

## 2 On the woody Boraginales: Cordiaceae and Ehretiaceae<sup>1</sup>

Cordiaceae R.BR. *ex* DUMORT., Anal. Fam. Pl.: 25 (1829), *nom. cons.*

Ehretiaceae MART. *ex* LINDL., Intr. Nat. Syst. Bot.: 242 (1830), *nom. cons.*

General description: Trees or shrubs, rarely subshrubs, lianas, or herbs. Indumentum sericeous or hispid, usually of simple, unicellular, eglandular trichomes, sometimes additionally with glandular trichomes, rarely glabrous. Leaves bifacial, alternate, petiolate or sessile, simple, mostly estipulate; deciduous or evergreen; sclerophyllous and coriaceous or membranaceous. Inflorescence terminal or axillary, thyrsoid, sometimes umbellate, globose, or spicate, rarely flowers solitary; usually ebracteose. Flowers perfect, actinomorphic, tetracyclic, chasmogamous, mostly bisexual, occasionally dioecious, sometimes dimorphic and dichogamous or cleistogamous, often fragrant; sessile or shortly pedicellate; perianth dichlamydeous, usually pentamerous. Calyx mostly synsepalous, calyx lobes equal, occasionally unequal; aestivation valvate or imbricate (quincuncial); calyx persistent, sometimes accrescent in mature fruit, then more or less enclosing the fruit, calyx lobes of varying outline. Corolla sympetalous, usually with a cylindrical or infundibuliform tube and spreading or reflexed limbs; corolla lobes of varying outline, altering with the sepals; often white, rarely orange, yellow or blue, aestivation mostly imbricate (quincuncial). Androecium usually haplostemonous, antesepalous and epipetalous; filaments linear; anthers tetrasporangiate, included or exserted, dorsifixed, opening *via* longitudinal slits. Gynoeceum superior, sessile, bicarpellate, syncarpous, with four ovules; ovules orthotropous or anatropous, unitegmic; style terminal, with one, two, or four stigmatic lobe(s). Fruit usually four-seeded (occasionally one or more seeds abortive), mostly indehiscent and drupaceous; endocarp undivided or separating into two or four endocarpids, each part enclosing four, two, or one seed(s), sometimes with additional sterile chambers; testa with transfer cells; embryo curved to straight; endosperm copious or absent; cotyledons flat or plicate.

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<sup>1</sup> Manuscript in preparation as GOTTSCHLING M, HH HILGER & M WEIGEND (in prep. b): Cordiaceae R. BR. *ex* DUMORT. – In: KUBITZKI K (ed.): Families of Flowering Plants. Berlin: Springer. It is considered to split the preliminary manuscript into two parts, Cordiaceae (= Cordioideae *sensu* GÜRKE 1893) and Ehretiaceae (= Ehretioideae *sensu* GÜRKE 1893, including Lennoaceae).

Own contributions: Compiling literature data, writing manuscript, drawings (partly).

Comprising 10 genera with approximately 500 species in the tropical and subtropical zones of all continents from tropical rain forest to dry savannah, most diverse in at least seasonally dry habitats.

## 2.1 Cordiaceae and Ehretiaceae

Vegetative Morphology. The vast majority of taxa are woody plants, mostly trees or shrubs with the only exception of the herbaceous *Coldenia*. Some species are scandent or scandent shrubs (*Bourreria p.p.*, *Varronia p.p.*). The bark is mostly dark, occasionally grey to almost white (e.g., in *Ehretia rigida*). The primary root is always well-developed and persists. In species of arid climates (e.g., *Coldenia*, *Tiquilia*) an extensive horizontal root system is developed enabling the plants to absorb rapidly the moisture from light showers. Underground rhizomes and xylopodia are occasionally developed in, e.g., *Bourreria* and *Cortesia*. Cordiaceae and Ehretiaceae have a range of different leaf shapes (linear, elliptic, ovate to widely ovate), and leaf morphology may vary within species (e.g., GAVIRIA 1987, MILLER 1989); some *Cordia* species have heteromorphic leaves. Generally, the leaf lamina is undivided (Figs. 2-1, 2-4, 2-6, 2-15 to 2-19, 2-21; some *Cordia* species rarely with compound leaves) with an entire margin (flat or revolute). In some species of *Cordia*, *Ehretia*, and *Varronia* the leaf margin is crenate, serrate, or dentate (Fig. 2-6), and in *Coldenia* the leaves are lobed (Fig. 2-17). The leaf apex is acute, acuminate, or rounded, and the base is subcordate, cuneate, or decurrent. Few taxa have highly derived leaf shapes, e.g., strongly coriaceous leaves with one lobe on each side (*Cortesia*, *Ehretia microphylla*, Figs. 2-16, 2-18). Usually, the leaves are flat, but plicate leaves are found in *Coldenia* (Fig. 2-17) and *Tiquilia*. The plants are mostly evergreen, but deciduous species are found in, e.g., *Cordia* and *Ehretia* growing in seasonally dry or temperate regions. Phyllotaxis is mostly alternate (Figs. 2-1, 2-4, 2-15), sometimes fasciculate [e.g., *Cordia americana* (= *Patagonula americana*), *Cordia nodosa*, *Ehretia microphylla*], rarely subopposite (*Cordia p.p.*).

Vegetative Anatomy. Wood anatomy in Cordiaceae and Ehretiaceae is not very diversified. Cork arises superficially from a cambium (METCALFE & CHALK 1950) and is generally well-developed. Annual growth rings are absent through very distinct depending on climate. The vessels are mostly diffuse, occasionally arranged in rings, both arrangements can be found in the same species. Vessels are solitary or in radial multiples, late wood vessels are solitary or in clusters (*Ehretia p.p.*) and are arranged in an ulmiform to dendritic pattern. Vessel-ray and vessel-parenchyma pits are similar, half-bordered, enlarged, or even perforated (in *Cordia p.p.*). Vasicentric tracheids and helical thickenings are present in some narrow vessels of *Ehretia* species. The fibres show minutely bordered pits and are mostly non-septate (exceptions with septate fibres are found in *Cordia p.p.*, *Ehretia p.p.*). Parenchyma is abundant and paratracheal to banded (in *Cordia p.p.*), predominantly apotracheal and diffuse-in-aggregates in *Ehretia* species. The rays are four- to six-seriate, heterocellular, with few rows of square to upright marginal

cells, through homocellular in some species of *Cordia* (BAAS in RIEDL 1997). Vestured pits have been reported for *Rocheportia* (MILLER 1977). The presence of calciumoxalat crystals in the wood is universal, and the distribution of these crystals is systematically informative. Ehretiaceae have crystal druses as solitary structures or arranged in rows, while in Cordiaceae crystal sand and prismatic crystals are found. Columnar crystals are restricted to the *Sebestena* subclade of *Cordia* and pyramidal crystals to *Varronia* (HEUBL *et al.* 1990, AL-SHEHBAZ 1991, GOTTSCHLING *et al.* subm. a). Specific functions of the different crystal arrangements are unknown. Leaves are bifacial, sclereids are sometimes present in *Cordia*. Leaf architecture appears to be originally brochidodromous, and craspedodromous venation is mostly restricted to species with serrate leaf margins. Palisade tissue is mostly one-layered, but more than one layer is found in some *Cordia* species and *Tiquilia*. The stomata are usually anomocytic. The vascular bundles are embedded in the mesophyll or are vertically transcurrent through sclerenchymatous bundle sheath extensions (in *Cordia p.p.*, *Ehretia*). The indumentum is variously pubescent to hispid, rarely absent, and usually consists of unicellular hairs often containing cystoliths (causing the typical roughness of the leaf surface). Unicellular and uniseriate hairs, without lithocysts, are also found, as are branched multicellular trichomes (in the *Sebestena* subclade of *Cordia*, *Rocheportia*, *Tiquilia*, *Varronia*) and stalked glandular trichomes with a single head cell (e.g., in *Coldenia*, on mature anthers of the *Myxa* subclade of *Cordia*, on immature anthers of *Varronia*). Trichomes often have a slightly bulbous base and vary in shape and surface structure (MEZ 1890). The density and composition of the indumentum may be variable, even within species, according to climate or habitat (GAVIRIA 1987).

**Inflorescence Structure.** The basic monotelic inflorescence architecture of Cordiaceae is rather conserved. Typically (in, e.g., *Bourreria*, *Cordia*, and *Ehretia*) there is a terminal, rarely axillary, acropetalous, ebracteose thyrsoid with mono- or dichasial paracladia (Figs. 2-1, 2-4, 2-15, 2-21). The flowers are pedicellate or sessile (Figs. 2-1, 2-23). Thyrsoids with dichasial paracladia and pedicellate flowers appear to represent the ancestral condition, while monochasial paracladia and sessile flowers are probably derived states. The more aberrant inflorescence types found in some taxa can be readily derived from this basic pattern (GAVIRIA 1987). In some species of *Cordia* morphologically terminal inflorescences are displaced into a lateral, internodal position due to recaulescence. The usually long internodes in the inflorescence can be very short resulting in apparently umbellate (*Cordia p.p.*, *Ehretia p.p.*) and finally paniculate syn-florescences (in some species of the *Sebestena* subclade of *Cordia*). Glomeruli are found in some *Tiquilia* species (RICHARDSON 1977). Also, inflorescences can be reduced to solitary, axillary flowers (*Bourreria p.p.*, *Cordia p.p.*, *Ehretia p.p.*, *Halgania p.p.*). In *Varronia* complex patterns of growth have led to strongly congested ('cephaloid', Figs. 1-4, 5-6), and 'spicate' inflorescences (Fig. 2-6), with basipetal anthesis (concaulescent-syndesmic), are derived from these congested inflorescences (UHLARZ & WEBERLING 1977, GOTTSCHLING *et al.* subm. a). Flowering can precede leaf development in deciduous species of the *Myxa* subclade of *Cordia* (GAVIRIA 1987).

**Flower Structure.** Usually the flowers do not exceed 15 mm in diameter, but large-flowered species are found in, e.g., *Bourreria* and the subclades *Collococcus* and *Sebestena* of *Cordia* (the largest flowers, with a diameter up to 10 cm, has *Cordia mairei* from the *Myxa* subclade of *Cordia*). Detailed studies on floral anatomy are rare (e.g., RAO & RANI 1987). The calyx is synsepalous, divided almost to base (many Ehretiaceae, Fig. 2-23) or forming a long tube (e.g., in *Cordia*, *Bourreria*, Figs. 2-1, 2-9 and 2-10, 2-22). The calyx tube is campanulate, urceolate, or cylindrical, and the lobes are lanceolate, triangular, or narrowly ovate. Calyx aestivation is often valvate (e.g., *Bourreria*, Cordiaceae), otherwise quincuncial imbricate (in, e.g., *Ehretia*, *Lepidocordia*, *Rocheportia*). Occasionally, the calyx is ruptured irregularly by the developing corolla, and no distinct calyx lobes can be observed (in some species of the *Myxa* subclade of *Cordia*). In *Cortesia* an involucre formed by bracts, with 10 to 15 teeth, is developed (FULVIO 1965). The calyx persists in fruit and encloses the fruit at least when young. The corolla is always sympetalous with a cylindrical or infundibuliform tube and spreading or reflexed lobes, which are ovate to suborbicular, sometimes long and narrow with margins entire to repand, sometimes involute (Figs. 2-2 and 2-3, 2-9 to 2-11, 2-22 and 2-23). Usually, the corolla tube exceeds the calyx in length (sometimes shorter in *Ehretia* and *Varronia*). The corolla lobes are mostly shorter than the tube. Aestivation is imbricate (quincuncial), occasionally contorted. There are usually five corolla lobes, but sometimes only four (e.g., *Coldenia*, *Cordia tetrandra*, *Rocheportia p.p.*, *Tiquilia p.p.*) or more than five (in some *Cordia* species). The corolla is mostly white, but yellow, orange (e.g., *Sebestena* subclade of *Cordia*), red (**titelpage**), purple or blue (e.g., *Halgania*, *Tiquilia p.p.*, Figs. 1-8 to 1-10) corollas also occur. The androecium is haplostemonous, filaments are united with the corolla tube and insert at different levels (Figs. 2-2 and 2-3, 2-9 and 2-10). In Cordiaceae and Ehretiaceae, there is usually a patch of trichomes at the point of attachment (also in some *Bourreria* species), and in some *Tiquilia* species the veins below the points of attachment are sometimes swollen or winged. The exerted anthers often exceed the style in length, but included anthers also occur. They are oblong, ovate, or cordate. A nectariferous disc is more or less developed (a voluminous disc is found in, e.g., *Bourreria* and *Cordia p.p.*). In *Halgania* anthers are connate into a cone around the style (Figs. 1-10, 2-20). The four microsporangia open *via* longitudinal slits (intrors). The ovary is bicarpellate, and the internal architecture results from the development of several additional septa (basal septa, apical septa, false septa), thus leading mostly to an imperfectly four-locular ovary. In *Halgania* only two locules are found, which is the result of the reduction of one half of each carpel (LAWRENCE 1937). The style is terminal and bifid in Ehretiaceae and twice bifid in Cordiaceae forming four stigmatic heads (**titelpage**, Fig. 1-5). The relative length of the two style branches varies from very short to almost to the base (in, e.g., *Ehretia microphylla*), occasionally varying in the same species. The placentas are well-developed (e.g., *Bourreria*, *Ehretia p.p.*) or scarce (e.g., Cordiaceae, *Tiquilia*). Placentation is basal (in, e.g., the *Sebestena* subclade of *Cordia*) through axile (most Ehretiaceae). Ovules are generally anatropous (epitropous, hanging, AGARDH 1858, GUSULEAC 1937), but orthotropous ovules are found in,

e.g., the *Sebestena* subclade of *Cordia*. In Ehretiaceae, they are exclusively crassinucellar, while both crassinucellar and tenuinucellar ovules are found in Cordiaceae (KHALEEL 1985).

**Embryology.** Knowledge on embryology is scarce in Cordiaceae and Ehretiaceae that goes beyond circumstantial evidence. The endothecium of the anthers develops fibrous thickenings. Microsporogenesis is simultaneous. The initial microspore is tetrahedral and decussate isobilateral. The anther wall has initially one middle layer, in some species it comprises 2 to 4 (sometimes 5) layers. The tapetum is multinucleate and glandular. Archespore functions directly (Cordiaceae) or cuts off a parietal cell (Ehretiaceae, KHALEEL 1985). In Ehretiaceae embryogeny corresponds to the crucifer- or chenopodiad-type. Embryo-sac development corresponds to the *Polygonum*- or *Allium*-type (RAO & RAO 1984). Polar nuclei fuse prior to fertilisation. Three ephemeral antipodal cells are formed, which do not proliferate. The synergids are hooked and are destroyed during the entry of the pollen tube. Fertilisation is porogamous. The endosperm (in Ehretiaceae) develops *ab initio* cellular and corresponds to the *Myosotis*-type. Both chalazal and micropylar haustoria are found. In some species one of them is more active than the other, while in others both of them are equally well-developed (SVENSSON 1925, KHALEEL 1985). For some species the presence of a placental obturator has been reported (KHALEEL 1982) as well as the presence of a suspensor, which is uniseriate, filamentous, and consists of 4 to 6 cells in *Ehretia acuminata* (KHALEEL 1977).

**Pollen Morphology.** Cordiaceae and Ehretiaceae are highly euryopalynous with many dimorphic and heteromorphic pollen types. Dimorphism regarding size and shape has been observed in distylous species of *Cordia* (AL-SHEHBAZ 1991). Pollen of Cordiaceae is oblate-spheroidal to subprolate in outline and usually 3–(rarely 4–)colpor(oid)ate and 20 to 60  $\mu\text{m}$  in diameter. *Varronia* has 3-porate pollen as also has, e.g., *Cordia lutea* (*Myxa* subclade of *Cordia*), but here it differs in size (up to 115  $\mu\text{m}$  in diameter), the presence of a thin exine, and a microreticulate tectum. Exine ornamentation is irregularly striate [*Cordia glazioviana* ( $\equiv$  *Auxemma glazioviana*)], rugulose [*Cordia oncocalyx* ( $\equiv$  *Auxemma oncocalyx*), *Cordia americana* ( $\equiv$  *Patagonula americana*)], reticulate with scabrae (*Varronia*), striate-reticulate (*Sebestena* subclade *p.p.* of *Cordia*), or variously spinulose and clavate (subclades *Sebestena p.p.* and *Myxa* of *Cordia*). BORRHIDI *et al.* (1988) distinguished three main types, HEUBL *et al.* (1990) five types, and NOWICKE & MILLER (1990) at least seven types of pollen in Cordiaceae, some of which correlate with molecular data (GOTTSCHLING *et al.* subm. a). Sticky pollen kit is abundant in, e.g., the *Myxa* subclade of *Cordia*, and obscures the exine structure. The (2– or) 3– (or 4–) colpor(oid)ate pollen of Ehretiaceae (except *Lepidocordia*) can usually be distinguished from those of Cordiaceae by the presence of pseudocolpi or pseudocolpoid depressions alternating with the colpi (SAHAY 1979, NOWICKE & MILLER 1990). Pollen shape is prolate-spheroidal to subprolate in outline with a diameter of 15 to 35  $\mu\text{m}$ . Exine ornamentation is granulate (e.g., *Bourreria*), scrobiculate (e.g., *Coldenia*), punctate (e.g. *Halgania*), finely reticulate (e.g., *Ehretia p.p.*), or faintly striate (e.g., *Ehretia p.p.*).

**Karyology.** Chromosome numbers of Cordiaceae are poorly studied, and records of only about 15% of the species are available. Although some reports are conflicting (even within species), the following generalised patterns emerge (e.g., HEUBL *et al.* 1990): Diploid Cordiaceae have base numbers of  $n = 7$  (*Myxa* subclade of *Cordia*),  $n = 8$  (*Sebestena* subclade of *Cordia*), or  $n = 9$  [*Cordia americana* ( $\equiv$  *Patagonula americana*), *Varronia*]. In some species of the *Sebestena* subclade of *Cordia*  $n = 15$  occurs, which can be interpreted as being derived from  $n = 7$  or 8. Two base numbers are readily recognised in Ehretiaceae:  $n = 8$  (*Ehretia*, *Tiquilia p.p.*) and  $n = 9$  (*Cortesia*, *Tiquilia p.p.*, RICHARDSON 1977, HEUBL *et al.* 1990). For *Bourreria*  $n = 19$  has been reported (AL-SHEHBAZ 1991). Polyploidisation (mostly tetraploidy) is a common feature in Cordiaceae and Ehretiaceae (e.g., in the subclades *Myxa* and *Sebestena* of *Cordia*, *Ehretia*, *Tiquilia*).

**Pollination.** The breeding systems are known to be very diverse (OPLER *et al.* 1975, GAVIRIA 1987, ASKINS *et al.* 1987, WARFA 1988). Some instructive examples of transitions between heterostyly (Figs. 2-9 and 2-10) and dioecy are found in *Cordia* (*Myxa* subclade, LLOYD 1979, VERDCOURT 1991, GOTTSCHLING *et al.* subm. a). Heterostyly is also known from some Ehretiaceae (e.g., *Ehretia saligna*, RANDELL 1993) as well as dioecy in, e.g., *Lepidocordia* (MILLER & NOWICKE 1990) and *Rochefortia*. Protandry is a frequent feature. Flower morphology and fragrance suggest that Cordiaceae are typically zoophilous. However, observations on pollination have been rarely published (FULVIO 1965, PERCIVAL 1974, OPLER *et al.* 1975, GAVIRIA 1987). For small, white flowers of many Ehretiaceae insects like hymenoptera, diptera, lepidoptera, coleoptera, or thysanoptera have been recorded. The blue flowers of, e.g., *Halgania* (Fig. 1-10) are probably visited by UV-sensible insects. The large, red flowers of the subclades *Collococcus p.p.* and *Sebestena p.p.* of *Cordia* (titelpage) suggest bird pollination. Furthermore, the frequent occurrence of exerted anthers indicate the possibility of wind pollination.

**Fruit and Seed.** Usually the fruit is drupaceous (Figs. 2-12 to 2-14, 2-24), schizocarps occur only in *Coldenia* and *Tiquilia*), and is differentiated into exocarp, mesocarp, and endocarp. The exocarp is thin to coriaceous, and the mesocarp is mostly fleshy to mucilaginous; only in some cases (e.g., *Bourreria p.p.*, *Coldenia*, *Sebestena* subclade *p.p.* of *Cordia*, *Tiquilia*) it is dry. Typically, each of four seeds is enclosed in a sclerenchymatic endocarpic layer. The fruits are usually small (10 mm in diameter or smaller), but in *Bourreria p.p.* (Fig. 1-11) and the *Sebestena* subclade of *Cordia* they are quite large (up to 5 cm in diameter). The fruit is often attractively coloured: it is orange or red in *Bourreria* (Fig. 1-12), *Ehretia*, and *Varronia*, white in some species of *Cordia* and in *Ehretia latifolia*, occasionally yellow or black in some species of *Bourreria*, *Cordia*, and *Ehretia*. Fruit anatomy yields important taxonomical characters (MILLER 1989, AL-SHEHBAZ 1991, GOTTSCHLING & HILGER 2001). The endocarp is either undivided (Cordiaceae, *Ehretia p.p.*, *Halgania p.p.*, *Lepidocordia*, Figs. 2-8, 2-27, 7-2) or divided into two (*Ehretia p.p.*, *Halgania p.p.*, Figs. 2-26, 7-1) or four parts (most Ehretiaceae, Figs. 2-25, 2-28, 7-1), which are called endocarpids (pyrenes). The abaxial surface of the endocarpids is glabrous,

rugose-sulcate, ridged, or composed of distinct lamella (e.g., *Bourreria*). Occasionally, the endocarp is quite thin-walled (*Cordia p.p.*, *Halgania*, *Lepidocordia*, *Tiquilia*). Sometimes, some endocarps and/or seeds abort (*Cordia p.p.*, *Ehretia p.p.*, *Halgania*, *Tiquilia p.p.*). Occasionally, additional sterile chambers are found (in, e.g., *Ehretia microphylla*, *Lepidocordia*, Fig. 2-27). The calyx persists in fruit (Figs. 1-2, 1-11, 2-24) and encloses the fruit at least when young. In many Cordiaceae it is accrescent, ultimately more or less enclosing the fruit (completely enclosed in the most species of the *Sebestena* subclade of *Cordia*, Figs. 2-4, 5-10). In some species the calyx lobes are elongated in fruit [e.g., *Ehretia microphylla*, *Cordia americana* (= *Patagonula americana*), Figs. 1-2, 2-5]. In most Cordiaceae and Ehretiaceae also the style (at least the base) persists in fruit (Figs. 1-11, 2-24). The testa epidermis consists of transfer cells with tangential and radial protuberances of the cell walls (DIANE *et al.* 2002b, GOTTSCHLING & HILGER *subm.*). The embryo is curved or straight. The endosperm is copious and fleshy in Ehretiaceae and is absent in Cordiaceae. The germination of the seed is epigeal and phanerocotylar. In Ehretiaceae cotyledons are flat, but plicate cotyledons have evolved from this in Cordiaceae (Figs. 1-1, 2-7). The first pair of foliage leaves is alternate or subopposite (GAVIRIA 1987, WARFA 1988).

Dispersal. The unit of dispersal is the entire fruit (exceptions are found in *Coldenia* and *Tiquilia*). It is dispersed mostly endozoochorically by birds (RIDLEY 1930, SCOTT & MARTIN 1984, AL-SHEHBAZ 1991) or sometimes by mammals. In some species of the *Sebestena* subclade of *Cordia* dispersal is by wind (AL-SHEHBAZ 1991). Hydrochoria is found in, e.g., *Cordia subcordata* with a corky mesocarp (JOHNSTON 1951) and *Coldenia* (RICHARDSON 1977).

Phytochemistry. Pyrrolizidine alkaloids (PAs, e.g., Ehretinine) and quinonoid or phenolic compounds are the most significant secondary metabolites in Cordiaceae (HEGNAUER in RIEDL 1997, STEGELMEIER *et al.* 1999). They all belong to the ester-type and are similar to, or identical with alkaloids also occurring in Asteraceae. The PAs are often concentrated in the youngest leaves and in flowers and inflorescences. PAs are a part of the plant's defence against herbivores, and they are used to increase floral constancy of visiting pollinators based on their volatility (HEGNAUER in RIEDL 1997). Both, the aminoalcohol part (necines) and the characteristic necic acids, derive from amino acids. Red alkannin as a key metabolite yields a whole array of quinonoid and/or phenolic constituents through different metabolic pathways, e.g., the allergenic cordiachromes, alliodorin, and glaziovianols (HEGNAUER 1989, HEGNAUER in RIEDL 1997, COSTA *et al.* 1999). These compounds, with antibiotic activities, were isolated in stems and roots. Cordiaquinones, ehretianones, and microphyllones are probably also derivatives of hydroquinone. Additional phenolic constituents were isolated in roots, stem bark, or seeds of several species of *Cordia* (HEGNAUER in RIEDL 1997). In stems, bark, and leaves of *Cordia* and *Ehretia*, triterpenes and triterpenoid saponins have been isolated. Caffeic and rosmarinic acid appears to be ubiquitous in Cordiaceae. Nitrile glucosides (ehretiosides) have been found in the stem bark of *Ehretia philippinensis*. The seeds are often very rich in allantoin (nitrogen storage)

and contain oleic acid (HEGNAUER 1989). Cordiaceae often deposit carbonate of calcium and/or silica in hairs and epidermis cells.

**Distribution and habits.** The distribution of Cordiaceae and Ehretiaceae closely correlates with climatic conditions, and they are largely restricted to tropical or subtropical regions. Minimum temperature and precipitation are limiting factors for geographical range. Only a few species occur in more temperate regions, and this is correlated with morphological features such as serrate leaves in, e.g., *Ehretia p.p.* (GOTTSCHLING & HILGER 2001) and *Cordia p.p.* Cordiaceae and Ehretiaceae have an originally Gondwanan distribution. Cordiaceae are mostly found in the New World with centres of diversity in Central and northern South America, whereas Ehretiaceae have centres of diversity both in the New World and in the Old World (Africa and East Asia). The habitats range from tropical rainforest (*Cordia*, *Ehretia p.p.*) to arid savannah (*Bourreria*, *Ehretia p.p.*, *Varronia*) and deserts (*Tiquilia*). Some taxa are adapted to extremely poor or toxic soils (some species of, e.g., *Bourreria* on serpentine in Cuba).

**Affinities.** Traditionally, Cordiaceae and Ehretiaceae have been treated as subfamilies of “Boraginaceae” *sensu* GÜRKE (1893). Current molecular studies suggest that “Boraginaceae” *sensu* GÜRKE (1893) are polyphyletic. In their current circumscription Boraginales comprise of Boraginaceae *s.str.*, Hydrophyllaceae *s.str.*, Heliotropiaceae, Cordiaceae, Ehretiaceae, and Lennoaceae (e.g., FERGUSON 1999, SMITH et al. 2000, GOTTSCHLING et al. 2001) and have an isolated and basal systematic position in the asterid clade. Based both on molecular and morphological data, Cordiaceae, Ehretiaceae (including Lennoaceae), and Heliotropiaceae constitute a monophylum, the Primarily Woody Boraginales (GOTTSCHLING et al. 2001, DIANE et al. 2002b, GOTTSCHLING & HILGER in prep.) with Cordiaceae and Ehretiaceae as sistergroups (previously suggested by, e.g., HUTCHINSON 1959, PARMAR 1991). Parasitic Lennoaceae are nested in Ehretiaceae on the basis both of molecular data and of apomorphic features such as the presence of pseudocolpi in pollen (YATSKIEVICH & ZAVADA 1986). The monophyly of Cordiaceae is well-supported by apomorphic traits such as the plicate cotyledons (Figs. 1-1, 2-7) and four stigmatic lobes (**titelpage**, Figs. 1-5, 2-11), while the monophyly of Ehretiaceae has been doubtful (no morphological apomorphy). Based on *trnL<sub>UAA</sub>* intron sequence data Ehretiaceae are monophyletic and comprise the following subordinate taxa (GOTTSCHLING & HILGER in prep.): *Bourreria*, *Ehretia* (including former *Carmona* and *Rotula*), *Halgania*, *Lennoa*, *Lepidocordia*, *Pholisma*, *Rochefortia*, and *Tiquilia*. Furthermore, *Cortesia* is possibly nested in *Ehretia* (based on fruit anatomy), and *Coldenia* possibly is closely allied to Cordiaceae (GOTTSCHLING & HILGER in prep.) comprising *Varronia* and *Cordia* (GOTTSCHLING et al. subm. a). The latter segregates into the three subclades *Collococcus*, *Myxa*, and *Sebestena* (including former *Auxemma*, *Patagonula*, and *Saccellium*). *Pteleocarpa* does not belong to Boraginales on the basis of molecular (GOTTSCHLING & HILGER in prep.) and wood anatomical data (GOTTWALD 1982).



Palaeobotany. Fossilised endocarpids of *Ehretia p.p.* are known from the European (England, France, Germany) Oligocene to Pliocene (CHANDLER 1961, 1962, 1964, MAI 1995), which closes the present-day distribution gap between North America and East Asia (GOTTSCHLING *et al.* 2002). There exist a few records of *Cordia* pollen from the Miocene of Spain and the Marshall Islands (MULLER 1981). Three species are known from the East Asian Palaeogene and Eocene. In the Flora of the Monterey Formation (Californian Miocene) some leaf imprints have been found as well as Quaternary seeds, fragmentary wood, and branches of *Cordia* species from the Caribbean (ITURRALDE-VINENT *et al.* 2000). From the Russian Eocene leaf imprints of *Cordia* have been described (CHELEBAJEVA 1984).

Economic importance. Several species of *Cordia* and *Ehretia* are valuable timber trees in East Asia and Central and South America. Their wood is used in constructions and in making furniture, flooring, tool handles, and musical instruments (AL-SHEHBAZ 1991). Alkannin can be used as a dye. The fleshy mesocarp of the fruit of many species is edible (WATT & BREYER-BRANDWIJK 1962, USHER 1971, FACCIOLA 1990). Furthermore, bark and leaves are sometimes used for the preparation of herbal teas or as condiments. Flowers and leaves are occasionally eaten as vegetables. Some species are cultivated as ornamentals [e.g., *Cordia lutea*, *Cordia saccellia* ( $\equiv$  *Saccellium lanceolatum*)]. Some species of Cordiaceae are used in folk medicine for wound-healing (QUISUMBING 1951, WATT & BREYER-BRANDWIJK 1962, LEWIS 1991, COSTA *et al.* 1999, DONG *et al.* 2000), or for treating infections of the urinary tract (NAYAR *et al.* 1999). Some compounds of Cordiaceae have psychoactive (NAYAR *et al.* 1999), antiallergic, or spasmolytic activity (HEGNAUER in RIEDL 1997). In Africa the root of *Cordia gharaf* and *Cordia quarensis* is used for abortions (WATT & BREYER-BRANDWIJK 1962).

## 2.2 Key to subordinate taxa

- |   |   |                              |
|---|---|------------------------------|
| 1 | Fruit never enclosed in accrescent calyx; style entire or once bifid; endocarp undivided, two-, or four-parted; cotyledons flat ( <b>Ehretiaceae</b> )  | □ 2                          |
| – | Fruit usually at least partly enclosed in accrescent calyx; style usually twice bifid (if once bifid, then fruit completely enclosed in accrescent calyx); endocarp undivided; cotyledons plicate ( <b>Cordiaceae</b> ) | □ 9                          |
| 2 | Herbs or shrubs up to 1 m tall; flowers crowded, inflorescences globose, rarely few-flowered; fruits dry, separating into four nutlets; leaves pinnately veined and bullate   | □ 3                          |
| – | Trees or shrubs; flowers not crowded, inflorescences branched, rarely few-flowered; fruits drupaceous at least when young, never separating into four nutlets; leaves sometimes pinnately veined but never bullate      | □ 4                          |
| 3 | Annual herbs with adventitious roots; lamina asymmetrical; flowers tetramerous; Old World   | <b>2 <i>Coldenia</i></b>     |
| – | Perennial herbs, subshrubs or shrubs; lamina symmetrical; flowers pentamerous; New World  | <b>9 <i>Tiquilia</i></b>     |
| 4 | Anthers connate in a cone surrounding the style; flowers mostly blue, rarely white, somewhat tilted; Australia  | <b>6 <i>Halgania</i></b>     |
| – | Anthers free; flowers usually white   | □ 5                          |
| 5 | Flowers unisexual; plants dioecious   | □ 6                          |
| – | Flowers all bisexual  | □ 7                          |
| 6 | Stem with spines  | <b>8 <i>Rochefortia</i></b>  |
| – | Stem without spines   | <b>7 <i>Lepidocordia</i></b> |
| 7 | Flowers partly enclosed in an involucre; calyx lobes free and spoon-shaped; two parted endocarp; Argentina  | <b>4 <i>Cortesia</i></b>     |
| – | Involucre absent; calyx lobes not spoon-shaped  | □ 8                          |
| 8 | Calyx aestivation valvate; fruit with 4 triangular endocarpids with an additional sterile chamber and distinct lamellae on the abaxial surface  | <b>1 <i>Bourreria</i></b>    |
| – | Calyx aestivation imbricate; fruit with 1 to 4 endocarpids, these without lamellae on the abaxial surface   | <b>5 <i>Ehretia</i></b>      |
| 9 | Inflorescence syndesmic, ‘cephaloid’, ‘spicate’ (or umbellate); leaves mostly serrate or dentate  | <b>10 <i>Varronia</i></b>    |
| – | Inflorescence mostly loose, with dichasial branches; leaves usually entire  | <b>3 <i>Cordia</i></b>       |

### 2.3 Subordinate taxa of Cordiaceae and Ehretiaceae (excluding *Lennoa* and *Pholisma*)

#### 1 *Bourreria* P.BR. (SCHULZ 1911, VERDCOURT 1991, Figs. 1-11 and 1-12, 2-21 and 2-22, 2-28)

*Bourreria* P.BR., Civ. Nat. Hist. Jam.: 168–169, tab. 15 (1756), *nom. cons.*

= *Morelosia* LA LLAVE & LEXARZA (1824)

= *Hilsenbergia* MEISSN. (1840)

= *Crematomia* MIERS (1869)

Trees or shrubs, occasionally climbers; leaves alternate or fasciculate, sometimes microphyllous, mostly obovate-oblong, apex rounded, rarely acuminate, smooth or scabrid, margin entire; thyrsoids terminal, rarely axillary, with dichasial paracladia, rarely few-flowered; flowers bisexual, white, small to quite large; calyx aestivation valvate, lobes sometimes irregular; corolla tube short or elongate, cylindrical, often broadened at the throat, lobes spreading or reflexed; anthers included or exerted, anthers ovate or oblong; style bifid or almost entire; drupe small to large; endocarp four-parted, endocarps with distinct lamellae on the abaxial surface and an additional sterile chamber. *n* = 19. About 40 species in the Caribbean and East Africa.

#### 2 *Coldenia* L. (RICHARDSON 1977, Fig. 2-17)

*Coldenia* L., Sp. Pl.: 125 (1753)

Procumbent herb with slender, branched stems, often with adventitious roots; leaves clustered, small, numerous, bullate, margin crenate; flowers bisexual, solitary, small, white or yellow, tetramerous; calyx deeply lobed; corolla tube cylindric, throat glabrous, lobes spreading; anthers included; style bifid; fruits small, dry, ovoid-conical, four-lobed, separating into four one-seeded apiculate nutlets, mesocarp spongiose, endocarp with spines. Monotypic (*Coldenia procumbens*), coastal, distributed in the Old World tropics.

**3** *Cordia* L. (JOHNSTON 1930, 1950, 1951, GAVIRIA 1987, WARFA 1988, VERDCOURT 1991, RIEDL 1997, GOTTSCHLING *et al.* subm. a, **titelpage**, Fig. **1-1** to **1-5**, **2-1** to **2-5**, **2-7** to **2-14**)

*Cordia* L., Sp. Pl.: 190 (1753)

= *Patagonula* L. (1753)

= *Collococcus* P.BR. (1756)

= *Gerascanthus* P.BR. (1756)

= *Sebestena* BOEHM. (1760)

= *Saccellium* HUMB. & BONPL. (1806)

= *Auxemma* MIERS (1875)

= *Lithocardium* (L.) KUNTZE (1891)

= *Myxa* (ENDL.) FRIESEN (1933)

Trees or shrubs; leaves alternate, rarely subopposite or fasciculate, ovate to lanceolate, with entire, crenate, or dentate margins; thyrsoids mostly terminal, occasionally axillary, with dichasial or monochasial paracladia, sometimes in corymbo-thyrsoids or apparently umbellate; flowers originally bisexual, often dichogamous or functionally monosexual, sometimes dioecious, large to small, showy, white, yellow, or red; calyx cylindrical, short to long, aestivation valvate; corolla sometimes persistent in fruit; anthers included or exerted; style twice bifid; drupe small to large, largely or almost completely enclosed by the enlarged calyx (this sometimes cupuliform) at maturity; endocarp undivided, often only one seed developed, the others abortive.  $n = 7, 8, 9$ . Approximately 300 species distributed pantropically with centres of diversity in the Caribbean, northern South America, and Africa.

Based on molecular data (GOTTSCHLING *et al.* subm. a) *Cordia* segregates into three clades, *Collococcus*, *Myxa*, and *Sebestena*. The exclusively New World *Collococcus* subclade represents JOHNSTON'S (1930) *Cordia* sects. *Pilicordia* and *Physoclada* (i.e., *C. nodosa*) together with the *Superbiflorae*. The *Myxa* subclade comprises species from the New World and the Old World of *Cordia* sect. *Myxa*. The *Sebestena* subclade consists of *Cordia* sects. *Cordia* and *Gerascanthus* and of former *Auxemma*, *Patagonula*, and *Saccellium*.

**4** *Cortesia* CAV. (Fig. 2-16)

*Cortesia* CAV., Icones 4: 53, tab. 377 (1797)

Shrub; leaves alternate or fasciculate, long-cuneiform with 2 to 3 lobes, lobe margin entire; flowers bisexual, terminal or axillary, mostly solitary, small, with an involucre with 10 to 15 teeth formed by bracts, persistent in fruit; calyx lobes free, spoon-shaped, caducous, aestivation imbricate; corolla equalling involucre; anthers exerted; style bifid; drupe small, endocarp two-parted.  $n = 9$ . Monotypic (*Cortesia cuneifolia*), Argentina.

Based on morphological data (syn-mericarpy) *Cortesia* is possibly nested in *Ehretia*.

**5** *Ehretia* P.BR. (MILLER 1989, VERDCOURT 1991, RIEDL 1997, GOTTSCHLING & HILGER 2001, Figs. 2-15, 2-18, 2-23 to 2-27)

*Ehretia* P.BR., Civ. Nat. Hist. Jam.: 168, tab. 16 (1756)

= *Rotula* LOUR. (1790)

= *Carmona* CAV. (1799)

= *Rhabdia* MART. (1826)

= *Traxilum* RAF. (1838)

Trees or shrubs; leaves alternate or fasciculate, ovate to lanceolate, smooth or scabrid, margin entire, crenate, or dentate; thyrsoids terminal or axillary with dichasial or monochasial paracladia, rarely few-flowered; flowers bisexual, sometimes dimorphic, small; calyx cylindrical, shallowly to deeply lobed, rarely accrescent, aestivation imbricate; corolla white, pale-yellow, pale-pink, or blue, the tube very short or exceeding the lobes in length, lobes spreading or reflexed; anthers usually exerted, sometimes included; style scarcely divided into two branches or divided to base; drupes small, endocarp four- or two-parted, or undivided, rarely with additional sterile chambers.  $n = 9$ . About 50 species in the tropics of the Old World and the New World, with centres of diversity in Africa and East Asia.

Based on molecular data *Ehretia* comprises two clades: the monophyletic *Ehretia* I (plants with a four-parted endocarp) with former *Rotula* species as its closest relatives, and the monophyletic *Ehretia* II (plants with a two-parted endocarp) with former *Carmona retusa* as its closest relative (GOTTSCHLING & HILGER 2001).

**6** *Halgania* GAUDICH. (Figs. **1-10**, **2-19** and **2-20**)

*Halgania* GAUDICH. in FREYC., Voy. Aut. Monde (Bot.): 448, tab. 59 (1826)

Shrubs; leaves alternate, lanceolate, margin entire or toothed to serrate; glandular hairs abundant; thyrsoids terminal, rarely few-flowered; flowers bisexual, small, showy, somewhat tilted; calyx campanulate; corolla white, blue to purple, tube short; anthers often yellow, connate, exceeding the style in length and forming a cone around it, tapering into five terminal appendages, which form a straight beak; gynoecium of two locules (by abortion of two half carpels), style shortly bifid; drupes small, two-seeded by abortion, endocarp thin-walled, undivided or rarely two-parted. About 20 species in Australia.

**7** *Lepidocordia* DUCKE (MILLER & NOWICKE 1990)

*Lepidocordia* DUCKE, Archiv. Bot. Río Janeiro **4**: 170, tab. 22 (1925)

= *Antrophora* I.M.JOHNST. (1950)

Trees; leaves alternate, ovate, margin entire; thyrsoids with dichasial paracladia, flowers small, unisexual, plants dioecious; calyx lobes nearly free to base, slightly unequal, imbricate in bud; corolla white, lobes spreading or reflexed; staminate morph with functional anthers and viable pollen, style absent, stigma very reduced; pistillate morph with smaller, shrivelled anthers and an elongated bifid style; drupe small, endocarp undivided, with sterile cavities. 2 species in Central America and Northern South America.

**8** *Rochefortia* SW.

*Rochefortia* SW., Prod. Veg. Ind. Occ.: 53 (1788)

Shrubs with axillary spines; leaves alternate or fasciculate, mostly ovate, with entire margin; thyrsoids terminal and often axillary with dichasial paracladia, flowers occasionally solitary; flowers white, small, unisexual, plants dioecious; calyx campanulate, aestivation imbricate; corolla tube short; anthers exerted; style bifid; drupe small, endocarp four-parted. About 3 species in Central America.

**9** *Tiquilia* PERS. (RICHARDSON 1977, Figs. 1-7 to 1-9)

*Tiquilia* PERS., Syn. Pl. 1: 157 (1805)

Shrubs or herbs, prostrate, spreading, or erect, densely branched; leaves microphyllous, often clustered near branch apices, bullate with lobed margins; inflorescences very dense (glomerules); flowers bisexual, small, sessile; calyx campanulate; corolla white to blue, often with a yellow throat; anthers included or exserted; style bifid; fruits drupaceous when young, later separating into four (or fewer by abortion) dry nutlets.  $n = 8, 9$ . About 25 species in North and South America.

**10** *Varronia* P.BR. (JOHNSTON 1930, 1951, GAVIRIA 1987, GOTTSCHLING *et al.* subm. a, Figs. 1-4, 2-6)

*Varronia* P.BR., Civ. Nat. Hist. Jam: 172, tab. 13, f. 2 (1756)

= *Montjolya* FRIESEN (1933)

= *Ulmarronia* FRIESEN (1933)

Shrubs or woody climbers; leaves alternate, ovate to lanceolate, with serrate margin; inflorescences terminal or axillary, capitate, spicate, or very shortly cymose umbellate to globose; flowers bisexual, small; calyx lobes thickened at the margin, frequently with appendages; corolla tube usually shorter than, or as long as the calyx, often with a trichome ring in the throat; anthers included; style twice bifid; drupes small, half to completely enclosed by the calyx, endocarp undivided.  $n = 9$ . About 100 species in the Neotropics, with centres of diversity in Mexico and Brazil.