

ANATOMICAL CONTRIBUTIONS TO PLANT TAXONOMY I¹).

Floral and vegetative anatomy of *Eliaea* from Madagascar and *Cratoxylum* from Indo-Malesia (Guttiferae)

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SUMMARY

The floral and vegetative anatomy of the closely allied guttiferous genera *Cratoxylum* (Indo-Malesia) and *Eliaea* (Madagascar) is described. Although the two taxa have many features in common, differences are substantial enough to recognize them as distinct genera, as appears from the following survey:

<i>Cratoxylum</i>	<i>Eliaea</i>
Ovary with 12 or more ovules	Ovary with 6(—8) ovules
Ovary with 3(or 4) incomplete true septa	Ovary with 6(or 8) incomplete septa, three being true, three false
Styles and filaments glabrous	Styles and filaments mostly villous
Secondary xylem with scarcely pitted fibres	Secondary xylem with densely pitted fibre-tracheids
Vessels solitary and in radial multiples	Vessels almost exclusively solitary
Silica bodies present in ray cells of wood	Silica bodies absent

The vascularization and insertion of the hypogynous scales in both genera favours the view that these structures may be interpreted as staminodial derivatives.

In some species of *Cratoxylum* a further differentiation into taxa of lower rank is suggested by the presence or absence of abaxial epidermal papillae on the leaves; this is related to geographical distribution.

Floral and xylem specialization of *Cratoxylum* and *Eliaea* are discussed. The xylem structure of *Eliaea* shows more primitive features than that of *Cratoxylum*, but the flowers seem to be more specialized. The possible implications of these findings for plant geography are discussed.

¹) This paper is the first of a series in which the, mainly vegetative, anatomy of dicotyledonous taxa of different ranks (families, genera, species) will be described and used to discuss their affinities. Anatomical studies on Carlemanniaceae, Dirachmaceae, Huaccaeae, Lophopyxis, Oncotheca, Phelline, and Sphenostemon are in progress.

In *Cratoxylum* the section *Isopterygium* (*C. arborescens* and *C. glaucum*) is very different in its wood anatomy from the other representatives of *Cratoxylum*. This difference (concerning parenchyma distribution) is correlated with the evergreen habit in the section *Isopterygium*. The other sections of *Cratoxylum* are deciduous. A comparison with some data from literature about other groups with deciduous and evergreen members is made.

INTRODUCTION

In his monograph of the genus *Cratoxylum* Blume (*Guttiferae, Hypericoideae, Cratoxyleae*) Gogelein (1968: 457) expressed his views on the relationship of this genus with the monotypic *Eliaea* Camb. from Madagascar: 'If I would have studied material of *Eliaea* before that genus was described, I doubt whether I would have made a separate genus of it, but would certainly have given it a distinction as a section or even subgenus close to sect. *Tridesmos*, most closest to *C. maingayi*'. He listed the distinctive characters of the two genera as follows:

<i>Cratoxylum</i>	<i>Eliaea</i>
Ovary with at least 12 ovules	Ovary with 6 ovules
Ovary incompletely 3-celled	Ovary incompletely 6-celled
Styles and filaments glabrous	Styles and filaments villous ('cottonny hairy')
Fruit with three valves, often partly caducous	Fruit with finally 6 semipersistent valves

Gogelein expressed some doubt about the true nature of the ovary of *Eliaea*, because of conflicting evidence given by Engler (1925) and Perrier de la Bâthie (1951). The former called the ovary and fruit three-celled and the latter reported in his key 'loges biovulées', which would refer to the three-celled condition, but in his generic description the ovary is said to have '6(—8) loges incomplètes uniovulées'. Gogelein himself suggested on the ground of his limited observations that the ovary of *Eliaea* possesses three true and three false, incomplete septa. He thus confirmed the original description of Cambessèdes (1830). Gogelein's plea for a further detailed study about the nature of the ovary finds its response in this paper. Moreover, a detailed study of the vegetative anatomy of both genera was undertaken in order to establish the mutual affinities with more certainty. The distribution pattern Indo-Malesia and Madagascar occurs in several plant genera (e.g. *Nepenthes*, *Allanthespermum*). A better understanding of the relationships within such groups, in order to be able to interpret this distribution pattern, is considered to be sufficiently important to justify an elaborate investigation of this kind.

Although a substantial amount of anatomical information on *Cratoxylum* and some notes on the secretory cavities in *Eliaea* have been published, a comprehensive account of the anatomy of these genera would add to our knowledge of *Guttiferae* anatomy. Accumulation of descriptive accounts of representatives of large families becomes more and more urgent, if comparative anatomists want to use their knowledge successfully in discussing the affinities of enigmatic small families.

Solereder (1899, 1908) and Metcalfe and Chalk (1950) comprehensively summarized the available information on *Hypericoideae* anatomy. Additional information on structure and applications of the timber can be found in Brazier and Franklin (1961), Chowdhury and Ghosh (1958), and Balan Menon, (1956, 1967). Schofield (1968) gave particulars on nodal and petiole anatomy. Chemotaxonomical data on *Cratoxylum* were summarized by Hegnauer (1966). Jacquemin *et al.* (1969) investigated some chemical compounds of *Eliaea*.

The anatomical descriptions in this paper were made according to a more or less standardized scheme largely following Metcalfe and Chalk's practice. Accounts of mature secondary xylem are more detailed than those of the secondary xylem of young twigs.

TECHNIQUES

For the study of the floral anatomy, series of pickled young buds and flowers, and in the case of *Eliaea* also fruits, were embedded in paraffin wax; serial sections from flower stalk to stigma were stained with auramin, safranin and astrablue according to Maáčz and Vágás (1961). In addition, other flowers and buds were cleared according to Vautier (1949) at 40° C in chloral-lactophenol to which were added some drops of 30 % hydrogen peroxide.

Leaf anatomy was studied in transverse sections through the middle of the lamina and the distal and basal part of the petiole. Epidermal characters were studied in scrapes and cuticular preparations (using a mixture of equal volumes of 20 % hydrogen peroxide and concentrated glacial acetic acid, at 60° C.)

Twig and wood anatomy were studied in transverse, radial and tangential sections. Quantitative features such as vessel member length and fibre length were measured in macerated material. The macerations were made in the same way as the cuticular preparations.

For wood elements the means are based on 25 measurements. Other means (stomatal diameter etc.) are based on 3—10 measurements. Illustrations were made using a Leitz Orthoplan microscope with drawing tube.

MATERIALS

In the following list of specimens, particulars are given about the investigations carried out on them. All material studied was derived from herbarium and wood specimens present at Leiden, unless stated otherwise. Institutional wood collections from which specimens were obtained are abbreviated according to Stern (1967). Slides for reference are available at the Rijksherbarium; duplicates of some of them have been deposited in the Kew slide collection.

Cratoxylum arborescens (Vahl) Blume. Pickled material from Kepong Arboretum (tree 253, line 5) (clearing and sectioning of flowers); Malaya, Kadim & Noor 155; Sumatra, For. Serv. bb 33096 (leaves and twigs); Borneo, S. H. SAN 25136; Fuchs 21290 and 21346 (wood samples).

C. cochinchinense (Lour.) Blume. Hongkong, Hallier s.n. (clearing of flowers); Sumatra, Alston 14359 (leaves and twigs); Borneo, Meyer SAN 25128 (wood sample).

C. formosum (Jack) Dyer ssp. *formosum*. Pickled material from Singapore Botanic Gardens (clearing and sectioning of flowers); Java, Cult. Hort. Bog. VI. C, 52a; Borneo, Buwalda 7979; Sumatra, Forbes 3298; Borneo, Meyer 53506 (leaves and twigs).

C. formosum (Jack) Dyer ssp. *pruniflorum*. Pickled material from Singapore Bot. Gardens (clearing and sectioning of flowers); Java, Cult. Hort. Bog. XV. J. A. XII. 3 (leaves and twigs).

C. formosum (Jack) Dyer. Borneo, SAN 19.6.61 (wood sample).

C. glaucum Kcrth. Borneo, Philip. Nat. Herb. 87634 (clearing of flowers); Borneo, Boschb. Proefst. bb 14411 (leaves and twigs) Boschb. Proefst. Bogor Number wood coll. 6468 (= bb 6770 of herbarium series) (wood sample ex RTIw).

C. maingayi Dyer. Singapore, Burkill HMB 2607 (clearing of flowers); Sumatra, Grashoff 991 (leaves and twigs); Malaya, WT 6732 (wood sample ex KEPw).

C. sumatranum (Jack) Blume ssp. *sumatranum*. Borneo, Darnton 577 (clearing of flowers); Java, Neth. Ind. For. Serv. bb 3939 (leaves and twigs).

C. sumatranum (Jack) Blume. Philippines, F.P.R.I., S.H. 321 (wood sample ex CLPw).

Eliaea articulata Camb. Pickled material of flowers and fruits collected by Dr. Capuron at Fort Dauphin,

Madagascar, 1967; Madagascar, d'Alleizette s.n. Aug. 1906 and Nov. 1906. Material from these 3 collections was used in clearing flowers. The first for serial sectioning. The latter two for vegetative anatomy. Madagascar, TEFw 14577 SF (wood sample ex TEFw).

RESULTS AND DISCUSSIONS

Anatomy of the flower in *Cratoxylum* (fig. 1a, 2)

The following account is based on serial sections of buds and flowers of *C. arborescens* and of *C. formosum* and on cleared material of all species of *Cratoxylum*. The arrangement of floral parts as seen in transverse section is illustrated in fig. 1a. Additional data are given below.

The hypogynous scales are inserted at the same level as the phalanges and receive several vestigial vascular bundles each from the same region of the stelar system as the phalanges. This seems to favour the view that they may be regarded as staminodial structures (cf. Engler, 1925: 183). The ovary of *Cratoxylum* is incompletely 3 (or 4) celled. The septa are fused at the very base of the gynoecium and are coherent (in *C. formosum*) or fused (in *C. arborescens*) below the styles. Placentation is axile; there are 3—18 ovules per cell (cf. Gogelein, 1968), which are attached to the placentae at the basal part of the septa in an ascendant anatropous way. Vascularization in the ovary of *Cratoxylum formosum* is shown in fig. 2. Below the loculi three major vascular bundles depart from a fragmented stelar cylinder. Each bundle branches over a very short distance (fig. 2a, b) into three bundles of which the median one forms the dorsal bundle and each of the other two bundles runs along the attachment of one of the septa ('lateral' bundles). Minor vascular bundles connected with these three carpellary bundles occur in varying numbers. The placentae are supplied with vascular bundles which are more or less linearly continuous with the stelar cylinder. Some vascular tissue extends to above the level of ovule insertion.

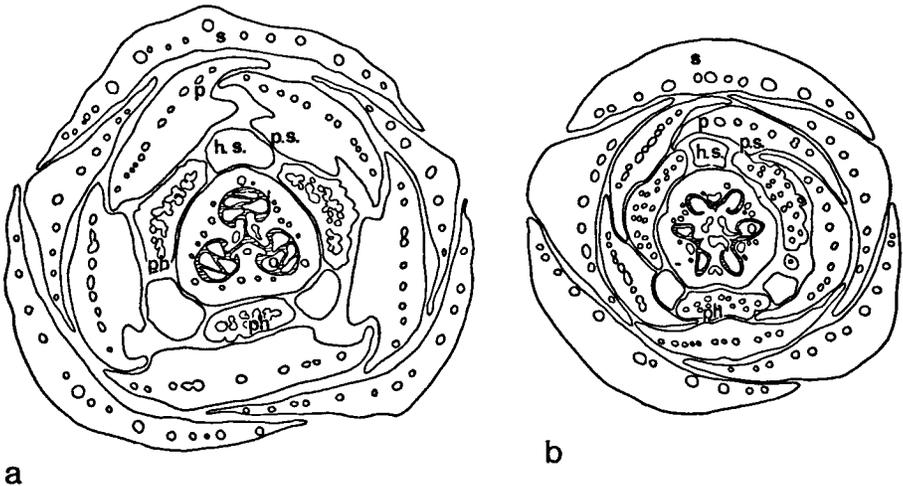


Fig. 1. Transverse sections through flower buds. a. *Cratoxylum formosum*, $\times 12$. b. *Eliaea articulata*, $\times 12$. h.s.: hypogynous scale; o: ovule; p: petal; p.s.: petal scale; ph: phalange; s: sepal. Loculi shaded; vascular bundles indicated where present.

The orientation of vascular bundles was very difficult to determine because of the very low number of differentiated xylem elements before and at the flowering stage. In those cases where orientation could be observed all peripheral vascular bundles (dorsal and lateral bundles plus derivatives) were found to have normal arrangement with xylem poles facing the loculi. In the placental vascular supply the situation is much more complicated and is obscured because there is no distinct boundary between the individual vascular bundles. In *C. arborescens* the bundles were found to be centric (amphicribal) above the level of ovule attachment. In the same species some minor vascular bundles with their xylem poles facing the axis of the ovary were observed running as a median line through the septa. These bundles, not found in the other species, are derived from the vascular system of the placentae. The course of vascular bundles was hardly observable in cleared material due to the scanty presence of differentiated xylem elements. The fusion of lateral vascular bundles from different carpels opposite the septa could be observed only in *C. maingayi*, but not in the other species. The dorsal and lateral bundles enter the styles. The dorsal bundles continue up to the stigmas where they branch profusely.

Secretory cavities and canals are abundant in the periphery of the ovary wall and occur also in the style. They are also abundantly present in the sepals, occur in various numbers in the petals (cf. Gogelein 1968), but are absent or very rare in the androecium (apart from special connective glands in *C. formosum* ssp. *pruniflorum*).

Anatomy of the flower in *Eliaea* (fig. 1b, 3)

The arrangement of floral parts in *Eliaea* is identical to that of *Cratoxylum* apart from some details in the gynoecium (see fig. 1b) Fig. 3 gives a series of transverse sections for comparison with those of *Cratoxylum*. The ovary is also incompletely 3 (or 4) celled, although the distance over which the septa are free is very short. There are three conspicuous false septa, composed of a bulky parenchymatous tissue situated abaxially to the dorsal vascular bundle. These septa give a superficial impression of the presence of 6(—8) loculi instead of the 3 (or 4) actually present. There are 6(—8) ovules in one ovary. As in *Cratoxylum* they are attached to the placentae at the basal part of the septa in an ascendant anatropous way. The vascularization of the ovary in *Eliaea* is fundamentally similar to that of *Cratoxylum*. There are some minor differences, however. The stelar cylinder is not broken up just below the level of insertion of carpellary bundles as in *Cratoxylum arborescens* and *formosum*. The lateral vascular bundles of two carpels are fused over some distance (see fig. 3d—f) in the distal part of the ovary. The vascular strands in the placentae appear to be double or centric above the level of ovule attachment (see fig. 3e). The lateral carpellary bundles do not continue into the styles. The dorsal bundles branch just below the stigmas. The distribution of secretory canals is similar to that in *Cratoxylum*.

Spherical glands (1 for each stamen) occur in the distal end of the connectives of the stamens. These are similar in structure to the two connective glands found in each stamen of *C. formosum* ssp. *pruniflorum* (cf. Gogelein, 1968, fig. 5k).

The vascularization of the hypogynous scales and the presence of petal scales in the corolla of *Eliaea* are among the other characters shared with *Cratoxylum*.

Vegetative Anatomy of *Cratoxylum*

Leaf (fig. 4d—k)

IN SURFACE VIEW: *Adaxial epidermis* glabrous in all material apart from *C. formosum* ssp. *pruniflorum*. Cells polygonal in outline with curved to straight anticlinal walls.

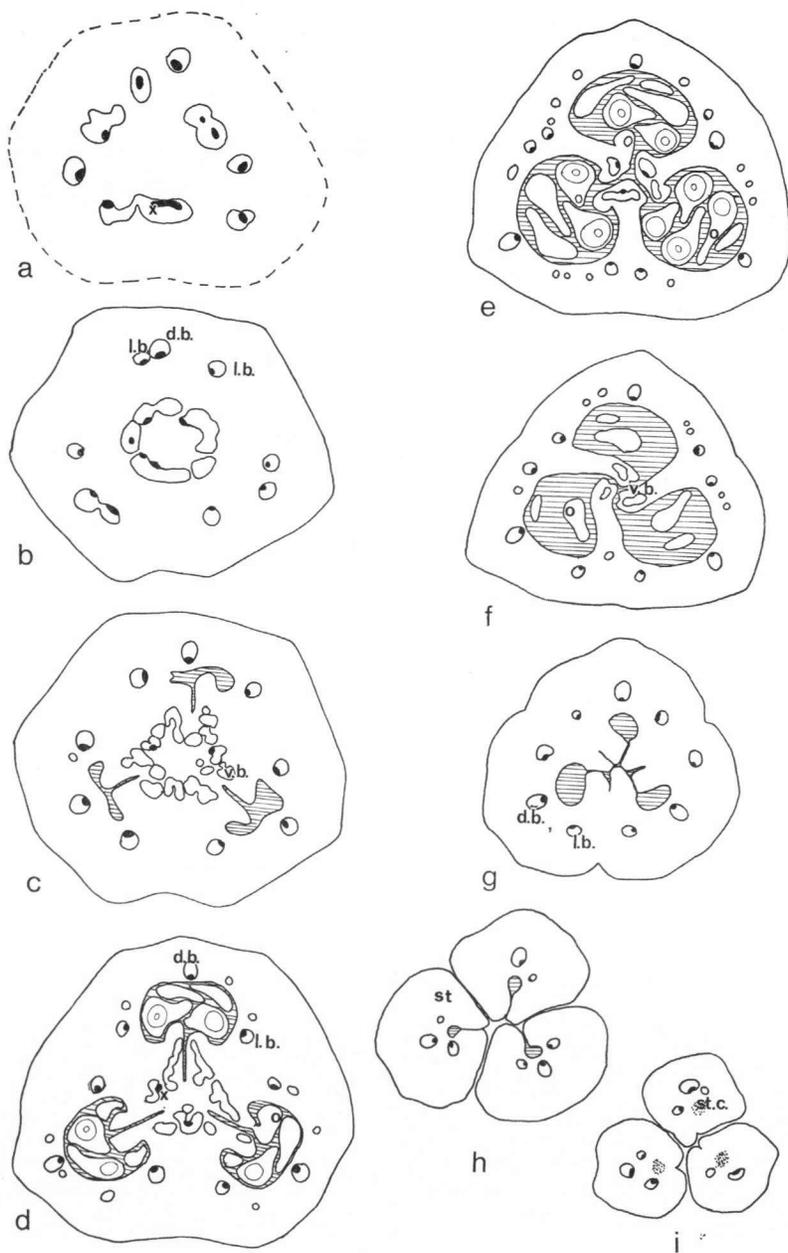


Fig. 2. Some transverse sections through the gynoecium of a flower of *Cratoxylum formosum* ssp. *formosum*, from bottom (a) to top; all $\times 29$. a. Vascular supply of central part of receptacle. b—i. Sections through ovary and styles. *d.b.*: dorsal bundle; *l.b.*: lateral bundle; *o*: ovule; *st*: style; *st.c.*: style canal; *v.b.*: vascular bundle; *x*: differentiated xylem element(s) (solid black). Loculi shaded.

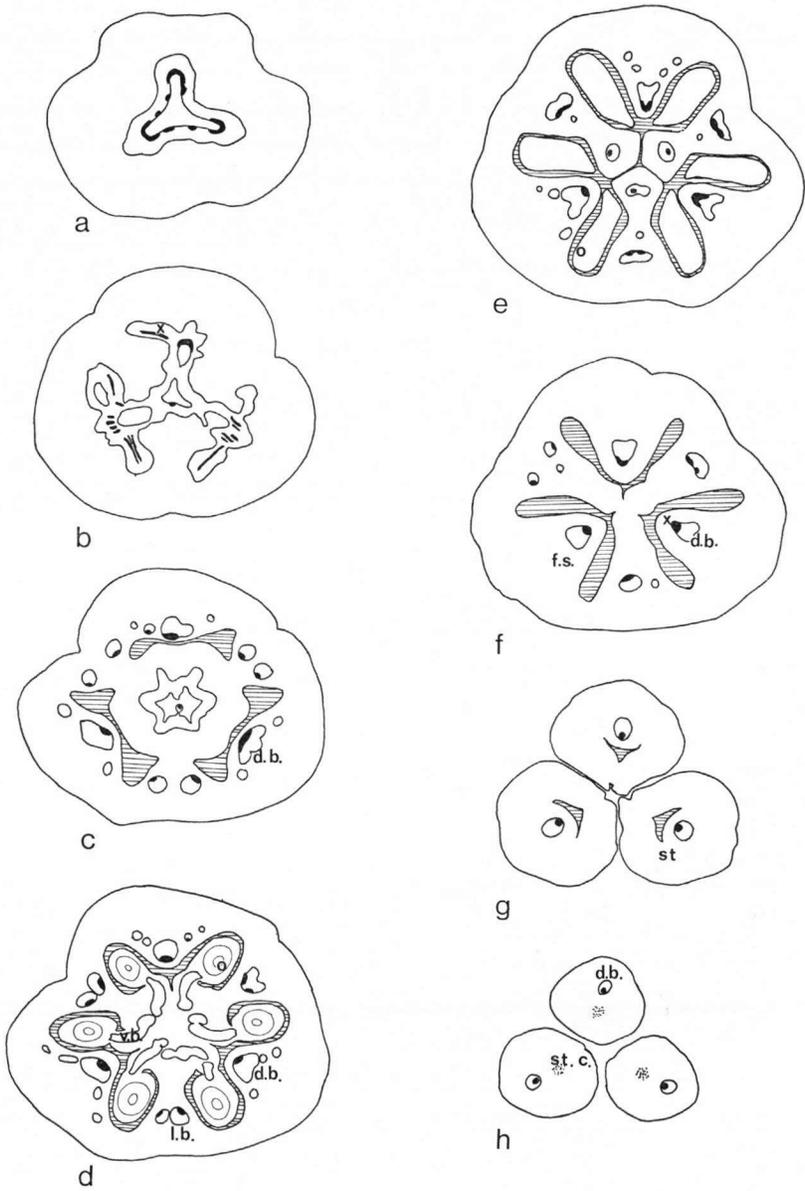


Fig. 3. Some transverse sections through the gynoecium of a flower of *Eliaea articulata* from bottom (a) to top; all $\times 29$. For legends see Fig. 2. *f.s.*: false septum.

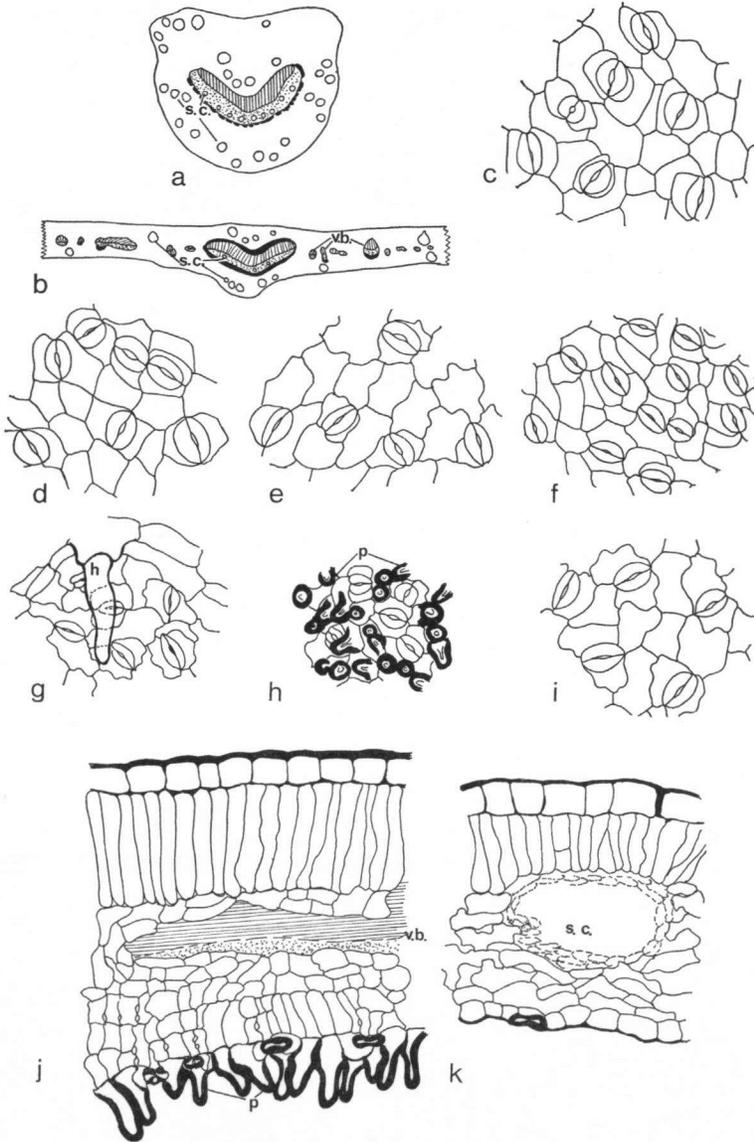


Fig. 4. Leaf anatomy of *Eliaea* and *Cratoxylum*. a—c. *Eliaea articulata* a. petiole through distal end, $\times 12$. b. lamina through midrib, $\times 12$. c. abaxial epidermis, $\times 200$. d. *C. sumatranum*, abaxial epidermis, $\times 200$. e. *C. maingayi*, abaxial epidermis, $\times 200$. f. *C. arborescens*, abaxial epidermis, $\times 200$. g. *C. formosum* ssp. *pruniflorum*, abaxial epidermis, $\times 200$. h. *C. formosum* ssp. *formosum*, Cult. Hort. Bog., abaxial epidermis, $\times 200$. i. *C. formosum* ssp. *formosum*, Buwalda 7979, abaxial epidermis, $\times 200$. j. *C. formosum* ssp. *formosum*, Cult. Hort. Bog., lamina, transverse section, $\times 200$. k. *ibid.*, Buwalda 7979. h: hair; p: papillae; s.c.: secretory cavity or canal; v.b.: vascular bundle. Xylem shaded; phloem dotted; sclerenchyma in a and b solid black.

Abaxial epidermis with indumentum of mainly uniseriate *hairs* with broad basal cells present in *C. formosum* ssp. *pruniflorum* (fig. 4g). In this sub-species hairs also infrequently present on adaxial leaf surface and low bluntly conical papillae present on abaxial surface. Tall to short \pm cylindrical *papillae* present on abaxial surface in part of the material of *C. cochinchinense*, *C. formosum* ssp. *formosum*, *C. glaucum*, *C. maingayi*, and *C. sumatranum* (see fig. 4h, j, Table III and discussion on p. 383). Papillae confined to unspecialized epidermal cells and absent from guard cells and subsidiary cells of stomata and from elongated cells overlying midrib and (if conspicuous on epidermis) major veins. Abaxial epidermis glabrous in remainder of material. Unspecialized cells polygonal in outline with almost straight to sinuous anticlinal walls (see fig. 4d—i). Cell outline often obscured by presence of papillae. *Stomata* confined to abaxial surface apart from some found on adaxial surface overlying the midrib in 1 specimen of *C. formosum* ssp. *formosum*; paracytic with low dome-shaped guard cells and subsidiary cells of various shapes. Outer anticlinal walls of subsidiary cells curved to sinous (see figs. 4d—i). Diameter of stomata perpendicular to the pore 10—20 μ (mean 14 μ); orientation random or tending to coincide with direction of major veins.

In transverse section: *Cuticle* 1—3 μ thick. *Epidermal cells* square to flattened, those of abaxial surface smaller than those of adaxial surface. *Hypodermis* (derived from protoderm and therefore representing the inner layer(s) of the multiple epidermis) of 1—3 irregularly arranged cell layers, adaxially present in *C. arborescens* and *C. glaucum*, absent from other material. *Mesophyll* composed of 1 or 2 layers of tall adaxial palisade cells; abaxial chlorenchyma cells of *C. cochinchinense* also tending to be palisade-like; in remainder of material abaxial tissue compact to fairly loose, composed of cubical to lobed or rounded chlorenchyma cells. *Leaf margins* pointed downwards to various extents. Mesophyll of margins composed of small amount of collenchyma. *Midrib* with shallow V—U shaped adaxial groove and prominently raised abaxial surface, supplied with single broadly V-shaped to crescentiform vascular strand with sclerenchymatous caps of thick walled fibres interspersed with thin-walled cells. Ground tissue of midrib collenchymatous at periphery to parenchymatous in more central parts. *Veins* with or without ad- and abaxial sclerenchyma caps. Sheath of translucent parenchyma cells present around vascular bundles and also including caps, if present. Vertical bundle sheath extensions associated with major veins present in all species apart from *C. maingayi*. *Petiole* \pm semi-circular to bean-shaped in T. S. through distal end, with concave to flat adaxial surface and convex abaxial surface. Vascular system composed of single \pm crescentiform strand, without incurved margin in material from the sections *Cratoxylum* and *Tridesmos*. 2(—4) additional latero-dorsal bundles present in the section *Isopterygium* (*C. arborescens* and *C. glaucum*). Ground tissue of petiole composed of collenchyma and thick walled parenchyma. *Crystals* present in varying amounts; druses predominant in abaxial part of mesophyll (often in cells which are larger than surrounding cells); clusters predominant in ground tissues of petiole and midrib and in mesophyll. Prismatic crystals less common. *Secretory cavities* of (sub)spherical shape, varying greatly in frequency confined to palisade or spongy part of mesophyll or present in both. In a few cases the anticlinal and/or periclinal cell walls of the epidermis thinner in places opposite secretory cavities than in remainder of epidermis. *Secretory canals* of small diameter present in phloem of midrib and petiole. Broader canals present in ground tissue of petiole and midrib. Epithelium of secretory cavities and canals badly preserved in most herbarium specimens.

Axis (twigs of c. 3—5 mm diameter; see also table I)

Epidermis, cortex and perivascular fibres caducous in all twigs which are 3 mm or more

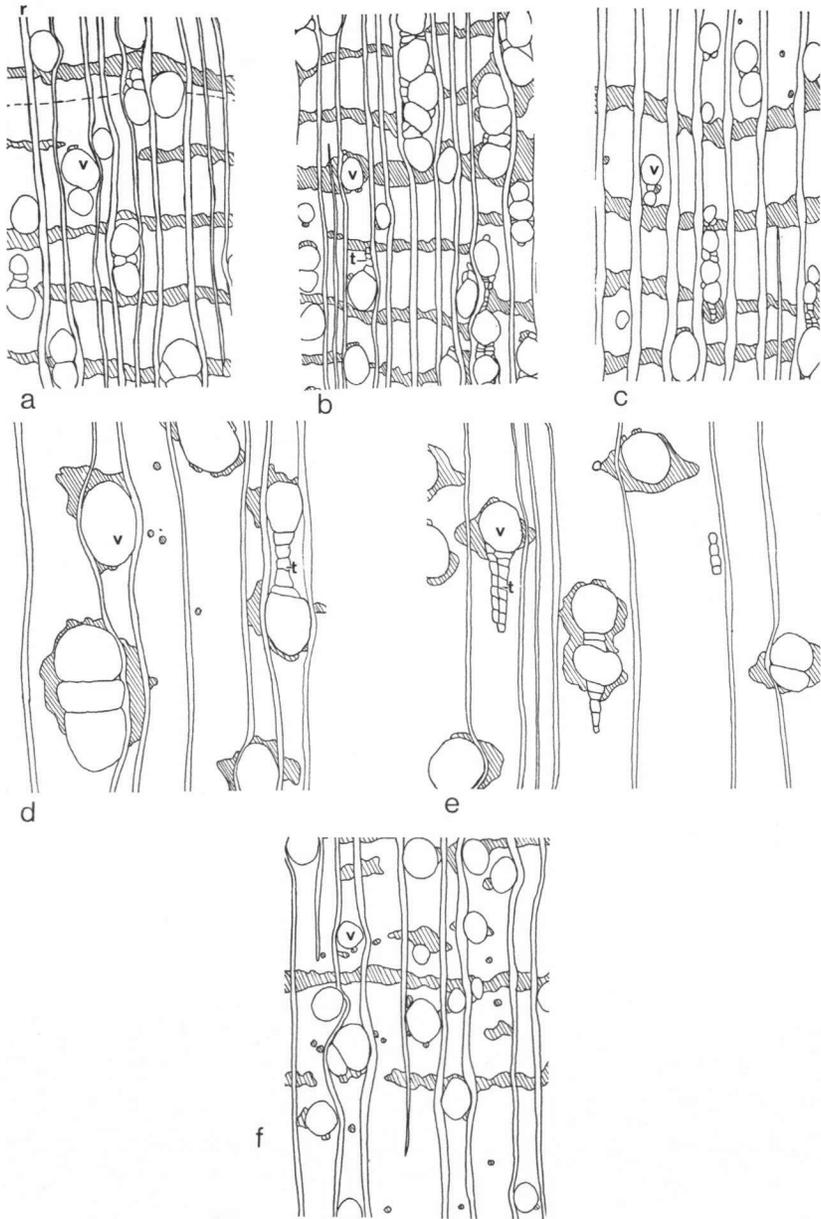


Fig. 5. Transverse sections of wood from *Cratoxylum* and *Eliaea*; all $\times 30$. — a. *C. sumatranum*. b. *C. cochinchinense*. c. *C. formosum*. d. *C. arborescens*, SAN 26136. e. *C. glaucum*. f. *Eliaea articulata*. r: ray; t: tracheid; v: vessel. Parenchyma shaded.

thick. These tissues were only seen in a very young twig of *C. arborescens*. *Cork* originating in pericycle between perivascular fibre sheath and phloem; composed of layers of approximately square to flattened cells with adaxially lignified \pm U-shaped and pitted wall thickenings; these layers are occasionally interspersed with layers of thin-walled cells. Cork cells \pm hexagonal in tangential view. Secondary *phloem* often badly preserved in herbarium specimens; composed of sieve-tubes, companion cells, parenchyma, secretory canals and rays with very slightly dilatating peripheral parts (due to tangential cell-elongation and/or the formation of an extra radial wall). Secondary *xylem*: *Growth rings* poorly defined or absent (varying intraspecifically). *Vessels* diffuse, solitary and in short oblique to radial multiples of 2 or 3 (—6); round to oval in T.S., mean tangential diameter 35—51 μ , mean vessel member length 255—365 μ . Perforations simple in the oblique to slightly oblique end walls. Lateral wall pits in transitional to alternate arrangement, small and round-oval (diameter 2—3 μ) or larger and slightly polygonal (diameter 3—4 μ). Vessel—ray pits polygonal or flattened and unilaterally compound, resulting in \pm reticulate wall pattern. *Tyloses* present in some of the specimens investigated. Solid amorphous brown *contents* present in some vessels of most specimens. *Tracheids* paratracheally arranged, very sparse to rather frequent ('vascular tracheids'). *Fibres* arranged in radial rows, constituting ground tissue of secondary xylem. Walls varying in thickness and very sparsely provided with simple to minutely bordered pits. Average fibre length 420—740 μ . *Parenchyma* present in varying amounts, predominantly in irregular, mainly apotracheal, bands in *C. cochinchinense*, *C. formosum*, *C. maingavi* and *C. sumatranum*; mainly paratracheal or confluent in *C. arborescens* and *C. glaucum*. *Rays* 15—25/mm at periphery of secondary xylem of twigs investigated, uniseriate or biseriata, (1—) 3— many cells high, heterogeneous, composed of square to upright cells. Primary xylem forming a continuous cylinder with conspicuous radial arrangement of vessels. *Node* unilacunar with a single leaf trace. *Pith* forming a flattened cylinder, composed of parenchyma cells which are rounded in T.S. and square to rectangular in L.S., interspersed with a varying number of secretory canals. *Crystals* present as clusters and prismatic types in pith. Prismatic types abundant in phloem. Amount and proportion of different crystal types varying infraspecifically *Silica bodies*, globose or of irregular shapes, noted in ray parenchyma cells of secondary xylem of part of the material investigated. *Secretory canals* with 1 or 2 layered epithelium; present in phloem and pith, the canals in the phloem being narrower than those in the pith.

Bark

Material: sample from bole of *C. arborescens*, Fuchs 21290

General features. Colour greyish brown or dark brown with yellow and reddish brown tones. 4—5 mm thick, with coarse shallow longitudinal fissures, which are more than 2 cm apart. Shedding in thin layers. In T.S. with numerous yellow tangential bands. For field characters see Foxworthy (1927).

Microscopic features: *Ground tissue* composed of sieve tubes, companion cells and (crystalliferous) parenchyma strands. *Rays* 1—4 seriate. *Secretory canals* numerous in ground tissue. Tangential bands (2—3 mm thick) composed of \pm cubical thick-walled and densely pitted *stone cells* ('phelloids'); occurring at various intervals (their distance varying from a few microns to 0.7 mm due to the rather wavy course of the bands). The discontinuous bands accompanied on both sides by layers of flattened suberized cells. Bands formed by *cork cambia* on their inner sides.

Wood (See also Table II, fig. 5, 6)

A. Section *Cratoxylum* and section *Tridesmos* (fig. 5a—c) Material investigated: samples of mature wood from boles of *C. sumatranum*, *C. cochinchinense*, *C. formosum* and *C. maingayi*.

General features: Wood heavy to very heavy (specific gravity exceeding 1 in *C. sumatranum*, *C. formosum* and *C. maingayi*). Colour dark brown in *C. maingayi*, light yellowish to pinkish brown in other three species. Texture fine.

Microscopic features: *Growth rings* absent to fairly conspicuous, *Vessels* diffuse, 7—18/mm², solitary and in radial to oblique multiples of 2—4(—6), forming an oblique pattern in *C. cochinchinense* and *C. maingayi*, round to oval (radially elongated) in T.S., mean tangential diameter 90—110 μ , radial diameter up to 140—190 μ , walls 3—4(—6) μ thick, vessel member length 290—710 μ (mean 460—600 μ). Perforations simple in the oblique to horizontal end walls. Lateral wall pits alternate. Inter-vessel pits predominantly round, sometimes oval to polygonal, diameter 3—5(—6) μ . Apertures slit-like, horizontal to oblique. Vessel-ray pits similar but half-bordered; sometimes unilaterally compound. Vessel—fibre pits very sparse and minute. Thin-walled *tyloses* and solid amorphous and granular brown *contents* noted in some heartwood vessels of *C. cochinchinense* and *C. maingayi* (also recorded for *C. sumatranum* and *C. formosum* by Moll and Janssonius, 1906). *Vascular tracheids* accompanying some of the vessels, sometimes arranged in radial 'tails' together with vessels of narrow diameter. Ground tissue composed of *fibres* with very few simple pits or bordered pits with strongly reduced borders and slit-like \pm vertical apertures. Fibres arranged in variously disturbed radial rows, hexagonal in T.S., diameter 10—32 μ , walls 2—8 μ thick; length 780—1690 μ (mean 1080—1320 μ). *Parenchyma* predominantly apotracheal in tangential bands of 1—4(—6) cells wide. Distance between bands 100—400 μ . Paratracheal parenchyma scanty. Diffuse parenchyma absent or very scanty. Parenchyma strands of 6—8 cells. *Rays* 10—13/mm, 1—many cells high, height not exceeding 1.1 mm, 1—2 seriate in *C. maingayi*, 1—3(or 4) seriate in other species, tending to be of two distinct sizes in *C. cochinchinense*, heterogeneous or tending to homogeneous, mainly composed of procumbent cells, but squarish cells occurring in low uniseriates and in tails of multiseriates. *Cystals absent*. *Silica bodies* with rough surface and of irregular shapes present in ray cells.

B. Section *Isopterygium* (fig. 5d, e, 6)

Material investigated: samples of mature wood of *C. arborescens* and *C. glaucum*.

General features: Wood rather light. Colour light pink to brick red. Texture fairly fine, but conspicuously coarser than in the other two sections.

Microscopic features: *Growth rings* not seen in material examined. *Vessels* diffuse, 2—5/mm², solitary and in radial multiples of 2—4(—5), oval in T.S. (radially elongated), mean tangential, diameter 125—200 μ , radial diameter up to 210—280 μ , walls 3—4(—6) μ thick, vessel member length 300—780 μ (mean 520—660 μ). Perforations simple in the oblique to horizontal end walls. Lateral wall pits alternate. Inter-vessel pits round to oval (diameter 3—6 μ) with oblique slit-like apertures. In *C. glaucum* the slits sometimes confluent with others from neighbouring pits. Pits to contiguous parenchyma cells (rays and axial parenchyma) half-bordered, similar to inter-vessel pits or occasionally unilaterally compound and then two pits on the parenchyma cell wall. Thin-walled *tyloses* and solid amorphous brown *contents* noted in some heartwood vessels. *Vascular tracheids* accompanying some of the vessels, sometimes arranged in radial 'tails' together with vessels of narrow diameter. Ground tissue composed of fibres with very few simple pits. Fibres more or less arranged in radial rows, rounded to rectangular in

T.S., diameter 20—38 μ in *C. arborescens*, 16—21 μ in *C. glaucum*; walls 2—4(—6) μ thick. Length 780—1560 μ (mean 1070—1210 μ). *Parenchyma* predominantly paratracheal, in 1—3 layers around the vessels to scanty, in *C. arborescens* tending to be aliform confluent in some places. Very few continuous bands, only seen in Fuchs 21346. In *C. glaucum* parenchyma mainly aliform. Diffuse parenchyma very scanty or absent. Parenchyma strands of 5—8 cells. *Rays* 10—11/mm, 1 to many cells high, height not exceeding 1.1 mm, 1—4 seriate and tending to be of two distinct sizes in *C. arborescens*, 1 or 2 (or 3) seriate in *C. glaucum*, heterogeneous or tending to homogeneous, mainly composed of procumbent cells, squarish cells present in most uniseriate rays and in the tails of multiseriate rays. *Crystals* absent. *Silica bodies* with rough surface and of irregular shapes present in ray cells.

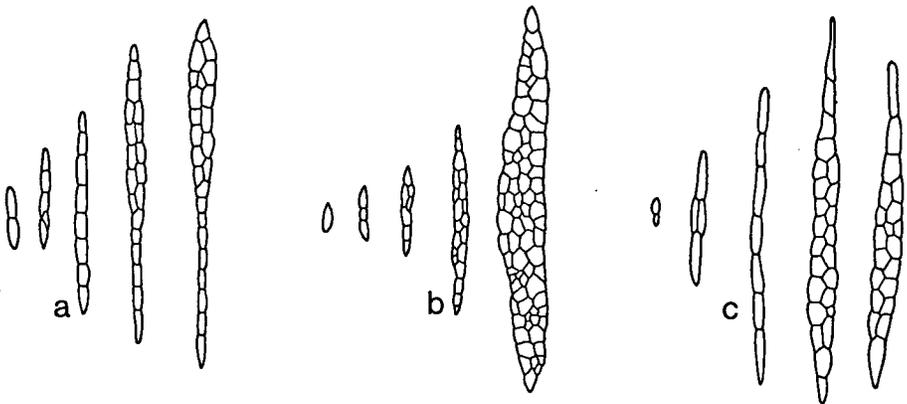


Fig. 6. Tangential sections through wood rays; $\times 77$. a. *C. glaucum*. b. *C. formosum*. c. *Eliaea articulata*.

Vegetative Anatomy of *Eliaea*

Leaf (fig. 4a—c)

In surface view: Adaxial and abaxial epidermis glabrous. Epidermal cells of adaxial surface and unspecialized cells of abaxial surface polygonal with straight anticlinal walls. Cells overlying midrib and major veins slightly elongated. *Stomata* confined to abaxial surface, paracytic with high dome-shaped subsidiary cells. Subsidiary cells often divided parallel to the pore. Diameter perpendicular to the pore 10—18 μ (mean 15 μ); orientation random.

In transverse section: *Cuticle* 2—5 μ thick. Adaxial epidermal cells larger than abaxial ones. *Multiple epidermis* with irregular collenchyma-like wall thickenings present in D'Alleizette, August 1906, absent in specimen D'Alleizette, Nov. 1906. *Mesophyll* composed of 1 or 2 layers of palisade cells and spongy tissue of inconspicuously lobed cells. *Leaf margins* pointed downwards. Mesophyll parenchymatous at margins. *Midrib* with slightly raised (almost flat) adaxial surface and convex abaxial surface, supplied with a single shallowly V-shaped vascular strand with or without incurved margin. Vascular strand with abaxial and adaxial sclerenchymatous caps, composed of thick-walled fibres interspersed with thin-walled cells. Ground tissue of midrib collenchymatous at abaxial periphery to parenchymatous in more central and adaxial parts. *Veins*

provided with sclerenchyma caps, which are most prominent opposite xylem, minor veins embedded in mesophyll. Sheath of translucent parenchyma cells present around vascular bundles and sclerenchyma caps. Bundle sheath extensions absent. *Petiole* \pm semi-circular in T.S. through distal end, with concave to flat adaxial surface and convex abaxial surface. Vascular system composed of single crescentiform strand, with or without additional incurved margins. Ground tissue collenchymatous. *Crystals* as in *Cratoxylum*. *Secretory cavities* of (sub)spherical shape present in both palisade and spongy tissue. Adaxial epidermal cells opposite secretory cavities with conspicuously thinner anticlinal and periclinal walls than remainder of epidermal cells. *Secretory canals* abundant and with a two-layered epithelium of large cells in ground tissue of midrib and petiole. Secretory canals in phloem of midrib and petiole narrow and very inconspicuous.

Axis (twigs of *c.* 3 mm diameter; see also table I)

Peripheral tissues as in *Cratoxylum*. Secondary *xylem*: *Growth rings* absent. *Vessels* diffuse, almost exclusively solitary; round in T.S., mean diameter 35—36 μ , mean vessel member length 390—450 μ . Perforations simple in the slightly oblique end walls. Lateral wall pits in alternate arrangement. Vessel-fibre pits round-oval, diameter *c.* 3 μ . Vessel-parenchyma and vessel-ray pits sometimes flattened and unilaterally compound. *Tyloses* and vessel *contents* not seen. Vascular *tracheids* rare. *Fibre-tracheids* arranged in radial rows, constituting ground tissue of secondary xylem. Walls thick and provided with numerous bordered pits. Average fibre length 670—780 μ . *Parenchyma* mainly irregularly banded; bands apotracheal or aliform confluent. Paratracheal parenchyma scanty. Rays *c.* 22/mm at periphery of secondary xylem, further as in *Cratoxylum*. Primary xylem, *node* and *pith* as in *Cratoxylum*. *Crystals* present as elongated prismatic types in phloem and as clusters in pith. *Silica bodies* absent. *Secretory canals* as in *Cratoxylum*.

Wood (see also Table II, fig. 5f, 6e)

Material investigated: outer part of stem of 5 cm diameter.

General features: Wood very heavy (specific gravity exceeding 1). Colour dark brown. Texture fine.

Microscopic features: *Growth rings* absent. *Vessels* diffuse, *c.* 12/mm², almost exclusively solitary, round in T.S., mean diameter 95 μ ; walls 4—7 μ thick; vessel member length 450—1200 μ (mean 780 μ). Perforations simple in the oblique to horizontal end walls. Lateral wall pits to contiguous fibre-tracheids in alternate arrangement, diameter 3—4 μ , apertures minute and round or slit-like. Vessel-ray and vessel-parenchyma pits similar but half-bordered or unilaterally compound. Vessels in heartwood with solid amorphous brown-yellow *contents*. *Tyloses* absent. *Vascular tracheids* not seen. Ground tissue composed of *fibre-tracheids*, arranged in radial rows, with numerous bordered pits with slit-like, almost vertical apertures; diameter of borders *c.* 3 μ . Fibres round to hexagonal in T.S., diameter 20—30 μ , walls 4—11 μ thick; length 900—1700 μ (mean 1290 μ). *Parenchyma* predominantly apotracheal in irregular tangential bands of 1—3 cells wide at various distances. Diffuse and paratracheal parenchyma scanty. Parenchyma strands of 5—8 cells. Rays *c.* 11/mm, 1 to many cells high (height not exceeding 0.8 mm), uni-biseriate, markedly heterogeneous, composed of procumbent to upright cells. *Crystals* of prismatic types infrequently present in axial parenchyma cells. *Silica bodies* absent.

Occurrence of papillae in *Cratoxylum*

In two out of four leaf samples of *C. formosum* ssp. *formosum* sectioned very conspicuous, tall epidermal papillae were noted on the abaxial leaf surface (fig. 4h, j). The leaves of the other two specimens were completely devoid of papillae (fig. 4i, k). The very striking differences in the abaxial epidermides of one subspecies led me to study all material of *Cratoxylum* present in the Rijksherbarium with a stereomicroscope (magn. $\times 60$) in order to establish the presence or absence of papillae. My aim was to know whether this character showed any relationship to geographical distribution of the specimens concerned and whether it could be used to trace taxa of infraspecific rank.

Results are listed in table III. Specimens listed under the question mark represent cases where no conspicuous papillae could be seen, but where the surface was not smooth either; when examined in transverse section such leaves were found to exhibit an intermediate condition with very low papillae. From table III it becomes evident that the presence of epidermal papillae is not a reliable diagnostic character for species of *Cratoxylum*, but that in some species a kind of geographical pattern exists for the occurrence of papillae. Such a pattern is very obvious in *C. formosum* ssp. *formosum*; here we find a high proportion of specimens with papillae in material from Java and Sumatra; in the material from Borneo and the Philippines this proportion is remarkably lower, whilst all specimens from Celebes and S.E. Asia lack papillae. It is tentatively suggested here that in this taxon the occurrence of papillae reflects a further differentiation into taxa of lower rank. If infraspecific variation patterns were to be investigated more extensively this character definitely deserves further attention. The comparatively high proportion of specimens of *C. cochinchinense* listed under the question mark could be an indication that differentiation of subspecific taxa has not progressed as far as in *C. formosum*.

The different patterns for the occurrence of papillae in different species growing under \pm similar conditions (cf. Gogelein, 1968) suggests that the presence or absence of papillae is not determined by the environment.

Floral and xylem specialization and related problems

In applying the general criteria for trends of phylogenetic flower specialization (see e.g. Takhtajan 1959) one has to regard the gynoeceium of *Eliaea* to be more specialized than that of *Cratoxylum* because of a reduced number of ovules in the former. The presence of false septa in *Eliaea* also seems to represent a specialization, rather than some vestigial character. A comparison with other *Hypericoideae* would be necessary for a good understanding of trends in floral specialization, but comprehensive data from literature are not available, as far as known to me.

Detailed data on xylem specialization are to be found in Bailey and Tupper (1918), Frost (1930), Tippe (1938), Metcalfe and Chalk (1950), and Carlquist (1961). For our purpose it suffices to summarize the following trends:

- 1) long fusiform elements (particularly vessel members) are more primitive than short ones;
- 2) fibre tracheids are more primitive than libriform fibres;
- 3) xylem with diffuse solitary vessels is more primitive than xylem with vessel multiples.

Bailey (1957) and Carlquist (1961) have pointed out the dangers of using these trends, which have been established for the higher categories of land plants to judge the degree of specialization within small groups of closely allied taxa. In my opinion these trends are, however, equally valuable for both closely and distantly related groups, perhaps even

more readily interpretable for small groups. In the higher categories such as families and orders, parallelism and different speeds of specialization may play a much more confusing part and members of different groups are often not comparable in their secondary xylem anatomy. These factors are apparently less important within a group of which we know on other grounds that its representatives are closely related. Of course we must not expect linear sequences, as if the more primitive member had been ancestral to the other species. The only result we may hope for is to find some representatives which are more like a possible common ancestor than others. Returning to *Cratoxylum* and *Eliaea*, we find that *Eliaea* shows the more primitive characters in the longer fusiform elements (tables I & II), in fibre tracheids with conspicuously bordered pits and in exclusively solitary vessels. Fibre length in *Eliaea*, though comparatively great, is equalled by *C. cochinchinense* (in twigs and mature wood) *C. formosum* (in twigs) and *C. maingayi* (in twigs and mature wood). It is known, however, that fibre length is not an accurate index for xylem specialization since considerable elongation of these cambial products takes place.

Here it should also be stressed that only a wood sample from a stem of 5 cm diameter was at our disposal in the case of *Eliaea*. Bole-samples as in *Cratoxylum* are not available since *Eliaea* is a shrub. It might well be that in branch wood of a similar diameter from *Cratoxylum* the quantitative values would be lower than in the material at my disposal; this would make the differences between *Cratoxylum* and *Eliaea* even more pronounced. Quantitative xylem characters as listed in tables I and II are not suitable for diagnostic purposes, because of a high intraspecific variation (e.g. table I: *C. formosum*; table II: *C. arborescens*). For our problem it is sufficient to know that in a wide range of values *Eliaea* occupies the maximal extremes. From the above we can tentatively conclude that the xylem of *Eliaea* resembles that of a possible common ancestor more closely than that of *Cratoxylum*. It is difficult to reconcile the contradictory conclusions from floral and wood anatomy. It should be mentioned, however, that the occurrence of a mixture of obviously advanced and primitive characters in plant taxa is by no means a rare phenomenon (see e.g. Cronquist 1968). The suggestion that floral and xylem anatomy in *Cratoxylum* and *Eliaea* show differently diverging lines implies that *Cratoxylum* and *Eliaea* are not so closely related as one might expect from gross morphology. Within the *Hypericoideae* they are, however, more closely related mutually than to any other genus. For the main differences in either gross morphology or vegetative anatomy from the other hypericoid genera: *Ascyrcum*, *Haronga*, *Hypericum*, *Psorospermum* or *Vismia* the reader is referred to Engler (1925) and Metcalfe and Chalk (1950). For each of these genera there are either flower and fruit or xylem characters which put them rather far apart from the *Cratoxyleae* (*Cratoxylum* and *Eliaea*).

Eliaea is a shrub found in the narrow strip of dunes along the east coast of Madagascar. Perrier de la Bâthie (1948: 114) stated: 'Ce genre monotypique est endémique, mais il est affine des *Cratoxylon* d'Asie et d'Océanie. C' est donc un type d'origine orientale,' etc. He tentatively ascribed its occurrence along the east coast to dispersal by seed of the winged seeds. The derivation of *Eliaea* from *Cratoxylum* is, however, most unlikely since the xylem of *Eliaea* is more primitive than that of *Cratoxylum*. If the presence of *Eliaea* on Madagascar must be explained by oriental origin it, or its ancestor, must have arrived at a time that *Cratoxyleae* in Indo-Malesia still showed the primitive xylem characters now found in *Eliaea*. An alternative hypothesis, already used by Danser (1928) for explaining the occurrence of primitive *Nepenthes* species on Madagascar, can also be used to understand the present distribution of *Eliaea*. This hypothesis implies that the distribution pattern Madagascar—Indo-Malesia goes back to the time that land connections

between the two areas were still present and that a common ancestor of *Cratoxylum* and *Eliaea* occupied the whole range (see also Schuchert 1932; Willis 1932; Van Steenis 1962 and Florin 1963). A later fragmenting of this Gondwana continent made an independent evolution of both *Cratoxylum* and *Eliaea* possible. During this process *Cratoxylum* retained primitive flower characters and *Eliaea* retained primitive xylem characters. *Dapania grandifolia* (Oxal.), an endemic form from Madagascar, resembles two *Dapania* species but also *Sarcotheca*, all from Malesia (Veldkamp 1958) and might call for a similar explanation. It is emphatically stressed here that the above mentioned hypothesis is merely a model in which the data known at present seem to fit fairly well. No factual evidence is available to support it. Obviously, much more research into plant groups with a similar distribution pattern is needed before it is possible to ascertain the probability of the explanation offered. Great care must also be observed in attaching too much weight to the phylogenetic trends of xylem specialization. The general trends of xylem specialization have been very elegantly established, but an absolute certainty of their irreversibility has only been claimed (Baily 1944) and was never proved.

Sectional delimitation and anatomy in the genus *Cratoxylum*

Den Berger (1925) suggested in a general paper that, on the grounds of wood anatomy, *Cratoxylum* should be split into two sections, different from those recognized by Engler (1925). Unfortunately he did not list any specific names or mention the decisive anatomical characters involved. Desch (1941) emphasized that *C. arborescens* differs wood-anatomically from the other species investigated by him (*C. formosum* and *C. ligustrinum* = *C. cochinchinense*) in having another type of parenchyma distribution. My own observations, together with wood descriptions from literature (Solereder 1899, Moll and Janssonius 1906, Metcalfe and Chalk 1950 and the papers cited therein), confirm the fact that wood anatomically only two groups can be distinguished in *Cratoxylum*. One group is represented by section *Tridesmos* (*C. formosum* and *C. maingayi*) and by section *Cratoxylum* (*C. sumatranum* and *C. cochinchinense*). The species of these sections possess comparatively narrow vessels, abundant predominantly banded parenchyma (see fig. 5a—c), and generally fairly thick-walled fibres (high specific gravity). The other group is represented by *C. arborescens* and *C. glaucum* constituting the section *Isopterygium*. Wood of these species is characterized by wide vessels, less abundant paratracheal parenchyma (fig. 5d, e), and thin-walled fibres (low specific gravity).

The fact that wood-anatomically only two groups can be distinguished instead of the three sections should not be interpreted as a disagreement between wood anatomy and gross morphology. That the sections *Tridesmos* and *Cratoxylum* cannot be separated on the basis of wood anatomy does not mean that they have no sound morphological basis. In fact, the great differences between the wood anatomy of section *Isopterygium* and that of the remainder of the genus are more surprising than the lack of such differences between the two other sections. It is most unlikely that, in the absence of flowering material, a wood sample of *C. arborescens* or *C. glaucum* would be related to other members of the genus. This indicates a rather isolated position of the section *Isopterygium* within the genus.

The distinction in wood anatomical structure coincides with another important feature: the representatives of the section *Isopterygium* are evergreen trees; those of the other two sections are deciduous. It would be very attractive to interpret the anatomical differences between the two groups in terms of a functional adaptation to the behaviour of the foliage. Initially, increased storage facilities in the abundant parenchyma cells of the deciduous group, useful for energy requirements during leafless periods, were consid-

ered. Some data from literature were collected about comparable cases in order to find out whether the situation in *Cratoxylum* is the example of a rule or whether there is no general relationship between parenchyma distribution and the evergreen or deciduous habit at all. Dadswell and Ingle (1954) described the wood anatomy of the genus *Nothofagus* and found wood parenchyma to be very abundant in the evergreen section from New Guinea, whilst it was very sparse in the deciduous sections and in a small evergreen section from New Zealand. This is a reversal, therefore, of what we found in *Cratoxylum*. Williams (1939) and Tilson and Muller (1942) tried to find wood-anatomical evidence for subgeneric segregation of American *Quercus*. They found no substantial difference between the wood of evergreen and of deciduous oaks, apart from a not surprisingly more pronounced ring-porousness in the former group of species. The above mentioned examples, though very few, remove any ground for accepting a functional explanation for the differences in wood anatomy in *Cratoxylum*. Suggestions on such topics require more knowledge of the autecology and cambial activity of the trees involved and such knowledge is only obtainable in field studies.

Returning to the xylem anatomy of *Cratoxylum*, it should be noted that the great differences found to exist in the mature secondary xylem are not paralleled by those in the juvenile secondary xylem of young twigs. In young twigs of *C. arborescens* and *C. glaucum* parenchyma may be banded to almost the same extent as in the other species and vessel diameter and frequency do not show deviations from the remainder of the genus. From this one might conclude that the mature xylem of *C. arborescens* and of *C. glaucum* represents a derived condition, considering that the first formed secondary xylem often retains the more primitive characters (see Bailey 1944). Such a conclusion seems to disagree with the quantitative features listed in table II where the vessel members of the mature secondary xylem of *C. arborescens* and *C. glaucum* belong to the longest in the genus. This again would imply a more primitive condition for the former two species. However, if we consider the data for young twigs we note that both *C. glaucum* and *C. arborescens* are within the limits of individual variability of *C. formosum*. It has been known from Sanio's time onwards (1872) that fusiform element length may increase from the first formed secondary xylem to the much later formed 'mature' secondary xylem. This increase in length, which varies from species to species (see e.g. Bailey and Tupper, 1918: 186) could interfere with our theories of vessel member length as related to phylogenetic specialization, and complicate the picture as in the case of *Cratoxylum*. Considering the wide vessels and paratracheal parenchyma in *C. arborescens* and *C. glaucum* one would be inclined to regard the section *Isopterygium* to be derived rather than primitive as compared with the other sections of *Cratoxylum* (cf. Carlquist, 1961, for trends of xylem specialization).

The considerations offered above do not affect the conclusions on page 384 about *Eliaea* having a more primitive xylem than *Cratoxylum* since the characters employed there are consistent for both young and mature secondary xylem.

Another anatomical character provided an argument for the rather isolated position of the *Isopterygium* species within the genus as a whole: in the distal end of the petiole of *C. arborescens* and *C. glaucum* 2(—4) latero-dorsal bundles occur which are absent in the other species of *Cratoxylum*. The presence of a multiple epidermis in leaves of species of the section *Isopterygium* would offer yet another character to distinguish them from the other species. The presence or absence of a multiple epidermis varies, however, quite often infraspecifically (e.g. in *Eliaea articulata*, see page 381), and this character could well break down in *Cratoxylum* as a diagnostic feature if more material is examined.

Cratoxylum and Eliaea as distinct genera

From the descriptive part of this paper it follows that there are many characters both in floral and vegetative structure shared by *Cratoxylum* and *Eliaea*. For instance petal scales, hypogynous glands, and stamens in phalanges; the general histology of leaf and axis is also essentially similar. However, quite a number of distinguishing characters are present as well. All characters as listed by Gogelein (see p. 370) could be confirmed and three more diagnostic characters could be added from vegetative anatomy: fibre-tracheids with numerous bordered pits, almost exclusively solitary vessels, and the absence of silica in the wood of *Eliaea*, as contrasted with scarcely pitted fibres and the common occurrence of vessel multiples and silica bodies in rays in the representatives of *Cratoxylum*.

The differences between *Cratoxylum* and *Eliaea* are more substantial than between the section *Isopterygium* and the other two sections of *Cratoxylum*. The two genera differ in both floral and wood characters, whilst the differential characters within *Cratoxylum* are mainly based on parenchyma distribution in the secondary xylem. The latter character may, moreover, be regarded as taxonomically less important than vessel grouping and type of fibres. Considering both floral and vegetative anatomy I see no grounds for combining *Eliaea* and *Cratoxylum* to form one genus.

I agree with Gogelein that within the genus *Cratoxylum*, *C. maingayi* is probably most closely related to *Eliaea*. Anatomically this view is supported by the fusion of lateral bundles in the ovary and the absence of vertical bundle sheath extensions in the veins of the leaves in both *Eliaea* and *C. maingayi*. These two features were not encountered in the other species of *Cratoxylum*. Moreover, *C. maingayi* possesses xylem fibres with pits that are most numerous and of which the borders are least reduced as compared with those of the other *Cratoxylum* species. These fibres are yet very different from the densely pitted fibre-tracheids in *Eliaea*, however.

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TABLE I: Quantitative characters of first formed secondary xylem of *Cratoxylum* and *Eliaea*

Standard deviations are not recorded in this table. They amount to 15—25 % for vessel member length, 10—35 % for vessel diameter, and 10—20 % for fibre length. Means of tracheid length are based on 10 measurements only.

	Vessel member length in μ		Vessel diameter in μ		Fibre length in μ		Tracheid length in μ	
	mean	range	mean	range	mean	range	mean	range
<i>Cratoxylum</i>								
Section <i>Cratoxylum</i> :								
<i>C. sumatranum</i>	310	215—440	42	16—84	600	470—820	340	
<i>C. cochinchinense</i>	315	255—435	45	31—68	740	650—850	340	
Section <i>Tridesmos</i> :								
<i>C. formosum</i> (5 specimens)	255—365	175—540	37—51	21—84	600—730	350—850	310—430	
<i>C. maingayi</i>	345	175—445	42	21—63	670	490—900	310	
Section <i>Isopterygium</i> :								
<i>C. arborescens</i> (2 specimens)	265—270	185—325	35—36	15—55	420—510	300—620	280—320	
<i>C. glaucum</i>	340	220—485	40	16—58	560	400—720	370	
<i>Eliaea articulata</i> (2 specimens)	390—450	225—650	35—36	26—52	670—780	420—960	410—510	

TABLE II: Quantitative characters of mature secondary xylem of *Cratoxylum* and *Eliaea*

Standard deviations are not recorded in this table. They amount to 13—24 % for vessel member length, 25—35 % for vessel diameter, and 11—17 % for fibre length.

	Vessel member length		Tangential vessel diameter		Fibre length		Fibre wall diameter thickness	
	mean	in μ range	mean	in μ range	mean	in μ range	mean	in μ range
<i>Cratoxylum</i>								
Section <i>Cratoxylum</i> :								
<i>C. sumatranum</i>	470	290—600	90	55—140	1190	910—1560	16—32	2—5
<i>C. cochinchinense</i>	460	365—560	90	30—125	1260	1040—1690	10—15	3—6
Section <i>Tridesmos</i>								
<i>C. formosum</i>	470	290—550	90	20—145	1080	780—1300	16—20	3—8
<i>C. maingayi</i>	600	400—710	110	30—160	1320	1100—1610	14—22	3—8
Section <i>Isopterygium</i> :								
<i>C. arborescens</i> SAN 25136	620	400—790	155	60—230	1120	910—1430	20—38	2—3
<i>C. arborescens</i> F 21290	520	300—715	180	60—270	1070	780—1430	20—30	2—4
<i>C. arborescens</i> F 21346	660	390—845	200	50—315	1210	1040—1560	20—28	2—3
<i>C. glaucum</i>	620	325—780	125	50—160	1120	780—1430	16—21	2—4
<i>Eliaea articulata</i>	780	450—1200	95	50—140	1290	900—1700	20—30	4—11

TABLE III: Epidermal papillae in *Cratoxylum*

+ = number of specimens with conspicuous epidermal papillae
 — = number of specimens without epidermal papillae
 ? = number of specimens in which papillae are doubtfully present when using $\times 60$ magnification of stereomicroscope,

Locality	<i>C. sumatranum</i> ssp. <i>nereifolium</i>		<i>C. cochinchinense</i>		<i>C. formosum</i> ssp. <i>formosum</i>		<i>C. maingayi</i>		<i>C. glaucum</i>	
	+	— ?	+	— ?	+	— ?	+	— ?	+	— ?
S.E. Asia (mainland)	2	1 2	6	6 9	0	4 0	2	1 0	—	—
Malaya	—	—	3	0 5	0	5 0	1	8 0	—	—
Sumatra	—	—	3	19 4	37	8 1	0	7 0	4	2 1
Java	—	—	—	—	8	0 0	—	—	—	—
Borneo	—	—	0	42 0	19	30 6	5	0 0	24	0 0
Celebes	—	—	—	—	0	8 0	—	—	—	—
Philippines	—	—	0	4 0	5	19 0	—	—	—	—

No papillae were found in *C. arborescens* (43 specimens) and *C. sumatranum* ssp. *blancoi* (7 specimens). Only one specimen from the Philippines of *C. sumatranum* ssp. *sumatranum* (170 specimens) showed papillae. *C. formosum* ssp. *pruiniflorum* does not possess conspicuous papillae (see description on p. 376).