On Certain Archaic Features in the Seed of *Taxus baccata*, with Remarks on the Antiquity of the Taxineae.

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With seven Figures in the Text.

INTRODUCTORY.

THE examination of *Taxus* seeds on which this paper is based was originally undertaken in connexion with an investigation of the New Caledonian genus *Acmopyle*, an account of which it is hoped to publish in the near future. In that paper the conclusion is expressed that the genera *Taxus*, *Torreya*, and *Cephalotaxus* are structurally so distinct from the Podocarps and other Conifers, that they deserve the rank of a separate phylum, Taxales,¹ having a clearer and more direct relation with *Ginkgo* and the Cordaitales than may be claimed for the remaining plants generally grouped under the Conifers. Since the following observations—which have a strong bearing upon the Cordaitan theory of the ancestry of Conifers—would have unduly lengthened my paper on *Acmopyle*, they are here published separately.

Professor Oliver's work (1903) has clearly shown that *Torreya* possesses one of the most primitively organized seeds known among living Gymnosperms. From his study of the seed of *Cephalotaxus* Worsdell (1900) has come to a similar conclusion with regard to this genus. These considerations, and the close similarity in general morphology between the ovuliferous shoots of *Cordaitea* and *Taxus*, impelled me to make a search for possible archaic features in the seed of *Taxus*, and to compare the latter with what we know of the structure of Cordaitan seeds.²

As a result of this comparison I have been led to conclude that, so far as seed-structure is concerned, (1) *Taxus* is in some respects more

¹ A name previously adopted by Lotsy (1911, p. 160), but not in the sense of a group equal in rank with the Coniferales.

² The previous investigations on the seed of this common plant, numerous as they are, have chiefly been conducted from the point of view of the structure and development of the nucellus, gametophytes, and embryo, while the minute study of the integument has been confined, so far as I know, to the comparatively young stages.

primitively organized than *Torreya*, and (2) the Taxales are in their affinities nearer to *Ginkgo* and to the Cordaitales than to any other known plants.¹ The general similarity which the seeds of *Torreya* and *Cephalotaxus* show to that of *Ginkgo* was recognized long ago (Lindley, 1836, p. 317; 1853, p. 231) by an association of these three genera in the same order (Taxaceae of Lindley), till the discovery of motile sperms in *Ginkgo* led to a separation of this genus as the sole survivor of an ancient phylum. The Ginkgoales are now universally regarded as being related on the one side to the Cycads, and on the other to the Cordaitales; especially to the latter group, of which they may claim to be more or less direct descendants. On the other hand, the retention of *Torreya* and *Cephalotaxus* in the position long ago assigned to them by Lindley (in the order Taxaceae, including such genera as *Dacrydium* and *Podocarpus*) has tended to emphasize their affinity with the Conifers. I venture to think that this emphasis has led to a false impression as to the affinities of the Yews, which, as already suggested, appear to lie rather with the Cordaitales and with *Ginkgo* than with the Podocarps. A further discussion of this question with special reference to the position of *Phyllocladus* will be given in my forthcoming paper on *Acmopyle*, but it may be stated here that the view that there is no close relation between the Yews and the Podocarps has previously been expressed by several authors, notably in a recent article by Dr. Scott (1911).

DESCRIPTIVE.

Ovule. The structure of the young ovule of *Taxus* is too well known to need further description. But the fact is worth recording, that in my microtome series of longitudinal sections (in the principal plane) a distinct vascular supply comes off from the two main supply bundles, and enters the base of the aril (Fig. 1). The aril supply is, however, so inconspicuous that it is not surprising that it escaped the notice of the earlier workers (Van Tieghem, 1869, p. 281; Strasburger, 1872, p. 4), who had only hand-sections at their disposal.

Young Seed. Owing to the hardness of the integument² the oldest stage of which coherent microtome sections were obtainable is that shown in Fig. 2. In this case the aril supply was completely obscured by the mass of very dark-staining tissue in that region. In the slightly earlier stage shown in Fig. 3 the supply to the aril is seen to consist of a row of scalariform tracheides; phloem could not be identified with certainty, so that the orientation of the aril supply is doubtful. In the figure the tracheides are shown in solid black, while the dotted region represents thin-walled elongated cells, possibly phloem.

¹ See also Lotsy (1911, p. 5), where a similar view has been expressed.

² It was necessary to keep the sliced seeds in melted paraffin (60°C. melting-point) for two to three months before sectioning.

After removal of the aril the bicarinate seed of *Taxus* shows a small elliptical disc slightly sunk into the base of the seed, and pierced by two ¹ minute foramina in the principal plane (Fig. 4, *a*). The longitudinal section shows that the disc consists of several layers of palisade-like simply pitted cells (Fig. 5, *a*) different from the thicker-walled and isodiametric stone-cells composing the rest of the shell (Fig. 5, *b*).

FIG. 1.

The foramina in the basal disc are the external openings of two straight canals which convey the two supply bundles of the seed obliquely upwards into the seed-cavity. In its further course towards the micropyle each strand steadily approaches the inner face of the shell, until at a short distance from the micropyle it actually comes into contact with the latter and runs along its inner surface for some little distance before dying out (compare the young stage in Fig. 1).

Special mention should be made of the fact that immediately after entering the seed-cavity each of the two supply bundles always shows

¹ Seeds with two or more planes of symmetry have a corresponding number of foramina (see Fig. 4, *b*, *c*).

a slight but easily noticeable thickening beyond which, instead of proceeding in the continuation of the canal, it bends sharply outwards so as to form a rather striking knee-like bend. The presence of these thickened angles in the bundles is a point on which I wish to lay stress, in spite of its apparent insignificance, for I have reason to believe that they mark the

FIG. 2.

points from which once branched off an 'internal' (nucellar) system of strands, now extinct in *Taxus*.¹

That I am able here to state my reason for this view, I owe to Prof. R. H. Compton, M.A., who very generously allowed me to examine the ovules of an extremely interesting new genus of Conifers recently

¹ It is indeed not impossible that if a sufficiently advanced stage of the seed could be sectioned—a process beset with practical difficulties owing to the bony sclerotesta—actual vestiges of an 'internal' vascular system might be discovered.

FIG. 3.

FIG. 5.

FIG. 4.

FIG. 6.

discovered by him in New Caledonia. So far as the female organs are concerned, this plant might at first be taken for a large-sized species of *Taxus*, the ovule being terminal on a bracteate axillary shoot, and the seed having a well-developed but free cup-shaped aril; but a noteworthy difference is that there is a distinct 'internal' (nucellar) vascular system. A fact of further significance from our point of view is that the nucellar strands branch off from the main bundles at points roughly corresponding to those in *Taxus*, which are here also marked by slightly thickened knee-like bends.

Attention may be drawn to the close proximity of the nucellus to the thickened knee-like bends in the strands of *Taxus* (Fig. 2). This part of the vascular supply is in fact nearer to the nucellus than is any other part.

Fig. 6 from a transverse section at the level ** in Fig. 2 is given to show the striking similarity to Sprecher's figure of *Ginkgo* (1907, p. 134, Fig. 143); the broken line shows the region along which, at a higher level, the aril separates off as a ring. The vascular bundles of the bracts are very close to the adaxial surface: in the inner pair of bracts they are extinct at this level, their positions being marked by crosses.

THEORETICAL.

In 1903 Professor Oliver, in his well-known paper on 'The Ovules of the Older Gymnosperms', showed how a seed like that of *Torreya* may be derived from a type such as the Palaeozoic *Cardiocarpus*, with a free nucellus and a centralized main vascular supply at the base, entering the seed-cavity through a single median foramen in the stone. He postulated longitudinal splitting of the main supply of the ancestral seed-type into the two strands which now pass into the seed-cavity through two foramina lying in the principal plane. At the same time it is supposed that during the ancestral history of *Torreya* the base of the seed underwent a marked transverse expansion,¹ with the result that these two foramina, while retaining their position in the principal plane, gradually receded from each other; and through the widening base of the seed the nucellus and megaspore bulged downwards into the apex of the seminiferous axis. This phylogenetically younger portion of the seed, conveniently termed by Professor Oliver the hyposperm, is in *Torreya* so large in proportion to the archisperm (defining the original limits of the seed) that the 'ancestral chalaza' is actually nearer to the micropyle than to the lower end of the entire seed.

¹ This transverse expansion of the seed-base must be distinguished from the longitudinal extension postulated by Professor Oliver in deriving the seed of *Cycas* from the same ancestral type. Both processes result in the intercalation of a new region at the base, but the main supply splits longitudinally in the one case, while in the other case it remains unaffected. In this paper we shall concern ourselves only with the former case.

If this has really been the course of events in the history of *Torreya*, the seed of this genus must belong to a truly isolated type, and would seem to be the result of specialization along a restricted side line. Nevertheless, the fact that the three known genera of *Taxales* so naturally fall into line with each other in most other respects justifies the expectation that it should be possible also to make the peculiar seed-organization of *Torreya* intelligible in terms of *Taxus* and *Cephalotaxus*. An attempt to do this is described in the following pages, which at the same time appear to corroborate in some detail the ingenious theory advanced by Professor Oliver sixteen years ago.

The two foramina in the basal disc of the sclerotesta of *Taxus* naturally recall those well known to occur in *Torreya* at a much higher level. Since it is tolerably certain that the paired ovular strands in both genera have been derived by a splitting of an original central main supply, it would seem that *Taxus* is nearer to the ancestral type in so far that in the former genus the 'chalazal foramina' are nearer the middle line than in the latter.

But in such a comparison between *Taxus* and *Torreya* there is one apparently insuperable difficulty, namely the fact that whereas in *Torreya* the strands of the 'outer system' are entirely outside the stone, in *Taxus* they are entirely inside the seed-cavity, for, as is well known, in this genus the outer flesh (if this name is at all applicable) is represented by only a thin membrane of unligified cells covering the stone.

How, then, is it possible to derive these two apparently divergent types from the same ancestral form?

We will, in the first instance, fix our attention upon certain well-preserved platyspermic seeds of Cordaitan affinity, described long ago by Ad. Brongniart (1874) from the Carboniferous of St. Étienne, and subsequently (1881) refigured to show the details of their structure. The original diagnoses have to some extent been recently modified by Professor C. E. Bertrand (1907, 1, 2, 3, 4, 1908, 1, 2, 3), who undertook a revision of Brongniart's types with the help of Renault's later preparations. More recently Mrs. Agnes Arber (1910) has made an interesting contribution to our knowledge of these ancient seeds, which exhibit a remarkable diversity of form without departing from the essentials of the plan upon which they are built.¹

¹ The further literature is referred to in Mrs. Arber's paper. The attribution of the seeds in question is, with the exception of *Cardiocarpus*, still a matter of conjecture, but there is a strong presumption in favour of the view that like *Cardiocarpus* they all belonged to members of the phylum Cordaitales. Apart from their agreeing with *Cardiocarpus* in their general plan of structure, they all possess a more or less well developed 'tent-pole'—an organ which appears to be of considerable importance in questions of relationship. In the case of one of these seeds (*Mitrospermum*) Dr. Scott has recently (1918–1919) discovered some indirect evidence to show that it was probably borne upon the highly specialized axillary shoots of the Cordaitan species *Mesoxylon multirame*.

On a general survey of this assemblage it was noticed that if a certain well-marked tendency (which I shall presently explain) was kept in view, it was possible to arrange the seeds in a series, as follows:

Cardiocarpus; ¹ *Cycadinocarpus*; *Rhabdospermum*; ² *Mitrospermum*; *Taxospermum*.

Of course, it is not by any means suggested that this series represents the actual course of evolution, but it appears as if the tendency it expresses may have been a real factor in the history of these ancient seeds, which, as already remarked, are all approximately of the same age. And this view at least acquires some interest when it is noticed that, so far as this tendency is concerned, the series appears to be continued into the living genera *Torreya* and *Cephalotaxus* in one direction, and into *Taxus* in another. See Fig. 7, Nos. 2-11.

A word of explanation is necessary in connexion with the figures referred to. All the figures are purely diagrammatic, but with two exceptions they do not represent any essential facts not already published. These exceptions are:

(a) The dotted lines in *Mitrospermum* (No. 6) represent the 'inner' (nucellar) vascular system, and have been inserted on the presumption that their absence in Mrs. Arber's material was due to imperfect preservation.³ The resemblance of *Mitrospermum* to *Rhabdospermum* (in which the 'inner' strands are clearly seen in Brongniart's figures) is far-reaching enough to justify this step.

(b) In *Taxospermum* (Fig. 7), too, which is likewise fundamentally similar to *Mitrospermum*, traces of an 'inner' system have been observed by C. E. Bertrand (1907, p. 216) at a level higher than the inner openings of the obliquely ascending lateral canals in the shell. The continuation downwards of these strands is thus not entirely unjustified, although their exact points of insertion must remain doubtful till better-preserved material is available.

It will be seen that whereas in the first member of the series (*Cardiocarpus*, Fig. 2) the 'outer' system of strands is entirely outside the stone, as we pass along the series its points of origin from the main supply

¹ As defined by Professor C. E. Bertrand (1908).

² A generic name proposed by Professor Seward (1917, p. 341) for seeds of the *Rhabdocarpus* type showing anatomical structure, Berger's original name *Rhabdocarpus* being reserved for impressions.

³ Since writing the above I have, through the great kindness of Dr. D. H. Scott, F.R.S., been able to examine some well-preserved sections of *Mitrospermum compressum*; although these sections did not show any sign of an internal vascular system, it may be stated that none of them happened to pass quite through the right plane. The question as to the existence of internal bundles in this seed is therefore open. It is quite possible that no internal bundles existed in *Mitrospermum*, which in this respect would hold the same relation to *Rhabdospermum* as, among living genera, *Taxus* does to the new Taxinean genus recently discovered in New Caledonia by Prof. Compton (*vide supra*).

gradually shifts nearer and nearer to the subnucellar pad of tracheides which also gives rise to the 'inner' system. During this process the basal parts of the two outer strands may be imagined to cut their way through the stone, somewhat like a hot piece of wire stretched tight and pressed against a block of wax, so that the regions through which it has passed have

FIG. 7. 1. *Ginkgo*. 2. *Cardiocrinocarpus*. 3. *Cycadinocarpus*. 4. *Rhabdospermum subunicatus*. 5. *Rhabdospermum cyclocaryon*. 6. *Mitrospermum*. 7. *Taxospermum*. 8. *Taxus*. 9. Pre-Torreya stage (hypothetical). 10. *Torreya*. 11. *Cephalotaxus*.

again solidified. In the figures these regions of the stone have for the sake of clearness been distinguished by a different method of shading. Thus we see that the proximal parts of these strands, ascending and entirely outside the stone in *Cardiocrinocarpus*, become horizontal and partly included in the

stone in *Cycadinocarpus*, while in *Rhabdospermum* they actually turn obliquely backwards and outwards to emerge from the stone through two foramina not far from the point where the main supply enters the stone. For convenience I propose to describe as excurrent and incurrent canals, respectively, those channels in the sclerotesta which afford egress or ingress to the vascular bundles.

Now, if we imagine that the outer openings of the excurrent canals of *Rhabdospermum* gradually move forward towards the micropyle, the conditions observed in *Mitrospermum* and *Taxospermum* will successively be arrived at: the canals will first become nearly horizontal as in *Mitrospermum* and then ascending as in *Taxospermum*. For our purpose the most important result of this tendency is that more and more of the 'outer' system of strands becomes included inside the shell-cavity. Thus in *Taxospermum* a considerable length of the 'outer' system is really inside the stone.

At this point I shall venture a suggestion which at first perhaps appears unwarranted, but which, as I hope to show presently, is not entirely without a foundation. Assuming that this acropetal tendency on the part of the excurrent canals did not become extinct in Palaeozoic times, is it not possible that the modern genus *Taxus* (in which the entire length of the 'outer' system of strands is inside the seed-cavity) may represent the culmination of this tendency? In other words, may it not be that in this plant the excurrent canals have actually reached the micropyle and become confluent with it? If this is so, it follows that that part of the stone which in *Taxospermum* lies distally to the excurrent canals (shown solid black in Fig. 7, No. 7) is entirely unrepresented in *Taxus*; and, further, that the proximal part of the stone of *Taxospermum* (shown dotted) corresponds to almost the whole of the shell of *Taxus*. The single incurrent canal of *Taxospermum* having split into the two incurrent canals of *Taxus*, that part of the stone of *Taxus* lying between these canals must be regarded as a newly intercalated piece.

Direct comparisons of this nature between plants so widely separated in time do not often lead to safe conclusions. But the suggestion here put forward is at any rate the only one that affords at all a satisfactory interpretation of the peculiar seed-structure of *Taxus*; and, as we shall see, it also makes it possible to compare the latter intelligibly with *Torreya*. When we realize the magnitude of the time-gap between *Taxospermum* and *Taxus* in the light of this suggestion, the structural gap between them becomes surprisingly small; and the vague comparison which Ad. Brongniart instituted between the two seeds as long ago as 1874, and which he expressed in the generic name *Taxospermum*, now acquires a phylogenetic significance. I wish to avoid conveying the impression that I regard *Taxospermum* as being necessarily a direct ancestor of the modern Yew,

for we are yet wholly ignorant as to the nature of the plant that bore the Palaeozoic seed, but the resemblances between the seeds certainly appear to be due to more than a chance. Such points of agreement as those in general shape and size may be ignored as being superficial. But it is at least a fact of some significance that, so far as known, of all the fossil seeds which show evidence of a Cordaitan affinity, it is *Taxospermum* that shows the greatest amount of fusion between nucellus and integument: an important advance in the direction of *Torreya* and *Taxus*. (See Bertrand, 1907, p. 216.)

Apart from the difference in the position of the 'outer' vascular system—which I have just attempted to explain—the most important difference between the two seeds is that in *Taxus* there are two basal supply bundles instead of the single one in *Taxospermum*. But there is every justification for the view that the two basal ovular strands, lying in the principal plane, which are a striking characteristic of the Ginkgoales, Taxales, and Coniferales, have been derived by the splitting of a single median bundle; for it is an observed fact that a centralized main supply prevails in the overwhelming majority of known Palaeozoic Gymnospermous seeds, whether platyspermic or radiospermic. If we imagine the two incurrent canals of *Taxus* to approach each other and fuse into a single median canal, the two contained bundles at the same time fusing into one, the thickened angles in these bundles would coalesce into a vascular mass exactly corresponding in position to the subnucellar tracheal pad characteristic of most Palaeozoic seeds with a centralized main supply. It is now easy to see the significance of the fact, to which attention was drawn in the descriptive part of the paper, that these thickened angles in the ovular strands of *Taxus* are situated nearer to the nucellus than any other part of the vascular supply.

The absence of a definite 'internal' (nucellar) system of strands in *Taxus* will hardly be taken as a serious objection to the comparison here instituted, for it is doubtless related to the absence of fertilization by motile sperms. I have already (p. 120) offered some reason for the view that the thickened angles in the ovular strands in *Taxus* probably mark the points of origin of the nucellar bundles in the ancestral type, although these bundles have become extinct in the modern genus.

Having considered whatever evidence there is for deriving the seed of *Taxus* from a type like *Taxospermum*, we shall now attempt to see in what relation the seeds of *Torreya* and *Cephalotaxus* stand towards either of the former seeds. Nos. 7–11 on Fig. 7 illustrate the view which I consider to be the most plausible. It will be noticed that I have attempted to derive the seed of *Torreya* also from the same source (*Taxospermum*) but along a line distinct from that of *Taxus*. At first sight the seed of *Torreya* appears so different from *Taxospermum* that it is difficult to see how a

comparison is possible. But if we agree with the conclusion reached by Professor Oliver, that the part of the seed lying below the level of the 'chalazal foramina' is a phylogenetically recent formation, the difference from *Taxospermum* does not appear so great. For the sake of clearness, I have interposed between these two seeds a hypothetical intermediate condition (Fig. 7, No. 9) which may for convenience be referred to as the pre-*Torreya* stage. Between *Taxospermum* and pre-*Torreya* there are only two points of difference. Firstly, pre-*Torreya* has at the base two strands which enter the stone through two incurrent canals, and between which an appreciable portion of the sclerotesta has been newly intercalated, just as in *Taxus*. Secondly, the excurrent canals in pre-*Torreya* are nearer to the micropyle than they are in *Taxospermum*—it has already been suggested that they have a tendency to move towards the micropyle. The dotted portion of the stone in Fig. 7, No. 9, may thus be described as having grown at the expense of the part shaded with lines, to the extent that the excurrent canals have moved forward. At the same time, however, the newly intercalated portion of the stone (shown cross-hatched) must be regarded as having increased in size at the expense of the dotted portion of the stone, for, ever since the splitting of the main supply bundle of the ancestral type, the two incurrent canals (conveying the resulting bundles) have also steadily travelled towards the micropyle.

Pre-*Torreya* is thus a strange kind of seed, in which the stone is pierced in the principal plane by two pairs of canals (one excurrent, the other incurrent), both of which are, in a phylogenetic sense, moving towards the micropyle. From this stage *Torreya* is only one step farther. We have only to imagine that the hinder pair of canals, having moved faster than the front pair, has overtaken the latter and become confluent with it. A glance at the figures will show that the obvious result of this process is that the dotted region of the stone is gradually squeezed out of existence. It will thus be seen that the incurrent canals of *Taxus* are not strictly comparable to those which convey the nucellar bundles of *Torreya* into the seed-cavity—a want of correspondence which is in keeping with the fact that the strands conveyed by the canals in the two genera are themselves not homologous, being the main supply bundles in the case of *Taxus* and nucellar bundles in *Torreya*.

It is of some interest to find that although we have derived the seed of *Torreya* from the *Cardiocarpus* type through a long succession of varying forms, our interpretation of this peculiar seed entirely agrees with that which Professor Oliver arrived at from a direct comparison between *Torreya* and *Cardiocarpus*. If we look back at the series of figures from *Torreya* to *Cardiocarpus*, it will be seen, from the conventional method of shading that we have throughout adopted, that in *Torreya* the small apical region of the stone is the representative of the entire stone of the ancestral type, which

has steadily undergone reduction, having been encroached upon in succession by two phylogenetically younger portions of the sclerotesta, intercalated one after the other at the base of the seed. Each of these newly formed portions of the stone has shown a persistent tendency to grow in the direction of the micropyle. The modern genus *Taxus* illustrates the triumph of the older of these, which forms almost the whole of the sclerotesta in this genus; in *Torreya* it is the younger of these newly created regions of the stone that protects nearly the whole of the seed.

Turning now to the third genus, *Cephalotaxus*, the question arises in what light we are to regard the stone of this seed. We have seen that in the ancestral history of *Torreya* the 'chalazal foramina' have probably shown a continual tendency to shift nearer and nearer to the micropyle. In *Cephalotaxus*, however, the most careful search reveals no trace of any perforations in the stone. May we conclude that in this genus the 'chalazal foramina' have actually passed beyond the micropyle—that the entire stone of *Cephalotaxus* corresponds to the newly intercalated portion of the stone of *Torreya* and to the small basal disc of *Taxus*? This, at any rate, seems to me the most natural conclusion, strange as the suggestion may appear. Of course, the alternative suggestion may be made that the seed of *Cephalotaxus* differs essentially from that of *Torreya* only in having lost its nucellar bundles by reduction *in situ*, and that consequently the 'chalazal foramina' which once admitted these strands have also become obliterated. If it were shown that the young seed contains vestiges of the nucellar bundles, or of foramina in the stone which become blocked up as development proceeds, this view would be indisputable. But in the absence of positive evidence on either side the conjecture first put forward is preferable, being more in conformity with the general line of argument previously adopted. The fact that there are in *Cephalotaxus*, as in *Torreya*, two separate supply bundles at the base would alone suggest that the part of the stone lying between them is a comparatively recent formation; and since the bundles run up as far as the micropyle without branching, this conclusion must evidently apply to the entire stone.

If the tendencies outlined above have had any significance in the evolution of the seeds in question, we have further evidence for the view—which is already well established on other grounds—that the Yews are descended from Cordaitalean ancestors. For the fact that it is possible to arrange these seeds into a more or less continuous series, helps us further to bridge the structural gap between the two groups, wide though the gap in time may be. The hope may therefore be well founded that rocks of an intermediate age will reveal evidence of the existence of seeds transitional between *Taxospermum* on the one hand, and *Torreya* and *Taxus* on the other.

The comparison of the seeds of the Taxales with the older seeds

appears, however, to fail in this respect, namely, that, so far as is known, the 'aril' was entirely unrepresented in the Cordaitales. But it is difficult to estimate the value of negative evidence, for, apart from the question of preservation, these fossil seeds are nearly always found detached, and the possibility is not excluded that if an aril was present it was left behind on the seminiferous axis when the seed was shed. At least in one of the few known cases where the attachment is preserved—namely, *Cordaianthus Williamsoni*—Renault's well-known figure (see Scott, 1909, p. 540) shows below the seed a differentiated pad of tissue terminating the seminiferous axis. May we regard this pad of tissue as the forerunner of an aril? Since I have not seen the original specimen this suggestion must be regarded as of the most tentative nature; but if the aril of *Taxus* is in origin a disc-like expansion of the apex of the seminiferous axis—and this view, held by Strasburger in 1872, is perhaps more plausible than any other¹—it is natural to expect that in such an ancient type as *Cardiocarpus* the aril would not be well differentiated from the rest of the axis. It would seem as if this disc, as it gradually became differentiated into a distinct organ, was in time completely appropriated by the seed, and was shed along with it as in *Taxus*.

Strasburger long ago (1879, p. 124) expressed the view that the seeds of Gymnosperms are often more or less deeply sunk into the seminiferous axis, so that it is no longer possible to define their real limits. This view found a remarkable illustration when Professor Oliver described the main features in the development of the seed of *Torreya*, and published his ingenious interpretation of this peculiar type of seed. In this genus that part of the seed which lies below the level of the 'chalazal foramina' in the stone is, according to Professor Oliver, phylogenetically younger than the apical region, which (in a figurative sense) may be described as having bulged downwards, through the widened seed-base, into a kind of 'brood-pouch' formed by what is strictly speaking the apex of the seminiferous axis. This expanded apex of the axis has, however, been so completely monopolized by the encroaching seed that it is now, to all appearance, an integral part of the integument; distally it is continued into the free part of the aril, which has had a similar origin at an earlier period, as suggested above in the case of *Taxus*.

If we keep in view this tendency on the part of the seed to bury itself deeper and deeper into the seminiferous axis, the seed of *Cephalotaxus* would appear to have gone even farther than that of *Torreya*, for the free portion of the nucellus which belongs to the archisperm (or phylogenetically older part of the seed) is in *Cephalotaxus* actually arched over by an

¹ Since *Ginkgo* is traceable to the same source as the Taxales, it is probable that the 'collar' of this genus is morphologically of the same origin as the 'aril' of *Taxus*. Sprecher (1907) actually employs the term 'aril' in describing the collar of *Ginkgo*.

integument which, as already suggested, is a comparatively recent formation.

In attempting to assign a place to *Ginkgo* in relation to the Cordaitales the fact must be taken into account that there is apparently nothing in the seed of this plant to represent the 'outer' vascular system. There may, however, be some significance in the fact, observed by Sprecher (1907, p. 137), that the superficial cells of the young sclerotesta of *Ginkgo* are histologically indistinguishable from tracheides (see Sprecher's Fig. 150, p. 137). May the outer vascular system of *Ginkgo* be regarded as having fused up with the outer surface of the stone? The following remark by Sprecher is of some interest in this connexion: 'Le noyau scléreux me paraît être en rapport avec le tissu de transfusion de l'arille; il est sa continuation dans l'arille.' If this view is justified *Ginkgo* would appear to make a remarkably near approach to the Palaeozoic seed *Cardiocarpus*, in which the 'outer' system of strands comes off from the main supply before the latter enters the stone (cf. Nos. 1 and 2 in Fig. 7). This would corroborate the low position of *Ginkgo* indicated by the motile sperms and the well-developed pollen-chamber and 'internal' vascular system, as well as by the presence of a well-developed 'tent-pole'. Another fact pointing in the same direction is the proximity of the two supply bundles to the middle line, which shows that the main supply has, in a phylogenetic sense, only recently undergone splitting.

SUMMARY AND CONCLUSIONS.

The present paper contains an elaboration of a theory developed by Professor Oliver in 1903, when he offered an interpretation of the seed-structure of *Torreya* in terms of the Palaeozoic seed *Cardiocarpus*, which was regarded as the ancestral type. It is suggested that the Palaeozoic seeds *Cycadinocarpus*, *Rhabdospermum*, *Mitrospermum*, and *Taxospermum*, all of which probably belong to the Cordaitan phylum, illustrate the general tendency that may have operated in producing the types of seed known to occur in the modern genera *Taxus*, *Torreya*, and *Cephalotaxus*. It is proposed to place these three genera in a distinct phylum, Taxales: the members of this phylum are regarded as the nearest existing relatives—apart from *Ginkgo*—of the Cordaitales, and like *Ginkgo* direct descendants of the Cordaitales. While accepting a Cordaitalean origin for the Coniferales, I regard the further question—whether the connexion was a direct one or whether the Conifers arose as a branch from the Taxales—as still *sub judice*, although I am inclined to favour a direct connexion. The problem as to the ultimate microphyllous or megaphyllous origin of the Cordaitales (and therefore also of the Conifers) is left untouched in this paper.

If the seeds of the Taxales have been derived from those of the

Cordaitales along the general tendencies outlined above, it is clear that we cannot strictly speak of a homology between the respective layers of the integument (outer flesh, stone, and inner flesh). A glance at the figure will show, for example, that in the so-called stone of *Taxus* there is nothing really comparable with the stone of *Cardiocarpus*. The region of the integument of *Taxus* which is comparable to the stone of the Palaeozoic type is no longer lignified and has become part of the inner flesh. It lies along a plane just inside the 'outer' vascular system, and would be represented by two lines joining the marks * * with the micropyle. In *Taxus*, therefore, what we are accustomed to call the 'stone' is really homologous with a portion of the 'outer flesh' of the ancestral type.

In comparing the seeds of the Taxales among themselves and with those of the Cordaitales the positions of the two vascular supply systems may safely be relied upon as determining the real homologies of the different parts of the integument.

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