

Phylogenetic relationships in Magnoliaceae subfam. Magnolioideae: a morphological cladistic analysis

J. Li¹ and J. G. Conran²

¹Kunming Division of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, Yunnan, P.R. China

²Centre for Evolutionary Biology and Biodiversity, Environmental Biology, School of Earth and Environmental Sciences, The University of Adelaide, South Australia

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Abstract. Relationships within Magnolioideae have been the subject of persistent debate; the main point at issue mostly being the disposition of tribes, genera and sections. A morphological cladistic analysis of the subfamily using *Liriodendron* as the out-group showed that Magnolioideae consisted of a large basal polytomy, but with five resolved and variously supported clades. *Manglietia* constituted a clade with sect. *Rytidospermum* of *Magnolia* subg. *Magnolia*. *Kmeria* and *Woonyoungia* formed a pair. *Pachylarnax*, *Parakmeria* and *Manglietiastrum* were grouped together, and sect. *Splendentes* and *Dugandiodendron* also formed a pair. The largest and best supported clade consisted of *Magnolia* subg. *Magnolia* sects. *Oyama* and *Maingola*, *Magnolia* subg. *Yulania*, *Michelia*, *Aromadendron*, *Alcimandra*, *Elmerrillia*, *Paramichelia* and *Tsoongiodendron*, with sect. *Oyama* of *Magnolia* subg. *Magnolia* is sister to the remainder. Although *Magnolia* sect. *Maingola*, *Aromadendron*, *Alcimandra* and *Elmerrillia* constituted a poorly resolved subclade, *Aromadendron* formed a monophyletic clade with *Alcimandra*. Within the *Michelia*/*Magnolia* subgen. *Yulania* subclade, *Paramichelia* was sister to *Tsoongiodendron*. These results are supported by similar placement of taxa within various molecular analyses of the family, but the low level of resolution indicates that more

morphological data are needed to improve phylogenetic signal. Our results support the molecular analyses in suggesting that *Magnolia* is best considered to be a large and diverse genus, but that the relationships between the taxa within it require more detailed clarification, with more extensive sampling and a combined molecular and morphological approach being needed.

Key words: Angiosperm, Magnoliaceae, Magnolioideae, Phylogeny, morphology, relationships, *Magnolia*.

Introduction

Magnoliaceae are a well-defined family of over 230 species characterised by annular stipular scars around the nodes, and floral parts spirally arranged on an elongated receptacle. The species are largely tropical and subtropical, but several extend into temperate regions, although greatest diversity is in subtropical to tropical Southeast Asia.

Because of extensive homogeneity and confusion of generic delimitation, there has been persistent debate and a number of taxonomic treatments, each differing in the disposition of

tribes, genera and sections (Chen and Nootboom 1993; Dandy 1927, 1964, 1978; Law 1984, 1996, 2000; Nootboom 1985, 1993, 2000). Dandy (1927, 1964, 1978) divided Magnoliaceae into two tribes: Liriodendreae (*Liriodendron* only) and Magnolieae with eleven genera: *Manglietia*, *Magnolia*, *Talauma*, *Alcimandra*, *Aromadendron*, *Pachylarnax*, *Kmeria*, *Elmerrillia*, *Michelia*, *Paramichelia* and *Tsoongiendendron*. Law (1984) subsequently added three new genera: *Manglietiastrum*, *Parakmeria* and *Dugandiodendron*, and modified Dandy's classification, dividing Magnoliaceae into two subfamilies: Magnolioideae and Liriodendroideae, the former consisting of two tribes (Magnolieae and Micheliaceae), four subtribes (Manglietiinae, Magnoliinae, Elmerrilliinae and Micheliinae) and 14 genera. He subsequently (Law 1997) moved *Alcimandra* from the Magnoliinae to the new subtribe Alcimandriinae. Nootboom (1985, 1993) agreed with Law (1984) at the subfamily level, but recognised only two tribes: Magnolieae and Micheliaceae, with only four genera (*Magnolia*, *Kmeria*, *Manglietia* and *Pachylarnax*) retained in the Magnolieae; the previously recognised genera *Talauma*, *Dugandiodendron*, *Aromadendron*, *Alcimandra*, *Manglietiastrum* placed as subgenera or sections within *Magnolia*. Two genera (*Michelia* and *Elmerrillia*) were included within Nootboom's Micheliaceae, with *Tsoongiendendron* and *Paramichelia* reduced to sections in *Michelia*. Chen and Nootboom (1993) modified Nootboom's (1985) system placing *Manglietiastrum* as a section of *Manglietia*, and Nootboom (2000) subsequently retained the subfamilies, but deleted all tribes and subtribes. Magnolioideae were reduced to two genera *Magnolia* and *Pachylarnax*, and *Magnolia* was reduced to two subgenera: subg. *Magnolia* and subg. *Yulania*, with all previously recognised genera treated as sections or subsections within *Magnolia*. *Michelia* was reduced to several sections within *Magnolia* subg. *Yulania*.

There is no disagreement about the status of Liriodendroideae, containing only *Liriodendron* with two intercontinental species. However, although there seems to be broad

agreement for two subfamilies, generic delimitations within Magnolioideae have been the subject of persistent debate and disagreement for at least half a century, with much of the basis for the confusion being the apparently homoplasious development of characters that were considered important by several taxonomists (Nootboom 2000).

Xu et al. (2000) undertook a morphology-based cladistic analysis of Magnoliaceae using 23 taxa and a range of characters. However, their analysis did not cover all of the taxa at sectional rank or higher within Magnolioideae, and since that study, there have been reconsiderations for some characters and their states within the family, especially shoots, floral development and fruits (e.g. Figlar 2000 and pers. comm., Zeng et al. 2001). In addition, molecular biologists have recently joined the debate (Azuma et al. 2000; Kim et al. 2001; Qiu et al. 1993, 1995a, 1995b; Shi et al. 2000; Ueda et al. 2000), suggesting further variations on relationships within the family.

Because much of the debate centres around the relative importance of different morphological characters in the family, the purpose of our study was to examine the infrafamilial groupings proposed by previous researchers, and to investigate intergeneric relationships within the Magnolioideae by a morphology-based cladistic analysis covering all taxa at sectional rank and above, using the revised information about characters and states, and comparing these results against those of the molecular studies by other researchers.

Materials and methods

Taxon sampling. Thirty-one genera or sections variously proposed by Dandy (1927, 1964, 1974, 1978), Law (1984, 1996, 2000), Nootboom (1985, 1993, 2000), Chen and Nootboom (1993), Yu (1994) or Zheng (1995) were included in the analysis (Table 1). Most of these sampled taxa are either monotypic or homogeneous for the character states used here, reducing possible problems that might be caused by polyphyly and or polymorphy.

Characters. Data were scored for twenty-eight morphological characters (Table 2) from both

Table 1. Taxa included in the analysis. Taxonomic treatment mainly follows Law (1984, 1996, 2000), but also includes other taxa variously recognised by Dandy (1927, 1964, 1978), Nootboom (1985, 1993, 2000) and Chen and Nootboom (1993)

Subfamily Magnolioideae	Species sampled
Tribe Magnolieae	
Subtribe Manglietinae	
<i>Manglietia</i>	<i>Manglietia grandis</i> Hu & Cheng <i>Manglietia decidua</i> Q. Y. Zheng
<i>Manglietiastrum</i>	<i>Manglietiastrum sinicum</i> Law
<i>Pachylarnax</i>	<i>Pachylarnax praecalva</i> Dandy
Subtribe Magnoliinae	
<i>Magnolia</i>	
Subgenus <i>Magnolia</i>	
Sect. <i>Magnolia</i>	<i>Magnolia virginiana</i> L.
Sect. <i>Splendentes</i>	<i>Magnolia splendens</i> Urb.
Sect. <i>Gwillimia</i>	<i>Magnolia delavayi</i> Franch.
Sect. <i>Lirianthe</i>	<i>Magnolia pterocarpa</i> Roxb.
Sect. <i>Rytidospermum</i>	<i>Magnolia officinalis</i> Rehd. & Wils.
Sect. <i>Oyama</i>	<i>Magnolia wilsonii</i> (Finet & Gagnep.) Rehd.
Sect. <i>Theorhodon</i>	<i>Magnolia grandiflora</i> L.
Sect. <i>Maingola</i>	<i>Magnolia maingayi</i> King
Subgenus <i>Yulania</i>	
Sect. <i>Yulania</i>	<i>Magnolia campbellii</i> Hook.f. & Thoms.
Sect. <i>Buergeria</i>	<i>Magnolia biondii</i> Pamp.
Sect. <i>Tulipastrum</i>	<i>Magnolia quinquepeta</i> (Buc'hoz) Dandy
<i>Talauma</i>	
Sect. <i>Talauma</i>	<i>Talauma mexicana</i> DC.
Sect. <i>Blumiana</i>	<i>Talauma candollii</i> Blume
<i>Dugandiodendron</i>	<i>Dugandiodendron mahechae</i> Lozano
<i>Aromadendron</i>	<i>Aromadendron elegans</i> Blume
<i>Parakmeria</i>	<i>Parakmeria nitida</i> (W. W. Smith) Law
<i>Kmeria</i>	<i>Kmeria duperreana</i> (Pierre) Dandy
<i>Woonyoungia</i>	<i>Woonyoungia septentrionalis</i> (Dandy) Law
Subtribe Alcimandriinae	
<i>Alcimandra</i>	<i>Alcimandra cathcartii</i> (Hook.f. & Thoms.) Dandy
Tribe Micheliaceae	
Subtribe Elmerrilliinae	
<i>Elmerrillia</i>	
Sect. <i>Elmerrillia</i>	<i>Elmerrillia tsiampacca</i> (L.) Dandy
Sect. <i>Pseudoaromadendron</i>	<i>Elmerrillia ovalis</i> (Miq.) Dandy
Subtribe Micheliinae	
<i>Michelia</i>	
Sect. <i>Michelia</i>	<i>Michelia champaca</i> L.
Sect. <i>Micheliopsis</i>	<i>Michelia figo</i> (Lour.) Sprengel
Sect. <i>Dichlamys</i>	<i>Michelia balansae</i> (A. DC) Dandy
Sect. <i>Anisochlamys</i>	<i>Michelia hypolampra</i> Dandy
<i>Paramichelia</i>	<i>Paramichelia baillonii</i> (Pierre) Hu
<i>Tsoongiodendron</i>	<i>Tsoongiodendron odorum</i> Chun

Table 2. Morphological characters and their states used in the cladistic analysis

1.	Habit: evergreen (0), deciduous (1);
2.	Leaf lobing: entire (0), lobed (1);
3.	Leaf arrangement: evenly arranged at the twigs (0), crowded into false whorls at the ends of the twigs (1);
4.	Leaf margin thin and not sclerophyllous (0), thick and sclerophyllous (1);
5.	Young leaf orientation in vegetative bud: erect (0), pendant (1);
6.	Young leaf vernation (prefoliation): conduplicate (0), flat or curved (1);
7.	Stipule attachment: adnate to the petiole (0), stipule free (or appearing free) from the petiole (1);
8.	Branching morphology: sylleptic (0), proleptic (1);
9.	Flower position: terminal on existing branches only (0), both terminal on existing branches and pseudoaxillary on proleptic brachyblasts (1);
10.	Flowering time: later in the season, over a longer period (0), precocious, mostly all at once (1);
11.	Sexuality: bisexual (0), androdioecious (1), unisexual monoecious (2), unisexual dioecious (3);
12.	Outer and inner tepals: subequal (0), unequal (1);
13.	Number of tepals: nine or more (0), six or fewer (1);
14.	Gynoecium exposure: not covered by the androecium (0), androecium covering the gynoecium (1);
15.	Gynophore: absent (0), present (1);
16.	Anther dehiscence: latrorse (0), introrse (1), extrorse (2);
17.	Anther connective shape: appendage short acute (<10 mm long) (0), connective blunt or retuse (1), appendage long (\geq 10 mm long) (2);
18.	Anther connective attachment: not embedded to the gynoecium (0), embedded to the gynoecium (1);
19.	Carpel number: \geq 10 (0), <10 (1);
20.	Carpel arrangement: many arranged spirally on the receptacle (0), singular in verticillate whorl (1);
21.	Pre-dehiscence fruiting carpel fusion: conerescent (0), separate (1);
22.	Number of ovules in each carpel: four or more (0), fewer than 4 (1);
23.	Fruiting carpel apices: beaked (0), not beaked (1);
24.	Fruit type: follicle (0), samaroid (1);
25.	Fruit dehiscence: indehiscent (0), apical parts mostly breaking / falling away circumscissile, singly or irregular masses, while also more or less parting along the dorsal / ventral suture (1), apical parts persistent, carpels splitting mostly via the dorsal / ventral suture (2), apical parts persistent, carpels splitting mostly via the ventral suture (3), apical parts persistent, carpels splitting mostly via the dorsal suture (4);
26.	Carpel rib upon carpel dehiscence: dehiscent (0), persistent (1);
27.	Fruit shape: ellipsoid, not usually distorted (0), cylindrical or oblong, usually more or less distorted (1);
28.	Testa from the endocarp (0), testa adherent to the endocarp (1).

living and herbarium specimens housed at IBSC, KUN, PE and SING (abbreviations follow Holmgren et al. 1990), or, where living or pressed plants were not available for examination, information

was taken from published literature (e.g. Chen and Nooteboom (1993), Chun (1963), Dandy (1927, 1964, 1974, 1978) Hu (1940), Hu and Cheng (1951), Law (1980, 1984, 1996, 2000), Law and Wu

(1996), Lozano-Contreras (1975, 1984), Nootboom (1985, 1993, 2000), Vazquez-Garcia (1994), Yu (1994) and Zheng (1995)).

Out-group. *Liriodendron* contains two intercontinentally disjunct species (one in SE North America, one in E Asia), and is characterised by lobed leaves, extrorse anthers and samaroid fruits. On the basis of both morphological and molecular data (Azuma et al. 2000; Chase et al. 1993; Chen and Nootboom 1993; Dandy 1927, 1964, 1978; Law 1984, 1996, 2000; Nootboom 1985, 1993, 2000; Qiu et al. 1993; Shi et al. 2000; Ueda et al. 2000), it is clearly distinct from all other Magnoliaceae (to the point that Barkley (1975) removed it to its own family), and the Asian *L. chinense* was chosen as the out-group for the analyses.

Phylogenetic analysis. The data matrix (Table 3) derived from the characters in Table 2 was analysed using PAUP* version 4.0b10 (Swofford 2001). In an initial analysis, all characters were treated as unordered, uninformative characters were deleted; a heuristic search option was utilized with random tree addition (1,000 replicates) and TBR branch swapping. Due to the high number of trees produced, a maximum of 10,000 trees per replicate was saved.

As a measure of which characters are more phylogenetically informative and which are more homoplasious, as well as to arrive at a more stable topology, an heuristic strategy designed to find optimal (parsimonious) trees was followed, the characters were re-weighted *a posteriori* based on their fit (consistency index, CI) to the trees produced in the analysis (Farris 1969). Bootstrap support was estimated using the same swapping options on a further 1,000 replicates.

Results

Character patterns. Within the characters sampled, there were a number of character states that showed distinctive distribution patterns within Magnolioideae as follows:

1. *Habit*: Evergreen leaves occur in most taxa within the family Magnoliaceae, but truly deciduous species are restricted to *Liriodendron*, *Magnolia* subg. *Yulania*, and subg. *Magnolia* sects. *Rytidospermum* and *Oyama*. A deciduous species of *Manglietia* was found in the mixed woods of Jiangxi, E China, and solely based on its deciduous habit, a new genus *Sinomanglietia* was established (Yu 1994), however, Zheng (1995) considered it to be within *Manglietia*. Although populations of *Magnolia virginiana* from the northern part of its range are facultatively deciduous, that is they may lose a few to most of their leaves depending on the severity of the winter, it is essentially evergreen.
2. **Leaf lobing*: Entire leaves are common throughout the family; *Liriodendron* is the only group in Magnoliaceae with “lobed” leaves. Although emarginate leaves occur in *Magnolia officinalis* of sect. *Rytidospermum* and *M. sargentiana* of sect. *Yulania*, they are not really lobed *sensu stricto*.
3. *Leaf arrangement*: Most taxa have evenly arranged leaves at the twigs, but *Magnolia* sect. *Rytidospermum* is characterised by leaves crowded into false whorls at the ends of the branchlets. False whorls are also encountered in several *Manglietia* spp. especially *M. grandis*, although there it is not as pronounced as in sect. *Rytidospermum* (Figlar pers. comm.)
4. **Leaf margin*: *Talauma* sect. *Blumiana* differs from sect. *Talauma* by the presence of thick sclerophyllous leaf margins, often including a vein. A thick marginal ridge also helps to identify certain species of *Manglietia*, *Michelia* and *Magnolia* subg. *Magnolia*. In addition, foliar sclereids are rare in *Alcimandra*, *Liriodendron*, *Paramichelia* and most species of *Elmerrillia* (Nootboom 1985, 1993).
5. **Young leaf orientation in vegetative bud*: According to Law (1984), young leaves are pendent while in bud in *Liriodendron*, but erect in the members of subfam. Magnolioideae.
6. *Young leaf veneration (prefoliation)*: Two kinds of veneration (also called prefoliation) occur in Magnoliaceae: conduplicate and flat-open. The former occurs in most taxa, whereas the latter is found in *Manglietiastrum*, *Pachylarnax* and *Parakmeria*. Although Law (1984) reported flat-open

Table 3. Data matrix of morphological characters used in the cladistic analysis. *indicates the outgroup taxon

Characters	1	11	11	11	11	12	22	22	22	22	22	22		
Taxa	12	34	56	78	90	12	34	56	78	90	12	34	56	78
<i>Manglietia grandis</i>	00	10	00	00	00	00	00	01	00	00	00	00	20	00
<i>Manglietia deciduas</i>	10	10	00	00	00	00	00	01	00	00	00	00	20	00
<i>Manglietiastrum sinicum</i>	00	00	01	10	00	00	00	11	00	00	01	00	30	00
<i>Pachylarnax praecalva</i>	00	00	01	10	00	00	01	01	00	11	00	00	30	00
<i>Magnolia virginiana</i>	00	00	00	00	00	00	00	01	00	00	01	00	20	00
<i>Magnolia splendens</i>	00	00	00	10	00	00	00	01	21	00	01	00	20	00
<i>Magnolia delavayi</i>	00	00	00	00	00	00	00	01	00	00	01	00	20	00
<i>Magnolia pterocarpa</i>	00	00	00	00	00	00	00	01	00	00	01	00	20	00
<i>Magnolia officinalis</i>	10	10	00	00	00	00	00	01	00	00	01	00	20	00
<i>Magnolia wilsonii</i>	10	00	00	01	00	00	00	01	10	00	01	00	20	00
<i>Magnolia grandiflora</i>	00	00	00	10	00	00	00	01	00	00	01	00	20	00
<i>Magnolia maingayi</i>	00	00	00	11	11	00	00	01	00	00	01	10	20	10
<i>Magnolia campbellii</i>	10	00	00	01	11	00	00	00	00	00	01	10	20	10
<i>Magnolia biondii</i>	10	00	00	01	11	01	00	00	00	00	01	10	20	10
<i>Magnolia quinquepeta</i>	10	00	00	01	11	01	00	00	00	00	01	10	20	10
<i>Talauma mexicana</i>	00	00	00	00	00	00	00	01	00	00	01	00	10	00
<i>Talauma candolli</i>	00	01	00	00	00	00	00	01	00	00	01	00	10	00
<i>Dugandiodendron mahechae</i>	00	00	00	10	00	00	00	01	20	10	01	00	10	00
<i>Aromadendron elegans</i>	00	00	00	11	11	00	00	11	20	00	01	10	10	10
<i>Parakmeria nitida</i>	00	00	01	10	00	10	00	11	00	00	01	10	20	00
<i>Kmeria duperreana</i>	00	00	00	00	00	20	10	01	00	00	01	00	30	00
<i>Woonyoungia septentrionalis</i>	00	00	00	00	00	30	10	01	00	10	01	00	40	00
<i>Alcimandra cathcartii</i>	00	00	00	11	11	00	01	11	00	00	01	10	20	10
<i>Elmerillia tsiampacca</i>	00	00	00	11	11	00	00	01	00	00	01	10	20	10
<i>Elmerillia ovalis</i>	00	00	00	11	11	00	00	01	00	00	01	10	10	10
<i>Michelia champaca</i>	00	00	00	01	11	00	00	10	00	00	10	10	20	10
<i>Michelia figo</i>	00	00	00	01	11	00	10	10	00	00	10	10	20	10
<i>Michelia balansae</i>	00	00	00	11	11	00	10	10	00	00	10	10	20	10
<i>Michelia hypolampra</i>	00	00	00	11	11	01	00	10	00	10	10	10	20	10
<i>Paramichelia baillonii</i>	00	00	00	01	11	00	00	10	00	00	00	10	11	00
<i>Tsoongiodendron odorum</i>	00	00	00	01	11	00	01	10	00	00	00	10	10	10
* <i>Liriodendron chinense</i>	11	00	10	10	00	00	00	02	00	00	01	?1	00	01

vernation in *Paramichelia*, Sima (2001) confirmed that it is conduplicate.

7. *Stipules*: Magnoliaceae stipules form a cap enclosing and protecting the bud. These rupture longitudinally, falling to leave an annular scar. Although free from the petiole in many taxa, the stipules are adnate to the petiole in *Magnolia* sects. *Magnolia*, *Gwillimia*, *Lirianthe*, *Rytidospermum* and *Oyama* of subg. *Magnolia*, sects. *Yulania*, *Buergeria* and *Tulipastrum* of subg. *Yulania* and *Talauma*, *Manglietia*,

Woonyoungia, *Kmeria*, *Paramichelia*, *Tsoongiodendron*, *Michelia* sect. *Micheliopsis* and some species of sect. *Michelia*.

8. *Branching morphology*: Two types of growth morphology occur in Magnoliaceae: syllepsis and prolepsis. As defined by Figlar (2000), sylleptic branches are produced directly from the current year's growth; whereas proleptic branches are produced from dormant lateral meristems in the leaf axils of the previous year's growth. Based on Figlar's observations

- (2000 and pers. comm.), sylleptic growth occurs in *Magnolia* subgen. *Magnolia* except for sects *Maingola* and *Oyama*. Proleptic branches occur in *Aromadendron*, *Alcimandra*, *Elmerrillia*, *Michelia*, *Paramichelia*, *Tsoongiodendron*, *Magnolia* subg. *Yulania* and subg. *Magnolia* sect. *Maingola* and sect. *Oyama*.
9. *Flower position*: Magnolioideae were divided traditionally into two tribes on the basis of the flower position: terminal in the Magnolieae and axillary in the Michelieae (Chen and Nooteboom 1993; Dandy 1927, 1964, 1978; Law 1984, 1996, 2000; Nooteboom 1985, 1993, 2000). Figlar (2000) confirmed that flower buds in *Magnolia* subg. *Yulania* are initiated from proleptic brachyblasts, as in the Michelieae, and more recently found that flowers in *Alcimandra*, *Aromadendron* and *Magnolia* subg. *Magnolia* sect. *Maingola* are also proleptic (Figlar pers. comm.).
 10. *Flowering time*: Precocious flowering has been one of the main characters used to separate *Magnolia* subg. *Yulania* from subg. *Magnolia*. Nevertheless, Figlar (2000) revealed “few new leaves are fully developed at the time of bloom in *Michelia* as in *Magnolia* subg. *Yulania*”. In addition, *Alcimandra*, *Aromadendron*, *Elmerrillia*, *Paramichelia*, *Tsoongiodendron* and *Magnolia* subg. *Magnolia* sect. *Maingola* are also precocious, and the leaves in *Magnolia* subg. *Yulania* sect. *Tulipastrum* are also expanded at flowering, albeit still in the early part of the growing season (Figlar pers. comm.)
 11. *Sexuality*: Although bisexual flowers are the normal condition in Magnoliaceae, these are androdioecious flowers in *Parakmeria*, monoecious flowers in *Kmeria* and dioecious flowers in *Woonyoungia*.
 12. *Outer and inner tepals*: In most Magnoliaceae, there is little difference between the outer and the inner tepals; however, those of the outer whorl form a calyx in *Michelia* sect. *Anisochlamys* and *Magnolia* subg. *Yulania* sects *Buergeria* and *Tulipastrum*.
 13. *Number of tepals*: The perianth typically consists of nine or more tepals arranged in whorls on an elongated pedicel. However, if there are six or fewer tepals, as happens in *Woonyoungia*, *Kmeria*, and *Michelia* sects *Dichlamys* and *Micheliopsis*, they show insertion in a single whorl.
 14. *Gynoecium exposure*: The subtribe Alcimandriinae characterised by the androecium covering the gynoecium was described by Law and Wu (1996). The same character is also seen in *Pachylarnax* and *Tsoongiodendron*.
 15. *Gynophore*: A gynophore occurs in *Alcimandra*, *Aromadendron*, *Manglietiastrum*, *Parakmeria*, *Michelia*, *Tsoongiodendron* and *Paramichelia*.
 16. *Anther dehiscence*: Comparative androecial anatomy of Annonaceae and Magnoliaceae suggested that latrorse dehiscence was plesiomorphic, with introrse and extrorse derived separately (Deroin 1991). Although most Magnoliaceae are introrse, latrorse anthers occur in *Magnolia* subg. *Yulania*, *Michelia*, *Paramichelia* and *Tsoongiodendron*, and *Liriodendron* is extrorse.
 17. *Anther connective shape*: The anther connective is produced into a short acute appendage in most Magnoliaceae, but anthers with blunt or retuse connectives occur in *Magnolia* sect. *Oyama*; and connectives with long appendages are found in *Dugandiodendron*, *Aromadendron* and *Magnolia* subg. *Magnolia* sect. *Splendentes*.
 18. **Anther connective attachment*: Sect. *Splendentes* is distinguished by stamens with the connective apex extending to become embedded in the gynoecium, supporting the stamen when it detaches at the base during anther dehiscence (Howard 1948, Vazques-Garcia 1994).
 19. *Carpel number*: Although most Magnoliaceae have numerous carpels, the flowers of *Pachylarnax*, *Dugandiodendron*, *Woonyoungia* and *Michelia hypolampra* of *Michelia* sect. *Anisochlamys* have fewer than ten carpels.

20. **Carpel arrangement*: The carpels are normally arranged spirally on the lengthened receptacle in Magnoliaceae, but they form a single verticillate whorl in *Pachylarnax*.
21. *Pre-dehiscence fruiting carpel fusion*: Figlar (pers. comm.) confirmed that the only taxon with free carpels is *Michelia sensu stricto*, where the carpels are arranged in a “least dense” pattern so that they do not touch. In all other Magnoliaceae, the carpels are connate (concreescent) to varying degrees before dehiscence.
22. *Number of ovules per carpel*: *Manglietia* mainly differs from *Magnolia* in possessing four or more ovules in each carpel, but *Pachylarnax*, *Michelia*, *Paramichelia* and *Tsoongiodendron* also have more than four ovules per carpel.
23. *Fruiting carpel apices*: Beaked carpels occur in *Manglietia*, *Manglietiastrum*, *Parchylanax*, *Magnolia* subg. *Magnolia* (except sect. *Maingola*), *Talauma*, *Dugandiodendron*, *Kmeria*, *Woonyoungia*. *Liriodendron* was coded as (?) as the character does not apply to this taxon.
24. **Fruit type*: Samaroid fruits occur in subfamily Liriodendroideae and follicles characterise subfamily Magnolioideae.
25. *Fruit dehiscence*: Describing dehiscence is difficult for most Magnoliaceae. For example, pre-dehiscent fruit of *Magnolia henryi* and *Talauma candollii* are difficult to distinguish, but at maturity, lignification develops in the mesocarp of *Talauma* so that upon drying it can only break circumscissile from the bases of the carpels, or sometimes also along the ventral/dorsal. In South American *Talauma* species, the mesocarp is often 10 to 15 mm thick, and it lignifies to such an extent that the carpels are irregularly apically circumscissile, few if any dehiscing along the dorsal/ventral suture. In *Magnolia cylindrica*, there is enough lignification to cause some circumscissile dehiscence in addition to the “normal” dorsal/ventral type, however, all the apical parts eventually fall off, as in *Talauma*. In *Magnolia macrophylla* there is significant mesocarp development (c. 10 mm between the carpel pockets and the exocarp) but it is weakly lignified and the carpels dehisce via the ventral and dorsal sutures. Therefore, there are five basic dehiscence mechanisms in Magnoliaceae: indehiscent in *Liriodendron*; apical parts mostly breaking/falling away circumscissile, singly or in irregular masses while also more/less parting along the dorsal/ventral suture (*Talauma*, *Dugandiodendron*, *Aromadendron*, *Elmerrillia* sect. *Pseudoaromadendron*, *Tsoongiodendron*, *Paramichelia*); apical parts persistent, carpels splitting mostly via dorsal/ventral suture occurred (mostly Magnolioideae); apical parts persistent, carpels splitting mostly via the ventral suture in (*Kmeria*, *Manglietiastrum* and *Pachylarnax*); and apical parts persistent, the carpels splitting mostly via the dorsal suture only (*Woonyoungia*).
26. **Carpel rib persistence*: The carpel rib is persistent after dehiscence in *Paramichelia*.
27. *Fruit shape*: Although ellipsoid fruits are seen in most taxa, *Magnolia* subg. *Yulania*, subg. *Magnolia* sect. *Maingola*, *Alcimandra*, *Michelia* and *Elmerrillia* sect. *Elmerrillia* have cylindrical or oblong, usually more or less distorted fruits, owing to their elongated receptacles. *Tsoongiodendron odorum* definitely has a cylindrical shaped fruit, but sometimes appears ellipsoid because of the large carpels which can distort if aborted. *Aromadendron* and *Elmerrillia ovalis* fruits are cylindrical, but their expanded mesocarp tends to make the fruit appear to be rounded or elliptical.
28. **Testa and endocarp*: The testa is free from the endocarp Magnolioideae, and adheres to the endocarp in Liriodendroideae.

Phylogenetic analyses. Following the deletion of nine uninformative characters (2, 4, 5, 11, 18, 20, 24, 26 and 28), cladistic analysis of the data resulted in 707 equally parsimonious trees 51 steps long (CI = 0.4706; RI = 0.8209).

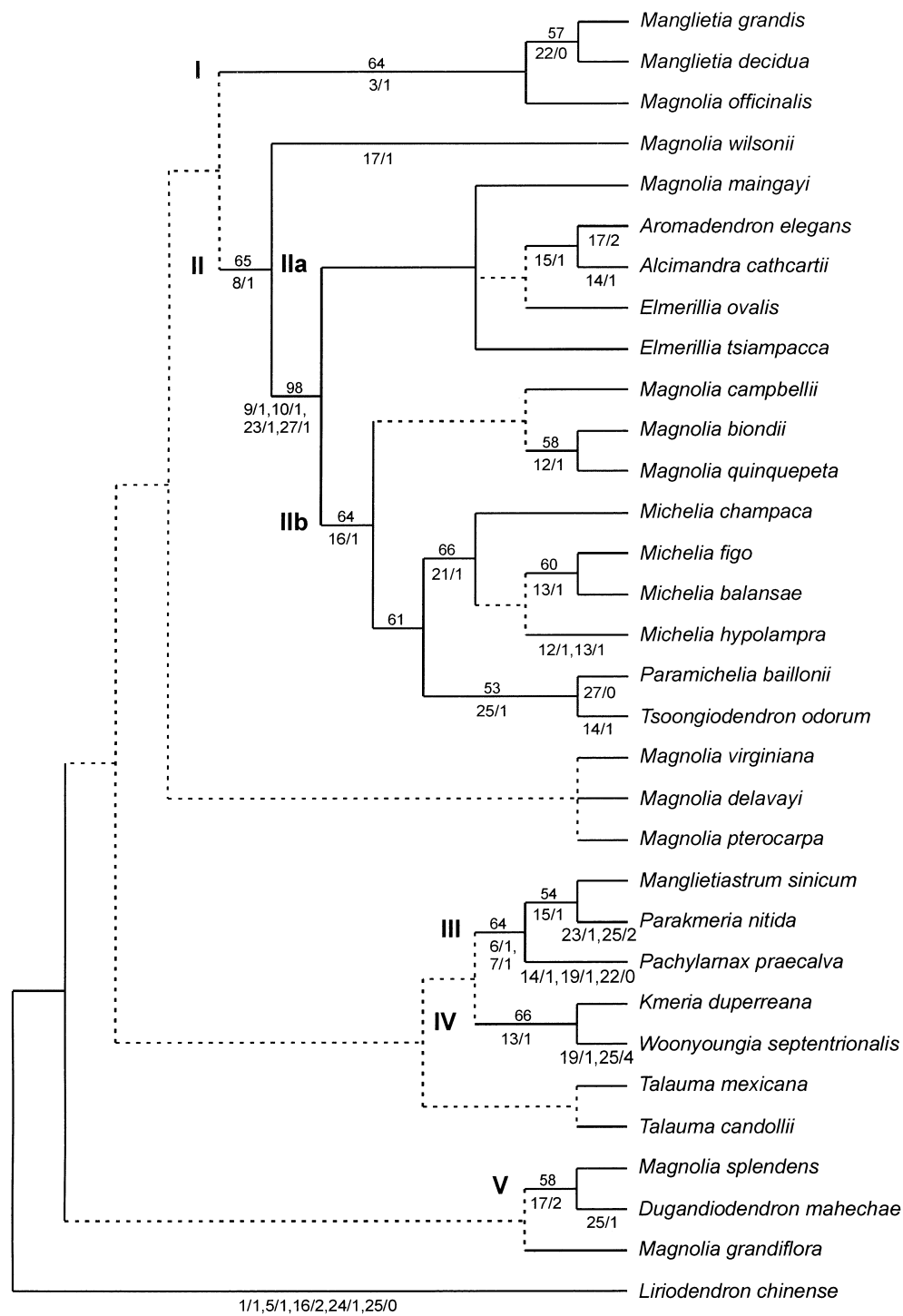


Fig. 1. Fully resolved majority rule tree derived from 168 most parsimonious trees produced by successive weighting. Solid branches are those also found in the strict consensus tree. Numbers above the branch are bootstrap support percentages, those below are the informative character/state conditions at that branch

168 equally most parsimonious trees were produced from *a posteriori* re-weighting analysis, with a length of 24,000 steps, consistency index (CI) of 0.622 and retention index (RI) of 0.894. The fully resolved majority-rule tree is shown as the best supported example tree for character exploration (Fig. 1), but with those branches indicated which also occurred in the strict consensus tree (and to which character/state discussion is limited).

The cladogram shows that Magnolioideae are poorly defined in terms of intergeneric relationships, with the main clades (I-V) and numerous individual taxa together forming a polytomy relative to the outgroup in the strict consensus tree. Bootstrap support was overall low (50–70%) although part of clade II was strongly supported at 98%.

The first clade (I) consisted of *Magnolia* subg. *Magnolia* sect. *Rytidospermum* sister to *Manglietia*, and was based on their shared possession of false leaf whorls at the ends of the branches.

Clade II was the largest and best supported of the clades, defined by the synapomorphy of proleptic branching. Sect. *Oyama* of *Magnolia* subg. *Magnolia* was basal and sister to the remainder of the clade, with low bootstrap support, but above this there were two subclades with 98% bootstrap support and the synapomorphies of pseudoaxillary (as well as terminal) flowers which are produced precociously, unbeaked carpels and cylindrical or oblong usually more or less distorted fruits. In the first of these subclades (IIA), *Magnolia* sect. *Maingola*, *Aromadendron*, *Alcimandra* and *Elmerrillia* formed a poorly supported polytomy. Within this, *Aromadendron* was sister to *Alcimandra*, as both possess a gynophore, although there was no bootstrap support for this pair. The second subclade (IIB) represented a polytomy of the taxa sampled from *Magnolia* subgen. *Yulania*, together with a sister pair representing *Michelia* (defined by free pre-dehiscence carpels) and a *Paramichelia* and *Tsoongiodendron* pair linked by the fruits dehiscing apically circumscissile along the dorsal/ventral suture.

Clade III was defined by flat/curved leaf venation and stipules which were free from the petioles. It consisted of *Pachylarnax* basal to a *Parakmeria*/*Manglietiastrum* pair, the latter two sharing possession of a gynophore. The fourth clade (IV) represented a *Kmeria* and *Woonyoungia* pair, united by having six or fewer tepals. In clade V, *Magnolia* sect. *Splendentes* and *Dugandiodendron* were united by the synapomorphy of long anther connective appendages.

Discussion

Subfamily Magnolioideae traditionally contained two tribes: Magnolieae with terminal flowers; and Michelieae with axillary flowers (Chen and Nootboom 1993; Law 1984, 1996, 2000; Nootboom 1985, 1993), however, our study did not support this separation. The cladistic analysis by Xu et al. (2000) found that *Magnolia* was polyphyletic, with sect. *Maingola* sister to *Manglietia*, sect. *Theorhodon* close to *Talauma*, *Alcimandra* sister to the Michelieae and *Liriodendron* isolated within Magnoliaceae suggesting its early divergence. Whereas our study also found polyphyly and placed *Alcimandra* with the same clade as the Michelieae, there was relatively little congruence with their results, and our analysis is instead more consistent with those of Kim et al. (2001) based on *ndhF* gene sequences.

In our analysis, *Magnolia* subg. *Yulania*, the Michelieae, *Alcimandra*, *Aromadendron*, *Magnolia* sects. *Oyama* and *Maingola* formed a monophyletic group characterised by proleptic branching. A close relationship between *Michelia* and *Magnolia* subg. *Yulania* was also proposed by Figlar (2000), based on shared proleptic branching and proleptic brachyblast flower production. Regardless of whether the flowers are axillary or terminal, the buds are terminal on a short brachyblast (peduncle) with the basal buds protected by deciduous spathaceous bracts which leave a conspicuous peduncle scar. The axillary brachyblast in the Michelieae is produced from a dormant previous year's bud by prolepsis, whereas the

terminal brachyblast in the remainder of *Magnolia* (except for *Magnolia* sect. *Oyama*) is produced directly from the current year's growth by syllepsis.

Magnolia subg. *Yulania* also differs from subg. *Magnolia* by having precocious flowering, and a successful hybrid between *Michelia* and *Magnolia* subg. *Yulania* supports this affinity (Figlar 2000, Savage 1989). On the basis of the sequences of several chloroplast DNA regions: *matK* and *trnK*3' intron, *trnL* intron, *trnT-trnL* IGS and *trnL-trnF* IGS, *psbA-trnK* and *atpB-rbcL* intergenic spacer regions, Ueda et al. (2000) and Azuma et al. (2000) also demonstrated a close relationship between subg. *Yulania* and the Michelieae. This relationship is supported in our analysis by the synapomorphies of laterally dehiscent anthers and cylindrical or oblong, usually more or less distorted fruit.

The systematic positions of *Paramichelia* and *Tsoongi dendron* have always been uncertain. They were treated as monotypic by Hu (1940), Chun (1963) and Law (1984, 1996, 2000) because of their distinctive, large syncarpous fruits, and were placed into the Michelieae because of their stipitate gynoecia. However, because concrescent carpels occur independently within different lineages of Magnoliaceae, Nootboom (1985) considered them to be congeneric with *Michelia*. Molecular phylogenetic analysis by Ueda et al. (2000) produced a *Michelia/Paramichelia* clade, and low divergence of *matK* sequences (2–6 bp) was found between *Michelia*, *Tsoongi dendron* and *Paramichelia* (Shi et al. 2000). In our study *Paramichelia* and *Tsoongi dendron* are placed inside the *Yulania/Michelia* clade, as in the *ndhF* sequence study of Kim et al. (2001).

Elmerrillia was polyphyletic in our analysis, with differences between its two sections, especially in fruit dehiscent morphology: sect. *Elmerrillia* possesses persistent apical parts of carpels; sect. *Pseudoaromadendron* has apical parts falling away in irregular masses. *Elmerrillia* sect. *Pseudoaromadendron* forms a sister pair with *Aromadendron* because of their

sharing the same way of fruit dehiscence. Unfortunately, only *E. ovalis* (sect. *Pseudoaromadendron*) was included in the molecular studies of Kim et al. (2001) and Shi et al. (2000), so the monophyly of the genus cannot be determined with certainty. Nevertheless, the taxa with which *Elmerrillia* was associated in those studies were the same ones which constituted our Clade II.

Nootboom (1985) considered that although *Aromadendron* could be characterised by its very long anther connective, concrescent, fleshy carpels, and seeds exposed in irregular masses, it should be a section of *Magnolia* subg. *Talauma*, and is morphologically close to sect. *Blumiana*. In contrast, our analysis indicates that *Aromadendron* does not show a close affinity to other sections of subg. *Talanma*, and is instead part of clade III. Similarly, the position of *Alcimandra* in that clade is supported by the *matK* study of Shi et al. (2000). The affinities between sect. *Maingola*, *Elmerrillia*, *Alcimandra* and *Aromadendron* seen in our analysis and based on fruit and flowering characters are also supported by the molecular studies of Kim et al. (2001) and Azuma et al. (2001).

Talauma was polyphyletic in the molecular study of (Kim et al. 2001), and in our analysis the two species included as representative of the subgenera were part of the basal polytomy within the Magnolioideae, suggesting that on the morphological character set chosen here, there were no synapomorphies which would unite them. This tends to support the molecular finding, although it may reflect the paucity of morphological characters with strong phylogenetic signal currently available in Magnoliaceae.

The affinity between *Dugandiodendron* and sect. *Splendentes* suggested in our analysis was based on their anther connective apices extending into a long setiform appendage (Howard 1948; Lozano-Contreras 1975, 1984; Vazquez-Garcia 1994). Although this is not unique, as most *Aromadendron* taxa have a similar setiform appendage atop the stamens (Nootboom 1987), a relationship between the two

groups is also supported by molecular analyses (Azuma et al. 2001, Kim et al. 2001).

The monoecious taxon *Kmeria* has been treated as an independent genus in many treatments (Chen and Nootboom 1993; Dandy 1927, 1964, 1978; Law 1984, 2000, 1996; Nootboom 1985, 1993, 2000), and Law (1997) further segregated *Kmeria septentrionalis* as the genus *Woonyoungia* as it is dioecious with fewer than ten carpels and has dorsally dehiscent fruit. The floral developmental study of Zeng et al. (2001) also found that the two genera were clearly very closely related, although they argued that *Woonyoungia* be maintained because it is so distinctive. Our study supports the recognition of *Kmeria* as distinct, but its close affinity with *Woonyoungia* seen in our analysis, and the molecular study of Kim et al. (2001) tend to argue for the return of the latter to synonymy.

Manglietiastrum has been variously considered as a separate genus (Law 1979, 1984, 1996, 2000); a section of *Magnolia* subg. *Talauma* (Nootboom 1985); or as a section of *Manglietia* (Chen and Nootboom 1993). Our results support neither an association with *Manglietia* nor *Talauma*, but place it instead as sister to *Parakmeria* in a subclade with *Pachylarnax*, with which it shares flat open prefoliation. An association between *Manglietiastrum*, *Parakmeria* and *Pachylarnax* was also found by the molecular study of Kim et al. (2001), and Shi et al. (2000) found that there are very low *matK* sequence divergences (0–5 bp) between *Woonyoungia*, *Manglietiastrum* and *Parakmeria* indicating closeness.

Manglietia was supported as monophyletic by several chloroplast DNA regions (Shi et al. 2000, Ueda et al. 2000) and *ndhF* data (Kim et al. 2001), although it has been placed previously within *Magnolia* (Baillon 1866, Keng 1978). Our analysis similarly supports the recognition of *Manglietia* as distinct, but with affinities to *Magnolia* sect. *Rytidospermum*, through shared false leaf whorls, and with which it is also variously associated in molecular phylogenetic studies (Azuma et al. 2001, 2000; Kim et al. 2001; Qiu et al. 1995a).

Conclusions

The conservative viewpoint of Magnoliaceae, represented by Nootboom (1985, 1993, 2000), reduces many segregate genera to subgenera or sections within *Magnolia* and could almost be regarded as a revival of Baillon's (1866) monogeneric concept. The alternative, exemplified by Law (1984, 1996, 2000) and Wu et al. (1998) supports and expands upon Dandy's (1927) generic concepts. The cladistic treatment of Xu et al. (2000) although more limited, found that if these segregate genera are recognised, then *Magnolia* s.str. becomes polyphyletic, and the recent molecular studies in the family (e.g. Azuma et al. 2000, Kim et al. 2001, Shi et al. 2000, Ueda et al. 2000) also support the inclusive approach of an expanded *Magnolia*. There is good agreement between our study and some of the molecular phylogenetic relationships seen by Kim et al. (2001) and Azuma et al. (2001), and our study similarly shows that whereas *Magnolia* s.l. is monophyletic, the recognition of Law's segregate genera would require the elevation of most sections of *Magnolia* to generic rank, which does not seem justified at this stage, especially given the poor bootstrap support for many of the clades within Magnolioideae.

This study, based on revised morphological data, shows that there is good congruence between the bootstrap and consensus-supported clades and many of those seen by the molecular studies. Nevertheless, there was much poorer resolution, especially at deep nodes within Magnolioideae, suggesting that the present morphological data lack sufficiently strong phylogenetic signal to reflect evolutionary pathways in the subfamily as a whole, and that more characters and wider sampling are needed, as well as a combined molecular and morphological study of the family to resolve in more detail the relationships within Magnolioideae.

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Addresses of the authors: Jie Li, Kunming Division of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan 650223, P. R. China. John G. Conran, Centre for

Evolutionary Biology and Biodiversity, Environmental Biology, School of Earth and Environmental Sciences, The University of Adelaide, SA 5005, South Australia.