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## A PHYLOGENETIC ANALYSIS OF THE MIMOSOIDEAE (LEGUMINOSAE) BASED ON CHLOROPLAST DNA SEQUENCE DATA

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### Abstract

A phylogenetic analysis of 134 exemplars of Mimosoideae and seven caesalpinoid outgroups was conducted using chloroplast DNA sequence data. Characters were drawn from the *trnL* and *trnK* intron and spacer regions, as well as the *matK* coding sequence. Parsimony analysis of the data resulted in 21,240 most parsimonious trees. None of the tribes of Bentham (1875) are monophyletic on the strict consensus tree. Parkieae are polyphyletic, with *Parkia* more closely related to various Ingeae and Mimoseae than to *Pentaclethra*. Tribe Mimoseae forms a paraphyletic grade in which are embedded both Acacieae and Ingeae. The genus *Acacia s.l.* is not monophyletic. *Acacia* subg. *Acacia* (*Acacia s.s.*) is strongly supported as monophyletic, and is not closely related either to other species of *Acacia s.l.* or the Ingeae. The remainder of the Acacieae and Ingeae form a monophyletic group, with the Australian acacias (segregate genus *Racosperma* or *Acacia* subg. *Phyllodineae*) also strongly supported as a monophyletic group. *Acacia* subg. *Aculeiferum* (*Senegalia*) is paraphyletic. Relationships among the Ingeae are poorly resolved and not well supported. This study highlights the inevitability of recognising segregate genera from *Acacia s.l.*, and the necessary abandonment of Bentham's longstanding tribal classification.

### Introduction

Mimosoids form one of the major groups of legumes and have been recognised either as the family Mimosaceae (e.g. Cronquist, 1981), or more often, as the subfamily Mimosoideae within the family Leguminosae. Comprised of about 80 genera, they are mostly tropical to subtropical in distribution, and major components of arid and semiarid regions throughout the world, where they are an important source of forage and fuel.

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Characters of the aestivation of sepals and petals have been of key importance in distinguishing subfamilies within the legumes. The Caesalpinioideae and Papilionoideae have imbricate aestivation of the sepals and petals, differing in the position of the standard petal (whether internal or external to the lateral petals). The Mimosoideae are characterised as having valvate aestivation of the petals and usually the sepals, although a number of mimosoid genera violate the latter generalisation. Tucker (1989) also showed that the median petal was abaxial in the mimosoids, and adaxial in the caesalpinoids and papilionoids. Most mimosoid legumes also have bipinnate leaves and small, regular flowers grouped into spicate or capitate inflorescences.

Classification within the Mimosoideae has until recently followed closely that of Bentham (1875). He recognised five tribes, based partly on aestivation of the sepals, but also on androecial characters. The Parkieae were a small tribe of two genera, *Parkia* and *Pentaclethra*, distinguished by imbricate aestivation of the sepal lobes; all other mimosoid tribes had valvate aestivation of the sepals. The Mimoseae and Piptadenieae, both tribes of moderate size, were characterised as having 10 stamens per flower. Originally Bentham (1841) segregated the Piptadenieae as possessing small glands at the apices of the anthers, while the Mimoseae lacked such glands. However in his final treatment of the Mimosoideae, Bentham (1875) redrew the line between these two tribes, using presence (Mimoseae) or absence (Piptadenieae) of endosperm in the seed as his primary character, which led to the reassignment of several genera. The other two tribes, Acacieae and Ingeae, were characterised as having an indefinite number of (i.e. many) stamens per flower, those of the Acacieae free and those of the Ingeae fused.

More recent treatments have not departed greatly from this system. Burkart (1939) added the new tribe Mimozygantheae to accommodate a monotypic South American genus with (supposedly) valvate petals and imbricate, free (as opposed to fused in the Parkieae) sepals. Hutchinson (1964) adhered to Bentham's original system by recognising the tribe Adenantherae (loosely corresponding to Bentham's original Piptadenieae) based on presence or absence of anther glands. Elias (1981) and Lewis and Elias (1981) fused Bentham's tribes Mimoseae and Piptadenieae, noting the unreliability of the endosperm character and how it separated genera that seemed to be closely related based on most other characters. They also presented a classification within this enlarged tribe Mimoseae, postulating 12 informal groups and the relationships among them.

The monophyly of the five tribes recognised by Elias (1981) is now seriously disputed. Cladistic analyses have shown the two genera of Parkieae to be only distantly related (Käss and Wink, 1996; Dayanandan *et al.*, 1997; Luckow *et al.*, 2000) and the tribe thus polyphyletic. The tribe Mimoseae has been widely considered a paraphyletic assemblage from which the Acacieae and Ingeae are derived (Polhill *et al.*, 1981). Guinet (1969, 1990) pointed out the similarities in pollen between *Acacia* and *Piptadeniopsis* in the Mimoseae, and hypothesised an origin for both the Acacieae and Ingeae within the *Piptadenia* group of Mimoseae. Recent cladistic analyses bear this out. Chappill and Maslin (1995) present a portion of a larger cladogram based on morphology in which members of the *Piptadenia* group are sister to a clade of Acacieae and Ingeae. The analysis of Luckow *et al.* (2000) also shows that Acacieae and Ingeae are nested in the *Piptadenia* group of Mimoseae.

The monophyly of the Acacieae, consisting of only the large genus *Acacia* (c. 1200 species) has also come under scrutiny. Predating any cladistic analysis of *Acacia*, Pedley (1986) divided *Acacia* into three genera: *Acacia*, *Senegalia* and *Racosperma*, the contents of which closely corresponded to the subgenera previously recognised by Vassal (1972). In Pedley's scheme, *Acacia* s.s. corresponded to *Acacia* subgenus *Acacia* (Table 1), *Senegalia* to *Acacia* subg. *Aculeiferum*, and *Racosperma* to *Acacia* subg. *Phyllodineae* (*Heterophyllum* in Vassal, 1972). Pedley argued that there were two independent lines in *Acacia* s.l., each sharing a common ancestor with a different

group of Ingeae. Such a scheme implies that the Ingeae are either paraphyletic or polyphyletic too. A cladistic analysis by Chappill and Maslin (1995) that concentrated on species of *Acacia* s.l. used morphological characters to show independent derivations of the *Acacia* subg. *Aculeiferum*/*Acacia* subg. *Phyllodineae* group and *Acacia* subg. *Acacia* from within the Ingeae. A similar analysis by Grimes (1999), but with a focus on genera of Ingeae, also showed two independently derived clades in *Acacia* s.l. Recent molecular analyses with intensive sampling of *Acacia* have likewise shown that some species of *Acacia* are more closely related to ingioid taxa than to other species of *Acacia* (Clarke *et al.*, 2000; Miller and Bayer, 2000, 2001, 2003; Robinson and Harris, 2000).

As is clear from the foregoing, evidence is accumulating that none of the tribes are monophyletic. What has been lacking, however, is a phylogenetic analysis of genera across the entire subfamily. Previous studies have focused on particular subgroups within the tribes, with inadequate sampling outside the tribe of interest. The goal of this study is to test the monophyly of the tribes in the Mimosoideae using a broad sample of representative genera and species drawn from throughout the subfamily.

### Methods and materials

One-hundred and forty-one taxa were included in the analysis and sampling of ingroup taxa was designed to be as comprehensive as possible across all tribes. Both genera in the Parkieae were sampled, and 30 of 37 genera in the Mimoseae. Sampling across the c. 1200 species of *Acacia* was directed by previous analyses of Miller and Bayer (2000, 2001) and Murphy *et al.* (2000). A total of 33 species representing all three subgenera (or genera of Pedley, 1986) and sections within the subgenera was sampled. The monotypic *Faidherbia albida* was also sampled. At the present time, sampling is weakest in the Ingeae, with only 30 species and 15 genera from a possible 32 genera. Also, we have yet to obtain material of the enigmatic *Mimozanthus* to examine its position as a monotypic tribe. Vouchers and Genbank accession numbers are listed in Table 1. Based on the analysis of Bruneau *et al.* (2001) possible outgroups to the Mimosoideae include members of tribe Caesalpinieae and seven species were used to root the tree. See Bruneau *et al.* (2001) for details on the outgroup sequences.

Characters for the ingroup taxa were sampled from two chloroplast regions: the *trnL* intron and spacer, the *matK* coding region and flanking *trnK* intron and spacer. Characteristics of these regions, primers, and procedures for amplification and sequencing are as described in Miller and Bayer (2000, 2001, 2003), Murphy *et al.* (2000) and Luckow *et al.*, (2000). Only *matK* has been sequenced thus far for most Parkieae and Mimoseae, and thus there were missing data for *trnK* for most of these taxa in the matrix (marked with an asterisk in Table 1). There were also a few taxa for which either the *matK* or *trnL* regions were missing, indicated in Table 1 as "no sequence". Only the *trnL* intron region was sampled for the Caesalpinieae (see Bruneau *et al.* (2001), for Genbank accession numbers and vouchers).

Chromatographic traces were edited in Sequencher 3.0 (Gene Codes Corporation, Ann Arbor, Michigan) to produce contiguous sequences. Sequences were submitted to Dialign (Genomatrix Software GmbH, Munich, <http://www.gsf.de/biodv/dialign.html>), then edited manually in Winclada ver. 0.9.99 (Nixon, 2001) to minimise gaps and base substitutions. The presence/absence of indels was scored as independent binary characters, except in homopolymer regions or where homology assessment was deemed arbitrary (Buroker *et al.*, 1990; Golenberg *et al.*, 1993). An aligned matrix is available from the first author upon request. Parsimony analyses were done spawning Nona ver. 2.0 (Goloboff, 1993) from Winclada, and employed a heuristic search strategy. Tree searches were performed with 1000 replicates, holding 20 trees in each search, with a maximum of 10,000 most parsimonious trees to be held

TABLE 1. Vouchers and Genbank Accession numbers for taxa sequenced for this study. Taxa are organised by tribe, segregate genus, and/or subgroup. Genbank accession numbers marked with an asterisk are taxa lacking a *trnK* sequence, otherwise missing sequences are indicated by “no sequence”. In a few cases two laboratories sequenced the same taxon: those marked “JM” were sequenced by Miller, those marked “ML” were sequenced in the Luckow laboratory. Herbarium acronyms are from *Index Herbariorum*.

Tribe	segregate genus (Acaciae)	subgenus/section (Acaciae) or group (Mimoseae)	Species and Authority	Voucher and Herbarium	<i>trnL</i> Genbank #	<i>trnK/ matK</i> Genbank #
Acaciae	Acacia s.s.	Acacia/ Acacia	<i>A. arven</i> (Molina) Molina	CANB 615552	AF522967	AF274131
			<i>A. cochlianthra</i> Humb., Bonpl. & Kunth ex Willd.	CANB 615587	AF522968	AF274133
			<i>A. constricta</i> Benth.	CANB 615588	AF522969	AF274135
			<i>A. farnesiana</i> (L.) Willd.	MEL 2045067, CANB 615606	AF195688, AF195669	AF523115
			<i>A. harroo</i> Hayne	CANB 615590	AF522972	AF274137
			<i>A. neaemerosa</i> Isley	CANB 615605	AF522970	AF523113
			<i>A. nilotica</i> (L.) Willd. ex Delile	CANB 615592	AF522973	AF274139
			<i>A. schottii</i> Torr.	CANB 615589	AF522971	AF274136
			<i>A. tortilis</i> (Forssk.) Hayne	CANB 615593	AF522974	AF274140
			<i>A. alata</i> R. Br.	MELU DM224, CANB 615610	AF195695, AF195676	AF523084
			<i>A. spinosens</i> Benth.	MELU DM246, CANB 615611	AF195706, AF195687	AF523082
			<i>A. elata</i> A. Cunn. ex Benth.	MELU DM234, CANB 615558	AF195683, AF195702	AF274149
			<i>A. mearnsii</i> De Wild.	MELU DM200, CANB 615612	AF195694, AF195675	AF523110
Racosperma		Phyllodineae/ Alatae	<i>A. longifolia</i> (Andrews) Willd.	MELU DM201, CANB 615613	AF195698, AF195679	AF523086
			<i>A. tumida</i> F. Muell. ex Benth.	MEL 2066637, CANB 615614	AF522986	AF523111*
			<i>A. colai</i> A. Cunn. ex G. Don	MEL 2066654, CANB 615564	AF522987	AF274215
		Phyllodineae/ Botrycephalae	<i>A. adoxa</i> Pedley	MEL 2041667, CANB 615615	AF195703, AF195684	AF523076
			<i>A. lycopodiifolia</i> Hook.	MEL 2044632, CANB 615616	AF195705, AF195686	AF523077
		Phyllodineae/ Phyllodineae	<i>A. euhycarpa</i> (J.M.Black) J.M. Black	MEL 2039729, CANB 615618	AF195689, AF195670	no sequence
			<i>A. amplexipes</i> Maslin	MEL 2066651, CANB 615617	AF522983	AF523074
		Phyllodineae/ Plumierius	<i>A. melanoxylon</i> R. Br.	MELU DM210, CANB 615580	AF195680, AF195699	AF274166
			<i>A. platycarpa</i> F. Muell.	MEL 2066655, CANB 615581	AF522985	AF274223
		Phyllodineae/ Pulchellae	<i>A. transiens</i> A. Cunn. ex Hook.	MEL 2066634, CANB 615619	AF522984	AF523087
			<i>A. drummondii</i> Lind.	MEL 2034627	AF195704, AF195685	AF523106*
		Aculeiferum	<i>A. pulchella</i> R. Br.	MELU DM268, CANB 615620	AF195692, AF195673	AF523100
			<i>A. visco</i> Lorenz ex Griseb.	CANB 615607	AF522982	AF523116
Senegalia		Aculeiferum/ Aculeiferum	<i>A. modesta</i> Wall.	CANB 615595	AF522975	AF274142
			<i>A. senegal</i> (L.) Willd.	CANB 615554	AF522976	AF274143
		Aculeiferum/ Filicinae	<i>A. botiniana</i> Rusby	CANB 615555	AF522981	AF274144

TABLE 1. continued

Tribe	segregate genus (Acaciae)	subgenus/section (Acaciae) or group (Mimoseae)	Species and Authority	Voucher and Herbarium	<i>trnL</i> Genbank #	<i>trnK/ matK</i> Genbank #
Acaciae	<i>Sengalia</i>	<i>Aulajferum/ Monacantha</i>				
			<i>A. berlandieri</i> Benth.	CANB 615596	AF529278	AF274145
			<i>A. glomerosa</i> Benth.	CANB 615556	AF529280	AF274147
			<i>A. roemeriana</i> Scheele	CANB 615608	AF529277	AF523099
			<i>A. schuavei</i> Benth. & Exell	CANB 615609	AF529279	AF523101
			<i>Faidherbia albida</i> (Delile)	CANB 632235	AF529254	AF274129
Ingeae (or Acaciae)			A. Chev.—JM			
			<i>Faidherbia albida</i> (Delile)	CANB 615551	no sequence	AF523081
			A. Chev.—337			
			<i>Albizia adinoccephala</i> (Donn. Sm.)	CANB 615621	AF529295	no sequence
			Britton & Rose			
			<i>Albizia harveyi</i> E. Fourn.	CANB 615623	AF529291	AF523075
			<i>Albizia kalkora</i> (Roxb.) Prain	CANB 615624	AF529245	AF523083
			<i>Albizia plurijuga</i> (Standl.)	CANB 615625	AF529293	AF523080
			Britton & Rose			
			<i>Albizia sindoensis</i> Britton & Rose	CANB 615543	AF529246	AF274121
			<i>Albizia tomentosa</i> (Micheli) Standl.	CANB 615626	AF529294	AF523093
			<i>Albizia versicolor</i> Welw. ex Oliv.	CANB 615627	no sequence	AF523112
			<i>Calliandra carbonaria</i> Benth.	B.B. Klugeard 622 (K)	AF278516	AF521815*
			<i>Calliandra longipetiolata</i> (McVaugh)	CANB 615629	no sequence	AF523107
			Macqueen & H.M. Hern.			
			<i>Calliandra physoclyx</i> H.M.	CANB 615630	no sequence	AF523102
			Hern. & M. Sousa			
			<i>Calliandra pittieri</i> var. <i>pittieri</i> Standl.	B.B. Klugeard 649 (K)	AF278515	no sequence
			<i>Calliandra surinamensis</i> Benth.	MEL 2066678	no sequence	AF523103
			<i>Calliandra umbellatum</i> (Vahl)	CANB 615544	AF529249	AF274122
			Kosterm.			
			<i>Cedrelinga cataeniformis</i> Ducke	B.B. Klugeard 698 (K)	AF278511	AF521818*
			<i>Chloroleucon mangense</i> (Jacq.)	CANB 615631	AF529250	AF523072
			Britton & Rose			
			<i>Ebenopsis ebano</i> (Berland.)	P. White 45 (BH)	no sequence	AY125853*
			Barneby & J.W. Grimes			
			<i>Ebenopsis ebano</i> (Berland.)	CANB 615545	AF529251	AF274123
			Barneby & J.W. Grimes			

TABLE 1. continued

Tribe	segregate genus (Acaciae)	subgenus/section (Acaciae) or group (Mimosae)	Species and Authority	Voucher and Herbarium Genbank #	trnL Genbank #	trnK/ matK
Ingeae			<i>Entolobium contortisiliquum</i> (Vell.) Morong	CANB 615546	AF522952	AF274124
			<i>Entolobium cyclocarpum</i> (Jacq.) Griseb.	<i>M. Lavin</i> 3205 (BH)	AF278518	AF521831*
			<i>Havardia albicans</i> (Kunth) Britton & Rose	CANB 61532	AF522956	AF523085
			<i>Havardia pallens</i> (Benth.) Britton & Rose	CANB 615547	AF522955	AF274125
			<i>Inga edulis</i> Mart.	MEL 2066677	AF522957	AF523078
			<i>Lysiloma acapulcense</i> (Kunth) Benth.	CANB 615584	AF522958	AF274126
			<i>Lysiloma divaricatum</i> (Jacq.) J.F. Macbr.	CANB 615633	AF522940	AF523088
			<i>Lysiloma largeminum</i> Benth.	CANB 615634	AF522959	AF523089
			<i>Parachidendron pruinatum</i> (Benth.) I.C. Nielsen	CANB 615549	AF522961	AF274127
			<i>Paraserianthes lophantha</i> subsp. <i>lophantha</i> (Willd.) I.C. Nielsen	CANB 615550	AF522962	AF274128
			<i>Pseudosamanea guachapete</i> (Kunth) Harms	MEL 2066675	AF522964	AF523079
			<i>Samanea saman</i> (Jacq.) Merr.	MEL 2066684	AF522965	AF523073
			<i>Zapoteca formosa</i> (Knuth) H.M. Hern.	Cultivated, conservatory (BH)	no sequence	AY125854*
			<i>Zapoteca tetragona</i> (Willd.) H.M. Hern.	CANB 615635	AF522966	AF523097
			<i>Neptunia gracilis</i> Benth.	Grimes 3168 (BH)	AF278494	AF521845
			<i>Neptunia monosperma</i> F. Muell. ex Benth. -JM	CANB 615542	AF522944	AF274209
			<i>Neptunia monosperma</i> F. Muell. ex Benth. -ML	<i>B. Jakes</i> s.n. (BH)	AF278495	AF521846*
			<i>Adenanthera pavonina</i> L.	Major Howell Seeds (BH)	AF278486	AF521808*
Mimosae			<i>Amblygonocarpus andongensis</i> (Welw. ex Oliv.) Exell & Torre	Silverhill Seeds (BH)	AF278487	AF521812*
			<i>Pseudoprosopis gillatii</i> (De Wilde) Villiers	<i>M.S.M. Sosef</i> 526 (BH)	AY125851	AF521861*

TABLE 1. continued

Tribe	segregate genus (Acaceae)	subgenus/section (Acaceae) or group (Mimosace)	Species and Authority	Voucher and Herbarium Genbank #	tmL Genbank #	trnK/ matK
Mimosace	<i>Adenanthera</i>		<i>Tetrapleura tetrapleura</i> (Schumach. & Thonn.) Taub.	BNBG 65-6191 (BR)	AF278510	AF521864*
			<i>Tetrapleura tetrapleura</i> (Schumach. & Thonn.) Taub.	M.S.M. Sosef 643 (BH)	AY125852	AF521865*
	<i>Dichrostachys</i>		<i>Alanisilodendron alluaudianum</i> (R. Vig.) Villiers	Luckow 4114 (BH)	AF278523	AF521809*
			<i>Alanisilodendron humbertii</i> (R. Vig.) Villiers	Luckow 4354 (BH)	AF278522	AF521810*
			<i>Alanisilodendron pilosum</i> Villiers	Luckow 4301 (BH)	AY125844	AF521811*
			<i>Calliandropsis nervosus</i> (Britton & Rose) H.M. Hern. & P. Guinet	Hernandez 2365 (BH)	AF278520	AF521816*
			<i>Dichrostachys paucifoliolata</i> (Scott-Elliott) Drake	Luckow 4157 (BH)	AF278526	AF521822*
			<i>Dichrostachys richardiana</i> Baill.	Luckow 4261 (BH)	AF278519	AF521823*
			<i>Dichrostachys spicata</i> (F. Muell.) Domin.	Dunlap 5853 (BH)	AF278524	AF521824*
			<i>Dichrostachys unijuga</i> Baker	Luckow 4279 (BH)	AF278525	AF521825*
			<i>Dichrostachys venosa</i> Villiers	Luckow 4188 (BH)	AF278521	AF521826*
			<i>Gagnebina bakoliae</i> Luckow & Du Puy	Luckow 4413 (BH)	AF278527	AF521834*
			<i>Gagnebina bernieriana</i> (Baill.) Luckow	Luckow 4243 (BH)	AY125848	AF521835*
			<i>Gagnebina commersoniana</i> (Baill.) R. Vig.	D. Potter 420809-01 (BH)	AF278529	AF521836*
			<i>Gagnebina pervillaana</i> (Baill.) G.P. Lewis & P. Guinet	Luckow 4221 (BH)	AF278528	AF521837*
			<i>Gagnebina perocarpa</i> (Lam.) Baill.	Carl Lewis 98-057 (BH)	AF278530	AF521838*
	<i>Dinizia</i> <i>Entada</i>		<i>Dinizia excelsa</i> Ducke	Sergio de Faria s.n. (BH)	AF278479	AF521827*
			<i>Elephantorrhiza elephantina</i> (Burch.) Skeels	Nat. Bot. Gardens Kirstenbosch 194 (BH)	AF278484	AF521828*
	<i>Fillaopsis</i>		<i>Entada abyssinica</i> Steud.	N-fixing Tree Assoc. 869 (KFSC)	AY125846	AF521829*
			<i>Entada rheedii</i> Spreng.	A. Bruneau 926 (BH)	AF278504	AF521830*
			<i>Fillaopsis discophora</i> Harms	D. Harris 4111 (E)	AF278508	AF521832*

TABLE 1. continued

Tribe	segregate genus (Acacieae)	subgenus/section (Acacieae) or group (Mimoseae)	Species and Authority	Voucher and Herbarium Genbank #	trnL Genbank #	trnK/ matK
Mimoseae	<i>Fillaeopsis</i>		<i>Fillaeopsis discophora</i> Harms (Sosef collection)	M.S.M. Sosef 518 (BH)	AY125847	AF521833*
		<i>Leucaena</i>	<i>Desmanthus acuminatus</i> (B. L. Turner) Luckow	Luckow 3527 (BH)	AF278490	AF521820*
	<i>Desmanthus balsensis</i> J.L. Contr.		Luckow 3532 (BH)	AF278531	AF521821*	
	<i>Desmanthus bicornutus</i> S. Watson		CANB 615637	AF522939	AF523108	
		<i>Kanaloa kalouagense</i> Lorence & K.R. Wood	<i>D. Lorence</i> 7380 (PTBG)	AF278489	AF521839*	
		<i>Leucaena greggii</i> S. Watson	<i>C. Hughes</i> 82/ 87 (BH)	AF278492	AF521840*	
		<i>Leucaena leucocephala</i> (Lam.) De Wit—ML	Luckow 3270 (BH)	AF278493	AF521841*	
		<i>Leucaena leucocephala</i> (Lam.) De Wit—JM	CANB 615639	AF522942	AF523094	
		<i>Schlenitzia insularum</i> (Guill.) Burkart	Waimanalo Res. Station, PI 282460 (BH)	AF278491	AF521862*	
	<i>Neatonia</i>	<i>Cylindrocarpus gabunensis</i> Harms	M.S.M. Sosef 645A (BH)	AY125845	AF521819*	
		<i>Neatonia buchananii</i> (Baker) G.C.C. Gilbert & Boutique	BNBG 69-6494 (BR)	AF278501	AF521847*	
		<i>Neatonia hildebrandtii</i> (Vatke) Brenan	BNBG 73-2891 (BR)	AF278502	AF521848*	
		<i>Piptadeniastrum africanum</i> (Hook.f.) Brenan	<i>D. Harris</i> 4319 (E)	AF278488	AF521857*	
	<i>Piptadenia</i>	<i>Anadenanthera colubrina</i> (Vell.) Brenan—JM	CANB 615636	AF522947	AF523114	
		<i>Anadenanthera colubrina</i> (Vell.) Brenan—ML	<i>R.T. Pennington</i> 845 (E)	AF278481	AF521813*	
<i>Anadenanthera peregrina</i> (L.) Speg. <i>Microlobius foetidus</i> (Jacq.) M. Sousa & G. Andrade—JM		BNBG 77-2925 (BR) CANB 615640	AF278480 AF522960	AF521814* AF523095		
<i>Microlobius foetidus</i> (Jacq.) M. Sousa & G. Andrade—ML		<i>D.J. Macqueen</i> 432 (FHO)	AF278506	AF521842*		
<i>Mimosa aculeaticarpa</i> var. <i>biuncifera</i> (Benth.) Barneby		Major Howell Seeds (BH)	AF278513	AF521843*		



TABLE 1. continued

Tribe	segregate genus (Acaciae)	subgenus/section (Acaciae) or group (Mimosae)	Species and Authority	Voucher and Herbarium Genbank #	trnL Genbank #	trnK/ matK
Mimosae		<i>Piptadenia</i>	<i>Mimosa albidia</i> var. <i>wildenovii</i> Humb. & Bonpl. ex Willd	<i>B.B. Klitgaard</i> 648 (K)	AF278512	no sequence
		<i>Mimosa quitensis</i> Benth.		<i>B.B. Klitgaard</i> 647 (K)	AF278514	AF521844*
		<i>Mimosa tenuiflora</i> (Willd.) Poir.		CANB 615541	AF529243	AF523104
		<i>Mimosa tenuiflora</i> (Willd.) Poir.		CANB 615541	as above	AF274120
		<i>Parapiptadenia rigida</i> (Benth.) Brenan		<i>A. Arambari</i> 215 (BH)	AF278505	AF521849*
		<i>Piptadenia moniliformis</i> Benth.		Kew Seed Bank 0049052 (K)	AF278496	AF521854*
		<i>Piptadenia obliqua</i> J.F. Macbr.		<i>D. Macqueen</i> 439 (FHO)	AY125855	AF521855*
		<i>Piptadenia viridiflora</i> (Kunth) Benth.		<i>C.E. Hughes</i> 1681 (FHO)	AF522963	AF521856*
		<i>Stryphnodendron</i> cf. <i>coriaceum</i> Benth.		<i>R.T. Pennington</i> 913 (E)	AF278497	AF521863*
<i>Plathymenia</i>		<i>Plathymenia reticulata</i> Benth.		<i>S. Bridgewater</i> 605 (E)	AF278509	AF521858*
<i>Prosopis</i>		<i>Prosopidastrium mexicanum</i> (Dressler) Burkart		Desert Legume Project (BH)	no sequence	AF521859*
		<i>Prosopis pallida</i> (Humb. & Bonpl. ex Willd.) Kunth		<i>M. Lavin</i> 3188 (BH)	AF278500	AF521860*
		<i>Calpocalyx dinklagei</i> Harms		<i>F.J. Brateler</i> 15461 (WAG)	AF278483	no sequence
<i>Xylia</i>		<i>Calpocalyx heitzii</i> Pellegr.		<i>F.J. Brateler</i> 13999 (WAG)	AF278482	AF521817*
		<i>Xylia africana</i> Harms		<i>P. Herendeen</i> & <i>F. Mbogo</i> 9-XII-97-5 (US)	AY125849	AF521866*
		<i>Xylia hoffmannii</i> (Vatke) Drake		<i>M. Luchow</i> 4414	no sequence	AF521867*
		<i>Parkia biglandulosa</i> (DC.) Merr.		Banana Tree Nursery (BH)	AF278498	AF521850*
		<i>Parkia speciosa</i> Hassk.		<i>A. Bruneau</i> 931 (BH)	AF278499	AF521851*
		<i>Parkia timoniana</i> (DC.) Merr.		MELU DM265	AF195701, AF195682	AF523091
		<i>Pentaclethra setuldeana</i> De Wild. & T. Durand		BNBG 65-6191 (BR)	AY125850	AF521852*
		<i>Pentaclethra macrophylla</i> Benth.—ML		BNBG 87-1143 (BR)	AF278485	AF521853*

Parkieae

at this stage. All most parsimonious trees from the search were then swapped to completion. Additional searches for islands of most parsimonious trees were conducted using the Parsimony Ratchet feature of Winclada (Nixon, 1999), with 1000 iterations, holding 5 trees per replicate and randomly reweighting 50 characters with each iteration. Strict-consensus bootstrap values were computed in Winclada and Nona with 1000 replicates and 10 tree bisection-reconnection searches and holding one tree per replicate. Strict-consensus bootstrap values (Soreng and Davis, 1998; Davis *et al.*, 1998) were rounded to percentages and mapped to the strict consensus tree in Winclada.

Results

Sequence characteristics are summarised in Table 2. The aligned length for the *trnL* region is 1474 bp, with 321 informative base substitutions and 38 informative indels. The aligned length of the *trnK/matK* region is 2688 bp long. There were 561 informative base substitutions, and 12 informative indels. Because of missing data for the *trnK* region among most Mimoseae, it is difficult to compare variability of the two regions. For example, complete *trnL* sequences were included for all but 8 of 141 taxa (c. 95%), so about 5% of the *trnL* matrix contained missing values. In contrast, *trnK* sequences were missing for 74 taxa (52%) and *matK* sequences were unknown for 14 taxa (c. 10%). Given this disparity, the *trnL* region still seems to have significantly more indels, and is probably more variable overall per length of sequence. There is a 300 bp deletion in the *trnL* spacer, flanked by two homopolymers, that has evolved independently at least five times in the Mimosoideae.

Parsimony analysis resulted in 21,240 equally most parsimonious trees of 2658 steps, CI = 0.49, RI = 0.72. The strict consensus tree is presented in Figs. 1–3, with strict consensus bootstrap values above the nodes. A summary diagram of this tree showing tribal relationships is shown in Fig. 4. As in previous analyses (Luckow *et al.*, 2000; Bruneau *et al.*, 2001), there is no support for the monophyly of the Mimosoideae (Fig. 1). In contrast to the previous analyses, *Dinizia excelsa* (Mimoseae) is sister to *Erythrophleum* (Caesalpinioideae), calling into question the former’s placement within the Mimosoideae.

TABLE 2. Sequence characteristics for the *trnL* and *trnK/matK* regions. Note that variability within regions is not comparable because the data sets are not completely parallel. The *trnK* intron has not yet been sequenced for a number of taxa in the Mimoseae, resulting in many missing values.

	<i>trnL</i>	<i>trnK/matK</i>
Aligned length (bp)	1474	2688
Length range (bp)	759–1102	2206–2332
Indels	38	12
Indel size range (bp)	1–c. 300	1–5
Base substitutions	321	561
Total potentially informative characters	359	573

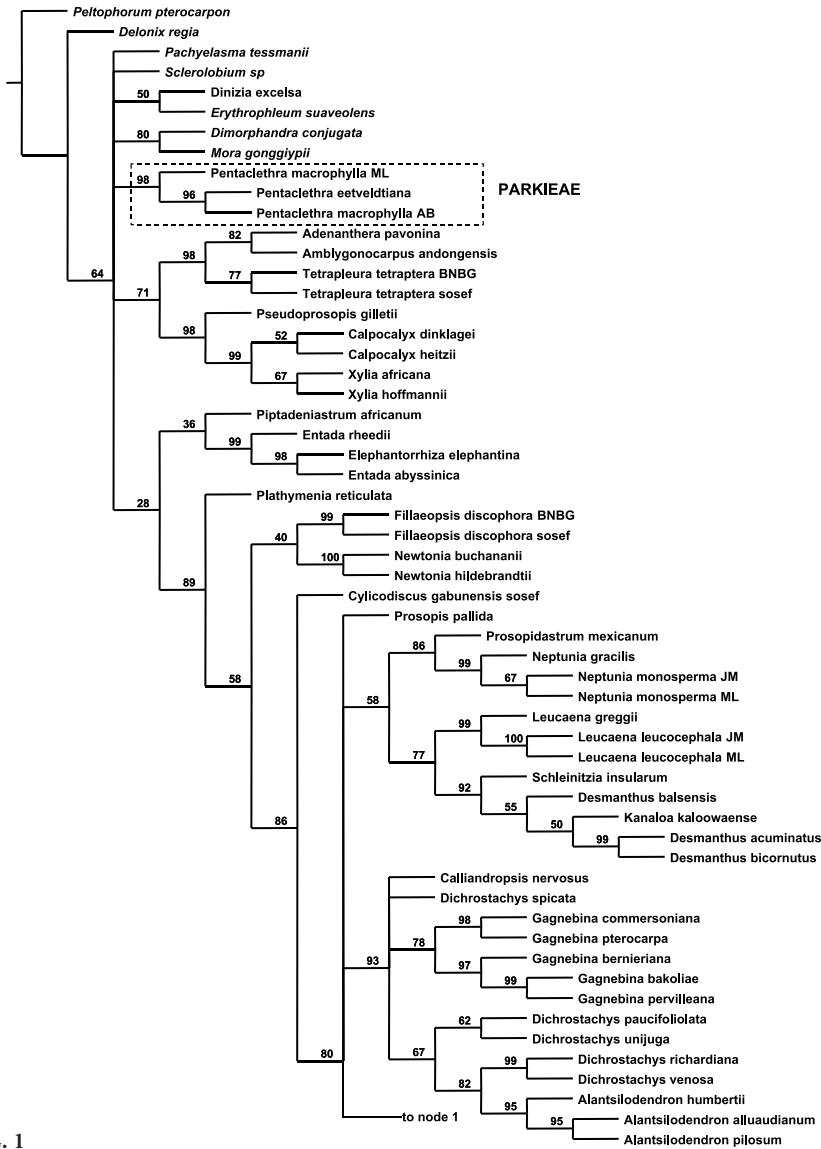


FIG. 1

FIGS. 1–3. Strict consensus tree of 21,240 equally most parsimonious trees, CI = 0.49, RI = 0.72. FIG. 1. Caesalpinoideae outgroup taxa (in *italics*) and basal genera of the tribe Mimosae. Species of *Pentaclethra*, formerly a genus in the tribe Parkieae, are in the dashed-box. FIG. 2. Genera of Mimosae, *Acacia* (boxes with solid lines) and the genus *Parkia* (box with dashed line). FIG. 3. Members of the Acacieae (box with solid lines) and Ingeae (shaded box). Bootstrap values are labelled above the nodes. Duplicate taxa are labelled “JM” if sequenced by Joe Miller; “ML” if sequenced in the Luckow laboratory, and “AB” if sequenced in the Anne Bruneau laboratory.

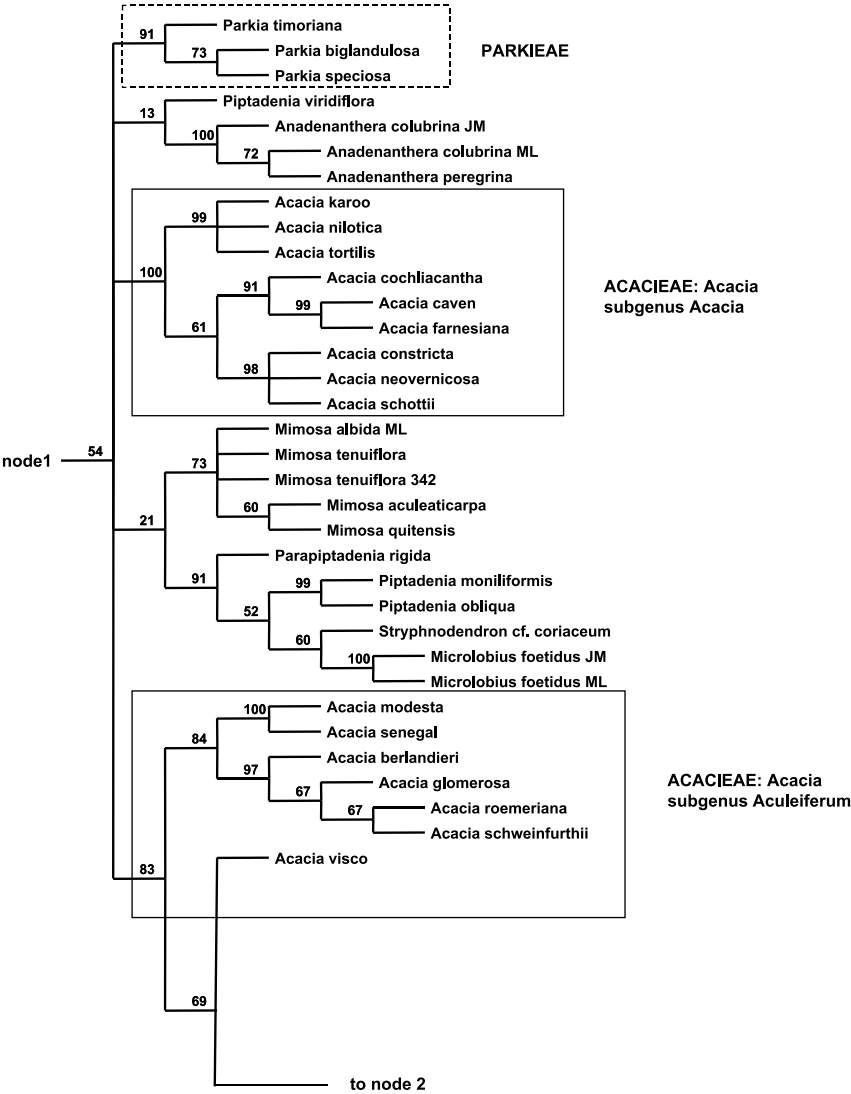


FIG. 2

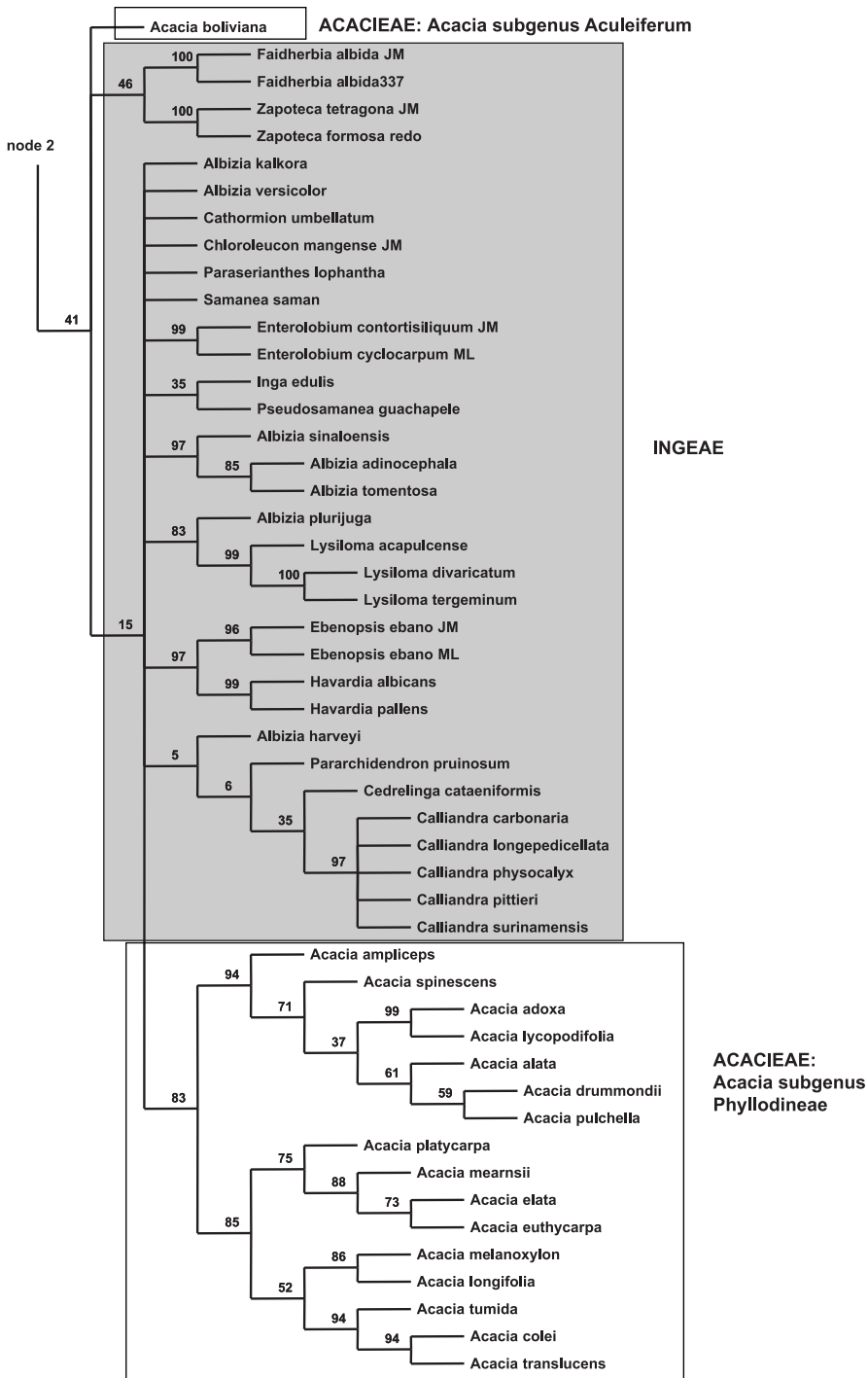


FIG. 3

This analysis also demonstrates that none of the recognised tribes are monophyletic (Fig. 4). It agrees with previous studies (Käss and Wink, 1996; Dayanandan *et al.*, 1997; Luckow *et al.*, 2000) in that the Parkieae are polyphyletic, with *Parkia* nested among the *Piptadenia* group of Mimoseae (Fig. 2) and *Pentaclethra* near the base of the mimosoids (Fig. 1). The Mimoseae form a basal grade, with the Ingeae and Acacieae nested within it (Fig. 4). The genus *Acacia* (and thus the tribe Acacieae) is at best paraphyletic; *Acacia* subg. *Acacia* is monophyletic (bs = 100%, Fig. 2) and part of a polytomy containing species from the *Piptadenia* group of Mimoseae, *Parkia*, and a clade of all other acacias and the Ingeae (Fig. 4). *Acacia* subg. *Aculeiferum* forms a grade at the base of a weakly supported clade containing *Acacia* subg. *Phyllodineae* and the Ingeae (Figs. 2, 3). *Faidherbia* is sister to *Zapoteca* (Ingeae), but with low bootstrap support (Fig. 3).

### Tribe Mimoseae

Although these results are quite consistent with the previous analysis of Luckow *et al.* (2000), there are a number of novel relationships. As mentioned above, *Dinizia excelsa* is weakly supported as sister to a member of the Caesalpinioideae in this analysis (Fig. 1); its relationship was unresolved in previous analyses. The cladogram of Luckow *et al.* (2000) showed *Xylia africana* as strongly supported as sister to a clade containing *Fillaeopsis* and *Newtonia*. The accession was resequenced to check our result, and we found that the previously reported sequence was a contaminant. The new *Xylia* sequence now indicates that the genus is most closely related to *Pseudoprosopis* and *Calpocalyx* (bs = 98%, Fig. 1), a result in close accord with morphology and the classification of Lewis and Elias (1981). *Piptadeniastrum* was not included in the previous analysis; it is shown to be most closely related to the *Entada* group rather than the *Newtonia* group as was postulated by Lewis and Elias (1981), although strict consensus bootstrap support is not high (36%, Fig. 1). *Prosopidastrum*, which was also part of the *Prosopis* group in the Lewis and Elias treatment is sister to *Neptunia* (bs = 86%) and this clade is sister to the *Leucaena* group (bs = 58%). The *Piptadenia* group of Mimoseae forms two clades that are unresolved relative to *Acacia* subg. *Acacia* and the genus *Parkia* (Fig. 2). Note that the genus *Piptadenia* is polyphyletic on this cladogram (Fig. 2), with *Piptadenia viridiflora* sister to *Anadenanthera*, and the other species nested in a clade with *Parapiptadenia*, *Stryphnodendron* and *Microlobius* (bs=91%).

### Tribe Acacieae

As postulated by Guinet (1990), members of the *Piptadenia* group of Mimoseae are most closely related to the Acacieae and Ingeae (Fig. 4). Although *Acacia* subg. *Acacia* is monophyletic, it is not resolved as sister to the well-supported clade containing other Acacieae and the Ingeae (Figs. 2, 3), and the Acacieae are paraphyletic at best. Guinet (1990) hypothesised that there were two lines in *Acacia* each independently derived from within the Mimoseae. Based on pollen characters, he hypothesised that *Acacia* subg. *Acacia* was most closely related to *Piptadeniopsis* (in the *Prosopis* group), whereas part of *Acacia* subg. *Aculeiferum* and *Acacia* subg. *Phyllodineae* were related to the *Piptadenia* group. We have yet to include *Piptadeniopsis* in our analysis, but *Acacia* subg. *Acacia* is not sister to any other members of the *Prosopis* group, i.e. *Prosopis* or *Prosopidastrum* (Figs. 1, 2). The *Acacia* subg. *Aculeiferum*/Ingeae/*Acacia* subg. *Phyllodineae* clade has moderate to high strict consensus bootstrap support (83%), as does the next node up which excludes the core *Acacia* subg. *Aculeiferum* from other Acacieae/Ingeae (bs = 69%, Fig. 4). *Faidherbia albida* was segregated from *Acacia* based on a number of characters (enumerated by Vassal, 1981). There has been debate about whether it belongs with the Ingeae or Acacieae. Here it is sister to *Zapoteca* (Ingeae) but with 46% bootstrap support (Fig. 3). Relationships within groups of *Acacia* are largely in agreement with the previously published analyses of Robinson and Harris (2000), Miller and Bayer (2001) and Murphy *et al.* (2000), although overlap of taxa among the various studies is minimal.

### Tribe Ingeae

Relationships are generally unresolved in the Ingeae and with few exceptions, clades are not strongly supported (Fig. 3). *Ebenopsis* and *Havardia* are sister taxa (bs = 97%), in agreement with Grimes (1995, 1999). *Albizia* is polyphyletic, also in agreement with Grimes (1999). The large polytomy in Fig. 3 has two strongly supported, monophyletic (>80% bs) clades of *Albizia*, and another species at the base of a clade containing *Calliandra*, but with low strict consensus bootstrap support.

## Discussion

### Mimoseae

The finding that *Dinizia excelsa* may be more closely related to caesalpinioids than mimosoids is congruent with morphology. *Dinizia* has a hypanthium, a stylar groove, and imbricate petals, characters either unusual or unknown among other mimosoids. Its placement within the Mimosoideae has rested on having pollen occasionally in tetrads and a valvate calyx. Polyads are found elsewhere in the Caesalpinioideae (Graham and Barker, 1981; Ferguson and Banks, 1994). The calyx of *Dinizia* is very short, and after careful examination of herbarium specimens, it is not clear that the sepals are truly valvate. More evidence from morphology and particularly floral development should be sought to explore the relationship of this taxon to the Caesalpinioideae.

As mentioned above, *Xylia* is now placed in a strongly supported clade with *Pseudoprosopis* and *Calpocalyx* (Fig. 1). There are numerous morphological synapomorphies for this clade. All three taxa have fruits with woody valves that recurve as they dehisce from the apex. The anther glands are also quite similar, with very large cells and a unique internal anatomy similar to that in the *Adenanthera* group (Luckow and Grimes, 1997). Guinet (1969, p. 31) noted unique similarities in pollen among the three genera, characterising it as elongate bitetrads. In contrast, there are few morphological similarities between *Piptadeniastrum africanum* and the *Entada* group, and given the low support from the molecular data, its affinities must remain uncertain pending further study.

*Prosopidastrum* has generally been united with other species having stipular spines as part of the *Prosopis* group (Lewis and Elias, 1981). This analysis indicates that it is more closely related to the unarmed genus *Neptunia* than to anything in the *Prosopis* group. Both genera are quite specialised, *Prosopidastrum* for extremely dry habitats and *Neptunia* for aquatic ones. *Prosopidastrum* lacks leaves for much of the year, relying instead on photosynthetic stems. *Neptunia* stems may be enlarged and aerenchymous when growing in water, and all species possess the usual bipinnate leaves. Flowers of *Prosopidastrum* are more like those of *Prosopis* than those of *Neptunia*, with an elongate pseudopedicel and pilose ovary. Nonetheless, all three genera share very similar anthers and anther glands, and the golden corky ridges on the stems of *Prosopidastrum* are reminiscent of those seen in *Neptunia*. Given the limited sampling and unresolved position of *Prosopis* in our cladogram (Fig. 2), it would be premature to assume that there is not a close relationship between *Prosopis* and *Prosopidastrum*. As mentioned in Luckow *et al.* (2000), sampling in the *Prosopis* group needs to be greatly expanded.

Relationships in the *Leucaena* and *Dichrostachys* groups are generally congruent with the previous study in the Mimoseae based on *trnL* only (Luckow *et al.*, 2000), although relationships of these groups relative to *Neptunia* has changed. In the current study, the *Neptunia*/*Prosopidastrum* clade is sister to the *Leucaena* group alone (Fig. 1), rather than unresolved relative to both the *Leucaena* and *Dichrostachys* groups. However, the former hypothesis is in conflict with the study of Hughes *et al.* (2003) based on ITS sequences, in which *Neptunia* is sister to a clade containing both the *Dichrostachys* and *Leucaena* groups. Although the sampling of species is denser in the Hughes *et al.* study, generic-level sampling is sparser than the study presented here; for example,

*Prosopidastrum* was not included. Since bootstrap values in both studies are not particularly convincing (58% *vs.* 65%), the relationship of *Neptunia*/*Prosopidastrum* clade to the *Dichrostachys* and *Leucaena* groups remains ambiguous.

Given the numerous generic realignments in *Piptadenia* in recent years (Brenan, 1955, 1963, 1986; de Lima and de Lima, 1984; Lewis and de Lima, 1991; Lewis 1991a, 1991b), it is surprising to discover that it is still not monophyletic as currently circumscribed. There is some morphological support for generic differentiation of the included taxa: *Piptadenia viridiflora* is armed with stipular spines and has a compressed, planar legume; *P. obliqua* and *P. moniliformis* are either unarmed or with spinescent stipules, but have legumes that are strongly constricted between the seeds. Additional sampling of *Piptadenia* is necessary, as there is yet a third group of species armed with aculei and without constricted pods whose status remains uncertain.

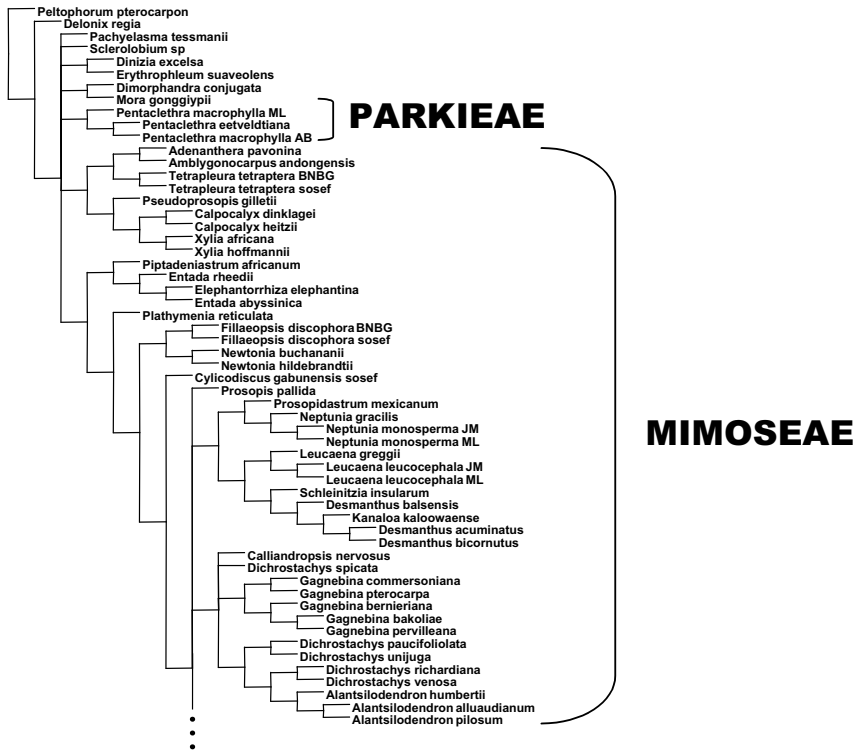


FIG. 4. Summary diagram of cladograms shown in Figs. 1–3 and illustrating the relative positions of the various tribes *sensu* Bentham (1875). The numbered nodes correspond to those in Figs. 1–3.



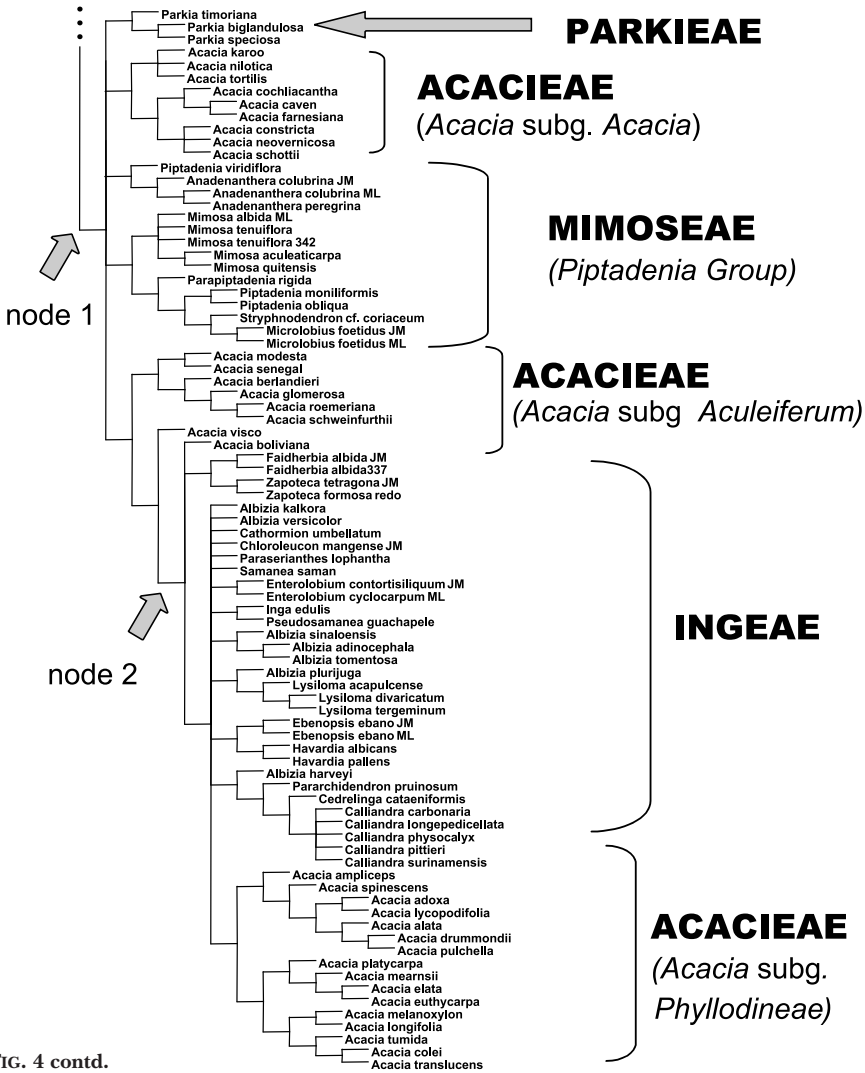


FIG. 4 contd.

## Acacieae

Perhaps the most significant finding of this study is the lack of monophyly of *Acacia* s.l. *Acacia* subg. *Acacia* is separated from *Acacia* subg. *Aculeiferum* and *Acacia* subg. *Phyllodineae* by a node with 83% strict consensus bootstrap support, and the core *Acacia* subg. *Aculeiferum* is separated from the *Acacia* subg. *Aculeiferum*/Ingeae/*Acacia* subg. *Phyllodineae* clade with 69% strict consensus bootstrap support. Thus, *Acacia* s.s. is positively paraphyletic and possibly polyphyletic given these data. As mentioned in the introduction, the polyphyly of *Acacia* has been suspected for some time (see Pedley, 1986; Maslin, 1988; Guinet, 1990; Polhill, 1990), but there has been controversy about how many and which groups should be recognised (see Pedley, 1987; Maslin, 1988; Vassal, 1988).

There has also been disagreement about the relationships of the groups to one another and to other genera of Ingeae. Pedley's (1986) reasons for splitting *Acacia* rested primarily on the significant differences among the subgenera rather than on notions of monophyly. *Acacia* s.s. was characterised by having corperate, columellate polyads, unique free amino acids in the seeds (N-acetyldjenkenkolic acid), and the presence of stipular spines. *Senegalia* had distinctive floral morphology, with the stamens inserted on a disc and a well-developed gynophore, as well as prickles on the stem and a different set of amino acids in the seeds. *Racosperma* usually had phyllodes and extraporate pollen, but also shared many characters with *Senegalia*. Pedley considered *Racosperma* and *Senegalia* to share a common ancestor with the ingioid genus *Calliandra*; indeed, he thought that *Racosperma* was derived from a senegalian ancestor (thus making *Senegalia* paraphyletic, Fig. 5A). He thought that *Acacia* s.s. was derived from a separate group of Ingeae, and shared a common ancestor with *Pithecellobium*.

The morphological cladistic analysis of Chappill and Maslin (1995) also showed independent derivations of the *Acacia* subg. *Phyllodineae*/*Acacia* subg. *Aculeiferum* group from *Acacia* subg. *Acacia* within the Ingeae, although their analysis differed from Pedley's in that *Acacia* subg. *Acacia* was sister to *Calliandra* (Fig. 5B). Note that in this scenario, *Acacia* subg. *Aculeiferum* and *Acacia* subg. *Phyllodineae* are sister taxa, and that *Acacia* subg. *Acacia* is nested among the Ingeae. This cladogram conflicted with one presented later in the same paper with much more intensive sampling of species of *Acacia* but few Ingeae (Fig. 5C). In the second analysis, the Ingeae and *Acacia* subg. *Acacia* form clades that are unresolved relative to one another, followed by a derived *Acacia* subg. *Aculeiferum*/*Acacia* subg. *Phyllodineae* clade. Although *Acacia* subg. *Acacia* and *Acacia* subg. *Phyllodineae* were monophyletic in both analyses, *Acacia* subg. *Aculeiferum* formed a paraphyletic grade at the base of the *Acacia* subg. *Phyllodineae* clade in the analysis with dense sampling of *Acacia*. Grimes (1999) sampled a large number of Ingeae genera and only "placeholder" taxa of *Acacia*, but nonetheless found that *Acacia* was biphyetic (Fig. 5D). His hypothesis disagrees with the previous two in showing *Acacia* subg. *Aculeiferum* as sister to *Acacia* subg. *Acacia* rather than *Acacia* subg. *Phyllodineae*.

*Acacia* subg. *Acacia* and *Acacia* subg. *Phyllodineae* have each been shown to be monophyletic in all molecular phylogenetic studies done to date, as well as in many of the above studies based on morphology. Clarke *et al.* (2000) in a cpDNA restriction site analysis found 100% bootstrap support for a monophyletic *Acacia* subg. *Acacia* clade, and strong support for a monophyletic *Acacia* subg. *Aculeiferum* clade, excluding the *Filicinae* group. The cladogram of Miller and Bayer (2001, summarised in Fig. 5E) is in closest agreement with hypothesis 2 of Chappill and Maslin (Fig. 5C), with 100% bootstrap support for a monophyletic *Acacia* subg. *Acacia*, somewhat less support (81%) for a monophyletic *Acacia* subg. *Aculeiferum* clade, excluding sect. *Filicinae*. The *Acacia* subg. *Phyllodineae* clade was also monophyletic (bs = 56%).

It is noteworthy that none of these analyses included significant numbers of Mimoseae genera, but concentrated on the Acacieae and Ingeae. Thus, the possibility that some *Acacia* might be most closely related to members of the Mimoseae was not tested. Furthermore, many analyses used *Mimosa* or *Parkia* to root the trees, and as is obvious from the cladogram presented here (Fig. 4), these taxa could be derived relative to *Acacia* subg. *Acacia*. The various analyses in Fig. 5 become much more congruent with one another if they are all rerooted at *Acacia* subg. *Acacia*.

The affinities of the monotypic genus *Faidherbia* have also been debated. *Faidherbia albida*, originally segregated from *Acacia* by Chevalier (1934), was resurrected by Vassal (1972), on the grounds that it differed from other species of *Acacia* in seedling and pollen morphology, as well as in the general anatomical and morphological features pointed out by Chevalier and others (summarised in Ross, 1979). Vassal (1972) suggested a monotypic tribe (Faidherbieae) to accommodate it; Polhill (1990) moved it to the Ingeae. Recent phylogenetic studies have been in conflict. Chappill

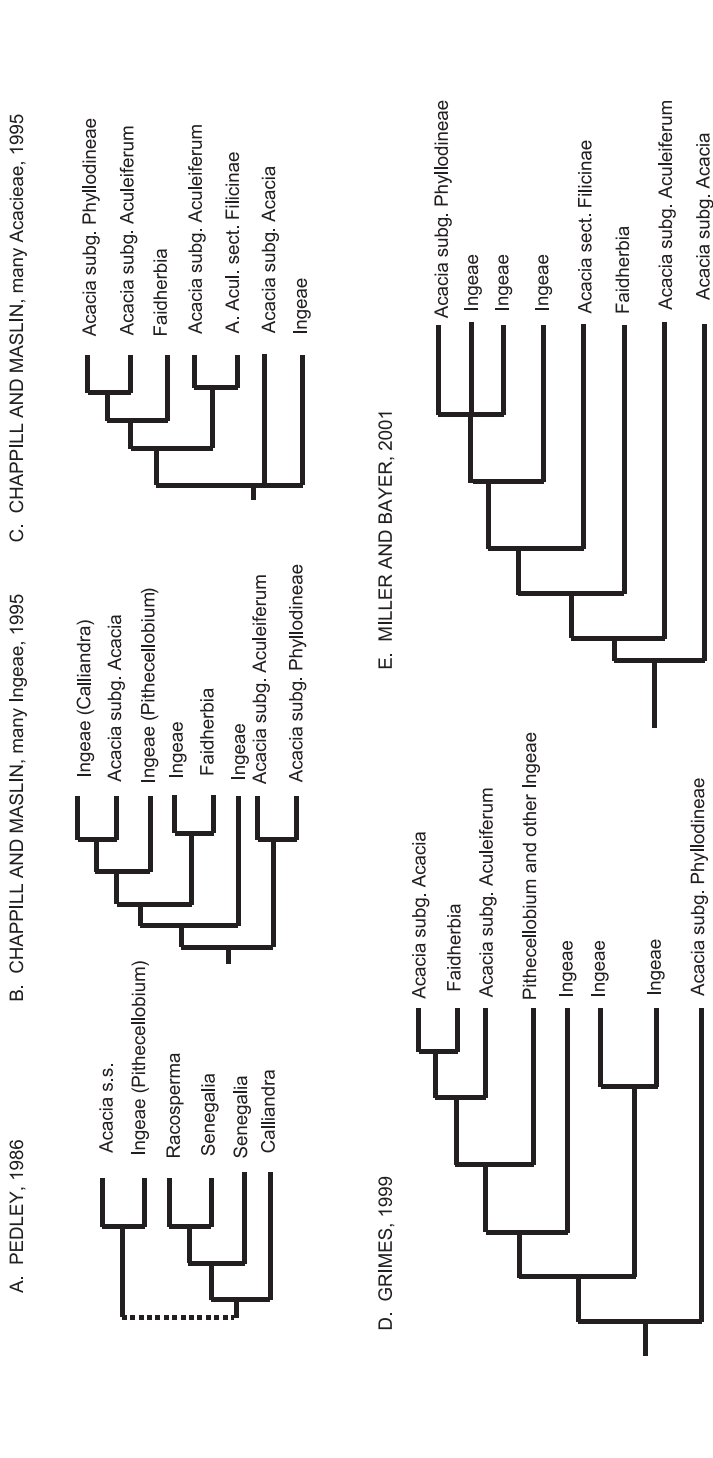


FIG. 5. Previous hypotheses of relationships in Acacieae. A. Pedley's 1986 scheme. Dotted line indicates presumed relationship, although this was not specified in the original paper. B, C. Summary of cladograms based on morphology and presented by Chappill and Maslin (1995). B shows the relationships from analysis of a matrix that included numerous exemplars of Ingeae, C a cladogram with many Acacieae and few Ingeae. D. Summary cladogram taken from Grimes (1999) with dense sampling of Ingeae and few Acacieae and based on morphological data. E. Summary cladogram from Miller and Bayer (2001), based on sequence data from the *trnK/matK* regions only.

and Maslin's (1995) two analyses conflicted in placing *Faidherbia* either as nested within the Ingeae (Fig. 5B) or as part of the *Acacia* subg. *Aculeiferum* grade (Fig. 5C). Grimes (1999) showed *Faidherbia* as sister to *Acacia* subg. *Acacia* (Fig. 5D). Robinson and Harris (2000) found *Faidherbia* to form part of a basal grade of Ingeae in which was nested *Acacia* subg. *Phyllodineae*, as did Miller and Bayer (2001), although *Acacia* subg. *Aculeiferum* sect. *Filicinae* also formed part of the basal grade in the latter analysis (Fig. 5E). As mentioned previously, the analysis presented in this paper weakly supports a relationship to *Zapoteca* (Ingeae; Fig. 3). Whether *Faidherbia* is more closely related to an acacia or to some member of the Ingeae, or is transitional between the two, awaits more conclusive data.

As mentioned above, our analysis of Acacieae is most consistent with Guinet's (1990) hypothesis that he based on pollen data. There is no evidence from our study that any part of *Acacia* is very closely related to *Calliandra*, in disagreement with Pedley (1986) and Chappill and Maslin (1995). *Acacia* subg. *Aculeiferum* is indeed paraphyletic as indicated by Pedley (1986), but it is not necessarily sister to *Acacia* subg. *Phyllodineae*. Support in this part of the cladogram is weak, so it is possible that the *Acacia* subg. *Phyllodineae* clade may be related somehow to a paraphyletic *Acacia* subg. *Aculeiferum*, but it is just as likely that any number of Ingeae genera are most closely related to *Acacia* subg. *Phyllodineae* as per Robinson and Harris (2000) and Miller and Bayer (2001). It is also highly likely that there are more than three lineages in *Acacia* s.l. There is 69% strict consensus bootstrap support for the clade that groups *Acacia visco*, *A. boliviana*, and the Ingeae/*Acacia* subg. *Phyllodineae* group, indicating that they are separate from the core *Acacia* subg. *Aculeiferum*.

In summary, there is strong agreement from most studies for a monophyletic *Acacia* subg. *Acacia* and a monophyletic *Acacia* subg. *Phyllodineae*. There are significant morphological synapomorphies for these clades (see above), and support is quite robust. Thus, their recognition presents no problem, at least from a phylogenetic viewpoint (but consider the impact of renaming some 900+ species of Australian *Acacia*). The problem arises when one considers *Acacia* subg. *Aculeiferum*. Although there is a core group of species that clearly belong to *Acacia* subg. *Aculeiferum*, other taxa form a grade on the cladogram, here represented by *A. visco* and *A. boliviana*. There is mounting evidence that *Acacia* subg. *Aculeiferum* sect. *Filicinae* (represented here by *A. boliviana*) is a separate lineage, but there is considerably less bootstrap support for the placement of *A. visco*. Although somewhat denser sampling in *Acacia* subg. *Aculeiferum* was done by Miller and Bayer (2003), relationships still are not well resolved and support for groups outside the core *Acacia* subg. *Aculeiferum* is weak.

We are thus in the position that although we can clearly delimit monophyletic clades for part of *Acacia* s.l., there exist significant gaps in our knowledge of other species groups. Denser sampling of both taxa and characters will be necessary to resolve these relationships. Nonetheless, our study indicates that monophyletic clades with strong support be segregated, i.e. *Acacia* subg. *Acacia*, the core *Acacia* subg. *Aculeiferum*, and *Acacia* subg. *Phyllodineae*. The molecular data presented here, in combination with morphological and chemical characters, are used by Maslin *et al.* (2003) to examine generic boundaries in *Acacia* s.l. Although they have not taken up Pedley's (1986) available names, they distinguish five lineages in *Acacia* s.l.: the three clades listed above, as well as two additional segregates from *Acacia* subg. *Aculeiferum*, *A. subg. Aculeiferum* sect. *Filicinae* (*A. boliviana* in this study), and the "couleri group" (Jawad *et al.*, 2000). Other species, such as *A. visco* will be considered *incertae sedis* pending additional study.

### Tribal system

The tribal system of Bentham (1875), although quite useful in the past, fails to accurately reflect evolutionary relationships. Certainly, the Lewis and Elias (1981) system of 12 informal "groups" of Mimoseae has proved superior as a natural

classification, and their groups require only minor modification to accurately represent the phylogeny presented here (see Luckow *et al.*, 2000). Such a system of classification needs to be implemented throughout the subfamily Mimosoideae, and should incorporate both morphological and molecular data. The present study, although providing a springboard from which to begin such a reclassification, lacks resolution and/or support among the Ingeae and part of the Acacieae, as well as any morphological component. Additional sampling of both characters and taxa are sorely needed in this portion of the tree before any such reorganisation can take place.

This study also indicates that it may not be feasible to recognise “tribes” within the Mimosoideae, unless one wishes to elevate the groups, such as those of Lewis and Elias (1981) and Luckow *et al.* (2000), to tribal status. Based on our current knowledge, one would be forced to recognise at least 13 tribes from the Mimoseae, while the lack of resolution in the terminal clade of Acacieae-Ingeae would mandate either the addition of numerous very small tribes or a very large, unwieldy one. Although additional study may resolve the latter problem, it may be that such groups will eventually receive formal recognition at the subtribal level, and that the Mimosoideae, as it has traditionally been defined, may itself become only a tribe within the Leguminosae.

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