TRIMENIACEAE (W. R. Philipson, Christchurch)

Trimenia was first described by SEEMANN as a genus related to the *Ternstroemiaceae*. BENTHAM & HOOKER *f.* (1880) regarded it as more closely related to the *Monimiaceae* without definitely placing it there. This was done by PERKINS & GILG (1901) who formed the tribe *Trimenieae* of that family. GIBBS (1917) created the family *Trimeniaceae* without stating grounds for the separation. GILG & SCHLECHTER (1923) disagreed, thinking the differences between *Trimenia* and other *Monimiaceae* too slight. However, a more complete study by MONEY, BAILEY & SWAMY (1950) firmly established the family which is now generally accepted. The work of ENDRESS & SAMPSON (1983) strengthened this conclusion and demonstrated the isolated position of the family by drawing attention to a number of features deviating from those generally found in the *Laurales*. These include absence of a floral cup; spiral floral phyllotaxis; caducous tepals; utriculate carpels; polyforate pollen; tectate-columellate exine; capitate stigma with multicellular papillae; vascularized outer integument. Chromosome number n = 8.

References: BENTHAM & HOOKER *f.*, Gen. Pl. 3 (1880) 143; ENDRESS & SAMPSON, J. Arn. Arb. 64 (1983) 447–473; GIBBS, Fl. Phyt. Arfak Mts (1917) 136; GILG & SCHLECHTER, Bot. Jahrb. 58 (1923) 245; MONEY, BAILEY & SWAMY, J. Arn. Arb. 31 (1950) 372–404; PERKINS & GILG, Pfl. R. Heft 4 (1901) 21.

1. TRIMENIA

SEEMANN, Fl. Vit. (1871) 425, t. 99; B. & H. Gen. Pl. 3 (1880) 143; PAX in E. & P., Nat. Pfl. Fam. 3, 2 (1889) 98; PERKINS & GILG, Pfl. R. Heft 4 (1901) 21, f. 4a–c; RIDL. Trans. Linn. Soc. Bot. II, 9 (1916) 144; GIBBS, Arfak (1917) 135; GILG & SCHLTR, Bot. Jahrb. 55 (1919) 195, f. 1–2; *ibid.* 58 (1923) 245, f. 1; PERKINS, Übersicht Gattungen Monim. (1925) 22; A.C. SMITH, J. Arn. Arb. 23 (1942) 442; RODENBURG, Blumea 19 (1971) 3. — *Piptocalyx* OLIV. *ex* BTH. Fl. Austr. 5 (1870) 292; PERKINS & GILG, Pfl. R. Heft 4 (1901) 22, f. 4d–f. — **Fig. 1–3.**

Small trees, shrubs or lianes, up to 20 m or more, young parts tomentose or glabrous. *Leaves* opposite, petiolate, exstipulate, ovate to ovate-lanceolate (obovate, *extra*-Mal.), base cuneate, apex acute to long acuminate, entire or serrate, with translucent dots, nerves connected near the margin. *Inflorescence* axillary or terminal, cymose, pleiochasial (racemose) or paniculate. *Flowers* unisexual or bisexual; receptacle continuous with the pedicel, slightly convex, glabrous; tepals caducous before or at anthesis, spirally arranged (outermost sometimes decussate), imbricate, 10–38, the lower ovate to ± orbicular or reniform, up to 3 mm long, base swollen and sometimes peltate, apex rounded or obtuse, grading upwards into longer, narrower and more membranous tepals, the uppermost spathulate, up to 5 mm long. *Stamens* 7–25, spirally arranged, filament shorter or as long as the anther, connective produced at apex, anthers tetrasporangiate, extrorse or latrorse, opening by two longitudinal slits. *Carpel* solitary (rarely 2), rudimentary or absent in male flowers, superior, barrel-shaped, glabrous or sparsely strigose; stigma sessile tufted-papillose, 1-celled; ovule 1, pendulous, anatropous. *Fruit* a small spherical, succulent berry. *Seed* hard, smooth or ridged; embryo small, apical; endosperm abundant.

Distr. Eastern Pacific (Marquesas), Polynesia (Samoa, Fiji), New Caledonia, E. Australia (New South

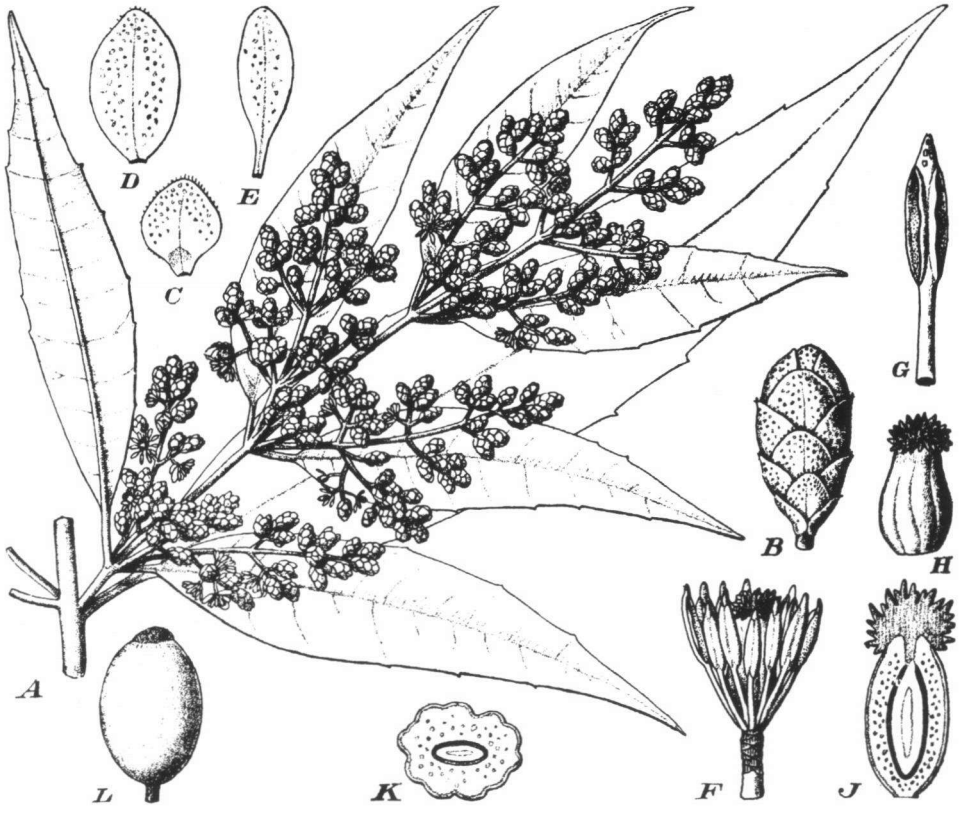

Fig. 1. *Trimenia papuana* RIDL. *A*. Habit, nat. size, *B*. bud, ×6, *C–E*. outer, middle and inner tepals, ×8, *F*. flower, after removal of tepals, ×7, *G*. stamen, from inside, ×10, *H*. ovary, ×7, *J*. *ditto* in LS, ×10, *K*. *ditto* in CS, ×12, *L*. fruit, ×3 (after GILG & SCHLECHTER, 1919).

Wales), Solomons (Bougainville) and *Malesia:* New Guinea (incl. New Britain & New Ireland), Moluccas (Ceram, Batjan) and Central Celebes. In all 5 *spp.* Fig. 2.

Fossils. MULLER (1981) considered that *Cretacaeiporites scabrabut* from West Africa and Brazil, which first appears in the Cretaceous (Albian-Cenomanian) (JARDINÉ & MAGLOIRE, 1963; HERNGREEN, 1973), may represent *Trimenia* pollen.

References: HERNGREEN, Pollen et Spores 15 (1973) 515–555; JARDINÉ *et al.*, Coll. Int. Micropal. Dakar (1963); MULLER, Bot. Rev. 47 (1981) 9.

Ecol. Small trees or climbers in forests, often on ridge crests or other exposed places and usually at moderate to high altitudes.

Floral biology. The flowers of *T. papuana* are scentless, produce no nectar and the pollen is dry. No insect visitors were observed (ENDRESS & SAMPSON, 1983). Presumably wind plays a major role in pollination. The outer tepals fall before flowering and at anthesis all the tepals have been shed. The other species probably have a similar biology. In all species some flowers are male, but the degree of separation of the sexes varies. In *T. papuana* most flowers are hermaphrodite with some male flowers present. In *T. neocaledonica* and *T. moorei* the proportion of male flowers is greater. The sexes are more completely separated in *T. weinmanniifolia* in which species all flowers are functionally either male or female. *Trimenia weinmanniifolia ssp. weinmanniifolia* is monoecious but the other two subspecies may be dioecious (RODENBURG, 1971).

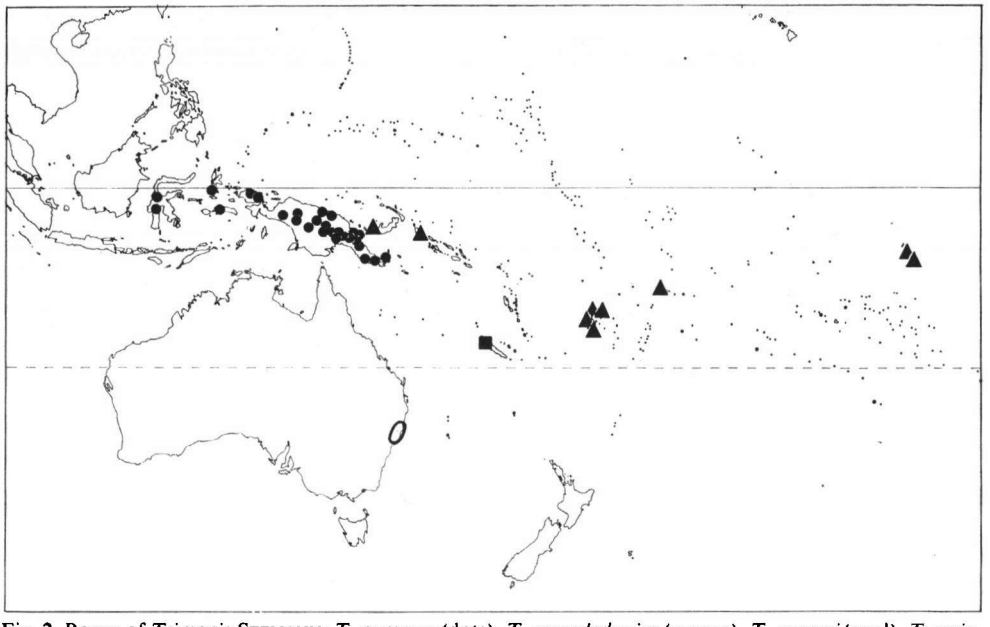

Fig. 2. Range of *Trimenia* SEEMANN: *T. papuana* (dots), *T. neocaledonica* (square), *T. moorei* (oval), *T. weinmanniifolia* (triangles), *T. macrura* (in New Guinea, not indicated).

Dispersal. The one-seeded succulent fruit has dark red to purple juice, and no doubt is distributed by birds.
References: ENDRESS & SAMPSON, J. Arn. Arb. 64 (1983) 447; RODENBURG, Blumea 19 (1971) 3–15.

Morph. The leaves are in decussate pairs and exstipulate. The lamina is tapered to an acute apex which in *T. macrura* is elongated into a delicate drip-tip. Inflorescences are lateral, or in some species also terminal. The inflorescence axes bear a terminal flower and either pairs of opposite flowers or branches which in turn bear a series of flower pairs, or even branches of a third order, when the inflorescence becomes a diffuse panicle.

Anat. Anatomical features are described by MONEY, BAILEY & SWAMY (1950), METCALFE & CHALK (1950), RODENBURG (1971) and CARLQUIST (1984). Hairs are unicellular or tricellular uniseriate and non-glandular. Stomata are paracytic. Oil cells and mucilage cells occur in the mesophyll of the leaf and in the axis. The leaf blade has no hypodermis and a palisade layer is not clearly defined from the spongy mesophyll. The leaf trace which departs from the single nodal gap comprises 2 or 4 bundles. Young stems develop no hippocrepiform sclereids (or only vestiges of them) in the pericycle opposite the interfascicular sectors. Elongated sclereids develop precociously in the secondary phloem. In the secondary xylem the vessel elements are long with high incidence of scalariform intercellular pitting. There are numerous uniseriate rays in addition to multiseriate rays (5 or 6 cells wide). Gelatinous fibres occur in the tension wood (KUČERA & PHILIPSON, 1977). Phloem plastids are of the S-type (BEHNKE, pers. comm.).

References: CARLQUIST, Pl. Syst. Evol. 144 (1984) 103–118; KUČERA & PHILIPSON, New Zeal. J. Bot. 15 (1977) 649–654; METCALFE & CHALK, Anatomy of the Dicotyledons 2 (1950); MONEY, BAILEY & SWAMY, J. Arn. Arb. 31 (1950) 372–404; RODENBURG, Blumea 19 (1971) 3–15.

Floral anatomy. The structure and development of the flower have been carefully described and discussed by ENDRESS & SAMPSON (1983). The tepals, stamens and carpel(s) are initiated in a spiral phyllotaxis. The perianth members show a gradation of form from below upwards without differentiation into sepals and petals. The anthers have neither lateral glands nor valvular dehiscence. The middle layer of the anther wall is only 1 or 2 cells thick, and the tapetum is glandular. Cytokinesis is successive and pollen is shed in the 2-celled condition. The mature carpel is markedly utriculate although early developmental stages pass through a chair-like form. The pendent, anatropous ovule is crassinucellar and bitegmic with the micropyle directed upwards. The archesporium is multicellular, but only one megagametophyte reaches maturity forming a long tube growing towards the micropyle. The fruit is a berry, the very juicy carpel wall enclosing a single seed with a very stony

outer coat. The small embryo is embedded in the apical part of the abundant endosperm. The cotyledons are rudimentary in the ripe seed and diverge slightly.

Reference: ENDRESS & SAMPSON, J. Arn. Arb. 64 (1983) 447–473.

Palyn. Earlier accounts of the pollen by MONEY, BAILEY & SWAMY (1950), ERDTMAN (1952) and WALKER (1976) are extended and fully discussed by SAMPSON & ENDRESS (1984). They report that *T. macrura, T. moorei* and *T. neocaledonica* have disulcate, globose-elliptic or globose-spherical to globose-elliptic grains, with finely reticulate or rugulose (*T. neocaledonica*) structure. *Trimenia papuana* has dimorphic pollen, with only one type on an individual plant, consisting of either globose-elliptic inaperturate grains, or globose-spherical polyforate grains. Both types have weakly rugulose structure, *T. weinmanniifolia* has globose-spherical polyforate pollen, with similar structure. Exine is tectate-columellate. In *T. papuana* and *T. weinmanniifolia* the innermost tectum, columellae and foot layer have a partly granular form. All taxa have a lamellate endexine in non-apertural regions. SAMPSON & ENDRESS compare the pollen of *Trimenia* with that of other families and conclude that pollen morphology confirms the comparatively isolated position of the family within the *Laurales*.

References: ERDTMAN, Pollen morphology and plant taxonomy (1952) 272–273, f. 157A; MONEY, BAILEY & SWAMY, J. Arn. Arb. 31 (1950) 372–404; SAMPSON & ENDRESS, Grana 23 (1984) 129–137; WALKER in Beck, Origin and early evolution of Angiosperms (1976) 241–299.

Chromosomes. *Trimenia papuana* (GOLDBLATT, 1974) and *T. moorei* (GOLDBLATT & BRIGGS, 1979) both give counts of n = 8.

References: GOLDBLATT, J. Arn. Arb. 55 (1974) 453–457; GOLDBLATT & BRIGGS, Ann. Mo. Bot. Gard. 66 (1979) 898–899.

Phytochem. The lignans (or neolignans) veraguensin and calopiptin have been isolated from *Trimenia papuana* and *Piptocalyx* (= *Trimenia*) *moorei* ('bitter vine') respectively. The nature of the bitter principles of bitter vine is still unknown, but a slightly sweet glucoside was isolated from its leaves and called piptoside; its aglucone was shown to be structurally related to the proteaceous metabolite leucodrin. CHENERY reported aluminium accumulation for one species of *Trimenia* (two investigated), but not for *Piptocalyx* (one species tested). The lack of benzylisoquinoline alkaloids in *Trimeniaceae* conforms with the exclusion of the taxon from *Monimiaceae*.

References: HEGNAUER, Chemotaxonomie der Pflanzen 5 (1969) 99–107, 457, and *ibid.* 8 (in prep.); family treated together with *Monimiaceae*. — R. HEGNAUER.

Taxon. *Generic limits.* Hitherto a second genus of the *Trimeniaceae*, *Piptocalyx*, has been recognized. First described from Australia (*P. moorei*) a second species (*P. macrurus*) is known from New Guinea. The climbing habit of these two species contrasts with the arboreal or shrubby habit of *Trimenia*, but the floral characters are closely alike. Careful comparisons of *Trimenia* and *Piptocalyx* by ENDRESS & SAMPSON (1983) revealed that some characters thought to separate the genera are indecisive. In particular they showed that the tepals of *Piptocalyx* are spiral, as in *Trimenia*, and not decussate. As *T. neocaledonica*, previously inadequately known, was found to be closer in some respects (*e.g.* pollen) to *Piptocalyx* than to other species of *Trimenia* they concluded that the only characters which separate the two genera are habit and the number of tepals (more than or fewer than 11). They preferred to leave the genera intact, to avoid name changes, but it is concluded here that the recognition of two genera is unjustifiable and the necessary new combination is made. I should add that also in *Monimiaceae* habit (erect or climbing) is variable within genera and sometimes even within a single species.

Trimenia moorei (OLIV. in BTH.) PHILIPSON, *comb. nov.* — *Piptocalyx moorei* OLIV. in BTH. Fl. Austr. 5 (1870) 292.

Specific delimitation. The treatment of the species adopted here follows that of RODENBURG (1971). A.C. SMITH (1978) was critical of RODENBURG's broad specific concept as regards both the Malesian and Polynesian species. RODENBURG's sinking of *T. arfakensis* and *T. myricoides* into *T. papuana* appears entirely justified. This conclusion has been reached after examination of very ample material. The treatment of RODENBURG's subspecies of *T. weinmanniifolia* does not concern this account except for *ssp. bougainvilleensis* which SMITH elevated to specific rank. In view of the wide geographical range of this complex and the indecisive nature of the characters involved, it appears wise to follow the more conservative treatment of RODENBURG.

References: BENTHAM & HOOKER *f.*, Gen. Pl. 3 (1880) 143; ENDRESS & SAMPSON, J. Arn. Arb. 64 (1983) 447–473; GILG & SCHLECHTER, Bot. Jahrb. 58 (1923) 244–248; GIBBS, Fl. Phyt. Arfak Mts (1917) 317; MONEY, BAILEY & SWAMY, J. Arn. Arb. 31 (1950) 372–404; SAMPSON & ENDRESS, Grana 23 (1984) 129–137; PERKINS & GILG, Pfl. R. Heft 4 (1901) 1–122; RODENBURG, Blumea 19 (1971) 3–15; A.C. SMITH, Allertonia 1 (1978) 311–314.

Fig. 3. *Trimenia papuana* RIDL. In Papua New Guinea (PHILIPSON 3692).

KEY TO THE SPECIES

1. Woody climber. Tepals 10 or fewer ..... **3. T. macrura**
1. Trees or shrubs. Tepals 13 or more.
2. Filaments relatively long and thin; mature anthers once or twice as long as the filaments. Seed smooth **1. T. papuana**
2. Filaments relatively short and broad; mature anthers at least 4 times as long as the filaments. Seed with longitudinal or reticulate ridges ..... **2. T. weinmanniifolia**

1. Trimenia papuana RIDL. Trans. Linn. Soc. Bot. II, 9 (1916) 144; GILG & SCHLTR, Bot. Jahrb. 55 (1919) 199, f. 1; A.C. SMITH, J. Arn. Arb. 23 (1942) 442; RODENBURG, Blumea 19 (1971) 9. — *T. arfakensis* GIBBS, Arfak (1917) 136; KANEH. & HATUS. Bot. Mag. Tokyo 56 (1942) 262, f. 10. — *T. myricoides* GILG & SCHLTR, Bot. Jahrb. 58 (1923) 248. — **Fig. 1, 3.**

Shrub or tree up to 20 m or more high; young branches reddish brown villous, becoming ± glabrous. *Leaves* narrowly elliptic to lanceolate, 2–1.25 by 0.7–3.5 cm, base cuneate, apex acuminate or acute, margin serrate or entire, yellowish brown when young, green at maturity becoming reddish, nerves numerous (*c.* 10–20 pairs), villous when young, becoming ± glabrous except for the midrib and nerves; petiole *c.* 6–12 mm, villous. *Inflorescence* axillary and terminal, paniculate, shorter than

the subtending leaf, *c.* 6.5 by 5.5 cm, peduncle up to 15 mm long, villous at first. Bracts *c.* 3 mm long, lower ovate-lanceolate, upper broader, caducous. *Flowers* uni- or bisexual, up to 4 by 2 mm, pedicel *c.* 1 mm long, villous; tepals 11–25(–28), in terminal flowers *c.* 6 outer decussate, in lateral flowers the outer 2 ± opposite, the remainder spirally arranged, the outer broadly ovate *c.* 1.5 mm long, peltate, grading into longer narrower tepals, the uppermost spathulate, *c.* 3 mm long, ciliate on the upper part, dark brown before anthesis, caducous. *Stamens* 9–25, *c.* 2–3.5 mm long, filament slender, *c.* 1 mm long, anthers to 2 mm long, white, pinkish white or cream at maturity, connective produced. *Carpel c.* 2 mm long, sparsely strigose, carpellode in male flowers rudimentary or absent. *Berry* to 7.5 by 5 mm, crimson to dark purple-black when ripe. *Seed* ovoid, *c.* 4 by 3 mm, smooth.

Distr. *Malesia:* Central Celebes, Moluccas (Ceram, Batjan), and throughout New Guinea. Fig. 2.

Ecol. Common on ridge crests and exposed places in primary low to mid-montane forests, 1000–2700 m. Also in regrowth after landslide and fire, and on infertile stony sand in riverside or stream bank vegetation.

Uses. The wood is used for fence posts and building. The leaves provide a treatment against dysentery (Okapa area).

Vern. *Arunan, nerch, tuna,* Enga, *butulye,* Eipomek, *daloe, moble,* Dani, *edigea,* Kapauko, *gial,* Chimbu, *guiamak,* Kasanombe, *kiluwe, kohbig,* Hagen, *kora kiyei,* Wonatabe, *kuje, porlyporl,* Mendi, *niebalaa,* Kebar, *pymbug,* Melpa, *paribara,* Gerebi, *sakolo,* Wapi, *taingaa, tan-ja,* Huli, *wonnai,* Maring.

Field notes. The bark is smooth and grey-brown, the blaze is pinkish straw to red-brown with few wide rays. The sapwood is pale straw to light reddish brown; the heartwood dark pink to red with conspicuous light brownish to white rays. The bark and crushed leaves have a peppermint-like odour and the leaves are bitter when chewed.

2. Trimenia weinmanniifolia SEEMAN *ssp.* **bougainvilleensis** RODENBURG, Blumea 19 (1971) 14. — *T. bougainvilleensis* (RODENBURG) A.C. SMITH, Allertonia 1 (1978) 154.

Small tree or shrub, up to 10 m; young branches reddish brown villous becoming ± glabrous. *Leaves* narrowly elliptic to lanceolate, 5–9 by 1.6–3 cm, base cuneate, tapered to an obtuse apex or acuminate, margin serrate, lateral nerves *c.* 14–20 pairs, glabrous at maturity, at first sparsely villous; petiole *c.* 10–15 mm, at first villous. *Inflorescence* axillary, paniculate, equal to or somewhat shorter than the subtending leaf, up to *c.* 85 by 55 mm, peduncle up to 25 mm, villous; lower bracts ovate, *c.* 2 mm long, upper broadly ovate, *c.* 1 mm long, strigose. ? Dioecious. *Flowers* up to 3.5 by 2 mm, pedicel 1 mm long; tepals 12–23, spirally arranged, the outer suborbicular, *c.* 1.5 mm ø, upper narrower and longer, the uppermost spathulate *c.* 2.5 mm long, sparsely ciliate. *Stamens* 9–16, *c.* 3 mm long in male flowers, filaments short, broad, anthers *c.* 2 mm long, whitish at anthesis, connective produced, staminodes in female flowers *c.* 2 mm long. *Carpel c.* 2 mm long, sparsely strigose, carpellode in male flowers *c.* 1 mm long. *Berry* dark crimson to black-purple. *Seed* ovoid, 2.5 by 1.7 mm, with distinct ridges.

Distr. Solomon Is. (Bougainville) and *Malesia:* Papua New Guinea (E. New Britain: Pomio Subdistr.). The two other subspecies of *T. weinmanniifolia* occur in Fiji and Samoa and the widely distant Marquesas Is. Fig. 2.

Ecol. In lower montane rain-forest and cloud forest, especially on exposed ridges, 1500–1700 m.

Vern. *Naligugu, naromalalawe,* New Britain.

Note. RODENBURG (1971) reserved judgement on material from New Britain, thinking it might represent another subspecies. Further material now available from New Britain indicates that this subspecies extends outside the island of Bougainville. The identification of collections from New Ireland remains in doubt.

3. Trimenia macrura (GILG & SCHLTR) PHILIPSON, *comb. nov.* — *Piptocalyx macrurus* GILG & SCHLTR, Bot. Jahrb. 55 (1919) 200, f. 2; *ibid.* 58 (1923) 246, f. 1.

Woody climber, with terete brown tomentose branches. *Leaves* elliptic-lanceolate, to *c.* 7–11 by 1.7–3 cm, chartaceous, base broadly cuneate to rounded, apex produced into long delicate acumen (*c.* 3 cm long), margin entire, nerves numerous, impressed above, reticulations of smaller veins prominent, becoming ± glabrous above, densely rufous-sericeous below; petiole *c.* 6–10 mm long, tomentose. *Inflorescence* axillary and terminal, shorter than the leaves, pleiochasia on long, brown-tomentose peduncles. *Flowers* evidently uni- and bisexual, *c.* 5 mm long, subsessile; tepals *c.* 8–10, ovate to obovate, obtuse, glabrous. *Stamens c.* 10–12, 3.5–4 mm long, filaments slender, the anthers somewhat longer than the filaments, white or pinkish at maturity, connective produced. *Carpel* solitary, *c.* 2–2.5 mm long, sparsely rigose, carpellode in male flowers rudimentary or absent. *Fruit* a succulent berry *c.* 7 by 5 mm, deep crimson.

Distr. *Malesia:* Papua New Guinea (West Sepik, Enga, Madang & Morobe Prov.).

Ecol. Climber in dense montane rain-forest and mossy forest, between 2000–3000 m.

Field notes. The tepals are brown and caducous. The stamens are white or pinkish.

Excluded

Idenburgia GIBBS, Fl. Arfak Mts (1917) 136 was reduced by VAN STEENIS, Svensk Bot. Tidskr. 49 (1955) 21 to *Sphenostemon* BAILL. (*Sphenostemonaceae*).

'Trimenia' grandifolia WARB., Index Kewensis, Suppl. 1 (1906) 439, *sphalm.* for *Trimeria grandifolia* (HOCHST.) WARB. (*Flacourtiaceae*).