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PHYLOGENETIC RELATIONSHIPS WITHIN THE TRIBE MALVEAE (MALVACEAE, SUBFAMILY MALVOIDEAE) AS INFERRED FROM ITS SEQUENCE DATA[1]

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Phylogenetic relationships among genera of tribe Malveae (Malvaceae, subfamily Malvoideae) were reconstructed using sequences of the internal transcribed spacer (ITS) region of the 18S–26S nuclear ribosomal repeat. Newly generated sequences were combined with those available from previous generic level studies to assess the current circumscription of the tribe, monophyly of some of the larger genera, and character evolution within the tribe. The ITS data do not support monophyly of most generic alliances as presently defined, nor do the data support monophyly of several Malveae genera. Two main well-supported clades were recovered, which correspond primarily to taxa that either possess or lack involucral bracts, respectively. Chromosomal evolution has been dynamic in the tribe with haploid numbers varying from $n = 5$ to 36. Aneuploid reduction, hybridization, and/or polyploidization have been important evolutionary processes in this group.

Key words: Bayesian analysis; ITS; Malvaceae; Malveae; Malvoideae; molecular phylogeny; parsimony analysis.

In recent years, morphological and molecular evidence have shown that many of the traditional families of the Malvales are not monophyletic (Judd and Manchester, 1997; Alverson et al., 1998, 1999; Bayer et al., 1999). As a result, an expanded circumscription of the Malvaceae has been created, which is composed of nine subfamilies: Bombacoideae (formerly Bombacaceae, in part), Brownlowioideae, Byttnerioideae, Dombeyoideae, Grewioideae, Helicteroideae, Malvoideae (formerly Malvaceae), Sterculioideae (formerly Sterculiaceae, in part), and Tilioideae (formerly Tiliaceae, in part) (Bayer et al., 1999; Bayer and Kubitzki, 2003). Subfamily Malvoideae (Eumalvoideae of Baum et al., 2004) has consistently emerged as a monophyletic group on the basis of both morphological and molecular data (Judd and Manchester, 1997; Alverson et al., 1999; Bayer et al., 1999). In the most recent treatment of Malvoideae, Bayer and Kutbitzki (2003) divide the subfamily into four tribes: Gossypieae, Hibisceae, Kydieae, and Malveae.

As considered here, tribe Malveae includes approximately 70 genera (~1000 species) that encompass the majority of the morphological and taxonomic diversity in the subfamily (Table 1) (Fryxell, 1997). Traditionally, members of the Malveae have been characterized by a combination of several morphological characters: schizocarpic fruits (sometimes a capsule), mericarps numbering 3 to over 20 and equal to the number of free styles, antheriferous apex of the staminal column, and the absence of lysigenous cavities (''gossypol glands'') (Fryxell, 1988; Bayer and Kubitzki, 2003). The genera of Malveae exhibit a broad geographic distribution, with representatives in both tropic and temperate areas exploiting a variety of habitats. Around 15 of the 70 Malveae genera have mostly temperate distributions, while some of the largest genera in the tribe (*Abutilon*, *Sida*, *Nototriche*) have primarily tropical distributions (Table 1).

Various interpretations of the composition and subdivision of tribe Malveae have been proposed. Table 2 outlines the major classification schemes, beginning with Bentham and Hooker (1862), for tribe Malveae and for genera currently placed in the tribe. Bentham and Hooker divided the tribe into four subtribes on the basis of carpel arrangement and ovule number and position: Abutilinae, Malopinae, Malvinae, and Sidinae (as Abutileae, Malopeae, Eumalveae, and Sideae, respectively). Schumann (1890) later reassigned three genera (*Malope*, *Kitaibela*, *Palaua*) to a separate tribe Malopeae due to the irregular arrangement of their carpels into superimposed verticils (i.e., not in single whorl). The remaining genera of the Malveae were placed into one of three subtribes by Schumann (Abutilinae, Malvinae, or Sidinae) based on carpel morphology. This classification was followed by Edlin (1935) and slightly modified by Kearney (1949, 1951) who erected a fourth subtribe, Corynabutilinae. Hutchinson (1967) further restructured the family and tribes by including the tribes Abutileae (composed of subtribes Abutilinae and Sidinae), Malopeae, and Malveae (containing subtribes Corynabutilinae and Malvinae). *Bastardia* and *Bastardiopsis*, the two Malveae genera that have capsules rather than schizocarps, were transferred

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TABLE 1. Genera of tribe Malveae (Malvaceae), their alliance associations, reported chromosome numbers and geographic distributions (Fryxell, 1997; Bayer and Kubitzki, 2003, with modification). Chromosome numbers in brackets are those reported in the literature, but are seemingly out of sync with numbers published for the rest of the genus.

Alliance	Genus	Number of species	Haploid chromosome numbers	Distribution
Abutilon	*Abutilon* Mill.	~160	*n* = 7, 8, 14, 16, 18, 21, 36	Pantropical
	Akrosida Fryxell & Fuertes	1	*n* = ?	Brazil
	Allosidastrum (Hochr.) Krapov., Fryxell & D.M. Bates	4	*n* = 7	Neotropics
	Allowissadula D.M. Bates	9	*n* = 8	Texas, Mexico
	Bastardia H.B.K.	3–4	*n* = 7, 14	Neotropics
	Bastardiastrum (Rose) D.M. Bates	8	*n* = 15	W Mexico
	Bastardiopsis (K. Schum.) Hassl.	10	*n* = 14	S America
	Billieturnera Fryxell	1	*n* = 8	S Texas to NE Mexico
	Corynabutilon (K. Schum.) Kearney	6	*n* = 8	Temperate Chile & Argentina
	Dendrosida Fryxell	7	*n* = 21	Colombia, Venezuela
	Herissantia Medik.	6+	*n* = 6, 7	Neotropics
	Hochreutinera Krapov.	2	*n* = 7	Mexico, Paraguay/Argentina
	Krapovickasia Fryxell	4	*n* = 8	SW Texas & NE Mexico, S America
	Malvella Jaub. & Spach	4	*n* = [11], 16?	W USA & Mexico, S America, Mediterranean
	Meximalva Fryxell	2	*n* = 8	S Texas to central Mexico
	Neobaclea Hochr.	1	*n* = 8	Temperate Argentina
	Pseudabutilon R.E. Fr.	19	*n* = 8, 16	USA to Argentina
	Rhynchosida Fryxell	2	*n* = 8	S Texas & N Mexico, Bolivia & Argentina
	Robinsonella Rose & Baker f.	15	*n* = 16	Mexico to Costa Rica
	Sida L.	~100	*n* = 6, 7, 8, 14, 16, 17, 21, 28	Pantropical
	Sidastrum Baker f.	8	*n* = 16	Mexico & West Indies to Argentina
	Tetrasida Ulbr.	2	*n* = ?	Ecuador & Peru
	Wissadula Medik.	26	*n* = 7	Neotropics
Anisodontea	*Anisodontea* Presl	20	*n* = 22	S Africa
Anoda	*Anoda* Cav.	24	*n* = 13, 14, 15, 18, 30, 45	S USA, Mexico, S America
	Periptera DC.	5	*n* = 13	W Mexico
Batesimalva	*Bakeridesia* Hochr.	20+	*n* = 15	Mexico, central America
	Batesimalva Fryxell	4	*n* = 12, 16	Mexico
	Briquetia Hochr.	5	*n* = 7	Mexico, S America
	Dirhamphis Krapov.	2	*n* = 7, 15	W Mexico, Bolivia/Paraguay
	Fryxellia D. M. Bates	1	*n* = 8	W Texas, N Mexico
	Horsfordia A. Gray	4	*n* = 15	SW USA, N Mexico, Baja California
Gaya	*Cristaria* Cav.	~75	*n* = 6, 12	Chile, also S Peru
	Gaya H.B.K.	33	*n* = 6, 12	Neotropics (Mexico, West Indies, Bolivia)
	Lecanophora Speg.	5	*n* = 6, 12, 18	Temperate Argentina
Kearnemalvastrum	*Kearnemalvastrum* D. M. Bates	2	*n* = 16	Mexico to Costa Rica, Colombia
Malacothamnus	*Iliamna* (Greene) Wiggins	7	*n* = 33	W USA & Canada, Illinois/Virginia
	Malacothamnus Greene	10	*n* = 17	California/Baja California
	Neobrittonia Hochr.	1	*n* = 16	Mexico to Panama
	Phymosia Desv. ex Ham.	8	*n* = 17	Mexico, Guatemala, Carribean
Malope	*Kitaibela* Willd.	2	*n* = 21, 22	E Europe, W Asia
	Malope Linn.	3	*n* = 22, 25	Mediterranean
Malva	*Alcea* L.	~60	*n* = 13, 21	Mediterranean to central Asia
	Althaea L.	12	*n* = 13, 14, 20, 21, 22, 25, 35, 42	Europe, Middle East, central Asia
	Lavatera L.	~13	*n* = 14, 21, 42, 56	Mediterranean, California/Baja California, Australia
	Malva L.	20+	*n* = 21, 38, 42, 56	Europe, Asia, N Africa
	Navaea Webb & Berthelot	1	*n* = 21, 22?	Macaronesia
Malvastrum	*Malvastrum* A. Gray	15	*n* = 6, 12, 18, 24	N America & S America

TABLE 1. Continued.

Alliance	Genus	Number of species	Haploid chromosome numbers	Distribution
Modiola	*Modiola* Moench	1	$n = 9$	Pantropical and subtropical, extending to temperate regions
	Modiolastrum K. Schum.	5	$n = 5, 15, 50$	S America
	Tropidococcus Krapov.	1	$n = 12$	
Plagianthus	*Asterotrichion* Klotzsch	1	$n = ?$	Tasmania
	Gynatrix Alef.	2	$n = ?$	Tasmania, S/SE Australia
	Hoheria A. Cunn	6	$n = 21$	New Zealand
	Lawrencia Hook.	12	$n = ?$	Australia
	Plagianthus J.R. & G. Forst.	2	$n = 21$	New Zealand
Sidalcea	*Callirhoë* Nutt.	9	$n = 12, 14, 15, 21, 28, 30, 34, 35, 42, 56$	central USA to NE Mexico
	Sidalcea A. Gray	~20	$n = 10, 20, 30$	W USA and NW Mexico
Sphaeralcea	*Acaulimalva* Krapov.	19	$n = 5$	Andes
	Andeimalva J. A. Tate	4	$n = 6$	Andes
	Calyculogygas Krapov.	1	$n = 5$	Uruguay
	Calyptraemalva Krapov.	1	$n = ?$	Brazil
	Eremalche Greene	3	$n = 10, 20$	S California, N Baja California
	Fuertesimalva Fryxell	14	$n = 5, 10, 15$	Andes, Mexico
	Monteiroa Krapov.	8	$n = 10$	S Brazil, N Argentina
	Napaea L.	1	$n = [14], 15$	E USA
	Nototriche Turcz.	~100	$n = 5, 10, 15, 20$	Andes
	Palaua Cav.	15	$n = 5$	Coastal Peru & Chile
	Sidasodes Fryxell & Fuertes	2	$n = 5$	Colombia, Ecuador, Peru
	Sphaeralcea St.-Hil.	~40	$n = 5, 10, 15, 25$	Temperate N & S America
	Tarasa Phil.	27	$n = 5, 10$	Andes, Mexico
	Urocarpidium Ulbr.	1	$n = 5$	Andes, Mexico

to tribe Hibisceae. Tribe Abutileae was created to accommodate genera with decurrent stigmas, while genera with apical stigmas remained in tribe Malveae. Hutchinson (1967) distinguished the subtribes of Abutileae and Malveae by ovule number and position.

Bates (1968) completely revised the classification scheme by eliminating the subtribes and creating 13 informal generic alliances within a single tribe Malveae (Table 2). Bates' generic alliances were based on morphology and chromosome number and were thought to reflect better phylogenetic affinities (Bates, 1968). Bates and Blanchard (1970) later expanded this classification scheme to include 16 alliances. In his treatment of the Mexican genera of Malvaceae, Fryxell (1988) slightly modified the classification of Bates and Blanchard. The major changes involved removing several genera from the *Abutilon* alliance and creating three new alliances (*Herrisantia*, *Robinsonella*, and *Sida*), segregating *Modiola* from the *Sphaeralcea* alliance into the *Modiola* alliance, reassigning *Callirhoë* to the *Sidalcea* alliance, renaming the *Malacothamnus* as the *Phymosia* alliance and adding *Neobrittonia* to it from the *Abutilon* alliance, and creating two new alliances for the newly described genera *Batesimalva* and *Fryxellia*.

Most recently, Bayer and Kubitzki (2003) provided a comprehensive treatment for the tribe, as well as for the entire subfamily and family. Fourteen Malveae alliances were maintained, but their generic compositions were altered somewhat (Table 2). The genera previously segregated into the *Herrisantia*, *Robinsonella*, and *Sida* alliances by Fryxell (1988) were subsumed into the *Abutilon* alliance. Members of the *Bakeridesia* and *Fryxellia* alliances were included with the *Batesimalva* alliance. The *Malacothamnus* alliance was maintained in name as originally proposed by Bates and Blanchard (1970), but its generic composition follows Fryxell (1988). The *Napaea* alliance was included with the *Sphaeralcea* alliance. In the present study, we will follow the taxonomy of Bayer and Kubitzki (2003) with slight modification to reflect recent taxonomic changes: the addition of *Navaea* to the *Malva* alliance (Fuertes Aguilar et al., 2003), *Tropidococcus* to the *Modiola* alliance (Fernandez et al., 2003; Krapovickas, 2003) and *Andeimalva* to the *Sphaeralcea* alliance (Tate, 2003).

Recent molecular studies of the Malvales and the Malvoideae (as Malvaceae sensu stricto) have provided preliminary evidence for phylogenetic relationships within the subfamily as well as within the tribe Malveae. Tribe Gossypieae was sister to Malveae based on *rbcL* and *atpB* (Bayer et al., 1999) and *ndhF* (Alverson et al., 1999) sequence data. All five tribes were represented in a recent phylogenetic analysis of tribe Hibisceae, using chloroplastic *ndhF* and *rpl16* intron sequences (Pfeil et al., 2002). Although only a few genera of Malveae were included, the resulting trees placed Malveae and Gossypieae at the base of an unresolved clade and sister to most of the Hibisceae. Another cpDNA based study, using restriction site data (La Duke and Doebley, 1995), sampled more extensively in the Malveae and placed the tribe in a clade that was sister to the remaining tribes of subfamily Malvoideae. Although La Duke and Doebley's study did not support monophyly of the Malveae alliances, it did identify two major clades: one composed of the *Abutilon* and *Sida* alliances and the other composed of the remaining alliances. A recent phylogenetic analysis based on sequence data from the internal transcribed spacer (ITS) regions of the 18–26S nuclear ribosomal repeat (Fuertes Aguilar et al., 2003) examined the phylogenetic relationships of the *Abutilon* and *Sida* alliances. Although their sampling was not exhaustive, neither alliance was supported as monophyletic (Fuertes Aguilar et al., 2003).

Previous studies have demonstrated that sufficient variation exists in ITS to resolve phylogenetic relationships within and between genera in the Malvoideae (Seelanan et al., 1997) and particularly in the Malveae (Ray, 1995; Whittall et al., 2000; Andreasen and Baldwin, 2001; Fuertes Aguilar et al., 2003; Tate and Simpson, 2003). Furthermore, several of these studies have also revealed that some genera are not monophyletic as currently circumscribed. Among these are *Abutilon* and *Sida* (Fuertes Aguilar et al., 2003), *Malva* and *Lavatera* (Ray, 1995), and *Tarasa* (Tate and Simpson, 2003). We extended these earlier studies with a broader sample representing most of the genera in tribe Malveae. The main objectives of this study were to reconstruct phylogenetic relationships in tribe Malveae, to assess the amount of congruence between the inferred relationships and the existing classification, to identify potential morphological synapomorphies that might support the reconstructed clades, and finally, to examine character evolution within the tribe.

MATERIALS AND METHODS

Taxon sampling—We sampled 68 genera (121 species) in our study representing all of the 14 alliances recognized by Bayer and Kubitzki (2003). To assess monophyly of the genera, as well as intrageneric variation, two or more species from the same genus were included when possible. The outgroups included *Gossypium*, *Kokia*, *Lebronnecia*, and *Thespesia* (tribe Gossypieae), and *Howittia* (incertae sedis fide Bayer and Kubitzki, 2003). Members of the Gossypieae were included based on previous molecular phylogenies for subfamily Malvoideae, which indicated that tribe Gossypieae is sister to Malveae (Alverson et al., 1999; Bayer et al., 1999). Originally, *Howittia* was included in the Malveae by Bentham and Hooker (1862), but later workers suggested that it should be placed in tribe Hibisceae (Edlin, 1935; Fryxell, 1968). Recent molecular analyses based on cpDNA sequence data found Hibisceae to be paraphyletic, with four Hibisceae genera (*Camptostemon*, *Radyera*, *Howittia*, and *Lagunaria*) placed sister to the remaining members of the Malvoideae (Pfeil et al., 2002). Tribes Malveae and Gossypieae (both of which were monophyletic) formed a clade sister to a clade containing tribes Decaschistieae, Malvavisceae, and the remaining Hibisceae genera (Pfeil et al., 2002). Although it is clear that *Howittia* does not belong in either tribe Hibisceae or Malveae, we include the genus here to represent a more distantly related lineage of Malvoideae.

The taxa sampled, voucher information, and GenBank accession numbers are available as a Data Supplement (Appendix 1) accompanying the online version of this article.

DNA extraction and ITS amplification—Total DNA was extracted from fresh material, herbarium specimens or silica—gel-dried material (Chase and Hills, 1991) by various modifications of the CTAB protocol (Doyle and Doyle, 1987). The internal transcribed spacer (ITS) region of the 18S–26S nuclear ribosomal repeat was amplified by the polymerase chain reaction (PCR) as previously described (Fuertes Aguilar et al., 2003; Tate and Simpson, 2003). Amplification products were separated on a 1% agarose gel, stained with ethidium bromide, and then visualized with UV on a transilluminator. PCR products were cleaned using QIAquick spin columns (Qiagen, Valencia, California, USA) following the manufacturer's instructions. Cycle sequencing was performed using Big Dye terminator chemistry (Applied Biosystems, Foster City, California, USA). Bidirectional automated sequencing using the forward and reverse amplification primers was conducted on an ABI 3700 or 377 at the DNA Analysis Laboratory at The University of Texas at Austin or an ABI 3100 at The University of North Dakota.

Sequence alignment and phylogenetic analysis—The boundaries of ITS were determined by comparison to a published *Gossypium* sequence in

TABLE 2. Historical classification of genera currently placed in tribe Malveae (see Table 1). n/a means not applicable (i.e., genus not found in geographical region under study). Genera are listed alphabetically within their current generic alliance (Bayer and Kubitzki, 2003).

Genus	Year described	Bentham and Hooker 1862	Schumann 1890	Edlin 1935	Kearney 1951 (American genera only)	Hutchinson 1967
		Tribe/subtribe	Tribe/subtribe	Tribe/subtribe	Tribe/subtribe	Tribe/subtribe
Abutilon	1754	Malveae/Abutilinae	Malveae/Abutilinae	Malveae/Abutilinae	Malveae/Abutilinae	Abutileae/Abutilinae
Akrosida	1992	–[a]	–	–	–	–
Allosidastrum	1988	–	–	–	–	–
Allowissadula	1978	–	–	–	–	–
Bastardia	1822	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	Hibisceae
Bastardiastrum	1978	–	–	–	–	–
Bastardiopsis	1910	–	–	Malveae/Sidinae	Malveae/Sidinae	Hibisceae
Billieturnera	1982	–	–	–	–	–
Corynabutilon	1949	–	–	–	Malveae/Corynabutilinae	Malveae/Corynabutilinae
Dendrosida	1971	–	–	–	–	–
Herrisantia	1788	–	–	Malveae/Sidinae[h]	Malveae/Abutilinae[i]	Abutileae/Abutilinae[m]
Hochreutinera	1970	–	–	–	–	–
Krapovickasia	1978	–	–	–	–	–
Malvella	1855	Malveae/Sidinae[b]	Malveae/Sidinae[b]	–	–	Abutileae/Sidinae
Meximalva	1975	–	–	–	–	–
Neobaclea	1929	–	–		Malveae/Corynabutilinae	Malveae/Corynabutilinae
Pseudabutilon	1908	–	–	Malveae/Abutilinae	Malveae/Abutilinae	Abutileae/Abutilinae
Rhynchosida	1978	–	–	–	–	–
Robinsonella	1897	–	–	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae
Sida	1753	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae
Sidastrum	1892	–	–	–	Malveae/Sidinae[b]	Malveae/Sidinae[b]
Tetrasida	1916	–	–	–	Malveae/Sidinae	Malveae/Sidinae
Wissadula	1787	Malveae/Abutilinae	Malveae/Abutilinae	Malveae/Abutilinae	Malveae/Abutilinae	Abutileae/Abutilinae
Anisodontea	1844	Malveae/Abutilinae[c]	Malveae/Abutilinae[c]	–	–	Abutileae/Abutilinae[c]
Anoda	1785	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	Abutileae/Sidinae
Periptera	1824	–	–	Malveae/Sidinae	Malveae/Sidinae	Abutileae/Sidinae
Bakeridesia	1913	–	–	Malveae/Abutilinae	Malveae/Abutilinae	Abutileae/Abutilinae
Batesimalva	1975	–	–	–	–	–
Briquetia	1902	–	–	Malveae/Sidinae	Malveae/Sidinae	Abutileae/Sidinae
Dirhamphis	1970	–	–	–	–	–
Fryxellia	1974	–	–	–	–	–
Horsfordia	1887	–	–	Malveae/Abutilinae	Malveae/Abutilinae	Abutileae/Abutilinae
Cristaria	1799	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	Abutileae/Sidinae
Gaya	1822	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	Abutileae/Sidinae
Lecanophora	1926	–	–	–	Malveae/Sidinae[j]	Malveae/Sidinae[j]
Kearnemalvastrum	1967	–	–	–	–	–
Iliamna	1906	–	–	–	Malveae/Abutilinae	Abutileae/Abutilinae
Malacothamnus	1906	–	–	–	Malveae/Abutilinae	Abutileae/Sidinae
Neobrittonia	1905	–	–	Malveae/Abutilinae	Malveae/Abutilinae	Abutileae/Abutilinae
Phymosia	1825	Malveae/Abutilinae[c]	Malveae/Abutilinae[c]	–	Malveae/Abutilinae	Abutileae/Abutilinae
Kitaibela	1802	Malopeae	Malopeae	Malopeae	n/a	Malopeae
Malope	1735	Malopeae	Malopeae	Malopeae	n/a	Malopeae
Alcea	1753	Malveae/Eumalvinae[d]	Malveae/Eumalvinae[d]	–	–	Malveae/Malvinae[d]
Althaea	1753	Malveae/Eumalvinae	Malveae/Malvinae	Malveae/Malvinae	Malveae/Malvinae	Malveae/Malvinae
Lavatera	1753	Malveae/Eumalvinae	Malveae/Malvinae	Malveae/Malvinae	Malveae/Malvinae	Malveae/Malvinae
Malva	1753	Malveae/Eumalvinae	Malveae/Malvinae	Malveae/Malvinae	Malveae/Malvinae	Malveae/Malvinae
Navaea	1836	Malveae/Eumalvinae[e]	Malveae/Malvinae[e]	–	n/a	–
Malvastrum	1849	Malveae/Eumalvinae	Malveae/Malvinae	Malveae/Malvinae	Malveae/Abutilinae	Abutileae/Sidinae
Modiola	1794	Malveae/Abutilinae	Malveae/Abutilinae	Malveae/Abutilinae	Malveae/Abutilinae	Abutileae/Abutilinae
Modiolastrum	1891	–	–	Malveae/Abutilinae	Malveae/Abutilinae[k]	Malveae/Abutilinae[k]
Asterotrichion	1841	Malveae/Sidinae[f]	Malveae/Sidinae[f]	–	n/a	Malveae/Malvinae
Gynatrix	1862	–	–	–	n/a	Malveae/Malvinae
Hoheria	1839	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	n/a	Malveae/Malvinae
Lawrencia	1840	Malveae/Sidinae[f]	Malveae/Sidinae[f]	Malveae/Sidinae	n/a	Malveae/Malvinae
Plagianthus	1775	Malveae/Sidinae	Malveae/Sidinae	Malveae/Sidinae	n/a	Malveae/Malvinae
Callirhoë	1821	Malveae/Eumalvinae	Malveae/Malvinae[g]	–	Malveae/Malvinae	Malveae/Malvinae

TABLE 2. Extended.

Bates 1968	Bates and Blanchard 1970	Fryxell 1988 (Mexican genera only)	Bayer and Kubitzki 2003
Generic alliance	Generic alliance	Generic alliance	Generic alliance
Abutilon	*Abutilon*	*Abutilon*	*Abutilon*
–	–	–	*Abutilon*
–	–	*Sida*	*Abutilon*
–	–	*Abutilon*	*Abutilon*
Abutilon	*Abutilon*	*Abutilon*	*Abutilon*
–	–	*Abutilon*	*Abutilon*
Abutilon	*Abutilon*	n/a	*Abutilon*
–	–	*Abutilon*	*Abutilon*
Abutilon	*Abutilon*	n/a	*Abutilon*
–	–	*Sida*	*Abutilon*
–	–	*Herrisantia*	*Abutilon*
–	–	*Abutilon*	*Abutilon*
–	–	*Sida*	*Abutilon*
–	–	*Sida*	*Abutilon*
–	–	*Sida*	*Abutilon*
Abutilon	*Abutilon*	n/a	*Abutilon*
Abutilon	*Abutilon*	n/a	*Abutilon*
–	–	*Sida*	*Abutilon*
Abutilon	*Abutilon*	*Robinsonella*	*Abutilon*
Abutilon	*Abutilon*	*Sida*	*Abutilon*
–	–	*Sida*	*Abutilon*
Abutilon	*Abutilon*	n/a	*Abutilon*
Abutilon	*Abutilon*	*Abutilon*	*Abutilon*
Anisodontea	*Anisodontea*	n/a	*Anisodontea*
Anoda	*Anoda*	*Anoda*	*Anoda*
Anoda	*Anoda*	*Anoda*	*Anoda*
Abutilon	*Bakeridesia*	*Bakeridesia*	*Batesimalva*
–	–	*Batesimalva*	*Batesimalva*
Abutilon	*Abutilon*	*Batesimalva*	*Batesimalva*
–	–	*Batesimalva*	*Batesimalva*
–	–	*Fryxellia*	*Batesimalva*
Sphaeralcea	*Bakeridesia*	*Batesimalva*	*Batesimalva*
Gaya	*Gaya*	n/a	*Gaya*
Gaya	*Gaya*	*Gaya*	*Gaya*
Gaya	*Gaya*	n/a	*Gaya*
Kearnemalvastrum	*Kearnemalvastrum*	*Kearnemalvastrum*	*Kearnemalvastrum*
Malacothamnus	*Malacothamnus*	n/a	*Malacothamnus*
Malacothamnus	*Malacothamnus*	*Phymosia*	*Malacothamnus*
Abutilon	*Abutilon*	*Phymosia*	*Malacothamnus*
Malacothamnus	*Malacothamnus*	*Phymosia*	*Malacothamnus*
Malope	*Malope*	n/a	*Malope*
Malope	*Malope*	n/a	*Malope*
–	–	*Malva*	*Malva*
Malva	*Malva*	n/a	*Malva*
Malva (in part), *Anisodontea* (in part)	*Malva* (in part), *Anisodontea* (in part)	*Malva*	*Malva*
Malva	*Malva*	*Malva*	*Malva*
–	–	–	–
Malvastrum (in part), *Sphaeralcea* (in part)	*Malvastrum* (in part), *Sphaeralcea* (in part)	*Malvastrum*	*Malvastrum*
Sphaeralcea	*Sphaeralcea*	*Modiola*	*Modiola*
Sphaeralcea	*Sphaeralcea*	n/a	*Modiola*
Plagianthus	*Plagianthus*	n/a	*Plagianthus*
Plagianthus	*Plagianthus*	n/a	*Plagianthus*
Plagianthus	*Plagianthus*	n/a	*Plagianthus*
Plagianthus	*Plagianthus*	n/a	*Plagianthus*
Plagianthus	*Plagianthus*	n/a	*Plagianthus*
Malva	*Callirhoe*	*Sidalcea*	*Sidalcea*
Sidalcea	*Sidalcea*	*Sidalcea*	*Sidalcea*

TABLE 2. Continued.

Genus	Year described	Bentham and Hooker 1862 Tribe/subtribe	Schumann 1890 Tribe/subtribe	Edlin 1935 Tribe/subtribe	Kearney 1951 (American genera only) Tribe/subtribe	Hutchinson 1967 Tribe/subtribe
Sidalcea	1849	Malveae/Eumalvinae	Malveae/Malvinae	Malveae/Malvinae	Malveae/Malvinae	Malveae Malvinae
Acaulimalva	1974	–	–	–	–	–
Andeimalva	2003	–	–	–	–	–
Calyculogygas	1960	–	–	–	–	Abutileae/Abutilinae
Calyptraemalva	1965	–	–	–	–	Abutileae/Abutilinae
Eremalche	1906	–	–	–	Malveae/Abutilinae[l]	Abutileae/Abutilinae
Fuertesimalva	1996	–	–	–	–	–
Monteiroa	1951	–	–	–	–	Abutileae/Abutilinae
Napaea	1753	Malveae/Eumalvinae	Malveae/Malvinae	Malveae/Malvinae	Malveae/Malvinae	Malvinae
Nototriche	1863	–	–	Malveae/Sidinae	Malveae/Abutilinae	Abutileae/Sidinae
Palaua	1785	Malopeae	Malopeae	Malopeae	Malopeae	Malopeae
Sidasodes	1992	–	–	–	–	–
Sphaeralcea	1825	Malveae/Abutilinae	Malveae/Abutilinae	Malveae/Abutilinae	Malveae/Abutilinae	Abutileae/Abutilinae
Tarasa	1891	–	–	Malveae/Sidinae	Malveae/Abutilinae	Abutileae/Sidinae
Urocarpidium	1916	–	–	–	Malveae/Abutilinae	Abutileae/Abutilinae

[a] –, genus not described yet or not included in treatment (details of synonymy not given).
[b] included under *Sida*.
[c] included under *Sphaeralcea*.
[d] included under *Althaea*.
[e] included under *Lavatera*.
[f] included under *Plagianthus*.
[g] included under *Malva*.
[h] as *Pseudobastardia* (see Bricicky, 1968).
[i] as *Gayoides* (see Bricicky, 1968).
[j] included under *Cristaria*.
[k] included under *Modiola*.
[l] included under *Malvastrum*.
[m] as *Bogenhardia* (see Bricicky, 1968).

GenBank (U12719, http://www.ncbi.nlm.nih.gov/). Forward and reverse sequences were assembled into contigs and edited using Sequencher (Gene Codes Corporation, 1995). The sequences were aligned using Clustal X (Thompson et al., 1997), with manual adjustments as needed. Conserved regions in ITS1 (Liu and Schardl, 1994) and ITS2 (Hershkovitz and Zimmer, 1996) were used to identify potential pseudogenes and confirm the alignment at those positions. Sequences that did not have these conserved regions were considered to be pseudogenes and were excluded from the phylogenetic analyses. The highly conserved 5.8S was not available for all sequences, so the region was excluded from the phylogenetic analyses. Because homology assessment for several nucleotide positions across distantly related genera was uncertain, we employed a conservative alignment strategy. By setting the gap penalty low, we favored introducing gaps, which created autapomorphies rather than forcing synapomorphies. We also conducted phylogenetic analyses with and without these uncertain regions as described next.

Both parsimony and Bayesian analyses of the ITS sequence data were conducted. For parsimony, heuristic tree searches were performed using PAUP* version 4.0b10 (Swofford, 2002) with 1000 random addition replicates, tree bisection reconnection (TBR) branch swapping, ACCTRAN character-state optimization, and gaps coded as missing. To reduce the amount of time spent swapping on suboptimal trees, only five trees were held at each replicate, to an arbitrary maximum of 10 000 trees saved. The best trees were then swapped to completion. Bootstrap support for the internal nodes was determined by 1000 bootstrap replications (Felsenstein, 1985) with uninformative characters excluded and using the maximum likelihood parameters estimated from Modeltest version 3.06 (Posada and Crandall, 1998) to conduct a neighbor-joining bootstrap.

Bayesian analyses were conducted using MrBayes 3.0 (Huelsenbeck and Ronquist, 2001), with the likelihood parameters estimated using Modeltest, the Markov chain Monte Carlo algorithm (Larget and Simon, 1999) with four simultaneous chains (three heated and one cold), and trees saved every 100 generations. Two independent runs of two million generations each (corresponding to at least five times the burn-in period) were performed to ensure the analyses converged on the same ''plateau.'' Trees from the burn-in period were discarded, and a 50% majority rule consensus tree was constructed from the remaining trees (Wilcox et al., 2002). Posterior probabilities for the clades reconstructed from each independent run were also compared to ensure proper mixing (Huelsenbeck et al., 2002).

RESULTS

ITS sequence characteristics and phylogeny reconstruction—The aligned region, including ITS1 and ITS2, contained 644 characters: 166 characters were constant, 98 were parsimony uninformative, and 380 were parsimony informative. ITS1 contributed 158 informative characters while ITS2 had 222. The ITS1 spacer varied in length from 253–297 base pairs (bp), while ITS2 varied from 207–231 bp. The GC content of ITS1 was 46.7–60.1% (mean 53.3%) and ITS2 was 50–67.8% (mean 56.9%).

From parsimony analyses, 10 000 most parsimonious (MP) trees of 2980 steps with a CI = 0.28 (excluding uninformative characters), RI = 0.67, and RC = 0.21 were saved. In the ITS tree, both Gossypieae and Malveae are monophyletic, with Malveae comprised of two main clades. One of the main clades (hereafter referred to as clade A) consists of genera placed in the *Abutilon*, *Anoda*, *Batesimalva*, *Gaya*, *Malacothamnus* (in part), *Plagianthus*, and *Sphaeralcea* (in part) alliances (Fig. 1). The second large clade (clade B) contains genera from the *Anisodontea*, *Kearnemalvastrum*, *Malacothamnus*, *Malope*, *Malva*, *Malvastrum*, *Modiola*, *Sidalcea*, and *Sphaeralcea* alliances (Fig. 2). Most of the infratribal alliances are not monophyletic and many of the genera are also not

TABLE 2. Continued extended.

Bates 1968	Bates and Blanchard 1970	Fryxell 1988 (Mexican genera only)	Bayer and Kubitzki 2003
Generic alliance	Generic alliance	Generic alliance	Generic alliance
–	–	n/a	*Sphaeralcea*
–	–	–	–
Sphaeralcea	*Sphaeralcea*	n/a	*Sphaeralcea*
Sphaeralcea	*Sphaeralcea*	n/a	*Sphaeralcea*
Sphaeralcea	*Sphaeralcea*	*Sphaeralcea*	*Sphaeralcea*
–	–	*Sphaeralcea*	*Sphaeralcea*
Sphaeralcea	*Sphaeralcea*	n/a	*Sphaeralcea*
Sidalcea	*Napaea*	n/a	*Sphaeralcea*
Sphaeralcea	*Sphaeralcea*	n/a	*Sphaeralcea*
Sphaeralcea	*Sphaeralcea*	n/a	*Sphaeralcea*
–	–	–	*Sphaeralcea*
Sphaeralcea	*Sphaeralcea*	*Sphaeralcea*	*Sphaeralcea*
Sphaeralcea	*Sphaeralcea*	*Sphaeralcea*	*Sphaeralcea*
Sphaeralcea	*Sphaeralcea*	*Sphaeralcea*	*Sphaeralcea*

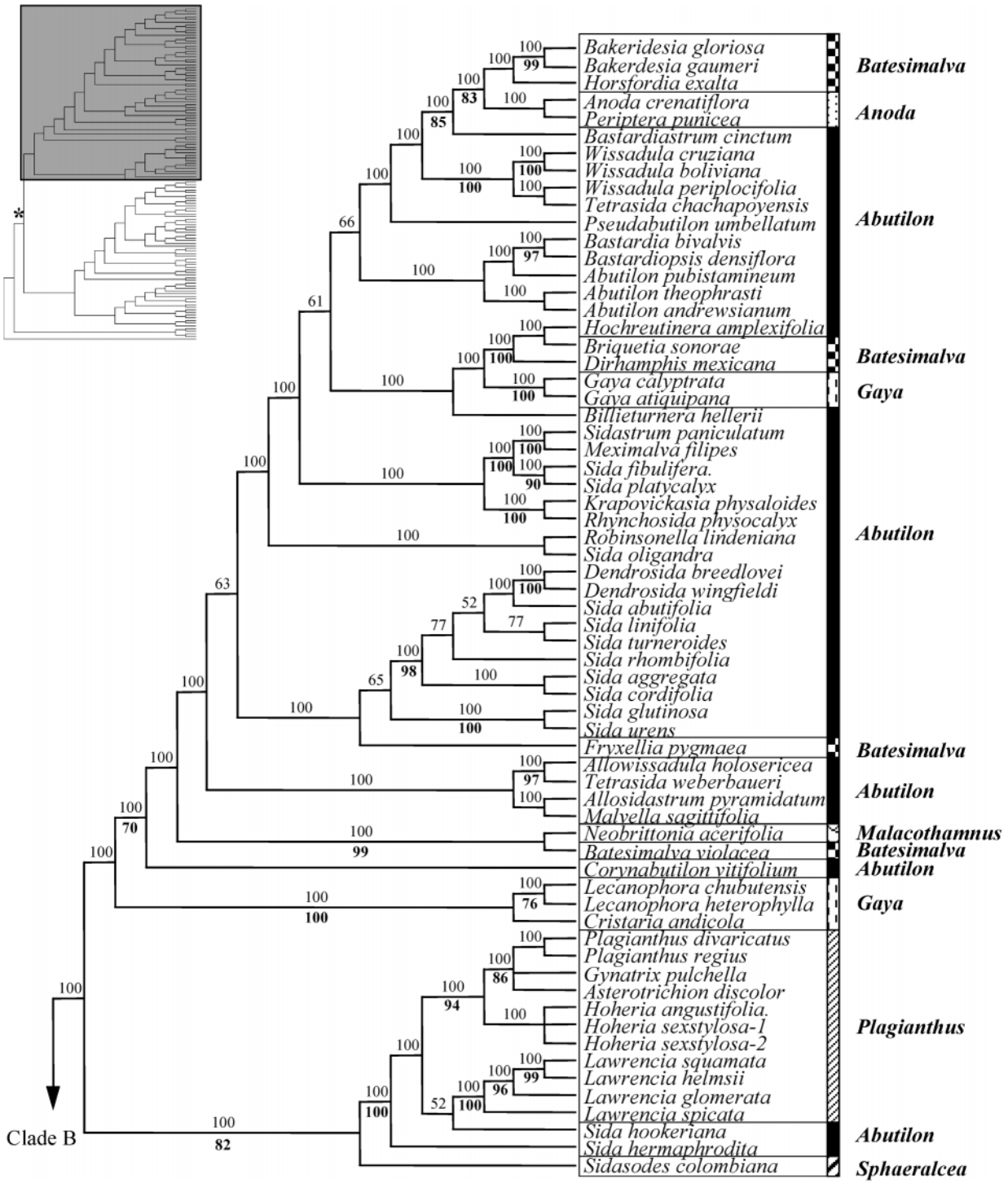
monophyletic, including *Abutilon*, *Iliamna*, *Sida*, *Tarasa*, *Tetrasida*, and *Wissadula*. Taxa from two of the alliances are found in both main clades, apart from the remainder of their alliance as currently circumscribed. *Sidasodes* is placed in clade A, while the remaining *Sphaeralcea* alliance genera are in clade B, and *Neobrittonia* is in clade A, whereas the rest of the *Malacothamnus* alliance is in clade B.

For Bayesian inference, the model that best fit the data set was TrN + G + I (Tamura and Nei, 1993), as determined by Modeltest. Trees corresponding to the burn-in period (approximately 200 000 generations) were discarded, and a 50% majority rule consensus was constructed from the remaining post-burn-in trees (Figs. 3, 4). The Bayesian analysis recovered a similar topology as the parsimony analyses, although a few of the generic placements differed. These differences include for clade A (Fig. 3): *Horsfordia* is unresolved in a clade with *Bakeridesia* and *Anoda* + *Periptera*, *Sida abutifolia* is sister to a clade containing *S. linifolia* + *S. turneroides* (rather than sister to *Dendrosida*), conversely *S. rhombifolia* is sister to *Dendrosida* (rather than sister *S. linifolia* + *S. turneroides*), *S. oligandra* is unresolved at the base of a large clade containing most of the *Abutilon* alliance (rather than sister to *Robinsonella*), *Malvella* is also unresolved (rather than being sister to *Allosidastrum*), and *S. hookeriana* and *S. hermaphrodita* are unresolved in the ''*Plagianthus*'' clade. In clade B (Fig. 4), the changes in the Bayesian topology include *Anisodontea* as sister to a clade containing *Callirhoë* + *Napaea* and *Alcea* + *Kitaibela* (rather than sister to a more inclusive clade containing *Malva* + *Lavatera* and *Malope*), the *Palaua* species are sister to *Fuertesimalva* + *Urocarpidium* (rather than sister to the large clade containing most of clade B), and *Tarasa trisecta* is unresolved with other *Tarasa* and *Nototriche* species (rather than sister to *Nototriche*).

DISCUSSION

Utility of ITS in tribe Malveae—In this study, we present the first comprehensive phylogeny for tribe Malveae. Studies in other angiosperm families have employed the ITS region for phylogenetic reconstructions at the tribal level, including one other Malvoideae tribe, Gossypieae (Seelanan et al., 1997). However, the utility of this region for phylogenetic reconstruction at higher taxonomic levels certainly will depend on the level of divergence for the genera under consideration. Across tribe Malveae, the use of the ITS region for phylogeny reconstruction is likely at its limit, given the alignment difficulties we experienced. For this same reason, the inclusion of genera from other tribes of Malvoideae, most notably the Hibisceae, was not feasible. Similarly, the high homoplasy levels [CI = 0.28 (excluding uninformative characters), RC = 0.21] indicate that this marker may be beyond the limit for a tribal level phylogeny. However, homoplasy levels have been shown to increase when a large number of taxa are analyzed (Sanderson and Donoghue, 1989). Moreover, when log transformed values for CI and number of taxa from our study are compared to the regression analyses conducted by Givnish and Sytsma (1997), our data fall within the range expected for DNA sequence data. The exclusion of troublesome areas in the Malveae alignment from the phylogenetic analyses did not produce conflicting relationships among the taxa, but did result in a lack of resolution for several areas of the tree. As demonstrated by previous studies in the Malveae, however, the ITS region does provide sufficient resolution at lower taxonomic levels (Ray, 1995; Andreasen and Baldwin, 2001, 2003; Fuertes Aguilar et al., 2003; Tate and Simpson, 2003).

The challenges of using ITS for phylogeny reconstruction in groups known or suspected to have experienced hybridization or polyploidization are widely appreciated (Baldwin et al., 1995; Wendel et al., 1995; Alvarez and Wendel, 2003; Fuertes Aguilar and Nieto Feliner, 2003). The ITS region, as part of the nuclear ribosomal repeat, is expected to undergo concerted evolution (Zimmer et al., 1980), and therefore, the repeats within a given taxon are often assumed to be homogeneous. In some cases, concerted evolution may fail to homogenize the repeats in hybrids or allopolyploids, particularly if these are recently formed entities (and sufficient time has not passed for homogenization of the repeats), if the repeats are located on different chromosomal segments (and interlocus concerted evolution does not occur) or if the hybrid or polyploid reproduces asexually (Baldwin, 1992; Alvarez and Wendel, 2003). Polyploidy has been well documented in tribe Malveae, not only within genera, but also within species (see Fryxell, 1997). Pseudogene formation, biased PCR amplification, and interlocus recombination are just a few of the processes that can potentially confound the use of ITS for phylogeny reconstruc-



Figs. 1–2. Majority rule (50%) consensus of 10 000 MP trees based on ITS sequence data of tribe Malveae. Frequency of reconstructed clades is indicated above the branches and bootstrap support (above 70%) for 1000 replicates is shown below the nodes. Alliance associations are shown at right and follow Bayer and Kubitski (2003) with slight modification (see Table 1). Clade A.

tion (reviewed in Alvarez and Wendel, 2003). Despite these potential shortcomings, the recovered generic relationships based on ITS sequence data are also supported by geography, chromosome number, and morphology (discussed later, Figs. 5, 6). Nonetheless, the findings presented here are preliminary and require further corroboration from one or more independent data sets, either from the chloroplast or from a low- or single-copy nuclear gene. As a conservative measure, we do not propose taxonomic changes for the tribe at present.

The traditional alliances are not monophyletic—The ITS phylogeny does not support any of the historical classification

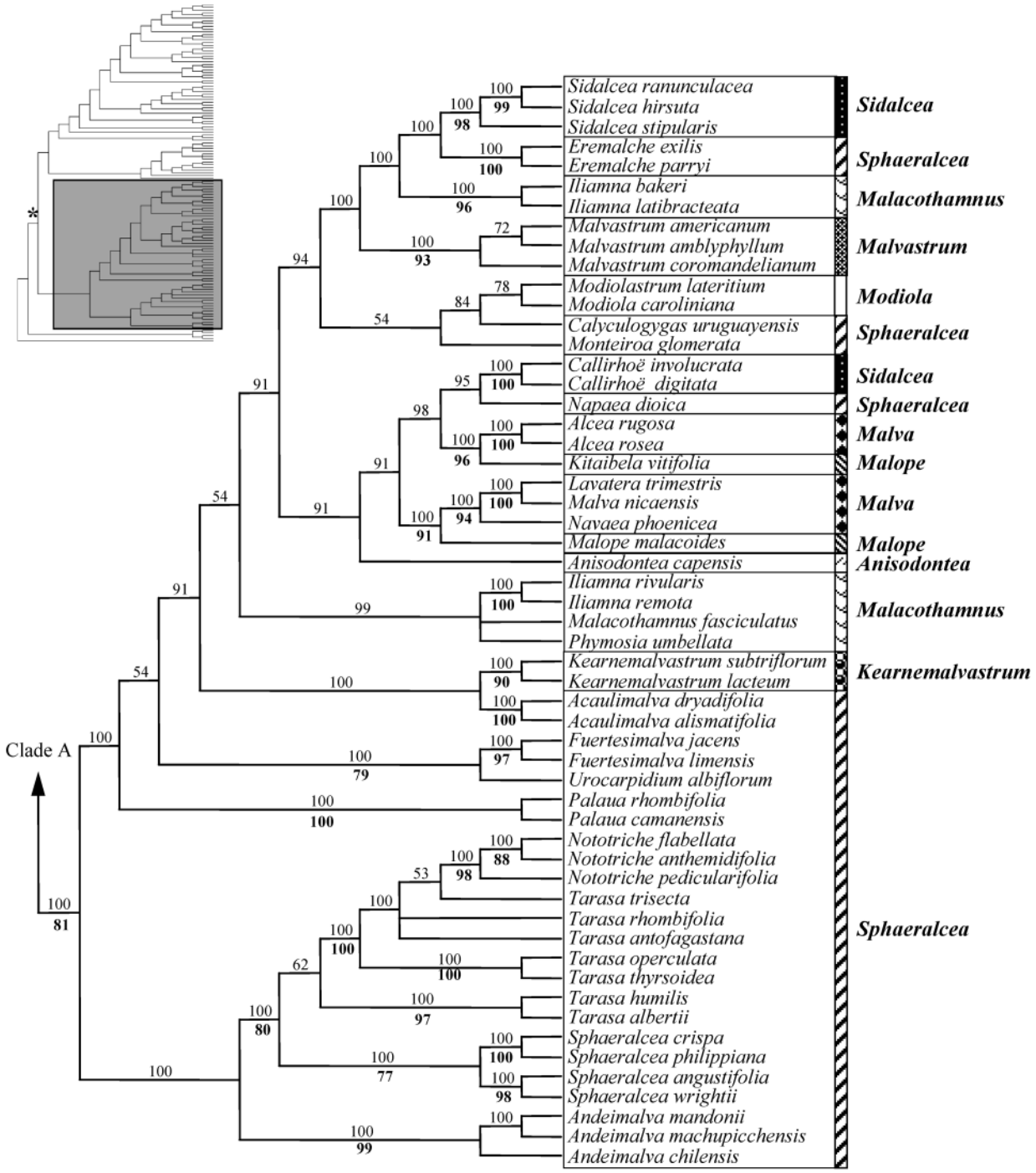
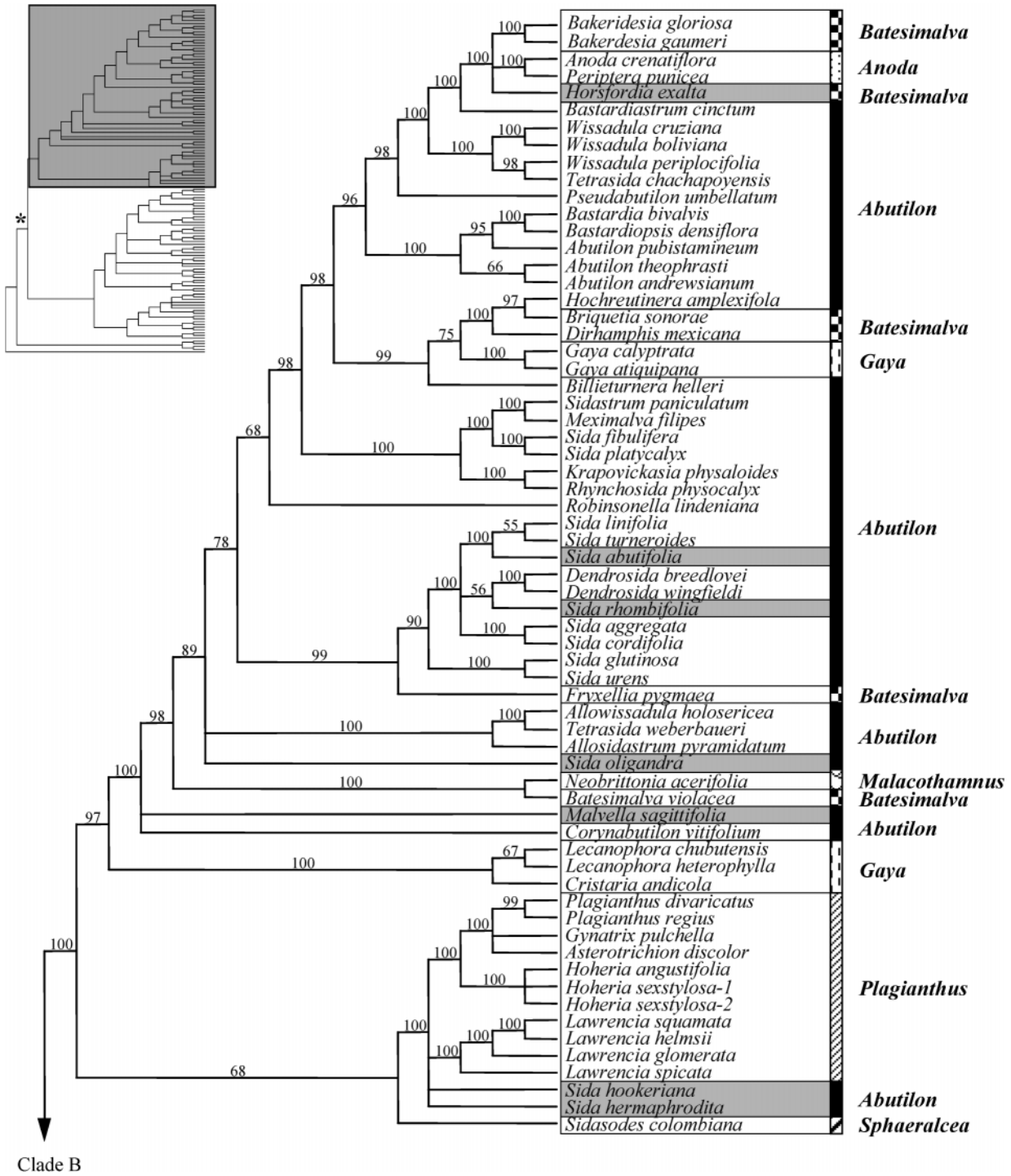


Fig. 2. Clade B.

schemes (Table 2). While several alliances are not monophyletic (i.e., are para- or polyphyletic), only two alliances (*Malacothamnus* and *Sphaeralcea*), as defined by Bayer and Kubitzki (2003), were found in both of the main clades. *Neobrittonia*, a member of the *Malacothamnus* alliance according to Fryxell (1988) and Bayer and Kubitzki (2003), was placed in clade A, while the remaining members of that alliance (*Iliamna*, *Malacothamnus*, and *Phymosia*) belong in clade B. Similarly, *Sidasodes* was aligned with genera of the *Sphaeralcea* alliance (Fryxell, 1997; Bayer and Kubitzki, 2003) because it shares a base chromosome number of $x = 5$ with the latter group. However, in the ITS phylogeny, *Sidasodes colombiana* was moderately supported (82% BS, 68% BPP) as sister to two outlier species of *Sida* plus the *Plagianthus* alliance in clade A. Other than these two cases, the remaining alliances are restricted to one of the two main clades. Within these two large clades, however, most of the alliances are not monophyletic. The exceptions are the *Anoda* alliance, with the genera *Anoda* and *Periptera* (clade A; Figs. 1, 3), and the *Modiola* alliance composed of *Modiola* and *Modiolastrum*



Figs. 3–4. Majority rule (50%) consensus of the post-burn in trees resulting from Bayesian analysis of ITS sequence data. Frequency of clades is shown above the branches and represent Bayesian posterior probabilities. Taxa that change position as compared to the parsimony analysis (Figs. 1–2) are outlined in grey. Clade A.

(clade B; Figs. 2, 4). Based on our present sampling, the monogeneric *Kearnemalvastrum* and *Malvastrum* alliances (clade B) are also monophyletic.

The non-monophyly of the alliances in the ITS phylogeny is generally consistent with a previous phylogeny based on cpDNA restriction site data for Malveae (La Duke and Doebley, 1995). In that study, two main clades were recovered: one containing *Abutilon* and *Sida* (*Abutilon* alliance) and a second containing *Alcea*, *Lavatera*, and *Malva* (*Malva* alliance), *Iliamna* and *Malacothamnus* (*Malacothamnus* alliance), *Modiola* and *Modiolastrum* (*Modiola* alliance), *Sphaeralcea*, *Tarasa*, and *Urocarpidium* (*Sphaeralcea* alliance), and *Callirhoë* (*Sidalcea* alliance). The taxon sampling here is more extensive than in the cpDNA study, but essentially the same

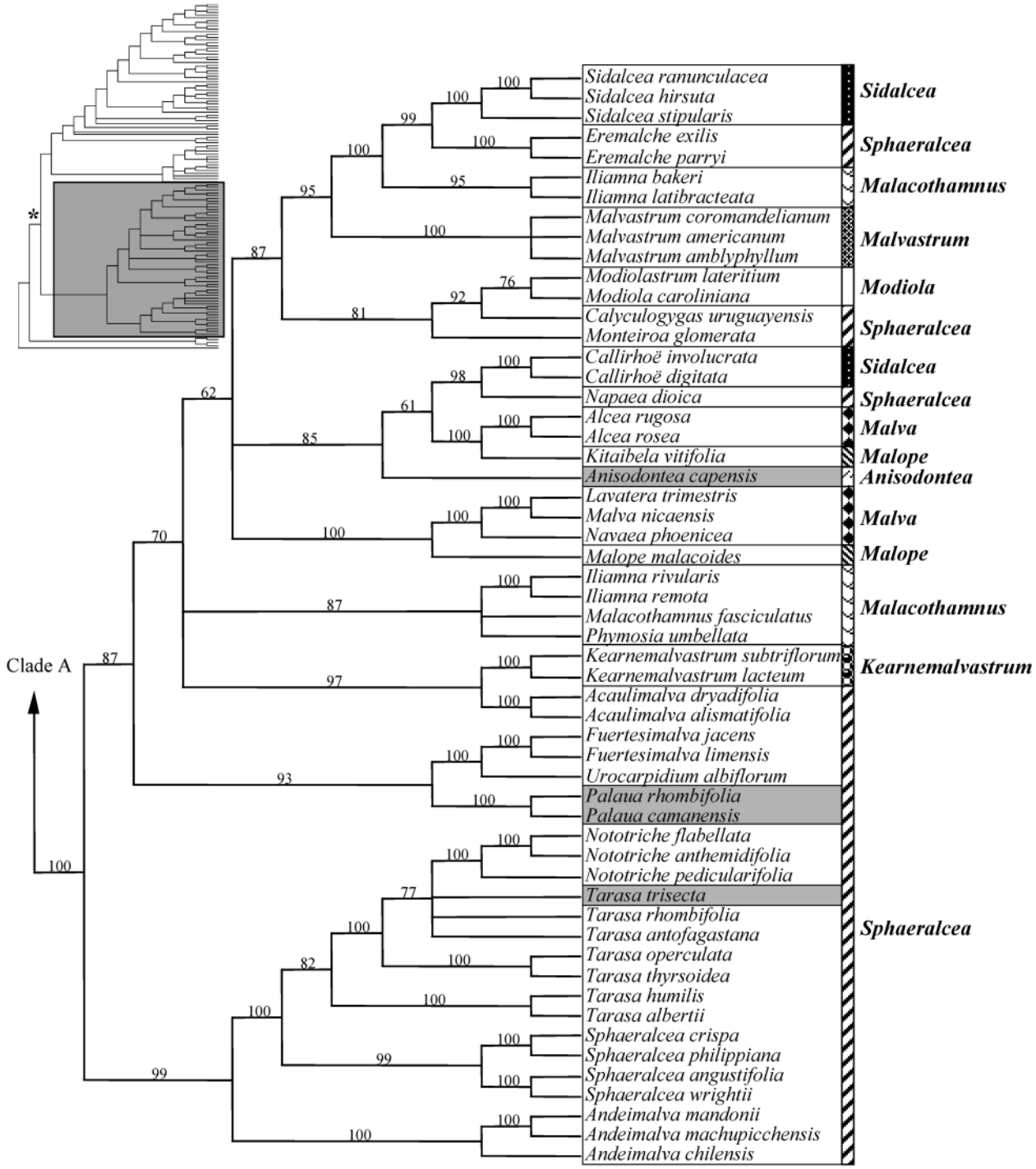
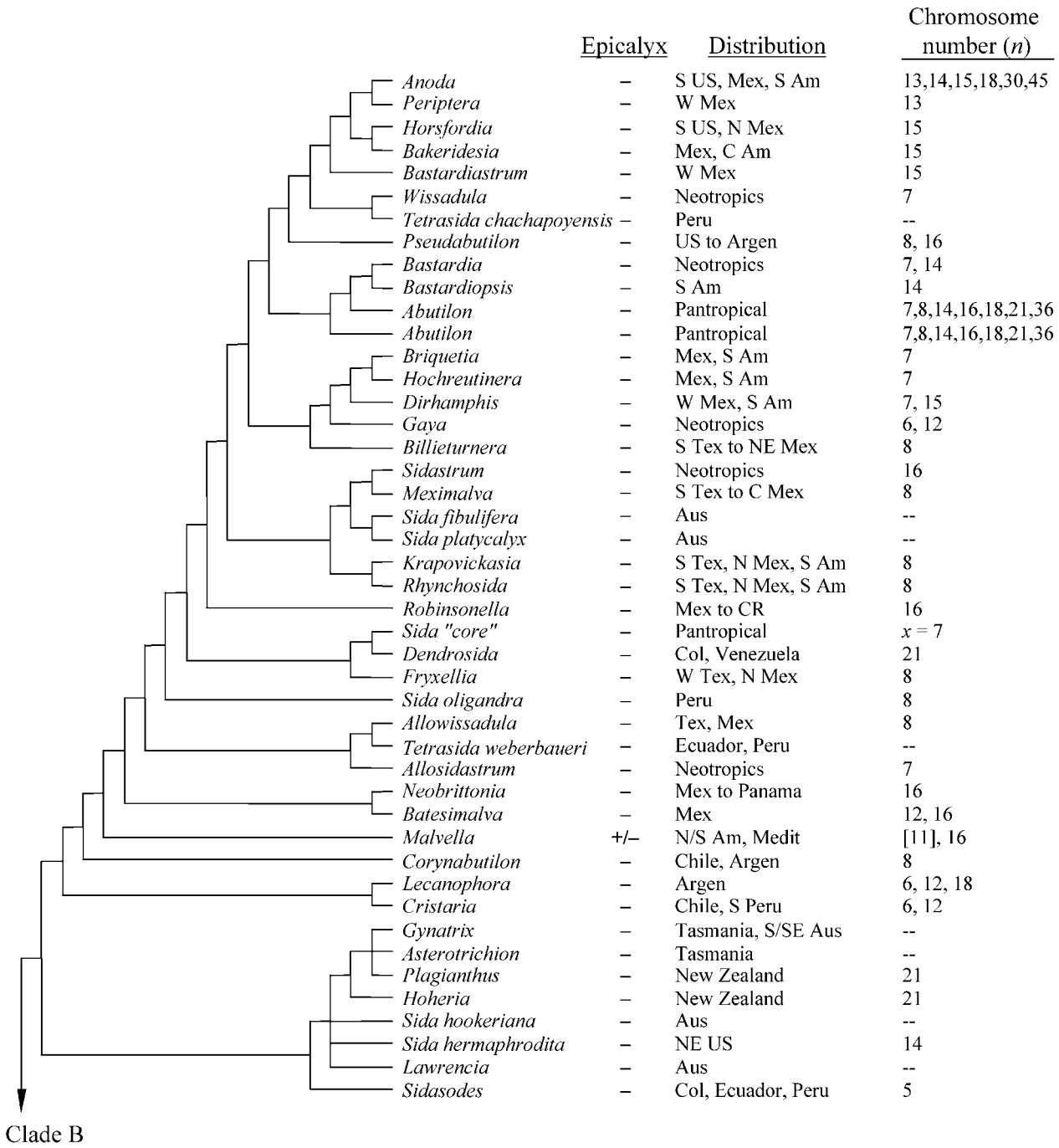


Fig. 4. Clade B.

topology is recovered: one clade (clade A) contains the *Abutilon*, *Anoda*, *Batesimalva*, *Gaya*, and *Plagianthus* alliances, with the aforementioned outliers from the *Malacothamnus* and *Sphaeralcea* alliances, and the second large clade (clade B) consists of genera from the *Anisodontea*, *Kearnemalvastrum*, *Malacothamnus*, *Malope*, *Malva*, *Malvastrum*, *Modiola*, *Sidalcea*, and *Sphaeralcea* alliances. These two clades correspond primarily to the absence (clade A) or presence (clade B) of involucral bracts subtending individual flowers (epicalyx) (Figs. 5, 6). However, this character is variable in species of *Malvella* (clade A, Fig. 5) and *Callirhoë* (clade B, Fig. 6) and is completely absent in species of *Nototriche* (clade B, Fig. 6). The loss of an epicalyx in *Nototriche* clearly represents an independent event, because this genus is firmly placed within clade B. The lability of the presence or absence of an epicalyx in *Malvella* and *Callirhoë* is an interesting question that merits further investigation, particularly from a developmental perspective. Within each of the main clades, other morpholog-



Figs. 5–6. Summary of generic relationships in tribe Malveae based on ITS sequence data, showing the presence or absence of an epicalyx, geographic distribution, and reported chromosome numbers. See also Table 1. Clade A.

ical characters (particularly those of the carpel previously emphasized for classification) appear to be quite labile, such that general trends presently cannot be well defined. Similarly, the lack of strong support, both bootstrap values and Bayesian posterior probabilities, at the base of clades A and B, makes rigorous character reconstructions tentative at this time. Early classifications of tribe Malveae (Bentham and Hooker, 1862, through Hutchinson, 1967) emphasized carpel morphology, specifically the number and position of ovules in each carpel. Bates (1968) proposed that the separation of uniovulate and pluriovulate genera into separate tribes was likely artificial and suggested that relationships between uniovulate and pluriovulate lineages should not be disregarded. Our findings based on ITS data, support Bates' astute observation that this character has been over-emphasized. Although paraphyly may be an expected outcome of phylogenetic analyses (e.g., Brummitt, 2002), we find support for many of the recovered generic relationships based on chromosome number and geographic distribution (Figs. 5, 6), two criteria used by Bates to delimit the alliances. For the remainder of the discussion, we will focus

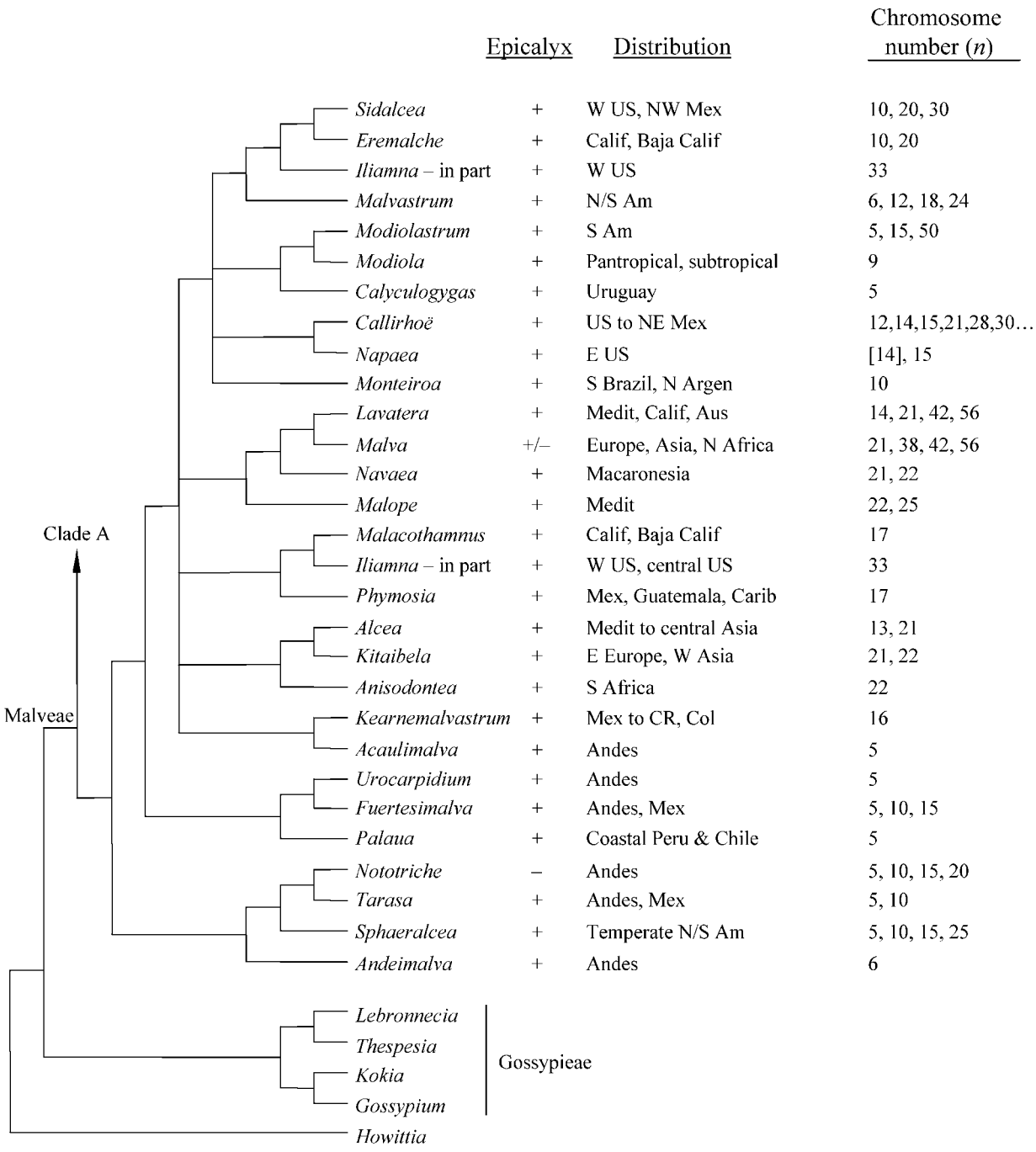


Fig. 6. Clade B. *Figure Abbreviations*: Am, America; Argen, Argentina; Aus, Australia; Calif, California; Carib, Caribbean; Col, Colombia; CR, Costa Rica; Medit, Mediterranean; Mex, Mexico; Tex, Texas; US, United States of America.

on the overall pattern of alliance and generic relatedness within clades A and B.

Alliances and genera of clade A—As mentioned, clade A contains those genera that lack involucral bracts and belong to the *Abutilon*, *Anoda*, *Batesimalva*, *Gaya*, *Malacothamnus*, *Plagianthus*, and *Sphaeralcea* alliances (Figs. 1, 3, 5). The clade as a whole is geographically and chromosomally diverse, with taxa distributed in the Americas and the South Pacific, and most with base chromosome numbers of $x = 6$, 7, and 8 (few with $x = 5$, 13, 15). Support for most of the basal nodes is relatively weak (no BS, but 100% BPP for clade A), with only a few receiving >70% BS (Figs. 1, 3). Only one alliance (*Anoda*) is monophyletic based on the ITS data. *Anoda* and *Periptera* were suggested to be closely related (Bates, 1987; Fryxell, 1997); both genera possess ephemeral mericarp walls (also found in *Cristaria*, to which they are not closely related) and are primarily distributed in Mexico. *Periptera* (only one species counted) has a haploid chromosome number of $n = 13$, while *Anoda* is more chromosomally diverse with $n = 13$, 14, 15, 18, 30, or 45 (Bates, 1987; Fryxell, 1997). Interestingly, Bates (1987) noted that the only $n = 13$ species of

Anoda (*A. thurberi*) forms a very robust hybrid (in greenhouse crosses) with *Periptera punicea* ($n = 13$) and that these may represent a lineage derived within *Anoda*.

The *Batesimalva* alliance, composed of six genera (~36 species), is dispersed throughout clade A. *Bakeridesia* and *Horsfordia* (both $n = 15$) form a clade sister to the *Anoda* alliance with good support (83% BS, 100% BPP) (Figs. 1, 3, 5). Both genera possess capitate stigmas and conspicuously ornamented mericarps (Fryxell, 1997), but in *Horsfordia* the wings are apical, and in *Bakeridesia* the wings are dorsal. No relationship between the two genera was previously suggested. Two other genera of the *Batesimalva* alliance, *Briquetia* ($n = 7$) and *Dirhamphis* ($n = 7, 15$), are included in a clade with *Hochreutinera* ($n = 7$, placed in the *Abutilon* alliance), plus *Gaya* ($n = 6, 12$, *Gaya* alliance) and *Billieturnera* ($n = 8$, *Abutilon* alliance). Krapovickas (1970) suggested a close relationship among *Dirhamphis*, *Briquetia*, and *Hochreutinera*, which is supported by the ITS data (100% BS, 100% BPP). Fryxell (1988) placed *Dirhamphis*, *Horsfordia*, *Batesimalva*, and *Briquetia* in the *Batesimalva* alliance, primarily on the basis of fruit morphology. Later, Fryxell and Stelly (1993) advised that this alliance might need modification, because new chromosome counts cast doubt on their association with one another. Further, they suggested that the two *Dirhamphis* species (one $n = 7$, the other $n = 15$) may not be congeneric.

In the ITS phylogeny, *Fryxellia* ($n = 8$) is at the base of a clade containing many *Sida* species ($n = 6, 7, 8, 14, 16, 28$) plus *Dendrosida* ($n = 21$, see later), although this clade receives no support (Figs. 1, 3, 5). Fryxell and Valdés (1991) speculated that *Fryxellia* could be related to *Batesimalva* or *Anoda* because it shares some morphological features with each genus. The placement of *Neobrittonia* (*Malacothamnus* alliance) as sister to *Batesimalva* (*Batesimalva* alliance) and not with the remaining *Malacothamnus* alliance in clade B (compare Figs. 1, 3 to 2, 4) is supported by several characters including a shared chromosome number of $n = 16$ (although one species of *Batesimalva* is $n = 12$), the absence of an epicalyx (involucral bracts) (Fig. 5), the presence of basal spines on the dehiscent mericarps, rough or warty seeds, and a pubescent staminal column, all of which are lacking in the *Malacothamnus* alliance. Fryxell (1988, 1997) did not indicate why he thought *Neobrittonia* should be included in the *Malacothamnus* alliance, but Bates (1968) originally placed *Neobrittonia* amongst the other pluriovulate genera of the *Abutilon* alliance (e.g., *Bakeridesia*, *Herissantia*, *Pseudabutilon*, and *Wissadula*).

Two of the three genera of the *Gaya* alliance ($x = 6$), *Lecanophora* and *Cristaria*, group together, while the third genus, *Gaya*, is well removed from these. *Cristaria* and *Lecanophora* have long been allied because they share the unique character of a carpocrater, a cup-shaped structure formed by expanded bases of the carpels, which are fused to the receptacle base (Bates, 1968; Fryxell, 1997). Although *Gaya* shares a common chromosome number with these two genera (Fig. 5), based on morphological characters, the genus is relatively isolated from other genera. Bates (1968) and Bates and Blanchard (1970) suggested that the genera of the *Gaya* alliance actually represent two distinct lineages, one composed of *Gaya* and the other of *Cristaria* + *Lecanophora*, which is supported here. In the ITS phylogeny, *Gaya* is sister to a clade composed of *Dirhamphis*, *Briquetia*, and *Hochreutinera*, although there is no bootstrap support and only low BPP (75%) for this relationship (Figs. 1, 3). The more inclusive clade of the taxa (with *Billieturnera*) also had no bootstrap support (Fig. 1), but the BPP was much higher (99%) (Fig. 3).

The *Abutilon* alliance with 23 genera (~400 species) is the largest in the tribe (Bayer and Kubitzki, 2003), and its members are also scattered throughout clade A (Figs. 1, 3). Several genera of this alliance are apparently not monophyletic, e.g., *Abutilon*, *Sida*, and *Tetrasida*. The *Abutilon-Sida* complex was the subject of a recent phylogenetic investigation using ITS (Fuertes Aguilar et al., 2003), which also revealed that the two genera were not monophyletic. *Sida* (100 spp.) has long been recognized as a heterogeneous assemblage (Fryxell, 1985). Attempts to create a more natural group have resulted in several segregate genera: *Allosidastrum*, *Bastardiopsis*, *Billieturnera*, *Dendrosida*, *Krapovickasia*, *Malvella*, *Meximalva*, *Rhynchosida*, *Sidastrum*, and *Tetrasida* (see Fryxell, 1997). In the ITS phylogeny, the remaining named *Sida* species still do not form a monophyletic group (Figs. 1, 3), which is consistent with the treatment of Fuertes Aguilar et al. (2003) and suggests that further taxonomic adjustments are needed. A ''core'' *Sida* clade (Fuertes Aguilar et al., 2003) was reconstructed with *Fryxellia* ($n = 8$) as its sister and *Dendrosida* ($n = 21$) derived within it (Fig. 5). These core *Sida* species have base chromosome numbers of both $x = 7$ and $x = 8$, and belong to different sections as outlined by Fryxell (1985): *S. cordifolia* (section *Cordifoliae*), *S. turneroides* (section *Ellipticifoliae*), *S. aggregata* (section *Muticae*), *S. glutinosa* and *S. urens* (section *Nelavagae*), *S. rhombifolia* (section *Sidae*), *S. abutifolia* (section *Spinosae*), and *S. linifolia* (section *Stenindae*). The remaining species of *Sida* are distributed throughout clade A (Fig. 1), including *S. fibulifera* and *S. platycalyx* (incertae sedis, fide Fuertes Aguilar et al., 2003), which are sister to the *Sidastrum* + *Meximalva* clade. Fryxell (1997) suggested that *Meximalva* and *Dendrosida* were potentially close relatives to *Sida*, and, in fact, both genera are closely related to species of *Sida*, but they occur in separate clades. Similarly, *S. oligandra* (section *Oligandrae*) is removed from the core *Sida* species and is either sister to *Robinsonella*, based on parsimony analyses (Fig. 1), or is unresolved at the base of the larger *Abutilon* alliance clade in the Bayesian analysis (Fig. 3). Two other *Sida* species, *S. hookeriana* (section *Hookeriana*) and *S. hermaphrodita* (section *Pseudo-Napaea*), are included with members of the *Plagianthus* alliance (100% BS, 100% BPP), plus *Sidasodes colombiana* of the *Sphaeralcea* alliance (82% BS) (Figs. 1, 3). *Sida hookeriana* is found in Australia, so its inclusion with the *Plagianthus* group is more tenable, although morphologically the two are disparate. The reconstruction of *S. hermaphrodita*, which is found in the northeastern United States, with the primarily South Pacific taxa of the *Plagianthus* alliance is somewhat perplexing. Fryxell (1997) suggested that this species might be better segregated into a distinct genus. Fryxell and Fuertes Aguilar (1992) noted the similarity of *Sidasodes* (from the Andes of Colombia and Peru) to *Sida hermaphrodita* on the basis of fruit morphology; however, these taxa were not thought to share other features. In the ITS study by Fuertes Aguilar et al. (2003), *S. hermaphrodita*, *S. hookeriana*, and *Sidasodes* also formed a clade sister to the other members of the *Abutilon* and *Sida* alliances, a finding that is corroborated here. Chloroplast sequence data also support the sister relationship of *S. hermaphrodita* and *S. hookeriana* to genera of the *Abutilon* and *Sida* alliances (J. Beck, R. Small, University of Tennessee, personal communication). Further

evaluation of these three species is needed to determine their systematic position.

One of the other two genera from the *Abutilon* alliance that is not monophyletic is *Abutilon* (160 spp.), one of the largest Malveae genera. Like *Sida*, several species were removed and new genera created, including *Bakeridesia*, *Bastardia*, *Corynabutilon*, *Herissantia*, *Hochreutinera*, *Pseudabutilon*, and *Tetrasida* (Fryxell, 1997), most of which were included in the present study. Only three species of *Abutilon* were sampled here; these do not form a monophyletic group, but are paraphyletic to *Bastardia* and *Bastardiopsis*, two of the segregate genera (Figs. 1, 3). These last two genera are the only ones in the tribe that possess capsular fruits; all other genera are schizocarpous (Fryxell, 1997). Expanded sampling within *Abutilon* certainly will be needed to determine if other species should be removed and elevated to generic status.

The third genus of the *Abutilon* alliance resolved as nonmonophyletic in the ITS phylogeny is *Tetrasida*. The genus is chromosomally unknown and currently contains five species (Fryxell and Fuertes Aguilar, 1992; Fryxell, 2002) found in Peru and Ecuador. Two species were included here to represent the genus: *T. chachapoyensis* clusters with species of *Wissadula* ($n = 7$), while *T. weberbaueri* is placed sister to *Allowissadula holosericea* ($n = 8$) (Figs. 1, 3, 5). Krapovickas (1969) included the species now considered as *Tetrasida* in *Abutilon* section *Tetrasida* because he believed the condition of a four-merous corolla (for which the genus was named) in the species was not sufficiently consistent to merit generic recognition. However, Fryxell and Fuertes Aguilar (1992) resurrected the genus, including two species, and later described three new species (Fryxell, 2002).

The *Plagianthus* alliance contains two genera from Australia (*Gynatrix*, *Lawrencia*), two from New Zealand (*Hoheria*, *Plagianthus*), and one from Tasmania (*Asterotrichion*) for a total of 23 species. Only *Hoheria* and *Plagianthus* have chromosome counts available and both are $n = 21$ (Bates and Blanchard, 1970). As discussed earlier, in the ITS phylogeny (Figs. 1, 3), this alliance forms a moderately supported clade (82% BS; 68% BPP) with *Sidasodes colombiana* (from the Andes of Colombia and Peru), *Sida hermaphrodita* (section *Pseudo-Napaea*, from the eastern United States), and *S. hookeriana* (section *Hookerianae*, from southwestern Australia). The genera of the *Plagianthus* alliance are morphologically diverse, ranging from annual herbs to prostrate subshrubs (*Lawrencia*) and large trees (*Plagianthus* and *Hoheria*) that differ considerably in flower and fruit structure (Melville, 1966; Lander, 1984). In this group, there is a tendency towards dioecy and a reduction in the number of locules in the ovary. *Plagianthus* is unilocular with a single (rarely two) pendulous ovule in each flower. The styles also show a gradation from the long linear stigmas of *Lawrencia* and *Gynatrix* to clavate forms in *Plagianthus*, *Asterotrichion*, and *Hoheria*.

Alliances and genera of clade B—Clade B was resolved as a well-supported group (81% BS, 100% BPP) and is composed of genera from the *Anisodontea*, *Kearnemalvastrum*, *Malacothamnus*, *Malope*, *Malva*, *Malvastrum*, *Modiola*, *Sidalcea*, and *Sphaeralcea* alliances (Figs. 2, 4). As mentioned, all members of this clade retain the symplesiomorphic character of having an epicalyx (with the exception of *Nototriche*, which lacks involucral bracts, but clearly belongs in this clade) (Fig. 6). Clade B contains primarily American taxa, but also includes European, Asian, and South African genera. The predominant base chromosome number is $x = 5$ (*Sphaeralcea* alliance, *Sidalcea*, *Modiolastrum*), although some clades are complex chromosomally (e.g., the clade that includes *Anisodontea* through *Callirhoë*, with $n = 12, 13, 14, 21, 22$, etc.) (Fig. 6). As with clade A, many of the basal nodes in clade B lack robust support (Figs. 2, 4). Relationships with the greatest support are those between congeneric taxa, although there is strong support for the *Malope* + *Navaea* + *Malva* + *Lavatera* clade (91% BS; 100% BPP) and the *Sphaeralcea* + *Tarasa* + *Nototriche* clade (80% BS; 100% BPP) (Figs. 2, 4). Three alliances in clade B are monophyletic: the *Modiola* alliance (78% BS, 76% BPP) composed of *Modiola* and *Modiolastrum*, and the monogeneric *Kearnemalvastrum* and *Malvastrum* alliances, although the sister groups to these latter alliances are not well supported.

The *Sphaeralcea* alliance, the largest of clade B with 12 genera (~230 species) (excluding *Sidasodes*, which is better aligned with genera of clade A), is not monophyletic (Figs. 2, 4). A clade composed of *Andeimalva* ($n = 6$), along with *Nototriche*, *Sphaeralcea*, and *Tarasa* (all $x = 5$) is sister to the rest of clade B. Other genera of the *Sphaeralcea* alliance occur in a grade (*Palaua*, *Urocarpidium*, *Fuertesimalva*, *Acaulimalva*), with the remaining genera (*Eremalche*, *Calyculogygas*, *Monteiroa*, and *Napaea*) scattered amongst genera from other alliances. In the case of *Eremalche*, the sister relationship to *Sidalcea* (*Sidalcea* alliance) is supported by geographic distribution (both are found primarily in California and northern Mexico), a morphological similarity and a shared basic chromosome number of $x = 5$ (Fig. 6). Two other genera of the *Sphaeralcea* alliance, *Calyculogygas* ($n = 5$) and *Monteiroa* ($n = 10$), are in a clade with *Modiola* ($n = 9$) and *Modiolastrum* ($n = 5, 15, 50$). The placement of these two genera with *Modiolastrum* is plausible given that they are all found in eastern South America (Argentina, Brazil, and Uruguay) and have a common base chromosome number (Fig. 6). *Modiola* is a monotypic genus that is widespread throughout pantropical America, extending into temperate areas, and is thought to represent an aneuploid lineage closely related to the $x = 5$ genera of the *Sphaeralcea* alliance (Bates, 1968). Krapovickas (1945) first suggested the close relationship of *Modiola* and *Modiolastrum* based on gross morphological features, and later noted that even their chromosomes were similar in size and satellite morphology (Krapovickas, 1949). Both genera were originally included in the *Sphaeralcea* alliance (Bates, 1968; Bates and Blanchard, 1970), but were later separated into their own generic alliance by Fryxell (1988). One other genus in the *Sphaeralcea* alliance that is relatively isolated is *Napaea* ($n = [14], 15$), a monotypic dioecious genus from the central United States. Although originally allied to *Sidalcea* (Iltis and Kawano, 1964; Bates, 1968), *Napaea* was later segregated into its own alliance by Bates and Blanchard (1970). Krebs (1993) noted that *Napaea dioica* shared pollen and fruit characters with *Sphaeralcea* and suggested that it was aligned better with genera of the *Sphaeralcea* alliance. In the ITS phylogeny, *Napaea* is sister to the cytologically complex genus *Callirhoë* (*Sidalcea* alliance, see Table 1), which is found in the central United States to northeastern Mexico (Dorr, 1990) (Fig. 6). Interestingly, gynodioecy, a rather rare phenomenon in the Malveae, occurs in several species of *Callirhoë* (Dorr, 1990). Although *Napaea* and *Callirhoë* were placed in separate alliances, a close relationship between them was suggested (Fryxell, 1997). As is found throughout the Malveae, the ITS phylogeny indicates that the phylogenetic relationships of many

genera of the *Sphaeralcea* alliance are supported more by geography and shared chromosome numbers than some previously emphasized morphological characters.

Within the *Sphaeralcea* alliance, only *Tarasa* ($n = 5, 10$) is not monophyletic in the ITS phylogeny (Figs. 2, 4), a finding consistent with a previous study based on ITS and chloroplast sequence data (Tate and Simpson, 2003; Tate, 2003). *Sphaeralcea* ($n = 5, 10, 15, 25$) is sister (80% BS, 100% BPP) to a clade containing *Tarasa* ($n = 5, 10$) and *Nototriche* ($n = 5, 10, 15, 20$) (no support for the next node, but the clade including *T. thyrsoidea* and *T. operculata* has 100% BS, 100% BPP) (Figs. 2, 4, 6). A close relationship among these three genera was proposed by Krapovickas (1960, 1971), but they were retained as separate genera because they were considered to be distinct from one another. Species of *Sphaeralcea* (~40 spp.) are herbs or shrubs found in temperate mid-elevation habitats of North and South America (Chile and Argentina) with one- to three-seeded mericarps that have a dehiscent, smooth upper portion and an indehiscent, laterally reticulate lower portion (Fryxell, 1997). *Tarasa* species (~27 spp.) are either annuals or perennial shrubs found at mid (800 m) to high (up to 4000 m) elevations in the Andes (Peru to Chile and Argentina) and have one-seeded mericarps that are completely dehiscent (Krapovickas 1954, 1960). *Nototriche* (~100 spp.) contains primarily acaulescent cushion plants (although a handful of annual species have been described) found above ~4000 m in the Andes from Ecuador to southern Chile and Argentina (Fryxell, 1997) and has one-seeded, dehiscent mericarps. Interestingly, the lower elevation perennial species of *Tarasa* are more similar morphologically to *Sphaeralcea*, while the high elevation annuals are more similar to *Nototriche* (Tate and Simpson, 2003). Additional data will be needed to define the boundaries of *Tarasa* and *Nototriche* or to determine if *Nototriche* should be considered a section of *Tarasa*.

Another finding in the ITS phylogeny related to *Tarasa* is the placement of *Urocarpidium albiflorum* with *Fuertesimalva* (Figs. 2, 4). This species, the type of the genus *Urocarpidium*, was suggested to be synonymous with *Tarasa operculata* due to its apically plumose awns on the mericarps (Fryxell, 1996). The genus *Fuertesimalva* was created to accommodate the remaining species of *Urocarpidium* (Fryxell, 1996) that do not possess this character. The results of the ITS phylogeny (and also chloroplast data, Tate and Simpson, 2003), do not support the separation of *U. albiflorum* from the remaining species of *Fuertesimalva*, nor its inclusion in *Tarasa* and argue for the original generic composition and name. Morphological characters that support the placement of *U. albiflorum* with *Fuertesimalva* rather than *Tarasa* include mericarps that are indehiscent, glabrous, and laterally ''ridged'' (vs. dehiscent, with stellate pubescence on the dorsal and apical surfaces, and the lateral walls that are smooth or faintly reticulate in *Tarasa*), and calyx trichomes that are simple and hirsute (vs. stellate stipitate in *Tarasa*). Thus, the occurrence of an apical awn on the mericarps of *U. albiflorum* and *Tarasa* species appears to be a convergent character, and we recognize the former as separate from the latter.

Most included members of the *Malacothamnus* alliance (*Iliamna*, *Malacothamnus*, and *Phymosia*, excluding *Neobrittonia*, which is a member of clade A), form a clade in the ITS phylogeny (Figs. 2, 4). However, *Iliamna* was also reconstructed as paraphyletic. Two species of *Iliamna* ($n = 33$) (*I. bakeri* and *I. latibracteata*) that are endemic to northern California/southern Oregon are more closely related to *Sidalcea* ($n = 10, 20, 30$) and *Eremalche* ($n = 10, 20$), which are distributed along the western coast of North America, than to the remaining members of *Iliamna* (Fig. 6). The other two species included here (*I. rivularis*, found in the Rocky Mountains of the United States, and *I. remota*, found in Illinois, Indiana, and Virginia), cluster with *Phymosia umbellata* (Mexico, Guatemala, and Caribbean) ($n = 17$) and *Malacothamnus fasciculatus* (California) ($n = 17$). Morphologically, *Iliamna* is distinct from *Sidalcea* and *Eremalche*. Characters distinguishing *Iliamna* from both genera include a perennial habit (annual *Eremalche*, annual or perennial in *Sidalcea*), deciduous stipules (persistent in both *Sidalcea* and *Eremalche*), carpels with multiple seeds (single in *Sidalcea* and *Eremalche*), and dehiscent mericarps (indehiscent in *Eremalche*). Chloroplast (*rpl16* intron and *trnL-F* spacer) sequence data place *Iliamna bakeri* and *I. latibracteata* in a clade with other western *Iliamna* species, while *I. remota* and *I. corei* are outside this ''core'' *Iliamna* clade with *Phymosia* (T. Bodo Slotta, unpublished data).

The *Malvastrum* alliance contains a single genus, *Malvastrum*, which, like *Abutilon* and *Sida*, was at one time a repository for many taxa that were difficult to place. Over the years, however, several species were removed from the heterogeneous *Malvastrum* and placed in other genera, including *Acaulimalva*, *Anisodontea*, *Malacothamnus*, *Monteiroa*, *Nototriche*, *Sphaeralcea*, *Tarasa*, and *Urocarpidium* (*Fuertesimalva*) (Hill, 1982; Fryxell, 1997). Since Hill's (1982) revision of *Malvastrum*, the genus is a cohesive American taxon of 15 species that share a base chromosome number of $x = 6$ (Fig. 6). Within the Malveae, *Malvastrum* appears to be rather isolated, but based on the ITS phylogeny, it is closely related to other North (*Eremalche*, *Sidalcea*) or South (*Calyculogygas*, *Modiola*, *Modiolastrum*, *Monteiroa*) American genera (Figs. 2, 4).

Like many of the other alliances in clade B, the *Malope* alliance, comprised of *Malope* and *Kitaibela*, is not monophyletic. Previously, these two genera, along with *Palaua* (*Sphaeralcea* alliance), were placed in a separate tribe Malopeae, because they shared the unique feature of multiverticillar carpels (Table 1). All three are members of clade B, but are not closely related to one another (Figs. 2, 4) , which suggests that this unusual morphological feature has evolved on three separate occasions. Bates (1968) placed *Palaua* in the *Sphaeralcea* alliance with the other $x = 5$ genera, while retaining *Kitaibela* and *Malope* as the sole members of the *Malope* alliance. He also proposed that the evolution of the carpels into superposed verticils in *Palaua* occurred independently from that of *Malope* and *Kitaibela*, a hypothesis supported here. In the ITS phylogeny, *Malope* ($n = 22, 25$) is included in a clade (91% BS, 100% BPP) with some members of the *Malva* alliance (*Lavatera*, *Malva*, and *Navaea*), which share a geographic distribution in the Mediterranean region (Fig. 6). *Kitaibela* ($n = 21, 22$) is sister to *Alcea* ($n = 13, 21$) from the *Malva* alliance (96% BS, 100% BPP); both of these genera are found in the Mediterranean, East European, and West Asian regions. Bates' (1968) discussion of the *Malva*, *Malope*, and *Anisodontea* alliances was included in the same section, as he suspected their close relationship.

The *Malva* alliance (five genera, ~100 species), as alluded to in the previous paragraph, is not monophyletic (Figs. 2, 4). The genera of this alliance are found predominantly in the Mediterranean/European region (although some *Lavatera* species occur in North America and Australia) and have various

multiples of an $x = 7$ base chromosome number, which is shared by most of the other closely related genera based on the ITS data (Fig. 6). *Lavatera*, *Malva*, and *Navaea phoenicea* form a strongly supported clade (94% BS, 100% BPP) with *Malope* as its sister (Figs. 2, 4). Two species of *Alcea* cluster together (100% BS, 100% BPP) and are sister to *Napaea dioica*. In a previous ITS phylogenetic study, Ray (1995) found that the individual genera *Malva* and *Lavatera* were not monophyletic, but that the North American species of *Lavatera* were more closely related to *Malva* than to the Old World *Lavatera* species. Subsequently, the New World species of *Lavatera* were transferred to *Malva* (Ray, 1998). The sister position of *Navaea* with *Lavatera* and *Malva* is also supported by cpDNA sequence data (Fuertes Aguilar et al., 2002). Morphological groups (Lavateroid and Malvoid groups) were outlined by Ray (1995), but clearly these two genera will require more extensive sampling of morphological and molecular data to sort out their boundaries.

General conclusions—Tribe Malveae is a geographically, chromosomally, and morphologically diverse clade. The ITS phylogeny presented here shows that the current circumscription of the tribe into 14 generic alliances is artificial. Instead, two clades can be defined by the presence or absence of involucral bracts, and, perhaps, only these two clades should be named formally. Given the lack of support for many nodes at the base of the tree, additional data (chloroplast and/or other nuclear markers) are needed to corroborate these relationships. Likewise, because many genera (and clades) contain polyploid or aneuploid lineages, more data will likely give insight into chromosome evolution, which already appears to have been rather complex within the tribe. Moreover, determination of the early-branching lineages of the Malveae should shed light on the biogeographic origin of the tribe, which centers in the Americas, but also contains South Pacific and European taxa, and the base chromosome number for the tribe, which has been postulated as $x = 8$ or 9 (Bates, 1968).

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