 1881.

re-discovered the pollen-chamber, a structure at that time not generally recognised in Gymnosperms *. This observation led to others upon recent Cycads, whilst some years later we have the suggestion of Renault that the simpler Gymnosperms possessed antherozoids †, a forecast amply justified by subsequent researches upon *Cycas*, *Ginkgo*, and other genera.

Perhaps no group of plants has ever travelled so rapidly to the forefront of botanical interest as have the Cycads. On the one hand, we have the great discovery of 1896 of the fact of their zoidiogamy, bringing the Gymnosperms into the closest relations with Pteridophytes. On the other, along the independent line of vegetative anatomy, Scott, co-operating in and continuing the investigations of Williamson into our Palæozoic fossil plants, has, through the Cycadofilices, shown the great probability of the Filicineous ancestry of the Cycads ‡. This progress in our knowledge of the Cycads themselves, as well as of the fossil fern-like forms which reach up to them, renders a re-examination of the fossil seeds a pressing necessity. Though the general organisation of these seeds has been made known, there remains much in which uncertainty prevails. In particular may be cited the precise relation of the nucellus to its integument, the details of nucellar structure, the fate of the pollen in the pollen-chamber, and so on. There is, of course, the chance—a remote one, seemingly—that some lucky section may reveal evidence justifying the reference of a seed to the plant to which it belonged.

Owing to the courtesy of Monsieur A. Roche, the Palæontologist of Autun, it has been possible for me to commence the investigation outlined above. M. Roche has with great liberality put at my disposition a considerable number of uncut pebbles from Grand' Croix as well as Autun. These, together with others which I have collected in both localities, form the basis of the present communication. Towards the cost of preparing microscopical sections of these fossils I am indebted to the Royal Society's Government Grant Committee for a grant in aid.

The present communication is restricted to a consideration of two seeds from the Stephanian of Grand' Croix and to the bearing of the facts elicited. These seeds are *Stephanospermum akenioides*, Brongn., and an apparently new seed which it is proposed to name *Stephanospermum caryoides*. Brongniart, in his 'Graines fossiles,' divided the silicified seeds into two groups:—(1) Those exhibiting bilateral symmetry, more or less flattened, and probably of Cordaitan affinity; (2) Forms with radial symmetry and sometimes provided with longitudinal ridges, wings, &c. It is to the latter group that these seeds belong.

In selecting *Stephanospermum* for first treatment I have been influenced partly by the fact that it was fairly abundant in the material at my disposal, but more particularly by the relative perfection of its preservation and the rather unusual characters of its organisation. In any case, a re-examination of *Stephanospermum* is appropriate on

* The pollen-chamber with pollen in it appears to have been first figured by Griffith in 1854 (Ic. Pl. As. tab. 378); see also Miquel, Journ. of Bot. vol. vii. 1869, p. 75. I am indebted to Sir William Thiselton-Dyer, K.C.M.G., for these references.

† 'Flore fossile d'Autun et d'Épinac,' pt. 2, p. 277.

‡ 'Studies in Fossil Botany,' Lecture xiv.

several grounds, whilst with the facts gained it may be possible to institute comparisons with other fossil seeds as well as with those of recent Gymnosperms. Taking first the general structure of *S. akenioides*, I shall proceed to a more detailed account of certain of its parts, and then, after describing the supposed new species, it will be possible to enter upon a more general discussion.

STEPHANOSPERMUM AKENIOIDES, Brongn.

General Structure.

The seed is ellipsoidal in form, circular in transverse section, and, so far as could be ascertained, possesses perfect radial symmetry, saving only in respect of the archegonia, which appear to be developed in one plane only. The longitudinal section represented in Pl. 41. figs. 1 A and B is quite typical. The whole structure is limited externally by a hard testa (*st.*), consisting largely of palisade-like stereides. This tegument, following the terminology of Brongniart, would be termed the endotesta, but, as there appears to be a layer internal to it, that term seems inappropriate. I shall speak of it as the sclerotesta, reserving the term endotesta for the more internally-placed soft layer. At the base of the seed the sclerotesta is relatively thick, and bears in median sections of good specimens a small papilla symmetrically placed upon its external surface (see Pl. 41. fig. 1 B, *pa.*). This is, no doubt, the point of attachment of the seed to the structure which bore it. At the papilla entered a delicate vascular bundle (*v.b.*) which, penetrating the testa, expands at the base of the nucellus into the basal tracheal plate (*t.d.*). From the horizontal part of the testa springs the nucellus, which appears to stand freely within the integument. Above the insertion of the nucellus the sclerotesta thins out to its normal dimensions. At the apex of the seed it tapers to a long sharp beak, which is perforated by a canal, the micropyle (Pl. 41. fig. 1 A, *m.*). At the base of this beak the testa expands into a circular collar or *crown* with sharp edge directed forwards (*c.*). The top of the seed, between beak and crown, is occupied by a circular perimicropylar trough.

Extreme length of seed from base to apex of beak 10 mm. Transverse diameter of seed at mid-height 4-4.5 mm.

Within the testa we recognise the nucellus standing erect and apparently free within it. Towards the apex the nucellus tapers and seems to end in a beak or canal which engages with the micropyle. Between the nucellus and the testa a space is present, broadest around the upper fifth of the nucellus. The apex of the nucellus (the upper $\frac{1}{5}$ — $\frac{1}{4}$) is the pollen-chamber (*p.c.*). It is cut off by a conspicuous transverse membrane from its main body, which was almost entirely filled with a prothallium. The whole nucellus is limited externally by an epidermis usually characterised by the carbonised contents of its cells (*ne.*). Of the tissue composing the nucellus little remains in the prothallial region. The megaspore by its enlargement has invaded and compressed the nucellar wall to such an extent that with one exception little is recognisable beyond the epidermis and a few flattened layers. The exception, and it is a notable one, is the tracheal mantle. The delicate bundle which enters at the chalazal end of the seed (Pl. 41. fig. 1 B, *v.b.*) expands into a wide tracheal plate, the margin of which is on every hand produced as a thin and

continuous mantle of spiral or scalariform tracheides. This mantle runs just below the epidermis of the nucellus, and reaches right up to the top of the macrospore. Here the tracheides pass into the lower region or extension of the pollen-chamber, paving its floor and lining its sides, but never penetrating to the upper portion or pollen-chamber proper. In the region of the pollen-chamber the lateral tissue of the nucellus is often preserved, forming an **S**-shaped pad of thin-walled, spindle-shaped cells right and left of the obtuse tapering apex (as seen in a median longitudinal section, *e.g.* in fig. 2, *sh.*). This tissue, however, dies out before the canal connecting the pollen-chamber and micropyle is reached.

At the junction of the nucellus and the narrow canal just mentioned there occurs almost invariably what at first sight appears to be a sort of collar folded down over the top of the nucellus like a small inverted funnel (Pl. 41. figs. 3 & 1 A, *co.*). The structure is very puzzling in all sections not ground to their ultimate fineness. It forms a characteristic feature in the Brongniartian drawings* like a pair of backwardly-directed antennæ, but no direct reference is made to it in the literature.

The macrospore is limited by a well-defined and fairly thick membrane in contact laterally with the attenuated residue of the nucellus; but at the apex always, and at the base frequently, it has undergone considerable contraction, so that in these regions it no longer follows the contour of the nucellus. In the living seed the base of the macrospore, no doubt, fitted on to the chalazal tissues; whilst at the apex it was convex, encroaching considerably upon what is loosely termed the pollen-chamber.

As regards the contents of the macrospore I have nothing to add to what is shown in Brongniart's figures. A prothallium more or less contracted from the wall is usually preserved (Pl. 41. fig. 3, *pr.*), and in lucky sections archegonia are found below the pollen-chamber (fig. 3, *ar.*). These seem to have been present to the number of two; and if this be really the case, the gametophyte alone in this seed exhibits bilateral rather than radial symmetry. But I was unable to settle this point by a critical section, such horizontal sections as have been obtained through this region being ill-served as regards the preservation of the prothallium. Though the egg-cell, which was large, and what is perhaps its nucleus, often shows as a striking cytological object (Pl. 41. fig. 3, *ar.*), no details of morphological value are recognisable.

Above is given in brief outline a general account of the more obvious features of the seed. I now pass on to speak in fuller detail of certain regions.

The Testa and the Chalaza.

Except at the chalaza and at the apex of the seed the sclerotesta has a uniform structure and thickness ($\cdot 33$ mm.). Externally there is a palisade-layer (Pl. 41. fig. 4, *p.*), in height about half the diameter of the sclerotesta. This layer is supported by a zone of short thick cells, whilst below these are several layers of fibres (*f.*) which run in the longitudinal direction. As a lining to the sclerotesta we find a well-marked layer of fairly large flattened cells with carbonised contents and clear refringent walls (*et.*). This

* 'Graines fossiles,' pl. 16. figs. 5, 8, &c.

layer, which may be termed the epithelioid layer of the sclerotesta, becomes continuous at the chalaza with the epidermis of the nucellus, and agrees with it in its histological characters (Pl. 43. fig. 21, *et. & ne.*). All the layers of the sclerotesta appear thick-walled and sclerotic, and all but the lining layer have brown cell-walls. The walls and contents of the former are often excellently preserved. The protoplasm is contracted away from the wall except at certain points where finger-like processes remained, as in fig. 22, which shows the ends of two sclerotic cells from the third layer from the surface. Fig. 23 represents another cell from immediately below the palisade-layer. In almost all the cells the nucleus appears to be represented by a dense body usually surrounded by a light contour. In the palisade-layer the preserved contents take the form of a long and often slightly sinuous filament with a local enlargement where the nucleus is contained (fig. 24, *n.*, also fig. 21, *lp.*). At the peripheral ends of these cells, with rare exceptions, and sometimes at their internal ends, the filament expands into a low, hollow, conical vesicle, the base of which is closely pressed against the limiting membrane (as at *v.*, fig. 24). More frequently we find at the internal ends paired finger-like processes (*p.*, fig. 24) which vividly recall pits. Occasionally, in the same position, there is a vesicle with a pair of short processes directed towards the cell corners. No doubt all these appearances were occasioned by the adhesion of the protoplasm to the wall, and it is difficult to resist the inference that a pitting of the end walls has been largely concerned in the production of the finger-like processes. But a detailed discussion of the matter would not be appropriate here. Palisade-cells are shown in transverse section in fig. 25. The apparent great thickness of the walls of the palisade and supporting cells of the sclerotesta is very probably exaggerated through preservation. The direction followed by the former is horizontal at the middle of the seed (where it is broadest); above this zone, and below, these cells gradually acquire an increasingly steep angle, till at the chalaza their course is parallel to the axis of the seed; whilst at the "crown" or perimicropylar ring they run up directly into this structure (*cf.* Pl. 41. figs. 1 A & B). The apex of the seed merits detailed description. The sharp ridge or crown which surrounds the micropylar beak is composed of an extension of the palisade-cells. The trough or moat which it contains is generally empty (figs. 1 A & B). Occasionally, however, the lining-surface of the trough bears a loose tangled feltwork of long filaments forming a brush inserted over the concave surface and reaching up to the micropyle (Pl. 41. figs. 2, 5, & Pl. 42. fig. 10). The component parts of the feltwork show little obvious indications of cellular structure. Two sorts of elements can be distinguished. First, there are indistinct remains of tubular cell-membranes much crumpled and distorted, and, mixed with these, filaments of extreme fineness, often following a sinuous course and occasionally expanding into small lenticular thickenings. Taken in conjunction with the normal type of preservation of the palisade-cells just described, the matted feltwork becomes intelligible. The membranes are the much-macerated walls, and the sinuous filaments the contracted contents of long cells or rows of cells. In some cases the membranous portion has been denuded away, and the tissue which once occupied the trough is represented by its protoplasmic contents alone. Of the original nature of this tissue it is difficult to judge. It may have consisted of tufts of real hairs, or of a spongy

thin-walled palisade, or perhaps of a succulent cushion. On the whole a delicate tissue seems indicated, for the filaments are rarely preserved although they occupy the most secluded position that the whole surface affords. The projecting rim may have been continued to the lip of the micropyle as a thin shell overlying a spongy tissue such as we know to have existed in *Ætheotesta elliptica* *. If so, the lid must have been caducous, as no indications of disintegration or splintering are found on the sharp edge of the crown. In these circumstances our seed must have presented a very close resemblance to *Ætheotesta*.

In this connection it is interesting to recall the fact that Renault has conjectured, from analogy with *Gnetopsis* (another seed from the same horizon), that the crown of *Stephanospermum* was the base of attachment of a plumed organ concerned in the dispersal of the seed †.

Whatever may have been the function of this micropylar organ, the fact is not without interest that the micropyle of this seed was more complicated than had previously been shown. Apart from the apex of the seed, no certain trace of a soft tissue external to the shell has been found. But, as it sometimes happens that even the hard sclerotesta of this seed shows evidence of superficial wear, it would be rash to conclude that a sarcotesta had not existed. From analogy with *Ætheotesta* ‡, *Trigonocarpus* §, and *Polylophospermum* ||, members of the *Stephanospermum*-group from the same horizon, the existence of such a layer is not wholly improbable.

As regards the lining of the integument, this layer of flattened cells with dark contents may be traced from the chalaza to the commencement of the micropylar canal. Here it seems to lose its characteristic appearance (*cf.* Pl. 43, fig. 29, and Pl. 41, fig. 4, *et.*), and is continued as an inconspicuous lining to the canal traceable with difficulty to the apex. That it was a sclerotic layer seems open to question.

The Chalaza ¶.—The base of the seed where nucellus and testa are confluent is not without interest. The sclerotesta in this region is much broader than elsewhere, due to the fact that the palisade-cells become about three times as deep here as elsewhere. At the centre, around the entering bundle with which these cells are parallel, they are undivided and have a length of .8 mm. (see Pl. 43, fig. 21, *lp.*), whilst further away from the bundle they are segmented into two or three storeys. Beyond, as we come level with the separation of sclerotesta and nucellus, the palisade-zone has become reduced to its normal proportions. Curved rows of short oblong cells of the same histological characters pass backwards from the chalaza and constitute the inner zone of the sclerotesta (see fig. 21, *st.*). Lying above the palisade-elements, and occupying the continuation of the plane of the gap between sclerotesta and nucellus, is a plate of not very thick-walled polygonal elements (*scl.*) stretching from the angle of confluence of the lining of the sclerotesta and

* Renault, 'Flore fossile d'Autun et d'Épinac,' pt. 2, p. 272.

† Cours de bot. fossile, vol. iv. 1885, pp. 184 & 186; also 'Études sur le terrain houiller de Commeny, Flore fossile,' pt. 2, 1890, pp. 669–670.

‡ Renault, 'Flore fossile d'Autun et d'Épinac,' pt. 2, p. 272, fig. 49.

§ Renault, *loc. cit.* p. 397.

|| Brongniart, 'Les Graines fossiles,' p. 28, and pl. C. figs. 6 & 7.

¶ Cf. Renault, 'Cours de bot. fossile,' vol. iv. pl. 22, fig. 1, & pp. 185, 186.

the nucellar epidermis, and sharing, in common with these two layers (with which it is continuous), the characteristic blackened structureless contents. Above this layer is a considerable zone of thin-walled parenchyma (*p.*), continuous in the peripheral direction with the hypodermal tissue of the nucellus. In the direction of the entering bundle this layer all but dies out, being intercepted by the longest of the palisade-cells of the sclerotesta in this region. Nevertheless it was probably continuous with the delicate one-layered parenchyma-sheath (or possibly phloem) which accompanied the tracheal strand into the seed. The layer of thin-walled parenchyma (*p.*) is very conspicuous in transverse sections of the seed cut in this plane, and occupies a large portion of such sections.

The tracheal bundle which enters at the little basal papilla is slender, and runs unaltered till the thick palisade-layer is traversed. In optical section it is found to be four or five elements across, each tracheal element being very narrow (10μ) and having rather close scalariform markings. A protoxylem was not detected. Level with the internal limit of the palisade it broadens out funnelwise, ultimately expanding into the broad tracheal plate, so usual a feature in the seeds of this period (*t.d.*). The elements composing the plate and the funnel are broad and short somewhat irregular tracheides (see Pl. 43. fig. 21, *t.d.*, and fig. 27), and they form a close plexus: $23\mu \times 40\mu$ are average dimensions. As the margins of the plate are approached the tracheides become longer and thinner and more regularly arranged, and as we draw level with the angle where the nucellus becomes free, the tracheal sheath has assumed the characters which, as regards form of elements, dimensions, and thickness, characterise it as a tracheal sheath or mantle enclosing the macrospore in its entirety. It is a continuous sheath without trace of local segregation into bundles. In the living seed the base of the macrospore rested on the tracheal plate, as indeed is often the case in the fossil. In the case rendered in the drawing (fig. 21), the spore-wall (*m.w.*) is withdrawn some little distance, and has carried with it residues of tissue. Not far above the level shown in fig. 21 the macrospore-wall is found in close contact with the remains of the nucellus (Pl. 41. fig. 7, *a*). Thus it appears that the delicate bundle expands into a thin but continuous sheath, which forms a complete investment to the macrospore; whilst the layer of parenchyma, which accompanies it into the seed after undergoing considerable augmentation below the tracheal plate, thins out and is continuous with the hypoderm of the nucellus.

The chalazal papilla (Pl. 41. figs. 1 B & 7) has a diameter of 120μ ; if this represent the full width of its attachment, the seed was doubtless pendulous. But it is premature to draw a conclusion until decisive evidence is forthcoming as to the existence of a sarcotesta.

The Endotesta.—For the existence of a layer interior to the sclerotesta adequate evidence exists. In Renault's figure of the chalaza * a delicate network of thin-walled cells is represented lying in the angle between the base of the nucellus and the lining of the sclerotesta, an observation confirmed by specimens that have passed through my hands. Unfortunately this network of cells is rarely preserved so as to make it possible to determine whether it was continuous with the tissues between which it lay. In the

* Renault, 'Cours de bot. fossile,' vol. iv. pl. 22. fig. 1.

majority of specimens this layer is represented by a structureless fold with occasional traces of cellular structure preserved in it. Thus in the median longitudinal section of the seed shown in Pl. 41. figs. 1 A & B the remains of what seems to be such an inner layer are represented by the light shade (*end.t.*) between nucellus and sclerotesta. In the right-hand half of the seed the shading is continuous from the apex of the nucellus to the chalaza, and for a large part of the distance is in contact with the sclerotesta. On the left-hand side of the nucellus a similar condition obtains, though the continuity of the layer in question is less perfect.

In Pl. 41. fig. 3 a similar fold is seen in contact with the sclerotesta lying to the left of the nucellar beak at *end.t.* A portion of this layer (*cc*) has become separated from the main part by a longitudinal fissure and lies near the pollen-chamber wall; lower down, however, this detached part is continuous with the main fold (*i.e.* with the downward prolongation of *end.t.*). Again, in Pl. 42. fig. 13, from a somewhat younger seed, the endotesta is well shown at *end.t.*—here evidently displaced from its continuity with the sclerotesta. This preparation demonstrates, perhaps better than any other, that the endotesta was continuous with the sclerotesta. Its relations with the nucellus are obscure, but no positive evidence of its continuity with the nucellar surface has been found. The point is one of some interest, as upon it depend the relations of nucellus and testa, whether free as in *Lepidocarpon* or joined as in *Cycas*. On the whole, I incline to the former view, which is embodied in the attempted restoration given in text-fig. 1, p. 372.

The Nucellus and Pollen-chamber.

Apart from the pollen-chamber and adjacent regions, in which the main interest centres, there is little to be said about the nucellus. As in so many gymnospermous seeds of corresponding age, its whole proximal portion has become transformed into a mere pouch for the accommodation of the large solitary macrospore. We rarely find preserved (restricting ourselves to the prothallial region) more than (1) the epidermis of thick flat cells with blackened contents; (2) a narrow zone within the epidermis, the elements of which are flattened and rarely recognisable; (3) the tracheal mantle of delicate tracheides with close-wound spiral and scalariform thickenings. The inner limit of the tracheal zone abuts almost directly on the thick wall of the macrospore. The hypoderm is continuous with the parenchyma at the chalaza, and in the best specimens it is evident that it consists of several layers of cells which have become flattened upon one another. The tracheides are of various length and have an average diameter of .01 mm. They are not readily seen in the nucellar wall, except in the very thinnest sections. When this condition is fulfilled the tracheides are found to be present in extraordinary abundance in all parts of the wall. In the aggregate they form a continuous mantle, two or three deep, from the chalaza to the pollen-chamber, and there is little doubt that they closely invested the top of the macrospore in the same way in the living seed (*cf.* text-fig. 1). Thus we find in this seed (and doubtless in some of the allied forms) a complete isolation of the inner parts of the nucellus, with the macrospore and prothallium therein contained, by a continuous sheet of tracheides. Two photographs in illustration of these tracheides

are appended. Pl. 42. fig. 8, from the upper part of the prothallial region, is from a section slightly tangential in plane. Above, it shows the tracheides in the nucellar wall (*tr.*); below, where the macrospore-wall (*m.w.*) curves away to form the floor of the pollen-chamber, we see the greater portion of the tracheides lying against the nucellar wall (*tr.*¹), a thin layer only remaining against the macrospore (*tr.*²). Pl. 41. fig. 9, on the other hand, is a completely tangential section taken at the junction of the prothallial and pollen-chamber regions. Its plane is that running obliquely down from *a*, fig. 10. At the bottom of the figure 9 the macrospore-wall is seen cut through (*m.w.*). Rising up above this for a distance of some 15 mm. (in the figure) a compact sheet of almost parallel tracheides is seen. Here they are emerging into the lower region of the pollen-chamber (supra-archegonial gap). The blank in the middle of the photograph is due to the fact that the tracheides run in a convex plane and consequently emerge from that of the section. On the flanks, however, the tracheides can be traced with little interruption till they disappear under the arching side of the pollen-chamber. The tattered cells (*ep.*) along the top and sides are the epidermal cells of this part of the pollen-chamber.

The Pollen-chamber.—We now pass on to speak more particularly of the *Pollen-chamber*. This term is rather loosely applied to the dome-shaped space occupying the distal extremity of the nucellus. In a typical case with fair preservation—as, for instance, that illustrated in Pl. 41. fig. 2—immediately upon the horizontally stretching upper portion of the macrospore-wall (*m.w.*) is a broad space contained laterally by the thin nucellar wall and tapering to an angle which lies just above the sudden curve of the macrospore-wall. Above, it is roofed over in part by a septum, of which the middle parts are wanting (*s.*). Through the broad opening where the septum is incomplete the lower space communicates with another space which occupies the apex of the nucellus. This upper chamber is the pollen-chamber, and it is here that the pollen is found; the lower chamber (*s.a.g.*), whose form approximates to that of a frustum of a sphere, is empty, except that the floor and sides are littered with tracheides with spiral thickenings. The distribution of these tracheides and their relative abundance vary from specimen to specimen. Sometimes the sloping sides of the space are plastered with them as in fig. 11, whilst on the floor there is but a sparse scattering of tracheal fragments and drawn-out spirals; or the reverse may be the case; or, finally, approximately equal shares may occur on floor and sides. In no case, however, do the tracheides extend beyond the septum. The tapering corners of the space are generally loosely filled with mutilated tracheides (Pl. 42. fig. 12, *tr.*), the actual angle of the space tapering down into that zone of the nucellar wall which is occupied by the tracheal mantle. The obvious inference to be drawn from the foregoing is that the space did not exist at all in the earlier stages of development in the living seed, and that it has been produced by the withdrawal or contraction of the top of the macrospore from the septum (or true floor of the pollen-chamber). The top of the macrospore was, no doubt, at an earlier stage overlaid with a tracheal covering which was merely a part of its general tracheal sheath or mantle (shown in the restoration, p. 372). It is the tracheal covering in this region that has become split, and the space merits the name of schizotracheal gap. The form and curvature and the occasional rupture of the macrospore-wall here are in

entire harmony with such a view. Whether the development of this space (or supra-archegonial gap) occurred naturally in the living seed, or whether it only occurred on the death of the seed previous to mineralisation, will be discussed below.

The true pollen-chamber is flanked by a considerable wall of nucellar tissue (Pl. 41. fig. 2, *sh.*) which is sometimes admirably preserved. The cells of this lateral cushion or *shoulder* are spindle-shaped, thin-walled, and unpitted, their long axes parallel to the slope of the wall (Pl. 42. fig. 11). The surface of this cushion abutting upon the pollen-chamber is always ragged and its condition indicates that the deeper-lying tissues have broken down. The roof of the chamber consists of a stratum of collapsed and blackened cells in which it is difficult to make out any structure. The degree of preservation of the shoulder varies from seed to seed. Sometimes, as in fig. 5, the ill-preserved remains of a tissue are seen, whilst occasionally (Pl. 41. fig. 1 A) maceration has proceeded much further. In sections which are cut at some distance from the median plane of the seed, *i. e.* tangential sections of the pollen-chamber, the shoulder appears to reach further into the pollen-chamber than is really the case (Pl. 42. fig. 12). Between such sections and cases like that represented in Pl. 42. fig. 13 a distinction must be drawn. In the latter, which, though slightly tangential, is not really very far from the median plane, the pollen-chamber is actually very small, and a great deal of nucellar tissue remains, not only at the sides, but below the chamber as well. This seems to indicate that we have here a somewhat younger stage in development. The supra-archegonial gap (*s.a.g.*), too, has less vertical development than in the majority of cases, whilst the splitting in the tissues to which the gap is due does not appear to have occurred quite normally. The plane of cleavage appears to have developed nearer the macrospore-membrane than usual, for (1) fragments of this membrane have remained behind on the nucellar tissue; (2) the cleft at the lateral angles is nearer the macrospore than we usually find, *i. e.* at the angles (it is the same on the right as on the left) the plane of cleavage lies below the tracheal sheath, instead of along it (*cf.* Pl. 42. fig. 13, *xx* show the plane of cleavage at two spots).

Comparing the manner of separation of the macrospore from the floor of the pollen-chamber in younger and older specimens, it appears that whilst in the usual later stages, which form the great majority of those found, the tracheal mantle itself was the fissile layer, in the younger stage (Pl. 42. fig. 13) there is a relatively greater cohesion between the tracheides than is the case later on. The macrospore in contracting and forming the supra-archegonial gap in these younger stages breaks away from the tracheal sheath altogether. From this it may be inferred that as development proceeded the tracheal mantle became more fissile, *i. e.* its elements in this region probably underwent a gradual solution prior to fertilisation. When, however, the macrospore separates locally from the nucellar wall along the sides or below, the fissile layer is not the tracheal mantle but the zone immediately within the mantle—precisely as in the younger stage (fig. 13). The normal condition of preservation is perhaps a result of the splitting of the tracheal layer in this softened condition. The solution of the tracheides had as a probable result the promotion of fertilisation. The actual production of a supra-archegonial gap may be regarded as a post-mortem change.

The Nucellar Beak.

The pollen-chamber is surmounted by a long canal which engages distally with the micropyle. At its base of insertion on the broader part of the nucellus this canal widens out into an inverted funnel, which overlies the pollen-chamber; but in thin median sections this funnel always presents the appearance of being detached from the wall of the pollen-chamber (Pl. 41. fig. 1 A, *co.*, and Pl. 43. fig. 29, *co.*). The tubular part of this structure is evidently perforated (fig. 29), whilst in fig. 3 a local swelling is shown (*p.g.*), due to a contained pollen-grain which has failed to reach the pollen-chamber. At the base of the tube the section falls just outside the cavity; higher up, the lumen is laid open (Pl. 43. fig. 29, from just above *b* to beyond *m.*), finally the surface of the tube comes into the section showing two long rectilinear cells with carbonised contents (Pl. 41. fig. 1 A, from the same preparation as fig. 29).

The funnel or collar is due to the sudden spreading of the sides of the tube above the pollen-chamber. It is one cell thick, and ends suddenly and always in the same way (Pl. 43. fig. 29, *xx*, also Pl. 41. figs. 2, *co.*, & 3, and Pl. 42. fig. 15 *). This was evidently the case in the specimens described by Brongniart†, though his figures are not highly magnified. The cells of the collar appear thick-walled and their contents strongly carbonised. Preservation ceases abruptly at a distance of about 4 mm. from the insertion of the tube and apparently in the middle of a cell (see fig. 29, *xx*). From this spot the collar is continued in the form of a structureless residue traceable down the flanks of the pollen-chamber for varying distances, and sometimes to the base of the seed where the space between the nucellus and sclerotesta dies out. This smear-like continuation of the collar is shown in Pl. 41. figs. 1 A (*end.t.*) and 3. In another specimen (not figured) traces of cellular structure are apparent in the residue.

The roof of the pollen-chamber immediately below the collar has all the appearance of a tissue without its delimiting layer (Pl. 42. fig. 14); *i.e.*, the collar is in all probability the missing epidermis which has become detached from the apex of the pollen-chamber. If this be the right interpretation, it follows that the true apex of the nucellus is beak-like and engages with the micropyle, whilst the tubular cavity of the beak is the entrance to the pollen-chamber. This view is corroborated by the specimen represented in Pl. 41. fig. 6. This section is as nearly as possible median. The distal portion of the beak had undergone maceration prior to mineralisation, but traces of several pollen-grains which it contained are present in the micropyle (but not shown in the photograph). Of the funnel or collar, three fragments are present in the section and are distinctly visible just above the pollen-chamber. Of these fragments the two on the right are detached portions of cells of the same character as *co.* in fig. 1 A. The third fragment, shown as a tooth at the apex, is *in situ*; it has not been drawn away from the subjacent tissues.

Figure 3, from another specimen, lends itself to interpretation in the same way. Here the epidermal layer of the pollen-chamber (*e., e.*) is continued up to the level from which the collar (*co.*) has been drawn away.

* Figure 15 should be examined with a hand-lens.

† 'Graines fossiles silicifiées,' pl. 16. figs. 4, 5, 7, & 9.

The reason for this severance of the beak and collar from the nucellus is to be sought probably in the fact that the nucellus underwent contraction on the death of the seed. The beak being trapped in the micropyle, with which it closely engages (Pl. 41. fig. 1 A), was unable to follow, consequently rupture occurred immediately below its insertion. The remarkable similarity to which attention has been drawn, between the detached collars of different specimens, may be interpreted as an indication of identity in the area over which the induration of the epidermal cells in this region spread. The whole phenomenon

Text-fig. 1.

Partial restoration of *Stephanospermum akenioides*, Brongn.

Showing the relations of nucellus and integument, the nucellar beak, and intact tracheal mantle.—*scl.t.*, sclerotesta; *end.t.*, endotesta; *m.*, micropyle; *g.*, gap between nucellus and testa; *n.e.*, nucellar epidermis; *nb.*, nucellar beak (indurated); *p.c.*, pollen-chamber; *sh.*, shoulder of pollen-chamber; *t.d.*, tracheal disc; *t.m.*, tracheal mantle; *t.m.'*, position in which schizotracheal gap developed on death of seed; *m.w.*, macrospore-wall; *a.*, archegonium. The spongy tissue of the trough is not shown.

seems to accentuate the fact that the epidermis at the apex of the nucellus was peculiar and coherent, recalling the apical patch of a Marattiaceous sporangium or Cycadean pollen-sac.

In this connection there is one peculiarity of preservation that requires a word of explanation. Reference has been made to the apparently structureless continuation of the collar (shown in Pl. 41. figs. 1 A, 3, and Pl. 43. fig. 29) which is occasionally to be traced to the base of the seed. Actually this continuation is not a portion of the collar at all—that is to say, the structureless residue does not indicate that a continuous stripping

of the nucellar epidermis has occurred, as the latter is often recognisable still clothing the nucellus within the former.

The origin of the appearance in question seems due to the fact that when the nucellar cap was detached its broken rim became involved in the more or less macerated remains of a soft layer (the endotesta) lying between the nucellus and sclerotesta. The apparent continuity of the two structures is a secondary effect.

In the adjacent text-fig. 1 the various regions of *Stephanospermum* are represented in the relation it may be supposed they occupied in the living seed. The endotesta is represented as a lightly shaded lining to the black sclerotesta. The apical beak and collar are restored to their original position upon the top of the pollen-chamber, the probable induration of their walls being emphasized by heavier shading. Finally, the supra-archegonial gap is not represented, as its origin seems due to post-mortem fission in the tracheal sheath above the embryo-sac; this sheath is therefore shown intact.

. STEPHANOSPERMUM CARYOIDES.

General Remarks.

This seed is represented by a solitary specimen which was wholly embedded in a large pebble from Grand' Croix. The block, which had already yielded a specimen of *S. akenioides* at the surface, on being broken in two in the search for other seeds was found to contain a large almost globular seed. It has been possible to obtain four complete longitudinal sections, all including the nucellus, together with some fifteen other sections through various parts. The seed is a very interesting one and apparently new; fortunately the preservation is above the average and it is possible to give a fairly full description.

Generally speaking, the relations here are as in *S. akenioides*, the chief differences being the greater size, the near approach to a globular form, and the abbreviation of the micropylar beak and peri-micropylar crown. A further point consists in the apparent strong retraction of the nucellus from the testa, so that a considerable space is left between the top of the pollen-chamber and the internal limit of the sclerotesta.

These relations are evident on glancing at the diagrammatic representation of a nearly median longitudinal section of this seed (text-fig. 2, p. 380).

The dimensions are $15\frac{1}{2}$ mm. long $\times$ $12\frac{1}{2}$ mm. across.

The transverse section is circular, judging from the form of the seed when exposed.

The sclerotesta has essentially the same structure as in *S. akenioides*, *i. e.* a peripheral palisade-layer and internal longitudinal layer of thick-walled cells. Internally it is defined by the usual cubical layer with carbonised contents. At the micropylar end the beak and trough of *S. akenioides* are represented by a depressed, circular, convex area, which, like the corresponding region in that seed, bears a feltwork of closely packed hairs or fibres. This region is represented in almost median longitudinal section in Pl. 44. fig. 36. The fibrous covering of the micropylar convexity seems to have a tufted insertion, bunches of hairs arising from distinct spots on the surface of the sclerotesta. Individual hairs are occasionally articulated and branched, as shown under considerable magnification in Pl. 44. fig. 37. The length of hair preserved in this seed is short, as compared with

S. akenioides (·65 mm. in *S. caryoides*, 1·6 mm. in *S. akenioides*). This difference probably corresponds with a difference in actual life in conformity with the absence of a micropylar beak. That the tuft represents a hairy plume seems improbable; its structure suggests a fibrous cushion, when some organ, now lost, may have been attached to the seed. Though there is no evidence to show that the surface of the seed was covered by a fleshy sarcotesta, there is nothing inconsistent with such a view should it seem probable from analogy with other seeds of like organisation. In this connection, however, see the remarks concerning *S. akenioides* (p. 366). The base of the most nearly median of the sections does not, unfortunately, coincide with the entering bundle, but there is no reason for supposing it to have departed materially from the type.

Endotesta.

A Layer within the Sclerotesta.—Of the existence of an endotesta beneath the sclerotesta there are some traces. There are, lining the carbonised epithelioid layer of the sclerotesta, definite traces of a thin-walled tissue (text-fig. 2, *end.t.*). These fragments are of the nature of a flattened macerated cell-reticulum, which appears to have been continuous with the epithelioid layer of the sclerotesta, but the discovery of additional specimens must be awaited before it is possible to speak confidently of the nature and extent of the endotesta in this seed.

Nucellus.

The *Nucellus* stands up freely from the base of the seed with a wide space between it and the sclerotesta. It shows the usual segmentation into prothallial and pollen-chamber regions. The embryo-sac is nearly globular, there being but a trifling difference between the transverse and vertical diameters. The pollen-chamber region is also broad and large, but its height, though actually exceeding that of the corresponding structure in *S. akenioides*, is, relative to the height of the whole nucellus, less than in that species. Here it is about $\frac{1}{7}$, in *S. akenioides* about $\frac{1}{5}$ of the whole. The summit of the nucellus tapers suddenly, *i. e.* into a short apiculus, the actual extremity of which is not, unfortunately, included in any of the sections. Consequently it must remain a matter for later determination whether the nucellar beak ended approximately as shown in Pl. 42. fig. 17 (at *a*), as seems probable, or whether it was continued further in the direction of the micropyle. The curved sides of the pollen-chamber are included in a well-marked epidermis consisting of cubical cells on the flanks, but becoming more columnar as the insertion of the beak is approached. This is well shown in Pl. 44. fig. 38, a faithful rendering of the top of the nucellus under a magnification of 65 diameters. The pointed summit is therefore surrounded by a circular zone of enlarged columnar epidermal cells suggesting the annulus in one of the Schizæaceæ. The sloping sides of the pollen-chamber are very well preserved in this seed, and consist of thin-walled, spindle-shaped cells, well shown in Pl. 42. fig. 17 and in more detail in fig. 18. The long axes of these cells converge towards the apex. The walls show occasional pitting, and in the parts adjacent to the macrospore a folding of the walls, as of a tissue which had lost its turgidity previous to fossilisation. The dome-shaped cavity of the pollen-chamber is

well-defined and symmetrical, its limits being marked out by the remains of its broken-down cells which had become absorbed in the excavation of the cavity. It is in this peripheral mucilage, especially, that the pollen-grains are found preserved. Their position, in a number of cases, is shown in text-fig. 2, *p.*, *p*², &c., whilst some are visible in Pl. 42. fig. 18. To this matter we shall return on p. 379. Of the cleft or gap below the pollen-chamber, so conspicuous a feature in *S. akenioides*, relatively small trace is found. A certain amount of splitting there has been, and the remains of the septum may be seen at *s.* (Pl. 42. fig. 18); the smaller photograph (fig. 17), with a hand-lens, shows it on the right-hand side as well (see also text-fig. 2, *s.a.g.*). The splitting is of the same nature as in *S. akenioides*, but less in degree. The floor of the supra-archegonial gap is practically destitute of tracheides, as are the sloping sides of this space, but the significance of this point of difference will be considered below. The main portion of the nucellus is, as usual in seeds of this period, reduced to a sheath or pouch enclosing the large macrospore. Similarly, an epidermis—well-defined, though at places detached from the nucellus—is present; at the chalaza it becomes continuous with the epithelioid lining the sclerotesta (text-fig. 2). As stated above, though the entering bundle is not included in any of the sections, there is no reason for supposing that it differed from that of *S. akenioides*. In the chalazal region of the nucellus there are ample remains of an extensive tracheal plate, the margins of which are continued up the nucellus as an unbroken sheath of tracheides, traceable up to the insertion of the sides of the pollen-chamber (text-fig. 2, *b*). The layer of tracheides lies just within the surface of the nucellus; between it and the epidermis are the compressed remains of a soft peripheral layer. In other words, the relations here are essentially as in the allied species. At one spot near the chalaza a large fragment of the nucellar wall has splintered away and been drawn into the cavity of the embryo-sac (Pl. 42. fig. 17, *f*). This is repeated in all three of the more median sections and is not due to shattering. The fragment of the macrospore and nucellar wall was evidently displaced anterior to mineralisation and in this position it has become embedded. The tracheides of this splinter have become somewhat fretted out and are in some degree isolated. They are unusually large and well preserved, and form most beautiful microscopic objects. Pl. 44. fig. 39 shows a group, whilst two of the tracheides are represented in Pl. 42. fig. 19. The rib-like thickenings of the walls show an unusual perfection of preservation. Occasionally the scalariform type gives place to a reticulated thickening as in fig. 39.

The average diameter of these cells is 20μ , so that they are much larger than in *S. akenioides* (where the diameter is about 14μ). This type of tracheide forms a continuous sheath of closely packed elements in the nucellar wall, some three deep, traceable to the insertion of the pollen-chamber, where they die out (text-fig. 2, *b*). It may be conjectured that on the top of the embryo-sac they have been absorbed, a change which, apparently, likewise took place in *S. akenioides* (*cf.* p. 370), where in older seeds they are sometimes less easy of observation and occasionally wanting altogether. That the solitary specimen of *S. caryoides* corresponds to a stage slightly older than the commonly occurring type of *Stephanospermum* there is good reason to suppose (*cf.* below, p. 387).

THE STRUCTURE OF THE POLLEN.

This part of the subject has been reserved for special consideration, and the observations drawn from the two species of seeds are given consecutively.

(1) *Pollen of Stephanospermum akenioides.*

In almost every pollen-chamber of this seed the characteristic pollen, so often mentioned by Renault, is present. These grains are usually congregated together in the apex of the chamber, as in Pl. 41. figs. 2, 3, 6, and Pl. 42. fig. 15. It is only exceptionally that a grain has been drawn down to the level of the diaphragm (*d.*) (as in fig. 3, *p.*¹) or below it, as with the isolated abortive grain (*p.*²) in the same photograph. The majority of the grains are large, possessing average dimensions of $160\ \mu \times 100\ \mu$, whilst occasional grains reach a length of $200\ \mu$ or even $210\ \mu$ (figs. 6 & 15). With these larger grains others of the same type are present, having an average length of $100\ \mu$. These may be regarded as grains which have failed to develop after reaching the chamber. In but a solitary instance has foreign pollen been found in the chamber. This case is illustrated in fig. 15, where, in addition to the large normal pollen-grain, two small grains are seen lying in the apex of the chamber just above it, whilst a third overlies its left-hand extremity. The upper left-hand grain shows a longitudinal furrow and is doubtless "foreign"; so, too, is its right-hand neighbour, but referable to the Cordaitan type; the third little grain is of the same nature. All these foreign pollen-grains seem to agree in remaining abortive, contrasting in this respect with the true pollen of *Stephanospermum*, which has undergone further development in this pollen-chamber.

The normal pollen shows an external finely granulated or sculptured coat, the exospore, whilst the contents are divided into a tissue of many cells. In this point of the multicellular nature of the pollen, concerning which there has been some question, I find myself in complete agreement with Renault, who described the grains in his 'Cours de bot. foss.' vol. iv. p. 185, and has adhered to his interpretation consistently ever since. The internal cells line the exospore everywhere, and surface views of the grains show the whole area mapped out by this internal tissue as in Renault's figures *, and here in Pl. 42. fig. 15 and in fig. 14, *p.*

A study of sections of the grains confirms the conclusions obtained from surface views. Pl. 42. figs. 14, *p.*², and 16, *p.*², represent a section of the same pollen-grain cut at right angles to its major axis. Here we are looking into the grain without the intervention of the surface, *ex.* (fig. 16) being the cut edge of the exospore. Within the grain, which is unusually well-preserved (fig. 16, *p.*²), a system of three convergent radial walls is evident. The internal organisation of this grain is further elucidated in Pl. 43. figs. 30 and 31. Fig. 30 is a view of the cut surface magnified about 180 diameters. The cut edge of the exospore (*ex.*) is seen as in fig. 16, and the three radial walls *a*, *b*, and *c*; traces of two more, *d* and *e*, are also discernible. Fig. 31 is an optical section of the same grain from a deeper plane and shows the walls *a*, *b*, *c*, and *d* as complete membranes, whilst *e*

* Notice sur les travaux scientifiques de M. B. Renault, 1896, pl. 6. fig. 8; Cours de bot. foss. iv. pl. 21. fig. 9.

is broken. From a study of this and similar preparations it would appear that there were about five rows of wedge-shaped cells disposed symmetrically about the longer axis of the grain. Turning now to a longitudinal section of a grain, we may consider in detail that marked *p.* in Pl. 41. fig. 6. The details are fully illustrated in Pl. 44. figures 32, 33, and 34. This grain is not cut in actual longitudinal section, but it is very nearly so. Figs. 32 and 34 represent the grain as seen from above and below respectively. The exospore (shaded) and its cut edge are evident in both figures, as also are the remains of the internal system of cell-walls, laid open by the section. Fig. 33 represents an optical section lying between the views rendered in figs. 32 and 34. Here are shown some eight cells lying around a central space (*c*) in which rests a dark nucleus-like body (*n*). The walls of the lining cells here show a copious perforation (as at *w*, fig. 33).

Another longitudinal section is represented in fig. 35, a drawing of pollen-grain *p.*³ (Pl. 42. figs. 14 & 16). As before, the cut edge of the exospore is shown (*ex.*) with traces of the internal cells (*c, c*), whilst in the middle of the figure is a spider-like body (*cb*), no doubt the same as *n* in fig. 33, but better preserved and also more typical—at any rate in the sections which have passed through my hands. The relation of the “legs” of the “spider” to the peripheral cells is suggestive, whilst at one place (*b*) the central body is continuous with the membrane.

The interpretation which may be placed on all these appearances (*i. e.*, those shown in figs. 30 to 35) is as follows:—The pollen-grain contains some five rows of internal cells (making some twenty cells in all), somewhat wedge-shaped in form, with the tapering apices of the wedges directed inwards. These cells, prior to mineralisation (whether in life or death is uncertain), underwent a certain degree of separation from one another at the centre, a separation which involved a fracture of the walls in that region. In this way there was left behind a sort of replum, which has been compared to a nucleus in fig. 33, and to a spider in fig. 35. This replum is far from uncommon. The transverse section (Pl. 42. fig. 16, *p.*², and Pl. 43. figs. 30 & 31) is perhaps not cut quite across the equator of the grain, but may coincide with a plane a little nearer one pole, as indicated at *d*, fig. 35. Finally, the pollen-grain *p.*¹, in fig. 14, is cut in transverse section, the transverse zone corresponding to that which would be included between the planes *e* and *f*, fig. 35. This section, according to the focal plane examined, shows either a free spider-like body or a condition of affairs resembling figs. 30 and 31. It thus removes all doubt as to the nature of the central body or “replum,” which consists of the coherent internal margins of the septa.

Recently, M. Renault * has directed attention to the pollen-grains of *Stephanospermum akenioides* and *Ætheotesta*. In both cases the grains are similarly organised, *i. e.*, many peripheral cells surrounding a central space, which often contains a nucleus-like body. In the case of *Ætheotesta* the grain is described. To quote the passage †:—“Celles-ci” (*i. e.*, the peripheral cells) “paraissent groupées assez régulièrement autour d’une cellule

* “Sur quelques pollens fossiles,” Soc. d’Hist. nat. d’Autun, Séance du 13 juin, 1901. “Sur quelques Cryptogames hétérospores,” *ibid.*, Séance du 22 sept., 1901.

† From the paper of Sept. 22, 1901, p. 7.

axiale tardive, où se trouve un noyau ? mal défini, appartenant peut-être à un Anthérozoïde. Dans la région polaire on remarque un bourrilet circulaire *t.p.* *, se prolongeant en un tube court et représentant les restes d'un tube pollinique ; autant qu'on en peut juger par transparence, ce tube serait en relation avec la cellule axiale." And further, " Il ne serait pas invraisemblable que les gros grains de pollen des *Stephanospermum* et des *Ætheotesta* aient ainsi produit un tube pollinique permettant la sortie des Anthérozoïdes emprisonnés dans une enveloppe épaisse et résistante."

In regard to *Ætheotesta* no comment is called for here, as this seed has not come under my observation. As regards *Stephanospermum akenioides* I have described in detail the critical preparations. That the body in the central space is nuclear in nature seems open to question, as indeed does the cellular nature of the space itself. It would seem possible that M. Renault may have had under observation pollen-grains of *Stephanospermum akenioides* sharing a condition of preservation corresponding to that represented in Pl. 44. figs. 32, 33, & 34. This, taken in connection with a tube-like orifice attached to one pole in the case of *Ætheotesta*, obviously suggested the inference which M. Renault draws, evidently with some reserve.

It may be pointed out that papilla-like outgrowths are not infrequent on the pollen-grains of *S. akenioides*, but they are not localised to a pole or any other spot in particular. One such is readily seen with a hand-lens on the lower side of the large pollen-grain in fig. 15. Another is present on the same grain immediately behind the foreign pollen-grain, and, of course, not shown in the photograph. The length of these little tubes does not exceed 20–25 μ . Whether they be mere accidents of preservation or the simple pollen-tubes of unspecialised multiple pollen-grains must remain, for the present, an open question.

Some allusion has been made to the perforation of the dissepiments in the interior of the pollen-grain. That they were abundant is seen from fig. 33, *w*. The raggedness of the walls cut in section, both here and in figs. 32 and 34, is due to the same cause. That these perforations are in any way connected with the liberation of possible antherozoids, can only be a matter of conjecture. The contents of the cells are not preserved in any of the specimens of *S. akenioides* that have passed through my hands. On the other hand, the fenestration of the walls may be readily conceived as the result of post-mortem, bacterial, or other destructive agency. Perforations of that kind are common enough in cuticularised epidermal membranes, parenchyma, &c. in the Grand' Croix pebbles. It is quite possible that in this species the seeds are preserved at a stage anterior to that at which antherozoids were liberated. But in any case the perforation of these internal walls is not wholly intelligible on any hypothesis of dehiscence ; for, in addition to actual tubes, large openings are found in the outer wall of the grain, quite adequate for the exit of antherozoids. These have been figured by Renault † for *Dolerophyllum*, and attributed by him to bacterial agency ; those produced here are in essential agreement. The only inference that can be safely drawn respecting the holes in the internal walls is that the walls of the pollen-grain complex were readily destructible,

* This refers to a figure showing a pollen-grain bearing a small excrecence at one pole.

† 'Flore fossile d'Autun et d'Épinac,' p. 269.

and adapted to freeing antherozoids if the necessity arose. In old-looking and probably much macerated pollen-grains, such as are occasionally to be observed, the whole system of internal walls appears to have broken down, leaving (in the rarest instances) what may possibly be small complexes of secondary cells. It is possible that here we have an indication of the formation of antherozoid mother-cells in considerable number in each. However, adequate data are lacking for a satisfactory hypothesis in this species. The subject will be alluded to again on p. 385, when dealing with *Stephanospermum caryoides*.

Renault has concluded that the pollen in this, as in other cases, underwent considerable growth in the pollen-chamber where it matured. He compared the dimensions of *Stephanospermum* pollen scattered in the matrix with that in the pollen-chamber, and infers a growth of about one third*.

As already stated, I have found numerous abortive grains present with the normal large grains in the pollen-chamber, and also, in certain cases, grains that have remained trapped in the micropyle.

I append a summary of the dimensions of these various grains, which wholly corroborates the view of M. Renault:—

Pollen-chamber shown in

Fig. 3	Average length of three normal grains in the pollen-chamber .	180 μ .
Fig. 3	Ditto of five abortive grains	100 μ .
Fig. 6	Average length of three normal grains in the pollen-chamber .	150 μ .
Fig. 6	Ditto of five trapped in the micropyle	66 μ .
Fig. 2	Length of largest grain	200 μ .
Fig. 15	Length of the large grain	210 μ .
General average of length of pollen-grains of this species scattered in the matrix . . .		60 μ .

(2) *Pollen of Stephanospermum caryoides.*

In the pollen-chamber of this seed eight pollen-grains or portions of pollen-grains have been found. They occur either attached to the lining of the chamber or very near to it. For convenience, the positions of seven of these bodies are represented in text-fig. 2, p. 380 (*p.-p.⁶*), as though they all occurred in a single section. They are really present in three sections, but for convenience of reference they are projected on to one plane. The eighth grain, which shows nothing, has not been included. The whole of these bodies appears to belong to one sort of pollen, a conclusion based on the dimensions of the various parts and on the nature of the sculpturings of the exospore; and as they show various developmental stages, and none of them is abortive, it is exceedingly probable that these grains really belong to the seed in the pollen-chamber of which they occur†.

Of the bodies mentioned, two are complete pollen-grains; the rest, fragments apparently in various phases of development. *p.* and *p.²* (text-fig. 2) are pollen-grains; *p.¹*, *p.³*, *p.⁴*, *p.⁵*, and *p.⁶* isolated internal cells of pollen-grains.

* 'Cours de botanique fossile,' vol. iv. p. 185.

† Unfortunately a second specimen is not available to test this assumption.

(a) *Complete Pollen-grains*.—The external features are shown by the grain $p.^2$ (text-fig. 2, and Pl. 44. fig. 42). It is oval and evidently flattened in the plane of the section. Its dimensions are $91\mu \times 72\mu$. Its area is divided into a peripheral gently convex region and a central strongly convex boss. Both the wing-like periphery and the central boss are sculptured. The former is marked with radially running lines, the latter with a reticulated sculpturing (fig. 42, $p.^2$). The grain is marked with a triradiate slit (fig. 42, $tr.s.$) on the convex central region, possibly an indication of its origin as a member of a tetrad.

Text-fig. 2.

Median longitudinal section of *Stephanospermum caryoides*.

Outside is the integument or sclerotesta ($st.$), with its epithelioid lining ($et.$); within it, fragments of the endotesta ($end.t.$) are represented; $m.$, micropyle. The broad nucellus contains the pollen-chamber ($p.c.$) above, a marking its apex; $sh.$, peripheral tissue (shoulder) of pollen-chamber with well-marked epidermis; $p.$, $p.^1$, &c., the various pollen-grains referred to in the text; $\times \times$, position of possible antherozoids; $s.a.g.$, supra-archegonial gap; $t.m.$, the tracheal mantle, ending at b ; $t.d.$, tracheal disc; $m.w.$, wall of macrospore. $\times 6\frac{1}{2}$.

This pollen-grain is rather opaque, but details of the internal structure are provided by $p.^1$, represented in fig. 40 (dimensions of $p.^1$, $110\mu \times 75\mu$). In this grain parts of the boss have been ground away in the preparation of the section. Focussing through the boss two internal cells are distinctly seen (a & b , Pl. 44. fig. 40), a smaller cell and a larger one partly surrounding it. The contents of the larger cell (a) seem to be preserved. The irregular space c , at the right-hand bottom corner of the grain, appears to be an extension of the outer cavity of the pollen-grain—to be a pollen-tube, in fact. Two alternatives to

this view are possible. First, that a fragment of the matrix has splintered away in the grinding of the preparation. This interpretation is untenable, as the matrix is actually present at *c*. The other alternative is that the excrescence is an accidental blister that originated prior to mineralisation*. As there is no means of determining from this isolated example whether the outgrowth was a natural or an accidental production, any conclusion as to its nature must be based on other considerations. Before this is possible the remaining stages have to be considered. Whatever may have been its nature, this tube was not very extensive. If we assume that the tube curved out of the plane of section, we should expect to find it in one of the two adjacent sections, if the appropriate regions be examined. No trace of it, however, is to be found. The tube consequently was of very limited extent. In the preparation it reaches to a distance of $22\ \mu$ from the pollen-grain. Traces of the triradiate slit are also present (Pl. 44, fig. 40, *tr.s.*).

(b) *Isolated internal Cells*.—The pollen evidently underwent some process of partial dissolution or rupture, for the isolated internal cells, agreeing approximately in dimensions with *a* and *b* of fig. 40, are common in the pollen-chamber. Those of importance to this account are shown at *p*.¹, *p*.³, *p*.⁶ (text-fig. 2).

p.¹—This is represented in fig. 41, and corresponds in dimensions ($40\ \mu \times 30\ \mu$) to the larger internal cell (*a*, fig. 40). It is still enclosed by the reticulated exospore of the convex part of the pollen-grain, and at *w* appears to show a small portion of the radiating sculpturing belonging to the flatter portion of the original pollen-grain. Within, a four-celled complex has been developed. These secondary cells show no contents. They have an average diameter of $15\ \mu$. The containing (sculptured) membrane of the complex is incomplete above, but the walls of the secondary cells appear to be complete.

p.³—This pollen-fragment consists of the pair of internal cells shown in fig. 42, *p*.³. The cells are still joined together, but their original relations in the pollen-grain seem to have undergone a slight alteration by the outward rotation of *b* from *a* (fig. 42) in the direction of the adjacent pollen-grain *p*.². The close association of *a* and *b* with this pollen-grain seems to be purely accidental—*p*.² is intact, *a* and *b* are the remains of another pollen-grain. The two joined cells of *p*.³ are laid open and present their concavities. Each contains the remains of a secondary cell-complex: that in *b*, relatively well-preserved (*b*, fig. 42), and somewhat displaced in relation to its containing membrane; that in *a* only recognisable as a crushed cell-group at *c* (fig. 42). Pl. 42, fig. 20 represents the cell-complex lying in the containing cell *b*, taken direct from the specimen.

The dimensions are as follows:—*a*, $37\ \mu \times 25\ \mu$; *b*, $34\ \mu \times 25\ \mu$. The larger cells of the reticulum contained in *b* have a diameter of about $15\ \mu$.

p.⁶—By itself, little importance would attach to this fragment. It consists of a broken containing-membrane with the remains of a possible secondary tissue lying close beside it; it is not figured.

p.⁵ essentially resembles *p*.¹, but is less well placed for observation.

From the foregoing exposition of the facts concerning the pollen-grains and pollen-

* A slight blistering has been observed in occasional instances in Cordaitan pollen-grains lying freely in the matrix.

fragments occurring in this pollen-chamber, it appears evident (1) that the pollen-grains, originally containing two internal cells and an extensive undivided residue (as shown in fig. 40, and as may be gathered also from scattered grains in the matrix), underwent a process of dehiscence by which the internal cells were liberated; (2) that the two internal cells concurrently produced secondary cell-complexes which may be regarded provisionally as antherozoid mother-cells. So far as the stages that have been found are concerned, the manner of freeing of the internal cells is obscure. That stage is wanting.

We may now return to *p*·, the pollen-grain represented in Pl. 44, fig. 40 with tube-like outgrowth, and consider whether it helps to bridge the lacuna in our series. Assuming for the moment that it is a naturally produced tube, it is easy to realise (from the point of view of the preservation of the pollen-fragments) that it may have constituted a weak spot from which decay may have started on the death of the seed, a decay which ultimately involved the whole peripheral part of the pollen-grain. Or, the changes in the outer cell of the pollen-grain which led to the production of a tube may have involved the whole of the peripheral part of the wall of the grain in decomposition. This is one hypothesis. On the other hand, it must be borne in mind that a solution of this part of the wall might have been achieved without the production of any tube. Finally, there is a third possibility. The triradiate mark or crack on the pollen-grain *p*·², represented also on *p*. (fig. 40, *t.r.s.*), and occasionally present on these grains in the matrix, *may* have offered the means of dehiscence, though the possibility seems a remote one. It is true that fern-spores with triradiate ridges use these lines for dehiscence at germination*, but there is no reason for supposing this method to have been perpetuated in seed-plants†.

But however this may be, it does not touch the present case, for the question is how the pollen-grains come to lose their wing-like expansions. The detached internal cells still bear their covering of exospore on one side. The decision arrived at depends on the view taken of the tube-like outgrowth in fig. 40. If this is a genuine tube (however rudimentary), then the structure of the grain would be intelligible. The outer cell is concerned in the production of a short tube through which the antherozoids, which may be supposed to have arisen in the secondary complexes (shown in *p*·³, fig. 42), were discharged. On this view the grain is differentiated into a generative portion consisting of the two internal cells, and a directive portion which developed a tube and perhaps started the antherozoids in the right direction.

Having traced events so far, we may pass on to the more conjectural question of the antherozoids themselves. In what is doubtless the fossilised mucilage of certain regions of this pollen-chamber, bodies are preserved which are susceptible of interpretation in this sense. The bodies in question are small ovoid vesicles having as average dimensions

* See Sadebeck, in Schenk's 'Handbuch d. Botanik,' vol. i. p. 154.

† See Coulter & Chamberlain, 'Morphology of Spermaphytes,' p. 91, fig. 69, c. The pollen-grains of *Pinus Laricio* are shown in the tetrad condition. From the position of the sac-like blisters of the extine, it would appear that the pollen-tube will arise on the side of the pollen-grain remote from the contact-angles of the members of the tetrad.

$17\mu \times 15\mu$. Two of them are represented in Pl. 44, fig. 43. Their position in the pollen-chamber is indicated by two little crosses close to the rent in the macrospore-wall (text-fig. 2, p. 380). Each body is delineated by a delicate membrane whose contour is slightly indented or crenate, the convexities of the crenations being directed towards the centre of the body. Within this membrane is a slightly carbonised reticulum, which may perhaps be regarded as the nucleus. Such types of nuclear preservation are sometimes met with in the cells of the female prothallium. Of cilia attached to these bodies there is no trace, though the radiate zone or halo of crystallisation occasionally found around them is not without some resemblance to a halo of cilia.

Whilst the size of these bodies supports the view that they may have escaped from the cells of the secondary complexes of the pollen-fragments, and their distribution, described below, is that which might be expected were they antherozoids, it is evident that in their actual preservation they do not closely resemble the antherozoids of any known Pteridophyte or Cycad. Traces of the spiral band are lacking. So far as general form is concerned, they are Cycadean rather than Filicinean. In their dimensions, however, they approach the Ferns. No positive determination is possible till similar and better preserved bodies of the kind have been studied in other specimens. The supposed antherozoids, oval in form, have a peculiar distribution. Three occur in the mucilage above the ruptured spot, and others at the spots indicated by small crosses in text-fig. 2. Of their distribution, it may be said that the antherozoids are met with either in the neighbourhood of those spots at which it is reasonable to suppose (in view of the other evidence) that antherozoids were liberated, or in the neighbourhood of the female prothallium, and nowhere else. Their dimensions harmonise with those of the secondary cell-complexes of the pollen-cells.

Though there seems little reason to doubt that the bodies in question represent nuclei enclosed in loose crenate envelopes, it must be borne in mind that the pollen-chamber itself has, no doubt, become excavated by a lysigenous breakdown of the tissues, and it would be difficult to prove that our nuclei may not have originated in that way. Or, again, it is possible they may be the free spores of one of the Fungi known to have attacked the tissues of the nucellus in more than one of the Palæozoic seeds. The most striking facts about them are their size and distribution. The attribution of these structures to antherozoids is conjectural, but the facts seem to justify allusion to them. Even if this seed were recent and not fossil, their occurrence would need further study and confirmation. In the present case, where so many pitfalls beset the investigator, such corroboration is, of course, more urgent.

The Question of Pollen-tubes.

If we look at the question from the wider standpoint of all the facts that have been so far elicited, how does the matter stand? In the case of the pollen of *Eltheotesta* we have Renault's interesting observation of a funnel-like process at one pole of the grain *. In *Codonospermum olivæforme* † the pollen-grains (stated to be derived from *Dolerophyllum*) are provided with an operculum. In both cases the indication would seem to

* 'Sur quelques Cryptogames hétérosporées,' p. 7, and fig. 13, p. 5.

† Renault, *loc. cit.* p. 7, and fig. 14, p. 5.

be that there was a certain local specialisation in connection with the discharge of the antherozoids. From a study of the structure of the pollen of *Stephanospermum akenioides*, Renault conjectures that a state of affairs may exist corresponding to *Ætheotesta*. I have endeavoured to show (p. 378) why such an interpretation of *S. akenioides* seems inadmissible. If the little tubular processes occasionally found projecting from the periphery of these grains (as in the large grain, fig. 15) be indeed naturally formed, the inference I would draw would be that this pollen was of a more generalized type, and that any of its cells could produce these tubes. In other words, that short multiple pollen-tubes were formed through which the antherozoids were discharged. As compared with this type, *Ætheotesta* and *Codonospermum*, each in its own way, shows a slight advance without departing from the *Stephanospermum*-type of pollen. Coming to *Stephanospermum caryoides*, reduction and specialisation are more complete. A considerable part of the pollen-grain remains undivided, as in recent Gymnosperms. This outer cell, whilst it may have possessed nutritive functions in connection with the maturing of the antherozoids, was doubtless concerned in promoting their discharge into the pollen-chamber. Whether this result was achieved through the agency of an incipient tube, as suggested by our preparation, or whether the internal cells were liberated through the deliquescence or dehiscence of the outer cell, must remain an open question till more evidence accrues.

The internal complexes of cells in the pollen of *Stephanospermum akenioides*, of *Cordaites*, and of *Stephanospermum caryoides* may thus represent different stages in the reduction of an archaic male gametophyte of a complexity not known in any Fern. It is true that the reticulations of the supposed "microspores" in *Botryopteris* and *Zygopteris* have been interpreted as an internal tissue*, thus offering an easy transition to the compound pollen of the early Gymnosperms. To this view of the reticulations there seem to be grave objections, and, after careful study of specimens, it is difficult to avoid sharing the doubt which has been expressed† whether these "microspores" justify the interpretation to which allusion has been made.

The main obstacle to definite and certain conclusions as to the behaviour of the pollen in these seeds is, of course, the fact that the seeds fell from the tree at a stage in development prior to fertilisation. The conditions are somewhat analogous to those that would obtain in the case of *Pinus sylvestris* were only first-year cones available for investigation. The mode of transport of the sexual cells is not yet fully declared. Nor, indeed, in *Stephanospermum akenioides*, do we know with certainty which *are* the sexual cells. The preparations that have come under observation, however, seem to indicate decisively that the "central body" is *not* of this nature (*cf.* p. 377). Of the twenty or more peripheral cells which compose the grain, it is impossible to select any as differing from the rest. They are all alike. Occasionally, short tubes are found—spout-like outgrowths from some of these cells. But their occurrence is too occasional as yet for acceptance as a normal stage in development. That pollen-tubes were produced penetrating the nucellar tissues as in recent Cycads and Conifers appears highly

* 'Flore fossile d'Autun et d'Épinac,' pp. 44, 54, 57.

† R. Zeiller, 'Éléments des Paléobotanique,' 1900, p. 74.

improbable. The pollen-grains of *Stephanospermum*, large from the first, have already, in the stage usually preserved, sojourned in the pollen-chamber for a considerable time, and have there undergone a further development. Had they formed rhizoid-like attachments to or actual tubes in the tissue of the wall of the chamber, indications could hardly be wanting. It may, I think, be safely assumed that structures of that kind were not produced. That mobile antherozoids were liberated in *Stephanospermum* may be inferred with some degree of confidence from the whole organisation of the pollen-chamber. Whether all or but a part of the internal cells of the pollen-grains were concerned in the production of antherozoids, there is no evidence to show. That papillæ (as in Pl. 42. fig. 15) arose from the periphery of these cells, liberating antherozoids, is not inherently improbable. To the occurrence of perforations, whether on the surface of the grains or, as is so frequently the case, on their partition-walls, just this significance may be attached, viz., that these walls were readily destructible, and that consequently a very limited number of papillæ might have served for the discharge of all the antherozoids produced in one of these multiple pollen-grains.

The view which I adopt in regard to this seed is that no tubular, rhizoid-like attachments were formed by the pollen-grains on the walls of the pollen-chamber, but that the large grains, after a process of maturing in the chamber, liberated antherozoids by some simple means, such, perhaps, as the extrusion of short papillæ, the tips of which became perforated. Finally, that the antherozoids were formed in considerable numbers and that the distance they had to traverse by swimming was relatively great—as compared with recent Cycads, for instance.

In *Stephanospermum caryoides* the number of primary internal cells is much reduced. They are partly enclosed in an extensive peripheral cell recalling the tube-cell of the pollen of recent Gymnosperms. The two internal cells produced secondary complexes of antherozoid mother-cells, whilst the outer cell seems to have facilitated the liberation of the antherozoids. Whether the blister-like outgrowth (*c*) of Pl. 44. fig. 40 indicates the natural means of exit of the antherozoids must remain an open question till additional specimens are available. In this seed, as in *S. akenioides*, the freedom of the pollen from special nutritive relations with the tissues of the nucellus seems to mark an archaic condition not preserved in any recent Gymnosperm. The discovery of this seed in a stage of development apparently more advanced than any of the numerous specimens of *S. akenioides* that have passed through my hands, encourages the hope that the phenomena attendant upon fertilisation in the seeds of this period may ultimately become known to botanical science.

The Difference in Pollen-structure.

From the description which has been given of the pollen-grains in the two *Stephanosperma*, it is evident that considerable divergence exists in their complexity in these two seeds. Whilst in the former the pollen-grains are filled with a tissue of some twenty cells or more, in the latter is contained a group of two. If, therefore, the close association of the two seeds be justified, as I incline to think on the near agreement of

their general characters, it follows that a considerable latitude in pollen-structure may co-exist within a fairly close cycle of affinity. Hitherto, two types of pollen have been recognised, the *Stephanospermum* (*akenioides*)-*Codonospermum*-type, filled with cells, and the Cordaitean type, in which there is an isolated prothallial or antheridial group*. It is premature to say whether the former type corresponds generally to the radially organised seeds of this period, the latter to the flattened. The problem does not appear to have been worked out in detail. The existence of a case like *S. caryoides*, where the pollen conforms rather to what I have referred to as the Cordaitean type, seems to indicate that seed- and pollen-structure do not run parallel in the two cases, and that the relations of the two broadly contrasting groups of seeds may be more complex than seemed probable.

Actually, the pollen of *S. caryoides* differs considerably from that of *Cordaites*. The primary internal complex of two cells (which is shown both in the matrix and in the pollen-chamber) would seem to mark a reduction from the Cordaitean type. Whether the secondary complexes, which later on appear within these primary cells in *S. caryoides*, represent merely a postponement in the appearance of elements present in *Cordaites*, even before escape from the pollen-sac, it seems hardly profitable to discuss in the present imperfect state of our knowledge.

CHARACTERS DISTINGUISHING STEPHANOSPERMUM CARYOIDES, n. sp.

STEPHANOSPERMUM CARYOIDES, n. sp.

This supposed new seed resembles *S. akenioides*, Brongn., in being circular in transverse section and in the possession of an apical crown and micropylar beak, though in an abbreviated form. As in that species, the perimicropylar area is closely set with hairs. Another feature in which the seeds agree is the continuous tracheal mantle of the nucellus.

S. caryoides is a large seed, approaching a globular form. Length $15\frac{1}{2}$ mm.; diameter $12\frac{1}{2}$ mm.

Its pollen-chamber is large and broad, with well-developed shoulders.

The peculiarities of the pollen have been noted above.

ON FERTILISATION AND THE TRACHEAL MANTLE.

The course in the foregoing seeds during life may be supposed to be somewhat as follows:—The pollen is caught at the apex of the ovule by a drop of mucilage which in any case must have been secreted here. There is no evidence to show what was the source of this drop, whether it welled up from the nucellar apex or was secreted at the micropyle. As the pollen-chamber developed and assumed the character of an extensive excavation in the nucellus, the peripheral tissue became sharply delimited from the central deliquescent area and formed the "shoulders." This flank or shoulder no doubt served the purpose of holding up the roof of the pollen-chamber, so that it should not collapse—a function

* Cf. Renault, 'Flore carbonifère,' 1879, pl. 17. fig. 15.

apparently discharged in quite another way by Hirase's "tentpole" in the case of *Ginkgo*, and by the central cone of nucellar tissue in *Lagenostoma*.

During the later stages of development the pollen has been maturing and has undergone considerable enlargement. The internal cells of the pollen underwent a subdivision into antherozoid mother-cells in *Stephanospermum caryoides*, perhaps in *S. akenioides* also. In the former the pollen appears to have undergone a process of dehiscence or fragmentation about this time, whilst in *S. akenioides* it became perforated. Ultimately the pollen-fragments of *Stephanospermum caryoides* were ruptured by the mother-cell reticula. From these, antherozoids escaped, leaving traces of the reticula behind. Bodies which might conceivably be the antherozoids have been observed in *S. caryoides* only. They occur associated with the pollen-fragments or on the floor of the pollen-chamber on the way to the archegonia.

Adequate supplies of moisture would be drawn from the tracheal sheath. If the mucilage began to dry up at any time, its greater concentration would lead to further supplies of water being absorbed from the tracheides. In the absence of pollen-tubes, fertilisation would depend on the pollen-chamber being nearly full of watery mucilage.

From the researches of Webber* we know that the pollen-chamber is dry, or, rather, saturated with vapour, not full of water, during the maturation of the antherozoids in recent Cycads. The same may have obtained in *Stephanospermum* during the earlier stages of development. As the antherozoids came to maturity, however, it would become necessary for the chamber to be filled, so that they might swim across the considerable interval. Meanwhile the pollen-chamber had been extending downward to the archegonia, and a quantity of damp mucilage would thus be always present. Finally, the tracheal sheath which overlies the prothallium itself underwent a breakdown, probably of the same kind, and disappeared from this region by fertilisation-time (*cf.* p. 369). This would explain the differences in fissibility in this region between younger and "normal" stages in *S. akenioides* noted at p. 370. In the younger seeds the tracheides formed a compact sheath, and the splitting in post-mortem contraction of the macrospore occurred in the least resistant plane, which was below the tracheides (see p. 370 and Pl. 42. fig. 13); in the older ones, which seem to have been preserved just prior to fertilisation, the tracheides below the chamber were already weakened, and so the split leading to the production of the supra-archegonial gap occurred in the tracheal layer itself (Pl. 42. figs. 8 & 12). Further, in *S. caryoides*, where the evidence points to ours being the actual fertilisation-stage, tracheides are wholly wanting from the floor of the pollen-chamber, though they begin just where the corner below the shoulder is turned. It may be conjectured they have disappeared from this region. By realising that the tracheides degenerated in this way as fertilisation-time approached two minor facts of observation are rendered intelligible: (1) the relative fissibility of different layers according to the age of the seed; (2) the almost total absence of tracheides from the supra-archegonial gap in *S. caryoides*. That the breakdown of the tracheides in this region should have impeded the outflow of water is hardly to be supposed. That the top of the macrospore should remain littered with tracheides and partly unrolled spirals is hardly consistent with zoidiogamy. Such

* H. J. Webber, 'Spermatogenesis and Fecundation of *Zamia*,' 1901.

entanglements would impede the movements of the antherozoids. The inferred degeneration of the tracheides, however, solves the difficulty. The view here stated, though somewhat hypothetical in character, rests in a measure on the observed facts.

It will be appropriate to consider here very briefly the fertilisation-mechanism of recent Cycads. In *Zamia* the archegonia open upon a shallow depression termed the archegonial chamber. The pollen-tubes hang down, so that their ends approximately touch the necks of the archegonia. As yet the chambers (the pollen- and archegonial chambers) are dry or merely moist. The pollen-tubes burst and the antherozoids are discharged together with the fluid that distends the pollen-tubes—a mechanism recalling that of the stinging-hair of a nettle. The necessary fluid for the antherozoids is therefore supplied from the pollen-tubes just before fertilisation. This mechanism is a special one correlated with the reduction in number of antherozoids produced by each pollen-grain, and marks a high degree of precision and certainty in bringing the antherozoids to the archegonia, indeed it is the perfection of attainable accuracy possible with free-swimming antherozoids.

In *Stephanospermum caryoides* the arrangement was more primitive. The antherozoids were liberated from the pollen-grains at a distance from the archegonia relatively remote. Correlated with the distance to be traversed by the antherozoids we note their production in larger numbers than in recent Cycads*. Whilst in the latter two are formed from each pollen-grain, in *S. caryoides*—assuming two internal cells to each pollen-grain and that each of them produces a packet of four or five antherozoid mother-cells—the minimum number of antherozoids per pollen-grain may safely be estimated at eight. In the pollen-chamber of our seed (not counting pollen-grains lost in the cutting and grinding of the sections) there are ten internal cells accounted for (see text-fig. 2, p. 380)—*i. e.*, ten packets of, say, four antherozoids each. This gives a minimum of forty antherozoids†, a number that would necessitate pollination in the Cycad by at least twenty pollen-grains.

The supposed antherozoids of *S. caryoides* are small, having average dimensions of $17\mu \times 15\mu$. These dimensions are confirmed by those of the individual cells of the secondary reticula. Those of Cycads are large and in some cases immense. They range from $82\mu \times 49\mu$ in *Ginkgo*, $160\mu \times 70\mu$ in *Cycas*, to $222\text{--}322\mu \times 222\text{--}306\mu$ in *Zamia*.

Whether *S. caryoides* belongs to a stock from which recent Cycads have originated, or whether, as seems probable, the series are distinct, they stand on quite different planes of remoteness from Pteridophytes. In the Cycads we have a highly specialised pollen-tube-antherozoid-mechanism with reduction in number and increase in size of the antherozoids. In *S. caryoides*, so far as the antherozoids are concerned, we have a type relatively near the Pteridophytes—a condition analogous to that which might obtain if, in such a type as *Selaginella*, a pollen-chamber and integument be superadded to the macrosporangium, and the microspores being introduced into this chamber followed their normal development. The antherozoids (if such they be) have dimensions comparable to those of Pteridophytes rather than those of Cycads, whilst all the facts observed are consistent with their liberation at a considerable distance from the archegonia.

* A point anticipated on general grounds by D. H. Scott, 'Studies in Fossil Botany,' p. 435.

† In *S. akenioides*, assuming one antherozoid to arise from each of the (say) twenty cells in a pollen-grain, we have in Pl. 41, fig. 3 seven non-abortive grains, *i. e.* one hundred and forty potential antherozoids.

COMPARISON WITH OTHER PALÆOZOIC SEEDS.

Just as among recent plants, where all seeds seem much on the same plane and the pollen-tube is the dominant mechanism of fertilisation, though in archaic forms like the Cycads we get the end of the zoidiogamic epoch, so in Palæozoic times—or, more precisely, in the later periods of the Permo-carboniferous—fertilisation-mechanisms would seem to be also much on a plane. We have in the remarkable constellation of seeds from Grand' Croix a fair sample of seeds probably in the zenith of their zoidiogamic phase of evolution. That amongst them the beginnings of siphonogamy may here occur is possible, so that if Renault's surmise of a specialised operculum in *Ætheotesta** prove correct, there would be distinct indications of a foreshadowing of a pollen-tube. That the Grand' Croix seeds were without pollen-tubes, as we understand them, seems more probable, in view of the statement of so careful and indefatigable an investigator as Renault, who tells us in more than one passage (prior to the year 1901) that of the 300 odd seeds that have passed through his hands this structure has never come under his observation.

It seems worth while to contrast *Stephanospermum* with the associated genera of seeds with a view to ascertaining in how far they present resemblances or differences in their general organisation, and to what extent they may be arranged under provisional groups.

Brongniart and, since his time, all botanists who have touched the subject distinguish between the seeds of this period possessing a bilateral symmetry and those which, on the other hand, are radially symmetrical.

The bilateral forms, which for convenient reference may be termed the PLATYSPERMÆ, include the types known as *Cardiocarpus*, *Rhabdocarpus*, *Diplotesta*, *Sarcotaxus*, *Leptocaryon*, *Taxospermum*, and *Cycadinocarpus*. Of these, many are probably Cordaitan in their affinity, whilst *Cycadinocarpus* may perhaps, as Renault supposes, approach the Cycads. They belong to one phase of evolution, and have in common more especially the complex chalazal plate from which the bundles both of testa and nucellus-wall take origin, the small pollen-chamber, and flattening more or less considerable.

Brongniart's other series, which we may term the RADIOSPERMÆ, include several groups based on the form of the transverse section:—

(1) <i>Stephanospermum</i> , <i>Ætheotesta</i> , <i>Gnetopsis</i>	Circular.
(2) <i>Trigonocarpus</i> , <i>Tripterospermum</i> , <i>Pachytesta</i>	3-ridged.
(3) <i>Eriotesta</i> , <i>Codonospermum</i>	Octagonal.
(4) <i>Polylophospermum</i> , <i>Polypterospermum</i> , <i>Hexaspermum</i> , <i>Ptychospermum</i> .	Hexagonal.

Of these many are much complicated by the presence of ridges and other emergences from the testa. These peculiar specialised forms may be left on one side for the present, but attention may be usefully directed to the members of groups (1) and (2).

Ætheotesta evidently, as a seed, very nearly resembles *Stephanospermum*. Two species have been described—*Æ. subglobosa*, Brongn., *Æ. elliptica*, B. Renault.

* Renault, "Sur quelques pollens fossiles," Soc. d'Hist. nat. d'Autun: extr. du Procès-verbal de la Séance du 13 juin, 1901.

Ætheotesta subglobosa, Brongn., is very imperfectly known. It is a globular seed, having a transv. diam. 12–15 mm. Brongniart sketches the general macroscopic characters of very imperfect specimens in figs. 16, 17, 18, pl. C., in his 'Graines fossiles.' The micropyle is not shown, but the apical end of the seed was flattened and hairy, though there does not seem to have been the shallow, trough-like depression that we get in *S. caryoides*. The basal end of the seed was peculiar, owing to the presence of an aril-like cushion around the point of insertion. The nucellus was much retracted and possessed a roomy pollen-chamber. Though differing in details, in its general characters this seed was not unlike *S. caryoides*. How near the resemblance goes can only be determined when the original specimens are compared*.

Æ. elliptica, B. Renault.—Of this seed Renault gives considerable details†. Though larger and relatively longer than *S. caryoides* it possesses the same broad type of pollen-chamber as that seed. The vascular supply of the nucellus, which is derived in the usual way from the chalazal bundle, is not a continuous mantle but consists of distinct strands. The pollen is interesting as the very large grains ($320\text{--}400\ \mu \times 270\text{--}310\ \mu$) are identified by Renault as being the spores of *Dolerophyllum* which have lost their extine. This author holds the view that the pollen of *Dolerophyllum* underwent dehiscence prior to pollination, and that the inner cell-complex alone penetrated to the pollen-chamber. The pollen-grains, except for their larger size, resemble those of *S. akenioides* and like these became profusely perforated.

There was an outer fleshy (?) coat with chief development at the two ends of the seed. At the micropylar end this layer was much chambered, an arrangement which Renault interprets as a floating mechanism. Though apparently very similar to *Stephanospermum*, this seed, apart from the lacunate sarcotesta, differs in the grouping of the nucellar tracheides into bundles.

Gnetopsis elliptica, R. Zeiller.—These are tiny seeds ($2\cdot5\text{ mm.} \times 1\cdot2\text{ mm.}$) bearing feathery arms at the micropyle like the nut of an *Abelia*. They have been found by Renault surrounded to the number of 3 and 4 by a two-membered cupule‡. The tracheal elements appear to be concentrated in four bundles, but whether they really belong to the nucellus seems open to question. The presence of the enclosing cupule here is an interesting fact, as it is the only instance as yet amongst the Radiosperms in which evidence has been obtained as to the kind of structure to which these seeds were attached. It does not appear, however, that the cupule exhibits any characteristic feature sufficient to warrant a reference to the plant upon which it was borne.

So far, then, as this group is concerned, we have smooth seeds, circular in transverse section, one with a definite sarcotesta (*Ætheotesta*), all with adaptations of one sort or another at the micropylar extremity. The *Stephanosperma* alone show a continuous tracheal mantle in the nucellus in contradistinction to discrete bundles in the other

* In the contingency of *Stephanospermum caryoides* eventually being recognised as identical with *Ætheotesta subglobosa*, Brongn., the discrepancy in respect of the pollen would still remain, as the pollen-grains of *Ætheotesta elliptica*, B. Renault, are stated to be of the *S. akenioides* type.

† 'Flore fossile d'Autun, &c.' pp. 272–278.

‡ 'Cours,' iv. pl. 20.

forms. In none of the forms other than the two seeds here described has any observation been put on record as to a layer internal to the sclerotesta. But perhaps special attention has not been directed to this point.

The second group of the Radiospermæ, which includes *Trigonocarpus*, *Tripterospermum*, and *Pachytesta*, is an interesting one demanding some consideration.

Tripterospermum, Brongn., seems to be as unspecialised a seed as any from the Palæozoic rocks. It is an oval seed with a beak-like micropyle and possessed a sarcotesta external to the sclerotesta. Longitudinally, there run three symmetrically placed ridges; ultimately dehiscence probably occurred along these lines. To this genus the *Trigonocarpon*s from the Lancashire Coalfield described by Sir J. D. Hooker and Binney* probably belonged, as Brongniart has suggested†.

The seed described by Williamson‡ under the name of *Trigonocarpon olivæforme*, though slightly larger than the Hooker and Binney specimens, unquestionably belongs to the same affinity. Consequently, for the purposes of the present discussion, both these *Trigonocarpon*s may conveniently rest in the Brongniartian genus *Tripterospermum* §.

Particular attention was drawn to the Hooker and Binney specimens from a study of pl. 4. figs. 5, 9, and 10 of their Memoir. Here is shown a circular ridge surrounding the base of the micropylar beak which recalls the crown of a *Stephanospermum*. On consulting the original specimens || I find that this apparent ridge is in reality due to a corrosion or decomposition of the tissue in this region, so that the marked resemblance is illusory. The only other point about these seeds calling for mention is that the tracheal elements ensheathing the nucellus are well preserved, though it is difficult to decide whether they formed a continuous mantle or separate bundles. The pollen-chamber is smaller relatively than in *Stephanospermum*.

Pachytesta ¶ was the largest of the Palæozoic seeds, approaching a hen's egg in dimensions as in form. The testa was massive and complicated, whilst the chalaza was remarkable in the presence of a conspicuous peduncle upon which the nucellus stood. Apart from the complexity of the testa, which possessed an extensive endotesta, this seed is characterized in that the nucellus appears to have borne longitudinal ridges which engaged with corresponding grooves in the endotesta. In view of these and other peculiarities, *Pachytesta* may perhaps be detached from the near alliance with *Trigonocarpus* and *Tripterospermum* implied in Brongniart's grouping of the genera.

Trigonocarpus, Brongn., may be provisionally placed in this section. *T. pusillus* was

* "On the Structure of certain Limestone Nodules, &c.," Phil. Trans. vol. 145 (1855), p. 149.

† 'Graines fossiles silicifiées,' p. 26, footnote.

‡ "On the Organisation of the Fossil Plants of the Coal-Measures: Part VIII.," Phil. Trans. 1877, p. 248.

§ I am in agreement with Williamson (*loc. cit.* p. 253) that a redundancy of genera has been created for the known Radiosperms.

|| It is owing to the kindness of Sir Joseph Hooker that I have been able to trace the originals to the Geological Department of the Natural History Museum. Here are to be found the specimens (all longitudinal sections) upon which are based figs. 6, 7, 8, and 9, pl. 4, of the Hooker and Binney Memoir. Sir Joseph Hooker's figures are drawn in natural size and are practically facsimile representations of the specimens.

¶ For full description see Brongniart, *loc. cit.* p. 25, pl. B. figs. 4 & 5, and pls. 18-21; also Renault, 'Flore fossile d'Autun et d'Épinac,' p. 389, and pls. 83 & 84. figs. 1 & 2.

the smallest of the seeds described by Brongniart *. It is three-ridged, but appears to resemble *Tripterosperrum* (with which, no doubt, it was closely allied) in the possession of a sarcotesta, of which traces are present.

Of the remaining genera of Radiosperms, the seed *Polylophospermum*, Brongn. †, may be cited as possessing, in essentials, a *Stephanospermum*-organisation, *i. e.* a vascular nucellus and a large broad pollen-chamber in conjunction with radial symmetry. The testa is complicated by chalazal and micropylar expansions, in addition to longitudinal ridges, whilst an outer fibrous or succulent "sarcotesta" enveloped the stone of the seed.

Beside this seed, *Codonospermum*, Brongn. ‡, naturally takes its place. As Renault has shown §, this seed also possessed a sarcotesta.

In addition to the above, the ridged seeds *Colpospermum*, B. Renault ||, *Ptychotesta*, Brongn. ¶, *Polypterosperrum*, Brongn. **, and *Hexapterosperrum*, Brongn. ††, and perhaps others, may be included as possessing the same general organisation as *Stephanospermum*, and as being marked out for retention in the same group.

To summarize the remarks, it may therefore be suggested that the following genera of Palæozoic seeds, having a like organisation, possess a bond of real affinity:—*Stephanospermum*, *Ætheotesta*, *Trigonocarpus*, *Tripterosperrum*, and the *Trigonocarpons* of Hooker & Binney and Williamson ‡‡, *Polylophospermum*, *Codonospermum*, *Colpospermum*, *Ptychospermum*, *Polypterosperrum*, and *Hexaspermum*. It is these forms, at present largely recruited from the French Permo-Carboniferous, that constitute the *Stephanospermum*-group of the Radiosperms.

The main features of this group are: radial symmetry; a nucellus traversed peripherally by a mantle, network, or distinct strands of tracheal elements; a relatively broad pollen-chamber; a stony testa with a tendency to be produced into transverse or longitudinal ridges, &c.; an outer fleshy or fibrous sarcotesta.

In the case of the type-genus, *Stephanospermum*, apart from the apex of the seed, evidence for the existence of the sarcotesta is lacking; but when the structure of this seed is considered as a whole (*cf.* p. 363), we can hardly avoid the conclusion that it resembled its contemporaries in this feature also.

During the passage of the present paper through the press, strong evidence has been adduced for referring the English Lower Coal-Measure seed, *Lagenostoma Lomaxi*, to the well-known fossil plant *Lyginodendron oldhamium* §§. Now this seed, and the

* Brongniart, 'Graines fossiles silicifiées,' p. 24.

† Brongniart, *loc. cit.* pl. C. figs. 6, 7, 8.

‡ Brongniart, *loc. cit.* pl. C. figs. 10, 11, 12; also Renault, 'Flore fossile d'Autun et d'Épinac,' p. 393, and pl. 87.

§ Renault, *loc. cit.* p. 394.

|| Renault, *loc. cit.* p. 400.

¶ Brongniart, *loc. cit.* pl. B. figs. 10, 11; also Renault, *loc. cit.* p. 401.

** Brongniart, *loc. cit.* pl. C. figs. 1, 2, 3.

†† Brongniart, *loc. cit.* pl. B. figs. 12, 13, 14.

‡‡ When the time arrives for a revision of these genera of seeds, the name *Trigonocarpus* may be appropriately associated with the Hooker and Binney specimens on the ground that the description of these petrified specimens holds unquestioned priority in the field of investigation of seeds with structure preserved.

§§ Oliver, F. W., and D. H. Scott, "On *Lagenostoma Lomaxi*, the Seed of *Lyginodendron*," Proc. Roy. Soc. vol. lxxi. (1904) p. 477.

other *Lagenostomas* of Williamson*, have a peculiar organisation that differentiates them from *Stephanospermum* and its allies, though they resemble the latter in their radial symmetry. Perhaps the most important feature of difference is the vascular system of the seed, which is *nucellar* in *Stephanospermum* but wholly *integumental* in *Lagenostoma*. When regard is had to the Cycadean character of the seed *Lagenostoma*, on the one hand, and of the vegetative organs known as *Lyginodendron*, the plant to which it belonged, on the other, little doubt can remain as to the close relations that must have existed between this plant and the ancestors of existing Cycads.

In addition to the *Lagenostomas*, possibly other seeds from the English Carboniferous rocks may be referred eventually to this group of seed-bearing Fern-like plants (the *Lyginodendreae*). The seed *Gnetopsis*, Renault, also may possibly belong to the same cycle of affinity—in any case it presents close agreement with *Lagenostoma* in several ways†.

The affinities of the *Stephanospermum*-group of seeds, however, are not yet known with certainty, though there are reasons for supposing that one of its members, the English *Trigonocarpon olivæforme*, may have belonged to the genus *Medullosa*‡. Further, there is Mr. Kidston's recent discovery of a seed, not wholly unlike a member of this group, in connection with the pinnules of *Neuropteris heterophylla*, a fern-frond also referable to the *Medulloseae*§.

Hence the position in respect of the radially organised seeds is as follows:—The *Lagenostoma*-group have been definitely referred to *Lyginodendron*, and take their place as the seeds of forms intermediate between true Ferns and Cycads. The rich series of seeds that conform to the *Stephanospermum*-type, on the other hand, are not yet so definitely referred, but it is a reasonable anticipation to suppose that they will eventually—through the *Trigonocarpons*—find a place in the *Medulloseae*.

It may perhaps be added that remains of *Alethopteris* pinnules and of *Myeloxylon* petioles are exceedingly abundant in the pebbles in which *Stephanospermum* occurs; but that, whilst the association of the last-named with the two former is very close and constant, no evidence of actual continuity has been discovered during the course of the present investigation.

The other French seeds described by Brongniart||, *Cardiocarpus*, *Rhabdocarpus*, and similar forms, are by common consent attributed to the *Cordaiteae*. As the organisation of these "Platysperms" is very uniform, and actual continuity with *Cordaitean* tissues has been established by Renault in certain instances¶, we may regard the position of these

* Williamson, "Organisation of the Fossil Plants of the Coal-Measures: Pt. VIII.," *Phil. Trans.* vol. 97, p. 233.

† See a forthcoming memoir in conjunction with D. H. Scott, F.R.S., "On the Structure of *Lagenostoma Lomaxi*, &c."

‡ G. Wild, "On *Trigonocarpon olivæforme*," *Trans. Manchester Geol. Soc.* vol. xxvi. 1900; D. H. Scott, "On the Origin of Seed-bearing Plants," Lecture delivered before Royal Institution of Great Britain, May 15, 1903, p. 11.

§ R. Kidston, F.R.S., "On the Fructification of *Neuropteris heterophylla*, Brongn.," *Proc. Roy. Soc.* vol. lxxii. (1904), p. 487.

|| *Loc. cit.*

¶ 'Flore carbonifère,' p. 311.

seeds as definitely settled. The resemblances which they present with the seeds of recent Cycads have been pointed out by various writers and are quite evident. Nevertheless, in view of the close Cycadean affinity offered by the *Lagenostoma-Lyginodendron* Cycadofilices in respect of reproductive and vegetative organs alike, it seems quite probable that the Cordaitæ and Cycadaceæ are less nearly related than has often been supposed. The former are an ancient group and retain relatively little of their Filicinean ancestry. The likeness in seed-structure may perhaps be regarded as a parallel development in related, but not very closely allied, lines of descent.

In the same way the agreement in details of seed-structure in Cycads on the one hand, and in *Stephanospermum* and similar forms on the other, should not be too closely pressed. For, in view of the position of *Lagenostoma*, the relation of *Stephanospermum* to *Cycas* is more remote than may have appeared to be the case before the sorting-out process began. For, if the Cycadean seed be interpreted in terms of *Lagenostoma*, as it needs must be, it is difficult to resist the conclusion that the inner system of vascular bundles in the former is, in reality, integumental in character rather than nucellar. Consequently, the homology of this system of strands with the vascular mantle of a *Stephanospermum*, an homology implied by the present writer on a former occasion *, stands in need of revision.

SUMMARY AND CONCLUSION.

In whatever respects the seeds of Palæozoic age may have differed among themselves, as in the structure of the integument and in the position of the vascular system, they all show marked agreement, as originally pointed out by Renault †, in the possession of a pollen-chamber. This applies to both provisional groups of the Radiospermic series (*Lyginodendreae* and *Stephanospermæ*) as also to the *Platysperms* (*Cordaitæ*). And in this respect they contrast in marked degree with recent plants, always excepting such archaic *Gymnosperms* as are fertilised by spermatozoids. The pollen-chamber was evidently an adaptation of the distal portion of the macrosporangium, connected with the reception and storing of the microspores and the liberation of spermatozoids. Indeed, it is difficult to conceive any essentially different method by which a seed could have been evolved, assuming always, of course, that fertilisation by spermatozoids was retained. And it would be improbable in the highest degree that the particular conjunction of factors that led to the production of a pollen-tube should have operated contemporaneously with those others which produced the pollen-chamber.

The old type of seed was of necessity, then, a complicated structure, as the microspores had to be collected and nursed, and provision made for the swimming of the spermatozoids. The pollen-chamber seems to have reached its zenith in *Permo-Carboniferous* times, and its decline was doubtless correlated with the evolution of pollen-tubes. The result we see in recent *Conifers*, with their simple reduced nucelli and siphonogamic methods.

* Cf. 'Annals of Botany,' vol. xvii. p. 466.

† 'Flore carbonifère,' p. 310.

Very few instances of early seed-like structures without pollen-chambers are at present known. *Lepidocarpon* alone has been at all fully described*; but even here nothing has been ascertained in regard to either pollination or fertilisation. In view of this paucity of data, a comparison of the two seed-types is hardly possible. It may be observed, however, with some confidence, that the *Lepidocarpon*-type has left no seed-bearing progeny, whilst there is at least equal probability for the assertion that the whole of existing Gymnosperms have originated from an ancestral type characterised by the possession of a pollen-chamber.

One reason for the predominance of the pollen-chamber may reside in the water-relations. The Pteridophytic alternation of generations, though a step in advance of the Algal condition, was not the ideal state for a dry-land flora. The early seed-habit, in its initiation, perhaps, largely a xerophilous adaptation, contained the germ of much else beside. The water-relations in question are very evident in the seeds of the *Stephanospermum*-type, where the ample sheath of transfusion-tracheides would provide such moisture as may have been required. But as yet the nutritive possibilities had not been realised in the way in which they are realised in recent plants. Already, before fertilisation, the seed seems to have reached maturity, and it is difficult to conceive how such a structure could have enlarged and accommodated rich supplies of food-material for the embryo. The real ovular stage was intercalated at a later date.

In point of fact our information as to the early developmental stages of Palæozoic seeds is exceedingly meagre. Renault has described young Cordaites seeds, and these were already pollinated; but we know nothing as to the time of pollination in *Stephanospermum*. The mature seeds contain pollen; two slightly younger stages, one figured in the present paper (Pl. 42. fig. 13), are without pollen; but these preparations are neither numerous nor favourable enough to justify any confident inference as to the time of pollination. Nor, on the other hand, can we assume that these seeds were pollinated, like *Cordaites*, whilst quite small; for the latter type is immensely old, and its seeds are not necessarily on quite the same plane of evolution as *Stephanospermum*.

If it be recognised that the nearest affinities of recent Cycads lie with the *Lyginodendron*-branch of the Cycadofilices rather than with the Stephanospermeæ, it almost follows that the latter have died out and are unrepresented in the existing flora. The apparent perfection of the vascular mantle in *Stephanospermum* may have proved an obstacle to further development. And if this type of seed should be shown to have belonged to a *Medullosa*-type of stem, have we not in their conjunction an over-elaborated organisation marked out for subsequent decline?

The phylogenetic history of so specialised a seed-type as *Stephanospermum* is extremely obscure. It may be conjectured that the pollen-chamber corresponds to some modification of sporangial dehiscence, whilst the tracheal mantle finds its analogue in an unassigned fossil sporangium with tracheal lining from the same horizon†. The morphological nature of the integument is no less obscure.

* D. H. Scott, "The Seed-like Fructification of *Lepidocarpon* &c.," Phil. Trans. series B, vol. 194, p. 291.

† "A Vascular Sporangium," New Phytologist, vol. i. 1902, p. 60.—A type of sporangium that may be termed conveniently *Tracheotheca*.

In conclusion, I would express my obligations to Dr. Smith Woodward, F.R.S., to whom I am indebted for access to the Williamson and other collections in the Geological Department of the Natural History Museum, and for facilities in preparing sections of some of the seeds in his custody; to Mrs. A. G. Tansley, who has rendered great assistance in preparing sections of recent plants for purposes of comparison; and to Dr. D. H. Scott, F.R.S., who has given me much encouragement in the course of this investigation. My thanks are also due to Mr. A. K. Coomáraswámy and to Mr. W. Tams for the photographs which accompany this paper.

[The opportunity afforded by the passage of this paper through the press has been utilised to revise certain portions in correspondence with the facts that have accrued since it was written.—F. W. O., *February* 1904.]

EXPLANATION OF THE PLATES.

Figures 1–16, *Stephanospermum akenioides*; 17–20, *Stephanospermum caryoides*: all taken direct from the sections. Almost all should be examined with the aid of a lens. Figures 1–16 are from photographs by Mr. W. Tams, of Cambridge; 17–20 by Mr. A. K. Coomáraswámy, B.Sc., F.L.S. Figures 29, 38, 41, and 43 are from drawings by Mr. G. T. Gwilliam.

PLATE 41.

Stephanospermum akenioides, Brongniart.

- Figs. 1, A & B. Median longitudinal section of apex and base. A narrow zone from the middle part of the seed alone is unrepresented in the two figures. The most noteworthy feature here shown is the relation of the collar to micropyle and nucellar apex. Shown on a large scale in Pl. 43. fig. 29. *c.*, crown; *co.*, collar; *end.t.*, remains of endotesta; *n.e.*, epidermis of nucellus; *pa.*, basal papilla; *p.c.*, pollen-chamber, much macerated; *t.d.*, tracheal disc at the chalaza; *v.b.*, the entering vascular bundle. $\times 15$. S 6 A *. (See pp. 363, 365.)
- Fig. 2. Median longitudinal section of micropyle and pollen-chamber. In the latter is a cluster of pollen-grains excellently preserved. Figs. 14 and 16 show the pollen under higher magnification, as also do figs. 30, 31, and 35. *co.*, collar, cut a little tangentially; *h.*, remains of hairs which lined the perimicropylar trough; *m.w.*, wall of macrospore; *s.* is level with the remains of septum between the pollen-chamber and the supra-archegonial gap (*s.a.g.*); *sh.*, shoulder (*i. e.*, tissue of nucellus forming side of pollen-chamber). A more highly magnified view of a portion of the shoulder is given in fig. 11. $\times 15$. S 7 A. (See p. 369.)
- Fig. 3. Median longitudinal section through pollen-chamber with pollen. Most of the grains are congregated near the apex of the chamber, a few (*p.*¹) with the small abortive grains adjacent to it and the abortive grain (*p.*²) have been drawn down, previous to mineralisation,

* The reference letter and number refer to the slides upon which the photographs or drawings are based. Where not specially indicated, the slides are in the University College collection.

to the level of the septum or diaphragm (*d.*) or even lower into the supra-archegonial gap. *pr.*, prothallium with a well-marked archegonium (*ar.*); *p.g.*, an abortive pollen-grain trapped in the nucellar canal; *co.*, the collar (*cf.* fig. 1 A), a persistent detached portion of the epidermis; *cc.*, ill-preserved remains of displaced endotesta; *e.*, epidermis of nucellus. $\times 30$. S 2. (See p. 371.)

- Fig. 4. Transverse section of the sclerotesta. *p.*, the palisade-layer showing the filamentous and often spiral contents with lenticular enlargements at places (*cf.* Pl. 43. figs. 22, 23, & 24); *f.*, longitudinally running fibrous layer; *et.*, epithelioid lining of the sclerotesta; *n.e.*, ill-preserved epidermis of the nucellus. The intermediate endotesta between *et.* and *n.e.* not shown. $\times 145$. S 17 c. (See p. 364.)
- Fig. 5. A somewhat tangential longitudinal section of the apex of a seed. Wall of pollen-chamber and sclerotesta badly preserved. Supra-archegonial gap and septum well shown. The strands within the crown (*h.*) are excellently shown. $\times 17$. S 1 A. (See p. 365.)
- Fig. 6. Median longitudinal section through the micropyle. *et.*, epithelioid lining of sclerotesta. The nucellar beak is not preserved, but two fragments of the collar are preserved to right of apex of nucellus. Within the pollen-chamber, three large normal pollen-grains and one abortive. The grain *p.* is much enlarged in Pl. 44. figs. 32, 33, & 34. $\times 14$. S 8 A. (See p. 371.)
- Fig. 7. Median longitudinal section through the base of the seed represented in fig. 6. The entering bundle and tracheal disc are well shown, as are the general relations of the parts at the base of the seed. *a*, point at which the macrospore has separated from the wall of nucellus. The chalaza is represented in detail in Pl. 43. fig. 21. $\times 15$. S 8 B. (See p. 367.)
- Fig. 9. Tangential section through corner of supra-archegonial gap, showing the tracheides passing into the space. The section follows the plane running obliquely down from *a* in fig. 10. A group of these tracheides is drawn much enlarged in Pl. 43. fig. 28. *m.w.*, macrospore-wall; *ep.*, epidermis of nucellus. $\times 80$. S 9 c. (See p. 369.)

PLATE 42.

- Fig. 8. Left-hand corner supra-archegonial gap—from the same specimen as fig. 10, but with the angle here directed upwards. Shows the tracheal sheath (*tr.*) splitting into an upper layer (*tr.*¹) lining the side of the gap, and a lower layer (*tr.*²) resting on the macrospore-wall (*m.w.*). *n.e.*, epidermis of nucellus. $\times 155$. S 12. (See p. 369.)
- Fig. 10. Tangential section through apex of seed. Shows strands on the summit. The epithelioid lining of the sclerotesta is admirably preserved. Of the pollen-chamber only the flanking tissue (shoulder) is shown. The supra-archegonial space is conspicuous. *a* to left-hand bottom corner, plane of section from which fig. 9 was taken. $\times 14$. S 12. (See p. 369.)
- Fig. 11. Longitudinal section of lower portions of shoulder from same section as fig. 2. *sh.*, tissue of shoulder; *p.c.*, corner of pollen-chamber; *s.*, septum (*i.e.*, remains of floor of pollen-chamber); *s.a.g.*, supra-archegonial gap; *tr.*, tracheides attached to the septum, also drawn-out spirals lying free in the gap. $\times 105$. S 7 A. (See p. 369.)
- Fig. 12. Longitudinal section very similar to fig. 10. The supra-archegonial gap has numerous drawn-out tracheides in the angle, admirably shown (*tr.*). $\times 30$. S 7 B. (See p. 369.)
- Fig. 13. Longitudinal section of apex of nucellus of a rather younger seed than those usually found. *end.t.*, endotesta; *s.t.*, sclerotesta; *p.c.*, the quite small pollen-chamber; *s.a.g.*, supra-archegonial gap—in this case developed by a splitting of the tissue immediately below the tracheal sheath, $\times \times$ mark the region of splitting; *e.t.*, displaced cell belonging to the epithelial lining of sclerotesta; *tr.*, the tracheal zone; *ar.*, archegonium. $\times 30$. S 3 A. (See p. 370.)

- Fig. 14. Apex of pollen-chamber and group of pollen-grains represented in fig. 2. $p.$, grain with internal cells in surface view; $p.^1$, longitudinal oblique section of a grain showing "replum"; $p.^2$, transverse section of a grain showing internal walls—this grain is drawn in Pl. 43. figs. 30 & 31; $p.^3$, grain in longitudinal section showing replum, drawn in Pl. 44. fig. 35; $p.^2$ and $p.^3$ also shown enlarged in fig. 16; $co.$, collar. $\times 58$. S 7 A. (See p. 376.)
- Fig. 15. Apex of nucellus in longitudinal section. Resting on the apex is the collar ($co.$). In the pollen-chamber a large pollen-grain with internal cells showing and a papilla on its underside; three abortive foreign pollen-grains are also present. $\times 16$. Williamson Collection 1486 a. (See p. 378.)
- Fig. 16. The two right-hand pollen-grains of figs. 2 and 14, much enlarged. $p.^2$, in transverse section, showing the internal walls; $ex.$, exospore: this grain is represented in Pl. 43. figs. 30 & 31. $p.^3$, in longitudinal section, showing replum within: this grain is represented in Pl. 44. fig. 35. $\times 100$. S 7 A. (See p. 376.)

Stephanospermum caryoides, n. sp.

- Fig. 17. Almost median longitudinal section of the seed. The black sclerotesta is in contact with the matrix. The micropyle, funnel-shaped, is seen at the summit. The nucellus is remote from the sclerotesta, except at the base, the space being somewhat increased, but not very much, owing to the three fissures in the preparation. The pollen-chamber is very broad, with well-preserved shoulder-tissue at the sides. The large embryo-sac contains the prothallium in its upper half. On the left-hand side of the embryo-sac the double membrane has resulted from the epithelium of the sclerotesta having separated from the latter till it touches the nucellar wall just where this is fractured. At f the dark fragments represent a portion of the macrospore-wall and overlying tracheal sheath that have become detached from their position and carried into the embryo-sac. This happened prior to mineralisation. a indicates the apex of the nucellus. In the matrix to the left is a Cordaitan bud. $\times 3$. S' 1 A. (See p. 374.)
- Fig. 18. Part of pollen-chamber and shoulder from the same specimen. Lying at the side of the pollen-chamber is an intact pollen-grain ($p.^2$) and a pair of internal cells from another grain ($p.^3$). $s.$, septum, *i.e.* lower limit of pollen-chamber, below which is the narrow supra-archegonial gap. On the right the macrospore is broken through (*cf.* fig. 17). $\times 20$. S' 1 A. (See p. 375.)
- Fig. 19. A pair of tracheides from the tracheal mantle. Their average diameter is about 27μ . $\times 165$. S' 1 A. (See p. 375.)
- Fig. 20. Secondary cell-reticulum contained in the cell b of Pl. 44. fig. 42. $\times 250$. S' 1 A. (See p. 381.)

PLATE 43.

Stephanospermum akenioides, Brongniart.

- Fig. 21. Median longitudinal section through a portion of the base of the seed shown in fig. 7. The entering vascular bundle ($v.b.$), tracheal disc ($t.d.$), and tracheal mantle ($t.m.$) are found in continuity. The bundle is accompanied by a layer of parenchyma ($sh.$), which expands below the tracheal disc into the parenchymatous layer ($p.$), which is continued as the crushed hypoderm of the nucellus. Below the parenchyma is a plate of sclerised cells with carbonaceous contents ($scl.$). Distally, this plate is attached to the angle of confluence of the

epithelioid lining of the sclerotesta (*e.t.*) and nucellar epidermis (*n.e.*). *s.t.*, sclerotesta; *l.p.*, long palisade-cells of this layer adjacent to the entering bundle; *m.w.*, retracted wall of macrospore. $\times 65$. S 8 B. (See p. 365.)

- Figs. 22, 23, and 24. Cells from the sclerotesta showing admirable "cytological" preservation. Fig. 22 represents the adjacent ends of two cells from one of the deeper-lying layers: the paired convergent processes on either side of the transverse wall resemble the protoplasmic processes occupying the pits; in the spindle-shaped enlargements nuclei are present. Fig. 23, one of the shorter cells from the second layer of the sclerotesta. Fig. 24, a palisade-cell with nuclear vesicle (*n.*) and spirally twisted protoplast. At the inner extremity are two pit-processes (*p.*); at the surface one of the broad conical vacuole-like structures (*v.*) so commonly found in this position. Cf. fig. 4. $\times 400$. S 8 B. (See p. 365.)
- Fig. 25. Tangential section through the palisade-layer of the sclerotesta. The middle lamella and thickening layers of the wall are shown, and in a few of the cells the thread-like protoplasts as dots in the cell-cavities. $\times 200$. S 19 A. (See p. 365.)
- Fig. 26. Tangential section through the epidermis of the nucellus, showing three cells with the characteristic carbonised contents. At the top of the figure the section traverses the tracheal mantle, portions of two of these elements being represented. $\times 240$. S 9 c.
- Fig. 27. Two of the short and rather irregular tracheides from the tracheal disc shown in fig. 21. $\times 550$. S 8 B. (See p. 367.)
- Fig. 28. A small portion of the tracheal mantle where the elements are somewhat isolated as they pass into the supra-archegonial gap. They are from the same specimen as fig. 9. $\times 285$. S 9 c. (See p. 369.)
- Fig. 29. Median longitudinal section of micropyle, collar, and apex of nucellus, showing these parts in greater detail than in fig. 1 A. *m.*, micropyle occupied by the nucellar beak, *b.*; *co.*, collar; *x, x*, the symmetrically placed regions on either side at which the preservation of the collar ceases; *p.c.*, upper part of pollen-chamber; *a.*, apex of residue of nucellus after detachment of funnel-like beak; *e.t.*, epithelioid lining sclerotesta. $\times 80$. S 6 A. (See p. 371.)
- Fig. 30. Pollen-grain cut in transverse section, showing internal walls (*a-e*) meeting at the centre of the section. *ex.*, exospore running obliquely towards the pole of the grain. The same pollen-grain is represented in fig. 16, *p.*² $\times 180$. S 7 A. (See p. 376.)
- Fig. 31. The same section drawn from a deeper optical plane. Lettering as in fig. 30.

PLATE 44.

- Figs. 32, 33, and 34. Three views of one pollen-grain cut in almost longitudinal section. Figs. 32 and 34 represent the two surfaces of the section, fig. 33 an optical section midway between them. The cells of the grain have come apart at the centre, leaving a space (fig. 33, *c*) in which the remains of the axis of union of the membranes is obscurely seen (*n*). *w.*, perforations in the walls of the internal cells. The pollen-grain here illustrated is marked *p.* in fig. 6. $\times 250$. S 8 A. (See p. 377.)
- Fig. 35. Pollen-grain marked *p.*³ in Pl. 42. figs. 14 & 16. *ex.*, exospore; *c.*, internal cells; *c.b.*, central body or remains of joined internal angles of the cells, at *b* still continuous with a radial wall. *d* indicates approximate plane of transv. section represented in fig. 16, *p.*², and figs. 30 & 31; *e, f*, approx. plane of section of pollen-grain, *p.*¹, fig. 14. $\times 235$. S 7 A. (See p. 377.)

Stephanospermum caryoides, n. sp.

- Fig. 36. Median longitudinal section of apex of seed, showing the micropyle (*m.*), perimicropylar area, and strands; *n*, summit of pollen-chamber. $\times 10$. S' 1 A. (See p. 373.)
- Fig. 37. Portion of a hair or branching strand of cells from the perimicropylar area. $\times 330$. S' 1 c. (See p. 374.)
- Fig. 38. Apex of nucellus with insertion of nucellar beak. *n.e.*, epidermis of nucellus; the pollen-chamber is below. A nearly horizontal fissure traverses two-thirds of the region drawn. $\times 65$. S' 1 B. (See p. 374.)
- Fig. 39. Tracheides from the nucellar wall. $\times 370$. S' 1 B. (See p. 375.)
- Fig. 40. Pollen-grain *p.* in text-fig. 2 (p. 380). *a* and *b*, internal cells; *c*, blister-like excrescence of outer wall; *tr.s.*, indication of triradiate mark on the grain. $\times 280$. S' 1 B. (See p. 380.)
- Fig. 41. Pollen-grain fragment *p.*¹ in text-fig. 2. The cell contains a secondary reticulum of possible antherozoid mother-cells. *w*, exospore. $\times 650$. S' 1 A. (See p. 381.)
- Fig. 42. Pollen-group *p.*², *p.*³ from fig. 18. *p.*², intact pollen-grain showing the triradiate mark; *p.*³, pollen-fragment of two internal cells, *a* and *b*, latter represented in fig. 20. $\times 310$. S' 1 A. (See p. 381.)
- Fig. 43. Two conjectured antherozoids in the petrified mucilage on the floor of the pollen-chamber. $\times 465$. S' 1 A. (See p. 383.)

F.W. Oliver &
G.T. Gwilliam del.

J.N. Fitch lith & imp.

STRUCTURE OF STEPHANOSPERMUM.

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