

A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific. 1. Introduction and an account of the species of Western Malesia, the Lesser Sunda Islands and the Moluccas

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ABSTRACT

About 40 species of the largely tropical, montane genus *Weinmannia* occur in Malesia and the Pacific belonging to two sections. Section *Fasciculata* is largely Malesian, extending eastwards to Fiji, and sect. *Leiospermum* is largely Pacific, occurring as far west as Papua New Guinea. The structure of the inflorescence provides previously unrecognised characters of taxonomic importance, especially at the sectional level. Because of the high levels of local endemism, species accounts for the whole region are divided into four parts. Descriptions, illustrations and distribution maps are provided here for four species: *W. fraxinea*, a widespread ochlo species; *W. clemensiae*, a local endemic on ultramafic substrates in Sabah; *W. aphanoneura*, from Borneo and Sumatra, and *W. hooglandii* H.C. Hopkins & J.C. Bradford, *sp. nov.*, from Peninsular Malaysia.

KEY WORDS

Weinmannia,
Cunoniaceae,
inflorescence structure,
Malesia,
Pacific.

RÉSUMÉ

La Malésie et le Pacifique renferment environ 40 espèces de *Weinmannia* (genre essentiellement tropical et montagneux), réparties dans deux sections : sect. *Fasciculata*, présente surtout en Malésie et répandue à l'est jusqu'à Fiji ; sect. *Leiospermum*, surtout Pacifique, s'étendant à l'ouest jusqu'à la Papouasie-Nouvelle-Guinée. La structure des inflorescences fournit des caractères d'importance taxonomique, surtout pour la distinction des sections, qui n'avaient pas été utilisés jusqu'à maintenant. En raison de l'importance de l'endémisme local, l'étude des espèces répandues dans l'ensemble de cette région est divisée en quatre parties. Des descriptions, illustrations et cartes de répartition sont fournies ici pour quatre espèces : *W. fraxinea* une ochloespèce largement répandue ; *W. clemensiae* endémique de Sabah, sur substrats ultramafiques ; *W. aphanoneura*, de Borneo et Sumatra, et *W. hooglandii* H.C. Hopkins & J.C. Bradford, *sp. nov.*, de la Péninsule malaise.

MOTS CLÉS

Weinmannia,
Cunoniaceae,
structure inflorescentielle,
Malésie,
Pacifique.

INTRODUCTION

Weinmannia is the largest and most widespread genus in the predominantly woody, southern hemisphere family, Cunoniaceae, and it contains almost half the 300 or so species of the family as it is currently circumscribed in BRUMMITT (1992). There are about 80 species in tropical America (BERNARDI 1961, 1963a), at least 30 in Madagascar and the Mascarene Islands (BERNARDI 1964, 1965; J.C. BRADFORD pers. comm.) and ca. 40 in Malesia and the Pacific (BERNARDI 1964 and this revision). The present day distribution of the genus is thus rather curious since it is absent from Africa, mainland Asia except for Peninsular Malaysia, and from Australia, which is part of the region of greatest generic diversity for the family. However, fossil leaves with affinities to *Weinmannia* (*Weinmanniaphyllum*) have been described from Oligocene deposits in Tasmania (CARPENTER & BUCHANAN 1993) suggesting that it may once have occurred in places where it is now extinct. *Weinmannia* is largely tropical and montane though it occurs in subtropical and temperate forest in South America and in New Zealand, and in lowland tropical forest in Madagascar. The taxonomic history of the genus was discussed by BERNARDI (1961).

In the most recent treatment of the Malesian-Pacific species, BERNARDI (1964) recognised 40 species in two sections but he rarely gave complete descriptions except for new taxa. In addition, much new material has become available since his work (e.g. 2/3 of the collections of *W. urdanetensis* Elmer and *W. pullei* Schltr. from the Highlands of New Guinea have been collected since 1959). R.D. HOOGLAND, who had a long-standing monographic interest in the family, started to revise *Weinmannia* for Malesia and the Pacific in the 1970s. The present study has drawn on his extensive collection of taxonomic literature, notes on morphology and typification, and a card index of specimens. However, the species concepts and descriptions are mine unless otherwise indicated.

My study was based largely on herbarium material with field observations in Malaysia, Fiji and New Caledonia. It is divided into four parts: this

paper presents background information, an account of the widespread and variable *Weinmannia fraxinea* (D. Don) Miq. and of the remaining species in Western Malesia, the Lesser Sunda Islands and the Moluccas; part 2 (HOPKINS 1998a) deals with the species of Sulawesi and the Philippines; part 3 (HOPKINS 1998b) describes the species that occur in New Guinea and the islands of the western Pacific; and part 4 (HOPKINS & FLORENCE 1998) deals with the islands of the central Pacific and presents an index to taxa, including synonyms. Where appropriate, regional papers have been further divided by island group, each with a separate key. This arrangement has been adopted in part to reflect the high degree of regional and island-group endemism, in part to reflect authorship of the accounts, and in part because the problems remaining in Samoa and the Cook Islands preclude a uniform treatment of all taxa in a single alphabetical list. Those wishing to see a comprehensive key and alphabetical treatment of species for Malesia will find this eventually in *Flora Malesiana*. In the meantime, the sectional keys of BERNARDI (1964) are helpful, with some minor adjustments for new and recircumscribed taxa. An identification list of specimens seen (excluding New Zealand, Samoa and the Cook Islands) will be deposited in major herbaria or available from P.

Only one species, *Weinmannia fraxinea*, is widespread in Malesia and the western Pacific, occurring from northern Sumatra to the Solomon Islands. It is described in some detail in this paper. Where this and other species occur in more than one region (e.g. *W. urdanetensis* in the Philippines and New Guinea; *W. exigua* A.C. Sm. in the Solomon Islands and Fiji), the description and synonymy are given only once.

My species concept is morphological (see MCDADE 1995) and aims to be consistent with the definition of CRONQUIST (1978) as the smallest group that is consistently and persistently distinct and distinguishable by ordinary means. It has been suggested that over reliance on leaf characters (especially size and number of leaflets) has led to taxonomic confusion and the over description of species in *Weinmannia*. However, there are few other characters available, as features of the flowers

and fruits are rarely taxonomically useful at the species level. Thus many taxa differ by combinations of quantitative characters, none of which is diagnostic on its own. The structure of the inflorescence has provided some new characters, particularly at the sectional level, but it is rather uniform amongst the species in Malesia.

There has been a wealth of anatomical work on Cunoniaceae and its relatives (e.g. DICKISON 1975a,b, 1977, 1980a,b, 1984; GOVIL & SAXENA 1976; HIDEUX & FERGUSON 1976; RAO & DICKISON 1985; RUTISHAUSER & DICKISON 1989) and many of the characters investigated have proved useful in understanding relationships within the family and with its close relatives (HUFFORD & DICKISON 1992). However, species delimitation in *Weinmannia* is aggravated by lack of strong morphological divergence, and anatomical characters are unlikely to be useful at this taxonomic level.

Within Cunoniaceae, *Weinmannia* is closely related to *Cunonia* (ENGLER 1930; HUFFORD & DICKISON 1992), with which it is sympatric in New Caledonia. It differs from *Cunonia* in the form of the floral disc (which is adnate to the base of the ovary in *Cunonia* and composed of either free lobes or a continuous ring, attached only at its base, in *Weinmannia*), the dehiscence of the fruit (dehiscing in a circle round the base and acropetally along the sutures, the valves remaining attached to the central column at the apex in *Cunonia*; dehiscing septically or septifragally from the apex, and the valves and central column remaining attached at the base in *Weinmannia*) and in the seeds (angular and often narrowly winged in *Cunonia*; ellipsoidal, comose at both ends or throughout and not winged in *Weinmannia*). HUFFORD & DICKISON's analysis also suggests a close affinity with *Pancheria* but this genus differs markedly from the other two in its capitate inflorescences.

Weinmannia has little economic importance in Malesia and the Pacific. The bark contains high levels of tannins and some species are used for tanning and firewood but few local uses are recorded. The flowers of *Weinmannia racemosa* L. f. are visited by bees which in turn produce honey on a commercial scale in New Zealand (J.C. BRADFORD pers. comm.).

ECOLOGY AND DISTRIBUTION

Weinmannia species are typically trees and shrubs of humid, montane forests, often growing where there is persistent cloud cover and quite high, well distributed rainfall. Twigs and leaf blades are often covered with mosses and other epiphytes. Within Malesia, the genus grows at mid to high elevations (up to 2600-2800 (-3000) m) in Borneo, Sulawesi and New Guinea) although a few species occur near sea level. In the Pacific, *Weinmannia* is absent from low coralline islands but widespread and sometimes abundant on the high volcanic ones. Vegetation zones here are more compressed than in Malesia, and *Weinmannia* is typically found at 300-750+ m. The genus also occurs on islands of continental origin, from 150-1550 m in New Caledonia, and from ca. 300-1180 m in New Zealand (*W. racemosa*, fide WARDLE 1966).

Weinmannia often occurs on ridges, steep slopes and in areas of disturbance due to tree falls, landslides or volcanic eruptions. It is sometimes an early coloniser on volcanic slopes and along roadsides (e.g. *W. fraxinea* in Sabah, *Weinmannia* sp. in central Viti Levu) where it tolerates high light intensity. While it is found on a range of soil types, it often occurs on ones with atypical mineral composition, including soils derived from ultramafic substrates and on the leached soils associated with disturbed sites in cloud forest. Frequent plant associates are the ferns *Gleichenia* and *Dicranopteris* which are typical of burnt or repeatedly cut sites on impoverished soils, often rich in aluminium.

A few species have very specific ecologies (e.g. *Weinmannia clemensiae* Steenis from stunted forest on ultramafic soil) while others show considerable ecological plasticity and are found over a broad altitudinal range (e.g. *W. fraxinea* in parts of Malesia and *W. parviflora* G. Forst. in Tahiti), and both these species are morphologically very variable. *Weinmannia croftii* H.C. Hopkins from the Bismarck Archipelago is found both as an early coloniser of volcanic deposits and in adjacent closed, montane forest (D. FRODIN pers. comm.).

Most species of Malesian-Pacific *Weinmannia* have quite restricted distributions and there is a

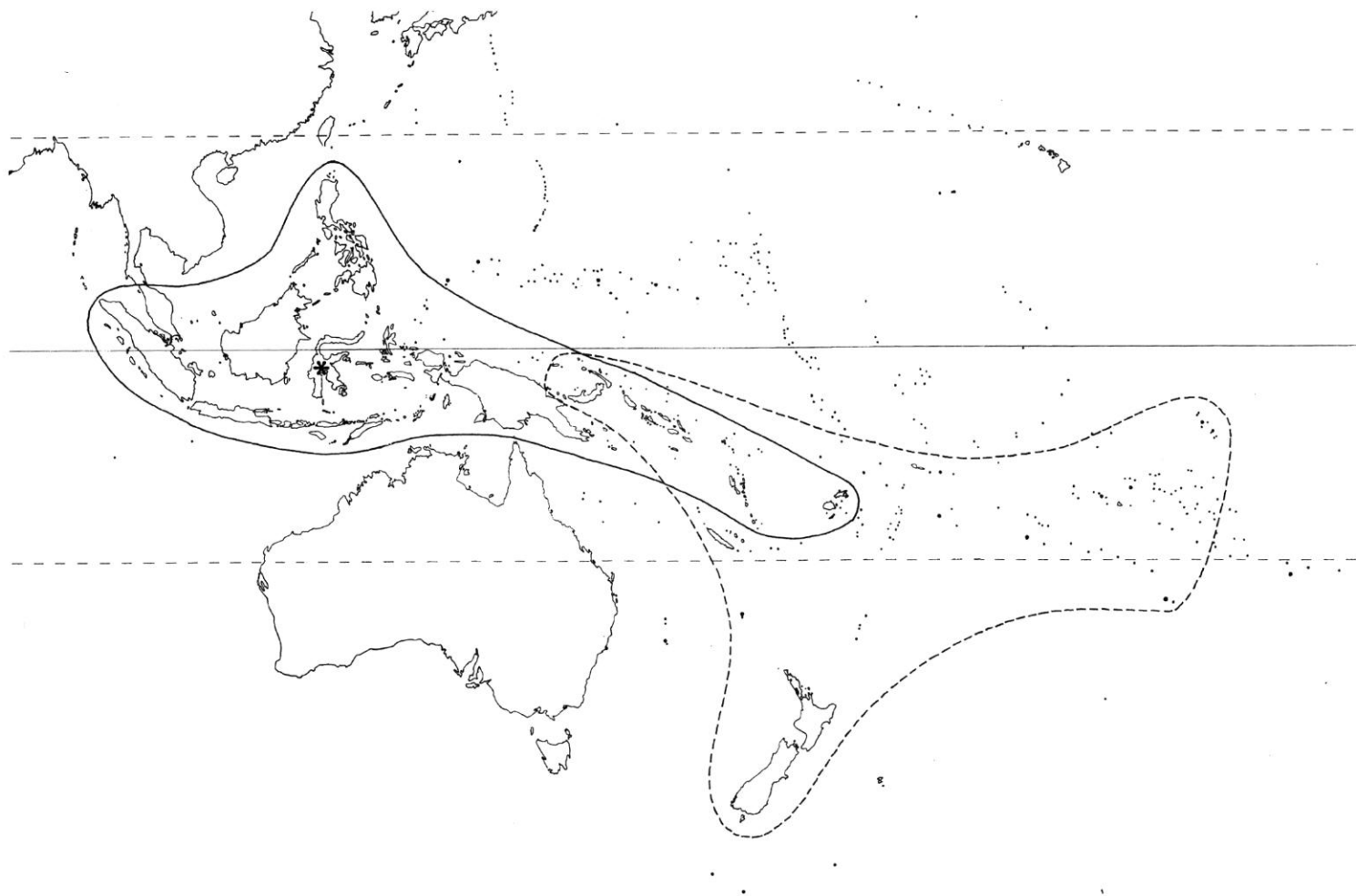


Fig. 1.—Distribution of *Weinmannia* sect. *Fasciculata* (solid line) and sect. *Leiospermum* (-----); *W. descombesiana* (*).

high degree of island or island-group endemism. Within Malesia, *W. fraxinea* is the only widespread species. In contrast with parts of the Andes and Madagascar (J.C. BRADFORD pers. comm.), there are few sympatric or co-occurring species of *Weinmannia* in any part of its Malesian-Pacific distribution. It is of note that there are only four species in New Caledonia, which is a centre of species richness for the Cunoniaceae, with a total of about 90 species. It seems likely that here, *Weinmannia* is at least partly replaced by *Cunonia*, which is morphologically similar in many respects.

Weinmannia has small seeds that are probably wind-dispersed (see below). Anemochory, possibly with the aid of cyclones, and the opportunistic ecological strategy of some species tie in well with dispersal to, and establishment on, groups of remote volcanic islands within the Pacific. Despite the role that the break up of Gondwanaland may have played in the worldwide distribution of the genus, more recent dispersal events have clearly also had an impact.

Weinmannia is an important component of the vegetation in some parts of its distribution, such as the Society and Marquesas Islands, and New Zealand. Those species that, like *W. fraxinea*, are tolerant of natural disturbance, are likely to become more abundant with increasing human impact. However, some restricted endemics may be of conservation interest including *W. clemensiae* from the Mt. Kinabalu massif in Sabah, *W. paitensis* Schltr., which is confined to a few mountains in central and southern New Caledonia and *W. ouaiemensis* (Guillaumin & Viot) Hoogland, known from only a single locality in north-eastern New Caledonia. Some other species are known from very few collections but we have too little information at present to assess their conservation status. Several species such as *W. rapensis* F. Br. and *W. raiaensis* J.W. Moore, are endemic to small Pacific islands, but they are not currently considered threatened.

RELATIONSHIPS OF THE MALESIAN-PACIFIC SPECIES

BERNARDI (1961, 1963a,b, 1964, 1965) pro-

posed an infrageneric classification of *Weinmannia* with six sections. According to BERNARDI, sections *Weinmannia*(e) and *Simplicifolia*(e) are principally American, with a few species in the Mascarene Islands (sect. *Weinmannia*); sections *Spicata*(e) and *Inspersa*(e) are confined to the western Indian Ocean (Madagascar and Comores); and the Malesian-Pacific species are placed in sections *Fasciculata*(e) and *Leiospermum* (referred to as sect. *Racemosae* by BERNARDI). The latter also contains two Malagasy species, *W. comorensis* Tul. and *W. baehniiana* Bernardi. Sections *Fasciculata* and *Leiospermum* are distinguished from the others by the form of the floral disc, which is composed of eight free lobes alternating with the filaments, rather than a continuous ring (BERNARDI 1964: 132). In sect. *Fasciculata*, the flowers are arranged in "pseudoracemes" whilst in sect. *Leiospermum* they are dispersed, on pedicels, in racemes or panicles (BERNARDI 1964: 132).

Preliminary results of phylogenetic studies in progress, based on morphological characters, especially of the inflorescence, and on DNA sequencing (BRADFORD in press and pers. comm.) support the monophyly of both sections *Leiospermum* (morphology; DNA still unresolved) and *Fasciculata* (strong support from DNA sequences), although their relationships with other sections are still unclear. A few species were misplaced by BERNARDI; the Indian Ocean species he placed in sect. *Leiospermum* belong with the Malagasy sect. *Spicata*, and *W. descombesiana* Bernardi, placed by BERNARDI in sect. *Leiospermum*, belongs with the Malesian sect. *Fasciculata* (BRADFORD pers. comm.).

Section *Fasciculata* is a cohesive group of species. In addition to having the flowers inserted in fascicles on the inflorescence axis (to form the "pseudoracemes" of BERNARDI), these species share a common, rather complex, inflorescence plan (see below). *Weinmannia descombesiana* is somewhat problematical since it combines some characters of both sections *Fasciculata* and *Leiospermum*. Section *Fasciculata* is mostly Malesian, extending as far as east as Fiji (Fig. 1).

Section *Leiospermum* is confined to the Pacific, extending westwards as far as the Bismarck

Archipelago and Karkar Island in Papua New Guinea (Fig. 1). Most Pacific species form a closely knit group (e.g. *W. parviflora*, *W. purpurea* L.M. Perry, *W. vitiensis* Seem.). Those from New Caledonia form another group with minor differences in the flowers, which are always bisexual, and the inflorescence structure. The New Zealand species form a third group. Their flowers are inserted singly but have a greater tendency to be perigynous and the structure of the inflorescence shows some differences from the remaining Pacific species. The species of the Marquesas Islands, at the extreme east of *Weinmannia*'s distribution in the Pacific, have their affinities with the other Pacific species, not the American ones.

NOTES ON MORPHOLOGY AND BIOLOGY

1. Vegetative axes

Branching in most species of *Weinmannia* is from axillary buds, accompanied by the continued growth of the apical bud, and the architecture conforms to Rau's model (KELLER 1996). However, in several species of sect. *Leiospermum* the apical bud of growing shoots can be aborted and branching is then dichotomous. Most of these species show a mixture of branching patterns, but in *Weinmannia dichotoma* Brongn. & Gris, branching is almost exclusively dichotomous. Occasionally four buds at a node will develop, producing four stems of equal dominance (e.g. *W. dichotoma*, *W. affinis* A. Gray). The buds that develop in this instance are lateral to the axillary buds, and in a plane perpendicular to the line: leaf - axil - (apical bud) - axil - leaf, and are referred to as lateral, auxiliary buds; again, the apical bud is aborted.

In *Weinmannia*, as in most other Cunoniaceae, there is a pair of small, flattish, usually rounded to ovate, leaf-like structures between the petioles at each node, usually referred to as interpetiolar stipules (RUTISHAUSER & DICKISON 1989; Fig. 2A,B; 3Q). MELVILLE (1972) described them as bud scales and considered that they were not true stipules but that each was equivalent to an entire leaf. At vegetative shoot apices, they cover the developing buds and can be either persistent or

caducous as the leaves enlarge; in the later case, they leave a distinctive annular scar. Similar structures cover developing (partial) inflorescences and are also found at nodes within the inflorescence in sect. *Leiospermum* where the leaves are wholly or partly suppressed. When found in the inflorescence, the stipules are usually more oblong-elliptic than at vegetative nodes.

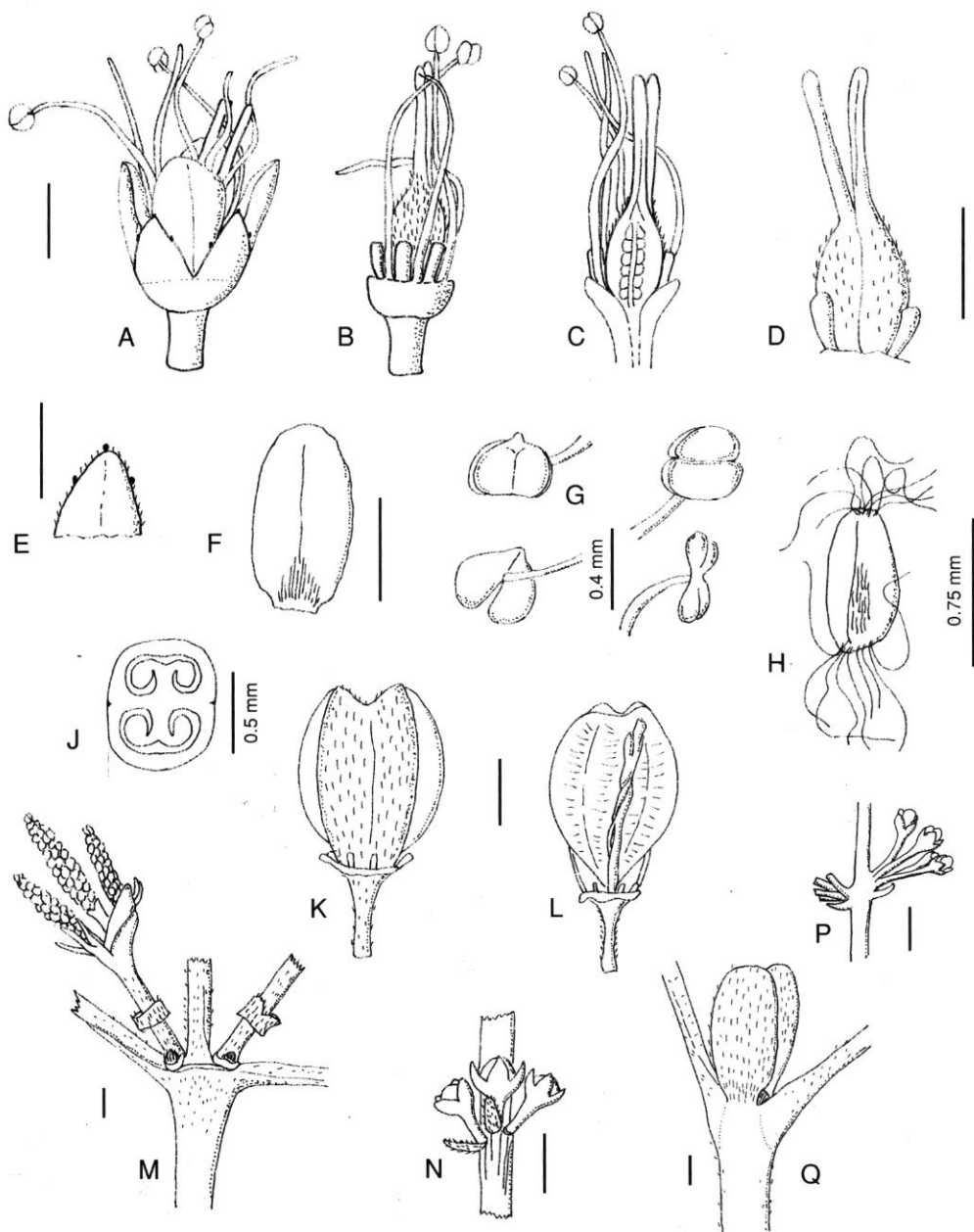
Stipules can be variable in size and shape on a single specimen and they are of varying value as taxonomic characters. They are often absent from the fertile shoots of some species and tend to be larger and more persistent on vegetative shoots.

The arrangement of leaves is always opposite and decussate, giving a distinctive appearance (Fig. 2A). Compound leaves are usually imparipinnate though the terminal leaflet is sometimes absent or fused to a lateral one. The petiole and leaf rachis can be winged or not, and sometimes the distinction between these two states is not marked. In Malesian and Pacific species, the wings are never as well developed as in some American ones. The size and shape of the leaves and leaflets, and the amount and distribution of indumentum, are often taxonomically significant. Leaflet size is small to medium, and in contrast to the Neotropics, no species is microphyllous. The margin is almost always distinctly dentate or crenate, and in *W. serrata* Brongn. & Gris, somewhat sinuate. In young leaflets the ends of the teeth are pronounced and probably glandular.

The venation is rather uniform. Secondary veins usually start to branch and anastomose

Fig. 2.—**A**, *Weinmannia fraxinea*, foliage of immature shoot, showing opposite and decussate compound leaves and large, rounded, salverform, interpetiolar stipules at nodes; young foliage reddish. (Hopkins et al. 5001a, Mt. Matang, Sarawak).—**B**, *Weinmannia clemensiae*, foliage and immature fruits. Inflorescence a pair of dyads with short peduncles. Note large, rounded stipules. (Hopkins & Bradford 5010, Pig Hill, Kinabalu, Sabah).—**C**, **D**, *Weinmannia fraxinea* "dulitensis": **C**, racemes of male flowers; **D**, base of inflorescence showing 4 dyads subtended by a pair of opposite petioles. Note flowers inserted in fascicles. (Hopkins & Bradford 5014, Pig Hill, Kinabalu, Sabah).—**E**, *Weinmannia richii*, fruits at dehiscence. Inflorescences of dyads with very short peduncles. (Hopkins & Bradford 5028, road N from Monosavu Dam, Viti Levu, Fiji).—**F**, *Weinmannia serrata*, immature fruits. Inflorescence a central pentad and one lateral triad, with one raceme missing. (Bradford 632, Col d'Amieu, New Caledonia).—All photos by J.C. BRADFORD.





before reaching margin but at least part of the vein terminates at the tip of a tooth. Tertiary and quaternary venation are strongly reticulate. Leaf/let texture is often coriaceous or at least chartaceous-coriaceous. Species that grow at high altitudes usually have more numerous, smaller, more coriaceous leaflets than those from lower elevations. Black dots, which are probably the bases of caducous hairs, are frequent on the underside of the leaves in some species. Such leaves are referred to as "punctate" in the species descriptions. Pustules are small, pale protuberances on both the upper and lower surfaces of leaflets and they can also occur on other organs, such as the calyx lobes. They do not appear to have any taxonomic significance nor to be an artefact of drying (cf. BERNARDI 1964: 162).

Juvenile foliage and sterile collections.

The characters that are diagnostic of adult foliage are rarely evident in juvenile and coppice shoots. For instance, a series of roadside collections from sterile individuals 1-3 m high near Monasavu Dam, central Viti Levu, Fiji (Hopkins & Bradford 5027a-b) show a range in variation in the number, size and shape of leaflets, length of

internodes, vestiture, shape of rachis, shape and persistence of stipules. Both *W. richii* and *W. affinis* occur in this area but the sterile collections were rarely consistent with the adult foliage of either of them. Some of this variation could perhaps be due to hybridization and the colonization of disturbed roadsides by hybrid swarms. Characters of mature foliage are best seen in leaves at the periphery of the crown in mature individuals (i.e. foliage from just below the inflorescences).

2. Structure of the inflorescence (with J.C. BRADFORD)

The parts of the inflorescence are organised hierarchically, and in *Weinmannia*, there are typically three levels of organisation: 1) flowers, borne along an unbranched axis, here termed a raceme; 2) racemes, organised into metameric units, each referred to here as a partial inflorescence (PI); 3) partial inflorescences, borne along the main stem. Together, the structure of a raceme, the way the racemes are organised into a PI, and the arrangement of the PIs along the main stem, constitute the inflorescence. Although there is some interaction amongst levels of organisation, with higher levels influencing lower ones, most variation within one level of organisation appears to be independent of variation at another level. For this reason, each level of organisation will be discussed separately.

There are several terms that require short definitions so that the descriptions of the inflorescences and their component parts can be made clearly and concisely. A bract is a minute, often carinate blade along the axis of a raceme and it subtends a flower or a group of flowers. A bud is an undeveloped shoot or flower, which in *Weinmannia* is normally enclosed by a bract (flowers) or a pair of stipules (shoots). A stipule is a small leaf-like structure at a node, decussate with the true leaves that may themselves be partially or wholly suppressed at nodes within the inflorescence. A metamer is a unit which consists of an internode, the node at its distal end, and the organs and meristems (buds) associated with that node. The term "main stem" is used for any dominant, linear axis of growth.

Fig. 3.—Details of the nodes, buds, flowers and fruits of *Weinmannia*: **A**, flower; **B**, flower with calyx and corolla removed to reveal disc lobes, filaments and gynoecium; **C**, l.s. through **B** to show ovules; **D**, gynoecium with syncarpous ovary and 2 disc lobes; note groove down style and down side of ovary; **E**, calyx lobe with ciliolate margin and 3 glands; **F**, petal; **G**, anthers, L.H.S. before dehiscence, R.H.S. after dehiscence; **H**, seed with hair tuft at each end and sculptured surface; note raphe down midline; **J**, t.s. ovary (**D**) to show developing ovules; **K**, outer surface of one valve of a capsule showing exocarp (central part strigose) and endocarp extended as wings at both sides, on receptacle, the calyx lobes fallen but disc lobes persistent; **L**, inner surface of **K**, note persistent central column and minutely sculptured shiny endocarp; **M**, developing inflorescence, one lateral triad shown in axil of petiole; note stipular scar between petioles, "collars" around lateral peduncles and conical ciliate buds at base of lateral peduncles (lateral auxiliary buds); at base of triad there is a stipule (partly folded back) and a pair of much reduced leaves; **N**, section of axis of a raceme typical of sect. *Leiospermum*, the pedicels inserted singly in the axils of the bracts; **P**, section of axis of a raceme in sect. *Fasciculata*, the pedicels inserted in fascicles in the axils of the bracts; **Q**, stipules between leaf petioles at most distal node of shoot protecting apical bud. Scale bars 1 mm unless otherwise indicated. [**A-F**, *J. W. paitensis* (McPherson 3403); **G**, *W. serrata* (Bernardi 12816); **H**, *W. serrata* (Balansa 204); **K**, *L. W. paitensis* (Veillon 296); **M**, *W. serrata* (Brinon 746); **N**, *W. serrata* (Balansa 2859); **P**, *W. fraxinea* ("dulitensis" (Hopkins & Bradford 5014); **Q**, *W. serrata* (Lécord s.n., reçu 20 Oct. 1879)].—Drawn by H.C.F. HOPKINS.

a) Racemes.—The flowers of the Malesian-Pacific species are pedicellate and borne in racemes ca. 5–12 cm long. The bracts usually fall when the flowers are still at the bud stage but occasionally they persist until fruiting. After they have fallen, a minute scar is usually visible. The individual flowers or fascicles are rather irregularly arranged on the axis of each raceme and insertion is never truly verticillate though it may superficially appear to be. Racemes may bear flowers for the whole of their length or usually they are devoid of flowers towards the base. The flowers in one raceme open more or less simultaneously.

— Sect. *Fasciculata*. Several pedicels are inserted in a small cluster in the axil of a bract (Fig. 3P). Occasionally flowers are inserted in fascicles for the most part but with some inserted singly towards the apex of the raceme, and in a few species, the fascicles tend to dissociate from the bracts during development. BERNARDI (1964: 132) used the term “pseudoraceme” in reference to sect. *Fasciculata*, but since this term is rather ambiguous, it is not used here.

— Sect. *Leiospermum*. The pedicels of the flowers are inserted singly in the axil of a bract (Fig. 3N).

b) Partial inflorescences.—In general, a PI is any subunit(s) into which the inflorescence can be divided. As used here, it consists of racemes and one or more sterile stem sections which form a developmentally integrated unit whose structure is predictable within different taxonomic groups. However, sometimes (though rarely in this region) the inflorescence of *Weinmannia* is composed of individual racemes inserted in leaf axils, in which case the racemes could be considered to be the PIs.

— Sect. *Fasciculata*. A partial inflorescence is limited to a single metamer. An even number of racemes (2 or 4) are inserted at the distal node of a short, sterile stem segment (referred to as a peduncle in the species descriptions) to form either a *dyad* (Fig. 4A) or a *tetrad* (Fig. 4B). Leaf production is usually totally suppressed at the node from which the racemes arise (exceptions seen in *W. pullei*).

There is typically a small bud in the angle between the central pair of racemes at the apex of the peduncle. This bud has the potential to continue

vegetative growth after flowering. Usually it is dormant during flowering (proleptic) or rarely sylleptic (i.e. no cessation of growth).

— Sect. *Leiospermum*. A partial inflorescence can consist of more than one metamer. Usually, an odd number of racemes are inserted at one or more nodes along the axis of the PI as the terminal meristem develops into a raceme. Therefore, when the PI consists of one metamer, there are 3 racemes (called a *triad*, Fig. 4F), when of two metamers, there are 5 racemes (a *pentad*, Fig. 4G), and when of three metamers, there are 7 racemes (a *heptad*). In a few species the PIs are dyads (Fig. 4H) and the bud between the bases of the racemes has aborted (i.e. failed to develop into a third raceme; exceptions in New Zealand are described below). The basal internode of a PI may be loosely termed the peduncle.

Leaf production can be either partially or totally suppressed within each PI and when leaves are produced, they are much reduced (e.g. Fig. 4J, level Y). There are often stipules at nodes within a PI. Quite often there are “collars” around the base of the peduncles of lateral PIs (Fig. 3M). These appear to be the remnants of a pair of stipules which once covered the developing PI and were fused to each other at the base. They are not usually seen around the peduncle of the central PI in sect. *Leiospermum*, nor around the peduncles in sect. *Fasciculata*.

c) Inflorescences.—An inflorescence is composed of one or more partial inflorescences. Usually all the flowers in one inflorescence open more or less simultaneously.

— Sect. *Fasciculata* (Fig. 4A–E). The PIs develop in opposite pairs from lateral meristems at a node on the main stem, i.e. they are usually in the axils of leaves. Each PI is a dyad or a tetrad. The most distal vegetative node on a stem usually produces more pairs of PIs than do subdistal nodes (see discussion of supernumerary buds below) and often the initiation of PIs is confined to the most distal node on the main stem.

Since the PIs are lateral, the apical meristem of the main stem remains indeterminate. It is normally dormant during flowering and continues vegetative growth after fruiting (prolepsis) or rarely it may be sylleptic. In exceptional cases, the apical meristem gives rise to a medial PI but

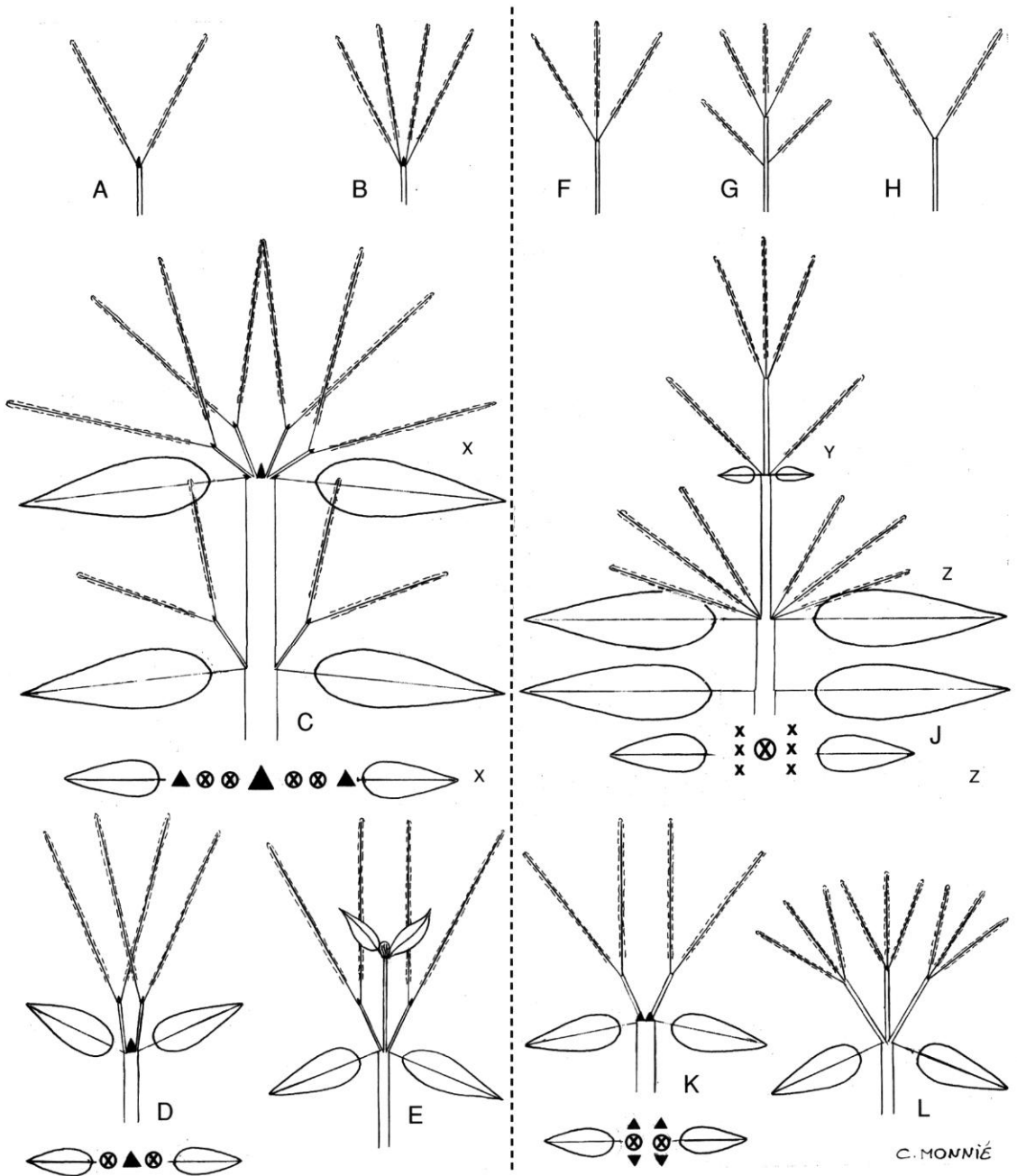


Fig. 4.—Inflorescence structure in *Weinmannia*. A-E, sect. *Fasciculata*: A, B, partial inflorescences: A, dyad; B, tetrad; C, inflorescence typical of *W. fraxinea* group, composed of 4 dyads and a pair of lateral supernumerary buds at the most distal vegetative node and single dyads in the axils of a pair of more proximal leaves; apical bud proleptic; D, inflorescence typical of *W. urdanetensis* group, composed of a pair of axillary dyads; apical bud proleptic; E, as D, but apical bud sylleptic. F-H, sect. *Leiospermum*: F-H, partial inflorescences: F, triad; G, pentad; H, dyad with central raceme aborted; J, inflorescence typical of *W. parviflora*, consisting of a heptad with 2 additional pairs of racemes inserted at node Z; partially suppressed leaves at node Y; K, inflorescence typical of *W. dichotoma*, with 2 axillary partial inflorescences (both dyads here) and apical bud aborted. Note prominent auxiliary buds in lateral positions at base of peduncles; L, inflorescence of 3 partial inflorescences (all triads). ▲: bud; ⊗: peduncle; x: raceme.—Drawn by C. MONNIÉ.

vegetative growth can again continue from the indeterminate apical meristem within that PI.

In most species (e.g. *W. fraxinea*, *W. hutchinsonii* Merr.) there is typically more than one bud per axil with the potential to produce a PI and these "supernumerary buds" are inserted in series. One, two or three buds may develop per axil, producing one to three pairs of PIs. Level X of Fig. 4C shows 2 pairs of dyads and one pair of dormant supernumerary buds. The racemes are arranged in a plane that is perpendicular to that formed by the line: leaf - (bud) - peduncle - peduncle - apical bud - peduncle - peduncle - (bud) - leaf (see Fig. 2D).

In another group of species (e.g. *W. urdanetensis*, *W. pullei*) there are typically only two PIs (here dyads) which are inserted in the opposite axils of the most distal pair of leaves (Fig. 4D). Sometimes there are additional PIs in the axils of more proximal leaves as well but there are no additional buds in series at the same nodes as the dyads (i.e. there is only one bud per leaf axil with the potential to produce a PI). The apical bud of the main stem can be either proleptic or sylleptic (Fig. 4E), in which case the dyads that were initially at the most distal node become subdistal.

— Sect. *Leiospermum* (Fig. 4F-L, 5). Partial inflorescences are usually positioned medially and often laterally too. In some cases, the apical bud of the main stem aborts and only lateral PIs are produced. The switch to flowering usually terminates the vegetative growth of the main

stem. In any one inflorescence there is usually an odd number of PIs (usually 1 or 3; rarely 2, a character state seen most frequently in some species in New Caledonia); when there is more than one, they are not always identical and the medial PI often contains more metamers than the lateral ones.

In the simplest examples (e.g. *Weinmannia marquesana* F. Br.) the inflorescence consists of a single PI (a triad or pentad) which develops from the apical bud of the main stem; the lower pair of racemes may be in the axils of either fully developed, partially suppressed or totally suppressed leaves. When an inflorescence consists of more than one PI, there are usually 3 triads (Fig. 4L) or a central pentad with a pair of axillary triads (as often seen in *W. serrata* and *W. affinis*), and occasionally more complex arrangements are found.

A unique structure is seen in *Weinmannia parviflora* (Fig. 4J). The inflorescence illustrated consists of a central heptad with a pair of partially suppressed leaves at one node, and 2 additional pairs of racemes at the lowest reproductive node. These additional racemes arise in a plane perpendicular to that formed by the line: leaf - raceme - central axis - raceme - leaf (see Fig. 4J, level Z), i.e. they are lateral to the axillary raceme and not inserted in series. One possible explanation for their presence is that the three racemes arising on either side of this node represent a pair of reduced triads in which the peduncle has not developed. Evidence for this is the occasional growth of a tiny section of peduncle in this axil

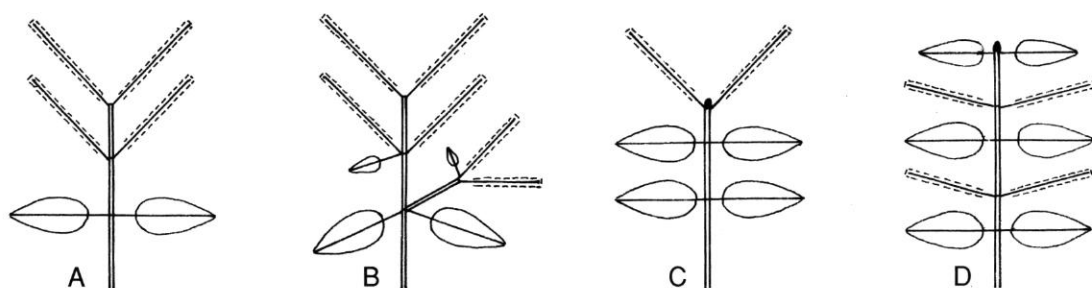


Fig. 5.—Inflorescence structure in the New Zealand species of *Weinmannia*. **A, B, *W. sylvicola***: **A**, 2 sequential pairs of dyads (pentad minus central raceme?); apical bud aborted; **B**, as **A** with an additional partial inflorescence (dyad) in an axillary position at subdistal node; **C, D, *W. racemosa***: **C**, inflorescence a median dyad, apical bud proleptic; **D**, as **C** but apical bud sylleptic, and continuing to produce dyads and leaves at sequential nodes.—Drawn by H.C.F. HOPKINS.

(see illustration of *W. rarotongensis* Hemsl., Fig. 7G in HOPKINS & FLORENCE 1998).

In three of the New Caledonian species and occasionally in other Pacific ones, the apical bud of the main stem may abort. In *Weinmannia dichotoma* for instance, the inflorescence frequently consists of two lateral PIs that develop at the most distal leaf-bearing node (Fig. 4K). These PIs can be either triads (Fig. 4F) or dyads (Fig. 4H,K), where the apical meristem within the PI has aborted also. At the node from which the PIs arise, there are often prominent lateral buds in a plane perpendicular to that of the leaves (lateral, auxiliary buds, Fig. 4K). They are most obvious in *W. dichotoma* but occur in other species as well.

In both species from New Zealand, *Weinmannia sylvicola* Sol. ex A. Cunn. and *W. racemosa*, the inflorescence structure is unique although it can still be understood as part of the pattern found in sect. *Leiospermum* (Fig. 5).

In *Weinmannia sylvicola*, the inflorescence is similar to those already described for sect. *Leiospermum* in which PIs consist of more than one metamer and they can develop in both medial and lateral positions. However, *W. sylvicola* is distinctive in that the apical meristem usually aborts (rarely not, e.g. *Colenso s.n.* where it appears dormant), so that the PI in a medial position resembles a pentad without the central raceme (Fig. 5A). In this instance, the apical meristem of both the PI and the main stem is the same. Apical meristems commonly abort in three of the species from New Caledonia but then the PI consists of only a single metamer, though in some other Pacific species where the apical meristem of the main stem sometimes aborts, lateral PIs may be pentads or heptads (e.g. *W. purpurea* L.M. Perry) and consist of more than one metamer. As in other pentad inflorescences, leaf production in *W. sylvicola* may be normal, partially or totally suppressed at the node from which the lower pair of racemes arise. When lateral PIs develop, they usually consist of only one metamer and often they develop at only one side to produce an asymmetrical inflorescence (Fig. 5B).

Superficially, the inflorescence of *Weinmannia racemosa* appears to have little in common with those of other members of the section. However,

its homology can be deduced if some assumptions are made about its evolutionary relationships. Here, we suggest that *W. racemosa* is most closely related to *W. sylvicola* (the only other New Zealand species), and that overlapping forms of these two species can be identified and used to link the unusual inflorescences in *W. racemosa* with those typical of sect. *Leiospermum*.

In *Weinmannia racemosa* there is always a single PI in a medial position and it can consist of either one (Fig. 5C) or two metamers. When two metamers develop the structure appears similar to a common variant of *W. sylvicola* in which there is no lateral PI (Fig. 5A), except that in this case, the apical bud is not aborted. There is thus a continuity in form between *W. racemosa* and *W. sylvicola*, and between *W. sylvicola* and other *Leiosperma*. The fate of the apical bud in *W. racemosa* makes it unique within sect. *Leiospermum* in that vegetative growth can continue from within the inflorescence. This, together with the absence of lateral PIs and the generally lesser number of metamers in any PI, is the reason for the unusual appearance of the inflorescence in *W. racemosa*. The apical bud (of both the PI and the main stem in this case) can be either dormant or commonly not, when it goes on to produce further leaves and PIs (Fig. 5D).

3. Flowers

While basic floral structure is extremely uniform among different species (see Fig. 3A-G), flowers can be morphologically bisexual (with filaments approximately the same length as the gynoecium so that anthers and stigmas are at about the same level, Fig. 6C), male (with long filaments, the anthers far exerted beyond the stigmas, the ovary small and the styles tiny and incurved, Fig. 6B) or female (with short filaments, the ovary often large and the styles far exceeding the stamens, either straight or curving outwards, Fig. 6A). However, there is often a considerable range in the length of the filaments and occasionally they are not clearly long or short, and then the gender of the flowers is equivocal. Usually the anthers are of similar size in male and female flowers, though unusually small anthers are found, for example, in the apparently

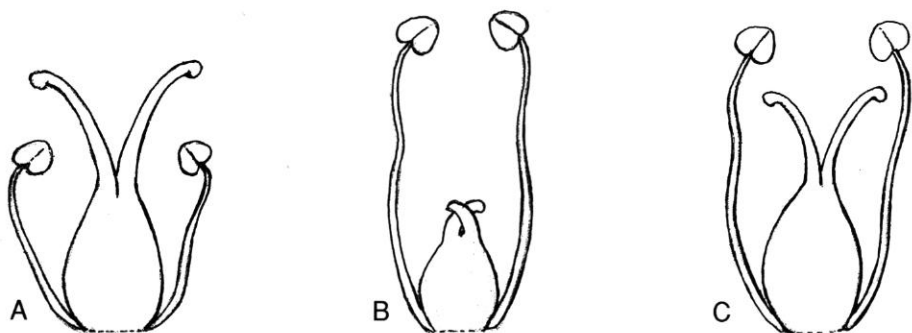


Fig. 6.—Androecium and gynoecium from morphologically female (A), male (B) and bisexual (C) flowers of *Weinmannia*.—Drawn by J. LEMEUX.

bisexual flowers of *W. fraxinea* from the Solomons.

There is only preliminary information on the functional potential of flowers of different morphological types. In *W. denhamii* Seem. from Vanuatu, the anthers of both male and female flowers contain pollen, although in the female flowers it appears to be less well formed (R.D. HOOGLAND in litt. to J. FLORENCE, 19 May 1987). In *W. parviflora* from Tahiti, no pollen was found in the anthers of morphologically female flowers (Florence 9089, 9091), while the anthers of morphologically male ones (Florence 9089, 9090) did contain pollen (R.D. HOOGLAND unpublished notes).

Sexual expression and breeding system. In many species, all the flowers on one herbarium specimen, which might contain several inflorescences each composed of several racemes, are of the same morphological type and there is no evidence to suggest that some species are not either simply dioecious (e.g. *W. hutchinsonii*, *W. luzoniensis* S. Vidal, *W. aphanoneura* Airy Shaw) or hermaphroditic (e.g. *W. serrata* and other species from New Caledonia, *W. racemosa* and *W. sylvicola* from New Zealand, *W. furfuracea* H.C. Hopkins and *W. descombesiana* from Sulawesi).

The expression of sex is more complex in some other species. For instance, a number are polygamodioecious (SMITH 1952), with male and female flowers on separate plants and some bisexual flowers, usually on staminate plants in this case (e.g. numerous species from small Pacific islands). In these species, bisexual flowers

are usually less common than unisexual ones, and they may either be mixed in the same inflorescence as the male flowers or in separate but contemporaneous inflorescences. In some species (e.g. *W. marquesana*, *W. denhamii*, *W. rapensis*) there are also temporal changes in gender, with cycles of different sorts of flowers on one plant, indicated by the presence of male flowers at anthesis and mature fruits (usually from bisexual flowers) in separate inflorescences. Temporally labile species may contain some stable individuals and others that change gender within and between seasons.

In some predominantly dioecious species (e.g. *Weinmannia urdanetensis*) a few individuals appear to be monoecious. The most complex pattern is seen in *W. fraxinea* where the sexual system varies geographically and some populations may perhaps be apomictic. Better description of the more complex sexual systems clearly requires detailed, long-term field studies.

Compatibility mechanisms have not been studied. There is circumstantial evidence of interspecific hybridization, e.g. in central Viti Levu, where small, infertile roadside plants showed a wide range of vegetative characters, and were likely to have been hybrids between *W. richii* (sect. *Fasciculata*) and *W. affinis* (sect. *Leiopsermum*) (HOPKINS & BRADFORD pers. obs.).

Floral biology and pollination. The flowers of *Weinmannia* are massed together in fairly dense, spike-like inflorescences that are arranged around the periphery of the crown, projecting upwards

(Fig. 2C). Individual flowers are bowl-shaped with the anthers and stigmas readily accessible to potential pollen vectors that land on the racemes (i.e. non-restrictive). The flowers are usually white or cream, sometimes pink, and described as scented or not. Nectar is produced in *Weinmannia racemosa* (THOMPSON cited in WARDLE 1966) although none was seen in *W. fraxinea* or *W. affinis* (HOPKINS & BRADFORD pers. obs.). The disc lobes are pale and inconspicuous in *W. fraxinea* in Borneo while in *W. affinis* and *W. vitiensis* in Fiji, they are dark and contrast strongly with the pale corolla. There have been no detailed studies of pollination but bees are probably the main pollen vectors. The flowers of *W. racemosa* in New Zealand are visited by insects including bees, and by the Parsonbird or "tui", *Prosthemadera novaeseelandiae* (WARDLE 1966). Racemes of *Weinmannia* also attract a variety of flies and beetles (pers. obs.). A high proportion of female or bisexual flowers on any raceme produces fruit.

4. Fruits and seeds

The capsules (Fig. 2E; 3K,L) are remarkably uniform, with only minor variation between species in size and indumentum. Variation in the persistence of the calyx lobes has been used as a taxonomic character but is variable in a few species. In sect. *Leiospermum*, there is a well developed persistent central column (GODLEY 1983; Fig. 3L) from which the lateral wings of the endocarp separate on dehiscence. In sect. *Fasciculata*, this column is often more weakly developed, or shorter or absent, when the tissue that otherwise forms the column remains attached to the endocarpic fringes of the valves. The capsules are usually referred to as septicidal, but the presence of a free central column after dehiscence means that they are septifragal (see SPJUT 1994).

The seeds are small and the surface of the testa has a complex pattern of sculpturing (DICKSON 1984; WEBB & SIMPSON 1991; Fig. 3H). In most species there is a tuft of comose hairs at each end, although in a few, there are short hairs widely distributed over the entire surface. There is some variation in the length and texture of the comose hairs which appears to affect the length of time

the seeds are retained within the capsule after dehiscence, and this may affect their dispersability.

Dispersal. The seeds are probably wind-dispersed (e.g. WARDLE 1966; HOPKINS & BRADFORD pers. obs. in Fiji) although exozoochory has been suggested (GUPPY in FLORENCE 1982: 32, for *Weinmannia parviflora*), the hairs on the seeds perhaps sticking to birds' feathers. Long-distance dispersal must be reasonably effective since the genus has reached many volcanic islands in the South Pacific.

5. Field characters

Life form is rather plastic in some species which can be trees, shrubs, dwarf shrubs and occasionally woody epiphytes, depending upon the vegetation type, altitude and exposure. Bark is often variable within species, and rarely distinctive. Inner bark is often pinkish, brown or reddish brown. Sap wood is white, straw, pinkish, sometimes orange-brown, sometimes turning purple; medium to hard. Heart wood is pink-cream to red or yellow-brown. Young stems and leaves are often conspicuously red (Fig. 2A), mature leaves often darkish green above, shiny; old leaves sometimes turning bright red. Inflorescence axes are sometimes reddish. Flower buds are light green to pink or red. Flowers are creamy white to pink (Fig. 2C,D), rarely light green or purple (*W. purpurea*), often with a slight sweet fragrance; the calyx is pale green, yellowish green or reddish; the corolla and filaments are usually white; the anthers pinkish, cream or straw; the disc yellow-orange or dark red-purple; the ovary light green or pinkish; the styles are pink at the base and the stigmas are white to brown or purplish. Young fruits are greenish, pink or reddish (Fig. 2B,F), turning crimson or rarely purplish green at maturity; dehiscent capsules are brown (Fig. 2E).

WEINMANNIA L.

Syst. Nat., ed. 10, 2: 997, 1005, 1367 (1759), nom. cons.; Juss., Gen. Pl.: 309 (1789); Lam., Tabl. Encycl. I 2, t. 313 (1793); Willd., Sp. Pl., ed. 4, 2: 296, 436 (1799); Benth. & Hook. f., Gen. Pl. 1: 653 (1865); Engl., Linnaea 36: 592 (1870); Engl., in C. Mart., Fl. Bras. 14 (2): 156 (1871); Engl., Nat. Pflanzenfam.,

III, 2a: 101 (1891), ed. 2, 18a: 250 (1930); Baill., Hist. Pl. 3: 373, 447 (1871); Bader, Nova Acta Leop. 23 (148): 170, 430 (1960); Bernardi, Candollea 17: 123 (1961), 18: 285 (1963); Bernardi, Adansonia, ser. 2, 3: 404 (1963); Bernardi Bot. Jahrb. Syst. 83: 126, 185 (1964); Bernardi, in Humbert, Fl. Madag., fam. 93: 3 (1965); Hutch., Gen. Fl. Pl. Dicot. 2: 9 (1967). *Windmannia* P. Browne, Civ. Nat. Hist. Jamaica: 212 (1756), nom rejic.; Kuntze, Revis. Gen. Pl. 1: 228 (1891). *Arnoldia* Blume, Bijdr. Fl. Ned. Ind.: 868 (1826), non Cass. (1824). *Leiospermum* D. Don, Edinburgh New Philos. J. 9: 91 (1830). *Pterophylla* D. Don, Edinburgh New Philos. J. 9: 93 (1830). *Ornithophus* Bojer ex Engl., Linnaea 36: 636 (1870), pro syn.

TYPE.—*Weinmannia pinnata* L. from Central and South America and the Antilles.

Generic description of *Weinmannia* in Malesia and the Pacific

Trees or shrubs, rarely epiphytes and perhaps rarely stranglers. Branching sometimes dichotomous in some species, usually so in a minority of species; shoots sometimes slightly thickened or flattened at nodes, internodes terete, the bark finely grooved; pale lenticels often prominent. Indumentum of simple hairs, variable in amount and distribution. Interpetiolar stipules 2 per node, elliptical, ovate, orbicular to subreniform, often with minute adpressed hairs, apex rounded or pointed, margin entire or toothed, a pair of opposite stipules often salverform in juvenile foliage, sometimes caducous in adult foliage, the bases leaving a prominent annular scar around stem at each node after abscission. Colleters purple-red, minute (< 0.1 mm long), frequent at nodes and visible after stipules have fallen, non-functional? Axillary and apical buds covered by a pair of velutinous or sericeous stipules (bud scales). Leaves opposite and decussate, simple (unifoliate?), trifoliate or imparipinnate (rarely paripinnate), usually petiolate; petiole and rachis terete, caniculate, or semiterete and flattened on adaxial side, sometimes narrowly winged, especially distally towards the point of insertion of each pair of leaflets; leaflets chartaceous to coriaceous; lateral leaflets often asymmetrical at

base, often smaller proximally in a given leaf; margin toothed or crenulate, the crenations acroscopic, margin usually minutely thickened and minutely revolute; secondary veins usually arcuate, branching before reaching margin, one branch arching towards apex and the other towards base to join with tertiary veins arising from a more proximal secondary vein; blade sometimes black-dotted below, sometimes pustulate.

Inflorescence composed of racemes, usually arranged in groups on a sterile axis on which leaf development is partially or wholly suppressed, to form a developmentally integrated unit, rarely not part of such a unit and arising directly from axillary buds on the main leaf-bearing stem; partial inflorescences either axillary or terminal or a combination. Racemes up to 12 cm long with up to 100 or more flowers, the basal part usually bare; axis of raceme longitudinally ridged and often minutely hairy (hairs < 0.1 mm long), sometimes densely so. Floral buds inserted on the axis of the racemes either singly or in small fascicles, each bud or fascicle subtended by a bract; bract often carinate, often histute on abaxial surface, often caducous. Flowers small, unisexual or bisexual, hypogynous or somewhat perigynous, perianth and androecium 4-merous or rarely a few flowers per raceme 5-merous (commonly 5-merous in some areas outside this region); pedicel usually filiform, often minutely hairy (hairs < 0.1 mm long); calyx of 4 lobes, imbricate in bud, \pm triangular, attached at their base to the hypanthium at the point of their greatest width, apex broadly acute or somewhat rounded, glabrous or hirsute on outer surface, slightly fleshy; corolla of 4 free petals, not caducous (in this region), usually elliptical, ovate or obovate, constricted at the base (attachment 0.1–0.2 mm across), apex rounded or irregularly emarginate, membranous, sometimes minutely ciliolate; androecium of 8 stamens, obdiplostemonous, the filaments filiform, inserted in a single whorl but alternate ones elongating asynchronously; anthers apiculate, versatile, dehiscing longitudinally, the valves of each thecum unequal; disc of 8 free lobes, alternating with the filaments, usually \pm oblong, obcuneate or slightly claviform, sometimes broadly oblong with flanges on either side so that lobes almost form a

continuous ring of tissue, glabrous; gynoecium of 2 (rarely 3) carpels fused at the level of the ovary; ovary ovoid, glabrous to densely hirsute, the hairs drying white; locules 2(-3); styles 2(-3), free, awl-shaped, glabrous except occasionally at the base, conduplicate and furrowed on adaxial side; stigmas terminal, small or sometimes capitate, papillose; ovules ca. 8-16 per locule, placentation axile.

Fruit small (< 6 mm long), a septicidal or usually septifragal capsule dehiscing from the apex into 2 parts which remain attached to the receptacle at their base to form a cup-shaped structure with the styles usually persistent at the apex; the valves composed of 2 layers: exocarp dark brown, pubescent, strigose or glabrous, smooth or minutely ridged; endocarp yellow, smooth, with minute transverse sculpturing on concave surface, usually completely adnate to exocarp or sometimes partially free especially towards the apex, the septum separating the locules extending as wing-like projections on either side of the exocarp at dehiscence; free central column formed from placenta often present and sometimes persisting after the valves have fallen; receptacle sometimes saucer-like at base; calyx lobes persistent or not; corolla and disc lobes occasionally persistent. Seeds small (< 1 mm long), elliptical in outline and circular in transverse section, generally 2 × as long as broad when fully mature, the surface minutely sculptured, raphe sometimes visible as a minute ridge, usually comose with straw-like hairs in a tuft at each end, sometimes hairs arising ± all over the surface, longer at the ends.

About 40 species in Malesia and the Pacific, belonging to two sections.

1. Sect. *Fasciculata* Bernardi ex Hoogland & H.C. Hopkins, **sect. nov.**

Sect. *Fasciculatae* Bernardi, Bot. Jahrb. Syst. 83: 132, 158 (1964), nom. inval., sine typus.

TYPE (here designated).—*Weinmannia fraxinea* (D. Don) Miq.

Flowers pedicellate and inserted on the axes of

the racemes entirely or largely in fascicles, i.e. several pedicels arising in a group, the group subtended by a single small bract (Fig. 3P), rarely inserted singly (*W. descombesiana*). Inflorescence composed of 1-3 opposite pairs of partial inflorescences inserted in series in the axils of the most distal pairs of leaves; each partial inflorescence consisting of a single metamer, which comprises a sterile peduncle and 2 or 4 racemes inserted at its distal end (to form a "dyad" or a "tetrad", see Fig. 4A,B); leaves at nodes from which racemes arise usually totally suppressed; stipules not usually present at nodes within partial inflorescences; "collars" around peduncles of partial inflorescences absent; bud within each partial inflorescence, at apex of peduncle between the central racemes, present and usually dormant during flowering; apical bud of main stem, between central peduncles, present and usually dormant during flowering; buds lateral to axillary buds at most distal leaf-bearing node (lateral auxiliary buds) absent.

Stipules often ± orbicular. Branching not dichotomous. Leaf blades not punctate below.

Capsules ± smooth and not ridged; indumentum on valves softly pubescent; after dehiscence, central column weakly developed; calyx lobes often but not always persistent in fruit.

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

2. Sect. *Leiospermum* (D. Don) Engl., Nat. Pflanzenfam. III 2a: 101 (1891), ed. 2, 18a: 256 (1930).

Sect. *Racemosae* Bernardi, Bot. Jahrb. Syst. 83: 132, 185 (1964), nom. superfl. et sine typus.

TYPE.—*Weinmannia racemosa* L. f.

Flowers pedicellate and inserted on the axes of the racemes singly, i.e. each pedicel arising in the axil of a small bract (Fig. 3N). Inflorescence composed 1-3(-5) partial inflorescences, usually inserted medially and laterally; lateral PIs usually consisting of one metamer [dyad (Fig. 4H,K) or triad (Fig. 4F,L)]; sometimes lacking the basal

sterile stem section in *W. parviflora*); medial PIs consisting of one metamer (dyad or triad), two metamers [tetrad (Fig. 5A) or pentad (Fig. 4G)] or three 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 (e.g. *W. racemosa*, Fig. 5C,D); 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 partial inflorescences often present (Fig. 3M); apical buds within each lateral PI 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.

Stipules often ligulate, elliptical or ovate, the apex rounded or pointed. Branching sometimes dichotomous. Leaf blades often punctate below.

Capsules often minutely ridged; indumentum on valves strigose or absent; after dehiscence, central column usually well developed and persistent; calyx lobes often falling in fruit.

There are 17-19 species in the Pacific, extending westwards to Papua New Guinea (Bismarck Archipelago and Karkar Island).

Notes on the species accounts

1. Vegetative characters. Because of variability in the leaves depending their position, even within the crown of one tree, and on the age of the plant, only leaves from fertile shoots are described. Dimensions given are for the largest leaves per specimen. Characters for juvenile or coppice shoots are given separately where known. Terminology for the indumentum follows HEWSON (1988).

2. Inflorescence. The most frequent structures are described but not all variants.

3. Flowers. The insertion of the pedicels on the axes of the racemes is scored in bud where possible as this is sometimes less clear after the flowers have opened and the bracts have fallen. The length of pedicels is given for flowers at anthesis and may be slightly longer in the fruiting stage.

The length of the calyx lobes is measured from their point of attachment to the receptacle to their apex (Fig. 3E). The length of the style includes the stigma.

4. Breeding system. Species are described as hermaphroditic, dioecious or polygamodioecious based on the morphology of the flowers (Fig. 6). The reproductive potential of flowers of different sorts has not been investigated.

5. Field characters. Many field characters are common across the genus and are not always repeated in each species account.

6. Types. In species accounts for which HCFH is the sole author, ! is used to indicate type specimens that have been studied. Collection details for types are not usually repeated in the list of material examined.

7. Specimen citations. For those species where I have seen relatively few collections, all material examined is listed. For those where there is much more material, a selection is cited to illustrate the morphological and geographical range of the species.

8. Abbreviations used in citations of specimens. Gn. = Gunung (mountain), Bt. = Bukit (hill), Mt. = mountain, Isls. = island, Kamp. = kampung (village), R. = river, Rd. = road, Sg. = Sungai (stream or small river); juv. = juvenile, fl. = flowers, fr. = fruits, yfr. = young fruits, st. = sterile; N = north, S = south, C = central, nr. = near, ft. = feet, Distr. = District, Prov. = Province, Div. = Division, Ond. afd. = Onderafdeling (subdivision).

Five species are recognised from western Malesia, the Lesser Sunda Islands and the Moluccas, all belonging to sect. *Fasciculata*. *Weinmannia fraxinea* is widespread and variable, and considerably more than half the collections from Malesia belong to this species. *Weinmannia clemenisae* is endemic to stunted forest on ultramafic soils on Mt. Kinabalu in Borneo, *W. aphanoneura* occurs in Borneo and Sumatra, and *W. hooglandii* is from high altitude in Peninsular Malaysia. *Weinmannia furfuracea* is known from this region by a single specimen from Seram (Rutten 2231) and is described with the other species which occur in Sulawesi, in Part 2 (HOPKINS 1998a).

Key to the species of the Malay Peninsula, Greater and Lesser Sunda Islands and Moluccas

1. Indumentum on young stems, leaf rachises, inflorescence axes and lower surface of leaflets red-brown, often scurfy; apex of lateral leaflets obtuse (Seram) **5. *W. furfuracea* (see p. 49)**
- 1'. Indumentum on young stems, leaf rachises, inflorescence axes and lower surface of leaflets grey to golden brown, puberulent to tomentose, not scurfy; apex of lateral leaflets acuminate, acute or obtuse 2
2. Lateral leaflets small, 1.4-2.7 × 0.5-1 cm, boat-shaped or ± oblong; young shoots tomentose-velutinous 3
- 2'. Lateral leaflets larger (2.2-4.2-8.5(-12) × (0.8-1.2-3.5(-4.5) cm, lanceolate, elliptical, narrowly obovate to ovate; young shoots ± glabrous, puberulent or tomentose 4
3. Leaflets bullate and the margin strongly recurved so leaflet is boat-shaped; lateral leaflets 6-13 pairs per leaf (Mt. Kinabalu, Sabah) **2. *W. clemensiae***
- 3'. Leaflets flat, not bullate and the margin flat or minutely revolute; lateral leaflets 4-8 pairs per leaf (Peninsular Malaysia) **4. *W. hooglandii***
4. Lateral leaflets narrowly elliptical to narrowly obovate, the base cuneate, the apex acute to obtuse, drying chestnut-brown, 1-4 pairs per leaf; leaf rachis sometimes narrowly winged; inflorescence of 1-2 pairs of dyads **3. *W. aphanoneura***
- 4'. Lateral leaflets, lanceolate, elliptical or ovate, not obovate, the base usually unequal and varying from cuneate to rounded, the apex narrowly acute to acuminate, usually drying greenish-brown, 1-8 pairs per leaf; leaf rachis terete, not winged; inflorescence of 1-3 pairs of dyads or tetrads **1. *W. fraxinea***

1. *Weinmannia fraxinea* (D. Don) Miq.

Fl. Ned. Ind. 1(1): 718 (1856); [Sm. ex D. Don, Edinburgh New. Philos. J. 9: 93 (1830) pro syn.]; Engl., Linnaea 36: 644 (1870), Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Scheff., Nat. Tijdschr. Ned. Ind. Batavia 34: 40 (1874); Pamp., Ann. Bot. (Rome) 2: 89 (1905); Merr., Interpr. Herb. Amboin.: 244 (1917); Bernardi, Bot. Jahrb. Syst. 83: 167 (1964).—*Pterophylla fraxinea* D. Don, Edinburgh New Philos. J. 9: 93 (1830); Walp., Repert. Bot. Syst. 2: 374 (1843), 5: 834 (1846); Müll. Berol., in Walp., Ann. Bot. Syst. 5: 31 (1858).—*Windmannia fraxinea* (D. Don) Kuntze, Revis. Gen. Pl. 1: 228 (1891).—Type: *C. Smith s.n.* (Moluccas), Honimoo, Apr. 1797 (holo-, LINN-SM!).

Arnoldia heterophylla Blume, Bijdr. Fl. Ned. Ind.: 869 (1826); DC., Prodr. 4: 12 (1830); G. Don, Gen. Hist. 3: 201 (1834); D. Dietr., Syn. Pl. 2: 1313 (1840); non *Weinmannia heterophylla* Kunth (1823).—*Weinmannia sundana* Miq., Fl. Ned. Ind. 1 (1): 718 (1856); Engl., Linnaea 36: 639 (1870), Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Scheff., Nat. Tijdschr. Ned. Ind. Batavia 34: 38 (1874); Koord. & Valetton, Bijdr. Boomsoort. Java: 403 (1900); Backer, Schoolfl. Java: 472 (1911); de Wit, Rumphius Memorial vol.: 411 (1959).—*Windmannia sundana* (Miq.) Kuntze, Revis. Gen. Pl. 1: 228 (1891).—Type ("in Javae sylvis montanis prov. Batam", probably in error): lecto-, here designated, chosen by HOOGLAND, *Reinwardt s.n.*, Amboina, July 1821, ! [Herb. Ludg. Bat. 908.239-...452].

Spiraea pinnata Blume, Catalogus: 76 (1823); Nees, Flora 8: 148 (1825); non Moench. (1794).—

Arnoldia pinnata Blume, Bijdr. Fl. Ned. Ind. (15):

868 (1826); DC., Prodr. 4: 12 (1830); G. Don, Gen. Hist. 3: 201 (1834); Hassk., Pl. Jav. Rar.: 324 (1848); Blume, Flora 41: 254 (1858); non *Weinmannia pinnata* L. (1759).—*Weinmannia blumei* Planch., Lond. J. Bot. 6: 470 (1847); Miq., Fl. Ned. Ind. 1 (1): 718 (1856); Engl., Linnaea 36: 640 (1870), Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Scheff., Nat. Tijdschr. Ned. Ind. Batavia 34: 39 (1874); King, Mat. Fl. Malay Penins. 9: 299 (1897); Koord. & Valetton, Bijdr. Boomsoort. Java: 399 (1900); Pamp., Ann. Bot. (Rome) 2: 89 (1905); Koord.-Schum., Syst. Verz. 1, Fam. 120: 4 (1913); Backer, Schoolfl. Java: 472 (1911); Koord., Exkurs-Fl. Java: 311 (1911); Koord. & Valetton, Atlas Baumart. Java 1: t. 200 (1913); Ridl., Fl. Malay. Penins. 1: 682 (1922); Corner, Wayside Trees Malaya 1: 201, t. 52 (ed. 1, 1940; ed. 2, 1952), 1: 224, t. 55 (ed. 3, 1988); Backer & Bakh. f., Fl. Java 1: 506 (1963); Bernardi, Bot. Jahrb. Syst. 83: 161 (1964); Whitmore, Guide For. Brit. Sol. Isl.: 59, 133, 152, 206 (1966); Steenis, Mount. Fl. Java: t. 13, fig. 7 (1972); Whitmore, Tree Fl. Malaya 1: 179 (1972).—*Weinmannia arnoldia* A. Gray, U.S. Expl. Exped., Phan. 1: 675 (1854).—*Windmannia blumei* (Planch.) Kuntze, Revis. Gen. Pl. 1: 228 (1891).—Type (Crescit in sylvis montanis Javae insulae): lecto-, here designated, chosen by HOOGLAND, *Blume 816a*, ! [Herb. Ludg. Bat. 908.238-...539]; *syn. nov.*

Weinmannia horsfieldii Miq., Fl. Ned. Ind. 1(1): 718 (1856); Engl., Linnaea 36: 642 (1870); Scheff., Nat. Tijdschr. Ned. Ind. Batavia: 39 (1874).—*Windmannia horsfieldii* (Miq.) Kuntze, Revis. Gen. Pl. 1: 228 (1891).—Type (Java, bij Soerabaja, door Horsfield ontdekt): *Horsfield s.n.* (holo-, BM!); *syn. nov.*

Arnoldia fraxinifolia Blume, Flora 41: 254 (1858);

- Müll. Berol., in Walp., Ann. Bot. Syst. 5: 31 (1858).—*Weinmannia fraxinifolia* (Blume) Miq., Fl. Ned. Ind. 1(1): 1095 (1858); Engl., Nat. Pflanzenfam., ed. 2, 18a: 255 (1930).—Type (In sylvis elatioribus Javae occidentalis): lecto-, here designated, chosen by HOOGLAND, *Blume s.n.*, Java, in cacumine montis, Malabar, L! [Herb. Ludg. Bat. 908.238-...577 & 908.238-...578]; *syn. nov.*
- Weinmannia papuana* Schltr., Bot. Jahrb. Syst. 52: 162 (1914); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930).—Type: *Ledermann 9784*, North East New Guinea, in dense humid forest on the April River, 200-400 m, Nov. 1912 (holo-, B; iso-, L!); *syn. nov.*
- Weinmannia ledermannii* Schltr., Bot. Jahrb. Syst. 52: 162 (1914); Lane-Poole, Rep. For. Res. Terr. Papua New Guinea: 63, 90, 91 (1925); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); L.M. Perry, J. Arnold Arbor. 30: 160 (1949).—Type: *Ledermann 9922*, North East New Guinea, in montane forest on Lordberge, ca. 1000 m, Nov. 1912 (holo-, B; iso-, K!, L!); *syn. nov.*
- Weinmannia tomentella* Schltr., Bot. Jahrb. Syst. 52: 163 (1914); Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); *Bernardi*, Bot. Jahrb. Syst. 83: 179, t. 28 (1964).—Type: *Ledermann 8172* (not 8173 as given by SCHLECHTER [1914]), North East New Guinea, in forest at foot of Hunstein peak, 200-400 m, Aug. 1912 (holo-, B!); *syn. nov.*
- Weinmannia blumei* Planch. var. *major* Ridl., Fl. Malay. Penins. 5: 307 (1925).—Type: *Ridley 16029*, Malay Peninsula, Pahang, Gunong Tahan, ca. 5500 ft., July 1911 (lecto-, here designated, chosen by HOOGLAND, SING!; isolecto-, BM!, K!, SING!); *syn. nov.*
- Weinmannia dictyoneura* Schltr., Bot. Jahrb. Syst. 52: 163 (1914), non Diels (1906).—*Weinmannia alta* Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); *Bernardi*, Bot. Jahrb. Syst. 83: 160 (1964).—Type: *Ledermann 10129*, North East New Guinea, in montane forest on Lordberge, ca. 1000 m, Dec. 1912 (holo-, B; iso-, K!); *syn. nov.*
- Weinmannia borneensis* Engl., Nat. Pflanzenfam., ed. 2, 18a: 256 (1930); Airy Shaw, Bull. Misc. Inform. 1940: 259 (1940); Heine, Mitt. Bot. Staatssamml. München 1: 212 (1953); *Bernardi*, Bot. Jahrb. Syst. 83: 164, t. 17 (1964).—Type: *Native Collector 722*, Sarawak, s.loc., s.d. [fide specimen in PNH: road to summit of Gunong Matang, 12 Aug. 1911, leg. *Dabongl*] (holo-, B; iso-, BM!, BO!, K!, L!, PNH); *syn. nov.*
- Weinmannia dulitensis* Airy Shaw, Bull. Misc. Inform. 1940: 259 (1940).—Type: *Native Collector 1671*, Sarawak, Dulit Ridge, forest nr. waterfall, ca. 1200 m, 10 Sep. 1932 (holo-, K!; iso-, L!, SING!); *syn. nov.*
- Weinmannia hypoglaucula* Kaneh. & Hatus., Bot. Mag. (Tokyo) 56: 111, t. 7 (1942).—Type: *Kanehira & Hatusima 12797* (Irian Jaya), Boemi, 40 km inward of Nabire, 400 m, 11 Mar. 1940 (holo-, FU, photo at K!; iso-, BO!, L!); *syn. nov.*
- Cortex papetarius* Rumph., Herb. Amboin. 3: 212, t. 137 (1743), nom. illeg.
- Small to large tree, up to 25(-40) m high. Young stems puberulent to tomentose, rarely glabrous, older stems glabrescent with numerous lenticels; branching not usually dichotomous. Stipules often caducous, ± orbicular to subreniform to broadly spatulate, 0.8×0.8 to 1.5×1.8 cm, narrowed at base, apex broadly rounded, abaxial surface shortly strigose especially towards base, adaxial surface glabrous. 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 on adaxial side or abaxial side or both; lateral leaflets ± sessile, usually broader towards the base, varying from lanceolate to narrowly elliptical to narrowly ovate to ovate, the largest per leaf $(2.2-4.2-8.5(-12) \times (0.8-1.2-3.5(-4.5))$ cm, proximal leaflets usually smaller than more distal ones, base frequently unequal to dimidiatus, rounded to cuneate on either side, apex acute to acuminate; terminal leaflet narrowly elliptical to narrowly ovate, $2.5-10 \times 1-3.3$ cm including petiolule of 0.3-1.5 cm, blade ± same size as largest lateral leaflets or larger, base attenuate into petiolule, apex acuminate; blades chartaceous to subcoriaceous, glabrous, not punctate below; margin crenate, 8-14 notches on each side in the lateral leaflets, crenations rounded and acroscopic or triangular and not acroscopic; midrib prominent and shortly hirsute below, indented above and sometimes hirsute towards base; secondary and tertiary veins ± flat above and minutely prominent below, sometimes drying paler than intervenium.
- Inflorescence 1-3 opposite pairs of lateral dyads or tetrads at most distal node of main stem, inserted in series when > 1 pair; apical bud of the main stem between the peduncles of the central dyads densely sericeous; bud at apex of peduncles in angle between the racemes sericeous; sometimes a few successive nodes on one shoot producing partial inflorescences simultaneously; peduncles 0.3-1.8 cm long; racemes 7.5-15 cm

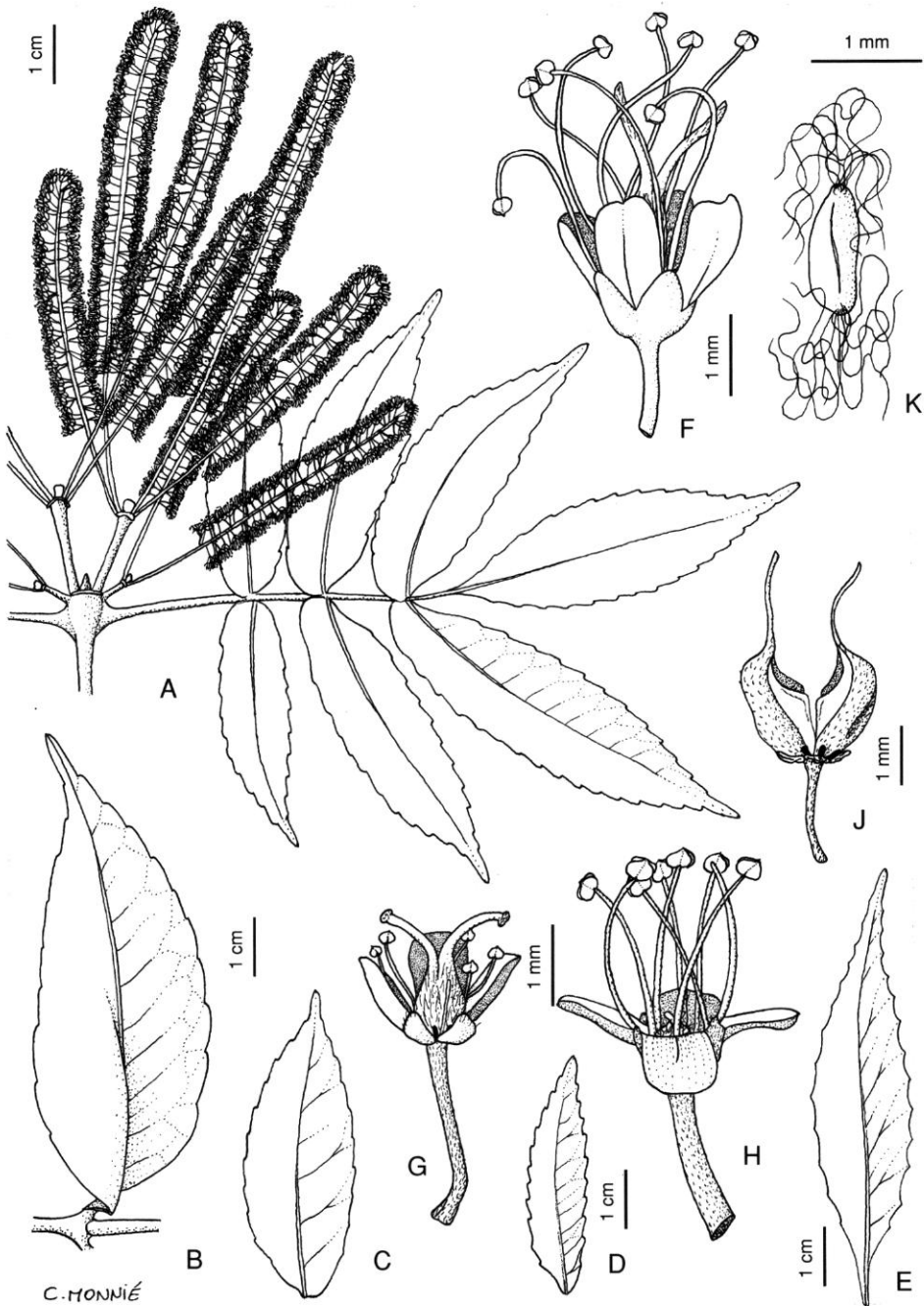


Fig. 7.—*Weinmannia fraxinea*: **A**, flowering shoot showing an inflorescence composed of 4 partial inflorescences (mixture of dyads and tetrads); note dormant apical bud and buds within each partial inflorescence; **B**, lateral leaflet, typical of *W. fraxinea* "dulitensis"; **C**, lateral leaflet, typical of *W. fraxinea* "borneensis"; **D**, lateral leaflet, typical of "blumei"; **E**, lateral leaflet, typical of *W. fraxinea* from the Moluccas; **F**, bisexual flower; **G**, female flower, one petal removed; **H**, male flower; **J**, dehiscent capsule, central column not evident; **K**, seed. (**A**, Hopkins & Bradford 5006; **B**, Hopkins & Bradford 5013; **C**, Meijer SAN 22106; **D**, Nousjet 670; **E**, Kuswata & Soepadmo 250; **F**, **J**, **K**, Dickson 215; **G**, Geesink 8953; **H**, Hopkins & Bradford 5006).—Drawn by C. MONNIÉ.

long; peduncles and axes of racemes minutely puberulent to tomentose. Floral buds inserted in fascicles; floral bracts ligulate-carinate 0.5-1 mm long, caducous, with short flattened hairs. Flowers unisexual or bisexual; pedicel (1.1-)1.5-3 mm long, minutely hairy; calyx lobes triangular, 0.6-0.9 mm long, hirsute at base; petals oblong to obovate, 1.1-1.8 × 0.7-1.2 mm, apex rounded or rarely emarginate, ciliolate or not; disc lobes free, oblong, 0.2-0.5 mm long, or rarely forming an almost complete disc; in male flowers: filaments ca. 2.9 mm long, anthers ca. 0.5 mm long, ovary ca. 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 (2-)2.5-4(-6) × 1.5-2(-3.1) mm at dehiscence, plus styles 1-2 mm long, the exocarp pubescent; calyx lobes usually persistent; central column weakly developed. Seeds 0.8-1.1 mm long, comose at both ends, the hairs up to 2 mm long.—Fig. 2A,C,D; 7A-K; 8.

JUVENILE FOLIAGE.—Small seedlings have 3-5 pairs of chartaceous leaflets tinged with red, the margin dentate and the teeth acroscopic; the stipules are persistent, ± round and often toothed (*Hopkins & Bradford 5017*, Borneo). Older seedlings have up to 12 pairs of leaflets with similar margins and the stipules are again often persistent and toothed (*Hopkins & Bradford 5003*, Borneo; *Verheijen 4397*, Flores; *Steenis 7398*, Java *p.p.*). Indumentum on the main stem and leaf rachises varies from almost glabrous to tomentose.

TABLE 1.—The number of herbarium specimens with flowers of different morphological types, as determined by the relative lengths of the styles and filaments, in *Weinmannia fraxinea* from various regions and two closely related species. Sex of flowers was determined at anthesis (columns 2-4) or rarely in fruit (column 5) but never prior to elongation of the filaments.

Geographical region	Male flowers	Bisexual flowers	Female flowers	Fruit with remnants of tiny stamens (i.e. from female flowers)	Breeding system (as indicated by morphology of flowers)
Sumatra	9	0	9	0	dioecious
Malay Peninsula	15	1	9	3	largely dioecious
Java	19	1 + 3 (male + bisexual)	16	0	polygamodioecious
Borneo	7	4	9	0	partly dioecious
Lesser Sunda Islands	4	0	2	0	dioecious
Moluccas	9	0	10	6	dioecious
New Guinea	3	21	1	1	largely hermaphroditic
Solomons	0	15	0	0	hermaphroditic
Sulawesi (<i>W. devogellii</i> , see part 2, p. 48)	3	0	4	0	dioecious
Vanuatu (<i>W. macgillivrayi</i> , see part 3, p. 85)	1	2 (male + bisexual)	1	4	polygamodioecious

BREEDING SYSTEM.—Varying with geography, either dioecious, polygamodioecious or hermaphroditic. See Table 1.

FIELD NOTES.—Small, often shrub-like tree 5–15 m tall at high altitude, to tall, slender tree up to 25(–40) m high \times 50 cm dbh at lower altitude. Buttresses usually absent; when present, up to 2 m, concave, rounded. Bark variable but frequently brownish and flaking; varying from dark brown, pink- or orange-brown, greyish, fawn, reddish purple to rich tawny rust, and the texture scaling, fissured, smooth, flaking or rugose-lenticellate. Inner bark variable, often reddish; also orange-yellow, brownish grey, golden-brown or reddish brown and fibrous. Slash wood dirty yellow-white; no exudate. Heart wood light orange to beefy red. Stipules sometimes prominent; young leaves, stems and stipules often pinkish, bright red or purplish. Mature leaves shining above, sometimes with red margins, the rachis brown-red, the stipules light green; old leaves bright red. Flower buds green, yellow, pink or red; inflorescence axes green or dull red; pedicels sometimes red. Flowers white, yellowish, pinkish or pale green; pedicels and calyx greenish or pinkish; petals and filaments white or creamy pink; disc yellowish; anthers white to sulphur; ovary red with styles pink or white, the hairs white; flowers lightly scented or not. Young fruit green, reddish green, yellow, bright red, purplish or red-brown; old fruits blackish; seeds yellowish white.

DISTRIBUTION AND ECOLOGY.—From northern Sumatra eastwards through Malesia (Malay Peninsula, Greater and Lesser Sunda Islands, Moluccas, New Guinea and Bismarck Archipelago) to the Solomon Islands; absent from Sulawesi and the Philippines. (0–)500–2000(–2700) m. In western Malesia, usually from mid to high elevations and more frequent at lower elevations in the eastern part of its range (Malay Peninsula: (450–)1000–2065 m; Sumatra: 500–2700 m; Java: 600–2400 m; Borneo: (0–)500–1970 m; Lesser Sunda Islands: 500–1500+ m; New Guinea: 10–1450(–2250) m; Solomons: 10–620 m).

In western Malesia, at lower elevations in primary and secondary forest, including with *Casuarina*. Locally common small tree above 500 m, in hill forest, often on ridges and spurs or

on slopes below ridge top. Varying in abundance from uncommon to one of main constituents of montane forest (e.g. *Jacobs* 8201, Sumatra), sometimes locally common and clumped. At higher altitude found in mossy heath forest, montane rain forest and dwarf, montane scrub and alpine shrubbery. Often on young volcanic soils and open, stony ground, sometimes recently burnt and dominated by ferns. Also grows on soils derived from sandstone, dacite and ultrabasics and recorded from acidic, water-logged sands in *Agathis* forest (*Kostermans* 12903), sandy, kerangas-like soil, and mixed peat swamp forest at sea level (Borneo).

SELECTED COLLECTIONS (from a total of 347 seen for this region).—**SUMATRA:** *Aceh:* *Steenis* 9543, Gayo lands, Gn. Kemiri, 1800–2000 m, st., 6 Mar. 1937 (BO); *Wilde & Wilde-Duyffes* 13087, Gn. Leuser Nat. Res., Gn. Bandahara, track from kamp. Seldok NE to blang S of summit, 25 km NNW of Kutatjane, 1800 m, yfl., 20 June 1972 (K, KEP, L); *Wilde & Wilde-Duyffes* 14151, Gn. Leuser Nat. Res., Gn. Ketambe, 8–15 km SW from mouth of Lau Ketambe, 40 km NW of Kutatjane, 2000 m, fl., 9 Aug. 1972 (K, KEP, L); *Wilde & Wilde-Duyffes* 16638, Gn. Leuser Nat. Res., Gn. Mamas, 9 km SW from mouth of Lau Ketambe, 30 km NW of Kutatjane, 1500 m, fl., 6 May 1975 (K, KEP, L). (**Tapanuli:**) *Alston* 14891, Baniara, S of Sidikalang, fl., fr., 28 Mar. 1954 (BM, L); *Mareman* 6, bb 5261, Toba plateau, nr. Pansurbatu, 2693 m, fl., 24 Jan. 1923 (BO, L). **W Sumatra:** *Abid gl. Malin Maradjo* 6, bb 18608, nr. Kerintiji Tengah, 1400 m, st., 20 Mar. 1934 (BO); *Bünnemeyer* 908, NW slope Talaman, Ophir Distr., 1900 m, fl., 28 May 1917 (BO); *Meijer* 5218, Mt. Singgalang nr. Bukittinggi, 2000–2200 m, fl., yfr., 1 July 1956 (L); *Meijer* 5898, Mt. Sago nr. Payakumbuh, 1500 m, yfr., 22 June 1957 (L). (**E coast:**) *Bangham & Bangham* 1020, Trail from Medan to top of Sibajak volcano, 4200–6500 ft., fl., 15 Feb. 1932 (K, SING); *Lörzing* 7941, Central Habinsaran, right bank of Kuwal between Parsoburan and Nassau, 850 m, buds, 15 Nov. 1920 (BO, L); *Teyssman s.n.*, Lingga, Mt. Tanda, st. (BO, L); *Yates* 2007, Brastagi, 4500 ft., fl., yfr., 12 Mar. 1926 (BO, L, SING). **Benkulu:** *Mesoerip* 20, bb 8753, Kroë, nr. Gn. Kewala, 800 m, st., 7 Mar. 1925 (BO); *Voogd* bb 17032, Lebong, nr. Bt. Daun, 1800 m, st., 1 Apr. 1932 (BO). **Palembang:** *Steenis* 3617, Gn. Pesagi, N ridge SSE of L. Ranau, 2000 m, st., 4 Nov. 1929 (BO). **Lampung:** *Jacobs* 8201, Mt. Tanggamus, 5°26'S–104°41'E, 1500 m, fl., 1 May 1968 (A, BISH, K, KEP, L).—**PENINSULAR MALAYSIA:** *Kedah:* *Wyatt-Smith* KEP 79272, top of Kedah Peak, 3950 ft., fl., 28 Apr. 1957 (K, KEP, L). *Perak:* *Ridley* 3027, top of

Gn. Hijau, fl., Mar. 1892 (BM, K, SING); *Wray* 3814, Gn. Babu, Larut, 5000 ft., fr., Mar. 1890 (K, P, SING). **Kelantan:** *Symington* KEP 37700, Gn. Stang, st., 10 Oct. 1934 (SING). **Trengganu:** *Cockburn* FRI 10828, E approach ridge Gn. Mandi Angin, 4200 ft., buds, 12 July 1962 (K, KEP, L); *Moysey & Kiah* SF 31040, Gn. Padang, 4000 ft., buds, June 1937 (KEP, SING). **Selangor:** *Maxwell* 78-318, Genting Highlands, Gn. Ulu Kali, 1700 m, fl., 3 June 1978 (L). **Pahang:** *Corner* SF 33161, Fraser's Hill, 4000 ft., fl., 10 Aug. 1937 (A, BO, L, SING); *Kloss* 126 or SF 12124, Gn. Tahan, Padang Sebrang, 4900 ft., fr., 6 July 1923 (SING); *Soepadmo* 950, between Wray's camp and the Padang, Taman Negara, 3000-5000 ft., fl., 4 Sep. 1970 (A, K, L, SAN, SAR); *Symington* SF? 36224, Cameron Highlands, summit of Gn. Terbakar, fr., 12 Apr. 1934 (K, KEP, SING); *Whitmore* FRI 3266, main NE ridge of Gn. Bebom, Krau Game Reserve boundary, 5000 ft., fr., 18 Mar. 1967 (A, K, KEP, L). **Malacca:** *Griffith* 2507, Gn. Toondot Ledang top, fl., 1861-62 (K, P); *Ridley* 3295, Mt. Ophir, buds, June 1892 (K, SING). **Johore:** *Mat Asri bin Ngah Sanah* FRI 38681, Gn. Ledang, nr. Telecom building, 450 m, fl., 20 Apr. 1993 (KEP); *Whitmore* FRI 12394, NW Johore, Gn. Ledang (Mt. Ophir), 3700 ft., fl., 17 July 1969 (A, K, KEP, L).—**JAVA** (W = west, C = central, E = east): *Arens* 79, E, Malang, Ardjuna, between Kokopan and Lalijiwo, 2400 m, fl., 15 Oct. 1915 (BO, L); *Backer* 7118, W, Bantam, Gn. Aseupan nr. Menes, 400-600 m, fr., 12 Mar. 1913 (BO); *Backer* 22969, W, Bogor, Gn. Beser, nr. Tidadap, S of Tibeber, 1050 m, buds, 10 Sep. 1917 (BO); *Backer* 37408, E, Malang, Pasuruan, Gn. Ardjuna, above Tjeter, 2000 m, fl., 3 Oct. 1927 (L); *Balgooy & Wiriadinata* 2913, W, Nirmala Estate, Gn. Halimun area, 1350 m, fl., 10 June 1980 (A, L); *Boschproefstation* 6691, E, Madiun, Kedunggalar forest, fr., Mar. 1927 (BO); *Burck* 483, W, Priangan, Garut/Karotjok, buds, fr., 4 July 1891 (BO, L); *Hochreutiner* 1941, W, Bogor, Mt. Salak, towards W on Gn. Bunder, 800 m, fl., 2 Oct. 1904 (L); *Junghuhn* s.n., C, Semarang, Medinie, Ungarang, yfr. (L); *Kalshoven* VI, W, Bogor, Tjiadhu (Gn. Salak), 900 m, fl., Nov. 1918 (BO); *Koorders* 7640, W, Bogor, Tjibodas, Tjiputri, fl., 22 Feb. 1890 (BO, L); *Koorders* 7645, W, Bogor, Takoka, 1100 m, fl., 3 Aug. 1890 (BO, L, P); *Koorders* 6746, W, Priangan, NW Galunggung, nr. top Pangentjongan-Telagabodas, 2229 m, fl., 1 Jan. 1891 (L); *Koorders* 7648, W, Bantam, Gn. Pulasari, Kihudjan, Pandeglang, 1050 m, fr., 13 June 1892 (BO, L); *Koorders* 7652, C, Semarang, Telomjo, Ambarawa, fl., fr., 9 Oct. 1888 (BO, K, L); *Koorders* 7653, C, Banyumas, nr. Pringombo, Bandjarnegara, yfr., 9 Nov. 1891 (BO); *Koorders* 7657, C, Banyumas, Midangan Mts. nr. Pringombo, 700-1000 m, fl., 15 Nov. 1891 (BO, L); *Koorders* 12441, E, Madiun, W Gn. Wilis, Ngebel, 1350 m, yfr., 22 Oct. 1892 (A, BO, L, SING); *Koorders* 26546, W, Priangan, Garut,

Wanaradja, Pasir, Pasanggrahan Pangentjongan, fr., 5 Feb. 1897 (BO, L); *Koorders* 27952, C, Semarang, Ambarawa, Telomojo, fl., 13 June 1897 (BO, L); *Koorders* 34183, E, Madiun, Ngebel, Ponorogo, fr., 19 Nov. 1900 (BO, L); *Koorders* 37915, E, Malang, Tengger, 1650 m, fl., 30 Oct. 1899 (BO, K); *Koorders* 38229, E, Malang, Gn. Ardjuno, Pasuruan, 2000 m, fr., 11 Nov. 1899 (BO, K, L); *Lörzing* 716, C, Tlerep, Prahui, N Sendara, 2000 m, buds, 24 Nov. 1912 (BO, L); *Steenis* 5110, W, Bogor, Tjiapuskloof, Gn. Salak, 800-1000 m, fl., 31 July 1932 (A, BO, K, L, SING); *Steenis* 17615, W, Bogor, Gn. Pangrango, 2500 m, st., 29 May 1950 (BO); *Winckel* 1559, W, Bogor, Tjadasmalang, nr. Tjidadap, S of Tjibeber, 1000 m, fl., fr., 11 Aug. 1923 (BO, K, L, SING).—**BORNEO:** **SABAH:** *Aban Gibot* SAN 60723, Distr. Ranau, Kamp. Kilimu Ranau, 2.5 miles E of Ranau along Poring Rd, 2000 ft., fr., 18 Sep. 1967 (BISH, SAN); *Aban Gibot* SAN 62024, Distr. Tuaran, Kampong Parad, fr., 18 May 1968 (L, SAN, SAR); *Aban Gibot* SAN 66831, Distr. Ranau, Copper Mining Area, Mamut, buds, 2 May 1970 (L, SAN); *Aban Gibot* SAN 95210, Distr. Beluran, Bt. Monkobo, 1950 m, st., 15 Mar. 1982 (SAN); *Alabazo* SH (SAN) A 3626, Forest Distr. Jambunah, Kg Zanateir, 2500 ft., fr., 26 Mar. 1952 (L, SING); *Carr* SF 27228, Mt. Kinabalu, nr. Bundu Tuhan, 4000 ft., fl., 3 May 1933 (SING); *Chew & Corner* RSBN 4398, Mt. Kinabalu, Bembangan R., 5400 ft., st., 20 Feb. 1964 (K, L, SAN); *Clemens & Clemens* 50693, Mt. Kinabalu, Gurulau Spur, 5500 ft., fr., 4 Dec. 1933 (A, BM); *Clemens & Clemens* 51173, Mt. Kinabalu, Penibukan ridge, 4000 ft., fl., 6 Nov. 1933 (A, BM, K); *Cockburn* SAN 84928, Distr. Lahad Datu, Summit trail of Gn. Tribulation, Sg. Segama, 900 m, fr., 18 Aug. 1976 (K, L, SAN, SAR); *Madani* SAN 89394, Distr. Ranau, foot Bt. Ampuan, 2500 ft., fl., 18 Nov. 1978 (L, SAN, SAR); *Meijer* SAN 51588, Distr. Sandakan, Mt. Melian nr. Kiabu Labuk, 2800 ft., juv., 14 May 1965 (SAN); *Mikil* SAN 31867, Distr. Tambunan, Trusmadi above Kionop, juv., 10 Oct. 1962 (KEP); *Mikil* SAN 37765, Distr. Penampang, Suran Trail, 890 ft., fr., 15 Dec. 1963 (L, SAN, SAR); *Sarie* SAN 28510, Distr. Ranau, spur of Kg Tamis Tenompaok F.R., 4700 ft., yfr., 19 Feb. 1962 (K, KEP, L, SAN, SAR); *Sundaling* SAN 129697, Distr. Lahad Datu, FR Malau, fl., 30 July 1990 (SAN).—**BRUNEI:** *Ashton* BRUN 1044, Bt. Pagon ridge, 4750 ft., fr., Mar. 1958 (K, L, SAR).—**SARAWAK:** *Ashton* S 21116, Bt. Lumut, Carapa Amau, Ulu Mujong, Hose Mts., 950 m, st., 14 Apr. 1964 (K, SAR); *Chai* S 18535, Gn. Matang, 800 m, fl., 31 July 1963 (A, K, KEP, L, SAN, SAR); *Chai* S 35503, Perupayang nr. foot of Apo Duat Range, Kelabit Highlands, Baram Distr., 4th Div., 1180 m, yfr., 14 Nov. 1974 (A, K, L, SAN); *Dyg. Awa & Lee* S 51142, Tama Abu Range, Bario, 4th Div., 1750 m, fl., 19 May 1988 (K, KEP, L, SAR); *Ilias Paie* S 26012, Ulu Ugong, Lawas, 2800 ft., fr., 19 Sep. 1967 (K, L, SAN, SAR); *Lee* S 52496, Bt. Tebunan, Ulu Trusan, Lawas,

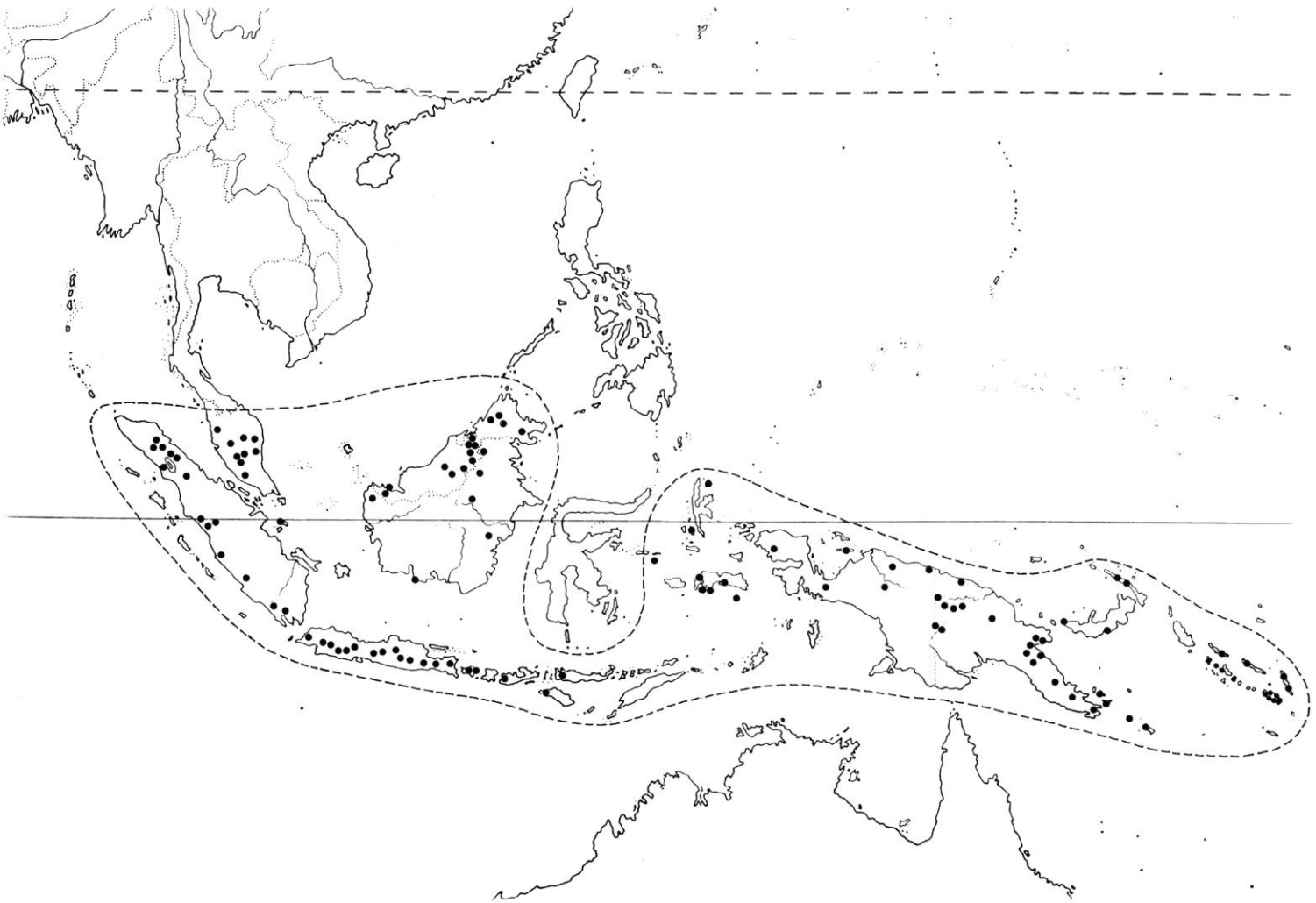


Fig. 8.—Distribution of *Weinmannia fraxinea*.

5th Div., 1450 m, fl., 9 May 1986 (K, L, SAN, SAR); *Martin S 37053*, Gn. Mulu National Park, Tutoh, Baram, 4th Div., 1310 m, fl., 24 Feb. 1976 (K, L, SAN, SAR); *Murthy & Ashton S 22621*, Usun Apau, Long Nyalau, Dapoi, Tinjar, 700 m, st., 4 Apr. 1965 (A, K, L, SAN, SAR); *Nooteboom & Chai 1696*, Kalabit Highlands, Bario, daka sina kaja hill, 1000 m, yfr., 25 Mar. 1970 (BISH, K, KEP, L, SAR); *Pickles S 3777*, Mt. Kalulong, 3°14'N-114°41'E, 4310 ft., fr., 19 Feb. 1956 (BM, SAR).—**KALIMANTAN**: *Enderi 3136*, W Kutei, L. Petak, 600 m, fl., 10 Sep. 1925 (BO, L); *Geesink 8953*, Kalimantan Timur, between Long Bawan and Panado, 3°52'N-115°42'E, 1000 m, fl., 7 July 1981 (L); *Jong bb 9670*, West Borneo, Ond. afd. Bengkajang, top Gn. Bawang, 1400 m, juv., st., 25 Mar. 1926 (BO); *Kostermans 7540*, Peak of Balikpapan, Gn. Beratus, 1200 m, st., 15 July 1952 (BO, K, L); *Kostermans 12903*, W. Kutei, Mt. Palimasan nr. Tabang on R. Belajan, 700 m, fr., 11 Sep. 1956 (BM, K, KEP, L); *Valkenburg & Stockdale 1082*, Kayan Mentarang Reserve, 2°51'N-115°55'E, 950 m, fl., 26 Nov. 1991 (A); *Yaeger 203*, Tanjung Puting, Kalimantan Tengah, 0 m, st., 16 Nov. 1985 (A).—**LESSER SUNDA ISLANDS**: *Bali*: *Kostermans et al. KK&SS 162*, Bedugul forest region, Mt. Batukan complex, 1300 m, fl., 25 June 1958 (A, BM, BO, K, L, P); *Meijer 10400*, Mt. Agung, 8°20'S-115°30'E, st., 17 June 1976 (L); *Seuff 17*, bb 17276, Klunbung, nr. Pengedjaran, 1200 m, fr., 22 Feb. 1933 (A, BO); *Steenis 8043*, Gn. Abang, 1500-2000 m, st., 9 Apr. 1936, (BO). **Sumbawa**: *Kostermans 18439*, W Sumbawa, Mt. Batulante, Brangbossang, trail from Batudulang to Pusu, 800-900 m, st., 24 Apr. 1961 (K, L). **Sumba**: *Verheijen 4028*, s.loc., buds (L); *Voogd 1901*, W Sumba, 500 m, fl., 30 Nov. 1934 (BO, L). **Flores**: *Hoogland 12646*, W Flores, Poco Raneka nr. Ruteng, 1400 m, fl., 25 June 1975 (CANB, L); *Kostermans 22091*, W Flores, SE part Mbengen, 600 m, buds, 10 May 1965 (K, L); *Schmutz 4588*, Nunang, 1100 m, fr., 2 Feb. 1980 (L); *Verheijen 4360*, Karat-Lelak, st., 16 July 1974 (L).—**MOLUCCAS**: *Morotai*: *Kostermans 1097*, Gn. Pare 2, 900 m, 26 May 1949, (BO, L). **Bacan**: *Haan 2*, bb 23122, nr. Masurung, 500 m, st., 12 Aug. 1937 (A, BO, L). **Sula Isls.**: *Atjeh (Exp. v. Hulstijn) 383*, Eil. Sulabesi (= Sanana), Gn. Patahoi, fl., 1913-14 (BO, L). **Seram**: *Burley et al. 4363*, 40 km E of Masohi in Wae Rutan/Wae Ruwata (Ruwa) catchment areas, 150 m, fl., 7 Dec. 1990 (A, K, KEP, L, P); *Rutten 1649*, W Ceram, W of Piru, 0-100 m, fl., 25 Sep. 1918 (BO, K, L); *Rutten 2221*, C Seram, H Elate S of Raiiliu, 400 m, fl., 13 May 1919 (BO, L). **Ambon**: *Burlage 253*, Gn. Tuna, fl., 17 July 1900 (BO); *Dumont d'Urville 131?*, s.loc., fl., Oct. 1823 (P); *Kornassi 1181*, Gn. Harumesen, 0-100 m, fl., 25 Apr. 1918 (BO, K, L); *Kuswata & Soepadmo 250*, Waai, slope of Mt. Salhutu, 100-200 m, fr., 7 July 1959 (A, BISH, BM, K, KEP, L, P); *Matatula 5*, bb 14261, nr. Puta, kamp. Hatu, 250 m, st., 14 Dec. 1929 (BO);

Rant 112, Karang panjang, behind Soja rd., fr., 30 May 1929 (BO); *Vriese & Teysmann s.n.*, s.loc., fl., 1859-1860 (L); *Wiljes-Hissink 21*, foothills of Salahutu Mt. nr. Wae, 200 m, buds, Apr. 1948 (A); *Zippel 72d*, s.loc., fr., Sep. 1828 (L). **Uli Asser Isls.**: *Malessij 4*, bb 14303, Haruku, nr. Taënenitu, 300 m, fl., 20 Mar. 1930 (BO). **Banda**: s.coll., s.n., s.loc., fl. (L). **Cult. in Hort. Bog. ex Moluccas**: *Forman 51*, J130, fr., 25 Feb. 1956 (A, BO, K, L); *Jacobs s.n.*, J130a, male fl., 12 Mar. 1958 (BM, K, L, P).

LOCAL NAMES.—**SUMATRA**: Antahasi or Atahasi (Batak language, Toba), Boertoba (Toba), Resak kero (Malay language), Boenga Loetih (Lampung lang.), Bringin tandoek (language?).—**MAL. PEN.**: Kasai bukit (*Burkill & Holttum SF 6853*), Sentang (*Whitmore FRI 3881*), Pa'ang (*Bidin CF 4200*).—**JAVA**: *Sundanese*: Ki merak(h), Karo tjok, Ki papatong, Kihiris, Kiringit, Tjirome, Tjeremeh, Ki Tjereme, Ki mèong, Angriet passang, Kibiroe, Ki adjag, Ki-papattong. *Javanese*: Dali kling or Dalikeling, Wlingi, Kelis, Pantjalkidang, Sampar kedang, Gagar, Ketjemé, Serak, Lere, Gringing, Damaran, ?Klis, ?djeng gitri, Nagasari gunung, Sap(i)enan, Sadan, Tembajang or Tembagan, S(e)riwalik, Wuru kunjat. **Language not specified**: Damaran (*Backer 16223*), Ki soeren goenoeng (*Koorders 26546*), Legarie Tjantigi (*Kalshoven VI*), Pasang kengkeng (*Voogd 721*), Kajoe djaran (*Winckel 1963*).—**BORNEO**: Tekaran(u) (Kelabit), Uban (Iban), Tansang Lang (Iban), tkaran (*Nooteboom & Chai 1696*), Kayu-papan (Murut).—**LESSER SUNDA ISLANDS**: Kémérak(h)an (Balinese lang.), Larang (Flores).—**MOLUCCAS**: Marah, k = Doka2ra = Sela, k (Tobela lang., Bacan), Daon mejang (Ambon), Kahoenar (Malay lang., Ambon), Lagoendi hoetan (Malay, Ambon dialect), Taheroe (Malay, Ambon dialect), Meongmerah (Malay, Ambon dialect), Moëtotoea (Haruku lang.).

LOCAL USES.—**BORNEO**: The leaves are used for dying cloth; they are boiled in water and then mixed with clay to make a blackish dye (*Chai S 35503*). Firewood.

NOMENCLATURE AND TYPIFICATION.—**HOOGLAND** worked extensively on the nomenclature and typification of *Weinmannia fraxinea* and its synonyms. Several lectotypes that he had chosen are formally designated here.

Under article 42.1 of the International Code of Botanical Nomenclature (GREUTER 1994), *Pterophylla fraxinea* D. Don, the basionym for *Weinmannia fraxinea*, was validly published in 1830 (*descriptio generico-specifica*) and should not be considered a *nomen nudum*.

For the names published by SCHLECHTER and placed in synonymy here, as well as for *W. borneensis* Engl., and for *W. pullei* Schltr. and *W. virgulata* Schltr. (see HOPKINS 1998b), the holotypes at Berlin have not been destroyed (see BERNARDI 1964).

TAXONOMY AND VARIATION.—As circumscribed here, *Weinmannia fraxinea* is a widespread species that shows a complex pattern of variation in the number, size, shape and texture of the leaflets and in the indumentum. *Weinmannia blumei*, the name usually applied to this species in western Malesia, is placed in synonymy with *W. fraxinea* here for the first time, as are several names from Borneo and New Guinea that were regarded by BERNARDI (1964) as distinct. The variation in *W. fraxinea* cannot be consistently divided into discrete units either morphologically or geographically, i.e. it shows “checkerboard” variation, and can thus be regarded as an ochlo-species (CRONK, in press; WHITE 1962). Since the variants grade into one another, division into infraspecific taxa is unwarranted. However, it is sometimes useful to be able to name variants, especially at a local level, and in this case I suggest following the example of HUXLEY & JEBB (1993) who propose the use of informal nicknames for the most distinctive variants of ochlo-species (e.g. “*dulitensis*” for the large, rubbery leafleted form; “*blumei*” for specimens with medium-sized, chartaceous leaves, etc.). However, there are too many intermediate collections for nicknames to be applied consistently to all the material in *W. fraxinea*.

The majority of collections from throughout the range have medium-sized, chartaceous to subcoriaceous leaflets, medium-sized and usually caducous stipules, and the indumentum on the axes varies from puberulent to tomentose (Fig. 7A). The flower buds are usually pinkish and the flowers whitish. In Sumatra, the Malay Peninsula, Java and New Guinea, some collections have smaller leaflets (Fig. 7D) (e.g. *Koorders* 7646, Java; *Steenis* 3617, *Rappard* S27, Sumatra; *Cockburn* FRI 11030, Malay Peninsula; *Stevens* LAE 58123, *Woods* 2718, New Guinea), the largest lateral leaflet per leaf exceptionally as small as 2.2×0.9 cm. These small-leafleted variants

usually occur at high altitude though specimens with medium-sized leaflets sometimes occur at similar elevation. The inflorescences tend to be short and less well developed than in material from lower elevation (i.e. fewer partial inflorescences; dyads not tetrads) and the flowers are usually white.

Other collections from these four areas and from Borneo have exceptionally large leaflets, up to 12×3.5 cm. The leaflets vary in texture from chartaceous to coriaceous, but when coriaceous, they often have minutely prominent or contrastingly coloured venation and a dense reticulum of tertiary and quaternary veins. In these specimens, the axes are glabrous or subglabrous and the stipules are larger and more persistent. In the Malay Peninsula material like this has been named *W. blumei* var. *major* (e.g. *Ridley* 16029, *Wray & Robinson* 5319); in Borneo, *W. dulitensis* (e.g. *Clemens* 51173, *Hopkins & Bradford* 5013); and in New Guinea, *W. alta* (e.g. *Smith* NGF 1355, *Lam* 1574). In Sumatra, collections include *de Wilde & de Wilde-Duyffes* 14151 from Gn. Leuser, Aceh Province. However, the shape of the lateral leaflets is not always the same, and varies from lanceolate or elliptical and \pm cuneate at the base, to ovate with the base rounded and conduplicate (Fig. 7B). In vivo, young stems and leaves are rubbery and difficult to press (HOPKINS & BRADFORD pers. obs.). In *W. fraxinea* “*dulitensis*” from Borneo, the inflorescence axes are reddish, the racemes long and robust, the flower buds pink or bright red and the flowers pinkish at anthesis (Fig. 2C,D).

Some other collections from Borneo have ovate lateral leaflets that are medium-sized, subcoriaceous, and the base is rounded on one or both sides but not conduplicate (Fig. 7C). They sometimes dry black and can be densely hirsute along the abaxial surface of the midrib. They correspond to *W. borneensis* (e.g. *Ampon et al.* SAN 71837, *Aban Gibot* SAN 56354, *J. & M.S. Clemens* 32641).

In Flores and Seram, the leaflet margins are rather distinctly crenate (e.g. *Hoogland* 12646, *Schmutz* 30621). Some specimens from the islands of Milne Bay Province, Papua New Guinea have leaflets with strongly acroscopic crenations (e.g. *Brass* 27428 and *Gideon* LAE 57278,

both from Misima Island) but the leaflets here are larger than in the Lesser Sunda Islands.

In the Moluccas, the leaflets are typically elliptical or lanceolate and the base of lateral leaflets, especially the most distal pair, is strongly unequal, being attenuate on one side and concave on the other (Fig. 7E) (e.g. *Kornassi* 1181, *Kuswata & Soepadmo* 250, *Malessij* bb 14281, *Teysmann s.n.*, Ambon; *Rutten* 2221, Seram). A few collections from the Cycloop Mts., Irian Jaya are rather similar (e.g. *Koster* BW 4302). In both the Moluccas and New Guinea some collections are glaucous on the underside of the leaflets (e.g. type of *W. hypoglaucula* from Irian Jaya; *de Wiljes-Hissink* 21, Ambon).

Weinmannia fraxinea is less variable than some other ochlo species, such as *Myrmecodia tuberosa* Jack in which 16 informal entities were recognised (HUXLEY & JEBB 1993), but nevertheless it shows many of the traits listed by CRONK (in press) as characteristic of this type of complex species. It has strongly polymorphic, non-hierarchical variation where the characters vary independently of one another and largely independently of geography and ecology. It has a widespread distribution and shows considerable ecological plasticity, occurring for instance in New Guinea from near sea level to over 2000 m on a variety of soil types. While distinct variants can sometimes be recognised at a local level, they intergrade when the whole range of the species is considered. Similar morphologies are often found in widely separated localities and sometimes appear to be polytopic, while other variants occur in only one region. In some cases, at a particular locality, there can be two distinct variants present which do not intergrade, although in another locality they do. In common with many ochlo species, *W. fraxinea* belongs to a large genus and has closely related, monomorphic satellites, such as *W. devogelii* H.C. Hopkins in Sulawesi and *W. macgillivrayi* Seem. in Vanuatu.

Although variation is not due to interspecific hybridization, nor does *Weinmannia fraxinea* appear to be a series of apomictic microspecies (see CRONK, in press), the morphology of flowers on herbarium specimens suggests a complex and variable breeding system (Table 1). Clearly field observations are needed but current evidence

indicates that *W. fraxinea* is predominantly dioecious or polygamodioecious in some regions and hermaphroditic in others. Successive cycles of flowers of different sexes on one plant, as seen in certain Sapindaceae (VAN WELZEN 1990) and which may occur in some of the Pacific species of *Weinmannia*, would not produce the pattern that has been observed in this species to date. For instance, herbarium specimens from plants in cultivation at the Botanical Garden at Bogor, which originated in the Moluccas where *W. fraxinea* is morphologically dioecious, are unisexual and provide no evidence that the trees change sex. It seems likely that variation in the breeding system contributes to taxonomic complexity and it is possible that some populations are apomictic. The fact that distinct variants sometimes do not intergrade where they occur together suggests a complex breeding system and at least partial barriers to gene flow.

CRONK (in press) discusses two hypotheses for the origin of ochlo species. The Prance hypothesis proposes that this type of polymorphic variation could have arisen in allopatric populations separated from one another in refugia during dry periods of the Pleistocene. The geographical region where *W. fraxinea* has its present distribution was certainly subject to considerable fluctuations in climate and sea level during this period. In a second hypothesis, CRONK (in press) proposes that the rapid expansion of a colonising species with wide ecological tolerance could give rise to the geographically unstructured variation seen in ochlo species. With time and outcrossing, this variation would become ecogeographically sorted and one or more less-variable species could emerge. This hypothesis seems particularly apt for *W. fraxinea* which has wide ecological tolerance and is often a pioneer. As suggested by CRONK, molecular techniques could be used to investigate the genetic structure and origin of ochlo species.

2. *Weinmannia clemensiae* Steenis

J. Bot. 72: 3 (1934); Bernardi, Bot. Jahrb. Syst. 83: 166, t. 18 (1964); Cockburn, in Kinabalu Summit of Borneo, chapter 7: 185, fig. only (1978).—Type: *J. &*

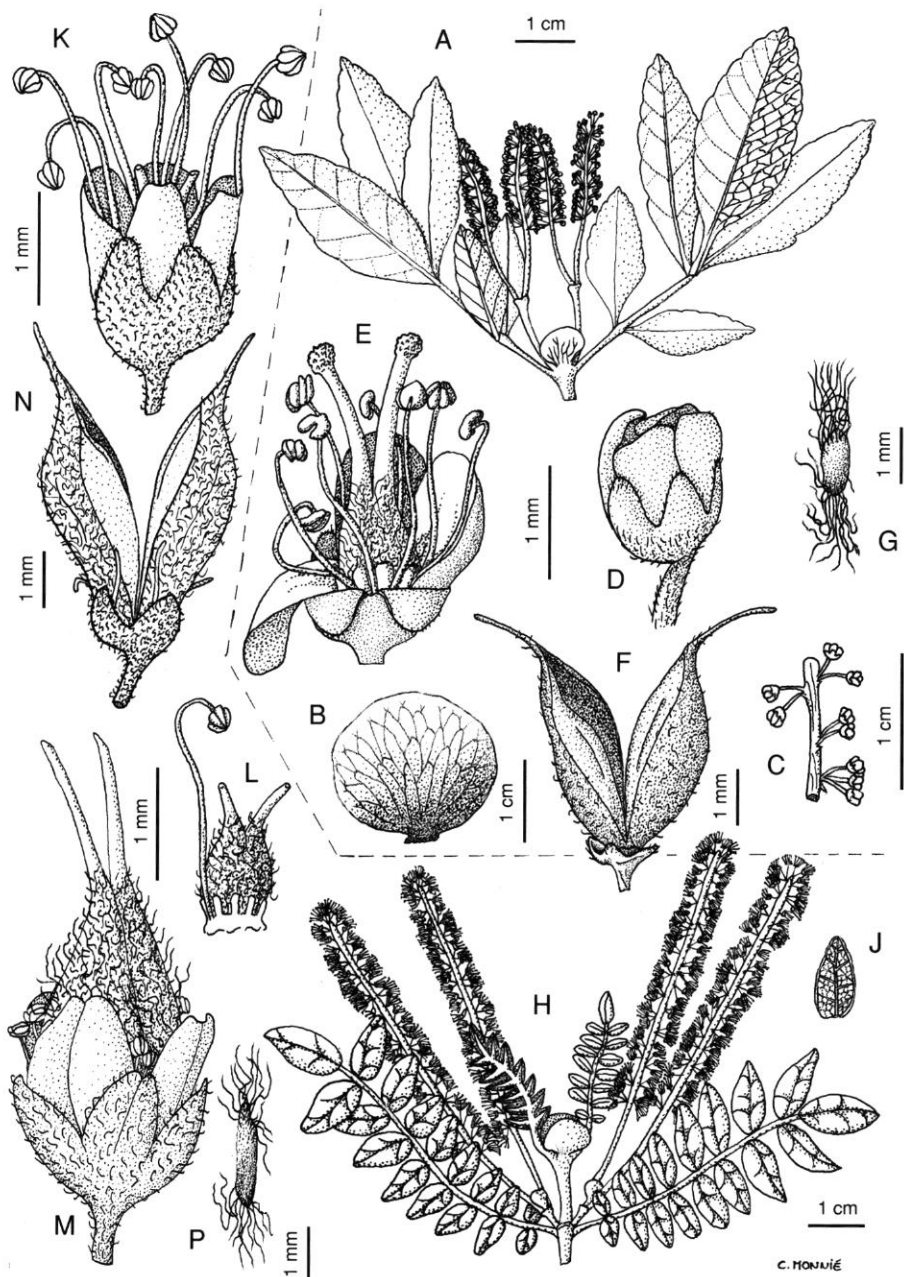


Fig. 9.—A-G, *Weinmannia aphanoneura*: A, flowering shoot with imparipinnate leaves, rounded stipule and inflorescence of two dyads; B, stipule; C, section of rachis of raceme showing flowers inserted in fascicles, the floral bracts already fallen; D, flower bud; E, female flower with one petal removed; F, dehiscid capsule; G, seed. (A, Chew Wee-Lek 380; B, E, Clemens 33076; C, D, Paie S26531; F, G, Endert 4125).—H-P, *Weinmannia clemensiae*: H, flowering shoot with imparipinnate leaves and an inflorescence of two dyads, the apical bud continuing to grow and producing a pair of young leaves; J, abaxial surface of a lateral leaflet; K, flower, probably male; L, detail of K with perianth removed to show gynoecium, disc lobes and a single stamen; M, female flower, note short filaments; N, dehiscid capsule; P, seed. (H-L, Beaman 9132; M, Chew & Corner RSNB 4508; N, P, Clemens 50877).—Drawn by C. MONNIÉ.

M.S. Clemens 27880 (Sabah), Mt. Kinabalu, in low jungle near Kamborangah, 2400 m, 7 Jan. 1932 (holo-, BO!; iso-, K! [photo at KEP], L!).

Treelet or tree, 1.5-10 m high. Young stems and leaf rachises densely tomentose-velutinous, older stems tomentose becoming \pm glabrous with numerous lenticels; stems terete, relatively thick, 3-5 mm diameter, nodes somewhat thickened and leaf scars prominent. Internodes often short, 0.5-1.7 cm. Branching not dichotomous. Stipules usually caducous, \pm orbicular, up to 1×1.2 cm, base narrowing, apex broadly rounded, abaxial surface densely sericeous especially towards the base, adaxial surface shortly velutinous. 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 segments terete, densely tomentose-velutinous, diverging from the stem at an angle of almost 90° especially at growing tips; leaflets bullate and carinate, the margins strongly recurved and often rolled; lateral leaflets oblong or somewhat ovate, the largest per leaf $1.4-2.7 \times 0.6-1$ cm, leaflets towards the base smaller, inserted \pm at 90° to leaf rachis, base equal, rounded to cordate, apex broadly acute; terminal leaflet elliptical, $1.9-3.3 \times 0.7-1$ cm including petiolule of 0.3-0.5 cm, blade scarcely larger than largest lateral leaflets, apex acute; blades coriaceous, the upper surface puberulent or glabrous when the cuticle thick, sparsely to densely pubescent below, the midrib sericeous; sometimes punctate (bases of hairs); margin crenate but crenations usually obscured, 5-7 notches on each side in the lateral leaflets; on upper surface midrib indented, secondary veins \pm at 90° to main vein, tertiary venation obscure; midrib prominent below.

Inflorescence a pair of opposite, lateral dyads, the apical bud of the main stem between the peduncles of the dyads densely sericeous, often continuing to grow vegetatively during flowering; bud at apex of peduncle in angle between the racemes sericeous; sometimes a few successive nodes on one shoot producing dyads simultaneously; peduncles 0.3-0.7 cm long; racemes up to 10.5 cm long; peduncles and axes of racemes densely tomentose-velutinous; inflorescences and

infructescences dense. Floral buds inserted in fascicles, floral bracts obovate-carinate, with short flattened hairs, up to 1-1.5 mm long, caducous. Flowers unisexual (or sometimes bisexual?); pedicel 1-1.5 mm long, with short erect hairs; calyx lobes $0.8-0.9 \times 0.6-0.8$ mm, hirsute; petals obovate or almost circular, $1.1-1.5 \times 1-1.1$ mm, rounded at apex, margin ciliolate; disc lobes 0.4-0.5 mm long, oblong or broadly oblong; in male flowers: filaments ca. 2.5 mm long, ovary ca. 0.6 mm, densely pubescent, styles 0.1 mm, incurved (some flowers in same inflorescence have ovary 0.9 mm long and styles 0.8 mm long, straight, and may be bisexual); in female flowers: filaments up to 1.9 mm long, ovary 1.5-2 mm long, densely pubescent, styles ca. 1 mm long, straight, pubescent at base.

Capsules up to $3.7-4.5 \times 1.8-2.2$ mm at dehiscence, plus styles up to 1.5 mm long, the exocarp densely pubescent; calyx lobes persistent; central column weakly developed. Seeds immature, ca. 0.9 mm long, comose at both ends.—Fig. 2B, 9H-P, 10.

JUVENILE FOLIAGE.—Seedling leaves: blade thin, chartaceous, margin strongly toothed and flat, not recurved; lateral leaflets few (ca. 4 pairs), mid green or reddish; stipules sometimes toothed (*Hopkins & Bradford 5015*). Saplings and coppice shoots: blade coriaceous, lateral leaflets up to 18 pairs, of similar size to those of adult foliage but scarcely recurved; venation indented above; margin distinctly toothed (*Hopkins & Bradford 5016*).

BREEDING SYSTEM.—Dioecious or polygamodioecious? Few collections have flowers at anthesis. Specimens with immature fruits have short filaments, suggesting they have developed from functionally female flowers.

FIELD CHARACTERS.—Adult foliage darkish green above, paler below with main vein brown or pink; leaf rachises and stems brown; stipules satiny mid green and paler than foliage. Buds green, white or brown from indumentum; new growth densely velutinous and sometimes reddish. Flowers pinkish brown or deep cream-pink; calyx blood red; corolla pink or pink-white; stamens cream; whole inflorescence pink and downy. Immature fruits pink with red styles, infructescence axis tinged pink.

DISTRIBUTION AND ECOLOGY.—Endemic to Mt. Kinabalu and Mt. Tambuyukon in Sabah. Restricted to stunted forest on strongly ultramafic soil at (1640-)1900-2600 m. Habitats described as low mossy and xerophyllous scrub forest, open ridges, oak-laurel forest, and forest dominated by *Leptospermum* and *Dacrydium*. Other associates include *Nepenthes rajah*. Probably all populations occur within the boundary of Kinabalu Park, whose protection is therefore crucial to the continued survival of this species.

MATERIAL EXAMINED.—**BORNEO: SABAH:** *Barkman & Buin 141*, Layang Layang, 2600 m, fl., 1 Mar. 1995 (*KIN); *Beaman 9132*, Ranau District, East Mesilau River, nr. Mesilau Cave, 6°03'N-116°36'E, 1950-2100 m, fl., 26 Mar. 1984 (K, L); *Beaman 9837*, Ranau District, Pig Hill on E side of Mt. Kinabalu, 6°03'N-116°36'E, 2000-2300 m, st., 25 May 1984 (A, K, L); *Chew & Corner RSNB 4364*, Mt. Kinabalu, Pig Hill, 7000 ft., fl., 18 Feb. 1964 (K, L, SAN); *Chew & Corner RSNB 4508*, *ibid.*, yfr., 24 Feb. 1964 (A, K, L, SAN); *Chew & Corner RSNB 4755*, Mt. Kinabalu, Mesilau Cave, 6000 ft., st., 29 Mar. 1964 (K, L, SAN); *J. & M.S. Clemens 50793*, Mt. Kinabalu, Gurulau spur, 7000-9000 ft., fl., 6 Dec. 1933 (A, BM, K, L); *J. & M.S. Clemens 50877*, *ibid.*, 8000 ft., fr., 8 Dec. 1933 (A, BM, K, L); *Hopkins & Bradford 5011*, Mt. Kinabalu, Pig Hill, 116°38'E-6°03'N, 2250 m, yfr., 5 Mar. 1996 (KIN, P, MO); *Meijer SAN 28737*, Ranau District, Mt. Tambuyokan, 6000-7000 ft., st., July 1961 (K, L, SAN); *Meijer SAN 34617*, *ibid.*, 6000 ft., st., July 1961 (SAN); *Meijer SAN 48098*, Mt. Kinabalu, Ranau District, opp. Kinabalu cave, Kinabalu Nat. Park, 8000 ft., st., 20 Feb. 1965 (K, L, SAN); *Mikil SAN 47041*, Ranau Dist. Kinabalu Park, Mesilau base camp, 5000 ft., st., June 1964 (SAN); *Nais et al. SNP 3675*, Kinabalu Park, Mt. Tambuyukon, 8000 ft., fl., 16 Mar. 1991 (KIN); *Nais et al. SNP 4896*, *ibid.*, between camp III and summit, fl., 6 Oct. 1990 (KIN); *Philips SNP 2318*, Mesilau landslide, fl., 28 May 1986 (KIN); *Whithead s.n.*, Kinabalu, 9000 ft., st., Mar. 1888 (BM).

(*KIN refers to the herbarium at Kinabalu Park HQ).

As noted in the type description, this species appears to be most closely related to *W. urdanetensis* from the Philippines and the Highlands of New Guinea. In both species there are numerous, small leaflets arranged at right-angles to the leaf rachis and the secondary veins are at right-angles to the midrib. *Weinmannia clemensiae* has characteristically bullate leaflets with the margins

recurved so that they can not be flattened. There is a slight tendency to bullate leaflets in *W. urdanetensis* but it is not nearly so pronounced. In both species the upper cuticle is sometimes thickened and the structure of the inflorescence is similar. The seeds of *W. clemensiae* are comose at each end, not hairy throughout as in *W. urdanetensis*.

3. *Weinmannia aphanoneura* Airy Shaw

Bull. Misc. Inform. 1940: 260 (1940); Bernardi, Bot. Jahrb. Syst. 83: 160 (1964).—Type: *P. W. Richards 1716* (not 6716 as given in protologue), Sarawak, Dulit Ridge, open moss forest, ca. 1400 m, 11 Sep. 1932 (holo-, K!, photo at KEP).

Shrub or tree 2-20 m high and up to 35 cm dbh. Young woody stems ± glabrous or adpressed puberulent, soon glabrescent, older ones glabrous with numerous lenticels, nodes sometimes ± thickened and leaf scars prominent; branching not usually dichotomous. Stipules often persistent at distal nodes, suborbicular and usually flat, not recurved, up to 1.7 × 1.9 cm (rarely spatulate, ca. 0.6 × 0.4), base constricted, apex broadly rounded, abaxial surface glabrous or shortly strigose especially towards the base, adaxial surface glabrous. 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 semiterete, adaxial side flattened, slightly ridged or channelled, sometimes narrowly winged, especially towards the point of insertion of the leaflets, wings extending outwards up to 1 mm on either side of mid line, petiole and rachis glabrous or tomentose either on adaxial or abaxial surface but not both, usually inserted at an acute acroscopic angle; lateral leaflets narrowly elliptical or narrowly obovate, the largest 2.4-7 × 0.6-1.9 cm, the base unequal, ± sessile, cuneate, apex acute to obtuse; apical leaflet narrowly elliptical, narrowly obovate to obovate, scarcely larger than the largest lateral leaflets, 3-9.4 × 0.7-2.7 cm including the narrowly cuneate to attenuate base 0.3-1.2 cm long, apex acute to obtuse; blades coriaceous, glabrous and sometimes shiny above, glabrous below, characteristically drying grey or

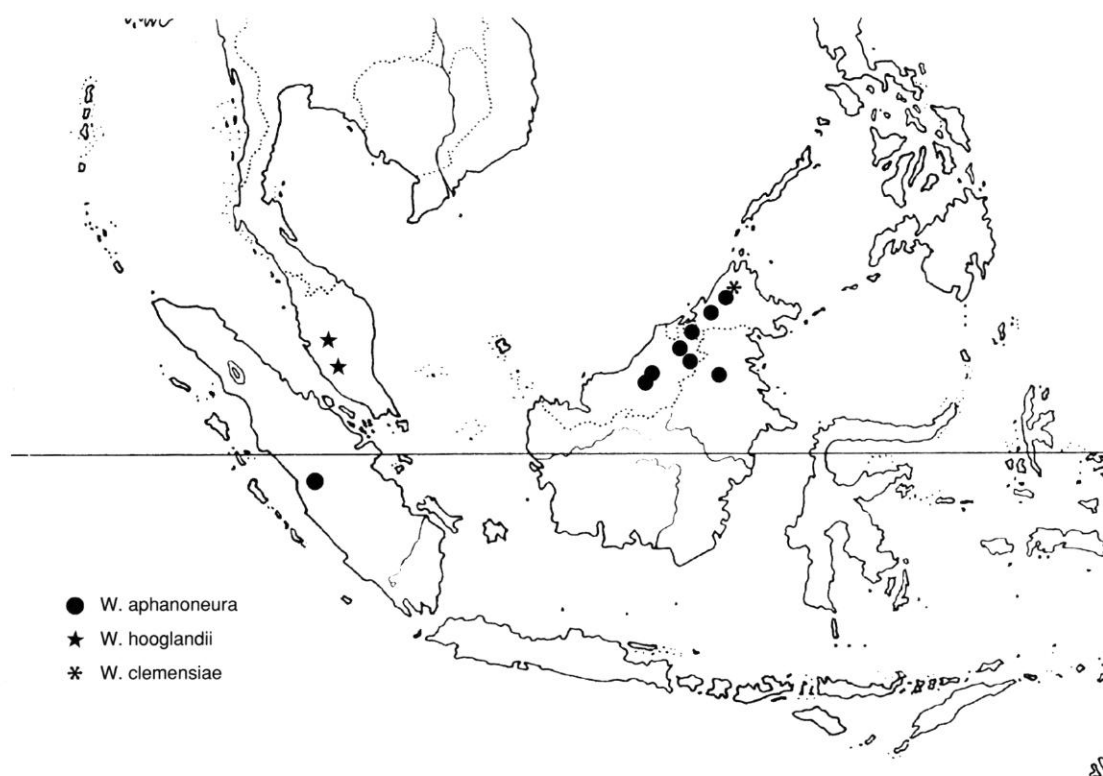


Fig. 10.—Distribution of *Weinmannia aphanoneura*, *W. clemensiae* and *W. hooglandii*.

dark chestnut above and chestnut below; not punctate; margin crenate, 6-11 notches on each side of the largest lateral leaflets; midrib slightly depressed above, prominent below and sometimes pubescent to tomentose at base, secondary and tertiary venation \pm flat on both surfaces or often obscured especially on the upper surface by the thick cuticle; reticulum not dense.

Inflorescence 1 or 2 pairs of opposite dyads, the apical bud of the main stem between the central dyads shortly sericeous, rarely continuing to grow vegetatively during flowering; bud at apex of peduncle in angle between racemes shortly sericeous; sometimes dyads produced in axils of leaves at subdistal nodes; peduncles ca. 0.3-1.9 cm long, racemes usually not longer than the leaves (7-8 cm) but sometimes up to 14 cm long; peduncles glabrous or adpressed puberulent, axes of racemes puberulent, rarely tomentose; stipules

at node at top of peduncle sometimes persistent and either free and orbicular or connate at base to form a cup-shaped structure. Floral buds inserted in fascicles; floral bracts carinate, ca. 1.6 mm long, margin with minute glandular teeth, shortly hairy on abaxial surface. Flowers unisexual; pedicel 1.8-3.6 mm long, puberulous; calyx lobes $0.5-0.8 \times 0.4-0.9$ mm, glabrous; corolla often rotate, petals oblong or irregularly obovate, $1.2-1.5 \times 0.7-0.8$ 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 that the 8 lobes 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 ca. 1 mm long, densely pubescent, styles ca. 1.8 mm long, straight, stigmas capitate, papillose.

Capsule 2.5-3.5 × 1.3-1.5 mm at dehiscence, the styles up to 1.5 mm long, the exocarp pubescent; calyx lobes persistent; central column sometimes present. Seeds ca. 0.9 mm long, comose at both ends, the hairs to 1.5 mm long.—Fig. 9A-G, 10.

BREEDING SYSTEM.—Dioecious.

FIELD CHARACTERS.—Bark scaly dark brown, outer bark reddish, inner bark brownish, sap wood pale yellow (*Pitty & Ogata SAN 63292*). Stem pink; petioles, midrib on underside of leaflets and inflorescence sometimes magenta. Buds red; flowers white to pink; calyx pink or red; corolla cream, pale pink or reddish; filaments white with pale pink anthers. Fruits crimson.

DISTRIBUTION AND ECOLOGY.—Montane forest in Borneo and Sumatra (one record), at 1175-2560 m. Habitats described as open moss forest, ridge top forest, submontane heath forest and ericaceous mossy forest. Locally common.

MATERIAL EXAMINED.—**SUMATRA:** *Nagamasu 3641*, West Sumatra, summit of Gn. Rasam, ca. 10 km S of Danau Diatas, 1°10'-11'S-100°44'-45'E, 2500-2565 m, fl., 18 Feb. 1989 (L).—**BORNEO: SABAH:** *Aban SAN 76507*, Mt. Kinabalu, Ranau District, above power station, st., 11 Mar. 1973 (SAN); *J. & M.S. Clemens 29476*, Mt. Kinabalu, Tenompok, 5000 ft., fl., 2 May 1932 (A, BM, K, L); *J. & M.S. Clemens 33076*, Mt. Kinabalu, Marai Parai, headwaters of Sadikan, 5000 ft., fl., yfr., 5 May 1933 (A, BM, K, L). **SARAWAK:** *Anderson 4507*, Baram District, Gn. Mulu, path from Melinau Paku, 4800 ft., buds, 30 June 1961 (A, K, L); *Brunig S 8785*, Bintulu District, Merurong plateau, Bt. Bandong, fl., 15 May 1960 (A, K, L); *Burt & Martin 5487*, 4th Div., Gn. Murud, 3°55'N-115°31'E, 7800 ft., fl., 12 Oct. 1967 (SAR); *Chew Wee-Lek 380*, Baram District, Gn. Mulu, 4°5'N-114°55'E, 5000 ft., buds, 16 June 1962 (A, K, L); *Chew Wee-Lek 388*, *ibid.*, fl., 16 June 1962 (A, K, L); *Ilias Paie S 26481*, Gn. Murut, Ba Kelalan, Lawas, 7700 ft., fl., 10 Oct. 1967 (K, L); *Ilias Paie S 26531*, Gn. Murut, Ulu Pahdappar, Ba Kelalan, Lawas, 7750 ft., fl., 13 Oct. 1967 (K, L). **KALIMANTAN:** *Enderd 4125*, Ond. Afd. W. Koetai, b/d Kemoel, 1500 m, fr., 14 Oct. 1925 (L).

W. cf. aphananoneura.—**BORNEO: SABAH:** *Pitty & Ogata S 63292*, Tenom District, Gn. Anginon Sapong, 3900 ft., fl., 20 Nov. 1968 (A); *Ogata 11614*, *ibid.*, 1175 m, 20 Nov. 1968 (L).

LOCAL NAME.—Maba (Iban).

4. *Weinmannia hooglandii* H.C. Hopkins & J.C. Bradford, *sp. nov.*

A W. fraxinea foliolis lateralibus parvioribus (maximis < 2 cm longis, non > (2.8-) 3.5 cm longis) oblongis apice late acuto (non lanceolatis apice anguste acuto), venatione reticulata conferta, areolis parvioribus, inflorescentia unica pare dyatum lateralium (non 2 nec 3 paribus dyatum vel tetratum) diversa.

TYPE.—*T.C. Whitmore FRI 12582*, Peninsular Malaysia, Pahang/Selangor, Gn. Ulu Kali, forested gully, 5600 ft., 9 Sep. 1969 (holo-, KEP!; iso-, A!, K!, L!, SAN!).

Shrub or small tree 1.2-5 m × 4 cm dbh. Young woody stems tomentose or velutinous, older ones glabrescent with numerous lenticels, branching not dichotomous. Stipules persistent or not at distal nodes, ± orbicular, up to 0.5 × 0.6 cm, base constricted, apex broadly rounded or flattened, abaxial surface shortly strigose especially towards the base, adaxial surface glabrous. Leaves imparipinnate, with 3-8 pairs of lateral leaflets, total length 5-7 cm long; petiole 0.8-1.5 cm long, rachis segments 0.4-0.8 cm long, petiole and rachis terete, slightly wider towards the point of insertion of the leaflets, often densely tomentose and especially so along adaxial side; lateral leaflets ± oblong to narrowly ovate, slightly imbricate the largest 1.6-2 × 0.5-0.6 cm, the most proximal leaflets smaller, ca. 0.7 × 0.4 cm, base unequal, sessile, cuneate, apex broadly acute; apical leaflet narrowly elliptical, scarcely larger than the largest lateral leaflets, 1.5-2.3 × 0.5-0.8 cm, base attenuate, apex acute; blades coriaceous, glabrous and sometimes shiny above, glabrous below, not punctate; margin crenate, ca. 3-7 notches on each side of the largest lateral leaflets, margin minutely revolute; midrib slightly depressed above, prominent below and sometimes shortly strigose especially towards the base, secondary and tertiary venation ± flat on both surfaces or often obscure on the upper surface, reticulum relatively dense and drying darker than the remainder of the blade.

Inflorescence a pair of lateral dyads, the apical bud of main stem between the peduncles shortly sericeous; bud at apex of peduncle between racemes shortly sericeous; peduncles ca. 0.4-0.5 cm long, strigose; racemes up to 6 cm long,

the axis pubescent or tomentose. Floral buds inserted in fascicles; floral bracts carinate, ca. 1 mm long, minutely hairy; pedicel 1.5-3 mm long, minutely hairy. Male flowers: calyx lobes ca. 0.8-0.9 × 0.6 mm, glabrous; petals ± obovate, 1.2-1.4 × 0.8-0.9 mm, apex rounded or emarginate, minutely ciliolate (at × 40); disc lobes 0.3-0.4 long, oblong or broadly oblong with thin flanges on either side of each lobe; filaments ca. 2.6-3 mm long; ovary minute, ca. 0.6 mm long, densely golden pubescent, styles 0.1-0.2 mm long, incurved. Fruit unknown.—Fig. 10, 11A-D.

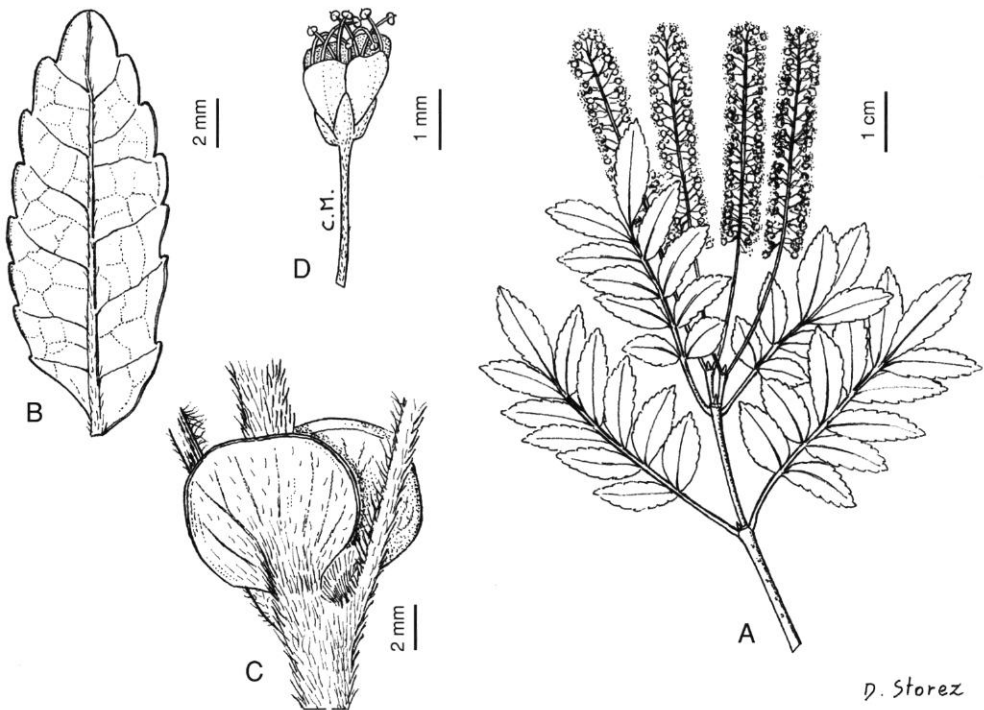
JUVENILE FOLIAGE.—Non-reproductive (coppice ?) shoots: axes tomentose, internodes long, often ca. 8 cm. Stipules orbicular to reniform and shortly stalked, up to 1 × 1.2 cm. Leaves up to 11 cm long, almost perpendicular to stem (not ± erect as in adult foliage), lateral leaflets in 8-10 pairs, ± oblong, up to 2 × 0.8(-1) cm,

chartaceous sometimes widely spaced on the rachis (not ± imbricate); rachis segments up to 0.9 cm. (See *Hoogland 12578*, *Siew Wei Hoe 15* and *Chiew Geok s.n.*). Juvenile leaves are longer than adult ones and have more pairs of leaflets.

BREEDING SYSTEM.—Probably dioecious, but female flowers have not been seen.

FIELD CHARACTERS.—The leaves are clustered towards the end of the twigs and held ± erect to form an even, dense, ball-like, congested crown (J.C. BRADFORD pers. obs.). Young branches and leaf rachises purplish or brown. Foliage dark green above, leathery. Flowers white on pink stalks (*Whitmore FRI 12582*), corolla and stamens white (*Ng FRI 6236*).

DISTRIBUTION AND ECOLOGY.—Known from mountains in western Peninsular Malaysia, from ca. 1680-2065 m. Habitats described as upper montane forest, moss forest and summit forest of low stature; locally common.



D. Storez

Fig. 11.—*Weinmannia hooglandii*: A, Flowering shoot showing inflorescence of two "dyads" (each of two racemes on a short peduncle) in opposite leaf axils at the most distal node of the shoot; B, Underside of a lateral leaflet; C, Node on a vegetative shoot showing a pair of stipules between opposite petioles with a sericeous bud in the axil of the right-hand petiole; D, Male flower, the filaments not fully extended. (A, B, D, *Whitmore FRI 12582*; C, *Bradford 580*).—Drawn by C. MONNIÉ and D. STOREZ.

MATERIAL EXAMINED.—**PENINSULAR MALAYSIA:** *Bradford* 579, 580, Pahang, Gn. Ulu Kali, Genting Highlands, 3°23'N-101°45'E, 1680 m, st., 18 Mar. 1996 (KEP, MO, P); *Chiew Geok s.n.*, Pahang, Genting Highlands, 5600 ft., st., 22 June 1974 (BISH); *Hoogland* 12578, Pahang, Summit Gn. Brinchang, 6300 ft., st., 1 Apr. 1975 (CANB); *Murdoch s.n.*, Selangor, Gn. Ulu Kali, st., 25 Mar. 1905 (K); *Ng FRI* 6236, Selangor, Summit Gn. Mengkuang, fl., 11 Jan. 1972 (KEP); *Siew Wei Hoe* 15, Gn. Ulu Kali, Genting Highlands, 5800 ft., st., 4 June 1977 (L); *Soepadmo & Suhaimi* S172, Gn. Ulu Kali, 3°27'N-103°48'E, 1772 m, st., 8 May 1990 (A); *Symington* 32246, Perak, Gn. Korbu F.R., Cameron Highlands, 5000-7000 ft., st., 22 July 1933 (KEP).

This species is named for R.D. HOOGLAND, specialist in the Cunoniaceae for over 35 years, who recognized his collection from Gunung Brinchang as "something interesting".

RELATIONSHIPS.—The material placed here in *Weinmannia hooglandii* had previously been regarded as a small-leafleted variant of the common and widespread *W. fraxinea* (D. Don) Miq. (synonym *W. blumei* Planch.) from high elevations. However, J.C. BRADFORD observed individuals of *W. hooglandii* growing next to *W. fraxinea* (with much larger, narrowly elliptical leaflets) at the same altitude and in the same habitat at Gn. Ulu Kali, Genting Highlands, in March 1996, suggesting that *W. hooglandii* is not merely an ecotype of the latter, and could be regarded as distinct. This observation is documented by *Bradford* 578 and 581 (*W. fraxinea*) and *Bradford* 579 and 580 (*W. hooglandii*).

Weinmannia hooglandii is distinguished from *W. fraxinea* by its smaller leaflets with more densely reticulate venation visible on the lower surface, and shorter internodes producing a congested, not diffuse, crown. The shape of the lateral leaflets is also different; in *W. fraxinea* in Peninsular Malaysia, the leaflets are usually lanceolate or narrowly elliptical [length to breadth ratio 1: 0.23-0.33(-0.38)] while in *W. hooglandii* distal leaflets are oblong or subfalcate (with the main vein asymmetrically placed) or sometimes suboblanceolate (length to breadth ratio 1: 0.30-0.39) and the proximal ones broadly elliptical. In addition, the stipules in *W. hooglandii* are smaller, being up to 6 mm broad, while the smallest

seen in *W. fraxinea* are 9 mm broad, though in many specimens they are not seen, having already fallen.

A further difference between *Weinmannia hooglandii* and *W. fraxinea* is the presence of supernumerary lateral buds at nodes, especially those bearing partial inflorescences, in the latter. Usually in *W. fraxinea* a reproductive node has two or three buds in each opposite leaf axil, and one, two or three pairs of partial inflorescences develop from them (each partial inflorescence being a dyad or a tetrad). In the few fertile specimens of *W. hooglandii* available, there is only one pair of buds at a reproductive node, and so the inflorescence that develops consists of a pair of dyads (Fig. 11A), as in *W. urdanetensis* (see below).

Although *Weinmannia hooglandii* and *W. fraxinea* can readily be distinguished from one another where they occur together, *W. fraxinea* is a complex and variable species that in some parts of its range has rather small leaves whose leaflets approach those of *W. hooglandii* in size [e.g. *Cockburn FRI* 11030, Peninsular Malaysia, Pahang, Summit Padang of Gn. Tapis, 4500 ft., fr., 11 Sep. 1968 (K, KEP, L); *Symington & Kiah SF* 28894, Pahang, Gn. Tapis, Kuantan, 4600 ft., fl., fr., 14 June 1934 (BO, SING)]. In these cases, leaflet shape and the venation are typical of *W. fraxinea*, and the leaflets are more widely spaced (not imbricate) along the rachis.

Weinmannia urdanetensis, which grows in montane forests in New Guinea and the Philippines, also has small leaflets, and like *W. hooglandii*, the inflorescence is typically a pair of dyads. Mature foliage of *W. hooglandii* differs from that of *W. urdanetensis* by its usually shorter leaves with fewer pairs of leaflets [4-8 not (2-)6-10(-19)], the leaves held at an acute angle to the stem in mature foliage (not more or less at right angles) and the leaflets positioned at an acute angle to the leaf rachis (not more or less at right angles).

Acknowledgements

The work by HCFH was financed by the Human Capital and Mobility Programme of the European Union via the network on Botanical Diversity of the Indo-Pacific. The following herbaria are thanked for access to specimens: A, B, BISH, BM, BO, CANB,

GH, K, KEP, L, LINN, MA, NOU, P, S, SAN, SAR, SING, SUVA, US, Z. Jason BRADFORD is grateful for financial support from Washington University, including the NSF Graduate Research Training Support Grant NSF BIR-9256779, and from the Missouri Botanical Garden, especially through the Mellon Foundation Fellowship. For assistance in our fieldwork in 1996, we are greatly indebted to John and Teffy BEAMAN (UNIMAS, Sarawak), Jamili NAIS and his staff (Kinabalu Park, Sabah), SAW LENG GUAN and his staff (FRIM, Peninsular Malaysia), Michael DOYLE (SUVA, Fiji) and the Fiji Electricity Authority (Monasavu Dam), the Directors of the "Service de l'Environnement" for the North and South Provinces in New Caledonia, and Tanguy JAFFRÉ and his staff at ORSTOM in Nouméa. HCFH also thanks the late R.D. HOOGLAND for his generosity in giving access to his unpublished notes, Jason BRADFORD for much interesting discussion on those parts of the text for which he is not cited as co-author, and for the photographs for Fig. 2, Petra HOFFMANN for advice on nomenclature, P. LOWRY & G. MCPHERSON for comments on all or part of the manuscript, Elsa ARMÈDE for help with typing, and Cécile MONNIÉ, Dominique STOREZ and Jacqueline LEMUEX for the illustrations.

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*Manuscript received 30 October 1997;
revised version accepted 27 February 1998.*