The Anatomy and Morphology of the Inflorescences and Flowers of Ephedra.

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With Plate LXXXV and twenty-one Figures in the Text.

WE undertook this investigation because it seemed to us that the genus *Ephedra* required re-examination for the sake of comparison with recent work on the other genera of the Gnetales.

The material on which our work is based is largely supplied from collections, embedded material, and slides previously made by one of us for other work on the embryology of the genus,[1] and includes four species, *Ephedra altissima, E. distachya, E. fragilis,* and *E. nebrodensis.* Additional inflorescences of *E. altissima* in various stages were obtained from the Manchester University Botanical Laboratory, and herbarium material of various other species, *E. alata, E. Torreyana, E. trifurca,* and others, was supplied from the Manchester University Herbarium.

I. General Morphology of the Inflorescences.[2]

The male inflorescence in *Ephedra* consists of an axis arising in the axil of one of the ordinary leaves, and often dichasially branched, bearing generally one terminal and two lateral strobili (Fig. 1, Pl. LXXXV). The bracts at the point of branching have acute apices, like those in a similar position in *Welwitschia.*

In *E. distachya, fragilis, nebrodensis,* and *antisyphilitica,*[3] &c., the female inflorescence axis also springs directly from the axil of a leaf on the

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[1] Berridge and Sanday : Oogenesis and Embryogeny in *Ephedra distachya.* New Phyt., vi. 1907.

[2] Strasburger, 1872, pp. 76 ff. and 132 ff.; Land, 1904.

[3] Coulter and Chamberlain, 1901, p. 372. In this and several other species the peduncle is so short that the strobilus appears to be sessile in the axil of the bract.

vegetative stem; it generally bears one strobilus only; in *E. distachya*, however, it is sometimes branched. In some cases, which are specially common in *E. fragilis*, two or three such peduncles appear in one axil; here the lateral ones are in reality branches of the median peduncle, the first internode of the latter having failed to elongate. This suppression of the first internode seems to be characteristic of the shrubby Ephedras; in *E. fragilis* as many as fourteen branches are sometimes found crowded together at a single node. In *E. altissima* the arrangement, though different in appearance, is the same in essentials; the tendency to suppression of internodes at the base of the branches is not so marked in the vegetative shoots and the peduncles branch freely, the strobili, some of which are abortive, drooping in loose clusters from the climbing stems (Fig. 2, Pl. LXXXV).

The frequent dichasial branching of the female inflorescences of this species is a feature of marked resemblance to the inflorescences of *Welwitschia*. It is interesting to find dichasial branching a recurrent feature in the Gnetales, as a comparison has already been made between the inflorescences of *Welwitschia*[1] and the dichasially branched inflorescences of *Wielandiella*,[2] the flower of which also approaches that of the Gnetales.[3]

In all the above species each female strobilus is made up of three pairs of decussate fused bracts which form three cupules, the lowest very small, the next larger, and the uppermost forming a large protective cup within which the ovules (or ovule) are enclosed (Figs. 2 and 3, Pl. LXXXV).

In the tribe Alatae, which includes some of the other species examined, the bracts of the female strobilus are more numerous and are not fused, but become during the ripening of the fruit chaffy and membranous instead of succulent[4] (Fig. 3 c, Pl. LXXXV, *E. Torreyana*; there were here ten pairs of bracts). In *E. Torreyana* there was one case with as many as five ovules in the strobilus, and examples with three were fairly frequent. In the strobili bearing three ovules the alternating whorls of bracts are sometimes trimerous throughout. Usually, however, even in these species, where the cones have numerous membranous bracts, there are only two ovules in each cone.

In the cones of *E. distachya* and *E. fragilis*[5] there are also two ovules, occurring one in the axil of each of the topmost pair of bracts, the main axis terminating in between them. In microtome series of *E. distachya* the true apex of the stem is visible between the ovules as a small projection of a few cells.

In *E. altissima*[6] there is commonly only a single terminal ovule.

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[1] Sykes, 1910.

[2] Nathorst, 1888 (*Williamsonia angustfolia*) and Nathorst, 1902, 1910, 1911.

[3] p. 975.

[4] See Stapf's monograph on the Ephedras, p. 23 and Pl. I–IV.

[5] Var. *campylopoda*, Strasburger, 1871; also *E. antisyphilitica*, Coulter and Chamberlain, 1901, *E. helvetica*, Jaccard, 1894, and many other species, Stapf, 1889.

[6] As in *E. trifurca*, Land, 1904; *E. Alte, E. campylopoda*, &c., Stapf.

Occasionally, however, a form with two ovules is met with in which the arrangement of the ovules is the same as that found in the other species; but in this case no sign of the stem apex could be detected, the two outer integuments being fused together at the base.

The ovule has two coverings similar in position and character to those immediately surrounding the ovules in the other Gnetales, and here regarded as the outer and inner integuments.

The male strobilus is similar to the young female, but above the single basal pair of sterile bracts there are several pairs of fertile bracts, in the axil of each of which is a male 'flower'. The male flower consists of two perianth segments and a stalk, frequently more or less bifid, bearing two groups of bilocular synangia (Figs. 4–6, Pl. LXXXV). The number of the synangia varies from eight in *E. distachya* and *nebrodensis* to two in *E. altissima*.

In *E. fragilis*, var. *campylopoda*, the strobilus is bisexual, with male flowers in the axils of the lower pairs of fertile bracts and ovules in the axils of the uppermost pair. The latter, however, never reach full development.

The strobili of *Ephedra* are obviously far more closely comparable with those of *Welwitschia*[1] than with those of *Gnetum*.[2] The branched male inflorescence with its compact strobili, and both male and female strobili with their basal sterile bracts and their upper fertile bracts with axillary sporangiophores, are strikingly similar in both genera, but in *Ephedra* the strobilus has a much more limited growth than in *Welwitschia*.

II. The Anatomy of the Inflorescences and Flowers.

(a) The Bracts.

The bracts of both male and female strobili are similar in character,[3] though those of the female are tougher in the early stages than those of the male, and also undergo later various changes connected with the ripening of the fruit, becoming, in the different species, succulent or chaffy, &c. The members of each pair are fused together in the female strobilus, but only slightly connate at the base in the male.

Each bract receives two vascular bundles, which run unbranched nearly to its apex. As in the vegetative leaves, the bundle is accompanied by a small number of reticulate transfusion tracheides, occurring laterally in two groups (Fig. 7, Pl. LXXXV). These increase in number and size towards the apex of the bract, where the bundles approach one another. Finally, the endings of the bundles are lost in one common group of transfusion tissue

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[1] Pearson, 1906, 1909; Sykes, 1910.   [2] Thoday (Sykes), 1911; Pearson, 1912.
[3] Stapf, 1889, pp. 25 ff.; Bertrand, Fig. 12, Pl. III, figure showing similar structure of vegetative leaf.

which extends for a short distance further into the apex (Text-fig. II. 5, 6, 7, 8).

Fibrous cells with lignified walls are scattered through the tissues of all the bracts and are especially numerous just under the inner epidermis, where in the cupules of the female strobilus they form a definite layer, one or two cells deep in the outer cupules, two, three or more cells deep in the inner cupules (Fig. 7, Pl. LXXXV).

The outer epidermis is very thick and strongly cuticularized. The outer wall consists of three layers, an inner cellulose, a middle containing crystals, and an outer cuticularized layer. The stomata are mainly in the outer epidermis, they are very small and deeply sunk, and the inner surface of the guard cells is strongly cuticularized (Fig. 8, Pl. LXXXV). The epidermis and stomata of the vegetative leaves are very similar in structure.

The structure of the bracts in *Ephedra* is closely comparable with that in *Welwitschia*,[1] the main differences being due to the unbranched nature of the vascular bundles in the former genus. The distribution of the fibrous cells, the curious character of the outer epidermis,[2] the structure of the stomata, and the transfusion tissue are all points of similarity.

(b) The Peduncle.

(i) *General.* The peduncle or naked axis of the inflorescence closely resembles the young vegetative stem. It has a strongly thickened and cuticularized epidermis with stomata similar to those of the bracts; the cortex is mainly composed of thin-walled assimilating cells, but contains also strands of hypodermal sclerenchyma which, however, do not project and form marked ridges as in the stem. The phloem of each bundle is accompanied by a strand of fibrous cells. In *E. altissima* the hypodermal strands of thickened cells are absent, but the pith is strongly lignified, the cells showing simple pits, and well-marked lignified strands accompany the vascular bundles; in *E. distachya*, on the other hand, the pith is thin-walled and the strands bordering on the phloem are reduced to a few fibrous cells, but the hypodermal groups are constant and regular, although smaller than in the vegetative stem. *E. fragilis* shows an intermediate condition; the hypodermal strands are irregular and scattered, while the pith and bundle strands are thick-walled but unlignified.

In the vegetative stem of *E. altissima* the lignification of the pith is confined to the region near the node, while in *E. distachya*, *E. fragilis*, and *E. nebrodensis* signs of lignification appear only at the margin of the pith in the neighbourhood of the bundles.

[1] Sykes, 1910, pp. 184–6, Figs. 5, 9 *a* and *b*, Pl. XVII.

[2] It compares still more closely with the epidermis of the vegetative leaves in *Welwitschia*. Ibid., Fig. 2, Pl. XVII.

The varied distribution of the lignified tissue in the different species of this genus is paralleled in *Welwitschia*, where in the male inflorescence the entire pith is lignified, while in the female inflorescence this happens only in the extreme base; elsewhere lignification is confined to strands of tissue on the periphery of the pith accompanying the vascular bundles.[1]

(ii) *Vascular Anatomy of Naked Axis.* In *E. distachya* the peduncle is traversed by eight collateral bundles, occurring in a regular ring and remaining unbranched except where, in the male inflorescence, branching of the axis occurs. At this level and at the branchings of the axis of the female inflorescence in *E. altissima*, the behaviour of the bundle system is similar to that described later in connexion with the vegetative buds in the axils of the ordinary vegetative leaves. In the upper branches of the female peduncle of *E. altissima* the structure is somewhat different; there are here four small bundles and two large ones, which latter are seen by their behaviour in the strobilus each to represent two of the bundles in the lower parts of the peduncle.
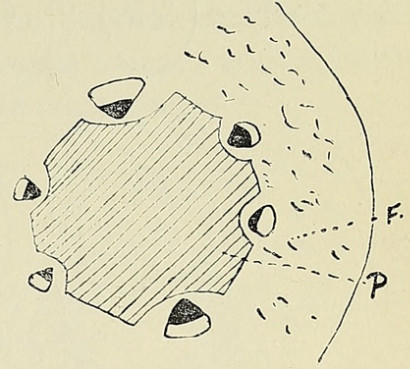
TEXT-FIG. I. Transverse section of peduncle of *E. altissima* near the base of a strobilus, showing six bundles, lignified pith (P), and fibres scattered in the cortex (F).

(c) Anatomy of the Female Strobilus.

The axis of the strobilus itself is similar in general structure, distribution of fibres, &c., to the naked axis bearing the strobilus. In describing the course of the vascular bundles in the axis of the female strobilus it will be necessary to treat the two species specially examined separately.

(i) *E. distachya.* The eight bundles which enter the base of the strobilus become arranged in two groups separated from one another by gaps in the ring (Text-fig. II. 1). Then the bundles on either side of each gap (Text-fig. II. 2 and 3, B) pass out to the first pair of bracts.
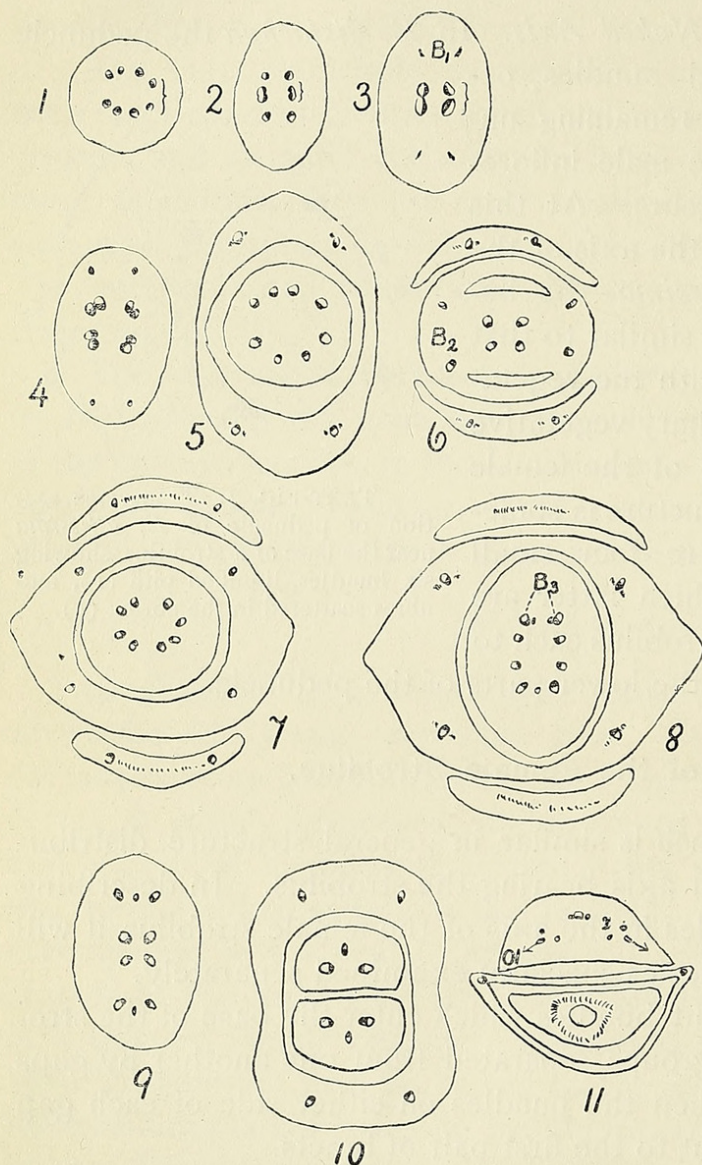
Four bundles are left in the axis; these now divide to form again the original number (Text-fig. II. 4). Next the eight bundles are rearranged into two groups at right angles to the previous arrangement, and two pairs of bundles pass out to the second pair of bracts (Text-fig. II. 5 and 6, B_2).

Four bundles are again left in the axis and once more divide to form eight, arranged in two groups corresponding in position to those below the first pair of bracts. Before, however, the lateral members of each group pass out to supply the third pair of bracts, a small bundle originates from each of them and fuses with the opposite one in the gap between the
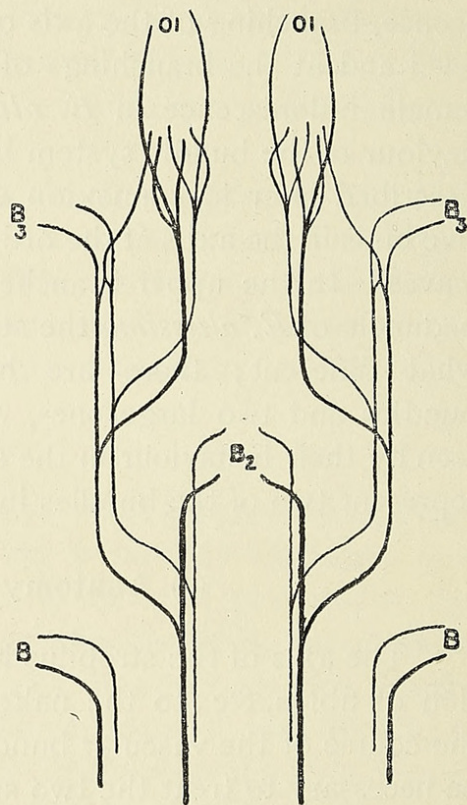
[1] Sykes, 1910, pp. 191 and 201–2.

groups (Text-fig. II. 8 and 9).   The two pairs of foliar bundles now pass
out in the ordinary way towards the bract, and the little median bundles
pass out a short distance with them (Text-fig. II. 9).   After the bundles
have entered the base of the bract the median bundle curves backwards
a little towards the centre of the axis and with two of the axial bundles

TEXT-FIG. III.   Plan of course of
vascular bundles in the female strobilus
of *E. distachya*; letters as in Text-fig. II.

TEXT-FIG. II.   I–II. Series of transverse sections
through the female strobilus of *E. distachya*, described
in text. B_1, B_2, and B_3 = bundles supplying lowest,
middle, and upper pairs of bracts respectively; OI =
bundles supplying outer integument.   The middle
cupule has been omitted in 9, and the upper cupule
in II.

enters the ovule.   With the formation of the two ovules the growth of the
axis ceases, and all the vascular elements are therefore used up in the
ovular supply (Text-fig. II. 10).

The behaviour of the bundle system at the level of origin of the ovule
is similar in essentials to its behaviour at the origin of an ordinary *vegetative*

axillary bud. The vegetative axillary bud receives a median trace,[1] derived from the two foliar bundles, which passes out first to the abaxial side of the bud and there divides into two again; also two lateral bundles which supply the adaxial side of the bud (Text-fig. IV. 1–5). The lateral traces are derived in some small part from the foliar bundles as they pass out to the subtending leaf, but chiefly from branches of the adjoining main bundles. In the case of the ovule none of the elements composing the two lateral traces are derived from the foliar bundles, and the adaxial side of each ovule is entirely supplied by two of the four main bundles left in the axis, which do not branch but themselves form the lateral traces; consequently no vascular elements remain to supply the minute stem apex.
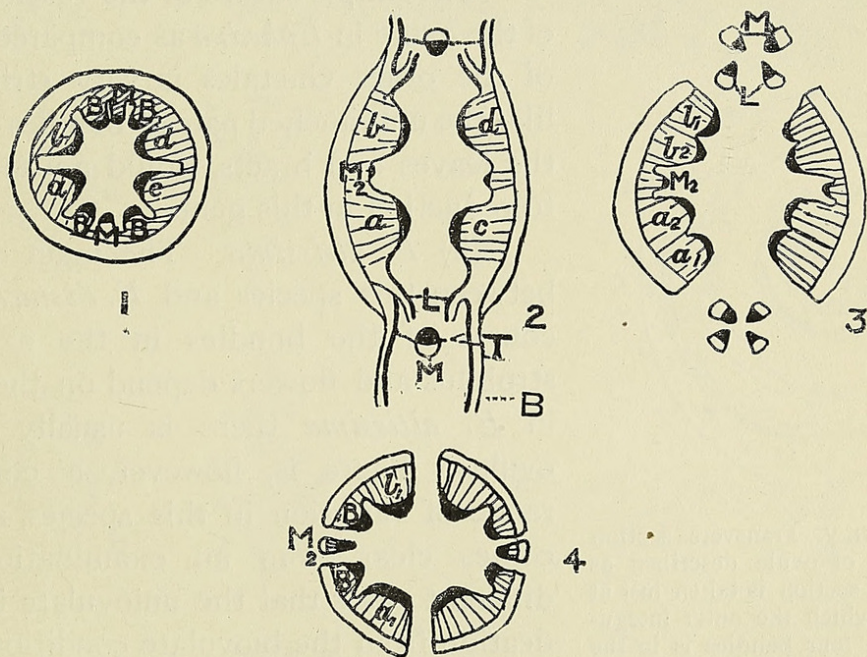
TEXT-FIG. IV. 1–5. Diagrams of series of transverse sections through the node of the vegetative stem (*E. nebrodensis*). M = median axillary bundle; L = lateral axillary bundle; B = bundle supply of subtending bract; a, b, c, d = four main bundles, which fork to form eight, $a_1a_2b_1b_2$, $c_1c_2d_1d_2$, in between each node; M_2 = median axillary bundle for axillary bud at next node; T = bridge of transfusion tracheides connecting the bract bundles with the median axillary bundle.

The course of the *bundle system in the ovule*[2] itself is very simple. The three bundles, one median axillary and two lateral, which enter the base of the ovule usually each branch into three; sometimes the median or abaxial one remains unbranched. In either case the median bundle does not contribute anything towards the supply of the outer integument, but the latter receives the middle branch from the other two groups only.[3] The outer integument thus receives two bundles which traverse the angles

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[1] The earlier account by Strasburger states that this is not the case: the vascular supply of the ovule differing in this respect from that of an ordinary axillary bud; 1872, pp. 78 ff.

[2] See also Strasburger, 1879, p. 99.

[3] The two bundles supplying the outer integument in *Welwitschia* originate in a very similar manner, each being derived from the middle bundle of a group of three; Sykes, 1910, p. 197, Diagram IX, especially Case 2.

adjoining its flattened side (Text-fig. II. 11) and run unbranched into the apex. In *E. fragilis* the median bundle does commonly contribute a small bundle to the outer integument.

In *E. alata* and *E. Torreyana* there are three large bundles in the outer integument, derived exactly alike from the three bundles entering the base of the ovule. The integument in these species has three large projecting wings, one in the median and two in the lateral planes.

The five or seven bundles left in the flower axis form a ring which dies out low down in the base of the ovule and does not as in *Welwitschia* and *Gnetum* run up into the base of the inner integument. From the position of the ring the constituent bundles here also are clearly integumental.[1]
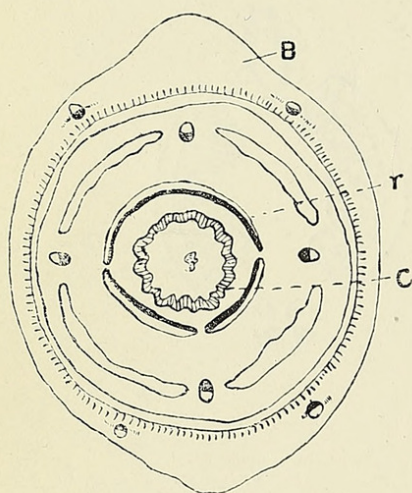
TEXT-FIG. V. Transverse section through base of ovule described as Case 2. The section is taken just at the level at which the outer integument with its four bundles is in the act of becoming free. B = upper cupule; *r* = 'ring of vascular tissue entering base of inner integument; C = suberized layer at the base of nucellus.

The simple nature of the vascular system of the ovule in *Ephedra* as compared with that of the other Gnetales is very striking, and, like the unbranched pair of bundles supplying the leaves and bracts, would appear to point to reduction in this genus.

(ii) *E. altissima*. The main differences between this species and *E. distachya* in the course of the bundles in the axis of the strobilus and flowers depend on the fact that in *E. altissima* there is usually only one ovule. There is, however, a considerable range of variation in this species, and it becomes clear from an examination of the different cases that the uniovulate is a modification from the biovulate condition.

Case I. Biovulate cones with both ovules fertile are occasionally found. In these cases the course of the vascular bundles is practically identical with that described in the cone of *E. distachya*, except that in the cases examined the integument always received three vascular bundles, and not two as is the rule in *E. distachya*, the median axillary bundle branching into three and contributing as well as the other two[2] to the integument.

Case 2. Among the material in the laboratory in Manchester, cases frequently occurred in which the single nut of the uniovulate cone had four angles instead of the normal three, and four bundles supplied the outer integument[3] (Text-fig. V), running up these four angles. The course of the

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[1] See pp. 966, 967. The tissues of nucellus and integument in *Ephedra* are differentiated from one another down to the base of the ovule.

[2] In *E. trifurca*, in which species also there is commonly only one ovule in the strobilus, biovulate cones also occasionally occur, in which the course of the bundles is the same as in Case 1 of *E. altissima*.   [3] This is the normal case in *E. trifurca* (see also Land, 1904).

vascular bundles in this case is seen in Text-fig. VI. 1–10. Text-fig. VI. 8 represents the level above the origin of the uppermost bracts (B_3), and it is seen that four bundles run into the base of the single ovule. Of these the two smaller represent the median traces derived from the bract bundles and the two larger each represent two of the main axial bundles fused together. In all the uniovulate cones of *E. altissima* examined, the course of the bundles in the cone axis below this level only differed from that in *E. distachya* in that six bundles instead of eight occurred in the internodes (six
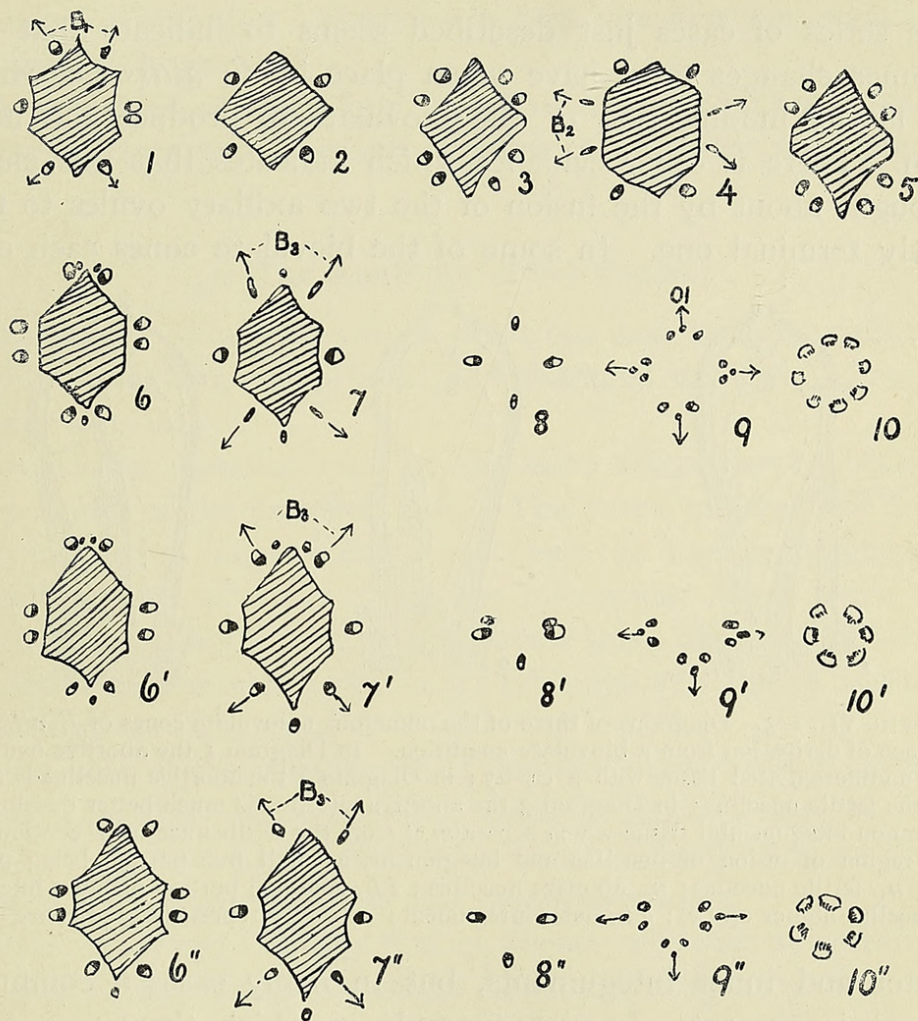
TEXT-FIG. VI. Illustrates three transverse series through the female strobilus of *E. altissima*, described in text. Case 2 = 1–10, Case 3 = 6′–10′, Case 4 = 6″–10″; letters as before.

is also the number in the peduncle, p. 957). This appears to be the result of the tendency of the four main axial bundles, which ultimately supply the two ovules in the biovulate cone, but which in the uniovulate cone fuse into two in the base of the ovule, to fuse into pairs lower down also.

Cases 3 and 4. In other uniovulate cones the integument is three-angled and receives three vascular bundles. The two median traces may still both be formed from the bract bundles as in Cases 1 and 2, but in Case 3 one of them divides into two in the base of the ovule, and the halves fuse with the two main bundles, so that three bundles run up into the ovule

instead of four (Text-fig. VI. 6′–10′). This case is intermediate between the first two cases and Case 4, in which one of the median axillary bundles is not formed at all, and only three bundles enter the base of the ovule (Text-fig. VI. 6″–10″). This is the case described by Strasburger [1] as normal, but it here seemed to be exceptional, for it only occurred in one ovule out of seven or eight. Case 3 was the most common.

(*d*) **Relation of E. altissima to E. distachya.**

The series of cases just described seems to indicate that in fairly recent times changes must have taken place in *E. altissima* which have resulted in the modification of the biovulate to produce the uniovulate condition. There is other evidence which indicates that this change has been brought about by the fusion of the two axillary ovules to form one apparently terminal one. In some of the biovulate cones each ovule has
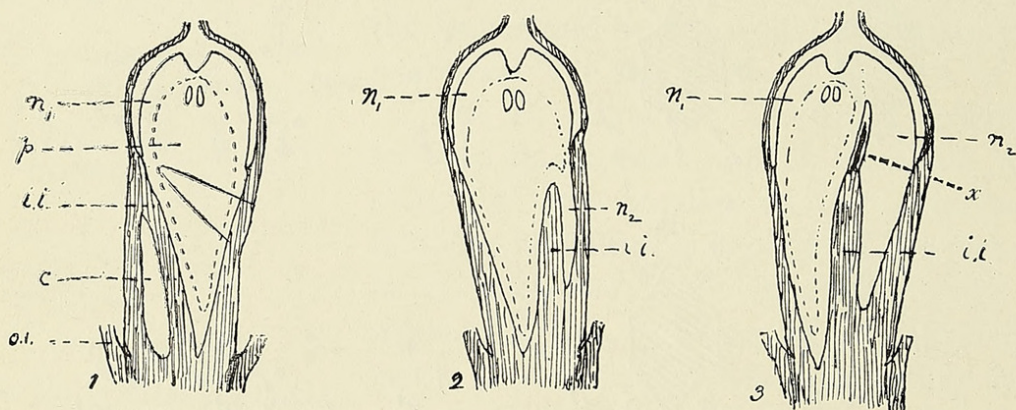
TEXT-FIG. VII. 1–3. Diagrams of three of the numerous uniovulate cones of *E. altissima* which show evidence of derivation from a biovulate condition. In Diagram 1 the abortive ovule is merely a mass of undifferentiated tissue with a cavity; in Diagram 2 the abortive nucellus is fused at the apex with the fertile nucellus; in Diagram 3 the abortive nucellus is much better developed and the wall of common integumental tissue which separates it from the fertile nucellus is continued upwards above the region of fusion of nucellus and integument, a small free portion being present. *p.*, prothallus; n_1, fertile nucellus; n_2, abortive nucellus; *i.i.*, common portion of inner integument free from the nucellus higher up (*x*); *o.i.*, outer integument; *c.*, cavity representing abortive nucellus.

both outer and inner integuments, but in many cases a common outer integument is present. In one example in which there was a common outer integument both ovules were fertile, but usually one is more or less abortive. This abortive ovule is often fused to the lower part of the inner integument of its fully developed companion, distorting and pressing aside its base; frequently it is merely a mass of undifferentiated tissue with a cavity in the middle (Text-fig. VII. 1), having an independent cup of suberized tissue at its base like that always found at the base of the fertile ovule. Sometimes, however, nucellar tissue [2] occurs within the cavity of the abortive ovule. This is the case in the example represented in Fig. 10,

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[1] Strasburger, 1872, Fig. 55 *a* and *b*, Taf. XVI.

[2] It is remarkably easy in *Ephedra* to distinguish the nucellar tissue from the surrounding layers of the inner integument, even in the common basal region; pp. 966, 967, Text-fig. XI. 2.

Pl. LXXXV, and in Text-fig. VII. 2.   Here the common wall of integumental tissue between the two nucelli is incomplete, and the small nucellar mass of the abortive ovule is fused at its apex with the fertile nucellus, so that in this section it appears as a long lobe of the latter extending downwards into the integumental tissue.

In a somewhat similar case (Text-fig. VII. 3) fusion of the two nucelli has only taken place at their extreme apices, and the common integumental wall runs up between them and ends in a small free lamina in the chink below the point of fusion.   Here again only one nucellus contains a pro-thallium with archegonia.

Fully one-third of thirty-four strobili of *E. altissima* examined showed traces of the presence of a second abortive ovule within the outer integument.

(e) The Anatomy of the Ovule.[1]

E. distachya.   The ovules in *E. distachya* and other biovulate species are roughly triangular, compressed and flattened on their adjacent sides, but rounded abaxially.

Two vascular bundles traverse the *outer integument,* running in the two sharp angles of the flattened side.   The outer epidermis of the integument is composed of large columnar cells and the inner epidermis of similar smaller cells except where it clasps the micropylar tube ; there each cell is drawn out into a papilla.   In the old ovule these become lignified and are firmly fused on to the micropylar tube (Text-figs. VIII and IX and especially XI. 3, and Fig. 11, Pl. LXXXV).

At the base of the integument it consists mainly of a layer of brown cells underneath the outer epidermis, which is continuous right round the bundles (Text-fig. VIII. 5), and internal to this is a band of tissue which even in the oldest ovule examined was still parenchymatous.

A little higher up (Text-fig. VIII. 4), fibrous cells with thick walls become differentiated in this parenchymatous band, and very soon there is a thick layer of fibrous cells on the inner side of the brown layer (Text-fig. VIII. 3). In the upper part of the outer integument there is, as well as the fibrous layer, a more conspicuous strand [2] of larger fibrous cells accompanying each vascular bundle on its inner side (Text-fig. VIII. 2) ; but at the tip, where the integument surrounds the micropylar tube, both the fibrous layer and the separate strands die out (Text-fig. VIII. 1).   The brown layer gradually diminishes in prominence till in this region it is represented only by two small bands of tissue alternating with the two vascular bundles.

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[1] Strasburger, 1872, pp. 86 ff., Pl. XVI, &c.

[2] In *E. nebrodensis,* the outer integument of which is very like that of *E. distachya,* these fibrous strands accompany the vascular bundles right to the base of the integument.   The fibrous layer is also well marked and strongly lignified.

The vascular bundles throughout the upper third of the ovule are accompanied by large wings of transfusion tissue, which extends some distance round the fibrous strands (Text-fig. VIII. 2), and at their termination the bundles are lost in two large groups of transfusion tracheides (Text-fig. VIII. 1, T).

The *inner integument*, which becomes free about two-thirds of the way up the nucellus, projects in the early stages considerably beyond the outer covering, but in the mature seed this projecting portion is generally broken
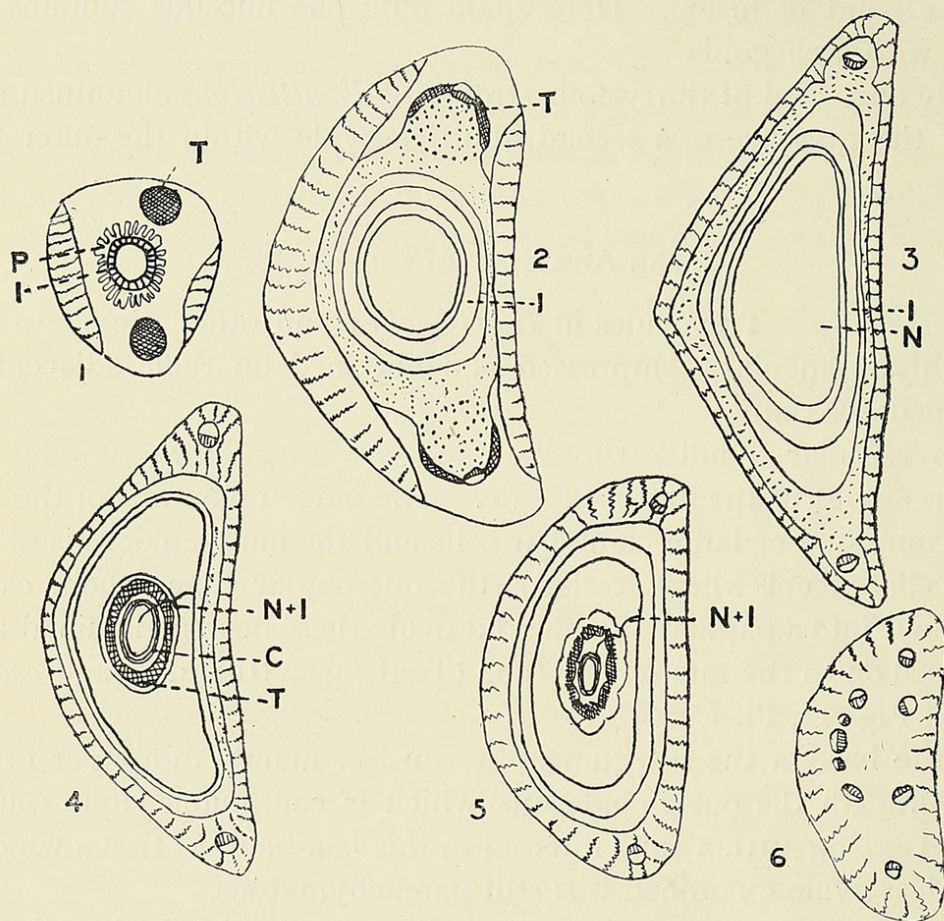
TEXT-FIG. VIII. 1–6. Diagram of series of transverse sections through the ovule of *E. distachya*. P = papillae; T = transfusion tissue; I = inner integument; N = nucellus; C = layer of suberized cells at base of nucellus; cross hatching = xylem; dots = fibres; jagged lines = brown tissue.

off. The whole integument is very thin and its base is made up of thin-walled parenchymatous cells only ; in the mycropylar tube there are three layers of cells, the inner epidermis, composed of large cells which are cuticularized to a most remarkable extent (Fig. 11, Pl. LXXXV), and two outer layers of much smaller cells whose walls are thickened in a minor degree, but not cuticularized. A little mucilage appears in the tube shortly before fertilization ; later this becomes hardened into a solid mass [1] which closes

[1] A similar secretion of mucilage is recorded by Pearson ('06) at the fertilization stage in *Welwitschia*; but it does not appear to be known whether this persists and becomes hardened afterwards.

the tip of the tube and which is continuous downwards as a thick mucilaginous lining to the tube. The chink between the micropylar tube and the integument is also closed by the papillae of the outer integument, and
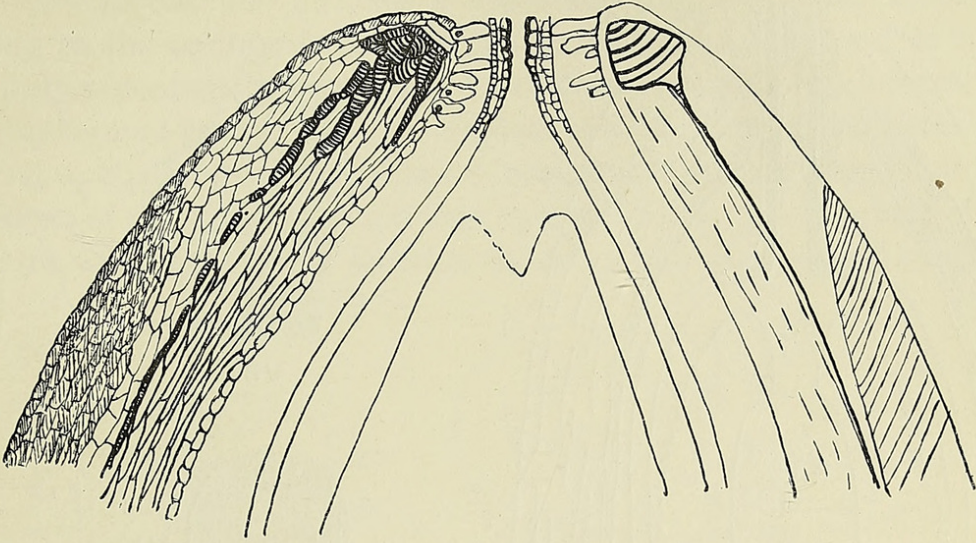
TEXT-FIG. IX. Longitudinal section of ovule of *E. distachya*, older than the one drawn in Text-fig. VIII. The fibres internal to the vascular bundles are seen to be strongly lignified.

in this manner the developing embryo would appear to be as effectively protected as in *Gnetum*[1] with its special apparatus.

The ring of vascular bundles which enters the base of the ovule does not run up as far as the free region of the inner integument, but terminates quite low down in a mass of transfusion tracheides. One of the most characteristic features of the *Ephedra* ovule is the sharp demarcation of the large empty cells of the nucellar tissue from the smaller celled tissue which forms the free part of the inner integument and is also prolonged downwards right round the base of the nucellus (Text-fig. XI. 2). The ring of vascular tissue is situated in the integumental region. This differentiation is not of course present in the earliest stages, its cause being the proximity and growth of the prothallus, in consequence of which the cells of the nucellus become flattened and empty. Still the differentiation is of some interest, nothing of the kind having been seen in *Gnetum* or *Welwitschia*.
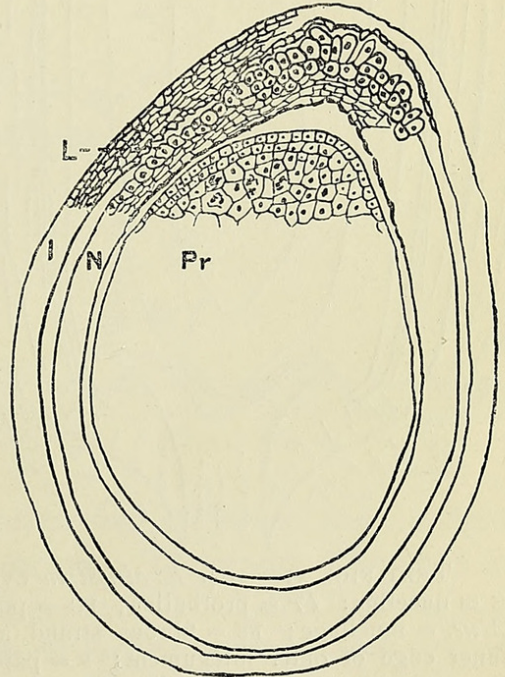
TEXT-FIG. X. Transverse section of nucellus and inner integument just above the level at which the integument becomes free. I = inner integument; N = nucellus; *Pr* = prothallus; L = layer of papillate cells on periphery of nucellus.

[1] Berridge, 1911; Thoday (Sykes), 1911.

The *nucellus* becomes very thin and papery in the seed, except at the apex, where it is still possible to distinguish the remains of the remarkably deep pollen-chamber, which has already been described in detail by other
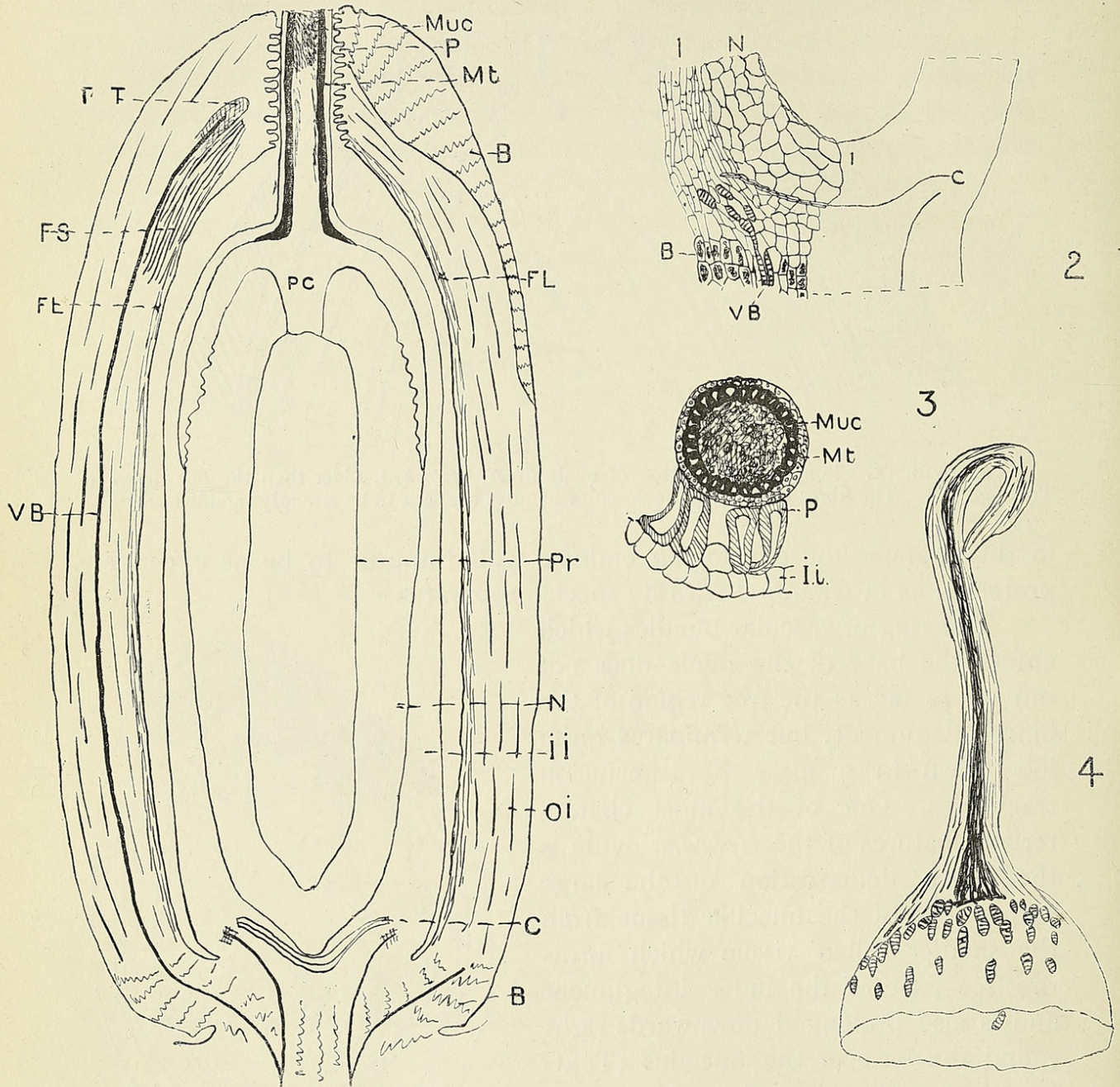
TEXT-FIG. XI. 1–4. *E. altissima* ovule. 1. Longitudinal section showing general structure. N = nucellus; *Pr* = prothallus; PC = pollen-chamber; *ii* = inner and *oi* = outer integument; *Muc.* = mucilage; FS = fibrous strand accompanying vascular bundle; FL = fibrous layer on inner edge of outer integument; P = papillae; *Mt* = micropylar tube; B = hypodermal tissue; C = cup; VB = vascular bundle; TT = transfusion tissue. 2. Base of fused nucellus and inner integument, showing sharp line of demarcation. 3. Transverse section through apex of micropylar tube, closed by hardened mucilage, and part of edge of inner integument showing lignified papillae attached to micropylar tube. 4. Free region of inner integument, showing coiled micropylar tube and reticulately thickened strengthening cells.

authors[1] (Figs. 9 and 12, Pl. LXXXV).   In the seed of some species the walls of the cells surrounding the pollen-chamber become thickened and lignified,

[1] Strasburger, 1872, Fig. 54, Taf. XVI ; Jaccard, 1894 ; Land, 1904 ; Berridge and Sanday, 1907.

forming a little cap as in *Gnetum.*[1] For some little distance above the level
at which the nucellus becomes free from the inner integument, the cells com-
posing its epidermal layer are drawn out into papilla-like outgrowths (Text-
fig. X).[2] At its base the nucellus is separated from the small-celled tissue
belonging to the region of the inner integument by a thin layer of crushed
cells, empty of contents, with suberized walls, which forms a cup, internal to the
larger cup formed by the vascular bundles and their transfusion tracheides,
extending upwards to about the same level, and separated from it by two or
three layers of parenchyma (Text-figs. V, C, and XI. 2, C). It is very difficult
to imagine what may be the function of such a cup of suberized cells.
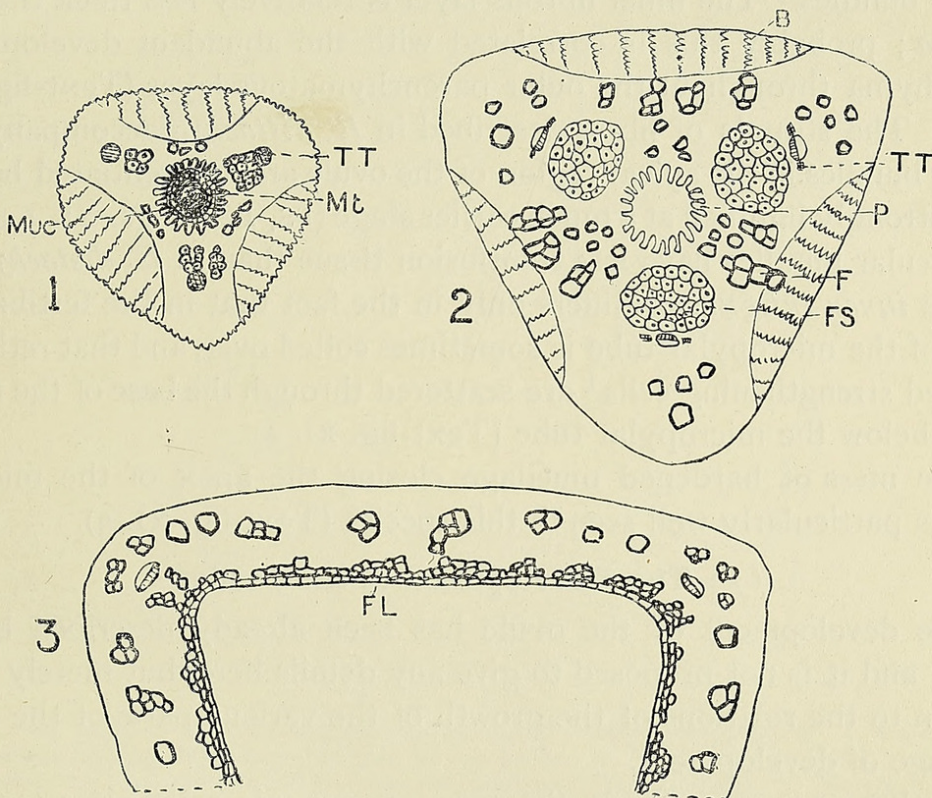
TEXT-FIG. XII. 1–3. *E. altissima.* Diagrams of transverse sections through ovule; 1 = through
apex of micropylar tube; 2 = through the outer integument at the level of the lower part of
micropylar tube; and 3 = at a level about half-way up the ovule. Letters as before.

E. altissima. The single ovule of *E. altissima* differs to some extent
from the ovule of the bisporangiate *E. distachya.* The great difference in
size may be seen by a comparison of Figs. 2 and 3 *a*, Pl. LXXXV, which are
magnified to the same scale. It is of course no longer laterally compressed
by the presence of another ovule, though it is still angled, its angles being

[1] Thoday (Sykes), 1911, pp. 1113–14.

[2] Pearson has suggested that during the disorganization of the nucellar apex in *Welwitschia*
a good deal of the mucilage afterwards found in the micropylar tube is formed, and he also produces
evidence to show that some of this mucilage is secreted by the outer layers of the nucellar cone
(1909, p. 343). It appears probable that in *Ephedra* also, while some of the mucilage originates
by disorganization to form the pollen-chamber, some of it is similarly secreted by the papillate cells
of the nucellar epidermis.

three or four in number, with a corresponding number of vascular bundles in the outer integument. The angles are not very prominent, but it is quite easy to tell their number by examination with the naked eye.

In the *outer integument* there is an outer soft and an inner fibrous layer as in *E. distachya.* In the outer layer the hypodermal brown tissue is only differentiated in the extreme base of the outer integument, where it forms a ring, and in the tip, where it is distributed in bands alternating with the vascular bundles. Text-fig. XI. 1 shows one of these bands cut longitudinally on the right side of the ovule, while on the left the section has passed through the region in between the bands and has cut one of the alternating vascular bundles. The inner fibrous layer is relatively less thick than in *E. distachya* ; probably this is correlated with the abundant development of sclerenchyma throughout the outer parenchymatous layer (Text-figs. XI. 1, and X). The strands of fibres described in *E. distachya* accompanying the vascular bundles in the apical region of the ovule are differentiated here also, but are strongly lignified at a much earlier stage (FS, Text-figs. XI. 1, and XII). The vascular bundles have less transfusion tissue than in *E. distachya.*

The *inner integument* differs only in the fact that in the fertilized seed the tip of the micropylar tube is sometimes coiled over, and that reticulately thickened strengthening cells[1] are scattered through the base of the thin free portion below the micropylar tube (Text-fig. XI. 4).

The mass of hardened mucilage closing the apex of the micropylar tube was particularly well seen in this species (Text-fig. XI. 3).

(*f*) The Development of the Ovule.

The development of the ovule has been already described by other authors, and it is not proposed to give any details here, but merely to draw attention to the relations of the growth of the various parts of the ovule at each stage of development.

In the very young ovule the two integuments arise close together at the base of the ovule ;[2] at the stage shown in Text-fig. XIII. 1 the bases of the two integuments are still almost on a level. From this stage onwards for some time the growth is mainly confined to the free apex of the nucellus, while very little development takes place in the region between the levels of origin of the two integuments. It will be seen that in Text-fig. XIII. 2, which is clearly a much older ovule than Text-fig. XIII. 1, this region has not begun to develop. Growth here begins about the time of cell-wall formation within the megaspore and continues with the enlargement of the prothallus ; in the ovule figured in Text-fig. XIII. 3, which is not yet fertilized, considerable growth of this region has taken place. From this stage onwards the nucellar apex enlarges less in proportion to the rest

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[1] It is probable that these were the cells once mistaken for tracheides. See reference in Thoday, 1911, p. 1117, note 3.

[2] See Fig. 2, Pl. XXII, in Berridge and Sanday, 1907.

of the ovule, and consequently the free part of the inner integument gets carried further up; in Text-fig. XIII. 3 its level of freedom is about half-way up the ovule, but in the ripe seed it is about two-thirds of the way up (Text-fig. XI. 1).[1] Even in the mature seed, however, the free apex of the nucellus is conspicuous and fairly massive.

It is interesting to compare the relative development of the different regions of the ovule in the three genera of the Gnetales. In *Gnetum* the method of development is similar to that in *Ephedra* in that the apical region of the ovule develops first, but in the later stages this region appears practically to cease to grow, and it is almost entirely to the great growth of
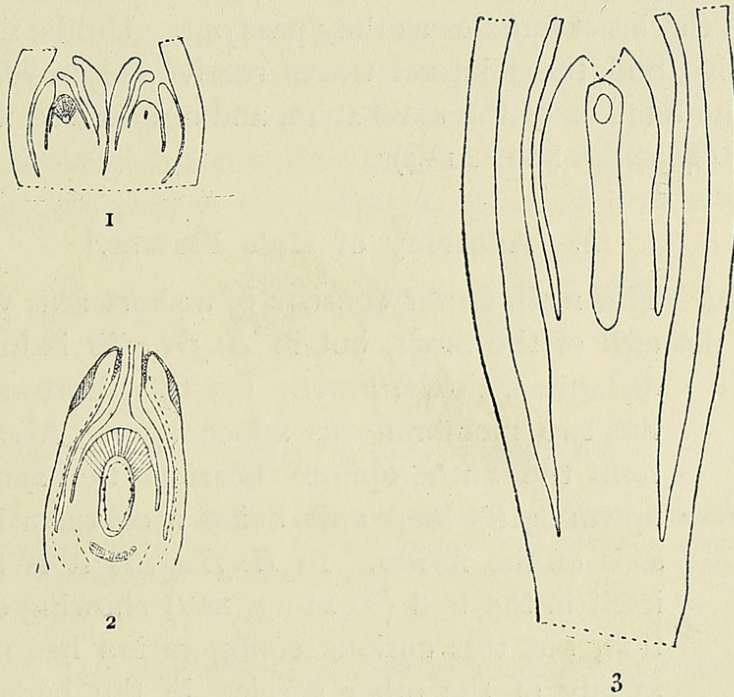
TEXT-FIG. XIII. 1-3. Three stages in the growth of the ovule in *Ephedra*. 1. Early stage with two integuments arising together at the base of the ovule. 2. Young ovule in which the apex has grown considerably, but the two integuments still originate close together. 3. Fertilization stage in which the region between the integuments has begun to enlarge.

the intermediate region, as in the Cycads, that the enlargement of the ovule is due. The apex of the nucellus after fertilization becomes hardened and withered, as it does also later and to a much smaller extent in *Ephedra*.

In *Welwitschia* we unfortunately know little of the earlier stages. In Text-fig. VIII, p. 196 of an earlier paper,[2] a stage is drawn in which the integuments are fairly close together. Here also the early growth in the apical region is followed by the enlargement of the intermediate region, but it also appears that here further great expansion of the apical region takes place, producing a massive nucellar apex far larger in size than that in *Ephedra*, though more like *Ephedra* than *Gnetum*. It has already been suggested [3] that the Angiosperms illustrate the further development of this tendency.

[1] Or even three-quarters, Strasburger, 1872, Fig. 50, Pl. XVI.
[2] Sykes, 1910.
[3] Sykes, 1910, pp. 218-19.

(*g*) Anatomy of Male Strobilus.

The anatomy of the male strobilus is similar in all essentials to that of the female. The pair of lower sterile bracts have usually no buds in their axils, and each is supplied with two bundles in the same way as the pairs of sterile bracts of the female strobilus. At the other nodes, at each of which arise two bracts and two male flowers, the course of the vascular bundles is closely comparable with that at the origin of a vegetative bud.[1] The male flower receives, similarly, three bundles : the median trace, derived itself from the fusion of two bundles and originating early from the two bundles which supply the subtending bract, and two lateral traces which originate from the bract bundles as they pass out. Unlike the lateral traces of the vegetative bud, these lateral traces receive only a very small contribution from the bundles of the main stem, and are derived mainly from the foliar bundles (Text-fig. XVIII. 1–4).

(*h*)   Anatomy of Male Flower.[2]

I. *General.* The male flower consists of a short axis which generally arises free in the axil of the bract, but in *E. fragilis* is fused for a short distance with the bract. On this short axis are inserted the two membraneous appendages. Above their insertion the antherophore bearing the synangia extends upwards, its long axis being a continuation of the long axis of the flower. In *E. fragilis* it is folded back on itself in the bud (Text-fig. XIV) showing circinate vernation, but this curious configuration has not been found in any of the other species, in the buds of which the axis is very short and straight (Fig. 5 *c*, Pl. LXXXV).
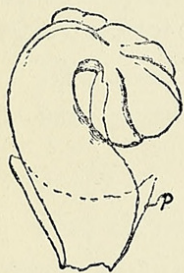
TEXT-FIG. XIV.
Sporangiophore of *E. fragilis* in bud, showing the manner in which it is folded over.   P = base of perianth.   × 23.

The antherophore varies considerably in the different species. It is generally cylindrical in the earliest stages, and it may remain so when mature, or may broaden out into a fairly wide lamina. In *E. Torreyana* (Text-fig. XVII) and *E. aspera*[3] this lamina is well developed, and the synangia are borne on long stalks. In *E. nebrodensis* also the sporangiophore is flattened, as it is in several of the species figured by Stapf. In *E. distachya* and *E. fragilis* it is much more cylindrical, and in *E. altissima*, where it is probably most reduced, it shows little if any sign of broadening out into a lamina.

In some species, e. g. *E. distachya*, *E. nebrodensis*, the antherophore is clearly bifid. Each half bears four synangia, situated on the side of the

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[1] p. 959 and Text-fig. IV.   [2] See also Strasburger, 1872, p. 132.
[3] Both of these species have female strobili with numerous membranous bracts, and are presumably (pp. 954 and 976) among the more primitive of the species of *Ephedra*.

antherophore away from the main axis of the strobilus, but borne some-what laterally and thus facing away from the axis of the antherophore. Apparently this arrangement represents the original form of the anthero-phore from which the other more reduced forms are derived by fusion of the synangia. The fused synangia are often bilocular, quadrilocular, or irregular in form. In *E. distachya* the division of the antherophore into two extends occasionally almost to its base,[1] but in other cases it may be quite absent, the two uppermost synangia being thus brought almost into contact with one another.

From this arrangement it is but a short step to the first stages of fusion and reduction in number of the synangia ; this has taken place in *E. Torreyana* (Text-fig. XVII) and *E. aspera*, in which the two uppermost synangia, one belonging to each half of the antherophore, are fused, giving rise to a single apical, commonly trilocular synangium (Text-fig. XV, C). There is often considerable variation within the limits of a single species, various stages of fusion occurring in the different antherophores even of the same
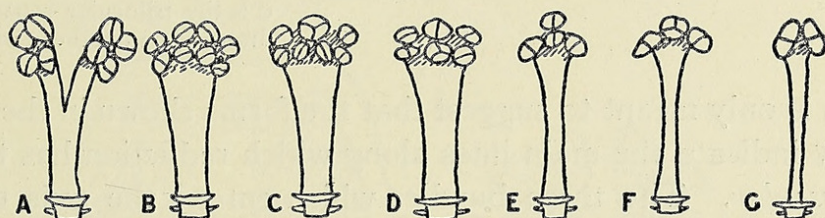
TEXT-FIG. XV. Diagram of antherophores of the various species, illustrating the reduction in number of the synangia by fusion.   A = *E. distachya*; B = *E. distachya, nebrodensis,* or *fragilis*; C = *E. aspera* or *E. Torreyana*; D = *E. aspera* or *E. Torreyana*; E = *E. Alte*; F = *E. aspera* or *E. altissima*; G = *E. altissima.*

strobilus. In *E. Torreyana*, for instance, cases occur in which the two inner synangia, like the uppermost pair, also fuse with one another (Text-fig. XV, D), so that there are two single median and two pairs of lateral synangia.

In *E. campylopoda*[2], a further fusion has occurred, the outer synangia of each half of the antherophore having fused with one another (Text-fig. XV, E), so that there are only four synangia, two median and two lateral. Next there are species in which the original eight synangia are represented only by three, one terminal and two lateral (*E. aspera, E. altissima, E. Alte* (Stapf), Text-fig. XV, F), and finally in *E. altissima* the terminal synangium, which when present is generally trilocular, is commonly abortive, and the antherophore bears only two lateral synangia (Text-fig. XV, G ; Figs. 6 *a* and 6 *b*, Pl. LXXXV).

It is not intended to assert that these fusions here described are the only possible fusions among the synangia, all kinds of irregular fusions occur, distributed among the various species; even in *E. distachya* and
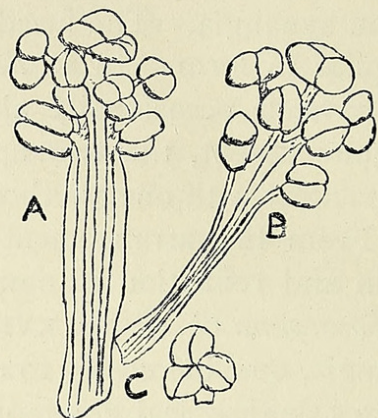
[1] Also recorded by Stapf, 1889, p. 21.   [2] Also in *E. Alte*, Stapf.

E. nebrodensis, cases were met with in which two otherwise independent synangia were fused by their adjacent ends. One of the most irregular species is *E. aspera*, in which occurred all the forms indicated in Text-
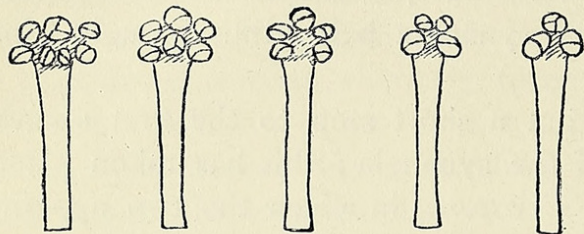

TEXT-FIG. XVI. Diagram of antherophores of *E. aspera*, showing the great variation in this species.

TEXT-FIG. XVII. Two anthero-phores of *E. Torreyana*, each show-ing a single terminal synangium, quadrilocular in A, trilocular in B. C is the trilocular synangium of B drawn from another point of view.

fig. XV. It is only meant to suggest that the forms shown in the diagram in Text-fig. XV indicate the main lines along which reduction has taken place.

II. *Vascular.* The three bundles which enter [1] the axis of the male flower fuse more or less completely into a single crescentic bundle (Text-fig.
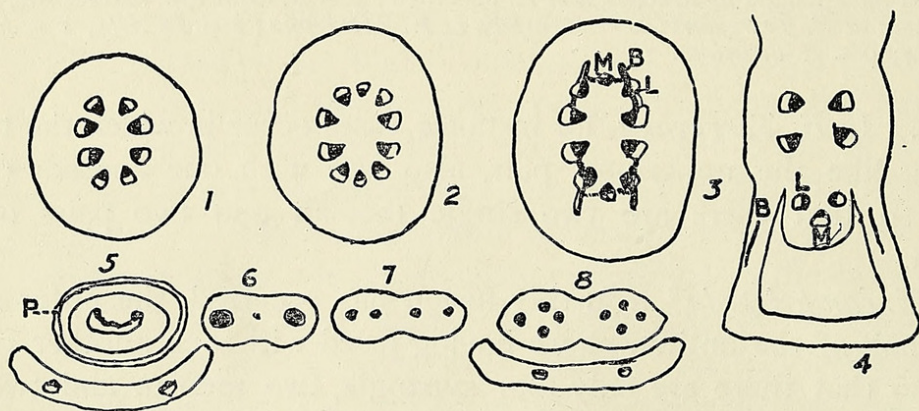

TEXT-FIG. XVIII. 1-8. Series of transverse sections through axis of male strobilus and anthero-phore of *E. nebrodensis*. 1-4 = axis of male strobilus, showing contribution of one median and two lateral traces to the antherophore, all being derived from the foliar traces. 5-8 = antherophore in axil of bract; 5 shows crescentic bundle, in 6 it has broken into two with a minute bundle between which dies out, in 7 the two have divided to form four, and in 8 to form eight. P = 'perianth'; other letters as before.

XVIII. 4, 5). The fusion lasts only for a very short time, and takes place just below the level of insertion of the two leaf-like appendages. The crescentic mass thus formed almost immediately separates again into two large bundles, and between these a minute third one is commonly found on the abaxial
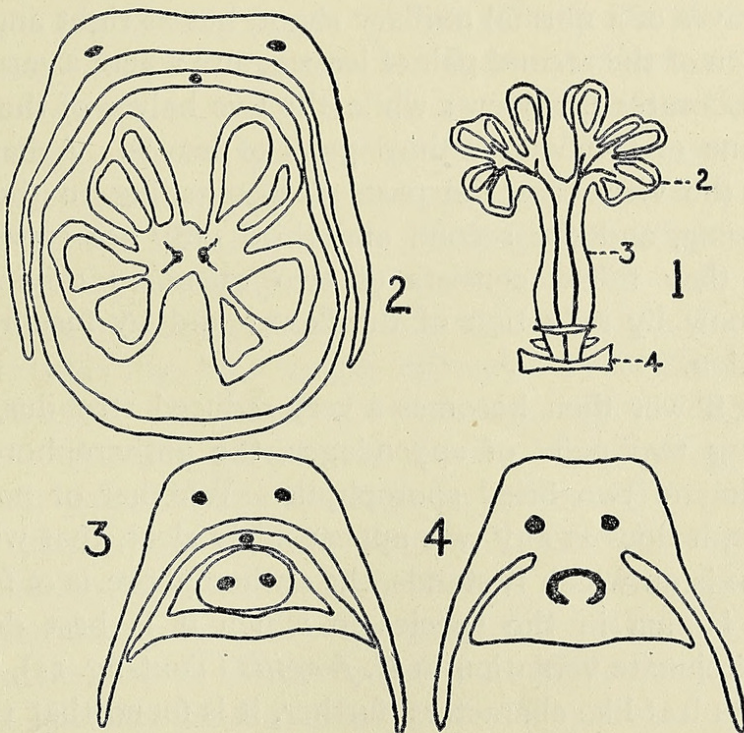
[1] p. 970.

side. In *E. fragilis* this minute bundle passes out into the adaxial ' perianth' member (Text-fig. XX. 3, 4), and rarely this may even receive two bundles, but the other member appears to be always without a vascular
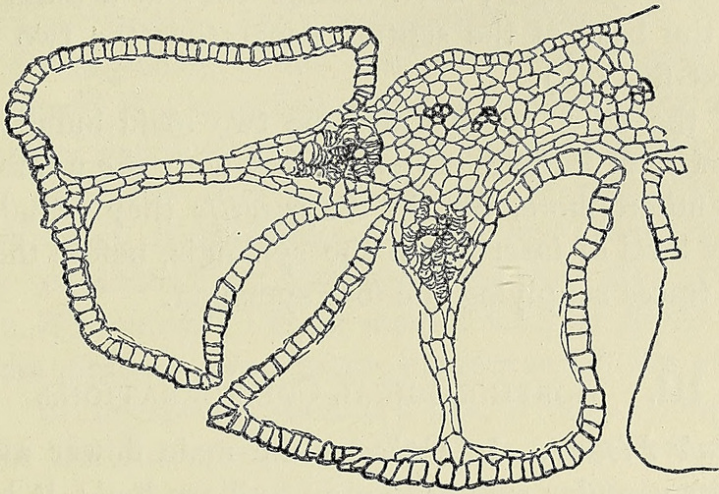
TEXT-FIG. XIX. Longitudinal section through two synangia of *E. nebrodensis*, showing transfusion tissue in septa.

TEXT-FIG. XX.[1] Diagram of male flower of *E. fragilis.*   1 = Longitudinal section ; 2, 3, 4 = transverse sections from levels 2, 3, 4 in Diagram 1.   The two bundles are seen to pass up unbranched to the level of origin of the synangia.   The third bundle supplying the perianth is seen in 3, and the fusion of the base of the flower-stalk with the bract in 4.   Higher up than 2 the perianth segments become separate from one another.   2, 3, 4 × 23.

supply.[2]   In all the other species the leaf-like appendages receive no bundles, and the minute third bundle dies out, while the two larger portions

[1] This figure is adapted from drawings kindly lent by Dr. Benson of Royal Holloway College.
[2] As in *Welwitschia*, but in *Gnetum* these structures have a vascular supply.

of the crescentic mass supply the two halves of the bifid antherophore. In each half in *E. distachya* and *E. nebrodensis*, the bundle branches into two and then again into four, the eight bundles thus formed supplying the two groups of four synangia; each bundle ends in a mass of transfusion tracheides[1] in the base of the septum separating the two loculi of each synangium (Text-fig. XIX).

In most of the other species also the two main bundles branch quite early into a number of bundles corresponding with the number of synangia borne on the antherophore, but in *E. fragilis* they remain unbranched almost up to the level of insertion of the synangia, before they each divide up to form four traces supplying the four synangia.

III. Morphological Considerations.

A. *The Male Flower.* In *Ephedra* the male flower axis is axillary, and it receives its vascular supply like an axillary bud; it bears two leafy appendages and a bifid antherophore. It therefore has the characteristics of an axillary shoot. The appendages are not however in the same plane as the first pair of leaves of a normal axillary shoot, but at right angles to it, that is in the position of the second pair of leaves; and where a vascular supply is present it corroborates this view: while the two halves of the antherophore are in the plane of the first or third pairs of leaves. Arber and Parkin[2] have adopted the view that the parts corresponding to the first pair of leaves are missing, and the second and third only are represented. The antherophore, they think, consists of two members originally standing laterally, but now by reduction of the flower and by fusion brought into a median position.

The male flower then becomes a very reduced strobilus, consisting of an axis bearing two pairs of appendages, the antherophore itself being a disc consisting of two fused sporophylls. Whether or no this view be the correct one, it does at any rate appear fairly clear, that whatever be the nature of the axis on which it stands, the antherophore is of foliar nature[3]: its broadened lamina in the species in which it is best developed, and especially its circinnate vernation in *E. fragilis* (Text-fig. 12), both combine to emphasize its leaf-like character: further, it is found that the two halves of the antherophore receive their bundles in the same manner as do the first and third pair of leaves of an axillary shoot, each half receiving at its base a contribution both from one of the lateral traces and from the median trace.

In view of the rapidly accumulating evidence[4] suggesting that the

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[1] Cf. *Welwitschia* antherophore; Sykes, 1910.
[2] Arber and Parkin, 1908, p. 499.
[3] Coulter and Chamberlain assume it to be axial; 1910, p. 471.
[4] Arber and Parkin, 1908; Sykes, 1910; Berridge, 1911; Thoday (Sykes), 1911.

Gnetales and Bennettitales are derived from the same stock, the leaf-like character of the disc of male organs in *Ephedra* and *Welwitschia* is of interest as tending to support this relationship. We now know, among the Bennettitales themselves, many examples of discs of male sporophylls much reduced from their original leafy and pinnate form. In *W. rajmahlensis*,[1] for example, the segments of the disc are few in number and no longer flattened, but consist of a branched axis-like structure, bearing each a row of bilocular synangia, seemingly very suggestive of the male organ in *Ephedra*. Wieland[2] also has lately drawn attention to the resemblance between the small male discs of *Wielandiella*, the reduced structure of which has recently been redescribed by Nathorst,[3] and the disc of six fused male sporophylls in *Welwitschia*. Such simple discs as those of *Williamsonia whitbiensis*[4] are perhaps even more suggestive of the staminate disc of *Welwitschia*. In this species there is a disc of fifteen simple leaf-like segments, fused at the base, projecting freely above; the free portion of each segment bears a row of paired bilocular synangia, while below the free portion this row is continued downwards by synangia which have become abortive. So that here reduction in the size of the segments and abortion of the lower synangia has already begun. Granted only the further continuation of reduction and abortion, the separate flattened segments of such a disc may easily be compared with one of the two flattened segments, fused below, free above, of the sporangiophore of such a species as *Ephedra distachya*, in which a row of only two pairs of bilocular synangia is borne by each half of the bipartite disc. *Welwitschia* differs in that the six members of its disc, similarly fused below, are continued upwards, not as flattened segments bearing paired bilocular synangia, but as cylindrical axes each terminating in a single trilocular synangium. In Wieland's staminate disc of El Consuelo,[5] in some respects less reduced than *W. whitbiensis*, the free portions of the disc are not flattened but cylindrical, and bear paired lateral synangia on stalks, and we have already seen in *Ephedra* itself[6] how easily a stage with paired lateral synangia can undergo reduction by fusion and abortion of the synangia, in the process of fusion trilocular synangia being produced. All that is required to derive the male disc of *Welwitschia* from Williamsonian discs such as these is the abortion of the lower pairs of synangia, already begun in *W. whitbiensis*, and the fusion of the topmost pair to form a trilocular synangium, such as is produced by fusion in *Ephedra*.

B. *The Female Strobilus* (cone). The restricted number of ovules in the female strobilus (cone) of *Ephedra* stands in marked contrast to the numerous ovules found in the strobili of the other Gnetales. In the groups of species in which the bracts are succulent the whole strobilus is very

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[1] Wieland, 1911, p. 461.　　　　[2] l. c., p. 438.　　　　[3] Nathorst, 1910.
[4] Nathorst, 1911, especially Fig. 3, p. 13.　　[5] Wieland, 1909, p. 433.　　[6] p. 971.

reduced in size, only three or four pairs of bracts being generally developed. The Alatae, however, the group in which numerous membranous bracts occur below the single fertile pair, is suggestive of an originally greater development than is found at present, which would be more comparable with the strobilus of *Welwitschia* with its numerous membranous bracts and axillary ovules. *E. alata, Torreyana*, &c., which have numerous bracts more or less loosely arranged and ovules which stand fairly free in the centre of the strobilus, are, we think, nearer the primitive form than the more reduced species. It is probable that more than a single whorl of bracts was originally fertile; indeed in one cone of *E. altissima* small masses of abortive tissue suggestive of undeveloped sporangiophores were found in the axils of the bracts next below the fertile ones; perhaps at the base of the strobilus there were male flowers as now in *E. fragilis*, var. *campylopoda*.

The increase in thickness and succulence of the bracts of groups other than the Alatae is accompanied by their decrease in number and by greater pressure on the ovules. These no longer stand free in the centre of the strobilus, but are tightly enclosed by the subtending bracts, and the three well-marked wings, each with its vascular bundle characteristic of the ovules of the Alatae, become modified by pressure. The ovules become laterally flattened, the two lateral wings being retained while the median one is lost; in *E. fragilis* and *E. nebrodensis* a small median wing with its vascular bundle is still present, but in *E. distachya* there is little trace of a median angle to the seed, and the median vascular bundle is hardly ever formed.

In *E. altissima* the very thick and succulent fertile bracts are fused together and tightly enclose in a cup the single ovule which has finally resulted from fusion of the two ovules originally present. The seed is no longer winged, but is round and almost smooth except at the apex where three or four slightly projecting ribs or angles can be distinguished.

C. *The Female Flower.* The ovule in *Ephedra*, like the male flower, is axillary in position, and perhaps as a consequence of this position it receives its bundles in the same manner as a vegetative axillary bud. Whether these facts can be regarded as proof that it is therefore the equivalent of a vegetative axillary bud is not easy to decide.

From a study of *Welwitschia* one of us [1] was inclined to conclude that it was wisest to term the axes of both male and female flowers 'sporangio-phores', but as has been said in the case of the male flower there is little to support this terminology, and the direct evidence as to the foliar nature of the flattened and bifid male sporangiophore in *Ephedra*, which is emphasized by the fern-like vernation of the organ in *E. fragilis* when in bud, is on the

[1] Sykes, 1910.

whole against it, and supports the view that the male flower represents an axillary strobilus.

Attempts have been made by various authors [1] to show that the coverings of the ovules represent fused bracts, and that the female flower is consequently an axillary bud bearing one or two whorls of bracts and terminating in an ovule. Some have also tried to prove that the ovule is not the termination of the axis of this bud, but is borne on one of the surrounding bracts, which represents a carpel.

Strasburger, in 1872, put forward the view that the outer covering in *Ephedra* and *Welwitschia* is the equivalent of a pair of leaves arranged, like the first leaves of an axillary shoot, transversely to the subtending bract. Jaccard also held the same view. According to it (Plan I, Text-fig. XXI) each half of the nut represents a leaf with a single median bundle instead of the pair of bundles formed in the normal vegetative leaf. But this sugges-tion is rendered unlikely by the fact that there is often a third bundle, situated in a position which would correspond to the fused margins of the leaves. Strasburger changed his opinion in 1879 and came to regard both coverings of the ovule as integu-ments.
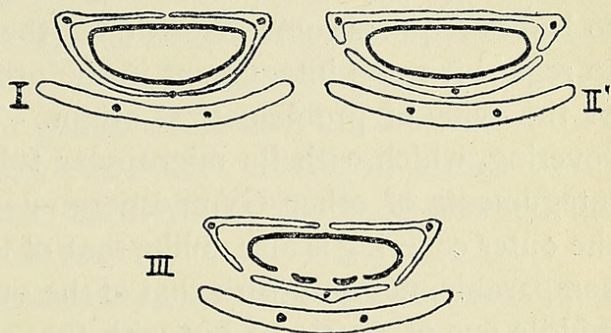
TEXT-FIG. XXI. Plans of the ovule of *E. distachya.* I. According to the view of Strasburger (first pair of leaves). II. According to the view of Van Tieghem (second pair of leaves). III. According to the view of Lignier (whorl of three leaves).

Van Tieghem regarded the outer covering as composed of two leaves, corresponding in posi-tion to the second pair of leaves of an axillary bud, in the same plane as the subtending bract ; the flattened surface of the nut with its two angles representing one leaf, traversed by two vascular bundles, the rounded, sometimes angled, outer portion representing the more or less abortive second leaf, sometimes supplied with a single vascular bundle. He regarded the ovule as borne on the inner leaf of the pair, a suggestion for which there is no evidence.

Lignier attempts to overcome the difficulties involved in demonstrating that the outer covering of the ovule represents a pair of leaves by the suggestion that it represents three leaves, the three vascular bundles belonging each to one of the three leaves ; the female flower would thus become trimerous, the outer of the three leaves being more or less abortive. The inner covering he also regards as representing a whorl of three bracts, forming a tricarpellary ovary, the inner bract being the most developed, the two outer more or less abortive. There is no evidence to support the latter suggestion, and trimery is very infrequent in *Ephedra.* His attempts to

[1] Strasburger, 1872 ; Van Tieghem, 1869 ; Jaccard, 1894 ; Lignier, 1901 ; Arber and Parkin, 1908.

use the four-angled ovules of *Ephedra altissima* to support his view are not successful in the light of the anatomical investigations described in the current paper ; for so far from it being possible that the outer covering in these cases represents only two of the leaves composing the outer covering in one of the ovules of the biovulate cones, it is found that it represents the fused outer coverings of both ovules, and its four vascular bundles represent the six bundles of the two ovules.

All theories which attempt to explain the outer coverings as composed of leaves do not meet the difficulty of the different method of vascular supply. Each of the bundles supplying the integument originates as the centre one of a group of three bundles formed from one of the bundles in the ovular base, the two lateral bundles remaining in the axis (Text-figs. II. 11, and III) ; the integumental bundles of *Welwitschia* are commonly formed in the same manner, but leaf-trace bundles do not arise in this way.

It appears to us that all attempts to compare the outer covering to leaves requires some distortion of the evidence, and that it is more correct to regard it as an integument in the ordinary sense of the word—a covering of the ovule of problematical origin. This is still more true of the inner covering, which with its micropylar tube is obviously comparable with the integuments of other Gymnospermous ovules. The complex structure of the outer covering is also unlike that of the ordinary leaves and is much more comparable, not only with that of the outer covering in *Welwitschia* and the middle one of *Gnetum*,[1] but with that of the outer covering of other ovules, more especially those of the Bennettitales. The resemblance [2] between the outer covering of *Gnetum* and the integument of *Bennettites* to which attention has already been drawn is still further emphasized in *Ephedra* ; for here the three or four fibrous strands representing the star-like rays of the fibrous layer in *Gnetum* and *Bennettites* each correspond to an external angling of the seed, such as is present in *Bennettites*.[3] The remarkably detailed resemblance in the structure of their outer integuments between the three members of the Gnetalean alliance, their leaves being so different, is alone a striking fact, and suggests that the coverings of the ovule are independent structures, less plastic than the leaves.

The ovule with its two integuments thus remains an isolated structure in the axil of the bract. There is no evidence to suggest that the ovule was ever borne on the subtending bract, and there is no direct evidence, except the analogy between its vascular supply and that of a vegetative bud, that

[1] It is clear from the structure that it is the middle covering of *Gnetum* which is homologous with the outer covering of the other two forms ; Thoday (Sykes), 1911.

[2] Berridge, 1911 ; Thoday (Sykes), 1911.

[3] Wieland's recent figures of the ovule in *Cycadeoidea turrita* (1911, p. 458, Fig. 15 *c*, and 1912, p. 90) still further strengthen the comparisons which have been made between the ovules of *Gnetum* and *Cycadeoidea*, though his comparison with *Gnetum*, 1911, p. 458, Fig. 15, *a* and *b*, is evidently based on some misapprehension.

the little axis on which it is borne represents an axillary bud, for it bears no leaves. But the male flower has already been compared with a little strobilus, and it seems probable in view of the evidence of reduction in the family that the female flower also represents a very reduced strobilus. If like the male flower it is to be compared with the strobilus of the Bennettitales, then the single ovule must represent the whole ovulate cone in that family ; the comparisons which have been made by other authors between the male flower of *Welwitschia* and the Bennettitean strobilus necessitate this presumption, and direct evidence of such a fusion of ovules and their coverings has here been recorded in *E. altissima*, where the single terminal ovule represents the two fused axillary ovules of other species.

It seems that while there is strong evidence that the male sporangia are foliar, we are driven to the view that the ovule terminates an axillary shoot. In the Bennettitales also the male sporangia are undoubtedly foliar, but we are still not certain as to the seed, though the view that the seed pedicel is the equivalent of an interseminal scale and therefore foliar appears to be gaining ground. If the single ovule in *Ephedra* and *Welwitschia* represent the mass of foliar ovules and scales in *Bennettites*, being derived by reduction and fusion from a strobiloid condition probably more simple than that actually found in that family, this difference between male and female sporangia would be accounted for.

The single ovule now differentiated direct from the plastic apex of the axillary bud would thus be the equivalent of more than one ovule, each originally borne on a foliar organ, but now fused together at the apex of an axis, much as the apical pair of synangia in *E. altissima* and perhaps the single trilocular synangium of *Welwitschia* are the equivalent of several pairs of synangia originally borne on foliar appendages, but now fused together at the top of what falsely appears to be a cylindrical axis since it shows so little trace of its primitively bifid and leaf-like condition. It may be that there is as yet insufficient evidence for this analogy between micro- and megasporangia, but at any rate the great amount of reduction which the microsporophyll has undergone, even among existing forms, as evidenced by its variation from a leaf-like organ bearing eight synangia to a small cylindrical axis carrying only two, renders it quite probable that in the female flower also we have the final stage of a long series of reductions, the last trace of which is still to be seen to-day in the fusion of ovules in *E. altissima*.

IV. Comparison of the Inflorescences of the Three Members of the Gnetales.

Of the three genera of the Gnetales it appears from their anatomy that *Ephedra* and *Welwitschia* are most closely related to one another. The dichasial branching of the male inflorescences of all species of *Ephedra*

and the more or less regular dichasial branching of the female inflorescences of *E. altissima* is a point of similarity with both the male and female inflorescences of *Welwitschia*. In *Welwitschia* the individual strobilus is elongated and produces numerous fertile bracts and flowers, fifty or thereabouts in the female and still more in the male [1] with a few sterile bracts at the base.[2] In *Ephedra* the male strobilus bears only ten to fifteen whorls of fertile bracts, and the female strobilus is of still more limited growth. It has already been remarked that the strobili of the Alatae with their numerous membranous bracts are suggestive of an originally greater development than is found at present, and even the bracts themselves in these species bear a close resemblance to those of *Welwitschia*.

In *Gnetum* also the male inflorescence is dichasially branched and both male and female inflorescences would seem from their general arrangement to be comparable with those of *Ephedra* and *Welwitschia*. But when we come to examine the individual strobili we find that the cupule at each node is the equivalent of the pair of bracts at the node in the other genera, subtending not two but a cushion bearing six or more ovules in the female inflorescence and numerous antherophores and abortive ovules in the male. There are many more points widening the gap between *Gnetum* and the other two genera : the ovule has an extra covering and both this and the outer integument are radially symmetrical and supplied by numerous vascular bundles ; the micropylar tube has a complex mechanism for closing it ; the membranous appendages of the male flower have a vascular supply. The complicated method of bundle supply [3] of the ovule and antherophores in *Gnetum* is also peculiarly characteristic, while the method of supplying these organs in the other two genera is very simple and quite comparable, there being, however, no median axillary bundle in *Welwitschia*.

In comparing the individual flowers of the three genera, it is again found that *Ephedra* and *Welwitschia* show most resemblance to one another, though here the signs of relationship are sufficiently clear to justify the placing of all three forms in the Gnetales.

In *Welwitschia* the male flower consists of an abortive ovule, surrounded by a disc of six male sporangiophores fused at their base, and four membranous appendages. In *Ephedra* the male flower bears two membranous appendages, and evidence has been brought forward to show that the antherophore probably consists of a disc of two fused sporophylls surrounding an abortive apex.[4] With respect to the form of its microsporophyll (as also in its gametophyte) *Ephedra* appears the more primitive of the two ; each

[1] Pearson, 1906.
[2] The lowest pair of sterile bracts is distinguished from the others by their acute apices; the same characteristic also occurs in the lowest pair of sterile bracts in the male strobilus of *Ephedra* (p. 953).
[3] Thoday (Sykes), 1911, and Pearson, 1912.
[4] Thibout, 1896, Part III ; Arber and Parkin, Part I, p. 502.

half of the antherophore with its paired bilocular synangia resembling far more closely one element of the disc of a *Williamsonia* than the microsporophyll of *Welwitschia* with its trilocular stalked synangium.

The ovules of *Ephedra* and *Welwitschia* being in similar compressed positions differ in some respects from the freely projecting ovule of *Gnetum*, but in other ways they show remarkable similarity. They all have an inner thin membranous covering, fused with the nucellus below, free above, and prolonged into a narrow tube, lined in *Ephedra*, *Welwitschia*, and some species of *Gnetum* by a thick cuticle. The inner ring of vascular bundles, which in *Gnetum* is prolonged into the free part of this inner integument, in *Welwitschia* terminates at the level at which it becomes free from the nucellus, and in *Ephedra* at a still lower level.

They all also have a thick outer covering. In *Ephedra* it is angled, and in *Welwitschia* it has two well developed wings; in *Gnetum* it is smooth. The stony layer of this outer covering is always strongly developed at points corresponding to the external angles, and even in the smooth seed of *Gnetum* it is angled.

Ephedra and *Gnetum* both have pollen-chambers, one of the signs of their greater primitiveness than *Welwitschia*, but even in *Welwitschia* there is some disorganization at the apex of the nucellus.[1]

The above evidence as to the reduced nature of *Ephedra* and its closer relationship to *Welwitschia* cannot be taken as indicating that it is reduced from *Welwitschia*. Its gymnospermous gametophyte and its well-developed pollen-chamber prohibit such a conclusion. But *Ephedra* and *Welwitschia* together appear to have retained in common numerous points which separate them off from *Gnetum* with its many singular characteristics.[2] Both genera show many signs of reduction, and *Welwitschia* has also, while retaining a less reduced strobilus than *Ephedra* and more primitive male flowers, undergone many remarkable vegetative modifications and a special elaboration of its ovules in the great growth of the nucellar apex correlated with its peculiar methods of fertilization.

V. SUMMARY.

1. The vascular system of the inflorescences and flowers of various species of *Ephedra* is described. It is found that the method of supply of the axillary flower buds is similar in essentials to that of the vegetative buds in the axils of the ordinary leaves. Each vegetative bud and each flower receives three bundles: a median abaxial bundle (afterwards branching into two in the vegetative bud), intimately connected with the bundles of the subtending leaf, and two adaxial bundles which originate partly or entirely from the adjoining bundles of the main stem.

[1] Pearson, 1906, Fig. 28, Pl. XIX, pp. 289-90.
[2] See also Pearson, 1912, p. 614; the male gametophyte, on the contrary, is most closely comparable in *Gnetum* and *Welwitschia*; l.c. p. 618.

2. The three bundles entering the axillary ovule branch each into three. In some species (*E. Torreyana, E. alata, E. fragilis*) the median bundle of each trio passes out into the outer covering ; in other species (*E. distachya*) the abaxial trio does not provide any contribution to the outer covering, which thus receives only two bundles. A special case is afforded by the uniovulate species, *E. altissima* and *E. trifurca*, in which the two fertile bracts enclose only a single ovule. This receives either four or three bundles, which clearly represent the fused vascular systems of the two ovules of the biovulate species.

3. That the single terminal ovule of these species is actually the product of the fusion of the two axillary ovules of the biovulate species is clearly demonstrated by a long series of intermediate forms in *E. altissima* ; among which occur biovulate cones, each ovule having two coverings, biovulate cones with a common outer covering, and uniovulate cones in which an abortive nucellus is more or less fused at the apex with a fertile one.

4. The structure of the outer covering and its method of vascular supply do not support the view that it represents the first whorl of leaves of an axillary shoot. It is here regarded as an integument. It is more or less angled in the various species and is composed, roughly, of an outer brown-celled layer and an inner fibrous layer. The vascular bundles traverse the angles and are accompanied towards the apex of the ovule by strands of fibres ; they terminate in transfusion tissue. The structure of the outer integument is thus very similar to that of *Gnetum* (middle covering), except that there is here no palisade layer and that the angling of the inner fibrous layer corresponds to the outer angling of the seed which does not occur in *Gnetum*, but is present in *Welwitschia*. The comparison formerly drawn between *Gnetum* and *Bennettites* is thus further emphasized by the study of *Ephedra*.

5. The inner covering has no vascular supply, the ring of bundles entering the ovule terminating near its base. It is free from the nucellus for the upper third of the ovule and is prolonged upwards as a micropylar tube with a very strongly cuticularized lining. The opening of the micropylar tube is closed in the fertilized ovule by a hardened plug of mucilage, and the chink between the two integuments is closed by papillae which grow out from the epidermis of the outer covering and firmly clasp the inner. The fertilized ovule is thus as efficiently protected as in *Gnetum* with its complex mechanism. Both arrangements are, physiologically, abortive attempts at Angiospermy.

6. The different species of *Ephedra* exhibit much variation in the number of male sporangia. In *E. distachya, E. fragilis, E. nebrodensis*, &c., the sporangiophore is clearly bifid, and each half bears four bilocular synangia. In some species such as *E. aspera, E. Torreyana*, &c., there is no clear separation into two halves, and the upper pair of synangia are fused

together. Other species exhibit further stages in this reduction process, more and more synangia fusing together, often forming in the process trilocular or even quadrilocular synangia, until *E. altissima* is arrived at with only two bilocular synangia. The formation of trilocular synangia as a result of fusion affords a link with *Welwitschia*, where terminal trilocular synangia are normally produced. In most species the synangia are nearly sessile, but in *E. Torreyana* and a few others they are borne on a stalk of some length, reminiscent again of the stalk freely projecting above the fused portion of the staminal whorl in *Welwitschia*.

7. From the evidence available it is concluded that the structures in the axils of the fertile bracts in the male cone are to be regarded as flowers, or little strobili, each consisting of one axis bearing four leaves. The first pair of leaves, which, except in *E. fragilis*, receive no vascular supply, are orientated like the second pair borne by a vegetative axillary bud, and the two flattened halves of the fertile organ thus appear to represent the third pair of leaves fused with one another back to back. In *E. fragilis* they exhibit circinnate vernation in the bud.

8. This bipartite sporangiophore with its paired bilocular synangia is compared with the six-partite disc of sporophylls in *Welwitschia* and with the multipartite disc in the Bennettitales. It is thought that we can trace the steps of a reduction series from the disc of *Cycadeoidea* with its bipinnate sporophylls, through such stages as *Williamsonia whitbiensis*, in which the segments are small and simple, and each bears a row of paired bilocular synangia, the lower of which are abortive ; and the disc of El Consuelo in which the freely projecting portions of the disc are no longer flattened but bear stalked synangia; to *Ephedra,* where the disc is reduced to two segments, each bearing two pairs of bilocular synangia, and *Welwitschia*, where it is composed of six segments, each with a stalked terminal trilocular synangium. From the reduction series in *Ephedra* itself it is seen how from the fusion of bilocular sporangia a single trilocular stalked synangia can be produced.

9. Whether the female flower also in *Ephedra* and *Welwitschia* is, like the male, morphologically a little strobilus and the equivalent of an axillary bud, it is not easy to decide, since it consists of an isolated ovule ; the more complicated relations occurring in *Gnetum* make the matter still more difficult. The male sporangiophores having been related with some show of probability to the disc of sporophylls in the Bennettitales, it seems justifiable, considering the many signs of reduction in the Gnetales, to suggest that the single ovule now developed at the apex of the axillary structure in the male and female flowers of *Welwitschia* and in the female flower of *Ephedra* represents the many ovules and interseminal scales of such a flower as *Cycadeoidea* fused together. This is rendered the more possible by the discovery that fusion of ovules actually occurs in *Ephedra,* resulting in the production of a uniovulate from a biovulate cone.

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DESCRIPTION OF PLATE LXXXV.

Illustrating the paper by Mrs. Thoday and Miss Berridge on the Inflorescences and Flowers of *Ephedra*.

Fig. 1. Young male inflorescence of *E. distachya*, consisting of peduncle bearing three strobili. *St.* = sterile bracts; B = fertile bracts, in the axils of which are the male flowers. The young synangia, enclosed in the two leaf-like appendages (P) are seen projecting a little way out between the bracts. × 16.

Fig. 2. Basal portion of female inflorescence of *E. altissima*, showing loose cluster of female strobili borne on a branched axis which hangs downwards from the climbing stem. × 2.

Fig. 3 *a*. Single female strobilus of *E. distachya*, detached from its position in the axil of a leaf on the ordinary vegetative stem. × 2.

Fig. 3 *b*. Single female strobilus of *E. fragilis* in situ. The micropylar tubes of the two ovules can be seen projecting from the enclosing bracts. × 16.

Fig. 3 *c*. Single female strobilus of *E. alata*, showing the numerous membranous bracts with prominent midribs, and two projecting ovules. × 2.

Fig. 3 *d*. Single ovule of *E. alata*, showing one of the three wings. × 2.

Fig. 4. Male sporangiophore of *E. distachya*, front view, bearing eight synangia. × 16.

Fig. 5 *a*. Male sporangiophore of *E. nebrodensis*, front view. × 16.

Fig. 5 *b*. Male sporangiophore of *E. nebrodensis*, back view. × 16.

Fig. 5 *c*. Young male sporangiophore of *E. nebrodensis*, seen in bud, enclosed by two leaf-like appendages. × 16.

Fig. 6 *a*. Male sporangiophore of *E. altissima*, young, bearing two synangia. × 16.

Fig. 6 *b*. Ditto, older. The long transparent stalk is seen to be traversed by two vascular bundles (*vb*). × 16.

Fig. 7. Transverse section through portion of bract of outer cupule. *Tr* = transfusion tissue. × 78.

Fig. 8. Longitudinal section through stoma of bract, showing cuticularized ridges. × 116.

Fig. 9. Apex of cone of *E. fragilis*, showing the two ovules with their integuments. *c* = cup of suberized cells. × 25.
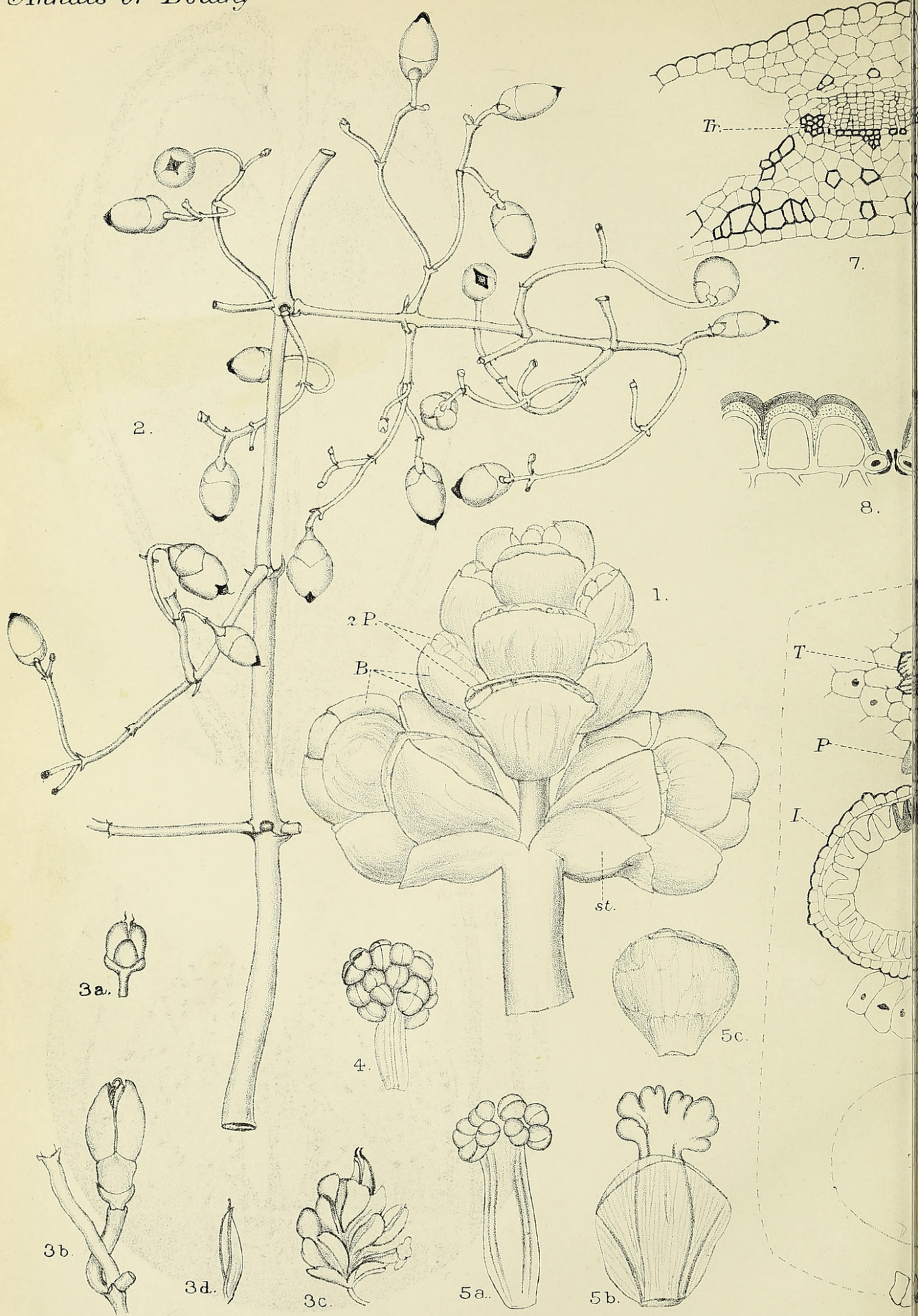
Fig. 10. Ovule of *E. altissima* with double nucellus, only the left-hand half of which is fertile ; the two inner integuments, free at the base, are fused at the apex into one. *d. n.* = double nucellus, the left-hand half of which contains a prothallus (*pro.*) ; *i.int.* = inner integument.

Fig. 11 *a*. Transverse section of apex of young unfertilized ovule of *E. distachya*. *b* = brown tissue ; I = still open micropylar tube with cuticularized lining ; *p* = papillae ; *Tr* = transfusion tissue. × 116.
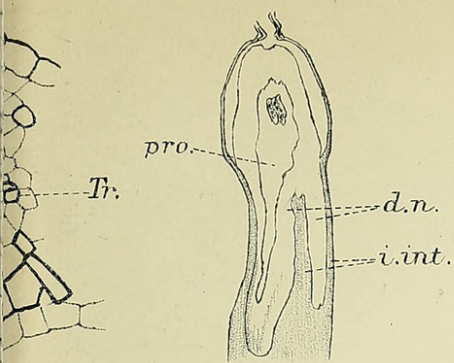
Fig. 11 *b*. External view of nut of *E. distachya*, showing small angles. × 16.

Fig. 12. Longitudinal section of apex of nucellus of *E. fragilis*, showing deep pollen-chamber. × 90.

2 P.

B.

1.

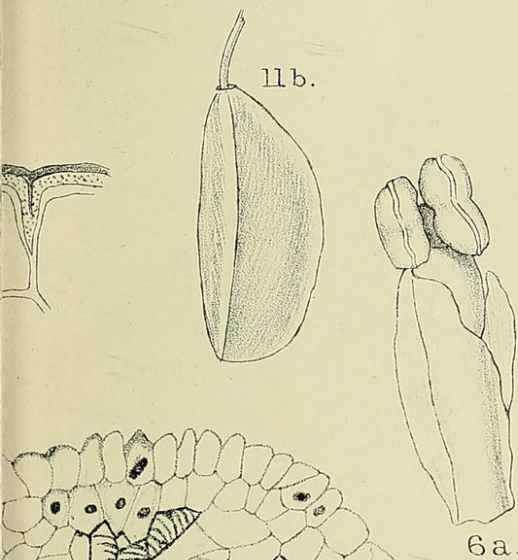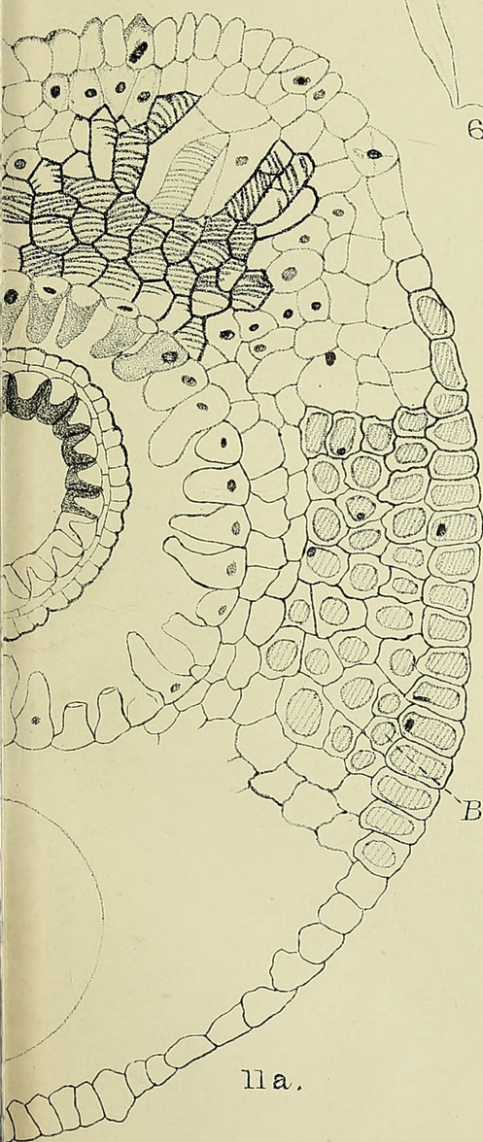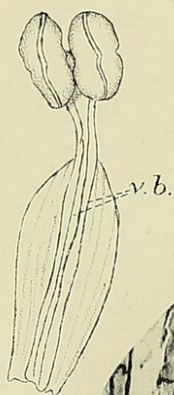2.

st.
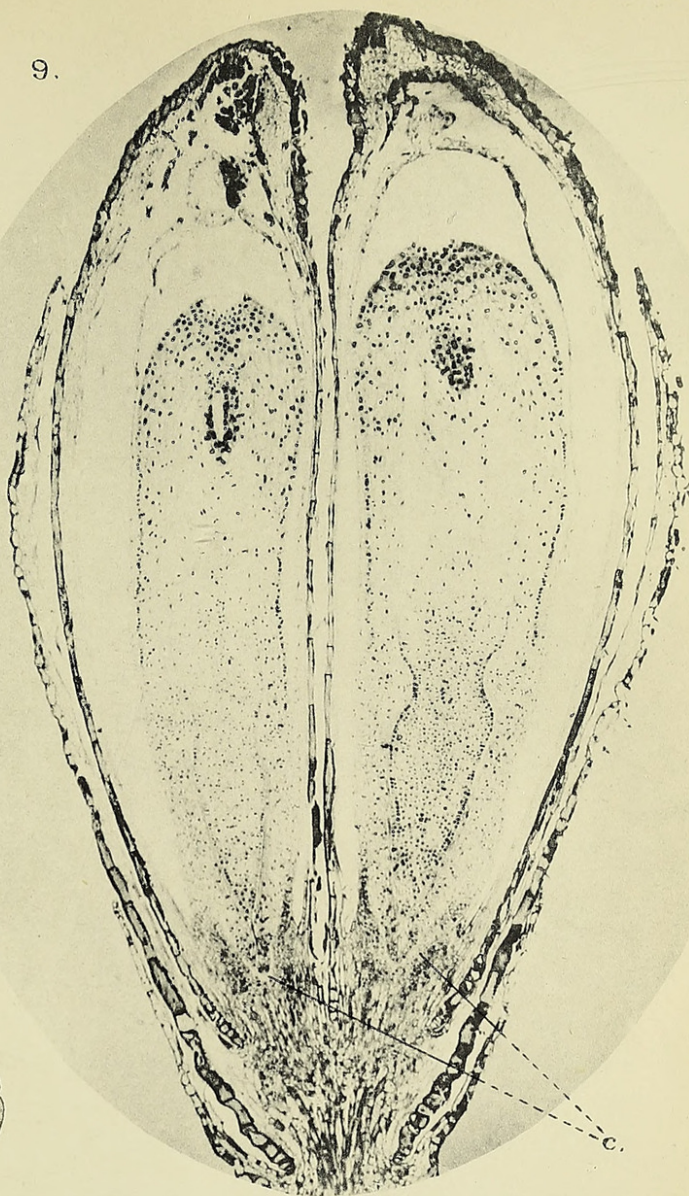
3a.

3b.

3d.

3c.

4.

5a.

5b.

5c.

Tr.

7.

8.

T.

P.

I.
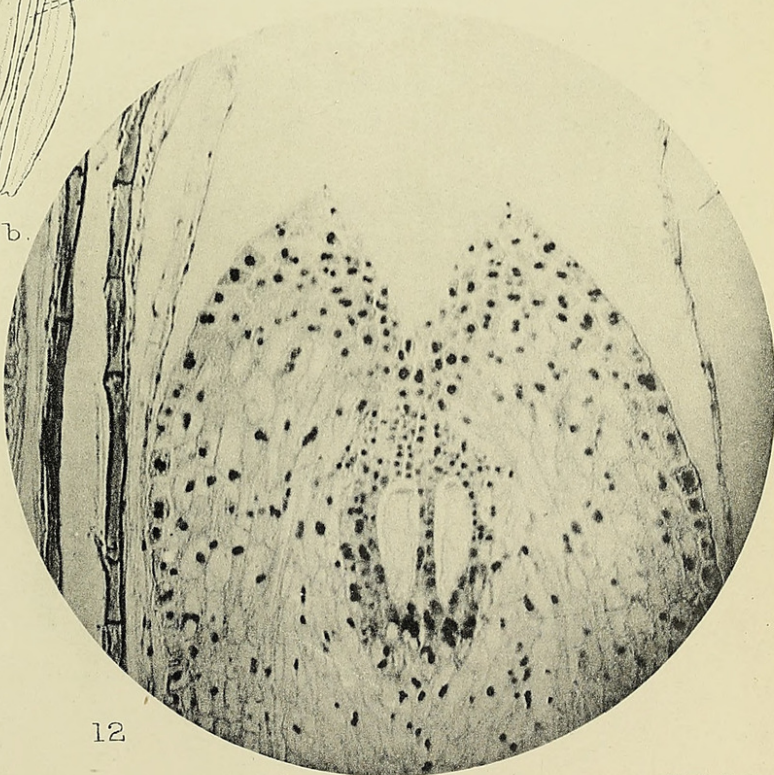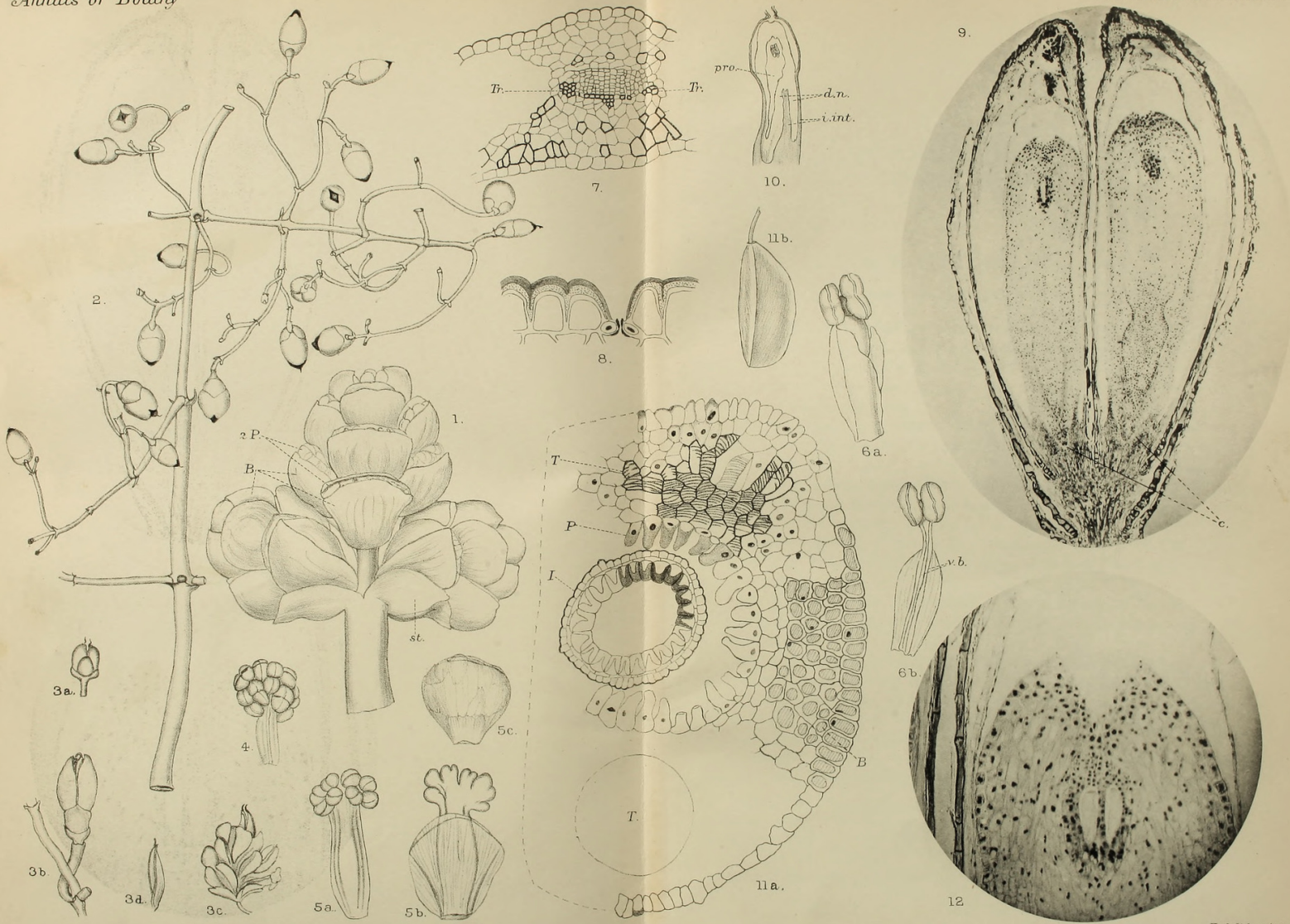
THODAY & BERRIDGE. —— EPHEDRA.

9.

10.

Tr.

pro.

d.n.

i.int.

11b.

6a.

B

11a.

v.b.

6b.

12

c.

Huth, lith et imp.