TAXONOMIC STUDIES ON BRAZILIAN SPECIES OF CORDIA L. (BORAGINACEAE)

Neusa Taroda

A Thesis Submitted for the Degree of PhD at the University of St Andrews

1984

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I - INTRODUCTION
I - Introduction

The family Boraginaceae s.l., to which the genus *Cordia* belongs, comprises some 100 genera and includes ca. 2000 species (Willis, 1973; Cronquist, 1983) with a more or less cosmopolitan distribution.

Bentham & Hooker (1876) divided the Boraginaceae into four tribes based primarily on the characteristics of the style and ovary:

1. **Cordieae** (style terminal, four-branched with each arm terminating in a clavate or capitate stigma; ovary unlobed);
2. **Ehretieae** (style terminal or lateral, stigma 4-lobed or bifid);
3. **Heliotropieae** (style terminal or lateral, stigma 4-lobed, elongate with a subapical depression, ovary unlobed);
4. **Borageae** (style gynobasic, stigma truncate or capitate, ovary distinctly 4-lobed).

Subsequently, these tribes were elevated to the category of subfamily by Gürke (1897, in Engler & Prantl, *Die Natürlichen Pflanzenfamilien*): (1) Cordioideae, (2) Ehretioideae: (3) Heliotropoideae and (4) Boraginoideae. This treatment of the family Boraginaceae was followed by Rendle (1925), Lawrence (1951) and Cronquist (1983).

Hutchinson (1959), combined Cordioideae and Ehretioideae in a distinct (largely woody) family Ehretiaceae with the remaining subfamilies comprising the (largely herbaceous) Boraginaceae s.str.

The treatment by Gürke (1897), however, has been more widely accepted, with the genus *Cordia* aligned with *Patagonula* and *Auxemma* under the subfamily Cordioideae.

The genus *Cordia* is particularly well represented in the large area of South America delimited by the Federal Republic of Brazil (some 65 species are recognised in the present revision, i.e. ca. one quarter of the total number of species in the whole genus).
The treatment of *Cordia* by Fresenius (1857) for von Martius' *Flora Brasiliensis* was unfortunate in being based in large part on a rather infelicitous view of the genus by De Candolle (1845) so that although this has been the standard taxonomic work for *Cordia* in Brazil, it suffers from many deficiencies. Of great value are the taxonomic studies by Johnston (1930-1956) which provided lucid accounts of the infrageneric taxa and species limits (see sect. II for detailed discussion). However, these accounts by Johnston are based on regional areas and extended over a period of 25 years during which this author changed his view of the taxonomy of generic, sectional and specific delimitations. The revision by Johnston (1930) consists the last treatment of the genus for part of Brazil, and thus there is no modern taxonomic account for *Cordia* for this country. It is this deficiency which the present study attempts to remedy.

The present revision is restricted to the Brazilian species of *Cordia*, but a view of the genus as a whole, in particular the status of infrageneric categories has also been evaluated.

Accompanying a formal revision based on external morphology, a palynological study of a number of species of the genus is provided, and also a discussion of the reproductive biology of some species, particularly with regard to the occurrence of heterostyly.

The entire genus *Cordia* presents many interesting aspects such as its diverse morphological features of habit, inflorescence pattern, flowers and fruits; the reproductive biology with heterostyly presumably evolving towards dioecy in many species and perhaps a high level of polyploidy.
II - HISTORICAL
II - HISTORICAL

I - Early taxonomic history.

The name *Cordia* was originally employed by Plumier (1703) for a plant described from the West Indies. Linnaeus (1737) in *Hortus Cliffortianus* and in the first edition of *Genera Plantarum* accepted the genus *Cordia* as recognised by Plumier (1703) and cited the name *Sebestena*, attributed to Dillenius, as a synonym.

Subsequently, Linnaeus (1753) in *Species Plantarum* (ed. 1), listed under *Cordia* three species: *C. myxa*, *C. sebestena* and *C. glabra*. With the fifth edition of *Genera Plantarum* (which is the starting point for generic nomenclature), Linnaeus (1754) provided the generic characteristics for *Cordia* Plum. (as it is cited); *Sebestena* Dill., again appeared as a synonym.

A contemporary botanist of Linnaeus, Browne (1756), in his studies of the Jamaican plants, in addition to recording *Cordia* L. for the island, described three new genera, *Collococcus*, *Gerascanthus* and *Varronia*. Under the genus *Varronia*, Browne (1756) recognised the species *Lantana "foliis alternis, floribus corymbosis"* of Linnaeus. *Gerascanthus* and *Collococcus* were almost immediately incorporated into *Cordia* by Linnaeus (1759, 1762), as *C. gerascanthus* and *C. collococcus*, respectively and curiously, Linnaeus replaced his former epithet *C. glabra* by *C. collococcus* in doing so. *Varronia*, however, continued to be treated as distinct from *Cordia* by Linnaeus (1759, 1762) and several subsequent authors.

During subsequent years, several authors such as Jacquin (1760, 1763), Aublet (1775) and Lamarck (1791) continued to recognise *Cordia* and *Varronia* as two distinct genera and added new species from West Indies and South America to each.

Ruiz & Pavon (1794) introduced the genus *Cerdana* to include
the species *Cerdana alliodora*. Although the name *Cerdana* appeared under *Cordia* in the account of Kunth (1818) and Chamisso (1833) these authors did not transfer the binomial *Cerdana alliodora* to *Cordia* and it was Oken (1841) who effectively made the transfer by using the epithet *Cordia alliodora* (R. & P.) Oken (fide Johnston, 1950).

A monograph of *Varronia* was presented by Desvaux (1808), who assembled 27 species in this taxon, ten of which were new. In this comprehensive work Desvaux (1808) followed Browne (1756), and divided the species in three groups according to the type of inflorescence viz. (1) "Flores spicati" (2) "Flores capitati" and also (3) "Flores cymosi".

Brown (1810) was the first author to recognise the relationship between *Cordia* and *Varronia*. He pointed out the common characteristics shared by these taxa: ovary with four ovules, style dichotomous and plicate colyledons. Probably influenced by this view, Kunth (1818) and Roemer & Schultes (1819) treated *Varronia* as a section under *Cordia*, and these authors provided the first comprehensive account of the genus *Cordia*.

Thus, Kunth (1818) divided the species of *Cordia* in four sections, based primarily on the nature of the inflorescence, calyx teeth and pilosity of the corolla mouth; (1) *Sebestenae*: inflorescence corymbose and paniculate, calyx teeth acute and corolla mouth glabrous - comprising the single species *C. sebestena*; (2) *Cordia verae*: inflorescence always corymbose, calyx teeth acute, corolla mouth hairy - with six species; (3) *Varroniae*: inflorescence spicate, calyx teeth acute, corolla mouth hairy; (4) *Dasyocephalae*: inflorescence capitate, calyx teeth subulate-setaceous, corolla mouth hairy. The sect. *Varroniae* was subdivided into (a) spike elongate - with ten species and (b) spike globose - with nine species,
recalling the original classification of Browne (1756) and Desvaux (1808).

In a parallel classification, Roemer and Schultes (1819) recognized 67 species of *Cordia*, which they separated into three sections in a slightly different way from Kunth (1818):

1. sect. "*Cordia genuina*" with 39 species, included all but one of the species not allied to *Varronia*;
2. sect. *Varronia*, which was strictly based on Desvaux (1808); and a new monospecific section, *Cerdanae*, with *C. cerdana* (R. & P.) R. & S.

Sprengel (1825) enlarged the genus *Cordia*, and listed some 72 species distributed in just two sections: *Cordia verae* and *Varronia*. He did not accept the monotypic sections *Sebestenae* of Kunth (1818) or *Cerdanae* of Roemer & Schultes (1819).

In his *Flora Fluminensis* Vellozo (1829) re-established *Varronia* as a distinct genus from *Cordia* and also described the genus *Cordiada* with the single species *Cordiada trichotoma*. However, Vellozo (1829) based his new genus on an abnormal specimen, with the style composed of six stigmas. The species *Cordiada trichotoma* was, subsequently, transferred to *Cordia* by Steudel (1840).

Chamisso (1829, 1830, 1833), in a series of papers, described a number of new Brazilian species of *Cordia* based on the material collected by Sellow. The major contribution of Chamisso (1829) was to segregate the species in groups (although the actual infra-generic rank is not clearly stated) as (1) "*Calyce decemstriato*" to comprise those taxa allied to the modern concept of sect. *Gerascanthus* (Browne) Don (1837), except for one species, *C. grandis* (presently a synonym under *C. trichocladia* DC. of sect. *Myxa*) and (2) "*Calyce laevi*" which was subdivided as (A) "*Flores cymoso-paniculati*" and (B) "*Flores glomerulati vel spicati*". The first group was further
subdivided into: *Macranthae*, to include species with large flowers and *Micranthae*, those with small flowers. The latter groups more or less correspond to sect. *Cordia* and sect. *Myxa* sensu Johnston (1930, 1951). The group "*Flores glomerulati vel capitati*" comprised species allied to sect. *Varronia*. Later, Chamisso (1930) treated *Gerascanthus* and *Varronia* as two subgenera of *Cordia*.

The account of *Cordia* by Don (1837), which was probably influenced by Chamisso, recorded some 130 species in a World-wide treatment. Basically he recognised four sections: *Sebestenae*, to include the species with a loose inflorescence and large flowers; *Micranthae*, similar to the preceding group but with smaller flowers; *Gerascanthus*, characterised by species with ten-ribbed calyx, large flowers and corymbose inflorescence and *Varronia*. The section *Gerascanthus* as recognised by Don was fairly homogeneous and with the exclusion of just a few species provides the basis for the modern concept of this group.

In *Genera Plantarum*, Endlicher (1839), provided only a sketch of the subgeneric rank of the genus, introducing the name *Myxa* for a subsection under section *Sebestena*.

De Candolle (1845) with the *Prodromus* provided the most detailed account of the genus *Cordia* until Johnston's recent studies. De Candolle much enlarged the genus to comprise 175 species which were classified into seven sections. The recognition by De Candolle of the marcescent corolla of the species included in sect. *Gerascanthus* consolidated the concept of this section. The new sections

*Habdocalyx*, with a single species - *C. elaegnoides* and *Physoclada*, with three species (presently reduced to one) have been accepted unaltered by recent authors. Another section introduced by De Candolle was *Pilicordia*. This section was expanded by Johnston
(1930) to include a number of New World species which had been classified by De Candolle in sect. Myxa, subsection Laxiflorae.

In sect. Sebestenoides, De Candolle included 12 species, which fall more or less into the sect. Cordia sensu Johnston (1930). In his large sect. Myxa, De Candolle assembled all the small-flowered species, in which he also included those belonging to the by now traditional Varronia group. This sect. Myxa was organised by De Candolle in four subsections defined according to the nature of the inflorescence: (1) Laxiflorae; (2) Spicaeformis; (3) Subapitatae; (4) Dasycephala. In another new sect. Cordiopsis, De Candolle assigned two species, C. parvifolia DC. and C. mirabiliflora A.DC., which are currently referred to Rabdocalyx and Varronia respectively.

Curiously, De Candolle applied the name Varronia for a generic concept which differs completely from all previous and subsequent authors, with the exception of Gürke (1897), who simply adopted his treatment. De Candolle included three species in his genus Varronia: (1) V. calyptrata, a synonym of C. dentata of sect. Pilicordia (Johnston, 1940); (2) V. rotundifolia and (3) V. abyssinica, both of which are currently treated as members of sect. Myxa sensu Johnston.

The account of the genus Cordia in Martius' Flora Brasiliensis was provided by Fresenius (1857), who accepted 66 species in Brazil. The infrageneric taxa recognised by Fresenius differed from De Candolle (1845) (on whose work his account is largely based) with regard to the establishment of a new sect. Corymbiformes, to include the species previously treated by De Candolle in sect. Myxa, subsect. Laxiflorae (of sect. Myxa), and sect. Sebestenoides; Fresenius also elevated De Candolle's subsect. Spicaeformis, Subcapitatae and Dasycephalae (of sect. Myxa) to sections. Warming (1867) in his study of Central Brazilian flora strictly followed
Fresenius (1857) with regard to sectional and subsectional treatment of *Cordia*.

Bentham & Hooker (1876) only provided a very brief account of *Cordia*. Their important contribution was to discuss the validity of some genera which had been proposed by earlier authors which they suggested were not distinguishable from *Cordia*. Among these are *Varronia* Browne and *Varronia* sensu De Candolle, *Gerascanthus* Browne, *Hemigynia* Griff., *Gynaion* A.DC., *Macria* Ten., *Plethostephia* Miers, *Paradigma* Miers, *Borelia* Neck., *Firesia* Neck. and *Macielia* Vand. In fact, most of these generic names have been transferred to *Cordia* and accepted as such by all subsequent authors, with the exception of *Varronia* Browne and *Gerascanthus* Browne which have continued to be subject to differences of opinion as to whether they are best treated at distinct generic rank or as infrageneric taxa within *Cordia*. 
II - Johnston and his treatment of *Cordia* s.l.

Any present day study of *Cordia* has to be undertaken with reference to the impressive series of papers by Ivan Johnston (1930, 1935a,b, 1937, 1940, 1948, 1949a,b, 1950, 1951 & 1956) which have so greatly contributed to our understanding of this large genus of *Boraginaceae*.

Johnston (1930) in his first work on the Cordias from Brazil, Uruguay, Paraguay and Argentina - perhaps the most comprehensive of his papers on the genus - created section *Euco~dia*, re-established sect. *Varronia*, and partially or completely redefined the sections previously proposed for the genus *Cordia* (*Gerascanthus*, *Pilico~dia*, *Physocladia*, *Calyptracordia* and *Rhabdocalyx*). To do this he made use of a larger number of attributes such as fruits, nature of inflorescence, corolla and calyx shape, size and persistence. These sectional concepts presented by Johnston (1930), at least for the Brazilian species, brought together related taxa and thus delimited very natural assemblages. In this paper Johnston accounted for 50 species (four of them new) for the area under review, and recognised 8 sections which were characterised as follows:

1. Sect. *Gerascanthus*: corolla marcescent; fruits ellipsoidal, with fiber-bearing chartaceous walls, completely and closely invested by the calyx and dispersed still enclosed in it.

2. Sect. *Rhabdocalyx*: corolla marcescent; fruits conic-ovoid, with bony walls, only loosely and partially enclosed by the calyx and dispersed naked.

3. Sect. *Varronia*: flowers in spikes, heads or glomerules, rarely in small open cymes; corolla withering after anthesis; fruits small (3-4 mm), partially or completely invested by the calyx.
4. Sect. *Eucordia*: flowers in panicles; corolla large (1.5-6.5 cm) withering after anthesis; calyx markedly accrescent, partially or completely investing the large fruit (6-16 mm).

5. Sect. *Calyptrocordia*: flowers in panicles; corolla small (5-15 mm), withering after anthesis, funnelform, lobes broader than long, emarginate; calyx 3-5-toothed, usually irregularly circumscissile at the apex, in fruiting becoming explanate scarcely accrescent, not investing the fruit.

6. Sect. *Physocorda*: similar to *Calyptrocordia* but differing in corolla salverform, lobes commonly longer than broad, apex rounded; stem with conspicuous subnodal swelling (*ant-domatia*); calyx irregularly ruptured by the corolla.

7. Sect. *Pilicorda*: similar to *Calyptrocordia* and *Physocorda* but lacking the subnodal swelling and calyx opening by 3-5 more or less regular teeth lobes.

8. Sect. *Myxa*: this section was not treated by Johnston (1930), since this paper was concerned only with the New World species of Brazil, Paraguay, Uruguay and Argentina. Johnston at that time regarded this section as restricted to the Old World, but pointed out that sect. *Myxa* was closely related to sect. *Pilicorda*.

A contemporary of Johnston, Friesen (1933), in his only paper on *Cordia*, proposed a completely different view of this taxon. In the first place, he argued that the name *Cordia* was illegitimate and therefore should be rejected, on the grounds that the illustration by Plumier on which Linnaeus based the description of the genus did not represent a *Cordia* species but rather a member of the *Loganiaceae*. In addition to this, Friesen desmembered the traditional genus *Cordia* into some ten segregate genera.
Johnston (1935a), in frank disagreement with Friesen (1933), investigated the manuscript and illustrations of Plumier and reached a completely different conclusion with regard to the suggested illegitimacy of the genus *Cordia*. In a lengthy discussion Johnston (loc. cit.), argued lucidly that the plant illustrated by Plumier, although inaccurate in some details (e.g. number of locules of the ovary) was intended to represent *C. sebestena*, the type species of *Cordia*. Johnston (1935a) also did not accept any of the segregate genera proposed by Friesen (1933), a view also taken by all subsequent authors. In this paper, which consisted of a revision of the Boraginaceae of Northeastern South America (i.e. British and French Guianas, Surinam and adjacent parts of Brazil), Johnston (1935a) also described six new species of *Cordia* from a total of 24 taxa for the genus from this area. Subsequently, Johnston (1935b, 1937) added, respectively, six and three new species of *Cordia* from Brazil, Peru, Bolivia and Guatemala.

In his account of *Cordia* sect. *Pilicordia* from Mexico and Central America, Johnston (1940) recorded 19 species (nine new species). He also provided some observations on the presence of dioecy and heterostyly in the genus and pointed out that heterostyly was common among the American Cordias, prevailing in those species with funnelform and salverform corollas, but that monomorphic condition predominated in sect. *Pilicordia* and in true "small-flowered" Varronias.

Two additional new Mexican species of sect. *Varronia* were described by Johnston (1948) and in the following year (Johnston, 1949a, b), in two separate papers, he revised the Mexican–Central American sect. *Varronia* and the Cordias of Southern West Indies, respectively. Subsequently, Johnston (1950) presented a revision of sect. *Gerascanthus* from Mexico and Central America in which he
described another five new species for this section.

In the treatment of *Cordia* from E. Asia, Johnston (1951) proposed the fusion of the previously recognised sect. *Pilicordia* with sect. *Myxa* and also suggested that *C. sebestena* and allies should be elevated to distinct generic status. In his last paper on *Cordia* Johnston (1956) published another additional five new species from America and Asia.

All of these papers by Johnston on the genus *Cordia* which were an integrated part of his additional studies on the family Boraginaceae not only greatly contributed to the enlargement of the genus (ca. 43 new species were described). Most importantly, Johnston redefined the limits of many obscure species. In order to do this he diligently traced the type specimens of the majority of the taxa involved in his studies, which provided him with a firm basis to recognise both new taxa and also to consign many names to synonymy. Furthermore, he also provided a key to the identification of the species in each area studied together with discussions on the affinities of each taxon in question. His works are also invaluable in providing, when necessary, a detailed analysis of the typification and/or nomenclature of various taxa, as is also the list of material examined for each species which was usually given together with citation of the type specimen.

However, as a natural consequence of dealing with such a large and complicated genus, Johnston in many cases did not manage to fully resolve all taxonomic problems. For example, the trio *C. curassavica/C. macrostachya/C. verbenacea* was first treated by him (Johnston, 1930) as distinct species. In subsequent paper Johnston (1935a) argued that *C. verbenacea* should, perhaps, be regarded as a mere form of *C. macrostachya* and eventually in 1949
he treated this latter species as a synonym of *C. curassavica*, without any comment on *C. verbenacea*.

In other cases, Johnston had to arbitrarily decide on species limits for taxa for which he either had insufficient material or could not resolve the variation pattern. For example, for the species *C. inornata* Johnst., *C. hintoni* Johnst. and *C. subvelutina* Johnst. Johnston (1940) commented "These three plants of western Mexico agree in habit and gross aspect and differ chiefly in pubescence. Perhaps they may represent forms of a single species". Conversely, in relation to *C. oaxacana* DC. (sect. *Varronia*) he cautiously pointed out that "specimens referred to it are rather diverse in appearance, but until more collections of it (he had seen some 13 exsicata) are accumulated and more is learned of its behaviour in the wild, I believe it had best be given the broad definition here accepted".

During the twenty odd years of progress with his studies on the genus, Johnston inevitably changed some of original taxonomic ideas, either at the specific (e.g. *C. polycephala*, *C. guazumaeolila* see discussion under these taxa) and at the sectional level, firstly merging the monotypic sect. *Physocladia* (and apparently sect. *Calptracordia*) in sect. *Pilicordia* (Johnston, 1935a, 1940) and subsequently joining this latter section with sect. *Myxa* (Johnston, 1951). In addition, as mentioned previously, Johnston (1951) also proposed to segregate *C. sebestena* and unspecified "allies" in a distinct genus, but simply with the comment: "*C. sebestena* and allies is a small group of West Indies species, aberrant to *Cordia* as a whole, which should be treated as generically distinct".

However, since such a move would split off the type species from the genus *Cordia*, Johnston (1951) proposed that *C. myxa* should
be considered instead \( C. \) sebestena as the type of the genus. This proposition was based on the fact that \( Cordia \) myxa was the first epithet mentioned in \textit{Species Plantarum} and probably the \( Cordia \) species which was most well known by Linnaeus (1753).

Johnston (1930) pointed out that sect. \textit{Varronia} was "a polymorphous group but evidently a natural one and because of the large number of species, their variability and their indefiniteness probably the most perplexing and poorly understood in the entire genus".

Thus, the comprehensive studies by Johnston provide the back cloth against which the present study of the Brazilian representatives of the genus \textit{Cordia}, with particular emphasis on the \textit{Varronia} group, was based.
III- TAXONOMIC PARAMETERS IN CORDIA
Cytology

Comparatively few species of *Cordia* (some 17 out of 250) have published chromosome numbers. Britton (1951), in his pioneer cytological study of the family Boraginaceae, was the first author to report the chromosome number of nine species of *Cordia*:

*C. glabra* Cham. (2n=28); *C. alba* R. & S., *C. angiocarpa* Rich., *C. boissieri* A.DC., *C. leucosebestena* Griseb. and *C. sebestena* L. (2n=32); *C. alliodora* (R. & P.) Oken and *C. rothii* (2n=72); *C. tremula* Griseb. (2n=80). Britton suggested that polyploidy was of frequent occurrence in the genus for which he proposed a base number of *x* = 8.

Further progress was slow since Federov (1969) reported the counts by Britton (1951) and only one additional species, *C. wallichii* G.Don (2n=42) by Gajapathy (1962). Bhattacharya (1968), studied the chromosomes of *C. sebestena*, confirming the count by Britton (1951) and reporting for the first time for *C. aubletii* DC. (2n=36). Mehra & Gill (1968) published the chromosome number for *C. dichotoma* Forst. (2n=48) and Bedi (1979) for *C. cylindrostachya* R. & S. (n=18).

Bawa (1973) enlarged the chromosome count records for *Cordia* and provided data for the following species: *C. collocococa* L., *C. panamensis* Riley, *C. inermis* (Mill.) Johnst. with n=14; *C. dentata* Poir. n=24 and *C. alliodora* (R. & P.) Oken, n=15 (this latter count in contrast to the one by Britton, 2n=72). These species have been regarded as tetraploids and hexaploids (Bawa, loc. cit.).

Table 1 shows the chromosome counts available for *Cordia* species listed according to the section they have been assigned by Johnston (1930, 1951).

The above picture confirms the view already stated by Britton
(1951) and Bawa (1973), that there is a considerable variation in chromosome number in *Cordia*. However, the data available are still very meagre to attempt any interpretation based on chromosome studies, with regard to the relationships among the taxa included in *Cordia*, and a survey involving many species assigned to different subgeneric categories is still very much a desideratum. Such a study could greatly contribute to clarifying relationships within the genus, and in particular it would be interesting to see whether cytology broadly correlates with palynological data.
Table 1: Chromosome numbers for *Cordia* species arranged according to the infrageneric classification of Johnston (1930, 1951).

<table>
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<tr>
<th>Sect.</th>
<th>Species</th>
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<th>2n</th>
<th>Location</th>
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<tr>
<td></td>
<td><em>C. angiocarpa</em> Rich.</td>
<td>32</td>
<td>Britton, 1951</td>
<td>Cuba</td>
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<td>Britton, 1951</td>
<td>Mexico</td>
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<td>Britton, 1951</td>
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<td>Britton, 1951</td>
<td>W. Indies</td>
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<td>Britton, 1951</td>
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<td></td>
<td><em>C. alliodora</em> (R. &amp; P.) Oken</td>
<td>72</td>
<td>Britton, 1951</td>
<td>Trop. America</td>
</tr>
<tr>
<td></td>
<td></td>
<td>15</td>
<td>Bawa, 1973</td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Myxa</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>C. collococca</em> L.</td>
<td>14</td>
<td>Bawa, 1973</td>
<td>Central America</td>
</tr>
<tr>
<td></td>
<td><em>C. panamensis</em> Riley</td>
<td>14</td>
<td>Bawa, 1973</td>
<td>Panama</td>
</tr>
<tr>
<td></td>
<td><em>C. dentata</em> Poir.</td>
<td>14</td>
<td>Bawa, 1973</td>
<td>Central America</td>
</tr>
<tr>
<td></td>
<td><em>C. alba</em> R. &amp; S.</td>
<td>32</td>
<td>Britton, 1951</td>
<td>Central America</td>
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<tr>
<td></td>
<td><em>C. rothii</em> R. &amp; S.</td>
<td>72</td>
<td>Britton, 1951</td>
<td>India</td>
</tr>
<tr>
<td></td>
<td><em>C. tremula</em> Griseb.</td>
<td>80</td>
<td>Britton, 1951</td>
<td>W. Indies</td>
</tr>
<tr>
<td></td>
<td><em>C. dichotoma</em> Forst.</td>
<td>48</td>
<td>Mehra &amp; Gill,</td>
<td>Eastern Asia</td>
</tr>
<tr>
<td></td>
<td><em>C. wallichii</em></td>
<td>42</td>
<td>Gajapathy, 1962</td>
<td>India</td>
</tr>
<tr>
<td></td>
<td><strong>Varronia</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>C. inermis</em> (Mill.) Johnst.</td>
<td>14</td>
<td>Bawa, 1973</td>
<td>Central America</td>
</tr>
<tr>
<td></td>
<td><em>C. abietii</em> DC.</td>
<td>36</td>
<td>Britton, 1951</td>
<td>Central America</td>
</tr>
<tr>
<td></td>
<td><em>C. cylindrostachya</em> R. &amp; S.</td>
<td>18</td>
<td>Bedi, 1979</td>
<td>Central America</td>
</tr>
</tbody>
</table>

1 *C. glabra* Cham. = *C. taguahydris* Vell. (Johnston, 1930).
Anatomy

Metcalf & Chalk (1950) in their encyclopaedic Anatomy of the Dicotyledons reviewed the scattered literature references to Cordia anatomy. Their brief synopsis indicates the very variable leaf and stem anatomy encountered in different Cordia species, and they drew attention to the presence of conspicuous crystal inclusions in leaf, stem cortex and pith, and wood parenchyma cells.

Gottwald (1983) reported a wood anatomical survey of 95 species of Cordia and this study is of particular interest both for its comprehensive scope, and also because the data are interpreted against a framework of the infrageneric classification proposed by Johnston (1930). The results obtained by him, summarised in Table 2, confirmed the considerable variation in the anatomical structure of the genus as pointed out by Metcalfe & Chalk (1950).

Perhaps because of this great variability, Gottwald (loc. cit.) put special emphasis on the taxonomic value of the crystalline inclusions and stated that their configuration allowed one to almost "redraw" the sections as accepted by Johnston (1930) as follows:

1. presence of sandy crystals alone characterises sections Varronia Pilicordia and Physocladia;
2. prismatic crystals alone occur in sections Rhabdocalyx, Gerasoanthus, Myxa and Calyptraecordia;
3. the remaining sect. Euordia is distinctive in having the two types of inclusions (sand and prismatic crystals). Gottwald (loc. cit.) illustrated diagramatically the distribution of the crystal inclusions among the sections, and his diagram with slight changes is presented overleaf.

The smaller circles attached to the larger ones represent some anomalous departures encountered in various species vis-a-vis
sand crystal
prismatic crystal
sand and prismatic crystal

Fig. 1. Distribution of crystal inclusions in the various sections of Cordia L., after Gottwald (1983).

their respective sections as follows: (I) C. diversifolia, C. lutea C. hintoni (sect. Pilicordia); (II) C. aspera, C. aurantiaca, C. dichotoma, C. macleodii, C. platythyrsea (sect. Myxa); (III) C. salvifolia (sect. Varronia); (IV) C. goeldiana (sect. Gerascanthus). Gottwald (1983) drew attention to the fact that these deviating species were also exceptional within their sections because of the distinctive characteristics of the flowers and fruits, as noted by Johnston.

It is interesting to note the overlapping between sect. Myxa and Pilicordia (Fig. 1) represented by some seven species.

Although this fact was taken into consideration in relation to the
Johnston's proposal to join these two sections, Gottwald (1983) was of the opinion that they were better treated separately. He also held the same conservative view with regard to the generic circumscriptions and did not agree with the segregation of Cordia in different genera as suggested by some previous authors (Friesen, 1933; Johnston, 1951 and Nowicke & Ridgway, 1973). Nevertheless, Gottwald (loc. cit.) did not explain in detail his reason for maintaining a conservative, essentially Johnston (1930) infrageneric classification. Rather, he stated that "a differentiation beyond the sectional level (referring to sect. Varronia), although possible, would not follow compelling evidence", "a segregation of this section (sect. Eucordia) would be practicable but not fully justified" and "the union of two sections (Myxa and Pilicordia) would not constitute a feasible solution".

However, the importance of the crystaline inclusions as a taxonomic character, considered in relation to the sectional level, have been, perhaps, over-emphasised by Gottwald (1983) and as with all characters it is necessary to study character correlations rather than isolated parameters. Thus, an equally viable interpretation of the occurrence of species with anomalous crystal inclusions in sect. Myxa and sect. Pilicordia would be to argue that these support uniting the two sections (indicated by arrows in Fig. 1) as proposed by Johnston (1951).
Table 2: Anatomical features of *Cordia* in relation to their occurrence in different sections.

<table>
<thead>
<tr>
<th>No. of species studied/total</th>
<th>Calyptraecordia</th>
<th>Eucordia</th>
<th>Gerascanthus</th>
<th>Myxa</th>
<th>Physolada</th>
<th>Filicordia</th>
<th>Rabdocalyx</th>
<th>Varronia</th>
</tr>
</thead>
<tbody>
<tr>
<td>1/1</td>
<td>8/12</td>
<td>7/12</td>
<td>23/50</td>
<td>1/1</td>
<td>42/90</td>
<td>1/3</td>
<td>13/60</td>
<td></td>
</tr>
<tr>
<td>Vessels</td>
<td>solitary or clustered + solitary</td>
<td>clustered + solitary</td>
<td>usually clustered</td>
<td>small clusters multiples + solitary</td>
<td>solitary + small clusters</td>
<td>diffuse clustered</td>
<td>solitary + small clusters</td>
<td></td>
</tr>
<tr>
<td>diameter</td>
<td>100-120</td>
<td>99-220</td>
<td>95-220</td>
<td>140-250 (-400)</td>
<td>115-150</td>
<td>100-310</td>
<td>80-240</td>
<td>85-240</td>
</tr>
<tr>
<td>pit diameter</td>
<td>4.5</td>
<td>4.5-5.5</td>
<td>4.5-6</td>
<td>5</td>
<td>5-6</td>
<td>4-7</td>
<td>5-6</td>
<td>3-4.5</td>
</tr>
<tr>
<td>perforations</td>
<td>mostly simple some ret.</td>
<td>simple horizontal</td>
<td>simple horizontal</td>
<td>simple + horizontal</td>
<td>simple reticulate</td>
<td>simple reticulate</td>
<td>simple + reticulate</td>
<td>simple horizontal</td>
</tr>
<tr>
<td>rays</td>
<td>± heterog.</td>
<td>=</td>
<td>=</td>
<td>=</td>
<td>heterog.</td>
<td>± heterog.</td>
<td>homog.</td>
<td>± homog.</td>
</tr>
<tr>
<td>sheath cells</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>seriate</td>
<td>(3-4)</td>
<td>(3-5)</td>
<td>(3-5)</td>
<td>(4-5)</td>
<td>(4-5)</td>
<td>3-5</td>
<td>4-5</td>
<td>2-5</td>
</tr>
<tr>
<td>tiloses</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>wall</td>
<td>2</td>
<td>2.5-4</td>
<td>2.5-4</td>
<td>2-4</td>
<td>2.5</td>
<td>2-3</td>
<td>4-5</td>
<td>2-3</td>
</tr>
<tr>
<td>pits</td>
<td>scattered</td>
<td>sparse</td>
<td>sparse</td>
<td>irregular</td>
<td>rare</td>
<td>sparse</td>
<td>large</td>
<td>scarce</td>
</tr>
<tr>
<td>crystals</td>
<td>mostly prismatic + sand</td>
<td>prismatic</td>
<td>mostly prismatic</td>
<td>mostly prismatic</td>
<td>sand</td>
<td>mostly sand</td>
<td>prismatic</td>
<td>mostly sand</td>
</tr>
</tbody>
</table>

1 sand crystal in: *C. goeldiana*.
2 sand crystal in: *C. aspera, C. macleodri, C. aurantiaca, C. platthyrea and C. dichotoma*.
3 prismatic crystals in: *C. diversifolia, C. lutea and C. hintoni*.
4 prismatic crystals in: *C. salvifolia*. 

21
Palynology

Most palynological references to *Cordia* are for isolated species, or small groups of species in comparative lists or surveys (e.g., Erdtman, 1952; Hammen & Gonzales, 1960; Barth & Silva, 1963; Marticorena, 1968; Salgado-Laboriau, 1973; Miranda et al., 1979-1982). Although providing additional data, none of these studies were directed to resolving taxonomic problems.

However, one study by Nowicke & Ridgway (1973) is of prime importance. These authors investigated the pollen morphology of some 40 species of *Cordia* by means of conventional light microscopy and also Scanning Electron Microscopy (SEM) and they attempted to correlate their results with the infra-generic classification of the genus proposed by Johnston (1930, 1951).

Nowicke & Ridgway (loc. cit.) found three distinct morphological pollen types which coincided with some of the sections recognised by Johnston on the basis of inflorescence, flower and fruit characters, thus: (1) three-porate grains with reticulate exine in species with condensed inflorescences, included in sect. *Varronia* (11/60);

(2) three-colpate to three-colporate grains with spinulose exine in species with paniculate inflorescences, medium to large flowers with salverform corollas, i.e. those included in sections *Gerascanthus* (6/12), *Myxa* (15/50), *Rhabdocalyx* (2/3) and *Physocalada* (1/1) together with another three species (*C. superba*, *C. rufescens* and *C. deaandra*) which were listed as "sect. assignment unknown" although all three were recognised under sect. *Eucordia* by Johnston (1930);

(3) three-colpate or three-colporoidate grains with striatoreticulate

---

¹Number of species studied by Nowicke & Ridgway (1973) out of estimated total.
exine in species with paniculate inflorescences, large flowers and fruits enclosed by an enlarged calyx were found in the species
C. sebestena, C. rickseckeri, C. boissieri and C. subcordata which they referred to sect. Eucordia.

Greatly influence by the discontinuities encountered in pollen morphology in Cordia, Nowicke & Ridgway (1973) proposed that three distinct genera should be recognised, with Cordia s.str. being reduced to sections Gerascanthus, Myxa, Rhabdocalyx and Physocalada, and sect. Varronia and sect. Eucordia being raised to generic status. However, they did not formally put this proposal to effect.

In the present account, Nowicke & Ridgway's survey has been augmented by the study of the pollen morphology of the majority of Brazilian species not included by these authors, comprising a total of 36 species referable to the sections Gerascanthus (3), Myxa (12), Eucordia* (3) and Varronia (18).

In this survey the mean polar and equatorial diameters of samples of acetolysed (Erdtman, 1952) pollen grains of each species were established using light microscopy and external exine morphology was studied by SEM (for methodology see appendix).

The results of this survey full accord with Nowicke & Ridgway's data in that all species of sect. Varronia were found to have pollen grains ranging from oblato-spheroidal to prolate shape, with 3-porate apertures and reticulate exine (Figs. 2, 3) in contrast to species of sect. Myxa, Gerascanthus and Eucordia which have prolate-spheroidal shape, three-colpate to colporate or colporoidate apertures with spinulose exine (Figs. 4, 5, 6). No species of the C. sebestena alliance are native in Brazil.

Data for polar versus equatorial diameter are given in Table 3. It is clear that heterostyly associated with differences in pollen
size between the floral morphs is common in the genus (see discussion below), and that species of the shrubby, condensed inflorescenced, but on the whole small-flowered sect. Varronia tend to have larger pollen grains than the tree species with paniculate inflorescences of sect. Gerascanthus and Myxa (Figs. 7, 8, 9). However, the bar diagrams also show that there is a considerable overlap in dimensions of the pollen grains of the three sections in consideration, which indicates that such variation in size does not correlate with the different patterns of exine morphology.

The striking correlation between the three types of exine sculpturing and the morphological features of the inflorescences, flowers and fruits has been accepted as being of fundamental importance in the present study, and is reflected in the infrageneric classification adopted (see sect. IV).

*It was not possible to take measurements of the pollen grains of species of sect. Eucordia due to collapse of the grains.*
Table 3: Pollen grain measurements of species of sect. Varronia, Myxa and Gerascanthus.

<table>
<thead>
<tr>
<th>sect. Varronia</th>
<th>Measurements (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Shape</td>
</tr>
<tr>
<td>(1) C. multispicata (S)</td>
<td>oblate-spheroidal</td>
</tr>
<tr>
<td>(2) C. curassavica (S)</td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(3) C. campestris (L)</td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(4) C. shomburgkii (L)</td>
<td>oblate-spheroidal</td>
</tr>
<tr>
<td>(5) C. truncata (L)</td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(6) C. calceophala (L)</td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(7) C. harleyi (S)</td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(8) C. harleyi (L)</td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(9) C. buddleioides (S)</td>
<td>oblate-spheroidal</td>
</tr>
<tr>
<td>Shape</td>
<td>PD (SD) × ED (SD)</td>
</tr>
<tr>
<td>---------------</td>
<td>--------------------------</td>
</tr>
<tr>
<td>(10) C. guazumaefolia (S) prolate-spheroidal</td>
<td>40.32(±3.26) × 37.40(±3.18)</td>
</tr>
<tr>
<td>(11) C. polycephala (S) prolate-spheroidal</td>
<td>35.36(±2.21) × 35.20(±2.08)</td>
</tr>
<tr>
<td>(12) C. discolor (S) prolate-spheroidal</td>
<td>41.72(±2.17) × 40.32(±2.24)</td>
</tr>
<tr>
<td>(13) C. monosperma (L) oblate-spheroidal</td>
<td>57.60(±3.27) × 57.40(±3.06)</td>
</tr>
<tr>
<td>(14) C. globosa (S) prolate-spheroidal</td>
<td>51.88(±2.78) × 52.00(±2.41)</td>
</tr>
<tr>
<td>(15) C. corchorifolia (L) oblate-spheroidal</td>
<td>40.60(±3.46) × 42.12(±2.29)</td>
</tr>
<tr>
<td>(16) C. mayii (L) prolate-spheroidal</td>
<td>55.48(±2.94) × 54.68(±3.07)</td>
</tr>
<tr>
<td>(17) C. leucocephala (S) prolate-spheroidal</td>
<td>65.04(±3.66) × 63.96(±4.19)</td>
</tr>
<tr>
<td>(18) C. grandiflora (S) prolate-spheroidal</td>
<td>71.68(±3.48) × 69.80(±2.53)</td>
</tr>
<tr>
<td>(19) C. poliophylla (L?) prolate-spheroidal</td>
<td>67.32(±3.41) × 66.12(±2.08)</td>
</tr>
<tr>
<td>sect. <em>Myxa</em></td>
<td>Shape</td>
</tr>
<tr>
<td>-------------</td>
<td>---------------</td>
</tr>
<tr>
<td>(20) <em>C. exaltada</em></td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(21) <em>C. lomatoloba</em></td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(22) <em>C. magnoliaefolia</em></td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(23) <em>C. scarifolia</em></td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(24) <em>C. sellowiana</em></td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(25) <em>C. sericicalyx</em></td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(26) <em>C. silvestris</em></td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(27) <em>C. sprucei</em></td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(28) <em>C. tetrandra</em></td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>(29) <em>C. toqueve</em></td>
<td>prolate-spheroidal</td>
</tr>
<tr>
<td>Shape</td>
<td>PD (SD)</td>
</tr>
<tr>
<td>-------------</td>
<td>-------------</td>
</tr>
<tr>
<td>C. trachyphylla</td>
<td>40.56(±2.14)</td>
</tr>
<tr>
<td>C. trichoclada</td>
<td>44.00(±2.23)</td>
</tr>
<tr>
<td>Sect. Gerascanthus</td>
<td></td>
</tr>
<tr>
<td>C. glabrata (L)</td>
<td>36.36(±1.11)</td>
</tr>
<tr>
<td>C. glabrata (S)</td>
<td>37.88(±2.31)</td>
</tr>
<tr>
<td>G. goeldiana (L)</td>
<td>29.08(±2.05)</td>
</tr>
<tr>
<td>G. goeldiana (S)</td>
<td>32.16(±1.28)</td>
</tr>
<tr>
<td>C. insignis (L)</td>
<td>42.08(±3.02)</td>
</tr>
<tr>
<td>C. insignis (S)</td>
<td>47.88(±2.83)</td>
</tr>
</tbody>
</table>

Note: PD = polar diameter; EP = equatorial diameter; SD = standard deviation; max = maximum; min = minimum; L = longstyle; S = shortstyle.
Fig. 2. SEM of *Cordia* pollen (sect. *Varronia*)

(a) *C. campestris* × 1000;
(b) *C. campestris* × 5000;
(c) *C. harleyi* (longstyle) × 1000;
(d) *C. harleyi* (longstyle) × 5000;
(e) *C. harleyi* (shortstyle) × 1000;
(f) *C. harleyi* (shortstyle) × 5000.
Fig. 3. SEM of *Cordia* pollen (sect. *Varronia*)

(a) *C. monosperma* × 2000;
(b) *C. discolor* × 2000;
(c) *C. guamanaefolia* × 2000.
Fig. 4. SEM of Cordia pollen (sect. Myxa)
(a) *C. magnoliaefolia* × 2000;
(b) *C. sericicalyx* × 2000;
(c) *C. toqueve* × 2000.
Fig. 5. SEM of *Cordia goeldiana* pollen (sect. *Gerascanthus*)

(a) shortstyle \( \times 2000 \);
(b) shortstyle \( \times 7500 \);
(c) longstyle \( \times 2000 \);
(d) longstyle \( \times 7500 \).
Fig. 6. SEM of *Cordia insignis*
(a) shortstyle × 2000;
(b) shortstyle × 7500;
(c) longstyle × 2000;
(d) longstyle × 7500.
Fig. 7. Range of Polar Diameter (PD) and Equatorial Diameter (ED) measurements showing 95% confidence interval of the pollen grains of sect. *Varronia* species. The numbers in brackets correspond to the numbers of the species given in the Table 3.
Fig. 8. Range of Polar Diameter (PD) and Equatorial Diameter (ED) measurements showing 95% confidence interval of pollen grains of sect. Myxa species. The numbers in brackets correspond to the number of the species given in the Table 3.
Fig. 9. Range of Polar Diameter (PD) and Equatorial Diameter (ED) measurements showing 95% confidence interval of pollen grains of sect. *Gerascanthus* species. The numbers in brackets correspond to the number of the species given in the Table 3.
Reproductive Biology

Darwin (1877) was the first author to record heterostyly in the family Boraginaceae when he described the dimorphic flowers of *Pulmonaria* (*P. angustifolia* and *P. officinalis*) and an unidentified *Cordia* species.

Heterostyly (or heteromorphic self-incompatibility), is a breeding system in which self-incompatibility is accompanied by floral dimorphism (occasionally trimorphism). It is usually described as in the classical example of *Primula*, with the occurrence of two types of flower in the population, i.e. one with long style and short stamens (pin) and the other with short style and long stamens (thrum). Only the cross pollinations between individuals bearing reciprocal types of flower result in successful seed set. In addition to the commonly encountered reciprocal differences in style/stamen length, other polymorphisms of pollen size or exine morphology, stigmatic papillae are also associated with heterostyly. However, as manifested in different taxa, these morphological components of heterostyly are expressed in an array of combinations, e.g. *Linum grandiflorum* (Linaceae) has the two style morphs but stamen height is constant (Lewis, 1979); in *Hedyotis caerulea* (Rubiaceae), the dimorphism is also expressed in the size of the stigmatic papillae and the size of the pollen grain in addition to distyly (Ornduff, 1980). Species of a single genus show marked differences in the manifestation of heterostyly. In the genus *Limonium* (Plumbaginaceae), whilst some species are characteristically dimorphic with regard to the style/stamen length and stigmatic papillae ("cob" versus "papillate" types) and pollen grain sculpturing (reticulate versus spinulose exine), other species are monomorphic for style and stamen
length with the heteromorphic SI mechanism only revealed by differences in pollen exine and stigmatic papillae morphology (Baker, 1966).

Aspects of this heteromorphic breeding system, including its genetics and varied morphological manifestation have been admirably reviewed by Vuilleumier (1967) and Ganders (1979). These authors have shown that heterostyly has a scattered distribution in some 24 angiosperm families and has almost certainly been produced by parallel evolution.

Subsequent to the early report by Darwin (1877), heterostyly was not reported in the genus *Cordia* until the study by Johnston (1940) who drew attention to the common occurrence of heterostyly in New World species. Johnston (loc. cit.) also described functional dioecy derived from heterostyly in *C. diversifolia* with the male plant producing flowers with conspicuous stamens but aborted ovary devoid of style; conversely, the female plant has flowers with well developed ovary with a long style and very reduced stamens. Furthermore, he reported that "similar dimorphism is found in the large group of the Old World species related to *C. myxa* L." (no author cited), and also that, according to this anonymous report, both kinds of flowers (pistillate and staminate) were surprisingly produced on the same plant. Nevertheless, Johnston himself only observed male and female flowers on different plants in the species he noted dioecious. *C. collococca*, however, differs from *C. diversifolia* in that the shortstyle flower the non functional ovary still retains a vestigial style and this condition is also found in *C. aymosa*, *C. toqueve*, *C. sericicalyx*, *C. macrophylla*, *C. sulcata* and *C. panamensis* (Johnston, 1940). In addition, Johnston (loc. cit.) also pointed out that monomorphic flowered species were
restricted to sect. *Pilicordia* and among the "true small-flowered" *Varronia*. Johnston (1950) noted that heterostyly was common in species of sect. *Gerascanthus* from Mexico and Central America, with *C. alliodora* as the only monomorphic exception.

Percival (1974) carried out field observations on four species of *Cordia* (*C. brownei*, *C. globosa* var. *humilis*, *C. gerascanthus* and *C. sebestena*) as part of her study of the floral ecology of scrublands in SE Jamaica. Each species revealed a different condition: *C. brownei* was reported as heterostylyous with the stamens exerted in both morphs; *C. globosa* var. *humilis* presented various degrees of heterostyly (long-, mid- and short-style with slight heterocellular, i.e. variation in corolla length); *C. sebestena* was reported to have the style length and stamen filament length remaining invariable but showing evident heterocellular, and *C. gerascanthus* as lacking heterostyly.

The most detailed field study of heterostyly in *Cordia* (including controlled pollination experiments) is that by Opler *et al.* (1975) which included eight species in Costa Rica. This study reported features of reproductive biology for the following species: (sect. *Varronia*) *C. curassavica* (Jacq.) R. & S., *C. inermis* (Mill.) Johnst., *C. pringlei* Robins; (sect. *Myza*) *C. colloococca* L., *C. dentata* Poir., *C. panamensis* Riley; (sect. *Gerascanthus*) *C. alliodora* and *C. gerascanthus*. Opler *et al.* (1975) observed that *C. inermis*, *C. colloococca* and *C. panamensis* were dioecious, but with the former species incompletely so, since the functional male plant (shortstyle) sometimes produced a few fruits. *C. curassavica*, *C. pringlei* and *C. dentata* were reported to be heterostylyous and *C. alliodora* as lacking distyly; curiously no data was given for *C. gerascanthus*, although the species is listed in the introduction.
and mentioned elsewhere in discussion. Their controlled pollination experiments with *C. dentata* demonstrated the classical result of heterostylous species, i.e. crosses between plants bearing the same morph produced no fruits but did result from reciprocal morph pollinations. However, these authors also found *C. alliodora* (according to them a homostylosus species) to show self-incompatibility and they commented "*C. alliodora* is the first species in which it seems that some degree of self-incompatibility has been retained despite the loss of heterostyly".

In the light of these earlier studies, special attention was given to the occurrence of heterostyly in the Brazilian species in the course of the present taxonomic revision. Such a study, based on herbarium material, can only record morphological features, and in some cases even this objective was frustrated due to a lack of sufficient material. Clearly, studies on a breeding system based solely on morphological characters must be treated with considerable caution, and controlled pollination experiments with *Cordia* species have a higher priority for future work with this genus.

The situation with regard to heterostyly in Brazilian Cordias can be summarised as follows:

(1) *Varronia*

Contrary to Johnston's view that "strictly monomorphic flowers, in fact, seem to predominate only in the section *Pilicordia* and among the true (small-flowered) *Varronia*", the majority, if not all, species of this section show evidence of heterostyly. However, in the Brazilian species for which sufficient material was available, whilst there is evidence of distyly, there is little variation in stamen filament length, such that whilst short-style morphs have the stigma borne well below the level of the anthers, the 'long-style'
morph has the stigma inserted more or less amongst, or a little above, the anthers.

This lack of dimorphic stamen lengths in the Brazilian taxa contrasts somewhat with the findings of Opler et al. (1975) for the Costa Rican species of Varronia, viz. C. pringlei, C. inermis and C. aurassavica, which they illustrate as having reciprocal short style/long stamen and long style/short stamen morphs. However, in their discussion, Opler et al. (loc. cit.) do point out that their species showed a wide range of intra-population variation of style and stamen length, particularly with a large overlap in stamen length between plants. This variation also seems to occur in C. globosa var. humilis/Jamaica as reported by Percival (1974). It is possible, therefore, that style dimorphy unaccompanied by strict stamen filament dimorphy is the rule in sect. Varronia.

It is interesting to note that in large-flowered Varronias, C. grandiflora, C. paucidentata and C. leucocephala, the stamens are inserted at different levels in the corolla tube, but still they present dimorphy in style length.

Heterostyly is accompanied by pollen size dimorphy in C. aurassavica, C. inermis, C. pringlei (Opler et al., 1975) and in C. harleyi as observed in the present study. However, dimorphism in exine sculpturing was not observed (Fig. 2).

With regard to corolla size, the unequal size between the morphs described by Opler et al. (1975) for C. inermis could not be established for the Brazilian Varronias due to the large overlap in size displayed by the specimens of a same species, which can be attributed to inter-population differences.

(2) Gerascanthus

The Brazilian species of sect. Gerascanthus are mostly markedly
heterostyrous and only *C. alliodora* has been repeatedly reported to be essentially homostylos (Johnston, 1950; Opler *et al.*, 1975). However, the presence of the shortstyle morph has been demonstrated by Gibbs & Taroda (1983), in a study based on a comprehensive number of exsiccatas from throughout the range of this species in South America. In *C. trichotoma* the occurrence of three morphs (short-long-homo-style) was reported (Gibbs & Taroda, *loc. cit.*), but the species *C. insignis*, *C. glabrata* and *C. goeldiana* are distinctly long- or short-style without the intermediate homostyle condition. However, the heterostyly in sect. *Gerascanthus*, as in *Varronia* species, is evidently primarily based on differences in the style length rather than the reciprocal differences in stamen length.

Polymorphism in corolla size or morphology, has not been observed in correlation with the different morphs but pollen grains of shortstyle are significantly larger than the longstyle flowers for the species investigated, *C. insignis*, *C. glabrata* and *C. goeldiana* (Table 3).

(3) *Pilicordia*

The situation in sect. *Pilicordia* Johnston with regard to the occurrence of heterostyly is much less clear cut than in sect. *Varronia* and *Gerascanthus*. Johnston (1940) regarded the section as monomorphic, and Opler *et al.* (1975) reported that the Costa Rican species *C. aff. lastocalyx* of this section showed only the shortstyle

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1Based on a small sample, *C. glabrata* and *C. insignis* were reported as not having significant differences between long- and short-style morphs by Gibbs & Taroda (1983). However, a survey of a wide range of material in the present study has established that there is dimorphism in pollen size in these two species.
morph. This situation also prevails in most of the Brazilian species for which sufficient specimens were available in the present study, viz. C. ecalyculata, C. sellowiana, C. scabrifolia and C. sprucei. However, the two species C. magnoliaefolia and C. trichocladata were found to have distinct short-style and long/homostyle morphs.

Opler et al. (1975) reported that the Central American species of this section, C. collococca and C. panamensis, were morphologically heterostylos but functionally dioecious (with only the long-style morph setting fruit) and Johnston (1940) also reported this condition (absence of style in the "short-style" morph) for C. diversifolia. (4) Eucordia

For this section sufficient herbarium material was available for the three species, C. superba, C. rufescens and C. tagualhyensis to indicate that they are distinctly heterostylos with short- and longstyle morphs.

Thus, all the Brazilian species of the sections Varronia, Gerascanthus, Eucordia and Pilicordia present some degree of heterostyly but in the large sect. Pilicordia, whilst some species are conspicuously dimorphic or functionally dioecious, the majority of species are monomorphic with fixation of the shortstyle morph.

The occurrence of functional dioecy in species of sect. Pilicordia presents an interesting change of breeding system which is at first sight perplexing since both heteromorphic SI and dioecy are outbreeding mechanisms. However, Beach & Bawa (1980) have recently proposed a very plausible hypothesis to explain this change of breeding system.

The components of Beach & Bawa's hypothesis are as follows:

(a) It is generally accepted that the morphological component of the heteromorphic self-incompatibility system - reciprocal style-
stamen length etc. - have been selected to promote disassortative pollen transfer between compatible genotypes (Canders, 1979).

(b) In Cordia, as in most (but not all, see Vuillémier, 1967) cases where heterostyly has evolved to dioecy it is the long-styled morph which converts to the pistillate flower and the short-style morph to the staminate flower (Lloyd, 1979; Beach & Bawa, 1980).

(c) Beach & Bawa (1980) argued that a breakdown in the reciprocal pollination of long- and short-style morphs can occur, perhaps by loss of a long-tongued vector, such that pollen is no longer removed from long-style morph anthers and/or not deposited on short-style stigmas. In this case long-style flowers will no longer be effective pollen donors but rather pollen receivers, i.e. effectively pistillate flowers, whilst short-style flowers will be pollen donors but not effective pollen receivers, i.e. effectively staminate flowers. In such a system, subsequent selection could be expected to stabilise the incipient dioecy.

Beach & Bawa (1980) supported their arguments by reference to studies on Coussarea (Rubiaceae) carried out by Frankie et al. (1974) and also on Cordia by Opler et al. (1975). In Coussarea distylos species were observed to be pollinated by a long-tongued moth species, whereas the dioecious C. talamancana (still bearing vestigial style and stamen) were visited by small (short-tongued) Hymenoptera. For Cordia species Opler et al. (loc. cit.) were unable to correlate each species to a presumed most effective pollinator due to a large number of visitors observed on them (C. gerasoanthus with ca. 20 and C. inermis ca. 300 insect species). However, they pointed out that "small short-tongued insects" touch the anthers/stigma generally by the head whilst the "long-tongued insects" carried the pollen on the mouth
parts. Beach & Bawa (1980) concluded their paper with the proposition that "a specific change in the pollination biology of these species is ultimately responsible for the evolution of unisexuality".

During the course of the present study, two cultivated individuals of the species *Cordia curassavica* (sect. *Varronia*) were available in flower in the glasshouse of the University Botanic Garden. Perversely, both plants were found to be short-style morphs! However, a series of controlled pollination experiments were performed, some of which were left for fruit-set, whilst styles of other such pollinated flowers were fixed in F.A.A. and studied for pollen tube growth by means of fluorescence microscopy (Martin, 1959).

(a) All self- and (same morph) cross-pollinations resulted in failure of fruit set, indicating a functioning heteromorphic self-incompatibility system.

(b) Self- and (same morph) cross-pollen tube growth was essentially similar: the pollen tube penetrated the stigmatic papillae and arrest of pollen tube growth took place in the apical region of the style (Fig.10).

This result is interesting, since in addition to having heteromorphic, and hence sporophytic self-incompatibility, *Cordia* species have trinucleate pollen (Brewbaker, 1957). Some authors have attempted to extend the correlation originally proposed by Brewbaker (1957) for homomorphic incompatibility, viz. gametophytic SI associated with binucleate pollen and stylar site of pollen tube inhibition versus sporophytic SI with trinucleate pollen and the site of incompatibility reaction at the stigma surface, to heteromorphic taxa. Thus, Brewbaker (1961) and Pandey (1960) have proposed that heteromorphic taxa with binucleate pollen (e.g. *Primula*
spp.) show inhibition in the style whilst taxa with trinucleate pollen (e.g. *Linum*) show inhibition at the stigma surface. It would seem, however, that *Cordia* species do not follow this rule.

Because of the preponderance of heterostylosous species in the genus, and occurrence of this self-incompatibility system in at least some taxa of all the infrageneric taxa recognised by Johnston, it would seem evident that heteromorphic SI is the basic breeding system in *Cordia*. However, the mode of functioning of the mechanism, occurrence of breakdown (homostyly) and evolution to dioecy, and the relationship between the breeding system and pollination biology are features which require further detailed study.

Fig. 10. Stigmatic branches of *C. curassavica* showing pollen (same morph) tube growth into the style after 27 hr of pollination.
IV- PROPOSED INFRAGENERIC CLASSIFICATION IN GORDIA
Proposed Infrageneric classification of *Cordia*.

As is clear from the historical review of the taxonomy of *Cordia* (outlined above), the genus has been subjected to different treatments by various authors (e.g. Kunth, 1818; De Candolle, 1845; Johnston, 1930), particularly with reference to its infrageneric classification but also with regard to generic circumscription, and there have been varying attempts to split it into distinct genera (Friesen, 1933; Johnston, 1951; Nowicke & Ridgway, 1973).

Johnston, in his series of regional revisions, provided a major contribution towards the consolidation of the infrageneric assemblages of *Cordia*. In his original work, Johnston (1930) recognised 8 sections which served the function of, on the one hand, grouping together numbers of species which share attributes in common and seem to be obviously related (e.g. *Gerascanthus*, sect. *Varronia*) and, on the other, isolating species with 'exceptional' characters (e.g. sect. *Physocladia*).

In subsequent treatments of the genus, Johnston (1935a, 1940) slightly changed his ideas and merged the monospecific sections *Physocladia* and apparently *Calyptracordia* in sect. *Pilicordia*. Then, Johnston (1951), in a more significant shift of opinion, united sect. *Pilicordia* with sect. *Myxa* and also suggested that *Cordia sebestena* (previously sect. *Cordia*) and related species warranted generic rank.

Nowicke & Ridgway (1973), much influenced by the results of their pollen studies (as discussed previously) have gone further than Johnston (1951) in recommending the dismemberment of *Cordia* into three distinct genera: the entire sect. *Varronia* would constitute one single genus, sect. *Myxa, Gerascanthus, Rhabdocalyx, Physocladia* and *Calyptracordia* together would comprise another, and a third genus would consist of the group of species allied to *C. sebestena*.
(C. subcordata, C. boissieri, C. ricksekeri). On the other hand, Gottwald (1983) on the basis of an extensive wood anatomical survey has proposed a very conservative approach with an infrageneric classification in line with Johnston (1930).

However, to raise infrageneric taxa within Cordia to generic level, as recommended by Johnston (1951) and, particularly, Nowicke & Ridgway (1973) would immediately raise a series of nomenclatural problems. Of one kind, would be the changes of epithets for a number of species of sect. Varronia (ca. 36 spp, or 60% of the total) if this were split off as a separate genus. More seriously, the generic name Cordia would be restricted to a handful of species (C. sebestena and allies) whilst the vast group of species comprising sects. Myxa, Gerascanthus and Eucordia would require a new generic name. Johnston (1951) at least was aware of this problem and attempted to argue with dubious nomenclatural legality that C. myxa should substitute C. sebestena as the type species of Cordia, despite the fact that he had argued with equal force previously (Johnston, 1935a) in favour of the latter species. This is a classical situation of the kind found, for example, in Cytisus (Leguminosae-Papilionoideae), where, if the genus is split into a number of splinter taxa as proposed by some authors (Frodin, 1965, fide Polhill, 1976), then the generic name Cytisus must be restricted to the species Cytisus scoparius (L.) Link. and a new name proposed for the bulk of the traditionally recognised Cytisus species.

In these circumstances, as pointed out by Davis & Heywood (1963) "... changes in binary names are undoubtedly a nuisance, and the raising of sections to genera or vice-versa, should not be undertaken unless there are strong taxonomic reasons for change".
Thus, whilst biological considerations are obviously more important than mere nomenclatural aspects, the elements of stability and user convenience which are part of the classificatory process mean that in cases like *Cordia* the arguments in favour of generic splitting should be particularly sound and compelling.

(1) The generic concept.

One of the fullest discussions of the generic concept and criteria for genera is that by Davis & Heywood (1963). These authors point out that three questions must be asked when deciding on generic concepts:

(i) "Is the group a natural one, and if not is it possible to make it so?" This criterion, of course, raises the contentious issue of 'naturalness' in taxonomy, but in general terms, as applied by Davis & Heywood it is a concept rather vaguely based on maximum correlation of characters.

(ii) "Where should the line be drawn between closely related genera?" As pointed out by Davis & Heywood, this causes no difficulty where genera are very distinct from each other (evolutionary extinction), but is a considerable problem if the separation is not clear cut. The authors counsel against the use of single arbitrary or artificial characters, but do not discuss the use of single biologically important characters.

(iii) "Is it practicable to recognise the group as a separate genus, or would it be better included in another?" As the authors point out, this question relates to (ii) above, but they focus here on aspects such as size and homogeneity of the groups and the number of intermediates between them, and traditional usage and classificatory stability.

Most authors treating with the genus concept emphasise the
difficulty of selecting from criteria, thus: "Between the family and the species there is no easy way of deciding on the appropriate degree of inclusiveness and there is no way of defining a genus, for example, in such a way that is not equally applicable to a subgenus or subfamily or tribe" (Heywood, 1976). Also, "Above the species level there is still less comparability between the taxa at one rank. Much has been written on the 'genus concept' ... but in fact it amounts to little more than personal judgement aimed at producing a workable classification" (Stace, 1980, p.202). This author goes on to cite the case of *Chamerion* (formerly *Chamaenerion*) which is sometimes recognised as a distinct genus from *Epilobium*, and sometimes not. On the grounds of the distinct discontinuity in floral morphology and crossability, it appears to be best considered a separate genus, but apart from the presence of this gap in the variation it seems scarcely more different from *Epilobium* than are some other groups of the genus. Raven talks of the 'generic balance' in the family Onagraceae and advocates the amalgamation of *Chamerion* and *Epilobium*" (Stace, 1980, p.202).

This elusive notion of 'generic balance' proposed by Raven (1976) is also considered by Raven & Mertens (1965) in a discussion of the taxonomic hierarchy. They pointed out that for ten species with varying degrees of 'similarity', the number of recognisable taxonomic units (genera, tribes etc.) can vary from one to ten, depending simply upon the criteria of similarity adopted for each rank in the hierarchy. They say: "This problem is solved in practice by arbitrarily deciding about how many levels of classification one wishes to use for the entire plant kingdom and then deciding at about what level of distinctness these will be used. Thus the genera into which species are grouped in the Rose Family, for example, have next
to nothing in common with the genera in the Oak Family. In each case the assemblages of plants are divided at what is thought to be a convenient level, taking into account the pattern of variation in the group being studied. Having used the system for over 200 years, we now find, for example, that the level of difference of which genera in Oak Family are recognised is fixed roughly by tradition. Where this level is fixed makes no difference as long as it does not give a false impression of what we know about the relationships to one another of the included groups".

(2) Generic concepts with Cordia.

(i) One problem with generic concept as applied to Cordia is that a distinct subfamily of Boraginaceae is usually identifiable as the genus Cordia. Thus, the criteria for subfamily Cordioideae and Cordia are largely identical since only two other, small (2 species each) neotropical genera, Auxema and Patagonula, occur in this subfamily. Certainly, both genera are readily distinguished by single, 'key' characters: viz. vastly accrescent calyx which enlarges by ten times its original size in Patagonula and a winged, inflated calyx in Auxema. Unfortunately, a detailed taxonomic study of both of these genera, and their relationships to Cordia is still needed. To what extent these diagnostic generic parameters are 'single, arbitrary' characters of the type criticised by Davis & Heywood (1963) needs to be determined. Certainly both characters state, i.e. accrescence of the calyx and a persistent inflated calyx which surrounds the fruit are both encountered to some degree in Cordia species.

Clearly, the degree of distinctness of Patagonula and Auxema is important as a comparable criterion when considering the appropriateness of infrageneric taxa within Cordia for generic
status (fide Raven's 'generic balance').

(ii) The proposals by Johnston (1951) and Nowicke and Ridgway (1973) to establish generic status for the Varronia group and C. sebestena group, represent a splitting off of these taxa from a 'Cordia core' group. Generic splitting in Cordia, therefore, largely concerns the distinctness and 'naturalness' of these two proposed segregates vis à vis the internal homogeneity and relative degree of distinctness of the remaining Cordia group, comprising sections Myxa (Piliaordia), Gerascanthus and Eucordia sensu Johnston (1930, 1935).

Thus, while it is possible to 'draw lines' around such groups by employing single characters such as pollen (Table 4) it is difficult to find even two still less three or more characters which are uniformly correlated and which would allow one to distinguish readily such groups at the generic level. For instance, the large flowers of few Varronia species resemble those of C. superba and allies; likewise, in each of the groups (Varronia, Myxa, Gerascanthus, Eucordia) some of the species have campanulate calyces.

At this stage, with lack of knowledge of Cordia species throughout its entire range and particularly with ignorance of cytological data and also absence of palynological data of Patagonula and Auxema (to be assessed in relation to Cordia) it seems premature to split up the traditional genus. The accumulated data on internal relationships, however, cannot be ignored so that in the present revision, three subgenera have been recognised to accommodate the more obviously distinct groups of species:

(1) Subgenus Varronia: comprising sect. Varronia alone elevated to subgeneric status.

(2) Subgenus Cordia: comprising C. sebestena, C. subcoordata,
C. ricksekeri, C. boissieri.


Section *Superbiflorae* was here established to accommodate those taxa allied to *C. superba*, which originally, together with those species related to *C. sebestena* (presently included in subg. *Cordia*) were aligned under the sect. *Eucordia*. However, species of sect. *Superbiflorae* have fruit and pollen characters which are distinct from subg. *Cordia*. Thus, sect. *Superbiflorae* together with sects. *Myxa* and *Gerascanthus* which share a common pollen morphology were aligned under the new subg. *Myxa*.

This taxonomic revision was based on studies of exsiccata from the following herbaria: Arnold Arboretum of Harvard University, Cambridge (A); The British Museum (Natural History), London (BM); Royal Botanic Garden, Edinburgh (E); Field Museum of Natural History, Chicago (F); Conservatoire et Jardin botaniques, Geneve (G); Gray Herbarium of Harvard University, Cambridge (GH); Royal Botanic Gardens, Kew (K); Missouri Botanical Garden, Saint Louis (MO); New York Botanical Garden, New York (NY); Museum National d'Histoire Naturelle, Paris (P); Institute of Systematic Botany, Utrecht (U); Departamento de Biologia Vegetal, Fundação Universidade de Brasília, Brasília (UB); Departamento de Morfologia e Sistemática Vegetais, Universidade Estadual de Campinas, Campinas (UES); United States National Herbarium, Department of Botany, Smithsonian Institution,
Washington (US); Naturhistorisches Museum, Botanische Abteilung, Wien (W).

(i) Species were characterised by reference to available keys and descriptions, with the studies by Ivan Johnston being, of course, particularly invaluable, but every effort was made to study the type material of all taxa.

(ii) As far as possible a traditional "morpho-geographical" concept of species (Du Reitz, 1930) has been followed such that species populations are distinctive in at least two morphological characters throughout their geographical range.

(iii) Botanical terminology used in the keys and descriptions follows essentially that of Radford et al. (1976) but in some particular cases the terminology employed by Johnston in his diverse contributions has been adopted.

(iv) In the following formal taxonomic sequence the geographical distributions of species are summarised according to the regions recognised by the Brazilian Institute of Geography and Statistics (IBGE) and exsidaia are cited by states and territories in alphabetical sequence as follows:
NORTH (N): Acre (AC); Amazonas (AM); Pará (PA); Rondônia (RO);
Amapá territory (AP) and Roraima territory (EE).
NORTHEAST (NE): Alagoas (AL); Bahia (BA); Ceará (CE); Maranhão
(MA); Paraíba (PB); Pernambuco (PE); Piauí (PI);
Rio Grande do Norte (RN) and Sergipe (SE).
WEST-CENTRAL (WC): Goiás (GO); Mato Grosso (MT) and Mato Grosso
do Sul (MS).
SOUTHEAST (SE): Espírito Santo (ES); Minas Gerais (MG); Rio de
Janeiro (RJ) and São Paulo (SP).
SOUTH (S): Paraná (PR); Santa Catarina (SC) and Rio Grande do
Sul (RS).
The bold line delimits the Brazilian geographical regions
referred in the species distribution.
(v) Maps for distributions of species are based on specimens seen
(dot maps) and do not necessarily represent the complete
distribution of any taxon.
Table 4: Comparison of morphological characters of the three proposed subgenera.

<table>
<thead>
<tr>
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<tbody>
<tr>
<td><strong>Habit</strong></td>
<td>shrub-sub-shrub</td>
<td>tree, occasionally shrub</td>
<td>tree, occasionally shrub</td>
</tr>
<tr>
<td><strong>Inflorescence</strong></td>
<td>condensed: spike capitules glomerule rarely small lax-panicle</td>
<td>lax-panicle</td>
<td>lax-panicle</td>
</tr>
<tr>
<td><strong>Calyx</strong></td>
<td>cupular or campanulate, smooth</td>
<td>campanulate sometimes cylindrical, smooth or occasionally ribbed</td>
<td>cylindric, occasionally campanulate ribbed, exceptionally smooth</td>
</tr>
<tr>
<td><strong>Corolla</strong></td>
<td>whitish small (ca. 1 cm) sometimes large (ca. 5 cm) tubular-cylindrical funnelform salverform not marcescent</td>
<td>whitish small (up 1 cm) campanulate</td>
<td>whitish ±large (1-4 cm) salverform</td>
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<td>------------------</td>
<td>--------------</td>
<td>----------------------</td>
<td>----------------------</td>
</tr>
<tr>
<td><strong>Style</strong></td>
<td>two times forked stigma-4</td>
<td>two times forked stigma-4</td>
<td>two times forked stigma-4</td>
</tr>
<tr>
<td><strong>Fruits</strong></td>
<td>conic, partially verrucose calyx persistent slightly accrescent enclosing the fruit partial or entirely</td>
<td>conic-smooth calyx persistent explanate or caducous</td>
<td>ellipsoidal-smooth calyx + corolla persistent, scarcely accrescent enclosing the fruit totally</td>
</tr>
<tr>
<td><strong>Seeds</strong></td>
<td>1, cotyledon plicate</td>
<td>1, cotyledon plicate</td>
<td>1 cotyledon plicate</td>
</tr>
<tr>
<td><strong>Pollen</strong></td>
<td>3-porate exine: reticulate</td>
<td>3-colpate exine: spinulose</td>
<td>3-colpate exine: spinulose</td>
</tr>
<tr>
<td><strong>Crystal inclusions</strong></td>
<td>sand</td>
<td>sand or prismatic</td>
<td>prismatic</td>
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Comparative Morphology

The following general comments on morphological characters in the genus *Cordia* are based primarily on herbarium material of Brazilian taxa, although many observations will also apply to the genus as a whole.

**Habit**: most species of *Cordia* consist of small to large trees (up to 30 m or so) but species of subg. *Varronia* are uniformly shrubby with some taxa such as *C. villicaulis* and *C. truncata* growing to 50 cm or less.

**Leaves**: with a few exceptions (*C. truncata*, *C. sessilisfolia*, *C. villicaulis*) all the Brazilian species of this genus have petiolate leaves, which are alternately disposed on the stem. On the whole, there is great variation in the dimension of the leaf blade from 1-30 cm long, but with smaller leaves prevailing in subg. *Varronia*. The shape is also very variable (e.g. elliptical, lanceolate, oblong, oblanceolate, ovate, obovate or orbicular). Leaf dimorphism occurs in *C. toqueve*, *C. sericocalyx* and *C. exaltata* in which the large, distinctly larger than broad more abundant leaves contrast with other smaller orbicular leaves.

The leaf margin is commonly variously toothed in subg. *Varronia* (except for *C. longifolia*) but mostly entire in sect. *Myxa* (*C. decipiens* and some specimens of *C. sellowiana* are toothed); in sect. *Superbaeae* most specimens of *C. superba* and *C. rufescens* have a coarsely dentate margin.

The majority of *Cordia* species are pubescent to some extent with only a few entirely glabrous species: *C. longifolia* (subg. *Varronia*); *C. aberrans* and *C. taguahyensis* (sect. *Superbaeaeae*); *C. latiloba* and *C. goeldiana* (sect. *Gerascanthus*); *C. ecalyculata*,...
C. magnolifolia and C. lomatoloba (sect. Myxa). The pubescence varies in density according to or within the same species and can be hirsute, tomentose or strigose. The hairs are simple in most species, but stellate hairs are encountered, for instance; in C. alliodora and C. trichotoma.

Venation is craspedodromous in subg. Varronia (except for C. longifolia and C. poliophylla with brochidodromous type) and in the remaining species the venation is brochidodromous.

Inflorescences: subg. Varronia is exceptional in that the flowers are produced in a congested inflorescence (spike, capitule, glomerule) as opposed to the loose and divaricate panicles which are characteristic of the species of the other sections.

In subg. Varronia the inflorescences can be terminal or axillary or internodal, i.e. arising from the stem without any subtending leaf. The spikes are sometimes very elongate, e.g. C. schomburgkii, or stout as in C. multiapicata. The capitules, as here accepted, are usually densely flowered and vary in shape from spherical to somewhat cylindrical or clavate. In a few species of this subgenus, e.g. C. discolor, C. urticaefolia and C. monosperma the inflorescences become laxer and panicle-like.

The well developed paniculate type of inflorescence is commonly produced in a terminal position but an axillary position can also occur. In C. aberrans and C. candida of sect. Superbi florae the panicles are very reduced, slender and produce only a few flowers.

Calyx: the calyx in Cordia species varies from tubular-campanulate to tubular-cylindrical or obconical. It can also be smooth or distinctly costate or ribbed, coriaceous or membranaceous in texture, and variously toothed. The teeth are usually somewhat
deltoid in shape, but in many species they are prolonged in a more or less extended linear apex. This situation is particularly common in species of subg. Varronia. In C. alliodora (sect. Gerascanthus) the teeth may be very much reduced to minute prolongations of the calyx ribs. The calyx, externally and internally, is usually variously hairy or occasionally totally glabrous.

Corolla: the species of Cordia have corollas varying from funnelform to salverform or they are tubular-cylindrical and then with the lobes almost inconspicuous. The corolla lobes in many species of sect. Superbiflorae and subg. Varronia are very shallow but in sects. Gerascanthus and Myxa they are distinctly cleft, oblong to orbicular in shape with rounded or truncate apex. However, C. latiloba (sect. Gerascanthus) is distinctive in having rhomboidal corolla lobes.

The dimensions of the corollas in Cordia species vary considerably, with the smallest ca. 4 mm long and the largest ca. 7 cm. Sect. Varronia shows the greatest range of corolla size although the majority of species are small flowered. In sect. Myxa the flowers are small (6-10 mm) and in sects. Gerascanthus and Superbiflorae they are usually large. The species of sect. Gerascanthus have the corollas invariably marcescent, which constitutes one of the diagnostic characters of this section.

Stamens: the Brazilian species of Cordia normally have 5 stamens with more or less equal height and inserted at the same level in the corolla tube. However, frequently in specimens of C. superba, C. rufescens and C. taguahyensis (sect. Superbiflorae) they are reduced to four and also in these species they occasionally present different heights with two of them evidently shorter than the other
two or three. Exceptionally, they are also inserted at different levels in *C. grandiflora*, *C. leucocephala* and *C. paucidentata* (subg. *Varronia*). Generally, the stamen filaments are basally provided with more or less long, somewhat villous hairs.

Particularly in sect. *Myxa* the stamens are always distinctly exerted, but in the remaining sections they are mostly included.

Ovary: the ovary in the entire genus does not show great variation, being globose or pyriform in shape and usually surrounded by a disc-like (probably nectary) structure. The ovary is pilose in some species of sect. *Myxa* (*C. toqueve*, *C. bicolor*, *C. sprucei*, *C. scabrifolia*) but the majority of the species in the genus have an entirely glabrous ovary. The style is characteristically twice-forked to terminate in 4 stigmas, clavate or capitate. The styles are glabrous, except for those species with hairy ovary, in which they are also basally pilose.

Fruit: although usually drupaceous and commonly ovoid in shape, the fruits show profound differences in the genus, particularly with reference to the development of the calyx, which continues to be attached to it and these are important infrageneric characters.

Thus, in subg. *Varronia* the fruit is relatively small (up to 10 mm), partially verrucose, the calyx always persistent and enclosing it partly or entirely. In sect. *Myxa* the fruits are not enclosed by the calyx to any extent, because it becomes somewhat flattened in shape (explanate) or sometimes the calyx does not persist. The drupe is usually glabrous but in some few species (*C. toqueve*, *C. sprucei*, *C. bicolor*, *C. scabrifolia*) they are clothed by a fine and somewhat stiff pubescence.

The species of sect. *Superbaeflorae* have the drupe similar to
those of *Myxa* but the calyx is always persistent and cupulate so that it more or less encloses the lower half of the fruit.

All species of sect. *Gerascanthus* have an elongated ellipsoidal fruit which is completely enclosed by the calyx and also by the characteristic marcescent corolla. (However, the fruit of *C. goeldiana*, which was originally described as globose, has not been observed in this study.)
V- TAXONOMIC TREATMENT
Cordia L. Gen. Pl. 87. ed. 5 (1754).

Trees, shrubs or subshrubs, variously pubescent, the hairs generally simple, occasionally stellate. Leaves alternate, usually homomorphic, sometimes dimorphic, petiolate or sessile. Flowers born in terminal, internodal or axillary panicles, spikes, capitules or glomerules; mostly heterostyloous but sometimes functionally dioecious. Calyx tubular-cylindrical, tubular-campanulate or campanulate, smooth or ribbed, variously 3-10 toothed. Corolla small (4 mm) to large (7 cm); funnelform, salverform or tubular-cylindrical, shallowly or deeply lobed, lobes mostly 5 occasionally 6-15, whitish to sometimes reddish. Stamens slender, usually 5 or as many as the corolla lobes, rarely reduced, inserted on the corolla tube, exserted or included. Ovary 2-carpellate with 4-locules and 4-ovules, only one developing; style slender, twice forked, terminating in 4 clavate or capitate stigmas. Fruits drupaceous, ellipsoidal but commonly ovoid, with the calyx rarely caducous, mostly persistent and variously developed covering the drupe partially or completely. Seed one, with plicate cotyledons.

Type species: C. sebestena L. Sp. Pl. 190 (1753).

Infrageneric key to Cordia.

1. Inflorescences usually in lax and well-developed panicles; fruit a large drupe, usually more than 10 mm long and smooth or slightly striate on drying, or if less than 10 mm, then with a persistent, marcescent corolla.

2. Corolla marcescent, persistent in fruiting. Fruit ellipsoidal. sect. Gerascanthus

2. Corolla withering soon after anthesis, not persistent in
fruition. Fruit ovoid.

3. Flowers reddish, calyx persistent and markedly accrescent and entirely enclosing the drupe. subg. Cordia

3. Flowers whitish to creamy, calyx sometimes caducous, usually persistent but scarcely accrescent, explanate (i.e. not surrounding the drupe) or cupulate (partially covering the drupe).

4. Flowers small, up to 10 mm. sect. Myxa

4. Flowers large, more than 10.5 mm. sect. Superbi_florae

1. Inflorescence usually congested, spike, capitules or glomerules, rarely becoming somewhat lax and turning to small panicles; fruit a small drupe, less than 10 mm long, partially verrucose on drying. subg. Varronia

Subgenus Myxa (Endl.) Taroda, subg. nov.

Trees or shrubs. Leaves petiolate, usually chartaceous or coriaceous in texture; mostly homomorphic sometimes dimorphic; margin entire rarely roughly dentate. Flowers in well developed loose panicles, occasionally becoming denser by the reduction of the inflorescence branches; heterostylous or apparently monomorphic, sometimes functionally dioecious. Calyx 3-5 toothed, smooth or ribbed. Corolla funnelform or salverform, small or large, 5-lobed. Stamens 5, rarely reduced to 4. Fruits ovoid or ellipsoidal. Pollen 3-colpate, 3-colporate or 3-colporoidate with spinulose exine.

Type species: C. myxa L. Sp._Pl.: 190 (1753).
Cordia section *Myxa* (Endl.) DC.

Section *Pilicordia* was established by De Candolle (1845) for a group of five species characterised by a 10-striate calyx. Johnston (1930) regarded this feature of the calyx as irrelevant as a sectional attribute and he expanded the concept of sect. *Pilicordia* to include not only four De Candolle species (one of the original five, *C. insignis*, was referred to sect. *Gerascanthus*), but also all the New World species of *Cordia* with small flowers in well developed, lax paniculate inflorescences and with the calyx, if persistent in the fruiting stage, becoming explanate and not enveloping the fruit to any extent. In this paper Johnston (1930) also commented that sect. *Pilicordia* was closely related to sect. *Myxa*, which included all species of the Old World (excepted *C. suboordata*), but pointed out that this relationship needed a more detailed study. Subsequently, Johnston (1951), in his account of the E Asian Cordias, briefly stated "it is now clear that a larger number of American species, those treated in my previous writings as belonging to the section *Pilicordia* also belong in the section *Myxa*". Johnston did not add any further discussion but the same set of characteristics which he had previously used for sect. *Pilicordia* were given in the key to distinguish sect. *Myxa* from *C. suboordata*, the only Old World species of his sect. *Sebestena*.

Subsequent authors, Nowicke & Ridgway (1973) and Opler et al. (1975) dealing, respectively, with pollen and breeding systems of *Cordia* species, have followed Johnston in uniting sect. *Pilicordia* with sect. *Myxa*. However, Gottwald (1973), on the basis of his anatomical studies of some 95 species of *Cordia* whilst noting the presence of "considerable variation within or overlap between *Myxa* and *Pilicordia*" concluded that "from the wood anatomical point of
view the union of the two sections would not constitute a feasible solution".

As noted previously, Gottwald (loc. cit.) tends to take a conservative approach to the infrageneric classification of Cordia. Although a detailed study of the relationships between the New and Old World taxa is clearly very desirable, since no characters of sectional value are known to the author which permit a separation of sect. Pilicordia *vis-a-vis* sect. Myxa, the view of Johnston (1951) has been formally adopted and the two sections united under sect. Myxa.

De Candolle (1845) recognised the sect. Physocladada for the three species *C. nodosa* Lam., *C. miranda* DC. and *C. hispidissima* DC., although the latter two are currently treated as mere synonyms of *C. nodosa*. Sect. Physocladada was characterised by a hispid, membranaceous calyx, the apex of which was irregularly ruptured by the emerging corolla bud, and by the hispid-pubescent branches with conspicuous ant-domatia.

Johnston (1930) originally accepted Physocladada as a monospecific section, but in a subsequent study, Johnston (1935) pointed out that the flowers and fruits of *C. nodosa* were very similar to *C. sprucei*, and considered that whilst the presence of ant-domatia and the bristly indumentum of the former species were striking characters, he proposed including *C. nodosa* in sect. Pilicordia.

This treatment of *C. nodosa* has been accepted in the present revision. The ant-domatia characteristic of this species also occur in *C. alliodora* (sect. Gerascanthus) whilst the ruptured calyx apex is also found in *C. superba* (sect. Superbaefolia), although in this species the calyx apex functions more or less like a circumsessile calyptra. Furthermore, the pollen of *C. nodosa* is 3-colporoidate.
with spinulose exine as in other species of sect. *Myxa* (Nowicke & Ridgway, 1973 and chapter III). *C. nodosa* has small flowers in a paniculate inflorescence with the calyx not enveloping the fruit, in fact not persistent in this species, all characters entirely in accord with sect. *Myxa*.


Certainly the Brazilian, and probably the New World species of sect. *Myxa* as a whole require further detailed study, and the limits of a number of taxa are still unsatisfactorily resolved. The present account must be taken, therefore, as only a provisional survey, based on a limited number of exsiccata and on the various studies by Johnston (1930, 1935, 1937 & 1951).


Small to large trees or shrubs. Leaves petiolate, variable in shape broadly to narrowly elliptical, oblong, ob lanceolate, ovate or obovate, base rounded, obtuse to acute, occasionally slightly cordate, apex acute, acuminate to long acuminate or obtuse; upper surface glabrous or variously sparsely to densely minute puberulent, strigillose or occasionally villous or appressed setaceous, undersurface glabrous or variously sparsely to densely
tomentose, hirsutulous or strigillose, occasionally villous, appressed-sericeous or hispid; margin (occasionally dentate in some specimens of *C. sellowiana*); venation brochidodromous; membranaceous, chartaceous or rigid-coriaceous in texture.

Flowers usually in well developed, divaricate panicles (sometimes the flowers are clustered in the reduced branchlets of the panicle). Calyx obconical-campanulate, usually 5-toothed (occasionally the lobes are pushed off by rupture); ribbed or smooth, externally glabrous or variously pubescent, internally glabrous or variously pubescent. Corolla small (up to 10 mm), more or less salverform with the lobes oblong. Stamens 5, exserted with the slender filaments somewhat villous at the base. Ovary pyriform, glabrous or apically villous or puberulent. Fruits with persistent explanate calyx.

Pollen prolate-spheroidal, spheroidal to oblate-spheroidal, 3-colpate to 3-colporoidate, exine spinulous.

Key to Brazilian species of sect. *Myxa*.

1. Calyx ribbed (but sometimes more or less obscured by its dense external indumentum).

2. Leaves bullate, usually markedly so. 1. *C. trichoclada*.

2. Leaves not bullate.

3. Branchlets strigillose; calyx densely strigillose; ovary glabrous. 2. *C. traehyphylla*.

3. Branchlets hirsute or tomentose; calyx densely tomentose; ovary pubescent (the ovary of *C. decipiens* has not been seen but the fruit is puberulent).

4. Upper surface of the leaves densely covered with somewhat setaceous hairs, conspicuously so at the margin which
appears more or less ciliate. 3. *C. gardneri*

4. Upper surface of the leaves sparsely strigose with stiff hairs.

5. Mature leaves less than 20 cm with the margin remotely dentate and not revolute. 4. *C. decipiens*

5. Mature leaves longer than 20 cm, with the margin entire and revolute. 5. *C. chamissoniana*

1. Calyx unribbed.

6. Stem, petiole, peduncle and calyx covered by long hispid hairs; (ant-domatia well developed). 6. *C. nodosa*

6. Stem, petiole, peduncle and calyx variously pubescent or glabrous but never hispid; (ant-domatia lacking).

7. Ovary with a somewhat villous or sericeous indumentum or puberulent, at least towards the apex.

8. Upper surface of leaves glabrate.

9. Lower surface of leaves with densely appressed hairs; ovary puberulent towards the apex. 10. *C. bicolor*

9. Lower surface of leaves sparsely tomentose; ovary densely villous. 7. *C. sprucei*

8. Upper surface of leaves pubescent.

10. Leaves commonly dimorphic, the larger broadly ovate and the smaller orbicular. Indumentum of leaf lower surface usually tomentose and not appressed. 8. *C. toqueve*

10. Leaves monomorphc, more or less narrowly
oblong-elliptical or ovate-oblong. Indumentum of the lower surface strongly appressed.

11. Lower surface of leaves provided with a minutely puberulent pubescence, the hairs predominantly on the veins and veinlets directed towards the centre of the alveolae but never covering them.

9. C. scabrifolia

11. Lower surface of leaves with a densely appressed sericeous indumentum which obscures the alveolae.

10. C. bicolor

7. Ovary totally glabrous.

12. Leaves with both surface glabrous or nearly so.

13. Calyx uniformly, sparingly minutely puberulent. Leaves decidedly ob lanceolate, broadest above the middle.

11. C. magnolii-folia

13. Calyx glabrous at least basally. Leaves oblong to elliptical, broadest at the middle.


12. C. ecalyculata

14. Calyx pyriform in bud, opening regularly with 5 teeth, pubescent at the teeth. Leaves more or less broadly oblong.

13. C. lomatoloba

12. Leaves with at least one surface distinctly pubescent.

15. Calyx distinctly and densely tomentose or sericeous.
16. Petiole more than 2 cm; leaf base usually slightly cordate-oblique.
   14. C. tetrandra

16. Petiole up to 1.5 cm (usually 0.3-1 cm); leaf base acute to rounded, never oblique.

17. Calyx tomentose. Leaf upper surface villosulous with slender ascending hairs, lower surface usually tomentose.
   15. C. sellowiana

17. Calyx with appressed indumentum. Leaf sparsely appressed puberulent on both surfaces.

18. Leaves evidently dimorphic: the larger oblong-elliptical, the smaller orbicular. Calyx, internally, densely sericeous.
   16. C. sericeoalyx

18. Leaves monomorphic, ovate to elliptical. Calyx, internally, with a sparse pubescence usually restricted to the teeth.
   17. C. naidophylla

15. Calyx sparsely and minutely puberulent or glabrescent.

19. Leaf upper surface minutely puberulent.

20. Leaves dimorphic: the larger oblong-elliptical or obovate, the smaller commonly orbicular; rigid-coriaceous in texture.
   18. C. exaltata

20. Leaves monomorphic elliptical; chartaceous in texture.
   22. C. ucayaliensis

19. Leaf upper surface glabrous.

21. Branchlets glabrous or glabrescent (very sparsely puberulent towards the apex).

22. Leaves obovate, membranaceous or chartaceous.
   19. C. silvestris

21. Leaves oblong or oblong-elliptical, rigid-
21. C. ochnacea

22. Coriaceous.

23. Branchlets tomentose or minutely puberulent.

24. Flowers in a well developed lax inflorescence. Ovary glabrous.

25. Flowers more or less clustered on short reduced branches. Ovary puberulent.

26. C. nervosa


C. grandiflora DC., Prodr. 9: 475 (1845). Type - Brazil: indefinite, Sellow (DC!).

Type - Brazil: Bahia, 1830, Salzmann (DC! holotype, MO! isotype).

Distribution: NE and SE Brazil. In forest.


INDEFINITE: 1815, Sellow (MO); Glaziou 1505 (MO, F).

Cordia trichoclada is one of five species of sect. Myxa which have a conspicuously ribbed calyx, the others being C. trachyphylla,
C. gardneri, C. chamissoniana and C. decipiens. These species, however, are quite distinctive and are easily distinguished by the characters used in the key.

2. **Cordia trachyphylla** Mart., *Flora Regenb.* 24 Bd. 2. Beibl. 6 (1841).


Distribution: NE and SE Brazil. In forests.


Type - Brazil: Minas Gerais, Arraial das Merces, x.1840, *Gardner* 5126 (K! holotype).

Distribution: known only from the type collection.

*C. gardneri*, although only known by the type specimen, is a very marked species. It can be easily separated from all other species with ribbed calyx because of the dense and long pubescence of the leaf upper surface, with the hairs spreading out from the margins which appear ciliate.


Type - Brazil: Amazonas, basin of Rio Madeira, municipality Manicore, near Santa Fé, 8-11.ix.1934, *Krukoff* 6048 (A holotype, MO! F! isotypes).

Distribution: known only from the type collection.
The present species has most of the leaves with the margin of the distal half coarsely dentate. This feature, and the soft pubescence of the lower surface are distinctive characters.


Type - Brazil: indefinite, Sellow (BD, fide Johnston, 1930).

Distribution: N Brazil.


Unfortunately the type of this species has not been seen. The collection here referred to *C. chamissoniana* fits in the original description by Don (1837). It was pointed out by Johnston (1930) that *C. chamissoniana* is related to *C. trichochada*, from which it differs by the comparatively much larger leaves and looser pubescence, smaller and more or less obscurely ribbed calyx. These differential characters hold for this material in relation to specimens of *C. trichochada* which have been studied.


Type - Brazil: Pará, Sieber 62 (BD, fide Johnston, 1930).

*C. miranda* DC., *Prodr.* 9: 475 (1845). Type - Brazil: Bahia, Salzmann (DC!).

*C. hispidissima* DC., *Prodr.* 9: 475 (1845). Type -
Brazil: Bahia, 1832, Blanchet 995 (DC!).

Type - French Guiana: indefinite, Aublet (BM!).

Distribution: N and NE Brazil extending Northwards to the Guianas and Venezuela.


BAHIA: Belmonte, 31.i.1967, Belém & Pinheiro 3246 (MO); without precise locality, xii.1944, Schery 715 (MO). MARANHÃO: Maracassume river region, 25.xi.1932, Froés 2002 (MO). MATO GROSSO: Aripuana, 5.ix.1976, Andrade 3408 (UEC); Santa Cruz da Barra, 3.iii.1894, Lindman 2821 (MO). PARA: Belém, grounds of IAN, Igarapé do Aura, 12.vi.1969, Austin 4192 (MO); Belém, 22.xii.1944, Froés 19890 (F); lower Cupari river, plateau between Xingu and Tapajós river, ix.1931,


Type - Brazil: Amazonas, Barra do Rio Negro, 1850-51. *Spruce* 1019 (F! Phototype).

Distribution: N Brazil and also extending to French Guiana.

AMAZONAS: Manaus-Porto Velho highway, km 160. 23.iii.1974, Campbell, Ongley & Ramos P20845 (MO, NY, U); Parantins, 4.i.1936, Ducke 116 (F, K, MO, US); Santo Antonio do Içá, 2.v.1945, Froés 20872 (F, NY, US); Manaus-Porto Velho highway, km 246, 14.iii.1974, Prance et al. 20520 (MO, NY, U); Manaus, INPA, Estrada do Aleixo, km 3, 27.xii.1973, Ramos P20140 (MO, NY, U); Barra-Martinho, i.1851, Spruce 1234 (K); Barra, xii-iii.1850-1851, Spruce (E).


Type - French Guiana: Cayenne, Herb. Poiret (P!).
**C. pubescens** Willd. ex R. & S., Syst. 4: 800 (1819).  
Type - not traced. (fide Johnston, 1930)

**C. hebecarpa** DC., Prodr. 9: 488 (1845). Type - Brazil: Bahia, 1831, Blanchet 44 (DC!).

Type - French Guiana, indefinite, Aublet (BM!).

Distribution: WC, NE and N Brazil, extending northwards to the Guianas. In forests.


*C. toqueue* shows dimorphism in leaf shape and size, i.e. besides the larger and broadly ovate leaves a few comparatively smaller and orbicular leaves can be observed in a single branch. Similar leaf dimorphism also occurs in *C. sericalyx* and *C. exaltata*, which are, apart from this particular trait, distinct from each other and readily differentiated by the dense pubescence of the calyx of the
former species in contrast to the sparse indumentum of the latter.
C. toqueve is easily distinguished from C. sericicalyx and
C. exaltata because it has a pubescent ovary.

Type - British Guiana: indefinite, 1840, Schomburgk 911 (DC!
holotype, E!, K!, BM!, P! isotypes).
Distribution: N Brazil, extending to British Guiana. In forests.
ACRE: Abunã-Rio Branco highway, km 242-246, vicinity of Campinas
18.vii.1968, Forero, Coelho & Farias 6366 (F, MO, NY, U); near mouth
of Rio Macauhan (tributary of Rio Yaco-Rio Purus Region), 8.viii.1933,
Krukoff 5336 (F, MO, NY, U); near mouth of Rio Macauhan (tributary
of Rio Yaco), 26.viii.1933, Krukoff 5672 (F, MO, NY, U).
AMAZONAS: Basin of Rio Demeni, vicinity of Totobi, 1.iii.1969, Prance
et al. 10381 (F, MO, NY, U). CEARÁ: without precise locality,
xi.1858, Gardner 911 (G). GOIÁS: Antoniana, regiã do Araguaïns,
17.viii.1961, Oliveira 1737 (UB). MARANHÃO: Maracassume river
region, 20.x.1932, Froes 1955 (NY, U). PARÁ: Belém, 26.1.1943,
Archer 8195 (NY); 10 km N of Igarape-Acu, 75 km E of Belém,
9.xii.1974, Gentry 13149 (MO); Ilha do Mosqueiro, 3-9.xi.1929,
Killip & Smith 30525 (NY); Rio Jari, Monte Dourado, 24.xi.1967,
Oliveira 3897 (NY, US); road BR 22, Capanema to Maranhão km 64,
vicinity of Piritoro, 4.xi.1965, Prance & Pennington 1976 (F, NY, U);
437 km from Tocantins to Belém, 14.xi.1963, Silva 57795 (NY).
RONDÔNIA: basin of Rio Madeira, km 167-169 of Madeira-Mamoré railroad,
near Mutumparanã, 4.vii.1968 (F, MO, NY, U).

Type - Surinam: indefinite, 1841, Hastmann 406 (DC! holotype, G! K!)
Pil isotypes).

Distribution: N, WC and NE Brazil, extending westward to Peru and Bolivia, and Venezuela, Guianas and Surinam to the North.

AMAZONAS: Borba, near Bela Vista, 4-6.ix.1934, Krukoff 5976 (MO); Manicore, near Santa Fé, 8-11.ix.1934, Krukoff 6045; Humaitá, near Livramento or river Livramento, 12.x-6.xi.1934, Krukoff 6846 (MO).


MATO GROSSO: Santa Ana das Chapadas, 2.v.1903, Malme 2455 (MO); 5 km E of town of Chapada dos Guimarães, 24.x.1973, Prance, Lleras & Coelho 1936 (F). PARÁ: rodovia Belém-Brasília, km 95, 17.ix.1959, Kuhlmann & Jimbo 244 (F); road BR 22, Capanema to Maranhão, km 64, vicinity of Piritoro, 3.i.1965, Prance & Pennington 1943 (F, K, MO).

RONDONIA: road from Rondônia to Porto Velho, 30.x.1973, Lleras, Coelho & Conceição P 19447 (MO).


C. diospyrifolia Cham., Linnaea 4: 477 (1829). Type - Brazil: indefinite, Sellow (CI Phototype).

Type - Brazil: indefinite, Sellow (BD - fide Johnston, 1930).

Distribution: S and SE Brazil.

MINAS GERAIS: Viçosa, road to São Miguel, 2.iv.1930, Mexia 4557 (NY); Viçosa, 3.vi.1930, Mexia 4780 (F, NY); Caldas, 12.i.1862, Regnell II 202 (MO): PARANÁ: Taconda Marumbi, 4.i.1914, Dusén
14287 (F, MO, NY); Cacatu-Serra Negra (Antonina), 23.iii.1966, Hatschbach 14127 (F); Campina Grande do Sul, 19.xii.1972, Hatschbach 31013 (NY); Cerro Azul, Barra do Tigre, 17.v.1977, Hatschbach 39891 (UEC); Cerro Azul, 8.viii.1966, Lindeman & Haas 2119 (U).

RIO DE JANEIRO: estrada de contorno de Petrópolis, 16.iii.1968, Sucre 2487 & Braga 329 (NY).


C. salicifolia Cham., Linnaea 4: 481 (1829). Type - Brazil: indefinite, Sellow (K! P!).


Type - not traced.

Distribution: NE (Southern Bahia), SE and S Brazil. Native in deciduous or gallery forest.

BAHIA: Itapebí, plant. de cacau, 10.xi.1966, Belém & Pinheiro 2782 (NY); Itabuna, 14.vii.1964, Silva 58381 (NY). MINAS GERAIS: Caparaó, 10.ii.1973, Hatschbach & Almada 31431 (NY); road to São Miguel,
22.x.1930, Mexia 5201 (F, MO, NY, U); Cart road to São Miguel, 9.i.1931, Mexia 5497 (F, MO, NY, U). PARANA: Ponta Grossa, 26.xii.1910, Dusén 11309 (F, MO, NY); Cianorte, Rio Ivaí, Barra São Tome, 1.v.1966, Hatschbach 14356 (F); Campo Grande do Sul, 24.v.1967, Hatschbach 16472 (NY); Cascavel, Santa Tereza, 8.ii.1969, Hatschbach 21063 (F); São José da Boa Vista, Rio Jaguariaiva, 19.xi.1970, Hatschbach & Guimarães 25517 (NY); Joaquin Távora, 20.xi.1976, Hatschbach 39288 (UEC); Miguel do Iguaçu, Inhunvera, Rio São Vicente, 27.iii.1977, Hatschbach 39859 (UEC); Santa Helena, Porto Verde, 9.xii.1977, Hatschbach 40541 (MO, UEC); 30 km E of Cianorte, S of Rio Ivaí, 16.iii.1966, Lindeman & Haas 569 (U); 30 km E of Cianorte, S of Rio Ivaí, 25.iii.1966, Lindeman & Haas 756 (U); Reserve on the Rio Ivaí, ca. 30 km E of Cianorte, N of Boa Esperança, 29.iii.1966, Lindeman & Haas 816 (U); near Vista Alegre, 15 km N of Francisco Beltrao, 15.v.1966, Lindeman & Haas 1375 (U); SE of Xambrê, faz. Estrela do Sul, 13.vi.1966, Lindeman & Haas 1502 (U); ca. 10 km NW of Xambrê, 15.vi.1966, Lindeman & Haas 1558 (U); ca. 25 km SE of Palotina, 30.vi.1966, Lindeman & Haas 1804 (U); Parque Nacional do Iguaçu, E of ferry Capanema, 21.xi.1966, Lindeman & Haas 3335 (U); Parque Nacional do Iguaçu, 5.xii.1966, Lindeman & Haas 3461 (U); Parque Nacional do Iguaçu, 10.xii.1966, Lindeman & Haas 3509 (F, U); by road from Icaraima to Porto Camargo, 20.i.1967, Lindeman, Haas & Hatschbach 4286 (NY, U); ca. 85 km SW of Guarapuava, 14.iii.1967, Lindeman & Haas 4894 (U); near Ubiratã, vicinity of Cava Funda, 31.v.1967, Lindeman & Haas 5383 (U); Xambrê, 10.xii.1965, Lindeman, Haas & Hatschbach 13303 (U); 15 km N of Fr. Westphalen, 12.xii.1960, Lindeman & Haas 3607 (NY, U). RIO GRANDE DO SUL: Santo Ângelo, 19.i.1893, Lindeman (MO); Porto Alegre, 11.xii.1901, Malme 817 (M); Morro das Abertas, 9.i.1949, Rambo 39644 (F); Estação Linha Bonita,
19.i.1949, Rambo 40042 (F); Itacolumí, near Gravataí, 11.i.1950, Rambo 45268 (F). SANTA CATARINA: Serra do Matador, Rio do Sul, 29.xii.1958, Reitz 6071 (NY); Matador, Rio do Sul, 23.xi.1958, Reitz & Klein 7577 (NY); Rio do Rastro, Lauro Müller, 16.xii.1958, Reitz & Klein 8046 (MO, NY, U); São Miguel d'Oeste, 19.xii.1964, Smith & Klein 14142 (MO, NY). SÃO PAULO: Santa Ernestina, 29.ix.1920, Gehrt 4520 (NY); Butantã, i.1921, Gehrt 5304 (F); Butantã, cult. no Horto Oswaldo Cruz, 10.xii.1924, Gehrt 18135 (NY); 25 km NW of Mogi-Guaçu, Estação Experimental de Mogi-Guaçu, 20.x.1977, Gibbs & Leitão Filho 6023 (F, UEC), Pirassununga, 29.x.1978, Martins 10033 (U, UEC); Serra do Caracol, 10.xii.1875, Mosén 4307 (MO).


Type - Brazil: Acre, near mouth of Rio Macauhan (tributary of Rio Yaco), 14.viii.1933, Krukoff 5497 (A holotype, MvIF! U! isotypes).

Distribution: N, NE and SE Brazil.


Type - Venezuela: Rio Apure near El Diamante, Bonpland 804 (P!).


*C. umbraculifera* DC., *Prodr.* 9: 484 (1845). Type - British Guiana, indefinite, 1837, Schomburgk 408 (DC! K!).

Type - French Guiana: Cayenne, Aublet (BM!).

Distribution: N and NE Brazil, extending to northern South America and southwards to Bolivia.

AMAZONAS: Esperança (boca do Javari), 18.12.1845, Ducke 1887 (K).


*C. brachypoda* DC., *Prodr.* 9: 487 (1845). Type - Brazil: Bahia, Blanchet (DC!).
Type - Brazil: indefinite, Sellow (BD, fide Johnston, 1930).
Distribution: N, WC, SE and S Brazil. The species is widely distributed throughout the country, growing predominantly in forest, sometimes in transition to cerrado, or in restinga.

FEDERAL DISTRICT:
Brasília, Granja do Ipê, 10.iv.1963, Heringer 9122 (UB); Corrego Monteiro, vicinity of Planaltina, 29.ix.1965, Irwin, Souza & Santos 8793 (NY).
GOIÁS: Goiânia-Goiás Velha, 14.vii.1964, Duarte 8245 & Mattos (UB); Serra do Caiapô, 42 km S of Caiapônia, 27.x.1964, France & Silva 59694 (NY).
MATO GROSSO: ca. 6 km S of Xavantina, 15.ix.1967, Argent et al. 6398 (E, NY).
Base Camp Square, 20.viii.1968, Argent 6739 (E, MO, NY); ca. 6 km SW of Xavantina, 4.viii.1967, Ratter & Ramos R 289 (E, NY); 10 km N of Base Camp of Expedition, 7.vi.1968, Ratter et al. 1684 (E, NY); 8 km NE of Base Camp of Expedition, 25.vi.1968, Ratter et al. R 1979 (E, MO, NY).
MINAS GERAIS: Serra do Espinhaco, ca. 15 km of São João da Chapada, 23.iii.1970, Irwin et al. 28113 (F, NY); Santo Antonio do Itambé, Pico do Itambé, 9.viii.1972, Hatschbach 30132 (MO, NY); Tombos, 6.viii.1935, Mello Barreto 1436 (F); Belo Horizonte, 31.viii.1932, Mello Barreto (F); São João del Rei, 24.iv.1957, Pereira 3130 & Pabst 3965 (F); without precise locality, 1854, Regnell III 907 (MO, U); without precise locality, 1845, Widgren 1198 (MO).
PARANÁ: Guaratuba, 31.xii.1911, Dusén (F, MO); Guarantuba, Morro dos Morretes, iv.1964, Hatschbach 10947 (U); Paranaguá-Ilha do Mel, 24.iv.1969, Hatschbach 21433 (NY); Bocaiuva do Sul, 24.iii.1970, Hatschbach 24050 (NY); Guaraqueçaba, caminho do Paraguara, 10.ii.1972,
Hatschbach 29138 (NY); Guaraqueçaba, Rio Murato, 7.xii.1972, 
Hatschbach 30950 (NY). SANTA CATARINA: Barra do Sul, Araguari, 
2.i.1954, Reitz & Klein (U); São Francisco do Sul, Mina Velha, 
7.xi.1957, Reitz & Klein 5652 (NY). SÃO PAULO: 6-10 km from 
Caverna do Diabo to Eldorado, 9.ix.1976, Davis et al. 60865 (UEC); 
Cananéia, 17.ii.1965, Eiten & Clayton 6165 (MO, US); Ubatuba, 
Morro Escuro, Fontella 88 & Moura (US); Mogi das Cruzes, 20.v.1889, 
Glaziou 17712 (NY); without precise locality, ii.1839, Guillemin 
423 (US); São Paulo, Jardim Botânico, 26.iii.1932, Hoehne 28776 
(F, NY, UB); Limeira-Campinas, 18.vi.1951, Hoehne (F); Campinas-
Limeira, 17.v.1979, Leitão Filho et al. 10091 (UEC). AMAPÁ 
INDEFINITE: Blanchet 648 (NY); Frolich (NY); Lalande (NY).


Type - British Guiana: indefinite, 1839, Schomburgk 109 (DC! 
holotype, E! F! P! isotypes).

Distribution: N Brazil. The species occurs predominantly in 
northern South America (Surinam, British and French Guiana and 
Venezuela), extending to the Brazilian territory of Roraima and 
Pará state.

PARÁ: without precise locality, ii-iv.1844, Kappler 1510 (MO, U). 
RORAIMA TERRITORY: Serra Tepequem, 17.ii.1967, France et al. 4446 
(F, MO, NY, U).


Type - Brazil: Amazonas, Manaus, 13.x.1929, Killip & Smith 30008 
(GH holotype).

Distribution: N Brazil.


Type - Brazil: Pará, near Santarém, Martius (K).

Type - French Guiana: indefinite, Richard (P herb. Lamarck).

Distribution: N, SE and WC Brazil.

ACRE: near mouth of Rio Mucauhan (tributary of Rio Yaco), 2.ix.1933, Krukoff 5743 (F, MO). AMAZONAS: Humaitá, near Tres Casas, 14.ix-11.x.1934, Krukoff 6435 (F, U); Rio Solimões, vicinity of Coari, 15.ii.1977, Mori et al. 8993 (NY, Y); Rios Pacajá & Muirapiranga, 23.ix.1965, Prance, Pennington & Silva 1462 (F, NY, U); Tapuruguara, 25.x.1971, Prance et al. 15836 (NY, U); Manaus-Porto Velho highway, 17.iii.1974, Prance et al. 2064 (F). ESPIRITO SANTO: Reserva Florestal de Sooretama, 10.viii.1965, Belém 1532 (E, MO, NY). MATO GROSSO: source of Jatuarana river, Machado river region, xii.1931, Krukoff 1566 (MO); source of Jatuarana river, Machado river region, xii.1931, Krukoff 1684 (MO). PARÁ: Belém, 17.v.1969, Austin 4032 (MO); Belém, iii-v.1929, Dahlgren & Sella 227 (F); Belém, ii-v.1929, Dahlgren & Sella 248 (F); Belém, iii-v.1929, Dahlgren & Sella 418 (F); Belém, iii-v.1929, Dahlgren & Sella 734 (F); Belém, 22.ix.1942, Froés 19892 (F, NY, US);


Type - Brazil: Minas Gerais, without precise locality, Martius 299 (3D, fide Johnston, 1930).

Distribution: S, SE and NE Brazil. In forest.

BAHIA: without precise locality, Bondar 2458 (F); without precise locality, vii.1911, Luetzelburg 2520 (F). PARANÁ: Rio Cubatão, 28.xii.1911, Dusén 13649 (F, MO); Antonina, Caix D'Água, 18.i.1966, Hatschbach, Lindeman & Haas 13533 (NY, U); Morretes, 3.i.1974, Hatschbach 33779 (MO, UEC); Morretes, São João da Graciosa, 23.iv.1974, Hatschbach 34343 (MO); Antonina, Manduira, 4.i.1979, Hatschbach
41828 (UEC). SANTA CATARINA: Cunhas, Itajaí, 8.i.1954, Klein
1153 (A); São Francisco do Sul, Garuva, Tres Barras, 28.i.1958,
Reitz & Klein 6504 (NY, U). SÃO PAULO: Ubatuba, 10.i.1979, Silva
10995 (UEC).

20. *Cordia ophthalmica* DC., Prodr. 9: 485 (1845).


Type - Brazil: Pernambuco, Rio São Francisco near
Joazeiro, iv.1818, Martius (BD, fide Johnston, 1930).

Type - Brazil: indefinite, Lhotsky (DC! holotype).

Distribution: N, SE Brazil and also reported for Pernambuco state
in NE in Johnston (1930) by a single collection dated from April
1818 by Martius.

PARA: Vicinity of Paragominas, Belém-Brasília highway km 161,
de Janeiro, ii.1815, Bowie & Cunningham (BM); Copacabana, 26.i.1870,
Glaziou 4149 (P); Morro da Babilônia-Botafogo, 29.iii.1891, Glaziou
18383 (P).


Type - Brazil: Acre, Rio Acre, Seringal São Francisco, iii.1911,
Ule 9716 (K! isotype).

Distribution: known only from the type specimen.

This species resembles *C. sprucei* in leaf shape, i.e.
commonly obovate, with the upper surface glabrate. However, in
*C. ulei* the ovary is glabrous while in *C. sprucei* it is conspicuously
hairy.

Type - Peru: Loreto, Yarina Cochas, 26.x.1925, *Tessmann* 5447 (Gl isotype).

Distribution: N Brazil, extending eastwards to Peru and Bolivia.


Johnston (1930) originally described this taxon as *C. ulei* var. *ucayaliensis*, with the leaf upper surface pubescent in contrast to the typical variety with the leaf glabrescent. Subsequently, Johnston (1935), elevated var. *ucayaliensis* to specific rank but without adding any new differential characters. From the limited material which has been seen of these two taxa it would seem that they can be only distinguished by this particular attribute of the leaf. Thus, although in the present revision they have been maintained as species, it is likely that a critical study of a large suite of material referable to them may establish that these two taxa are conspecific.


Type - French Guiana: indefinite, Herb. Lamarck (P!).

Distribution: N Brazil, and widely distributed in the Guianas.

*C. nervosa* is easily recognised because the veinlets are completely immersed in the lower surface of the leaves, although the midrib and secondary veins are prominent. The relatively small, clustered inflorescence is also distinctive.

Section *Gerascanthus* was established by Don (1837) for a group of 17 species with distinctly ribbed or striate calyx and largish flowers in dense, corymbose inflorescences. The section as recognised by Don was heterogeneous and included only remotely related species, e.g. *C. sellowiana* Don\(^1\) and *C. chamissoniana* Don which are now referred to sect. *Myxa*, and *C. lutea* which is referred to sect. *Cordia*.

Johnston (1930) much improved the concept of sect. *Gerascanthus* by drawing attention to the distinctive fruit, which is cylindrical, thin walled, and enclosed in a persistent calyx and marcescent corolla. Sect. *Gerascanthus* sensu Johnston is a very natural group of 12 New World species of which five are endemic to Brazil (*C. goeldiana* Hub., *C. glabrata* (Mart.) DC., *C. insignis* Cham., *C. latiloba* Johnst. and *C. trichotoma* (Vell.) Arrab. ex Steud.) and a sixth species, *C. alliodora* (R. & P.) Oken, extends from Brazil into NW South America and Central America. All the species are quite distinct with the exception of the pair *C. alliodora*-*C. trichotoma* which show some breakdown of the differential corolla size, particularly where the two taxa are sympatric in Minas Gerais.

\(^1\)Inexplicably, Don described the species now referred to as *C. trichocladada* DC. under the name *C. sellowiana*, an epithet he had already applied to another species in the same paper. The epithet *C. trichocladada* was later used by De Candolle (1845) who was apparently unaware of Don's description. In any case, the species described as *C. sellowiana* by Don is a later homonym of *C. sellowiana* Chamisso (1829).


Small to large trees or sometimes shrubs. Leaves distinctly petiolate, lanceolate, elliptical, oblong, ovate, obovate or sometimes orbicular; base acute, obtuse or truncate, very often oblique, apex acute, acuminate or rounded; upper surface glabrescent or stellate-tomentose, lower surface glabrous, sparsely to densely tomentose or stellate-tomentose, or obscurely to densely appressed sericeous; margin entire; venation brochidodromous; usually coriaceous in texture.

Flowers commonly in lax, paniculate inflorescences (occasionally clustered on the much reduced branches of the panicle). Calyx tubular-cylindrical or campanulate, strongly ribbed (except *C. goeldiana*) variously 3-5(-10)-toothed, externally densely tomentose to minutely puberulent; internally sericeous. Corolla relatively large (1.5-4.5 cm), with the lobes oblong, rounded or rhombiform. Stamens 5 with the base dilated and hairy. Ovary pyriform or globose, glabrous. Fruits cylindrical enveloped by the calyx and the marcescent corolla. Pollen prolato- to oblato-spheroidal, 3-colpate or 3-colporate, exine spinulose.

All flowers are heterostylosous, but stamen height is not usually very variable between longstyle and shortstyle morphs.

Type species: *C. gerascanthus* L., *Syst.* ed. 10: 936 (1759).
Key to Brazilian species of sect. *Gerascanthus*.

1. Calyx unribbed (sometimes slightly striate).  
   1. *C. goeldiana*

1. Calyx strongly ribbed.

2. Corolla lobes rhombiform with the apex more or less acute.  
   Leaves glabrous on both surfaces.  
   2. *C. latiloba*

2. Corolla lobes oblong to rounded, with the apex truncate or rounded. Leaves pubescent at least on the lower surface.

3. Pubescence exclusively of simple hairs.

4. Lower surface of the leaves with strongly appressed sericeous pubescence and veins inconspicuous, more or less immersed in the lamina. Corolla 2-3 cm.  
   3. *C. glabrata*

4. Lower surface of the leaves tomentose (hairs never appressed) and veins prominent, not immersed in the lamina. Corolla 3.5-4.5 cm.  
   4. *C. insignis*

3. Pubescence mostly of stellate hairs.

5. Corolla lobes less than 3.5 mm. Ant-domatia usually present just below the inflorescence.  
   5. *C. alliodora*

5. Corolla lobes 4.0 mm or more. Ant-domatia usually lacking.  
   6. *C. trichotoma*


Type - Brazil: Pará, Peixeboi, railroad between Pará and Bragança, 23.ix.1907, *Goeldi* 8319 (RB, BM, G!).

Distribution: N Brazil. In forests.

PARÁ: Rio Xingu, between Boa Vista and Altamira, 20.viii.1919, *Ducke* (US); Belém, Campo Lyra Castro, 22.viii.1941, *Ducke* 788 (F, NY, US);
Belém, bosque Municipal, 10.ix.1945, Ducke 2345 (F, NY, US); Belém, IAN, mata do Cafezal, 15.ix.1949, Pires 1785 (NY); Rio Pacajá and Muirapiranga, line SW of Ilha de Breves, 28.ix.1965, Prance et al. 1492 (F, NY).


Within sect. Gerascanthus, *C. goeldiana* is exceptional because it has the calyx campanulate and smooth, in contrast to the remaining species with prominent ribbed, cylindrical calyx. In addition, the leaves are glabrous on both surfaces, a feature shared only with *C. latiloba*.

In the original description of *C. goeldiana* Huber (1909) described the fruit as globose, ca. 2 cm in diameter. Johnston (1930) argued that as this species is so clearly a member of sect. Gerascanthus, he strongly suspected that the fruit described by Huber did not belong to *C. goeldiana*. This point still needs to be clarified but, unfortunately, no fruiting material was available for this present study. However, if the fruit should be as described by Huber, then the sectional concept would need to be re-evaluated, or perhaps *C. goeldiana* transferred to section Rabdocalyx a group of 3 species from Mexico, which also have a marcescent corolla but with conic-ovoid fruits.


Type - Brazil: Rio de Janeiro, without precise locality, Glaziou 1106 (K!).

The species is known only from the type specimen and two additional collections, one of which, collected by Riedel, also from
Rio de Janeiro, was listed by Johnston (1930). The other specimen, seen at Paris during the present revision, was collected by St. Hilaire but with no indication of its provenance. The species must be very rare since the area around Rio de Janeiro has been well collected and, in spite of this, no new collections of *C. latiloba* have been made. The species is, nevertheless, a very distinct one with the corolla lobes rhombiform and with an acutish apex, a unique feature among the species of section *Gerascanthus*.

3. *Cordia glabrata* (Mart.) DC.

Syn.: *Gerascanthus glabrata* Mart., *Flora Regenb.* 21, Bd. 2, Beibl. 87 (1838) - (basionym).


*C. longituba* Chod., *Bull. Soc. bot. Gèneve* ser. 2.12: 213 (1921). Type - Paraguay: Rincon between Conception and Horqueta, 1914, Chodat 363 (G!).

Type - Brazil: Minas Gerais, near Contendas, Martius Herb. Bras. 1569 (BD - fide Johnston).

Distribution: NE, WC and SE. Predominantly in cerrado vegetation.

GOIÁS: 100 km south of Guará, along Belém-Brasília highway, 12.viii.1963, Basset Maguire et al. 56118 (NY); near Padre Bernardo, 20.vii.1971, Gifford & Fonseca G 210 (E); Serra Dourada, 1.viii.1895, Glaziou 21782 (NY, P); Piranhas, 15 km E, 27.vii.1977, Hatschbach 40134 (UEC); Padre Bernardo, 120 km of Brasília, 11.viii.1974, Meringer & Paula 13922-B (UEC); Mun. Niquelândia, Trairas, 27.vii.1952, Macedo 3623
4. **Cordia insignis** Cham., *Linnaea* 8: 122 (1833)


*C. jucunda* Moore, *Trans. Linn. Soc.* ser. 2. 4: 401 (1893). Type - Brazil: Mato Grosso, 1886, Leeson (BM!).
Type - Brazil: Minas Gerais, without precise locality, Lotzky (F! phototype).

Distribution: NE and WC Brazil. In cerrado vegetation.


GOIÁS: Olaria 5 km from Xavantina, 28.vii.1967, Sidney 194 (NY, UB).

MATO GROSSO: ca. 35 km (straight line), ENE of Barra do Garça, 4.v.1973, Anderson 9693 (F, NY); Cuiabá, Coxipó, 18.v.1973, ca. 60 km Hatschbach 32080 (NY, US); Xavantina-Caximbo road, 65 km Xavantina, 24.v.1966, Hunt & Ramos 5534 (K, NY); ca. 60 km N of Xavantina; 24.v.1966, Irwin et al. 15920 (F, NY, US); ca. 86 km of Xavantina, 4.vi.1966, Irwin et al. 16619 (F, NY, US); ca. 2 km NE of Xavantina, 7.vi.1966, Irwin et al. 16719 (F, NY, US); ca. 20 km S of Xavantina, 9.vi.1966, Irwin et al. 16806 (F, NY); 75 km S of Xavantina, lower slopes of Serra Azul, 17.vi.1966, Irwin et al. 17316 (F, NY, US); 15 km N of Barra do Garça on road to Xavantina, 2.v.1968, Ratter et al. 1267 (E, K, NY); Córrego do Gato, 220 km N of Xavantina on the Xavantina-São Félix road, 30.v.1968, Ratter et al. 1558 (E, K, NY).


*C. cujabensis* Manso & Lhotzk. ex Cham., *Linnaea* 8: 121 (1833). Type - Brazil: Mato Grosso, Cuiabá, vi.1832, Manso & Lhotzk 13 (DC!).

(1838). Type - Brazil: Mato Grosso, Martius Herb. Fl. Bras. 268 (E! P!).

Type - not traced.

Distribution, N, WC Brazil.


This species was described by Johnston (1950) and Opler et al. (1975) as homostylos. However, the survey carried out by Gibbs and Taroda (1983), based on floral dissection of some 51 specimens from South America, revealed the presence of shortstyle and homostyle morphs in C. alliodora.


Syn.: Cordiada trichotoma Vell. Fl. Flum.: 98 (1829) and Icones 2: 156 (1831).


C. excelsa A.DC., Prodr. 9: 473 (1845). Based on Gerascanthus excelsa.

C. chamissoniana Steud., Nom. ed. 2: 417 (1840), not Don (1837). Type - Brazil: Ceará, viii-xi.1838, Gardner 1780 (G! NY!).

C. hypoleuca DC., Prodr. 9: 472 (1845). Type - Brazil: Rio de Janeiro, 1844, Lund 66 (DC!).

Type - not traced.

Distribution: NE, WC, SE and S Brazil. In cerrado and gallery forest; also caatinga.


MATO GROSSO: Rio Paraguai, Pantanal, 27.viii.1977, Schaller 36 (NY). MATO GROSSO DO SUL: Dourados-Ponta Porã, Rio Dourados, 19.vii.1977, Gibbs et al. 5317 (UEC); Sidrolândia, 12.vii.1969, Hartschbach 21783 & Guimarães (MO); BR-262, 20 km W of Aquidauana, 12.v.1976, Hartschbach 38615 (UEC). MINAS GERAIS: without precise locality, 1841, Gardner 5040 (E, NY, US); without precise locality, 10.xi.1884, Glaziou 14144 (NY); Barbacena, 8.xi.14145, Glaziou 14145 (NY); Ituiutaba, 23.v.1945, Macedo 679 (MO); Santa Luzia-Piteiras, 1.v.1934, Mello Barreto 2129 (F); Santa Luzia, 3.v.1934, Mello Barreto 2130 (F); Tombos, 14.vii.1935, Mello Barreto 5129 (F); Santa Luzia-Vespaziano, 26.v.1935, Mello Barreto 5131 (F); Patos, 19.vi.1936, Mello Barreto 5132 (F); Caldas, 10.v.1874, Mosen 1917 (MO, U); Curvelo-Diamantina, 6.vi.1973, Orchioni 5477 (F); without precise...
locality, 3.v.1878, Regnell 1690 (US); Entre Rios de Minas, 26.iii.1981, Sarti 12548 (UEC); Venda Nova-Vespaziano (mun. Santa Luzia), 22.x.1945, Williams & Assis 6741 (F, MO, NY). PARANÁ: Jaguariaiva, 3.vii.1910, Dusén 10024 (MO, NY); Jaguariaiva, 20.iv.1911, Dusén 11743 (F, MO); Jaguariaiva, 3.vi.1914, Dusén 497a (MO); Imbuial, Alto da Bela Vista, 25.iv.1947, Hatschbach & O'Curial 720 (U); Laranjeiras do Sul, v.1964, Hatschbach 11196 (U); Alto Paraná, 21.vi.1966, Hatschbach 14424 (F, NY); Río Cedro, Mun. Guaratequêbaraba, 30.i.1968, Hatschbach 18515 (MO, NY); Laranjeiras do Sul, Río Iguazu near Barra do Perdido, 12.vi.1968, Hatschbach & Guimaraes 19394 (F); Laranjeiras do Sul, 8.ix.1975, Hatschbach 36601 (UEC); Adrianópolis, 21.i.1978, Hatschbach 41043 (UEC); Jaguariaiva, 3.vi.1914, Jonsson 497a (NY); Mariana, rio Laranjinha, 31.iii.1974, Kummrow 539 (MO); ca. 30 km E of Cianorte, 29.iii.1966, Lindemann & Haas 817 (U); 30 km E of Cianorte, 30.iii.1966, Lindemann & Haas 825 (F, NY, U, US); Porto Mendes, 21.vi.1967, Lindemann & Haas 5483 (U); Ivai, 15.iii.1937, Tessman 6105 (U). PERNAMBUCO: Taquaritinga W of Recife, 19.vii.1967, Lindemann & Haas 6169 (F, NY, U); Tapera, 10.ix.1932, Pickel 3113 (F, US). RIO GRANDE DO SUL: São Leopoldo, i.1941, Eugenio 278 (NY); São Leopoldo, v.1940, Leite 270 (NY), Santa Rosa-Giruá, 3.iii.1971, Porto & Oliveira 9651 (U). RIO DE JANEIRO: Guanabara, Floresta da Tijuca, 3.iv.1962, Angeli 287 (F); Rio de Janeiro, Armand 14833 (US); Rio de Janeiro, 27.iii.1886, Glaziou 16278 (NY); Guanabara-Jacarepaguá, 11.v.1963, Lanna 631 & Castellanos (F); Barra da Tijuca, 25.ii.1959, Pereira 4489 (F); Guanabara, morro do Bico do Papagaio, 14.vi.1969, Sucre 5286 (F, UEC). SANTA CATARINA: São Miguel do Oeste, 2.iii.1964, Castellanos 24837 (F); Ibirama, 3.iii.1956, Reitz & Klein 2604 (NY, U); Barra de Areia-Vidal Ramos, Reitz & Klein 6597 (US); Novo Horizonte, 15.i.1959, Reitz & Klein 8239 (F); Serra do Matador-Rio do Sul,
25.i.1959, Reitz & Klein 8295 (NY); Sanga da Areia, Jacinto Machado, 27.i.1960, Reitz & Klein 9414 (NY); Joaçaba, 10.ii.1957, Smith, Reitz & Klein 11167 (US); Rio do Sul, Braço do Trombudo, 13.ii.1957, Smith, Reitz & Klein 11359 (NY). SÃO PAULO: Matão, 18.vi.1961, Eiten et al. 3002 (MO, NY, US); Itapira, 26.v.1936, Gehrt (F); Campinas, 14.vi.1977, Gibbs 4781 (F, UEC); Campinas, 1904-1906, Heiner (MO); Campinas, Heiner (MO); São José do Barreiro, 29.iv.1926, Höhne & Gehrt 17642 (US); Mogi Mirim, 9.vi.1932, Höhne 29737 (F); Pirassununga, 1.v.1979, Martins 10004 (E, UEC); Campinas, 3.vii.1979, Martins 10873 (UEC); São José dos Campos, 29.iv.1961, Mattos 8909 & Mattos (F); subida para os campos de Bocaina, 1.v.1959, Pabst 11032 (F); Jundiaí, Serra do Japi, 9.v.1977, Traldi & Souza 25 (UEC); São Paulo-Rio de Janeiro, 1861, Weir 254 (F). INDEFINITE: Riedel 572 (NY).

*C. alliodora* is morphologically very similar to *C. trichotoma*. They were distinguished by Johnston (1930) on the basis of corolla lobe width (1.5-2.5 mm in *C. alliodora*, 3-7 mm in *C. trichotoma*), distribution and also the presence of a conspicuous ant-domatia developed below the inflorescence in *C. alliodora*, which are absent in *C. trichotoma*. Subsequently, however, Johnston (1935), preferred to treat *C. trichotoma* as a variety of *C. alliodora* with the earliest name available at varietal rank being *C. alliodora* var. tomentosa

Gibbs and Taroda (1983) in a critical study of *C. alliodora*—*C. trichotoma* observed that, although the presence of ant-domatia was not always consistent in *C. alliodora* and there were some intermediates between the two species with regard to corolla size, the two taxa differed in the expression of heterostyly. *C. alliodora* shows a range from shortstyle to homostyle flowers whereas *C. trichotoma* has distinctly short-, long- and homostyle flowers.
It was therefore argued that it is preferable to maintain the two taxa as distinct species for the present, pending controlled pollination studies on the functioning of the heteromorphic breeding system.
Section *Superbiflorae* sect. nov.


Small trees or shrubs. Leaves distinctly petiolate; elliptical, oblong-elliptical, oblanceolate, ovate to obovate; base and apex rounded, obtuse or acute; upper surface glabrous to puberulent, undersurface glabrous, minutely puberulent to sparsely to densely tomentose; margin entire or coarsely dentate; venation brochidodromous.

Flowers usually in terminal, robust and well-developed multiflowered panicles, but sometimes axillary, slender and few-flowered. Calyx tubular-campanulate, lobes 3-5 irregularly divided (except for *C. aberrans* with 5 equal lobes); externally minutely puberulent to densely tomentose, internally glabrous or puberulent. Corolla usually very large (up to 7 cm), funnelform, with the lobes more or less rounded and shallow or sometimes deeply oblong. Stamens 4-5, usually two shorter and three longer but sometimes all of equal length, villous at the base. Ovary pyriform, glabrous. Fruits conical-ovate, halfway or totally surrounded by the persisting calyx. Pollen 3-colpate to 3-colporate with spinulose exine.

Flowers heterostylos probable in all species.

Type species: *C. superba* Cham., *Linnaea* 4: 474 (1829).

Key to Brazilian species of sect. *Superbiflorae*.

1. Calyx regularly 5-lobed, lobes acuminate, mucronate, internally puberulent, with the mid-vein prominent.  
   1. *C. aberrans*
1. Calyx irregularly 3-5 lobed, lobes more or less rounded; internally glabrous, the middle vein immersed not prominent.

2. Panicles very slender, few flowered, axillary or apparently so.
   2. C. candida

2. Panicles robust, well developed, multiflowered, always terminal.

3. Corolla less than 2.5 cm, lobes deeply divided, oblong.
   6. C. anabaptista

3. Corolla more than 3.0 cm, lobes rather shallow, rounded.

4. Leaves glabrous on both surfaces, with entire margin.
   3. C. taguahyensis

4. Leaves pubescent at least on the lower surface, margin frequently coarsely dentate towards the apex.

5. Calyx minutely puberulent.
   4. C. superba

5. Calyx densely tomentose.
   5. C. rufescens


Syn.: C. mucronata Fresen., Fl. Bras. 8 (1): 9 (1857); not Poiret (1818).

Type – Brazil: "inter Vittoria et Bahia", Sellow 572 (M, GH! phototype).


The species was described by Fresenius (1857) but it was redescribed by Johnston (1935), due to the existence of an earlier homonym. C. aberrans is a very distinctive species of this section
and has the calyx with 5 lobes distinctly outlined, the mid-vein prominent on the inner surface of each. In addition, it has the leaves glabrous on both surface, but with a peculiar tuft of hairs restricted to the axil of the secondary veins.


Type - not traced.

Distribution: SE Brazil. The species occur at coastal localities around Rio de Janeiro and Espírito Santo.


*C. candida* resembles *C. aberrans* in that the panicles in both species are slender and fewer flowered in comparison with those of the other species in the section. They are, however, readily distinguished by the calyx characteristics used in the key and the leaf lower surface, which in *C. candida* is pubescent, contrasting with the glabrous leaves of *C. aberrans*.


*According to Johnston (1935) the type of *C. amplifolia* is at Munich and it is only a very large-leaved northern form of *C. taguahyensis*.
A. De Candolle (1845).

Type - not traced.

Distribution: NE, SE Brazil. Forest and gallery forest.


RIO DE JANEIRO: Monte de Santa Tereza, 11.ii.1815, Bowie & Cunningham (P); without precise locality, Gardner (US); without precise locality, 1841, Martius 462 (NY, P), without precise locality, 19.ii.1880, Netto 14236 (US), without precise locality, Regnel 149 (NY); without precise locality, v-vi.1832, Riedel 571 (US); without precise locality, 1844, Wildgren (MO). RONDÔNIA: basin of Rio Madeira, km 12, road Guajará-Mirim to Abuna, 5.8.1968, Prance et al. 6804 (MO).


*Syn.: C. superba var. cuneata* Cham., *Linnaea* 4: 474 (1829).

Type - Brazil: indefinite, Sellow (DC! G! K!).
C. superba var. elliptica Cham., Linnaea 4: 474 (1829).
Type - Brazil: indefinite, Sellow (G!).

C. blanchettii DC., Prodr. 9: 477 (1845). Type - Brazil: Bahia, Jacobina, Blanchet 2618 (DC!).

Type - Brazil: Rio de Janeiro, cultivated, Claziou 12087 (BD - fide Johnston, 1930).

C. ipomoeaeflora Hook., Bot. Mag. 84: t. 5027 (1858).
Type - pat. ignot., ex Hort. Kew (K!).

Type - Brazil: indefinite, Sellow (K!).

Distribution: NE, WC, SE and S Brazil. In forest or forest-cerrado margins.

GOIAS: MARANHÃO: Balsas, 13.iii.1962, Eiten & Eiten 3609 (US); Lorêto, Ilha das Balsas region, between Rio das Balsas and Rio Parnaiba, Eiten & Eiten 4201 (US); Lorêto, 31.v.1962, Eiten & Eiten 4781 (US).
RIO DE JANEIRO: Floresta da Tijuca, 22.i.1960, Angeli 99 (F).
SAO PAULO: Batovi, iii.1918, Andrade 1632 (NY); Mogi-Guaçu, faz. Campininha, 28.xii.1961, Mattos 9618 (F); Pirassununga, Chácara São Sebastião, 30.iv.1978, Monteiro 7707 (UEC); no locality given, 10.xii.1875, Mosén 4306 (MO); Louveira, 26.xi.1974, Sazima 980 (UEC).
INDEFINITE: 1836-1841, Gardner 1782 (NY).
The leaves of *C. superba* vary very much in size and shape and may be obovate, oblanceolate or elliptical. The species is very similar to *C. rufescens* and can be distinguished only by the denser (tomentose) pubescence of the leaf lower surface and calyx of the latter. Possibly a more detailed study of these two taxa will indicate that they are conspecific with *C. rufescens* as a mere variety of *C. superba*.

*C. anabaptista* approaches *C. superba* in general morphology of the leaves which are also variable in shape and size. They are, however, easily distinguished by the smaller corolla (less than 2.5 cm) with oblong lobes of *C. anabaptista*. The corolla of *C. superba* is much larger (more than 3 cm) and the lobes are shallow and more or less rounded.


Type - Brazil: Piaui, Martius (BD - fide Johnston, 1930).

Type - Brazil: Bahia, Serra Assuruá, 1838, Blanchet 2821 (G! K! P!).

Distribution: NE, SE and S Brazil. In forest and gallery forest.

BAHIA: Jacobina, Blanchet 3607 (BM, K, MO); Serra do Curral, 3 km NW Lagoinha, 5.iii.1974, Harley et al. 16744 (E, K, MO, NY); Serra da Água Rega, 25.ii.1971, Irwin, Harley & Smith 31052 (MO), Serra do Tombador, ca. 6 km S of Morro do Chapéu town, 18.ii.1971, Irwin, Harley & Smith 32469 (E, MO, NY).

CEARÁ: ca. 7 km from Missão Velha, 22.vii.1964, Castelhanos 25223 (F).

PARANÁ: Jaguariaiva, 1.i.1915, Dusén 16248 (MO, US); Rio Jaguariaiva, São José da Boa Vista, 19.xi.1970, Hatschbach 25519 (US); Quatiguá, 19.xi.1976, Hatschbach 39243 (UEC); Cerro Azul, Jaguatirica, 21.xi.1979, Hatschbach 42562
(UEC); Jaguariaiva, 17.i.1965, Smith, Klein & Hatschbach 14646 (US).
SÃO PAULO: ca. 50 km S of Itapetininga, road to Registro, Reserva
Florestal Carlos Botelho, 26.x.1976, Gibbs, Leitão Filho & Taroda
3253 (F, UEC); Itapetininga, 20.xii.1978, Giannotti 6818 (UEC).


Type - Brazil: indefinite, Sellow (P! isotype).
Distribution: NE, WC and SE Brazil. In forest or cerrado.

BAHIA: Santa Cruz da Cabralia, 8.ii.1967, Belém & Pinheiro 3293 (MO);
Valley of Rio das Ondas, Espigão Mestre, ca. 32 km W of Barreira,
5.iii.1971, Irwin, Harley & Smith 31527 (US). GOIÁS: ca. 2 km of Araguaina,
12.iii.1968, Irwin, Maxwell & Wasshausen 21076 (US); S of Miracema do Norte,
29.vii.1964, France & Silva 58483 (US).
SÃO PAULO: Ribeirão Preto, Estação Experimental de Ribeirão Preto,
19.i.1939, Viegas 3871 (US).


Mostly shrubs of less than 2 m but some small trees up to 5 m.

Leaves petiolate or sessile, membranaceous or chartaceous in texture, margin serrate, dentate or crenate, occasionally entire; venation craspedodromous (brochidodromous in *C. longifolia* and *C. poliophylla*).

Flowers in congested inflorescences (spicate, capitate or glomerulate) or sometimes in small, loose panicle. Calyx variable in shape, 5-toothed, teeth deltoid frequently prolonged in a long acumen, internally glabrous. Corolla variable in shape, villous below the point of the insertion of the stamens. Stamens 5, usually inserted at the same level on the corolla tube (at different levels in *C. grandiflora*, *C. leucocephala* and *C. paucidentata*). Ovary pyriform, glabrous. Fruits conical or cylindrical, coarsely verrucose at least the half basal part, but with a longitudinal, slightly striate band. Pollen, spheroidal to oblate spheroidal, 3-porate, exine reticulate.
All the species seem to be heterostyloous, but with the stamen length scarcely variable.

Type species: *Cordia globosa* (Jacq.) HBK., *Nov. Gen. et Sp.* 3: 76 (1818).*

*Although a contemporary of Linnaeus, Browne (1756) in his work dealing with the Jamaican plants, did not adopt the binomial nomenclature. In establishing the genus *Varronia*, Browne (1756) described two taxa: the first of these "the round spiked *Varronia" was subsequently treated under the name *Varronia humilis* by Jacquin (1763) and in doing so he specifically cited the first taxon of Browne. Johnston (1949) reduced *V. humilis* to a varietal rank of *Cordia globosa* (Jacq.) HBK. *Cordia globosa* has its basionym in *Varronia globosa* Jacq., which in the sequence of Jacquin's work precedes the description of *V. humilis*. In any case, the first described taxon by Browne under *Varronia* is the one now bearing the name of *C. globosa var. humilis* (Jacq.) Johnst. The second species by Browne (1756) "the *Varronia with oblong spikes", was also given a binomial by Jacquin (1763) with the name of *Varronia curassavica* which was subsequently transferred to *Cordia* by Roemer and Schultes (1819).
Key to the species of subgenus Varronia.

1. Inflorescence spicate, elongate, more than 3 times longer than broad.

2. Petiole of the leaves decurrent on the peduncles of the inflorescences and young side branchlets.

3. Leaves evidently dentate or crenate. Spike generally stout and densely flowered; calyx teeth usually acuminate.
   1. *C. multispicata*

3. Leaves entire, ondulate or at most inconspicuously denticulate.
   Spike slender, very elongate and loosely flowered; calyx teeth triangular.
   2. *C. euchomburgkii*

2. Petiole of the leaves not decurrent on either peduncles of the inflorescences or young side branchlets.

4. Leaves triangular-ovate, base truncate. Corolla lobes more or less rounded and shallow, reflexed.
   3. *C. dardani*

4. Leaves elliptical, elongate, base attenuate or acute.
   Corolla lobes more or less triangular, strongly reflexed.
   (*C. aurassavica group.)*

5. Stem very densely hirsute. Leaf upper surface densely tomentose. Calyx abundantly hirsute.
   4. *C. intonsa*

5. Stem glabrate-puberulent, or with generally rigid, appressed hairs. Leaf upper surface glabrate or abundantly strigose, sometimes sparsely villosulous.

6. Leaf upper surface mostly glabrate. Calyx teeth acute; corolla with wrinkled lobes.
   5. *C. aurassavica*

6. Leaf upper surface with abundant strigose-setose
hairs. Calyx teeth acuminate; corolla lobes smooth.

6. *C. campastris*

1. Inflorescence variously capitate, glomerulate, elongate-cylindrical or clavate (in this case flowers always very congested) or sometimes small loosely paniculate.

7. Flowers with corollas more than 2.5 cm long.

8. Sepal tip prolonged in a long filiform apex.

9. Leaves sessile, oblanceolate or obovate. Calyx puberulent at the base becoming densely hirsute towards the teeth. 7. *C. paucidentata*

9. Leaves petiolate, triangular-ovate. Calyx uniformly long setaceo-strigose. 8. *C. grandiflora*

8. Sepal tip lacking a long filiform apex. 9. *C. leucocephala*

7. Flowers with corollas 2.0 cm long or less.

10. Calyx funnelform; corolla with a narrow tube, ca. 2 mm in diameter and 10 mm long, expanding abruptly in a well developed limb with deeply divided lobes.

11. Stem, leaves on both surfaces and calyx glabrous. 10. *C. longifolia*

11. Stem, leaves and calyx pubescent. 11. *C. poliophylla*

10. Calyx campanulate or obconical; corolla variously tubular-cylindrical, funnelform or when salverform the tube is 5 mm long or less, lobes shallow sometimes almost inconspicuous.

12. Leaves sessile, or subsessile with the petiole 2 mm or less.
13. Inflorescence clearly elongate-cylindrical, 2 times longer than broad. 13. *C. villicaulis*

13. Inflorescence capitate or clavate, sometimes shortly-cylindrical but always less than 2 times longer than broad.

14. Stem densely hirsute with spreading hairs. Leaves narrowly to broadly lanceolate, upper surface hirsute or more or less villous. Calyx teeth in most cases prolonged in a filiform apex (rarely lacking). 14. *C. sessilifolia*

14. Stem with appressed, setose or strigose hairs. Leaves usually ovate or obovate, sometimes elliptical, upper surface appressed setose or strigose. Calyx teeth acuminate.

15. Calyx basally glabrate-puberulent, becoming hirsute towards the teeth. Corolla funnelform with the limb reflexed. 15. *C. truncata*


12. Leaves evidently petiolate, petiole 3 mm or more.

16. *Sepal* tip prolonged in a long filiform apex

17. Stem, leaves and calyx with stipitate glands.

18. Calyx sparsely strigose. Corolla limb not reflexed. Inflorescence less than 1 cm in diameter. 18. *C. corchorifolia*

18. Calyx densely whitish hirsute, at least at the teeth. Corolla limb reflexed. Inflorescence more than 1 cm in diameter. 19. *C. caput-medusae*

17. Stem, leaves and calyx without stipitate glands.
19. Inflorescence usually elongate-cylindrical or clavate, occasionally spherical, very much congested. Stem robust and few branched, densely hairy.  

17. C. calocephala

19. Inflorescence spherical or globose. Stem slender, much branched, usually sparsely hairy.

17. C. caZocephaZa

20. Leaves with upper surface glabrous (very rarely sparsely appressed puberulent), margin usually entire, occasionally remotely serrulate. Inflorescence mostly axillary with the peduncle decurrent on the petiole of subtended leaf.

26. C. buddleioiZes

20. Leaves with upper surface conspicuously pubescent, strigose or hirsute, margin evidently serrate or serrulate. Inflorescence internodal or terminal.


20. C. globosa


12. C. setigera


22. Lower surface of the leaves evidently whitish-floccose. Stem and calyx with fine covering of whitish cotton-like hairs.

23. Leaves larger than 8 cm x 3.5 cm.

21. C. leucomalla

23. Leaves less than 5 cm x 2 cm.

22. C. leucomalloiZes

22. Lower surface of the leaves variously hairy but never floccose. Stem and calyx lacking whitish cotton like hairs.

24. Corolla salverform with a well developed and reflexed limb. Inflorescence clavate, congested.  

23. C. harleyi
24. Corolla tubular-cylindrical with the limb not reflexed. Inflorescence capitate-glomerulate or small loosely paniculate.

25. Corolla ca. 12 mm. Calyx exceeding 5 mm, whitish sericeous-tomentose. 24. *C. mayoi*

25. Corolla 5 mm or less. Calyx less than 5 mm, hirsute, strigose or puberulent.

26. Calyx basally glabrous or puberulent, becoming hirsute towards the teeth.

27. Leaves with upper surface densely strigose, hirsute or villosulous and margin usually distinctly serrate. Calyx teeth acute to acuminate never with a filiform apex. 25. *C. guazumaefolia*

27. Leaves with upper surface glabrous except for the midrib (very rarely appressed puberulent) and margin usually entire, rarely remotely serrulate. Calyx teeth with a filiform apex, very rarely lacking. 26. *C. buddleioiides*


28. Inflorescence internodal, not subtended by a leaf. 29. *C. monosperma*

28. Inflorescence axillary, subtended by a leaf or terminal.

29. Flowers in capitate-glomerulate heads which are usually in racemes or panicles, sometimes solitary. 27. *C. polycephala*

29. Flowers in small panicles, sometimes becoming rather denser.

30. Stem abundantly hirsute; inflorescence borne on robust, straight, evidently
axillary peduncle. Calyx usually hirsute. 29. *C. urticaefolia*

30. Stem mostly appressed strigose or strigillose; inflorescence mostly terminal (very rarely some additional inflorescences are internodal or axillary). Calyx usually puberulent.

28. *C. discolor*

Syn.: *C. bahiensis* DC., *Prodr.* 9: 489 (1845). Type - Brazil: Bahia, without precise locality, 1830, Salzmann 376 (DC! P!).

Branchlets covered by a mixture of strigose, incurved hairs and slender, soft hairs, occasionally with dense, stiff-appressed pubescence. Leaves (6-)7-10(-13) × (3-)4-5(-7.5) cm; ovate or sometimes almost orbicular, base acute or abruptly attenuate, apex acute or acuminate; upper surface strigose to strigillose, tuberculations present and variously developed, rarely absent, undersurface tomentose; margin dentate or crenate. Petiole (3-)5-7(15) mm, decurrent on the peduncle of the inflorescence or young branchlets. Inflorescence spicate, usually stout and densely flowered, axillary or terminal, solitary or in cluster of two or three; peduncles (1-)2-6(-9) cm. Calyx 3-5 mm, obconical-campanulate, teeth acuminate; hirsutulous towards the apex. Corolla 5-6 mm, funnelform with lobes slightly emarginate and reflexed. Stamens ca. 2 mm, filaments slender. Ovary ca. 1.5 mm, style ca. 2 mm in shortstyle and ca. 4 mm in longstyle flowers. Fruits conical.

Type: Brazil, indefinite, Sellow (GH! phototype).

Distribution: N and NE of Brazil. Map 1, fig. 11.


BAHIA: 16 km de Itabuna (mun. de Ilhéus), 19.i.1965, Belém & Mendes 172 (UB); Bom Jesus, 1.i.1929, Hoehne 24015 (GH); without precise locality, 1831, Salzmann (E, K, MO); Mun. de Alagoinhas, i.1944, Schery 481 (GH, MO); Vittoria, Sellow (GH); Nazaré, collector unknown.
Among the Brazilian spicate Varronias, *C. multispicata* is one of the most distinctive species. The spike is very stout and the leaf petiole is decurrent on the peduncle of the inflorescence and branchlets. *C. multispicata* differs from *C. schomburgkii*, the only other species to have this characteristic, in having stout, densely flowered spikes in contrast to the long, laxly flowered spikes of *C. schomburgkii*.

*C. bahiensis* DC is a clear synonym of *C. multispicata*, since the type material is virtually identical with type specimen of *C. multispicata*. 
Fig. 11. *C. multispicata*

(a) habit; (b) flower (longstyle); (c) dissected corolla; (d) gynoecium (homostyle); (e) gynoecium (shortstyle) / Archer, 8097 (K) [b,c,d]; Drouet 2088 (GH) [e].

Branchlets finely tomentose, frequently with a mixture of strigillose hairs. **Leaves** (4-)6-8(-10.5) x (2-)3.5-(-7.5) cm, ovate, ovate-lanceolate or sometimes orbicular, base generally rounded, apex acute; upper surface minute strigillose, tuberculations generally present, undersurface finely tomentose, hairs mainly on the veins; margin entire, occasionally serrate or serrulate. **Petiole** 6-10 mm long decurrent on the peduncle of the inflorescence or branchlets.

**Inflorescence** spicate, very much elongate, slender, loosely flowered, axillary or terminal, solitary or in clusters of two or three; peduncle (2-)4-6(-10) cm. **Calyx** ca. 4 mm, campanulate or funnelform, teeth with acute apex; puberulent. **Corolla** ca. 5 mm, funnelform with lobes very shallow, slightly reflexed. **Stamens** ca. 2 mm. **Ovary** 1.5 mm, style ca. 2 mm in shortstyle and ca. 3.5 mm in longstyle flowers. Fruits conical.


3. *Cordia dardani* sp. nov.

"*C. curassavicae*, *C. intonsae* et *C. campestris* forma corolla similis est sed foliis ovato-triangularibus et spicis laxis praesertidiffert."

Branchlets densely and finely hirsutulous. Leaves 2.3-4 × 1.5-2.0 cm; triangular-ovate to ovate, base truncate, apex acute; upper surface abundantly minute-strigillose, undersurface densely tomentose; margin serrulate. Petiole 5-10 mm. Inflorescence spicate, slender, somewhat lax, terminal; peduncle 2.0-3.5 cm. Calyx ca. 3.5 mm, obconical-campanulate, teeth acute, uniformly densely hirsutulous. Corolla ca. 6 mm, somewhat funnelform with lobes somewhat rounded and marginate, slightly reflexed. Stamens ca. 2 mm. Ovary 1.5 mm, style ca. 3.5 mm in longstyle flowers, shortstyles not observed. Fruits cylindrical.

Type - Brazil: Pernambuco, estrada Salgueiro-Carqueja, Serra de São Gonçalo, 23.v.1971. E.P. Heringer et al. 862 (UB holotype).

Distribution: NE Brazil. Caatinga vegetation. Map 1; fig. 12.


This species is named in honour of the Brazilian botanist Dr. Dardano Andrade-Lima, distinguished specialist of the flora of NE Brazil.

Although *C. dardani* is only known from the type and one other collection, these specimens show clear differences which separate from all the other spicate *Varronia*, viz. small triangular-ovate leaves with the upper surface minutely strigillose and the inflorescences laxly flowered.

In *C. dardani* the corolla is similar to that of *C. curassavica*, *C. intonsa* and *C. campestris*. However, these latter species have distinctly lanceolate leaves which clearly distinguish them from *C. dardani*. 
Fig. 12. *C. dardani*

(a) habit; (b) flower; (c) dissected flower;
(d) gynoecium (homostyle)/Heringer et al. 862 (UB)
[b,c,d].

Non *C. hirsuta* Willd. (1798).

Branchlets densely soft hirsute. Leaves 4-10 × 1.2-3.0 cm, lanceolate to elliptic-lanceolate, base cuneate to long attenuate, apex acute; upper surfaces very densely tomentose, tuberculate, underside densely tomentose; margin serrate to serrulate. Petiole 2-10 mm.

Inflorescence spicate, densely flowered, terminal or internodal; peduncle 2-4 cm. Calyx ca. 4.5 mm, obconical-campanulate, teeth apex acute; densely hirsute. Corolla ca. 7 mm, somewhat salverform with the lobes more or less triangular and strongly reflexed, wrinkled. Stamens ca. 1.5 mm. Ovary 1.5 mm, style ca. 3.0 mm in longstyle flowers shortstyle flowers and fruits not seen.

Type - Brazil: Minas Gerais, between Salgado and Vao do Paranan; ix.1818, Martius (BD) - fide Johnston (1930).

Distribution: SE Brazil. Map 1; fig. 13.


The present species, formerly described by Fresenius as *Cordia hirsuta*, was correctly renamed by Johnston (1930) as *Cordia intonsa*. *C. hirsuta* Fresen is a later homonym of *C. hirsuta* Willdenow (1798) which is here treated as a synonym of *C. nodosa* (p.74).

*C. intonsa* very closely resembles *C. curassavica* from which it can only be distinguished by the conspicuous and densely-hirsute indumentum.

The Martius type specimen at Berlin-Dahlem was probably destroyed, in which case the specimen *St. Hilaire* 662 should be chosen as lectotype.
Fig. 13. *C. intona*

(a) habit; (b) flower; (c) dissected flower; (d) gynoecium (homostyle)/St. Hilaire 662 (P) [b, c, d].
Map 1: Distribution of *C. multispicata* (○), *C. schomburgkii* (▲), *C. dardani* (○) and *C. intonsa* (□).


*C. verbenacea* DC., *Prodr.* 9: 491 (1845). Type - Brazil: Rio de Janeiro, 1834, Gaudichaud 532 (DC!).

*C. salicinia* DC., *Prodr.* 9: 492 (1845). Type - Brazil: Rio de Janeiro, 1833, Vauthier 204 (DC! G! P!).


Branchlets usually puberulent, sometimes strigillose or hirsutullous. Leaves (4-)6-7(-12.5) x (1-)1.5-2.5(-3.0) cm, varying in shape from lanceolate, ovate-lanceolate to oblong-elliptical, base long to short attenuate, apex acute to obtuse; upper surface commonly glabrous occasionally strigillose or hirsutullous, tuberculate, under-surface sparsely to very dense tomentose; margin serrulate, serrate or crenulate. **Petiole** (2-)3-4(-10) mm. **Inflorescence** spicate, usually densely flowered internodal or terminal; peduncles (1.5-)2-6(-12) cm. **Calyx** 3-5 mm, obconical-campanulate, teeth apex acute, puberulent, occasionally hirsutullous. **Corolla** 5-8 mm, funnelform or somewhat salverform, lobes deeply divided, wrinkled, strongly reflexed. **Stamens** 1.5-3 mm. **Ovary** ca. 2.5 mm, style ca. 3.6 mm in shortstyle and ca. 5.2 mm in longstyle flowers. **Fruits** conical.

Type: not traced.

Distribution: widely distributed throughout Brazil (N, NE, WC, SE, S): found in a wide range of habitats, e.g. cerrado, restinga and
forest. Map 2; fig. 14.

AMAZONAS: Rio Cauamé, afluente Rio Branco, 6.ix.1943, Ducke 1311 (F, GH); São Carlos, Rio Negro, 1853-54, Spruce 3012 (E, K). BAHIA: Barreiras, 24.xii.1954, Black 54-17780 (A); without precise locality, v.1866, Blanchet 3608 (GH, K, MO); without precise locality, 29.v.1928, Bondar 23566 (GH); Porto Seguro, 21.iii.1974, Harley et al. 17224 (MO); Itacaré, near the mouth of Rio das Contas, 31.iii.1974, Harley et al. 17584 (MO); Serra do Síncora, Lagoa Encantada, 19 km NE of Ibicoara near Brejão, 1.ii.1974, Harley 15790 (MO); 20 km E of Camaleão, on the Itiuba-Cansaça road, 21.ii.1974, Harley 16456 (MO); Serra da Água Rega, 22 km N of Seabra road to Água Rega, 26.ii.1971, Irwin, Harley & Smith 31109 (UB); Valley of the Rio das Ondas, ca. 4 km N of Barreiras, road to Sta. Rita de Cassia, 5.v.1971, Irwin, Harley & Smith 31583 (UB); Serra do Tombador, Morro do Chapéu, ca. 6 km S of town of Morro do Chapéu, 18.i.1971, Irwin, Harley & Smith 32447, (UB), munic. de Almadina, 18.vii.1978, Mori, Hage & White 10259 (UEC); Esplanada, xii.1944, Schery 712 (GH, MO); munic. Itabuna, 25 km of Buerarema, 10.vii.1964, Silva 58349; Caldeirão, x.1906, Ule 7263 (G, K). ESPÍRITO SANTO: Cachoeiro do Itapemirim, 8.ii.1973, Hatschbach 31374 & Ahumada (K); ca. 60 km NW of Colatina, Vale de Pancas, 8.ix.1977, Shepherd et al. 5874 (F, UEC); 60 km S of Vitória, between Anchieta & Pídua, 9.ix.1977, Shepherd et al. 5880 (F, UEC). GOIÁS: Monte Alegre de Goiás, 13.iii.1973, Anderson 6979 (E, MO, UB); 50 km N of Corumbá de Goiás on road to Niquelândia, in valley of rio Maranhão, 24.i.1968, Irwin, Maxwell & Wasshausen 19119 (K, MO). MINAS GERAIS: ca. 8 km N of Gouveia on road to Diamantina, 4.ii.1972, Anderson, Stieber & Kirkbride (UB); Serra do Cipó, 17.ii.1972, Anderson, Stieber & Kirkbride 36076 (K, UB); munic. Sta. Luzia, 25.x.1945, Assis 35 (A, GH, MO); munic. Sta. Luzia, 13.xii.1945, Assis 238 (GH); munic.
Nova Lima, Serra da Mutuca, 10.ii.1945, Assis 5726 (GH); without precise locality, iv.1840, Claussen (K); near Paraopeba, 28.xii.1976, Fonsêca & Fonsêca FF6 (E, UB); S'Ana do Riacho, 25.x.1964, Hatschbach 35334 & Koczicki (MO); Paraopeba, 28.ii.1955, Heringer 3717 (UB); Belo Horizonte, Holway 1323 (A); Serra do Cipó, 135 km N of Belo Horizonte, 20.ii.1968, Irwin et al. 20556 (A, MO, UB); ca. 28 km SW of Diamantina on road to Gouveia, 15.i.1969, Irwin et al. 21992 (UB); Serra do Espinhaço, ca. 8 km W of Graõ Mogol, 16.ii.1969, Irwin et al. 23364 (GH, MO); base of Serra da Piedade, ca. 35 km E of Belo Horizonte. road to Caeté, 13.i.1971, Irwin et al. 30266 (UB); Ituiutaba, 23.1.1949, Maciel 2033 (MO); Belo Horizonte, 8.xi.1932, Mello Barreto 5139 (A); Belo Horizonte, 7.vii.1940, Mulford & Foster 554 (GH); munic. Jaboticatubas, km 126 Lagoa Santa-Conceição do Mato Dentro, 14.xii.1971, Semir & Sazima 552 (UEC); munic. Jaboticatubas, km 126 Lagoa Santa - Conceição do Mato Dentro, 15.xii.1973, Semir & Lima 4822 (UEC); Santo Hipólito-Diamantina km 45, 30.xi.1976, Shepherd et al. 3834 (UEC); road Curvelo-Sete Lagoas km 40, 2.xii.1976, Shepherd 3994 (E, UEC); Belo Horizonte, 4.iii.1945, Williams & Assis 5976 (GH, K); 10 km N of Belo Horizonte, 16.iii.1945, Williams & Assis 6041 (GH).


RIO GRANDE DO SUL: Vila Manresa, near Porto Alegre, 22.ix.1948, Rambo 37730 (GH); Toca do Tigre, 27.ix.1950, Rambo 48851 (K); without
precise locality, 1832, Tweedie (GH). RIO DE JANEIRO: Cabo Frio, 16.x.1938, Alston-Lutz 27 (A); without precise locality, Banks 1768 (A); Nova Friburgo, 1918, Curran 729 (A); Niterói, 25.xii.1901, Dusén 144 (G, MO); Magé-Mauá beach on Guanabara bay, 20.xi.1966, Eiten & Eiten 7846 (US); Rio de Janeiro, Glaziou 4963 (A); Jacarepaguá, 29.i.1962, Lanna 521 (F); Rio de Janeiro, x.1832, MacGillivray 323 (K); Barra da Tijuca, 7.vi.1960, Martins 158 (F); Guanabara, 17.viii.1961, Martins 224 (F); Rio de Janeiro, Riedel (A); Niteroi, Morro do Cavalaó, 17.iv.1929, Smith & Brade 2318 (A); Campos - Morro do Coco, 8.xii.1964, Trinta 1028 & Fromm 2104 (M); Rio de Janeiro, 1844, Widgren (MO). SANTA CATARINA: Itajuba, 6.i.1974, Conrad 2089 & Dietrich (MO); Florianópolis, 15.vii.1951, Rambo 50304 (A); Laguna, 19.ix.1951, Reitz & Klein 41 (GH); Laguna, 3.vii.1952, Reitz & Klein 277 (GH), munic. Itajai, 28.vi.1954, Klein 788 (A); Itajai, 15.vii.1953, Reitz & Klein 822 (A, UB); Araguari, Barra do Sul, 10.viii.1953, Reitz & Klein 915 (A); Palhoça, 24.ix.1953, Reitz & Klein 981 (A); munic. Itajai, 1.x.1953, Reitz & Klein 1090 (A); Palhoça, 5.xi.1953, Reitz & Klein 1221 (A, G); Barra do Sai-Guacú, S. Francisco, 3.i.1954, Reitz & Klein 1469 (A); Araguari, 2.i.1954, Reitz & Klein 1478 (A); Palhoça, 18.xii.1952, Reitz 4877 (A).

SAO PAULO: Ilha Queimada, 5.iv.1920, Amaral & Domingues 13 (A), Guarujá, 17.i.1924, Bailey & Bailey 942 (A); Santos, Ball (E); Ilha do Cardoso, 3.xi.1978, Cruz et al. 8997 (UEC), between Caraguatatuba & Ubatuba, 22.viii.1976, Davis et al. 59886 (E, UEC); Ilha do Cardoso, 7.ix.1976, Davis et al. 60653 (E, UEC); Ilha do Cardoso, 8.ix.1976, Davis et al. 60701 (E, UEC); São Paulo - Cananéia, 16.i.1965, Eiten & Clayton 6150 (MO, US); Santos, Ilha da Queimada Grande, 3.xi.1920, Gher 4530 (A); São Sebastião-Bertioga, 10.xi.1976, Gibbs et al. 3517 (UEC); Ubatuba, 24.ix.1978, Gibbs & Joly 8440 (UEC);
Iguape, 21.ix.1929, Hoehne 24269 (A); Ubatuba, 1.v.1977, Joly et al. 6791 (F, UEC); Atibaia, 6.ix.1939, Foster (A, US); Itanhaen, 13.ix.1894, Loefgren & Edwall 11307 (A); Ilha dos Alcatrazes, x.1920, Luederwaldt & Fonseca 11281 (GH); Guarujá, 9.i.1961, Pedersen 5768 (A); Ubatuba, 12.ii.1976, Taroda 2171 (UEC); Guarujá, 13.i.1907, Usteri 11280 (A).

Curiously, *C. aurassaviaa* has never been cited from Brazil. Johnston (1930), in his extensive study of Brazilian Cordias, did not include this species, but in his treatment of *C. verbenacea* he pointed out the close relationship of this latter species to *C. aurassaviaa* and *C. macrostachya*, and Johnston (1935a), in a study of Cordias in NE South America, suggested that *C. verbenacea* should be best treated as a mere forma of *C. macrostachya*.

Subsequently, Johnston (1949b), in a paper treating with the Mexican Varronias, discussed at length the early history of *C. aurassaviaa* and provided a long list of synonyms for this species which included *C. macrostachya*, but with no mention of *C. verbenacea*. In this discussion of *C. aurassaviaa* Johnston (loc. cit.) argued that *C. macrostachya* should be regarded as a "mesophytic phase" of the species (i.e. presumably a shade-form ecotype). In fact, the broader and more membranaceous leaves described for *C. macrostachya* intergrade with the typical narrower and chartaceous leaves of *C. aurassaviaa*.

Unfortunately, the type specimen of *C. aurassaviaa* has not been traced, so that it is not possible to make comparison with the type material of *C. verbenacea*. However, a critical comparison of a range of material referred to *C. aurassaviaa* from the Caribbean with specimens previously referred to *C. verbenacea* or *C. macrostachya* has not revealed any substantial character differences. It is
therefore proposed to treat *C. verbenacea* and *C. macrostachya* as synonyms of the widespread species *C. curassavica*. 
Fig. 14. *C. curassavica*

(a) habit; (b) flower; (c) dissected flower;
(d) dynoecium (short style); (e) gynoecium (long style)/
St. Andrews Botanic Garden [b,c,d]; Reitz & Klein
12 & 1 (G) [e].
Map 2: Distribution of *C. curassavica* (●).

Branchlets hirsute or tomentose. Leaves (4.5)9-13(-18) \times (2-)3-4(-6) cm, usually broadly elliptical, sometimes lanceolate to ovate-lanceolate, base long attenuate, somewhat oblique, apex acute; upper surface generally strigose-hirsutulous or at times hairs rigid-appressed with tubercles usually present, undersurface tomentose; margin irregularly dentate. Petiole (2-)3-7(-9) mm. Inflorescence spicate, elongate and densely flowered, terminal or occasionally internodal; peduncle 2-6 cm. Calyx 4-5.5 mm, teeth with acuminate apex, uniformly hirsute, rarely hirsutulous and then only distally or puberulent. Corolla 507 mm, funnelform to somewhat salverform, lobes more or less deeply oblong and reflexed. Stamens 2-3 mm. Ovary ca. 1.5 mm, style ca. 3 mm in shortstyle and ca. 6 mm in longstyle flowers. Fruits conical.

Type - Brazil; Minas Gerais, Lagoa Santa-Pinhoês, 28.i.1866, Warming (C. holotype).

Distribution: N, WC & SE. Predominantly in Minas Gerais and Goiás; cerrado vegetation. Map 3; fig. 15.

GOIÁS: munic. de Posse, 220 km of Formosa, 8.i.1965, Belém & Mendes 92 (UB); munic. de Porangatu 67 km N of Santa Tereza de Goiás, 25.xii.1969, Eiten & Eiten 9982 (US); munic. de Gurupi, 26.xii.1969, Eiten & Eiten 10014 (US); without precise locality, 1896, Glaziou 21781 (K); 70 km N of Corumbá de Goiás on road to Niquelândia, 20.i.1968, Irwin, Maxwell & Wasshausen 18906 (MO, UB), ca. 15 km S of Niquelândia, 22.i.1972, Irwin et al. 34767 (MO). MINAS GERAIS: between Várzea da Palma and Pirapora, 31.i.1965, Belém & Mendes 439 (UB); without precise locality, 1838, Clausen 221 (P); ca. 25 km
W of Montes Claros, road to Água Boa, 23.ii.1969, Irwin et al. 23717 (UB); ca. 48 km W of Montes Claros, road to Água Boa, 26.ii.1969, Irwin et al. 23944 (UB); Serra do Cabral, ca. 3 km E of Cantoni, 10.ii.1970, Irwin et al. 27723 (K, UB); ca. 5 km SE of Paracatú, 6.ii.1970, Irwin et al. 26212 (UB); Formigas, 1816-1821, St. Hilaire (P); Lagoa Santa, 1869, Warming (P). PARÁ: Belém, 3.xii.1963, Silva 57801 (UB).

The species shows strong affinities to *C. curassavica*, but is easily distinguished by its long acuminate calyx. *C. campestris* also resembles *C. multispicata* in leaf size and dentation, but is easily distinguished since the latter species has the peduncle of the inflorescence decurrent on the petiole of the subtended leaf.
Fig. 15. *C. campestris*

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium (short style); (e) gynoecium (long style)
Eiten & Eiten 10014 (US) [b, c, d]; Irwin et al. 18906 (MO) [c].
Map 3: Distribution of *C. campestris* (●).

Syn.: *C. sessilifolia* var. *macrantha* Cham., *Linnaea* 8: 130 (1833).

Branchlets densely hirsute, mixed with appressed, strigose hairs. Leaves 3.5-8.5 × 1.3-2.3 cm, oblanceolate, base long-attenuate, apex acute; upper surface densely strigose, usually with well developed tuberculae, undersurface densely strigose; margin dentate to crenate. Petiole lacking. Inflorescence capitately globose, congested, terminal or internodal; peduncle 2.5-10 cm. Calyx ca. 11 mm, obconical-campanulate, with teeth prolonged into a long filiform apices; puberulent at the base, densely hirsute towards the apex. Corolla ca. 3 cm, funnelform, the lobes very shallow. Stamens ca. 6 mm, inserted at different levels on the corolla tube. Ovary ca. 21 mm, style ca. 18 mm (longstyle). Fruits cylindrical.

Type - Brazil: indefinite, *Sellow* (K!).

Distribution: WC and S. Brazil, extending westwards to Paraguay where it has been more frequently collected. Map 4; fig. 16.


RIO GRANDE DO SUL: without precise locality, 1816-1821, St. Hilaire, C2 2586 (P); without precise locality, 1816-1821, St. Hilaire C2 2667 (P); without precise locality, 1816-1821, St. Hilaire C2 2697 (P).

INDEFINITE: *Sellow* (K).

Fresenius (1857) described his new taxon based on *C. sessilifolia* var. *macrantha* Cham., which is in fact specifically distinct from the var. *micrantha*, particularly by the conspicuous difference in corolla size (3 × 1.3 cm).
Cordia paucidentata is distinctive among the large-flowered Brazilian Varronia species in having sessile leaves. There is some variation in the indentation of the leaf margin and the shape of the calyx teeth, but otherwise the species is unexceptional. Insufficient material has been available for dissection to determine the length of the style of the shortstyle morph.
Fig. 16. *C. paucidentata*:

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium/Hatschbach 23632 (MO) [b,c,d].

**Syn.**: *Varronia grandiflora* Desv., *Jour. de Bot.* 1: 273 (1809).

Branchlets more or less densely long-strigose or with appressed setaceous hairs. **Leaves** (6-)7-9(-11) × (2.5-)3.5-5(-6) cm; triangular-ovate, base abruptly attenuate, apex acute or slightly acuminate, mucronate; upper surface densely setaceous-strigose, undersurface tomentose; margin crenate. **Petiole** 1-2 cm. **Inflorescence** capitate globose, densely flowered, terminal sometimes internodal; peduncles 4-10 cm. **Calyx** 10-20 mm, cylindrical-campanulate, teeth prolonged into a very long filiform apex; densely appressed setaceous-strigose. **Corolla** 3.5-5 cm, funnelform with a narrow cylindrical tube 8-10 × 2-2.5 mm which expands abruptly to a throat 2-2.7 × 1.2-1.6 cm, lobes very shallow and emarginate. **Stamens** 5-10 mm, inserted at different levels on the corolla tube. **Ovary** ca. 3.5 mm, (short) style ca. 7.5 mm. Fruits cylindrical.

**Type** - Venezuela: Rio Apure, Humboldt & Blonpland 805 (P!).

**Distribution**: In Brazil the species is only known from Pará. Map 4; fig. 17.

**PARÁ**: Cacaual grande, Canal Maroja Netto, Rio Amazonas, 10.ii.1952, Black 52-15617 (A); Cacaual grande Santarém, 19.xi.1949, Murça Pires 1811 (A); Óbidos, xii.1849, Spruce 515 (E, G, K).

*Cordia grandiflora* is distinctive in having the largest flowers of the species of subg. *Varrinia*. The combination of white, funnelform flowers of 3.5-5 cm, setaceous-pubescent calyx with a long filiform apex and triangular-ovate leaves with abruptly attenuate base and crenate margin render this species easily recognisable. Insufficient flowers were available for dissection to determine the length of the longstyle morph.
Fig. 17. *C. grandiflora*

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium/Busby & Squires 14 (GH) [b,c,d].


Type: not traced.


Type - Brazil: Bahia, cachoeira, 1819, Martius (BD isotype) – fide Johnston (1930).


Type - Brazil: Bahia, serv do Assuruá, 1838, Blanchet 2854 (K! BM!).

Branchlets with dense, minute, canescent hairs mixed with sparse, hirsute or appressed, strigose hairs. Leaves 7-11 × 3.5-5.5 mm, ovate to ovate-lanceolate, base obtuse to rounded, slightly oblique, apex acute to acuminate; upper surface strigose and finely puberulent, undersurface sparsely tomentose; margin finely and irregularly serrulate. Petiole 10-20 mm. Inflorescence capitate, globose-congested, terminal or internodal; peduncles 3.5-6 cm. Calyx ca. 8 mm, obconical-campanulate, teeth with apex shortly apiculate, finely and densely tomentose at the apex mixed with sparse strigose or hirsute hairs. Corolla 2.5-3.5 cm, funnelform, lobes very shallow, emarginate. Stamens 2-4 mm. Ovary ca. 4 mm, style ca. 3.0 cm. (longstyle). Fruits not seen.

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1The illustration (t.7) provided by Fresenius (1857), clearly shows its conspecificity with *C. leucocephala.*
Type - Brazil: Bahia, Pouco d'Areia near Jacobina, Blanchet 3880
(G! holotype, P! BM! isotype).
Distribution: NE Brazil. In caatinga vegetation and on sandy soils.
Map 4: fig. 18.

BAHIA: Serra Assurua, Rio Sao Francisco, 1838, Blanchet 2854
(BM, G, K); Pouco d'Areia, vi.1844, Blanchet 3879 (G); BA630 highway,
23 km S of Ara tatu between Vitória da Conquista and Brumado, 13.i.1974,
Harley 15021 (K); 64 km N of Senhor do Bonfim on BA130 highway to
Juazeiro, 25.ii.1974, Harley 16311 (K); 26 km NW of Lagoinha on
side road to Minas do Mimoso, 7.iii.1974, Harley 16904 (K); road
Petrolina-Remanso, 25.iv.1971, Heringer et al. 361 (UB). PARAIBA:
Esperança, vii.1939, Gardner 2265 (BM, K).

The combination of characters minutely serrulate leaf margin,
calyx with felty, whitish pubescence mixed with coarser hairs and
teeth which lack a long, linear apex differenciate C. leucocephala
from the other two related large flowered \textit{Varronia} species,
\textit{C. grandiflora} and \textit{C. paucidentata}.

Although \textit{C. leucocephala} is not a particularly variable taxon,
Fresenius (1857) in his treatment of the Brazilian Cordias described
three splinter species related to this taxon. The present account
agrees with Johnston (1930) in treating these as synonyms of
\textit{C. leucocephala}. As with \textit{C. paucidentata} and \textit{C. grandiflora},
insufficient flowers were available on the specimens studied to permit
dissections to determine the length of the style on both morphs.
Fig. 18. *C. leucocephala*

(a) habit; (b) dissected corolla; (c) calyx;
(d) gynoecium/Eiten & Eiten 10851 (US) [b,c,d].

Branchlets glabrous, puberulent on the young parts. Leaves 9-20 × 2-5 cm, lanceolate elliptic, base acute, apex acuminate to caudate; upper surface glabrous, occasionally sparsely tubercululate, undersurface glabrous; margin entire, undulate. Petiole 3-10 mm. Inflorescence capitate slightly elongate, densely flowered, terminal or internodal; peduncles 4-7 mm. Calyx ca. 7 mm, funnelform, teeth apex acute, glabrous-puberulent. Corolla ca. 2 cm, salverform with lobes deeply divided, wrinkled. Stamens ca. 2 mm and inserted at the top of corolla tube. Ovary ca. 2 mm, style ca. 6 mm. Fruits cylindrical.

Type - Brazil: Bahia, 1834, Blanchet 1739 (DC! holotype, BM! G! K! isotypes).

Distribution: Known only from Bahia. Map 4; fig. 17.

BAHIA: without precise locality, Blanchet 268 (G); without precise locality, 1840, Blanchet 3190 (G); Muritiba, 1847, Blanchet 3986 (G, K, MO); Feira de S. Ana, Blanchet (G); Almadina, 17.vii.1978, Mori, Hage & White 10275 (F).

*Cordia longifolia* is very distinct since it is the only species of subg. *Varronia* which is totally glabrous. It most closely resembles *C. poliophylla*: both species have a funnel-shaped calyx and corolla with a very narrow tube which expands abruptly into a well developed limb with deeply divided lobes, and also stamens with very short filaments inserted in the mouth of the corolla tube. (See also observations under *C. poliophylla*.) It is not known whether the species is heterostylos.
Fig. 19. *C. longifolia*

(a) habit; (b) flower; (c) gynoecium/Mori, Hage & White 10275 (F) [b,c].

Branchlets densely covered with short, incurved hairs. Leaves 7-13 x 1.9-3 cm, lanceolate or elliptical, base acute or cuneate, apex acute; upper surface sub-glabrous, sparsely strigillose or strigose, sometimes tuberculate, undersurface finely and densely minutely tomentose or tomentose; margin sub-entire or very sparsely serrate, usually slightly revolute. Petiole 3-10 mm. Inflorescence capitate globose, occasionally slightly elongate, densely flowered, terminal or internodal; peduncles 2.5-3.5 cm. Calyx ca. 7 mm, funnelform, teeth apex acuminate, puberulent or sericeous-canescence. Corolla 1.5-2 cm, salverform, lobes deeply divided, emarginate. Stamens ca. 2 mm, inserted at the top of corolla tube. Ovary ca. 2 mm, style ca. 8 mm. Fruits not seen.

Type - Brazil: "in silvarum Oceano conterminarum margine et in saepilus inter Victoria et Bahiam": Sellow (GI Phototype).

Distribution: NE Brazil. Known only from Bahia, in forests. Map 4; fig. 20.

BAHIA: between Itiruçu and Maracás, 22.i.1965, Belém & Mendes 227 (UB); Belmonte, 6.vii.1966, Belém & Pinheiro 2468 (UB); Belmonte, 31.i.1967, Belém & Pinheiro 3226 (UB); without precise locality, Blanchet (G); ca. 26 km SW of Belmonte along road to Itapebi, 25.iii.1974, Harley 17396 (K).

*Cordia poliophylla* together with *C. longifolia* differ from the other brazilian species of subg. *Varronia* in having brochydodromous rather than craspedodromous leaf venation. This character gives a marked difference to the appearance of the leaves and the plants as a whole. The flowers in two species are also distinctive because of the deeply divided corolla lobes: in the other large-flowered
Varronias (C. grandiflora, C. leucocephala and C. paucidentata) the corolla lobes are shallow. Furthermore, these latter species have stamens filaments which are inserted at different levels in the corolla tube whereas in C. poliophylla and C. longifolia the stamens are all inserted at the top of the corolla tube.

Because of these features C. longifolia and C. poliophylla stand apart from the other species of subgenus Varronia. However, the they do share)characteristic capitate-globose shortly cylindrical inflorescence and also the pollen grains are 3-porate with reticulate exine.

Insufficient flowering material was available to determine whether C. poliophylla is heterostylos.
Fig. 20. *C. poliophylla*

- (a) habit; (b) flower; (c) dissected corolla;
- (d) gynoecium/Belem & Mendes 227 (UB) [b,c,d].
Map 4: Distribution of *C. paucidentata* (●), *C. grandiflora* (○), *C. leucocephala* (△), *C. longifolia* (■) and *C. poliophylla* (▲).

**Branchlets strigillose.** Leaves 2.5-6.5 × 1.0-2.5 cm; elliptical, base and apex acute; upper surface sparse to densely strigose and conspicuously tuberculate, undersurface densely strigose; margin serrate. **Petiole 1.5 mm.** **Inflorescence** capitate-globose, more or less densely flowered, terminal or internodal; peduncles 1-7 cm. Calyx ca. 6 mm, tubular-campanulate, teeth prolonged in a filiform apex, uniformly appressed strigose. **Corolla** 1.5-1.8 cm, funnelform. The type material is very sparsely flowered and a dissection could not be effected. Johnston (1935) did not give any information with regard to the stamens, ovary and style of this species.

**Type** - Brazil: Minas Gerais, near fazenda Bom Jardim, rio Jequitinhonha, 1817, St. Hilaire Bl 1478 (P! holotype).

**Distribution:** Known only from the type specimen. Map 5.

Although only known from the type collection *Cordia setigera* seems to be a good species. Some specimens of *C. paucidentata* resembles *C. setigera* in leaf shape and distinctly tuberculate upper surface, but the slender habit, and uniformly sparsely strigose calyx of *C. setigera* clearly distinguish it from *C. paucidentata.*


Branchlets densely strigose or hirsute. Leaves 4-9 × 2.5-5.5 cm, generally broadly elliptical or obovate, base obtuse or cuneate, apex obtuse or rounded; upper surface with sparsely to densely appressed setaceous hairs, lower surface very densely villosulous; margin crenate. Petiole ca. 2 mm or lacking. Inflorescence capitate elongate-cylindrical, densely flowered, terminal; peduncles 3-6 cm. Calyx ca. 7 mm, obconical-campanulate, teeth apex acute; puberulent at the base, becoming densely brownish-hirsute towards the apex. Corolla ca. 10 mm, funnelform, lobes very shallow and inconspicuous. Stamens ca. 4 mm. Ovary ca. 3.5 mm, style ca. 5.5 mm. Fruits not seen.

*Type* - Brazil: Goiás, serra de São Pedro, near rio Paranaiba, Pohl 1740 (K1).

Distribution: EC Brazil (the type locality in Goiás State) extending to Paraná, and also, according to Johnston (1980) the SE (São Paulo State) and westwards to Paraguay. A very poorly collected species despite this extensive distribution. Map 5; fig. 21.
PARANÁ: between Tingés and Itararé, 10.xii.1910, Dusén 10936 (GH, K, MO).

*Cordia villicaulis* Fresen. together with *C. villicaulis* var. *tomentosa* Chod. & Hass. were treated by Johnston (1930) as synonyms of *C. sessilifolia* var. *tomentosa* on the grounds that *C. villicaulis* was merely a broad-leaved variety of *C. sessilifolia*. However, although *C. villicaulis* resembles *C. sessilifolia* in general features and floral morphology they can be distinguished by a number of characters: the inflorescence, in *C. villicaulis*, is distinctly elongate, the calyx lacks a filiform apex and the leaves are usually broader (i.e. more than 3 cm wide) and have a crenate margin; in contrast, *C. sessilifolia* has a globose inflorescence, in most specimens the calyx teeth are prolonged in a filiform apex and the leaves are generally narrow (1-2.6 cm wide) and have a serrate margin.

Type material of *C. caaguazuensis* Chod. & Hass. has been examined and since this falls completely within the range of variation of *C. villicaulis* is must be regarded as a synonym of this species. Likewise, it is considered that *C. villicaulis* var. *tomentosa* Chod. & Hass. cannot be sustained as a distinct taxon.
Fig. 21. *C. villicaulis*

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium/Dusem 10936 (MO) [b,c,d].

*C. sessilifolia* var. *micrantha* Cham., *Linnaea* 4: 129 (1933).

Type - not traced.

Branchlets densely hirsute. Leaves 4–10 × 1–2.6 cm, generally narrowly lanceolate but sometimes broadly so, base cuneate or acute, apex acute or obtuse; upper surface usually densely hirsute but in some specimens the hairs become somewhat appressed, undersurface densely hirsute or tomentose; margin irregularly serrate. Petiole lacking. Inflorescence capitate-globose, very rarely slightly elongate, congested, terminal; peduncles 1–5 cm. Calyx ca. 8 mm obconical campanulate, teeth usually prolonged in a filiform apex but sometimes merely long-acuminate, puberulent at the base densely hirsute towards the apex. Corolla ca. 1.3 cm, funnelform, lobes very shallow, emarginate. Stamens ca. 2 mm. Ovary ca. 2 mm, style ca. 4 mm in shortstyle and ca. 12 mm in longstyle flowers.

Fruits cylindrical.

Type - Brazil: Minas Gerais, Quartel de S. Antonio, 1818, Sellow B1562, C.655 (GH! phototype).

Distribution: WC and SE Brazil. In cerrado vegetation. Map 5; fig. 22.

Fig. 22. *C. nessilifolia*

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium/Sellow s/l (f) [b,c,d].

Branchlets generally appressed-setose but occasionally becoming somewhat hirsute with spreading hairs towards the apex. Leaves (2.4-)5.5-7.5(-10) × (1-)2-3(-4) cm, usually obovate or ovate, sometimes lanceolate, base cuneate to long cuneate, apex obtuse to acute; upper surface more or less appressed setose, undersurface tomentose or somewhat villous (rarely, the hairs rigid and bristle-like); margin dentate to serrate or finely serrate. Petiole lacking. Inflorescence capitate clavate, shortly cylindrical or occasionally spherical, congested, terminal or sometimes internodal; peduncles 2-7 mm. Calyx 7 mm obconical-campanulate, teeth with acuminate apex, puberulent at the base, densely hirsute towards the apex. Corolla ca. 10 mm, funnelform, lobes very shallow and emarginate, limb reflexed. Stamens 2-3 mm. Ovary ca. 2 mm, style ca. 4 mm in shortstyle and ca. 9 mm in longstyle flowers. Fruits conical.

Type - Brazil: Goiás, Serra dos Cristais, Pohl 1741 (K!).

Distribution: WC and SE Brazil. In cerrado vegetation. Map 5; fig. 23.

FEDERAL DISTRICT: fazenda Água Limpa, 22.i.1980, Cezar 51 (E, UB); Brasília, 17.ii.1975, Hatschbach et al. 36213 (MO) Brasília, 30.i.1975, Heringer 14445 (UB, UEC); Brasília, xi.1967, Lima 28 (UB); Brasília, 17.x.1965, Sucre 861 (UB); Brasília, x-xi.1971, Taxonomy class of UB 298 (UB); Brasília, 16.x.1977, Taxonomy class of UB 538 (UB). GOIÁS: Rio Cristal, 44 km by road SE of Cristalina, 6.iv.1973, Anderson 8285 (UB); Chico-Lobo-Rio Torto, 19.xi.1894, Glaziou 21779 (G, K, P); Portolândia, 15.ii.1974, Hatschbach 34238 (MO); 3 km W of Cristalina, 3.xi.1965, Irwin, Souza & Santos 9835 (UB); Serra do Rio Petro, 16.xi.1965, Irwin, Souza & Santos 10306 (UB); Serra do Rio Petro, 19.xi.1965, Irwin, Souza & Santos 10545 (UB); Serra dos

*Cordia truncata* seems to be a well delimited species. Some few specimens which have spherical rather than the more typical clavate or shortly cylindrical inflorescence and also lanceolate rather than obovate to ovate leaves approach *C. sessilifolia*. However, these specimens retain the appressed hairy stem and soft, whitish pubescence of the calyx of *C. truncata* in contrast to the distinctly hirsute stem and rigid, brownish pubescence of the calyx of *C. sessilifolia*. 
Fig. 23. *C. truncata*

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium/Thy. class of UB 538 (UB) [b, c, d].
The diagram shows several parts of a plant. It includes a leaf with a scale of 5 cm for reference. The images labeled 'a', 'b', 'c', and 'd' seem to depict different stages or parts of the plant. The diagram appears to be educational, possibly used for botanical study or classification.

Branchlets abundantly appressed strigose. Leaves 2–4 × 0.1–1.6 cm, obovate or elliptical, base long-attenuate, apex obtuse to rounded; upper surface sparsely but uniformly rigid-strigose, usually distinctly tuberculate, lower surface also sparsely and uniformly rigid-strigose; margin serrate. Petiole lacking. Inflorescence capitate globose, more or less densely flowered, terminal; peduncle 2–7.5 cm. Calyx ca. 5 mm, obconical-campanulate, teeth apex shortly subulate; puberulent at the base and appressed rigid-strigose towards the apex. Corolla ca. 1.2 cm, funnelform, lobes emarginate. Stamens 2–3 mm, two of them inserted at a lower, two at an intermediate and one at a higher level. Ovary 1.5 mm, style ca. 6.5 mm. Fruits cylindrical.

Type – Brazil: Minas Gerais, Corinto beyond Retiro, fazenda do Diamante, 14.iv.1931, Mexia 5617 (GH holotype, A, K! GI MO! isotypes).

Distribution: known only from the type collections. Map 5; fig. 24.

*Cordia bracelinae* is a distinctive species because of its much branched low spreading habit and its uniformly short, rigid-strigose leaves.

It resembles *C. paucidentata* in the sparsely dentate leaf margin but not in any other characters. Seemingly heterostylosous but insufficient material to verify this.
Fig. 24. *C. bracelinae*

(a) habit; (b) flower; (c) dissected corolla; (d) gynoecium/Mexia 5617 (G) [b, c, d].
Map 5: Distribution of *C. truncata* (●), *C. sessilifolia* (○), *C. bracteata* (■) and *C. villicaulis* (▲), and *C. setigera* (△).

Branchlets dense hirsute or softly hirsute. Leaves (4-)5-8(-10) x (2.5-)3.5-5(-6) cm, usually broadly ovate, rarely elliptical, base abruptly shortly attenuate, apex rounded or obtuse; upper surface commonly villosulous, but occasionally the hairs become appressed and more rigid, lower surface usually densely tomentose, sometimes hirsute or villosulous, canescent; margin dentate or serrate. Petiole (0.5-)0.7-1.2(-3) cm. Inflorescence capitate-clavate or cylindrical, sometimes spherical, very congested, terminal, peduncles (1.5-)4-7(-9) cm. Calyx 5-6 mm, obconical, glabrous at the base, densely hirsute towards the apex. Corolla 1-12 mm, funnelform, lobes very shallow and emarginate, the limb strongly reflexed. Stamens ca. 4 mm. Ovary ca. 2.5 mm, style ca. 9 mm in shortstyle and ca. 15 mm in longstyle flowers. Fruits cylindrical.

Type - Brazil, locality not given, *Sellow* 5611 (GH! phototype).

Distribution: WC and SE Brazil. In cerrado vegetation. Map 6; fig. 25.


GOIÁS: Chapada dos Veadeiros, 6-7 km E of Alto Paraíso on road to Nova Roma, 7.iii.1973, *Anderson* 6560 (E, MO, UB), ca. 25 km by road SW of Monte Alegre de Goiás, 13.iii.1973, *Anderson* 6997 (E, MO); near Almas, 1839, *Gardner* 3366 (K); without precise locality, *Gardner* 3912 (K); without precise locality, 1841, *Gardner* 3913 (K); Chapada dos Veadeiros, 5 km of Alto Paraíso, 24.i.1979, *Gates & Estabrook* 15 (UB); between Chico-Lobo and Rio Torto, 19.xi.1894, *Glaziou* 21780 (K, P); Chapada dos Veadeiros, Alto Paraíso, 21.xii.1968, *Graziela, M. José & Ana Lima* 820 (UB); Chapada dos Veadeiros, 21.xii.1968, *Harley & Barroso* 11444 (K); Serra Dourada, 19.i.1966, *Irwin, Souza & Santos* 11785 (K, UB); Chapada dos Veadeiros ca. 12 km S of Cavalcante,
9.iii.1969, Irwin et al. 24166 (UB); Chapada dos Veadeiros, 10 km of Alto Paraíso, 18.iii.1976, Semir 993 (UEC). MATO GROSSO: Serra do Roncador, muníc. Barra do Garças, 6.xii.1969, Eiten & Eiten 9776 (US); ca. 1 km SE of km 264, Xavantina-Caximbo road, 19.xi.1967, Philcox, Ramos & Souza 3141 (MO). MINAS GERAIS: without precise locality, 1838, Claussen 222 (GH, P); Caldas, 27.xii.1862, Regnell III 213 (MO); without precise locality, 1816-1821, St. Hilaire C1 298 (P); Lagoa Santa, Warming (P). SÃO PAULO: without precise locality, Breice (P). INDEFINITE: Burchell 6699 (K); Burchell 8300 (K), Lund (GH).

*Cordia calocephala* can be distinguished by the following combination of characters: robust habit, extremely congested, usually elongate, more or less cylindrical inflorescence, calyx teeth prolonged in a long filiform apex, and leaves which are broadly ovate and densely hairy.

*C. villicaulis* resembles *C. calocephala* in the elongate, brownish inflorescence, but the former species is readily distinguished by its sessile or subsessile leaves and absence of filiform calyx teeth.
Fig. 25. *C. calocphala*

(a) habit; (b) flower; (c) gynoecium; (d) dissected corolla/Philcox et al. 3141 (MO) [b,c,d].

Branchlets finely and densely covered by stipitate glands, mixed with sparse, hirsute hairs. Leaves 2.3-5 × 1-2 cm, commonly ovate, base truncate or obscurely cordate, apex acuminate; upper surface strigillose or strigose mixed with an abundant covering of stipitate glands, undersurface sparsely strigose and strigillose, usually with abundant stipitate glands although in some specimens these are restricted to the midrib and veins; margin serrate, rarely subentire. Petiole 3-12 mm. Inflorescence capitate-globose, lax to densely flowered, terminal or internodal; peduncle 6-25 mm. Calyx ca. 5 mm, campanulate with the teeth prolonged in rather long filiform apex, sparsely strigose and densely glandular, the margin barbellate. Corolla ca. 7 mm, funnelform, lobes shallow, inconspicuous. Stamens ca. 2 mm long. Ovary ca. 2 mm, style ca. 3.5 mm. Fruits not seen.

Type - Brazil, indefinite, Douville (DC! holotype).

Distribution: NE Brazil. Map 6; fig. 26.

ALAGOAS: banks of Rio S. Francisco near Penedo, iii.1838, Gardner 1364 (BM, G, K). BAHIA: without precise locality, 1833, Blanchet 1073 (DC); without precise locality, Blanchet 2073 (G); without precise locality, 1856, Blanchet (G).

Flowers seemingly heterostylous but insufficient flowering specimens available to determine this.
Fig. 26. *C. corchorifolia*

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium/Gardner 1364 (G) [b,c,d].


Branchlets finely covered by stipitate glands mixed with some sparse hirsute hairs. Leaves 4-7 × 2-3 cm; ovate, base shortly truncate or slightly cordate, apex acute to acuminate; upper surface densely hirsute mixed with stipitate glands, undersurface less densely hirsute also mixed with stipitate glands; margin irregularly serrate. Petiole 5-15 mm. Inflorescence capitate-globose, congested, terminal or axillary; peduncles 2-3.5 cm long. Calyx obconical-campanulate with the teeth prolonged in filiform apex. No flowers were available for dissection.

Type - Brazil: Minas Gerais, Gandarela, Glaziou 15273 (K! isotype).

Known only from the type collection. *C. caput-medusae* has the distinctive finely stipitate-glandular indumentum which is found only in *C. corchorifolia* and both species also have a similar leaf morphology. *C. caput-medusae* is distinguished by its larger, congested multiflowered inflorescence and the densely hirsute (puberulent in *C. corchorifolia*) calyx.


Branchlets appressed strigose or hirsute, mixed with very short and fine hairs. Leaves 1.5-9.2 × 0.8-3.5 cm, usually ovate or narrow elliptical, base acute to truncate, acute to obtuse; upper surface strigose or hirsute and sometimes distinctly tuberculate, undersurface hirsute; margin serrate to serrulate. **Petiole** 3-4 mm. **Inflorescence** capitate globose, densely flowered, terminal or internodal; peduncle 1-5 cm. **Calyx** 4-6 mm, obconical, teeth prolonged in a filiform apex; puberulent at the base, softly appressed hirsute towards the apex, becoming denser at the margins of the teeth. **Corolla** 6-10 mm, funnelform, very shallow emarginate lobes. **Stamens** ca. 2 mm. **Ovary** ca. 1.5 mm, style ca. 4 mm in shortstyle and ca. 8.5 mm in longstyle flowers. Fruits globose.

Type - Not traced: According to Johnston (1949) the type of *Varronia globosa* Jacq. is not preserved.

Distribution: NE Brazil. In caatinga vegetation. Map 6; fig. 27.

**ALAGOAS:** without precise locality, 1838, Gardner 1367 (K). **BAHIA:** Serra de Itiúba about 6 km E of Itiúba, 19.ii.1974, Harley et al. 16194 (K); 64 km N of Senhor do Bonfim on the BA130 highway to Juazeiro, 25.ii.1974, Harley et al. 16345 (K). **CEARÁ:** Serra do Pocinho, 16.ii.1957, Guedes 421 (UB). **PERNAMBUCO:** without precise locality, ii.1838, Gardner 1367 (K); vicinity of Petrolina, 18.iv.1971, Heringer et al. 94 (UB); Tapera, 30.iii.1932, Pickel 2966 (GH); Tapera, 18.vii.1932, Pickel 3048 (GH, P). **FERNANDO DE NORONHA TERRITORY:** 20.viii.1887, Ridley & Ramage 89 (K).

According to Johnston (1949b) this is a wide ranging species
distributed from Florida, Central America, Caribbean islands and Northern South America. Johnston (loc. cit.) recognised two varieties but only the typical variety occurs in Brazil. The Brazilian material which has been studied in the present account is relatively homogeneous, varying only slightly in the length of the filiform apex of the calyx.
Fig. 27. *C. globosa*

(a) habit; (b) flower; (c) dissected corolla; (d) gynoecium/Harley 16194 (K) [b,c,d].
Map 6: Distribution of *C. globosa* (○), *C. calocephala* (●) and *C. corchorifolia* (■).

Branchlets hirsute, towards the apex densely mixed with fine, whitish hairs. Leaves 8-12 x 3.5-5 cm; ovate to elliptical, base abruptly, short-attenuate, apex acute to acuminate; upper surface densely hirsute-tomentose, undersurface white-floccose, mixed with sparse-hirsute hairs on the veins; margin crenate-dentate. Petiole 5-10 mm. Inflorescence capitate-subglobose to shortly clavate, densely flowered; peduncles 5.5-7.5 cm. Calyx ca. 4 mm, teeth acute apex; whitish-floccose, mixed with brownish stiff-hirsute hairs. Corolla ca. 6 mm salverform, with the lobes strongly reflexed and wrinkled. No flowers were available for dissection and, consequently, it is not known whether the species is heterostylous.

Type - Brazil: Rio de Janeiro, Laranjeiras, Glaziou 4146 (K! isotype).

Distribution: known only from Rio de Janeiro. Map 7.

RIO DE JANEIRO: Copacabana beach, ii.1841, Gardner 5563 (K, BM); Pedreira, vii.1878, Miers 3931 (K); Morro do Flamengo, 1879, Miers (BM).

*C. leucomalla* is quite distinctive on account of its conspicuous leaves (at least 8 x 3 cm) and the whitish, floccose hairs on the undersurface of the leaves and young stems.
22. *Cordia leucomalloides* sp. nov.

"C. *leucomalloa* valde affinis, sed foliis multo minoribus (minus quam dimidium longitudinis) et capitulis axillaribus differt."

Branchlets abundantly hirsute, mixed with dense, fine, whitish hairs, towards the apex. Leaves 2.5-4.0 x 1.0-1.5 cm, ovate to elliptical, base acute, apex obtuse to acute; upper surface tomentose or abundantly soft-hirsutulous, undersurface densely floccose, mixed on the veins with sparse, hirsute hairs; margin crenulate. Petiole 3-4 mm. Inflorescence capitate globose, densely flowered, axillary (same terminal also present), peduncle 6-20 mm. Calyx ca. 3 mm, campanulate, teeth apex acuminate; very densely whitish floccose. Corolla ca. 5 mm, salverform, lobes triangular, strongly reflexed and wrinkled. Stamens ca. 1 mm. Ovary ca. 1 mm, style ca. 3 mm. Fruits not observed. Insufficient material available to determine whether heterostyly is present; flowers examined all homostyloous.

Type - Brazil: Bahia, 6 km from Filadelfia on the BA 385 to Itiuba, 18.ii.1974, Harley 16143.

Distribution: NE Brazil. In caatinga vegetation. Map 7; fig. 28.

PARAIBA: Areia, Escola de Agronomia do Nordeste, 12.vi.1953, Morais 813 (P); Areia, 18.x.1958, Morais 1875 (A).

*Cordia leucomalloides*, from NE Brazil resembles *C. leucomalla* from Rio de Janeiro, and the two taxa are probably vicariads. Although probably closely related, *C. leucomalloides* has been described as a distinct species on account of its similar leaves (less than half the size of those of *C. leucomalla*) and regular presence of axillary inflorescences in contrast to the strictly terminal inflorescences of *C. leucomalla*. 
Fig. 28. *C. leucomalloides*

(a) habit; (b) flower; (c) dissected corolla; (d) gynoecium/Morais 1875 (A) [b,c,d].
23. Cordia harleyi sp. nov.

"C. truncatae capitulis clavatis similis est sed foliis petiolatis et supra minute strigillosis, calicibus minute tomentosis et corolla hypocretiformis statim dignoscenda."

Branchlets minute strigillose, puberulent. Leaves 2.5-4.5 x 1.5-3.5 cm, ovate or ovate-triangular, base truncate, apex obtuse or rounded; upper surface sparsely puberulent and minutely, inconspicuously strigillose, undersurface densely villosulous; margin crenate or dentate. Petiole 4-7 mm. Inflorescence capitater clavate, densely flowered, terminal or internodal; peduncles 2.3-7.0 cm. Calyx obconical, teeth with acute apex, densely and finely minute-tomentose, whitish at the base, brownish at the teeth. Corolla 11 mm, salverform (limb very ample), lobes very shallow, emarginate. Stamens ca. 1 mm. Ovary 2-1.5 mm, style ca. 6.5 mm in shortstyle and ca. 8.0 mm in longstyle flowers. Fruits globose.

Type - Brazil: Bahia, Morro do Chapéu, ca. 8 km SW of the town Morro do Chapéu, to the W of the road to Utinga, 3.iii.1977, Harley et al. 19312 (CEPEC! holotype, K!, E! isotypes).

Distribution: known only from Bahia. Map 7; fig. 29.

BAHIA: Serra do Rio das Contas, Pico das Almas, ca. 25 km NW of the town of Rio das Contas, 22.i.1974, Harley et al. 15409 (K); 19.5 km SE of the town Morro do Chapéu, on the BA 052 road to Novo Mundo, 2.iii.1977, Harley et al. 19241 (K, E). Serra dos Lençóis, munic. Palmeiras, 24.v.1980, Harley 22527 (K); Morro do Chapéu, ca. 8 km SW of the town of Morro do Chapéu, to the W of the road to Utinga, 30.v.1980, Harley et al. 22749 (K, E).

Cordia harleyi is a very distinct species, resembling only
remotely *C. truncata* in the shape of clavate inflorescence. Otherwise they are very much dissimilar, particularly because of the evidently petiolate leaves of *C. harleyi*.

*C. harleyi* is easily recognised by the following combination of characters: the minute and almost inconspicuous pubescence of the upper surface of the ovate leaves, inflorescence clavate, calyx finely minute-tomentose and the salverform corolla with a rather well developed limb.

This species is named after the Kew botanist Raymond Harley who has organised a number of plant collecting expeditions in the NE of Brazil.
Fig. 29. *C. harleyi*

(a) habit; (b) flower; (c) dissected corolla;

(d) gynoecium/Harley 22149 (E) [b, c, d].
24. *Cordia mayoi* sp. nov.

"Species propria, calicis dentibus longiacuminatis et pubescentia sericeo-villulosa canescenti et corolla longissima (ultra 7 mm) tubuloso-cylindrica dignoscenda."

**Branchlets** finely, densely villosulous. **Leaves** 2-6 × 0.8-4.5 cm, ovate, base truncate, apex acute to rounded; upper surface abundantly sericeous-tomentose, canescent, lower surface finely and densely villosulous; margin irregularly serrate. **Petiole** 3-5 mm. **Inflorescence** capitate globose or somewhat elongate, more or less densely flowered, terminal or internodal; peduncle 10-20 mm. **Calyx** ca. 8 mm, campanulate finely and densely canescent sericeous-villosulous, teeth with long acuminate apices. **Corolla** ca. 12 mm, tubular-cylindrical, lobes very shallow. **Stamen** ca. 3 mm. **Ovary** ca. 2 mm, style* ca. 10 mm. Fruits unknown.

**Type** - Brazil: Bahia, 1.5 km of São Ignácio on Gentio do Ouro road, 24.ii.1977, Harley et al. 18983 (CEPEG holotype, K!, E! isotype).

**Distribution**: known only from Bahia. Map 7; fig. 30.

**BAHIA**: Serra do Assurúa, 1830, Blanchet 2909 (G, K); Serra do São Inácio, ii.1907, Ule 7549 (G, K).

The recent collection by Harley et al. agrees with older material collected by Ule in the same locality and from another in Bahia by Blanchet to confirm the status of this new species.

*Cordia mayoi* is characterised by a calyx with long acuminate

*The material with flowers available for dissection has apparently long style flower.
teeth with a sericeous-villosulous indumentum and by a distinctly long tubular-cylindrical corolla, more than 7 mm.

This species is named after the Kew botanist Simon Mayo who has taken part in a number of plant collecting expeditions to NE Brazil.
Fig. 30. *C. mayoi*

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium/Harley 18983 (K) [b,c,d].
Map 7: Distribution of *C. leucomalla* (○), *C. leucomalloides* (△)m
*C. mayoi* (○) and *C. harleyi* (■).

**Syn.:** *Varronia guazumaefolia* Desv., *Jour. de Bot.* 1: 276. (1809).

*C. patens* var. *monocephala* Cham., *Linnaea* 4: 486 (1829).
Type - Brazil: indefinite, Sellow (K BM!).

*C. patens* var. *polycephala* Cham., *Linnaea* 4: 486 (1829).
Type - Brazil: indefinite, Sellow (K!).

Based on *C. patens* var. *monocephala* Cham.

*C. axillaris* var. *gymnocarpa* Johnst., *Contr. Gray Herb.* 92: 35 (1930). Type - Brazil: Minas Gerais, without precise locality, 1840, Claussen (K!).

Branchlets generally densely ferrugineous-hirsute. Leaves (3-5)-9(-13) × (1.5-2.5)-4(-6) cm, elliptical, elliptical-oblung or sometimes ovate, base cuneate, obtuse to rounded, apex acute to acuminate; upper surface usually densely strigose-hirsute, sometimes somewhat strigose-villosulous, usually tuberculate, undersurface tomentose to very densely tomentose; margin evidently to remotely serrate. Petiole (3-)4-7(-12) mm. Inflorescence capitate-globose, sometimes shortly-clavate, densely flowered, axillary or terminal; peduncle (1-)3.5-6(-8) cm. Calyx ca. 4 mm, campanulate, teeth with acute apex; glabrous or puberulent at the base, becoming densely hirsute towards the tip. Corolla 4-5 mm tubular-cylindrical, lobes shallow and inconspicuous. Stamens ca. 2 mm. Ovary ca. 2 mm, style ca. 2.5 mm shortstyle and ca. 4 mm in longstyle flowers. Fruits globose.
Type - Brazil: no locality given, Vandelli 1790 (P. JU!).

Distribution: WC, SE, S Brazil. Banks of rivers, forest margins or cerrado. Map 8; fig. 31.


SÃO PAULO: between Ubatuba & Caraguatatuba, 22.viii.1976, Davis et al. 5884 (E, UEC); Taubaté, 9.ix.1892, Loefgren & Edwall 11313 (GH); Campinas, 24.viii.1977, Yamamoto 5665 (UEC). INDEFINITE: Burchell 5695 (K); Sellow 1564 (GH); Sellow 15 (GH), Sellow (E). [Sellow specimens are probably fragments from a single collection.]

_Cordia guazumaeefolia_ was first described by Desvaux (1809) under the genus _Varronia_, and subsequently accepted as a _Cordia_ by Roemer & Schultes (1819) and Don (1837), although in each case these authors merely repeated the original diagnosis.
A chain of confusion was begun when Chamisso (1829) created two varieties of *C. patens* HBK., var. *monocephala* and var. *polycephala* without realising these taxa were conspecific with *C. guazumaefolia*. Subsequently, De Candolle (1845) relegated *C. guazumaefolia* to a synonym of *C. urticaefolia* and this treatment was followed by Fresenius (1857).

Johnston (1930) treated *C. guazumaefolia* as a synonym of *C. corymbosa* (L.) Don, but he also described a new species, *C. axillaris*, which was based on *C. patens* var. *monocephala* Cham., and also described a new variety of *C. axillaris*, *C. axillaris* var. *gymnocarpa*.

However, after he had the opportunity to study the Desvaux type specimens in the Jussieu herbarium at Paris, Johnston (1935b) recognised *C. guazumaefolia* as a distinct species, to which he relegated his *C. axillaris* var. *gymnocarpa* although in this treatment he maintained without comment *C. axillaris* as a distinct species.

A critical study of exsicatae of this group, including type specimens of *C. guazumaefolia*, *C. axillaris* and *C. axillaris* var. *gymnocarpa* has led to the conclusion that only a single species can be recognised for which the name *C. guazumaefolia* must be used.

Some specimens, particularly from Minas Gerais, have the inflorescence obovate rather than spherical, a variation which is paralleled in other species of subg. *Varronia*.
Fig. 31. *C. guamanecifolia*

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium (short style); (e) gynoecium (long style)/

Davis et al. 59884 (E) [b,c,e]; Loefgren & Idawal
11313 (GH) [d].

Branchlets generally densely ferrugineous-hirsute or rarely with appressed hairs. Leaves (4-)6-9(-16) x (3-)3.5-4.5(-6.5) cm, elliptic or elliptic-oblong, base acute, apex acute to acuminate; upper surface usually scabrous, glabrous except for the midrib, very rarely sparsely appressed-puberulent; undersurface hirsute; margin entire or remotely serrate. Petiole (3-)4-7(-10) mm. Inflorescence usually a raceme of globose, densely flowered capitulae (occasionally of solitary capitulae) axillary; peduncles (1-)3-4(-5) cm, decurrent with the petiole of the subtended leaf. Calyx ca. 3 mm obconical-campanulate, teeth prolonged in a filiform apex; glabrous or puberulent at the base, densely long-hirsute towards the teeth. Corolla tubular-cylindrical, the lobes shallow or inconspicuous. Stamens ca. 2 mm. Ovary ca. 1.5 mm, style ca. 2.5 mm in shortstyle and ca. 4.1 mm in longstyle flowers. Fruits cylindrical.

Type - Bolivia: La Paz, Mapiri, vii-liii.1872, Bang 1530 (NY holotype, K! isotype).

Distribution: N Brazil. Map 8; fig. 32.


AMAZONAS: Esperança, mouth of Rio Javari, Ducke 1129 (MO).

INDEFINITE: Blanchet 2471 (MO).

Specimens of typical *C. buddleioides*, i.e. with the calyx with a conspicuous filiform apex and leaves with the upper surface glabrescent, occur in Peru and Northern Bolivia. In the few collections from North Brazil, these diagnostic characters of *C. buddleioides* lose their conspicuousness with the calyx teeth apex shorter and upper surface of the leaves sparsely hairy. These
brazilian specimens of *C. buddleioides* approach *C. guamaefolia* although this latter species remains distinguishable because of its densely hairy leaf upper surface and distinctly serrate margin. In addition, the two species have different distributions, with *C. guamaefolia* in Central, South and Southeast Brazil and *C. buddleioides* in North Brazil.
Fig. 32. *C. biddleioides*

(a) habit; (b) flower; (c) dissected corolla;

(d) gynoecium (short style); (e) gynoecium (long style)

Herbario Marin 1714 (F) [b, c, d]; Kurzack 2502 (F) [c].
Map 8: Distribution of *C. guamumae folia* (•) and *C. buddleioides* (○).

Syn: *Varronia polypephala* Lam. excl. syn. "Plunkenet t.328 fig. 5?".

Branchlets generally appressed-strigose or strigillose, very rarely hirsute. Leaves 5-9 × 1.5-4.5 cm, ovate to ovate-lanceolate, base acute to rounded, apex acuminate; upper surface usually appressed-strigose, occasionally strigillose or glabescent, usually tuberculate, undersurface finely and minutely tomentose mixed with sparse coarse strigose hairs; margin distinctly to indistinctly serrate. Petiole (3-)4-5(-6). Inflorescence panicles or racemes of relatively small, rather few-flowered glomerules (occasionally solitary), axillary or terminal; peduncles (1-)3-4(-6) cm. Calyx ca. 3 mm, obconical-campanulate, teeth acute, usually appressed pubescent or tomentose. Corolla 3.5-4 mm, tubular-cylindrical, lobes very shallow and inconspicuous. Stamens 1.5-2 mm. Ovary ca. 1 mm, style 1-1.5 mm in shortstyle and ca. 3.5 mm in longstyle flowers. Fruits conical.

Type - not traced.

Distribution: N, NE, WC, SE Brazil. In forest, gallery forest and cerrado. Map 9; fig. 34.

ACRE: munic. Tarauacá, 23.ix.1968, France, Ramos & Farias 7486 (MO);
(US); without precise locality, 1841, Gardner 3368 (E, G, K); ca. 1 km
S of Araguaina, at Rio das Lontras, 15.iii.1968, Irwin, Maxwell &
Wasshausen 21220 (UB); ca. 15 km S of Araguaina, 16.iii.1968, Irwin,
Maxwell & Wasshausen 21277 (UB); ca. 27 km S of Paraíso, 23.iii.1968,
Irwin, Maxwell & Wasshausen 21718 (GH, MO, UB). MARANHÃO: without
precise locality, 12.vi.1909, Lima 2273 (UB). MATO GROSSO;
entroncamento das rodovias Cuiabá-Santarém-Porto Velho, 5.ii.1979,
Silva & Pinheiro 4451 (UB, UEC). MINAS GERAIS: Lavras, 9.xii.1980,
Leitão Filho, Shepherd & Martins 11690 (UEC). PARÁ: Marabá, Rio
Tocantins, 9.vi.1949, Froes & Black 24345 (UB); Santarém, iii.1850,
Spruce (E, G); Taperinha, Santarém, 15.vi.1927, Zerny 882 (W).
RORAIMA TERRITORY: Serra da Lua, 12.i.1969, Prance et al. 9226 (GH,
MO); Rio Mucajai, vicinity of Mucajai airstrip, 13.ii.1971, Prance
et al. 10914 (GH, K, MO); Posto Mucajaí, Rio Mucajaí, 17.iii.1971,
Prance et al. 11076 (GH, MO).

Johnston (1930) in his account of Cordias from Brazil, Paraguay, Uruguay and Argentina treated this species under the name
Cordia corymbosa (L.) Don. The species concept accepted by Johnston for this taxon was a very wide one (some 16 synonyms included under it), and in his use of the name C. corymbosa he followed Urban (1910) who cited Lantana corymbosa L. as a basionym.

However, Johnston (1935a) subsequently realised that the epithet corymbosa as employed by Urban was a later homonym of C. corymbosa (Desv.) Don. In a lengthy nomenclatural discussion Johnston (loc. cit.) traced the history of Lantana corymbosa (see below), and he proposed that the earliest name for the widespread southern Brazilian-Argentinian species was Varronia polycephala Lam. which he transferred to Cordia. Subsequently, however, Johnston (1949a,b) restricted his idea of C. polycephala (Lam.) Johnst. and
excluded a number of taxa: *C. lineata* (L.) R. & S., *C. bifurcata* R. & S., *C. discolor* Cham., *C. urticaefolia* Cham., *C. patens* HBK. and *C. boliviana* Gandog. The criteria employed by Johnston to split his original *C. polycephala* into this series of segregates was basically the nature of the inflorescence (axillary, internodal or terminal) and also geographical distribution.

In the present revision *C. polycephala* has been accepted in the restricted concept as proposed by Johnston (1949a,b) and, accordingly, *C. discolor* and *C. urticaefolia* are treated as distinct species. The extra-brazilian segregate *C. bifurcata* R. & S. seems to be a good species and was certainly accepted as such by Nowicke (1969) in her revision for the *Flora of Panama*. There is no recent reference to *C. boliviana* Gandog. and no specimens assignable to this taxon have been seen.

The remaining segregates split off by Johnston (1949a,b) were *C. lineata* (L.) R. & S. and *C. patens* HBK., both with distributions in the Caribbean, and the complicated nomenclature/taxonomy is partially entangled with *C. polycephala* (Lam.) Johnst.

Lamarck (1791) described *Varronia polycephala* as follows:

"VARRONIA polycephala, v. foliis ovato-lanceolatis, serratis; pedunculis lateralibus; spicis globosis. Ex America. Pluk. t.328. f.5?".

The Plukenet illustration 't.328 f.5', was also referred by Linnaeus (1753) for his *Lantana corymbosa* as follows:

"corymbosa 6. LANTANA foliis alternis, floribus corymbosis. †

Periclymenum rectum, salviae foliis majoribus oblongis mucronatis subtus villosis alternatim sitis, flore 7 fructu minoribus. Sloan. jam. 104. hist. 2. p.83. t.194. f.3. Raj. dendr. 30."
Ulmi angustifoliae facie baccifera jamaicensis, foliis supernae scabris, subtus villosis alternatim sitis, floribus parvis perpusillis, fructu botryoide monospermo. Pluk. alm. 393, t.328. f.5.

Habitat in Jamaica.

Refertur ex fide Sloanei; De floris structura nulla mihi certitudo'.

The illustrations by Plukenet t.328 and Sloane, t.194, depict rather different plants (see fig.33). Johnston (1949a) lectotypified Lantana corymbosa L. by the Plukenet plant and commented that the Sloane plant "most suggested the Cordia polycaphala". However, since it was not possible to transfer Linnaeus Lantana corymbosa to Cordia, Johnston accepted the name Varronia lineata L. as the next available epithet for the species in question. Varronia lineata was a substitute used by Linnaeus himself in 1759 for his L. corymbosa after he had accepted Browne's genus Varronia. In this study, therefore, Johnston (1949a,b) distinguished between Cordia polycaphala (Lam.) Johnst. and Cordia lineata (L.) R. & S.

Stearn (1971), in a study of Jamaican Cordias, reinvestigated the nomenclatural history of C. lineata (L.) R. & S. and Lantana corymbosa L. In this paper, Stearn lectotypified Lantana corymbosa by the Sloane illustration, arguing that Linnaeus has particularly referred to this specimen "refertur ex fide Sloane", and he noted that the Sloane specimen "belongs to the species later named C. polycaphala (Lam.) Johnst.". Stearn also pointed out that Varronia lineata was an illegitimate substitute by Linnaeus for his earlier L. corymbosa and as such could not be transferred to Cordia. He proposed, therefore, a new species C. Linnaei, and thereby a description and type specimen for what was in effect a very old 'species'.
However, whilst studying material in the Paris herbarium, the present author encountered a specimen, in the Humboldt & Bonpland Herbarium, determined as *Cordia patens* from "Caripe". This specimen, which bears a type label, is almost certainly the type specimen of *C. patens* which was described from "Novae Andalusiae, inter Guanaguana et coenobium Caripense".

From the above account, it can be seen that according to Johnston's (1949a) lectotypification of *Lantana corymbosa* L. by the Plukenet illustration this taxon becomes a synonym of *C. patens* HBK., whereas, according to Stearn's dubiously legal relectotypification of *L. corymbosa* by Sloane illustration, *L. corymbosa* becomes a synonym of *C. polycephala*. The argument is an academic one since the epithet *corymbosa* cannot be taken into *Cordia*, but is of some interest because Lamarck cited the Plukenet t.328. f.5. with a query in his description of *Varronia polycephala*.

The Plukenet illustration, showing solitary glomerules in an axillary position, is very similar to *C. linnaei* Stearn and undoubtedly referable to it. The illustration by Sloane represents most of the inflorescence in a position immediately above a leaf, perhaps implying an axillary position, but also with most of the glomerules in a somewhat paniculate arrangement. This plant (in spite of the 'pseudo axillary' inflorescence) resembles *C. polycephala* as here accepted, i.e. axillary or terminal panicles or racemes of glomerules (the glomerules occasionally, one or two in a branch, may be solitary).

Lamarck's use of a question mark for the Plukenet illustration implies that he based his species in something else and doubted whether the Plukenet plant was the same species, but exactly what *Varronia polycephala* as based on is unknown since there is no
specimen labelled *polycephala* in the Lamarck herbarium (IDC microfiche 450-451). This lack of a firm link to a type specimen or illustration is unfortunate since Lamarck's descriptive phrase could apply equally well to a number of Caribbean *Varronia* species. In the final analysis, the use of the name *Varronia polycephala* by Johnston (1949b) and accepted in the present account is based on traditional usage, and because there do not seem to be any good grounds for rejecting the epithet.

Despite the fact that *C. patens* HBK. as represented by the type in Paris (and also by the type of *C. linnaei* Stearn, and other materials cited for this species by Stearn) differs from *C. polycephala* as recognised in Brazil, a detailed study of these taxa throughout their range is still highly desirable. It is possible that such study could reveal that *C. polycephala* s.str. and *C. patens* are geographically vicariants in a wide-ranging species complex.
Fig. 33: Illustration of "Periclymenum rectum, salviae foliis majoribus ..." by Sloane (a) and of "Ulmi angustifolieae, facie baccifera ..." by Plunket (b).
Fig. 34. *C. polycantha*

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium (long style); (e) gynoecium (short style)/
Gardner 3368 (K) [b,c,e]; Zerny 882 (W) [d].
Map 9: Distribution of *C. polycephala* (O) and *C. urticaefolia* (O).

Syn.: *C. hermanniiifolia* Cham., *Linnaea* 4: 489 (1829). Type - Brazil: indefinite, Sellow (K! BM! G!)

*C. hermanniiifolia* var. *caulocina* Cham., *Linnaea* 4: 486 (1829). Type - Brazil: indefinite, Sellow (K!).

*C. salzmannii* DC., *Prodr.* 9: 494 (1845). Type - Brazil: Bahia, without precise locality, 1830, *Salzmann* 377 (DC!).


Branchlets usually appressed strigillose, sometimes hirsute.

Leaves (3-)4-6(7) × (1-)2-4(-4) cm, generally narrowly elliptical, lanceolate or ovate-lanceolate, base acute to rounded, apex acuminate; upper surface appressed strigose or strigillose and tuberculate, undersurface minute and densely minute tomentose mixed with coarse, strigose hairs which vary in abundance; margin usually serrulate, occasionally serrate. Petiole 3-5 mm. Inflorescence usually of small lax panicles, but occasionally with the branches very much reduced and becoming glomerulate, always terminal on the main and side branchlets (occasionally in a branch some axillary or internodal inflorescences may also occur); peduncle 1.5-3 cm. Calyx 3-4.5 mm, obconical-campanulate, teeth with acute apex, puberulent or rigid-tomentose. Corolla 4.5-5 mm, tubular-cylindrical, lobes very shallow, inconspicuous. Stamens 1-1.5 mm. Ovary ca. 1 mm, style ca. 1.5 mm in shortstyle and ca. 4.5 mm in longstyle flowers. Fruits conical.

Type - Brazil: locality not given, Sellow (K!, BM!, G!).
Distribution: NE, WC, SE and S Brazil. In capoeira, restinga, cerrado and forest clearings. Map 10; fig. 35.

BAHIA: without precise locality, Blanchet 841 (W). GOIÁS: Chapada dos Veadeiros, 6-7 km E of Alto Paraíso on road to Nova Roma, 7.iii.1932, Anderson 6586 (E, MO, UB). MINAS GERAIS: Porto Novo, i-.ii.1932, Frambach 103 (GH); Serra do Espinhaço, ca. 27 km of Serro on road to Diamantina, 26.ii.1968, Irwin, Maxwell & Wasshausen 20937 (GH, MO, UB); Caldas, 17.ii.1847, Regnell II 908 (K, MO). RIO GRANDE DO SUL: Porto Alegre, 24.x.1897, Czermak & Reineck 143 (E, G); Porto Alegre, 11.iii.1892, Malme 256 (MO); Osório, 11.ix.1950, Rambo 48758 (MO). RIO DE JANEIRO: Rio de Janeiro, Tijuca, 21-23.vii.1882, Ball (K); Rio de Janeiro, 1768, Banks (A, GH); Magé, 1837, Casaretto 1487 (G); Guanabara, Pedra Branca, 7.iv.1963, Castelhanos 23860 (F); Nova Friburgo, x.1842, Claussen 70 (G); Nova Friburgo, 1818, Curran 730 (GH); Corcovado, 18.ii.1862, Glaziou 206 (P); without precise locality, 1838, Martius 125 (E, K, MO); Copacabana, vii.1878, Miers 3674 (K); without precise locality, 21.vii.1873, Mosén 234 (MO); Baia de Sepetiba, Ilha Furtada, 2.ii.1967, Sucre 1806 (UB); Alto da Boa Vista, 26.ii.1967, Sucre 1981 (UB); Itaperuna, faz. S. José, Strang 858 & Castellanos 26147 (K); without precise locality, 1858, Weddell 393 (G). PARANÁ: Serra do Mar, Volta Grande, 27.vii.1914, Dusén 756 a (MO); Jacarei, 28.ix.1908, Dusén 6624 (GH, K, MO); Adrianópolis, 26.ix.1962, Hatschbach 9282 (K); near Altonia, muníc. Xambrê, 10.xii.1965, Hatschbach, Lindeman & Haas 13310 (A); road from Praia do Leste to Morretes, 3.x.1966, Lindeman & Haas 2632 (K).

SANTA CATARINA: without precise locality, 1832, Gaudichaud 161 (G); without precise locality, iv.1869, Mueller 306 (K); Camp do Massiambú, Palhoça, 16.vii.1963, Reitz & Klein 837 (UB); Campo do Massiambú, Palhoça, 24.ix.1963, Reitz & Klein 1044 (UB); Ibirama, 18.vii.1956,
Cordia discolor is rather variable in leaf size and shape and pubescence, and this variation has been the basis for a number of 
segregate taxa: C. hermanniaefolia Cham., C. hermanniaefolia var. 
calyicina Cham., C. salzmanni DC. and C. salzmanni var. lanceolata 
Fresen. On the basis of isotypes and other material studied these 
are all considered to fall within the range of C. discolor.
Fig. 35. *C. discolor*

(a) habit; (b) flower; (c) dissected corolla;

(d) gynoecium (short style); (e) gynoecium (long style)/

Reitz & Klein 4952 (A) [b, c, d]; Tweedie 981 (L) [e].
Map 10: Distribution of *C. discolor* (●).


*V. corymbosa* Desv., *Jour. de Bot.* 1: 275 (1809).


Branchlets appressed setulose, frequently hirsute. Leaves 3.2-6.5 x 1.7-3 cm, ovate, ovate-lanceolate to elliptic-oblong, base obtuse or somewhat rounded, apex acute to acuminate; upper surface usually appressed strigose and minute strigillose, tuberculate, undersurface finely and minutely tomentose mixed with abundant strigose hairs; margin distinctly to inconspicuously serrate. Petiole (3-)4-6(-7) cm. Inflorescence scropioid-corymbose, lax or more or less glomerulate, internodal, peduncles 1.5-4 cm. Calyx 3-3.5 cm, obconical-campanulate; teeth with acuminate apex, usually densely setulose, occasionally puberulent. Corolla 3-4.5 mm, tubular-cylindrical with shallow or inconspicuous lobes. Stamens 1-1.5 mm. Ovary ca. 1 mm, style ca. 3 mm in shortstyle and ca. 4 mm in longstyle flowers. Fruits ovoid

Type: type specimen not traced.

Distribution: NE, SE & S Brazil. Map 11; fig. 36.


This species was described by Jacquin (1797) as *Varronia monosperma* but was subsequently illegally renamed by Desvaux (1807) as *Varronia corymbosa* on the grounds that Jacquin's epithet referred to an attribute shared by all species of *Varronia*.

Don (1837) transferred Desvaux's *Varronia corymbosa* to *Cordia*, apparently unaware that Roemer & Schultes (1819) had previously transferred *Varronia monosperma* to *Cordia*.

Johnston (1935a) relegated *C. monosperma* (Jacq.) R. & S., together with a number of other species epithets, as synonyms under his wide concept of *C. polycophala* (Lam.) Johnst., but subsequently, (Johnston 1949b) he referred *C. monosperma* to *C. urticaefolia*. Johnston seems to have misinterpreted *C. monosperma* (see discussion under *C. urticaefolia*) since this appears to be a distinct species which agrees well with the original illustration provided by Jacquin, i.e. with the inflorescence clearly internodal with patent peduncles.

Curiously, however, Jacquin (1797) cited his species as originating from Caracas. No material has been seen from northern South America.
Fig. 36. *C. monosperma*

(a) habit; (b) flower; (c) dissected corolla;
(e) gynoecium (short style); (e) gynoecium (long style)/

Gibbs et al. 8215 (UEC) [b,c,e]; Usteri 11307 (CH) [d].
Map 11: Distribution of *C. monosperma* (○).

Branchlets densely to very densely hirsute-villose. Leaves 4–8 x 2–3.7 cm, commonly ovate, sometimes broadly oblong-elliptical, base obtuse, apex acute to acuminate; upper surface usually hirsute-tomentose, regularly appressed-setose or strigose, tuberculate, lower surface sparsely to densely hirsutulous; margin serrate. Petiole (3–)4–5(–6). Inflorescence scorioid-corymbose, lax or more or less glomerulate, axillary; peduncle 1–4.5 cm. Calyx 3.5–4 mm, obconical-campanulate, teeth apex acute, densely hirsute. Corolla 4.5–5 mm, lobes very shallow or inconspicuous. Stamens 1.5 mm. Ovary 1–1.3 mm, style ca. 2 mm in shortstyle, ca. 3.7 mm in longstyle flowers. Fruits conical.

Type: Chamisso (1829) - "E Brasilia aequinocialimisit Sellowius specimina paucha, male servata, foliis ut plurimum, amissis e ramis superioribus florifera ex inferiori fructifera". Brasilia tropica Sellow - Photo (G!). As a duplicate from the Berlin Herbarium: "Rio de Janeiro (1814–15), Sumidoro, Ex reliqui Sellowianis IB 397" (P!). See discussion below.

Distribution: SE, S Brazil. Map 9; fig. 37.


*Cordia urticifolia* has been previously treated by Johnston (1930) under his wide concept of *C. corymbosa*, subsequently regarded as *C. polycephala* (see discussion under this taxon). Johnston (1949b)
split this broadly conceived *C. polycephala* and revalidated *C. urticaefolia* stating that it "is a coarsely strigose representative of the group in Brazil and Paraguay". Unfortunately, he seems to regard *C. urticaefolia* as having an "extra-axillary inflorescence" which is a mistake, since Chamisso, the author of the species, described the inflorescence in an axillary position. This point of regarding the inflorescence as "extra-axillary" led him to confuse the present species with *C. monosperma*. Probably influenced by Johnston's comments, Smith (1970), in his treatment of *Cordia* for the *Flora Catarinensis*, included present species under *C. monosperma*.

In agreement with Johnston (1949), *C. urticaefolia* has been treated as a separate species in this account but one characterised by a clearly axillary inflorescence. This decision was confirmed by study of a specimen which most likely was that seen by Chamisso to describe his *C. urticaefolia*.

Apart from being clearly axillary, the inflorescence is characteristically born on a rather robust somewhat straight peduncle, and also it is generally lax, sometimes glomerulate, but never capitate, but rather of scorpioid -corymbose type. The peduncle bifurcates two or three times in relatively well developed branches.
Fig. 37. *C. actinophylla*

(a) habit; (b) flower; (c) dissected corolla;
(d) gynoecium (short style); (e) gynoecium (long style)/
Sucre 1190 (US) [b, c, d]; Irwin 3053B (US) [e].
Excluded or doubtful species.


According to Johnston (1935b), this taxon is a well marked *Varronia* species with the large corolla similar to that of a remotely related species, *C. paucidentata*.

Apparently De Candolle (1845) based this species on *Varronia macrocephala* Nees et Mart. but he did not provide an accurate citation to its publication ('*V. macrocephala* Nees et Mart. act. n. cur. xi. p.8').

Johnston (1935b) mentioned that the type specimen is at Brussels, but he did not refer to this specimen or cite any other material for this species. Unfortunately, it was not possible to obtain this anonymous specimen for study and no other specimen which fits the original description by De Candolle (1845) or that by Johnston (loc. cit.) was encountered among the exsiccate available for study in the present revision.


Rizzini (1974) characterised this species by its crenate leaves and described the inflorescences as "globose aggregate cymes disposed in lax panicles". In his comments he pointed out that *C. crenatifolia* approached *C. salsmanni*, *C. discolor*, *C. hermanniaefolia* and *C. urticaefolia*. All those taxa, as discussed previously under the appropriate species, are part of the *C. polycephala* complex (sensu Johnston, 1935a). It is possible, therefore, that *C. crenatifolia* Rizz. is merely a variant of *C. polycephala* (see description). However, the type specimen of this taxon, which is apparently preserved at The Botanical Garden of Rio de Janeiro will have to be studied in order to decide if it constitutes a


These two species described by Fresenius (1857) were given as dubious synonyms of *C. superba* by Johnston (1930), who mentioned that he had inferred this status entirely based on the published descriptions of these two taxa. Types of either species have not been traced.


Johnston (1930) studied the type material at Berlin and recognised this species. He noted that *C. acutifolia* was related to *C. sellowiana*. No material which could be undoubtedly referable to *C. acutifolia*, however, was encountered during the course of the present study.


As previously discussed by Johnston (1930), the illustration of *C. tetraphylla* provided by Aublet (1775) does not represent a member of the genus *Cordia*. 
Appendix

Methods employed in pollen analysis of Cordia species.

The pollen grains of the studied species were taken from well developed buds of herbarium specimens which are listed below:

subg. Varronia

1. C. multiopicata  Burchell 9987 (K)
2. C. curassavica  Botanic Garden, University of St. Andrews
3. C. campestris  Irwin et al. 18906 (MO)
4. C. schomburgkii  Prance et al. 9765 (MO)
5. C. truncata  Tax. class of UB 538 (UB)
6. C. calocephala  Eiten & Eiten 9776 (US)
7. C. harleyi (L)  Harley et al. 19241 (E)
8. C. harleyi (B)  Harley et al. 22749 (E)
9. C. buddeioiides  Beck 1667 (E)
10. C. guanumaefolia  Loefgren & Edwal 11313 (GH)
11. C. polycephala  Gardner 3368 (K)
12. C. discolor  Gibbs et al. 6667 (UEC)
13. C. monosperma  Gibbs 82/5 (UEC)
14. C. globosa  Pickel 2966 (GH)
15. C. oorchorifolia  Gardner 1364 (DC)
16. C. mayoi  Harley et al. 18983 (E)
17. C. leucoccephala  Eiten & Eiten 10851 (US)
18. C. grandiflora  Rusby & Squires 14 (A)
19. C. poliophylla  Belem & Pinheiro 3226 (UB)

sect. Myxa

20. C. exaltata  Maguire et al. 56038 (P)
21. C. lomatoloba  Krukoff 5497 (K)
22. *C. magnoliifolia* Hatschbach 14127 (F)
23. *C. searcefolia* Prance et al. 10381 (MO)
24. *C. sellowiana* Leitão Filho 10091 (UEC)
25. *C. sericocalyx* Smith 3049 (MO)
26. *S. silvestris* Hatschbach 33779 (MO)
27. *S. sprucei* Ducke 116 (US)
28. *C. tetrandra* Prance et al. 4092 (F)
29. *C. toquere* Prance et al. 4336 (U)
30. *C. trachyphylla* Belem 3843 (F)
31. *C. triochlada* Gerht 7979 (F)

sect. *Cerascanthus*

32. *C. glabrata* (L) Hatschbach 32456 (MO)
33. *C. glabrata* (S) Maguire et al. 56118 (MO)
34. *C. goeldiana* (L) Ducke 2345 (US)
35. *C. goeldiana* (S) Prance et al. 1492 (F)
36. *C. insignis* (L) Ratter et al. 1267 (E)
37. *C. insignis* Irwin et al. 16619 (F)

The sample for each species was acetolyzed according to Erdtman (1952). Pollen walls of *Cordia* species were found to be very fragile and a minimum acetolysis time was necessary. Even so, many grains were found to have collapsed walls. For the purpose of observation and measurements of the polar and equatorial diameters by light microscopy, samples of grains were mounted on slides in glycerol jelly and the coverslip sealed with paraffin wax (Erdtman, 1952). The measurements of the polar and equatorial diameters were taken from 25 pollen grains, for each diameter, of each sample.

With samples for observation with the SEM the acetolysed pollen
grains were transferred to ca. 5 ml of absolute ethanol and a
droplet of absolute ethanol containing a suspension of pollen grains
was deposited on the surface of an SEM stub and allowed to air
dry. Grains were then coated with gold in a conventional vacuum
coating unit and observed at various magnifications in a Cambridge
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Abstract

The present study consists of a taxonomic revision of the genus *Cordia* in Brazil with particular emphasis on the *Varronia* group.


A synopsis of the group, together with keys for the identification of Brazilian species is provided for subg. *Myxa*, whilst subg. *Varronia* is revised in detail, with a key, species descriptions and distribution maps for all Brazilian species. In these two subgenera, 65 species in Brazil are recognised.

In parallel to the taxonomic studies, a survey of pollen morphology by means of light and scanning electron microscope is presented together with an assessment of other taxonomic parameters such as anatomy, cytology, reproductive biology and comparative morphology.
REFERENCES


Williams & Norgate. P.574-581.


