

THE TAXOIDEÆ; A PHYLOGENETIC STUDY.

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[WITH PLATE I.]

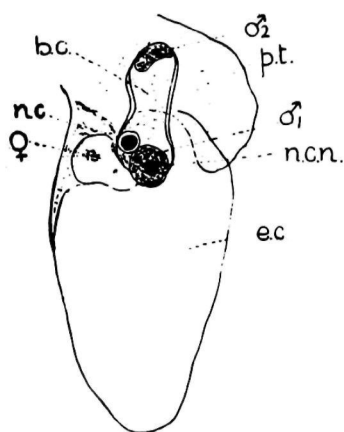
I.—INTRODUCTION.

EARLY in 1904, at the suggestion of Professor F. W. Oliver, I began to make a study of the Taxoideæ. At that time the minute structure and development of the reproductive organs of the group were not known with any completeness except in *Taxus*, but in the course of the last three years several papers have appeared on the subject, culminating quite recently in Professor A. A. Lawson's interesting study of *Cephalotaxus*, (see Literature Citations, 16, 17, 18, 19, 26). We are now acquainted with at least the main outlines of the reproductive processes of these plants, and a considerable mass of information has accumulated as to their floral morphology, anatomy, etc., so that it seems as if the moment has come to enquire what bearing this knowledge may have upon our ideas as to the phylogeny of the group. I have made some attempt to do this in the following pages. I should like to take this opportunity of thanking Professor F. W. Oliver for the help and encouragement which he has constantly given me in the study of the group. Before entering on any general discussion I have a correction to make and a few observations to record.

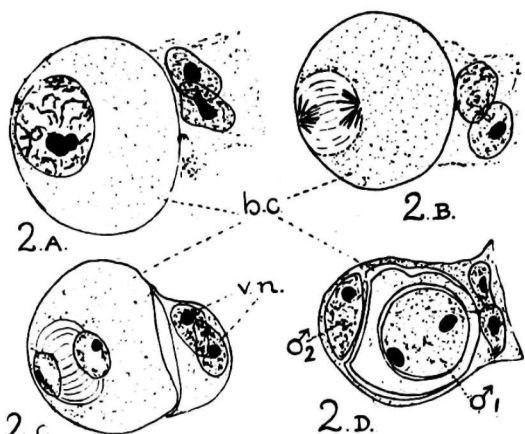
II.—OBSERVATIONS.

(a). *Torreya californica*. Torr.

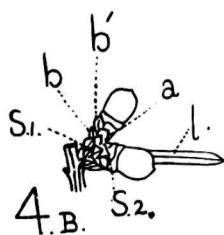
I wish to begin these notes by correcting an error into which I fell in a paper on *Torreya californica* (17) published in this journal in 1904. I stated there that the division of the "body cell" nucleus of the pollen tube gave rise to two sperm nuclei of equal size. Since my paper was published an account of *Torreya taxifolia* by Coulter and Land (19) has appeared, in which the division of the body cell in this species is described as *unequal*, thus resembling that of *Taxus*, in which the functional male nucleus is greatly larger than the functionless one. The discrepancy on this point between my results and those of Coulter and Land, made me re-examine my preparations, and I have come to the conclusion that my statement of 1904 was incorrect. Pollen tubes were comparatively scarce in my material, and I chiefly based my statement on



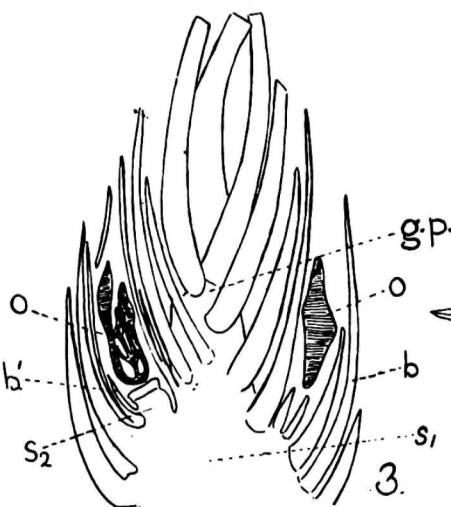
TORREYA



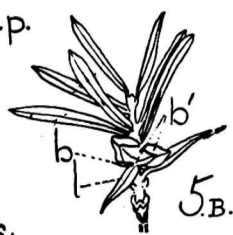
TAXUS



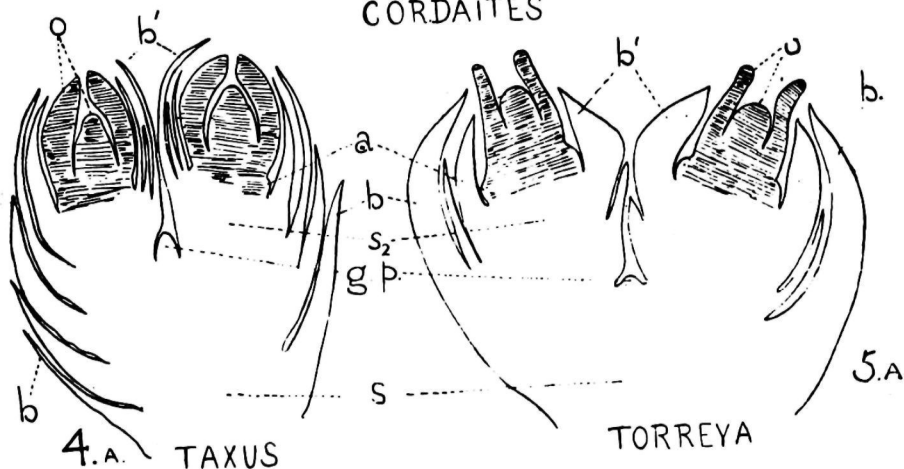
TAXUS



CORDAITES



TORREYA



TAXUS

TORREYA

the two preparations represented in Pl. 8, figs. 17 and 18 of the paper referred to; I now think that the nuclei there figured were wrongly identified. The two nuclei which I interpreted as the second male nucleus and a vegetative nucleus I now regard as respectively the functional male nucleus and the smaller second male nucleus, while the nucleus which I labelled " σ_1 ," I now believe to be merely a vegetative nucleus. I particularly regret this mistake as I had in my possession at the time of writing the paper a preparation and sketch made by Mrs. Tansley in the previous year, in which the entry of the sperm into the archegonium was shewn, and the smaller size of the second male nucleus was distinctly indicated. This drawing Mrs. Tansley has kindly given me permission to reproduce (Fig. 1).

(b.) *Taxus baccata*. L.

The development of the reproductive organs of *Taxus baccata* has already been investigated with considerable completeness by several workers (Belajeff, 4; Strasburger, 6 and 18; Jäger, 7), but since microtome methods have not been applied to the more interesting stages I thought it might be worth while to re-examine the ovules. My thanks are due to the Director of the Royal Gardens, Kew, for allowing me to collect material during the summers of 1905 and 1906. I used chiefly Juel's fixative (2 grs. zinc chloride, 2 c.c. glacial acetic acid, 100 c.c. 45-50% alcohol) which seems particularly well adapted for Gymnosperm ovules, followed by Flemming's triple stain. My results on the whole have simply confirmed previous work. Apparently the presence of more than one embryo sac is fairly common in *Taxus* ovules; cases are described by Hofmeister (1), Jäger (7) and Thomson (21), and I have met with one such example in my 1905 material. The ovules which I examined were abundantly penetrated by pollen-tubes, whose great swollen ends often pressed the prothallus quite out of shape, and sometimes grew right down its flank. As might have been expected, the dates of the various stages of the ovular development given by Jäger for material grown in the neighbourhood of Zurich do not apply accurately to that collected in England. The division of the body cell, and fertilisation, which Jäger describes as occurring at the end of May or beginning of June did not take place in my 1906 ovules until June 18th. The actual division of the body cell seems never to have been figured, so I have shown it in Figs. 2A, B, C, D. These figures bring out the

rather interesting point that the division itself is perfectly symmetrical, and it is only the great subsequent growth of the functional male nucleus which brings about the inequality.

Hofmeister (1) gives the number of archegonia in *Taxus baccata* as 5 to 8. Jäger (7) confirms this as the normal number, but says that he found cases of 9, 10 and 11. In my 1906 material I met with an embryo-sac containing 17 archegonia! Two archegonia sometimes occur with no intervening prothallial cells. I have not detected any trace of a ventral canal cell nucleus.

According to Jäger, wall-formation does not occur in the pro-embryo until 16 to 32 nuclei have been formed. My observations confirm this. One ovule contained 7 proembryos! Three of these were binucleate, two were 8-nucleate, one shewed 16 daughter nuclei still connected in pairs, and in the seventh there were 16 resting daughter nuclei, but still no trace of wall-formation.

III.—AFFINITIES AND PHYLOGENY.

According to the most recent classification of the Taxaceæ (that of Pilger, 15), this group is divided into three sub-families:—

1. Podocarpoideæ.
2. Phyllocladoideæ.
3. Taxoideæ.

Other authors however do not place *Phyllocladus* in a sub-family of its own; Coulter and Chamberlain (9) include this genus in the Taxoideæ, while Strasburger (2) attaches it to the *Podocarpus* group. The result of some observations on *Phyllocladus alpinus* (Robertson, 22) has been to convince me that the older of these two views more nearly expresses the true relationship, and that *Phyllocladus* is intermediate between the Podocarpoideæ and Taxoideæ, but with somewhat greater affinity for the former. The Taxoideæ are sub-divided by Pilger as follows:—

CEPHALOTAXEÆ.

Cephalotaxus,

TAXEÆ.

Torreya.

Taxus.

Ginkgo used to be included with the genus *Cephalotaxus* (cf. Veitch, 8), but modern work, especially the discovery of the motile sperms, has emphasized the uniqueness of the Maidenhair Tree among the Conifers, and its resemblance to the Cycads, and it has been removed from the near neighbourhood of *Cephalotaxus* into an alliance of its own,—the Ginkgoales.

The relation of *Cephalotaxus*, *Torreya*, and *Taxus* to the other Conifers has been the subject of much controversy. According to our present imperfect knowledge of the geological history of the Coniferales, the Taxaceæ appear at a somewhat later period than the Abietineæ; more complete information however is needed before we can draw trustworthy deductions as to the history of the group.

There are two contrasting views as to the position of the Taxoideæ:—

1. That the Taxoideæ are a group retaining relatively primitive characters (Strasburger, 5; Coulter and Chamberlain 9; Worsdell, 10, etc.) Those who take this view commonly regard the Taxoideæ as descended from some group of the Fern-Cycad alliance.

2. That the Taxoideæ are relatively specialised, while it is rather the Abietineæ which should be regarded as a primitive group. (Jeffrey, 20; Thomson, 21; Lawson, 26.)

We will begin by considering the evidence for the first view.

The anatomy of the three genera offers some distinctly primitive features. More traces of centripetal xylem are found here than in any other family of Conifers. (For references on this point see Robertson 22, p. 263). Strasburger (5) has shewn that *Taxus* has no albuminoid elements in its secondary phloem rays, that is to say the secondary structure of the phloem is *not* more specialised than the primary structure. This character, which is shared by *Ginkgo* and *Araucaria*, he regards as an indication of primitiveness, contrasting with the specialised anatomy of the Abietineæ, in which the albuminoid cells of the secondary phloem are confined to the rays. Strasburger looks upon this anatomical evidence as a confirmation of his view that any explanation of the floral structure of the Coniferæ must start from the Taxads.

The large erect seeds of the Taxoideæ recall those of *Cycas* and *Ginkgo* in their macroscopic characters. Professor F. W. Oliver (14) who has worked out the structure in the case of *Torreya* and has compared it with palæozoic seeds, describes the vascular anatomy as peculiar and isolated among recent plants, and regards the seed as of a distinctly archaic type.

The stamens of the Taxoideæ, like those of *Araucaria*, are characterised by possessing more than two pollen sacs. This is probably a relatively primitive character, representing in a very general sense a stage between numerous pollen sacs, such as we find for instance in the Cycadales, and the definitely bisporangiate condition met with in such a Conifer as *Pinus*. But it is necessary

to bear in mind that the evolution of the microsporophylls of the Gymnosperms is still very obscure; there are great gaps between the microsporophyll of the Cycad, with its numerous clustered sori on the lower surface,—the pinnate synangia-bearing microsporophyll of *Bennettites* (Wieland, 25, Fig. 87 p. 164),—the erect stalked cluster of pollen sacs of *Cordaitea*,—and the stamen of any of the Coniferales.

The minute structure of the reproductive organs does not give much positive evidence for the idea that the group is a primitive one, except in a single point to which I am disposed to attach some importance. This is the mode of development of the proembryo (see Coulter and Chamberlain, 13). In the Cycads and *Ginkgo* and probably *Bennettites* (Wieland 25, p. 125 and Pl. XXX.) the fertilised egg nucleus divides repeatedly before any walls are formed; but in *Pinus* as soon as four nuclei are produced they become separated by walls. *Taxus* and *Cephalotaxus* recall the Cycadean condition in that no walls are formed until at least sixteen free nuclei have arisen by division from the fusion nucleus.

The mature embryo of the Taxaceæ has two cotyledons; a similar dicotyledonous condition prevails throughout the Cycads, *Bennettites*, and *Ginkgo*, while polycotyledony is characteristic of the Abietineæ.

A further point in favour of the view that the Taxoideæ are a relatively primitive group is the resemblance which exists between the female "flowers" of *Taxus* and *Cordaitea*. To this point I will return later.

The most important arguments brought forward by those who believe that the Taxoideæ are specialised rather than primitive are concerned with the structure of the megaspore and the female gametophyte. Dr. R. B. Thomson of Toronto has recently drawn attention to the "megaspore membrane" of the Gymnosperms (21). In common with other authors he regards the Gymnosperms as ultimately descended from forms in which the megaspores were set free from the sporangium; in such cases a firm protective spore coat would obviously be of use, but it would lose its function in the later stages of evolution when the megaspore became embedded in the nucellus. Hence Dr. Thomson looks upon the megaspore membrane of the Conifers as a vestigial structure, retained in the more primitive forms and gradually lost in the more advanced. He finds that the megaspore membrane is present, associated with a tapetum which he regards as of sporogenous origin, in the Cycads,

Ginkgo, and the Abietineæ, while it is absent or very poorly developed in the Taxoideæ. While admitting the possibility that the megaspore membrane may have the phylogenetic value which Dr. Thomson attributes to it, I should like to point out that it is by no means certain that it is not an adaptive character. The Cycads have a very large and watery prothallus and they are characteristically xerophytes, so that in their case the well-developed megaspore membrane may have an important protective function. Also the fact that according to Dr. Thomson's observations the megaspore membrane is always associated with a tapetum, suggests that it may have some significance in connection with nutrition.

There are two other points in the structure of the female gametophyte of Taxoideæ on which Professor A. A. Lawson has laid some stress in his study of *Cephalotaxus* (26), as showing that this genus "represents a very recent type of Conifer." The first of these is the absence of the ventral canal cell. In *Cephalotaxus* there is a ventral canal nucleus, but it is *not* separated by a wall from the egg cell, while in *Taxus* and *Torreya* even the nucleus occurs rarely or never. In the Abietineæ on the other hand a well-marked ventral canal cell is cut off. The second point is that "prothallial" nuclei are absent from the pollen grains of Taxoideæ, while they are present in the Abietineæ. Lawson concludes "If the retention of such evanescent vestigial structures as the prothallial cells in the pollen or the membrane of the ventral canal-cell has any phylogenetic bearing, then we have an argument in support of the primitive character of the Abietineæ as a group." Another point which might perhaps be brought forward is that the differentiation between the two sperm nuclei in *Taxus* and *Torreya* is a decidedly sophisticated character. All these arguments seem to me to carry considerable weight, and to show at least that the Taxoideæ have specialised a great deal along their own particular lines, but nevertheless I am disposed to think that the balance of evidence is in favour of the view that the Taxoideæ have retained a greater number of primitive characters than the Abietineæ. One point which Professor Lawson brings forward, the absence of prothallial cells in the pollen grains of Taxoideæ, may, as I have tried to show elsewhere, (Robertson, 16, p. 139) find its explanation in the almost universal association of the *winged* character of the pollen grain with the presence of prothallial nuclei. (For criticisms of this hypothesis see Seward and Ford, 24, p. 392 and Lawson, 26, p. 4.)

The problem of the relation of the three genera of Taxoideæ to one

another is a very difficult one. The connection between *Taxus* and *Torreya* seems to be considerably closer than that between either of them and *Cephalotaxus*, while on the other hand *Cephalotaxus* shews clear indications of affinity with *Ginkgo*. As regards the minute structure of the reproductive organs, *Taxus* and *Torreya* agree in the inequality of the sperm nuclei, and the absence or rare development of the ventral canal nucleus, while *Cephalotaxus* resembles *Ginkgo* in the equality of its sperm nuclei and the presence of a ventral canal nucleus. A curious little anatomical peculiarity shared by *Cephalotaxus* and *Ginkgo* is the presence of a central resin duct in the pith.

The female "flowers" of the Taxoideæ differ a great deal from those of other Gymnosperms. In *Taxus* the ovules are each borne in an apparently terminal position on a short leafy axis known as the "primary shoot." They are really however lateral on the primary shoot, being produced at the end of a much abbreviated secondary shoot, arising in the axil of the uppermost bract of the primary shoot. The growing point of the primary shoot is pushed to one side, so that the ovule seems to be terminal on it. Fairly often the two uppermost bracts of the primary shoot are fertile and in such cases the morphology of the structure is much clearer than in the reduced and more normal form (Figs. 4A and B). *Torreya* closely resembles *Taxus* (Figs. 5A and B). *Cephalotaxus* bears its female reproductive organs in cones, and though superficially very unlike *Ginkgo*, can really be more closely homologised with this archaic Gymnosperm than with the other Taxoideæ. The cone consists of a number of leaves each with two erect ovules in its axil.

Celakovsky's view as to the morphology of the female "flower" in the Taxoideæ, which is clearly expounded by Worsdell (10 p. 641, etc.) seems to me to be far better founded and more luminous than the other hypotheses that have been put forward. According to this view "the primary shoot of *Taxus* and *Torreya* . . . is the homologue of the entire plant of Cycads and the brachyblast of *Ginkgo*; the secondary shoots are the homologues of the Cycadean cone and the ovuliferous axis of *Ginkgo*." The cone of *Cephalotaxus* is regarded as corresponding to the "primary-shoot" of *Taxus* or *Torreya*, or to an aggregate of the ovuliferous axes of *Ginkgo* with their subtending leaves. The belief that *Ginkgo* and *Cephalotaxus* can truly be homologised on these lines has been strengthened of late years by additional observations on abnormal "flowers" of the

two genera. Spiess (12) has found in both cases that when more than two ovules are present the extra ones are arranged decussately with reference to the normal pair.

In nearly all the points in which *Taxus* and *Torreya* differ from one another, *Taxus* is the less specialised, but in the structure of the mature seed the reverse seems to hold good. Professor F. W. Oliver (14) says of the seed of *Torreya*, "In the apparent retention of old features it exceeds either *Taxus* or *Cephalotaxus*." It is possible that the comparatively small size of the *Taxus* seed and its coloured aril (said to be attractive to birds) may have something to do with its wide distribution, while on the other hand *Torreya* and *Cephalotaxus* may partly owe their restricted habitats to the handicap of their cumbrous seeds. The radially symmetrical peltate stamens of the Yew, with their numerous pollen sacs, are represented in *Torreya* by dorsiventral stamens bearing four pollen-sacs on the lower side. That this is phylogenetically a case of reduction is strongly indicated by Coulter and Land's interesting observation (19) that the dorsal resin cavity in the stamen of *Torreya taxifolia* is formed ontogenetically by abortion and fusion of three rudimentary sporangia. The number of archegonia shows reduction as we pass from *Taxus* to *Torreya*. In the Yew ovule there are normally five to eight, but the number may rise to seventeen, whereas in *Torreya californica* three are commonly found, and in *T. taxifolia* only one. Again, the development of the proembryo of *Taxus* is less specialised than that of *Torreya*; *Taxus* produces sixteen to thirty-two free nuclei before forming cell-walls, while in *Torreya* wall formation is initiated at the four-nucleate stage.

The morphology of the female flower of *Taxus* and *Torreya* is also best explained on the view that *Torreya* is one degree more specialised than *Taxus*. In the case of *Taxus* the so-called "primary shoot" bearing bracts arises in the axil of a foliage leaf, while from the axils of the two uppermost bracts on this shoot secondary axes arise, each bearing three pairs of bracteoles and terminating in an ovule (Fig. 4). One of the secondary axes commonly aborts. In *Torreya* we meet with precisely the same arrangement, except that the axes are telescoped down, the number of scale leaves is reduced, and two secondary axes are normally, instead of occasionally produced (Fig. 5). The erect ovule placed terminally at the end of a secondary bracteole-bearing axis, which itself arises from a primary bract-bearing axis produced laterally on an axis

of higher order, exactly recalls the arrangement described by Renault (3) for *Cordaianthus*, the female "flower" of the palæozoic Gymnosperm *Cordaites* (Fig. 3). *Taxus* is somewhat reduced from this type, in that the growing point of the primary shoot aborts after producing a certain number of sterile bracts, and either one or two ovule-bearing axes, whereas in *Cordaites* it produces, besides sterile bracts, several ovuliferous secondary axes, and then (instead of being reduced to a little barren cone) continues its growth and produces some more leaves, Fig. 3 (see also Renault 3, Pl. XV, Figs 1 and 3).

The morphology of the male "flower" of *Cordaites* is obscure, but it seems clear that the pollen-sacs were borne in an erect tuft at the end of a slender pedicel. The pollen-sacs of *Taxus* on the contrary are pendulous, but they resemble those of *Cordaites* (Renault 3, Pl. XIV., Fig 2), and differ from those of all other Gymnosperms in their radial symmetry with respect to the pedicel that bears them.

There seems to be no doubt that *Cordaites* was descended from ancestors belonging to the Fern-Cycad alliance. We have anatomical evidence for this in the structure of the stems of *Pitys*, a tree from the lower Carboniferous. Dr. Scott (11) regards it as a primitive member of the Cordaitean family, but with mesarch strands of primary xylem. In Dr. Scott's words, "The *Pitys* trees appear to afford a new link, as far as stem structure is concerned, between the Cycadofilices of the family Lyginodendreae and the true Cordaiteæ." The seeds of *Cordaites* are said to "shew a marked parallelism with the ovules of recent Cycads." (Oliver 14).

Between the dying out of *Cordaites* at the top of the Palæozoic and the appearance of the Taxaceæ in the Cretaceous, there is a considerable gap in point of time, which may conceivably be bridged later on by the discovery of intermediate types.

CONCLUSION.

The evidence which we have been considering seems to point to the conclusion that the Taxoideæ are a group retaining many relatively primitive characters, though considerably specialised along their own lines. Phylogenetically they may be regarded as an offshoot from the Cordaitean stock, which is itself a branch of the Cycadofilicinean plexus. This descent is indicated by the marked resemblance of *Cephalotaxus* to *Ginkgo*, and of *Taxus* to *Cordaianthus*.

The relation between *Cephalotaxus* and *Ginkgo* has long been

recognised, and Dr. Scott (23), has pointed out that *Ginkgo* thus forms a bond uniting the Taxaceæ to the Cordaitan phylum.

It seems, however, not impossible that there is an even more direct connection between this phylum and the Taxaceæ—a connection indicated by the fact that the *general morphology of the female "flower" of Taxus more closely recalls that of Cordaites, than that of any other known plant.* I do not of course intend to suggest that *Cordaites* is actually the direct ancestor of *Taxus* (from which it differs in a number of important points), but I think that there is reason to suppose that *Cordaites* and *Taxus* are descended from the same primitive stock, and that *Cordaianthus* gives some idea of one of the stages passed through by the female "flower" of the Taxoideæ in the course of its evolution towards the reduced and specialised forms of the present day.

*. Since this Paper was written my attention has been called to a memoir which I had overlooked, "Fertilization and Embryogeny in *Cephalotaxus Fortunei*," W.C. Coker, Bot. Gaz. XLIII., Jan., 1907. The observations in this paper are in agreement with those of Professor Lawson, published in the Annals of Botany for the same month, except that the author reports *inequality* of the sperm cells.

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EXPLANATION OF PLATE I.,

ILLUSTRATING MISS AGNES ROBERTSON'S PAPER ON THE TAXOIDEÆ.

- Fig. 1. *Torreya californica*. Fertilisation stage. Egg cell (*e.c.*) and pollentube (*p.t.*) from longitudinal section of ovule gathered September 17th, 1902, shewing entry of functional male nucleus (σ_1). The second male nucleus (σ_2), distinguished by its smaller size, remains in the rear of body cell (*b.c.*). The egg nucleus (φ) and the remains of two neck cells (*n.c.* and *n.c.n.*) are shewn. (Preparation and drawing by Mrs. Tansley).
- Fig. 2, A, B, C, D. *Taxus baccata*. Stages in the division of the body cell. *v.n.*, vegetative nucleus. From sections of ovules gathered June 18th and 21st, 1906. (\times about 500).
- Figs. 3, 4, 5. Comparison of female "flower" of *Cordaites*, *Taxus* and *Torreya*. *o*, ovule; *a*, arillus; *b*, bract; *b'* bracteole; *g p.*, growing point; *l*, leaf subtending primary shoot; *s*₁, primary shoot; *s*₂, secondary shoot.
- Fig. 3. Diagrammatic longitudinal section through the "primary shoot" of *Corduaianthus Williamsoni* (after Renault.)
- Fig. 4A. Diagrammatic longitudinal section through "primary shoot" of *Taxus baccata*, illustrating a case in which the second ovuliferous axis (which usually aborts) has developed. (From a preparation by Miss T. L. Pranker.)
- Fig. 4B. External view of a biovulate primary shoot of *Taxus baccata*, cf. Fig. 4A. (after Pilger.)
- Fig. 5A. Diagrammatic longitudinal section through the "primary shoot" of *Torreya californica*.
- Fig. 5B. External view of shoot of *Torreya californica* with biovulate primary shoot in axil of leaf *l*, cf. Fig 5A.

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