

## A LEAF ANATOMICAL CONTRIBUTION TO THE CLASSIFICATION OF THE LINACEAE COMPLEX

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### SUMMARY

The leaf anatomy of the Linaceae complex (Linaceae s.s., Hugoniaceae, Ixonanthaceae, Humiriaceae and Erythroxylaceae) and putative allies (*Ctenolophon*, *Lepidobotrys*, Irvingiaceae) is surveyed, mostly on the basis of original observations (72 specimens, 27 genera), partly from data in the literature.

Diversity in stomatal type, midrib and petiole vascularisation, sclerenchyma support, foliar sclereids, mucilage cells, secretory cavities, and cristarque cells provide evidence in favour of a separate family status of the members of the Linaceae complex. *Allantospermum* and *Cyrrilopsis* are best accommodated in the Ixonanthaceae. Irvingiaceae (often treated in or near Simaroubaceae) show similarities with the Linaceae complex, albeit more closely to the Hugoniaceae than to the Ixonanthaceae to which they have been transferred by some authors. *Ctenolophon* seems unrelated, but leaf anatomy gives no strong clues for its true affinities. *Lepidobotrys* may be related to the Linaceae complex, but its leaf anatomy is also in good agreement with treatment in or near the Oxalidaceae. Within the Ixonanthaceae, *Phyllocosmus* deserves generic status next to *Ochthocosmus* on account of the exclusive occurrence of tracheoidal idioblasts in the latter and lack thereof in the former. The results are discussed in connection with evidence from other sources of enquiry.

### INTRODUCTION

The Linaceae *sensu lato* are currently being revised for Flora Malesiana (Kool, 1980; Van Hooren & Nootboom, 1984) and the present leaf anatomical study on a world-wide basis was undertaken as a complementary means to provide arguments in the debate of taxonomic delimitation above the genus level. Over the years the Linaceae complex has been treated very differently by various authors. Without going into a detailed historical account, the controversial issues can be summarised as follows:

1. Are the various suprageneric taxa (Linoideae or Linaceae s.s., Hugonioideae or Hugoniaceae, Ixonanthoideae or Ixonanthaceae, and Erythroxylloideae or Erythroxylaceae) and various isolated genera (*Ctenolophon*, *Lepidobotrys*) sufficiently distinct to merit family status, and how are their mutual, phylogenetic affinities? For diverging views see Bentham & Hooker (1862), Hallier (1923), Winkler (1931),

Léonard (1950), Exell & Mendonça (1951a), Hutchinson (1959), Scholz (1964), Airy Shaw (1973), Takhtajan (1980), Dahlgren (1980), Thorne (1981), Cronquist (1981), and Young (in Bedell & Reveal, 1982).

2. Are *Ctenolophon* and *Lepidobotrys* at all related to the Linaceae complex, and if not which are their closest living relatives? Compare opinions by Oliver (1873), Engler (1903), Hallier (1912, 1923), Knuth (1931), Winkler (1931), Léonard (1950), and Exell & Mendonça (1951b).
3. Which are the relationships between the Linaceae complex and the Irvingiaceae (or Irvingioideae of the Simaroubaceae) of the order Rurales (or Geraniales)? This question has become a moot point since the genus *Allantospermum* has been treated by various authors as an ally of the Irvingiaceae (Capuron, 1965; Nootboom, 1967) or the Ixonanthaceae (Forman, 1965) and since Forman (l.c.) even proposed to treat the Irvingioideae as a subfamily in the Ixonanthaceae.

Throughout the taxonomic history of these alliances, micromorphological characters, including leaf anatomical ones, have played an important role (Solereder, 1899 & 1908; Jadin, 1901; Van Tieghem, 1903; Boas, 1913; Winkler, 1931; Metcalfe & Chalk, 1950; Metcalfe et al., 1968). However, an integral discussion of the problems at hand using leaf anatomical data of all groups has never been given, and much of the descriptive information is in need of updating. Our present study is restricted to a rather low number of samples and species, but information on the most poorly sampled groups (Humiriaceae, Erythroxylaceae and Simaroubaceae) could be complemented with data from the literature (Rury, 1981a & b; Boas, 1913; Vilhena, 1978).

For easy reference, and anticipating the conclusions of this study the following classification at the basis of the suprageneric nomenclature adopted throughout this paper, is given here.

<i>Family</i> (total number of genera)	<i>Genera studied</i>	<i>Other treatments in the literature</i>
Linaceae s.s. (6)	<i>Hesperolinon</i> <i>Linum</i> <i>Radiola</i> <i>Reinwardtia</i> <i>Tirpitzia</i> <i>Anisadenia</i>	Linoideae in Linaceae s.l.
Hugoniaceae (5)	<i>Hebepetalum</i> <i>Hugonia</i> <i>Indorouchera</i> <i>Roucheria</i> <i>Philbornea</i>	Hugonioideae in Linaceae s.l.

Ixonanthaceae (5)	<i>Cyrillopsis</i> <i>Ixonanthes</i> <i>Ochthocosmus</i> <i>Phyllocosmus</i> — — subgenus of <i>Ochthocosmus</i> <i>Allantospermum</i> — — in Irvingiaceae	Ixonanthoideae in Linaceae s.l.
Lepidobotryaceae (1)	<i>Lepidobotrys</i>	in Oxalidaceae
Ctenolophonaceae (1)	<i>Ctenolophon</i>	in Linaceae s.l. or Hugoniaceae
Humiriaceae (8)	<i>Humiria</i>	Humirioideae in Linaceae s.l.
Erythroxyloaceae (4)	<i>Aneulophus</i> <i>Erythroxyllum</i>	Erythroxyloideae in Linaceae s.l.
Irvingiaceae (3)	<i>Desbordesia</i> <i>Irvingia</i> <i>Klainedoxa</i>	Irvingioideae in Simaroubaceae or in Ixonanthaceae
Simaroubaceae (c. 20)	<i>Eurycoma</i> <i>Simarouba</i>	

## MATERIAL AND METHODS

Herbarium material studied is mainly from the Rijksherbarium at Leiden (L) unless stated otherwise (Utrecht: U). Mature leaves were rehydrated by boiling in water. Transverse sections of the middle portion of the lamina (including midrib and one leaf margin) and of distal and basal parts of the petiole were prepared on a sledge microtome and partly bleached in household bleach. These and paradermal free hand sections of the upper and lower leaf surface were stained with a safranin/haematoxylin mixture (vols. 95 : 5) and mounted in euparal together with unbleached, unstained sections upon dehydration in an alcohol series. In addition Sudan IV-stained cuticular macerations obtained after incubation overnight in a mixture of equal volumes of 30% hydrogen peroxide and glacial acetic acid, and unstained leaf clearings prepared in chloral-lactophenol enriched with hydrogen peroxide were studied.

The specimens studied are listed below:

- Allantospermum borneense* Forman: Malaya, FRI 6120; Borneo, Sibat ak Luang 24560. — *A. multicaule* (Capuron) Nooteboom: Madagascar, Capuron SF 23944.  
*Aneulophus africana* Benth.: Gabon, Courtet s.n. (Herb. d'Alleizette).  
*Anisadenia saxatilis* Wall.: India, Hooker & Thomson s.n.  
*Ctenolophon parvifolius* Oliv.: New Guinea, Boumann 3355; Philippines, PNH 6385.

- Cyrillopsis paraensis* Kuhlm.: Brazil, Ducke 10705, Prance et al. 3783 and Froes 22149.  
*Desbordesia glaucescens* (Engl.) Pierre: Zaire, Wagenmans 990.  
*Durandea* Planchon: see *Hugonia*.  
*Erythroxylum cuneatum* (Miq.) Kurz: Borneo, S 17894. – *E. ecarinatum* Hochr.: New Guinea, BW 9763.  
*Eurycoma longifolia* Jack: Borneo, Fuchs 21334.  
*Hebepetatum humiriifolium* (Planch.) Benth.: Surinam, Schulz 7934 (U); British Guyana, A.C. Smith 2717 (U).  
*Hesperolinon adenophyllum* (Gray) Small: California, Sharsmith 4398. – *H. drymarioides* (Curran) Small: California, Sharsmith 4162.  
*Hugonia afzelii* R.Br. ex Planch.: Ivory Coast, Leeuwenberg 2893. – *H. castanea* Baill.: Madagascar, Lam & Meeuse 95632. – *H. costata* Miq.: Sumatra, Forbes 2814. – *H. cf. costata* Miq.: Borneo, SAN 44657 and Leighton 1010. – *H. jenkinsii* F.v.M.: New Guinea, Van Royen & Sleumer 5794. – *H. racemosa* Schlechter (*Durandea deplanchei* Stapf): New Caledonia, Balansa 2372.  
*Humiria balsamifera* St. Hil.: French Guyana, Herb. Paris s.n. (1838).  
*Indorouchera contestiana* (Pierre) Hall. f.: Borneo, Van Niel 4034 and Haviland & Hose 2840. – *I. griffithiana* (Planch.) Hall. f.: Borneo, SAN 39257; Java, Bakhuizen van den Brink f. 5485.  
*Iringia grandifolia* Engl.: Cameroun, Zenker 3328. – *I. malayana* Oliv.: Borneo, SAN 26093.  
*Ixonanthes icosandra* Jack: Burma, Griffith 7841; Sumatra, Bunnemeijer 7687. – *I. petiolaris* Bl.: Borneo, BS 528; Philippines, Olsen 843. – *I. reticulata* Jack: New Guinea, Pullen 7364; China, How 70738; Borneo, Kostermans 7932 and S 12066.  
*Klainedoxa gabonensis* Pierre var. *oblongifolia* Engl. ex De Wild.: Zaire, Louis 6151.  
*Lepidobotrys staudtii* Engl.: Cameroun, Zenker 2951 (isotype); Africa, Le Testu 1265.  
*Linum corymbiferum* Desf.: Algeria, Battandier & Trabut 129. – *L. dolomiticum* Borb.: Hungary, Filarzky et al. 51. – *L. usitatissimum* L.: Crete, Van Soest 305.  
*Ochthocosmus barrae* Hall. f.: Brazil, Froes 25178 (paradermal sections only). – *O. floribundus* Cleason: Venezuela, Steyermark 94198 (ibid.) and Steyermark & Dunsterville s.n. (1977). – *O. multiflorus* Ducke: Venezuela, Wurdack & Adderley 42755 (paradermal sections only); Brazil, Ducke 29033. – *O. roraimae* Benth.: Brazil, Ducke 23421; British Guyana, Maguire & Fanshawe 23348.  
*Philbornea magnifolia* (Stapf) Hall. f.: Sumatra, Toroes 5059; Borneo, S 26203.  
*Phyllocosmus africanus* Klotzsch: Ivory Coast, Leeuwenberg 4556; Zaire, Karmann s.n. – *P. congolensis* (De Wild. & Th. Dur.) Th. & H. Dur.: Zaire, Dacremont 281. – *P. dewevrei* Engl.: Zaire, Karmann s.n. – *P. sessiliflorus* Oliv.: Gabon, Courtet s.n. (Herb. d'Alleizette 903); Cameroun, Zenker 3274 (= type of *Ochthocosmus zenkeri* Hallier f.).  
*Radiola linooides* Roth: Germany, Larsen et al. 69.  
*Reinwardtia cicanoba* (Buch.-Ham. ex D. Don) Hara: India, Hooker & Thomson s.n.: the Netherlands, cult. hort. Leiden s.n. – *R. indica* Dum.: Sri Lanka, Hallier C 249; Nepal, Polunin et al. 3681.  
*Roucheria columbiana* Hall. f.: Columbia, Lehman B.T. 951. – *R. laxiflora* Winkler: Bolivia, Buchtien s.n. – *R. parviflora* Ducke: Brazil, Herb. Rio de Janeiro 23423 (U).  
*Simarouba glauca* D.C.: Florida, Lakela 29580 and Long 1493.  
*Tirpitzia sinensis* Hallier: China, Yunnan, Tsai 61751; Tonkin, Bon 1754/5.

## RESULTS AND DISCUSSIONS

In view of the limited number of species studied per genus, we refrain from detailed generic leaf anatomical descriptions but present the descriptive data in tabular form (tables 1 and 2). Some information not included in the tables will be discussed in the survey of characters. The leaf anatomical diversity in the Linaceae complex lends

itself well for diagnostic purposes, but more material should be studied to test the value of the differences reported here. This lack of comprehensiveness does not invalidate the use of our data for a discussion of overall leaf anatomical similarities or differences in relation to taxonomic delimitation and affinities above the genus level.

### Survey of the leaf anatomical characters with comments on diagnostic and taxonomic value

#### *Indumentum and papillae* (Fig. 1a–d)

Most taxa studied have glabrous leaves. Papillae occur in *Anisadenia* and *Tirpitzia* (here variable below the species level) of the Linaceae s.s., several *Erythroxylum* species (cf. Rury, 1981a & b), *Irvingia* and *Desbordesia* of the Irvingiaceae, and in some Simaroubaceae. Trichomes of the following types occur: (1) Simple unicellular hairs (usually small, sometimes fairly tall) in *Anisadenia* and *Hesperolinon* (Linaceae s.s.), *Hugonia jenkinsii*, and some Simaroubaceae. Unusual, unicellular prickly hairs (i.e., inflated, acuminate cells) characterise *Linum corymbiferum*. (2) Uniseriate hairs occur in *Reinwardtia indica* (Linaceae s.s., in combination with glandular hairs), *Hugonia* section *Hugonia* (with a number of short basal cells and a long top cell), and several Simaroubaceae (Boas, 1913; Metcalfe & Chalk, 1950). (3) Biseriate hairs with multicellular, glandular heads along the leaf margin of *Reinwardtia indica* (numerous in one specimen, exceedingly rare in the other material of this species). (4) Comparable glandular hairs but with thicker multiseriate stalks in *Hesperolinon* (in combination with long, unicellular hairs). Stalked glandular hairs are also reported for some Simaroubaceae (Metcalfe & Chalk, 1950). (5) Tufted hairs are typical for *Ctenolophon* but are restricted to young shoots and floral parts. The mature leaves of *Ctenolophon* are glabrous.

The indumentum of mature leaves is of very limited taxonomic value or above the genus level. Below the genus level the variation in *Linum*, *Reinwardtia* and *Hugonia* is interesting and either coincides with sectional delimitation (*Hugonia*) or perhaps species boundaries (*Linum*, *Reinwardtia*). Further study of more species and specimens would be required to test this and to see whether the remarkable indumentum of *Hesperolinon* is constant for the whole genus. Although absent from the mature leaves, the tufted hairs (stellate in appearance) on young vegetative and mature floral parts of *Ctenolophon* provide an additional argument for the isolated position and family status of this genus.

#### *Epidermal cells (including mucilage and crystalliferous cells)*

The unspecialised epidermal cells vary greatly in size and outline in the taxa studied. Anticlinal walls may be straight to strongly undulating (table 1). As far as tested the genera appear to be fairly constant for this feature, which is surprising in view of the reputedly variable nature of anticlinal epidermal wall outline in many plant groups (cf. Baas et al., 1982: 160).

Cell size varies from  $10 \times 8$ – $146 \times 88 \mu\text{m}$  in the adaxial epidermis, and from  $8 \times 8$ – $125 \times 70 \mu\text{m}$  in the abaxial epidermis. Herbs and shrubs tend to have larger cells than trees.

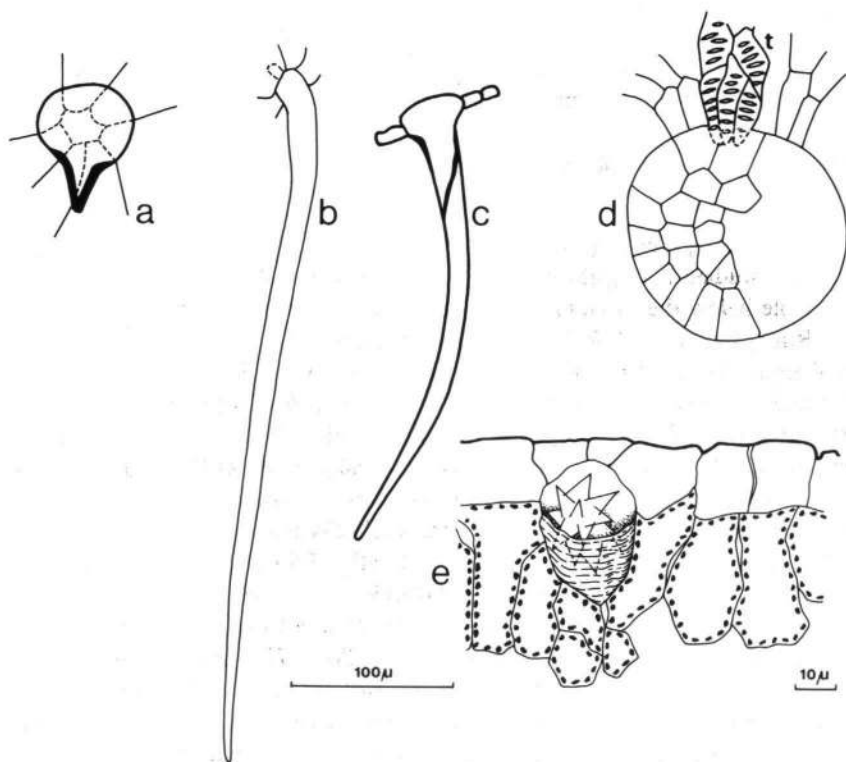


Fig. 1. a–d. Hair types in the Linaceae complex. a. Prickle hair of *Linum corymbiferum*; b. Long unicellular hair of *Anisadenia saxatilis*; c. Uniseriate hair of *Hugonia costata*; d. Stalked gland of *Hesperolinon drymarioides*, t = tracheids in stalk of gland. – e. Subepidermal, inflated cristaque idioblast of *Roucheria laxiflora*. Palisade cells dotted.

Thin, straight anticlinal or periclinal division walls are common in a number of taxa, especially in the adaxial epidermis. Only the occurrence of anticlinal division walls is listed in table 1. They appear to be common, but not constant in the Hugoniaceae and Ixonanthaceae. Their absence is typical for Linaceae s.s. Periclinal division walls are often associated with mucilage cells. The latter are then the internal daughter cells of the subdivided epidermal cells. Undivided epidermal cells may also develop into mucilage cells. The degree of inflation of the mucilage cells varies greatly. Linaceae s.s. and most Hugoniaceae (except two *Hugonia* species and the *Roucheria* species studied by us) are characterised by mucilaginous epidermal cells. Metcalfe and Chalk (1950) reported mucilage cells also for *Roucheria*. The Irvingiaceae, Ixonanthaceae, Erythroxylaceae and Simaroubaceae are variable for presence or absence of mucilage cells (table 1 and data from literature cited in the introduction). *Cteno-*

*lophon* and *Lepidobotrys* lack mucilage cells. The variability of presence or absence of mucilage cells within individual genera (e.g. *Hugonia*, *Erythroxyton*, *Roucheria*) and groups of closely related genera obviously limits the taxonomic value of the character. Yet one can recognise a salient trend for the undisputed Linaceae allies (Linaceae s.s. and Hugoniaceae) to possess mucilage cells. This in turn weakens the case for inclusion of *Lepidobotrys* and *Ctenolophon* in this alliance.

Crystalliferous epidermal cells are of rare occurrence in the Linaceae complex. In the material studied by us cells with druses are confined to species of *Hugonia* (especially *H. afzelii* and *H. costata*). Boas (1931) recorded epidermal cells containing solitary crystals for two genera of the Simaroubaceae: *Rigiostachys* (= *Recchia*) and *Perriera*. Some *Erythroxyton* species are also known to have a similar type of crystalliferous epidermal cells (Solereeder, 1908; Rury, 1981 a & b). In view of the variability below the genus level, presence or absence of crystalliferous epidermal cells cannot be used in the discussion of classification at subfamily or family level.

#### *The stomatal complex* (Figs. 4–12)

Stomata are mostly confined to the abaxial epidermis. Only rarely some woody taxa show infrequent adaxial stomata in the midrib region. In the herbaceous genera *Linum*, *Radiola* and *Hesperolinon* (Linaceae s.s.) adaxial stomata are abundant all over the adaxial surface in addition to abaxial ones. In *Linum* adaxial stomata are apparently not constant for the genus (Rehfous, 1917; Ozhatay, 1981). *Linum tenuifolium* is reported to have only adaxial stomata (Luquet, 1928) in its leaves which are adnate to the stem.

The stomatal type is predominantly paracytic or parallelocytic (2–4 subsidiary cells parallel to the pore). All Linaceae s.s., Hugoniaceae, Erythroxytonaceae, Irvingiaceae and most Ixonanthaceae are constant in this respect. Two species of *Phyllocosmus* and *Humiria balsamifera* have paracytic stomata embedded in an anisocytic to cyclocytic pattern of neighbouring cells (table 1, fig. 6 & 7). In *Lepidobotrys* the stomata are paracytic to laterocytic (terminology according to Den Hartog-Van Ter Tholen & Baas, 1978). *Ctenolophon* has anomocytic to anisocytic stomata. The Humiriaceae and Simaroubaceae are heterogeneous for stomatal type. Humiriaceae are on record to have paracytic, anomocytic to cyclocytic and anisocytic stomata (Solereeder, 1899; Winkler, 1931; Vilhena, 1978) in addition to the special type reported here for *Humiria balsamifera*. Simaroubaceae have anomocytic stomata in several genera (Solereeder, 1899; Metcalfe & Chalk, 1950; Smith & Stern, 1962), but paracytic stomata occur in at least one genus (*Picramnia*; Pyykkö, 1979) and Solereeder's description (1908) of the stomatal complex of *Suriana* is suggestive of anisocytic to cyclocytic stomata. Within the Linaceae complex itself the paracytic stomatal type is an important taxonomic marker, and the anomocytic to anisocytic stomata of *Ctenolophon* provide additional evidence to treat this genus as a separate family.

In the taxa with paracytic stomata, the subsidiary cells usually do not touch at the poles, except in *Cyrrilopsis* and to a lesser extent in some other species in the Ixonanthaceae and Irvingiaceae.

All Hugoniaceae show a remarkable feature of the subsidiary cells: the anticlinal

walls underlying the guard cells are sinuous and show 3 or 4 lobes each (fig. 8). Slightly similar, but less regular lobes (1–6 per subsidiary cell) were found in *Linum dolomiticum*, whilst *Allantospermum borneense* shows one lobe per subsidiary cell (fig. 9). For the Hugoniaceae the regular lobing of the subsidiary cells is highly diagnostic.

In transverse section the stomata are in level with the epidermis. The cuticular ledges vary in conspicuousness. Usually the herbaceous species and small shrubs have less well developed outer and inner ledges than the tree species. Lignified guard cells are diagnostic for *Hugonia*. In *Hebepetalum*, *Roucheria* and *Philbornea* of the Hugoniaceae they also occur, but inconspicuously so in the two former genera. In *Allantospermum* the lignified stomata are not a constant feature (table 1). The literature on Humiriaceae leaf anatomy does not record lignified guard cells, but this character is often neglected; our material of *Humiria* shows weakly lignified guard cells.

#### *The hypodermis*

A complete hypodermis below the entire adaxial surface of the lamina is restricted to *Ochthocosmus* (Ixonanthaceae) and *Hugonia afzelii* (Hugoniaceae). Local hypodermal development in the midrib region as a few translucent parenchymatous to collenchymatous cells is far more common (table 1). The variation pattern of hypodermal development in the Linaceae complex and putative allies is such that it cannot be used for classification at and above the genus level.

#### *The mesophyll*

Most taxa studied have dorsiventral leaves with adaxial palisade tissue of 1–4 cell layers and abaxial spongy tissue of varying compactness. In *Hesperolinon*, *Linum* and *Radiola* the mesophyll is isobilateral in association with the amphistomatic condition of the leaves. In *Irvingia* and *Klainedoxa* (Irvingiaceae) all mesophyll cells are palisade-like.

In the leaf margin the mesophyll is usually modified and consists of translucent, often rather thick-walled isodiametric cells, sometimes transitional towards palisade cells. In *Hesperolinon*, *Linum*, *Radiola*, *Anisadenia* (i.e., all Linaceae except *Tirpitzia*) and *Humiria* the mesophyll of the leaf margin consists of unmodified chlorenchyma.

#### *Midrib and petiole* (figs. 2, 17–19)

The range of vascular patterns in the midrib is illustrated diagrammatically in figure 2. The most simple type of collateral bundle is typical of all Linaceae s.s. A simple arc of collateral vascular tissue occurs in the Hugoniaceae p.p., Ixonanthaceae p.p., *Ctenolophon* and Erythroxylaceae p.p. (Ballard, 1926; Rury, 1981 a & b). This type has also been recorded for *Picramnia* of the Simaroubaceae (Pyykkö, 1979). Arcs with strongly incurved margins intergrade with simple, closed vascular systems in which often an abaxial arc and adaxial 'plate' can be distinguished (most Hugoniaceae, Ixonanthaceae p.p., *Lepidobotrys*, Humiriaceae (cf. Colozza, 1904), Simaroubaceae p.p. (Boas, 1913) and *Desbordesia* of the Irvingiaceae. Complex vascular patterns with 'pith' bundles are relatively rare: *Ochthocosmus* p.p. (Ixonanthaceae),



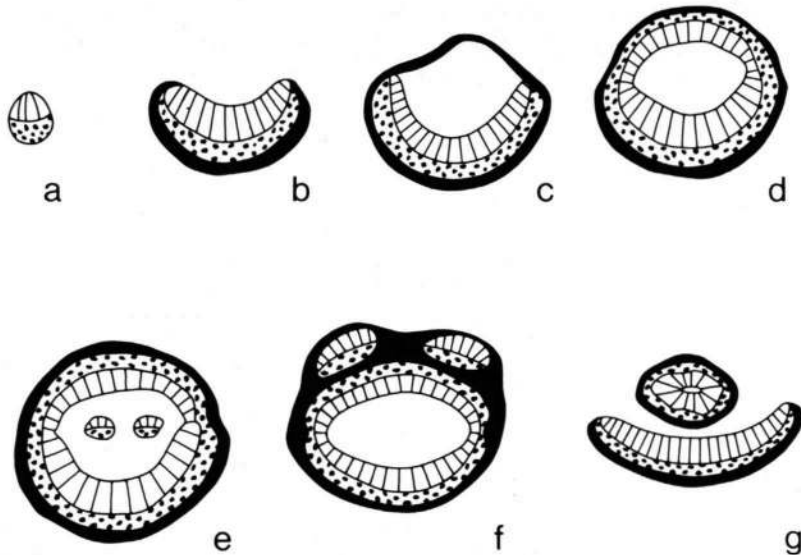


Fig. 2. Types of vascular systems in midrib and distal end of petiole in the Linaceae complex. Xylem hatched; phloem dotted; sclerenchyma black. — a–c. Simple open systems (marked S in table 1); a. ‘reduced’ and without sclerenchyma support; b. with abaxial sclerenchyma; c. with continuous sclerenchyma sheath enclosing adaxial parenchyma (marked +c in table 1). — d. Simple closed (marked C). — e. Complex closed with included bundles (marked CCi). — f. Complex closed with additional adaxial bundles (marked CCA). — g. Complex as in *Allantospermum borneense*.

one *Erythroxyllum* species (Rury, 1981 a & b) and many Simaroubaceae (cf. Jadin, 1901; Boas, 1913; Spiekerkoetter, 1924). Complex systems with adaxial bundles superposed on the more or less cylindrical main system are restricted to the Irvingiaceae and *Hebepetalum* p.p. (Hugoniaceae). In *Allantospermum borneense* the complexity is yet of another type (fig. 1).

The small collateral bundles of the Linaceae s.s. in correlation with the herbaceous or subshrub habit is probably a result of reduction. This is also born out by the total lack of sclerenchyma support in the midrib of most Linaceae s.s.: another likely reduction (cf. Baas et al., 1982 for comparable and argued reductions in the Olacaceae). Within the Hugoniaceae and Ixonanthaceae the simple open vascular systems are provided with a complete cylindrical fibre sheath, enclosing parenchymatous ground tissue like the ‘pith’ parenchyma of taxa with completely closed vascular systems. This might be taken as an indication that these simple open vascular systems are derived from simple closed systems. The more complex systems might also be derived from these simple cylindrical (stelar) systems. It is, however,

likely that increased complexity or reduction evolved as parallel specialisations several times in the Linaceae complex and other related or unrelated assemblages. Judging from the variation within the genera *Allantospermum*, *Ochthocosmus* and *Hugonia*, and within the species *Hebepetalum humiriifolium* (table 1) the steps from one character state to another must have occurred several times within closely knit groups (table 1).

The vascular system of the petiole is basically similar to that of the midrib. At the basis it is commonly more open and provided with less sclerenchyma fibres. At the distal part it is virtually identical to the midrib pattern halfway the lamina. *Desbordesia* (Irvingiaceae) is exceptional in showing a complex vascular system with adaxial bundles in the petiole and a simple closed system in the midrib.

#### *Secondary and minor veins*

As in most dicotyledons the secondary and minor veins are provided with collateral bundles with a varying amount of supporting sclerenchyma. Only the Linaceae s.s. without sclerenchyma support in the midrib also lack sclerenchyma fibres in the other veins (see above and table 1). Apart from a (partial) sclerenchymatous bundle sheath, there is an outer parenchymatous bundle sheath which is often crystalliferous (see under crystals).

Two characters of the veins are of taxonomic interest, viz., presence or absence of vertical bundle sheath extensions (resulting in so-called vertically transcurrent veins), and of a continuous marginal bundle heavily provided with, or almost entirely consisting of sclerenchyma fibres. Vertical bundle sheath extensions linking the veins either to the upper epidermis only, or to both epidermises are a feature of several Ixonanthaceae, *Erythroxyllum* p.p. (cf. Rury, 1981 a & b), Irvingiaceae, *Lepidobotrys*, and *Philbornea* of the Hugoniaceae. Fibrous marginal bundles were found in *Anisadenia* (Linaceae s.s.), several Ixonanthaceae (cf. table 1), *Lepidobotrys*, *Ctenolophon* p.p., and the Irvingiaceae.

#### *Crystals and cristarque cells* (Figs. 1e, 13, 14)

The crystal complement in the taxa studied shows the usual types of solitary, rhomboidal crystals and druses (intergrading with clustered crystals) either in combination or with only one type represented (table 1). Three genera of the Linaceae s.s. typically lack crystals (table 1).

Cristarque cells, i.e., crystalliferous cells with a unilaterally thickened and lignified cell wall (Van Tieghem, 1902, 1903) occur in various degrees of conspicuousness and in different distribution patterns:

1. cells containing solitary crystals and restricted to bundle sheath cells in *Anisadenia*, *Hebepetalum*, *Allantospermum* p.p., *Lepidobotrys*, *Ctenolophon* and Erythroxyllaceae p.p. This type of distribution pattern renders the cristarque cells very inconspicuous because the lignified wall portions adjoin the lignified fibres of the inner sclerenchymatous bundle sheath (fig. 14).
2. as 1, but also dispersed throughout the ground tissue of petiole and midrib, or especially numerous in subepidermal layers of the petiole. This distribution pat-

tern makes the cristarque cells a quite striking feature of the leaf anatomy in most Hugoniaceae, *Phyllocosmus* p.p. (Ixonanthaceae), Erythroxylaceae p.p., and all Irvingiaceae (fig. 13).

3. inflated cristarque cells containing druses in the mesophyll directly below the epidermis of *Roucheria* (Hugoniaceae, fig. 1 e).

As pointed out before (Baas, 1972) cristarque cells are more common in woody dicotyledons than apparent from the descriptive literature. Especially the cristarque cells of bundle sheaths have often been overlooked probably because of the similar staining properties of the unilateral wall thickenings and the fibres they adjoin. Their abundance in the ground tissue of Hugoniaceae and Irvingiaceae is of great taxonomic interest. Their sporadic occurrence in species of other families of the Linaceae complex is more difficult to evaluate.

#### *Sclereids* (Figs. 15, 16)

Thin- to thick-walled brachysclereids confined to the ground tissue of petiole and midrib are of rare and variable occurrence in some of the Hugoniaceae (*Hebepetalum*, *Indorouchera*, *Philbornea*) and Ixonanthaceae (*Cyriolopsis*, *Ixonanthes*, *Ochthocosmus*). In none of these genera they are constant; sometimes presence or absence even varies below the species level.

Mesophyll sclereids are of greater diagnostic value in the taxa studied. Slender, filiform sclereids occur in *Roucheria* (Hugoniaceae), *Ochthocosmus*, *Phyllocosmus* (Ixonanthaceae) and several Simaroubaceae (our data and literature cited before; other Simaroubaceae lack sclereids). In the literature there are also records of mesophyll sclereids in Humiriaceae (Colozza, 1904; Hallier, 1923), in Erythroxylaceae (Ballard, 1926; Rury, 1981 a & b) and Irvingiaceae. The latter record may be doubtful, because Hallier (1923) erroneously reported foliar sclereids as a constant feature of Irvingiaceae, and presence of subepidermal sclereids in two *Irvingia* species (Jadin, 1901) was later contradicted by Van Tieghem (1903). Our material of *Irvingia* only showed sporadic, very inconspicuous sclerified cells branching away from the bundle sheaths, but these are not comparable with the foliar sclereids found in the other families. The latter show various degrees of branching, thus forming a three-dimensional network of varying density or are largely unbranched as in *Roucheria* (Hugoniaceae) and *Eurycoma* (Simaroubaceae).

A very special type of sclereid is found in *Ochthocosmus* (Ixonanthaceae), viz. tracheoidal idioblasts (fig. 15). Solereder (1899) already referred to these spindle-shaped cells with densely coiled spiral secondary walls as 'eigentümliche Spiraltracheiden'. In the literature similar cells have been described for *Xanthophyllum* (Dickison, 1973), *Nepenthes* (Solereder, 1899), *Pogonophora* (Foster, 1956), and several Orchidaceae (Olatunji & Nengim, 1980). In *Ochthocosmus* they are independent of the vascular bundles of the veins, and are scattered in the mesophyll together with 'normal' branched foliar sclereids. Their constant occurrence in *Ochthocosmus* provides a strong argument against lumping *Phyllocosmus* (where they are always absent) with the former genus as proposed by Hallier (1923) and Kool (1980).

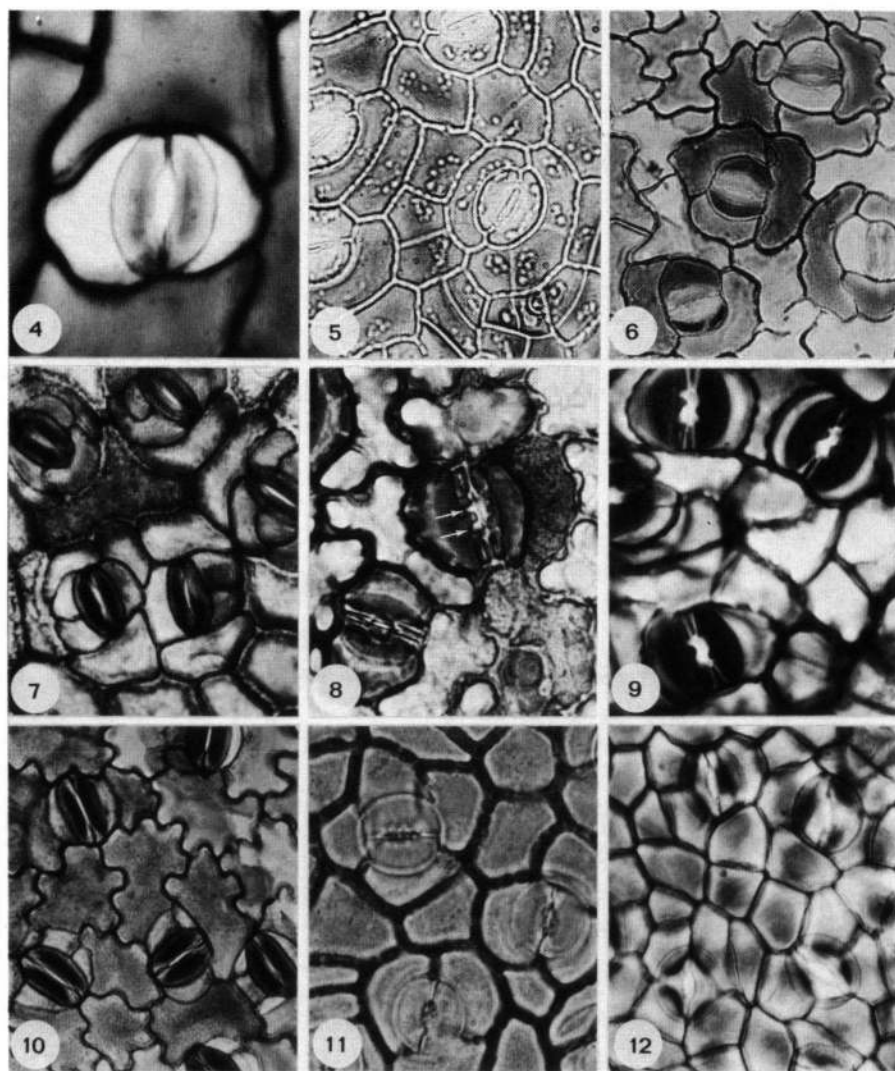


Fig. 4–12. — 4. *Linum corymbiferum*. Paracytic stomatal complex;  $\times 550$ . — 5. *Cyrallopsis parapsis*. Parallelocytic stomata with subsidiary cells touching at the poles;  $\times 350$ . — 6. *Phyllocosmos sessiliflorus*. Paracytic stomata embedded in anisocytic pattern;  $\times 350$ . — 7. *Humiria balsamifera*. Paracytic to laterocytic stomata embedded in anisocytic pattern;  $\times 350$ . — 8. *Hugonia castanea*. Paracytic stomata with lobing of subsidiary cells below guard cells (arrows);  $\times 550$ . — 9. *Allantospermum borneense*. Paracytic stomata with one lobe per subsidiary cell beneath each guard cell;  $\times 550$ . — 10. *Lepidobotrys staudtii*. Laterocytic to paracytic stomata;  $\times 350$ . — 11. *Ctenolophon parvifolius*. Anisocytic to anomocytic stomata;  $\times 550$ . — 12. *Eurycoma longifolia*. Anomocytic stomata;  $\times 350$ .

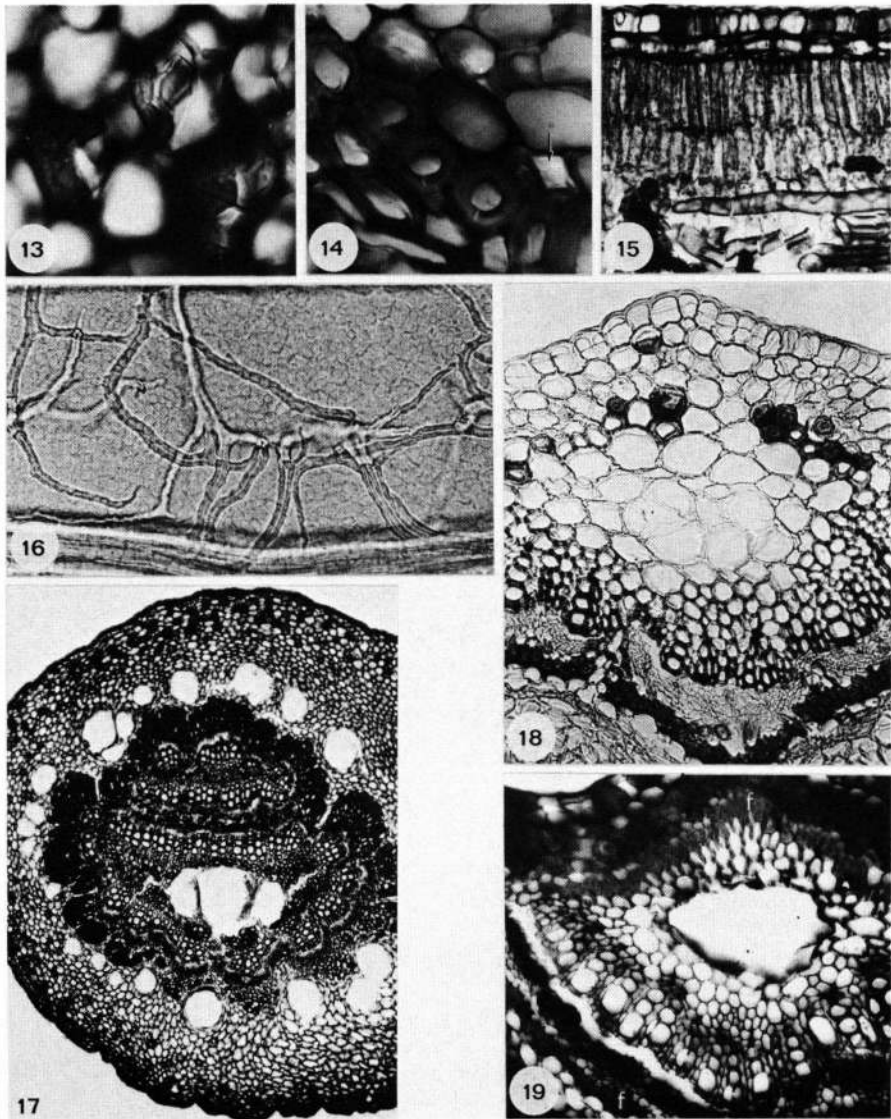


Fig. 13–19. – 13. *Indorouchera griffithiana*. Conspicuous cristarque cells in peripheral ground tissue of petiole;  $\times 220$ . – 14. *Lepidobotrys staudtii*. Inconspicuous cristarque cell (arrow) adjoining fibre sheath in midrib;  $\times 550$ . – 15. *Ochthocosmus roraimae*. Tracheoidal idioblast in mesophyll;  $\times 140$ . – 16. *Phyllocosmus dewevrei*. Foliar sclereids in leaf clearing;  $\times 140$ . – 17. *Irvingia grandifolia*. Petiole with complex vascular system and mucilage cavities;  $\times 35$ . – 18. *Indorouchera contestiana*. Midrib with thin-walled cells in central ground tissue;  $\times 140$ . – 19. *Indorouchera griffithiana*. Midrib with central cavity and traces of collapsed cells (f = fibres);  $\times 140$ .



<b>Hugoniaceae</b>												
<i>Hebepetalum humiritifolium</i>												
<i>Hugonia</i> section <i>Hugonia</i>												
<i>H. afzelii</i>	u	-	-	-	-	-	-	-	-	-	-	r, d
<i>H. castanea</i>	u	+	-	+	+	+	+	+	+	+	+	r, d
<i>H. costata</i>	u	-	+	+	+	+	+	+	+	+	+	r, d
<i>Hugonia</i> section <i>Durandea</i>												
<i>H. jenkinsii</i>	s-c	+	±	+	+	+	+	+	+	+	+	r, d
<i>H. racemosa</i>	s-c	+	±	+	+	+	+	+	+	+	+	r, d
<i>Indorouchera</i>												
<i>I. contestiana</i>	c-u	+	-	+	+	+	+	+	+	+	+	r, d
<i>I. griffithiana</i>	c-u	+	-	+	+	+	+	+	+	+	+	r, d
<i>Philbornea magnifolia</i>	c-u	+/-	+/-	+	+	+	+	±	-/±	+	+	r, d
<i>Roucheria</i>												
<i>R. columbiana</i>	s	±	-	+	±	+	-	-	-	±	-	d
<i>R. laxiflora</i>	s-c	-	-	+	±	+	-	-	-	±	-	d
<i>R. parviflora</i>	s-c	-	-	+	±	+	-	-	-	+	-	r, d
<b>Ixonanthaceae</b>												
<i>Allantospermum</i>												
<i>A. borneense</i>	c-u	+/-	-	+	±	+/-	+	+	+	+	+	r, d
<i>A. multicaule</i>	c-u	-	-	-	-	-	-	-	-	-	-	r, (d)
<i>Cyrtolopsis paraensis</i>	s-c	+	-	-	+	+	+	±	±	±	±	r
<i>Ixonanthes</i>												
<i>I. icosandra</i>	s-c	-	-	-	±	-	-	-	-	-	-	r, d
<i>I. petiolaris</i>	s	+	+	-	-	-	-	±	-	-	-	r, d
<i>I. reticulata</i>	s	+	+/-	-	-	-	-	-	-	-	-	r, d/-
<i>Occhocosmus</i>												
<i>O. barrae</i> (paradermal)	s-c	±	-	-	-	-	-	-	-	+	+	r, d
<i>O. floribundus</i>	s-c	±	-	-	-	-	-	-	-	+	+	r, d
<i>O. multiflorus</i>	s-c	±	-	-	-	-	-	-	-	+	+	r, d

(continued on the next pages)

(Table 1 continued)

Species studied	epidermis				stomata														
	antichlinal wall outline	antichlinal division walls	mucilage cells	crystaliferous cells	axially common	type(s)	lighted guard cells	lobes on subsidiary cells	subsidiary cells touching at poles	hypodermis	vascular system of midrib and petiole	sclerenchyma support in midrib	continuous, sclerenchymatous marginal bundle	veins vertically transcurrent	secretory cavities or ducts	mesophyll sclereids	tracheoidal idioblasts	crystal cells	crystal complement
<i>O[chthocosmus] rorainae</i>	s-c	±	-	-	-	P	-	-	±/-	+/1	CCi	+	-	-	-	+	+	-	r, d
<i>Phyllocosmus</i>																			
<i>P. africanus</i>	c-u	+	+	-	-	P	-	-	±	-	C	+	-	-	-	+	+gt	-	r, d
<i>P. congolensis</i>	c-u	+	-	-	-	P	-	-	±	-	C	+	-	-	-	+	+gt	-	r
<i>P. deweyrei</i>	s-u	+	-	-	-	P	-	-	-	1	C	+	-	-	-	+	+gt	-	r
<i>P. sessiliflorus</i>	c-u	+	-	-	-	PAi	-	-	-	-	C	+	+	-	-	+	-	-	r, d
<i>P. zenkeri</i>	c-u	+	-	-	-	PAi	-	-	-	1	C	+	+	-	-	+	-	-	r, d
<b>Humiriaceae</b>																			
<i>Humiria balsamifera</i>	s	+	+	-	-	PAi	±	-	-	1	C	+	-	-	-	-	-	-	(r), d
<b>Erythroxylaceae</b>																			
<i>Aneulophus africana</i>	s-u	-	+	-	-	P	-	-	-	1	S	+c	-	-	-	-	+	(gt)	r, (d)
<i>Erythroxylum</i>																			
<i>E. cuneatum</i>	s	-	+	-	-	P	-	-	-	1	S	+	-	-	-	-	-	-	r, (d)
<i>E. ecartnatum</i>	s-c	-	±	-	-	P	-	-	-	1	S(-C)	+	-	-	-	-	-	-	r



<b>Irvingiaceae</b>																				
<i>Desbordesia glaucescens</i>	u	-	+	-	-	P	-	-	±	-	CCa-C	+	±	+	-	-	-	+gt	-	r
<i>Irvingia</i>																				
<i>I. grandifolia</i>	c-u	+	+	-	-	P	-	-	±	-	CCa	+	+	+	-	-	-	+gt	-	r
<i>I. malayana</i>	s-u	-	+	-	-	P	-	-	±	-	CCa	+	+	+	-	-	-	+gt	-	r, (d)
<i>Klainedoxa gabonensis</i>	c-u	±	+	-	-	P	-	-	±	-	CCa	+	±	+	-	-	-	+gt	-	r, d
<b>Lepidobotryaceae</b>																				
<i>Lepidobotrys staudtii</i>	u	-	-	-	-	P-L	-	-	-	-	l	C	+	±	(±)	-	-	+	-	r, (d)
<b>Ctenolophonaceae</b>																				
<i>Ctenolophon parvifolius</i>	s	-	-	-	-	Al-o	-	-	-	-	-	S	+c	±/-	-	-	-	±	-	r, (d)
<b>Simaroubaceae</b>																				
<i>Eurycoma longifolia</i>	c-u	-	-	-	-	Al	-	-	-	-	l	CCi	+	-	-	-	+	-	-	r, d
<i>Simarouba glauca</i>	s	-	±	-	-	Al	-	-	-	-	l	CCi	+	-	-	+	+	-	-	(r), d

*Explanation of symbols:* + = character present; - = character absent; ± and () = character poorly developed or infrequent. Anticlinal wall outline: c = curved, s = straight, u = undulating. Stomatal type: Ai = anisocytic; Ao = anomocytic; C = cyclocytic; L = laterocytic; P = paracytic; PAi = paracytic embedded in anisocytically arranged surrounding cells. Lobes on subsidiary cells: + = 3-4 regular lobes per cell; i = irregularly lobed; l = one lobe per cell. Hypodermis: l = locally developed in midrib region only. Vascular system of midrib: S = simple open; C = simple closed; CC = complex closed, a = with adaxial bundles, i = with medullary bundles, \* = special type, see fig. 2. Sclerenchyma support: +c = sclerenchyma forming a complete or almost complete cylinder enclosing parenchymatous ground tissue adaxially from the simple open vascular system. Cristarque cells: + = present in bundle sheath only; gt = present throughout ground tissue. Crystals: d = druses or clusters; r = rhomboidal, solitary crystals. Ranges and transitional character states are hyphenated. Variability below the species level is indicated as e.g. +/-.

### *Secretory structures* (Figs. 17–19)

External secretory structures in the form of glandular teeth along the leaf margin, or extrafloral nectaries are widespread in the Linaceae complex and also in the Simaroubaceae. Their anatomy has been discussed by Bélin-Depoux (1978) and their presence is routinely recorded in the taxonomic literature (e.g., Van Hooren & Nooteboom, 1984; Steyermark & Luteyn, 1980). Here they will not be further discussed. For glandular hairs see above under indumentum.

Apart from the mucilage cells derived from the epidermis (see above) several Linaceae s.s. (*Reinwardtia*, *Tirpitzia*) and Hugoniaceae (*Hebepetalum*, *Indorouchera*, *Philbornea*, and doubtfully also *Roucheria* p.p.) have mucilage cells scattered in the ground tissue of midrib and/or petiole. In *Hebepetalum* they even occur scattered in the mesophyll of the lamina.

Secretory cells containing oil or resin occur in the petiole of several Simaroubaceae according to Solereder (1899) and Metcalfe & Chalk (1950) but are by no means a constant feature of that family.

Secretory canals or cavities are a well-known feature of the petiole and midrib ground tissue of the Irvingiaceae and several Simaroubaceae (Solereder, 1899; Metcalfe & Chalk, 1950). In Irvingiaceae they contain mucilage. For Simaroubaceae the contents have been described as resinous. In *Indorouchera* p.p., *Roucheria parvifolia* and *Philbornea* p.p. (Hugoniaceae) poorly defined cavities were observed (figs. 18 & 19) in the central ground tissue of the midrib, possibly originating through the breakdown of thin-walled cells. These cavities might be considered transitional between the conspicuous mucilage ducts of the Irvingiaceae and complete absence of secretory cavities. Similar 'incipient' cavities were found in the peripheral ground tissue of *Lepidobotrys*, but here they were probably of traumatic origin.

## DISCUSSIONS

### *Taxonomic implications*

In the following the leaf anatomical diversity in the Linaceae complex and their putative relatives will be discussed in relation to taxonomic delimitation at and above the genus level. Since it is impossible and undesirable to base a classification on leaf anatomical characters alone, the traditionally recognised suprageneric taxa (tribes, subfamilies or families) will be surveyed first. Their possible mutual relationships as based on leaf anatomical characters in addition to vegetative, pollen and flower morphology and wood anatomy will be subsequently discussed.

### *Linaceae s. s.*

The six Linaceae genera form a leaf anatomically coherent group characterised by paracytic stomata, epidermal mucilage cells, simple vascularisation of the midrib and total absence or at least paucity of mechanical tissue. *Hesperolinon*, *Linum* and *Radiola* moreover share adaxial stomata, isobilateral mesophyll and absence of crystals. *Tirpitzia* is exceptional with fairly well developed sclerenchyma support of the vascular bundle of the midrib. *Anisadenia* also has some midrib sclerenchyma and stands

out within this group through its fibrous marginal bundle and cristarque cells. These features can be used in support of a somewhat isolated position of *Anisadenia* in the Linaceae, as also implied in Hallier's (1923) distinction of 'Anisadenieen' and Winkler's (1931) recognition of a separate tribe for the genus. *Tirpitzia* is sometimes said to be intermediate between *Anisadenia* and the other Linaceae s.s., but its leaf anatomy is not truly intermediate, although within the Linaceae s.s., *Anisadenia* shares the midrib sclerenchyma. Both *Anisadenia* and *Tirpitzia* provide links between the leaf anatomically very simple (presumably reduced) and more elaborate (presumably more primitive) groups of the Linaceae complex. The predominant absence of sclerenchyma and crystals and presence of amphistomatic leaves in three genera is related to habit (herbs or small shrubs) in this group.

### *Hugoniaceae*

The Hugoniaceae are leaf anatomically very strictly defined by their shared possession of lobed subsidiary cells and cristarque cells in the ground tissue of petiole and midrib (only in *Hebepetalum* the cristarque cells are restricted to bundle sheaths); paracytic stomata are another constant feature of this group. Variable characters which yet predominate in the Hugoniaceae are mucilage cells, lignified guard cells, and a simple closed vascular system of the midrib. If the vascular system is open, there is still a continuous cylinder of sclerenchyma fibres.

Other leaf anatomical characters help to define genera or sections: *Roucheria* stands out on account of its subepidermal cristarque cells containing druses and its mesophyll sclereids; *Indorouchera* has unligified guard cells; *Philbornea* has partly vertically transcurrent veins; within the genus *Hugonia*, section *Hugonia* differs from section *Durandea* because of its indumentum of uniseriate hairs and undulating anticlinal epidermal cell walls (cf. survey of characters and table 1).

The ill-defined cavities presumably resulting from the break-down of the central ground tissue of the midrib in *Indorouchera* p.p. and *Philbornea* p.p. might be indicative of a tendency to form lysigenous secretory cavities.

### *Ixonanthaceae and Allantospermum*

The Ixonanthaceae are leaf anatomically rather diverse. They could only be defined by the absence of characters which define the putatively related groups and constant presence of characters which are also of quite common occurrence outside the Ixonanthaceae (cf. tables 1 and 2). Positive characters for most Ixonanthaceae are presence of anticlinal division walls, paracytic stomata (embedded in an anisocytic pattern of surrounding cells in two *Phyllocosmus* species only) and some form of hypodermal development. Negative characters include unligified guard cells, unlobed subsidiary cells (except *Allantospermum* where the subsidiary cells have one lobe each in one species) and absence of secretory cavities. The various midrib and petiole vascular systems are not so different if one considers the simple open systems with continuous, cylindrical fibre sheaths in *Cyrillopsis* and *Ixonanthes* as a reduction of the simple closed system as occurs in *Phyllocosmus* and *Ochthocosmus* p.p. The complex system with included medullary bundles of *Ochthocosmus* p.p. can be interpreted as an elaboration on this basic pattern.

The two species of *Allantospermum* are rather different from each other, but leaf anatomically they could both be included in the Ixonanthaceae without increasing its heterogeneity to any great extent (cf. tables 1 and 2).

*Cyrillopsis*, only recently incorporated in the Ixonanthaceae (for supporting evidence see Forman, 1965; Nooteboom, 1967; Hutchinson, 1973, and Kool, 1980) fits well leaf anatomically, and is especially close to *Ixonanthes*. Previous assignments to Irvingiaceae (Robson & Airy Shaw, 1962), Celastraceae and Cyrillaceae would find less leaf anatomical support. This conclusion is based on comparing slides of representatives of these families in the Rijksherbarium reference collection and on data from the literature.

The subdivision of *Ixonanthes* into two sections: *Brewstera* (*I. icosandra*) and *Ixonanthes* (the other two species) as suggested by Hallier (1923) and maintained by Kool (1980) finds some support in leaf anatomy: *I. icosandra* stands out through its lack of anticlinal divisions in the epidermal cells, of mucilage cells (also absent from one *I. reticulata* specimen) and of a locally developed hypodermis (cf. table 1).

The genera *Ochthocosmus* and *Phyllocosmus* have been combined by Hallier (1923) and again by Kool (1980) in opposition to Forman (1965). Through the shared branched foliar sclereids the two genera are indeed mutually close, but the remarkable tracheoidal idioblasts, constant and exclusive for *Ochthocosmus* s.s. provide a significant argument to keep both genera apart. Within *Phyllocosmus* the two sections *Decastemon* (in our material represented by *P. sessiliflorus* and *P. zenkeri*) and *Phyllocosmus* (the other species) differ somewhat in their leaf anatomy. Section *Phyllocosmus* has cristarque cells albeit in low frequency and indistinct, whilst these are absent from *Decastemon*. The latter section moreover stands out on account of its epidermal cell pattern of the stomatal complex (paracytic in anisocytic pattern of surrounding cells). Yet these differences are in our opinion less significant than the major difference between the genera *Ochthocosmus* and *Phyllocosmus*.

#### *Lepidobotryaceae*

This monotypic family has a leaf anatomy without striking features. Within the families studied, *Lepidobotrys* stands out somewhat through its tendency for laterocytic stomata in addition to paracytic ones. Other noteworthy characters are the vertical bundle sheath extensions of some of the veins and the cristarque cells. This combination of characters is quite common in the Ixonanthaceae but leaf anatomy by itself is too 'characterless' in *Lepidobotrys* to oppose claims for closer affinity with Oxalidaceae by several authors (Hallier, 1923; Knuth, 1931) or to support Léonard's (1950, 1958) family concept for the genus. Leaf anatomy is neutral with respect to treatment in or near the Oxalidaceae or between Linaceae s.s. and Erythroxylaceae (as suggested by Léonard l.c.). See Metcalfe & Chalk (1950) for an account of Oxalidaceae leaf anatomy.

#### *Ctenolophonaceae*

*Ctenolophon* differs from the Linaceae complex through its anomocytic to anisocytic stomata. Other leaf anatomical characters of this monogeneric family are of a very common nature and do not allow conclusions of phylogenetic affinity. The in-

dumentum of the calyx and young vegetative parts (stellate hair tufts) also separate *Ctenolophon* from the Linaceae and its close allies, as well as from all other families considered in this study. Affinities with the Linaceae complex as reflected in the alignment of Ctenolophonaceae in the same order in most recent classification systems of angiosperms cannot be refuted in view of much larger leaf anatomical ranges in other doubtlessly natural groups (cf. Baas, 1975 and Baas et al., 1982 for diversity within the single genus *Ilex*, and the coherent family of the Olacaceae). The sporadic occurrence of cristarque cells might even be cited in favour of such an alliance, although these cells are also known to occur in Celastraceae (Jansen & Baas, 1973) and Olacaceae (Baas et al., 1982); families to which *Ctenolophon* was once assigned (Oliver, 1873; Hallier, 1912, 1923).

#### *Humiriaceae*

The Humiriaceae are leaf anatomically quite diverse (cf. Solereder, 1899, 1908; Colozza, 1904; Metcalfe & Chalk, 1950; Vilhena, 1978 in addition to our data on one species only). Especially the range of stomatal types is considerable and together with a rather general combination of other leaf anatomical characters this opens possibilities to advocate affinities with almost all the taxa considered in this study. The paracytic stomata embedded in an anisocytic pattern of surrounding epidermal cells of *Humiria* recall *Phyllocosmus* p.p. of the Ixonanthaceae; the stomata of *Endopleura* (Vilhena, 1978) could be compared to the anomocytic to anisocytic stomata of *Ctenolophon*; the tendency towards laterocytic stomata in *Humiriastrum* (Vilhena, 1978) and to some extent also in *Humiria* are reminiscent of *Lepidobotrys*. The paracytic stomata of *Vantanea* (Metcalfe & Chalk, 1950) link the family to the Linaceae complex.

In most modern systems the Humiriaceae are treated as a separate family in the same order as the Linaceae. Thorne (1981) and Melchior (1964) consider it a subfamily of the Linaceae. Leaf anatomy is neutral to either treatment, and certainly not in conflict with presumed affinities between Humiriaceae and Linaceae. A comprehensive study of all species would doubtlessly be rewarding as a contribution towards generic characterisation and to indicate which members of the Linaceae complex are closest to the Humiriaceae.

#### *Erythroxylaceae*

There is a general consensus of opinion to treat Erythroxylaceae as a separate family in the same order as the Linaceae. Leaf anatomy comprehensively studied by Rury (1981a & b) and our own results (table 1) fully confirm the affinities with Linaceae s.s., Ixonanthaceae and Humiriaceae. Within the family there is an interesting diversity which can partly be interpreted as ecological adaptations (Rury, l.c.).

#### *Irvingiaceae, Simaroubaceae and Allantospermum*

Mostly treated as a subfamily in the Simaroubaceae, the Irvingioideae or Irvingiaceae constitute a leaf anatomically very coherent group, characterised by epidermal mucilage cells, paracytic stomata, mostly complex vascular systems in petiole and midrib with adaxial bundles in addition to a closed cylinder, vertically transcurrent

Table 2. Summary table of important leaf anatomical characters based on table 1 and data from the literature cited in the text. Legend as table 1.

	Mucilage cells	Stomatal type	Lobes on subsidiary cells	Midrib vascular system	Sclerenchyma support of midrib	Veins vertically transcurrent	Secretory cavities or ducts	Cristarque cells
Linaceae s.s.	+	P	-(i)	S	-(+)	-	-	-(+)
Hugoniaceae	+/-	P	+	S-C(-CCa)	+	-(±)	-(±)	+gt(+)
Ixonanthaceae	+/-	P(PAi)	-	S-C-CCi	+	-(±)	-	-(+gt)
Allantospermum	-	P	-(1)	S-CC*	+	+/-	-	+/-
Humiriaceae	+/-	P/Ai/Ao/C	-	S-C	+	-	-	-
Erythroxylaceae	+/-	P	-	S-C(-CCi)	+	+/-	-	-/+gt)
Irvingiaceae	+	P	-	(C-)CCa	+	+	+	+gt
Lepidobotryaceae	-	P-L	-	C	+	±	(±)	+
Ctenolophonaceae	-	Ai-o	-	S	+	-	-	±
Simaroubaceae	+/-	Ao/Ai/C/P	-	S-C-CCi	+	-?	+/-	-?

veins, conspicuous mucilage ducts in petiole and midrib, and abundant conspicuous cristarque cells throughout petiole and midrib. This combination of characters is typically absent in the Simaroubaceae s.s., but in view of the rather great leaf anatomical diversity in the Simaroubaceae affinities with Irvingiaceae cannot be absolutely denied. The secretory ducts which characterise several Simaroubaceae are apparently different from those of the Irvingiaceae because of their resinous or fatty contents and possibly also in their ontogeny. Jadin (1901) and Boas (1913) have already stressed the leaf anatomical distinction of the *Irvingia* alliance from the Simaroubaceae as based on a much more representative sample than studied by us. The recognition of the family Irvingiaceae (cf. Pierre, 1886; Van Tieghem, 1905; Cronquist, 1981) as distinct from the Simaroubaceae is therefore fully supported by leaf anatomy. The problem of assigning the family to the Rutales or Sapindales (where Simaroubaceae belong) or to the Linaceae alliance is more complex, as discussed below.

Capuron (1965), Nooteboom (1967) and Muller (1972) have advocated a position of *Allantospermum* in the Irvingiaceae as opposed to the treatment by Forman (1965) of the genus in the Ixonanthaceae, a view partly supported by anatomical evidence by Metcalfe et al. (1968) and Rojo (1968) and adopted by Airy Shaw (1973), Hutchinson (1973) and Cronquist (1981). The leaf anatomical evidence favours the

latter treatment. *Allantospermum* lacks the mucilage canals and profuse cristarque cells in the ground tissue of petiole and midrib, so typical for the Irvingiaceae, whilst there are no major differences with Ixonanthaceae.

For similar reasons why Irvingiaceae should be considered distinct from the Simaroubaceae, their treatment as Irvingioideae in the Ixonanthaceae advocated by Forman (1965) and Airy Shaw (1973) cannot be supported. However, the implied recognition of affinities between Irvingiaceae and the Linaceae complex does find support in leaf anatomy. In their foliar anatomy the Hugoniaceae are, however, closer to the Irvingiaceae than the latter are to the Ixonanthaceae. This is mainly through the shared, profuse cristarque cells and incipient (?) mucilage cavities of some Hugoniaceae (cf. tables 1 and 2).

The possibilities of fairly close affinities of Irvingiaceae with both the Simaroubaceae and the Linaceae complex would support a broad ordinal concept of Geraniales as adopted in several classical systems, including both Geraniales s.s., Linales and Rutales of some modern systems.

#### Preferred taxonomic treatment and arguments from other disciplines

The leaf anatomical diversity combined with alternative suggestions on family delimitation in the literature have induced us to favour the following treatment:

<i>Family (number of genera)</i>	<i>Affinity</i>
Linaceae s.s. (6)	Linaceae complex
Hugoniaceae (5)	Linaceae complex
Ixonanthaceae (5, including <i>Allantospermum</i> and <i>Cyrillopsis</i> )	Linaceae complex
Humiriaceae (8)	Linaceae complex
Erythroxylaceae (4)	Linaceae complex
Ctenolophonaceae (1)	Doubtful
Lepidobotryaceae (1)	Doubtful, Oxalidaceae or Linaceae complex
Irvingiaceae (3)	Linaceae complex or Rutales, or both
Simaroubaceae (c. 20)	Rutales

Wood anatomy (cf. Heimsch, 1942; Heimsch & Tschabold, 1972; Metcalfe & Chalk, 1950; Webber, 1936; Thomas, 1960, and Rojo, 1968) is not in conflict with this treatment. All members of the Linaceae complex are characterised by fibres with distinctly bordered pits and tend to have large and simple vessel-ray pits. The vessel perforations are scalariform (Hugoniaceae p.p., Humiriaceae), exclusively simple or simple with occasional scalariform or vestigially scalariform plates. The rays are typically heterocellular (Kribs heterogeneous types I–III) or entirely composed of erect cells in the small shrubs and herbs of the Linaceae s.s. *Hugonia* and *Allantospermum* are exceptional with small, half-bordered vessel-ray pits. The wood of *Ctenolophon* resembles that of Humiriaceae in essential characters, but since these are all unspecialised, this does not necessarily imply true affinity. Simaroubaceae and Irvingiaceae have libriform fibres, but Irvingiaceae share the large vessel-ray pits with the Lina-

ceae complex. Although *Allantospermum* is somewhat apart from the other Ixonanthaceae its wood fits this family better than the Irvingiaceae (Rojo, 1968 and original observations). The wood of *Lepidobotrys* is too poorly known to enter the discussion here.

Pollen morphology (Erdman, 1952; Metcalfe et al., 1968; Oltmann, 1971; Saad, 1962a & b) can be variously interpreted if one considers that the affinities of *Allantospermum* have been advocated to be with Ixonanthaceae by Lobreau (in Metcalfe et al., 1968) and Oltmann (1971) and with Irvingiaceae by Muller (1972) emphasising different aspects of the same pollen types. In these papers the pollen morphology is interpreted in favour of either a Linaceae alliance or a Simaroubaceae alliance for both Irvingiaceae and Ixonanthaceae. According to Oltmann all members here regarded as families in the Linaceae complex and Irvingiaceae, *Ctenolophon* and *Lepidobotrys* have sufficiently distinct pollen to advocate their family status. The pollen of *Cyrillopsis* (Ixonanthaceae) has been described as belonging to the 'Celastraceae type' (Thomas, 1960), and the pollen of *Lepidobotrys* has been found similar to that of the Oxalidaceae genera *Dapania* and *Sarcotheca* (Oltmann, 1971).

On a combination of various characters such as petal appendages, number of ovules per locule, presence or absence of an obturator and an intra- or extrastaminal disk, the different taxa of the Linaceae complex and their putative allies are readily separable, which is reflected in the suprageneric rank (tribe, subfamily or family) awarded to them in all systematic treatments.

Balancing the leaf anatomical evidence with the multitude of data from other disciplines (only fragmentarily cited above, but all taken into account in our analysis) is very difficult, partly because the leaf anatomy in itself does not provide unambiguous arguments to stress either the similarities or differences between the groups. For instance, the sporadic occurrence of cristarque cells (*Anisadenia*) and sclerenchyma support of the midrib (*Tirpitzia*) can be cited in favour of affinities of the Linaceae s.s. with Hugoniaceae, Erythroxylaceae and Ixonanthaceae. On the other hand, the remaining gaps in leaf anatomical characters between Linaceae s.s., Hugoniaceae, Ixonanthaceae and Erythroxylaceae (cf. tables 1 and 2) can be stressed to support their separate family status. Cronquist (1981) probably provided the most sensible argument for recognition of a number of separate families when he commented on the coherence and distinctness of the Humiriaceae in the order Linales as understood by him (= our Linaceae complex): 'Once the Humiriaceae are removed from the Linaceae, the Ixonanthaceae and Hugoniaceae also appear as aberrant groups that might more reasonably be treated as separate families. Each of the five families of the order then appears as a well defined group' (l.c. p. 752). With our results this argument can be expanded: the Hugoniaceae are leaf anatomically the most distinct and coherent group of the Linaceae complex, and differ more from the Linaceae s.s. than the latter do from Erythroxylaceae and Humiriaceae (table 2). Accepting the latter two as distinct families, requires the recognition of Hugoniaceae and consequently also Ixonanthaceae for reasons of consistency and here we disagree with Van Hooren and Nootboom's treatment (1984). The alternative, which also finds some support in leaf anatomy is to revert to the broadest possible family con-



cept with as subfamilies the Linoideae, Hugonioideae, Ixonanthoideae, Humirioideae and Erythroxyloideae, possibly even the Irvingioideae. However, the precise taxonomic level of the suprageneric groups is hardly of interest as long as their equal status and phylogenetic affinities are recognised.

Leaf anatomy favours the exclusion of *Ctenolophon* from this alliance, but can offer as yet no alternatives for treatment in another order for lack of distinctive characters and positive enough candidates. The Celastraceae and Olacaceae suggested in the older literature do not provide closer leaf anatomical or wood anatomical similarities than the Linaceae complex (cf. Metcalfe & Chalk, 1950; Den Hartog-Van Ter Tholen & Baas, 1978; Baas et al., 1982).

Lepidobotryaceae cannot be excluded from the Linaceae alliance on account of its leaf anatomy, but treatment in the Geraniales close to or even in the Oxalidaceae does not meet with any leaf anatomical, pollen morphological and probably also wood anatomical obstacle either, and seems to be a better match macromorphologically as judged from the common inclusion in this family by most recent students of angiosperm classification.

The anatomical evidence tips the balance for treatment of *Allantospermum* in the Ixonanthaceae, and not in the Irvingiaceae. The affinities of the latter with either the Linaceae complex or the Simaroubaceae and other Rutales, or with both alliances should be the subject for further multidisciplinary study. The problem is beyond the scope of this paper and could easily ramify into the sort of study embracing many groups of angiosperms as in Hallier's paper of 1923 on the Linaceae and their putative relatives. It should be acknowledged that many of the suggestions in that classic, but very complicated paper are confirmed by the leaf anatomical evidence presented here.

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