ULMACEAE (E. Soepadmo, Kuala Lumpur)

Monoecious or dioecious (?), evergreen, deciduous or semideciduous shrubs or trees, (in Mal.) unarmed and often buttressed. Growth habit (in Mal.) flush-wise, except for *Trema* and *Parasponia*. Indumentum of simple, bulbous-based unicellular hairs and/or multicellular glandular hairs. Stipules caducous or rarely rather long persistent and completely enclosing the bud, extrapetiolar or intrapetiolar, basally attached or rarely peltately attached to the nodes, free or connate. *Leaves* simple, (in Mal.) alternately arranged, petioled, pinnately nerved or triplinerved at base, often asymmetrical at base, entire or variously serrate. *Inflorescences* 1-many-flowered, ♂, ♀, ♂♀, or ♂☿, axillary, subterminal, or borne on leafless, older branchlets or on short, lateral, leafless new shoots, paniculate, racemose, thyrsoid, cymoid, or rarely capitate, bracteate; bracts minute, caducous. Flowers functionally ♂, ♀, or ☿. — ♂ *Flowers* solitary or in condensed cymoid clusters along the rachis, sessile or short-pedicelled; perianth (4–)5(–7)-lobed, lobes free or variously connate, imbricate or induplicate-valvate in bud; stamens as many as tepals, attached to the base of and opposite the perianth lobes, straight or incurved in bud; anthers ovoid, ellipsoid or subreniform, apiculate or non-apiculate, initially tetrasporangiate, later becoming 2-celled, dehiscing lengthwise, introrse or extrorse; pistillode present or absent, if present either rather well developed or rudimentary, densely whitish to silvery, soft or hirsute pubescent. — ♀ & ☿ *Flowers* sessile or stalked, solitary in the axils of the upper new leaves or arranged in various types of inflorescences; perianth herbaceous or thin-coriaceous, (4–)5(–7)-lobed, lobes always imbricate in bud and connate at base, (in Mal.) long persistent; staminodes or stamens as many as perianth lobes or absent; ovary superior, 2-carpellate, (in Mal.) 1-celled, sessile or stipitate; style 1, tubular, short or absent, stigmatic arms 2, slender, often bifid to deeply lobed at the tip, adaxially papillose-stigmatic for their entire length; ovule 1, anatropous to hemi-anatropous, subapical, pendulous, bitegmic. *Fruit* a drupe or a samara, faintly angular or flat and winged. *Seed* mostly exalbuminous; embryo large, straight or curved; cotyledons flat-convex, fleshy, straight or variously folded, often foliaceous. Germination mostly epigeal.

Distribution. There are 15 genera, *c.* 200 *spp.*, widely distributed in the tropics, subtropics, and temperate regions of Europe (as far north as 70°, Scandinavia), Africa (South of Sahara), continental Asia, Malesia, Australia (Queensland and New South Wales), Pacific Islands (as far as Tahiti; incl. also Hawaii and the Galapagos Is.), North, Central, and South America (as far south as 40°, Argentina). Fig. 1.

Fossils. Various macrofossils (woods, drupes, and leaf-impressions) and microfossils (pollen grains) attributed to *Ulmaceae* have been reported by different authors from various localities in Alaska, North America, Europe, continental Asia, and Japan. Amongst the older records are pollen grains of the *Ulmus-Zelkova*-type from Golden Valley Formation in North Dakota and Rocky Mountains, U.S.A. (Paleocene) and wood and leaf-impressions attributed to *Ulmus* from Rocky Mountains and to *Planera* from Alaska (Late Paleocene). By the middle of the Eocene and throughout the Miocene and Pliocene fossils of *Ulmaceae* become more abundant (common) in the northern hemisphere, especially in Europe and North America. However, very little is known about the geological history of the family in Asia.

Of the Malesian genera belonging to the tribe *Celtoideae*, fossil records of *Gironniera* (identification very doubtful) go back to Middle Eocene (Alaska), that of *Celtis* to Miocene (Japan), and *Trema* to Upper Oligocene (Japan). — *Literature:* Berry, Tree Ancestor (1923) 146; Watari, Jap. J. Bot. 11 (1941) 385; J. Fac. Sc. Un. Tokyo III, 6 (1952) 97; La Motte, Mem. Geol. Soc. Am. 51 (1952) 112, 260, 346, 360; Prakash & Barghoorn, J. Arn. Arb. 42 (1961) 185, 347; Greguss, Tert. Angios. Hung., Ak. Kiado Budapest (1969) 83; Ferguson, Verh. Kon. Ned.

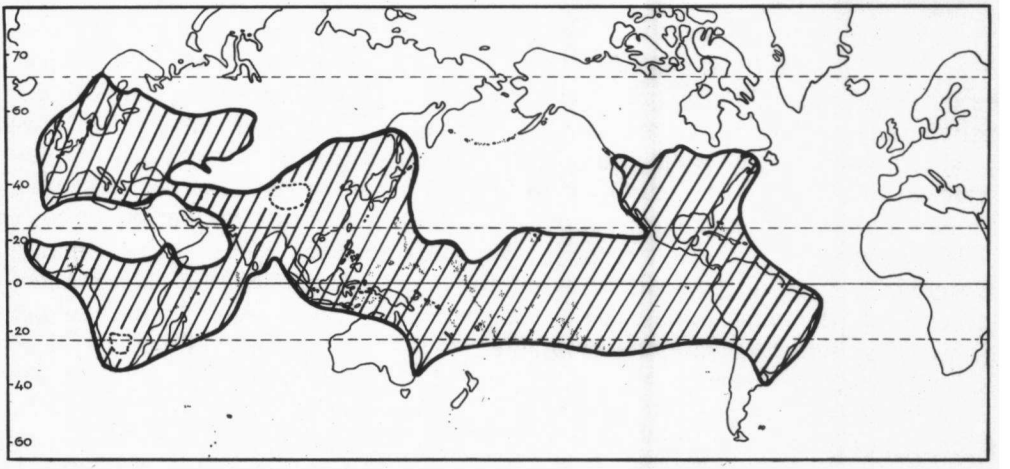

Fig. 1. Approximate range of *Ulmaceae*.

Ak. Wet. sect. II, 60 (1971) 103; LEOPOLD & MACGINITIE in Graham, Flor. & Paleofl. Asia & N.E. America (1972) 147; WOLFE, *l.c.* 200; TANAI, *l.c.* 235; WOLFE, Brittonia 25 (1973) 334.

Ecology. In Malesia species of the *Ulmaceae* may be found in both primary and secondary forests, from sea-level up to 2000 m; they are more common in the lowlands and hills.

Apart from *Ulmus lanceaefolia*, *Celtis rigescens*, *Gironniera nervosa* and *G. subaequalis* which may attain up to 45 m in height and 100 cm in diameter, all species are understorey shrubs or trees. Of the 6 genera occurring in Malesia, species of *Aphananthe*, *Celtis*, *Gironniera* and *Ulmus* are basically primary forests inhabitants, though they may survive and thrive in secondary forests as well. Of these, *Celtis* and *Gironniera* species are the most widely spread and may be found growing on various types of soils, including those derived from limestone.

In Malesia *Ulmaceae* are found under both everwet and more seasonal climatic conditions, but some show preference for one or the other. In *Celtis* two groups of species may be distinguished, *viz* the group of *C. tetrandra*, *timorensis* and *rubrovenia*, and that of *C. philippensis*. The former is either semideciduous or deciduous and found mainly under a drier and more seasonal climate, while the latter is evergreen and grows better in more humid environmental conditions. *Aphananthe* and *Ulmus* species are mainly found in regions subject to a rather distinct seasonal climate, and they are either semideciduous or deciduous. Members of the genera *Parasponia* and *Trema* are pioneer plants preferring and thriving well in newly opened up habitats, *e.g.* forest clearings, thickets, roadsides, flood-plains, on volcanic ashes, *etc.* Fig. 10, 11, 17. They are usually short-lived (at least in Malaya, 5–7 years) and soon will die out, particularly when over-grown by the other more aggressive and long-lived pioneer plants, *e.g.* species of *Macaranga*, *Mallotus*, and *Grewia*, *etc.* For this reason species of *Trema* and perhaps also those of *Parasponia* are usually not or rarely found in old secondary forest. It also may be noted here that most *Trema* species grow, thrive, and are more widely spread in the western parts of Malesia, while *Parasponias* are more common in the eastern parts, especially in New Guinea.

The structure and position of the inflorescence and flowers, particularly the amount of pollen grains produced and the structure of the stigmas, and also the absence of nectary, seem to suggest that pollination is most likely affected by wind, though insects may not be ruled out altogether as possible agents for pollination.

Except for *Ulmus*, which produces a dry, flat, winged fruit, the other Malesian genera have various types of fleshy drupes which turn to bright yellow, orange, or deep-red in colour when ripe. These drupes are most probably dispersed by various species of frugivorous birds or arboreous mammals. Alternatively, at least in some species, *e.g. Celtis philippensis var. wightii* which is very common in coastal vegetation, fruit dispersal may be carried out by water currents. In *Ulmus* the winged fruits are easily dispersed by wind.

It should be noted here that there is a very high percentage of seed abortion in Malesian genera for reasons unknown. This is made good by the production of a great number of flowers and fruits, produced regularly throughout the year or at least twice a year. Except for *Ulmus*, the embryo is protected by a strong, hard and durable endocarp. In all genera endosperm is usually scanty or absent.

Anatomy. For general surveys also covering the older literature see SOLEREDER, Syst. Anat. Dicot. Stuttgart (1899) 860–865 and *ibid.* (1908) 295; METCALFE & CHALK, Anat. Dicot. Oxford (1950) 1271–1278; SWEITZER, J. Arn. Arb. 52 (1971) 523–585. Additional selected references: DEHAY, l'Appareil conducteur foliaire des Urticacées, des Moracées et des Ulmacées (Ordre des Urticales), Arras (1934); JANSSONIUS, Mikr. 6, Leiden (1934) 1–308 (wood anatomy, under *Urticaceae*); LEROY, Bull. Mus. Nat. Hist. Nat. Paris sér. 2, 18 (1946) 118–123 & 180–184 (taxonomy, and anatomy of *Aphananthe*); DEN BERGER, Determinatietabel Malesië, Veenman, Wageningen (1949) (wood identification); RAO, GOVINDU & THIRUMALACHAR, J. Indian Bot. Soc. 29 (1950) 224–226 (aerial roots, *Trema*); JANSSONIUS, Blumea 6 (1950) 407–464 (wood anatomical affinities); DESCH, Mal. For. Rec. 15 (1954) 618–620 (wood); JUTTE, Nova Guinea n.s. 10 (1959) 241–278 (wood); MOSELEY, Brittonia 25 (1973) 356–379 (anatomy and relationships).

SWEITZER's study (*l.c.*) is the most up-to-date survey of leaf and wood anatomy of the *Ulmaceae*. Although his extensive research materials included very few Malesian species his general conclusions are probably largely applicable to the Malesian species as well.

The wood anatomy is indicative of the mutual affinities of all Ulmaceous genera. Shared characters are: predominantly simple vessel perforations, short vessel members, alternate intervessel pits. Fibres with simple to slightly bordered slit-like pits. Parenchyma at least partly vasicentric. Genera of the tribe *Ulmeae* (in Malesia only represented by *Ulmus lanceaefolia*) have exclusively homocellular rays. In *Celteae* (in Malesia all other genera) at least part of the ray tissue is heterocellular.

The wood of *Ulmus lanceaefolia* differs from all species described in literature in lacking the ring porosity and the typical ulmiform arrangement of vessel clusters (original observation). Instead, its vessel distribution resembles the diffuse porous group of tropical *Celtis* species. In *Celtis* the very striking differences in vessel distribution between tropical and extratropical species are well documented (*cf.* SWEITZER, *l.c.*). Although from SWEITZER's and other publications some quantitative and qualitative differences between Malesian genera of *Celteae* can be deduced, our knowledge is still based on too limited materials to allow conclusions on diagnostic and systematic implications.

The leaf anatomy of *Ulmaceae* at the same time supports its coherence as a family and provides an interesting diversity, of great potential diagnostic and systematic value. All *Ulmaceae* share the dorsiventral leaf architecture. The stomata are confined to the abaxial epidermis and are of the anomocytic type. The indumentum includes bulbous-based unicellular trichomes the walls of which are usually silicified. Mineral inclusions of calcium carbonate or silica in cystoliths (with or without pegs) are of common occurrence. The trichome-complement, presence or absence of mucilage cells, crystal complement, loose or compact structure of the spongy tissue, petiole and midrib vasculature show a considerable diversity. SWEITZER's data and other reports from the literature do not yet allow a leaf anatomical characterization of the individual Malesian taxa, but preliminary studies are indicative that this will be possible if more material is studied.

The entire evidence from vegetative anatomy supports the traditional placement of *Ulmaceae* in *Urticales*. — P. BAAS.

Palynology. Based on size, sculpturing of exine and number of pores, pollen grains of *Ulmaceae* may be divided into two major morphological types, namely the *Ulmus*-type and the *Celtis*-type. In the *Ulmus*-type the pollen are oblate to subspherical, amb convex or straight; (4–)5(–7)-porate, 20–30 by (26–)28–38(–51) μm, pore circular to elliptic, *c.* 2–3 by 3–4 μm, slightly thickened around its margin; exine rugulate-reticulate. Genera with this type of pollen grains are: *Ampelocera*, *Hemiptelea*, *Holoptelea*, *Phyllostylon*, *Planera*, *Ulmus*, and *Zelkova*. In the *Celtis*-type the pollen is suboblate to spherical, amb convex; (2–)3–4(–5)-porate, pores circular or elliptic (elongated towards the poles), often annular and protruding, *c.* 2–3 by 3–4 μm; 17–25 by 19–30 μm; exine more or less smooth but for very fine (1–1.5 μm) scabrae. This type is found in *Aphananthe*, *Celtis*, *Chaetacme*, *Gironniera*, *Lozanella*, *Parasponia*, *Ptero-*

celtis and *Trema*. It may be noted here that pollen grains of *Gironniera*, *Parasponia* and *Trema* are usually slightly smaller and have finer exine sculpturing than those of other genera with *Celtis*-type of pollen, while the pollen grains of the Malesian species of *Trema* and those of *Parasponia parviflora* MIQ. are predominantly diporate. As for pollen grains, *Ulmaceae* are very closely allied to *Moraceae* and *Urticaceae*, particularly to the former. According to NAIR (1967) the pollen type found in *Ulmaceae*, *Moraceae* and *Urticaceae* is derived from a tricolpate type of Ranalean stock. — *Literature:* ERDTMAN, Pollen Morph. & Taxon. 1 (1956) 442; IKUSE, Pollen Grains of Japan (1956) 62; PRAGLOWSKI, Grana Palyn. 3 (1962) 45–65; KUPRIANOVA, Kom. Bot. Inst. Ac. Sc. USSR 1 (1965) 54–58; NAIR & SHARMA, Bot. Notis. 118 (1965) 177–186; STRAKA, Pollen et Spores 8 (1966) 241–264; NAIR, Rev. Palaeobot. & Palyn. 3 (1967) 81–91; MALLIK & CHAUDHURI, Bull. Bot. Soc. Beng. 22 (1968) 105–108; TSUKADA, Bot. Mag. Tokyo 81 (1968) 385–395; RAO & LEE, Pacif. Sc. 24 (1970) 255–268; HUANG, Pollen Fl. Pl. Taiwan (1972) 235; SOWUNMI, Grana Palyn. 13 (1973) 145–186; ADAMS & MORTON, Atl. Pollen Trees & Shrubs Canad. & U.S. 9 (1974) pl. 17; STOCKMARR, Grana Palyn. 14 (1974) 103–107; KEDVES & PARDUTZ, Acta Biol. Szeged. 20 (1974); HAMILTON, Pollen et Spores 18 (1976) 54–57.

Embryology. Apart from several species of *Ulmus* and *Holoptelea* very little is known about the sporogenesis and embryogenesis of the *Ulmaceae*. From a very limited information so far published it appears that the anthers are initially tetrasporangiate but become bisporangiate just before anthesis through the breakdown of the adjoining wall between the locules. The anther-wall development conforms with the so-called basic-type in which the parietal cells divide both anticlinally and periclinally to form the endothesium layer, two (*Trema* and *Ulmus*) or three to four (*Holoptelea integrifolia*) middle-layers and glandular tapetum. Simultaneous cytokinesis in the microspore mother-cells follows meiosis and as a result the pollen grains are initially arranged in either tetrahedral or decussate tetrads. At anthesis the pollen grains are either 2-celled (*Holoptelea* and *Trema*) or 3-celled (*Ulmus*). In *Celtis*, *Holoptelea* and *Trema* up to 80% of the pollen grains produced are sterile or imperfectly developed. The ovule is anatropous to hemianatropous, bitegmic, crassinucellar or tenuinucellar (in a few species of *Ulmus*) with the micropyle formed by both integuments (*Celtis* and *Trema*) or by the inner integument only (*Holoptelea* and *Ulmus*). In *Holoptelea* and *Trema* the megaspore mother-cell divides into 4 daughter cells arranged in a linear tetrad, and of these only the chalazal megaspore develops into *Polygonum*-type of embryo-sac. In *Ulmus*, however, the embryo-sac is tetrasporic and either belongs to *Adoxa*- or *Drusa*-type or variation of these two types with 4–12 antipodal cells. The pollen tube enters the ovule either through the micropyle, the integuments or the chalaza. Endosperm formation is nuclear and the tissue is either diploid or triploid and later becomes cellular. Embryo development conforms with the Onagrad-type in *Holoptelea* and Solanad-type in *Ulmus*. Polyembryony is a common phenomenon, especially in *Ulmus*. The mature embryo is straight with broad, flat or plano-convex, equal or slightly unequal cotyledons in *Holoptelea*, *Planera*, *Phyllostylon*, *Ulmus*, and *Zelkova*, or curved with ascending hypocotyle and narrow, incurved or induplicate-plicate or variously folded cotyledons which are mostly unequal in length in *Ampelocera*, *Aphananthe*, *Celtis*, *Gironniera*, *Parasponia*, *Pteroceltis* and *Trema*. — *Literature:* SHATTUCK, Bot. Gaz. 40 (1905) 205–223; LELIVELD, Rec. Trav. Bot. Néerl. 32 (1935) 543–573; CAPOOR, Beih. Bot. Centralbl. 57 (1937) 233–249; WALKER, Am. J. Bot. 37 (1950) 47–52; HJELMQVIST & GAZZI, Bot. Notis. 118 (1965) 329–360; DAVIS, Syst. Embryol. Angiosp. (1967) 266–267.

Chromosomes. From various published data it seems that the chromosome number in the *Ulmeae* (*Holoptelea*, *Ulmus*, and *Zelkova*) is n = 14 and 2n = 28, 42, and 56, though reports of n = 15 and 30 have been made on *Ulmus americana*. In the *Celtideae* the number seems to be less constant varying from n = 10, 2n = 20, 28, 40 in *Celtis* (9 *spp.*); n = 30, 2n = 84 in *Chaetacme* (2 *spp.*); to n = 10, 10 + B, 18, 20, and 80 in *Trema* (3 *spp.*). It may be noted here that as for chromosome number, *Ulmaceae* seems to be closely related to *Moraceae* where n = 12–16, 2n = 24, 26, 28, 42, 56, and 84, and to *Urticaceae* of which n = 14, 28 and 2n = 22, 24, 28, 52, and 84. — *Literature:* KRAUSE, Ber. Deut. Bot. Ges. 48 (1930) 9–13; Planta 13 (1931) 29–84; WALKER, Science 75 (1932) 107; SAX, J. Arn. Arb. 14 (1933) 82–84; BOWDEN, Am. J. Bot. 32 (1945) 195; DARLINGTON & WYLIE, Chromos. Atlas Fl. Pl. (1955) 182–183; MANGENOT & MANGENOT, Bull. Jard. Bot. Brux. 28 (1958) 315–329; ARORA, Bull. Bot. Surv. India 2 (1960)

305; GAJAPATHY, Bull. Bot. Surv. India 3 (1961) 49–51; GRUDZINSKAJA & ZAKHARYEVA, Bot. Zhurn. 52 (1967) 641–651; HSU, Taiwania 13 (1967) 117–129; MEHRA & GILL, Taxon 17 (1968) 574–576; J. Arn. Arb. 55 (1974) 663–677; FEDOROV (ed.), Chromos. Numb. Fl. Pl. (1969) 710–711; GADELLA *c.s.* Acta Bot. Neerl. 18 (1969) 74–83; MEHRA & HANS, Taxon 18 (1969) 310–315; TATAYUK & TURCHANINOVA, Tsitologia & Genetika 4 (1970) 397–401; HANS, Cytologia 36 (1971) 341–345; NIEHAUS, Taxon 20 (1971) 355; MEHRA, Nucleus 15 (1972) 64–83; SARKAR, Taxon 22 (1973) 652.

Chemotaxonomy. SOLEREDER mentioned the more or less general occurrence of cystoliths and cystolith-like structures (SiO_2 + $CaCO_3$) in *Ulmaceae*. The tendency to accumulate carbonate of lime seems to be very strong in this family; $CaCO_3$ is deposited in wall structures (*e.g.* hairs, cystoliths) and in cell lumina (*e.g.* in heartwood of *Ulmus* and *Celtis*; in seed coat cells of *Celtis*). Often oxalate of lime is also present in large amounts; solitary and clustered crystals occur in the family. Anatomically easily detectable internal excretion comprises also mucilage production. The mucilage is deposited in epidermal cells (many taxa) or in mucilage idioblasts in the mesophyll of some genera and in barks and flowers of most species of *Ulmus*. The bark of *Ulmus rubra* MUHL. ('Slippery Elm') was used formerly as a mucilaginosum in official medicine. In mucilage-rich elm barks large mucilage idioblasts may develop to lysigenous mucilage cavities. Chemically elm bark mucilages are characterized by a high content of galacturonic acid, galactose, 3-O-methylgalactose and rhamnose. *Ulmaceae* are moderately strong accumulators of polyphenolic compounds. Derivatives of caffeic acid, catechins, pro-anthocyanidins (formerly leucoanthocyanidins), flavonols (especially glycosides of kaempferol and quercetin) and condensed (= flavanoid) tannins seem to occur more or less ubiquiteous in leaves, fruits, barks and woods. According to LEBRETON flavonoid constituents with a trihydroxylated B-ring (in casu myricetin and prodelphinidin), an assumedly primitive feature, are restricted to *Celtideae*. (+)-Catechin was definitely identified in leaves, twigs and barks of European elms and its 7-xyloside was isolated from the stem-bark of *Ulmus americana* L. C-Glycoflavons (tremasperin) occur in leaves of *Trema aspera* BL., and the wood of *Zelkova serrata* (THUNB.) MAKINO contains large amounts of the fungistatic 6–C-glucoflavonoids keyakinin and keyakinol. Tannin contents of woods, barks, leaves and fruits are moderate (mostly less than 10%). There is only one report in literature indicating a possible co-occurrence of galli- and ellagitannins with condensed tannins in *Ulmaceae*; bark and wood of *Celtis australis* L. contain gallic acid and derivatives of ellagic acid according to CHARI *c.s.* (1968).

Much chemical work was performed with elm barks and especially elm woods in connection with 'Dutch Elm Disease'. Cadinane-type oxigenated sesquiterpenes seem to be present in the young wood of every species. On aging (heartwood formation) or after fungal infection, synthesis and accumulation of fully aromatic (cadalenal, hydroxycadalenal) and (or) *o*-quinonoid (the mansonones) cadinane derivatives take place in American elm species belonging to the sections *Trichoptelea*, *Microptelea* and *Chaetoptelea*; they seem to be absent from the sections *Blepharocarpus* and *Madocarpus* in which all European elms are included. It deserves mentioning that the antifungal cadalenals and mansonones represent phytoalexin-like stress compounds in *Ulmus*, and occur at the same time as normal heartwood constituents in *Ulmus* and *Zelkova* (but not in *Celtis*); they are chemically identical with, or biochemically closely related to the gossypol-mansonone-group of constituents of many *Malvaceae*, *Bombacaceae* and *Sterculiaceae* (mansonones were first detected in the wood of *Mansonia altissima* A. CHEV.). It was recently shown that hemigossypol, the precursor of the long-known gossypol, is a phytoalexin in many malvaceous plants and that *p*-quinonoid derivatives of hemigossypol are engaged in the plants resistance against attack by several phytophagous insects (J. R. GRAY *c.s.* J. C. S. Chem. Commun. 1976, 109; J. A. VEECH *c.s. l.c.* 144). As far as ecological chemistry (defensive substances) is concerned, *Ulmaceae* much resemble members of the order *Malvales*. Leaf, bark and wood waxes were investigated by several authors in recent time. They seem to consist mainly of alkanes, long-chain fatty acids, wax alcohols and phytosterins. Additionally pentacyclic triterpenes are often present; β-amyrin (i), lupeol (ii), betulin (iii), friedelin (iv), friedelanol (v), moretenol (vi), simiarenol (vii) and simiarenon (viii) were reported from leaves and (or) barks of *Celtis australis* L. (iii), *C. laevigata* WILLD. (vi), *Holoptelea integrifolia* PLANCH. (iv, v), *Trema guineensis* FICALHO (reported as *T. orientalis* BL.; vii, viii), *Ulmus americana* L. (ii, esterified with cerotinic acid) and *Zelkova*

serrata MAKINO (iv). The heartwood of *Holoptelea integrifolia* PLANCH. yielded 2α-hydroxy-3-epioleanolic acid (G. MISRA *c.s.* Planta Medica 27, 1975, 290); this is the only triterpenic acid isolated hitherto from *Ulmaceae*. Seeds of *Ulmaceae* seem to store predominantly proteins and fatty oils. The oils have linolic (*Celtis*, *Chaetacme*, *Trema*), oleic (*Holoptelea*) or capric (*Ulmus*, *Zelkova*) acids as main fatty acid. Species of *Celtis* and *Pteroceltis* accumulate small amounts of quebrachitol in leaves; this cyclitol could not be detected in leaves of species of *Ulmus* and *Zelkova* (*Hemiptelea* included). Alkaloid-like compounds are recorded in literature from members of *Ampelocera*, *Aphananthe*, *Celtis*, *Gironniera*, *Trema* and *Ulmus*, but only in the case of *Ampelocera ruizii* KLOTZSCH an alkaloid-like compound isolated from leaves was chemically identified; it proved to be an α-pyridone derivative related to trigonelline (R. H. BURNELL *c.s.* Lloydia 38, 1975, 444). The foetid smell of some *Celtis* woods of India, Indonesia ('*kaju tai*') and Africa is caused by skatol. Several species of *Ulmaceae* are reported to be toxic in literature. GRESHOFF isolated a toxic bitter principle from the leaves of *Aphananthe aspera* (THUNB.) PLANCH. (= *Homoioceltis aspera* BL.) which he compared with his streblide (from *Streblus asper* LOUR.; strebloside is now known to be a cardenolide). Leaves of *Trema cannabina* LOUR. (= *Sponia virgata* PLANCH.) and of *T. aspera* BL. (= *T. cannabina*) were reported to be cyanophoric; both species, however, are polymorphic with regard to cyanogenesis if the botanical identification of all plant samples investigated hitherto was correct. Leaves of *T. aspera* (= *T. cannabina*) contain another toxic principle called trematoxin; its chemical structure is not yet known.

From the taxonomic point of view three facts deserve special mentioning: (1) *Ulmaceae* are generally included in *Urticales*; their chemistry agrees rather well with such a classification as is indicated by patterns of mineralisation and phenolic compounds. (2) The chemistry of *Ulmaceae* resembles members of *Malvales* in several respects: chemistry of stress compounds; mucilages with high contents of galactose, rhamnose and galacturonic acid; some features of the polyphenolic and triterpenic patterns. (3) The classification of *Ulmaceae* in *Ulmoideae* and *Celtidoideae* (ENGLER's Syllabus 2, 1964) or *Ulmeae* and *Celtideae* (HUTCHINSON, General of Flowering Plants 2, 1967) is not very satisfactory from the chemical point of view (see cadinane-type sesquiterpenes including mansonones and capric acid as main fatty acid in seed oils in *Ulmus* and *Zelkova*, but not in *Celtis*).

For more phytochemical details and references see my 'Chemotaxonomie der Pflanzen' 6 (1973) 545–554, 762–763, 791, 796. — R. HEGNAUER.

Taxonomy. The family name *Ulmaceae* was first introduced and defined by MIRBEL in 1815, at which time it included only *Celtis* and *Ulmus*. LINK (1831) proposed splitting *Ulmaceae* into two separate families, *i.e.* *Ulmaceae* to include *Ulmus* and related genera, and *Celtidaceae* comprising *Celtis* and its allies, an opinion which was supported by GRUDZINSKAYA (1967). However, all contemporary taxonomists generally agree to regard *Ulmaceae* as a natural taxon closely related to *Moraceae* and *Urticaceae* and to include these families in the order *Urticales*. Any difference of opinion is usually restricted to the inclusion or exclusion of a few genera in the family. In the most recent treatise, HUTCHINSON (1967) divided the family into two tribes, namely the *Ulmeae* (flowers bisexual, fruit not drupaceous, embryo straight, cotyledons flat or longitudinally folded) to include: *Holoptelea*, *Planera*, *Phyllostylon*, and *Ulmus*, and the *Celtideae* (flowers unisexual or sometimes bisexual, fruit drupaceous, embryo curved, cotyledons mostly variously folded) comprising *Ampelocera*, *Aphananthe*, *Celtis*, *Chaetacme*, *Gironniera*, *Hemiptelea*, *Lozanella*, *Mirandaceltis*, *Parasponia*, *Pteroceltis*, *Trema* and *Zelkova*. This subdivision was supported by SWEITZER (1971) who studied the anatomy of leaf and wood. However, as has been mentioned under Embryology and Palynology, the embryo of *Zelkova* is straight, and the pollen (also of *Ampelocera* and *Hemiptelea*) belongs to the *Ulmus*-type (see also ERDTMAN, 1956). Furthermore in many species of *Celtis* the flowers are bisexual, and in *Ulmus lanceaefolia* and *U. parvifolia* the flowers are either functionally male or female. This seems to indicate that the tribal subdivision as proposed by HUTCHINSON is not a clear cut case, but that *Ulmaceae* is a natural taxon. It should be noted further that the Mexican genus *Mirandaceltis* is in the present study regarded as congeneric with *Aphananthe*.

As for phylogenetic relationship, there seems to be two different opinions. BESSEY (1915) and THORNE (1968, 1973) placed *Ulmaceae* along with *Moraceae* and *Urticaceae* in the superorder

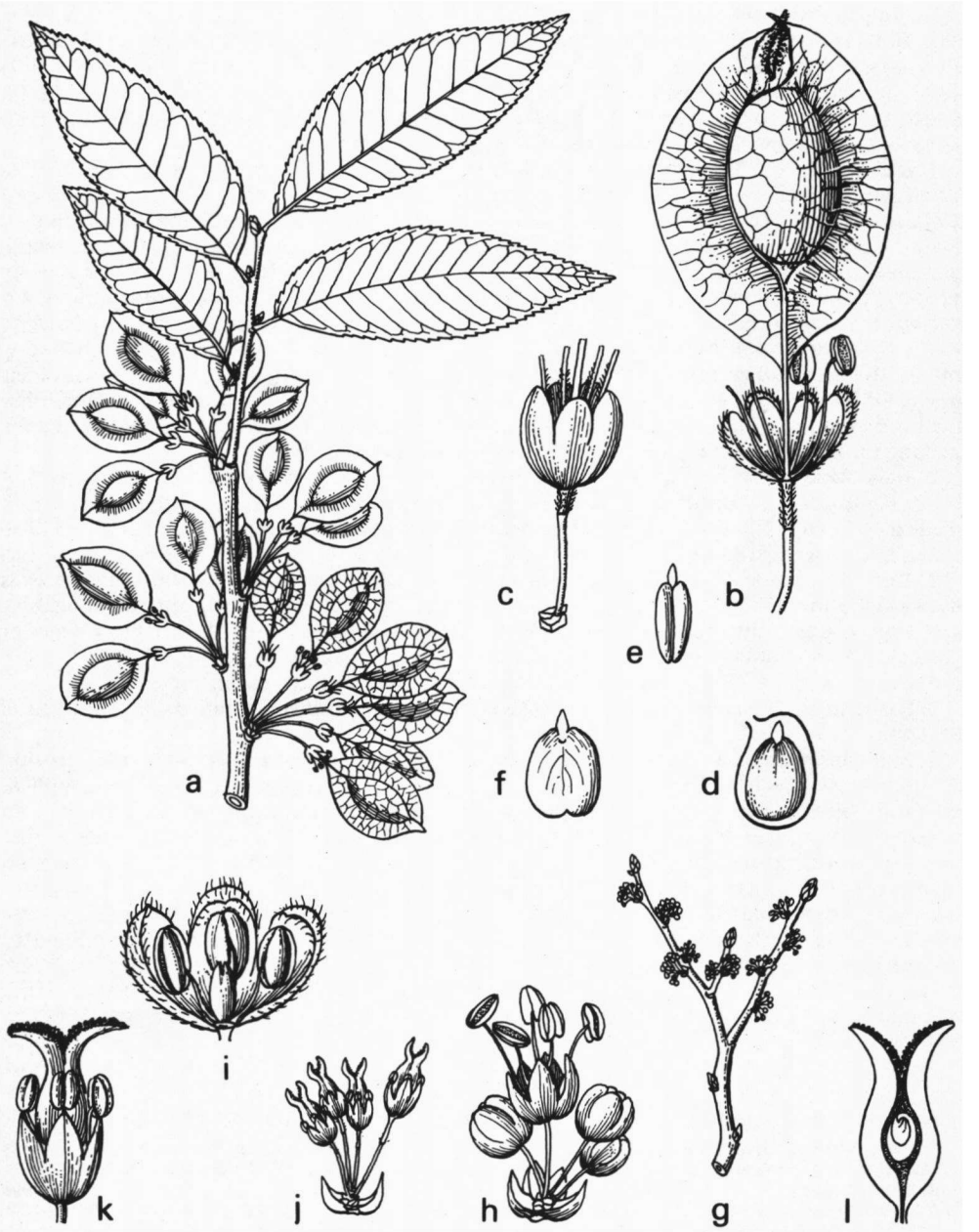

Fig. 2. *Ulmus lanceaefolia* ROXB. *ex* WALL. a. Habit, nat. size, b. fruit, × 2, c. persistent cup-shaped perianth, × 2, d–e. embryo, nat. size, g. flowering twig, × $^2/_3$, h. cluster of ♂ flowers, × 8, i. ♂ flower, × 14, j. cluster of ☿ flowers, × 2, k–l. ☿ flower, × 6 (*a–f* HANSEN *c.s.* 11265, *g–i* SCHMUTZ 3024, *j–l* LISTER 31).

Malviiflorae, and considered them as families having a very close affinity to or derived from the *Malvales*. On the other hand, authors such as HUTCHINSON (1967), CRONQUIST (1968), TAKHTAJAN (1969), SWEITZER (1971), *etc.*, are of the opinion that *Ulmaceae*, *Moraceae*, and *Urticaceae* are closely allied to or have been derived from the *Hamamelidales*. — *Literature:* MIRBEL, Elém. Phys. Veg. Bot. (1815) 905; LINK, Handb. 2 (1831) 445; BESSEY, Ann. Mo. Bot. Gard. 2 (1915) 109–164; ERDTMAN, Pollen Morph. & Pl. Tax. (1956) 442–443; GRUDZINSKAYA, Bot. Zhurn. 52 (1967) 144–150; HUTCHINSON, Genera of Flowering Plants 2 (1967); CRONQUIST, Evol. & Class. Fl. Pl. (1968) 166–167; THORNE, Aliso 6 (1968) 57–66; Brittonia 25 (1973) 395–405; TAKHTAJAN, Fl. Pl. Orig. & Disp. (1969) 210–212; SWEITZER, J. Arn. Arb. 52 (1971).

Uses. 1. Timber. Throughout the north temperate regions the tough, strong and durable wood with attractive appearance and excellent bending quality of many species of *Celtis* and *Ulmus* is extensively used for various purposes including shipbuilding, panelling, furniture, boxes, crates, veneers, *etc.* and that of *Zelkova* and *Phyllostylon* for making weaver's shuttles, scales, piano-keys, *etc.* In Central America timber of *Chaetoptelea* (= *?Ulmus*) is used for railway sleepers, frames and wheels of vehicles. In Africa and India wood of *Holoptelea* is utilized for various building purposes. In Malesia and neighbouring countries except *Aphananthe cuspidata*, *Celtis rigescens*, *C. hildebrandii*, *C. tetrandra*, *Gironniera nervosa*, *Ulmus lanceaefolia* and a few others, the trees seldom reach timber size, and as a consequence very little is known about their usage. Of these species the timber is locally used for making planks in house-building and other light constructions. The soft wood of *Trema* and other species of *Gironniera* is used locally for making tea-chests and match-sticks, for firewood and charcoal.

2. Bark. Due to the high content of mucilagenous substances, decoction of barks of *Holoptelea*, *Parasponia*, *Trema* and *Ulmus* mixed with some other ingredients is used in local folk medicines to cure ailments such as inflammation of mucous membrane, rheumatism, *etc.* The tough fiber is known to be used locally for making ropes.

3. Root. Decoction of roots of *Gironniera* and *Trema* species mixed with other substances is used to cure sore mouth, diarrhoea, and also applied as protective medicine after child-birth.

4. Leaves. Especially of *Trema* species leaves are used as fodder, though due to the presence of glucocides they could be poisonous if consumed in a large quantity.

5. Fruits. In India fruits of *Celtis* and *Holoptelea* are known to be eaten.

6. Shade trees. *Trema* has been used for shade in coffee and cocoa plantations in various parts of Asia.

7. Soil conservation. In South Africa *Trema* has been planted to protect soils against erosion (SCHEEPERS *c.s.*). As both *Trema* and *Parasponia* species come up in dense seral stands on eruptiva, on fresh volcanic ash, are sometimes pioneers on lavastreams, and are almost invariably an important constituent of thickets, seral regrowths, and secondary forest, I would emphasize that they may represent an untapped cheap source for soil conservation for poor, eroded soils and old mining lands. They have all the favourable qualities of pioneer plants, indifference to soil, producing abundant seed, and that already at a very early age, and furthermore they are available almost throughout the year. Curiously I do not know of experiments by the Indonesian Forestry Service in this respect. — *Literature:* BURKILL, Dict. Econ. Prod. Mal. Pen. (1935) 513–514, 1088–1089, 2213–2214; METCALFE & CHALK, Anat. Dicot. (1950) 1277; SCHEEPERS *c.s.* Tijd. Natuurwet. S. Afrika Akad. Wet. & Kunst. 8 (1968) 105–120; SWEITZER, J. Arn. Arb. 52(1971) 525.

KEY TO THE GENERA

1. Flowers always borne on bare older branches, and organized in a condensed cluster on short leafless lateral shoots; perianth cup-shaped, 5–7-lobed; ovary (fruit) stipitate. Fruit a dry, flat, winged samara. Embryo straight . . . . . **1. Ulmus**
1. Flowers axillary, or rarely borne in a condensed capitate thyrse on older branches (*Gironniera celtidifolia*); perianth 4–5-lobed, with the lobes free from one another except for their base; ovary sessile. Fruit a fleshy drupe. Embryo variously curved.
2. Leaves triplinerved at base, or if pinnately nerved the stipules do not leave a circular scar around the node; lateral nerves less than 5 pairs.
3. Stipules intrapetiolar, connate . . . . . **2. Parasponia**
3. Stipules extrapetiolar, free.

4. Female flowers borne in condensed, multiflowered raceme. Perianth of male flower induplicate-valvate. Fruit compressed, elliptic lens-shaped in cross-section . . . . . **3. Trema**
4. Female flowers solitary in the axils of leaves or borne in a cymoid cluster of 2–3. Perianth lobes of male flowers imbricate. Fruit faintly 3–5-angular in cross-section.
5. Male flowers borne in a 2–3-flowered cymoid inflorescence or in a much-branched paniculate, subterminal inflorescence. Female flowers borne in a racemose cluster of 2–10 or in a ♂♀, much-branched racemose inflorescence; staminodes mostly present. Cotyledons broad, variously folded or curved . . . . . **4. Celtis**
5. Male flowers organized in a condensed, multiflowered raceme. Female flowers always solitary or rarely borne in a 2–3-flowered racemose, ♂♀ inflorescence; staminodes always absent. Cotyledons narrow, incurved . . . . . **5. Aphananthe**
2. Leaves pinnately nerved; lateral nerves more than 5 pairs; stipules free but overlapping each other, in falling leaving circular scar around the node . . . . . **6. Gironniera**

1. ULMUS

LINNÉ, Gen. Pl. ed. 5 (1754) 106; ENDL. Gen. Pl. (1837) 276, Suppl. 2 (1842) 29; PLANCH. Ann. Sc. Nat. III, 10 (1848) 259; in DC. Prod. 17 (1873) 154; BAILL. Hist. Pl. 6 (1877) 137; B. & H. Gen. Pl. 3 (1880) 351; HOOK. *f.* Fl. Br. Ind. 5 (1888) 480; ENGL. in E. & P. Nat. Pfl. Fam. 3, 1 (1888) 62; BERNARD, Bull. Herb. Boiss. II, 5 (1905) 1097; ibid. 6 (1906) 23; SCHNEIDER, Oest. Bot. Z. 66 (1916) 21, 65; in Sargent, Pl. Wils. 3 (1917) 238; GAGNEP. Fl. Gén. I.-C. 5 (1927) 674; TUTIN, Fl. Europ. 1 (1964) 65; HUTCH. Gen. Fl. Pl. 2 (1967) 147; TOUW & STEEN. Blumea 16 (1968) 84. — **Fig. 2, 4–6.**

Deciduous or semideciduous trees or shrubs. *Innovations* densely set with greyish to brownish simple hairs, glabrescent. Buds ovoid-conical or obovoid-globose, scales imbricate, hard and tough, glabrous. Stipules extrapetiolar, caducous. *Leaves* pinnately nerved, variously serrate to crenate, thin- to thick-coriaceous and rigid, glabrous or variously sparsely hairy at least beneath. *Flowers* ☿ but of two kinds, one functionally ♂ and the other functionally ♀, variously stalked and spirally arranged in fascicles of 3–15 on short lateral shoots. Perianth mostly campanulate, variously 4–8-lobed. Anthers glabrous, reniform, extrorse. *Ovary* compressed, sometimes stipitate; style short. Ovule 1, anatropous to amphitropous. *Fruit* a dry and compressed nutlet surrounded by a membranous reticulate-venose wing. *Seed:* endosperm absent, embryo straight with planoconvex cotyledons. Germination epigeal.

Distr. About 20–25 *spp.*, distributed in Europe (as far north as 68°), W. & SW. Russia, N. & NE. India, Burma, China, Korea, Japan, Formosa, Indo-China, N. Thailand, and in North America from N. Mexico to the U.S.A. east of the Rocky Mts as far north as 60°. In *Malesia:* 1 *sp.* so far known from a few localities in N. Sumatra, the Lesser Sunda Is. (Flores), and Central & S. Celebes.

As has been indicated by SCHNEIDER, *l.c.*, there seem to be three centres of distribution, *i.e.* the European centre (5–6 *spp.*), the Indian-E. Asian centre (10–15 *spp.*), and the North American centre (4–5 *spp.*). Fig. 3.

Fossils. Numerous fossils (pollen grains, leaf-impressions, and wood fragments) have been reported from various late Cretaceous and Tertiary deposits in Europe, Russia, China, Japan, North America, and Greenland. Fig. 3.

Ecol. In Malesia the genus is so far known only from areas more or less subject to a seasonal climate at 200–1450 m.

Taxon. Currently there is not a single worldwide monograph of the genus available for reference. The latest and perhaps the most comprehensive revision since PLANCHON's work (1873) is that by SCHNEIDER (1916). He distinguished 26 *spp.* and recognized 5 distinct sections in the genus based on morphological characters derived from inflorescence, flowers, and fruits.

When more specimens from China become available for further studies, I believe the number of species occurring in the Indian-E. Asian centre will have to be reduced considerably.

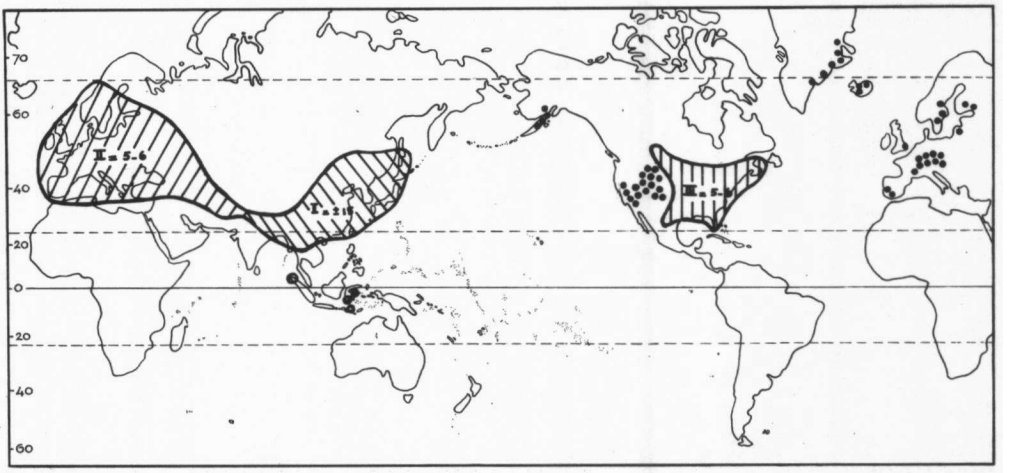

Fig. 3. Approximate range of *Ulmus* L. with number of *spp.* in each of the three centres, Malesian localities belonging to a species of the Asian centre. Fossil localities outside the present range indicated by dots; adopted from BERNARD, *l.c.*; GREGUSS (Tert. Angios. Hung., Ak. Kiado Budapest, 1969, 83), and LA MOTTE (Mem. Geol. Soc. Am. 51, 1952, 346).

Fig. 4. Peeling bark of *Ulmus lanceaefolia* ROXB. *ex* WALL., × 1/8 (Photogr. SCHMUTZ, 5 Nov. 1972, Flores, Nunang).

1. Ulmus lanceaefolia ROXB. *ex* WALL. Pl. As. Rar. 2 (1831) 86, t. 200; ROXB. Fl. Ind. ed. Carey 2 (1832) 66 (*'lancifolia'*); PLANCH. Ann. Sc. Nat. III, 10 (1848) 281; in DC. Prod. 17 (1873) 162; KURZ, For. Fl. Burma 2 (1877) 473; GAMBLE, Man. Ind. Timb. ed. 1 (1881) 342; HOOK. *f.* Fl. Br. Ind. 5 (1888) 480; HEMSL. J. Linn. Soc. Bot. 26 (1894) 447; PRAIN, Beng. Pl. (1903) 718; BRANDIS, Ind. Trees (1906) 594; SCHNEIDER, Oest. Bot. Z. 66 (1916) 32; in Sargent, Pl. Wils. 3 (1917) 263; MERR. Contr. Arn. Arb. 8 (1934) 44; TOUW & STEEN. Blumea 16 (1968) 84; MELVILLE & HEYBROEK, Kew Bull. 26 (1971) 24 (*'lanceifolia'*). — *U. hookeriana* PLANCH. in DC. Prod. 17 (1873) 162; ENGL. in E. & P. Nat. Pfl. Fam. 3, 1 (1888) 62. — *U. tonkinensis* GAGNEP. Fl. Gén. I.-C. 5 (1927) 674. — **Fig. 2, 4–6.**

Small to large tree up to 48 m, 70 cm ∅, often with fluted trunk. Bark rough, pustulate, with large warty lenticels. Branchlets initially densely set with greyish to brownish curly simple hairs, later glabrous and sparsely warty lenticellate. Buds obovoid-globose, *c.* 2–3 mm ∅; bracts dark brown. Stipules linear-lanceolate acute, *c.* 4–5 by 1–1½ mm, soon caducous. *Leaves* thin- to thick-coriaceous, lanceolate to ovate-lanceolate, (2–)4–6(–9) by (1–)2–3 (–3½) cm (index 2–2½), broadest at or slightly below the middle, more or less glabrous, glossy; base rounded to attenuate-acute, unequal; margin serrulate to serrulate-crenulate; apex acute with blunt tip; midrib raised beneath and flattish to impressed above, as the petiole initially densely greyish, curly hairy on both surfaces, glabrescent; nerves (6–)10–12(–14) pairs, subparallel, often rather irregularly spaced, slightly raised beneath, flattish to impressed above, often forked near and towards the leaf-margin; reticulations fine, areolate; petiole (2–)3–4(–6) by ½–1 mm. Flowers in fascicles of 3–10. — Functionally ♂ *flowers* globose before anthesis, 1½–2 mm ∅, subglabrous; lobes 5–6, obovate-lanceolate, *c.* 2 by 1 mm; filaments

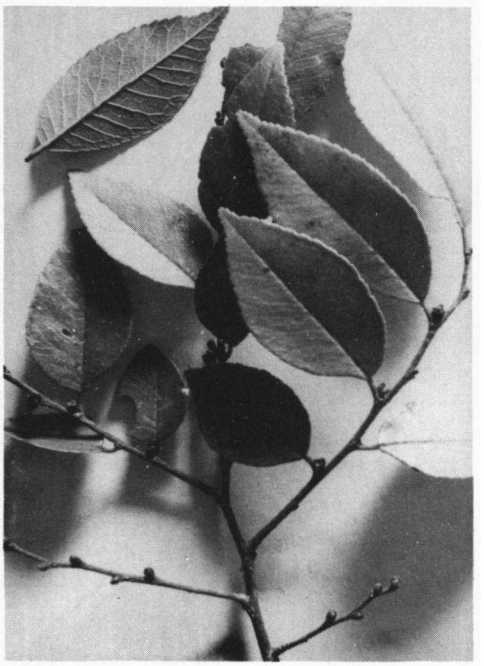

Fig. 5. *Ulmus lanceaefolia* ROXB. *ex* WALL. with old leaves at Nunang (Photogr. SCHMUTZ, 15 Oct. 1972, Flores).

glabrous, slender, *c.* 1 mm; anthers *c.* 1 by $^1/_2$ mm, glabrous; pistillode compressed obovate-elliptic, glabrous. — Functionally ♀ *flowers* (as seen under a very young fruit): perianth campanulate, lobes 5–6, rounded-elliptic, hairy along the margin; filaments slender, glabrous, 3–5 mm, anthers as in ♂ flower; ovary stipitate, glabrous, ± obovate-elliptic. *Fruit* obovate-elliptic, glabrous, including the wing 2–3$^1/_2$ by 1$^1/_2$–2 cm, stalk 5–10 mm, articulate, lower part hairy.

Distr. China (?), India (E. Himalaya, Sikkim, Bhutan, Khasia Hills, Manipur, Assam), Bangladesh, Burma (Hukong Valley, Chittagong Hills), Thailand (northern parts), Laos, Vietnam (Mt Bavi); in *Malesia:* N. Sumatra (Gajo- & Karo-Batak Lands), Lesser Sunda Is. (Flores), and Celebes (Poso; Bonthain). Fig. 7.

Ecol. Scattered tree in lowland to submontane forest, 200–1450 m. In Thailand it is confined to forests along streams and in Flores it has been found on limestone. *Fl. fr.* in the northern hemisphere Febr.–April; in Flores Nov.

Taxon. *U. lanceaefolia* is very closely allied to *U. parvifolia* JACQ. from China and Japan. It differs from the latter by its narrow leaves with a shorter petiole, serrulate to serrulate-crenulate margin, and fewer lateral nerves, obovoid-globose buds, the campanulate perianth of the functionally ♀ flower, and the reticulate venation of the fruit; see fig. 2.

Uses. Very little is known about the usage of this species, but judging from the enormous size it can attain it must have been a useful timber in house-building, construction, *etc.*, at least to the local inhabitants.

Vern. Sumatra: *pĕngki(h)*, *poki*, Karo-Batak, *pongki*, Toba-Batak; Lesser Sunda Is.: *ngguling*, *nggulung*, Flores; Celebes: *mota*, Bonthain.

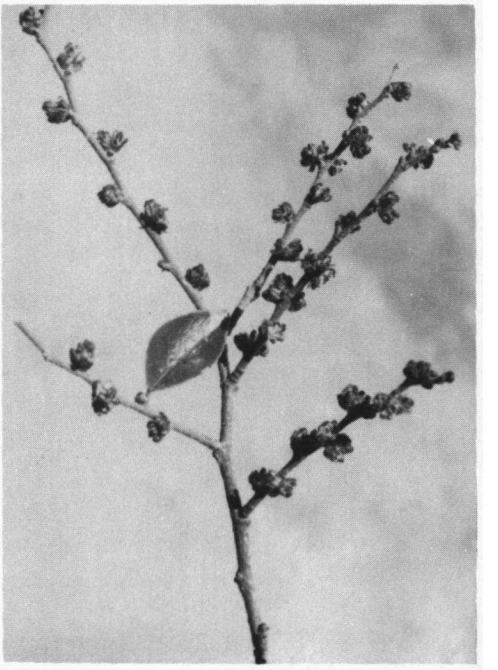

Fig. 6. *Ulmus lanceaefolia* ROXB. *ex* WALL., leafless, in flower, ± × $^2/_3$, at Nunang (Photogr. SCHMUTZ, 5 Nov. 1972, Flores).

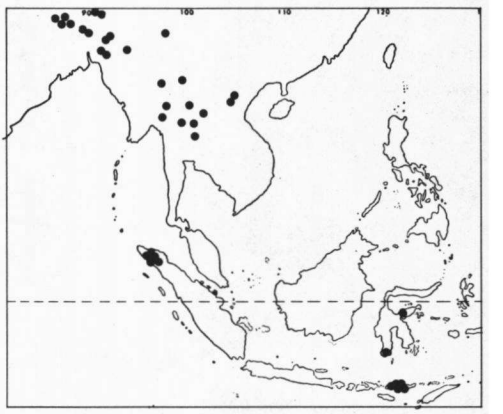

Fig. 7. Range of *Ulmus lanceaefolia* ROXB. *ex* WALL.

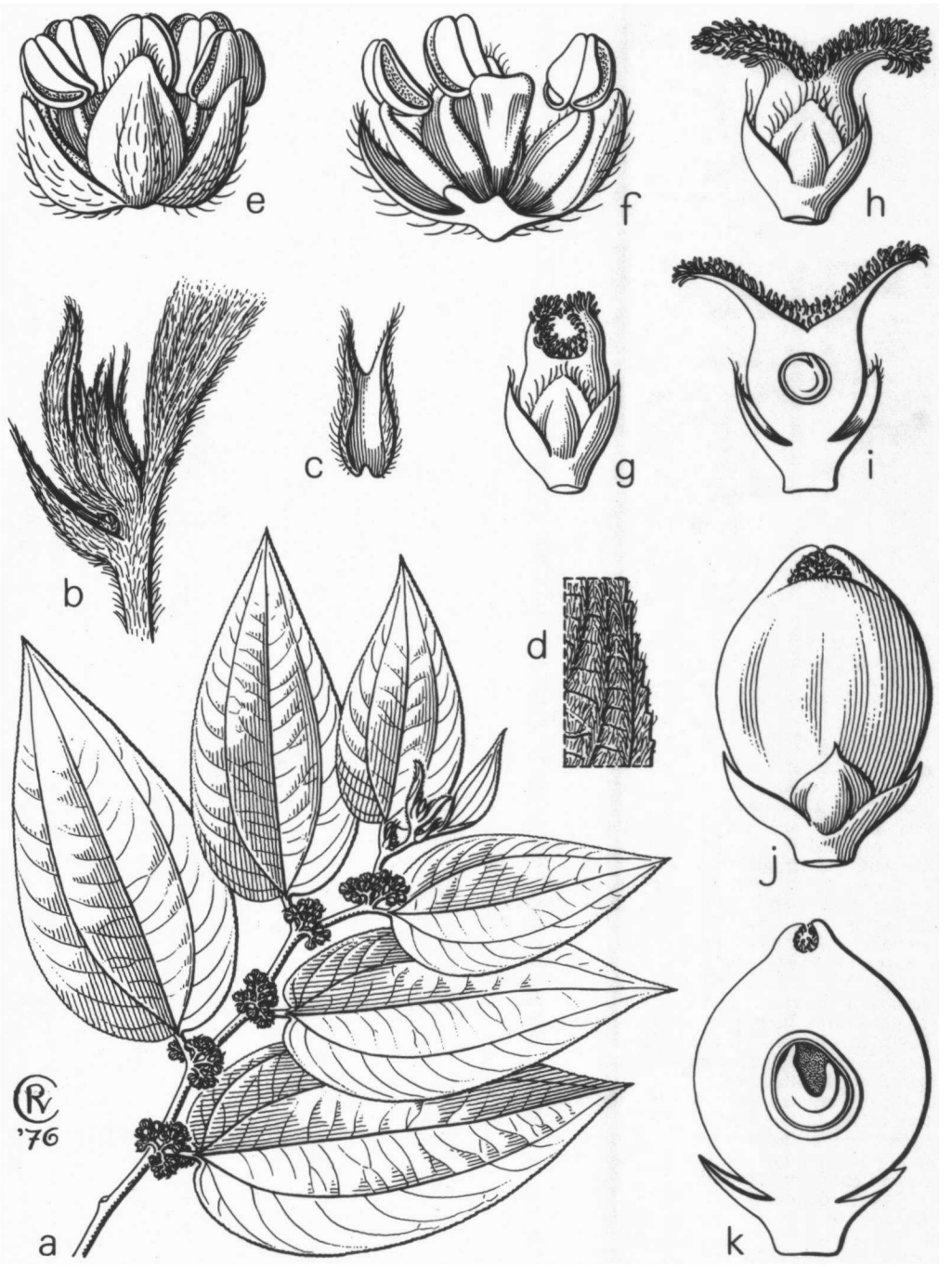

Fig. 8. *Parasponia rigida* MERR. & PERRY. a. Habit, × ²/₃, b. twig-tip with stipules, c. connate stipules, from inside, d. detail of leaf undersurface, all × 3, e. ♂ flower, f. *ditto* in LS. g. young ♀ flower, h. mature ♀ flower, i. *ditto* in LS, all × 12, j. fruit, k. *ditto* in LS, both × 12 (*a–f* ANU 6463, *g–k* SCHODDE 4828).

2. PARASPONIA

MIQ. Pl. Jungh. (1851) 68; Fl. Ind. Bat. 1, 2 (1859) 218; BL. Mus. Bot. 2 (1856) 65; PLANCH. in DC. Prod. 17 (1873) 194; ENGL. in E. & P. Nat. Pfl. Fam. 3, 1 (1888) 65; J. J. SMITH in K. & V. Bijdr. 12 (1910) 662; BACK. & BAKH. *f.* Fl. Java 2 (1965) 12; HUTCH. Gen. Fl. Pl. 2 (1967) 149. — **Fig. 8, 10–11.**

Shrubs to medium-sized trees. Bark grey-brown, smooth to finely fissured; inner bark fibrous and tough. *Innovations* with dense appressed, silvery to greyish hairs. Stipules intrapetiolar, connate into a bifurcate unit and together enclosing the terminal bud, caducous. *Leaves* (in Mal.) triplinerved at base, concolorous, above non-scabrous to variously scabrous, mostly glabrous except for the midrib and lateral nerves, lower surface variously pubescent. *Inflorescences* axillary, ♂, ♀, or ♂♀, much-branched, many-flowered, paniculate or thyrsoid, including the bracts densely short greyish appressed-pubescent. Flowers 5-merous. — ♂ *Flower* ± globose, perianth lobes imbricate in bud; stamens glabrous, introrse; filaments subulate, glabrous; anthers reniform to subglobose, sub-basifixed, glabrous; pistillode obovoid-conical, compressed, surrounded by hirsute hairs at its base. — ♀ *Flower* ovoid-conical; staminodes absent; ovary ovoid, slightly compressed; stigmatic arms short, simple; ovule anatropous. *Drupe* ovoid, slightly compressed pericarp fleshy and fibrous, endocarp hard and stony. *Seed:* endosperm scanty or copious; embryo curved, cotyledons equal, hypocotyle ascending.

Distr. 5 *spp.*, in Polynesia (Tahiti) and Melanesia (Fiji, New Hebrides, Solomons); in *Malesia:* New Guinea (incl. New Britain), Moluccas (Ternate, Banda), Philippines, Celebes, Lesser Sunda Is. (Lombok, Bali), Java, and S. Sumatra (Palembang). Fig. 9, 12.

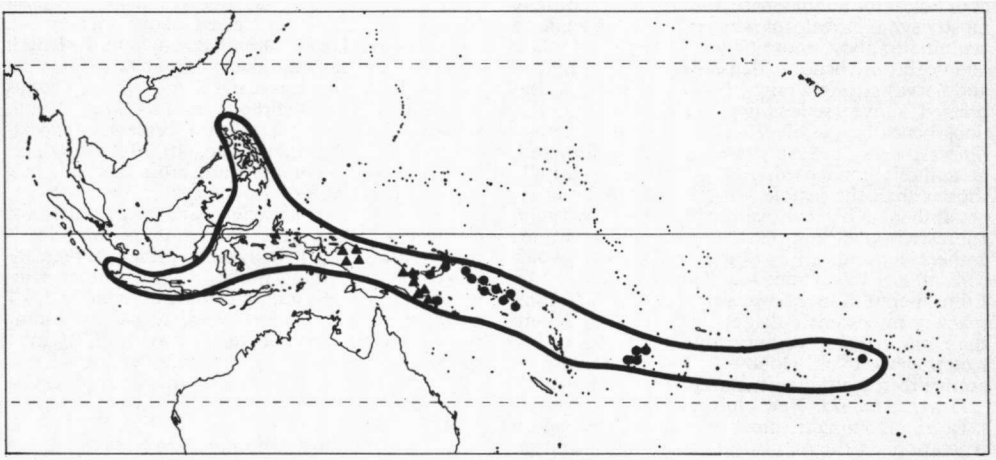

Fig. 9. Approximate range of the genus *Parasponia* MIQ. (line); localities of *P. andersonii* (PLANCH.) PLANCH. (dots) and *P. melastomatifolia* J. J. S. (triangles).

Ecol. In New Guinea and the Pacific islands the genus is found as a pioneer plant invading and occupying newly available habitats from the lowland up to 2000 m. In Java the same situation was described by E. W. CLASON from natural regeneration on volcanic ash of Mt Kelud, together with *Trema* (Bull. Jard. Bot. Btzg III, 13, 1935, 509). Fig. 10, 11. Recorded as a pioneer on lavastreams of Mt Batur in Bali by DE VOOGD (Trop. Natuur 29, 1940, 48, f. 12). Grows well in all types of soils, including volcanic ash and limestone, very often gregariously together with *Trema spp.* and forming a dense thicket on ridges, hills and along river-banks.

TAXON. *Parasponia* is morphologically very similar to *Trema* but can easily be distinguished from the latter by its imbricate perianth lobes of the male flowers and intrapetiolar, connate stipules enclosing the terminal bud.

KEY TO THE SPECIES

1. Basal nerves running up throughout the length of the leaf or nearly so.
 2. Leaf thick-coriaceous, lower surface densely set with soft erect hairs; margin distinctly serrate; reticulations prominent beneath. Inflorescence ♂ or ♀, at anthesis condensed and shorter than the petiole . . . . . **1. P. rigida**
 2. Leaf chartaceous to thin-coriaceous, lower surface glabrous or sparsely appressed-hairy; margin finely serrulate to subentire; reticulations obscure. Inflorescence ♂ or ♂♀, at anthesis lax and longer than the petiole. . . . . **2. P. melastomatifolia**
1. Basal nerves running up to $^1/_2$–$^2/_3$ the length of the leaf.
 3. Leaf thick-coriaceous, upper surface strongly rugose and scabrous, lower surface densely pubescent; midrib, nerves, and reticulations prominent beneath . . . . . **3. P. rugosa**
 3. Leaf chartaceous to thin-coriaceous, upper surface not or hardly rugose nor scabrous, lower surface sparsely appressed pubescent or glabrous; midrib, nerves, and reticulations only slightly raised beneath.
  4. Leaf elliptic-lanceolate, more or less glabrous; nerves more than 4 on each side, straight and ascending at a narrow angle (less than 40°) from the midrib. Inflorescences mostly ♂♀, very rarely ♂ or ♀ **4. P. parviflora**
  4. Leaves ovate to ovate-elliptic, underneath sparsely appressed pubescent; nerves less than 4, usually 3 on each side, arcuating at a wider angle (*c.* 45–60°) from the midrib. Inflorescences ♂ or ♀, rarely ♂♀ **5. P. andersonii**

1. Parasponia rigida MERR. & PERRY, J. Arn. Arb. 22 (1941) 254. — **Fig. 8.**

Small tree, up to 10 m, 10 cm ⌀. Branchlets initially densely silver-appressed-hairy, glabrescent and sparsely warty lenticellate. Stipules ovate-lanceolate, 8–10 by 2–3 mm. *Leaves* elliptic to ovate-lanceolate, thick-coriaceous, (5–)8–10(–12) by (1$^1/_2$–)2–3$^1/_2$(–4$^1/_2$) cm (index 2$^1/_2$–3$^1/_2$), broadest at or below the middle; base rounded to subcordate, mostly symmetrical; margin serrate; apex acute to acuminate; above more or less glabrous, rugulose and scabrous, beneath densely soft-hairy; midrib and nerves strongly raised beneath, flattish to impressed above; reticulations subscalariform, distinct beneath; petiole 10–12 by 2–3 mm, terete. *Inflorescences* ♂ or ♀, very rarely ♂♀, 10–50-flowered, at anthesis condensed, *c.* $^1/_2$–1 cm long, usually shorter than the petiole. — ♂ *Flowers* 1–2 mm ⌀, perianth lobes narrow-ovate, concave, *c.* 2 by 1 mm, appressed-pubescent outside; filaments *c.* 1 mm; anthers ellipsoid, *c.* 1 by $^1/_2$ mm, pistillode obovoid-conical, *c.* 1 by $^1/_2$ mm. — ♀ *Flower* ovoid, *c.* 2 by 1 mm; perianth lobes ovate-acute, *c.* $^3/_4$ by $^1/_2$ mm, sparsely pubescent outside; ovary *c.* 2 by 1 mm, stigmatic arms spreading, long-papillose, *c.* $^1/_2$–1 mm. *Drupe* ovoid-globose, *c.* 3–4 mm ⌀, turning orange to red when ripe. Endosperm copious.

Distr. *Malesia:* New Guinea. Fig. 12.

Ecol. Dominant pioneer tree in secondary vegetation on ridges, also in mossy forest and on limestone hills, 1000–2000 m. *Fl. fr.* Jan.–Dec.

Vern. *Bĕsukan*, Hattam lang., *golan*, Finschhafen dial., Morobe Distr.

2. Parasponia melastomatifolia J. J. SMITH, Nova Guinea 8, 2 (1914) 891, t. 158. — *P. simulans* MERR. & PERRY, J. Arn. Arb. 22 (1941) 255.

Shrub to small tree, up to 6 m, with spreading and brittle branches. Branchlets initially densely appressed-silvery-hairy, glabrescent and sparsely lenticellate. Stipules ovate-elliptic, 4–5 by 2–3 mm. *Leaves* elliptic-lanceolate to ovate-elliptic, (5–)6–8(–10) by (1$^1/_2$–)2$^1/_2$–3$^1/_2$(–4$^1/_2$) cm (index 2–3), broadest at or slightly below the middle; chartaceous to thin-coriaceous, above more or less glabrous, hardly scabrous and often with mineral deposits on the epidermis, beneath sparsely appressed-hairy especially on midrib and nerves, or completely glabrous; base more or less rounded, symmetrical; margin finely serrulate to ± entire; apex acute; midrib and nerves slightly raised beneath, flattish to impressed above; nerves 1–2 pairs, the basal ones running throughout the length of the leaf or nearly so, at an acute angle of less than 45°; reticulations subscalariform, inconspicuous on both surfaces; petiole (5–)8–12(–15) by 1 mm, sulcate, sparsely appressed-pubescent. *Inflorescences* ♂ or ♂♀, paniculate, 10–20-flowered, at anthesis lax, 2–3 cm long and across, axes *c.* 1 mm ⌀, densely appressed-pubescent; bracts ovate, *c.* 1$^1/_2$ by 1 mm, sparsely appressed-pubescent outside. — ♂ *Flowers c.* 1–2 mm ⌀, perianth lobes ovate-acute, *c.* $^1/_2$–1 by $^1/_2$ mm, sparsely appressed-hairy outside; filaments *c.* 1 mm, anther subglobose, *c.* 1 by $^1/_2$ mm, pistillode obovoid, *c.* $^1/_2$–1 by $^1/_2$ mm. — ♀ *Flower* ovoid, *c.* 1–2 by 1 mm; perianth lobes ovate-acute, *c.* $^1/_2$–1 by $^1/_4$–$^1/_2$ mm, sparsely appressed-hairy outside; ovary ovoid, *c.* 2 by 1 mm; stigmatic arms *c.* 1 mm, incurved. *Drupe* ovoid-globose, *c.* 3 by 2 mm. Endosperm scanty.

Distr. *Malesia:* New Guinea. Fig. 9.

Ecol. Common and dominant in seral vegetation in gullies and river-banks, 200–1000 m. *Fl. fr.* Jan.–Dec.

Vern. *Kwatoro*, Onjob lang., Northern Distr., E. New Guinea.

3. Parasponia rugosa BL. Mus. Bot. 2 (1856) 66. — *P. aspera* BL. *l.c.* 66; MIQ. Fl. Ind. Bat. 1, 2 (1859) 218. — *Trema vulcanica* MERR. Philip. J. Sc. 7 (1912) Bot. 260. — *Trema philippinensis* ELMER, Leafl. Philip. Bot. 9 (1934) 3218. — *P. parviflora* (*non* MIQ.) STEEN. Philip. J. Sc. 91 (1962) 507. — **Fig. 10–11.**

Shrub or medium-sized tree, up to 20 m, 30 cm ∅, with spreading branches. Bark smooth, grey-brown; inner bark tough, brownish. Branchlets densely, silvery, appressed, long-hairy, subglabrescent. Stipules ovate-lanceolate, (6–)8(–10) by 2–3 mm. *Leaves* ovate-lanceolate, (7–)8–10(–12) by (2–)$2^1/_2$–$3^1/_2$(–5) cm (index $2^1/_2$–3), broadest at or below the middle, thick-coriaceous; above rugose and scabrous, sparsely hairy especially on midrib and nerves, beneath densely silvery hairy by soft, erect hairs; base rounded to cordate, equal to slightly unequal; margin serrate, apex acute to acuminate, the acumen up to 2 cm; midrib and nerves strongly raised and prominent beneath, flattish to impressed above; nerves 2–4 pairs, arcuate and ascending, the basal ones running up to $^1/_2$–$^2/_3$ the length of the leaf; reticulations dense, areolate, prominent beneath; petiole 7–10 by 2–3 mm, subterete, densely appressed-pubescent. *Inflorescences* ♂ or ♂♀, 10–50-flowered, densely silvery appressed-hairy, at anthesis condensed, axes *c.* $^1/_2$–$1^1/_2$ cm long, 1–2 mm ∅; bracts ovate-acute, *c.* $1^1/_2$–1 mm. — ♂ *Flower* *c.* 1–2 mm ∅; perianth lobes ovate-acute, *c.* 1–2 by 1 mm, sparsely hairy outside; filaments 1–$1^1/_2$ mm, anthers ovoid-reniform, *c.* 1 mm ∅; pistillode ovoid, compressed, *c.* 1–2 by 1 mm. — ♀ *Flower* ovoid-conical, *c.* 1–$1^1/_2$ by 1 mm; perianth lobes narrow ovate-acute, *c.* 1–$1^1/_2$ by 1 mm, sparsely appressed-hairy outside; ovary ovoid, *c.* 1–2 by 1 mm, stigmatic arms *c.* 1 mm, spreading. *Drupe* ovoid, 2–3 by 2 mm, turning red when ripe. Endosperm copious.

Distr. *Malesia:* East Java (Mts Kelud & Lamongan), Lesser Sunda Is. (Bali, Lombok), Philippines (Luzon, Leyte, Mindanao), Celebes (near Makassar; Tondano, Menado), Moluccas (Ternate, Banda), New Guinea (W. & E. Highlands and Morobe Distr., incl. New Britain). Fig. 12.

Fig. 10. Pioneer vegetation on the volcanic ash of Mt Kelud, East Java, of *Saccharum spontaneum* and *Parasponia rugosa* BL. (Photogr. CLASON).

Ecol. Rather common and often dominant or co-dominant pioneer plant in seral vegetation on various types of soils including volcanic ash, 50–1900 m. *Fl. fr.* Jan.–Dec. Fig. 10, 11.

Uses. Strips of the inner bark are used as ropes in house and fence building by local inhabitants.

Vern. Java: *anggring*, *anggris*, J; Philippines: *analdung*, If.; Moluccas: *kayu kuli*, Banda; New Guinea: *wanep*, Enga lang., W. Highlands Distr., *la karabi*, W. Nakanai, New Britain.

Fig. 11. Older pioneer forest on Mt Kelud of *Parasponia rugosa* BL., *Trema*, *Cyathea contaminans*, and *Amomum* (Photogr. CLASON).

4. Parasponia parviflora MIQ. Pl. Jungh. (1851) 69; Fl. Ind. Bat. 1, 2 (1859) 218, t. 16; BL. Mus. Bot. 2 (1856) 65, f. 35; PLANCH. in DC. Prod. 17 (1873) 194; J. J. SMITH in K. & V. Bijdr. 12 (1910) 663, *p.p excl. syn. P. aspera* BL.; BACK. & BAKH. *f.* Fl. Java 2 (1965) 12. — *P. similis* BL. Mus. Bot. 2 (1856) 66.

Small to medium-sized tree, up to 15 m. Branchlets initially densely silvery or grey appressed-hairy, glabrescent, smooth. Stipules ovate, 5–10 by 2–4 mm, sparsely hairy outside. *Leaves* lanceolate to narrow ovate-lanceolate, (3–)5–8(–10) by (1–)2–3(–3¹/₂) cm (index 3–4), broadest at or below the middle; chartaceous to thin-coriaceous, above ± glabrous, not scabrous, beneath initially appressed-hairy, later glabrous except for the midrib and nerves; base rounded, more or less equal; margin finely serrate, apex acute; midrib and nerves slightly raised beneath, impressed and inconspicuous above; nerves 4–6 pairs, straight, ascending and parallel, at a narrow angle (30–40°), basal ones running up to ± half the length of the leaf; reticulations fine, subscalariform, indistinct on both surfaces; petiole terete, densely appressed-hairy, 5–10 by 1 mm. *Inflorescences* ♂, ♀, or ♂♀, 5–30-flowered, at anthesis condensed, shorter than or as long as the petiole, as the bracts densely short-hairy; bracts ovate-acute, 1–1¹/₂ by ¹/₂–1 mm. — ♂ *Flowers* glabrous, 1–2 mm ∅; perianth lobes *c.* 1–1¹/₂ by ¹/₂ mm; filaments ¹/₂–1 mm, anthers subglobular, *c.* 1 by ¹/₂ mm; pistillode ovoid-conical, compressed, 1–1¹/₂ by ¹/₂ mm. — ♀ *Flowers* ovoid-conical, *c.* 2 by 1¹/₂ mm, ± glabrous except for the inner base of the perianth lobes; perianth lobes ovate-acute, *c.* 1 by ¹/₂ mm; ovary ovoid, *c.* 1¹/₂ by 1 mm; stigmatic arms spreading, *c.* ¹/₂–1 mm. *Drupe* ovoid-conical, slightly compressed, 1¹/₂–2 by 1¹/₂ mm. Endosperm scanty.

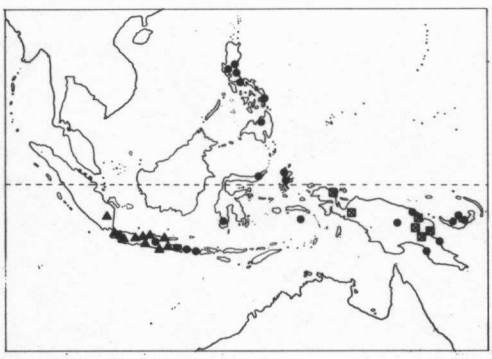

Fig. 12. Localities of *Parasponia rugosa* BL. (dots), *P. parviflora* MIQ. (triangles), and *P. rigida* MERR. & PERRY (squares).

Distr. *Malesia:* S. Sumatra (Palembang, very rare), Java (common). Fig. 12.

Ecol. In secondary or seral vegetation on exposed habitats, also in teak forest, often rather common and dominant locally especially on soils derived from volcanic ash, 500–2000 m. *Fl. fr.* Jan.–Dec.

Vern. *Kurai, k. lělaki, k. tjangkrèng*, S, *anggring, anggris, anggrung*, J.

5. Parasponia andersonii (PLANCH.) PLANCH. in DC. Prod. 17 (1873) 193. — *Sponia andersonii* PLANCH. Ann. Sc. Nat. III, 10 (1848) 336; SEEMANN, Fl. Vit. (1867) 235; PARHAM, Pl. Fiji Isl. (1972) 133. — *P. paucinervia* MERR. & PERRY, J. Arn. Arb. 20 (1939) 324.

Shrub to medium-sized tree, up to 15 m and 30 cm ∅. Branches spreading and drooping, initially densely set with erect but soft, silvery hairs, subglabrescent and sparsely warty lenticellate. Bark smooth to nodular, grey-brown; inner bark fibrous, tough, orange to brownish. Stipules ovate-acute, sparsely hairy outside, 6–10 by 3–4 mm. *Leaves* ovate to elliptic, thin-coriaceous, (5–)8–12 (–14) by (2–)3–4(–6) cm (index 2–3), broadest below or at the middle; above subglabrous, scabrous, often covered with mineral deposits, beneath sparsely set (rarely rather densely) with short and soft hairs especially on midrib and nerves; base rounded to subcordate, equal, rarely unequal; margin serrate, apex acute to acuminate; midrib and nerves slightly raised beneath and impressed above; nerves 3–4 pairs, arcuating and ascending at an angle of 45–60°, basal extending up to *c.* ²/₃ the length of the leaf; reticulations fine, subscalariform, rather distinct below; petiole (7–)10–15(–20) by 1–2 mm, densely set with silvery, soft, erect hairs, flat or sulcate. *Inflorescences* ♂, ♀, or rarely ♂♀, 10–30-flowered, at anthesis condensed or lax, shorter than or as long as the petiole, including the bracts densely silvery, soft-hairy; bracts ovate-acute, *c.* 1 by ¹/₂ mm. — ♂ *Flowers c.* 1¹/₂–2 mm ∅; perianth lobes ovate-elliptic, *c.* 1 by ¹/₂ mm; stamens glabrous; filaments *c.* 1 mm, anthers subreniform to subglobular, *c.* 1 by ¹/₂ mm; pistillode subovoid-conical, *c.* 1¹/₂ by ¹/₂ mm. — ♀ Flowers ovoid-ellipsoid, *c.* 1¹/₂ by 1 mm; perianth lobes ovate-acute, *c.* 1 by ¹/₂ mm; ovary ovoid, slightly compressed, *c.* 1 by ¹/₂ mm; stigmatic arms *c.* ¹/₂ mm, spreading and short-papillose. *Drupe* ovoid, slightly compressed, 2–4 by 2–3 mm. Endosperm copious.

Distr. Polynesia (Tahiti), Melanesia (Fiji, New Hebrides, Solomons, very common), ? New Caledonia (no specimen seen but *cf.* GUILLAUMIN, Fl. Nouv.-Caléd. 1948, 94); in *Malesia:* New Guinea (several islands off Madang and Milne Bay) and New Britain. Fig. 9.

Ecol. Primary as well as secondary forests, on various types of soils including limestone, 0–1500 m. *Fl. fr.* Jan.–Dec.

Uses. In the Solomons the bark is reputed to have medicinal properties.

Vern. New Britain: *ip, ivu*; Solomons: *bulasisi, bulsisi*, Kwara lang.; Fiji: *ndroi, ndrou.*

3. TREMA

LOUR. Fl. Coch. 2 (1790) 562; BL. Mus. Bot. 2 (1856) 58; BTH. Fl. Austr. 6 (1873) 157; B. & H. Gen. Pl. 3 (1880) 355; ENGL. in E. & P. Nat. Pfl. Fam. 3, 1 (1888) 65; BERNARD, Bull. Herb. Boiss. II, 6 (1906) 31, maps 19–21; J. J. SMITH in K. & V. Bijdr. 12 (1910) 649; RENDLE, Fl. Trop. Afr. 6, 2 (1917) 10; DE WIT, Bull. Bot. Gard. Btzg III, 18 (1949) 184; HUTCH. Gen. Fl. Pl. 2 (1967) 148; ELIAS, J. Arn. Arb. 51 (1970) 37, f. 2; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 420. — *Sponia* COMMERS. *ex* LAMK, Dict. 4 (1795) 138; ENDL. Gen. Pl. 4 (1837) 276; PLANCH. Ann. Sc. Nat. III, 10 (1848) 264; in DC. Prod. 17 (1873) 195. — **Fig. 13, 16–17.**

Trees or shrubs, often buttressed and with spreading and drooping branches, monoecious. *Innovations* variously and densely set with simple bulbose-based hairs or/and with short multicellular capitate-glandular hairs. Terminal buds ovoid-conical, enclosed by overlapping but free extrapetiolar, caducous stipules. *Leaves* penninerved; above ± glabrous, variously scabrate, beneath glabrous, subglabrous, or variously densely set with bulbous-based hairs and/or with short multicellular glandular hairs; base triplinerved, cordate to acute, often unequal-sided; margin variously serrate or denticulate; apex acute to acuminate or caudate; petiole sulcate. *Inflorescence* axillary, paniculate or thyrsoid, many-flowered, condensed or lax at anthesis, ♂, ♀, ♂♀, densely and variously pubescent; bracts minute, ovate-acute, caducous. — ♂ *Flower* globular; perianth 4–5-lobed, lobes induplicate-valvate in bud, boat-shaped; stamens glabrous, introrse; filament subulate, glabrous, incurved in bud; anthers subglobular to reniform, glabrous, dorsifixed near the base; pistillode present, hirsute at base. — ♀ *Flower* ovoid; perianth 4–5-lobed; staminodes absent or very rarely present; ovary ovoid, (in Mal.) glabrous, slightly compressed, sessile; style short; ovule ana- to amphitropous. *Drupe* ovoid or subglobose, (in Mal.) slightly compressed, glabrous; exocarp fleshy and fibrous, endocarp stony and very hard. *Seed* with a rather scanty or copious endosperm; embryo curved or nearly involute; hypocotyle ascending; cotyledons equal. Germination epigeal.

Distr. About 10–15 *spp.*, widely distributed throughout the tropics and subtropics. In Asia (with 6–7 *spp.*) from the warmer parts of the Himalayas, extending north-eastwards to China (incl. Hainan, Hongkong, Formosa) and S. Japan and south and south-eastwards through India, Burma, Thailand, Indo-China, and Malesia to the tropical and subtropical parts of Australia and the Pacific islands as far east as Tahiti (31° N–37° S). In Africa (with 3–4 *spp.*) it occurs south of the Sahara to S. Africa and Madagascar (22° N–28° S). In America (with 4–5 *spp.*) the genus is known from Central & S. Florida and Mexico, extending south-eastwards through Central America, Bermuda, and the Bahamas, the Greater Antilles and southwards to South America as far south as the northern parts of Argentina (26° N–25° S). In *Malesia:* 4 *spp.*, widely spread. Fig. 14, 15.

Ecol. Throughout its range of distribution the genus seems to grow well and often gregariously in newly opened up habitats on various types of soils ranging from heavy laterite to limestone soils and soils derived from volcanic ash (fig. 17), from sea-level up to 2000 m.

Pollination is probably affected by wind and small insects.

The fruits which turn orange, red or black when ripe are dispersed by various species of bulbuls.

In East Java CLASON (Bull. Jard. Bot. Btzg III, 13, 1935, 509, f. III) reported that following the frequent eruptions of Mt Kelud, *Trema spp.* together with *Parasponia spp.* formed a dominant association in the regrowths on volcanic ash.

Taxon. The genus is homogeneous and closely related to *Parasponia* and *Celtis*. This is corroborated by the anatomy of the wood and leaves. Reports on the cytology are, however, suggesting that the number of chromosomes is not constant.

Embryology. Very little is known about the sporogenesis and embryogenesis of the genus. A preliminary study carried out recently on *Trema cannabina* and *T. tomentosa* in the Malay Peninsula indicates that the development of the anther and microspores follow the so-called dicotyledon-type, and that of the embryo-sac conforms with the *Polygonum*-type.

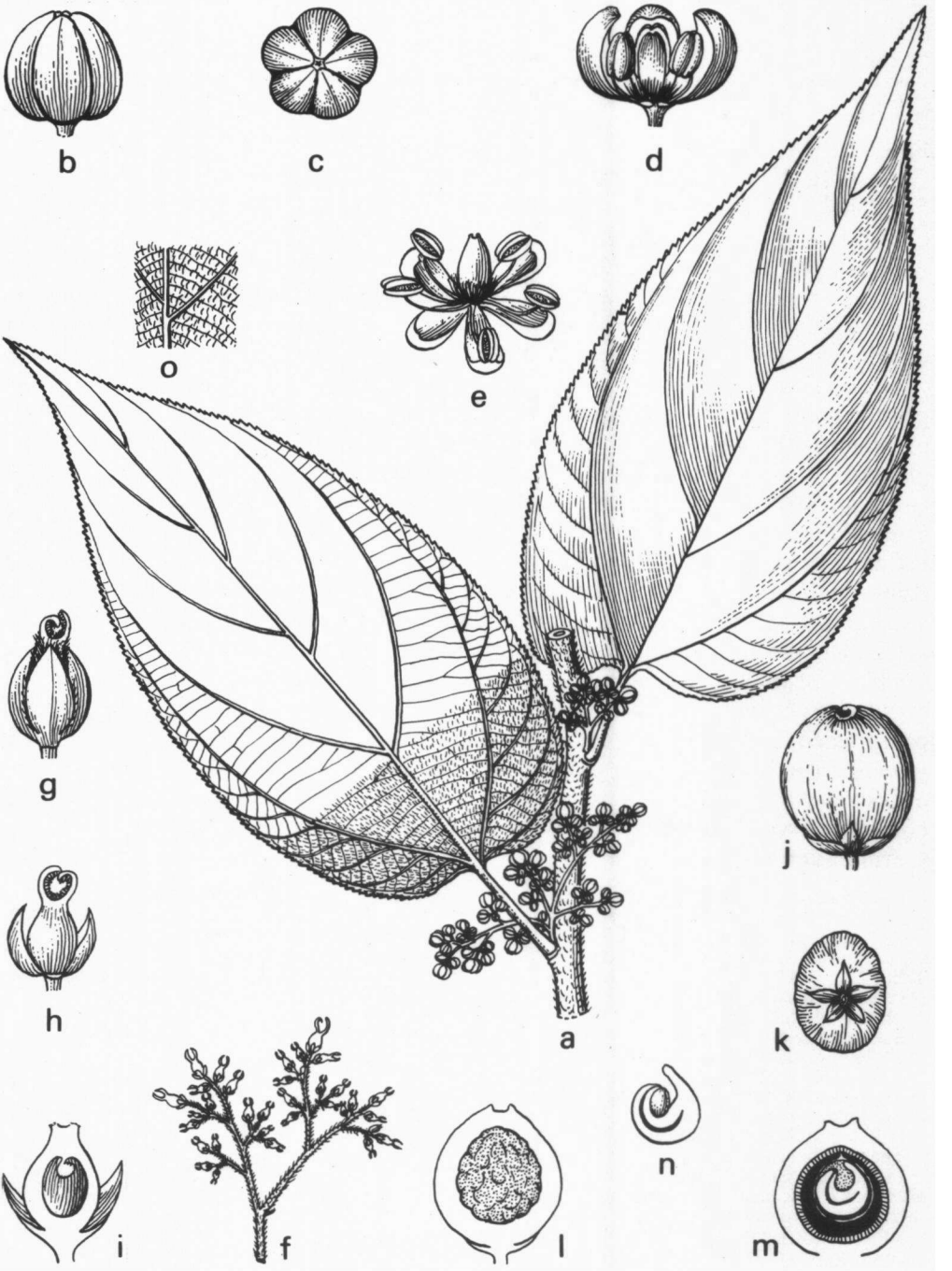

Fig. 13. *Trema orientalis* (L.) Bl. a. Habit, with functionally ♂ flowers, × ²/₃, b–e. ♂ flowers at various stages of development, all × 8, f. ♀ inflorescence, × ²/₃, g. ♀ flower, h. older ♀ flower, 2 tepals removed, i. *ditto* in LS, j–k. mature fruit, l. *ditto*, exocarp halfway removed, showing stone, m. *ditto* in LS, n. embryo, o. detail of lower leaf surface, all × 8 (*a–e* BW 13889, *f–i* BW 7019, *j–n* Brass 6496).

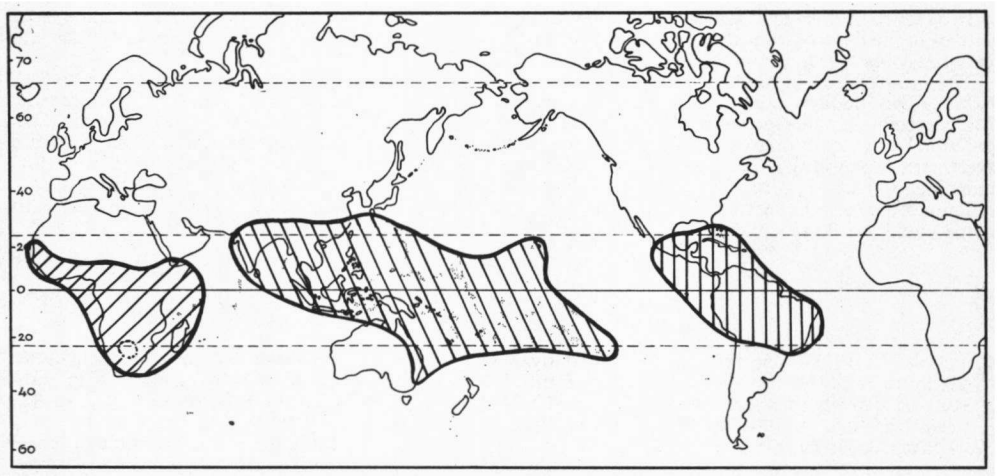

Fig. 14. Approximate range of *Trema* LOUR.

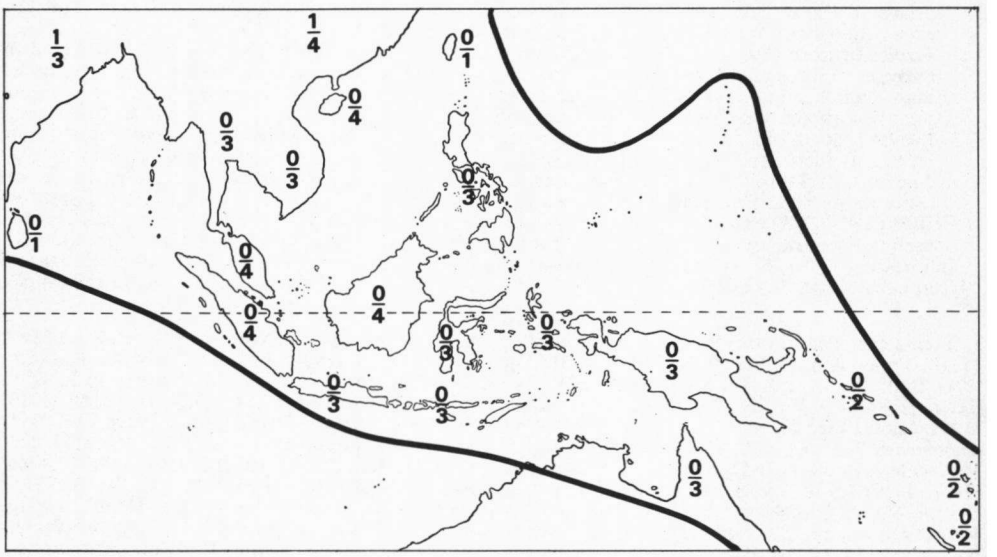

Fig. 15. Species density of *Trema* LOUR. in Indo-Australia; above the hyphen the number of endemic *spp.*, below it the number of non-endemic *spp.*

Chromosomes. A few counts on the chromosome number which have been reported by various cytologists suggest that cytogenetically the genus is rather variable. In *Trema politoria* from India n = 10+B (MEHRA & GILL, Taxon 17, 1968, 574; J. Arn. Arb. 55, 1974, 663); in *T. orientalis* n = 18 (ARORA, Bull. Bot. Surv. India 2, 1960, 305), or n = 20 (GAJAPATHY, *ibid.* 3, 1961, 49; HSU, Taiwania 13, 1967, 117), or n = 10 (MEHRA & HANS, Taxon 18, 1969, 310; HANS, Cytologia 36, 1971, 341); and in *T. tomentosa* (cited as *T. amboinensis*) n = 10 or 80 (HANS, *l.c.*; MEHRA, Nucleus 15, 1972, 64).

Specific delimitation has proved to be difficult and has led to more than 50 names in the genus. This was partly due to the various interpretations of the early described species. There is still no unanimity of opinion about the number of good species in the continents. In Africa, for example, ENGLER (Pfl. Welt Afr. 3 (1), 1915, 11) estimated the number for Africa at 5–7, following BLUME (1856), but RENDLE (1917) and POLHILL (Kew Bull. 19, 1964, 143) accept only one, either under the specific name *T. guineensis* or *T. orientalis*.

In absence of a critical, reliable world monograph there is a similar uncertainty about the number of species in the neotropics and in Indo-Malesia. For Malesia out of 20–25 published names of species and varieties, only 4 *spp.* are recognized here.

The proliferation of name giving in Malesia is mainly due to the fact that *Trema spp.* have a growth habit of continuously producing lateral and terminal new shoots on which flowers and fruits are borne. Many specimens collected were from these young shoots in which the indumentum and leaf-shape is often different from that of mature leaves. For accurate identification leaves, inflorescences, and fruits of mature specimens are essential. Besides, the indumentum was in earlier descriptions mostly derived from low magnification observations, but to differentiate sterile material of *T. orientalis* and *T. tomentosa* the difference in the indumentum becomes only clear under at least 40 × magnification. It is impossible to name young sterile specimens.

KEY TO THE SPECIES

(Based on mature leaves, inflorescences, and fruits)

1. Petiole (7–)10–15(–25) mm. Leaves broad ovate-elliptic, rarely narrow lanceolate (but then either glabrous or silvery brown tomentose beneath), (3–)5–10(–13) by (1½–)2–4(–5½) cm (and then glabrous or sparsely pubescent beneath) or (5–)10–15(–19) by (2–)3–7(–10) cm. Inflorescence ♂, ♀, or ♂♀, at anthesis lax, 10–100-flowered, 1½–5 cm long. Mature fruit 3–5 by 2–4 mm.
2. Leaves (3–)5–10(–13) by (1½–)2–4(–5½) cm, glabrous or rarely sparsely pubescent beneath, chartaceous to thin-coriaceous; base rounded, rounded-attenuate, truncate, or very rarely subcordate, mostly symmetrical; nerves 2–4(–5) pairs. Inflorescence always with a slender axis. Mature fruit *c.* 3 by 2 mm, orange or red in colour . . . . . **1. T. cannabina**
2. Leaves (5–)10–15(–19) by (2–)3–7(–10) cm, densely and variously hairy beneath, thin- to thick-coriaceous; base cordate, subcordate or rounded, mostly asymmetrical; nerves 4–8 pairs. Inflorescence with a stout or slender axis. Mature fruit black, 3–5 by 3–4 mm.
3. Leaves beneath (fig. 16) completely covered with matted glaucous to silvery straight appressed or curly, erect hairs and short, multicellular capitate-glandular hairs (epidermis invisible even under high magnification), very often distinctly discolorous with the upper surface darker in colour and weakly scabrate. ♂ Inflorescence up to 2½ cm. Fruit ± globular. . . . . **2. T. orientalis**
3. Leaves beneath (fig. 16) densely or sparsely (but not completely) set with velvety greyish-brown erect hairs only (epidermis clearly visible between the hairs even under low magnification), mostly concolorous, dark-brown to blackish in dried specimens; upper surface strongly scabrate. ♂ Inflorescence up to 5 cm. Fruits ovoid, compressed . . . . . **3. T. tomentosa**
1. Petiole (2–)3–6 (–8) mm. Leaves narrow ovate-lanceolate, (4–)5–6(–11) by (1¼–)2–3(–4) cm, beneath densely tomentose by short, matted, rufous, 1-celled and multicellular glandular hairs (hoary). Inflorescence ♂ or ♂♀, at anthesis condensed and shorter or as long as petiole, 5–15-flowered. Mature fruit subglobose, 2–3 by 2 mm. . . . . **4. T. angustifolia**

1. Trema cannabina LOUR. Fl. Coch. 2 (1790) 563; MERR. Trans. Am. Phil. Soc. 24, 2 (1935) 131; DE WIT, Bull. Bot. Gard. Btzg III, 18 (1949) 184; BACK. & BAKH. *f.* Fl. Java 2 (1965) 12; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 421. — *Celtis amboinensis* WILLD. Sp. Pl. 4, 2 (1805) 997. — *Celtis commersonii* BRONGN. in Duperrey, Voy. Bot. Coq. Phan. (1829) 215. — *Sponia commersonii* (BRONGN.) DECNE, Nouv. Ann. Mus. Hist. Nat. III, 3 (1834) 498; PLANCH. Ann. Sc. Nat. III, 10 (1848) 317; in DC. Prod. 17 (1873) 198. — *Sponia timorensis* DECNE, Nouv. Ann. Mus. Hist. Nat. III, 3 (1834) 498; PLANCH. Ann. Sc. Nat. III, 10 (1848) 318; in DC. Prod. 17 (1873) 196; MIQ. Fl. Ind. Bat. 1, 2 (1859) 216. — *Sponia amboinensis* (WILLD.) DECNE, Nouv. Ann. Mus. Hist. Nat. III, 3 (1834) 498, *quoad nomen.* — *Sponia virgata* PLANCH. Ann. Sc. Nat. III, 10 (1848) 316; in DC. Prod. 17 (1873) 195, *incl. var. major* PLANCH. *l.c.* 196; MIQ. Fl. Ind. Bat. 1, 2 (1859) 216; KURZ, For. Fl. Burma 2 (1877) 469. — *Sponia glabrescens* PLANCH. Ann. Sc. Nat. III, 10 (1848) 317; MIQ. Fl. Ind. Bat. 1, 2 (1859) 217. — *Sponia viridis* PLANCH. Ann. Sc. Nat. III, 10 (1848) 319. — *T. commersonii* (BRONGN.) BL. Mus. Bot. 2 (1856) 60. — *T. timorensis* (DECNE) BL. *l.c.* 60; HOOK. *f.* Fl. Br. Ind. 5 (1888) 483; HEMSL. J. Linn. Soc. Bot. 26 (1894) 452; LAUT. Bot. Jahrb. 50 (1913) 317, *incl. var. carinata* (BL.) LAUT. *et var. pallida* (BL.) LAUT.; HAND.-MAZZ. Symb. Sin. 7 (1929) 107. — *T. virgata* (PLANCH.) BL. Mus. Bot. 2 (1856) 59; J. J. SMITH in K. & V. Bijdr. 12 (1910) 652; LAUT. Bot. Jahrb. 50 (1913) 313, *incl. var. pubigera* (BL.) LAUT. *l.c.* 315; SCHNEIDER in Sargent, Pl. Wils. 3 (1917) 289; RIDL. Fl. Mal. Pen. 3 (1924) 319; GAGNEP. Fl. Gén. I.-C. 5 (1927) 686; HAND.-MAZZ. Symb. Sin. 7 (1929) 106; CORNER, Ways. Trees (1940) 694; LI, Woody Fl. Taiwan (1963) 109. — *T. amboinensis* (WILLD.) BL. Mus. Bot. 2 (1856) 61, *quoad nomen, excl. syn. et sched.*; MERR. Int. Rumph. (1917) 187. — *T. viridis* (PLANCH.) BL. Mus. Bot. 2 (1856) 58. — *T. glabrescens* (PLANCH.) BL. *l.c.* 58. — *T. carinata* BL. *l.c.* 59. — *T. pallida* BL. *l.c.* 60. — *T. pubigera* BL. *l.c.* 60. — *T. morifolia* BL. *l.c.* 59; LAUT. Bot. Jahrb. 50 (1913) 318. — *Sponia pallida* (BL.) MIQ. Fl. Ind. Bat. 1, 2 (1859) 215; PLANCH. in DC. Prod. 17 (1873) 196. — *Sponia carinata* (BL.) MIQ. Fl. Ind. Bat. 1, 2 (1859) 215; PLANCH. in DC. Prod. 17 (1873) 202. — *Sponia pubigera* (BL.) MIQ. Fl. Ind. Bat. 1, 2 (1859) 216; PLANCH. in DC. Prod. 17 (1873) 197. — *Sponia morifolia* (BL.) PLANCH. in DC. Prod. 17 (1873) 196. — *Sponia vieillardii* PLANCH. *l.c.* 201. — *Sponia aspera var. viridis* (PLANCH.) BTH. Fl. Austr. 6 (1873) 158. — *T. orientalis var. amboinensis* (WILLD.) KURZ, For. Fl. Burma 2 (1877) 469, *quoad nomen.* — *T. vieil-*

lardii (PLANCH.) SCHLTR, Bot. Jahrb. 36 (1905) 31.

Shrub or small much-branched tree up to 6 m, 15 cm ø. Bark smooth, grey-brown. Branchlets slender, spreading, often drooping, initially densely silvery-hairy, glabrescent and sparsely lenticellate. Stipules linear-lanceolate, 5–7 by 1–2 mm. *Leaves* chartaceous to thin-coriaceous, narrow ovate-caudate to broad ovate-acute, or elliptic-lanceolate, (3–)5–10(–13) by (1½–)2–4(–5½) cm (index 2–3 (–4)), broadest below or at the middle; base rounded to attenuate and acute, rarely subcordate, slightly contracted and more or less symmetrical; margin serrulate to denticulate for its entire length; apex with a sharp tip; above glabrous and variously scabrate, beneath glabrous or sparsely appressed-hairy; midrib and nerves raised beneath, impressed above; nerves (2–)3–4(–5) pairs, arcuate and subparallel, basal ones running up to ± ⅔ the length of the leaf; reticulations fine, subscalariform, obscure to visible beneath; petiole (5–)8–12(–15) by 1–2 mm, glabrescent. *Inflorescence* ♂ or ♂♀, with slender axes, 10–15-flowered, at anthesis lax, *c.* 1–2½ cm long, densely greyish appressed-hairy; bracts ovate-acute, *c.* 2–3 by 1 mm. — ♂ *Flowers* *c.* 1–2 mm ø, outside sparsely hairy, glabrescent; perianth lobes 4–5, membranous, oblong-lanceolate, *c.* 1–1½ by ½–1 mm; filaments *c.* 1 mm, anthers *c.* 1 by ½ mm; pistillode obovoid, compressed, *c.* 1 by ½ mm. — ♀ *Flowers* *c.* 1½–2 by 1–1½ mm; perianth lobes mostly 5, membranous, glabrous, ovate-acute, *c.* 1–1½ by ½ mm; staminode absent; ovary *c.* 1 by ½ mm; stigmatic arms spreading or incurved. *Drupe* 2–3 by 2 mm, turning deep-orange or red when ripe. Endosperm copious.

Distr. Burma, China, Formosa, Hainan, Indo-China, Thailand, common throughout *Malesia* to Australia, Melanesia (Solomons, New Caledonia, New Hebrides), W. Polynesia (Fiji, Samoa), and Micronesia.

Ecol. Common as a pioneer in newly opened up habitats along roadsides, edges of forests, regrowths, thickets, and in young secondary vegetation, from sea-level up to 1200 m. *Fl. fr.* Jan.–Dec. At least in Malaya pollination is affected by wind and by small insects (diptera). Ripe fruits are dispersed by various species of bulbuls.

Taxon. In Malesia there seem to be three rather but not completely distinct entities. These can be defined as follows: (i) specimens which have a completely glabrous, chartaceous and narrow-ovate leaf of (3–)5–8(–10) by (1½–)2–3(–4) cm with an index of 2½–3, more or less non-scabrate upper surface, and 2–3 lateral nerves (*T. cannabina* and *T. virgata*); (ii) specimens with a thin-coriaceous, narrow ovate-lanceolate to elliptic-lanceolate leaf of (6–)7–10(–12) by (1½–)2–3(–3½) cm, with an index of 4–5, slightly scabrate upper surface and sparsely hairy lower surface, and 4–5 lateral nerves which are straight and ascending and forming a narrow angle (less than 40°) with the midrib (*T. timorensis*, *T. virgata var. scabra*, and *T. cannabina var. scabra*); (iii) those with a broad ovate and coriaceous leaf of (8–)9–11(–13) by (3–)4–4½(–5½) cm, with an index of 2½–3, rugose and slightly scabrate upper surface and sparsely pubescent beneath, and 3–4 lateral nerves forming a broad angle (more than 45°) with the midrib (*T. glabrescens*, *T. viridis*, and *T. vieillardii*). Various intermediates are however present, making it difficult to recognize them as distinct infra-specific taxa.

Vern. Malaya: *měnĕrong*, *měngkirai*, M; S. Sumatra: *dĕlung*, M, Palembang; Java: *anggrung*, J; N. Borneo: *bintanong*, Murud; Lesser Sunda Is.: *rĕdong kué*, Flores, *pĕpaka*, Alor; Moluccas: *loli-sawu*, Halmaheira; Solomons: *bulasisi*, Kwara.

2. Trema orientalis (L.) BL. Mus. Bot. 2 (1856) 62; BTH. Fl. Austr. 6 (1873) 158; HOOK. *f.* Fl. Br. Ind. 5 (1888) 484; J. J. SMITH in K. & V. Bijdr. 12 (1910) 655, *p.p., excl. syn. T. commersonii et T. griffithii*; LAUT. Bot. Jahrb. 50 (1913) 320, *p.p., incl. var. rigida* (BL.) LAUT. *l.c.* 322, *excl. var. viridis et var. amboinensis*; CORNER, Ways. Trees (1940) 694, pl. 211, *p.p. excl. syn.*; DE WIT, Bull. Bot. Gard. Btzg III, 18 (1949) 189, *p.p., incl. var. bicornis* DE WIT, *l.c.* 190, *excl. var. bicolor et syn. T. angustifolia*, *T. imbricata et T. velutina*; BACK. & BAKH. *f.* Fl. Java 2 (1965) 12, *p.p., excl. syn. T. amboinensis auct. non* (WILLD.) BL.; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 421. — *Celtis orientalis* LINNÉ, Sp. Pl. 2 (1753) 1044; ROXB. Fl. Ind. ed. Carey 2 (1832) 65. — *Celtis rigida* BL. Bijdr. (1825) 486. — *Celtis discolor* BRONGN. in Duperrey, Bot. Voy. Coq. Phan. (1829) 215, pl. 47B. — *Sponia discolor* (BRONGN.) DECNE, Nouv. Ann. Mus. Hist. Nat. III, 3 (1834) 498; PLANCH. Ann. Sc. Nat. III, 10 (1848) 324; in DC. Prod. 17 (1873) 201. — *Sponia orientalis* (L.) DECNE, Nouv. Ann. Mus. Hist. Nat. III, 3 (1834) 498; PLANCH. Ann. Sc. Nat. III, 10 (1848) 323; in DC. Prod. 17 (1873) 200. — *Sponia rigida* (BL.) DECNE, Nouv. Ann. Mus. Hist. Nat. III, 3 (1834) 498; PLANCH. Ann. Sc. Nat. III, 10 (1848) 336; MIQ. Fl. Ind. Bat. 1, 2 (1859) 217. — *Sponia argentea* PLANCH. Ann. Sc. Nat. III, 10 (1848) 323; in DC. Prod. 17 (1873) 201. — *Sponia wightii* PLANCH. Ann. Sc. Nat. III, 10 (1848) 322; WIGHT, Ic. 6 (1853) t. 1971. — *T. argentea* (PLANCH.) BL. Mus. Bot. 2 (1865) 58. — *T. burmannii* BL. *l.c.* 62. — *T. rigida* (BL.) BL. *l.c.* 61. — *T. scaberrima* BL. *l.c.* 63. — *T. wightii* (PLANCH.) BL. *l.c.* 58. — *T. discolor* (BRONGN.) BL. *l.c.* 58; LAUT. Bot. Jahrb. 50 (1913) 319. — *Sponia scaberrima* (BL.) MIQ. Fl. Ind. Bat. 1, 2 (1859) 217; PLANCH. in DC. Prod. 17 (1873) 202. — *Sponia burmannii* (BL.) PLANCH. in DC. 17 (1873) 200. — **Fig. 13, 16.**

Shrub to large tree, 3–36 m, 10–90 cm ø. Buttresses, if present, up to 1¼ m. Bark smooth to finely fissured, lenticellate, grey-brown or whitish-grey. Branchlets, stipules, petioles, and inflorescences densely set with appressed and matted or erect silvery to glaucous 1-celled hairs and short multicellular glandular hairs. Stipules linear-lanceolate to ovate-acute, 3–4 by 1–2 mm. *Leaves* thin- to thick-coriaceous, often rigid and brittle, ovate, ovate-lanceolate to narrow elliptic, lanceolate, (6–)10–15(–18) by (1½–)2½–6(–10) cm, index (2–)3–4(–5½), broadest at or mostly below the middle, mostly discolorous, above dull grey-brown or grey-green in dried specimens, scabrate and sparsely set with bulbous-based hairs, beneath densely tomentose by a combination of silvery, glaucous or grey-brown, appressed 1-celled hairs and shorter multicellular glandular hairs (fig. 16); base cordate, rounded, or sometimes truncate, often contracted, asymmetrical or symmetrical; margin serrate to denticulate for its entire length;

apex acute to acuminate-caudate; midrib and nerves raised beneath and impressed above; nerves 4–6(–8) pairs, the lowest pair arcuating and running up to $^1/_2$–$^2/_3$ the length of the leaf; reticulations subscalariform to subareolate, sometimes strongly raised and distinct beneath; petiole (7–)10–15(–18) by 1–2 mm, densely short pubescent. *Inflorescences* either ♂ or ♀ borne on separate vegetative branches, a much-branched panicle or thyrse, at anthesis lax or condensed, axes 1–2 mm thick; bracts ovate-acute, 2–3 by 1 mm. Flowers 5-merous. — ♂ *Inflorescences* up to 3–5 cm long, 20–100-flowered; ♂ flower *c.* $1^1/_2$–2 mm ∅; perianth lobes ciliate, $1^1/_2$–2 by 1 mm; filaments 1–$1^1/_2$ mm, anthers *c.* 1 by $^1/_2$ mm, pistillode obovoid-conical, compressed, 1–$1^1/_2$ by $^1/_2$–1 mm. — ♀ *Inflorescences* 5–15-flowered, $1^1/_2$–$2^1/_2$ cm long, axes 1–2 mm thick; ♀ flower *c.* 2–3 by 1–2 mm; perianth lobes ovate acute, *c.* 1–$1^1/_2$ by $^1/_2$ mm, ciliate and densely short pubescent, glabrescent; staminode absent; ovary ovoid-conical, *c.* 2 by 1 mm; stigmatic arms slender, *c.* 1–$1^1/_2$ mm., spreading. *Drupe* 3–5 by 2–4 mm, turning black when ripe. Endosperm scanty to copious.

Distr. ?Tropical Africa, SE. Asia (Ceylon, India: from W. Himalayas to Bombay and Malabar; Burma, Thailand, Indo-China, China, also Hainan, Formosa, to S. Japan), through Malesia to Queensland, Melanesia (Solomons), Micronesia (Marianas), and Polynesia (Fiji, Tonga, Tahiti). In *Malesia:* Malay Peninsula and Sumatra (rather rare), Java (rather common in the hills and submontane regions), Lesser Sunda Islands (rare), Borneo (common), Philippines (rather common), Celebes (rather rare), Moluccas (rare), and New Guinea (incl. New Britain, rare).

Ecol. In W. Malesia and continental Asia the species is more common in the hills and montane regions between 600–2000 m, whereas in E. Malesia, Australia, and Pacific Islands it is more common in the lowlands. The ripe fruits which turn to deep purple or black are dispersed by various species of birds, particularly bulbuls. *Fl. fr.* Jan.–Dec.

Taxon. Three rather but not completely distinct entities may be recognized. These are: (i) specimens from continental Asia and W. Malesia which have been variously identified as *T. orientalis, rigida, argentea,* and *wightii* by previous authors. They are characterized by: thick-coriaceous, broadly ovate to ovate-elliptic leaves with grey-brown to glaucous indumentum, slightly asymmetrical to symmetrical cordate, subcordate or rounded base, rugose upper surface, and acute to acuminate apex; and by a relatively larger fruit of *c.* 4–5 by 3–4 mm and stouter inflorescence axes.

(ii) Specimens from S. Japan, Formosa, Hainan, the Philippines, New Guinea, Micronesia, Melanesia, and Polynesia, and Australia, which have been included in the so-called *T. discolor*, characterized by: thin-coriaceous, narrow-ovate leaves with strongly asymmetrical cordate base, hardly scabrate upper surface, short and matted silvery to grey-brown indumentum, lax inflorescence with slender axes, and fruits *c.* 3–4 by 2–3 mm.

(iii) A few specimens from scattered localities in S. China, Thailand, Sumatra, and Borneo, which have been described by DE WIT (1949) as *T. orientalis ssp. bicornis*, characterized by: very narrow, ovate-lanceolate thin-coriaceous leaves with silvery appressed and matted dense indumentum on the lower surface and non-scabrate upper surface, 6–8 pairs of nerves, and the shorter and few-flowered inflorescence.

Several intermediates are present however, making formal infraspecific distinction not advisable.

Vern. Sumatra: *endrung, ndĕrung,* Karo, *indarung,* Pajakumbu, *bandorung,* Tapanuli, *landojung,* Simelungun, *ĕndĕlung,* Palembang, Bencoolen, *magĕlong, nĕlung,* Bencoolen, *nĕriung,* Lampong. Java: *gorai, kuraj,* S, *anggrung, njampu,* J. Lesser Sunda Is.: *lĕnggung,* Bali, *rĕdong,* Flores, *tabĕlah,* W. Sumbawa. Borneo: *randagong,*

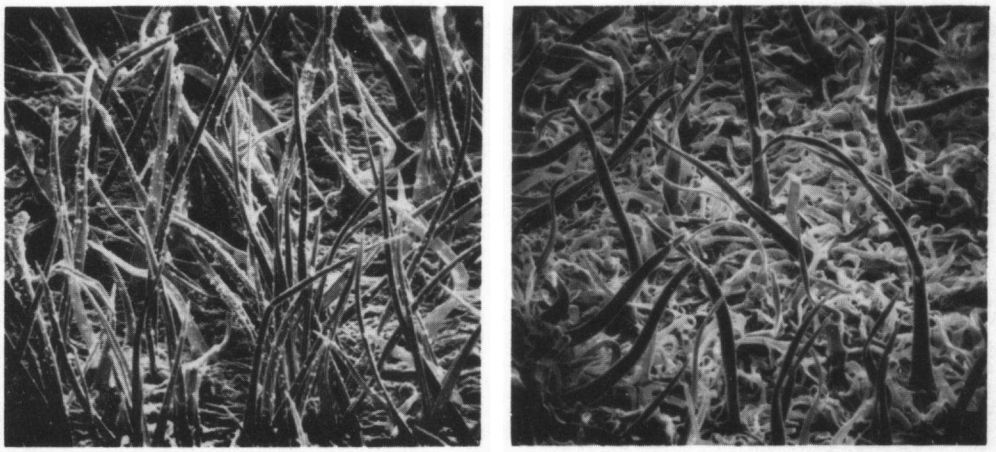

Fig. 16. Indument of lower leaf-surface, strongly enlarged. Left: only unicellular hairs of *Trema tomentosa* (ROXB.) HARA, between which the epidermis is visible. Right: *T. orientalis* (L.) BL., with long unicellular hairs and crowded multicellular crisped hairs covering the epidermis.

tandago, Dusun; *bĕngkirai*, E. Kutai. Philippines: *anadgong*, Bis. Celebes: *ngawoi*, Malili, *mawa*, Bonthain, *kantu*, Toradja, *tajapu*. Moluccas: *rufu*, Ternate, *laei*, Tidore, *soka soka*, E. Ceram. West New Guinea: *bĕsuwai*, Hattam lang., *karara*, Ambai, *kaniem*, *mier*, Kebar lang.

3. Trema tomentosa (ROXB.) HARA, Fl. E. Himal. 2 (1971) 19; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 423. — *Celtis orientalis* (*non* L.) BL. Bijdr. (1825) 485. — *Celtis amboinensis* (*non* WILLD.) BRONGN. in Duperrey, Bot. Voy. Coq. Phan. (1829) 212, pl. 47A, *p.p., excl. specim. ex Ventenat, Amboina.* — *Celtis tomentosa* ROXB. Fl. Ind. ed. Carey 2 (1832) 66. — *Sponia amboinensis* (WILLD.) DECNE, Nouv. Ann. Mus. Hist. Nat. III, 3 (1834) 498, *quoad specim.*; PLANCH. Ann. Sc. Nat. III, 10 (1848) 321; MIQ. Fl. Ind. Bat. 1, 2 (1859) 216; PLANCH. in DC. Prod. 17 (1873) 198. — *Celtis lima* (*non* SW.) BLANCO, Fl. Filip. 2 (1837) 139. — *Sponia griffithii* PLANCH. Ann. Sc. Nat. III, 10 (1848) 324. — *Sponia tomentosa* (ROXB.) PLANCH. *l.c.* 336. — *Sponia velutina* PLANCH. *l.c.* 327, *p.p., excl. specim. Cuming 1232 ex Luzon.* — *Sponia blancoi* PLANCH. *l.c.* 327; MIQ. Fl. Ind. Bat. 1, 2 (1859) 218. — *T. griffithii* (PLANCH.) BL. Mus. Bot. 2 (1856) 58. — *T. blancoi* (PLANCH.) BL. *l.c.* 58. — *T. imbricata* BL. *l.c.* 63. — *T. velutina* (PLANCH.) BL. *l.c.* 58; GAGNEP. Fl. Gén. I.-C. 5 (1927) 689; LI, Woody Fl. Taiwan (1963) 109. — *T. amboinensis* (WILLD.) BL. Mus. Bot. 2 (1856) 61, *quoad specim.*; BTH. Fl. Austr. 6 (1873) 159; HOOK. *f.* Fl. Br. Ind. 5 (1888) 484; K. SCH. & LAUT. Fl. Schutzgeb. (1900) 264; J. J. SMITH in K. & V. Bijdr. 12 (1910) 659, *p.p., excl. syn. Celtis amboinensis* WILLD. *et Trema burmannii* BL.; MERR. En. Born. (1921) 217; RIDL. Fl. Mal. Pen. 3 (1924) 319. — *Sponia imbricata* (BL.) PLANCH. in DC. Prod. 17 (1873) 199. — *T. orientalis var. amboinensis* (WILLD.) KURZ, For. Fl. Burma 2 (1877) 469, *quoad specim.*; LAUT. Bot. Jahrb. 50 (1913) 321. — *T. orientalis* (*non* (L.) BL.) MERR. Sp. Blanc. (1918) 121. — *T. dielsiana* HAND.-MAZZ. Symb. Sin. 7 (1929) 106; P'EI, Bot. Bull. Ac. Sin. 1 (1947) 289. — **Fig. 16.**

Shrub to medium-sized tree of 5–15(–24) m, 5–30(–50) cm ∅. Bark grey-brown, smooth to finely fissured, lenticellate. Branchlets, inflorescences, petioles, stipules, and underside of leaves densely and thickly set with greyish, erect, velvety hairs. Stipules linear-lanceolate, *c.* 5 by 1 mm. *Leaves* thin- to thick-coriaceous, broadly ovate to ovate-elliptic, (5–)8–15(–19) by (2–)4–7(–9) cm, index $2^1/_2$–3, broadest mostly below the middle; more or less concolorous, drying dark-chocolate brown to blackish brown; above strongly scabrate; base cordate, rarely subcordate or rounded, mostly strongly asymmetrical, rarely symmetrical; margin serrate throughout, apex acute to acuminate-caudate, acumen sharp, 1–3 cm; midrib and nerves raised beneath (often very strongly), impressed and hairy above; nerves 4–6 pairs, ascending and subparallel, at an angle of ± 45°, the lowest pair running to ± $^1/_2$–$^2/_3$ the length of the leaf; reticulations subscalariform to subareolate, often rather distinct beneath; petiole 1–$1^1/_2$ cm by 1–2 mm, densely pubescent. *Inflorescences* ♂, ♀, or ♂♀, either on the same or on different vegetative branches; bracts ovate-acute, *c.* 1 by $^1/_2$ mm. — At anthesis ♂ and ♂♀ axes of the inflorescences lax, $2^1/_2$–$4^1/_2$ cm long, 20–100-flowered; ♂ flower *c.* $1^1/_2$–2 mm ∅; perianth lobes mostly 5, elliptic, *c.* $1^1/_2$ by 1 mm; filaments *c.* 1 mm, flat, glabrous, anthers *c.* 1 by $^1/_2$ mm; pistillode obovoid-ellipsoid, compressed, $1^1/_2$ by $^1/_2$ mm. — ♀ *Inflorescence* 1–2 cm long, axes 1–2 mm thick, 5–15-flowered; ♀ flower *c.* 2 by 1 mm; perianth lobes 4–5, ovate-acute, *c.* 1 by $^1/_2$ mm; staminode mostly absent, if present strongly reduced in size and non-functional; ovary *c.* $1^1/_2$ by $^1/_2$–1 mm, stigmatic arms slender, *c.* 1 mm, spreading. *Drupe c.* 3 by 2 mm, maturing black. Endosperm copious.

Distr. East tropical Africa, Madagascar, SE. Asia: Pakistan, India, Bangladesh, Burma, Thailand, Indo-China, China (incl. Hainan), Hongkong, Formosa, Ryu Kyu Is. (Okinawa), throughout *Malesia* to Queensland, Melanesia (New Caledonia), Micronesia, and Polynesia (Fiji, Tonga, and Hawaii).

Ecol. Common in the lowlands and hills, at sea-level up to 1000 m, as a pioneer plant invading and occupying newly opened up habitats on all kind of soils, including limestones. *Fl. fr.* Jan.–Dec. At least in Malaya pollination is affected by wind and small insects (diptera). The ripe black fruit is dispersed by various species of birds.

Taxon. Evidently, *T. tomentosa* is closely allied to *T. orientalis*, and it is possible that, when more field data become available in the future, the former may prove to be only representing a juvenile ontogenetical form of the latter. Except for a few specimens from the Philippines (*e.g.* WHITFORD 681, BS 37313, 48355, ELMER 8417) and from New Guinea (*e.g.* ANU 2075, 2752, 6240, HARTLEY 10937, MANNER & STREET 270, NGF 29353, SCHODDE 1419, and BW 16510) in which the leaves are thick-coriaceous and with a more or less symmetrical base and pale grey-brown in colour, specimens of *T. tomentosa* can be easily distinguished from those of *T. orientalis* by the characters mentioned in the key. Fig. 16. It is also interesting to note that according to HANS (Cytologia 36, 1971, 341) and MEHRA (Nucleus 15, 1972, 64) the chromosome number in *T. tomentosa* is n = 10 or 80, whereas that of *T. orientalis* is n = 10, 18, or 20.

Vern. Malay Peninsula: *mĕnarong*, *mĕndarong*, *mĕngkirai*, M. Sumatra: *bĕngkirai*, Gajo, *ĕndĕlung*, Palembang, *eĕmaha*, Enggano, *hana(w)e*, Batak, *kamĕsèn silai*, Simalur, *mangkirai*, Pajakumbu, *manghirei*, *mĕnkirei*, Lingga, *mudĕn sabu*, Djambi, *(n)dĕr(r)ung*, Karo-Batak, *randurung*, Toba, *sangkiraja*, Batak, *tindjau*, Riouw. Java: *anggrung*, J, *kuraj*, *k. awèwèna*, S. Lesser Sunda Is.: *rĕdong*, *damot*, Flores, *ruka parak*, Sumba. Borneo: Sarawak: *murieng*, Bidajuh, *kĕrĕnènog*, Iban, *tuku baroh*, Land Dayak; N. Borneo: *anjalakat*, Kedayan; Brunei: *balèk balèk angin jantan*, *balik angin*, *rundagong*, Brunei, *bintanong*, Murut, *damai*, Suluk, *entimon*, Iban, *lindagong*, Kedayan, *landagong*, Dusun Tambato & Kayan, *lundagong*, *salimuak*, Dusun, *randagong*, Tenggara, *rĕndagong*, Dusun Labuk; E. Borneo: *bangĕrai*, *bangkirai*, *tjalundung*, E. Kutai; W. Borneo: *ĕngkirai*, *butu*. Philippines: *anaginong*, Mang., *anugdon*, Tag-Bis., *anabiong*, *hanagdong*, Tag., *karangyan*, *karayangyang*, Tagb. Moluccas: *mandalirung'a*, Talaud, *pohon rupong*, Banda, *rufut*, Buru. West New Guinea: *fidukwa*, Manokwari, *hormas*, Sorong; East New Guinea: *komukai*, Maring name, *natua*,

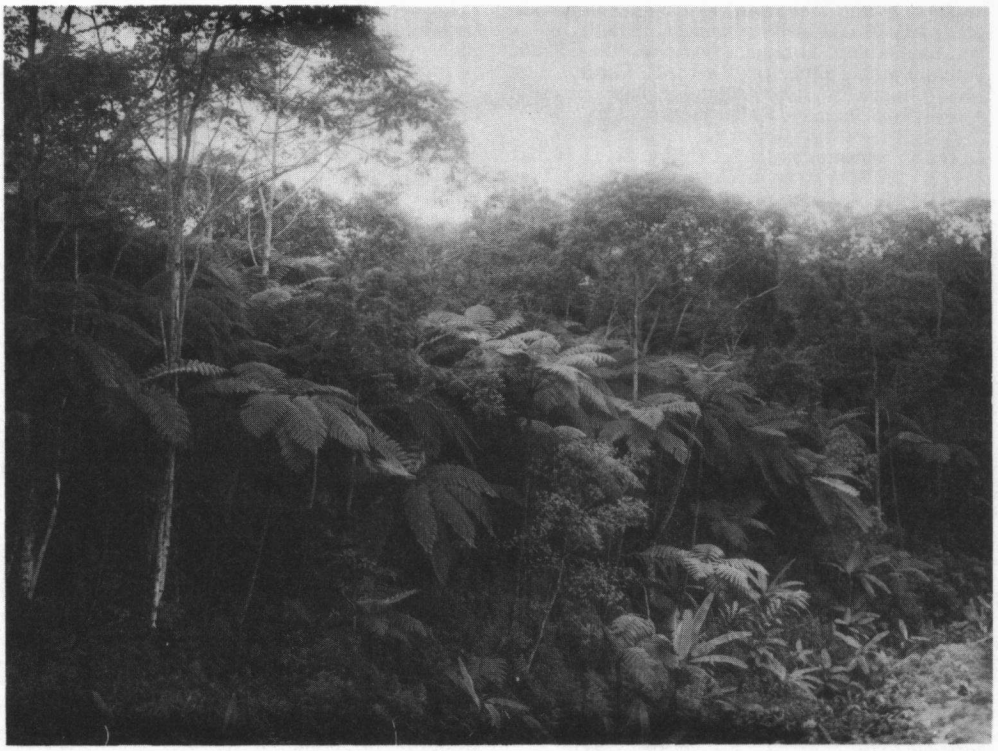

Fig. 17. Young blukar (regrowth or secondary forest) on an abandoned tea estate near Tapos, West Java, *c.* 1000 m, consisting of three layers: 2 m high stand of *Eupatorium inulifolium*, 5–6 m high tree ferns of *Cyathea contaminans*, above which is an open canopy of *Trema orientalis* (L.) BL. (Photogr. VAN STEENIS).

Kainantu, *seraun*, Daga-Bonenau, *wanip*, Enga lang., *wantip*, Medlpa, Wahgi, *wan'um*, Mendi.

4. Trema angustifolia (PLANCH.) BL. Mus. Bot. 2 (1856) 58; HOOK. *f.* Fl. Br. Ind. 5 (1888) 484; GAGNEP. Fl. Gén. I.-C. 5 (1927) 686; HAND.-MAZZ. Symb. Sin. 7 (1929) 108. — *Sponia angustifolia* PLANCH. Ann. Sc. Nat. III, 10 (1848) 326; MIQ. Fl. Ind. Bat. 1, 2 (1859) 215; PLANCH. in DC. Prod. 17 (1873) 202. — *Sponia acuminatissima* MIQ. Sumatra (1861) 410; PLANCH. in DC. Prod. 17 (1873) 202. — *Sponia sampsonii* HANCE, Ann. Sc. Nat. V, 5 (1866) 242. — *T. acuminatissima* (MIQ.) BOERL. Handl. 3 (1900) 358. — *T. lanceolata* MERR. Lingn. Sc. J. 7 (1931) 302. — *T. sampsonii* (HANCE) MERR. & CHUN, Sunyatsenia 5 (1940) 40. — *T. orientalis var. bicolor* DE WIT, Bull. Bot. Gard. Btzg III, 18 (1949) 190.

Shrub or small tree with spreading and drooping branches, 3–7 m, 5–15 cm ∅. Branchlets densely set with rufous multicellular glandular hairs and glaucous short and matted 1-celled hairs, subglabrescent. Stipules linear-lanceolate, 3–4 by 1 mm. *Leaves* chartaceous to thin-coriaceous, narrow ovate-lanceolate to lanceolate, (3–)5–8(–10) by (1–)2–3(–4) cm, index 3–3$^1/_2$, broadest below or at the middle; discolorous, upper surface strongly scabrate, dark chocolate-brown to blackish-brown, lower surface densely set with short and matted rufous to glaucous 1-celled and multicellular glandular hairs; base rounded to attenuate, symmetrical; margin finely serrate throughout; apex acute to acuminate; midrib and nerves slightly raised beneath, impressed above; nerves 4–5 pairs, straight, ascending at 30–40°; reticulations fine, subscalariform to subareolate, obscure above and faintly visible beneath; petiole (2–)3–6(–8) by 1 mm, densely short hairy. *Inflorescences* ♂ or ♂♀, densely set with a short rufous indumentum, much-branched, (5–)10–15(–30)-flowered, at anthesis condensed, shorter than or as long as the petiole; bracts narrow ovate-acute, *c.* $^1/_2$–1 by $^1/_4$–$^1/_2$ mm. — ♂ *Flowers c.* 1–1$^1/_2$ mm ∅; perianth lobes 5, elliptic, *c.* 1–1$^1/_2$ by 1 mm; filaments *c.* 1 mm long, *c.* $^1/_2$–1 mm ∅; pistillode obovoid-ellipsoid, strongly compressed, *c.* $^1/_2$–1 by $^1/_4$ mm. — ♀ *Flowers* ovoid-conical, *c.* 2 by 1 mm; perianth lobes 5, narrow-lanceolate, acute, $^1/_2$–1 by $^1/_4$–$^1/_2$ mm; staminode absent; ovary *c.* 1–2 by 1 mm; stigmatic arms *c.* $^1/_2$–1 mm, spreading or incurved. *Drupe c.* 1$^1/_2$–2 mm ∅, turning orange to red when ripe. Endosperm copious.

Distr. China (Yunnan, Hainan), Thailand, and Indo-China; in *Malesia:* Malay Peninsula (common), Sumatra (rare), Borneo (rare), Celebes (very rare).

Ecol. Scattered in newly available habitats in the lowlands to submontane regions, from sea-level to 1200 m. *Fl. fr.* Jan.–Dec. Ripe fruits are dispersed by various species of bulbuls.

Vern. Malaya: *mĕnarong*, *mĕngkirai*, M; Sumatra: *kayu anggurung*, M, Eastcoast, *mangkirai kĕtjil*, M, Palembang.

Excluded

Trema (*Parasponia*) *lancifolia* RIDL. J. Mal. Br. R. As. Soc. 1 (1923) 91 = *Debregeasia longifolia* (BURM. *f.*) WEDD. (*Urticaceae*).

4. CELTIS

LINNÉ, Gen. Pl. ed. 5 (1754) 467; Sp. Pl. 2 (1753) 1043; PLANCH. Ann. Sc. Nat. III, 10 (1848) 262; BL. Mus. Bot. 2 (1856) 70; MIQ. Fl. Ind. Bat. 1, 2 (1859) 220; PLANCH. in DC. Prod. 17 (1873) 168; B. & H. Gen. Pl. 3 (1880) 354; ENGL. in E. & P. Nat. Pfl. Fam. 3, 1 (1888) 63; BERNARD, Bull. Herb. Boiss. II, 5 (1905) 1112, maps 9–15; J. J. SMITH in K. & V. Bijdr. 12 (1910) 639; LEROY, Fl. Madag. et Com. Fam. 54 (1952) 3; POLHILL, Kew Bull. 19 (1964) 139; HUTCH. Gen. Fl. Pl. 2 (1967) 147; ELIAS, J. Arn. Arb. 51 (1970) 32; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 414. — *Solenostigma* ENDL. Prod. Fl. Norf. (1833) 41; BL. Mus. Bot. 2 (1856) 66; MIQ. Fl. Ind. Bat. 1, 2 (1859) 219. — **Fig. 18, 20, 22–23.**

Small to large monoecious or polygamo-monoecious trees, often buttressed. Bark smooth or finely fissured, often conspicuously warty lenticellate. Branches (in Mal.) unarmed, initially densely yellow-brown or rufous-hairy, glabrescent; hairs 1-celled. Buds enclosed by the overlapping stipules or naked. Stipules thick and tough, peltately attached or free and scarious, caducous. *Leaves* entire or not, 3-nerved at base, semideciduous or persistent. *Inflorescenes* ♂, ♀, or ♂♀, branched racemes or panicles, few- to many-flowered, axillary or subterminal on the new shoot; staminate inflorescences borne on the lower and leafless part or in the axil of leaves of the new shoot; in the ♂♀ inflorescence the ♀ flowers are borne on the distal ends of the axes; bracts minute, caducous. — *Staminate* (♂) *flowers* globular, pedicelled or sessile; perianth lobes 4–5, imbricate in bud, membraneous, boat-shaped, outside sparsely pubescent, at anthesis recurved, caducous; stamens glabrous, inserted on the densely pilose receptacle; filaments subulate, incurved in bud and spreading elastically, exserted at anthesis; anthers ovoid to subreniform, dorsifixed just above the emarginate base, extrorse; pistillode present or absent. — ♀ *Flowers* ovoid, pedicelled; perianth lobes 4–5, imbricate in bud, connate at base, membranous, outside sparsely pubescent, boat-shaped, at anthesis recurved, caducous; stamens well-developed and functional or rudimentary, other characters as in ♂ flowers; ovary ovoid-ellipsoid, sessile, style short or ± absent; stigmatic arms elongate, divergent, the tips entire to deeply bifid; ovule anatropous. *Drupe* fleshy, ovoid, ellipsoid or globose; exocarp thick and firm, mesocarp thin and fleshy, containing slimy substances; endocarp hard and persistent, smooth or variously ridged or pitted. *Seed:* coat membranous, chalazal area broad, dark-coloured and close to the minute hilum; endosperm scanty or wanting, oily or gelatinous, nearly enclosed between the folds of the cotyledons. Embryo curved, cotyledons broad, foliaceous, equal or unequal in thickness, flat or conduplicate, variously folded, incumbent on or embracing the short superior and ascending radicle. Germination epigeal.

Distr. About 50–60 *spp.*, widely distributed in tropical and temperate regions of the world, the majority of species (30–40) in the Old and New World tropics, throughout *Malesia* (9 *spp.*). Fig. 19, 21.

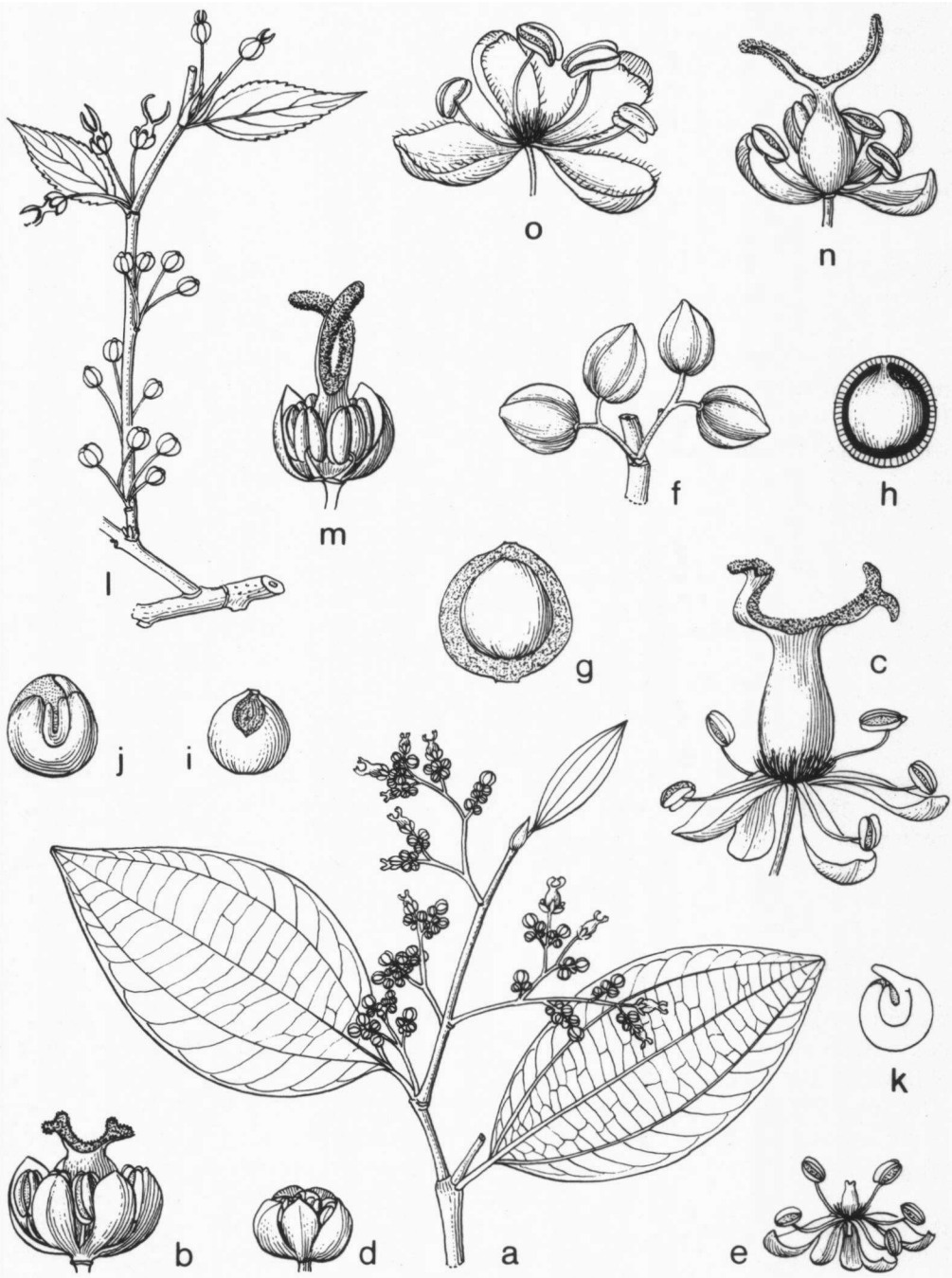

Fig. 18. *Celtis philippensis* BLANCO. a. New shoot bearing flowers, × ²/₃, b–c. ☿ flowers, × 8, d–e. ♂ flowers, × 10, f. fruits, × ²/₃, g. fruit, exocarp in LS, × 1¹/₃, h. stone, endocarp in LS, × 1¹/₃, i. seed showing testa and chalaza, nat. size, j. *ditto* in LS showing folded cotyledons, shaded oily endosperm, × 1¹/₃, k. embryo in LS, × 1¹/₃. — *C. tetrandra* ROXB. l. New shoot bearing flowers, × ²/₃, m-n. ☿ flowers, × 8, o. ♂. flowers, × 10 (*a–c* MERRILL 52, *d–e* BS 1920, *f–k* BARTLETT 15071, *l–o* SCHMUTZ 1666).

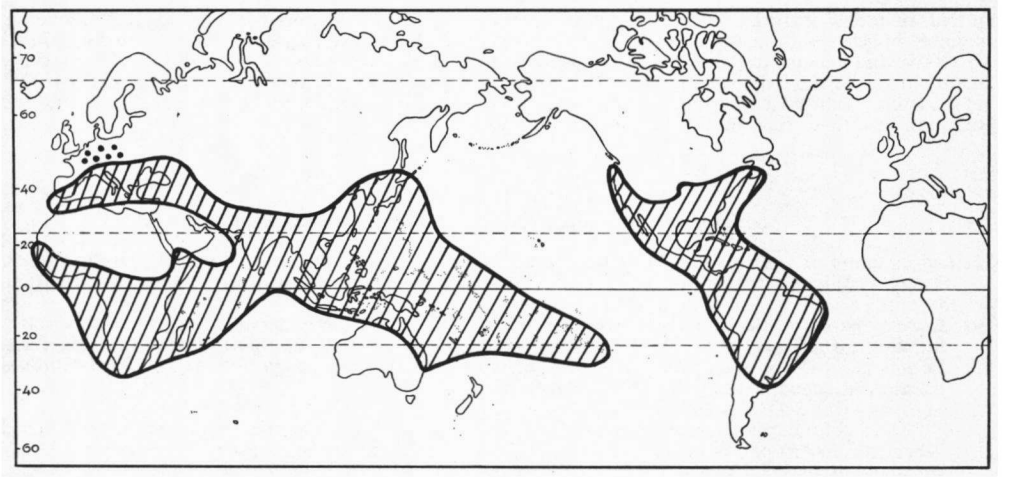

Fig. 19. Approximate range of *Celtis* L. Fossil records are indicated by dots.

Fossils. Numerous fossilized wood-fragments, leaf-impressions, drupes and pollen grains have been discovered in various localities in Europe, the U.S.A., and in Asia. According to ELIAS *l.c.* the first (oldest) records are apparently from the early Eocene in Wyoming and the late Eocene in Georgia, U.S.A. Continuing through the Oligocene, *Celtis spp.* are best known from the Miocene, fossilized material of younger age is relatively sparse at least in the U.S.A. — References: A. GRAHAM (ed.), Floristics and Paleofloristics of Asia & Eastern North America (1972) 147; GREGUSS, Tert. Angios. Hung., Ak. Kiado Budapest (1969) 83; LA MOTTE, Mem. Geol. Soc. Am. 51 (1952) 112. Fig. 19.

Ecol. Malesian species of *Celtis* may be classified into two rather distinct ecological groups, *i.e.* the *C. philippensis var. philippensis* and *C. tetrandra* groups. The first group, which includes also *C. hildebrandii*, *C. latifolia*, *C. luzonica*, *C. paniculata*, and *C. rigescens*, is found mainly in the lowland forests, both primary and secondary, and is an important constituent of the understorey tree community in moist areas. The *C. tetrandra* group, which includes *C. rubrovenia*, *C. timorensis*, and *C. philippensis var. wightii*, is confined to areas which are subject to a rather pronounced seasonal climate, or if they occur in wetter regions, they grow on strongly drained substrates, *e.g.* rocky shores, limestone, *etc.* In tune with this environmental preference, the second group shows a more prominent flush-wise growth habit and its species are completely or partly deciduous. In Malaya, species of *Celtis* are producing flowers around July-September, while fruit ripens January–March.

How pollination is affected is not certain, but judging from the structure and position of the inflorescence, some species (*e.g. C. philippensis var. philippensis*, *C. hildebrandii*, and *C. latifolia*) may be pollinated by insects, while others (*C. tetrandra*, *C. timorensis*, *C. rubrovenia*, and *C. rigescens*) may be pollinated by wind.

The ripe fleshy drupes which turn to orange, red or bluish-black may be dispersed by birds, or alternatively they may be dispersed by water as the embryo is protected by the hard, persistent and durable endocarp.

Morph. Except for *C. paniculata* the stamens of the pistillate flowers are well-developed and functional. In the male or staminate flowers the pistillode is rudimentary or completely absent in *C. tetrandra*, *C. timorensis*, and *C. rubrovenia*. In the other species the pistillode is present and relatively rather well-developed though non-functional.

Chromosomes. The chromosome numbers reported are: n = 10 (2n = 20) (*C. australis var. eriocarpa*, *C. inguana*, *C. laevigata*, *C. occidentalis*, *C. sinensis*, and *C. timorensis* (under *C. cinnamomea*)); 2n = 22 (*C. spinosa*); 2n = 28 (*C. occidentalis*); 2n = 40 (*C. australis* and *C. tupalangi*). — References: SAX, J. Arn. Arb. 14 (1933) 82; BOWDEN, Am. J. Bot. 32 (1945) 195; DARLINGTON & WYLIE, Chromos. Atlas (1955) 182; MEHRA & GILL, Taxon 17 (1968) 574; GADELLA *et al.* Acta Bot. Neerl. 18 (1969) 74; MEHRA & HANS, Taxon 18 (1969) 310; FEDOROV (ed.), Chromos. Numbers Flow. Pl. (1969) 710; MEHRA & GILL, J. Arn. Arb. 55 (1974) 663.

According to SAX *l.c.* there seems to be at least in *C. occidentalis* a high degree of pollen sterility and a high incidence of meiotic irregularity. This may be one of the causes why in *Celtis* there is a very high percentage of barren seeds production, even among tropical species.

Embryology. No detailed study on the microsporogenesis, megasporogenesis and embryogenesis of *Celtis* species has ever been carried out. In Malesia the solitary ovule is bitegmic, anatropous and inserted just below the apex of the locule. After fertilization both integuments develop into thin membranous seed coats with a broad, dark-coloured, more or less circular chalaza. The endocarp becomes woody and very hard and impregnated by mineral deposits. It is persistent and becomes variously sculptured (ridged,

pitted, or nearly smooth). The embryo is strongly curved with the hypocotyle superior and ascending, situated in between or nearly enclosed by the broad, thick, foliaceous cotyledons. The cotyledonar lobes are somewhat unequal in thickness, and they are either induplicate or variously folded. Endosperm is very scanty to absent and either gelatinous or oily. Especially in *C. paniculata* and *C. tetrandra*, at least 70–80% of the fruits produced are barren. Though the fruits are developed normally, the embryo fails to grow and becomes shrivelled. As a result the fruits are empty.

KEY TO THE SPECIES

(Measurements of leaf and fruit based on fully mature material)

1. Leaves entire or nearly so. ♂ Inflorescence a much-branched many-flowered panicle with up to 150 flowers. Pistillode rather well-developed, *c.* 1–1½ by ½–1 mm. Stigmatic arms bilobed or bifid at the tip.
2. Leaves rugose, brittle, sparsely pubescent beneath; midrib and lateral nerves strongly raised beneath. Stipules not peltately attached, free from one another. Fruit densely appressed-hairy. **1. C. rigescens**
2. Leaves not rugose, not brittle, glabrous; midrib and nerves only slightly raised beneath. Stipules peltately attached, overlapping. Fruit glabrous.
3. Leaves with (2–)3–5 pairs of nerves.
4. Leaves elliptic-orbicular or elliptic-oblong, index (1¼–)1½(–2); midrib and nerves slightly raised beneath; lowest pair of nerves running to ⅔–¾ the length of the leaf, upper pairs of nerves ascending and arcuating. Stigmatic arms shallowly bilobed at the tip. Fruit globose, 16–20 by 14–18 mm. **2. C. luzonica**
4. Leaves elliptic or ovate-eliptic, index (1½–)2–2½(–3); midrib and nerves flattish beneath; lowest pairs of nerves running up to ⅓–½(–⅔) the length of the leaf; upper pairs of nerves weak, subhorizontal. Stigmatic arms deeply bifid at the tip. Fruit ovoid or ellipsoid, 7–12 by 5–8 mm.
5. Nerves 3–5 pairs; lowest pair running to ⅓–½ the length of the leaf. Inflorescence mostly ♂ or ☿. Stamens of ☿ flower rudimentary, non-functional. Fruit ovoid, feebly 4–5-angular in CS; endocarp with reticulate ridges. . . . . **3. C. paniculata**
5. Nerves 1–2(–3) pairs; lowest pair running up to ⅔ the length of the leaf. Inflorescence ♂ or ♂☿. Stamens of ☿ flower well-developed and functional. Fruit ellipsoid, ± terete; endocarp smooth. **4b. C. philippensis *var.* wightii**
3. Leaves with 1 pair of nerves.
6. Leaf symmetrical. Inflorescence ♂ or ♂☿. ♂ Inflorescence 15–40-flowered. Cotyledons curved but not folded.
7. Leaves (4–)8–14(–18) by (2–)3–6(–8) cm; reticulations fine, dense. Ovary glabrous. Fruit 8–15 by 7–12 mm; endocarp smooth . . . . . **4a. C. philippensis *var.* philippensis**
7. Leaves (8–)15–18(–25) by (6–)8–12(–18) cm; reticulations coarse, wide-spaced. Ovary densely appressed-pubescent. Fruit 15–25 by 10–18 mm; endocarp pitted . . . . . **5. C. latifolia**
6. Leaf oblique. Inflorescence ♂ and ☿. ♂ Inflorescence 60–150-flowered. Cotyledons curved and many times folded. . . . . **6. C. hildebrandii**
1. Leaves serrulate to denticulate at least in the upper half. ♂ Inflorescence racemose, 5–20-flowered. Pistillode strongly reduced in size or absent. Stigmatic arms entire.
8. Leaf not strongly oblique in outline; nerves 1–2(–3) pairs. Inflorescence ♂ and ♂☿; ♂ flower 5-merous.
9. Leaves (6–)10–12(–17) by (2½–)4–5(–8) cm, index 1½–2½. ♂ Inflorescence 10–20-flowered. Ovary glabrous. Infructescence 4–5 cm long. Fruit ovoid, strongly beaked, 5–10 by 3–6 mm. **7. C. timorensis**
9. Leaves (3–)4–5(–6½) by (1¼–)1½–2½(–3½) cm, index 2–3.3. ♂ Inflorescence 5–7-flowered. Ovary densely hairy. Infructescence *c.* 1½ cm. long. Fruit globose, not beaked, *c.* 3 by 3 mm **8. C. rubrovenia**
8. Leaf strongly oblique; nerves 3–4 pairs. Inflorescence ♂ and ☿; ♂ flower 4-merous.. **9. C. tetrandra**

1. Celtis rigescens (MIQ.) PLANCH. in DC. Prod. 17 (1873) 182; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 416. — *Solenostigma rigescens* MIQ. Sumatra (1861) 411. — *Solenostigma sumatrana* MIQ. *l.c.* 411. — *C. sumatrana* (MIQ.) PLANCH. in DC. Prod. 17 (1873) 181. — *C. nymanii* K.SCH. in K.Sch. & Laut. Fl. Schutzgeb. Nachtr. (1905) 240; LAUT. Bot. Jahrb. 50 (1913) 311. — *C. asperifolia* MERR. Philip. J. Sc. 17 (1920) 246; En. Philip. 2 (1923) 32. — **Fig. 20e, 23a–b.**

Large tree up to 45 m, 1 m ∅. Buttresses up to 6 m tall, 3 m out, 5 cm thick. Bark grey-brown, smooth, finely fissured to pustulate and lenticellate. Innovations densely yellowish brown to rufous simple hairy. Older twigs glabrous, finely striate and sparsely minute lenticellate. Terminal buds ovoid-conical, *c.* 3 by 2 mm, scales densely yellowish-brown tomentose. Stipules linear-lanceolate, 4–5 by 1–1½ mm. Mature *leaves* thick-coriaceous, strongly rugose, stiff and brittle when dry, ovate-elliptic to elliptic-oblong, (5–)8–12(–15) by (2½–)3–5(–6½) cm (index 1½–2½), broadest at or slightly below the middle; above glabrous, shining, beneath sparsely yellowish-brown pubescent especially on midrib and nerves; base rounded to subcordate, symmetrical, rarely attenuate-rounded and slightly asymmetrical; margin undulate, entire or distantly serrate in the upper half, very often incurved; apex rounded-acute to acuminate; midrib and nerves strongly raised beneath, flattish

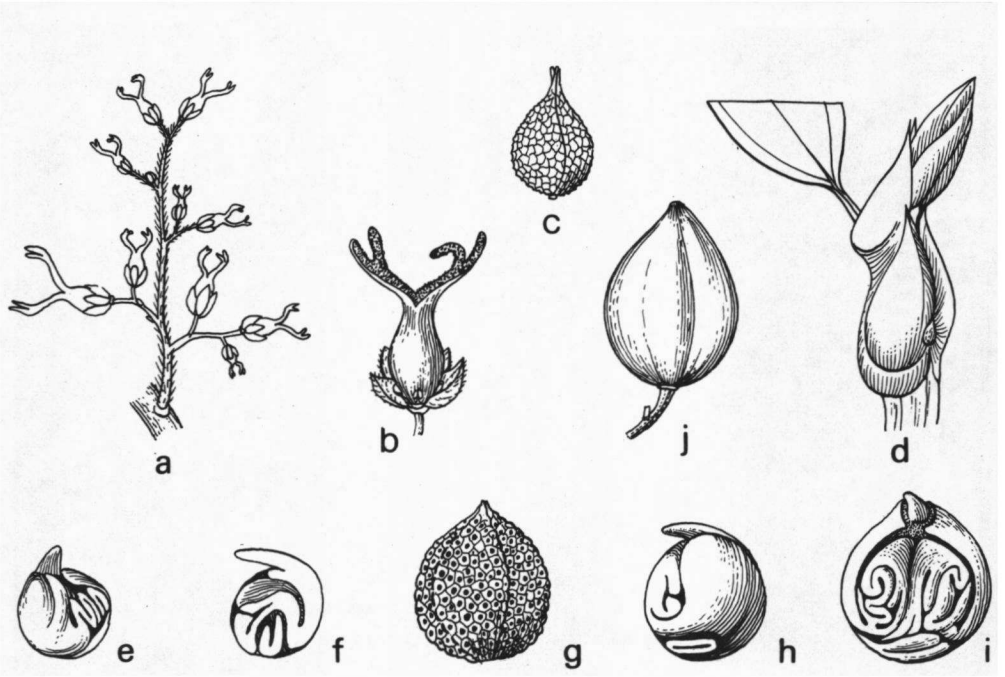

Fig. 20. *Celtis paniculata* (ENDL.) SPACH. a. ♀ Inflorescence, × 8, b. flower, × 14, c. fruit, × 1 1/3, d. shoot apex showing terminal bud above 2 pairs of overlapping stipules, × 5. — *C. rigescens* (MIQ.) PLANCH. e. Embryo, folded cotyledons, × 1 1/3. — *C. timorensis* SPAN. f. Embryo in LS, × 2. — *C. hildebrandii* SOEPADMO. g. Pitted endocarp, × 3, h–i. embryos, × 4. — *C. latifolia* (BL.) PLANCH. j. Fruit, nat. size (*a–b* KORNASSI 463, *c.* KOSTERMANS & SOEGENG 352, *d* PLEYTE 73, *e* BLOEMBERGEN 4231, *f* FORBES 1073, *g–i* CLEMENS 8375, *j* BSIP 11768).

to deeply impressed above; main nerves (2–)3(–4) pairs, ascending and arcuating, anastomosing along the margin, the lowest pair running up to 1/2–3/4 the length of the leaf; reticulations subscalariform to subareolate, distinct beneath; petiole 6–10 by 1–2 mm, shallow-sulcate, densely appressed yellowish-brown pubescent, glabrescent. *Inflorescence* ♂ or ♀ or rarely mixed, 1 1/2–5 cm long; bracts ovate, *c.* 1/2–1 by 1/2 mm. — ♂ *Inflorescence* a much-branched, multiflorous (up to *c.* 70) panicle up to 5 cm long, axes slender, flexuous, borne on the lower and leafless part of the new shoot or in the axils of lower new leaves; ♂ flower 1 1/2–2 mm ∅, subsessile; perianth lobes (4–)5, elliptic, *c.* 1–1 1/2 by 1 mm; filaments 1–1 1/2 mm long, anthers reniform, *c.* 1 by 1/2 mm; pistillode minute, surrounded by dense pale yellowish-brown hirsute hairs. In a mixed inflorescence, the few ♀ flowers are situated near the tip of the axis. — ♀ *Inflorescences* borne in the axils of leaves of the new shoot, 1–1 1/2 cm long with up to 5 flowers; ♀ flower ovoid, *c.* 2 by 1 mm; perianth lobes (4–)5, elliptic-rounded, *c.* 1 1/2 by 1 mm, stamens (4–)5; filaments *c.* 1 mm, anthers *c.* 1/2 by 1/2 mm; ovary slightly compressed, densely pale yellowish-brown appressed-hairy; stigmatic arms spreading, bifurcate at the tip. *Infructescence* up to 2–3 cm long, axes up to 2 mm thick, with (1–)2(–3) fruits. *Fruit* ellipsoid, faintly 5-angular, *c.* 15 by 10 mm, appressed-pubescent, glabrescent; exocarp 2–3 mm ∅, rather woody, occasionally lenticellate, turning deep-red when ripe, containing slimy substances when boiled. Embryo curved, cotyledons foliaceous, folded, equal. Endosperm scanty.

Distr. Solomons (common); in *Malesia:* New Guinea (incl. New Britain, common), Moluccas (Ceram, Buru, Sula, Morotai), NE. Celebes (Minahasa), E. Borneo (W. Kutei), W. Java (Bantam), Central & S. Sumatra, Anambas Is., and Malaya (Perak, Selangor, Pahang, Johore).

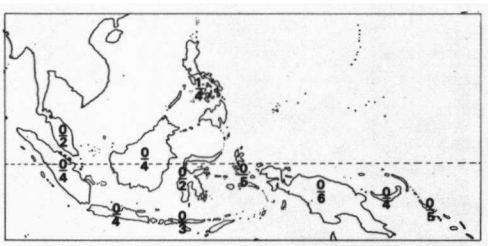

Fig. 21. Species density of *Celtis* L. in Malesia; above the hyphen endemic *spp.*, below it the non-endemic ones.

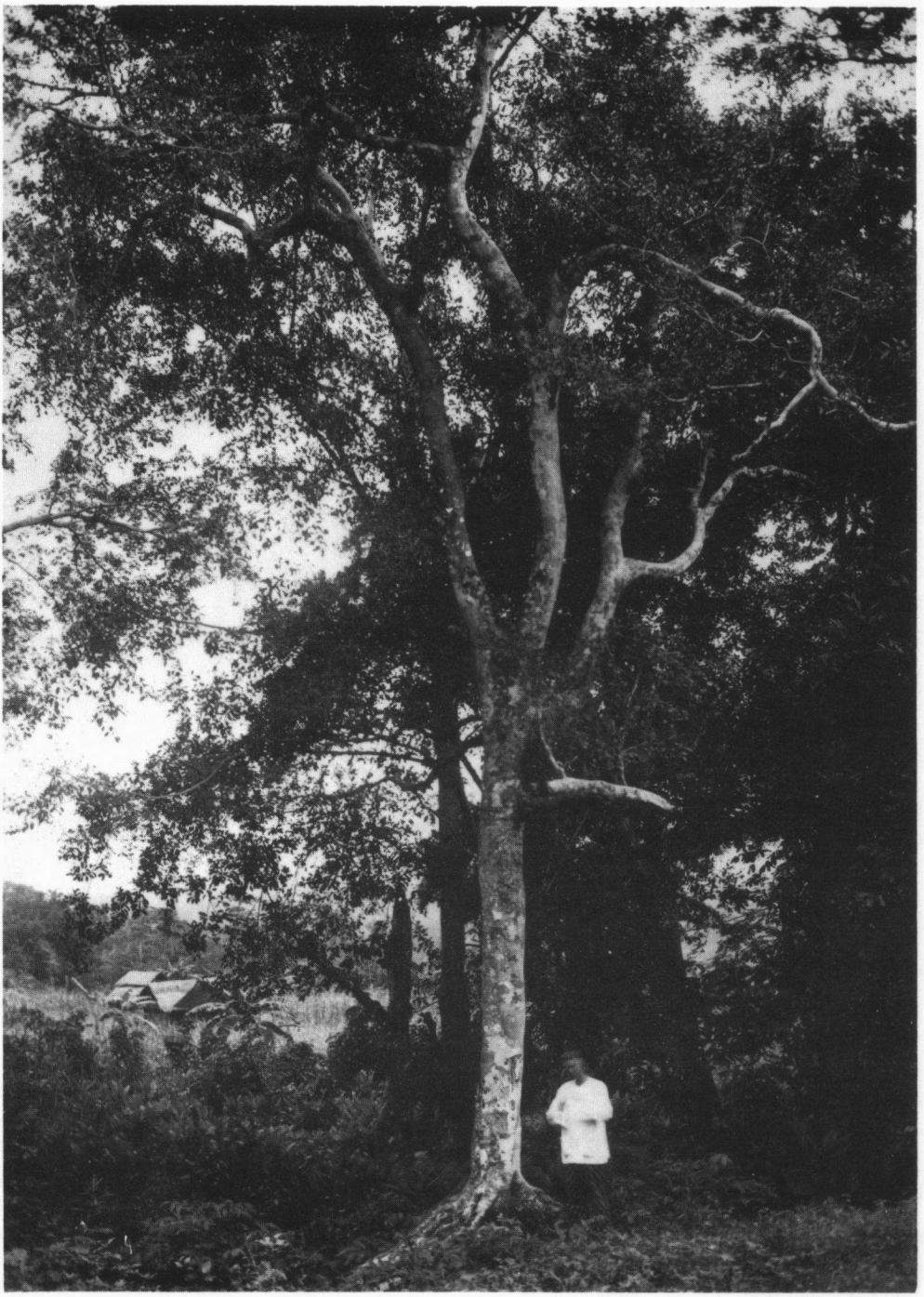

Fig. 22. *Celtis philippensis* BLANCO *var. wightii* (PLANCH.) SOEPADMO at Atasangin, Bodjonegoro (Photogr. WIND, Jan. 1925).

Ecol. In primary and secondary forest, 0–1500 m, on various types of soils including limestone. Often rather common locally (W. New Guinea and Solomons). *Fl.* (March–April) Sept., Dec., *fr.* Dec.–Aug.

Vern. Malay Peninsula: *mĕmpĕlas bulan*, Abor., *rĕmpĕlas*, M. Sumatra: *klutum*, *marsĕkan*, *rĕmpĕlas*, M. Palembang, *asin asin*, Anambas. West New Guinea: *sĕhiega*, *sĕriega*, Manikiong lang., *wennèmaram*, Berik lang., Hollandia, *bĕgèk*, Oransbari, Hattam lang., *pieh(h)*, Kebar, *bipa*, Wandammen lang., Adi I., *ainam*, Key lang., *hajanggwij*, *manji*, *sĕkika*, Manokwari, *pimar*, Sidei lang., *warĕn*, *siempai*, *wiempai*, Biak lang., *walik*, *walis*, Mooi lang.; East New Guinea: *gairama*, *watot*, Waria dial., Moresby, Madang Distr., *koru*, Bambi, *suri*, Madang, *bagibib*, Kaigorin, *aban*, *bison*, *sam*, Bilia, *baigu(p)*, Amele, *bagibip*, *kara*, *sungung*, *susuik*, Dumpu, *goga*, *mutum*, *sawan*, Faita, *tapang*, Washuk, Sepik Distr.; *ailee*, Urin, S. New Britain; *gwalafalisi*, *lausi*, Kwara lang., Solomons.

Note. Sterile specimens, especially those with young leaves only, may easily be mistaken as belonging to *Grewia* or *Microcos* (*Tiliaceae*) or to *Ziziphus angustifolius* (BL.) HATUS.

2. Celtis luzonica WARB. in Perkins, Fragm. Fl. Philip. (1905) 164; MERR. En. Philip. 2 (1923) 32. — **Fig. 23c.**

Tree up to 30 m, 90 cm ⌀. Bark smooth yellowish-grey. Innovations sparsely set with minute simple hairs, glabrescent. Terminal bud ovoid, *c.* 6–10 by 3–5 mm. Stipules ovate, thick, glabrous, peltately attached and overlapping, *c.* 5–10 by 3–5 mm. *Leaves* broad elliptic to elliptic-oblong, thick-coriaceous, glabrous, (8–)12–16(–19) by (5–)8–10 (–12) cm, index $(1^1/_4–)1^1/_2(–2)$; base rounded, symmetrical; margin entire, undulate, apex rounded with blunt and sometimes emarginate tip; midrib and nerves raised beneath, flattish to shallowly impressed above; nerves 2–3 pairs, ascending and arcuating, at least at an angle of 55° with the midrib, anastomosing and looped along the margin, the lowest pair running up to $^2/_3–^3/_4$ the length of the leaf; reticulations irregular to subscalariform, sparse, distinct beneath or obscure on both surfaces; petiole 10–20 by $1^1/_2–2(–3)$ mm, flat or shallowly sulcate. Flowers 5-merous. *Inflorescences* ♂ or ♂♀, much-branched panicles or racemose, up to 150-flowered, up to 10 cm long, axillary or subterminal, including the bracts sparsely puberulous, glabrescent; bracts ovate, minute, *c.* 1 by $^1/_2$ mm. — ♂ *Flower c.* $1^1/_2–2$ mm ⌀; perianth lobes *c.* $1^1/_2–2$ by 1 mm; filaments $1^1/_2–2$ mm, anthers subreniform, *c.* $1–1^1/_2$ by $^1/_2–1$ mm; pistillode ovoid-conical, compressed, *c.* 1 by $^1/_2$ mm. — ♀ *Flowers* ovoid-conical, borne at the distal parts of the inflorescence, $2^1/_2–3$ by $2–2^1/_2$ mm; perianth lobes *c.* $1^1/_2–2$ by $1–1^1/_2$ mm; filaments *c.* $1–1^1/_2$ mm, anthers *c.* $^3/_4$ by $^1/_2$ mm; ovary ± compressed, sparsely pubescent apically, *c.* $2–2^1/_2$ by $1–1^1/_2$ mm; stigmatic arms spreading or incurved, broadened and shallowly bifid at the tip. *Infructescence* with a stout axis 2–3 mm thick, bearing up to 10 fruits. *Fruit* globose, glabrous, 16–20 by 14–18 mm, ± terete, reddish-brown when ripe; endocarp 4-lobed and splitting at maturity; embryo curved, hypocotyle ascending, cotyledons foliaceous, equal, folded; endosperm very scanty to nearly absent.

Distr. *Malesia:* Philippines (Luzon, Surigao, Mindanao, Mindoro, Samar, Masbate).

Ecol. In thickets and forests at low altitude. *Fl. fr.* March–July.

Vern. Philippines: *malaikmo*, *malaitmo*, Tag., *daloo*, Todaya.

3. Celtis paniculata (ENDL.) PLANCH. Ann. Sc. Nat. III, 10 (1848) 305; in DC. Prod. 17 (1873) 182; BTH. Fl. Austr. 6 (1873) 156; NADEAUD, En. Pl. Tahiti (1873) 42; LAUT. Bot. Jahrb. 50 (1913) 310; KANEH. Fl. Micron. (1933) 82, f. 14; FRANCIS, Austr. Rain-forest Trees ed. 2 (1951) 67. — *Solenostigma paniculatum* ENDL. Prod. Fl. Norf. (1833) 42. — *C. pacifica* PLANCH. Ann. Sc. Nat. III, 10 (1848) 308; in DC. Prod. 17 (1873) 184. — *C. ingens* F.v.M. Fragm. 4 (1864) 88. — *C. vitiensis* A. C. SMITH, Bull. Torr. Bot. Cl. 70 (1943) 536; J. Arn. Arb. 31 (1950) 150; PARHAM, Pl. Fiji Isl. (1964) 88. — **Fig. 20a–d, 23i.**

Small to large tree, up to 36 m, 70 cm ⌀. Buttresses occasionally present, up to $1^1/_4$ m. Bark smooth to finely fissured, light- to dark-brown. Innovations sparsely appressed-puberulous, glabrescent. Older twigs glabrous, sparsely lenticellate. Stipules overlapping, embracing the twig and enclosing the bud, broad-ovate-acute, thick, *c.* 4–5 by 3–4 mm. *Leaves* elliptic to ovate-elliptic, (5–)8–11(–13) by $(2^1/_2–)3–5(–6)$ cm, index $(1^1/_2–)2(–2^1/_2)$; coriaceous, glabrous, dull grey-green when dried; base attenuate-rounded, mostly symmetrical, margin entire, often undulate, apex bluntly acute to rounded-acute; midrib and nerves only slightly raised beneath, flattish to shallowly impressed above; main nerves 3–5 pairs, ascending and arcuating at an angle of over 50° with the midrib, anastomosing and looped along the margin, the lowest pair running up to $^1/_3–^1/_2$ the length of the leaf; reticulations fine, irregular, obscure on both surfaces; petiole 6–15 by $1–1^1/_2$ mm, flat to ± sulcate. Flowers 5-merous. *Inflorescences* ♂ or ♀ or rarely mixed, axillary or subterminal, much-branched, 5–60-flowered, including the bracts sparsely appressed-puberulous; bracts ovate-acute, *c.* 2 by 1 mm. — ♂ *Inflorescences* up to 4 cm long, borne on the lower and leafless part or axillary on the lower leaf of the new shoot, paniculate, 30–60-flowered; ♂ flowers subsessile, *c.* $1–1^1/_2$ mm ⌀; perianth lobes transparent, *c.* $1–1^1/_2$ by $^1/_2$ mm; filaments *c.* 1 mm, anthers subreniform, *c.* $^3/_4–1$ by $^1/_2$ mm; pistillode minute, compressed. — *Mixed* or ♀ *inflorescences* axillary on the upper parts of the new shoot, racemose, 5–10-flowered; ♀ flower ovoid-conical, *c.* 2 by 1 mm; perianth lobes ovate-acute, *c.* $^1/_2–1$ by $^1/_2$ mm, subglabrous; staminodes rudimentary, very much shorter than the perianth; ovary ± compressed, subglabrous, *c.* $1^1/_2–2$ by 1 mm; stigmatic arms spreading, bifid at the tip. *Fruit* ovoid, faintly 4–5-angular, beaked, glabrous, 7–12 by 5–8 mm, bluish to glaucous when ripe, mostly sterile.

Distr. Australia (Queensland, Norfolk I.), Melanesia (Solomons, New Hebrides, New Caledonia), Polynesia (Fiji, Tonga, Tahiti, Cook Is., Pitcairn, Mangarawa I., Tuamotus, Marquesas), Micronesia (Marianas); in *Malesia*: Lesser Sunda Islands (Wetar), Borneo (Mt Kinabalu, very rare), Moluccas (Morotai, Ceram, Ambon, Tanimbar),

New Guinea (common in West, apparently rare in East).

Ecol. Primary and secondary forest, 0–900 m, on well drained soils including coral limestone, very often common locally (W. New Guinea and Solomons). *Fl. fr.* July–May.

Vern. New Guinea: *wiempai*, Biak, *sĕhiega*, Manikiong; Solomons: *lausiasi*, Kwara; Fiji: *marasa*, Sabalu.

4. Celtis philippensis BLANCO, Fl. Filip. (1837) 197; PLANCH. Ann. Sc. Nat. III, 10 (1848) 306; in DC. Prod. 17 (1873) 184 (*'philippinensis'*); BTH. Fl. Austr. 6 (1873) 156; VIDAL, Rev. Pl. Vasc. Filip. (1886) 248; MERR. Philip. J. Sc. 1 (1906) Suppl. 42; Sp. Blanc. (1918) 122; En. Philip. 2 (1923) 32; LEROY, Bull. I.F.A.N. 10 (1948) 212, *incl. var. consimile* (BL.) LEROY; Fl. Madag. Fam. 54 (1952) 3; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 416. — *C. wightii* PLANCH. Ann. Sc. Nat. III, 10 (1848) 307; WIGHT, Ic. Pl. (1853) t. 1969; PLANCH. in DC. Prod. 17 (1873) 184; HOOK. *f.* Fl. Br. Ind. 5 (1888) 483; BRANDIS, Ind. Trees (1906) 594; J. J. SMITH in K. & V. Bijdr. 12 (1910) 647; GAGNEP. Fl. Gén. I.-C. 5 (1927) 683; POLHILL, Kew Bull. 19 (1964) 141; BACK. & BAKH. *f.* Fl. Java 2 (1965) 11. — *C. strychnoides* PLANCH. Ann. Sc. Nat. III, 10 (1848) 306; in DC. Prod. 17 (1873) 185; WARB. Bot. Jahrb. 13 (1891) 287; LAUT. in K.Sch. & Laut. Fl. Schutzgeb. (1900) 264. — *C. mauritiana* PLANCH. Ann. Sc. Nat. III, 10 (1848) 307; in DC. Prod. 17 (1873) 184. — *Sponia strychnifolia* TEYSM. & BINN. Nat. Tijd. N. I. 4 (1853) 394; Ned. Kruidk. Arch. 3 (1855) 392. — *Solenostigma brevinerve* BL. Mus. Bot. 2 (1856) 67. — *Solenostigma laurifolium* BL. *l.c.* 68; MIQ. Fl. Ind. Bat. 1, 2 (1859) 220, *incl. var. constricta* MIQ. — *Solenostigma hasseltii* BL. Mus. Bot. 2 (1856) 68. — *Solenostigma consimile* BL. *l.c.* 68. — *Solenostigma djungiel* BL. *l.c.* 69. — *Solenostigma philippinensis* (BLANCO) MIQ. Fl. Ind. Bat. 1, 2 (1859) 220. — *Solenostigma wightii* (PLANCH.) MIQ. *l.c.* 220. — *C. brevinervis* (BL). PLANCH. in DC. Prod. 17 (1873) 183. — *C. laurifolia* (BL.) PLANCH. *l.c.* 185. — *C. hasseltii* (BL.) PLANCH. *l.c.* 185. — *C. djungiel* (BL.) PLANCH. *l.c.* 185. — *C. mindanaensis* ELMER, Leafl. Philip. Bot. 8 (1915) 2842. — *C. collinsae* CRAIB, Kew Bull. (1918) 370; RIDL. Fl. Mal. Pen. 3 (1924) 322. — *C. multifolia* ELMER, Leafl. Philip. Bot. 10 (1939) 3796, *angl.*, *inval.* — **Fig. 18a–k, 22.**

Small to large tree, up to 30 m, 80 cm ⌀. Buttresses if present up to $2^1/_2$ m tall, 2 m wide and 10 cm thick. Bark smooth to finely fissured, pale grey to grey-brown. Innovations initially sparsely to densely set with yellowish-brown appressed or/and woolly hairs, glabrescent. Stipules ovate-acute, 6–10 by 2–4 mm, thick, peltately attached, overlapping and enclosing the bud. *Leaves* thick-coriaceous, glabrous, full grey when dried, elliptic-oblong to suborbicular, (4–)8–14(–18) by (2–)3–6(–8) cm, index ($1^1/_2$–)2–3; base rounded or attenuate-rounded, mostly symmetrical; margin entire often undulate (immature leaves very rarely distantly serrulate at the upper half); apex rounded to acute; midrib and nerves raised beneath, impressed to flattish above; main nerves 1 pair, ascending, arcuating and running throughout the length of the leaf (*var. philippensis*) or 1–3 pairs, the lowest pair ascending, arcuating, and running up to about $^2/_3$ the length of the leaf and then anastomosing with the 1–2 weaker and more or less horizontal upper nerves (*var. wightii*); reticulations fine, dense, subscalariform or subareolate, usually rather distinct beneath; petiole 6–15 by 1–2 mm, sulcate. *Inflorescences* ♂ or ♂♀, much-branched panicles, many-flowered, including the bracts densely yellow-brown to rufous soft-hairy; bracts ovate-acute, *c.* 3 by 1 mm. In the ♂♀ inflorescence the ♀ flowers are borne on the distal parts of the inflorescence. — ♂ *Inflorescences* borne on the lower part of the new shoots, 2–4 cm long, with up to 40 flowers; ♂ flowers *c.* 2 mm ⌀; perianth lobes ovate-elliptic, *c.* $1^1/_2$–2 by 1 mm; filaments 1–$1^1/_2$ mm long, anthers subreniform, *c.* $^1/_2$–1 mm by $^1/_2$ mm; pistillode ovoid-cylindrical, compressed, *c.* 1–$1^1/_2$ by $^1/_2$ mm. — *Mixed inflorescence* up to 5 cm long, up to 50-flowered, borne on the upper part of the new shoots; ♀ flowers ovoid, *c.* 2–$2^1/_2$ by 2 mm; perianth lobes ovate-elliptic, *c.* 2–$2^1/_2$ by 1 mm; filaments 1–2 mm, anthers $^1/_2$–1 mm ⌀; ovary ovoid-cylindrical, *c.* 2–$2^1/_2$ by $1^1/_2$–2 mm, glabrous except at the base; stigmatic arms spreading, *c.* 1–$1^1/_2$ mm long, bilobed to bifid at the tip. *Infructescence* up to 4–5 cm long, carrying 1–3 fruits, axes 1–2 mm thick. *Fruit* ovoid, glabrous, 8–15 by 7–12 mm, beaked when young; exocarp less than 1 mm ⌀, sometimes lenticellate, turning orange to red when ripe; endocarp ± smooth; embryo curved, hypocotyle ascending, cotyledons broad, foliaceous, unequal in thickness, not folded; endosperm oily, scanty to absent.

Distr. Tropical Africa to Madagascar, Indian Ocean (Réunion, Mauritius, *etc.*), India, Burma, ? SE. China, Hongkong, Taiwan, Indo-China, Thailand, throughout Malesia to NE. Australia and the Solomons.

Taxon. A rather variable, widely spread species with two rather but not completely distinct varieties. These are:

a. *var.* philippensis, characterized by larger leaves of (7–)9–12(–18) by 4–8 cm with one pair of nerves usually running more or less throughout the length of the leaf, subscalariform reticulation, and larger fruit of 10–15 by 8–12 mm;

b. *var.* wightii (PLANCH.) SOEPADMO, *comb. nov.* (basionym: *C. wightii* PLANCH. *l.c. supra*). Fig. 22. Characterized by smaller leaves, (4–)5–7(–9) by (2–)3–4(–$5^1/_2$) cm with 1–3 pairs of nerves and the lowest pair mostly running up to $^2/_3$ the length of the leaf, and slightly smaller fruit, 8–12 by 6–10 mm.

It should be noted, that the distinguishing characters mentioned above should be applied in combination; if taken individually they may not be clearly well defined. For example, there are several specimens (*e.g.* GARDNER *s.n.*, THWAITES CP 50 from Ceylon; KING *s.n.* and BROWNE *s.n.* from India; PARKINSON 214 from the Andamans; UNESCO 214 from Malaya; JACOBS 4709, 4711, and KOSTERMANS 23061 from Java; KOSTERMANS & WIRAWAN 61 from the Lesser Sunda Is.; NGF 19100 & 30787 from New Guinea; MERRILL Sp. Blanc. 52 from the Philippines, *etc.*) which have both types of venation. As for the fruit, the smaller size in *var. wightii* may be due in part to the fact that they are not fully ripe, as the majority of them are empty (without embryo). Furthermore, it was also noticed that most specimens of *var. wightii*

have been collected from localities under a strong seasonal climate or from trees growing on well-drained and poor soils (rocky or sandy beach, limestone hills, *etc.*).

Ecol. Understorey tree in primary and secondary forests, on various types of soils, at low altitudes (0–650 m); often gregarious and very common locally. *Fl. fr.* mostly July–April,. The fruits which turn to orange or red when ripe may be dispersed by birds, but in the case of *var. wightii*, which mostly grows in the very coastal forest, they may be dispersed by sea-water as well; (the endocarp is woody, hard, and persistent).

Uses. Though not durable, the wood is locally used for house-building.

Vern. Java: *ki-ĕndog*, *ki-howè*, S, W. Java, *kĕraja*, *pusutan*, *sĕntok*, *sĕpat*, *sĕprèh*, *tjĕngkèk*, *wuluh*, J, Central & E. Java; N. Borneo: *nyelepi*; Philippines: *malaitmo*, *narabagsay*, Tag.; Celebes: *kao lulu*, Malili; Moluccas: *horo*, Morotai; Lesser Sunda Is.: *menulang*, Sumba, *nemu*, Flores; New Guinea: *pièh*, Kebar, *marmar*, Tor, Berik, *sehiega*, Manikiong, *bĕpiejĕt*, Hattam, *warĕn*, Biak, *ikai*, *ikoi*, Kemtuk, *mĕlawar*, Mooi, *etc.*

5. Celtis latifolia (BL.) PLANCH. in DC. Prod. 17 (1873) 186; WARB. Bot. Jahrb. 13 (1891) 287; LAUT. in K. Sch. & Laut. Fl. Schutzgeb. (1900) 264; Bot. Jahrb. 50 (1913) 311. — *Solenostigma latifolium* BL. Mus. Bot. 2 (1856) 67; MIQ. Fl. Ind. Bat. 1, 2 (1859) 219. — *Solenostigma zippelii* BL. Mus. Bot. 2 (1856) 67. — *C. zippelii* (BL.) PLANCH. in DC. Prod. 17 (1873) 186. — *C. kajewskii* MERR. & PERRY, J. Arn. Arb. 22 (1941) 254. — **Fig. 20j, 23k.**

Tree up to 35 m, 80 cm ⌀. Buttresses plank-like, up to 2 m tall, $2^1/_2$ m out and 6 cm ⌀. Bark smooth to finely fissured, pustulate-lenticellate, light-brown to grey-brown. Innovations densely yellowish-brown hairy, glabrescent. Young twigs blackish when dry, older ones greyish, glabrous and sparsely lenticellate. Terminal buds ovoid-conical, acute, 10–15 by 4–5 mm. Stipules peltately attached, overlapping, thick, ovate-acute, *c.* 10 by 5 mm. *Leaves* thick-coriaceous, glabrous or sparsely pubescent beneath, especially on midrib and nerves, broadly ovate to elliptic-orbicular, (8–)15–18(–25) by (6–)8–12(–18) cm, index $1^1/_2$–$2^1/_2$; base rounded to subcordate, symmetrical to ± asymmetrical; margin entire, undulate, often recurved; apex bluntly rounded or acute to acuminate; midrib and nerves strongly raised beneath, impressed above; nerves 1–2 pairs, ascending and arcuating, the lowest pair running through $^3/_4$ of the length of the leaf; reticulations coarse, wide-spaced, subscalariform, distinct beneath; petiole 10–20 by 2–3 mm, glabrous, shallowly sulcate. Flowers 5-merous. *Inflorescence* ♂ or ♂♀, axillary or borne on the lower part of the new shoot, 10–30-flowered, including the bracts densely yellowish-brown appressed-hairy; bracts ovate, *c.* 2 by 1 mm. — ♂ *Inflorescence* (not fully developed) up to 2 cm long, 15–30-flowered, paniculate; ♂ flowers *c.* $1^1/_2$–2 mm ⌀; perianth lobes *c.* $1^1/_2$–2 by 1 mm; filaments *c.* 1 mm, anthers *c.* $^1/_2$–1 by $^1/_2$ mm; pistillode compressed ovoid, *c.* 1 by $^1/_2$ mm. — ♂♀ *Inflorescence* racemose, 5–10-flowered, slender, up to 7 cm long, few-branched; ♀ flower ovoid-ellipsoid, borne on the distal part of the inflorescence, *c.* 2–3 by 2 mm; perianth lobes ovate-lanceolate, *c.* 2–$2^1/_2$ by 1 mm, at anthesis recurved; filaments up to $1^1/_2$ mm, anthers *c.* $^1/_2$–$^3/_4$ by $^1/_2$ mm; ovary ovoid-cylindrical, *c.* 2–3 by 1–$1^1/_2$ mm, initially densely appressed-hairy, glabrescent except for the basal part; stigmatic arms spreading, shallowly bilobed at the tip. *Infructescence* up to 5 cm long, carrying 1–5 fruits, axes sturdy *c.* 2–3 mm thick. *Fruit* ovoid, faintly 4–5-angular, glabrous, $1^1/_2$–$2^1/_2$ by 1–$1^3/_4$ cm, exocarp occasionally lenticellate, up to 2 mm ⌀, turning to orange or deep-red when mature. Embryo curved, cotyledons fleshy, unequal in thickness, hypocotyle ascending; endosperm absent.

Distr. Solomons (very common); in *Malesia:* Philippines (Palawan), Moluccas (Morotai, Tidore), and New Guinea (in West very common in the vicinity of Manokwari and Hollandia; in East in Sepik and Morobe Districts; New Britain).

Ecol. Primary and secondary forests on sandy clay soils, 0–400 m. *Fl. fr.* mostly Jan.–Aug.

Vern. Moluccas: *tohu*, Morotai; New Guinea: *sehiega*, Manikiong, *marmar*, Berik, *bepiet*, Hattam; Solomons: *lae-lae*, Kwara.

6. Celtis hildebrandii SOEPADMO, *sp. nov.* — **Fig. 20g–i, 23l.**

Species valde affinis C. philippensi var. philippensi et C. latifoliae, sed ab eis differt folio asymmetrico, inflorescentia ♂ valde ramosa multiflora, et cotyledonibus multiplicatis. T: BW 7936.

Arbor magna usque ad 45 m alta et 1 m diam. Folia tenuiter coriacea, oblique ovato-elliptica, (5–)8–11(–14) × (3–)4–6(–8) cm, ind. 1,5–2, glabra, nervis lateralibus uniparibus usque ad $^4/_5$ partem laminae longitudinis ascendentibus, reticulatione laxa subscalariformi; petiolus applanatus vel ± sulcatus, 8–15 × 1–1,5 mm. Inflorescentiae ♂ et ♀; ♂ multiramosae, 60–150-florae; ♀ 5–10-florae. Fructus ovoideo-globosus, ± 4– vel 5–angulatus, 10–12 × 8–10 mm; endospermium nullum; cotyledones multiplicati; embryo curvatus.

Large tree up to 45 m, 100 cm ⌀. Buttresses up to $2^3/_4$ m tall, 2 m out and 10 cm ⌀. Bark smooth to finely fissured, often pustullate, light-brown to grey-brown. Innovations densely rufous to yellowish-brown appressed-hairy, glabrescent. Terminal buds ovoid-conical, acute, *c.* 4–6 by 3 mm. Stipules ovate-acute, peltately attached and overlapping, thick, *c.* 5 by 3 mm. *Leaves* thin-coriaceous, obliquely ovate-elliptic, (5–)8–11(–14) by (3–)4–6(–8) cm, index $1^1/_2$–2; glabrous; often discolorous, upper surface dull grey-green, lower surface dull chocolate- or grey-brown; base attenuate-rounded, mostly asymmetrical; margin entire, often undulate; apex acute to acuminate; midrib and main lateral nerves raised beneath, impressed or flattish above; nerves one pair, ascending and arcuating, running up to $^4/_5$ or the entire length of the leaf; reticulations lax, subscalariform, rather distinct beneath; petiole glabrous, 8–15 by 1–$1^1/_2$ mm, flat, ± sulcate. *Inflorescence* ♂ or ♂♀, axillary or subterminal on new shoots, much-branched, many-flowered, including the bracts rather densely yellowish-brown to rufous appressed-hairy, glabrescent; bracts ovate-acute, *c.* 2–3 by 1–$1^1/_2$ mm. Flowers 5-merous. — ♂ *Inflorescences* much-branched panicle, 60–150-flowered; ♂ flower *c.* 2 mm ⌀; perianth lobes *c.* $1^1/_2$–2 by 1 mm; filaments 1–$1^1/_2$

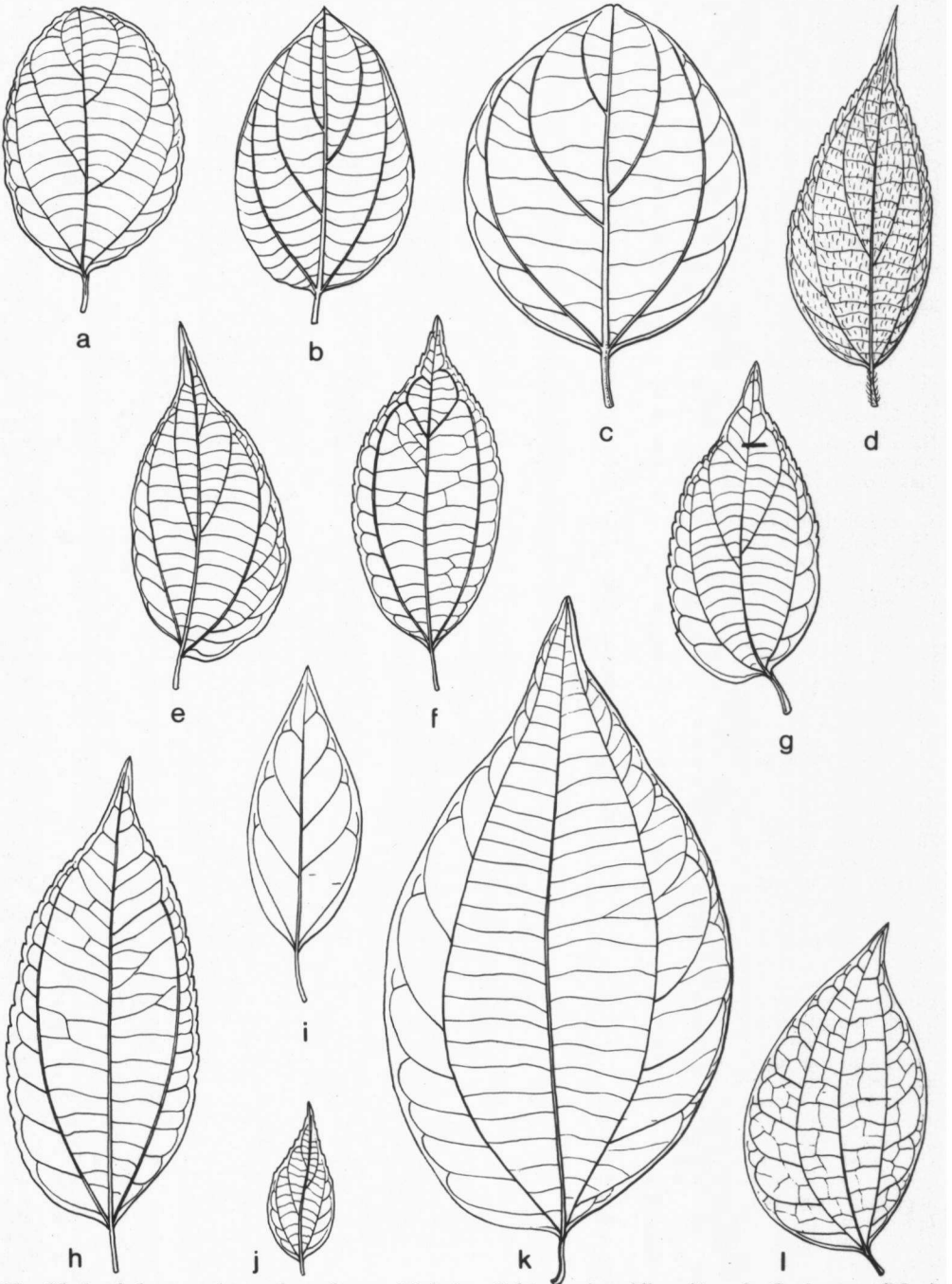

Fig. 23. Leaf shape and venation of some Malesian *Celtis* species. All × ½. a–b. *C. rigescens* (MIQ.) PLANCH. — c. *C. luzonica* WARB. — d–e. *C. tetrandra* ROXB. — f–h. *C. timorensis* SPAN. — i. *C. paniculata* (ENDL.) PLANCH. — j. *C. rubrovenia* ELMER. — k. *C. latifolia* (BL.) PLANCH. — l. *C. hildebrandii* SOEPADMO (*a–b* bb T.1012, *c* BS 1633, *d* KOORDERS 8771, *e* KOORDERS 26516, *f* KOORDERS 38755, *g* JUNGHUHN *s.n.*, *h* BLUME *s.n.*, *i* bb 33845, *j* BRASS & VERSTEEGH 11168, *k* LAM 3635, *l* BRASS 28860).

mm, anthers subreniform, *c.* 3/4–1 by 1/2 mm; pistillode ovoid-cylindrical, compressed, *c.* 3/4 by 1/2 mm. — ☿ *Inflorescence* a much-branched raceme, up to 4–5 cm long, 5–10-flowered; ☿ flower ellipsoid, *c.* 3 by 2 mm; perianth lobes ovate-acute, *c.* 2–3 by 1 mm; filaments 1–1 1/2 mm, anthers *c.* 1/2 by 1/2 mm; ovary ovoid-ellipsoid, *c.* 2 by 1 mm, slightly compressed, initially densely hairy, glabrescent; stigmatic arms initially curved, later spreading, *c.* 1–1 1/2 mm long, broadened and shallowly bilobed at the tip. *Infructescence* 3–5 cm long, axes glabrous, *c.* 1–2 mm ∅, bearing 2–5 fruits. *Fruit* ovoid-globose, glabrous, ± 4–5-angular, slightly beaked, 10–12 by 8–10 mm; exocarp thin, endocarp pitted; embryo curved, hypocotyle ascending, cotyledons broad, foliaceous, folded; endosperm absent.

Distr. Solomons (common); in *Malesia:* Moluccas (Buru, rare), New Guinea (W. & E. parts, common; New Britain).

Ecol. In both primary and secondary forests at 0–1000 m; often very common and gregarious locally; on various types of soil. Male flowers appear with new shoots around Nov.–Dec., and ☿ ones around Jan.–Feb.; fruits mature by May–June. The ripe fruits, which turn deep purple or bluish black, may be dispersed by birds.

Vern. New Guinea: *běhěg*, Hattam, *walik*, Mooi, *sehiega*, Manikiong, *pièh*, Kebar, *biempai*, Biak; Solomons: *laussi*, *lai-lai*, Kwara.

7. Celtis timorensis SPAN. Linnaea 15 (1841) 343; PLANCH. Ann. Sc. Nat. III, 10 (1848) 315; BL. Mus. Bot. 2 (1856) 71; MIQ. Fl. Ind. Bat. 1, 2 (1859) 22; PLANCH. in DC. Prod. 17 (1873) 180. — *C. cinnamomea* LINDL. *ex* PLANCH. Ann. Sc. Nat. III, 10 (1848) 303; BL. Mus. Bot. 2 (1856) 72; PLANCH. in DC. Prod. 17 (1873) 181; KURZ, For. Fl. Burma 2 (1877) 472; HOOK. *f.* Fl. Br. Ind. 5 (1888) 482; PRAIN, Beng. Pl. 2 (1903) 719; BRANDIS, Ind. Trees (1906) 596; J. J. SMITH in K. & V. Bijdr. 12 (1910) 644; MERR. En. Philip. 2 (1923) 32; GAGNEP. Fl. Gén. I.-C. 5 (1927) 682; BACK. & BAKH. *f.* Fl. Java 2 (1965) 11. — *C. reticulosa* MIQ. Pl. Jungh. (1851) 69; Fl. Ind. Bat. 1, 2 (1859) 222. — *C. hamata* BL. Mus. Bot. 2 (1856) 72; PLANCH. in DC. Prod. 17 (1873) 180. — *C. waitzii* BL. Mus. Bot. 2 (1856) 71; MIQ. Fl. Ind. Bat. 1, 2 (1859) 221; PLANCH. in DC. Prod. 17 (1873) 180. — *C. dysodoxylon* THW. En. Pl. Zeyl. (1861) 267. — *C. crenato-serrata* MERR. Philip. J. Sc. 5 (1910) Bot. 174. — **Fig. 20f, 23f–h.**

Medium-sized tree up to 20 m, 30 cm ∅. Bark smooth, grey. Innovations densely rufous-hairy. Branchlets glabrous, rather densely lenticellate. Terminal buds ovoid-conical, *c.* 3–4 by 2 mm. Stipules linear-lanceolate, 5–10 by 1–2 mm. *Leaves* thin-coriaceous, ovate-elliptic to elliptic-oblong, (6–)10–12(–17) by (2 1/2–)4–5(–8) cm, index 1 1/2–2 1/2; except for the midrib and nerves glabrous, discolorous, upper surface dull grey to blackish, lower surface chocolate-brown; base rounded to subcordate, mostly asymmetrical, margin undulate, distantly serrulate to crenate at least for the upper half; apex acute to acuminate; midrib and nerves flattish to impressed above, raised beneath; nerves 1–2(–3) pairs, arcuating and ascending, the lowest pair running to (1/2–)2/3(–4/5) the length of the leaf, anastomosing along the margin; reticulations subscalariform, sparse, rather distinct beneath; petiole 5–15 by 1–2 mm, sulcate. Flowers 5-merous. *Inflorescence* ♂ or ♂☿, racemose, lax, axes slender, always longer than the petiole, including the bracts sparsely rufous-hairy; bracts narrow ovate-acute, *c.* 3–5 by 1–2 mm. — ♂ *Inflorescences* borne on the lower and leafless parts of the new shoots, much-branched, 10–20-flowered, up to 3 cm long; ♂ flower *c.* 2 mm ∅; perianth lobes *c.* 1 1/2–2 by 1 mm; filaments 1–1 1/2 mm, anthers reniform, *c.* 1 by 1/2 mm; pistillode present but strongly reduced in size. — ☿ *Inflorescences* borne in the axils of new leaves, 4–7-flowered, up to 2–3 cm long; ☿ flower *c.* 2–3 mm ∅; perianth lobes *c.* 1 1/2–2 by 1 mm; filaments *c.* 1/2–1 mm, anthers subreniform, *c.* 1/2–3/4 by 1/2 mm; ovary ovoid-ellipsoid, *c.* 2 by 1 mm; stigmatic arms *c.* 1–1 1/2 mm, spreading. *Infructescence* up to 4–5 cm long. *Fruit* ovoid, terete or 4-angular, beaked, 5–10 by 3–6 mm, glabrous. Embryo curved, hypocotyle ascending; cotyledons broad, folded, equal; endosperm scanty.

Distr. Ceylon, India, Bangladesh, Burma, Thailand, Indo-China; in *Malesia:* Central Sumatra (rare), Java (common; incl. Christmas I.), Lesser Sunda Islands (Flores, Timor), N. Borneo (Mt Kinabalu), Philippines (Luzon).

Ecol. Outside Malesia the species grows in evergreen forests or along streams in deciduous forests. In Malesia it is more common in areas with a rather prominent seasonal climate, 0–1500 m. *Fl. fr.* Nov.–April.

Vern. Central Sumatra: *ki tondok*, *si tjakik*; Java: *jeungil*, *ki tamiang*, S, *tjèngkèk*, *tjitik*, J; Philippines: *takulao*, Ibn., *malabutulan*, Tag.

8. Celtis rubrovenia ELMER, Leafl. Philip. Bot. 2 (1908) 464: MERR. En. Philip. 2 (1923) 33. — *C. similis* MERR. & PERRY, J. Arn. Arb. 22 (1941) 253. — **Fig. 23j.**

Deciduous tree up to 30 m, 60 cm ∅. Bark grey-brown, smooth. Innovations densely rufous appressed-hairy, glabrescent. Older branchlets glabrous, sparsely lenticellate. Buds ovoid-conical, *c.* 3 by 2 mm, bracts ovate, imbricate, *c.* 1 by 1/2 mm. Stipules subulate, *c.* 3–4 by 1 mm. *Leaves* (fully developed ones) thick-coriaceous, rigid, brittle, ovate to ovate-elliptic, (3–)4–5(–6 1/2) by (1 1/4–)1 1/2–2 1/2(–3 1/2) cm, index 2–3.3; sparsely appressed-hairy especially on the midrib and nerves, glabrescent; base attenuate-rounded to rounded, symmetrical to asymmetrical; margin of young leaves serrate to crenate at least at the upper half, that of old leaves entire or distantly serrate in the upper half only; apex acute, acuminate to caudate, tip usually very sharp; midrib and nerves strongly raised beneath (reddish in fresh specimens), impressed above; nerves (1–)2(–3) pairs, arcuating, ascending, at a narrow angle with the midrib less than 45°, lowest pair running to *c.* 2/3 the length of the leaf; reticulations fine, subareolate, obscure on both surfaces; petiole (3–)4–6(–8) by 1 mm, deeply sulcate. Flowers 4-merous. *Inflorescences* ♂ or ♂☿, racemose, 1–2 cm long, 4–7-flowered. — ♂ *Inflorescence* borne on the lower and leafless parts of the new shoot, 5–7-flowered; ♂ flower *c.* 2 mm ∅; perianth lobes *c.* 1 1/2 by 1 mm, ciliate; filaments 1–1 1/2 mm long, anthers reniform, *c.* 1 by 3/4 mm; pistillode minute. — *Mixed* (♂☿) *inflorescences* 4–5-flowered, borne in the axil of

new leaves; ♀ flower borne on the upper part of the inflorescence, *c.* 2–2½ mm ∅; perianth lobes *c.* 1½–2 by 1 mm, ciliate; stamens slightly smaller in size than those of the ♂ flower; ovary ovoid, 1½–2 by 1 mm, densely hirsute; stigmatic arms spreading, 1½–2 mm long. *Infructescences* up to 1½ cm long, carrying (1–)2(–3) fruits. *Fruit* globose, *c.* 3 by 3 mm, glabrous, ± 4-angular. Endosperm scanty, oily, transparent. Embryo curved, hypocotyle ascending; cotyledons equal, foliaceous, folded.

Distr. *Malesia:* Philippines (Luzon), New Guinea (Kebar Valley, Baliem R.; Morobe Distr.).

Ecol. In primary forests on hills, ridges between 500–1800 m. In New Guinea sometimes rather common locally. *Fl. fr.* Sept.–March.

Vern. Philippines: *palek*; W. New Guinea: *dotjoni, nitjoni*, Kebar.

9. Celtis tetrandra ROXB. Fl. Ind. ed. Carey 2 (1832) 63; PLANCH. Ann. Sc. Nat. III, 10 (1848) 300; in DC. Prod. 17 (1873) 179; KURZ, For. Fl. Burma 2 (1877) 472; GAMBLE, Man. Ind. Timb. ed. 1 (1881) 344; HOOK. *f.* Fl. Br. Ind. 5 (1888) 482, *incl. var. hamiltonii* HOOK. *f. et var. mollis* (PLANCH.) HOOK. *f.*; PRAIN, Beng. Pl. 2 (1903) 719; BRANDIS, Ind. Trees (1906) 596; J. J. SMITH in K. & V. Bijdr. 12 (1910) 641; GAGNEP. Fl. Gén. I.-C. 5 (1927) 681; BACK. & BAKH. *f.* Fl. Java 2 (1965) 11. — *C. trinervia* ROXB. Fl. Ind. ed. Carey 2 (1832) 65, *non* LAMK, 1797. — *C. acata* HAMILT. Trans. Linn. Soc. 17 (1834) 211; PLANCH. Ann. Sc. Nat. III, 10 (1848) 299. — *Sponia tetrandra* (ROXB.) VOIGT, Hort. Suburb. Calc. (1845) 294. — *C. napalensis* PLANCH. Ann. Sc. Nat. III, 10 (1848) 298. — *C. glabra* PLANCH. *l.c.* 298. — *C. roxburghii* PLANCH. *l.c.* 302. — *C. hamiltonii* PLANCH. *l.c.* 301; in DC. Prod. 17 (1873) 179. — *C. mollis* PLANCH. Ann. Sc. Nat. III, 10 (1848) 297, *p.p., quoad specim. ex Wallich 7203*; in DC. Prod. 17 (1873) 179. — *C. serotina* PLANCH. Ann. Sc. Nat. III, 10 (1848) 301; WIGHT, Ic. 4, 4 (1850) t. 1570. — **Fig. 18i–o, 23d–e.**

Semi-deciduous tree up to 40 m and 100 cm ∅. Bark smooth to rough, grey-brown. Innovations densely rufous-hairy, glabrescent. Terminal bud ovoid-globose, 2–3 mm ∅. Stipules linear, *c.* 5 by 1 mm. *Leaves* coriaceous, oblique ovate-elliptic, (4–)6–10(–13) by (1½–)2½–3½(–5) cm, index 2–3, broadest at or below the middle; slightly discolorous, above glabrous, dull grey in drying, beneath glabrous or sparsely rufous-pubescent especially on midrib and nerves, yellow grey-green in drying; base rounded-attenuate, strongly asymmetrical; margin denticulate or distinctly serrate at the upper half, or subentire; apex acute, acuminate, to caudate; midrib and nerves flat to impressed above, raised beneath; nerves 3–4 pairs, ascending and arcuating, anastomosing near the margin, the lowest pair running to *c.* ⅓–⅔ the length of the leaf; reticulations fine, subscalariform, rather distinct beneath; petiole 5–12 by 1–2 mm; slightly sulcate. *Inflorescence* ♂ or ♀, cymoid, including the bracts densely rufous-hairy. — ♂ *Inflorescence* borne on the lower and leafless part of the new shoot, 2–5-flowered, occasionally several of them are clustered together on leafless short lateral new shoots giving rise to a raceme of cymes; ♂ flower *c.* 2–3 mm ∅; perianth lobes 4(–5), *c.* 1½–2 by 1 mm, ciliate; filaments ½–1 mm, anthers reniform, *c.* 1 by ½ mm, sparsely sericeous; pistillode very much reduced. — ♀ *Inflorescences* 2–5-flowered, axes slender, in the axils of new leaves; ♀ flower *c.* 2 mm ∅; perianth lobes ciliate, *c.* 2 by 1 mm; stamens as in the ♂ flower; ovary ovoid, *c.* 2 by 1 mm, sparsely minute pubescent; stigmatic arms *c.* 2 mm long, ½ mm broad, spreading. *Fruit* ± globose, 5–8 mm ∅, glabrous, turning deep-red or black when ripe. Endosperm scanty.

Distr. India, Bangladesh, Burma, Thailand, Indo-China; in *Malesia:* N. Sumatra (Gajo and Karo Lands) Java (West: G. Galunggung; Central: G. Muria; East: Bodjonegoro, Mts Kawi & Idjen, Besuki, *etc.*), Lesser Sunda Islands (Bali, Sumbawa, Flores).

Ecol. In primary and secondary forests, 0–2000 m. In Burma and Thailand very often in evergreen or semi-deciduous forest along river-banks. In Malesia the preference seems to be largely to areas subject to a seasonal climate. *Fl. fr.* Aug.–April.

Vern. Sumatra: *ndokum, sigar*, Karo, *bitatar*, Toba, *tĕmung*, M; W. Java: *ki djeungkil, ki tamiang*, S, *tĕritih, tritih*, J; Lesser Sunda Is.: *pusu*, Sumbawa, *namut*, Flores.

Excluded

Celtis grewioides WARB. Bot. Jahrb. 13 (1891) 287 = *Ziziphus angustifolius* (MIQ.) HATUS. Nova Guinea Bot. *n.* 3 (1960) 13.

Solenostigma angustifolium MIQ. Sumatra (1861) 412. — *C. angustifolia* (MIQ.) PLANCH. in DC. Prod. 17 (1873) 186, *non* LINDL. *ex* WALL. Cat. (1831) *n.* 3691, *nomen* = *Ziziphus angustifolius* (MIQ.) HATUS. Nova Guinea Bot. *n.* 3 (1960) 13.

5. APHANANTHE, *nom. gen. cons.*

PLANCH. Ann. Sc. Nat. III, 10 (1848) 265, *non* LINK, 1821; MIQ. Fl. Ind. Bat. 1, 2 (1859) 218; PLANCH. in DC. Prod. 17 (1873) 207; HOOK. *f.* in B. & H. Gen. Pl. 3 (1880) 355; ENGL. in E. & P. Nat. Pfl. Fam. 3, 1 (1888) 66; BERNARD, Bull. Herb. Boiss. II, 6 (1906) 34; GAGNEP. Fl. Gén. I.–C. 5 (1927) 690; LEROY, Bull. Mus. Hist. Nat. Paris II, 18 (1946) 118, 180; Fl. Madag. Fam. 54 (1952) 12; J. Agr. Trop. Bot. Appl. 8 (1961) 72; LI, Woody Fl. Taiwan (1963) 105; HUTCH. Gen. Fl.

Pl. 2 (1967) 149. — *Homoioceltis* BL. Mus. Bot. 2 (1856) 64. — *Galumpita* BL. *l.c.* 73; MIQ. Fl. Ind. Bat. 1, 2 (1859) 223. — *Gironniera subg. Galumpita* HOOK. *f.* in B. & H. Gen. Pl. 3 (1880) 356; ENGL. in E. & P. Nat. Pfl. Fam. 3, 1 (1888) 66. — *Mirandaceltis* A. J. SHARP, Bol. Soc. Bot. Mex. 23 (1958) 38, f. 1–4. — **Fig. 24.**

Monoecious, deciduous or semideciduous shrubs or trees, often buttressed. *Innovations* densely or sparsely, whitish-grey to rufous, appressed-pubescent. Indumentum consisting of bulbous-based, unicellular, finely tuberculate hairs and multicellular, glandular hairs. Older branches glabrous, lenticellate, bearing lateral and terminal buds. Stipules lateral, extrapetiolar, subulate, caducous. *Leaves* alternate, petioled, glabrous, coriaceous, triplinerved at base or pinnately nerved. *Inflorescences* ♂, ♀, or very rarely ♂♀, axillary; bracts minute, caducous. — ♂ *Inflorescences* a condensed, multi-flowered raceme, borne on the lower parts of the new shoots; ♂ flowers short-stalked, globular, 4–5-merous; perianth lobes membranous, imbricate in bud, sparsely appressed pubescent outside; stamens glabrous, filaments subulate, inflexed in bud, anthers ovoid-subreniform, non-apiculate, introrse; pistillode absent, replaced by a cluster of whitish to silvery, erect, soft, simple hairs. — ♀ *Flowers* solitary in the axil of the upper leaves of the new shoot, or borne in a 2–3-flowered mixed (♂♀) racemose inflorescence; long-stalked; perianth lobes 4–5, long-persistent; staminode absent; ovary sessile, ovoid-ellipsoid, terete to angular; stigmatic arms tubular; ovule anatropous. *Drupe* fleshy, ovoid-globose, faintly 3–5-angular or ± terete, glabrous; endocarp hard and persistent. *Seed* exalbuminous, coat membranous, few cells thick; embryo curved, hypocotyle ascending, cotyledons more or less equal, involute. Mode of germination unknown.

Distr. About 4–5 *spp.* Mexico, Madagascar, Ceylon, India, Burma, China (also Hainan), Korea, Japan, Taiwan, Hongkong, Indo-China, Thailand, Andamans, through Malesia to Australia (Queensland and New South Wales) and Solomons. Throughout *Malesia* (except Malaya and Moluccas): 2 *spp.* Fig. 25.

Ecol. In Malesia mainly found in areas subject to a rather strong seasonal climate, on various types of soil in the coastal lowlands, hills, and gallery forests, 0–750 m, locally often abundant and forming dense thickets.

In the north temperate and subtropical regions the species flower in April–May and drupes ripen in July–August. Tropical species produce flowers twice a year, *viz* around March–April and Sept.–Oct. and fruit ripens in June–July or Nov.–Dec.

The deciduous or semideciduous habit, flush-wise mode of growth, structure, size, colour of the inflorescence and flowers suggest that pollination is affected by wind. The drupes which turn to a deep red colour when ripe are possibly dispersed by frugivorous birds.

KEY TO THE SPECIES

1. Leaves ovate, elliptic or obovate, (2–)4–6(–10) by (1–)2–3(–4) cm, triplinerved at base, margin variously serrate or dentate, very rarely subentire; nerves (3–)4–5(–6) pairs, at a 30–45° angle with the midrib. Mature fruit 6–10 by 4–7 mm, beak 1–3 mm . . . . . **1. A. philippinensis**
1. Leaves ovate-elliptic or elliptic-oblong, (5–)10–14(–20) by (2–)3–6 (–8) cm, pinnately nerved, margin entire or very rarely distantly, minute serrulate at the upper half; nerves (5–)7–8(–10) pairs, at an angle of more than 60° with the midrib. Mature fruit 15–20 by 8–12 mm, beak up to 5 mm. . **2. A. cuspidata**

1. Aphananthe philippinensis PLANCH. Ann. Sc. Nat. III, 10 (1848) 337; MIQ. Fl. Ind. Bat. 1, 2 (1859) 219; PLANCH. in DC. Prod. 17 (1873) 208; BTH. Fl. Austr. 6 (1873) 160; HOOK. *f.* Icon. III, 2 (1876) 65, t. 1741; MERR. En. Philip. 2 (1923) 34; FRANCIS, Austr. Rain-forest Trees ed. 2 (1951) f. 24 & 25. — *Taxotrophis rectinervia* F.v.M. Fragm. 6 (1863) 192. — *A. rectinervia* (F.v.M.) PLANCH. in DC. Prod. 17 (1873) 208. — **Fig. 24j–n.**

Shrub to medium-sized tree up to 28 m, 40 cm ⌀. Trunk often fluted, low-buttressed, occasionally producing suckers. Bark smooth to finely fissured, peeling off into rectangular flakes, lenticellate. Young parts densely or sparsely greyish-brown or rufous, short, simple pubescent. Stipules subulate, 2–3 by 1/4 mm. *Leaves* glabrous, thin- to thick-coriaceous, ovate, elliptic, or obovate, (2–)3–6(–10) by (1–)2–3(–4) cm, index 2–2.6; base attenuate

Fig. 24. *Aphananthe cuspidata* (BL.) PLANCH. a. Habit, nat. size, b. LS of mature fruit, × 1 1/3, c. basal view of fruit, nat. size, d. flowering young shoot, nat. size, e. ♂ flower before anthesis, × 6, f. *ditto* in section, × 9, g. ♂ flower at anthesis, × 13, h. ♀ flower, × 8, i. *ditto* in section, × 16. — *A. philippinensis* PLANCH. j. mature fruit, × 2, k. *ditto*, basal view, × 1 2/3, l–n. variation of leaf-form, × 2/3 (*a–c* KOORDERS 21330, *d–i* KOORDERS 30071, *j, k, m, n* BORDEN FB 1286, *l* RAMOS BS 27383).

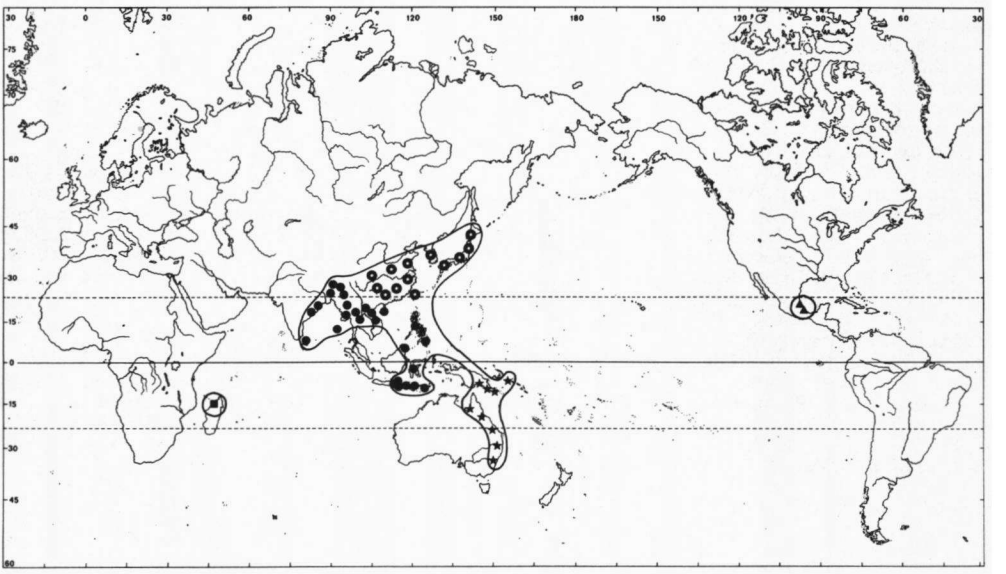

Fig. 25. Range of *Aphananthe* PLANCH. — *A. cuspidata* (BL.) PLANCH. (dots), *A. philippinensis* PLANCH. (stars), *A. sakalava* LEROY (square), *A. aspera* ENGL. (circles), *A. monoica* (HEMSL.) LEROY (triangles).

or rounded, more or less equal-sided; margin serrate, dentate, or rarely subentire, ends of serration occasionally developing into sharply mucronate structures; apex acute, or rounded, tip blunt; midrib and nerves strongly raised beneath, flattish above; nerves (3–)4–5(–7) pairs, ascending, straight or arcuating, subparallel, at 30–45° with the midrib, not anastomosing near the margin; reticulations fine, lax, subscalariform, faintly visible beneath; petiole (2–)3–5(–7) by 1 mm, adaxially flat or shallowly sulcate. — ♂ *Inflorescence* 1–3 cm ∅, 10–50-flowered; bracts linear-acute or narrow ovate-acute, $^1/_2$–1 by $^1/_4$ mm; ♂ flowers 1–1$^1/_2$ mm ∅; perianth lobes ovate-lanceolate, 1–1$^1/_2$ by $^1/_2$–1 mm; filaments $^1/_2$–$^3/_4$ mm, anthers *c.* $^3/_4$ by $^1/_2$ mm. — ♀ *Flowers* always solitary, ovoid-ellipsoid, 1–1$^1/_2$ by 1 mm, *c.* 5 mm pedicelled; perianth lobes narrow ovate-acute, $^1/_2$–1 by $^1/_2$ mm; ovary 1–1$^1/_2$ by 1 mm, densely appressed-hairy; stigmatic arms 2–3 mm. *Fruit* ovoid-globose, 6–8 by 4–6 mm, 3–4-angular, sparsely appressed-pubescent, glabrescent, pedicel *c.* 5–10 mm.

Distr. Australia (Queensland and New South Wales) and Solomons; in *Malesia:* New Guinea and Philippines (Luzon). Fig. 25.

Ecol. In primary and secondary forest subject to a rather strong seasonal climate, 0–750 m. In New Guinea it is often found in semi-deciduous gallery- or mixed *Eucalyptus*-forest, occasionally forming dense thickets especially on hillsides. *Fl.* Apr.–May and Sept.–Oct., *fr.* mature in July–Aug. and Nov.–Dec.

2. Aphananthe cuspidata (BL.) PLANCH. in DC. Prod. 17 (1873) 209. — *Cyclostemon cuspidatum* BL. Bijdr. (1825) 599. — *Galumpita cuspidata* (BL.) BL. Mus. Bot. 2 (1856) 73; MIQ. Fl. Ind. Bat. 1, 2 (1859) 224. — *Gironniera nitida* BTH. Fl. Hongk. (1861) 324. — *Gironniera reticulata* THW. En. Pl. Zeyl. 1 (1861) 268; HOOK. *f.* Fl. Br. Ind. 5 (1888) 486. — *Gironniera lucida* KURZ, For. Fl. Burma 2 (1877) 470; HOOK. *f.* Fl. Br. Ind. 5 (1888) 486. — *Gironniera cuspidata* (BL.) KURZ, For. Fl. Burma 2 (1877) 470; J. J. SMITH in K. & V. Bijdr. 12 (1910) 688; MERR. En. Philip. 2 (1923) 35; BACK. & BAKH. *f.* Fl. Java 2 (1965) 12. — *Gironniera curranii* MERR. Philip. J. Sc. 4 (1909) Bot. 251. — *A. lissophylla* GAGNEP. Bull. Soc. Bot. Fr. 72 (1925) 804; Fl. Gén. I.-C. 5 (1927) 690. — *Gironniera thompsoni* KING *ex* A. M. & J. M. COWAN, Trees N. Bengal (1929) 122. — ?*Gironniera yunnanensis* HU, Bull. Fan Mem. Inst. Biol. Bot. Ser. 10 (1940) 150. — ?*A. yunnanensis* (HU) GRUDZ. Nov. Syst. Pl. Vasc. USSR (1964) 66. — **Fig. 24a–i.**

Small to medium-sized tree up to 30 m, 60 cm ∅. Buttresses up to 1 m tall, and 2 m out. Bark surface rough, grey-brown, often flaky. Young branchlets sparsely, minutely, appressed-pubescent, glabrescent; older branchlets sparsely lenticellate. Stipules narrow ovate-acute, 2–3 by 1 mm. *Leaves* coriaceous, glabrous, ovate-elliptic to elliptic-oblong, (5–)10–14(–20) by (2–)3–6(–8) cm, index 2$^1/_2$–3; base rounded, subcordate, or attenuate, equal-sided or occasionally slightly unequal; margin entire, rarely distantly, minute serrulate in the upper half, often undulate; apex acute, acuminate, or cuspidate, acumen up to 2 cm, sharp-tipped; midrib strongly raised and prominent beneath, impressed to flattish above; nerves (5–)7–8(–10) pairs, slightly raised beneath, flattish above, subparallel, arcuating, at an angle of more than 60° with the midrib, weakly anastomosing near the margin; reticulations fine, indistinct on both surfaces, subscalariform to sub-areolate; petiole glabrous, (5–)8–12(–15) by 1–2 mm, sulcate. — ♂

Inflorescence up to 4 cm, 10–30-flowered; bracts ovate-acute, $^1/_4$–$^1/_2$ by $^1/_4$ mm; ♂ flower $1^1/_2$–2 mm ⌀, short-stalked; perianth lobes obovate-lanceolate, *c.* 2 by 1 mm; filaments 1–$1^1/_2$ mm, anthers ovoid-subreniform, *c.* 1 mm ⌀. — ♀ *Flower* solitary or borne in a 2–3-flowered mixed inflorescence, ovoid-ellipsoid, *c.* 2 by 1 mm; pedicels up to 10 mm; perianth lobes coriaceous, ovate-acute, *c.* 2 by 1 mm; ovary ovoid, glabrous, *c.* $1^1/_2$ by 1 mm; stigmatic arms 2–3 mm. *Fruit* ovoid, glabrous, including the beak 15–20 by 8–12 mm, beak up to 5 mm; pedicel up to 3 cm, 1 mm ⌀.

Distr. Ceylon, India, Burma, Andaman Is., ? China, Hainan, Hongkong, Indo-China, Thailand; in *Malesia:* NE. Sumatra (Sibolangit, doubtfully native), Java (mainly N. Central & E. parts), Lesser Sunda Islands (Bali, Sumbawa, Flores, Timor, rather common), Borneo (very rare, Kinabalu area), Philippines (Mindanao, rare), Celebes (rare). Fig. 25.

Ecol. In primary lowland to submontane forest, 0–1300 m. In Malesia it is mainly confined to lowland forests subject to a rather pronounced seasonal climate. In Thailand it occurs mainly in the evergreen or semi-deciduous forests along streams. Outside Malesia flowering in March–April and fruits mature in July–August. In Malesia it flowers twice yearly, *viz* in Febr.–March and Sept.–Oct., fruits maturing in June–July and Nov.–Dec.

Vern. Java: *suluh*, *wuluh*; Lesser Sunda Is.: *sulu*, Bali, *k. belikat*, Sumbawa, *k. loko*, Flores.

Note. Though I have not been able to examine any of the specimens cited by HU (1940), judging from the description given it is likely that *Gironniera yunnanensis* HU must be referred to this species.

Excluded

Aphananthe negrosensis ELMER, Leafl. Philip. Bot. 2 (1909) 575. — *Calaunia negrosensis* (ELMER) GRUDZ. Nov. Syst. Pl. Vasc. USSR (1964) 54 = *Streblus glaber* (MERR.) CORNER, Gard. Bull. Sing. 19 (1962) 221 (*Moraceae*).

6. GIRONNIERA

GAUDICH. Voy. Bonite (1844) t. 85; PLANCH. Ann. Sc. Nat. III, 10 (1848) 338; BL. Mus. Bot. 2 (1856) 72; MIQ. Fl. Ind. Bat. 1, 2 (1859) 222; PLANCH. in DC. Prod. 17 (1873) 205; HOOK. *f.* in B. & H. Gen. Pl. 3 (1880) 356; Fl. Br. Ind. 5 (1888) 485; ENGL. in E. & P. Nat. Pfl. Fam. 3, 1 (1888) 66; BERNARD, Bull. Herb. Boiss. II, 6 (1906) 34, map 24; J. J. SMITH in K. & V. Bijdr. 12 (1910) 665; HUTCH. Gen. Fl. Pl. 2 (1967) 149; PHUPHATHANAPHONG, Thai For. Bull. 6 (1972) 49; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 417. — *Nemostigma* PLANCH. Ann. Sc. Nat. III, 10 (1848) 265, *cf.* p. 338. — *Helminthospermum* THW. in Hook. J. Bot. Kew Misc. 6 (1854) 301, t. 9c. — **Fig. 26.**

Shrubs or large-sized trees, very rarely buttressed. Bark smooth to finely fissured, grey-brown, often lenticellate. *Innovations* densely or sparsely set with golden yellow or yellowish-brown indumentum consisting of simple bulbous-based, finely tuberculate, appressed or erect hairs and multicellular capitate-glandular hairs. Stipules extrapetiolar, free but overlapping each other and completely enclosing the bud, on falling leaving a circular scar around the node. *Leaves* pinnately nerved, nerves parallel, regularly well-spaced. *Inflorescence* ♂ or ♀, very rarely ♂♀, axillary or borne on older, leafless branchlets, 1-many-flowered, paniculate, racemose, thyrsoid, or capitate; bracts ovate-acute, minute, caducous, but rather long persistent in the ♀ inflorescence. — ♂ *Flower* globular, sessile or short-stalked along the axes; perianth lobes 5, imbricate in bud; stamens glabrous, anthers introrse; filament subulate, inflexed; anthers ovoid-reniform, apiculate, sub-basifixed; pistillode present, rather well-developed or very rudimentary, densely set with whitish or silky erect hairs. — ♀ *Flower* ovoid-ellipsoid, compressed; perianth lobes 4–5, usually unequal in size, long persistent; staminodes absent; ovary ovoid-ellipsoid, strongly compressed, sessile, densely or sparsely appressed-hairy, glabrescent; stigmatic arms up to $1^1/_2$ cm long, curled in bud, later spreading, rather long persistent; ovule anatropous. *Drupe* ovoid-globose, convex elliptic lens-shaped; exocarp thin, strongly adnate to the hard and persistent endocarp. *Seed*

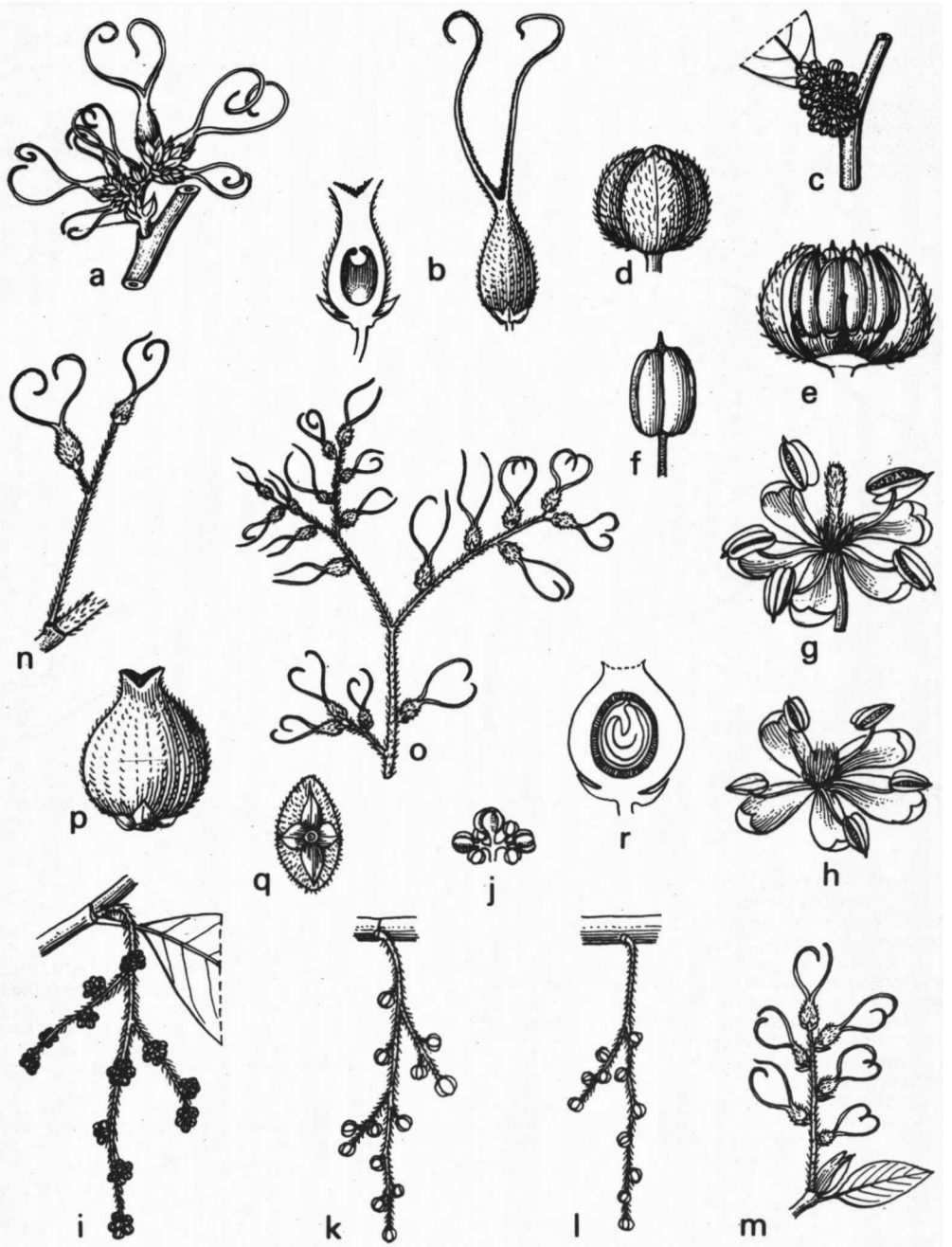

Fig. 26. *Gironniera celtidifolia* GAUDICH. a–b. ♀ Flowers, one in CS, c–g. ♂ flowers, various details. — *G. subaequalis* PLANCH. h. ♂ Flower, m. young infructescence, p-r. fruits, one in LS. — *G. nervosa* PLANCH. i–j. ♂ Flowers. — *G. parvifolia* PLANCH. k. ♂ Inflorescence, n. young infructescence. — *G. rhamnifolia* BL. l. ♂ Inflorescence. — *G. hirta* RIDL. o. Young infructescence. *a*, *c*, *m–r* × $^2/_3$, *b* × 3, *d–e*, *g–h* × 7, *f* × 9, *i* × $^2/_3$, *j* × 2, *k–l* × $1^1/_3$ (*a–b* BS 48861, *c–g* MALIWANAG 119, *h* RAHMAT SI BOEEA 9311, *i–j* KEP/FRI 14582, *k* KEP/FRI 18017, *l* ZIPPELIUS *s.n.*, *m* MOH. SHAH 519, *n* SF 34908, *o* bb 30873, *p–r* KEP/FRI 99766).

coat membranous, a few cells thick; endosperm absent; embryo curved, hypocotyle ascending; cotyledons fleshy, narrow, equal. Mode of germination unknown.

Distr. 6 *spp.*, SE. Asia: Ceylon, Andaman Is., Burma, Thailand, Indo-China, China (Yunnan, Kwangtung, Canton, Hainan, Hongkong), Micronesia (Palau and Ponape Is.), Melanesia (Solomons), Polynesia (Samoa, Fiji); in *Malesia:* throughout the region except for the eastern part of Java, the Lesser Sunda Islands, and the SE. Moluccas. Fig. 27.

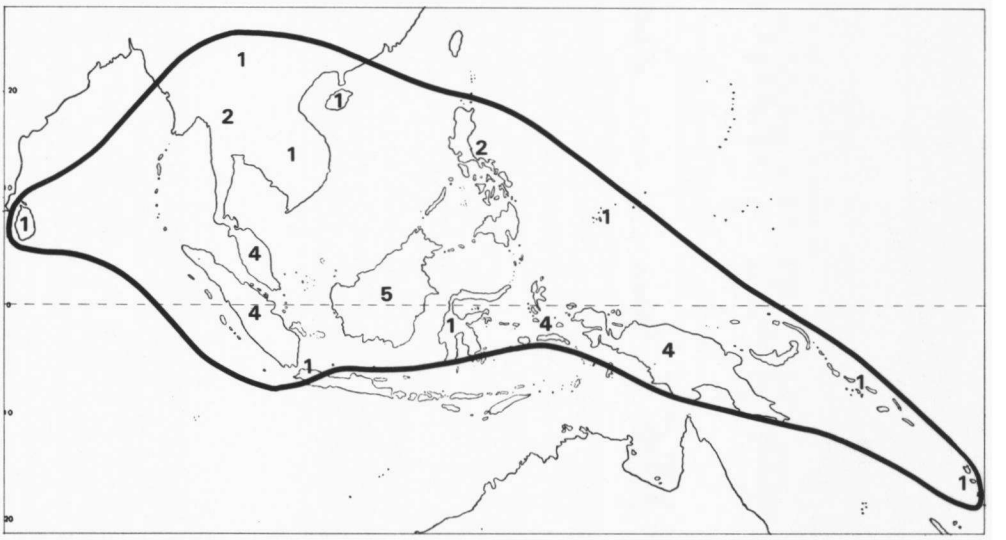

Fig. 27. Approximate range of the genus *Gironniera* GAUDICH. with the number of species in each island or partial area. There are no endemic species.

Fossils. WOLFE (in Graham, Flor. & Paleoflor. Asia & N.E. America, 1972, 200, pl. IV, f. 2) reported leaf-impressions attributed to *Gironniera* from the Early Ravenian Flora of Alaska (Middle Eocene). However, in examining the published photograph (p. 211), I am very much in doubt whether the specimen belongs to the genus at all.

Ecol. Understorey shrubs or trees in both primary and secondary forests, at 0–1300 m, often abundant and gregarious; on various types of soil, including those derived from limestone. In areas where the seasonal climate is prominent mainly found in the evergreen forest along streams.

Judging from the structure of the flower and inflorescence, it is inferred that the pollination may be affected by wind. The drupes which turn to bright yellow or orange in colour when ripe are mostly barren, and they may be dispersed by various species of frugivorous birds. Direct observations in the field are, however, wanting.

Notes. *Gironniera spp.* have a continuous, flush-wise growth habit and have the ability to produce flowers and fruits at a very young (sapling) stage (2–3 m tall). Since the plants are often very common locally both in the primary and secondary forests, produce flowers and fruits regularly, and are very easy to collect, most of the examined specimens were gathered from these young plants. The presence of so many specimens collected from juvenile plants hampers proper identification even when they are fertile.

In the present revision, the characters used in the key were taken from specimens collected from mature or fully grown trees, while those mentioned in the description of each species include also data from specimens collected from the young plants, thus to include the total morphological variability.

On the material and field notes so far available it is impossible at this stage to determine whether the genus is strictly monoecious or dioecious. In most cases, the specimens display only fruits or ♂ inflorescences, thus giving the impression that the genus is dioecious. However, there are a few collections (in all species but *G. hirta*) which have both ♂ influorescences and infructescences attached to the same branchlet, or they are borne on separate branchlets belonging to a single collecting number.

Mrs. PHUPHATHANAPHONG *l.c.* accommodated the Malesian specimens into two species, *G. nervosa* and *G. celtidifolia*, without argumentation. I cannot agree with this view.

KEY TO THE SPECIES

(Based on specimens from mature trees)

1. ♂ & ♀ Inflorescence and infructescence a condensed, capitate thyrse or panicle, axillary or borne on older leafless branchlets. ♂ Flower with a rather well-developed pistillode. Leaves thick-leathery, distantly serrate or subentire. Terminal bud (stipules) up to $4^1/_2$ by $^1/_2$ cm . . . . . **1. G. celtidifolia**
1. ♂ & ♀ Inflorescence and infructescence a lax, branched or unbranched panicle, raceme, or thyrse, always axillary. ♂ Flower with a strongly rudimentary pistillode. Leaves chartaceous to thick leathery, in Mal. specimens mostly entire. Terminal bud less than 3 cm by less than 0.3 cm.
2. Mature leaf densely pubescent beneath. ♂ Inflorescence a much-branched thyrse; ♂ flowers arranged in condensed cymoid clusters of 5–10 along the axes.
3. Young branchlets densely short appressed-hairy. Leaves elliptic-lanceolate to elliptic-oblong, index $2^1/_2$–3, broadest at the middle; nerves (12–)15(–17) pairs, parallel, straight, 5–8 mm spaced, not or only weakly anastomosing along the margin. Well-developed ♀ inflorescence (thus also the infructescence) mostly an unbranched panicle, *c.* 3 cm long, bearing less than 10 flowers (fruits). **2. G. nervosa**
3. Young branchlets densely set with long, erect hairs. Leaves mostly ovate-elliptic, rarely elliptic-oblong, index *c.* 2, broadest below or rarely at the middle; nerves (8–)10–12(–14) pairs, subparallel, 10–15 mm spaced, arcuating and anastomosing towards the margin. Well-developed ♀ inflorescence (*cq.* infructescence) a mostly much-branched panicle 5–10 cm long, bearing up to 20 fruits **3. G. hirta**
2. Mature leaf glabrous. ♂ Inflorescence unbranched or a branched raceme or panicle; ♂ flowers solitary along the axes.
4. Mature leaf thick-coriaceous, broad-ovate, elliptic, or elliptic-oblong, broadest below or at the middle, index 2–$2^1/_2$, base unequal-sided. Terminal bud 2–3 by 0.2–0.4 cm. Well-developed ♂ inflorescence a much-branched panicle, carrying 40–100 flowers. Well-developed ♀ inflorescence (*cq.* infructescence) carrying (2–)5–10(–15) flowers (fruits). Mature fruits 10–12 by 9 by 5 mm. **4. G. subaequalis**
4. Mature leaf chartaceous to thin-coriaceous, elliptic-lanceolate or elliptic-obovate, broadest at or slightly above the middle, index ($2^1/_2$–)3(–$3^1/_2$), base more or less equal-sided. Terminal bud 2 by $^1/_2$ cm. Well-developed ♂ inflorescence an unbranched panicle carrying 15–30 flowers. Well-developed ♀ inflorescence (*cq.* infructescence) carrying 1–3(–5) flowers (fruits). Mature fruits 7–8 by 5–6 by 3–4 mm.
5. Nerves (5–)6–8(–9) pairs. ♂ Flowers short-stalked. Axes of ♀ inflorescence (infructescence) slender and thin (less than 0.3 mm), 4–10 cm long, carrying 1–3(–5) flowers (fruits). . . **5. G. parvifolia**
5. Nerves 10–12 pairs. ♂ Flowers sessile along the axes. Axes of ♀ inflorescence (infructescence) $^1/_2$–1 mm thick, 3–4 cm long, carrying (1–)3–5 flowers (fruits). . . . . **6. G. rhamnifolia**

1. Gironniera celtidifolia GAUDICH. Voy. Bonite (1844) t. 85; PLANCH. Ann. Sc. Nat. III, 10 (1848) 340; MIQ. Fl. Ind. Bat. 1, 2 (1859) 223; SEEM. Fl. Vit. (1865) 236; PLANCH. in DC. Prod. 17 (1873) 207; LAUT. Bot. Jahrb. 50 (1913) 326; MERR. En. Philip. 2 (1923) 35; PARHAM, Pl. Fiji Is. (1964) 88. — *G. sibuyanensis* ELMER, Leafl. Philip. Bot. 5 (1913) 1845; MERR. En. Philip. 2 (1923) 35. — *G. grandifolia* MERR. & PERRY, J. Arn. Arb. 20 (1939) 325. — *G. retinervia* MERR. & PERRY, *l.c.* 326. — **Fig. 26a–g.**

Shrub or medium-sized tree up to 18 m tall and 25 cm ∅. Bark greyish-brown to dark-brown, smooth or finely fissured. Terminal buds *c.* 4–$4^1/_2$ by $^1/_2$ cm; stipules narrow lanceolate-acute, *c.* 4–$4^1/_2$ by $^1/_4$–$^1/_2$ cm. *Leaves* thick-coriaceous, elliptic-, lanceolate-, or obovate-oblong, (8–)15–25(–42) by (4–)6–12(–19) cm, index $2^1/_2$–$3^1/_2$, broadest at or above the middle; base unequal-sided, attenuate, rounded, or cordate-auriculate; margin distantly serrate at least for the upper half or subentire; apex rounded, acute, or acuminate-caudate, acumen up to 4 cm long; glabrous above, sparsely appressed-hairy beneath especially on midrib and nerves, glabrescent; midrib and nerves strongly raised beneath, flattish to shallowly impressed above; nerves (8–)12–16(–19) pairs, anastomosing along the margin; reticulations subscalariform, evenly spaced, distinct beneath; petiole (3–)5–12(–15) by (1–)$1^1/_2$–$2^1/_2$(–4) mm, terete or adaxially flat near the base, strigose, glabrescent. *Inflorescences* a condensed, capitate, much-branched panicle or thyrse, axillary or borne on older, leafless branchlets, many-flowered, ♂ or ♀, very rarely ♂♀, including the bracts densely appressed-hairy; bracts 2–4 by 2 mm. — ♂ *Flower c.* $1^1/_2$–2 mm ∅, sessile or short-stalked along the axes, perianth lobes ovate-elliptic, concave, *c.* $1^1/_2$–2 by 1–$1^1/_2$ mm; filaments $1^1/_2$–2 mm, anthers 1–$1^1/_2$ by 1 mm; pistillode cylindrical, $1^1/_2$–2 by $^1/_2$ mm, at base surrounded by dense, whitish, erect hairs. — ♀ *Flower* 2–3 by 2 mm; perianth lobes ovate, 1–$1^1/_2$ by $^1/_2$–1 mm; ovary 2–3 by $1^1/_2$–2 mm, densely appressed-hairy; stigmatic arms 1–$1^1/_2$ cm, slender. *Fruit* ovoid-ellipsoid, sparsely appressed-hairy, glabrescent, 5–8 by 4–6 by 3–4 mm, beak up to 5 mm.

Distr. Micronesia (Palau, Ponape), Melanesia (Solomons), Polynesia (Samoa, Fiji); in *Malesia:* Borneo (doubtful record), Philippines (common and widespread), Moluccas (Morotai, Halmaheira), New Guinea (common in W. & E.; also in Admiralty, Misima, Sudest, and Rossel Is.).

Ecol. In both primary and secondary forests, 0–1200 m; often locally abundant as understorey shrub or tree. *Fl. fr.* Jan.–Dec.

Vern. Philippines: *ablang*, Mang., *dita*, Tag., *mangabau*, Bis., *tanguntungan*, Mbo.; Moluccas: *koko*, Morotai; New Guinea: *aimarwirieh*, Biak, *taun*, Wapil lang., Sepik Distr.; Solomons:

aisulia, Kwara; Fiji: *masivau*, *sisisi*; Samoa: *pua-pua*, *puluvao*.

Notes. In most specimens examined, the ♂ inflorescence shows abnormal development and produces a malformed structure consisting of numerous superimposed bracts in the axils of which are found sterile structures resembling in size and shape that of the pistillode in the normally developed and functionally ♂ flowers. Well-developed and functionally ♂ flowers are to be found only at the distal parts of these abnormally developed inflorescences. In a ♂♀ inflorescence, which is very rarely present, the functionally ♀ flowers are borne on the central main axis and they are flanked by two or more lateral, functionally ♂ flowers. Most of the fruits so far examined (more than 95%) are barren.

Size and shape of the leaf are rather variable. In general, specimens collected from a higher altitude or from a more exposed habitat have a smaller leaf and less pairs of nerves than those gathered from lowland and shady localities. Intermediates are, however, not uncommon, and for this reason *G. sibuyanensis*, *G. grandifolia*, and *G. retinervia* are here reduced.

2. Gironniera nervosa PLANCH. Ann. Sc. Nat. III, 10 (1848) 338; BL. Mus. Bot. 2 (1856) 74; MIQ. Fl. Ind. Bat. 1, 2 (1859) 222; PLANCH. in DC. Prod. 17 (1873) 206; KURZ, For. Fl. Burma 2 (1877) 469; HOOK. *f.* Fl. Br. Ind. 5 (1888) 485; MERR. En. Born. (1921) 216; RIDL. Fl. Mal. Pen. 3 (1924) 320; CORNER, Ways. Trees (1940) 688; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 419, f. 2. — *G. penangiana* GANDOG. Bull. Soc. Bot. Fr. 66 (1919) 289. — *G. sponioides* GANDOG. *l.c.* 289. — **Fig. 26i–j.**

Small to large-sized tree up to 40 m, 60 cm ⌀. Buttresses sometimes present, low. Bark smooth or finely fissured, grey-green to dark grey-brown, often hoop-marked and lenticellate. Terminal bud 1–2 by $^1/_4$–$^1/_2$ cm; stipules $1^1/_2$–2 by $^1/_4$–$^1/_2$ cm. *Leaves* thick-coriaceous, rigid, elliptic-lanceolate to elliptic-oblong, (6$^1/_2$–)10–15(–18) by (2$^1/_2$–)4–6 (–8) cm, broadest at the middle, index 2$^1/_2$–3; except for the midrib and lateral nerves glabrous above, densely set with yellowish-brown, soft, slender hairs beneath; base rounded or attenuate, unequal-sided; margin entire, often recurved; apex rounded to acute; midrib and nerves strongly raised beneath, flattish or impressed above; nerves (12–)14–16(–17) pairs, 5–8 mm spaced, arcuating but not anastomosing near the margin, forming an angle of up to 60° with the midrib; reticulations dense, regularly spaced, scalariform or subscalariform, strongly raised and prominent beneath, obscure to faintly visible above; petiole 5–10 by 1–2 mm, subterete, densely yellowish-brown appressed, pubescent. *Inflorescences* ♂ or ♀, axillary, borne on separate shoots, including the bracts densely yellowish-brown, appressed-pubescent; bracts narrow ovate-acute, *c.* 1–2 by 1 mm. — ♂ *Inflorescence* a slender, lax, pendent, branched panicle of condensed cymes, up to 7 cm long, bearing 20–100 flowers; ♂ flowers in clusters of 5–10 along the axes, *c.* 2 by 2 mm; perianth lobes broad ovate-acute, *c.* 1–1$^1/_2$ by 1 mm, densely, short appressed-hairy outside; filaments 1–1$^1/_2$ mm, anthers ovoid, *c.* 1 mm ⌀; pistillode strongly rudimentary. — ♀ *Inflorescence* a simple or branched panicle, up to 2$^1/_2$ cm long, 5–10-flowered; ♀ flowers sessile along the axes, compressed ovoid-conical, 2–3 by 1$^1/_2$–2 mm; perianth lobes ovate-acute, densely appressed-hairy outside, 1$^1/_2$–2 by 1 mm; ovary densely appressed-hairy, 1$^1/_2$–3 by 1–1$^1/_2$ mm; stigmatic arms 5–10 mm. *Infructescence* up to 3 cm long, bearing (2–)4–6(–8) fruits. *Fruit* subglobose or ovoid, densely appressed-pubescent, 5–8 by 4–6 by 3–4 mm, short-beaked.

Distr. Thailand; in *Malesia:* Malay Peninsula (incl. Singapore; common), Sumatra (rather rare), Borneo (common).

Ecol. In primary and secondary forests, 0–1300 m, mostly below 500 m; often common locally as understorey tree in lowland forests. In Thailand it occurs mainly in the evergreen forest along streams. *Fl. fr.* Jan.–Dec., but mainly during July–Dec.

Vern. Malaya: *mĕdang berbulu*, *m. kasap*, *tapis*, M; N. Borneo: *luazon*, Kadasan, *hugot-hugot*, Dusun; Kalimantan: *kayu ruas*, Bandjar, *gagas*, Bassap.

3. Gironniera hirta RIDL. J. Str. Br. R. As. Soc. *n.* 82 (1920) 194; Fl. Mal. Pen. 3 (1924) 321; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 417, f. 2. — **Fig. 26o.**

Shrub to medium-sized tree up to 30 m, 30 cm ⌀. Bark smooth, light to grey-brown. Young branchlets, petiole, stipules, terminal bud densely set with golden yellow, long, soft, erect hairs. Terminal buds ovoid-conical, 1$^1/_2$–3 by $^1/_4$–$^1/_2$ cm; stipules 1$^1/_2$–3 by $^1/_2$ cm. *Leaves* thick-coriaceous, rigid, ovate-elliptic or rarely elliptic-oblong, (6–)14–18 (–23) by (3–)5–8(–12) cm, index *c.* 2; base rounded, subcordate or attenuate, unequal-sided; margin entire, rarely distantly serrulate in the upper half; apex rounded, acute to acuminate; except for the midrib and nerves which are densely or sparsely set with long, appressed or erect, soft hairs, glabrous above, densely soft-pubescent beneath; midrib and nerves raised and distinct beneath, flattish or impressed above; nerves (8–)10–12(–14) pairs, 10–15 mm spaced, arcuating towards and anastomosing near the margin; reticulation subscalariform to subareolate, well-spaced, distinct beneath, obscure above; petiole 2–10 by 1–3 mm, terete or flat above near the base. *Inflorescences* ♂ or ♀, axillary, borne on separate branches, including the bracts densely golden yellow pubescent; bracts ovate-acute, 1–1$^1/_2$ by $^1/_2$–1 mm. — ♂ *Inflorescence* slender, lax, branched, thyrsoid, up to 8 cm long, bearing up to 100 flowers; ♂ flower 1$^1/_2$–2 mm ⌀, sessile along the axes, in cymoid clusters of 3–10; perianth lobes 1$^1/_2$–2 by 1 mm, densely appressed-hairy outside; filaments 1–1$^1/_2$ mm, anthers ovoid-reniform, *c.* 1 mm ⌀; pistillode strongly rudimentary. — ♀ *Inflorescence* (as seen in a very young infructescence) a branched panicle, up to 5 cm, carrying 2–20, sessile or short-stalked flowers; perianth lobes narrow ovate-acute, *c.* 2 by 1 mm, densely appressed short-hairy outside; ovary (young fruit) ovoid, densely short-, appressed-hairy, *c.* 3 by 2 mm; stigmatic arms up to 1 cm. *Infructescence* up to 10 cm long, axes *c.* 1 mm thick, bearing (2–)5–15(–20) fruits. *Drupe* ovoid-compressed, densely short-appressed-pubescent, 8–10 by 6–8 by 3–5 mm, short-beaked.

Distr. *Malesia:* Malaya (rather rare), Sumatra (rare), Borneo (common), Moluccas (rare), New Guinea (rare, mainly in W.).

Ecol. Scattered as an understorey shrub or tree in lowland forests, 0–700 m. *Fl. fr.* Jan.–Dec.

Vern. Malaya & Sumatra: *hampas tĕbu, hampĕlas burung, mĕdang berbulu, m. kasap,* M; Kalimantan: *kayu ruas, lĕmpung bulu,* Bandjar; Sarawak: *puloh,* Iban; New Guinea: *warpis,* Biak.

Note. Closely related to *G. nervosa,* but readily distinguished from the latter by the characters mentioned in the key. Specimens from Malaya (mainly from the Kluang area in Johore and Pahang), including the type, have much thinner leaves with a distantly serrulate margin than those from Sumatra, Borneo, and New Guinea. Since in most cases the field notes of the Malayan specimens indicate that the height of the tree was never more than 3 m, it is assumed that these specimens have been collected from saplings.

4. Gironniera subaequalis PLANCH. Ann. Sc. Nat. III, 10 (1848) 339, *p.p., excl. var. ceylanica*; BL. Mus. Bot. 2 (1856) 73, *incl. var. brevistylis* BL., *var. scabrida* BL. *et var. serrulata* BL. *l.c.* 74; MIQ. Fl. Ind. Bat. 1, 2 (1859) 222; PLANCH. in DC. Prod. 17 (1873) 206; HOOK. *f.* Fl. Br. Ind. 5 (1888) 485; HEMSL. J. Linn. Soc. Bot. 26 (1894) 452; BRANDIS, Ind. Trees (1906) 596; J. J. SMITH in K. & V. Bijdr. 12 (1910) 666; Nova Guinea 8 (1912) 892, *incl. var. papuana* J. J. S.; LAUT. Bot. Jahrb. 50 (1913) 326; MERR. En. Born. (1921) 217; En. Philip. 2 (1923) 35; RIDL. Fl. Mal. Pen. 3 (1924) 320; GAGNEP. Fl. Gén. I.-C. 5 (1927) 678; CORNER, Ways. Trees (1940) 690; BACK. & BAKH. *f.* Fl. Java 2 (1965) 12; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 419, f. 2. — *Sponia annulata* TEYSM. & BINN. Ned. Kruidk. Arch. 3 (1855) 408. — *G. costata* MIQ. in Zoll. Syst. Verz. (1855) 88; Fl. Ind. Bat. 1, 2 (1859) 223. — *G. chinensis* BTH. Fl. Hongk. (1861) 324. — *G. nervosa var. subaequalis* (PLANCH.) KURZ, For. Fl. Burma 2 (1877) 470. — *G. amboinensis* LAUT. Bot. Jahrb. 50 (1913) 326. — *G. longifolia* CRAIB, Kew Bull. (1918) 371. — *G. sumatrana* GANDOG. Bull. Soc. Bot. Fr. 66 (1919) 288. — *G. blumei* GANDOG. *l.c.* 288. — *G. borneensis* GANDOG. *l.c.* 288. — *G. ferruginea* GANDOG. *l.c.* 289. — **Fig. 26h, m, p–r.**

Small to large-sized tree up to 40 m, 60 cm ø. Bark smooth to finely fissured, pustular or lenticellate. Terminal bud 2–3 by $^1/_4$–$^1/_2$ cm; stipules linear-lanceolate, $1^1/_2$–$2^1/_2$ by $^1/_4$–$^1/_2$ cm. *Leaves* thick-coriaceous, broad ovate-elliptic or elliptic-oblong, (6–)12–16(–21) by $(3^1/_2$–$)5$–$8(-13)$ cm, index 2–$2^1/_2$, except for midrib and nerves glabrous; base attenuate or rounded, unequal-sided; margin entire or occasionally, especially when young, distantly serrulate at least for the upper half; apex rounded or attenuate-acute; midrib and nerves raised beneath, flattish above, sparsely or densely yellowish-brown appressed short-hairy beneath; nerves (6–)8(–10) pairs, 10–15 mm spaced, at more than 60° with the midrib, arcuating and anastomosing along the margin; reticulations subscalariform, fine, dense or rather well-spaced, slightly and clearly visible beneath, flattish and faintly visible above or obscure; petiole 5–15 by 1–2 mm, terete or adaxially flat near the base, sparsely or densely appressed, simple, short, yellowish-brown pubescent, glabrescent. *Inflorescence* ♂ or ♀, axillary, borne on separate branchlets or rarely on the same branchlet, including the bracts sparsely to densely short, yellowish-brown, appressed-hairy, glabrescent; bracts ovate-acute, 1–2 by $^1/_2$–1 mm. — ♂ *Inflorescence* paniculate, pendent, much-branched, 40–100-flowered, axes up to 3–7 cm long, $^1/_2$–1 mm thick; ♂ flowers $1^1/_2$–$2^1/_2$ mm ø, sessile and solitary along the axes or in clusters of 3–5 on short, condensed secondary branches of the panicle; perianth lobes sparsely short appressed-pubescent, glabrescent, broadly ovate-rounded, 2–$2^1/_2$ by $1^1/_2$–2 mm; filaments $1^1/_2$–2 mm, anthers ovoid-subreniform, *c.* 1 by 1 mm; pistillode strongly rudimentary. — ♀ *Inflorescence* racemose, unbranched or more commonly branched, axes 3–6 cm long, 1–$1^1/_2$ mm thick, bearing (2–)5–10 (–15) flowers; ♀ flowers solitary and short-stalked along the axes, 2–4 by 2 mm; perianth lobes broadly ovate-acute, $1^1/_2$–2 by $1^1/_2$ mm, sparsely appressed-pubescent outside; ovary 2–3 by 2 mm, densely appressed-pubescent, glabrescent; stigmatic arms up to 2 cm. *Infructescence* with a sturdy axis up to 2 mm thick, 5–10 cm long, bearing (2–)5–8 (–10) fruits. *Fruit* 1–$1^1/_4$ by 8–9 by 5–6 mm, sparsely appressed-pubescent, glabrescent, beak 2–5 mm.

Distr. A rather variable species widely distributed in the Andaman Is., Burma, China (Yunnan, Kwangtung, Canton, Hainan), Hongkong, Indo-China, Thailand, throughout *Malesia* (except the Lesser Sunda Is.).

Ecol. Understorey shrub or tree in primary and secondary forest, 0–1300 m, more commonly in the lowland between 200–500 m. *Fl. fr.* Jan.–Dec.

Vern. Malaya: *hampas tĕbu, mĕdang kasap,* M; Sumatra: *silu, siluk,* M; W. Java: *ki bulu,* S; N. Borneo: *kuayun, ruwayon,* Dusun, *untoh bulu,* Iban; Kalimantan: *katul,* Bulungan; Anambas Is.: *pupoh,* M; W. New Guinea: *gawa, gĕwa, mĕgawa,* Mooi, *nadjun, nitjun,* Kebar, *bobohufeka,* Manikiong, *warpis,* Biak.

5. Gironniera parvifolia PLANCH. Ann. Sc. Nat. III, 10 (1848) 338 ('*parvifolium*'); MIQ. Fl. Ind. Bat. 1, 2 (1859) 223; PLANCH. in DC. Prod. 17 (1873) 206; HOOK. *f.* Fl. Br. Ind. 5 (1888) 486; RIDL. Fl. Mal. Pen. 3 (1924) 321; CORNER, Ways. Trees (1940) 689; SOEPADMO in Whitmore, Tree Fl. Mal. 2 (1973) 419, f. 2. — *G. subaequalis var. ceylanica* PLANCH. Ann. Sc. Nat. III, 10 (1848) 339; THW. En. Pl. Zeyl. (1861) 268; HOOK. *f.* Fl. Br. Ind. 5 (1888) 485. — *Helminthospermum scabridum* THW. in Hook. J. Bot. Kew Misc. 6 (1854) 303, t. 9c. — *G. paucinervia* MERR. J. Str. Br. R. As. Soc. *n.* 77 (1917) 189; En. Born. (1921) 217. — *G. zeylanica* GANDOG. Bull. Soc. Bot. Fr. 66 (1919) 288. — *G. scabrida* (THW.) ALSTON in Trimen, Fl. Ceyl. 6 (1931) 267. — **Fig. 26k, n.**

Shrub or small-sized tree up to 15 m, 20 cm ø. Bark smooth to finely fissured, lenticellate, grey-green or grey-brown. Terminal bud (5–)8–15(–18) by 1–3 mm; stipules linear-acute, 8–15 by 2–3 mm. *Leaves* chartaceous to thin-coriaceous, rarely coriaceous, elliptic-lanceolate or elliptic-obovate, very rarely ovate-elliptic, (4–)8–12(–16) by $(1^1/_2$–$)$ 3–4(–5) cm, index 3–$3^1/_2$, glabrous,; base attenuate or rounded, more or less equal-sided; margin entire or sometimes minutely and distantly serrulate

in the upper half (extra-Mal. and young specimens); apex attenuate-acute or rounded-acuminate; midrib and nerves slightly raised beneath, flattish above; nerves (5–)6–8(–9) pairs, 7–10 mm spaced, at up to 60° with the midrib, arcuating and anastomosing along the margin; reticulations subareolate, fine, dense, visible beneath, obscure above; petiole 5–7 by 1–1½ mm, sulcate. *Inflorescences* ♂ or ♀, axillary, borne on separate branchlets, including the bracts sparsely, short, appressed-pubescent, glabrescent; bracts ovate-acute, membranous, *c.* 1 by ½ mm. — ♂ *Inflorescence* a slender, pendulous, simple or branched raceme, bearing 15–30 flowers, axes up to 5 cm long, 0.2–0.3 mm thick; ♂ flowers solitary along the axes, short-stalked, 1½–2 mm ∅; perianth lobes broad ovate, *c.* 1½–2 by 1–1½ mm; filaments 1–1½ mm long, anthers ovoid-reniform, ¾–1 mm ∅; pistillode strongly rudimentary. — ♀ *Inflorescence* a slender, 1–3(–5)-flowered raceme, 4–10 cm long, axes 0.2–0.3 mm thick; ♀ flower 2–3 by 2 mm, short-stalked; perianth lobes mostly 4, unequal in size, 1½–2½ by 1–2 mm; ovary sparsely short appressed-pubescent, 2–3 by 2 mm; stigmatic arms up to 1½ mm. *Infructescences* slender, up to 10 cm long, bearing 1–3(–5) fruits, axes thinner than 1 mm. *Fruit c.* 8 by 6 by 4 mm, sparsely, short appressed-pubescent, glabrescent; beak up to 5 mm.

Distr. Ceylon; in *Malesia:* Malay Peninsula (incl. Singapore; very common), Sumatra (rare), Borneo (common).

Ecol. In primary as well as in secondary forest, 0–1300 m, but mostly in the lowland, on various types of soil including those derived from limestone. *Fl.* Jan.–April, *fr.* Oct.–Dec.

Vern. Malaya: *hampas tĕbu, mĕdang kasap*, M; Sarawak: *tĕpadĕ*, Kelabit.

Note. As in other species of the genus, most of the specimens so far available suggest that the plant is monoecious. However, in MAINGAY K.D. 1470 from Malaya both the ♂ inflorescence and infructescence are found on separate branchlets of the same collection number. Assuming that these branchlets were collected from the same tree, it would suggest that the species is monoecious but producing ♂ and ♀ flowers at different stages of its growth. More field work is required to determine its breeding system.

6. Gironniera rhamnifolia BL. Mus. Bot. 2 (1856) 74, t. 25; MIQ. Fl. Ind. Bat. 1, 2 (1859) 223; PLANCH. in DC. Prod. 17 (1873) 206; LAUT. Bot. Jahrb. 50 (1913) 326. — **Fig. 26l.**

Shrub to medium-sized tree, up to 25 m, 40 cm ∅. Bark smooth, pale grey-brown. Branchlets initially densely set with simple, yellowish-brown, soft, erect hairs, glabrescent. Terminal buds 1–1½ by 0.2–0.3 cm; stipules narrow elliptic-lanceolate, *c.* 1½ by ¼ cm. *Leaves* chartaceous to thin-coriaceous, glabrous, elliptic-lanceolate or rarely ovate-elliptic, (5–)8–15(–17) by (2–)4–6(–8) cm, index 2½–3½; base rounded or attenuate, ± equal-sided; margin entire; apex acute to acuminate; midrib and nerves slightly raised beneath, flattish to slightly impressed above, often densely, short, appressed-hairy; nerves 10–13 pairs, at an angle of over 60° with the midrib, arcuating and anastomosing towards the margin; reticulations fine, lax, subscalariform to subareolate, faintly visible beneath; petiole 5–10 by 1–1½ mm, glabrous, shallowly furrowed or flat above near the base. *Inflorescences* ♂ or ♀, axillary, including the bracts sparsely short, yellowish-brown appressed-pubescent; bracts narrow ovate-acute, *c.* 1 by ½ mm. — ♂ *Inflorescence* an unbranched or branched panicle, 3–5 cm long, bearing 15–30 flowers; ♂ flowers sessile and solitary along the axes, *c.* 1–1½ mm ∅; perianth lobes ovate, 1½–2 by 1 mm, sparsely short, appressed-pubescent outside; filaments 1½–2 mm, anthers ovoid-reniform, ½–1 mm ∅; pistillode strongly rudimentary. — ♀ *Inflorescence* an unbranched, (1–)3–5-flowered panicle, 3–4 cm long with the axes *c.* ½–1 mm thick; ♀ flowers 2–3 by 2 mm; perianth lobes 5, ovate, 1½–2 by 1 mm; ovary 2–3 by 2 mm, densely short, appressed-pubescent, glabrescent; stigmatic arms up to 1½ cm. *Infructescence* up to 5 cm long, axes *c.* 1 mm or thicker, bearing (1–)3–5 fruits. *Fruit* ± glabrous, *c.* 7 by 6 by 3 mm, short-beaked.

Distr. *Malesia:* N. Moluccas (Morotai), New Guinea (incl. Biak, Japen, and Polima Is.).

Ecol. Primary and secondary forests, locally often very common in rocky or stony habitats including limestone, 0–1000 m. *Fl. fr.* Jan.–Dec.

Vern. W. New Guinea: *warpis*, Biak, *tamanpara*, Japen, *ramé*, Iko.

Excluded

Gironniera glabra MERR. Philip. J. Sc. 1 (1906) Suppl. 42 = *Paratrophis glabra* STEEN. J. Bot. 72 (1934) 8 = *Chevalierodendron glabrum* LEROY, C. R. Ac. Sc. Paris 227 (1948) 146 = *Streblus glaber* (MERR.) CORNER, Gard. Bull. Sing. 19 (1962) 221 (*Moraceae*).