

The application of a cladistic analysis to the classification and identification of *Weinmannia* (Cunoniaceae) in Madagascar and the Comoro Islands

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ABSTRACT

Weinmannia species from Madagascar are currently difficult to identify with available published accounts due to both a paucity of qualitative characters used in identification keys, and a large number of undescribed species. However, newly recognized morphological characters, especially of the inflorescence, can be used to diagnose Malagasy sect. and species-groups. These characters, used previously for a comprehensive cladistic analysis of the genus *Weinmannia* (BRADFORD 1998), are applied here in diagnoses and a key to the resulting sections and species-groups of *Weinmannia* in Madagascar.

RÉSUMÉ

Application d'une analyse cladistique à la classification et l'identification des Weinmannia (Cunoniaceae) à Madagascar et aux Comores.

Les espèces malgaches de *Weinmannia* sont actuellement difficiles à identifier avec les publications disponibles en raison de la fois de la pauvreté des caractères qualificatifs utilisés dans les clés d'identification et d'un nombre élevé d'espèces non décrites. Cependant, des caractères morphologiques nouvellement reconnus, en particulier ceux de l'inflorescence, peuvent être utilisés pour les diagnoses des sections et des groupes d'espèces malgaches. Ces caractères, employés précédemment pour une analyse cladistique du genre *Weinmannia* (BRADFORD 1998) sont appliqués ici dans les diagnoses et une clé de détermination des sections et groupes d'espèces de *Weinmannia* à Madagascar.

MOTS CLÉS

Weinmannia,
Cunoniaceae,
cladistique,
classification,
clés taxonomiques,
inflorescence,
Madagascar,
Comores.

INTRODUCTION

Cunoniaceae, a southern hemisphere family with 26 genera and c. 300 species (BRADFORD &

BARNES 2001), is represented in Madagascar solely by its largest genus, *Weinmannia* L., with c. 150 species worldwide. Most *Weinmannia* species are trees and shrubs of tropical montane

forests, although tropical lowland species occur in Madagascar, and temperate species in Chile, Argentina, Australia, New Zealand and South Africa. *Cunonia* L. and *Platylophus* D. Don, from South Africa, are the only African members of the family.

Cunoniaceae have been the subject of recent phylogenetic and revisionary investigations, with most attention given thus far to *Weinmannia* (BRADFORD 1998; HOPKINS 1998a, 1998b, 1998c; HOPKINS & FLORENCE 1998). Based on cladistic studies (discussed below), the infra-generic classification of BERNARDI (1961, 1964) and the placement of some species has been slightly modified to make sections monophyletic. BRADFORD (1998) recognized five sections of *Weinmannia* that circumscribe species from the Americas plus two species from the Mascarenes (sect. *Weinmannia*), Malesia and Melanesia (sect. *Fasciculata* Bernardi), the South Pacific (sect. *Leiospermum* D. Don), and Madagascar and the Comores (sect. *Spicata* Bernardi and *Inspersa* Bernardi; see also HOPKINS 1998a). Taxonomic changes affect a few Malagasy species.

Malagasy *Weinmannia* species were last treated by BERNARDI (1964, 1965, 1969). He established two endemic sections *Spicata* and *Inspersa*, and placed a few species in the more widespread sections *Weinmannia* and *Leiospermum* (sect. *Leiospermum* has priority over BERNARDI's equivalent sect. *Racemosa*, see HOPKINS 1998a). However, BERNARDI's assignment of some Malagasy-Comoral species to sections normally found outside of Madagascar has been proven incorrect. *Weinmannia baehniiana* Bernardi and *W. comorensis* Tul., which BERNARDI placed in sect. *Leiospermum*, belong instead in sect. *Spicata*, and the species he included in sect. *Weinmannia*, *W. rutenbergii* Engl. and *W. venusta* Bernardi, belong in sect. *Inspersa* (see BRADFORD 1998 and below). Both a morphological cladistic analysis of *Weinmannia* species-groups and sections (BRADFORD 1998) and molecular systematic work on the genus (BRADFORD 2000; BRADFORD & BARNES 2001) support the monophyly of sections *Spicata* and *Inspersa* as now circumscribed and provide evidence that they are sister taxa.

As exemplified by the number of species found during field work at Marojejy (BRADFORD & MILLER 2001), Madagascar is one of the most species-dense areas in the world for *Weinmannia*, with levels of sympatry similar to that found in Andean forests. Unlike other parts of the world, however, the species richness of Malagasy *Weinmannia* is accompanied by a diversity of morphological characters that enable relatively rapid identification of species.

Study of available herbarium specimens and field work indicate that 35-40 *Weinmannia* species occur in Madagascar, 15-20 more than were known to BERNARDI (1965, 1969). Given the large number of undescribed species and the limited array of qualitative characters used by BERNARDI in his keys, it is difficult to identify *Weinmannia* species. The present paper addresses this problem by: (1) describing and illustrating previously overlooked qualitative character variation among Malagasy *Weinmannia*, (2) presenting a synoptic key to the sections and species-groups of *Weinmannia* in Madagascar and the Comores, (3) providing diagnostic features for each section and species-group, and (4) listing all presently described species in each species-group. Because a number of *Weinmannia* species remain to be described from Madagascar, it would be premature to write a key to the species level. Instead, the key given below aids species-level identification by reducing the number of species with which one must compare an unidentified specimen. This synoptic key has proven useful as the basis for a species-level key of *Weinmannia* from the Marojejy massif (BRADFORD & MILLER 2001), and could be applied to other regions and eventually the entire genus in Madagascar.

The key and diagnoses are largely based on a recent morphological cladistic study (BRADFORD 1998) that found several characters not discussed by BERNARDI (1964, 1965). In Madagascar, several groups of species can be recognized that share unique combinations of these qualitative characters. The key and diagnoses for the Malagasy species-groups utilize inflorescence terminology that may not be familiar. For this reason, figures, illustrations and a discussion of important characters precede the key.

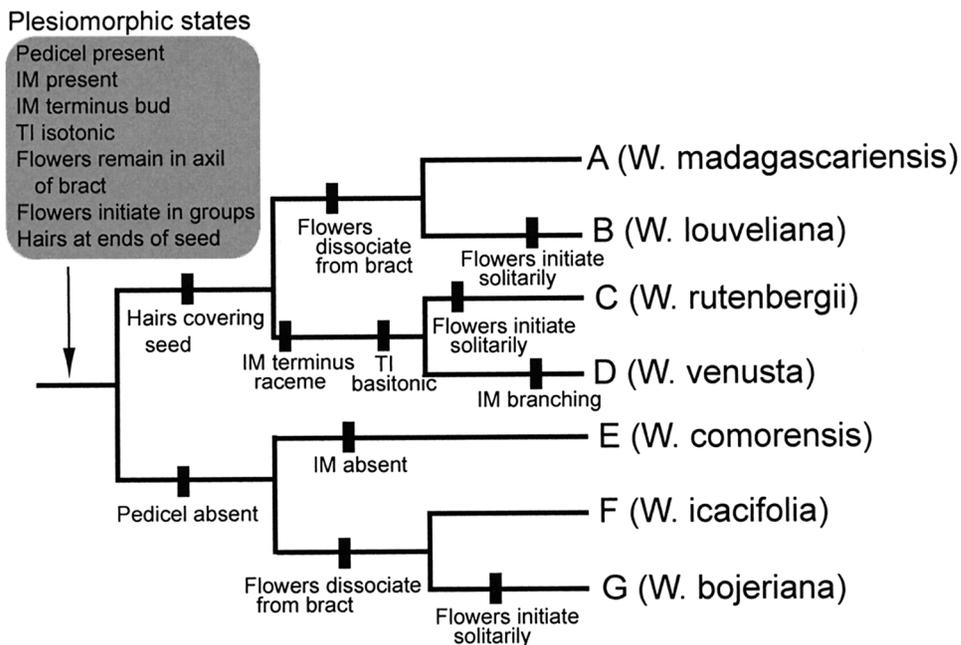


Fig. 1. — Cladogram of *Weinmannia* species-groups (with representative species) based on morphology (from BRADFORD 1998). The main characters used in the key are plotted on the tree.

FROM CLADOGRAMS TO KEYS

Prior to conducting a cladistic analysis of *Weinmannia* and the related genus *Cunonia*, specimens representing all known species of these genera were examined to find unique combinations of qualitative morphological characters among species (see vouchers in BRADFORD 1998). This process led to the recognition of species-groups, each representing from one to many species, that served as a terminal units in the cladistic analysis. Seven species-groups were recognized in Madagascar and the Comores, five of which have apparent autapomorphies, whereas two lack clearly apomorphic features (see character states in Fig. 1). Species-groups B, C, D, E, and G (see below) may therefore be monophyletic, whereas no characters have been found that support the monophyly of species-groups A and F.

Classifications communicate grouping information, but phylogenetic systematics also requires that formally recognized groups be

monophyletic. At present, not enough is known about the phyletic relationships of *Weinmannia* species-groups A-G to give them formal taxonomic names and rank, which would violate the principles of phylogenetic systematics and probably lead to taxonomic instability. Nevertheless, a real need exists to communicate group information on this complex genus, which can be done by informally recognizing species-groups A-G for the purpose of discussion. Such informal taxonomies have a long history (e.g. BENTHAM & HOOKER 1862-1883) and are commonly used in phylogenetic systematics when cladistic resolution is lacking or clades are poorly supported (e.g. Angiosperm Phylogeny Group 1998). By acknowledging uncertainty, informal classifications may actually communicate information more effectively than do some rigid systems that require all individuals to be part of a formal taxon at each hierarchical rank.

Cladograms can be applied towards taxonomic identification by including in a standard dichotomous key the qualitative characters of the data

matrix as plotted on a dichotomously branching tree. The key presented below is organized using character states as mapped on the cladogram from more general characters to more specific ones. In other words, synapomorphies of the largest clades are used in the first order couplet, followed by more exclusive synapomorphies in second order couplets, and terminating with apomorphic or diagnostic characters for a species-group (Fig. 1).

It may not always be practical to apply the characters used in a cladistic analysis to taxonomic keys if, for example, most of them are anatomical and therefore difficult to use with herbarium specimens or on material in the field. The case of *Weinmannia* provides a good example. The first couplets use inflorescence and pedicel characters that can readily be seen. Some couplets also emphasize structural features of the flower-bearing axis that can be used whether the material is in bud, flower or fruit. By contrast, the key in BERNARDI (1965) emphasizes the floral nectary, the pubescence of the ovary, and the distribution of trichomes on seeds.

This paper provides detailed illustrations and discussions of important features in Malagasy species of *Weinmannia*. BRADFORD (1998) may be referred to for a more general discussion of characters in the genus and cladistic methods used to study them. Figure 1 shows the inferred plesiomorphic and derived conditions for several qualitative traits that differ among Malagasy species-groups. Figures 2-4 illustrate and compare these characters (except for seed indumentum), which are discussed below.

INFLORESCENCE FEATURES

Architecture

Weinmannia inflorescences can be described at three architectural levels: the Total Inflorescence, the Inflorescence Module, and the Raceme (Fig. 2) (BRADFORD 1998). The term Raceme (with capital "R") is used generally to describe the unbranched, ultimate flower-bearing axes in *Weinmannia*, which have also been called pseudoracemes or spikes (BERNARDI 1964). Racemes are

often organized into compound structures borne on a peduncle, and these are called Inflorescence Modules (IMs). Among sections or species-groups, IMs may have distinct patterns of organization along the main stem. The Total Inflorescence (TI) is formed by the architectural arrangement of the IMs and Racemes (Fig. 2). Figure 2 does not show the full range of TI variation among Malagasy species, but is sufficient to diagnose species-groups.

Most of the species-groups in Madagascar (A, B, F, G; see below) have similar architectural features, in that IMs consist of a single metamer (i.e. an internode plus a node and associated organs) with an opposite pair of Racemes and a terminal vegetative bud. The number of IMs and their position may vary somewhat among species. For example, the TI may be reduced to a terminal IM or a pair of lateral IMs (Fig. 2).

Species-groups C and D can be recognized by a terminal Raceme in the IM, although they are variable and may have the more general IM form (i.e. that found in A, B, F, G). Even when the IMs are of the general form, members of groups C and D can often be recognized by a prolific TI, in which IMs occur at several subdistal nodes along the main stem. Prolific TIs are especially common in *W. rutenbergii*, which is indicated by the broken lines and arrow in Fig. 2. Species in group D have a branched IM, whereas branching is rare in group C. In both groups C and D, the TI is basitonic (i.e. IMs are larger at basal nodes and smaller at terminal nodes).

Group E is easily recognized by the absence of IMs. Racemes are borne from leaf axils along the main stem.

Flower-bearing axis

The two sections of *Weinmannia* in Madagascar can be distinguished by whether the flowers are subtended by a pedicel (sect. *Inspersa*) or are sessile along the Raceme (sect. *Spicata*). BERNARDI (1964, 1965) instead emphasized the form of the floral nectary to circumscribe sections, which is why he placed some Malagasy species in sections otherwise from the Malesian-Pacific region. However, nectary form is homo-

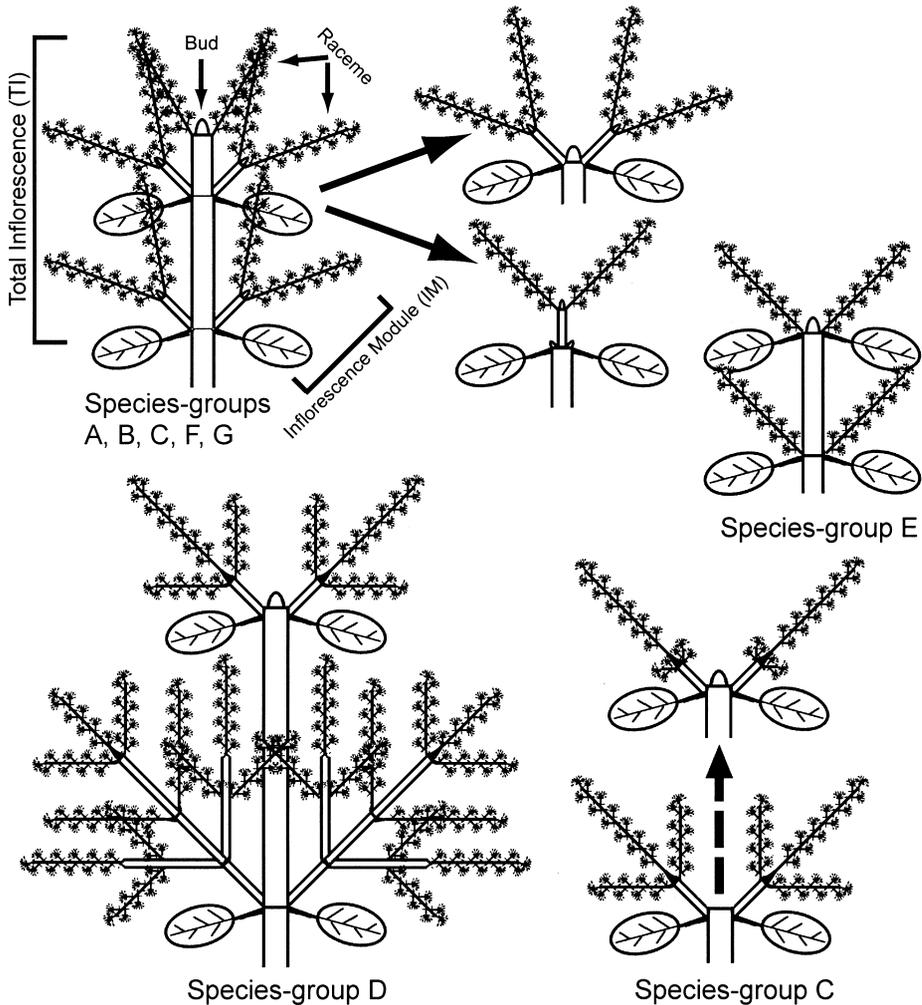


Fig. 2. — Inflorescence architecture among *Weinmannia* species-groups in Madagascar. See main text for the discussion of features and the list of species in each group.

plasia and varies within Malagasy sections (BRADFORD 1998), although it can be useful to diagnose Malagasy species-groups.

The organization of flowers along the Raceme varies in two important ways: (1) whether flowers are initiated solitarily or in a group, and (2) whether flowers remain near their point of initiation or dissociate from it. Characters of the Raceme are often easiest to see when flowers are in bud, or when mature flowers or fruits are removed to view clearly their positional relationships (Figs. 3, 4). Even when flowers initiated in

the axil of a bract dissociate during elongation of the flower-bearing axis, the relationship between a flower and its bract can usually be traced by a ridge or differently-colored linear zone between them. Flowers are often clustered in groups of four, and appear to develop from decussate pairs of buds (see Fig. 4, Group E). When floral groups dissociate during axis elongation, the pair of flowers perpendicular to the floral bract is spread apart more so than the pair of flowers borne in the same plane as the bract (see Fig. 4, Group F).

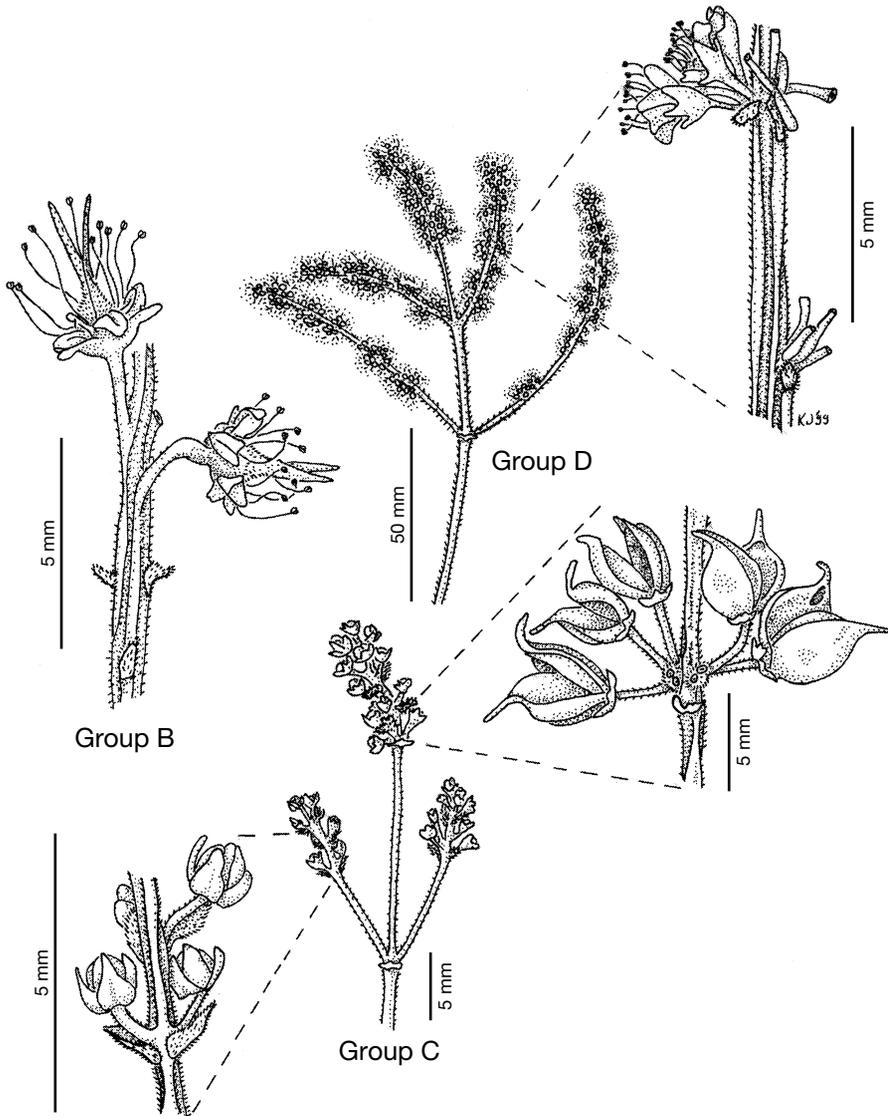


Fig. 3. — The relationship between flowers and floral bracts as illustrated for *Weinmannia* sect. *Inspersa* species-groups: **Group B:** *Weinmannia lowryana* with a single flower dissociating from a bract (Humbert 23057, MO 05006602); **Group C:** *Weinmannia rutenbergii* for portion shown in bud (Bradford 699, MO 05079575), and for portion in fruit, racemes often in threes, flowers mostly solitary and in the axil of a bract [shown in bud to left] or flowers grouped at the base of the medial raceme [shown in fruit on right] (Bradford 701, MO 05079557); **Group D:** *Weinmannia venusta*, with inflorescence modules usually branched (only one portion shown), and flowers grouped in the axil of a bract (Service Forestier (Capuron) 27632, MO 05006598). Some flowers have been removed to see pedicels clearly.

Bracts may fall at floral or fruit maturity, but because bract scars are shaped differently than floral scars the positional and numerical relationships between these structures remain clear. Floral

scars are round, with the vascular cylinder especially visible in species of sect. *Spicata*. Bract scars are more difficult to see, but they may be crescent-shaped, or small, irregular protrusions along

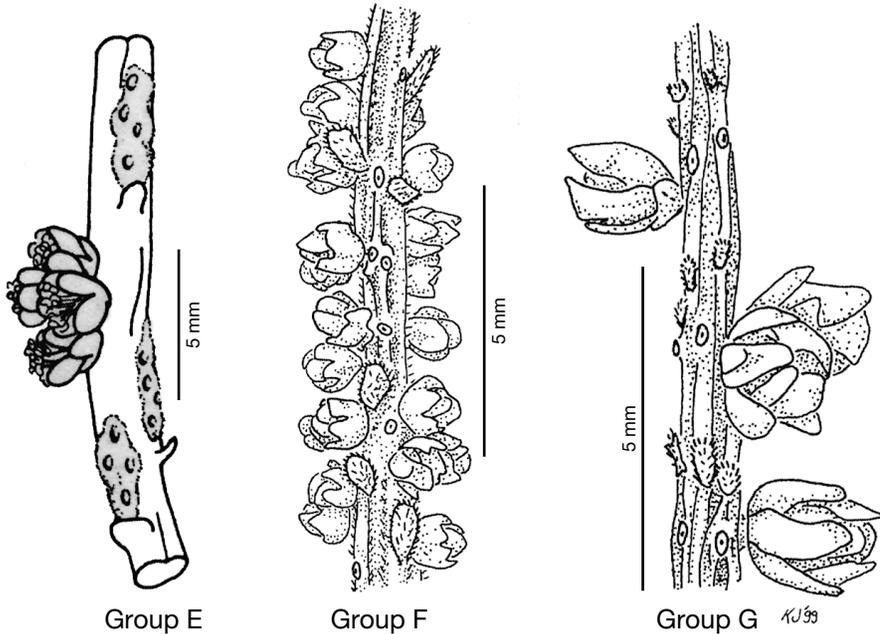


Fig. 4. — The relationship between flowers and floral bracts as illustrated for *Weinmannia* sect. *Spicata* species-groups. A central portion of a spike is shown: **Group E:** *Weinmannia lucens* (voucher unknown) with groups of flowers clustered near bract; **Group F:** *Weinmannia hildebrandii*, with groups of flowers dissociating from a bract (Service Forestier (Capuron) 24417, MO 05012268); **Group G:** *Weinmannia arguta*, with a single flower dissociated from a bract (Miller & Randrianasolo 4659, MO 3759761). Flowers removed to see positional relationships more clearly, leaving a circular scar with a point in the middle. (Illustration of *Weinmannia lucens* from BERNARDI 1965)

the Raceme. In sect. *Inspersa*, remaining bases of pedicels show the locations of flowers.

The structure of the central portion of the flower-bearing axis is most consistent and useful for identification. Often flowers will arise in clusters at the very base of a Raceme but will otherwise be solitary (e.g. Fig. 3, Group C illustration on right). Usually, the distal portion of a flower-bearing axis bears solitary flowers no matter what the rest of the axis is like.

One species, *W. rutenbergii* (Group C), may sometimes key out to species-group D because of variation in the number of flowers per bract (although the IM rarely branches in members of species-group C as it does in those of D, see Fig. 2). Often in *W. rutenbergii*, at the base of the terminal Raceme a large, stipular bract can be seen that subtends clusters of flowers (Figs. 2, 3). Between this cluster of flowers and other flowers on the axis a sterile gap can be observed.

Comparing the position of flower clusters in *W. rutenbergii* to that of lateral Racemes in a close relative, *W. venusta*, suggests that they are homologous. Flowers along other parts of the Raceme in *W. rutenbergii* are usually solitary, although pairs of flowers do occur sometimes in many specimens.

The key below includes six new species described and one new species-level combination made for *Weinmannia* from the Marojej massif (BRADFORD & MILLER 2001). These new taxa represent three of the seven species groups, with four of the novelties found in group G alone. Because group G is so species-rich in general, additional couplets are provided to subdivide it into more manageable groups, although these are not based on cladistic characters (Fig. 1). Authors of the recognized taxa are given below following the diagnoses of each species-group.

Key to sections and species-groups of Malagasy *Weinmannia*

1. Pedicels distinct, easily visible and slender; seeds with surfaces more or less evenly covered with trichomes 2, sect. **Inspersa**
- 1'. Pedicels lacking, very short, or thick as if an extension of the receptacle; seeds usually comose at ends only, sometimes more or less covered with trichomes throughout 5, sect. **Spicata**
2. Flowers positioned away from the floral bract at maturity; IMs equal in size; racemes borne in pairs from a short internode with a vegetative bud between them 3
- 2'. Flowers positioned in the axil of the floral bract at maturity; IMs larger basally; racemes borne in threes or at the ends of a decussate branching system with multiple internodes that usually terminate in a raceme, or racemes in pairs with a vegetative bud between them 4
3. Floral bracts subtending groups of flowers **species-group A**
- 3'. Floral bracts subtending solitary flowers **species-group B**
4. IM unbranched; floral bracts subtending solitary flowers or less often groups of flowers **species-group C**
- 4'. IM branched; floral bracts subtending groups of flowers **species-group D**
5. Spikes borne solitarily in leaf axils; floral nectary composed of more or less distinct segments; flowers distributed near each other and the floral bract, borne in clusters of usually four **species-group E**
- 5'. Spikes borne in pairs from a short internode in leaf axils or terminally; floral nectary usually an entire, membranous disc (rarely segmented); flowers not distributed in clusters, but spread in a line away from the floral bract 6
6. Floral bracts subtending multiple flowers; floral nectary sometimes easily broken into segments **species-group F**
- 6'. Floral bracts subtend a single flower; nectary usually entire and membranous **species-group G**

DESCRIPTION OF *WEINMANNIA* AND DIAGNOSTIC FEATURES OF MALAGASY CLADE, SECTIONS AND SPECIES-GROUPS

WEINMANNIA L.

Trees and shrubs, sometimes hemiepiphytic and strangling. Populations monoecious and flowers bisexual, dioecious or polygamodioecious. Leaves decussate in pairs or rarely whorls, imparipinnate or unifoliolate, rachis alate or not, leaf margins toothed or rarely mostly entire. Inflorescence racemose (including spikes and pseudoracemes); borne solitary in leaf axils or in compound units of various forms, compound units borne axillary or terminal. Flowers initiated solitarily or grouped in the axil of a small bract, remaining near bract or dissociating from it during elongation of the flower-bearing axis; pedicellate or sessile; bisexual or unisexual; perianth of sepals and petals, 4-5-merous, hypogynous or perigynous, imbricate, calyx lobes free or barely fused basally, petals persistent or caducous; floral nectary annular or segmented; androecium diplostemonous (rarely one whorl of stamens), filaments slender, equal to or exceeding petals, anthers dorsifixed, bithecal with an apical con-

nective, longitudinally dehiscent; ovary bicarpellate, carpels fused to the level of the styles, locules two, each with an axile placenta, ovules 2 to numerous in two rows per locule, styles slender and diverging, stigmas small and terminal. Fruits capsular, carpels diverging and opening along their ventral sutures; calyx persistent or caducous; placenta often remaining upright between separate carpels; endocarp and exocarp separating in old fruits or remaining adherent; seeds comose or trichomes more or less covering the surface, lacking wings.

MALAGASY CLADE OF *WEINMANNIA* (sections *Inspersa* and *Spicata*)

Flowers mostly pentamerous, hypogynous, bisexual, petals persistent, calyx persistent, endocarp and exocarp usually separating in old fruits.

Weinmannia sect. **Inspersa** Bernardi

Flowers pedicellate, floral nectary usually annular and ribbed; seed surface with dense indumentum throughout.

species-group A. — *Weinmannia henricorum* Bernardi, *W. madagascariensis* DC. ex Ser.

TI isotonic, IM terminating in a bud, flowers borne in clusters that dissociate from bract.

species-group B. — *Weinmannia commersonii* Bernardi, *W. loweliana* Bernardi, *W. lowryana* J.C. Bradford.

TI isotonic, IM terminates in a bud, flowers borne solitarily and dissociate from bract.

species-group C. — *Weinmannia hepaticarum* Bernardi, *W. rutenbergii* Engl.

TI basitonic, IM terminating in a raceme or a bud, IM sometimes branched, flowers borne solitarily or sometimes in small groups and remaining in axil of bract.

species-group D. — *Weinmannia venusta* Bernardi.

TI basitonic, IM terminating in a raceme or a bud, IM branched, flowers borne in groups and remaining in axil of bract.

Weinmannia sect. **Spicata** Bernardi

Flowers sessile; seeds comose, only rarely seed surface with indumentum throughout.

species-group E. — *Weinmannia lucens* Baker, *W. minutiflora* Baker, *W. comorensis* Tul., *W. baehniiana* Bernardi.

Spikes borne in leaf axils, flowers borne in clusters that remain in axil of bract, nectary composed of more or less distinct segments.

species-group F. — *Weinmannia hildebrandtii* Baill., *W. icacifolia* Bernardi, *W. marojejyensis* J.S. Mill. & J.C. Bradford, *W. rakotomalazana* J.C. Bradford.

Spikes borne in IMs, flowers initiated in groups that dissociate from bract, nectary annular and thin or composed of more or less distinct segments.

species-group G. — Species are listed within the key given below. Spikes borne in IMs, flowers borne solitarily and usually dissociate from axil of bract, nectary usually annular and thin.

- | | |
|---|---|
| 1. Leaves unifoliolate | 2 |
| 1'. Leaves imparipinnate | 3 |
| 2. Ovaries glabrous | <i>W. humbertiana</i> Bernardi |
| 2'. Ovaries pubescent | <i>W. bojeriana</i> Tul., <i>W. mammea</i> Bernardi, <i>W. pauciflora</i> , J.C. Bradford, <i>W. integrifolia</i> J.C. Bradford |
| 3. Ovaries glabrous | <i>W. decora</i> Tul. |
| 3'. Ovaries pubescent | 4 |
| 4. Hairs on seeds restricted to ends | <i>W. humblottii</i> Baill.,
..... <i>W. sanguisugarum</i> Bernardi, <i>W. arguta</i> (Bernardi) J.C. Bradford, <i>W. venosa</i> J.C. Bradford |
| 4'. Hairs on seeds widely distributed | <i>W. eriocarpa</i> Tul., <i>W. stenostachya</i> Baker |

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