

HERNANDIACEAE

(Brigitta E.E. Duyfjes, Leiden)¹

Hernandiaceae Blume, Bijdr. (1826) 550, '*Hernandieae*'; Backer & Bakh. f., Fl. Java 1 (1963) 135–137; Kubitzki, Bot. Jahrb. 89 (1969) 78–209, 51 fig.; in Fl. Camb., Laos & Vietnam 12 (1970) 3–22, fig.; Ng in Tree Fl. Malaya 2 (1973) 244–247, fig.; Croft in Handb. Fl. Papua New Guinea 2 (1981) 190–201, fig.; A.C. Sm., Fl. Vit. Nov. 2 (1981) 108–113, 143–145, fig.; Du Puy & Telford in Fl. Austral. 50 (1993) 69–73, fig.; Kubitzki et al. (eds.), The families and genera of vascular plants 2, X (1993) 334. — Type genus: *Hernandia* L.

Trees, shrubs, or woody climbers, with bisexual or unisexual flowers. *Leaves* alternate or spirally arranged, petiolate, without stipules, simple, lobed or unlobed, or palmately compound, margin entire. *Inflorescences* usually axillary, much-branched, compound cymes, sometimes corymbose; with or without bracts. *Perianth* sepaloid with 3–8 imbricate or valvate segments (tepals) in 1 or 2 whorls. *Stamens* 3–7 in a single whorl opposite the tepals, or in a double whorl inserted opposite the outer tepals; filaments with two basal glands, or with one dorsal gland, or without glands; anthers 2-locular, dehiscent with 2 lateral or apical valves; interstaminal staminodes present or absent. *Ovary* inferior, 1-locular; ovule 1, pendulous; style simple, in male flowers absent or reduced; stigma discoid and oblique or capitate. *Fruits* dry, indehiscent, nut- or drupe-like, unwinged and enclosed by inflated, fleshy, expanded cupule (*Hernandia*) or not, or with 2–4 lateral wings (*Illigera*) or with 2 apical wings (*Gyrocarpus*). Seed 1, without endosperm; embryo straight; cotyledons large.

DISTRIBUTION

A family of 4 genera, *Gyrocarpus* (3 species) and *Hernandia* (24 species) both tricentric-tropical, *Illigera* (c. 20 species) in the African–Asian–Malesian region, and *Sparattanthelium* (13 species) in Central America and Mexico.

HABITAT AND ECOLOGY

Habitat — Mostly confined to the everwet tropics, but several species are characteristic of areas with a marked periodical drought (*Gyrocarpus*, some species of *Illigera*). The majority of the species occurs in the tropical lowland areas, only some SE Asian *Illigera* species and some local-endemic Pacific *Hernandia* species reach the submontane zone.

Pollination — No observations are recorded, but the flowers of *Hernandia* and *Illigera* are often reported to be fragrant and the staminal appendages of *Illigera* seem to function as nectaries; the pollen grains of both genera are large and sticky. These characters suggest that the *Hernandia* and *Illigera* species may be entomogamous. The flowers of *Gyrocarpus* and *Sparattanthelium* are small and numerous, especially the male ones.

1) With contributions by P. Baas, Leiden (vegetative anatomy), R.W.J.M. van der Ham, Leiden (paleontology), and R. Hegnauer, Leiden (phytochemistry).

They are not fragrant and pollen grains are small and powdery; these genera are possibly anemogamous.

Dispersal — All *Hernandiaceae* have more or less drupaceous fruits which are winged in *Illigera* and *Gyrocarpus*. The fruits may be drifted by the wind over short distances. Fruits of *G. americanus* and *H. nymphaeifolia* have been observed drifting in the sea, and can retain their buoyancy for several months; in both species the buoyancy is apparently effected by the spongy testa.

TAXONOMY

The genera here recognized in *Hernandiaceae* have a checkered taxonomic history. Kubitzki (1969) comprehensively dealt with it. Most authors agree upon a relation with *Lauraceae*. *Gyrocarpus* is often placed in a separate family, *Gyrocarpaceae*. Pax (1889) established *Hernandiaceae* in the present sense, with four genera, divided into two sub-families, *Hernandioideae* (*Hernandia* and *Illigera*) and *Gyrocarpoideae* (*Gyrocarpus* and *Sparattanthelium*); this was followed by Kubitzki (1969). See also page 761.

References: Kubitzki, K., Bot. Jahrb. 89 (1969) 78–209. — Pax, F.A., in Engler & Prantl, Nat. Pflanzenfam. 3, 2 (1889) 129.

VEGETATIVE ANATOMY

(P. Baas)

Leaf anatomy — Metcalfe (1987) gave a detailed leaf anatomical account of all genera, incorporating information from the literature. Below follows a summary for the three genera occurring in Malesia. Nonglandular, simple hairs range from straight to curved or hooked. Glandular hairs are absent from *Gyrocarpus*; in *Hernandia* and *Illigera* they are globular or pear-shaped with a unicellular stalk and a unicellular or multicellular body. Stomata paracytic in *Illigera* and *Hernandia*; the anomocytic stomata in *Gyrocarpus* have parallel cuticular flanges, recalling paracytic stomata. Cystoliths present in *Gyrocarpus*, absent in *Hernandia* and *Illigera*.

Wood anatomy — For full bibliographies on the wood anatomy of *Hernandiaceae*, see Gregory (1994) and Metcalfe (1987). Growth rings absent to distinct. Vessels diffuse, solitary and in radial multiples, with simple perforations. Intervessel pits alternate, vessel–ray pits coarse and with reduced borders. Fibres thin-walled in most species, with minutely bordered to simple pits (*Gyrocarpus*, *Hernandia*) or distinctly bordered ones (*Illigera*). Parenchyma paratracheal, vasicentric to aliform (*Gyrocarpus* and *Hernandia*) or scanty (*Illigera*). Rays mostly multiseriate, homocellular to heterocellular. Secretory (oil or mucilage) cells present in varying frequency among the axial parenchyma in *Gyrocarpus* and *Hernandia*, among ray parenchyma in *Illigera*. Crystalliferous cells noted in rays of some species of *Hernandia*.

Taxonomic aspects — On balance the anatomical evidence is inconclusive with respect to the status of *Gyrocarpus* and the New World genus *Sparattanthelium* as a separate

family, *Gyrocarpaceae*. In their leaf anatomy the latter share the presence of cystoliths (also present in the wood of *Sparattanthelium*) but in wood anatomy they do not differ substantially from *Hernandia*; *Illigera* appears more isolated.

References: Gregory, M., Bibliography of systematic wood anatomy of Dicotyledons, IAWA J. Suppl. 1 (1994). — Metcalfe, C.R., Anatomy of the Dicotyledons, ed. 2, 3 (1987) 174–184.

PALYNOLOGY

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

Pollen of the *Hernandiaceae* has been more or less extensively described and illustrated with light micrographs or drawings by Agababian (1969), Kubitzki (1969) and Mitroiu (1970). Scanning electron micrographs of *Illigera* pollen were included by Walker (1976a, b), Straka & Friedrich (1988) and Tang & Shang (1995).

The pollen grains of the *Hernandiaceae* are small to very large (19–168 μm), spheroidal and inaperturate (functionally omniaperturate). The exine is very thin, intectate, and loosely to densely covered with warts (*Sparattanthelium*) or 1.8 to 9.6 μm long spines. A transmission electron micrograph of the wall of *Hernandia* pollen (Hesse & Kubitzki 1983) shows a c. 0.4 μm thick granular exine with a solid conical spine. In *Illigera* pollen the spines have flattened contiguous bases. The intine is always distinctly thicker than the exine. In *Hernandia* and *Illigera* it consists of a thin homogeneous inner layer and a thick outer channeled layer. In the other two genera the intine seems to be homogeneous throughout (Kubitzki 1969).

Two pollen types may be distinguished: *Hernandia* and *Illigera* have large (83–168 μm) pollen grains, provided with pollenkitt and a stratified intine, while *Gyrocarpus* and *Sparattanthelium* have smaller (19–64 μm) grains, without pollenkitt, and, as far as known, a homogeneous intine. These differences are probably associated with contrasting pollination types: entomogamy and anemogamy respectively.

The pollen grains of *Hernandia* and *Illigera* are very similar. However, no special characters indicating the monophyly of the family in its present circumscription have been found. Pollen of the *Hernandiaceae* is like that of several *Lauraceae*, and the pollen of *Hernandia* and *Illigera* also resembles that of *Peumus* of the *Monimiaceae* (Erdtman 1952; Shutts 1960; Walker 1976a, b; Hesse & Kubitzki 1983; Tang & Shang 1995). A cladistic analysis of 49 taxa of *Magnoliidae* by Loconte & Stevenson (1991) using 104 characters confirmed the monophyly of the *Hernandiaceae* and the above subdivision of the family, and indicated a sister group relation to the *Lauraceae*. However, pollen morphology did not contribute to these results, because the ten pollen characters used were coded similarly in the *Lauraceae* and the four genera of the *Hernandiaceae*.

References: Agababian, V.S., Biol. Zh. Armenii 22, 3 (1969) 45–58. — Erdtman, G., Pollen morphology and plant taxonomy (1952). — Hesse, M. & K. Kubitzki, Pl. Syst. Evol. 141 (1983) 299–311. — Kubitzki, K., Bot. Jahrb. 89 (1969) 78–148. — Loconte, H. & D.W. Stevenson, Cladistics 7 (1991) 267–296. — Mitroiu, N., Acta Bot. Hort. Bucurest. 1969 (1970) 3–243. — Shutts, C.F., Trop. Woods 113 (1960) 85–123. — Straka, H. & B. Friedrich, Trop. Subtrop. Pflanzenwelt 61 (1988) 5–117. — Tang, G.G. & C.B. Shang, Acta Phytotax. Sinica 33 (1995) 161–170. — Walker, J.W., Linn. Soc. Symp. Ser. 1 (1976a) 251–308; in C.B. Beck, Origin and early evolution of Angiosperms (1976b) 241–299.

PHYTOCHEMISTRY

(R. Hegnauer)

Several reviews of the chemistry of the family are available (Hegnauer 1966, 1989; Kubitzki 1969; Pernet 1971; Gottlieb et al. 1993). It has to be stressed, however, that thorough chemical investigations are restricted to a few species of *Illigera* and *Hernandia* and to alkaloids of *Gyrocarpus americanus* and *Sparattanthelium uncigerum*. A summary of presently known chemical data follows.

Kubitzki (1969) investigated phenolics in hydrolized leaf extracts and reported genus-characteristic patterns. Kaempferol, quercetin and its 3'-methylether isorhamnetin were detected in 14 taxa of *Hernandia* and occurred erratically and usually in trace amounts only in *Illigera* (16 taxa investigated), *Gyrocarpus americanus* and *jatrophifolius* and *Sparattanthelium* (12 taxa). Vitexin-like C-glycoflavones were present in *Hernandia albiflora* and in all taxa of *Illigera* and in trace amounts in 7 taxa of *Sparattanthelium*. Proanthocyanidins were present in large to moderate amounts in 7 taxa of *Hernandia*, 14 taxa of *Illigera*, but were totally lacking in *Gyrocarpus* and *Sparattanthelium*. Ferulic and sinapic acids were detected in trace to moderate amounts in practically all taxa of *Hernandia*, *Gyrocarpus* and *Sparattanthelium* and were lacking in *Illigera*. The apparent absence of the wide-spread *p*-coumaric and caffeic acids and the greatly reduced or totally suppressed production of flavonols and flavones in *Gyrocarpus* and *Sparattanthelium* represent notable features of phenolic metabolism of *Hernandiaceae*. Concerning flavonoids it should not be forgotten, however, that screening procedures of the type applied by Kubitzki and making use of herbarium material are useless for the detection of flavanones and flavanonols (= 2,3-dihydroflavonols). Indeed, prenylated and/or geranylated flavanones, the nymphaeols -A to -C, were isolated from *H. nymphaeifolia* (Presl) Kubitzki (= *H. peltata*; Japanese name 'Hasunoha-giri') (Yakushijin et al. 1980).

One class of compounds is relatively well known from the family. Alkaloids have been detected in all four to five genera. They belong to the phenylalanine-tyrosine-derived family of isoquinoline alkaloids and are represented by the benzyloisoquinoline-, aporphine-, oxo-aporphine-, N,N-dimethylaminoethyl-phenanthrene-types and by dimeric derivatives of these monomers. A strange compound is 3-cyano-4-methoxypyridine from *H. nymphaeifolia* (Yakushijin et al. 1980); as yet its biogenesis is not known.

Lignans seem to occur frequently in stems, leaves and seeds of many species of *Hernandia*. Hitherto they were not yet isolated from representatives of other hernandiaceous genera. Known *Hernandia* lignans belong to several types: furofuranoid-, tetralin (= tetrahydronaphthalene)-, naphthalene- and bibenzylbutanolide-types; examples (isolated from *Hernandia* taxa) are epimagnolin, podophyllotoxin, 1,2,3,4-tetrahydrodehydroxy-podophyllotoxin and podorhizol. Two new lignans, dimethylmatairesinol and 5'-methoxypodorhizol, were isolated from seeds of *H. ovigera*; seeds of this taxon yielded eleven lignans till today (Tanoguchi et al. 1991). Neolignans were not yet detected in the family.

Oil cells of the magnolioid type are wide-spread in the family; they occur mainly in leaves and in the primary cortex and pith of stems (Kubitzki 1969) and perhaps also in roots and fruits. Their presence indicates that essential oils should be of common occurrence. However, only a few investigations of essential oils are reported in literature. *Hernandia peltata* yielded essential oils from roots, stems and fruits in Madagascar; the wood oil (2%) had perillaldehyde as main compound and myrtenal, cineol and limonene as additional monoterpenes. The smell of perillaldehyde is described in literature as cumin-like or as camphoraceous (Gildemeister & Hoffmann 1959, 1963; Guenther 1949; Weber 1974). Perillaldehyde is also the principal constituent of the essential oil of bark and twigs of Madagascan *H. voyroni* [= *Hazomalania voyroni* (Jumelle) Capuron] (Weber 1974).

Metcalf (1987) stated "oil cells have been reported in all genera and species and they are sometimes accompanied by mucilage cells." The last-mentioned feature reminds of *Lauraceae* and explains observations made by Greshoff that the bark of *H. ovigera* and *H. sonora* is mucilaginous.

Hernandiaceae have seeds without endosperm (all ?) containing embryos with large cotyledons. Some hints can be found in literature that several species store large amounts of fatty oils in their seeds, but exact information is scarce. According to Netolitzki (1926) *Hernandiaceae* (which?) store fatty oils, protein bodies and starch in cotyledons. Corner (1976) stressed the fact that hitherto only seeds of *Hernandia* were studied in some detail and drew attention to similarities between seeds of *Hernandia* and those of *Myristicaceae*.

Usually affinities of *Hernandiaceae* with *Lauraceae* and *Monimiaceae* are assumed. As far as chemical data are available they do not contradict such a relationship.

References: Corner, E.J.H., The seeds of dicotyledons, vol. 1 (1976) 152. — Gildemeister, E. & F. Hoffmann, Die ätherischen Öle, ed. 4 (ed. W. Treibs), 3 (1963) 115 (Perillaaldehyd); 5 (1959) 149–151 (*Hernandiaceae*). — Gottlieb, O.R., et al., pp. 20–31, 337 in K. Kubitzki et al. (eds.), The families and genera of flowering plants, vol. 2 (1993). — Guenther, E., The essential oils 2 (1949) 342 (perillaldehyde). — Hegnauer, R., Chemotaxonomie der Pflanzen 4 (1966) 246–249, 502; 8 (1989) 557–562. — Kubitzki, K., Monographie der Hernandiaceen, Bot. Jahrb. 89 (1969) 78–209 (Chemische Merkmale 97–105). — Kubitzki, K., *Hernandiaceae*, pp. 334–338 in K. Kubitzki et al. (eds.), The families and genera of flowering plants, vol. 2 (1993). — Metcalfe, C.R., Anatomy of the Dicotyledons, ed. 2, 3 (1987) 174–184 (*Hernandiaceae*). — Netolitzki, F., Anatomie der Angiospermen-Samen, in Linsbauers Handbuch der Pflanzenanatomie 10 (1926). — Pernet, R., Revue des Hernandiacees, Planta Medica 20 (1971) 314–319. — Tanoguchi, M., et al., Chem. Pharm. Bull. 39 (1991) 1873. — Weber, N., Phytochemistry 13 (1974) 2006. — Yakushijin et al., Heterocycles 14 (1980) 161; Phytochemistry 19 (1980) 161.

USES

Some *Hernandia* species and *Gyrocarpus americanus* produce a rather soft and not very valuable wood, used for making canoes and as timberwood. The oil of the seeds of *Hernandia nymphaeifolia* is used locally as lampoil, but is of inferior quality (Heyne 1950).

Reference: Heyne, K., Nutt. Pl. Indon., ed. 3 (1950) 674.

KEY TO THE GENERA

- 1a. Woody climbers. Leaves palmately compound, petioles twisting. Fruits with 2–4 lateral wings (wings sometimes ridge-like) **Illigera** (p. 751)
- b. Trees. Leaves simple, petioles not twisting. Fruits with 2 apical wings or fruits surrounded by an inflated cupule 2
- 2a. Deciduous trees. Inflorescences without bracts, flowers minute, buds less than 1.5 mm diameter. Fruits with 2 apical wings **Gyrocarpus** (p. 742)
- b. Evergreen trees. Inflorescences with bracts, flowers conspicuous, buds more than 2 mm diameter. Fruits surrounded by an inflated cupule **Hernandia** (p. 744)

GYROCARPUS

Gyrocarpus Jacq., Select. Stirp. Amer. (1763) 282; Kubitzki, Bot. Jahrb. 89 (1969) 181; Kubitzki et al. (eds.), The families and genera of vascular plants 2, X (1993) 337. — Type species: *Gyrocarpus americanus* Jacq.

Deciduous trees. *Leaves* simple, entire or 3(–5)-lobed; veining palmate. *Inflorescence* axillary or terminal, a more or less repeatedly dichotomous corymbose thyrse, ebracteate, sometimes precocious. *Flowers* bisexual or unisexual (mostly male), numerous, small (less than 1.5 mm). *Bisexual* and *female flowers* with (6–)7(–8) perianth segments (tepals), four of these forming an opposite pair, each pair consisting of two adjacent tepals with common basal meristem growing out during and after anthesis into two spatulate wings on top of the nut; style sigmoid, stigma capitate; *stamens* 4 or 5, or less, filaments provided with small dorsal glands or not; clavate staminodes alternating with stamens. *Male flowers* similar to bisexual flowers, with 4–7 perianth segments (tepals); ovary and style reduced or absent; wings absent; *stamens* 4–7, more conspicuous than in bisexual flowers; staminodes 4 or 5, free and alternating with stamens or (not in Malesia) fused. *Fruit* a samara; nut ovoid or elongate-ellipsoid with two large apical spatulate wings; pericarp hard, rather thick. *Seeds* with spongy testa (in one American species membranous); cotyledons contortuplicate.

Distribution — A pantropical genus of 3 species: *G. jatrophifolius* Chiov. in Central America; *G. hababensis* Domin in E Africa; *G. americanus* widely distributed throughout the tropics.

Habitat — Open, often rocky places, in light or deciduous forests, sometimes in rain forests; also at the shore.

Dispersal — The falling fruit quickly rotates, the wings being stretched out in an angle of 120–140°, facilitating a steady fall created by the air-resistance, and achieving dispersal over short distances (Von Wahl 1897, Biblioth. Bot. 40: 14). The fruits of *G. americanus* and *G. hababensis* can be carried by water, the buoyancy due to the spongy seed-coat. Testified by the wide coastal distribution of these species, this kind of dispersal apparently is effective.



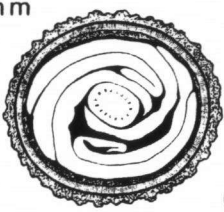
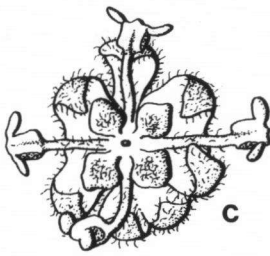
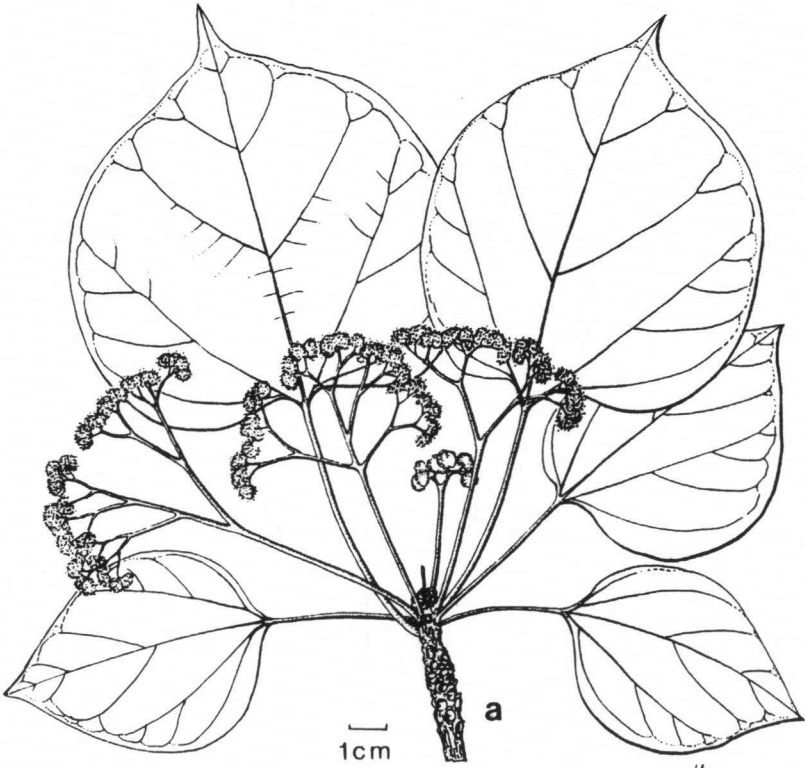
Fig. 1. *Gyrocarpus americanus* Jacq. Leafy twig and infructescence. Sri Lanka. Photo T.B. Worthington, 1965.

***Gyrocarpus americanus* Jacq.**

Gyrocarpus americanus Jacq., Select. Stirp. Amer. (1763) 282, t. 178, f. 80; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 205; Backer & Bakh. f., Fl. Java 1 (1964) 136; Kubitzki, Bot. Jahrb. 89 (1969) 182; Ng in Tree Fl. Malaya, 2 (1973) 244, f. 1. — *Gyrocarpus americanus* subsp. *americanus*: Kubitzki, Bot. Jahrb. 89 (1969) 183, f. 45; Croft in Handb. Fl. Papua New Guinea 2 (1981) 191, f. 42; A. C. Sm., Fl. Vit. Nov. 2 (1981) 143, f. 46; Du Puy & Telford in Fl. Austral. 50 (1993) 72. — Type: *Jacquin s.n.* (BM), Colombia, Cartagena.

Gyrocarpus jacquini Gaertn., Fruct. 2 (1791) 92, t. 97, nom. illeg.; Ridley, Fl. Malay Penins. 3 (1924) 139. — Type: 'E collectione Sem. Banksiana'.

Gyrocarpus lobatus Blanco, Fl. Filip. 2 (1845) 54; Merr., Sp. Blanc. (1918) 155. — Type: destroyed; neotype, illustrative specimen: *Merrill Sp. Blanc. 755*, Philippines.



Gyrocarpus asiaticus Willd. var. *?javanicus* Meisn. in A.DC., Prodr. 15 (1864) 248. — *Gyrocarpus jacquini* Gaertn. var. *javanicus* Domin, Bibl. Bot. 89 (1925) 680. — Type: Zollinger 2889 (A, BM, BR, FI, NY), Java.

Gyrocarpus rugosus R. Br. var. *?philippinensis* Meisn. in A.DC., Prodr. 15 (1864) 248. — Type: Llanos s.n., 1853 (NY, fragm. ex G-DC), Philippines.

Tree 3–30 m high, dbh 20–100 cm, trunk smooth or with coarse scales, pale grey or nearly white. *Leaves*: petiole 4–19.5 cm long; leaf-blade coriaceous or chartaceous, entire, or in young trees with 3 or 5 acute lobes, cordate to ovate, 7–24 by 4–21 cm, base cordate to broadly rounded to cuneate, apex c. 1 cm acuminate, pubescent on both surfaces or the upper surface glabrous, nerves conspicuous, 3- or 5-palminerved, with ladder-like tertiary veining. *Inflorescence* (including 3–6 cm long peduncle) 5–17 cm long, the flowers compact, all parts more or less pubescent. *Flowers* 4-merous, small (mature bud less than 1.5 mm diam.), bisexual and unisexual (only male flowers), pale green or creamy; filaments in female flowers c. 1.5 mm long, in male flowers c. 2 mm long with 4 alternating small glands, 0.5–1 mm long. *Fruits*: nut ovoid, 1.4–2 by 0.8–1.3 cm, longitudinally 8-ribbed, topped with a pair of spatulate wings, 6.5–9 cm long, 2–3 mm wide at base, 0.8–1.1 cm wide at widest part, resembling those of certain dipterocarps, yellowish green; the whole fruit thinly up to thickly pubescent, seldom glabrous. — **Fig. 1, 2.**

Distribution — Pantropical, in regions with a monsoon climate; in *Malesia*: Peninsular Malaysia, E Java, Philippines, Lesser Sunda Islands, Papua New Guinea (around Port Moresby and in Ramu Valley).

Habitat & Ecology — Frequently found near the shore: on beach, on rocky slopes, in dune scrub; also in savanna, sclerophyll forest on calcareous soil, poor monsoon forest on low hills, stony crests, limestone hills, and banks of gulleys; 0–200 m altitude.

Fieldnotes — Branches ascending with drooping branchlets. Slashed wood with creamy or yellowish exudate; bruised tissue with unpleasant smell. Frequently mentioned as flowering or fruiting while the tree is leafless. The leaves are convex at the time they are falling off. According to *Merrill Sp. Blanc. 755*, the species is in the Philippines widely distributed, but nowhere abundant.

Notes — Kubitzki (1969) distinguished 7 subspecies in *G. americanus* on characters of outline and hair-covering of the leaves, with in the Malesian area 2 subspecies: subsp. *americanus*, occurring in the whole area, and subsp. *sphenopteris* (R.Br.) Kubitzki in the Lesser Sunda Islands (Sumbawa) and the Philippines (Luzon). More field observations are needed to clarify the position of these taxa.

Fig. 2. *Gyrocarpus americanus* Jacq. a. Flowering twig; b. bisexual flower; c. male flower, seen from above; d. fruits; e. fruit, transverse section showing contortuplicate cotyledons (a: Cuatrecasas 25451; d: Calderón 1674; b, c, e from living material). Reproduced with permission of Bot. Jahrb. 89 (1969).

HERNANDIA

Hernandia L., Sp. Pl. (1753) 981; Kubitzki, Bot. Jahrb. 89 (1969) 122; in Fl. Camb., Laos & Vietnam 12 (1970) 17; Kubitzki et al. (eds.), The families and genera of vascular plants 2, X (1993) 337. — Type species: *Hernandia sonora* L.

Biasolettia Presl, Rel. Haenk. 2 (1835) 141. — Type species: *Biasolettia nymphaeifolia* Presl.

Trees or shrubs. *Leaves* simple, undivided (seldom 3–5-lobed), peltate (*H. nymphaeifolia* in Malesia) or not, venation palmate or with 3–7 pairs of lateral veins, arching towards the apex. *Inflorescence* usually at and towards the tips of branchlets, the peduncles distinct (rarely short), the ultimate partial inflorescences comprising of modified cincinni and these usually subtended by an involucre of 4 bracts comprising 3 flowers: 2 lateral (rarely 1) pedicelled male flowers, and 1 central sessile female flower (rarely 1 bisexual flower). All parts of inflorescence finely pubescent, rarely glabrous. *Bracteoles* of male flowers more or less equal, those of female flowers united into a cupule partly or wholly surrounding the ovary, accrescent at maturity, or female bracteoles seldom free (*H. bivalvis* Benth., Australia; *H. voyroni* Jum., Madagascar). Outer tepals quincuncial or imbricate, the inner ones partly valvate. *Male flowers* 3–5(–6)-merous; ovary and style lacking or style rudimentary; *stamens* 3–5(–6), filaments free or partly connate, each with two basal glands free or glands connate. *Female flowers* 4–6-merous; *ovary* somewhat compressed laterally, without staminodes; style sigmoid or straight, at base often thickened and surrounded by 4–5(–10–12) free or connate glands; stigma dilated or irregularly lobed. *Drupe* ovoid to ellipsoid, often inconspicuously longitudinally ribbed, with or without an umbo (wart) at apex, at maturity enclosed by the inflated, fleshy cupule, or not (*H. bivalvis*, *H. voyroni*, not in Malesia). *Seeds* with a hard, sometimes spongy testa; cotyledons free or (in Malesia) fused, ruminant.

Distribution — Pantropical genus of 24 species (Kubitzki 1969); in *Malesia* 3 species.

Habitat & Ecology — Mostly in primary and secondary lowland rain forest, coastal forest. In the Pacific some species reach the submontane zone, up to 1500 m altitude.

KEY TO THE SPECIES

- 1a. Leaves peltate **2. *H. nymphaeifolia***
- b. Leaves not peltate 2
- 2a. Leaf-base cordate or broadly rounded, domatia absent. Mature cupule of fruit 3–8 cm long, margin of orifice 2- (or -3)-toothed **3. *H. ovigera***
- b. Leaf-base acute or rounded, domatia present. Mature cupule of fruit 2.5–3 cm long, margin of orifice entire **1. *H. moerenhoutiana***

1. *Hernandia moerenhoutiana* Guill.

Hernandia moerenhoutiana Guill., Ann. Sc. Nat. Bot. II, 7 (1837) 189; Kubitzki, Bot. Jahrb. 89 (1969) 127, f. 23–25 (3 subsp.). — Type: *Bertero & Moerenhout s.n.* (G, P), Tahiti.

Hernandia moerenhoutiana Guill. subsp. *samoensis* auct. non (Hochr.) Kubitzki; Croft in Handb. Fl. Papua New Guinea 2 (1981) 194 (see the note).

Tree, 12–30 m high, c. 30 cm dbh. *Leaves*: petiole 3–6 cm; blade coriaceous, elliptic to oblong, 6–13.5 by 3.5–6 cm, apex broadly rounded (seldom truncate) or obtuse, or acute, base acute or rounded, margin revolute, glabrous on both surfaces but lower surface of young leaves hairy, basal nerves 3, palmate, and midrib with 2 pairs of arching lateral ones, whitish or yellow; domatia present. *Inflorescence* including the 6–13 cm long peduncle 10–20 cm long; involucre bracts elliptic to obovate, 10–11 by 5–8 mm; flower buds globose-ovoid, 3–5 mm in diam. *Flowers* 4- or 5-merous, white, sweetly fragrant. *Male flowers*: pedicel c. 4 mm long, tepals c. 6 mm long, *stamens* 5, filaments c. 1.5 mm long, laxly pilose, each at base with two stiped glands, c. 1 mm long, stipe 0.5 mm long. *Female flowers*: pedicel c. 1 mm long, flower (including ovary) 7.5–8.5 mm long, ovary entirely enveloped by the cupule, tepals c. 5.5 mm long, style c. 2 mm long, surrounding glands 5 (sometimes more glands, but then smaller), firm, c. 1 mm long; cupule in anthesis 2–3 by 4 mm, faintly ribbed, in fruit inflated, loosely enclosing the drupe, green turning red, 2.7–3 cm long, the orifice 1.5–2.5 cm diam., margin irregularly undulate. *Drupe* shorter than the cupule, ovoid, laterally compressed, c. 2 by 1.5 cm, faintly 10-ribbed, the apex with a half-rounded umbo, which is contracted at the beak.

Distribution — Widespread in the Pacific from Manus I. eastward to the Society Islands; in *Malesia*: Papua New Guinea (Manus I., New Britain).

Habitat & Ecology — Found in lowland rain forest on ridges, in colline rain forest on limestone boulders; 100–830 m altitude.

Note — *Hernandia moerenhoutiana* is common and widespread in the Pacific. Kubitzki (1969) accepted in this species three subspecies, viz. subsp. *moerenhoutiana* (Tahiti, Cook Is.), subsp. *campanulata* (Tonga Is., Fiji, Samoa) and subsp. *samoensis* (Solomon Is., Santa Cruz, Samoa). A much related species, *H. cordigera* Vieillard, is restricted to New Caledonia. Kubitzki distinguished these two species on the dimensions of the cupule at anthesis: broader than long leads to *H. cordigera* and longer than broad to *H. moerenhoutiana*. Croft (1981) put the Malesian material into subsp. *samoensis*, but I doubt whether this is correct: the cupules are broader than long and the leaf apices also do not match. The Malesian material very much resembles *H. cordigera*, and pending the availability of more material I prefer to leave it in *H. moerenhoutiana* s.l.; possibly the Malesian and part of the Solomon material represents a fourth subspecies, as yet undescribed.

2. *Hernandia nymphaeifolia* (Presl) Kubitzki

Hernandia nymphaeifolia (Presl) Kubitzki, Bot. Jahrb. 90 (1970) 272; Ng in Tree Fl. Malaya 2 (1973) 245, f. 2; Croft in Handb. Fl. Papua New Guinea 2 (1981) 193, f. 43; A.C. Sm., Fl. Vit. Nov. 2 (1981) 110, f. 39; Corner, Wayside Trees 1, 3 (1988) 363, f. 120; Du Puy & Telford in Fl. Austral. 50 (1993) 71. — *Biasolettia nymphaeaeifolia* Presl, Rel. Haenk. 2 (1835) 142. — Type: *Haenke s.n.* (PR), Guam.

Hernandia peltata Meisn. in A.D.C., Prodr. 15 (1864) 263; Koord. & Valetton, Atlas 1 (1913) f. 184; Backer & Bakh.f., Fl. Java 1 (1964) 137, excl. syn. *H. javanica* Tuyama; Kubitzki, Bot. Jahrb. 89 (1969) 153. — Type: *Thwaites CP 2914* (G-DC lecto; B, BM, G, L, W), Sri Lanka.

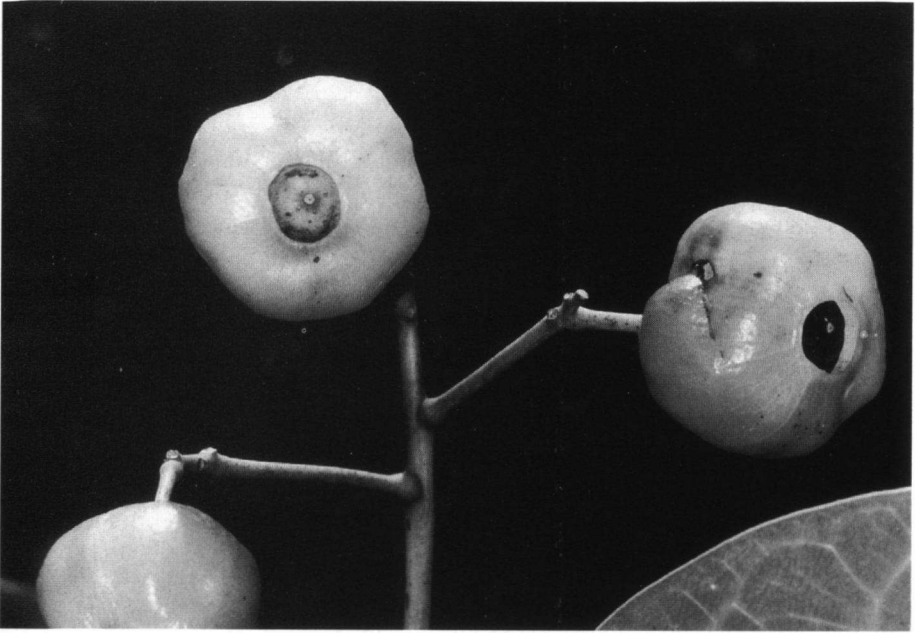


Fig. 3. *Hermandia nymphaeifolia* (Presl) Kubitzki. Part of infructescence showing three fruits enclosed by the inflated cupules. Tree along the southcoast of Java. Photo W. J. J. O. de Wilde, 1995.

Shrub or tree 5–22 m high, dbh up to 90 cm (in Fiji up to 200 cm, A. C. Smith 1981). *Leaves*: petiole 5–17 cm long, peltately attached 0.5–3 cm from the margin; blade chartaceous or thinly coriaceous, shining above, dull beneath, narrowly or broadly ovate, or subcircular, 7–33 by 6–29 cm, apex acute or slightly acuminate, glabrous on both surfaces, nerves 5–9, palmate, conspicuously white or yellow, the central nerve with 2–4 lateral nerves per side, arching towards apex, domatia absent. *Inflorescence* including the 6–20 cm long peduncle 10–30 cm long; involucre bracts elliptic to obovate, 2–6 by 1–3.5 mm. *Flowers* 3-merous (male) or 4-merous (female), greenish or white, fragrant. *Male flowers*: pedicel 4–4.5 mm long, tepals c. 5 mm long; anthers yellow, filaments c. 3 mm long, each basally with two subspathulate glands c. 1 mm long, free or pairwise fused between the stamens. *Female flowers*: pedicel absent; flower (including the ovary) 8–10 mm long, ovary up to halfway enveloped by the cupule; tepals c. 5 mm long, style papillose, c. 3 mm long, surrounding glands 4 (sometimes more), firm, c. 1 mm long, free or fused, stigma pink; cupule in anthesis c. 2 by 3 mm, the margin entire or slightly undulate, in fruit loosely enclosing the drupe, inflated, bell-shaped, fleshy and waxy white or reddish, the margin of the orifice entire and slightly revolute. *Drupe* as long as the cupule or somewhat exserted, ellipsoid, 2.5–3 by 1.5–2.3 cm, faintly longitudinally 8-ribbed, slightly stalked or not, apex with an umbo, 8–10 mm wide, 2–3 mm high. — Fig. 3.

Distribution — E Africa, Madagascar, Sri Lanka, Andaman & Nicobar Islands, Thailand, Cambodia, Vietnam, Taiwan, Micronesia (northward to Ryukyu & Bonin Islands), Melanesia, Polynesia; in *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java, Christmas Island (Indian Ocean), Lesser Sunda Islands, Philippines, Celebes, Moluccas, New Guinea.

Habitat & Ecology — Occurs exclusively in coastal areas: along the sea-shore (recorded as leaning over the sea and even sometimes immersed by sea water), in primary and secondary littoral forest (*Barringtonia asiatica* association), also behind the beach in swampy places; on sand, coral beach, or pebbles; at low altitude.

Notes — 1. The wood is soft and light in weight and of little use as timber; in some parts of the Pacific it is used for making canoes.

2. According to Kubitzki (1969) the species seems to hybridize with *H. ovigera*.

3. *Hernandia ovigera* L.

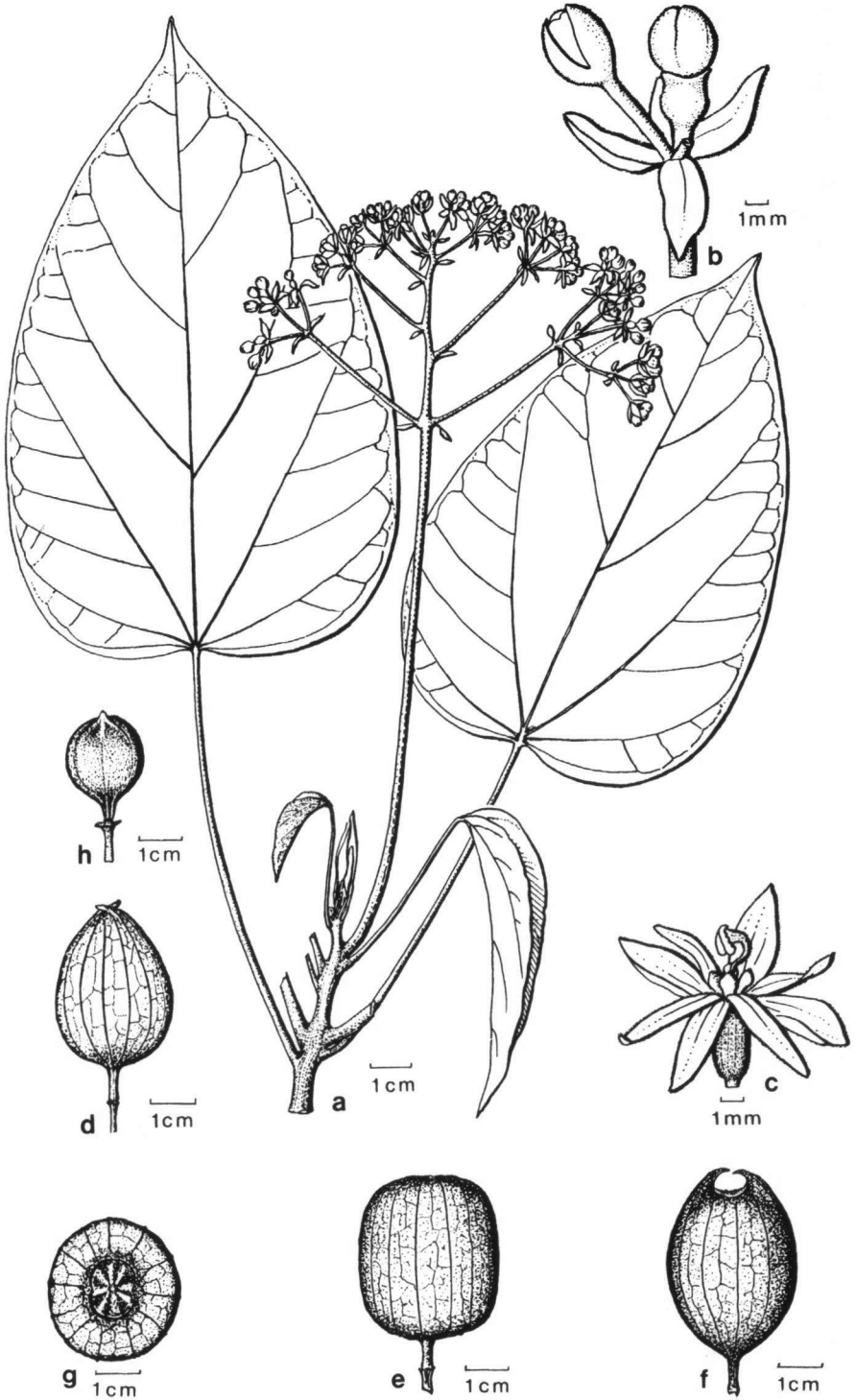
Hernandia ovigera L. (Diss. O. Stickman), Herb. Amboin. (1754) 14; Rumph., Herb. Amboin. 3 (1743) 193, t. 123; Koord. & Valetton, Atlas 1 (1913) f. 185; Backer & Bakh.f., Fl. Java 1 (1964) 137; Kubitzki, Bot. Jahrb. 89 (1969) 138, f. 31; Croft in Handb. Fl. Papua New Guinea 2 (1981) 196, f. 44; Du Puy & Telford in Fl. Austral. 50 (1993) 70, f. 32 F–H. — Type: Rumphius (1743: t. 123).

Hernandia papuana C.T. White, J. Arnold Arbor. 10 (1929) 216. — Type: *Brass 1073* (A), Papua New Guinea, Madang.

Hernandia javanica Tuyama, Bull. Sigenkagaku Kenkyusyo 1 (1943) 44. — Type: not indicated.

Tree, 20–40 m high, dbh 50–100 cm. *Leaves*: petiole 7–19 cm; blade chartaceous or coriaceous, broadly lanceolate to broadly ovate, 10–25(–40) by 6–21(–30) cm, apex 0.5–1(–2) cm acuminate, base more or less cordate or broadly rounded, shining and glabrous on both surfaces but nerves on lower surface pubescent, nerves 5 (or 7), palmate, the midrib with 3–6 pairs of lateral nerves; domatia absent. *Inflorescence* including the 6–18 cm long peduncle 15–30 cm long; involucre bracts elliptic or obovate, 4–7 by 1–3 mm. Flower buds ellipsoid. *Flowers* 3-merous (male), or 4-merous (female), creamy-white, fragrant. *Male flowers*: pedicel 4–5 mm long, tepals c. 7 mm long, *stamens* 3, filaments sparsely pilose or glabrous, each filament with 2 glands c. 1 mm long. *Female flowers*: pedicel c. 1.5 mm long, flower including the ovary c. 1 cm long, ovary entirely enveloped by the cupule, tepals 4–5 mm long, style c. 5 mm long, at the base surrounded by 4 unstiped glands, free, c. 1 mm long; cupule in anthesis fleshy, green, 3–5 by c. 2.5 mm, the margin 2-lobed, in fruit inflated, loosely enclosing the drupe, egg-shaped, 3–8 cm long, turning white or tinged red, the margin with 2(–4) conspicuous teeth. *Drupe* much shorter than the cupule, subglobose to broadly elliptic or ovate, somewhat compressed laterally, 2–2.5 by 1.7–2.2 cm, dark brown, or black, faintly longitudinally 8-ribbed, abruptly tapering into a stalk 2–6 mm long, umbo absent. — Fig. 4.

Distribution — Mariana Is., Solomon Is.; in *Malesia*: scattered collections seen from Simeulue, Enggano (W of Sumatra), Java, Christmas I. (Indian Ocean), Philippines (Luzon), Celebes, Bali, Moluccas (Bacan, Sula I.), common in New Guinea (Irian Jaya):



Vogelkop, western and northern part, Japen I., near Jayapura; Papua New Guinea: Sepik, Madang, Morobe, Milne Bay Prov., New Britain, Woodlark I.).

Habitat & Ecology — Tree from lowland rain forest on coastal plains and alluvial flats; often on riverbanks, or ridges, also in old secondary forest, in hill forest and on steep mountain slopes; recorded from peaty soil, rocky clay, clay, and sandy clay. Found from sea level up to 1000 m altitude, but most collections are from the lowland.

Notes — 1. Kubitzki (1969) discussed the complicated typification of *H. ovigera*. He also noted that the present species seems to hybridize with *H. nymphaeifolia*, especially so in and near New Guinea.

2. Two collections from Christmas I. (Indian Ocean), *Powell 21* and *Mitchell 30*, show the cupules curiously and deceptively dissected but the phenomenon appeared artificial.

ILLIGERA

Illigera Blume, Bijdr. (1826) 1153; Hutch., Gen. Flow. Pl. 1 (1964) 145; Kubitzki, Bot. Jahrb. 89 (1969) 157; Kubitzki et al. (eds.), The families and genera of vascular plants 2, X (1993) 337. — Type species: *Illigera appendiculata* (lectotype, see Hutchinson 1964).

Henschelia Presl, Rel. Haenk. 2 (1835) 81, t. 63. — Type species: *Henschelia luzonensis* Presl.

Gronovia Blanco, Fl. Filip. (1837) 186. — Type species: *Gronovia ternata* Blanco.

Corysadenia Griff., Proc. Linn. Soc. 1 (1846) 281; Not. Pl. As. (1854) 356 ('*Corysadenia*'). — Type species: *Corysadenia trifoliata* Griff.

Generally medium-sized woody climbers, climbing with the aid of twisted petioles. *Leaves* 3(–5)-foliolate, seldom simple and 3-lobed (not in Malesia); leaflets petioluled, top mostly acuminate, veins loop-like with midrib and lateral nerves curved towards apex or basal. *Inflorescence* terminal and axillary, many- or few-flowered; partial inflorescences cincinni, paired or simple, with bracts; bracts persistent (or caducous). *Flowers* bisexual, 5-merous, perianth segments (tepals) in two rows, valvate in bud, oblong, inner ones linear, deciduous; outer ones 3–5-nerved, inner ones 1–3-nerved; *ovary* ovoid, 4-angled, in fruit the angles grown out into 2 or 4 wings, style filiform; *stamens* 5, inserted opposite the outer tepals and alternating with sessile glands, or glands absent (*I. celebica*); filaments straight and slightly flattened, or inwardly coiled and conspicuously flattened, each at base with two inflated, membranous, shortly stiped appendages, or appendages clavate and solid; anthers ovoid. *Fruit* a samara; the nut with 2 longer and 2 shorter lateral wings (or wings sometimes absent), wings membranous, suborbicular or lingulate. *Seeds* with membranous testa; cotyledons free, more or less planoconvex, or slightly unequal.

Distribution — About 20 species, the majority in the Sinohimalayan region; in *Malesia* 9 species; in Africa and Madagascar 3 species.

Fig. 4. *Hernandia ovigera* L. a. Flowering twig; b. partial inflorescence, one male flower fallen off; c. female flower, cupule removed; d, e, f. inflated cupule; g. cupule and drupe seen from above; h. drupe (a, b: *Brass* 28620; c: *van Royen* 5096; d, h: *NGF* 7040; e, g: *BW* 358; f: *NGF* 4743). Reproduced with permission of Bot. Jahrb. 89 (1969).

Habitat & Ecology — Climbers in forests, or forest edges, in bushes and in thickets; some species in everwet regions, others in areas with periodical draught. Most species grow in the lower tropical zone, but in the Sinohimalayan region some may ascend up to 3300 m altitude.

KEY TO THE SPECIES

- 1a. Angle of lateral nerves with main nerve almost right, 80–90° **8. I. pulchra**
 b. Angle of lateral nerves (basal nerves excepted), with main nerve much sharper, c. 30–60° 2
- 2a. Flower buds globose; stamens in bud and in young flower inwardly coiled, conspicuously protruding in anthesis; staminal appendages solid and clavate 3
 b. Flower buds ovoid or ellipsoid; stamens in bud straight or sigmoid, in young flowers straight, not or slightly protruding in anthesis; staminal appendages inflated and petaloid 4
- 3a. Filaments broad, tepal-like, at base 1.5–2.5 mm wide, the margins curved around the staminal appendages; interstaminal glands absent **2. I. celebica**
 b. Filaments narrow, not tepal-like, at base c. 0.5 mm wide, the margins not curved around the staminal appendages; interstaminal glands present **7. I. parviflora**
- 4a. Staminal appendages dorsally entire, not cleft 5
 b. Staminal appendages dorsally cleft 6
- 5a. Rim of staminal appendages conspicuously finger-like fringed, the fringes c. 0.5 mm long, inner perianth segments narrow, much narrower than outer perianth segments, c. 0.8 mm wide. Christmas I. (Indian Ocean) **3. I. elegans**
 b. Rim of staminal appendages with short fringes, c. 0.2 mm long; inner perianth segments about as wide as outer segments, c. 2 mm wide. Papua New Guinea **6. I. novoguineensis**
- 6a. Fruit wings lingulate, 3.5–6 cm long **5. I. megaptera**
 b. Fruit wings hemi-orbicular, or sublingulate, 1.5–4 cm long 7
- 7a. Staminal appendages pointed at the top, not curved; perianth segments c. 2 mm acuminate **1. I. appendiculata**
 b. Staminal appendages spathe-like, more or less hooded towards outside; perianth segments acute, or c. 0.5 mm acuminate 8
- 8a. Flowers 10–12 mm long, subglabrous; leaves usually drying blackish-brown **4. I. luzonensis**
 b. Flowers 7–9 mm long, hairy; leaves drying brown **9. I. trifoliata**

1. Illigera appendiculata Blume

Illigera appendiculata Blume, Bijdr. (1826) 1153; Dunn, J. Linn. Soc. Bot. 38 (1908) 294; Backer, Bull. Jard. Bot. Buitenzorg II, 12 (1913) 19; Backer & Bakh. f., Fl. Java 1 (1964) 136; Kubitzki, Bot. Jahrb. 89 (1969) 164, f. 39. — Type: *Blume 1472* (L), Java.

Leaves: petiole 3–13 cm, petiolules 0.5–1.5 cm, brown villose; leaflets chartaceous to coriaceous, lanceolate, elliptic, or ovate (or obovate), 6–14 by 3–9 cm, apex faintly

acute or with an acumen 3–10 mm long, base cordate or rounded (or cuneate), upper surface dull, both surfaces glabrous or sparsely hairy, but nerves on lower surface, especially midrib, hairy, domatia present; nerves: 3–6 pairs (at an angle of c. 45° with the midrib). Thyrses brownish tomentose. *Flower buds* ellipsoid, 6–9 mm long, with short brown hairs. Bracteoles c. 2.5 by 1.5 mm. *Perianth* in anthesis greenish, tinged purplish or pinkish. Tepals acute, up to 2 mm acuminate, both sides with short brown hairs, especially so towards the top; outer tepals 9–11 by 2–4 mm, 5-nerved, inner ones 9–10 by c. 2.5 mm, 3-nerved. *Filaments* ± filiform, slightly hairy, c. 4 mm long; *staminal appendages* including the c. 0.5 mm long stipe 2–2.5 mm long, inflated, ventrally with a pointed apex, dorsally broadly cleft, rim slightly denticulate; interstaminal glands present. *Fruits* reddish in living plants, cinnamon-coloured when dry, nut 2.5–3 cm long, 4-winged, but only one pair fully developed, the other pair obsolete or ridge-like; wings lingulate (subsp. *appendiculata*) or hemi-orbicular (subsp. *stenoptera*).

Distribution — *Malesia*: Sumatra, E Kalimantan (Kutai), Java, SW Celebes, Kangean I., Lesser Sunda Islands (Lombok, Sumbawa, Flores, Timor); see also note 2 under subsp. *stenoptera*.

Note — There are two closely resembling subspecies, distinct by differences in the wings of the fruit.

KEY TO THE SUBSPECIES

- a. Wings of nut lingulate, 2–3.5 cm long a. subsp. **appendiculata**
 b. Wings of nut hemi-orbicular, c. 2.5 cm in diameter b. subsp. **stenoptera**

a. subsp. **appendiculata**

Fruit wings well developed, lingulate, very finely and regularly striated, 2–3 cm long. A good illustration is given by Kubitzki (l.c.: f. 39 II).

Distribution — *Malesia*: Sumatra, W Java.

Habitat & Ecology — Foothill forest, primary dryland forest on flat alluvial soil; 30–800 m altitude.

b. subsp. **stenoptera** Kubitzki

Illigera appendiculata Blume subsp. *stenoptera* Kubitzki, Bot. Jahrb. 89 (1969) 164, f. 39 VII. — Type: *Sujarto* 79 (L), Sumbawa.

Illigera dubia Span., Linnaea 15 (1841) 187. — Type: *Spanoghe* 22 (L holo), Timor.

Fruit wings well developed, hemi-orbicular, c. 2.5 cm in diameter, striated, but less finely and regularly as in subsp. *appendiculata*.

Distribution — *Malesia*: E Java? (no collections seen), Kangean I., Lesser Sunda Islands (Lombok, Sumbawa, Flores, Timor).

Habitat & Ecology — In primary monsoon forest, in semi-dry forest and in secondary forest; 400–900 m altitude.

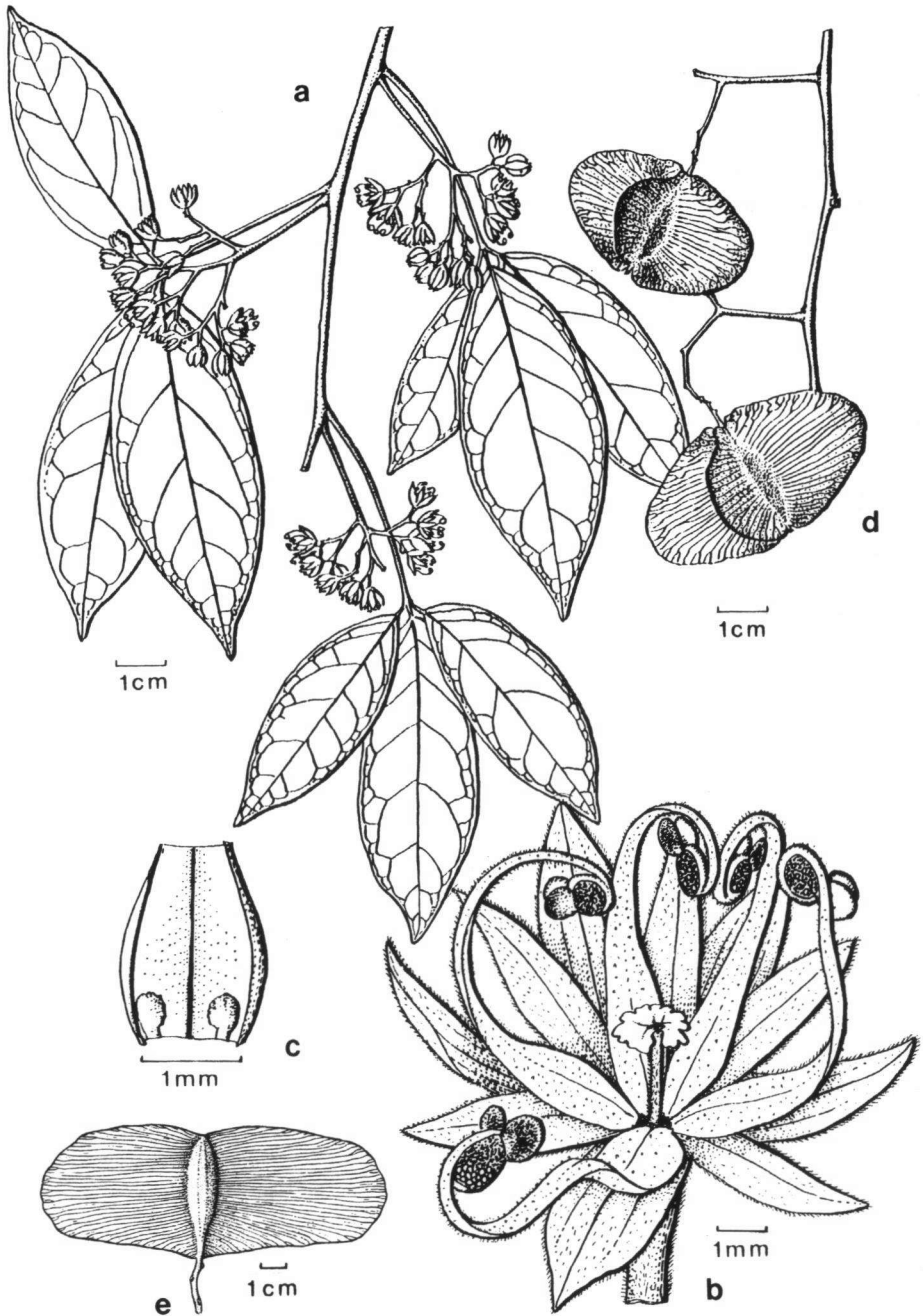


Fig. 5. *Illigera celebica* Miq. a. Flowering twig; b. flower; c. basal part of filament, showing staminal appendages; d. fruits. — *Illigera megaptera* Merr. e. Fruit (a, b, c: *Ebalo* 521; d: *Tsang* 26529; e: *Elmer* 13362). Reproduced (a–d) with permission of Bot. Jahrb. 89 (1969); e: drawing by J.H. van Os (L).

Notes — 1. *Illigera appendiculata* as a whole seems of rare occurrence; there are but a few recent collections. This was already observed by Backer (1913) for Java and by Schmutz for Sumbawa; the latter noted on the field label that he found the species only twice.

2. The only collections seen from East Kalimantan (*Endert 5140*, *Kostermans 6822*), as well as the one from Celebes (*Bünnemeijer 10580*), concern flowering specimens, and it cannot yet be decided to which subspecies they belong.

3. The majority of the herbarium collections concerns flowering material. Fruits of subsp. *appendiculata* are known only of two collections (Sumatra and W Java); subsp. *stenoptera* is known from three fruiting collections (Kangean I., Sumbawa and Flores) only, and more fruit-bearing material is needed to ascertain the status of the latter subspecies.

2. *Illigera celebica* Miq.

Illigera celebica Miq., Ann. Mus. Bot. Lugd.-Bat. 2 (1866) 215; Merr., J. Str. Br. Roy. As. Soc. 85 (1922) 197; Koord., Suppl. Overz. Flora NO Celebes 2 (1922) 10; Merr., Pl. Elmer. Born. (1929) 91; Kubitzki, Bot. Jahrb. 89 (1969) 178, f. 44. — Type: *Forsten s.n.* (L), Celebes, Likupang, Sept. 1840.

Illigera platyandra Dunn, J. Linn. Soc. Bot. 38 (1908) 296; Gagnep. in Fl. Gén. Indo-Chine 2 (1920) 785; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 206. — Type: *Balansa 3161* (L), Tonkin.

Illigera ovatifolia Quisumb. & Merr., Philipp. J. Sc. 37 (1928) 149, p.p., quoad specim. *BS 47166* (K).

Leaves: petiole 4–11.5 cm, petiolules 1–2.5 cm, glabrous or partly palish hairy; leaflets thinly or thickly chartaceous, lanceolate or lanceolate-ovate, 7–17 by 2–8.5 cm, acumen 0.5–1 cm long, base cuneate or subcordate, glabrous on both surfaces, conspicuously olivaceous when dry, often shining above, nerves on lower surface glabrous or hairy, domatia absent, nerves: 4–7 per side, at angles of 40–60° with midrib and arching towards the apex; thyrses slightly pubescent. *Flower buds* globose, 2–5 mm in diameter; stamens in bud inwardly coiled. Bracteoles early falling, c. 1.5 by 0.5 mm. *Perianth*: green, white, pinkish, or violet, all parts more or less hairy (see note 1); tepals lanceolate, acute, outer ones 5–7 by c. 2 mm, inner ones 4.5–6 by c. 1 mm. *Filaments* reddish, tepal-like, filiform towards apex, 10–13 mm long, dilated towards the base, 1.5–2.5 mm wide, margins curved around the staminal appendages; *staminal appendages* clavate, dorsally inserted on the bases of the broad filaments, c. 0.6 mm long; interstaminal glands absent. *Fruits* unequally 4-winged, nut 2–3.3 cm long; longer wings lingulate, 2–2.7 cm long, shorter ones 1–1.4 cm long. — **Fig. 5a–d.**

Distribution — S China, Honkong, Thailand, N & S Vietnam; in *Malesia*: Borneo (Sabah, NE Kalimantan), Celebes, Philippines (Luzon, Palawan, Cebu), NW Irian Jaya.

Habitat & Ecology — Steep slopes in rain forest, disturbed and secondary forest, on riverbanks, in thickets, shrubs and underwood; on sand, limestone and ultrabasic rock; sea level up to 1000 m (Mt Kinabalu).

Notes — 1. The outer surface of the inner perianth segments is conspicuously white because of a thick, felt-like layer of short hairs, easily to be seen in herbarium specimens. The base of the inner perianth segments is much narrower than the base of the filaments.

2. Most of the herbarium material is in flower, while fruit-bearing specimens are under-represented.

3. *Illigera elegans* Duyfjes

Illigera elegans Duyfjes, *Blumea* 38 (1994) 407. — Type: *Powell 541* (K holotype).

Creeper or climber. *Leaves*: petiole c. 11 cm, glabrous; petiolules 2–2.5 cm, glabrous; leaflets chartaceous, suborbicular, 6–9 by 6–7.5 cm, acumen c. 0.5 cm long, base cuneate or cordate, dull and glabrous above, but upper nerves with short hairs, lower surface with domatia, lateral nerves 4 or 5 pairs, at angles of 20–40° with midrib. Thyrses hairy. *Flower buds* ovoid, c. 5 mm long; stamens in bud straight. Bracteoles c. 1 by 0.5 mm. Perianth colour not known, outer and inner tepals unequal, slightly hairy towards the tips, outer tepals ovate-lanceolate, c. 6.5 by 2 mm, c. 0.5 mm acuminate, inner ones much narrower, c. 5 by 0.8 mm acute. *Filaments* filiform, c. 3 mm long; *staminal appendages* dorsally not cleft, the rim finger-like fringed, 1.5 mm long including the 0.5 mm long stipe; interstaminal glands present. *Fruits* with two large wings and with two obsolete wings or ridges, nut 0.8–1 cm long; larger wings more or less hemi-orbicular, c. 2 cm in diameter, the short ones 0.2–0.7 cm wide.

Distribution — *Malesia*: Christmas I. (Indian Ocean), S of Java. Only few collections seen.

Habitat & Ecology — On cliffs and ridges, and in high marginal growth of railway; 180–220 m altitude.

Note — In Malesia both *I. elegans* and *I. novoguineensis* have staminal appendages which are dorsally uncleft; outside Malesia this character is only found in *I. madagascariensis* Perrier de la Bâthie [Kubitzki, *Bot. Jahrb.* 89 (1969) 159]. Kubitzki suggested that the uncleft staminal appendages in the group of species with petaloid and hollow staminal appendages would be a primitive character, supported by the disjunct distribution of the species concerned.

4. *Illigera luzonensis* (Presl) Merr.

Illigera luzonensis (Presl) Merr., *Philipp. Gov. Lab. Bur. Bull.* 17 (1904) 18; *Fl. Manila* (1912) 212; *Sp. Blanc.* (1918) 156; *Enum. Philipp. Flow. Pl.* 2 (1923) 205; *Li, Fl. Taiwan* (1976) 472; Kubitzki, *Bot. Jahrb.* 89 (1969) 163. — *Henschelia luzonensis* Presl, *Rel. Haenk.* 2 (1835) 81, t. 63. — Type: *Haenke 60* (B, W), Luzon.

Illigera meyeniana Kunth ex Walp. in *Meyen, Nov. Act. Acad. Caes. Leop.-Carol. Nat. Cur.* 19, Suppl. 1 (1843) 410. — Type: *Meyen s.n.*, 1831 (B), Manila.

Illigera ternata (Blanco) Dunn, *J. Linn. Soc. Bot.* 38 (1908) 294; Merr., *Sp. Blanc.* (1918) 156. — *Gronovia ternata* Blanco, *Fl. Filip.* 1 (1837) 186. — *Halesia ternata* Blanco, *Fl. Filip.* 1 (1837) 399. — Type: not indicated, illustrative specimens: *Merrill, Sp. Blanc.* 297 & 663 (both L).

Illigera cardiophylla Merr., *Philipp. J. Sc., Bot.* 9 (1914) 292; Kubitzki, *Bot. Jahrb.* 89 (1969) 161, f. 38. — Type: *Fénix BS 4082* (lost); neotype: *Edaño BS 79156* (NY, chosen by Kubitzki, 1969).

Illigera pubescens Merr., *Philipp. J. Sc., Bot.* 9 (1914) 446. — Type: *Vanoverbergh 2135* (P), Bontoc.

Illigera reticulata Merr., *Philipp. J. Sc., Bot.* 9 (1914) 291. — Type: *Curran & Merritt FB 7761*, Luzon.

Illigera ovatifolia Quisumb. & Merr., *Philipp. J. Sc.* 37 (1928) 150, p.p., excl. *Ramos & Edaño BS 47166* (= *I. celebica*, K). — Type: *BS 46712* (BM), Luzon.

Leaves: petiole 4–12 cm, petiolules 0.5–3 cm, glabrous or velutinous; leaflets thinly chartaceous or chartaceous, (sub)orbicular, or ovate, 4–13 by 3–10.5 cm, acute or with an 0.5–1 cm long acumen, base truncate, cordate, or cuneate, the upper surface drying (blackish) brown, the lower surface conspicuously paler, both surfaces glabrous or (sparsely) hairy, especially the midrib; domatia sometimes present; lateral nerves 3–5 pairs, at angles of c. 30° with the midrib; leaflets of flowering lateral shoots smaller, 4–7 by 2.5–5.5 cm, ovate or suborbicular with base almost rounded (rarely subcuneate). Thyrses glabrous or towards the flowers (and fruits) velutinous. *Flower buds* ovoid or ellipsoid, (5–)8 mm long. Bracteoles 1.5–2 by 0.8–1 mm, glabrous or velutinous. *Perianth* in anthesis green or pale pink, glabrous or somewhat hairy; inner and outer tepals slightly unequal, outer tepals lanceolate, 10–12.5 by 3–4 mm, acute or 0.5 mm mucronate, inner ones 9–11 by 2.5–3 mm, narrow at the base. *Filaments* ± filiform, 7–7.5 mm long; *staminal appendages* inflated, spathe-like, dorsally cleft, including the 0.5–1 mm long stipe 2.5–3.5 mm long; interstaminal glands present. *Fruits* with 2 large wings and with (one or) two obsolete wings or ridges; nut 1.5–3.5 cm long, wings variable, hemi-orbicular or sublingulate, longer wings 1.5–2.5 cm long, shorter ones 0.5(–1) cm long.

Distribution — Taiwan and southern Ryukyu Islands; in *Malesia*: Philippines (Babuyan Is., Luzon, Palawan, Mindoro, Samar).

Habitat & Ecology — Mountain and ridge slopes, also in secondary growth and forest plantations; altitude sea level to c. 1300 m.

Notes — 1. A remarkable character is the colour of the dried leaves: upper surface black-brown, lower surface contrastingly lighter. The comparatively rather large flowers are noteworthy.

2. The sterile collection *PNH 19128* (Mindoro) is somewhat deviating, with both leaf surfaces with rather long hairs.

5. *Illigera megaptera* Merr.

Illigera megaptera Merr., Philipp. J. Sc., Bot. 9 (1914) 290; Enum. Philipp. Flow. Pl. 2 (1923) 206; Kubitzki, Bot. Jahrb. 89 (1969) 170. — Type: *BS 21511* (K), Mindanao.

Illigera elliptifolia Merr., Philipp. J. Sc., Bot. 9 (1914) 291. — Type: *FB 20571* (US), Miranda.

Illigera diptera Elmer, Leaflet Philipp. Bot. 7 (1915) 2687. — Type: *Elmer 13362* (B, F, L, NY, U, UC, US, W), Cabadbaran.

Leaves: petiole 6–10.5 cm; petiolules 0.7–2.5 cm, glabrous or sparsely set with short hairs; leaflets chartaceous or coriaceous, ovate or oblong, 8–18 by 5.5–11 cm, acumen up to 1 cm long, base cordate or rounded, upper surface shiny or dull, lower surface dull, glabrous on both surfaces or lower midrib somewhat hairy towards the base, nerves 4 or 5 pairs, at angles of 60–80° with the midrib; domatia present or absent. Thyrses velutinous, especially near flowers and fruits, or partly glabrous. *Flower buds* ellipsoid, c. 6 by 4 mm. Bracteoles coriaceous, ovate, 2–5.5 by 1.2–3 mm, rusty velutinous on both surfaces. *Perianth* in anthesis pink, outer and inner tepals unequal, mucronate, outer surface hairy, especially towards the tips; outer tepals lanceolate, 7–10.5 by 3–3.5 mm, 5-nerved, inner ones spatulate, 6.5–9 by 2–2.5 mm, 3-nerved.

Filaments ± filiform, c. 7 mm long; *staminal appendages* inflated, spathe-like, dorsally cleft, nearly to the base, including the c. 1 mm long stipe 2.5–3 mm long; interstaminal appendages present. *Fruits* with 2 wings and 2 ridges; nut 3–4 cm long, wings linguulate, 3.5–6 cm long. — Fig. 5e.

Distribution — *Malesia*: Borneo (Sabah), Philippines (Luzon, Mindoro, Samar, Mindanao).

Habitat & Ecology — Recorded as a large liana of slopes, ridges and steep forested valleys; also in disturbed forest. Altitude 20–600(–1660) m; see note 4.

Notes — 1. Apparently a rare species and seldom collected in flower. Merrill (1914) described fruits only. I have seen only two collections with flowers: *Ridsdale 1171* (immature flowers, Mindoro) and *Nordin Abas SAN 85879* (Sabah).

2. Kubitzki (1969) regarded the presence or absence of domatia taxonomically an important character; I found that they are mostly absent in *I. megaptera* from the Philippines, but in the Sabah material they are present.

3. *Illigera megaptera* resembles *I. luzonensis*, the latter differs e.g. by shorter leaflets and shorter fruit wings (hemi-orbicular or sublingulate).

4. Doubtful specimens are *Clemens 26185* and *51587*, both from Mt Kinabalu, with flowers only. Their resemblance in habit with *I. megaptera* is evident, so I named them provisionally under that species, although fruits are unknown. Their provenance, from an exceptionally high altitude, c. 1700 m, urged Kubitzki (1969) to place these two Clemens specimens under *I. khasiana* Clarke, a species from mountainous continental SE Asia. To me this seems unlikely, and more complete material from Mt Kinabalu is needed for a final decision.

6. *Illigera novoguineensis* Kubitzki

Illigera novoguineensis Kubitzki, Bot. Jahrb. 89 (1969) 161, f. 37 v. — Type: *Nyman 258* (B, C, S), Papua New Guinea, Madang.

Illigera appendiculata auct. non Blume: K. Schum. & Lauterb., Fl. Deutsch. Schutzgeb. Südsee (1900) 335.

Leaves: petiole 4–11 cm, petiolules 0.7–2.2 cm, pubescent; leaflets chartaceous, ovate to elliptic, 5–10 by 3–7.5 cm, acumen 0.3–0.7 cm long, base cuneate, subcordate or rounded, upper surface glabrous or slightly pubescent, the midrib shortly and densely hairy, lower surface laxly pilose; domatia present; nerves 3–4(–5) pairs at angles of 40–60° with midrib. Thyrses slightly pubescent. *Flower buds* ovoid, pear-shaped just before anthesis, 3–4 mm long. Bracteoles c. 1.5 by 0.5 mm. *Perianth* colour unknown; tepals all more or less equal, outer tepals ovate, c. 6 by 2.2 mm, 5-nerved, slightly hairy towards the tips, inner ones c. 5 by 2 mm, 3-nerved. *Filaments* ± filiform, glabrous, c. 3 mm long; *staminal appendages* dorsally not cleft, urceolate, rim very shortly (c. 0.2 mm) fringed, including the c. 0.3 mm long stipe, c. 1.5 mm long; interstaminal glands present. *Fruits* greyish brown, 2-winged and (1- or) 2-ridged; nut c. 2 cm long, wings hemi-orbicular, 2–2.5 cm diam., ridges c. 0.7 cm long.

Distribution — *Malesia*: Papua New Guinea (Madang Prov., S of Madang).

Habitat & Ecology — Rain forest; up to 700 m altitude.

Notes — 1. Only three collections known, all collected round 1900.

2. The species is strongly resembling *I. appendiculata*, but the staminal appendages are different: not fissured in *I. novoguineensis* and dorsally fissured in *I. appendiculata*. See also the note under *I. elegans*.

7. *Illigera parviflora* Dunn

Illigera parviflora Dunn, J. Linn. Soc. Bot. 38 (1908) 296; Kubitzki, Bot. Jahrb. 89 (1969) 177; Ng in Tree Fl. Malaya 2 (1973) 247. — Type: Ford 260 (K), Kwantung.

Illigera appendiculata auct. non Blume: Ridley, Fl. Malay Penins. 3 (1924) 139, f. 146.

Illigera lucida auct. non Teijsm. & Binnend.: M.R. Hend., Gard. Bull. Str. Settl. 4 (1926) 102.

Leaves: petiole 8–9 cm; petiolules 1.5–2 cm, glabrous or with some hairs; leaflets chartaceous, ovate or lanceolate, 7–11 by 3.5–6.5 cm, acumen c. 0.5 cm long, base cuneate or rounded; drying brownish, upper surface dull, glabrous, lower surface with short hairs on midrib, lateral nerves c. 4 pairs, at angles of 30–45° with midrib. Thyrses densely pubescent. *Flower buds* globose, 2–3 mm diam.; stamens in bud inwardly coiled. *Perianth* in anthesis white; tepals unequal, acute, with short hairs towards the tips, outer tepals ovate 3.2–4 by c. 2.2 mm, 3–5-nerved, inner ones lanceolate, 3–3.2 by c. 1 mm, at base narrow, c. 0.4 mm wide, 3-nerved. *Filaments* ± filiform, 4.5–6 mm long, at base c. 0.5 mm wide, protruding; *staminal appendages* very inconspicuous, clavate, including stipe 0.3–0.6 mm long; interstaminal glands present, small. *Fruits* unequally 4-winged, nut 2–3 cm long; longer wings more or less hemi-orbicular, c. 2 cm long, shorter ones c. 0.5 cm long.

Distribution — China, Vietnam; in *Malesia*: Peninsular Malaysia (Perak, Pahang).

Habitat & Ecology — Lowland forest, in underwood and thickets and in mountainous places in open wood; up to 1260 m altitude.

8. *Illigera pulchra* Blume

Illigera pulchra Blume, Bijdr. (1826) 1154; Backer & Bakh. f., Fl. Java 1 (1964) 136; Kubitzki, Bot. Jahrb. 89 (1969) 174, f. 42; Ng in Tree Fl. Malaya 2 (1973) 247. — Type: Blume s.n. (L), Java.

Illigera lucida Teijsm. & Binnend., Nat. Tijds. Ned. Ind. 27 (1864) 29; Kurz, Nat. Tijds. Ned. Ind. 27 (1864) 168; Ridley, Fl. Malay Penins. 3 (1924) 140. — Type: Teijsmann s.n. (BM), Bangka.

Leaves: petiole 4–8 cm; petiolules 0.5–1.3 cm; glabrous or partially hairy; leaflets thickly chartaceous, lanceolate or elliptical, 5–15 by 2–5 cm, acumen 0.3–1.5 cm long, base rounded or cordate, glabrous on both surfaces or slightly hairy on the lower surface, upper surface shiny, olivaceous when dry; nerves 7–9(–15) pairs, looped, at angles of 80–90° with midrib. Thyrses slightly pubescent. *Flower buds* subglobose, ovoid, or pear-shaped, 3–5 mm long. Bracteoles c. 1.5 by 0.5 mm. *Perianth* in anthesis: outer and inner tepals unequal, inner surface towards the base with palish c. 1 mm long hairs; outer tepals ovate or lanceolate, connate at base, 6–6.5 by 2–2.5 mm, inner ones linear, 5–6 by 0.6–0.8 mm. *Filaments* ± filiform, c. 2 mm long, with c. 1 mm long hairs in the lower part; *staminal appendages* inconspicuous, solid, clavate, c. 0.25 mm long; interstaminal glands present. *Fruits* 2-winged and 2-ridged, nut 1.5–2.5 cm long; wings lingulate, 3–3.7 cm long, ridges c. 0.5 cm long.

Distribution — *Malesia*: Sumatra, Peninsular Malaysia, Bangka, W Java, Celebes (see note).

Habitat & Ecology — Lowland forest, in bushes and thickets; often on limestone; up to c. 100 m altitude.

Note — Kubitzki (1969) mentioned for its provenance also Celebes (Sulawesi), but I have seen no collections. Apparently a rare species; there are no collections made after the 1930s.

9. *Illigera trifoliata* (Griff.) Dunn

Illigera trifoliata (Griff.) Dunn, J. Linn. Soc. Bot. 38 (1908) 294; Kubitzki, Bot. Jahrb. 89 (1969) 169; Ng in Tree Fl. Malaya 2 (1973) 247, f. 3. — *Corysadenia trifoliata* Griff., Not. Pl. As. 4 (1854) 356.

Illigera corysadenia Meisn. in A. DC., Prodr. 15, 1 (1864) 251. — Type: *Griffith s.n.* (K), Madamaca I., Mergui Archipel.

Illigera dasyphylla Miq., Fl. Ind. Bat. 1, 1 (1858) 169; *ibid.*, Suppl. (1861) 333, t. 1. — *Illigera trifoliata* var. *dasyphylla* (Miq.) Kubitzki, Bot. Jahrb. 89 (1969) 169. — Type: *Teijsmann H.B. 1036* (BO, L, U), Sumatra, Solok.

Illigera kurzii Clarke in Hook. f., Fl. Brit. India 2 (1878) 460. — Type: *Maingay 649* (K), Malay Peninsula.

Illigera appendiculata auct. non Blume: Kanjilal c.s., Fl. Assam 4 (1940) 103; M.R. Hend., Malayan Wild Flow. Dicot. 1 (1959) 445, f. 402.

Strong climber or creeper. *Leaves*: petioles 8–10 cm, petiolules 0.8–2 cm, slightly or densely hairy; leaflets chartaceous, ovate, 5–15 by 3.5–8 cm, apex acute, base rounded or cordate, upper surface glabrous or sparsely hairy in many gradations, and often with short hairs on the nerves, the lower surface hairy in many gradations: only sparsely hairy, especially on and near the nerves; domatia present; nerves curved, c. 6 pairs, at angles of 60–80° with midrib. Thyrses velutinous. *Flower buds* ovoid, 4.5–5 mm long. Bracteoles c. 2 by 1 mm. *Perianth* in anthesis with tepals pinkish white or pale greenish with purplish midnerve; outer and inner tepals unequal, outer surface densely hairy or (somewhat) hairy towards the tips only, acute, outer tepals 6.5–9 by 1.8–2 mm, inner ones 5–7 by 0.5–1.8 mm, at the base c. 0.5 mm wide. *Filaments* filiform, somewhat papillose, 6–6.5 mm long; *staminal appendages* inflated, spathe-like with an entire rim, dorsally cleft, including the 0.5–1 mm long stipe 2–3 mm long; interstaminal glands present. *Fruits* cinnamon-coloured when dry, 2-winged and with 2 ridges, often with short hairs; nut 3–4 cm long; wings lingulate, 3.5–4 cm long, the ridges c. 0.2 cm.

Distribution — Andaman Islands, Laos, Thailand; in *Malesia*: Sumatra, Peninsular Malaysia (Perak, Selangor).

Habitat & Ecology — Margins of evergreen forest, forest edges in open sunny places, in ravines, also in secondary growth such as roadsides, etc. Found on loamy soil and granite bedrock. Altitude 100–800(–1050, Thailand) m.

Note — The indumentum of the leaves is very variable. Older stems may reach a diameter of c. 1.5 cm, with scaly bark (*Maxwell 10-8755*, Thailand).

Postscript

EMBRYOLOGY AND TAXONOMIC POSITION OF HERNANDIACEAE

A recent study (Heo & Tobe 1995) on the embryology of *Gyrocarpus* (*G. jatrophifolius*) and *Hernandia* (*H. cordigera*, *H. nymphaeifolia*) disclosed that no synapomorphies exist for these two genera. They are rather divergent in various characters, which supports the prevalent acceptance of two subfamilies in the *Hernandiaceae*: a derived subfamily *Hernandioideae* and a less specialized subfamily *Gyrocarpoideae* (see under Taxonomy, page 738). Nevertheless, *Hernandiaceae* evidently is one separate family belonging in the *Laurales*, because both *Gyrocarpus* and *Hernandia* share various synapomorphies with other lauralian families, as was also previously supported by cladistic and DNA analyses. However, embryologically no evidence was found to separate *Hernandiaceae* from *Lauraceae*, whereas the genus *Hernandia* shares two synapomorphies with the latter family, viz. pachychalazy (ramified raphal vascular bundles at the chalaza) and ruminant cotyledons.

Reference: Heo, K. & H. Tobe, Embryology and relationships of *Gyrocarpus* and *Hernandia* (*Hernandiaceae*), J. Plant Res. 108 (1995) 327.