
A CLADISTIC ANALYSIS OF
SPECIES GROUPS IN
WEINMANNIA
(CUNONIACEAE) BASED ON
MORPHOLOGY AND
INFLORESCENCE
ARCHITECTURE¹

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ABSTRACT

Weinmannia (Cunoniaceae) is a woody genus of about 150 species widely distributed in the tropics and the southern temperate zone. Herbarium and living specimens were examined to determine characters for a cladistic analysis to test the monophyly of the genus and its sections. A matrix of 28 taxa and 31 morphological characters was analyzed to find the most parsimonious trees. The strict consensus cladogram supports the monophyly of the genus *Weinmannia* and sections *Leiospermum*, *Weinmannia* (including sect. *Simplicifolia*), *Inspersa*, and *Spicata*, but section *Fasciculata* is paraphyletic with respect to a highly derived section *Weinmannia*. Section *Leiospermum* from the South Pacific is the sister taxon to the rest of the genus. Some of the most parsimonious trees support a monophyletic clade from Madagascar of sections *Inspersa* and *Spicata*, but this node is unresolved in the strict consensus tree. Although the deep nodes of the phylogeny are not well supported, and few evolutionary interpretations are ventured, it appears that dioecy has arisen independently at least three times in the genus. The method and theory used to analyze variation in inflorescence architecture, which emerges from the metameric construction of plants and positional homology, are emphasized. The cladistic coding of positional characters and the tracing of their evolution on the cladogram are a study in heterotopy, i.e., evolutionary change in the position of development. Heterotopic evolution in the inflorescence is common in *Weinmannia*, suggesting a role for an evolutionary-developmental process that has typically been overlooked in favor of heterochrony.

SYSTEMATIC BACKGROUND

Weinmannia is a genus of canopy trees and shrubs common to montane tropical and southern temperate floras. With approximately 150 species, it is the largest genus in the Cunoniaceae, a morphologically diverse family that includes 27 genera and ca. 370 species. The family has been considered a distinct, isolated lineage within the Rosidae (Dickison & Rutishauser, 1990) that is morphologically recognized by its woody habit, usually interpetiolar stipules, toothed leaves, and decussate leaf arrangement (Hufford & Dickison, 1992). A cladistic analysis using morphological and anatomical characters (Hufford & Dickison, 1992) supports the monophyly of the Cunoniaceae only when a few

genera that have been treated as separate but related families are included (*Bauera*, *Brunellia*, *Eucryphia*). However, Orozco (1997) advocated splitting the family to exclude *Brunellia* and its putative Cunoniaceae relatives. *Davidsonia* may also belong in a monophyletic Cunoniaceae (Doweld, 1998). Hufford and Dickison's (1992) consensus cladogram placed *Weinmannia* in a small clade with *Cunonia* and *Pancheria*, which was nested among a large, monophyletic group of genera characterized by the presence of a styler canal and a fused, bicarpellate ovary.

The Cunoniaceae are austral in distribution: 15 of the genera occur in Australia and Tasmania, 9 in New Guinea, 11 in the South Pacific, and

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only 5 (3 endemic) in South America. Like the Cunoniaceae in general, the present-day distribution of *Weinmannia* suggests a Gondwanaland origin (Raven & Axelrod, 1974). *Weinmannia* is widespread relative to other genera in the family, and its distribution includes the following geographic regions: Central and South America and the Caribbean islands; Madagascar, the Comores, and the Mascarenes; Malesia (the Malay Peninsula, Greater and Lesser Sundas, the Philippines, Celebes, Moluccas, New Guinea, and the Bismarck Archipelago); and the South Pacific high-elevation islands, from the Solomons and Vanuatu in the west to the Societies and Marquesas in the east, including New Caledonia and New Zealand. About half of the species occur in tropical America, a quarter are concentrated in Madagascar, and another quarter are distributed in the vast Malesian-Pacific region.

Sympatric species of *Weinmannia* are common in middle- to upper-elevation montane forests of the Andes and Madagascar (Humbert & Darne, 1965; Rios, 1986; Kelly et al., 1994; Gentry, 1995). Species can have radically distinct life forms that correspond to local habitats. For example, at upper elevations, especially in exposed, windswept conditions, *Weinmannia* species are typically small, sometimes prostrate shrubs, whereas in eastern Madagascar some species are among the largest trees in the lowlands. *Weinmannia* is not as locally species-rich in Malesia and the Pacific, but species are often locally abundant in this region, especially in the Society Islands (Florence, 1982; Fosberg, 1992) and New Zealand (Wardle & MacRae, 1966). The genus typically has small, fragrant flowers that attract bees (Renner, 1989; Bradford, pers. obs.), and small, hairy seeds easily dispersed by wind (J. Bradford & H. C. F. Hopkins, pers. obs.).

Engler's (1928) revision of *Weinmannia* divided the genus into two sections, section *Leiospermum* and section *Euweinmannia*, based upon variation in the persistence of the calyx in fruit. Bernardi (1961, 1963b, 1964) incorporated variation in the form of the floral nectary, raceme structure, and leaf complexity to recognize six sections: section *Racemosa*, which corresponds to Engler's section *Leiospermum* and has caducous sepals, and five other sections corresponding to Engler's section *Euweinmannia*. [*Euweinmannia* is an illegal name (see Greuter et al., 1994, Article 21.3) and is no longer used.] In general, the classification of Bernardi is followed, although it is recognized that Engler's section *Leiospermum* has priority over Bernardi's section *Racemosa*. Also, Bernardi's section *Simplicifoliae* has been sunk into section *Weinmannia*. Section *Simplicifoliae* separates species with

Table 1. A comparison of previous sectional classifications of *Weinmannia* vs. the one used here.

Bradford (present paper)	Bernardi (1961, 1963b, 1964)	Engler (1928)
<i>Leiospermum</i>	<i>Racemosae</i>	<i>Leiospermum</i>
<i>Weinmannia</i>	<i>Weinmanniae</i>	<i>Euweinmannia</i>
<i>Weinmannia</i>	<i>Simplicifoliae</i>	<i>Euweinmannia</i>
<i>Fasciculata</i>	<i>Fasciculatae</i>	<i>Euweinmannia</i>
<i>Spicata</i>	<i>Spicatae</i>	<i>Euweinmannia</i>
<i>Inspersa</i>	<i>Inspersae</i>	<i>Euweinmannia</i>

simple leaves from the compound-leaved species in section *Weinmannia* and appears to have been erected by Bernardi for taxonomic convenience. However, the number of leaflets often varies within individuals, is extremely homoplastic among species, and, therefore, has little taxonomic value at the sectional level. Previous and current classifications are compared in Table 1.

PURPOSE

Recent systematic studies of *Weinmannia* have identified more characters than were used by Bernardi (1961, 1963b, 1964) to circumscribe sections. Many new characters, especially from inflorescence architecture, are described here. Thirty-one qualitative characters are used in a cladistic analysis to resolve these systematic questions: (1) Is *Weinmannia* monophyletic? (2) Are the sections monophyletic? (3) How are sections related to each other? and (4) What morphological character states support what clade?

Answers to these questions may help interpret biogeographic and character-distribution patterns. For example, a dioecious to polygamodioecious breeding system is nearly ubiquitous in the Malesian section *Fasciculata*, among most species of the South Pacific section *Leiospermum*, and in the Mascarene island species of section *Weinmannia*. An understanding of whether dioecy is derived or basal within the genus and the number of times it has evolved depends upon the relationships inferred among taxa. Because most sectional delimitations are congruent with particular geographic regions (e.g., sects. *Inspersa* and *Spicata* are endemic to Madagascar and the Comores), the cladistic relationships among species groups of *Weinmannia* may inform us about area relationships among southern continents.

To understand the cladistic coding and the evolution of the inflorescence in *Weinmannia*, it is necessary to describe inflorescence characters in detail, and to discuss the methods and theory behind

determinations of homology. Three points are emphasized: (1) the inflorescence is formed by the spatial arrangement of nested sets of parts, (2) the coding of inflorescence characters usually requires an assessment of positional homology (at least for this study), and (3) evolutionary change in the position of inflorescence units is a form of heterotopy.

OVERVIEW OF INFLORESCENCE ARCHITECTURE IN *WEINMANNIA*

An attempt to apply general inflorescence terminology, such as that of Briggs and Johnson (1979) and Weberling (1989), was not satisfactory. Structural definitions only approximate many inflorescence features of *Weinmannia*, or terms cannot be applied consistently among species. In a later section, I discuss why standard terminology does not work in *Weinmannia*, especially when the goal is identifying cladistic characters. But first, the terminology used here to describe *Weinmannia* inflorescences is introduced.

Following the system of Briggs and Johnson (1979), flower-bearing axes in *Weinmannia* and *Cunonia* can precisely be called "anauxotelic botrya," which includes forms of "spikes" and "pseudoracemes." To avoid these cumbersome terms in all subsequent discussion, the term "raceme" is used broadly to include any unbranched, flower-bearing axis. The terms Inflorescence Module (IM) and Total Inflorescence (TI) will refer to two other distinct levels of organization. Architectural variation in the *Weinmannia* inflorescence occurs at up to three hierarchical levels: (1) the organization of flowers along a "raceme," (2) the development of racemes in conjunction with supporting stems and buds (IM), and (3) the position these raceme-stem units occupy in relation to the main stem axis (TI).

Flowers vary in their organization along the raceme in two ways: (1) how they are initiated and (2) whether their relative positions change during axis elongation (Fig. 1). Flowers are initiated solitarily or grouped, in the axil of a bract. During elongation of the raceme axis, flowers may remain in the axil of the bract or move away from it and each other. Differences in the positional relationships among flowers give distinct forms to the raceme.

In most sections, racemes usually develop as parts of developmentally integrated units (modules) composed of internodes, nodes, meristems, and racemes. Within a species-group, raceme-stem units are organized predictably and may be repeated along the main stem axis in predictable patterns (Fig. 2). Each of these raceme-stem units will be

referred to as an Inflorescence Module (IM). The term "module" has had more or less precise usage (see White, 1979; Grimes, 1992; Barlow, 1994). Here it refers to a particular level of organization, or integration of a group of metamers, to form a natural structural unit (Wagner, 1996). Of course higher and lower levels of organization, such as the raceme, are modules, but may already have useful names. The IM is at an intermediate level of organization, above the raceme but below the entire inflorescence. Within a locally dominant stem system, the structure of the racemes, the organization of racemes into an IM, and the arrangement of IMs along the main axis constitute the Total Inflorescence (TI).

DESCRIPTION OF INFLORESCENCE ARCHITECTURES IN *WEINMANNIA*

Inflorescence architecture is taxonomically informative and may help identify an entire section, or a portion of a section, or distinguish a single species from other members of its section. Variation occurs in: (1) whether racemes develop as part of an IM or directly along the main stem axis, (2) the form of the IM, (3) the number of main stem metamers that bear racemes or IMs, and (4) the position of IMs relative to the main stem axis. There are 17 terminal taxa of *Weinmannia* in the data matrix (Appendix 4). When variation within the raceme (i.e., that shown in Fig. 1) is ignored, there are about 11 distinct inflorescence architectures among taxa, which are described below.

(A) Twelve of 18 species in section *Fasciculata* have supernumerary lateral buds that develop into lateral IMs in series at a node (e.g., *W. fraxinea*). These IMs each consist of one metamer with an opposite pair of racemes and a vegetative bud between them. The apical meristem of the main stem axis usually remains vegetative, although vegetative growth is usually suspended during reproduction. The TI is acrotonic in that the distal node of the TI usually has more IMs per series than occur at subdistal nodes (Fig. 3a).

(B) Most other members of section *Fasciculata* have similar IM morphology, but do not develop IMs in a series at a node. Also, while it is rare for IMs to form in medial positions in the *W. fraxinea* group, this is common in some other species in the section (Fig. 2b).

(C) *Weinmannia descombesiana* has a highly variable inflorescence architecture that may appear most similar to that of the *W. fraxinea* group (Fig. 3a) or other members of section *Fasciculata* (Fig. 2b).

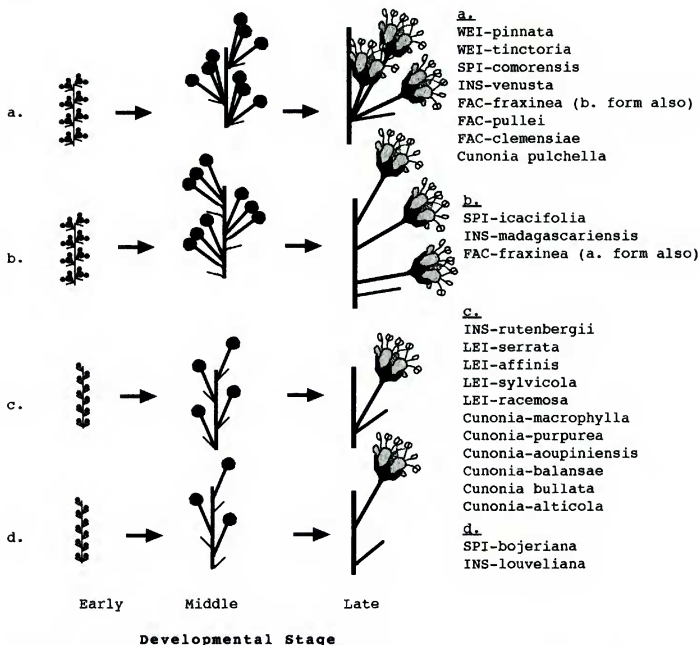


Figure 1. The distribution of flowers along a "raceme" is determined by the number of flowers initiated in the axil of a bract and whether the flowers remain in the axil as the axis elongates: —a. Fasciculate inception + bract fidelity. —b. Fasciculate inception + floral migration. —c. Solitary inception + bract fidelity. —d. Solitary inception + floral migration. Parts not necessarily to scale and only a portion of the axis is shown. The adjoining table lists each *Weinmannia* and *Cunonia* OTU in the cladistic analysis with its raceme form. Flowers are sessile in section *Spicata* (SPI). See discussion of characters 19 and 20 (Appendix 3) and the character matrix (Appendix 4).

(D) Nearly half the species in the genus are in section *Weinmannia*, which can be recognized by its unique inflorescences. In this section, the inflorescence is limited to a pair of racemes developing from axillary buds at the most distal node of the main stem (Fig. 2c). There is no IM in this group and much variation in the suppression of leaf development at the node bearing the racemes. Within individual plants leaves may be fully developed at the raceme-bearing node or extremely reduced.

(E) About 20 species in section *Leiospermum* have a characteristic inflorescence in which the apical meristem within an IM either develops into a raceme or aborts. In many species this is fixed one way or the other [e.g., the bud almost always

aborts in *W. dichotoma* (Fig. 3b)], but in several species this character varies within individual plants. Also typical of this section is that the IM may consist of sequentially arranged metamers with long internodes. The position of the IMs along the main stem is both lateral and terminal. The TI is acrotomic, with the terminal IM often developing more metamers than the laterals (Fig. 2a). Leaf development is suppressed within the IM, but generally less so at nodes proximal to the main stem when the IM consists of sequential metamers.

(F) Two species endemic to New Zealand have distinctive inflorescences. *Weinmannia sylvicola* is similar to *W. dichotoma* in that the IMs terminate with an aborted meristem, but differs in that the

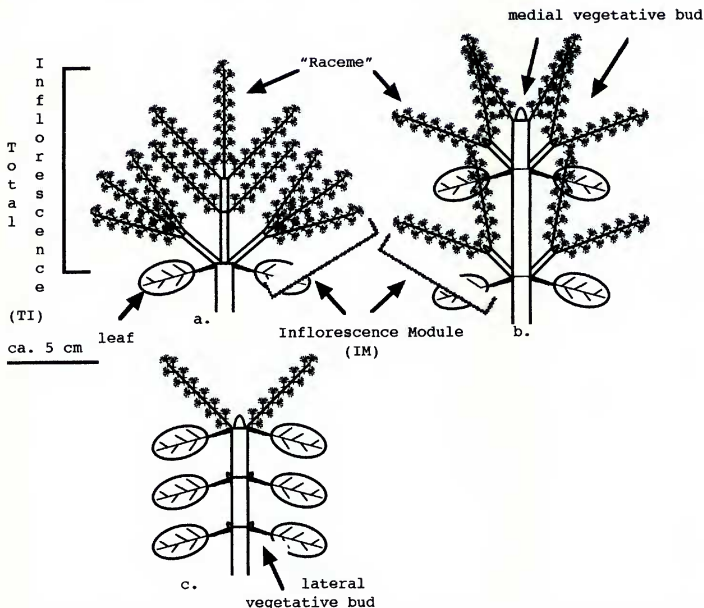


Figure 2. Diagram of inflorescence terms and examples of inflorescence architecture in *Weinmannia*. —a. Section *Leiospermum*, with IMs potentially consisting of sequential metamers, terminating with a raceme, and positioned laterally and medially. —b. Parts of sections *Inspersa*, *Spicata*, and *Fasciculata*, with IMs of one metamer, terminating with a vegetative bud, and borne medially and laterally at distal and subdistal nodes. —c. Section *Weinmannia*, with racemes borne laterally at vegetative nodes. See text for more complete descriptions of architectural variation within species groups, as not all patterns are shown. Actual leaves may be simple or compound. Although the figures are in two dimensions, the actual arrangement is decussate.

medial IM often produces two metamers. Also, there is usually only one lateral IM (Fig. 3c).

(G) The other New Zealand species, *Weinmannia racemosa*, is unique within section *Leiospermum* in that the IM does not terminate in a raceme or abort, but produces a vegetative bud (Fig. 9b). This is the only species within the section in which vegetative growth continues beyond the inflorescence. Furthermore, the IM is only borne in a medial position. A more detailed discussion of the inflorescence in sections *Fasciculata* and *Leiospermum* is given in Hopkins and Bradford (in Hopkins, 1998a).

(H) Most species in the two Madagascan sections, *Inspersa* and *Spicata*, have similar inflorescences. About 22 species in section *Spicata* and 5 species in section *Inspersa* have IMs consisting of

one metamer with an opposite pair of racemes and a vegetative bud between them. These IMs may be positioned laterally at both distal and subdistal nodes along the main stem, as well as medially at the distal node. Racemes can also develop directly from axillary buds, but only at the most distal node of the TI (Fig. 2b).

(I) Five species in section *Spicata* (two of which, *W. comorensis* and *W. baehniiana*, were placed in sect. *Leiospermum* by Bernardi, 1964) develop racemes from axillary buds along the main stem at sequential nodes (Fig. 3d).

(J) *Weinmannia rutenbergii* (not illustrated) in section *Inspersa* has extremely plastic inflorescence development. IMs may be of one or more metamers, sometimes branched but usually not, and may ter-

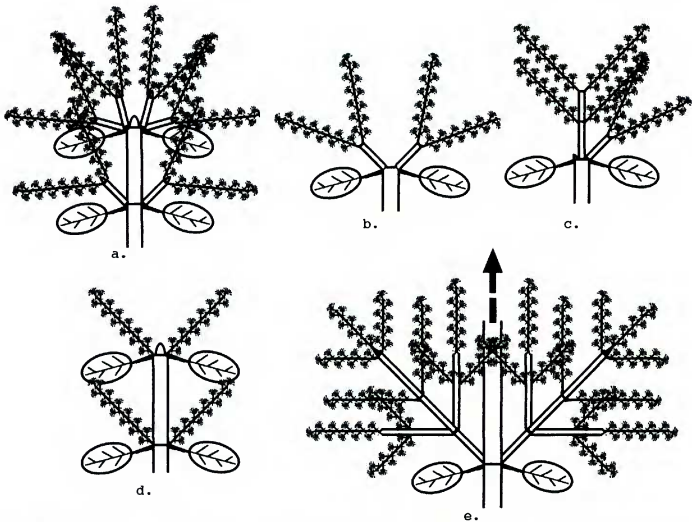


Figure 3. Examples of inflorescence architecture among *Weinmannia* species groups. —a. *W. fraxinea* (sect. *Fasciculata*). —b. *W. dichotoma* (sect. *Leiospermum*). —c. *W. sylvicola* (sect. *Leiospermum*). —d. *W. comorensis* (sect. *Spicata*). —e. *W. venusta* (sect. *Inpersa*). Note that b and c have aborted terminal meristems in the IM. See text for full descriptions.

minate in a bud or a raceme. When reproduction is prolific, IMs develop at several nodes and may vary in form within a TI. In general, larger IMs develop from lower nodes. *Weinmannia hepaticarum*, known only from the type collection, appears to be closely related to *W. rutenbergii*, but its inflorescence variability is unknown. Bernardi (1964, 1965) placed *W. rutenbergii* in section *Weinmannia*.

(K) Two species in section *Inpersa*, *W. venusta* and *W. sp. nov. I*, have branched IMs that bear racemes. The length of these racemes is variable within an IM. The IM may terminate either in a raceme or in a vegetative bud. The position of IMs along the main stem may be lateral and medial. The TI is basitonic, with the largest IMs developing at lower nodes (one of the variants is shown in Fig. 3e and includes only a subdistal node of the TI). Bernardi (1964, 1965) placed *W. venusta* in section *Weinmannia*.

Most species in the closely related genus *Cunonia* have an inflorescence architecture similar to that depicted in Figure 9c, but often with IMs at two successive nodes of the TI. However, several

species diverge from this pattern (see illustrations in Hoogland et al., 1997, and coding in character matrix, Appendix 4).

The photos in Plate 1 show some common forms of the inflorescence among *Weinmannia* sections. Additional color plates will be available from the World Wide Web by searching the species name in W/TROPICOS at <http://www.mobot.org>.

THE USE OF INFLORESCENCE ARCHITECTURE IN CLADISTICS

The hierarchy of inflorescence architecture and its systematic importance have been recognized in diverse groups (Venkata Rao, 1965; Mabberley, 1975; Weberling, 1977; Briggs & Johnson, 1979; Kaul & Abbe, 1984; Tucker, 1987; Weber, 1988; Weberling, 1988; Schlessman et al., 1990; Grimes, 1992; Liede & Weberling, 1995; Tortosa et al., 1996; Timonen, 1998). While many studies have proposed pathways of inflorescence evolution based on comparative morphology and development, few have used cladistic methodology to do so.

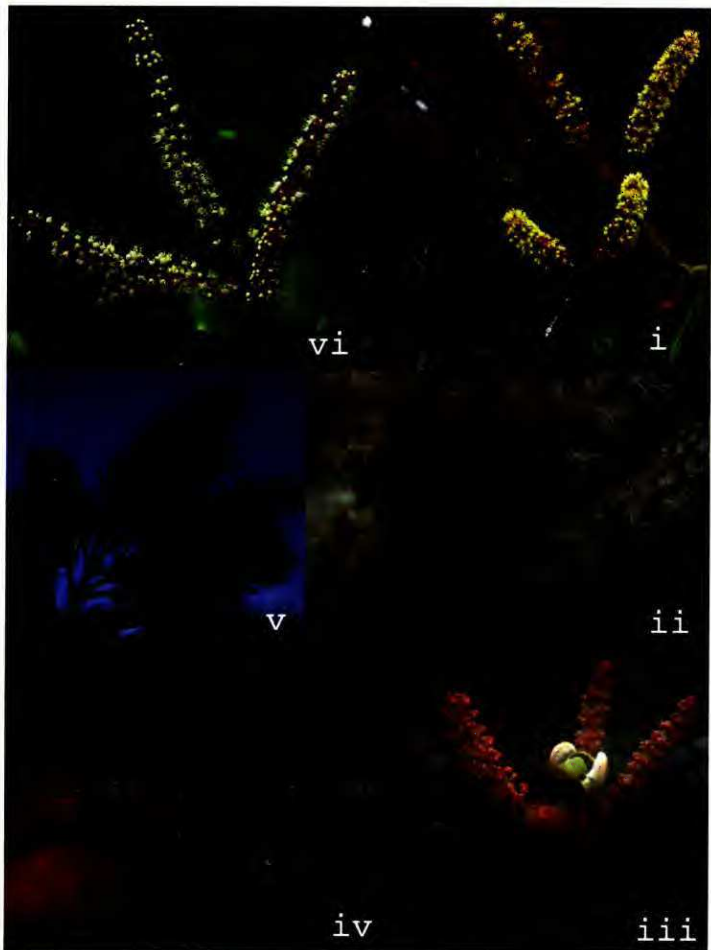


Plate 1. Photos documenting *Weinmannia* inflorescence architecture illustrated in Figures 2, 3, and 9. —i. Section *Weinmannia*; *W. dryadifolia* (J. C. Bradford 160); compare with Figure 2c. ii, iii, Section *Fasciculata*. —ii. *W. fraxinea* (J. C. Bradford 830); compare with Figure 3a. —iii. *W. clemensiae* (H. F. Hopkins 5011); compare with Figure 9c. —iv. Section *Spicata*; *W. stenostachya* (J. C. Bradford 650); compare with Figure 2b. v, vi, Section *Leiospermum*. —v. *W. sylvicola* (J. C. Bradford 732); compare with Figure 3c. —vi. *W. parviflora* (J. C. Bradford 919); compare with Figure 9a.

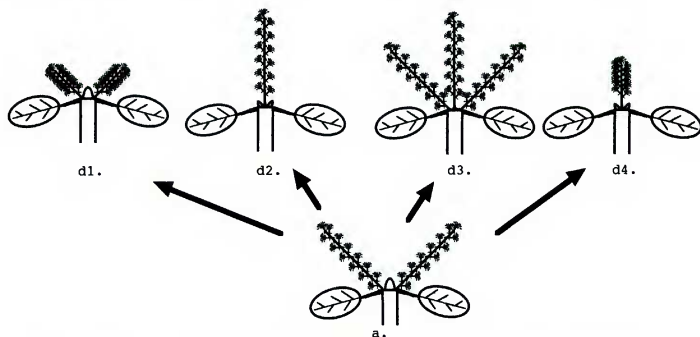


Figure 4. Morphological evolution occurs through temporal and spatial modification of development. As shown here, the ancestor (a) has racemes developing from the leaf axils. The descendants (d1–d4) are heterochronic, heterotopic, or both. —d1. Heterochronic, paedomorphic form in which the raceme axes are constricted. —d2. Heterotopic form in which the racemes develop from the terminal bud and not the axillary ones. —d3. Heterotopic form in which the racemes develop in their plesiomorphic, axillary position, and from a new position, at the terminus. —d4. Heterochronic and heterotopic form. Heterotopy is recognized by changes in the relative position of parts (d2, d3), not just quantitative shifts that are probably heterochronic (d1).

Although inflorescence architecture is diverse in many taxa, cladists may have avoided inflorescence characters because of difficulties in assessing homology. Progress came when Grimes (1992) analyzed the inflorescence of the *Pithecellobium*-complex by breaking it into nested, repeated units. Similarly, *Weinmannia* inflorescences have nested components and, in order to identify cladistic characters, the relative positions of parts within each component can be compared. Recognizing positional homologies is the key to coding inflorescence characters. As a consequence of recognizing positional homologies, evolutionary changes in the positions at which parts develop, i.e., heterotopy (Haeckel, 1905; Gould, 1977; Sattler, 1988), can be inferred by tracing character transformations on the phylogeny. Therefore, this work advances a view of evolutionary development that recognizes both temporal and spatial transformation (see also Zelditch & Fink, 1996).

HETEROTOPY: DOES IT HAPPEN?

While it is well accepted that heterochrony causes the modification of form (Jong & Burt, 1975; Gould, 1977; Raff & Wray, 1989; Kellogg, 1990; Boughton et al., 1991; McKinney & McNamara, 1991), positional changes in development have often been either ignored or considered byproducts of underlying heterochrony (see discussions in Raff,

1996; Zelditch & Fink, 1996). Heterotopic patterns are recognized by qualitative shifts in the positional relationships among parts, not just quantitative changes in relative distances among parts, which may often be due to heterochrony (Fig. 4).

For example, reproductive structures can shift from lateral to terminal positions, or from distal branches to the trunk. A possible outcome may be the evolution of monocarpy from polycarpy, or changes in how flowers are pollinated and fruit is dispersed. Distinct inflorescence modules that develop either male or female flowers are common in monoecious breeding systems [e.g., pistillate vs. staminate spikes in *Quercus* (Kaul & Abbe, 1984), and in corn]. Once male and female modules are established, they can be expressed at separate positions within the plant, which may have functional benefits.

Even though heterotopy has been mostly overlooked by evolutionary biologists, some obvious (and bizarre) examples of morphological changes in plants appear to be purely heterotopic. These include: the switch in position of leaves and lateral buds in *Utricularia* (Sattler, 1994); the positional reversal of stamens and carpels in *Lacandonia schismatica* (Martínez & Ramos, 1989); and epiphyllous inflorescences (Dickinson & Sattler, 1974, 1975).

Plant morphologists have long accepted that spa-

tial and temporal changes in development contribute to morphological evolution. For example, heterotopy has also been called "translocation" (Leavitt, 1905) and "phylogenetic shifting" (including homeosis, Zimmermann, 1961). In discussing the "morphogenetic" basis of plant form, Sachs (1982) suggested that mutations affecting gene regulation could change the spatial and temporal expression of developmental processes to account for morphological evolution. This notion is supported by developmental-genetic studies that show how sets of genes, especially ones encoding transcription factors (Sommer et al., 1990; Yanofsky et al., 1990), act to establish the position in which an organ will form (Bradley et al., 1997; Meyerowitz, 1997). Sattler (1988) discussed how both heterochrony and heterotopy are related to homeosis. The potential for heterotopy is also embodied in Sattler's term "homotopy," referring to homology of position (Sattler, 1994).

Taken together, the data from systematists, plant morphologists, and plant molecular biologists show that heterotopy is widespread among plants. This provides the conceptual and empirical framework on which positional homologies of inflorescence architecture are here coded.

MATERIALS AND METHODS

SAMPLING METHODS

Except for recent work by H. C. F. Hopkins (1998a-c; Hopkins & Florence, 1998) in the Malesian-Pacific region, *Weinmannia* has not been revised at the species-level since Bernardi (1961, 1963b, 1964, 1965). Numerous recent collections show that many currently recognized taxa are poorly circumscribed. Sampling of specimens was done to cover the distribution of phylogenetically informative characters independently of previous species circumscriptions or determinations. For this reason, some taxa recognized as varieties of the same species by previous authors are members of different terminal taxa in this analysis. Because there will be changes in nomenclature and new species descriptions, both specific names and a set of specimens examined are listed in Appendix 1.

My goal was to examine at least one specimen of each species of *Weinmannia*. The lack of a recent treatment of Malagasy and American species made sampling more uncertain in these areas. Data come from field studies in tropical America, Madagascar, Malaysia, and the South Pacific, and examination of herbarium specimens primarily at the Laboratoire de Phanérogamie in Paris (P) and the Missouri Botanical Garden (MO). Type material was avail-

able for nearly all species from Madagascar and the Malesian-Pacific region. Several American species are known only from type specimens that were not available, but most of the characters used in this analysis were at least seen in illustrations or photos. Furthermore, the Neotropics are well represented by recent collections at MO and F, and I have collected extensively in the region. Species sampling of *Cunonia* relied on the taxonomy of R. Hoogland and his unpublished monograph of the genus at P. This study has revealed several undescribed species, each of which can be placed in an Operational Taxonomic Unit (OTU) with at least one described species.

Many inflorescence characters are coded based on developmental potential, which is fixed in some taxa but variable in others (e.g., see discussion of character 23, Appendix 3; description of *W. rutenbergii*, inflorescence J). To accurately code these taxa, groups with greater complexity and variety of inflorescence architecture, such as section *Leiospermum*, were sampled more intensively than those with less, such as section *Weinmannia*. Poorly represented species that are not known for all of their characteristics (e.g., of which fruits have never been collected) could be provisionally placed into an OTU, since an intact inflorescence with either flowers or fruits is sufficient to discriminate among the OTUs.

The observed morphological characteristics of hundreds of specimens were managed in two ways. Sketches and notes of specimens were made, and descriptive information on specimens was entered into a computerized database. The database fields were used to search for unique combinations of character states among species, and characters were reconfirmed by checking sketches and by repeated specimen examination. The OTUs in the cladistic analysis were circumscribed according to the possession of unique combinations of character states for the current character matrix. If an OTU was polymorphic for a character, it was due to polymorphism within some species of that OTU.

Identifying OTUs by unique combinations of characters could yield paraphyletic OTUs. Therefore, each ingroup OTU was studied for potential autapomorphies, which are listed in Appendix 2. Most OTUs were arguably monophyletic, but a few were not. A separate cladistic analysis was run that removed the following OTUs to see if their absence affected the tree topology: FAC-descombesiana (possible hybrid taxon), FAC-clemensiae, SPI-icafolia, INS-madagascariensis, LEI-serrata, Cunonia-purpurea.

CHOICE OF OUTGROUPS

The character matrix and cladograms of Hufford and Dickison (1992) were used to choose outgroups. All outgroups were part of the large clade that includes *Weinmannia*. Two of them, *Caldcluvia paniculata* and *Spiraeopsis celebica*, were considered useful because they apparently lack many derived floral, inflorescence, or fruit characters that would make comparison with *Weinmannia* difficult. Within the Cunoniaceae, *Spiraeopsis* (with 6 species) has the autapomorphy of stellate pubescence on the leaves, but no obvious autapomorphies exist for the monotypic *Caldcluvia* s. str. (Hufford & Dickison, 1992). Within this data set, *Caldcluvia paniculata* is unique in possessing four stipules per node, as opposed to two stipules per node in other taxa (Dickison & Rutishauser, 1990).

In Hufford and Dickison's (1992) analysis, the position of the monotypic *Vesselowskyia* was poorly resolved, but in some trees this was the sister taxon of the *Cunonia*(*Pancheria*–*Weinmannia*) clade and, therefore, was included here. However, their matrix had some incorrect scoring of characters in *Vesselowskyia*, which has palmately compound leaves, flowers borne in racemes, and valvate sepals. These traits suggest a close relationship between *Vesselowskyia* and the *Lamanonia*/*Geissois*–*Pseudoweinmannia* clade, rather than the *Cunonia*(*Pancheria*–*Weinmannia*) clade. The *Lamanonia*/*Geissois*–*Pseudoweinmannia* clade has two features shared with *Cunonia* and *Weinmannia*: a racemose floral axis and a fused vascular bundle between the fruit carpels, the latter not included by Hufford and Dickison (1992). Possible autapomorphies for *Vesselowskyia* are its 3-merous perianth and androecium, and its decurrent stigmas.

Ackama rosifolia was examined because this genus (with 3 species) is the only one in the Cunoniaceae other than *Weinmannia* with hairy seeds. However, for these hairs to be homologous with those of *Weinmannia* would require that *Ackama* be the sister taxon to *Weinmannia*, adding five steps to the shortest trees of Hufford and Dickison (1992). In fact, *Ackama* shares some possibly derived leaf trichome and domatium features with *Spiraeopsis*.

The monophyly of *Weinmannia* with respect to *Cunonia* was tested by treating *Cunonia* as part of the ingroup. *Pancheria* was excluded because its many derived floral and inflorescence features (Hufford & Dickison, 1992) make it difficult to recognize corresponding structures in *Weinmannia*. For example, *Pancheria* has whorled phyllotaxy, flowers arranged in spherical heads, unisexual flow-

ers with a reduced number of parts, and an apocarpous gynoecium. In contrast, *Weinmannia* and *Cunonia* have similar floral structures and inflorescences composed of racemes. Including *Pancheria* in an analysis with *Weinmannia* and *Cunonia* would require that many characters be scored as inapplicable in *Pancheria*, and vice versa. Therefore, despite the possibility that *Pancheria* is the sister genus to *Weinmannia*, it was not useful to include it in a morphological analysis at this level.

CODING OF CHARACTERS

Because phylogenetic studies attempt to discover relationships at different hierarchical levels, characters that vary within one set of taxa may be inapplicable in other taxa (what Pleijel, 1995, termed "hierarchical dependence"). Other coding problems may arise when there is non-independence of characters due to developmental or functional coupling. For example, stem architecture may be coded separately from inflorescence architecture, although one may influence the other. The scoring of "complex characters" has generated some recent discussion (Pleijel, 1995; Wilkinson, 1995), which has recognized the different assumptions and tradeoffs in different coding methods. For example, multi-state coding may reduce the problem of non-independence among characters, but may compound problems of inapplicable characters among taxa. Reductive coding (such as presence vs. absence) eliminates the problem of inapplicable characters among taxa, but may increase the frequency of non-independence among characters. Which tradeoffs or assumptions are most acceptable for a particular analysis may be difficult or impossible to know a priori.

Within this data set it was decided to adopt a moderate, consistent approach, as recommended by Hawkins et al. (1997). For features present and variable among some taxa and absent in others, the information was coded into two characters: a presence/absence character and a character denoting character-state variation for those taxa for which the character was present. Taxa for which the complex character was absent were denoted as inapplicable for variation within the character by a dash ("–") in the data matrix, and taxa for which character data were missing were denoted by a question mark ("?"). For features that may be developmentally related, the strength of this relationship was considered before establishing a character (e.g., see discussion about *W. dichotoma* for characters 3 and 27, Appendix 3). However, developmental studies

have not been done, nor are the pleiotropic effects of trait evolution known.

The characters used in the cladistic analysis are discussed in Appendix 3. Several conspicuous characters that were not used also merit some discussion. Leaf characters, such as imparipinnate vs. unifoliate leaves, winged vs. unwinged leaf rachis, and entire vs. toothed margins, varied within most species-rich OTUs used here and, therefore, could not test the monophyly of sections or their relationships. Variation in leaf complexity was considered to divide the species-rich OTU of American section *Weinmannia*, but these characters were difficult to score qualitatively (see discussion about Bernardi's sect. *Simplicifoliae*) and would require the breakup of nearly all other multi-species OTUs. Another potential character that differed within the American OTU was caducous vs. persistent petals. However, this appeared related to the degree of opening of the sepals, a character more difficult to define, and not to the absence of petal abscission. Other characters that could not be defined with precision or were difficult to score for the majority of species included: variation in the thickness of the pericarp, whether the endocarp detaches in fruit, stipule shape, and leaf anatomical characters, such as whether areolation is complete, presence or absence of a hypodermis, and the degree of lignification of tertiary vascular bundles. Such characters may be found useful with more detailed anatomical, morphological, or developmental information.

CLADISTIC METHODS

Data were entered into MacClade (Maddison & Maddison, 1992), and analyses used PAUP version 3.1.1 (Swofford, 1993) run on an Apple PowerMac 7500/100. All characters were scored as unordered (nonadditive) except for "Morphology of branches" (see discussion of character 2, Appendix 3), which was treated as an ordered ("Wagner") character. No data were missing, but inapplicable entries accounted for ca. 7% of the data and were treated as "unknown" in the analysis. Polymorphisms were treated as "uncertainties," because of the way character data were partitioned in the data set. In PAUP, polymorphism is intended to represent variation among monophyletic clades (Swofford & Begle, 1993), such as between species, whereas the coding in this data set represents variation at the population level (i.e., variation within species). The heuristic-search option was implemented with 100 replicates of random-taxon addition using the TBR branch-swapping algorithm. Zero-length branches

were collapsed. All shortest trees were saved, and PAUP was used to make consensus trees.

A bootstrap analysis (Felsenstein, 1985) was done with 1000 replicates, with one round of random-taxon addition for each replicate, using the heuristic-search option and TBR branch swapping. To prevent some searches from never swapping to completion, the "maxtrees" setting was held at 500 trees. Decay analyses were done by saving all trees one, and then two steps longer than the most parsimonious trees.

RESULTS

The first round of taxon addition found 192 most-parsimonious trees of 90 steps [Consistency Index (C.I.) = 0.456, Retention Index (R.I.) = 0.745], and all subsequent searches located the same island of trees. Among the outgroups, *Caldcluvia* is arbitrarily used to root the cladogram. The strict consensus tree is shown in Figure 5 and includes bootstrap values of 50% or greater and decay values. The search for trees two steps longer than parsimony could not be completed because the number of possible trees filled available memory. One of the most parsimonious trees is shown in Figures 6 and 7, and was chosen to represent the Malagasy OTUs (sects. *Spicata* + *Inspersa*) as forming a monophyletic group.

When the six possibly non-monophyletic OTUs were removed, the strict consensus cladogram was less resolved than the one shown in Figure 5. Unresolved nodes included the monophyly of *Weinmannia* and the monophylies of sections *Spicata* and *Inspersa*. The node uniting sections *Fasciculata* and *Weinmannia* collapsed. The poorer resolution probably resulted from an inability to polarize character states when plesiomorphic taxa were removed, but the results were congruent with the complete matrix tree.

The monophyly of *Weinmannia* is supported with *Cunonia* as the sister taxon. One character synapomorphic for the *Weinmannia*-*Cunonia* clade, imbricate calyx aestivation, was expected, but other synapomorphies are homoplastic within the clade, including fused lateral stipules and medial meristem abortion. An unbranched floral axis (e.g., raceme), a fused fruit column, and IM development are synapomorphies for a *Vesselowskya* (*Weinmannia*-*Cunonia*) clade.

Cunonia has three distinctive apomorphies: a nectary whorl adnate to the carpel wall, circum-basal dehiscence of fruits, and a double internode on branches.

Monophyly of *Weinmannia* is supported by the

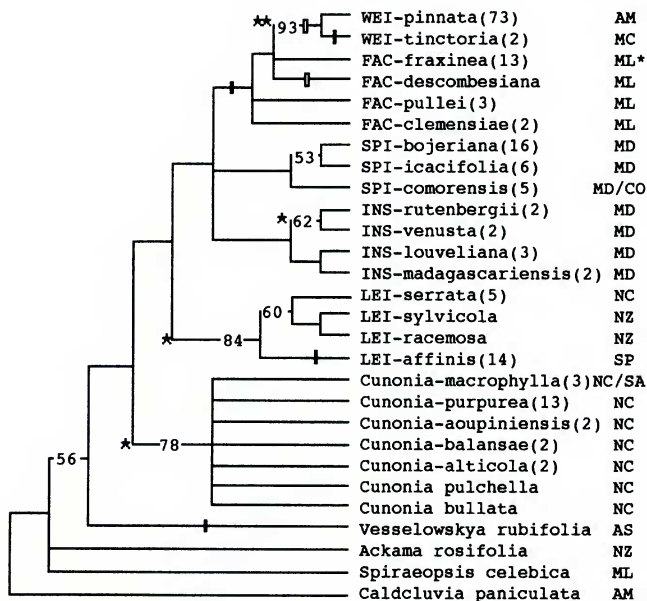


Figure 5. Strict consensus of 192 most parsimonious trees, and taxon-area cladogram. OTUs of species groups in *Weinmannia* are shown with the first three letters of their section capitalized followed by the name of one species. WEI = *Weinmannia*, FAC = *Fasciculata*, SPI = *Spicata*, INS = *Inspersa*, LEI = *Leiospermum*. The total number of species in each OTU is given in parentheses. For areas: AM = Americas, MC = Mascarenes, ML = Malesia (*with a few species in Melanesia), MD = Madagascar, CO = Comores, NC = New Caledonia, NZ = New Zealand, SP = South Pacific (Melanesia and Polynesia), AS = Australia, SA = South Africa. Numbers on branches are bootstrap values. Decay values are 1, unless indicated by a star at the node, with * = decay value of 2 and ** = decay value probably >2. As reconstructed on the cladogram, unisexual flowers have evolved from bisexual ones at least three times in *Weinmannia* (solid bars), and the reverse has happened twice (open bars).

absence of seed wings and the presence of seed hairs, even though these characters are also present in *Ackama*. Another supporting character is the development of IMs in lateral and medial positions, but this character is relatively homoplastic overall.

The first split within the *Weinmannia* clade is between the South Pacific section *Leiospermum* and the rest of the genus. Section *Leiospermum* appears to be monophyletic based upon two characters of the inflorescence architecture: sequential arrangement of metamers within the IMs, and acrotonic development of IMs in the medial position. Within this section is a group of 14 species with unisexual flowers widespread in Melanesia and Polynesia, and a clade of 7 species with bisexual flowers and

a perigynous perianth found only in New Caledonia and New Zealand. The two New Zealand species are further distinguished by their inflorescences (as previously discussed).

Four unambiguous synapomorphies unite all other *Weinmannia* species: calyx persistent in fruit, fasciculate flowers, persistent floral bracts, and short IM shoots. Except for the character of fasciculate/solitary floral inception (which changes 6 times in all most parsimonious trees), these characters are not very homoplastic, as each changes only 2–3 times in all most parsimonious trees (Fig. 8). However, this clade is not supported by bootstrap or decay analyses (Fig. 5).

Relationships within this larger *Weinmannia*

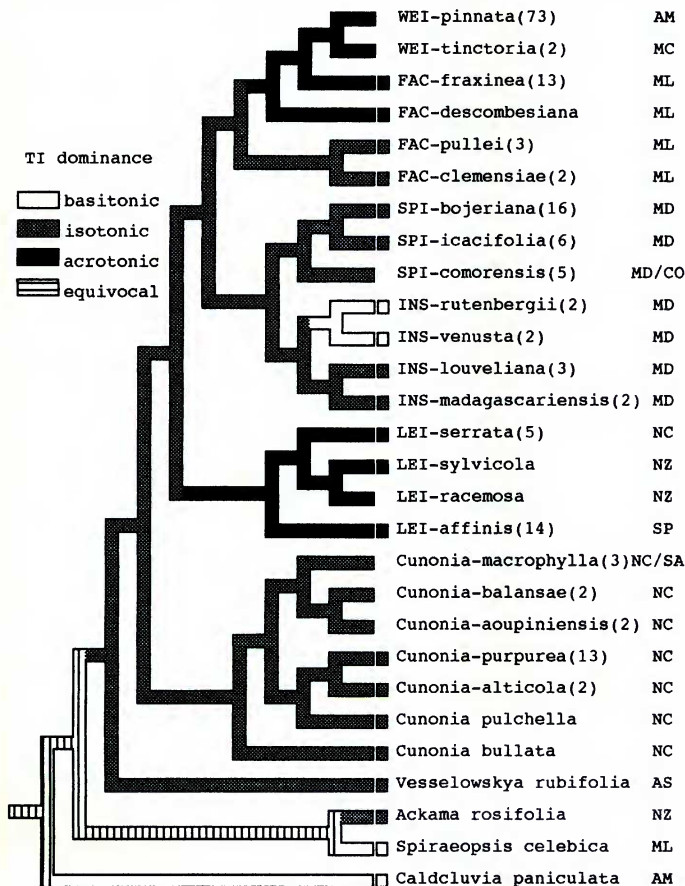


Figure 6. One of the most-parsimonious trees showing a monophyletic group from Madagascar and tracing the evolution of character 31: "TI dominance."

clade are not fully resolved. Although the monophyly of sections *Inspira* and *Spicata* is supported, the relationship of these clades to one another and to the *Weinmannia-Fasciculata* clade is uncertain. Assuming that the Malagasy sections are most closely related to one another can resolve this po-

lytomy as shown in Figures 6 and 7. However, there are no unambiguous synapomorphies for the Malagasy clade. Section *Spicata* has only one recognized apomorphy, sessile flowers. Section *Inspira* has two apomorphies, ribbed nectaries (also present in sect. *Weinmannia* and erratically in sect. *Fas-*

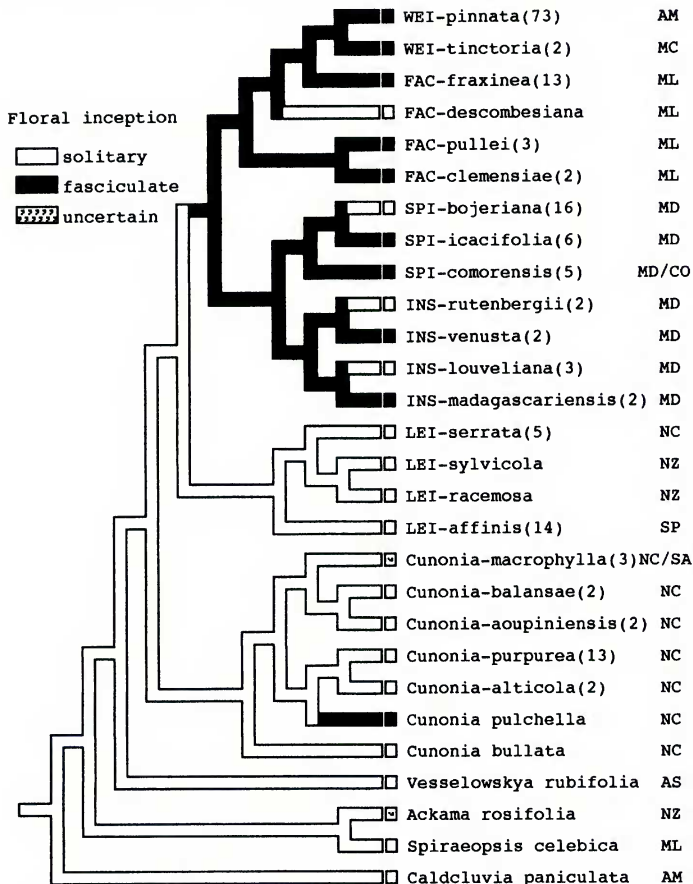


Figure 7. Floral inception (character 19) traced on one of the most-parsimonious cladograms.

ciculata) and seeds covered with dense hairs (sometimes found in sect. *Fasciculata*). In general, species-groups in Madagascar show a great diversity of characters relative to other taxa.

No most-parsimonious reconstruction supports the monophyly of section *Fasciculata*, which in this analysis is paraphyletic with respect to a highly

differentiated section *Weinmannia*. These two sections are united by the absence of persistent, fused lateral stipules and the absence of a bud at the base of the axillary shoots.

The node uniting the species of section *Weinmannia*, which are disjunct between the Americas and the Mascarene Islands, is the best supported,

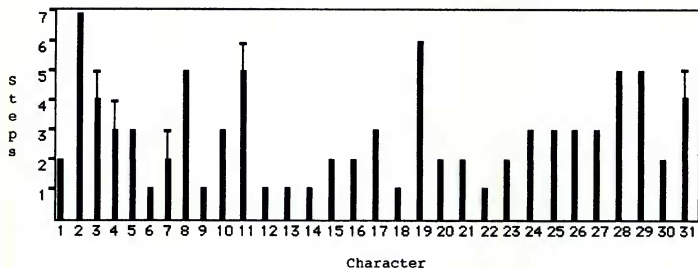


Figure 8. The number of steps (y axis) per character (x axis) calculated over all most-parsimonious trees, showing the upper bound and minimum values. Characters 24–31 represent variation in the inflorescence architecture above the level of the raceme axis (as shown in Figs. 2, 3, 9). These characters comprise 26% of the characters in the matrix (8/31), and about 29% of the total number of steps (26–27/90). When all inflorescence characters are included (characters 19–31), these values are 42% (13/31) and 44% (39–40/90), respectively, demonstrating that they do not have levels of homoplasy significantly different from traditionally used characters.

with a bootstrap support of 93% and a decay index of >2 (Fig. 5). This node has six unambiguous changes: ribbed nectaries, sparsely distributed seed hairs, reniform seed shape, absence of IM development, presence of development of racemes along the main stem axis, and only one TI metamer. Within section *Weinmannia*, the Mascarene species have two distinguishing characters: unisexual flowers formed by late suppression, and 5-merous flowers (in contrast to bisexual, 4-merous flowers in American species). As noted previously, most American species have caducous petals and may be a monophyletic sister taxon to the Mascarene clade. The American species appear monomorphic in this analysis, which relied on qualitative character variation, but are highly diversified in terms of leaf shape, distribution and form of pubescence, and size of racemes.

DISCUSSION

SYSTEMATIC IMPLICATIONS

At the generic level, this analysis supports the continued recognition of *Weinmannia* and *Cunonia* as separate genera, a distinction that has been questioned by some systematists (Cronquist, 1981: 547). However, more systematic studies within the family are needed to be more certain of cladistic relationships among genera.

Within *Weinmannia*, the sections proposed by Bernardi (1961, 1963b, 1964) appear monophyletic, with the exception of section *Fasciculata*, with some rearrangement of species indicated. Specifically, *Weinmannia descombesiana* on the one hand,

and *W. comorensis* and *W. baehnia*, on the other, do not belong in section *Leiospermum*, but in sections *Fasciculata* and *Spicata*, respectively. *Weinmannia venusta* and *W. rutenbergii* do not belong in section *Weinmannia*, but in section *Inspersa* (see Appendix 1). With these rearrangements, the monophyly of sections *Leiospermum*, *Spicata*, *Inspersa*, and *Weinmannia* (including sect. *Simplicifolia*) is supported. Section *Fasciculata* is paraphyletic with respect to section *Weinmannia*, but several characters were scored as inapplicable in section *Weinmannia* (since this section lacks IM development) and may have skewed patterns within section *Fasciculata*. Furthermore, preliminary results of molecular-systematic studies (Bradford, unpublished) strongly support the monophyly of section *Fasciculata*.

The poor resolution in *Cunonia* may have been due to the selection of characters in *Weinmannia*. An analysis focusing on *Cunonia* might be more informative. Interestingly, the South African *Cunonia capensis*, the only *Cunonia* species outside of New Caledonia, shares many characters with two other species, *C. macrophylla* and *C. schinziana*. Furthermore, these three species appear very distinctive when compared to other *Cunonia* species.

UTILITY OF ARCHITECTURAL CHARACTERS FOR WEINMANNIA SYSTEMATICS

As judged by relative levels of homoplasy, inflorescence architecture is as informative as other sources of variation, such as vegetative, floral, and fruit characters (Fig. 8).

Parts of the cladogram rely heavily on inflorescence characters. For example, the monophyly of section *Leiospermum* is supported by inflorescence architecture alone, and section *Weinmannia* is supported by three inflorescence characters.

The inclusion of inflorescence characters has permitted the resolution of relationships within sections for the first time. This is especially true in the species-rich section *Spicata*, which can be divided into three groups largely on the basis of inflorescence differences. Inflorescence characters are also useful at the species level in section *Inspersa*. It is often easier to recognize species using qualitative differences in the inflorescence than using differences in leaves, which may be fairly similar among species and highly plastic within species.

The fact that inflorescence characters have been overlooked is illustrated by Smith (1985), who considered *W. richii* and *W. vitiensis*, both from Fiji, as fairly indistinct based upon leaves and flowers. However, at a glance one can recognize that racemes terminate the IMs of *W. vitiensis* (sect. *Leiospermum*), whereas the IMs terminate in a bud and are borne serially in *W. richii* (sect. *Fasciculata*). Although these characters have gone unnoticed, they are macroscopic, with clear patterns discernible by the naked eye and not requiring rehydration and dissection of parts, as is often necessary for flowers and fruits.

THE CONCEPT OF POSITIONAL HOMOLOGY: IMPLICATIONS AND BENEFITS

Heterotopy is the development of an organ in a different position in a descendant than where it had developed in the ancestor. This definition views the organ as primary and the position as secondary. Another perspective of heterotopy is: at a given position, a different organ develops in the descendant than that which had developed in the ancestor. This view gives primacy to positional homology, and with this perspective it may be easier to understand that an organ can develop in its plesiomorphic position and in an apomorphic position within a plant. Consideration of the homology of position has two important implications: (1) it draws attention to a broader set of characters, and (2) it may lead to more precise formulation of characters. The coding of the inflorescence using positional homology exemplifies these points.

Often, the use of inflorescence characters in systematics is vague (e.g., "inflorescence terminal or not") because the level of organization is not specified. By contrast, consider character 26, "Fate of

IM terminus," which accounts for the organ (raceme, bud, or aborted meristem) that forms at a particular position, the terminus of an IM. This coding specifies topographic information in the proper hierarchic context. Because such characters are positional, patterns of heterotopy can be studied from cladograms. The mapping of character 31, "TI dominance," on the cladogram (Fig. 6) shows that TIs are generally isotonic within *Canonia* and *Weinmannia*, but that acrotonic TIs have evolved twice (Figs. 2a, 3a) and basitonic TIs once (Fig. 3e). At the TI level, this is a *positional* change in dominance, but it is expressed by differences among IMs possibly caused by unequal *timing* of development. In other words, timing differences are among serially homologous IMs within a TI, whereas positional differences are among clades within *Weinmannia*.

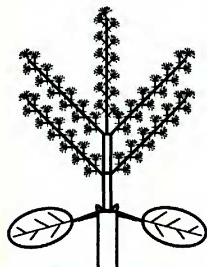
It should be stressed that nothing is being implied about the underlying molecular development of these characters. Heterotopy is only being used to describe patterns observed at the morphological level in a phylogenetic context. However, because the deep nodes of the cladograms are not well supported (Fig. 5), extensive discussion of character evolution is not warranted.

ORIGIN OF RACEMES

In the discussion of character 22 ("Flower-bearing axis: branched/unbranched") it was suggested that if fasciated flowers (character 19) were plesiomorphic in the cladogram, then the hypothesis that floral fascicles are homologous to flower-bearing short shoots would be supported. Mapping of character 19 on the cladograms does not support this hypothesis (Fig. 7). Fasciated flowers appear derived within the sister clade to section *Leiospermum*, but within this clade there are four reversals. The hypothesis is not completely rejected, however, due to the high level of homoplasy of character 19 and the lack of support for deep nodes.

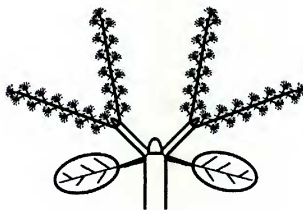
INFLORESCENCE CLASSIFICATION AND CLADISTICS: SOME OBSERVATIONS AND CAUTIONS

Standard inflorescence terminology may inadequately describe cladistic characters because traditional terms frequently confound distinct characters and levels of organization. For instance, previous descriptions of inflorescence variation in *Weinmannia* (Bernardi, 1963a) recognized three forms: "racemes," "pseudoracemes," and "spikes." The first pair of terms refers to the final stage of floral position along the axis but mixes the characters "Floral inception" (character 19) and "Bract fidelity" (character 20; Fig. 1). The term "spike"



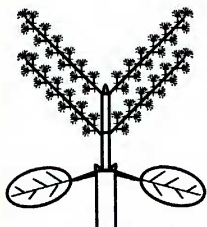
a. *Weinmannia marquesana*

Heterothetic compound raceme



c. *Weinmannia clemensiae*

Homothetic compound raceme



b. *Weinmannia racemosa*

Homothetic compound raceme

Character/Species	a.	b.	c.
IM position	medial	medial	lateral
IM metamers	two	two	one
IM terminus	raceme	bud	bud

Figure 9. Inflorescence typology and cladistics. Three species and their inflorescences are shown, with two labeled "homothetic compound racemes," and one "heterothetic compound raceme," following Weberling (1989). Of three characters coded using the methodology in this paper, standard terminology accounts for only one, IM terminus. That is why standard terminology classifies b and c the same, whereas this analysis suggests that a and b are most closely related.

specifies flowers borne on an unbranched axis without pedicels and is therefore unrelated to variation in the distribution of flowers along the axis that is dealt with (poorly) by the other two terms. A cladistic analysis that codified traditional terminology would therefore be comparing non-homologous parts.

As mentioned in the description of inflorescence architecture, general systems of inflorescence classification do not apply to many structures in *Weinmannia*. The various forms of the IM may loosely be termed "compound racemes" following Weberling (1989), although they do not fit the definition exactly. Standard terminology cannot be expected to describe in detail the unique aspects of a group, but details are crucial for cladistics. For example,

compare the inflorescences shown in Figure 9, which are common in *W. marquesana* (Fig. 9a) and *W. racemosa* (Fig. 9b; sect. *Leiospermum*) and *W. clemensiae* (Fig. 9c; sect. *Fasciculata*). The inflorescence of *W. marquesana* can be called a "heterothetic compound raceme," and the others can be called "homothetic compound racemes." The standard terminology addresses whether the terminus of the IM produces a bud or a raceme. This fails to convey other characters important in *Weinmannia*, such as the number of IM metamers and the position the IM occupies within the TI.

It is also difficult to apply standard names to the inflorescences of some highly plastic species, such as *W. rutenbergii*, especially since variation is rampant at different levels of organization. However, by

breaking down a complex structure into its parts, variation relevant to different hierarchical levels can be distinguished.

EVOLUTION OF DIOECY

The cladogram (Fig. 5) shows that bisexual flowers are plesiomorphic in *Weinmannia*. Two clearly monophyletic groups (corresponding to sects. *Weinmannia* and *Leiospermum*) have some members with bisexual and others with unisexual flowers (and which are more or less dioecious). Unisexual flowers are also most common in section *Fasciculata*, but because relationships in this portion of the tree are not well resolved, the pattern of character evolution is unclear. Minimally, unisexual flowers have arisen three times, with a possible reversal in *W. descombesiana* and in the branch of the section *Weinmannia* clade.

Weinmannia flowers are small, simply structured, and mature more or less simultaneously within an inflorescence. The pollinators of *Weinmannia* probably conform to the "generalist" category of small insects, especially bees, that Bawa (1994) and Beach (1981) suggested drove the evolution of dioecy from bisexuality. The best evidence for bee pollination of *Weinmannia* is the commercial production of honey in New Zealand (Matheson, 1991; Walsh, 1978) and Madagascar (Ralimanana, 1994).

It is noteworthy that dioecy is prevalent on islands, which has been suggested as a general trend (Baker, 1967; Baker & Cox, 1984). The only dioecious species in section *Weinmannia* occur on the Mascarene Islands, and the dioecious members of section *Leiospermum* are distributed among the smaller South Pacific islands, with bisexual species on the relatively larger islands of New Caledonia and New Zealand. In the South Pacific, dioecy is usually imperfect (e.g., "leaky dioecy" or polygamodioecy), which may promote the colonization of small, ephemeral islands (Baker & Cox, 1984).

BIOGEOGRAPHY

Weinmannia has attracted the interest of biogeographers because its distribution suggests that the genus was widespread on Gondwanaland, and its current disjunctions may have much to do with plate-tectonic processes and resultant continental vicariance (Good, 1950; Bernardi, 1963a; van Balgooy, 1971; Raven & Axelrod, 1974). However, extensive distribution among South Pacific volcanic islands shows that long-distance dispersal can also be important in this genus.

Because deep phylogeny of *Weinmannia* is not well supported, no firm conclusions about Gond-

wana-area relationships can be made. However, the well-supported sister-group relationship between American and Mascarene taxa is impossible to explain without invoking dispersal, because the Mascarene Islands are of relatively recent, hot-spot volcanic origin (Patriat & Seqoufin, 1988). This disjunction can be explained by one of two general classes of hypotheses: (1) long-distance dispersal between the Americas and the Mascarenes, or (2) short-distance dispersal from a non-extant source area from Africa, Madagascar, or other, older islands in the Indian Ocean. The second hypothesis implies an historically more widespread occurrence of section *Weinmannia*, with intervening extinction.

If section *Weinmannia* is in fact a relatively young, highly derived lineage, as its current position in the cladogram suggests, then the long-distance dispersal hypothesis may be favored. However, the hypothesis of formerly widespread occurrence and short-distance dispersal gains some support from fossils. Oligocene whole-leaf fossils of either *Weinmannia* or *Cunonia* from Tasmania (Carpenter & Buchanan, 1993) look very similar to *W. trichosperma* from southern Chile.

CONCLUSIONS AND FUTURE DIRECTIONS

This cladistic study of morphological characters has identified congruent patterns of variation both within and among previous taxonomic groupings of *Weinmannia*. This helps to focus research into the origin and transformation of characters within *Weinmannia* and related genera. While good support exists for the monophyly of some sections, cladistic relationships and patterns of character evolution among sections are still poorly understood. However, molecular-systematic work will be aided by a better understanding of the disparity in morphological diversity and species richness among clades, and the overall congruence of character variation with geography.

It is likely that the methods used here to identify and cladistically code inflorescence architecture in *Weinmannia* and *Cunonia* will be useful in other taxa. This is certainly true within and among other genera of Cunoniaceae. An understanding of the nested, modular construction of plants and the potential for heterotopy in evolution may often be required to code inflorescence architecture for cladistic analysis. It is suggested that heterotopic patterns are prevalent in inflorescence evolution, and that coding of positional homologies is an effective way to infer character-state polarities of inflorescence features.

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APPENDIX 1

List of species assigned to each OTU and a selected list of specimens examined. Only the name of the first collector is given. An estimate of the number of species in each OTU includes preliminary studies of undescribed species. New species are listed and specimens are cited only if they are mentioned in the text. Types are holotypes or isotypes unless indicated otherwise. Herbaria holding specimens are given in parentheses.

Section *Weinmannia*

WEI-pinnata 73 species (in addition to the species cited below there are ca. 10 undescribed species)

- Weinmannia anisophylla* Standl. & L. O. Williams, *Smith* P2622 (F; type), Costa Rica
- Weinmannia auriculata* D. Don, *Bradford* 392 (MO), Venezuela; *Jørgensen* 1260 (MO), Ecuador
- Weinmannia auriculifera* Hieron., *Cuatrecasas* 6313 (F), Colombia
- Weinmannia balbisiana* Kunth, *Bradford* 459 (MO), Venezuela
- Weinmannia bangii* Rusby, *Bradford* 525 (MO), Bolivia; *Solomon* 10683 (MO), Bolivia
- Weinmannia boliviensis* R. E. Fr., *Solomon* 10591 (MO), Bolivia
- Weinmannia bogotensis* Cuatrec., *Bradford* 746 (MO), Colombia; *Cuatrecasas* 8005 (COL, F; type), Colombia
- Weinmannia burserifolia* Standl., *Bello* 1338 (MO), Costa Rica; *Bradford* 97 (MO), Costa Rica
- Weinmannia cochenis* Hieron., *Bradford* 3 (MO), Ecuador; *Bradford* 339 (MO), Ecuador; *Bradford* 762 (MO), Colombia
- Weinmannia corocoroensis* P. E. Berry & J. C. Bradford, *Huber* 12296 (MO), Venezuela
- Weinmannia costulata* Cuatrec., *Steyermark* 53545 (F; type), Ecuador
- Weinmannia crassifolia* Ruiz & Pav., *Bradford* 510 (MO), Bolivia; *Solomon* 17344 (MO), Bolivia
- Weinmannia cundinamarcaensis* Cuatrec., *Cuatrecasas* 12033 (COL, F; type), Colombia
- Weinmannia cymbifolia* Diels, *Díaz* 2654 (MO), Peru; *Llantas Quiroz* 2625 (MO), Peru
- Weinmannia discolor* Gardner, *Davidson* 5020 (MO), Bolivia; *Hatschbach* 43003 (MO), Brazil
- Weinmannia dryadifolia* Moric., *Bradford* 150 (MO), Ecuador; *Gentry* 61436 (MO), Peru; *Smith* 5011 (F, MO), Peru
- Weinmannia ellatantha* Diels, *Bradford* 538 (MO), Bolivia; *Gentry* 52076 (MO), Bolivia
- Weinmannia elliptica* Kunth, *Bradford* 351 (MO), Ecuador
- Weinmannia fagaroides* Kunth, *Bradford* 295 (MO), Ecuador
- Weinmannia glabra* L.f., *Breedlove* 19958 (F), Mexico
- Weinmannia glomerata* C. Presl, *Gentry* 19302 (F), Peru; *Gentry* 44877 (F, MO), Peru; *Young* 593 (F, MO), Peru
- Weinmannia guyanensis* Klotzsch ex Engl., *Delascio* 11861 (MO), Venezuela; *Huber* 9085 (US), Venezuela
- Weinmannia haenkeana* Engl., *Llantas Quiroz* 1320 (F), Peru; *Smith* 5039 (MO), Peru
- Weinmannia humilis* Engl., *Hatschbach* 26323 (MO), Brazil
- Weinmannia ilutepuiensis* J. C. Bradford & P. E. Berry, *Liesner* 23338 (MO), Venezuela; *Liesner* 23413 (MO; type), Venezuela; *Maguire* 33508 (US), Venezuela
- Weinmannia intermedia* Schltr. & Cham., *Ventura* 1089 (F), Mexico
- Weinmannia jelskii* Szyszyl., *Gentry* 80472 (MO), Ecuador; *Smith* 7789 (MO), Peru
- Weinmannia karsteniana* Szyszyl., *Bradford* 383 (MO), Venezuela
- Weinmannia kunthiana* D. Don, *Jaramillo Mejia* 167 (F, MO), Colombia
- Weinmannia latifolia* C. Presl, *Cuatrecasas* 23723 (F), Colombia; *Smith* 7937 (MO), Peru
- Weinmannia laurina* Kunth, *Mori* 7686 (MO), Panama
- Weinmannia laxiramea* Killip & A. C. Sm., *Steyermark* 128321 (MO), Venezuela; *Steyermark* 129882 (US), Venezuela
- Weinmannia lentisifolia* C. Presl, *Palacios* 4128 (MO), Ecuador
- Weinmannia macrophylla* Kunth, *Jørgensen* 92729 (MO), Ecuador
- Weinmannia magnifolia* Cuatrec., *Cuatrecasas* 8590 (COL, F; type), Colombia; *Palacios* 13415 (MO), Ecuador
- Weinmannia mariquitae* Szyszyl., *Bradford* 208 (MO), Ecuador; *Romoleux* 253 (MO), Ecuador
- Weinmannia microphylla* Ruiz & Pav., *Bradford* 492 (MO), Bolivia
- Weinmannia multijuga* Killip & A. C. Sm., *Brujin* 1296 (MO), Venezuela; *Penland* 1198 (F), Ecuador
- Weinmannia myrtifolia* Cuatrec., *Bradford* 745 (MO), Colombia; *Cuatrecasas* 9451 (COL; type), Colombia
- Weinmannia organensis* Gardner, *Irwin* 8601 (MO), Brazil
- Weinmannia orata* Cav., *Bradford* 541 (MO), Bolivia; *D'Arcy* 13770 (MO), Peru
- Weinmannia parvifoliolata* Cuatrec., *Cuatrecasas* 8486-A (COL, F; type), Colombia
- Weinmannia paulliniifolia* Pohl ex Ser., *Pohl s.n.* (P; type), Brazil; *Sucre* 6824 (MO), Brazil
- Weinmannia pentaphylla* Ruiz & Pav., *Gentry* 43227 (MO), Peru
- Weinmannia pinnata* L., *Wilbur* 7952 (MO), Dominica
- Weinmannia platyptera* Diels, *Smith* 4459 (F, MO), Peru
- Weinmannia polyphylla* Moric. ex Ser., *Bradford* 2 (MO), Ecuador; *Luteyn* 5631 (F, MO), Ecuador
- Weinmannia producta* Moric. ex Ser., *Núñez* 7146 (MO), Peru; *Sagástegui* 7766 (MO), Peru
- Weinmannia pubescens* Kunth, *Bradford* 13 (MO), Ecuador; *Palacios* 9648 (MO), Ecuador
- Weinmannia reticulata* Ruiz & Pav., *Bradford* 296 (MO), Ecuador
- Weinmannia rhoifolia* Rusby, *Lectae* 1989 (MO; type), Bolivia
- Weinmannia rollottii* Killip, *Bradford* 357 (MO), Ecuador; *Bradford* 747 (MO), Colombia
- Weinmannia sibudoya* Cuatrec., *Cuatrecasas* 11624 (F; type), Colombia; *Cuatrecasas* 11817 (F), Colombia; *Cuatrecasas* 19308 (MO), Colombia
- Weinmannia sorbifolia* Kunth, *Solomon* 15997 (MO), Bolivia
- Weinmannia subsessiliflora* Ruiz & Pav. *Schultes* 5329 (COL), Colombia
- Weinmannia ternata* Engl., *Stein* 2114 (MO), Peru; *Woytkowski* 8314 (MO), Peru
- Weinmannia tolimensis* Cuatrec., *Cuatrecasas* 20424 (MO), Colombia; *Wilson Deria* 663 (MO), Colombia
- Weinmannia tomentosa* L.f., *Berry* 175 (MO), Venezuela; *Bradford* 751 (MO), Colombia; *Gentry* 34725 (MO), Colombia

Weinmannia trianaea Wedd., *Cuatrecasas* 11635 (COL, F), Colombia; *Cuatrecasas* 8431 (COL, F), Colombia; *Vargas* 438 (MO), Ecuador
Weinmannia trichocarpa Pamp., *Wurdack* 704 (MO), Peru
Weinmannia trichosperma Cav., *Baum* 4537 (MO), Argentina; *West* 4679 (MO), Chile
Weinmannia velutina O. Schmidt, *Steyermark* 104504 (F, US), Venezuela; *Steyermark* 92437 (F), Venezuela
Weinmannia wercklei Standl., *Haber* 2438 (MO), Costa Rica

WEI-tinctoria 2 species

Weinmannia biriniana Tul., *Badré* 932 (P), Mascarenes; *Bourbon s.n.* (P), Mascarenes; *Cadet* 1704 (P), Mascarenes; *Frappier* 395 (P), Mascarenes; *Friedmann* 2482 (P), Mascarenes
Weinmannia tinctoria Sm., *Barthe s.n.* (P), Mascarenes; *Destruix s.n.* (P), Mascarenes; *Frappier* 397 (P), Mascarenes; *Kramer* 9299 (MO), Mascarenes; *Lorence* 2427 (MO), Mascarenes; *Lorence* 2676 (MO), Mascarenes

Section Fasciculata**FAC-fraxinea** 13 species

Weinmannia aphanoneura Airy Shaw, *Brunig* S 8785 (L), Malaysia, Sarawak; *Chew Wee-Lek* 380 (L), Malaysia, Sarawak; *Clemens* 29476 (L), Malaysia, Sabah; *Clemens* 33076 (L), Malaysia, Sabah; *Endert* 4125 (L), Indonesia, Kalimantan; *Paie* S 26531 (L), Malaysia, Sarawak
Weinmannia coodei H. C. Hopkins, *Coode* 6197 (L; type), Indonesia, Sulawesi
Weinmannia detogelii H. C. Hopkins, *Balgooy* 3809 (L), Indonesia, Sulawesi; *de Vogel* 5682 (L), Indonesia, Sulawesi; *de Vogel* 5959 (L), Indonesia, Sulawesi; *de Vogel* 6122 (L; type) Indonesia, Sulawesi; *Meijer* 11147 (L), Indonesia, Sulawesi; *Schmid* 5512 (L, P), Indonesia, Sulawesi
Weinmannia dulitensis Airy Shaw, *Hopkins* 5014 (MO), Malaysia, Sabah
Weinmannia exigua A. C. Sm., *Howard* 89 (BISH), Fiji; *Whitmore* BSIP 995 (BSIP, L), Solomon Islands
Weinmannia fraxinea Sm. ex D. Don, *Bradford* 830 (MO), Solomon Islands; *Hopkins* 5004 (MO), Malaysia, Sarawak; *Hopkins* 5006 (MO), Malaysia, Sarawak; *Sargent s.n.* (MO), Indonesia "Journey Round the World"; *Takeuchi* 7135 (MO), Papua New Guinea
Weinmannia furfuracea H. C. Hopkins, *Balgooy* 3255 (L; paratype), Indonesia, Sulawesi; *Balgooy* 3464 (L; paratype), Indonesia, Sulawesi; *bb* 20787 (BO; paratype), Indonesia, Sulawesi; *Rutten* 2231 (BO, L; paratype), Indonesia, Seram; *Tantra* 1595 (L; type), Indonesia, Sulawesi
Weinmannia hutchinsonii Merr., *Elmer* 14228 (MO), Philippines; *Elmer* 14918 (MO), Philippines; *Ramos* BS 23494 (MO), Philippines; *Wenzel* 1088 (MO), Philippines
Weinmannia luzonensis Vidal, *Elmer* 18024 (MO), Philippines; *Vanoverbergh* 1253 (MO), Philippines
Weinmannia macgillivrayi Seem., *Bourdy* 322 (P), Vanuatu; *Kajewski* 735 (BISH, P), Vanuatu; *Schmid* 3557 (P), Vanuatu; *Schmid* 5083 (NOU), Vanuatu
Weinmannia negrosensis Elmer, *Ramos* BS 1287 (MO), Philippines; *Wenzel* 1057 (MO), Philippines
Weinmannia richii A. Gray, *Hopkins* 5023 (MO), Fiji; *De-gener* 14379 (F, MO), Fiji; *Smith* 6813 (L, P), Fiji

Weinmannia ysabelensis Perry, *Brass* 3215 (BO, L; type), Solomons

FAC-descombesiana 1 species

Weinmannia descombesiana Bernardi, *bb* 20870 (L), Indonesia, Sulawesi; *bb* 22981 (L, P; paratype), Indonesia, Sulawesi; *bb* 26643 (L), Indonesia, Sulawesi; *bb s.n.* (L), Indonesia, Sulawesi; *Eyma* 3590 (L), Indonesia, Sulawesi; *Kjellberg* 1618 (S; type), Indonesia, Sulawesi

FAC-pullei 3 species

Weinmannia eymaena H. C. Hopkins, *Eyma* 3578 (BO, L; type), Indonesia, Sulawesi
Weinmannia pullei Schltr., *Hoogland* 6979 (BISH, BO, L), Papua New Guinea; *Hoogland* 7685 (L), Papua New Guinea; *Kalkman* 4859 (BO, L), Papua New Guinea; *Robbins* 3056 (L), Papua New Guinea; *Veldkamp* 5493 (BISH, L), Papua New Guinea; *Vink* 17098 (BO, L, P), Papua New Guinea; *Frodin* NGF 26964 (BISH, L), Papua New Guinea
Weinmannia urdanetensis Elmer, *Bowers* 401 (L), Papua New Guinea; *Hoogland* 5463 (BISH, L), Papua New Guinea; *Hoogland* 7254 (L), Papua New Guinea; *Kostermaers* 2304 (BO, L), Indonesia, Irian Jaya; *Paijmans* 1315 (L), Papua New Guinea; *Sterly* 80-40 (L), Papua New Guinea; *BW* 5588 (L), Indonesia, Irian Jaya; *Robbins* 191 (L), Papua New Guinea; *Takeuchi* 6340 (MO), Papua New Guinea; *Wade* ANU 7663 (L), Papua New Guinea; *Womersley* NGF 15240 (L), Papua New Guinea

FAC-clemensiae 2 species

Weinmannia clemensiae Steenis, *Beaman* 9132 (L), Malaysia, Sabah; *Beaman* 9837 (L), Malaysia, Sabah; *Clemens* 50793 (L), Malaysia, Sabah; *Clemens* 50877 (L), Malaysia, Sabah; *Hopkins* 5011 (MO), Malaysia, Sabah; *Chew* RSNB 4508 (L, SAN), Malaysia, Sabah; *Chew* RSNB 4755 (L, SAN), Malaysia, Sabah
Weinmannia hooglandii H. C. Hopkins & J. C. Bradford, *Symington* 32246 (KEP), Peninsular Malaysia; *Whitmore* FRI 12582 (KEP, L, SAN; type), Peninsular Malaysia

Section Spicata**SPI-bojeriana** 16 species (in addition to the species cited below there are 7 undescribed species)

Weinmannia bojeriana Tul., *Bojer s.n.* (P; type), Madagascar; *Bosser* 13321 (P), Madagascar; *Bradford* 639 (MO), Madagascar; *Decary* 5010 (P), Madagascar; *Decary* 5366 (P), Madagascar; *Humbert* 4849 (P), Madagascar; *Malcomber* 1031 (MO), Madagascar; *Perrier* 6433 (P), Madagascar
Weinmannia decora Tul., *Bernardi* 11961 (P), Madagascar; *Bernier* 324 (P; type), Madagascar; *R.N.* 3452 (P), Madagascar; *S.F.* 10167 (P), Madagascar; *SF* 13228 (P), Madagascar
Weinmannia eriocarpa Tul., *Baillon s.n.* (P), Madagascar; *Bojer s.n.* (P; type), Madagascar; *Decary* 15104 (P), Madagascar; *Dequaire* 27809 (P), Madagascar; *Hildebrandt* 3562 (P), Madagascar; *Baron* 1674 (P), Madagascar
Weinmannia hildebrandtii Baill. var. *arguta* Bernardi, *Bradford* 642 (MO), Madagascar; *S.F.* 8848 (P; type of variety), Madagascar
Weinmannia humbertiana Bernardi, *Bradford* 703 (MO), Madagascar; *Humbert* 23532 (P), Madagascar; *Hum-*

- bert* 23814 (P; type), Madagascar; *Humbert* 22505 (P), Madagascar
- Weinmannia humblotii* Baill. var. *humblotii*, *Baron* 4434 (P; type of *W. leptostachya*), Madagascar; *Humbert* 12074 (P), Madagascar; *Humbert* 613 (P; type), Madagascar; *Weinmannia humblotii* var. *anceps* Bernardi, *Bradford* 705 (MO), Madagascar; *Perrier de la Bâthie* 6421 (P), Madagascar
- Weinmannia mammea* Bernardi, *Louvel* 191 (P; type), Madagascar; *Morat* 2803 (P), Madagascar; *Humbert* 24496 (P), Madagascar; *Humbert* 24781 (P), Madagascar
- Weinmannia sanguisugarum* Bernardi, *Bernardi* 11999 (P; type), Madagascar; *Humbert* 3823 (P), Madagascar; *Malcomber* 2363 (MO), Madagascar
- Weinmannia stenostachya* Baker, *Baron* 3148 (P; type of *W. fraxinifolia*), Madagascar; *Baron* 6406 (P; type), Madagascar; *Benoist* 1345 (P), Madagascar; *Leandri* 1737 (P), Madagascar; *Perrier* 6422 (P), Madagascar; *S.F.* 12547 (P), Madagascar; *S.F.* 3 (P), Madagascar

SPI-icacifolia 6 species (in addition to the species cited below there are 4 undescribed species)

- Weinmannia hildebrandtii* Baill., *Cours* 4792 (P), Madagascar; *Hildebrandt* 3695 (P; type), Madagascar; *S.F.* 5809 (P), Madagascar; *S.F.* 6240 (P), Madagascar
- Weinmannia icacifolia* Bernardi, *Perrier de la Bâthie* 15346 (P), Madagascar; *Perrier de la Bâthie* 16122 (P), Madagascar; *Perrier de la Bâthie* 16464 (P; type), Madagascar

SPI-comorensis 5 species (in addition to the species cited below there is 1 undescribed species)

- Weinmannia baehniiana* Bernardi, *Perrier de la Bâthie* 6431 (P), Madagascar; *R.N.* 1398 (P), Madagascar; *R.N.* 1837 (P), Madagascar; *S.F.* 10198 (P), Madagascar
- Weinmannia comorensis* Tul., *Boivin s.n.* (P; type), Madagascar; *Bosser* 17997 (P), Madagascar; *Boureau* 68 (TEF), Madagascar; *S.F.* 16591 (P), Madagascar
- Weinmannia lucens* Baker, *Decary* 13241 (P), Madagascar; *Humbert* 28744 (P), Madagascar
- Weinmannia minutiflora* Baker, *Baron* 2542 (P; type), Madagascar; *Jardin Botanique* 4710 (P), Madagascar; *S.F.* 9044 (P), Madagascar

Section *Inspersa*

INS-rutenbergii

- Weinmannia hepaticarum* Bernardi, *Humbert* 23545 (P; type), Madagascar
- Weinmannia rutenbergii* Engl., *Chauvet* 429 (P), Madagascar; *R.N.* 1786 (P), Madagascar; *SF* 13518 (P), Madagascar; *SF* 18382 (P), Madagascar; *SF* 21468 (P), Madagascar; *Cloisel* 227 (P), Madagascar

INS-venusta

- Weinmannia* sp. nov. 1, *R.N.* 111 (MO, P), Madagascar; *Bradford* 655 (MO), Madagascar; *R.N.* 2853 (P), Madagascar; *S.F.* 5464 (P), Madagascar; *S.F.* 24061 (P), Madagascar; *Raharimalala* 295 (P), Madagascar
- Weinmannia venusta* Bernardi, *Humbert* 21944 (P; type), Madagascar; *Capuron*, *S.F.* 27632 (P), Madagascar; *Christophe S.F.* 17610 (TEF), Madagascar; *S.F.* 17231 (TEF), Madagascar

INS-louveliana 3 species (in addition to the species cited below there is 1 undescribed species)

- Weinmannia commersonii* Bernardi, *S.F.* 16718 (TEF), Madagascar; *S.F.* 21528 (TEF), Madagascar; *Vegreux* 42 (P), Madagascar; *Perrier de la Bâthie* 14263 (P; type), Madagascar; *S.F.* 10164 (P), Madagascar
- Weinmannia louveliana* Bernardi, *S.F.* 9669 (P), Madagascar; *S.F.* 5182 (P), Madagascar; *R.N.* 6211 (P; type), Madagascar; *S.F.* 10402 (P), Madagascar

INS-madagascariensis 2 species

- Weinmannia henricorum* Bernardi, *Humbert* 7018 (P; type), Madagascar
- Weinmannia madagascariensis* DC. ex Ser., *S.F.* 17814 (P), Madagascar; *Bradford* 660 (MO), Madagascar; *Dumetz* 535 (P), Madagascar; *S.F.* 17814 (P), Madagascar; *Weinmannia madagascariensis* var. *aniba* Bernardi, *R.N.* 9765 (P; type of variety *aniba*), Madagascar

Section *Leiospermum*

LEI-serrata 5 species

- Weinmannia dichotoma* Brongn. & Gris, *MacKee* 15000 (P), New Caledonia; *MacKee* 18867 (P), New Caledonia; *MacKee* 31635 (P), New Caledonia; *Schmid* 4135 (P), New Caledonia; *Veillon* 1914 (P), New Caledonia; *Veillon* 3839 (P), New Caledonia
- Weinmannia monticola* Däniker, *Aubrèville* 230 (P), New Caledonia; *Hürlimann* 1875 (P), New Caledonia; *Jaffré* 2707 (P), New Caledonia; *MacKee* 44406 (P), New Caledonia; *McPherson* 5809 (MO), New Caledonia; *Veillon* 750 (P), New Caledonia
- Weinmannia ouaiemensis* (Guill. & Viro) Hoogland, *MacKee* 18670 (P), New Caledonia; *MacKee* 34088 (P), New Caledonia; *MacKee* 35993 (P), New Caledonia; *MacKee* 36001 (P), New Caledonia; *Schmid* 3370 (P), New Caledonia; *Veillon* 2273 (P), New Caledonia; *Viro* 731 (P; type), New Caledonia
- Weinmannia paitensis* Schltr., *Bernardi* 9881 (P), New Caledonia; *McPherson* 3403 (MO), New Caledonia; *Schlechter* 14941 (P; type), New Caledonia; *Thorne* 28733 (P), New Caledonia
- Weinmannia serrata* Brongn. & Gris, *Balansa* 2298 (P), New Caledonia; *Bernardi* 12816 (P), New Caledonia; *Bradford* 627 (MO), New Caledonia; *Brinson* 746 (P), New Caledonia; *MacKee* 35545 (P), New Caledonia; *Raynal* 16608 (P), New Caledonia; *Thiebaud* 22 (P), New Caledonia

LEI-sylvicola 1 species

- Weinmannia sylvicola* Sol. ex A. Cunn., *Bradford* 912 (MO), New Zealand; *Gardner* 1621 (MO), New Zealand; *Gardner* 2659 (MO), New Zealand; *Gardner* 5384 (MO), New Zealand; *Orchard* 4048 (MO), New Zealand; *Walker* 5243 (MO), New Zealand

LEI-racemosa 1 species

- Weinmannia racemosa* Lf., *Bradford* 910 (MO), New Zealand; *Chapman CHR* 258594 (MO), New Zealand; *Loh CHR* 359035 (MO), New Zealand; *Gardner* 169 (MO), New Zealand; *Gardner* 5350 (MO), New Zealand; *Thompson* 526 (MO), New Zealand; *Wood* 31653 (MO), New Zealand

LEI-affinis 15 species (in addition to the species cited below there are 2 undescribed species)

- Weinmannia affinis* A. Gray, *Bradford* 597 (MO), Fiji; *Gibbs* 642 (BISH), Fiji; *Hopkins* 5022 (MO), Fiji; *Seemann* 200 (P), Fiji; *Smith* 4905 (BISH, L, P), Fiji;

- Smith 7608 (BISH, L. P. SUVA), Fiji; U.S. Expl. Exped. US 48070 (US; type), Fiji
- Weinmannia croftii* H. C. Hopkins, *Clunie LAE 63017* (K, L; paratype), Papua New Guinea; *Ridsdale NGF 33981* (BISH, L; type) Papua New Guinea; *Stevens LAE 51252* (L; paratype) Papua New Guinea; *Vinas LAE 59724* (BISH, L; paratype), Papua New Guinea
- Weinmannia denhamii* Seem., *Aubert de la Rüe s.n.* (P), Vanuatu; *Bernardi 13258* (L, P), Vanuatu; *Morat 5897* (NOU, P), Vanuatu; *Kajewski 317* (BISH, P), Vanuatu; *MacGillivray 45* (P; isolectotype), Vanuatu
- Weinmannia marquesana* F. Br., *N. Hallé 2057* (P), Marquesas; *Perlman 10259* (BISH, MO, P), Marquesas; *Weinmannia marquesana* var. *myrsinites*, *Florence 9667* (MO), Marquesas
- Weinmannia parviflora* G. Forst., *Bradford 920* (MO), Society Islands, Tahiti; *Florence 3110* (P), Society Islands, Tahiti; *Florence 7935* (P), Society Islands; *Fosberg 62927* (BISH, P), Society Islands, Tahiti
- Weinmannia purpurea* Perry, *Kajewski 1738* (L; type), Papua New Guinea; *Kajewski s.n.* (L), Solomon Islands; *Maurias BSIP 12092* (BSIP, L), Solomons
- Weinmannia raiatensis* J. W. Moore, *Bradford 929* (MO), Society Islands, Raiatea; *Florence 3554* (P), Society Islands, Raiatea; *Florence 3746* (P), Society Islands, Raiatea; *Florence 3754* (P), Society Islands, Raiatea; *Florence 8945* (P), Society Islands, Raiatea; *B. H. Gagné 1457 bis* (P), Society Islands, Raiatea
- Weinmannia rapensis* F. Br., *Florence 6395* (MO), Rapa; *Florence 6514* (P), Rapa; *Hallé 7517* (P), Rapa; *N. Hallé 7700* (P), Rapa; *St. John 15304* (P), Rapa; *St. John 15305* (P), Rapa
- Weinmannia rarotongensis* Hemsl. ex Cheeseman, *Gardner 2503* (MO), Rarotonga; *MacKee 44191* (P), Rarotonga; *MacKee 44309* (MO, P), Rarotonga
- Weinmannia samoensis* A. Gray, *Bradford 800* (MO), Upolu, Western Samoa; *Bradford 807* (MO), Savaii, Western Samoa; *Christophersen 1943* (BISH, MO), Samoa; U.S. Expl. Exped. US 48072 (US; type), Samoa
- Weinmannia tremuloides* H. C. Hopkins & Florence, *Florence 9581* (P; type), Marquesas Islands
- Weinmannia vescoi* Drake, *Bradford 932* (MO), Society Islands, Raiatea; *Florence 8991* (P), Society Islands, Raiatea; *Morat 6990* (P), Society Islands, Raiatea; *St. John 17255* (P), Society Islands, Raiatea; *Vescoi s.n.* (P; type), Society Islands
- Weinmannia rutiensis* Seem., *Bryan 317* (BISH), Fiji; *Hopkins 5041* (MO), Fiji; *Seemann 199* (P; type), Fiji
- Cunonia**
- Cunonia-macrophylla** 3 species
- Cunonia macrophylla* Brongn. & Gris, *Bradford 607* (MO), New Caledonia; *McPherson 5387* (MO), New Caledonia; *McPherson 2277* (MO), New Caledonia
- Cunonia capensis* L., *Bradford 735* (MO), United States (Cultivated); *Goldblatt 1387* (MO), South Africa; *Rouske 734* (MO), South Africa; *Werdemann 2441* (MO), South Africa
- Cunonia schinziana* Däniker, *Däniker 506* (P; type), New Caledonia; *MacKee 17799* (P), New Caledonia; *MacKee 27546* (P), New Caledonia; *MacKee 38224* (P), New Caledonia
- Cunonia-purpurea** 13 species
- Cunonia atrorubens* Schltr., *Bradford 614* (MO), New Caledonia; *McPherson 2004* (MO), New Caledonia; *McPherson 2227* (MO), New Caledonia; *McPherson 4442* (MO), New Caledonia
- Cunonia austrocaledonia* Brongn. ex Guill., *Hoogland 12904* (MO), New Caledonia; *McPherson 1876* (MO), New Caledonia; *McPherson 1944* (MO), New Caledonia; *McPherson 3434* (MO), New Caledonia
- Cunonia cerifera* Hoogland, *McPherson 4450* (P; paratype), New Caledonia
- Cunonia deplanchei* Brongn. & Gris, *McPherson 4364* (MO), New Caledonia; *McPherson 6429* (MO), New Caledonia
- Cunonia lenormandii* Vieill. ex Brongn. & Gris, *McPherson 6418* (MO), New Caledonia
- Cunonia linearisepala* (Guill.) Bernardi, *McPherson 2878* (MO), New Caledonia
- Cunonia nervosa* Hoogland, *MacKee 15715* (P; type), New Caledonia
- Cunonia pseudoverticillata* Guill., *Blanchon 196* (P), New Caledonia
- Cunonia pterophylla* Schltr., *McPherson 2119* (MO), New Caledonia; *McPherson 4445* (MO), New Caledonia; *McPherson 2163* (MO), New Caledonia
- Cunonia purpurea* Brongn. & Gris, *McPherson 2082* (MO), New Caledonia; *McPherson 2637* (MO), New Caledonia; *McPherson 4396* (MO), New Caledonia
- Cunonia rupicola* Hoogland, *MacKee 19129* (P; type), New Caledonia
- Cunonia varijuga* Hoogland, *MacKee 22886* (P; type), New Caledonia
- Cunonia vieillardii* Brongn. & Gris, *McPherson 3998* (P), New Caledonia; *McPherson 4634* (MO), New Caledonia; *McPherson 4535* (MO), New Caledonia
- Cunonia-aoupiniensis** 2 species
- Cunonia aoupiniensis* Hoogland, *Morat 7977* (P; paratype), New Caledonia
- Cunonia montana* Schltr., *Bradford 609* (MO), New Caledonia; *McPherson 2930* (MO), New Caledonia; *Bernardi 12729* (MO), New Caledonia
- Cunonia-balansae** 2 species
- Cunonia balansae* Brongn. & Gris, *Bradford 617* (MO), New Caledonia; *McPherson 3313* (MO), New Caledonia; *McPherson 4127* (MO), New Caledonia; *Hoogland 12731* (MO), New Caledonia
- Cunonia rotundifolia* Däniker, *Jaffré 1954* (P), New Caledonia
- Cunonia-alticola** 2 species
- Cunonia alticola* Guill., *Bradford 611* (MO), New Caledonia
- Cunonia bernieri* Guill., *Morat 7660* (P), New Caledonia
- Cunonia-pulchella**
- Cunonia pulchella* Brongn. & Gris, *Bradford 635* (MO), New Caledonia; *McPherson 4037* (MO), New Caledonia; *McPherson 6034* (MO), New Caledonia
- Cunonia-bullata**
- Cunonia bullata* Brongn. & Gris, *McPherson 2241* (MO), New Caledonia
- Outgroups**
- Ackama**
- Ackama rosifolia* A. Cunn., *Bradford 909*, New Zealand

(MO); *Gardner 358*, New Zealand (MO); *Jessup s.n.*, New Zealand (MO#1616100); *Orchard 4040*, New Zealand (MO)

Caldeluvia

Caldeluvia paniculata D. Don, *Landrum 4476* (MO), Chile; *Morrison 17552* (MO), Chile; *Werdermann 681* (MO), Chile; *Werdermann 1855* (MO), Chile; *Zöllner 9639* (MO), Chile

Spiraeopsis

Spiraeopsis celebica Blume, *Bradford 834* (MO), Solomon Islands; *Bradford 840* (MO), Solomon Islands; *Elmer 11402* (MO), Philippines; *Elmer 14157* (MO), Philippines; *Elmer 15184* (MO), Philippines; *Wenzel 1087* (MO), Philippines

Vesselowskya

Vesselowskya rubifolia Pamp., *Boorman NSW 104729* (NSW), Australia; *Bradford 879* (MO), Australia; *Bradford 882* (MO), Australia; *Coveny 5676* (MO, NSW), Australia; *Coveny 10877* (MO, NSW), Australia; *Fraser s.n. NSW 104749* (MO, NSW), Australia; *Webb 11474* (MO), Australia

APPENDIX 2

List of possible autapomorphies for each ingroup OTU. Some assumptions of relationships were needed to hypothesize derived states. For example, comparisons of character states were made within sections, and the most generalized character state was usually considered primitive.

- WEI-pinnata: caducous petals (not present in all species, see discussion)
- WEI-tinctoria: unisexual flowers
- SPI-bojeriana: solitary flowers, double internode of branches
- SPI-icatifolia: no clear autapomorphies
- SPI-comorensis: no IM
- INS-rutenbergii: double internode of branches
- INS-louveliiana: solitary flowers
- INS-madagascariensis: no clear autapomorphies
- INS-venusta: IM branching
- FAC-fraxinea: fixed supernumerary IMs
- FAC-descombesiana: solitary flowers (has hybrid-like characteristics between sects. *Fasciculata* and *Leiospermum*)
- FAC-pullei: abortion of medial meristem
- FAC-clemensiae: no clear autapomorphies
- LEI-serrata: no clear autapomorphies
- LEI-affinis: unisexual flowers
- LEI-sylvicola: IM with two internodes and terminal abortion
- LEI-racemosa: no lateral IMs, IM terminus a bud
- Cunonia-macrophylla: large flowers, no medial meristem abortion, racemes borne directly along main stem
- Cunonia-purpurea: no clear autapomorphies
- Cunonia-aoupinienensis: lateral and medial IMs
- Cunonia-balansae: medial IMs only
- Cunonia bullata: IM with terminal raceme
- Cunonia-alticola: sessile flowers
- Cunonia pulchella: fasciated flowers

APPENDIX 3

CHARACTERS USED IN THE CLADISTIC ANALYSIS.

Numbers after character states refer to the coding in the data matrix as shown in Appendix 4. The plesiomor-

phic condition implied by the outgroups is listed first (state 0). Illustrations for many of these characters can be found in Bernardi (1961, 1963b, 1964, 1965) and Hopkins (1998a).

Vegetative Characters

- (1) Persistent, fused lateral stipules: present (0), absent (1).
- Stipule pairs that enclose lateral buds may be fused at their base. Even when most of the stipule has fallen off, the fused tissue may leave a "collar" around the base of the young branches. The lateral stipules may rarely be barely fused in section *Fasciculata*, but they do not persist as "collars."
- (2) Morphology of branches: basal bud absent (0), basal bud present (1), double internode present (2).

Three different branch morphologies were observed. In one, the first metamer produced by the lateral bud consists of an internode of normal length with a normal pair of leaves at the first node. In another pattern, a first internode of normal length is formed, but with buds at the base of this internode that are oriented in a plane perpendicular to the leaf axil ("basal bud" form). These basal buds appear to be homologous to axillary buds at a node. This homology becomes apparent in the third pattern of branch development. Here, the first metamer consists of a short internode without leaf development at the node, but with axillary buds produced ("double internode" form). Only the second metamer of this type of branch shows standard development of internode and leaves. This is treated as an ordered character, because the basal bud form is considered intermediate between the other conditions.

Taxa with basal buds often produce stems from them. This is especially true for section *Leiospermum*, in which the dominant medial and distal-lateral meristems are committed to reproduction. The double internode form is most pronounced in *Cunonia*.

- (3) Abortion of medial meristem: absent (0), present (1).
- Some groups have the tendency to abort the medial meristem. This branching pattern produces two new dominant stems, rather than a medial dominant stem plus a pair of suppressed lateral stems. Whenever this occurs as part of the branching pattern of a species it is scored as present. Only the New Caledonian species *W. dichotoma* and *W. monticola* branch this way at every node.
- (4) Lateral bud formation: additional pair(s) (0), one pair only (1).

Among OTUs, the number of axillary buds formed at a node varies. In some OTUs, only a single, usually prominent bud is formed. In other groups, a large axillary bud develops along with a second, smaller bud that is positioned between the large bud and the adaxial leaf surface. Because of its small size, this bud is often difficult to see, but when the large bud develops into a lateral branch the small bud may enlarge. Usually the small bud does not develop and may fall off quickly or persist during stem thickening. In section *Fasciculata*, many species also produce additional axillary buds at a node, but with no clear dominance among buds so that the extra buds are more easily visible. The additional buds in many species of section *Fasciculata* often develop into lateral IMs to form a series of IMs at a node. This is scored by character 31.

Flower and Fruit Characters

- (5) Pedicels: present (0), absent (1).
- In section *Spicata* the pedicel is so short that the receptacle lies against the axis of the raceme, although it is

not fused to the axis. This condition is scored as "pedicel absent." However, this character must be scored in flower, as some species develop a slender pedicel in fruit. A few species (e.g., *W. comorensis*) have a narrow, elongate receptacle that resembles a pedicel but is here considered non-homologous. See Bernardi (1964: tabs. 1-9; 1965: figs. 1-7) for illustrations.

(6) Calyx aestivation: valvate (0), imbricate (1).

Imbricate calyx aestivation is considered a synapomorphy for the *Canonia* (*Pancheria-Weinmannia*) clade. Hufford and Dickson (1992) reported imbricate calyx aestivation in *Vesselowskyia*, but the specimens examined for this study show valvate aestivation.

(7) Calyx persistence in fruit: present (0), absent (1).

This character is scored during fruit maturation. A score of "present" indicates that the calyx remains on mature fruits, while "absent" means that the calyx falls off during fruit maturation.

(8) Number of perianth parts: 5-merous (0), 4-merous (1), 3-merous (2).

In most OTUs the perianth tends to be either 4-merous or 5-merous, with the same number of sepals as petals. Only *Vesselowskyia* has a 3-merous perianth.

(9) Free nectary disk: present (0), absent (1).

The floral receptacle bears tissue between the staminal whorl and the gynoecium, or as ribbed outgrowths at the base of the outer carpel wall. Traditionally, these tissues have been called nectaries. Whether nectar is produced has not been examined carefully, but it is likely since commercial honey is produced from *Weinmannia* flowers (Walsh, 1978; Matheson, 1991; Ralimanana, 1994). Most Cunoniaceae have free nectaries, developing unattached to the carpel wall. The nectaries of *Canonia* are adnate to the carpel wall.

(10) Form of the nectary: segmented (0), ribbed (1), membranous (2).

Free nectaries are found in different shapes. Ribbed nectaries form a complete ring with alternating, longitudinal costae of varying thickness corresponding to the position of stamens. Membranous nectaries form an entire ring of thin tissue. Segmented nectaries do not form a continuous ring, but are composed of more or less separate, often slender parts usually positioned between the stamens.

(11) Floral sexuality: bisexual only (0), early unisexual (1), late unisexual (2), complete unisexual (3).

The sexual system of *Weinmannia* has been little studied. In most species with unisexual flowers, it appears that unisexual flowers are mostly distributed on different individuals (i.e., dioecious), but strict dioecy probably breaks down often. For example, sometimes both sexes, or bisexual and unisexual flowers, are found on the same plant (i.e., "leaky dioecy" or polygamodioecy). For this analysis, the potential to develop unisexual flowers was scored, even when bisexual flowers were known from a species. When unisexual flowers were unknown this was coded as bisexual only. See illustrations in Bernardi (1964).

There seem to be two distinct kinds of unisexual flowers in *Weinmannia*. The most common has relatively early suppression of the opposite sex, so that the carpels are very tiny in male flowers and the stamens weakly developed in female flowers. Two species of section *Weinmannia* from the Mascarene islands have flowers that are less conspicuously unisexual because sexual dimorphism is not very great. These are coded as a distinct kind of unisexual flower that is presumably caused by late suppres-

sion of the opposite sex. A third type of development is found in *Vesselowskyia rubifolia*, which has extreme suppression of parts of the opposite sex so that stamens do not develop in female flowers and carpels do not develop in male flowers.

(12) Position of the perianth: hypogynous (0), perigynous (1).

Most OTUs have hypogynous flowers with a fairly broad, flat receptacle upon which the carpel is borne at the same level as the perianth. In several species of section *Leiospermum* the carpel is sunken slightly into a narrowly concave receptacle with the perianth borne above the base of the carpel. These are scored as being perigynous.

(13) Fruit dehiscence: basipetal (0), circumbasal (1).

Circumbasal fruit dehiscence occurs when a zone at the base of the carpel splits from the receptacle. Usually this results in acropetal dehiscence (i.e., the capsule opens from the bottom up) along the sutures between the carpels, but circumbasal dehiscence is a more precise description of the difference between *Canonia* and most other Cunoniaceae. Most *Canonia* have styles that remain connate at the base, causing acropetal fruit dehiscence. A few *Canonia* species lack styler fusion, and the dehiscence is non-directional along the longitudinal suture between the carpels although circumbasal dehiscence is present. When the capsule splits open from the top, dehiscence is basipetal, as in *Weinmannia* and most other capsular-fruited Cunoniaceae.

(14) Fruit column: split pair (0), fused (1).

All OTUs have fruits composed of two united carpels that dehisce along their sutures, exposing two locules full of seeds. The seeds are borne in two rows in each locule, along axile placentae (Dickison, 1975, 1984). The degree of fusion of the placentae varies, being completely fused into a single column, or fused into a pair of bundles, with each bundle composed of the opposing edges of adjacent carpels. This character is easily visible as the carpels split in the mature fruit.

Weinmannia, *Canonia*, and *Vesselowskyia* have a single central column. In many species this central column is prominent because it remains intact and upright between the separate carpels after fruit dehiscence. In other groups the column is less conspicuous because it remains partially attached to one edge of a carpel, and after fruit dehiscence only a single, short stub remains near the receptacle. *Ackama* has a pair of columns that adheres to the carpels during dehiscence. Only by examining the fruit near the receptacle can the pair of columns be seen. In contrast, *Caldcluvia* and *Spiravopsis* have conspicuous pairs of columns that are detached from the carpel edges in fruit, but remain attached to the styles. These different patterns of fruit column morphology were illustrated by Godley (1983), although he did not notice the subtle vascular pair in *Ackama* and its underlying similarity to the columns of *Caldcluvia*.

(15) Seed wings: present (0), absent (1).

When flattened tissue extends around the seed then wings were coded as "present." Many *Weinmannia* species have a minute raphe along one side of the seed coat that may be homologous with the wings of other taxa (Dickison, 1984; Webb & Simpson, 1991). These were not coded as wings "present" because they are very small. Because minute wings occur, wings and hairs appear to be ontogenetically unrelated, and the two features were treated as separate characters, although they may serve the same function in seed dispersal.

(16) Seed hairs: absent (0), present (1).

Long, slender, unicellular outgrowths from the seed coat are found in all species of *Weinmannia* and *Ackama* (Dickson, 1984; Webb & Simpson, 1991).

(17) Distribution of hairs on seeds: sparse and widely distributed (0), comose at both ends (1), dense and widely distributed (2).

According to Dickson (1984), there are three basic patterns of hair distribution and density in *Weinmannia*. This more extensive survey largely agrees, although the distinction between the patterns is not always clear. Comose seeds have hairs concentrated at both ends in dense tufts. Otherwise, hairs are more or less evenly distributed around the seed and may be either so dense that the seed surface is obscured, or sparse, with the seed surface visible.

Many species are fixed for one of these patterns, but a few are highly variable and must be scored as polymorphic. For example, many members of section *Spicata* have comose hairs and hairs sparsely distributed on the same seed. In a few species of section *Fasciculata*, some specimens have comose seeds and other specimens have seeds with dense hairs all over the surface.

(18) Seed shape: straight (0), reniform (1).

Most seeds are straight or only slightly asymmetrical. Asymmetry is most pronounced in section *Weinmannia*, in which the seeds have a curved shape so that a line from one pole to the other would pass far from the center.

Floral Axis/Raceme Characters

(19) Floral inception: solitary (0), fasciculate (1).

Floral meristems develop in the axils of small bracts in all OTUs (Fig. 1). In some groups, a few to several floral meristems develop in each bract axil, and in others only a single floral meristem develops. The development of multiple floral meristems at a bract often results in fasciculate flowers (but see character 20 "bract fidelity"), while a solitary flower develops from a single meristem. Taxa with fasciculate inception of flowers have a large bract subtending the entire fascicle and smaller "bracteoles" subtending the individual flowers.

This character may vary within a raceme, but this variation is usually minor and occurs predictably, with solitary flowers at the very tip of the raceme and fasciculate flowers along most of the axis. A few American species of section *Weinmannia* living in extremely exposed, upland habitats have highly reduced racemes with relatively few flowers. In these species the flowers all arise solitarily. Because this feature is correlated with specialized ecology, solitary flowers within section *Weinmannia* are assumed to be a derived condition and were not scored in the matrix.

(20) Bract fidelity: present (0), absent (1).

Although flowers are initiated from bract axils, not all flowers remain in this position during the development of the raceme (Fig. 1). The elongation of the raceme axis may cause the separation from one another of flowers that were initiated at the same position. When mature flowers remain in the axil of their bract, then bract fidelity is said to be "present." When flowers move relative to the bract, due to a visible zone of elongation among the flowers, then bract fidelity is "absent."

(21) Persistence of floral bract: absent (0), present (1).

This character is scored around the time of floral maturity, such as when the anthers dehisce. Precise timing is difficult, because specimens are not collected at uniform developmental stages. If the bracts are consistently or firmly attached to the axis, not just hanging on loosely after abscission, persistence is coded as "present."

(22) Flower-bearing axis: branched (0), unbranched (1).

Vegetative branching in Cunoniaceae is almost uniformly decussate. In contrast, flower-bearing axes usually have a spiral arrangement of nodes. A distinction can be made between unbranched flower-bearing axes, which bear floral meristems only at the nodes, and branched axes, which give rise to both lateral inflorescence branches and floral meristems.

The term "raceme" is used here to denote any unbranched, flower-bearing axis. Family-level cladograms (Hufford & Dickson, 1992) imply that racemes are derived from branched flower-bearing axes. In fact, the morphology of fascicled-flowered racemes (character 19) suggests that they may be derived from branched flower-bearing axes through the suppression of lateral branching and elongation of the primary axis. For example, on occasion lateral branching is not totally suppressed in a fascicled-flowered raceme, and at the base of an axis short branches may arise. This implies that a group of fascicled flowers may be homologous to a short shoot of solitary ones, an hypothesis that also accounts for the presence of bracteoles subtending individual flowers in a fascicle. If fascicled-flowered racemes are derived from branched flower-bearing axes, then this character state (see character 19) is expected to be plesiomorphic in *Weinmannia*.

(23) Racemes arising as split pairs: present (0), absent (1).

In some taxa, raceme meristems have the tendency (i.e., this character is not always expressed) to split and form a pair of racemes from a single initial. Often, the pair of racemes is united by common rachis tissue near their base.

Inflorescence-Module (IM) Characters

(24) Development of flower-bearing axes as part of IMs: present (0), absent (1).

Species of section *Weinmannia* (Fig. 2c) and a few of section *Spicata* (Fig. 3d) have flower-bearing axes only developing directly from axillary buds along the main stem. Other taxa develop racemes as parts of an IM. IMs are recognized as distinct from vegetative metamers by such characteristics as usually shortened internodes, complete or partial suppression of leaf development, and distinct branch morphology.

(25) IM shoot: long (0), short (1).

The internodes within an IM are very short relative to vegetative internodes in most *Weinmannia* species. In sections *Leiospermum* and *Cunonia*, IM internodes are similar in length to vegetative ones.

(26) Fate of IM terminus: flower-bearing axis (0), vegetative bud (1), aborted (2).

This character accounts for what happens to the dominant apical meristem within an IM. There are three meristem fates: vegetative bud (Figs. 2b, 3a), flower-bearing axis (Figs. 2a, 3c), or aborted (Fig. 3b, c). Taxa that have vegetative buds terminating the IM often develop vegetative branches after fruiting.

(27) IM metamer development: branched (0), sequential (1), unimodal (2).

IMs may be composed of one to several metamers. In many species of *Weinmannia* and *Cunonia*, the IM is limited to a single raceme-bearing metamer (unimodal; Figs. 2b, 3a, b). Species in section *Leiospermum* and some members of section *Inspersa* have IMs with the potential to develop more than one metamer in a sequence, without branching, and with racemes at each node (sequential:

Figs. 2a, 3c). A pair of species in section *Inspersa* have racemes borne at the ends of a decussate-branched module (branched; Fig. 3c).

As mentioned previously, *Weinmannia dichotoma* and *W. monticola* have a fixed vegetative architecture in which the medial meristem at each node is aborted (Fig. 3b). This architecture is carried into the inflorescence in these species and precludes development of two medial metamers in a sequence. Here, this is regarded as a derived condition and is not included in the data matrix. Instead *W. dichotoma* and *W. monticola* have been placed in an OTU with all other New Caledonian species (*W. ouaiemensis*, *W. paitensis*, and *W. serrata*).

Total Inflorescence (TI) Characters

(28) Flower-bearing axis borne along the main stem: absent (0), present (1).

This character distinguishes whether nodes along the main stem axis bear racemes directly from axillary buds. However, direct development of racemes from axillary buds of the main stem does not preclude the development of racemes as part of an IM.

(29) Position of IM: lateral only (0), lateral and medial (1), medial only (2).

This refers to the location of IMs relative to the main

axis of stem growth. Lateral IMs develop from axillary buds. A medial IM develops from medial, apical buds. This character is inapplicable when racemes only develop directly from meristems along the main stem, e.g., in section *Weinmannia* (Fig. 2c) and the *W. comorensis* group (Fig. 3d) of section *Spicata*, for which characters 24 and 28 are coded as state 1.

(30) TI formed by more than one main stem metamer: present (0), absent (1).

This character scores whether the main stem produces racemes or IMs at successive nodes. For example, this character is scored "absent" for Figure 2c and "present" for Figure 3d.

(31) TI dominance: basitonic (0), isotonic (1), acrotonic (2)

The size or proliferation of IMs or flower-bearing axes may depend on their position within the TI. Isotonic TIs have IMs or flower-bearing axes of the same size at all nodes. Basitonic TIs have larger basal, subdistal metamers, while acrotonic TIs have larger distal metamers.

Acrotonic development is manifested in two distinct ways in *Weinmannia*, but scored as the same character state: variation in the number of metamers within an IM (e.g., sect. *Leiospermum*, Fig. 2a), and variation in the number of IMs at a node in response to the position within the TI (e.g., sect. *Fasciculata*, Fig. 3a).

APPENDIX 4

Character matrix. See Appendix 1 for composition of OTUs, and Appendix 3 for discussion of characters.

OTUs/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31		
<i>WEI-pinnata</i> (73 sp)	1	0	0	0	1	0	1	0	1	0	0	0	1	1	1	0	1	1	0	1	0	1	1	0	1	-	-	1	-	1	-		
<i>WEI-tinctoria</i> (2 sp)	1	0	0	0	1	0	0	0	1	2	0	0	1	1	1	0	1	1	0	1	0	1	1	0	1	-	-	1	-	1	-		
<i>SPI-bojeriana</i> (16 sp)	0	2	1	1	1	0	0	0	2	0	0	0	1	1	1	0/1	0	0	0	1	0/1	1	1	0	1	1	2	1	1	0	1		
<i>SPI-icacifolia</i> (6 sp)	0	1	1	1	1	0	0	2	0	0	1	1	1	1	1	1	0	0	1	1	0/1	1	1	0	1	1	2	1	1	0	1		
<i>SPI-comorensis</i> (5 sp)	0	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	0/1	1	1	1	-	-	1	-	1	-	0		
<i>INS-rutenbergii</i> (2 sp)	0	2	1	1	0	0	0	1	0	0	0	1	1	1	1	2	0	0	0	1	1	1	0	1	0/1	0/1	0/1	0	0	0	0		
<i>INS-louveliana</i> (3sp)	0	1	1	1	0	1	0	0	1	0	0	0	1	1	1	2	0	0	1	1	1	1	0	1	1	1	2	1	1	0	1		
<i>INS-madagascariensis</i> (2 sp)	0	1	1	0	1	0	0	1	0	0	1	0	0	1	1	2	0	0	1	1	1	1	0	1	1	1	2	1	1	0	1		
<i>INS-venusta</i> (2 sp)	0	1	1	1	0	0	1	0	0	1	0	0	1	1	1	2	0	1	0	1	1	1	0	1	1	0/1	0/1	0	1	0	0		
<i>FAC-fraxinea</i> (12 sp)	1	0	0	0	1	0/1	0	1	0	0	1	1	1	1	1	1	0	1	0/1	0/1	0	1	0	0	1	1	2	0	1	0	2		
<i>FAC-descombesiana</i> (1 sp)	1	0	1	0	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	1	1	0	0	1	1	0	1	2	0	1	0	2	
<i>FAC-pullei</i> (3 sp)	1	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0/1/2	0	1	0	1	1	1	0	1	1	1	1	2	0	1	0	1	
<i>FAC-clemensiae</i> (2 sp)	1	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0/1	0	1	0	1	0	1	1	0	1	1	1	2	0	1	0	1	
<i>LEI-serrata</i> (5 sp)	0	1	1	0	1	1	0	0	1	0	0	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0/2	1	0	1	0	2	
<i>LEI-affinis</i> (14 sp)	0	1	1	0	1	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	0	2
<i>LEI-sylvicola</i> (1 sp)	0	1	1	0	1	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	1	1	0	1	2	1	0	1	0	2	
<i>LEI-racemosa</i> (1 sp)	0	1	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0	1	1	0	1	1/2	1	0	2	-	-	
<i>Cunonia-macrophylla</i> (3 sp)	0	2	0	1	0	1	1	0	1	-	0/1	1	1	0	0	-	0	0/1	0	0	0	1	1	0	1	0/1	1	2	1	0	1	-	
<i>Cunonia-purpurea</i> (13 sp)	0	2	1	1	0	1	0	1	0	1	-	0	1	1	0	0	-	0	0	0	0	0	1	1	0	0	1	2	0	0	0	1	
<i>Cunonia-acupiniensis</i> (2 sp)	0	2	1	1	0	1	0	1	0	1	-	0	1	1	0	0	-	0	0	0	0	0	1	1	0	0	1	2	0	1	-	-	
<i>Cunonia-balansae</i> (2 sp)	0	2	1	1	0	1	0	1	-	0	1	1	0	0	0	-	-	0	0	0	0	0	1	1	0	0	1	2	0	0	1	-	
<i>Cunonia bullata</i> (1 sp)	0	2	1	1	0	1	0	1	-	0	0	1	1	0	0	-	-	0	0	0	0	0	1	1	0	0	1	2	0	0	1	-	
<i>Cunonia-aiticola</i> (2 sp)	0	2	1	1	1	0	1	0	1	-	0	0	1	1	0	0	-	0	0	0	0	0	1	1	0	0	1	2	0	0	0	1	
<i>Cunonia pulchella</i> (1 sp)	0	2	1	1	0	1	0	1	-	0	0	1	1	0	0	-	-	0	1	0	0	1	1	0	0	1	2	0	0	0	1	-	
<i>Caldcluvia paniculata</i>	1	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	1	0	-	1	-	-	-	1	-	0	0		
<i>Spiracopsis celebica</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0/1	0	0	0	0	-	1	-	-	-	1	-	0	1		
<i>Vesselowskyia rubifolia</i>	1	0	0	0	1	2	0	0	3	0	0	1	0	0	0	0	-	0	0	0	0/1	0	0	0	0	0/1	0	0	0	0	1	0	
<i>Ackama rosifolia</i>	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	-	1	-	-	-	1	-	0	0	0	