

Anatomy of *Gnetum africanum*.¹

BY

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With Plates LVII-LIX.

THE following account of the anatomy of *Gnetum africanum* is based on material collected by Professor H. H. W. Pearson in Montobello, on April 7, 1909. My thanks are due to Professor Pearson for handing over the material to me for investigation, and for much helpful advice with regard to the work.

In view of the systematic position of *Gnetum* and the difficulty of obtaining suitable material for investigation, it seemed worth while to place on record the facts ascertained with regard to the anatomy.

BRIEF REVIEW OF THE MORE IMPORTANT PUBLISHED WORK ON GNETUM ANATOMY.

Griffith's 'Remarks on *Gnetum*', which appeared in the Linnean Society's Transactions of 1859, contains a few references to the anatomy of the genus. Professor Bower in 1882 published an account of the germination and seedling structure of *G. Gnemon*, while the seedlings of *G. scandens* and *G. moluccense* have been investigated recently by Hill and de Fraine. A few references to the anatomy of *G. Gnemon*, *G. scandens*, and *G. Thoa* occur in de Bary's 'Comparative Anatomy of Phanerogams and Ferns'. Strasburger, in 1872, investigated the course of the bundles in leaf and stem, and the vascular supply of the axillary buds in several species of *Gnetum*. In 1894 Boodle and Worsdell published a paper on the 'Comparative Anatomy of the Casuarineae, with special reference to the Gnetaceae and Cupuliferae'. The species of *Gnetum* examined were—*G. Gnemon*, *G. paniculatum*, *G. scandens*, *G. neglectum*, and *G. Thoa*.

EXTERNAL CHARACTERS.

The genus *Gnetum* comprises between 20 and 30 species of tropical trees and climbers, two of which—*G. africanum* and *G. Buchholzianum*—are natives of the African continent. *G. africanum* was first discovered

¹ Percy Sladen Memorial Expedition in South-West Africa, 1908-9, Report No. 20.

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by Welwitsch in the Cazengo district of Central Angola in 1858, and was described by him in the Linnean Transactions of 1869. The species is a climber with long slender stems which are swollen and jointed at the nodes; the much elongated internodes are sometimes more than 15 cm. long. The plant exhibits marked heterophylly. In the material examined the lateral branches spring from the axils of short, opposite scale leaves; while the expanded foliage leaves produce only abortive buds in their axils. On superficial examination the scale leaves resemble the persistent bases of the petioles of foliage leaves, and were apparently mistaken for such by Welwitsch.¹ No root material was available.

STEM.

The oldest material examined shows a stem 5 mm. in diameter, its surface covered with a thin layer of cork. The younger internodes are marked with numerous, irregularly arranged dots and striations of a dark brown colour, while the youngest branches are smooth and green. The secondary thickening is perfectly normal; there is no trace of the successively renewed thickening rings which are present in *G. scandens*² and *G. Thoa*. It is possible that this abnormality may occur in older stems than those investigated. The number of vascular bundles seen in transverse section of the axis varies considerably; from 12 to 20 were observed in the internodes examined.

Xylem. The wedge-shaped xylem-masses are separated by conspicuous medullary rays (Pl. LVII, Fig. 1). The first-formed elements of the protoxylem have loosely coiled, spiral thickenings occasionally combined with annular markings. Those formed later have very close spiral or reticulate thickenings and often communicate by means of a row of large pits on the oblique walls. Reticulately thickened tracheides are specially abundant in the region of the node. Boodle and Worsdell³ have pointed out that in *Gnetum* the vessels first formed by the cambium have usually several perforations in their end walls, resembling in this respect the well-known vessels of *Ephedra*. In several cases two rows of large, circular, bordered pits were seen in the sloping end of a reticulate nodal tracheide of *G. africanum*, and one of the vessels was found to possess two rows of perforations on the oblique wall, as described by the above authors in the node of *G. paniculatum*. In general, however, only a single row of perforations occurs in these first-formed vessels. Transitional stages between pitted tracheides with a row of large, closed, bordered pits on their terminal wall, and true vessels were observed, the central pits of the oblique walls being perforated, those at the ends closed. Transitional stages between vessels with several circular perforations and those with a single long narrow one

¹ Welwitsch (9).

² De Bary (3).

³ Boodle and Worsdell (1).

were also noticed (Pl. LVIII, Fig. 8, *a-d*). The later formed vessels usually have inclined end walls with a single oval or circular perforation (Fig. 8, *e-f*). In one case two large circular openings were observed. In transverse sections the remains of the oblique septa of the vessels with their perforated bordered pits are often seen (Pl. LVII, Fig. 1). Associated with the true vessels of the secondary xylem are numerous gymnospermous tracheides. The thickness of the walls and the size and shape of the bordered pits in both vessels and tracheides vary considerably. In addition to the tracheal elements large numbers of elongated cells with protoplasmic contents and simple pits occur in the secondary xylem. They do not contain starch, but occasionally numerous minute crystals of calcium oxalate are found in them. Near the cambium these parenchymatous cells are usually seen to be arranged in regular rows continuous with the albuminous cells in the phloem (Pl. LVIII, Figs. 9, 12); in the older wood they are scattered, apparently owing to the enlargement of the vessels. Occasionally, the lumina of the vessels were found to be blocked with resinous substances.

Phloem. The boundary between the xylem and phloem masses of the vascular bundles, as seen in transverse section of the younger internodes, has the shape of an arc whose concave side is directed outwards. In older internodes this appearance is generally lost. The phloem elements are extremely regular;¹ but when sections are placed in water, considerable swelling and distortion occurs. No hard bast elements are present. The large sieve tubes are arranged in radial rows (Figs. 9, 10, 12). Compound sieve plates occur in large numbers on the very oblique end walls, but are less numerous on the vertical walls (Figs. 13 and 14). On staining with iodine after heating in glycerine, minute starch grains may be seen in the albuminous contents of many of the sieve tubes. Considerable callus formation covers the older sieve plates (Figs. 15, 17, 18). These callus pads stained readily with water blue, Russow's callus reagent, and corallin soda, but were unaffected even after prolonged staining with aqueous solutions of aniline blue and eosin. Particularly good results were obtained with water blue.

The albuminous cells are also arranged radially, and, as was remarked above, they are generally continuous with the elongated parenchymatous cells of the xylem (Fig. 12). In longitudinal section they are seen to be long and narrow, with dense proteid contents and well-defined, often elongated, nuclei (Fig. 14). Their end walls are at first transverse, but later become oblique. Numerous minute crystals of calcium oxalate are often collected at one end of these cells, and small starch grains are occasionally present. A doubling of the radial rows of albuminous cells and sieve tubes often takes place. In the older phloem, owing to the displacement of the elements, the albuminous cells come to lie at the corners of the sieve tubes

¹ Boodle and Worsdell (1).

and the likeness to companion cells is then very marked (Fig. 12). At the periphery of the bundle lies the crushed mass of protophloem. In tangential sections through the phloem of older stems, fusiform rays are often seen. These vary much in size, some of them being only one cell wide and from one to three cells high; others are several cells wide and higher in proportion (Figs. 11, 16). These rays are specially numerous near the nodes of old stems. The cells are thin-walled, with protoplasmic contents, and are packed with minute crystals of calcium oxalate. A few starch grains are occasionally present. Intermediate stages were observed between the smaller rays and albuminous cells with crystallogenous contents (Fig. 16).

Pith. The pith consists of elongated cylindrical cells with pitted walls which are conspicuously lignified in the region of the vascular ring. In most of the older internodes the central thinner-walled cells have been disorganized (Pl. LVII, Figs. 1, 4), though this is not always the case. The older stems have the pith cells packed with rounded starch grains; these are entirely absent from the pith of the younger internodes. In the pith region below the growing point, and in the pith of the nodes, large numbers of crystals of calcium oxalate were found. Running longitudinally through the pith are latex tubes similar to those of the cortex which will be described below. In the pith of the node large numbers of branched, lignified, fibrous cells occur (Fig. 5). Similar sparingly branched lignified elements are very occasionally found in the pith of the internode.

Primary Medullary Rays. As is well known, the primary medullary rays are very conspicuous, and extend from pith to cortex, gradually broadening outwards (Fig. 1). Their width varies considerably in different internodes. These rays are composed of parenchymatous cells which are often radially elongated. Many of the cells are lignified and provided with simple pits; others are packed with calcium oxalate crystals and crystal sand. The amount of lignification of the ray varies. In young stems most of the ray cells are lignified; all have conspicuous protoplasmic contents, and some are packed with crystals. Between the phloem masses large thin-walled crystallogenous cells are very numerous. In older internodes a very large number of thin-walled crystallogenous cells occur, and in the wider parts of the ray there are stone cells with lignified, pitted, and conspicuously striated walls (Fig. 1). These sclerosed cells are very numerous in the ray parenchyma between the masses of bast. Starch was found to be absent from the rays of the young internodes, but is present in considerable quantities in those of older stems. The crystals in the ray cells are usually rhombic in surface view and vary greatly in size (Pl. LIX, Fig. 30), many of them being extremely minute. They resemble closely those found in the crystal sacs of phloem and cortex. In tangential section the rays are often seen to be broken up into partial rays by vascular tissue (Pl. LVII, Fig. 2). Single bridging xylem elements were frequently observed (Figs. 2, 3). In one

section a large pitted vessel was seen bridging a ray, and in a few cases bridging phloem elements were also noted.

Cortex. The ground tissue lying next to the phloem masses consists, in young stems, of thin-walled parenchymatous cells through which a few latex tubes and fibres are scattered. In older stems an irregular ring of large parenchymatous cells becomes strongly lignified, forming the conspicuous sclerenchymatous zone (Fig. 1 and Pl. LVIII, Fig. 9). The walls of these stone cells are stratified and pitted, and resemble the sclerotic elements of the old medullary rays. The fibres are elongated and unbranched, with cellulose walls and pointed ends. They are very numerous in the outer cortex, but are occasionally found inside the zone of stone cells. The white lustrous thickening layer is often found to have separated from the primary wall (Pl. LIX, Fig. 27). The marked contraction which sometimes occurs may have been caused by the alcohol in which the material was preserved. The cell lumina of many of the fibres are almost entirely obliterated; the walls of some show well-marked stratification (Fig. 27). In the cortex of the node, stellate fibrous cells also occur (Pl. LVII, Fig. 5), but they are extremely rare in the internode. In the younger internodes the parenchyma of the cortex, especially near the epidermis, contains numerous chloroplasts. A considerable quantity of storage starch is present in the cortex of older stems, and is very abundant in the parenchyma between the zone of stone cells and the phloem masses. Crystallogenous cells, similar to those of the rays, also occur in the cortex.

Latex Tubes. Among the most striking elements of the cortex are unbranched secretory tubes similar to those found in the pith and leaf-stalk. These laticiferous vessels of *Gnetum africanum* do not differ from those of *Gnetum Gnemon* described by Bower.¹ Their origin from vertical rows of elongated parenchymatous cells was observed in microtome sections of the young stem below the apical cone. Two or three nuclei were observed in several of these cells. Occasionally short, lateral protrusions of these vertical tubes were found forcing themselves between the neighbouring cells. The coagulated, albuminous contents turn a golden yellow on treatment with iodine. On placing longitudinal sections of the stem in strong sulphuric acid, the cellulose walls are dissolved and the strands of coagulated latex show up very distinctly. After prolonged treatment with alkanet tincture the contents of the tubes turn a reddish brown.

Epidermis of Stem. The epidermal cells of the young internodes are papillate, with much thickened outer wall and well-defined cuticle. The wall thickening in older internodes often projects irregularly into the cell cavity. The stomata are arranged in vertical rows and sunk below the level of the epidermis (Pl. LIX, Fig. 23). Their structure resembles that of the leaf stomata which will be described below.

¹ Bower (2).

Cork. The formation of cork in the internodes of *G. africanum* was found to be very irregular. The phellogen originates in circumscribed areas of the stem epidermis (the dots and striations mentioned above) and then spreads peripherally (Pl. LVIII, Fig. 21). It is not unusual to find part of an internode covered with 8–10 layers of cork and the rest with no sign of phellogen formation. This is probably connected with the climbing habit of the species. Some of the older internodes are surrounded by a thin and regular mantle of cork whose surface shows many minute cracks. In several of the stems examined, however, periderm formation cuts deeper and deeper into the cortex at certain points, and thus cortical fibres and secretory tubes come to be embedded in the outer cork. Occasionally, groups of fibres are completely isolated by cork cells (Pl. LVII, Fig. 4). In longitudinal sections these cork rings are found to be connected with the peripheral layer of cork. Similar cork rings surrounding a core of fibres were found in *G. scandens* and *G. Buchholzianum*. Layers of thick-walled phelloderma cells containing numerous crystals are sometimes found inside the phellogen. In several internodes the ground tissue cells inside the sclerenchymatous zone were found to have undergone division, often to such an extent that part of the zone of stone cells was ruptured and pushed out to the periphery of the stem, while large parenchymatous cells next to the phloem masses had become sclerosed. If an anomalous zone of xylem and phloem occurs in this species, the cambium must arise in this secondary tissue inside the zone of sclerenchyma (Pl. LVIII, Figs. 19, 20). A curious feature of some of the sections examined was the mucilaginous disorganization of groups of parenchymatous cells in the region of the protophloem masses (Fig. 20).

Stem Apex. According to Stapf,¹ Dingler² made the surprising statement that he had traced the growth of the stem apex of *Ephedra* to a 4-sided apical cell. Microtome sections were cut through the apical cone of branches of *G. africanum*, but in every case a small-celled meristem was found.

LEAF.

As was mentioned above, *G. africanum* possesses pairs of scale leaves in addition to the expanded foliage leaves. In transverse sections of the node below the swollen bases of the foliage leaves, eight bundles are seen to leave the stele, four passing into the base of each leaf. The two median leaf-traces are the first to separate from the vascular ring (Pl. LVII, Fig. 5). Sections through the bases of the pair of scale leaves immediately below the female cone showed the same bundle supply. On tracing the bundles through the scale leaf they were seen to fuse laterally, so that near the apex the separate strands could no longer be distinguished. A small twig which possessed six pairs of scale leaves was also examined. The vascular supply resembled that described above. Undeveloped buds were

¹ Stapf (7).

² Dingler (4).

found in the axils of these leaves. Sections were also cut through old nodes with opposite lateral branches in the axils of the scale leaves. Again eight bundles leave the stele as in the cases already described. These bundles branch in passing through the cortex,¹ the median leaf-traces often bifurcating before the lateral are quite clear of the vascular ring. A number of these branches enter the axillary bud, while others pass into the leaves. The material available did not admit of all the details of the leaf and axillary branch supply being made out, but in the sections examined a brush of xylem elements appears to pass up into the free part of each scale leaf.

Petiole. The short petiole of the foliage leaf is slightly furrowed above and convex beneath. Numerous latex tubes and fibres traverse the petiole and pass into the midrib. A few lignified spicular cells are also present. The four leaf-trace bundles remain distinct through the entire length of the petiole. A considerable amount of secondary tissue is formed by the cambium of each of these bundles.

Lamina. The four bundles of the petiole enter the base of the lamina and fuse laterally in pairs about one-fourth of the way up the midrib. Complete fusion occurs at some little distance above this point. The cambium of the midrib forms a considerable amount of secondary xylem and phloem. As is well known, the reticulate venation of the *Gnetum* leaf is of the normal dicotyledonous type (Figs. 6, 7). The leaf lamina, though fairly thin, is extremely tough. Below the cuticularized upper epidermis lies a single row of short palisade cells. The many-armed, spongy mesophyll occupies a considerable part of the substance of the leaf. The sclerenchymatous framework of the lamina consists of branched acicular cells and elongated fibres. The former have lignified, finely striated walls, occasionally perforated by simple pits. They are stellately branched and differ from the spicular cells of *Welwitschia* in the absence of an outer crystal-bearing layer of cellulose from their walls (Pl. LIX, Fig. 29). They occur for the most part in the stellate parenchyma close to the lower epidermis, the more prominent arms usually lying in the plane of the lamina. The fibres, which are far more numerous, are of enormous length. Their cellulose walls are so strongly thickened that in places the cell lumen is almost entirely obliterated. On isolating these fibres after maceration the ends are frequently found to be shortly and unequally branched. Similar branches occasionally occur at other points, but are seldom of great length (Figs. 28, 31). A bundle of these fibres strengthens the leaf margin and prevents tearing. These marginal fibres resemble those of the axis in being much straighter than the fibres described above and entirely unbranched.

The ordinary epidermal cells of both surfaces have strongly undulated walls (Pl. LVIII, Fig. 22), but opposite the larger veins they are narrower and more regular in outline. Nodose thickenings of the walls are fairly common.

¹ Strasburger (8).

The epidermis is provided with a well-marked cuticle which shows up distinctly on treatment with alkanet root or a fresh solution of chlorophyll.

The stomata are small, numerous, and arranged irregularly over the whole of the under surface with the exception of the veins and veinlets. A few are also present on the upper surface over the midrib.¹ They occur on the scale leaves as well as on the foliage leaves. Each stoma is accompanied by two subsidiary cells lying parallel to the pore (Fig. 22), but the material did not admit of the determination of the origin of the subsidiary cells. Several cases of 'twin stomata' were observed. In the leaf the stomata are about on a level with the subsidiary cells (Pl. LIX, Fig. 24), but in the young stems the stomata, which are here placed parallel to the longitudinal axis, are considerably sunken (Fig. 23). Seen from above the stoma often bears a striking resemblance to the under surface of a cowrie shell (Pl. LVIII, Fig. 22). The outer wall of each guard cell is provided with a lignified flap marked by delicate striations (Fig. 22). The guard cells, as seen in longitudinal section, are enlarged at the ends and somewhat contracted in the middle (Pl. LIX, Fig. 25). They contain large quantities of starch. As in most investigated Gymnosperms, ridge-like protuberances of the membrane are absent.

SUMMARY.

Gnetum africanum is heterophyllous, producing pairs of scale leaves which subtend the lateral branches, and foliage leaves with abortive buds in their axils. The stems examined showed normal secondary thickening.

The number of vascular bundles seen in transverse section of the axis varies considerably.

The first-formed vessels have several perforations on their sloping end walls, and transitional stages were found between these and the later-formed vessels with a single circular perforation. As is usual in climbers, the vessels of the secondary wood are of considerable size.

The phloem tissue is composed of regular rows of sieve tubes alternating with rows of elongated albuminous cells. Numerous compound sieve plates occur on the oblique end walls and also on the lateral walls of the sieve tubes. Considerable callus formation takes place.

In addition to the conspicuous primary medullary rays, smaller fusiform rays packed with calcium oxalate crystals are sometimes found. Transitional forms between the latter and the elongated albuminous cells of the phloem occur. Rhombic crystals of calcium oxalate, which vary greatly in size, are present in large numbers in certain cells of the xylem, phloem, medullary rays, cortex, and phelloderma, also in the pith of the nodes.

Sclerenchymatous elements of various forms occur in the stem. Stone cells with lignified and pitted walls form a conspicuous zone outside the

¹ Griffiths (5).

vascular bundles, and also occur in the broader parts of old medullary rays. Branched acicular cells with lignified and finely striated walls occur in the pith and cortex of the nodes. Elongated fibres with enormously thickened cellulose walls are present in large numbers in the cortex.

Latex vessels with cellulose walls and dense albuminous contents occur in pith and cortex, also in petiole and lamina of the foliage leaf.

Cork formation is exceedingly irregular. The phellogen originates in circumscribed areas of the epidermis and spreads peripherally. It is not unusual to find periderm formation cutting deep into the cortex at certain points, and occasionally groups of fibres are completely isolated by cork cells. Division of the ground tissue cells within the sclerenchymatous zone was observed.

The stem apex was found to possess a small-celled meristem.

Four bundles pass into the base of each foliage leaf, the median leaf-traces being the first to leave the vascular ring. The bundles which supply the scale leaves subtending the lateral shoots branch on passing through the cortex, a number of the bundles passing into the axillary shoots.

The reticulate venation is of the usual Dicotyledonous type.

A single layer of short, palisade cells occurs below the upper epidermis. The spongy parenchyma consists of many-armed, loosely packed cells.

Fibres and branched acicular cells are present in large numbers in the mesophyll of the leaf.

The stomata are arranged irregularly over the under surface of the lamina with the exception of the veins and veinlets. They also occur on the upper surface over the midrib, and are about on a level with the surrounding epidermal cells. The outer wall of each guard cell is provided with a lignified flap. The stomata of the young stems are sunken below the level of the epidermis.

LITERATURE CITED.¹

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¹ In several cases the entire paper was not available and extracts only were seen.

EXPLANATION OF FIGURES IN PLATES LVII-LIX.

Illustrating Miss Duthie's paper on the Anatomy of *Gnetum africanum*.

PLATE LVII.

- Fig. 1. Part of a transverse section of the stem. $\times 165$.
 Fig. 2. Part of a longitudinal section of the stem, showing vessels of the xylem and medullary rays. $\times 500$.
 Fig. 3. Part of a medullary ray with bridging xylem tracheides. $\times 500$.
 Fig. 4. Transverse section of stem, showing irregular cork formation and cork rings.
 Fig. 5. Transverse section through node, showing leaf-trace bundles.
 Fig. 6. Photograph of skeleton of young leaf. Natural size.
 Fig. 7. Portion of above. $\times 3$.

PLATE LVIII.

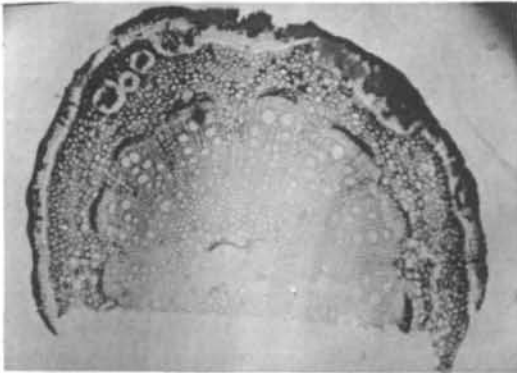
- Fig. 8 *a*. Terminal wall of pitted vessel with row of circular perforations. $\times 375$.
 Fig. 8 *b, c*. Terminal walls of segments of vessels, showing fusion of circular pits. $\times 375$.
 Fig. 8 *d-f*. Terminal walls of vessels of old wood with single perforations. $\times 220$.
 Fig. 9. Transverse section through phloem mass, showing radial rows of sieve tubes and albuminous cells. $\times 375$.
 Fig. 10. Transverse section through a portion of a bundle, showing medullary ray cells packed with crystals of calcium oxalate. $\times 375$.
 Fig. 11. Tangential section through medullary rays in phloem. $\times 375$.
 Fig. 12. Transverse section through a portion of a bundle, showing albuminous cells packed with crystals of calcium oxalate. $\times 375$.
 Fig. 13. Radial section through phloem, showing compound sieve plates on sloping terminal walls. $\times 375$.
 Figs. 14 and 15. Tangential section through phloem, showing sieve tubes and albuminous cells. $\times 375$.
 Fig. 16. Tangential section through phloem, showing short parenchymatous cells filled with crystals abutting on elongated albuminous cells. $\times 375$.
 Fig. 17. Transverse section through phloem, showing large callus pads on walls of sieve tubes. $\times 375$.
 Fig. 18. Tangential section through phloem, showing large callus pads on sloping end walls of sieve tubes. $\times 375$.
 Fig. 19. Transverse section through part of stem, showing formation of phelloderm and cork in the ground tissue inside zone of stone cells. $\times 240$.
 Fig. 20. Transverse section through part of stem, showing formation of mucilage cavity and secondary tissue inside zone of stone cells. $\times 240$.
 Fig. 21. Portion of a transverse section of a stem, showing origin of phellogen in epidermis. $\times 375$.
 Fig. 22. Surface view of stoma. $\times 800$.

PLATE LIX.

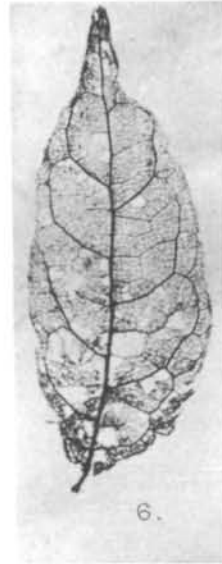
- Fig. 23. Median transverse section through sunken stoma of young stem. $\times 800$.
 Fig. 24. Median transverse section through stoma of leaf. $\times 800$.
 Fig. 25. Longitudinal section through stoma of leaf. $\times 800$.
 Fig. 26. Transverse section through end of stoma of leaf. $\times 800$.
 Fig. 27. Transverse section of stem cortex with fibres. The thickened walls are unshaded. $\times 375$.
 Fig. 28 *a*. Bone-shaped end of elongated fibre of leaf. $\times 220$.
 Figs. 28 *b* and 31. Fibres of leaf with short branches. $\times 220$.
 Fig. 29. Branched acicular cell of leaf. $\times 220$.
 Fig. 30. Cell of medullary ray with rhombic crystals of calcium oxalate. $\times 375$.



2.



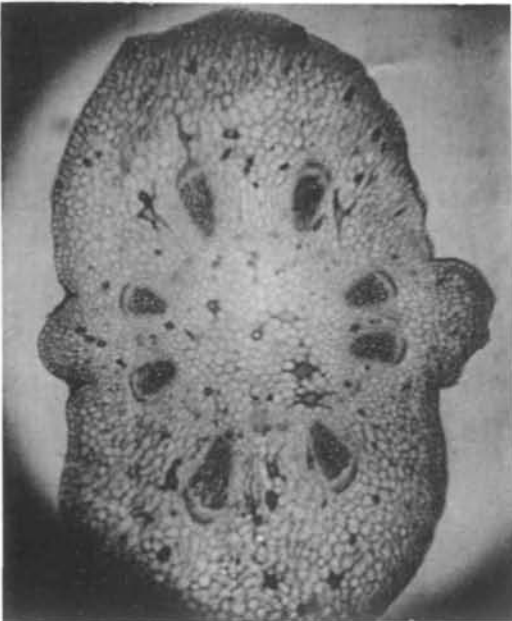
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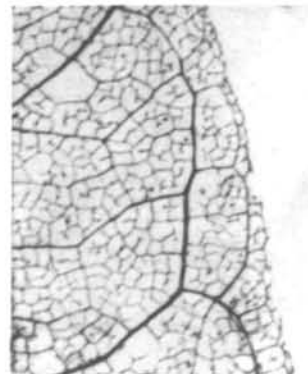
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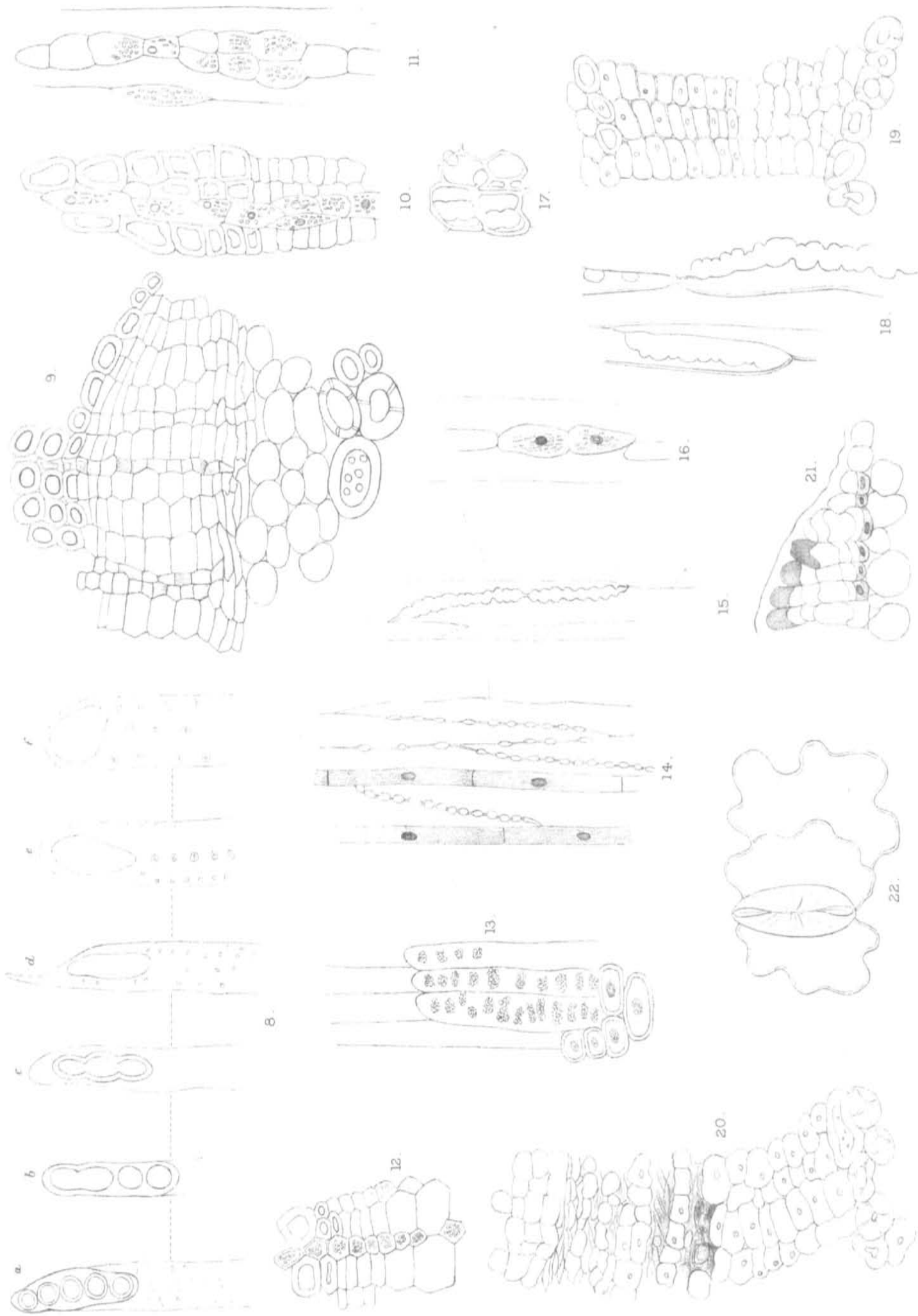
5.



7.

High cell

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GNETUM — DUTHIE

