WOOD ANATOMICAL STUDIES OF BORAGINACEAE (s.l.). I. CORDIOIDEAE

by

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Summary

The wood anatomy of 98 species of the subfamily Cordioideae is described. On a generic basis Auxemma, Cordia and Patagonula can be clearly identified whereas within these genera only species groups can be differentiated.

In Cordia various crystal configurations of constant occurrence possess a much higher taxonomic value than other structural features. The grouping based on different forms and combinations of inorganic inclusions is in good accordance with the subdivision into 8 sections proposed by Johnston using flower, inflorescence and fruit characters. Most of the few species not corresponding to the respective crystalline pattern are also exceptional in their floral characters. In addition to the remarkable crystal formations all species are characterised by sheath cells and paratracheal parenchyma. According to xylem anatomy the subfamily is phylogenetically advanced and shows a close affinity to many families of the superorder Lamianae of Takhtajan.

Introduction

Considering the size and diversity of Boraginaceae comprising more than 2000 species, previous wood anatomical work is rather limited. This is mainly due to the fact that woody plants make up less than 1/3 of the family, and that only recently very few industrially exploited species have gained economic importance. Presumably for this reason most investigations are concerned with individual species or small species groups; only some relate to the occurrence of specific structural characters or attempt a rudimentary portrayal of the family on account of only a small number of species from several genera.

The present investigation aims at a more complete picture of the anatomy of the secondary xylem of Boraginaceae taking into account the largest possible number of species from all genera consisting entirely or mostly of woody plants. It also attempts the construction of a supra-regional generic key and, finally, correlates occurrence and distribution of structural characters with existing classifications of the family. Subsequently these data are to be used for assembling a list of technically promising timbers. — The present investigation of Cordioideae is to be followed later by a second part treating the remaining subfamilies and featuring a discussion of the whole family of Boraginaceae.

Synopsis of the Boraginaceae

Botanical classification: The first consolidated morphological and systematic treatise of the family was published by Gürke (1897) in Engler & Prantl's Natürliche Pflanzenfamilien. It already covered 84 genera, and even nowadays its underlying ideas are widely acknowledged. Gürke's delimitation of Boraginaceae and its division into four subfamilies was maintained through the subsequent revision by Melchior (1964) and its systematic position was firmly established by the recognised relationship with Hydrophylaceae. There were, however, repeated attempts to segregate parts of the family sensu Gürke by giving more weight to habitual and morphological differences (e.g. Hutchinson, 1959; van Tieghem, 1906), or to split up the large genus Cordia (Friesen, 1933; Nowicke & Ridgway, 1973). Some of these endeavours are commonly accepted such as the separation and elevation to family rank of Wellstedia (Merxmüller, 1960) whose attribution to Boraginaceae was already met with considerable hesitation by Gürke. Other suggestions related to the contention that the diversity observed in Boraginaceae is not compatible with the concept of natural familial uniformity are generally not followed. According to the above cited traditional interpretation of the boraginaceeous assembly to which Johnston adheres in his 30 treatises (1923–1959) the subfamilies Cordioideae and Ehretioidae consist entirely of woody plants; in the former nearly all, in the latter only part are trees. The other two subfamilies are composed mostly of herbaceous species; the few woody plants rarely reach tree size in Heliotropioideae while attaining at the most shrubby habit in Boraginoideae.
**Distribution:** Boraginaceae occur on all continents and may be found in warm, temperate or subarctic climates without being dominant in any particular region. Some genera show a rather limited to endemic (Antrophora) distribution, others are clearly climate dependent as for instance the largest genus *Cordia* with mainly tropical, occasionally subtropical species. The semi-arid character of many genera is indicated by their manifold presence in the Mediterranean and in southeastern North America as well as by the relatively frequent occurrence of individual taxa in tropical dry forests (Opler et al., 1980).

**Utilisation:** Meanwhile quite a few species are employed for a variety of purposes none of which is in any sense outstanding. In particular, species of *Cordia* are being preferred in ornamental gardening because of their blossoming at an early age, aromatic flowers and sometimes edible fruits. Among the herbaceous taxa some are put to medical use while others serve as vegetable, forage and ornamental flowers.

The most important utilisation is that of the timber of all species with well-sized stems, mostly belonging to the genera *Cordia*, *Patagonula* and *Ehretia*. Due to their appearance and the often above average properties these are likened to certain species of Verbenaceae and Bignoniaceae. Particularly, *Cordia* species are considered useful because they lend themselves for plantations within and outside their natural range of distribution; they are easily cultivated, fast growing, and reach fertility at an early age (Melchior, 1977).

**Wood structure:** Up to date approximately 50 species of Boraginaceae have been described (Abbate, 1964; Brehme, 1966; Carliquist, 1970; Cellai, 1971; Corothie, 1967; Dadswell & Eckersley, 1935; Dechamps, 1979; Detienne et al., 1982; Fasolo, 1939–1940; Gottwald, 1980, 1982; Janssornius, 1926, 1940; Lebaciq & Dechamps, 1964; Mainieri, 1978; Miles, 1978; Morales, 1981; Normand, 1960; Normand & Paquis, 1976; Pearson & Brown, 1932; Pfeiffer, 1926; Record & Hess, 1941, 1943; Reyes, 1938; Solereder, 1899; Sudo, 1959; Tortorelli, 1956; Wagemann, 1948). Unfortunately only about half of these descriptions contain sufficient data for taxonomic evaluation based on microstructural features.

Although this previous work covers less than 5% of the boraginaceous woody plants the features herein described already suggest different structural groups within the family: Vessels may be solitary or arranged in groups; their distribution ranges from ring-porous through radially oriented to fully diffuse-porous. Vertical parenchyma may either be apotracheal, paratracheal or conspicuously banded. Fibres are described as either purely libiriform or as fibretrechedoids. Considerable intrageneric variation was also reported with regard to specific features such as: average vessel diameter, size of intervacular pits, quantity of parenchyma, height and width of wood rays, presence of sheath cells and vented pits (Miller, 1977). Furthermore, the overall structural heterogeneity of the family is given particular weight by the sporadic occurrence of silica particles in rays (Gottwald, 1980; Morales, 1981), fibre arrangement or reticulate vessel perforations. The results of most of the earlier investigations on Boraginaceae are summarised in the well-known "Anatomy of the Dicotyledons" by Metcalfe and Chalk (1950).

**Material and Methods**

The present investigation is based on 318 wood samples representing 98 species from 3 genera. Further data regarding the sample material is given at the beginning of the respective generic descriptions jointly with other pertinent parameters such as taxon size, species distribution, etc. The number of specimens studied per species is indicated between brackets. More than 2/3 of all samples are accompanied by herbarium vouchers. Because of the enormous quantity of data related to this material no details on herbarium specimens are included; corresponding information can be made available by the author upon request.

Small wood blocks were boiled in demineralised water and subsequently sectioned with a sliding microtome. For microscopic observations 5 sets of transverse, tangential and radial sections were prepared, two of which were double stained with 0.5% alcoholic solutions of Astra Blue and Safranin B. Macroscopic observations were carried out using samples with planed surface at about 8% moisture content. Specific gravity values referred to in the descriptions are based on oven dry weight and volume. Microscopic analysis of silica and crystalline inclusions was aided by bleaching sections in ordinary chlorinated household bleach and embedding in clove oil (ter Welle, 1976). Sillicium and calcium were traced with a scanning electron microscope (SEM) using gold-sputtered blocks for observation and X-ray micro-analysis. Quantitative values given in the text represent the average from approximately 50 measurements. Whenever several samples of one species were available the italicised mean is based on individual averages. The mean is followed by
the averaged maxima, as for instance: Vessel diameter 80–100 μm (adjusted to every 5 μm); in the other cases it represents the full range. Pit vestures were observed with the SEM after thorough removal of organic cell contents and debris, again using bleaching agent. The terminology adopted is in accordance with the standards developed by the International Association of Wood Anatomists (IAWA, 1964) and by the Standard List of Characters suitable for Computerized Hardwood Identification (Miller & Baas, 1981). The sequence of descriptions follows alphabetical order and adheres to the systematic hierarchy from subfamily, via genus, to section.

Results (Subfamily Cordioideae)

*Auxemma* Miers – 2 species; trees; Brazil.

Species studied: A. glazioviana Taub. (2); A. oncocalyx (Miers) Baill. (2).

Macroscopy: Sapwood grey to light brown; 2.5–3 cm wide (*A. oncocalyx*). Heartwood clearly differentiated, brown to dark brown. Pores visible in all planes; ring- to semi-ring-porous (Fig. 1). Rays distinct on radial faces. Specific gravity 0.66–0.78 g/cm³.

Microscopy: Vessels in the earlywood solitary, clustered or in short multiples, diameter 210–230 μm (*A. glazioviana*), 185–200 μm (*A. oncocalyx*); in the latewood mostly in clusters or partly in ulmiform arrangement, diameter 80–100 μm. Pits alternate, round, diameter 4–4.5 μm, not vestured. Perforations simple, in wide vessels almost horizontal. Reddish brown, gum-like substances, often as layers of different thickness, partly shaped like tyloses. Rays heterogeneous with sheath cells of variable frequency; 5-seriate, uniseriates rare; height 0.7–0.9 mm. Pits to vessels similar to intervacular pits. Large (30–70 μm) prismatic crystals present partly together with small (5–10 μm) ones. Reddish brown gum-like substances rare. Parenchyma mostly irregularly aliform, partly vasicentric or locally confluent. Crystals not as numerous as in rays. Fibres in earlywood about 18 μm in diameter, in latewood 15 μm; walls 3 μm thick; septa of variable frequency (Fig. 2); pits rare, inconspicuously bordered, diameter 3 μm.

Conclusion: According the overlapping features of both species their differentiation is not possible; *Auxemma* is a homogeneous genus, characterised by the tangential arrangement of the vessels, slightly heterogeneous rays with sheath cells and septate fibres. Thus the descriptions given by Miller (1977) and Record and Hess (1941) are confirmed; Metcalfe and Chalk (1950) did not mention the septa, but they reported tyloses as occurring frequently; the latter might have been a misinterpretation of gums with foam-like appearance. *Auxemma* has all signs of a wood anatomically advanced taxon.

*Cordia* Linn. – c. 230 species; trees and shrubs; Africa, Asia, Australia, America.

Species studied: 95 (304 specimens).

Section *Calyptrocarpa* (Britt.) I.M. Johnst. – 1 species; shrubs or trees; West Indies, Central and northern South America.


Macroscopy: Sapwood and heartwood not clearly differentiated, yellowish grey to light olive. Pores mostly diffuse, partly semi-ring-porous (Fig. 3). Rays clearly visible. Growth rings not distinct. Specific gravity low: 0.47 g/cm³.

Microscopy: Vessels in small clusters or solitary with thin-walled tyloses; diameters 100–120 μm; pits alternate, round, diameter 4.5 μm, not vestured; perforations horizontal and mostly simple, partly reticulate (Fig. 4). Rays slightly heterogeneous, sheath cells present; 3- to 4-seriate, uniseriates rare; height 0.6–0.7 mm; pits to vessels similar to intervacular pits. Prismatic crystals (20–40 μm) abundant, partly with smaller ones (5 μm) in the same cell. Parenchyma mostly loosely aliform, partly confluent, often two cells per strand and tending to storied arrangement; pits sometimes scalariform. Fibre diameter 18–20 μm, walls about 2 μm thick; pits scattered, inconspicuously bordered, 2–3 μm in diameter.

Conclusion: This monospecific section is characterised by vessels with medium diameter and partly reticulate perforations, paratracheal parenchyma, heterogeneous rays with sheath cells and prismatic crystals. Section *Calyptrocarpa* has an advanced structure but also remnants of primitive features.

Section *Eucordia* I.M. Johnst. – c. 12 species; shrubs and trees; Madagascar, tropical Asia/ Australia (1), southern USA (2), tropical to subtropical Central and South America (c. 9).

Species studied: 8. Cordia angiocarpa A. Rich. (1); C. boisierii A.D.C. (4); C. decandra Hook. & Arn. (1); C. dodecandra DC. (5); C. ensifolia Urb. (1); C. rufescens A.D.C. (1); C. sebestena L. (4); C. subcordata Lamb. (9).

Macroscopy: Sapwood yellowish, 2–5 cm wide. Heartwood sharply demarcated, brown to dark brown with irregular darker veins. Pores visible. Rays inconspicuous. Growth layers in *C. subcordata* pronounced. Specific gravity high: 0.70–0.94 g/cm³.
Microscopy: Vessels diffuse or wood semi-ring-porous; vessels clustered and solitary, often with thin-walled and brown-layered tyloses; diameter in earlywood 90 \( \mu \text{m} \) (C. boisieri) to 220 \( \mu \text{m} \) (C. dodecandra), in latewood 80–170 \( \mu \text{m} \); pits round, alternate, diameter 4.5–5.5 \( \mu \text{m} \), notusted; perforations simple and horizontal, slightly oblique in latewood. Rays homogeneous to slightly heterogeneous, always with sheath cells (Fig. 6); 3- to 5-seriate, 0.5–0.8 mm high; pits to vessels similar to intervacular pits. Prismatic crystals and crystal sand present in all species (Fig. 5 & 6). Parenchyma vasicentric to irregularly aliform, partly short confluent and terminal; crystals and crystal sand not as frequent as in rays. Fibre diameter 15–18 \( \mu \text{m} \); walls 2.5–4 \( \mu \text{m} \) thick, latewood fibres radially flattened; pits sparse, finely bordered, 2–2.5 \( \mu \text{m} \) in diameter.

Conclusion: Except for the differences in vessel diameter and distribution, all other features are alike in this section; special attention is called to the constant occurrence of both types of crystal-configurations in all species including the single one occurring naturally in Asia while all other species are of American origin. The density variation of the wood is mainly caused by the differences in fibre wall thickness and the amount of gum-like inclusions. Eucordia is best characterised by a pronounced colouration, high density and the constant occurrence of two types of crystals. This section shows advanced wood structural features.

Section Gerascanthus (P. Browne) Don — c. 12 species; trees; tropical America.

Species studied: 7. Cordia alliodora (R. & P.) Cham. ex DC. (22); C. gerascanthus L. (5); C. glabrata (Mart.) A.DC. (9); C. goeldiana Huber (8); C. megalantha Blake (2); C. sonorae Rose (4); C. trichotoma (Vell.) Arab. ex Steud. (7).

Macroscopy: Sapwood yellowish grey to light brown, 2.5–4 cm wide. Heartwood clearly differentiated; in C. goeldiana light brown, in the others brown to dark brown and often with dark veins. Rays distinct only in C. goeldiana. Growth rings often pronounced in C. alliodora & C. trichotoma. Specific gravity medium to high: 0.5 g/cm\(^3\) (C. goeldiana) to 0.86 g/cm\(^3\) (C. glabrata).

Microscopy: Vessels often in small clusters: wood partly semi-ring-porous (Fig. 7); vessel diameter 95 \( \mu \text{m} \) (C. sonorae) to 220 \( \mu \text{m} \) (C. goeldiana), mostly with thin-walled tyloses containing shell-like silica (Fig. 8) or compact silica grains (Fig. 9) in C. sonorae; pits round, alternate, not vested, diameter 4.5–6 \( \mu \text{m} \), apertures in C. goeldiana partly coalescent; perforations simple and horizontal (earlywood) to oblique (latewood). Rays slightly heterogeneous with sheath cells (Fig. 10), very pronounced in C. goeldiana; sclerotic cells scattered in C. glabrata, C. gerascanthus & C. sonorae; 3- to 5-seriate; 0.6–1 mm high (C. goeldiana), pits to vessels

(text continued on page 170)
similar to intervacular pits. Prismatic crystals numerous in all species, also as crystal sand in *C. goeldiana*, and with silica bodies in addition in *C. glabrata* & *C. sonorae*. Parenchyma vasicentric to irregularly aliform, seldom locally confluent, partly terminal; strands of 4 cells, partly storied in *C. geranacanthus* & *C. goeldiana*: prismatic crystals not as frequent as in rays. Fibre diameter 18–22 μm (*C. goeldiana*), walls 2.5 μm (*C. goeldiana*) to 4 μm thick; latetwood fibres very much flattened; pits sparse, finely bordered, 2–2.5 μm in diameter.

**Conclusion:** Section *Geranacanthus* has a uniform structure, characterised by thick-walled fibres and prismatic crystals. Exceptions are the occurrence of silica in *C. glabrata*, *C. sonorae* and the extreme cell dimensions and sand occurring beside large crystals in *C. goeldiana*. The difference in density is mainly caused by the thickness of fibre walls. *Geranacanthus* is advanced in all wood anatomical aspects.


**Species studied:** 23. *Cordia africana* Lam. (14); *C. aspera* Forst. (1); *C. aurantiaca* Baker (5); *C. caffra* Sond. (3); *C. crenata* (Jacq.) R. & S. (2); *C. dichotoma* Forst. f. (12); *C. fragrans-tissima* Kurz (3); *C. gharaf* (Forsk.) Ehrenb. (4); *C. goetzei* Gürke (1); *C. grandis* Roxb. (1); *C. macleoidii* (Griff.) Hook. f. & Thoms. (2); *C. millenii* Bakh. (4); *C. ?mipea* (1); *C. monoca* Roxb. (1); *C. myxa* L. (4); *C. myxa* L. var. *brunnea* Kurz (1); *C. obliqua* Willd. (3); *C. oblongifolia* Thw. (1); *C. odorata* Gürke (1); *C. ovalis* R. Br. ex A.DC. (3); *C. platytherys* Bakh. (8); *C. senegalensis* Juss. (3); *C. vestita* Hook. f. & Thoms. (1).

**Macroscopy:** Sapwood greyish to yellowish grey, 1–8 cm wide. Heartwood light brown (*C. millenii*) to dark brown and partly with darker veins (*C. fragrans-tissima*). Pores mostly prominent on all faces and often more or less tangentially arranged. Rays pronounced on the radial plane. Parenchyma visible as light-coloured tissue in species with dark heartwood. Specific gravity low to mostly high: 0.35 g/cm³ (*C. aspera*) to 0.62 g/cm³ (*C. dichotoma*) to 0.82 g/cm³ (*C. caffra*).

**Microscopy:** Vessels in small clusters and solitary, diameter 140–170 μm in *C. goetzei*, *C. gharaf*, *C. ovalis*, in the other species 200–250 μm with individual pores up to 400 μm; often with tyloses, partly sclerotic (Fig. 16) in *C. gharaf*, *C. macleoidii* & *C. vestita*, including large crystals in *C. fragrans-tissima*, *C. gharaf*, *C. macleoidii*, *C. oblongifolia*, *C. ovalis*, *C. senegalensis* & *C. vestita* (Fig. 12 & 13), also with crys-

tal sand in *C. oblongifolia* (Fig. 14); pits round, alternate, diameter 5 μm (*C. senegalensis*) to 6 μm (*C. grandis*), partly coalescent, not ventrusted; perforations simple and horizontal, also reticulate in *C. aurantiaca*, *C. dichotoma*, *C. fragrans-tissima*, *C. goetzei*, *C. macleoidii*, *C. ?mipea* & *C. platytherys*. Rays with sheath cells and slightly heterogeneous; 4- to 5-seriate, height 450–950 μm; pits to vessels often enlarged and perforated. Prismatic crystals of varying size in all species. Parenchyma in *C. aspera* aliform, in all other species confluent and often developing into broad bands (Fig. 15); partly storied; pits often irregularly enlarged. Crystal sand in *C. aspera*, *C. aurantiaca*, *C. dichotoma*, *C. macleoidii* & *C. platytherys*; prismatic crystals partly present. Fibres often with irregular, polygonal cross-section, in the latetwood mostly flattened; diameter 15 μm (*C. gharaf*) to 30 μm (*C. aspera*); walls 2 μm (*C. aurantiaca*) to 4 μm (*C. vestita*) thick; pits irregularly distributed, in wide fibres locally up to three in a row, indistinctly bordered, about 2 μm in diameter.

**Conclusion:** The variable diameters of the vessels, the very different thickness of the fibre walls together with the often reticulate perforations and the very wide range of tyloses formation (sclerotic, containing crystals and/or sand) as well as the highly variable density and colour of the heartwood make section *Myxa* a heterogeneous taxon. Nevertheless, the constant occurrence of large prismatic crystals and the relatively high amount of axial parenchyma constitute a stable combination of features which is absent from *C. aspera* only. The latter species also deviates in other features. The pronounced heartwood including the tendency to ring porosity reflect the distribution of the section in areas with high temperatures and seasonal rains. The often heterogeneous rays, the enlarged parenchyma pits and the partly reticulate perforations in one third of the species show relics of a low degree of advancement; altogether the structure of *Myxa* is still to be considered advanced.

Section *Physocladia* DC. — 1 species; shrub or small tree; northern South America except Colombia.

**Species studied:** Cordia nodosa Lam. (5).

**Macroscopy:** Sapwood greyish merging into the light brown heartwood. Pores mediumsized and evenly distributed. Rays distinct on radial faces. Growth layers not developed. Specific gravity medium: 0.7 g/cm³.

**Microscopy:** Vessels in small clusters or short multiples and solitary with thin-walled tyloses (Fig. 17); diameter 115–150 μm; pits round, alternate, diameter 5–6 μm, not vestur-
ed; perforations simple and partly reticulate, mostly horizontal. Rays mostly heterogeneous with 1 or 2 marginal rows of upright cells, sheath cells present; 4- to 5-seriate; height 0.8–1 mm, some up to 2.5 mm (Fig. 18); pits to vessels similar to intervascular pits. Crystal sand in all samples but in small quantities. Parenchyma alliform to locally confluent, and terminal (Fig. 17). Fibres polygonal, diameter 18 μm, walls 2.5 μm thick, pits rare, inconspicuously bordered, diameter 2 μm.

Conclusion: The monospecific section Physocladia is characterised by diffuse and medium-sized pores with simple or reticulate perforations, paratracheal parenchyma, heterogeneous rays with sheath cells and crystal sand. Physocladia is advanced but also shows some primitive features.

Section Pilicordia A.DC. – c. 90 species; shrubs and mostly small trees; tropical America.

Species studied: 41. Cordia bicolor A.DC. (6); C. borinquensis Urb. (1); C. citricroca L.O. Will. (1); C. collococa L. (6); C. columbiana Killip (2); C. decipiens Johnst. (1); C. diversifolia Pav. (2); C. dyweri Nowiecke (1); C. ecalyculata Vell. (5); C. erioistigma Pitt. (2); C. exaltata Lam. (4); C. exaltata var. melaneura (Kl.) Johnst. (4); C. fallax Johnst. (2); C. fulva Johnst. (1); C. hebeclada Johnst. (1); C. hintoni Johnst. (1); C. hirta Johnst. (2); C. laevifrons Johnst. (3); C. laevigata Lam. (2); C. lasioalyx Pitt. (2); C. lomatoloba Johnst. (3); C. lucidula Johnst. (2); C. lutea Lam. (1); C. macrophylla L. (1); C. magnoliaefolia Cham. (2); C. nervosa Lam. (2); C. nitida (L.) Vahl (4); C. panamensis Riley (1); C. paniculata Rudge (2); C. sagotti Johnst. (4); C. scabifolia A.DC. (2); C. sellowiana Cham. (3); C. sericoclyx A.DC. (3); C. silvestris Tresen (2); C. stellifera Johnst. (2); C. sulfurata DC. (3); C. tetrandra Aubl. (8); C. toqueve Aubl. (5); C. trichoclada DC. (1); C. ucalaiennis Johnst. (4); C. ulei Johnst. (1).

Macroscopy: Sapwood light grey to yellowish. Heartwood weakly demarcated, light brown. Pores visible on all faces, diffuse or with slight tangential arrangement. Rays visible only on radial planes. Growth rings partly distinct. Specific gravity low to medium: 0.35 g/cm³ (C. dyweri) to 0.63 g/cm³ (C. hintoni).

Microscopy: Vessels solitary and in small clusters (Fig. 19), tyloses common; diameter 100 μm (C. borinquensis) to 310 μm (C. citricroca); pits round, alternate and partly coalescent, diameters 4 μm (C. hintoni) to 7 μm (C. bicolor), not vented; perforations mostly simple, also reticulate in C. citricroca, C. ecalyculata, C. scabifolia & C. silvestris, with extra small perforations (smaller than 10 μm) on the lateral walls in C. citricroca (Fig. 22); silica as layers or as compact particles filling the vessels in C. hintoni. Additional circular perforations in side walls along the rim of normal perforations in C. citricroca (Figs. 21–23). Rays with sheath cells, slightly heterogeneous to homogeneous; 3- to 5-seriate, height 0.5–1 mm. Parenchyma mostly vascentric to alliform, locally confluent (C. hintoni), also terminal in continuous or semi-continuous narrow bands; strands often stored, length very variable, 200–350 μm (Fig. 20). Crystal sand in all species except C. diversifolia, C. hintoni & C. lutea which always contain large prismatic crystals. Fibre diameter 18–25 μm (C. exaltata); between earlywood and latewood mostly flattened; walls about 2 μm thick and 3 μm in C. hintoni; pits sparse, finely bordered, 2 μm in diameter.

Conclusion: The vessel and pit diameter as well as ray type show a wide variation: on the other hand the constant occurrence of crystal sand in 36 species (out of 39) constitutes a feature of high taxonomic value. The other 3 species possess large crystals. Among the latter C. hintoni presents all sectional extremes in vessel and pit diameter, thickness of fibre walls, density, and also in the occurrence of silica, which is very rare in Cordia. These three distinct species are also exceptional otherwise: C. hintoni is defined by Johnst (XV/1940) as the Mexican form of C. diversifolia, itself outstanding in Pilicordia: ‘Flowers of similar dimorphism are found in the large group of Old World species, related to C. myxa L.’. C. lutea is the only species with a distribution outside America where otherwise only species of Myxa are of natural occurrence; its placement in Pilicordia is preliminary and based on the relationship to C. ucayaliensis. C. citricroca, finally occupies a special position in Cordia due to the additional lateral perforations.

Section Rhabdocalyx DC. – 3 species; small to medium-sized trees or shrubs; western Mexico, Peru.

Species studied: Cordia elaeagnoides DC. (4).

Macroscopy: Sapwood a dull yellowish brown, 2–4 cm wide. Heartwood sharply differentiated, brown with black stripes. Pores prominent, diffuse to semi-ring-porous. Rays nearly indistinct; growth layers present. Specific gravity high: 0.88 g/cm³.

Microscopy: Vessels diffuse, clustered, partly in short tangential aggregates (Fig. 24); tyloses present often with thin layers of gum; diameter in earlywood 210–240 μm, in latewood 110–80 μm; pits round, alternate, diameter 5–6 μm, not vented; perforations simple and
horizontal, oblique in latewood. Rays with sheath cells, homogeneous or with one marginal row of upright cells; 4- to 5-seriate, height 0.5–0.6 mm; pits to vessels similar to intervacular pits. Large prismatic crystals common, partly together with smaller ones (less than 5 μm) in the same cells. Parenchyma vasicentric to irregularly aliform and terminal; crystals not as frequent as in rays. Fibre diameter 15–18 μm, walls 4–5 μm thick; pits sparse, finely bordered, 2.5 μm in diameter.

Conclusion: This species is characterised by high density, dark colour and crystals. The wood structure of *Rhabdocalyx* is phylogenetically advanced.

Section *Varronia* (O. Browne) Don. – c. 60 species; shrubs; tropical America.

Species studied: 13. Cordia angustifolia R. & S. (1); C. calicola Urb. (1); C. caracasana DC. (1); C. curassavica (Jacq.) R. & S. (3); C. cylindristachya (R. & P.) R. & S. (3); C. globosa (Jacq.) H.B.K. (3); C. leucophylitis Hook. f. (1); C. mollissima Killip (1); C. polycéphala (Lam.) I.M. Johnst. (2); C. salvifolia Juss. ex Poir. (2); C. schomburgkii DC. (3); C. spinescens L. (1); C. verbenacea DC. (1).

Macroscopy: Sapwood grey to light yellowish brown; heartwood not seen. Pores clearly visible only in *C. caracasana* & *C. mollissima*. Rays, parenchyma and growth rings indistinct. Specific gravity medium: 0.5 g/cm³ (*C. cylindristachya*) to 0.68 g/cm³ (*C. caracasana*). These are approximate values because of the small volumes and the reaction wood common in shrub specimens.

Microscopy: Pores solitary and in small clusters; wood in part tending to semi-ring-porosity (Fig. 25); vessel diameter 85 μm (*C. verbenacea*) to 200 μm (*C. mollissima*); tyloses rare; pits round, alternate, weakly vaulted only in *C. schomburgkii* (Fig. 27), diameter 3–4.5 μm; perforations simple, horizontal to oblique. Rays with sheath cells, homogeneous to slightly heterogeneous (*C. globosa*); 2- to 5-seriate, height 0.2–1 mm; pits to vessels similar to intervacular pits; large prismatic crystals only in *C. salvifolia*. Parenchyma vasicentric to locally confluent and partly terminal; strands of 2–4 cells, often storied, partly fusiform. Crystal sand in all species (Fig. 26), in *C. schomburgkii* rare. Fibre diameter 15–20 μm, walls 2–3 μm thick, flattened in the latewood; pits scarce, finely bordered, diameter 2 μm.

Conclusion: Due to the shrubby to scandent habit, all features influenced by habit such as size of vessels and rays are highly variable. Contrary, other features like pits and inclusions demonstrate a high degree of constancy. Only *C. salvifolia* differs by the additional occurrence of large prismatic crystals besides sand; this structurally unique species is also described by Johnston (VIII/1949) as ‘... a very distinct member of the section Varronia ... readily distinguished from all immediate relatives ...’. The slightly developed pit vessels in *C. schomburgkii* can be considered a deviation of degree only, as many species show similar finely sculptured pit apertures as reported by Miller (1977).

*Patagonula* Linn. – 2 species; trees; southeastern South America.

Species studied: *P. americana* Linn. (10).

Macroscopy: Sapwood yellowish grey, 4–8 cm wide. Heartwood clearly separated, brown and partly with darker stripes. Pores visible on cross-sections as ulmiform bands, tangentially as prominent light coloured feather-like structures, and radially as very fine stripes. Rays conspicuous on radial faces only. Specific gravity high: 0.75 g/cm³.

Microscopy: Vessels clustered and arranged in tangential aggregates; diameter 70–80 μm (Fig. 28); pits round, alternate, diameter 3 μm, not vaulted; perforations simple, horizontal to oblique; partly with tyloses. Reddish brown gums present in layers of variable thickness lining the walls. Rays homogeneous to weakly heterogeneous, sheath cells present; 3- to 4-seriate, height 0.35–0.4 mm; pits to vessels similar to intervacular pits. Crystal sand in sheath cells common. Parenchyma mainly vasicentric, locally irregularly confluent; strands of 2–4 cells, partly storied. Crystal sand in extremely thin-walled (less than 1 μm), fibre-like cells, the latter 250–350 μm in length and about 20 μm in diameter, often dispersed between regular fibres (Fig. 29). Fibre diameter 14–18 μm, walls 3–3.5 μm thick; in last-formed latewood flattened; pits inconspicuously bordered, diameter 2.5 μm.

Conclusion: The species not available (*P. bahiensis* Moric), endemic to eastern Brazil, is said to possess the same structure and to differ only by the lesser colouration of heartwood. Accordingly the genus is characterised by the ulmiform arrangement of small pores, the minute pits and the crystal sand in extremely thin-walled cells. The septate fibres, mentioned by Metcalfe and Chalk (1950) and Tortorelli (1956) could not be observed. Both authors, however, reported the frequent occurrence of crystal sand mentioned before by Solererder (1899), as a specific feature in leaves of this genus. *Patagonula* has a clearly advanced structure.
Table 1. Specific features of the sections of *Cordia*.

<table>
<thead>
<tr>
<th>Sections</th>
<th>Vessel pit diameter</th>
<th>Multiple perforations</th>
<th>Sclerotic tyloses</th>
<th>Rays multiserate and with sheath cells</th>
<th>Parenchyma vascinsect</th>
<th>Parenchyma banded (broad)</th>
<th>Crystal sand (diameter less than 2 μm)</th>
<th>Prismatic crystals (diameter over 2 μm)</th>
<th>Overdry weight/volume (g/cm³)</th>
<th>Heartwood dark-coloured</th>
<th>Deviating species</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Calyptracodia</em></td>
<td>4.5</td>
<td>(+)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.47</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eucordia</em></td>
<td>4.5-5.5</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td>0.70-0.94</td>
<td>+</td>
<td>C. glabrata, C. sonorae, *C. goeldiana</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gerascanthus</em></td>
<td>4.5-6</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td>0.58-0.86</td>
<td>+</td>
<td></td>
<td>*C. aspera, *C. macleodii, *C. aurantia-ca, *C. platythrysa, *C. dichotoma</td>
<td></td>
</tr>
<tr>
<td><em>Myxa</em></td>
<td>5-6</td>
<td>(+) (+) (+) (+) (+)</td>
<td>-</td>
<td>+</td>
<td></td>
<td></td>
<td>0.62-0.82</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Physocladia</em></td>
<td>5.5</td>
<td>(+)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pilicordia</em></td>
<td>5-7</td>
<td>(+)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.35-0.65</td>
<td>-</td>
<td>*C. diversifolia, *C. lutea, *C. hintoni</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Rhabdocalyx</em></td>
<td>5.5</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td>0.88</td>
<td>+</td>
<td></td>
<td>*C. salvifolia</td>
<td></td>
</tr>
<tr>
<td><em>Varronia</em></td>
<td>3-4.5</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td>0.5-0.68</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(+): not occurring in all species; *: deviating from oxalate pattern of the section.

Discussion

*Auxemma* (see commentary on page 163)

*Cordia* (s.l.)

Anatomy — According to the anatomical features observed in all 8 sections the following overall generic picture can be drawn: Vessel diameter medium to large; pores simultaneously solitary and in multiples; predominantly diffuse to sometimes nearly ring-porous; tyloses common, mostly thin-walled, in part sclerotic; perforations simple and horizontal, rarely in combination with reticulate perforations; intervascular pits minute to medium-sized, compact, circular to angular in outline, in a single species with few vesture. Rays non-storied, predominantly multiserate in combination with few uniseriates; sheath cells present in all species in variable proportions, extremely thin-walled; tending to heterogeneity (*Kribs He IIA to Ho II*), but never conspicuously so; vessel-ray pitting essentially unchanged, slightly enlarged in few species of section *Myxa*. Parenchyma paratracheal in all configurations varying from weakly vascinsect to loosely aliform to broadly banded; terminal bands fine and only in part conspicuous; strands of mostly 2 to 4 cells with tendency to storied arrangement. Fibres extremely variable in diameter and wall thickness; pits fine and inconspicuously bordered; non septate. Organic inclusions as amorphous particles or compact sediments, generally rare; silica particles of regular occurrence in two species; Ca-oxalate in all species, either as large crystals, as crystal sand or both forms simultaneously present in the same species (see also Table 1).

Taxonomy — The above described features can be combined into a structural principle characterised by medium-sized, solitary and multiple pores in varying proportions, paratracheal parenchyma and multiserate rays. This
pattern is rather unspecific as it can be observed not only in other families of the superorder Lamianae (Takhtajan, 1980) such as Bignoniaceae and Verbenaceae but also in Moraceae, Leguminosae, Asteraceae and other unrelated families. In addition, this indistinctness of *Cordia* is further enhanced by a considerable quantitative variation from species to species. Some taxonomic geographical significance may be attributed to parenchyma distribution: Confluent banded parenchyma occurs exclusively in Old World species (section *Myxa*). Such distinction becomes even more conspicuous when considering the comparatively small number of species distributed over such a large area (Fig. 30).

Contrary to the rather indeterminate picture based on overall structure the genus *Cordia* shows several remarkable special characters. One is the constant occurrence of sheath cells, which are present in all species, albeit quantitatively variable. Other such features include silica, sclerotic tyloses with Ca-oxalate crystals and, especially, the common but variable distribution of crystals in parenchymatic tissues. In combination they allow for the delimitation of species and/or sectional groups within *Cordia*. In synthesis in this genus general structural parameters are of much less diagnostic value than inorganic inclusions. Given a few exceptions this feature alone in its differing habit and configurations makes it possible to nearly 'redraw' as it were the subdivision into 8 sections introduced by Johnston (Fig. 31). Accordingly, sections *Varronia*, *Pilicordia* and *Physocladia* are characterised by crystal sand while *Rhabdocalyx*, *Gerascanthus*, *Myxa* and *Calyptracordia* are distinct in containing large rhomboidal crystals. Finally, in section *Eucordia* both crystalline configurations occur simultaneously.

Few individual species (indicated in Fig. 31 by letters a, b, c, d) deviate from this remarkable coincidence of botanical taxonomic grouping and distributional pattern of crystals in the secondary xylem. Incidentally, most of these species (a, b, c) occupy a special position in their respective sections due to atypical features.

Fig. 30. The distribution of the genus *Cordia* and number of species per area. I: more than 120; II: 30–100; III: 20–30; IV: 10–20; V: less than 10 species.

Fig. 31. The sections of *Cordia* arranged according to crystal features, advancement and frequency of axial parenchyma with special reference to deviating groups (a: *C. salvifolia*, b: *C. goeldiana*, c: *C. diversifolia*, *C. lutea*, *C. hintoni*, d: *C. aspera*, *C. aurantiaca*, *C. dichotoma*, *C. macleodii*, *C. platythyrsa*). Vertical lines: prismatic crystals; horizontal lines: crystal sand; cross-hatched: crystals and sand. Mp: species below the dotted line also with multiple perforations; Pa: species to the right of the dotted line with prominent confluent parenchyma.
of flowers or fruit. No such agreement can be found in the case of species group 'd' as being different from the general pattern in section *Myxa*. Possibly this might be explained by the fact that because of its vast distribution this taxon has not received the same intensive treatment by botanists as the others. Four of the five species in group 'd' are characterised by sporadically occurring reticulate vessel perforations. The far reaching concurrence between taxon delimitation based 1) on exomorphological evidence and 2) on crystal distribution in the secondary xylem is of particular significance in view of the repeated attempts to break up the genus *Cordia* in a different manner, even to the point of creating several new genera. The segregation of sections *Varronia* and *Eucordia* as independent genera was discussed more than once (Friesen, 1933; Nowicke & Ridgway, 1973); Johnston (1930) describes his section *Varronia* as 'polymorphous' and adds with regard to the species involved: 'their variability and their indefiniteness (are) perhaps the most perplexing and poorly understood in the entire genus'. However, when considering crystalline inclusions *Varronia*, except Cordia *salvifolia*, constitutes the most uniform section and differs from all others by its minute intervascular pits. Hence, this section offers a second common feature serving delimitation beside crystal type. Although in wood anatomy vessel pit diameter is usually considered a stable and therefore important diagnostic character on the generic level, in *Cordia* it is somewhat deprived of its significance due to the ever so gradual increase in pit diameter through the sections (see Table 1). Consequently, a differentiation beyond the sectional level according to this feature, although possible, would not follow compelling evidence. Wood anatomical reasoning thus conforms partly to the viewpoint expressed by Johnston with regard to *Varronia*.

The section *Eucordia*, previously discussed as one of the taxa to be elevated to generic level, also occupies a special position on the basis of its crystals. Only the species belonging to this section constantly feature both types of crystalline configurations in the secondary xylem, and thus could be singled out as having no equal within *Cordia*. Again a segregation of this section on anatomical grounds would be practicable but not fully justified. Rather, the rank of subgenus must be considered appropriate for both sections: *Varronia* and *Eucordia*, and would fully accommodate wood anatomical evidence. There is also good agreement between xylem-based intersectional relations as featured in Fig. 31 and Johnston's placement of sections *Gerocanthus* and *Rhabdocalyx* relative to each other: According to both sets of criteria the two taxa must be considered closely related.

Contrary to the above cited parallels of exomorphological and xylem anatomical traits no such agreement can be found with regard to the repeatedly suggested junction of sections *Myxa* and *Pilocardia*, for instance by Nowicke and Ridgway (1973), this time based on pollen characters of 40 species. From a wood anatomical point of view the union of the latter two sections would not constitute a feasible solution, notwithstanding the considerable variation within or overlap between *Myxa* and *Pilocardia* caused by a relatively high (7) number of species deviating from the respective section-al structural patterns (Fig. 31).

Phylogeny – The secondary xylem features of the 8 sections studied offer few hints to be followed when tracing evolutionary trends within *Cordia*. Only the sections *Calyptracordia* and *Physocladia* with more heterogeneous rays and partly reticulate vessel perforations show a somewhat lower degree of advancement. This might signal no more than a slight polarity of those two sections as opposed to *Eucordia*, *Rhabdocalyx*, *Varronia* and *Gerocanthus*. Between these marginally placed sections the large taxa *Myxa* and *Pilocardia* could be assigned an intermediate position since both contain species with partly reticulate perforations.

Altogether the genus *Cordia* must be seen as definitely advanced while showing a limited infrageneric gradient in terms of evolutionary changes. This situation is comparable to that of several genera of Bignoniaceae and Verbenaceae which, in a similar way, appear to have maintained some reticulate vessel perforations as more primitive remnants within their otherwise uniformly advanced wood.

Ecology – There is no positive indication of a possible influence ecological site conditions may have on wood structure. In fact, incomplete data on the ecology of the species studied, the small number of specimens per species, and perhaps superimposed strong habitual influences make it impossible to draw any conclusions. On the other hand, the distribution of annual precipitation definitely seems to affect tangential vessel arrangement: Species from monsoon forests show a strong tendency towards ring porosity.

Identification – The wood structure of the genus *Cordia* is in many respects homogeneous or else of such gradual variation that — without resorting to crystal characters — proper identification within the genus is nearly impossible. Even then the determination of individual species is very much restricted and may be
Table 2. Important features of the genera of Cordioideae.

<table>
<thead>
<tr>
<th>Feature</th>
<th>Auxemma</th>
<th>Cordia</th>
<th>Patagonula</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vessels in uniform pattern</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Vessel diameter over 80 μm</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Vessel pits smaller than 8 μm</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Multiple perforations</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Sclerotic tyloses</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Rays multiseriate and with sheath cells</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Parenchyma paratracheal</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Fibres septate</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Crystal sand</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Prismatic crystals</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Silicon bodies (in vessels or rays)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ovendry weight/volume</td>
<td>0.65–0.8</td>
<td>0.35–0.94</td>
<td>0.75</td>
</tr>
</tbody>
</table>

(+): sporadic and not in all species.

successful only with the two species representing sections Calyptracordia and Physocladia. Otherwise only species groups can be separated, as for instance those with reticulate vessel perforations in sections Myxa and Pilicordia. Beyond this, identification will at best reach down to sectional level where the few outsiders (a, b, c, d — Fig. 31) might still be critical in terms of structural overlap. In this general context of identification it is important to note that all diagnostically decisive features are already present in the latest formed sapwood.

Record and Hess (1943) have classified Cordia woods in two property related groups: ‘hard-wooded, dark coloured’ (A) and ‘soft-wooded, light coloured’ (B). This classification may equally be applied to the much larger number of species studied in the present investigation. Species belonging to the sections Euclordia and Rhabdocalyx exclusively furnish woods of type A while those of sections Calyptracordia, Physocladia, Pilicordia and Varronia belong to type B. Finally, sections Gerascanthus and Myxa are mixed taxa containing species of both types of wood.

Patagonula (see commentary on page 172)

Subfamily Cordioideae

The three genera belonging to this subfamily, Auxemma, Cordia and Patagonula, constitute a rather uniform entity when considering the general structural principle and individual characters discussed above. The more important common features are the constant paratracheal parenchyma, multi-seriate rays with sheath cells, and the diagnostically valuable crystalline inclusions. Hence, Cordioideae is to be regarded a coherent ‘natural’ assembly also according to secondary xylem features. Notwithstanding such homogeneity each of the three genera can be differentiated by its own specific character combination (Table 2).

Comparison with other genera or groups of genera outside Boraginaceae is facilitated by the structural coherence of the subfamily Cordioideae. Such comparison shows that many taxa, particularly among those belonging to the families of Bignoniaceae, Hydrophyllaceae and Verbenaceae, manifest considerable similarity with genera of Cordioideae not only in terms of general structure but also in specific features; in a more restricted way, a structural relation can also be found with various genera of Labiatae and Solanaceae. Thus this subfamily, also according to wood structure, appears as a typical representative of the superorder Lamianae (Takhtajan, 1980). Concerning their status of phylogenetic advancement the three genera cannot be clearly segregated. The gradual specialisation in parts of Cordia suggests no more than that this genus could possibly occupy a somewhat basal position when compared to the other two genera.

In synthesis, the subfamily Cordioideae presents a taxon with remarkable agreement between exomorphological and wood anatomical classification.
Acknowledgements
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