The Female Inflorescence and Ovules of *Gnetum africanum*,¹ with Notes on *Gnetum scandens*.

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With Plates LXXXVI and LXXXVII and sixteen Figures in the Text.

FOR the material on which this investigation is based I am indebted to Professor H. H. Pearson, of the South African College, Cape Town, who collected and preserved it during the recent Percy Sladen Memorial Expedition in South-West Africa.

The material of *G. africanum* includes many stages in the development of the ovules (most of the younger ovules are, however, unfortunately aborted); also large fertilized ovules containing well-developed endosperm, but no embryos. As other authors have given comparatively few details of their investigations of the ovules of various species of *Gnetum*, it is not possible to say how far this species, here for the first time described, differs from those already known. In the morphology of the inflorescences, and in the general structure of the ovule and its integuments, it agrees with the species described by Strasburger² and Lotsy.³ Strasburger's material appears to have included only young stages of the ovule, and he was not able to give an account of the mature seed.

Some material of *G. scandens* (comprising small portions of the female inflorescences with young, unfertilized ovules all nearly at the same stage, one mature fertilized seed on its stalk and male inflorescences) has been examined for comparison, and Miss Berridge's recent description of the ovule of *G. Gnemon* appears opportunely. It is hoped that the ovules and inflorescences of other species may be investigated later. From Karsten's

¹ A short preliminary account of the ovules of this species was given at the Sheffield Meeting of the British Association, 1910. The Morphology of the Ovule of *Gnetum africanum*. Report, p. 783.

² Strasburger, 1872, 1879.

³ Lotsy, 1899.

description of the macroscopic features of the ovules, it appears likely that the detailed structure of the integuments in the various species¹ would differ widely, and such differences may well prove of value in comparison with other seeds both fossil and recent.

The present paper includes an account of the vascular system in the female inflorescences of *G. africanum* and *G. scandens*, and of the male inflorescence of *G. scandens*. Several interesting points serve to recall the structure in the allied genus *Welwitschia* and in the Cycads.

The structure of the ovules in *G. africanum* has many points of interest. A short description of these was given at the Sheffield meeting of the British Association, where attention was also drawn to the remarkable detailed resemblance between the ovules of this species and those of *Bennettites*.

I. RECAPITULATION OF THE GENERAL MORPHOLOGY OF INFLORESCENCE AND OVULE IN GNETUM.

The inflorescence in most species² is a spike, bearing at its base two bracts, in the axils of which other inflorescences, buds or flowers may occur. At each node of the inflorescence axis is a cupule derived from two fused bracts,³ in the axil of which the flowers are borne on a ring-shaped swelling of the inflorescence axis. The swelling or cushion arises from a ring of meristematic tissue in the axil of the young cupule, and the flowers are developed by further localized growth of portions of this tissue.⁴ Between and below the flowers the cushion is covered with numerous multicellular hairs (Fig. 3 A, Pl. LXXXVI).

In the female inflorescence, the presence of five to eight flowers in a ring is general throughout the genus. Five to seven are common numbers in *G. africanum* and six appears to be usual in *G. scandens*.

In the early stages the cupules with their axillary swellings are crowded together, but later they are usually more or less separated from one another by the growth of the internodes. In *G. scandens*, the nodes become very widely separated (Fig. 1, Pl. LXXXVI); in *G. africanum*, on the other hand (Fig. 2, Pl. LXXXVI), the internode is very short and the nodal swelling extends over a relatively very large area.

The bases of the young flowers are sunk deeply into the swollen axis, so that the portions of the cushion intervening between them appear in transverse section as peltate projections (Pl. LXXXVI, Fig. 3 B, *G. africanum*).

¹ Karsten, 1893 (1) and (2). One difference remarked is that seeds may be angular and pointed at the apex, or smooth and rounded at the apex. The species described here both belong to the latter class.

² See Strasburger, 1872, 1879; Karsten, 1893; Lotsy, 1899, &c. In some species, such as *G. scandens*, *G. Ula*, and *G. Rumphianum*, the stalks of the mature seeds are so much elongated that the inflorescence becomes at length a raceme.

³ Karsten: Cohn's Beiträge, 1893, p. 340, &c.

⁴ Lotsy, 1897, p. 84.

In *Gnetum scandens* the fertilized ovule is later carried out on a stout stalk (Fig. 1 A, Pl. LXXXVI). Each female flower consists of an ovule enclosed in three coverings, the outer of which is, according to the species, green, orange or red,¹ and more or less succulent, resembling in texture the bracts and cupule, while the two inner are more specialized and are referred to in this paper as the outer and inner integument.

The female inflorescence is said² commonly to terminate in a flower; this has been once observed to be apparently the case in *G. africanum*.

In the male inflorescence the cushion bears a ring of stamens, and above these a number of abortive ovules each consisting of a nucellus with two coverings.

II. ANATOMY OF INFLORESCENCE AXIS AND CUPULES IN *G. AFRICANUM* AND *G. SCANDENS*.

(a) The *general structure* in the node and in the internode of the inflorescence axis is strikingly different.³ In the internode of a young inflorescence the structure resembles in all particulars, except a greatly increased diameter, that of the naked peduncle on which the cone is borne.

The *peduncle and the internodes of the young inflorescence axis* are made up of thin-walled parenchymatous tissue, in which a few branched fibres with lignified walls are scattered at intervals,⁴ and are traversed by a ring of simple collateral vascular bundles, each of which grows in thickness by means of a cambium. In the older inflorescences there are a few concentric groups of bundles outside the main ring; these may be continuous throughout the internode.⁵

The simple main ring of bundles characteristic of the internode runs up into the node; the number of bundles in the ring increases to some extent with the age of the inflorescence, but there is no regular interfascicular cambium. In *G. africanum* there are generally 8–12 bundles in the ring, and there does not appear to be any further increase in number in the oldest inflorescences in my material; in *G. scandens* as many as 16–20 may occur in quite young inflorescences, and new bundles are still being inserted between the old ones, according as the appendicular organs require a larger vascular supply.

¹ Lotsy, 1899, p. 53; Griffith, 1859, p. 303, &c.; Karsten, 1893 (1).

² Strasburger, 1879, p. 118.

³ This account applies mainly to the female inflorescence axis of *G. africanum*; the material of *G. scandens* showed much the same features, but, owing to the inflorescence being younger, they were less marked.

⁴ These fibres resemble the 'spicular cells' in *Welwitschia*, but have no crystals embedded in their walls; Sykes, 1910 (1), p. 181.

⁵ Cf. Worsdell, 1901, p. 772. In *Welwitschia* such concentric strands are numerous; see *ibid.*, and also Sykes, 1910 (1), p. 194, &c., and (2) p. 341.

Each bundle is made up chiefly of secondary elements; the crushed primary phloem and the torn spiral protoxylem are, however, clearly recognizable.¹ The secondary xylem throughout the inflorescences is mainly composed of narrow reticulately thickened elements.

The structure at the node is much more complicated. Besides the main ring of bundles there are two outer rings concentric with it, the middle one being orientated inversely to the other two. The two outer rings are concerned with the supply of cupules and flowers; they are connected with the main series, and in the older inflorescences are also continuous with the small additional concentric bundles found in the internodes. Below the bracts at the base of the spike and below each bract cupule, the pith tends to become lignified, the lignification spreading centripetally from the xylem of the main bundles.² In the older inflorescences of *G. africanum*³ this tendency to lignification of the pith extends throughout the internode; while at the nodes, probably owing to the tissue tensions brought about by the rapid growth of the cushion, the pith is torn and hollow (Text-figs. 2 and 5). The tension under which the node has increased in size has also resulted in the development of large spaces in the pericyclic region of each bundle; these spaces are crossed at intervals by trabeculae (Fig. 4, Pl. LXXXVI). Throughout the node the thick-walled fibres increase greatly in number, both in the pith and more especially in the outer layers of the cortex, where they form a more or less continuous strengthening band.

Text-fig. 3 is a longitudinal section through a node, and shows the hollow pith with its numerous fibres, and the ovular bases sunk in the swollen cushion in the axil of the bract cupule. Fig. 3 A, Pl. LXXXVI, is taken from a section through the base of the node and shows the cushion, covered with hairs, surrounded by the free apex of the cupule. Fig. 3 B, Pl. LXXXVI, through the middle of the node, shows the sunken ovule and the interovular portions of the cushion which are peltate in transverse sections.

Bracts and Cupule. Both the basal pair of bracts and the cupule are specialized for protective functions. The epidermis is thick-walled, and corky excrescences appear in places. Stomata are very rare, occurring mainly on the decurrent bases of the cupules and bracts, but being entirely absent from the free tip. Numerous branched fibres with lignified walls occur throughout the tissues. The free portion of the cupule has a mucilaginous subepidermal layer on its inner surface (M, Fig. 5, Pl. LXXXVI).

The vascular bundles supplying the cupules pass out horizontally from the main bundles and then run downwards, afterwards turning sharply upwards into the free tip. They are thus often cut twice in a transverse

¹ Contrast the absence of protoxylem in the cone axis of *Welwitschia*; Sykes, 1910 (2), p. 339.

² See Worsdell, 1901, p. 772.

³ The material of *G. scandens* was too young for comparison with this stage.

section. They branch freely, they are small and numerous, and associated with them are many transfusion tracheides which occur chiefly laterally on the phloem side of the bundle (*Tr.*, Fig. 5, Pl. LXXXVI).¹

(b) *The Course of the Bundles.* The bundles run straight up the peduncle and internodes of the inflorescence without anastomosing. As they reach the base of the inflorescence they branch, and from two opposite points in the stele two single, usually concentric bundles arise. Each of these first bundles forms the median bundle of a bract supply and is speedily supplemented by numerous other bundles, arising on each side of it from others of the bundles of the main axis. Many of the bundles, including the single median one, have a double origin from two of the bundles of the main axis, as shown in Text-fig. 1.²

TEXT-FIG. 1, A, B, C, shows the origin of one of the concentric bract bundles from two bundles of the main axis.

I had only two whole spikes among my material and in both cases there were no buds in the axils of the two basal bracts, so the vascular supply of axillary organs other than the flowers could not be investigated.

The bundles supplying the bract cupules arise in a manner very similar to those supplying the bracts; the median bundle is, however, not often clearly distinguishable, the bundles are more numerous and the general arrangement more irregular. The chief interest in the vascular system of the inflorescence of *Gnetum* lies in the origin of the two outer nodal rings of bundles and the method of formation of the bundle supply of the flowers. Worsdell³ compares 'these transitory extra-fascicular rings of bundles with the more fixed extra-fascicular rings of bundles in the vegetative axes of the Cycads'; the former are almost all used up at each node by the bract and flower supplies, the latter are concerned with the leaf supplies and are therefore not persistent above the youngest leaf-trace.

The course of the bundles through the node of the older inflorescences of *Gnetum africanum* is exceedingly complex, so the younger inflorescences of *G. scandens* will first be described. In *G. scandens* the simple ring of fibrovascular bundles has a long undisturbed course through the elongated internode, and the small size of the cushion at the node brings the insertion of the ovules closer in the axil of the cupule (see Fig. 1, Pl. LXXXVI).

¹ As in *Welwitschia*; Sykes, 1910 (1), p. 186. Cf. Worsdell, 1901, p. 767, on *Ephedra distachya*, where he found a few tracheides of centripetal xylem in the bract of the female inflorescence.

² A similar double origin of bundles is common throughout the inflorescence. Cf. *Welwitschia*, Sykes, 1910 (1), pp. 193, 204, &c.

³ Worsdell, 1901, pp. 767-8.

In the simplest case¹ examined (Text-fig. 2, right-hand side), a ring of bract bundles (B) arose from the main axial bundles (M) and passed out into the cupule, first running upwards and then turning sharply downwards. During their outward course two series of bundles were given off, the outer of which (OB) was orientated in the same way as the main bundles and supplied the lower half of the ovular bases, and the inner of which was inversely orientated (BIV), running up higher into the cortex of the main axis and then turning outwards to supply the upper half of the ovular base. The inverse series arises from the bract bundles at some distance from the main bundles and is never closely attached to the latter as it is in *G. africanum* (Text-fig. 4).

In a rather older node of *G. scandens*, the inverse series (Text-fig. 2, BIV, left-hand side) receives further contributions (OM and MIV) from the bundles of the main axis, some of which become more or less inversely concentric.²

TEXT-FIG. 2. Course of bundles in female inflorescence of *G. scandens*. The right-hand side represents a somewhat younger ovule than the left. M = bundles of main axis; B = supply of bract cupule; OB = outer series of bundles supplying ovule and arising from B; BIV = inner series of inversely orientated bundles arising from B and supplying ovule; MIV and OM = bundles arising from main bundles and augmenting the inverse series supplying ovule. (Black lines = phloem; stroked lines = xylem.)

It is probable that in older inflorescences than are found among my material a more complicated structure approaching that seen in *G. africanum* would be developed.

In the male inflorescence of *G. scandens* all the cases examined had a simple arrangement similar in essentials to that shown on the right-hand side of Text-fig. 1. Numerous bundles supply the bract cupules as in the female inflorescence, and from them arise an outer series of bundles, mostly concentric, which give off branches to the stamens and then supply some of the abortive ovules;³ and also, nearer the main bundles, an inner inversely orientated series which also supplies both stamens and ovules. As the bundles divide to form staminal and ovular traces, an anastomosing ring is formed such as is shown in the photograph in Fig. 17, Pl. LXXXVII. The stamens each receive a simple concentric bundle,⁴ the abortive ovules a little ring of bundles.

¹ Strasburger, 1879, pp. 116-18, Figs. 15-23, Taf. XXI.

² See Sykes, on *Welwitschia*, 1910 (1), p. 192.

³ As described by Strasburger, 1879, p. 106, and Taf. XXV, Figs. 65 and 67.

⁴ Cf. *Welwitschia* stamens and *Bennettites* ovules, Worsdell, 1901, p. 763, and Sykes, 1901 (1), p. 187.

In the younger examples of female inflorescences of *G. africanum*, the state of affairs is similar to that in *G. scandens*. The great extent of the node in this species (Fig. 2, Pl. LXXXVI) is, however correlated with a disturbance of the arrangement of the vascular system over a greater distance, and indeed the course of the undisturbed ring characteristic of the internode is in this species relatively very short.

In Text-fig. 3 is seen a diagram of the course of the bundles

TEXT-FIG. 3. Letters as before; also F = branched fibres; H = hollow stem opposite ovule; BC = bract cupule; C = nodal cushion; TR = transfusion tissue; LOM = small bundles arising from main series and augmenting series OB; OM = bundle arising from main series and augmenting series OIV; OIV = inverse series turning down to supply ovule; P, O.IN, I.IN = bundles supplying perianth, inner integument and outer integument respectively.

through the node of an old female inflorescence of *G. africanum*. As before, the bract bundles (B) are seen to originate from the main bundles, and as they pass out they give rise first to a series of inversely orientated bundles (BIV) and then to some normally orientated ones (OB), both of which supply the ovule. Both series are augmented from the main series. In the oldest inflorescence I examined, only a few small bundles (LOM) were added to the outer series, which still is chiefly composed of bundles derived from the bract bundles. But a large number of the inversely orientated bundles forming the inner series come directly (MIV) from the main bundles

at intervals throughout their long course up the node and remain closely associated with them till at the top of the node they pass out to the ovules. There they are joined by a number of additional bundles from the main axis (OM), at about the level at which they turn downwards (OIV), making a sharp angle with their former course, and run into the upper edge of the ovule. In *G. scandens* the inverse series does not make this sharp bend, but

TEXT-FIG. 4. A-E. Series of transverse sections through a node and internode of an inflorescence of *G. africanum*. (Letters as before; also X = concentric bundles in internode; Z = bundles with double origin¹; VBT = bract bundles with transfusion tissue; OV = ovule.) A is from the base of an internode; some of the bundles are already dividing in preparation for the next node. B = base of bract cupule, cut obliquely, with axillary cushion covered with hairs. C = lower part of cushion, three series of bundles, some of the outer series are concentric. D is through the median plane of the ovules, showing some of the ovular supply cut in longitudinal section, but only two series in main axis. E = near top of ovule, showing some of the bundles supplying the upper part of ovule, cut both in their downward course near the edge of the section, and in their upward course attached to the main bundle as part of the inverse series. A concentric bundle is being re-formed in the cortex at the level of fusion between an ovular bundle and a main bundle.

its whole course is in a straight line; sloping gently outwards from the point of origin from the bract bundles (Text-fig. 3).

A series of transverse sections through the node shows, first, above the level of the origin of the bract bundles, three concentric series of bundles; then the median sections through the ovules show only the two series, the outer being in the act of passing out into the ovules; finally, above this level three series again appear (the new outer ring being formed by the

¹ See p. 1105.

bundles which enter from the upper part of the ovule and, after passing upwards, turn down again to join the inverse series, the bundles of which are thus cut twice in these upper sections). Text-fig. 4 is a series of transverse sections illustrating this; the sections are obtained from an older part of the inflorescence than that shown in Text-fig. 3, and the pith has become hollowed out to a greater extent, only a very small part of the internode remaining solid, but the levels of the sections roughly correspond to B, C, D, E respectively in Text-fig. 3. The most interesting feature in this series is the concentric groups of bundles (xx), outside the main ring, which are persistent throughout the internode. At the base of the node these concentric groups become involved with the bract bundles and the lower part of the

TEXT-FIG. 5 is from a tangential section of the female inflorescence axis, showing the ring of bundles destined for a single ovule in process of formation. Letters as before; C = bundles entering from intermediate portion of cupule.

TEXT-FIG. 6 is a still more tangential section, showing the now fully formed ring nearly at the base of the ovular stalk. Ha = hairs on cushion; OM and OIV may be taken to represent bundles entering from above the ovule, OB and M those entering from below the ovule.

ovular supply, and are not continued as such into the node. They are formed again at the top of the node from the inverse series and main bundles at the level at which the former turns downwards towards the ovule (Text-fig. 4 E, x). Text-figs. 4 C and D show the close connexion formed in many cases between the inverse series and the main bundles, many of them being fused together so as to constitute a large inversely concentric bundle.

In tangential sections through the inflorescence axis it is seen that the bundles destined for each ovule are collected into a little ring (see Text-fig. 5). The upper and lower bundles, those derived respectively from the inverse series (OM and OIV) and the outer series (OB), form the upper and lower groups of the ring. At the sides of the ring are smaller bundles (C), which, derived at first from the upper and lower groups, have moved outwards into the intermediate portions of the cushion and then inwards again into the ovular base. The entry of such a bundle into the ovule is seen in Text-fig. 13 C, p. 1121.

The completely formed ring of bundles is seen in the still more tan-

gential section shown in Text-fig. 7, and the further course of the ring of 8-10 bundles thus entering the ovular axis may be followed in the series of sections through the ovular stalk shown in Text-fig. 7.

III. ANATOMY OF STALK OF OVULE.

The young ovule is almost sessile in the axil of the cupule, and its base is deeply embedded in the tissues of the cushion. In even the oldest ovules among my material of *G. africanum* the outermost covering originated very near the base of the short stalk, as in *G. Gnemon*. I do not know whether in *G. africanum* the stalk ever grows any longer; Professor Pearson tells me he has seen no signs of any further growth. The fully mature ovule of *G. scandens* had a stalk equal in length to about a third of the total length of the ovule.¹

The flower-stalk receives from the main axis a simple ring of bundles, varying in number in very young flowers from about ten to thirteen (Text-fig. 7 A). Numerous sclerenchymatous fibres with lignified walls are gradually developed in the peripheral layers of the cortex, and lignification appears in the pith at a very early stage, becoming more and more strongly pronounced, till in the short stalk of the old ovule of *G. africanum* the pith is entirely composed of sclerified elements. In the long seed-stalk of *G. scandens* this lignification is found only in the upper portion of the stalk.

Below the base of the outer flower-covering the vascular bundles branch, and a number of small bundles pass out to supply the outer covering. Many of the bundles left behind in the axis become inversely concentric and irregularly orientated (Text-fig. 7 B). A ring of lignified cells appears in the cortex between the two rings of bundles, and the outermost covering is separated off along the outer edge of this ring.

Above the origin of the outer covering parenchymatous cells appear in the centre of the lignified pith. Text-fig. 7 C shows the parenchymatous pith surrounded by a ring of lignified tissue. The vascular bundles are now divided up rather irregularly into numerous smaller bundles, which become separated into an outer and an inner ring. During this process many more of the bundles become concentric or more commonly inversely concentric, or a few collateral bundles may be arranged to form a concentric group.

The ring of lignified tissue surrounding the pith next moves outwards and separates the two rings of bundles (Text-fig. 7 D, and Fig. 6, Pl. LXXXVI, *lf*); it finally becomes the inner layer of the outer integument. Text-fig. 7 E represents the base of the ovule just below the level of freedom of

¹ It would appear that *G. Ula*, figured by Karsten, Cohn's Beitrage, 1893, resembles *G. scandens* in having a long stalk; in that species the abortive ovules fall off, and the old inflorescence presents the appearance of a raceme.

TEXT-FIG. 7, A-E. Series of transverse sections through the stalk of an ovule of *G. africanum*.
F = fibres, L = lignified tissue, B = tissue with darkly coloured walls, P = palisade layer.

the outer integument; the figure passes through the base of the embryo-sac, and the inner ring of bundles is seen running in the tissues of the fused nucellus and inner integument. The complex outer integument is already differentiated into three zones: (1) the innermost composed of fibrous cells, which are unligified in the very young ovule, but become partly ligified at an early stage; (2) a palisade layer; and (3) the outer layer, containing strands of parenchymatous tissue each traversed by a bundle, alternating with larger strands of cells with brownish indurated walls. The structure of the outer integument shown in this diagram is continued upwards for some distance above its level of freedom, and the chief difference as far as the level of origin of the inner integument is that in the upper half of the ovule the fibrous zone, and consequently the palisade layer, assumes a rayed outline, projecting outwards opposite each vascular bundle (Text-fig. 10, p. 1114).¹

IV. THE SEED.

The seed in both species of *Gnetum* is straight and cylindrical, circular in transverse section, and tapering slightly towards the apex where a conical projection marks the position of the micropyle. The oldest seed of *G. africanum* among my material was about 1.2 cm. long (Fig. 2, Pl. LXXXVI), the single mature seed of *G. scandens* was about 2.7 cm. in length (Fig. 1 A, Pl. LXXXVI). It will be best to describe these seeds separately, though their development is similar and the older stages only differ in minor details.

G. africanum.

Text-fig. 9 is a diagrammatic representation of one of the oldest seeds examined; it is of course possible that further development may take place later.

The *nucellus*, which is fused for about two-thirds of its length with the inner integument, is composed at this stage of a few layers of thin-walled parenchymatous tissue. The inner series of vascular bundles traverses the fused region of nucellus and inner integument, clearly in the region of the integument, and there is no vascular supply to any part of the nucellus itself. The latter is almost filled by the embryo-sac, which is full of endosperm. The endosperm has a slightly corrugated outline, and at the apex of the embryo-sac it projects upwards and forms a sort of small 'tent-pole'² supporting the tip of the nucellus

¹ Exactly the same stages occur in *G. scandens*; but as the ligification of the pith is only developed in the upper part of the long stalk of that species it will be realized that the ligified tissue which forms the sort of cup at the base of the ovule is there exactly comparable to the cup of fibrous tissue at the base of the long-stalked ovule of *Bennettites*; see pp. 1125, 1126.

² Cf. *Ginkgo*, Seward and Gowan, 1900.

(TP, Text-fig. 9); the cell-walls of the 'tent-pole' are often thickened and lignified, to fit them for their supporting function (Fig. 8, Pl. LXXXVI). The

TEXT-FIG. 8. Oldest ovule of *G. africanum*. Endosperm and adhering nucellar cap from which integuments have been removed by dissection. about twice natural size. NC = nucellar cap; PC = remains of pollen chamber; TP = tent-pole; DP = lignified cells in basal projection of endosperm; c = paths made by pollen tubes.

TEXT-FIG. 9. Diagram of median longitudinal section through seed of *G. africanum*. C = outermost covering; O = outer integument; I = inner integument; F = fused nucellus and inner integument; E = corrugated endosperm; TP = tent-pole; NC = nucellar cap; S = closed micropyle; R = down-growing flange of micropylar tube.

cells of the nucellus in this region have thick lignified walls and form a sort of nucellar cap¹ (NC, Text-figs. 8 and 9) which, being attached at its base to

¹ Griffith, 1859, p. 303, Taf. LV, Figs. 25 and 26; Coulter and Chamberlain, p. 383, Fig. 430.

the inner integument only by two or three layers of thin-walled cells, is very easily lifted off, when the seed is dissected, like a tent from its supporting pole (see Text-fig. 8). At the apex of the nucellar cap some signs of disintegration are generally visible, and represent the remains of the pollen chamber; in the tissues both of the cap itself and in the apical region of the endosperm it is generally possible still to distinguish traces of the paths made by the pollen tubes.

The seed has three coverings.

The *outermost covering* arises from the base of the seed and is free to

TEXT-FIG. 10. Transverse section through upper half of ovule. Part of same series as Text-fig. 7 A-E, and Text-fig. 11. For lettering see Text-fig. 7.

its apex; it is green, fleshy, and succulent, and is chiefly composed of homogeneous parenchymatous tissue among which are scattered numerous branched fibres with lignified walls (Fig. 11, Pl. LXXXVI). Numerous repeatedly branched vascular strands run up to its tip, and stomata are occasionally found in its outer epidermis; altogether it resembles the bracts forming the cupular ring in the axil of which the ovule is borne.

The middle covering or *outer integument* is complex in structure, and contains the hard protective layer of the seed. It arises just above the outermost covering and continues upwards, uniform in thickness till it expands at the apex and surrounds the micropylar tube. It is traversed throughout its length by numerous vascular bundles which branch at intervals and run almost up into the tip. Text-fig. 10 represents a transverse section through the upper half of the ovule. The structure of the outer integument at this level is very similar to that already described, at the base of the ovule, before it was free from the nucellus (p. 1112, Text-fig. 7 E);

Fig. 11, Pl. LXXXVI (OI) shows the structure of the free outer integument between these two levels.

The outer zone of the outer integument is traversed by the vascular bundles, each of which is accompanied by a strand of parenchyma and alternates with strands of tissue composed of isodiametric cells with brown indurated walls (Text-fig. 10, B, Text-fig. 11, and Fig. 11, Pl. LXXXVI, D). Next comes a continuous palisade layer which at the base of the ovule is smooth, but in the upper part of the ovule projects outwards and makes an angle opposite each bundle. Inside this is the inner fibrous zone, the outline of which corresponds with that of the palisade layer. In my oldest ovules of *G. africanum* the palisade and fibrous layers were unlignified from the base of the ovule to near the apex, or only very slightly lignified in places, but in the mature ovule of *G. scandens* both layers were lignified throughout, and it is probable that there would be more lignification in *G. africanum* when mature.

As the upper part of the seed is approached the hypodermal strands of indurated tissue diminish in size and prominence, while the fibrous layer increases. The outward projections of the fibrous and palisade layers opposite each vascular bundle become individually more and more strongly pronounced, but as the vascular bundles die out the projections are also gradually reduced in number, there being always a projection opposite each remaining vascular bundle (Text-fig. 11).¹

When the integument thickens at the apex and clasps the micropylar tube the hypodermal strands are lost sight of, and the palisade layer entirely disappears. By this time the fibrous layer occupies the greater portion of the thickness of the integument and its rays are reduced to four or five, opposite some of which the last remaining tracheides of the vascular bundles may still be detected. A characteristic star-like structure (Fig. 16, Pl. LXXXVII, and Text-fig. 11, p. 1116) is thus obtained, which reminds one of Lignier's figures of *Bennettites* and also of *Trigonocarpus*. At this level the radial section of the ovule (Text-fig. 9, p. 1113, Fig. 7, Pl. LXXXVI, and Fig. 15, Pl. LXXXVII) shows that the ends of the cells constituting the fibrous zone have arranged themselves to form a close series of cells elongated at right angles to the surface of the integument, and having their walls strongly lignified and pitted; the walls of the inner epidermal cells are similarly lignified and pitted (Fig. 7, Pl. LXXXVI).

Outside the fibrous zone the expanded portion of the integument is composed of parenchyma only, the cells of which show some tendency towards arrangement in rows at right angles to the epidermis, though not so clearly as in *G. Gnemon*.² The general configuration of this layer

¹ For similar ribbed fibrous layers in integument, see *Conostoma* (Oliver, 1911), *Trigonocarpus* (Scott, 1907, &c.), and other ancient seeds. A similar tendency to the reduction in number of the angles towards the seed apex is seen in *Conostoma anglogermanicum*, Oliver and Salisbury, 1911, p. 26.

² Berridge, 1911, Fig. 1.

reminds one of the 'assise rayonnante' in *Bennettites Morierei* as described by Lignier.¹

At the extreme tip of the integument the fibrous layer dies out, and only a thin band of parenchymatous tissue remains, tightly clasped round the micropylar tube.

TEXT-FIG. 11, A-K. Transverse sections through apex of ovule. A (slightly oblique) level of freedom of inner integument and termination of its vascular bundles; outer integument already shows some reduction in the number of its bundles. B through nucellar cap; B₁ is through extreme tip of nucellar cap and base of micropylar tube. C shows star-like arrangement of fibrous layer in outer integument; palisade layer and hypodermal strands have died out. D = termination of fibrous layer. E = parenchymatous tip of outer integument; micropylar opening reduced to a mere slit. F = micropylar tube almost solid. G = solid micropylar tube, enclosed by tip of outer integument, surrounded by base of down-growing flange. H = solid micropylar tube with wide flange, separate on one side, showing tip of outer integument projecting upwards. I = cavity beginning to reappear in micropylar tube; radial lines indicate divisions to form flange. K = just below withered tip of micropylar tube.

The innermost covering or inner integument is coalescent with the nucellus for about two-thirds of the length of the latter; its free portion encircles the nucellar cap and projects for some distance beyond the nucellus as the micropylar tube. At this stage the tip of the tube

¹ Thoday: Brit. Ass., Sheffield, 1910; also Berridge, 1911.

is withered ; it only projects a little distance beyond the outer integument and does not overtop the outermost covering as it does in the younger stages.¹

4 In my oldest ovule of *G. africanum* the innermost integument is composed almost entirely of parenchymatous cells, though in the micropylar tube (Fig. 11, Pl. LXXXVI) a few short cells with lignified walls are scattered ; and it is probable that these would increase in number later, as they do in *G. scandens*.

A ring of numerous well-developed and branching vascular bundles traverse the common base of the integument and nucellus, running, however, distinctly in the region of the integument ; as a rule the principal part of the bundles terminates just at the level of freedom of the integument, but one or more spirally thickened tracheides have been in several cases traced quite into the base of the free portion of the integument (Fig. 10, Pl. LXXXVI), and in most cases a few elongated cells with dense contents, such as accompany the xylem elements throughout the course of the bundles, continue past their termination for some little distance into the integument.² The integumentary nature of the vascular strands³ is still more clearly seen in the younger ovules (see photograph shown in Fig. 13, Pl. LXXXVII), where the procambial strands extend right into the base of the integument.

The micropylar tube is closed at this stage⁴ for a short distance opposite the tip of the outer integument. Above this level the cavity can still be distinguished in the withered tip ; the cells lining the cavity are cuticularized. Below this level the cavity again appears and is at first slit-like, thus imparting to the seed a small amount of bilateral symmetry. A projecting flange⁵ extends downwards from the closed part of the micropylar tube and is wrapped over the tip of the outer integument, locking the two firmly together.

This method of closing the micropyle, of which details will be given later, resembles that recently described by Miss Berridge in *G. Gnemon*. The tip of the inner integument appears to be withered lower down in my species, and all the structures at the apex are less conical and pointed than in *G. Gnemon* (cf. Text-fig. 9, p. 1113, with Berridge, Fig. 1, p. 140). In *G. africanum* the withering of the micropylar tube seems very rapid ; in most of my smallest ovules the micropylar tube had already withered below the level of the outermost covering (Fig. 14, Pl. LXXXVII).

¹ Griffith, p. 302, Taf. LV, Fig. 18, shows the long tube of the inner integument before it withers ; also Lotsy, 1889, Fig. 18, Pl. III.

² See also Lignier, 1911, p. 3.

³ Miss Berridge tells me that isolated tracheides occur in the inner integument of *Ephedra*.

⁴ Griffith, p. 302 ; Karsten, p. 200 ; Berridge, 1911.

⁵ Described by Karsten in *G. Rumphianum* and *G. ovalifolium*. Cohn's Beiträge, 1893, p. 377 ; Thoday, 1910 ; Berridge, 1911.

Gnetum scandens.

The resemblance between the oldest seeds of *G. africanum* and the mature seed of *G. scandens* is very close in most respects. The chief difference is the fusion of the two outer coverings of the seed to form one, the single covering thus formed having a double vascular supply. Karsten¹ noted the variation in number of the integuments in various species of *Gnetum*, and enumerates three species with their two outer coverings fused (*G. verrucosum*, *G. Rumphianum*, *G. ovalifolium*); the other species he examined had an independent middle covering. It is probable that these three species, like *G. scandens*, would have three separate coverings when young.

The middle covering (outer integument) is entirely composed of lignified cells, and forms a hard, stony layer; the different kinds of tissues, palisade layer, hypodermal strands, fibres, &c., being now only recognizable by the shapes of the cells composing them.

The level of freedom of the inner integument is nearer the apex of the ovule than in the oldest seed of *G. africanum*, and the cavity between the micropylar tube and the nucellus is thus proportionately smaller.

The micropyle is closed, as in *G. africanum*; the solid mass of cells in the closed region is entirely lignified, as is also the greater part of the micropylar tube. There is altogether a great deal more lignification in this species than in *G. africanum*. It is not possible to say whether lignification of the integumentary tissues would ever develop to such an extent in mature ovules of the latter species, but it seems probable that it would not, since the young ovules of *G. scandens* have already more thickened tissues than older ovules of *G. africanum*.

V. DEVELOPMENT OF THE OVULE.

A. The youngest ovules among my material were those of *G. scandens* shown in Fig. 1, Pl. LXXXVI. In these (Fig. 13, Pl. LXXXVII) the micropyle is widely opened and fertilization has not yet taken place. The embryo-sac contains a few nuclei in a peripheral position, and disorganization at the apex to form a pollen chamber has hardly begun. The three coverings arise close together from the base of the seed. The outer covering is already well developed, and is traversed by a network of vascular bundles. The middle and inner coverings are still undifferentiated; more or less definite strands of meristem traverse the middle covering and run into the base of the inner.

¹ Karsten: Cohn's Beiträge, 1893, p. 377.

The nucellus is here composed of a very small basal region, from which arise the three coverings and a comparatively very large free apical portion.

The inner series of bundles is hardly yet developed. It is interesting to find that, at this very young stage, the open micropylar tube is circular in transverse section and is lined by cells whose outer walls are already thickly cuticularized¹ (Text-fig. 12).

B. The next stage was seen in the youngest ovules among my material of *G. africanum*. Their micropyles are already either closed or nearly so. The three integuments still arise near together at the base of the ovule. The vascular system, except in the outermost covering, still consists only of strands of cambial tissue, which extend to the tip of the outer integument, and run for some distance into the inner integument. The integumentary nature of the inner series of vascular bundles is clearly seen in the photograph shown in Fig. 14, Pl. LXXXVII.

The tip of the micropylar tube is already withered, and so firmly interlocked by means of the flange with the outer integument, that it is often difficult to make sure that there is no actual continuity of tissue between them.

The lining of the micropylar tube has probably never been so thickly cuticularized as it was in the young ovule of *G. scandens*. In the closed region there is often little or no sign of cuticularization to be seen at this stage, but in the withered tip, and often for a short distance below the closed region, the epidermis has a thinly cuticularized wall.

A well-developed pollen chamber is present at the apex of the nucellus² (Fig. 14, Pl. LXXXVII). At this stage the embryo-sac is considerably enlarged, and extends from the level of origin of the middle covering to some distance above the origin of the inner integument.

C. The *later stages of development* were mostly seen in abortive ovules (see Text-figs. 13 A, B, C). The greatest change which takes place consists in the gradual stretching and growth of the region between the inner and middle coverings. The basal region develops hardly at all in length, and the apical or free region of the nucellus also develops comparatively very little, but becomes gradually encroached upon by the growing endosperm: thus nearly all the growth in length of the seed

TEXT-FIG. 12. Transverse section of micropylar tube of young unfertilized ovule of *G. scandens*, showing thick cuticularized lining.

¹ The thickness of the cuticle is here more comparable with that in *Welwitschia* than in other species of *Gnetum*; Sykes, 1910 (2), p. 196, Fig. 10, Pl. XVII.

² Lotsy, 1899, p. 94, Fig. 35, Pl. V.

between stage B and the mature ovule takes place in the middle region between the two integuments.¹

The other changes in the development of the ovule consist in the differentiation of the elements of the vascular-bundle system and of the tissues of the outer integument, the complete closure of the micropylar tube and further withering of the tip, the disintegration of the pollen chamber and hardening of the apex of the nucellus.² A diagram of the mature ovule is given on p. 1113.

Text-fig. 14 is drawn from part of a section through an abortive ovule in which these changes were almost complete. The ovule was about 1.5 mm. long, and a good deal of stretching of the region between the two integuments had already taken place. It is possible to distinguish the remains of the pollen chamber.

D. *Details of method of closing micropyle.* The method of closing the micropyle in *G. africanum* is in some respects different from that described recently in *G. Gnemon* by Miss Berridge;³ in *G. scandens* I only saw very young stages and the mature stage with fully closed micropyle, but it would appear as if in that species the resemblance is closer. The closed micropylar tube of the mature ovule, of which the tissues are strongly lignified, is shown in Fig. 12, Pl. LXXXVI. The epidermal cells lining the canal appear to have elongated and interlocked with those opposite them, and thus to have obliterated the cavity.

In *G. africanum* the actual ingrowth of separate epidermal cells as hairs or papillae plays only a small part in the closure of the micropyle. This is due mainly to the rapid division of the epidermis to form radial rows of cells, the pressure of which rapidly closes the micropyle. The innermost elements of the radial rows occasionally project inwards, and sometimes appear to have therefore got crushed together. As a rule, however, this only happens above the region of the flange—that is to say, where the micropylar tube is clasped only by the outermost covering, and is not so tightly compressed as lower down.

The down-growing flange is the result of rapid cell-division in the outer layer of the micropylar tube; it is fringed with short hairs. It adheres so closely to the outer edge of the outer integument that without close examination the tissues appear to be continuous.

¹ Earlier authors have noticed that the depth of attachment of the inner integument varies in *Gnetum*, but they appear to have regarded the difference as specific and not to have realized that they were dealing with different developmental stages. E. g. Karsten : Cohn's Beiträge, 1893, p. 397. The stretching of the ovule and consequent change in position of the level at which the inner integument becomes free is indicated in Coulter's diagrams (Figs. 2 A, 3 A, 6 A), but not referred to in his text; Coulter, 1908; see also Strasburger, 1879, p. 101.

² No sign of the development of a pedicel between the bases of the two outer coverings which is described by Coulter (1908, p. 381, Fig. 6 A) in *G. Gnemon* was seen by Miss Berridge or by me.

³ Berridge, 1911. This method of closing the micropyle is analogous to that described in some Conifers, e. g. *Widdringtonia*, figured by Saxton, 1910, Fig. 2, Pl. I.

Text-fig. 15 represents a series of sections through the micropylar tube of an ovule of *G. africanum*, probably preserved soon after fertilization.

TEXT-FIG. 13. A. Ovule in which the micropylar tube is closed, and the nucellar cap is hardening, but stretching has hardly yet begun. B. The region between the two integuments has undergone considerable extension. C (shown *in situ*) is about the same stage as B, but the free nucellar apex is unusually long and narrow. The closing tissue of the micropyle forms a conspicuous lignified rod. *Ab. ES.* = abortive embryo-sac; *CUS* = interovular portion of cushion; *c* = bundle which has bent outwards into the interovular portion of cushion, and is now bending inwards again to enter ovule (see p. 1109); large black dots (*p*) = phloem of bundles.

Above the closed region of the tube there are already signs of withering (w, Text-fig. 15 F); the canal is open and lined by a thin cuticle. Text-

TEXT-FIG. 14. Longitudinal section through apex of abortive ovule of *G. africanum*, 1.5 mm. long. Ab. ES. = part of abortive embryo-sac; NC = nucellar cap; PC = remains of pollen chamber; F = flange. The micropylar canal is open at the withered tip O, closed at C; it is almost closed and lined with a cuticularized epidermis at L, and is open below.

fig. 15 E shows the beginning of radial divisions in the outer epidermis to form the flange, and the ingrowth of some of the cells of the inner epidermis. Text-fig. 15 D passes through the closed region and shows the radial rows of cells which have been derived from the inner epidermis. At the lower edge of the figure is seen the free part of the flange and the tip of the outer integument (OI) projecting upwards between it and the central portion of the micropylar tube. Below the flange (Fig. 15 C) the tube is nearly closed, but there is a narrow crevice between the epidermis of the two sides. The micropylar canal lower down is always slit-like (Fig. 16, Pl. LXXXVII). It gradually loses its lining of columnar cuticularized cells and its epidermis becomes thin-walled, made up of cells which are elongated in the tangential direction (Text-fig. 15 B). Just above the nucellar tip it becomes irregular in outline (Text-fig. 15 A). Nowhere is the epidermis torn or decayed, so that there is nothing com-

TEXT-FIG. 15, A-F. Series of transverse sections through micropylar tube of fertilized ovule of *G. africanum*, described in text. OI = outer integument.

parable with the 'lysigenous' region described in *G. Gnemon* by Miss Berridge.

In the above series of sections it will be seen that some of the cells composing the micropylar tube are already lignified, especially the radial rows of cells derived from the inner epidermis. Lignification of these often begins on one side only, as in Text-fig. 15 C. Fig. 9, Pl. LXXXVI, shows a transverse section through the micropylar tube of an older ovule, in which there is a solid central core of lignified cells surrounded by a zone of regular thin-walled cells. Presumably this solid core was derived from the radial rows of cells closing the micropyle and formed by the division of the epidermis, while the regular zone of cells outside (S.C.) is the sub-epidermal layer.

In none of the ovules of *G. africanum* examined was the whole tube lignified as in the mature ovule of *G. scandens* (Fig. 12, Pl. LXXXVI).

VI. THE ABORTIVE OVULES OF THE MALE INFLORESCENCE OF *G. SCANDENS*.

The abortive ovules of the male inflorescence resemble those of other species of *Gnetum*. The nucellus is undifferentiated and composed of thin-walled cells with large nuclei. The outer covering contains many fibres and is obviously homologous with the outer covering in the fertile female flower. The inner covering appears to be generally homologized with the inner integument, the outer integument being absent. I have no evidence one way or the other, except that the general form of the inner covering in the abortive ovule of the male inflorescence is more comparable with the outer than the inner integument of the fertile ovule,¹ as will be seen from the figure.

On the other hand, Karsten² states that the middle envelope always appears in a rudimentary condition during the development of the abortive ovules, and Lotsy³ also makes a similar statement, though in the figure which he gives of the developing ovule the rudiment of the middle envelope is almost negligible.

TEXT-FIG. 16. Abortive ovule from male inflorescence of *G. scandens*.

¹ Cf. *Welwitschia*, Sykes, 1910 (1), pp. 207-8.

² Karsten, 1893, (1) and (2).

³ Lotsy, 1899, Fig. 14, Pl. II.

VII. COMPARISON OF THE FEMALE 'FLOWER' OF GNETUM WITH THAT OF WELWITSCHIA. PRIMITIVE FEATURES.

The ovule of *Gnetum*, while in some respects, at any rate, not so primitive as that of *Ephedra*, is certainly more primitive than that of *Welwitschia*. It is not intended now to enter into a comparison with *Ephedra*, as some work on that species is in progress.

The differences between the general form of the ovule in *Gnetum* and *Welwitschia* are probably dependent largely on the different positions of the two. The ovule of *Welwitschia* is closely appressed in the axil of a bract, and it is therefore from the beginning bilaterally compressed. Hence the bilateral symmetry of the outer covering, both external and internal, with its two wings, each traversed by one large group of fibrous cells and one vascular bundle. The inner integument and nucellus still retain the probably more primitive radial symmetry. The ovule of *Gnetum*, which is not laterally compressed, but protected all round by the nodal cushion and its outgrowths, is radially symmetrical, and the fibrous cells in the outer integument form an uninterrupted layer which has an outward projection corresponding to each vascular bundle.

Both *Welwitschia* and *Gnetum* have two integuments; the outer is free, the inner is in the mature ovule fused for about two-thirds of the length of the ovule, while its free apical portion forms the elongated micro-pylar tube with its characteristically cuticularized lining. There was no material of *Welwitschia* young enough to show whether in the earlier stages, here as in *Gnetum*, the inner integument arises near the outer from the base of the seed. The outer integument in both seeds has a bundle system throughout its length, but the small bundles supplying the inner integument terminate at the base of the free portion in *Welwitschia*, while in *Gnetum* (*africanum*) they are well developed and run for a short distance into the base of the free portion. This greater development of the inner system of *Gnetum*, also the more complex outer integument with its stony layer and the development of a pollen chamber, are all probably primitive features which mark the wide gap between the two genera.

The short free apical portion of the nucellus in *Gnetum* is also in great contrast with the elongated apical region of the nucellus in *Welwitschia*. This latter is probably a specialized development to form a spacious brood chamber for the embryo, and may be regarded as a step towards the Angiosperms.

An attempt has recently¹ been made to show that the *Welwitschia* ovule is built up on the same primitive ground plan as such a seed as *Lagenostoma*. It will be seen that all that has been said applies with still greater force to *Gnetum* the prolongation of the inner system of strands into

¹ Sykes, 1910 (1).

the inner integument proves them to be without doubt integumentary. Further, the complex nature of the outer integument in *Gnetum* makes the comparison there made between the seeds of the Gnetales, the Cycads, and some of the older types more striking,¹ and supports the attempt to refer them all to the same ground plan. The pollen chamber in *Gnetum* is clearly comparable with that described in the Cycads.² Other Cycadean features in the *Gnetum* inflorescence are the presence of the three concentric rings of bundles at the nodes, the middle one being inversely orientated to the others, and the occurrence of occasional concentric single bundles.³ Similar features have been described in the 'peduncles' of *Welwitschia*. The seed characters, however, of the recent Cycads suggest that any connexion between the two families is remote, probably only through common Pteridospermic ancestors.

The seed characters in *Gnetum* also give most striking support to the other comparison drawn, in a former paper, between *Welwitschia* and the Bennettitales.

VIII. COMPARISON BETWEEN THE SEEDS OF GNETUM AND THOSE OF THE BENNETTITALES.

Conflicting and confusing as the accounts of the seeds of the Bennettitales at present necessarily are, the points of resemblance between them and *Gnetum* are even so most remarkable.

(i) It will be well first to recall the *detailed structure of the integument* in *Bennettites Morierei*. There is an outer layer which is expanded at the apex of the seed to form a palisaded tissue, which is considerably thickened ('assise rayonnante').⁴ The inner layer of the integument is complex; next to the outer layer is a palisaded layer with thin walls (Lignier's 'assise plissée'), and internal to it are thin-walled cells which are brownish in colour ('tissu charnu') and a distinct fibrous layer. The fibrous layer, composed of elongated cells, extends downwards into the peduncle, and passes inside the vascular bundles, forming the pith of the upper portion of the peduncle; in this region it is composed of much shorter cells with very thick walls. *Bennettites Gibsonianus* would appear to agree with *B. Morierei*, except that the expanded portion of the outer layer is there composed of oblong cells which are not so distinctly palisaded.

Cycadeoidea Wielandii has a much thinner outer integument, also com-

¹ Coulter, 1908, p. 47, compares the seeds of *Gnetum* with those of *Cycas* and *Ginkgo*, since they all have a two-layered integument, the inner layer of which is stony, and both layers have a vascular supply. He regards the differentiation of the inner layer as a separate integument in *Gnetum* as a special development. I should regard it as a primitive feature, reminiscent of the *Lagenostoma* ground plan from which I believe all these seeds to have been derived.

² Lang, 1900.

³ *Ante*, pp. 1103, 1119; cf. concentric rings in the stems of Cycads.

⁴ According to Lignier this outer layer is composed of 'tubular' cells, but Wieland refers the 'assise tubuleuse' to the interseminal scales, and gives no special description of the outer layer in *Bennettites* except at the apex of the seed.

posed of two layers: the outer, thick-walled and more or less clearly palisaded throughout, shows some sign of expansion at the tip of the ovule (Fig. 4, Pl. XXVIII, Wieland); the inner layer, which is composed of 'string elements', probably corresponds to the fibrous layer in *Bennettites*, and is similarly prolonged downwards into the peduncle.

In *Gnetum* the integument is also made up of two layers. The outer layer contains alternating vertical strands of parenchyma and dark coloured tissue, and is expanded at the apex of the integument, but is not thickened. In *G. africanum* and *G. scandens* there is only an indication of a radial arrangement of the cells at the apex, similar to that occurring in *Bennettites*, but in *G. Gnemon*¹ this is much more marked. The inner layer in *G. africanum* and *G. scandens* consists of a palisaded thin-walled layer, like that recorded in *Bennettites*, and a fibrous or stony layer, also as in *Bennettites* and *Cycadeoidea*: the arrangement of the latter layer appears to be exactly similar to that described in the fossil seeds; it extends downwards into the stalk of the ovule, where it passes inside the vascular bundles and forms the pith of the upper portion of the peduncle, in the integument its cells are elongated and run irregularly in the horizontal direction, while in the peduncle they become short and very thick-walled. The fibrous layer is lignified in the peduncle of the quite young ovule, and in *G. africanum* at the apex of the seed also, where it forms a palisade layer. In the old ovule of *G. africanum* this layer shows signs of lignification throughout: in the mature ovule of *G. scandens* the whole inner integument is lignified.

The distribution of the fibrous layer at the apex of the seeds in *Bennettites Morierei* is another point of resemblance to *G. africanum*.² It will be remembered that the former seed has four or five wings, while the latter has not. In both, however, the fibrous layer develops four or five wings which project outwards, and in *B. Morierei* extend into the outer wings. A comparison between Fig. 16, Pl. LXXXVII, of this paper and Lignier's Fig. 6, p. 41, &c., speaks for itself.³ The wings of fibres in both seeds decrease in prominence lower down, forming small projecting angles which gradually die out, till the layer of fibres forms a smooth zone; cf. Text-figs. 7 C, and 10 of this paper with Lignier's Fig. 7, p. 42, Fig. 45, Pl. IV, &c.

Opposite each of the wings of fibres in *G. africanum* is a vascular bundle; Lignier could not certainly distinguish any vascular bundles in the upper part of the seed of *B. Morierei*, but states that there were suggestions of their presence opposite the outer point of each wing of fibres.

To sum up, the integuments of these three seeds agree in the possession

¹ Berridge, 1911.

² In *G. scandens* the star-like distribution of the fibres at the apex of the outer integument was not so striking as in *G. africanum*. In *G. Gnemon*, Miss Berridge tells me that she was also able to make out the star-like distribution, but no lignification had occurred.

³ In *G. africanum* it is only in the extreme apex that the number of angles is reduced to five; lower down the seed these increase in number.

of an inner fibrous layer which is similarly distributed in the peduncle, main body, and apex of all three seeds, except that in *Gnetum* it forms at the tip of the seed a more definite palisade, which in *G. africanum* is lignified very early. *B. Morierei* and *Gnetum* have a middle palisade layer. In the seeds of the Bennettitales the stony layer tends to be formed from the outer layer of the integument; in *Gnetum* the inner layer shows the earliest signs of lignification.

(ii) The comparison of the *nucellus* and *inner integument* of the seed of *Gnetum* with the main body of the seed in *Bennettites* involves more difficult questions. In both seeds there is a projecting *micropylar tube*, which in *Gnetum* is derived from the inner integument and projects beyond the outer, but is fastened firmly on to it by means of the downward projecting flange. Lignier's figures of *Bennettites* are suggestive of the same arrangement in that seed, the relation¹ of the micropylar tube to the expanded portion of the integument being identical with that found in *Gnetum*. Lignier attempts to trace continuity between 'the integument' (outer integument?) and micropylar tube; he states, however, that the micropylar tube is homogeneous in structure, sclerified in the fertile seeds, not sclerified in the aborted, and shows no resemblance to the complex structure of the rest of the integument; continuity with the rest of the integument could not be demonstrated. This description would equally apply to *Gnetum*. The difficulty of investigating the apex of the seed may possibly be due to a similar withering of the apex after fertilization, and if it be true that the micropylar tube in *Bennettites* is also fastened by a flange to the top of the outer integument, as in *Gnetum*, it is easy to understand the confusion as to the boundary between the two. The description of the micropylar tube agrees with that of *Gnetum*, the canal being cylindrical below, with an epidermis composed of small thin-walled cells, irregularly slit-like above, with an epidermis which consists of narrow radially elongated cells, and is cuticularized (cf. Figs. 31, 32, Pl. III, Lignier, with Fig. 16, Pl. LXXXVII, of this paper). Opposite the expanded portion of the outer integument the canal is closed as in *Gnetum*.

The micropylar tube of *Cycadeoidea Wielandii* is not clearly comparable with either *Bennettites* or the mature seed of *Gnetum*. It is open, and it may be, as Miss Berridge has suggested, that the seeds figured are at an earlier stage and should be compared with unfertilized ovules of *Gnetum*. A greater difficulty is that the outer thickened layer of the (outer?) integument extends upwards and clothes the micropylar tube. It is, of course, possible that the seed is so young that the inner integument does not yet protrude beyond the outer, but this does not seem likely in view of the differentiation which has already taken place in the integument. It is more

¹ This comparison was made in detail by the author at the Sheffield meeting of the British Association, 1910; and a similar one has also been drawn by Miss Berridge, 1911.

probable that there is in this seed a different relation between the integument and tube.

That the micropylar tube in *Cycadeoidea* also, however, corresponds with the inner integument in *Gnetum*, there seems to me little doubt. Wieland says that 'the interior layer of the micropylar tube is regarded as a continuation of the wall of the nucellus'; that is to say, that it becomes free from the nucellus at a given level, but is fused with it below. It may be that in *Cycadeoidea* the external layers of the micropylar tube were fused with the palisaded outer integument, as in the mature ovules of such species as *G. scandens*. The outlines sketched in Wieland's Fig. 63 (2), p. 122, suggest this. It appears that the palisaded stony layer must have been prolonged upwards in this form, clothing the tube.

Owing to the difficulties in interpreting the material, the account of the relations of the nucellus with the micropylar tube and integument in *Bennettites* is very confusing.¹ Lignier describes a small cavity, 'corpuscular mass,' in the apex of the main body of the nucellus and also, above the main body, a large 'lysigenous' pollen chamber, beyond which the nucellus is prolonged upwards as a beak.¹ This beak projects into the micropylar tube. Miss Berridge has suggested that Lignier's 'corpuscular mass' is the true pollen chamber, agreeing in position with the pollen chamber of *Gnetum*. On the other hand, she regards the 'nucellar beak' as probably homologous with the secondary closing tissue which fills up the micropylar tube in *Gnetum*, and which has here become separated from the tube by an accident of preservation; and she regards the space between the beak and main body of the nucellus, not as a pollen chamber, but as comparable with the large space between the micropylar tube (or inner integument) and nucellus in *Gnetum*, which occurs also in Wieland's *Cycadeoidea* where no nucellar beak is figured.² In *G. Gnemon* the lower part of the micropylar tube below the closed portion is lined by a ragged torn layer of cells, and is very suggestive of Lignier's 'pollen chamber'; in *G. africanum* the thin-walled epidermis is still intact, but it is easy to see how, if not well preserved, it would become torn and ragged.

¹ Wieland does not describe any such complex structure in *Cycadeoidea*.

² Here the micropylar tube is open and the ovule is probably young, so that if the nucellar beak corresponds with closing tissue its presence would not be expected. Another point of difference between Wieland and Lignier's account supports Miss Berridge's theory. Lignier's Fig. 35, Pl. II, passes through the base of the so-called 'mucron nucellaire' and the 'pollen chamber'. It is clearly surrounded only by the (outer) integument, and there is nothing at this level representing the micropylar tube, which, according to him, has fused on to the (outer) integument. But Wieland describes the continuity of the inner layers of the micropylar tube and the nucellus. If Wieland's account is true this hollow 'beak', which is fused below with the nucellus, must represent the base of the micropylar tube below the closed portion. It corresponds exactly with Miss Berridge's figure of *G. Gnemon* at this level, and even its small transverse section, so striking in contrast with Figs. 32 and 31 of the upper portion of the micropylar tube, is another suggestive point, since the latter sections would pass through the flange and the former would be taken from the lower, narrower portion of the tube.

The closed upper portion of the micropylar tube in *Gnetum* is similar to the part of the tube which Lignier describes as closed in *Bennettites*, but it is not at first sight easy to see how below this the nucellar beak, which, it is suggested, represents the closing tissue, could have become so sharply separated off as an individual organ, as it is in Lignier's figures, apparently surrounded by a distinct epidermis of its own. Miss Berridge drew my attention to a point in some of my series of slides of *G. africanum* which affords a possible explanation of this difficulty. In Fig. 9, Pl. LXXXVI, a transverse section through the lower part of the closed region of the tube, the closing tissue derived from the original epidermis of the tube forms a solid cylinder of lignified cells which is separated off from the rest of the tube by the still intact and regular subepidermal layer. It would only be necessary for this delicate layer to be split off from the central rod in order to get the effect shown in Lignier's Fig. 32, Pl. III, a solid rod enclosed by the hollow micropylar tube.

In the absence of more perfectly preserved material of *B. Morierei*, we cannot regard this theory of the nucellar beak as proved, but in view on the one hand of the other resemblances between the seed and that of *Gnetum*, and on the other of Wieland's account of the young *Cycadeoidea* without a nucellar beak, it must be regarded, at any rate, as a brilliant hypothesis which has every appearance of probability.

(iii) The structures surrounding and protecting the ovule in *Gnetum* and *Bennettites* may be compared. It will be seen that while the ovule in the latter is enclosed at the base by the 'coque' or basal husk, this extends upwards only for a short distance, and it is the interseminal scales, with which the whole is surrounded, that give the ovule efficient protection. On the other hand, the interovular portions of the nodal cushion in *Gnetum*, which completely protect the young ovule, and in transverse sections of the axis remind one forcibly of the interseminal scales in *Bennettites*, do not continue to enlarge with its growth; and it is the extra outer covering, comparable in position with the basal husk in *Bennettites*, which is the efficient protective organ of the mature ovule. It is not necessarily intended here to homologize the basal husk with the extra outer covering or the interseminal scales¹ with the projecting portions of the cushion, but physiologically the comparison between them has some force.

The long stalk of *G. scandens* is suggestive of the long pedicel of the *Bennettites* ovule. Coulter² states that there is a short pedicel between the 'perianth' and outer integument in *G. Gnemon*, but neither Miss Berridge nor I have seen any trace of it.

¹ The interseminal scales have already been compared morphologically with the bracts in *Welwitschia*; Sykes, 1910 (1).

² Coulter, 1908, p. 381.

IX. OTHER RESEMBLANCES BETWEEN GNETUM AND THE BENNETTITALES.

The method of vascular supply of the peduncle of the whole cone of *Cycadeoidea Wielandii*, and of the single *Gnetum* flower is very similar, as may be seen when Text-fig. 3, p. 1107, is compared with Wieland's Fig. 59, p. 113. The two figures are both drawn from radial sections, and two sets of bundles are seen running out into the axillary stalk. Wieland says that the lower bundles, which are seen from transverse sections to be orientated similarly to the main bundles, are 'either directly connected with, or envelop the supply of the leaf-base';¹ he calls them 'the axillary portion of the leaf bundles'. The upper series is orientated inversely to the other two and is chiefly derived from the main bundles. This description is strikingly like that of *Gnetum* given on pp. 1106 ff. of this paper. Transverse sections show that the bundle supply of each peduncle² is arranged in a ring, the outer members of the ring orientated like the main bundles, the inner inversely orientated. In *Gnetum* the outer series passes out more rapidly, and the whole of the ring supplying any given ovule cannot be cut in transverse sections of the stem, but only in tangential.

X. SUMMARY.

1. The vascular system of the female inflorescences and flowers of *G. africanum* and *G. scandens*, and of the male inflorescence of *G. scandens* is described. The most interesting points are the presence of *three concentric rings* of bundles in the nodes, the middle one of which is *orientated inversely* to the other two. The method of vascular supply to the single female flower in *G. africanum* bears a remarkably close resemblance to the method of supply to the axillary inflorescence in *Bennettites*.

2. Concentric bundles occur fairly frequently in the two outer rings of bundles and are sometimes continuous throughout the internode.

3. Each ovule receives a ring of bundles; these traverse the stalk and branch at the base of the ovule to form three series; the two outer series traverse the outer and middle coverings to their tips, the inner series run up to the level of freedom of the inner covering and sometimes for a little distance into its base. In the young ovule *strands of meristem* run a considerable way up *into the free portion of the inner integument*.

4. Throughout the short ovular stalk of *G. africanum* and in the upper part of the long stalk of *G. scandens*, the centre of the pith is lignified. At the base of the ovule the lignification spreads outwards, while parenchyma appears in the centre of the pith. The layer of lignified tissue then passes outwards between the bundles into the region separating the bases of the two integuments, and is higher up continuous

¹ Wieland, p. 113.² Ibid., pp. 69-71.

with the fibrous layer of the outer integument (middle covering). Thus, at the base of the ovule the fibrous layer forms a sort of cup just as it does in *Bennettites*.

5. The outer integument (middle covering) is complex in structure: in *G. africanum* it remains independent, but in *G. scandens* it becomes fused with the outermost covering. In *G. africanum* it is composed of an outer zone which is made up of alternating strands of parenchyma, each containing a vascular bundle, and indurated tissue; and an inner zone which becomes the stony layer of the seed. The inner zone contains a palisade layer and a fibrous layer. The fibrous layer is angled in the upper part of the seed, there being an angle opposite each vascular bundle. These angles, along with the number of vascular bundles, are gradually reduced in number, till at the tip of the integument there are only four or five. Here the integument clasps the micropylar tube, and the five-angled fibrous zone forms a sort of star, of which all the cells are lignified at a very early stage. A similar arrangement of the fibrous layer and a similar palisade layer is found in *Bennettites Morierei*.

6. A well-developed pollen chamber is present in the young ovule; as it decays the apex of the nucellus hardens and forms a pointed cap of lignified tissue.

7. In the young ovule the three coverings arise close together at the base of the nucellus, and the free apical portion of the nucellus is by far the largest part of the ovule. As the seed grows the region between the two integuments becomes much stretched and forms the greater portion of the mature ovule, so that the innermost covering becomes free about two-thirds of the way up the nucellus. The free portion of the nucellus in the mature seed is very small in proportion to the part developed by intercalary growth. The embryo-sac develops between the levels of freedom of the two inner coverings; it is as it expands that the intervening region stretches. In the mature seed it projects into the free portion of the nucellus.

8. The open micropylar tube of the youngest ovules (*G. scandens*) is circular in section, and its lining is strongly cuticularized. After fertilization the tube is closed for some distance by means of a tissue formed by division of the epidermal cells, and a 'flange' is also produced which fits tightly over the outer integument. In the older ovule and seeds the micropylar canal, where it is still open, is slit-like. The tissues of the tube become gradually lignified; the closing tissue becomes lignified first and forms a solid thick-walled central rod. The micropylar tube is remarkably similar to that of *Bennettites Morierei*, and this central rod is compared with the 'nucellar beak' in that seed.

9. The radial structure of the seed, the short free apical portion of the nucellus, the presence of a pollen chamber, the extension of the bundle system into the free portion of the inner integument, the complex structure

of the outer integument are all points of contrast with *Welwitschia* and probably indicate the more primitive nature of the *Gnetum* ovule.

10. The attempt to refer the seed of *Welwitschia* to the same ground plan as that of such Pteridosperms as *Lagenostoma* and such recent seeds as the Cycads is thus supported by the study of *Gnetum*. Between *Gnetum* and *Bennettites* there are still more obvious resemblances. None of these forms are of course regarded as directly derived from one another, but the seed characters render it probable that they derive their origin from common ancestors.

My thanks are due to Mr. Mangham for the five photographs forming Pl. LXXXVII illustrating this paper.

BOTANY SCHOOL, CAMBRIDGE,
July 28, 1911.

ADDITIONAL NOTE.

Since the above was written two publications have appeared which bear on the subjects discussed, and which require some notice here.

I. Wieland's most recent paper on the American Fossil Cycads, 'Further Notes on Seed Structures,'¹ is chiefly concerned with the minute structure of their integuments. His account of *Bennettites Morierei*, especially his description of the base of the seed, is full of resemblances to *G. africanum*. But he seems quite convinced that the middle or stony layer of the seed, at any rate in *Cycadeoidea*, is continuous with the micropylar tube (see especially Fig. 5, p. 144), which is therefore not the prolongation of the inner flesh only, as it should be were it to be closely homologized with the inner integument in *Gnetum*. On the other hand, he gives a diagram (Fig. 3 C, p. 141) showing the micropylar tube clothed with the stony palisaded layer, but made up mainly of thin-walled tissue. The latter may be chiefly closing tissue, but must consist partly of prolonged inner flesh; he does not discuss the question fully. There appears to me nothing incredible in the suggestion (p. 1128 of the present paper) that the micropylar tube, so delicate in most species, should in *Cycadeoidea* have become protected by a firm hard layer derived from the outgrowth of some of the tissues of the outer integument.

Whether or no the attempts at homologies between Gnetalean and Bennettitalean seeds made in the present paper prove of any ultimate value, the remarkable resemblances in the detailed structure of the integuments and micropylar tubes are too great to be lost sight of.

II. Schuster's paper² on 'Weltrichia und die Bennettitales' contains

¹ The American Journal of Science, xxxii, 1911.

² Kungl. Svenska Vetenskapsakademiens Handlingar, Band 46, No. 11. Stockholm and Upsala, 1911.

a hypothesis of the origin of the Bennettitalean 'flower' which is given in so graphic a manner and is so fully in accordance with the forthcoming evidence that it carries conviction with it. That the interseminal scale finds its progenitor in the fern sporophyll is altogether probable, and is of course a belief which is commonly held, but it is harder to follow the writer in his derivation of the angiospermous carpel from the actual interseminal scale now found in the Bennettitales. The carpel of such Angiosperms as the Ranalean series seems more naturally related to the sporophyll of Schuster's 'Urtypus' of *Bennettites*, which is almost a Pteridophyte, than to the specialized scale of the known types. In view of the growing belief in the polyphyletic origin of the Angiosperms it may well be that in other forms without marginal ovules the carpel found its origin in a more specialized organ; possibly resembling more nearly the 'bract' in *Welwitschia*, as has been already suggested in a previous paper.

Oct. 10, 1911.

LITERATURE QUOTED.

- BECCARI, O.: Della organogenia dei fiori feminei del *Gnetum gnemon*. Il Nuovo Giorn. Bot. Ital., vol. vii, 1877.
- BERRIDGE, E. M.: On some Points of Resemblance between Gnetalean and Bennettitean Seeds. New Phyt., vol. x, 1911.
- BERTRAND, C. E.: Anatomie des Gnétacées et des Conifères. Paris, 1874; and Ann. des Sci. Nat., Bot., sér. 5, vol. xx, 1874.
- COULTER, J. M.: The Embryo-sac and Embryo of *Gnetum gnemon*. Botanical Gazette, vol. xlv, 1908.
- COULTER, J. M., and CHAMBERLAIN, C. J.: Morphology of Gymnosperms. Chicago, 1910.
- GRIFFITH, W.: Remarks on *Gnetum*. Trans. Linn. Soc., vol. xxii, 1859.
- KARSTEN, G. (1): Untersuchungen über die Gattung *Gnetum*. Ann. Jard. Bot. de Buit., vol. xi, 1893.
- (2): Zur Entwickelungs-Geschichte der Gattung *Gnetum*. Cohn's Beiträge, vol. vi, 1893.
- LANG, W. H.: The Morphology of Cycadean Sporangia. The Ovule of *Stangeria*. Annals of Bot., vol. xiv, 1900.
- LIGNIER, O.: Végétaux fossiles de Normandie. Structure et affinités du *Bennettites Morierei*. Bull. de la Soc. Linn. de Nor., Caen, 1894.
- LIGNIER, O., and TISON, A.: Les Gnétales sont des Angiospermes apétales. Comptes rendus, 1911.
- LOTSY, J. P.: Contributions to the Life History of the Genus *Gnetum*. Ann. Jard. Bot. Buit., (2), vol. i, 1899.
- OLIVER, F. W.: Notes on *Trigonocarpus* and *Polylophospermum*. New Phyt., vol. iii, 1904.
- OLIVER, F. W., and SALISBURY, E. J.: On the Structure and Affinities of the Palaeozoic Seeds of the *Conostoma* Group. Annals of Botany, vol. xxv, 1911.
- OLIVER, F. W., and SCOTT, D. H.: On the Structure of the Palaeozoic Seed *Lagenostoma Lomaxi*. Phil. Trans., B, vol. cxcvii, 1904.
- PEARSON, H. H. W.: Some Observations on *Welwitschia mirabilis*. Phil. Trans., B, vol. cxcviii, 1906.
- : Further Observations on *Welwitschia mirabilis*. Phil. Trans., B, vol. cci, 1909.
- SAXTON, W. T.: Contributions to the Life History of *Widdringtonia cupressoides*. Botanical Gazette, 1910.

- SCOTT, D. H., and MASLEN, A. J.: The Structure of the Palaeozoic Seeds *Trigonocarpus Parkinsonii*, B., and *Trigonocarpus Oliveri*, sp. nov. Ann. of Bot., vol. xxi, 1907.
- SEWARD, A. C., and GOWAN, J.: The Maidenhair Tree, *Ginkgo biloba*. Annals of Botany, vol. xiv, 1900.
- STOPES, M. C.: Beiträge zur Kenntniss der Fortpflanzung der Cycadeen. Flora, 1904.
- STRASBURGER, E.: Die Coniferen und die Gnetaceen. Jena, 1872.
- : Die Angiospermen und die Gymnospermen. Jena, 1879.
- : Ueber das Verhalten des Pollens und die Befruchtungsvorgänge bei den Gymnospermen. Hist. Beitr., Jena, 1892.
- SYKES, M. G. (THODAY, M. G.) (1): On the Anatomy and Morphology of the Leaves and Inflorescences of *Welwitschia mirabilis*. Phil. Trans., B., vol. cci, 1910.
- (2): On the Anatomy of *Welwitschia mirabilis* in its Seedling and Adult Stages. Trans. Linn. Soc., series 2, Botany, vol. vii, 1910.
- THODAY, M. G. (SYKES, M. G.): The Morphology of the Ovule of *Gnetum africanum*. Brit. Ass. Report, Sheffield, 1910.
- WIELAND, G. R.: American Fossil Cycads. Carnegie Institute, Washington, 1906.
- WORSDELL, W. C.: The Vascular Structure of the Flowers of the Gnetaceae. Annals of Botany, vol. xv, 1901.

DESCRIPTION OF PLATES LXXXVI AND LXXXVII.

Illustrating Mrs. Thoday's paper on the Female Inflorescence and Ovules of *Gnetum*.

PLATE LXXXVI.

Fig. 1. Single node of inflorescence of *Gnetum scandens*, showing young ovules with projecting micropyles borne on a cushion (Cus.) in the axil of the cupule of bracts (Cup.). In. = internode. In the right-hand figure are shown the gaps in the cushion from which two of the sunken ovules have been removed. (Rather larger than natural size.)

Fig. 1 A. Single mature ovule of *G. scandens* on stalk. (Natural size.)

Fig. 2. Lower portion of inflorescence of *G. africanum*, borne on naked peduncle. At the base of the inflorescence are two bracts in the axil of which was a cushion, but no buds or ovules. In. = the very short internode; B.C. = the cupule of bracts; C = large swollen axillary nodal cushion; A.Ov. = abortive ovules; F.Ov. = fertile ovules. (Natural size.)

Fig. 3 A. Diagram of transverse section through lowest part of node, showing free edge of cupule, and base of axillary cushion covered with hairs. Shaded patches on cupule (Cup.) represent corky tissue; c = hairs; shaded lines on inner edge of cupule = mucilaginous layer of cells. $\times 6$.

Fig. 3 B. Diagram of transverse section through middle of node. The two inner series of bundles are seen in pith of main stem; the outer series has just passed out into the ovules. A.O. = abortive ovule with free integuments arising from base; c = peltate projecting portion of cushion; F.O. = fertile ovule; P = outer covering; O.I. = outer integument; C.M. = closed micropylar tube; N.C. = nucellar cap; E = embryo-sac. $\times 6$.

Fig. 4. Single bundle from peduncle, showing space in pericycle (Pcy.Sp.) crossed by trabeculae; small space on inner edge of bundle (Sp.). V.B. = vascular bundle; F = fibre. $\times 400$.

Fig. 5. Section through portion of bract cupule. M = mucilaginous layer under upper epidermis; Tr. = transfusion tissue at sides of bundles; F = fibres. $\times 78$.

Fig. 6. Part of transverse section through base of ovule, just below level of freedom of outer integument (O.I.). N + I.i. = nucellus and inner integument; l.f. = lignified fibres, here marking the line of separation of outer integument and becoming later the inner zone of the outer integument; p = palisade layer; v.b. = vascular bundle; to the left of the bundle is a hypodermal strand of tissue with dark-coloured cell-walls. $\times 78$.

Fig. 7. Longitudinal section through apex of expanded portion of outer integument. F = parenchymatous tip; L = lignified series of cells at the termination of fibrous layer; a.r. = outer

parenchymatous zone showing arrangement into radial rows (cf. Lignier's 'assise rayonnante').
× 116.

Fig. 8. Longitudinal section through apex of ovule, showing nucellar cap and 'tent-pole' of endosperm. T.P. = tent-pole; N = remains of nucellar tissue; T = tapetum; I.i. = inner integument. × 78.

Fig. 9. Transverse section through micropylar tube at the base of the closed region; a minute slit is just reappearing. The ovule is rather older than the one figured in the text (Text-fig. 9, p. 1113); the almost solid central core of cuticularized cells is probably due to the division and subsequent cuticularization of the epidermal cells originally forming the lining of the tube; the beginning of the cuticularization is seen in Fig. 15, Pl. LXXXVII. The more or less definite layer surrounding the solid core represents what was originally the subepidermal layer (*s.e.*). × 336.

Fig. 10. Longitudinal section passing through base of inner and outer integuments at level of origin from nucellus. I = inner, M = outer integument; Tr. = tracheides at termination of a bundle running into the base of the inner integument. × 116.

Fig. 11. Part of transverse section through mature ovule near its base. E = endosperm; N = remains of nucellus still fused with the inner integument; O.I. = outer integument; P = outermost covering; Sz. = branched fibres; V.B. = vascular bundle; D = hypodermal strand of brownish tissue; P = palisade layer; F = fibrous zone. × 116.

G. scandens.

Fig. 12. Transverse section through closed micropylar tube of mature seed just below flange (Fig. 1A). All the cell-walls are lignified. The epidermal cells are elongated and now fit tightly together. × 400.

PLATE LXXXVII.

Fig. 13. Longitudinal section through young ovule of *G. scandens*. Shows open micropylar tube with cuticularized lining.

Fig. 14. Longitudinal section through young fertilized ovule of *G. africanum* in situ. Shows pollen chamber, and prolongation of strands of meristem into inner integument.

Fig. 15. Longitudinal section through apex of older ovule (abortive). Shows closed micropylar tube, flange, beginning of sclerified nucellar cap, lignification of inner fibrous palisade in outer integument.

Fig. 16. Transverse section through apex of outer integument of old fertilized ovule. Shows star of lignified tissue in outer integument, and slit-like micropyle.

Fig. 17. Transverse section through node of axis of male inflorescence of *G. scandens*, showing anastomosis of bundles.

M.G.Thoday (Sykes) del.

M.G. Thoday (Sykes) del.

Huth, lith. et imp.

13.

14.

15.

16.

17.

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Sykes, Mary Gladys. 1911. "The female inflorescence and ovules of *Gnetum africanum* with notes on *Gnetum scandens*." *Annals of botany* 25, 1101–1135.
<https://doi.org/10.1093/oxfordjournals.aob.a089365>.

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