The Ovules of the older Gymnosperms [1].

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With Plate XXIV and a Figure in the Text.

THE seeds of most recent Conifers are fully siphonogamous, and their organization exhibits an adaptation in complete harmony with this type of fertilization—the most perfect that has been evolved by aërial plants. But if there is any conclusion in phylogeny on which we may confidently rely, it is that the method of fertilization by pollen-tubes has been evolved from zoidiogamy, the type of fertilization characteristic of an aquatic ancestor. The discovery of motile spermatozoids in the Cycads and in *Ginkgo* indeed places a coping-stone on the edifice of Hofmeister's generalizations.

The pollen-tube of the Conifer affords so simple and direct a means of effecting fertilization that we recognize that an ovule of relatively simple construction offers adequate facilities for the accomplishment of this process. But the instant we turn to *Cycas* or *Ginkgo*, where zoidiogamy prevails, the ovule is seen to be much more complex. Not only do we find a special chamber excavated in the apex of the nucellus for the reception of the pollen, but the ovule is also provided

[1] This article is based on a lecture delivered by the writer before the Botanical Section of the British Association for the Advancement of Science at its meeting in Belfast, September, 1902.

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with a fairly complicated vascular system. When we pass from these most archaic of living Phanerogams to the various Gymnospermous seeds found in the palaeozoic rocks, seeds which there is every reason to believe possessed an even less specialized type of zoidiogamy than obtains in recent Cycads, we are struck with the importance and dimensions of the pollen-chamber and with the very complicated vascular system which embraces the body of the nucellus. These older seeds needed to be complex to neutralize the disadvantages of their ancestry. In them, whilst the macrospore is retained, the microspore still liberates spermatozoids on the nucellus. The arrangement, viewed in the light of what we find in more recent plants, may be a clumsy makeshift, but it was probably an essential link in the evolution of more perfect arrangements. The central principle of zoidiogamy is still there, hedged about by contrivances so that it may be carried out, independent of chance water-supply, by land-growing plants. With the appearance of siphonogamy these contrivances became obsolete, and the modern ovule is a reduced and comparatively simple structure from which traces of the ancestral history have in large degree vanished.

The object of the present paper is to draw attention to the details of some of these older seeds, and to trace the modifications that seem to have occurred *pari passu* with the evolution of more perfect methods in the transportation of the male cells. And in so doing it is hardly possible to ignore certain other changes that have taken place in the structure of the ovule, changes involving an enlargement of its functions so that it has become as well a temporary resting-place or brood-chamber for the embryo. The discussion in the following pages will include a consideration (1) of the ordinary palaeozoic types of seed so well represented in the French permo-carboniferous and described by Brongniart and Renault; (2) of *Lagenostoma*, a peculiar type found in the lower coal-measures of Lancashire and Yorkshire, and standing somewhat apart from the French palaeozoic seeds; (3) of recent Cycads; and (4) of *Torreya*, a remark-

able genus of Taxaceae, which though siphonogamous yet appears to retain marked traces of those contrivances which usually became obsolete when siphonogamy appeared. Finally we can hardly close this article without some allusion to such elementary seed-like structures as have been described, with a view to linking up the Seed Plants with the true Pteridophytes. But in this department, though facts that will be of the greatest value hereafter have already come to light, some time must elapse before we are able to realize step by step the manner of origination of the earliest seeds.

1. Ordinary Palaeozoic Seed Types.

These in their simplest form are represented by *Stephanospermum* [1], a small unassigned seed some 10 mm. in length, 5 mm. in diameter, and circular in transverse section. This seed may be taken as the type of a group of radially symmetrical seeds—many with ridges and other excrescences often fantastic in character. For convenience all such forms were ranged together provisionally by Brongniart, and for the sake of easy reference may be termed the Radiospermeae (=Brongniart's Group B) [2], in contradistinction to the flattened seeds or Platyspermeae (=Brongniart's Group A) of which a few are known to belong to the Cordaiteae.

The members of these two provisional groups differ in other respects than in their form. Whilst the Radiospermeae, with rare exceptions [3], possessed a bony integument only, the Platyspermeae were in all cases provided with an additional external fleshy layer, the sarcotesta. And there were further differences in the internal organization of these two groups, though they are not of such a character as to upset the broad general resemblance that embraces all these seeds. In the briefest possible manner a type from each group may now be

[1] Cf. Brongniart, Les graines fossiles silicifiées, Pl. XVI.

[2] Brongniart, loc. cit., p. 20.

[3] *Trigonocarpus pusillus*, Brongniart, and *Tripterospermum*, in the sense of Brongniart. Cf. loc. cit., p. 26, footnote. These had a sarcotesta in addition to a bony scelerotesta.

described, *Stephanospermum* as a Radiosperm, *Cardiocarpus* as a Platysperm.

Stephanospermum is a small cylindrical seed with sharply-pointed apex. It consists of a straight nucellus enclosed in a hard bony integument. The chalaza is at the base, the micropyle at the apex. Its general organization may be apprehended by reference to Pl. XXIV, Fig. 10. This diagram is drawn for another purpose, but if the outer light layer of the integument and the red strand which runs along its inner margin be ignored, and the entering chalazal bundle be regarded as quite simple (as it is in Fig. 1), then we have an ordinary Radiosperm. A special study of *Stephanospermum* seems to show that the nucellus stands up freely within the integument, and though this is a point of some importance it is one that has been definitely ascertained in relatively few of these seeds. The apex of the nucellus is occupied by an extensive pollen-chamber which is accurately centred to the micropyle, with which its perforated apex seems to have engaged. The body of the nucellus is occupied by the macrospore and its contained prothallium. The chalazal strand of tracheides expands at the base of the nucellus into a tracheal plate, the margins of which are continued in the wall of the nucellus right up to the pollen-chamber, the floor of which is paved with tracheides. The contained macrospore is thus completely invested in a thin mantle of tracheides. This mantle is exposed in Fig. 10, and is represented by a wash of red. Whilst some of the Radiosperms resembled *Stephanospermum* in possessing a continuous tracheal mantle, there were others in which the tracheides had become segregated into distinct strands[1] (as shown in the nucellus of Fig. 1).

The pollen-chamber often contains a number of large pluricellular pollen-grains that had been sucked into it no doubt in the ordinary way. Here it would seem they underwent a

[1] This was the case in *Tripterospermum*, *Gnetopsis*, *Codonospermum*, and *Aetheotesta*. In *Polylophospermum*, the intermediate condition of a coarse-meshed reticulum is sometimes found, perhaps the result of an enlargement of the nucellus.

period of maturation, and in due course liberated free-swimming spermatozoids. It is true spermatozoids have never been certainly recognized in these seeds, but that is a matter of small importance. The apex of the nucellus of *Cycas* and *Ginkgo* is similarly organized as a pollen-chamber, and in these cases it is well known that spermatozoids were liberated. But *Stephanospermum* is an older seed and exhibits more primitive characters than do the Cycads. Were fertilization effected by pollen-tubes the whole structure of the seed would be a contradiction. Whether or no the discharge of spermatozoids was accompanied by pustule-like projections from the surface of the grain is an open question. Such projections, very small in relation to the diameter of the pollen-grain, have been occasionally observed. The stage at which almost all these seeds have been preserved is that just preceding fertilization; only occasional specimens being met with in a slightly earlier stage of development. In referring to them the term *seed* is usually employed, though in recent Gymnosperms the corresponding stage would be called an unfertilized ovule. This usage in terminology has doubtless arisen from the appearance of maturity which their integumentary tissues present, a maturity which seems to preclude all possibility of subsequent expansion. In course of evolution, probably, the time of hardening of the integument was postponed till embryonic stages had set in, so that well-marked ovular and seed phases became recognizable; but in the palaeozoic seeds known to us such a distinction can hardly be drawn.

Whatever their differences in detail, the Radiosperms agree in that the nucellus is invested in a tracheal mantle or a number of tracheal strands, which, arising from the chalazal bundle, meet below the pollen-chamber, the floor of which they seem to have paved. Nor does their function seem difficult of interpretation. It was that of a mechanism for bringing water to the pollen-chamber. This would be important during the period of pollen-maturation and vital to the transport of motile spermatozoids at fertilization.

The pollen-chamber shows every indication of having been

excavated in the apex of the nucellus through a mucilaginous breakdown of the tissue there; and should the watery mucilage tend to concentrate through desiccation, fresh supplies of water would be drawn up from the tracheal system. Ultimately there is reason for supposing that the way to the archegonia (which lie much as in *Cycas*) was cleared for the passage of the spermatozoids by a further mucilaginous breakdown in that portion of the tracheal sheath which overlaid the summit of the macrospore; but in the tracheides outside the area of the pollen-chamber no such change is indicated. Whether it may not have happened in allied seeds that the nucellar tracheides stopped short from the first at the margin of the pollen-chamber, so that the necessity for their solution prior to fertilization did not arise, is a question difficult to answer. For it must be borne in mind that it would be difficult to discriminate between such a case, and one in which the tracheides had been locally absorbed. That is, of course, unless the state of preservation were remarkably good and the appropriate developmental stages forthcoming.

As regards the number of pollen-grains usually present in a pollen-chamber, it is impossible to speak other than broadly in consequence of the fact that even when a series of sections is obtained there is a considerable loss as a result of cutting and grinding. In the case of *Stephanospermum*, from twelve to twenty does not seem too generous an estimate; and if each of the twenty cells or so of which each pollen-grain consists be regarded as producing a single spermatozoid, that would allow from 240 to 400 of the latter. The distance to be traversed in the passage from the pollen-grain to the archegonium varies in this seed from ·5 to ·85 mm.

It will have been gathered from the foregoing that whilst the problem of water-supply in relation to free-swimming spermatozoids stood on a satisfactory footing, there still remained room for advance in the direction of greater precision in the mechanism as a whole. We still appear to have the promiscuous liberation of motile spermatozoids reminiscent of a heterosporous Pteridophyte.

Turning now to the Platysperms, we may take *Cardiocarpus* as their type. It is characterized by its flattened, heart-like form, and by the possession of a sarcotesta. As the supply-bundle enters at the chalaza and traverses the sarcotesta, it gives off a pair of bundles which run along the inner limit of that layer to the micropyle (as in Fig. 1). The plane in which these two bundles run is the plane of flattening, generally designated the principal plane of the seed [1]. The main bundle continues to the base of the nucellus, where it expands into the tracheal plate. From the margins of this plate a number of nucellar strands pass off peripherally in the wall of the nucellus and extend a variable distance in the direction of the pollen-chamber. And now we come to a difficulty not infrequent in the investigation of fossil seeds, the inadequacy of the preservation. In the first place there is some uncertainty as to the extent of freedom that obtained between nucellus and integument, and secondly as to the actual extent of the nucellar vascular system. If we turn to the works of the French investigators who have described these seeds, the impression gained is that the lower part of the nucellus is fused with the testa and that the tracheal strands travel upwards in the plane of fusion, ceasing where the nucellus becomes free. Brongniart's figure of one of these seeds, *Taxospermum Gruneri* [2], shows very clearly that the fusion in this case involved the basal fifth of the nucellus, but unfortunately the tracheides are not represented in his plate. Renault makes some allusion to the question, and speaks of the nucellar bundles reaching up to about one-third the height of the nucellus [3]. So that as far as the data are available it would seem quite probable that a certain

[1] In others of the Platyspermeae the entering bundle passes unbranched to the tracheal plate, the margins of which supply the nucellus in the usual way. The bundles for the sarcotesta, however, are inserted upon the under face of the tracheal plate, and running outwards and backwards penetrate the sclerotesta and curve round into the sarcotesta. This type is only a slight modification of that figured, and the two types occur in seeds so nearly resembling one another as to have been included by Brongniart under the same genus.

[2] Brongniart, loc. cit., Pl. XV, Figs. 1 and 2.

[3] B. Renault, Cours de bot. fossile, I, 1881, pp. 100–1c.

amount of fusion obtained amongst the Platysperms, and that the internal vascular system was restricted approximately to that zone. But it would be interesting to know, should the preservation permit of it, whether, and if so to what extent, the tracheal elements passed beyond the line of separation of nucellus and integument. For the structure of the seeds and the relations of the bundles recall in a very marked degree Cycadean characters (cf. Figs. 4 and 6). It is known that in certain Cycads (e.g. *Bowenia* and *Stangeria*[1]) the inner system of bundles does not lie quite in the plane of fusion of nucellus and integument, but that the bundles exhibit a centrifugal tendency and actually lie outside the arbitrary province of the nucellus, as determined by the downward continuation of the plane of separation of the free regions of nucellus and integument. Renault has noticed this centrifugal tendency in Brongniart's seed *Cardiocarpus Augustodunensis*, and in view of this point of contact with certain Cycads he has founded the new genus *Cycadinocarpus* for its reception[2].

In other respects, too, the Platysperms exhibit Cycadean features, among which may be mentioned the relatively small pollen-chamber as compared with the Radiosperms, whilst often, as W. H. Lang has pointed out, the cells of the beak of the nucellus are thickened in a corresponding manner[3]. The pollen in the pollen-chambers of these seeds is generally smaller in size than the elliptical multicellular pollen so frequently associated with the Radiosperms. Here, too, there is an internal cell-group, but it by no means fills the entire grain. That it was antheridial in nature, as suggested by D. H. Scott[4], rather than a vegetative prothallium, seems very probable. Whether spermatozoids were liberated directly from these pollen-grains, as has been suggested in the case of *Stephanospermum*, or whether they were led part of the way to the archegonia in tubes, as in recent Cycads, is a question

[1] I am indebted to Dr. W. H. Lang for much information concerning these and other Cycadean ovules.

[2] Flore fossile d'Autun et d'Épinac, pt. ii, p. 385.

[3] W. H. Lang, Annals of Botany, vol. xiv, p. 286.

[4] D. H. Scott, Studies in Fossil Botany, 1900, p. 436.

that cannot be considered, owing to the lack of data. It is just possible, of course, in view of the distinctly Cycadean tendencies of the Cordaitean seeds themselves, that this parallelism also involved the pollen; or, on the other hand, as D. H. Scott points out, the pollen-grains of *Cordaites* may have been a stage nearer the Cryptogamic microspore than those of *Cycas* or *Ginkgo*[1].

From what has been stated above it is evident that the Platyspermic (or Cordaitean) seeds must be carefully discriminated from the Radiospermic. The former show a marked approach to a parallelism with the ovules of recent Cycads, whilst the latter appear to exhibit more general and perhaps more primitive characters. That all these seeds belonged to plants of common if remote ancestry there can be little reasonable doubt in view of their general striking unity of organization. The types of seed possessed by these remote ancestors may have to a certain extent combined the characters of both these groups, as in the hypothetical Figures 1 and 10. Actually the seeds represented in these figures are symmetrical about a principal plane, but that modification has been introduced for purposes of comparison with certain recent seeds; here, regarding them as possible ancestral forms of the Radiospermeae and Platyspermeae, this implied flattening may be disregarded.

2. Lagenostoma.

This seed, belonging to the lower coal-measures, was in point of time considerably earlier than Brongniart's seeds from the French permo-carboniferous. Nevertheless, it shows marked and unusual peculiarities, and evidently stands somewhat apart from the generality of palaeozoic seeds. In consequence, it seems fitting to treat it apart from the other seeds of the primary rocks, though regarding it as a type analogous to the Cycad in certain respects.

The general organization of this seed is known from Wil-

[1] D. H. Scott, loc. cit., p. 435.

liamson's description of *Lagenostoma ovoides*[1]. It is a small seed, some $4\frac{1}{2}$ mm. × $2\frac{1}{2}$ mm., circular in transverse section, and belonging to the type with adnate integument and nucellus. These parts are free from one another in the region of the pollen-chamber alone, about one-fifth the whole length of the seed. The relations of the parts in median longitudinal section are given diagrammatically in Fig. 9. The free apex of the nucellus, the 'lagenostome' of Williamson, is transformed into a pollen-chamber (Fig. 9, *pc.*). The nucellar epidermis persists as the wall of the chamber (*pcw.*), the cavity of which has arisen by the separation of the central tissue from the wall. This central mass stands up freely from the floor as a cone of tissue (*cc.*), so that the actual pollen-chamber, in which numerous pollen-grains frequently occur, is a crevice that may be likened to the true cavity of a 'Sachsian bell-jar.'

Surrounding the pollen-chamber is the very complicated integument, of which only the general relations are seen in the longitudinal section. In the transverse section of the apex of the seed, represented in the adjacent text-figure, the integument is seen to consist of an outer zone *t.*, which is circular in transverse section, and an inner zone of (in the case figured) nine symmetrically disposed chambers which are separated from one another by strong radial plates. The internal angle of each chamber is convex, and their internal containing-walls form collectively a fluted membrane (*c.*) which was termed by Williamson the 'canopy.' The convexities of the canopy engage with corresponding concavities of the pollen-chamber wall. The space *g.* between the two membranes is the natural gap between nucellus and integument. The chambers which formed the canopy were occupied by soft parenchyma, whilst in each chamber a single tracheal strand ran longitudinally (*v.*, Text-fig. 20). These strands were direct prolongations of the system of strands which diverged from the entering supply-bundle of the chalaza, and ran up near the plane of 'fusion' of nucellus and integument

[1] On the Organization of the Fossil Plants of the Coal-Measures, pt. viii, Phil. Trans. 1877, pp. 233–43, and Figs. 53–75.

(Fig. 9). The seed appears to lack a sarcotesta, and so far agrees with such members of the Radiospermeae as had distinct nucellar bundles. But the chambered apex of the seed with its vascular prolongations constitutes an organ unique amongst the palaeozoic seeds. The peculiar form of the pollen-chamber is correlated with the distribution of the archegonia, which seem to have occupied a ring immediately beneath the bell-shaped crevice (as suggested in Fig. 9).

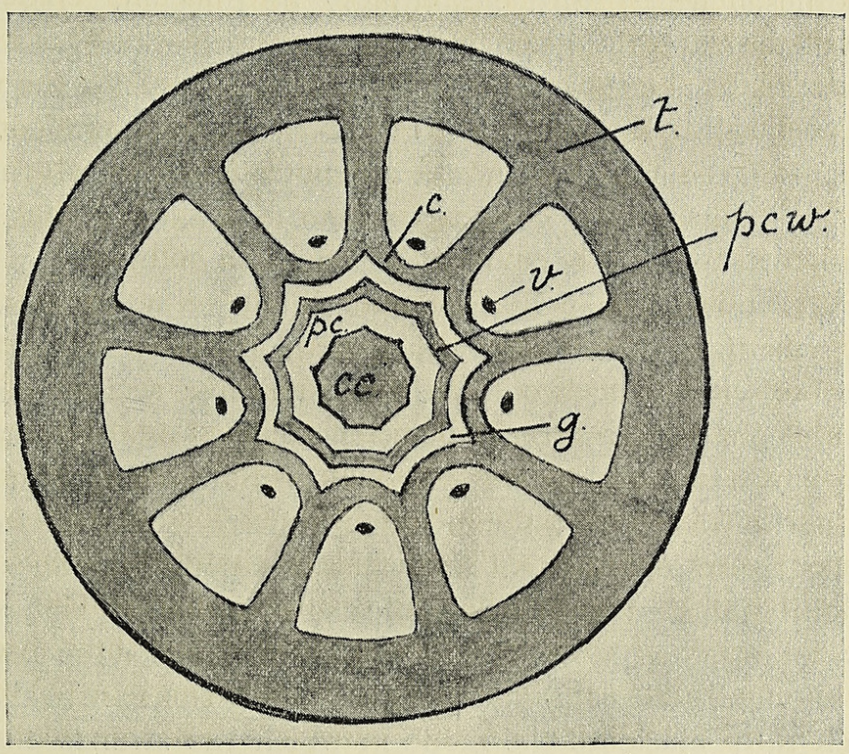


FIG. 20.—Transverse section of *Lagenostoma* cut near the apex at *v* in Fig. 9 (Pl. XXIV). The section traverses the pollen-chamber *pc.*, enclosed in its wall *pcw.*; *cc.* is the central cone of nucellar tissue; *t.* testa; *c.*, the fluted 'canopy'; *v.*, vascular strands running in the chambers of the 'canopy'; *g.*, chink between canopy and pollen-chamber wall. × 30 (From the 'New Phytologist.')

Compared with the ordinary palaeozoic type of seed, *Lagenostoma* seems peculiar in the lack of tracheal supply beneath its pollen-chamber. Assuming that this deficiency is real and not due to imperfect preservation, there are at least two possibilities open in respect of the course of events in the pollen-chamber. The pollen-grains themselves, though

not yet fully studied, seem to have been filled with a tissue as in the well-known case of *Stephanospermum*[1]. They would in that case belong to the old type, and it may reasonably be suspected that they liberated spermatozoids. A consideration of the relations of this pollen-chamber at one time suggested that perhaps the pollen-grains formed haustorial attachments in the central cone of parenchyma and behaved somewhat as in Cycads, but the best specimens give no support to such an hypothesis, which must accordingly be rejected. Another view is based on the peculiar relations of the micropyle. As shown in Fig. 9, the micropyle is plugged by the summit of the nucellus, so much so that if this condition obtained at pollination the intervention of a micropyle would be dispensed with. If, now, there were any reason for believing that the apices of the chambers of the canopy were porous, if the tracheal strands could be supposed to end in hydathodes, all the essentials of a contrivance for supplying the pollen-chamber with water would be present. For whatever may have been the natural position of the seed (pendent or erect), a drop of water at the summit would inevitably be drawn into the narrow crevice of the pollen-chamber. The specimens convey the impression that the wall of the pollen-chamber was so tightly jammed in the micropyle as to exclude the siphoning of water into the space *g*. (Fig. 9) which lies between the canopy and the true pollen-chamber. As yet no sections are available which fully elucidate the mode in which the strands end at the micropyle; but the preservation of this seed occasionally reaches such a high standard of excellence as to encourage the hope that such sections may eventually be forthcoming.

Sufficient has been said regarding *Lagenostoma* to show that whilst it resembled Cycads in the considerable area of 'fusion' that obtains between the nucellus and testa, as well as in the presence of vascular strands in the plane of 'fusion,' it is yet marked by peculiarities all its own. The confined form of the pollen-chamber marks an advance in precision on the open type of the ordinary palaeozoic seed,

[1] Cf. Renault, Cours de bot. fossile, IV, Pl. XXI, p. 99.

whilst in the canopy we seem to have a structure whose homology, like its function, is at present obscure. It would be premature to enter into any discussion as to the relations of this seed until its structure has been more fully elucidated.

3. Cycads.

The ovule in this group offers so general an agreement with the usual palaeozoic type that any view of its affinities seems inadmissible which excludes relationship with the Radiospermeae and Platyspermeae. The main difference is found in the fact that only at the apex are nucellus and integument free from one another.

The pollen on its entry into the pollen-chamber becomes rooted by haustorial attachments in the wall of the chamber. It thus obtains adequate nourishment for its further development. In due course the pollen-grain extremities of these tubes undergo a stretching, so that the sperm-cells are brought down close to the necks of the archegonia. Here they are liberated, the necessary fluid for their swimming being supplied, in some cases at any rate, from the tubes as they burst [1].

The distribution of the vascular system in the Cycadean ovule demands some consideration. Though the general plan is fundamentally the same throughout the group, there is considerable variation in detail in the different genera and even species. The case here set forth is that of *Cycas Rumphii* [2] (Figs. 4–8). The common supply-bundle gives off the branches to the integument before its actual entry into the ovule (Fig. 4 *sb.*), and then continues its course into the chalaza (*cb.*). The integumental bundles are two in number and run in the sarcotesta undivided to the micropyle. The plane in which they run is known as the principal plane of the ovule. Before these integumental bundles pass beyond the chalazal region, however, each gives off an internal

[1] H. J. Webber, Spermatogenesis and fecundation of Zamia, 1901.

[2] I have to acknowledge much assistance from Miss Edith Chick, in the study of the structure of Cycadean ovules.

bundle (*nb'*.) which constitutes the nucellar supply in the regions adjacent to the principal plane. The nucellar ring of bundles is completed by the strands which originate from the central chalazal bundle. Fig. 4 is a section in the principal plane, Fig. 5, in the plane at right angles to the principal plane. The nucellus is thus invested in a system of bundles of double origin. One portion, and here the chief portion, of the bundles has its origin in the central chalazal cord ; whilst on the flanks, i. e. adjacent to the principal plane, a limited number of bundles is supplied from the strands of the integument. These relations are fully exposed in Fig. 6, which represents an ovule with the integument of one side dissected away so that the nucellar bundles are laid bare. The principal plane is indicated by the line *p*., consequently the relations shown by this dissection are those that would obtain if Fig. 5 be imagined built up into a solid figure and not merely a section. For the sake of clearness the main supply-bundle (*sb*.) and the two groups of nucellar bundles which arise directly from its continuation are drawn in *black* in this figure (the same holds in Figs. 7 and 8), whilst those nucellar bundles that take their origin from the integumental bundle on the exposed side are coloured *red*. The point of insertion of the integumental bundle on the main supply-bundle is shown as a red spot (*ib*.), but the intervening connexions with the nucellar bundles *nb'*. (readily understood from Fig. 4) are for obvious reasons not represented. The transverse sections cut at the levels *A* and *B* (in Fig. 6) show that the series of bundles from the central cord (black in Figs. 8 and 7) reach nearer the pollen-chamber than those inserted upon the integumentary bundles (red in those Figs.). This disparity in the upward extension of the nucellar bundles is correlated with the fact that the groove between the free nucellus and integument extends considerably further down in the neighbourhood of the principal plane than it does elsewhere (cf. Fig. 6). The significance of this peculiarity in the course of the groove (which recurs also in *Torreya*, see p. 468) is obscure.

The arrangement of the strands in *Cycas Rumphii* is in close agreement with that shown by Warming to exist in *Cycas circinalis*[1]. But many other different types obtain according to the manner of joining up of the vascular strands at the chalaza. Thus in *Zamia* sp. (a complex case) the ovular supply is constituted from two bundles, each of which forks and joins again as they pass into the chalaza. Of these two reunited bundles, one supplies one-third of the integument and nothing more; the other gives off two bundles which supply the remaining two-thirds of the integument, whilst its continuation breaks up, supplying two-thirds of the nucellus. The remaining one-third of the nucellar ring is derived, relatively high up, from one of the two integumental bundles which arose lower down from this same system.

These varying types of chalazal branching seem consistent with the assumption that the whole of the body of the ovule, below the level at which the nucellus becomes free, is phylogenetically younger than its apical parts—that between the original ovule and its insertion a new region has been intercalated. This suggestion is embodied in Figs. 1, 2, and 3. In Fig. 1 is shown the conjectured ancestral palaeozoic type as described in the first section, but so far modified by the assumption of a plane of symmetry as to bring it in touch with a Cycadean ovule such as that of *C. Rumphii*. In Fig. 2 the possible mode of intercalation of a new zone is indicated by the broken lines (included under the bracket *b*.), all the structures of nucellus and integument being continued across this new zone. As the zone of stretching lies below the insertion of the nucellus, the gap between nucellus and integument finds no place in the new insertion. For the rest, however, it is a mere extension of the tissues of integument and nucellus. An ideal case is represented in Fig. 2, perhaps never realized, in which the bundles are all connected at the chalaza exactly as in the palaeozoic type (Fig. 1). With the basal extension of the ovule fresh distributions of the

[1] E. Warming, Recherches et remarques sur les Cycadées, 1877, p. 21 and Pl. III, Figs. 6–12.

bundles could take place, and in an instance like *Cycas Rumphii* it is readily comprehensible that a certain number of the nucellar strands in the neighbourhood of the principal plane might have joined up with the integumental bundles as shown in Fig. 3. In other cases, as in *Stangeria* where nucellar and integumental bundles appear to arise in common, the whole of the nucellar bundles may have undergone this change of insertion; whilst even in the complex *Zamia* it is possible to understand that the growing basal zone gave opportunity for the production of the anastomoses outlined above. But of course no attempt is made to offer a special explanation for each several case—that is out of the question. The suggestion made is a general inference from the facts, and its validity must depend on the degree in which it renders the structure of the Cycad ovules more intelligible than it was before. The main significance of this intercalation is probably nutritive—the provision of a suitable brood-chamber for the nursing of the embryo.

The other point that calls for notice here is the retreat of the nucellar bundles from the pollen-chamber (cf. Figs. 1, 2, and 3). In the Cycadean ovule they are no longer needed so urgently as in the palaeozoic seeds (especially the Radiosperms), mainly because the pollen effects haustorial attachments in the nucellar tissues, obtaining thus the water required in further development, and even for the swimming of the spermatozoids in their brief journey to the archegonium. In part, perhaps, the broader surface of continuity of the tissues of nucellus and integument (a result of the basal extension) would be a contributing factor in the decline of the water-excreting tracheal contrivance which was so conspicuous in palaeozoic times.

4. Torreya.

The facts of the vascular anatomy in the seeds of this genus of Taxaceae are peculiar and isolated among recent plants, and in the light of palaeozoic seeds would mark it as an archaic type even were *Torreya* not recognized as far back as

the lower Cretaceous. In the apparent retention of old features it exceeds either *Taxus* or *Cephalotaxus*, and its inaccessibility as an object of detailed investigation has left a regrettable lacuna in our knowledge of the Taxaceae. Whilst all details are reserved for treatment in a special memoir[1], certain of the facts of its ovular morphology may be outlined here.

Already in the winter buds the rudiments of nucellus and integument are discernible. By the beginning of May the latter overtops the former. Towards the end of this month basal stretching ensues, so that nucellus and integument are raised up slightly from the enclosing scales. From this intercalated zone a circular cushion projects, this is the future arillus. At the beginning of June the buds open, exposing the micropyles, and pollen is collected in the usual way. The arillus now grows rapidly and meets above the micropyle before the end of July. By this time pollen-tubes have developed, and these reach the embryo-sac early in September. Before the winter resting-period pro-embryos have been formed in the archegonia, whilst the base of the young seed has undergone considerable expansion. This expansion and further embryonic development is continued in the following spring. The most striking phase is that shown in July, when enormous expansion of the seed-base is manifested. This is followed by the differentiation of the stone, and by the autumn the drupe-like seed ripens and falls. During this second year a marked rumination of the endosperm develops, but this feature need not be described here.

The vascular system, indicated in the first year by strands of desmogen, undergoes no marked degree of differentiation till the approach of seed-ripening. Its distribution is indicated in red in Fig. 12. This diagram is a longitudinal section of a ripening seed cut in the principal plane, but the central light-red area must be regarded as convex as it represents the exposed surface of the nucellus. At the top of the figure

[1] For some time I have, in conjunction with Miss Edith Chick, been occupied upon an investigation of this genus, and it is with her sanction that I am enabled to utilize some of our results here.

are seen the free arillus (*a.*) and integument (*i.*) covering the free portion of the nucellus. The wall of the nucellus is thin, and the contained embryo-sac and endosperm are continued towards the base of the seed, as also are the arillus and integument. Two bundles enter the seed at the base, and whilst each may divide into two or more branches [1] in passing upwards, these branches unite again below the level at which arillus and integument are free from one another in the principal plane of the seed (*f.*). At this point the central portion of the reunited bundle dips suddenly inwards, penetrating the stony layer at a special shield-like area.

The two shield-like areas, right and left of and a little below the micropyle, form characteristic marks on the stone of the ripe seed when stripped of its fleshy arillus. The view of the stone in Fig. 13 shows one of these shields with the foramen (a dot) perforating it. The crescent-shaped area at the top of the seed, often covered by a thin translucent membrane, represents the outer surface of the integument where it is free from the arillus. It is noticeable that this area attains its greatest downward extension in the plane at right angles to the principal plane, whilst in the principal plane (*p.*) (i. e. the one which traverses the foramina) it is much narrower. Identical relations obtain between nucellus and integument.

After its passage through the stony layer of the integument, and as it traverses the soft tissue which lies between the internal aperture of the foramen and the base of the groove between nucellus and integument, the tracheal strand forks, the branches turning sharply away from the principal plane of the seed. These branches direct their course towards the groove between the nucellus and integument, striking the furrow of the groove a little below its highest point. These relations are somewhat elucidated in Fig. 14, a nearly transverse section across the seed at the level of the foramina. Outside is the arillus, then the stone (shaded dark) with a lining of soft parenchyma. The bridge which traverses the figure vertically is the nucellus joined to the integument above

[1] This branching is very marked in *T. nucifera.*

and below. The semicircular gaps (*g.*) on either side owe their existence to the fact that the nucellus is not at this level wholly merged in the integument. The bundle (red) is seen (below) traversing a foramen. The subsequent forking of the strand and the direction taken by its two branches are shown as though happening in one plane. On the other side (above) the section is so drawn as to show what happens at a slightly lower level. The integumental bundle is cut below the foramen of that side, whilst within the stone the descending branches of the strand that has penetrated the foramen (in a higher plane) are represented as red dots (*x*) in contact with the furrow between nucellus and integument.

It has been explained that the groove corresponding to the line of separation of nucellus and integument is highest opposite the foramen, lowest in the plane at right angles to the principal plane[1]. Here in the nearly ripe seed the bundle seems to lose itself in the curious hypoderm of the nucellus. Though the bundle at this stage cannot be traced further, in a younger seed (May of the second year), when only desmogen is present and tracheides are as yet not differentiated in the upper part of the seed, the desmogen-strands may be traced close to the angle of the groove right across till they meet the corresponding branches from the opposite side. The course followed by these desmogen-strands may be compared to that of the side ropes of a hammock, the two poles from which the hammock is suspended standing for the two main bundles of the seed which run outside the stone. In other words the strands from the foramina encircle the base of the free apex of the nucellus (cf. Fig. 12, the horizontal red line passing across). But true lignified tracheides do not seem to differentiate in these strands much beyond the point of forking of the primary strand, i. e. only quite a short distance within the interior aperture of the foramen. And in development differentiation comes late in the region of the foramen—coinciding with the hardening of the stone. As the summer advances there comes a period when tracheides are well shown in the bundle

[1] In *Cycas* this groove dips in the principal plane, see Fig. 6.

outside the foramen, but it was only by the middle of August of the second year that these elements could be recognized in the actual foramen and continuing to the place of forking.

A seed freshly picked at this stage and stood with its cut base in a watery solution of eosin sucked up the eosin by its xylem, and the pigment was drawn right through the foramina and a little distance further, i. e. up to the limit of differentiation of tracheides.

It has been stated that the desmogen-strands run right across from one foramen to the other, encircling the base of the free nucellus, but in the nearly ripe seed they can no longer be traced all the way. Running in the hypoderm of the nucellus in the angle of the groove between nucellus and integument they become merged in the peculiar hypoderm of the nucellus which becomes prominent in July. This tissue consists of large, thick-walled, mucilaginous, pitted cells of remarkable appearance which first arise in the nucellus adjacent to the trough, but ultimately appear in the downward continuation of the nucellus, everywhere enclosing the prothallium in a continuous sheath or mantle. This layer is very characteristic, and its protoplasm becomes filled with oily granules. Its actual signification is obscure without special investigation, but its appearance suggests that it serves in some way as a go-between in respect of food that is being transferred from the green assimilating layer of the arillus to the prothallium. Perhaps it may be termed provisionally a 'digestive layer.' It is in this layer that the strands from the foramina become lost. Indeed as a strand is followed from the forking-place the tracheides slowly die out and large mucilage cells begin, the impression gained from a study of these transition regions being that the mucilage cells and tracheides mutually exclude one another—that they are produced from identical structures.

For the completion of this brief account of the vascular system of the seed in *Torreya* one point remains to be added. It was stated at p. 468 that only the central portion of the reunited bundle turned sharply inwards and traversed the

foramen (cf. Fig. 12, *f.*). The flanks continue their course for an appreciable distance in the pulp outside the stone, and end in a mass of transfusion-tracheides at a point a little below the level at which the arillus becomes free from the integument (Fig. 12, *t.*).

The remarkable course of the bundles shown in this seed suggests a comparison with that found in Cycads and the palaeozoic seeds. At first sight *Torreya* seems so different that such a comparison must be vain. But bearing in mind the conclusion reached in the section dealing with the Cycads, as to the probability of the lower part of the seed being phylogenetically younger than the apex where nucellus and integument are free, and applying the same principle to *Torreya*, it seems possible to describe the latter in terms of the palaeozoic seed. For the purposes of this elucidation it is convenient to start with a form slightly modified from the supposed ancestral palaeozoic seed as in Fig. 10, a form differing from the type (Fig. 1) in that, instead of a single supply-bundle entering at the chalaza, we assume that there is a pair. Such a seed is shown cut longitudinally in the principal plane in Fig. 10. It resembles that given as the starting-point of *Cycas* in all other respects, except that the nucellar investment of tracheides is rendered as a continuous mantle and not as discrete bundles. (The red shade over the nucellus is to be regarded as representing the surface of the nucellus covered with its tracheal mantle.) From such a type *Torreya* may be derived by supposing that, at the time when a basal stretching of the ovule set in, this was accompanied by a marked rotation of the bundles which immediately connected with the tracheal plate at the base of the nucellus, so that one was carried some 80° to the right and the other a similar amount to the left. This process is sufficiently represented in the transitional Fig. 11, where the intercalated zone (under the bracket *b.*) is drawn in broken lines. It may be said that a marked feature of the evolution of this seed was the transverse expansion of the inner part of the chalaza which accompanied the general basal extension.

Concurrently the embryo-sac has extended down (as represented by arrows in Fig. 11) and occupied all the available space. To interpret the facts literally the tracheal plate (at the base of the nucellus in Fig. 10) has become stretched and split into a ring, and the embryo-sac has obtained an outle by extending right through this ring (Fig. 11). In the seed of *Torreya* the tracheal plate may be still represented by the desmogen-strands which appear in development reaching from one foramen to the other (Fig. 12). Here then we have a seed in which the stone ends blindly below, and the water-supply for the nucellus is brought up round the outside and led through the foramina to the base of the free apex. These two foramina represent the ancestral chalaza, which by a strange evolutionary freak now finds itself close to the apex of the orthotropous seed[1]!

As for the integumental bundles of the ancestral type, these have dwindled down in *Torreya* and are represented by the spurs *t.* (Fig. 12).

Finally, there is a temptation to wonder whether the peculiar 'digestive layer' of the nucellus which invests the embryo-sac may not be the palaeozoic tracheal mantle modified to meet present requirements. Its pitted, mucilaginous character indicates that it probably performs some transfusion function in connexion with the water supplied by the tracheal strands which penetrate the foramina, whilst the nature of its contents suggests that it also plays a part in some metabolic process. Though the surface of the nucellus is coloured red in Fig. 12, thus emphasizing this view, the suggestion is necessarily of the most tentative character.

From what has been written it would seem possible to derive the very dissimilar seeds of a Cycad and *Torreya* from something approximately identical with the supposed ancestral

[1] The actual relations of base and apex in the seed of *Torreya*, as well as some matters of minor detail, would appear to have been misapprehended by former writers. Cf. C. E. Bertrand, Ann. des sciences nat., Bot., 6e sér., tom. vii, pp. 72, 76, and Pl. XI, Figs. 1–6; also Bull. Soc. Bot. de France, 1883, p. 293. The same assertions appear in Renault's Cours de bot. fossile, IV, 1885, p. 77.

palaeozoic type. If this be true, it should be possible to realize at every stage in the evolution the factors that have led to a modification of the ancestral type or to the persistence of some of its characters. In the case of the Cycads this is beset with less difficulty. The chief factors suggested above were the attachment of the pollen-grains to the wall of the pollen-chamber by haustoria and the need for increased space for the nutrition of the embryo. In *Torreya*, however, the factors are less evident, though the presence of the enlarging embryo midway between the foramina just as the stone is hardening (end of July) may not be without significance (cf. Fig. 14, *e.*). The retention of the nucellar tracheal sheath as a mucilage layer (if it be homologous with the palaeozoic mantle) may be correlated with the exiguous nature of the water-supply, whilst its possible digestive function may also have a bearing. Otherwise the interior of the seed might become prematurely isolated from water-supplies. For, being completely siphonogamous like the other Taxaceae (*Taxus* and *Cephalotaxus*), its retention here cannot be attributed to the requirements of spermatozoids.

As for the other Conifers, they have lost their nucellar vascular systems, whilst the pollen-chamber is either quite obsolete or represented by the merest pouch. The base of the ovule has, however, generally undergone a marked extension.

The problem of the limit of the real ovule in Gymnosperms is not a new one. Strasburger made some allusion to the question years ago [1].

In another place I have emphasized the distinction drawn between the original ovule and the phylogenetically younger intercalation by proposing the terms *Archisperm* and *Hyposperm* to designate these regions. The phylogenetic history of a gymnospermous ovule may be compared to the case of an island rising out of the sea which becomes an inhabited centre of activity. As the elevation continues the original island becomes a remote mountain summit, whilst the newly-won

[1] Die Angiospermen und die Gymnospermen, pp. 124 and 134.

ground in its turn becomes the scene of active operations. In time the summit is little more than a land-mark, and is ultimately denuded away.

Whilst the consideration of these seeds from the palaeozoic rocks, together with those of recent Cycads and Taxaceae, tends to confirm the view that is held on many hands as to their common origin, it is evident that even the oldest forms show a marked advance on the condition that probably obtained in their pteridophytic ancestors. Whilst the work of recent years has tended to carry the lower limit of the Gymnosperms deep down into the Ferns, we are still in search of fern-sporangia exhibiting a tendency or capacity for seed-like adaptation. Along the line of the Lycopodineae such structures have become known to us in *Lepidocarpon*, the evident strobilus of a *Lepidodendron* bearing seed-like structures [1]. But in view of the probable Filicinean affinities of the Cycads and of the other Gymnosperms, *Lepidocarpon* is only of value for the moment as an analogy. It cannot be supposed that the Gymnosperms were evolved from the Lycopodinean phylum. A structure standing in the same relation to the probable fern-like ancestors of the Gymnosperms as *Lepidocarpon* does to the Lycopodineae has yet to be discovered. Whether the transverse section of an unidentified sporangium [2] showing a belt of tracheal elements between the sporangial wall and the mass of developing spores is likely to furnish a clue must await the identification of that sporangium. In any case the condition of vascularity in a fern-sporangium, which this specimen proves to have actually existed, may have been an important antecedent to the evolution of the vascular nucellus that played so considerable a part among the earlier Gymnosperms, and from which it may be reasonably supposed the ordinary Coniferous type of nucellus has been derived.

University College, London,
January, 1903.

[1] D. H. Scott, The Seed-like Fructification of Lepidocarpon. Phil. Trans., 1901, p. 291.

[2] A Vascular Sporangium, The New Phytologist, Vol. i, p. 60.

EXPLANATION OF THE FIGURES IN PLATE XXIV.

Illustrating Professor F. W. Oliver's paper on the Ovules of Gymnosperms.

In all cases red colour indicates tracheal tissues.

Fig. 1. A conjectural synthetic type of seed embodying the characters of such a seed as *Stephanospermum* with those of a *Cardiocarpus*.

Fig. 2. Hypothetic stage connecting the Cycadean ovule with the palaeozoic type. *b.*, the supposed intercalated younger zone.

Fig. 3. Ovule of *Cycas Rumphii*, cut in the principal plane. The dotted lines beneath the pollen-chamber indicate the shrinkage of the original nucellar strands.

Fig. 4. Section of ovule of *Cycas Rumphii* cut in the principal plane. *sb.*, main supply-bundle; *nb.*, insertion of nucellar bundles on the main strand; *nb'.*, nucellar bundle inserted on an integumental bundle; *ib.*, integumental bundle; *st.*, stone or sclerotesta.

Fig. 5. The same ovule cut in the plane at right angles to the principal plane. References as in Fig. 4.

Fig. 6. Ovule of *Cycas Rumphii* dissected so as to show the vascular system of the nucellus. The dotted line *p.* indicates the position of the principal plane of the ovule. The nucellar bundles (*nb'.*) that arise from an integumental bundle *are alone coloured red.* *ib.*, place of insertion of integumental bundle on the main supply-bundle. *AA.*, *B.B.*, heights at which the transverse sections represented in Figs. 8 and 7 respectively were cut. Other references as in Fig. 4.

Figs. 7 and 8. Transverse sections of the ovule represented in Fig. 6 at the heights *B* and *A*. The red dots in the nucellar circle of bundles in Fig. 7 are those which are inserted upon the integumental bundles. They have died out at the height at which Fig. 8 is cut.

Fig. 9. Diagrammatic median longitudinal section of *Lagenostoma*. *pc.*, pollen-chamber containing pollen-grains; *pcw.*, wall of pollen-chamber; *cc.*, the central cone of nucellar tissue in the pollen-chamber; *g.*, space between pollen-chamber wall and canopy; *c.*, canopy; *v.*, tracheal strand here running in a chamber of the canopy; *t.*, testa; *a.*, archegonium. The unshaded cavity of the chambers contained a soft parenchyma; the tissue within the shaded layer of the testa in the body of the seed was probably of the same character.

Fig. 10. Median longitudinal section of palaeozoic seed type for comparison with *Torreya*. The light red shade on the nucellus is to indicate a continuous tracheal mantle. Beneath the nucellus is the tracheal plate (dark red), and two supply-bundles each of which originates an integumental bundle.

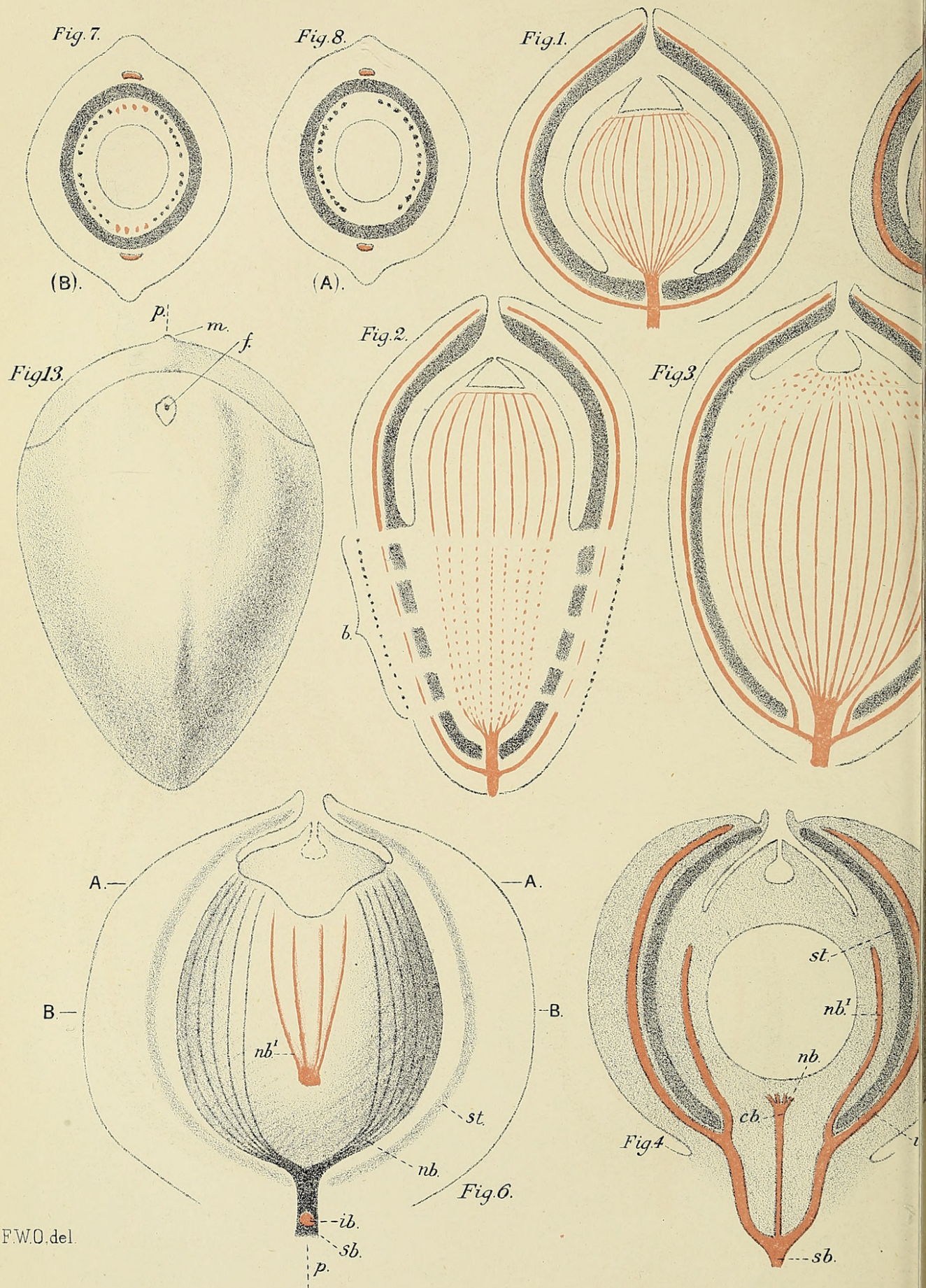
Fig. 11. Transitional type connecting with *Torreya*. At *b.* the broken lines indicate the position of the supposed intercalated zone. The dark red horizontal stripe across the nucellus is the stretched tracheal plate, now a ring. The arrows show the downward extension of the nucellus and embryo-sac.

Fig. 12. Median longitudinal section of seed of *Torreya* through the principal plane. *a.*, arillus; *i.*, integument becoming hardened; it is continued as a dark shaded layer right round the seed; *f.*, foramen perforating sclerotesta and allowing

vascular strand to pass to the base of the nucellus; the dark red stripe joining the two foramina represents the supposed traces of the tracheal plate; *t.*, mass of transfusion-tracheides; the old integumental bundles are supposed to be reduced to these spurs.

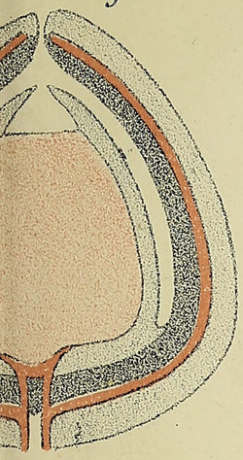
Fig. 13. View of stone of *Torreya Myristica* stripped of its fleshy arillus. The shield with foramen (*f.*) is near the apex; *m.*, micropyle; *p.*, principal plane. × 2.

Fig. 14. Cross-section of seed of *Torreya Myristica* so cut as to lie in the plane of one foramen (towards the bottom of the figure) and to pass *below* the other. The section is consequently not quite transverse. The red T (below) is the bundle traversing the foramen and its two branches which pass right and left in the direction of the furrows of the gaps (*g.*) here present on the flanks between nucellus and integument. The foot of the T represents the portion of the bundle which remains outside the stone (=*t.*, Fig. 12). On the other side of the seed the bundle is cut through a little below the foramen. The two detached red spots are the cross-sections of the strands which follow the groove. As these strands sag a good deal they can only be followed from *x* to *y* by examining a series of transverse sections. *e.*, embryo; *p.* prothallium; *ml.*, coloured pale red, represents the mucilage-layer of the nucellar wall; *i.*, integument, the dark shaded ring is the stone (sclerotesta), the lighter ring within it is also a part of the integument but of soft parenchyma (endotesta); *a.*, arillus. Had the section been cut a little nearer the apex, gaps would have appeared right and left between the integument and arillus. × 2.



OLIVER.— ON OLD GYMNOSPERMOUS SEEDS.

Fig.10.



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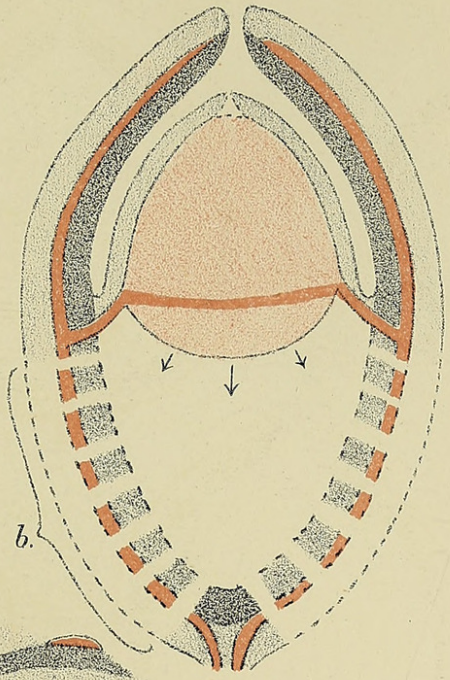
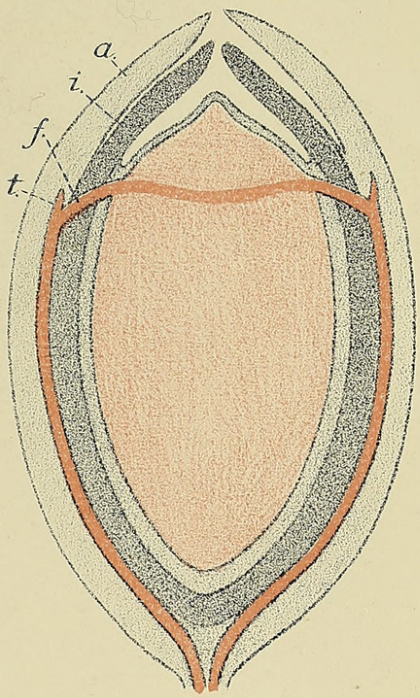


Fig.12.



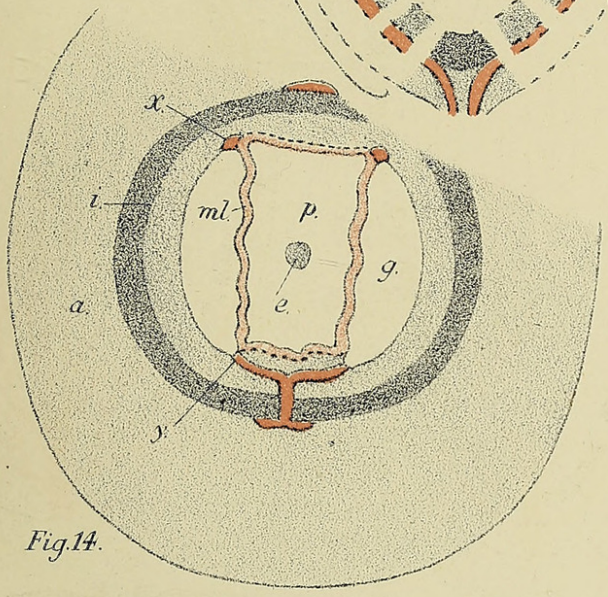
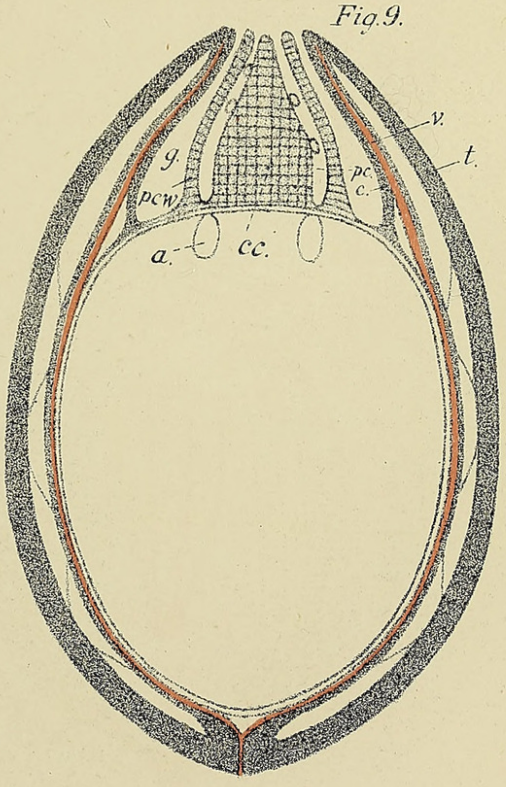


Fig.14.

Fig.9.



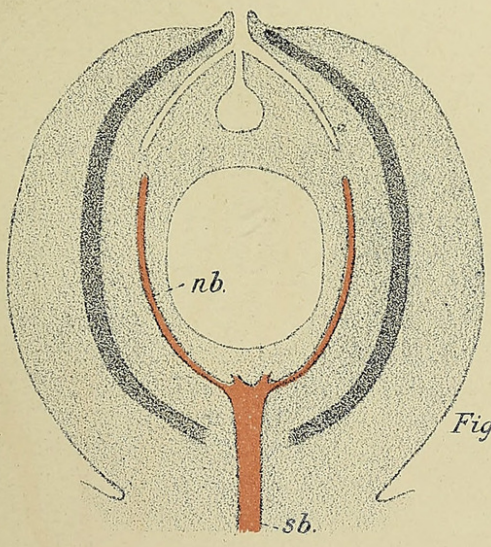


Fig.5.

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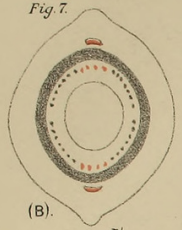

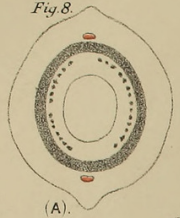

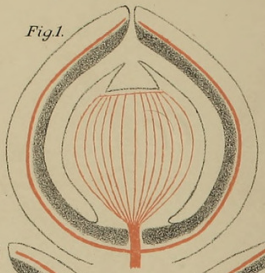

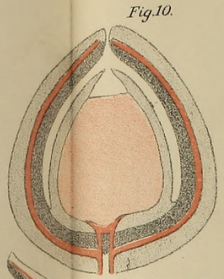

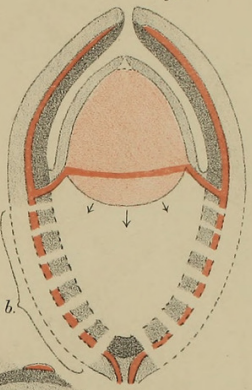

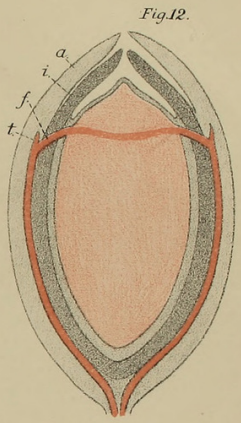

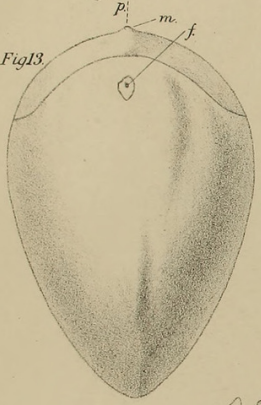

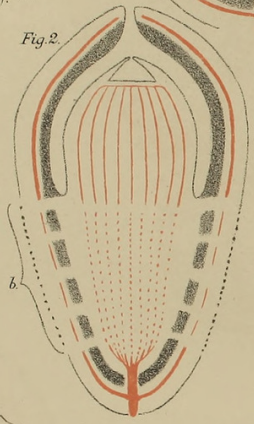

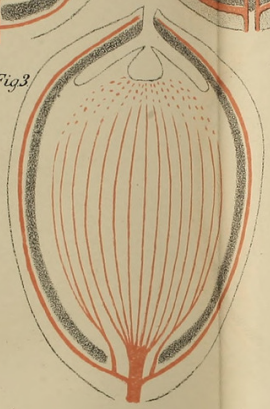

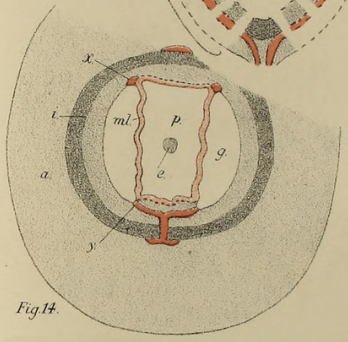

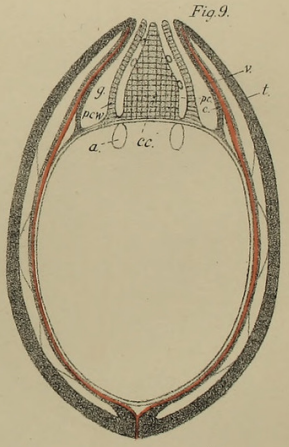

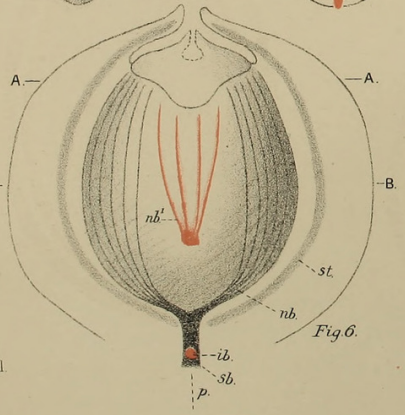

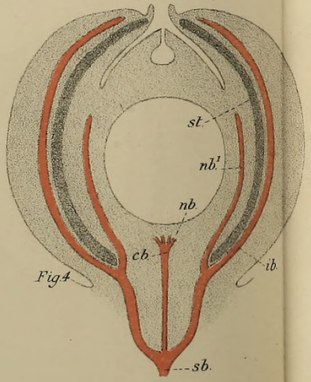

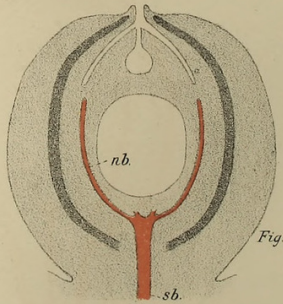

F.W.O. del.

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