JUGLANDACEAE (M. Jacobs, Leyden)

Juglandaceae represent a characteristic northern hemisphere family, in the New World going south to Central America (Mexico, Costa Rica, Guatemala, Panama, Cuba, Hispaniola and found S of the equator as fas as *c.* 30° S, absent from Africa, and overstepping the equator also in the Malaysian region where *Engelhardia* extends to Java and New Guinea. This distribution shows a remarkable resemblance with that of the *Fagaceae-Castaneae* which though absent S of the equator in the Americas, occur in Africa in the Mediterranean part only, and though rather well represented as far as New Guinea are also absent in Australia and the Pacific islands. A noteworthy detail of this parallel is that although both are well represented in the Himalayan region and the Indo-Chinese Peninsula no representative of either group is found in Ceylon and the Deccan Peninsula!

Northwards the family extended much farther in Tertiary time and fossils are known from Sakhalin, E. Siberia to 61° N (where at present *Juglans* occurs to 51° N), also Alaska (pollen grains), Greenland, and Spitsbergen. Several genera which are now confined to East Asia or North America occurred in Europe from the Upper Cretaceous until the Pliocene but became gradually extinct there during the Pleistocene Ice Age. See also under *Engelhardia.*

Taxonomy. The family comprises 6 genera with *c.* 58 *spp.*. *Platycarya* and *Pterocarya* are Asiatic, *Alfaroa* is American, while *Engelhardia*, *Carya*, and *Juglans* occur in both the Old and the New World. As for the disputed monotypic genus *Annamocarya* CHEV. (synonyms: *Caryojuglans* KIRCHH., *Juglandicarya* REID & CHANDLER, *Rhamphocarya* KUANG), described in 1941 from S. China and Tonkin, we refer to LEROY, Mém. Mus. Hist. Nat. n.s. Bot. 6 (1955) 66.

The family is a coherent one. *Engelhardia* and *Alfaroa* form a natural and rather primitive group.

Thusfar three systems of subdivision for the *Juglandaceae* have been proposed. The first is by OERSTED, Vid. Medd. Nat. For. Kjøbenhavn (1870) 159–174. The second is by KOIDZUMI, who gives a complete subdivision with a taxonomic survey of the genera in Acta Phytotax. & Geobot. 6 (1937) 1–16. The third is by LEROY, *l.c.* 1–246. The three systems have in common, that they always keep *Engelhardia* together with *Pterocarya*, and *Carya* together with *Juglans.*

The affinity of the *Juglandaceae* within the *Amentiferae* seems to be closest with the *Myricaceae.*

Palynology. According to ERDTMAN (Pollen Morph. & Pl. Tax. 1952, 216) the pollen grains have several characters in common with those in *Betulaceae*, *Casuarinaceae*, *Myricaceae*, and *Rhoipteleaceae*; those of *Fagaceae etc.* are less similar.

Phytochemistry. This family is known to accumulate different types of polyphenolic compounds. The most characteristic constituent of *Juglandaceae* is naphtoquinon juglon. It has been proved to occur in species of *Juglans*, *Carya*, and *Pterocarya.* In the tissues juglon is present as a monoglucoside of the reduced form of the quinon (dihydrojuglon). Enzymatically dihydrojuglonglucoside is split very rapidly and dihydrojuglon set free is concurrently oxydized to juglon. Juglon is very toxic to fungi and seedlings of higher plants. It is also toxic to animals and may well be the ichthyotoxic principle of *Juglandaceae*; fresh barks and leaves of *Juglans rupestris* ENGELM., *Carya illinoensis* (WANG) K. KOCH, *Engelhardia spicata* BL., and *Engelhardia polystachya* RADLK. are reported in literature to be used as fish poison.

Besides juglon, flavonoid compounds and tannins are known to accumulate in considerable amounts in *Juglandaceae.* The bark of *Engelhardia formosana* HAYATA contains up to 7.5 % of flavonoid glycosides (engelitin, isoengelitin, afzelin, astilbin, quercitrin). Similar compounds were isolated from leaves of *Juglans spp.* The tannins of *Juglandaceae* have been investigated in recent years. They seem to belong to the hydrolyzable class and hydrolysis gives rise to gallic acid, ellagic acid, and glucose. One tannin, juglanin, was proved to be isomeric with corilagin. Ellagic acid and gallic acid occur also in the free state in the wood of *Juglans sieboldiana* and *Platycarya strobilacea.*

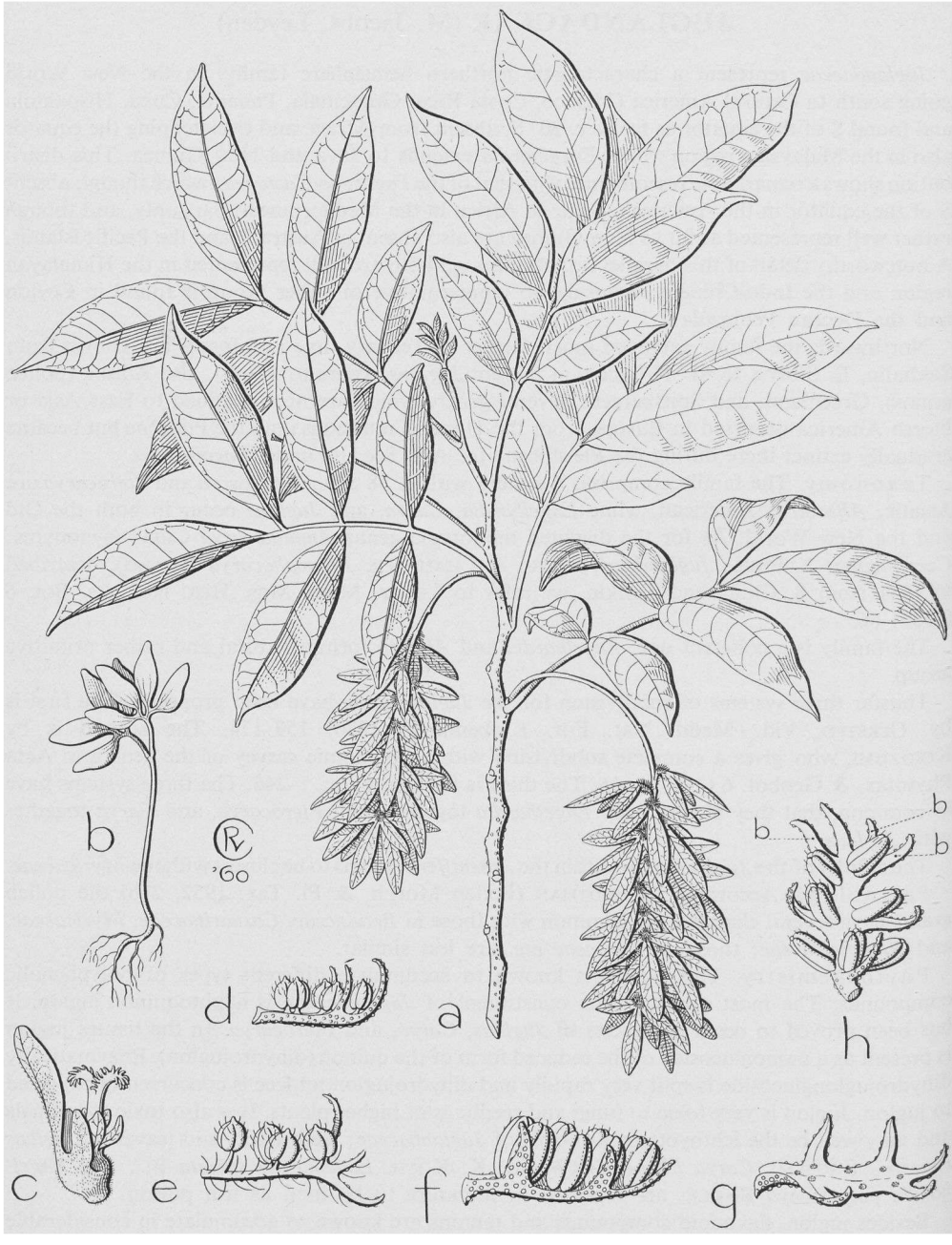

Fig. 1. *Engelhardia rigida* BL. *a*. Fruiting twig, × ½, *d–f*. variation in the ♂ flowers, all × 6, *g*. ♂ flower after removal of the stamens, with 2 perianth lobes and 3 bract lobes, *h*. ♂ flower from above, with the bract lobes (b) and 4 perianth lobes.—*E. serrata* BL. (?) *b*. Seedling, × ½.—*E. spicata* LECHEN. *ex* BL. *c*. ♀ Flower, × 6 (*a* BRASS 11061, *b* BURKILL 9984, *c* KOORDERS 29792, *d* ENDERT 3447, *e* ENDERT 4407, *f–h* CLEMENS 494).

The high ascorbic acid contents (= vitamin-C) of different organs of *Juglans regia* reported in literature are greatly exaggerated because juglon interferes strongly in the usual determination of ascorbic acid.

The available data permit the characterization of the *Juglandaceae* phytochemically as a family which accumulates many types of tannin-like polyphenolyc compounds. In this respect it resembles many other woody families, *e.g. Hamamelidaceae, Fagaceae, etc.*—R. HEGNAUER.

1. ENGELHARDIA

LECHEN. *ex* BLUME, Bijdr. 10 (1825) 528; Fl. Jav. Jugl. (1829) 5, '*Engelhardtia*'; C.DC. Ann. Sc. Nat. IV, 18 (1862) 35; Prod. 16, 2 (1864) 140; NAGEL, Bot. Jahrb. 50 (1914) 475.—*Pterilema* REINW. Syll. 2 (1826) 13.—*Oreomunnea* OERST. Vid. Medd. Nat. For. Kjøbenh. (1856) 52.—**Fig. 1-9.**

Trees, mostly lepidote with golden yellow, glandular scales 0.1–0.2 mm diam. Pith solid. Leaf buds naked, with a resemblance to hands. Young twigs densely brownish tomentellous, young leaves mostly reddish. Stipules none. *Leaves* spirally arranged (in Asiatic members), paripinnate; leaflets slightly asymmetrical, the acroscopic side being mostly wider with higher inserted base than the basiscopic side; midrib above flattish with a narrow, raised keel, nerves camptodromous. Monoecious or dioecious. *Flowers* small, in catkins (each flower solitary) which are often arranged to lateral or terminal panicles, the flower fused with a 3-lobed bract; perianth 4-lobed.—♂ *Flowers:* perianth often reduced and irregular; stamens 4–13 (in Asiatic members), (sub)sessile.—♀ *Flowers:* perianth lobes in 2 whorls partly connate with the ovary, the median pair exterior; ovary 2-carpellate, the carpel sutures median, 1-locular with an incomplete, simple (in Asiatic members), transverse septum, sometimes also with an abortive median septum; ovule 1, erect, at the top of the main septum, conical with broad base, atropous, with 1 integument. Style in *sect. Engelhardia* well-developed with 2(–4) transversal elongate, papillose, persistent stigmas, in *sect. Psilocarpeae* the 4 stigmas small and sessile. In *fruit* the strongly accrescent bract forms a 3-lobed, obovate, scarious wing with midribs and reticulate venation and partly adnate to the nut; the central (abaxial) lobe is about twice as large as the lateral ones, sometimes a smaller adaxial simple or irregularly dissected lobe is present. Nut indehiscent, pea-sized; pericarp cartilaginous, mostly hispid with itching hairs. *Seed* filling the space between the septa; testa forming an even covering of the seed; cotyledons strongly plicate and divided into 4 lobes, later epigeal, radicle superior, endosperm none.

Distr. Five *spp.* in the Old World, from the W. Himalaya to China S of ± 30° N, all over the Indo-Chinese Peninsula, Malaysia, and Formosa; in America 2–3 *spp.* in Mexico, Costa Rica, and Guatemala. Fig. 2.

Ecol. Trees, mostly small or medium but sometimes growing very large, in evergreen, primary dryland forest, apparently not on limestone. In Malaysia they prefer the mountains between *c.* 1000 and 2000 m, although sometimes found in the lowlands.

Though *Engelhardia* is a regular constituent of the fagolauraceous montane rain-forest in Java, none of the species occurs gregarious or dominant, but in open grassy places they may occur in groups in anthropogenous pseudosavannahs. VAN STEENIS observed on Mt Patuha (W. Java) abundant regeneration of seedlings *c.* 10–200 cm high in a dense thicket of *Eupatorium inulifolium* on abandoned cinchona plantations near Tjipadaruum, at *c.* 1800 m; the seeds were derived from three old fruiting trees which happened to be in the adjacent forest border. See further under *E. spicata.*

Often (always?) shortly deciduous and then flowering. Pollination and seed dispersal are clearly adapted to wind. However, the matter may be not so simple as that. Dr P. VAN ROYEN told me that in New Guinea, where *E. rigida* is very common, he repeatedly found all the fruiting catkins, shed as a whole, on the ground under the trees.

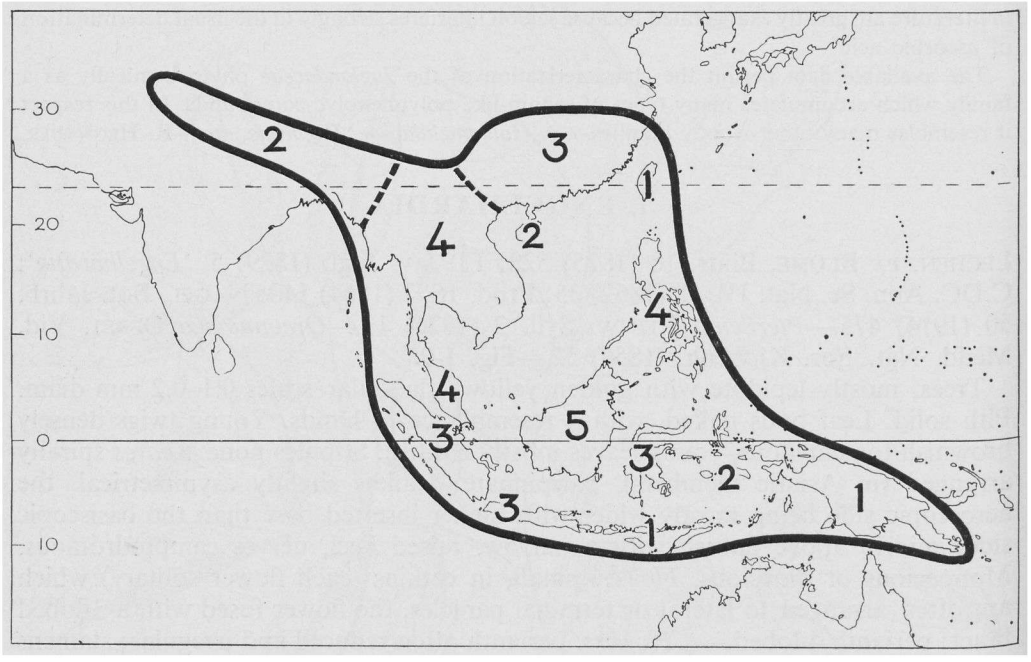

Fig. 2. Distribution of *Engelhardia* LECHEN. *ex* BL. in the Old World, with number of species indicated for each subarea.

Wood-anat. BEEKMAN, Meded. Proefstat. Boschw. 5 (1920) 96; DEN BERGER, Meded. Proefstat. Boschw. 13 (1926) 13, Determinatietabel van Malesië, Veenman, Wageningen (1949) 62 (hand lens.) HEIMSCH, Lilloa 8 (1942) 164; KRIBS, Trop. Woods 12 (1927) 16; METCALFE & CHALK, Anat. Dic. 2 (1950) 1287; MOLL & JANSSONIUS, Mikr. Holzes 6 (1936) 308; TIPPO, Bot. Gaz. 100 (1938) 42. For various opinions about the affinities of the family see METCALFE & CHALK, *l.c.*—C.A.R.-G.

Morph. Not all authorities agree on the nature of the floral parts, called by MANNING the floral envelope, in his opinion consisting, when complete, of a 3-lobed bract, 2 bracteoles, and a 4-lobed perianth. Other authors hold the view that the flower is surrounded by a 1-lobed bract with 2 bracteoles, and a 4-lobed perianth, the lobes of which are some times called sepals. The nature of the bracteoles is subject to interpretation. The smaller and facultative adaxial lobe of the fruit is, in my opinion, too variable to represent anything but an outgrowth of the two adaxial margins of the bract lobes.

HJELMQVIST, basing his opinion on a comparison with the *Myricaceae*, supposed that the flower was originally unisexual and of a pseudanthic nature, *i.e.* it has arisen through union of a number of simply built flowers. NAGEL and MANNING suppose that the flower was initially bisexual and has become unisexual by reduction. This is supported by the fact that, very rarely, seemingly ♂ catkins are found where part of the flowers have a prolonged bract. Such flowers often show both a reduced androecium and a reduced gynoecium, *i.e.* a sterile stigmatiferous ovary surrounded by a subnormal number of stamens.

The nut is also regarded as a sort of drupe with thin flesh which, however, is derived from the involucre or perianth and not from carpel tissue.

The ovule seems only to be basal on a columella. Virtually it is not truly basal, but modified axile, at the apex of one of the primary septa.

According to HJELMQVIST the integument is protracted upwards to a narrow tube in *E. spicata* and *E. parvifolia* (the latter here reduced to *E. serrata*).

Several important studies have been published, all covering the whole family. We mention NAGEL, Bot. Jahrb. 50 (1914) 459–530; MANNING, Amer. J. Bot. 25 (1938) 407–419 on the inflorescence, *ibid.* 27 (1940) 839–852 on the ♀ flowers, *ibid.* 35 (1948) 606–621 on the ♂ flowers, Bull. Torrey Bot. Club 86 (1959) 190–198 on *Engelhardia* and *Alfaroa* in America; HJELMQVIST, Bot. Notis. Suppl. 2[1] (1948) 5–171; LEROY, Mém. Mus. Hist. Nat. n.s. Bot. 6 (1955) 1–246.

Fossils. Many records prove the wide occurrence of *Engelhardia* in the warmer parts of Europe

and also of N. America in the Tertiary. Dr W. H. ZAGWIJN kindly informed me, that *Engelhardia* pollen forms an important part (up to 20 %) of the anemophilous elements of a flora which existed in the SE. part of the Netherlands and the adjacent region in Germany. This flora, of the Miocene and Pliocene clay and browncoal formations, is remarkable for its strong E. Asiatic and American affinities, and for the many tropical and subtropical elements it contains, especially in the Mid-Miocene, where these make up about 50 % of the flora. See also ZAGWIJN, Aspects of the Pliocene and early Pleistocene Vegetation in the Netherlands, thesis Leiden 1960. An endocarp of †*E. nucifera* (LUDWIG) MÄDLER is depicted in Fortschr. Geol. Rheinl. u. Westf. 4 (1959) t. 1, by the same author.

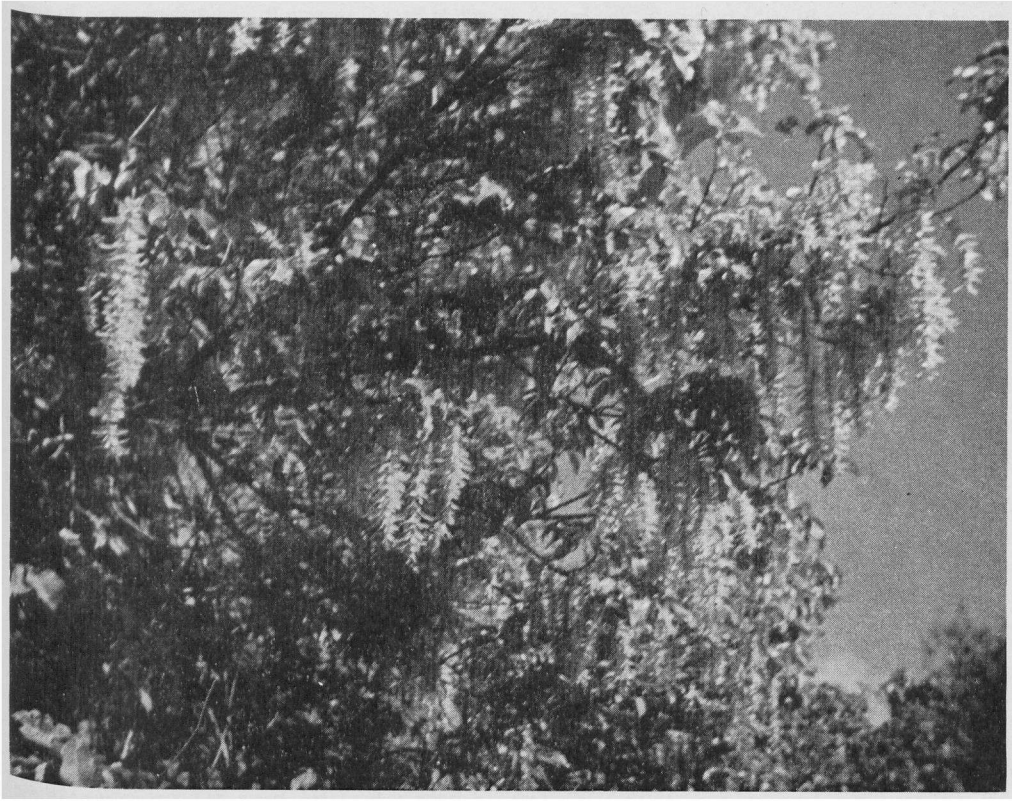

Fig. 3. Fruiting *Engelhardia spicata* LECHEN. *ex* BL. above Sembalun, Mt Rindjani, Lombok, *c.* 2000 m (DE VOOGD).

variability. There is a significant difference between juvenile and adult leaves. The juvenile leaves, on young trees and suckers, bear more pairs of leaflets, are thinner, longer acuminate, more serrate, and denser hairy than those of mature trees. This holds for both the American species and at least for part of the Malaysian ones.

The numerous field data on bark characters vary so much that it was found impossible to make reliable descriptions.

In reproductive parts there is an astounding variation. The panicles of catkins are variously reduced, often the single ♀ catkin or the few ♂ catkins remaining. In *sect. Engelhardia* the perianth is often liable to much reduction. In the ♂ flowers some stamens in a row may be lacking, or the individual stamens are reduced in size. In the nuts part of the perianth lobes may be wanting, or, on the other hand, may have grown out excessively, up to nearly the length of the lateral wing lobes. The variation displayed by the adaxial lobes is practically beyond description.

In the descriptions the ♀ flowers are not mentioned because they are considered rather irrelevant for diagnostic purpose. Their size varies much in the course of development and it is difficult to define

in dry material the exact moment when the stigmas are receptive; material with ♀ flowers is, moreover, very rare in herbaria. The collecting of ♀ flowers and the making of observations on their anthesis is strongly recommended to the attention of field workers.

Taxon. Several authors have, in the course of time, contributed to the present subdivision into 3 sections.

Sect. **1. Engelhardia.**—*Sect. Pterilema* (REINW.) C. DC.—*Sect. Trichotocarpeae* NAGEL. Leaves spirally arranged. Inflorescences lateral. Male flowers: subsessile; bract with 3 distinct narrow lobes; receptacle elongate; perianth flat, irregular, reduced, often obscure; stamens in transversal rows of 2–3, hirsute. Female flowers: stigmas commissural, hence transversal, linear, style far exceeding the perianth lobes. Nut hispid, (sub)sessile, about halfway adnate to the wing, 2(–4)-celled at the base. Here belong *E. spicata* LECHEN. *ex* BL. (the type *sp.* of the genus), *E. rigida* BL., *E. serrata* BL., and *E. apoensis* ELMER *ex* NAGEL.

Sect. **2. Psilocarpeae** NAGEL *emend.* LEROY. Leaves spirally arranged. Inflorescences terminal, sometimes also lateral. Male flowers: stalked; bract very obscurely 3-lobed; receptacle orbicular; perianth regular, 4-lobed, lobes cucullate, stamens (2–)3 at the base of each lobe, glabrous. Female flowers: stigmas split-carinal, cushion-like, concealed by the perianth-lobes; no style. Nut scaly, not hairy, stalked, hardly adnate to the wing, 2(–4)-celled at the base. Here belongs *E. roxburghiana* WALL.

Sect. **3. Oreomunnea** (OERST.) C. DC. (only American and not incorporated in the above generic description). Leaves opposite or whorled. Inflorescence lateral. Male flowers: subsessile; bract obscurely 3-lobed; receptacle elongate, periant 2–4-lobed, flattish; stamens ± 16–19(–23), irregularly arranged, glabrous. Female flowers: septa nearly complete, ramified, one true septum transversal, a false septum median; stigmas carinal, hence median, cushion-like on short styles just or almost exceeding the perianth lobes. Nut (sub)sessile, not hairy but obscurely scaly, 8-celled at the base, 4-celled in the middle, 1-celled at the apex; the testa attached to all irregularities in the pericarp; wing for ± ⅓ adnate to the nut, often very large, with a large simple adaxial lobe completely concealing the nut. This section, which comprises the 2–3 American *spp.*, is considered to represent the most primitive group in the genus.

Oreomunnea OERSTED, often spelled *Oreamunoa*, which is more correct from an etymological but not from a nomenclatural point of view, is by several authors kept apart. MANNING gave reasons for its reduction to *Engelhardia* in Bull. Torrey Bot. Club 76 (1949) 196–209; in the same paper he commented on characters in *Alfaroa* and *Engelhardia*.

Uses. The wood is locally applied for timber but considered of inferior quality. The bark is occasionally used for fish-poison.

Notes. An attempt has been made to evaluate all names given to Asiatic *Engelhardias*. I was not able to place *E. mollis* HU, Bull. Fan Mem. Inst. Biol. Peiping, Bot. 10 (1940) 161, from SW. Yunnan.

The author is greatly indebted to Professor Dr WAYNE E. MANNING, Lewisburg, Penns., U.S.A., who spent much time to go through the MS and put the fruits of his lifelong work in the *Juglandaceae* at our disposal in a most generous and liberal way.

KEY TO THE SPECIES

1. Nut hispid, (sub)sessile, with distinct style and stigmas. Bract of the ♂ flowers with 3 distinct narrow lobes. Stamens hairy. Inflorescences lateral.
 2. Leaflets underneath more or less densely set with yellow scales (hand lens!). Fruiting catkins on a slender subterete stalk.
  3. Nut subglobose, 3–5 mm long, wing up to 4, rarely to 6 cm long. Leaflets widest about the middle or above, the base acutish to obtuse. Stamens 3–7. Dioecious.
   4. Leaflets entire . . . . . **1. E. rigida**
   4. Leaflets (more or less distinctly) serrate or crenate . . . . . **2. E. serrata**
  3. Nut elongate, ovoid, 6–8 mm long, wing 5½—7½ cm long. Leaflets ovate, the base subcordate to rounded. (Flowers unknown) . . . . . **3. E. apoensis**
 2. Leaflets underneath sometimes with minute greyish (not yellow) scales, but mostly with hairs only or glabrous. Stamens 8–13. Fruiting catkins on a vigorous, angular stalk. Monoecious. **4. E. spicata**
1. Nut scaly, not hairy, stalked, stigmas concealed. Bract of the ♂ flowers obscurely lobed, but 4 perianth lobes distinct. Stamens glabrous. Inflorescence terminal, sometimes also lateral. **5. E. roxburghiana**

1. Engelhardia rigida BL. Bijdr. 10 (1825) 528; Fl. Jav. Jugl. (1829) 13, t. 3; MIQ. Fl. Ind. Bat. 1, 1 (1856) 842; C. DC. Prod. 16, 2 (1864) 142; K. & V. Bijdr. 5 (1900) 175; KOORD. Exk. Fl. Java 2 (1912) 53; BACK. Bull. Jard. Bot. Btzg II, *n.* 12 (1913) 16; NAGEL, Bot. Jahrb. 50 (1914) 476; KOORD. Atlas 4 (1916) t. 698; BAKH. *f.* in Back. Bekn. Fl. Java (em. ed.) 7A (1948) fam. 155 p. 2.—*E. subsimplicifolia* MERR. Govt Lab. Publ. Philip. *n.* 34 (1906) 6; Philip. J. Sc. 1 (1906) Suppl. 41; NAGEL, Bot. Jahrb. 50 (1914) 477; MERR. En. Philip. 2 (1923) 24.—*E. lepidota* SCHLTR, Bot. Jahrb. 50 (1913) 66, f. 1; NAGEL, Bot. Jahrb. 50 (1914) 477; RENDLE, J. Bot. 61 (1923) Suppl. 53.—*E. zambalensis* ELMER, Leafl. Philip. Bot. 9 (1934) 3195.—**Fig. 1a, d-h, 4c-f.**

Tree 15–30(–47) m, sometimes with buttresses up to 3 m high and 2 m out; the bark once reported decorticating in small flakes. *Leaf* rachis vigorous, blackish, (1½–)3–6(–21) cm, mostly glabrous or scaly, rarely puberulous, (1–)2–3(–5)-jugate; leaflets rather thick-coriaceous, sessile to 5 mm stalked, blade 2¼–3½(–4) times as long as wide, widest at the middle or rarely above, 5½–10½(–16½) by 2½–4(–7½) cm; base acutish, top subacuminate, tip acute; margin entire (in New Guinea exceptionally crenate towards the top), surfaces more or less densely set with golden yellow glandular-scales, especially underneath, otherwise glabrous or rarely hairy on the nerves. Dioecious. Catkins lateral on leafy and on slightly older twigs, rarely serial in twos. *Male catkins* solitary or 2–3 on a ½–1 cm long stalk, 1½–5 cm long, rachis scaly and/or hairy. Bract 2–4 mm, scaly, lobes irregular, narrow. Perianth 4-lobed, the lobes resembling those of the bract, to completely reduced. Stamens (3–)4–6(–7), the anthers equal or unequal, (½–)1 mm, more or less hispid, connective not or shortly protruding; if there is a single proximal stamen, this has sometimes a filament up to 1 mm, the others being sessile. *Fruiting catkins* (6–)10–15(–22) cm including a peduncle 2–3(–7) cm; peduncle subterete, in the basal half with 2 scars; rachis rather slender, more or less densely scaly and/or puberulous. Nut (sub)sessile, ± 3 mm diam., hispid, wing (2–)2½–3(–6) cm long with the nut, 3–8 mm wide; perianth lobes sometimes very unequal, one or both of the median lobes sometimes attaining half the length of the wing; style about as long as the stigmas, the whole 2–4 mm long.

Distr. *Malaysia*: W. Java (rare), Borneo, Philippines (W. Luzon, N. Mindanao), Central and SW. Celebes (also Banggai Arch.), Moluccas (Halmaheira, Morotai), New Guinea (also Japen and Numfoor). In New Guinea rather common, elsewhere rare.

Ecol. Primary forest, only once reported from secondary forest, *c.* 1000–1800(–2300) m.

Vern. *Ki hudjan*, S, *sibiri*, Papua.

Uses. The wood is used for canoes, native buildings, *etc.*

Notes. Only in Borneo, the Philippines, and Celebes occur specimens with 1-jugate leaves.

Closely related to *E. serrata*, and arguments could be advanced to regard the two as subspecies. Separation based on reproductive characters is practically impossible. However, apart from the different distribution, either species has its own particular pattern of variability, as has been pointed out in the descriptions. For separation two characters have been found, notably the leaf margin, which is entire or serrate, and the decreasing in size of the leaflets towards the leaf base; this feature is generally far more pronounced in *E. serrata*, where the basal leaflets are about half as long as the largest ones. These characters mostly concur. In the cases where they do not, I am inclined to take the leaf margin character as decisive, since in a few *E. rigida* specimens from New Guinea and elsewhere such small basal leaflets were also found. *Engelhardia zambalensis*, described on a specimen with entire leaflets but much reduced towards the leaf base, is therefore placed by me under *E. rigida*, but if one accepts the narrowing leaf base as the key character, it would come under *E. serrata*.

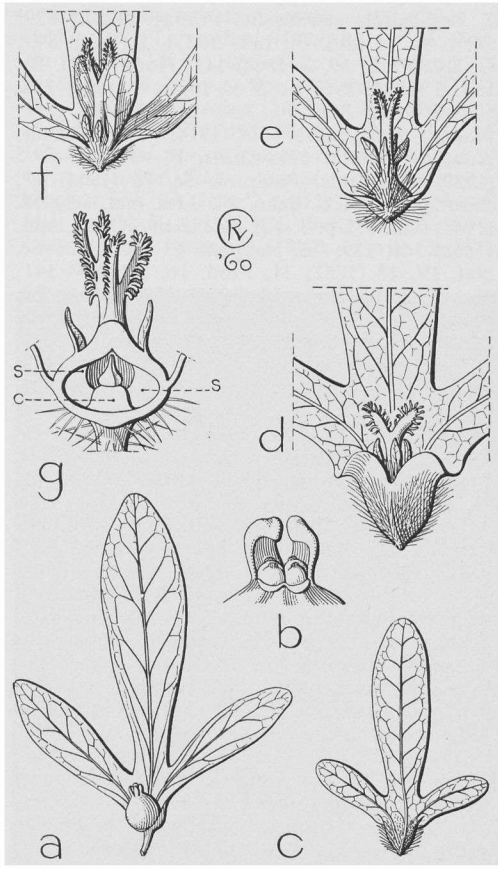

Fig. 4. Fruits of *Engelhardia*. *a. E. roxburghiana* WALL., ventrally, nat. size, *b.* the stigmas, shown by removal of 2 perianth lobes, × 4.—*E. rigida* BL. *c.* Fruit dorsally, × 2, *d–f*, fruits ventrally, showing variation in perianth and adaxial lobe, × 2.—*E. serrata* BL. *g.* Longitudinal section of fruit, showing ovulum on columella (c) and partial septa (s), × 4 (*a–b* CLEMENS 27250, *c–d* WINCKEL 1540*β*, *e* BRASS 11051, *f* KALKMAN 4363, *g* JACOBS 4677).

Two sterile specimens from Japen and Numfoor are believed to belong here, notwithstanding they lack scales on the underside of the leaves.

In ENDERT 3833 and KOSTERMANS 7648, both from E. Borneo, the fruit bears no long hairs, only a soft pubescence and scales. From *E. roxburghiana* these specimens are distinguished by well-developed style and stigmas. In ROBBINS 569 from New Guinea even the anthers bear scales.

2. Engelhardia serrata BL. Fl. Jav. Jugl. (1829) 14, t. 4, 5c; MIQ. Fl. Ind. Bat. 1, 1 (1856) 843; C. DC. Prod. 16, 2 (1864) 141; HOOK. *f.* Fl. Br. Ind. 5 (1888) 596; K. & V. Bijdr. 5 (1900) 172, 174; KOORD. Exk. Fl. Java 2 (1912) 53, f. 7; NAGEL, Bot. Jahrb. 50 (1914) 477; KOORD. Atlas 4 (1916) t. 699; DODE, Fl. Gén. I.-C. 5 (1930) 928; QUIS. Philip. J. Sc. 76 (1944) 37; BAKH. *f.* in Back. Bekn. Fl. Java (em. ed.) 7A (1948) fam. 155 p. 3.—*E. palembanica* MIQ. Sum. (1861) 346, 139.—*E. parvifolia* C. DC. Ann. Sc. Nat. IV, 18 (1862) 34; Prod. 16, 2 (1864) 141; NAGEL, Bot. Jahrb. 50 (1914) 477; MERR. En. Philip. 2 (1923) 23.—*E. nudiflora* HOOK. *f.* Ic. Pl. 18 (March 1888) t. 1747; Fl. Br. Ind. 5 (Dec. 1888) 597; NAGEL, Bot. Jahrb. 50 (1914) 477; GAMBLE, J. As. Soc. Beng. 75, ii (1915) 401, *incl. var. crenata* HOOK. *f. ex* GAMBLE; RIDL. Fl. Mal. Pen. 3 (1924) 369, f. 158; CORNER, Ways. Trees (1940) 333, f. 117.—*E. permicrophylla* ELMER, Leafl. Philip. Bot. 9 (1934) 3194.—**Fig. 1b, 4g, 5.**

Tree (2–)20–25(–42) m, sometimes with buttresses up to 3–4 m high and 1½ m out. *Leaf* rachis (3–)5–18(–21) cm, more or less hairy, 3–7(–9)-jugate; leaflets varying from small, coriaceous, and glabrous to large, herbaceous, and hirsute (mainly on the nerves), (sub)sessile, markedly decreasing in size towards the leaf-base, the basal leaflets attaining about half the length of the largest ones, 1½–3 times as long as wide, widest at the middle or above, (1–)2–13½ by (½–)1–4 cm; base narrowed, acutish to obtuse, top acutish to subacuminate; margin crenate or serrate sometimes from the base but at any rate towards the top; surface dull, underneath more or less densely set with golden yellow glandular scales. Dioecious. Catkins lateral on leafy and on slightly older twigs, the peduncles solitary in the leaf axil or serial by twos or threes. *Male catkins* in bundles of 2–3, sessile to 3 cm stalked, 3–10 cm long; perianth completely reduced or almost so; stamens (3–)5–7, sessile to ⅓ mm stalked, anthers sometimes unequal, ½–1 mm, sparsely hirsute, connective not or hardly protruding. *Fruiting catkins* 9–14 cm long in all, 2–5 cm stalked, rachis as thick as that of the leaves, shallowly grooved. Nut (sub)sessile, ± 3 mm diam., hispid, wing 1½–3¼(–3¾) cm long with the nut, 5–10 mm wide; perianth lobes rather equal, often not adnate to the style, style about as long as the stigmas, the whole 2–4 mm long.

Distr. Upper Burma, N. Siam, Indo-China (Laos, Cambodia), in *Malaysia*: Malay Peninsula, Sumatra (S of Lake Toba, also Bengkalis, Banka, Billiton), W. Java, Borneo, Philippines (Luzon to N. Mindanao), Celebes, Moluccas (W. Ceram).

Ecol. Primary dryland forest (rarely secondary forest) on sandy or clayey soil, from sea-level to 2200 m. In Malaya the leaves are shed at the end of a dry spell without fading into autumn tints (CORNER).

Vern. *Ki hudjan*, (*lang*)*kědi*, (*bě*)*běri*, M, *ki keper*, S.

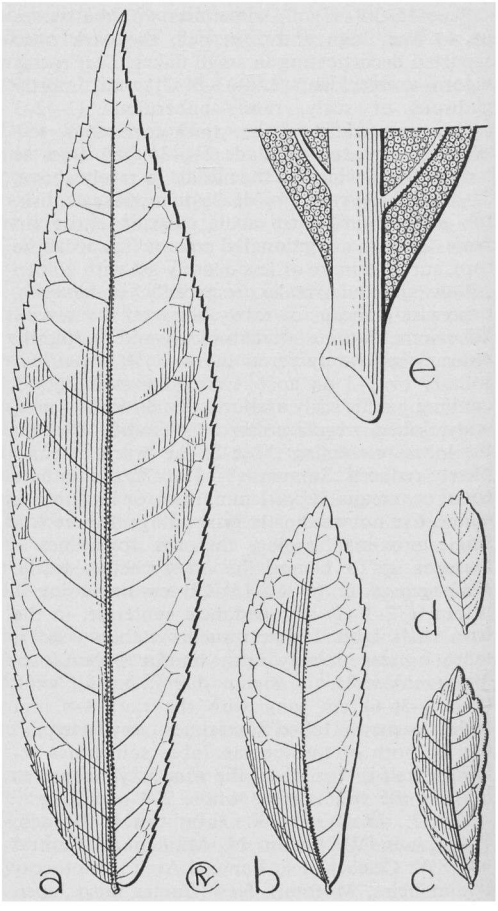

Fig. 5. Variation in leaflets of *E. serrata* BL., the acroscopic side on the left, *a–d.* × ⅔, *e.* leaf base densely set with glandular scales (*a* Houtsoorten Gedeh 126, *b* SULIT 21595, *c*, *e* HOLTTUM 14857, *d* CLEMENS 16888).

Notes. In the Philippines several collections possess very small leaflets, glabrous, *viz* 2–3 cm, the fruit wing being ± 15–21 mm long. In Celebes specimens occur in which the leaflets are slightly larger and 2–3-jugate, the fruit wing being slightly smaller. In Malaya, Sumatra, Banka, and Billiton the leaflets are generally 5–7 cm and glabrous. In Java the leaflets are thin in texture, up to 9-jugate, 8–13½ cm long, serrate from the base, and hirsute, especially on the nerves. Intergrading specimens occur throughout the area.

PIERRE 3301, from Cambodia, is a very bad specimen with entire, acuminate leaves glandular-scaly on both sides. Most probably it belongs here.

JACOBS 4677, from Mt Sago in W. Sumatra, in fruit, is the only specimen with entire leaflets. The leaf rachis is sparsely hairy, the leaflets are 4 times as long as wide, the perianth lobes are not connate with the style. It tallies with a

specimen from the same locality that has serrate leaves.

Most of the extra-Malaysian specimens, especially those from N. Siam, are very densely brown-pubescent on the twigs, the rachises of leaves and catkins, on the leaflets underneath and the nerves above. The largest leaflet seen was 17½ by 5½ cm. The leaflets are sometimes nearly entire, with their indument resembling *E. spicata var. colebrookeana*, but have always yellow scales below.

3. Engelhardia apoensis ELMER *ex* NAGEL, Bot. Jahrb. 50 (1914) 477; ELMER, Leafl. Philip. Bot. 7 (1915) 2693.—*Engelhardtia sp.* CORNER, Ways. Trees (1940) 333, f. 117.—**Fig. 6.**

Leaf rachis 13–23 cm, more or less densely set with scales and small hairs. Leaflets alternate, 7–10, thinly coriaceous, 2–4 mm stalked; blade ± 2½–3 times as long as wide, ovate, (7–)9–13 by 2¼–3(–5) cm; base rounded to subcordate, top narrowed; margin comparatively finely serrate, especially in the basal part; surface above glossy, below glabrous or (in the type specimen) with some minute tomentum on the nerves. Flowers not known; inflorescences presumably lateral. *Fruiting catkins* 12–30 cm long in all, stalk 4–6 cm. Nut ± 6–8 by 5–6 mm, the body ovoid, elongate, wing (5½–)6–7½ cm long with the nut, 11–18 mm wide, adaxial lobe well developed, 4–6(–15) mm long, style 2–3 mm, stigmas 10 mm long.

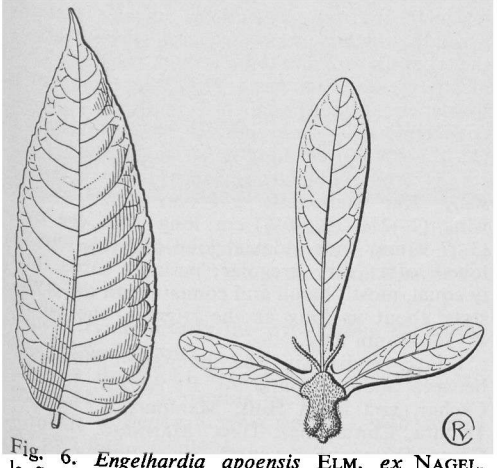

Fig. 6. *Engelhardia apoensis* ELM. *ex* NAGEL, leaflet and fruit, × ⅔ (CF 24424 SYMINGTON).

Distr. *Malaysia*: Malay Peninsula, Borneo (N. Sarawak), Philippines (Mindanao: Mt Apo).

Notes. This taxon is remarkable for its ovate leaflets and elongate nut.

The 7 examined specimens from Malaya match the type specimen from Mindanao, ELMER 11744, very well, the Malayan plants having somewhat longer catkins and larger fruits. In RICHARDS 1521 from N. Sarawak the leaves are entire.

4. Engelhardia spicata LECHEN. *ex* BL. Bijdr. 10 (1825) 528; Fl. Jav. Jugl. (1829) 8, t. 1, 5A; MIQ. Fl. Ind. Bat. 1, 1 (1856) 842; C. DC. Prod. 16, 2 (1864) 140; KURZ, For. Fl. Burma 2 (1877) 491; VIDAL, Sin. Atlas (1883) t. 90A; HOOK. *f.* Fl. Br. Ind. 5 (1888) 595; K. & V. Bijdr. 5 (1900) 165, 170, *incl. var. α genuina et var. β aceriflora, var. γ colebrookiana quoad specim. tantum*; KOORD. Exk. Fl. Java 2 (1912) 51, f. 6; NAGEL, Bot. Jahrb. 50 (1914) 476, *incl. var. aceriflora*; LEEFM. Trop. Natuur 3 (1914) 46 with fig., 77;

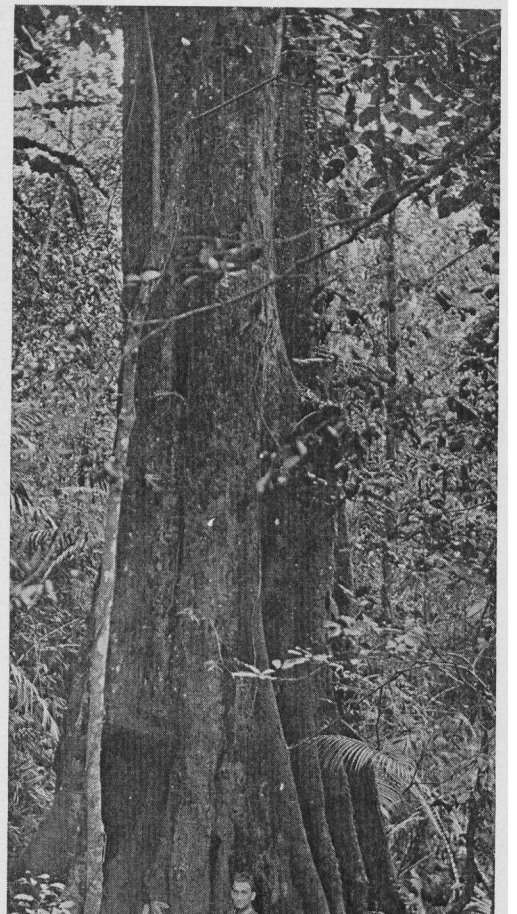

Fig. 7. *Engelhardia spicata* LECHEN. *ex* BL. Large tree, over 40 m tall, in primary forest near Tjikahuripan, Mt Gedeh, W. Java; stem base 8.84 m in girth, dbh 2.8 m (F. KRAMER, who is standing in front).

GAMBLE, J. As. Soc. Beng. 75, ii (1915) 400; KOORD. Atlas 4 (1916) t. 700; MERR. Sp. Blanc. (1918) 120; En. Philip. 2 (1923) 24; KOORD. Fl. Tjibodas 7 (1923) 10, *var. aceriflora* (REINW.) K. & V.; RIDL. Fl. Mal. Pen. 3 (1924) 368; DOCTERS VAN LEEUWEN, Zoocecidia (1926) 103; DODE, Fl. Gén. I.–C. 5 (1930) 930, f. 107, 3–7; CHUN, Sunyatsenia 4 (1940) 245; CORNER, Ways. Trees (1940) 333, f. 117; KANJ. *c.s.* Fl. Assam 4 (1940) 229; DE VOOGD, Trop. Natuur 30 (1941) 103, f. 5–6, 125; BAKH. *f.* in Back. Bekn. Fl. Java (em. ed.) 7A (1948) fam. 155 p. 2.—*Pterilema aceriflorum* REINW. Sylloge 2 (1826) 13.—*E. aceriflora* BL. Fl. Jav. Jugl. (1829) 11, t. 2, 5B; MIQ. Fl. Ind. Bat. 1, 1 (1856) 842; C. DC. Prod. 16, 2 (1864) 141; HOOK. *f.* Fl. Br. Ind. 5 (1888) 596, '*acerifolia*'; FORBES & HEMSL. J. Linn. Soc. Bot. 26 (1899) 495; VON MALM, Fedde Rep. 34 (1934) 271.—*E. roxburghiana* LINDL. *ex* WALL. Pl. As. Rar. 2 (1831) 85, t. 199 f. 7, *quoad fruct.*—*Juglans pterococca* ROXB. Fl. Ind. (ed. Carey) 3 (1832) 631, *quoad fruct.*, '*pterococca*'.—*Girocarpus pendulos* BLANCO, Fl. Filip. ed. 2 (1845) 55, ed. 3 (1877) 104, t. 387.—*E. philippinensis* C. DC. Ann. Sc. Nat. IV, 18 (1862) 34, t. 2 f. 15; Prod. 16, 2 (1864) 141.—**Fig. 1c, 3, 7-9.**

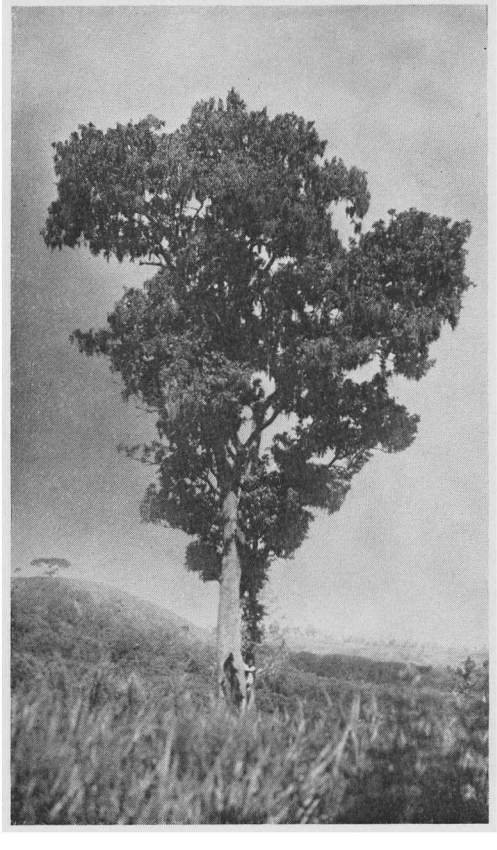

Fig. 8. *Engelhardia spicata* LECHEN. *ex* BL. in clearing of coffee estate Kalisat, Mt Idjen, E. Java (J. H. COERT).

Tree (5–)12–30(–36) m, sometimes with small buttresses. *Leaf* rachis vigorous, blackish, (5½–)10–30(–40) cm, glabrous and/or scaly to hirsute and/or tomentose, (2–)4–5(–7)-jugate; leaflets firmly herbaceous to coriaceous, sessile to 5(—15) mm stalked, blade (1.7–)2.4–3.0(–3.4) times as long as wide, widest about the middle or rarely above, (6–)8½–16(–30) by (3–)5½–6(–8) cm; base very unequal, acute to subcordate, top shortly acuminate, the tip obtuse to acute, rarely the top rounded to acutish; margin entire, rarely serrate; surfaces glabrous to hirsute, especially underneath and on the nerves, sometimes underneath with domatia and/or thin flat greyish (never yellow) scales. In juvenile specimens and suckers leaves large, the leaflets serrate, hirsute. Inflorescences mostly bisexual, paniculate, lateral on leafy and on slightly older twigs, with 1(–0) central ♀ catkin and 2–5 basal ♂ catkins subtended by a caducous subulate bract 3–5 mm, rarely the basal catkins also ♀. *Male catkins* (5–)10–18 cm long in all, 0–1 cm stalked; bracts 2–4 mm, the apical lobe sometimes mucro-like, the lateral lobes very irregular, narrow, sometimes much reduced, perianth whether or not reduced, very irregular, the lobes up to 2 mm long, a small proximal lobe mostly present. Stamens 8–12(–13), anthers (sub)-sessile, equal or unequal, ± 1 mm long, hirsute, connective ¼–½ mm pointed. *Fruiting catkins* (12–)21–40(–60) cm long in all, peduncle 2–10½ cm, vigorous, angular, glabrous and/or greyish-scaly. Nut (sub)sessile, 3–4 mm diam., hispid, wing (2–)2¾–3¾(–6½) cm long with the nut, (3–)7–9 mm wide, adaxial lobe undivided to 5-lobed, often very irregular; perianth lobes fairly equal, mostly small and connate with the style; style about as long as the stigmas, the whole ± 3½–9 mm long.

Distr. India (in the montane Himalayas between about 75° and 90° E; Assam: Khasia, Cachar, and Naga Hills, Manipur; E. Bengal: Tripura, Chittagong), Tibet (MANNING, *in litt.*), China (Yunnan, Kwangsi, *n.v.*), Burma (S of about 25° N), Siam, Indo-China (Laos, Cambodia, Cochin-China), Hainan, in *Malaysia*: Sumatra (Medan to Bencoolen), Malay Peninsula (Perak), Java (W to E, very common), Lesser Sunda Islands (Bali, Lombok, Sumbawa, Sumba, Flores), Borneo (scattered), Philippines (Luzon, Mindoro, Negros, Panay, Cebu, Mindanao; rather common).

Ecol. Primary evergreen forest. Seems to prefer the mountains up to 2000(–2500) m, especially frequent in the *Casuarina* forests on the volcanoes in Central and East Java. On the W. side of Mt Jang in E. Java it is known to form locally pure stands. Similar local dominance has been observed by DE VOOGD, *l.c.*, on Mt Rindjani in Lombok; he also observed it pioneering in mountain savannahs. The dominance is due to succession and seral; with *Pittosporum*, *Homalanthus giganteus*, *Vernonia arborea*, *Dodonaea*, *Wendlandia*, *etc.* belonging to the pioneers of the rain-forest

Fig. 9. *Engelhardia spicata* LECHEN. *ex* BL. in pyrogenous mountain savannah near Sembalun, Mt Rindjani, Lombok, *c.* 2000 m (DE VOOGD).

which try to invade the pyrogenous *Casuarina junghuhniana* stands.

Often deciduous for a short time and then flowering, not in definite periods.

Vern. *Ki hudjan*, S, *sowo*, *donglu*, J, with various prefixes and variations.

Note. Easily distinguished from other species by lacking the golden-yellow glandular scales on the lower surface of the leaves. If scales are present, these are flat, greyish and never golden-yellow.

var. colebrookeana (LINDL. *ex* WALL.) O. KUNTZE, Rev. Gen. Pl. 1 (1891) 637, *non* K. & V. Bijdr. 5 (1900) 169, 172.—*E. colebrookeana* LINDL. *ex* WALL. Pl. As. Rar. 3 (1832) 4, t. 208; BRANDIS, For. Fl. NW. & C. India (1874) 499; HOOK. *f.* Fl. Br. Ind. 5 (1888) 596; DODE, Fl. Gén. I.-C. 5 (1930) 929; MERR. En. Philip. 2 (1923) 23.—*E. villosa* KURZ, For. Fl. Burma 2 (1877) 491, *incl. var. integra* (according to MANNING *in litt.*).—*E. esquirolii* LÉV. in Fedde Rep. 12 (1913) 507, *cf.* REHDER, J. Arn. Arb. 10 (1929) 118.—**Fig. 4a-b.**

Differs from *E. spicata var. spicata* in the following characters: tree mostly comparatively small; twigs, leaf rachis, and leaflets underneath densely hirsute, leaflets with rounded top, often grey-greenish when dry. Fruiting catkins 16–26 cm long in all, 2½–8 cm stalked, the rachis densely hirsute.

Distr. India (largely the same area as *var. spicata*, but not known from E. Bengal), S. China (Kwangsi), Hainan, Burma (KURZ), N. and E. Siam, Indo-China (Annam, Laos); in *Malaysia*: Philippines (Luzon, see below).

Notes. The material on which the Malaysian record is based, PARAISO 25483 and RAMOS & EDAÑO 37939, was identified by Dr MANNING; I have not seen it.

E. spicata is a very variable species and the variation of its characters seems to occur more or less at random and not bound to a geographical pattern. The reason that the combination of characters described above has received taxonomic recognition is solely because the specimens representing this combination are conspicuous. All these characters, however, were also found to occur separately, and in other combinations as well. Therefore I adhere no more taxonomic value to this variety than as a random assemblage of marked paramorphs.

In East Java, apart from the common form, a form dominates with densely hairy leaves, which has incorrectly been referred to *var. colebrookeana* by KOORDERS & VALETON. In my opinion this form represents a local tendency in the population that originated independently from the paramorphs on the Asiatic continent. Moreover, a complete series of intergrades exists between the glabrous and the hairy form in Java.

5. Engelhardia roxburghiana WALL. Pl. As. Rar. 2 (1831) 85, t. 199, *excl. fruct.*; BRANDIS, For. Fl. NW. & C. India (1874) 500.—*Juglans pterococca* ROXB. Hort. Beng. (1814) 68, *nomen*; Fl. Ind. (ed. Carey) 3 (1832) 631, *'pterococca', descr., excl. fruct.—E. chrysolepis* HANCE, Ann. Sc. Nat. IV, 15 (1861) 227; NAGEL, Bot. Jahrb. 50 (1914) 475; CORNER, Ways. Trees (1940) 333, f. 117; METCALFE, Fl. Fukien 1 (1942) 45; P'EI, Bot. Bull. Acad. Sin. 1 (1947) 208.—*E. wallichiana* [LINDL. *ex* WALL. Cat. (1831/2) *no* 4942] C. DC. Prod. 16, 2 (1864) 141, *incl. β chrysolepis*; HOOK. *f.* Fl. Br. Ind. 5 (1888) 596; FORBES & HEMSL. J. Linn. Soc. Bot. 26 (1899) 195; NAGEL, Bot. Jahrb. 50 (1914) 475; GAMBLE, J. As. Soc. Bengal 75, ii (1915) 402; RIDL. Fl. Mal. Pen. 3 (1924) 370; DODE, Fl. Gén. I.-C. 5 (1930) 931.—*E. polystachya* RADLK. Sitz. Ber. Bayer. Ak. Wiss. Math.-Phys. Kl. 8 (1878) 385, *ex descr.*; BRANDIS, Ind. Trees (1906) 620; KANJ. *c.s.* Fl. Assam 4 (1940) 301.—*E. pterococca* O.K. Rev. Gen. Pl. 2 (1891) 637, *quoad nomen et var. α roxburghiana* O.K.—*E. spicata var. formosana* HAY. Fl. Mont. Form. (1908) 199.—*E. formosana* HAY. Ic. Pl. Form. 6 (1916) 61; KANEH. Form. Trees (1936) 80, f. 35.—*E. fenzelii* MERR. Lingn. Sc. J. 7 (1931) 300, *ex descr.*; METCALFE, Fl. Fukien 1 (1942) 45.

Tree ± 5–20 m, sometimes with low, rounded buttresses. Innovations bronze-coloured with golden yellow glandular scales which become brown when older. *Leaf* rachis 5½–14 cm, as the twig glabrous to sometimes densely brown puberulous, 2–4-jugate; leaflets coriaceous, on a stalk 6–12 mm forming mostly a distinct joint with the rachis; blade (2.4–)2.8–3.6(–4.0) times as long as wide, widest mostly below the middle, sometimes halfway, (8–)10–16(–23) by (2–)3½–5(–7½) cm; base very unequal, acute, often basiscopically somewhat decurrent, top narrowed, gradually bluntly acuminate; midrib narrowly raised above; margin entire, surfaces in dry state never even-coloured, but with dull shades of greenish, greyish, brownish, or blackish, glabrous but underneath yellow to brown glandular-scaly. Probably sometimes dioecious, but mostly the inflorescences bisexual, paniculate, terminal on normal or slightly weaker lateral twigs, 2–4 cm peduncled, with central ♀ catkin (which may be wanting) and 2–6 basal ♂ catkins subtended by early caducuous bracts; rarely the ♀ catkin solitary. Flowers scaly. *Male catkins* 8–12 cm long in all, ½–2 cm stalked; rachis slender, scaly, not hairy; bract ± 2 by 1 mm, obscurely 3-lobed at the top, perianth lobes 4, not reduced, strongly cucullate, 1–1¼ cm diam., with membranous margin; stamens (8–)12, inserted with (2–)3 at the base of each perianth lobe, filament and anther both ½ mm long, in some stamens reduced to ⅓ mm, glabrous. *Fruiting catkins* 12–22 cm long in all, peduncle 2–5½ cm, slender, rachis tomentose, sometimes also scaly. Nut 4–8 mm stalked, transversely ellipsoid, 4–5 mm diam., scaly, not hairy; wing (3–)5–5½ cm long with the nut, 0.7–1.4(–1.8) cm wide, hardly connate with the nut, adaxial lobe almost none; perianth lobes very equal and regular, 1–2 mm long, on top of the nut together enclosing the 4 sessile stigmas.

Distr. India (Assam), S. China (all provinces S of about 30° N lat.), Hainan, Formosa, Indo-China (Tonkin, Laos, Annam), in *Malaysia*: Sumatra (in the N. part especially, S to Bencoolen), Malay Peninsula (Kedah, Perak, Pahang, Penang), Borneo (Brunei and Kinabalu region). Everywhere more or less rare.

Ecol. Primary forests in hilly country between about 700 and 1500 m alt. Flowers and fruits not at definite times.

Uses. In Sumatra said to be a fish-poison.

Note. WALLICH's treatment of this species comprises three elements: a two-line diagnosis from LINDLEY's MS, an extensive analysis after ROXBURGH's MS (the latter was to be published again, under the name *Juglans plerococca*, in 1832), and a plate which is a copy of ROXBURGH's drawing. The diagnosis that WALLICH took from LINDLEY refers, as HOOKER has already pointed out, to *E. spicata* and the same is true for that part of ROXBURGH's plate and description where the fruit is given as hairy. The remaining part of ROXBURGH's plate and description clearly refer to *E. roxburghiana* in the present sense. Since only a minor part of WALLICH's *mixtum* belongs to *E. spicata*, it is thought correct to accept WALLICH's *E. roxburghiana pro majore parte.*

Excluded

Engelhardia selanica BL. Fl. Jav. Jugl. (1829) 8 = *Shorea selanica* BL. Mus. Bot. 2 (1852) 33 (*Dipterocarpaceae*).