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BORAGINACEAE

(H. Riedl, Vienna)[1]

Boraginaceae Juss., Gen. Pl. (1789) 128 ('*Borragineae*'); Brand in Engl., Pflanzenr., fam. IV.252 (1921) 1–183 (*Cynoglosseae*); ibid. (1931) 1–236 (*Cryptantheae*); Heine in Fl. Nouv.-Caléd. 7 (1976) 95–118; I.M. Johnston, Contr. Gray Herb. 73 (1924) 42–73; Ridl., Fl. Malay Penins. 2 (1923) 438–442; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 687–698; Van Royen, Pac. Sc. 29 (1975) 79–98.

Trees, shrubs, subshrubs, woody climbers, perennial or annual herbs usually covered by hairs or bristles on the herbaceous parts, woody species sometimes entirely glabrous. *Leaves* alternate, very rarely opposite (in *Tournefortia*), exstipulate, undivided, usually entire, in a very few species serrate, with reticulate venation of which only the main nerves are clearly detectable in most cases. *Inflorescence* either a simple cyme or compound, cymes arranged dichotomously or in racemes or panicles, with or without bracts, terminal or lateral, sometimes single flowers in the axils of upper leaves. *Flowers* hermaphroditic, rarely unisexual and plants monoecious, composed of calyx and corolla, pentamerous, rarely tetramerous, actinomorphous, in some genera slightly zygomorphous. *Calyx* campanulate to cup-shaped, lobes entirely free or more or less coherent, sometimes accrescent or spreading after flowering, sessile or distinctly stalked. *Corolla* coherent in lower part (tube), lobes free, erect or spreading in the upper part (limb), with an intermediate, gradually widening zone (throat), tubular, campanulate to funnel-shaped or rotate, lobes usually imbricate in bud, rarely valvate, bent into the throat (in some *Heliotropium* spp.) or contorted (in *Myosotis*). In many genera, scale-like invaginations (fornices) present in the throat. In some genera, a basal nectary ring, scale-like appendages (that are not hollow invaginations) or variously distributed hairs inside the corolla present. *Stamens* of the same number as corolla lobes, alternating with them, included in or exserted from the corolla; anthers sessile or on distinct filaments, sometimes with a sterile tip of connective tissue or produced to an awn-like structure, awns of one flower twisted or not, anthers bilocular, dorsally fixed to the corolla or the filament, opening longitudinally. *Ovary* superior, often fixed either to a disc-like base or base produced to a conical or pyramidal structure (gynobasis), bicarpellate as a rule, undivided, entire or with four deep furrows, breaking into two biovulate halves or into four uni-ovulate mericarps ('nutlets'), sometimes part of the locules aborted, rarely a greater number of carpels developed (e.g., in *Trigonotis procumbens*); placentation axillary; ovules erect or nearly horizontal, rarely pendent. *Style* single, either terminal on the undivided ovary or free at last on top of the 4-partite ovary, or fixed basally on the disc-like base between the nutlets or apically on the conical to pyramidate gynobasis, undi-

1) With contributions by: P. Baas, Leiden (vegetative anatomy), R.W.J.M. van der Ham, Leiden (palynology), R. Hegnauer, Leiden (phytochemistry and chemotaxonomy). Most drawings are by Ms. N. Spitteler; origin of photographs is as indicated.

vided or once to twice forked, sometimes cleft nearly to the base; stigma absent or disc-to cushion-shaped terminating the style, or (in *Heliotropium* and *Tournefortia*) forming a ring round the style at various levels (for convenience' sake the ring together with the terminal part of the style above the ring is called stigma as a rule); heterostyly rather frequent (in groups outside Malesia). *Fruit* drupaceous or a berry or divided into 2–4 mericarps surrounded by a hard outer wall, sometimes adherent to the style and separating with an awn; surface smooth, warty, or rugulose, often tuberculate or spiny, sometimes divided into a disc-like outer and a convex inner side, the outer disc surrounded by a thickened margin or not, sometimes glochids present on the whole or certain parts of the surface or nutlets winged. *Seeds* usually without albumen.

DISTRIBUTION

About 100 to 115 genera with a total of about 2,400 species in all climatic regions of the earth. The woody genera of subfamilies *Cordioideae*, *Ehretioideae* and *Heliotropioideae* are predominant in tropical and subtropical regions, *Heliotropium* is widespread in tropical and temperate regions, while herbs and subshrubs belonging to *Boraginoideae* are most numerous in temperate regions, in the tropics mainly confined to higher altitudes or growing as weeds and also represented in the arctic with a few species (involves only *Boraginoideae*).

In the Malesian region, 12 genera are indigenous, two more introduced. Of these, *Crucicaryum* is of rather doubtful value and only known from one collection, which has been lost. *Pteleocarpa*, sometimes regarded as a member of *Boraginaceae*, is not included in this family by the present author. The number of species acknowledged in this account, is 77, of which 64 or 65 are indigenous, the other 12 or 13 having been introduced either for economical and/or ornamental uses or as weeds.

HABITAT

Boraginaceae are widespread in a great number of different habitats from sandy sea shores to mountain forests, wet meadows, desertic or semidesertic regions and stony slopes. In tropical countries, they are absent from lowland rain forests as a rule as well as from vegetation types derived from them. Subfamily *Boraginoideae* is confined to mountainous areas at higher altitudes in the tropics and subtropics as mentioned above. Several species are introduced into new areas of distribution as weeds.

ECOLOGY

Pollination is performed by insects of various groups in a great majority of cases though special adaptations to particular pollinators are lacking. Faucal appendages prevent insects with a short proboscis from pollinating the flowers in many genera, however. These appendages serve as guide to the nectar in the basal part of the corolla. Selfing is observed in a number of taxa, but is prevented by heterostyly in others. Heterostyly is combined with self-incompatibility as a rule, in some genera also with pollen dimorphism. In large-flowered *Cordia* species bats may act as pollinators.

There are several ways of dispersal found within the family. Nutlets bearing glochids are well adapted to epizoochorous dispersal. Comparatively small, hard nutlets are eaten by birds and transported in their digestive tract over longer or shorter distances, while the fruits of *Cordia* are partly digested by mammals and the endocarp is excreted in a viable state. Species of the sea coast such as *Tournefortia argentea* with a spongy pericarp are dispersed by seawater. Winged nutlets are transported by the wind. The same is true sometimes in plants with single surviving nutlets that are shed together with the enlarged calyx.

FOSSILS

There are only a few records of pollen of *Cordia* and *Tournefortia* from the Oligocene and Miocene from Mexico, Puerto Rico and the Marshall Islands. Nutlets of still extant and of extinct genera have been reported from the Miocene. Among the latter, epecially *Prolithospermum* is of interest for the phylogeny of present-day *Boraginaceae* as demonstrated by Johnston (1954).

Literature: Gabel, M.L., Amer. J. Bot. 74 (1987) 1690–1693. — Graham, A. & D.M. Jarzen, Ann. Missouri Bot. Gard. 56 (1969) 308–357; ibid. 63 (1976) 787–842. — Johnston, I.M., J. Arnold Arbor. 35 (1954) 1–81.

MORPHOLOGY AND ANATOMY

Hairs — Hairs are among the most generally distributed features in the family. Unicellular hairs are always present, but they are not the only type of hairs in many species. Typical for unicellular hairs are agglomerations of calciumcarbonate or cystoliths in their lumen. To maintain their flexibility, there are various devices, most often a specific distribution of thin and thickened segments of the cell wall. In many cases, most characteristically in members of tribe *Lithospermeae*, the hairs are surrounded by one to several circles of so called 'accessory cells' with calcified cell walls, that may also be different in the ratio of length to width from other epidermal cells. Widespread are bristle-like hairs with one longitudinal series of cells the terminal cell of which may be horizontal or oblique. These are glochids mainly found on fruits in order to attach them to the fur of animals. Other types of hairs less common are capitate hairs which are characterized by undivided heads in *Boraginaceae*, stellate hairs and hairs composed of more than one series of cells.

Literature: Hummel, K. & K. Staesche, Verbreitung Haartypen. In: Handb. Pflanzenanat., ed. 2, IV, 5 (1962).

Inflorescence — The most peculiar morphological feature of *Boraginaceae* is their inflorescence, which has sometimes been called 'boragoid'. It is sympodial with a straightened axis. The main axis is terminated by a single flower. From the axil of the uppermost leaves one or two side branches originate, which in turn are terminated by a flower. In *Boraginaceae*, either single bracts are developed or bracts are utterly suppressed. The composite axis of the inflorescence is continued by a branch originating from the axil of

the bract if present. This is not obvious in most cases, however, as the true origin of the side branch is obscured by concaulescence, that means, the two axes are connate in part. In most members of *Heliotropioideae* and *Boraginoideae* at least, the flowers are all directed to one side, so that the resultant inflorescence is scorpioid at least when young, the terminal flowers being arranged in a whorl. Morphologically, this type of inflorescence can be derived from that of many *Solanaceae*, in which normally two leaves or bracts are developed at the point of origin of the side branch.

Literature: Troll, W., Prakt. Einf. Pflanzenmorph. 2 (1957) 357–361.

Fruit attachment — While the undivided or divided fruits are attached to the receptacle and separate from it at maturity as a rule in *Cordioideae*, *Ehretioideae* and *Heliotropioideae*, in *Boraginoideae* part of the outer layers of the wall of the carpel remains coherent with the receptacle, so that at maturity the wall is split. Sometimes, these outer tissues form a conical to subulate structure in the centre between the separating nutlets, that bears the style and is called gynobasis by most authors. It has wrongly been interpreted as part of the receptacle.

Literature: Hilger, H., Bot. Jahrb. Syst. 105 (1985) 323–378.

Anatomy of the nutlets — The ovary of *Boraginaceae* is supplied by 10 vascular bundles, which may be modified in relation to special morphological features of the nutlets, such as wing formation. The wall of the nutlets displays a constant sequence of a number of distinct layers. The outermost single-celled layer or exocarp produces the various types of sculpturing on the surface and may be multilayered in the protuberances thus formed. In *Lithospermeae* it consists of palisade-shaped sclereids. The wall thickenings are typically undulated. In most groups the following mesocarp is composed of parenchymatous cells, while in *Lithospermeae* there is an outer part of elliptic sclereids in several layers and an inner parenchymatous part. In *Trichodesma*, the innermost layer is thick-walled. In some groups, especially *Cynoglosseae*, the endocarp has U-shaped thickenings, while it is thin-walled in most other groups. It is always single-layered. The seed coat itself consists of thin-walled cells covered by a cuticle or not.

Literature: Lawrence, J.R., Amer. J. Bot. 24 (1937) 433–444. — Roth, I., Encycl. Plant Anat. 10/1 (1977) 330–336 (earlier literature is reviewed in detail in this publication).

VEGETATIVE ANATOMY

(P. Baas)

Leaf anatomy — The leaf anatomy of the Malesiana *Boraginaceae* is very poorly known. The account given below derives from the general family survey by Metcalfe & Chalk (1950), with additional data from Inamdar & Patel (1973), Patel & Inamdar (1971), and Uphof et al. (1962).

Indumentum diverse, but typically including unicellular hairs containing cystoliths ('boraginaceous hairs', causing the typical roughness of the leaf surface); non-lithocyst

unicellular and uniseriate hairs also occur as well as branched multicellular hairs (*Cordia* p.p.) and short- or long-stalked glandular hairs with unicellular heads (e.g. in *Coldenia*, *Cordia* p.p., and *Heliotropium*). Stomata usually anomocytic, but anisocytic, paracytic and diacytic types also occur, often in the same leaf, as well as stomata with a single subsidiary cell. Mesophyll isobilateral or dorsiventral, occasionally including sclereids in *Cordia* spp. Vascular bundles of the veins embedded in the mesophyll or vertically trancurrent through sclerenchymatous bundle sheath extensions in *Cordia* p.p., *Ehretia*, *Heliotropium* p.p., and *Tournefortia*. Vascular system of midrib and petiole ranging from a single strand to a cylinder of vascular bundles enclosing medullary bundles. Crystals usually present as either crystal sand, solitary crystals or clusters and druses.

Wood anatomy — For a full bibliography on the wood anatomy of *Boraginaceae*, see Gregory (1994). Selected references for Asian *Boraginaceae* are Baas et al. (1984), Burgess (1966), Gottwald (1982, 1983), Heubl et al. (1990), Ilic (1991). Kanehira (1921), Metcalfe & Chalk (1950), Miller (1977), Moll & Janssonius (1926); Pearson & Brown (1932), Sudo (1963, 1988) and Versteegh (1968). Only the wood anatomy of *Cordia, Ehretia, Pteleocarpa,* and *Tournefortia* is well documented; that of the other Malesian genera (mainly herbaceous ones) is very poorly known.

Growth rings range from absent to distinct (and are then marked by thick-walled latewood fibres, marginal parenchyma, and/or ring-porosity). Vessels mostly diffuse; exclusively solitary in *Pteleocarpa*; solitary and in radial multiples in other genera, latewood vessels in *Ehretia* also in clusters and in an ulmiform to dendritic pattern. Perforations all simple, or with sporadic reticulate plates in *Cordia* spp. Intervessel pits vestured (*Pteleocarpa*) or non-vestured (other Malesian genera as far as known), alternate; vessel–ray and vessel–parenchyma pits similar but half-bordered or (partly) enlarged or even perforated in *Cordia* p.p. Helical thickenings present in some narrow vessels of *Ehretia*. Vasicentric tracheids present in *Ehretia*. Fibres either with distinctly bordered pits (*Pteleocarpa*) or with minutely bordered pits (other genera), mostly non-septate, but some septate fibres present in *Cordia* p.p. and *Ehretia* p.p. Parenchyma abundantly paratracheal to banded in *Cordia*, predominantly apotracheal and diffuse-in-aggregates in *Ehretia*, narrowly banded and paratracheal in *Tournefortia*, and in fine unilateral paratracheal lines in *Pteleocarpa*. Rays (1–)2–3-seriate in *Pteleocarpa* and *Tournefortia*, up to 4–6-seriate in *Cordia* and *Ehretia*, heterocellular with few rows of square to upright marginal cells to homocellular in some species of *Cordia* and *Tournefortia*. Crystal sand and/or prismatic crystals in ray cells, axial parenchyma and/or tyloses of *Cordia* p.p. Heubl et al. (1990) also recorded clustered crystals in the wood of some taxa but probably only observed them in pith or bark and not in the secondary xylem. Parenchyma and fibres (weakly) storied in *Cordia* p.p. and *Tournefortia*.

Taxonomic note — As emphasised by Gottwald (1982) the genus *Pteleocarpa* is wood anatomically aberrant in the *Boraginaceae* on account of its solitary vessels, fibre pitting (fibre-tracheids) and parenchyma distribution, supporting the exclusion of this genus from the *Boraginaceae* (cf. Veldkamp 1988). As demonstrated by Gottwald (1983),

Heubl et al. (1990) and Patel & Inamdar (1971) the anatomical diversity within the *Boraginaceae* is of great, yet largely untapped, systematic potential.

References: Baas, P., Lee Chenglee, Zhang Xinying, Cui Keming & Den Yuefen, IAWA Bull. n.s. 5 (1984) 45–63 (*Carmona,* wood anatomy). — Burgess, P.F., Timbers of Sabah, Sabah For. Rec. No. 6 (1966) (*Cordia,* wood properties). — Gottwald, H.E., IAWA Bull. n.s. 3 (1982) 161–165 (*Pteleocarpa,* wood anatomy); IAWA Bull. n.s. 4 (1983) 161–178 (*Cordioidieae,* wood anatomy). — Gregory, M., Bibliography of Systematic Wood Anatomy of Dicotyledons (1994). — Heubl, G.R., J.C. Gaviris & G. Wanner, Bot. Jahrb. Syst. 112 (1990) 129–165 (crystals). — Ilic, J., CSIRO Atlas of hardwoods, Crawford House and CSIRO, Melbourne (1991) (*Cordia. Ehretia, Tournefortia*). — Inamdar, J.A. & R.C. Patel, Feddes Repert. 83 (1973) 473–488 (hairs). — Kanehira, R., Anatomical characters and identification of Formosan woods. Govt. Formosa, Taihoko (1921) (*Cordia, Ehretia*). — Metcalfe, C.R. & L. Chalk, Anatomy of the Dicotyledons (1950). — Miller, R.B., IAWA Bull. 1977/3 (1977) 43–48 (vestured pits). — Moll, J.W. & H.J. Janssonius, Mikrographie des Holzes der auf Java vorkommenden Baumarten, vol. 4 (1926) 683–709 (*Cordia, Ehretia*). — Patel, R.C. & J.A. Inamdar, Ann. Bot. 35 (1971) 389–409 (stomata). — Pearson, R.S. & H.P. Brown, Commercial timbers of India, Govt. India, Calcutta (1932) 750–762 (*Cordia, Ehretia*). — Sudo, S., Identification of tropical woods. Bull. Govt. Exp. Sta. Meguro No. 157 (1963) (*Cordia, Ehretia*); Anatomical characters and identification of Papua New Guinea timber species. Bull. Forestry Forest Products Res. Inst., Tsukuba No. 350 (1988) (*Cordia*). — Uphof, J.C.T, Plant hairs, & Hummel, K. & K. Staesche, Verbreitung Haartypen; in: Handb. Pflanzenanat., ed. 2, IV, 5 (1962). — Veldkamp, J.F., Flora Males. Bull. 10 (1988) 47–50. — Versteegh, C., Acta Bot. Neerl. 17 (1968) 151–159 (*Cordia,* wood anatomy).

PALYNOLOGY

(R.W.J.M. van der Ham)

Erdtman et al. (1961) considered the *Boraginaceae* as rather stenopalynous. However, in the last decades it appeared to be one of the more eurypalynous families, even in a more strict taxonomic (*Boraginoideae*) or geographic (Malesia, NW Europe) delimitation. A single work dealing with the entire family is not available. Due to its heterogeneity, it is hardly possible to characterise the family in a comprehensive description. Based on a literature survey covering 80 genera (c. 3/5 of the total number) listed in the bibliographic index to angiosperm pollen (Tissot & Van der Ham 1994) characteristics and remarkable pollen types of all subfamilies and tribes are given. All genera surveyed and a selection from the literature are mentioned. The term heterocolpate indicates the occurrence of compound apertures (colpi with endoapertures) alternating with simple apertures (relatively long colpi).

Pollen of the *Cordioideae* is oblate-spheroidal to subprolate (*Auxemma, Patagonula*: 18–25 µm; *Cordia*: 28–52 µm) and usually 3- (or 4-)colpor(oid)ate (Heubl et al. 1990; Nowicke & Miller 1990). Section *Varronia* of *Cordia* has 3-porate pollen. Ornamentation is striate-reticulate, reticulate with scabrae, irregularly striate, rugulate or variously echinate or clavate. Seven pollen types based on aperture and ornamentation features can be distinguished.

Pollen of the *Ehretioideae* (*Bourreria, Carmona*: own observations, *Coldenia, Ehretia, Halgania, Lepidocordia, Rotula, Saccellium, Tiquilia*) is prolate-spheroidal to subprolate (15–50 µm) and usually (2- or) 3-colpor(oid)ate, mostly with relatively thin mesocolpium centres: pseudocolpi (Heubl et al. 1990; Nowicke & Miller 1990; Sahay

1979). The colpi in *Rotula* pollen each have two poroid endoapertures, and are sometimes fused at the poles. *Coldenia*, which shows more affinities to the *Boraginoideae* than any other genus of the *Ehretioideae*, has 6-heterocolpate pollen (Qureshi & Khan 1985). Most *Ehretioideae* can be distinguished from most *Cordioideae* by the presence of pseudocolpi. *Lepidocordia* pollen is 3-colporate without pseudocolpi and perforate (Miller & Nowicke 1990), and is therefore in the *Ehretioideae* nearest to that of the problematical genus *Pteleocarpa* (not accepted as a *Boraginaceae* in the present work). *Pteleocarpa* pollen is deviating in possessing small endoapertures with acuminate lateral sides, a more reticulate tectum and a more developed infratectum (Lobreau 1969, 1975). *Saccellium*, tentatively assigned to the *Cordioideae* by Takhtajan (1987), has pollen much alike that of *Patagonula*.

Pollen of the *Heliotropioideae* is oblate-spheroidal to prolate (13–45 µm). *Ixorhea* (Di Fulvio 1980) and *Heliotropium* pollen are 6-heterocolpate, except for *H. indicum* which is 3-brevicolporate (Sahay 1973). Ornamentation is psilate/perforate in these genera. Pollen of *Tournefortia* is strikingly divergent. Four types have been distinguished (Nowicke & Skvarla 1974). The aperture system is mostly 6-heterocolpate or 3- (or 4-) colporate and the ornamentation more or less psilate. One type is 3-porate with clavate ornamentation. Another type has conspicuous psilate polar caps and protruding apertures. Pollen morphology does not support the separation of the *Argusia/Mallotonia/Messerschmidia* group. It confirms the close relationship with *Heliotropium*. Most *Heliotropioideae* can be distinguished from the *Cordioideae* and *Ehretioideae* by their 6-heterocolpate pollen. Within the family the 3-porate condition is restricted to a few species of *Cordia* and *Tournefortia*.

Pollen of the monotypic *Wellstedioideae* is suboblate (15–20 µm), 3 colporoidate, with a hexagonal equatorial outline (Erdtman 1952), which suggests the presence of pseudocolpi. According to Hunt (1969) the pollen of *Wellstedia* is not boraginaceous (s.s.) but more ehretiaceous, being fairly similar to that of for example *Ehretia rigida*.

The *Boraginoideae*, being the largest subfamily, is clearly the most diverse. Usually its pollen is distinctly prolate (5–65 µm), often more or less rectangular to equatorially constricted (Clarke 1977; Díez 1987). Of all dicots several species of *Myosotis* and *Trigonotis* have the smallest pollen grains (P × E = 5 × 2 µm). The ornamentation is mostly psilate to scabrate, and often slightly different in the equatorial zone (ectocingulus). A basic distinction is between tribes with colporate pollen (*Lithospermeae*, *Borageineae*, *Trichodesmeae* p.p.) and tribes with heterocolpate pollen (*Eritrichieae*, *Cynoglosseae*, *Trigonotideae*, *Myosotideae*).

The *Lithospermeae* (*Alkanna*, *Arnebia*, *Buglossoides*, *Cerinthe*, *Cystostemon*, *Echiochilon*, *Echium*, *Lasiarrhenum*, *Lithodora*, *Lithospermum*, *Lobostemon*, *Macromeria*, *Maharanga*, *Moltkia*, *Onosma*, *Onosmodium*) have (2–)3–7(–11)-colporate variously shaped pollen. *Alkanna*, *Cystostemon*, *Echium*, *Lobostemon*, *Onosma* spp. and *Onosmodium* have heteropolar pear-shaped pollen (see also Díez et al. 1986; Pérez de Paz 1995; Popova & Zemskova 1995). *Echiochilon* pollen is 2-colporate. *Lithospermum* pollen is heteropolar in having the endoapertures situated near one of the poles. In *Arnebia* pollen the colpi are very wide, diporate and sometimes fused at the poles (Qureshi

et al. 1989). Syncolpate pollen is also found in *Onosma* spp. (Ning et al. 1995). Pollen dimorphism occurs in many heterostyled *Arnebia* species (Nowicke & Miller 1988).

The *Boragineae* (*Anchusa, Borago, Elizaldia, Gastrocotyle, Nonea, Pentaglottis, Pulmonaria, Symphytum, Trachystemon*) the pollen is (3–)4–6(–15)-colporate and never constricted (see also Harmata 1977, 1981; Ning et al. 1992). In most genera the endoapertures may be fused to form a continuous circular aperture (endocingulus). *Borago* pollen has complex apertures and very distinct columellae (Ben Saad-Limam & Nabli 1984).

The *Eritrichieae* (*Amsinckia, Asperugo, Craniospermum, Cryptantha, Eritrichium, Hackelia, Lappula, Microula, Myosotidium, Nesocaryum, Plagiobotrys, Rochelia, Selkirkia*) usually have 6(–8)-heterocolpate constricted pollen (see also Díez et Valdés 1991; Marticorena 1968; Ning et al. 1993). In *Amsinckia* it is elliptic or pear-shaped. *Craniospermum* might be 3-colporate (Johnston 1956). In *Lappula* and *Rochelia* the three endoapertures are offset from the equatorial plane, two to one pole and one to the other; in *L. patula* each colpus has two pores.

Pollen of the *Cynoglosseae* (*Actinocarya, Antiotrema, Cynoglossum, Gyrocaryum, Lindelofia, Omphalodes, Paracaryum, Pardoglossum, Pectocarya, Rindera, Solenanthus, Thyrocarpus*) is much alike that of the *Eritrichieae*: 6-heterocolpate, although mostly not constricted (Barbier & Mathez 1973; Díez & Valdés 1991; Marticorena 1968). *Cynoglossum* spp., *Pardoglossum* and *Rindera* have poro-colpate pollen: three compound pori alternating with three simple colpi (Clarke et al. 1979).

Pollen in the *Trigonotideae* (*Bothriospermum, Brachybotrys, Mertensia, Moltkiopsis, Neatostema, Ogastemma, Omphalotrigonotis, Sericostoma, Sinojohnstonia, Trigonotis*) is diverse. Usually it is 6(–8)-heterocolpate, but it is 6-colporate in *Moltkiopsis* (Popova & Zemskova 1995), (6-) 7- (8-)colporate in *Neatostoma* (Díez et al. 1986), 2-colporate in *Sericostoma* and 3-(col?)porate in *Ogastemma*. Palynologically these genera would be better placed in the *Lithospermeae*, where they were initially accommodated by Johnston (1953, 1957). The 3-colporate pollen with distinctly protruding apertures of *Omphalotrigonotis* (Xi 1984) does not fit in the *Trigonotideae*, nor in any other tribe of the *Boraginoideae*. It rather resembles the pollen of *Tournefortia setacea* (Nowicke & Skvarla 1974, fig. 14) of the *Heliotropioideae*.

Pollen in the *Myosotideae* (*Myosotis*) is diverse: 6-, 8-, 10- (12-)heterocolpate, sometimes (para)syncolpate, constricted or not (Díez & Valdés 1991; Grau & Leins 1968; Grau & Schwab 1982).

Pollen in the *Trichodesmeae* is 6-heterocolpate (*Suchtelenia*) or 3-colpor(oid)ate (*Caccinia, Trichodesma*) and not constricted (Barbier & Mathez 1973; Bonnefille & Riollet 1980).

Although palynologically most of the subfamilies can be characterised fairly well, their mutual relationships are less clear. The 3-colpor(oid)ate pollen in the *Cordioideae* is a basic angiosperm pollen type, and might be considered basic in the *Boraginaceae* as well. The frequent occurrence of pseudocolpi makes the *Ehretioideae* more derived. However, it is unknown whether the common 6-heterocolpate type of the *Heliotropioideae* and *Boraginoideae* evolved from a 3-colpor(oid)ate/pseudocolpate type like in the

Ehretioideae (and *Wellstedioideae*?) or was derived 'de novo' from a basic 3-colpor-(oid)ate type as in the *Cordioideae*. *Coldenia*, intermediate between the *Ehretioideae* and the *Boraginoideae*, has 6-heterocolpate pollen, which suggests derivation from the pseudocolpate type. In contrast, *Lepidocordia*, intermediate between *Ehretioideae* and *Heliotropioideae*, has 3-colporate pollen without pseudocolpi, which indicates a 3-colporate origin of the heterocolpate type. It would be interesting to analyse *Heliotropium* and *Tournefortia*, where both colporate and heterocolpate pollen occur within a single genus. Significant for a more inclusive point of view is whether the *Lithospermeae* (colporate) or the *Trigonotideae* (heterocolpate) are considered basal in the *Boraginoideae* (see discussion by Al-Shehbaz 1991). It appears that pollen morphology has a clear potential in a phylogenetic analysis, as it characterises groups of taxa on various taxonomic levels.

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EMBRYOLOGY

Embryology has played a major part in the discussion whether *Boraginaceae* should be divided into at least two separate families or not. In subfamily *Boraginaceae* the endosperm may be nuclear, cellular or of an intermediate type, in the remaining subfamilies (as far as is known) it is always cellular. In *Boraginoideae*, an endosperm haustorium is lacking, while it is present in the remaining subfamilies. The suspensor is short in *Boraginoideae*, long in the rest. As already mentioned, pollen characters are not necessarily correlated with embryology, as *Trichodesma* likewise has two nuclei instead of three as in most of the other *Boraginoideae*. Mainly for embryological reasons, *Heliotropiaceae*

Schrader as a separate family are advocated by several authors. Position of the embryo is correlated to attachment of nutlets and not always easy to interpret, therefore.

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CHROMOSOMES

Polyploidy is confined to a certain limited number of genera within the family, while aneuploidy seems to be of great importance. In *Cordioideae*, only diploids are known with n = 8, 14, 16. In *Ehretioideae*, the basic number x may be 7–11, 13 and 21. In *Heliotropioideae* and *Boraginoideae* together, all basic numbers are known from x = 4 to 13. While it is often argued that the base number of the family as a whole is 12 because of its wide distribution within *Boraginoideae*, this is certainly not the case for the other subfamilies, in which x = 8 is much more likely the primary base number. There is no clear correlation between aneuploidy and systematic position within subfamily *Boraginoideae*, though x = 12 is most common in *Cynoglosseae* and probably also in *Eritrichieae*, while it is much less common in *Lithospermeae*. The lowest diploid number known in the family is 2n = 8, while the highest is 2n = 144.

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PHYTOCHEMISTRY AND CHEMOTAXONOMY

(R. Hegnauer)

Pyrrolizidine alkaloids and quinonoid or phenolic compounds biogenetically derived from C-prenylated or -geranylated or -farnesylated 4-hydroxybenzoic acid are the most striking secondary metabolites of this family. The isomeric red pigments alkannin and shikonin are the best known representatives of such hydroxybenzoic acid derivatives. Synthesis and accumulation of pyrrolizidines and of alkannin-related compounds occur in all four subfamilies commonly accepted within the *Boraginaceae*; they form a biochemical link between *Cordioideae, Ehretioideae, Heliotropioideae* and *Boraginoideae*

Boraginoideae and *Heliotropioideae* were most thoroughly studied by plant physiologists and phytochemists. This resulted in the detection of several metabolic features which should also interest plant taxonomists. In this respect phenolics, triterpenes and triterpene-based saponins, triglycerides of seeds, carbohydrate storage products and some N-containing compounds other than pyrrolizidines have to be mentioned. Phytochemical reviews of the family are available in Hegnauer (1964, 1989). In the following summary references are usually only given if not available in these two chemotaxonomic treatments.

Boraginoid Pyrrolizidine Alkaloids — These (PAs) belong to the ester-type and are similar to or identical with alkaloids also occurring in *Compositae–Eupatorieae* and *–Senecioneae* and in the papilionoid genus *Crotalaria*. Periodical reviews of these often

hepatotoxic alkaloids are published in Natural Products Reports [last review in 11 (1994) 613–619; covers the period July 1992–June 1993). Another review we owe to Hartmann and Witte (1994). Nowaday much attention is paid to biosynthesis, ecological functions and pharmacology of PAs. Both, the aminoalcohol part, the so-called necines, and the characteristic necic acids of these ester alkaloids derive from amino acids. Moreover, PAs often contain also organic acids other than necic acids. Acetylations occur rather frequently; an example being 7-acetyl-9-latifolylretronecine from *Hackelia californica*. Ehretinine, a PA of *Ehretia aspera*, has replaced the necic acid by 4-methoxybenzoic acid. In plants PAs are often concentrated in the youngest leaves and in flowers and inflorescences. Plant parts with large amounts of PAs are impalatable to many herbivores; PAs form part of the plants defence against herbivory. Some specialists, e.g. many arctiid moths, were able to adapt to this chemical barrier and subsequently evolved means to make use of these toxins for their own defence against potential predators. Larvae of some arctiid moths even transesterify PAs of their host plants to callimorphine or creatonotine, two alkaloids hitherto only known from butterflies feeding on PA-containing plants. Examples are *Gnophaela latipennis* feeding on *Hackelia californica* which contains the already mentioned 7,9-diester of retronecine (L'Empereur et al. 1989) and *Creatonotos transiens* reared on *Gynura scandens* (*Compositae–Senecioneae*) which has gynuramine, a macrocyclic 7,9-diester of retronecine with an isomer of isatinecic acid, a dihydroxynecic acid with two carboxylic groups, as main alkaloid. *Gnophaela* stores predominantly callimorphine by replacing the necic acid latifolic acid of the PAs of its host plant by 2-acetoxy-2-methylbutanoic acid, and *Creatonotos* stores the monoesters creatonotine and isocreatonotine by replacing the isatinecic acid isomer of gynuramine by 2-hydroxy-3-methylpentanoic acid. The new acids of the butterfly alkaloids generated in the larvae by transesterifications are assumed to be insect metabolites (Hartmann et al. 1990). Both, plants and insects, are able to N-oxidize PAs; N-oxides are main transport and storage forms of these alkaloids. PAs are also present in the nectar of some plants. This feature was interpreted as a mean a plant can use to increase floral constancy of visiting pollinators: generalists are deterred and specialists, e.g. butterflies needing PAs for defence and/or pheromone production (necine-part only), are attracted (Masters 1991).

Alkannin and shikonin and biogenetically related secondary metabolites — Alkannin, a liposoluble red 1,4-naphthoquinone derivative occurs in many *Boraginaceae*. Its biogenesis starts with 3-geranylation of 4-hydroxybenzoic acid and subsequent oxidative decarboxylation yielding C-geranylhydroquinone which has been isolated from wood of *Cordia elaeagnoides*. This key metabolite yields along different routes a whole array of quinonoid and/or phenolic constituents: alkannin-shikonin-like naphthoquinones, arnebifuranone-type 1,4-benzoquinones, the allergic cordiachromones, arnebinol-type phenols, biphenolic shikonofuran-type esters and still other structural variants derivable from geranylhydroquinone. Formerly a tincture made from *Alkanna* roots was used for staining lipids in histochemical work. The lipophilic red pigments known as alkannareds are mixtures of monoesters of alkannin and/or its enantiomer, shikonin. They occur mainly in a number of perennial *Boraginoideae*. Their original sources were roots of

Alkanna tinctoria and roots of *Lithospermum erythrorhizon*. The latter yielded in Japan a crude drug called 'Shikon' (Kariyone-Koiso 1971) or 'Koshikon' to discern it from the imported crude drug 'Nanshikon', which is the dried root of *Macrotomia euchroma* [*Lithospermum euchromon* = *Arnebia euchroma* (Xin-Sheng Yao et al. 1991)]. Alkannareds are often produced and stored by plants in roots, but deposition of red pigments is also known from stems and leaves of several species of the American genus *Plagiobothrys*; leaves of *P. arizonica* yielded acetylalkannin. According to recent investigations (Okamoto et al. 1995) biogenesis of shikonin in roots of *Lithospermum erythrorhizon* starts with phenylalanin and subsequently yields geranyl-4-hydroxybenzoic acid, geranylhydroquinone and deoxyshikonin. Ultimately shikonin is produced by introduction of a hydroxyl group in the aliphatic side chain; it is this alcoholic hydroxyl which is esterified in the genuine esters of alkannareds or lithospermumreds. Another recent investigation (Ikeda et al. 1991) established the fact that all boraginoid reds are mixtures of esters of the enantiomers alkannin and shikonin; in reds of roots of *Alkanna tinctoria* and *Arnebia euchroma* esters of alkannin dominate (> 95%), and in roots of *Lithospermum erythrorhizon* esters of shikonin are predominant (84–93%). The cordiachromones and closely related compounds were isolated from wood of species of the genus *Cordia*. Microphyllone from *Ehretia microphylla* is probably a derivative of prenylated hydroquinone. A recent investigation of this Philippine medicinal plant resulted in the isolation of the flavonol glycosides astragalin and nicotiflorin, of rosmarinic acid, and of four dimeric monoprenylated *p*-benzoquinones, i.e. microphyllone and three chemically and biosynthetically related compounds; two of the microphyllone-type constituent and rosmarinic acid showed good spasmolytic activity; this perhaps accounts for the use of this plant as antiallergic remedy (Yamamura et al. 1995). The antibiotically active cordiaquinones A to D are C_{26}-compounds which probably derive from farnesylhydroquinone; these compounds were called meroterpenoids, because only part of their structure is of isoprenoid origin (hydroquinone derived from phenylalanin + a sesquiterpenoid unit). In cordiaquinones A, B en D the sesquiterpenoid moiety of the molecules shows an unusual type of rearrangement (Bieber et al. 1990, 1994; Silva Filho et al. 1993). Still another type of compounds generated by this pathway was isolated from the resinous exudate of *Heliotropium filifolium* of arid regions of Chile. This exudate yielded two flavonoids and filifolinol which was shown to be a derivative of a C-geranylated methylester of 4-hydroxybenzoic acid (Torres et al. 1994). Similar compounds seem to occur together with lipophilic flavonoids in *H. stenophyllum* (Urzúa et al. 1993).

Phenolic constituents — Glycosides of the flavonols kaempferol, quercetin and isorhamnetin were reported to be the main flavonoids of *Boraginoideae*, but flavones are not lacking. Apigenin was detected in *Echium simplex*, and *Onosma heterophylla* yielded apigenin, luteolin and chrysoeriol besides quercetin (Mellidis et al. 1993). The 7-glucoside of luteolin was isolated from *Heliotropium tenellum*. Flower anthocyanins are predominantly based on cyanidin, delphinidin and malvidin. Dry leaves of *Cordia verbenacea* yielded the lipophilic exudate flavones artemetin (= 5-hydroxy-3,6,7,3',4'-pentamethoxyflavone) and 6'-hydroxyartemetin. Derivatives of the falvanone hesperetin, of the dihydroflavonol taxifolin and yellow chalcone dimers were isolated from roots, stem-

bark or seeds of several species of *Cordia*. Resinous exudates of *Heliotropium chenopodiaceum* yielded 5 lipophilic flavonoids, i.e. rhamnocitrin, ayanin, and kumatakenin which are methyl ethers of the flavonols kaempferol and quercetin, and the 7,3'-dimethylether of the flavanone eriodictyol, and sakuranetin, the 7-methyl ether of 2,3-dihydrokaempferol; the two exudate flavonoids of *H. filifolium* were identified with galangin, a flavonol with a non-hydroxylated B-ring, and 3-methylgalangin (Urzúa et al. 1993).

Caffeic acid seems to be ubiquitous in the family. It occurs esterified with quinic acid as chlorogenic acids and with α-hydroxydihydrocaffeic acid (formally caffeic acid + H_2O) as rosmarinic acid. Lithospermic acid was isolated from several taxa of *Boraginoideae*; it is a trimeric constituent in which rosmarinic acid is conjugated with a third molecule of caffeic acid by one -C-C- and one -C-O-C-bond, and is therefore a neolignanoid compound containing a benzofuran moiety. *Onosma heterophylla* also yielded an ester of caffeic acid with a 4-phenyl-butan-2-ol derivative and an ester of isoferulic acid with 3-phenylpropan-2-ol (Mellidis et al. 1993). Roots of *Macrotomia euchroma*, an antiflammatory Chinese crude drug, yielded two isomeric lignanoid caffeic acid tetramers, one of which proved to be identical with rabdosiin formerly isolated from *Rabdosia japonica* (*Labiatae*; Nishizawa et al. 1990). Rabdosiin and its isomers are rosmarinic acid dimers (or caffeic acid tetramers) present as sodium and potassium salts in roots; these salts were shown to inhibit propagation of human immunodeficiency virus (HIV) (Kashiwada et al. 1995).

Triterpenes and triterpenoid saponins — Free pentacyclic triterpene-monols or their acetates seem to occur frequently. Bauerenol and its acetate, isobauerenol, lupeol, betulin, β-amyrin acetate and α- and β-amyrin were detected in *Ehretia*- and *Symphytum*-taxa (Jaarsma et al. 1989, 1990) and *Sericostoma pauciflorum* (Ayatollahi et al. 1991). Barks of some species of *Ehretia* also yielded betulinic and ursolic acids. Cordialin A and B are multioxygenated tetracyclic dammarane-type triterpenes from leaves of *Cordia verbenacea*. Saponins with triterpenoid sapogenins were isolated from *Anchusa officinalis, Caccinia glauca, Cordia obliqua, Symphytum officinale* (Ahmad et al. 1993; Noorwala et al. 1994; Mohammad et al. 1995) and *Trichodesma africanum* (Omar et al. 1983). Sapogenins were identified with oleanolic acid, hederagenin (= 23-hydroxyoleanolic acid), caccigenin (= 2,19,23-trihydroxyoleanolic acid) and 23-desoxycaccigenin. One of the many saponins of *Anchusa* had 2,19,23-trihydroxyursolic acid as aglycone. The *Cordia*-saponin is based on lupeol and a second *Trichodesma* saponin has β-amyrin as sapogenin. Present knowledge favours the assumption that boraginaceous saponins are mainly based on the pentacyclic oleanolic acid and some of its hydroxylated derivatives. In two instances triterpenic alcohols (β-amyrin, lupeol) replaced triterpenic acids as sapogenins.

Seed oils — Seeds (nutlets) store proteins and fatty oils but lack starch. Seeds of *Boraginoideae* store a specific type of triglycerides characterized by substantial amounts of γ-linolenic acid (18:3,*all-cis* Δ6,9,12) and of a corresponding tetraenic acid [18:4,*all-cis* Δ6,9,12,15, called stearidonic acid by Sewón and Tyystjärvi (1993)]. *Cordioideae, Ehretioideae* and *Heliotropioideae* seem not to store such seed oils; oleic and linoleic acid are main fatty acids of their triglycerides. Within *Boraginoideae* fatty acid patterns of

seed oils seem to offer taxonomically useful information, e.g. seed oils of *Cynoglosseae* and *Anchuseae* additionally contain considerable amounts of 20:1 and 22:1 acids. A new type of seed triglycerides was recently detected in *Trichodesma zeylanicum*; the seed oil of this taxon has a totally different pattern of fatty acids, i.e. 12:0 = 7%, 14:0 = 4%, 16:0 = 21%, 18:0 = 12%, 18:1 = 4%, 18:2 = 14%, ricinoleic (= 12-hydroxyoleic) acid = 22% and 16% of Halphen-positive cyclopropene fatty acids (malvalic and sterculic acids; Hosamani 1994). We do not yet know whether other species of *Trichodesma* produce similar seed oils. It is remarkable that the unusual triglycerides with a high proportion of Δ6-trienoic and tetraenoic C_{18} acids are not restricted to seeds; such acids often predominate also in leaf lipids. A recent analysis of the fatty acids of lipids of the edible leaves of *Borago officinalis* showed that they contain mainly palmatic, ordinary linolenic and stearidonic (c. 20% of total) acids and that γ-linolenic acid is present in lesser amounts (1–6% of total acids depending on leaf age) (Sewón & Tyystjärvi 1993).

Carbohydrates including cyclitols — (-)-Bornesitol, a monomethyl ether of myoinositol seems to be present in most species of *Boraginoideae*; it was not yet detected in members of other subfamilies. Scyllitol accompanies bornesitol in several *Boraginoideae* and seems to replace it in a few. Flowers and roots of *Cordia boissieri* yielded pinitol.

Starch and inulin-type fructans are predominant carbohydrate storage products in vegetative plant parts except for annual species. Starch occurs in all four subfamilies and fructans are restricted to *Boraginoideae* where they occur together with starch or totally replace the latter. *Symphytum* belongs to the genera storing starch and fructans in rootstocks, roots and stems; recent detailed fructan investigations were reported for *S. officinale* (Abou-Mandour et al. 1987), *S. palaestinum* (Sitton & Chaouat 1989) and *S. asperum* (Barbakadze et al. 1990).

Allantoin — Probably all *Boraginaceae* contain allantoin in taxon- and plantpart-dependent amounts. This ureide is synthesized by partial degradation of purines. Allantoin is a N-rich metabolite which is used by some taxa of higher plants for temporary storage and for transport of nitrogen. Boraginaceous seeds are often very rich in allantoin.

Miscellaneous compounds — Cyanogenesis occurs erratically in this family. The cyanogenic glucoside dhurrin was isolated from young leaves of *Borago officinalis*. Moreover, making use of reliable tests cyanogenesis was demonstrated for leaves or aerial parts of *Cordia revoluta* (one of two samples), *C. scouleri, Heliotropium anderssonii, Tournefortia polystachya, pubescens* and *rufo-sericea* of the Galapagos Islands and for Australian *Heliotropium amplexicaule* (one of four tested samples).

Another type of nitrile glucosides occurs in roots of several *Lithospermum* taxa: *L. purpureocoeruleum* (*Buglossoides purpureocoeruleum*) (Sosa et al. 1955; Sosa et al. 1977), *L. ruderale* (Gorman et al. 1956) and *L. officinale* (Sosa et al. 1977). This glucoside was called lithospermoside in 1977. A series of related compounds was isolated from the stembark of *Ehretia philippinensis* by Simpol et al. (1994): ehretiosides A1, A2 en A3, ehretioside B and simmondsin which was already known from *Simmondsia californica* (*Buxaceae* s.l.). Compare for this strange type of non-cyanogenic cyanoglucosides sub *Caesalpiniaceae* (Flora Malesiana I, 12 (2) 1995: 16). Ehretioside B is the

first lithospermoside-like compound in which the cyclohexene ring is replaced by a fully aromatic ring; this suggests that phenylacetonitriles derived from amino acids (phenylalanine, tyrosine) may be precursors of simmondsin- and lithospermoside-like plant constituents. Moreover, bark of *E. phillippinensis* yielded rosmarinic acid just as did bark of *E. microphylla* (Simpol et al. 1994).

Prenylation, geranylation and farnesylation of 4-hydroxybenzoic acid and/or hydroquinone is common in the family. It is not surprising therefore that besides such meroterpenoids with hemiterpene, monoterpene and sesquiterpene moieties essential oils containing mainly mono- and sesquiterpenes are produced in appreciable amounts by some members of *Boraginaceae*. Such essential oils were described for the wood of *Cordia chacoensis* and for leaves of *C. cylindrostachya* (Fun & Baerheim Svendsen 1990).

Boraginaceae tend to deposit carbonate of calcium and/or silica in hairs and ordinary epidermis cells. Moreover, it was shown that leaves and nutlets of many members of the family contain an unusual amount of a water-soluble form of SiO_2. According to Seibert (1978) deposition of large amounts of carbonate of calcium in the peripheral nutlet layers is a character of tribe *Lithospermeae* if some exceptions (the genera *Echium, Halacsya* and *Lobostemon* and a few species of *Moltkia* and *Lithodora*) are accepted.

Chemotaxonomy — There are but a few peculiar tendencies of primary and secondary metabolisms which are valid for the family as a whole, i.e. synthesis and storage of the ureide allantoin, of pyrrolizidine alkaloids, and of meroterpenoids based on phenylalanine-derived 4-hydroxybenzoic acid and its oxidative decarboxylation product hydroquinone and a hemi-, mono- or sesquiterpenoid moiety (alkannin, cordiachromones, cordiaquinones and biogenetically related compounds). Perhaps metabolites of caffeic acid, such as dimeric rosmarinic acid, trimeric lithospermic acids and tetrameric rabdosiins are also widespread in *Boraginaceae*; this has, however, only been established for *Boraginoideae* and *Ehretioideae*. Other chemical peculiarities, such as the composition of seed oils, of carbohydrate reserves, accumulation of cyclitols and still other ones appear to be of potential taxonomic use at subfamiliar and tribal levels rather than at familiar rank. The position of the family in the system of angiosperms is still somewhat doubtful. In recent time *Boraginaceae* are affiliated to *Solanaceae* rather than to *Labiatae* by some authors. Compare *Solanales-Boraginineae* of Thorne (1992) with *Lamiales* (incl. *Boraginaceae*) of Cronquist (1988). Chemistry of secondary metabolites is not very helpful in this respect. The boraginaceous meroterpenoids confirm the generally accepted strong affinities with *Hydrophyllaceae*, but do not yield unequivocal hints regarding solanaceous or lamiaceous affinities. By rosmarinic acid and the rabdosiins the family is biochemically linked with *Labiatae*, but other metabolic tendencies discussed above and a total lack of iridoid compounds rather favour Thorne's classification.

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USES

Alkannin has been used as a dye in widely distant parts of the world. Species of *Cordia* provide edible fruits and timber. For the latter, South American species have been introduced into culture in Indonesia such as *C. alliodora* and *C. gerascanthus*. Recently, alkannin esters of various organic acids have been introduced into pharmacology for their wound healing properties. *Borago officinalis* is used as a spice.

Literature: Al-Shehbaz, I.A., J. Arnold Arbor., Suppl. Ser. 1 (1991) 1–169. — Papageorgiou, V.P., Planta Medica 38 (1980) 193–203.

TAXONOMY

Delimitation of *Boraginaceae* as a whole is still controversial. While a majority of authors regard them as a natural entity that can further be subdivided into five subfamilies, i.e., *Wellstedioideae*, *Cordioideae*, *Ehretioideae*, *Heliotropioideae* and *Boraginoideae*, others take some of these subfamilies as separate families which are even assigned to different

orders by Hutchinson and his followers. As an example, Takhtajan (1987) may be cited, who excludes the primarily woody *Cordioideae* and *Ehretioideae* as well as the tetramerous *Wellstedioideae* from *Boraginaceae* in the strict sense, which are divided into *Heliotropioideae* and *Boraginoideae*. On the other hand, embryologists advocate recognition of a distinct family *Heliotropiaceae* including *Cordioideae* and *Ehretioideae*. There is little doubt that all these groups are closely related to each other. In the present author's opinion, there are no compelling reasons for dividing *Boraginaceae* into several separate families, and they are treated as an entity here.

Boraginoideae are divided into a number of tribes, some of which have been adopted in all newer treatments of the subfamily. These are *Lithospermeae*, *Boragineae* (= *Anchuseae* of older literature), *Eritrichieae* and *Cynoglosseae*. To include some genera ancestral to these tribes and probably closely related among each other, Riedl (1968) adopted an additional tribe originally proposed by Popov (1953) under the name *Trigonotideae*. *Myosotis* is different from all other genera of *Boraginaceae* by its contorted aestivation and is best regarded as the only member of tribe *Myosotideae*.

Synopsis of subfamilies, tribes and genera of *Boraginaceae* represented in Malesia:

Subfamily ***Cordioideae***

Trees or shrubs. Fruit a drupe with one quadrilocular or four unilocular pyrenes. Style terminal, twice forked.

In Malesia: *Cordia*.

Subfamily ***Ehretioideae***

Trees, shrubs, climbers or rarely herbs. Fruit a drupe with two bilocular or rarely four unilocular pyrenes. Style terminal, simply forked or two styles.

In Malesia: *Carmona, Coldenia, Ehretia, Rotula*.

Subfamily ***Heliotropioideae***

Trees, shrubs, subshrubs, climbers, perennial or annual herbs. Fruit with a fleshy, rarely a spongy pericarp and two bilocular or four unilocular pyrenes or hard, usually breaking up into four unilocular nutlets, rarely into two mericarps or not at all. Style terminal, surrounded by the annuliform stigma, entire or forked.

In Malesia: *Heliotropium, Tournefortia* (including *Argusia*).

Subfamily ***Boraginoideae***

Annual or perennial herbs, rarely subshrubs. Fruit breaking up into four unilocular nutlets, rarely nutlets 1–3 by abortion. Style basifixed between the nutlets and coherent to gynoecial tissue that is covering the receptacle and separating from the inner layers of the fruit wall, sometimes on top of a pyramidate to subulate gynobasis formed by that gynoecial tissue, undivided or once to twice forked.

Tribus ***Trigonotideae***

Gynobasis flat, slightly concave or slightly convex in its centre. Ventral (inner) side of the nutlets angular, with an open furrow upwards from the subbasal areola at the

angle, or with a simple keel or angle and stipitate areola, or umbilicate ventrally, umbilicus with a thickened margin.

In Malesia: *Bothriospermum, Trigonotis.*

Tribus ***Boragineae***

Gynobasis flat or nearly flat. Nutlets with a basal areola often surrounded by a thickened margin.

In Malesia: *Borago.*

Tribus ***Cynoglosseae***

Gynobasis conical to pyramidate. Nutlets attached for their whole length or only slightly surpassing the gynobasis, free from an early stage.

In Malesia: *Trichodesma, Cynoglossum, Omphalodes* (*?Crucicaryum*).

Tribus ***Myosotideae***

Gynobasis flat, small. Nutlets smooth with a minute subbasal, oblique areola. Corolla-lobes contorted in aestivation.

Only *Myosotis.*

Pteleocarpa is not considered as a member of *Boraginaceae*. It is treated here as a genus of uncertain position at the end of the family.

While there is little doubt that *Boraginaceae* are most closely related to *Hydrophyllaceae* and *Lennoaceae,* their assignment to a particular order is still controversial. Hutchinson (1973) included the woody *Ehretiaceae* in *Verbenales* ancestral to *Verbenaceae,* while *Boraginaceae* s.str. were considered as the only family of a monotypic order *Boraginales* derived from *Polemoniales.*

As has been argued, the woody groups are certainly closely related to the herbaceous ones and should not be placed into a different order. Cronquist (1981) and Thorne (1976) united them with *Labiatae* and *Verbenaceae* in the order *Lamiales.* The alternate leaves, actinomorphic corolla and number of stamens equal to that of corolla lobes along with the presence of pyrrolizidine and not-iridioid alkaloids are strong arguments against this decision as has been pointed out by Dahlgren (1977, 1983) and Thorne (1983), who included the family in *Solanales,* among others. The soundest solution seems to keep *Boraginales* with the families mentioned above as a separate order as proposed by Takhtajan (1980, 1987) and Dahlgren. It is also justified for embryological and anatomical reasons according to Al-Shehbaz (1991). *Boraginales* probably are derived from *Polemoniales* in close vicinity of which they are also placed by Takhtajan (1987).

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KEY TO THE GENERA

1a. Style terminal on top of the undivided or divided fruit 2
b. Style basal between the 4 or rarely fewer separate nutlets. Herbs 9
2a. Fruits 2, laterally compressed capsules with a wide wing, bilocular, with one larger erect and one smaller pendent ovule ..... *(Pteleocarpa, p. 141)*
b. Fruit drupaceous or separating into 4 unilocular nutlets or two 2-locular mericarps, or undivided, hard 3
3a. Style once or twice forked, with or without a distinct stigma, sometimes undivided with 2 stigmata. Fruit drupaceous with 1 to 4 pyrenes and 4 seeds 4
b. Style simple or forked, surrounded by an annular stigma. Fruit drupaceous or separating into 4 nutlets or 2 mericarps 8
4a. Style twice forked. Fruit with a single 4-locular pyrene. Trees, shrubs or woody climbers ..... **Cordia** *(p. 68)*
b. Style simply forked or styles 2. Fruit with two 2-seeded or four 1-seeded pyrenes or remaining entire 5
5a. Creeping herb ..... **Coldenia** *(p. 67)*
b. Trees, shrubs or climbers 6
6a. Fruit breaking up into two 2-seeded pyrenes. Style forked .... **Ehretia** *(p. 91)*
b. Fruit breaking up into four 1-seeded pyrenes or endocarp remaining entire ... 7
7a. Style undivided, with 4 capitate stigmata. Fruit breaking up into four 1-seeded pyrenes. Flowers in a loose, scorpioid inflorescence ..... **Rotula** *(p. 114)*
b. Style forked to below middle, stigmata indistinct. Endocarp of fruit remaining entire with 4 seeds. Flowers single or a few in fascicles ..... **Carmona** *(p. 65)*
8a. Fruit drupaceous. Pericarp corky or fleshy. Trees, shrubs or climbers (in Malesia) ..... **Tournefortia** *(p. 116)*
b. Fruit separating into 4 nutlets or two 2-seeded mericarps, rarely undivided with mostly 1 locule by abortion ..... **Heliotropium** *(p. 99)*
9a. Anthers with long, twisted awns. Fruit separating into nutlets only at a late stage ..... **Trichodesma** *(p. 124)*
b. Anthers without awns. Fruits with 4 separate locules already at an early stage 10
10a. Nutlets perfectly smooth 11
b. Nutlets warty, with spines, tubercles or glochids 12
11a. Nutlets with a ventral keel or angle and a shortly stipitate basal, horizontal areola ..... **Trigonotis** *(p. 127)*
b. Nutlets without a ventral keel or angle. Areola minute, oblique, not stipitate .... **Myosotis** *(p. 109)*
12a. Filaments with an erect appendix; anthers forming a column, usually subacute. Nutlets with a basal areola surrounded by a thick, tumidulous margin; gynobasis flat ..... **Borago** *(p. 62)*
b. Filaments without an appendix; anthers not forming a column, obtuse. Nutlets with a subventral areola, gynobasis short conical to pyramidate 13

13a. Nutlets without glochids 14
b. Nutlets flat to convex dorsally, not cup-shaped, with glochids at least marginally and on ventral side 15
14a. Nutlets concave dorsally, much larger than 1 mm ..... **Omphalodes** *(p. 113)*
b. Nutlets ellipsoidal, scarcely larger than 1 mm ..... **Bothriospermum** *(p. 63)*
15a. Narrowly pyramidate stylar column present between the nutlets ..... **Cynoglossum** *(p. 79)*
b. Stylar column absent between the nutlets that are inserted on a flat disc ..... *(Crucicaryum, p. 141)*

BORAGO

Borago L., Sp. Pl. (1753) 137; Gen. Pl., ed. 5 (1754) 172. — Type species: *Borago officinalis* L.

Annual or perennial herbs with long, patent, rigid, bristly hairs in all parts. *Leaves* alternate, lanceolate. *Cymes* many-flowered, bracteate or leafy, combined into a broad, corymb-like structure. *Flowers* on long, spreading or deflexed pedicels, pentamerous. *Calyx* deeply divided, with narrow lobes. *Corolla* with short tube and stellate or campanulate limb, with 5 scales (fornices) in the throat. *Stamens* with long, broad filaments abruptly tapering in their uppermost parts and with an erect, subulate appendage at apex; anthers exserted for the greatest part, laterally coherent, connective produced into a mucro. *Pistil*: style long, filiform. *Nutlets* 4, erect on a flat receptacle, with concave areola.

Distribution — Small genus of 3 species native in the Mediterranean region. *Borago officinalis* is widely cultivated throughout the world.

Notes — 1. The basic chromosome number x = 8. There are diploid and tetraploid species.

2. The genus has been treated taxonomically by Gusuleac, Bul. Fac. Stiinte Cernauti 2 (1928) 394.

Borago officinalis L.

Borago officinalis L., Sp. Pl. (1753) 137; Backer & Bakh. f., Fl. Java 2 (1965) 464. — Type: Herb. Cliff. (BM).

Annual, hispid herbs. Stem erect, branched, angular, hollow, 20–120 cm high. *Leaves* alternate, crowded in lower part of stem rosetta-like, lower leaves stalked, petiole 2–8 cm long, upper leaves sessile; blade 3–10 by 2–5(–8) cm, oblong or elliptic, margin entire or sinuate-wavy, obtuse, bristly hairy, nerves especially distinct on lower side, forming a dense network between primary nerves. *Inflorescence* subcorymbose-paniculoid, with few small, lanceolate leaves near base, composed of scorpioid, leafless cymes; pedicels 0.5–2 cm long, patent or recurved. *Calyx* 10–12 mm long, explanate in flower, accrescent to 15–20 mm and forming a tube in fruit, cleft nearly to the base into lanceolate, obtuse lobes with long spreading hairs along margin and on surface.

Corolla 15–25 mm across, blue, tube very short, white, throat with 5 exserted, large fornices, limb stellately spreading, with oblong-lanceolate to lanceolate, acute lobes. *Stamens:* filaments strongly widening towards base, shorter than anthers, with a spur-like appendix, anthers with an acute apex, 7 mm long, dark violet. *Pistil:* style filiform, stigma capitate. *Nutlets* 5, 7–10 mm long, oblong-ovoid, ventrally keeled, dorsally ribbed, with vertical rows of warts, areola with a white strophiole surrounded by a prominent ring.

Distribution — Of Mediterranean origin, now widely cultivated and sometimes naturalized in Europe, Asia and northern Africa; *Malesia:* Java, cultivated in mountain regions.

BOTHRIOSPERMUM

Bothriospermum Bunge, Enum. Pl. Chin. Bor. (1832) 47. — Type species: *Bothriospermum chinense* Bunge.

Annual or biennial plants. *Leaves* alternate. *Flowers* small, pentamerous, solitary, extra-axillary, forming a kind of leafy raceme in the distal part of the branches. *Calyx* cleft to the base. *Corolla* with scales (fornices) in the throat, with a short tube and spreading limb divided into 5 obtuse lobes. *Stamens* included in the corolla, with short, obtuse anthers. *Pistil:* style short, with small, capitate stigma. *Nutlets* very small, erect, with a tiny areola attached to the flat or nearly flat receptacle, surface usually sculptured, ventral side with a large navel surrounded by a prominent margin.

Distribution — A genus of 5 species with its centre of distribution in China.

Bothriospermum zeylanicum (J. Jacq.) Druce

Bothriospermum zeylanicum (J. Jacq.) Druce, Rep. Bot. Exch. Cl. Brit. Is. 1916 (1917) 610. — *Anchusa zeylanica* J. Jacq., Eclogae 1 (1813) 47, t. 29. — Type: Plate in J. Jacquin, l. c.

Bothriospermum tenellum (Hornem.) Fischer & C. A. Meyer, Index Sem. Hort. Petrop. 1 (1855) 23; C. B. Rob., Philipp. J. Sc., Bot. 4 (1909) 697; Backer & Bakh. f., Fl. Java 2 (1965) 463. — Type in Herb. Vahl (as *Anchusa zeylanica*), 'Hab. in China' (C).

Annual, with numerous stems and subappressed hairs that are only more patent in the petioles and leaf margins. Stems prostrate, 8–25 cm long, slender, simple or nearly simple. Basal *leaves* soon dry and often vanishing, stem leaves 15–30 by 3–8 mm, decreasing in size upwards, with wavy margin and acute apex, the lower ones stalked, ovate-lanceolate to lanceolate, the upper ones sessile, lanceolate. *Inflorescence* leafy, leaves 7–8 mm by c. 2 mm. *Flowers* not strictly axillary; pedicels 3–5 mm long. *Calyx* c. 2 mm long, with linear-lanceolate lobes. *Corolla* c. 2.5 mm long, salver-shaped, tube shorter than calyx, lobes 5, rounded, explanate; fornices 5, trapeze-shaped, emarginate at apex. *Pistil:* style short, stigma capitate. *Nutlets* 1–1.2 mm long. — **Fig. 1.**

Distribution — Afghanistan, Pakistan, India, China and adjacent parts of the former URSS, Japan; *Malesia:* Java (naturalized, according to Backer & Bakh. f., l.c.), Philippines.

Habitat — In fields.

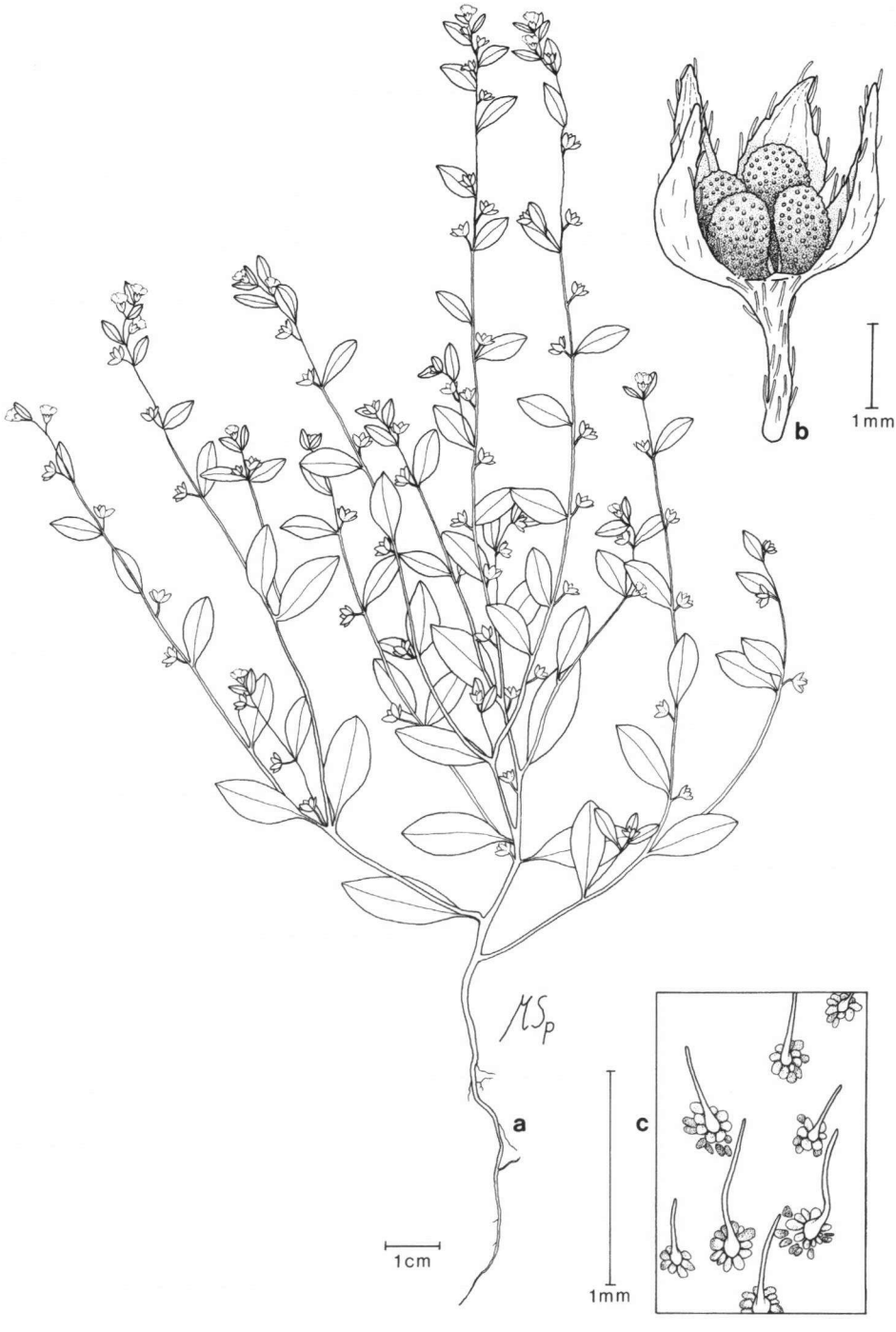

Fig. 1. *Bothriospermum zeylanicum* (J. Jacq.) Druce. a. Habit of plant; b. fruits in calyx; c. upper leaf surface (*Backer 21529*). Drawing M. Spitteler.

CARMONA

Carmona Cav., Ic. 5 (1799) 22, t. 438; I.M. Johnston, J. Arnold Arbor. 32 (1951) 16; Backer & Bakh. f., Fl. Java 2 (1965) 459; Ng in Tree Fl. Malaya 4 (1989) 59. — Type species: *Carmona heterophylla* Cav. [= *C. retusa* (Vahl) Masamune].

Shrubs or small trees. Branches slender, bearing short shoots with dense clusters of leaves and inflorescences in the leaf-axils. *Leaves* comparatively small, roughly toothed at apex. *Flowers* 2–6 in a short, bractless, glomerulate inflorescence. *Corolla* white, with a short tube and broad, spreading lobes. *Stamens:* anthers exserted. *Ovary:* style terminal, cleft to near base into two slender, elongate arms bearing minute, subcapitate stigmas. *Fruit* globose, drupaceous, red or yellow, with 1–4 seeds, endocarp bony, not breaking up into pyrenes. — **Fig. 2.**

Distribution — A monotypic genus of SE Asia, spreading northwards to southern China, westwards to India, eastwards to New Guinea and the Solomon Islands.

Habitat — Confined to dry places in coastal sands, on rocks, in open woodlands.

Note — *Carmona* has been included in *Ehretia* by most authors prior to Johnston (1951). The most peculiar feature, by which *Carmona* is separated from *Ehretia*, is the undivided, shortly beaked endocarp. Internal cavities are changing in arrangement from base to top. There are 4 large cavities for the seeds extending for the whole length of the endocarp. Near the base of the endocarp they are accompanied by 5 sterile cavities, two large ones on the dorso-ventral line, a small central one and a small cavity to the left and right of both pairs of fertile cavities. At a higher level the number of the last mentioned cavities is increased to 3 on both sides, there are also 2 tiny central cavities between the members of each pair of fertile cavities. In the upper half of the endocarp, the 2 large sterile cavities are replaced by 3, the central tiny cavities are lacking, finally the lateral small sterile cavities are disappearing also below the apex. The number of fertile cavities may be reduced by abortion in rare cases (see also Johnston, l.c.).

Carmona retusa (Vahl) Masam.

Carmona retusa (Vahl) Masam., Trans. Nat. Hist. Soc. Formosa 30 (1940) 61; Backer & Bakh. f., Fl. Java 2 (1965) 459; Ng in Tree Fl. Malaya 4 (1989) 59. — *Cordia retusa* Vahl, Symb. Bot. 2 (1791) 42. — Type: Plukenet, Phytographia, tab. 31, fig. 1 ('Habitat in India Orientali').

Ehretia microphylla Lam., Tabl. Encycl. 1 (1792) 425; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 692. — *Carmona microphylla* (Lam.) G. Don, Gen. Syst. 4 (1837) 391; I.M. Johnston, J. Arnold Arbor. 32 (1951) 17. — Type: unknown.

Ehretia buxifolia Roxb., Pl. Corom. 1 (1796) 42; Ridl., Fl. Malay Penins. 2 (1923) 442. — Type: unknown.

Shrub or tree, 1–4(–10) m high, much branched. Juvenile branches hispid, sometimes in addition puberulent, with tomentose buds or short shoots producing clusters of leaves and inflorescences. *Leaves:* petiole 1–5(–10) mm long; blade 0.8–6(–10) by 0.5–2.5(–4) cm, obovate to spathulate, broadest in upper third and gradually narrowing towards petiole, rounded, obtuse or rarely acute, toothed or crenate towards apex, bearing short, rigid, more or less appressed hairs from clusters of mineralized cells. *Inflores-*

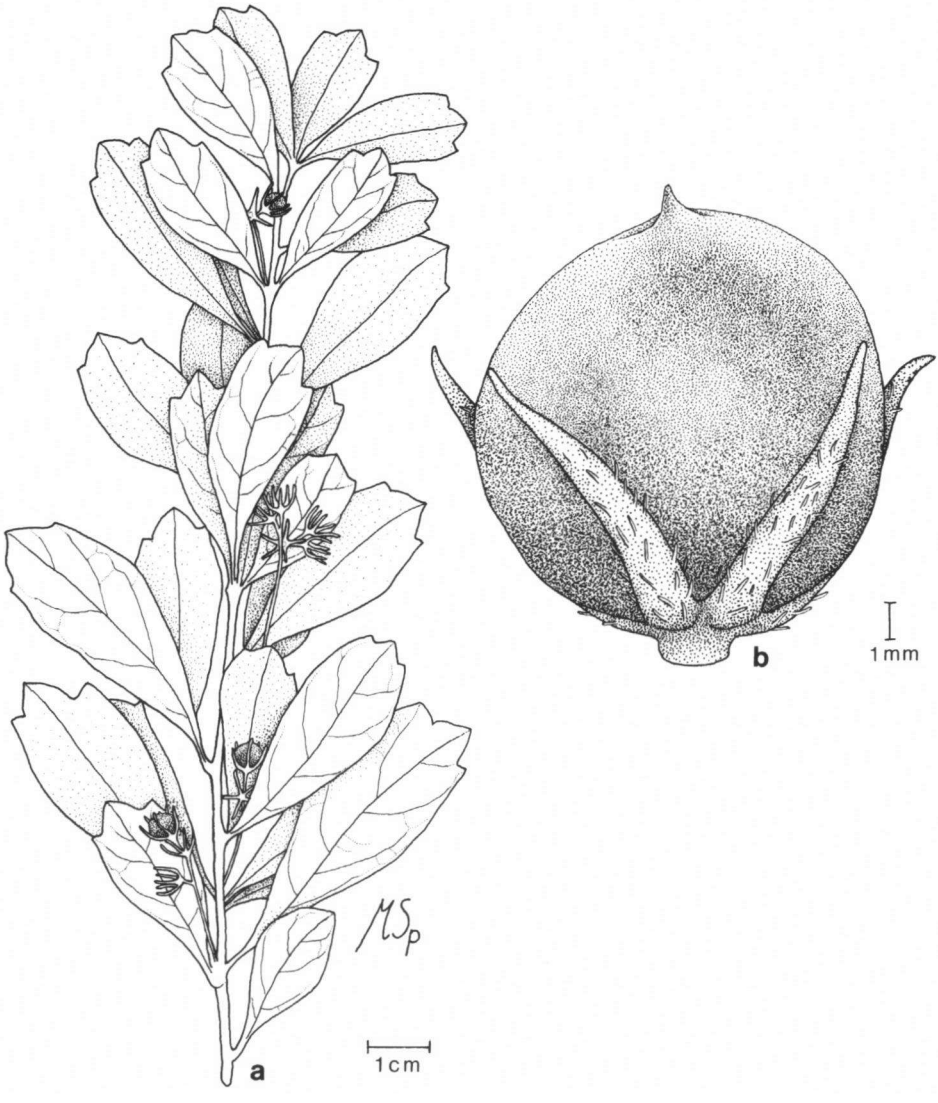

Fig. 2. *Carmona retusa* (Vahl) Masam. a. Fruiting twig, most calyces empty; b. fruit in calyx, style broken (*Britton 140*). Drawing M. Spitteler.

cence: peduncle arising from leaf-axils or apex of short shoots, slender, 0.2–2.5(–4) cm long; flowers 2–6 fascicled or in a scantily branched cyme; pedicels 0–7 mm long. *Calyx* 3–6 mm long, sparsely hispidulous outside, densely hairy inside, lobes linear to linear-spathulate. *Corolla* white, 4.5–6.5 mm long, tube 1.7–2 mm, widening from base upwards, limb 6–9 mm in diam., lobes spreading, 2.5–4.5 mm long. *Stamens:* filaments 2.5–3.5 mm long, the anthers oblong. *Ovary:* style 4.5–6 mm long, bifid, branches 3–5 mm long. *Fruit* globose, 5–6 mm in diam. — **Fig. 2.**

Distribution — India, Sri Lanka, Burma, Thailand, Indo-China, China (Hainan, Kwangtung), Taiwan, Japan (Ryukyu Islands); *Malesia:* Sumatra, Peninsular Malaysia, Java, Philippines, Celebes, Lesser Sunda Islands (Sumba, Flores), Moluccas, New Guinea, Solomon Islands. Often cultivated in gardens for ornamental purposes.

Habitat — Dry regions, sunny forests.

COLDENIA

Coldenia L., Sp. Pl. (1753) 125; Gen. Pl., ed. 5 (1754) 61. — Type species: *Coldenia procumbens* L.

Annual, prostrate herbs with dorsiventrally compressed, ascendingly branched stems. *Leaves* small, crenate-dentate or lobulate, asymmetric. *Flowers* tiny, disposited between the leaves or bracts, neither axillary nor opposed to them, tetramerous. *Corolla* white, with cylindric tube and diminute lobes. *Stamens:* anthers broad, included in the corolla, on 4 short filaments attached to about the middle of the corolla tube. *Ovary* glandular villose, pyramidate; styles terminal, 2, united at base, with tiny stigmas at the apex. *Fruit* rostrate, dividing into two 2-seeded halves first, later halves again divided into single-seeded nutlets; ventral side of nutlets with a sharp angle, dorsal side with corky, vesicular mesocarp; endocarp thick with strong ridges and protuberances.

Note — *Coldenia* was described by Linnaeus as monotypic with the single species *C. procumbens*. In later times, up to as many as 20 American species have been included, until Richardson demonstrated in 1976 that there are marked differences between them and the original *Coldenia*. For the American species, the generic name *Tiquilia* was available. *Tiquilia* species are perennial herbs or subshrubs with symmetric leaves and pentamerous flowers. The endocarp is thin, a mesocarp is entirely lacking.

Literature: Johnston, I.M., Contr. Gray Herb. 70 (1924) 55. — Richardson, A., Sida (Contr. Bot.) 6 (1976) 235; Rhodora 79 (1977) 467.

Coldenia procumbens L.

Coldenia procumbens L., Sp. Pl. (1753) 125; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 693; Ridl., Fl. Malay Penins. 2 (1923) 442; I.M. Johnston, J. Arnold Arbor. 32 (1951) 13; Backer & Bakh. f., Fl. Java 2 (1965) 460. — Type: Plukenet, Phytographia, tab. 64, f. 6.

Stems ascendingly branched, 10–50 cm long, greyish hairy. *Leaves:* petiole 0–5 mm long; blade 5–30 by 3–15 mm, asymmetric, oblong or obovate, crenate-dentate to lobulate, veins 4–6 on each side, impressed above, prominent beneath, strigose between veins, hairs often with bulbose base on upper, spreading on lower surface. *Flowers* subsessile. *Calyx* 1.5 mm long, slightly accrescent in fruit, lobes 4, lanceolate or ovate-lanceolate. *Corolla* white, glabrous, 1.5–1.8 mm long, tube 1–1.3 mm long, lobes ascending, 0.2–0.4 mm long, rounded. *Stamens:* filaments inserted above middle of corolla, included, longer than the anthers. *Ovary* glandular-villous; style bifid nearly to the base. *Fruit* 3–4 mm long, pyramidal, 4-lobed, nutlets beaked, strongly convex by vesicular, corky mesocarp dorsally, sharply angulate ventrally, with one large and one small commissural face. — **Fig. 3.**

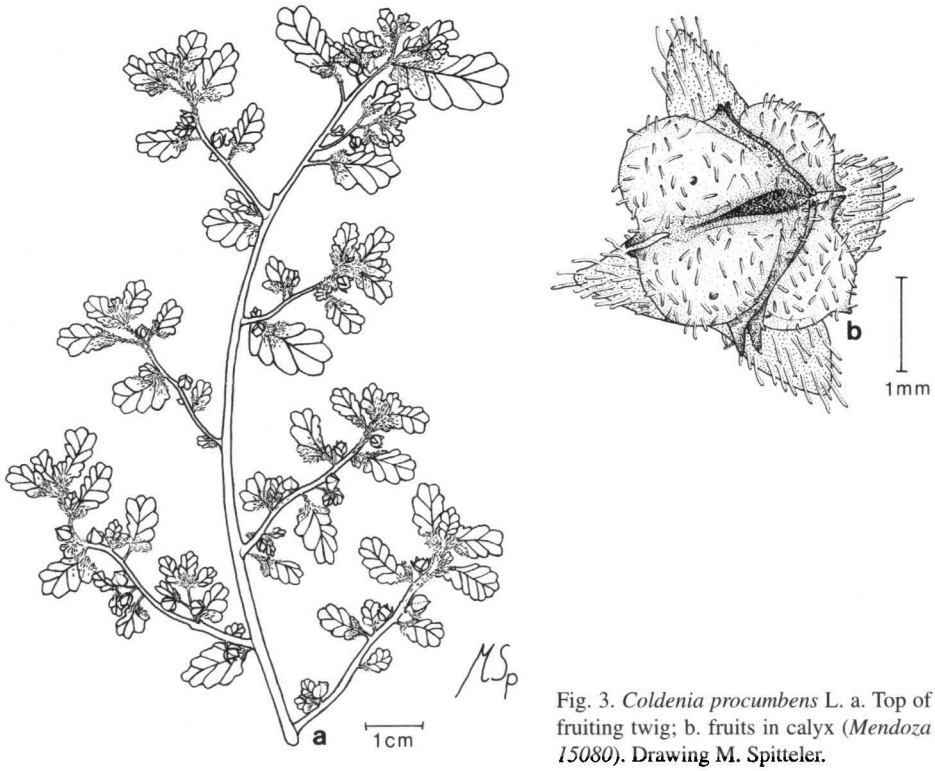

Fig. 3. *Coldenia procumbens* L. a. Top of fruiting twig; b. fruits in calyx (*Mendoza 15080*). Drawing M. Spitteler.

Distribution — India, Sri Lanka, Thailand, Burma, Indochina, China (Hainan), Taiwan; *Malesia:* Malay Peninsula, Borneo, Java (incl. Madura), Lesser Sunda Islands (Flores, Timor), Moluccas, New Guinea. Widespread in tropical and subtropical SE Asia, Africa and Australia.

Habitat — On desiccating land subject to seasonal floodings, rice-fields, etc.

Ecology — A plant of seasonally flooded places, but also able to stand extreme heat and drought. It is a common weed in dry rice-fields. The corky mesocarp may be useful for dispersal in ponds and ditches.

CORDIA

Cordia L., Sp. Pl. (1753) 190; Gen. Pl., ed. 5 (1754) 87; I.M. Johnston, J. Arnold Arbor. 32 (1951) 2; Heine in Fl. Nouv.-Caléd. 7 (1976) 97; Borhidi et al., Acta Bot. Hung. 34 (1988) 375–423; Ng in Tree Fl. Malaya 4 (1988) 60; Heubl et al., Bot. Jahrb. Syst. 112 (1990) 129. — Type species: *Cordia sebestena* L.

Medium sized trees, shrubs or woody climbers. *Leaves* alternate, rarely subopposite, stalked, unsually entire, sometimes indistinctly crenate. *Inflorescences* terminal or axillary, panicled to corymbose, sometimes very few-flowered, subglobose, with scorpioid branches. *Flowers* with a short, distinct pedicel or subsessile, (4–)5–16-merous, bisex-

ual, sometimes functionally monosexual and dioecious. In male flowers the ovary reduced and style absent, in female flowers the anthers sterile. *Calyx* cup-shaped to campanulate or tubular, lobes either irregular, 3–12, or regular, 5, or very short and reduced to a membranous, irregular margin, in some species growing with the mature fruit and becoming fleshy. *Corolla* hypocrateriform or funnel-shaped, large or small; lobes imbricate or nearly contorted in bud. *Stamens* of same number as corolla-lobes, included or exserted; filaments glabrous or pubescent at base; anthers oblong, ovate to subquadrate. *Ovary* 4-locular with one erect ovule in each locule; style twice forked, terminal; stigma elongate on each branch or subcapitate. *Fruit* drupaceous, as a rule partially included in the persistent, cupuliform calyx. *Pollen grains* 3-colpate, 3-colporate or 3-colporoidate, sexine tectate to semi-tectate, striate-reticulate or spiny and tuberculate in the Malesian species, 3-porate to pantoporate with semitectate, reticulate sexine bearing microtubercules in the exclusively American subgenus *Varronia*. — **Fig. 4.**

Distribution — A pantropical genus of about 250–300 species. In *Malesia* represented by 8 indigenous species and 4 species introduced from tropical America.

Morphology and anatomy — Certain anatomical features seem to be of taxonomic value. Crystals present in the secondary xylem can either be described as crystal sand, or there are prismatic crystals either additionally or as the only type, or a special columnar type of crystals is developed. As far as known, only *C. subcordata* is characterized by crystal druses.

In the leaves, cystoliths either are confined to epidermal cells or also found in the basal part of trichomes.

Hairs, especially of the axis, are simply strigillose or with two horizontal, apical branches, or they are stellate (especially in subg. *Gerascanthus*), sometimes, especially in American groups, bearing glandular heads.

Chromosome numbers are derived from the basic numbers 7 (in subg. *Myxa*), 8 (in subg. *Cordia* and in some species of subg. *Gerascanthus*), 9 (in subg. *Varronia*) and 15 (in some species of subg. *Gerascanthus*). Polyploidy is not infrequent. The highest diploid number counted is 'more than 80' in *C. rothii* (subg. *Myxa*).

Literature: Gottwald, H., IAWA Bull., new ser. 4 (1983) 161. — Heubl, G.R. et al., Bot. Jahrb. 112 (1990) 129. — Mez, C.C., Bot. Jahrb. 12 (1890) 526.

Uses — Some *Cordia* species are cultivated for their timber. Medicinal use is mentioned for *C. dichotoma* and *C. 'myxa'* (Jansen et al. 1991).

Reference: Jansen, P.C.M., et al. (eds.), Plant Resources of South-East Asia (PROSEA). Basic List (1991) 227.

Taxonomy — The delimitation of the genus *Cordia* has varied a great deal in the past from author to author. It has been split into as many as ten different genera (Friesen 1933), while I.M. Johnston (1930 to 1951) accepted it in a broad sense dividing it into 5 sections. The most recent treatment by Borhidi et al. (1988) takes an intermediate path acknowledging three genera: *Cordia*, *Varronia* and *Gerascanthus*. *Cordia* is not subdivided any further, in the exclusively American genus *Varronia* three sections are recog-

nized, in *Gerascanthus* two subgenera. Unfortunately, the very thorough morphological, anatomical and cytological paper of Heubl et al. (1990) was not yet known to them. Taking into account obvious correlations in chromosome numbers, pollen morphology and crystal pattern in the wood among each other and with other characters, it seems better to include *Gerascanthus* in *Cordia* and ascribe generic rank to the much more different *Varronia*, as has been proposed already by De Candolle in 1845. In the Malesian area, only true *Cordia* is found according to that proposal. It is further divided into three subgenera in the following way.

Cordia L. subg. *Cordia*

Cordia L. subg. *Cordia*. — *Sebesten* [Dill. ex] Adans., Fam. Pl. — *Cordia* L. sect. *Sebestenoides* DC., Prodr. 9 (1845) 476.

Large flowered. Fruit with corky mesocarp, completely enclosed by the calyx. Pollen 3-colpate to 3-colporoidate, exine striate-reticulate. In the secondary xylem and pith, columnar crystals (united to druses in *C. subcordata*) present along with crystal sand. x = 8.

In Malesia only *C. subcordata*.

Cordia L. subg. *Cerascanthus* (P. Browne) Cham.

Cordia L. subg. *Gerascanthus* (P. Browne) Cham., Linnaea 5 (1831) 115. — *Gerascanthus* P. Browne, Civ. Nat. Hist. Jamaica (1756) 170. — *Cerdana* Ruiz & Pavon, Prodr. (1794) 37. — *Cordiada* Vellozo, Fl. Flumin. (1829) 98. — *Cordia* sect. *Cerdanae* (Ruiz & Pavon) Roem. & Schult., Syst. 4 (1818) 499.

Small flowered. Fruit single-seeded with a thin, fibrous, chartaceous carpel-wall, at the mature state surrounded by the cylindrical calyx and the tube of the marcescent corolla. Pollen 3-colpate or 3-colporoidate, exine spinulose. Secondary xylem with medium-sized crystals often in groups of 2–8. x = 8 or 15.

Exclusively American, but some species (*C. alliodora*, *C. gerascanthus*) also cultivated in SE Asia.

Cordia L. subg. *Myxa* (Endl.) Taroda

Cordia L. subg. *Myxa* (Endl.) Taroda, Rev. Bras. Bot. 9 (1986) 38. — *Collococcus* P. Browne, Civ. Nat. Hist. Jamaica (1756) 167. — *Cordia* sect. *Myxa* Endl., Gen. Plant. (1840) 644. — *Cordia* sect. *Pilicordia* A.DC. in DC., Prodr. 9 (1845) 474. — *Calyptracordia* Britton, Sci. Surv. Porto Rico 6 (1925) 122. — *Myxa* (Endl.) Friesen, Bull. Soc. Bot. Genève 24 (1933) 136.

Small flowered, flowers often dimorphic. Fruit with a watery or viscid endocarp, frequently dispersed by birds or mammals. Pollen 3-colpate to 3-colporate, exine finely spinulose to verrucose. Usually, only crystal sand present in the secondary xylem, but rarely also prismatic crystals. x = 7.

References: Johnston, I.M., Contr. Gray Herbarium 92 (1930) 1; J. Arnold Arbor. 21 (1940) 336; ibid. 30 (1949) 85; ibid. 31 (1950) 172; ibid. 32 (1951) 1, 99. — Friesen, F.C.V., Bull. Soc. Bot. Genève II, 24 (1933) 117. — Borhidi, A., et al., Acta Bot. Hung. 34 (1988) 375. — Heubl, G.R., et al., Bot. Jahrb. 112 (1990) 129.

KEY TO THE SPECIES

1a. Inflorescence a simple, unbranched cyme ..... **5. C. curassavica**
b. Inflorescence branched in various ways 2
2a. All the herbaceous parts covered by stellate, appressed and longer, simple, patent hairs. Inflorescence paniculate ..... **1. C. alliodora**
b. Stellate hairs absent. Inflorescence more or less corymbose, rarely paniculate.. 3
3a. Corolla 2–4 cm long. Calyx cylindrical 4
b. Corolla shorter than 2 cm. Calyx never cylindrical 5
4a. Inflorescence paniculate. Leaves more than 3 times as long as wide, lanceolate ... . **7. C. gerascanthus**
b. Inflorescence more or less corymbose. Leaves ovate, acute, usually less than twice as long as wide ..... **9. C. subcordata**
5a. Leaves glabrous to nearly glabrous except along nerves on lower side..... 6
b. Leaves hairy, at least on the whole lower side 7
6a. Fruit 20–30 mm long. Calyx glabrous, campanulate .... **4. C. cochinchinensis**
b. Fruit up to 15 mm long. Calyx hairy to glabrescent, cup-shaped **6. C. dichotoma**
7a. Leaves coriaceous, upper side glabrous, lower side tomentose with hairs brown when dry ..... **3. C. bantamensis**
b. Leaves not markedly coriaceous, upper side hairy at least at a younger stage, lower side with hairs of various types..... 8
8a. Leaves green on both sides. Hairs reddish brown in all parts. Inflorescence always terminal ..... **2. C. aspera**
b. Leaves much paler on the lower side. Hairs whitish to greyish, leaving calcareous tubercles on the upper side. Inflorescence terminal or axillary .... **8. C. monoica**

1. **Cordia alliodora** (Ruiz & Pavon) Oken

Cordia alliodora (Ruiz & Pavon) Oken, Allgem. Naturgesch. 2 (1841) 1098. — *Cerdana alliodora* Ruiz & Pavon, Fl. Peruv. II (1799) 47, t. 184. — *Gerascanthus alliodorus* (Ruiz & Pavon) Borhidi, Acta Bot. Hung. 34 (1988) 396. — Type: *Ruiz & Pavon s.n.* (MA holo; F), Peru.

Tree up to 20 m high, with grey, fissured bark. All herbaceous parts densely covered by very short, stellate hairs, especially the inflorescence. *Leaves:* petiole 1–3 cm long; blade broadly elliptic, 10–55 by 5–25(–30) cm, base obliquely truncate, subacute, apex subacute to acuminate, coriaceous, margin entire, upper surface glabrous, with slightly impressed nerves, lower surface stellate-pubescent with prominent nerves. *Inflorescence* terminal, laxly branched, with numerous, crowded flowers. *Calyx* subglobose, greyish pubescent, with 10 prominent ribs, 6–7(–14) mm long, truncate with indistinct teeth. *Corolla* tube longer than calyx, lobes oblong, rounded, 5–10 by c. 3 mm. *Fruit* 5 mm long, c. 3 mm in diam., deciduous together with calyx and corolla.

Distribution — Native in Central and South America south to Bolivia, north to Mexico, and in the West Indies. *Malesia:* in Sabah (Distr. Sandakan) introduced as a plantation tree.

Ecology — Remarkable for its myrmecophily; swellings are formed on branches and sometimes also in inflorescences, which serve as domatia for ants. Ants use to cut the leaves into small pieces.

2. Cordia aspera G. Forst.

Cordia aspera G. Forst., Fl. Ins. Austr. (1786) 18, nr. 109. — Type: 'Tongatabu' in *herb. Forster* (BM holo).
Cordia cumingiana Vidal, Phan. Cuming. Philipp. (1885) 187; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 689. — Types: *Cuming 1012, 1647, 1653*, no lectotype selected.
Cordia propinqua Merr., Philipp. Govt. Lab. Bur. Bull. 35 (1906) 60. — Type: unknown.

Small tree or scrambling shrub. Young branches with a greenish brown bark and dense, patent, bristly hairs. *Leaves:* petiole 0.7–8 cm long; blade ovate-acute, (2.5–)5–22 by 1.5–16 cm, margin finely serrate with cuspidate teeth, base obliquely to subhorizontally truncate or rounded, apex acute to acuminate, rarely subobtuse, nerves (3–)4–6 on each side, darker upper surface short strigillose, pale lower surface tomentose. *Inflorescence* subcorymbose, lateral, subterminal or in fork of uppermost branches; peduncle 0.7–3.5 cm long. *Flowers* numerous; pedicels less than 1 mm long. *Calyx* subcylindrical to cylindrical-campanulate, with 10 distinct, longitudinal ribs, 3–3.5 mm long, 2–2.5 mm wide in flower, widened to 3.5(–4) mm in fruit, with 5 distinct, triangular, acute lobes, reddish tomentose. *Corolla* 3 mm long, tube cylindrical, lobes revolute, 2 mm long, scarcely 1 mm wide, oblong. *Stamens* with short filaments, anthers exserted from the corolla. *Fruit* ovoid, acute, (5–)8 by (4–)5 mm.

Distribution — Solomon, Tonga, Fiji, Samoa Islands, New Caledonia, Australia; *Malesia:* Borneo, Philippines, Celebes, Lesser Sunda Islands (Sumbawa, Flores, Timor), Moluccas, New Guinea.

Habitat & Ecology — No data available.

Note — One of the most characteristic qualities of this species are the 10 well marked ribs of the calyx. This is also one of the main reasons to include *C. cumingiana* Vidal in *C. aspera.*

KEY TO THE SUBSPECIES

1a. Leaves ovate to suborbicular-acuminate, 10–12 cm long. Fruit only 5(–6) mm long, 4 mm wide ..... **b.** subsp. **microcarpa**
b. Leaves markedly longer than wide, up to 22 cm long. Fruit 8 mm long, 5 mm wide 2
2a. Leaves very loosely strigillose to glabrescent on upper, loosely tomentose on lower side, acuminate. Calyx in flower 4 mm in diameter, campanulate to cup-shaped .. .. **c.** subsp. **miquelii**
b. Leaves densely strigillose on upper, densely tomentose on lower side, acute. Calyx in flower subcylindrical, not more than 3.5 mm in diameter .... **a.** subsp. **aspera**

a. subsp. **aspera**

Leaves up to 22 mm long, markedly longer than wide, ovate, acute, densely tomentose on lower surface. Number of flowers in inflorescence very great. Flowering calyx subcylindrical, fruiting calyx obconical. Fruit 8 mm long.

Distribution — Solomon, Tonga, Fiji, Samoa Islands, New Caledonia, Australia; *Malesia:* Borneo, Philippines, Moluccas, New Guinea.

b. subsp. **microcarpa** Riedl

Cordia aspera G. Forst. subsp. *microcarpa* Riedl, Blumea 38 (1994) 461. — Type: *Verheijen 4495* (L holo), Flores.

Leaves 10–12 mm long, ovate to suborbicular, acuminate; hairs as in subsp. *aspera*. Fruiting calyx flat cup-shaped to nearly saucer-shaped, c. 5 mm in diam. Fruit 5(–6) by 4 mm.

Distribution — *Malesia:* Lesser Sunda Islands (Sumbawa, Flores, Timor)

c. subsp. **miquelii** Riedl

Cordia aspera G. Forst. subsp. *miquelii* Riedl, Blumea 38 (1994) 461. — *Cordia miquelii* Meijer Drees, nomen in herb. L. — Type: *Koorders 16283/3* (L holo), Celebes, Minahasa.

Leaves up to 15(–20) cm long, distinctly longer than wide, ovate to oblong-acuminate, apart from young ones much less densely tomentose on the lower surface than the typical subspecies. Flowering calyx campanulate to cup-shaped, with revolute lobes after flowering. Inflorescence composed of a much smaller number of flowers than in the typical subspecies, with often thickened branchlets. Fruit c. 8 mm long.

Distribution — *Malesia:* Celebes.

3. Cordia bantamensis Blume

Cordia bantamensis Blume, Bijdr. (1826) 843; Backer & Bakh. f., Fl. Java 2 (1965) 459. — Type: *Blume s. n.* (L holo), Java, Tjikandie.

Cordia calocoma Miq., Fl. Ind. Bat. 2 (1856) 916. — Type: *Horsfield s. n.* from Java, Surakarta.

Tree or climber, 3–10 m high. Branches with a grey to tawny bark, tomentose while still herbaceous. *Leaves:* petiole 1.2–6 cm long; blade elliptical to ovate, 7–22 by 4–12 cm, margin entire to wavy, base rounded-decurrent to rounded or subcordate, apex obtuse to acuminate, nerves 4 or 5 on each side, darker than surroundings when dry on lower surface, glabrous on the upper, tomentose on the lower surface. *Inflorescence* paniculoid, with 10–12 flowers subcapitate at end of (up to 5) branches, axillary, on a 2–3 cm long peduncle; pedicels 1–3 mm long. *Calyx* campanulate, 6–7 mm long, c. 4 mm wide in flower, broadly cup-shaped, 8–9 mm long and up to 15 mm wide in fruit, tomentose, with 5 triangular lobes in flower, that become broadly triangular to indistinct in fruit. *Corolla* cylindrical with reflexed lobes, tube shorter than calyx, transverse diam-

eter c. 7 mm, lobes broadly rounded, c. 4 mm long. *Stamens* with short filaments, included in the corolla. *Fruit* ovoid, rostrate, 15–18 by c. 10 mm.

Distribution — *Malesia:* Sumatra, Java, Lesser Sunda Islands (Bali, Flores, Timor).

Habitat & Ecology —Periodically dry areas, brushwoods, sunny forest (Backer & Bakhuizen f., l.c.).

Note — On Timor, leaves are often comparatively narrow for their length and show fine white, calcareous dots under a lens similar to *C. dichotoma.*

4. **Cordia cochinchinensis** Gagnep.

Cordia cochinchinensis Gagnep. in Fl. Indo-Chine 4 (1914) 203. — Type: *Pierre 413* (P lecto), Bavia, Cochinchina.

Cordia premnifolia Ridl., J. Roy. As. Soc. Straits Br. 68 (1915) 12; Fl. Malay Penins. 2 (1923) 439. — Type: unknown.

Tree, 10–12 m high, or scrambling shrub. Branches soon lignescent, first dark reddish brown, later pale yellowish to greyish brown, glabrous. *Leaves:* petiole 1.5–4 cm long; blades of two kinds: those more distant from apex of branches often broader, 9–12 cm long, w/l ratio about 2/3 to 3/4, with 5 nerves on each side, the rest 5–11 cm long, up to half as wide as long, with c. 8 nerves on each side, all with entire margin, base rounded to transversely truncate or subcordate, apex acute to acuminate, nerves forming a dense network on lower side, glabrous on the upper, with few hairs along the primary nerves on the lower side. *Inflorescence* dichotomously branched, cymes with 2 to 5 flowers, terminal, rarely lateral on short branches; pedicels 1–2 mm long. *Calyx* 3 mm long and wide immediately after flowering, 8–10 mm long, 10–15 mm wide in fruit. *Corolla* (according to Gagnepain) elongate, 15 mm long, tube 8 mm, straight, often broadening towards base round the ovary, lobes 4, ovate-lanceolate, 3 mm long, recurved. *Stamens* 4; filaments exserted. *Fruit* ovoid, up to 3 cm long, 22 mm in diam., tapering towards apex.

Distribution — Cambodia, Vietnam, Thailand; *Malesia:* Peninsular Malaysia.

Habitat & Ecology — No data available.

5. **Cordia curassavica** (Jacq.) Roem. & Schult.

Cordia curassavica (Jacq.) Roem. & Schult., Syst. Veg. 4 (1819) 460. — *Varronia curassavica* Jacq., Enum. (1760) 14; Sel. Stirp. (1763) 40. — Type from Curaçao.

Cordia cylindristachya auct. florae Malaysiae non (Ruiz & Pavon) Roem. & Schult.: Corner, Wayside Trees (1940) 176; Ng in Tree Fl. Malaya 4 (1989) 60.

Shrub, c. 1–4 m high. Young branches rough hispidulous, becoming reddish brown. *Leaves:* petiole 5–6 mm long, blade 3–10(–15) by 2–4(–5) cm, lanceolate to ovate-lanceolate, margin serrate, tapering and acute at both ends, glabrous to sparsely hispid and with tiny white tubercles on upper side, paler and soft pubescent beneath. *Inflorescence* unbranched, spike-like scorpioid, developing basipetally, terminal, 5–15(–25) cm long. *Calyx* sessile, 3–4(–5) mm long, finely pubescent or papillose, lobes triangular,

1.5 mm long. *Corolla* tubular, 4–5 mm long, white, with small, reflexed lobes 2 mm long and wide. *Fruit* globose, 5 mm in diam., hidden in the calyx.

Distribution — Central America, Antilles, northern South America. In *Malesia* introduced in W Malaysia, Singapore and Borneo at the end of last century.

Habitat & Ecology — No data available.

Note — All Malesian specimens examined clearly belong to *C. curassavica*. This species is distinct from *C. cylindristachya*, under which name it is found in the herbaria and cited in literature, by narrower leaves that are never velvety or tomentose but rough, exclusively terminal, often longer inflorescences and smaller calyces and corollas. The hairs on the calyx are much shorter than those in *C. cylindristachya*.

6. **Cordia dichotoma** G. Forst.

Cordia dichotoma G. Forst., Fl. Ins. Austr. (1786) 18, nr. 110; I.M. Johnston, J. Arnold Arbor. 32 (1951) 8; Backer & Bakh. f., Fl. Java 2 (1965) 459; Ng in Tree Fl. Malaya 4 (1989) 60, excl. syn. *Cordia suaveolens* Blume; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 98, f. 2. — Type: *Forster s.n.*, New Caledonia.

Cordia blancoi Vidal, Rev. Pl. Vasc. Filip. (1886) 192; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 688. — Type: not extant, neotype never selected.

Cordia myxa auct. non L.: Koord., Exk. Fl. Java 3 (1912) 127; Merr., Fl. Manila (1912) 393.

Cordia obliqua auct. non Willd.: Koord., Exk. Fl. Java 3 (1912) 127; Ridl., Fl. Malay Penins. 2 (1923) 439.

Cordia subdentata Miq., Sumatra (1860) 571. — Type: *Diepenhorst s.n.* from W Sumatra.

Cordia griffithii C.B. Clarke in Hook. f., Fl. Brit. India 4 (1885) 139; Ridl., Fl. Malay Penins. 2 (1923) 439. — Type: *Griffith s.n.*, Malacca.

Tree or shrub, 6–20(–27) m high. Younger branches grey, greyish brown to brownish, glabrous. *Leaves:* petiole 1–4.5 cm long; blade ovate, ovate-lanceolate, broadly ovate, rarely suborbicular, 2–12(–16 in sterile branches) by 1.2–10 cm, margin entire, wavy, sometimes crenulate towards apex, papyraceous to coriaceous, base rounded-decurrent to oblique truncate to subcordate, apex acute, acuminate, obtuse to rounded, nerves (3–)4–5 on each side, prominent below, mostly small whitish, flat groups of mineralized cells in 2 circles on upper, sparsely hairy or with more numerous hairs along nerves on lower side. *Inflorescence* subcorymbose to subthyrsoid, with pseudodichotomous branching, terminal on slender lateral branches with 2–4 leaves, rarely lateral, with a highly variable number of flowers. *Calyx* cup-shaped, expanded in fruit from a narrow base, 3–5 mm long, slightly accrescent in fruit, 3–4 mm wide in flower, 6–10 mm in fruit, with short, dense hairs in flower, later glabrescent, lobes shortly triangular, reflexed. *Corolla* cylindrical-campanulate, white, 5–6(–8) mm long, tube 3 mm, limb 5 mm in diam., lobes 5, oblong, reflexed, 2 by 1 mm. *Stamens* long exserted. *Fruit* ovoid, c. 10(–15) mm long, c. 8(–10) mm in transverse diam. — **Fig. 4.**

Distribution — New Caledonia; *Malesia:* Sumatra, Peninsular Malaysia, Singapore, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands (Bali, Lombok, Sumbawa, Flores, Alor, Timor), Moluccas, New Guinea.

Habitat — Mainly at low altitudes from sea level upwards to about 500 m, an aberrant specimen from New Guinea also on mountain top in sunny position.

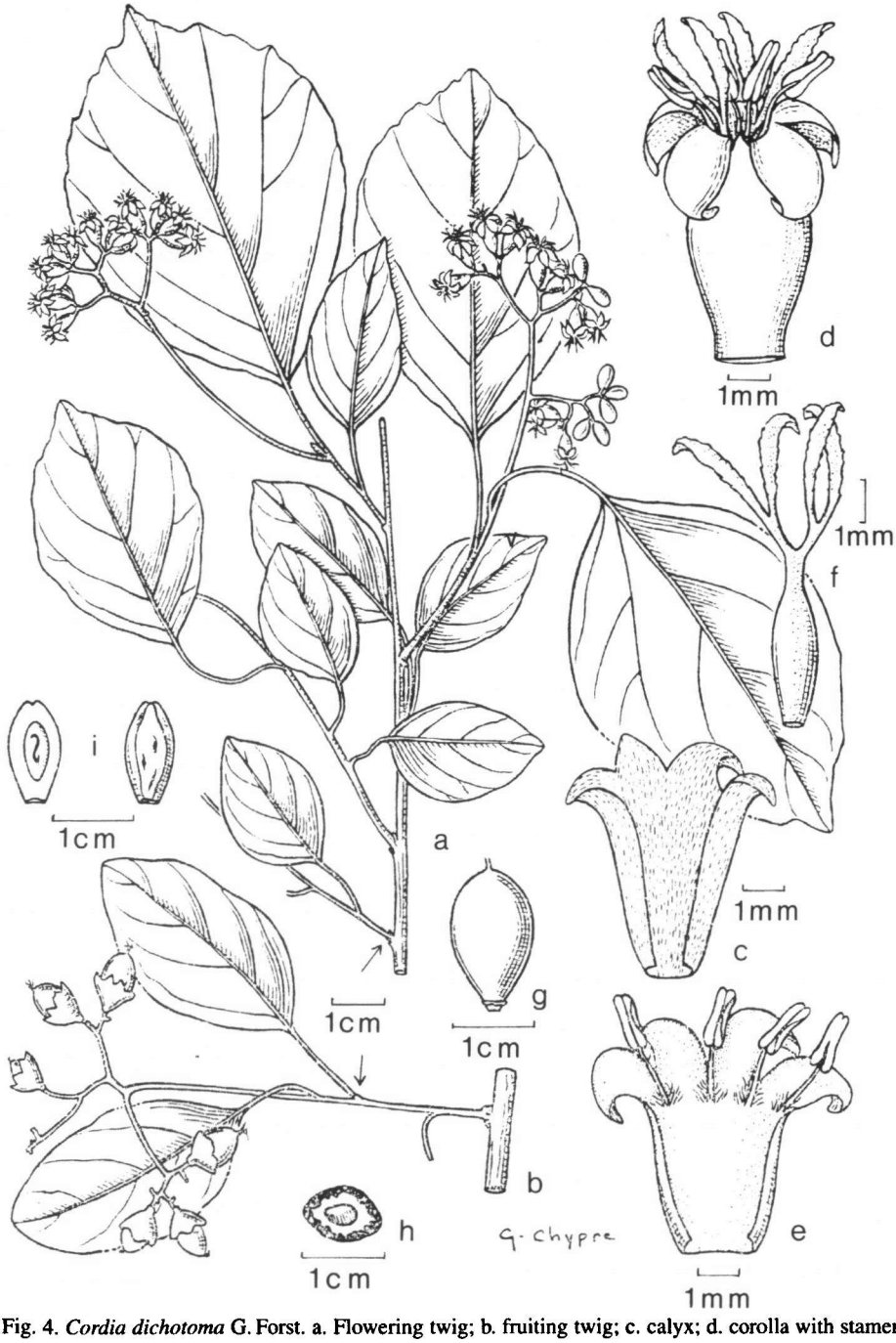

Fig. 4. *Cordia dichotoma* G. Forst. a. Flowering twig; b. fruiting twig; c. calyx; d. corolla with stamens and styles; e. opened corolla with stamens; f. pistil; g. fruit; h. fruit, cross section; i. endocarp (left) with length section (a, c–f *Catala 7458*, b, g–i *MacKee 13770*). Drawing G. Chypre. Reproduced with permission from Fl. Nouvelle-Calédonie 7.

Notes — 1. In general, variability of this extremely polymorphic species increases from West to East. In the Philippines, leaves are usually strictly flat and entire at the margin. On New Guinea, there are also species with very large (long and broad), entire leaves.

2. Especially unusual collections include: *Vera Santos 4707* (Philippines, Cagayan du Sulu, Mt Kamutyajan) with ovate, grossly dentate, leathery leaves, flowers 8 mm long, calyx 6 mm long, 6–7 mm wide already in flower; *Gebo UPNG 234* (New Guinea, Central Province, Port Moresby District, on mountain summit) with dark brown twigs, broadly ovate to suborbicular, grossly dentate leaves, calyx c. 4 mm long, corollas included in calyx.

7. **Cordia gerascanthus** L.

Cordia gerascanthus L., Syst. Veg., ed. 10 (1759) 936. — Type: P. Browne, Civ. Nat. Hist. Jamaica (1756) t. 19, f. 3.

Tree, 10–15(–30) m high. Branches glabrous. *Leaves:* petiole 1.5–2.5 cm; blade lanceolate, lanceolate-ovate or elliptic-oblong, 5–12 by 1.5–4 cm, margin entire, base acute, apex acute to acuminate, glabrous on both sides. *Inflorescence* paniculoid, composed of dense, much branched cymes. *Calyx* sessile, tubular, 7–10 mm long, with 10 distinct longitudinal ribs, sparsely hirsute with short hairs or glabrescent, lobes 5, deltoid. *Corolla* funnel-shaped, 15–25 mm long, white, becoming lavender and, when getting dry, brown, tube cylindrical, as long as calyx, lobes obovate, apically truncate to retuse. *Stamens* exserted, filaments inserted below throat, pubescent, woolly at base, anthers sagittate. *Ovary*: style deeply bifid. *Fruit* enclosed by persistent corolla and calyx.

Distribution — Mexico, Central America, West Indies, Colombia. In *Malesia* introduced in cultivation in the Philippines.

8. **Cordia monoica** Roxb.

Cordia monoica Roxb., Pl. Corom. 1 (1796) 43, t. 58; Backer & Bakh. f., Fl. Java 2 (1965) 458.

In *Malesia* one of the subspecies (but see note 2).

subsp. **subpubescens** (Decne.) Riedl

Cordia monoica Roxb. subsp. *subpubescens* (Decne.) Riedl, Blumea 38 (1994) 461. — *Cordia subpubescens* Decne., Herb. Timor. 67; Nouv. Ann. Mus. Hist. Nat. III, 3 (1834) 395, t. 16–21; Miq., Fl. Ind. Bat. 2 (1856) 918. — Type: *Guichenot 322, bois no. 41* (P lecto), Timor.

? Cordia trichostemon DC., Prodr. 9 (1845) 482; Miq., Fl. Ind. Bat. 2 (1856) 916. — Type: *Exp. Baudin* (P), Timor.

Cordia leucocoma Miq., Fl. Ind. Bat. 2 (1856) 917. — Type: *Teijsmann s.n.*, Java, Besuki.

Tree, 5–10 m high. Younger branches reddish brown, with few longer, patent, flexuous hairs and brownish or white pubescence, older ones brownish, glabrescent. *Leaves:* petiole (2–)5–30 mm; blade broadly ovate to suborbicular or oblong-ovate, (0.8–)1.5–10 by (0.7–)1–6.5 cm, margin irregularly crenate to grossly dentate, sometimes undu-

late, base rounded, truncate to subcordate, rarely decurrent into petiole, apex acute, acuminate or broadly rounded, with 3–5 nerves on each side, short dense hairs and longer hairs arising from groups of mineralized cells on upper side (denser in what has been called *Cordia leucocoma*), either equally distributed soft, longer hairs or hairs confined to nerves on lower side. *Inflorescence* corymbose to paniculoid, from 2.5 cm in lateral to 12 cm in terminal position wide, with a very large number of flowers; pedicels 1–3 cm long. *Calyx* campanulate, 4 mm long, 3 mm wide in flower, broadly cup-shaped, 4 mm long, 6–7 mm wide in fruit, lobes 3–5, broadly triangular, brownish or whitish pubescent. *Corolla* salver-shaped, with cylindrical tube and explanate to reflexed lobes, white, 3.5–4.5 mm long, c. 5 mm in diam., lobes obovate-spathulate, 2.5 by 1.5 mm. *Stamens:* filaments slightly exserted from the tube. *Fruit* broadly ovoid, rostrate, 6 mm long, 5 mm in diam.

Distribution — *Malesia:* Java, Kangean Archipelago, Lesser Sunda Islands (Bali, Sumbawa, Flores, Timor).

Notes — 1. Subsp. *subpubescens* is different from subsp. *monoica* (India, Sri Lanka) by its short, more or less appressed pubescence combined with longer, patent hairs on branches (subsp. *monoica* has stiff, patent, shorter and longer hairs). The pyrenes are 9–12 mm long in subsp. *monoica*.

2. Plants with only white pubescence on branches and dense hairs with larger groups of mineralized cells on upper surface of leaves have been called *Cordia leucocoma*. They may represent a separate variety.

9. Cordia subcordata Lam.

Cordia subcordata Lam., Tabl. Encycl. 1 (1792) 421; Miq., Fl. Ind. Bat. 2 (1856) 914; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 689; Ridl., Fl. Malay Penins. 2 (1923) 439; I.M. Johnston, J. Arnold Arbor. 3 (1951) 3; Ng in Tree Fl. Malaya 4 (1989) 62; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 100. — Type: *Commerson s.n.* (P-JU), 'ex insulis Praliniis'.

Cordia moluccana Roxb., Fl. Ind., ed. Carey & Wall., 2 (1824) 337; Miq., Fl. Ind. Bat. 2 (1856) 916. — Type: not indicated.

Cordia rumphii Blume, Bijdr. (1826) 843. — Type: ?*Blume s.n.* from W Java.

Cordia banalo Blanco, Fl. Filip. (1837) 124. — Type: not extant.

Tree, 2–15 m high. Branches grey to light brown, wood orange. *Leaves* with a 2–8 cm long petiole; blade ovate to elliptic, 8–20 by 5–15 cm, entire or rarely with few teeth, base obtuse to rounded, rarely subcordate, apex obtuse to rounded, rarely acute and shortly acuminate, with 4–5(–6) primary nerves on each side, upper surface slightly nitidulous, with very short, appressed hairs, sometimes with small groups of mineralized cells at base of hairs, lower surface velutinous or even tomentose along median and primary nerves. *Inflorescence* terminal, composed of 6–20 flowers, with a short peduncle. *Calyx* cylindrical, 10–20 mm long, 4–8 mm wide, glabrous or with few short, rigid hairs, with 3 short, triangular lobes, persistent, strongly accrescent and envelopping the fruit. *Corolla* 3.5–5 cm long and wide, orange, the lobes 5–7, large, rounded-truncate. *Stamens:* filaments inserted above middle and at base of limb of corolla, exserted. *Fruit* obovoid to subglobose, 20–30 mm long, 15–25 mm in diam.

Distribution — E coast of Africa, India, Cambodia, Vietnam, Pacific Islands; *Malesia:* Borneo, Java, Philippines, Celebes, Kangean Islands, Lesser Sunda Islands (Sumbawa, Flores, Alor, Timor), Moluccas, New Guinea

Habitat — Sandy or gravelly beach, beach forests.

Vernacular name — Salimolé (Java).

EXCLUDED OR DOUBTFUL NAMES

Cordia ? dubiosa Blume, Bijdr. (1826) 844.

Note — According to Koorders, Exk. Fl. Java 3 (1912) 127, who had examined the very incomplete type specimen at Leiden, it belongs to a species of *Elaeocarpus*, probably *E. floribunda.*

Cordia olitoria Blanco, Fl. Filip. (1837) 123.

Note — According to Blanco's notes to the description, the species is characterized mainly by its greenish white leaves. The name is not mentioned in later publications, and not even Merrill tried to identify it with any known species.

CYNOGLOSSUM

Cynoglossum L., Sp. Pl. (1753) 134; Gen. Pl., ed. 5 (1754) 168; Brand in Engl., Pflanzenr., fam. IV. 252 (1921) 114; Popov in Fl. URSS 19 (1953) 657; Riedl, Österr. Bot. Z. 109 (1962) 385; Backer & Bakh. f., Fl. Java 2 (1965) 463; Riedl in Fl. Iran. 81 (1967) 142. — Type species: *Cynoglossum officinale* L.

Paracynoglossum Popov in Fl. URSS 19 (1953) 717; R.R. Mill, Notes Roy. Bot. Gard. Edinb. 41 (1984) 473.

Annual, biennial or perennial herbs with alternate, entire *leaves*; basal leaves usually already withered at flowering time. *Cymes* with or without bracts, terminal and axillary, terminal ones often in pairs. *Flowers* extra-axillary, pentamerous, on longer or shorter, but nearly always distinct pedicels. *Calyx* divided beyond middle, often nearly to the base. *Corolla* cylindrical, campanulate, funnel-shaped or rotate, white, blue or purple, sometimes white with blue or purple veins, with 5 distinct scales in the throat. *Stamens* always inserted below the scales, included in the corolla, with very short filaments and short, ellipsoidal, rounded anthers. *Pistil:* style long or short, with or without a distinct stigma, sometimes nearly hidden between the nutlets. *Nutlets* 4, attached to the conical receptacle by an areola that is markedly shorter than the inner side of the nutlet, sometimes additionally with an awn; outer (ventral) side sometimes surrounded by a tumidulous margin or the widening, joined bases of the innermost series of marginal glochids, concave, flat or convex, often less densely covered by glochids than the rest of the nutlet, or not different at all. — **Fig. 5.**

Distribution — 50 to 60 species in the warmer and temperate regions of all continents.

Habitat — The species of this genus display a great variety of habitat preferences.

Uses — *Cynoglossum amabile* Stapf from southern China is used as an ornamental plant in many areas, e.g. most parts of Europe, Indonesia, etc.

Notes — 1. The basic chromosome number is x = 12 with most species being diploid, only a few tetraploid.

2. Delimitation of the genus has become controversial in recent years. While the European and N African *Pardoglossum* Barbier & Mathez and the Australian *Austrocynoglossum* R. Mill are very natural groups clearly different from true *Cynoglossum*, *Paracynoglossum* Popov is hard to separate even on the subgeneric level. The main distinguishing character, presence of an awn united with the receptacle and separating from it at maturity of the nutlets in *Cynoglossum* s.str., is not always recognizable. The only other difference, smaller nutlets and often also corollas in *Paracynoglossum*, is working only on a statistical basis, and there are intermediates such as *C. microglochin* Benth. The present author prefers to retain *Paracynoglossum* for the time being on a subgeneric level, though a final decision is still impossible. Especially African species like *C. coeruleum* Hochst. or *C. johnstonii* Bak. assigned to sect. *Eleutherostylum* by Brand are very closely related to typical members of *Paracynoglossum* and have been transferred to it by Mill.

In the Malesian region, the genus is represented by the two subgenera *Paracynoglossum* and *Eleutherostylum*.

Cynoglossum L. subg. ***Paracynoglossum*** (Popov) Riedl

Cynoglossum L. subg. *Paracynoglossum* (Popov) Riedl, Osterr. Bot. Z. 109 (1962) 392.

Nutlets connected to receptacle or style by an awn. Nutlets small, usually not longer than 3–3.5 mm, but with few exceptions up to 4.5 mm. Style usually much longer than nutlets.

The Malesian species *C. furcatum*, *hellwigii*, *javanicum*, *lanceolatum*, *timorense*, and probably also *C. amabilis* belong to this subgenus.

Cynoglossum L. subg. ***Eleutherostylum*** Brand

Cynoglossum L. subg. *Eleutherostylum* Brand in Engl., Pflanzenr. fam. IV.252 (1921) 115, 140.

Nutlets not connected to receptacle or style by an awn. Nutlets usually bigger, 4 mm or longer. Receptacle distinctly surpassed by the apex of the nutlets, style often very short.

KEY TO THE SPECIES

1a. Branches of inflorescence crowded at apex, at acute angles. Leaves greyish-white, velvety ..... **1. C. amabile**

b. Branches of inflorescence at different levels, often furcate at apex. Hairs of leaves different 2

2a. Corolla broadly cylindrical, up to 10 mm long. Nutlets 6 mm in diam., with a distinct margin ..... **11. C. papuanum**
b. Corolla campanulate, funnel-shaped or rotate, shorter. Nutlets rarely up to 6 mm 3

3a. Corolla with a short tube and a wide, rotate limb c. 8–10 mm in diam. Leaves glabrescent, with mineralized pustules at a later state. Calyx-lobes glabrous on their outer surface ..... **5. C. glabellum**
b. Corolla either of different shape and size or leaves markedly hairy, not glabrescent. Calyx-lobes hairy on outer surface 4

4a. Nutlets 5(–6) mm long. Robust plant at least 75 cm high .... **2. C. castaneum**
b. Nutlets smaller 5

5a. Corolla c. 12 mm in transverse diam. Plant 50–75 cm high. Nutlets c. 4–4.5 mm long ..... **10. C. novoguineense**
b. Corolla (and usually the whole plant) smaller. Nutlets 1.5–4.5 mm long 6

6a. Whole plant golden silky-tomentose. Corolla white ..... **3. C. celebicum**
b. Plant with different kind of hairs. Corolla blue to dark purple at least in part .. 7

7a. Style distinctly shorter than nutlets. Nutlets with very short, few, slender, subulate spines, attached to the receptacle with a very small, apical areola. Lobes of corolla 3.5 mm long and wide ..... **9. C. macrolimbe**
b. Style longer than nutlets. Nutlets with longer and usually more numerous glochids. Attachment to receptacle different. Corolla lobes smaller 8

8a. Lowermost pedicel 1–1.5 cm long, recurved. Inflorescence few-flowered, flowers remote. Flowers and nutlets very small ..... **13. C. spec. A**
b. Pedicels fairly equal or the lowermost pedicel a little longer, but not as much as 10 mm. Flowers more or less dense 9

9a. Nutlets c. 1.5–2.2 mm long, with short pedicels or nearly sessile ..... **8. C. lanceolatum**
b. Nutlets 2.5–3(–3.5) mm long, with longer or short, distinct pedicels 10

10a. Fruiting cymes spreading, rigid, uppermost forked, lower ones subhorizontal 11
b. Fruiting cymes not spreading nor rigid, at least uppermost at acute angles, suberect 12

11a. Corolla campanulate to funnel-shaped, up to 3 mm long. Nutlets 2–3 mm long .. **6. C. hellwigii**
b. Corolla campanulate, up to 5 mm long. Nutlets 3–4 mm long ..... **4. C. furcatum**

12a. Pedicels filiform, recurved, longer than calyx. Nutlets c. 2–2.5 mm long ..... **12. C. timorense**
b. Pedicels stouter, recurved or patent, not longer than calyx. Nutlets 3(–3.5) mm long ..... **7. C. javanicum**

1. Cynoglossum amabile Stapf & Drumm.

Cynoglossum amabile Stapf & Drumm., Kew Bull. (1906) 202; Backer & Bakh. f., Fl. Java 2 (1965) 463. — Syntypes: *Hancock 133, Henry 9365, Soulié 861, Pratt 887* (K), China.

Perennial herbs, 15–60 cm high. Stems single, rarely several, erect, with dense, spreading hairs. *Leaves* velvety, greyish white, with distinct nerves on lower side, basal ones with a long petiole, 5–20 cm long, 2–3.5(–4) cm wide, oblong-lanceolate to lanceolate, acute at the apex, tapering into petiole; cauline leaves sessile with broad, rounded base, oblong to lanceolate, (2–)3–10 by up to 2.5 cm. Lowest *cymes* in the axils of upper leaves, upper ones crowded, at acute angles, erect, ebracteate; pedicels 2–3 mm long in flower, elongated to c. 4 mm and curved downwards in fruit. *Calyx* 2.5–3.5 mm long, greyish pubescent, lobes ovate, acutish, free to base. *Corolla* blue, rarely white, 5–6 mm long; tube c. 2.5 mm long, limb spreading, 7–10 mm in diam.; fornices papillate, trapeziform. *Stamens:* anthers subsessile between fornices, 1 mm long. *Pistil:* style twice as long as nutlets. *Nutlets* whitish, ovate in outline, 3–4 mm long, dorsally slightly concave to slightly convex, covered equally by glochids all over, the marginal glochids confluent at the base, nearly forming a wing; areola above middle of ventral surface.

Distribution — A native of southern China, now widely cultivated; *Malesia:* cultivated in Java.

2. Cynoglossum castaneum Riedl

Cynoglossum castaneum Riedl, Blumea 38 (1994) 462. — Type: *Afriastini 488* (BO, K), Central Java, Mt Lawu.

Biennial or perennial herb (base unknown), at least 75 cm high. Stem with several elongate branches, covered with short, appressed, usually retrorse hairs. Basal *leaves* not known, stem leaves sessile, acute, linear-lanceolate, covered by short, strigillose, antrorse hairs on the upper, by similar, irregularly directed hairs on the lower side, nerves more or less distinct on lower side only, middle ones 10–12 cm long, 1.5 cm wide, tapering towards base, upper ones 2.5–5.5 cm long, 0.5–1.5 cm wide, semiamplexicaulous. *Cymes* elongate after flower, ebracteate; pedicels 1.5 mm long in flower (at top of cyme), up to 5 mm in fruit (near base). *Calyx* 2.5 mm long in flower, 3(–3.5) mm in fruit, strigillose with antrorse hairs, lobes free to base, ovate, up to 2 mm wide, subacute. *Corolla* funnel- to salver-shaped, with bluish veins on whitish ground, 3.5–4 mm long, 7 mm in diam., tube about as long as calyx, lobes oblong-obovate, rounded, c. 2 mm long, glabrous; fornices sub-trapeziform to sub-quadrate, involute and emarginate at apex. *Stamens:* anthers ovoid or ellipsoid, 1 mm long, subsessile. *Pistil*: style 0.8 mm in flower, c. 2.5 mm in fruit, without distinct stigma. *Nutlets* ovate in outline, shining castaneous brown, glochids dense and confluent at base at margins, more or less evenly distributed on dorsal and ventral surfaces, areola small, subapical.

Distribution — *Malesia:* Central Java. Known only from the type collection.

Habitat — No data available.

3. Cynoglossum celebicum Brand

Cynoglossum celebicum Brand in Engl., Pflanzenr., fam. IV.252 (1921) 147. — Type: *Sarasin 1289* (B, destroyed), Celebes.

Biennial or perennial (base not known). Whole plant golden sericeous tomentose. Stem more than 40 cm high, upright, angulate, branched in the upper part. Basal *leaves* unknown; stem leaves tapering gradually into a short petiole or semiamplexicaulous, lanceolate-oblong to oblong, 15–20 cm long with petiole, 1.2–4.5 mm wide, sligtly attenuate at apex. *Cymes* terminal and axillary, dense, ebracteate, on long peduncles; flowers subsessile, fruiting pedicels very short, slightly bent downwards. *Calyx* 3.5 mm long, sepals free to the base. *Corolla* white, cylindrical-campanulate, 4 mm long, lobes ovate, as long as tube; fornices subquadrate. *Stamens:* anthers subsessile in the middle of the tube. *Pistil*: style very short, but much longer than the nutlets. Immature *nutlets* only known, very small, rounded, with very short glochids, inserted at base of the elongated gynobase.

Distribution — *Malesia:* Celebes. Known only from the type collection.

Note — The description is taken from the original diagnosis.

4. Cynoglossum furcatum Wall.

Cynoglossum furcatum Wall. in Roxb., Fl. Ind., ed. Carey & Wall., 2 (1824) 6; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 696. — Type: Described from a plant in the Botanical Garden, Calcutta, native in Nepal.

Cynoglossum zeylanicum Brand in Engl., Pflanzenr., fam. IV.252 (1921) 134, p.p., non Thunb. ex Lehm. (1817), nomen in syn. = *Echinospermum zeylanicum* Lehm.

Biennial or perennial. Stems up to 1 m or more high, with numerous branches especially in the upper part, covered by soft, more or less appressed hairs. Stem *leaves* sessile, lanceolate or ovate-lanceolate or lanceolate-oblong, lower and middle ones 7–8 by 2.5–3 cm, upper ones 1.5–4 by 0.8–1.5 cm, all gradually tapering towards base, sometimes semiamplexicaulous, acute, with very distinct nerves and with soft, appressed, more or less distinctly retrorse hairs densest along the nerves on both sides. *Cymes* terminal on main stem and lateral branches, mostly paired, divaricate, densely scorpioid in the beginning, straight in fruit, ebracteate; pedicels 1–3 mm long, bent downwards after flowering, covered with very dense, antrorse hairs. *Calyx* c. 2.5 mm long in flower, lobes 2 mm long, 1 mm wide in flower, 4.5–5 by 2(–2.5) mm in fruit, very densely covered by antrorse hairs. *Corolla* campanulate, blue, 4–5 mm long, 5–7 mm in diam., glabrous, tube shorter than calyx, lobes suborbicular, c. 2 mm in diam.; fornices subquadrate, large. *Stamens:* anthers subsessile, much smaller than fornices, inserted below them. *Pistil:* style c. 2 mm long in fruit (without gynobase), stigma small, like a helmet on top of the style. *Nutlets* ovate in outline, 3–4 mm long, c. 2.5 mm wide, dorsally slightly convex, with glochids fairly equally distributed all over the surface.

Distribution — Afghanistan, Pakistan, Himalayas, India, China, Japan; *Malesia:* Java, Philippines.

Habitat — No data available.

5. Cynoglossum glabellum Riedl

Cynoglossum glabellum Riedl, Blumea 38 (1994) 462. — Type: *Veldkamp & Stevens 5554* (L holo), New Guinea, Mt Suckling.

Perennial; rhizome divided into creeping branches. Stems several, ascendent, 40–45 cm high, unbranched or with a single branch, glabrous below, strigose with short retrorse hairs in the inflorescence. Apart from the stems there are sterile rosettes of leaves. *Leaves* lanceolate to lanceolate-oblong, acute, on the upper side with numerous, on the lower side with a few groups of mineralized cells very rarely bearing short hairs, ciliate in the margins; leaves of basal rosettes stalked, petiole 3–5 cm long, lamina 5–7 by 1–1.8 cm; lower stem leaves already dry at flowering time, middle ones 3–6 by 0.7–1.4 cm with narrowing base, upper ones 1.8–3 by 0.7–1 cm. *Inflorescence* bifurcate with erect branches or simple, loose, 1.5–8 cm long, composed of only 7–11 flowers, ebracteate; pedicels 4–6 mm long, recurved in fruit. *Calyx* 2 mm long in flower, 4 mm in fruit, crispulate hairy at the very base, lobes 1.3 mm wide in flower, up to 2 mm wide in fruit, subobtuse, with reticulate veins, ciliate at margins. *Corolla* mauve in bud, then deep blue, salver-shaped, 4–5 mm long, 8–9 mm in diam., glabrous, tube about as long as calyx or a little shorter, lobes obovate, 3–3.5 mm long, with reticulate veins; fornices quadrate, emarginate, papillate at margin. *Stamens:* filaments distinct, 0.2 mm long, anthers oblong to ovate-oblong, 0.8 mm long, inserted below fornices. *Pistil:* style 2.5 mm long in fruit, without stigma. *Nutlets* ovate in outline, 4–4.5 mm long, 2.5 mm wide, with dense glochids ventrally and at margin and loosely arranged glochids on the flat dorsal disc.

Distribution — *Malesia:* New Guinea, known from two collections.

Habitat — On dry and rocky flats or on treefern grassland, usually along rivers.

Note — A very distinct endemic species without any close relatives.

6. Cynoglossum hellwigii Brand

Cynoglossum hellwigii Brand in Fedde, Repert. 13 (1915) 546. — Type: *Hellwig 362* (B, destroyed), New Guinea, Finisterre Mts.

Cynoglossum javanicum auct. non Thunb. ex Lehm.: Van Royen, Pac. Sc. 29 (1975) 95; Alpine Fl. New Guinea 4 (1983) 3123.

Annual or biennial herb. Stem 8–100 cm high, branched very much, hirsute with dense, more or less distinctly retrorse hairs in the lower, antrorse hairs in the upper part of stem and branches. *Leaves* elliptical oblong, oblong, elliptical, oblong-lanceolate or lanceolate; petiole 4–7 cm long in lower leaves, gradually decreasing in length upwards; blade 12–15 by 3.5–5 cm, long tapering towards petiole in lower leaves, 7–10 by 1–3 cm in middle, 1.5–6 by 0.3–1.5 cm, sessile with narrow base in upper leaves, obtuse to subacute, with numerous, very distinct nerves on both sides, strigose with antrorse longer and shorter hairs, the longer ones arising from groups of mineralized cells on upper, with soft, spreading hairs denser along the nerves on lower side. *Inflorescence* much branched, cymes divaricate, ebracteate; pedicels less than 1 mm in flower, 1–3 mm in fruit, patent or curved downwards, densely hairy. *Calyx* 1.5–2 mm long in

flower, lobes 2.5 mm long, 0.8–1 mm wide in fruit, obtuse, hairs subappressed, antrorse. *Corolla* white or pale blue, campanulate to funnel-shaped, glabrous, 2.5–3 mm long, 3.5–4 mm in diam., tube slightly shorter or equal to calyx, lobes oblong, 1.5–1.8 mm long, 1–1.2 mm wide; fornices large, subquadrate. *Stamens:* filaments very short, anthers ovate, half the size of the fornices, reaching their bases. *Pistil:* style 1.5 mm long, stigma small, bilobed. *Nutlets* ovate in outline, convex dorsally, 2–3 mm long, 1.5–2 mm wide, glochids equally distributed or slightly looser dorsally.

Distribution — *Malesia:* New Guinea, widespread, endemic.

Habitat — Swampy grassland along river, open places, 1200–1300 m altitude.

Vernacular name — Mai Rokh.

Uses — Used locally for adornment of wigs.

7. **Cynoglossum javanicum** Lehm.

Cynoglossum javanicum Thunb. ex Lehm., Neue Schr. Naturf. Ges. Halle 3 (1817) 21; Pl. Asperif. (1818) 118, in syn.; Backer & Bakh. f., Fl. Java 2 (1965) 463; Van Royen, Pac. Sc. 29 (1975) 95, p. min. p.; Alpine Fl. New Guinea 4 (1983) 3123, p. min. p. — Type: *Herb. Thunberg*, Java.

Biennial (?) herb. Stem 30–100 cm high, branched, with antrorse to patent hairs arising from groups of mineralized cells. *Leaves* oblong to ovate-oblong or oblong-lanceolate or lanceolate, petiole 1–1.5 cm long in lower leaves, absent in upper, blade up to 12 cm long, (0.7–)1–2.5(–3) cm wide in lower, 4–9 by 0.5–2.5 cm in middle, 2–4 by 0.25–2 cm in upper leaves, tapering towards petiole, in uppermost leaves sessile with narrow or broad base, acute, more rarely obtuse, nerves distinct on both sides, hairs antrorse, arising from a group of mineralized cells on upper, antrorse, denser along nerves on lower side. *Inflorescence* terminal on main stem and lateral branches, cymes more or less upright, at sharp angles, ebracteate, sometimes with a single leaf above lowermost flower; pedicels 1 mm in flower, 2.5–3(–5) mm in fruit, curved downwards. *Calyx* 1.5–2 mm long in flower, lobes ovate, 2.5 mm long, 1.2 mm wide in fruit, obtuse, rounded at apex, with antrorse hairs. *Corolla* dilute blue or pink, campanulate to funnel-shaped, 3–4(–5) mm long, c. 6 mm in diam., lobes suborbicular, 1.5–2 mm by 2 mm, papillate on inner side; fornices trapeziform, large, as long as wide, sometimes slightly bilobed, involute and papillate at upper margin. *Stamens:* filaments very short, anthers oblong, below fornices. *Pistil:* style 1–1.5 mm long, stigma indistinct. *Nutlets* broadly ovate in outline, 3 mm long and wide, glochids equally distributed, conical, sometimes bases of marginal glochids widened, confluent. — **Fig. 5.**

Distribution — *Malesia:* Sumatra, Java, ?Bali, ?Lombok.

Habitat — *Casuarina* forests, waste fields (acc. to Backer & Bakhuizen f., l.c.).

Notes — 1. Specimens from the Tengger Mts, E Java, have remarkably narrow leaves and small nutlets with a distinct rim formed by the bases of marginal glochids. Specimens from Bali and Lombok (only one seen from each) are very untypical with more patent, rough indument and may represent a local subspecies.

2. There are plants that have a general habit intermediate between *C. javanicum* and *C. lanceolatum*, between *C. javanicum* and *C. furcatum* as well as between *C. javani-*

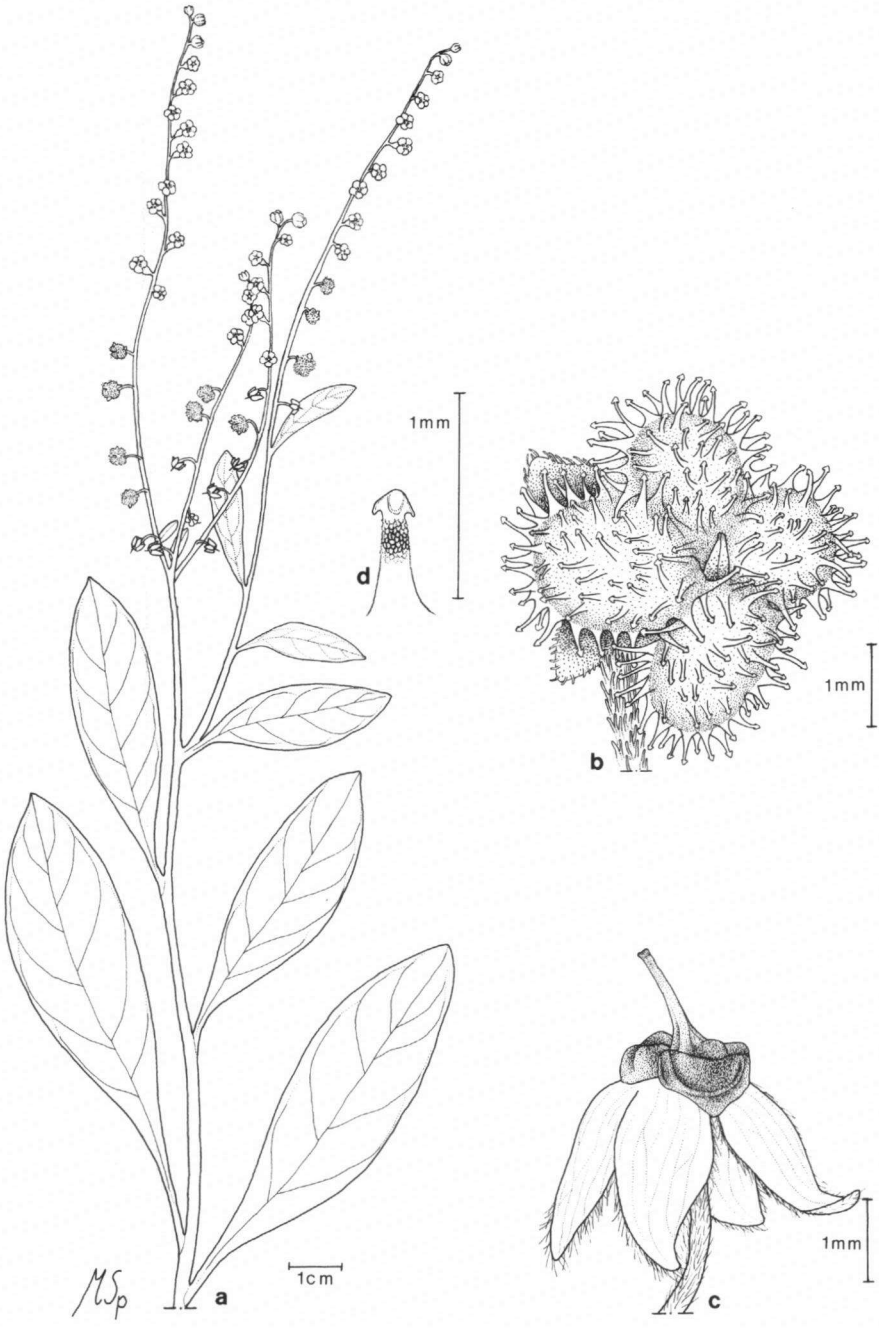

Fig. 5. *Cynoglossum javanicum* Lehm. a. Top of plant in flower and fruit; b. fruit with detail of barbed spine (d); c. fruiting calyx, nutlets fallen (*Danser 6585*). Drawing M. Spitteler; a: adapted from an old drawing in L.

cum and *C. timorense*. The delimitation of the species is still far from clear, and it may prove necessary to divide it into several subspecies, as geographical correlations seem to exist in many cases, or even into several species. On the other hand, *C. timorense* and *C. hellwigii* may prove as mere subspecies, though at the moment the differences seem to be constant.

8. Cynoglossum lanceolatum Forssk.

Cynoglossum lanceolatum Forssk., Fl. Aegypt.-Arab. (1775) 41; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 94. — Type: *Forsskål* (C), Yemen, Hadie.
Cynoglossum micranthum Desf., Tabl. Ec. Bot. (1804) 220; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 696. — Type: *Hb. Forsskål 312* (C).

Biennial (?) herb. Stems up to 100(–150) cm high, much branched, with longer, patent and shorter, antrorse hairs. *Leaves* lanceolate or oblong-lanceolate, petiole 1.5–3 cm long in lower, 0–1 cm in upper leaves, blade up to 10–11 by 3–3.5 cm in lower, 5–9 by 1.3–1.8 cm in middle, 1.5–6 by 0.3–1 cm in upper leaves, tapering towards base, acute, nerves very distinctly impressed on upper, prominent on lower side, upper side strigose with hairs arising from groups of mineralized cells, hairs on lower side subpatent, a few longer, numerous shorter, denser along nerves. *Inflorescences* terminal on main stem and branches, furcate, cymes divaricate, scorpioid in flower, 3–10 cm long in fruit, ebracteate; pedicels c. 1 mm long in fruit, curved downwards. *Calyx* 1–1.5 mm long in flower, 1.5 mm long in fruit, divided to base, lobes 0.5–0.8 mm wide, acute. *Corolla* white or dilute bluish, funnel-shaped, 2–3(–4) mm long, c. 3–4 mm in diam., glabrous, lobes ovate-suborbicular, 1(–1.5) mm long; fornices transverse linear, much wider than long. *Stamens:* filaments and anthers very short, anthers broadly ovate, much smaller than fornices, not reaching their base. *Pistil:* style very short, stigma indistinct. *Nutlets* ovate in outline, with nearly flat disc, 1.5–2.2 mm long, glochids equally distributed or less dense on disc, bases joined along margin.

Distribution — Widespread in NE, E and southern Africa, Arabia, Afghanistan, Pakistan, Himalayas, India, China, Japan, Taiwan, Indochina, Burma, Thailand; *Malesia:* Sumatra, Borneo, Java, Philippines, Celebes.

Habitat — Not very specialized.

9. Cynoglossum macrolimbe Riedl

Cynoglossum macrolimbe Riedl, Linzer Biol. Beitr. 22 (1990) 310. — Type: *Brass 22460* (A, LAE), Papua New Guinea, Dayman Mts.

Basal parts and main stem not known, but obviously a much branched stout herb. Branches c. 30 cm long, covered especially in their lower part densely by retrorse or distally by spreading, in dried state brownish hairs. *Leaves* darker green on upper, paler on lower side, with appressed antrorse hairs on the upper, less closely appressed, irregularly directed, along the nerves denser hairs on the lower side, middle leaves lanceolate, rounded-truncate at base, widest below middle, 10–11 by 2.8–3 cm, acute, the upper leaves 4–7 by 1–2 cm. *Cymes* first scorpioid-contracted, later elongate, loose, straight,

composed of about 10 flowers, with horizontally spreading, brownish hairs; pedicels 1.5–3 mm in flower, 12–15 mm long in fruit, more or less bent downwards. *Calyx* 3–3.5 mm long in flower, 6–6.5 mm later on, lobes coherent only at the very base, acute, first 1.5, later 1.8–2 mm wide, covered by antrorse, later on more patent hairs. *Corolla* funnel- to salver-shaped, 4.5–5 mm long, lavender, tube 2 mm long, distinctly shorter than limb, lobes free beyond the middle of the limb, broadly rounded, c. 3.5 mm long and wide, orbicular-obovate to ovate-oblong, spreading; fornices very short and broad, nearly semilunate, c. 0.8 mm wide. *Stamens:* filaments very short but distinct, attached to middle of tube, anthers slightly incurved at apex, scarcely reaching base of fornices. *Pistil:* style 2.5–3 mm long, shorter than the nutlets but surpassing them, stigma very small, subcapitate. *Nutlets* slightly immature only known, ovate in outline, 3–3.5 mm long, 2.5 mm wide, with few, very short spines or glochids on the dorsal disc, with several concentric rows of basally widening and partly confluent glochids ventrally and along margin, attached to the short gynobase by the small, apical areola.

Distribution — *Malesia:* New Guinea. Known only from the type collection.

Habitat — No data available.

10. **Cynoglossum novoguineense** Riedl

Cynoglossum novoguineense Riedl, Linzer Biol. Beitr. 22 (1990) 307. — Type: *Cruttwell 754* (K), Papua New Guinea, Mt Maneao.

Stout, biennial or perennial plant (base unknown), 50–75 cm at least high. Stem upright, branched in upper part, densely leafy, covered with nearly appressed, antrorse hairs in lower, retrorse hairs in middle and nearly horizontally spreading, white hairs of scarcely 1 mm length in upper part. Basal *leaves* not seen, stem leaves dark green with short, appressed, soft, antrorse hairs on upper, pale green with irregularly directed, especially along nerves very dense, short, appressed hairs on the lower side, lower stem leaves already dry and vanishing at flowering time, but some still remaining, 6–7.5 by 1.5–2.1 cm, lanceolate, sessile, base rounded or obliquely truncate, widest below middle, acute, middle and upper leaves slightly smaller, 3–6 by up to 1.5 cm wide, even smaller on lateral branches. *Cymes* either crowded at apex or in subdichotomous pairs with a single flower between them, reduced cymes also in axils of upper leaves, sometimes repeatedly branched, scorpioid-contracted at flowering time, later on elongated, straight, leafy in their lower part with smaller leaves than below, with 12–15 flowers in the main cymes; pedicels very short, densely hairy at flowering time, c. 1 mm long, later bent downwards, 6–7 mm long, the lowermost up to 12 mm. *Calyx* 3–3.5 mm long in flower, lobes free to the base or coherent at the very base only, lobes linear-oblong, acute, antrorsely hairy, later accrescent, 6–8 mm long, lobes coherent for the fourth or fifth part, c. 2 mm wide, lanceolate, slightly recurved. *Corolla* intensely blue, salver-shaped or nearly funnel-shaped, 4–5 mm long, 12 mm in diam., tube 2–2.5 mm long, hidden by the calyx, limb spreading, divided at least to the middle into broadly rounded, 4–4.5 mm long and 3–4 mm wide lobes; fornices trapeziform, slightly shorter

than wide, puberulent. *Stamens:* filaments very short, attached slightly below base of fornices, anthers oblong, scarcely 1 mm long. *Pistil:* style 2–2.5 mm long; stigma very small, capitate. *Nutlets* ovate in outline, subacute, 4.5 mm long, 3.5–4 mm wide, with loosely arranged, slender spines or glochids on dorsal disc, very dense glochids along margin and dense, slender conical glochids or spines ventrally, attached to the gynobase by an areola that covers more than half the length of the ventral surface.

Distribution — *Malesia:* New Guinea, endemic, only known from the type specimen.

Habitat — No data available.

11. Cynoglossum papuanum O. Brand

Cynoglossum papuanum Schltr. ex O. Brand, Bot. Jahrb. 62 (1929) 489. — Type: *Keysser 22* (B, destroyed), Papua New Guinea, Saruwaged Mts.

Erect, sparsely hairy herb. Base and lower *leaves* unknown, upper leaves obovate or oblong, 4–6 by 1.5–2 cm, semiamplexicaulous, acute, covered densely by groups of mineralized cells. *Cymes* terminal, loose, ebracteate or with few bracts near base; lower pedicels longer than calyx and bent downwards in fruit. *Sepals* ovate, acute, sparsely appressed hairy, 5 mm long, after flowering elongated to 6–7 mm. *Corolla* shortly and broadly cylindrical, twice as long as calyx; fornices large, trapeziform. *Stamens* inserted at the middle of the tube. *Gynobasis* depressed pyramidate, with 4 large excavations, about as long as style. *Nutlets* 6 mm in diam., marginate, densely spiny, spines denser in the margin and ventrally than on the dorsal surface; embryo 4 mm long with nearly orbicular cotyledons and very short rootlet.

Distribution — *Malesia:* New Guinea, only known from the type collection.

Note — As the type has been destroyed and no new material is available, the above description is a translation of the original diagnosis, in which several important characters have not been mentioned while other, unusual characters are described in detail.

12. Cynoglossum timorense Riedl

Cynoglossum timorense Riedl, Blumea 38 (1994) 463. — Type: *van Steenis 18303* (L holo), Timor, Mt Perdido.

Annual (?), 30–40 cm high. Stem branched from near the base, covered by patent or retrorse hairs in the lower, antrorse hairs in the upper part. *Leaves* lanceolate to obovate or oblong, tapering towards petiole, acute to shortly acuminate, nervature distinct, reticulate on lower side, covered by nearly spreading, stiff, bristly hairs, petiole of lower leaves 5–10 mm long, blade 1.5 by 0.7 cm, petiole of middle leaves shorter, blade 3–3.5 by 0.9–1 cm, petiole of upper leaves 0–2 mm long, blade 1.5–2.5 by 0.6 cm. *Inflorescence* loose, elongated up to 15 cm after flowering, with leafy bracts in the lower, ebracteate in the upper part; pedicels filiform, 1 mm long in flower, elongated to 3–7 (–15) mm in fruit, curved downwards. *Calyx* 1.5–2 mm in flower, 2–2.5 mm in fruit, antrorsely strigillose, lobes free to the base, 0.8–1 mm wide, subacute or acute. *Corolla*

campanulate to funnel-shaped, 2.5(–3) mm long, 4.5 mm in diam., glabrous, tube shorter than calyx, lobes elliptical, 1.5 mm long; fornices trapeziform to subquadrate, indistinctly emarginate, subinvolute at apex. *Stamens:* anthers subsessile a little below the fornices, ovoid, 0.6 mm long. *Pistil:* style 0.3 mm long in flower, hidden by the nutlets, without distinct stigma. *Nutlets* ovate in outline, 2–2.5 mm long, 1.5 mm wide, with a flat dorsal disc, densely glochidiate in margin with confluent bases of glochids, glochids evenly distributed on disc.

Distribution — *Malesia:* Lesser Sunda Islands (Lombok, Flores, Timor).

Habitat — On naked limestone peak (type), roadsides at 1750–2100 m altitude.

Notes — 1. A specimen from Sumbawa is characterized by larger leaves that are subserrate by the thickened bases of marginal bristles and distinctly larger calyx with sharply acute lobes, that are spreading star-like. It is not clear whether this is within the normal amplitude of variation or whether this plant represents a separate taxon probably on the infraspecific level.

2. Several plants from Java are similar to *C. timorense* in their small nutlets, comparatively long, slender fruiting pedicels and small leaves. It is not quite clear whether they should be assigned to *C. javanicum*, that seems to be extremely variable, or to *C. timorense*.

13. Cynoglossum spec. A

Perennial herbs, stems arising from rooting, subhorizontal, subterranean shoots, 40–50 cm high, with few branches, with long, spreading to retrorse, fairly dense, flexuous hairs. *Leaves* ovate-lanceolate to lanceolate, petiole 0.5–1 cm in lower, 0–0.3 cm in upper leaves, blade 7–8 by 2–2.5 cm in lower, 2.5–5 by 0.6–1.2 cm in upper leaves, 2–6.5 by 0.6–1.2 cm in sterile, lateral branchlets, tapering towards base or rounded, sessile, acute, with 5–7 pairs of primary lateral nerves especially distinct on lower side, hairs subpatent, irregularly directed on upper, rigid, arising from mineralized cells on lower side. *Cymes* in main stem paired, in lateral branches single, ebracteate, short, very loose, lowermost flower below uppermost leaves, extra-axillary; pedicel of lowermost flower 2–2.5 cm long, others 0.4–1.2 cm after flowering, very short in flower, with very long, curved, spreading hairs. *Calyx* c. 2.5 mm long in flower, scarcely accrescent, divided to base, lobes ovate, 1–1.2 mm wide, acute, with dense, long, spreading to antrorse hairs crowded in centre of lobes. *Corolla* short campanulate to funnel-shaped, colour not known, 3.5 mm long, 5–5.5 mm in diam., glabrous or with few spreading hairs on lobes, tube included in calyx, lobes oblong, c. 1.5 mm long, 1.2 mm wide; fornices transversely linear, 0.5–0.6 mm wide, 0.15 mm long. *Stamens:* anthers nearly sessile, placed below fornices. *Pistil:* style not surpassing ovary in juvenile state. *Nutlets* (immature only known) ovate-suborbicular in outline, c. 2 mm long, glochids dense ventrally and along margin, few on flat disc.

Distribution — Known only from a single collection from Lombok, *Elbert 1366*, 27 May 1909 (seen from L).

Habitat — Bushy grassland, 3200–3500 m altitude, on loose, volcanic gravel.

EHRETIA

Ehretia L., Syst., ed. 10 (1759) 936; I.M. Johnston, J. Arnold Arbor. 32 (1951) 19. — Type species: *Ehretia tinifolia* L.

Trees or shrubs. *Leaves* small to large, alternate, margin entire or serrate, sometimes wavy. *Inflorescences* terminal and/or lateral, branched or unbranched, sometimes arranged in corymb- or panicle-like structures. *Calyx*-lobes 5, separate from the beginning. *Corolla* white or pale yellow, with elongate-cylindrical or campanulate tube and spreading to recurved lobes. *Stamens:* anthers exserted as a rule, on filiform filaments. *Ovary:* style terminal, with two branches free in the uppermost part or to the middle; stigmas 2, capitate or elongate. *Fruit* a subglobose drupe, yellow, orange or reddish, with two separate pyrenes sometimes divided again into 4 one-seeded parts. *Pollen* spheroidal to prolate-spheroidal or subprolate, finely reticulate or striate-reticulate, 3-colpate or 3-colporoidate. — **Fig. 6.**

Distribution — About 50 species in the tropics and subtropics of Africa, Asia and Australia, 3 species in America. In *Malesia* 12 species.

Uses — Medicinal use is mentioned for *E. philippinensis* and *E. resinosa* in Jansen et al. (eds.), Plant Resources of SE Asia (PROSEA Handb.), Basic List (1991) 230.

Notes — 1. Crystal druses present in vascular parenchyma.

2. Chromosome numbers given as 2n = 26, 32, 40.

3. The genera *Ehretia* and *Bourreria* are very close to each other. The latter generally has been regarded as exclusively American, but Thulin (1987) found that also some African species belong to it. The main distinguishing character is the calyx of the young bud which is undivided in *Bourreria* splitting into 2 to 5 lobes when opening, while 5 separate lobes are present from the beginning in true *Ehretia*. The pyrenes are always separating into two one-seeded units in *Bourreria*, while in *Ehretia* there are two sections, *Ehretia* s.str. with 2 two-seeded pyrenes not further dividing at maturity, and *Bourreroides* Benth. & Hook.f. with 4 separate units in the end.

Reference: Thulin, M., Nordic J. Bot. 7 (1987) 413.

KEY TO THE SPECIES

1a. Leaves serrate to irregularly dentate. Inflorescence paniculoid or thyrsoid ..... **1. E. acuminata**

b. Leaves entire or with few irregular teeth. Inflorescence corymbose or with few cymose branches 2

2a. Cymes few-flowered, always axillary, bracteate; lower bracts up to 10 mm long .. **8. E. papuana**

b. Inflorescence terminal or axillary, with branched or unbranched cymes or corymbose, without or with few bracts at base of branches 3

3a. Tube of corolla 3.5–5 times as long as the calyx; lobes one third, rarely up to half as long as tube, recurved. Fruit up to 10 mm long ..... **4. E. javanica**

b. Tube of the corolla shorter compared to the calyx and lobes. Fruit 8 mm long or shorter 4
4a. Anthers sagittate, with a narrow but distinct sinus between their lower ends. Often also veins of higher order distinct, forming a dense network ... **11. E. resinosa**
b. Anthers not sagittate, linear, sometimes widened and rounded at base. Only primary nerves prominent 5
5a. Inflorescence branched, with 1–5 flowers all on one side of each branch, on short pedicels (0.5–1 mm) 6
b. Inflorescence branched, flowers single (rarely 2 or 3) terminal on branches of ultimate order, not all on one side of main branches 8
6a. Inflorescence glabrous ..... **3. E. dichotoma**
b. Inflorescence shortly pubescent, sometimes with glands 7
7a. Leaves ovate to lanceolate, with distant primary nerves usually 1 cm or more apart at their base ..... **6. E. laevis**
b. Leaves obovate to oblanceolate, sometimes emarginate at apex, with very dense primary nerves less than 1 cm apart at their base ..... **9. E. parallela**
8a. Inflorescence glabrous or nearly glabrous 9
b. Inflorescence hairy 10
9a. Leaves acute or acuminate. Calyx 1.2–1.5 mm long, cleft to middle or a little beyond, lobes glabrous or with few hairs along margin. Style cleft for about 0.8 mm ..... **10. E. philippinensis**
b. Leaves rarely acute, usually obtuse or emarginate. Calyx 2.5 mm long, cleft for about 2 mm, lobes densely ciliate along margin. Style cleft for most of its length ..... **12. E. timorensis**
10a. Scandent shrubs. Calyx densely covered with very short reddish, strigillose hairs. Young branches with loose patent bristles sometimes thorn-like with broader base ..... **2. E. asperula**
b. Trees. Calyx without reddish hairs, sometimes ciliate along margin and/or covered with white pustules. Young branches glabrous 11
11a. Corolla-tube distinctly longer than calyx. Calyx lobes with patent, long hairs along margin, glabrous on surface ..... **7. E. moluccana**
b. Corolla-tube included in calyx. Calyx lobes ciliate along margin, white pustulate on surface ..... **5. E. keyensis**

1. Ehretia acuminata R.Br.

Ehretia acuminata R.Br., Prodr. Fl. Nov. Holl. (1810) 497; C.B.Rob., Philipp. J. Sc., Bot. 4 (1909) 690; I.M.Johnston, J. Arnold Arbor. 32 (1951) 21; Backer & Bakh.f., Fl. Java 2 (1965) 459. — Type: *R. Brown s.n.* (K holo), Australia, Port Jackson.

Ehretia serrata Roxb., Hort. Beng. (1814) 17, nomen; Fl. Ind., ed. Carey & Wall., 2 (1824) 340, descr.; Miq., Fl. Ind. Bat. 2 (1856) 920; Koord., Exk. Fl. Java 3 (1912) 127. — Type: Cultivated in Calcutta Bot. Garden.

Ehretia ovalifolia Hassk., Cat. Hort. Bogor. (1844) 137. — Type: Cultivated in Bogor (Buitenzorg) Bot. Garden, ex Japan.

Ehretia polyantha DC., Prodr. 9 (1845) 503; Miq., Fl. Ind. Bat. 2 (1856) 920. — *Ehretia acuminata* R. Br. var. *polyantha* (DC.) I.M. Johnston, J. Arnold Arbor. 32 (1951) 24. — Type: *Perrottet* (GE), Philippines.

Ehretia acuminata R. Br. var. *pyrifolia* (D. Don) I.M. Johnston, J. Arnold Arbor. 32 (1951) 23. — Type: *Wallich* (K), Nepal.

Tree up to 25 m high. Young branches (blackish) brown, glabrous, older branches grey. *Leaves* lanceolate to ovate-lanceolate or oblong, (3–)5–15(–18) by (1.5–)2–8 cm, finely serrate, serrate, crenate-dentate to grossly dentate, indistinctly petiolate, base obliquely truncate to rounded, apex acute, with 4–7 nerves on each side, upper side glabrous, lower side with hairs along main nerves. *Inflorescence* terminal on main and lateral branches, paniculoid, with numerous flowers; pedicels 1–2.5 mm long. *Calyx* cup-shaped, 1.5 mm long, 2 mm wide in flower, lobes 5, free beyond middle, laterally overlapping in flower, with hairs along margin. *Corolla* funnel-shaped, 2–2.5 mm long, 4–5 mm in diam., lobes oblong, obtuse, 1.5(–2) mm long. *Stamens* exserted. *Pistil:* style divided for 1/3, branches widening towards indistinct stigmata. *Fruit* globose, c. 7 mm in diam.

Distribution — Australia, China; *Malesia:* Java, Philippines, Lesser Sunda Islands (Bali, Sumbawa, Flores, Timor), Moluccas, New Guinea.

Habitat — In forests.

Note — The species is highly variable, but variation does not follow any geographical pattern as supposed by Johnston (1951). The assumption that Malesian specimens can be separated in a var. *pyrifolia* does not hold.

2. **Ehretia asperula** Zoll. & Mor.

Ehretia asperula Zoll. & Mor. in Mor., Syst. Verz. Zoll. (1845–46) 52; I.M. Johnston, J. Arnold Arbor. 32 (1951) 106; Backer & Bakh. f., Fl. Java 2 (1965) 460, in adnot. — Type: *Zollinger 1548*, Java.

Climbing shrub. Young branches reddish to greyish brown, covered with loose patent bristles that often have a bulbous base. *Leaves:* petiole (0.5–)0.8–1(–1.5) cm; blade lanceolate to oblong-lanceolate, (1.5–)3–15 by 0.8–5.5 cm, entire or widely repanded dentate, base narrowly rounded to obliquely truncate, apex acuminate, nerves (4–)5(–6) on each side, glabrous on both sides or with few hairs along nerves beneath. *Inflorescence* terminal and lateral on short branches, loosely corymbose to paniculoid, patent bristly, with numerous flowers; pedicels 0.8–3 mm long. *Calyx* cup-shaped, 1.2–1.5 mm long, 2.5–3 mm wide, lobes free for 1/3 to 1/2, triangular, densely strigillose with very short, reddish hairs. *Corolla* broadly and shortly campanulate, white, 1.5–1.8 mm long, 3.5–4 mm in diam., lobes wider than long, 1 mm long, c. 2 mm wide, broadly rounded. *Stamens* very long exserted. *Pistil:* style 3.5 mm long, the branches free for 1/3 or a little more, the stigmata indistinct. *Fruit* globose to subglobose, c. 3.5 mm in diameter.

Distribution — Hainan, Vietnam; *Malesia:* Sumatra, Peninsular Malaysia (Johore), Borneo, Java.

Habitat — Primary forest, upper dipterocarpous forest.

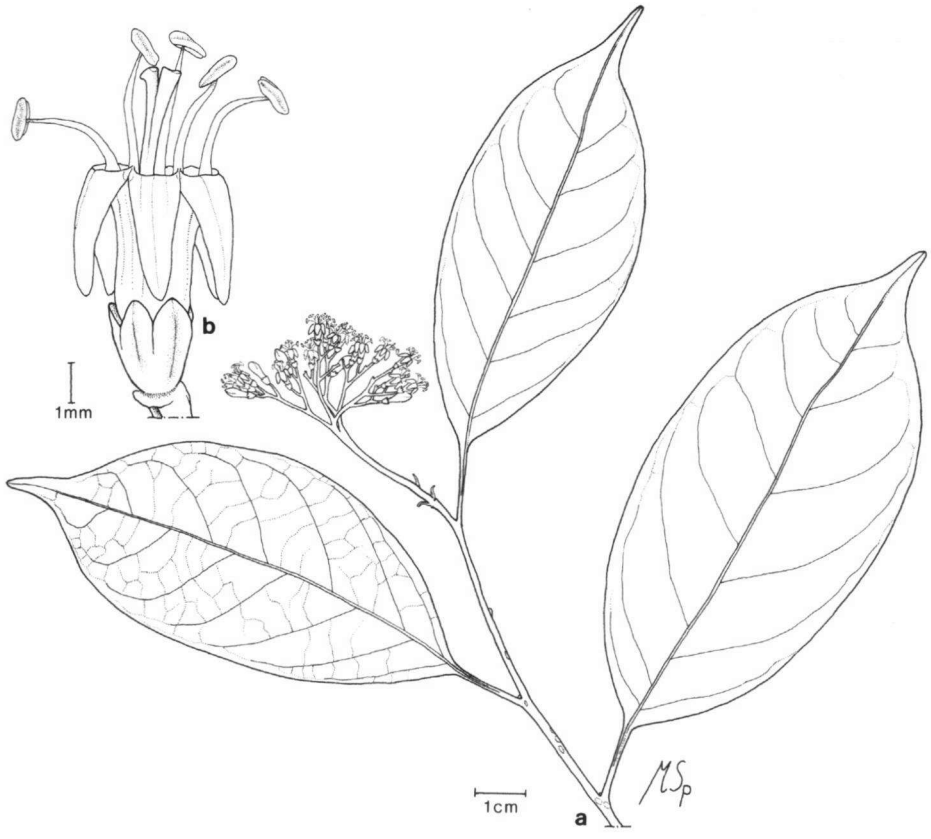

Fig. 6. *Ehretia dichotoma* Blume. a. Top of flowering twig; b. flower (*Blume 692*). Drawing by M. Spitteler.

3. Ehretia dichotoma Blume

Ehretia dichotoma Blume, Bijdr. (1826) 842; I. M. Johnston, J. Arnold Arbor. 32 (1951) 109; Backer & Bakh. f., Fl. Java 2 (1965) 460. — Type: *Blume s. n.* (L holo), Java, Mt Burangrang.

Ehretia laurifolia Decne., Nouv. Ann. Mus. Paris 3 (1834) 395. — Type: *Herb. Timor. 67.*

? Ehretia lucida Span., Linnaea 15 (1841) 334. — Type: not indicated.

Ehretia timorensis auct. non Decne.: Ng in Tree Fl. Malaya 4 (1989) 62; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1966) 101, f. 3 (see note).

Tree, rarely more than 15 m high. Branches brownish to greyish, youngest parts sometimes dark brown, glabrous. *Leaves:* petiole 6–15 mm; blade lanceolate, rarely ovate-lanceolate, 2.5–12 by 1–6 cm, entire, wavy or very rarely repanded-dentate, obliquely rounded to truncate at base, apex acute to acuminate, nerves 5–7 on each side, at wide angles to midrib, the same colour on both sides or paler beneath, glabrous on upper, with hairs in axils of primary nerves at lower side, sometimes folded along midrib. *Inflorescence* terminal on young, lateral branches or axillary, subcorymbose, flowers all at one side of branches of last order, sparsely hairy, with few to numerous flowers; pedi-

cels less than 1 mm. *Calyx* campanulate, 2(–2.5) mm long, 2.25 mm wide, lobes free for 1/3, hairs along margins. *Corolla* white, 4–4.5 mm long, upper border of tube 3.5 mm wide, tube subcylindrical-obconical, lobes reflexed, 2.5 mm long, with revolute margins. *Stamens* very long exserted. *Pistil:* style 5–5.5 mm long, free branches 1–1.25 mm, stigmata 2, discoid-subcapitate, distinct also by colour. *Fruit* globose, 3.5–4(–5) mm in diam. — **Fig. 6.**

Distribution — Andaman Islands, Vietnam; *Malesia:* Sumatra, Malay Peninsula, Borneo, Java, Celebes, Lesser Sunda Islands (Flores, Timor).

Habitat — Dry, evergreen forests, plains, below 1000 m altitude.

Note — In literature on the Malay Peninsula and also in the Tree Flora Sabah & Sarawak, the species has been called *E. timorensis* or *E. laevis* var. *timorensis*, from which it is widely different.

4. **Ehretia javanica** Blume

Ehretia javanica Blume, Bijdr. (1826) 842; Backer & Bakh. f., Fl. Java 2 (1965) 460. — Type: *Blume s.n.* (L holo), Java.

Tree up to 30 m high. Youngest branches dark reddish brown, older ones greyish brown, glabrous. *Leaves:* petioles 1–3.5 cm long; blade broadly lanceolate, ovate-lanceolate, oblong-lanceolate, obovate or suborbicular, 2–13 by 1–7.5 cm, margin entire or somewhat wavy, base obliquely truncate to rounded, apex acute, acuminate or obtuse, nerves 4–6(–7) on each side of midrib, upper side glabrous or with a very few hairs, lower side glabrous. *Inflorescence* terminal on short, lateral branches, subcorymbose, branchlets of last order at very acute angles, glabrous or with very few hairs; pedicels 1–3 cm long. *Calyx* obconical to cup-shaped, sepals 2–3, mostly 2.5 mm long and wide, loosely strigillose, lobes free for 2/3, narrowly triangular with revolute margins. *Corolla* funnel-shaped, 9–10 mm long, 7–8 mm in diam., tube cylindrical-campanulate, lobes explanate, 3 mm long, rounded at apex. *Stamens* shortly exserted (?). *Pistil:* style 12–13 mm long, branches suberect, 2 mm long, stigmata indistinct. *Fruit* ellipsoidal, 10 mm long, 7–8 mm in diam. when compressed.

Distribution — *Malesia:* Java, (Borneo?), Lesser Sunda Islands (Bali, Sumbawa, Flores).

Habitat — Forest, mountain slopes, between 500 and 1200 m altitude.

5. **Ehretia keyensis** Warb.

Ehretia keyensis Warb., Bot. Jahrb. 13 (1891) 424. — Type: from Key Islands (B holo, destroyed).

Tree, 5–10 m high. Branches dilute greyish brown to dark brown and patchy pale grey to fawn, glabrous. *Leaves:* petiole 0.5–2 cm; blade lanceolate to ovate-lanceolate, 2.5–13 by 0.8–7 cm, margin entire, base obliquely truncate to broadly rounded, apex acute to acuminate, nerves 4–7 on each side, glabrous on both sides. *Inflorescence* subterminal to axillary, loosely corymbose with numerous branches, branches with long, stiff, patent hairs, flowers very numerous; pedicels 0.5–5 mm long. *Calyx* cup-shaped,

later flattish salver-shaped, 1.2 mm long, 1.5 mm wide in flower, up to 4 mm in fruit, white pustulate on surface, ciliate along margin of lobes, lobes free beyond middle, triangular to oblong lanceolate. *Corolla* white, as long as calyx, tube slightly shorter than calyx, campanulate, limb 3.5 mm in diam., lobes explanate to slightly recurved, rounded, 1.3 by 1.1 mm. *Stamens* exserted. *Pistil:* style c. 1.5 mm long, divided for 2/3; stigmata subcapitate. *Fruit* globose, 2–2.5 mm in diam.

Distribution — *Malesia:* Key Islands, New Guinea.

Habitat — Swamp fringes, forest remnants, regrowth, thicket and scrubland.

6. **Ehretia laevis** Roxb.

Ehretia laevis Roxb., Pl. Corom. 1 (1796) 42, t. 56; I.M. Johnston, J. Arnold Arbor. 32 (1951) 107. — Type: Plate in Roxburgh, l.c. 'Serigade of the Telingas'.

Shrub or tree. Branches greyish, the youngest ones dark reddish brown, glabrous. *Leaves:* petiole c. 1–2.5 cm long; blade oblong to suborbicular or oblong-lanceolate, 3–9 (–18) by 3–5(–11) cm, margin entire, base broadly rounded to truncate, apex acuminate, rounded or emarginate, nerves 4 or 5 on each side, upper side glabrous, lower side with hairs in the axils of lowest primary nerves. *Inflorescence* axillary, corymbose, with very short hairs, flowers few to many. *Flowers* subsessile or pedicels up to 1 mm long. *Calyx* cup-shaped, (1.2–)1.5–1.8 mm long, c. 3 mm wide, glabrescent, lobes lanceolate, obtuse, free for 2/3. *Corolla* white, 2–2.3 mm long, up to 5 mm in diam., tube cylindrical, surpassing calyx for c. 0.5 mm, lobes explanate to recurved, c. 2 mm long, longer than wide, rounded with often revolute margins. *Stamens* exserted. *Pistil*: style 2.5 mm long, divaricately forked to at least middle, stigmata indistinct. *Fruit* globose, 3–4 mm in diam.

Distribution — India, Hainan, Vietnam, Burma; *Malesia:* Malay Peninsula.

Habitat — No data available.

7. **Ehretia moluccana** Riedl

Ehretia moluccana Riedl, Blumea 38 (1994) 463. — Type: *Beguin 1695* (L holo), Ternate.

Tree (?). Young branches first dark brown, later greyish, glabrous. *Leaves:* petiole 0.5–3 cm; blade lanceolate to oblong-lanceolate or ovate-lanceolate, (3–)5–18 by 1.5–9 cm, margin entire to wavy, base truncate, apex acute to acuminate, nerves 5–7 on each side, glabrous on both sides. *Inflorescence* axillary or terminal on short branches, corymbose with long primary branches, at length broadly expanded, flowers numerous in subcapitate groups crowded at end of branches, with loose, white, patent hairs; pedicels less than 1 mm long. *Calyx* broadly cup-shaped, 1.5 mm long, 2 mm in diam., with loose, patent hairs along margin of lobes, lobes free for 3/4, lanceolate. *Corolla* white, 3.5 mm long, c. 5 mm in diam., tube cylindrical-campanulate, gradually widening towards apex, lobes reflexed to subexplanate, 2.5 mm long, 1 mm wide at base, rounded, but seemingly acute by revolute margins. *Stamens:* filaments long exserted, anthers linear, 1 mm long. *Pistil:* style 4–4.5 mm long, forked for 0.8–1 mm, branches more or less erect; stigmata small, subcapitate, fairly indistinct. *Fruit* not seen.

Distribution — *Malesia:* Moluccas (Ceram, Ternate, Halmahera).
Habitat — Primary forest at very low altitude.
Vernacular name — Gomadedeo.
Uses — Local use as a disinfectant after child-birth and as a contraceptive.

8. Ehretia papuana S. Moore

Ehretia papuana S. Moore, J. Bot. 61 (1923) Suppl., 36. — Type: *Forbes s.n.* (BM holo), New Guinea, Kerepunu.

Shrub (?). Branches fistulose, somewhat compressed, glabrous. *Leaves:* petiole slender, 3–6 cm long; blade broadly ovate-rounded, 6–8 by 5–7 cm, margin entire or somewhat repanded-dentate, base broadly truncate, apex obtuse, nerves 4 or 5 on each side, between main nerves densely reticulate on lower side, glabrous on both sides. *Inflorescence* axillary, shorter than the subtending leaves, few-flowered; bracts leafy, lanceolate, 0.2–1 cm long; pedicels c. 2.5 mm long. *Calyx* 5.5 mm long, lobes free to nearly the middle, ovate, more or less obtuse. *Corolla* short-campanulate, tube slightly shorter than calyx, lobes oblong-spathulate, 3 mm long. *Stamens* shortly exserted, anthers oblong, 1.25 mm long. *Pistil:* style 2.5 mm long, forked divaricately for about 0.25 mm. Mature *nutlets* not seen.

Distribution — *Malesia:* New Guinea.
Habitat — No data available.
Note — The species seems to be known only from the type collection (not seen), but is very distinct from all others as far as can be judged from the author's description, that is translated here.

9. Ehretia parallela C.B. Clarke

Ehretia parallela C.B. Clarke in Hook. f., Fl. Brit. India 4 (1885) 143; Ridl., Fl. Malay Penins. 2 (1923) 442; Ng in Tree Fl. Malaya 4 (1989) 63. — Type: *Griffith K.D. 6004* (K holo; W), Burma, Irawaddy.

Tree. Branches glabrous, greyish. *Leaves:* petiole 0.3–0.5 mm; blade obovate, 1.2–4 by 0.5–2.2 cm, margin entire, base obliquely truncate, apex broadly rounded to obtuse, nerves parallel, 6–9 on each side, glabrous on both sides. *Inflorescence* axillary on a short peduncle (1–2.5 cm), with patent hairs; flowers all on one side of branches of last order, subsessile or on pedicels of 0.5 mm. *Calyx* 2 mm long, shortly strigillose, lobes free for at least 2/3, triangular. *Corolla* white, 7–10 mm long. *Fruit* depressed globose, 2.5 mm long, 3 mm in diam.

Distribution — Burma; *Malesia:* Malay Peninsula.
Habitat — No data available.

10. Ehretia philippinensis A.DC.

Ehretia philippinensis A.DC. in DC., Prodr. 9 (1845) 504; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 691. — Type: *Cuming 471* (G holo), Philippines.

Small tree 4–5 m high. Young branches brown to greenish brown, glabrous. *Leaves:* petiole 1–3 cm long; blade broadly lanceolate to oblong-lanceolate or ovate-lanceolate, (3–)4–15 by 1.5–7.5(–8) cm, margin entire, base attenuate, obliquely truncate, apex acute or acuminate, nerves 4–6 on each side, glabrous or subglabrous on both sides. *Inflorescence* on short, lateral branches or axillary, corymbose, with numerous flowers. *Calyx* broadly cup-shaped, 1.25–1.5 mm long, 1.25–2 mm wide, glabrous or with few hairs along margin of lobes, lobes free to the middle or beyond, triangular. *Corolla* white, 3.5–4(–5) mm long, c. 5 mm in diam., tube cylindrical-campanulate, lobes more or less reflexed, broadly rounded, c. 2.5 mm long. *Stamens* long exserted. *Pistil:* style 4.5–6 mm long, forked for 0.8 mm; stigmata capitate, distinct. *Fruit* subglobose, 3–4 mm in diam.

Distribution — *Malesia:* Philippines (Luzon, Mindanao, Palawan).

Habitat — In forests along rivers and secondary growth at low and medium altitudes.

Note — In the type collection the flowers are especially small.

11. **Ehretia resinosa** Hance

Ehretia resinosa Hance, J. Bot. 18 (1880) 299; I.M. Johnston, J. Arnold Arbor. 32 (1951) 103. — Type: *Swinhoe 12333*, Taiwan.
Ehretia navesii Vidal, Rev. Pl. Vasc. Filip. (1886) 194. — Types: *Vidal 471, 473.*

Tree. Branches dark brown first, greyish to brownish at a later stage, glabrous. *Leaves:* petiole 0.8–3 cm long; blade broadly ovate to ovate-lanceolate, 2–20 by 1.2–10 cm, margin entire, base broadly rounded to subcordate, apex subacute, acute to acuminate, 5–7 primary nerves on each side, with a dense network of minor nerves between them, glabrous to subglabrous on upper side, subglabrous or sparsely hairy mainly along nerves on lower side, young leaves with very dense hairs on lower side. *Inflorescences* on short, lateral branches, densely corymbose, with dense, patent hairs, flowers numerous; pedicels 1–4 mm long. *Calyx* campanulate, 3–4 mm long, c. 2 mm wide in flower, later on lobes patent, 5 mm in diam., densely covered by patent hairs, lobes linear-oblong, obtuse, free to near base. *Corolla* white, 5–6 mm long, up to 9 mm in diam., tube cylindrical-campanulate, lobes 4.5–5 mm long, rounded, reflexed to sub-explanate. *Stamens* long exserted, anthers sagittate. *Pistil:* styles 7 mm long, widened towards apex, forked for 1.5 mm, stigmata fairly indistinct. *Fruit* subglobose, 4–5 mm in diam.

Distribution — Taiwan; *Malesia*: Philippines (Luzon).

Habitat — No data available.

Note — A comparison of plants from Taiwan and from Luzon shows practically no differences, as already Johnston (1951) has suggested.

12. **Ehretia timorensis** Decne.

Ehretia timorensis Decne., Nouv. Ann. Mus. Paris. 3 (1834) 395, non Ridley, Fl. Malay Penins. 2 (1923) 442, nec Ng in Tree Fl. Malaya 4 (1989) 63. — Type: *Anonymous* (P holo), Timor.

Tree (?). Youngest branches dark reddish brown or blackish brown when dry, older ones brownish to greyish brown, often fissured, glabrous. *Leaves:* petiole 0.8–2.2 cm long; blade broadly ovate-lanceolate to obovate, 3–7 by 1.5–4.5 cm, base obliquely truncate, apex obtuse or emarginate, often cuspidate, sometimes folded along midrib, nerves distinct only on lower side, (5–)6–7 on each side, glabrous or with a very few hairs on upper, tomentose in the axils of the primary nerves on the lower side. *Inflorescence* subapical or on lateral branches, corymbose-paniculoid, glabrous, often with flexuous branches, loose, many-flowered; pedicels 0.5–5 mm (in fruit). Fruiting *calyx* up to 2.5 mm long, 4.5 mm in diam., lobes 2 mm long, triangular, ciliate along margins. *Fruit* globose or a little depressed, 4–5 mm in diam., keeled at margin of carpels, with the remnants of the style that is breaking at point of branching.

Distribution — *Malesia:* Lesser Sunda Islands (Timor).

Note — The species is only known from the type collection from which the description was prepared. Flowers are unknown. There are marked differences with all other species in the Malesian area.

DOUBTFUL SPECIES, PROBABLY TO BE EXCLUDED

Ehretia uniflora Roxb., Hort. Beng. (1814) 84, nomen; Fl. Ind., ed. Carey & Wall., 2 (1824) 344. — Type not indicated.

"Shrubby, twiggy. Leaves crowded, subsessile, oblong, entire, hairy. Flowers solitary, sub-sessile. Drupe with 4 one-celled nuts."

Distribution — *Malesia:* Moluccas.

Note — Probably not an *Ehretia.*

HELIOTROPIUM

Heliotropium L., Sp. Pl. (1753) 130; Gen. Pl., ed. 5 (1754) 164. — Type species: *Heliotropium europaeum* L.

Annual or perennial herbs or subshrubs. *Leaves* large to small, alternate, petiolate or sessile. *Inflorescence* usually a unilateral, scorpioid cyme, sometimes 2 cymes close together on dichotomous branches or even a greater number of short cymes crowded together in a head-like manner, with or without bracts that may be foliose or very small and sometimes confined to lower part of cyme. *Corolla* tubular, funnel-shaped or hypocrateriform, white, yellowish to yellow, purple or purplish violet, tube often with an inflated part where the anthers are inserted. *Stamens* included with very short filaments. *Pistil:* style apical, sometimes strongly reduced to nearly absent below stigma, free from the ovary as soon as the pyrenes are separating; stigma[1] a ring-like structure round the style. Mature *nutlets* either remaining undivided with 4 locules or by reduction finally

1) For the sake of convenience the whole structure from the stigmatic ring upwards is as a rule called stigma; it may be cylindric with a basal disc, conical, or cushion-shaped.

with only one fertile locule, or separating into two bilocular pyrenes, most often these pyrenes again separating into 2 unilocular nutlets; surface of nutlets smooth or sculptured in various ways. — **Fig. 7, 8.**

Distribution — A genus of about 250 species in the warm and warm temperate zones of all continents.

Habitat — *Heliotropium* species occur in very diverse habitats, though in general drier places are preferred. Some species are weeds, often introduced from the New World at an early date and now widespread in the palaeotropics.

Uses — *Heliotropium indicum* is reported to be used as a medicinal plant and also sometimes for the production of beverages and dyes [Jansen et al. (eds.), Plant Resources of SE Asia (PROSEA Handb.), Basic List (1991) 234]. *Heliotropium arborescens*, better known under its synonym *H. peruvianum*, is widely cultivated as an ornamental plant and may have escaped cultivation in some places, as it is mentioned for the Malesian region, though cultivation seems to have become obsolete.

Chromosomes — At least four basic chromosome numbers are known in the genus that are not closely related to the taxonomic position of the species from the scattered data available. There are polyploid series known from the basic numbers x = 7 and 8, while from the basic numbers x = 9, 11 and 13 only diploids were found so far.

Notes — 1. *Cochranea* Miers is sometimes regarded as a separate genus mainly South American in distribution, but extending to the Malesian region with *Heliotropium anchusaefolium*. The differences, however, do not seem to justify separation, as they are by no means more profound than those existing between subgenera and sections normally included in *Heliotropium*; *H. anchusaefolium* is the type species of section *Heliophytum*, moreover, and does not even belong to *Cochranea*.

2. Infrageneric classification suffers from the absence of a recent treatment including both Old World and New World species since the time of De Candolle's Prodromus. There is a lack of correspondence between the various local treatments. Malesian native and introduced species belong to sections *Heliophytum*, *Tiaridium*, *Halmyrophila* (= *Platygyne*), *Heliothamnus* and *Orthostachys* according to the most recent system of Johnston [Contr. Gray Herb. 81 (1928) 4], which, however, covers South American taxa only.

KEY TO THE SPECIES

1a. Stigma an umbrella-shaped disc on a short style. Plant more or less succulent .... **4. H. curassavicum**

b. Stigma conical or a ring-like structure surpassed by a tubular apical part. Plants not succulent 2

2a. Leaves broad, ovate to oblong 3

b. Leaves narrowly linear to lanceolate. Fruit not ribbed, separating into 4 nutlets. 6

3a. Fruit separating into 2 bilocular pyrenes. Corolla villous inside .... **1. H. amplexicaule**

b. Fruit not dividing at all or separating into 4 unilocular nutlets. Corolla not villous inside 4
4a. Inflorescence corymbose, composed of branched cymes. Fruit separating into 4 nutlets ..... **2. H. arborescens**
b. Inflorescence spike-like, elongate, not corymbose. Fruit remaining undivided. 5
5a. Apex of carpels profoundly bidentate; carpels 2.5–3 mm long, strongly divergent at last ..... **6. H. indicum**
b. Apex of carpels entire or slightly bidentate; carpels 4–5 mm long, not or scarcely divergent at last ..... **5. H. elongatum**
6a. Inflorescence without bracts. Leaves elliptic to obovate, with silky hairs ..... **8. H. ovalifolium**
b. Inflorescence with bracts, or flowers in axils of leaves 7
7a. Stems and branches more or less prostrate 8
b. Stems and branches erect or branches more or less divaricate 9
8a. Flowers single in axils of leaves, crowded apically ..... **10. H. scabrum**
b. Flowers in terminal short, straight cymes, bracts and flowers alternating on each side ..... **3. H. brevifolium**
9a. Flowers in very dense cymes without any free space between them. Bracts sharply acute, needle-like. Tube of corolla long and slender, strongly inflated by the stamens, surpassing the calyx in length ..... **11. H. ventricosum**
b. Flowers not so dense, arranged in 3–8 mm distance of each other. Bracts not so sharply acute, not needle-like. Tube of corolla shorter, usually not or scarcely surpassing the calyx, only weakly inflated by stamens 10
10a. Style about 1.5 to 2.5 times as long as stigma. Calyx c. 2.5 mm long ..... **9. H. paniculatum**
b. Style about as long as stigma. Calyx c. 1.5 mm long ..... **7. H. madurense**

1. **Heliotropium amplexicaule** Vahl

Heliotropium amplexicaule Vahl, Symb. Bot. 3 (1794) 21; I.M. Johnston, Contr. Gray Herb. 81 (1928) 21. — Type: *Thouin*, Brazil.
Heliotropium anchusaefolium Poir., Encycl. Suppl. 3 (1813) 23. — *Cochranea anchusifolia* (Poir.) Guerke in Engl. & Prantl, Nat. Pflanzenfam. 4, 3a (1894) 97; Backer & Bakh. f., Fl. Java 2 (1965) 462.

Perennial herb, 30–50 cm high. Stem ascending, much branched. *Leaves* more or less crowded, sessile, 4–7 cm long, 1–2 mm wide, oblong, tapering towards base, apex acute, nerves impressed above, prominent beneath, covered with patent bristles on both sides. *Cymes* terminal, branched, 10–15 cm long, with short glandular and longer normal hairs, without bracts. *Calyx* 4 mm long in flower, slightly accrescent, with 5 linear lobes free to near the base, hairs like inflorescence. *Corolla* hairy outside, tube yellow, slightly longer than calyx, hairy above anthers inside, limb explanate, dark purple from a pale base, 6–8 mm in diam., with 5 shallow lobes, plicate. *Stamens* 5, anthers nearly sessile, oblong. *Pistil:* style shorter than the stigma; stigma conical from an annulate

base. *Fruit* breaking up into 2 two-loculate carpels, with membranous pericarp, glabrous, with 2 longitudinal grooves, 3 mm high.

Distribution — South America. Now widespread in tropical regions; *Malesia:* Java, formerly cultivated, now as an escape near Bogor (according to Backer & Bakhuizen f., l.c.).

Habitat — No data available.

2. Heliotropium arborescens L.

Heliotropium arborescens L., Syst. Nat., ed. 10 (1759) 913. — *Heliotropium peruvianum* L., Sp. Pl., ed. 2 (1762) 187, nom. superfl.; Backer & Bakh. f., Fl. Java 2 (1965) 461. — Type: Plate in Mill., Gard. Dict. (1757) 96, pl. 144.

Perennial herb, sometimes with woody base, in its original home also shrub up to 2 m high. Stem much branched. *Leaves* ovate to oblong-elliptic; petiole short, rarely 1–2 cm long; blade 4–8 by 2–4.5 cm, decurrent towards petiole, acute, upper side pubescent or becoming glabrous, lower side paler, with distinct nerves. *Inflorescences* with many short branchlets, scorpioid, dense, scarcely elongated in fruit, strigose to villous, ebracteate. *Calyx* nearly sessile, 3–3.5 mm long, not accrescent after flowering, lobes 5, free to the base, subulate-linear. *Corolla* lavender-purple, tube appressed strigulose, twice as long as calyx, limb 4–5 mm in diam., lobes glabrescent, rounded. *Stamens:* anthers subsessile, crested dorsally by a wavy, antrorse trichome. *Pistil:* style longer than stigma. *Nutlets* 4, pitted, ellipsoid.

Distribution — Peru. Widely cultivated in tropical and temperate countries. *Malesia:* cultivated in Java and possibly elsewhere.

3. Heliotropium brevifolium Wall.

Heliotropium brevifolium Wall. in Roxb., Fl. Ind., ed. Carey & Wall., 2 (1824) 2. — *Heliotropium strigosum* Willd. var. *brevifolium* (Wall.) C.B. Clarke in Hook. f., Fl. Brit. India 4 (1885) 151. — Type: *Wallich Cat. 914* (K holo).

Perennial or annual, decumbent herb. Stems 3–10(–15) cm long, branched mainly in the inflorescence, covered by stiff, antrorsely appressed hairs. *Leaves* sessile, linear, horizontally arranged left and right from the stems, 4–10 by 0.8–1 mm, tapering towards base, acute, with revolute margins, both sides with antrorse, appressed hairs. *Inflorescence* 0.5–3 cm long, spike-like, with 3–12 flowers; bracts similar to leaves, the lowermost excluded shorter than the calyx; pedicels 0.5–0.8 mm long. *Calyx* 1.8–2 mm long in flower, 2.5 mm in fruit, lobes free to base, 0.8 mm wide, subacute, hairs as in the leaves. *Corolla* campanulate, white, 2.5 mm long, hairy outside, tube shorter than calyx, lobes broadly ovoid, rounded. *Stamens:* anthers subsessile, included in the tube. *Pistil:* style a little shorter than stigma; stigma conical from a discoid base, with minute papillae. *Nutlets* 1–1.1 mm high, ovoid, smooth, very densely covered by appressed hairs.

Distribution — India, ?Nepal; *Malesia:* Philippines (Luzon).

Note — The distribution is not yet clear, as *H. brevifolium* has not been recognized as a species separate from *H. strigosum* by many authors. It seems to be most common

in the Philippines, where the greatest number of herbarium specimens comes from, but there are also collections from northern India. Whether there is really a gap between this area and the Philippines seems doubtful.

Already Johnston [J. Arnold Arbor. 32 (1951) 113] pointed out several differences between African and Asian collections of *H. strigosum*. Nevertheless, *H. brevifolium* seems to be different also from the Asian plants mentioned under this name, as, for instance, Johnston describes the ovary as glabrous. In the Malesian area, *H. paniculatum* R.Br. has often erroneously been identified as *H. strigosum*, but Johnston's plants are different from that either.

According to Clarke in Hooker f. (1885), *H. brevifolium*, which he assigns the rank of a variety, is more common throughout India than true *H. strigosum*. Further investigations based on material from all the south-eastern Asian countries are necessary to define species and their area of distribution more exactly.

4. Heliotropium curassavicum L.

Heliotropium curassavicum L., Sp. Pl. (1753) 130; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 695; Backer & Bakh. f., Fl. Java 2 (1965) 461. — Type: *Herb. Cliff. 45* (BM), 'Habitat in Americae calidioris maritimis'.

Annual, prostrate to ascending, more or less succulent herb. Stems much branched, 5–50 cm or more long, glabrous. *Leaves* shortly stalked to sessile, oblong, spathulate, lanceolate to linear, glaucous, 1–5 by 0.3–1 cm, glabrous. *Cymes* spike-like, 3–10 cm long, dense, ebracteate, usually forked once. *Calyx* subsessile, short, cleft to the base into 5 linear, acute lobes, glabrous. *Corolla* 1–2.5(–3) mm long, white or bluish with a yellow centre, tube broadening towards base, longer or equalling the calyx, lobes 5, rounded. *Stamens:* anthers subsessile, sagittate, mucronate at apex. *Pistil:* style indistinct, stigma 0.2 mm long, with a broad, discoid base. *Fruit* breaking up into 4 nutlets; nutlets 1.6–1.8 mm long, wedge-shaped, smooth at first, later sometimes rugulose, glabrous.

Distribution — A native of the Americas from Patagonia to the United States and the West Indies; *Malesia:* occassionally occurring as a weed in widely different places such as Java (near Bogor) and the Philippines.

Habitat — In its native countries in wet places, along the sea shore, etc.

5. Heliotropium elongatum (Lehm.) Cham.

Heliotropium elongatum (Lehm.) Willd. ex Cham., Linnaea 4 (1829) 452; Backer & Bakh. f., Fl. Java 2 (1965) 462. — *Tiaridium elongatum* Lehm., Pl. Asperif. Nucif. (1818) 16. — Type: not indicated.
Heliotropium decipiens Steenis ex Backer, nomen in Backer & Bakh. f., Fl. Java 2 (1965) 462, in syn.

Annual herb up to 60 cm high. Stem simple or with 1 or 2 branches, with few patent, white, bristly hairs and short hairs. *Leaves:* petiole 1.5–4 cm long; blade ovate, 2.5–8 (–10) by 1.5–6 cm, base horizontally truncate, long decurrent, apex acute, with 4–5 primary nerves on each side and a network of nerves of higher order, short strigillose on upper, appressed hairy with longer bristles along main nerves on the lower side. *In-*

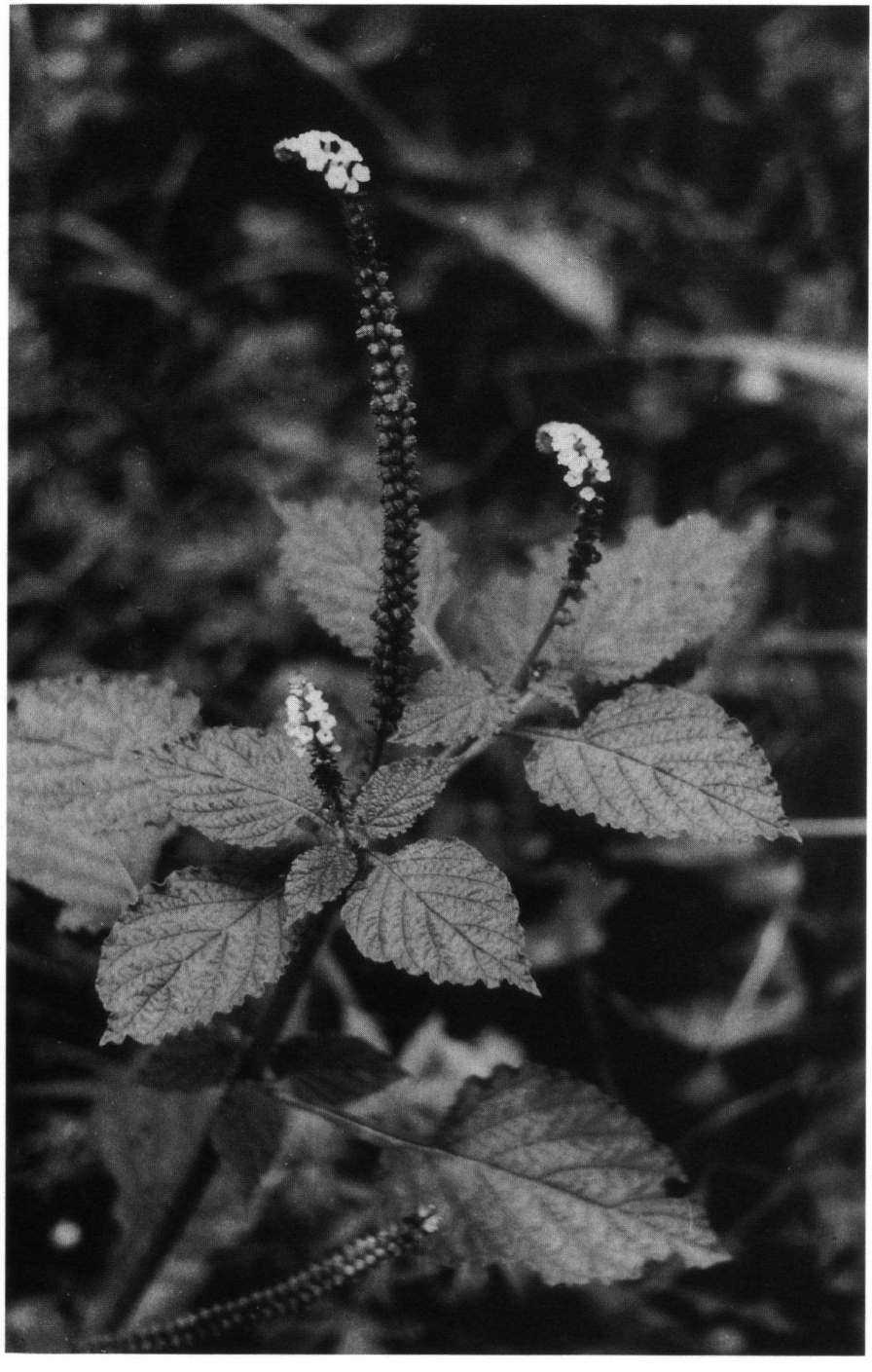

Fig. 7. *Heliotropium indicum* L. Flowering twig. Pontianak, weed in garden. Photo A. Elsener, 1961.

florescence simple, spike-like, elongate, ebracteate. *Calyx* sessile, 2–2.5 mm long, with longer and shorter patent hairs, cleft to the base into 5 linear, acute lobes 0.5 mm wide. *Corolla* salver-shaped, tube 4.5–5 mm long, limb c. 3 mm in diam., first purple, then pale yellowish with a darker centre, at last purple again, lobes rounded, c. 1 mm long. *Stamens:* anthers subsessile at about the middle of the tube. *Fruit* shallowly two-lobed with margins of lobes meeting each other above middle of fruit, parting into 2 two-locular halves.

Distribution — A native of South America; in *Malesia* naturalized in parts of Java (from Bogor to Depok in the West, near Malang and Puger in the East).

Habitat — No data available.

6. Heliotropium indicum L.

Heliotropium indicum L., Sp. Pl. (1753) 130; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 695; Ridl., Fl. Malay Penins. 2 (1923) 441; I.M. Johnston, J. Arnold Arbor. 32 (1951) 111; Backer & Bakh. f., Fl. Java 2 (1965) 462; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 94. — Type: probably in *Herb. Cliff.* (BM), 'Habitat in India utraque'.

Annual herb 15–60 cm high. Stem simple or with few branches, with few patent, bristly hairs and shorter, irregularly directed or retrorse hairs. *Leaves:* petiole 1–9 cm long; blade ovate, (1.5–)2–10(–12) by 0.8–8(–9) cm, base horizontally truncate, long decurrent, apex acute, primary nerves 4–7 on each side, between them a dense network of nerves of higher order, upper side with bristles arising from white tubercles of mineralized cells and short hairs, lower side with dense, white tubercles of mineralized cells and bristly hairs along the nerves. *Inflorescence* spike-like, elongate, cymes 1 to several, 5–20 cm long, ebracteate. *Calyx* sessile, 1.5–2 mm long, with patent, white, bristly hairs, lobes free to base, less than 0.5 mm wide, acute. *Corolla* salver-shaped, with appressed white hairs outside, tube 3–4.5 mm long, limb pale violet, blue or white, throat sometimes orange-yellow, lobes rounded, c. 1 mm long. *Stamens:* anthers subsessile at about middle of tube. *Pistil:* style slightly longer than stigma, the stigma short conical, broadly obtuse. *Fruit* 2–3 mm long, deeply bifid, margins of lobes meeting far below middle of fruit or at very base only, apices divergent, fruit-halves two-celled, cells two-locular, outer partition with one seed, inner one larger, empty. — **Fig. 7.**

Distribution — Probably a native of tropical America, now widespread in all the tropical regions of the world; *Malesia:* Sumatra, Malay Peninsula, Singapore, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands (Lombok, Sumbawa, Sumba, Flores, Timor), Moluccas, New Guinea.

Habitat — Waste lands, botanical gardens, close to ponds, in disturbed areas, etc.

7. Heliotropium madurense Riedl

Heliotropium madurense Riedl, Blumea 38 (1994) 463. — Type: *Backer 20943* (L holo), Madura.
Heliotropium paniculatum auct. non R.Br.: Backer & Bakh. f., Fl. Java 2 (1965) 462.

Annual, 6–35 cm high. Stems reddish brown, branched mainly in the upper half but with few branches often also from near base appearing at a later stage, with short, an-

trorsely appressed hairs. *Leaves* sessile, soon evanescent, linear, 0.7–1.5 by c. 0.1 mm, tapering towards base, apex subacute to obtusish, midrib deeply impressed, no lateral nerves present, margins revolute, covered by antrorse, bristly hairs on lower side arising from one circle of mineralized cells, white incrustations sometimes also present along margins. *Inflorescence* spike-like; lower bracts 2.5 mm, upper ones 1.5 mm long; pedicels 1–1.2 mm long at least in fruit, arising at about 2–3 mm distance from each other, divaricate to suberect. *Calyx* 1.5 mm long, with few appressed, bristly hairs, lobes free to base, ovate, 0.8 mm wide, subobtuse. *Corolla* funnel-shaped, white, 1.8–2 mm long, 1.5 mm in diam., white-powdery with bristly hairs outside, tube as long as calyx, lobes ovate to obovate, subvalvate in bud, 0.8 mm long. *Stamens:* anthers subsessile in upper part of tube, ovate. *Pistil:* style 0.3 mm long, stigma 0.4 mm with a broad disc and a central, obtuse cone. *Fruit* separating into 4 nutlets, constricted at margins of nutlets, 1 mm high, white-powdery on surface. — **Fig. 8.**

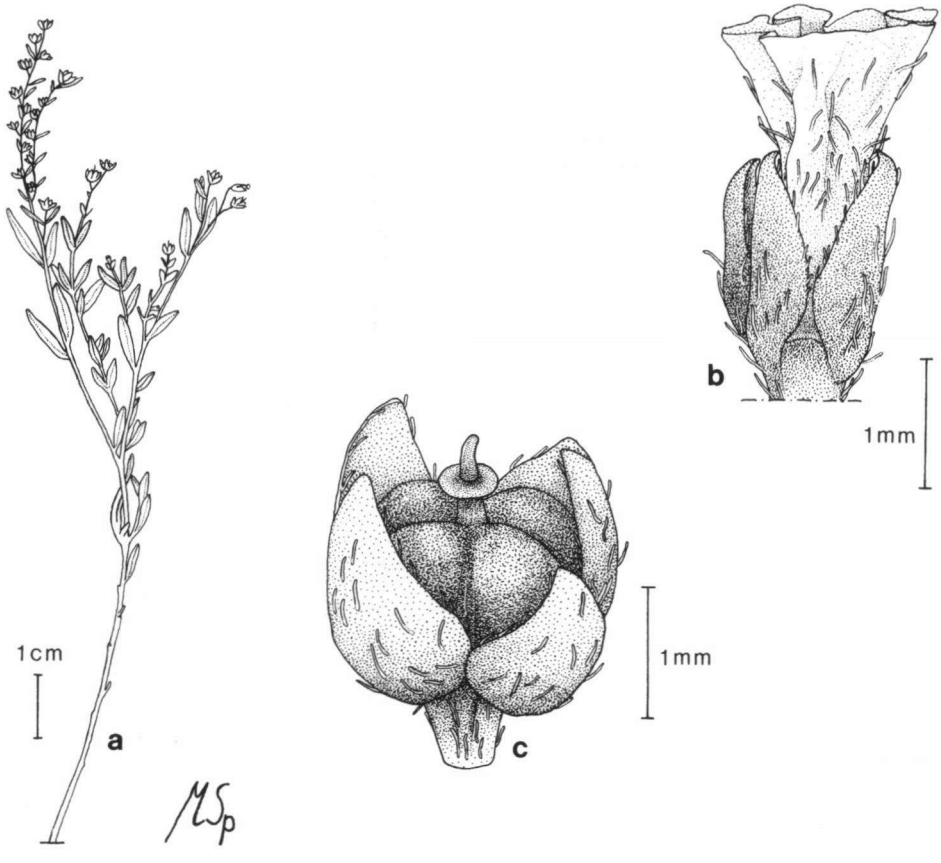

Fig. 8. *Heliotropium madurense* Riedl. a. Top of flowering branch; b. flower; c. fruit in calyx (*Backer 20943*). Drawing M. Spitteler.

Distribution — *Malesia:* endemic to Madura.

Note — The specimens seen are obviously identical with what Backer & Bakhuizen van den Brink (1965) called *H. paniculatum.* These authors also mention as only occurrence the island of Madura.

8. Heliotropium ovalifolium Forssk.

Heliotropium ovalifolium Forssk., Fl. Aegypt.-Arab. (1775) 38. — Type: *Forsskål s.n.* (C holo), Yemen, Hadie.

Perennial herb, sometimes with woody base. Stems up to 40 cm high, much branched, covered by antrorsely appressed, short hairs. *Leaves:* petiole 1–5 mm long; blade oblong-obovate, 10–15 by 3–4 mm, tapering gradually towards base, apex obtuse, rarely subacute, nerves indistinct, hairs on both sides white, silky, antrorse, sometimes a little patent. *Inflorescence* a spike-like, ebracteate cyme, flowers more or less dense, arranged in two ranks; pedicels usually less than 0.5 mm. *Calyx* 2 mm long, cleft to the base, covered densely by antrorse hairs, lobes 0.5–0.6 mm wide, slightly unequal. *Corolla* funnel-shaped, white, 3 mm long, 2 mm in diam., with dense, antrorse hairs outside, lobes ovate-triangular to ovate, 0.8 mm long. *Stamens:* anthers subsessile at middle of tube. *Pistil:* stigma sessile or subsessile, conical from a wider base. *Nutlets* 4, ovoid, densely antrorse hairy.

Distribution — Tropical Africa, Arabian Peninsula, India, Vietnam, Solomon Islands; *Malesia:* Lesser Sunda Islands (Sumba, Timor).

Habitat — In valleys, on road sides, in dried pond, etc.

9. Heliotropium paniculatum R.Br.

Heliotropium paniculatum R.Br., Prodr. Fl. Nov. Holl. 1 (1810) 494. — Type: *R. Brown s.n.* (K holo), tropical Australia.

Perennial, sometimes with woody base, (10–)15–40 cm high. Stem much branched, branches upright to divaricate, stem and branches covered by long, appressed, bristly hairs. *Leaves* sessile, linear to linear-subulate, (0.7–)0.8–2.5(–3) cm long, c. 1 mm wide, base attenuate, apex acute, margin revolute, both sides covered by long appressed bristly hairs. *Cymes* elongate; bracts linear, 3–4 mm long; pedicels 0.5–1 mm long. *Calyx* c. 2.2 mm long, hairs as on leaves, lobes free to the base, lanceolate, acute, 0.8 mm wide. *Corolla* funnel-shaped, white, 2.5–3.3 mm long, 1.5–2 mm in diam., outside with few hairs, tube shorter than calyx, lobes rounded, 0.7–0.8 mm long. *Stamens:* anthers subsessile in tube. *Pistil:* style 1.5–3 times as long as stigma, stigma subulate from a discoid base. *Fruit* separating into 4 nutlets, nutlets ovoid, 0.8–1 mm high, covered with very short, appressed hairs.

Distribution — Australia; *Malesia:* ?Lesser Sunda Islands (Flores, a very untypical specimen, that cannot be assigned to the present species with certainty), New Guinea.

Notes — 1. The species is flowering already in the first year and can, therefore, be mistaken for annual.

2. The plants from Madura under this name belong to *H. madurense*. The specimens from New Guinea have mostly been misidentified as *H. strigosum*, which does not seem to occur in the Malesian region.

10. Heliotropium scabrum Retz.

Heliotropium scabrum Retz., Observ. 2 (1781) 8. — Type: not indicated.
Heliotropium marifolium Retz., l.c.; Backer & Bakh.f., Fl. Java 2 (1965) 462. — Type: *Koenig*.
Heliotropium cyrtostachyum Miq., Fl. Ind. Bat. 2 (1856) 924. — Type: *Horsfield*, Java.

Perennial. Stems prostrate, 5–30 cm long, branched from the base, upper branches very short, covered with antrorsely appressed, white, bristly hairs. *Leaves*: petiole 0–3 mm long; blade linear to lanceolate or lanceolate-oblong, 5–20 by 1–5 mm, base either narrow or rounded, apex acute, margin revolute, hairs as on stem on both sides. *Cymes* subcapitate at end of stems and branches, with leaf-like bracts; pedicels up to 1 mm long. *Calyx* 2.5–3 mm long, lobes free to the base, lanceolate to triangular-lanceolate or ovate-lanceolate, acute, 0.6–0.7 mm wide in flower, up to 1.2 mm in fruit, hairs as in stem. *Corolla* funnel-shaped, white, sometimes with a yellow eye, 3–3.5 mm long, outside covered with stiff hairs, tube much shorter than calyx, lobes ovate-oblong, with wavy margin, 1–1.2 mm long. *Stamens:* anthers subsessile in tube, ovate-oblong, acute, 0.6 mm long. *Pistil:* style 0.4 mm long, stigma slightly longer than style. *Fruit* separating into 4 nutlets, nutlets 1.8–2 mm long, 1.4–1.5 mm wide, ovoid-acute, covered dorsally with short, dense, more or less patent hairs.

Distribution — Pakistan, India, Sri Lanka, Cambodia, Hainan; *Malesia:* Java, Celebes? (identification highly uncertain), Lesser Sunda Islands (Flores). Johnston's (1951) assumption that it also occurs on New Guinea could not be verified.

Habitat — In dunes.

11. Heliotropium ventricosum R.Br.

Heliotropium ventricosum R.Br., Prodr. Fl. Nov. Holl. 1 (1810) 494. — Type: *R. Brown s.n.* (K holo), tropical Australia.

Annual herb. Stem erect, 5–18 cm high, with numerous short, erect branches, with white, more or less patent or appressed hairs. *Leaves* sessile, linear-lanceolate, needle-like, 0.5–1.8 by c. 1 mm, tapering towards base, acute, with revolute margins, hairs dense, white on both sides as in stem. *Cymes* with densely crowded flowers, 1.5–2.5 cm long; bracts leaf-like, longer than calyx; pedicels less than 1 mm. *Calyx* cleft to the base into slightly unequal lobes, 4 lobes 3.5 mm, the fifth 4 mm long, 0.8–1 mm wide, sharply acute, with hairs as in leaves. *Corolla* white, hairy as calyx outside, 4.5–5 mm long, 2.5–3 mm in diam., tube very narrow, strongly inflated above middle by the anthers, lobes elliptical to ovate, 1.2 mm long, curved inwards when young. *Stamens:* anthers subsessile, ovoid, 0.5–0.6 mm long, inserted at about 2/3 of length of tube above base. *Pistil:* style long, filiform in upper part, breaking after flowering above

conical base that is persistent in fruit; stigma short conical. *Fruit* breaking up into 4 nutlets; nutlets short-ovoid, covered with very short, appressed hairs in upper part.

Distribution — Australia; *Malesia:* Lesser Sunda Islands (Timor), Moluccas (Aru), New Guinea.

DOUBTFUL SPECIES

Heliotropium orientale L., Sp. Pl. (1753) 131. — *Lithospermum javanicum* Spreng., Syst. Veg. 1 (1825) 547, nom. illeg.

Annual. Leaves linear, glabrous, without veins, with few lateral flowers.

Note — The species is based on a collection of Houttuyn from Java (Linnaeus only mentions 'Asia'). It seems to be a glabrescent specimen of *Heliotropium scabrum* Retz., and certainly not a member of *Lithospermum*, as Sprengel suggested.

MYOSOTIS

Myosotis L., Sp. Pl. (1753) 131; Gen. Pl., ed. 5 (1754) 165; Stroh, Beih. Bot. Centralbl. 61B (1941) 317; Grau & Leins, Ber. Deutsch. Bot. Ges. 81 (1968) 107; Grau & Schwab, Mitt. Bot. Staatssamml. München 18 (1982) 9. — Type species: *Myosotis scorpioides* L.

Perennial, biennial or annual herbs with alternate, lanceolate, oblanceolate or oblong leaves. Basal *leaves* stalked, stem leaves usually sessile or nearly sessile. *Inflorescence* scorpioid or terminated by a single flower, usually without bracts. *Calyx* on a distinct pedicel, with 5 lobes not free to the base, with straight or hooked appressed or spreading hairs, rarely almost glabrous. *Corolla* rotate or rarely campanulate, usually blue or white, limb 5-lobed, lobes spirally arranged in bud, overlapping marginally; scales (fornices) always present in the throat. *Stamens* with distinct filaments and anthers, that often have a rounded apical, more or less hood-shaped, hyaline appendix. *Ovary* 4-lobed, stigma either distinct, cushion-shaped, or indistinct, club-shaped. *Nutlets* 4, compressed ovoid, smooth, shiny, in the upper part with or without a flat, narrow keel-like margin; areola minute, basal to subbasal, attached to the flat receptacle, with or without caruncula. *Pollen* 3- to 5-colporate, with distinct sculptured areas. — **Fig. 9, 10.**

Distribution — More than 100 species, most common in temperate and subarctic regions of the Old World, but also in the tropics at higher altitudes, section *Exarrhena* with its centre in New Zealand. A few species are also found in temperate North America, one species in Patagonia.

Habitat — Many species grow under humid conditions and there are scarcely any xerophytic groups, but otherwise occurring in a great variety of habitats.

Notes — 1. The genus is unique within the whole family by the spiral arrangement of the corolla lobes in bud. Another unusual feature is the sterile apical appendix of the anthers that consists of several layers of hyaline cells beyond the end of the vascular bundles. It is covered by the epidermis continuous with the rest of the anther and may

Fig. 9. *Myosotis australis* R. Br. a. Plant in flower; b. fruits in calyx (*Stevens & Coode LAE 54511*). Drawing M. Spitteler.

be either semicircular and dome-like or nearly ovoid and longer than wide. Its shape seems to offer a reliable distinctive character for various groups within the genus (Grau & Schwab 1982). Over-all shape as well as length and distribution of papillae of scales and stigma are likewise criteria of importance for systematics and lead to similar groups.

2. There are two distinct types of pollen size. Large-sized pollen is characteristic for species of the southern hemisphere together with the *M. discolor* group in the northern. It seems best suited to characterize section *Exarrhena* in a natural way.

3. Polyploidy is frequent on the basic numbers x = 9, 10, 11, 12. See A.A. Fedorov (ed.), Chromosome numbers of flowering plants (1969) 160.

Taxonomy — As said above, *Myosotis* holds a very isolated position within the *Boraginaceae* and is best taken as the only member of the monotypic tribe *Myosotideae* Rchb. Closest affinities seem to be with *Trigonocaryum* formerly included in *Myosotis* as sect. *Phyllocephalum* Boiss., and probably also with *Trigonotis*.

Strophiostoma DC. was kept as a separate section for the presence of a distinct caruncula, which is a difference in quantity, not in quality, however, as there are small similar structures found also in other groups. At present, only two sections are discerned by authors such as Grau & Schwab (1982). I follow their descriptions here.

Section *Myosotis:* Stigma with small, well differentiated papillae, usually bilobed. Pollen grains small. Scales in corolla throat with long papillae: *M. scorpioides* L.

Section *Exarrhena* DC.: Stigma with large, clavate papillae, usually simple. Pollen grains large. Scales in corolla throat short: *M. australis* R.Br.

Uses — *Myosotis* spp. are frequently grown as ornamentals.

KEY TO THE SPECIES

1a. Hairs of calyx spreading, mostly hooked at apex ..... **1. M. australis**
b. Calyx covered by straight, appressed hairs ..... **2. M. scorpioides**

1. Myosotis australis R.Br.

Myosotis australis R.Br., Prodr. Fl. Nov. Holl. (1810) 494; Van Royen, Pac. Sc. 29 (1975) 80; Alpine Fl. New Guinea 4 (1983) 3090. — Type: *R. Brown* (K), Australia, Port Jackson.

Myosotis saruwagedica Schltr. ex O. Brand in Diels, Bot. Jahrb. 62 (1929) 490. — Type: *Keysser 21* (B, destroyed), New Guinea, Saruwaged Mts.

Perennial herb. Stems arising either round a central rosetta of leaves or at the end of long, subterranean, creeping runners, ascendent, 10–40 cm high, simple or with 1 or 2 branches, hairs spreading in lower, more or less antrorse in uppermost part. *Leaves* oblong, spathulate-oblong or lanceolate-oblong, petiole winged, 1–4(–6) cm long in rosetta leaves, 0–0.5 cm in stem leaves, blade 5–10 by 0.5–1.2 cm in rosetta leaves, 2.5–3.5 by 0.3–0.8 cm in lower, 0.8–2 by 0.3–0.5 cm in upper stem leaves, tapering towards base, obtuse to subacute, hairs denser, antrorse or irregular, arising from a group of mineralized cells or not on lower, looser except on midrib, antrorse or slightly irregular, rarely spreading on upper side. *Inflorescence* short, indistinctly scorpioid first,

Fig. 10. *Myosotis australis* R. Br. Flowering plants (*van Royen 30020*). Murray Pass, Papua New Guinea. Photo P. van Royen, 1965.

strongly elongated, fairly straight later on, rhachis with antrorse hairs sometimes hooked at apex, ebracteate; pedicels 1–2 mm long, hairy. *Calyx* campanulate, 2–2.5 mm long in flower, 3–4 mm soon afterwards, deciduous with nutlets, divided to 4/5 into lanceolate, 0.5–0.8(–1) mm wide, subacute to obtusish lobes; hairs near base reflexed-spreading, others spreading, with hooked apex especially in lower part of calyx, but sometimes in its whole length. *Corolla* funnel-shaped, white to pink, yellowish, bluish, 3.5–4 mm long, about 3 mm in diam., tube 2.5–3 mm long, lobes rounded orbicular, 1–1.5 mm in diam., glabrous; fornices kidney-shaped, yellow. *Stamens:* anthers subsessile, oblong, sometimes apiculate, 1.5 mm long. *Pistil:* style 2.5–4 mm long, filiform, stigma small, clavate. *Nutlets* ovate in outline, compressed, 1.5 mm long, 1 mm wide, in upper part with a flat, broadly obtuse rim, smooth, shining. — **Fig. 9, 10.**

Distribution — New Zealand, Tasmania, temperate Australia; *Malesia:* mountains of New Guinea.

Habitat — Montane to alpine altitudes, in wetter part of grasslands, landslides, deserted gardens (according to Van Royen).

Notes — 1. *Myosotis saruwagedica* has been separated from *M. australis* mainly for differences in the indument. It should have longer, soft hairs especially along the margin. This difference does not hold, when more numerous specimens are compared. Even plants from the Saruwaged mountains do not show the typical characters. No other distinguishing characters could be found.

2. The most obvious peculiarity of the species in the wide sense is the deciduous calyx. In older plants, there are only the pedicels remaining in the lower part of the cymes.

3. According to Grau & Schwab (1982), *M. australis* has pollen grains characterized by a rhomboidal area on the colpi and only loosely verruculous surface, while the rhomboidal area is less distinct and wartlets are dense in the otherwise closely related *M. saruwagedica*. As no correlations to other characters could be found, the value of this difference seems to be rather doubtful.

2. Myosotis scorpioides L.

Myosotis scorpioides L., Sp. Pl. (1753) 131; Backer & Bakh. f., Fl. Java 2 (1965) 464. — Type: *Herb. Cliff. 46* (*β palustris*) (BM).

Perennial with a creeping rhizome, often stoloniferous. Stem erect or ascendent, 15–45 cm high, angular, more or less hairy. Lower *leaves* 4–7 cm long, oblong-lanceolate to obovate-lanceolate, subobtuse, tapering towards base, usually sessile, nearly glabrous or with few appressed hairs; the upper leaves narrowly oblong, often apiculate, smaller. *Cymes* without bracts, single or bifurcate; fruiting pedicels as long as to twice as long as the calyx, spreading (especially in upper flowers) or reflexed. *Calyx* campanulate, 2.5–3 mm long in flower, 4–5 mm in fruit, covered by appressed hairs, cleft to 1/3 or 1/2 into triangular teeth. *Flowers* female or hermaphroditic, distinctly larger in the first case, salver-shaped with a short tube included in the calyx, limb rotate, explanate, 4–10 mm in diam., first pink, later sky-blue, rarely white, lobes rounded-emarginate; fornices yellow. *Stamens:* anthers lanceolate, included in the corolla. *Pistil*: style about as long as tube of calyx or surpassing the calyx in length. *Nutlets* narrowly ovate in outline, obtuse, 1.5 mm long, 1 mm wide, with a narow, flattened border, black, shining.

Distribution — Nearly all Europe, Asia south to N India, N Africa, N America; *Malesia:* introduced in Java and, maybe, other parts of the Malesian area.

Habitat — Often cultivated, especially in mountain areas.

OMPHALODES

Omphalodes Moench, Meth. (1794) 419; Brand in Engl., Pflanzenr., fam. IV.252 (1921) 96. — Type species: *Cynoglossum omphalodes* L. [= *Omphalodes verna* Moench].

Perennial herbs, often with a creeping rhizome, or annuals. *Leaves* alternate, basal leaves or leaves of sterile creepers often different in shape from stem leaves. *Flowers* solitary in the axils of upper leaves or in loose, raceme-like cymes, usually without bracts, pentamerous. *Calyx*-lobes free to the base. *Corolla* cylindrical-campanulate or more often rotate with a short tube and spreading limb; scales in the throat well devel-

oped. *Stamens:* anthers nearly sessile, ovoid. *Pistil:* style shorter than the calyx, usually with a cushion-shaped stigma. *Nutlets* umbilicate dorsally, attached to the small, pyramidate receptacle and surpassing it in length several times, depressed globose to ovoid, with an incurved, entire or toothed margin; embryo straight or rarely curved.

Distribution — About 25 species mainly in the Mediterranean region, Mexico and China, but with few species in Central Europe, Caucasus, etc. *Omphalodes linifolia* is widely cultivated and sometimes escapes from culture.

Note — Basic chromosome numbers seem to be x = 6, 7, 11, but no diploids are known apart from one species with 2n = 22.

Omphalodes linifolia (L.) Moench

Omphalodes linifolia (L.) Moench, Meth. (1794) 419; Backer & Bakh.f., Fl. Java 2 (1965) 463.
Cynoglossum linifolium L., Sp. Pl. (1753) 134. — Type: *Herb. Cliff.* (BM)

Annual; stem slender, 8–30 cm high, simple or branched, slightly angulate. Basal *leaves* stalked, cuneiform, stem leaves linear to lanceolate, rarely ovate, 1–5 by 1–1.6 cm, margin ciliate, surface glabrous on both sides, sometimes with small tubercles of mineralized cells. *Cymes* elongate, without bracts or with one or two bracts at the very base, loose; pedicels much longer than calyx, horizontally spreading at last. *Calyx* 3 mm long in flower, 4–4.5 mm in fruit, cleft to the base into lanceolate-subulate, ciliate lobes. *Corolla* white, rarely bluish, 5.5–7.5 mm long, 8–13 mm in diam., limb divided to middle into rounded lobes; fornices nearly trapeziform. *Pistil:* style very short. *Nutlets* depressed globose, 4 mm in diam., ciliate, crenate-dentate at margin, with a large umbilicus.

Distribution — Southern France, Portugal, Spain; *Malesia:* introduced in Java in cultivation.

Note — No specimens from the Malesian area could be examined. The description is taken from Brand in Engler, Pflanzenreich. According to Backer and Bakhuizen van den Brink, l.c., the plants from Java belong to var. *obtusata* DC., Prodr. 10 (1846) 161 and are described a little different in some details: Plants 15–60 cm high. Leaves elongate-spathulate, 2–10 cm long, 0.25–1.5 cm wide, glaucous, rough from few, scattered hairs. Calyx 4–5 mm long at flowering time, strongly accrescent, with spreading lobes, up to 1.5 cm across. Nutlets ovoid, 4.5–5 mm long, acutely keeled.

ROTULA

Rotula Lour., Fl. Cochinch. (1790) 121; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 693; I.M. Johnston, J. Arnold Arbor. 32 (1951) 14. — Type species: *Rotula aquatica* Lour.
Rhabdia Mart., Nov. Gen. 2 (1827) 136, t. 195; Vidal, Rev. Pl. Vasc. Filip. (1886) 194; Ridl., Fl. Malay Penins. 5 (1925) 323. — Type species: *Rhabdia lycioides* Mart. [= *Rotula aquatica* Lour.].

Shrub with several slender, ascending to prostrate, virgate stems. *Leaves* small, subcoriaceous, sessile or subsessile, on short lateral branchlets. *Inflorescence* a small cyme

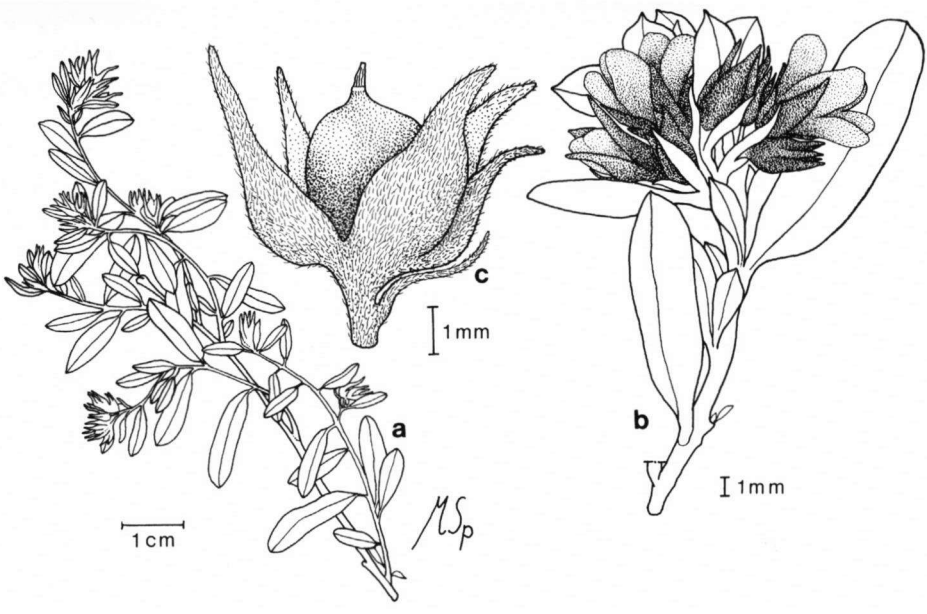

Fig. 11. *Rotula aquatica* Lour. a. Habit of twig; b. inflorescence; c. fruit in calyx (*van Steenis 19578*). Drawing M. Spitteler.

terminating the branchlets and main branches. *Corolla* with a short tube included in the 5-lobed calyx, with 5 spreading, rounded lobes. *Stamens* exserted with filiform, elongate, glabrous filaments. *Pistil:* style apical, slender, undivided, with an indistinctly bilobed stigma. *Fruit* drupaceous, red, with a strongly 4-lobed endocarp breaking up into 4 single-seeded pyrenes at an early stage. — **Fig. 11.**

Distribution — A small genus of 2 (or 3) species occurring in SE Asia, W Africa and eastern Brazil.

Habitat — The species of *Rotula* are restricted to forested, tropical areas, where they grow in rocky, gravelly to sandy places along streams that are periodically inundated for shorter or even longer periods.

Note — Among the SE Asian woody members of *Boraginaceae*, *Rotula* is characterized by leafy short shoots markedly different from the virgate long shoots, similar to the situation in *Carmona*. Its most important distinguishing character from *Ehretia,* to which it is closely related, is the undivided style.

Rotula aquatica Lour.

Rotula aquatica Lour., Fl. Cochinch. (1790) 121; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 693; I.M Johnston, J. Arnold Arbor. 32 (1951) 15. — Type: not indicated.

Rhabdia lycioides Mart., Nov. Gen. 2 (1827) 136; Vidal, Rev. Pl. Vasc. Filip. (1886) 194. — Type: *Martius* (M?), Bahia.

Shrub with many elongate, terete shoots. *Leaves* crowded on numerous lateral short-shoots, subcoriaceous; petiole 0.5–3 mm long; blade 0.6–2.5 by 0.2–0.9 cm, oblanceolate to oblong, strigose or woolly strigillose, rarely glabrous, with indistinct nerves. *Inflorescence* a short, terminal, few-flowered cyme; pedicels in axils of bracts. *Calyx* 4–5 mm long, lobes unequal in width, 0.5–1.5 mm wide. *Corolla* pink to purplish, 5–7 mm long, tube 1–2 mm long, lobes rounded, explanate. *Stamens:* filaments attached above middle of corolla-tube. *Pistil:* style undivided, 4–5 mm long. *Fruit* red, drupaceous, subglobose, 3–4 mm in diam. — **Fig. 11.**

Distribution — Tropical Africa, India, Sri Lanka, southern China, Vietnam, Laos, Thailand, Burma; *Malesia:* Malay Peninsula, Borneo, Philippines, Celebes, New Guinea.

Habitat — See under the genus.

Uses — Medicinal use is recorded in Jansen et al. (eds.), Plant Resources of SE Asia (PROSEA Handb.), Basic List (1991) 244.

TOURNEFORTIA

Tournefortia L., Sp. Pl. (1753) 140; Gen. Pl., ed. 5 (1754) 68; I.M. Johnston, J. Arnold Arbor. 16 (1935) 145; Backer & Bakh. f., Fl. Java 2 (1965) 460. — Type species: *Tournefortia hirsutissima* L.

Tetrandra (DC.) Miq., Fl. Ind. Bat. 2 (1858) 928. — Type species: *Tetrandra wallichii* Miq. [= *Tournefortia tetrandra* Blume].

Messerschmidia L. ex Hebenstr., Nov. Comm. Acad. Sci. Imp. Petrop. 8 (1763) 315, t. 11; I.M. Johnston, J. Arnold Arbor. 16 (1935) 161; 32 (1951) 118; Backer & Bakh. f., Fl. Java 2 (1965) 461; Ng in Tree Fl. Malaya 4 (1989) 58. — Type species: unknown.

Argusia Boehm. in Ludwig, Defin. Gen., ed. Boehmer (1760) 507; Dandy, Reg. Veg. 51 (1967) 28, 121; Bot. J. Linn. Soc. 65 (1972) 256; Heine in Fl. Nouv.-Caléd. 7 (1976) 108; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 95. — Type species: *Argusia sibirica* (L.) Dandy [= *Tournefortia sibirica* L.].

Mallotonia (Griseb.) Britt., Ann. Missouri Bot. Gard. 2 (1915) 47; Heubl et al., Bot. Jahrb. 112 (1990) 154. — Type species: *Tournefortia gnaphalodes* R. Br.

Trees, shrubs (often scandent) or herbs. *Leaves* large or small, alternate or more rarely opposite, sometimes crowded apically on the branches, sessile with narrow base or stalked. *Inflorescences* terminal or lateral, usually dichotomously or trichotomously branched, composed of unilateral cymes without bracts. *Flowers* tetra- or pentamerous. *Corolla* with a short or elongate, cylindrical or sometimes campanulate tube and spreading lobes usually conduplicate in bud. *Stamens* included in the corolla, with very short filaments, sometimes mucronulate at apex. *Pistil:* style almost lacking, stigma with a fertile, basal ring and a sterile apical portion, often bilobed at apex. *Fruit* either a white drupe with juicy mesocarp (sect. *Tournefortia* and sect. *Tetrandra*) or dry, with a corky, vesicular mesocarp, endocarp breaking up into two 2-seeded or four 1-seeded pyrenes. — **Fig. 12, 13.**

Distribution — About 150 species, most of which are native in America, about 15 species in the Old World.

Habitat & Ecology — There are 4 species with corky mesocarp that are confined to coastal areas. Obviously, the special anatomy of the fruit is an adaptation to dispersal by water. Other groups are inhabitants of forested country or rocky places.

Uses — *Tournefortia argentea* is used as a vegetable and the fruits are sometimes also eaten and have antihistaminic properties. *Tournefortia sarmentosa* also has medicinal applications. See Heine in Fl. Nouv.-Caléd. 7 (1976) 110; Jansen et al. (eds.), Plant Resources of SE Asia (PROSEA Handb.), Basic List (1991) 201, 248.

Note — In most publications of more recent times, the genus *Tournefortia* is confined to species with fleshy endocarp, while those with corky endocarp are assigned to *Argusia* Boehm. (= *Messerschmidia* Hebenstr.) with the type species *A. sibirica* (L.) Dandy. *Argusia sibirica* from the coast of the Black Sea to the Pacific coast of Siberia and N China on one side has not much in common with *A. argentea* (L. f.) Heine from the eastern coast of Africa to Australia and Polynesia and *A. gnaphalodes* (L.) Heine from the West Indies (type species of *Mallotonia*) on the other. Either three genera have to be recognized or *Tournefortia* must be taken in a wide sense to include all three as sections. The present author prefers to adopt the latter solution of the problem.

KEY TO THE SPECIES

1a. Endocarp spongy. Trees ..... **1. T. argentea**
b. Endocarp fleshy, fruit a drupe. Usually climbing shrubs 2
2a. Flowers tetramerous. Leaves paler on lower side, nerves forming a dark reddish brown pattern when dry ..... **7. T. tetrandra**
b. Flowers pentamerous. Leaves not like that on lower side 3
3a. Leaves distinctly opposite. Flowers sessile 4
b. Leaves alternate. Flowers sessile or shortly stalked 5
4a. Base of leaves cordate to horizontally truncate, or, if rounded, leaves lanceolate. Calyx lobes triangular to lanceolate-triangular, free for two thirds of their langth .. .. **2. T. luzonica**
b. Base of leaves rounded, rarely obliquely truncate. Calyx lobes linear lanceolate, free for most of their length, at least for three quarters ..... **5. T. oppositifolia**
5a. Corolla only 2.5 mm long ..... **3. T. minutiflora**
b. Corolla at least 5 mm long 6
6a. Flowers with a short pedicel. Fruit breaking up into 2 two-celled pyrenes. Leaves greyish tomentose on lower side ..... **4. T. muelleri**
b. Flowers sessile. Fruit breaking up into 4 one-celled nutlets. Leaves not tomentose on lower side, the same colour as above or a little paler ..... **6. T. sarmentosa**

1. Tournefortia argentea L. f.

Tournefortia argentea L. f., Suppl. Plant. (1781) 133; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 693; Ridl., Fl. Malay Penins. 2 (1923) 440. — *Messerschmidia argentea* (L. f.) I.M. Johnston, J. Arnold Arbor. 16 (1935) 164; 32 (1951) 121; Backer & Bakh. f., Fl. Java 2 (1965) 461; Ng in Tree Fl. Malaya 4 (1989) 64. — *Argusia argentea* (L. f.) Heine in Fl. Nouv.-Caléd. 7 (1976) 109; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 95, f. 1. — Type: *Koenig*, Sri Lanka.

Tree or shrub, 1–10 m high. Branches greyish, densely covered by soft, greyish white hairs. *Leaves* crowded at apex of branches; petiole 5–25 mm long, winged; blade

Fig. 12. *Tournefortia argentea* L. f. Flowering plants. Photo from Flora Malesiana archives, origin unknown.

oblanceolate to obovate, 10–20 by 3–8 cm, with entire margin, base long tapering towards petiole, apex obtuse to broadly rounded, nerves more or less distinct, both sides greyish white tomentose. *Inflorescence* terminal, subcorymbose to paniculoid, branched several times successively in dicho-, tricho- and tetrachotomies, branches of last order scorpioid cymes, peduncle 5–15 cm long. *Flowers* numerous in two ranks, sessile. *Calyx* 1.5–2 mm long, tomentose from dense, appressed hairs outside, glabrous inside, with 5 triangular-lanceolate to suborbicular lobes. *Corolla* white to pinkish white, 3–4 mm long, 4–7 mm in diam., salver-shaped, tube campanulate, about as long as calyx, lobes ovate to orbicular, pubescent outside. *Stamens:* filaments inserted 0.4–0.8 mm above base of tube, anthers exserted for half their length. *Pistil:* stigma sessile, with 2 conical apices. *Fruit* depressed-globose, 5–8 mm in diameter, with spongy wall. — **Fig. 12.**

Distribution — Coasts of E Africa, across the Indian Ocean, Ryukyu, Taiwan, Hainan, Vietnam, northern Australia to Polynesia, New Caledonia; *Malesia:* Sumatra, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands (Bali, Lombok, Timor), Moluccas, New Guinea.

Habitat — Sandy beaches, etc.

2. Tournefortia luzonica I.M. Johnston

Tournefortia luzonica I.M. Johnston, J. Arnold Arbor. 16 (1935) 156. — Type: *Adduru 237* (A, K), Luzon.

Creeper or liana. Branches dark reddish brown, with very dense, crispulate hairs. *Leaves* arranged strictly opposite; petiole 8–15 mm, blade ovate to oblong-lanceolate, 4–12 by 1.2–5.5 cm, entire, base horizontally truncate to subcordate, apex acute to acuminate, densely covered by subappressed, irregularly directed hairs on both sides or hairs sparse. *Inflorescences* terminal and axillary, composed of short, very dense cymes, branches of last order dichotomous, divaricate, not elongated in fruit. *Flowers* sessile, arranged in 2 ranks. *Calyx* 3–3.5 mm long (Johnston: 1–2.5 mm), covered by very dense, patent hairs, lobes 5, free to the base, linear, 0.6–0.7 mm wide. *Corolla* greenish, salver-shaped, 9–10 mm long, 3.5–4 mm in diam. (Johnston: 5 by 2–2.5 mm), densely appressed hairy outside, tube cylindrical, lobes ovate, rounded, 1.5 mm long. *Fruit* ovoid-globose, 2.5 mm long, 2 mm in diam. when dry, wall fleshy.

Distribution — *Malesia:* Philippines (Luzon), New Guinea (Biak I.).

Habitat — Mountainous regions.

Note — Johnston (1935) gives much smaller measurements (in brackets in the above description) for calyx and corolla than were found in material from Leiden. The identity, however, is clear from the strictly opposite leaves.

KEY TO THE SUBSPECIES

1a. Leaves greyish from dense, short hairs ..... **a.** subsp. **luzonica**
b. Leaves never greyish, subglabrous to scabridulous hairy 2
2a. Leaves only with very few hairs, shining, ovate to ovate-oblong or ovate-lanceolate ..... **c.** subsp. **sublucens**
b. Leaves scabridulous on upper, densely hairy along nerves on lower side, more or less lanceolate ..... **b.** subsp. **angustissima**

a. subsp. **luzonica**

Greyish from dense short hairs.

Distribution — Northern, East-central and Southern Luzon, New Guinea (Biak I.).

b. subsp. **angustissima** Riedl

Tournefortia luzonica I.M. Johnston subsp. *angustissima* Riedl, Blumea 41 (1996) 443. — Type: *Ridsdale 1477* (L holo).

Distribution — Luzon, only known from type locality: prov. Zambales, Santa Cruz.

Ecology — On ultrabasic soils.

c. subsp. **sublucens** (I.M. Johnston) Riedl

Tournefortia luzonica I.M. Johnston subsp. *sublucens* (I.M. Johnston) Riedl, Blumea 41 (1996) 443. — *Tournefortia luzonica* var. *sublucens* I.M. Johnston, J. Arnold Arbor. 16 (1935) 157. — Type: *Ramos & Edaño 44553* (A, BM, K), Zambales Prov.

Distribution — West-central Luzon.

3. Tournefortia minutiflora Riedl

Tournefortia minutiflora Riedl, Blumea 41 (1996) 443. — Type: *Ivalaoa UPNG 7752* (L holo; K, LAE, UPNG), Papua New Guinea, Gulf Prov.

Shrub with very long, rope-like branches resting upon each other (climbing shrub?). Branches dark purple-brown with short, white, conical hairs bulbous at base. *Leaves* alternate, petiole 1–2 cm long, blade (3–)6–14 by (1–)2–7 cm, ovate to ovate-oblong, shortly acuminate, rounded at base, glabrous and shining on upper, asperulous with short, stiff hairs along middle nerve on lower side like petiole, nerves 8–10 on each side. *Inflorescence* sublateral, repeatedly dichotomously branched, with asperulous axes; branches of last order bearing flowers in two rows on their whole length, scorpioid, 2.5–3 cm long. *Calyx* sessile, 1–1.2 mm long, shortly patent-hairy, divided into short, lanceolate, acute lobes in its distal half. *Corolla* 2.5 mm long, folded longitudinally in juvenile state, salver-shaped, densely, more or less appressed hairy outside, tube nearly cylindrical, 2 mm long, limb up to 1.5 mm wide, with very short, acute lobes. *Fruit* not seen.

Distribution — Papua New Guinea, only known from the type collection.

Habitat — Tidal regrowth.

4. Tournefortia muelleri I.M. Johnston

Tournefortia muelleri I.M. Johnston, J. Arnold Arbor. 16 (1935) 157. — *Tournefortia mollis* F. Muell., Fragm. 1 (1858) 59, nom. illeg., nec Bertoloni (1852). — Type: *F. von Mueller* (K iso), Australia, Burdekin R.

Shrub or subshrub, 1–2.5 m high. Branches reddish brown, with dense, white, short, patent hairs. *Leaves:* petiole 5–25 mm long; blade ovate-lanceolate, ovate or rarely lanceolate, 2.5–10 by 1–6.5 cm, margin entire, base oblique to horizontally truncate, sometimes slightly decurrent in petiole, apex acute, acuminate or rarely obtuse, nerves impressed above, prominent below, upper side slightly rough from few appressed stiff hairs, lower side densely soft tomentose. *Inflorescence* composed of 3–5 more or less distinctly stalked cymes on 2 or 3 dichotomies, not much elongated after flower, terminal or lateral, with numerous sessile flowers in 2 ranks. *Calyx* campanulate, 2.5 mm long, 1.5 mm wide, densely strigulose outside and inside, lobes lanceolate from a wider base, 0.7–0.8 mm wide, acute, free to base. *Corolla* salver-shaped, white, 5–8 mm long, 3.5(–4) mm wide, densely strigulose outside, tube cylindrical, lobes ovate-oblong, rounded, entire, 1.2 mm long. *Stamens* inserted at or above middle of tube. *Pistil:* stigma subsessile, conical. *Fruit* depressed-subglobose to subglobose-pear-shaped, 2.5 mm long and wide or 2.7 mm wide when dry, wall fleshy.

Distribution — Northern Australia; *Malesia:* ?Java (Merapi), Philippines, Lesser Sunda Islands (?Bali, Sumba), New Guinea. In the case of Java, only Merapi is mentioned on the label, but no particular island. In the case of Bali, the identification is a little doubtful.

Habitat — Along rivers and in tidal area.

5. Tournefortia oppositifolia Riedl

Tournefortia oppositifolia Riedl, Blumea 41 (1996) 444. — Type: *van Balgooy 4885*, Moluccas, Buru.

Climber. Young twigs, petioles, leaves and inflorescence nearly glabrous or with a few, rarely more numerous hairs. Branches dark brown, finely longitudinally sulcate. Apart from the two uppermost ones *leaves* opposite or subopposite, ovate to ovate-lanceolate; petiole 5–20 mm long, sometimes flexuous as if used to attach to some minor branches; blade 3–10 by 1.5–5.5 cm, acuminate, broadly rounded at base, subglabrous or more or less densely short hairy especially on lower side, with 6 to 7 primary nerves on each side. *Inflorescence* terminal or sublateral, dichotomously branched several times, contracted or with long, divaricate primary branches, with dense, sessile or shortly (up to 1 mm) stalked in one and the same plant. *Calyx* 1.5—1.8 mm long, shortly hairy, lobes 5, spreading, narrowly linear-lanceolate to linear, acute, free to near base or at least for three quarters. *Corolla* white, c. 8 mm long, shortly hairy, tube narrowly cylindrical, limb short, salver-shaped, 1.8(–2) mm in diam., lobes triangular, acute. *Fruit* breaking up into two 2-celled pyrenes with a distinct keel at suture, only known in immature state, at that time ovoid, 2 mm long, 1.3 mm wide, green, white in mature state according to collector; stigma sessile, narrowly conical, c. 0.8 mm long, with a widened, deeply bilobed apex.

Distribution — *Malesia:* Moluccas, Buru, only known from type locality: SE of Bara (NW Buru).

Habitat — Riverine forests dominated by *Casuarina* at about 200–250 m altitude.

6. Tournefortia sarmentosa Lam.

Tournefortia sarmentosa Lam., Tab. Encycl. 1 (1791) 416; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 694; I.M. Johnston, J. Arnold Arbor. 16 (1935) 147; 32 (1951) 115; Backer & Bakh. f., Fl. Java 2 (1965) 460. — Type: *Sonnerat* (P holo), Mauritius, cultivated.

Tournefortia tetrandra Blume, Bijdr. (1826) 845. — Type: unknown.

Tournefortia urvilleana Cham., Linnaea 4 (1829) 465; Miq., Fl. Ind. Bat. 2 (1858) 927. — Type: *Chamisso* (LE), Luzon.

Tournefortia hirsuta Reinw. ex Boerl., Handl. Fl. Ned. Ind. 2 (1899) 487, nomen, in syn.

Tournefortia horsfieldii Miq., Fl. Ind. Bat. 2 (1858) 927; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 694. — Type: *Horsfield*, Java.

Tournefortia macrophylla K. Schum. & Lauterb., Fl. Deutsch. Schutzgeb. Südsee (1901) 520. — Type: *Lauterbach 2003* (B, destroyed), Papua New Guinea.

Tournefortia sarmentosa Lam. var. *magnifolia* Domin, Bibl. Bot. 89 (1928) 1097. — Type: *Dietrich 724*, Queensland.

Tournefortia glabrifolia Domin, BIbl. Bot. 89 (1928) 1098. — Type: *Domin*, Queensland.

Creeper or liana. Young branches dark brown, covered loosely by short, patent to subappressed hairs. *Leaves:* petiole 7–20 mm long; blade oblong-lanceolate to ovate lanceolate, 4–15 by 1.7–7 cm, margin entire, base rounded to truncate, apex acuminate, main nerves distinct especially below, upper side with a very few hairs, dense, minute whitish groups of mineralized cells usually present, lower side loosely appressed strigulose with irregularly directed hairs. *Inflorescence* dichotomously branched several times,

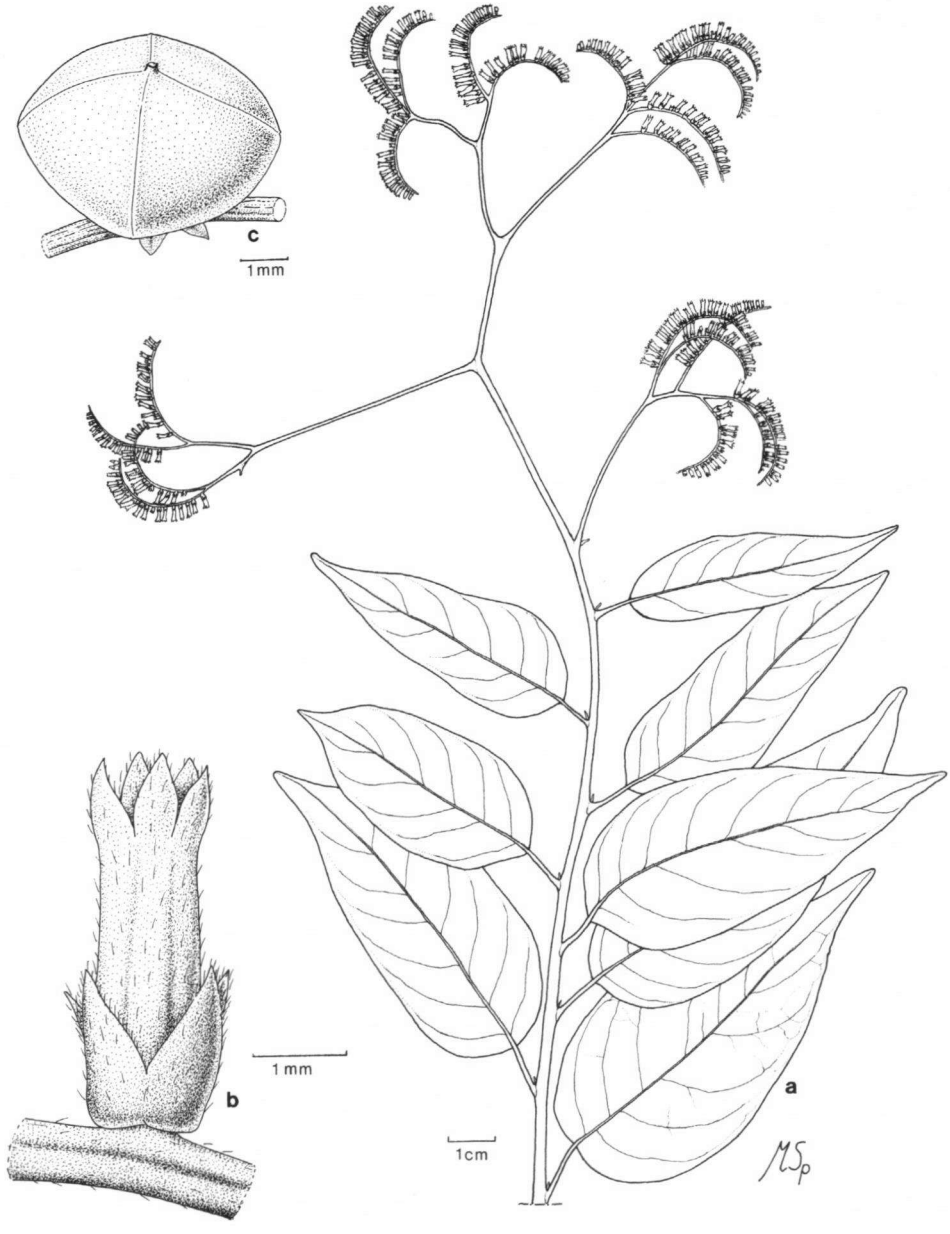

Fig. 13. *Tournefortia sarmentosa* Lam. a. Flowering branch; b. flower; c. fruit (*Sulit & Conklin PNH 16900*). Drawing M. Spitteler (a), J.H. van Os (b, c).

cymes dense when flowering, strongly accrescent and loose in fruit, terminal and axillary. *Flowers* numerous in 2 ranks, sessile. *Calyx* cup-shaped, 1.5–2 mm long, 3 mm wide, with appressed to patent short hairs on outer and inner side, lobes 5, free to base,

ovate-acuminate, 0.7–0.8 mm wide. *Corolla* salver-shaped, 6–9(–10) mm long, 4 mm in diam., densely strigulose outside, tube cylindrical, slightly narrower in lowest third, lobes plicate, ovate, acuminate, up to 2 mm long. *Stamens* inserted above middle of tube. *Fruit* depressed ovoid-subglobose, ribbed at border of pyrenes, rostrate, 2.5 mm long, 2.8 mm in diam. when dry, wall fleshy. — **Fig. 13.**

Distribution — Australia (N Queensland), Taiwan; *Malesia:* Sumatra, Malay Peninsula, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands (Lombok, Flores, Timor, Alor, Wetar), Moluccas, New Guinea.

Habitat — Dry areas, especially near sea; thickets (Backer & Bakhuizen f., l.c.).

7. **Tournefortia tetrandra** Blume

Tournefortia tetrandra Blume, Bijdr. (1826) 845; Steud., Nomencl. ed. 2, 2 (1841) 694 (*'tetragona'*); I.M. Johnston, J. Arnold Arbor. 16 (1935) 150; Backer & Bakh. f., Fl. Java 2 (1965) 460; Ng in Tree Fl. Malaya 4 (1989) 65. — Type: *Blume s.n.* (L holo), Java.

Heliotropium scandens Noronha, Verh. Bat. Genootsch. 5 (1827) 78; Hassk., Cat. Hort. Bog. (1844) 137. — Type: not indicated.

Tournefortia tetrandra Blume var. *glabra* Hassk., Flora 25/2, (1842), Beibl. 27; Cat. Hort. Bog. (1844) 77; Pl. Jav. Rar. (1848) 492. — *Tournefortia glabra* (Hassk.) Zoll. & Mor. ex Zoll., Nat. Geneesk. Arch. Ned. Ind. 2 (1845) 5. — *Tetrandra glabra* (Hassk.) Miq., Fl. Ind. Bat. 2 (1858) 929. — Type: *Hasskarl*, Java.

Tournefortia wallichii DC., Prodr. 9 (1845) 527. — *Tetrandra wallichii* (DC.) Miq., Fl. Ind. Bat. 2 (1858) 928. — Type: *Wallich 911*, Singapore.

Tournefortia tetrandra Blume var. *angustifolia* Mor., Syst. Verz. (1845-46) 52, nomen nudum.

Tournefortia tetrandra Blume var. *longiflora* Hassk., Pl. Jav. Rar. (1848) 492. — Type: unknown.

Tetrandra zollingeri Miq., Fl. Ind. Bat. 2 (1858) 928. — Type: to be typified.

Creeper or liana. Branches smooth, greenish or reddish brown, with short, appressed hairs in herbaceous parts. *Leaves:* petiole 4–10 mm; blade ovate-lanceolate to lanceolate, 3–10 by 1–5 cm, margin entire to crenulate, base obliquely truncate, rarely subcordate, apex acute, nerves distinct on both sides, prominent and darker on pale lower surface when dry, short stiff hairs arising from tubercles of mineralized cells and such tubercles without hairs on upper, few stiff, short, appressed hairs mainly along nerves on lower side. *Inflorescence* branched, bearing cymes as branches of last order, terminal and/or lateral. *Flowers* subsessile, numerous in 2 ranks. *Calyx* narrowly cylindrical and tapering towards apex in flower, more explanate in fruit, 2.5 mm long, with few hairs mainly along margins, densely strigose on inner side, lobes 4, acuminate from a wider base, 0.7–0.8 mm wide. *Corolla* cylindrical, greenish to yellow, 9–10 mm long, 1–1.2 mm wide, lobes 4, erect, acute, folded along the middle. *Stamens* inserted at about the middle of the tube. *Fruit* depressed globose, with 2 beaks, 4 mm long and in diam., wall fleshy.

Distribution — Nicobar Islands, Sri Lanka; *Malesia:* Anambas and Natuna Islands, Sumatra, Malay Peninsula (according to Johnston 1935), Borneo, Java, Philippines, New Guinea.

Habitat — Mountain forests and scrubs.

Vernacular name — Ojot sisier (Sumatra).

TRICHODESMA

Trichodesma R.Br., Prodr. Fl. Nov. Holl. (1810) 496; Brand in Engl., Pflanzenr., fam. IV.252 (1921) 19. — Type species: *Borago zeylanica* Burm. f. [= *Trichodesma zeylanicum* (Burm. f.) R.Br.].

Annual or perennial herbs, sometimes suffrutescent. *Leaves* alternate or opposite, sessile or stalked. *Cymes* loose, often many-flowered, usually with bracts that may be similar to the upper stem leaves. *Flowers* pentamerous. *Calyx* on distinct, often fairly long pedicels, strongly accrescent in fruit, lobes free to the base or united in part. *Corolla* more or less rotate to funnel-shaped with a short tube and long-acuminate to cuspidate lobes, without scales in the throat. *Stamens:* anthers subsessile in the tube, oblong to linear, with long sterile awns that are twisted round each other. *Ovary* not divided in flower; style filiform, stigma small, globose. *Nutlets* 4, ovoid, triquetrous or nearly globose, smooth or rugose, sometimes hairy, with or without a distinct margin. — **Fig. 14, 15.**

Distribution — About 40 species in subtropical and tropical regions of Africa, Asia and Australia.

Uses — Both species from the Malesian region are used for medicinal purposes.

Notes — 1. Basic chromosome numbers are x = 7, 11, 12.

2. Brand (l.c.) divided the genus into 6 sections exclusively on characters of the fruits such as glabrous, bristly or hairy, marginate or immarginate, smooth or rugose. Both Malesian species belong to section *Leiocaryum* A.DC., which, including the type species *T. zeylanicum*, however, has to repeat the generic name *Trichodesma*. The section is characterized by smooth, shiny, immarginate nutlets.

KEY TO THE SPECIES

1a. All leaves sessile with a broad base. Calyx sagittate at base ..... **1. T. indicum**

b. Lower leaves with a short stalk or at least tapering towards base. Calyx truncate at base ..... **2. T. zeylanicum**

1. Trichodesma indicum (L.) Sm.

Trichodesma indicum (L.) Sm. in Rees, Cyclop. 36/1 (1817) n. 1; C.B.Rob., Philipp. J. Sc., Bot. 4 (1909) 696; Brand in Engl., Pflanzenr., fam. IV.252 (1921) 38. — *Borago indica* L., Sp. Pl. (1753) 137. — Type: *Herb. Linn. 188/2* (LINN).

Annual herb. Stems 15–40 cm high, much branched, with spreading, not very dense hairs. *Leaves* sessile, oblong, lanceolate or lanceolate-oblong, lower leaves 5–8 by 0.8–2.2 cm, upper leaves 2–4.5 by 0.3–1.2 cm, base in lowermost leaves narrow, in the others broadly rounded, semiamplexicaulous, apex acute or obtusish, midrib distinct, sometimes also a few other nerves visible, hairs spreading-antrorse, arising from groups of mineralized cells on upper side, loose, crispulate on lower side. *Inflorescence* terminal on stem and branches, leafy, flowers axillary; pedicels 0.8–1.8 cm, curved downwards in fruit, with long, dense, spreading hairs. *Calyx* c. 1 cm long in flower, up to 1.3 cm in fruit, cleft to the base into narrowly triangular, basally sagittate lobes 1.2 mm

wide in flower, 2 mm wide in fruit, hairs loose, spreading from mineralized cells. *Corolla* funnel-shaped, lilac, tube c. 5 mm long, limb 1.3–1.5 cm in diam., lobes broadly rounded-acuminate, 7 mm long and wide. *Stamens:* anthers oblong, sterile, twisted apex 4–5 mm long, densely woolly. *Pistil:* style as long as calyx. *Nutlets* oblong ovoid, 5 mm long, 2–3 mm wide, smooth, whitish.

Distribution — Afghanistan, Pakistan, India, Burma (a separate variety), Mascarene Islands; *Malesia:* Philippines.

Habitat — Dry, sunny places, fields.

2. **Trichodesma zeylanicum** (Burm. f.) R.Br.

Trichodesma zeylanicum (Burm. f.) R.Br., Prodr. Fl. Nov. Holl. (1810) 496; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 696; Brand in Engl., Pflanzenr., fam. IV.252 (1921) 40; Backer & Bakh. f., Fl. Java 2 (1965) 462. — *Borago zeylanica* Burm. f., Fl. Ind. (1768) 41. — Type: Burman f., Fl. Indica t. 14, f. 2.

KEY TO THE VARIETIES

1a. Leaves oblong, oblong-lanceolate or broadly lanceolate, 0.8–4 cm wide ..... **a.** var. **zeylanicum**

b. Leaves linear to narrowly linear-lanceolate, sericeous, up to 0.5 cm wide ..... **b.** var. **sericeum**

a. var. **zeylanicum**

Trichodesma zeylanicum (Burm. f.) R.Br. subsp. *eu-zeylanicum* Brand var. *vulgare* Brand f. *typicum* Brand & f. *longifolium* Brand in Engl., Pflanzenr., fam. IV.252 (1921) 41.

Annual, up to 1.75 m high. Stem much branched, angular, covered by spreading long hairs from groups of mineralized cells and very numerous short hairs. *Leaves* sessile, broadly lanceolate, lower leaves 6–12(–16) by 1–3(–5.5) cm, upper leaves 3–6 by 0.3–1.5 cm, base narrow, rounded, apex acute, midrib and several primary nerves strongly protruding on lower side, strigose to spreading bristly with hairs from groups of mineralized cells on upper, with few spreading, long bristles and denser, often antrorse, short hairs on lower side. *Cymes* scorpioid towards apex, rhachis with spreading long and appressed short hairs or only appressed hairs, basally leafy, leaves gradually decreasing in size, becoming bract-like towards apex; pedicels 0.8–3 cm long, with soft, appressed to spreading, flexuous hairs turning fuscous in plants from Madura. *Calyx* (1.2–)1.5–1.8 cm in flower, up to 2 cm in fruit, cleft to the base into long acute, 3(–4) mm long lobes, hairs appressed, silky, to spreading, usually white, turning fuscous in plants from Madura. *Corolla* funnel-shaped, bluish with 5 red dots, or violet, pink, or white, tube c. 8 mm long, limb 1.5–2(–2.5) cm in diam., lobes suborbicular or wider than long, 0.7–1 cm long, apiculate. *Stamens:* anthers shorter than awns, awns twisted, 0.8–1 cm long, with long hairs horizontally wound around anthers. *Pistil:* style 0.6–1.2 cm long, filiform. *Nutlets* ovoid, 5 mm long, c. 2 mm wide, smooth, shining, brown. — **Fig. 14, 15.**

Distribution — NE and E Africa, Comores, Madagascar, Mascarene Islands, India, Sri Lanka; *Malesia:* Java (Madura), Philippines, Lesser Sunda Islands (Flores, Sumba, Timor, Alor), New Guinea.

Fig. 14. *Trichodesma zeylanicum* (Burm. f.) R. Br. a. Flowering plant; b. flower; c. fruit in calyx (*Turner s.n.*). Drawing M. Spitteler.

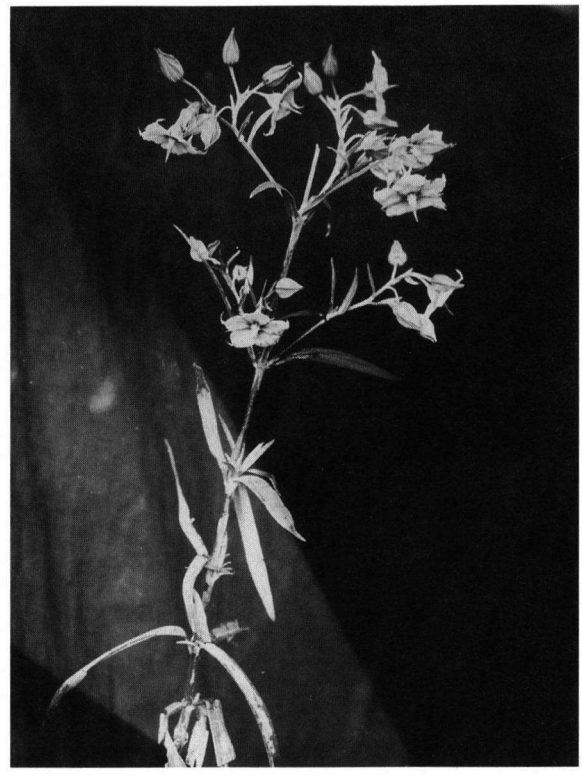

Fig. 15. *Trichodesma zeylanicum* (Burm. f.) R. Br. Top of flowering stem. Flores. Photo L. van der Pijl.

b. var. **sericeum** (Lindl.) Benth.

Trichodesma zeylanicum (Burm. f.) R. Br. var. *sericeum* (Lindl.) Benth., Fl. Austral. 4 (1869) 405. — *Trichodesma sericeum* Lindl. in Mitch., J. Trop. Austral. (1848) 258. — *Trichodesma zeylanicum* subsp. *eu-zeylanicum* Brand var. *australe* Brand f. *sericeum* (Lindl.) Brand in Engl., Pflanzenr., fam. IV. 252 (1921) 42. — Type: *Mitchell*, Australia, Belyando River.

Leaves 3–6.5 by 0.2–0.3 cm, with revolute margins. Indument in all parts silky, hairs partly from groups of mineralized cells, but covering them completely, very dense, of nearly equal length, appressed antrorse. Calyx usually 1.2–1.3 cm long.

Distribution — Australia; *Malesia:* Lesser Sunda Islands (Flores, Sumba, Timor).

TRIGONOTIS

Trigonotis Steven, Bull. Soc. Nat. Moscou 24, 1 (1851) 603; I.M. Johnston, J. Arnold Arbor. 21 (1940) 57; 33 (1952) 68; P. Royen, Pac. Sc. 29 (1975) 81. — Type species: *Trigonotis clavata* Steven [= *Trigonotis pedunculare* (Trev.) Benth.].

Zoelleria Warb., Bot. Jahrb. 16 (1893) 28. — Type species: *Zoelleria procumbens* Warb. [= *Trigonotis procumbens* (Warb.) I.M. Johnston].

Havilandia Stapf, Trans. Linn. Soc. Lond. II, Bot. 4 (1894) 209; I.M. Johnston, J. Arnold Arbor. 16 (1935) 190. — Type species: *Havilandia borneensis* Stapf [= *Trigonotis borneensis* (Stapf) I.M. Johnston].

Creeping, decumbent or ascending herbs with simple or branched stems, sometimes forming large mats or cushions. *Leaves* either in basal rosettes or cauline, alternate, stalked or not, in creeping species sometimes all in one plane by twisting of the petioles. *Flowers* solitary, axillary or extra-axillary, or in elongated, terminal or lateral, scorpioid cymes without leaves or bracts, or with the lowermost flowers in the axils of leaf-like bracts. *Calyx* with 5 lobes imbricate in bud. *Corolla* lobes 5 or 6, invaginate at base, forming hollow appendages bulging into the throat. *Stamens* isomerous with corolla, filaments very short, inserted in the tube of corolla, anthers opening introrsely with two longitudinal slits. *Ovary* composed of 4 or (7–)8–10 carpels on a cup-shaped receptacle, style short, stigma bilobed. *Nutlets* 4 or (7–)8–10, either with a sharp angle dorsally, dorso-ventrally compressed, or rounded dorsally, slightly compressed laterally, ribs sometimes with a narrow wing, smooth or finely papillate to tuberculate, glabrous or with hairs along the margins, shiny or dull. — **Fig. 16, 17.**

Distribution — About 50 species in Central Asia, China, Japan to *Malesia:* Borneo, Philippines, and New Guinea.

Habitat — Most of the species grow at higher altitudes, mainly in the montane and subalpine zone, a few also lower down or in the alpine zone.

Notes — 1. In the few species counted polyploidy is prevalent with the diploid numbers 2n = 36 or 48.

2. *Trigonotis* was usually regarded as a member of *Lithospermeae*, but Riedl (1968) made it the type genus of a separate tribe *Trigonotideae*, in which it is the sole member of subtribe *Trigonotidinae*. *Trigonotideae* include all those genera which are nearest to the root of the other tribes within *Boraginoideae*. Its closest relatives outside *Trigonotideae* seem to be *Trigonocaryum* and *Myosotis*. As in the latter, in some of its species nutlets are pyramidate with the areola shortly stipitate.

3. *Zoelleria* Warb. has been regarded as the type of a separate, monotypic tribe *Zoellerieae* by Gürke (1897) for the aberrant number of carpels (7–10), but agrees in all other characters with what Stapf described as a new genus *Havilandia*. *Havilandia* was characterized by dorsally rounded, laterally compressed nutlets, while in typical *Trigonotis* they are dorsally angulate and compressed dorso-ventrally. Along with this difference went the growth habit: creeping with solitary, axillary flowers in *Havilandia*, apically erect with naked or nearly naked cymes in *Trigonotis* s.str. With the discovery of *Trigonotis abata* I.M. Johnston, this correlation did not hold any longer: it combined the growth habit of *Havilandia* with the shape of the nutlets of *Trigonotis*. For this reason, Johnston united all three genera in 1940. *Trigonotis minuta* seems to keep a similar intermediate position according to Van Royen's description of the nutlets. The present treatment closely follows the two excellent papers of Johnston (1940) and Van Royen (1975).

References: Gürke, M., Borraginaceae, in Engl. & Prantl, Nat. Pflanzenfam. 4, 3a (1897) 71–131; Stapf, O., Trans. Linn. Soc. Lond. II, Bot. 4 (1894) 209; Johnston, I.M., J. Arnold Arbor. 21 (1940) 59; Riedl, H., Österr. Bot. Z. 115 (1968) 291; Van Royen, P., Pac. Sc. 29 (1975) 81; Alpine Fl. New Guinea 4 (1983) 3094.

KEY TO THE SPECIES

1a. Ovary 7–10-lobed, nutlets 7–10 2
b. Ovary 4-lobed; nutlets 4 3
2a. Corolla 7–9 mm in diam. Leaves elliptic- to obovate-oblong, strigose on margin and midrib, otherwise glabrous ..... **13. T. pleiomera**
b. Corolla c. 4 mm in diam. Leaves orbicular to ovate, conspicuously strigose on both faces ..... **14. T. procumbens**
3a. Leaves linear to linear-lanceolate, acute, not longer than 9 mm ... **9. T. minuta**
b. Leaves wider, oblong-obovate to oblanceolate, if linear then much longer than 9 mm 4
4a. Nutlets angulate dorsally, dorso-ventrally compressed; plants prostrate, flowers solitary above axils of upper leaves ..... **1. T. abata**
b. Nutlets either angulate dorsally, dorso-ventrally compressed and plants upright in upper part with elongated cymes or nutlets rounded dorsally, or plants prostrate with solitary flowers in axils of upper leaves 5
5a. Nutlets angulate dorsally, dorso-ventrally compressed; plants upright in the upper part, with elongated cymes 6
b. Nutlets rounded dorsally, laterally slightly compressed; plants creeping, prostrate; flowers solitary in the axils of upper leaves 12
6a. Bases of lower leaves decurrent, upper leaves stalked 7
b. Bases of lower leaves rounded or tapering into a petiole 8
7a. Leaves strigose along margins only; cymes axillary with 4–6 flowers; stems glabrous ..... **17. T. vestita**
b. Stems and leaves hirsute on whole surface; cymes terminal, often bifurcate, with more numerous flowers ..... **7. T. hirsuta**
8a. Ovary and fruit finely hairy; leaves linear to oblong or oblong-lanceolate ..... **6. T. haackii**
b. Ovary and fruit glabrous; leaves oblong to elliptic 9
9a. Calyx united for half of its length, lobes ovate-triangular ..... **2. T. apoense**
b. Calyx united for less than half of its length, lobes narrowly ovate to ovate-lanceolate 10
10a. Stem densely patent hairy in its lower part, hairs reddish brown when dry. Leaves of flowering stems 0–1, broadest near base, semiamplexicaulous ..... **16. T. subrosulata**
b. Stem with more or less appressed, antrorse hairs in its whole length, hairs permanently white. All leaves tapering towards base, stalked 11
11a. Corolla 4 mm long, tube c. 2 mm; both leaf surfaces densely strigose ..... **12. T. philippinensis**
b. Corolla 3–9 mm long, tube 2–3(–5) mm; upper leaf surface laxly strigose, hairs sometimes in irregular patches ..... **8. T. inoblita**
12a. Nutlets ciliolate along their margins ..... **4. T. ciliolata**
b. Nutlets glabrous or minutely papillate 13

13a. Plant pulvinate with short stems crowded densely together. Leaves not longer than 8 mm ..... **5. T. culminicola**
b. Plant not pulvinate, with elongate, more or less creeping stems. Leaves distinctly longer 14
14a. Nutlets minutely papillate, gray or light-brown, dull 15
b. Nutlets smooth, blackish or black, rarely ivory white, shiny 16
15a. Pedicels 0.5–1 mm long. Corolla 3–3.5 mm long, 4.5 mm across **10. T. opaca**
b. Pedicels 8–12 mm long in flower, up to 18 mm in fruit. Corolla 9 mm long, 12 mm across ..... **15. T. robusta**
16a. Leaves oblanceolate, gradually contracted into the petiole; nutlets lanceolate. Pedicels 2–5 mm long ..... **3. T. borneensis**
b. Leaves obovate to elliptic, abruptly contracted into a short, sheathing petiole; nutlets short. Pedicels 1–3 mm in flower, up to 7 mm in fruit .... **11. T. papuana**

1. Trigonotis abata I.M. Johnston

Trigonotis abata I.M. Johnston, J. Arnold Arbor. 21 (1940) 58; Van Royen, Pac. Sc. 29 (1975) 88; Alpine Fl. New Guinea 4 (1983) 3106. — Type: *Brass & Meijer Drees 9838* (A), Irian Jaya, Mt Trikora (Wilhelmina).

Creeping herbs, rooting at nodes. Stems up to 30 cm long, antrorse strigose, finally glabrescent. *Leaves* ovate or elliptic, (0.4–)0.8-2.2 by (0.2–)0.4–1 cm, sometimes slightly asymmetric, base rounded, abruptly tapering into the 1–2 mm long, sheathing, often twisted petiole or sessile, lateral nerves 1 or 2 on either side of midrib, leaves antrorse strigose on both side, more patent on upper side, denser on midrib below. *Flowers* solitary, extra-axillary; pedicels 3–4 mm long in flower, 7–12 mm in fruit, antrorse strigose. *Calyx* 1.5–2.5 mm in flower, up to 3 mm in fruit, antrorse hairy on the whole surface or along midrib of lobes only, lobes ovate-lanceolate to ovate, c. 1.5 mm long, 1 mm wide, acute to acuminate, with a black, linear gland outside below tip. *Corolla* white with yellow throat, 4–5 mm across, lobes obovate; fornices kidney-shaped, finely ciliate. *Stamens* c. 1 mm long, anthers 0.5 mm. *Pistil:* style c. 1 mm long. *Nutlets* 4, pyramidal, dorsally convex, ventrally with a sharp angle, 2–3 mm long, 1–1.5 mm wide, brownish black, with 3 narrow, acute crests.

Distribution — *Malesia:* mountains of New Guinea, endemic.

Habitat — In damp places on landslides, open, sandy beds of streams, in moss cushions of subalpine shrubberies, 1670–3650 m altitude.

Note — Some specimens with very small, nearly sessile leaves usually not longer than 4–6 mm and densely crowded, shorter stems forming mats like *T. culminicola* seem to belong to this species, but may represent a separate variety or subspecies. Further investigations in this matter are necessary.

2. Trigonotis apoensis Elmer

Trigonotis apoensis Elmer, Leafl. Philipp. Bot. 7 (1915) 2562. — Type: *Elmer 11500* (not seen), Mindanao.

Creeping, biennial herbs with prostrate, rooting, branched stems, lateral branches or tufts of leaves arising from bracts at the nodes. Stems slightly succulent, glabrous or subglabrous, with erect ends. *Leaves* alternate along runners, tufted distally, narrowly elliptic to broadly oblong, petiole 2–8 cm long, sheathing the stem, greyish strigose, lamina up to 6 by 3 cm, but usually much smaller, rounded at base, apex rounded-apiculate, with 3–5 lateral nerves on either side paler below, with appressed, white hairs on both sides, denser along the midrib below. *Cymes* arising from the uppermost leaf axils, with a distinct peduncle, leafy bracteate, flowers crowded towards scorpioid top; bracts elliptic, acute, 5 mm long, 2.5 mm wide; pedicels 3–4 mm long, minutely strigose. *Calyx* 4 mm long and wide, divided to the middle into 5 ovate-triangular, slightly unequal teeth overlapping towards base, sparsely strigose. *Corolla* 3.5 mm long, tube about as long as limb, lobes elliptic to shortly obovate, 1.5 mm long; fornices short and broad. *Stamens:* filaments less than 0.5 mm, anthers 0.75 mm. *Pistil:* style 1–1.5 mm long, stigma minute. *Nutlets* pyramidal, dark brown, not seen at maturity.

Distribution — *Malesia:* Philippines (Mindanao).

Habitat — Fertile, moist humus at banks of creeks.

Vernacular name — Salimbangande.

Note — The description is taken from Elmer's diagnosis of the species, that does not seem to have been collected in more recent times.

3. Trigonotis borneensis (Stapf) I.M. Johnston

Trigonotis borneensis (Stapf) I.M. Johnston, J. Arnold Arbor. 21 (1940) 63; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 94. — *Havilandia borneensis* Stapf, Trans. Linn. Soc. Lond. II, 4 (1894) 209, t. 16. — *Lithospermum borneense* (Stapf) Boerl., Handl. Fl. Ned. Ind. 2 (1899) 488. — *Plagiobothrys borneensis* (Stapf) I.M. Johnston, Contr. Gray Herb. 73 (1924) 78. — Type: *Haviland 1059* (K holo), Sabah, Mt Kinabalu.

Stems long prostrate or creeping, sometimes rooting, in their lower parts naked, in their distal part with a few dichotomous branches, with distichous leaves, appressed greyish strigillose. *Leaves* sessile, semi-amplexicaulous and nearly sheathing the stem, 1.5–2.5 by 0.4–0.7 cm, slightly emarginate at apex, in apical part appressed, towards base spreading ciliate at margin, on upper side appressed strigillose near apex, on lower side glabrous except along midrib, without lateral veins. *Flowers* single in the axils of leaves; pedicel 2–5 mm long, appressed strigillose. *Calyx* at last 6–7 mm long, cleft for two thirds, lobes bristly-ciliate, spreading in fruit. *Corolla* funnel-shaped, 3.5–4 mm long, lobes as long as tube, obovate. *Stamens:* anthers subsessile, c. 0.5 mm long. *Pistil:* style c. 1 mm long. *Nutlets* c. 2 mm long, pyramidal, substipitate, sharply angled ventrally.

Distribution — *Malesia:* Borneo, only known from Mt Kinabalu area.

Habitat — Marshy places.

4. Trigonotis ciliolata I.M. Johnston

Trigonotis ciliolata I.M. Johnston, J. Arnold Arbor. 33 (1952) 68; Van Royen, Pac. Sc. 29 (1975) 88; Alpine Fl. New Guinea 4 (1983) 3108. — Type: *Kanehira & Hatusima 13883*, Irian Jaya, Arfak Mts.

Small creeping herbs. Stems densely patently strigose. *Leaves* shortly petiolate, petiole 2–6 mm long, blade ovate, 1.6–2.6 by 0.8–2.2 cm, base rounded, abruptly tapering into the petiole, acute to apiculate at apex, subappressed strigose, densest along midrib on lower side. *Flowers* solitary, extra-axillary; pedicels antrorse strigose, 12–15 mm long. *Calyx* 3.5–5 mm long, antrorse strigose on outer and to a lesser degree on inner side, lobes lanceolate, 3–3.5 by 1–1.5 mm, acute, elongated to 4.5 mm in fruit. *Corolla* white, glabrous, 5–7 mm long, tube 2.2–2.5 mm, lobes orbicular, 3–4 mm in diam., fornices kidney-shaped, 1 mm broad, finely hairy. *Stamens* 1.2 mm long, anthers 0.7 mm. *Pistil:* style 1–1.3 mm long. *Nutlets* pyramidal, c. 1 mm long, dorsal side convex, the other surfaces flat, 2 mm wide, margins acute, ciliolate, black, smooth.

Distribution — *Malesia:* endemic in western New Guinea.

Habitat — Probably wet, open grasslands, about 1900 m altitude.

5. Trigonotis culminicola P. Royen

Trigonotis culminicola P. Royen, Pac. Sc. 29 (1975) 90; Alpine Fl. New Guinea 4 (1983) 3112. — Type: *Hoogland & Pullen 5790* (L holo), Papua New Guinea, Mt Wilhelm.

Small, creeping herbs forming dense cushions or mats. Stems short, numerous, densely antrorse stigose. *Leaves* obovate, spathulate or oblong, 5–8 by 0.3–0.4 mm, base gradually tapering into the 1–3 mm long, sheath-like petiole, apex rounded, retuse or mucronulate, without lateral veins, sparsely antrorse strigose above, glabrous below except midrib and margins. *Flowers* solitary, extra-axillary; pedicels spreading strigose, 2–3.5 mm long in flower, up to 4.5 mm in fruit. *Calyx* 2.5–3.5 mm long in flower, coherent base 0.5–1 mm in flower, accrescent to 1.5–2 mm in fruit, lobes 1–1.5 mm wide, not accrescent, acutish or obtuse, apiculate, with a black gland at tip, white antrorse strigose on outside along midrib and margins. *Corolla* white or pink or lavender, throat yellow, glabrous, tube 1.5–2.5 mm long, lobes orbicular, 1.5 mm in diam., rounded or retuse; fornices kidney-shaped, ciliate. *Stamens* c. 1 mm long, anthers oblong-ovoid, c. 0.7 mm long. *Pistil:* style c. 0.5 mm. *Nutlets* pyriform, dorsally rounded, c. 1.2 mm long, black, smooth.

Distribution — *Malesia:* mountains of New Guinea, endemic.

Habitat — Moist ground among gravel and in rock crevices, 3150–4480 m altitude.

6. Trigonotis haackii F. Muell.

Trigonotis haackii F. Muell., Trans. Roy. Soc. Vict., N. S. I/2 (1889) 30; Van Royen, Pac. Sc. 29 (1975) 83; Alpine Fl. New Guinea 4 (1983) 3097. — Type: *MacGregor s.n.* (MEL holo), Papua New Guinea, Mt Victoria.

Erect or decumbent herbs. Stems up to 35 cm high, covered with appressed, white hairs. *Leaves* nearly opposite to alternate, linear-spathulate to elongate-spathulate, 1.8–4 by 0.2–0.4 cm, tapering towards base into a very short petiole, acute at apex, without distinct lateral veins, sparsely appressed white strigose above, subglabrous with more hairs only along midrib below. *Cymes* up to 5 cm long, ebracteate; pedicels 2.5–4 mm

long, strigose. *Calyx* 3.5–5 mm long, divided to near base into ovate to ovate-elliptic, acute lobes with black glands at the very tip, strigose outside mainly along midrib and margins, glabrous inside. *Corolla* glabrous, tube 2.5–3 mm long, lobes orbicular to broadly ovate, 2–2.5 mm in diam.; fornices bilobed, finely papillate. *Stamens:* filaments short, anthers c. 1 mm long, oblong. *Pistil:* style 1–1.5 mm long, stigma slightly bilobed. *Nutlets* obliquely pyriform, c. 1 mm long, rounded dorsally, with a sharp angle ventrally, dull brown, with few fine hairs.

Distribution — *Malesia:* New Guinea, endemic.

Habitat — Open, wet grasslands.

7. **Trigonotis hirsuta** Steenis

Trigonotis hirsuta Steenis, Bot. Jahrb. 86 (1967) 398. — Type: *van Steenis 6202* (L holo; BO), N Sumatra.

Prostrate herb. Stems densely covered with long, patent, rigid hairs. *Leaves* oblong to broadly spathulate, petiole 1–2 cm long, blade 3–5 by 1.5–2 cm, decurrent at base, apex rounded, scarcely acute, sometimes mucronulate, with patent, rigid hairs on white tubercles on lower side and on upper side along veins. *Cymes* often forked, ebracteate; pedicels 1–1.5 mm long, patent hirsute. *Calyx* hirsute as other parts, c. 1.5 mm long, divided to base into spathulate-oblong, obtuse or acutish lobes. *Corolla* glabrous, tube as long as calyx, lobes rounded, suborbicular, 1.5 mm in diam. *Stamens:* anthers oblong, on very short filaments. *Pistil:* style c. 1 mm long, stigma minute, capitulate. *Nutlets* tetrahedral, 1 mm long, with 3 distinctly costate angles, brown, smooth, shiny, glabrous.

Distribution — *Malesia:* N Sumatra, endemic.

Habitat — Found, for instance, in elephant trails together with *Urticaceae* and *Amaranthaceae*, at 1300–2000 m altitude.

8. **Trigonotis inoblita** F. Muell.

Trigonotis inoblita F. Muell., Trans. Roy. Soc. Vict., N.S. I/2 (1889) 31; Van Royen, Pac. Sc. 29 (1975) 83; Alpine Fl. New Guinea 4 (1983) 3097. — Type: *MacGregor s.n.* (MEL), Papua New Guinea, Owen Stanley Range.

Decumbent or more commonly erect herbs. Stems up to 40 cm high, simple or branched, leafy mainly in the upper half, densely, often antrorse appressed strigose. *Leaves* broadly or narrowly elliptic, spathulate, obovate, oblong, elliptic- or obovate-oblong to oblong-ovate, petiole 0.5–3.5 cm long, glabrous above, strigose below, blade 2–12 by 0.7–3 cm, tapering into a petiole at base, obtuse or rounded and apiculate or acuminate at apex, with 5–7 lateral nerves on either side of midrib, sparsely strigose above, strigose below and along margins, denser along midrib. *Cymes* terminal or axillary, simple or branched, with 10–40 flowers, ebracteate, rhachis densely strigose; pedicels 1–7 mm long, densely strigose. *Calyx* 1.5–4 mm long, cleft to the base into 5 ovate to ovate-lanceolate, oblong or oblong-elliptic lobes 0.5–1 mm wide, with acute tips and a black gland just below tip, appressed strigose outside, sometimes only along ribs, glabrous

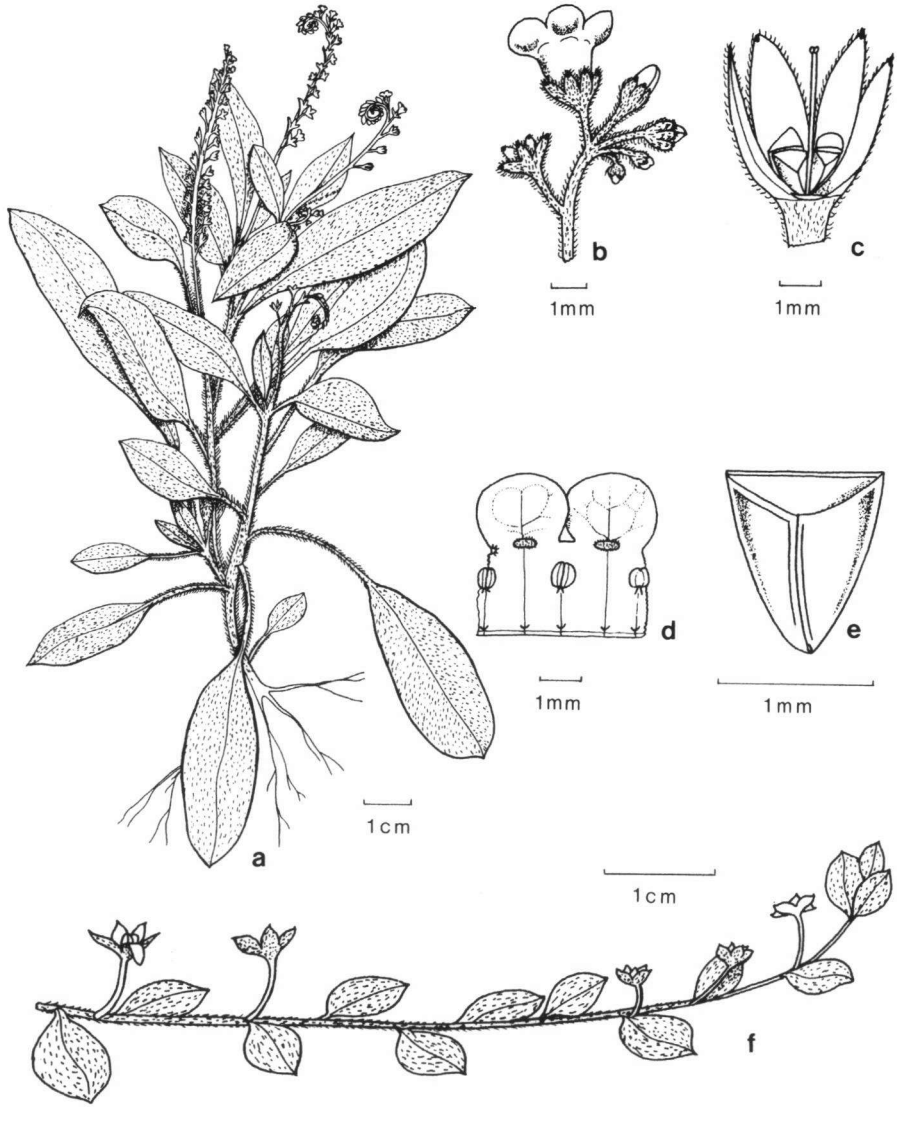

Fig. 16. *Trigonotis inoblita* F. Muell. var. *inoblita*. a. Flowering plant; b. top of inflorescence; c. calyx with fruits; d. part of corolla with stamens; e. fruit (a, e: *Hoogland & Schodde 6911*; b–d: *Brass 31358*). — *T. procumbens* (Warb.) I.M. Johnston. f. Apical part of plant (*Hellwig 331*). Drawing P. van Royen. Reproduced from Van Royen, Alpine Flora New Guinea 4.

inside. *Corolla* white or lobes pale purple at apex, throat pale yellow, 3–9 mm long, 5–12 mm in diam., tube 2–3(–5) mm long, lobes suborbicular to orbicular, 1.5–5 mm wide; fornices kidney-shaped, c. 1 mm wide, finely ciliate. *Stamens:* filaments very short, anthers c. 0.7 mm long. *Pistil:* style slightly shorter than calyx, stigma bilobed. *Nutlets* pyramidal, 1–1.5 mm long, dark brown, smooth, with ribbed angles. — **Fig. 16 a–e.**

Distribution — *Malesia:* throughout New Guinea, endemic.

Habitat — Damp, shady places, along rivulets, in alpine grassland, under boulders, in mossy slopes, under trees.

KEY TO THE VARIETIES

1a. Flowers 3–3.5 mm long, 3 mm across. Pedicels 1–4 mm long . **a.** var. **inoblita**
b. Flowers 4–8 mm long, 5–12 mm across. Pedicels 3–7 mm long ..... **b.** var. **archboldii**

a. var. **inoblita**

P. Royen, Pac. Sc. 29 (1975) 84; Alpine Fl. New Guinea 4 (1983) 3101.

Distribution — Whole area of the species.

b. var. **archboldii** (I.M. Johnston) P. Royen

Trigonotis inoblita F.Muell. var. *archboldii* (I.M. Johnston) P. Royen, Pac. Sc. 29 (1975) 88; Alpine Fl. New Guinea 4 (1983) 3102. — *Trigonotis archboldii* I.M. Johnston, J. Arnold Arbor. 21 (1940) 58. — Type: *Brass & Meijer Drees 9838* (A holo), Irian Jaya, Mt Trikora (Wilhelmina).

Distribution — *Malesia:* New Guinea.

9. Trigonotis minuta (Wernham) I.M. Johnston

Trigonotis minuta (Wernham) I.M Johnston, Contr. Gray Herb. 81 (1928) 81; Van Royen, Pac. Sc. 29 (1975) 87; Alpine Fl. New Guinea 4 (1983) 3103. — *Lithospermum minutus* Wernham, Trans. Linn. Soc. Lond. II, 9 (1916) 118. — Type: *Boden Kloss (Wollaston Exp.)*, Irian Jaya, Mt Jaya (Carstensz).

Small, erect herb. Stem 4 cm high. *Leaves* densely arranged along whole length of stem, linear, sessile with broad base, clasping stem, 6–9 by 0.1–0.2 mm, acute, only midrib distinct, ciliate along margin and midrib below, with longer hairs towards base. *Flowers* solitary, terminal. *Calyx* 2–3 mm long, cleft to the base, lobes lanceolate, acuminate, 1–1.5 mm wide, ciliate along midrib and margin. *Corolla* glabrous, tube 1.5–2 mm long, lobes orbicular, c. 2.5 mm wide; fornices kidney-shaped, papillate. *Stamens* 0.5–0.8 mm long, anthers ovoid, 0.5 mm. *Nutlets* pyramidal, 1 mm long, 0.7 mm wide, with sharp angles, blackish, smooth, shiny.

Distribution — *Malesia:* New Guinea, only known from the type collection.

Habitat — Open moraines and alpine grasslands, 3140–4400 m altitude.

10. Trigonotis opaca (I.M. Johnston) I.M. Johnston

Trigonotis opaca (I.M. Johnston) I.M. Johnston, J. Arnold Arbor. 21 (1940) 62; Van Royen, Pac. Sc. 29 (1975) 92; Alpine Fl. New Guinea 4 (1983) 3116. — *Havilandia opaca* I.M. Johnston, J. Arnold Arbor. 16 (1935) 190. — Type: *Brass 4178* (A holo), Papua New Guinea, Wharton Range.

Small, creeping herbs forming large, more or less dense mats. Stems much branched, densely appressed, white, antrorse strigose. *Leaves* oblong to oblong-ovate, petiole 1–2 mm long, blade 4–7 by 0.2–0.4 mm, base cuneate, abruptly narrowed into the petiole, apex rounded or retuse, with 3 or 4 lateral veins on either side of midrib, glabrous except lower side of petiole, margins and midrib on lower side, which are densely strigose. *Flowers* solitary in leaf axils; pedicels 0.5–1 mm long, antrorse strigose. *Calyx* 3–3.5 mm long, lobes ovate-elliptic, 1.7–2.5 by 1 mm, acute, strigose along margins and midrib. *Corolla* white, as long as calyx, up to 4.5 mm in diam., tube 1.5–2 mm, lobes rounded obovate, 1.2–1.5 mm wide, finely papillate inside; fornices trapeziform, yellow, c. 0.5 mm wide, finely papillate. *Stamens* c. 0.7 mm, anthers 0.4–0.6 mm long. *Pistil:* style c. 0.7 mm long. *Nutlets* 4, ovoid, 1 mm long, 0.5 mm wide, dorsally rounded, with a ventral crest and sharp, lateral angles, light brown to grey, dull, minutely papillate.

Distribution — *Malesia:* Papua New Guinea, endemic.

Habitat — Open, wet graslands on black, peaty soils, once found on dead tree-fern, 2660–2950 m altitude.

11. **Trigonotis papuana** (Hemsl.) I.M. Johnston

Trigonotis papuana (Hemsl.) I.M. Johnston, J. Arnold Arbor. 21 (1940) 63; P. Royen, Pac. Sc. 29 (1975) 93; Alpine Fl. New Guinea 4 (1983) 3118. — *Havilandia papuana* Hemsl., Kew Bull. (1899) 107. — Syntypes: *Giulianetti s.n.*, *English s.n.* (K), Papua New Guinea.

Fig. 17. *Trigonotis papuana* (Hemsl.) I.M. Johnston. Flowering plant. Naitmambi Range, Papua New Guinea. Photo P. van Royen, 1976.

Creeping herbs, often forming large mats. Stems much branched, appressed antrorse strigose. *Leaves* in two rows flat on the ground by twisting of the sheath-like, clasping petiole, petiole 1–7 mm long, blade oblong, oblong-ovate or spathulate, 0.4–2 by 0.2–0.9 cm, abruptly narrowed into petiole, apex rounded or often retuse, glabrous above, strigose along midrib alone below, margins antrorse strigose. *Flowers* solitary, axillary or extra-axillary; pedicels 1–3 mm long in flower, up to 7 mm in fruit, antrorse strigose. *Calyx* 3.5–4.5 cm long, divided to about 1–1.5 mm above base into ovate to lanceolate, 1–1.5 mm wide, acutish lobes with black gland outside below apex, antrorse strigose outside along midrib and margins. *Corolla* white or pink, purple or white with bluish tinge, tube 1–1.5 mm long, lobes ovate-orbicular or sometimes spathulate, 1.5–3 by 1.5–2.5 mm, rounded, finely papillate inside; fornices yellow, kidney-shaped, c. 0.5 mm wide, 0.2 mm long, finely ciliate. *Stamens* 1 mm long, anthers 0.8 mm. *Pistil:* style 0.7-1 mm long. *Nutlets* obpyriform, 1–1.5 mm long, c. 1 mm wide, acute, dorsally rounded, with a narrow crest ventrally, dark brown, rarely ivory white, smooth, glabrous. — **Fig. 17.**

Distribution — *Malesia:* New Guinea, widespread, endemic.

Habitat — Wet, open places in grasslands, swamps, seepage slopes, along rivulets, wet landslides, 2900–4100 m altitude.

Vernacular name — Kua'pepo (Mendi).

Note — Obviously the most common species on New Guinea.

12. Trigonotis philippinensis Merr.

Trigonotis philippinensis Merr., Philipp. J. Sc. 1, Suppl. (1906) 228; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 697. — Type: *Merrill 4700*, Luzon.

Erect or slightly prostrate. Stems up to 25 cm high, with few branches, more or lesss hispid pubescent. *Leaves* oblong, elliptical, oblong-obovate or subspathulate, tapering into a distinct, slender, 0.4–2.5 cm long petiole, blade 0.8–3 by 0.6–1.3 cm, apex acute or rounded to retuse, distinctly apiculate, lateral veins indistinct, antrorse white strigose on upper as well as midrib and margins on lower side, with few scattered hairs on lower surface. *Cymes* lateral, solitary, ebracteate, with distinct peduncle, rhachis antrorsely strigose; pedicels antrorse strigose, less than 1 mm long in flower, elongated to 3 mm, in the lowermost flowers to 5–6 mm in fruit. *Calyx* 1.5–2 mm long in flower, up to 3 mm long in fruit, strigose, lobes narrowly ovate, acute, c. 2 mm long at last. *Corolla* white, 4 mm long, tube nearly 2 mm long, lobes obovate to suborbicular, broadly rounded, c. 2 mm wide; fornices fairly broad. *Stamens:* filaments very short, anthers oblong, c. 0.8 mm long. *Pistil:* style c. 1 mm long. *Nutlets* tetrahedral with 4 sharp angles, c. 1 mm long, black, shiny, glabrous.

Distribution — *Malesia:* Philippines (N Luzon), endemic.

Habitat — Damp, mossy cliffs just below limit of mossy forest at about 1900 m altitude.

Note — Specimens from the classical localities do not quite agree with Merrill's diagnosis. The most important difference are the cymes arising from the axils of some of the

lowermost, long since withered leaves and not terminal as Merrill says. The calyx is 3 mm long only at the very last stage of fruiting. Nevertheless, there can be little doubt about their identity.

13. Trigonotis pleiomera I.M. Johnston

Trigonotis pleiomera I.M. Johnston, J. Arnold Arbor. 21 (1940) 61; Van Royen, Pac. Sc. 29 (1975) 94; Alpine Fl. New Guinea 4 (1983) 3120. — *Clemens 5989* (A holo), Papua New Guinea, Mt Sarawaket.

Creeping, much branched herbs growing solitary or in dense mats. Stems up to 35 cm long, appressed strigose. *Leaves* usually seemingly distichous due to twisted petioles, petioles 1–3 mm long, blade elliptic, obovate, oblong or elliptic- to obovate-oblong, 0.8–2 by 0.3–1 cm, tapering towards base, tips rounded or obtuse, apiculate, lateral nerves 3 or 4 on each side of midrib, sparsely appressed antrorse strigose along margins and on midrib below. *Flowers* solitary, extra-axillary; pedicels appressed antrorse strigose, 8–15 mm long. *Calyx* 3–5 mm long, divided to near base into ovate or oblong-ovate, 2–2.5 mm wide, acute lobes, antrorse strigose along margins and midribs. *Corolla* white, purplish, pink or pale purple blue, 7–9 mm diam., tube 3–4 mm long, lobes 5 or 6, glabrous, orbicular-ovate, rounded, 4–5 by 3.5–4.5 mm; fornices kidney-shaped, c. 0.5 mm wide, finely hairy. *Stamens* 1–1.5 mm long, anthers oblong-ovoid, 1 mm long. *Pistil:* style 1–1.5 mm long. *Nutlets* 7–10, obliquely ovoid, 1–1.5 mm long, 0.5–1 mm wide, acute, dorsally convex, with sharp crest, light grey, shiny, smooth.

Distribution — *Malesia:* New Guinea, endemic.

Habitat — Slightly shaded, wet parts of grasslands, open places in montane forests, 2130–4100 m altitude.

14. Trigonotis procumbens (Warb.) I.M. Johnston

Trigonotis procumbens (Warb.) I.M. Johnston, J. Arnold Arbor. 21 (1940) 62; Van Royen, Pac. Sc. 29 (1975) 89; Alpine Fl. New Guinea 4 (1983) 3109. — *Zoelleria procumbens* Warb., Bot. Jahrb. 17 (1893) 28. — Type: *Hellwig 331* (B holo, destroyed), Papua New Guinea, Finisterre Mts.

Creeping herbs, sometimes growing in clumps. Stems long, slender, much branched with suberect distal part, green or purple, antrorse strigose. *Leaves* ovate, elliptic or intermediate, sometimes suborbicular, petiole 1–12 mm long, densely or sparsely strigose, blade 0.3–4.5 by 0.2–3 cm, base cuneate, abruptly contracted to petiole, apex rounded or obtuse and apiculate, with 3 or 4 lateral nerves on each side of midrib, appressed antrorse strigose on both sides, often denser along midrib below. *Flowers* solitary, axillary; pedicels 3–8 mm long, appressed antrorse strigose. *Calyx* appressed strigose outside and inside, basal tube 0.5–1 mm long in flower, up to 2 mm in fruit, lobes ovate, ovate-lanceolate or elliptic, 2–3 by 1 mm, acute, with a black gland below apex. *Corolla* white, pale mauve, or violet, or only tip of lobes pink, tube c. 2 mm long, finely papillate inside, lobes ovate-lanceolate or elliptic, 2–3 by 1–2 mm, obtuse, glabrous; fornices

indistinctly bilobed, 0.5 mm wide, 0.2 mm long, ciliolate. *Stamens* very short, 0.5–0.8 mm, anthers 0.5 mm, ovoid. *Pistil:* style c. 1 mm long. *Nutlets* 7–10, pyriform, c. 0.8 mm long, dorsally rounded, brownish grey or blackish brown, smooth, shiny, rarely dorsally with few hairs. — **Fig. 16f.**

Distribution — *Malesia:* New Guinea, endemic.

Habitat — Open, wet places, sometimes in a light shade, in grassy clearings in forests, at forest edges, creek banks, etc., 1400–3350 m altitude.

Note — Type species of the monotypic genus *Zoelleria*, which was described for the increased number of nutlets, but is not distinct from *Trigonotis* (species formerly included in *Havilandia*) in any other character.

15. Trigonotis robusta (I.M. Johnston) I.M. Johnston

Trigonotis robusta (I.M. Johnston) I.M. Johnston, J. Arnold Arbor. 21 (1940) 62; Van Royen, Pac. Sc. 29 (1975) 91; Alpine Fl. New Guinea 4 (1983) 3112. — *Havilandia robusta* I.M. Johnston, J. Arnold Arbor. 16 (1935) 191. — Type: *Brass 5681* (A holo), Papua New Guinea, Mt Albert Edward.

Large, lax herbs often growing in large groups. Stems more or less ascendent, up to 30 cm high, with few branches and lower leaves already withered at flowering time, appressed antrorse strigose. *Leaves* spathulate, spathulate-oblong to oblong, petioles 0.5–1.2 cm long, blade 1.5–4.5 by 0.4–0.7 cm, obliquely truncate at base, rounded or retuse at apex, with 3 nerves on either side of midrib and 2 basal ones, sparsely antrorse strigose in distal part above, with only few hairs, more numerous only along midrib below. *Flowers* solitary in axils of upper leaves. *Calyx* 5–6 mm long, lobes 4–6 by 1–1.5 mm, narrowly lanceolate to elliptic, acute, with a black gland below apex, antrorse strigose along midrib and margins. *Corolla* pink or blue, throat white, or entirely white, or white with blue tips, up to 9 mm long, 12 mm diam., tube 4–6 mm long, lobes broadly spathulate-obovate, 4–6 mm wide, papillate on the inner side; fornices kidney-shaped, 0.5–1 mm wide, ciliolate. *Stamens* c. 1 mm long, the anthers 0.8 mm long. *Pistil:* style 1–1.5 mm long. *Nutlets* angulate-ovoid, c. 1 mm long, dorsally rounded, with sharp angles, dull grey, finely papillate.

Distribution — *Malesia:* Papua New Guinea, endemic.

Habitat — Wet places in grasslands, along rivulets, 2000–3680 m altitude.

16. Trigonotis subrosulata Riedl

Trigonotis subrosulata Riedl, Blumea 38 (1994) 464. — Type: *Mc Gregor BS 19575* (L holo), Luzon, Mt Polis.

Base not known, but obviously more or less decumbent. Stems erect or ascending, 12–17 cm high, simple or branched at the very base, with subrosulate leaves, densely covered by patent hairs turning fulvous when dry in the lower part, appressed antrorse strigose with white hairs in upper part. *Leaves* oblong to elliptic, lanceolate-oblong or obovate-oblong, petiole 0.5–2.5 cm long, distinctly winged, with dense, long, patent hairs along the margin, blade 2–7 by 0.7–2.2 cm, rosetta leaves tapering gradually into

petiole at base, the single leaf of flowering stems sessile with broadly rounded base or semi-amplexicaulous, long acuminate at apex, lateral nerves indistinct, upper side dark green with often fairly lax, appressed, in the lower half irregularly directed, in the distal part antrorse hairs, lower side pale with antrorse hairs especially dense on midrib and along margins. *Cymes* always paired, terminal or on lateral branches arising from near base, bractless, either naked in lowermost part or with a single flower in the axil between two cymes and with more flowers in their whole length; pedicels 0.5–3 mm long, that of axillary flower up to 5 mm, densely strigose. *Calyx* 2.5–3 mm in flower, up to 4.5 mm in fruit, lobes 2–2.5 by 0.8 mm in flower, 3–3.5 by up to 1.1 mm in fruit, ovate-lanceolate, acute, antrorse strigose especially at base, along midrib and margins. *Corolla* white, 4 mm long, tube c. 2 mm long, lobes suborbicular, broadly rounded, c. 2 mm wide, glabrous; fornices c. 0.8 mm wide, 0.3 mm long, finely papillate. *Stamens* c. 1 mm long, anthers 0.8 mm, oblong, protruding from throat. *Pistil:* style c. 1 mm long, stigma distinct. *Nutlets* tetrahedral, c. 1 mm long, blackish brown, smooth, shiny, angles costate, ribs light brown.

Distribution — *Malesia:* Philippines (N Luzon). Only known from the type-collection.

Note — Closely related to *T. philippinensis* and *T. oblita*, from which it differs by the patent hairs growing fulvous in the lower part of the stems, from the former, which grows in the same area of Luzon, especially by the nearly rosulate, larger leaves, the winged petioles with dense, patent hairs, the longer calyx with narrower lobes and the light brown ribs of the nutlets.

17. Trigonotis vestita P. Royen

Trigonotis vestita P. Royen, Pac. Sc. 29 (1975) 85; Alpine Fl. New Guinea 4 (1983) 3102. — Type: *Lam 1658* (L holo), Irian Jaya, Mt Doorman.

Small, erect or ascendent herb. Stems up to 25 cm high, branched, the stems and branches glabrous, with leaves confined to the youngest parts, lower down with remnants of old leaves. *Leaves* close to each other, lanceolate, base widening into a sheath-like part, 1–2.2 by 0.15–0.3 cm, often curved downwards, acute, truncate and thickened at the very apex, one-nerved, subappressed strigose along margins only with longer hairs towards the base. *Cymes* axillary, 4–6-flowered, scorpioid while young, straight later on, usually with 1 or 2 bracts; peduncles, rhachis and pedicels angulate, appressed strigose; pedicels 3–6 mm long, in fruit curving downwards. *Calyx* 3.5–4 mm long, divided to the base, lobes elliptic, 1.5(–2) mm wide, obtuse, antrorse strigose along midrib and margins only, with a black gland below the apex. *Corolla* white, glabrous, 4–5 mm long, tube 2–2.5 mm long, lobes broadly obovate, rounded; fornices kidney-shaped, c. 1 mm wide, 0.5 mm long, papillate. *Stamens* c. 1 mm long, anthers 0.5 mm. *Pistil:* style c. 0.5 mm long. *Nutlets* tetrahedral with sharp angles, c. 1 mm long, brown, smooth.

Distribution — *Malesia:* New Guinea. Known only from the type locality.

Habitat — In swampy places between ferns and grasses in alpine grasslands, 3200–3520 m altitude.

DUBIOUS GENUS

CRUCICARYUM

Crucicaryum O. Brand in Diels, Bot. Jahrb. 62 (1929) 489; P. Royen, Pac. Sc. 29 (1975) 96. — Type species: *Crucicaryum papuanum* O. Brand.

Small, erect herbs, stems appressed villose. *Leaves* lanceolate, upper ones sessile, lower ones unknown. *Inflorescences* subthyrsoidal cincinni, bracteate. *Flowers* numerous, stalked. *Calyx* 5-lobed (?), widely cylindric, lobes ovate, throat-scales 5 (?), semilunate. *Stamens* 5 (?), inserted in tube. *Carpels* 4, connate at base only to the style; style shortly claviform. *Receptacle* flat, indistinct. *Nutlets* plano-compressed, shortly hairy with hooked hairs, horizontally spreading.

Distribution — A monotypic genus, endemic in New Guinea.

Note — Nothing is known of this genus except the original description translated into English with slight alterations by Van Royen. His text is followed here word for word. Van Royen's suspicion that it represents a poor form of *Cynoglossum javanicum* (Lehm.) Thunb. (*C. hellwigii* O. Brand in the interpretation adopted in this treatment), may be correct, though it does not explain the flat receptacle and the bracteate inflorescence. However, does Brand's description mean that it is bracteate throughout? Bracts may be present in the lower part of the inflorescence in any case. If there is no stylar column the genus would have to be included in *Lithospermeae* otherwise not represented in the area, or maybe in *Trigonotideae*. No final conclusion can be reached before additional new material becomes known from the alpine zone of the Sarawaket Range in the northeastern part of Papua New Guinea.

Crucicaryum papuanum O. Brand in Diels, Bot. Jahrb. 62 (1929) 489; P. Royen, Pac. Sc. 29 (1975) 96.

Herb. *Leaves* lanceolate, c. 3 by 0.5 cm, acute, sessile. *Pedicels* known in fruit only and as long as calyx. *Sepals* ovate, 1.5–2 mm long. *Corolla* 3 mm long. *Nutlets* orbicular, hardly 1 mm long.

Distribution — Known only from the type collection, Papua New Guinea, Sarawaket Range, 3600–4000 m (*Keysser 41*, destroyed in B).

EXCLUDED GENUS, OF UNCERTAIN AFFINITIES

PTELEOCARPA

Pteleocarpa Oliv., Trans. Linn. Soc. 28 (1873) 515; Ridl., Fl. Malay Penins. 2 (1923) 464; Veldkamp, Fl. Males. Bull. 10, 1 (1988) 47; Ng in Tree Fl. Malaya 4 (1989) 64; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 103. — Type species: *Pteleocarpa malaccensis* Oliv. [= *Pteleocarpa lamponga* (Miq.) Bakh. ex K. Heyne].

Glabrous trees. *Leaves* alternate, lanceolate to ovate-lanceolate. *Inflorescence* paniculoid, many-flowered, terminal, without bracts. *Flowers* on a short stalk. *Calyx* 5-lobed,

imbricate. *Corolla* yellow, with a short tube and 5 oblong, rounded, imbricate lobes sometimes slightly different in size. *Stamens* 5, exserted from the throat, with sagittate anthers. *Ovary* undivided, bilocular, each locule with a small upright and a bigger pendulous ovule; style divided to the base into two branches, each bearing a capitate stigma. *Fruit* broadly elliptic to suborbicular, with a wide, cartilaginous, radially veined wing, one-seeded. *Seed* elongate. — **Fig. 18.**

Distribution — A monotypic genus, see under the species.

Note — The most peculiar features of the genus which clearly show that it cannot be a member of *Boraginaceae* are the radially veined wings of the single fruit and especially the two different ovules, one pendent and one upright. This latter character is very rare in general and found, e.g., in the genus *Maytenus* of *Celastraceae*.

Pteleocarpa was included in *Olacaceae* by its original author, but there are many important differences. Veldkamp, l.c., discusses possible relationships to *Boraginaceae*, *Icacinaceae*, *Olacaceae*, *Cardiopteridaceae*, *Lophopyxidaceae* and *Sapindaceae*, but he arrives at the conclusion that it does not belong to any of them. It may prove necessary to describe a new family for it, the position of which will remain uncertain again, however.

Pteleocarpa lamponga (Miq.) K. Heyne

Pteleocarpa lamponga (Miq.) Bakh. ex K. Heyne, Nutt. Pl. Ned. Indië, ed. 2 (1927) 1309; Veldkamp, Fl. Males. Bull. 10, 1 (1988) 47; Ng in Tree Fl. Malaya 4 (1989) 64; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 103, f. 4. — *Dodonaea lamponga* Miq., Sumatra (1862) 511. — Type: *Teijsmann s.n.* (BO holo; L), Sumatra.

Pteleocarpa malaccensis Oliv., Trans. Linn. Soc. 28 (1873) 515; Ridl., Fl. Malay Penins. 2 (1923) 464. — Type: unknown.

Pteleocarpa longistyla Becc., Malesia 1 (1877) 130. — Type: unknown.

Tree, up to 30 m high. Trunk 40–60 cm in diam. Bark superficially fissured, yellowish to greenish grey, inner bark pale brown to pale orange, wood pale yellowish to reddish brown; branches reddish brown, youngest, herbaceous shoots minutely papillose. *Leaves* obovate, obovate-lanceolate or lanceolate, petiole 0.7–1 cm long, blade 2.5–10 by 1.2–6 cm, margin entire, base gradually tapering into petiole, apex usually long acuminate, rarely subobtuse to emarginate, 5 or 6 primary nerves on each side of midrib (following the pattern of *Ehretia*), glabrous on upper and lower side. *Inflorescence* terminal, paniculate to thyrsoid-paniculate, with short peduncle, rhachis densely pubescent, flowers numerous; pedicels 2–8 mm long, densely pubescent. *Calyx* campanulate, 1.8–2 mm long, 1.8 mm wide, lobes free for 3/4 of calyx length, ovate to triangular, acute, sometimes imbricate, with few hairs along the margin. *Corolla* yellow, rarely red, tube shorter than calyx, lobes explanate, c. 5 by 1.8–2 mm, obovate-oblong, broadly rounded. *Stamens* inserted at upper end of tube, filaments filiform, about thrice as long as anthers, anthers basifixed, linear, bilobed at base, dehiscent longitudinally, obtuse. *Pistil:* styles 2, 3–4 mm long, filiform, stigmas indistinct; ovary sitting on an ovoid, sterile disc. *Fruit* single, broadly winged, wing suborbicular to ob-

ovate in outline, 3–4.5 cm in diam., fertile locules 2, oblong, 1.3–2 cm long, laterally compressed, wing densely radially veined, slightly emarginate to deeply bifid at apex, continuous also below locules; only the big, pendulous ovule developing into a seed. — **Fig. 18.**

Distribution — S Thailand; *Malesia:* Sumatra (incl. Bangka), Malay Peninsula, Singapore, Borneo.

Habitat — Tree of primary lowland and hill forests.

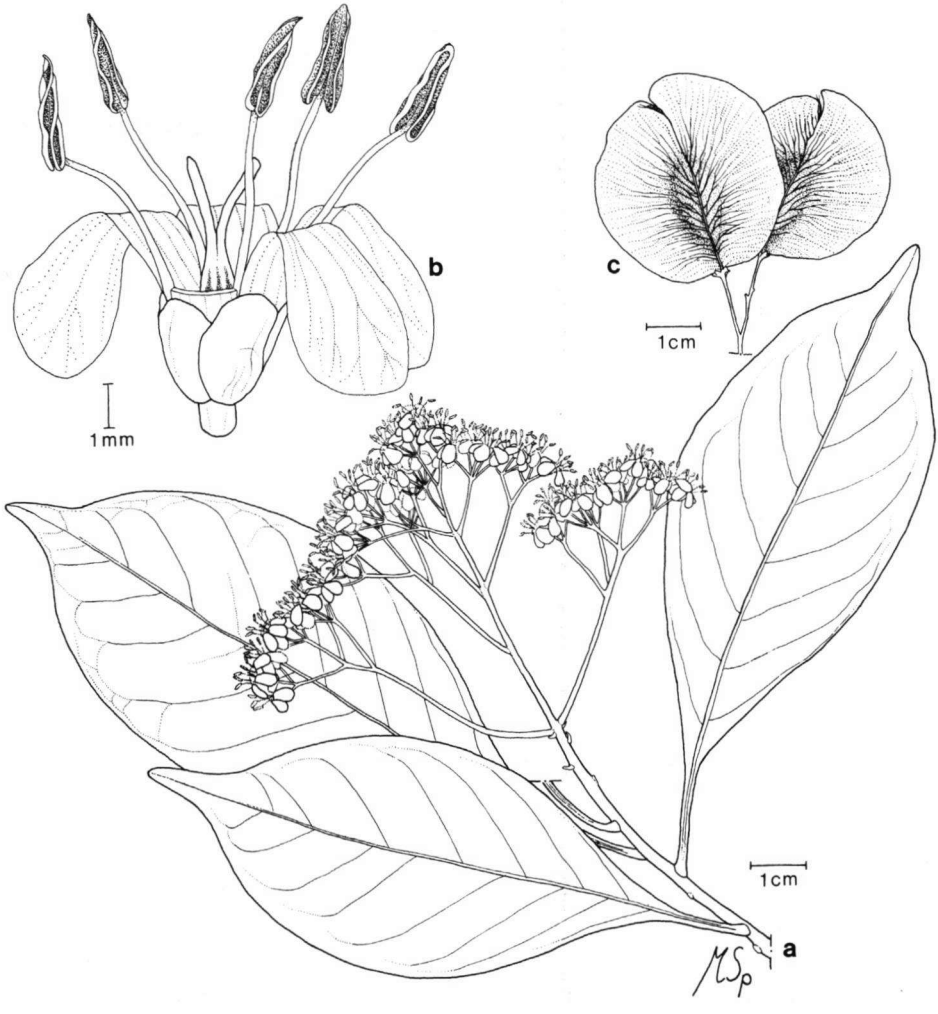

Fig. 18. *Pteleocarpa lamponga* (Miq.) K. Heyne. a. Top of flowering twig; b. flower; c. ripe fruits (a, b: *Lajangah 44630*; c: *Brand SAN 30871*). Drawing M. Spitteler.

DOUBTFUL OR ERRONEOUS RECORDS

Lithospermum zollingeri A.DC., Prodr. 10 (1846) 587. — Type: *Zollinger 352*, Java.

Note — *Lithospermum zollingeri* is a well-defined species from China, that has not been found in Java by anyone since Zollinger. Either it had been introduced there by chance and has vanished long since, or the label data of the type specimen are erroneous.

'Lithospermum' corsonianum G. Don in Loudon, Gard. Mag. (1842) 371. — Type: *Corson 1839*, Batagoda.

Erect, hispidulous-strigose, branched at apex, with linear leaves and paired, terminal, bracteate spikes, acuminate segments of the calyx and the tube of corolla as long as the calyx. Annual with simple base, 4–5 inches high. Flowers small, yellow.

Note — From the above description, no conclusion as to the identity of the species can be drawn. Certainly it is no *Lithospermum*, as it is far from the area of distribution of that genus. The type specimen had been kept at the Linnean Society in London, but apparently was among those plants that have been sold in 1863. All attempts to locate it have been in vain so far. According to Index Kewensis it came from Timor.