The Systematic Anatomy of the genus Canephora.

By

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With 7 figures in the text.

The examination from the systematic standpoint of the specimens of *Canephora* in the National and Kew Herbaria [1]) has led me to investigate the anatomy of these curious plants as fully as may have been consistent with the scanty and somewhat poor material available, which was taken from herbarium specimens. The bulk of the tissues, being more or less lignified, is tolerably well preserved; but the softer portions, particularly the phloem, have perished to a considerable extent.

This rare genus of *Rubiaceae* is, so far as our present knowledge extends, confined to Madagascar.

The five species hitherto described all reveal more or less strongly marked xerophytic characters; they are shrubs or trees, with leathery leaves, and destitute of indumentum. The rather small campanulate flowers are borne two or three together in the hollowed apices of axillary flattened branches (Fig. 1). The corolla is contorted in aestivation, and the bilocular ovary contains a few ovules, maturing into a few-seeded berry, so that the genus finds a place in the section *Cinchonoideae-Gardeniinae-Gardenieae.* [2])

We may proceed forthwith to such anatomical details as have been ascertained in the course of the enquiry. Three only of the five known species have been available for the purpose of this investigation — *C. madagascariensis* Gmelin, upon which the genus was founded; *C. angustifolia* and *C. Goudotii*, described by myself in the Journal of Botany (loc. cit.).

[1]) Wernham, Journ. of Botany. Vol. XLIX. 1911. p. 77—82.
[2]) Schumann, K., u. Engler, A., Nat. Pflanzenfam. IV. 4. p. 80.

Fig. 1. *Canephora madagascariensis.*

A. Portion of the shoot, shewing the inflorescence borne on flattened axillary peduncles (*i. p.*).

B. Inflorescence enlarged, the peduncle (*i. p.*) bearing five flowers in the hollowed apex, associated with an involucre of bracts (*br.*).

The parts examined respectively for each species were of corresponding age and maturity of development.

C. madagascariensis Gmelin.

I. Stem (Fig. 2). — The pith consists of rounded cells with rather large lumina and with distinct intercellular spaces. The

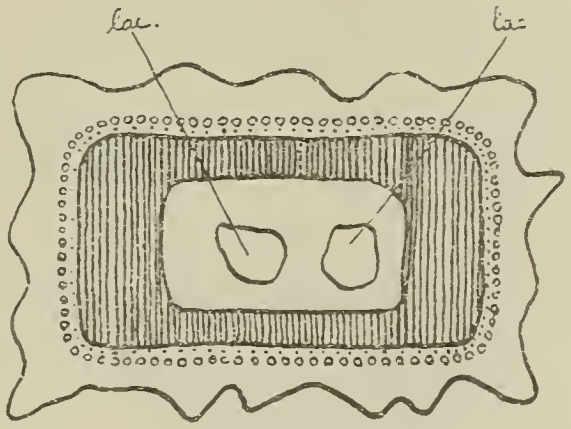

Fig. 2, *b*.

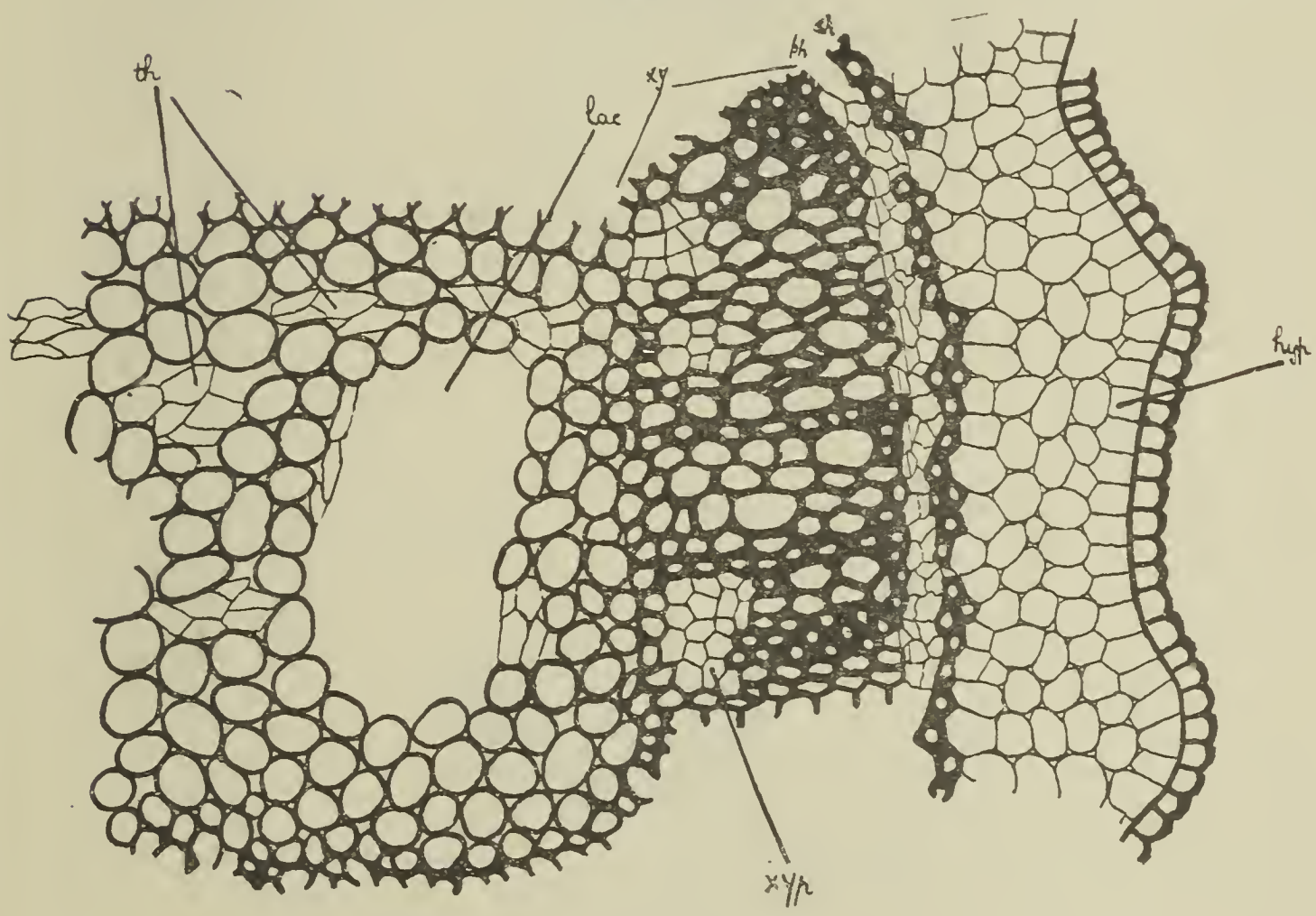

Fig. 2, *a*.

Fig. 2. *Canephora madagascariensis*.

a. A portion of the stem in transverse section; for explanation of lettering, see text.

b. Diagram of the whole stem in transverse section.

Lac., lacunae in the pith; other signs as in Fig. 3.

walls are for the most part thick and lignified, especially in the peripheral zone where the pith passes more or less insensibly into the primary xylem. In the central part of the pith, groups of thin-walled cells *(th.)* appear; and two large lacunae *(lac.)*, which

occupy the centre of the transverse section, may probably mark the position of two large groups of thin-walled cells which have perished.

A good deal of tannin is present, and a certain amount of calcium oxalate, which appears in a few of the cells in the form

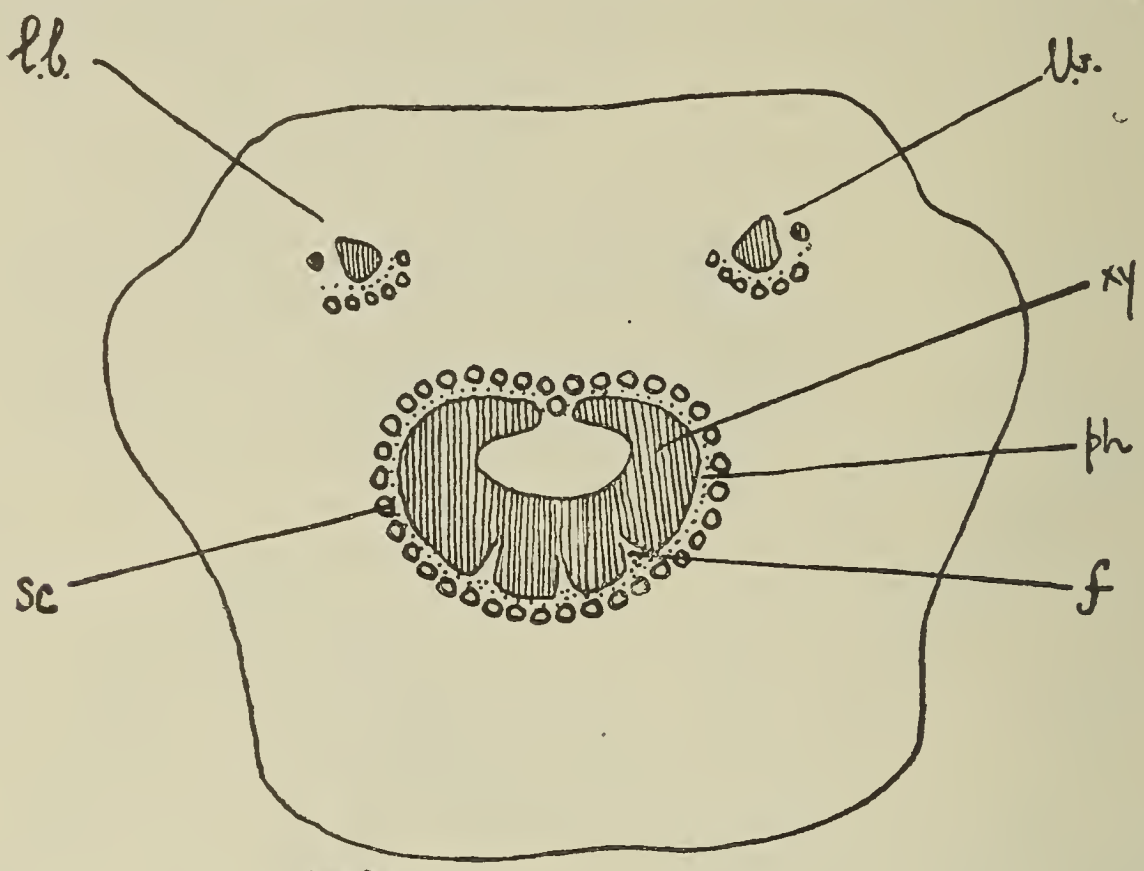

Fig. 3, *a*.

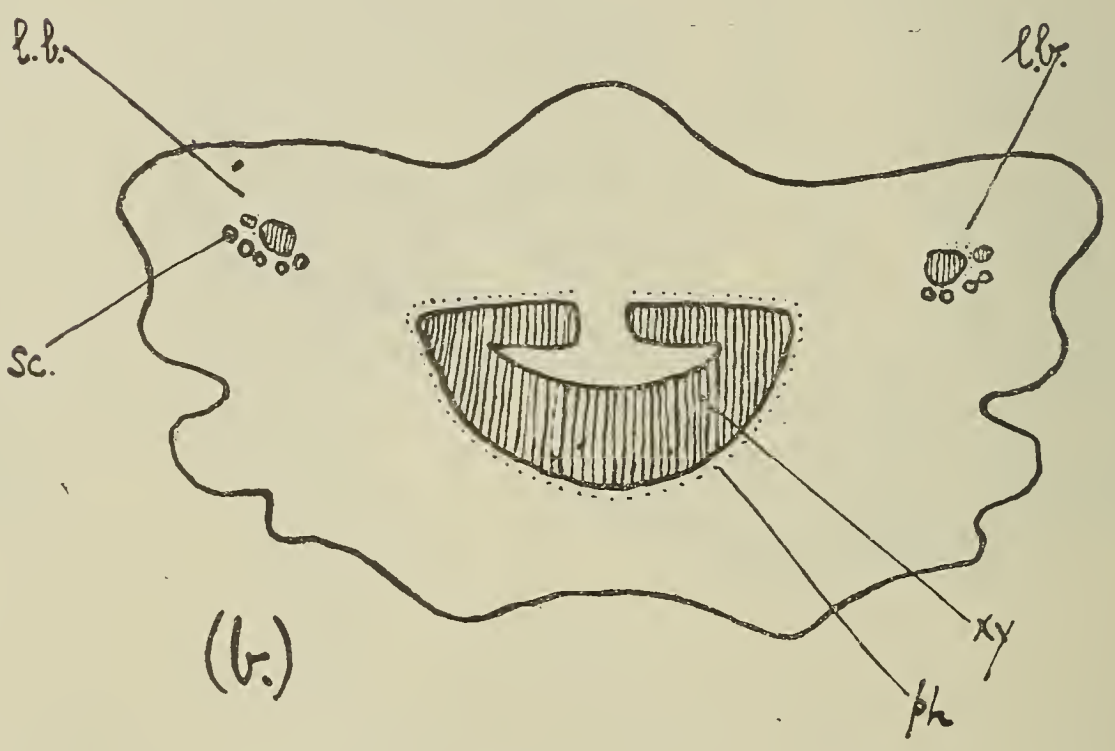

Fig. 3, *b*.

of crystal sand. This sand displays a noticeable tendency to aggregate into amorphous clusters; and one or two "cluster-crystals" of typical appearance, but quite small, are to be seen.

The xylem *(xy)* is very dense. The vessels are small and few in number; there are numerous fibres, with very thick walls.

At more or less frequent intervals, associated with the primary xylem, are patches of parenchymatous tissue *(xy. p.)*, consisting of small thin-walled cells of polygonal outline. This may represent xylem parenchyma, but in the absence of developmental details no definite assertion can be made. There are no medullary rays, but the wood is interrupted at frequent intervals by rays of fibres, sometimes as much as three cells wide as seen in transverse section.

The phloem, which is too perished to be investigated with much profit, takes the form of a narrow band surrounding the

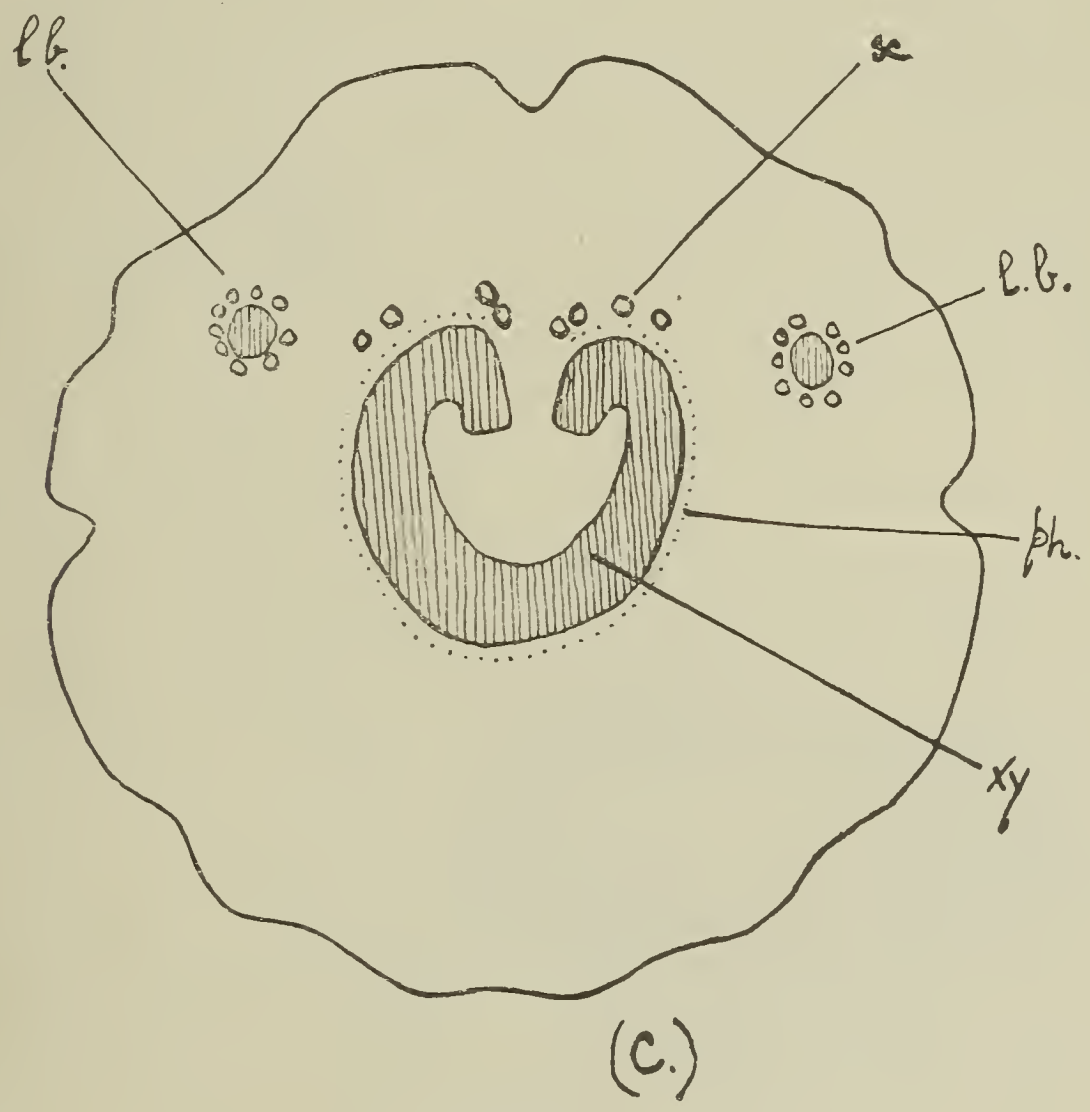

Fig. 3, *c*.

Fig. 3. Diagrams of the petioles of (*a*) *Canephora madagascariensis*, (*b*) *C. angustifolia*, (*c*) *C. Goudotii*, in transverse section.

xy. Xylem, lined; *ph*. phloem, dotted; *sc*. fibres, small circles; ground parenchyma left blank; *l.b*. lateral vascular strands; for *f*. see text and Fig. 4.

xylem; the cell-walls are thin, and tannin is abundant. Calcium oxalate, in the form of crystal sand, occurs but is relatively rare in the phloem.

Immediately external to the phloem in transverse section appears an unbroken sheath *(sh.)*, one to two cells broad, of rather small sclerenchymatous fibres, with very thick walls and lumina almost obliterated.

The cortex consists of large round cells, as seen in transverse section, with relatively thin walls. Tannin is abundant, especially

near the periphery; and calcium oxalate, chiefly in the form of crystal-sand, with a few small true cluster-crystals, is fairly plentiful. No sclerenchyma is present in the cortex external to the fibrous sheath just described.

There is a well-marked hypodermis *(hyp.)* of rather large square cells filled with tannin. The epidermis is of cells of similar

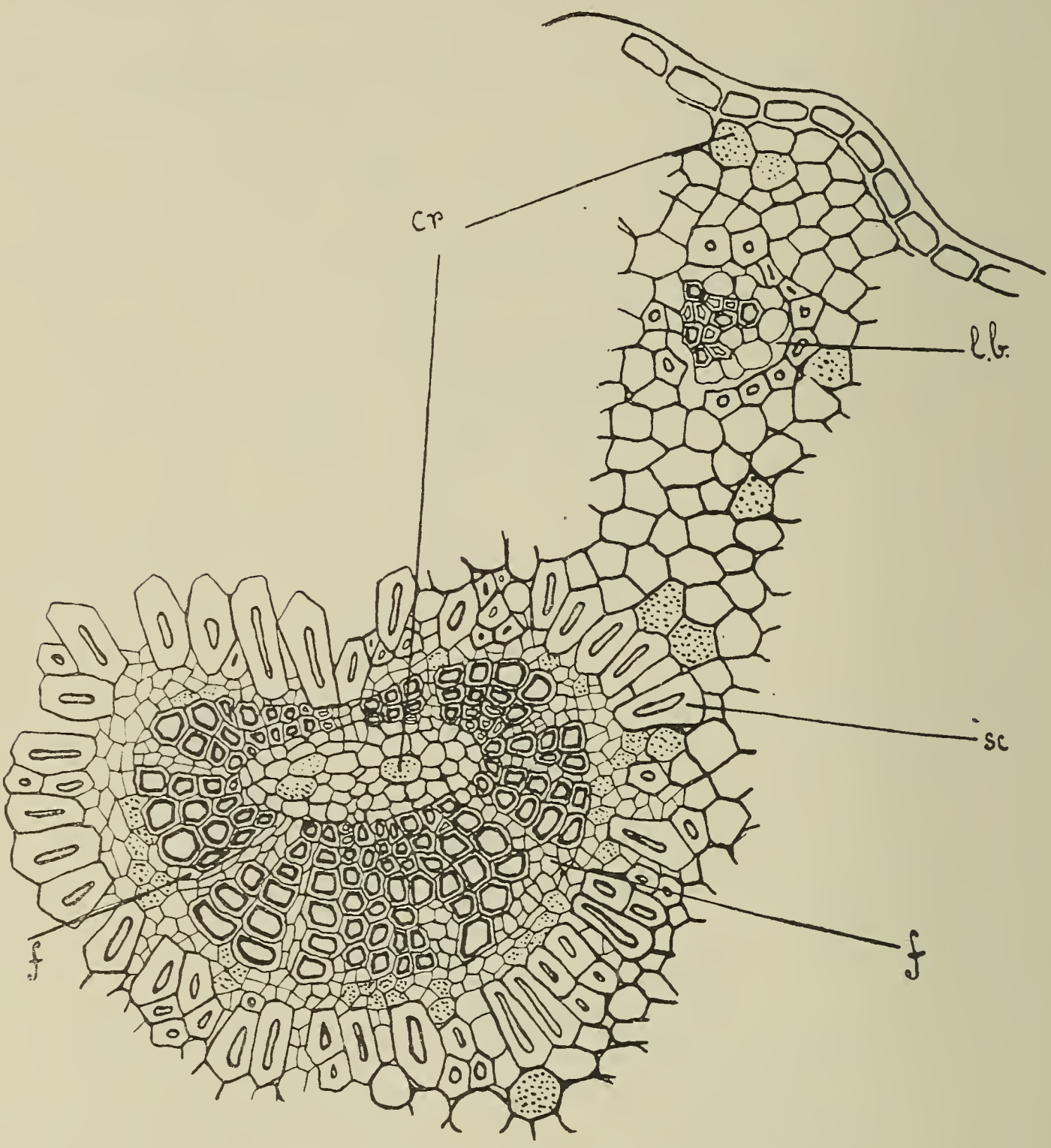

Fig. 4. *Canephora madagascariensis.*

Portion of petiole in transverse section, shewing the main vascular strand and one of the lateral strands (*l. b.*). *Sc.* fibres of the sheath; *f.* fans of parenchyma terminating the medullary rays; *cr.* cells containing crystal-sand of calcium oxalate.

shape but smaller; all the walls are remarkably thick and lignified, and the cuticle is extremely thick.

II. Leaf. a) Petiole. The general shape and structure of the petiole is represented in Fig. 3, *a* and 4. The vascular system comprises one large median bundle, with two ventro-lateral, quite small, bundles.

The xylem of the main bundle forms an almost unbroken hollow cylinder, interrupted only by a small ventral gap which is almost completely blocked by sclerenchymatous fibres. The wood consists for the most part of secondary vessels, four to five elements broad, in regular radial arrangement. As compared with the stem, the wood in the petiole is comparatively loose in texture, being intersected by several conspicuous parenchymatous medullary rays, in some cases three to four cells broad. At one or two points these rays "fan out" (Fig. 3, *a*, 4, *f.*) into patches of parenchyma; this parenchyma has no crystal contents. There are few or no fibres in the xylem.

The central tissue in the concavity of the xylem is composed of cells rather large in section, with rather thick walls which show signs of lignification. Tannin and calcium oxalate are fairly abundant, the latter in the form, principally, of cluster-crystals; crystal-sand, displaying a strong tendency to aggregation, also occurs.

The phloem appears to be coextensive with the xylem, the periphery of which it follows as far as the edge of the gap. In some parts the phloem is four to six cells broad, consisting of sieve-tube tissue and parenchyma. Tannin and calcium oxalate of the nature already described are very abundant.

The phloem is surrounded by an almost continuous sheath of large conspicuous fibres with very thick walls (Fig. 3, *a*; 4, *sc.*), many of them being radially elongated as seen in transverse section. This petiolar sheath, and the nature of its elements, seems to be characteristic for this species.

The "concavity-tissue" is continuous through the gap with the ground tissue in which the vascular system is imbedded. This consists of thick-walled cells of varying size and shape, but there is no definite sclerenchyma. Calcium oxalate is very abundant as crystal-sand aggregated into irregular masses, with a few small true cluster-crystals. Tannin is plentiful, especially in the outer zone.

The epidermis is similar to that of the stem; but no definite hypodermis appears to be differentiated.

The lateral vascular bundles consist chiefly of xylem arranged in a fan of three or four rays of about three vessels in each ray, the narrow part of the fan being ventrally situated; one or two vessels, isolated from this main group, also appear. This xylem is associated with a small amount of parenchyma, and one or two elements which appear to be sieve-tubes, on the dorsal side. This parenchyma contains crystal-sand of calcium oxalate.

The lateral bundles are associated also with a few fibres, much of the type found in the neighbourhood of the median bundle. These are situated for the most part dorsally, and in some cases are radially elongated as seen in section.

b) Midrib (Fig. 5, *a*). A large projecting rib (*v. r.*) runs ventrally, the dorsal side being relatively flat and ungrooved.

The vascular system consists of a main bundle from which branches emerge to serve the secondary veins. The bulk of the

main bundle is occupied by a closed wood cylinder, semilunar in transverse section, with plane ventral surface. The xylem is relatively loose in texture, with regular radial arrangement on the

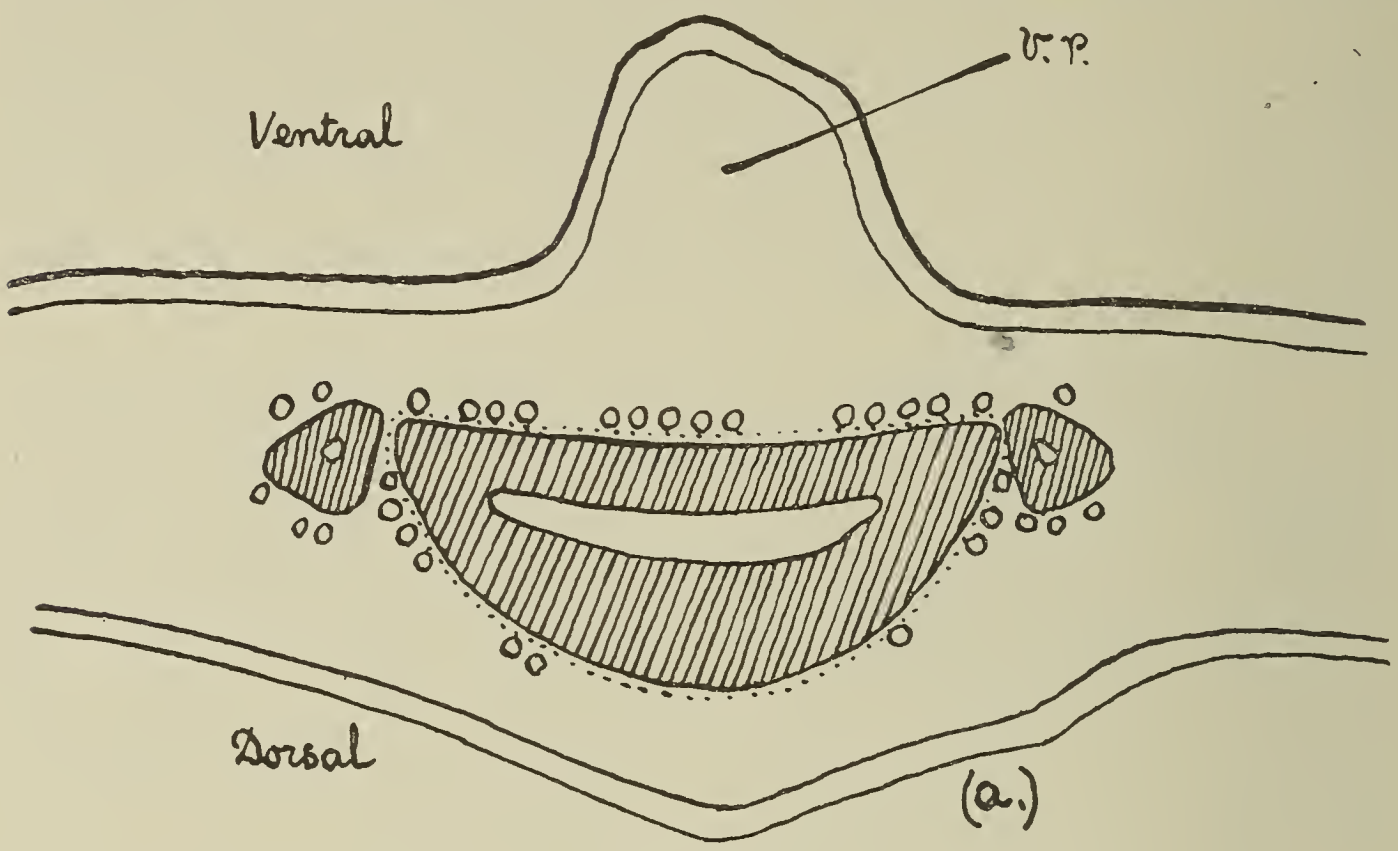

Fig. 5, *a*.

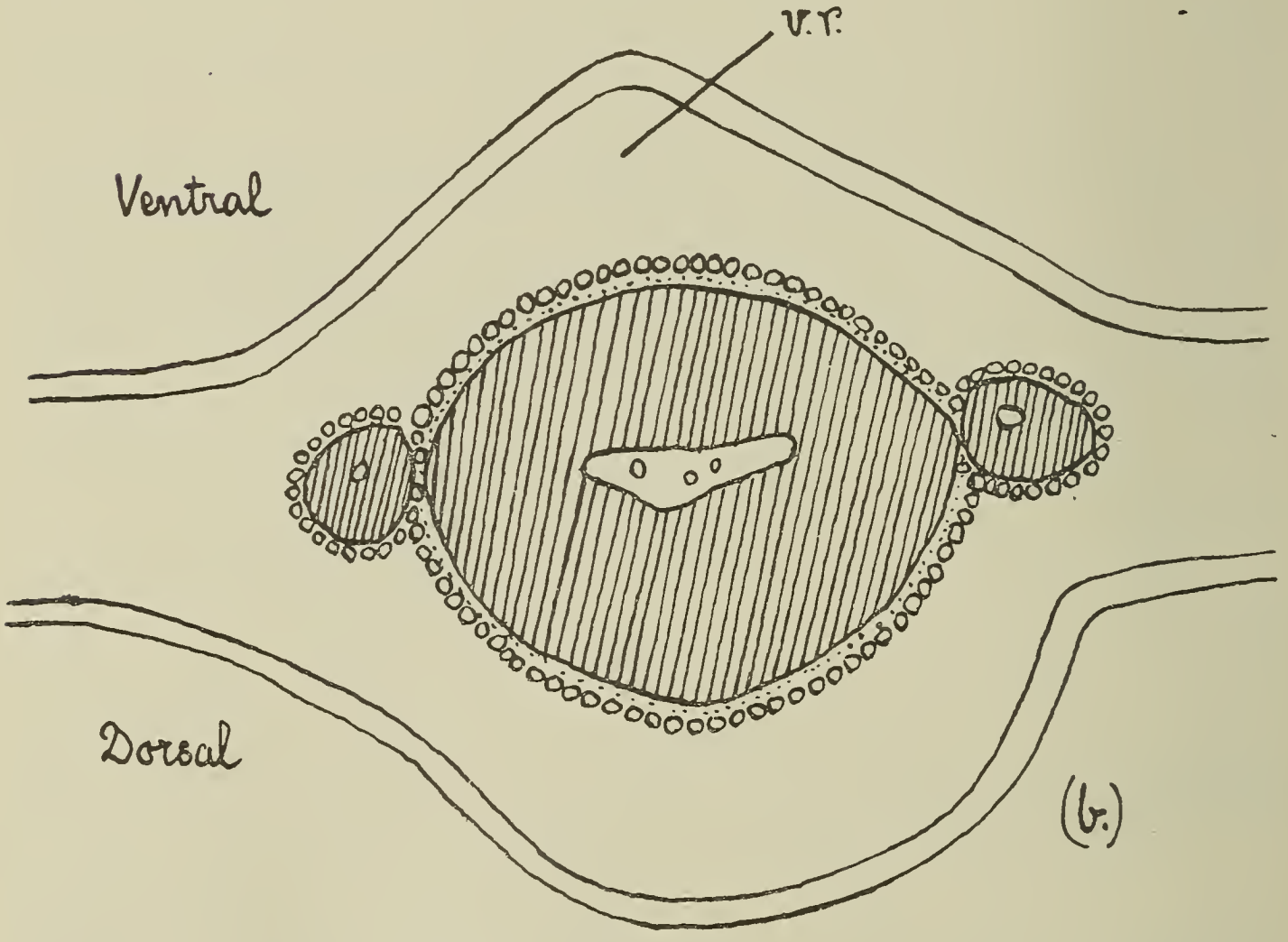

Fig. 5, *b*.

dorsal side, the ventral vessels being irregularly disposed and interspersed with one or two fibres. The vessels are comparatively large, and but three broad at most.

The phloem is of one or two layers only. These are densely packed with tannin and calcium oxalate chiefly in the form of crystal-sand. The phloem apparently surrounds the wood-cylinder almost completely. The intra-xylary tissue consists for the most part of cells with very thick walls, among which groups of thin-walled cells are interspersed, as in the stem. A certain amount of tannin and crystal-sand of calcium oxalate occurs in this tissue.

There is no continuous fibrous sheath in the midrib as in the stem and petiole. A few fibres appear here and there, associated with the main bundle, principally on the ventral side where they form a broken series.

The extra-stelar ground tissue is of more or less large parenchymatous cells, many with relatively thin walls. A number of thick-walled elements also appear, especially in the neighbourhood

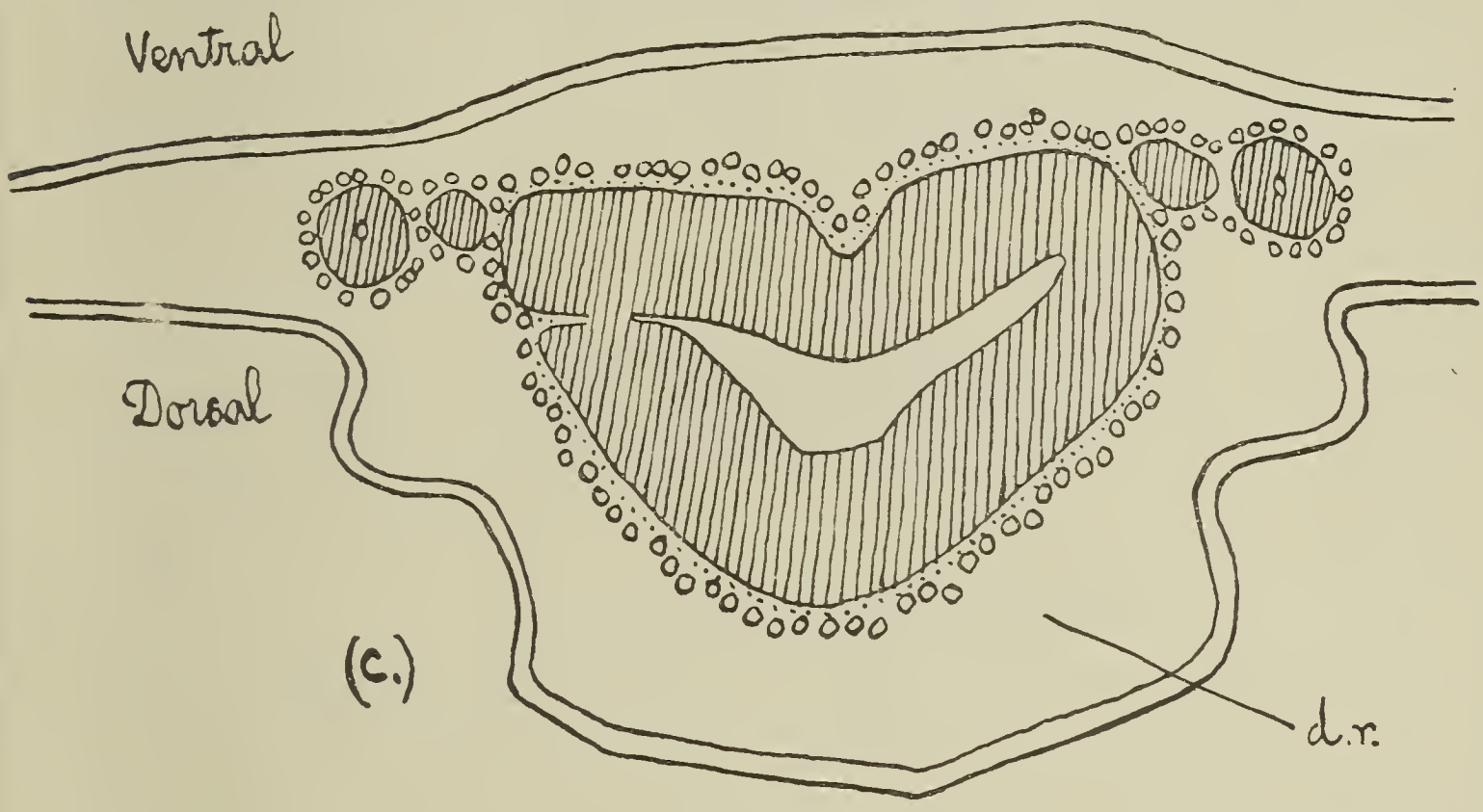

Fig. 5, *c*.

Fig. 5. Diagrams of leaf-midrib in (*a*) *Canephora madagascariensis*, (*b*) *C. angustifolia*, (*c*) *C. Goudotii*, in transverse section.
V. r. ventral rib; *d. r.* dorsal rib; other signs as in Fig. 3.

of the bundle, where they doubtless take the place of a more definite fibrous sheath; the latter we shall meet in the case of the other two species. No definite sclerenchymatous fibrous tissue is present in the ground tissue. Tannin is abundant in this ground tissue, especially in the ventral rib. Crystal-sand of calcium oxalate, more or less loosely aggregated, is fairly plentiful.

The epidermis on both sides is similar to that of the stem, but the cuticle is even thicker.

c) Lamina. (Fig. 6, *a*.) The leaf is relatively thick. The palisade is clearly differentiated from the "spongy" tissue, but the lacunar system in the latter is but feebly developed.

A single row of fibre-bundles appears at frequent intervals in transverse section running in different directions in the interior

of the leaf; the fibres have sometimes comparatively large lumina. Relatively few vascular bundles are to be seen in section in the

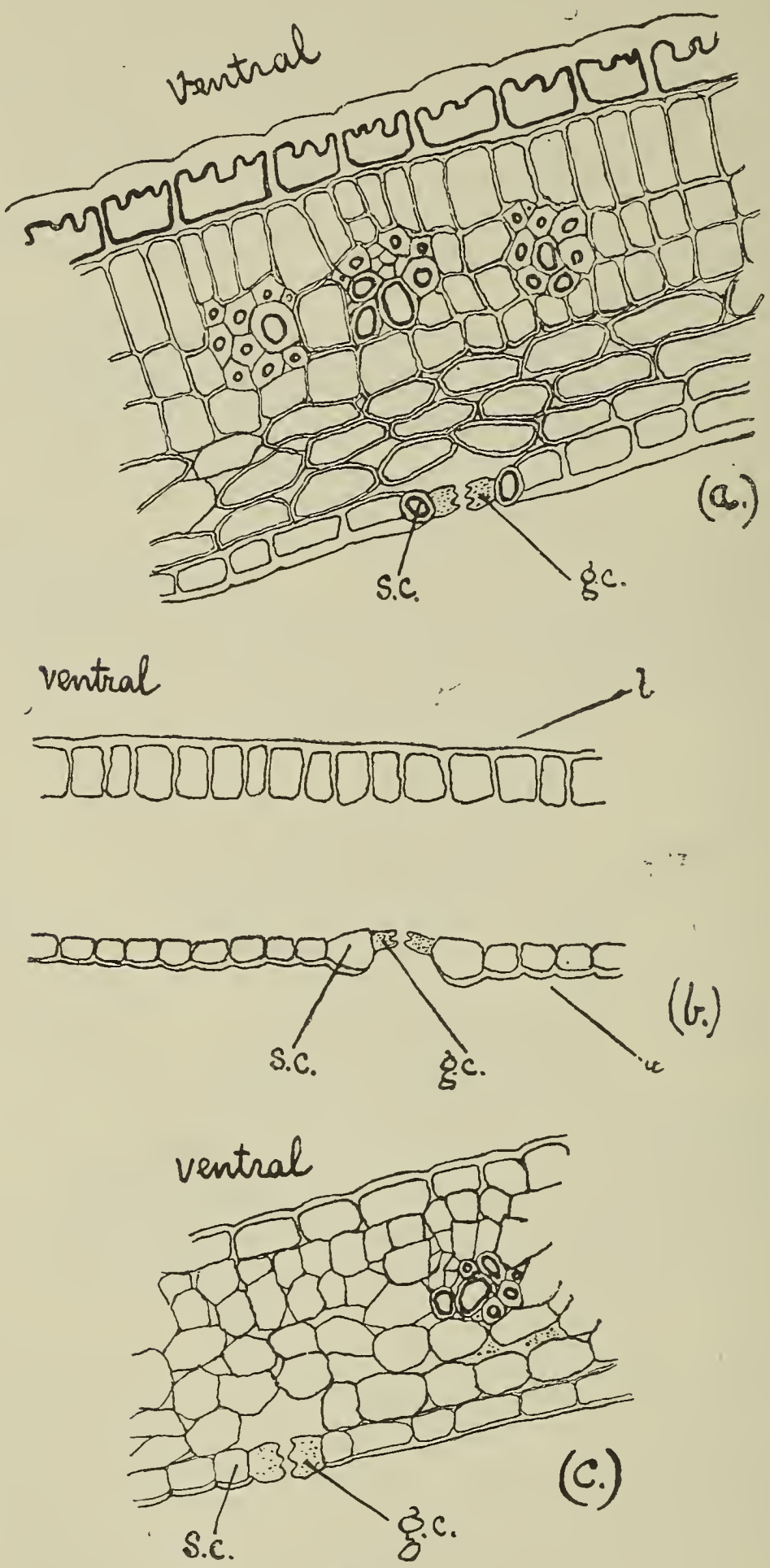

Fig. 6.

Portions of leaf lamina of (*a*) *Canephora madagascariensis*, (*b*) *C. angustifolia* (*c*) *C. Goudotii*, in transverse section, each shewing a stoma.

G. c. guard-cell; *S. c.* subsidiary cell; other signs as in Fig. 3.

blade; these comprise two or three vessels associated with a few phloem elements and fibres.

The parenchyma is generally rather thick-walled. The palisade tissue consists of about three layers, the upper of cells elongated perpendicularly to the surface, the lower of one to two layers of closely packed square cells.

Tannin is especially abundant in the palisade tissue. The "spongy" parenchyma comprises rather large cells, which appear flattened parallel to the surface. Tannin occurs in this region, but not so abundantly as in the ventral portion of the leaf. Calcium oxalate occurs chiefly in the upper layers of the spongy tissue; it takes the form principally of small aggregations of crystal-sand, but a few minute cluster-crystals are to be seen.

The upper epidermis is of rather large thick-walled brick-like cells with extremely thick cuticle, the inner surface of which is corrugated into irregular folds. There appear to be no stomata upon the ventral surface. The lower epidermis differs from the upper in consisting of smaller, flatter cells, with cuticle less strongly developed. A few stomata are visible. The guard-cells are relatively large and are not at all sunk; each is associated with a spheroidal

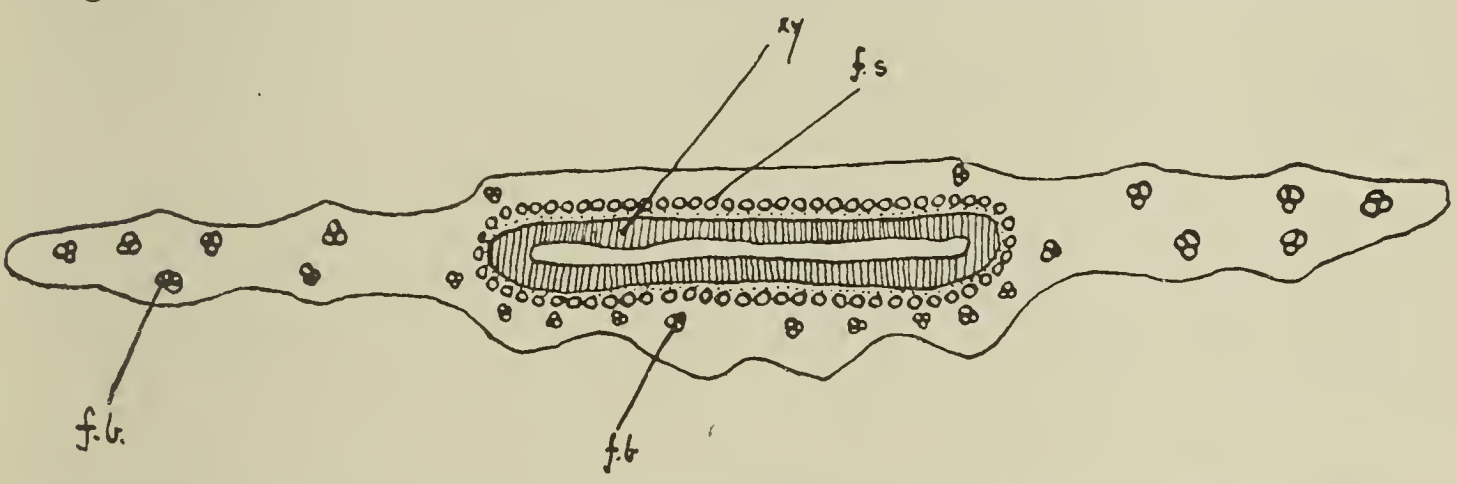

Fig. 7. *Canephora madagascariensis*. Diagramm of transverse section taken near the middle of the inflorescence peduncle.
F. s. fibrous sheath; *f. b.* fibrous strands; other signs as in Fig. 3.

auxiliary cell with rather strongly lignified walls. The stomata, we shall find, are characteristic for each of the three species under description.

III. Peduncle. The shape of the transverse section, shown in Fig. 7, offers a certain suggestion of dorsiventrality, although the organ in question presents its edge to the mother axis, at least so far as can be judged from the dried and pressed material; one surface of the swollen central portion is comparatively even, and the other folded and irregular. This suggestion, we shall see, is borne out to some extent by the internal structure.

The most conspicuous feature in the section is the flattened vascular bundle which traverses the central region. The bulk of this bundle consists of a wood-band, completely closed, the breadth being occupied by three or four xylem elements arranged in a more or less regular radial manner. The narrow space enclosed by this band is filled with large, rather thin-walled parenchyma, containing a certain amount of tannin, but no calcium oxalate.

Externally the xylem is surrounded by a practically continuous

sheath of one to two layers of small fibres; these display a nature and arrangement similar to the corresponding elements in the stem. Between this and the xylem appears a very narrow band of perished tissue which may be phloem; this contains tannin, but no calcium oxalate.

The external ground tissue, which is of limited extent, consists of large thin-walled cells resembling those of the intra-xylary parenchyma. Along the outside of one surface of the vascular bundle, and at a short distance in the ground tissue from it, about ten bundles of fibres run, at approximately equal intervals from each other; on the outer side only two fibrous bundles appear, and these are placed towards the extremities of the bundle-section. This appears to be the only anatomical indication of the dorsiventrality referred to above; we shall return to this point in the summary.

The "wings" of the peduncle show no differentiation into a ventral and dorsal surface. Both surfaces are uneven (see Fig. 7). The ground tissue is of thick-walled parenchyma, and is traversed by several fibrous bundles, irregularly disposed at frequent intervals. These bundles are vascular in some cases, including a few vessels, sometimes associated with small-celled parenchyma with thin walls.

The epidermis is the same on both sides; the cuticle is very thick, and no stomata are to be seen. Tannin is abundant throughout the peduncle, but calcium oxalate appears to be confined to the wings; here it occurs as fairly large cluster-crystals, often contained in rather large sacs of lysigenous origin.

C. angustifolia Wernham.

I. Stem. As in *C. madagascariensis* the pith consists of rather large rounded cells; but the walls are thick and sclerenchymatous throughout, no thin-walled tissue appearing. The centre of the section is, however, occupied by a lacuna, and this may represent degraded thin-walled tissue as suggested in the case of *C. madagascariensis*.

The xylem is dense — perhaps not quite so dense as in the last-named species — and the vessels and fibres are of similar character and occurrence; in this case, again, the xylem passes almost insensibly into the pith. No groups of thin-walled tissue are to be seen in association with the primary xylem; but at intervals lacunae occur, including part of the primary and secondary wood. In some cases loose sections of xylem vessels appear in these lacunae, in a manner recalling the carinal cavities of *Equisetum*. These lacunae may not impossibly represent degraded xylem-parenchyma, or at any rate degraded soft tissue analogous to that observed in *C. madagascariensis* (supra, p. 457).

A few medullary rays, each of a single layer of rather narrow cells often infiltrated with tannin, traverse the xylem ring.

The phloem consists of two or three layers, for the most part, apparently, of sieve-tube tissue. This is rich in tannin, and calcium

oxalate is very abundant, taking the form of crystal-sand and small cluster-crystals.

The phloem is surrounded by a sheath of fibres with extremely thick walls and lumina almost obliterated. This sheath is not so regularly continuous as in the case of *C. madagascariensis*. The constituent fibres are irregularly associated in groups, which, taken, together, form the more or less discontinuous sheath. The gaps in this sheath are, however, small, and are occupied by parenchyma; the latter, together with the fibres, appear from their position and arrangement to belong to the phloem.

The cortex is, in contrast with *C. madagascariensis*, for the most part of thick-walled lignified elements. Tannin is plentiful, especially in the outer zone. Calcium oxalate occurs as crystal-sand, with a fair number of cluster crystals, but is apparently less abundant than in *C. madagascariensis*.

The epidermis is very similar to that in the stem of the first species, except that the elements are relatively rather larger. There appears, moreover, to be no indication of the existence of a definite hypodermis.

II. Leaf. a) Petiole. The general anatomical structure is similar to that of the first species; there is a large median bundle, and two small lateral ones (Fig. 3, *b*).

The xylem-arc presents but little difference from that in the petiole of *C. madagascariensis*, but the ventral gap is broader. No parenchyma is associated with the xylem, as in the latter species. The medullary rays are filled with tannin. The phloem appears as a narrow band of sieve-tubes, which follows the periphery of the xylem as far as the edge of the gap. The cells are densely packed with calcium oxalate — crystal-sand and small clusters.

No definite sclerotic sheath surrounds the phloem as in the first species, but the cells of the ground-tissue in the region immediately external to the main bundle have very thick walls. This ground-tissue, which is continuous with the tissue in the concavity of the bundle-gap, is relatively thick-walled throughout. Calcium oxalate and tannin both occur abundantly, the latter especially in the outer, sub-epidermal layers.

The epidermis presents no critical differences from that in *C. madagascariensis;* there is no definite hypodermis.

Each of the small lateral bundles consists of about fifteen xylem vessels, more or less separated into two groups, associated with very little phloem. Fibrous elements, nine to twelve in number, form a discontinuous arc on the dorsal side.

b) Midrib (Fig. 5, *b*). There is a ventral rib, triangular in transverse section, with apical angle of about 120°; the dorsal side is relatively flat.

The main vascular bundle consists of a closed ring of wood, completely surrounded by phloem. The xylem-ring is roughly circular in section, and is made up of vessels much smaller and much more numerous than in *C. madagascariensis* — about six vessels broad throughout. These are arranged in a regular radial manner,

and the ring is encircled by a sheath of wood fibres, from which radial lines invade the xylem. The latter is traversed by medullary rays rich in tannin.

The phloem appears as a continuous layer some two to three cells broad, and is packed with tannin and calcium oxalate in the form of crystal-sand.

The intra-xylary ground tissue consists of rather large cells of circular section, with one or two sclerenchymatous fibres. This ground tissue is thick-walled for the most part, but a few thin-walled elements also appear. Tannin and calcium oxalate are present, the latter in the form of crystal-sand, both loose and in amorphous clusters.

Immediately external to the phloem is an unbroken sclerenchymatous sheath, a single layer of small fibres with lumina obliterated as the result of the thickness of the walls.

The extra-stelar ground tissue is of uniform parenchyma consisting of rather small thick-walled cells. There is a good deal of crystal-sand of calcium oxalate in this tissue, especially in the neighbourhood of the vascular bundle; this displays a strong tendency to aggregation into clusters. Tannin is somewhat scarce except in the ventral sub-epidermal region.

The epidermis on the ventral side is distinct from that on the dorsal. The former is composed of large cells, elongated perpendicularly to the surface as seen in section, and with thick cuticle. The dorsal epidermis consists of relatively small cells with roughly circular lumina. No hypodermis is differentiated.

c) Lamina (Fig. 6, *b*). Like that of the previous species, the leaf is of a distinctly thick type; the nature and arrangement of the tissues is essentially similar, and the parenchyma is thick-walled. Tannin abounds, especially in the palisade tissue, and also in the region underlying the dorsal surface. Calcium oxalate, in the form of crystal-sand aggregations and minute clusters, is more abundant than in *C. madagascariensis*, particularly in the interior of the leaf and in the spongy parenchyma.

The ventral epidermis consists of conspicuously large cells, square or, in some cases, elongated radially. The cuticle is not so thick as in *C. madagascariensis*. The dorsal epidermis is very distinct from the ventral, being composed of smaller, brick-like cells, with relatively thin cuticle. The small guard-cells of the stomata are appreciably sunk; each is associated with a large subsidiary cell which, apart from the cuticle, has comparatively thin walls. This type of stoma is, therefore, very different from that found in the last species.

III. Peduncle. This is essentially similar in anatomical structure to that of *C. madagascariensis*, with the important exception that the row of fibre-bundles which accompanies the main bundle in the inflorescence-peduncle of that species is absent in *C. angustifolia*.

C. Goudotii Wernham.

I. Stem. The pith is relatively much bulkier than in the other two species. The cells are roughly circular in section, and are thick-walled throughout; no lacunae appear, and this may indicate the absence of thin-walled tissue in the pith of the living plant, in contrast with the species dealt with above. Not much tannin is present in the pith; calcium oxalate is fairly abundant, a good deal of it appearing as crystal-sand, but mostly, perhaps, in the form of small cluster crystals.

The stem xylem is essentially similar to that of the other two species, but the primary wood is more sharply distinguished from the pith, its elements being considerably smaller. The fibres are very thick-walled and the vessels smaller in section. The wood-ring is perforated by a good many medullary rays, of the type described for *C. angustifolia*; there is no other parenchyma associated with the xylem, but a few small lacunae are to be seen in the region of the primary xylem.

The phloem consists of a narrow band almost obliterated with tannin, and containing also an abundance of crystal-sand. Immediately surrounding this is a fairly continuous fibrous sheath, as in the other species; this comprises only a single layer for the greater part of its extent.

The cortex is composed mostly of thick-walled cells. Tannin is not so conspicuous a feature of the cell-contents as in the other species, but calcium oxalate, in the form of crystal-sand and small cluster crystals, is very abundant. This is contained mostly in cells which appear to be larger than their neighbours, and in some cases definite sacs, formed apparently from two or three cells, are receptacles for an abundance of calcium oxalate.

The epidermis displays no distinctive features; no hypodermis appears to be differentiated.

II. Leaf. a) Petiole. This, unlike the two already described, is approximately circular in section (Fig. 3, *c*). The vascular system consists, as in the previous species, of one large median bundle and two lateral small ones. The extremities of the former are involute, and are separated by a relatively broad gap.

The xylem of the median bundle is dense, consisting entirely of vessels, which are traversed by narrow medullary rays infiltrated with tannin. The phloem appears to be composed almost entirely of sieve-tube tissue, appearing as a two to four-layered band extending continuously round the wood ring as far as the edges of the gap; this tissue is packed with crystal-sand of calcium oxalate. At several points the phloem "invades" the xylem.

As in *C. angustifolia,* no definite fibrous sheath surrounds the phloem; a few large fibres, isolated for the most part, appear in the neighbourhood of the gap.

The gap is in reality but one cell-layer broad, its relatively great width being due to the large size of the lumina of the cells composing this layer. The tissue in the concavity of the bundle

is similar to the external ground-tissue; the cells are more or less circular in section, with rather thick walls. There is, however, no special thickening of the cell-walls in the neighbourhood of the median bundle, such as we have observed in *C. angustifolia*. Calcium oxalate is abundant throughout the parenchymatous tissue; its mode of occurrence is essentially similar to that in the last-named species. There is a marked tendency for the crystal-sand to become aggregated, and a few quite large cluster crystals occur. Tannin is not very plentiful; most of it appears in a sub-epidermal band of four or five cell-layers.

The epidermis presents no special features, except that the cuticle is appreciably thinner than in the previous species.

The lateral bundles consist each of some fifteen to twenty vessels, with but little associated parenchyma. This group, moreover, is surrounded by a discontinuous set of large fibres, disposed more or less regularly.

b) Midrib (Fig. 5, *c*). The shape in transverse section is distinctive; as compared with the other species the ventral side is flat, approximately flush with the lamina. Dorsally the section presents a very prominent rib, of furrowed and folded outline.

The main vascular bundle occupies the greater part of the sectional area. The xylem forms a broad ring, the secondary elements presenting a regular radial arrangement and extending over about one half of the breadth; the primary wood is a conspicuous feature in the midrib of this species. The vessels are small and much more numerous than in either of the other two species, the xylem-band being from ten to twelve vessels broad. The fibrous system of the wood is similar to that of *C. angustifolia*, but there are more fibres towards the inner side of the ring than in that species, particularly in the ventral region. The medullary rays are very few in number, and impregnated with tannin.

The phloem is represented by a narrow band, densely packed with tannin; calcium oxalate also abounds, in the form of aggregations of crystal sand. The intra-xylary ground parenchyma consists of a few very large cells with thin walls; neither tannin nor calcium oxalate is plentiful in this tissue — the latter occurring in small sand-masses. The same applies to the extra-stelar ground tissue, except that the cells are not so large; here the tannin is confined for the most part to one or two layers immediately subjacent to the epidermis. The main bundle, and the branch bundles also, are surrounded each by a well-marked sclerotic sheath of one layer of small fibres; these are rather loosely arranged.

The upper and lower epidermal surfaces are similar, of small square cells, much as in *C. madagascariensis;* the cuticle is, however, relatively thin.

c) Lamina (Fig. 6, *c*). The blade may be described as submembranous, being of a thinner type than in the other two species described. Palisade and spongy tissue are not clearly differentiated; the former comprises two or three layers of cells rather smaller and richer in tannin than the underlying layers. The cell-walls

are thin; and the lacunar system is more extensive than in either *C. madagascariensis* or *C. angustifolia*.

Calcium oxalate is only fairly abundant in the lamina, but it takes the form frequently of relatively large cluster-crystals.

The central line of the transverse section is occupied by a row of vascular bundles, as in the other two species; but these are appreciably smaller, and associated with fewer fibres.

The ventral epidermis is composed of cells distinctly larger than those of the dorsal. In both, the cells are brick-shaped, with narrower ones interspersed. The cuticles are relatively thin.

The stomata are much more numerous than in the other species, as one would reasonably expect in view of the relatively mesophilous nature of this leaf. The guard-cells are not at all sunk, and each is associated with a subsidiary cell slightly smaller than the ordinary epidermal cells. The cell-walls are invariably thin in every case.

III. Peduncle. Unfortunately no material is available at present for the purpose of anatomical investigation.

Summary.

A. Characters peculiar to each species.

Each species appears to possess several anatomical characters which distinguish it from the other two; these are summarised below. How far these characters may be constant is a question which can be decided only by further investigation with more plentiful material. Taken collectively, however, the characters should at least serve to uphold the position as true species of the three forms described, thus maintaining the conclusions based upon external features.

C. madagascariensis. I. Stem. The pith contains groups of thin-walled cells. The primary xylem is associated with patches of thin-walled parenchyma, which may be xylem-parenchyma. The xylem is particularly dense, and there are no definite medullary rays. A regular and continuous sclerotic sheath immediately surrounds the phloem. The cortex is relatively thin-walled throughout. A definite hypodermis, very rich in tannin, is differentiated. Calcium oxalate is, generally, less plentiful than in the stems of the other two species.

II. Leaf. a) Petiole. The xylem of the main bundle forms an almost continuous cylinder, the ventral gap being extremely narrow. "Xylem-parenchyma" occurs at one or two points on the ring, each group passing into one of the medullary rays. The latter are conspicuous and numerous, each being some three or four cells broad.

The phloem is in some parts from four to six cells broad. A very definite and continuous sclerotic sheath surrounds the main bundle; the constituent fibres are very large, and often radially elongated in transverse section. The xylem-gap is almost completely blocked by two or three of these fibres.

b) Midrib. The main vascular bundle is shaped like the segment of a circle, with flat ventral side. No definite fibrous sheath surrounds the bundle. The xylem is somewhat loose in texture, and the ring is at most only three vessels broad; the vessels are relatively large. On the ventral side the wood is irregularly arranged, on the dorsal side it is disposed radially. There are very few fibres in the xylem.

c) Lamina. The cuticles are remarkably thick, and the inner side of the wall is irregularly wrinkled and folded. Calcium oxalate occurs chiefly in the form of crystal-sand. The stomata are not at all sunk; each of the rather large guard-cells is associated with a rounded subsidiary cell with lignified walls.

III. Peduncle. A row of fibrous bundles runs parallel with one of the flat sides of the main bundle, at a short distance from it, in the cortex.

C. angustifolia I. Stem. Calcium oxalate is of rare occurrence in the pith, and is not very abundant in the cortex. The primary xylem is associated with lacunae, which may represent degraded parenchymatous tissue.

II. Leaf. No definite sclerenchymatous sheath surrounds the main vascular bundle of the petiole, but the walls of the ground-parenchyma cells in the neighbourhood of the bundle are thickened and lignified. The wood of the main midrib-bundle is about six cells broad. The ground-tissue in the midrib is thick-walled throughout. In both midrib and lamina the ventral epidermis is readily distinguishable from the dorsal, the former consisting of relatively large cells of rectangular section, often elongated perpendicularly to the leaf-surface, while the latter is composed of much smaller cells which appear rounded in section. Calcium oxalate appears mostly as minute cluster crystals. The guard-cells of the stomata are quite small and sunk; each is more or less overarched by a large subsidiary cell with lignified walls.

C. Goudotii. I. Stem. The pith is conspicuously larger than that of the other two species, and it is not lacunar. The xylem is sharply defined from the pith. Calcium oxalate occurs in the stem mostly as small cluster crystals.

II. Leaf. a) Petiole. This is roughly circular in transverse section; the extremities of the median vascular bundle are involute. The phloem tends to invade the xylem at a few points. There is no fibrous sheath as in

C. madagascariensis, nor are the walls of the extra-stelar parenchyma-cells specially thickened near this bundle as in *C. angustifolia*. Tannin is not remarkably plentiful; a few large cluster-crystals of calcium oxalate are to be seen.

b) Midrib. The shape in transverse section is distinctive; the ventral surface is approximately flat, and there is a prominent dorsal rib. The primary xylem forms a broad band, and the wood-ring is ten to twelve vessels broad. The concavity of the bundle is occupied by a few thin-walled cells with large lumina, and the ground tissue generally is of thin-walled, relatively large cells.

c) Lamina. The leaf is comparatively thin, of a more or less mesophilous type; palisade and spongy tissue are not clearly differentiated, but the lacunar system is rela, tively well-developed. The vascular bundles are small-with few fibres. Fairly large cluster-crystals of calcium oxalate are common. The stomata are not sunk; the guard-cells are flattened parallel with the leaf surface, and each is adjacent to a small subsidiary cell with thin walls.

B. Anatomical Characters of the genus.

These are, as is to expected from the general external habit of these plants, of a nature usually associated with xerophily. Thus, the parenchyma is for the most part of thick-walled elements; the intercellular space-system is inconspicuous, even in the leaves where the lacunae are but feebly developed; the epidermis in all parts is provided with a remarkably thick cuticle; the fibres everywhere have exceptionally thick walls, with lumina almost or quite obliterated; the xylem vessels, too, are small as seen in section, and have small lumina.

A more or less continuous sclerenchymatous sheath, not improbably of phloem-fibres, occurs immediately external to the phloem of the stem, comprising a single layer for the greater part of its circumference; no other definite stereom is present.

The petiole is traversed by three vascular bundles—one large median strand and two quite small lateral ones; the main bundle is cylindrical and hollow, the continuity of the cylinder being interrupted by a narrow gap on the ventral side. The main bundle of the midrib consists of a continuous cylinder of xylem surrounded by phloem.

The leaf-blade is comparatively thick in all the species examined, although *C. Goudotii* shows some leaning to a thinner type. The guard-cells of the stomata are always associated each with a subsidiary cell placed

parallel to the pore and so the stomata conform to the so-called "Rubiaceous" type.[1])

The peduncle of the inflorescence is invariably borne in the axil of a leaf (see fig. 1), and so must be regarded morphologically as a stem-structure; this estimate of its nature is borne out by the fact that the main bundle is a completely-closed cylinder. The faint suggestion of dorsi-ventrality, both internally and externally, is curious (supra, p. 463).

As regards the cell-contents, tannin is plentiful, especially in the exterior layers (excepting, of course, the epidermis). It abounds in the phloem of all parts, and occurs throughout the ground-parenchyma, pith, and intra-stelar tissue generally, and frequently in the medullary rays. In the leaf, tannin is especially abundant in the palisade tissue.

Calcium oxalate occurs in the form either of crystal-sand or of cluster-crystals; the former, moreover, displays a marked tendency to become aggregated into amorphous masses. No raphides were observed. Crystal-sand is present generally in the ground tissue, both intra- and extra-stelar (pith, cortex etc.); it is usually very abundant in the phloem.

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[1]) v. Solereder, Systematic Anatomy of the Dicotyledons. Transl. Oxford, (Boodle and Fritsch) 1908. II. p. 1078.