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CUNONIACEAE

(H.C. Fortune Hopkins, Lancaster University, United Kingdom and R.D. Hoogland†)[1]

Cunoniaceae R. Br., Voy. Terra Austral., 2 (appendix 3) (1814) 548; D. Don, Edinburgh New Philos. J. 23 (1830) 85; Pamp., Ann. Bot. (Rome) 2 (1905) 43; Schltr., Bot. Jahrb. Syst. 52 (1914) 139; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 229; L.M. Perry, J. Arnold Arbor. 30 (1949) 139; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 4; A.C. Sm., Fl. Vit. Nova 3 (1985) 5; Hufford & Dickison, Syst. Bot. 17 (1992) 181; J.C. Bradford & R.W. Barnes, Syst. Bot. 26 (2001) 354; nom. cons.
Baueraceae Lindl., Intr. Nat. Syst. Bot. (1830) 50.
Eucryphiaceae Endl., Ench. Bot. (1841) 528; nom. cons.
Davidsoniaceae Bange, Blumea 7 (1952) 294.

Woody plants, from small shrubs to tall upper canopy trees, rarely hemi-epiphytes and stranglers, evergreen or rarely deciduous. Twigs generally ± flattened or angular (following the phyllotaxis) when young, to terete with lenticels and longitudinal fissures when older. Leaves opposite and decussate, or verticillate in alternate whorls, or rarely alternate (*Davidsonia*), pinnately or palmately compound (the latter outside Malesia), usually with a terminal leaflet, or trifoliolate, or simple/unifoliolate, the leaflet margins crenate-serrate or entire; venation pinnate. Indumentum generally of simple hairs, or occasionally stellate and peltate trichomes or rarely stinging hairs (*Davidsonia*), or small spherical glands. Stipules present, mostly one pair of interpetiolar stipules per node between petiole bases (or the number of stipules equal to the number of leaves where the phyllotaxis is whorled), usually triangular-ovate or ± orbicular, sometimes bifurcate to deeply divided at apex, rarely intrapetiolar (outside Malesia), or 4 lateral stipules per node, foliaceous; usually caducous, leaving a scar in the form of a continuous arc between adjoining leaf bases (rarely, outside Malesia, arc interrupted). Colleters often present at nodes and base of adaxial surface of stipules, sometimes secretory. Inflorescences various; often axillary, sometimes 2 or more serially arranged, terminal, or false-terminal, often a paniculate or corymbose thyrse with major branching following the phyllotaxis and ultimate branching ± spirally arranged, or racemose usually with several racemes together in one inflorescence, or capitate, or outside Malesia, rarely flowers solitary and axillary. Flowers bisexual, sometimes distinctly protandrous, or unisexual in dioecious or polygamous plants, actinomorphic. Sepals 3–6(–9), usually 4 or 5, valvate or imbricate, in some genera enlarged in fruit, in others persistent or caducous. Petals alterni-

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1) With contributions on palaeobotany and leaf morphology by R.W. Barnes (Hobart), palynology by J. Muller† (Leiden), wood anatomy by P. Baas (Leiden) and phytochemistry by R. Hegnauer (Leiden).
RDH's study of *Cunoniaceae* was funded initially by CSIRO, Canberra, and subsequently in Leiden by ZWO. HCFH's work on *Weinmannia* was funded by the EU Human Capital and Mobility Fund, and on *Schizomeria* by the Kostermans Bequest. HCFH also thanks Jason Bradford for discussions on *Cunoniaceae* and for access to unpublished data.
Line drawings are by Ruth van Crevel and Jan van Os (Leiden).
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sepalous, entire or deeply incised, and then rarely with terminal glands (*Gillbeea*), or absent. Stamens usually twice as many as the calyx lobes, the alternipetalous ones often slightly longer than the alternisepalous ones, outside Malesia also ∞ or rarely equal to the number of calyx lobes or irregular in number; filaments usually long and thin; anthers cordate-ovate, generally incised at base and the connective often shortly extended at apex into a blunt point or apex emarginate, versatile, dorsifixed, opening with lateral longitudinal slits. Disc between androecium and gynoecium either annular and free or adnate to the gynoecium, or variously lobed, the lobes rounded or oblong when appearing to alternate with the filaments, or rarely indistinct or absent. Ovary superior to half-inferior, 2–6(–14)-celled, syncarpous or occasionally apocarpous, each cell with its own style, styles often diverging and ending in a small inconspicuous stigma, or rarely stigmas decurrent. Ovules 1–∞, generally in 2 rows on axile or apical-axile placentas. Fruit dehiscent or not, usually small, fruit wall glabrous or hairy; in apocarpous gynoecia, fruitlets ventrally dehiscent; in syncarpous ones either dehiscent (various forms of capsule) or indehiscent (drupe, samara, pseudosamara, etc.); fruit rarely compound, fruitlets dehiscent (*Pancheria*). Seeds 1–∞, fusiform to ellipsoid, smooth or papillate, rarely with elaiosomes (*Pseudoweinmannia*), in dehiscent fruits usually with wings at one or both ends or hairy without wings; embryo embedded in starchy endosperm (except *Davidsonia*).

INTRODUCTORY NOTE

RDH started monographic work on *Cunoniaceae* while working for CSIRO in Canberra in the 1950s. His interest developed during numerous collecting expeditions with the Resources Survey to what became Papua New Guinea, where the family is relatively diverse. He published accounts for several genera, and his notes on others are deposited at the Laboratoire de Phanérogamie (P), Museum National d'Histoire Naturelle, Paris.

While based at the Rijksherbarium, Leiden in 1976–77, RDH prepared a manuscript for Flora Malesiana covering all the genera except *Weinmannia* and *Schizomeria*. HCFH revised Malesian *Weinmannia* at the Laboratoire de Phanérogamie, Paris in 1994–96 and *Schizomeria* at Lancaster University, U.K. in 1998–99. All species concepts and descriptions in the genera treated by RDH remain his although the generic limits have been altered slightly in line with recent phylogenetic studies. The introductory sections were written by HCFH where not otherwise attributed, incorporating notes by RDH and information published since 1977.

DISTRIBUTION

About 300 species in about 26 genera, with c. 40 species in 10 genera in Malesia; mainly in the southern hemisphere, extending into the tropics in Central America and the West Indies, Madagascar and the Mascarenes, the Pacific Islands, and throughout Malesia; absent from North America, Europe, continental Asia (except Peninsular Malaysia and Thailand) and continental Africa except South Africa. The family is most diverse in E Malesia, SW Pacific and E Australia and the only genera whose distributions lie exclusively outside this region are *Platylophus* (1 species, southern Africa), *Lamanonia* (5 species, Brazil, Paraguay, Argentina) and *Caldcluvia* (1 species, Chile, Argentina). There are endemic genera in New Caledonia (*Codia, Pancheria*) and Australia (*Acrophyllum, Anodopetalum, Bauera, Callicoma, Davidsonia, Pseudoweinmannia, Vesselowskya*).

HABITAT

Most tropical species are found in lower montane forest extending upwards into the subalpine zone. Some Australian and most New Caledonian taxa are found in open shrubby vegetation ('maquis') on sandstone or in the latter region on ultramafic substrates ('serpentine'). In Malesia the family occurs from near sea level to 3500 m, but is best represented in forest between 1000 and 2500 m. *Spiraeopsis celebica* and *Weinmannia fraxinea* sometimes display weedy tendencies and can be invasive in secondary grassland. *Weinmannia* and *Opocunonia* are occasionally reported as dominant in vegetation.

Most Malesian genera contain species with wide altitudinal ranges from lowland or foothills forest to upper montane forest and the edge of subalpine grasslands (*Acsmithia, Aistopetalum, Gillbeea, Opocunonia, Pullea, Spiraeopsis* and *Weinmannia*). Some species show a marked decrease in leaf size with increasing altitude (*Pullea glabra, Schizomeria ilicina, S. gorumensis*, and to a lesser extent, *Weinmannia fraxinea*). In *Opocunonia nymanii*, the density of the indumentum increases with altitude while the leaflet size decreases.

Many tree species can flower while the plant is still only quite small, e.g. 2 m tall in a species which may reach 30 m, in particular when it is growing in the open, in regrowth vegetation, on the forest edge, or in subalpine grassland. Within the forest they may have to grow somewhat taller, e.g. 5 m, but here too they flower long before reaching maximum size. The same applies to several *Cunoniaceae*, including *Pullea stutzeri* (F. Muell.) Gibbs and *Callicoma serratifolia* Andrews, in Eastern Australian temperate rain forests where this phenomenon occurs in other families such as *Proteaceae* and *Myrtaceae*. While *Cunoniaceae* in Malesia and elsewhere are typically evergreen, at least one is deciduous, *Eucryphia glutinosa* (Poepp. & Endl.) Baill. from the Andean foothills (see Taylor & Hill 1996).

Association with ultramafic substrates — Members of several genera occur in 'serpentine' floras. This is particularly apparent in New Caledonia, where outcrops of ultramafic occupy about one third of the total surface area (Brooks 1987) and is seen to a limited extent in Malesia and New Zealand.

Two Malesian species of *Weinmannia* appear to be confined to ultramafic, *W. clemensiae* on Mt Kinabalu in Borneo and *W. devogelii* from near Lake Matano in Sulawesi (Hopkins 1998a & b). *Weinmannia clemensiae* is a distinctive species with small, thick, bullate leaflets which occurs in localised patches of dwarf forest with a rather open canopy, at 1900–2600 m altitude. In contrast, *W. devogelii* is a satellite of the widespread and variable *W. fraxinea*, and is a medium to large tree in lowland forest, with a leaf texture typical for the genus. The forests of the region around Lake Matano are described in Van Balgooy & Tantra (1986).

Weinmannia fraxinea has a variable ecology and is occasionally found in forest in proximity to ultramafic outcrops, e.g. on Mt Kinabalu (Hopkins & Bradford, pers. obs.) and Kamiali, Morobe Province, Papua New Guinea (W. Takeuchi, pers. comm.). Another widespread species, *Schizomeria serrata*, occurs occasionally on ultramafic in the Solomon Islands, and on Obi Island, North Moluccas, in rather open, low forest on red porous nickel soil (*de Vogel 4230*). Analysis of leaves from Obi Island showed elevated levels of Co, Ni and Mn (Wither 1977), but the level of Ni (590 µg/g of dried leaf material) is not high enough for it to be categorised as a hyperaccumulator (> 1000 µg/g). The ultramafic outcrops of New Guinea have been little studied (Brooks 1987).

Outside Malesia, *Weinmannia racemosa* L.f. occurs in several serpentine areas in South Island, New Zealand, sometimes as a dwarf shrub only 2 m high in transition forest, as well as on non-ultramafic substrates (see references in Brooks 1987). In New Caledonia, *Cunoniaceae* is represented by about 90 species in 6 genera and there is a strong association with ultramafic. For instance, *Codia* and *Pancheria* are endemic and have radiated in ultramafic maquis scrub, and some species in both genera are typical of particular ultramafic communities (Jaffré 1980), though others are found on different substrates and some, e.g. *Codia montana* J.R. Forst. & G. Forst., have a variable ecology. Hyperaccumulation of Ni has been demonstrated in *Geissois* and *Pancheria* (Jaffré 1980). There is no association between *Cunoniaceae* and ultramafic in southern Africa, and I have found no information for Madagascar and Australia.

The accumulation of aluminium has been reported in several Malesian genera, including *Schizomeria, Ceratopetalum* and *Gillbeea*, as well as in *Anodopetalum, Platylophus* and *Acrophyllum* outside Malesia (Chenery 1948; Webb 1954). Malesian genera which tested negative for Al-accumulation included *Opocunonia, Spiraeopsis* and *Spiraeanthemum.*

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TAXONOMY AND PHYLOGENY

Circumscription of the family — Although the circumscription of the family has until recently remained almost unchanged since Engler's treatment (1928), the placement of some genera has been problematical. This stimulated considerable work on morphology and anatomy, largely by W.C. Dickison and co-workers, and now, with additional data from molecular sequences, a revised circumscription has been produced (Bradford & Barnes 2001).

According to Brummitt (1992) and Gunn et al. (1992), with the exclusion from the former of *Gumillea* Ruiz & Pavon to *Simaroubaceae* (Hoogland in Gunn et al. 1992), *Cunoniaceae* is generally considered to comprise 22 genera. Amongst these, *Bauera* has sometimes been accorded familial status or included in *Saxifragaceae* (see Dickison 1975; Prakash & McAlister 1977), and the inclusion of *Aphanopetalum* has been questioned (Hoogland, unpublished notes; Dickison et al. 1994). Three other genera, *Brunellia* from tropical America, *Davidsonia* from E Australia, and *Eucryphia* from temperate South America and E Australia, are each usually accorded the status of a separate family with close affinities to the *Cunoniaceae* or included in the family (Bange 1952; Cronquist 1981; Dickison 1978, 1989; Hufford & Dickison 1992; Orozco 1997; Doweld 1998). Studies of molecular sequence data demonstrate that *Bauera, Eucryphia* and *Davidsonia* all lie within the main body of *Cunoniaceae* and confirm that *Aphanopetalum* should be excluded, while *Brunellia* is maintained as a distinct family, and sister group to *Cephalotaceae* (Bradford & Barnes 2001). However, these changes in circumscription have no implications for Malesia.

Relationships within the family — Bradford & Barnes (2001) recognise six tribes, each of which corresponds to a major clade within the family, and leave six genera unplaced. This new tribal classification supersedes that of Engler (1928), which has for some time appeared artificial (see Dickison 1984; Hufford & Dickison 1992; Orozco 1997).

According to Bradford and Barnes, the Malesian genera are distributed amongst most of the major clades: *Acsmithia* and *Spiraeanthemum* are sister taxa near the base of the family (tribe *Spiraeanthemeae*); *Schizomeria* and *Ceratopetalum* form a clade with *Platylophus* and *Anodopetalum* (tribe *Schizomerieae*); *Opocunonia* and *Spiraeopsis* belong to the *Caldcluvieae*, together with *Caldcluvia* s. s. and *Ackama*; *Pullea* is in the same lineage as *Codia* and *Callicoma* (tribe *Codieae*); while *Weinmannia* is part of a derived clade with *Pancheria, Cunonia* and *Vesselowskya* (tribe *Cunonieae*). In this classification, *Gillbeea* and *Aistopetalum* are unplaced, as are four non-Malesian genera. The only major clade unrepresented in Malesia is the tribe *Geissoieae* (comprising *Geissois, Lamanonia* and *Pseudoweinmannia*).

Relationships of the family — The family was included in the *Saxifragaceae* by Bentham & Hooker (1865) but most subsequent authors have accepted it as distinct. The recent classification of the angiosperms based on molecular sequence data places it in the order *Oxalidales* (higher Eurosids I), together with *Cephalotaceae, Connaraceae, Elaeocarpaceae, Oxalidaceae* and *Tremandraceae* (APG 1998). This is a fairly radical shift in our view of the affinities of the *Cunoniaceae*, which has traditionally been considered close to the saxifragaceous complex, in a basal position within the *Rosales* (see Dickison 1989). Morphological apomorphies for the revised order *Oxalidales* remain to be clarified.

The characteristics of the families placed around the *Saxifragaceae* had always been somewhat vague, and the study of features other than those of external morphology, such as pollen structure (Hideux & Ferguson 1976) and flavonoid chemistry (Jay 1968), failed to clarify family distinctions and, instead, emphasised the overlapping features of the segregate families of *Saxifragaceae* s.l. Molecular data now place *Saxifragales* in the Core Eudicots, at some distance from the *Oxalidales* (APG 1998). Dickison (1989) discussed putative relationships of *Cunoniaceae*, as representing the primitive rosids, looking at evolutionary trends in structure and biology both within the family and within the larger assemblage.

Generic circumscription — Generic limits are discussed by Bradford & Barnes (2001), who provide a list of currently accepted genera and their apomorphies. Their study rejects all of the generic mergers suggested by Hufford & Dickison (1992), though it upholds the partition of *Caldcluvia* s.l.

Hoogland (1979) united several small, rather confused genera into *Caldcluvia* on the basis of: valvate sepals, entire petals, obdiplostemonous androecium, and loosely connate carpels separating while dehiscing with a ventral split (1979: 482). However, none of these characters provides an obvious apomorphy for the genus (Hufford & Dickison 1992), and *Caldcluvia* sensu Hoogland has not always been accepted by others (Godley 1983; Webb & Simpson 1991; Hufford & Dickison 1992). With the exception of valvate sepals, three of the characters which define the genus are also seen in *Weinmannia*.

Four distinct groups can be recognised within *Caldcluvia* s.l.: *Caldcluvia* s.s. [1 species, *C. paniculata* (Cav.) D. Don, Chile and Argentina], *Spiraeopsis* (6 species, Philippines to Solomon Islands), *Ackama* (3 species, Australia and New Zealand) and *Opocunonia* (1 species, *O. nymanii*, New Guinea and New Britain). General morphology supports the idea that these segregate groups are closely related and several characters have a reticulate pattern of occurrence (e.g. protandry, replum in the fruit). In the analysis of Bradford and Barnes, they form a clade, defined as the tribe *Caldcluvieae*.

Caldcluvia s.l. is clearly more heterogeneous than most other genera in the family. Although Hoogland (1984) considered that the species groups merited no more than infrageneric recognition, there appears to be a general consensus amongst those currently working in the family that more narrowly defined genera are useful, and the Malesian species of *Caldcluvia* s.l. are therefore treated in their segregate genera in this account.

Note on Types — The types for numerous species, especially from New Guinea, are cited as present at B. For names in *Schizomeria*, the continued existence of these specimens has been verified by HCFH and for all other names, indication of their presence at B after WW2 comes from the notes and publications of RDH. All types cited have been seen by one of the authors unless 'n.v.' is indicated. For some taxa in *Weinmannia* from the Philippines no lectotype has been designated as only a handful of the numerous isotypes has been studied.

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LEAF MORPHOLOGY

(R.W. Barnes)

General form

Leaves, whether compound or simple, are generally petiolate and often stiff to coriaceous, though there are some exceptions to both. The petiole is often inflated at the point where it attaches to the stem and is particularly pronounced in some *Pullea*, *Ceratopetalum* and *Schizomeria*. Leaves are usually imparipinnate, formed by 1 to 10 leaflet pairs and an elongated terminal leaflet, or may be trifoliolate (most *Ceratopetalum*), palmate (New Caledonian *Geissois*), unifoliolate or simple. The leaflets in compound leaves are shortly petiolulate (*Spiraeopsis, Aistopetalum*), sessile (most *Weinmannia*) or both in the same genus (*Ceratopetalum*). Leaves are unifoliolate when there is an articulation between the petiole and lamina (e.g. *Ceratopetalum apetalum* D.Don in Australia) or simple when this articulation is absent (*Acsmithia, Pullea, Schizomeria, Spiraeanthemum* and some Australian endemic genera).

Stipels occur at the base of each leaflet on the rachis in *Spiraeopsis*, Australian *Ackama* species, *Davidsonia* and in *Geissoieae* (Bradford & Barnes 2001). Small stipels at the base of each leaflet also occur in the Vanuatu endemic *Weinmannia macgillirayi* Seem. (Hopkins 1998b). The rachis is sometimes winged between successive leaflets in some *Weinmannia* and *Cunonia*, but this trait in *Weinmannia* is only slightly developed in a few Malesian taxa (Hopkins 1998a) and is more developed in some neotropical species (Bradford 1998).

In Malesian genera the leaf or leaflet margin is irregularly serrate, dentate or rarely crenate or entire (*Gillbeea papuana* Schltr. and some *Acsmithia* and *Spiraeanthemum*). Tooth apices, when present, are usually glandular and may have a spinose extension (some *Schizomeria* and *Ceratopetalum* species).

Venation patterns

Primary venation is pinnate. Secondary venation is usually of the semicraspedodromous type, where secondary veins loop within the leaf margin to form an arch from which another vein originates to vascularise the sinus or tooth apex (Dickison 1975; Hufford & Dickison 1992; Bradford & Barnes 2001). Brochidodromous venation occurs when the leaf margin is entire, as in *Gillbeea papuana* and some *Acsmithia* and *Spiraeanthemum* species. Craspedodromous venation occurs in some *Spiraeanthemum, Acsmithia* and *Weinmannia* where the secondary vein terminates at the leaf margin, either at a sinus or at a tooth apex, and is the exclusive type in some endemic Australian genera (*Acrophyllum, Callicoma, Vesselowskya*).

Tertiary venation in Malesian taxa is percurrent (*Acsmithia, Gillbeea*), random reticulate (*Ceratopetalum, Schizomeria, Weinmannia*) or rarely a mixture of admedial ramified to random reticulate (*Pullea*), and there is occasionally a composite intersecondary vein (*Aistopetalum, Ceratopetalum, Gillbeea*). Tertiary venation patterns are often never absolute and the leaves on a single specimen may vary between venation types (e.g. *Spiraeanthemum*). Areolation can often be seen in most leaves/leaflets in the field, with areoles either well developed (*Ceratopetalum, Schizomeria*), imperfect or rarely incomplete (*Aistopetalum* and some *Weinmannia*). Veinlet endings are sheathed in parenchymatous or sclerenchymatous cells (Dickison 1975), or these may be absent (*Aistopetalum*).

Indumentum

Simple, unicellular trichomes with thick walls, variable in length, occur in most genera either alone or with other types of trichome (Fig. 1A; Dickison 1975; Barnes & Hill 1999). In *Spiraeopsis*, 6 to 25 unicellular trichomes are clustered to form stellate hairs which are often abundant and readily seen with a lens on the leaf lamina and veins (Fig. 1B; Dickison 1975) and on the inflorescence or floral parts, such as the calyx. These stellate hairs are present on the young stem, inflorescence and fruits of *Gillbeea* but I

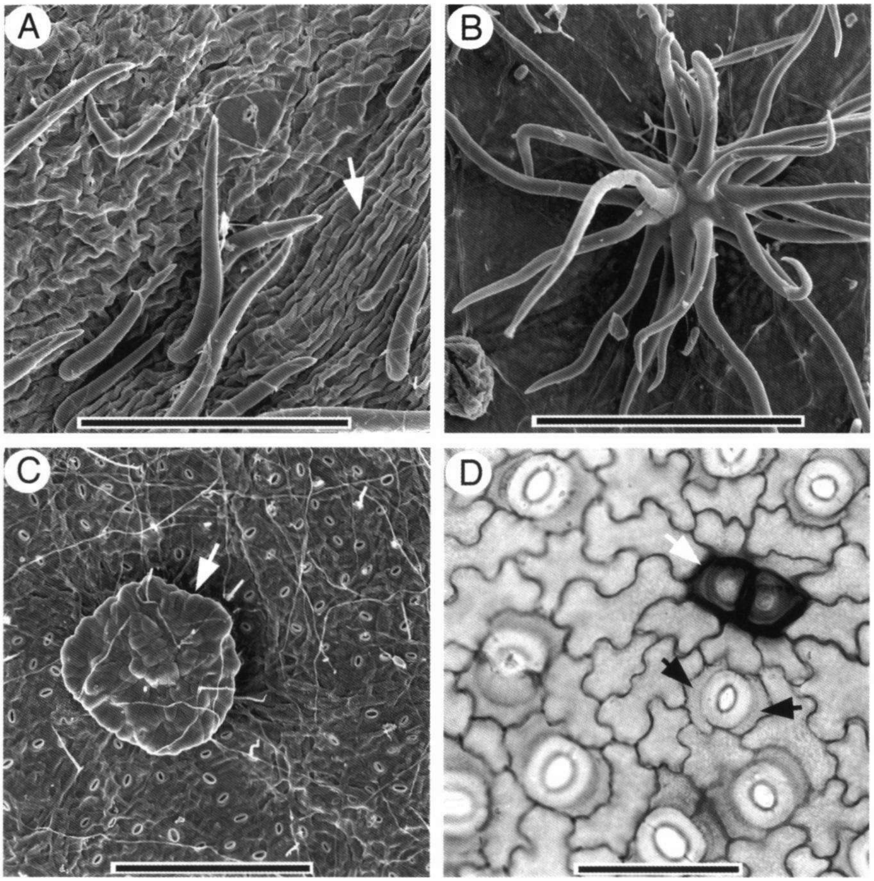
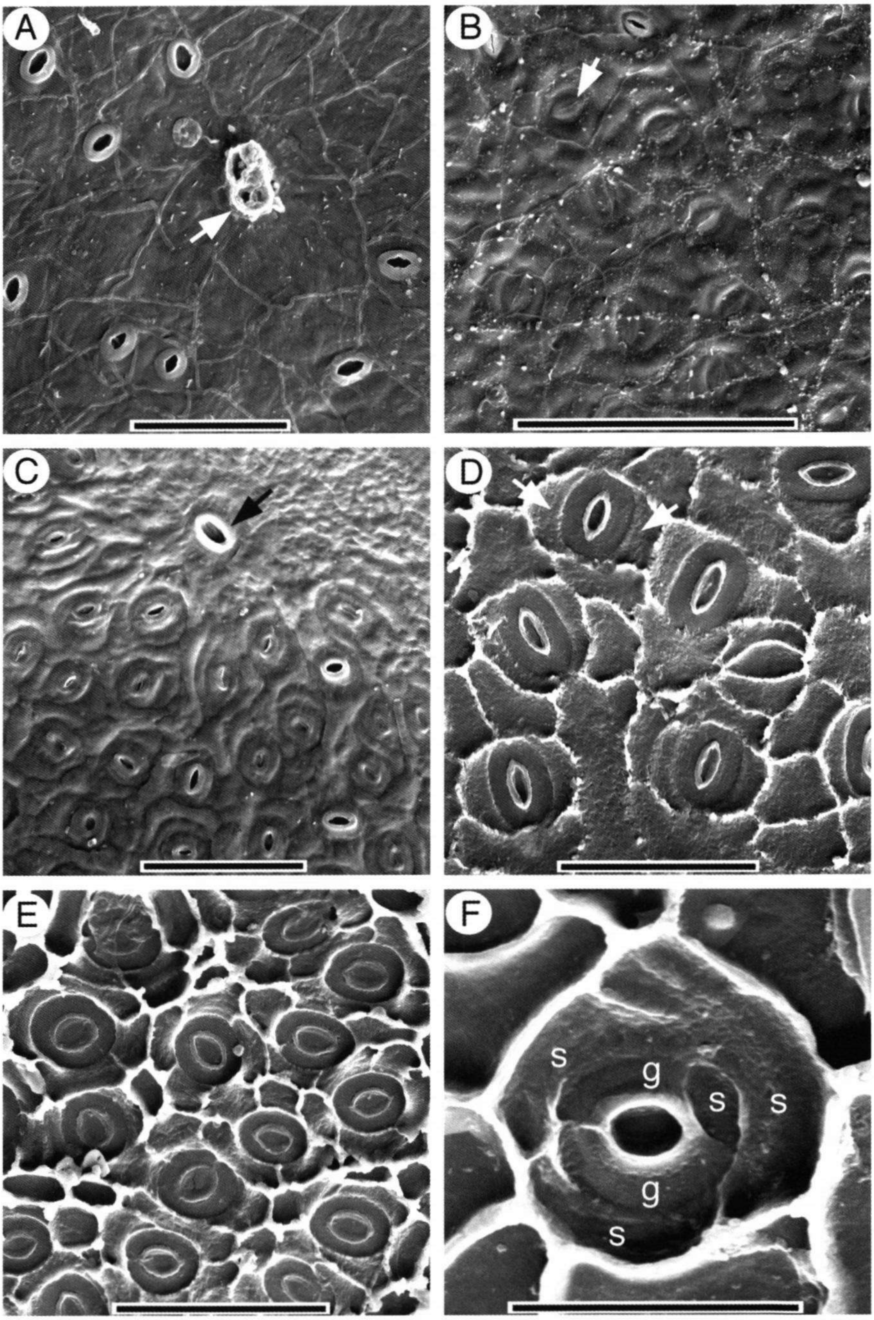


Fig. 1. Scanning electron micrographs of structures on the leaf surface of selected Malesian *Cunoniaceae* genera. – A. Unicellular trichomes on a secondary vein (arrow) in *Gillbeea papuana* (*Coode & Lelean NGF 29903*). Scale bar = 150 µm. – B. Stellate hair in *Spiraeopsis rufa* (*Womersely NGF 17906*). Scale bar = 150 µm. – C. Multicellular peltate trichome (arrow) on the leaf surface of *Spiraeopsis celebica* (*Wheeler ANU 6511*). Scale bar = 150 µm. – D. Secretory gland formed by two modified epidermal cells on the lamina (white arrow) of *Acsmithia integrifolia* (*Henty, Ridsdale & Galore NGF 31910*). Note the brachyparacytic arrangement of the subsidiary cells (black arrows indicate the position of subsidiary cells around the guard cells). Scale bar = 50 µm.

Fig. 2. Scanning electron micrographs of the leaf cuticular and stomatal morphology of selected Malesian *Cunoniaceae* genera. – A. Secretory gland formed by two modified epidermal cells on the lamina (arrow) of *Acsmithia integrifolia* (*Henty, Ridsdale & Galore NGF 31910*). Note superficial stomata and strands of epicuticular wax. Scale bar = 50 µm. – B. Outer abaxial leaf surface of *Aistopetalum multiflorum* (*Hoogland & Craven 10826*) showing superficial stomata (arrow). Scale bar = 100 µm. – C. Outer abaxial leaf surface of *Pullea mollis* (*Gideon s.n.*) showing hydathode (arrow) and superficial stomata. Scale bar = 50 µm. – D. Inner abaxial cuticle of *Opocunonia nymanii* (*Womersley & Eddowes LAE 55281*) showing a brachyparacytic subsidiary cell arrangement (arrows indicate the position of subsidiary cells). Scale bar = 50 µm. – E. Inner abaxial cuticle of



Pullea glabra var. *glabra* (*Havel NGF 17293*) showing stomata with an anomocytic subsidiary cell arrangement. Scale bar = 50 µm. – F. Inner abaxial surface of a single stoma in *Weinmannia humblotii* var. *humblotii* (*Turk, Solo & Randrianasolo 319* [MO]) from Madagascar. Note the anisocytic arrangement of the subsidiary cells (s) around the guard cells (g). Scale bar = 25 µm.

have not found them in *Ackama* as suggested by Dickison (1975). Multicellular peltate hairs with a short stalk commonly occur on the leaves of *Spiraeopsis* and *Ackama* (Fig. 1C; Dickison 1975; R.W. Barnes, pers. obs.) and some *Schizomeria* species (e.g. *S. gorumensis*). The peltate hairs are formed by a short multicellular stalk with circular head formed by numerous small cells that collapse when dehydrated (Fig. 1C). Peltate hair bases are formed by 3 to 4 circular epidermal cells that are smaller than the surrounding cells. The distribution and density of peltate hairs in *Spiraeopsis* and *Ackama* species is often variable between species but relatively constant within a species.

Several *Weinmannia* have large multicellular trichome bases with a central, non-glandular unicellular trichome (Barnes et al. 2001) which were referred to as 'black dots' by Hopkins (1998a). *Acsmithia* and *Spiraeanthemum* have secretory glands on the leaf lamina and veins that are formed by two modified epidermal cells (Fig. 1D & 2A; Carpenter & Pole 1995; Barnes et al. 2001), and are not trichomes or trichome bases as reported by Dickison (1975).

In Australia, rigid urticating hairs occur in *Davidsonia* (Bange 1952; Dickison 1989) and paired curly unicellular hairs occur in *Callicoma* and in the juvenile leaves of some New Caledonian *Codia* (Barnes & Hill 1999). Glandular hairs and colleters do not occur on the leaves of *Pancheria* and *Cunonia* as reported by Dickison (1975).

Cuticle morphology

The abaxial cuticle is usually smooth and non-ornamented with superficial stomata (e.g. Fig. 1C, 2A–C) generally occurring in areoles. Epicuticular wax often occurs as long strands on both leaf surfaces (e.g. Fig. 1C & 2A), with cuticular striations present on the veins of some genera (*Ceratopetalum, Gillbeea*). Peltiform cuticular extensions occur in evergreen *Eucryphia* species (Hill 1991; Barnes & Jordan 2000). Epidermal cells are rectangular, rhomboidal, pentagonal or isodiametric in shape and may be of unequal sizes, especially on the adaxial surface.

Subsidiary cell arrangement in Malesian taxa is usually brachyparacytic (*Acsmithia* (Fig. 1D), *Aistopetalum, Ceratopetalum, Opocunonia* (Fig. 2D), *Schizomeria, Spiraeanthemum* and *Spiraeopsis*). *Pullea* is anomocytic (Fig. 2E) while *Weinmannia* species can be anomocytic, brachyparacytic, encyclocytic or rarely anisocytic (*W. fraxinea*), which is more common in Malagasy species (e.g. *W. humblotii* Baill., Fig. 2F). Subsidiary cell arrangement is equally variable between genera outside Malesia (see Bradford & Barnes 2001). Hydathodes, or water stomates, are present on the veins, and rarely in the areoles, of most *Cunoniaceae* (e.g. Fig. 2C), and are particularly abundant in *Schizomeria* and some *Ceratopetalum*.

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GENERAL MORPHOLOGY

These notes apply primarily to the Malesian species unless otherwise indicated and expand characters given in the description of the family.

Our knowledge of the micromorphology and anatomy of the *Cunoniaceae* is due in large part to the work of W.C. Dickison† and collaborators, and in addition to papers on stipules, fruits and seeds, and wood anatomy cited below, he has dealt with vegetative characters (e.g. Dickison 1975a; Rao & Dickison 1985) and floral anatomy (Dickison 1975b). An overview of the anatomy of the family is provided by Gregory (1998).

Architecture

Some *Cunoniaceae* are distinctive in the field because of the opposite, decussate phyllotaxis and often compound leaves. Stipules occur either as interpetiolar pairs or as four lateral structures per node (see below). Young growth and sometimes old leaves can be reddish. Architecturally, *Pancheria* and some *Weinmannia* species demonstrate Attim's model with a monopodial trunk, continuous branching, and branches orthotropic and monopodial, while other *Weinmannia* species conform to Rauh's model (Keller 1996).

Leaf domatia

Specialised chambers in the axils of secondary veins, usually on the underside of a leaf, occur in several genera. They are formed either by a tuft of hairs or by invaginations or outgrowths of tissue, or sometimes both. These chambers are also known as acarodomatia because they billet predaceous and fungivorous mites that prey on plant enemies (O'Dowd & Willson 1989). Typically, domatia are not present on every leaf of a specimen nor on every specimen of a species for which they are reported.

Leaf domatia have been variously classified into morphological types including pit, pouch, pocket and tuft (Jacobs 1966, f. 1; O'Dowd & Willson 1989, f. 2; Brouwer & Clifford 1990). However, differences between types are not clear-cut in some *Cunoniaceae* and, for instance, in *Acsmithia*, there is a range of structures although hairs are almost always present. Some anatomical variation in the cells lining the domatia has been reported in *Ackama* (Dickison 1975a; Sampson & McLean 1965) but few species have been investigated so far.

Within Malesia, domatia have been found in five genera (*Acsmithia, Spiraeanthemum, Opocunonia, Pullea, Spiraeopsis*). Figure 3 illustrates the various types found in *Acsmithia*. Here the base and margins of the domatia are modified as pits, pockets, pouches or 'igloos' (see below) with trichomes usually present. The different forms are not species specific and there is often a continuum of form on a single herbarium sheet.

1) Simple tuft of hairs in axil of secondary vein (e.g. *A. reticulata, Brass 27417*, Fig. 3e; *A. pulleana, Robbins 281*).
2) Pit with hairs: the floor of the domatium is indented into the leaf surface and is visible as a bump on the adaxial surface, sometimes drying a different colour to the rest of the lower leaf surface (e.g. *A. reticulata, Kostermans & Soegeng 722*, Fig. 3c).
3) Pocket with hairs: a flap of tissue extends between the midrib and the secondary vein (*A. parvifolia, Schodde 5447*, Fig. 3d) – most common type.

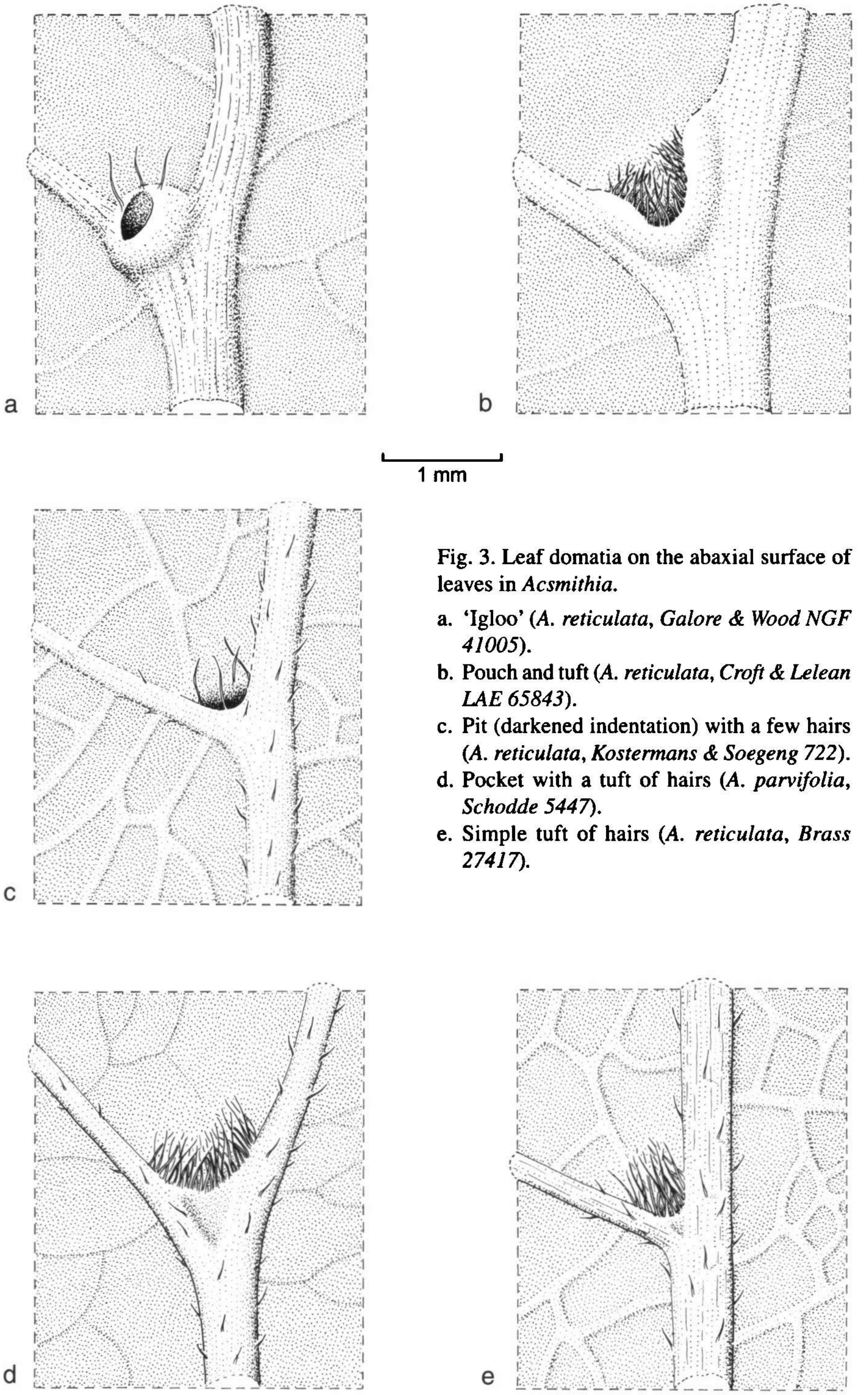

Fig. 3. Leaf domatia on the abaxial surface of leaves in *Acsmithia*.

a. 'Igloo' (*A. reticulata, Galore & Wood NGF 41005*).
b. Pouch and tuft (*A. reticulata, Croft & Lelean LAE 65843*).
c. Pit (darkened indentation) with a few hairs (*A. reticulata, Kostermans & Soegeng 722*).
d. Pocket with a tuft of hairs (*A. parvifolia, Schodde 5447*).
e. Simple tuft of hairs (*A. reticulata, Brass 27417*).

4) Pit-pouch with hairs: the bottom of the domatium is indented and the swollen sides of the veins form a partial covering (e.g. *A. reticulata, Croft & Lelean LAE 65843,* Fig. 3b; this is an intermediate step towards an 'igloo', and igloos are present on the same sheet) – rare.
5) 'Igloo': a hemispherical raised bump with a small lateral entrance, with or without hairs around the entrance (e.g. *A. reticulata, Galore & Wood NGF 41005,* Fig. 3a) – uncommon. 'Igloos' probably correspond to the domed pits of Brouwer & Clifford (1990).

In *Spiraeanthemum* the range in form is similar to that in *Acsmithia* but this genus is unusual in that occasionally domatia are sometimes also present in the axils of the tertiary veins (e.g. *Sands 2477, S. macgillivrayi,* New Ireland). Here the domatia are flat pouches generally with some hairs inside, or intermediate between pits and pouches. In *S. bougainvillense* Hoogland (*Kajewski 2082,* Bougainville), pockets with hairs occur in the axils of both secondary and tertiary veins, and in *S. graeffei* Seem. (*Smith 5800,* Fiji) there are pouches with or without hairs.

In *Opocunonia,* the domatia are either small pockets, or a very slight pocket with a tuft of hairs (e.g. *Pullen 207*) and in *Spiraeopsis,* some species have simple tufts of hairs while others lack domatia. *Pullea glabra* occasionally has tuft-domatia (e.g. *Burley & Ismail 4539, Carr 13843*).

Outside Malesia, domatia have been recorded in Ackama in Australia and New Zealand. *Ackama rosifolia* A.Cunn. has pockets with a dense mass of trichomes including peltate scales (Sampson & McLean 1965), while *A. australiensis* (Schltr.) C.T. White and *A. paniculosa* (F. Muell.) Beuzeville & C.T.White have hair-tufts (O'Dowd & Willson 1989, as *Caldcluvia*; Brouwer & Clifford 1990). Domatia also occur in *Lamanonia* in South America (Zickel & Leitão Filho 1993), some species of *Geissois,* and in *Vesselowskya* in Australia (Rozefelds et al. 2001).

Stipules

In most genera of *Cunoniaceae,* interpetiolar (or interfoliar) stipules occupy a position between the areas of insertion of opposite or whorled leaves (Rutishauser & Dickison 1989). Where the leaves are opposite, each node of the stem typically bears two petioles and two stipules (one pair), and when the leaves are whorled, the number of stipules is usually the same as the number of leaves. These interpetiolar stipules are sometimes referred to as 'fused' but since each arises from a single primordium, i.e. is entire from its inception (Dickison & Rutishauser 1990), this terminology is somewhat confusing. The mature stipules may be triangular, ovate, lingulate, reniform, spoon-shaped with a narrow base, or bifid (*Opocunonia*), and the margin is usually entire or occasionally toothed. The stipules arise simultaneously with, or slightly later than, the accompanying leaf primordia and generally enclose the developing leaves of the same node and the terminal bud (Rutishauser & Dickison 1989). Stipules may be either caducous, usually leaving a distinctive scar between the petioles, or sometimes persistent, and they are often more persistent in juvenile foliage than in the adult. Colleters are often associated with the stipules and nodes, and in *Ceratopetalum* and *Schizomeria* they are adnate to the stipules to form glandular ribs over part of the adaxial surface (Rutishauser & Dickison 1989); their secretions often result in varnished buds and nodes, which are also apparent in some species of *Eucryphia* and in *Anodopetalum* (R.W. Barnes, pers. comm.).

While this general type of interpetiolar stipule is characteristic for the family there is some variation in the position and number of the primordia (Rutishauser & Dickison 1989). Intrapetiolar stipules (one pair per node) arise in the axils of the petioles of *Geissois* p.p. (western Pacific Islands), or occasionally four lateral stipular primordia coalesce to produce a pair of bifid mature stipules (*Geissois* p.p., Australia; *Pseudoweinmannia*, Australia). In Malesia and Australia, *Gillbeea* has four lateral stipular primordia at each node and they usually remain as independent structures at maturity (i.e. two pairs per node, see Fig. 16a) (Hoogland 1960; Dickison & Rutishauser 1990; Rozefelds & Pellow 2000). Each stipule is quite large and strongly asymmetrical with the side nearer the petiole the narrower one, and they are narrowly attached at the base; the venation is prominent, consisting of a distinct midrib and lateral veins (Hoogland 1960; Dickison & Rutishauser 1990). In the *Caldcluvieae*, there is one pair of interpetiolar stipules per node in *Spiraeopsis, Opocunonia* and *Ackama*, while in *Caldcluvia* s.s. there are two pairs of lateral, leafy stipules per node, as in *Gillbeea* (Rutishauser & Dickison 1989, pers. obs.).

Inflorescences

The structure of the inflorescence is quite variable. Inflorescences have been described in detail elsewhere for *Weinmannia* (Bradford 1998; Hopkins & Bradford 1998), *Schizomeria* (Hopkins in prep.), *Cunonia* (Hoogland et al. 1997) and *Anodopetalum* (Barnes & Rozefelds 2000).

The flowers are frequently pedicellate, the pedicels often articulating around the midpoint or towards the base, and sometimes widening gradually into the hypanthium. More or less sessile flowers occur in some species of *Schizomeria, Spiraeopsis* and *Pullea*, and small fascicles of flowers are found in some species of *Spiraeopsis* and most Malesian species of *Weinmannia*. Capitula and glomerules occur in *Pullea*. Axes within the inflorescence can be terete or ridged; they often bear indumentum, and lateral segments are often articulated at the nodes. Nodes typically bear bracts (subtending lateral axes and individual flowers or fascicles of flowers) and especially at lower nodes with opposite branching, they also bear 'stipules', i.e. a pair of opposite bracts in a lateral position at the node, between the insertions of the opposite axes, resembling stipules in shape and position but associated with reduced leaves or bracts and not with fully developed leaves.

The most common type of inflorescence, which is probably plesiomorphic in the family, is paniculate. In many cases there is a change in phyllotaxis from opposite and decussate branching at the lower nodes to alternate (spiral) at distal nodes, although the level at which this occurs within the inflorescence varies. The most distal, flower-bearing subunits are often cymose and this type of inflorescence is thus a thyrse in the terminology of Weberling (1989). Such inflorescences vary in shape from broadly triangular/ paniculate to corymbose and in size from small (c. 5 cm across in *Schizomeria gorumensis*) to quite large (e.g. up to 50 by 30 cm in *Spiraeopsis celebica*). Their position (axillary, terminal etc.) is variable or fixed in different species. In Malesia, paniculate or corymbose inflorescences occur in all genera except *Weinmannia*.

According to Bradford & Barnes (2001), genera can be divided into two groups depending upon the timing of floral maturation. Within Malesia, ± synchronous maturation along the flower-bearing axes occurs in all genera except *Aistopetalum, Ceratopetalum, Gillbeea* and *Schizomeria*, in which the terminal flowers mature first (centrifugal maturation). In these latter genera, the distal subunits of the inflorescence are clearly cymes; in the genera with paniculate/corymbose inflorescences and ± synchronous floral maturation, the structure of the distal subunits is less clear.

In the following examples, typical inflorescence structures are described for the Malesian genera, but not all possible variations are included.

Genera with centrifugal maturation of flowers

Ceratopetalum — The inflorescence is a thyrse; branching is primarily opposite (Fig. 4a) with some distal branching subopposite to alternate, and the most distal flower-bearing subunits are cymose. Generally the dominance at any node is ± equal, the median axis being only slightly more strongly developed than the two lateral ones. In *C. succirubrum* in New Guinea, the inflorescence is usually terminal with the lower lateral branches developing in the axils of full-sized or reduced leaves (Fig. 4a).

Gillbeea — In *G. adenopetala* (Australia), the inflorescence is usually terminal with the lower lateral branches developing in the axils of the most distal pair of leaves, as in *Ceratopetalum succirubrum*. However, while the inflorescence is occasionally terminal in *G. papuana*, more usually the apical bud of a flowering shoot aborts or remains dormant (false-terminal), or sometimes continues vegetative growth during flowering. In the latter case, the inflorescence is then subdistal, with the principal axes all axillary (Fig. 4b). Especially where the apical bud has aborted or is dormant the dominance of the lateral branches can be rather irregular. The switch from opposite to alternate branching within the inflorescence is shown in Fig. 4b'.

Schizomeria — The inflorescence may be 1) axillary, where the principal inflorescence axes develop from opposite, axillary buds, often of the most distal pair of leaves on a shoot, the apical bud remaining dormant before resuming vegetative growth; 2) terminal, i.e. developing in a median position from the apical bud of a shoot and terminat-

Fig. 4. Inflorescence structure.

a. ***Ceratopetalum succirubrum.*** Principal axes of inflorescence are borne in axils at distal nodes. – a'. Reduced leaves are present at some nodes within inflorescence (*Lelean & Stevens LAE 51156*).

b. ***Gillbeea papuana.*** Principal axes are borne in series in axils of subdistal nodes. – b'. Phyllotaxis changes from opposite and decussate (proximally) to alternate (distally) (*Coode & Lelean NGF 29903*).

c. ***Aistopetalum viticoides.*** Principal axes are borne in axils at most distal node. – c'. Branching is opposite and decussate throughout; ultimate subunits are dichasia (*Brass & Versteegh 13170*).

d. ***Pullea glabra.*** Principal axes are borne in series in leaf axils; the flowers tend to aggregate distally along each flower-bearing axis to form glomerules. Branching is opposite, with flower-bearing axes inserted in series at nodes within the inflorescence (*Havel NGF 9128*).

e. ***Pullea mollis.*** As above, but the flowers are aggregated into distinct capitula (*Hartley 12878*).

f. ***Weinmannia fraxinea.*** Flowers are arranged in small fascicles along unbranched axes. These flower-bearing axes are borne in pairs (or fours) on a sterile peduncle, with a small bud at its apex. The peduncles are axillary, in series, at the most distal node of a shoot whose apical bud is dormant. Inflorescence structure typical for *Weinmannia* sect. *Fasciculatae*.

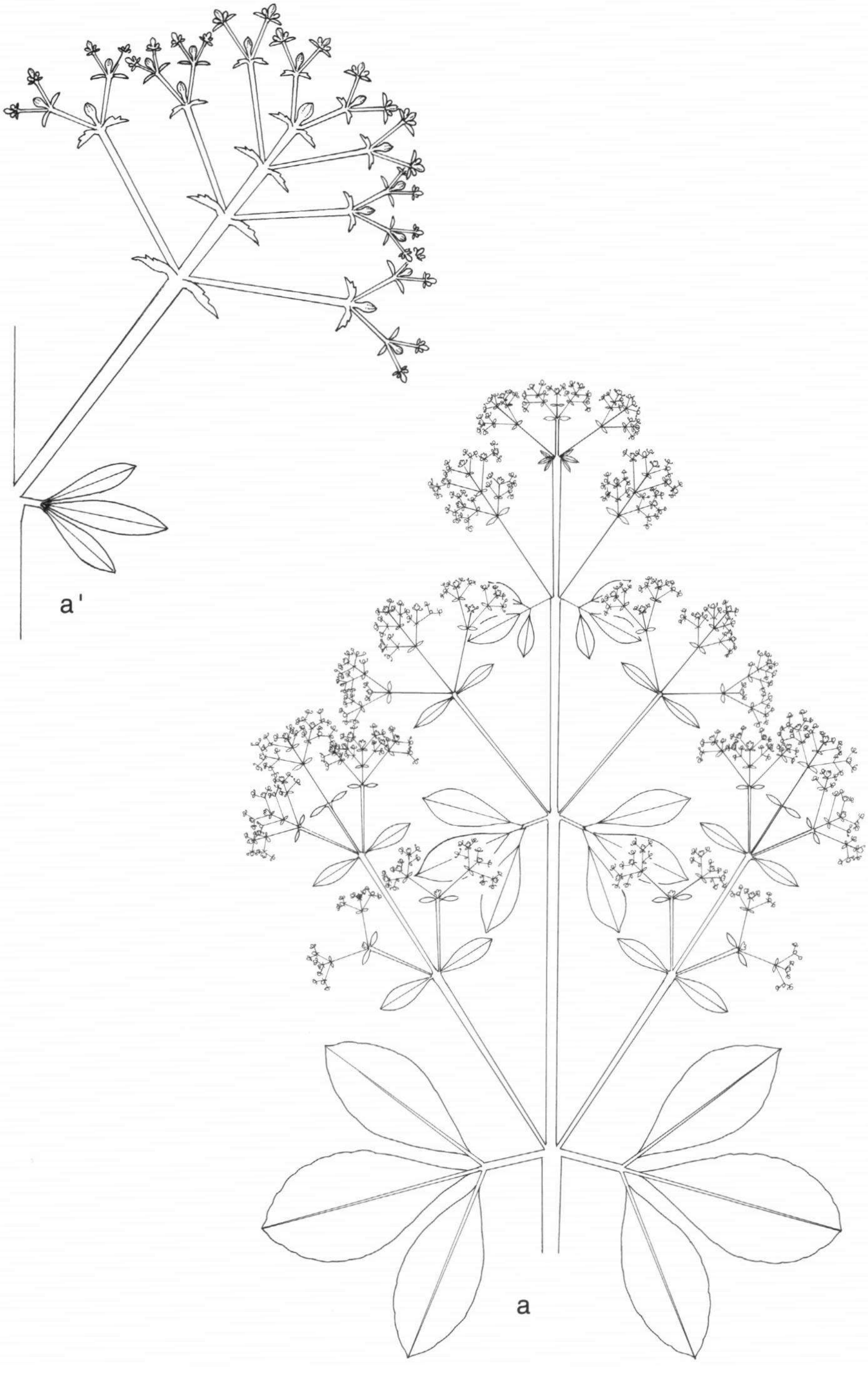

Fig. 4a & a'. *Ceratopetalum succirubrum*. – See the legend on page 67.

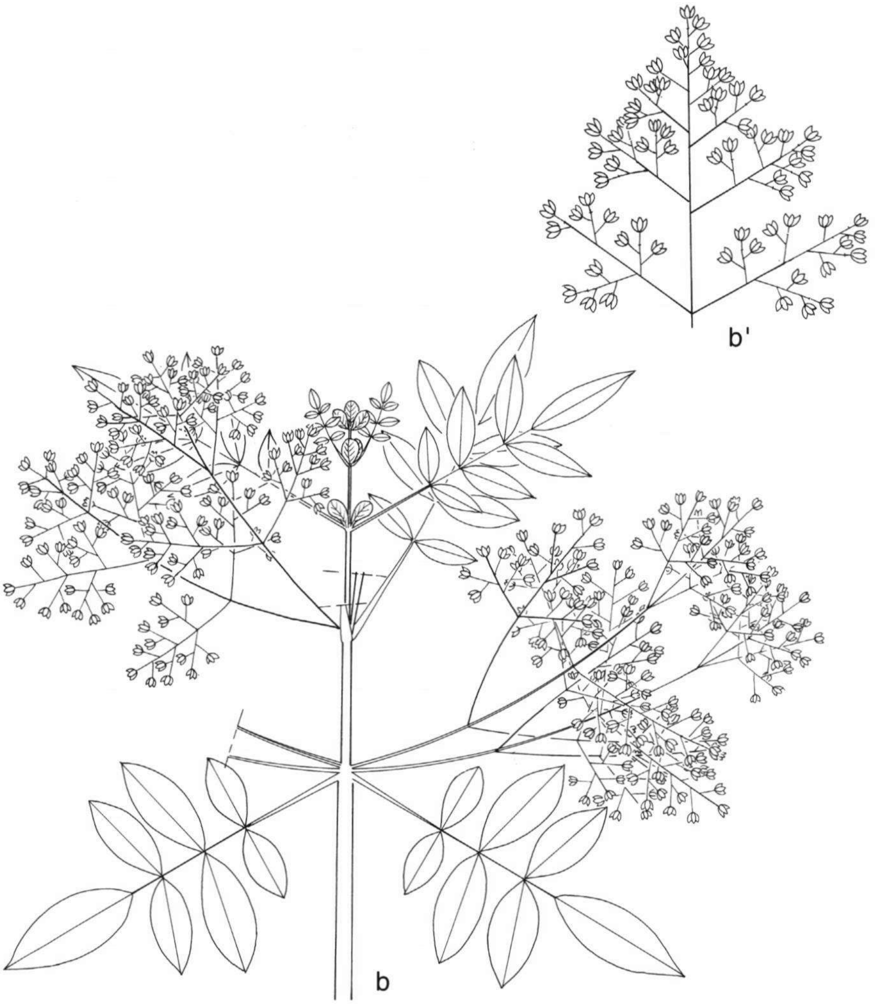

Fig. 4b & b'. *Gillbeea papuana*. – See the legend on page 67.

ing its growth; or 3) false-terminal, i.e. again developing in a median position, but the apical bud either aborts, remains dormant, or resumes vegetative growth during flowering.

Aistopetalum — Fig. 4c. The structure is unusual since opposite, decussate branching is usually retained throughout (Fig. 4c'). Generally a pair of opposite principal axes develop in the axils of the most distal pair of leaves and/or sometimes in subdistal leaf-axils. The apical bud of the shoot is usually dormant or occasionally aborted. At major nodes within the inflorescence, the median axis is slightly more dominant than the two lateral ones. In *A. multiflorum* the inflorescence has up to seven orders of branching and

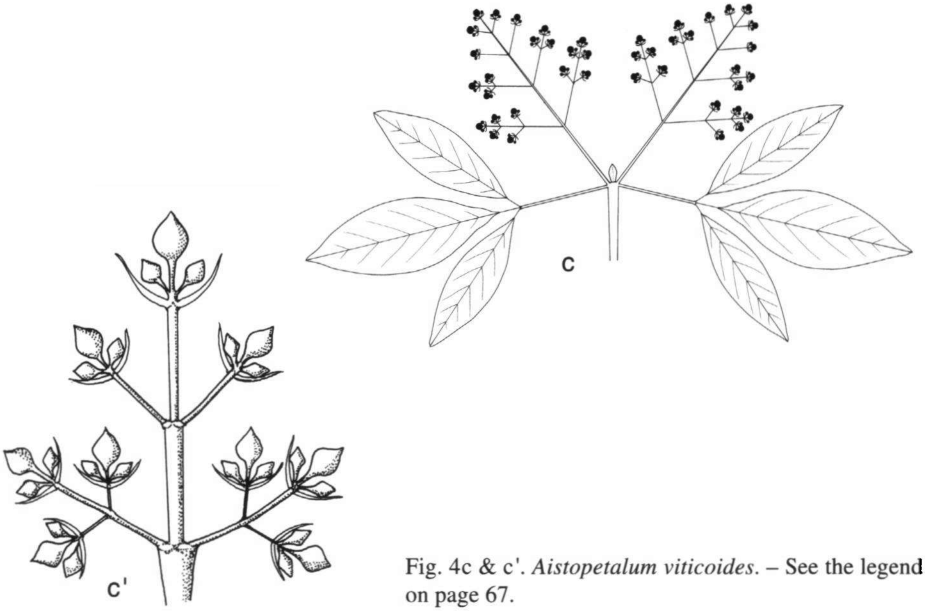

Fig. 4c & c'. *Aistopetalum viticoides*. – See the legend on page 67.

well developed articulations at nodes give a highly jointed appearance, while in *A. viticoides* it is little branched, with only c. 3 or 4 orders of branching, and the ultimate subunits are 3-flowered cymes.

Genera with more or less synchronous maturation of flowers

Opocunonia — Corymbose, the flat-topped form being due to the length and angle of insertion of the lower branches.

Acsmithia — Paniculate, the whorled phyllotaxis of the leaves continuing within the inflorescence at the proximal nodes, while branching at the peripheral nodes is ± alternate. Inflorescences can be axillary or terminal and they are usually smaller than in most other Malesian genera.

Spiraeanthemum — Paniculate, usually axillary, also sometimes terminal? Phyllotaxis follows the usual pattern, i.e. opposite towards the base and alternate to ± irregular distally.

Spiraeopsis — Paniculate, axillary. The flowers are shortly pedicellate to ± sessile, and inserted singly or in fascicles. In bud, caducous bracts subtend fascicles of flowers and each individual flower. Three features give a distinctive appearance in this genus:

1) Branching pattern switches from opposite and decussate to alternate more proximally than in most other genera.
2) Lateral axes are often ± at right angles to the median ones, rather than inserted with an acute acropetal angle.

3) After the change in phyllotaxis, the main sterile segments of the axes are usually strongly dominant and the lateral flower-bearing segments that arise from them are much less so, i.e. the flower-bearing axes are much shorter than the axis from which they arise, so that the inflorescence and each major subdivision within it is ± triangular in outline. In most other genera, the median axis at any node is only slightly more dominant than the lateral ones, so that each axis appears to branch ± equally into three at each node.

Pullea — This genus shows a gradation in inflorescence structure from a well-branched, fairly lax panicle with the flowers inserted ± singly along the most distal branches (some *P. glabra*, New Guinea and Fiji, Fig. 4d), through protocapitula with some or all of the flowers in glomerules at the ends of the axes (some *P. glabra*, especially New Guinea), to well developed spherical capitula terminating each distal axis and organised into complex units (*P. mollis*, New Guinea, Fig. 4e).

In *Pullea* the principal axes of the inflorescence are usually inserted in series in opposite leaf axils along a vegetative stem. In *Pullea mollis*, the principal axes typically consists of three metamers, where a metamer comprises an internode, the node at its distal end and the organs and meristems (buds) associated with that node. The basal metamer (M1) often has five axes (M2s) inserted at its distal end, a median axis and two pairs of lateral ones in series. The two outer M2s on each side terminate in a small, spherical capitulum of about 16 flowers, while the median M2 has three axes in series at its distal end (M3s), each of which terminates in a capitulum (see Fig. 4e). Thus the principal axis typically bears seven capitula in each of which the individual flowers are densely packed. These principal axes arise in the opposite axils of leaves at several successive subdistal nodes, and there are often up to three axes inserted in series per axil, the largest and best

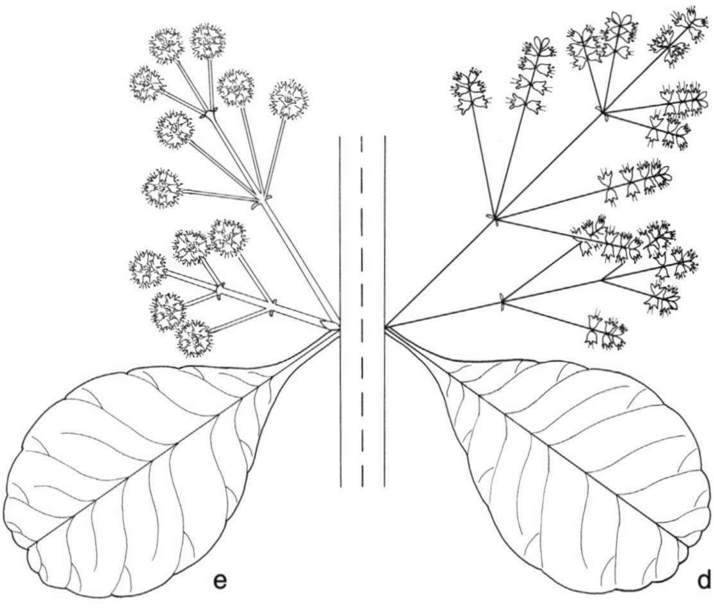

Fig. 4d & e. – d: *Pullea glabra*. – e: *Pullea mollis*. – See the legend on page 67.

developed being closest to the main stem. Occasionally there is an extra order of branching, resulting in a corresponding increase in the number of capitula, up to c. 25, and in *Hartley 12714* there is a large, dormant bud in a median position at the apex of the M1.

In *P. glabra*, the inflorescence has a similar structure but the axes are generally longer and more slender, giving a more lax appearance. In a typical principal axis (e.g. *Havel NGF 9128, Pullen 206*), the basal segment (M1) bears five or seven axes (M2s) at its apex, and the lateral M2s terminate in a cluster of flowers or glomerule. Frequently there are also a few flowers inserted singly along the distal part of the axis, and sometimes these M2s have short, slender side branches (M3s) bearing flowers. In all cases the individual flowers are easily distinguished, i.e. they are not densely packed. The median M2 is sterile and bears three (or five) M3 axes. The pattern of the previous node is repeated with the lateral M3s bearing flowers distally and the median one bearing three M4 axes which terminate in flowers. Where the median M2 bears five M3 axes, there may be an additional order of branching, but the pattern is the same (see Fig. 4d). As in *P. mollis*, two or three axes are usually inserted in series in opposite leaf axils, but while some small inflorescences are produced at subdistal nodes, the ones at the most distal node are often larger and better developed. Axes with the same structure as axillary ones are occasionally found in a terminal position (e.g. *Sayers NGF 21588*).

In the examples of *P. glabra* described so far, the branching is opposite except for the final insertion of the flowers, which is alternate. However, sometimes in well developed inflorescences the most distal lateral axes are alternate (e.g. *Sayers NGF 21588*). The general pattern of branching within the inflorecences of *P. glabra* var. *verticillata* is opposite, not verticillate. In *Pullea stutzeri* (F. Muell.) Gibbs from NE Queensland, the inflorescence is very similar to that of *P. glabra*, with the flowers in relatively loose glomerules though the bracts and 'stipules' are more persistent.

Although initially appearing unique amongst Malesian *Cunoniaceae*, this type of inflorescence is fairly closely related to those in other genera. For instance, a reduction in the number of orders of branching and the dispersal of the flowers along the axes would transform *Hartley 12714* (*P. mollis*), with a dormant median bud at the apex of the M1, into a similar structure to the partial inflorescences of *Weinmannia* sect. *Fasciculatae*. A reduction in the number of lateral axes per node (from four or six, to two) would transform the inflorescence in *Sayers NGF 21588* (*Pullea glabra* var. *verticillata*) to one similar to those of *Schizomeria*, as in both, distal branching is alternate, not opposite. A shift in the dominance of the axes would also modify the appearance of the inflorescence. In *Pullea*, the axes at any node are usually ± equally developed, the median one being only slightly longer than laterals, but occasionally lateral axes are shorter and less dominant than median ones, producing a resemblance to *Spiraeopsis*.

The inflorescence in *Pullea* could be derived from the supposed plesiomorphic type (a well-branched panicle or thyrse) by 1) multiplication of lateral axes at the basal nodes, 2) gradual suppression of the distal alternate origin of the flowers and their aggregation into lax protocapitula and then further aggregation into dense, spherical capitula, and 3) a shift in dominance of the axes arising at any node from median-one-most-dominant to dominance ± equal.

Outside Malesia, capitulate inflorescences also occur in *Codia* and *Pancheria* (New Caledonia) and *Callicoma* (Australia).

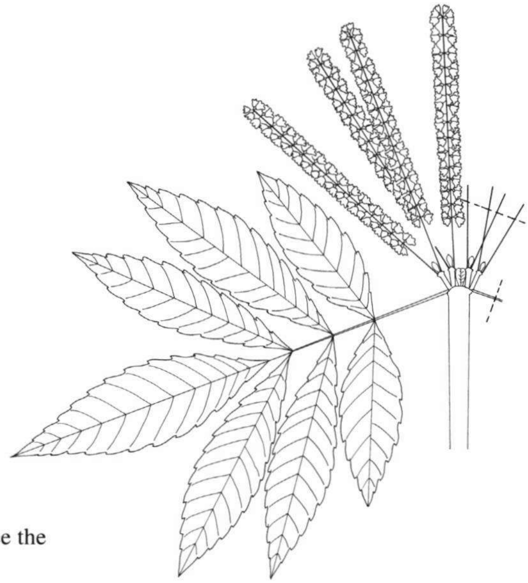

Fig. 4f. *Weinmannia fraxinea.* — See the legend on page 67.

Weinmannia — Fig. 4f. The flowers are arranged in racemes. In most species of *Weinmannia* outside America, these racemes are organised into complex units with a distinct and predictable structure, usually with one or more sterile stem sections (Bradford 1998; Hopkins & Bradford 1998), here referred to as partial inflorescences [PIs]. In section *Fasciculatae*, which contains the majority of the Malesian species, the racemes are usually in pairs or fours and borne on a sterile stem segment (M1) or 'peduncle' to form dyads or tetrads, and these inflorescence subunits or PIs typically develop from the axillary buds of the most distal pair of leaves; sometimes two or more PIs develop in series in a single axil and sometimes PIs also arise in subdistal axils. The apical bud of the shoot remains vegetative and is usually dormant during flowering (rare exceptions). The apical bud within each dyad or tetrad, at the distal end of the peduncle, is usually aborted or dormant (rare exceptions). Each dyad or tetrad consists of a single metamer.

In section *Leiospermum* the inflorescence usually develops in a median position from the apical bud of the shoot and so terminates its growth (exceptions in New Zealand) or the apical bud aborts (especially in New Caledonia), and the inflorescence subunits generally consist of two metamers. In *W. croftii*, the only Malesian species in sect. *Leiospermum*, the inflorescence is typical for the section, median in position, and usually a pentad, i.e. with five racemes (M1 bearing two racemes and a sterile M2, which itself bears three racemes, one in a terminal position and two laterals).

Outside Malesia, inflorescences composed of simple racemes or racemes organised into complex units occur in *Cunonia* (Hoogland et al. 1997; Bradford 1998), as well as *Geissois, Lamanonia, Pseudoweinmannia* and *Vesselowskya.*

Flowers

In Malesia, the calyx, corolla when present, androecium and disc usually show the same merosity as one another, typically 4–5 but varying from 3–7. The number of carpels forming the gynoecium is typically 2 but sometimes 3–8 in Malesia (and up to 14 or rarely 18 in *Eucryphia*; Bausch 1938; Dickison 1978).

The calyx arises from a hypanthium which varies from very short to cone- or cup-shaped. The calyx lobes are sometimes shortly connate at the base and they are often hirsute on the outer surface and/or hirsute on the inner one also. They are sometimes persistent, and sometimes enlarged in fruit (e.g. *Ceratopetalum*).

A corolla of free petals is uniformly present in some genera, absent in others, and variable in occurrence in *Ceratopetalum*. In Malesia, the petals are quite small, often membranous and rather inconspicuous, usually ovate, obovate or spathulate, sometimes ciliolate, and sometimes toothed (*Schizomeria, Gillbeea*), the teeth being glandular in *Gillbeea*.

The stamens are twice as many as the calyx lobes in all the Malesian species and inserted in a single series (see Dickison 1989, f. 4.1D). Outside Malesia, stamens may be equal to the number of calyx lobes (in some species of *Weinmannia* and *Cunonia*), few but irregular in number [*Acsmithia austro-caledonica* (Brongn. & Gris) Hoogland] or numerous (in several genera including *Geissois, Lamanonia, Pseudoweinmannia, Eucryphia, Bauera*), described as complex polyandry by Ronse Decraene & Smets (1992), and sometimes inserted in more than a single series. The filaments are typically long, thin or sometimes fleshy, and subulate, usually shortly exserted beyond the perianth (occasionally far exserted, in some *Geissois* and some *Cunonia*, or included in *Davidsonia*). The anthers are small, the base is often incised and the apex rounded, emarginate or apiculate with an extended connective. The anthers of several genera of *Cunoniaceae* were illustrated by Endress & Stumpf (1991).

The disc is somewhat variable. Where it consists of free lobes, their number is usually equal to the number of filaments (e.g. *Weinmannia* in Malesia). Sometimes it is a continuous but deeply lobed ring, the indentations corresponding to the bases of the filaments. In these cases, the lobes are often paired and more united with the adjacent lobe on one side than on the other (e.g. in some *Schizomeria* and male flowers of *Spiraeanthemum*). If the incision between the lobes is not deep, the bases of the filaments are impressed. Entire or slightly indented toral discs occur in several genera, either as a fleshy, free ring (*Gillbeea*), as a fleshy ring, strongly adpressed to the gynoecium (*Aistopetalum*), or attached to the upper surface of the ovary (*Ceratopetalum*). In *Lamanonia* (South America), the disc is indistinct and visible only as a ring of darkened tissue at the base of the ovary.

The gynoecium is apocarpous in *Acsmithia* and *Spiraeanthemum* though the carpels are slightly adaxially connate at the base (Hoogland 1979, f. 2; Dickison 1989, f. 4.1C). In the Australian shrub *Acrophyllum* the carpels appear at least sometimes to be strongly adpressed rather than fused. In New Caledonia, the endemic genus *Pancheria* also has an apocarpous ovary.

Where the gynoecium is syncarpous, the carpels are united at the level of the ovary, and each carpel is surmounted by a free style or stylulus. In some genera with syncarpous ovaries, the number of carpels is clearly visible from suture lines on the ovary wall (e.g. *Weinmannia*); in others, the suture lines are not visible (e.g. *Schizomeria*). Semi-inferior ovaries occur in *Ceratopetalum* and *Pullea*, and in *Schizomeria* there is a slight tendency towards a partially inferior ovary in some species. The styles are usually long, filiform and furrowed on the adaxial side or rarely short, thick and adpressed (*Aistopetalum*).

Stigmas are generally small and terminal, sometimes clavate (e.g. *Acsmithia, Gillbeea, Spiraeanthemum, Weinmannia*) and papillate, though there is variation in shape and distribution of papillae (illustrated in Dickison 1989). Outside Malesia, decurrent stigmas occur in *Vesselowskya* (Dickison 1989, f. 4.3E).

The ovules are typically bitegmic, crassinucellate and anatropous, though occasionally hemitropous or campylotropous (Cronquist 1981), usually apotropous but reported as epitropous in *Acsmithia, Davidsonia, Eucryphia* and *Spiraeanthemum*, as they are in *Brunellia* (Bange 1952; Cuatrecasas 1970; Cronquist 1981; Smith 1985; Dickison 1989). The embryology of *Weinmannia fraxinea* was described by Govil & Saxena (1976).

Fruits and seeds

Fruits and seeds of *Cunoniaceae* were reviewed by Dickison (1984). Fruit type is rather uniform within each genus and genera can thus be divided into those with dehiscent or indehiscent fruits, and about half the Malesian genera fall into each category. Fruits of *Cunoniaceae* are generally small, especially the capsular ones, and the largest fruits in Malesia are found in *Schizomeria*, whose drupes can be up to 5 cm diameter. The typological categories of Spjut (1994) have been employed here as useful short-hand terms although they tend to emphasise differences between rather similar structures and may thus mask relationships between them.

Dehiscent fruits — These are derived from either apocarpous or syncarpous ovaries. Those developing from the apocarpous ovaries of *Acsmithia* and *Spiraeanthemum* have 2–5 carpels, each dehiscing along its adaxial suture. The term follicle has usually been applied to each of these fruitlets (Hoogland 1979; Dickison 1984), though strictly speaking this term applies to a simple fruit, and follicetum better describes this type of multiple fruit (see Spjut 1994). Spjut (1994: 75) cited *Spiraeanthemum* as an example of a follicarium, but apparently based on false information about the styles, which are free and not united in the flowering stage.

In Malesia, dehiscent fruits developing from syncarpous ovaries are found in *Weinmannia, Spiraeopsis* and *Opocunonia*. The capsules of *Weinmannia* often have a central column arising from the base of the fruit and which is free from the valves after dehiscence, and they are thus septifragal. This column appears to be derived from the placentae and vasculature and in some cases this tissue remains attached to the margins of the valves. Variation depends partly upon taxonomic group, and the column is more strongly developed in sect. *Leiospermum* (e.g. Godley 1983, f. 3) than in sect. *Fasciculatae*. Occasionally there is no sign of central column remnants, in which case 'septicidal capsule' would be the correct term. Similar capsules occur in *Opocunonia nymanii* where a central column is absent or represented only by a few weak strands of tissue. This is in contrast to *Spiraeopsis* in which the margins of the valves often form a persistent 'replum', which is free from the valves at the base but attached to the free margin of the adjacent valve, then entirely free distally, and finally attached to the persistent style at the apex of the valve (see Fig. 27). Similar structures are seen in *Caldcluvia* s. s. (Godley 1983, f. 2). The presence of replum makes this fruit a ceratium although the placentation is not parietal as is usual in ceratia. Other forms of dehiscent fruits occur outside Malesia in *Cunonia, Bauera, Eucryphia* and *Anodopetalum* (Dickison 1984; Barnes & Rozefelds 2000).

The seeds in dehiscent fruits are generally winged (most genera) or hairy (*Weinmannia, Ackama*; see Webb & Simpson 1991), with the exception of *Acrophyllum* (Dickison 1984) and *Anodopetalum* (Barnes & Rozefelds 2000). In winged seeds the wing may be terminal or at both ends (rarely all round the seed, *Geissois hirsuta* Brongn. & Gris, New Caledonia). Hairy seeds occur in *Ackama* and throughout *Weinmannia* where typically there is a tuft of hairs at either end of the seed (comose) or occasionally the hairs are distributed all over the surface. The surface of the seeds may be smooth or variously sculptured appearing striate, warty or papillate in scanning electron micrographs (Dickison 1984).

Indehiscent fruits — These are found in five Malesian genera. Drupes occur in *Schizomeria* and *Aistopetalum*, the pericarp being fleshy to rather fibrous or coarsely farinaceous. The endocarps in *Schizomeria* vary from deeply and irregularly sculptured with resinous vacuoles to unsculptured with a rough surface, especially in the species with smaller fruits. In *Aistopetalum*, the endocarp is stoney with a rough surface and faint lines where the carpels are fused (*A. multiflorum, Streiman LAE 51814*).

The fruit in *Gillbeea* is a samara, with wings developing from the wall of the ovary, while the fruits of *Ceratopetalum* are pseudosamaras, the 'helicopter' wings being the spreading, elongated calyx lobes.

The fruits of *Pullea* have proved difficult to define. When mature they appear little changed from the ovary at the flowering stage except that the chartaceous calyx lobes are slightly enlarged and the styles are elongated, stiff and diverging. This structure was described by Dickison (1984) as an indehiscent capsule and it is not very different from an undehisced capsule of *Weinmannia*. Smith (1985: 23) described it as "drupaceous, probably becoming a tardily dehiscent capsule ..., containing 2 collateral pyrenes, these flattened ovoid, the endocarp cartilaginous or crustaceous" but I have found no evidence of dehiscence. In Spjut's terminology, it is probably a carcerulus since the pericarp does not adhere to the several, small seeds. The calyx lobes are usually more enlarged in a pseudosamara.

Outside Malesia various other types of indehiscent fruits occur, for example in *Platylophus, Pseudoweinmannia* and *Codia*.

The surface of the seeds in indehiscent fruits may be smooth (e.g. *Pseudoweinmannia*), reticulate (*Pullea, Codia*), papillate (*Gillbeea*) (Dickison 1984) or striate (*Schizomeria*) (Barnes & Rozefelds 2000).

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REPRODUCTIVE BIOLOGY

Floral biology and pollination — Most genera in Malesia have small to very small, dish- or bowl-shaped flowers massed into showy inflorescences, and they are generally pale (white, cream, pinkish, greenish, or yellowish) to red or purple (some species of *Spiraeopsis*). Scent is reported as pleasant or absent, or occasionally musty. Visual attraction is provided by the perianth, the shortly exserted stamens, sometimes by the disc, and in *Gillbeea*, perhaps also by the glistening, secretory glands on the petals (Endress 1994). At least sometimes the disc is nectariferous.

Non-restrictive flowers of this sort fit into a general pattern of generalised entomophily, and pollinators are likely to be short-tongued social bees and a variety of other promiscuous insects and perhaps some vertebrates. Within Malesia there have been no detailed field studies and rather little information is available. For *Weinmannia*, herbarium labels occasionally report bees visiting flowers (e.g. *Weinmannia furfuracea, Tantra 1595*, Sulawesi), and beetles and flies have also been observed (at *W. fraxinea* '*dulitensis*', Pig Hill, Sabah, Hopkins & Bradford, pers. obs., 1996). In the same genus outside Malesia, honey-producing bees and the Parsonbird (*Meliphagidae: Prosthemadera novaeseelandiae*) visit the flowers of *W. racemosa* in New Zealand (Wardle 1966), and halictid and meliponine bees and syrphid flies take nectar from the pale pink flowers of *W. velutina* O.C. Schmidt in Venezuela (Renner 1989). The flowers of *Spiraeopsis celebica* in New Guinea attract numerous beetles (*Vink 16874*) and for *Opocunonia nymanii, Schodde 5673* (Efogi, Central Distr., 1300 m, secondary growth on ridge) says that floral nectar is sought by the following birds: *Myzomela rosenbergii, M. cruentata, Oedistoma pygmaeum* and *Melidectes torquatus*, which are all members of the Australo-Pacific family of Honeyeaters, the *Meliphagidae*.

Some extra-Malesian genera show a greater range in the form and colour of the flowers and the structure of the inflorescence, and a range of floral visitors has been reported. For instance *Cunonia capensis* L. and *Platylophus trifoliatus* (Thunb.) D. Don in South Africa are visited by various bees, *Lepidoptera* and nectar-feeding birds (Phillips 1926), and in the SW Pacific, ornithophily has been reported for the bright red, bottle-brush inflorescences of *Geissois* (Hoogland, unpublished notes; Wheatley 1992). The flowers are again non-restrictive and reported to attract insects (e.g. bees, *MacKee 46128*), pteropodid bats (e.g. *MacKee 44393*) and geckos (Bavay 1869; S. Zona, pers. comm.). Capitulate inflorescences are found in *Pullea*, *Codia* and *Pancheria* (both New Caledonia) and *Callicoma* (Australia) but as yet their pollinators are unknown. Large, white, showy petals are found in *Eucryphia* (Australia and Chile), whose flowers are visited by honey-producing bees (Barnsley 1983), and small, magenta or white petals occur in *Bauera* (Australia and Tasmania).

There is some circumstantial evidence for anemophily in the dioecious genus *Vesselowskya* (Australia), which has catkin-like inflorescences and decurrent stigmas, but experimental studies are lacking.

Sexual expression — The majority of genera have bisexual, homogamous flowers. In Malesia, dioecy occurs in *Spiraeanthemum* (all species dioecious), but not in its sister taxon *Acsmithia*, and in most species of *Weinmannia*. Polygamodioecy (= subandroecy), including rare evidence of gender lability, and monoecy occur occasionally in Malesian *Weinmannia*, and a few species have bisexual flowers. Sexual expression is complex in *W. fraxinea* where male, female and bisexual flowers are recorded in different proportions in different populations (Hopkins 1998). In the Pacific, polygamodioecy, including temporal changes in sexual expression, occurs in several species, but outside the Malesian-Pacific region, almost all species of *Weinmannia* have morphologically bisexual flowers (Bradford 1998). Other dioecious genera include *Pancheria* and *Vesselowskya*.

Andromonoecy, with male and bisexual flowers in the same inflorescence, occurs in at least some species of *Schizomeria*, and is perhaps to be expected where a few relatively large fruits develop from an inflorescence composed of many small flowers.

Dicliny occurs in the tribe *Caldcluvieae* which shows strong protandry in *Spiraeopsis*, *Opocunonia* and perhaps *Ackama*, though not in *Caldcluvia* s.s. There may sometimes be a slight degree of protandry in some specimens of *Weinmannia* (Smith 1985) and in *Pullea*. In the latter, the styles are sometimes quite short at the time of anther dehiscence, and later they become longer, stiff and outcurving. The time of stigmatic receptivity is not known.

Dispersal — Morphology and anecdotal information suggest that anemochory is the dominant mode of dispersal in the family and there is a range of specialised structures (Dickison 1984, 1989).

In genera with dry, indehiscent fruits (*Ceratopetalum*, *Gillbeea* and *Pullea* in Malesia) the fruit is the unit of dispersal. In those with dehiscent fruits (*Acsmithia*, *Opocunonia*, *Spiraeanthemum*, *Spiraeopsis* and *Weinmannia*), the small, light seeds are the units of dispersal, whether winged (most genera) or hairy (*Weinmannia*). Besides the possibility of anemochory, exozoochory on the feet of birds has been proposed for the seeds of *Weinmannia* (see Florence 1982) and *Cunonia capensis* L. (Coates Palgrave 1970), but field observations appear to be lacking and there are no fleshy structures to attract birds to the fruits.

In Malesia, the indehiscent, fleshy, whitish or brownish drupes of *Schizomeria* are dispersed by bats, arboreal marsupials and birds, including terrestrial flightless cassowaries (Rumphius 1755, under *Arbor vespertilionum*; Pratt 1983; D. Wright, pers. comm.). I have found no data on dispersal in *Aistopetalum*, the only other genus in Malesia with drupes, although the fleshy, purple fruits of *Davidsonia pruriens* F. Muell. from Australia are eaten by cassowaries (Crome 1976; Stocker & Irvine 1983).

Outside Malesia, other mechanisms of dispersal have been reported. In Australia, the densely hairy, indehiscent fruits of *Pseudoweinmannia* are considered anemochorous and the seeds may be secondarily dispersed by ants since they have elaiosomes, while in South Africa the inflated, indehiscent fruits of *Platylophus* are probably dispersed by flowing water, as well as being consumed by pigs and birds (Coates Palgrave 1977; Dickison 1984).

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CYTOLOGY

No counts are given for any Malesian taxa in the various indices of plant chromosome numbers. For taxa outside our region, 2n = 32 has been reported in several genera [*Ackama rosifolia* A. Cunn., *Bauera rubioides* Andrews, *Ceratopetalum gummiferum* Sm., *Cunonia capensis* L., *Geissois pruinosa* Brongn. & Gris and *Lamanonia speciosa* (Cambess.) L.B. Sm. (= *L. ternata* Vell.); Smith-White in Darlington & Wylie 1955; Hair & Beuzenberg 1960; Hamel 1961; Guillaumin & Hamel 1963; Gadella et al. 1969], 2n = 30 for *Weinmannia racemosa* L.f. and *W. sylvicola* Sol. ex A. Cunn. (Hair & Beuzenberg 1960) and *Eucryphia lucida* (Labill.) Baill. (Goldblatt 1976), and 2n = 24 for *Pancheria sebertii* Guillaumin (Hamel 1952). In the related *Brunelliaceae*, 2n = 28 occurs in *Brunellia comocladiifolia* Humb. & Bonpl., *B. mexicana* Standl. and *B. sibundoya* Cuatrec. (Ehrendorfer et al. 1984; Orozco 1991).

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PALYNOLOGY

(J. Muller†, updated by R.W. Barnes)

Pollen grains are small (10–13 µm), generally tricolporate (*Cunonia, Opocunonia, Spiraeanthemum, Weinmannia*) and dicolp(or)ate (*Ceratopetalum, Geissois, Pullea, Schizomeria*) but syncolpate in *Gillbeea*. Shape may vary from suboblate to subprolate, generally with a circular equatorial outline, but sometimes dicolp(or)ate grains are bilaterally flattened (*Ceratopetalum, Schizomeria*). Only *Cunonia capensis* has oblate, angulaperturate grains which differ markedly from the normal suboblate grains with a circular outline found in the New Caledonian species of *Cunonia*.

Ectoapertures are colpate (except *Gillbeea*) or indistinct, as in *Pullea*. Endoapertures vary in Malesian taxa from indistinct or simply constructed (*Ceratopetalum, Pullea, Schizomeria*) to simple-complex/complex (*Aistopetalum, Opocunonia, Spiraeanthemum, Spiraeopsis, Weinmannia*).

Tectum sculpture in Malesian taxa varies from uniformly perforate (homogeneous) or finely reticulate (*Opocunonia, Pullea, Spiraeopsis*, some *Weinmannia*) to partial and coarsely reticulate (heterogeneous) in the centre of the mesocolpia (*Ceratopetalum, Gillbeea*, some *Schizomeria*) (Hideux & Ferguson 1976). In some genera the sculpture in the centre of the mesocolpia tends towards rugulate (*Schizomeria*).

Reference: Hideux, M. J. & I. K. Ferguson, pp. 327–377 in I. K. Ferguson & J. Muller (eds.), The evolutionary significance of the exine. Linn. Soc. Symp. Series 1, Great Britain (1976).

PHYTOCHEMISTRY

(R. Hegnauer)

For a long time *Cunoniaceae* were badly neglected by phytochemists. In 1964 only a few chemical tendencies could be mentioned for the family; these referred to the production of flavonols in leaves, of proanthocyanidins (formerly called leucoanthocyanidins) and related condensed tannins in leaves and barks, to the storage of rather large amounts of aluminium in leaves and to the deposition of mucilage in leaves (see Hegnauer 1964).

A more comprehensive chemotaxonomic study of *Cunoniaceae*, including *Baueraceae* and *Davidsoniaceae*, was published by Bate-Smith (1977), and was essentially based on leaf phenolics; as a whole the family is rather uniform in this respect. Most species contain much tannin in the leaves, together with glycosides of kaemferol and quercetin. Tannins are mostly based on procyanidins and (or) ellagic acid. The flavonoids with a trihydroxylated B-ring, prodelphinidins and myricetin, occur only exceptionally in *Cunoniaceae*; appreciable amounts of myricetin were only observed in *Ceratopetalum apetalum* D. Don and *Weinmannia organensis* Gardner and large amounts occur in leaves of *Bauera rubioides* Andrews and *Davidsonia pruriens* F. Muell. '*Ackama paniculata* (F. Muell.) Engl.' [nom. illeg. = *Ackama paniculosa* (F. Muell.) Beuzev. & C.T.White)] and *Bauera rubioides* contain proanthocyanidins which on acid treatment generate a compound which was formerly confused with delphinidin (e.g. Jay 1968). The correction of this error is taxonomically important because most research workers in the field of chemotaxonomy attach much importance to characters such as 'presence' or 'absence' of prodelphinidin. Presence of flavonoids with a trihydroxylated B-ring (i.e. prodelphinidins and myricetin) is interpreted as an evolutionarily very primitive character. A higher level is supposed to be represented by taxa which have trihydroxylation only in their hydrolizable tannins which are based on gallic and ellagic acid. The highest level of evolution with regard to this class of plant phenolics is supposed to be represented by plants which do not produce flavonoids with a trihydroxylated B-ring and which at the same time lack tannins. In the *Cunoniaceae* mainly the second of these three levels is represented.

According to Bate-Smith (1977) the chemotaxonomic characters of *Cunoniaceae* suggested a position in the rosalean assemblage, and he mentioned chemical similarities between *Cunoniaceae* and the genus *Ribes*. The presence of azaleatin (= 5-methyl quercetin) in a few *Cunoniaceae* and in some species of *Eucryphia* indicated a chemical link between these two groups which is now supported by phylogenetic analyses (see Taxonomy and Phylogeny). An interesting feature of some species of *Cunoniaceae* is the presence of ellagitannins based on mono- and di-0-methylellagic acids; such tannins are very widespread in the *Myrtales*.

Bate-Smith investigated about 50 species of *Cunoniaceae* representing a wide sample of genera and tribes; based on the pattern of leaf phenolics he regarded the genus *Ceratopetalum* as the most primitive since it lacks ellagitannins and contains both myretin and prodelphinidin.

A recent study of leaf and bud exudates discussed relationships in *Eucryphia* based on the distribution of 28 flavonoids (Wollenweber et al. 2000).

References: Bate-Smith, E.C., Biochem. Syst. Ecol. 5 (1977) 95–105. — Hegnauer, R., Chemotaxonomie der Pflanzen 3 (1964) 625–628. — Jay, M., Taxon 17 (1968) 489–495. — Wollenweber, E., M. Dörr, A.C. Rozefelds, P. Minchin & P.I. Forster, Biochem. Syst. Ecol. 28 (2000) 111–118.

WOOD ANATOMY

(P. Baas)

Detailed studies by Dickison (1977, 1980) and Ingle & Dadswell (1956) were recently summarised by Cutler & Gregory (1998). Below the most salient features for the Malesian genera – as far as ever studied in wood anatomical detail – are abstracted from these sources.

Growth rings are absent or poorly defined. The wood is diffuse porous with vessels solitary and in radial multipes (almost exclusively solitary in *Acsmithia, Spiraeanthemum* and *Weinmannia*). The perforations are exclusively scalariform in *Acsmithia, Gillbeea, Pullea, Spiraeanthemum* and *Weinmannia* p.p., and mixed simple and scalariform (in varying proportions) in the remaining taxa. Intervessel pitting is often scalariform to opposite in taxa with exclusively scalariform perforations, but opposite to alternate in woods with predominantly simple perforations. The vessel-ray pits are coarse and scalariform to opposite. The fibres are typically (fairly) thick-walled, nonseptate, and have distinctly bordered pits, except in *Aistopetalum, Ceratopetalum, Gillbeea, Schizomeria* and *Spiraeopsis* where the pit borders are (strongly) reduced and usually confined to the radial walls. Septate fibres have been reported for *Weinmannia*. Axial parenchyma is mainly diffuse, diffuse-in-aggregates and scanty paratracheal. *Aistopetalum* and *Ceratopetalum* have banded parenchyma in addition.The rays are both uni- and multiseriate and heterocellular. Sheath cells have been recorded in *Pullea*. Prismatic crystals are frequently present in chambered axial parenchyma cells.

This wood anatomical syndrome supports earlier views of close phylogenetic relationships between *Cunoniaceae* and *Eucryphiaceae* & *Davidsoniaceae* (from Takhtajan's *Cunoniales*). Recent molecular analyses include *Davidsoniaceae* and *Eucryphiaceae* in the *Cunoniaceae*, and are thus in agreement with wood anatomical evidence (Savolainen et al. 2000). The wider molecular affinities of *Cunoniaceae* in the newly delimited *Oxalidales* with *Brunelliaceae, Cephalotaceae, Connaraceae, Elaeocarpaceae* and *Oxalidaceae* are not clearly supported by wood anatomical synapomorphies.

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USES

Timber — A number of species in Australia and New Zealand are used for construction purposes or in particular for furniture, cabinet work and turnery, and several of the larger tree species in New Guinea are also considered promising. Within Malesia, *Ceratopetalum, Schizomeria* and *Weinmannia* are discussed by Dickison (1998, q.v. for details and references) as lesser known timbers. *Ceratopetalum succirubrum* and *Schizomeria* species are both used in furniture making and cabinet work, for interior finishes and house building, and the timber is also considered suitable for plywood and packing cases (Dickison 1998). Small quantities of logs of both genera are exported from Papua New Guinea. In Australia, *Schizomeria ovata* D. Don is traded domestically but is less valuable than *Ceratopetalum apetalum* D. Don known as coachwood. The timber of *Weinmannia* species (mostly *W. fraxinea*) is used in house construction as poles and beams, and for utility furniture and house interiors but on a local scale only (Heyne 1950; Dickison 1998). In Papua New Guinea, the timber of *Spiraeopsis*, including *S. celebica*, is used locally for building in the Chimbu and Jimi regions, and *Schizomeria* is used, again in Chimbu, as rope for construction and timber for building (Powell 1976).

Other uses — In Ambon, the bark of *Weinmannia fraxinea* (as *W. sundana*) is dried and stored in bundles, then used to colour papéda, a porridge made from sago, during cooking or to improve the flavour of old sago, while *Schizomeria serrata* is used for tanning fishnets (Heyne 1950). In the Philippines the bark of *Weinmannia luzoniensis* is also used in tanning (Brown 1954). *Pullea glabra* is used in the Chimbu region of Papua New Guinea for making tools and weapons, and in personal adornment, although details are not given (Powell 1976).

Outside Malesia the flowers of *Eucryphia, Platylophus* and *Weinmannia* are visited by bees from whose nests honey is obtained (e.g. Wardle 1966; Coates Palgrave 1977; Barnsley 1983), sometimes on a commercial scale.

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PALAEOBOTANY

(R.W. Barnes)

No macro- or microfossils of *Cunoniaceae* have been recorded from Malesia although they have been documented from Australia, New Zealand, Antarctica, North and South America and Europe.

Macrofossils

Eleven genera are represented as macrofossils in Australian Cainozoic sediments (Barnes et al. 2001), of which 5 genera are extant in Malesia (*Acsmithia, Ceratopetalum, Schizomeria, Spiraeanthemum/Acsmithia, Weinmannia*). The extinct species *Acsmithia grandiflora* R.J. Carp. & A.M.M. Buchan. and *Schizomeria tasmaniensis* R.J. Carp. & A.M.M. Buchan. are represented by Early Oligocene (Cethana) flower compressions in Tasmania (Carpenter & Buchanan 1993). *Ceratopetalum* is represented by 4 fossil fruit species located within different deposits aged between Middle Eocene and late Early–Late Miocene in Australia (Barnes & Hill 1999a; Holmes & Holmes 1992).

A coalified compression of an imparipinnate *Weinmannia* leaf has been recorded from the Early Oligocene (Wilson's Creek) of Central Tasmania (Barnes et al. 2001). Early Oligocene (Cethana) leaf impressions in Tasmania with affinities to some *Weinmannia* and *Cunonia* have been described as a single taxon within the fossil genus *Weinmanniaphyllum, W. bernardii* R.J. Carp. & A.M.M. Buchan. (Carpenter & Buchanan 1993). Dispersed foliar cuticle identified as *Spiraeanthemum/Acsmithia* has been recovered from 2 cores of the Pidinga Formation (aged at late Middle Eocene, and late Middle Eocene to early Late Eocene) in Western Australia (Barnes et al. 2001; Carpenter & Pole 1995).

Incomplete leaf (?stipule) macrofossils from near the Antarctic Peninsula (Early Tertiary) assigned to the fossil taxon *Caldcluvia mirabilis* Dusén (Dusén 1908; Czajkowski & Rosler 1986) have been re-assigned to *Lomatia mirabilis* (*Proteaceae*) (Li 1994). Cainozoic fossil wood of *Caldcluvioxylon* (e.g. Shanzhen & Qingzhi 1994) and *Weinmannioxylon* (Petriella 1972; Petriella & Archangelsky 1975; Rancusi et al. 1987) has been recorded from Antarctica, although their exact taxonomic relationship to extant *Caldcluvia* (and related genera *Ackama, Opocunonia* and *Spiraeopsis*) and *Weinmannia* is unresolved. More recent fossil wood identifications include *Weinmannioxylon eucryphioides* from Eocene sediments at King George Island (Poole et al. 2001) which has strong affinities to *Eucryphia*, and two *Weinmannioxylon* species from Late Cretaceous sediments in Antarctica (Poole et al. 2000; Poole & Cantrill 2001). Two species of the fossil genus *Cunonioxylon* have been described from European Tertiary sediments. *Cunonioxylon weinmannioides* (Oligocene of Austria) has affinities to *Weinmannia* (Hoffman 1952) while Gottwald (1992) directly compared *C. parenchymatosum* (Eocene of Lower Saxony in Germany) to wood of extant *Cunonia*. There is significant taxonomic confusion generated by *Cunoniaceae* fossil wood identifications as a single genus may contain species with affinities to several extant genera. On this basis, *Cunoniaceae* fossil wood species should not be considered to represent extant genera. Late Pleistocene lacustrine sediments from Ecuadorian Amazonia have yielded fossil wood of the *Weinmannia*-type, although these may equally represent *Symplocos* or *Laplacea* (Bush et al. 1990).

There is no documented macrofossil record for the remaining Malesian genera (*Aistopetalum, Gillbeea, Opocunonia, Pullea, Spiraeopsis*). Some non-Malesian extant taxa including *Anodopetalum, Callicoma, Codia, Bauera, Eucryphia* and *Vesselowskya* have an often extensive macrofossil record in Australia (e.g. Hill 1991; Carpenter & Buchanan 1993; Barnes & Hill 1999a, 1999b; Barnes & Jordan 2000; Barnes et al. 2001). The macrofossils of vegetative organs of *Weinmannia, Callicoma* and *Cunonia* from Europe and North America have generally been reassigned to other families (e.g. Givulescu & Rüffle 1971; Mai 1995). A Late Cretaceous fossil flower from Sweden has been assigned to a fossil genus within *Cunoniaceae, Platydiscus* Schonenberger & Friis (Schonenberger et al. 2001).

Microfossils

Cunoniaceae fossil pollen has been recorded from all southern hemisphere continental landmasses except Africa. Fossil *Cunoniaceae* pollen is temporally widespread with records dating throughout the Cainozoic (e.g. Cranwell 1959; Stover & Partridge 1973; Petriella & Archangelsky 1975; Luly et al. 1980; Hill & Macphail 1983; Truswell et al. 1985; Sluiter 1991; Macphail et al. 1995). Quaternary records are common (Dodson 1978; McGlone & Bathgate 1983; Kershaw 1985; Markgraf et al. 1986; Colhoun & Van de Geer 1986; Colhoun et al. 1989), especially in South America (e.g. Heusser 1964; Schreve-Brinkman 1978; Van der Hammen et al. 1980; Villagran 1988; Bush et al. 1990; Van der Hammen & Absy 1994; Hansen et al. 1994; Heusser et al. 1996).

The occurrence and relative abundance of *Cunoniaceae* fossil pollen has been used to interpret vegetation history (Villagran 1988; Bush et al. 1990; Sluiter 1991), regional extinctions (Hill & Macphail 1983), plant migration and dispersal (Truswell et al. 1987) and glacial events (Heusser 1964; Helmens & Kuhry 1986; Hooghiemstra 1989; Heusser et al. 1996).

Specifically, the fossil pollen taxon *Concolpites leptos* represents *Gillbeea* (Stover & Partridge 1973) and has been recovered from sediments in Santa Cruz Province (Eocene), Argentina (Romero & Castro 1986), and the Gippsland Basin (Eocene to Early Oligocene), Australia (Stover & Partridge 1973). Late Paleocene *Cunoniaceae* pollen has been recovered from Seymour Island (cf. *Weinmannia*, Cranwell 1959) and Argentina (*Rhoipites* sp. aff. *Weinmannia*, Petriella & Archangelsky 1975).

Weinmannia fossil pollen records are particularly abundant and have been made from New Zealand (Late Oligocene, Pocknall 1982; Quaternary, McGlone 1983; McGlone & Bathgate 1983; Mildenhall 1994), Chile (Quaternary, Godley & Moar 1973; Heusser 1974; Villagran 1988) and Colombia (Upper Pliocene, Hooghiemstra 1989; Quaternary, Schreve-Brinkman 1978; Hooghiemstra & Ran 1994; Van der Hammen et al. 1980).

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PLANT GEOGRAPHY

While *Cunoniaceae* is a relatively small component of the Malesian flora, eastern Malesia and especially New Guinea are important regions for the diversity of the family. All genera recorded from Malesia occur on the island of New Guinea with the exception of *Spiraeanthemum* (New Britain and New Ireland eastwards). *Aistopetalum* (2 species, New Guinea mainland) and *Opocunonia* (1 species, New Guinea and New Britain) are endemic.

All the Malesian genera are confined to the SW Pacific and eastern Australia except for *Weinmannia*. As several Malesian genera also occur in Australia, it is remarkable that *Weinmannia*, though found in New Caledonia and New Zealand, is unknown from the present-day flora of Australia, all species previously recorded now being placed in other genera. Generic distribution maps for *Acsmithia, Caldcluvia* s.l., *Geissois, Pullea* and *Spiraeanthemum* were provided by Hoogland (1984), and some preliminary species maps were given in Hoogland (1972), in the context of phytogeographical relationships between New Guinea and Australia. Distribution maps are provided here for all species except those in *Weinmannia* (see Hopkins 1998) and *Schizomeria* (Hopkins, in prep.) and for *Spiraeanthemum.*

Most Malesian species are endemic to the region. Those that are not are: *Weinmannia fraxinea* (also in the Solomon Islands), *Schizomeria serrata* and *S. ilicina* (Solomons), *Ceratopetalum succirubrum* (Australia), *Spiraeanthemum macgillivrayi* (Solomons), *Spiraeopsis celebica* (Solomons) and *Pullea glabra* (Fiji).

Biogeography — In general, the family has a Gondwanan distribution. South American–Australasian links are seen within the genera *Weinmannia* and *Eucryphia*, and between the closely related genera *Lamanonia* (S America) and *Geissois* (SW Pacific and Australia); *Caldcluvia* s.s. (S America) and *Ackama, Spiraeopsis* and *Opocunonia* (all SW Pacific). Connections between the SW Pacific and southern Africa/Indian Ocean islands are evident in *Weinmannia* (Madagascar–Mascarenes and Malesia–SW Pacific) and *Cunonia* (S Africa and New Caledonia). The family is absent from the mainland of Asia except for *Weinmannia* in Peninsular Malaysia and the peninsula of Thailand, and is poorly represented in western Malesia where only *Weinmannia* occurs to the west of the Philippines and is represented by only a handful of species. The relationships of Malesian *Cunoniaceae* are thus clearly austral, not Asian. In Australia, there are 16 genera but only about 35–40 extant species, suggesting it may be a relictual element in the flora.

While the current distribution of the family supports the idea that continental drift has been important in its history, anemochory has also contributed to its distribution. For example, *Weinmannia* occurs on volcanic Pacific islands south of the equator, with no continental connections. At both species and generic levels, anemochory is probably the predominant mode of dispersal in the family.

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CONSERVATION

Logging and conversion of forests to agricultural land will affect some species at lower altitudes in Malesia, but since many *Cunoniaceae* occur in predominantly montane forest, around the upper limit of agriculture and often on steep slopes where logging is more difficult, they may be less at risk of genetic erosion and extinction.

Potentially threatened species are thus likely to be those known from few collections and those with very limited distributions. In New Guinea, *Aistopetalum multiflorum, Spiraeopsis clemensiae* and *Pullea mollis* are all known from few collections and could be considered rare. The Vogelkop is a significant region for the conservation of *Cunoniaceae* as several collections are either atypical of the species into which they have been placed or perhaps represent undescribed taxa (examples in *Weinmannia* and

Schizomeria). In Sulawesi *Weinmannia coodei* and *W. eymaeana* have very limited distributions, and in Borneo, *W. clemensiae* is a distinctive endemic on the Mt Kinabalu massif confined to ultramafic substrates.

In situ conservation in reserves is appropriate for some taxa, such as *W. clemensiae* in Kinabalu Park and the various taxa from the Vogelkop. Ex situ conservation in seed banks and as live plants in botanical gardens should also be encouraged. Though nothing is known about compatibility mechanisms, most genera are likely to have generalised insect-pollinators and seed set may be possible for montane species in subtropical botanical gardens.

KEY TO THE GENERA BASED ON FLOWERING MATERIAL

1a. Leaves verticillate 2
b. Leaves opposite and decussate 3
2a. Sepals imbricate. Ovary semi-inferior with 2(–3) connate carpels **Pullea** *(p. 111)*
b. Sepals valvate. Ovary superior, with 2–5 free carpels . . . . **Acsmithia** *(p. 90)*
3a. Sepals imbricate 4
b. Sepals valvate 5
4a. Ovary semi-inferior, 2(–3)-carpellate. Flowers apetalous . . . . . . **Pullea** *(p. 111)*
b. Ovary superior, 2-carpellate. Petals small, ± obovate-spathulate . . . . **Weinmannia** *(p. 141)*
5a. Leaves simple or unifoliolate 6
b. Leaves trifoliolate or pinnately compound (occasionally some simple/unifoliolate leaves on the same tree) 7
6a. Flowers apetalous and unisexual (plants dioecious). Ovary with 2–5 free carpels . . . . **Spiraeanthemum** *(p. 127)*
b. Flowers with petals, each split distally into 3 acute lobes; flowers bisexual or male (plants hermaphrodite or andromonoecious). Ovary with 2–3 connate carpels . . . . **Schizomeria** *(p. 117)*
7a. Flowers apetalous 8
b. Flowers with petals 9
8a. Flowers 4–7(–8)-merous; ovary superior with as many carpels as sepals; styles short-conical, closely adpressed . . . . **Aistopetalum** *(p. 96)*
b. Flowers 4(–5)-merous (4–6-merous outside Malesia); ovary semi-inferior, 2-carpellate; styles subulate-terete, spreading . . . . **Ceratopetalum** *(p. 100)*
9a. Flowers protandrous. Petals ± obovate-spathulate, apex rounded, often with a few hairs along the midline on lower surface. Stipules 1 pair per node, interpetiolar 10
b. Flowers homogamous. Petals cuneate, bifurcating towards apex, each tooth with a small gland. Stipules 4 per node, lateral . . . . **Gillbeea** *(p. 104)*
10a. Carpels 2–6, the styles not far exserted beyond the perianth. Ovules 6–16 per locule. Indumentum including stellate hairs and in most species spherical glandular trichomes. Stipules ± orbicular with a rounded apex or reniform, not stalked . . . . **Spiraeopsis** *(p. 128)*
b. Carpels 2, the styles far exserted beyond the perianth. Ovules up to 40 per locule. Indumentum of simple hairs only. Stipules obovate to reniform, the apex usually bifid with two obtuse apices and the base distinctly stalked **Opocunonia** *(p. 107)*

KEY TO THE GENERA BASED ON FRUITING MATERIAL

1a. Fruits indehiscent 2
b. Fruits dehiscent 6
2a. Fruit a woody or fleshy drupe, spherical to ellipsoid 3
b. Fruit variously winged or enclosed within the calyx lobes, not a drupe 4
3a. Leaves always simple .... **Schizomeria** *(p. 117)*
b. Leaves trifoliolate or pinnate .... **Aistopetalum** *(p. 96)*
4a. Fruit outwardly little different from flowers, the calyx lobes scarcely enlarged and not or only slightly spreading, the styles long and protruding .... **Pullea** *(p. 111)*
b. Fruit markedly different from flowers, the wings well developed 5
5a. Fruit a samara, the carpel wall laterally extended into 3 chartaceous wings with distinct reticulate venation .... **Gillbeea** *(p. 104)*
b. Fruit a pseudosamara, the ovary little enlarged from the flowering stage, supported by 4 considerably enlarged, spreading woody sepals ... **Ceratopetalum** *(p. 100)*
6a. Leaves verticillate .... **Acsmithia** *(p. 90)*
b. Leaves opposite and decussate 7
7a. Carpels 2; seeds hairy, not winged .... **Weinmannia** *(p. 141)*
b. Carpels 2–6; seeds glabrous, winged 8
8a. Indumentum including stellate hairs and often spherical glandular trichomes that dry orange. Valves of capsule sometimes joined by a replum after dehiscence .... **Spiraeopsis** *(p. 128)*
b. Indumentum of simple hairs only and lacking spherical orange glandular trichomes. Valves of capsule not joined by a replum after dehiscence 9
9a. Fruit simple; carpels always 2 and seeds up to 40 per locule (New Guinea and New Britain) .... **Opocunonia** *(p. 107)*
b. Fruit multiple; carpels 2–5 and seeds 1 to few per locule (New Britain and New Ireland) .... **Spiraeanthemum** *(p. 127)*

SPOT CHARACTERS

Family: within Malesia, the family can usually be recognised by the following rule of thumb: Leaves opposite and decussate (sometimes whorled), pinnate, trifoliolate or simple, toothed, with interpetiolar stipules (see below for exceptions).

Genera: the following characters are seen in a few genera only, though not necessarily in all species of the genus. This list refers to the Malesian species only.

A) Leaves
  1) leaves in whorls – *Acsmithia, Pullea.*
  2) leaves:
    (a) simple/unifoliolate - *Acsmithia, Pullea, Schizomeria, Spiraeanthemum, Weinmannia.*
    (b) trifoliolate – *Aistopetalum, Ceratopetalum, Opocunonia, Spiraeopsis, Weinmannia.*
    (c) imparipinnate – *Aistopetalum, Gillbeea, Opocunonia, Spiraeopsis, Weinmannia.*
  3) domatia (tufts of hairs or pockets) in axil of secondary veins on underside of leaf – *Acsmithia, Opocunonia, Pullea, Spiraeanthemum, Spiraeopsis.*

B) Stipules
  - 4) 4 stipules per node – *Gillbeea.*
  - 5) stipules
    - (a) orbicular or ± spoon-shaped – *Spiraeopsis, Weinmannia.*
    - (b) bilobed at apex, with a short stalk – *Opocunonia.*
  - 6) stipules secretory (i.e. with adnate glandular colleters), nodes varnished – *Ceratopetalum, Schizomeria.*

C) Indumentum
  - 7) stellate hairs – *Gillbeea* (fruits and inflorescences only), *Spiraeopsis* (leaves, fruits and inflorescences).
  - 8) 'glands', and related structures, especially on lower leaf surface – *Acsmithia* (secretory glands, appearing as red dots), *Schizomeria*, especially *S. gorumensis* (spherical glands or reddish resin dots), *Spiraeanthemum* (secretory glands, appearing as red dots), *Spiraeopsis* (orange, spherical, multicellular, peltate hairs), *Weinmannia*, especially sect. *Leiospermum* (trichomes with multicellular hair bases that appear as black dots).

D) Inflorescence
  - 9) flowers in small heads or glomerules – *Pullea.*
  - 10) inflorescence of dyads or tetrads (2 or 4 racemes on short peduncle) – *Weinmannia.*

E) Flowers
  - 11) aestivation of calyx lobes imbricate – *Pullea, Weinmannia.*
  - 12) petals
    - (a) absent – *Acsmithia, Aistopetalum, Ceratopetalum, Pullea, Spiraeanthemum.*
    - (b) toothed – *Gillbeea* (teeth glandular), *Schizomeria.*
    - (c) considerably longer than calyx – *Opocunonia, Weinmannia.*
  - 13) gynoecium
    - (a) apocarpous – *Acsmithia, Spiraeanthemum.*
    - (b) syncarpous and carpels 2 (only very rarely 3) – *Ceratopetalum, Opocunonia, Pullea, Weinmannia.*
    - (c) syncarpous and carpels 2–6+ – *Aistopetalum* (4–7[–8]), *Gillbeea* (3), *Schizomeria* (2–3), *Spiraeopsis* (2–6).
  - 14) ovules per locule numerous (up to c. 40) – *Opocunonia.*

F) Sexual expression
  - 15) flowers unisexual – *Schizomeria* (bisexual and male), *Spiraeanthemum* (all dioecious or perhaps sometimes polygamodioecious), *Weinmannia* (most dioecious, sometimes bisexual).
  - 16) flowers strongly protandrous – *Opocunonia, Spiraeopsis.*

G) Fruits and seeds
  - 17) fruit a fleshy or woody drupe – *Aistopetalum, Schizomeria.*
  - 18) fruit a 3-winged samara – *Gillbeea.*
  - 19) fruit a 4-winged pseudosamara ('helicopter') – *Ceratopetalum.*
  - 20) fruit capsular with
    - (a) free central column – *Weinmannia.*
    - (b) replum – *Spiraeopsis.*
    - (c) neither (a) nor (b), at most a few small central strands – *Opocunonia.*
  - 21) fruit capsular with seeds
    - (a) hairy – *Weinmannia.*
    - (b) winged – *Acsmithia, Opocunonia, Spiraeanthemum, Spiraeopsis.*
  - 22) fruit an 'indehiscent capsule' or carcerulus – *Pullea.*

ACSMITHIA

Acsmithia Hoogland, Blumea 25 (1979) 492, f. 1; Fl. Nouv.-Caléd. m.s. at P. — Type: *Acsmithia pulleana* (Schltr.) Hoogland.

Spiraeanthemum A. Gray, Proc. Amer. Acad. Arts 3 (May 1854) 128; U.S. Explor. Exped., Phan. 1 (June 1854) 66 et Atlas (1865) t. 83 B: specie lectotypica exclusa; et sensu: Schltr., Bot. Jahrb. Syst. 52 (1914) 139; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 237, p.p.; A.C. Sm., J. Arnold Arbor. 33 (1952) 139, p.p.; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 8, p.p.

Shrubs or small trees, or less commonly medium-sized to tall trees. Twigs often with thickened nodes. Indumentum of simple hairs, with secretory glands visible as red dots on leaf surface and veins. Leaves verticillate in alternate whorls of 3 or 4, occasionally 5, simple, margin entire or crenate-serrate; tuft-domatia in axils of secondary veins often present in all Malesian species. Stipules interpetiolar, the number per node equal to the number of petioles or rarely otherwise, simple, narrowly triangular, caducous. Inflorescences axillary and solitary or two subunits serially inserted, or less commonly terminal, paniculate, with branching at proximal nodes whorled and at peripheral nodes less regular and ± alternate, many-flowered, with peduncles up to half of total length, the axes bearing small caducous bracts at nodes. Flowers bisexual, 4–5(–6)-merous, apetalous, pedicellate. Sepals valvate, subcoriaceous, connate at base for 1/4–1/2 of their length. Stamens with filaments subulate, glabrous and anthers broadly cordate, retuse at apex and incised at base. Disc consisting of free lobes alternating with stamens (or frequently 2 adjoining lobes connate inside alternisepalous stamens), glabrous or rarely with a few hairs. Ovary superior, ± apocarpous, with 2–5 carpels, frequently not all maturing to fruiting stage; carpels ovoid, hairy, each with 1–4(–6) ovules; styles continuous with ovary, terete, glabrous; stigma small, terminal, clavate, papillose. Fruit multiple, a follicetum with 2–5 free follicle-like fruitlets attached to receptacle at base and each dehiscing along the full length of the adaxial suture, the valves boat-shaped, stiff-coriaceous, their margins minutely thickened, the styles and calyx persistent. Seeds 1–4 per carpel, oblong, glabrous, with a lateral to terminal wing. — **Fig. 3, 5–9.**

Distribution — 16 species; from Fiji (1 species), New Caledonia (10 species) and NE Australia (1 species) to *Malesia:* Moluccas and New Guinea; absent from the Bismarck Archipelago, Solomon Islands and Vanuatu.

Ecology — In New Caledonia on serpentine in maquis and in mesophyll forest, particularly along creeks; in Fiji in lower montane rain forest between 500 and 1200 m altitude; in Australia in rain forest from near sea level up to 1500 m; in Malesia: in lowland and lower montane rain forest, in shrub layer or understorey, less commonly in canopy; in low mossy forest often in canopy, and in low scrub on exposed ridges or mountain tops; from c. 150 up to 2700 m.

Notes — 1. Distinguished immediately from *Spiraeanthemum*, which in Malesia has been found only in the Bismarck Archipelago (New Britain and New Ireland), by the verticillate leaves. The only other genus in Malesia in which verticillate leaves regularly occur is *Pullea*, which is easily recognised in flower or fruit by the half-inferior ovary and imbricate calyx lobes. Only in a single Malesian case, in *Acsmithia reticulata*, have opposite and verticillate leaves both been found within the same individual, but here the opposite, as well as ± alternate, leaves are suspected to be teratological.

2. In several Malesian species the leaves vary from small, coriaceous and sometimes bullate to larger, papyraceous and flat. This is probably related to habitat and exposure, and all Malesian species occur over a considerable altitudinal range.

3. The inflorescences are generally shorter than in most other Malesian genera, and flowering is often profuse. The flowers are fragrant and usually described as pale, varying from white, greenish cream to yellowish, the calyx being cream, yellow, yellow-green or rarely reddish (flowers old?), the filaments yellow or white and the stigmas white. The buds vary from creamy white to pale yellowish green. Young fruits are green or reddish, and mature, dehisced fruitlets are brown. Young leaves are sometimes pink.

4. Venation. In the Malesian species there are comparatively few lateral veins per leaf, commonly c. 5, opposite or alternate, on each side of the midrib. The main lateral veins form an acute acroscopic angle with the midrib, and in addition, sometimes there are much weaker veins ± at right angles to midrib in between prominent laterals or arising near their base. The midrib is sometimes not completely straight towards the apex.

5. The number of stipules per node is typically equal to the number of leaves although in *A. davidsonii* (F. Muell.) Hoogland in Australia it is sometimes twice the number of leaves (R.W. Barnes, pers. comm.).

6. Species delimitation in Malesia is not straightforward and the key relies in part on characters that are difficult to observe (e.g. ovule number).

KEY TO THE SPECIES

1a. Tomentum on twigs dense, relatively long-persistent, consisting of patent hairs 0.2–0.6 mm long 2

b. Tomentum on twigs dense to open (twigs almost glabrous), consisting of ± adpressed hairs or very short patent hairs less than 0.1 mm long 3

2a. Abaxial surface of calyx sparsely hirsute or strigose-hirsute throughout. Upper surface of leaves hirsute along midrib and nerves with tomentum ± persistent; intervenium on both surfaces bearing an evanescent tomentum .... **3. A. pulleana**

b. Abaxial surface of calyx glabrous or at most very sparsely strigose near base only. Upper surface of leaves glabrous or with few usually caducous hairs on midrib and nerves; intervenium on both surfaces glabrous .... **2. A. parvifolia**

3a. Ovules 2 per cell .... **4. A. reticulata**

b. Ovules 4 per cell .... **1. A. integrifolia**

1. Acsmithia integrifolia (Pulle) Hoogland

Acsmithia integrifolia (Pulle) Hoogland, Blumea 25 (1979) 496. — *Spiraeanthemum integrifolium* Pulle, Nova Guinea 8 (1912) 646; Schltr., Bot. Jahrb. Syst. 52 (1914) 142. — Type: *von Römer 936* (L lecto of Hoogland 1979; BO), Hellwig Mts, Irian Jaya.

Spiraeanthemum lanceolatum L. M. Perry, J. Arnold Arbor. 30 (1949) 142. — Type: *Brass 13615* (A holo; BM, BO, BRI, L, LAE), 2 km SW of Bernhard Camp, Idenburg R., Irian Jaya.

Spiraeanthemum reticulatum auct. non Schltr.: L. M. Perry, J. Arnold Arbor. 30 (1949) 141.

Shrub or small tree to 15 m by 20 cm diameter. Twigs shortly strigose-hirsute, glabrescent. Leaves in whorls of 3 or 4. Petiole 3–13(–20) mm, sparsely short-strigose.

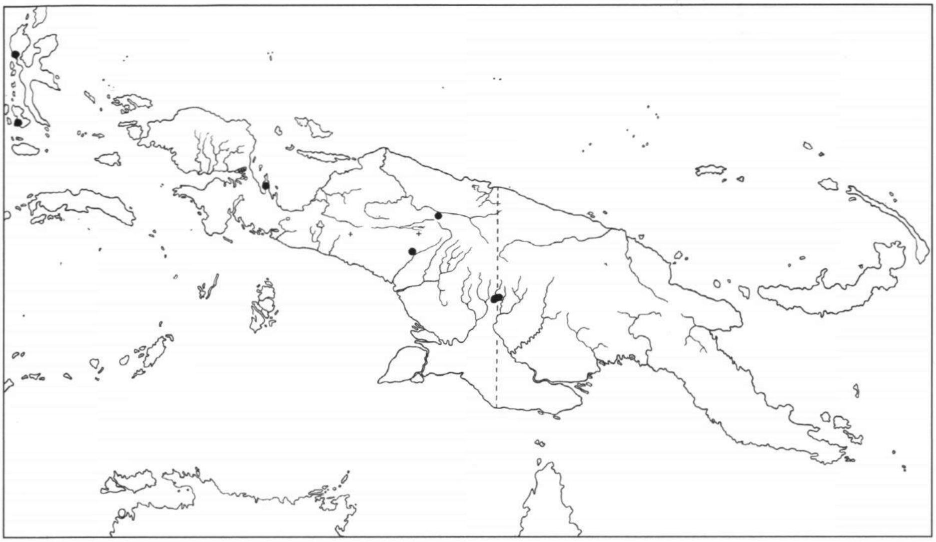

Fig. 5. Distribution of *Acsmithia integrifolia* (Pulle) Hoogland.

Blade elliptic-oblong or lanceolate, (3–)5–15(–20) by (1.5–)2–6(–8) cm, apex acute to obtuse or rounded, base obtuse to broadly acute and decurrent; margin entire; sparsely short-strigose along midrib and lower part of nerves on underside, glabrescent; nerves (6–)8–10(–12) pairs, midrib and nerves sunken above. Stipules lanceolate, up to c. 3 by 1 mm. Inflorescences axillary, up to 12 by 4 cm, up to c. 75-flowered. Flowers with pedicel 0.7–1.8 mm long above articulation. Sepals 1.7–2.1 by 0.6–1 mm, connate for 0.3–0.5 mm, glabrous. Stamens with filaments 2–3.5 mm long and anthers c. 0.2 by 0.3 by 0.15 mm. Disc 0.4–0.5 mm high, 0.05–0.1 mm thick. Ovary 2–4-carpellate, mostly 3-carpellate, with carpels 0.6–0.8 by 0.3–0.4 mm, ± densely strigose-hirsute, each with 4 ovules; styles 1.5–2.2 mm long. Fruit with fruitlets each c. 3 by 1.2 mm, with few seeds. Seeds including wings c. 1.5 mm long by 0.4 mm diameter, smooth.

Distribution — *Malesia:* Moluccas (Halmahera, Bacan) and Irian Jaya up to the border with Papua New Guinea. — Fig. 5.

Ecology — In lowland or lower montane forest, in the understorey, and in the canopy of mossy forest, 150–2200 m altitude.

2. Acsmithia parvifolia (Schltr.) Hoogland

Acsmithia parvifolia (Schltr.) Hoogland, Blumea 25 (1979) 498. — *Spiraeanthemum parvifolium* Schltr., Bot. Jahrb. Syst. 52 (1914) 140, f. 1A–E; Steenis, Bull. Jard. Bot. Buitenzorg III, 13 (1934) 196 '*parviflorum*'. — Type: *Ledermann 12761* (B holo), Felsspitze, Sepik, Papua New Guinea.

Tree to 18 m, the bole to 12 m by 30 cm diameter. Twigs densely hirsute, the hairs 0.2–0.3 mm long. Leaves in whorls of 3 (rarely 4). Petiole 1–5(–15) mm, fairly densely hirsute. Blade elliptic or obovate, 2–8(–13) by 1.3–3(–5) cm, apex rounded to obtuse, base rounded to obtuse and shortly decurrent, margin undulate to coarsely crenate-den-

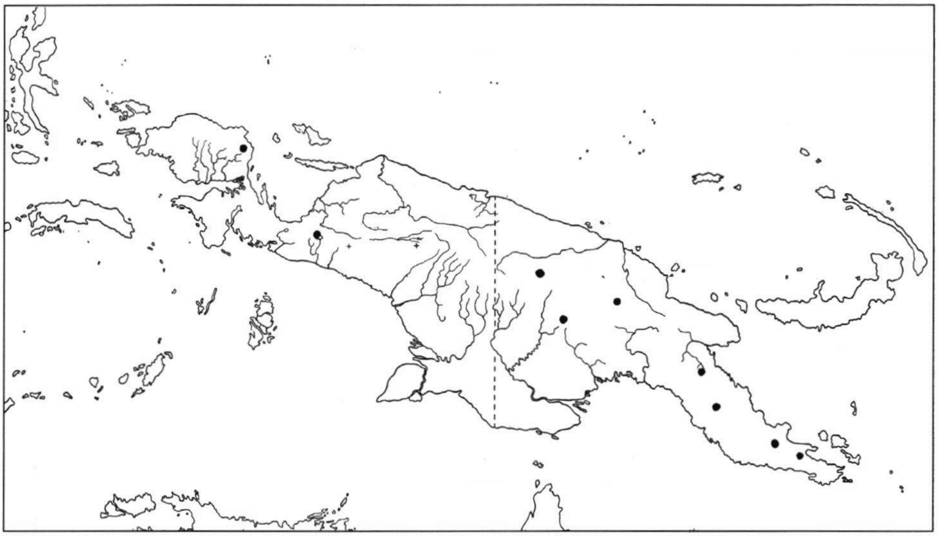

Fig. 6. Distribution of *Acsmithia parvifolia* (Schltr.) Hoogland.

tate, in small-leaved plants sometimes ± bullate; nerves 4–6(–8) pairs; on both sides, midrib and lower part of nerves sparsely hirsute, intervenium glabrous. Stipules ovate-elliptic or lanceolate, 1–3 by 0.3–1 mm. Inflorescences axillary or terminal, up to 14 by 5 cm, up to 400-flowered, but usually much smaller. Flowers with pedicels 0.5–1.5 mm long above articulation. Sepals 1.8–2.3 by 0.6–1.8 mm, connate for 0.5–1 mm, glabrous or sparsely puberulous near base only. Stamens with filaments 2.8–3.2 mm long and anthers 0.2–0.3 by 0.3–0.4 by 0.1–0.2 mm. Disc 0.4–0.6 mm high and 0.05–0.1 mm thick. Ovary (2–)3–4-carpellate with carpels 0.6–0.7 by 0.3–0.4 mm, rather sparsely hirsute, each with 2 ovules; styles 1–1.5 mm long. Fruit with fruitlets each c. 2.7 by 1.2 mm, with 1 or 2 seeds. Seeds including wings c. 1.5 mm long by 0.4 mm diameter, smooth.

Distribution — *Malesia:* scattered in mainland New Guinea from the Arfak Mts in the west to Mt Simpson in the southeast. — Fig. 6.

Ecology — In primary and disturbed forests and on forest edges between 500 and 2000 m altitude.

Uses — The bark is used for stomach ache (*Widjaja 4365*).

3. **Acsmithia pulleana** (Schltr.) Hoogland

Acsmithia pulleana (Schltr.) Hoogland, Blumea 25 (1979) 499. — *Spiraeanthemum pulleana* Schltr., Bot. Jahrb. Syst. 52 (1914) 140; Nova Guinea 12 (1917) 491, t. 191; Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 111, f. 6; L.M. Perry, J. Arnold Arbor. 30 (1949) 141. — Type: *Gjellerup 1214* (B holo; BO, L, U), Anggi Lakes, Arfak Mts, Irian Jaya.

Spiraeanthemum bullatum Gibbs, Fl. Arfak Mts (1917) 142. — Type: *Gibbs 5543* (BM holo; K), Anggi Lakes, Arfak Mts, Irian Jaya.

Shrub or small tree, rarely to 21 m tall. Twigs densely hirsute, hairs c. 0.5 mm long. Leaves in whorls of 3 or 4. Petiole 2–15 mm, ± densely hirsute. Blade elliptic to ovate or

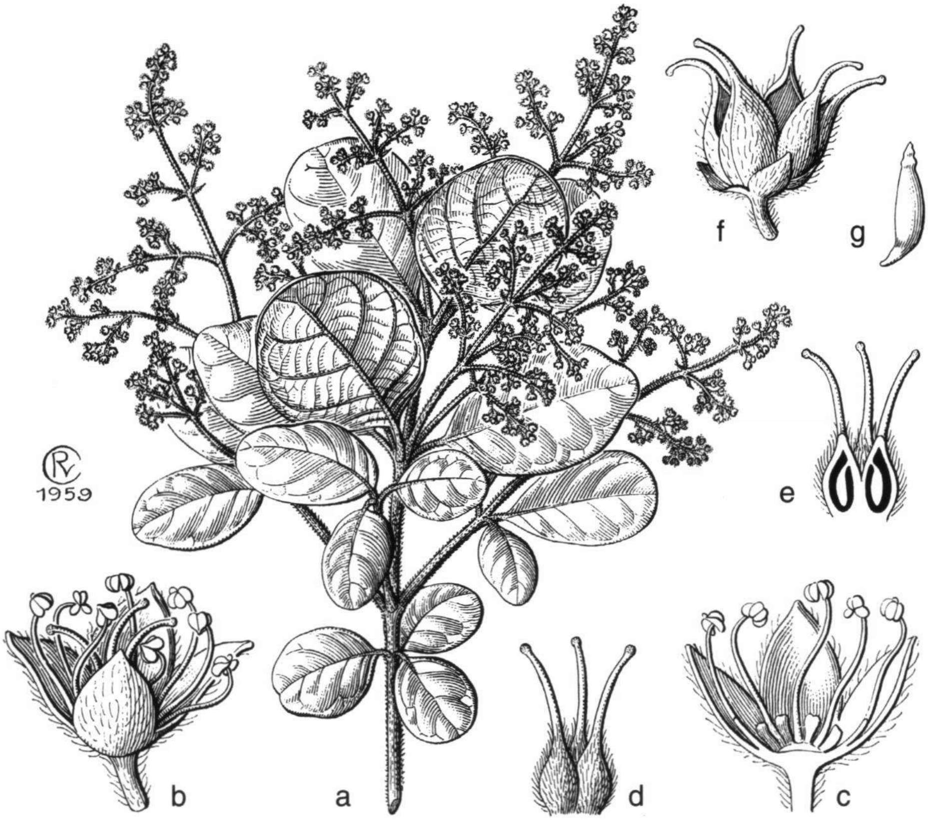

Fig. 7. *Acsmithia pulleana* (Schltr.) Hoogland. a. Flowering shoot; b. flower; c. longitudinal section of flower with the gynoecium removed; d. gynoecium; e. longitudinal section of gynoecium; f. mature fruit, the fruitlets dehisced; g. seed (a–e: *Brass & Versteegh 11923*; f, g: *CANB 41742*). a × 0.66; b–e, g × 10; f × 7.

obovate, 2–6(–8) by 1.5–3.5(–4) cm, sometimes strongly bullate, both apex and base rounded to obtuse; margin entire, vaguely undulate, or minutely serrate; nerves (3–)5–7 pairs; midrib near base densely hirsute, with tomentum long-persistent; intervenium and nerves sparsely to densely villose-hirsute, ± glabrescent above and ± persistent below. Stipules lanceolate, up to 3 by 1 mm. Inflorescences axillary and sometimes terminal, up to 12 by 5 cm, up to 150-flowered. Flowers with pedicels 0.8–1.2 mm long above articulation. Sepals 1.9–2.2 by 0.6–1.3 mm, connate for 0.3–0.8 mm, hirsute beneath. Stamens with filaments 1.8–3.2 mm long and anthers c. 0.3 by 0.4 by 0.2 mm. Disc 0.3–0.5 mm high, 0.1 mm thick. Ovary 2–5-carpellate, usually 3- or 4-carpellate, the carpels 0.7–1 by 0.3–0.5 mm, strigose, each with 2 (or 3) ovules; style 1.3–1.6 mm long. Fruit with fruitlets each c. 2.5 by 1.3 mm, containing 1 or 2 seeds. Seeds including wings c. 1.4 mm long by 0.4 mm diameter, smooth. — **Fig. 7.**

Distribution — *Malesia:* New Guinea, widespread from the Vogelkop Peninsula to Mt Albert Edward. — Fig. 8.

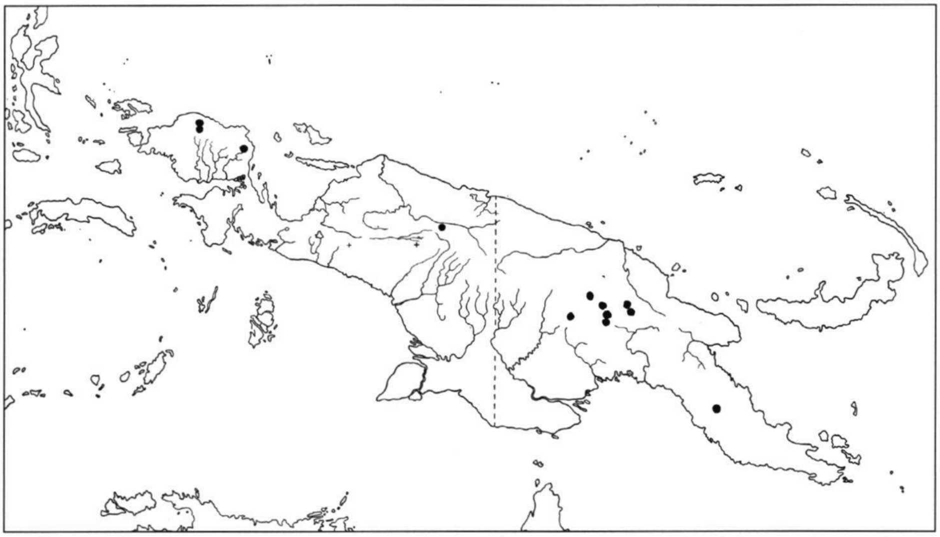

Fig. 8. Distribution of *Acsmithia pulleana* (Schltr.) Hoogland.

Ecology — From 700 to 2650 m, in low shrubby vegetation on stony ridges, in woody regrowth, secondary forest, low mossy forest, and tall rain forest. On the Arfak Mts particularly common in fire-affected shrubby vegetation above 2000 m.

Note — The holotype of *Dendromyza puberula* Stauffer (*Santalaceae*) (*van Royen & Sleumer 7340*) was collected from this species (*van Royen & Sleumer 7341*).

4. **Acsmithia reticulata** (Schltr.) Hoogland

Acsmithia reticulata (Schltr.) Hoogland, Blumea 25 (1979) 500. — *Spiraeanthemum reticulatum* Schltr., Bot. Jahrb. Syst. 52 (1914) 140, f. 1F–K. — Type: *Ledermann 10941* (B holo), Mt Hunstein, Papua New Guinea.

Spiraeanthemum idenburgense L.M. Perry, J. Arnold Arbor. 30 (1949) 141. — Type: *Brass & Versteegh 11938* (A holo; BM, K, L, LAE), 15 km SW of Bernhard Camp, Idenburg R., Irian Jaya.

Spiraeanthemum novoguineense L.M. Perry, J. Arnold Arbor. 30 (1949) 142. — Type: *Brass 11860* (A holo; BM, L, LAE), 15 km SW of Bernhard Camp, Idenburg R., Irian Jaya.

Shrub or tree up to 16 m tall by 20 cm diameter. Twigs very shortly strigose, early glabrescent. Leaves in whorls of 3 or 4. Petiole 5–10(–15) mm, sparsely and shortly strigose. Blade elliptic, occasionally nearly orbicular, to oblong, 2.5–7(–11) by 1.5–3.5(–6) cm, apex rounded to obtuse or broadly acute (and then slightly tapered), base obtuse to acute, decurrent; margin entire or undulate to distinctly serrate; midrib and nerves sunken above; lower part of midrib sparsely short-hirsute or wholly glabrous above, sparsely short-strigose or strigose-hirsute beneath. Stipules linear-lanceolate, up to c. 2.5 by 0.5 mm. Inflorescences axillary or terminal, up to 8(–13) by 4(–7) cm, 20–100-flowered. Flowers with pedicels 0.8–1.8 mm above articulation. Sepals 1.6–2.2 by 0.6–1.5 mm, connate for 0.4–0.8 mm, on abaxial surface glabrous or sparsely short-hirsute near base only. Stamens with filaments 1.4–2.7 mm long and anthers 0.3–0.5 by 0.4–0.6 by 0.15–0.2

mm. Disc 0.3–0.6 mm high, 0.1 mm thick. Ovary 3–4(–5)-carpellate with carpels 0.7–1.2 by 0.3–0.4 mm, strigose, each with 2 (or 3) ovules; style 0.6–1.5 mm. Fruit with fruitlets each 2.2–2.8 by 1–1.3 mm, 1–2-seeded. Seeds including wings c. 1 mm long by 0.3 mm diameter, smooth.

Distribution — *Malesia:* New Guinea, scattered from the Wissel Lakes to Misima Island in the Louisiade Archipelago. — Fig. 9.

Ecology — Subsidiary tree in lower montane forest or canopy tree in low mossy forest, 900–2500 m altitude; once collected in the lowlands as canopy tree in rain forest at 350 m (Misima Island).

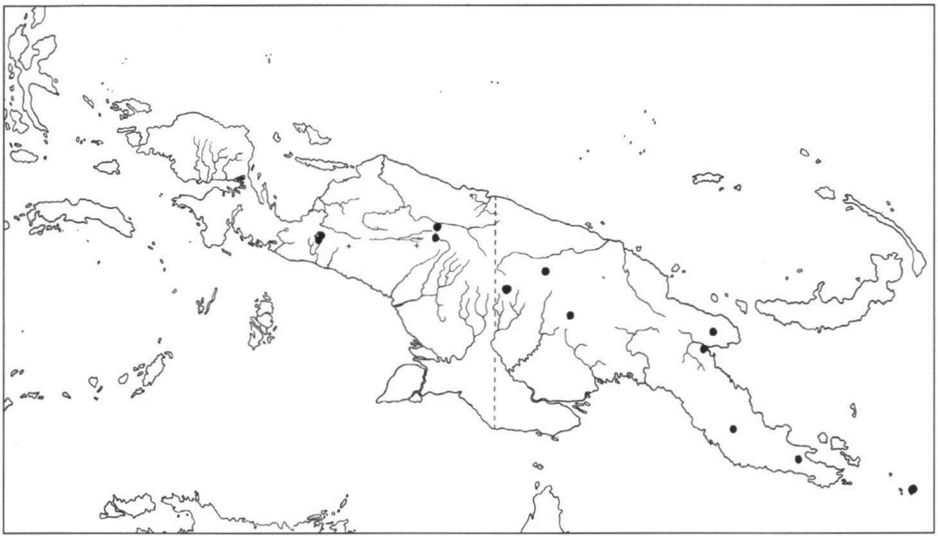

Fig. 9. Distribution of *Acsmithia reticulata* (Schltr.) Hoogland.

AISTOPETALUM

Aistopetalum Schltr., Bot. Jahrb. Syst. 52 (1914) 142, f. 2; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 239, f. 138; L.M. Perry, J. Arnold Arbor. 30 (1949) 158; Hoogland, Austral. J. Bot. 8 (1960) 333, f. 5, 6; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 8. — Type: *Aistopetalum viticoides* Schltr. (lectotype of Hoogland 1960).

Tall trees. Leaves opposite and decussate, imparipinnate, 1–2(–3)-jugate with lateral leaflets subopposite, the terminal leaflets generally larger than the lateral ones, and upper lateral leaflets larger than lower ones, occasionally unifoliolate; without domatia; margin crenate, serrate to subentire. Stipules interpetiolar, one pair per node, early caducous. Inflorescence axillary, paniculate, with opposite branching pattern to outermost extremities, many-flowered, with small caducous bracts. Flowers bisexual, 4–7(–8)-merous, apetalous, with short pedicel gradually widening into discoid receptacle. Sepals valvate, coriaceous. Stamens with subulate filaments and anthers ovoid or cordate. Disc annular, ± angular following the calyx, often ± lobed with shallow radial groove inside all stamens. Ovary superior, syncarpous, with as many carpels as sepals, truncated-conical, each cell with one ovule; styles one at apex of each cell, short-conical, free, each erect or all adpressed to each other to form single conical style surface at apex of ovary. Fruit a drupe with dry-leathery exocarp and woody endocarp, the styles remaining as protruding small horns or sometimes hardly noticeable around central-apical depression. Seeds 4–8, oblong. — **Fig. 4c, 10–12.**

Distribution — *Malesia:* 2 species in New Guinea; not recorded from any of the surrounding islands.

Ecology — Tall trees reaching canopy size in lowland and lower montane rain forest, up to 2200 m.

KEY TO THE SPECIES

1a. Leaflets 18–30-nerved; inflorescence many-flowered (250 or more flowers); disc densely and shortly hirsute .... **1. A. multiflorum**

b. Leaflets 10–15(–18)-nerved; inflorescence relatively few-flowered (up to about c. 100 flowers); disc glabrous .... **2. A. viticoides**

1. **Aistopetalum multiflorum** Schltr.

Aistopetalum multiflorum Schltr., Bot. Jahrb. Syst. 52 (1914) 143, f. 2G–L; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 239, f. 138G–L; Hoogland, Austral. J. Bot. 8 (1960) 334. — Type: *Ledermann 8531* (B holo), Quellenlager, Mt Hunstein, Papua New Guinea.

Trees up to 40 m tall, bole 25 m, buttressed. Twigs sparsely minutely strigose, early glabrescent. Leaves with petiole 2.5–6 cm and internodes of rachis 1.5–3 cm, terete, channelled above. Leaflets oblong or obovate-oblong, 6–18 by 2–6 cm, apex acuminate,

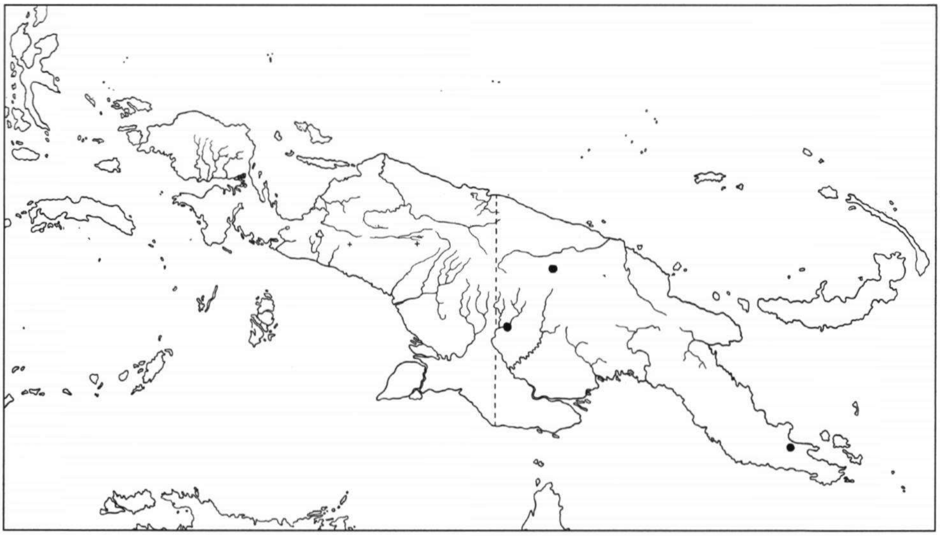

Fig. 10. Distribution of *Aistopetalum multiflorum* Schltr.

base acute to obtuse, somewhat decurrent, margin serrate, nerves 18–30 on each side of midrib, sparely minutely strigose to glabrous; petiolule 4–10 mm. Stipules triangular-ovate to ovate-oblong, c. 3 by 0.5 mm. Inflorescence of c. 250 flowers or more, up to 12 by 12 cm, subunits inserted in opposite axils of most distal pair of leaves; peduncle up to 3 cm; branches sparsely and minutely strigose at base to densely so in ultimate branchlets. Flowers with short pedicel from 0.5 mm thick merging into receptacle to 1.5 mm in diameter. Sepals ovate, 1.7–2.8 by 1.5–2.2 mm, acute, shortly strigose beneath, densely short-hirsute above. Stamens with filaments 0.8–1.7 mm long and 0.2–0.3 mm wide at base, anthers ovoid, retuse to faintly apiculate at apex, obtuse to retuse at base, 0.5–0.7 by 0.4–0.5 by 0.3 mm. Disc 0.2–0.5 mm tall, 0.4–0.8 mm thick, densely short-hirsute. Ovary 0.6–0.9 by 0.5–0.7 mm, fairly densely short-hirsute; styles 0.2–0.3 by 0.05–0.2 mm, glabrous. Fruit ovoid, c. 28 by 24 mm, slightly asymmetrical around apex, surface glabrous with some white warty patches, the persistent styles only visible as minute protrusions around apex.

Distribution — *Malesia:* Papua New Guinea, only known from 3 localities (Mt Hunstein, East Sepik; Kiunga, Western; W of Biniguni, Milne Bay). — Fig. 10.

Ecology — In rain forest at low to moderate altitude (30–800 m).

Note — Well developed articulations at nodes throughout the inflorescence give it a highly jointed appearance. The flowers are pale olivaceous outside and the calyx is cream inside, the stamens are cream, the disc yellow-green, and the ovary pale yellow; the fragrance is honey-like. Young fruits are green.

2. Aistopetalum viticoides Schltr.

Aistopetalum viticoides Schltr., Bot. Jahrb. Syst. 52 (1914) 144, f. 2A–F; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 239, f. 138A–F; L.M. Perry, J. Arnold Arbor. 30 (1949) 159; Hoogland, Austral. J. Bot. 8 (1960) 335, f. 6. — Type: *Ledermann 12177* (B holo), Mt Schrader, Papua New Guinea.

Aistopetalum tetramerum Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 105, f. 1. — Type: *Kanehira & Hatusima 12803* (FU holo n.v., photo at K; A, BO), Boemi, 40 km S of Nabire, Irian Jaya.

Trees up to 40 m tall, bole 20 m by 60 cm diameter, with or without buttresses. Twigs minutely strigose-puberulous, glabrescent. Leaves with petiole (1–)1.5–4(–7) cm, internodes of rachis 1–3 cm, terete, channelled above, minutely strigose-puberulous. Leaflets oblong, 3–18 by 1–7 cm, apex acuminate, base acute to obtuse and decurrent, margin shallowly crenate-serrate to subentire, nerves 8–15(–18) on each side of midrib, blade sparsely puberulous to glabrous above, fairly densely so to glabrous beneath, glabrescent; petiolule 3–12 mm. Stipules ovate-oblong, up to 7 by 3 mm, densely minutely puberulous beneath. Inflorescences of c. 25–100 flowers, up to 16 by 8 cm, subunits usually in opposite axils of most distal pair of leaves or in subdistal axils; peduncle up to 3 cm; branches sparsely to densely puberulous, most densely so towards ultimate branchlets. Flowers with pedicel up to 2.5 mm long and from 0.7 mm thick merging into receptacle to 1.8 mm in diameter. Sepals ovate to lanceolate, 2.7–3.6 by 1.2–2.6 mm, glabrous to shortly strigose or strigose-hirsute beneath, ± densely shortly strigose above. Stamens with filaments 1.4–2.2 mm long, 0.2–0.3 mm wide at base, anthers cordate, obtuse or submucronate at apex, retuse at base, 0.6–0.8 by 0.6–0.7 by 0.3–0.4 mm. Disc 0.5–1.2 mm tall, 0.5–1 mm thick, glabrous. Ovary 0.7–1.2 by 1–1.5 mm, glabrous ex-

Fig. 11. *Aistopetalum viticoides* Schltr. a. Flowering shoot; b. flower; c. longitudinal section of flower; d. fruit (a–d: *Hoogland & Pullen 5883*). — a × 0.66; b, c × 5; d × 1.32.

cept for row of hairs along outside centre of each cell; styles 0.3–0.4 by 0.2–0.3 mm, glabrous. Fruit ovoid to globular, up to 20 by 13–20 mm, glabrous, the styles slightly prominent around central-apical depression; in transverse section, fleshy layer c. 1–2 mm thick when dried, locules (4–)5–7 in a ring towards centre, each containing a single seed. Seeds oblong, c. 6 by 1.5 mm. — **Fig. 4c, 11.**

Distribution — *Malesia:* New Guinea, fairly widespread from Vogelkop to central and southern Papua New Guinea (absent from the tail). — Fig. 12.

Ecology — In primary forest from near sea level up to 2200 m. In Western Prov., Papua New Guinea, at c. 70 m asl, where associates include *Acacia.*

Note— The flowers are greenish yellow, the calyx pale green, the disc yellow and the ovary and stigmas yellow or green. The fruits are pale, sordid yellow or orange when ripe, rarely greenish white, with rather soft, juiceless pulp and a very hard kernel. Young growth is olive-green.

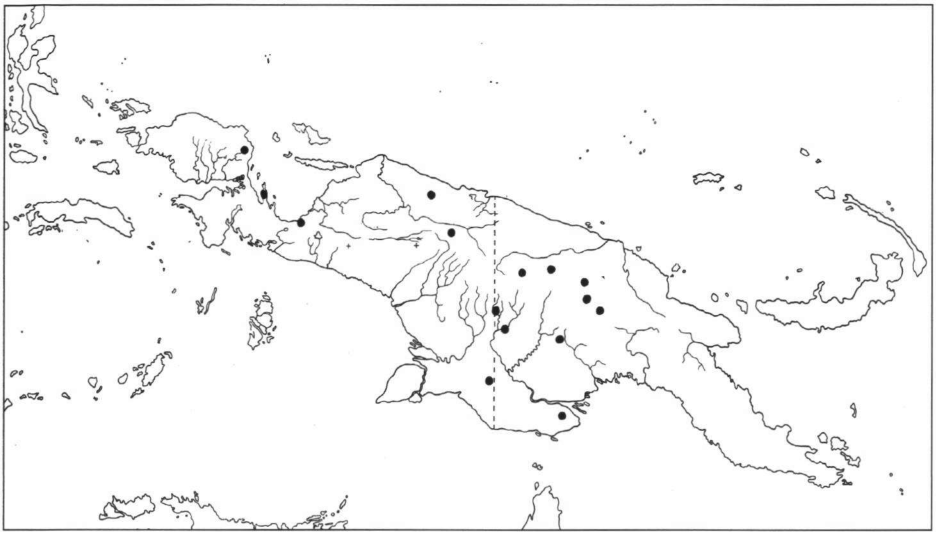

Fig. 12. Distribution of *Aistopetalum viticoides* Schltr.

CERATOPETALUM

Ceratopetalum Sm., Spec. Bot. New Holland (1793) 9, t. 3; Benth., Fl. Austral. 2 (1864) 442; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248; Hoogland, Austral. J. Bot. 8 (1960) 318, f. 1, 2; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 12; Willis, Austral. Pl. 1 (5) (1960) 4; Hyland & Wiffin, Austral. Trop. Rain Forest Trees (1993) 83. — Type: *Ceratopetalum gummiferum* Sm. (Australia).

Trees to canopy size (in Australia also shrubs). Leaves opposite and decussate, trifoliolate (occasionally bifoliolate) or (in Australia) unifoliolate, with nerves and venation prominent on both surfaces; domatia absent; margin serrate to crenate or almost entire. Stipules interpetiolar, one pair per node, resinous, early caducous. Inflorescences terminal and/or axillary, proximal branching opposite and decussate and ultimate branching cymose, ± corymbose in shape, many-flowered, with small caducous bracts. Flowers 4–6-merous (except gynoecium), bisexual, with short pedicel gradually widening into discoid receptacle. Sepals valvate, ± reduplicate, coriaceous, substantially enlarged and woody in fruit. Petals in one Australian species 3–5-furcate, in all others absent. Stamens with subulate filaments and cordate anthers. Disc annular, attached to the upper surface of the ovary. Ovary semi-inferior, syncarpous, 2-carpellate, superior part conical; each cell with 4 ovules in 2 longitudinal rows; styles subulate-terete, spreading. Fruit indehiscent, a pseudosamara, surrounded by radiating enlarged woody sepals; styles per-sistent, conical; carpels slightly woody, each usually with a single seed. — **Fig. 4a, 13–15.**

Distribution — 8 species, 2 in SE Australia and 6 in NE Australia (including 2 as yet undescribed), one of which extends to *Malesia:* New Guinea and New Britain.

Ecology — Most species are typically tall rain forest trees but one of the Australian species (*C. gummiferum* Sm.) is a shrub to small tree, usually found in drier sclerophyll forest and heathland on sandstone, and in NE Australia some species occur on exposed ridges and in steep rocky habitats at higher altitude on poor soils (R.W. Barnes, pers. comm.).

Uses — The genus has some importance as a source of timber and in horticulture. A summary for Malesia is given by Dickison (Timber trees: lesser-known timbers, PROSEA 5 [3] [1998] 153). In New Guinea, *C. succirubrum* is of local commercial importance though supplies are limited. It is widely used in furniture and cabinet work, house building, general turnery and carving, and it is also suitable for plywood. The timber of *C. apetalum* D. Don from Australia is highly valued for furniture and less so as a general building hardwood. It is also used as outer veneer in high quality plywood for furniture. It was previously used in coach building, hence the Australian name 'Coachwood'. In *C. gummiferum*, the calyx lobes are bright red and contrast with the deep green foliage, and the species is valued as Christmas decoration, hence the name 'Christmas Bush' (see Austral. Pl. 1, 5 [1960] 2–6).

Ceratopetalum succirubrum C.T. White

Ceratopetalum succirubrum C.T. White, Proc. Roy. Soc. Queensland 47 (1936) 59; Francis, Austral. Rain Forest Trees ed. 2 (1951) & ed. 3 (1970) 413, f. 253, 254; Hoogland, Austral. J. Bot. 8 (1960) 325, f. 2. — Type: *Tardent s.n.* (BRI holo; A, B, K, NY), Gadgarra, Atherton Tableland, NE Queensland, Australia.

Ceratopetalum tetrapterum Mattf., J. Arnold Arbor. 20 (1939) 432; Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 108, f. 3; L.M. Perry, J. Arnold Arbor. 30 (1949) 150. — Type: *Brass 7405* (B holo; A, BM, BO, BRI, L), Oroville Camp, Fly R., 30 miles above d'Albertis Junction, Papua New Guinea.

Trees up to 35 m tall, the bole to 27 m by 60 cm diameter, often with small buttresses, the bark exuding a red sap slowly turning colourless. Twigs glabrous. Leaves trifoliolate, petiolate; petiole 1–5 cm, terete, channelled above; leaflets obovate-oblong or oblong to ovate-lanceolate or lanceolate, (3.5–)5.5–13(–26) by (1–)2–6(–10) cm, acute to obtuse or rounded at apex, acute and decurrent at base, the margin faintly serrate to entire; secondary veins 25–35 of varying thickness on each side of midrib; petiolule (1–)3–15 mm; leaf glabrous except sometimes lower part of petiole sparsely strigose. Stipules triangular-ovate, 3–13 by 2.5–6 mm, usually early caducous. Inflorescences terminal, often with adjoining axillary ones, many-flowered, up to c. 30 by 20 cm, sometimes with one or more pairs of reduced leaves at subdistal nodes, sometimes 1 or 2 additional collateral or serial branches at lowest nodes; branches with persistent short pubescence increasing in density towards ultimate branchlets, with small distinctly less hairy ± caducous bracts. Flowers 4(–5)-merous, apetalous, with short hirsute pedicel 0.5 mm thick, articulating at base of hypanthium or up to 1 mm below it. Hypanthium conical, 0.8–1.2 mm tall, 1.7–2 mm diameter, strigose-hirsute. Calyx lobes ovate to lanceolate, 2.6–3.2 by 1.8–2.5 mm, acute, strigose beneath, sparsely so towards apex, ± densely hirsute above; stamens with filaments 0.9–1.8 mm long, at base 0.2–0.3 mm wide; anthers bluntly acuminate with extended connective at most 0.1 mm long, incised at base, 0.3–0.5 by 0.3–0.5 by 0.15–0.2 mm. Disc 0.3–0.5 mm tall, 0.3–0.5 mm wide, glabrous, fairly thick-fleshy, slightly indented. Superior part of ovary 0.5–0.8 by 0.7–1 mm, ± densely hirsute; styles 0.8–1.8 mm, glabrous. Fruit with ovary c. 5 by 3 mm, the styles up to 3 mm long, and the sepals enlarged up to 15 by 5 mm. — **Fig. 4a, 13, 14.**

Fig. 13. *Ceratopetalum succirubrum* C.T. White. a. Flowering shoot; b. flower and pedicel, note articulation and bracteoles; c. longitudinal section of flower; d. fruit, the calyx lobes enlarged into wings (a: *van Royen 3198*; b, c: *Koster BW 1163*; d: *Brass 7405*). — a: × 0.66; b, c × 7; d × 1.32.

Distribution — NE Australia (Atherton Tablelands) and *Malesia:* widespread in New Guinea, including Waigeo and the islands of Geelvink Bay (Teluk Cendrawasih) in the west and Normanby I. and New Britain in the east. — Fig. 15.

Ecology — Rain forest from near sea level up to c. 1800 m altitude. Appears to be localised but common where it occurs.

Fig. 14. *Ceratopetalum succirubrum* C.T. White. Leaves and trunk of a small tree (Kamiali Wildlife Management Area, Morobe Prov., Papua New Guinea). Photo by W. Takeuchi.

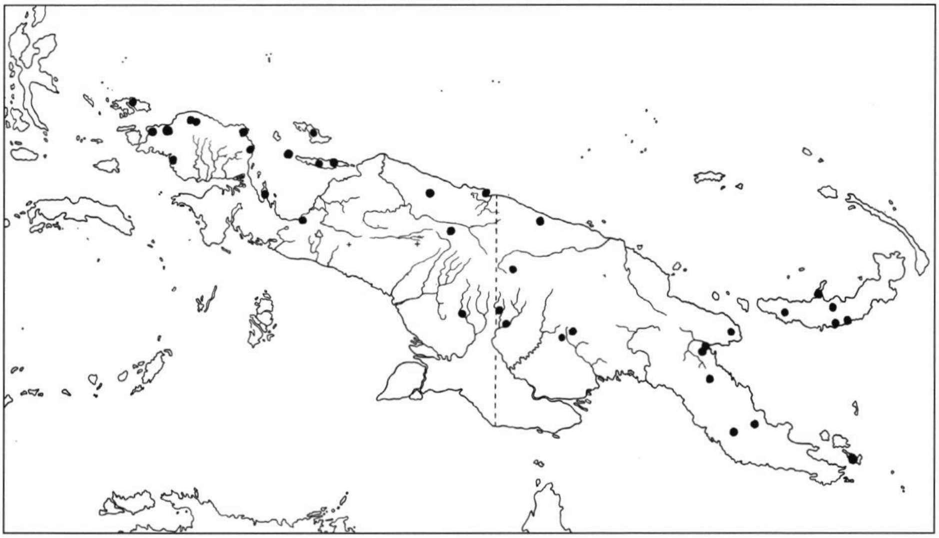

Fig. 15. Distribution of *Ceratopetalum succirubrum* C.T. White.

Vernacular names — Many names have been recorded none of which appear to be of more than restricted local use.

Notes — 1. The flowers are creamish or white with a greenish disc. In fruit the calyx lobes are purplish, purplish green, or crimson with a green centre (perhaps immature).

2. Perry (1949) mentioned that leaflets in specimens from Australia tend to be smaller than in those from New Guinea, and that the anthers have a slightly more prominent apex in Australia. A.C. Rozefelds (pers. comm.) suggests that differences in the morphology of the anthers between the types of *C. succirubrum* from Australia and *C. tetrapterum* from New Guinea may have taxonomic significance, as may variation in the size of the fruits within New Guinea.

GILLBEEA

Gillbeea F.Muell., Fragm. 5 (1865) 17; Schltr., Bot. Jahrb. Syst. 52 (1914) 144, f. 3; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 241, f. 141, 142; Hoogland, Austral. J. Bot. 8 (1960) 328, f. 3, 4; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 8; Rozefelds & Pellow, Nordic J. Bot. 20 (2000) 435. — Type: *Gillbeea adenopetala* F.Muell.

Medium to tall trees. Leaves opposite and decussate, imparipinnate, up to 6-jugate, with lateral leaflets subopposite; without domatia. Stipules 4 per node, lateral, ± foliaceous with main vein asymmetrically placed, leaving 2 contiguous interpetiolar scars on either side between adjoining leaf bases. Inflorescences terminal or axillary, paniculate, many-flowered, with terete branches and small caducous bracts, the branching varying from decussate in major branches through subopposite to ± spirally arranged in ultimate branchlets. Flowers bisexual, (4–)5(–6)-merous (except gynoecium), shortly pedicellate. Sepals valvate, subcoriaceous. Petals shorter than sepals, membranaceous, cuneate, bifid, with small glands at the apices. Stamens with subulate-terete filaments and oval to cordate anthers. Disc annular, upper surface ± smooth and with distinct impressions from filaments on outer edge or somewhat lobed. Ovary superior, syncarpous, 3(–4)-carpellate, each cell with a free subulate style and 2 or (3–)4 ovules. Fruit indehiscent, a 3(–4)-winged samara, obcordate in outline, the apex deeply incised, each wing formed by lateral expansion of the carpel wall; wings chartaceous with distinct reticulate venation; each locule usually with only a single seed, 1–3 seeds per fruit. Seeds oblong, the surface minutely papillate. — **Fig. 4b, 16, 17.**

Distribution — 3 species, 2 in Australia (NE Queensland) and 1 in *Malesia:* New Guinea.

Ecology — Rain forest trees.

Notes — 1. The Malesian species is quite similar to *G. adenopetala* F.Muell. from Australia, the most reliable distinguishing character being the number of ovules per locule (4, occasionally 3 in *G. adenopetala*; 2 in *G. papuana*). Both the Australian species also differ in having ciliate petals, somewhat larger flowers, a glabrous ovary (though tomentum may develop in young fruit of *G. whypallana* Rozefelds & Pellow), and terminal inflorescences, and the margin of leaflets is usually toothed or crenate (not entire), but none of these differences is fully diagnostic.

2. Schlechter (1914) illustrated the stipules in *G. papauana* as interpetiolar, with one pair per node, but this appears to be an error (and see discussion in Rozefelds & Pellow 2000).

Fig. 16. *Gillbeea papuana* Schltr. a. Shoot with flowers and fruits; note foliaceous stipules at nodes; b. flower; c. longitudinal section of flower; d, e. bilobed petal with glands on apices of lobes, d = abaxial surface, e = adaxial surface; f. fruit, the ovary wall expanded into 3 wings (a: *Ledermann 10694*; b–e: *Hoogland 5873*; f: *Ledermann 6772*). — a × 0.5; b, c × 5; d, e × 7; f × 1.

Gillbeea papuana Schltr.

Gillbeea papuana Schltr., Bot. Jahrb. Syst. 52 (1914) 146, f. 3; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 241, f. 141; Hoogland, Austral. J. Bot. 8 (1960) 331, f. 4. — Type: *Schlechter 17191* (B holo; P), Kani Mts, Papua New Guinea.

Gillbeea ledermannii Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 241. — Type: *Ledermann 10694* (B lecto of Hoogland 1960), Hauptlager Malu (= Ambunti), Papua New Guinea.

Trees up to 30 m tall, bole 18 m by 75 cm diameter. Twigs densely and shortly strigose-hirsute, glabrescent. Leaves with petiole 2.5–7 cm, internodes of rachis 1–4 cm. Leaflets ovate or elliptic, 5–14 by 2–6 cm, acute to obtuse, slightly acuminate at apex, obtuse and slightly decurrent at base, with entire margin, (8–)10–15 nerves on each side of midrib, leaf variously strigose or strigose-hirsute, glabrescent. Stipules obovate or suborbicular, strongly unequal-sided, 8–12 by 7–10 mm, often long-persistent. Inflorescence usually false terminal or axillary, occasionally terminal, often 2 partial inflorescences developing serially in an axil and then the upper one usually about twice as strong as the lower one, up to 25 by 15 cm; branches sparsely short hirsute at base to densely so in ultimate branchlets. Flowers with densely stellate-hirsute pedicel to 2 mm long above articulation, 0.5 mm thick, sharply separated from calyx. Sepals ovate or broad-ovate, 2.8–4 by 1.2–3.3 mm, densely and shortly stellate-hirsute beneath, hirsute above. Petals 1.2–2.6 by 0.6–1.7 mm, glabrous, the glands about half the size of the anthers. Stamens with filaments 1 by 2.4 mm long and anthers oval, rounded to retuse at apex and base, 0.3–0.4 by 0.3–0.5 by 0.2–0.3 mm. Disc 0.4–0.6 mm tall, 0.3–0.8 mm thick, glabrous. Ovary ovoid, 0.8–1.2 by 0.8–1 mm, shortly hirsute, each cell with 2 ovules; styles 0.4–0.5 mm, stigmas club-shaped. Fruit with reddish obovate wings coherent along central axis for 14–16 mm; wings at maturity 16–18 by 6 mm, rounded at apex, with entire slightly undulate margin and numerous groups of short stellate hairs. Seeds c. 5 by 0.8 mm. — **Fig. 4b, 16.**

Distribution — *Malesia:* Papua New Guinea, mainland only. — Fig. 17.

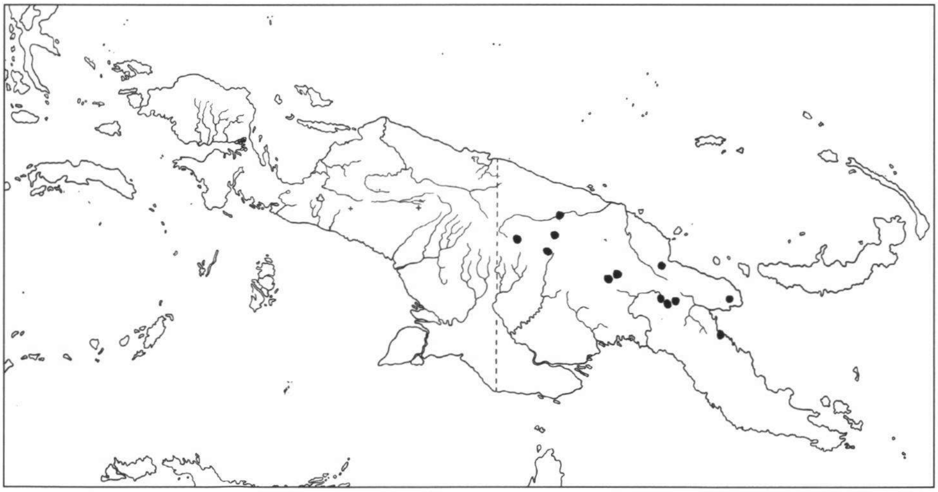

Fig. 17. Distribution of *Gillbeea papuana* Schltr.

Ecology — In rain forest at 50–2300 m altitude, often on creek banks.

Notes — 1. Herbarium labels record the flowers as white, yellowish or greenish and fragrant, the sepals being brownish cream and the petals white. The glands on the petals in the Australian species glisten and resemble nectaries (Endress, Diversity and evolutionary biology of tropical flowers [1994] 179, f. 5.12.4-6).

2. The seeds produce a dark, resinous substance while still within the fruit (pers. obs.; Dickison, J. Arnold Arbor. 65 [1984] 149–190).

OPOCUNONIA

Opocunonia Schltr., Bot. Jahrb. Syst. 52 (1914) 159; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248; L.M. Perry, J. Arnold Arbor. 30 (1949) 143; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 11. — Type: *Opocunonia kaniensis* Schltr. (lecto of Hutchinson 1967).

Stollaea Schltr., Bot. Jahrb. Syst. 52 (1914) 154; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 244; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 10. — Type: *Stollaea papuana* Schltr.

Caldcluvia D. Don p.p., sensu Hoogland, Blumea 25 (1979) 481.

Trees. Indumentum of simple hairs. Leaves opposite and decussate, imparipinnate, trifoliolate or rarely unifoliolate; leaf domatia very small pockets, with or without hairs, or absent. Stipules interpetiolar, one pair per node, reniform or bilobed, caducous. Inflorescence axillary, corymbiform, many-flowered, branching at proximal nodes opposite, then subopposite and then alternate, most distal floral subunits cymose, peduncle 1/3–1/2 of total length. Flowers 5–6-merous (except for gynoecium), petaliferous, pedicellate, bisexual but generally markedly protandrous; in male stage, calyx lobes incurved at apex to ± erect, filaments exserted, styles shortish, curved; in female stage, calyx lobes

Fig. 18. *Opocunonia nymanii* (K. Schum.) Schltr. Flowering shoots (*Hoogland & Pullen 5416*, Daulo, Papua New Guinea). Photo by R.D. Hoogland.

± erect, petals persistent, stamens fallen, styles elongated, straight. Sepals valvate, ovate to triangular, attached to hypanthium at their greatest width, not connate, glabrous above. Petals ovate to oblong, longer than calyx, not fugaceous. Stamens twice as many as sepals, with filaments thin, subulate, glabrous and anthers broadly cordate, the connective shortly extended. Disc ± distinctly lobed, the number of lobes equal to the number of stamens and sometimes united in pairs, the pairs separated by the alternipetalous stamens and with the alternisepalous stamens deeply impressed on the outer surface, glabrous. Ovary syncarpous, superior, 2-carpellate, hairy, each cell bearing a glabrous, cylindrical style; locules each containing numerous ovules arranged in 2 rows; stigma terminal, small, clavate, papillose. Fruit dehiscent, a septicidal capsule, the valves 2, boat-shaped, coriaceous in central part and thin at the edges (lateral extensions of the endocarp), the margins (placentae) of each valve remaining attached to the endocarp; endocarp often splitting at apex, just below style; central column absent or at most a few strands of tissue at the base of fruit; calyx and styles persistent, the styles divergent. Seeds numerous, small, elongate, with narrow, subequal terminal wings. — **Fig. 18–20.**

Distribution — *Malesia:* endemic to New Guinea and New Britain; one very variable species.

Ecology — Montane forest, occasionally at low elevations.

Opocunonia nymanii (K. Schum.) Schltr.

Opocunonia nymanii (K. Schum.) Schltr., Bot. Jahrb. Syst. 52 (1914) 159; L.M. Perry, J. Arnold Arbor. 30 (1949) 144. — *Ackama nymanii* K. Schum. in K. Schum. & Lauterb., Nachtr. Fl. Deut. Schutzgeb. (1905) 272. — *Caldcluvia nymanii* (K.Schum.) Hoogland, Blumea 25 (1979) 486. — Type: *Nyman 543* (B holo), Sattelberg, Morobe, Papua New Guinea.

Stollaea papuana Schltr., Bot. Jahrb. Syst. 52 (1914) 154, f. 6. — Type: *Ledermann 8724* (B lecto of Hoogland 1979; K), April R., East Sepik, Papua New Guinea.

Opocunonia kaniensis Schltr., Bot. Jahrb. Syst. 52 (1914) 160, f. 8A–G; L.M. Perry, J. Arnold Arbor. 30 (1949) 143. — Type: *Schlechter 17898* (B lecto of Hoogland 1979; P, UC), Kani Mts, Madang, Papua New Guinea.

Opocunonia trifoliolata Schltr., Bot. Jahrb. Syst. 52 (1914) 161, f. 8H–N; L.M. Perry, J. Arnold Arbor. 30 (1949) 145. — Type: *Ledermann 12896* (B holo; BM, K, L), near Felsspitze camp, East Sepik, Papua New Guinea.

Opocunonia papuana Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 108, f. 4; L.M. Perry, J. Arnold Arbor. 30 (1949) 144. — Type: *Kanehira & Hatusima 11756* (FU holo, n.v., photo K; A), Chaban, c. 30 km inward of Nabire, Irian Jaya.

Opocunonia? nov. sp.? Schltr., Bot. Jahrb. Syst. 52 (1914) 161.

Tree up to 45 m tall, often with a considerable length of bole, to 90 cm diameter. Twigs ± densely short-strigose, occasionally villose-hirsute, glabrescent. Leaves 1–3 (–4)-jugate, rarely unifoliolate. Petiole 2–6(–7.5) cm, internodes of rachis 1–2.5(–4) cm, with tomentum as on twigs. Leaflets ovate to ovate-oblong, rarely obovate, 4–12(–16) by 2–5(–7) cm, apex acute or often slightly acuminate or rarely rounded, base acute to rounded or subcordate, slightly decurrent; margin serrate to subentire; secondary veins (7–)8–11 on either side of midrib; petiolule 8–20(–25) mm in terminal leaflets, 2–10 (–13) mm in lateral ones; blades above glabrous to sparsely short-hirsute, glabrescent, the venation slightly prominent, beneath sparsely and very shortly strigose or strigose-hirsute, or less commonly hirsute, the hairs up to 1.5 mm long, tomentum subpersistent.

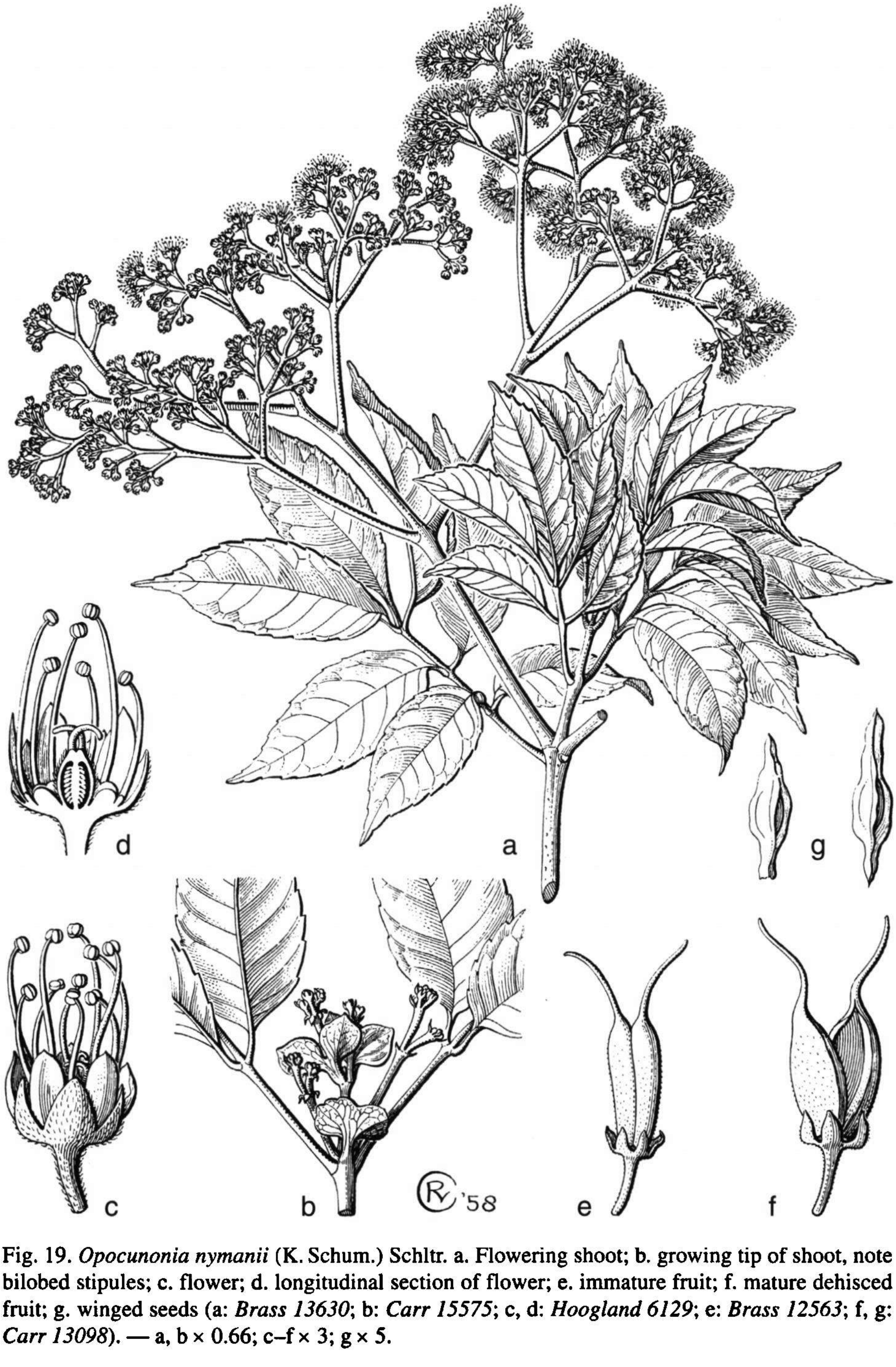

Fig. 19. *Opocunonia nymanii* (K. Schum.) Schltr. a. Flowering shoot; b. growing tip of shoot, note bilobed stipules; c. flower; d. longitudinal section of flower; e. immature fruit; f. mature dehisced fruit; g. winged seeds (a: *Brass 13630*; b: *Carr 15575*; c, d: *Hoogland 6129*; e: *Brass 12563*; f, g: *Carr 13098*). — a, b × 0.66; c–f × 3; g × 5.

Stipules obovate to reniform, (5–)9–15 by (4–)7–18 mm, apex rounded or more often bifid with two obtuse apices, base distinctly stalked 2–4 mm long, tomentum as in leaflets. Inflorescences most commonly corymbiform, to thyrsiform, up to c. 25 by 25 cm, inserted at distal or subdistal nodes; branches glabrous to densely short-hirsute, rarely long hirsute. Flowers pedicellate, the pedicels 1–5 mm long. Sepals 1.7–2.8 by 1–2.1 mm, ± densely short-strigose or rarely fairly densely hirsute beneath. Petals ovate to oblong, 2.2–3.8 by 1.1–2 mm, sometimes with a central line of hairs on outer surface. Stamens with filaments 4.5–6.5 mm long and anthers 0.4–0.7 by 0.4–0.7 by 0.3 mm. Disc 0.3–0.6 mm high and thick. Ovary 1–2 by 1–1.4 mm, ± densely strigose or strigose-hirsute, each cell with 35–50 ovules; style 1.8–2.6 mm. Fruit with valves 4–8 mm long, 2.5–3.5 mm wide, containing many seeds. Seeds including wings 3.5–5 mm long, smooth. — **Fig. 18, 19.**

Distribution — *Malesia:* widespread in New Guinea (except the Vogelkop Peninsula) and New Britain. — Fig. 20.

Ecology — In lowland and more commonly in lower montane rain forest, from 30 to 2800 m altitude; above 1500 m often one of the major constituents of the forest as a canopy or subcanopy tree, for instance in *Nothofagus* forest; also sometimes in secondary forest or on forest edge and occasionally planted as a roadside or village tree.

Notes – 1. This species is very variable, particularly in the size of the flowers and leaves. Small leaflets in trifoliolate leaves seem to be especially associated with exposed sites. There is also substantial variation in the density of the tomentum, and in the area from the Southern Highlands to Goroka a number of trees have a much denser and more hirsute type of tomentum.

2. Flowering is often profuse and the flowers are reported as fragrant or weakly so. They are usually white or cream, occasionally yellow-green, with the calyx pale olive, the corolla cream-white or rarely maroon bordered with white, the filaments pink, cream or white, the anthers yellow, and the ovary, styles and stigmas light green.

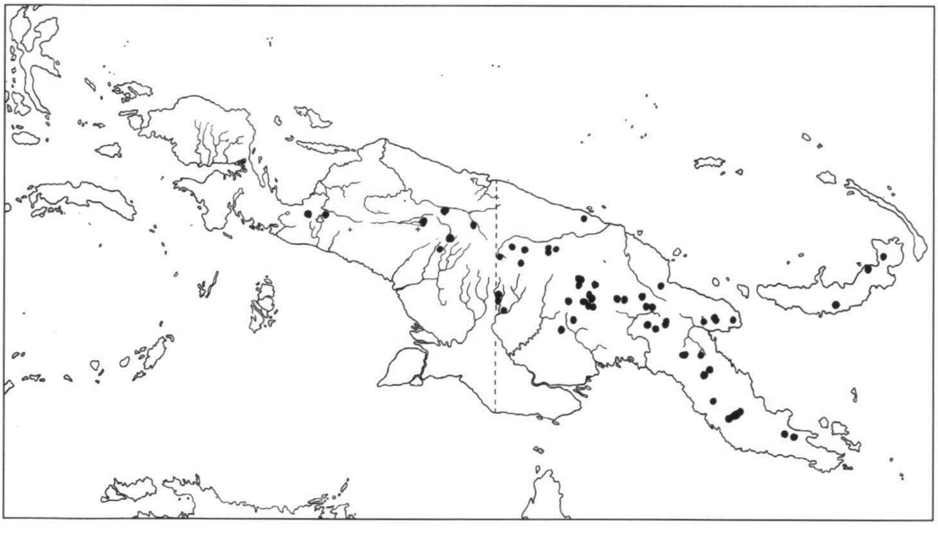

Fig. 20. Distribution of *Opcunonia nymanii* (K. Schum.) Schltr.

PULLEA

Pullea Schltr., Bot. Jahrb. Syst. 52 (1914) 164, f. 9; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 260, f. 151; L.M. Perry, J. Arnold Arbor. 30 (1949) 163; A.C. Sm., J. Arnold Arbor. 33 (1952) 148; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 9; Hoogland, Blumea 25 (1979) 490; A.C. Sm., Fl. Vit. Nova 3 (1985) 23, f. 6, 7 — Type: *Pullea mollis* Schltr. (lecto of Hutchinson 1967).

Small to moderately large trees, up to 30 m. Leaves opposite and decussate or less commonly whorled, simple, entire or shallowly crenate, petiolate; tuft domatia occasional. Stipules ovate or oblong, entire, early caducous. Inflorescences usually axillary, frequently composed of 2 or 3 subunits arranged in series in opposite axils of leaves with upper one largest, and rarely terminal, each subunit paniculate with peduncle c. 1/4–1/2 of length of inflorescence, the major branches serially arranged, the flowers in dense terminal clusters of up to c. 16, or in lax, subspherical clusters with some scattered subdistal flowers (racemes), with small caducous bracts at nodes and subtending the flowers. Flowers bisexual, (4–)5(–6)-merous (except for gynoecium), apetalous, appearing slightly protandrous. Hypanthium conical. Calyx lobes imbricate. Stamens with filaments thin, subulate and anthers broadly reniform, with a shortly extended connective at the apex and deeply incised at the base. Disc consisting of free glabrous lobes alternating with stamens, or lobes paired and some or all pairs of lobes connate inside altemisepalous stamens. Ovary semi-inferior, hirsute, 2- or rarely 3-carpellate, the cells in superior part loosely connate, each cell with usually 4 (6 in Australian species) ovules in 2 rows; styles conical and hirsute at base, to cylindrical and glabrous at apex. Fruit indehiscent, the pericarp not adhering to the seeds, not or scarcely larger than the ovary in flower, the calyx lobes persistent, slightly enlarged, chartaceous, erect or somewhat spreading, the styles persistent, elongated, stiff, exserted; endocarp cartilaginous. Seeds minute, glabrous, flattened, perhaps slightly winged. — **Fig. 4d, e, 21–24.**

Distribution — 3 or 4 species in *E Malesia*, NE Australia, and Fiji. The reported occurrence from the Solomon Islands (Whitmore, Guide For. Brit. Sol. Isls [1966] 59) is based on a wrongly identified specimen of *Spiraeanthemum.*

Ecology — In lower montane rain forest and on creek banks, sometimes descending into the lowlands, occurring from 300 to 2400 m altitude in Malesia and from sea level upwards in NE Australia.

Notes — 1. *Pullea* was originally described as unique in the family because of its inferior ovary, subsequently more correctly indicated as semi-inferior by Engler (1928). However, the ovary in *Ceratopetalum* is also semi-inferior and there is a tendency in this direction also in *Schizomeria* where the ovary is sunk into the receptacle to a varying degree. *Pullea* differs from these genera by the imbricate aestivation of the calyx lobes, which is clearly visible in bud and still recognisable in flower and even in fruit.

2. The flowers appear to be slightly protandrous, at least in *P. glabra* and *P. stutzeri* (F. Muell.) Gibbs, the styles remaining relatively short and incurved when the anthers dehisce, but they are not markedly diclinous.

3. The fruit is perhaps a carcerulus ('indehiscent capsule'). It might also be described as a pseudosamara, but the calyx lobes are only slightly enlarged.

KEY TO THE SPECIES

1a. Twigs, lower side of leaves, hypanthium, and lower side of calyx lobes sparsely to moderately densely strigose-hirsute or villose, the hairs ± adpressed, up to 0.2 (rarely to 0.5) mm long. Calyx lobes elliptic or obovate, at base distinctly narrower than at maximum width, the apex rounded .... **1. P. glabra**

b. Twigs, lower side of leaves, hypanthium, and lower side of calyx lobes densely hirsute, some of the hairs erect, c. 0.5 mm long. Calyx lobes triangular-ovate, at base very little or not narrower than at maximum width, the apex obtuse .. **2. P. mollis**

1. **Pullea glabra** Schltr.

Tree to 30 m tall with bole 22 m by 60 cm diameter. Twigs strigose or strigose-hirsute to subglabrous, glabrescent. Leaves subcoriaceous to coriaceous, sometimes somewhat bullate, broad-elliptic to elliptic or obovate, (2–)4–12(–18) by (1.5–)2–7(–9) cm, 6–11-nerved, rounded or obtuse and then often somewhat tapered at apex, obtuse to acute at base, decurrent along petiole, with coarsely undulate-serrate to entire margin, glabrous to sparsely strigose-hirsute, glabrescent, sometimes with tuft domatia in axils of secondary veins on abaxial surface. Petiole (5–)10–20 mm, sparsely strigose-hirsute. Stipules oblong or ovate-oblong, 3–6(–10) by 1–4(–7) mm, strigose beneath, glabrous above, rounded-obtuse at apex. Inflorescences of up to c. 75 flowers, subunits inserted in series in opposite axils of distal and frequently subdistal leaves and also rarely terminal, each subunit up to 8 (rarely 12) by 6(–8) cm, orders of branching 2–4, axes bearing flowers either dispersed along their distal part and/or in small, lax, subspherical clusters, each 4–6 mm diameter in flowering stage when dry and composed of c. 5 or more flowers; axes strigose or strigose-hirsute. Flowers sessile or with pedicel up to 1 mm long. Hypanthium 0.8–1.4 mm, shortly strigose-hirsute. Calyx lobes elliptic, ovate, or obovate, 1.7–2.5 by 0.8–1.4 mm, 0.4–1 mm wide at base, rounded at apex, strigose-hirsute to villose. Stamens with filaments (1.8–)2.5–3.4 mm and anthers 0.2–0.3 by 0.3–0.4 by 0.2 mm. Disc lobes 0.4–0.5 mm long. Ovary 1.2–2 mm long, hirsute, styles c. 2.5 mm long. Fruit with 'ovary' c. 2 mm diameter, styles up to 4 mm long. Seed c. 0.5 mm long. — **Fig. 4d, 21.**

Distribution — Perhaps Fiji; *Malesia:* New Guinea and Moluccas? (Morotai).

Ecology — See under the varieties.

Notes — 1. The perianth is greenish or white, becoming greenish yellow when old, the styles and filaments are white, the disc lobes bright red, and the anthers yellow.

2. Tuft domatia occur occasionally but are far from universal.

3. A recent collection from Mt Rossel, Rossel Island, Milne Bay Prov., Papua New Guinea, *Gideon LAE 76009*, appears to combine features of *P. mollis* and *P. glabra*. The flowers are in glomerules not capitula while the ± abundant indumentum on the young stems, leaves, inflorescence axes etc. is of long straight, patent hairs, but the leaf shape is closer to *P. glabra*.

KEY TO THE VARIETIES

1a. Leaves opposite and decussate .... **a.** var. **glabra**

b. Leaves verticillate in whorls of 3 or 4 .... **b.** var. **verticillata**

Fig. 21. ***Pullea glabra*** Schltr. var. *glabra*. a. Flowering shoot; b. flower; c. longitudinal section of flower; d. fruit, note slightly enlarged sepals and elongated styles (a–c: *Robbins 921*; d: *Hoogland & Pullen 5876*). — a × 0.66; b–d × 7.

a. var. glabra

Pullea glabra Schltr., Bot. Jahrb. Syst. 52 (1914) 166; Nova Guinea 12 (1917) 492; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 260; L.M. Perry, J. Arnold Arbor. 30 (1949) 163, in key; Hoogland, Blumea 25 (1979) 491. — Type: *Pulle 787* (B lecto of Hoogland 1979; B, BO, CANB, K, L), Hellwig Mts, Irian Jaya.

Pullea papuana Gibbs, Fl. Arfak Mts (1917) 141; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 260; L.M. Perry, J. Arnold Arbor. 30 (1949) 163, in key. — Type: *Gibbs 5576* (BM holo; K, L), Anggi Gita Lake, Arfak Mts, Irian Jaya.

Pullea decipiens L.M. Perry, J. Arnold Arbor. 30 (1949) 163. — Type: *Brass & Versteegh 13115* (A holo; L, LAE), 4 km SW Bernhard camp, Idenburg R., Irian Jaya.

Pullea versteeghii L.M. Perry, J. Arnold Arbor. 30 (1949) 164. — Type: *Brass & Versteegh 11146* (A holo; L, LAE), Bele R., 18 km N of Lake Habbema, Irian Jaya.

Pullea clemensiae L.M. Perry, J. Arnold Arbor. 30 (1949) 165. — Type: *Clemens 9068* (A holo; L), Samanzing, Morobe, Papua New Guinea.

Pullea perryana A.C. Sm., J. Arnold Arbor. 33 (1952) 148; Parham, Pl. Fiji Isls (1964) 78, f. 32 & ed. 2 (1972) 122, f. 34; A.C. Sm., Contr. U.S. Natl. Herb. 37 (1967) 71. — Type: *Tothill 472* (K holo; BISH, K, US), Central Road, Suva, Viti Levu, Fiji [N.B.: extra limital synonym].

Distribution — Fiji (see Note) and *Malesia:* widespread in New Guinea and adjoining islands (including Japen and those of Milne Bay Province), and probably on Morotai, Moluccas. Material from the latter locality is sterile and placed in *P. glabra* on the basis of its venation, though it is otherwise similar to sterile material of *Schizomeria serrata*. — Fig. 22.

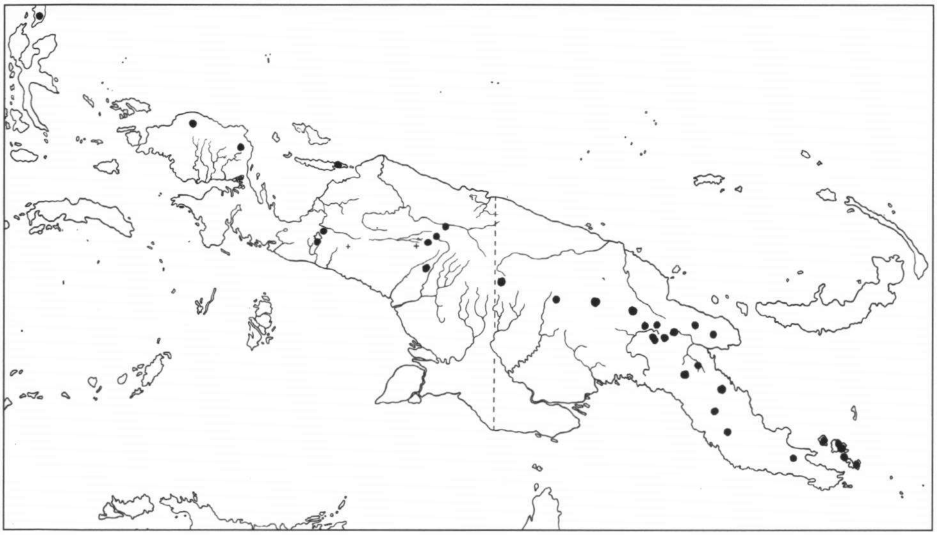

Fig. 22. Distribution of *Pullea glabra* Schltr. var. *glabra.*

Ecology — In primary forest, also often on creek banks, occasionally also in secondary forest, in New Guinea generally between 750 and 2400 m altitude, occasionally in the lowlands down to 50 m on Japen, and on Morotai at 1000 m.

Note — Hoogland (1979) placed *Pullea perryana* A.C. Sm. from Fiji into synonomy with *P. glabra* var. *glabra* but this was rejected by Smith (Fl. Vit. Nova 3 [1985] 25), who cited several small differences. In particular, inflorescences in material from Fiji tend to have the flowers dispersed in racemes or with only 2 or 3 flowers together at most, rather than aggregated into several-flowered capitula, and the leaves are somewhat different in shape. However, there is a range in the degree of clustering of the flowers in New Guinea, including this type of more lax inflorescence (e.g. *Brass 27818*, Sudest Island).

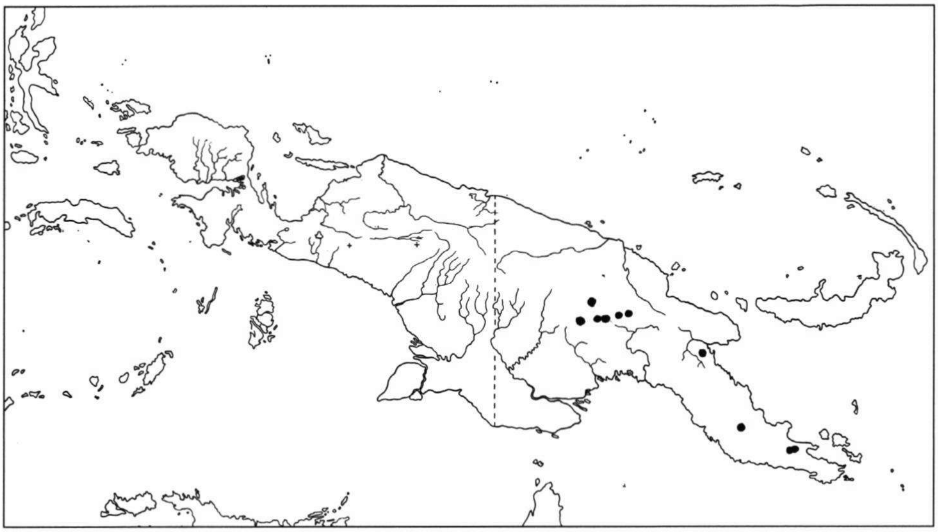

Fig. 23. Distribution of *Pullea glabra* Schltr. var. *verticillata* Hoogland.

b. var. **verticillata** Hoogland

Pullea glabra Schltr. var. *verticillata* Hoogland, Blumea 25 (1979) 492. — Type: *Pullen 206* (L holo; A, B, BISH, BM, BO, BRI, CANB, G, K, LAE, MEL, P, PNH, US), Mt Olga, Western Highlands, Papua New Guinea.

Distribution — *Malesia:* Papua New Guinea, fairly widespread on the mainland. — Fig. 23.

Ecology — In lower montane rain forest or mossy forest between 1450 and 2700 m altitude, occasionally also in regrowth.

Notes — 1. The species shows a great deal of variation in shape, size and consistency of its leaves and density of the tomentum, but is essentially constant in its floral morphology. It is closely related to *P. stutzeri* (F. Muell.) Gibbs from NE Australia which differs mainly in having 6 rather than 4 ovules per cell. The texture and venation of the leaves are often characteristic, being somewhat coriaceous with the venation drying yellow and contrasting with the intervenium, which is often brownish beneath and greenish above. The size of the leaves decreases with altitude and in the most extreme examples the leaves resemble small coins.

2. The occurrence of opposite and verticillate leaves within one genus also occurs rarely in *Weinmannia*, except for teratological modifications or occasional cultivated individuals. Much of the variation in var. *glabra* is repeated in var. *verticillata*, and apart from phyllotaxis, no other differences between these taxa are apparent. It appears likely that it is merely an environmentally induced modification, though var. *verticillata* tends to occur at the higher altitudes. These two have only been found in close proximity to each other on Mt Dayman, at 2230 m (var. *glabra*) and 2350 m (var. *verticillata*).

2. Pullea mollis Schltr.

Pullea mollis Schltr., Bot. Jahrb. Syst. 52 (1914) 165, f. 9; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 260, f. 151; L.M. Perry, J. Arnold Arbor. 30 (1949) 163; Hoogland, Blumea 25 (1979) 491. — Type: *Ledermann 11396* (B holo), Mt Hunstein, Papua New Guinea.

Tree to 20 m tall, 60 cm diameter. Twigs hirsute with hairs generally tufted and at least partly distinctly erect. Leaves elliptic or more commonly obovate, 4–9 by 2.5–6 cm, 7–10-nerved, rounded or slightly retuse at the apex, obtuse to acute at the base, decurrent along petiole, with faintly undulate margin, ± densely hirsute above and beneath, the tomentum at least partly long-persisting. Petiole 7–20 mm. Stipules ovate, 5 by 3 mm, densely strigose-hirsute beneath, glabrous above, rounded at the apex. Inflorescence of up to c. 200–300 flowers, subunits inserted in series in opposite axils of subdistal leaves, each subunit up to 5 by 4 cm, orders of branching 2–3, axes terminating in dense, spherical heads of flowers, each 6–8 mm diameter in flowering stage when dry and composed of c. 16 flowers; peduncle and branches densely and shortly hirsute. Flowers sessile. Hypanthium 0.5–0.7 mm, densely strigose-hirsute to hirsute. Calyx lobes triangular-ovate, 0.9–1.5 by 0.5–0.9 mm, at base hardly narrower, obtuse at apex, strigose-hirsute. Stamens with filaments 1.8–3.5 mm and anthers 0.2 by 0.4 by 0.2 mm. Disc lobes 0.3–0.5 mm long. Ovary 0.8–1.4 mm long, densely hirsute, the styles up to 1 mm long. Fruit with 'ovary' c. 1.5 mm diameter, the styles up to 4 mm long. Seed c. 0.5 mm long. — **Fig. 4e.**

Distribution — *Malesia:* New Guinea, only known from two localities in Papua New Guinea (Mt Hunstein, East Sepik, and Garaina, Morobe). — Fig. 24.

Ecology — In rain forest of the lower montane zone, 1300–2100 m altitude.

Note — Flowers white, sometimes tinged with pink.

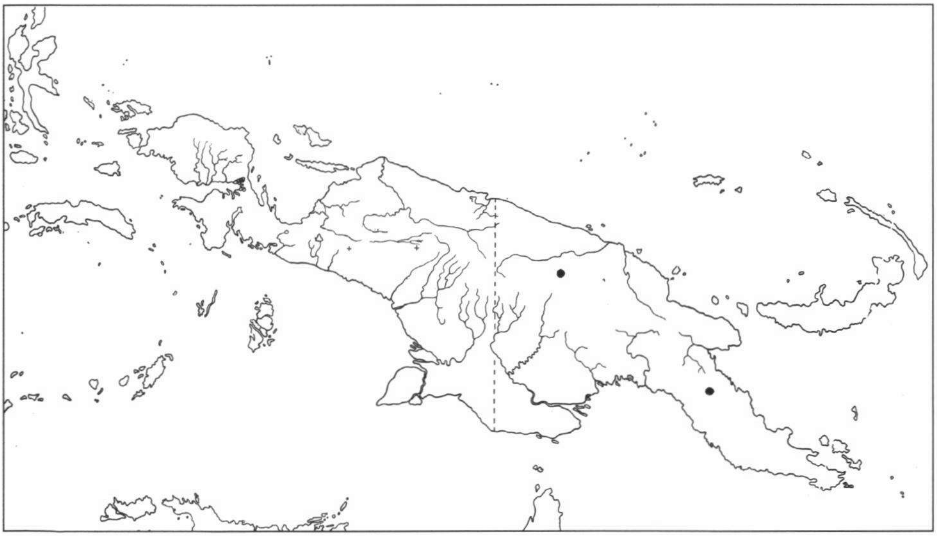

Fig. 24. Distribution of *Pullea mollis* Schltr.

SCHIZOMERIA

Schizomeria D. Don, Edinburgh New Philos. J. 9 (1830) 94; Benth., Fl. Austral. 2 (1864) 442; Schltr., Bot. Jahrb. Syst. 52 (1914) 156; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 247, f. 145; L.M. Perry, J. Arnold Arbor. 30 (1949) 151. — Type: *Schizomeria ovata* D. Don.

Cremnobates Ridl., Trans. Linn. Soc. London, Bot. 9 (1916) 41, t. 3, 4, f. 55–63. — Type: *Cremnobates ilicina* Ridl.

Small to large trees or occasionally shrubs. Indumentum of simple hairs, pubescent to crispate or tomentose. Leaves simple, opposite and decussate, petiolate, the margin serrate or crenate to sub-entire. Glands on the underside of blade in some species, minute, spherical or oblate, sometimes reddish and resinous, visible at × 40; domatia absent. Stipules interpetiolar, one pair per node, sometimes secretory and then the nodes and buds varnished, usually caducous. Inflorescence a thyrse, paniculate or corymbose, either terminal, or false-terminal, the apical bud aborted, dormant or vegetative, or axillary and then often small and lax. Pedicels articulated, graduating into hypanthium above articulation, or ± absent. Flowers bisexual or sometimes male, petaliferous, 4–6-, mostly 5-merous (except for gynoecium); hypanthium cup- to dish-shaped. Sepals 4–6, triangular to ovate, thick or membranous, aestivation valvate. Petals 4–6, alternating with the calyx lobes, membranous, the base elongated and narrow, the distal part laciniate; teeth usually 3, acute to acuminate, sometimes irregular. Stamens twice as many as sepals; filaments subulate, glabrous; anthers versatile, usually apiculate. Disc annular and deeply incised into 8, 10 or 12 fleshy and rounded or thin and flattened lobes; lobes ± free or sometimes clearly connate at their bases, sometimes semi-united in pairs. Gynoecium 2–3-carpellate, the carpels fused at level of ovary; ovary superior to half-embedded in hypanthium; styles 2–3, apical, free or sometimes connate towards the base, subulate, furrowed on adaxial side, usually glabrous, at least distally; stigmas terminal, minute; locules 2–3, ovules pendulous, 2–4(–6) per locule in 2 rows. In bisexual flowers, gynoecium well-developed and styles usually out-curving; in male flowers, ovary reduced or ± absent, the styles much reduced or absent, the ovules not developed. Fruit a drupe, ellipsoid or globose-oblate, often somewhat irregular, usually with a small annular depression at base corresponding to hypanthium and margin of hypanthium forming a minutely protruding annular scar with remnants of the persistent calyx lobes at its rim; epicarp thin, smooth or warty; mesocarp fleshy or granular; endocarp usually stony, sculpturing superficial to deep, irregular, sometimes with dark, resinous vacuoles or indentations. Seeds 1(–3). — **Fig. 25, 26.**

Distribution — About 10 species in eastern Australia, Solomon Islands and *Malesia:* Moluccas, New Guinea and the Bismarck Archipelago.

Ecology — In forest, occasionally extending into secondary vegetation, scrub, or at the edge of savanna or alpine grassland. From sea level to 3300 m. In Malesia, *S. serrata* is widespread at low elevation, the remaining species occur in montane forest.

Notes — 1. The combination of laciniate petals and drupaceous fruits is unique within *Cunoniaceae. Schizomeria* is closely related to *Ceratopetalum*, but readily distinguished from it in Malesia where the latter has trifoliolate leaves, and by the fruits. Vegetative material is occasionally confused with *Pullea glabra.*

2. Most species are quite variable, and vegetative characters are not always species specific, though the pattern of venation is often useful. Some unplaced material may represent additional taxa.

3. The flowers are greenish white to cream or somewhat brownish in species with dense indumentum. The disc lobes are yellow or green, and clearly visible in those species with rather dish-shaped flowers, while the anthers are often purple-black or brown, contrasting with the cream filaments and perianth. The fruits are usually ivory white or fawn at maturity, and brownish when immature, with a smooth or often warty surface. The rather granular-fibrous flesh usually adheres quite strongly to the endocarp.

4. A red exudate is commonly reported from close to the cambium.

KEY TO THE SPECIES

1a. Fruits narrowly ovoid, truncate at base and pointed at apex, 2.9–3.7 by 1.4–1.8 cm .... **6. S. orthophlebia**

b. Fruits globose to somewhat ellipsoid, 1–5 by 0.8–5.8 cm, if pointed at the apex then < 2 by 1.5 cm 2

2a. Ovary glabrous; plants mostly above 1100 m .... **4. S. ilicina**

b. Ovary pubescent, pilose or tomentose, or rarely almost glabrous and then plants at low altitude (< 100 m) 3

3a. Inflorescence usually axillary, small, lax, delicate; petals markedly shorter than calyx lobes; leaves often with minute ± spherical, sometimes reddish resinous glands on the lower surface, especially when young .... **3. S. gorumensis**

b. Inflorescence usually terminal or false-terminal and well branched, ± robust; petals extending as far as the calyx lobes; leaves usually lacking glands 4

4a. Ovary pubescent to pilose, rarely almost glabrous (TransFly region); leaves usually chartaceous to subcoriaceous, rarely coriaceous, usually acute at the apex .... **7. S. serrata**

b. Ovary tomentose; leaves usually coriaceous or subcoriaceous, usually rounded at the apex 5

5a. Inflorescence axes densely and persistently tomentose; flowers sessile .... **8. S. versteeghii**

b. Inflorescence axes pubescent or sparsely to moderately tomentose, if the latter then the indumentum not persistent; flowers subsessile to pedicellate 6

6a. Leaves glabrous and eglandular, or if hirsute then fruits large, 2.5–5 by 2.5–5.8 cm .... **2. S. clemensiae**

b. Leaves with reddish or brownish tomentum and/or glands, especially when young; fruits small, 1.6–2 by 1.6–2.2 cm 7

7a. Inflorescence terminal; lateral vegetative branches almost as dominant as median axis of shoot; indumentum reddish .... **1. S. carrii**

b. Inflorescence false-terminal; lateral vegetative branches not as dominant as median axis of shoot; indumentum fawn to brown, not reddish .... **5. S. novoguineensis**

1. Schizomeria carrii H.C. Hopkins

Schizomeria carrii H.C. Hopkins, Blumea 46 (2001) 185, f. 1. — Type: *Carr 14175* (L holo; BM, K), Alola, Northern Prov., Papua New Guinea.

Trees up to 30 m high, buttresses absent. Lateral stems almost as dominant as median axis; twigs floccose, the hairs red-brown, later more sparsely hairy. Leaves with petiole 0.3–0.7 cm and blade subcoriaceous to coriaceous, (3–)3.5–6(–9.3) by (1.7–)2–4(–5.3) cm, elliptic, ovate or oblong-elliptic, with the base obtuse or broadly acute and the apex obtuse or rounded; indumentum often floccose near midrib, irregularly persistent, red-brown; minute glands rare; margin crenulate; secondary veins in 11–15 pairs, generally evenly spaced. Stipules narrowly triangular to ovate, 5–8 mm long. Inflorescence terminal; median axes up to 9.5 cm long by 2–4 mm diameter, usually with 3–4 pairs of major lateral branches, bearing red-brown, tomentose indumentum. Flowers bisexual, 5–8 mm diameter, 5-merous (except for gynoecium); almost sessile to pedicellate, pedicel 0.5–2 mm long; hypanthium tomentose, up to c. 0.5 mm high; calyx lobes 2–2.6 by 1–2 mm, outer surface almost glabrous; petals with the basal part c. 1 mm long, lobes up to 0.6–0.8 mm long; filaments 1.7–2.5 mm, anthers 0.6–0.8 mm long; disc lobes c. 0.6 mm diameter; ovary superior, 2-carpellate, ± spherical, 1–2 by 1–2.5 mm, tomentose; styles 0.8–1.1 mm long. Fruit ± spherical, somewhat irregular, up to c. 1.6 by 1.6 cm but perhaps not yet fully mature; epicarp smooth to warty.

Distribution — *Malesia:* Owen Stanley Mountains of Papua New Guinea, from Myola and Alola in the central part of the range and Mts Dayman and Suckling in the southeast.

Ecology — A canopy tree in mossy montane forest, 1800–2425 m altitude.

Note — The branching pattern and rather persistent reddish brown indumentum are distinctive.

2. Schizomeria clemensiae L.M. Perry

Schizomeria clemensiae L.M. Perry, J. Arnold Arbor. 30 (1949) 157. — Type: *Clemens 439* (A holo; L), Sattelberg, Morobe Prov., Papua New Guinea.

Tree 12–35 m high, lacking buttresses. Twigs somewhat flattened at nodes, usually glabrous; buds in distal leaf nodes relatively large. Leaf with petiole 0.3–4.5 cm long, and blade subcoriaceous to coriaceous, 7.5–23+ (leaf broken) by 3.8–13.5 cm, usually elliptic to broadly elliptic, occasionally narrowly elliptic or ovate, the base obtuse, rounded, slightly cordate, truncate or cuneate especially in narrow leaves and the apex broadly acute, obtuse, rounded, apiculate or sometimes acute, especially in narrow leaves; intervenium flat or somewhat bullate, sometimes drying ± shiny, yellow-green above; upper surface usually glabrous, lower one either ± glabrous or with rusty tomentum near veins, or rarely floccosely evanescent; glands absent; margin crenulate-dentate to subentire; secondary veins in 14–20 pairs, evenly spaced to somewhat irregular. Stipules triangular-ovate to ligulate, 0.5–1.3 by 0.4–0.5 cm, caducous, abaxial surface tomentose or sparsely pubescent. Inflorescence either false-terminal or terminal; when false-terminal, apical bud dormant or aborted, and median axis 0.5–5.5 cm long by 0.5–1 cm diameter, usually thicker in fruiting stage, with 1–4 pairs of major lateral branches; when terminal, median axis 9–18 cm long by 0.4–0.5 cm diameter, remaining relatively slender in fruit, with c. 3–6 pairs of opposite, lateral branches, up to 11 cm long; axes, outer surface of bracts and buds brown-tomentose, the indumentum evanescent on lower internodes and often much reduced by fruiting stage. Flowers bisexual and male, 5–8 mm diameter; 5–6-merous (except gynoecium); flowers sessile or pedicellate, the pedicel 1.5–3.5 mm long; calyx lobes 2.5–4.5 by 1.5–2.5 mm, outer surface densely to rather sparsely tomentose; petals 2.2–3.5 mm long, the basal part 1–2 mm plus teeth 1–2 mm long, petals as long as calyx lobes and teeth glabrous or rarely petals shorter than calyx and teeth hairy; filaments 2.5–4.5 mm long; anthers apiculate; disc lobes c. 1 mm diameter; ovary 2–3(–4)-carpellate, in bisexual flowers globose-conical, 2–3.5 mm diameter by 1.5–3 mm high, densely tomentose at anthesis, the hairs easily detaching; styles 2–3 mm long; ovules 2–3 per locule. Fruits ellipsoid or irregularly globose-oblate, up to 2.5–5 cm long by 2.5–5.8 cm diameter; epicarp rough, with numerous pale warty lenticels. — **Fig. 25.**

Fig 25. *Schizomeria clemensiae* L.M. Perry. Leaves and fruit (*Bulmer 85/203*, Schrader Range Papua New Guinea). Photo by R.N.H. Bulmer.

Distribution — *Malesia:* mountains of New Guinea.

Ecology — In primary and secondary mixed montane forest and forest edge, 700–2900 m altitude.

Note — This is a rather variable and perhaps heterogeneous species with large fruits, probably closely related to *S. versteeghii*, which has much denser indumentum on the inflorescence. A distinctive population with terminal, rather than false-terminal inflorescences and rather bullate leaves (Fig. 25) occurs on Mt Giluwe and the Schrader Range at 2000–2500 m, and another variant has some floccose indumentum on the leaves.

3. Schizomeria gorumensis Schltr.

Schizomeria gorumensis Schltr., Bot. Jahrb. Syst. 52 (1914) 157, f. 7; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248, f. 145; L.M. Perry, J. Arnold Arbor. 30 (1949) 153. — Type: *Schlechter 18837* (B holo), Gorum, 2100 m, Bismarck Range, Papua New Guinea.

Schizomeria ledermannii Schltr., Bot. Jahrb. Syst. 52 (1914) 158, f. 7; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248, f. 145. — Type: *Ledermann 12077* (B holo), Schrader Mts, 2070 m, Papua New Guinea.

?*Schizomeria pulleana* O.C. Schmidt, Nova Guinea 14 (1924) 150; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248. — Type: *Pulle 1474* (B holo; BO, K?, L), Doormantop, region of Mamberamo R., 1420 m, Irian Jaya.

Schizomeria adenophylla L.M. Perry, J. Arnold Arbor. 30 (1949) 153. — Type: *Brass 4661* (A holo; BO), Murray Pass, Wharton Range, Central Prov., Papua New Guinea.

Shrub or small slender to large tree, 2–25 m high, lacking buttresses. Twigs sparsely pubescent. Bracts sometimes united to form a bilobed, persistent cup around stem. Leaves with petiole (0.3–)0.5–1(–1.3) cm and blade chartaceous to subcoriaceous, either broadly elliptic, 2.5–4 by 1.5–2.5 cm, both base and apex rounded, or elliptic to ovate, (3.5–)5–10(–12.5) by (2.2–)3.5–4(–4.5) cm, the base cuneate to rounded and the apex obtuse or acute, or narrowly elliptic-lanceolate, 3.5–7.7 by 1.3–3 cm, the base attenuate or rounded and the apex narrowly acute or acuminate; lower surface often bearing minute ± spherical pale or reddish resinous glands and rarely sparse indumentum; margin crenulate to subentire; secondary veins in 8–10(–12) pairs, quite well spaced. Stipules triangular, 2–5 mm long, usually varnished. Inflorescence axillary or occasionally terminal or false-terminal; when axillary, median axes 3–5.5(–7.5) cm long by c. 1 mm diameter, and few-flowered (15 or more flowers), often slender and lax, or denser when axes shorter; when false-terminal, median axes bearing 1–2(–4) pairs of major lateral branches and the apical bud aborted, dormant or vegetative. Flowers bisexual and male, 4.5–7 mm diameter; 4–5-merous (except for gynoecium); almost sessile to pedicellate, the pedicel up to 4 mm long; hypanthium and outside of calyx often sparsely pubescent; calyx lobes 1.8–2.5 by 1–2 mm; petals with basal part 0.6–1.1 mm long, teeth 0.3–0.5 mm long; filaments 1–2 mm long, anthers 0.4–0.6 mm long, apiculate; disc lobes globose, fleshy, 0.5–0.7 mm diameter; ovary 2(–3)-carpellate, in bisexual flowers superior to slightly embedded in hypanthium, ± spherical, 0.8–1.2 by 1–1.5 mm, densely pubescent or rarely glabrous; styles 0.5–1.2 mm long; ovules 2 per locule; ovary in male flowers 0.7 by 1 mm, styles c. 0.3(–0.5) mm long. Fruits ovoid-ellipsoid and pointed at apex or rarely ± spherical, the apex rounded, 1.1–1.4 by 0.7–0.9(–1.1) cm, with bases of styles often persistent; epicarp warty.

Distribution — *Malesia:* widespread in the mountains of New Guinea.

Ecology — In primary and regrowth montane forest, often in the understorey, and in scrub on ridge crests at the highest altitudes; quite common in parts of the Central Highlands and the Owen Stanley Mts, from 2000–3300 m, occasionally as low as 1100 m, and from (570–)800–2000 m in Irian Jaya.

Notes — 1. Frequently a small, sometimes bushy tree or slender treelet, flowering when 3–10 m high; occasionally a tall canopy tree up to 25 m high and 50 cm diameter; rarely a shrub 2–3 m high in mossy scrub at high altitude.

2. The presence of small, pale, spherical glands or reddish resin dots on the underside of mature leaves is characteristic of this species but not completely diagnostic. Sometimes the glands are seen only in young leaves and rarely glands are not seen in material otherwise identical to other collections of *S. gorumensis*. Glands occur occasionally in some other species of the genus, especially *S. novoguineensis*, but usually less consistently. The texture, venation and yellowish-green coloration of the leaves in *S. gorumensis* are also often distinctive, as is the small, axillary inflorescence. Young growth is sometimes pale grey-green.

3. At high altitude the leaves are often small and rounded, as in *S. ilicina*, but in *S. gorumensis*, the venation is minutely prominent and the texture less coriaceous.

4. **Schizomeria ilicina** (Ridl.) Schltr.

Schizomeria ilicina (Ridl.) Schltr., Bot. Jahrb. Syst. 55 (1918) 194; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248; L.M. Perry, J. Arnold Arbor. 30 (1949) 155. — *Cremnobates ilicina* Ridl., Trans. Linn. Soc. London, Bot. 9 (1916) 41, pl. 3, f. 56–63; pl. 4, f. 55. — Type: *Kloss s.n.* (BM holo n.v.), Wollaston Expedition, Camp VIc (Mt Carstensz region), Irian Jaya.

Schizomeria parvifolia L.M. Perry, J. Arnold Arbor. 30 (1949) 152. — Type: *Brass 4576* (A holo; BO), Murray Pass, Wharton Range, Central Prov., Papua New Guinea.

Schizomeria nov. sp. (species no. 4) Schltr., Bot. Jahrb. Syst. 52 (1914) 158. — Specimen cited: *Ledermann 9983* (L), Lordberg, Papua New Guinea.

Tree or rarely shrubby, (3–)10–35 m high, buttresses absent. Twigs glabrous or with very short hairs. Leaves with petiole 0.2–1.7(–2) cm and blade usually coriaceous, 1.7–11.5(–16.5) by 1–7(–8.5) cm, elliptic, oblong, ovate or obovate, with the base cuneate to truncate, rounded or rarely ± cordate and the apex usually rounded or obtuse, sometimes emarginate, rarely acute; glabrous; glands rare; margin crenulate; secondary veins in 9–15 pairs, usually straight and unbranched almost to margin, often ± perpendicular to midrib towards base of blade, subparallel, often closely spaced especially towards base, 2–3 mm apart in small to medium leaves, up to 7 mm apart in larger leaves. Stipules lingulate or narrowly triangular, 4–12 by 1–2.5 mm, glabrous. Inflorescence terminal, well-developed to compact, paniculate to corymbose; median axis 2.5–14 cm long by 2–3(–5) mm diameter, (4–5 mm diameter in fruiting stage), bearing 3–6 pairs of major lateral branches; axes sparsely to densely pubescent. Flowers usually bisexual, (4.5–)6–7 mm diameter; 5–6-merous (except for gynoecium); almost sessile to shortly pedicellate, pedicel below articulation 0.5–2 mm, above 1–2 mm; hypanthium sparsely pubescent; calyx lobes 2.5–3.5 by (1.2–)1.5–2.5 mm, ± glabrous on outer surface; petals (1–)2–4 mm long, basal part 1–2.5 plus teeth 0.5–2 mm; filaments (2–)2.5–3 mm long; disc lobes fleshy, sometimes paired, 0.5–1 mm diameter; ovary 2–3-carpellate, globose to ovate, 1–2 mm diameter, glabrous; styles 1.5–3 mm; ovules c. 10 per ovary. Fruit usu-

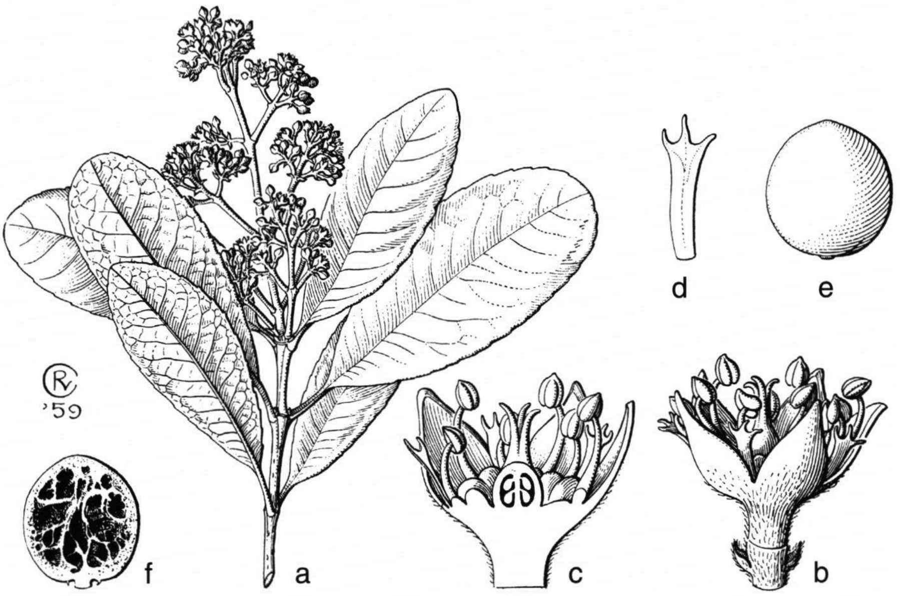

Fig. 26. *Schizomeria ilicina* (Ridl.) Schltr. a. Flowering shoot; b. flower and pedicel, note articulation and bracteoles; c. longitudinal section of flower; d. laciniate petal; e. fruit; f. longitudinal section of fruit, showing vacuoles in endocarp (a–f: *Hoogland & Pullen 5913*). — a × 0.66; b, c × 5; d × 8; e, f × 1.

ally ± spherical, sometimes misshapen, sometimes ellipsoid or oblate, 1.6–3 by 1.3–2.5 cm; epicarp often warty or cracked. — **Fig. 26.**

Distribution — Mt Popomanasiu, Guadalcanal, Solomon Islands and *Malesia:* widespread in the Highlands of New Guinea.

Ecology — Subcanopy, canopy and emergent tree or rarely shrubby, in mixed montane rain forest from (525–)1100–3280 m.

Notes — 1. A variable but often distinctive species, especially at high altitude. The size of the leaves usually decreases with altitude. The pattern of venation, with the secondary veins ± perpendicular to the midrib towards the base of the blade, straight rather than arcuate, and more closely spaced towards the base of the blade than distally, is often characteristic but does occur occasionally in other species. The leaves are usually ± glabrous, except for two collections from the Vogelkop with reddish floccose indumentum.

2. At medium elevations, *S. ilicina* is not always easily distinguished from *S. serrata* except by the ovary, which is normally glabrous in *S. ilicina* and pubescent in *S. serrata*. In addition, the leaves of *S. ilicina* are usually smaller and more coriaceous, often with a rounded rather than a pointed apex.

5. **Schizomeria novoguineensis** L.M. Perry

Schizomeria novoguineensis L.M. Perry, J. Arnold Arbor. 30 (1949) 154. — Type: *Clemens 4763* (A holo; B, K, L), Ogeramnang, Morobe Prov., Papua New Guinea.

Tree 16–40 m high, the bole up to 70 cm diameter, buttresses absent. Twigs sparsely to densely pubescent, later glabrous. Leaves with petiole 0.9–1.7 cm and blade subcoriaceous to coriaceous, 5–11 by 2.5–5.8 cm, elliptic or ovate-elliptic, rarely broadly or narrowly elliptic, with the base acute or rarely somewhat truncate and the apex acute or rarely obtuse; indumentum in mature leaves sparse or absent, and minute glands occasionally present beneath; in young leaves, indumentum sometimes dense and woolly, red-brown; margin crenulate to crenate; secondary veins in 15–20 pairs, generally evenly spaced, prominent beneath. Stipules 0.9–1.5 cm long, broad at base (2–5 mm) and tapering to a narrow tongue 1.5–2 mm wide, rounded at apex, with dense adpressed indumentum on abaxial surface. Inflorescence usually false-terminal, the apical bud aborted, dormant or vegetative; sometimes lateral axes also terminating in a dormant bud or young vegetative growth; median axes up to 11 cm long by 4 mm diameter, bearing up to 4 pairs of major lateral branches; indumentum of short, adpressed to erect or woolly hairs on axes and abaxial surface of bracts. Flowers bisexual or rarely male (?), 4–5 mm diameter; (4- or) 5-merous (except for gynoecium); subsessile or the pedicel 1–2 mm long; calyx lobes 1.3–1.7(–2.5) by 1.1–1.6(–2.7) mm, outer surface somewhat hirsute; petals 1.2–1.6 mm long, the basal part 0.8–1 mm plus teeth 0.4–0.6 mm; filaments 1.1–1.7(–2.3) mm long, anthers 0.5–0.6 mm long, apiculate; disc lobes 0.3–0.5(–0.7) mm diameter; ovary 2-carpellate, half-embedded in hypanthium, somewhat flattened above, c. 1.5(–2) mm diameter by 0.7(–1) mm high (above hypanthium), upper surface densely hirsute, indumentum quickly shed as young fruit develops; styles up to 0.6(–1) mm long; ovules 2–4 per locule. Fruit spherical or slightly oblate, somewhat irregular, up to c. 2 by 2.2 cm; epicarp rough, with numerous pale, circular, warty makings.

Distribution — *Malesia:* Highlands of New Guinea.

Ecology — In montane forest, from 1600–2230 m.

Note — The structure of the inflorescence is unusual and where the apical bud is vegetative, it starts to produce young leaves during flowering. This means that while the flowers are around the edge of the foliage, the fruits will be formed amongst young leaves.

6. Schizomeria orthophlebia L.M. Perry

Schizomeria orthophlebia L.M. Perry, J. Arnold Arbor. 30 (1949) 154. — Type: *Brass & Versteegh 10463* (A holo; BM, L), 9 km NE of Lake Habbema, Irian Jaya.

Tree 32 m high, dbh 55 cm. Twigs with nodes somewhat thickened by an annular scar; internodes glabrous, the most distal ones pruinose. Leaves with petiole 1–2 cm long and blade coriaceous, 5.8–10.8 by 3.9–5.3 cm, oblong-elliptic, with the base truncate and the apex obtuse, rounded or emarginate; glabrous; lacking glands; margin crenate to subentire; secondary veins in 14–22 pairs, ± parallel, the basal ones almost perpendicular to midrib and the distal ones somewhat ascending, not branching until 4/5 distance to margin, generally regularly spaced 0.4–0.8 mm apart. Stipules triangular, c. 8 by 4 mm, glabrous. Flowers not seen. Infructescence terminal or false-terminal, the median axes c. 4 cm long by 4 mm diameter, pubescent. Fruits ovate-ellipsoid, somewhat irregular, the base rather flattened and the apex markedly acute, 2.9–3.7 by 1.4–1.8 cm; epicarp smooth with lenticular dots, probably immature.

Distribution — *Malesia:* known only from the type in the Highlands of Irian Jaya.

Ecology — Montane forest at 2750 m.

Note — The elongated fruits are unique in the genus.

7. Schizomeria serrata (Hochr.) Hochr.

Schizomeria serrata (Hochr.) Hochr., Annuaire Conserv. Jard. Bot. Genève 10 (1907) 118; Valeton, Icon. Bogor. 3 (1907) 69, t. 228; Hochr., Ann. Jard. Bot. Buitenzorg, Suppl. 3 (1910) 859; Merr., Interpr. Herb. Amboin. (1917) 244; Whitmore, Guide to forests of British Solomon Islands (1966) 60; Gard. Bull. Singapore 22 (1967) 5. — *Acronychia serrata* Hochr., Pl. Bogor. Exs. (1904) 49; Bull. Inst. Bot. Buitenzorg 22 (1905) 89. — Type: *Hochreutiner 103* (G holo n.v.; B?, BO, K, L), cultivated in Hort. Bogor., Java, originating from Ambon, Moluccas.

Schizomeria floribunda Schltr., Bot. Jahrb. Syst. 52 (1914) 156, f. 7; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248, f. 145. — Type: *Ledermann 9763* (B holo; K, L), April R., East Sepik Prov., Papua New Guinea.

Schizomeria katastega Mattf., J. Arnold Arbor. 20 (1939) 433; L.M. Perry, J. Arnold Arbor. 30 (1949) 157. — Type: *Brass 7898* (B holo; L), Lake Daviumbu, Middle Fly R., Western Prov., Papua New Guinea.

Schizomeria tegens Mattf., J. Arnold Arbor. 20 (1939) 434. — Type: *Brass 7429* (B holo; BO, L), Oroville Camp, Fly R., Western Prov., Papua New Guinea.

Schizomeria brassii Mattf., J. Arnold Arbor. 20 (1939) 435; L.M. Perry, J. Arnold Arbor. 30 (1949) 157. — Type: *Brass 713* (B? holo n.v.; A, K), Iaritari, Central Prov., Papua New Guinea.

Schizomeria homaliiformis Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 109, f. 5. — Type: *Kanehira & Hatusima 13031* (FU holo n.v., photo at K; BO), Waren, 60 miles S of Manokwari, Vogelkop, Irian Jaya.

[*Tanarius major* Rumph., Herb. Amboin. 3 (1743) 192, t. 122].

[*Arbor verspertilionum altera oppositifolia* Rumph., Herb. Amboin. 7 (1755) 17, t. 10].

Small to large trees, 8–45 m; buttresses frequent, up to 1.5 m high by 2 m wide by 10 cm thick. Twigs terete, glabrous, sometimes pruinose; very young stems pubescent, quickly glabrescent. Leaves with petiole 1–3.3(–4.7) cm and blade chartaceous to subcoriaceous or occasionally coriaceous, (5–)8.5–22.5(–26) by (2–)3.3–9.5 cm, ovate to broadly elliptic, with the base obtuse, truncate or cuneate and the apex usually acute or obtuse, or rarely acuminate, rounded or emarginate; hairs absent; very rarely glandular; margin crenate, crenulate or almost entire, occasionally undulate; secondary veins in 10–15 or more pairs, usually widely spaced, 0.8–1.5 cm apart in mid part of blade, arcuate. Stipules narrowly to broadly triangular, lingulate or ovate, 4–12 by 3–6 mm, glabrous except for ciliolate margin. Inflorescence usually terminal, rarely otherwise; median axes 5.5–16.5(–26.5) cm long, 2–4 mm diameter at base, (up to 4 mm diameter in fruit), with 4–7(–10) pairs of major lateral branches, the lowest ones often in axils of most distal leaves; axes glabrous to pubescent. Flowers mostly bisexual, 4–5(–7) mm diameter; (4–)5(–6)-merous (except for gynoecium); pedicel above articulation c. 1 mm, below 1.5–3 mm; hypanthium and calyx sparsely pubescent to glabrous; calyx lobes 1.8–3(–3.5) by 1.5–2 mm, membranous or not; petals 1.5–2.5(–3) mm long, usually equal to or just shorter than calyx lobes; filaments 1.5–3(–3.5) mm long, anthers c. 0.5 mm long; disc lobes fleshy, 0.5–0.8 mm diameter; ovary 2-carpellate, 1–1.5 mm diameter, usually densely pubescent to pilose, the hairs often reddish, occasionally ± glabrous; styles 0.7–1.5(–3) mm long; ovules 6–8 per ovary. Fruits spherical, ovate or ellipsoid, 1–1.8(–2) by 1–1.5(–1.8) cm, apex rounded or occasionally pointed; epicarp smooth, warty or sometimes with resinous patches.

Distribution — Solomon Islands, including Bougainville, and *Malesia:* Moluccas, New Guinea, Louisiade Archipelago, Bismarck Archipelago (New Britain only).

Ecology — Usually in lowland and foothills primary rain forest, occasionally extending to montane forest, also in strand forest (Vogelkop), savanna woodland with *Melaleuca*, swampy areas with standing water, or forest patches in savanna (Aru Islands and TransFly region). Occasionally reported from ultramafic soils. Sometimes locally common. Generally at low altitude, usually 0–750 m, or rarely up to 1000 m on Morotai and perhaps 1600 m in New Britain.

Notes — 1. This is a variable species, but the only one commonly found at low altitude in Malesia. At medium elevation, vegetative and fruiting material may be difficult to distinguish from *S. ilicina.*

2. In the TransFly region the flowers and inflorescences sometimes approach those of *S. ovata* D. Don from eastern Australia, and the ecology is rather different from elsewhere.

8. Schizomeria versteeghii L. M. Perry

Schizomeria versteeghii L.M. Perry, J. Arnold Arbor. 30 (1949) 158. — Type: *Brass & Versteegh 11129* (A holo; L), Bele R., 18 km NE of Lake Habbema, Irian Jaya.

Tree 12–27 m high. Twigs somewhat flattened at nodes, sometimes pubescent. Leaves with petiole 0.7–1.5 cm and blade coriaceous, 6–21+ (leaf broken) by 3.3–13.7 cm, elliptic or ovate-elliptic, sometimes conduplicate, with the base rounded to truncate and the apex acute-apiculate to acuminate, drying yellowish or yellow-green above, glabrous above and almost so below; glands absent; margin dentate-crenate; secondary veins in 11–20 pairs, for the most part ± evenly spaced, 5–17 mm apart in mid part of blade. Stipules not seen. Inflorescence false-terminal, the apical bud dormant or perhaps aborted; median axis 2.5–4 cm long by 0.6–0.9 cm diameter, with c. 3 pairs of major lateral branches, 3–14.5 cm long; axes, abaxial surface of bracts and buds densely golden brown floccose. Flowers bisexual and male, 8.5–11 mm diameter; 5–6(–7)-merous (except for gynoecium), sessile; calyx lobes 3–5 by 2–3.5 mm, outer surface densely tomentose; petals 3–4.5 mm long, the basal part 1.5–2.5 mm plus teeth 1.5–2.5 mm long; filaments 3.5–4 mm long; anthers c. 1 by 0.8 by 0.5 mm, apiculate; disc lobes 1–1.2 mm diameter; ovary 2–3-carpellate, in bisexual flowers ± conical, 2–3 mm diameter by 1.5–2 mm high, densely tomentose at anthesis, the hairs c. 1 mm long, easily detached; styles 2–3 mm long, glabrous; ovules up to c. 17 (5–6 per locule). Fruit ± spherical, 2.5–2.9 by 2.4–2.7 cm; epicarp warty.

Distribution — *Malesia:* Highlands of New Guinea.

Ecology — In primary and secondary mixed montane forest, at 1900–2780 m altitude.

Note — Most similar to *S. clemensiae*, differing largely in the density of the indumentum, especially on the inflorescence, and in the length of the pedicels (see Perry 1949).

SPIRAEANTHEMUM

Spiraeanthemum A. Gray, Proc. Amer. Acad. Arts 3 (May 1854) 128; U.S. Explor. Exped., Phan. 1 (June 1854) 66 & Atlas (1856) t. 83A; Ann. Sci. Nat. IV Bot. 4 (1855) 176, p.p. as to the lectotype; Seem., Fl. Vit. (1865) 110, t. 17, p.p.; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 237, p.p.; A.C. Sm., J. Arnold Arbor. 33 (1952) 139, p.p.; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 8, p.p.; Hoogland, Blumea 25 (1979) 501, f. 2; A.C. Sm., Fl. Vit. Nova 3 (1985) 6, f. 1, 2A. — Type: *Spiraeanthemum samoensis* A. Gray (lecto of A.C. Smith 1952).

Shrubs or small to medium-sized trees. Twigs somewhat thickened at nodes. Indumentum of simple hairs with secretory glands on leaf surface and veins visible as red dots. Leaves simple, opposite and decussate, the margin entire or crenate-serrate; domatia in axils of veins often present. Stipules interpetiolar, one pair per node, simple, triangular-ovate, caducous. Inflorescences axillary and solitary or occasionally two subunits serially inserted, rarely terminal, paniculate, with branching at proximal nodes opposite and decussate and at peripheral nodes ± alternate, many-flowered, with peduncles 1/5–1/2 of total length, the axes bearing small caducous bracts at nodes. Flowers 3–5-, mostly 4-merous, apetalous, pedicellate, unisexual and plants dioecious. Sepals valvate, subcoriaceous, connate for 1/4–1/2 of their length. Stamens with filaments subulate, glabrous and anthers transverse-oval, incised at apex and base, in female flowers reduced to about half size and probably sterile. Disc in male flower lobed, the number of lobes equal to the number of stamens but united in pairs, the pairs separated by the alternipetalous stamens and with the alternisepalous stamens deeply impressed on the outer surface, ± closely adpressed to form an inverted cone in centre of flower; in female flower lobed, the lobes either free, oblong, as many as and alternating with the filaments, or some or all lobes united in pairs, connate inside alternisepalous stamens. Ovary in male flower absent; in female flower superior, apocarpous, carpels 2–5 and usually equal to the number of sepals, ovoid, hairy, each with 2 ovules; styles continuous with ovary, terete, glabrous or with some hairs in lower part only; stigma terminal, inconspicuous, clavate, papillose. Fruit multiple, a follicetum with (2–)3–5 free follicle-like fruitlets, attached to receptacle at base and each dehiscing along the full length of the adaxial suture, the valves boat-shaped, stiff-coriaceous, their margins minutely thickened, the styles, calyx and sometimes stamens persistent. Seeds 1–few per carpel, glabrous, with a small pointed wing at both ends.

Distribution — 6 species ranging from New Britain through the Solomon Islands, Vanuatu, and Fiji to Samoa; in *Malesia:* a single species in New Britain and New Ireland.

Ecology — In rain forest; in New Britain, New Ireland and the Solomon Islands (including Bougainville) between 700 and 2250 m, elsewhere in the Pacific also occasionally at lower altitudes and in drier vegetation types.

Notes — 1. Smith (1985) suggested that the plants may sometimes be polygamodioecious, the 'female' flowers possibly sometimes having fertile anthers. However, in most specimens, the anthers in female flowers are much reduced compared with those in male flowers.

2. Reference to the occurrence of this genus in Milne Bay Province, Papua New Guinea (Smith 1985) appears to be based on a misidentified specimen of *Pullea*.

Spiraeanthemum macgillivrayi Seem.

Spiraeanthemum macgillivrayi Seem., Fl. Vit. (1866) 111, Hoogland, Blumea 25 (1979) 504. — Type: *McGillivray 59* (BM holo; G, P), Aneityum, Vanuatu.

subsp. **kajewskii** (L.M. Perry) Hoogland, Blumea 25 (1979) 504.

Spiraeanthemum kajewskii L.M. Perry, J. Arnold Arbor. 30 (1949) 139. — Type: *Kajewski 1700* (A holo; BISH, BM, BO, BRI, G, L, P), Kupei Gold Field, Bougainville, Papua New Guinea.

Shrub or slender tree up to 20 m with 10 m bole. Twigs with open tomentum of thin, ± adpressed hairs, glabrescent; the hairs short (c. 0.1 mm) or longer (c. 0.5+ mm), the longer ones mainly immediately below and on abaxial side of stipules. Leaves with petiole (8–)15–30(–35) mm, the blade elliptic to oblong or ovate, (4.5–)6–13(–15) by 2–5 (–6.5) cm, the nerves (7–)10–14(–16) on either side of midrib; apex and base obtuse to broadly acute, the base slightly decurrent along petiole; margin shallowly to distinctly dentate; indumentum lacking. or midrib and nerves on both surfaces very shortly hirsute, early glabrescent; domatia in axils of secondary and sometimes tertiary veins, usually with hairs. Stipules ovate-lanceolate, 8–14 by 4–5 mm, villose with adpressed hairs to 0.5 mm long beneath, glabrous above, rounded at apex. Inflorescence up to 15 by 10 cm, with up to c. 400 flowers; peduncle and branches fairly densely and very shortly hirsute near base, to more sparingly so towards extremities. Flowers with pedicel 0.4–2.5 mm long, distinctly articulated, glabrous above articulation. Calyx 1.4–2.2 mm long, glabrous; lobes ovate, 0.6–1 mm wide, acute. Stamens in male flowers with filaments 1.8–2.8 mm long and anthers 0.2–0.35 by 0.4–0.5 by 0.15–0.2 mm. Disc lobes in male flowers 0.6–1 mm long, 0.2–0.25 mm wide at base, 0.3–0.4 mm wide at apex, with some stiff hairs up to 0.4 mm long near apex or wholly glabrous; in female flowers disc lobes 0.4–0.6 mm long, 0.15–0.2 mm wide at base and 0.2–0.3 mm at apex, glabrous. Ovary 2–5-, usually 4-carpellate; carpels 0.8–1 by 0.35–0.4 mm, fairly densely and shortly strigose-hirsute, the hairs c. 0.2 mm long, the styles 0.4–0.5 mm long. Fruit with fruitlets each 3–3.5 by 1–1.2 mm, each with 2 seeds. Seeds ovoid, c. 0.9 by 0.4 mm, the terminal wings 0.8 mm long.

Distribution — Solomon Islands and in *Malesia:* New Britain and New Ireland; subsp. *macgillivrayi* occurs in Vanuatu.

Ecology — In lower montane forest, 900–1830 m, with *Nothofagus* species.

Notes — 1. The buds are yellowish green and the flowers are white to yellow-cream, the perianth being light green or cream, the filaments and anthers, styles and stigmas white, the ovary light green and the pedicels pink. The scent is described as fresh or slightly musty.

2. The venation is usually distinctive and characteristic, with each secondary vein branching into two towards the margin, and each of the two branches reaching the margin at adjacent sinuses, i.e. simple craspedodromous.

SPIRAEOPSIS

Spiraeopsis Miq., Fl. Ned. Ind. 1 (1) (1856) 719; in De Vriese, Pl. Ind. Bat. Orient. (1857) 155; Baill., Adansonia 10 (1871) 152; Boerl., Handl. Fl. Ned. Ind. 1 (2) (1890) 443; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 244; L.M. Perry, J. Arnold Arbor. 30 (1949) 145; Hutch., Gen.

Flow. Pl. Dicot. 2 (1967) 11. — *Dirhynchosia* Blume, Flora 41 (1858) 254; in C. Muell., Walp. Ann. Bot. Syst. 5 (1858) 31 '*Dichynchosia*'. — Type: *Cunonia celebica* Blume = *Spiraeopsis celebica* (Blume) Miq. = *Dirhynchosia celebica* (Blume) Blume.

Betchea Schltr., Bot. Jahrb. Syst. 52 (1914) 146; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 241; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 10. — Type: *Betchea rufa* Schltr. (lecto of Hutchinson 1967).

Caldcluvia D. Don p.p., sensu Hoogland, Blumea 25 (1979) 481.

Shrub or small to large trees. Twigs often densely hirsute, glabrescent or sometimes subglabrous. Indumentum of stellate and simple hairs; orbicular peltate trichomes present but variable in density and distribution on leaves and inflorescence. Leaves opposite and decussate, imparipinnate (commonly 2–4-jugate) or trifoliolate; tuft-domatia frequently present in axils of secondary veins in some species. Stipules interpetiolar, one pair per node, ± orbicular with apex rounded and somewhat curled back, or reniform, ± caducous. Stipels sometimes present at bases of leaflets. Inflorescences axillary, paniculate thyrses, many-flowered, branching at the proximal nodes opposite, then often soon becoming alternate, the main axes often strongly dominant and flowers borne singly or in small fascicles on relatively short, lateral axes. Flowers 4–5-merous (except gynoecium), petaliferous, ± sessile or shortly pedicellate, bisexual but markedly protandrous; in male stage, calyx lobes just separated, filaments exserted, styles very short, incurved; in female stage, calyx lobes spreading, corolla and filaments fallen, styles gradually elongating and straightening. Sepals valvate, ovate to triangular, attached to hypanthium at their greatest width, not connate, glabrous above. Petals elliptic with the base attenuate, to obovate, ± equal in length to sepals, fugaceous. Stamens with filaments thin, subulate, glabrous and anthers broadly cordate, the connective shortly extended. Disc annular to ± distinctly lobed, the number of lobes equal to the number of stamens and sometimes united in pairs, the pairs separated by the alternipetalous stamens and with the alternisepalous stamens deeply impressed on the outer surface, glabrous. Ovary syncarpous, superior, carpels 2–5, hairy, each bearing a glabrous, cylindrical style; locules each containing 6–16 ovules arranged in 2 rows; stigma terminal, small. Fruit dehiscent, capsular, the valves boat-shaped, as many as carpels, coriaceous in central part and thin at the edges (lateral extensions of the endocarp), the margins (placentae) of each valve often partially detaching to form a persistent replum, the margin on each side of a valve detached from valve at base but connate with margin of adjacent valve, then distally free from both valve and adjacent margin, and finally reunited with valve at apex; calyx and base of styles persistent. Seeds several, small, elongate, with narrow, sub-equal wings at each end. — **Fig. 27–34.**

Distribution — Solomon Islands and *Malesia:* Philippines, Sulawesi, Moluccas, New Guinea, New Britain & New Ireland. Six species, one of which is widespread; the others are confined to New Guinea.

Ecology — Mainly in the lower montane forest zone, occurring inside the forest either as a canopy tree or in the lower or middle understorey, or outside the forest in secondary growth. Some species descend to the lowlands while others extend to the subalpine zone where they occur as shrubs or small trees on the forest edge or in the subalpine grassland. From 250–3300 m in Malesia; from 100 m upwards in the Solomon Islands.

Notes — 1. In addition to the stellate hairs, shortly stalked, orbicular, glandular, peltate hairs occur in this genus (see p. 60–62). They are especially noticeable in *Spiraeopsis celebica* and *S. clemensiae*, where they are most obvious on the lower surface of the leaves, but they may occur also on the upper leaf surface, on vegetative branchlets, on the inflorescence up to the pedicel and outer surface of the calyx, and sometimes amongst the hairs on the ovary. In herbarium material they are usually bright orange and appear ± spherical at low magnification. They are referred to in the key and descriptions as glandular trichomes or glandular hairs.

2. In the open flowers, the alternisepalous stamens are slightly longer and less deeply impressed in the outer edge of the disc than are the alternipetalous ones. In bud however, the alternipetalous stamens are distinctly longer and apparently more advanced than the alternisepalous ones.

3. Protandry is marked in most flowering collections. Usually all flowers in one inflorescence, and often most inflorescences on one tree, are at approximately the same stage, thereby giving the impression that the species are dioecious.

KEY TO THE SPECIES

1a. Ovary 2-carpellate, at most an occasional flower on the same plant 3-carpellate 2
b. Ovary 3–5-carpellate, at most an occasional flower on the same plant 2-carpellate 3
2a. Venation distinctly sunken on upper leaf surface; lower surface of leaf hirsute (hairs simple or mainly stellate) without glandular trichomes .... **1. S. brassii**
b. Venation slightly prominent on upper leaf surface; lower leaf surface (and usually many other parts also) with glandular trichomes .... **2. S. celebica**
3a. Leaves densely velutinous beneath, the tomentum consisting of a closed underlayer of very short pale (fulvous) hairs from between which short stellate hair groups emerge; flowers (4- or) 5-carpellate .... **4. S. fulva**
b. Leaves fairly densely stellate-hairy with intervenium mostly clearly visible between hairs to glabrous beneath; flowers 2–4-carpellate 4
4a. Flowers minute (e.g. sepals c. 0.6–0.8 mm long); younger twigs and peduncles with tomentum consisting of simple hairs up to 3 mm long and/or very short stellate hairs up to 0.1 mm long, or glabrous .... **5. S. papuana**
b. Flowers small (e.g. sepals c. 1–1.3 mm long); younger twigs and peduncles with fairly dense to dense tomentum consisting of very short or longer stellate hairs, up to 1 mm long 5
5a. Leaflets fairly large, generally 8–17 by 2.5–9 cm; tomentum on lower side of leaflets stellate with hairs 0.2 mm long or more, sometimes with some glandular trichomes .... **6. S. rufa**
b. Leaflets fairly small, generally 4–7 by 1.5–3.2 cm; tomentum on lower side of leaflets stellate with hairs up to 0.1 mm long with some longer simple hairs, and always with conspicuous glandular trichomes .... **3. S. clemensiae**

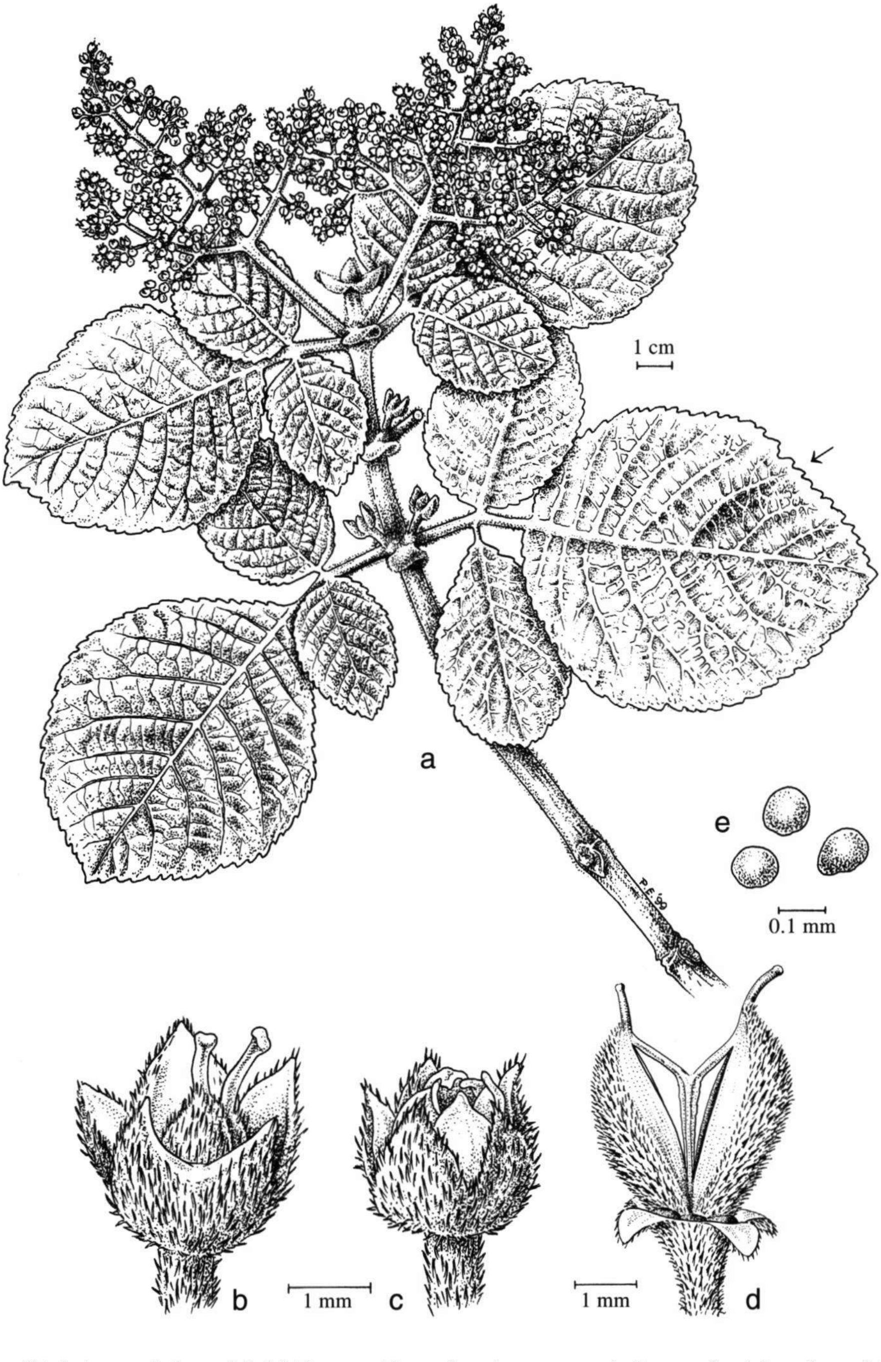

Fig. 27. *Spiraeopsis brassii* L.M. Perry. a. Flowering shoot, arrow indicates abaxial surface of the leaf; b. flower at female stage; c. flower at male stage; d. mature dehisced fruit, note 'replum'; e. seeds (a–e: *Streimann 8575*, L).

1. Spiraeopsis brassii L.M. Perry

Spiraeopsis brassii L.M. Perry, J. Arnold Arbor. 30 (1949) 147. — *Caldcluvia brassii* (L.M. Perry) Hoogland, Blumea 25 (1979) 484. — Type: *Brass 4852* (A holo; BO, BRI, NY, US), Mt Tafa, Central Prov., Papua New Guinea.

Spiraeopsis pubescens L.M. Perry, J. Arnold Arbor. 30 (1949) 148. — Type: *Clemens 3429* (A holo; B, G, L), Yoangen, Huon Peninsula, Papua New Guinea.

Shrub or small to large tree, up to 30 m tall. Twigs densely hirsute, hairs rusty brown, later glabrescent. Leaves 1–2-jugate, occasionally some on the same plant unifoliolate. Petiole 2.5–5(–7) cm, densely hirsute; rachis, if present, 3–5(–7.5) cm. Leaflets elliptic, sometimes ± rhomboidal or nearly orbicular to oblong, 5–11(–18) by 2.5–7(–13) cm, the terminal leaflet generally larger than the laterals, apex obtuse to acute or sometimes slightly acuminate, base obtuse and decurrent or rarely rounded; petiolule 1–2 (– 4) cm long in terminal leaflets and 1–3(–8) mm long in lateral ones; margin distinctly serrate; nerves in 7–12(–17) pairs. Upper surface of leaflets glabrous, with venation distinctly sunken; lower surface very densely to rather sparsely rusty hirsute, lateglabrescent (often in patches), with prominent venation. Domatia absent. Stipules broadly ovate or reniform, 8–12 by 10–15 mm, sessile or with a very short stalk, apex rounded, margin ± deeply dentate, surface densely hirsute. Inflorescence thryrsiform, up to c. 40 by 20 cm; usually one subunit per axil, at distal or subdistal nodes; branches densely hirsute throughout. Flowers shortly pedicellate, the pedicel up to 1.2 mm long, densely hairy. Sepals 1–1.6 by 0.8–1.5 mm, densely stellate-hirsute below. Petals narrowly obovate or oblanceolate, 1.1–1.5 by 0.4–0.5 mm. Stamens with filaments c. 1.8 mm long and anthers 0.3 by 0.3 by 0.2 mm. Disc 0.4–0.8 mm high, 0.2–0.3 mm thick. Ovary 2-carpellate, 0.7–1.3 by 0.5–1.1 mm, densely stellate-hirsute, often with rounded glands; ovules 10–14 per locule; style 0.9–1.2 mm. Fruit with valves 3.5–6 mm long, 2–3 mm wide, with several seeds. Seeds including wings c. 1.8 mm long, surface papillose. — **Fig. 27.**

Distribution — *Malesia:* thus far only known from the eastern half of New Guinea. — Fig. 28.

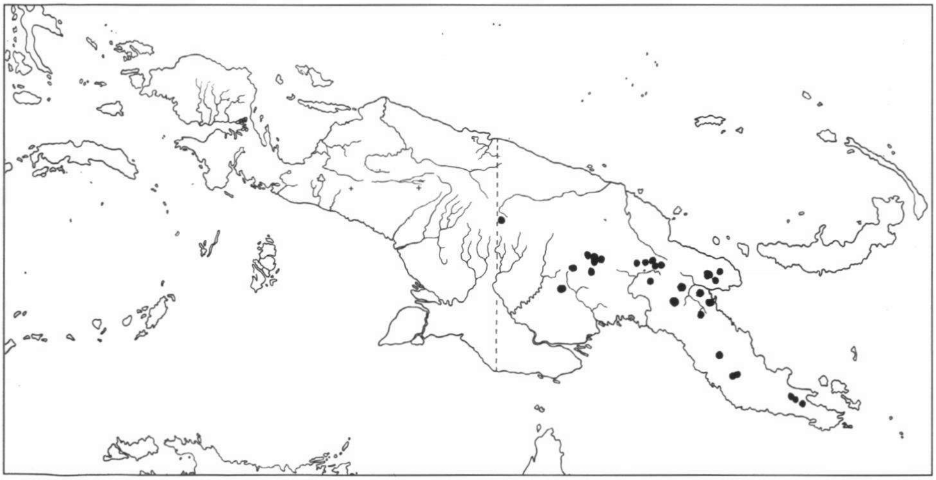

Fig. 28. Distribution of *Spiraeopsis brassii* L.M. Perry.

Ecology — In lower montane forest from (1400–)1800 m upwards to 3300 m as an upper canopy tree or in the understorey; at higher altitudes frequently in forest regrowth, on landslides, on the forest-grassland edge, in low mossy forest, or even in subalpine grassland.

Notes — 1. The plant is often very distinctive because of the dense, rusty brown indumentum on the axes and lower sides of the leaves.

2. The flowers are generally olive-brown, the sepals rusty brown outside and purple-red inside, the petals are pink to white but fugacious, the filaments are purple, the anthers white or yellow, the disc deep purple, and the styles purple. Young fruits are pale green to pale brown.

3. Used for construction (*Vaii NGF 17157*).

2. Spiraeopsis celebica (Blume) Miq.

Spiraeopsis celebica (Blume) Miq., Fl. Ned. Ind. 1 (1) (1856) 719; in De Vriese, Pl. Ind. Bat. Orient. (1857) 155; Koord., Meded. Lands Plantentium 19 (1898) 450; Merr. & Rolfe, Philipp. J. Sci., Bot. 3 (1908) 101; Koord., Suppl. Fl. Celebes 1 (1918) 21, t. 7a-b; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 224; Burtt, Bull. Misc. Inf. Kew 1936 (1936) 462; L.M. Perry, J. Arnold Arbor. 30 (1949) 145. — *Dirhynchosia celebica* (Blume) Blume, Flora 41 (1858) 254; in C. Muell., Walp. Ann. Bot. Syst. 5 (1858) 31, '*Dichynchosia*'. — *Caldcluvia celebica* (Blume) Hoogland, Blumea 25 (1979) 485. — *Cunonia celebica* Blume, Bijdr. Fl. Ned. Ind. (1826) 868. — *Spiraea arborea* Reinw. ex Miq. in De Vriese, Pl. Ind. Bat. Orient. (1857) 156, pro syn.; Reinw. (ed. De Vriese), Reis Oostel. Ged. Ind. Arch. (1858) 594, nom. nud. — Type: *Reinwardt 1549* (L lecto of Hoogland 1979), Lukon and Rumagang Mts, N Sulawesi.

Spiraeopsis philippinensis Elmer, Leafl. Philipp. Bot. 8 (1915) 2826. — Type: *Elmer 14157* (L lecto of Hoogland 1979; A, B, BISH, BM, FI, G, K, NSW, NY, US, W, Z), Cabadbaran (Mt Urdaneta), Agusan Prov., Mindanao, Philippines.

Spiraeopsis glabrescens L.M. Perry, J. Arnold Arbor. 30 (1949) 149. — Type: *Clemens 7052A* (A holo; B, L), Sambanga, Huon Peninsula, Papua New Guinea.

Spiraeopsis luzonensis Elmer, Leafl. Philipp. Bot. 10 (1939) 3810, pro syn.

Tree to 40 m tall, bole 80 cm diameter. Twigs densely hirsute, the hairs simple, up to 2 mm long, and/or very short, stellate; orange glandular hairs or their bases present; glabrescent. Leaves 1–4-jugate. Petiole 3–9(–11) cm, internodes of the rachis 2–4(–6) cm, hirsute and/or shortly stellate-hirsute. Leaflets oblong to obovate-oblong or ovate-oblong, 8–15(–25) by 4–7(–12) cm, the apex acute or often slightly acuminate, the base acute and decurrent to rounded; margin distinctly serrate to subentire; nerves 12–15 (–20) on either side of midrib; petiolule in terminal leaflet 1–2(–2.5) cm long, in lateral leaflets 3–6 mm; each lateral leaflet often with a small stipel; leaflets above sparsely short-hirsute, glabrescent, with slightly prominent venation; leaflets below glabrous or with closed to sparse tomentum of very short lanose hairs mainly on intervenium, and longer hirsute hairs mainly along midrib and major veins, also with ± numerous orange glandular hairs or their bases, the venation prominent. Tuft-domatia often present in axils of secondary veins. Stipules broadly ovate to reniform, sessile or with short stalk, 5–18 by 7–24 mm, apex obtuse to rounded or retuse, margin entire to dentate, upper surface sparsely hirsute to glabrous, lower surface hirsute and with orbicular glandular trichomes. Inflorescences paniculate/thyrsiform, up to c. 50 by 30 cm, usually maturing in subdistal nodes; branches ± densely hirsute, most densely so at extremities. Flowers

Fig. 29. *Spiraeopsis celebica* (Blume) Miq. Shoot with immature inflorescence (*Bradford 840*, Kolombangara, Solomon Islands). Photo by J.C. Bradford.

sessile or pedicellate, the pedicels up to 2 mm long. Sepals 0.9–1.3 by 0.6–1.1 mm, stellate-hairy and with glandular trichomes beneath. Petals obovate-spathulate to oblanceolate-oblong, 0.8–1.4 by 0.4–0.5 mm. Stamens with filaments 1.6–3.2 mm long and anthers c. 0.3 by 0.3 by 0.2 mm. Disc 0.3–0.4 mm high, 0.1–0.2 mm thick. Ovary 2(–3)-carpellate, 0.6–0.8 by 0.6–1 mm, densely stellate-hirsute, often with glandular trichomes; ovules 8–16 per locule; style 0.6–1.7 mm. Fruit with valves 2.5–4 mm long, 1.5–2 mm wide, with several seeds. Seeds including wings to c. 1.6 mm long, papillose. — **Fig. 29.**

Distribution — Solomon Islands and in *Malesia:* from the Philippines (SE Luzon to Mindanao) and Sulawesi through the Moluccas (Halmahera, Ternate) to New Guinea (rare in the western half), New Britain and New Ireland. — Fig. 30a, b.

Ecology — In primary and secondary forest, generally between 500 and 2000 m, in New Guinea up to 2800 m, in New Britain down to 250 m and in the Solomon Islands to 100 m. Sometimes an early invader of secondary grassland.

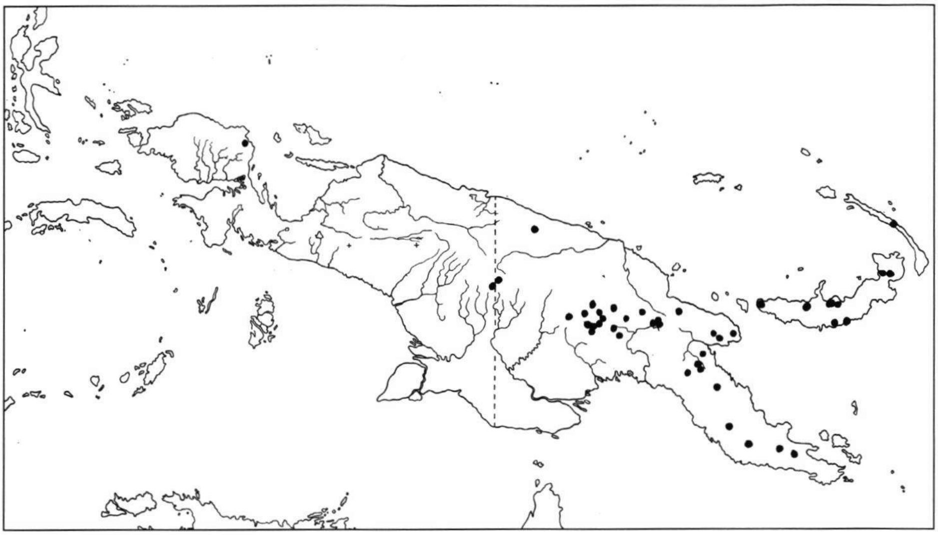

Fig. 30a. Distribution of *Spiraeopsis celebica* (Blume) Miq. in New Guinea and the Bismarck Archipelago only.

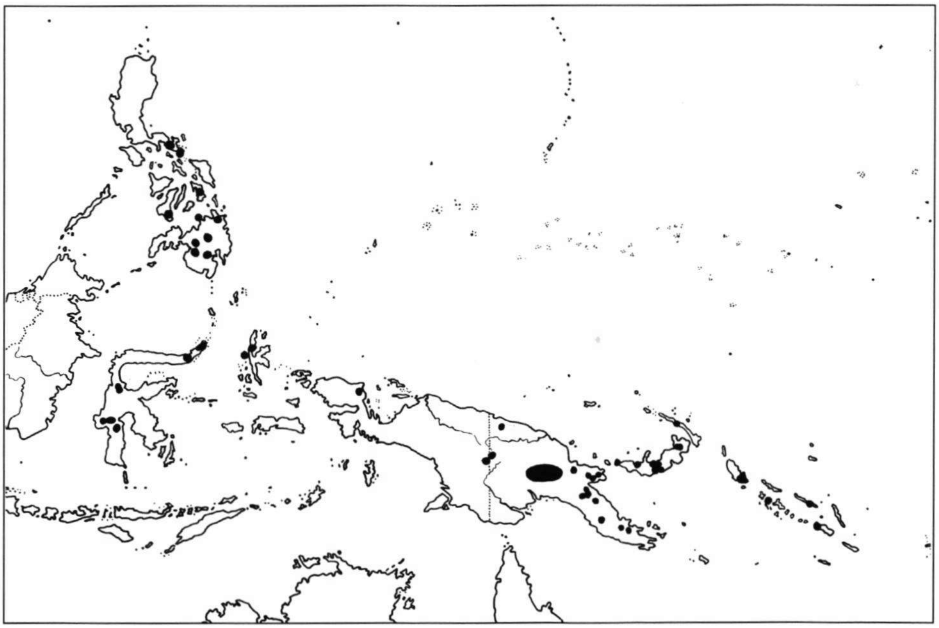

Fig. 30b. Distribution of *Spiraeopsis celebica* (Blume) Miq.

Notes — 1. The number of leaflet pairs varies geographically, 3 or 4 pairs being most common in the western part and 1 or 2 pairs in the eastern part. A 6-jugate leaf is known only from a young plant found in Sulawesi.

2. The flowers are rather variable in colour, ranging from cream, whitish-brown, -green, or -yellow to deep mauve or crimson, the stamens being white or pale straw with yellow anthers, and the styles purplish brown or red. They are reported as sweetly scented or not (e.g. *Stevens LAE 58476*; *Endress 4065*). Young fruit are yellow-green or green tinged with red, and brownish at maturity. Young leaves are purplish or red.

3. Formerly used for carving of wooden plates (*Havel & Kairo NGF 17084*, Bulolo).

3. **Spiraeopsis clemensiae** L.M. Perry

Spiraeopsis clemensiae L.M. Perry, J. Arnold Arbor. 30 (1949) 149. — *Caldcluvia clemensiae* (L.M. Perry) Hoogland, Blumea 25 (1979) 486. — Type: *Clemens 7568* (A holo; '*7558*' B), Sattelberg, Masak R., Huon Peninsula, Papua New Guinea.

Tree to 20 m tall. Twigs densely hirsute with very short and a few longer stellate hairs to 0.3 mm, glabrescent. Leaves 2–3-jugate. Petiole 1.2–3 cm, internodes of rachis 0.8–2 cm, densely and very shortly stellate-hirsute. Leaflets elliptic, 2.5–7 by 1.5–3.2 cm, apex obtuse and shortly acuminate, base obtuse to rounded or subcordate, very shortly decurrent; margin serrate; secondary veins 8–12 on either side of midrib; indumentum of stellate hairs above and beneath, glabrescent, with fairly numerous glandular trichomes on lower surface; the major venation sunken above and beneath. Petiolule in terminal leaflets 8–15 mm, 3–6 mm in lateral ones. Tuft-domatia sometimes present in axils of secondary veins. Stipules orbicular to ovate, 7–12 by 7–10 mm, apex rounded, margin entire, glabrous above, fairly densely stellate-hirsute below. Inflorescences paniculate, up to c. 25 by 15 cm, inserted at subdistal nodes; branches densely stellate-hirsute. Flowers pedicellate, the pedicels 0.8–2 mm long. Sepals c. 1.2 by 0.9 mm, fairly densely stellate-hirsute beneath. Petals obovate, c. 1.3 by 0.6 mm, narrowed at base. Stamens with filaments c. 1.8 mm long and anthers c. 0.4 by 0.4 by 0.2 mm. Disc c. 0.4 mm high, 0.3 mm thick. Ovary 3- or 4-carpellate, c. 0.8 by 1 mm, densely stellate-hirsute; ovules 8–10 per locule; style c. 0.8 mm. Fruit with valves 2.5–3 mm long by 1–1.2 mm wide, containing several seeds. Seeds including wings c. 1.5 mm long, smooth.

Distribution — *Malesia:* restricted to NE New Guinea, in the Central Highlands from Mt Wilhelm to Goroka, in the Finisterre Range, and in the mountains of the Huon Peninsula from Mt Sarawaket eastwards. — Fig. 31.

Ecology — In lower montane forest, including *Podocarpus* and *Nothofagus* forest, as a canopy tree or usually in the second storey; also in secondary forest and low mossy forest. Locally common. From 2100–2850 m.

Note — Flowers cream or brown with pinkish brown calyx and cream stamens. Young leaves red.

4. **Spiraeopsis fulva** (Schltr.) L.M. Perry

Spiraeopsis fulva (Schltr.) L.M. Perry, J. Arnold Arbor. 30 (1949) 147. — *Betchea fulva* Schltr., Bot. Jahrb. Syst. 52 (1914) 148. — *Caldcluvia fulva* (Schltr.) Hoogland, Blumea 25 (1979) 486. — Type: *Ledermann 12160* (B holo), Schrader Mt, East Sepik, Papua New Guinea.

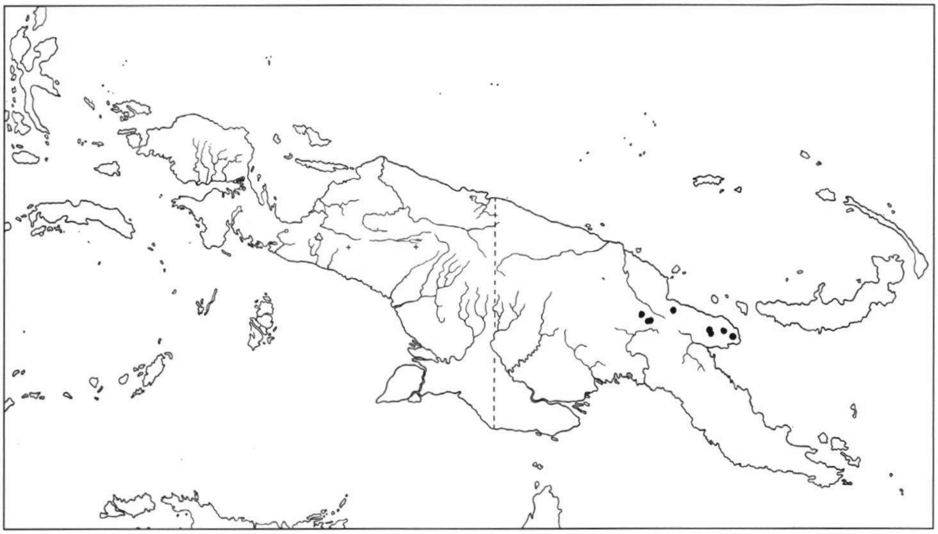

Fig. 31. Distribution of *Spiraeopsis clemensiae* L.M. Perry.

Betchea aglaiaeformis Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 106, f. 2. — Type: *Kanehira & Hatusima 13907* (FU holo n.v., photo K; A), Anggi Giji Lake, Arfak Mts, Irian Jaya.

Tree to 34 m tall, bole 45 cm diameter. Twigs densely velutinous with very short stellate hairs, glabrescent. Leaves 1–2-jugate. Petiole 3–9 cm, rachis if present 2–3.5 cm, densely stellate-velutinous. Leaflets ovate to oblong, 5–14 by 2.5–6.5 cm, apex acute to slightly acuminate, base obtuse to rounded, shortly decurrent; margin serrate to subentire; secondary veins 9–20 on either side of midrib; petiolule 10–17 mm in terminal leaflets and 1–3 mm in lateral ones; stipels minute or absent; blades above stellate-hairy with sunken venation, beneath very densely stellate-velutinous, the tomentum of dense layers of pale short curly hairs and scattered emergent ones together with ± numerous glandular trichomes, the venation prominent; domatia absent. Stipules orbicular or ovate-oblong, 7–17 by 7–10 mm, rounded at apex, entire, sessile, densely stellate-velutinous above and beneath. Inflorescence paniculate, up to c. 30 by 20 cm, subunits inserted at subdistal nodes; branches densely velutinous. Flowers pedicellate, the pedicels 1–1.5 mm long. Sepals 0.8–1.1 by 0.6–0.8 mm, densely stellate-hirsute below. Petals obovate-oblong or oblanceolate, 1.1–1.2 by 0.2–0.7 mm. Stamens with filaments 1.2–1.8 mm long and anthers c. 0.3 by 0.4 by 0.2 mm. Disc 0.2–0.4 mm high, 0.1–0.2 mm thick. Ovary (3–)4–5-carpellate, 0.6–0.8 by 0.5–0.7 mm, densely stellate-hirsute, each cell with c. 10 ovules; style 0.4–0.5 mm. Fruit with valves c. 4 by 1.2 mm, with several seeds. Seeds including wings c. 1.8 mm long, glabrous.

Distribution — *Malesia:* fairly widespread throughout New Guinea, from the Vogelkop to the SE peninsula. — Fig. 32.

Ecology — In mixed lower montane forest, including *Nothofagus* forest, also in open forest, secondary growth, and on forest edge, between 1600 and 2900 m altitude.

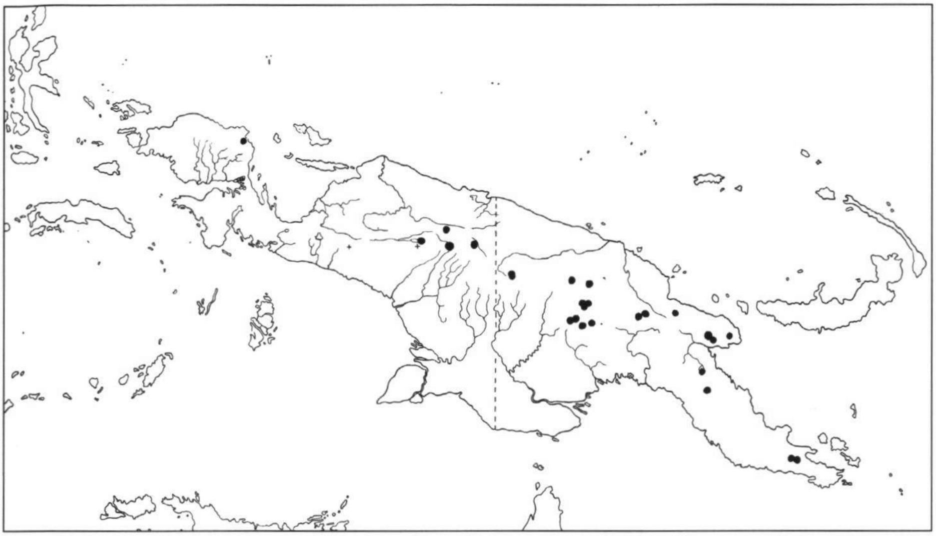

Fig. 32. Distribution of *Spiraeopsis fulva* (Schltr.) L.M. Perry.

Notes — 1. The flowers are whitish cream to dull yellow with light brown pubescence, with a weak scent of honey (*Jacobs 8604*). The filaments are white, the anthers white to yellow, the ovary reddish, the styles white or purplish and the stigmas pinkish. Mature fruits are greenish brown or yellowish brown. Young leaves and shoots are tinged ochre or pale brown.

2. The leaves often dry reddish brown, pale brown or yellowish on the underside, while the upperside dries much darker. The venation is often rather distinctive, with fairly numerous straight, parallel secondary veins reaching unbranched almost to the margin.

5. Spiraeopsis papuana (Pulle) L.M. Perry

Spiraeopsis papuana (Pulle) L.M. Perry, J. Arnold Arbor. 30 (1949) 150. — *Ackama papuana* Pulle, Nova Guinea 8 (1912) 645. — *Betchea papuana* (Pulle) Schltr., Bot. Jahrb. Syst. 52 (1914) 150; Nova Guinea 12 (1917) 491. — *Caldcluvia papuana* (Pulle) Hoogland, Blumea 25 (1979) 489. — Type: *von Römer 819* (U holo; B, L), foothills of Hellwig Mts, Irian Jaya.

Betchea myriantha Schltr., Bot. Jahrb. Syst. 52 (1914) 150. — *Spiraeopsis myriantha* (Schltr.) L.M. Perry, J. Arnold Arbor. 30 (1949) 150. — Type: *Ledermann 8469* (B holo), Mt Hunstein, East Sepik, Papua New Guinea.

Spiraeopsis pometiiformis Ridl., Trans. Linn. Soc. London, Bot. 9 (1916) 37. — Type: *Kloss s.n.* (BM holo; K), Utakwa R. to Mt Carstensz, Camp VIb, Irian Jaya.

Tree to 25 m tall, 35 cm diameter. Twigs with few short stellate hairs and/or simple erect hairs up to 3 mm long, to subglabrous. Leaves 2–5(–7)-jugate. Petiole 2–6 cm, internodes of rachis 1.5–5 cm, with tomentum as on the twigs. Leaflets ovate-oblong or elliptic to oblong, 4.5–16 by 3–6 cm, apex acute and slightly to distinctly acuminate, base obtuse to rounded and only slightly or not decurrent; margin serrate to subentire; petiolule 1–2 cm in terminal leaflets and up to 5 mm in lateral ones; small stipels sometimes present; secondary veins 9–16 on either side of midrib; leaflet blades above mostly glabrous with venation slightly prominent, beneath shortly stellate-hairy and/or hirsute, mainly along midrib and nerves, or glabrous, sometimes also with glandular trichomes, the venation prominent; tuft-domatia in axils of secondary veins absent or occasionally weakly developed. Stipules reniform to orbicular or broadly ovate, 3–15 by 3–18 mm, rounded at apex, entire, sessile, glabrous above with tomentum beneath similar to that on lower surface of leaflets. Inflorescence paniculate/thyrsiform, up to c. 50(–76) by 30 cm; at distal or subdistal nodes; indumentum on axes varying from sparsely short stellate-hirsute and/or hirsute with hairs up to 3 mm long on peduncle to densely and shortly stellate-hirsute in distal branchlets. Flowers pedicellate, the pedicels 0.2–0.7 mm long. Sepals 0.6–0.8 by 0.4–0.5 mm, fairly densely stellate-hirsute outside. Petals oval to obovate to oblanceolate, 0.6–1.1 by 0.3–0.4 mm. Stamens with filaments 1.3–1.7 mm long and anthers 0.2–0.3 by 0.2–0.4 by 0.1–0.2 mm. Disc 0.1–0.2 mm high, 0.1 mm thick. Ovary 3- (or 4-)carpellate, 0.4–0.7 by 0.4–0.8 mm, ± densely stellate-hirsute, each cell with 8–14 ovules; style 0.3–0.6 mm. Fruit with valves c. 3.5 mm long, 1.3 mm wide, with several seeds. Seeds including wings to c. 1.8 mm long, glabrous.

Distribution — *Malesia:* in the central mountain range of New Guinea from Mt Jaya (Carstensz) and Mt Trikora (Wilhelmina) eastwards. — Fig. 33.

Ecology — In lower montane forest (including *Castanopsis* and *Nothofagus* forest) extending into the lowland, foothill forest, between 450 and 2350 m; also in secondary forest of the same zone.

Notes — 1. The species varies a great deal in its tomentum, with a particularly hirsute form occurring in the Telefomin area.

2. The flowers are usually reported as pink to red (pale purple-pink, deep pink or maroon) or occasionally green, the perianth reddish with conspicuous cream to white filaments, the anthers cream to yellow, the ovary maroon and the stigmas pink. The fruits are dull red. Young leaves are conspicuously red, and the branchlets dark purple.

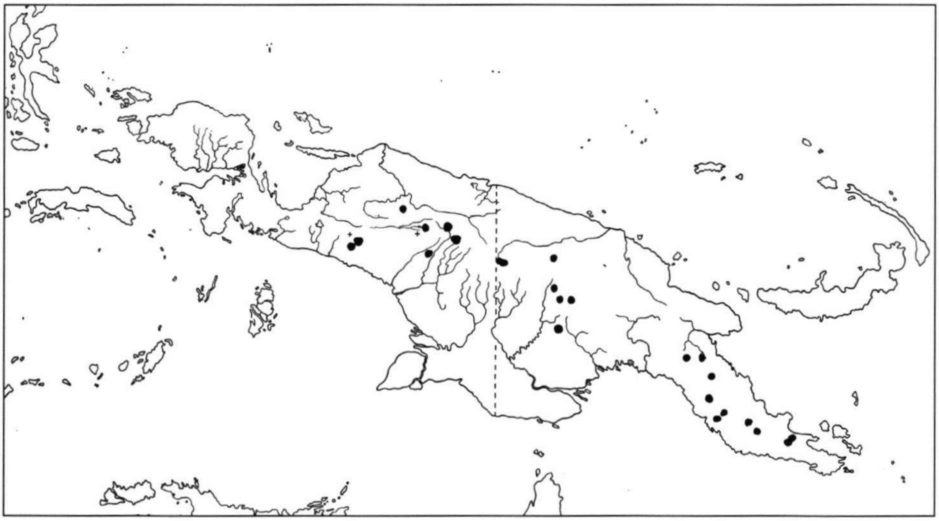

Fig. 33. Distribution of *Spiraeopsis papuana* (Pulle) L.M. Perry.

6. Spiraeopsis rufa (Schltr.) L.M. Perry

Spiraeopsis rufa (Schltr.) L.M. Perry, J. Arnold Arbor. 30 (1949) 147. — ***Betchea rufa*** Schltr., Bot. Jahrb. Syst. 52 (1914) 148, f. 4A–G. — ***Caldcluvia rufa*** (Schltr.) Hoogland, Blumea 25 (1979) 489. — Type: *Schlechter 17780* (B lecto of Hoogland 1979; K, P, UC, all as *17780a*), Kani Mts, Madang, Papua New Guinea.

Spiraeopsis canariifolia Ridl., Trans. Linn. Soc. London, Bot. 9 (1916) 37. — Type: *Kloss s.n.* (BM lecto of Hoogland 1979), Utakwa R. to Mt Carstensz, Camp III-VIII, Irian Jaya.

Tree to 35 m tall, 50 cm diameter. Twigs densely velutinous with short stellate hairs, glabrescent. Leaves 1–3-, mostly 2-jugate. Petiole 2–7 cm, internodes of rachis 1.5–5 cm, densely velutinous. Leaflets ovate-oblong, 4.5–17 by 2–9 cm, 10–15-nerved, apex acute or slightly acuminate, base obtuse to rounded or subcordate; margin minutely serrate; petiolule 1.5–4 cm in terminal leaflets, 2–5 mm in lateral ones; blades above sparsely to densely stellate-hirsute, glabrescent, with venation slightly sunken, below ± densely stellate-hirsute and sometimes with ± abundant glandular trichomes, the venation distinctly prominent; domatia absent. Stipules reniform or orbicular to ovate, 10–15 by 10–12 mm, rounded at apex, entire, sessile, sparsely stellate-hirsute or glabrous above, densely velutinous beneath. Inflorescences thyrsiform, c. 40–30 mm, inserted at subdistal nodes; branches densely stellate-velutinous, towards extremities sometimes with small glands. Flowers pedicellate, pedicels 0.3–1.2 mm long. Sepals 0.9–1.3 by 0.6–1 mm, ± densely stellate-hairy beneath. Petals obovate, elliptic-oblong or obovate-oblanceolate, 0.8–1.5 by 0.3–0.5 mm. Stamens with filaments 1.7–2.2 mm long and anthers 0.3–0.4 by 0.3–0.4 by 0.15–0.3 mm. Disc 0.2–0.3 high, 0.1 mm thick. Ovary 2–4-, mostly 3-carpellate, 0.6–0.7 by 0.5 mm, densely hairy, each cell with 8–10 ovules; styles 0.4–0.8 mm. Fruit with valves 2.8–3 by 1.1–1.2 mm, with several seeds. Seeds including wings c. 1.7–1.8 mm long, faintly papillose to glabrous.

Distribution — *Malesia:* scattered in the eastern half of New Guinea and in Irian Jaya only known from the Mt Jaya (Carstensz) area and the Arfak Mts. — Fig. 34.

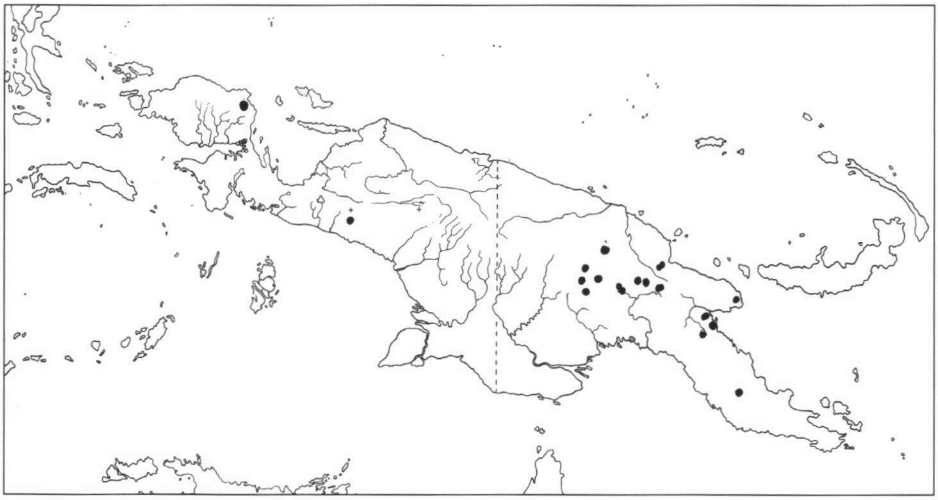

Fig. 34. Distribution of *Spiraeopsis rufa* (Schltr.) L.M. Perry.

Ecology — In lower montane forest (including mixed coniferous, *Nothofagus* and *Castanopsis* forest), between 750 and 3100 m; also in secondary forest, particularly at the lower altitudes.

Notes — 1. The flowers are reported as scented, creamy, yellow, pinkish fawn to maroon or purple, the perianth pale brown outside and purple or reddish inside, the stamens pink, bright red or purple, or white to pale yellow, the anthers white, the ovary yellow-green covered in rufous hairs, and the styles bright red or purple.

2. The leaflets are conspicuously rusty brown beneath.

WEINMANNIA

Weinmannia L., Syst. Nat. ed. 10, 2 (1759) 997, 1005, 1367, nom. cons.; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 250; Bernardi, Candollea 17 (1961) 123; 18 (1963) 285; Adansonia n.s. 3 (1963) 404; Bot. Jahrb. Syst. 83 (1964) 126, 185; in Humbert, Fl. Madag. 93 (1965) 3; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 9; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 5, 43, 67, 107; J.C. Bradford, Ann. Missouri Bot. Gard. 85 (1998) 565. — Type: *Weinmannia pinnata* L.

Windmannia P. Browne, Civ. Nat. Hist. Jamaica (1756) 212, nom. rejic.; Kuntze, Revis. Gen. Pl. 1 (1891) 228.

Trees or shrubs, rarely epiphytes and stranglers. Branching sometimes dichotomous; twigs sometimes slightly thickened or flattened at nodes; pale lenticels often prominent. Indumentum of simple hairs. Leaves opposite and decussate or very rarely whorled (outside Malesia), simple, trifoliolate or imparipinnate, usually petiolate; petiole and rachis sometimes winged; lateral leaflets opposite, often asymmetrical at base, frequently smaller proximally in a given leaf; terminal leaflet generally somewhat larger than lateral ones; margin toothed or crenulate; domatia absent; blade with or without multicellular trichome bases. Stipules interpetiolar, one pair per node, elliptic, ovate, orbicular to subreniform, often constricted at the base, often caducous in adult foliage; a pair of opposite stipules often salverform, amplexicaul and ± persistent in juvenile foliage; indumentum on abaxial surface usually more dense towards the base. Inflorescence racemose; racemes simple and axillary (outside Malesia) or arranged in groups on a sterile axis (peduncle), and then the basal axis either axillary and often inserted in series at distal node(s), or terminal, or a combination. Individual racemes up to 14 cm long with up to 100 or more flowers. Floral buds inserted singly or in small fascicles, each bud or fascicle subtended by a carinate, often caducous bract. Flowers unisexual or bisexual, hypogynous or somewhat perigynous, petaliferous, pedicellate, 4(–5)-merous or commonly 5-merous outside Malesia except for gynoecium. Calyx lobes 4(–5), ± triangular, with the apex broadly acute or rounded; aestivation imbricate. Petals 4(–5), sometimes fugaceous (outside Malesia), usually elliptic, ovate or obovate, constricted at the base, rounded or irregularly emarginate at the apex, membranous, often ciliolate. Stamens twice as many as calyx lobes; filaments filiform; anthers broadly cordate, deeply incised at base and apiculate at apex. Disc annular (outside Malesia) or divided into 8(–10) free lobes alternating with the filaments, each lobe oblong to obcuneate, sometimes broadly oblong with flanges on either side, usually glabrous. Gynoecium of 2 (or 3) carpels fused at the level of ovary; ovary ovoid; locules 2 (or 3); styles 2 (or 3), free, subulate, glabrous, furrowed on adaxial side; stigmas terminal, small or sometimes capitate and papillose; ovules 8–16 per locule, placentation axile. Fruit a septicidal or septifragal capsule dehiscing from the apex; free central column often present; valves coriaceous, boat-shaped, with a dark exocarp and smooth, yellow endocarp with extended margins; styles usually persistent; calyx lobes persistent or not. Seeds elliptic in outline and circular in transverse section, minutely sculptured, usually comose with a tuft of hairs at each end or sometimes hairs arising all over. — **Fig. 4f, 35–40.**

Distribution — Widespread in Latin America (c. 80 species), the islands of the western Indian Ocean (c. 30 species) and the southern Pacific (c. 25 species), and throughout *Malesia* (c. 17 species), though represented by few species in the western part. Absent from Africa, mainland Asia (except Peninsular Malaysia and Thailand) and Australia.

Ecology — Forest trees, at tropical latitudes mostly in montane forest, from c. 500–2500(–3250) m in Malesia, though sometimes from sea level, and in temperate rain forest in southern South America and New Zealand. In Malesia occasionally associated with serpentine (especially *W. clemensiae* and *W. devogelii*) and volcanic soils (*W. croftii*). Sometimes locally common.

Taxonomy — Bernardi (1961, 1963, 1964) divided the genus into six sections. A phylogenetic study by Bradford (1998) confirmed the utility of five of these, with minor modifications. In Malesia, most species belong to sect. *Fasciculatae* Hoogland & H.C. Hopkins, which is largely Malesian but extends into the Pacific as far as Fiji, and a single Malesian species, *W. croftii*, belongs to sect. *Leiospermum* (D. Don) Engl. (sect. *Racemosae* of Bernardi), which is predominantly Pacific and found on most of the high islands or island groups south of the equator, including New Caledonia and New Zealand, as far E as the Marquesas. Sections *Fasciculatae* and *Leiospermum* can be readily distinguished from each other by the structure of the inflorescence. In addition, the flowers are usually inserted on the axes of the racemes singly in sect. *Leiospermum* and in small fascicles in sect. *Fasciculatae* (exception in *W. descombesiana*).

Notes — 1. *Weinmannia* is the largest genus in the family, containing about half the species. With the exception of *W. fraxinea*, most Malesian species have a rather limited geographical distribution and Sulawesi, with seven species, has the highest number of taxa of any island within our area. The number of taxa recognised within Malesia depends partly on the circumscription of *W. fraxinea*, a widespread, variable species, and its satellites. In addition to the named taxa described here, unplaced material from Sulawesi and Irian Jaya may represent a handful of additional species (see Hopkins 1998).

2. Within Malesia, *Weinmannia* appears to be predominantly dioecious, individuals bearing morphologically unisexual flowers. Exceptions include *W. descombesiana, W. furfuracea* and some populations of *W. fraxinea*, which have morphologically hermaphrodite flowers. Evidence for polygamodioecy (or subandroecy?, with male and hermaphrodite flowers on the same plant) is rare in Malesia, but this condition appears to occur sometimes in *W. eymaeana*, *W. fraxinea* and *W. urdanetensis*.

3. Flowers and fruits within Malesia are remarkably uniform in structure. Dimensions are included for all species but they provide few useful characters.

4. The flowers are typically white, cream or pale pink, or occasionally bright pink, with a slight sweet fragrance. The disc lobes may be either pale and inconspicuous or dark and contrasting with the pale corolla, and at least in some species they are nectariferous. A high proportion of female or hermaphrodite flowers in any raceme produces fruit. Young stems and leaves are often conspicuously tinged red.

5. Two collections from Irian Jaya are highly unusual in having flowers arranged not in racemes but appearing directly from woody stems, i.e. cauliflorous.

KEY TO THE SPECIES

(Leaf characters refer to mature foliage on reproductive shoots, usually the pairs of leaves just below the inflorescence)

1a. Inflorescence usually a median triad or pentad developing from the apical bud of the shoot (Bismarck Archipelago & Karkar Island, Papua New Guinea); section *Leiospermum* . . . . **17. W. croftii**
b. Inflorescence composed of 1–3 pairs of dyads or tetrads inserted in the opposite axils of the most distal pair of leaves and sometimes in axils of subdistal leaves; apical bud of shoot, between central peduncles of the partial inflorescences, present and usually dormant, rarely developing vegetatively during reproduction (throughout Malesia); section *Fasciculatae* 2
2a. Flowers inserted on the inflorescence axes singly, each individual pedicel subtended by a bract; leaves simple . . . . **5. W. descombesiana**
b. Flowers inserted on the inflorescence axes in fascicles, each fascicle subtended by a bract; leaves usually imparipinnate, less often simple or trifoliolate 3
3a. Leaves simple or trifoliolate, the blades 4–9.5 by 1.7–4.4 cm, glabrous (Philippines, Sulawesi) . . . . **14. W. negrosensis**
b. Leaves imparipinnate, lateral leaflets in 1–19 pairs, only occasional leaves trifoliolate or if regularly trifoliolate, then leaflets smaller and densely hirsute (*W.* cf. *pullei*, New Guinea) 4
4a. Leaflets small, the largest laterals 0.6–3.2 by 0.2–1.5 cm, often in numerous pairs (2–19) 5
b. Leaflets medium-sized, the largest laterals 2.4–10 by 0.6–3.7 cm, usually in fewer pairs (1–8) 9
5a. Leaflets bullate and carinate, the margins strongly recurved and revolute (Mt Kinabalu) . . . . **3. W. clemensiae**
b. Leaflets flat or if slightly bullate then the margins not rolled back 6
6a. Petiole and rachis segments narrowly winged and leaflets numerous, 3–20 pairs; stems and leaflets glabrous . . . . **7. W. eymaeana**
b. Petiole and rachis segments terete or semiterete, or if narrowly winged then leaflets fewer, 1–6 pairs; young stems and young leaflets tomentose, velutinous or sericeous, sometimes glabrescent 7
7a. Leaflets inserted at almost 90° to rachis, and secondary veins at almost 90° to midrib . . . . **16. W. urdanetensis**
b. Leaflets inserted at an acute acroscopic angle and secondary veins at an acute acroscopic angle to midrib 8
8a. Lateral leaflets obovate or oblanceolate (New Guinea) . . . . **15. W. pullei**
b. Lateral leaflets oblong to narrowly ovate (Peninsular Malaysia) **10. W. hooglandii**
9a. Indumentum on young twigs pilose and on leaves pilose and pubescent 10
b. Indumentum on young twigs and leaves absent or pubescent to villous-tomentose, not pilose 12

10a. Terminal leaflet markedly rhomboidal and distinctly larger than the largest laterals . . . . **13. W. luzoniensis**
b. Terminal leaflet narrowly elliptic, only slightly larger than the largest laterals 11
11a. Lateral leaflets usually in 5–7 pairs, the largest 2–6.5 by 0.6–1.4 cm, decreasing in size proximally along the rachis; margin of stipules often wavy or coarsely toothed (Philippines) . . . . **11. W. hutchinsonii**
b. Lateral leaflets in 3–6 pairs, the largest 3–5 by 1–1.6 cm, not markedly decreasing in size proximally; margin of stipules entire (N Sulawesi) . . . . **2. W. celebica**
12a. Leaflets drying grey or dark chestnut above and chestnut beneath, lateral ones in 1–4 pairs, the largest 2.4–7 by 0.6–1.9 cm; petiole and rachis sometimes narrowly winged . . . . **1. W. aphanoneura**
b. Leaflets drying dark green or brown but not chestnut, lateral ones in 1–8 pairs, the largest 4.2–10 by 1.4–3.5 cm; petiole and rachis not winged 13
13a. Underside of leaflets bearing short scurfy hairs; indumentum on growing tips, stipules, leaf rachises and inflorescence axes dense rusty or golden brown villous-tomentose; lateral leaflets elliptic to obovate, the base ± symmetrical and the apex rounded or obtuse . . . . **9. W. furfuracea**
b. Underside of leaflets glabrous; indumentum on growing tips, stipules, leaf rachises and inflorescence axes puberulent to tomentose or absent, not rusty or golden brown; lateral leaflets lanceolate to elliptic or ovate, the base usually asymmetrical and the apex usually acute or acuminate 14
14a. Lateral leaflets lanceolate, narrowly elliptic to ovate, in 1–8 pairs 15
b. Lateral leaflets narrowly to broadly elliptic, not broader towards to base, in 2–3 pairs 16
15a. Pedicels 1.5–3 mm long (widespread in Malesia except Sulawesi and the Philippines) . . . . **8. W. fraxinea**
b. Pedicels very short, 0.2–0.5 mm (Sulawesi) . . . . **6. W. devogelii**
16a. Lateral leaflets attenuate into a petiolule at base, often conduplicate, 5–8.5 by 2–3.7 cm . . . . **12. W. lucida**
b. Lateral leaflets acute at base, ± sessile, not conduplicate, 4.8–6.4 by 1.4–2.1 cm . . . . **4. W. coodei**

Section Fasciculatae

Weinmannia sect. *Fasciculatae* Bernardi, Bot. Jahrb. Syst. 83 (1964) 132, 158, nom. inval., sine typo, ex Hoogland & H.C. Hopkins, Adansonia sér. 3, 20 (1998) 21. — Type: *Weinmannia fraxinea* (D. Don) Miq.

Arnoldia Blume, Bijdr. Fl. Ned. Ind.(1826) 868, non Cass. (1824). — Type: *Arnoldia heterophylla* Blume.

Pterophylla D. Don, Edinb. New Philos. J. 9 (1930) 93. — Type: *Pterophylla fraxinea* D. Don.

Branching not dichotomous. Stipules usually ± orbicular, constricted at base and rounded at apex. Inflorescence of 1–3 opposite pairs of partial inflorescences (PIs) inserted in series in axils of most distal pairs of leaves; each PI a single metamer, comprising a sterile peduncle and 2 or 4 racemes at its distal end (dyad or tetrad); leaves at nodes from which racemes arise usually totally suppressed; stipules not usually present at nodes within PIs; 'collars' (partially fused stipules) around peduncles absent; bud at apex of peduncle and apical bud of main stem usually dormant during flowering; buds lateral to axillary buds at most distal leaf-bearing node (lateral auxiliary buds) absent. Flowers pedicellate and inserted entirely or largely in fascicles, i.e. several pedicels arising in a group, the group subtended by a single small bract, or rarely inserted singly (*W. descombesiana*). Capsules with valves ± smooth and indumentum softly pubescent; after dehiscence, central column weakly developed; calyx lobes often persistent in fruit.

Distribution — About 20 species in Malesia and the western Pacific, extending as far east as Fiji.

1. Weinmannia aphanoneura Airy Shaw

Weinmannia aphanoneura Airy Shaw, Bull. Misc. Inform. (1940) 260; Bernardi, Bot. Jahrb. Syst. 83 (1964) 160; H.C. Hopkins, Adansonia sér 3, 20 (1998) 35, f. 9, 10. — Type: *Richards 1716* (not *6716* as given in protologue) (K holo, photo at KEP), Dulit Ridge, Sarawak, Borneo.

Shrub or tree 2–20 m high, up to 35 cm dbh. Twigs ± glabrous or adpressed puberulent. Leaves imparipinnate with (0–)1–4(–5) pairs of lateral leaflets; total length up to 16 cm including petiole of 0.7–2.8 cm; rachis segments 0.5–1.9 cm long; petiole and rachis sometimes narrowly winged, wings extending up to 1 mm from midline; leaflets coriaceous, with upper cuticle appearing quite thick, glabrous except for some hairs on midrib beneath, sometimes shiny above, characteristically drying grey or dark chestnut above and chestnut beneath; lateral leaflets narrowly elliptic or narrowly obovate, the largest 2.4–7 by 0.6–1.9 cm, base unequal, ± sessile, cuneate, apex acute to obtuse; apical leaflets narrowly elliptic to obovate, scarcely larger than largest laterals, 3–9.4 by 0.7–2.7 cm including the narrowly cuneate to attenuate base 0.3–1.2 cm long, apex acute to obtuse; margin crenate, 6–11 notches on each side of the largest lateral leaflets; midrib slightly depressed above and prominent beneath; secondary and tertiary venation flat on both sides. Stipules suborbicular, usually flat, up to 1.7 by 1.9 cm (rarely spathulate, c. 0.6 by 0.4 cm). Inflorescence usually 1 or 2 pairs of opposite dyads; peduncles 0.3–1.9 cm long, racemes usually not longer than the leaves (7–8 cm), rarely up to 14 cm long; peduncles glabrous or adpressed puberulent, axes of racemes puberulent, rarely tomentose. Flowers unisexual and plants dioecious; pedicel 1.8–3.6 mm long, puberulous; calyx lobes 0.5–0.8 by 0.4–0.9 mm, glabrous; corolla often rotate, petals oblong or irregularly obovate, 1.2–1.5 by 0.7–0.8 mm, rounded or emarginate at apex; disc lobes 0.3–0.5 mm long, oblong and discrete or with thin flanges on either side so they form an almost continuous disc; in male flowers: filaments 2.1–2.6 mm long, ovary 0.5–0.7 mm long, pubescent, styles 0.1–0.2 mm long, incurved; in female flowers: filaments up to 1.7 mm long, ovary c. 1 mm long, densely pubescent, styles c. 1.8 mm long, straight, stigmas capitate, papillose. Capsule with valves 2.5–3.5 by 1.3–1.5 mm at dehiscence; exocarp pubescent; calyx lobes persistent. Seeds c. 0.9 mm long, comose at both ends.

Distribution — *Malesia:* Borneo and Sumatra (one record).

Ecology — Montane mossy forest and heath forest at 1175–2560 m altitude.

2. Weinmannia celebica Koord.

Weinmannia celebica Koord., Meded. Lands Plantentuin. 19 (1898) 640 [& 450]; Koord.-Schum., Syst. Verz. 3 (1914) 51; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 256; Bernardi, Bot. Jahrb.

Syst. 83 (1964) 165; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 54, f. 2.— Type: *Koorders 18022b* (BO lecto of Hopkins 1998; BO, L), Loeloemboelan near Pahoe oere, Residentie Menado, N Sulawesi.

Tree 5–27 m, up to 45 cm dbh. Young twigs pilose, the hairs up to 0.5 mm long, older twigs sparsely pilose to glabrescent. Leaves imparipinnate with 3–6 pairs of lateral leaflets; total length up to 14 cm including petiole of 1.5–2 cm; rachis segments 0.8–1.1 cm long; petiole and rachis segments semiterete, often pilose; leaflets chartaceous to subcoriaceous, glabrous above, pilose beneath; lateral leaflets lanceolate or narrowly elliptic, the largest 3–5 by 1–1.6 cm, base unequal and ± sessile, apex acuminate; apical leaflet narrowly elliptic, 5.2–7 by 1.4–2 cm, base attenuate into a petiolule c. 0.7 cm long, apex acuminate; margin crenulate, 11–14 notches on each side of the largest lateral leaflets; midrib slightly depressed above, puberulent at base, prominent beneath and pilose; secondary and tertiary venation slightly raised on both surfaces. Stipules few in mature foliage, suborbicular, up to 0.45 cm diameter. Inflorescence a pair of opposite dyads; peduncles c. 1 cm long, strigose-puberulous; axes of racemes up to 11 cm long, puberulous. Flowers probably unisexual; pedicel 1.8–2 mm long, puberulous to glabrous; in old female flowers/young fruit, calyx lobes 0.8 by 0.6 mm, glabrous; corolla oblong, c. 1.5 by 0.8 mm, apex rounded; disc lobes 0.2 mm long, oblong; filaments 1.6 mm long; ovary 1.2 mm long, densely pubescent; styles 1.3 mm long, straight or divergent; stigmas papillose. Mature fruits not seen.

Distribution — *Malesia:* known from the northern peninsula of Sulawesi around Menado.

Ecology — In forest at 600–1500 m altitude. Scarce to locally common.

Note — This species is distinguished from *W. fraxinea* by the pilose indumentum on the underside of the leaflets and from *W. devogelii* by the longer pedicels. Its affinities seem to be with *W. hutchinsonii* and *W. luzoniensis* from the Philippines but better collections are needed to determine whether it is in fact worthy of specific rank.

3. Weinmannia clemensiae Steenis

Weinmannia clemensiae Steenis, J. Bot. 72 (1934) 3; Bernardi, Bot. Jahrb. Syst. 83 (1964) 166, t. 18; Cockburn, Kinabalu Summit Borneo, chapt. 7 (1978) 185 (fig. only); H.C. Hopkins, Adansonia sér. 3, 20 (1998) 32, f. 9, 10. — Type: *J. & M.S. Clemens 27880* (BO holo; K, L), near Kamborangah, Mt Kinabalu, Sabah, Borneo.

Treelet or tree, 1.5–10 m high. Twigs and leaf rachises densely tomentose-velutinous; stems terete, relatively thick, 3–5 mm diameter and internodes often short, 0.5–1.7 cm. Leaves imparipinnate with 6–13 pairs of lateral leaflets; total length up to 13 cm including petiole 0.5–1 cm long; rachis segments 0.4–0.9 cm long; petiole and rachis terete, densely tomentose-velutinous, petiole diverging from shoot at angle of almost 90° especially at growing tips; leaflets coriaceous, bullate and carinate, with margins strongly recurved and often rolled, upper surface puberulent or glabrous when the cuticle thick, lower surface sparsely to densely pubescent, the midrib sericeous; lateral leaflets oblong or somewhat ovate, the largest 1.4–2.7 by 0.6–1 cm, with the base symmetrical, rounded to cordate and the apex broadly acute, inserted ± at 90° to leaf rachis; terminal leaflet elliptic, scarcely larger than largest laterals, 1.9–3.3 by 0.7–1 cm including petiolule of 0.3–0.5 cm, apex acute; margin crenate but usually obscured, 5–7 notches on each side in the largest lateral leaflets; midrib indented on upper surface and prominent beneath; secondary veins ± at 90° angle to midrib. Stipules ± orbicular, up to 1 by 1.2 cm, adaxial surface shortly velutinous. Inflorescence one pair of opposite dyads, the apical bud of the main stem (between the peduncles of the dyads) often continuing to grow vegetatively during flowering; peduncles 0.3–0.7 cm long; racemes up to 10.5 cm long; axes densely tomentose-velutinous; inflorescences and infructescences usually dense. Flowers unisexual (or sometimes bisexual?); pedicel 1–1.5 mm long, with short erect hairs; calyx lobes 0.8–0.9 by 0.6–0.8 mm, hirsute; petals obovate to ± circular, 1.1–1.5 by 1–1.1 mm, rounded at apex, margin ciliolate; disc lobes 0.4–0.5 mm long, oblong or broadly oblong; in male flowers: filaments c. 2.5 mm long, ovary c. 0.6 mm, densely pubescent, styles 0.1 mm, incurved; in female flowers: filaments up to 1.9 mm long, ovary 1.5–2 mm long, densely pubescent, styles c. 1 mm long, straight, pubescent at base. Capsules with valves up to 3.7–4.5 by 1.8–2.2 mm at dehiscence; exocarp densely pubescent; calyx lobes persistent. Seeds immature, c. 0.9 mm long, comose at both ends. — **Fig. 35.**

Distribution — Endemic to Mt Kinabalu and Mt Tambuyukon in Sabah. Probably all populations occur within the boundary of Kinabalu Park, whose protection is therefore crucial to the continued survival of this species.

Ecology — Restricted to stunted forest on strongly ultramafic soil at (1640–)1900–2600 m.

Notes — 1. A distinctive species due to the boat-shaped and bullate leaflets and dense tomentose-velutinous indumentum.

Fig. 35. *Weinmannia clemensiae* Steenis. Leaves and young fruit (*Hopkins & Bradford 5010*, Mt Kinabalu, Sabah). Photo by J. C. Bradford.

2. Plants are mostly unisexual but one collection with predominantly morphologically male flowers has some possibly bisexual flowers mixed in.

3. Adult foliage is darkish green above and paler beneath with the main vein brown or pink. The stipules are satiny mid-green and paler than the foliage. New growth is densely velutinous and sometimes reddish. The flowers are pinkish brown or deep cream-pink, with a blood red calyx, pinkish corolla and cream stamens; the whole inflorescence is pink and downy. Immature fruits are pink with red styles.

4. **Weinmannia coodei** H.C. Hopkins

Weinmannia coodei H.C. Hopkins, Adansonia sér. 3, 20 (1998) 52, f. 2, 4A–D. — Type: *Coode 6197* (L holo; A, K), Gn. Watuwila foothills above Sanggona, Gn. Sopura, Kolaka area, SE Sulawesi.

Small tree 6 m high, 35 cm dbh. Twigs glabrous, ridged, nodes thickened. Leaves imparipinnate, with (1 or) 2 pairs of lateral leaflets; total length up to 13 cm including petiole of 1.4–2 cm; rachis segments 1–1.5 cm long; petiole and rachis segments semiterete or channelled; leaflets subcoriaceous, glabrous above and beneath; lateral leaflets narrowly elliptic, the largest per leaf 4.8–6.4 by 1.4–2.1 cm, base unequal, ± sessile, acute, apex acute to obtuse; apical leaflet elliptic to obovate, 5–6.2 by 1.4–2.3 cm including base attenuate into a petiolule c. 1 cm long, apex obtuse; margin crenulate, 9–18 notches on each side of the largest lateral leaflets; midrib indented above, prominent beneath, glabrous; secondary and tertiary venation ± flat above and somewhat raised beneath. Stipules not seen, caducous. Inflorescence a pair of dyads; peduncles up to 1 mm long, glabrous; axes of racemes puberulous, up to 7.5 cm long; stipules at apex of peduncle sericeous and partially fused at their lateral margins to form a cup-shaped structure. Flowers with pedicel 1–1.5 mm long, puberulous; calyx lobes 0.7 by 0.6 mm, pubescent on outer surface; corolla irregularly obovate to oblong, 1.4 by 0.8 mm, apex rounded; disc lobes 0.3–0.4 mm long, oblong or sometimes fused into an almost continuous ring; filaments up to 1.6 mm long; ovary 0.5–0.7 mm long, densely pubescent; styles 1.3 mm long, straight; stigmas capitate, papillose. Capsule with valves 3.5–4 by 2 mm at dehiscence; exocarp densely pubescent; calyx lobes persistent. Immature seeds 0.6–0.8 mm long, either comose at both ends or with hairs all over surface, longest at the ends.

Distribution — *Malesia:* SE peninsula of Sulawesi. Known only from the type.

Ecology — Mossy ridge forest with deep leaf-litter on schist at 1600 m; canopy tree at 6 m.

Note — The breeding system has not been determined.

5. **Weinmannia descombesiana** Bernardi

Weinmannia descombesiana Bernardi, Bot. Jahrb. Syst. 83 (1964) 190, t. 33; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 44, f. 1G–L, 2. — Type: *Kjellberg 1618* (S holo; BO), Pasoei–Rante Lemo, SW Sulawesi.

Shrub or tree, 2.6–30 m high, up to 30 cm dbh. Twigs glabrous or puberulous, black, shiny; branching sometimes dichotomous. Leaves unifoliolate, usually with an articulation between blade and petiole; petiole 0.5–1 cm long, semiterete, rarely very narrowly winged, almost glabrous; leaf blade subcoriaceous or chartaceous, elliptic, 4–9.5(–11) by 1.7–4.4(–4.8) cm, with base acute and apex acuminate, glabrous on both surfaces; margin sometimes minutely thickened and revolute, crenate, c. 8–19 notches on each side; midrib flat or slightly depressed above, glabrous, prominent beneath with sparse indumentum, secondary and tertiary venation flat above and beneath, reticulum dense. Stipules obovate, ligulate or spathulate, c. 0.7 by 0.4 cm. Inflorescence usually a pair of dyads, sometimes a few successive nodes reproductive; peduncles 0.2–1.6 cm long, sparsely puberulent; axes of racemes up to 8.5 cm long, puberulent; floral buds inserted singly. Flowers bisexual; pedicel 1–1.2 mm long in flower, 1.4–2.6 mm long in fruit, almost glabrous; calyx lobes 0.5 by 0.4 mm, sparsely hairy on outer surface, ciliate; petals oblong, 1.2 by 0.6 mm, apex rounded; disc lobes 0.2–0.3 mm long, oblong, minutely strigose; filaments c. 2.2 mm long; ovary c. 1 mm long, densely pubescent; styles c. 1 mm long, diverging; stigmas capitate, papillose. Capsule with valves 2–2.5 by 1.2–1.6 mm at dehiscence; exocarp strigose-pubescent; calyx lobes persistent. Seeds 0.5–0.6 mm long, c. 8 per capsule, often persisting in capsules after dehiscence, comose at both ends, the hairs to 1.5 mm long, hairs almost 'sticky'.

Distribution — *Malesia:* mountains of South and Central Sulawesi.

Ecology — In primary and secondary forest at 1000–1800 m altitude.

Note — Although placed here in sect. *Fasciculatae*, *W. descombesiana* was originally referred to sect. *Leiospermum* (as sect. *Racemosae*) by Bernardi (1964) as the flowers are arranged singly on the axes of the racemes. Other features characteristic of sect. *Leiospermum* seen in this species include: branching sometimes dichotomous and stipules ovate-ligulate-spathulate in adult foliage. However, the inflorescence structure is typical of sect. *Fasciculatae*, and other characters that suggest its affinities include the type of indumentum on the capsules (pubescent not strigose), the calyx lobes in fruit (persistent not caducous), and the absence of 'collars', which are remnants of partially fused stipules, around the inflorescence axes.

6. **Weinmannia devogelii** H.C. Hopkins

Weinmannia devogelii H.C. Hopkins, Adansonia sér. 3, 20 (1998) 48, f. 1A–F, 2. — Type: *de Vogel 6122* (L holo; K), Bonemaitu, E of Nuha, N shore of Lake Matano, S Sulawesi.

Tree 5–20 m high, up to 40 cm dbh. Twigs with sparse indumentum. Leaves imparipinnate with (0–)2–6 pairs of lateral leaflets; total length up to 22 cm including petiole of 1.5–3.5 cm; rachis segments 1.2–2.5 cm long; petiole and rachis segments terete to semiterete, densely pubescent on upper side; leaflets chartaceous to subcoriaceous, glabrous above and beneath; lateral leaflets lanceolate, narrowly ovate or narrowly elliptic, the largest 4.5–10 by 1–3 cm, base unequal, ± sessile or shortly petiolulate, apex acuminate; apical leaflet narrowly elliptic, 5.5–9.5 by 1.5–2 cm, base attenuate into a petiolule c. 0.7 cm long, apex acuminate; margin almost entire to crenulate, 10–15 notches on each side of the largest lateral leaflets; midrib slightly depressed above, puberulent at base, prominent beneath and sparsely strigose; secondary and tertiary venation slightly raised on both surfaces. Stipules ± orbicular and larger ones amplexicaul, up to 1.4 by 1.6 cm. Inflorescence of 1–3 pairs of dyads or tetrads, sometimes a few successive nodes flowering; peduncles 0.2–1.3 cm long, puberulous; axes of racemes up to 11.5 cm long, densely puberulous. Flowers unisexual and plants dioecious; pedicel 0.2–0.5 mm long, minutely strigose or puberulous; calyx lobes 0.5–0.7 by 0.4–0.5 mm, minutely strigose on outer surface; corolla obovate, 1.1–1.5 by 0.7–1.1 mm, apex rounded or irregularly emarginate; disc lobes 0.2–0.3 mm long, oblong; in male flowers: filaments 3.3–3.7 mm long, ovary 0.4–0.5 mm long, pubescent, styles 0.1–0.2 mm long, incurved; in female flowers: filaments 0.6–0.9 mm long, ovary 0.9–1.1 mm long, densely pubescent, styles 0.9–1.1 mm long, straight, stigmas papillose. Capsule with valves 1.9–2.5 by 1.2–1.5 mm at dehiscence; exocarp pubescent; calyx lobes persistent. Seeds ellipsoid to broadly ellipsoid, 0.5–0.7 mm long, 4 per capsule, comose at both ends, the hairs to 2 mm long.

Distribution — *Malesia:* Eastern South Sulawesi near Malili and Lake Matano.

Ecology — In primary and secondary forest at 0–700 m. On peridotite and ultrabasic laterite; also in patches of coastal vegetation along the lake on limestone and on red clayey soil derived from conglomerate bedrock. Locally common.

Notes — 1. *Weinmannia devogelii* is a satellite of widespread and variable *W. fraxinea*, and the differences between them are not great. However, *W. devogelii* has a unique morphological feature (the very short pedicel) not seen in *W. fraxinea*, a distinctive ecology, and an allopatric distribution. The leaf characters of *W. devogelii* fall within the range for *W. fraxinea* and sterile specimens cannot be distinguished; the latter species is assumed to be absent from Sulawesi as no fertile material has yet been identified as belonging to it.

2. Buttresses few or absent. Flowers usually described as pink, or rarely white.

7. **Weinmannia eymaeana** H.C. Hopkins

Weinmannia eymaeana H.C. Hopkins, Adansonia sér. 3, 20 (1998) 50, f. 2, 3E–J. — Type: *Eyma 3578* (L holo; A, BO, K, U), Biv. II–III, Gn. Loemoet, Tusschen, Poso, Central Sulawesi.

Shrub? Twigs glabrous. Leaves imparipinnate with 3–20 pairs of lateral leaflets; total length up to 6 cm long; petiole and rachis segments 0.3–0.6 cm long, glabrous, channelled above, narrowly winged, the wings extending 0.5 mm from midline and incurved; leaflets coriaceous, glabrous, cuticle on upper surface thick and shiny; lateral leaflets narrowly elliptic or elliptic, (0.45–)0.7–1.9 by 0.2–0.5 cm, of ± equal size in one leaf, base ± equal, cuneate, apex acute; terminal leaflet narrowly elliptic to elliptic, 0.7–2.3 by 0.25–0.8 cm, scarcely larger than the largest laterals, base sessile or petiolulate, the petiolule c. 0.3 cm long, apex acute; margin recurved, entire or sparsely crenate-dentate with 0–7 notches on each side in the lateral leaflets; on upper surface, midrib and secondary veins depressed into cuticle; on lower surface, midrib slightly prominent. Stipules ± orbicular, up to 0.8 by 0.8 cm, glabrous. Inflorescence usually a pair of opposite dyads; apical bud of shoot glabrous, sometimes continuing to grow vegetatively during flowering; peduncles 0.1–0.3 cm long, ± glabrous; racemes up to 8 cm long, puberulent. Flowers apparently unisexual, only male flowers seen: pedicel 1–2.3 mm long, glabrous or puberulent; calyx lobes 0.7 by 0.5 mm, glabrous; petals oblong, 1.4–1.6 by 0.6 mm, ± emarginate at apex; disc lobes 0.3 mm long, narrowly oblong; filaments up to 2.9 mm long; ovary c. 0.4 mm long, pubescent; styles 0.1 mm long, incurved. Capsules with valves 3.5–4 by 1.8 mm long just prior to dehiscence; exocarp densely pubescent; calyx and disc lobes persistent. Seeds immature, flat, c. 0.6 mm long, comose at both ends.

Distribution and Ecology — *Malesia:* known from only two collections, both from Gn. Lumut (Loemoet), Sulawesi, at about 2200 m. Habitat not recorded.

Note — This species may be polygamodioecious since male flowers and fruits are present on *Eyma 3578*, though not on the same twig.

8. Weinmannia fraxinea (D. Don) Miq.

Weinmannia fraxinea (D. Don) Miq., Fl. Ned. Ind. 1, 1 (1856) 718; [Sm. ex D. Don, Edinb. New. Philos. J. 9 (1830) 93, pro syn.]; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 23 (f. 7, 8), 69. — *Pterophylla fraxinea* D. Don, Edinb. New Philos. J. 9 (1830) 93. — *Windmannia fraxinea* (D. Don) Kuntze, Revis. Gen. Pl. 1 (1891) 228. — Type: *C. Smith s. n.* (LINN-SM holo), Honimoa, Moluccas.

Arnoldia heterophylla Blume, Bijdr. Fl. Ned. Ind. (1826) 869, non *Weinmannia heterophylla* Kunth (1823). — *Weinmannia sundana* Miq., Fl. Ned. Ind. 1, 1 (1856) 718. — *Windmannia sundana* (Miq.) Kuntze, Revis. Gen. Pl. 1 (1891) 228. — Type: *Reinwardt s. n.* (L lecto of Hoogland in Hopkins 1998), Amboina, Moluccas.

Spiraea pinnata Blume, Cat. (1823) 76. — *Arnoldia pinnata* Blume, Bijdr. Fl. Ned. Ind. (1826) 868, non *Weinmannia pinnata* L. (1759). — *Weinmannia blumei* Planch., Lond. J. Bot. 6 (1847) 470; Bernardi, Bot. Jahrb. Syst. 83 (1964) 161. — *Weinmannia arnoldia* A. Gray, U.S. Expl. Exped., Phan. 1 (1854) 675. — *Windmannia blumei* (Planch.) Kuntze, Revis. Gen. Pl. 1 (1891) 228. — Type: *Blume 816a* (L lecto of Hoogland in Hopkins 1998), Java.

Weinmannia horsfieldii Miq., Fl. Ned. Ind. 1, 1 (1856) 718. — *Windmannia horsfieldii* (Miq.) Kuntze, Revis. Gen. Pl. 1 (1891) 228. — Type: *Horsfield s. n.* (BM holo), Soerabaja, Java.

Arnoldia fraxinifolia Blume, Flora 41 (1858) 254. — *Weinmannia fraxinifolia* (Blume) Miq., Fl. Ned. Ind. 1, 1 (1858) 1095. — Type: *Blume s. n.* (L lecto of Hoogland in Hopkins 1998), Malabar, Java.

Weinmannia papuana Schltr., Bot. Jahrb. Syst. 52 (1914) 162. — Type: *Ledermann 9784* (B holo; L), April R., Papua New Guinea.

Weinmannia ledermannii Schltr., Bot. Jahrb. Syst. 52 (1914) 162. — Type: *Ledermann 9922* (B holo; K, L), Lordberg, Papua New Guinea.

Weinmannia tomentella Schltr., Bot. Jahrb. Syst. 52 (1914) 163. — Type: *Ledermann 8172* (not *8173* as given by Schltr. [1914]) (B holo), Mt Hunstein, Papua New Guinea.

Weinmannia blumei Planch. var. *major* Ridl., Fl. Malay Penins. 5 (1925) 307. — Type: *Ridley 16029* (SING lecto of Hoogland in Hopkins 1998; BM, K, SING), Gn. Tahan, Pahang, Malay Peninsula.

Weinmannia dictyoneura Schltr., Bot. Jahrb. Syst. 52 (1914) 163, non Diels (1906). — *Weinmannia alta* Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 256. — Type: *Ledermann 10129* (B holo; K), Lordberg, Papua New Guinea.

Weinmannia borneensis Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 256. — Type: *Native Collector 722* (B holo; BM, BO, K, L, PNH), Sarawak, Borneo. (fide PNH: road up Gn. Matang, leg. Dabong).

Weinmannia dulitensis Airy Shaw, Bull. Misc. Inform. (1940) 259. — Type: *Native Collector 1671* (K holo; L, SING), Dulit Ridge, Sarawak, Borneo.

Weinmannia hypoglauca Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 111, t. 7. — Type: *Kanehira & Hatusima 12797* (FU holo n.v., photo at K; BO, L), Boemi, 40 km inward of Nabire, Irian Jaya.

[*Cortex papetarius* Rumph., Herb. Amboin. 3 (1743) 212, t. 137.]

Small to large tree, up to 25(–40) m high. Young twigs puberulent to tomentose, rarely glabrous, older stems glabrescent. Leaves imparipinnate with (0–)1–8 pairs of lateral leaflets; total length 5.5–15.5 cm including petiole of 1–3 cm; rachis segments 1–2.5 cm long; petiole and rachis segments terete, indumentum varying from glabrous to tomentose-velutinous; leaflets chartaceous to subcoriaceous, glabrous, sometimes ± shiny above;

Fig. 36. *Weinmannia fraxinea* (D. Don) Miq. Large tree in flower (*Hoogland 12565*, Fraser's Hill, Peninsular Malaysia). Photo by R.D. Hoogland.

lateral leaflets ± sessile, usually broader towards the base, varying from lanceolate to narrowly elliptic to narrowly ovate to ovate, the largest per leaf (2.2–)4.2–8.5(–12) by (0.8–)1.2–3.5(–4.5) cm, base frequently somewhat to markedly unequal, rounded to cuneate on either side, apex acute to acuminate; terminal leaflets narrowly elliptic to narrowly ovate, 2.5–10 by 1–3.3 cm including petiolule of 0.3–1.5 cm, ± equal in size to largest lateral leaflets or larger, base attenuate into petiolule, apex acuminate; margin crenate, 8–14 notches on each side in the lateral leaflets, crenations rounded or triangular; midrib prominent and shortly hirsute beneath, indented above and sometimes hirsute towards base; secondary and tertiary veins ± flat above and minutely prominent beneath, sometimes drying paler than intervenium. Stipules ± orbicular, subreniform or broadly spathulate, 0.8 by 0.8 to 1.5 by 1.8 cm. Inflorescence 1–3 opposite pairs of lateral dyads or tetrads; peduncles 0.3–1.8 cm long; racemes 7.5–15 cm long; peduncles and axes of racemes minutely puberulent to tomentose. Flowers unisexual or hermaphrodite; pedicel (1.1–)1.5–3 mm long, minutely hairy; calyx lobes 0.6–0.9 mm long, hirsute at base; petals oblong to obovate, 1.1–1.8 by 0.7–1.2 mm, apex rounded or rarely emarginate; disc lobes free and oblong, 0.2–0.5 mm long, or rarely forming an almost complete ring; in male flowers: filaments c. 2.9 mm long, anthers c. 0.5 mm long, ovary c. 0.5 mm, densely pubescent, styles 0.1 mm, incurved; in female flowers: filaments 0.6–1.2 mm long, anthers 0.3 mm long, ovary 0.6–1.2 mm long, densely pubescent, styles 1–1.3 mm long, straight; in bisexual flowers: filaments 3–3.5 mm long, ovary 0.6–0.8 mm long, pubescent, styles 1.5–2 mm long. Capsules with valves 2.5–4(–6) by 1.5–2(–3.1) mm at dehiscence; exocarp pubescent; calyx lobes usually persistent. Seeds 0.8–1.1 mm long, comose at both ends, hairs up to 2 mm long. — **Fig. 4f, 36–38.**

Distribution — Solomon Islands and *Malesia:* from Peninsular Malaysia, Thailand and Sumatra to New Guinea; absent from Sulawesi and the Philippines.

Ecology — In forest and sometimes disturbed areas (e.g. roadsides) (0–)500–2000 (–2700) m. At lower elevations in primary and secondary forest, and locally common as a small to medium tree above 500 m. At higher altitude in mossy montane forest, heath forest, and subalpine shrubbery. Varying in abundance from uncommon to one of the main constituents of montane forest. On various substrates including young volcanic soils, open, stony ground, sometimes recently burnt and dominated by ferns. Occasionally on soils derived from ultramafics and on acidic, water-logged sands and in mixed peat swamp forest at sea level (Borneo).

Taxonomy — This is the most widespread and abundant *Weinmannia* in Malesia. The leaflets are variable in number, size, shape, texture and indumentum, but usually they

Fig. 37. *Weinmannia fraxinea* (D. Don) Miq. Flowering branch with inflorescences both mature and in bud (*Coode 7566*, Gn. Pagon, Brunei). Photo by M.J.E. Coode.

Fig. 38. *Weinmannia fraxinea* (D. Don) Miq. a. Leaves and inflorescence; b. base of inflorescence, showing racemes in pairs on short peduncles, the latter inserted in series in the most distal leaf axils (*Bradford 830*, Kolombangara, Solomon Islands). Photos by J.C. Bradford.

are broader towards the unequal base and the apex is acuminate. The inflorescence of dyads and tetrads is often well developed. The name *W. blumei* has often been applied to this taxon in western Malesia. Closely related satellite species which are maintained as distinct for the present include *W. devogelii* (Sulawesi), *W. hooglandii* (Peninsular Malaysia) and *W. macgillivrayi* Seem. (Vanuatu).

The majority of collections from throughout the range have medium-sized, chartaceous to subcoriaceous leaflets, with medium-sized and usually caducous stipules, and the indumentum on the axes varies from puberulent to tomentose. At high altitudes, leaflets tend to be smaller, the largest lateral leaflet per leaf exceptionally as small as 2.2 by 0.9 cm, and the inflorescences tend to be shorter and less well developed. At medium elevations, some collections from Sumatra to New Guinea have exceptionally large leaflets, up to 12 by 3.5 cm, that vary in texture from chartaceous to coriaceous. When coriaceous, they often have minutely prominent or contrastingly coloured venation and a dense reticulum, the axes are glabrous or subglabrous, sometimes with an almost rubbery consistency, and the stipules are larger and more persistent. Elsewhere there are variants with lanceolate leaflets (especially in the Moluccas).

Distinct variants can sometimes be recognised at a local level but they tend to intergrade when the whole range of *W. fraxinea* is considered. Similar morphologies can be found in widely separated localities, while other variants occur in only one region. In some cases, there appear to be two distinct variants which do not intergrade, although in another locality they appear to do so. In this type of polymorphic, non-hierarchical variation, where characters vary independently of one another and largely independently of geography and ecology, formal infraspecific taxa are unwarranted although it may sometimes be useful to apply informal 'nicknames' to distinguish between variants as has been done for some other ochlospecies (e.g. Huxley & Jebb, Blumea 37 [1993] 271). However, there are too many intermediate collections for nicknames to be applied consistently to all the material in *W. fraxinea.*

Notes — 1. The breeding system can be dioecious or hermaphrodite, or very rarely polygamodioecious, and the proportion of individuals bearing flowers with different sexual expression varies geographically (largely dioecious in Western Malesia, dioecious in the Moluccas, largely hermaphrodite in New Guinea and the Solomon Islands). Variation in the breeding system, as deduced from the morphology of the flowers, is not correlated with variation in any other morphological characters.

2. Field characters: Small, often shrub-like tree 5–15 m tall at high altitude, to a tall, slender tree up to 25(–40) m high by 50 cm dbh at lower altitude. Buttresses usually absent. Flowers white, yellowish, pale green or pale pink, occasionally bright pink.

9. Weinmannia furfuracea H.C. Hopkins

Weinmannia furfuracea H.C. Hopkins, Adansonia sér. 3, 20 (1998) 49, f. 2, 3A–D. — Type: *Tantra 1595* (L holo; BO), W slope Mt Roroka Timbu, SE of Palu, Central Sulawesi.

Tree 16–45 m high, up to 60 cm dbh. Twigs, leaves, stipules, leaf rachises and inflorescence axes covered with dense rusty or golden brown villous-tomentose indumentum, the longest hairs up to 1 mm; older stems tomentose or puberulous, finally glabrescent. Leaves imparipinnate with (1–)2–4 pairs of lateral leaflets; total length up to 20 cm including a petiole 1–4 cm long; rachis segments 1–3.2 cm long; leaflets subcoriaceous, glabrous above and with an indumentum of short, scurfy hairs beneath, sometimes glabrescent; lateral leaflets elliptic to obovate, the largest 4–7.8 by 1.9–3 cm, base almost equal, ± sessile or shortly petiolulate, apex rounded or obtuse (acute in immature foliage); apical leaflet elliptic to obovate, 5–9(–11) by 1.9–3.6(–4.8) cm including base attenuate into a petiolule c. 1 cm long, apex rounded or obtuse; margin subentire to crenulate, with 20–25 notches on each side of the largest lateral leaflets; midrib ± flat above and prominent beneath, bearing villous to scurfy hairs; secondary and tertiary venation ± flat above and somewhat raised beneath. Stipules ± orbicular, recurved, up to c. 0.9 by 1.1 cm. Inflorescence 1 or 2 pairs of opposite dyads or tetrads, the apical bud between the central peduncles often continuing to grow vegetatively during flowering; sometimes a few successive nodes flowering simultaneously; peduncles 0.6–2.5 cm long, villous-tomentose; axes of racemes up to 11.5 cm long, tomentose. Flowers bisexual; pedicel 1–1.7 mm long, tomentose; calyx lobes 0.7 by 0.5–0.6 mm, tomentose on outer surface; corolla irregularly obovate to almost circular, 1–1.2 by 0.8–1 mm, apex rounded or irregularly emarginate, puberulous on outer surface; disc lobes 0.3–0.4 mm long, oblong, sometimes with thin flanges on either side to form an almost continuous ring; filaments 2.2–2.4 mm long; ovary 1.1–1.8 mm long, densely pubescent; styles 1.1–1.8 mm long, divergent then later straight; stigmas capitate, papillose. Capsule with valves 3–4 by 1.5 mm just prior to dehiscence; exocarp densely pubescent; calyx lobes persistent. Immature seeds 0.6–0.8 mm long, comose at both ends.

Distribution — *Malesia:* Sulawesi and Seram.

Ecology — Primary montane forest at 1700–2000 m altitude. Locally common.

Note — The scurfy indumentum is distinctive and in the field the leaves are golden from below, becoming glaucous when old.

10. **Weinmannia hooglandii** H.C. Hopkins & J.C. Bradford

Weinmannia hooglandii H.C. Hopkins & J.C. Bradford, Adansonia sér. 3, 20 (1998) 37, f. 10, 11. — Type: *Whitmore FRI 12582* (KEP holo; A, K, L, SAN), Gn. Ulu Kali, Pahang/Selangor, Peninsular Malaysia.

Shrub or small tree 1.2–5 m high, 4 cm dbh. Twigs tomentose or velutinous. Leaves imparipinnate with 4–8 pairs of lateral leaflets; total length 5–7 cm including a petiole 0.8–1.5 cm long; rachis segments 0.4–0.8 cm long; petiole and rachis terete, often densely tomentose; leaflets coriaceous, glabrous and sometimes shiny above, glabrous beneath; lateral leaflets ± oblong to narrowly ovate, the largest 1.6–2 by 0.5–0.6 cm, base unequal, sessile, cuneate, apex broadly acute; apical leaflet narrowly elliptic, scarcely larger than the largest lateral leaflets, 1.5–2.3 by 0.5–0.8 cm, base attenuate, apex acute; margin crenate, 3–7 notches on each side of the largest lateral leaflets, minutely revolute; midrib slightly depressed above, prominent beneath and sometimes shortly strigose especially towards the base; secondary and tertiary venation ± flat on both surfaces or obscure on the upper one. Stipules ± orbicular, up to 0.5 by 0.6 cm, apex broadly rounded or flattened. Inflorescence a pair of opposite dyads; peduncles 0.4–0.5 cm long, strigose; racemes up to 6 cm long, the axis pubescent or tomentose. Flowers unisexual? (only male ones seen); male flowers: pedicel 1.5–3 mm long, minutely hairy; calyx lobes 0.8–0.9 by 0.6 mm, glabrous; petals ± obovate, 1.2–1.4 by 0.8–0.9 mm, apex rounded or emarginate; disc lobes 0.3–0.4 long, oblong or broadly oblong with thin flanges on either side; filaments 2.6–3 mm long; ovary minute, 0.6 mm long, densely golden pubescent, styles 0.1–0.2 mm long, incurved. Fruit not seen.

Distribution — *Malesia:* mountains in western Peninsular Malaysia (Gn. Ulu Kali and Gn. Brinchang).

Ecology — Upper montane forest and mossy forest of low stature, 1680–2065 m altitude; locally common.

Notes — 1. The leaves are clustered towards the end of the twigs and held ± erect to form an even, dense, ball-like, congested crown. Young branches and leaf rachises are purplish or brown and adult foliage is dark green above and leathery.

2. Probably dioecious but so far only male flowers have been found.

3. Appears to be closely related to *W. fraxinea*, and resembles somewhat small-leafleted variants of that species which occur in some localities at high altitude. However, on Gn. Ulu Kali both taxa grow in close proximity and can be readily distinguished, as *W. fraxinea* has much larger, narrowly elliptic leaflets.

11. Weinmannia hutchinsonii Merr.

Weinmannia hutchinsonii Merr., Philipp. J. Sci., Bot. 2 (1907) 275; Enum. Philipp. Flow. Pl. 2 (1923) 224; Bernardi, Bot. Jahbr. Syst. 83 (1964) 169, t. 20; H.C. Hopkins, Adansonia sér. 3, 20 (1998): 56, f. 4E–K, 5. — Type: *Merrill 5753* (FI, K, NY, P, US), Mt Halcon, Mindoro, Philippines.

Weinmannia camiguinensis Elmer, Leafl. Philipp. Bot. 7 (1915) 2607. — Type: *Elmer 14228* (A, BM, BO, GH, K, L, P, PNH and others), Mambajao, Camiguin, Mindanao, Philippines.

Weinmannia bulusanensis Elmer, Leafl. Philipp. Bot. 10 (1939) 3723; nom. invalid, description in English. — Collection cited: *Elmer 17293* (A, BM, BO, GH, L, P and others), Irosin (Mt Bulusan), Prov. Sorsogon, Luzon, Philippines.

Weinmannia irosinensis Elmer, Leafl. Philipp. Bot. 10 (1939) 3725; nom. invalid, description in English. — Collection cited: *Elmer 14918* (BM, BO, GH, L, P and others), Irosin (Mt Bulusan), Prov. Sorsogon, Luzon, Philippines.

Tree 7–12 m high, 12–40 cm dbh. Twigs pilose, the hairs up to 0.8 mm long, older ones more sparsely pilose to glabrescent or puberulous. Leaves imparipinnate with (2–)5–7(–8) pairs of lateral leaflets; total length up to 14 cm including a petiole 1.3–2.5 cm long; rachis segments 0.6–1.5 cm long; petiole and rachis segments semiterete, pilose and/or puberulent; leaflets chartaceous to subcoriaceous, glabrous above, sparsely pilose beneath; lateral leaflets narrowly elliptic, the largest per leaf 2–6.5 by 0.6–1.4 cm, base unequal, ± sessile, apex narrowly acute; apical leaflet narrowly elliptic, (2.2–)4.1–8.3 by (0.7–)0.9–2.3 cm, base shortly attenuate to petiolulate, apex narrowly acute; margin crenate to serrate, 7–11 notches on each side of the largest lateral leaflets; midrib slightly depressed above, puberulent at base, prominent beneath and pilose. Stipules suborbicular or reniform, up to 1.2 by 1.9 cm, the margin wavy or coarsely toothed. Inflorescence of 1–3 pairs of dyads, sometimes a few sequential nodes flowering simultaneously; peduncles 0.4–1.5 cm long, puberulous; axes of racemes up to 12 cm long, densely puberulous. Flowers unisexual and plants dioecious; pedicel 0.8–1.5 mm long, puberulous; calyx lobes 0.5–0.7 by 0.4–0.5 mm, hirsute on outer surface; corolla obovate or almost circular, 1–1.3 by 0.7–0.9 mm, rounded at apex; disc lobes 0.2–0.3 mm long, broadly oblong; in male flowers: filaments 2.8–3 mm long, ovary 0.4 mm long, pubescent, styles 0.1 mm long, incurved; in female flowers: filaments c. 0.9 mm long, ovary c. 1 mm long, densely pubescent, styles c. 0.9 mm long, straight, stigmas papillose. Capsule with valves 2–2.5 by 1.4–2 mm at dehiscence; exocarp pubescent; calyx lobes often caducous. Seeds c. 0.6 mm long, comose at both ends.

Distribution — *Malesia:* Philippines (Luzon, Catanduanes, Leyte, Negros, Mindoro and Mindanao).

Ecology — In forest on ridges and slopes, including open, disturbed areas from 325–1150 m; sometimes common.

12. **Weinmannia lucida** Merr.

Weinmannia lucida Merr., Philipp. J. Sci., Bot. 10 (1915) 7; Enum. Philipp. Flow. Pl. 2 (1923) 225; Bernardi, Bot. Jahrb. Syst. 83 (1964) 170, t. 21; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 64, f. 8. — Type: *Ramos, Philipp. Pl. 1109* (FI, G, JE, M, U, US, Z), Dahican, Prov. Laguna, Luzon, Philippines.

Shrub or small tree 3–10 m high. Twigs ± glabrous. Leaves imparipinnate with (1–) 2–3 pairs of lateral leaflets; total length up to 18 cm including petiole of 1.5–3.5 cm; rachis segments 1.2–3 cm long, petiole and rachis segments subterete, sometimes densely puberulent; leaflets subcoriaceous, glabrous and shiny on both surfaces, drying dark brown above and reddish brown beneath, often conduplicate; lateral leaflets elliptic to broadly elliptic, 5–8.5 by 2–3.7 cm, the blade narrowing unequally at the base into a petiolule c. 0.5 cm long, apex acuminate; apical leaflet elliptic to broadly elliptic, 7–9.5 by 2.5–3.5 cm, not markedly larger than the largest laterals, base attenuate to form a petiolule c. 1 cm long, apex acuminate; margin sometimes minutely revolute, crenate, 8–10 notches on each side of a leaflet; midrib slightly depressed above, prominent beneath, secondary and tertiary venation slightly raised on both surfaces. Stipules suborbicular, up to 0.7 by 0.9 cm. Inflorescence usually 4 dyads or tetrads, sometimes a few successive nodes flowering simultaneously; peduncles 0.5–1 cm long, shortly puberulous; axes of racemes up to 12 cm long, puberulous. Flowers unisexual? (only female ones seen); female flowers: pedicel 3 mm long, puberulous; calyx lobes 0.6 by 0.5 mm, glabrous; corolla oblong, 1.1 by 0.8 mm; disc lobes 0.3 mm long, broadly oblong; filaments 1 mm long; ovary 1.1 mm long, densely pubescent; styles 1.4 mm long, straight; stigmas capitate, papillose. Capsules with valves 2.5 by 1.5 mm at dehiscence; exocarp densely pubescent; calyx lobes caducous. Seeds c. 0.8 mm long, comose at both ends, the hairs to 1.5–2 mm long.

Distribution — *Malesia:* Philippines (Luzon and ?Samar).

Ecology — Forest at 650 m, perhaps as low as 230 m on Samar.

Notes — 1. A poorly defined species somewhat intermediate between *W. negrosensis* and *W. luzoniensis*. More collections and better ecological information are required before it can either be equated with another taxon or more clearly distinguished.

2. Probably dioecious but so far only female flowers have been found.

13. **Weinmannia luzoniensis** S. Vidal

Weinmannia luzoniensis S. Vidal, Révis. Pl. Vasc. Filip. (1886) 125; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 225; Bernardi, Bot. Jahrb. Syst. 83 (1964) 172; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 58, f. 6A–C, 7. — Type: *Vidal y Soler 314* (MA lecto of Hopkins 1998, photo at P; A, FI, L, MA), Lucban, Tayabas Prov., Philippines.

Weinmannia luzoniensis S. Vidal var. *puberula* Elmer, Leafl. Philipp. Bot. 8 (1919) 3078. — Type: *Elmer 18066* (A, BM, BO, K, L, P, PNH and others), Los Baños, Mt Maquiling, Laguna Prov., Philippines.

Tree 8–20 m high, 10–50 cm dbh. Young twigs pilose, the hairs up to 0.8 mm long, older ones more sparsely pilose to glabrescent or puberulous. Leaves imparipinnate with 2–3(–4) pairs of lateral leaflets; total length up to 19 cm including petiole of 2–2.5 cm; rachis segments 0.5–1.5 cm long, petiole and rachis segments semiterete, usually somewhat pubescent or pilose; leaflets chartaceous to subcoriaceous, glabrous and sometimes shiny above, sparsely pilose beneath; lateral leaflets elliptic, the largest 4.5–8.4 by 1.5–3.5 cm, base unequal, ± sessile, apex acuminate; apical leaflet elliptic or usually markedly rhomboidal, 6.7–12 by 2.2–5 cm, base shortly attenuate to form a winged petiolule up to 1 cm long, apex acuminate; margin markedly crenate, 13–17 notches on each side of the largest lateral leaflets; midrib slightly depressed above, prominent and pilose beneath, secondary and tertiary venation slightly raised on both surfaces. Stipules suborbicular, up to 1.7 by 2.2 cm. Inflorescence usually 4 dyads or tetrads, sometimes a few successive nodes flowering simultaneously; peduncles puberulous; axes of racemes up to 9 cm long, densely puberulous. Flowers unisexual and plants dioecious; pedicel 0.8–1.5 mm long, puberulous; calyx lobes 0.6–0.7 by 0.4–0.6 mm, hirsute on outer surface; corolla oblong or irregularly obovate, 1–1.2 by 0.6–0.8 mm, rounded or emarginate at apex; disc lobes c. 0.3 mm long, broadly oblong; in male flowers: filaments 2.2–3.4 mm long, ovary 0.4–0.6 mm long, pubescent, styles 0.1–0.4 mm long, incurved; in female flowers: filaments 0.7–1.2 mm long, ovary 1–1.2 mm long, densely pubescent, styles 0.9–1.1 mm long, straight, stigmas capitate, papillose. Capsule with valves 2–2.7 by 1.3–1.5 mm at dehiscence; exocarp densely pubescent to velutinous; calyx lobes caducous or not. Seeds c. 0.7 mm long, comose at both ends, the hairs to 1 mm long.

Distribution — *Malesia:* Philippines (Luzon and one record from Mindanao).

Ecology — Primary and secondary montane forest, from 500–2000 m. Fairly common in some localities in the mountains of Luzon.

Notes — 1. A distinctive species, because of the combination of a rhomboidal terminal leaflet and longish hairs on several organs (pilose).

2. Flowers described as yellowish or red (*Conklin & Buwaya PNH 80387*).

14. Weinmannia negrosensis Elmer

Weinmannia negrosensis Elmer, Leafl. Philipp. Bot. 2 (1909) 577; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 225; Bernardi, Bot. Jahrb. Syst. 83 (1964) 174, t. 23 (var. *negrosensis*); H.C. Hopkins, Adansonia sér. 3, 20 (1998) 62, f. 6D–K. — Type: *Elmer 9656* (A, BM, E, FI, G, LE, Z), Cuernos Mts, Dumaguete, Negros Oriental Prov., Philippines.

Weinmannia simplicifolia Merr., Philipp. J. Sci., Bot. 12 (1917) 268; Enum. Philipp. Flow. Pl. 2 (1923) 225. — *Weinmannia negrosensis* Elmer var. *simplicifolia* (Merr.) Bernardi, Bot. Jahrb. Syst. 83 (1964) 175, t. 24. — Type: *Ramos & Edaño BS 26531* (A, K), Mt Dingalan, Tayabas Prov., Philippines.

Weinmannia cuneatifolia Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 252. — Type: *Ramos Philipp. Pl. 1287* (B holo; BM, L, P and others), Mindanao, Philippines.

Shrub or tree 3–25 m high, up to 30 cm dhb when 12 m high. Twigs glabrous. Leaves simple or trifoliolate; total length up to 19 cm in trifoliolate leaves, including petiole of 1–4 cm; petiole subterete, slightly flattened or channelled on adaxial side, glabrous or puberulent; leaf(let) blades coriaceous, glabrous on both surfaces, elliptic to obovate; in trifoliolate leaves, lateral leaflets 4.5–11.5 by 1.6–3.4 cm, base shortly attenuate, apex acute or acuminate; apical leaflet 6–15.5 by 2.4–6 cm, base long-attenuate (constricted region up to 1.7 cm long), apex acute or acuminate; unifoliolate leaves 4.5–13 by 1.7–6.5 cm, base attenuate (constricted region 0.6–1.5 cm long); margin sometimes minutely thickened and revolute, crenate, 11–15 notches on each side of a leaflet; midrib sometimes slightly depressed above, prominent beneath, glabrous, secondary and tertiary venation flat or raised above and raised beneath. Stipules suborbicular, up to 1.5 by 1.7 cm. Inflorescence usually 4 dyads or tetrads, sometimes a few successive nodes flowering simultaneously; peduncles 0.3–1.3(–3) cm long, puberulent; axes of racemes up to 12 cm long, puberulent. Flowers unisexual and plants dioecious; pedicel 1–1.7 mm long, puberulent; calyx lobes 0.6–1 by 0.6–0.8 mm, glabrous on outer surface, ciliate; petals obovate, apex rounded, 1–1.4 by 0.7–0.9 mm; disc lobes 0.3–0.4 mm long, broadly oblong; in male flowers: filaments 2.7–3.2 mm long, ovary c. 0.5 mm long, pubescent, styles 0.1–0.2 mm long, incurved; in female flowers: filaments 0.9–1.7 mm long, ovary 1.1–1.4 mm long, pubescent, styles 1.3–1.9 mm long, straight, stigmas capitate, papillose. Capsule with valves 2–2.5 by 1.3–1.5 mm at dehiscence; exocarp pubescent or densely so; calyx lobes usually but not always persistent. Seeds 0.8–0.9 mm long, comose at both ends, the hairs to c. 1 mm long.

Distribution — *Malesia:* Philippines (Luzon, Mindanao, Sibuyan, Negros, Leyte, Mindoro) and Sulawesi (1 collection).

Ecology — Recorded from montane mossy forest and dense windswept shrubberies at 1200–1960 m.

15. Weinmannia pullei Schltr.

Weinmannia pullei Schltr., Bot. Jahrb. Syst. 52 (1914) 164; Nova Guinea 12 (1917) 492, t. 192; Bernardi, Bot. Jahrb. Syst. 83 (1964) 176, t. 25; P. Royen, Alpine Fl. New Guinea 4 (1983) 2539, t. 739; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 70, f. 1J–Q, 2. — Type: *Pulle 470* (B holo; BM, BO, K, L), Mt Perameles, Irian Jaya.

Weinmannia virgulata Schltr., Bot. Jahrb. Syst. 52 (1914) 164; Nova Guinea 12 (1917) 492. — Type: *Pulle 692* (B holo; BO, L), Mt Hellwig, Irian Jaya.

Weinmannia versteeghii L.M. Perry, J. Arnold Arbor. 30 (1949) 162; Bernardi, Bot. Jahrb. Syst. 83 (1964) 183. — Type: *Brass & Versteegh 10469* (A holo; BM, BO, K, L), 9 km NE of Lake Habbema, Irian Jaya.

Shrub or tree (1.75–)4–27 m high, up to 30 cm dbh, rarely epiphytic. Twigs, buds and young leaves sericeous, later glabrescent. Leaves imparipinnate with 1–6(–10) pairs of lateral leaflets; total length up to 10.5 cm including petiole 0.7–1 cm long; rachis segments c. 0.8 cm long; petiole and rachis diverging from the stem at an acute acroscopic angle, terete, semiterete or sometimes narrowly winged, the wings extending to 0.8 mm from midline; leaflets subcoriaceous, usually glabrous on both surfaces or sometimes sparsely strigose on underside especially along midrib, flat; lateral leaflets obovate or oblanceolate, 0.6–3.2 by 0.3–1.5 cm, inserted at an acute acroscopic angle to the leaf rachis, of ± equal size in one leaf, base equal, apex acute to obtuse; terminal leaflet narrowly elliptic to elliptic, 0.8–4.8 by 0.3–1.7 cm, base attenuate, apex acute; margin crenulate or rarely dentate with 3–7 notches on each side in the lateral leaflets; midrib and secondary veins ± flat above, secondary veins at an acute acroscopic angle to the midrib. Stipules ligulate to ± orbicular or reniform, up to 0.8 by 1 cm. Inflorescence usually of 2 dyads, the apical bud of main stem sometimes aborting or continuing to grow vegetatively, or rarely of 2 or 4 individual racemes; sometimes a few successive nodes flowering simultaneously; a pair of reduced leaves and a pair of stipules usually present at base of the racemes in each dyad; peduncles 0.6–2 cm long, sparsely puberulent; racemes up to 12 cm long, sparsely puberulent; bud at apex of peduncles minute, velutinous, sometimes commencing growth during reproduction. Flowers mostly unisexual, sometimes bisexual; pedicel 1.5–3.5 mm long, puberulent or ± glabrous; calyx lobes c. 0.5 by 0.4–1.4 by 1.1 mm, glabrous or with ciliate margin; petals elliptic, 1.1–2.3 by 0.7–1.5 mm; disc lobes 0.3–0.6 mm long; in male flowers: filaments up to 4 mm long, ovary 0.5–1 mm, pubescent, styles 0.2 mm long, incurved; in female flowers: filaments up to c. 0.8 mm long, ovary 0.5–1 mm long, pubescent, styles c. 0.9 mm long, straight, puberulent at least at base, stigmas capitate, papillose; in bisexual flowers: filaments c. 4 mm long, ovary c. 1 mm long, styles c. 1 mm long, straight. Capsules with valves 3–4.5 by 2.5–2.8 mm at dehiscence; exocarp densely pubescent; calyx lobes persistent. Seeds c. 1 mm long, bearing hairs all over surface, longest at ends.

Distribution — *Malesia:* New Guinea.

Ecology — Grows as a tree in montane forest and as a small tree or shrub in mountain-top shrubbery; from 1100–2100 m in Irian Jaya and 2800–3200 m in Papua New Guinea. Locally common.

Notes — 1. *Weinmannia pullei* appears most closely related to the largely sympatric *W. urdanetensis*; however, it has rather few, obovate leaflets while *W. urdanetensis* usually has more numerous elliptic or oblong ones; the leaflets also differ in their angle of insertion. These two species share the following characters: inflorescence primarily of dyads; floral bracts often persisting to fruiting stage; flowers usually unisexual but sometimes bisexual; fruits with the valves densely pubescent; seeds with hairs all over their surface (not confined to the ends). The structure of the inflorescence is particularly variable in *W. pullei.*

2. A few collections from Irian Jaya (Wissel Lakes and Vogelkop) with largely trifoliolate leaves are provisionally placed here although they may prove to be distinct.

16. **Weinmannia urdanetensis** Elmer

Weinmannia urdanetensis Elmer, Leafl. Philipp. Bot. 7 (1915) 2608; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 225; L.M. Perry, J. Arnold Arbor. 30 (1949) 160; Bernardi, Bot. Jahrb. Syst. 83 (1964) 181, excl. t. 29; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 65, 74, f. 1A–H, 3. — Type: *Elmer 13701* (A, BISH, BM, BO, K, L and others), Cabadbaran (Mt Urdaneta), Agusan Prov., Mindanao, Philippines.

Weinmannia trichophora L.M. Perry, J. Arnold Arbor. 30 (1949) 161; Bernardi, Bot. Jahrb. Syst. 83 (1964) 181. — Type: *Clemens 9498* (A holo; B), Samanzing, Morobe Prov., Papua New Guinea.

Weinmannia novoguineensis L.M. Perry, J. Arnold Arbor. 30 (1949) 161. — Type: *Clemens 7517* (A holo; B), Sarawaket, Morobe Prov., Papua New Guinea.

Shrub or tree 3–26 m high, up to 43 cm dbh, variable in form from bushy to gnarled to slender. Twigs velutinous, axillary buds and young leaves sericeous. Leaves imparipinnate with 2–19 pairs of lateral leaflets; total length up to 10.5 cm, including petiole c. 0.5 cm long; rachis segments 0.3–1 cm long; petiole and rachis diverging from the

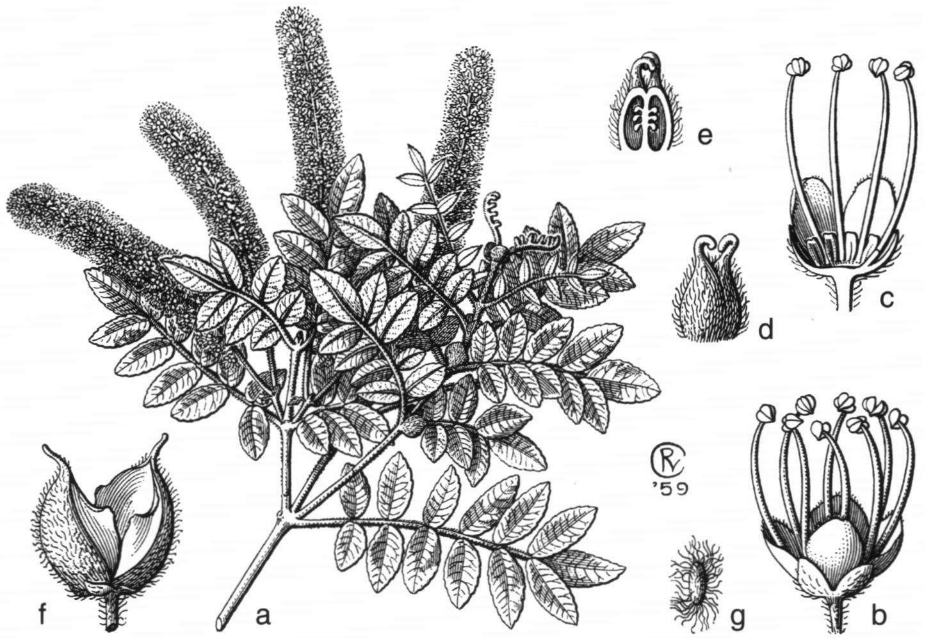

Fig. 39. *Weinmannia urdanetensis* Elmer. a. Flowering shoot, the flowers in racemes; b. flower; c. longitudinal section of flower, the gynoecium removed; note disc lobes alternating with filaments; d. gynoecium; e. longitudinal section through gynoecium; f. mature, dehisced capsule; g. seed, with hairs all over surface (a: *CSIRO New Guinea 1946*; b–e: *Hoogland 5463*; f, g: *Pullen 374*). — a × 0.66; b, d, f, g × 7; d, e × 13.

stem at an angle of almost 90° especially at growing tips; petiole and rachis segments terete, densely velutinous, the hairs erect, up to 0.5 mm long; leaflets coriaceous, imbricate or not, flat or revolute, usually glabrous or puberulent above, the cuticle thick and shiny, sparsely to densely strigose-velutinous beneath, the midrib velutinous; lateral leaflets elliptic, oblong or somewhat ovate, with margins ± parallel, 0.6–2.6 by 0.3–1.1 cm, inserted ± at 90° to leaf rachis, of ± equal size in one leaf, base symmetrical or not, cuneate to square to cordate, apex broadly acute; terminal leaflet narrowly elliptic to elliptic, 0.9–3 by 0.3–1.2 cm, base petiolulate, the petiolule c. 0.3 cm long, apex acute; margin crenulate with 4–7 notches on each side in the lateral leaflets; midrib and secondary veins depressed into cuticle above; secondary veins ± at 90° to midrib; tertiary venation obscure. Stipules ± orbicular or reniform, up to 0.8 by 1.1 cm. Inflorescence a pair of dyads (rarely a pair of tetrads, or 4 dyads, or 4 individual racemes), sometimes a few successive nodes flowering simultaneously; the apical bud of the main stem densely velutinous and often continuing to grow vegetatively during flowering; peduncles 0.3–0.4 cm long, densely velutinous; racemes up to 9 cm long, densely velutinous. Flowers unisexual or rarely bisexual; pedicel 0.5–1 mm long, puberulent or ± glabrous; calyx lobes 0.7–1 by 0.6–0.9 mm, hirsute; petals elliptic, oblong or almost circular, 1–1.9 by 0.7–1.2 mm, rounded or notched at apex; disc lobes 0.3–0.6 mm long; in male flowers: filaments 2.2–3.6 mm long, ovary c. 0.6–1 mm, pubescent, styles 0.2–0.5 mm, incurved;

in female flowers: filaments 0.8–1.7 mm long, ovary 1–1.5 mm long, pubescent, styles 0.5–1 mm long, straight, puberulent at least at base, stigmas capitate, papillose; in bisexual flowers: filaments 2.6+ mm long, ovary 1–1.5 mm long, the styles 1–1.8 mm long, straight. Capsules with valves 2.5–4 by 1.5–2 mm at dehiscence; exocarp densely pubescent; calyx lobes persistent. Seeds c. 1 mm long, bearing hairs all over the surface, longest at ends. — **Fig. 39.**

Distribution — *Malesia:* Philippines (Luzon and Mindanao) and New Guinea.

Ecology — In lower montane and montane forest, also secondary forest and open scrub on limestone, abundant and gregarious, at 1000–3250 m, at higher altitude in the Central Highlands of New Guinea.

Notes — 1. Appears to be closely related to *W. pullei* from New Guinea and *W. clemensiae* from Mt Kinabalu in Borneo, which it resembles in its branching pattern and somewhat bullate leaflets.

2. The breeding system is largely dioecious with some exceptions (monoecious, polygamodioecious etc.).

3. Specimens from the western part of the distribution tend to have more numerous pairs of longer, narrower leaflets (Philippines and Irian Jaya; also Torricellis and Mt Hunstein but the latter are sterile). In the Central Highlands of Papua New Guinea, leaflets on fertile specimens tend to be shorter and broader, often more densely pubescent ('*W. trichophora*') and there are fewer pairs per leaf. A number of specimens from the Central Highlands have comparatively large leaflets, approaching *W. pullei.*

Section Leiospermum

Weinmannia sect. *Leiospermum* (D. Don) Engl., Nat. Pflanzenfam. III, 2a (1891) 101; ed. 2, 18a (1928) 256; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 21. — *Leiospermum* D. Don, Edinb. New Philos. J. 9 (1830) 91. — Type: *Weinmannia racemosa* L.f. (lecto of Hopkins 1998).
Weinmannia sect. *Racemosae* Bernardi, Bot. Jahrb. Syst. 83 (1964) 132, 158.

Branching sometimes dichotomous. Stipules often ligulate, elliptic or ovate, the apex rounded or pointed. Inflorescence composed 1–3 partial inflorescences, usually inserted medially and laterally; lateral PIs usually consisting of 1 metamer (dyad or triad); median PIs of 1 metamer (dyad or triad), 2 metamers (tetrad or pentad) or 3 metamers (heptad); apical bud of shoot usually fertile (developing into a raceme in triads, pentads and heptads), sometimes aborted (in dyads and tetrads) or rarely dormant or vegetative (New Zealand); leaves at nodes from which racemes arise not suppressed, partially suppressed or totally suppressed; stipules sometimes present at nodes within partial inflorescences; 'collars' around peduncles of lateral PIs often present; apical buds within lateral PIs either developed into a medial raceme or aborted; lateral auxiliary buds (i.e. lateral to axillary buds) present at most distal leaf-bearing node and often at other nodes also. Flowers pedicellate, inserted on axes of racemes singly, each pedicel subtended by a small bract. Capsules with valves often minutely ridged and indumentum strigose or absent; after dehiscence, central column usually well developed and persistent; calyx lobes often falling in fruit.

Distribution — 17–19 species in the Pacific, extending westwards to Papua New Guinea (Bismarck Archipelago and Karkar Island) and eastwards to the Marquesas.

17. **Weinmannia croftii** H.C. Hopkins

Weinmannia croftii H.C. Hopkins, Adansonia sér. 3, 20 (1998) 76, f. 4, 5. — Type: *Ridsdale NGF 36706* (L holo; A, BISH, K), Karkar Island, Madang Prov., Papua New Guinea.

Shrub or tree 2–20 m high. Twigs shortly hairy and finely ridged; branching sometimes dichotomous. Leaves trifoliolate or imparipinnate with 1–3 pairs of leaflets; up to 14 cm long including petiole of 1.3–2.5 cm; rachis segments 0.8–1.7 cm long; petiole and rachis segments semiterete, usually bearded above and narrowly winged, the wings extending c. 1 mm from midline; blade subcoriaceous to coriaceous, glabrous on both surfaces, usually punctate beneath; lateral leaflets lanceolate to narrowly elliptic, 2.9–6.7 by 0.9–1.7 cm, apex acute, base asymmetrical, the distal side acute to attenuate, proximal side obtuse; terminal leaflet narrowly elliptic to narrowly obovate, (2.8–)4.3–11 by (0.9–)1.2–2.3 cm, apex acute, base attenuate; margin somewhat thickened and minutely revolute, crenate especially towards the apex with 14–17 notches on each side; midrib narrowly prominent above and slightly prominent beneath, when sometimes hirsute. Stipules usually elliptic, ligulate or rhomboidal, c. 0.7 by 0.4 cm, obtuse to broadly acute at apex. Inflorescence a central triad or usually pentad, the lower racemes in the

Fig. 40. *Weinmannia sp. A* Flowering shoot (*Bradford 811*, Vangunu, New Georgia Group, Solomon Islands). Photo by J. C. Bradford.

axils of leaves or not; peduncles and rachis segments 0.9–1.6 cm long; racemes 5–9 cm long; inflorescences axes puberulent. Flowers unisexual and plants dioecious; pedicel 1–2 mm long, puberulent; calyx lobes 0.7–1.1 by 0.6–0.9 mm, ± glabrous; petals elliptic, 1.1–1.7 by 0.7–1 mm; disc lobes 0.4–0.8 mm long; in male flowers: filaments 2.4–3 mm long, ovary 0.6–1 mm long ± glabrous, styles minute, 0.2 mm long and curved inwards; in female flowers: filaments 0.9–2 mm long, ovary 1–1.8 mm long, almost glabrous, styles 0.9–1.5 mm long, stigmas capitate and papillose. Capsules distinctly supported by receptacle, valves 2–4 by 1.3–1.8 mm at dehiscence; exocarp minutely ridged, almost glabrous (few minute strigose hairs); calyx lobes not persistent. Seeds 0.8–1 mm long, 16 per capsule, comose at both ends, the hairs c. 0.5 mm long.

Distribution — *Malesia:* Papua New Guinea (Karkar Is., Manus and New Britain).

Ecology — In mossy montane forest and as an early coloniser on volcanic substrates where it is sometimes very abundant. On Manus and Karkar, from 530–720 m and 820–1050 m respectively, and in New Britain from 1200–2100 m.

Notes — 1. A shrub in open areas such as scoria slopes, or a tree in forest.

2. Appears to be closely related to *W. denhamii* Seem. from Vanuatu and *W. vitiensis* Seem. from Fiji and possibly conspecific with un-named material from the Solomons (Fig. 40). All have imparipinnate, coriaceous leaves with a narrowly winged petiole and predominantly unisexual flowers. *Weinmannia denhamii* usually has more numerous, shorter leaflets than *W. croftii,* and *W. vitiensis* has trifoliolate leaves with rather broader leaflets. The mean values for foliage characters are different for each species though the ranges overlap.

3. Not yet recorded from New Ireland, where so far only *W. fraxinea* is known.

EXCLUDED

Adenilema Blume, Bijdr. Fl. Ned. Ind. (1827) 1120, described as probably belonging to the *Cunoniaceae*, is now commonly included in *Neillia* D. Don (*Rosaceae*).

Pellacalyx Korth., Tijdschr. Natuurl. Gesch. Physiol. 3 (1836) 20, was placed by the author in the *Cunoniaceae*, to which he also transferred *Carallia* Roxb. Both these genera are now included in the *Rhizophoraceae* (see Ding Hou, Fl. Males. ser. I, 5 [1958] 481, 490).

"*Cunoniaceae*" Griff., Not. Pl. Asiat. 4 (1854) 429 & Ic. Pl. Asiat. 4 (1854) t. 486, represent *Pellacalyx* Korth.

Kaernbachia Schltr., Bot. Jahrb. Syst. 52 (1914) 151, f. 5; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 241; non O. Kuntze (1891). Originally described as a new genus in the *Cunoniaceae*, it has been shown to be synonymous with *Turpinia* Vent. (*Staphyleaceae*) (see Van Steenis, Nova Guinea n.s. 10 [1959] 211 and Van der Linden, l.c. 212 & Fl. Males. ser. I, 6 [1960] 51).