ERYTHROXYLACEAE (J. P. D. W. Payens, Leyden)

1. ERYTHROXYLUM

P. BROWNE, Hist. Jamaica 1 (1756) 278; LINNÉ, Syst. Nat. ed. 10, 2 (1759) 1035 (*Erythroxylon*); O. E. SCHULZ, Pfl. R. Heft 29 (1907); E. & P. Pfl. Fam. ed. 2, 19a (1931) 130.—**Fig. 1–4.**

Shrubs or trees. Youngest branchlets compressed, older branches terete; base of the lateral twigs often provided with small distichous 'bracts' (*ramenta*) sometimes also occurring between the leaves. *Leaves* simple, alternate (distichous), entire, involute in bud, the margins leaving a more or less permanent trace as 2 longitudinal lines on the upper leaf surface ('areolate'). Stipules mostly entirely connate, rarely bifid, intrapetiolar, often bicarinate, sometimes emarginate or 2-toothed at the apex, long-persistent or early caducous, inserted ± semi-amplexicaulous and leaving a distinct, mostly oblique scar. *Flowers* axillary, solitary or in clusters, often dimorphous, or even 3–4-morphous, 5-merous, actinomorphic, bisexual. Pedicels more or less thickened, often only under the calyx, provided with 2 bracteoles at the base. *Calyx* persistent, campanulate, (in Mal.) ± halfway divided into 5 lobes imbricate in bud. *Petals* 5, free, caducous, alternating with the calyx lobes, quincuncial in bud, nearly always provided with an emarginate or 3-lobed ligule inserted on the apex of the claw of the petal. *Stamens* 10, in two whorls of 5, persistent; filaments towards the base connate into a staminal tube often with a toothed margin; anthers ellipsoid, basifixed, cordate at the base, 2-celled, opening lengthwise. latrorse. *Ovary* (1–)3-celled, each cell with 1 ovule, normally only 1 cell fertile, but the other empty cells sometimes distinctly enlarged in fruit; styles 3, erect, free or partly connate or stigmas ± sessile; stigmas flattened (often oblique) or (in extra-Mal. *spp.*) clavate, blunt or rarely acute. Ovules pendulous, anatropous, with a ventral raphe. *Fruit* a drupe. *Seed* with or without endosperm; embryo oblong, erect; cotyledons flat to plano-convex; no plumule, but a distinct radicle.

Distr. The *Erythroxylaceae* comprise three exclusively tropical genera. *Aneulophus* BENTH. is monotypic and restricted to West Africa. *Nectaropetalum* BENTH. (*Peglera* BOLUS) has a few species in SE. Africa (*cf.* STAPF, Kew Bull. 1909, 188).

Erythroxylum occurs throughout the tropical regions of the world, distinctly centering, both to sections and species, in South America where 9 sections out of 19 are represented.

About 200 *spp.* have been distinguished in the genus, but the number of good species will possibly be less. Africa is poor in species, Madagascar relatively rich, Asia, Malaysia, and Queensland poor; in the Pacific obviously only represented in Melanesia (Solomons and New Caledonia) and not reported from Fiji, Samoa, or Micronesia.

All Malaysian *spp.* belong to the *sect. Coelocarpus*, which includes also Australian and African *spp.* Two South American *spp.* of *sect. Archerythroxylum* are cultivated in Java.

Ecol. The Malaysian *spp.* are confined to the substage of the primary rain-forest up to *c.* 1600 m, obviously avoiding areas subject to a dry season; of *E. cuneatum* only two specimens have been collected in the seasonal area of the Lesser Sunda Islands, *viz* on an islet of the Kangean group and on Sumbawa. In Africa and Australia some xerophytic species are known under arid climatic conditions.

E. cuneatum is often found in the coastal forest along the beach or behind the mangrove as a small tree.

Galls. Among New Guinean material of *E. ecarinatum* an undescribed flower gall was found in which the pedicels are swollen into globular galls with a lignified wall.

Morph. The *ramenta* occurring in certain species represent stipules of leaves with early arrested development; the rudimentary leaf blade is sometimes present as a minute thick awn concealed in the dorsal groove between the 2 nerves of the ramentum. In most species ramenta occur in great number and are closely set at the base of the lateral twigs, but they may also be found between the leaves higher up the twig; naturally they are alternate. In certain cases they may bear flowers. In Malaysia clearly developed ramenta are only found in *E. coca*.

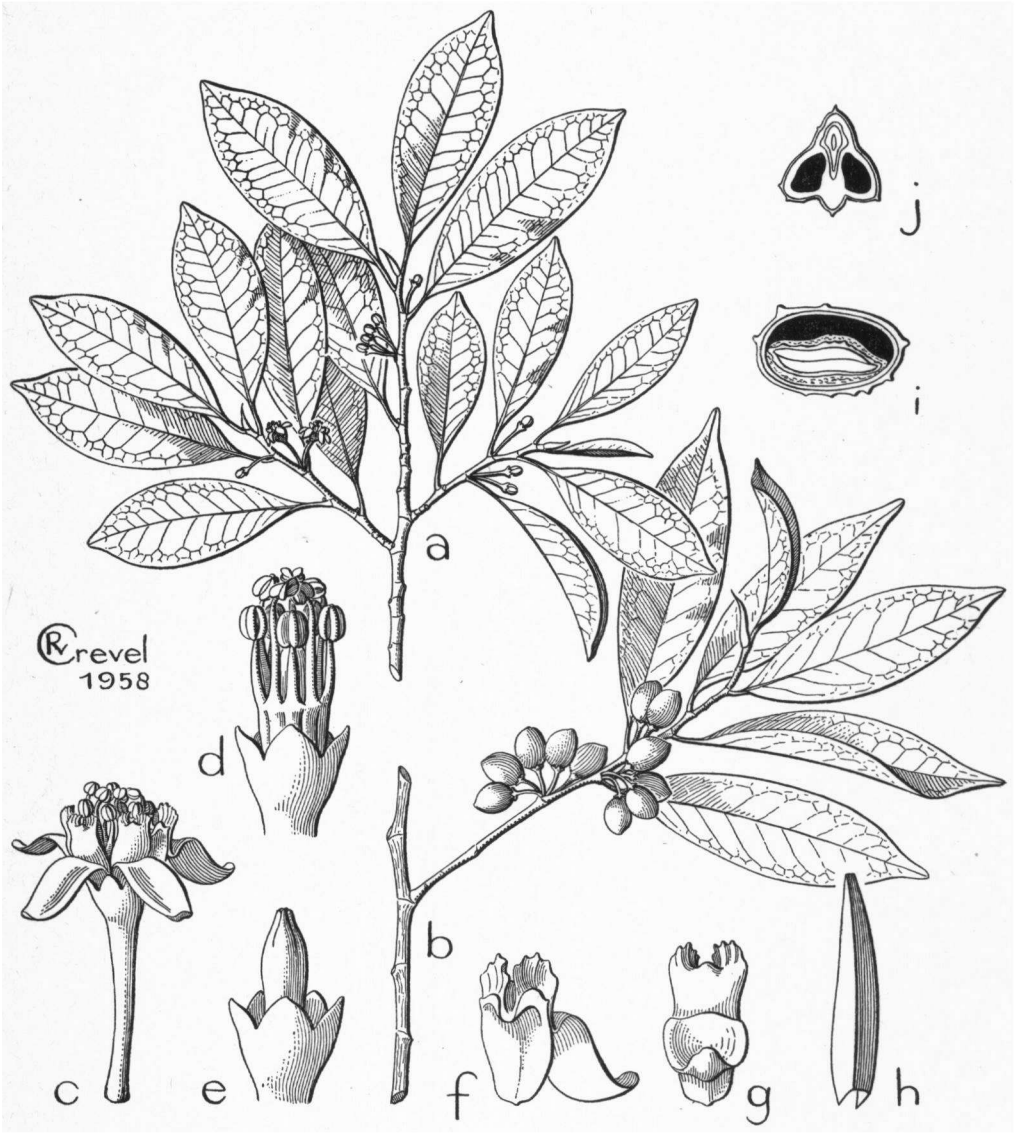

Fig. 1. *Erythroxylum ecarinatum* BURCK. *a.* Flowering twig, × 2/3, *b. ditto* fruiting, × 2/3, *c.* flower, × 4, *d. ditto*, petals removed, × 7, *e.* calyx and gynoecium, × 7, *f–g.* petal, lateral and dorsal, × 7, *h.* stipule with flattened dorsal, 2-nerved face, × 7, *i.* the 1-celled fruit in cross-section, the seed shrunk, × 3.—*Erythroxylum cuneatum* (MIQ.) KURZ. *j.* The 3-celled fruit in cross section, 2 lateral cells empty, × 3 (*a, c–h* BRASS 28561, *b, i* BRASS 7679, *j* HOCHREUTINER 78).

Several species possess dimorphous flowers: *brachystylous* (short-styled) and *dolichostylous* (long-styled). See fig. 4. *E. cuneatum* (MIQ.) KURZ possesses even four types of flowers.

In brachystylous flowers the stamens are either all equal in size and shape (*E. cuneatum*) or unequal ('*E. densinerve*'). In dolichostylous flowers the stamens are sometimes all equal, but in other specimens 5 stamens are short and 5 are long. In the case of unequal stamens the anthers of the shorter filaments are always larger than those on the longer filaments. The heteromorphism is specific but each specimen has one type of flowers and is either brachystylous or dolichostylous.

BURCK has described the details of the remarkable heterostylism in *Erythroxylum* (Ned. Kruidk. Arch. 6, 1895, 254–262, in Dutch). He observed abundant fruiting in *E. novogranatense* of which only dolichostylous flowers occurred in Java; the same phenomenon was found in *E. coca* (*l.c.* p. 261–262).

Also from the restricted geographical distribution pattern of brachystylous and dolichostylous flowers in Malaysia I conclude that the genetics of this character are not random.

Wood-anat. DESCH, Mal. For. Rec. 15[1] (1941) 155 (hand lens). HEIMSCH, Lilloa 8 (1942) 100; METCALFE & CHALK, 1 (1950) 273; NORMAND, Atlas des Bois de la Cote d'Ivoire 1 (1950) 145; RECORD & HESS, Timbers of the New World, Yale Univ., New Haven (1947) 149.—HEIMSCH considers, that the wood anatomy suggests close affinity with the *Linaceae*, but that the two families are distinct.—C.A.R.-G.

Dispersal. In all probability the drupes will be dispersed by animals, though the empty, air-filled cavities of the sterile cells might be advantageous for providing buoyancy capacity in waterborne dispersal. The habitat, however, does not indicate that this potentiality is effective in nature. From the experiments with the cultivated *spp.* it appears that the germination capacity is rapidly lost.

Uses. *E. coca* LAMK and *E. novogranatense* (MORRIS) HIERON. are very important because of the high content in valuable alkaloids found in their leaves. Cocaine is used nowadays medicinally throughout the world as a stimulant and as an anaesthetic, specially in eye-surgery.

In Malaysia only *E. novogranatense* is grown for coca. In trade it is generally known as 'Java coca' or 'Truxillo coca'.

E. cuneatum (MIQ.) KURZ furnishes a hard and durable, pink-coloured timber, which is through its often small dimension and quantity of minor importance.

Taxon. The *Erythroxylaceae* have in the past been incorporated in several families. At first A. L. DE JUSSIEU tentatively referred the genus *Erythroxylum* to the *Malpighiaceae* (Gen. Pl. 1789, 281).

In 1821 KUNTH described it as representing a separate family, including the genera *Erythroxylum* and *Sethia;* the latter genus contained one Indian species, *S. indica* DC. = *E. monogynum* ROXB. (in H.B.K. Nov. Gen. 5, 1821), now recognized as the single representative of *sect. Sethia.*

In 1862 BENTHAM incorporated the genera *Erythroxylum, Aneulophus* (and *Hebepetalum,* which is retained in *Linaceae*) in the *Linaceae* as a separate tribe (in B. & H. Gen. Pl. 1, 1862, 244); he was followed by BAILLON and later still by SOLEREDER (Syst. Anat. Dikot. 1899).

In 1878 EICHLER (Blütendiagr.) and PEYRITSCH (in Fl. Bras. 12, 1) re-established the *Erythroxylaceae* definitely as a distinct family, a point of view retained to the present day.

Several authors recognize the close affinity to the *Linaceae* and this is obviously sustained by the wood-anatomy according to HEIMISCH (Lilloa 8, 1942, 100), though he admitted that the differences should be given family rank: *Erythroxylaceae* lack scalariform vessel perforations and have more uniform ray types.

HUTCHINSON revived JUSSIEU's opinion and accepted a close affinity with the *Malpighiaceae,* arranging them with the *Humiriaceae* in the *Malpighiales* (Fam. Fl. Pl. 1926) instead of with the *Linaceae* in the *Geraniales.*

ERDTMAN stated that palynologically *Erythroxylaceae* are more or less closely related to the *Linaceae* (except the genus *Nectaropetalum*), the *Malpighiaceae,* and the *Trigoniaceae,* without giving further preference.

The genus *Erythroxylum* is very homogeneous and it has not been possible to distinguish subgenera within it. O. E. SCHULZ (1907, *l.c.*) has subdivided it into 19 different sections.

P. BROWNE (1756) attributed two unnamed species to the genus, one of which was named by LINNAEUS in 1759 *E. areolatum* L. (Syst. Nat. ed. 10, p. 1035). This is therefore the type species of the genus. Consequently *sect. Heterogyne* O. E. SCHULZ (1907, *l.c.*, p. 63) becomes the type section *Erythroxylum.*

SCHULZ distinguished the sections primarily on characters of the stipule which he considered, through its constancy, as the most important one from the taxonomical point of view. He found great difficulty in the distinction of the species caused by the variable morphology of the flowers and the plasticity of the foliage. It appears that his keys to both sections and species contain many 'feeble' places as for instance between his sections 7 to 11, where all characters mentioned are a matter of (mostly overlapping) quantity rather than of quality. Consequently, the sections represent rather natural but grading groups of allied species of certain geographical areas than sharply defined taxa. It seems rather strange that *E. ecarinatum* is inserted without comment in *sect. Coelocarpus* though it differs in a set of important characters from the other *spp.* of this section by its sessile stigmas, the structure of the exalbuminous embryo, and the remarkable fact that the ovary is 1-celled without vestiges of other cells.

My impression is that with the abundant material collected posterior to SCHULZ's monograph, it has appeared that many species have become connected by intergrades and consequently must be united.

KEY TO THE SPECIES

1. Stipules persistent. Styles free. Sterile cells of the drupe inconspicuous, very much smaller than the fertile cell (*sect. Archerythroxylum* O. E. SCHULZ).
2. Leaves oblong-obovate, long persistent, bright green above. Ramenta none or few. Flowers white. Fruits on leafy branches. Young twigs not warty . . . . . **1. E. novogranatense**
2. Leaves broad-elliptic, soon falling, dark green above. Ramenta numerous. Flowers yellowish-green. Fruits almost always on bare branches. Young twigs warty . . . . . **2. E. coca**
1. Stipules early caducous. Styles more or less connate or stigmas almost sessile. Sterile cells of the drupe either conspicuous (as large as or even larger than the fertile cell) or absent (*sect. Coelocarpus* O. E. SCHULZ).
3. Styles almost absent, stigmas sessile. Ovary 1-celled. Drupe biconvex, compressed. Seed without endosperm. Midrib of the leaves prominent on both sides . . . . . **3. E. ecarinatum**
3. Styles well developed. Ovary 3-celled. Drupe trigonous, not compressed. Sterile cells as large as or larger than the fertile one. Seed with endosperm. Midrib of the leaves prominent beneath, not prominent (usually sunken) above . . . . . **4. E. cuneatum**

1. Erythroxylum novogranatense (MORRIS) HIERON. Bot. Jahrb. 20, Beibl. 49 (1895) 35; O. E. SCHULZ, in Urban, Symb. Ant. 5 (1907) 199; Pfl. R. Heft 29 (1907) 85; BACK. Schoolfl. (1911) 164; KOORD. Exk. Fl. Java 2 (1912) 416; VAN GORKOM, Oost-Ind. Cult. 3 (1913) 163; HEYNE, Nutt. Pl. (1927) 855; BURK. Dict. 1 (1935) 950; BACK. Bekn. Fl. Java (em. ed.) 4c (1943) fam. 111, p. 1.—*E. coca var. novogranatense* MORRIS, Kew Bull. (1889) 5; J. Linn. Soc. Bot. 25 (1890) 384; BURCK, Teysmannia 1 (1890) 385, 449.—*E. coca var. spruceanum* BURCK, Teysmannia 1 (1890) 456.—*E. truxillense* RUSBY, Druggist's Circular Chemic. Gaz. (1900) 220; (1901) 48.

Bush or shrub *c.* 1–3 m. Lenticels on the branches minute. *Leaves* abundant along the twigs, not soon falling, obovate-oblong, bright green above, paler and glaucous beneath, *c.* (2–)3–6(–7) by 1–3 cm; rounded or sometimes emarginate, always with a mucronate tip or notch, attenuate at the base; midrib rather prominent beneath, specially at the base, nerves numerous, on both surfaces equally distinct, venation delicately anastomosing, central part included between the areolation lines slightly concave and of a paler colour on both surfaces; petiole thin, *c.* 3–7 mm. Stipules green, triangular, shorter or half as long as the petiole, *c.* 2½–4 by 2–3 mm, slightly bicarinate, persistent, on old branches brown, top emarginate, 2-toothed, margin more or less fimbriate. Ramenta none or occasionally a few. *Flowers* in clusters of 1–4(–8). Bracteoles green, deltoid, acuminate, scarious, up to *c.* 2½ by 1 mm, margin delicately fimbriate. Pedicels thickened, *c.* 5–10 mm. *Calyx* green, the tube 1–1½ mm, lobes triangular-ovate, acuminate, *c.* 1½–2 by 1 mm. *Petals* white or greenish-white, oblong, convex *c.* (3½–)4(–5) by 2 mm; ligule 3-lobed, with crisped lobes, half as long as the blade of the petal; claw *c.* ⅕–¼ the length of the petal.

Brachystylous flowers.—Staminal tube pale green *c.* 1 mm. Stamens equal, filaments *c.* 3½–5½ mm, anthers *c.* ½ by ⅓ mm. *Ovary* distinctly longer than the staminal tube, *c.* 2 by 1 mm; styles free, *c.* 1 mm.

Dolichostylous flowers.—Staminal tube 1 mm. Stamens unequal, episepalous filaments ½–¾–1 mm, epipetalous ones ½–1½–2 mm, anthers ¾–½ by ½–¼ and ½ by ¼ mm respectively. *Ovary* longer than the staminal tube, *c.* 1½ by 1 mm; styles free, *c.* 2–3 mm.

Drupe red, elliptic-oblong, in the fresh state 9–11 by 4–5 mm; stone narrower, pointed, obtusely trigonous, with 4–6 ribs and furrows, *c.* 8–10 by 3–4 mm; sterile cells hardly distinct, fertile cell almost triangular in section. *Seed* with 3 distinct ribs; endosperm abundant; embryo central, small, *c.* 6–7 by 1 mm, flattened; cotyledons lanceolate, *c.* 3–4 mm; radicle *c.* 2–3 by ½ mm.

Distr. Native in South America, cultivated elsewhere in the tropics; in *Malaysia*: in the Malay Peninsula (Perak, Selangor), W. and E. Java, Br. N. Borneo, Celebes (Minahasa), and the Philippines (Luzon).

Ecol. In *Malaysia* often grown as a hedge plant, up to 750 m. *Fl.-fr.* Jan.–Dec.

Uses. Cultivated in Java since 1875 in the Botanic Garden at Bogor, when the first seeds were received. In 1885 after many difficulties and contradictory reports and advices an experimental plantation was started in the Tjikeumeuh Agricultural Garden at Bogor from seeds imported by the firm of Herman Linden & Co, which proved successful. Since 1886 many seeds were distributed to new plantations. The culture never gained great importance in Java; the price of the leaves rapidly decreased in the early twenties. Several estates used the species as hedges and as accessory crop. According to CORNER (Ways. Trees 1, 1940, 220) cultivation was prohibited in the Malay Peninsula.

From the dried leaves medicinal tinctures were prepared and by refining these alkaloids are obtained of which the main one is cocaine, which is used as a stimulant and as an anaesthetic mainly for eye-surgery. In Java a factory was built to prepare the crude alkaloid for export in order to avoid the costs of transport of the leaves to Europe (BURKILL, *l.c.* p. 952).

Vern. *Coca, truxillo coca, Java coca*, D, E.

Notes. O. E. SCHULZ described 3 varieties based on the size of the leaves. This is, however, very much depending on the environment (soil, altitude, moisture, and temperature) and also on the amount of shade; they have no taxonomical

value. *E. novogranatense* adapts itself better to moist and warm tropical conditions than *E. coca* LAMK. Both are grown in their native countries in South America up to high altitudes to over 2000 m.

Though according to PRESCOTT (History of the Conquest of Peru 1, 1847, 129) both *E. coca* and *E. novogranatense* have been cultivated on a large scale in S. America from time immemorial and have never been found in a truly wild state, Peru has been accepted as the native country. In the Inca culture the plants were originally held sacred and reserved only for kings and priests. This reservation was later abandoned and leaves were chewed freely by the people, specially by carriers and messengers for avoiding a heavy food and water supply during far, rapid journeys over the mountains.

2. Erythroxylum coca LAMK, Enc. Méth. Bot. 2 (1786) 393; Cav. Diss. 7 (1789) 402; DC. Prod. 1 (1824) 575; HOOK. Comp. Bot. Mag. 1 (1835) 161; 2 (1836) 25; MARTIUS, Abh. Ak. München 3 (1841) 367; GOSSE, Mém. Cour. Acad. Roy. Belg. 12 (1861); PEYRITSCH, Fl. Bras. 12, 1 (1878) 156; BERKHOUT, Tijd. Nijv. Landb. N.I. 31 (1885) 251; TRIM. Ceyl. Adm. Rep. (1887) 13; MORRIS, Kew Bull. 3 (1889) 3, 221; J. Linn. Soc. Bot. 25 (1890) 381; BURCK, Teysmannia 1 (1890) 385, 449; HOOK. *f.* Bot. Mag. 50 (1894) t. 7334; BACK. Fl. Bat. 1 (1907) 210; O. E. SCHULZ, Pfl. R. Heft 29 (1907) 83; BACK. Schoolfl. Java (1911) 164; MERR. Fl. Manila (1912) 267; KOORD. Exk. Fl. Java 2 (1912) 416; VAN GORKUM, Oost-Ind. Cult. 3 (1913) 171; BURK. Dict. 1 (1935) 950; KANEHIRA, J. Dept Agr. Kyushu Imp. Un. 4 (1935) 341; BROWN, Useful Pl. Philip. (1950) 190.—*E. peruvianum* PRESCOTT, Hist. Conquest of Peru 1 (1847) 129, *nom. nud.*—*E. bolivianum* BURCK, Teysmannia 1 (1890) 456.

Small tree or shrub up to 2½ m. Lenticels on the branches sometimes warty, very prominent. *Leaves* chiefly at the ends of the twigs, soon falling, broad-elliptic, *c.* 3–8 by 2–4 cm, dark green above, paler and glaucous beneath, acuminate or rounded with a mucronate tip, cuneate at the base; midrib prominent beneath; nerves numerous, very faint on both sides, venation delicately anastomosing, two lines giving a clearly distinguishable, slightly concave areolation of a paler colour; petiole *c.* 2–6 mm. Stipules triangular, more or less bicarinate, shorter than or as long as the petiole, *c.* 3–5 by 3–5 mm, persistent, on old branches brown and stiff, top acute, 2-toothed. Ramenta numerous. *Flowers* in clusters of 6–12, rarely more, in the axil of leaves or ramenta. Bracteoles deltoid small and scarious. Pedicels thickened, *c.* 4–6 mm. *Calyx* green, the tube 2–1 mm, lobes triangular-ovate, acute, *c.* 1–2 mm. *Petals* yellow or yellowish green, oblong, convex, *c.* 4–4½ by 2 mm; ligule 3-lobed (2 lobes crisped), half as long as the blade, claw broad, *c.* ⅕ of the petal.

Brachystylous flowers.—Staminal tube *c.* 1½ mm. Stamens equal; filaments 4 mm, anthers ½ by ⅓ mm. *Ovary* ellipsoid, slightly longer than the staminal tube, *c.* 2 by 1½ mm; styles free, *c.* 2 mm.

Dolichostylous flowers.—Stamens unequal; episepalous filaments 2 mm, epipetalous ones 3 mm; anthers ¾ by ½ and ½ by ¼ mm respectively. Styles free, 4 mm.

Drupe red, oblong-ovoid, pointed, when dry obtusely trigonous, furrowed, *c.* 7–10 by 3–4½ mm; sterile cells not very distinct, fertile cell large, almost triquetrous in section. *Seed* with 3 distinct ribs; endosperm abundant; embryo central, small, *c.* 6 by 1½ mm, flattened, cotyledons lanceolate *c.* 4 mm; radicle *c.* 2 mm.

Distr. Native in South America, cultivated in various other tropical countries, in *Malaysia* obviously only cultivated in a few Botanic Gardens but not used as a crop in plantations.

Ecol. At Bogor it produces abundant fruit but not much foliage as it does at higher altitudes, for example in tropical South America, where it is grown on red clay soils up to 1600 m. *Fl.-fr.* Jan.-Dec.

Uses. In S. America chewed by the Indians as a stimulant, leaves being exported for distillation abroad.

Vern. *Peru coca, coca,* D, E.

3. Erythroxylum ecarinatum BURCK, Ann. Jard. Bot. Btzg 11 (1893) 191; HOCHR. Pl. Bog. Exs. (1904) 79; O. E. SCHULZ, Pfl. R. Heft 29 (1907) 141; MERR. Philip. J. Sc. 11 (1917) Bot. 277; O. E. SCHULZ, Bot. Jahrb. 58 (1923) 249; HEYNE, Nutt. Pl. (1927) 855; C. T. WHITE, Contr. Arn. Arb. 4 (1933) 47; FRANCIS, Austr. Rain-for. Trees (1951) 419.—*E. sp.* TEYSM. & BINN. Cat. Hort. Bog. (1866) 214.—*E. montanum* TEYSM. & BINN. *ex* EYKMAN, Ann. Jard. Bot. Btzg 7 (1888) 225, *nomen*; MORRIS, Kew Bull. 3 (1889) 11, *nomen.*—*E. moluccanum* TEYSM. & BINN. *ex* SCHULZ, Pfl. R. Heft 29 (1907) 141, *nomen in synon.*—*E. salomonense* WHITE, J. Arn. Arb. 31 (1950) 89. —Fig. 1.

Tree 7–37 m; crown small, not widely spreading. Bark brown or greyish brown, often soft-suberose and thin (2–6 mm), fissured lengthwise or scaly. Branches 2–3(–4) mm diam., with large lenticels in the light brown bark, sometimes giving a warty appearance; very young branchlets 1–2 mm diam. *Leaves* abundant at the ends of the twigs, narrowly elliptic, *c.* 6–12(–17) by 1–4(–5) cm; dark green often shining above, light green and less shining beneath, acuminate with an obtuse tip, base cuneate, midrib always more or less prominent above, very prominent and yellowish beneath; nerves on both sides slightly prominent, venation delicate; areolation often distinct; petiole *c.* 4–8 mm. Stipules oblong-lanceolate, longer than or as long as the petiole, rarely somewhat carinate, *c.* (4–)8–11(–20) by (1–)2–4(–5) mm; top more or less falcate. Ramenta none. *Flowers* in clusters of (2–)4–8(–20). Bracteoles triangular, scarious, rather large, sometimes up to 2 mm. Pedicels thickened towards the calyx, *c.* 5–10 mm. *Calyx* tube *c.* 2½–1½ mm high, lobes triangular, *c.* ½–1½ mm; acuminate with a bluntish tip. *Petals* white, yellow to greenish yellow and cream, outside light brown, oblong, convex, 1-nerved with 2 lateral

nerves in the blade, *c.* 4–5 by 1¼–2 mm; ligule 3-lobed, half as long as the blade, claw *c.* ⅓ as long as the petal.

Brachystylous flowers.—Staminal tube *c.* 1¼–2 mm; stamens unequal; episepalous filaments *c.* ½–1 mm, epipetalous ones *c.* 1–2 mm; anthers light purple, *c.* ½–1 by ½ and ¼–½ by ¼–½ mm respectively. *Ovary* 1-celled, oblong, exceeding the staminal tube, *c.* 2–3 by ¼–¾ mm, light yellow; style none or very short, stigmas (2–)3, brown, clavate, *c.* ½ mm.

Drupe ovoid or broadly ovoid, often curved, when maturing turning from yellow via orange to red; more or less compressed, sometimes slightly oblique with a rounded top, *c.* 8–12(–17) by 5–7(–8) mm and *c.* 4–5 mm thick. *Seeds* without endosperm; embryo *c.* 6–9(–15) by 3–5(–6) mm with more or less ovate, thick cotyledons *c.* 5–7½ by 3–5 mm and a distinct radicle *c.* 1–2 by ½ mm.

Distr. Queensland and Melanesia (Solomon Islands: New Georgia), in *E. Malaysia:* Celebes, Moluccas (Halmaheira, Sula Isl., Buru, Ceram, Ambon), and New Guinea.

Ecol. A very common subsidiary tree of scattered occurrence in the Moluccas and New Guinea, from the lowland up to 2000 m in primary rainforests on slopes and mountain ridges, on rocky and clayey soils, in Halmaheira on coral rock. *Fl.-fr.* Jan.–Dec.

Uses. In Celebes used as a medicine (*obat jaguar*). The timber is used in New Guinea for boat and house building. The latter use is also reported from the Solomon Islands.

Vern. *Liqelique*, Solomons; *lowa waino* (= woman), *lowa motea* (= hard), Tobelo lang., *samainding*, Madi lang., Celebes; *dodojo*, *gemi*, Tobelo lang., Halmaheira; *kasoeli*, Sula Isl.; *naniwar*, Ceram; *kahunar*, *naniwar*, Ambon; *aibon*, Numfoor lang., *biyu*, Anona lang., *dora*, West Papuan, *irèpo*, Tariè lang., *ruachwau*, Karas lang., New Guinea.

Galls. Some specimens from Ambon and many from New Guinea have flower galls, in which the calyx is swollen into a very hard, orange, globular gall.

Notes. Sapwood white or yellow to brown, abruptly set off against the brown or brownred heartwood.

O. E. SCHULZ (*l.c.* 1923, p. 249) distinguished a *var. ledermannii*, based on LEDERMANN 12028, 12135, and 12176 from New Guinea. I have not succeeded in obtaining duplicates for study; the holotypes were obviously lost during the war. According to the description it would differ mostly by the smaller petals (3 mm) and fewer flowers (1–2 per axil).

As far as I could observe the ovary is 1-celled without vestiges of other cells and the drupe is 1-seeded. In herbarium specimens there appears, through shrinkage of the seed, some space between the pale brown testa and the light yellow endocarp. This space gives the false appearance of representing reduced empty cells.

In a remarkably high percentage of specimens the fruits are fully developed but do not contain seed.

4. Erythroxylum cuneatum (MIQ.) KURZ, J. As. Soc. Beng. 43, ii (1847) 135; O. E. SCHULZ, Pfl. R. Heft 29 (1907) 146, *incl. var. bancanum* (BURCK)

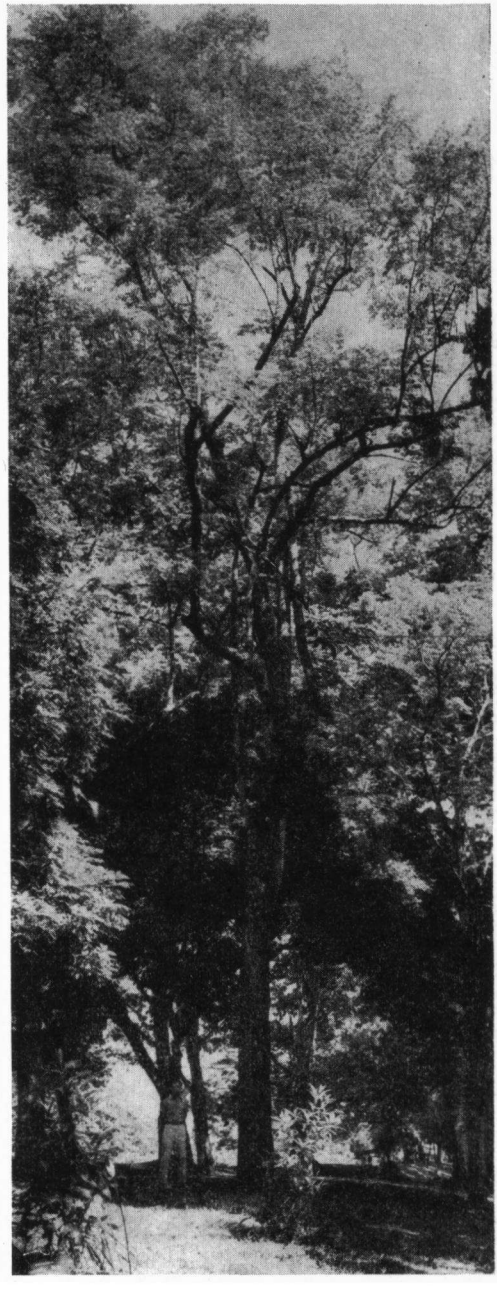

Fig. 2. *Erythroxylon cuneatum* (MIQ.) KURZ. Cultivated tree in Kebun Raya Indonesia (III. K. 5a), Nov. 1957.

O. E. SCHULZ, *l.c.* 148; MERR. Philip. J. Sc. 3 (1908) Bot. 232; BACK. Schoolfl. (1911) 164; GUILLAUMIN, Fl. Gén. I.-C. 1 (1911) 591; MERR. En. Philip. 2 (1923) 325; CRAIB, Fl. Siam. En. 1 (1926) 199; HEYNE, Nutt. Pl. (1927) 855; BURK. Dict. (1935) 950; CORNER, Ways. Trees (1940) 220; BACK. Bekn. Fl. Java (em. ed.) IV C (1943) fam. 111, p. 1; TARDIEU-BLOT, Fl. Gén. I.-C. Suppl. 1 (1945) 516; QUIS. Philip. J. Sc. 77 (1947) 153.—*Ficus cuneata* WALL. Cat. (1828) *no* 4534, *nom. nud.*—*Urostigma ? cuneatum* MIQ. in Hook. Lond. J. Bot. 6 (1847) 585.—*E. burmanicum* GRIFF. Posth. Papers, Not. Pl. As. 4 (1854) 468, t. 581, fig. 3; KURZ, J. As. Soc. Beng. 39, ii (1870) 68; SCHEFF. Nat. Tijd. N.I. 32 (1873) 409; HOOK. *f.* Fl. Br. Ind. 1 (1874) 414; SCHEFF. Nat. Tijd. N.I. 34 (1874) 95; KURZ, For. Fl. Burma 1 (1877) 171; BURCK, Ann. Jard. Bot. Btzg 11 (1893) 190; KING, J. As. Soc. Beng. 62, ii (1893) 190; RIDL. J. Str. Br. R. As. Soc. *no* 33 (1900) 55; HOCHR. Pl. Bog. Exs. (1904) 78; CRAIB, Kew Bull. (1911) 24; RIDL. Fl. Mal. Pen. 1 (1922) 325.—*E. sumatranum* MIQ. Sum. 1 (1861) 200, 512; Illustr. (1871) 71.—*E. retusum* BAUER *ex* TEYSM. & BINN. Cat. Hort. Bog. (1866) 214, *nom.*; Nat. Tijd. N.I. 29 (1867) 254, *descr.*[1]; MORRIS, Kew Bull. (1889) 11.—*E. bancanum* BURCK, Ann. Jard. Bot. Btzg 11 (1893) 192, t. 16.—*E. latifolium* BURCK, Ann. Jard. Bot. Btzg 11 (1893) 192, *incl. var. longipetiolatum* BOERL. & KOORD. Ic. Bog. 1 (1897) t. 6; O. E. SCHULZ, Pfl. R. Heft 29 (1907) 144, *incl. var. angustatum* O. E. SCHULZ; MERR. En. Born. (1921) 313; MASAMUNE, En. Phan. Born. (1942) 357.—*E. longistipulatum* BURCK, Ann. Jard. Bot. Btzg 11 (1893) 193.—*E. densinerve* O. E. SCHULZ, Pfl. R. Heft 29 (1907) 142; MERR. En. Born. (1921) 313; MASAMUNE, En. Phan. Born. (1942) 357.—*E. platyphyllum* MERR. Philip. J. Sc. 3 (1908) Bot. 232; En. Philip. 2 (1923) 325.—*E. iwahigense* ELM. Leafl. Philip. Bot. 5 (1913) 1776; MERR. En. Philip. 2 (1923) 325.—*E. borneense* MERR. Pl. Elm. Born. (1929) 112; MASAMUNE, En. Phan. Born. (1942) 357.—**Fig. 1j, 2–4.**

Small to large tree or a shrub, (1–)8–40(–45) m, up to 35–55 cm diam. Bark noted to be grey to brown often with vertical grooves, inner bark yellow to reddish brown. Branches 1½–4 mm diam., brown to black when dried, the tips 1–3 mm diam. *Leaves* very variable in size and shape, even on the same twig, mostly obovate, elliptic or oblong, *c.* (3–)5–11(–18) by 2–3(–7) cm; dark green to greenish brown often shining above, dull light green beneath, shortly acuminate or rounded with a more or less emarginate, mostly mucronate tip, base attenuate or cuneate; midrib nearly always sunken above, very prominent beneath; nerves on both sides equally distinct, often almost horizontal and close together giving a dense nervation, venation delicate; areolation often distinct; petiole 2–7(–9) mm. *Stipules* triangular to lanceolate, mostly as long as the petiole, not divided, entire, distinctly bicarinate *c.* 2–7(–9) mm, top mostly curved. Ramenta very rarely a few. *Flowers* in clusters of 1–8, mostly in pairs, faintly scented. Bracteoles deltoid, scarious, *c.* 1 mm long, 1-nerved. Pedicels thickened towards the calyx, *c.* (1–)4–10 or in fruit even to 35 mm (in the Philippines). *Calyx tube c.* 2–1½ mm high; lobes triangular, *c.* ½–1½ mm, acuminate with a bluntish tip. *Petals* white, whitish green to light green and yellow (also pink recorded from Central Celebes), oblong or oblong-elliptic, convex, *c.* 3–4 by 1½–2 mm; ligule 3-lobed, half as long as the blade; claw often distinctly narrowing towards the base, *c.* ⅓ as long as the petal. Flowers dimorphous, both types either with equal or unequal stamens.

Brachystylous flowers.—Staminal tube *c.* 1–2 mm. *Stamens equal*; filaments *c.* 2–3½ mm; anthers *c.* ½ by ½ mm. Ovary ellipsoid or ovoid, somewhat longer than staminal tube, *c.* 2 by 1 mm, top often truncate; styles (2–)3, *c.* 1–2 mm, shortly connate or only connate at the base, stigmas capitate, often flattened, broader than the style.

Brachystylous flowers.—Staminal tube 1–1½ mm. *Stamens unequal*; episepalous filaments *c.* 1½–4 mm, epipetalous ones *c.* 2–4½ mm; anthers ⅓ by ⅓ mm. Ovary ovoid to subglobular somewhat longer than staminal tube, *c.* 1¼–2 by 1–1½ mm; styles *c.* 1¼–2 mm, very shortly connate at the base; stigmas oblong-ovate, broader than the style.

Dolichostylous flowers.—Staminal tube *c.* 1–2 mm. *Stamens equal*; filaments *c.* 2–4 mm, sometimes thickened at the base. Ovary ellipsoid to subglobular, somewhat longer than staminal tube, *c.* 2–1½ by 1 mm, styles *c.* 2–5 mm, connate from ⅓ to ⅔ of their length, stigmas capitate, often flattened, broader than the style.

Dolichostylous flowers.—Staminal tube *c.* 1½–2 mm. *Stamens unequal;* episepalous filaments *c.* ½–¾ mm, epipetalous ones *c.* 1–1¼ mm; anthers *c.* ½ by ½ and ½ by ¼ mm respectively. Ovary ellipsoid to subglobular, somewhat longer than the staminal tube, *c.* 2–1½ by 1 mm, styles *c.* 2–4 mm, connate to various degree from ½ to ⅛ of their length, stigmas capitate, often flattened, broader than the style.

Drupe oblong-ovoid, often somewhat curved, red, when dry obtusely trigonous, distinctly furrowed, top pointed, *c.* 7–12 by 3–6 mm; fertile cell as large as or smaller than sterile cell, bilaterally compressed, sterile cells distinct and large, on both sides of the fertile cell. *Seed* flattened often somewhat curved, with distinct furrows, *c.* 5–10 by 1–2½ mm, endosperm little; embryo flattened, slightly curved or straight, green, *c.* 4–8 by ½–1½ mm; cotyledons linear, very thin, *c.* 2½–6 by ½–1½ mm; radicle distinct 1½–3½ mm.

Distr. Burma (Tenasserim, Moulmein, Mergui, and Andaman Isl.), Siam, and Cochinchina, in *Malaysia:* Sumatra (throughout), Malay Peninsula, Banka, Billiton, Riouw & Lingga Arch., West Java, Lesser Sunda Islands (Kangean,

(1) *E. retusum* BAILL. *ex* SCHULZ, Pfl. R. Heft 29 (1907) 137, *non* BAUER *ex* TEYSM. & BINN. 1867 *l.c.*, from Madagascar = *Erythroxylum leandrianum* PAYENS, *nov. nom.*

Fig. 3. *Erythroxylum cuneatum* (MIQ.) KURZ. Flowering and fruiting twig in Kebun Raya Indonesia (III. K. 5), Nov. 1957.

Sumbawa), Anambas and Natuna Isl., Philippines (Palawan, Luzon, Mindanao), Central Celebes (also Muna Isl.), Moluccas (Halmaheira, Ternate, Ceram), West New Guinea (the islands of Waigeo and Misool), but not yet found on the mainland of New Guinea.

Ecol. Very tolerant and found in a variety of habitats. It is often a tree or shrub behind sandy beaches or rocky shores; in Johore it is a characteristic constituent of the *Eugenia grandis* coastal forest. Also inland it is found under various conditions: sandy or rocky hills, average dryland forest, inundated peat-forest, sometimes on exposed limestone summits, both in primary and secondary vegetation. Sometimes in groups, more often scattered and nowhere dominant, from sea-level up to 900 m. *Fl.-fr.* Jan.–Nov.

Uses. The sapwood is white to yellow, abruptly set off against the brown heart-wood which is very durable and easy to work; it shrinks, tears, and warps very little and the timber is used for house-building in the Malay Peninsula, and in Sumatra also for bridges. Beams are said to be very durable but can seldom be obtained in quantity. The fresh wood sinks in water. In Trengganu, according to HOLTTUM, the leaves are pounded and applied on the forehead of women after miscarriage. In Bunguran leaves are reported to be used in sajur (vegetable soup).

Vern. *Ankara mula, garu lanang, g. abang, gĕlundi, kaju urang, k. katjang, kĕpitis, ngĕlĕgundi, pietis, pulas, tĕlung, tĕnara punai* (= *pepitis*), *tenaropunang*, M (Sum.); *kayu mutoh*, Banka, *membĕntaän* or *nĕmbĕntahan*, Billiton; *baka, chinta mola* (*mula, mulah*, or *mulek*), *inai-inai, mansira, mĕdang* or *bunga langundi, payoli* (also *mĕdang bunga langundi payoli*), *poko buluntas bukit, sri mula*, Mal. Pen.; *ki beureum*, S; Borneo: *asan, djĕnging*, Tidung lang., *gĕrongan*, Dusun Kinabatangan, *liduja, mahui*, Bekumpai lang., *paris, piling, tailan, tĕbakan*, Sarawak, *kaju sapat*, Bandjar.; Philippines: *baransiágau*, Ilk., *manambo, salñgen*, Bik., *sáleng*, Tag.; *bugunran, horu malako* or *malau*, Ternate.

Galls. On a specimen from Singapore and from Atjeh flower galls were found, giving a thickening of the pedicels.

Notes. The large variety of ecological conditions under which this species is found must be held partly responsible for the variability in habit and leaf shape and size of this vegetatively plastic species. Specimens collected on rich soils (heavy black soil, yellow clay, or old volcanic soils) are often small trees or shrubs already flowering and they possess large leaves which remain green when dried. Other large-leaved specimens showing this were collected as shrubs on coastal karst-limestone in Waigeo and along mangrove swamps in Mindanao and Bunguran Isl.. A few times it has been collected on exposed limestone summits (Philippines and a hill in Perak) scrambling as a very small-leaved, almost xerophytic shrub in the open. Trees over 15 m height always possess small or relatively small and thicker leaves, specially where the habitat is dry sandy soils, high forest, or inundated peat-swamp.

I got the rather remarkable impression that from Tenasserim to the Malay Peninsula it is always recorded as a medium-sized tree, but in Sumatra, Borneo, and Java either as a tree or a shrub. In the Philippines the data are insufficient to judge, but in East Malaysia it has never been recorded as a high tree.

The leaf apex may differ considerably in leaves from one branch, ranging from distinctly rounded to acuminate, the tip being always emarginate. In Borneo there were some specimens with exclusively either rounded or acuminate leaves.

The vegetative reaction to habitat and the fact that juvenile specimens freely flower and fruit in the open are held responsible for the variation of the leaf shape and size. Several authors have given specific or varietal names to certain leaf types or extremes but, after an intensive study of a large amount of specimens, I am perfectly satisfied that the leaf cannot be used for specific discrimination.

Characters for specific distinction can only be found in the fruit, the stipules, and to a certain extent in the structure of the flower.

The fruit proves to be very constant in structure, the fertile cell being accompanied on both sides by a large sterile cell. I found only one deviating specimen (Palembang: DUMAS 1564) which possessed very large drupes, measuring 15–17 by 7–8 mm, in which no embryo was developed; its absence may account for the abnormal size of the pericarp which in cross-section leaves no doubt that it belongs to *E. cuneatum*.

The flower has appeared to be more variable than formerly assumed. I have dissected flowers from all specimens and if material permitted of a number of flowers of one specimen. It has appeared that the flowers of one tree or twig are identical!

O. E. SCHULZ, in his key (Pfl. R. *l.c.* 139–140), has used the relation between the length of the staminal tube and that of the calyx as a character for distinguishing species but I believe this to be unreliable: in the majority of flowers the staminal tube exceeds the calyx, sometimes it was equal in length with the calyx, very rarely it was shorter.

Hitherto the flowers of *E. cuneatum* have been accepted to be 3-morphous, as found by BURCK. It has appeared, however, that they are 4-morphous. Fig. 4.

There are two major groups, *brachystylous* and *dolichostylous* flowers, but within either group

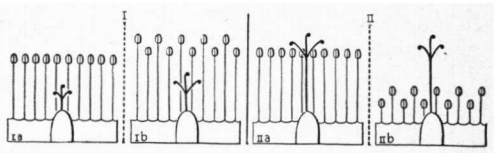

Fig. 4. Schematic drawing of the 4 flower types of *Erythroxylum cuneatum* (MIQ.) KURZ. I. *Brachystylous* flowers, *ia* stamens equal, *ib* stamens unequal. II. *Dolichostylous* flowers, *iia* stamens equal, *iib* stamens unequal. All × 3.

there are specimens with equal and specimens with unequal filaments, resulting into 4 subgroups.

Within both major groups the length of styles and degree of their coalescence is very variable, ranging from almost free or very shortly connate at the base in some brachystylous flowers to almost entirely connate in some dolichostylous ones.

Among brachystylous flowers the stamens are mostly equal and rarely unequal. Also among the dolichostylous flowers equal stamens predominate, but unequal stamens are less rare.

As far as adequate flowering material was available, the frequency of the flower forms turned out to be as follows: *form Ia, brachystylous flowers, stamens equal*, 46 specimens, *form Ib, ditto, stamens unequal*, 5 specimens, *form IIa, dolichostylous flowers, stamens equal*, 16 specimens, *form IIb, ditto, stamens unequal*, 11 specimens.

I have tried to correlate the four flower forms with geographical distribution: In Tenasserim, Burma, and Siam (3 specimens) I found only specimens of form Ia. In the Malay Peninsula (20 specimens) only forms Ia and IIa are found. In Sumatra (19 specimens) all forms occur except IIb. In Borneo (12 specimens) and the Philippines (11 specimens) all forms are represented, in Central Celebes (2 specimens) only the forms Ia and IIb, and in the Moluccas & West New Guinea (11 specimens) only form Ia.

Obviously the distribution of the flower types is not entirely random.

Affinities of E. cuneatum with SE. Asiatic species. —*E. cuneatum* can easily be distinguished from *E. monogynum* ROXB. by its caducous, entire stipules which are in the latter species persistent and finely serrate.

More difficult is its delimitation against the group *E. acuminatum* (ARN.) WALP., *E. obtusifolium* (WIGHT) HOOK. *f.* and *E. lanceolatum* (WIGHT) WALP. which belong with *E. cuneatum to* § *Coelocarpus*. All former authors have had trouble to distinguish these species from one another, and from *E. cuneatum*. I am inclined to look upon this triplet as representing one species, but I have not made a sufficiently thorough study of them for reaching a final conclusion. All three differ from *E. cuneatum* in the same difference in the fruit which in cross-section offers a large fertile cell flanked by 2 very small sterile cells.

E. kunthianum KURZ differs from *E. cuneatum* by very deeply bifid stipules with a serrate margin (entire and undivided in *E. cuneatum*).

Excluded

Ixonanthes JACK was inserted in the *Lineae trib. Ixonantheae* by BENTHAM & HOOKER *f.* in their 'Genera plantarum' and, though their delimitation of this family is no longer upheld in its original concept, the genus *Ixonanthes* is by some British authors still considered to make part of a segregate of these *Lineae* and referred to the *Erythroxylaceae*, for example by RIDLEY (1900), HUTCHINSON (1926), and BROWNE (1955). HALLIER *f.* (1923) inserted *Ixonanthes* in his *Linaceae sens. lat.* in the tribe *Ixonantheae* but placed *Erythroxylum* in a separate tribe with *Hugonieae*.