

CTENOLOPHONACEAE

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The systematic place of the tropical lowland rain-forest tree *Ctenolophon* OLIVER has a chequered history.

Originally it was referred to affinity with *Olacaceae* (OLIVER, 1873; MASTERS, 1875; ENGLER, 1889; BAILLON, 1892) or *Icacinaceae* (BECCARI, 1877). HALLIER *f.* (1912, 1918) held another view and arranged the genus in the *Celastrales*, deriving this group from *Linaceae*. HUTCHINSON (1959, 1973) referred the genus to the *Malvales*.

In a meticulous exposé of the anatomy, flower and fruit structure, PIERRE (1893) concluded that the affinity of *Ctenolophon* is with the *Linaceae* and he was followed by ENGLER (1907), EXELL (1927), and HUB.WINKLER (1931).

At present *Ctenolophon* is almost unanimously recognized as belonging to the Linaceous affinity, together with *Ixonanthaceae*. Within *Linaceae* HUB.WINKLER (1931) had raised the genus to the rank of a monogeneric subfamily. Later EXELL & MENDONÇA (1951) recognized it as representing a family of its own, a view now almost unanimously accepted, as fully discussed by VAN HOOREN & NOOTEBOOM (1984).

In the treatment of the family *Linaceae* (page 607, see there) the families *Linaceae*, *Ixonanthaceae*, and *Ctenolophonaceae* are opposed by concise diagnoses.

On account of studies of special features some other affinities have been put forward. HEIMSCHE (1942) found a remarkable resemblance in xylem structure with *Humiriaceae*. CRONQUIST (1981) referred to *Ctenolophon* as an aberrant member of *Hugoniaceae*, a view with which we cannot agree. VAN WELZEN & BAAS (1984) compared the leaf anatomy of *Ctenolophon* with that of *Humiria* and some *Malpighiaceae* and found that it is very different from both *Humiriaceae* and *Malpighiaceae*, but also from other *Linaceae*, and they supported the status of a family of its own, adding that close affinities are still unknown.

References: BAILLON, *Hist. Pl.* 11 (1892) 445; BECCARI, *Malesia* 1 (1877) 119; CRONQUIST, *Integrated system etc.* (1981) 759; ENGLER, *Nat. Pfl. Fam.* 3, 1 (1889) 237; *ibid.*, *Nachtr.* 3 (1907) 204; EXELL, *J. Bot.* 65 (1927) *Suppl.* 1: 50; EXELL & MENDONÇA, *Conspectus flora Angolensis* 1, 2 (1951) 248, 392; HALLIER *f. Arch. Néerl.* III B, 1 (1912) 109; *Meded. Rijksherb.* 35 (1918) 28; HEIMSCHE, *Lilloa* 8 (1942) 83; VAN HOOREN & NOOTEBOOM, *Blumea* 29 (1984) 547; HUTCHINSON, *Fam. Fl. Pl.* 1 (1959) 265; ed. 3 (1973) 324; MASTERS, *Fl. Br. India* 1 (1875) 577; OLIVER, *Trans. Linn. Soc.* 28 (1873) 516; PIERRE, *Fl. For. Coch.* (1893) t. 281; VAN WELZEN & BAAS, *Blumea* 29 (1984) 477; HUB.WINKLER in *E. & P. Nat. Pfl. Fam.* ed. 2, 19a (1931) 122.

1. CTENOLOPHON

OLIVER, *Trans. Linn. Soc.* 28 (1873) 516; HUB.WINKLER in *E. & P. Nat. Pfl. Fam.* ed. 2, 19a (1931) 122; BULLOCK, *Kew Bull.* 14 (1960) 41; VAN HOOREN & NOOTEBOOM, *Blumea* 29 (1984) 547. — Fig. 1, 2.

Trees. Hairs stellately tufted and simple. Stipules interpetiolar, caducous. *Leaves* entire, opposite, petiolate, simple, pinnately nerved. *Inflorescence* an axillary or terminal cymoid panicle. Bracts present, bracteoles absent. *Flowers* bisexual, 5-merous, actinomorphic, hypogynous. *Sepals* basally shortly connate, quincuncially imbricate, subequal, indurate, swollen and persistent in fruit, with stellate hair tufts. *Petals* free, contorted, caducous, often shortly clawed. *Disk* extrastaminal. *Stamens* 10, free, inserted halfway the disk, alternately longer and shorter, the longer epipetalous and the shorter episepalous; anthers dorso-versatile, 2-celled, introrse; connective protruding, acute-triangular. Extrastaminal nectary glands absent. *Ovary* superior, 2-celled; style 1, apically

forked with 2 capitate stigmas; ovules 2 per cell, axile, collateral, pendent, epitropous. *Fruit* a 1-celled capsule, the woody pericarp finally lengthwise splitting into 2 valves. *Seed* 1, persisting after falling of pericarp and pendulous from the top of a filiform columella; ariloid papillose, surrounding lower half of the seed. Endosperm copious. Embryo straight.

Distr. Two species, one (*C. engleriana* MILDBR.) in West Africa (Angola, Zaire, Nigeria, Gabon) and one throughout *Malesia* (but not in Java and Lesser Sunda Islands and not yet reported from Celebes and Moluccas, where it is expected to occur). For *Malesia* see fig. 3.

Ecol. Mixed lowland rain-forest.

Vegetative anatomy. *Ctenolophon* has glabrous leaves, but the young shoots and floral parts have tufted, stellate hairs. Stomata are anisocytic to anomocytic. Crystals are mainly solitary and rhomboidal, more rarely clusters intergrading with druses. Crystalliferous bundle sheath cells have unilateral sclerified thickenings (cristarque cells). The petiole and midrib have a simple collateral vascular strand.

The wood of *Ctenolophon* is characterized by solitary vessels with scalariform perforations, fibres with distinctly bordered pits, parenchyma which is scanty paratracheal and diffuse-in-aggregates, and heterocellular 1–3-seriate rays.

The above attributes are not very helpful in determining the phylogenetic affinity of this monogeneric family *Ctenolophonaceae*. Its stomatal type removes it from the *Linaceae* complex, but other leaf anatomical characters are of common occurrence throughout the dicotyledons, including the *Linaceae*. The wood anatomy of *Ctenolophon* is very plesiomorphic and cannot therefore be used to support or reject various suggestions of natural affinity of the genus, although similarities with *Humiriaceae* have been pointed out by HEIMSCH & TSCHABOLD (1972) and METCALFE & CHALK (1950).

References: HEIMSCH & TSCHABOLD, Bot. Gaz. 133 (1972) 242–253; METCALFE & CHALK, Anatomy of the Dicotyledons I (1950) 268–273; SAAD, Bot. Notis. 115 (1962) 44–57; VAN WELZEN & BAAS, Blumea 29 (1984) 453–479. — P. BAAS.

Palynology. Pollen of *Ctenolophonaceae* shows two types: the *Ctenolophon englerianus* type and the *C. parvifolius* type. Pollen grains of both types measure 31–66 µm. The apertural system is zonocolporate ('stephanocolporate'), the number of apertures ranging from 3–8 in the *parvifolius* type and 5–9 in the *englerianus* type. Contrary to the rounded subspherical *parvifolius* type, the *englerianus* type shows distinct thickenings on its mesocolpia and polar areas, making this type characteristically angular and barrel-shaped.

Exine thickness ranges from 3–6 µm. Exine stratification is rather obscure in the light microscope and difficult to determine, especially in the *englerianus* type. A thick nexine can mostly be observed. The infratactal layer appears labyrinthine, sometimes exhibiting granulate-columellate structures. The tectum is psilate or finely perforate in the *englerianus* type, perforate to foveolate in the *parvifolius* type (THANIKAIMONI *c.s.*, 1984).

SAAD (1962) noted striking resemblance with pollen of some *Malpighiaceae*, which led him to the conclusion that *Ctenolophon* may be considered as related to *Malpighiaceae*. Pollen morphological affinity to *Linaceae* and *Humiriaceae* is regarded as respectively being absent and not close. Here, it is put forward that pollen of *Ctenolophon* is neither close to that of *Malpighiaceae*, as the bipartite nature of wall stratification in both *Ctenolophon* and some *Malpighiaceae* noted by SAAD (*l.c.*) actually represents only superficial similarity. Pollen of *Ctenolophon* cannot be convincingly connected with that of other families, which supports attribution of family rank to the taxon.

Fossils. The distinctness of *Ctenolophon* pollen is illustrated by its extensive fossil record. Both types can be easily recognized (MULLER, 1981; THANIKAIMONI *c.s.*, *l.c.*). The *englerianus* type (*Ctenolophonidites*) occurred in Africa nearly uninterruptedly from the Upper Cretaceous onwards, and can be linked with the recent area of distribution of *C. englerianus*. The type was also present in South America (Paleocene, Eocene) and India (Eocene, Miocene), but disappeared from those areas in the course of the Tertiary. In recent time the *englerianus* type also exists in the Philippines on Samar, in *C. parvifolius* (THANIKAIMONI *c.s.*, *l.c.*, as *C. philippinensis*, PNH 6385). This Samar material is distinct from that of Africa by having mostly less apertures (5 to 7 versus 5 to 9) and by showing a perforate rather than a psilate or finely perforate tectum. Another collection from Samar (PNH 6146) shows pollen which seems to be intermediate between PNH 6385 and the *parvifolius* type (original observation).

The *parvifolius* type (*Retistephanocolpites*) was first recorded from the Paleocene of Africa. In India it occurred in the Paleocene and the Eocene, while it is known from Borneo starting from the Upper Eocene continuing up to the present (MORLEY, 1977; manuscript comm. MORLEY).

The fossil record of both types clearly demonstrates the relic nature of the present area of distribution of *Ctenolophonaceae*. It points to separation of the two types in the Upper Cretaceous in Africa (GERMERAAD *c.s.*, 1968: 276). However, the Samar collections may reflect another, much more recent as well as easterly contact between both types. Possibly, the Indian *englerianus* stock did not become extinct in the Miocene before branching off into the Malesian area. Probably the Indian *parvifolius* stock branched off into Malesia as early as the Eocene, becoming extinct in India at the Eocene-Oligocene transition. Macromorphological difference between recent *C. englerianus* and *C. parvifolius* is very small. The occurrence of intermediate pollen between the *englerianus* and the *parvifolius* type is suggestive of introgression between the two species, although independent origin of the *englerianus* type on Samar cannot be excluded.

References: GERMERAAD, HOPPING & MULLER, *Rev. Palaeobot. Palynol.* 6 (1968) 189–348; MORLEY, *Proc. Indon. Petr. Ass.*, 6th Ann. Conv. (1977) 255–276; MULLER, *Bot. Review* 47 (1981) 73–74; SAAD, *Bot. Notis.* 115 (1962) 49–57; THANIKAIMONI, CARATINI, VENKATACHALA, RAMANUJAM & KAR, *Trav. Sect. Sci. et Techn. Inst. Franç. Pondichéry* 19 (1984) 23, 80. — R.W.J.M. VAN DER HAM.

Notes. 1. The African species *C. englerianus* MILDBR. is hardly different from the Malesian species, *C. parvifolius*. The only differences observed are the simple cymose panicle and the stamens being up to 15 mm long in *C. englerianus*, versus the compound cymose panicle and the stamens up to 10 mm in *C. parvifolius*.

2. The fruit and seed structure was wrongly described by HUTCHINSON and by HUB. WINKLER, who said that the seed dangles from a long funicle. The so-called funicle, however, is a filiform columella on which the seed is attached apically.

1. *Ctenolophon parvifolius* OLIVER, *Trans. Linn. Soc.* 28 (1873) 516, t. 43, f. 1–7; MAST, *Fl. Br. India* 1 (1875) 577; BECC. *Malesia* 1 (1877) 120; KING, *J. As. Soc. Beng.* 62, ii (1895) 106; RIDLEY, *Fl. Mal. Pen.* 1 (1922) 423; BURK. *Dict.* (1935) 695; ed. 2 (1966) 705; DESCH, *Man. Mal. Timbers* 2 (1954) 15; BULLOCK, *Kew Bull.* 14 (1960) 41; MEIJER, *Bull. Herb. For. Dep. Sandakan* 10 (1968) 151, fig.; COCKBURN, *Gard. Bull. Sing.* 24 (1969) 6; *Tree Fl. Malaya* 1 (1972) 306; *Sabah For. Rec.* 10 (1976) 205; ANDERSON, *Checklist Trees Sarawak* (1983) 239; VAN HOOREN & NOOTEBOOM, *Blumea* 29 (1984) 547. — *C. grandifolius* OLIVER, *Trans. Linn. Soc.* 28 (1873) 517, t. 43, f. 8–10; MAST, *Fl. Br. India* 1 (1875) 577; BECC. *Malesia* 1 (1877) 119; KING, *J. As. Soc. Beng.* 62, ii (1895) 106; RIDLEY, *Fl. Mal. Pen.* 1 (1922) 423. — *C. philippinensis* HALL, *f. ex SCHNEIDER*, *Philipp. Bur. For. Bull.* 14 (1916) 127, *nomen*; MERR. *Enum. Philip.* 2 (1923) 326. — **Fig. 1, 2.**

Tree, 12–40 m, 15–120 cm diam., buttressed. Twigs with distinct leaf-scars and thickened at the insertion of the buds, glabrous. Innovations marginally and apically tufted-hairy, hairs to 1 mm long. Stipules boat-shaped, triangular to ovate, 1.5–2.5(–3) by 1–1.5 mm; entire, apex rounded to emarginate. *Leaves* glabrous, narrowly ovate to elliptic, sometimes obovate, often with \pm parallel margins, 5–15 by 2–6 cm; base broadly cuneate, sometimes rounded; margin often \pm thickened; apex broadly acute to obtusely acuminate, sometimes rounded, acuminate to 2.5 cm; nerves (5–)7–10(–12) pairs, slightly curving upwards to near the margin, often meeting in 1 (or 2) looped intramarginal veins; reticulation rather lax to dense; petiole sulcate above, 4–10(–15) mm. *Panicles* rather densely flowered, terminal and up to 7 together, or 2–3 in the axil of a leaf near the end of the twigs, sometimes ramiflorous, up to 3 times

branched, broadly ovoid to depressed obovoid, 3–9(–16) cm long. Axes patently tufted hairy, especially above the nodes. *Bracts* caducous just below the articulation, densely or sparsely appressedly to patently tufted-hairy without, especially on margin and midrib, more or less boat-shaped, narrowly ovate-liguliform to triangular, 1–3.5 by 0.5–1.7 mm; base with a row of bristles within. Pedicel articulate, grooved, swollen in fruit, 1–1.5(–2.5) mm. Hypanthium thickened. *Sepals* appressed, densely appressedly to patently tufted-hairy to (the inner 3 marginally) glabrous, glabrous within but inner base with a row of up to 0.8 mm long bristles, boat-shaped, obovate to depressed ovate, ciliate, 1–2.5 by 1.5–4.7 mm, the outer two smallest. *Petals* recurved and more or less twisted in anthesis, stout, thin-leathery, densely appressedly tufted-hairy without except the overlapping margin and the base, glabrous within, slightly asymmetric, narrowly elliptic to narrowly ovate, 7–12 by 2–2.5 mm; claw absent or indistinct, at most 1 by 1 mm; margin sometimes with simple hairs towards its base. *Disk* membranous or slightly fleshy, cup-shaped, 1–1.5 mm high; margin often more or less dentate to undulate. *Stamens* inserted halfway up to just below the margin of the disk, short filaments 3.7–6.5 mm, long filaments 4.5–7.5 mm. *Pistil* up to halfway the style covered with straight, up to 2 mm long simple hairs; style straight, rather stout, slightly flattened, equalling to up to 3 mm exceeding the long stamens, sometimes as long as the short stamens, 5–10 mm long. *Ovary* \pm constricted at base, ellipsoid to ovoid, 1.5–3 by 1–2 mm. *Fruit* 1-celled, densely appressedly tufted-hairy, ellipsoid to obovoid, 13–24 by 6–13 mm, sometimes basally curved; pericarp woody, ribbed, smooth inside, consisting of 4 layers, 1.5–2 mm diam. *Seed* ellipsoid to obovoid, 12–20 by 5–9 mm,

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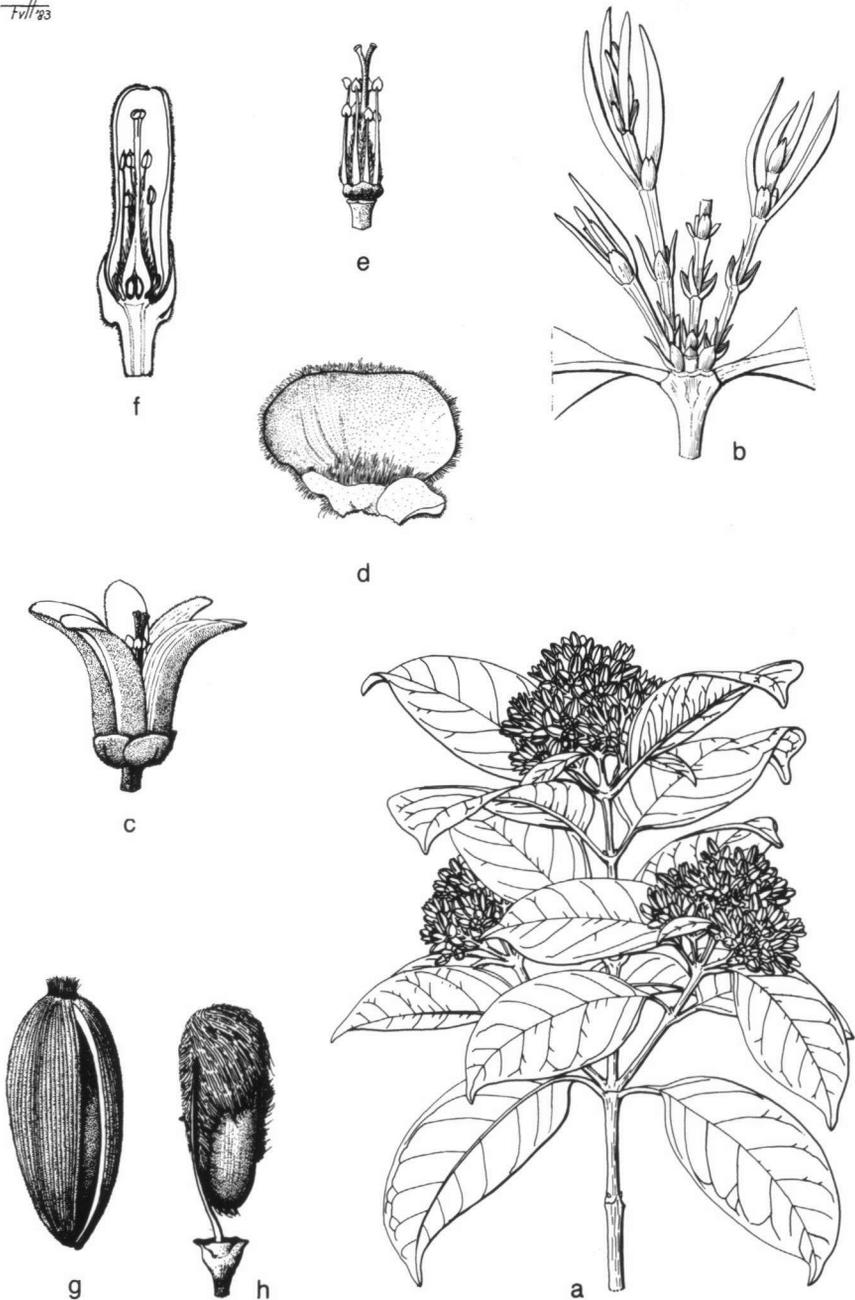


Fig. 1. *Ctenolophon parvifolius* OLIVER. *a.* Habit, $\times 0.5$; *b.* innovations, with budscales, stipules and plicate leaves; *c.* flower, $\times 3$; *d.* sepal from inside, $\times 12$; *e.* flower (sepals and petals removed), $\times 3$; *f.* flower in LS, $\times 5$; *g.* fruit, $\times 2$; *h.* seed, $\times 2$ (*a* from OLIVER (1873), *b* DUMAS 1513, *c-f* SAN 4595, *g, h* LAMBACH 1251).

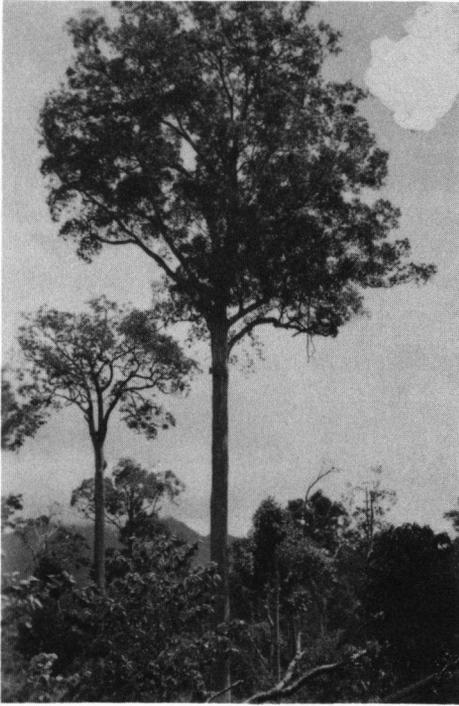


Fig. 2. *Ctenolophon parvifolius* OLIVER. A large mature tree at Dolok Puhutan Lajan, Tapanuli, E. Central Sumatra (Photo G.A.L. DE HAAN, 1939; coll. no. 697).

dangling from a filiform columella (10–)15–20 mm long; hilum apical, slightly protruding from testa, obtriangular, 4–7 by 2–2.5 mm; ariloid from slightly above the base up to around the hilum, oblong triangular, up to 5 by 5 mm, with hair-like papillae which are reddish when dry, surrounded by a gelatinous transparent layer. Testa 0.1–0.2 mm thick, outer layer smooth, crustaceous, dark olive-brown to purple black when dry, sometimes fissured, finally covered by a thin membrane; second and third layer reddish-brown, free from the outer wall. Endosperm fleshy, spongy. Embryo stout; cotyledons elliptic to obovate, 8–10.5 by 4.7–5 mm; radicle (1–)2–2.5 mm long.

Distr. *Malesia*: Sumatra, Malay Peninsula, Borneo, Philippines (Samar, Leyte, Mindanao), and New Guinea (incl. Japen I.). Fig. 3.

Ecol. Mixed primary forest, also in heath and swamp forest, indifferent to soils (latosols, humic podsols, loam, ultrabasic) and also frequent on sand (Banka, Borneo), locally common to sometimes very common in lowland and on hills, generally below 850 m, but in Borneo rarely up to 1650 m. Fl. fr. Feb.–Dec. Fig. 2.

Field notes. Bole up to 35 m; buttresses, if present, up to 4 m high and wide up to 12.5 cm thick. Bark reddish brown to black, often greyish, very variable in appearance, scaly or cracked, often peeling off, hard. Inner bark reddish to pink, granular or fibrous. Exudate colourless to iodine-coloured, clear, slowly appearing, thick, or absent. Heartwood often reddish or brown, rather hard, heavy, sinks in water. Corolla from white to yellow, orange or

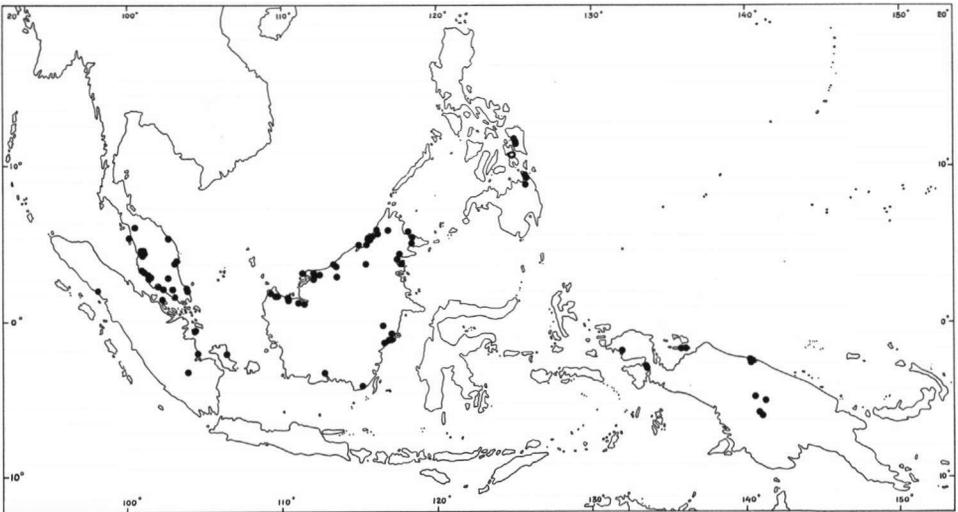


Fig. 3. Localities of *Ctenolophon parvifolius* OLIVER.

bright red. Style pinkish. Fruit yellow to pink, later brown. Seed brown or glossy black; ariloid white to orange or brilliant vermilion.

Uses. The hard and very durable timber is used for house construction and as general purpose timber (SCHNEIDER, 1916; RIDLEY, 1922; DESCH, 1954; BURKILL, 1966).

Vern. Sumatra: *babi kurus*, *batu*, *djambu ayer*, *jinkinai*, *kaju batu*, *k. bawang*, *kalek bung cung*, *klawar*, *medang tembatu*, *petjah pingan*; Malay Peninsula: *bunga tanjong hutan*, *kumus beruang*,

mata ulat, *membatu hitam*, *perichat*, Malaya; *ban(g)kal*, *bankal paya*, *kas*, Mersing; *karu karu*, *kelabau*, Perak; *kelat*, *k. bukit*, *pompong paya*, Pahang, *kelat hitam*, *mertas*, Kuala Lumpur, *mertas kuning*, Kuala Trengganu; *jambu paya*, Johore; Borneo: *belama'a*, *tamana'a*, Sarawak: *litoi*, Iban; *besi*, *obah*, Sabah; *merandi*, W. Kalimantan; *jarmgin*, *kayu batu*, *latak manuk*, E. & SE. Kalimantan. New Guinea: *gun*, Iwur I.; *kodawu*, *kodowu*, *kotawu*, Ingembit I.; *mamdai*, *tora*, Ormu dial., *dnok*, *nook*, Tehid I.; *samber*, *sosopi*, Japen dial.